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BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 173 : ARTICLE 3 NEW YORK : 1982

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Volume 173, article 3, pages 177–336, figures 1–50, tables 1–34
Issued July 30, 1982
Price: $11.30 a copy

ISSN 0003-0090

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ABSTRACT

Eleven native and five introduced species of *Rattus* occur in New Guinea. The native species are represented by 23 subspecies or monotypic species, all of which are endemic, and ally as three major species groups: (1) *R. niobe, R. richardsoni,* and *R. verecundus*; (2) *R. praetor, R. mordax, R. leucopus, R. steini, R. giluwensis, R. novaeguineae,* and *R. jobiensis*; and (3) *R. sordidus.* The first species group is largely montane (to 4500 m. altitude) in distribution, the second includes both montane and lowland species, whereas the third, *R. sordidus,* is restricted to southern lowlands.

One new species, *R. novaeguineae,* and two new subspecies, *R. steini baliemensis* and *R. verecundus vandeuseni,* are proposed and described in this revision. *Rattus giluwensis, R. jobiensis,* and *R. steini* are elevated to the rank of full species.

Among the native species, we recognize two subspecies of *Rattus niobe*: *R. n. niobe* (synonyms = *Stenomys rufulus* and *Stenomys niobe stevensi*), and *R. n. arrogans* (synonyms = *Rattus niobe haymani* [=*klossi*], *Stenomys niobe arfakiensis,* and *Rattus niobe pococki* [=*clarae*]); *Rattus richardsoni* as monotypic (synonym = *Rattus omichlodes*); four subspecies of *Rattus verecundus*: *R. v. verecundus, R. v. mollis* (synonym = *Rattus verecundus tomba*), *R. v. unicolor,* and *R. v. vandeuseni,* new subspecies Taylor and Calaby; two subspecies of *Rattus praetor*: *R. p. praetor* (synonyms = *Rattus praetor mediocris* and *Rattus purdiensis*), and *R. p. coenorum* (synonyms = *Rattus mordax tramitius, Rattus bandiculus, Rattus leucopus utakwa,* and *Rattus sansapor*); two subspecies of *Rattus mordax*: *R. m. mordax* and *R. m. fergussoniensis*; three subspecies of *Rattus leucopus*: *R. l. ringens, R. l. ratticolor,* and *R. l. dobodurae*; four subspecies of *Rattus steini*: *R. s. steini, R. s. foersteri, R. s. hageni* (synonym = *Rattus rosalinda*), and *R. s. baliemensis,* new subspecies Taylor and Calaby; *Rattus giluwensis* as monotypic; *Rattus novaeguineae,* new species Taylor and Calaby as monotypic; *Rattus jobiensis* as monotypic (synonyms = *Rattus owiensis* and *Rattus biakensis*); and two subspecies of *Rattus sordidus*: *R. s. gestri* (synonyms = *Rattus brachyrhinus* and *Rattus gestri bunae*) and *R. s. aramia.*

The five introduced species are *R. exulans, R. nitidus, R. rattus, R. norvegicus,* and *R. argentiventer,* and all are commensals of human beings. *Rattus exulans* is represented by a single widespread subspecies in New Guinea, *R. e. browni,* and its establishment here probably antedates that of the others by several thousand years. It is the only introduced species that we assessed in detail taxonomically and regard it as the senior synonym of the following: *Mus? echimyoides, Rattus concolor lassacquèrei, Rattus concolor manoquarius, Rattus browni praecelsus, Rattus browni aitape, Rattus browni suffectus, Rattus browni tibicen, Rattus browni gawae,* and *Rattus rennelli.*

INTRODUCTION

Rattus, as currently understood, is the largest mammalian genus and presumably originated in southeast Asia where the greatest number of species of *Rattus* and *Rattus*-like genera occurs. Musser (1981a) emphasizes, however, that *Rattus* is "an assemblage of great morphological diversity and geographical spread" and is inadequately defined. His contributions to the difficult quest of rational definitions of this and related genera are significant. He speculates that endemic *Rattus* of Australia and New Guinea may prove to be generically distinct from *Rattus* and that their *Rattus*-like features could have been independently derived in a manner analogous to those of species on the Lesser Sunda Islands (Musser, 1981b). Our taxonomic revision is at the levels of species and subspecies and for our purposes we adopt the traditional broad view of *Rattus* (Ellerman, 1941, 1949).

On New Guinea, with its mountainous spine and vast forests, grasslands, and lowland swamps, *Rattus* has radiated into endemic species, one or more of which occur virtually throughout this large island. Fossil evidence to provide a dating for the initial invasion is lacking; however, two autochthonous species occur in fossil deposits dating 8000–2000 B.P. (J. Hope, 1976) and indicate that speciation of *Rattus* was by then well advanced. Late Pleistocene *Rattus* are recorded from Australia (Tedford, 1967), but whether their progenitors came from New Guinea via the intermittent land bridge in the Pleistocene (Jennings, 1972), or from elsewhere, is unknown.

As in Australia, immigration of *Rattus* to New Guinea was successful even though the genus confronted results of earlier adaptive radiations of the Muridae, whose ancestors had arrived at least by the Pliocene (Plane, 1967), and a much older marsupial fauna. Lidicker (1968, 1973) has phenetic evidence to support his phylogenetic hypothesis that *Rattus* is a peripheral member of the murids in New Guinea. That *Rattus* was capable of dispersal and speciation in the face of a diverse mammalian fauna signifies its inherent adaptability. Whether it became established following one major invasion or several will probably never be established. From an evolutionary standpoint it is not germane for likely progenitors from the southeast Asian mainland are unknown. Faunal connections with Australia are far more evident and a land bridge occurred as recently as about 8000–6500 B.P. (Jennings, 1972). Our investigation focuses on the systematics of these oldest and truly native *Rattus* of New Guinea.

In addition, five species of *Rattus* now established in New Guinea are commensals of human beings. Their arrivals are also undocumented, but were undoubtedly assisted by this relationship. *Rattus exulans* apparently came with the indigenous people several thousand years ago, and *R. rattus, R. nitidus, R. argentiventer,* and *R. norvegicus* arrived more recently. Our treatment of all introduced species but *R. exulans* is minimal, except for discussion of *R. nitidus* and *R. rattus* in their masquerade as native species.

Detailed biological exploration of New Guinea began later than in most countries; only three native species of *Rattus* were recorded before 1900. For a long period only small numbers of specimens from widely separated localities reached museums. These were usually briefly described, inadequately compared to previously recorded specimens, and this has resulted in considerable synonymy. Prior to the late 1930s, scarcity of specimens precluded serious revisionary studies. Only two major revisions have utilized a reasonable number of specimens, those of Rümmler (1938) and Tate (1951). Ellerman's (1941, 1949) revision was based largely on type specimens. These reviews differ widely in their treatments of described forms. The standard checklist is that of Laurie and Hill (1954).

We have examined every museum collection known to us to contain *Rattus* of New Guinea and have studied all primary types in our re-evaluation of the genus. We have relied upon the harvests of numerous collec-

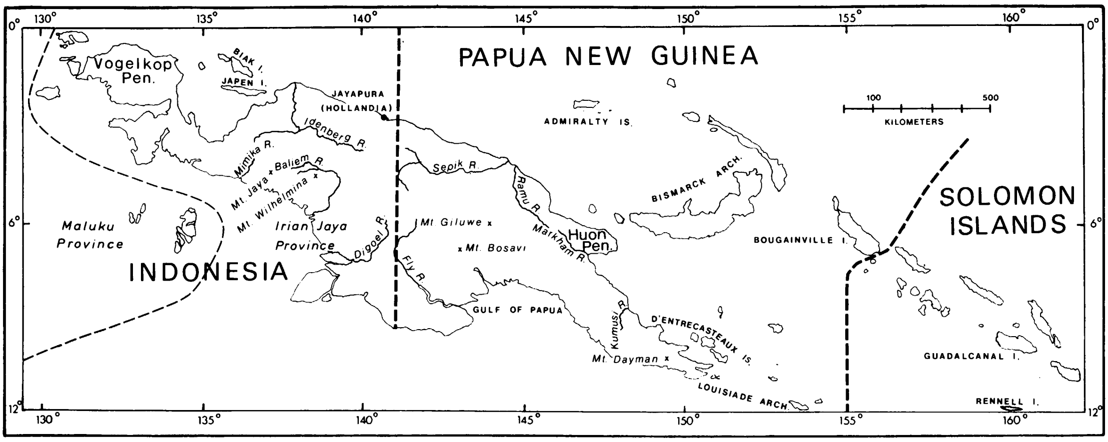

FIG. 1. Map of New Guinean region that defines geographical limits of the study and indicates certain landmarks important to this investigation.

tors who have preserved this material for posterity, often under the most adverse field conditions. It is not without deep awareness of major problems yet unresolved that we now propose a relatively new perspective of evolutionary relationships of the *Rattus* of New Guinea. It is a rapidly evolving genus that is widespread over a geographical region unequaled in potential for altitudinal and insular barriers to gene flow. There emerge more questions than answers in this study, but it is our hope to bring relationships within this genus into sharper focus and to define problems that will require critical evaluation in future studies.

In this paper "New Guinea" is used in a geographical sense and means the whole main island and all the adjacent smaller islands that are included within the boundaries of our distribution maps. The area covered by our study, as defined by these limits, includes all or part of three separate and independent countries. The western half of New Guinea and nearby islands is the Irian Jaya Province of the Republic of Indonesia, and the Aru and Kei islands are part of the Maluku Province of Indonesia. Papua New Guinea consists of the eastern half of New Guinea and nearby small islands, the Admiralty Islands, the Bismarck Archipelago, and the two most northerly islands, Buka and Bougainville, in the Solomon Islands chain. The remaining islands in the Solomons chain and Rennell Island are the independent country known as Solomon Islands (fig. 1).

Laurie and Hill's (1954) checklist contains a species called *Rattus shawmayeri* Hinton, 1943. A study by J. A. Mahoney of the holotype and only known specimen has shown it to be an example of *ruemmleri* Tate and Archbold, 1941, a species now listed in *Pogonomelomys* [Mahoney, in George (1979); personal commun.]. It is therefore removed from further consideration.

The descriptions of the three new taxa proposed in this paper were prepared by Taylor and Calaby, and only those authors should be cited as the authorities for the names.

ACKNOWLEDGMENTS

We express our profound gratitude to the many people who have helped us in the various phases of this study. They volunteered their time and expertise most generously in behalf of our work on the re-evaluation of the genus *Rattus* of New Guinea.

The following people provided valuable information regarding the locations and physiography of certain collecting sites: Captain E. H. Bryan, Jr., Manager, Pacific Science Information Center, Bernice P. Bishop Museum, Honolulu; Dr. J. M. Diamond, De-

partment of Physiology, University of California at Los Angeles; Mr. Lawrence Foanaota, Assistant Curator, Solomon Islands Museum, Honiara; Mr. J. E. Hill, Mammal Section, British Museum (Natural History), London; Dr. W. Z. Lidicker, Jr., Museum of Vertebrate Zoology, Berkeley; Dr. J. I. Menzies, formerly of Department of Biology, University of Papua New Guinea, Port Moresby; Dr. L. P. Richards, Department of Biology, Eastern Michigan University, Ypsilanti; Dr. G. K. Rutherford, Department of Geography, Queens University, Kingston; the late Professor Dr. Georg H. W. Stein, Natur-Museum und Forschungsinstitut, Frankfurt am Main; Dr. A. C. Ziegler, Bernice P. Bishop Museum, Honolulu.

Dr. J. W. Kamp, Department of Science Education, The University of British Columbia, provided us with numerous references on geology and climatology of New Guinea which were valuable in this investigation. Professor A. L. Bloom, Department of Geological Sciences, Cornell University, Ithaca, and Dr. D. Hopley, Department of Geography, James Cook University, Townsville, assisted us in a search for information on the geology of insular regions in Papua New Guinea and related sea level changes.

Mr. J. H. Bjerring, Assistant Director, The University of British Columbia Computing Centre, spent many hours helping us to implement and evaluate statistical methods used in multivariate analyses. In addition, we acknowledge the help of Mr. Stanley Kita, Mrs. I. Nissen, and Miss Joanne Bell, also of this Centre.

We are especially grateful to Mrs. Susan Harrison, of the Biology Data Centre of The University of British Columbia, for writing special programs for our data and for aiding us in computerizing raw data. Mr. William Webb, Systems Analyst of the Centre, kindly implemented the NT-SYS program on The University of British Columbia computer system. The late Mr. Stephen Bordan, Computer Analyst of the Centre, assisted us in the initial organization of the data and in generating locality maps from digitized coordinates. Mrs. Shirley Graystone, also of this Centre, gave us willing assistance in several aspects of the computer portion of this study. Dr. S.-S. Lee, Faculty of Education, The University of British Columbia, Mr. Bob Footit, Department of Biological Sciences, Simon Fraser University, and Dr. D. P. Snyder, Department of Zoology, University of Massachusetts, provided helpful information regarding computer programs.

The advice given by Dr. Leslie F. Marcus, Department of Invertebrates, Miss Nancy A. Neff, Department of Vertebrate Paleontology, both of the American Museum of Natural History, and by Dr. F. James Rohlf, Department of Ecology and Evolution, State University of New York–Stony Brook, regarding options among appropriate multivariate packages suitable for handling a large data base is greatly appreciated. Miss Marla Weston, Department of Zoology, The University of British Columbia, generously shared her knowledge and expertise in times of difficulty with particular computer runs.

Services by the library staff at The University of British Columbia were extensive, both in obtaining interlibrary loans and in assisting in our quest for locality sites. We especially thank the librarians in the Map Division for their help.

The long term loan of half of the New Guinean *Rattus* in the collection of the Bernice P. Bishop Museum was made possible by Dr. A. C. Ziegler, Vertebrate Zoologist of that museum. It became our primary available reference collection in the course of our reevaluation of this group.

Mrs. Wendy Hindmarsh Jones, technical assistant in the first stages of this project, aided in data transcription, locality identification, and preparation of typescripts of important papers that were translated for this project.

Mr. Nasar Din, Curatorial Assistant, The Cowan Vertebrate Museum at The University of British Columbia, helped extensively in the shipment and unpacking of specimens loaned from various museums.

Joan Miller prepared the skull drawings and locality maps for this project. Her care and interest in the preparation of these illus-

trations are greatly appreciated. Mr. Peter Rowlinson, printer for the Faculty of Education of The University of British Columbia, kindly duplicated the base map for the locality site figures.

The following persons generously assisted us by providing access to museum specimens of *Rattus* of New Guinea: Dr. S. Anderson, Dr. G. G. Musser, Dr. R. G. Van Gelder, and Ms. Marie Lawrence, all of the American Museum of Natural History, New York; Mr. B. J. Marlow, Australian Museum, Sydney; Dr. A. C. Ziegler, Bernice P. Bishop Museum, Honolulu; Dr. G. B. Corbet, Mr. J. E. Hill, Miss D. M. Hills, and Miss P. D. Jenkins, British Museum (Natural History), London; Dr. Luis de la Torre, Field Museum of Natural History, Chicago; Dr. L. Cahen and Dr. X. Misonne, Institut Royal des Sciences Naturelles de Belgique, Brussels; Professor E. Tortonese, Museo Civico di Storia Naturale, Genoa; Dr. B. Lawrence, Museum of Comparative Zoology, Cambridge; Dr. W. Z. Lidicker, Jr., Museum of Vertebrate Zoology, Berkeley; Dr. S. Kadarsan, Museum Zoologicum Bogoriense, Bogor; Dr. U. Rahm, Naturhistorisches Museum, Basel; Dr. Heinz Felten, Natur-Museum und Forschungsinstitut, Senckenberg, Frankfurt am Main; Dr. Eric Lindgren, Papua New Guinea Museum, Boroko; Dr. A. M. Husson and Dr. C. Smeenk, Rijksmuseum van Natuurlijke Historie, Leiden; Dr. G. Topal, Természettudományi Múzeum Állattára, Budapest; Dr. C. O. Handley, Jr., United States National Museum, Washington, D.C.; Dr. F. W. Braestrup and Dr. P. Valentin-Jensen, Universitetets Zoologiske Museum, Copenhagen; Dr. W. Forster, the late Dr. T. Haltenorth, and Dr. I. Weigel, Zoologische Sammlung des Bayerischenstaates, Munich; Dr. R. Hutterer, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; and Dr. R. Angermann, Zoologisches Museum der Humboldt-Universität zu Berlin.

We are deeply grateful to the persons who reviewed our manuscript and offered many constructive suggestions. They are: Dr. Karl F. Koopman, Dr. Leslie F. Marcus, Dr. Guy G. Musser, and Miss Nancy A. Neff, all of the American Museum of Natural History, and Dr. Michael D. Carleton, Smithsonian Institution. Although interpretations and conclusions are our own and we take full responsibility for errors, we benefited immeasurably from the reviewers' comments that led us to improve and clarify important aspects of our presentation. To Dr. Guy G. Musser we owe special thanks for his interest, encouragement, and challenging discussions throughout all phases of this study.

Financial support for this project was provided by the National Sciences and Engineering Research Council of Canada grant A3462 (Taylor) and by a Killam Senior Research Fellowship (Taylor). Access to computer facilities was made available by The University of British Columbia. These generous sources of support are gratefully acknowledged. Mrs. Kathleen Taylor and Dr. J. W. Kamp kindly helped read proof, and the judicious editing by Ms. Florence Brauner is appreciated.

DEDICATION

We dedicate this work to Mrs. Sarah C. Smith, research assistant for the major portion of this study, to express our deep appreciation for the many ways she aided us. She took the initiative to learn a spectrum of technical procedures in the course of this investigation. She was meticulous in her work, rendered help in preparation of the figures, typed the manuscript, helped to proofread, offered many excellent suggestions, and assisted in numerous other aspects of the study. Her cheerful smile, sense of humor, and genuine interest in this project are appreciated beyond measure and became salvation on days when computer runs went awry. It is both this personal side and her outstanding competence which we wish to acknowledge. Our gratitude to her is immeasurable.

TABLE 1
Subspecies of *Rattus* from New Guinea Listed by Number of Localities and by Number and Nature of Specimens

Subspecies	Total Localities	Total Animals (♂, ♀, Sex Unknown)	Skins & Skulls, or Skulls Only		Skins Only, or Skulls in Skins (Skulls not Measured*)		Age Unknown
			Adults	Juv.	Adults	Juv.	
Rattus niobe niobe	91	1993 (983, 976, 34)	1503	157	199	56	78
Rattus niobe arrogans	19	637 (353, 278, 6)	186	4	391*	18*	38
Rattus richardsoni	8	65 (34, 31, 0)	62	2	1	0	0
Rattus verecundus verecundus	19	86 (44, 37, 5)	80	3	2	1	0
Rattus verecundus mollis	38	219 (101, 115, 3)	158	48	10	0	3
Rattus verecundus unicolor	4	59 (32, 23, 4)	55	2	2	0	0
Rattus verecundus vandeuseni	1	8 (5, 3, 0)	8	0	0	0	0
Rattus praetor praetor	16	49 (23, 22, 4)	33	4	11	0	1
Rattus praetor coenorum	34	184 (97, 76, 11)	117	45	17	5	0
Rattus mordax mordax	52	269 (116, 148, 5)	207	47	10	4	1
Rattus mordax fergussoniensis	8	37 (15, 21, 1)	26	11	0	0	0
Rattus leucopus ringens	22	194 (80, 95, 19)	149	24	16	3	2
Rattus leucopus ratticolor	17	60 (29, 31, 0)	54	5	1	0	0
Rattus leucopus dobodurae	23	200 (101, 99, 0)	162	33	5	0	0
Rattus steini steini	6	282 (122, 107, 53)	203	66	7	5	1
Rattus steini foersteri	9	26 (12, 9, 5)	20	3	0	0	3
Rattus steini hageni	105	612 (268, 312, 32)	408	111	50	38	5
Rattus steini baliemensis	7	218 (109, 106, 3)	174	41	3	0	0
Rattus giluwensis	6	20 (8, 12, 0)	15	5	0	0	0
Rattus novaeguineae	23	171 (81, 86, 4)	116	38	7	10	0
Rattus jobiensis	5	18 (9, 9, 0)	8	10	0	0	0

TABLE 1—(*Continued*)

Subspecies	Total Localities	Total Animals (♂, ♀, Sex Unknown)	Skins & Skulls, or Skulls Only		Skins Only, or Skulls in Skins (Skulls not Measured*)		Age Unknown
			Adults	Juv.	Adults	Juv.	
Rattus sordidus gestri	12	51 (37, 13, 1)	34	12	4	1	0
Rattus sordidus aramia	19	248 (130, 102, 16)	169	43	20	10	6
Rattus exulans browni	242	1677 (868, 728, 81)	1170	335	112	60	0
Rattus nitidus	4	20 (6, 13, 1)	8	10	2	0	0
Rattus rattus	40	177 (75, 86, 16)	116	35	17	7	2

MATERIALS AND METHODS

This study is based on the examination of 7580 specimens of *Rattus* from New Guinea from the collections of the following museums: Australian Museum, Sydney (AM); American Museum of Natural History, Department of Mammalogy, New York (AMNH); Australian National Wildlife Collection, Division of Wildlife Research, CSIRO, Canberra (ANWC); Bernice P. Bishop Museum, Honolulu (BBM); British Museum (Natural History), London (BM); Naturhistorisches Museum, Basel (BNM); Universitetets Zoologiske Museum, Copenhagen (CZM); Field Museum of Natural History, Chicago (FMNH); Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels (KNMB); Museo Civico di Storia Naturale, Genoa (MCSN); Museum of Comparative Zoology, Harvard College, Cambridge (MCZ); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Museum Zoologicum Bogoriense, Bogor (MZB); Papua New Guinea Museum, Boroko (PNG); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); Natur-Museum und Forschungsinstitut, Senckenberg, Frankfurt am Main (SMF): Terméşzettudományi Múzeum Állattára, Budapest (UNM); United States National Museum, Smithsonian Institution, Washington, D.C. (USNM); Zoologisches Museum der Humboldt-Universität zu Berlin (ZM); Zoologische Sammlung des Bayerischenstaates, Munich (ZS).

Specimens examined of each subspecies (table 1) are listed by locality and by museum registration number in the section entitled Museum Specimens Examined and Localities.

Twenty skull measurements were taken on each specimen and recorded to the nearest 0.1 mm. on needlepoint dial calipers. All but 50 of the 6335 skulls were measured by Taylor to maximize consistency of measurements. The measurements are as follows:

1. Occipitonasal length: dorsal measurement from anterior tip of nasals to posterior point of occiput.
2. Condylobasal length: ventral measurement from anterior faces of upper incisors to posterior margins of occipital condyles.
3. Basal length: ventral measurement from anterior faces of upper incisors to midventral margin of foramen magnum.
4. Zygomatic width: greatest width across zygomatic arches.
5. Interorbital width: dorsal measurement of minimum distance across frontals between orbital fossae.
6. Interparietal length: middorsal measurement of interparietal taken from point of con-

tact with sagittal suture of parietals to its posterior limit anterior to the lambdoidal crest.

7. Interparietal width: dorsal measurement across interparietal at its points of junction with parietals and occipital.

8. Braincase width: dorsal measurement from one squamosal to the other immediately posterior to termination of the zygomatic arch.

9. Mastoid width: dorsal measurement across occipital immediately posterior to the 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 the sagittal or parasagittal plane determined by the nasal tip. (Paired features were measured on side indicated except where complete only on other side.)

11. Nasal width: dorsal measurement across the two nasals at anterior points of contact with premaxillae.

12. Palatal length: ventral measurement taken from face of left upper incisor to most anterior 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 the 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 most posterior 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.

Whenever possible, pelage assessment was made from the most recently prepared specimens available that had apparently not been subjected to spirit preservation.

Two age categories, adult and juvenile, were established for each subspecies to separate specimens of sexually mature size from those that were sexually immature. The distinctions were made in part on scrotal size and teat development on skins and, in a few cases, on embryo records. Occipitonasal lengths were then correlated with these soft part criteria to establish the two age categories solely on the basis of this specific skull measurement. This dimension was thus extended to allow assignment of specimens without skins or whose skins lacked aging criteria. The value that separates these age categories is provided for each subspecies in the Mean Measurements section.

Each of the 547 localities represented in this study is defined by longitude, latitude, and elevation. These geographical criteria are included in the listing of the museum specimens and form a gazetteer within this listing.

A map of New Guinea and the locality coordinates, longitude and latitude, were recorded on an Instronics Gradicon Digitizer. The computer data were used to generate cartographic plots on a Calcomp Plotter 565 operating from a PDP 11/45 computer running on UNIX. These computerized distribution maps formed the basis for the drafting of the map illustrations. These final maps show localities as generalized dots, and the lines circumscribing the distributions of subspecies or single species are visual aids only and are not intended to define precise limits of distribution.

Final numerical analyses of the taxa at both the subspecies and species levels are based on 20 skull measurements of 3800 adult specimens, although more specimens were used in trial runs. All juveniles (1312), all specimens with incomplete or missing skulls (2328), and those unidentifiable as to age category (140), were deleted from the total of 7580 specimens examined. Measurements of the skulls used in the analyses are summarized and listed by subspecies in tables 2 through 22 and 24 through 28.

All numerical analyses were run on an Amdahl 470 V/6 Model 2 computer on the Michigan Time Sharing operating system at The University of British Columbia. A review of numerical methods that were explored, which either led to our final selection of specific analyses or to their rejection, follows.

The original mensural data were first entered into a missing data analysis, BMDPAM (Dixon, 1975) using the twostep option. A maximum of 20 variables measured on each of 5233 adult cases constituted the data matrix. Patterns and estimations of missing data were generated for the more than 1400 cases that lacked one or more variables. Although the highest percentages of estimates were for variables that seemed particularly valuable (i.e., occipitonasal, condylobasal, and basal lengths), we chose to use both estimated and real variables in the data matrix for a preliminary run.

The data matrix was entered into a principal components analysis (PCA), BMDP4M (Dixon, 1975), using a covariance matrix. A score for each case was calculated by dividing the distance-squared (approximately Chi-square) by the number of variables (20); each case in which this score exceeded 4.0 was considered an outlier. Although this score was arbitrary, it established an obvious upper limit of a spectrum of lower scores. Less than 3 percent of the cases exceeded this threshold and, of these, most did so by an increment of 1 or more. The large scores of the outliers, which were from various taxa, had initially been measured on different occasions, and usually indicated a mensural transcription error, keypunch error, or skull anomaly. The PCA was rerun and adjusted, by remeasurement or deletion, until all cases to be used were below the threshold. The score on the first component, which primarily reflected size, was extracted as output for each case.

A matrix, consisting of the values for the mean-centered 20 variables plus the score for the first component for each case, was entered into a discriminant analysis, BMDP7M (Dixon, 1975). The primary function of this analysis was to test the discriminatory success of these variables in assigning cases to species and subspecies levels that had been determined *a priori* by facies determination. The analysis, which assigns the cases as "correctly" or "incorrectly" classified, provides a Mahalanobis D^2 value from each case to each *a priori* group. This measure was informative because it suggested possible trends in alliances of a given taxon to other than its own group. Canonical variates for individual cases and for the centroids of the *a priori* groups were also generated.

Initially, 5233 cases produced the matrix for the discriminant analysis. The *a priori* groupings were established to represent the level of subspecies. Two aspects of the input, estimation of missing data and widely differing sample sizes (5 to 1433), presented problems. Another problem was that within certain taxa, rats near upper or lower limits of cranial size showed some tendency to affiliate with other taxa that shared similar skull sizes. The resulting "correct" scores for the classification matrix and jackknifed classification were in the lower 60 percent range.

The next runs of BMDP7M employed only complete original measurements (3835 cases) which were mean-centered and rerun through PCA. Decision to eliminate the estimated data established our priority for real measurements at the sacrifice of number of cases. It was a substantial compromise since both locality representation and mensural variability within a locality were reduced. The first principal component was again extracted and scores computed from this component plus the 20 variables for each case were used in matrices entered for some discriminant analyses. An attempt to lessen the influence of skull size in some runs was made by deleting the score for the first component from the matrix. Nonetheless, assignments related to size problems were only marginally improved, for now skulls of large-bodied subspecies allied anomalously with those of small size. The *a priori* groupings varied in sample size from 3 to 1208. Before attempting to enter *a priori* groups in accordance with our initial facies analysis, we deliberately overestimated the number of groups to examine their scores as entities. These earlier runs scored lower "correct" assignments than subsequent, more refined groupings. Assignments improved to a maximum of 70 percent correct (classification matrix) and 67 percent correct (jackknifed classification) in the last set of these runs that retained scores for the first principal component.

The influence of skull size was lessened further by transforming the original variables of all complete cases to their logarithmic equivalents. A data matrix based upon this transformation was then entered into a PCA. In this analysis, 2.5 was designated the threshold score. Only 1 percent of the cases surpassed it, and did so by at least 0.5. These 35 outliers were rejected from further consideration. A discriminant analysis (BMDP7M) was run for 3800 cases on the logarithmic matrix for the refined, 26 *a priori* subspecies groups. The resulting classification and jackknifed classification matrices were now 87.0 and 85.2 percent correct, respectively. A regrouping of these 3800 cases into 14 species groups resulted in classification and jackknifed classification matrices of 89.6 and 89.2 percent correct, respectively. We accepted these levels as reasonable assignments to our facies grouping choices.

Entry into numerical analyses that generate taxonomic structure is a problem when the data matrix is very large, as was true in our study. The number of cases had to be reduced to below at least 1000 OTUs (Operational Taxonomic Units; Sokal and Sneath, 1963) before routines within the NT-SYS program (Rohlf, Kishpaugh, and Kirk, 1968) could be used (Rohlf, personal commun.) Initial trials with cluster analysis (SIMINT-TAXON routines of NT-SYS) were based upon the 20 mean-standardized variables of individuals. The clustering strategy was UPGMA (unweighted pair-group arithmetic average), using a Mahalanobis distance coefficient. Complete samples of only a few subspecies at a time could be analyzed per run due to space limitations of the routine. Some runs included cases for which estimates of missing data had been made (from BMDPAM) and others were restricted to complete data cases only. Attempts to include all subspecies in a single run were made by designating one specimen per locality as an OTU or, in cases of low sample sizes of certain subspecies, all specimens as OTUs. The results of all of these runs were of limited value since only subspecies of small skull size grouped well.

Reduction of OTUs and of the influence of skull size was next achieved by generating group means of the logarithm of the value for each subspecies according to localities. The number of OTUs for all 3800 complete cases was now 516. Principal components were extracted using NT-SYS. The number of components sufficient to account for about 98 percent of the correlation among variables was selected for each run.

Using the scores of the OTUs on the components in the reduced set, the single linkage cluster method was explored initially (MSTSNGL routine of NT-SYS) for it is a much more economical run than is average linkage clustering. Both Mahalanobis distances (which maximize size differences) and correlation coefficients (which reduce size differences in favor of shape) were employed with the 516 OTUs. The results were disappointing because the OTUs were even less compatible with the results of the facies analysis than they were in the previous cluster runs. The subspecies of the three smallest-sized species were the only members to be structured well within their own groups.

The following analyses were also performed upon the scores of the 516 OTUs on the principal components. Again, Mahalanobis distance and correlation coefficient matrices were formed and, using the TAXON routine of NT-SYS, three types of sequential agglomerative hierarchal cluster analyses were performed upon each matrix: UPGMA (unweighted pair-group method using arithmetic averages), WPGMA (weighted pair-group method using arithmetic averages), and WPGMC (weighted pair-group method using centroids). Of these, UPGMA method on distances was the most compatible with the facies analysis and WPGMA on correlations was second best. UPGMA on distances produced well-defined clusters of the smaller and mid-sized rats at the level of subspecies that agreed with the facies analysis. In the remaining areas of the phenograms, the larger rats were intermingled without detectable pattern. Data subsets, each run on the appropriate number of principal components describing 97.5 percent accumulated percent correlation among variables and consisting of various combinations of subspecies, were similarly clustered. The object was to examine whether relationships among OTUs would become more clearly defined by working with reduced numbers of groups. Little was gained by this subset approach although, again, UPGMA, based on distance coefficients, was a more satisfactory method than WPGMA.

In a further attempt to attain some clarification of phenetic relationships, particularly of the larger rats, the data matrix was reduced to the form in which each OTU represented the group mean of one of the 26 subspecies or of the 14 species. Data were prepared for these phenetic analyses in three ways: 1) as means of the logarithmic transformations of the variables, 2) as the scores on that number of components from a principal components analysis of the logarithmic data matrix accounting for 98 percent of the correlation among variables, and 3) as the scores on that number of canonical variates, evaluated at group means from the discriminant analyses, that contain more than 98 percent of the among-groups variance. The discriminant analyses had been run on the logarithmic matrix of 3800 complete cases and were grouped either at the level of the 26 subspecies or of the 14 species.

UPGMA on Mahalanobis distances, based on the mean logarithmic data, clustered subspecies or species largely by size criteria. The results were less compatible with our facies analysis than were those for UPGMA runs on 516 OTUs. UPGMAs on distances, calculated from scores on principal components, also sorted the subspecies or species OTUs mainly by size. The third type of input, scores on the first eight canonical variates for subspecies or first six for species, was entered into several structure-finding strategies. One was the minimum spanning tree and single linkage cluster routine (MSTSNGL). Both types of spatial structure based on canonical variate scores were considerable improvements over those generated from the first two types of input data. This type of cluster analysis still grouped the large-bodied subspecies or species with more sensitivity to size than it did the smaller rats. The minimum spanning tree structure was, however, much more effective for both small and large species and this method has been included in our final treatment. The canonical variate scores for the group means were entered into NT-SYS UPGMA and WPGMA using both Mahalanobis distance and correlation coefficient matrices. Of these, UPGMA on distances showed the greatest strength in clustering subspecies of larger-bodied taxa with their conspecifics while maintaining good clustering of the smaller rats.

Since both UPGMA and the minimum spanning tree (MST) method provided results that basically reinforced our facies assessment, we then explored the possibility of a cladistic approach to structural representation. Wagner trees (MINT package; Rohlf, 1971) at both subspecies and species levels were created from a Mahalanobis distance matrix. The matrix consisted of the canonical variates evaluated at the group means, since this matrix had provided the most acceptable phenetic structure when using UPGMA or the MST strategy. Since entry into this cladistic analysis was based strictly on mensural variables and no designation of "primitive" or "advanced" could be ascribed to such character states, the most critical aspect of the input was lacking, namely, an evolutionary ordering of variables. Interpretation from such a postulated ordering for this young genus in New Guinea at the current status of knowledge, even if non-mensural characters were used, would most likely be more misleading than constructive and we rejected the idea. Alternatively, the trees were rooted by selecting *Rattus exulans browni* as the surrogate ancestral OTU for input to the program. This rat is not one of the old endemics of New Guinea, but presumably arrived by human agency. It also extends geographically beyond the New Guinea–Australia limits and is well represented in sample size. We elected it to serve as the "ex-group" (Ross, 1974), or the most distant, in an evolutionary sense, from the endemics. The HTU (Hypothetical Taxonomic Unit; Farris, 1970) generated between this OTU and the rest was positioned as the root. The resultant Wagner trees were effective in associating only those OTUs that had already shown strong degrees of neighborliness in other types of structural analysis, and further exploration into numerical cladistics was not carried out.

The nature of the material upon which this revision is based is limited and imposes considerable restriction on the foundations for re-evaluating this group of rodents. The type of data most available for numerical analysis that permits use of the majority of specimens is craniometric. Its greatest asset is that it is obtained by the investigator and, since it comes from hard part anatomy which is least affected by preparation and subsequent storage, is very reliable. These points are critical when some taxa are represented by only a few skulls and oxidized deteriorating skins, and when opportunities for further collecting are financially prohibitive to most museums and investigators. The numerical assessment is thus based solely on craniometric variables. The facies assessment is founded upon those features that could be reliably evaluated from preserved skins and from general skull conformations. Incomplete skulls, skins lacking skulls, and juvenile specimens could be included in this latter assessment, details of which are presented in the accounts of species.

Series of juvenile skulls exhibit disproportionate growth between rostrum and cranium. Since no aging data are available to define this growth function, juveniles had to be culled out from numerical analyses on the basis of size and absence of reproductive activity. Since most species of *Rattus* in New Guinea are not seasonal breeders in these tropics (Taylor, Calaby, and Smith, unpubl. data), sexual maturation is generally not delayed by the intervention of a lull in seasonal breeding, as it is in most polyestrous rodents in temperate regions. Thus, young rats can enter the breeding adult status while still in an active growth phase and while relative skull proportions may still be shifting. Furthermore, adult *Rattus* is evergrowing and, even though the skull proportions become more stable as the animal ages, cranial crests and processes develop and enlarge, particulary in old specimens of large species, and can affect certain measurements. The larger species also undergo greater morphometric changes than do the smaller, both in maturing and in older individuals. The extent of tolerance of the numerical procedures we employed to such osteological changes is, however, unknown. For specimens differing greatly in size, transformation to the logarithmic form of their variables results in closer correspondence in their standard deviations and, thereby, reduces heterogeneity of variance (Neff and Marcus, 1980).

In summary, the numerical procedures that we selected were discriminant analysis (BMDP7M), SIMINT-TAXON routine for an UPGMA clustering strategy, and minimum spanning tree routine (MSTSNGL), the last two from NT-SYS. The discriminant analyses were run on the logarithmic equivalents of the original variables. The NT-SYS routines were based on scores of canonical variates of group means at the subspecies and species levels which were generated by the discriminant analyses. The results of these discriminant and cluster analyses are presented in the section on Multivariate Analysis.

RESULTS

DESIGNATION OF SPECIES AND SUBSPECIES

The genus *Rattus,* known to occupy New Guinea only since the Pleistocene, has radiated vigorously in every major portion of this complex, vertically-stratified region. Severe earthquakes and regional volcanic activity are common here, as are erosion and major landslides. Their impact upon the biota and the mosaic of habitats is unfathomable. We envision the effect on *Rattus* of

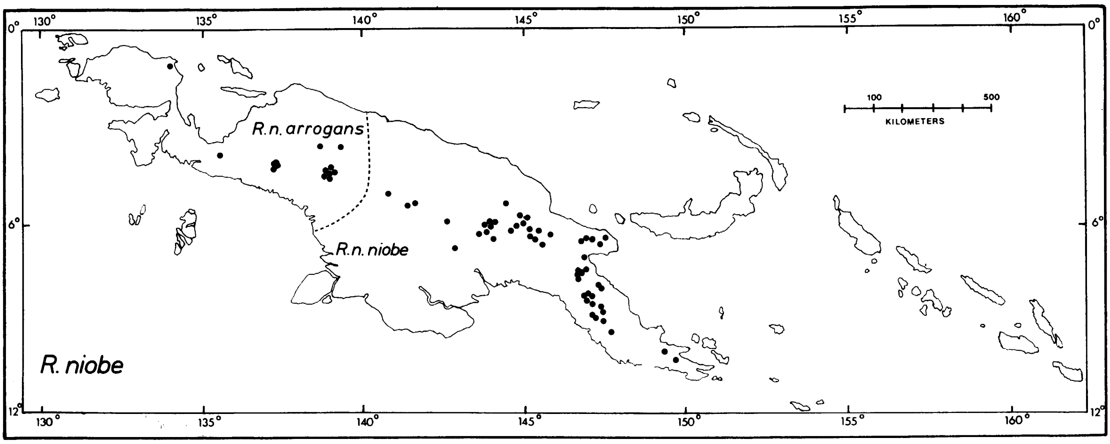

FIG. 2. Distribution map of *Rattus niobe*. Locality records for each of the two subspecies are indicated by dots.

such frequent perturbations as one of fragmenting and juxtaposing anew local populations that are differentiating under selective pressures of prevailing microhabitats. Although frequent restructuring of components in populations and the development of new faunal interfaces may accelerate or suppress the process of radiation, we have nonetheless attempted to revise this genus in New Guinea within a rational taxonomic framework of species and subspecies.

Whenever possible, on the basis of museum records of sympatry, we have used the biological species criterion (Mayr, 1963) for most of the species we recognize, including a new species. With or without the availability of sympatric evidence, we have also tried to estimate some magnitude of interspecific dissimilarity that can be demonstrated in the facies and numerical analyses.

The decision to recognize subspecies in our revision stems from two goals. One is to acknowledge entities within a species that are phenotypically differentiated from conspecifics, as well as geographically isolated by distance and/or topography. Based on current collections, they indicate some measure of evolutionary diversification within species of this rapidly evolving genus. Secondly, it formalizes by nomenclatorial means our views regarding treatments by earlier investigators, an important documentation since we have reorganized and synonymized a large number of taxa. Again, both facies and numerical analyses are combined to aid us in our assessment and to attempt some quantitative and qualitative foundation for making these difficult assignments.

ACCOUNTS OF SPECIES

Rattus niobe (Thomas)

DISTRIBUTION: Virtually all montane areas of the island of New Guinea, including the Huon Peninsula. Records are sparse west of 137° E longitude where only four localities are represented in museum collections. Ranges in altitude from 762 to 4050 m.; most records are from above 1500 m. (fig. 2).

GENERAL DESCRIPTION: This species is the smallest of the *Rattus* endemic to New Guinea. Only the widespread commensal, *R. exulans browni,* is smaller and the two are readily separated on morphological characters. The pelage is very soft and fine in *niobe* and body coloration is dark brown. Usually there is a tinge of rufous dorsally and one of buff or cinnamon ventrally. Spines are absent. Ears, feet, and tail are also dark, although the feet may have some silvery hairs middorsally. The hind feet are narrow and the tail is usually equal to, or longer than, the head and body length.

The mammary formula is 1 + 2 = 6.

The skull is the most delicate of all the native *Rattus* (fig. 3). The rostral area is

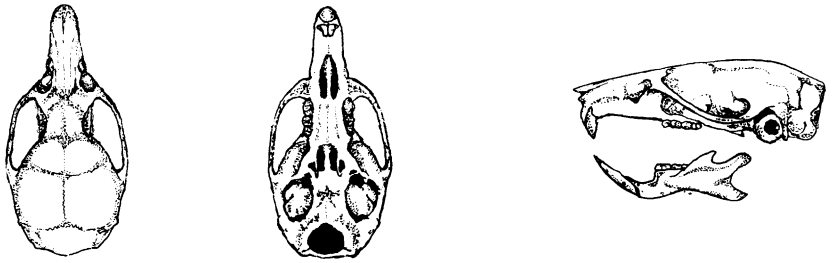

FIG. 3. Dorsal, ventral, and lateral views of skull of adult *Rattus niobe niobe,* BBM 96738, from Bulldog Road. Occipitonasal length 33.0 mm.

elongated and the cranium is relatively inflated and is composed of very thin bone. In some specimens the mid-dorsal cranium is translucent. The zygomata are thin and fragile. The nasals and premaxillaries extend anterior to the incisors. The dorsal skull is smooth and supraorbital ridging, if present, is barely discernible. The incisive foramina are short and usually relatively wide. They may reach the level of the molar row or fall short of it. This is highly variable and the differences are not of subspecific value. The palate terminates 1–2 mm. posterior to the molar row. The bullae are small and relatively uninflated, and they average 17.1–17.5 percent of the basal skull length. The molars and incisors are narrow and delicate. The anterolateral cusp of m^2 is absent or weakly developed, a feature shared with *R. verecundus.*

DIAGNOSTIC CHARACTERS: This is the smallest of the somber-furred *Rattus* of New Guinea. There are only two species with which it might be confused, *R. e. browni,* that is almost the same size, and *R. verecundus,* which is larger. *Rattus niobe* is readily distinguished from *R. e. browni* by its darker and softer dorsal pelage, dark coloration on venter and feet, lower mammary formula, more delicate skull, and smaller bullae relative to basal length. It is distinguished from *R. verecundus* by its smaller size, darker ventral pelage without white marking, less pointed rostrum with less nasal overhang, and by its slightly larger bullae. Juvenile *R. verecundus* that lack distinctive white marking can be difficult to distinguish from adult *niobe.* Skull features, such as shape of the incisive foramina, which are narrow in juvenile *verecundus,* and tooth wear relative to skull length, should, however, clarify species identification.

TAXONOMIC HISTORY: The species was originally described as *Mus niobe* by Thomas (1906). His description was based upon a young adult and he regarded the species as a close ally of *Mus verecundus.* Thomas (1910a) then placed both *niobe* and *verecundus* in the genus *Stenomys.* A new species, *Stenomys klossii,* was proposed by Thomas (1913) and he viewed it as similar to *S. niobe* in external features. Thomas (1922a, 1922b) added two more species to *Stenomys, S. arrogans* and *S. rufulus,* and noted strong similarities between *rufulus* and *niobe.* Later, in the same year, Thomas (1922c) provided an extended description of *arrogans* and mentioned its strong resemblance to *klossi.* Rümmler (1935) described three subspecies, all of which he placed in *S. niobe*: *S. n. stevensi, S. n. arfakiensis,* and *S. n. clarae.* He then added *rufulus, arrogans,* and *klossi* to *S. niobe* and thus recognized seven subspecies (Rümmler, 1938). Ellerman (1941) shifted the entire group to *Rattus,* and as a result nomenclatorial problems emerged in that the names *klossi* and *clarae* were preoccupied in *Rattus.* Ellerman (1941) renamed these forms *haymani* and *pococki,* respectively. Ellerman (1949) placed all seven subspecies of *R. niobe* in the subgenus *Apomys* along with forms that ranged westward to Ceylon. Tate (1951) proposed a *Rattus niobe* Group containing all seven subspecies of *niobe,* al-

TABLE 2
Measurements (in Millimeters) of Adult *Rattus niobe niobe*
(N = 825 for skin measurements; N = 1253 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	120.1 ± 0.25	7.08	98.0–150.0
Tail length	123.5 ± 0.38	10.83	92.0–157.0
Hind foot (s.u.) length	28.1 ± 0.05	1.38	24.5–32.0
Occipitonasal length of skull	32.6 ± 0.03	0.99	30.0–35.8
Condylobasal length	30.0 ± 0.03	0.98	27.0–33.1
Basal length	27.3 ± 0.03	0.93	24.3–30.3
Zygomatic width	15.2 ± 0.01	0.51	13.7–17.0
Interorbital width	5.6 ± 0.01	0.24	4.9–6.8
Interparietal length	4.2 ± 0.01	0.46	2.9–5.9
Interparietal width	9.4 ± 0.02	0.67	7.0–11.2
Braincase width	14.2 ± 0.01	0.39	13.0–15.5
Mastoid width	12.2 ± 0.01	0.41	10.9–13.8
Nasal length	12.2 ± 0.02	0.57	10.2–14.0
Nasal width	3.4 ± 0.01	0.27	2.5–4.2
Palatal length	16.7 ± 0.02	0.65	14.2–19.0
Incisive foramen length	4.4 ± 0.01	0.41	3.0–5.7
Incisive foramina width	1.7 ± 0.01	0.24	0.9–2.3
Inside m^{1-1} width	2.8 ± 0.01	0.31	1.9–3.8
Outside m^{1-1} width	6.7 ± 0.01	0.28	5.9–7.7
Bulla length	4.7 ± 0.01	0.28	3.6–5.9
Crowns m^{1-3} length	4.9 ± 0.01	0.23	4.1–5.7
Alveoli m^{1-3} length	5.2 ± 0.01	0.24	4.4–5.9
Crowns m_{1-2} length	4.0 ± 0.01	0.26	3.0–4.8

though he doubted the validity of *haymani, arrogans,* and *stevensi,* and added his newly described species, *Rattus richardsoni.* Laurie and Hill (1954) placed all the members of Tate's *R. niobe* Group under the subgenus *Lenothrix,* questioned the validity of *stevensi,* and to the subgenus added two more species from Sulawesi. Since 1935 seven subspecies have been recognized in *R. niobe.* Although the validity of some has been questioned, no synonymies have been proposed until now.

We recognize two subspecies, *R. n. niobe* and *R. n. arrogans.*

Rattus niobe niobe (Thomas)

Mus niobe Thomas, 1906, p. 327.
Stenomys niobe: Thomas, 1910a, p. 507.
Stenomys rufulus Thomas, 1922b, p. 669.
Stenomys niobe stevensi Rümmler, 1935, p. 117.
Stenomys niobe niobe: Rümmler, 1938, p. 200.
Stenomys niobe rufulus: Rümmler, 1938, p. 201.
Rattus niobe niobe: Ellerman, 1941, p. 206.
Rattus niobe rufulus: Ellerman, 1941, p. 206.
Rattus niobe stevensi: Ellerman, 1941, p. 206.

HOLOTYPE: Skin and slightly damaged skull, young adult female, BM 5.11.28.7, collected November 15, 1904, by A. S. Meek, at Owgarra, Angabunga River, Papua New Guinea, 2750 m.

DISTRIBUTION: Montane habitat from the southeastern extremity of New Guinea northward and westward to 141° E longitude; also in the Saruwaged Mountains of the Huon Peninsula. Altitude records range from 762 to 4000 m. (fig. 2).

MEAN MEASUREMENTS (IN MM.): External: head and body 120; tail 124; hind foot (*sans unguis*) 28.1. Skull: occipitonasal length 32.6; braincase width 14.2; bulla length 4.7; crowns m^{1-3} length 4.9. (See table 2 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 30.5 or less.

DESCRIPTION: This is the smaller of the two subspecies, although the size difference is not appreciable. The soft, dark brown, rufous-tipped, dorsal pelage is about 14 mm. long. It is dark gray for most of its length and for the last 2 mm. is dark brown with rufous tipping. The degree of development of the tipping varies individually and accounts for slight differences in coloration that Rümmler (1938) viewed as of subspecific value. Examination of large series demonstrates that such variation can occur even at a restricted locality. The fine black guard hairs are inconspicuous and measure to 20 mm. The facial vibrissae measure to 30 mm., and the ears are dark brown. The ventral pelage is dark gray-brown with cream to rufous tipping; since the darker color predominates, the overall ventral coloration is only slightly lighter than the dorsal pelage. Ventral fur measures about 7 mm. long, of which the last 1.5 mm. is tipped. The tail is uniformly dark brown and tail scales measure about 15–17 rows per cm. Tail hairs are very short and fine and difficult to see without magnification. The feet are lightly clothed dorsally with a mixture of silvery and brown hairs.

The juvenile pelage is very similar to that of the adult except hair tipping and guard hairs are less well developed and the overall color is duller.

The skull is as described for the species and differs from that of the other subspecies, *R. n. arrogans,* in having narrower molars and a smaller bulla that averages 17.1 percent of the basal skull length (fig. 3).

PREVIOUS DESCRIPTIVE ACCOUNTS: When Thomas (1906) proposed *Mus niobe,* he provided a full description of the single skin and skull and noted the resemblance to *Mus verecundus* that he had described two years earlier. He recognized that the holotype was a young animal, and did not indicate either the sex or the mammary formula. Jentink (1908) noted that, unlike most *Mus* from New Guinea, this species and *verecundus* had tails that exceeded the length of the head and body. The description of a slightly larger specimen, as *Stenomys rufulus,* included details of the mature adult pelage of cinnamon brown, in contrast to the darker brown color of the young *Mus niobe* holotype (Thomas, 1922b). Le Souef and Burrell (1926) gave a slight rewording of Thomas's original description.

When Rümmler (1935) proposed *S. n. stevensi,* he indicated that it exceeded the holotype of *Mus niobe* in skull length, and provided a good description of adult features. Tate (1936, figs. 19–21) figured ventral and lateral views of the skull of *S. niobe* and a crown view of the right upper molars. He also examined and measured specimens from Mt. Tafa that he related most closely to the holotype of *M. niobe.* Rümmler (1938, Pl. IX, Illus. 7) identified the holotype of *M. niobe* as a female and illustrated the skull. His redescription was based solely upon this specimen. He redescribed *S. n. stevensi,* however, from the holotype plus 11 other topotypical specimens. He also illustrated the skull of the holotype (Rümmler, 1938, Pl. IX, Illus. 8). His description of *S. n. rufulus* was based upon the holotype plus four additional specimens, but no illustration was provided. Sody (1941) was the first to give the mammary formula of 1 + 2 = 6 for *S. n. niobe.* In his redescription of the subspecies of *R. niobe,* Tate (1951) cast doubt upon the reddish coloration of the skin of *rufulus* and suggested that it may be an artifact resulting from "some treatment." Lidicker (1968) has illustrated and provided mensural features of the phallus of *R. n. niobe.* Lidicker and Ziegler (1968, table 5) summarized a few skin and skull measurements of 15 individuals. They discussed the few reproductive data that they were able to obtain and the variation in pelage coloration. Menzies (1973) noted that occasionally the tail tip may be white, a feature that produces greater similarity to *verecundus.* Dwyer (1975) has analyzed breeding parameters and body weights for *niobe,* and Dennis and Menzies (1978, fig. 1) have illustrated the karyotype and found it identical with those of *R. verecundus* and *R. ruber* (*R. s. hageni* and *R. m. fergussoniensis*).

REMARKS: All the studies to date have been based upon the examination of very few specimens or larger series from only a small number of localities. This has led to limited appreciation of the extent of variation in this

FIG. 4. Habitat of *Rattus niobe niobe* in alpine grassland on Mt. Albert Edward. Tree line in distance is about 3800 m. (Archbold and Rand, 1935). Photograph taken June–July 1933, on 1933–1934 Archbold Expedition.

subspecies. Lidicker and Ziegler (1968) were the first to suspect this as a problem when they assigned their series from Edie Creek to *R. n. stevensi* on the basis of proximity to the type locality. Our own concept of *R. n. niobe* is broadly defined since we are unable to perceive patterns or trends that distinguish regional variation from that of contiguous populations. We admit to the possibility of lumping more than a single subspecies under *R. n. niobe*. The problem is compounded because of major geographic gaps in collecting and in wide variation in sample sizes from those areas that have been collected. We have grouped these rats in full recognition that clinal situations may override the possibility of clear subspecific distinctions. We have attempted to provide a grouping that can be defended statistically according to the material currently at hand.

HABITS AND HABITAT: This subspecies occupies the cloud forest zone of the Saruwaged Mountains (Rümmler, 1938) and is a high altitude occupant of mossy forests (Lidicker and Ziegler, 1968). Wade and McVean (1969) describe them as most frequent in grassland on Mt. Wilhelm. They found numerous small mounds of friable peat associated with their burrows and recorded the rat as abundant to the summit. They also observed them as scavengers of discarded food cans on the tundra. Menzies and Dennis (1979) record them as extremely abundant inhabitants of montane forest and alpine grassland above the tree line (fig. 4). They describe their burrows as U-shaped with two entrance holes in the ground or among the thick moss layer on the forest floor. They also give a brief account of breeding biology. Ziegler (1971) applied the vernacular name Moss-forest Rat to this rodent. Records from specimen labels indicate that it also occurs in oak-beech forest.

SYMPATRY: *Rattus niobe niobe* is sympatric with *Rattus verecundus mollis, Rattus verecundus vandeuseni, Rattus steini hageni, Rattus novaeguineae, Rattus mordax mordax, Rattus giluwensis* (Mt. Giluwe and Kagaba), and *Rattus exulans browni*.

TAXONOMIC HISTORY: Following the original description of *Mus niobe* (Thomas, 1906), and its generic transfer to *Stenomys* (Thomas, 1910a), Thomas (1922b) described *Stenomys rufulus* from the Huon Peninsula. The description was based upon two specimens which he recorded as having the "size and essential characters as *S. niobe*" but distinguished by more cinnamon coloration when compared to that of *S. niobe*. The latter was apparently still represented only by the holotype, a young specimen in which the pelage tipping is probably incompletely developed. Furthermore, there was no basis at that time for comparison of range of pelage coloration within a series. Rümmler (1935), when he described the new subspecies *S. n. stevensi,* distinguished it from *S. niobe* solely on the basis of its longer, narrower skull. Again, this new rat was compared solely with the holotype of *S. niobe,* for no other specimens were available, and his comparison reflected the differences in growth stages. Tate (1936) was the first to describe a series of *S. niobe*. Rümmler (1938) brought *rufulus* into the species *Stenomys niobe* and retained it as a distinct race on the basis of pelage coloration. Ellerman (1941) transferred these three subspecies into the genus *Rattus,* but continued to regard them as racially differentiated. Although Tate (1951) had before him a large series of *R. n. niobe,* most of which are adults, he did not question the status of *rufulus,* although he viewed *stevensi* as a questionable race. Laurie (1952) identified a specimen of *R. n. niobe* from Yanca as *R. n. haymani,* known before only from Utakwa River, Irian Jaya. This misidentification was again used by Laurie and Hill (1954) who otherwise followed Tate's (1951) treatment of *niobe, rufulus,* and *stevensi.* Lidicker and Ziegler (1968), who assigned their series from Edie Creek to *R. n. stevensi,* suggested that it might well be referred to the nominate race when better information on geographic variation is available.

The series of this eastern race now available in museums led us to take into consideration the substantial variation in pelage color and in the length of incisive foramina within and between population samples. Our analysis, using craniometric parameters, revealed no distinct groups. If valid subspecies can be demonstrated in this group, a wider spectrum of parameters, that includes nonmensural features, will probably be necessary. Thus, in the absence of demonstrable differences, we have brought *rufulus* and *stevensi* into synonymy with the nominate race.

Rattus niobe arrogans (Thomas)

Stenomys klossii Thomas, 1913, p. 207 (not *Rattus klossi* Bonhote, 1906).

Stenomys arrogans Thomas, 1922a, p. 263.

Stenomys niobe arfakiensis Rümmler, 1935, p. 118.

Stenomys niobe clarae Rümmler, 1935, p. 118.

Stenomys niobe klossi: Rümmler, 1938, p. 202.

Stenomys niobe arrogans: Rümmler, 1938, p. 201.

Rattus niobe arrogans: Ellerman, 1941, p. 206.

Rattus niobe haymani Ellerman, 1941, p. 206 (new name for *klossi,* preoccupied).

Rattus niobe pococki Ellerman, 1941, p. 206 (new name for *clarae,* preoccupied).

Rattus niobe arfakiensis: Ellerman, 1941, p. 206.

HOLOTYPE: Skin and skull, complete except for damage to right zygoma and anterior of left nasal, young adult female, BM 22.2.2.24, collected October 31, 1920, by W. C. van Heurn, at Doormanpad-bivak, Irian Jaya Province, Indonesia, 2400 m.

DISTRIBUTION: Arfak Mountains of Vogelkop Peninsula, Weyland Mountains, Carstensz Mountains, upper Utakwa River, and eastward to longitude 139°11′ E. All localities mid- to upper-montane and range in altitude from 1500 to 4050 m. (fig. 2).

MEAN MEASUREMENTS (IN MM.): External: head and body 131; tail 114; hind foot (s.u.) 27.6. Skull: occipitonasal length 34.2; braincase width 14.9; bulla length 5.1; crowns m^{1-3} length 5.2. (See table 3 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 31.0 or less.

DESCRIPTION: This subspecies is slightly larger than the nominate one. The dorsal pel-

TABLE 3
Measurements (in Millimeters) of Adult *Rattus niobe arrogans*
(N = 147 for skin measurements; N = 168 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	130.6 ± 0.68	8.19	111.0–146.0
Tail length	113.6 ± 0.69	8.32	90.0–135.0
Hind foot (s.u.) length	27.6 ± 0.08	1.02	25.0–30.0
Occipitonasal length of skull	34.2 ± 0.10	1.24	30.6–37.0
Condylobasal length	31.5 ± 0.10	1.25	28.2–34.8
Basal length	29.0 ± 0.09	1.22	25.8–31.8
Zygomatic width	16.1 ± 0.05	0.61	13.8–18.0
Interorbital width	5.9 ± 0.03	0.37	4.9–6.7
Interparietal length	4.4 ± 0.04	0.49	3.0–5.8
Interparietal width	9.6 ± 0.05	0.70	7.4–11.4
Braincase width	14.9 ± 0.04	0.53	13.7–17.0
Mastoid width	12.6 ± 0.04	0.45	11.2–14.2
Nasal length	12.6 ± 0.06	0.80	10.4–14.5
Nasal width	3.7 ± 0.02	0.27	3.0–4.4
Palatal length	17.4 ± 0.05	0.70	15.0–19.0
Incisive foramen length	4.5 ± 0.04	0.46	3.5–5.9
Incisive foramina width	1.6 ± 0.02	0.26	1.0–2.2
Inside m^{1-1} width	2.5 ± 0.03	0.35	1.8–3.5
Outside m^{1-1} width	7.1 ± 0.03	0.33	6.4–8.1
Bulla length	5.1 ± 0.03	0.33	4.3–5.9
Crowns m^{1-3} length	5.2 ± 0.02	0.31	4.3–5.9
Alveoli m^{1-3} length	5.6 ± 0.02	0.30	4.8–6.3
Crowns m^{1-2} length	4.2 ± 0.02	0.31	3.3–4.9

age is dark as in *n. niobe* and in some localities is almost black with just a slight suggestion of rust tipping to the fur. There are 14–16 rows of tail scales per cm. In all other features it resembles *n. niobe.*

The skull is very similar to that of *R. n. niobe.* In his description of *klossii,* Thomas (1913) stated that when compared with *niobe,* the interorbital region is broader, the incisive foramina are longer, and the braincase is more inflated. He gave the key feature of the type of *arrogans* as a "remarkably swollen braincase" (Thomas, 1922a). Our comparisons do not support such differences. In addition to the larger absolute size of *arrogans,* it has wider molars and larger bullae than *n. niobe.* Bulla length averages 17.5 percent of the basal skull length in *arrogans.* All other features are very similar.

PREVIOUS DESCRIPTIVE ACCOUNTS: Thomas (1913) first described a member of this subspecies as *S. klossii,* on the basis of features that largely reflect the fact that its holotype is adult and that of *niobe* a young specimen. His proposal of *S. arrogans* was very brief and provided little more than a few measurements and the observation that the cranium was inflated (Thomas, 1922a). He had made a similar comment about *klossii,* although later (Thomas, 1922c) he stated that *arrogans* could be distinguished from *klossi* [*sic*] on this basis. In a more expanded description of *arrogans* in this same paper, he gave the mammary formula as 1 + 2 = 6. Rümmler (1935) distinguished *arfakiensis* from the nominate race on the basis of size and his other new subspecies *clarae* (=*pococki*) on the basis of its darker color. Later, Rümmler (1938) expanded the descriptions of all subspecies of *niobe* and relied heavily again on color and absolute size differences to distinguish the western races. He was limited to a maximum of seven specimens for *clarae* and *klossi,* two of *arrogans,* and one of *arfakiensis* in drawing his comparisons. Ellerman (1949) was troubled by the fact that *R. niobe* would not fit comfortably into the subgeneric group of *Rattus* in which he

FIG. 5. General habitat of *Rattus niobe arrogans* and *Rattus richardsoni* at Lake Habbema, 3225 m., on sandy banks of stream. Alpine grassland, chiefly tussock sedges (*Gahnia*); tree fern (*Cyathea*) and, at foot of ridge, *Libocedrus*. Photograph taken August 1938, on 1938–1939 Archbold Expedition.

placed it because of the long incisive foramina of the holotype of *arfakiensis*. He did not give a measurement, but we have determined its length as 5.9 mm. Tate (1951) redescribed the races and, although he had available much larger series, he also was struck by the length of the incisive foramina of the holotype of *arfakiensis*. Although this is the longest foraminal length among the complete skulls we examined, we measured a large specimen from Mt. Wilhelmina (MZB 8274), with incomplete nasals that had an incisive foraminal length of 6.3 mm. Misonne (1979) gave a measurement of 6.1 mm. for one from the Carstensz Mountains. Thus, *arfakiensis*, still represented by only the holotype, is not unique in this feature. Jeanette Hope (1976) and Misonne (1979) have given skin and skull measurements of a small series of *arrogans* taken in the Carstensz Mountains, and Misonne (1969) has illustrated the upper and lower molars of a specimen from the upper Utakwa River very near the type locality (Pl. XX, fig. 118).

REMARKS: The chief problem with western *niobe*, here all designated *R. n. arrogans*, is the difficulty of obtaining adequate measures of the range in geographic variation. Far less collecting has been done in Irian Jaya than in Papua New Guinea, although series taken by the Archbold Expedition at Bernhard Camp, Lake Habbema, Ibele River, and Mt. Wilhelmina are among the largest in existence. Elsewhere in Irian Jaya, however,

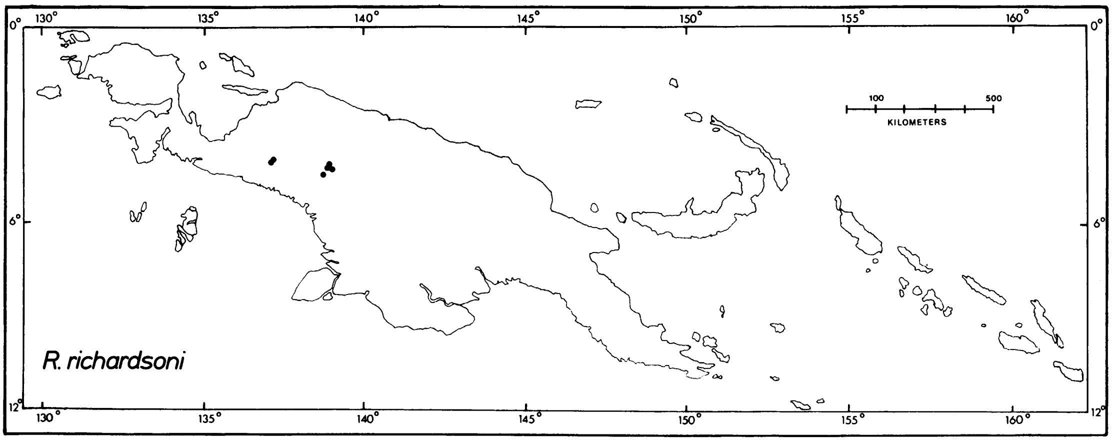

FIG. 6. Distribution map of *Rattus richardsoni*. Locality records are indicated by dots.

there are very few collecting sites and the material available is extremely limited in both numbers and in geographical representation.

HABITS AND HABITAT: One of the collectors, W. C. van Heurn, found this rat in thick mossy undergrowth at an altitude of 2400 m. (Thomas, 1922c). It has also been taken in tussock grassland (J. Hope, 1976), montane moss forests, and alpine meadows (Misonne, 1979) (figs. 5 and 8).

SYMPATRY: *Rattus niobe arrogans* is sympatric with *Rattus steini baliemensis, Rattus praetor coenorum, Rattus richardsoni, Rattus verecundus unicolor,* and *Rattus exulans browni* (Arfak Mountains).

TAXONOMIC HISTORY: Following the original description of this subspecies as *Stenomys klossii* (Thomas, 1913), a further new species, *Stenomys arrogans,* was proposed by the same author (Thomas, 1922a). In the meantime he (Thomas, 1914) emended the spelling of *klossii* to *klossi*. Rümmler (1935) described two subspecies of *Stenomys niobe, S. n. arfakiensis* and *S. n. clarae,* and later (Rümmler, 1938) treated *klossi* and *arrogans* as subspecies of *S. niobe*. Sody (1941) followed this placement of *arrogans*. Ellerman (1941) concurred also with Rümmler's move, except that he placed all forms of *niobe* in the genus *Rattus*. In so doing, the names *klossi* and *clarae* became preoccupied, as already described under the taxonomic history of the species, and were replaced by *haymani* and *pococki,* respectively (Ellerman, 1941). Tate (1951) viewed *niobe* and *pococki* as valid, but doubted the validity of *haymani* and *arrogans*. Laurie (1952) and Laurie and Hill (1954) regarded *haymani* as a subspecies that extended to the Central Highlands of northeastern New Guinea. The specimen on which they based this decision (BM 50.1765) is in our view *R. n. niobe,* judged by molar width and by sympatry with the nominate race on Mt. Hagen. Otherwise, Laurie and Hill (1954) followed Ellerman's (1941, 1949) classification of the western races in all respects.

We recognize only *Rattus niobe arrogans* in the western portion of New Guinea and have brought *haymani, pococki,* and *arfakiensis* into synonymy with it.

Rattus richardsoni Tate

Rattus richardsoni Tate, 1949, p. 1.
Rattus omichlodes Misonne, 1979, p. 6.

HOLOTYPE: Skin and complete skull, adult male, AMNH 150701, collected August 2, 1938 by W. B. Richardson, near Lake Habbema, Irian Jaya Province, Indonesia, 3225 m.

DISTRIBUTION: *Rattus richardsoni* is currently known from only three major localities, all of which are in Irian Jaya Province. It occurs on high montane slopes between

TABLE 4
Measurements (in Millimeters) of Adult *Rattus richardsoni*
(N = 51 for skin measurements; N = 41 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	143.4 ± 1.22	8.73	126.0–164.0
Tail length	131.8 ± 1.68	11.99	92.0–147.0
Hind foot (s.u.) length	35.5 ± 0.23	1.65	30.0–39.0
Occipitonasal length of skull	37.2 ± 0.23	1.45	33.9–39.8
Condylobasal length	34.3 ± 0.24	1.54	30.1–37.0
Basal length	31.6 ± 0.23	1.44	28.6–34.1
Zygomatic width	17.1 ± 0.10	0.66	15.6–18.3
Interorbital width	6.2 ± 0.04	0.25	5.6–6.8
Interparietal length	4.8 ± 0.07	0.47	3.6–5.9
Interparietal width	9.8 ± 0.11	0.68	8.2–11.8
Braincase width	15.8 ± 0.06	0.39	15.1–16.7
Mastoid width	13.4 ± 0.07	0.42	12.5–14.0
Nasal length	14.2 ± 0.12	0.76	12.5–15.7
Nasal width	3.9 ± 0.04	0.28	3.3–4.6
Palatal length	18.4 ± 0.14	0.87	16.5–20.9
Incisive foramen length	5.7 ± 0.09	0.57	4.7–6.8
Incisive foramina width	2.0 ± 0.05	0.31	1.2–2.6
Inside m$^{1-1}$ width	2.7 ± 0.05	0.31	2.0–3.3
Outside m$^{1-1}$ width	7.3 ± 0.04	0.28	6.6–8.2
Bulla length	5.6 ± 0.06	0.36	4.9–6.3
Crowns m$^{1-3}$ length	5.6 ± 0.04	0.25	5.0–6.0
Alveoli m$^{1-3}$ length	6.0 ± 0.04	0.23	5.4–6.4
Crowns m$^{1-2}$ length	4.6 ± 0.04	0.25	4.0–5.0

Lake Habbema and Mt. Wilhelmina (Mt. Trikora), a distance of 14 air km., at altitudes of 3225–4050 m. The third major locality is Gunung (Mt.) Jaya in the Carstensz Range 160 km. west of Lake Habbema. Mt. Jaya (4884 m.) is not only the highest mountain in New Guinea but also in the entire southeast Asian and western Pacific regions (G. S. Hope, 1976). This rat has been recorded here at 3450–4500 m., on specific mountain sites (J. Hope, 1976), and at 3350–3400 m. at Ertsberg (Misonne, 1979) (fig. 6).

MEAN MEASUREMENTS (IN MM.): External: head and body 143; tail 132; hind foot (s.u.) 35.5. Skull: occipitonasal length 37.2; braincase width 15.8; bulla length 5.6; crowns m$^{1-3}$ length 5.6. (See table 4 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 34 or less.

DESCRIPTION: The pelage is very soft and is more dense than that of any other *Rattus* in New Guinea. The dorsal pelage is a warm brown mixture of chestnut and rufous coloration. All but the brown tipping is dark steel gray measuring about 16 mm. The chestnut-to-rufous tipping is about 4 mm. The fine black guard hairs are about 25 mm. long, but may be as long as 35 mm. in the rump region. Their basal portion is steel gray. Spinous hair is absent. The dorsal facial region is the same overall color as the dorsal body and the ears are self colored and sparsely covered by short (1–2 mm.) dark fur. The black facial vibrissae extend to 45 mm. in length. The pelage blends to a conspicuous region of lighter rufous brown laterally and to buffy white ventrally, retaining its thick quality throughout. The dark steel gray of the proximal region of the ventral pelage is 9–10 mm. long with a light tipping of 3 mm. This tipping is usually buffy but may be tinged with rufous which is variably developed. The dark gray basal portion of the fur is readily seen beneath the tipping. The ventral facial region is similarly colored.

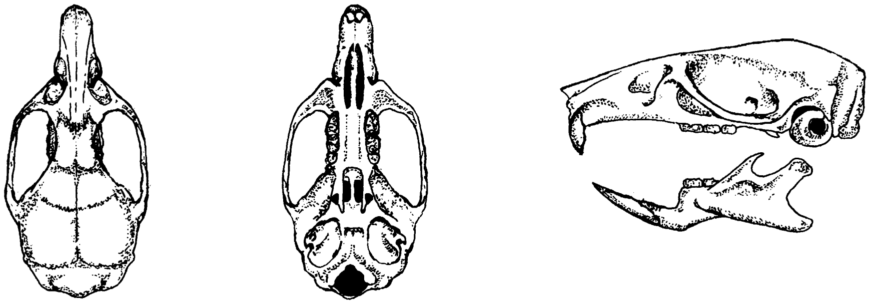

FIG. 7. Dorsal, ventral, and lateral views of skull of adult *Rattus richardsoni,* AMNH 110179, from 2 km. E of Mt. Wilhelmina. Occipitonasal length 38.9 mm.

The tail is a rich brown dorsally and may be slightly lighter ventrally. The tail hairs are conspicuous and are 1.5–2 mm. long, and there are about 14 tail scales per cm. All four feet are silvery white dorsally.

The juvenile pelage is darker dorsally since the rich brown pelage tipping is less well developed. The overall dorsal coloration of these younger rats is more chocolate brown.

The mammary formula is 2 + 2 = 8.

The skull is elongate and there is a prominent dorsal convex curvature when viewed in profile (fig. 7). The rostral region is long and the breadths of the zygomata and cranium are relatively narrow. Although the skull is convex in profile, it is narrow dorsoventrally and becomes broadest at the level of the mid-dorsal suture of the parietals. The cranium is composed of thin bone (0.2 mm. thick) and, although narrow, is somewhat inflated relative to the rostrum. The incisive foramina are slightly bowed midway and from here maintain uniform width as they extend posteriorly. Only the anterior portion is narrow. These foramina terminate posteriorly in line with the anterior face of the molar row. The palate terminates in line with the posterior face of the molar row. Supraorbital ridging is absent. The interorbital region is relatively narrow. The nasal bones are narrow and attenuated distally. Interbullar distance is relatively great when compared to that of *R. niobe*.

In the juvenile skull the cranium is more inflated relative to rostral size than in the adult, and the incisive foramina are narrower for their length.

DIAGNOSTIC CHARACTERS: The combination of thick and soft pelage of this rat is unequaled in any other species of *Rattus* in New Guinea. Only *R. giluwensis* approaches *R. richardsoni* in this character. The tail length is about 92 percent that of the head and body (compare with *R. giluwensis*). The convex dorsal profile of the skull is a good diagnostic feature that readily separates *R. richardsoni* from any other *Rattus* native to New Guinea. The thin-boned, slightly inflated cranium is a feature shared with *R. niobe* and *R. giluwensis* and, to some extent, with *R. verecundus*.

The overall likeness of this species to *Rattus giluwensis* is a striking example of convergence of two allopatric species occupying somewhat similar high montane habitats. Close examination of both skin and skull features readily indicates that the resemblance is superficial and not indicative of conspecificity.

PREVIOUS DESCRIPTIVE ACCOUNTS: Tate (1949) provided a description of the type when he originally proposed the species and later (Tate, 1951) when he revised the rodents of the Australasian Region. The first measurements of specimens obtained from Gunung Jaya were published by J. Hope (1976). The mammary formula was first given by Dennis and Menzies (1978). Misonne (1979), who obtained 13 additional specimens (identified as *R. richardsoni* and *R. omichlodes,* new species) from the Carstensz

FIG. 8. Habitat of *Rattus richardsoni* and *Rattus niobe arrogans* on Mt. Wilhelmina in subalpine limestone region of grass, *Vaccinium* and *Coprosma*. Photograph taken at 3800 m. by L. J. Brass, September 1938, on 1938–1939 Archbold Expedition.

Mountains has published brief tables of a few skin and skull measurements and has illustrated the upper and lower molars (Misonne, 1979, figs. 2 and 3).

HABITS AND HABITAT: In the Carstensz Range this species occurs in tussock grassland and in bare tundra-like habitat that is largely rock or gravel widely interspersed with mats of herbs and grasstufts (J. Hope, 1976). On Gunung Jaya at Meren Valley, the latter habitat has been uncovered by glacial retreat for only 35 years. Hope also describes remains of this rat in recent fissure deposits and in feces from feral dogs at these high elevations. Misonne (1979) describes it as an occupant of the upper bush and grass edge of the montane forest and of the open regions above the tree line including shallow marshes (figs. 5 and 8). The current lower limit of glaciation is 4350–4400 m. (Allison and Kruss, 1977).

At altitudes above 3600 m. needle ice and soil heaves form during the frequent freezing temperatures at night, and the daily maximum temperatures range between about 8 and 12° C. year round (Schodde et al., 1975). Annual rainfall is about 3800 mm. in glaciated areas and may bring snowfall temporarily down to 4000 m. (*ibid.*). The habitat occupied by *R. richardsoni* is cold and wet throughout the year and varies little either in temperature or amount of rainfall from month to month.

No notes of habits or habitat accompany the specimens that were collected by the 1938–1939 Archbold Expedition at Lake

Habbema and Mt. Wilhelmina. We have relied upon the detailed botanical analysis of collecting sites for inferences about the habitat of this species (Archbold, Rand, and Brass, 1942). Lake Habbema is bordered in part by open marsh grass and sedges. Extensive grassy hollows occur between ridges openly timbered by subalpine trees up to 15 m. high and between small patches of closed forest. The three collecting sites on Mt. Wilhelmina (3560 m., 3800 m., 4050 m.) are typically clothed by large expanses of tussock grass on the slopes and by grassy amphitheaters. At 3800 m. the subalpine forest becomes scant and very stunted, and trees are absent at the summit. Talus slopes are common at these two higher sites where older talus slopes become overgrown by tussock grass. Much of the area is bare sandstone and limestone (fig. 8).

Rattus richardsoni occurs in all these areas that provide grassy expanses, whether or not patches of forest are present. The species is primarily an alpine grassland form which may opportunistically utilize the upper limit of subalpine forest habitat as well. An aerial reconnaissance of this area made by members of the 1938–1939 Archbold Expedition indicated that this type of habitat appears to be continuous from Mt. Wilhelmina–Lake Habbema to the Carstensz Range (Archbold, Rand, and Brass, 1942).

Although Dennis and Menzies (1978) include this species among rats that are primarily forest dwellers, this ecological assignment is without basis. Gressitt and Ziegler (1973) include it among the endemic rodents of the moss forest, but do not assign it primarily to this habitat.

Rattus richardsoni appears to be expanding into new grassland habitat that develops as glaciers recede and substrate is exposed. Such expansion is historically apparent in Meren Valley (J. Hope, 1976). In geological time, 13,000 years ago both Mt. Wilhelmina and Carstensz Top had a snowline of 3485 m.; snow and ice would have virtually covered the habitat occupied today by this rat. The existing snowline is now 4650 m. on Carstensz Top and 4750 m. on Mt. Wilhelmina (Koopmans and Stauffer, 1968), and *R. richardsoni* can probably be found at the very edge of it.

SYMPATRY: *Rattus richardsoni* is sympatric with *Rattus niobe arrogans* in all but summit localities of Mt. Wilhelmina (3900–4050 m.). On Gunung Jaya it is sympatric with *R. n. arrogans* at altitudes of 3350–3750 m. (Misonne, 1979). The highest record for *R. n. arrogans* in sympatry with *R. richardsoni* was one of remains retrieved from feral dog feces at 4250 m. which may be a misleading representation of the upper altitudinal extent of *arrogans* (J. Hope, 1976). At the lowest elevation on record for *R. richardsoni*, Lake Habbema (3225 m.), it is sympatric with *Rattus steini baliemensis*.

TAXONOMIC HISTORY: The Third Archbold Expedition (1938–1939) returned with an extensive collection of rodents from the northern slopes of the Snow Mountains as well as from mid and lower elevations of the Idenberg River drainage. At the highest elevations that were successfully trapped, Mt. Wilhelmina and Lake Habbema, a series of densely furred dark rats were taken along with the more common small *R. niobe arrogans*. This series of 56 larger rats formed the basis of the description of a new species, *Rattus richardsoni*, by Tate (1949). He noted at the time that it showed no close affinity to any other species of *Rattus* from New Guinea. His assignment of *Rattus richardsoni* to the status of full species has held to the present time (Laurie and Hill, 1954; Ziegler, 1971; Gressitt and Ziegler, 1973; J. Hope, 1976; Dennis and Menzies, 1978; Misonne, 1979). Until recently, *R. richardsoni* was known only from the high montane areas of Mt. Wilhelmina and Lake Habbema at 3225–4050 m. Jeanette Hope (1976) has now described a series from Gunung (Mt.) Jaya that accounts for not only the highest altitudinal records known for this species (4500 m.), but also for any species of *Rattus* in New Guinea.

Misonne (1979) proposed the new species *Rattus omichlodes* from seven specimens taken at Ertsberg. He regarded them as related to both *R. niobe* and *R. richardsoni*. Only one skull of this series appears to be intact (Field no. 997). We have examined

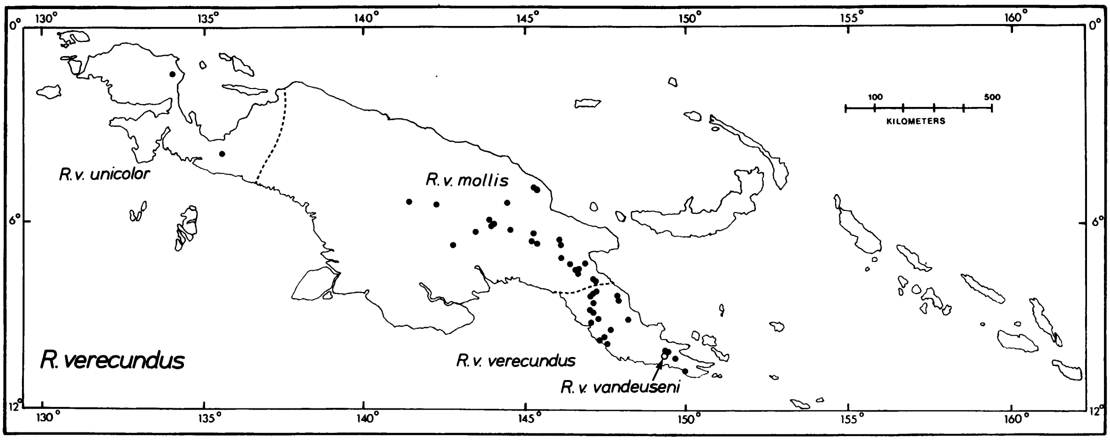

FIG. 9. Distribution map of *Rattus verecundus*. Locality records for three of the four subspecies are indicated by dots, and the fourth by an open circle.

two paratypes, nos. 997 and 999, that are now registered as KNMB 4030 and 4031, respectively. These two specimens fall well within the pelage variation expected for the species, and the characteristic dome-shaped cranial convexity of *richardsoni* is readily apparent. All other skull features are also the same as in earlier described *richardsoni*. The two are examples that fall into the smaller end of the adult size spectrum of *richardsoni*.

We recognize *R. richardsoni* as a monotypic species.

Rattus verecundus (Thomas)

DISTRIBUTION: Records are mainly east of 141° longitude in montane situations, and into the lowlands in association with the drainage systems of the Owen Stanley Range. In the west, has been taken at one site in the Vogelkop (Sururai) and two in the Weyland Mountains (Kunupi and Sumuri). No specimens have been taken from the Huon Peninsula. Altitude records are from 150 to 2750 m. (fig. 9).

GENERAL DESCRIPTION: This is a soft-furred, medium-sized rat that is somber in overall coloration except for the presence of narrow white feet and the usual occurrence of a white tail tip. Only in one of the two larger subspecies, *R. v. verecundus*, which occupies low elevations as well as mid-montane sites, is there any suggestion of development of fine spines in the dorsal pelage. The dorsal pelage is mid- to deep-brown or even black-brown. The fur is shiny, very smooth to the touch, and in both glossiness and texture is unlike that of any other *Rattus* in New Guinea. The ventral pelage is light to dark gray tinged with rust or yellow. White pectoral marking is common. The feet are long, narrow, and delicate and are clothed in white fur dorsally or a mixture of white and brown mid-dorsally. The dark brown tail is usually white distally and as long or longer than the head and body length. Although Menzies (1973) claims that it always has a white tail tip, and Menzies and Dennis (1979) state that it "nearly always" does, we have examined many specimens from eastern New Guinea, as well as the western portion, that lack this feature. The dark brown ears are relatively inconspicuous.

The mammary formula is $1 + 2 = 6$ or $0 + 2 = 4$.

The skull is smooth in contour and the cranium is relatively large compared to the rostral region (fig. 10). The rostrum is narrow and elongate and both premaxillae and nasals extend anterior to the incisors. The incisive foramina are moderately flared and extend posteriorly to the anterior face of the molar row. The incisors and molars are narrow and

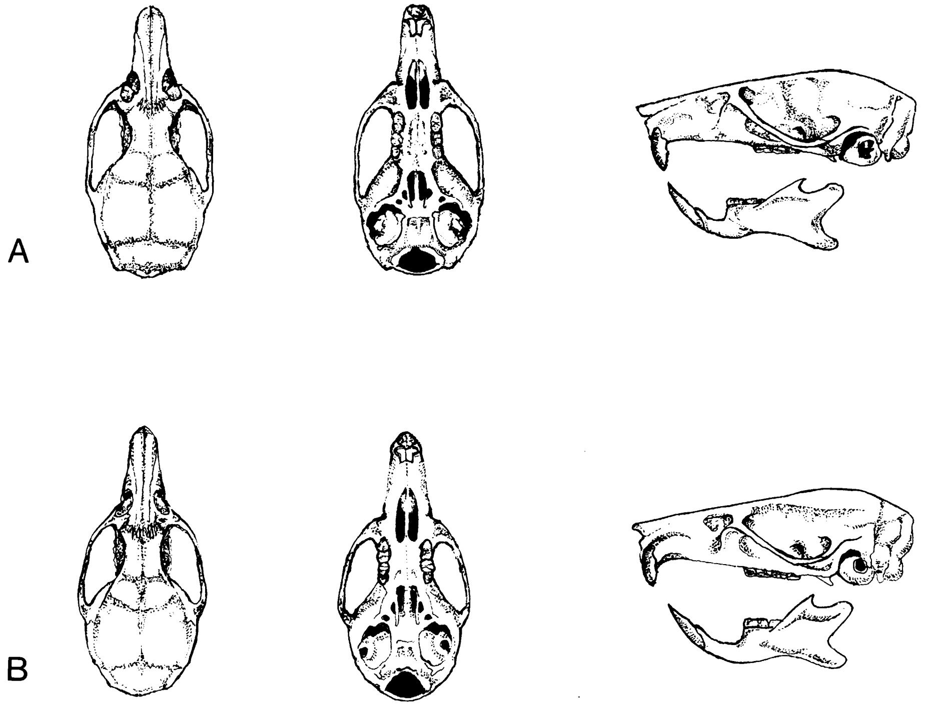

FIG. 10A, B. Dorsal, ventral, and lateral views of adult skulls of two subspecies of *Rattus verecundus*. A. *Rattus v. mollis*, BBM 97895, from Hawate. Occipitonasal length 36.8 mm. B. Holotype of *R. v. vandeuseni*, new subspecies, AMNH 157905, from Mt. Dayman, Middle Camp. Occipitonasal length 36.4 mm.

the bullae are small. The palate terminates 1 to 2 mm. posterior to the molar row. Supraorbital ridging, if present, is only lightly developed. In common with *R. niobe,* this species usually lacks an anterolateral cusp on m^2.

DIAGNOSTIC CHARACTERS: *Rattus verecundus* is most likely to be confused with only two other native species, *R. leucopus* juveniles and *R. niobe*. The hind feet are narrow and delicate in *R. verecundus,* whereas they are wide and heavy in juvenile *leucopus*. The molars are narrower in *verecundus* and the incisive foramina are more bowed. Comparison of relative tooth wear with occipitonasal length will also distinguish the two species, for *leucopus* is a much larger rat. Young adult *R. verecundus* and *R. niobe* are more difficult to distinguish. The pelage is softer, duller, and completely spineless in all *niobe* although the similarity to *verecundus* in coloration may be great. The hind feet are lighter in *verecundus* and so, usually, is the ventral pelage. The tail of *niobe* is not mottled, whereas it is usually so in *verecundus*. The skull of *niobe* is more delicate and the cranial bones are extremely thin. The incisive foramina usually terminate anterior to the molar row and are shorter than those of *verecundus*. Supraorbital ridging is usually not visible in *niobe*. *Rattus verecundus* is a larger rat than *niobe* so comparison of molar wear with occipitonasal length is useful in distinguishing the two.

TAXONOMIC HISTORY: When Thomas (1904b) described the new species, *Mus verecundus,* he questioned its placement in *Mus* but was reluctant to erect a new genus for it at that time, an arrangement accepted by Jentink (1907a, 1908). Later Thomas (1910a) concluded that *verecundus* did not belong in *Mus* and defined a new genus, *Stenomys,* with *M. verecundus* as type species, and included *Mus niobe* as well. At that time he was in the process of breaking up the large genus *Mus* into more rational units, and in the following issue of the same journal he (Thomas, 1910b) relegated other New Guinean species of *Mus* to a more restricted genus, *Epimys,* first proposed by Trouessart (1897). Longman (1916) and Le Souef and Burrell (1926) accepted the new genus. Rümmler (1935) added three new subspecies to *S. verecundus, S. v. mollis, S. v. unicolor,* and *S. v. försteri.* Tate (1936) supported the use of *Stenomys* and provided skull and molar views of *S. verecundus.* Rümmler (1938) added groups to *Stenomys* that had formerly been placed in *Rattus,* although he recognized that the differences between the genera were small. Among New Guinean *Rattus,* this affected *leucopus* (*sensu lato*) which then became known as *S. leucopus* (see Taxonomic History of *R. leucopus*). Ellerman (1941) rejected *Stenomys* as a genus distinct from *Rattus* and transferred all four subspecies of *verecundus* into *Rattus.* Frechkop (1948) disagreed with this move. Ellerman (1949) later softened his stand when he recommended that *Stenomys* become a subgenus of *Rattus* under which he included the New Guinean species, *R. verecundus, R. ringens* (=*R. leucopus*), and *R. ruber* (=*R. praetor*), but he excluded *niobe.* Under his *R. leucopus* Group Tate (1951) included *R. verecundus* and *R. leucopus* as species. Although he could find very little to distinguish the subspecies *R. v. verecundus, R. v. försteri,* and *R. v. unicolor,* he recognized all of them along with *R. v. mollis.* The last subspecies to be described was *R. v. tomba,* by Laurie (1952) who allied it most closely with *mollis.* Up to the time of our own assessment there has been general recognition of five weakly differentiated subspecies of *R. verecundus.*

We recognize four subspecies, *R. v. verecundus, R. v. mollis, R. v. unicolor,* and *R. v. vandeuseni,* new subspecies. The subspecies *foersteri* is not a *verecundus* but rather belongs to a separate species, *R. steini.* The type specimen of *foersteri* (RMNH 292/2) is readily distinguished by the presence of a conspicuous antero-external cusp on m^2, a feature that Thomas (1910a) claimed to be absent in all *verecundus* and *niobe.* In fact, if present, it is poorly developed in these two species.

Rattus verecundus verecundus (Thomas)

Mus verecundus Thomas, 1904b, p. 598.
Stenomys verecundus: Thomas, 1910a, p. 507.
Stenomys verecundus verecundus: Rümmler, 1935, p. 117.
Rattus verecundus verecundus: Ellerman, 1941, p. 205.

HOLOTYPE: Skin, lacking ears and left hind foot, and skull, complete except for broken zygomata, adult female, BM 3.12.1.1, collected May 31, 1903, by A. S. Meek, at Avera, Aroa River, Papua New Guinea, 200 m.

DISTRIBUTION: Occurs in low- and mid-elevations on either side of the Owen Stanley Range from about 8° S to the southeastern extremity. It is known from 150 to 1830 m. in altitude (fig. 9).

MEAN MEASUREMENTS (IN MM.): External: head and body 144; tail 161; hind foot (s.u.) 34.1. Skull: occipitonasal length 37.6; braincase width 15.4; bulla length 5.4; crowns m^{1-3} length 5.8. (See table 5 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 34.0 or less.

DESCRIPTION: This is one of the larger subspecies of *R. verecundus* and the pelage is less soft than the others. Fine translucent spines are usually present in the dorsal pelage. They are flexible and do not impart a harsh quality to the fur. The dorsal coloration is medium to dark brown and the pelage is about 15–17 mm. long. The hair is medium gray for most of its length and is tipped with 2–3 mm. of rust color. The translucent spines are of comparable length. Fine, black guard hairs that measure 16–17 mm. endow the pelage with the darker hue and are relatively inconspicuous. The ears are medium brown and clothed in very short, fine brown hair. The muzzle vibrissae measure to 55 mm. The ventral pelage, which is 8–9 mm. long, is medium gray and tipped

TABLE 5
Measurements (in Millimeters) of Adult *Rattus verecundus verecundus*
(N = 55 for skin measurements; N = 59 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	143.5 ± 1.83	13.57	114.0–168.0
Tail length'	160.8 ± 2.21	16.37	129.0–194.0
Hind foot (s.u.) length	34.1 ± 0.39	2.88	29.0–39.0
Occipitonasal length of skull	37.6 ± 0.26	1.98	33.6–41.8
Condylobasal length	34.7 ± 0.25	1.91	30.9–38.6
Basal length	32.1 ± 0.24	1.81	28.2–35.8
Zygomatic width	17.2 ± 0.10	0.79	15.2–18.5
Interorbital width	5.8 ± 0.04	0.29	5.1–6.6
Interparietal length	4.9 ± 0.06	0.44	3.9–6.3
Interparietal width	10.2 ± 0.11	0.82	8.7–11.9
Braincase width	15.4 ± 0.07	0.57	13.8–16.9
Mastoid width	12.9 ± 0.07	0.54	11.7–13.9
Nasal length	14.0 ± 0.13	0.99	11.9–16.2
Nasal width	4.0 ± 0.04	0.31	3.4–4.6
Palatal length	19.9 ± 0.14	1.08	17.1–21.9
Incisive foramen length	6.2 ± 0.07	0.54	5.1–7.8
Incisive foramina width	2.5 ± 0.04	0.32	1.9–3.0
Inside m^{1-1} width	3.5 ± 0.04	0.32	2.6–4.2
Outside m^{1-1} width	7.7 ± 0.05	0.37	6.8–8.3
Bulla length	5.4 ± 0.04	0.32	4.7–6.1
Crowns m^{1-3} length	5.8 ± 0.04	0.31	5.2–6.6
Alveoli m^{1-3} length	6.2 ± 0.04	0.33	5.4–6.8
Crowns m^{1-2} length	4.8 ± 0.04	0.33	4.0–5.7

with light cream to rufous for the last 2–3 mm. A white pectoral area may be present. The tail is medium brown for most of its length, but up to one-third of the distal portion may be white. There are 10–11 rows of tail scales per cm. and the short tail hairs are inconspicuous. The feet are covered dorsally by white or light brown hairs.

The juvenile pelage is darker dorsally with less rust tipping. The ventral pelage is grayer and the tipping is white. Spines are absent, and the guard hairs are less conspicuous. Otherwise, the pelage is similar to that of the adult.

The mammary formula is 1 + 2 = 6.

Supraorbital beading is either absent or barely discernible on skulls less than 38 mm. in occipitonasal length. This subspecies has the largest bulla relative to basal length, the ratio being 16.9 percent. It is, however, closely followed by *vandeuseni* and *mollis*. All other major features are the same as described for the species.

PREVIOUS DESCRIPTIVE ACCOUNTS: Thomas (1904b) gave a full description of *Mus verecundus*, including the mammary formula, when he proposed it as a new species. His description was based on four specimens. Jentink (1908) pointed out that *verecundus* and *niobe* were exceptional among *Mus* of New Guinea in having a tail length greater than that of the head and body. When Thomas (1910a) proposed the new genus *Stenomys*, he designated *M. verecundus* as type species, and gave a new description of the species. Tate (1936, figs. 19–21) illustrated ventral and lateral views of the skull and the occlusal view of the right upper molars. Rümmler (1938, Pl. IX, Illus. 5) included photographs of the dorsal, ventral, and lateral views of the skull when he provided additional description of *Stenomys v. verecundus*. Tate (1951) discussed the status of *Stenomys* at some length and, when defending the use of *Rattus* rather than *Stenomys* as the genus for *verecundus* and in his discussion of *R. v. verecundus,* provided a further descriptive account. He included measurements of skins and skulls of four specimens including the holotype.

REMARKS: *Rattus verecundus verecundus* occupies more lowland situations than do the other subspecies. It appears to be successful in utilizing border vegetation of drainage areas where mid-montane habitat may extend down into the lowlands. It is the one subspecies which can be confused with a sympatric species, *R. l. dobodurae,* in that *verecundus* may be misidentified as juvenile *dobodurae*. Both species usually have white tail tips, but the difference in width of the hind foot readily serves to distinguish the two, for *verecundus* has a much more slender pes.

HABITS AND HABITAT: This subspecies occupies the coastal and hill forest zone (Rümmler, 1938) of southeastern New Guinea and rain forests of the Astrolabe Range (Tate, 1951). It has also been taken in rejuvenated primary forest and "in bush on ridge" (specimen label data).

SYMPATRY: *Rattus verecundus verecundus* is sympatric with *Rattus mordax mordax, Rattus exulans browni, Rattus niobe niobe, Rattus leucopus dobodurae,* and *Rattus sordidus gestri.*

TAXONOMIC HISTORY: For the taxonomic history of this subspecies see that of the species. Since Rümmler (1935) described three further subspecies of *Stenomys verecundus* and Ellerman (1941) placed *v. verecundus* in *Rattus,* there have been no subsequent assessments.

Rattus verecundus mollis (Rümmler)

Stenomys verecundus mollis Rümmler, 1935, p. 116.
Rattus verecundus mollis: Ellerman, 1941, p. 205.
Rattus verecundus tomba Laurie, 1952, p. 305.

HOLOTYPE: Skin and complete skull, adult female, MCZ 29905, collected April 14, 1933, by H. Stevens, at Mt. Misim, Papua New Guinea, 1900 m.

DISTRIBUTION: A mid-montane rat that occurs from Tifalmin eastward along the Central Highlands and southeast to the Bowutu Mountains. Also inhabits the Adelbert Range near the northeast coast, but apparently absent from the Huon Peninsula. Altitudinal records range from 1150 to 2750 m. (fig. 9).

MEAN MEASUREMENTS (IN MM.): External: head and body 135; tail 153; hind foot (s.u.) 32.5. Skull: occipitonasal length 36.1; braincase width 14.8; bulla length 5.1; crowns m^{1-3} length 5.6. (See table 6 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 33.5 or less.

DESCRIPTION: This subspecies has very soft fur and is smaller than both *R. v. verecundus* and *R. v. unicolor.* No spines occur in the pelage. The dorsal coloration is dark brown tipped in rust. Mid-dorsal hairs measure about 15 mm., of which 12 mm. are dark gray and the terminal 2 mm. portion is rust. Fine black or deep brown guard hairs measure to 20 mm. and are abundant but relatively inconspicuous. The ventral pelage measures to 11 mm. long. Most of its length is dark gray and the tipping of 2–3 mm. is cream white or buff. Tail scales measure about 15 rows per cm. The distal one-third of the tail is usually white. In all other skin features it is like *R. v. verecundus.*

The mammary formula is 1 + 2 = 6.

The skull is smaller and more delicate than that of *R. v. verecundus* or *R. v. unicolor,* and the molars are narrower than those of the other subspecies. The molars are usually well worn at 35 mm. occipitonasal length and supraorbital beading is only evident on the skulls measuring 36 mm. occipitonasal length or more. The bulla length is 16.6 percent of the basal skull length (fig. 10A).

PREVIOUS DESCRIPTIVE ACCOUNTS: Following Rümmler's (1935) original description of this subspecies, he later gave further details and illustrated dorsal, ventral, and lateral views of the skull of the holotype (Rümmler, 1938, Pl. IX, Illus. 6). Ellerman (1941) stated that the mammary formula for *R. verecundus* is 1 + 2 = 6, but it is not clear whether he actually checked this feature on *R. v. mollis.* Tate (1951) provided a brief description of *mollis* and noted that a small white pectoral spot may be present. He provided measurements of the holotype. Laurie (1952) described features and mea-

TABLE 6

Measurements (in Millimeters) of Adult *Rattus verecundus mollis*

(N = 110 for skin measurements; N = 160 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	134.7 ± 0.79	8.32	111.0–154.0
Tail length	153.1 ± 1.04	10.93	132.0–188.0
Hind foot (s.u.) length	32.5 ± 0.13	1.31	29.0–36.0
Occipitonasal length of skull	36.1 ± 0.08	1.02	33.6–38.7
Condylobasal length	33.1 ± 0.08	1.03	30.7–35.6
Basal length	30.5 ± 0.08	0.99	28.0–32.8
Zygomatic width	16.6 ± 0.04	0.48	15.3–17.8
Interorbital width	5.5 ± 0.02	0.23	5.0–6.3
Interparietal length	4.9 ± 0.03	0.37	3.9–5.8
Interparietal width	10.2 ± 0.05	0.65	7.9–11.7
Braincase width	14.8 ± 0.03	0.40	13.8–16.1
Mastoid width	12.5 ± 0.02	0.31	11.9–13.4
Nasal length	13.1 ± 0.05	0.62	11.3–14.6
Nasal width	3.7 ± 0.02	0.29	3.0–4.6
Palatal length	19.0 ± 0.05	0.62	17.2–20.6
Incisive foramen length	5.6 ± 0.03	0.35	4.6–6.8
Incisive foramina width	2.4 ± 0.02	0.25	1.7–3.0
Inside m^{1-1} width	3.7 ± 0.03	0.37	2.8–4.8
Outside m^{1-1} width	7.7 ± 0.02	0.31	6.5–8.5
Bulla length	5.1 ± 0.02	0.22	4.4–5.7
Crowns m^{1-3} length	5.6 ± 0.02	0.20	5.1–6.1
Alveoli m^{1-3} length	5.9 ± 0.02	0.20	5.4–6.4
Crowns m^{1-2} length	4.6 ± 0.02	0.25	4.0–5.2

surements of a single specimen when she proposed *R. v. tomba*. Live *R. v. mollis* is said to be distinguished with ease from other *Rattus* of the Schrader Range by its long and slender snout (Bulmer and Menzies, 1973). Dennis and Menzies (1978, fig. 3) have illustrated the karyotype of this subspecies which they found to be identical with those of *R. niobe* and *R. ruber* (their *ruber* sample = *R. mordax fergussoniensis, R. steini hageni,* and possibly *R. novaeguineae*).

REMARKS: Mid-montane rats are easily isolated by geographical barriers, such as valleys and river systems, and this subspecies is no exception. For example, the population on the Adelbert Range is probably completely isolated by the Ramu River and Valley from those of the Central Highlands. Similar examples can be drawn from Mt. Bosavi as well as within the Central Cordillera. None of our statistical analyses justified breakdown of this subspecies into geographical isolates, such as recognition of *R. v. tomba,* but part of the difficulty relates to small sample sizes. Our prediction is that some future study may demonstrate that this subspecies is actually multiracial.

HABITS AND HABITAT: This rat has been trapped in forests, native gardens at the edge of forests, bush fallow, and stream sides, and it has been dug out of subterranean nests and burrows (Bulmer and Menzies, 1972, 1973). Menzies and Dennis (1979) found many insects and a small amount of seeds in stomach contents. They do not record the area from which their samples were obtained and their records may apply to *R. v. verecundus.* Breeding data obtained by Dwyer (1975) suggest that it has a seasonal reproductive pattern and undergoes sexual regression in winter and early spring.

SYMPATRY: *Rattus verecundus mollis* is sympatric with *Rattus steini hageni, Rattus niobe niobe, Rattus exulans browni,* and *Rattus novaeguineae.*

TAXONOMIC HISTORY: There has been no critical review of this subspecies since the original description and a later expanded one

TABLE 7
Measurements (in Millimeters) of Adult *Rattus verecundus unicolor*
(N = 17 for skin measurements; N = 19 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	153.2 ± 3.13	12.89	120.0–170.0
Tail length	150.5 ± 3.03	12.51	123.0–172.0
Hind foot (s.u.) length	33.0 ± 0.47	1.94	30.0–36.0
Occipitonasal length of skull	38.1 ± 0.33	1.42	35.4–40.2
Condylobasal length	35.0 ± 0.37	1.63	31.6–37.6
Basal length	32.2 ± 0.32	1.40	29.3–34.5
Zygomatic width	17.2 ± 0.15	0.66	16.1–18.1
Interorbital width	5.8 ± 0.09	0.39	5.1–6.5
Interparietal length	5.4 ± 0.11	0.50	4.7–6.4
Interparietal width	10.6 ± 0.10	0.44	9.7–11.2
Braincase width	15.4 ± 0.11	0.50	14.3–16.4
Mastoid width	13.4 ± 0.11	0.46	12.6–14.3
Nasal length	13.9 ± 0.18	0.78	12.4–15.3
Nasal width	3.6 ± 0.05	0.22	3.3–3.9
Palatal length	19.4 ± 0.17	0.75	17.9–21.0
Incisive foramen length	5.8 ± 0.10	0.44	4.9–6.4
Incisive foramina width	2.0 ± 0.06	0.25	1.5–2.4
Inside m^{1-1} width	3.4 ± 0.07	0.29	2.6–3.8
Outside m^{1-1} width	7.5 ± 0.06	0.24	7.0–7.9
Bulla length	5.1 ± 0.06	0.24	4.7–5.7
Crowns m^{1-3} length	5.6 ± 0.06	0.28	5.0–6.0
Alveoli m^{1-3} length	6.0 ± 0.07	0.32	5.4–6.5
Crowns m^{1-2} length	4.5 ± 0.08	0.35	3.8–5.1

(Rümmler, 1935, 1938), and Ellerman's (1941) removal of it from *Stenomys* to *Rattus*. Laurie (1952) described a new subspecies, *R. v. tomba,* which she likened to *mollis,* but she provided no justification for distinguishing the new form. Her comparison of differences is, instead, drawn between *tomba* and *R. v. verecundus*. Laurie and Hill (1954) recognized *tomba* and this is the last assessment that has been made. We find no statistical or morphological evidence to distinguish *tomba* from *mollis* and therefore place *tomba* in synonymy.

Rattus verecundus unicolor (Rümmler)

Stenomys verecundus unicolor Rümmler, 1935, p. 117.

Rattus verecundus unicolor: Ellerman, 1941, p. 205.

HOLOTYPE: Skin and complete skull, adult male, ZM 45678, collected September 11, 1931, by Georg Stein, Kunupi, Weyland Mountains, Irian Jaya Province, Indonesia, 1400–1800 m.

DISTRIBUTION: Known from Kunupi, Sumuri, and Sururai, all in western Irian Jaya, from 1000 to 2500 m. Misonne (1979) has identified a juvenile rat from Enarotali as this subspecies, but we have not examined the specimen (fig. 9).

MEAN MEASUREMENTS (IN MM.): External: head and body 153; tail 151; hind foot (s.u.) 33.0. Skull: occipitonasal length 38.1; braincase width 15.4; bulla length 5.1; crowns m^{1-3} length 5.6. (See table 7 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 35.0 or less.

DESCRIPTION: This subspecies is very soft-furred, and the dark brown pelage is tipped with rust. Except for white patches, the ventral pelage is only slightly lighter than the dorsum and is tipped with buff. In all specimens examined, the tail is dark brown for its entire length. The tail scales measure about 13 rows per cm. It is the largest subspecies of *verecundus* and exceeds *v. verecundus* slightly in this regard. In all other features, it is similar to those described for the species.

The mammary formula is 1 + 2 = 6.

Supraorbital ridging is indistinct, even on large skulls. This subspecies has the smallest bulla relative to basal length of any *verecundus*; the bulla is 16.0 percent of the latter in length.

PREVIOUS DESCRIPTIVE ACCOUNTS: Rümmler (1935, 1938), who described *unicolor*, distinguished it from other *verecundus* on the basis of its narrower incisive foramina. Tate (1951) gave a brief description that included skin and skull measurements of the holotype. Although he regarded *unicolor* as smaller than *v. verecundus*, comparison of the skull measurements he gave does not support his statement. Misonne (1979) is the only other investigator to mention this subspecies. He has given measurements of a juvenile specimen that he refers to *unicolor*.

REMARKS: Rümmler's (1935, 1938) separation of *unicolor* from other subspecies on the basis of its relatively narrower incisive foramina appears to be valid when means of the other groups of *verecundus* he was examining are compared. *Rattus v. vandeuseni*, new subspecies, which was unknown to Rümmler, has even narrower foramina. The most distinctive feature of the skull of *unicolor*, the smallest bullae relative to basal skull length, has not previously been mentioned.

A skin feature shared only with *vandeuseni* is the absence of white on the tail. This, combined with the rather darker ventral pelage, lends endorsement to the sagacious choice of the name *unicolor*.

HABITS AND HABITAT: This subspecies lives in the mountain rain forest zone in the Weyland Mountains (Rümmler, 1938). No other information is available.

SYMPATRY: *Rattus verecundus unicolor* is sympatric with *Rattus steini steini*, *Rattus niobe arrogans*, and *Rattus exulans browni* (Sururai).

TAXONOMIC HISTORY: Rümmler (1935) described this subspecies as *Stenomys verecundus unicolor*. Ellerman (1941) removed it to *Rattus* and later (Ellerman, 1949) included it under the subgenus *Stenomys* of *Rattus*. Tate (1951) concurred with the generic alliance, but did not recognize the subgeneric arrangement. He placed all forms of *R. verecundus*, including *unicolor*, in his *R. leucopus* Group that included the two species *R. verecundus* and *R. leucopus*. Laurie and Hill (1954) followed Ellerman (1949) in listing *unicolor* and the other subspecies of *verecundus* under the subgenus *Stenomys*. Their work is the most recent treatment of *unicolor*.

Rattus verecundus vandeuseni,
New Subspecies
Taylor and Calaby

HOLOTYPE: Skin and complete skull, adult female, AMNH 157905, collected July 10, 1953, by Hobart M. Van Deusen, Middle Camp, north slope of Mt. Dayman, Maneau Range, 1540 m.

DISTRIBUTION: Known only from the type locality (fig. 9).

MEAN MEASUREMENTS (IN MM.): External: head and body 130; tail 145; hind foot (s.u.) 30.8. Skull: occipitonasal length 35.5; braincase width 14.8; bulla length 5.1; crowns m^{1-3} length 5.8. (See table 8 for complete list of measurements and statistical presentation.) Juveniles: unknown.

DESCRIPTION: This is the smallest subspecies of *R. verecundus* judged by the limited series of specimens currently available, most of which have moderate to well worn molars. Skin measurements taken when the holotype was collected were 269 mm. (total length), 134 mm. (tail length), 31 mm. [hind foot (s.u.)], 15 mm. (ear from notch), and body weight was 2.4 oz. (68 g.). The 20 skull measurements of the holotype (listed in mm. and in the same order as in table 8) are: 36.4, 33.7, 31.3, 16.4, 5.4, 4.8, 10.5, 14.8, 12.3, 14.9, 3.7, 19.7, 5.8, 2.2, 3.3, 8.0, 4.9, 5.8, 6.2, 4.8, and the molars are well worn. The holotype is the largest of the series. The mammary formula, determined by Van Deusen at the time of collection, is 0 + 2 = 4.

TABLE 8

Measurements (in Millimeters) of Adult *Rattus verecundus vandeuseni*

(N = 8 for skin measurements; N = 6 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	130.1 ± 1.70	4.79	121.0–135.0
Tail length	145.1 ± 3.14	8.87	134.0–160.0
Hind foot (s.u.) length	30.8 ± 0.37	1.03	29.5–32.5
Occipitonasal length of skull	35.5 ± 0.30	0.72	34.5–36.4
Condylobasal length	32.7 ± 0.37	0.90	31.5–33.7
Basal length	30.3 ± 0.38	0.93	29.0–31.3
Zygomatic width	16.3 ± 0.14	0.35	15.7–16.7
Interorbital width	5.6 ± 0.09	0.23	5.3–5.8
Interparietal length	4.6 ± 0.25	0.61	3.9–5.4
Interparietal width	10.4 ± 0.26	0.65	9.6–11.4
Braincase width	14.8 ± 0.11	0.26	14.3–15.0
Mastoid width	12.6 ± 0.16	0.39	12.2–13.3
Nasal length	13.6 ± 0.36	0.88	12.4–14.9
Nasal width	3.8 ± 0.15	0.38	3.5–4.5
Palatal length	18.8 ± 0.35	0.86	17.7–19.7
Incisive foramen length	5.4 ± 0.15	0.38	5.0–5.8
Incisive foramina width	1.8 ± 0.15	0.38	1.2–2.2
Inside m^{1-1} width	3.1 ± 0.11	0.26	2.7–3.4
Outside m^{1-1} width	7.5 ± 0.20	0.49	6.8–8.1
Bulla length	5.1 ± 0.14	0.35	4.8–5.7
Crowns m^{1-3} length	5.8 ± 0.03	0.06	5.7–5.9
Alveoli m^{1-3} length	6.1 ± 0.06	0.15	5.9–6.3
Crowns m^{1-2} length	4.5 ± 0.14	0.35	4.0–4.8

This is a soft-furred rat which lacks spines. The dorsal coloration is dark brown tinged with rust-colored tipping. The dorsal hairs are about 17 mm. long. The basal portion is dark gray and the terminal 2 mm. are rust colored. The black guard hairs are inconspicuous and are only 1–2 mm. longer than the regular hairs. Fine gray underfur is also present. The muzzle vibrissae measure to 50 mm. in length. The ears are dull medium-brown and are finely clothed in short hairs. Laterally, the pelage becomes slightly more rust and the basal portion of the fur is medium gray. The ventral pelage is tipped in reddish buff and is somewhat lighter than other regions of the body. The length of this pelage is 9–10 mm., of which the basal portion is medium gray and the tipping is 2 mm. The long tail is a uniform medium brown for its entire length. There are 12–13 scale rows per cm., and the tail is sparsely clothed in short brown hairs. The dorsal surface of the feet is a mixture of brown and white hairs.

Juvenile pelage is unknown.

The mammary formula of all three females of the series is 0 + 2 = 4. The count was originally determined by the collector on fresh skins and has been reconfirmed by us on the dried study skins.

The skull is typical of the species (fig. 10B). Supraorbital beading is barely discernible. The bulla is 16.8 percent of the basal skull length and in this regard is very close to *R. v. verecundus* and is relatively larger than either *R. v. mollis* (16.6 percent) or *R. v. unicolor* (16.0 percent). *Rattus verecundus vandeuseni* has longer nasal bones relative to basal length of the skull (44.8 percent) than any of the other subspecies of *verecundus* (43.0–43.5 percent), and narrower palatal foramina (see tables 5–8).

The juvenile skull is unknown.

PREVIOUS DESCRIPTIVE ACCOUNTS: None.

REMARKS: This new subspecies has the lowest mammary formula recorded for any species of *Rattus* of New Guinea. Were it

FIG. 11. Hobart Van Deusen and field assistants skinning mammals in Middle Camp, 1550 m., north slope of Mt. Dayman. Photograph taken June–July of 1953 Archbold Expedition.

not for the fact that Van Deusen, who placed considerable value on such formulae in rodents, had taken the counts on fresh material, we would have been reluctant to accept as verification our own results on dried skins.

On the same mountain at an altitude of 700 m., *R. v. verecundus* is present; it is a larger subspecies, which not only has a higher mammary formula and a white tail tip, but differs in both absolute size and in certain relative skull proportions. It also occupies a different forest zone on this mountain (see Habits and Habitat for *R. v. vandeuseni*). Because the subspecies *R. v. verecundus* and *R. v. vandeuseni* occur so close to each other, we do not exclude the possibility that *verecundus* and *vandeuseni* could be distinct species. At present, however, only 12 *R. v. verecundus* have been collected on Mt. Dayman, all at 700 m., and the eight *R. v. vandeuseni* specimens that are known to exist were all taken at 1540 m. The question can only be solved by detailed collecting along the altitudinal gradient, or perhaps by a study of tissue enzymes. The eight specimens of this new mid-montane rat are so close in general morphology to all the other subspecies of *R. verecundus* that, in balance with our assessments of other species at the level of subspecies, it is more appropriately designated as a subspecies of *R. verecundus* in our revisionary study. Although *vandeuseni,* with its relatively low sample size, is a poor candidate for our numerical analyses (see section on Multivariate Analysis), in all it is linked more closely to at least one other subspecies of *R. verecundus* than it is to any other taxon.

HABITS AND HABITAT: *Rattus verecundus vandeuseni* was trapped in oak forest characterized by many large trees over 30 m. tall, numerous dead trees covered by ferns and mosses, and regular mists (Brass, 1956). This

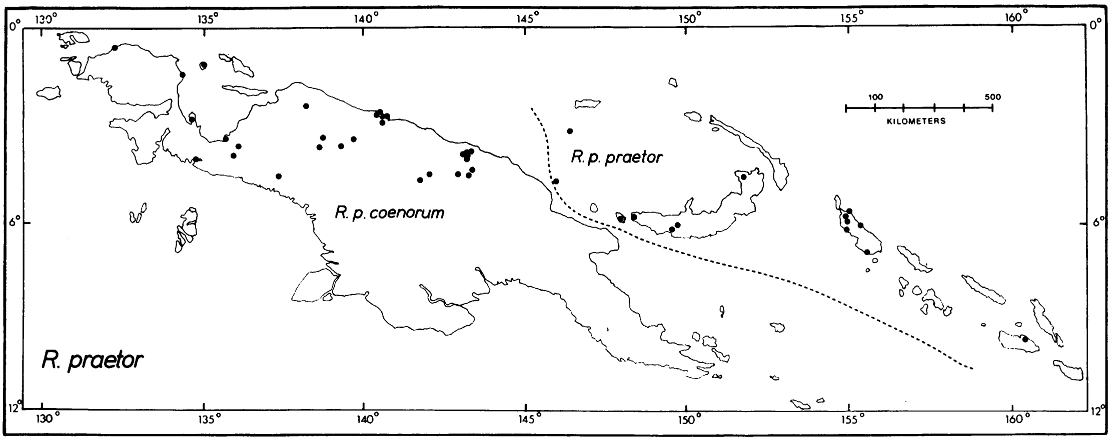

FIG. 12. Distribution map of *Rattus praetor*. Locality records for each of the two subspecies are indicated by dots.

habitat contrasts with that at 700 m. where *R. v. verecundus* was taken. The latter is mixed rain forest that is less open than the oak forest and is below the zone of regular mists.

SYMPATRY: *Rattus verecundus vandeuseni* is sympatric with *Rattus niobe niobe*.

TAXONOMIC HISTORY: Specimens of *R. verecundus* from this locality have never been described and thus there is no historical background that pertains to *R. v. vandeuseni*. In recognition of our late colleague and joint author, Hobart Merritt Van Deusen, who not only collected this series but also firmly believed that it represented a new taxon, we (Taylor and Calaby) take special pleasure in naming this subspecies after him (fig. 11).

Rattus praetor (Thomas)

DISTRIBUTION: Both a mainland and an insular rat. On the mainland occurs from Vogelkop Peninsula eastward along the lowlands of the northern portion of New Guinea to the Sepik-Ramu drainage. Known only from Etna Bay in the lowlands of the south coast, although at higher elevations, up to 1525 m., it occurs on both sides of the major central mountain ranges of Irian Jaya. Insular distribution includes offshore islands near the mainland, Bismarck Archipelago, Admiralty Islands, New Britain and the Solomon Islands, from sea level to 1900 m. (fig. 12).

GENERAL DESCRIPTION: *Rattus praetor* is a coarse-haired spinous rat that in lowland situations may equal the large *R. jobiensis* in size. At higher elevations body size is smaller and spines in the pelage, although still abundant, are less fully developed. The pelage is medium to dark brown and becomes a rich dark brown at higher elevations. Regular body hair and spines may be rufous tipped which gives a somewhat grizzled effect. Ventral coloration is gray or yellowish ivory. White pectoral or other ventral spotting is common. In lowland rats the ventral pelage is very spinous but this feature diminishes or may not even be present in those from higher altitudes. The ears and tail are medium brown, and the feet are clothed by light or medium brown hair.

The mammary formula is $2 + 2 = 8$.

Larger specimens have strongly developed supraorbital-temporal and supraoccipital ridging, whereas smaller adults may possess only a modest development of these ridges. Such variable development may make the skulls look remarkably different and, unless a good age series is examined, may produce deceptive features in identification. The incisive foramina are bowed, especially in larger specimens, and the palate terminates 0.5 to 2.5 mm. posterior to the molar rows. The

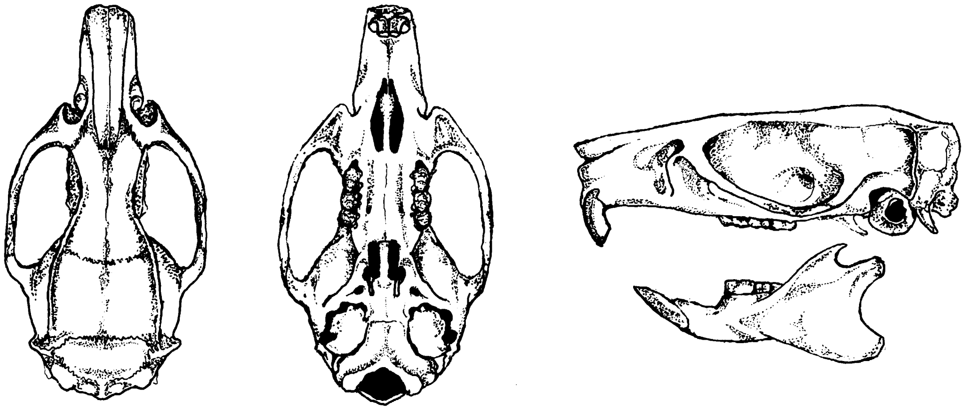

FIG. 13. Dorsal, ventral, and lateral views of skull of adult *Rattus praetor coenorum,* AMNH 143837, from Sansapor. Occipitonasal length 51.5 mm.

molars are unenlarged (see General Description of *R. mordax* for comparison). The nasal bones flare distally and terminate in line with the anterior face of the incisors or just beyond. The bullae are relatively small (fig. 13).

DIAGNOSTIC FEATURES: In the lowlands this species is readily confused with the other large lowland rats, *R. jobiensis, R. mordax,* and *R. leucopus,* and at higher elevations, with *R. steini.* The mammary formula readily distinguishes it from *R. leucopus* and *R. steini,* and the plain tail will usually separate it from *R. leucopus. Rattus steini* has almost no development of supraorbital ridging. *Rattus mordax* has substantially wider molars and narrower straight-sided incisive foramina, whereas *R. jobiensis* has a more elongate skull and greater nasal overhang. *Rattus praetor* is, among New Guinean rats, one of the most responsive in ecotypical characters. Changes in adult body size and pelage quality can be broadly correlated with altitudinal and accompanying climatic differences. This type of variation is evident, not only on the mainland but also in insular situations (e.g., Tinputz, 5 m., and Mt. Balbi, 1900–2300 m., Bougainville) and it presents difficulty in attempting to provide adequate taxonomic assessment of this species.

TAXONOMIC HISTORY: This was the second species of rat to be described from the New Guinean region that is indigenous there and now included in *Rattus.* Thomas (1888) proposed it as *Mus praetor* from two specimens collected at Aola in the Solomon Islands. He designated the female as the type and provided its mammary formula, 2 + 2 = 8, one of the features by which he distinguished it from *M. terrae-reginae* (=*R. leucopus*). He expanded this description in a later paper (Thomas, 1889) and recorded a specimen from New Britain.

In 1897, Thomas identified two specimens from Haveri as *M. praetor,* but this was before he had described *M. mordax,* to which they belong. When Thomas (1904a) described *M. mordax,* he allied it closely to *M. praetor.* In 1910 Thomas shifted *praetor* to *Epimys,* a move that Longman (1916) followed, and then to *Rattus* (Thomas, 1916). In 1922 Thomas described two new species and one subspecies, *R. coenorum, R. bandiculus,* and *R. mordax tramitius,* all of which are *praetor,* and later in the same year, he (Thomas, 1922c) expanded the descriptions of these three taxa. Le Souef and Burrell (1926) mention only *R. praetor.* Rümmler (1935) described a new subspecies, *R. leucopus utakwa,* that also belongs in *praetor.* Tate (1936) had doubts about *R. praetor* and in it he included not only true *praetor,* but also five specimens of *R. m. mordax* (AMNH 104228–30, 104232–33), one of *R. steini foersteri* (AMNH 79761), and one of *R. leucopus ringens* (AMNH 104537). He recognized *R. coenorum* as well. Troughton (1936) described a new subspecies from

Bougainville which he named *R. praetor mediocris*.

In 1938 Rümmler's major revision of the murid rodents of New Guinea was published and in this work he recognized a number of taxa as subspecies under the name *Stenomys leucopus*. In this species he placed *praetor, utakwa, tramitius,* and *coenorum,* along with several others. He realized that the type of *bandiculus* was but a larger example of *coenorum* and listed it in synonymy under *coenorum*. Among the additional taxa that he included in *S. leucopus* was the single specimen known of *ruber* which Jentink had described as *Mus ruber* in 1880. Tate (1940) examined the holotype of *ruber,* viewed it as related to *praetor,* and retained it as a full species, *R. ruber*. Ellerman (1941) followed Rümmler's proposal that *ruber, praetor, utakwa, tramitius,* and *coenorum* all be recognized as subspecies within a single species, but as *Rattus leucopus* rather than as *Stenomys leucopus*. Sody (1941) placed both *coenorum* and *tramitius* (incorrectly printed as *Rattus rattus tramitius*) under *Rattus mordax*.

Troughton (1946), who argued strongly in favor of recognizing *mordax* as a species distinct from *ringens* or *leucopus,* described two new species, *Rattus purdiensis,* from Bat Island near the Admiralty group, and *Rattus sansapor,* from the Vogelkop region of the mainland. He expressed the belief that *purdiensis* was somewhat intermediate between *mordax* and *praetor*. Frechkop (1948) followed Rümmler's (1938) proposal of placing *praetor* as a subspecies of *Stenomys leucopus* and he synonymized Troughton's (1936) *mediocris* with *praetor,* but made no reference to Troughton's more recent work.

Ellerman (1949) divided his *Stenomys leucopus* and used the name *Rattus ringens* when he removed the New Guinean rats from the Australian *leucopus*. In *R. ringens* he included all or most of the same subspecies of New Guinean rats that he had grouped earlier under *Stenomys ringens*. He acknowledged the possibility that *bandiculus* was a synonym of *coenorum,* but of greater consequence was his treatment of *ruber*. Since he had not seen the type, Ellerman this time retained it as a full species, but remarked that since it is an older name than *ringens,* the subspecies now under *ringens* may actually belong in *Rattus ruber*.

Tate (1951) provisionally placed *praetor, coenorum* (including *bandiculus*), *tramitius* (=*utakwa*), *mediocris, purdiensis,* and *jobiensis* (regarding *sansapor* and *biakensis* as synonyms), along with *mordax, hageni, steini,* and *rosalinda,* all under *Rattus ruber*. With but minor variation in treatment, *Rattus ruber* has stood as the species name for a large and diverse group of rats in New Guinea and is currently a name in common usage.

We have examined the holotype of *R. ruber* (RMNH a), which consists of a mounted skin and a skull. Except for a broken zygoma and a small portion of the posterior palate, the skull is intact. It represents an adult specimen and possesses well-worn molars. The pelage is soft and lacks spines, characters so different from those of the lowland *praetor* of the Vogelkop region from where this specimen comes, that these features must have influenced Rümmler (1938) into believing that it was subadult. The holotype of *R. ruber* is a specimen of a southeast Asian commensal rat, *Rattus nitidus,* that is known from only a few localities in New Guinea, all in the western portion. Musser (1973, 1977) has described its distribution in Irian Jaya and has shown that the type of *Rattus vanheurni* is another example of *R. nitidus*. *Rattus nitidus* was described by Hodgson in 1845 and its name thus has nomenclatorial priority over *Rattus ruber*. The next available name for the New Guinean rats that Tate (1951) and Laurie and Hill (1954) grouped within *R. ruber,* is *R. praetor*. We have reviewed this nomenclatorial problem in a separate paper and have included photographs of the skulls of the holotype of *R. ruber* and of a specimen of *R. praetor* from the Vogelkop region (Calaby and Taylor, 1980).

In addition to this nomenclatorial problem that has caused confusion in this group, there is a more serious problem of interpretation that warrants attention. We have taken a broad view in dividing *R. praetor* into only two subspecies. The problem, in part, as with any of the *Rattus* of New Guinea, stems from the formidable distributional gaps due to lack of sampling and inadequacy of numbers of specimens. In part, the problem is also one of insular distribution along a vast archipelago system in which intervening ocean represents a potential barrier to genetic continuity between adjacent islands. The strength of these barriers weakens when a rat is a commensal of man, such as *R. exulans*. That *R. praetor* is an opportunist in man's environment is documented by captures in food supplies and in buildings made of native materials. That it travels in man's cargo across ocean straits is undocumented. There remains in both the insular distribution and on the mainland, where mountain systems and climatic differences can carve up habitats into ecological islands, the strong possibility that *R. praetor* is far more diverse in subspecific representation than we have allowed for in our formal interpretation. We admit, also, to arbitrariness in dividing the subspecies according to insular and mainland distributions. It is unlikely that a realistic interpretation of evolution within *R. praetor* can be made until extensive collections are procured and biochemical markers of populations are obtained to aid in the analysis of the systematics of this complex group.

We recognize two subspecies of *Rattus praetor, R. p. praetor* and *R. p. coenorum*.

Rattus praetor praetor (Thomas)

Mus praetor Thomas, 1888, p. 158.
Epimys praetor: Thomas, 1910b, p. 605.
Rattus praetor: Thomas, 1916, p. 240.
Rattus praetor mediocris Troughton, 1936, p. 343.
Stenomys leucopus praetor: Rümmler, 1938, p. 191.
Rattus leucopus praetor: Ellerman, 1941, p. 205.
Rattus purdiensis Troughton, 1946, p. 408.
Rattus ringens praetor: Ellerman, 1949, p. 69.
Rattus ruber praetor: Tate, 1951, p. 334.
Rattus ruber mediocris: Tate, 1951, p. 334.
Rattus ruber purdiensis: Tate, 1951, p. 333.

HOLOTYPE: Skin in alcohol and intact skull with one broken zygoma, adult female, BM 88.1.5.39, collected at an unspecified date, by C. M. Woodford, at Aola, Guadalcanal, Solomon Islands, about 150 m.

DISTRIBUTION: Insular in distribution and known from islands off the coast of northeastern New Guinea near the mouth of the Sepik and Ramu rivers, northward to Bat Island, in New Britain and the Solomon Islands to as far southeast as Aola, Guadalcanal (type locality), from sea level to 1900 m. (fig. 12).

MEAN MEASUREMENTS (IN MM.): External: head and body 187; tail 146; hind foot (s.u.) 37.5. Skull: occipitonasal length 43.3; braincase width 16.5; bulla length 6.2; crowns m^{1-3} length 6.7. (See table 9 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 39.0 or less.

DESCRIPTION: This is a large spinous rat, medium to dark brown, and grizzled in appearance due to pale brown or cinnamon tipping of the hairs. The length of the dorsal hairs, which are mostly grayish, translucent and spinous, is about 15 mm., of which the last 2 mm. are tipped as described. Black guard hairs, that are conspicuous but not especially abundant, are up to 45 mm. in length. The ears are medium brown and lightly haired. Muzzle vibrissae measure to 45 mm. The pelage becomes a warm buff laterally and blends into a ventral color of cream to yellow. Ventral hairs are pale gray basally, measure about 10 mm. long, and are tipped with cream to yellow for about 2 mm. Larger adults may be very spinous ventrally and these spines may be cream-colored for their entire length. Ventral blotching of one or occasionally more areas of white is common, particularly in the pectoral region. The tail is dark brown and is lightly covered with brown hair about 1.5 mm. in length, and scale rows that number 7 per cm. The feet are clothed dorsally with both brown and white hairs.

The juvenile pelage is very similar except for the lack of spines and the tendency for a grayer ventral coloration.

The mammary formula is $2 + 2 = 8$.

TABLE 9
Measurements (in Millimeters) of Adult *Rattus praetor praetor*
(N = 32 for skin measurements; N = 20 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	187.0 ± 2.67	15.09	157.0–212.0
Tail length	146.1 ± 2.55	14.41	118.0–180.0
Hind foot (s.u.) length	37.5 ± 0.38	2.17	32.0–41.0
Occipitonasal length of skull	43.3 ± 0.64	2.88	39.0–49.4
Condylobasal length	41.0 ± 0.60	2.69	37.0–46.3
Basal length	38.2 ± 0.59	2.64	34.3–43.4
Zygomatic width	20.9 ± 0.36	1.63	18.3–24.5
Interorbital width	6.2 ± 0.07	0.33	5.8–7.0
Interparietal length	5.5 ± 0.09	0.42	4.9–6.7
Interparietal width	10.9 ± 0.17	0.78	9.7–12.4
Braincase width	16.5 ± 0.13	0.57	15.5–17.5
Mastoid width	14.6 ± 0.17	0.76	13.0–16.0
Nasal length	16.2 ± 0.27	1.21	14.5–19.1
Nasal width	4.9 ± 0.11	0.51	4.0–5.9
Palatal length	23.5 ± 0.34	1.53	21.2–26.8
Incisive foramen length	7.8 ± 0.14	0.60	6.8–9.0
Incisive foramina width	2.9 ± 0.10	0.43	2.1–3.9
Inside m^{1-1} width	4.1 ± 0.12	0.53	3.3–5.3
Outside m^{1-1} width	9.1 ± 0.14	0.62	8.2–10.5
Bulla length	6.2 ± 0.10	0.45	5.5–7.4
Crowns m^{1-3} length	6.7 ± 0.07	0.31	6.1–7.3
Alveoli m^{1-3} length	7.4 ± 0.07	0.32	6.6–8.0
Crowns m^{1-2} length	5.5 ± 0.06	0.28	4.9–6.0

The skull is heavy, well ridged both in the supraorbital-temporal and the supraoccipital regions, and the supraorbital ridging may rise 1 mm. or more from the skull surface. The incisive foramina are well bowed and the rostral area is relatively heavy. The nasals are flared distally, but there is little or no nasal overhang. The palate terminates 1 mm. behind the end of the molar row. The interorbital region is constricted, and the bullae and molars are relatively small. The juvenile skull lacks ridging, the incisive foramina are less bowed, and it bears remarkable overall similarity to that of adults of *R. steini.*

Previous Descriptive Accounts: The original description of *R. praetor* by Thomas (1888) was brief and was in part concerned with distinguishing this large lowland rat from an earlier described one from Australia, *Mus terrae-reginae* (*Rattus leucopus*). The year following, Thomas augmented this description and added an illustration (Thomas, 1889, Pl. XXII, fig. 6). The holotype (BM 88.1.5.39) is a young adult female that is considerably smaller than the male paratype (BM 88.1.5.38). The choice of this specimen as the holotype was very likely made because it is a lactating female with prominent teats. Since the mammary formula differs from that of *M. terrae-reginae,* a feature that Thomas (1888) noted in his initial description and could be verified without doubt on this lactating individual, its selection as holotype is significant. Jentink (1907a) quoted Thomas's (1888) original description almost verbatim, and Le Souef and Burrell (1926) slightly reworded it.

Tate (1936) commented upon the "diversified nature" of *Rattus praetor,* a conclusion he reached in part because he was including specimens of *mordax, foersteri,* and *leucopus ringens* as *praetor,* even though he claimed that *praetor* could be distinguished from *ringens* and *mordax* by its longer rostrum, smaller molars, and smaller bullae.

When Troughton (1936) described *R. praetor mediocris,* he worked from young adult specimens (holotype, AM M5761) that were slightly larger than the holotype of *R. p. praetor*. His descriptions of somewhat larger dimensions and greater development of supraorbital ridging reflect the larger body size. Rümmler (1938) added further to the description of the holotype of *R. p. praetor* as well as to three other specimens, two of which came from New Britain. When Troughton (1946) proposed *Rattus purdiensis* as a new species, he based his description on the features of a holotype (AM M7183) and a paratype (M7184), both of which are younger than either of the other two subspecies proposed. His description of less spinous pelage, and a smaller and less ridged skull with smaller nasals and incisive foramina, reflects the features of younger specimens. Johnson (1946) added more to the description of *R. p. mediocris* and commented upon the white pectoral or belly patch that is so common in these insular rats. Frechkop (1948) gave a very brief description of three specimens from Buin, and Tate (1951) added descriptive remarks about a paratype of *Mus praetor*. Koopman (1979) has identified two mandibles of this rat from Kar Kar, off the northeast coast of the mainland. Our placement of this insular record in *R. p. praetor* is purely arbitrary.

REMARKS: One difficulty is assessing the amount of variation in *R. p. praetor* is the lack of adequate series (see Museum Specimen Examined and Localities). Another is a bias in sampling that is reflected in the generally young material from which descriptions have been made. It is unlikely that the present series available in museums adequately portrays the range of size in adults.

The tendency for occupants of high altitudes (i.e., Mt. Balbi) to be smaller and less spinous in adulthood, a feature that has already been discussed for the species, is an excellent demonstration in these insular rats of their ability to adapt both morphologically and ecologically in the absence of strong competition. The Mt. Balbi specimens that occupy rain forest in these higher elevations, have as adults retained the juvenile features of relatively soft fur, darker underparts, and smaller body size.

HABITS AND HABITAT: This rat is a strong burrower and uses the burrow systems to shelter its young (Troughton, 1946). On Cape Torokina, Johnson (1946) found that the rats were relatively abundant in a semi-marsh area by a lagoon and bordering a jungle. He described their burrows in sandy soil of ridges covered by jungle between marshy areas. They would come to forage among troop dugouts and low, round concrete and steel shelters. They were suspected carriers of scrub typhus and tsutsugamushi diseases and were infested with chiggers of trombiculine mites.

SYMPATRY: *Rattus praetor praetor* is sympatric with *Rattus exulans browni* and *Rattus rattus*.

TAXONOMIC HISTORY: Thomas's (1888) description of *Mus praetor* from Guadalcanal and its subsequent confusion with *M. mordax* from mainland New Guinea has been reviewed previously. Troughton (1936) considered that his new subspecies, *Rattus praetor mediocris* from another of the Solomon Islands, Bougainville, was larger than the form from Guadalcanal. He thought that the new subspecies might be intermediate between the type and another specimen, without skull, that Thomas (1889) had mentioned from the Duke of York Islands.

Rümmler (1938) placed *praetor* as a subspecies of *Stenomys leucopus* and viewed *mediocris* as a synonym of *praetor*. He dismissed the difference on the grounds that the skin of the type of *praetor* was in alcohol, whereas that of *mediocris* had been prepared as a dry skin. Ellerman (1941) accepted Rümmler's synonymy and his placement of *praetor* in *leucopus*, but retained it in the genus *Rattus*.

When Troughton (1946) described *Rattus purdiensis*, he assessed its status as intermediate between *R. praetor* and *R. mordax*. Tooth wear is light on both the holotype and allotype of *purdiensis*, but Troughton did not recognize that some of the differences he was describing were merely features of young specimens. Although he described *R. sansapor* at the same time, he seemed to detect no affinity between this and *purdiensis* and perhaps it was because the holotype of *sansapor* is a much larger adult. Frechkop (1948) followed Rümmler's (1938) nomenclature and synonymy in his treatment of *prae-*

tor. When Ellerman (1949) removed the Australian *leucopus* as a monotypic species, he placed *praetor,* along with a number of other taxa, as a subspecies of *Rattus ringens*. He was apparently unaware of Troughton's (1946) new species, for he makes no mention of them anywhere in his revision.

Tate (1951) was the first to express the crux of the problem with this group. By this time, he realized that variation in body size and in pelage texture imposed difficulties in assessing the relationships of large lowland rats of eastern and western geographical distributions to each other and to altitudinally higher forms. He took a broad view and placed many in *Ruttus ruber,* including *praetor, mediocris,* and *purdiensis,* each as a subspecies. He found little difference between these three insular subspecies and *mordax* of the mainland, although he treated each separately as a subspecies of *Rattus ruber*. Laurie and Hill (1954) followed Tate's nomenclature in this regard.

We have synonymized *purdiensis* and *mediocris* with *R. p. praetor*. Our rationalization is that there are no morphological grounds at this stage on which to distinguish more subspecies. Present museum collections contain a paucity of specimens from this archipelago that is over 1600 km. long. This subspecies has spread far along island chains that have been formidable barriers to other lowland rats, such as *R. leucopus* or *R. sordidus*. We know so little about its habits, including its ability to become an opportunistic stowaway with cargo on native boats going from island to island, that the existence of genetic barriers, if any, is untested. One extreme possibility is that every island or insular cluster contains a different subspecies of *R. praetor*; on the other hand, it may be sensible to regard the entire insular population as a single subspecies. It is also probable that various characters vary clinally along these island chains. The material is not yet at hand for any realistic subdivisions of these island populations into entities that can be viewed as discrete. We take the position that the most appropriate stand is to regard this entire insular group as a single subspecies until such time that convincing evidence to the contrary is forthcoming.

Rattus praetor coenorum Thomas

Rattus coenorum Thomas, 1922a, p. 262.
Rattus mordax tramitius Thomas, 1922a, p. 262.
Rattus bandiculus Thomas, 1922a, p. 262.
Rattus leucopus utakwa Rümmler, 1935, p. 115.
Stenomys leucopus tramitius: Rümmler, 1938, p. 189.
Stenomys leucopus coenorum: Rümmler, 1938, p. 188.
Stenomys leucopus utakwa: Rümmler, 1938, p. 185.
Rattus mordax coenorum: Sody, 1941, p. 310.
Rattus rattus [*sic*] *tramitius*: Sody, 1941, p. 310 (under *Rattus mordax*).
Rattus leucopus coenorum: Ellerman, 1941, p. 205.
Rattus leucopus tramitius: Ellerman, 1941, p. 205.
Rattus sansapor Troughton, 1946, p. 409.
Rattus ringens tramitius: Ellerman, 1949, p. 69.
Rattus ringens coenorum: Ellerman, 1949, p. 69.
Rattus ringens utakwa: Ellerman, 1949, p. 69.
Rattus ruber tramitius: Tate, 1951, p. 332.
Rattus ruber coenorum: Tate, 1951, p. 332.
Rattus ruber jobiensis: Tate, 1951, p. 331 (specimens previously identified as *sansapor,* not *Rattus leucopus jobiensis* Rümmler).

HOLOTYPE: Skin and complete skull, young adult male, BM 22.2.2.19, collected December 18, 1920, by W. C. van Heurn, at Pionier-bivak, Mamberamo River, Irian Jaya Province, Indonesia, 50 m.

DISTRIBUTION: Irian Jaya and in the northern lowlands of Papua New Guinea. In Irian Jaya known from the north and east coasts of the Vogelkop region, Etna Bay on the south coast, and in low- and mid-land situations both north and south of the central cordillera, from sea level to 1525 m. Extends eastward across the northern lowlands into Papua New Guinea and as far east as the Sepik-Ramu drainage on the coast (fig. 12).

MEAN MEASUREMENTS (IN MM.): External: head and body 196; tail 175; hind foot (s.u.) 39.3. Skull: occipitonasal length 44.6; braincase width 17.3; bulla length 6.3; crowns m^{1-3} length 6.9. (See table 10 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 38.0 or less.

DESCRIPTION: This rat attains a large size in lowland situations and becomes very spinous, whereas at known maximum altitudes it is smaller and somewhat less spinous.

TABLE 10

Measurements (in Millimeters) of Adult *Rattus praetor coenorum*

(N = 83 for skin measurements; N = 69 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	195.9 ± 2.57	23.42	150.0–260.0
Tail length	175.2 ± 2.47	22.47	125.0–234.0
Hind foot (s.u.) length	39.3 ± 0.48	4.41	30.0–50.0
Occipitonasal length of skull	44.6 ± 0.47	3.92	37.4–54.9
Condylobasal length	42.3 ± 0.48	3.95	35.2–53.7
Basal length	39.2 ± 0.47	3.88	32.7–50.7
Zygomatic width	21.3 ± 0.24	2.02	18.1–27.1
Interorbital width	6.3 ± 0.05	0.43	5.4–7.3
Interparietal length	5.8 ± 0.07	0.60	4.5–7.5
Interparietal width	10.9 ± 0.11	0.92	8.9–13.4
Braincase width	17.3 ± 0.11	0.94	15.7–19.7
Mastoid width	14.8 ± 0.11	0.91	13.3–17.5
Nasal length	16.5 ± 0.25	2.08	12.9–22.0
Nasal width	5.0 ± 0.09	0.77	3.9–7.3
Palatal length	24.2 ± 0.29	2.40	19.8–31.3
Incisive foramen length	7.7 ± 0.10	0.80	6.2–9.8
Incisive foramina width	2.9 ± 0.06	0.50	2.0–4.2
Inside m^{1-1} width	4.3 ± 0.08	0.63	3.3–5.9
Outside m^{1-1} width	9.3 ± 0.10	0.81	7.9–11.4
Bulla length	6.3 ± 0.06	0.50	5.4–8.1
Crowns m^{1-3} length	6.9 ± 0.06	0.52	5.9–8.7
Alveoli m^{1-3} length	7.4 ± 0.07	0.57	6.1–9.3
Crowns m^{1-2} length	5.6 ± 0.06	0.46	4.4–6.5

Overall dorsal color is dark brown with a grizzled effect due to buff or cinnamon tipping of spines and regular hair. The dorsal pelage measures 15 mm., of which the basal portion is gray if it is regular hair and translucent if spinous. The tipping occurs on the terminal 2–3 mm. Black guard hairs measure to 35 mm. The ears are medium brown and sparsely haired. The muzzle vibrissae measure to 60 mm. The pelage blends to a yellowish ivory ventrally with a background of gray. The ventral pelage is also spinous; the spines are yellowish ivory in color, and a sparse layer of underfur provides a gray cast. The ventral pelage measures to 11 mm. Ventral white marking is very common, especially in the pectoral area. Occasionally, white marking may also occur dorsally. The holotype of *R. sansapor* has a white blaze on the forehead. The tail is medium brown and is lightly covered by dark brown hairs measuring to 2 mm. Tail scales measure 8 rows per cm. The feet are dark dorsally and are covered by both brown and white hairs.

The juvenile pelage lacks spines, pelage tipping is minimal, and the ventral region is usually gray, although white spotting may occur.

The mammary formula is 2 + 2 = 8.

The large skull has prominent supraorbital-temporal and supraoccipital ridging on large specimens that rises to 1.5 mm. above the skull surface (fig. 13). The rostral region is heavy and the nasal bones flare terminally, but do not overhang appreciably. The incisive foramina are well bowed. The palate terminates about 0.5–1.5 mm. posterior to the molar row. The bullae and the molars are small relative to skull size. The juvenile skull has little ridging, the nasals are less flared, and the incisive foramina are less bowed.

Previous Descriptive Accounts: After Thomas (1922a, 1922c) provided a description of *tramitius, coenorum,* and *bandiculus,* a distinction that reflected so heavily the age differences of this subspecies and, in part, altitudinal variation, Rümmler (1935) added further details when he proposed *utakwa*. It was the first mention of white pectoral spotting, a pelage marking that, although not exclusive to *R. praetor*, is very frequent and geographically widespread in this species. Rümmler (1938) was the first to re-examine and redescribe the types that Thomas (1922a) had proposed and the first to publish photographs of dorsal, ventral, and lateral views of the skulls of the types of *coenorum, utakwa,* and *tramitius*.

Troughton (1946) provided a good description of *sansapor,* and included its mammary formula of 2 + 2 = 8. Tate (1951) redescribed *coenorum* and *tramitius* (=*utakwa*). He demonstrated an appreciation for the size to which *coenorum* can grow, but, also on the grounds of size, retained *tramitius* as a distinct mountain race. He was inconsistent in his handling of *sansapor*. In the text he treated it as a synonym of *jobiensis*. In his table of measurements, however, he listed it as a separate subspecies of *ruber*. This table provides a useful set of measurements of all of the types included here. Laurie's (1952) description of *tramitius* should be discounted here since she was actually including both *hageni* and *mordax* under this name.

REMARKS: *Rattus praetor coenorum* affords a greater opportunity to study ecogeographic changes in both skin and skull features in relation to altitude, than any other *Rattus* in New Guinea. An altitudinally based set of transects on the Nassau Range would offer such an opportunity. No such study has yet been done; the nearest approach is found in a series in the 1938–1939 Archbold Collection taken at several altitudes at Bernhard Camp in which a gradient in characters can be detected. A similar, but much more obvious gradient in these features occurs at the interspecific level in *Rattus,* but in that case the potential of genetic confluence or clinal interchange is lost. An intraspecific study of this large rat is critical to providing the type of information now required at the interpretive level of the systematics of this group. It is essential to obtain adequate measures of informative parameters, the nature of these variations, and their relationships to microclimatic changes in habitat.

HABITS AND HABITAT: This species has been seen to climb over rocks and logs while foraging at the base of trees in the very dry substrate of the Weyland Mountains at 1000 m. (Stein, 1933). Rümmler (1938) stated that it inhabits coastal and mountain rain forest. No other information is available except a photograph of a collecting site (fig. 14).

SYMPATRY: *Rattus praetor coenorum* is sympatric with *Rattus exulans browni* and *Rattus rattus*. At inland and higher elevations, it is also sympatric with *Rattus steini steini* (Bernhard Camp, 850–1200 m.), *Rattus verecundus unicolor* (Kunupi, 1400–1800 m.), and *Rattus niobe arrogans* (Doormanpad-bivak, 1410 m.).

TAXONOMIC HISTORY: Thomas's (1922a) original description of *R. coenorum* was very brief and provided only a few measurements and pelage features. In the same article he also proposed two other new forms, *Rattus mordax tramitius* (BM 22.2.2.13) from Doormanpad-bivak (1410 m.) and *Rattus bandiculus* (BM 22.2.2.22) from the same locality as *R. coenorum*. He did not recognize *R. coenorum,* a young male, and *R. bandiculus,* an old male, as conspecifics; nor did he entertain the view that either resembled *tramitius*. He did, however, liken both *tramitius* and *coenorum* to *mordax*. In his later expanded description of all three forms (Thomas, 1922c) he provided the mammary formula for *coenorum* as 2 + 2 = 8. The holotype of *tramitius* is too young to discern the mammary formula, although he did not mention this point, and the single specimen of *bandiculus* was a male. The extraordinary development of cranial ridges and expanding incisive foramina and the increment in the flaring of the distal rostrum that characterize aging in lowland endemic *Rattus* in New Guinea, misled Thomas into believing that *bandiculus* was another species. He recognized, however, that it was similar in pelage color to older examples of *R. coenorum*.

Rümmler (1935), who had a broad concept of *R. leucopus,* described *Rattus leucopus*

FIG. 14. Habitat of *Rattus praetor coenorum* in interior rain forest of flood plain, 4 km. southwest of Bernhard Camp, 850 m. Photograph taken March 1939, by L. J. Brass on 1938–1939 Archbold Expedition.

utakwa from the south side of the Nassau Range. He chose as holotype, BM 13.6.18.65, a breeding adult male from Utakwa River (Camp 3) at an altitude of 762 m. This may have been one of the specimens from the south side of the Nassau Range that Thomas (1922c) referred to as appearing to belong to *tramitius*. It is unclear whether external measurements were made by the collector on fresh material or later on preserved or dried skins. Rümmler (1935) made no reference to any alliance with *tramitius*. Stein (1933), however, collected one of these rats from the Weyland Mountains at 1000 m., and identified it as *R. coenorum*, and Tate (1936) identified a specimen from Wasior in the same general region, as *R. coenorum*.

Rümmler (1938) placed *tramitius, coenorum,* and *utakwa* all as subspecies in his large *Stenomys leucopus,* and synonymized *bandiculus* with *coenorum*. He also thought that the specimens identified by Rothschild and Dollman (1933) as *tramitius* were specimens of *coenorum*. He provided the mammary formula for *tramitius* (2 + 2 = 8) in this work.

Sody (1941) objected to Rümmler's use of *Stenomys* for rats with a mammary formula of 2 + 2 = 8, and placed both *tramitius* and *coenorum* in *Rattus mordax*. He identified specimens from Hollandia and from all of northern New Guinea as *coenorum*.

Ellerman (1941) included *tramitius, coenorum* (=*bandiculus*), and *utakwa* all under *Rattus leucopus*.

Troughton (1946) proposed a new species, *Rattus sansapor* (holotype, AM M7195) from sea level in the Vogelkop region. Although his description was based upon an adult male and a younger male paratype, he was able to provide the mammary formula of 2 + 2 = 8 from other material. Troughton stated that it had the body dimensions of *coenorum* but the cranial dimensions of *bandiculus*. Apparently, he continued to regard these as different species, and this was probably what he had in mind when establishing *sansapor* as yet another species.

In his monographic revision of the rodents, Ellerman (1949) treated *tramitius, coenorum,* and *utakwa* all as subspecies of *Rattus ringens*. Thus, except for the species nomenclature, his view of these groups remained essentially unchanged. He made no mention of *sansapor*.

Tate (1951) included *tramitius* and *coenorum* under *Rattus ruber*. He synonymized *utakwa* with *tramitius,* and *sansapor* with *R. jobiensis* as *Rattus ruber jobiensis*. Included in his *jobiensis* were specimens from Sansapor and also from Wasior that Tate (1936) had earlier identified as *coenorum*. In the membership of *coenorum,* he placed five rats from 1200 m. and 1500 m. near Bernhard Camp, that we have re-examined and have identified as *Rattus steini steini*.

Laurie (1952) expanded Tate's (1951) view of *tramitius* and included not only *utakwa* but also *hageni* as *Rattus ruber tramitius*. This new synonymy followed a suggestion made by Tate (1951) that *hageni* might be a synonym of *tramitius,* although he had not formally endorsed such a move. When Laurie proposed this synonymy, she identified 19 specimens as *tramitius,* all of which belong to other groups. The 12 specimens from Saiko and the one from Boneno are *R. m. mordax*. The specimen from Enaena (BM 47.1156) is a skin of *R. m. mordax* mismatched with a skull of *R. v. verecundus*. The remaining five are *Rattus steini hageni*.

Laurie and Hill (1954) perpetuated this unfortunate synonym proposed by the senior author. They recognized *tramitius* and *coenorum* as subspecies of *Rattus ruber,* and concurred with Tate (1951) that *sansapor* was a synonym of *Rattus ruber jobiensis* (see Taxonomic History of *Rattus jobiensis*). Lidicker and Ziegler (1968) followed Laurie and Hill (1954) in their use of *tramitius,* but they were wary about the species boundaries of these rats. In consequence, they synonymized their *hageni* material under *tramitius*.

We have synonymized *tramitius, bandiculus, utakwa,* and *sansapor* with *coenorum* and treat them as a single subspecies. This, like *R. p. praetor,* may prove to be more than a single taxon, but the material is not yet adequate to justify separation. Of the two available names proposed in the same work, *coenorum* and *tramitius,* we select *coenorum* from a lowland locality as it better rep-

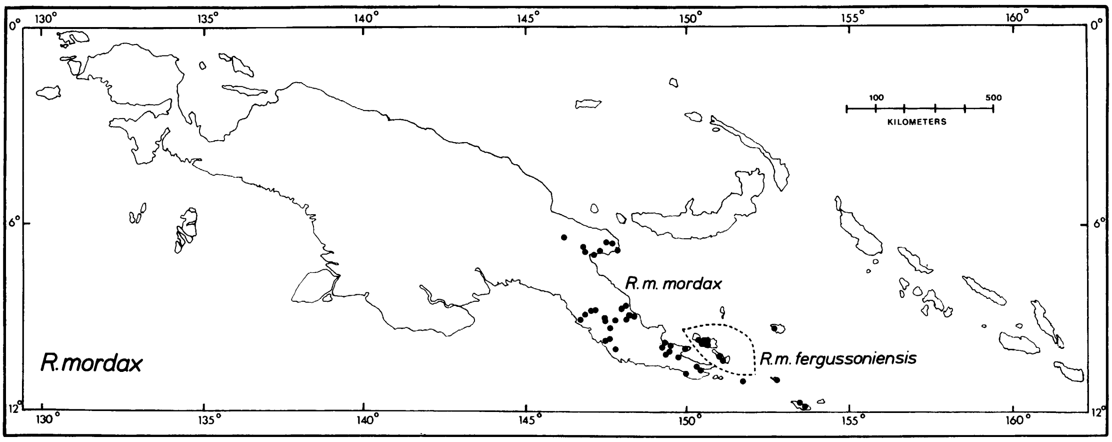

FIG. 15. Distribution map of *Rattus mordax*. Locality records for each of the two subspecies are indicated by dots.

resents the popular view that *praetor* in New Guinea is a large, spiny lowland species.

Rattus mordax (Thomas)

DISTRIBUTION: Southeastern New Guinea on both sides of the Owen Stanley Range, from Baroka on the west coast and north to the tip of the Huon Peninsula. The distributional gap along the coastal lowlands between the Huon Peninsula and southeastern Papuan occurrences is probably due to lack of collecting; we lack records of any species of *Rattus* along this coastal gap. Insular distribution of *R. mordax* is in the D'Entrecasteaux Islands, Louisiade Archipelago, and Woodlark Island in the Trobriand group. Altitudinally from sea level to 1000 m. except in the Owen Stanley Range where it extends to 2750 m. along semicleared tracks (fig. 15).

GENERAL DESCRIPTION: The two subspecies of *R. mordax* are large lowland rats with spinous pelage. The pelage is a deep rust brown and typically grizzled due to the tipping of yellowish brown both on regular hairs and on spines. Adults from sea level are usually larger and more spinous than those from higher elevations. The ears and tail are medium brown and are sparsely haired. The ventral pelage is a dull cream with the gray underfur providing a somber background to the lighter coloration. The ventral pelage may or may not possess spines and, if so, they are relatively soft and flexible. Frequently, a red-brown area occurs in the chin and anterior pectoral region. Some investigators (i.e., Tate, 1951) attribute this to food stain. The feet are clothed in short brownish hairs. White pectoral spotting, such as occurs in *R. praetor,* is very infrequent in this species.

The broad massive skull is very distinctive, particularly since the conspicuous supraorbital-temporal ridging develops a lateral projection at the posterior supraorbital region in mature specimens that is unique to this species of New Guinean *Rattus* (fig. 16). The incisive foramina are narrow and straight-sided on all but old specimens. The foramina tend to bow as the rat ages. The nasals flare terminally and usually end in line with the anterior incisive foramina or overhang slightly. The bullae are relatively small, and the molars are heavy and broad.

DIAGNOSTIC CHARACTERS: *Rattus mordax* is most frequently confused with another large, spinous lowland rat, *R. praetor.* The two species are allopatric. *Rattus praetor* is basically northern and western in distribution, and *R. mordax* is its southeastern counterpart. Both species have representation both on the mainland of New Guinea and on archipelago systems. *Rattus mordax* is a smaller rat that is most readily separated

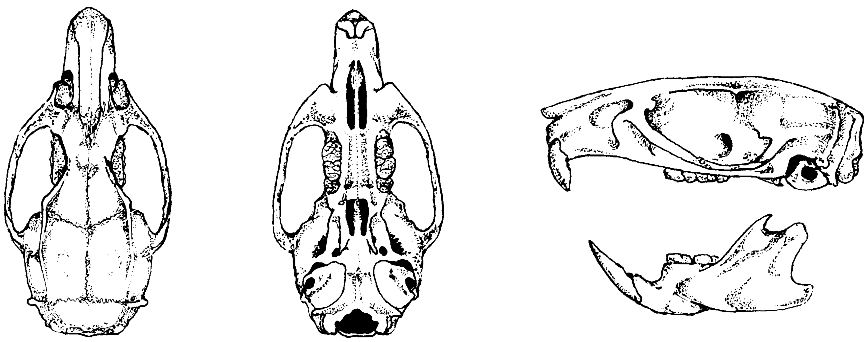

FIG. 16. Dorsal, ventral, and lateral views of skull of adult *Rattus mordax mordax*, AMNH 158038, from Gwariu River. Occipitonasal length 42.8 mm.

from *R. praetor* by its posterior supraorbital lateral projections and by the narrower and more straight-sided incisive foramina. *Rattus mordax* is sympatric with *R. l. dobodurae* which it resembles in skin characters of dry specimens. *Rattus mordax* has a relatively shorter and plain brown tail, it is not as light ventrally, and the mammary formula is higher. The skull of *R. mordax* is distinguished from that of *R. l. dobodurae* by its smaller bullae, narrower incisive foramina, configuration of supraorbital-temporal ridging, wider molars, and lack of appreciable nasal overhang. It is readily distinguished from a third lowland rat, *R. s. gestri,* by its smaller bullae, lighter pelage, and lower mammary formula.

TAXONOMIC HISTORY: This species was described by Thomas (1904a) on the basis of a single complete specimen that he designated holotype and an incomplete skull. He also included a specimen from the Conflict Islands. Thomas allied his new species most strongly with *Mus praetor* from the Solomon Islands that he had described 16 years earlier. Later, he (Thomas, 1916) transferred *mordax* to the genus *Rattus*. As mentioned previously, Thomas (1922a) described a new subspecies, *R. mordax tramitius,* from western New Guinea, but this is a form of *R. praetor*. Tate (1936) regarded *mordax* as a subspecies of *R. ringens*.

Troughton (1937) described another subspecies, *R. mordax hageni,* from the highlands but this is a form of *R. steini* (see later). Rümmler (1938) placed *mordax* as a subspecies of his very diverse species, *Stenomys leucopus*. Sody (1941) did not support this view and considered *mordax* a full species (of *Rattus*), with *coenorum* (=*R. praetor coenorum*) as a subspecies.

Ellerman (1941) followed Rümmler and treated *mordax* as a subspecies of *leucopus,* using *Rattus* as the genus, but later (Ellerman, 1949) placed it as a subspecies of *ringens*. Troughton (1946) argued strongly in support of recognizing *mordax* as a full species distinct from *leucopus* or *ringens*.

In his major revision, Tate (1951) admitted his earlier (1936) mistake of associating *mordax* with *ringens* and *leucopus,* and placed it under *R. ruber* (see Taxonomic History of *R. praetor*). He suggested that it may extend into northeast New Guinea away from the coast. No reference localities are provided which would allow the determination of the region to which he refers, except the eastern end of the Central Range between 150 and 600 m. Laurie and Hill (1954) followed Tate's treatment of *mordax*.

A new subspecies was described by Laurie (1952) from Faralulu, Fergusson Island, which she called *R. ruber fergussoniensis*. She allied it most closely to *R. ringens feliceus* and *R. ringens coenorum* (of Ellerman's 1949 classification).

We recognize two subspecies of *Rattus mordax, R. m. mordax* and *R. m. fergussoniensis*.

TABLE 11

Measurements (in Millimeters) of Adult *Rattus mordax mordax*

(N = 119 for skin measurements; N = 101 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	176.0 ± 1.64	17.91	142.0–254.0
Tail length	147.0 ± 1.28	14.00	115.0–203.0
Hind foot (s.u.) length	35.3 ± 0.27	2.97	28.0–44.0
Occipitonasal length of skull	42.0 ± 0.26	2.65	37.4–48.7
Condylobasal length	40.0 ± 0.27	2.69	35.0–47.1
Basal length	37.4 ± 0.26	2.60	32.5–44.2
Zygomatic width	21.0 ± 0.13	1.28	18.3–25.5
Interorbital width	6.0 ± 0.03	0.33	5.2–7.1
Interparietal length	4.6 ± 0.05	0.52	3.5–6.1
Interparietal width	10.3 ± 0.08	0.83	7.5–12.3
Braincase width	16.9 ± 0.07	0.69	15.2–18.4
Mastoid width	14.5 ± 0.06	0.65	13.2–16.0
Nasal length	15.6 ± 0.12	1.22	13.0–19.7
Nasal width	4.6 ± 0.04	0.43	3.8–5.9
Palatal length	23.1 ± 0.15	1.52	20.0–26.6
Incisive foramen length	7.3 ± 0.07	0.72	5.8–9.0
Incisive foramina width	2.3 ± 0.04	0.41	1.3–3.5
Inside m^{1-1} width	3.6 ± 0.05	0.51	2.4–5.1
Outside m^{1-1} width	9.2 ± 0.05	0.50	7.8–10.4
Bulla length	6.2 ± 0.04	0.37	5.5–7.1
Crowns m^{1-3} length	6.9 ± 0.04	0.38	5.8–7.8
Alveoli m^{1-3} length	7.4 ± 0.04	0.40	6.3–8.3
Crowns m^{1-2} length	5.5 ± 0.04	0.36	4.4–6.6

Rattus mordax mordax (Thomas)

Mus mordax Thomas, 1904a, p. 398.
Epimys mordax: Thomas, 1910b, p. 605.
Rattus mordax: Thomas, 1916, p. 240.
Rattus ringens mordax: Tate, 1936, p. 205.
Stenomys leucopus mordax: Rümmler, 1938, p. 186.
Rattus leucopus mordax: Ellerman, 1941, p. 205.
Rattus ruber mordax: Tate, 1951, p. 333.

HOLOTYPE: Skin and incomplete skull with hind skull missing, old adult female, BM 4.8.3.1, collected 14 November 1903, by C. A. W. Monckton, 08°30′ S, 148°20′ E, Papua New Guinea, 172 m. As discussed by Tate (1951) the accuracy of the type locality is in doubt, but is probably the middle reaches of the Kumusi River. Monckton published three volumes of reminiscences but gave no details, although in one of these books (Monckton, 1922) he reprinted Thomas's original description.

DISTRIBUTION: *Rattus mordax mordax* occurs from the tip of Huon Peninsula southward in lowland areas to the southeastern tip of the mainland of New Guinea, and up the west side to the vicinity of Baroka. It also occupies lower portions of the Owen Stanley Range away from the coast. It is recorded from sea level to 2750 m.; most records are below 600 m. It is also recorded from the islands of the Louisiade Archipelago, and Woodlark Island of the Trobriand group from sea level to 350 m. (fig. 15).

MEAN MEASUREMENTS (IN MM.): External: head and body 176; tail 147; hind foot (s.u) 35.3. Skull: occipitonasal length 42.0; braincase width 16.9; bulla length 6.2; crowns m^{1-3} length 6.9. (See table 11 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 37.5 or less.

DESCRIPTION: This is a large, dark brown rat with grizzled fur due to the buff or rufous brown tipping of the pelage. Coarse translucent spines are prevalent in the dorsal pelage. The dorsal hair is about 20 mm., of which the basal portion is slate gray and the terminal 3 mm. is buff or brown. The black guard hairs measure to 25 mm. The ears are medium brown and finely haired. Muzzle vibrissae measure to 50 mm. The pelage blends laterally into the lighter ventral fur. The ventral pelage may or may not contain spines. The ventral color is yellowish ivory with the medium gray underfur showing beneath. The hairs are about 10 mm. long and are usually ivory to the base, or may be steel gray basally. A rufous-colored area may be present in the throat region. The tail is dark brown, lightly covered by brown hairs up to 2.5 mm. long, and there are 7–8 scale rows per cm. The feet are usually brown dorsally and are covered by a mixture of buff and brown hairs although they may be lighter and covered by cream-colored hairs.

Juveniles have a soft non-spinous fur with rufous ticking dorsally. The pelage is considerably darker than that of adults. The ventral pelage is dull gray with cream ticking. Except for the darker body pelage, the juvenile coloration is similar to that of the adult.

The wide heavy skull is distinguished most readily on larger adults by the slight lateral projection of the posterior supraorbital ridging (fig. 16). This ridging is less developed in younger specimens and the projection is not apparent. Supraorbital ridging measures to 1 mm. in elevation on larger specimens. The incisive foramina are typically narrow and straight-sided, but not as narrow as those of *R. sordidus gestri*. The palate terminates about 1 mm. posterior to the molar row. The molars are relatively wide. The nasals are somewhat flared distally and overhang the rostral area slightly. The zygomata are heavy and broad, the rostrum is relatively short, and these features give the skull the appearance of being compact and wide. The bullae are relatively small. The juvenile skull lacks supraorbital ridging, or it is only minimally developed, and the incisive foramina are very narrow.

PREVIOUS DESCRIPTIVE ACCOUNTS: Prior to his recognition of *mordax* as a distinct species, Thomas (1897) had identified two rats from Haveri as *Mus praetor*; however, in 1904 he proposed *Mus mordax* as a new species and provided a full description. He made a careful comparison between it and another large rat, *Mus praetor,* to which he thought it might be allied. Thomas (1904a) gave the mammary formula as 2 + 2 = 8. Le Souef and Burrell's (1926) brief description is a rewording of the original.

Tate (1936) provided skin and skull measurements of additional specimens and illustrated the skull in ventral (Tate, 1936, fig. 3B) and lateral (*ibid.,* fig. 4B) views. Five of the rats identified as *praetor,* and for which he gave measurements (AMNH 104228–30, 104232–33), are *R. mordax* (*ibid.,* p. 662).

Rümmler (1938) added further details to the description of *mordax* as a member of *Stenomys leucopus*. He photographed dorsal, ventral, and lateral views of the type skull (Rümmler, 1938, Pl. IX, Illus. 3). The photograph shows that a portion is missing from the hind skull. This fragment seems to have been missing at the time Thomas (1904a) first described it, for he gives no full length measurements. The teeth are well worn on this skull and it is that of a fully adult female [not a young adult, as Troughton (1937) suggested]. In most *mordax* the incisive foramina are almost parallel-sided, a feature pointed out in the original description. Rümmler (1938) made an important observation when he realized that with increasing age of adult *mordax* these foramina gradually widen and the parallel nature of their boundaries becomes less conspicuous. The type skull is such an example. This feature of the type is, undoubtedly, responsible for assessments that link *mordax* and *praetor* (or "*ruber*") as conspecific.

Troughton (1946) prepared a brief key to distinguish *mordax* from *ringens* (=*leucopus*). Tate (1951) provided additional measurements of specimens and a brief description. He appears to have been the first to appreciate the range of size among adults of *mordax*.

REMARKS: Some *mordax* are included among rats collected by Shaw Mayer and identified by Laurie (1952) as *R. ruber tramitius*. They are BM 47.1159 from Boneno, BM

FIG. 17. Habitat of *Rattus mordax mordax* in rain forest on Mt. Sisa. Photograph taken July 1956, by L. J. Brass on 1956–1957 Archbold Expedition.

50.1208–10 from Saiko, and a skin of BM 47.1156 (the skull is *R. v. verecundus*) from Enaena.

One feature of this rat that aids in the identification of skin material of both young and adults is the relatively wide hind feet. This feature is particularly helpful in distinguishing *R. s. hageni* from young of *mordax*. The width is relative to body size; thus, direct comparison of comparable body sizes of the two species is necessary to appreciate this feature.

HABITS AND HABITAT: There are no published accounts of the habits and habitat of this subspecies. The information here comes from notes on the collecting labels of specimens. These rats occur in gallery rain forest, kunai grassland, scrub, eucalyptus savannah, and coastal and lake-edge grasslands (fig. 17). They invade native gardens, native houses where they are attracted to stored rice and sweet potato, pastures, and cacao plantations. They are said to feed on fruit in the bush.

SYMPATRY: *Rattus mordax mordax* is sympatric with *Rattus leucopus dobodurae, Rattus exulans browni, Rattus sordidus gestri, Rattus verecundus verecundus, Rattus niobe niobe,* and *Rattus rattus*.

TAXONOMIC HISTORY: Thomas's (1904a) original association of a specimen from the Conflict Islands, Louisiade Archipelago, with his type material of *Mus mordax* from the Kumusi River area, is endorsed by our own assessment of the relationship of these insular and mainland rats. Thomas provided a good description that included the mammary formula. Jentink (1907a) accepted Thomas's proposal and quoted him verbatim. Thomas (1914) subsequently listed 16 specimens from Utakwa River as *mordax*; these were later reidentified and removed from this species (Rümmler, 1935), but not before Longman (1916) and Le Souef and Burrell (1926) included this supposed western record.

Tate (1936) seemed unsure of the limits of *mordax* for he not only placed it as a subspecies of his *R. ringens,* but also identified a group of specimens of *R. mordax* as ?*R. praetor.*

The later assessments of the taxonomic status of *mordax* (Rümmler, 1938; Sody, 1941; Ellerman, 1941, 1949; Troughton, 1946; Tate, 1951; Laurie and Hill, 1954) have been reviewed previously under *R. mordax.*

With the material available, we were unable to distinguish mainland specimens from those from the Louisiade Archipelago and Woodlark Island. The Archipelago is a submerged extension of the Owen Stanley Range (Rumens, 1972). The Woodlark specimens (six adults and two juveniles from Kulumadau) are the most distant geographically from either subspecies of *R. mordax.* Their remote insular distribution is possibly the result of overwater dispersal by human, or other, agency. A pattern of prevailing warm currents moves north-northwestward toward Woodlark Island from the eastern portion of the Louisiade Archipelago (Oceanographic Office, Dept. of the Navy, 1969) in conjunction with the southeasterly trade winds. We do not preclude the possibility that when larger collections are available more than one subspecies may ultimately be recognized among these insular rats.

Rattus mordax fergussoniensis Laurie

Rattus ruber fergussoniensis Laurie, 1952, p. 304.

HOLOTYPE: Skin and complete skull, adult male, BM 50.1211, collected July 31, 1935, by F. Shaw Mayer, at Faralulu district, West Fergusson Island, D'Entrecasteaux group, Papua New Guinea, about 550 m.

DISTRIBUTION: Known only from the D'Entrecasteaux Islands of Fergusson, Goodenough, and Normanby. Records extend from sea level to 900 m. (fig. 15).

MEAN MEASUREMENTS (IN MM.): External: head and body 193; tail 159; hind foot (s.u.) 37.4. Skull: occipitonasal length 46.7; braincase width 17.7; bulla length 6.6; crown m^{1-3} length 7.8. (See table 12 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 40.5 or less.

DESCRIPTION: This subspecies differs from *R. m. mordax* mainly in body size. The larger size is apparent on the three islands from which this subspecies is known, and is in sharp contrast with specimens from the mainland, Woodlark Island, and the Louisiade Archipelago. It is so similar to *R. m. mordax* in most features of the skin and skull that a complete description is unwarranted. This account will be confined to those features that are at variance with the nominate subspecies.

The dorsal pelage is even more densely spinous in large adults and the ventral pelage is also more spinous. Tail scales measure 5–6 rows per cm., and tail hairs measure to 3 mm. The skull looks more elongate due in part to the well developed ridging. The supraorbital-temporal ridging usually rises 1 mm. or more and extends posteriorly to end in line with the interparietal bone. The palate extends 1.5 mm. posterior to the molar row.

PREVIOUS DESCRIPTIVE ACCOUNTS: Laurie (1952) provided a brief description and measurements of the type and paratype of *R. ruber fergussoniensis.* This is the only description that has been published. Dennis and Menzies (1978) prepared a karyotype of *R. m. fergussoniensis* from Fergusson Island which they identified as *Rattus ruber* (UPNG 938). They state that the karyotypes of all their *R. ruber,* both highland and lowland, were identical.

REMARKS: The last major sea level rise, which was of the magnitude of 180 m., occurred within the past 10,000–15,000 years (Galloway and Löffler, 1972). As the sea rose, most of the eastern extremity of the Owen Stanley Range was submerged, and the exposed peaks are now represented by the Louisiade Archipelago (Rumens, 1972). A wide platform less than 200 m. below sea level exists today between the Louisiade Archipelago and the mainland (Ryan, 1972). One far more restricted in extent and deeper

TABLE 12

Measurements (in Millimeters) of Adult *Rattus mordax fergussoniensis*

(N = 15 for skin measurements; N = 10 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	193.3 ± 6.84	26.48	153.0–239.0
Tail length	158.7 ± 4.21	16.29	135.0–194.0
Hind foot (s.u.) length	37.4 ± 0.47	1.81	35.0–41.0
Occipitonasal length of skull	46.7 ± 1.15	3.64	41.0–51.9
Condylobasal length	44.6 ± 1.23	3.89	38.3–49.9
Basal length	41.8 ± 1.21	3.84	35.4–46.7
Zygomatic width	23.0 ± 0.54	1.70	20.6–25.0
Interorbital width	6.4 ± 0.12	0.39	5.7–7.0
Interparietal length	5.3 ± 0.17	0.54	4.6–6.2
Interparietal width	11.0 ± 0.36	1.15	8.7–12.4
Braincase width	17.7 ± 0.20	0.63	16.8–18.8
Mastoid width	15.4 ± 0.29	0.91	14.0–17.2
Nasal length	17.5 ± 0.51	1.62	15.4–19.8
Nasal width	5.2 ± 0.23	0.72	4.3–6.0
Palatal length	25.8 ± 0.66	2.08	22.4–28.5
Incisive foramen length	8.4 ± 0.19	0.61	7.4–9.3
Incisive foramina width	3.0 ± 0.12	0.37	2.1–3.5
Inside m^{1-1} width	4.2 ± 0.20	0.64	3.1–5.3
Outside m^{1-1} width	10.1 ± 0.27	0.85	8.8–11.6
Bulla length	6.6 ± 0.14	0.45	6.0–7.4
Crowns m^{1-3} length	7.8 ± 0.19	0.59	6.9–8.8
Alveoli m^{1-3} length	8.4 ± 0.22	0.70	7.6–9.7
Crowns m^{1-2} length	6.1 ± 0.15	0.48	5.3–6.8

(200–1000 m.) occurs between the D'Entrecasteaux Islands and the mainland (*ibid.*). This deeper channel indicates that the D'Entrecasteaux Islands have probably been separated from the mainland for a greater length of time than has the Louisiade chain. This longer period of isolation appears to have created the opportunity for evolutionary radiation of the D'Entrecasteaux *mordax* from mainland populations to the extent of recognition as a distinct subspecies.

Habits and Habitat: Almost nothing has been published about the habits and habitat of this subspecies and specimen labels of the material we examined lacked such information. Brass (1959) mentions collecting "*Rattus ruber*" in the low mossy scrub of Mt. Pabinima, Normanby Island, and in oak forest and savannas on Fergusson Island.

Sympatry: *Rattus mordax fergussoniensis* is sympatric with *Rattus exulans browni.*

Taxonomic History: Specimens from Fergusson Island had been collected in 1935, but they were not described as a new subspecies until 1952 when Laurie proposed *Rattus ruber fergussoniensis.* Although she described the straight and narrow incisive foramina, so characteristic of *mordax,* she assessed *fergussoniensis* as a close ally of *R. ringens feliceus* from Ceram and of *R. ringens coenorum* from Pionier-bivak, Irian Jaya. She was undoubtedly strongly influenced by their common features of large size and spinous pelage. Her identification in the same paper of some *R. m. mordax* specimens as *R. ruber tramitius* suggests that her concept of the species *mordax* was unclear. Laurie and Hill (1954) refer to *fergussoniensis* as *R. ruber fergussoniensis* and this appears to be the last reference of taxonomic significance in the literature.

We regard *R. m. fergussoniensis* as a distinct subspecies that is primarily distinguished on the basis of size. Although size alone can be an expression of seasons of collecting, the fact that at the same time of year

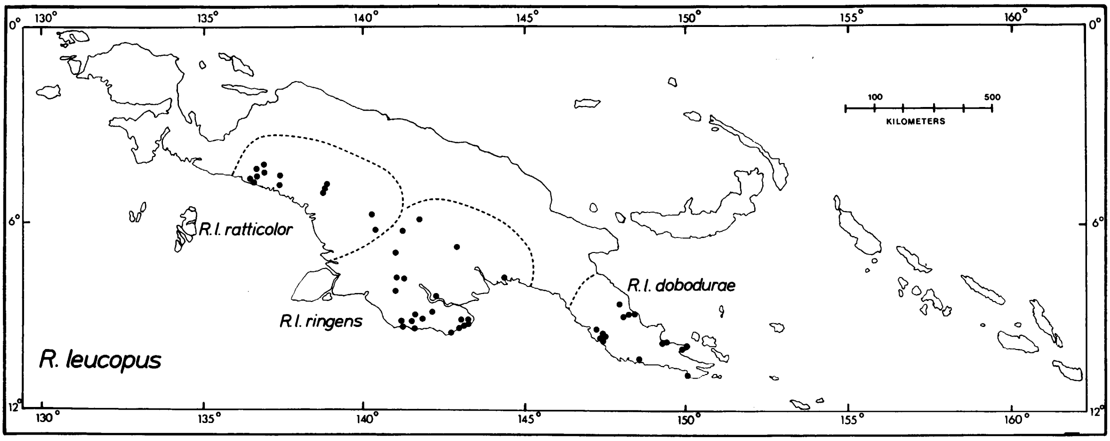

FIG. 18. Distribution map of *Rattus leucopus* in New Guinea. Locality records for each of the three subspecies are indicated by dots.

the specimens from these islands are consistently larger than either those collected from the Louisiade Archipelago or from the mainland (1953 and 1956 Archbold Expeditions) lends credibility to the recognition of the size difference as a genuine one that reflects genetic difference. Because both are primarily lowland forms, the influence of altitude is not a factor here. It is on this basis that we justify our recognition of *fergussoniensis* as a distinct subspecies of *R. mordax.*

Rattus leucopus (Gray)

DISTRIBUTION: Widespread in the southern half of New Guinea, generally south of the Central Highlands and at altitudes ranging from sea level to 900 m. In the west inhabits the lowland region south of the Snow Mountains, from 136° E eastward to 144° E. A break occurs in its known distribution east of this point until it appears again in lowland areas of both south and north coasts that fringe the Owen Stanley Range. On the north coast ranges as far north as 08°30′ S at the Kumusi River (fig. 18).

In Australia occurs only on the eastern half of Cape York, from the apex of the peninsula to about 22° S latitude. Its distribution there is the most limited of any of the native species of *Rattus* on that continent.

GENERAL DESCRIPTION: This species is one of the large lowland rats. The pelage is coarse and spinous dorsally and somewhat spinous ventrally on mature specimens. The dorsum is yellow-brown and the hairs are tipped in a deeper cinnamon brown. Conspicuous dark brown to black guard hairs provide a grizzled appearance to the pelage. A light gray underfur is present both dorsally and ventrally. The ventral pelage is yellowish white or gray with buff tipping. The spines are yellowish white for their entire length. The feet are covered dorsally by dull white hairs, a feature that is acknowledged in the specific name. The hind feet are relatively broad. The dull brown tail is about 20 mm. shorter than the length of the head and body and is usually, but not always, mottled with white or is white distally. The ears are also dull brown and sparsely covered with hair.

The mammary formula is $1 + 2 = 6$ in all three subspecies from New Guinea.

The skull is moderately elongated and the nasals flare slightly and overhang the incisors (fig. 19). The incisive foramina are relatively wide, especially in the mid-region and usually taper slightly as they extend posteriorly. They terminate in line with the occlusal surface of m^1. The palate terminates 1 to 2 mm. posterior to the molar row. Supraorbital-temporal ridging is conspicuous and extends posteriorly to the posterior limit of the parietals. The bullae are unenlarged, and the

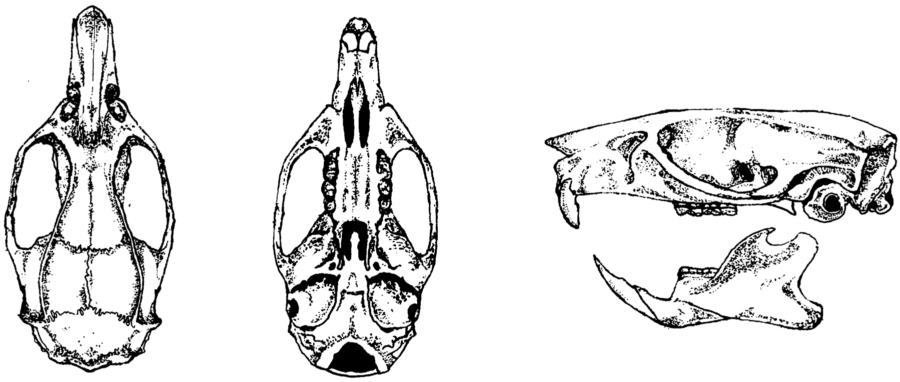

FIG. 19. Dorsal, ventral, and lateral views of skull of adult *Rattus leucopus ringens*, AMNH 105613, from Oroville Camp, upper Fly River. Occipitonasal length 47.8 mm.

molars are distinctly narrower than those of either of the large sympatric species *R. sordidus* and *R. mordax*.

Juveniles can be confused with *R. verecundus*, but several features distinguish them. Usually, by the age at which *R. leucopus* are independent, adult pelage is beginning to erupt and the spinous quality of hair readily separates it from *R. verecundus*. The hind feet are also broader and shorter in *leucopus* of the same head and body length as *R. verecundus*. The molars and rostrum are wider in *R. leucopus*.

DIAGNOSTIC CHARACTERS: The mammary formula separates this species from all other larger *Rattus* of New Guinea except *R. jobiensis* and *R. steini*. No other larger *Rattus* has a white tail tip or conspicuous mottling along the tail. The skull can be distinguished from that of *R. m. mordax*, a sympatric species with which it can be most readily confused, by its wider interorbital breadth, wider incisive foramina, and narrower molars. It can be distinguished from that of *R. jobiensis*, a species often allied to *leucopus*, by less nasal flare and overhang, by shorter incisive foramina, and by relatively larger bullae.

TAXONOMIC HISTORY: The taxonomic history of the Australian subspecies of *R. leucopus* has been reviewed by Taylor and Horner (1973). The species was described by Gray in 1867 from Cape York, Australia, as *Acanthomys leucopus*. When *leucopus* was later placed in *Mus* it became a junior homonym, and a replacement name, *terraereginae*, was introduced by Alston in 1879. In 1920, Thomas transferred the species to *Rattus* and reinstated the name *leucopus* for Australian material, and since then virtually all authors have used that name in preference to *terraereginae*. As a result of applications to the International Commission on Zoological Nomenclature, initially by Calaby, Horner, and Taylor (1966), and later by Ride (1974), the name *leucopus* was validated for this species by the Commission (Melville, 1979). A detailed description of this nomenclatorial problem and the use of the name *leucopus* is given by Calaby, Horner, and Taylor (1966). The two subspecies in Australia were recently assessed by Taylor and Horner (1973) and will not be treated further here.

The first member of this species known from New Guinea was described by Peters and Doria (1881) as *Mus ringens*. Thomas (1897, 1904a) and Jentink (1907a) recognized that *Mus ringens*, in which they included specimens from the region occupied by the later-described *R. leucopus dobodurae*, was conspecific with *R. leucopus*, then known as *Mus terraereginae*. In 1908 Jentink described a new species, *Mus ratticolor*, based upon a single juvenile female, which he viewed as distinct from adults from the same locality that he identified as *Mus terraereginae*. Thomas (1914) regarded *ratticolor* and New Guinean *terraereginae* as synonymous and included both under *Epimys ringens* for, by then, he considered *terraereginae* of Australia as a distinct species. Longman (1916) followed this recommendation.

Thomas (1920) reintroduced the name *leucopus* for Australian rats, but continued to regard the New Guinean representative, *ringens,* as a distinct species, and both Le Souef and Burrell (1926) and Tate (1936) agreed. Tate (1936) thought that *mordax* should probably be regarded as a subspecies of *R. ringens.* This was the first in a series of inclusions of other species groups within *ringens.*

Rümmler (1935), who treated *ringens* under *R. leucopus,* described three new rats, *utakwa, steini,* and *jobiensis,* as subspecies of *R. leucopus.* He then (Rümmler, 1938) transferred *leucopus* from *Rattus* to *Stenomys,* and placed 10 named subspecies from New Guinea plus one unnamed questionable subspecies under *S. leucopus,* as follows: *ringens, ratticolor, utakwa* (=*R. p. coenorum*), *steini* (=*R. steini*), *jobiensis* (=*R. jobiensis*), *mordax* (=*R. m. mordax*), *coenorum* (=*R. p. coenorum*), *tramitius* (=*R. p. coenorum*), *ruber* (=*R. nitidus*), *praetor* (=*R. p. praetor*), and a doubtful subspecies from the Aru Islands. Ellerman (1941) followed Rümmler's subspecific treatment but retained *leucopus* in *Rattus.* Later, Ellerman (1949) restricted the name *leucopus* to Queensland rats, and transferred all New Guinean forms listed above, except *R. ruber,* to *R. ringens.* At the same time he moved *R. ringens,* but not *R. leucopus,* to the subgenus *Stenomys.*

Troughton (1946) described a new subspecies, *R. ringens dobodurae,* from southeastern New Guinea. In the same paper he stated that *mordax* should be regarded as a distinct species and that Tate (1936) was in error in including it under *ringens.* He also expressed the view that Rümmler's inclusion of *mordax* and *ringens* under the genus *Stenomys* was unwarranted, as was Ellerman's (1941) inclusion of both under *R. leucopus.* Tate (1951) accepted the removal of *mordax.* He treated the group under *R. leucopus* and in it included as subspecies *ringens* (with *ratticolor* as a synonym), *dobodurae, owiensis,* and *doboensis* (tentatively), as well as three from Queensland. More than one species has been included in *owiensis* and *doboensis* (see Taxonomic Histories of *R. praetor, R. exulans,* and *R. rattus*). *Rattus owiensis* is not a form of *leucopus* at all, and Tate's conception of *doboensis* includes representatives of *ringens* from the Western Province of Papua New Guinea as well as another species.

Laurie and Hill (1954) followed Ellerman (1949) to some extent, but included even more subspecies, all of which they placed in *R. ruber,* a name that has priority over *ringens.* Laurie and Hill's (1954) conception of the subgenus *Stenomys* included both *R. ruber* and several other species from New Guinea, Moluccas, and Sulawesi. They removed both *doboensis* and *owiensis* from their *R. ruber,* although they considered *doboensis* as a possible subspecies. They then included all the subspecies which Ellerman (1949) had placed under *ringens,* except that they synonymized *ratticolor* under *R. ruber ringens* and, in addition, included *mediocris, rosalinda, dobodurae, purdiensis, fergussoniensis,* and described a new subspecies *R. ruber melanurus* (see Taxonomic Histories of *R. praetor, R. steini, R. mordax,* and *R. giluwensis* for discussions of these taxa). There have been no further revisions of this large group of forms. By now, *R. leucopus* has become such a composite of species that it warrants detailed revision.

We recognize three subspecies of *R. leucopus* in New Guinea, *R. l. ringens, R. l. ratticolor,* and *R. l. dobodurae.*

Rattus leucopus ringens (Peters and Doria)

Mus ringens Peters and Doria, 1881, p. 700.
Mus terraereginae Jentink, 1908, p. 7.
Epimys ringens: Thomas, 1914, p. 319.
Rattus ringens: Thomas, 1920, p. 424.
Stenomys leucopus ringens: Rümmler, 1938, p. 183.
Rattus leucopus ringens: Ellerman, 1941, p. 204.
Rattus ringens ringens: Ellerman, 1949, p. 69.
Rattus ruber ringens: Laurie and Hill, 1954, p. 110.

TABLE 13

Measurements (in Millimeters) of Adult *Rattus leucopus ringens*

(N = 97 for skin measurements; N = 97 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	168.8 ± 1.60	15.80	142.0–215.0
Tail length	151.6 ± 1.25	12.26	126.0–195.0
Hind foot (s.u.) length	35.6 ± 0.24	2.32	32.0–44.0
Occipitonasal length of skull	41.6 ± 0.25	2.42	37.5–48.4
Condylobasal length	39.1 ± 0.25	2.42	35.3–45.7
Basal length	36.2 ± 0.24	2.39	32.4–42.8
Zygomatic width	20.0 ± 0.13	1.24	17.8–23.3
Interorbital width	6.2 ± 0.04	0.38	5.5–7.1
Interparietal length	5.2 ± 0.06	0.56	3.9–6.6
Interparietal width	10.7 ± 0.08	0.81	7.9–12.5
Braincase width	16.8 ± 0.07	0.69	15.2–18.8
Mastoid width	14.1 ± 0.06	0.63	13.0–16.6
Nasal length	15.2 ± 0.11	1.10	13.3–18.7
Nasal width	4.5 ± 0.04	0.38	3.9–5.9
Palatal length	22.1 ± 0.15	1.44	19.5–25.9
Incisive foramen length	6.9 ± 0.07	0.66	5.3–8.3
Incisive foramina width	2.8 ± 0.04	0.36	2.0–3.7
Inside m^{1-1} width	4.0 ± 0.04	0.43	2.9–5.1
Outside m^{1-1} width	8.7 ± 0.05	0.53	7.6–10.1
Bulla length	6.6 ± 0.04	0.38	5.9–7.7
Crowns m^{1-3} length	6.6 ± 0.04	0.38	5.6–7.5
Alveoli m^{1-3} length	7.0 ± 0.04	0.38	5.9–8.0
Crowns m^{1-2} length	5.4 ± 0.04	0.38	4.5–6.5

HOLOTYPE: Dry skin (prepared from alcohol in June 1937) and incomplete skull, adult female, MCSN MSNG3460, collected by L. M. D'Albertis, Fly River, Papua New Guinea, 100 m. or less.

DISTRIBUTION: Known from the central lowlands of southern New Guinea, from Eramboe eastward to Aird Hills; ranges inland to the upper Fly River and the lower elevations of Mt. Bosavi. Distributed in lowland areas from sea level to 900 m. (fig. 18).

MEAN MEASUREMENTS (IN MM.): External: head and body 169; tail 152; hind foot (s.u.) 35.6. Skull: occipitonasal length 41.6; braincase width 16.8; bulla length 6.6; crowns m^{1-3} length 6.6. (See table 13 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 38.0 or less.

DESCRIPTION: The pelage is moderately coarse and spinous. The spines are very dense but are sufficiently pliable that the pelage can be bent in reverse to its direction of growth. Dorsal coloration is a combination of rust and yellow-brown with a mixture of long deep brown to black guard hairs. Dorsal pelage, composed mainly of spines, is 15–20 mm. in length, of which the terminal 3–5 mm. is rust color or yellow-brown. The spines are translucent or grayish basally and frequently have a subterminal band of dark brown. The guard hairs are particularly conspicuous in the rump region where they measure to 45 mm. Woolly grayish underfur is inconspicuous both dorsally and ventrally. The ears are dull medium brown and lightly haired, and the muzzle vibrissae measure to 65 mm. The ventral pelage is cream to the base except for the inconspicuous gray underfur. It consists of coarse hair and fine spines measuring to 12 mm. long. A reddish brown pectoral area may be present. The medium brown tail has 9–10 scales per cm., short self-colored hairs, and is usually white terminally or has a white band about midway along its length. It may be mottled, however, or in a few instances may lack white marking altogether. The feet are clothed dorsally by dull white hairs.

The juvenile pelage is medium or dark brown dorsally with a slight tipping of rust. It is soft and is without spines, or spines are just beginning to erupt. This pelage lacks the warmth of color of the adult. The ventral pelage is either pure white or a mixture of white and gray. The feet are covered dorsally by white hairs, and white markings, if present, are conspicuous on the tail.

The skull is moderately elongate due to a relatively long rostrum and narrow cranial region (fig. 19). The incisive foramina are expanded laterally and in many cases remain expanded to their posterior termination. Larger individuals tend to have more expanded foramina. They terminate in line with the most anterior root of m^1. The palate terminates well behind the molar row, usually 2–3 mm. posterior to the molars. Supraorbital-temporal ridging is distinct and becomes very prominent on larger skulls. It curves laterally as a smooth beading from the anterior supraorbital region and along the parietals to their posterior extent. Occasionally, the beading forms a slight dorsolateral thickening at the junctures of the interorbital and parietals, but it is rarely pronounced. The nasals expand moderately at the anterior portion and project beyond the premaxillaries about 1 mm. The bullae are moderately inflated (18.2 percent of the basal length). The molars are narrow.

The juvenile skull has relatively narrower incisive foramina, a proportionately expanded cranium, and no development of supraorbital beading.

PREVIOUS DESCRIPTIVE ACCOUNTS: Descriptions of the morphology of *R. l. ringens* have been given by Peters and Doria (1881), Tate (1936), and Rümmler (1938). Tate (1951) included *ratticolor* under *ringens,* but described the holotypes separately.

The mammary formula was provided in the original description (Peters and Doria, 1881). We have found no exception. Peters and Doria (1881) prepared their description from a single specimen and thus had no basis for evaluation of morphological variation of this subspecies. They remarked upon the yellow bands along the tail, a feature common to all subspecies of *R. leucopus*; however, it may be absent, and hence is not a completely reliable character.

Although their measurements do not support their statement, Peters and Doria (1881) claimed that the tail was the length of the body (=head and body). Tate (1936) stated that the tail was either longer or shorter than the head and body in his *R. ringens* Group. Although he was including the shorter tailed *mordax* in this Group, his table of measurements of *R. ringens ringens* (that excludes *mordax*) reveals that all specimens from near the type locality have shorter tails. Our analysis of 60 specimens confirms this point. This feature contrasts with the Australian subspecies of *R. leucopus* in which the tail is approximately equal to, or slightly longer than, the head and body (Taylor and Horner, 1973).

REMARKS: *Rattus leucopus ratticolor* has been synonymized under *R. l. ringens,* and specimens from the range of the later described *R. l. dobodurae* have also been placed in *R. l. ringens* (e.g., Thomas, 1904a; Jentink, 1907a). Part of the confusion rests upon the fact that the holotype of *ratticolor* was juvenile, and at the time of its description (Jentink, 1908) adults of *ratticolor* were identified as *Mus terraereginae* under which *R. ringens* was synonymized (Jentink, 1907a). Our comparison of adults of *ringens* and *ratticolor* reveals that *ringens* is a smaller subspecies, more likely to have a mottled tail, and is widely sympatric with another common lowland species, *R. s. aramia,* a rat that appears to be ecologically excluded from *ratticolor* habitat farther west.

The holotype of *ringens* is badly faded from long alcohol immersion. The skull is damaged for the right zygoma is missing, the palate is largely gone, the left bulla and most of the right are missing, and the occipital bone and foramen magnum are missing. Supraorbital ridging is pronounced and the molars are very worn and without occlusal patterning. The characters are those of an old individual.

HABITS AND HABITAT: *Rattus leucopus*

FIG. 20. Habitat of *Rattus leucopus ringens* in swampy rain forest inland from lower Fly River and dominated by the large trees, *Erythrina*. Photograph taken in dry season, October 1936, by L. J. Brass on 1936–1937 Archbold Expedition.

ringens is primarily a rat of the forest, both dense rain forest and river edge bush (fig. 20). It is a widespread inhabitant of lowland situations that include lower montane slopes. This information is obtained solely from notes on specimen labels.

SYMPATRY: *Rattus leucopus ringens* is sympatric with *Rattus sordidus aramia, Rattus steini hageni* (Mt. Bosavi), and *Rattus rattus*.

TAXONOMIC HISTORY: *Mus ringens* was the first indigenous species that is now included in *Rattus* to be described from the New Guinean region although it was known previously from Australia under other names. The taxon *ringens* soon came to include all *leucopus* (=*terraereginae*) from New Guinea, and its original geographic restriction to southwestern Papua and southeastern Irian Jaya became obscured. Thomas (1914) synonymized *ratticolor* with *ringens,* a move that was not generally accepted until the time of the studies of Tate (1951) and Laurie and Hill (1954).

As recently as 1954, Laurie and Hill included rats from Japen Island under their *R. ruber ringens* (see Taxonomic History of *R. jobiensis*). Tate (1951) tentatively placed series from localities occupied by both *R. l. ringens* and *R. l. ratticolor* under *R. l. doboensis*. The type of *doboensis,* which Tate did not examine, is a *R. rattus* from Dobo,

TABLE 14
Measurements (in Millimeters) of Adult *Rattus leucopus ratticolor*
(N = 38 for skin measurements; N = 40 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	211.0 ± 3.27	20.13	170.0–250.0
Tail length	178.8 ± 2.97	18.32	135.0–218.0
Hind foot (s.u.) length	41.7 ± 0.38	2.31	37.5–47.0
Occipitonasal length of skull	48.5 ± 0.48	3.02	39.6–54.2
Condylobasal length	46.1 ± 0.52	3.28	36.7–52.4
Basal length	42.9 ± 0.53	3.34	33.9–48.9
Zygomatic width	22.8 ± 0.26	1.67	18.4–25.9
Interorbital width	7.2 ± 0.07	0.47	6.3–8.2
Interparietal length	6.0 ± 0.11	0.68	4.9–7.6
Interparietal width	11.2 ± 0.17	1.10	7.2–12.9
Braincase width	18.0 ± 0.12	0.75	16.1–19.7
Mastoid width	15.5 ± 0.12	0.76	13.1–16.9
Nasal length	18.1 ± 0.24	1.54	14.1–21.0
Nasal width	5.3 ± 0.08	0.54	4.2–6.3
Palatal length	25.9 ± 0.32	2.01	20.0–29.2
Incisive foramen length	8.3 ± 0.10	0.65	6.5–9.5
Incisive foramina width	3.5 ± 0.08	0.48	2.5–4.7
Inside m^{1-1} width	4.8 ± 0.10	0.63	3.7–6.0
Outside m^{1-1} width	9.9 ± 0.10	0.66	8.3–11.1
Bulla length	7.0 ± 0.08	0.51	6.0–8.1
Crowns m^{1-3} length	7.3 ± 0.05	0.33	6.5–8.0
Alveoli m^{1-3} length	7.9 ± 0.06	0.37	7.0–8.7
Crowns m^{1-2} length	5.9 ± 0.05	0.34	5.2–6.5

Aru Island. Nonetheless, Laurie and Hill (1954) must have been influenced by Tate's erroneous alliance for they suggested that *R. doboensis* might be a subspecies of *R. ruber* in which they included all subspecies of *leucopus*. At the present time a rational concept of *ringens* has generally become lost by the shifting back and forth of this name at specific and subspecific levels, and by the inclusion of more and more taxa under the names *R. ringens* or *R. leucopus*.

Rattus leucopus ratticolor (Jentink)

Mus ratticolor Jentink, 1908, p. 7.
Rattus ratticolor: Thomas, 1920, p. 424.
Stenomys leucopus ratticolor: Rümmler, 1938, p. 184.
Rattus leucopus ratticolor: Ellerman, 1941, p. 204.
Rattus ringens ratticolor: Ellerman, 1949, p. 51.

HOLOTYPE: Skin and incomplete crushed skull, juvenile female, RMNH 84, collected June 18, 1907, by H. A. Lorentz at van Weel's Camp, Lorentz River, Irian Jaya Province, Indonesia, near sea level.

DISTRIBUTION: The most westerly race of *R. leucopus,* extending across lowlands south of the Snow Mountains in Irian Jaya. Occurs from Tiponé eastward to Digoel and from sea level to 215 m. Distribution largely in association with river drainages (fig. 18).

MEAN MEASUREMENTS (IN MM.): External: head and body 211; tail 179; hind foot (s.u.) 41.7. Skull: occipitonasal length 48.5; braincase width 18.0; bulla length 7.0; crowns m^{1-3} length 7.3. (See table 14 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 42.5 or less.

DESCRIPTION: This is the largest of the subspecies of *R. leucopus* in New Guinea, and it is unfortunate that the holotype is both juvenile and damaged and an inadequate representative of this subspecies. Adults are very spinous and are similar to *ringens* in coloration and thus a full separate description is not warranted. Dorsal pelage measures to 18 mm. in length and the black guard hairs to 50 mm. The ventral pelage length is 10–12 mm. All specimens that we have examined had a white tail tip of one-third or more of its length, or some white mottling along the tail. The tail scales are large, measuring 7–9 rows per cm.

This subspecies has the most massive skull and is most readily distinguished by the development and shape of the supraorbital-temporal ridging. The ridging forms a constriction in the anterior interorbital region that is most evident on larger skulls. This beading rises 0.8 to 1.0 mm. above the skull contour, is rough and unevenly developed, and is almost parallel to the long axis of the skull in the parietal region. Smaller adult skulls, of occipitonasal length less than 47 mm., also have conspicuous beading but it is smoother and more bowed laterally along the parietals. Among *leucopus, R. l. ratticolor* has the smallest bulla relative to basal skull length and is 16.3 percent.

PREVIOUS DESCRIPTIVE ACCOUNTS: Jentink's (1908) unique holotype of *ratticolor* was a juvenile female. The color of the juvenile pelage, superficially similar to that of the softer furred *rattus,* was the reason for the name *ratticolor*. It was also for this reason that he distinguished it from adult specimens from this and other localities. The immature nulliparous condition led him to distinguish only four inguinal teats and thus to specify the mammary formula as 0 + 2 = 4. He illustrated the palatine ridging on the broken skull and noted that it was unlike that of *rattus*. He provided skin and skull measurements of a series of larger *ratticolor* that he identified as *M. terraereginae,* and from these he was able to record the mammary formula of 1 + 2 = 6. A further series collected in 1909–1910 from the same area is described briefly and skin measurements are given (Jentink, 1911). The measurements are of special note since they give a firmer idea of the large size attained by adults, some of which are over 1.5 times the length of the holotype of *ratticolor*.

Thomas (1914) listed a few more specimens of *ratticolor* (as *Epimys ringens*) and said that Jentink had informed him that the correct mammary formula of the holotype of *ratticolor* was 1 + 2 = 6 rather than 0 + 2 = 4. Rümmler (1938) was the first to provide a full description of both the skin and skull of *ratticolor* and he illustrated the skull in dorsal, ventral, and lateral views (Pl. IX, Illus. 1). Tate (1951) gave a brief description of the holotype of *ratticolor,* although he included it under *R. l. ringens*. Misonne (1979) collected a series of young specimens 105 km. southwest of the type locality, all of which are the same size or smaller than the holotype of *ratticolor*. He compared them briefly with the holotypes of both *ratticolor* and *ringens* and tentatively concluded that they were *ratticolor*. He gave a few skull measurements of the larger members of this young series, and a comparison of these with those made by Jentink (1908, 1911) demonstrates that all of Misonne's series are juvenile to subadult.

REMARKS: This is the largest subspecies of *R. leucopus* and one of the largest of all the *Rattus* of New Guinea, being exceeded only by *R. jobiensis*. It appears to be the sole representative of *Rattus* in the southwestern lowlands of New Guinea in the watershed of the Snow Mountains. There are no records of the other lowland rat, *R. praetor coenorum,* in sympatry with *R. l. ratticolor* although *coenorum* is known from higher elevations of 750 m. to 1000 m. on the south slope of the Snow Mountains and at Etna Bay on the south coast west of the known distribution of *R. l. ratticolor. Rattus leucopus ratticolor* and the northern larger lowland *Rattus, R. jobiensis,* have been viewed as conspecific by some investigators (Rümmler, 1935, 1938; Ellerman, 1941, 1949) because they show convergence in certain morphological features that characterize large lowland *Rattus*.

HABITS AND HABITAT: The only information available on the habitat of this rat comes from notations on specimen labels made by the collectors. It occupies rain forest borders of river systems from sea level to 215 m. It has also been trapped in man-modified environments including gardens and even a

TABLE 15
Measurements (in Millimeters) of Adult *Rattus leucopus dobodurae*
(N = 110 for skin measurements; N = 107 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	183.6 ± 1.69	17.68	149.0–249.0
Tail length	161.4 ± 1.28	13.42	130.0–201.0
Hind foot (s.u.) length	39.4 ± 0.21	2.19	35.0–45.0
Occipitonasal length of skull	43.7 ± 0.24	2.50	38.1–50.4
Condylobasal length	41.2 ± 0.24	2.45	35.7–47.3
Basal length	38.4 ± 0.24	2.48	32.9–44.3
Zygomatic width	20.7 ± 0.13	1.34	17.9–23.9
Interorbital width	6.5 ± 0.04	0.40	5.6–7.5
Interparietal length	5.3 ± 0.05	0.48	3.9–6.3
Interparietal width	10.9 ± 0.09	0.88	8.5–13.3
Braincase width	17.2 ± 0.07	0.69	15.6–19.8
Mastoid width	14.5 ± 0.06	0.65	12.9–16.3
Nasal length	15.9 ± 0.12	1.24	13.2–19.5
Nasal width	4.9 ± 0.04	0.45	3.9–6.2
Palatal length	23.3 ± 0.14	1.44	20.2–26.8
Incisive foramen length	7.3 ± 0.06	0.65	5.9–8.7
Incisive foramina width	2.8 ± 0.04	0.43	1.8–3.9
Inside m^{1-1} width	4.0 ± 0.05	0.52	2.9–5.3
Outside m^{1-1} width	9.1 ± 0.05	0.52	7.9–10.3
Bulla length	6.4 ± 0.04	0.37	5.5–7.3
Crowns m^{1-3} length	6.6 ± 0.03	0.32	5.9–7.2
Alveoli m^{1-3} length	7.1 ± 0.03	0.31	6.2–7.9
Crowns m^{1-2} length	5.3 ± 0.03	0.35	4.4–6.2

store (Wakatimi). In the latter situation, the surrounding countryside was flat and was subject to periodic flooding.

SYMPATRY: *Rattus leucopus ratticolor* is sympatric with *Rattus rattus* (Musser, 1973) at Tanah Merah (06°07′ S, 140°18′ E). No further records of sympatry with this or other species of *Rattus* are known.

TAXONOMIC HISTORY: When Jentink (1908) proposed *Mus ratticolor* as a new species and recorded *M. terraereginae* from the same locality, he failed to recognize that he was dealing with differences in morphology between a juvenile and adults. Nevertheless, this western *leucopus* is, in our view, sufficiently different from *R. l. ringens* to warrant subspecific recognition. It is thus unfortunate that the juvenile holotype, with its crushed and incomplete skull, is quite unrepresentative of several fundamental features of adults of this subspecies. Jentink (1911) continued to classify adults of *ratticolor* as *Mus terraereginae* when he described additional material. Thomas (1914) transferred both adults and the holotype of *ratticolor* described by Jentink (1908, 1911) to *Epimys ringens* and later (Thomas, 1922c) added further specimens, all of which he placed under *R. ringens*.

Rümmler (1938) was the first to treat all the western *leucopus* as *ratticolor*. He recognized that mature adults were the largest of all *leucopus* and regarded only those *ratticolor* 400 mm. or more in total length as adults. Ellerman (1941, 1949) also treated *ratticolor* as a distinct subspecies, first under *R. leucopus* and later under *R. ringens*. Tate (1951), however, viewed *ratticolor* as a synonym of *ringens* and placed it as *R. leucopus ringens*. Laurie and Hill (1954) followed this synonymy but listed them under *R. ruber ringens*. Ziegler (1971) followed Tate's (1951) treatment. Misonne (1979), who collected only subadults and juveniles, as judged by Rümmler's (1938) age grouping, tentatively referred his collection to *ratticolor* and presumably agrees with Jentink (1908) that it is a distinct species.

Rattus leucopus dobodurae Troughton

Rattus ringens dobodurae Troughton, 1946, p. 407.
Rattus leucopus dobodurae: Tate, 1951, p. 338.
Rattus ruber dobodurae: Laurie and Hill, 1954, p. 111.

HOLOTYPE: Skin and skull in good condition except for incomplete zygomata, adult male, AM M6960, collected April 25, 1944, by G. M. Kohls for the United States Typhus Commission, from Dobodura, Papua New Guinea, 150 m.

DISTRIBUTION: Occurs in the lowlands both north and south of the Owen Stanley Range. On the southern side known as far north as Brown River and on the northern side northward to the Kumusi River. Ranges in altitude from sea level to 600 m. (fig. 18).

MEAN MEASUREMENTS (IN MM.): External: head and body 184; tail 161; hind foot (s.u.) 39.4. Skull: occipitonasal length 43.7; braincase width 17.2; bulla length 6.4; crowns m^{1-3} length 6.6. (See table 15 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 38.0 or less.

DESCRIPTION: Troughton (1946) described this subspecies as more robust than *ringens,* and this is substantiated by our data. The pelage is very spinous, generally more so than in either *ringens* or *ratticolor.* The dorsum is dark brown tipped by yellowish rust. The hairs are brown for most of their length, whereas the spines are translucent dull gray. Both are about 15 mm. in length and are tipped in yellow-rust color for the last 2 mm. The black guard hairs measure to 40 mm. and are moderately conspicuous. Ears are medium brown and lightly haired and the muzzle vibrissae measure to 60 mm. A sparse covering of woolly gray underfur occurs both dorsally and ventrally. The ventral pelage is moderately harsh, may possess light spines, and is 10 mm. long. Ventral hair is cream white to the base except for the presence of gray underfur. A reddish brown color is common in the pectoral region. The tail is medium brown and is usually white-tipped. Tail scales are 8–10 per cm. and the tail hairs are short and sparse. They match the background color of the scales. The dorsal surface of the feet is covered by dull white hairs.

The juvenile pelage is soft and dark gray with only faint rust tipping and lacks the gloss of the adult pelage. The ventral pelage is usually gray basally and tipped by white. A pure white pectoral area occurs on some specimens. The feet are clothed in white dorsally and white tail marking is evident on most specimens.

The skull of *R. l. dobodurae* is very similar to that of *R. l. ringens,* but a couple of distinctive features are apparent The interorbital constriction is more pronounced in *dobodurae* at about midway along the interorbital length in a fashion similar to that of the Australian *leucopus* (Taylor and Horner, 1973), whereas in *ringens* it forms a smooth curve. The bulla is relatively smaller and is 16.8 percent of the basal length.

PREVIOUS DESCRIPTIVE ACCOUNTS: Troughton (1946) provided a brief description of this subspecies when he proposed it. He pointed out that the hind foot was larger than that of typical *ringens.* He also thought that the tail was proportionately longer, although this is not supported in our assessment. Tate (1951) extended the range of this subspecies to include the *leucopus* on the southern side of the Owen Stanley Range. He pointed out that Thomas (1897) had earlier identified material from this side as *terraereginae,* and later (Thomas, 1904a) had identified as *ringens* rats from near the type locality of *dobodurae.* Tate (1951) provided additional descriptive comments and some measurements of skins and skulls of four specimens. Yosida (1973) and Dennis and Menzies (1978) have illustrated the karyotype of this subspecies. They present somewhat different interpretations of the nature of the chromosomal fissions. The skull has never been illustrated.

REMARKS: The skull of the type specimen of *dobodurae* is the only holotype of a *R. leucopus* of New Guinea that could be said to be representative of the subspecies, for

FIG. 21. Habitat of *Rattus leucopus dobodurae* in pockets of relict rain forest near Menapi. *Rattus mordax mordax* and *Rattus sordidus gestri* are sympatric here. Photograph taken at 150 m., from hill behind Menapi across Goodenough Bay, March–May, by L. J. Brass, on 1953 Archbold Expedition.

the others are broken or immature. It is unfortunate that Troughton (1946) provided such a limited description when he proposed this subspecies. His comment about lack of a reddish brown chest patch in the Dobodura series should not be construed as typical of this subspecies for it was common among the material we examined from other localities. It is absent in juveniles. Tate (1951) has suggested that it is caused by fruit stains but Menzies and Dennis (1979) think it more likely that it is a glandular secretion. We support Menzies and Dennis and believe that it may be associated with a development of cutaneous glands that have a communicatory function in adults. The possibility warrants histological analysis.

Since this subspecies appears to be the most spinous of the forms of *leucopus,* this feature deserves brief discussion. The degree of development of spines is associated with the maturation of the pelage and within a sample from a given locality the largest specimens typically have the most spinous pelage. There may also be differences between localities among adults of the same size. Rümmler (1938) has suggested that the spinous condition becomes reduced with an increase in elevation. To a certain extent this appears to be the case, however, no studies of *Rattus* of New Guinea have addressed this problem. Since spinous fur is undoubtedly associated with pelage insulation, variation can be expected in association with local climatic differences and perhaps even with seasonal changes. Thus, degree of spinousness is limited in diagnostic value.

HABITS AND HABITAT: *Rattus leucopus dobodurae* inhabits rain forest, scrub, bush along river banks, and even grassland adja-

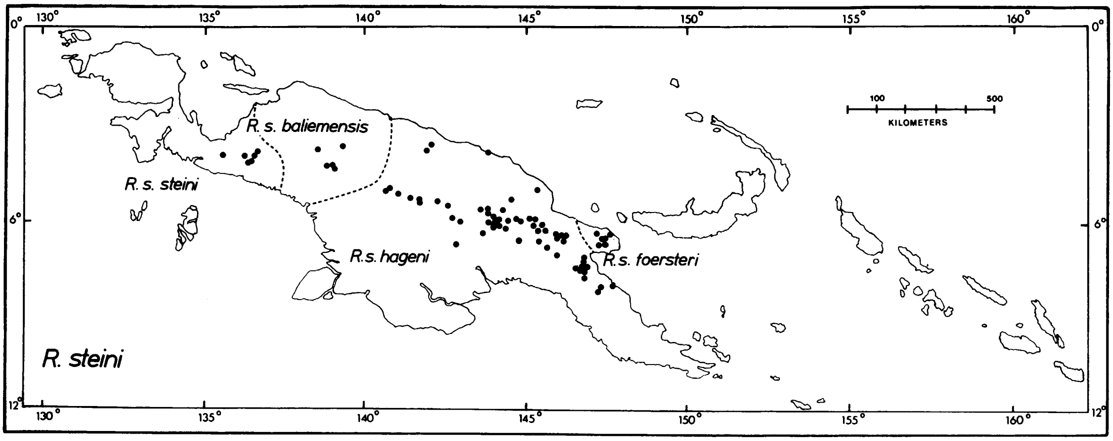

FIG. 22. Distribution map of *Rattus steini*. Locality records for each of the four subspecies are indicated by dots.

cent to forests (fig. 21). It is reported to invade man-modified areas, such a forest plantations and rest houses. These data are all from label notations on specimens.

SYMPATRY: *Rattus leucopus dobodurae* is sympatric with *Rattus sordidus gestri, Rattus exulans browni, Rattus mordax mordax, Rattus verecundus verecundus,* and *Rattus rattus.*

TAXONOMIC HISTORY: Following the original description of this subspecies by Troughton (1946) as *R. ringens dobodurae,* Tate (1951) agreed to its validity and placed it as *R. leucopus dobodurae.* Ellerman (1949), however, made no mention of it. Laurie and Hill (1954) included it as a subspecies under their greatly extended species *R. ruber.* Ziegler (1971), Bulmer and Menzies (1972), Menzies (1973), Yosida (1973), Gressitt and Ziegler (1973), and Dennis and Menzies (1978) have all followed Tate's classification of this subspecies. We also concur with this treatment.

Rattus steini Rümmler, New Status

DISTRIBUTION: A mid-montane rat widely distributed in the central cordillera of Irian Jaya and Papua New Guinea; also occurring in the mountains of the Huon Peninsula. In its eastward distribution, extending as far south as the Bowutu Mountains. Altitudinally, known from 20 to 2800 m. (fig. 22).

GENERAL DESCRIPTION: *Rattus steini* is a medium-sized relatively soft-furred rat. Spinous fur is present on larger specimens, but the spines are sparsely distributed, thin and flexible. The dorsal color is a grizzled dark brown with rufous tipping. Soft gray underfur is much more prevalent than it is in any of the lowland rats. Fine guard hairs are distributed over the entire dorsal surface and are most conspicuous in the rump area. The ventral pelage lacks spines, and is gray with yellowish buff tipping. A white pectoral spot occurs frequently. The ears and tail are dark brown. The feet are clothed dorsally in cream-colored or light buff hairs.

The mammary formula is either $1 + 2 = 6$ or $2 + 2 = 8$ and varies according to subspecies.

The skull is characterized by slightly or moderately bowed incisive foramina, relatively heavy molars, average sized bullae and a palate that terminates about 1 mm. behind the molar row (fig. 23). Supraorbital ridging is very light, about 0.8 mm. above the skull surface, and varies according to overall size. The nasal bones flare slightly as they extend distally. The nasals terminate in line with the anterior face of the incisors or overhang slightly.

DIAGNOSTIC CHARACTERS: This species is not readily confused with other mid-montane rats, such as *R. niobe* and *R. verecundus,*

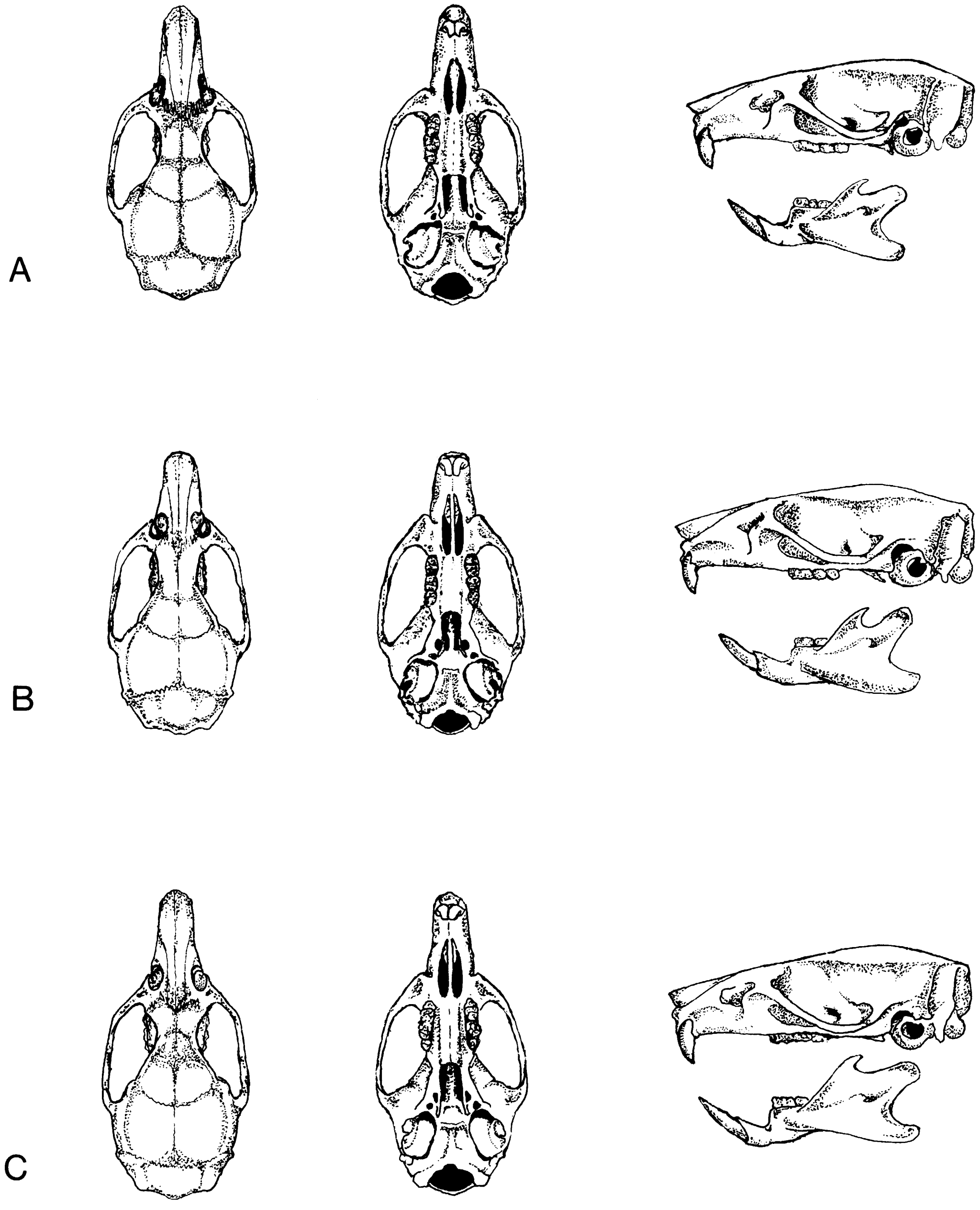

FIG. 23A, B, C. Dorsal, ventral, and lateral views of skulls of adult *Rattus steini*. A. *Rattus steini foersteri*, AMNH 195122, from Gang Creek. Occipitonasal length 39.2 mm. B. *Rattus steini hageni*, BBM 60758, from Murmur Pass. Occipitonasal length 39.4 mm. C. *Rattus steini baliemensis*, new subspecies, AMNH 110218, from Baliem River. Occipitonasal length 41.8 mm.

which have much more delicate skulls and longer rostra, or with those from higher altitudes, such as *R. richardsoni* and *R. giluwensis*, which have a more expanded cranium and more delicate molars. *Rattus steini* is most readily confused with smaller examples of lowland species, such as *R. praetor, R. mordax,* or *R. novaeguineae,* new

TABLE 16
Measurements (in Millimeters) of Adult *Rattus steini steini*
(N = 89 for skin measurements; N = 149 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	165.9 ± 1.45	13.69	139.0–199.0
Tail length	146.1 ± 1.19	11.25	112.0–166.0
Hind foot (s.u.) length	33.9 ± 0.16	1.52	30.0–38.0
Occipitonasal length of skull	40.9 ± 0.15	1.82	36.9–44.9
Condylobasal length	38.3 ± 0.16	1.90	33.3–42.9
Basal length	35.8 ± 0.16	1.94	30.7–40.3
Zygomatic width	19.6 ± 0.08	0.96	17.3–22.2
Interorbital width	6.2 ± 0.02	0.25	5.3–7.2
Interparietal length	5.7 ± 0.04	0.46	4.4–6.9
Interparietal width	10.9 ± 0.06	0.69	9.2–13.2
Braincase width	16.8 ± 0.04	0.52	15.7–18.9
Mastoid width	14.1 ± 0.04	0.50	12.9–15.8
Nasal length	15.3 ± 0.09	1.05	12.9–18.3
Nasal width	4.6 ± 0.03	0.39	3.8–5.6
Palatal length	22.1 ± 0.09	1.16	19.1–25.0
Incisive foramen length	7.6 ± 0.04	0.54	6.3–9.0
Incisive foramina width	2.9 ± 0.02	0.27	2.3–3.9
Inside m^{1-1} width	3.8 ± 0.03	0.35	3.0–4.9
Outside m^{1-1} width	8.7 ± 0.03	0.38	7.7–9.6
Bulla length	6.2 ± 0.02	0.26	5.4–6.8
Crowns m^{1-3} length	6.7 ± 0.02	0.27	6.0–7.3
Alveoli m^{1-3} length	7.2 ± 0.02	0.26	6.6–7.8
Crowns m^{1-2} length	5.4 ± 0.02	0.29	4.7–6.0

species. The parallel-sided incisive foramina and heavier molars of *mordax* will usually serve to distinguish it from *steini. Rattus novaeguineae* has a relatively longer tail, whiter venter, more delicate molars, flatter dorsal skull profile, longer rostrum with greater nasal overhang, and more bowed incisive foramina. Young *R. praetor* can be distinguished from *steini* only with great difficulty. Overall size is one of the best criteria. *Rattus praetor* has relatively wider hind feet and the pelage is much more spinous.

TAXONOMIC HISTORY: This species was described by Rümmler (1935) as *R. leucopus steini* from specimens collected by Georg Stein at Kunupi, 1400–1800 m. In the same paper, he also described a new montane subspecies from the Huon Peninsula that he placed under his *R. verecundus* as *R. v. förster*i. Another new subspecies from the eastern portion of the New Guinean highlands was proposed by Troughton (1937) as *R. mordax hageni.* When Rümmler (1938) moved *steini* along with a number of other subspecies, including *mordax,* into *Stenomys leucopus,* he was apparently unaware of Troughton's new subspecies for he makes no mention of *hageni.* Hinton (1943) proposed *Rattus rosalinda* for a montane rat of northeastern New Guinea. We recognize *Rattus steini* as a full species with four subspecies: *R. s. steini, R. s. foersteri, R. s. hageni* (=*R. rosalinda*), and *R. s. baliemensis,* new subspecies.

Rattus steini steini Rümmler

Rattus leucopus steini Rümmler, 1935, p. 115.
Stenomys leucopus steini: Rümmler, 1938, p. 189.
Rattus ringens steini: Ellerman, 1949, p. 69.
Rattus ruber steini: Tate, 1951, p. 332.

HOLOTYPE: Skin and incomplete skull (basioccipital broken), adult male, ZM 45676, collected October 5, 1931, by Georg Stein, Kunupi, Weyland Mountains, Irian Jaya Province, Indonesia, 1400–1800 m.

DISTRIBUTION: A montane rat known only from the Weyland and Nassau Ranges of Irian Jaya between altitudes of 1400/1800 (range only, given) and 1765 m. (fig. 22).

MEAN MEASUREMENTS (IN MM.): External: head and body 166; tail 146; hind foot (s.u.) 33.9. Skull: occipitonasal length 40.9; braincase width 16.8; bulla length 6.2; crowns m^{1-3} length 6.7. (See table 16 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 36.0 or less.

DESCRIPTION: The pelage is slightly spinous and moderately reversible. The overall color dorsally is grizzled dark brown and rufous orange to golden. The dorsal coloration is similar, but duller, to that of *R. p. coenorum*. Dorsal body hair is medium gray basally for about 12 mm. and is tipped with rufous to golden for about 3–4 mm. A light covering of underfur of medium gray is present but is inconspicuous. The guard hairs are dark brown to black and may be tipped with rufous. They measure up to 35 mm. long and are distributed well over the dorsum, being most conspicuous in the rump. The spines are translucent basally and are dark brown to black in the terminal one-third. They are fine, less than 1 mm. in width, and are not a conspicuous component of the pelage. The facial region is the same coloration as the body and the rostral vibrissae measure to 55 mm. The ears are lightly covered by short hairs and blend with the dorsal color. The lateral body pelage blends into the lighter gray ventral pelage. The venter lacks spines. Its gray hue may be interrupted by white ventral markings. Usually the white marking is a single pectoral splotch, but it may occur as a long ventral streak or other configuration. The ventral hairs are gray basally for about 6 mm. and are tipped by buff for about 3 mm. The brown tail is evenly colored and the inconspicuous brown tail hairs are about 1.5 mm. long. The tail scales are 10 per cm. The feet are covered by light buff hairs.

The juvenile pelage lacks spines and the guard hairs are not conspicuous. It is the same color as that of adults except the rufous tipping is more subdued.

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

The skull is very lightly to moderately ridged supraorbitally, and on younger rats the ridging is usually not measurable. The incisive foramina tend to be more bowed than those of *hageni* from the same altitudinal range. The palate terminates about 0.5 mm. posterior to the molar row. The most distinctive feature is the narrow interorbital breadth. The narrowest region is in line with the ossification centers of the supraorbital bones, as it is in *baliemensis*, whereas in *hageni* and in *foersteri* it tends to be posterior to this level. The bullae are of average size. The juvenile skull lacks supraorbital ridging, the incisive foramina are narrower, and the narrow interorbital region has not yet developed into a distinctive feature.

PREVIOUS DESCRIPTIVE ACCOUNTS: Rümmler (1935) provided the original description, and later (Rümmler, 1938) expanded it and included the mammary formula. Tate (1951) appears not to have examined *steini* since he placed his brief description in quotations. Presumably, it represents his translation of excerpts from Rümmler (1935, 1938). There are no further published accounts.

REMARKS: The existence of *steini* as a taxonomic entity has been generally acknowledged but it has remained poorly understood since Rümmler's time. Although he removed *steini* from *R. leucopus* to *R. ringens* in 1949, Ellerman (1941, 1949) essentially followed Rümmler's treatment and did not expand upon it. Tate (1951), who presumably never examined the holotype or any of the series lodged in museum collections, placed *steini* as a subspecies of *R. ruber*. The specimen that Tate examined as representative of *R. ruber steini* (AMNH 101964) is actually an example of the somewhat smaller, less spiny upland form of *R. praetor coenorum* that he recognized as *R. p. tramitius*. No doubt, this accounted for his statement that *steini* and *tramitius* are very closely related (Tate, 1951).

HABITS AND HABITAT: This is a mid-montane form that occurs mainly near lakes and river systems. The only records on the habitat are notes on specimen labels and in one published account. It has been trapped in grassland, forest, and scrub. Rümmler (1938) states that it occurs in the mountain rain forest zone of the Weyland Mountains.

SYMPATRY: *Rattus steini steini* is sympatric with *Rattus verecundus unicolor* and *Rattus praetor coenorum.*

TAXONOMIC HISTORY: When Rümmler (1935) described *R. leucopus steini,* his concept of *leucopus* was very broad and included what we now regard as several different species. The holotype (ZM 45676) is an adult of about the same size as *utakwa* (=*R. p. coenorum*). Rümmler (1935) took care in distinguishing the two subspecies. Ellerman (1941) did not accept Rümmler's (1938) move of *R. leucopus steini* and others to the genus *Stenomys,* but rather retained *Rattus* as the genus. When he later regarded the Australian *R. leucopus* as specifically distinct, he removed the New Guinean subspecies formerly included in *leucopus* to *Rattus ringens,* a transfer that involved *steini* (Ellerman, 1949). Tate (1951) included *steini* as a subspecies under *R. ruber,* as the name *ruber* has priority over *ringens.*

Our assessment of *R. s. steini* as one of four subspecies that extend across the backbone of New Guinea at mid-montane elevations is a substantially different treatment from earlier ones but, as discussed under *R. s. baliemensis,* it is in part foreshadowed in other investigations (Tate, 1951; Laurie, 1952).

Rattus steini foersteri (Rümmler)

Stenomys verecundus försteri Rümmler, 1935, p. 117.

Rattus verecundus forsteri: Ellerman, 1941, p. 205.

Rattus verecundus försteri: Tate, 1951, p. 339.

Rattus verecundus foersteri: Laurie and Hill, 1954, p. 114.

HOLOTYPE: Dry flat skin with tail that appears complete, incomplete skull with ventroposterior cranium missing, young adult female, RMNH 292/2, collected February 22, 1913, by F. Förster, at source of Bulung River, Huon Peninsula, Papua New Guinea, 1800–2000 m. (fig. 22).

DISTRIBUTION: Known only from mountainous portions of the Huon Peninsula, and to date recorded from less than 10 localities at altitudes between 1160 and 1800/2000 m. Its western extent is the Saruwaged Mountains (fig. 22).

MEAN MEASUREMENTS (IN MM.): External: head and body 148; tail 150; hind foot (s.u.) 34.3 Skull: occipitonasal length 38.1; braincase width 15.8; bulla length 5.5; crowns m^{1-3} length 6.2. (See table 17 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 35.0 or less.

DESCRIPTION: This is a medium-sized rat with relatively soft and sleek fur. The dorsal color is a warm dark brown tipped with 2 mm. of rust. The pelage is 14 mm. long, of which all but the tipping is dark gray. Gray underfur is also present. Fine, flexible translucent spines are usually present, and the black guard hairs are relatively inconspicuous and measure about 20 mm. long. The ears are medium brown, and the muzzle vibrissae measure to 40 mm. in length. The ventral pelage is medium gray with cream-colored tipping. A white pectoral spot or white mid-ventral streak is common. The ventral pelage is about 9 mm. long, of which the last 2 mm. is light. The tail is medium brown with 10 scale rows per cm., and the fine tail hairs are 1.5 mm. long. All material we examined had plain tails, although Rümmler (1935) commented that the tip was sometimes whitish. The feet are covered dorsally by white or ivory-colored hairs.

The juvenile pelage is more somber and softer, and no spines are present.

The mammary formula is 2 + 2 = 8.

The skull is relatively delicate, and the supraorbital ridging is very fine or undeveloped (fig. 23A). The incisive foramina are slightly bowed and the palate terminates about 1 mm. posterior to the molar rows. The relatively narrow interorbital breadth and relatively wide zygomatic breadth help to distinguish this from *R. verecundus,* with which it has been formerly allied, but the differences are subtle. The nasals flare terminally and overhang the rostrum slightly. The skull is intermediate in a number of features be-

TABLE 17
Measurements (in Millimeters) of Adult *Rattus steini foersteri*
(N = 16 for skin measurements; N = 17 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	147.7 ± 2.89	11.54	132.0–180.0
Tail length	149.9 ± 3.30	13.18	120.0–171.0
Hind foot (s.u.) length	34.3 ± 0.36	1.42	33.0–38.0
Occipitonasal length of skull	38.1 ± 0.42	1.73	35.2–41.9
Condylobasal length	35.4 ± 0.37	1.54	32.9–38.7
Basal length	33.1 ± 0.36	1.48	30.6–36.0
Zygomatic width	18.0 ± 0.17	0.70	16.9–19.0
Interorbital width	5.7 ± 0.05	0.22	5.4–6.1
Interparietal length	5.0 ± 0.07	0.31	4.3–5.5
Interparietal width	10.7 ± 0.16	0.68	9.8–12.0
Braincase width	15.8 ± 0.12	0.48	15.0–16.8
Mastoid width	13.3 ± 0.12	0.51	12.4–14.4
Nasal length	14.1 ± 0.26	1.08	12.5–16.8
Nasal width	4.4 ± 0.09	0.39	3.9–5.3
Palatal length	20.6 ± 0.25	1.02	19.0–22.2
Incisive foramen length	6.1 ± 0.13	0.52	5.3–7.3
Incisive foramina width	2.3 ± 0.07	0.29	1.9–2.8
Inside m^{1-1} width	3.3 ± 0.07	0.28	3.0–3.9
Outside m^{1-1} width	8.2 ± 0.10	0.41	7.5–8.9
Bulla length	5.5 ± 0.07	0.28	5.0–5.9
Crowns m^{1-3} length	6.2 ± 0.09	0.37	5.6–6.9
Alveoli m^{1-3} length	6.5 ± 0.08	0.35	5.9–7.1
Crowns m^{1-2} length	4.9 ± 0.11	0.45	4.2–5.8

tween *steini* and *verecundus* and it is only with difficulty that its stronger alliance with *steini* can be discerned.

PREVIOUS DESCRIPTIVE ACCOUNTS: Rümmler (1938) expanded his description of *foersteri* following his original proposal of it as a new subspecies of *Stenomys verecundus* (Rümmler, 1935). In this last study, he referred to eight additional specimens. There are no further descriptive accounts. Until our present study, the mammary formula was unknown.

REMARKS: When Rümmler (1935) proposed this subspecies he had before him a single specimen represented by a flat skin, and the rostral and anterior cranial attachments only. The collector had provided no body measurements. From this material, Rümmler supplied what skull measurements he could and a brief description of the skin. He was of the opinion that the tail was incomplete. He made no reference to another specimen (RMNH 292/5) that presently exists in the museum collection, probably because it is a younger example. Both skin and skull are as poorly preserved as the holotype, but it reinforces our opinion that the tail was probably not incomplete in the holotype. The tail length is by nature about subequal to that of the head and body. *Rattus verecundus,* the species to which Rümmler allied this rat subspecifically, has a tail that is characteristically longer than the head and body length, and this may have influenced him in his view that the tail of the holotype was incomplete.

Two skull features that Rümmler (1935, 1938) specified are the wider zygomatic arch and the narrower incisive foramina. He viewed these as characters that separate *R. v. unicolor* and *R. v. mollis* from *foersteri* at the subspecific level. Our opportunity to examine a large series of *R. verecundus* has led us to conclude that all members of this species have flared incisive foramina and narrow elongated skulls. The absence of

FIG. 24. Habitat of *Rattus steini foersteri* in rain forest at Gang Creek, 1311 m. Photograph taken in June by S. O. Grierson on 1964 Archbold Expedition.

these features in *foersteri* and the relatively short tail led us to cast doubt upon Rümmler's assessment. We have the distinct advantage that we have available a series of *foersteri* collected after Rümmler's time by the Seventh Archbold Expedition in 1964. This additional material has confirmed our suspicions and enabled us to place *foersteri* as a subspecies of *R. steini*.

HABITS AND HABITAT: This rat lives in the mountain rain forest zone of the Huon Peninsula (Rümmler, 1938). The only other information available is an unpublished note in Van Deusen's diary (May 15, 1964) that records the rat in rain forest near a small creek (fig. 24).

SYMPATRY: *Rattus steini foersteri* is sympatric with *Rattus exulans browni*.

TAXONOMIC HISTORY: Rümmler's (1935, 1938) view that *foersteri* is a subspecies of *Stenomys verecundus* has until now never been questioned except at the generic level. Ellerman (1941, 1949) placed it in *Rattus* as *R. v. forsteri* and Tate (1951) restored the umlaut to *försteri*. Laurie and Hill (1954) correctly anglicized the name to *foersteri*. It is unclear whether these later investigators ever re-examined the holotype or other *foersteri* specimens.

Rattus steini hageni Troughton

Rattus mordax hageni Troughton, 1937, p. 120.
Rattus rosalinda Hinton, 1943, p. 557.
Rattus ruber hageni: Tate, 1951, p. 333.
Rattus ruber rosalinda: Tate, 1951, p. 334.

HOLOTYPE: Skin and complete skull, adult male, AM M6102, collected May 1936, by G. A. M. Heydon, on the southern slopes of Mt. Hagen, Mt. Hagen District, Papua New Guinea, 1500–1800 m.

DISTRIBUTION: A mid-montane rat occurring from the Star Mountains in the western part of its range, across the Central Highlands, and to the Bowutu Mountains south

TABLE 18
Measurements (in Millimeters) of Adult *Rattus steini hageni*
(N = 272 for skin measurements; N = 275 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	153.5 ± 0.74	12.17	122.0–188.0
Tail length	134.1 ± 0.70	11.60	100.0–174.0
Hind foot (s.u.) length	32.8 ± 0.12	1.93	25.0–38.0
Occipitonasal length of skull	37.6 ± 0.10	1.70	33.3–42.5
Condylobasal length	35.8 ± 0.10	1.66	32.0–40.8
Basal length	33.1 ± 0.10	1.65	29.0–38.4
Zygomatic width	19.1 ± 0.05	0.82	17.0–21.1
Interorbital width	5.7 ± 0.02	0.27	4.9–6.5
Interparietal length	4.8 ± 0.03	0.51	3.5–6.5
Interparietal width	10.2 ± 0.05	0.78	8.0–12.3
Braincase width	16.1 ± 0.03	0.56	14.4–17.5
Mastoid width	13.6 ± 0.03	0.48	12.4–14.9
Nasal length	13.5 ± 0.06	0.93	10.8–16.2
Nasal width	4.2 ± 0.02	0.34	3.3–5.3
Palatal length	20.4 ± 0.06	1.01	17.6–23.6
Incisive foramen length	6.3 ± 0.03	0.58	4.9–8.0
Incisive foramina width	2.3 ± 0.02	0.28	1.6–3.2
Inside m^{1-1} width	3.5 ± 0.03	0.44	2.4–4.7
Outside m^{1-1} width	8.3 ± 0.03	0.44	7.1–9.6
Bulla length	5.8 ± 0.02	0.31	4.9–6.9
Crowns m^{1-3} length	6.3 ± 0.02	0.31	5.5–7.1
Alveoli m^{1-3} length	6.7 ± 0.02	0.33	6.0–7.7
Crowns m^{1-2} length	5.2 ± 0.02	0.30	4.3–6.0

of Wau. Also present in the Adelbert Range. Altitudinal records range from 450 to 2800 m., except for two northern localities, Wewak and Yellow River, at 20 to 250 m. (fig. 22).

MEAN MEASUREMENTS (IN MM.): External: head and body 154; tail 134; hind foot (s.u.) 32.8. Skull: occipitonasal length 37.6; braincase width 16.1; bulla length 5.8; crowns m^{1-3} length 6.3. (See table 18 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 35.0 or less.

DESCRIPTION: This is a medium-sized, soft-furred rat. The pelage is dark brown and flecked by cinnamon buff tipping. The dorsal pelage is about 18 mm. long; the basal portion is dark gray and the tipping is on the terminal 2 mm. Black guard hairs are abundant and measure 30 mm. The larger rats, particularly those from lower altitudes, have fine, flexible translucent spines in the dorsal pelage. Slate-gray underfur lies beneath the surface pelage. The ears are dark brown, and the muzzle vibrissae measure to 40 mm. Ventrally, the overall pelage color is gray basally and tipped for the last 2 mm. with ivory. This ventral pelage is about 7–9 mm. long. A white pectoral spot is not uncommon. The dark brown tail has about 10 scale rows per cm. and is lightly covered by brown hairs about 2 mm. long. The feet are covered dorsally by white or medium brown hairs and their overall color is light brown.

The juvenile pelage is softer and darker, and the development of lighter tipping is minimal. White pectoral spotting may be present.

The mammary formula is 2 + 2 = 8.

The skull is faintly ridged in the supraorbital region and is much more delicate in appearance than that of any lowland rat (fig. 23B). The incisive foramina are usually slightly bowed, but in younger rats may be fairly straight-sided. The palate terminates about 0.5 mm. behind the molar rows. The molars are relatively wide and robust for the skull size and are one of the best characters on which to distinguish this subspecies from a sympatric rat, *R. novaeguineae,* new species. The terminal portion of the nasals is flared and there is little or no nasal projection beyond the anterior face of the incisors. The bullae are slightly inflated and there is a marked constriction in the interorbital region. The juvenile skull lacks ridging and the incisive foramina are more slit-shaped.

PREVIOUS DESCRIPTIVE ACCOUNTS: The original description by Troughton (1937) was largely one of comparison with typical *mordax* since he viewed *hageni* as a subspecies of *mordax*. His description included the mammary formula, and provided skin and skull measurements as well as qualitative details.

In describing the new species *R. rosalinda,* Hinton (1943) made comparison with *R. leucopus* to which he thought it was most closely allied. His description is briefer than that of Troughton (1937), but he includes external and skull measurements as well as the mammary formula.

Tate (1951) provided almost no descriptive account for *hageni* and furthermore stated that the mammary formula was still unknown, an erroneous remark that led him to suggest that, if not an ally of *tramitius* (= *coenorum*), it might be one of *verecundus*.

Although Laurie (1952) provided some external and skull measurements of *hageni* (under the misidentification *R. ruber tramitius*) they are of limited value since she may have included *mordax* (BM 47.1156 skin; 47.1159 skin and skull; 50.1208–10 skin and skull) or *verecundus* (BM 47.1156 skull) in the calculations. Lidicker (1968) has described the phallic morphology of *hageni* under the name of *R. ruber*.

The most comprehensive description is that of Lidicker and Ziegler (1968) under the name *R. r. tramitius*. They were aware that the name *R. ruber* was at that time being applied to a complex of species, but it is clear from their description that the one they dealt with was a single form and that it was *hageni*. In fact, they stated that their material was most closely related to *R. r. hageni* that had been synonymized with *tramitius* by Laurie (1952). Their description includes information on reproduction. A brief description was provided by Menzies (1973). Dwyer (1975) has examined aspects of breeding and population composition in *hageni* under the name *R. ruber*. The karyotypes of montane rats from Wau identified as *R. ruber* (=*R. s. hageni*) and of lowland rats from Fergusson Island also identified as *R. ruber* (=*R. mordax fergussoniensis*) are composed of 32 chromosomes, are said to be identical, and to share similar autosomal components with *R. niobe* and *R. verecundus* (Dennis and Menzies, 1978).

REMARKS: Although it has been buried in the literature, probably more is known about the general biology of *hageni* than perhaps any other *Rattus* endemic to New Guinea. As our brief review of previous descriptive accounts suggests, knowledge of it has been eclipsed by its incorporation under other nomenclatorial entities, such as *tramitius, mordax,* and *ruber,* which themselves were usually contaminated by the inclusion of more than one species.

Since this subspecies is one of the best represented in museum collections, ecogeographic variations in certain features emerge to some degree. Specimens from lower altitudes tend to be larger, contain more fine spines in the pelage, have a longer tail, longer rostrum, and more bowed incisive foramina. Those from higher elevations are softer, darker, the tail is shorter relative to head and body length, the skull is more compact since the rostrum is shorter, and the incisive foramina are more slitlike. This type of morphological variation warrants a full scale study that takes into account microclimatic variables, minimizes the effects of seasonal trapping, and systematically measures the most important morphological variables for statistical correlation.

HABITS AND HABITAT: This montane rat was first described from specimens taken in cane grass and at the time was reputed not to enter human habitations (Troughton, 1937). Lidicker and Ziegler (1968) collected two specimens in a tall grass marsh at 700 m. elevation, but suggested that it may not

FIG. 25. Habitat of *Rattus steini hageni* in kunai grassland 1 mi. WNW of Bulolo. Photograph taken October 27, 1962, by W. Z. Lidicker.

be representative habitat at higher elevations where the rat is more plentiful and marshes are less so. Bulmer and Menzies (1973) found *hageni* (identified as *R. ruber*) in gardens or bushfallow in the Schrader Mountains. The local people claimed that they also occur along streamsides but do not enter houses. A brief description of a burrow system has also been described (Bulmer and Menzies, 1973). Dwyer (1975) found *hageni* (identified as *R. ruber*) most commonly in cane grass (pitpit) below the forest line and in gardens near the cane grass. He found it less commonly in kunai grassland (fig. 25) and absent from rain forest. In the vicinity of Wau at higher altitudes, records from skin labels state that they were trapped on the ground in moss forest and in sugarcane fields.

SYMPATRY: *Rattus steini hageni* is sympatric with *Rattus exulans browni, Rattus verecundus verecundus* (Garaina, 800 m.), *Rattus verecundus mollis, Rattus niobe niobe, Rattus novaeguineae, Rattus leucopus ringens* (Mt. Bosavi), and *Rattus giluwensis* (Kagaba).

TAXONOMIC HISTORY: After Troughton (1937) described *hageni* as *R. mordax hageni,* no reference to it occurs in the literature until Tate (1951) recognized it as *R. ruber hageni. Rattus rosalinda,* however, described in 1943 by Hinton, was cited by Ellerman (1949) who retained it as a full species. Tate (1951), on the other hand, reduced *rosalinda* to a subspecies of *R. ruber* and likened it to *mordax*. Laurie (1952) dealt with a collection that was largely composed of *hageni* (non-*hageni* material is listed under Previous Descriptive Accounts) which she synonymized under *R. ruber tramitius*. Laurie and Hill (1954) followed this treatment.

Since then, most investigators have simply

TABLE 19
Measurements (in Millimeters) of Adult *Rattus steini baliemensis*
(N = 105 for skin measurements; N = 150 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	161.1 ± 0.98	10.08	137.0–186.0
Tail length	138.5 ± 0.87	8.96	105.0–165.0
Hind foot (s.u.) length	32.1 ± 0.13	1.28	29.0–35.0
Occipitonasal length of skull	38.5 ± 0.13	1.60	34.8–42.0
Condylobasal length	36.2 ± 0.13	1.60	32.1–39.6
Basal length	33.6 ± 0.13	1.60	29.7–37.1
Zygomatic width	18.6 ± 0.07	0.86	16.0–20.3
Interorbital width	5.8 ± 0.02	0.24	5.2–6.3
Interparietal length	5.0 ± 0.04	0.45	4.0–6.3
Interparietal width	10.3 ± 0.06	0.71	7.7–12.2
Braincase width	15.9 ± 0.04	0.52	14.5–17.0
Mastoid width	13.6 ± 0.04	0.51	12.2–15.2
Nasal length	14.1 ± 0.07	0.82	12.0–16.7
Nasal width	4.2 ± 0.03	0.36	3.1–5.2
Palatal length	20.6 ± 0.08	0.93	18.3–22.8
Incisive foramen length	6.3 ± 0.04	0.47	4.7–7.1
Incisive foramina width	2.2 ± 0.03	0.38	1.3–3.1
Inside m^{1-1} width	3.3 ± 0.03	0.40	2.5–4.4
Outside m^{1-1} width	8.3 ± 0.04	0.48	7.0–9.3
Bulla length	5.5 ± 0.03	0.32	4.8–6.2
Crowns m^{1-3} length	6.0 ± 0.03	0.33	5.0–6.9
Alveoli m^{1-3} length	6.4 ± 0.03	0.34	5.5–7.2
Crowns m^{1-2} length	4.9 ± 0.03	0.35	3.9–5.8

identified *hageni* specimens as *R. ruber* without subspecific assignment (i.e., Lidicker, 1968; Bulmer and Menzies, 1973; Dwyer, 1975; Dennis and Menzies, 1978) or have queried the use of *R. ruber tramitius* to designate this eastern form (i.e., Lidicker and Ziegler, 1968). This generally non-committal treatment for the last 25 years, of material representing *hageni,* reflected the doubts that most investigators had about *R. ruber* in general and particularly about the affinity of *hageni* to other *Rattus*. A reassessment of this complex problem was one of the challenges that encouraged us to attempt this present revision of *Rattus* of New Guinea.

Rattus steini baliemensis, New Subspecies
Taylor and Calaby

HOLOTYPE: Skin and complete skull, adult female, AMNH 110283, collected December 14, 1938, by W. B. Richardson, Baliem River, Irian Jaya, Indonesia, 1600 m.

DISTRIBUTION: Known only from the north slope of the Snow Mountains of Irian Jaya, from 03°31′ S to 04°10′ S and 138°25′ E to 139°11′ E, and ranging in altitude from 850–1200 m. (Bernhard Camp) to 2800 m. (Lake Habbema) (fig. 22).

MEAN MEASUREMENTS (IN MM.): External: head and body 161; tail 139; hind foot (s.u.) 32.1. Skull: occipitonasal length 38.5; braincase width 15.9; bulla length 5.5; crowns m^{1-3} length 6.0. (See table 19 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 35.0 or less.

DESCRIPTION: This subspecies is very similar to *R. s. steini* that occurs farther west, but it is smaller in body size and the pelage is slightly softer. Skin measurements of the holotype are 301 mm. (total length), 136 mm. (tail length), 33 mm. [hind foot length (s.u.)], and 18 mm. (ear length). The 20 skull measurements of the holotype (listed in mm. in the same order as in table 19) are: 39.8, 37.6, 34.8, 18.8, 5.9, 4.7, 9.1, 16.1, 13.9, 14.5, 4.5, 21.2, 6.6, 2.6, 3.3, 8.1, 5.6, 5.9, 6.3, 4.8, and the molars are moderately worn. The mammary formula is 1 + 2 = 6 on the holotype.

The coloration of *R. s. baliemensis* is essentially like that of *R. s. steini*, including the frequent occurrence of white pectoral spotting. It shares with *R. s. steini* the mammary formula of 1 + 2 = 6. On the basis of skins alone, we are unable to distinguish this subspecies from *R. s. steini*.

The distinctive features of *R. s. baliemensis* rest mainly in skull differences (fig. 23C). The average absolute size of the skull in *baliemensis* approximates those of *hageni* and *foersteri* but is smaller than that of *R. s. steini*. There are also certain differences in proportions. The most obvious are the relative size and shape of the incisive foramina of *baliemensis* which closely resemble those of *foersteri* in length but, relative to skull basal length, are shorter (18.5 percent) than they are in *steini* or *hageni* (19.2–21.2 percent) and narrower (6.5 percent) than in the other three subspecies (6.8–8.1 percent). The bulla and the molar row are also smaller in *baliemensis* relative to basal length (16.1 and 17.8 percent, respectively) than in the other three subspecies (16.8–17.3 and 18.7–19.2 percent, respectively).

PREVIOUS DESCRIPTIVE ACCOUNTS: None.

REMARKS: This subspecies is the eastern form of the two subspecies of *R. steini* in Irian Jaya, and the remaining two subspecies of *steini* occupy the montane habitat of the western half of Papua New Guinea. A large geographical gap in collecting sites occurs between the two Irian Jaya subspecies which restricts our interpretation of the relationships of these forms. An even wider gap occurs between *baliemensis* and *hageni*, but in this situation the Baliem Valley forms a major ecogeographic break in montane continuity.

HABITS AND HABITAT: The only habitat data come from notes on specimen labels at Bernhard Camp where at lower elevations this rat was taken in mixed rain forest and at 1500 m. and above in beech forest (fig. 26). The 1938–1939 Archbold Expedition collected a large number but they were purchased from the local people (Archbold, Rand, and Brass, 1942).

SYMPATRY: *Rattus steini baliemensis* is sympatric with *Rattus niobe arrogans, Rattus praetor coenorum,* and *Rattus rattus.*

TAXONOMIC HISTORY: Tate (1951) was the first to examine this series of rats that we are now proposing as a new subspecies. He identified most of them as *Rattus ruber tramitius* and a few from high elevations of Bernhard Camp as *Rattus ruber coenorum.* He likened *tramitius* to the southeastern *mordax* which he also placed in *R. ruber.* He did, however, regard *tramitius* as a close relative of *R. ruber steini* (=*R. s. steini*) as well, although, as mentioned previously, Tate presumably had never seen the holotype or any other specimens of this subspecies.

Tate's statement (1951, p. 331) that *tramitius, hageni,* and *rosalinda* are closely related is based upon his identification of *R. steini baliemensis* material as *tramitius.* Laurie's (1952) determination of *hageni* material as *tramitius* was undoubtedly the consequence of Tate's identification. Our view that *R. s. baliemensis* is one of two western montane subspecies and that *R. s. hageni* (=*R. rosalinda*) is one of the two eastern montane subspecies, presents a new taxonomic arrangement but not an entirely new recognition of the alliance of these montane subspecies.

To our knowledge, there are no other references in the literature to the series we now describe as a new subspecies.

Rattus giluwensis Hill, New Status

Rattus ruber melanurus Laurie and Hill, 1954, p. 112.

Rattus ruber giluwensis Hill, 1960, p. 277 (new name for *melanurus,* preoccupied).

HOLOTYPE: Skin and complete skull, adult male, BM 53.256, collected June 2, 1951, by F. Shaw Mayer, Mt. Giluwe, Papua New Guinea, 3350–3660 m.

DISTRIBUTION: Known from only six altitudes at four geographical place names: Mt. Giluwe, the adjoining Lamende Range, Ka-

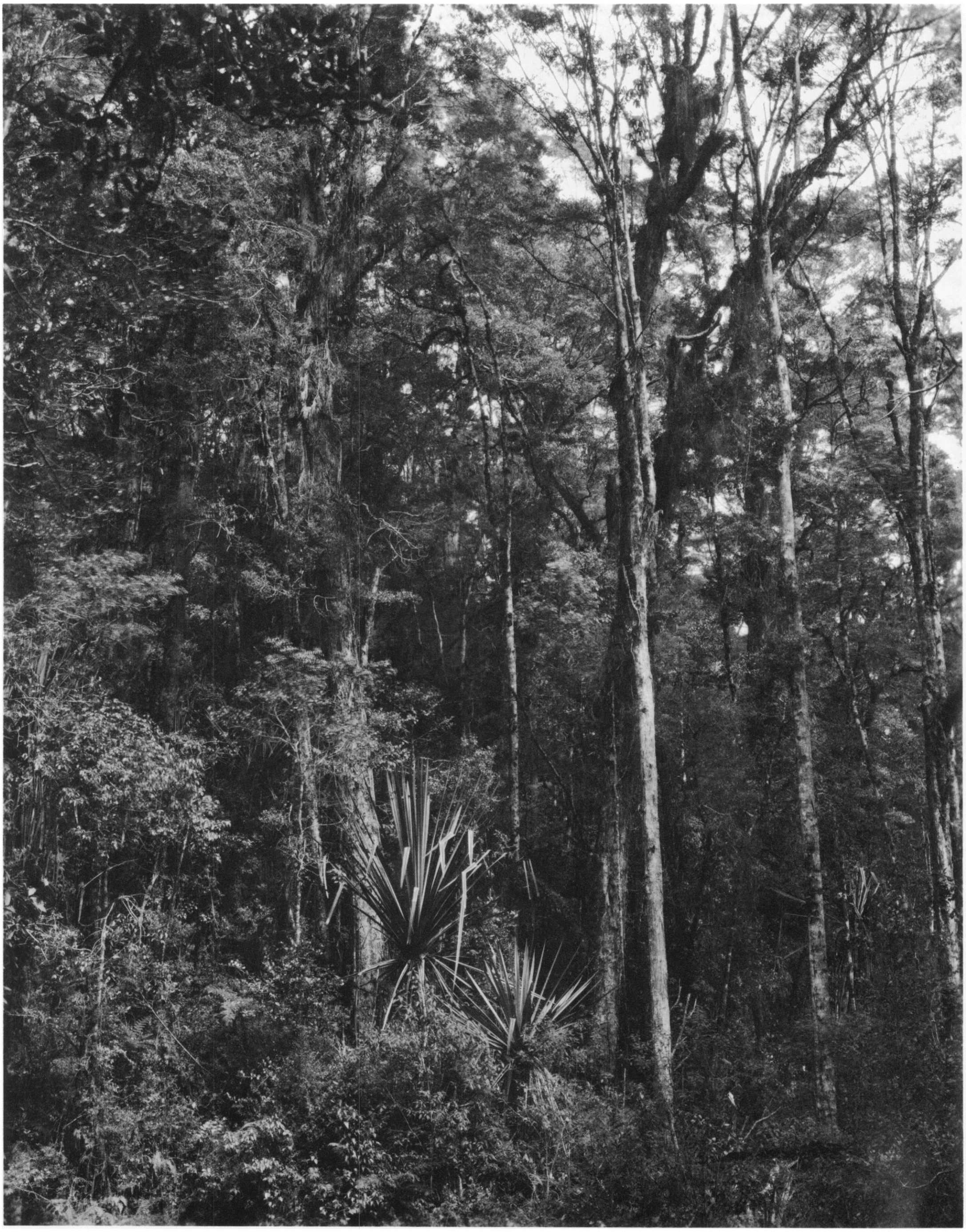

FIG. 26. Habitat of *Rattus steini baliemensis* in beech (*Nothofagus*) forest, 9 km. northeast of Lake Habbema, 2800 m. Photograph taken October 1938, by L. J. Brass on 1938–1939 Archbold Expedition.

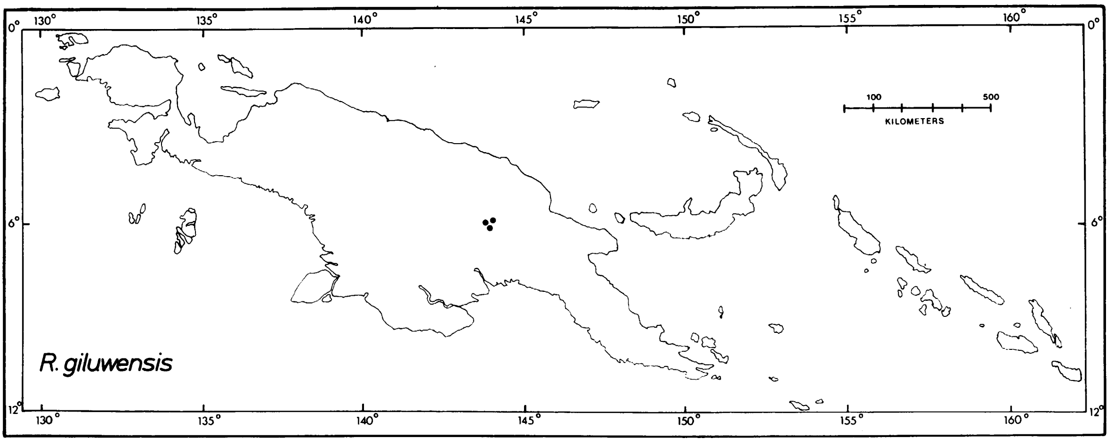

FIG. 27. Distribution map of *Rattus giluwensis*. Locality records are indicated by dots.

gaba, and Kawongu, ranging between 2195 and 3600/3660 m. These sites are all within 12′ S or E of one another (fig. 27).

MEAN MEASUREMENTS (IN MM.): External: head and body 151; tail 99; hind foot (s.u.) 30. Skull: occipitonasal length 36.4; braincase width 16.0; bulla length 6.1; crowns m$^{1-3}$ length 6.2. (See table 20 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 35 or less.

DESCRIPTION: *Rattus giluwensis* is one of the smaller species of *Rattus* in New Guinea. The pelage is very thick and soft and no spines are present. The dorsal pelage is a rich cinnamon brown and is well mixed with longer black guard hairs. Length of the fur middorsally is 15–22 mm. of which all but the last 3 mm. is dark gray. The terminal 3-mm. segment is a rich rufous brown. The black guard hairs measure to 30 mm. and are particularly conspicuous posterodorsally. The facial region and ears are similarly colored, and the ears are lightly clothed in short brown hairs. The black muzzle vibrissae measure to 35 mm. The dorsal pelage blends to a yellowish gray in the ventral region where the pelage is also thick and relatively long. All but the apical 2 mm. of the ventral fur is dark- or steel-gray and the hairs are tipped with yellow-buff to cinnamon. Ventral fur length is about 10 mm. No guard hairs occur ventrally. The short, dark brown tail is uniformly colored. It has 7 scales per cm. and the relatively inconspicuous tail hairs are about 2–2.5 mm. long. All feet are dark brown and are covered dorsally by light brown hairs.

The mammary formula, hitherto unpublished, is $2 + 2 = 8$.

The juvenile pelage closely resembles that of the adult except for less well-developed guard hairs and less rich cinnamon brown coloration.

The delicate, thinly boned skull has a relatively large cranial region when compared to the rostrum (fig. 28). The incisive foramina are long, narrow, and almost straight-sided. They terminate 0.5–1.0 mm. posterior to the anterior face of m^1. The palate extends posteriorly to about 1.0 mm. beyond the posterior face of m^3. Supraorbital ridging is indistinct and the interorbital width is narrow. The nasals are slightly flared and the auditory bullae are relatively expanded compared to most other species of New Guinean *Rattus* of this size.

DIAGNOSTIC CHARACTERS: This species has the shortest relative tail length (65 percent of head and body length) of any *Rattus* native to New Guinea. It shares with *R. richardsoni* the feature of relatively long, soft and dense pelage, although it is not as well developed in *R. giluwensis*. The long straight-sided appearance of the incisive foramina is distinctive among native *Rattus* of

TABLE 20
Measurements (in Millimeters) of Adult *Rattus giluwensis*
(N = 14 for skin measurements; N = 12 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	151.3 ± 3.39	12.69	136.0–187.0
Tail length	98.9 ± 1.58	5.93	84.0–108.0
Hind foot (s.u.) length	29.9 ± 0.36	1.36	28.0–32.0
Occipitonasal length of skull	36.4 ± 0.23	0.81	34.8–37.8
Condylobasal length	34.0 ± 0.23	0.81	32.3–35.4
Basal length	31.4 ± 0.27	0.92	29.8–33.0
Zygomatic width	18.6 ± 0.12	0.42	17.9–19.2
Interorbital width	5.4 ± 0.06	0.22	5.0–5.7
Interparietal length	4.5 ± 0.10	0.33	3.9–4.9
Interparietal width	9.5 ± 0.19	0.67	8.2–10.5
Braincase width	16.0 ± 0.08	0.28	15.4–16.5
Mastoid width	13.3 ± 0.08	0.28	12.9–13.7
Nasal length	13.4 ± 0.17	0.58	12.7–14.5
Nasal width	3.8 ± 0.05	0.17	3.6–4.0
Palatal length	19.2 ± 0.16	0.56	18.4–20.0
Incisive foramen length	6.7 ± 0.07	0.25	6.2–7.0
Incisive foramina width	2.1 ± 0.06	0.21	1.8–2.5
Inside m^{1-1} width	3.1 ± 0.09	0.32	2.5–3.7
Outside m^{1-1} width	7.6 ± 0.05	0.18	7.2–7.8
Bulla length	6.1 ± 0.07	0.24	5.8–6.7
Crowns m^{1-3} length	6.2 ± 0.03	0.11	6.1–6.5
Alveoli m^{1-3} length	6.6 ± 0.04	0.14	6.4–6.9
Crowns m^{1-2} length	5.0 ± 0.06	0.20	4.6–5.3

this size. The skull can be distinguished also, particularly from *R. s. hageni,* with which this species is sympatric, and from its ecological counterpart, *R. richardsoni,* by its narrower interorbital breadth and narrower incisive foramina.

PREVIOUS DESCRIPTIVE ACCOUNTS: The only description prior to this present treatment is that given by Laurie and Hill (1954) when they proposed it as a subspecies of *R. ruber.* Their description is based upon the holotype and nine paratypes. The two specimens from Kagaba and the single one from Kawongu that are included in our study, had not been collected at the time of the species' description. Misonne (1969, Pl. XX, fig. 119) has illustrated the upper and lower sets of molars of *R. giluwensis* (BM 53.264) as those of *R. ruber.*

HABITS AND HABITAT: The collector of the original specimens, F. Shaw Mayer, noted that these rats occupied subalpine grassland from Mt. Giluwe to the adjoining Lamende Range. They were also found in the forest (moss forest, presumably) on Mt. Giluwe and moss forest (3600 m.) and beech-moss forest (2800 m.) at Kagaba (A. B. Mirza—notation on specimen labels). On Mt. Giluwe these rats constructed shallow tunnels along the ground that led to nests among the tussock grass, and appeared to be eating grass seeds and small buds and flowers of alpine plants (F. Shaw Mayer, unpubl. notes of June 10, 1951).

Subalpine grasslands generally begin at 3050 m. (Rutherford, 1964). Pockets of subalpine grasslands may also invade lower altitudes to about 2285 m. These lower reaches may be the effect of localized frost hollows (Henty, 1972). The subalpine tussock grasslands are above the cloud forest zone and cover the summit area.

The known altitude range for the rat is 2195 m. to 3600 m. and it shares with *R.*

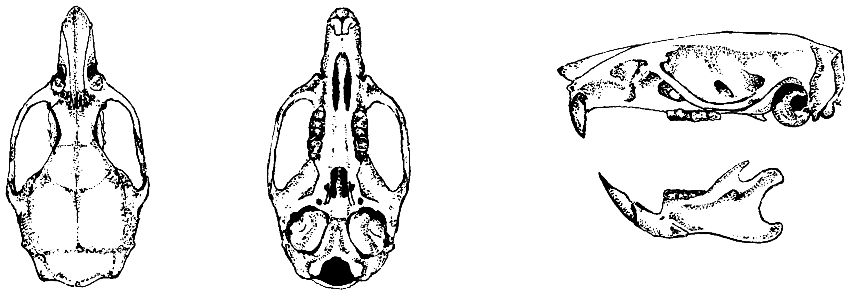

FIG. 28. Dorsal, ventral, and lateral views of skull of adult *Rattus giluwensis*, BBM 101939, from Mt. Giluwe. Occipitonasal length 36.9 mm.

niobe the highest known altitude for any *Rattus* in Papua New Guinea. In Irian Jaya, where *R. giluwensis* has never been recorded, only *R. richardsoni* and *R. niobe* reach higher altitudes.

The climate on Mt. Giluwe is cold and wet, and the surface humus, in which the tussock grasses grow, is subject to constant fracturing and reshaping by needle ice (G. S. Hope, 1976). The rats must utilize natural crevices and form burrow systems and extensive runways throughout the friable humus. Alpine bogs are common on at least the western slopes of Mt. Giluwe and thus much of the soil is continuously waterlogged (Wade and McVean, 1969).

SYMPATRY: *Rattus giluwensis* is sympatric with *Rattus niobe niobe* and, in Kagaba, also with *Rattus steini hageni.*

TAXONOMIC HISTORY: *Rattus giluwensis* was first described by Laurie and Hill (1954) as *Rattus ruber melanurus* from a collection obtained three years earlier by F. Shaw Mayer. Later, Hill (1960) discovered that the name was preoccupied and proposed *Rattus ruber giluwensis* as a replacement. Laurie and Hill (1954) noted a strong resemblance between *R. ruber giluwensis* and *R. ruber rosalinda,* but they judged the distinctions to be subspecific in nature. *Rattus ruber rosalinda* is a synonym of *Rattus steini hageni* (see Discussion of *R. s. hageni*). The sym-

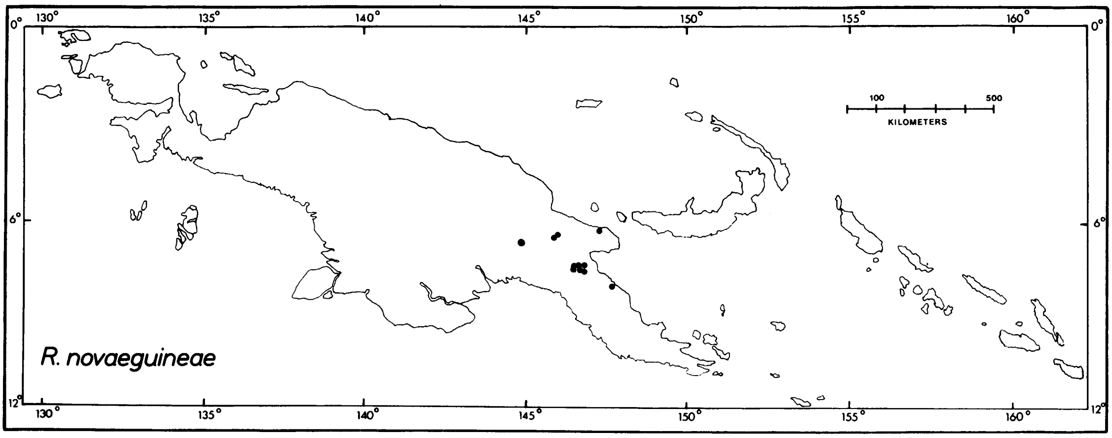

FIG. 29. Distribution map of *Rattus novaeguineae*, new species. Locality records are indicated by dots.

TABLE 21

Measurements (in Millimeters) of Adult *Rattus novaeguineae*

(N = 81 for skin measurements; N = 78 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	168.1 ± 1.65	14.84	135.0–200.0
Tail length	159.9 ± 1.38	12.39	131.0–185.0
Hind foot (s.u.) length	37.4 ± 0.17	1.53	34.0–41.0
Occipitonasal length of skull	41.1 ± 0.24	2.15	36.2–45.0
Condylobasal length	38.7 ± 0.25	2.19	33.4–42.6
Basal length	35.7 ± 0.25	2.22	30.6–39.6
Zygomatic width	19.4 ± 0.10	0.92	17.1–21.4
Interorbital width	5.8 ± 0.03	0.28	5.2–6.7
Interparietal length	5.5 ± 0.05	0.40	4.3–6.3
Interparietal width	10.8 ± 0.07	0.66	9.3–12.6
Braincase width	16.4 ± 0.06	0.53	15.0–17.8
Mastoid width	14.0 ± 0.05	0.46	13.2–15.3
Nasal length	15.4 ± 0.11	1.01	12.7–17.7
Nasal width	5.1 ± 0.05	0.41	4.3–6.3
Palatal length	21.9 ± 0.15	1.32	18.9–24.6
Incisive foramen length	6.7 ± 0.06	0.56	5.4–8.2
Incisive foramina width	2.7 ± 0.03	0.28	2.2–3.4
Inside m^{1-1} width	4.1 ± 0.05	0.45	3.0–5.0
Outside m^{1-1} width	8.7 ± 0.05	0.43	7.8–9.7
Bulla length	6.0 ± 0.03	0.27	5.3–6.7
Crowns m^{1-3} length	6.4 ± 0.03	0.25	5.8–6.9
Alveoli m^{1-3} length	6.8 ± 0.03	0.25	6.1–7.5
Crowns m^{1-2} length	5.3 ± 0.03	0.26	4.8–5.8

patry of this with *R. giluwensis* at Kagaba confirms their integrity as distinct taxa at the level of full species.

Rattus novaeguineae, New Species
Taylor and Calaby

HOLOTYPE: Skin and complete skull, adult male, BBM 54518, collected September 14, 1967, by A. B. Mirza, Kalolo Creek, Papua New Guinea, 1070 m.

DISTRIBUTION: *Rattus novaeguineae,* as presently known from museum collections, has a restricted distribution both geographically and altitudinally. Occurs from Kassam westward to Karimui in the north, and southward to Koranga, at altitudes ranging from 740 to 1525 m. (fig. 29).

MEAN MEASUREMENTS (IN MM.): External: head and body 168; tail 160; hind foot (s.u.) 37.4. Skull: occipitonasal length 41.1; braincase width 16.4; bulla length 6.0; crowns m^{1-3} length 6.4. (See table 21 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 36.0 or less.

DESCRIPTION: The holotype was collected at a locality that is in the center of the known distribution of this species. The skin measurements are 350 mm. (total length), 165 mm. (tail length), 40 mm. [hind foot (s.u.)], 22 mm. (ear from notch), and 16 mm. (ear from crown). The 20 skull measurements of the holotype (listed in mm. and in the same order as in table 21) are: 42.3, 39.7, 36.8, 19.3, 5.6, 5.6, 11.7, 16.7, 14.0, 16.3, 4.8, 22.6, 7.1, 2.9, 4.2, 8.5, 6.2, 6.4, 6.6, 5.2, and the molars are moderately to well worn.

This is a fairly harsh-furred, medium-sized rat which as an adult possesses spinous pelage both dorsally and, to a lesser extent, ventrally. Dorsal coloration is deep brown tinged by cinnamon-colored tipping. It is almost identical in dorsal body coloration to that of the sympatric species, *R. s. hageni,* with which it has been lumped until now under the misunderstood complex formerly

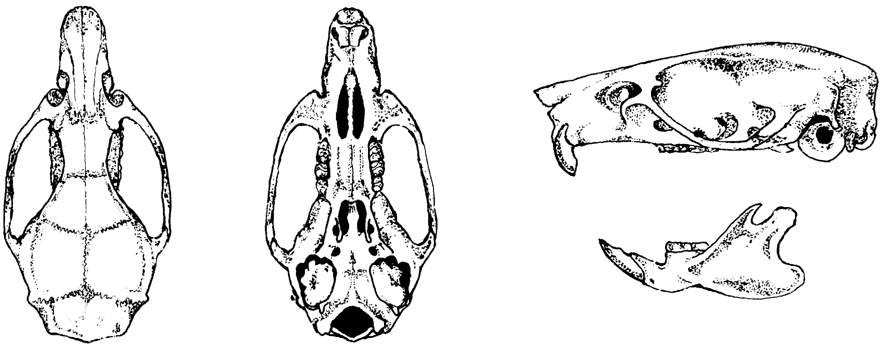

FIG. 30. Dorsal, ventral, and lateral views of skull of adult *Rattus novaeguineae*, new species, BBM 97912, from Minava. Occipitonasal length 43.0 mm.

called *ruber*. Dorsal hairs are 14–16 mm. long, of which the last 2 mm. forms the tipping, and the remaining part of the hair is translucent and forms the harsher broader portion of the spine. Short medium gray underfur is present as well as black-tipped guard hairs that measure to 30 mm. The facial region is also spinous, and the muzzle vibrissae measure to 60 mm. The ears are self-colored and are sparsely covered by very short brown hairs. The ventral pelage is usually white or yellow to the base and contrasts sharply with that of the dorsal side. Only when considerable gray underfur extends ventrolaterally is the demarcation less obvious. Even in this condition, there is, with rare exception, a white or yellow midventral lengthwise streak from fore to hind legs. The ventral spinous pelage measures 9–10 mm. long and is white or yellow for its entire length. In light-bellied individuals, the underfur is also the same color. The long tail is usually a uniform medium brown for its entire length, although white tipping or mottling occasionally occurs (e.g., AMNH 222579, 222582). There are 10 rows of tail scales per cm., and the tail is sparsely covered by very short hairs. The dorsal surface of the feet is covered by white hairs.

The juvenile pelage is soft and is dark brown-gray, and the cinnamon tipping is only faintly developed. The ventral pelage is white to the base either over the entire venter or at least midventrally. We examined one juvenile (BBM 54047) which had a white tail tip of 15 mm.

The mammary formula is 2 + 2 = 8 on all adult females.

The skull most closely resembles that of smaller individuals of *Rattus leucopus* and *R. novaeguineae* may be most closely related to that species. The skull is slightly elongate with a robust rostral region and a relatively narrow interorbital width (fig. 30). The incisive foramina are bowed laterally and extend posteriorly to a position in line with the anterior face of the molar rows. The palate terminates 1.5 mm. posterior to the molar rows. Supraorbital-temporal ridging is discernible but not very conspicuous and rises about 0.5 mm. above the cranium. The nasals are long and flare at their terminus. The bullae are relatively small.

The juvenile skull also possesses bowed foramina and is similar to that of the adult except for a proportionally larger cranium and absence of supraorbital-temporal ridging.

PREVIOUS DESCRIPTIVE ACCOUNTS: None.

REMARKS: *Rattus novaeguineae* warrants comparison with both *R. s. hageni* and *R. leucopus* because of its superficial resemblance to these two taxa, only one of which, *R. s. hageni*, is sympatric with it.

External body proportions will readily distinguish *R. novaeguineae* from *R. s. hageni*. *Rattus novaeguineae* is not only a larger rat in absolute size, but more importantly for identification the tail averages 95 percent of the head and body length and the hind foot is 22.3 percent of that length. *Rattus steini hageni,* on the other hand, has an average tail length that is 87 percent of the head and body length and a hind foot that is 21.4 percent of that length.

Pelage color and quality also aid in separating the two species. *Rattus steini hageni* does not have the pure white or yellow lightly spinous venter that contrasts sharply with the dorsum, that is found in *R. novaeguineae.* If white occurs at all on the venter of the former species, it is as a white pectoral spot or streak and the ventral pelage is soft. The feet of *novaeguineae* are lighter and lack brown hairs.

The skull of *novaeguineae* has a relatively long wide rostrum and the molars are relatively narrow in comparison to total length. *Rattus steini hageni,* on the other hand, has a short rostrum and relatively robust molars, as well as greater convex curvature of the dorsal skull profile. The bullae of *novaeguineae* are relatively smaller (16.9 percent of basal length of skull) than they are in *hageni* (17.4 percent), the nasals are longer (43.1 percent) than those of *hageni* (40.9 percent), and the molars are narrower (6.4 percent) than they are in *hageni* (7.4 percent).

The following comparisons can be made with New Guinean *R. leucopus.* The most obvious external differences are the mammary formula that is 2 + 2 = 8 in *novaeguineae* and 1 + 2 = 6 in *leucopus,* the customarily plain tail of *novaeguineae* and the usually mottled tail of *leucopus,* and the relatively longer tail in *novaeguineae* (95 percent of the head and body length) compared to that of *leucopus* subspecies (85–88 percent). The pelage coloring, both dorsally and ventrally, is very similar.

The skulls of the two species have a strong resemblance in that they both are somewhat elongate, the incisive foramina are bowed, the molars are narrow, and the nasals are elongate and flared terminally. Relative to basal skull length, the interorbital width is 16.3 percent in *novaeguineae* and ranges from 16.8 to 17.2 percent in the three subspecies of *leucopus,* the nasal length is 43.1 percent in *novaeguineae* and ranges from 41.5 to 42.1 percent in *leucopus,* the nasal width is 14.3 percent in *novaeguineae* and ranges from 12.4 to 12.7 percent in *leucopus.*

HABITS AND HABITAT: The only habitat information available is from notes on specimen labels. They indicate that this species occurs in primary forest, secondary forest, and in grassland. It is recorded in association with brush along streams or along river banks in montane forest. It appears to be a ground dweller, but there is one record of a specimen on a fallen log six feet aboveground.

SYMPATRY: *Rattus novaeguineae* is sympatric with *Rattus exulans browni, Rattus steini hageni, Rattus rattus, Rattus verecundus mollis,* and *Rattus niobe niobe.*

TAXONOMIC HISTORY: This new species has no formal taxonomic history. *Rattus novaeguineae* has been identified in collections as *R. ruber,* less frequently as *R. leucopus,* or no assignment has been made. Specimens are currently held only in the collections of the American Museum of Natural History and the Bernice P. Bishop Museum. Lidicker and Ziegler (1968) suspected that more than one species referred to *R. ruber* existed in the Wau-Bulolo area and they were correct in identifying the specimens they recorded as belonging to only one of these species (*R. s. hageni*). Possibly the new species proposed here is the rat that provoked their comment.

Rattus jobiensis Rümmler, New Status

Rattus leucopus jobiensis Rümmler, 1935, p. 116.
Stenomys leucopus jobiensis: Rümmler, 1938, p. 191.
Rattus owiensis Troughton, 1945, p. 374.
Rattus biakensis Troughton, 1946, p. 409.
Rattus ringens jobiensis: Ellerman, 1949, p. 69.
Rattus ruber jobiensis: Tate, 1951, p. 331 (excluding specimens previously identified as *Rattus sansapor* Troughton).

HOLOTYPE: Skin and complete skull, adult male, ZM 45677, collected March 28, 1931, by Georg Stein, Japen (Jobi) Island, Schouten Group, Geelvinck Bay, Irian Jaya Province, Indonesia, presumably near sea level.

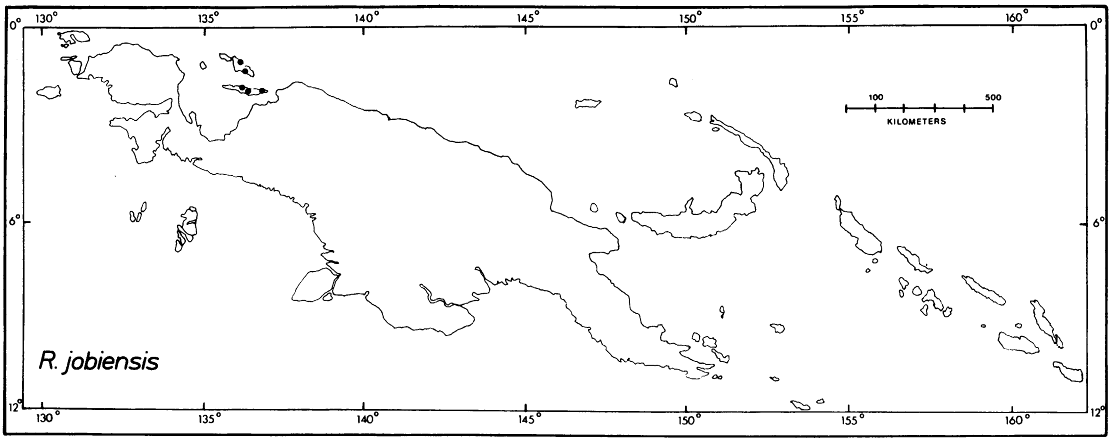

FIG. 31. Distribution map of *Rattus jobiensis*. Locality records are indicated by dots.

DISTRIBUTION: Confined to islands in Geelvinck Bay. Known only from Biak, Owi and Japen Islands, from sea level to 610 m. (fig. 31).

MEAN MEASUREMENTS (IN MM.): External: head and body 230; tail 212; hind foot (s.u.) 46.7. Skull: occipitonasal length 50.8; braincase width 18.1; bulla length 6.8; crowns m^{1-3} length 7.6. (See table 22 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 46 or less.

DESCRIPTION: The pelage of this large rat is very coarse and spinous and consists largely of spines and guard hairs with very little regular hair or underfur. Dorsally, it is a grizzled medium to dark brown, this appearance being mainly due to the pale brown tips of many of the translucent colorless spines which contrast sharply with the blackish- or tan-tipped guard hairs that are steel gray basally. The spinous portion of the dorsal pelage measures about 18 mm. in length, and the guard hairs are very long, reaching up to 50 mm. The sparse underfur is medium gray. The dark brown ears are sparsely clothed in short brown hair. Muzzle vibrissae may attain 60–70 mm. in length. The pelage blends laterally to develop into a buff or dusky yellow-white ventral pelage with a tendency to more rufous coloration in the pectoral and chin area on some specimens. The ventral hairs are about 10 mm. long and are composed primarily of spines. Beneath the spinous overlay is a sparsely distributed layer of fine, light to medium gray underfur. The tail is a uniform dark brown and, although it appears naked superficially, is sparsely covered by brown hairs up to 2 mm. long. There are about seven tail scales per cm. The dorsal surface of all four feet is lightly covered by white to light buff hairs.

The juvenile pelage is very similar, although it is steel gray rather than brown dorsally and the grizzled appearance and robust quality of the spines are less well developed.

The mammary formula is either 1 + 2 = 6 (Japen and Owi Islands) or 2 + 2 = 8 (Biak Island).

The large skull is elongate, particularly due to the presence of a long narrow rostrum, long nasal bones that protrude well beyond the anterior face of the upper incisors, and a relatively narrow zygomatic breadth (fig. 32). The incisive foramina are both longer and wider than they are in a similar species, *Rattus praetor,* and they terminate just posterior to the level of the anterior face of the molar rows. The palate ends about 2 mm. posterior to the molars. Supraorbital-temporal ridging is distinct but only lightly developed, even in the largest specimens. The molar rows are both relatively short and narrow in proportion to the size of the skull, and the bullae are in average proportion to overall skull size.

TABLE 22
Measurements (in Millimeters) of Adult *Rattus jobiensis*
(N = 6 for skin measurements; N = 8 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	230.2 ± 5.34	13.08	212.0–252.0
Tail length	211.8 ± 6.05	14.82	186.0–227.0
Hind foot (s.u.) length	46.7 ± 1.05	2.58	44.0–51.0
Occipitonasal length of skull	50.8 ± 0.81	2.28	45.9–53.1
Condylobasal length	47.9 ± 0.79	2.24	43.3–49.9
Basal length	44.8 ± 0.76	2.15	40.4–46.7
Zygomatic width	23.7 ± 0.39	1.12	22.4–25.7
Interorbital width	7.0 ± 0.13	0.36	6.2–7.3
Interparietal length	5.7 ± 0.34	0.98	4.6–7.1
Interparietal width	11.7 ± 0.31	0.88	10.0–12.9
Braincase width	18.1 ± 0.16	0.45	17.5–18.7
Mastoid width	16.0 ± 0.11	0.32	15.6–16.5
Nasal length	19.2 ± 0.48	1.35	16.9–21.0
Nasal width	5.3 ± 0.14	0.39	4.8–6.0
Palatal length	27.5 ± 0.45	1.27	25.0–28.7
Incisive foramen length	8.6 ± 0.26	0.74	7.4–9.7
Incisive foramina width	3.5 ± 0.18	0.50	2.8–4.2
Inside m^{1-1} width	4.6 ± 0.17	0.49	4.0–5.5
Outside m^{1-1} width	10.2 ± 0.14	0.40	9.6–10.8
Bulla length	6.8 ± 0.07	0.20	6.5–7.0
Crowns m^{1-3} length	7.6 ± 0.09	0.25	7.1–7.8
Alveoli m^{1-3} length	8.3 ± 0.08	0.21	7.9–8.5
Crowns m^{1-2} length	6.2 ± 0.12	0.35	5.6–6.6

The juvenile skull lacks supraorbital ridging, the incisive foramina are less bowed, and the nasal overhang is less conspicuous.

PREVIOUS DESCRIPTIVE ACCOUNTS: Rümmler (1935) proposed *jobiensis* as a subspecies of *R. leucopus* and described it largely or entirely from the type specimen. His additional description (Rümmler, 1938) referred to three more specimens, also from Japen Island, and he expanded upon skull features.

Troughton (1945, 1946), in proposing two new species, *R. owiensis* and *R. biakensis,* was actually providing further descriptions of *jobiensis*. One feature he noted was that *biakensis* had a larger hind foot than *jobiensis*. This was a reasonable distinction to use since he had apparently not seen the holotype of *jobiensis*. When Rümmler (1935) described the holotype, he made a mensural or typographical error of at least 7 mm. in the hind foot length, a mistake that was not detected until our own examination of this holotype. The hind foot is 44 mm. now on the dry skin and not 37 mm. as published (R. Angermann, personal commun.). Troughton (1946) provided the mammary formula of *biakensis* as 2 + 2 = 8.

Tate (1951) treated *jobiensis* as a subspecies of *Rattus ruber*. He added further descriptive features although, since he included *sansapor* as well as *biakensis* in the synonymy of *jobiensis,* the description is composite. Tate (1951) supplied skin and skull measurements of *owiensis* (holotype and allotype), *sansapor* (includes holotype), and *biakensis* (holotype). Measurements of the types were taken from Troughton's published accounts, so it is possible that Tate never examined this material himself. Furthermore, in his listing of measurements, Tate (1951, table 5) referred to *biakensis* as *R. ruber biakensis,* whereas he synonymized it under *R. ruber jobiensis* in the text. This was probably because it was type material. Tate (1951, table 5) also gave measurements

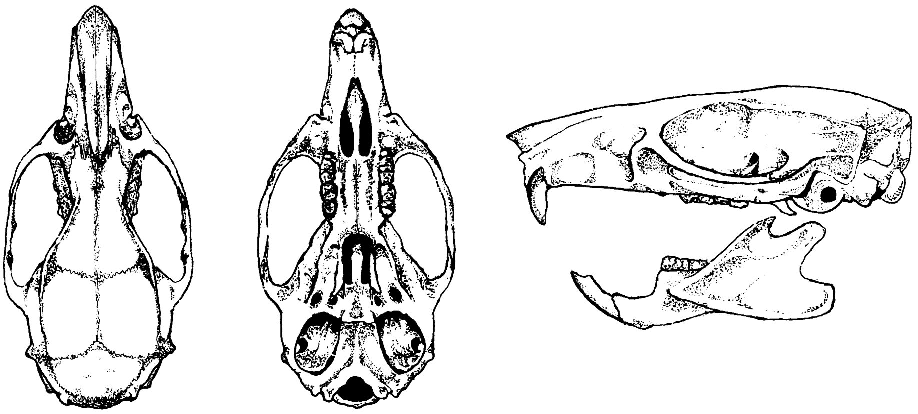

FIG. 32. Dorsal, ventral, and lateral views of skull of adult *Rattus jobiensis,* AMNH 222241, from Biak Island. Occipitonasal length 52.8 mm.

of the holotype of *jobiensis,* that includes 38 mm. for the hind foot measurement.

HABITS AND HABITAT: No description exists of the habits and habitat of *jobiensis,* but there are a few data on specimen labels. It has been trapped at the edge of jungle, in a native garden, and around a village. It appears to be strictly insular and a lowland inhabitant.

SYMPATRY: *Rattus jobiensis* is sympatric with *Rattus exulans browni* and *Rattus rattus.*

TAXONOMIC HISTORY: This species was first proposed (Rümmler, 1935) as *Rattus leucopus jobiensis.* Rümmler had a very broad view of the species *leucopus* and included several taxa that are now recognized as distinct species (Tate, 1951; Laurie and Hill, 1954; present study). Rümmler (1938) transferred *jobiensis,* along with the rest of his *leucopus* subspecies, to the genus *Stenomys.* Although Ellerman (1941, 1949) never acknowledged *Stenomys* as a genus, in his later study he included *jobiensis* under the subgenus *Stenomys,* in the *callitrichus* Group, and he placed it in the species *Rattus ringens.* In so doing, he was removing it from close affinity with *R. leucopus* from Australia. He was apparently unaware of *R. owiensis* and *R. biakensis* described by Troughton (1945, 1946).

Rattus owiensis was based on a subadult male holotype (AM M6993) and a subadult female allotype (AM M6992) from Owi Island. These are examples of young *R. jobiensis.* The two specimens in the collection that are labeled as the paratypes (AM M6994 male, M6996 male) are actually *Rattus exulans browni.*

Troughton (1946) was, with good reason, struck by the differences between the two other new species he had described, *R. biakensis* and *R. sansapor.* He recognized that *biakensis* had relatively narrower zygomatic dimensions, larger incisive foramina, a shorter molar row, and more elongate nasals than *sansapor.* He had apparently never seen the holotype or other specimens of *jobiensis* and did not realize that both *owiensis* and *biakensis* belonged to the same species. His *sansapor* is a *Rattus praetor coenorum,* but at that time he was comparing it with descriptions of mature (*bandiculus*) and immature (*coenorum*) examples of lowland *coenorum* that he viewed as distinct species. Troughton (1946) believed that *biakensis, sansapor,* and *bandiculus* had no racial alliance with either *R. mordax* or *R. ringens.* He would have disagreed with Ellerman's (1949) proposal to include all under *R. ringens.*

Tate (1951) recognized that *biakensis* was synonymous with *jobiensis,* but he also included *sansapor* as another synonym. He removed *jobiensis* from close affinity with

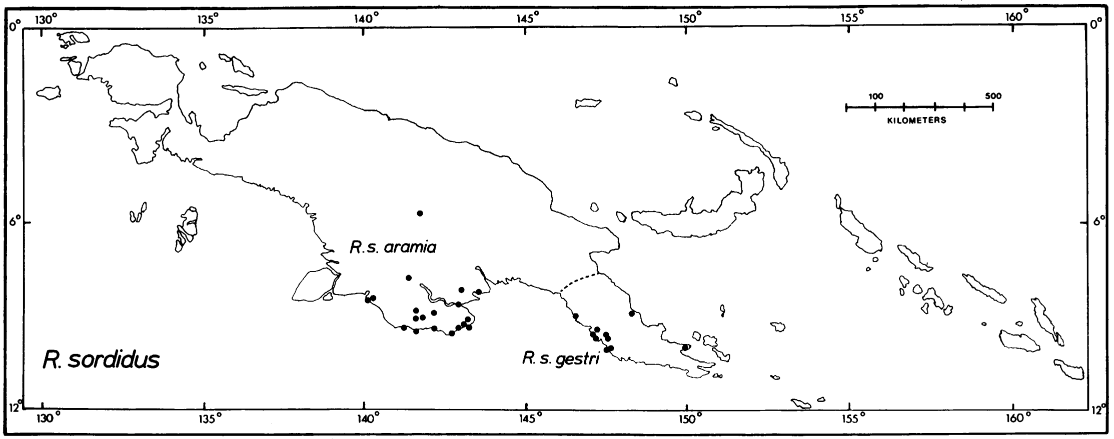

FIG. 33. Distribution map of *Rattus sordidus* in New Guinea. Locality records for each of the two subspecies are indicated by dots.

R. ringens (which he placed under *R. leucopus*) and, along with 10 other races, placed it under *Rattus ruber*. Tate (1951) regarded *owiensis* as belonging to *R. leucopus*, an assessment based primarily upon apparent agreement in the published mammary formula (1 + 2 = 6). He erred in the location of Owi Island, believing it to be one of the eastern Schouten Islands near the mouth of the Sepik River. The occurrence of a subspecies of *R. leucopus* so far to the north led Tate to suggest that as an alternative *owiensis* might be a *Rattus verecundus*. It seems unlikely that he ever studied the type material.

Laurie and Hill (1954) followed Tate's treatment of *jobiensis*. They kept *owiensis* as a full species but, like Tate (1951), suggested that it might be a race of *verecundus*. Ziegler (1971) also retained *owiensis* as a full species.

For nomenclatorial reasons that are explained in the section under Taxonomic History of *Rattus praetor,* neither *jobiensis* nor any other subspecies that Tate (1951) or Laurie and Hill (1954) included in this group can remain in *Rattus ruber*. Although *jobiensis* and *praetor* (the valid name of the group that includes their "*ruber*") are both large lowland rats and convergent, not only in their size relationships but also in the development of spinous pelage, they are morphologically discrete and thus *jobiensis* requires the status of a full species. Although its known distribution in New Guinea is extremely limited (Geelvinck Bay) and totally insular, it may actually be related to *Rattus* of the Indo-Malaysian region, a fauna that is extralimital to our investigation.

Rattus sordidus (Gould)

DISTRIBUTION: Southern New Guinea and Australia, in the latter country almost entirely east of 130° E longitude (Taylor and Horner, 1973). In New Guinea, restricted to the lowlands south of the major central cordillera that forms the backbone of the island; from Dobodura in eastern Papua New Guinea and coastally around the southeastern tip and northward and westward to Koembé, Irian Jaya. The two subspecies in New Guinea are geographically separated by a hiatus in their distribution around the Gulf of Papua, a region of very wet swamp forest. All localities are between sea level and 670 m. (fig. 33).

GENERAL DESCRIPTION: *Rattus sordidus* in New Guinea is, like its Australian ally, a large rat in which the tail is about 25 percent shorter than the head and the body length. The coarse and usually spinous pelage is grizzled dark brown or yellow-brown dorsally while ventrally it becomes yellowish gray. Both ears and tail are dark or medium brown, and the latter is relatively hairy for

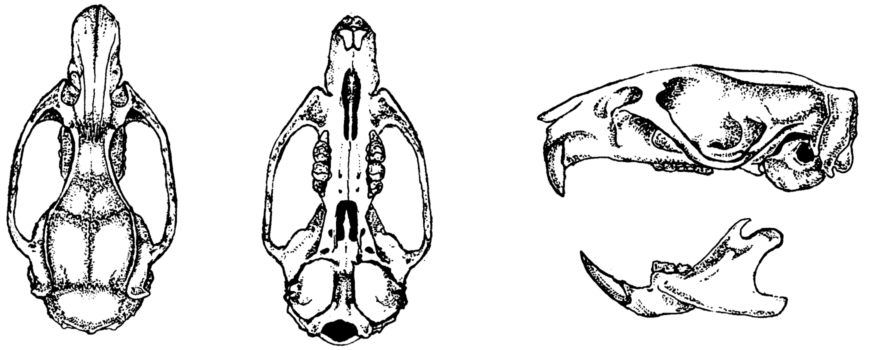

FIG. 34. Dorsal, ventral, and lateral views of skull of adult *Rattus sordidus aramia,* AMNH 105698, from Lake Daviumbu. Occipitonasal length 42.8 mm.

a *Rattus* of New Guinea. The mammary formula is 3 + 3 = 12.

The robust skull is very distinctive and readily separable from that of any other *Rattus* from New Guinea (fig. 34). It is wide and compact in conformation. The nasals terminate abruptly in line with, or just beyond, the anterior face of the incisors, and the zygomata are wide. The supraorbital ridging extends posteriorly as temporal ridging and rises about 0.5 mm. above the skull surface. Ventrally, the slitlike incisive foramina extend posteriorly at least to the level of the molar row and often to the posterior face of the first loph. The molars are wide, and the palate terminates immediately posterior to the end of the molar rows. The bullae are inflated to a greater degree, both absolutely and relatively, than in any other *Rattus* of New Guinea and in length average 21.8 percent of the basal skull length.

DIAGNOSTIC CHARACTERS: The inflated auditory bullae, prominent supraorbital-temporal ridging, narrow and long incisive foramina, and the mammary count of 3 + 3 = 12 together distinguish this species from all other native Australasian *Rattus.*

TAXONOMIC HISTORY: The earliest material of *Rattus sordidus* to be collected and described came from sites in Australia, and its taxonomic history has been reviewed in detail by Taylor and Horner (1973), who recognize three subspecies in Australia: *R. s. sordidus, R. s. villosissimus,* and *R. s. colletti.* The first specimens from New Guinea were collected at Kapa Kapa by Lamberto Loria, and described as a new species, *Mus gestri,* by Thomas (1897), who recognized its affinity to Australian rats typified by *Mus greyii.* This alliance was logical at the time since he was probably using Collett's (1887) description of *R. s. sordidus,* misidentified as *Mus greyii,* from Coomooboolaroo, Queensland, as the basis for comparison. No good description or access to specimens of *Mus sordidus* was available to Collett at that time. One of Collett's series (Zoologisk Museum, Oslo, No. 99) has since been reidentified as *R. s. sordidus* by Taylor and Horner (1973). This sequence of events explains the temporary and peripheral involvement of the name *Mus greyii* in the taxonomic history of *M. gestri.*

Jentink (1907a, 1908) recognized *M. gestri* as a valid species in his studies of mammals of New Guinea.

Both *gestri* and *sordidus* were shifted in succession to the genera *Epimys* Trouessart, 1881 (Thomas, 1910b; Longman, 1916) and *Rattus* Fischer, 1803, following the division of the large genus *Mus*, and the discovery of *Rattus* as a prior name (Thomas, 1916). Thomas (1921) selected one of the two syntypes of *R. sordidus* from the Darling Downs, Queensland, as the lectotype (BM 58.11.24.6), but did not select one from the two "co-types" of *gestri* that he designated when he described the species. His failure to do so was probably deliberate and motivated by the permission he had received to retain one of the "co-types" (BM 97.8.7.36 female) in the collection of the British Museum (Natural History). The other "co-type" (MCSN 3501 skin/3501a skull, male) remains in Italy.

Le Souef and Burrell (1926) listed both rats as *R. gestri* and *R. sordidus*.

The 1933–1934 Archbold Expedition collected a series from Baroka, Rona (Laloki River), and Wuroi (Oriomo River), all in southern coastal New Guinea, which was described as a new species, *Rattus brachyrhinus*, by Tate and Archbold (1935). They expressed surprise that a species so distinctive and abundant had never been described, and commented on the unusual mammary formula of 3 + 3 = 12. Obviously they had no suspicion that their new species might be *M. gestri*, but suggested that it may be identical to a species from Queensland. Tate (1936) pursued this alliance further by declaring that *R. brachyrhinus* was a member of the *Rattus tunneyi* Group and that it may be in the northernmost representative. In doing this he was now basing his assessment more on skull morphology than on mammary formula, which was reported to be lower in the Australian *tunneyi* Group. Again, he suggested that its closest relative was "an unidentified form occurring in North Queensland." This unidentified form was undoubtedly *R. s. sordidus* which also has a mammary formula of 3 + 3 = 12. Tate (1936) had no inkling at this time that *R. brachyrhinus* was identical with *R. gestri*. In fact, he suggested that *R. gestri* and *R. vanheurni* (=*R. nitidus*) were conspecific and related to the *diardii-neglectus* subgroup of his *Rattus rattus* Group. The presumed "topotype" of *vanheurni*, on which he based this assessment, was FMNH 31842 which we have seen and identified as *Rattus rattus*.

Troughton (1937) was the first to suggest that *R. gestri* and *R. brachyrhinus* were conspecifics, and he was also the first to recognize that Thomas (1897) had in part based his description of *R. gestri* on a young series. He viewed *R. vanheurni* as distinct from *R. gestri* at the species level. New material of *R. gestri*, this time from southwestern Papua (Aramia River) formed the basis of Troughton's (1937) description of a new subspecies, *R. g. aramia*.

Rümmler (1938) proposed that *gestri*, *brachyrhinus*, and *vanheurni* were all subspecies of *R. gestri*, but was apparently unaware of the recently described *R. g. aramia*. He stated that the mammary formula was either 2 + 3 = 10 or 3 + 3 = 12. Rümmler commented on Thomas's (1897) statement that *gestri* might be allied to the Australian *M. greyii*, and Tate and Archbold's (1935) suggestion that it should be included in the *tunneyi* Group of Australian rats, but was unwilling to endorse either view. Instead, he resolved the issue by simply stating that *R. gestri* is probably the same as some of the Australian *Rattus*. He felt unable to assess the relationships of the three subspecies that he included under *R. gestri* because of insufficient study material. He examined only the type and two other specimens of *R. gestri* and depended entirely upon the published descriptions of *brachyrhinus* and *vanheurni* for comparison. A final point about Rümmler's assessment of *R. gestri* is his suggestion that it might also be related to *Tryphomys adustus* from Luzon and to *Rattus rattus brevicaudatus* from Java.

Sody (1941), who was strongly influenced by mammary formulae in his assessments of murid relationships, proposed (it seems primarily on the basis of Thomas's count of 2 + 3 = 10 for *M. gestri* in the original description) a new genus, *Geromys*, and designated *Mus gestri* Thomas as type species. Fortunately, no one has subsequently supported this move. Sody recognized *Rattus brachyrhinus*, but he opposed Rümmler's (1938) inclusion of *brachyrhinus* and *vanheurni* as subspecies of *R. gestri*.

Ellerman (1941) formally endorsed Tate's (1936) proposal that *R. g. gestri* belonged to the *rattus* Group, even though he suggested that it might alternatively belong to the *tunneyi* Group. He recognized that Tate's unidentified northern Queensland rat was *R. sordidus* and placed it, *R. brachyrhinus*, and 11 other Australian taxa together under his *tunneyi-villosissimus* Group, and *R. g. gestri* and *R. g. vanheurni* in his *rattus* Group. Later, Ellerman (1949) adopted a different view. He listed *gestri, brachyrhinus,* and *vanheurni* as subspecies of *R. sordidus* along with 10 other Australian taxa, thereby transferring *gestri* and *vanheurni* out of his *R. rattus* Group. It is not clear whether Ellerman ever examined specimens of *vanheurni* or the *R. rattus* specimen that Tate (1936) had misidentified as *vanheurni*.

The last of the subspecies in this group to be described was *Rattus gestri bunae* by Troughton (1946). At the same time he reversed his earlier decision (Troughton, 1937) and now regarded *gestri* and *brachyrhinus* as distinct species largely on the basis of reputed differences in mammary formula, and in consequence was obliged to move his earlier proposed subspecies, *aramia,* from *gestri* to *brachyrhinus*. He relied heavily upon mammary formula in his evaluations, although he recognized the extreme to which Sody (1941) had gone in this regard. Troughton (1946) placed his new subspecies *bunae* in *R. gestri* because he believed that they shared a mammary formula of 2 + 3 = 10, but continued to regard *vanheurni* as a distinct species.

Dennis and Menzies (1978) proposed that the *R. sordidus* Group has membership in three species in New Guinea: *R. s. sordidus, R. gestroi,* and *R. bunae*. On the grounds of sharing identical karyotypes with the Australian *R. sordidus sordidus,* these authors place the western form from New Guinea in that subspecies. They consider the six known specimens of *R. bunae* to be close to this western form, but retain *bunae* as a species of doubtful affinity since the two are not sympatric (Menzies and Dennis, 1979). The third is *R. gestroi,* which they found, compared to *R. s. sordidus,* has a higher number of chromosomes, less rough and lighter pelage, smaller body size, and has a karyotype similar to that of *R. sordidus colletti* of Australia. They use molar row length (specifically, m^{1-3} alveolar length) as the measure for size comparisons.

We recognize two subspecies of *R. sordidus* in New Guinea, *R. s. gestri* and *R. s. aramia,* as well as the three subspecies known from Australia (Taylor and Horner, 1973). Our rejection of the recent proposal by Dennis and Menzies (1978) is on the following grounds. Measurements we took of m^{1-3} alveolar lengths are not all in agreement with those taken by Dennis and Menzies (1978, table 1) which they use to distinguish the groups (table 23). All three groupings of rats have similar mean m^{1-3} alveolar lengths by our measurements, a result that lends no support to the proposal by Dennis and Menzies (1978). Furthermore, mean head and body length for the six *bunae* specimens, 164 mm., is nearer to that of *gestri* (168 mm.) than to *aramia* (174 mm.) (*R. s. aramia* = *R. s. sordidus* in New Guinea, according to Dennis and Menzies, 1978). Among adults, minor differences in coloration and in degree of coarseness of the pelage are common and are exhibited even in samples from adjacent localities. We view these as inadequate discriminators at the species level. We, too, observed a tendency for *R. s. aramia* to be slightly more somber and spinous than *R. s. gestri,* and discuss this in more detail under the accounts of these subspecies, but do not treat these differences as robust distinguishing characters.

Their presentation of karyotypic differences between *R. s. aramia* (=*R. s. sordidus* in New Guinea of Dennis and Menzies, 1978) and *R. s. gestri* (=*R. gestroi* minus *bunae* of Dennis and Menzies, 1978), is unclear since their photographic plate labeled *R. sordidus* is that of *R. leucopus* (Dennis and Menzies, 1978, fig. 6). Difference in the diploid numbers of these two *R. sordidus* subspecies, 32 and 44 (Dennis and Menzies, 1978), also appears in the three Australian subspecies of *sordidus,* as designated by Taylor and Horner (1973). Recent work reinforces this earlier treatment of the Australian forms as monophyletic for, although the diploid states for the three subspecies are 32, 42, and 50, the subspecies all readily crossbreed in captivity and share karyotypic features that are unique among *Rattus* (Baverstock et al., 1977; Watts and Aslin, 1981). Critical tests of fertility and meiotic behavior between pair

TABLE 23

Mean Length of m^{1-3} Alveolar Measurement in Subdivisions of *Rattus sordidus*

Taxonomic Designation			Mean m^{1-3} Alveolar Length (in mm.)	
Dennis and Menzies (1978)		Present Revision	Dennis and Menzies (1978)	Present Revision
R. bunae	=	same six specimens and included in *R. s gestri*	7.50 (N = 6)	7.02 (N = 6)
R. gestroi	=	remaining specimens of *R. s. gestri*	6.97 (N = 23)	6.91 (N = 12)
R. s. sordidus in New Guinea	=	*R. s. aramia*	7.43 (N = 27)	7.10 (N = 102)

combinations of these Australian subspecies are being made (Baverstock et al., 1977).

Rattus sordidus gestri (Thomas)

Mus gestri Thomas, 1897, p. 611.
Rattus brachyrhinus Tate and Archbold, 1935, p. 4.
Rattus gestri brachyrhinus: Troughton, 1937, p. 119.
Geromys gestri: Sody, 1941, p. 260.
Rattus gestri bunae Troughton, 1946, p. 408.
Rattus gestri gestri: Tate, 1951, p. 349.
Rattus bunae: Tate, 1951, p. 351.
Rattus sordidus gestroi: Laurie and Hill, 1954, p. 109.
Rattus gestroi: Dennis and Menzies, 1978, p. 204.

LECTOTYPE: Skin and complete skull (except for small segment of right zygoma), adult female, BM 97.8.7.36, collected July 1891, by L. Loria, at Kapa Kapa, Papua New Guinea, presumably near sea level. We hereby select this lectotype from the syntypes (BM 97.8.7.36 female, and MCSN 3501 skin/3501a skull male) as the better preserved specimen.

DISTRIBUTION: *Rattus sordidus gestri* extends, from sea level to 670 m., over the coastal southeastern lowlands from Yule Island to Rigo on the western side of the Astrolabe Range and Menapi and Dobodura on the eastern side (fig. 33). The paucity of collecting in lowland areas from Rigo to Menapi limits our knowledge of the full extent of its range. Patches of suitable habitat in the form of savanna and grassland are intermixed with forests throughout the lowland area (White, 1975).

MEAN MEASUREMENTS (IN MM.): External: head and body 168; tail 131; hind foot (s.u.) 30.6. Skull: occipitonasal length 38.3; braincase width 15.6; bulla length 7.5; crowns m^{1-3} length 6.4. (See table 24 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 35 or less.

DESCRIPTION: Fine spines are intermixed with the coarse dark brown, or yellow-brown, grizzled fur. Average length of the dorsal hair is 16–18 mm., of which the basal portion is medium gray and the last 3 mm. are brown or yellow-rust. The spines are relatively soft and thin and are generally translucent. In most dorsal regions the fine black guard hairs are up to 30 mm. long and up to 40 mm. long on the rump. Dark gray underfur is present but not visible on the surface. The ears are an inconspicuous dull brown and are lightly covered by short brown hairs. The muzzle vibrissae are up to 40 mm. in length. The lateral portion of the body is grayish brown and ventrally the pelage is cream with the gray basal portion in evidence beneath the cream. Ventral body hairs are about 10 mm. long, of which the basal 8 mm. are medium gray and the terminal 2 mm. are cream. Spines are absent ventrally. The tail is medium to dark brown throughout and is covered by scale rows measuring 10

TABLE 24

Measurements (in Millimeters) of Adult *Rattus sordidus gestri*

(N = 24 for skin measurements; N = 15 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	167.7 ± 3.54	17.36	140.0–198.0
Tail length	131.2 ± 3.13	15.34	100.0–167.0
Hind foot (s.u.) length	30.6 ± 0.45	2.19	27.5–37.0
Occipitonasal length of skull	38.3 ± 0.40	1.56	35.6–40.8
Condylobasal length	37.2 ± 0.43	1.67	34.4–39.7
Basal length	34.6 ± 0.43	1.67	32.1–37.2
Zygomatic width	19.4 ± 0.26	0.99	17.6–21.0
Interorbital width	5.0 ± 0.07	0.28	4.5–5.5
Interparietal length	4.4 ± 0.13	0.52	3.6–5.2
Interparietal width	9.5 ± 0.17	0.66	8.5–10.8
Braincase width	15.6 ± 0.15	0.58	14.4–16.5
Mastoid width	13.6 ± 0.12	0.48	12.9–14.5
Nasal length	14.1 ± 0.20	0.77	13.2–16.3
Nasal width	4.4 ± 0.08	0.32	4.0–5.1
Palatal length	20.5 ± 0.23	0.90	18.9–21.9
Incisive foramen length	7.6 ± 0.13	0.49	7.0–8.8
Incisive foramina width	2.0 ± 0.07	0.26	1.6–2.6
Inside m^{1-1} width	2.8 ± 0.10	0.41	2.3–3.7
Outside m^{1-1} width	7.9 ± 0.11	0.43	7.2–8.5
Bulla length	7.5 ± 0.11	0.41	6.9–8.4
Crowns m^{1-3} length	6.4 ± 0.09	0.35	5.7–6.9
Alveoli m^{1-3} length	7.0 ± 0.11	0.42	6.0–7.5
Crowns m^{1-2} length	5.2 ± 0.07	0.27	4.8–5.8

per cm. Dark brown tail hairs measure 1.5–2 mm. long. The feet are covered dorsally by dull cream-colored and light brown hairs.

The juvenile pelage lacks spines, is more somber, and the hair tips are grayish rather than a shade of brown.

The mammary formula is 3 + 3 = 12.

The robust skull is slightly smaller in average size than that of *R. g. aramia*. Otherwise, the two are extremely similar and our description provided for this species adequately documents its major features. The juvenile skull has relatively wider molars and less well developed supraorbital-temporal ridging.

Previous Descriptive Accounts: Morphological accounts have been given by Thomas (1897), Le Souef and Burrell (1926), Tate and Archbold (1935), Tate (1936), Troughton (1937), Menzies (1973), Dennis and Menzies (1978), and Menzies and Dennis (1979). Most are rewordings of earlier descriptions. Tate (1936) provides some measurements of the syntypes.

The greatest controversy has been about the mammary formula and this feature has been used heavily in systematic assessments (see section on Taxonomic History).

Rümmler (1938, Pl. VI, Illus. 7) has illustrated dorsal, ventral, and lateral views of the skull of the syntype BM 97.8.7.36, Tate (1936, fig. 8) illustrated the ventral and lateral views of *R. brachyrhinus* (AMNH 104224) from Baroka, Dennis and Menzies (1978, fig. 5) have photographed the karyotype, and Menzies and Dennis (1979, Pl. 3a) have published a colored photograph of a live specimen.

Remarks: The southwestern and southeastern coastal regions of southeastern Papua New Guinea have been poorly collected, especially at sea level sites. Much of this area is lowland forest interspersed with grassland and some is mangrove swamp. There appears to be nothing to prevent *R. s.*

gestri from extending sporadically right to the southern tip and up the east coast to at least Dobodura. There are no morphological features in the samples collected at Menapi and Dobodura, the two east coast localities from which the rat is recorded, to warrant separation at the subspecies level from those near the type locality, Kapa Kapa, on the west coast of this region. *Rattus sordidus bunae* is, in our view, a synonym of *R. s. gestri*. Features that Troughton (1946) used to distinguish *bunae* as a subspecies fall within the normal variation of *gestri*.

HABITS AND HABITAT: *Rattus sordidus gestri* is basically a grassland rat. It occurs in open *Eucalyptus* forest associated with kunae (*Imperata cylindrica*) savanna and in the lowest edges of rain forest that abut savanna (fig. 21). It is known to occur from sea level to 670 m. Except for short notations on a few specimen labels, as just given, there is no description of the habits or habitat of this rat except that Dennis and Menzies (1978) and Menzies and Dennis (1979) describe it as adapting mainly to a woodland type of habitat.

SYMPATRY: *Rattus sordidus gestri* is sympatric with *Rattus exulans browni, Rattus mordax mordax, Rattus leucopus doboduroae, Rattus verecundus verecundus,* and *Rattus rattus*.

TAXONOMIC HISTORY: Following Thomas's (1897) description of *M. gestri* no further specimens were collected until the 1933–1934 Archbold Expedition. In the intervening period such comments as were published (Jentink, 1907a, 1908; Thomas, 1910b, 1916; Longman, 1916; Le Souef and Burrell, 1926) were merely listings, generic name changes, or brief descriptions based on the original. Tate and Archbold (1935) described the Archbold material as a new species, *R. brachyrhinus*. During the following couple of decades there was a great upsurge in the study of the rodents of New Guinea and eastern Indonesia based on new collections and some re-examination of the older specimens. In the new material were specimens from a new locality, that Troughton (1946) described as *R. g. bunae,* and reported the mammary formula as 2 + 3 = 10.

The failure to appreciate the identity of *R. gestri* and *R. brachyrhinus* and the various alignments of these two nominal species with *R. vanheurni* and the *tunneyi* and *rattus* groups by a number of authors (Tate, 1936; Troughton, 1937, 1946; Rümmler, 1938; Sody, 1941; Ellerman, 1941, 1949) has been discussed previously. The mammary formula was used as one of the key diagnostic features in these arguments, and Thomas's (1897) erroneous recording of that of *M. gestri,* which was not questioned, was central to the whole problem.

Thomas (1897) had before him 20 specimens from Kapa Kapa which, according to Tate (1951), contained a female of another species with the mammary formula of 2 + 3 = 10. Troughton (1937) suggested that Thomas's series were young rats. We have re-examined all we could locate of the original series, eight specimens, including the syntypes, and agree with Troughton that they are young animals. The largest, which are the syntypes, have occipitonasal lengths that are almost 2 mm. less than the mean of *R. s. gestri*. All but one other small adult are subadults. Contrary to Tate's (1951) statement that the series contained more than one species, all the specimens we saw belong to a single taxon. The only mammary formula that we could obtain from this original series was one of 3 + 3 = 12. Tate (1951), however, said that the syntype BM 97.8.7.36 had a mammary formula of 3 + 3 = 12, a count that we could not verify on that specimen. The probable reason for Thomas's record of a lower formula is that it is often difficult or impossible to locate the anterior pectoral teats on the dry skin of young nulliparous female.

In his 1951 monograph Tate made some progress in solving the true relationships of the various forms. He sank his *R. brachyrhinus* in the synonymy of *R. g. gestri,* listed *R. g. aramia* as an "extremely weak race" of *R. gestri,* and no longer regarded *R. vanheurni* as a relative of *R. gestri*. According to Tate the type of *R. vanheurni* was a young animal and, although he made no decision on its taxonomic status, he thought that it would probably prove to be conspecific with one of the species of *Rattus* found on the Vogelkop Peninsula. With Troughton's incorrect mammary formula in mind he raised *bunae* to the status of a full species and thus questioned its affinity to *gestri*. Instead, he suggested that it might be related to *lacus* (a subspecies of the Australian *R. lutreolus* that is not known in New Guinea), or perhaps to *R. rattus*.

Laurie and Hill's (1954) list of the various forms was based on the work of Ellerman (1949) and Tate (1951). They followed Ellerman in including *gestri* under *R. sordidus*. In doing so they emended the spelling *gestri* to *gestroi*, as the name was based on that of R. G. Gestro, Acting Director of the Museum at Genoa. In our view the spelling *gestri* was deliberate on Thomas's part and we do not regard it as an inadvertent error, and therefore we maintain the original spelling. Laurie and Hill viewed *brachyrhinus* as a synonym of *R. s. gestroi* and listed both *aramia* and *bunae* as subspecies of *R. sordidus*. However, they doubted that *R. s. aramia* was a valid subspecies and that *R. s. bunae* belonged with *R. sordidus*.

Misonne (1969) took the view that *R. gestri* might be a subspecies of *R. sordidus*, but made no assessment of the group. Ziegler (1971), Gressitt and Ziegler (1973), and Menzies (1973) list only *R. sordidus* as the name for this entire group and thus follow Laurie and Hill (1954).

Recently, Dennis and Menzies (1978) have determined the karyotypes of a number of *Rattus* species of New Guinea. They recognize three species in the *R. sordidus* Group in New Guinea: *R. s. sordidus* (also in Australia), *R. gestroi*, and *R. bunae*. *Rattus gestroi* is given full species status primarily on the basis that it has 44 chromosomes, whereas *R. s. sordidus* of Australia and their material from the Western Province of Papua New Guinea have 32. The comparison is not illustrated for apparently a mix-up has occurred in the karyotype plates since their figure 6 of *R. sordidus* from the Western Province is identical with their figure 4 of *Rattus leucopus* and both depict the latter species. They were unable to determine the karyotype of *bunae* and tentatively regard it as a full species of doubtful affinity. Dennis and Menzies claim that *R. gestroi* has a variable mammary formula of 2 + 3 = 10 or 3 + 3 = 12. In examining the specimens that Troughton (1946) used in describing this as a subspecies of *R. gestri*, they discovered that on the only specimen on which the teats were distinct, the mammary formula was 3 + 3 = 12 and not 2 + 3 = 10, as stated in the original description.

We have examined all museum specimens known to us that have been identified as *gestri*, *brachyrhinus*, or *bunae*. None of them provided us with convincing evidence that the mammary formula varies between 3 + 3 = 12 and 2 + 3 = 10. That a mammary formula can occasionally be variable and even asymmetrical in *Rattus* is well documented in Australian *Rattus* (Taylor and Horner, 1973) but is not the issue here. None of the New Guinean adult specimens of this rat that we examined demonstrated an alternate formula of 2 + 3 = 10, but rather showed a remarkable consistency of 3 + 3 = 12. Although we do not endorse the use of the mammary formula as a pivotal character in the assessment of *Rattus* and have used craniometric and other morphological features as the basis of our conclusion that *bunae* and *brachyrhinus* are synonyms of *R. s. gestri*, the mammary formula does in this case provide further evidence for the integrity of this subspecies.

Rattus sordidus aramia Troughton

Rattus gestri aramia Troughton, 1937, p. 119.

Rattus brachyrhinus aramia: Troughton, 1946, p. 408.

Rattus sordidus sordidus: Dennis and Menzies, 1978, p. 204.

HOLOTYPE: Skin and complete skull, young adult male, AM M4893, collected December 26, 1922, by Allan R. McCulloch, at Totani Village near the mouth of the Aramia River, Papua New Guinea, near sea level.

DISTRIBUTION: From Koembé, Irian Jaya Province of Indonesia, in the western portion of the south coast eastward to Totani Village, Papua New Guinea, and northward to the upper Fly River. All localities are from sea level to 100 m. (fig. 33).

TABLE 25
Measurements (in Millimeters) of Adult *Rattus sordidus aramia*
(N = 107 for skin measurements; N = 102 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	173.9 ± 1.69	17.52	142.0–220.0
Tail length	128.2 ± 1.10	11.39	103.0–166.0
Hind foot (s.u.) length	30.6 ± 0.17	1.74	27.0–36.0
Occipitonasal length of skull	38.7 ± 0.19	1.96	34.8–43.6
Condylobasal length	37.9 ± 0.20	2.00	33.9–43.0
Basal length	35.5 ± 0.20	2.01	31.3–40.6
Zygomatic width	19.7 ± 0.10	0.97	17.8–23.0
Interorbital width	5.3 ± 0.02	0.19	4.9–5.8
Interparietal length	4.6 ± 0.04	0.44	3.4–6.1
Interparietal width	9.6 ± 0.06	0.64	8.2–11.0
Braincase width	15.8 ± 0.05	0.48	14.5–17.5
Mastoid width	13.7 ± 0.05	0.50	12.4–15.1
Nasal length	14.1 ± 0.10	1.02	11.6–16.5
Nasal width	4.9 ± 0.04	0.41	4.1–6.2
Palatal length	21.3 ± 0.12	1.18	18.9–25.0
Incisive foramen length	7.8 ± 0.06	0.60	6.3–9.3
Incisive foramina width	2.1 ± 0.03	0.31	1.1–3.0
Inside m^{1-1} width	3.0 ± 0.03	0.34	2.1–4.1
Outside m^{1-1} width	8.2 ± 0.04	0.39	7.1–9.5
Bulla length	7.7 ± 0.04	0.44	6.7–9.0
Crowns m^{1-3} length	6.5 ± 0.03	0.30	5.8–7.5
Alveoli m^{1-3} length	7.1 ± 0.03	0.33	6.3–8.2
Crowns m^{1-2} length	5.3 ± 0.04	0.36	4.4–6.2

MEAN MEASUREMENTS (IN MM.): External: head and body 174; tail 128; hind foot (s.u.) 30.6. Skull: occipitonasal length 38.7; braincase width 15.8; bulla length 7.8; crowns m^{1-3} length 6.5. (See table 25 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 34.5 or less.

DESCRIPTION: The pelage is coarse and spinous. It is a dark brown color relieved by tan-rust tipping of the fur that gives it a grizzled appearance. The length of the dorsal pelage is about 14 mm.; the basal region is gray and the apical 2 mm. are tipped in rust. Spines are numerous, but are relatively fine and flexible. Fine black guard hairs are up to 30 mm. in length. Ears are dull brown and lightly covered with brown hairs. The black muzzle vibrissae measure to 35 mm. The sides are grayish brown and are considerably lighter than the mid-dorsal region. The ventral area is a mixture of cream and gray, for the hairs are either entirely cream or are gray-based and tipped in cream. The ventral area is lighter in overall color than that of *R. s. gestri*. The ventral hairs are about 9 mm. long and, if tipped, only at the terminal 2 mm. The ventral fur is coarse on larger adults, but is usually free of spines. The dark or medium brown tail is finely covered by dark brown hairs 2–3 mm. long and the tail gives the appearance of being relatively hairy for *Rattus* of New Guinea. The feet are covered by dull cream-white hairs often mixed with darker hairs.

The juvenile pelage is soft and spineless. It is less grizzled than the adult largely due to less development of brown tipping dorsally.

The mammary formula is 3 + 3 = 12.

The skull averages slightly larger than that of *R. s. gestri* but is virtually indistinguishable from it morphologically (fig. 34). Our description of the skull for the species is adequate for this subspecies.

PREVIOUS DESCRIPTIVE ACCOUNTS: Tate

FIG. 35. Aerial view of rain forest, savanna, and savanna forest in which *Rattus sordidus aramia* and *Rattus leucopus ringens* occur sympatrically. Photograph taken of left limb of Oriomo River, March–May 1936, by R. Archbold on 1936–1937 Archbold Expedition.

and Archbold (1935) viewed this subspecies merely as a western representative of *R. brachyrhinus* and, in their original description of the species, stated that this western group closely resembled the type series in dorsal coloration, but were slightly lighter ventrally.

Following the original description by Troughton (1937), this subspecies was largely dismissed until recently, except by Troughton himself. In 1946, he shifted the subspecies to *brachyrhinus* on the basis of his evaluations of the mammary formula, but provided no further diagnostic characters. It was not until Dennis and Menzies (1978) reevaluated this group, using karyotype evidence, that serious attention has been redirected to *aramia*. Unfortunately, the karyotype that is labeled "*R. sordidus,* from Daru, Western Province" (Dennis and Menzies, 1978, fig. 6) is that of *R. leucopus,* so it remains unillustrated. Menzies and Dennis (1979) have given a brief description of this form, illustrated with a colored photograph (Pl. 3b) of a live specimen.

REMARKS: *Rattus sordidus aramia* is a slightly larger and more robust rat than *R. s. gestri* and the pelage is more spinous, and in these features it shows stronger resemblance to *R. s. sordidus* of Australia. Geo-

FIG. 36. Habitat of *Rattus sordidus aramia* in savanna forest at Tarara. Grass is mainly *Imperata* and trees are chiefly *Melaleuca*. Photograph taken January 1937, by L. J. Brass on 1936–1937 Archbold Expedition.

graphically, it is closer to *R. s. sordidus* of Cape York, Australia, than is *R. s. gestri* and, by extrapolation from the geological record, its progenitors had potential access to Cape York about 6500–8000 years B.P. via a land bridge across the Torres Strait (Jennings, 1972). Whether or not *R. s. aramia* should be viewed as a synonym of *R. s. sordidus,* as suggested by Dennis and Menzies (1978) is currently being assessed (Taylor, Calaby, and Smith, MS).

HABITS AND HABITAT: *Rattus sordidus aramia* occupies the largest swamp country in the world (fig. 35). Fortunately, several collections have been made in this vast lowland and they provide some evidence that this subspecies is wide-ranging in the lowlands. Virtually nothing has been recorded about the habits and habitat of *aramia* except that it is a grassland inhabitant (fig. 36). Its progenitors some 6500–8000 years B.P. had access to what is presently the Arafura Sea (Jennings, 1972) and presumably were confluent with progenitors of populations that continue to inhabit the north coast of Australia (Taylor and Horner, 1973). The savanna land and fluvial plains of this southern coast of New Guinea are subject to strong seasonal changes. It has a monsoonal type of climate with a wet season in December through March and a drier period from May through August (Bowler et al., 1976). The seasonal climate is similar on the north coast of Australia.

SYMPATRY: *Rattus sordidus aramia* is sympatric with *Rattus leucopus ringens, Rattus leucopus ratticolor,* and *Rattus rattus.*

TAXONOMIC HISTORY: The first specimens of *aramia* were collected on the First Archbold Expedition of 1933–1934. A mixed series of this subspecies and *R. s. gestri* formed the basis of the description of *R. brachyrhinus* (Tate and Archbold, 1935). Not until Troughton (1937) culled out the western group, on the basis of material collected by one of his Australian Museum colleagues, did it become recognized as a subspecies, *R. gestri aramia*. Later, Troughton (1946) shifted *aramia* from *R. gestri* to *R. brachyrhinus* since he recognized that both shared the mammary formula of 3 + 3 = 12. He recognized, too, that *aramia* was the subspecies that the First Archbold Expedition collected in the western portion of Papua. Neither Rümmler (1938) nor Ellerman (1941, 1949) mention *aramia* in their assessments of *Rattus*. As stated previously, Tate (1951) doubted the validity of *aramia* as a distinct subspecies. He discounted Troughton's transfer of *aramia* to *R. brachyrhinus,* for by then Tate (1951) had sunk his earlier described *R. brachyrhinus* (Tate and Archbold, 1935) into the synonymy of *R. gestri*. Laurie and Hill (1954) also cast doubt upon the subspecific distinction of *aramia* and treated it as a possible synonym of *R. s. gestroi*.

In their recent work Dennis and Menzies (1978) treat *aramia* as a synonym of the Australian *R. s. sordidus* (see Taylor and Horner, 1973, for its distribution in Australia). They base their judgment primarily upon the fact that its karyotype is identical with that of *R. s. sordidus* of Australia and that the length of the molar rows of the two taxa are not significantly different (Dennis and Menzies, 1978, table 1). They believe that the disjunct savanna habitat of the Central and Western provinces of Papua New Guinea have been separated for a sufficiently long time to permit *R. gestroi* (=*R. s. gestri*) of the Central Province to become distinct at the species level. Dennis and Menzies (1978) thus imply that the invading Arafura Sea which separated New Guinea from Australia 8000 years B.P. (Nix and Kalma, 1972) did so too recently to permit even subspecific differentiation between *R. sordidus* populations inhabiting the two land masses.

We retain *R. s. aramia* as the valid name for the western subspecies of *R. sordidus* in New Guinea, as will be discussed in our separate study (Taylor, Calaby, and Smith, MS).

Rattus exulans (Peale)

Rattus exulans is a small rat, widely distributed in the southeast Asian mainland, the Philippines, Indonesia, and through the New Guinean region to the islands of the Pacific. The extremes of its Pacific range include Stewart Island, New Zealand, Easter Island, the Hawaiian Islands, and Kure Atoll. In this vast area *R. exulans* has been redescribed many times under different specific or subspecific names (Ellerman, 1941, 1949; Ellerman and Morrison-Scott, 1951; Tate, 1935; Laurie and Hill, 1954). It is presumably native to southeast Asia, and there is no doubt that it was introduced into much of its present range along with human exploration in prehistoric times.

Because a number of endemic subspecies have been described from various parts of New Guinea (Alston, 1877; Sody, 1933, 1934; Troughton, 1937, 1945), and this species has been there for a sufficiently long time that some geographical variation has evolved (Lidicker, 1968), we have treated it in the same way as the endemic species.

We have not compared material from New Guinea with *R. exulans* from other major regions.

Rattus exulans browni (Alston)

Mus browni Alston, 1877, p. 123.
Mus? echimyoides Ramsay, 1877, p. 15.
Rattus concolor lassacquèrei Sody, 1933, p. 433.
Rattus concolor manoquarius Sody, 1934, p. 175.
Rattus browni praecelsus Troughton, 1937, p. 121.
Rattus browni aitape Troughton, 1937, p. 122.
Rattus browni suffectus Troughton, 1937, p. 122.
Rattus browni tibicen Troughton, 1937, p. 123.
Rattus exulans browni: Rümmler, 1938, p. 211.
Rattus browni gawae Troughton, 1945, p. 374.

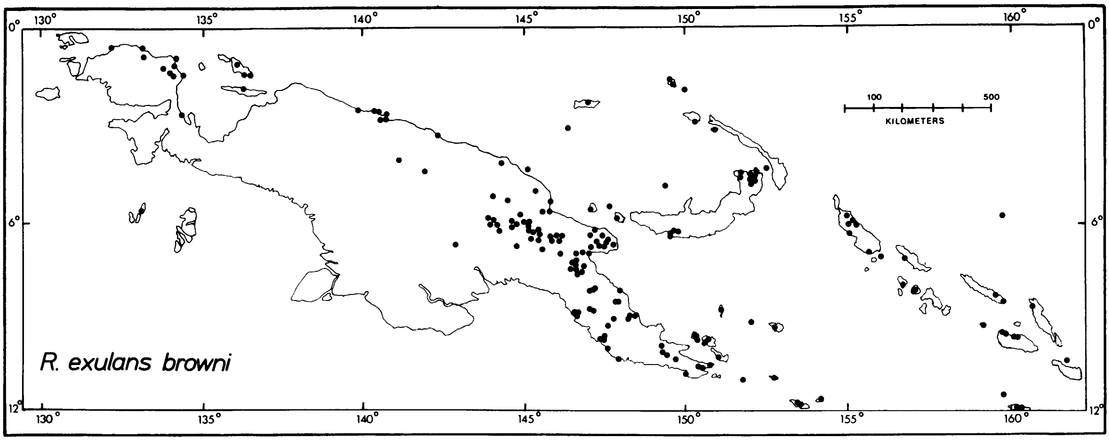

FIG. 37. Distribution map of *Rattus exulans browni*. Locality records are indicated by dots.

Rattus rennelli Troughton, 1945, p. 375.
Rattus exulans rennelli: Hill, 1956, p. 82.

LECTOTYPE: Skin and incomplete skull lacking hind skull and mandibles, young adult female, BMNH 77.7.18.26, collected on unknown date, by Reverend G. Brown, Duke of York Island or adjacent part of New Britain or New Ireland, Papua New Guinea, presumably near sea level.

DISTRIBUTION: From the northern part of the Vogelkop Peninsula and islands in Geelvinck Bay, eastward along the northern half of New Guinea to the southeastern extremity of the island. Its known distribution along the south coast is restricted to the area east of 146° E longitude. No records are known along the entire remaining part of the south coast, although it has been taken southward at Gu Daal, Great Kei Island. Occurs throughout the New Britain–Solomon Islands chain, the D'Entrecasteaux and Louisiade Archipelago, and on Murray Islands, within the political boundaries of Queensland, Australia. It is the most widely distributed of all *Rattus* of New Guinea (fig. 37). It ranges in altitude from sea level to 2880 m. on the mainland and from sea level to 2300 m. in its insular distribution. The extent of its distribution beyond Australasia is unknown.

MEAN MEASUREMENTS (IN MM.): External: head and body 127; tail 128; hind foot (s.u.) 26.1. Skull: occipitonasal length 31.9; braincase width 13.5; bulla length 5.7; crowns m^{1-3} length 4.8. (See table 26 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 29.5 or less.

DESCRIPTION: The quality and color of the pelage are highly variable in *R. e. browni*. At elevations near sea level the fur may be moderately harsh and spinous, whereas at 1500 m. and above the pelage is softer and may lack spines altogether. The dorsal pelage is medium brown at lower elevations and is usually slightly darker brown in rats occurring at the higher elevations. In all cases, the mid-dorsal pelage tends to be somewhat darker than the lateral portion. Melanistic individuals occur near sea level in populations from Hollandia (Jayapura) (AMNH 110099–110103, 150919) and Torokina, Bougainville Island (USNM 276907). Dorsal pelage measures 9–15 mm., the longer fur being generally associated with higher elevations. It is dark or medium gray for most of its length and the terminal 2 mm. is tipped in rust-brown or brown. The translucent spines, when present, are tipped in brown, and their length approximates that of the regular dorsal pelage. The underfur is steel gray. Dark brown to black guard hairs exceed the regular pelage in length by about 4 mm. The ears are self-colored and finely clothed with short, medium brown hairs. Black muzzle vibrissae are 30–50 mm. in length. The ven-

TABLE 26
Measurements (in Millimeters) of Adult *Rattus exulans browni*
(N = 656 for skin measurements; N = 763 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	126.6 ± 0.45	11.58	99.0–195.0
Tail length	128.3 ± 0.48	12.34	85.0–180.0
Hind foot (s.u.) length	26.1 ± 0.06	1.66	22.0–32.0
Occipitonasal length of skull	31.9 ± 0.07	1.83	28.3–38.2
Condylobasal length	29.6 ± 0.07	1.80	26.0–35.8
Basal length	27.3 ± 0.06	1.78	23.8–33.8
Zygomatic width	15.0 ± 0.03	0.74	13.3–17.6
Interorbital width	4.8 ± 0.01	0.29	4.1–5.8
Interparietal length	4.8 ± 0.01	0.39	3.5–6.4
Interparietal width	9.7 ± 0.02	0.55	8.2–11.3
Braincase width	13.5 ± 0.02	0.47	12.1–14.9
Mastoid width	11.5 ± 0.02	0.44	10.3–12.8
Nasal length	11.4 ± 0.03	0.92	8.6–14.9
Nasal width	3.5 ± 0.01	0.38	2.5–4.9
Palatal length	16.5 ± 0.04	1.05	14.3–20.1
Incisive foramen length	5.3 ± 0.02	0.51	4.0–7.0
Incisive foramina width	1.9 ± 0.01	0.26	1.2–2.9
Inside m^{1-1} width	2.6 ± 0.01	0.31	1.9–3.9
Outside m^{1-1} width	6.3 ± 0.01	0.37	5.4–7.7
Bulla length	5.7 ± 0.01	0.31	4.7–6.7
Crowns m^{1-3} length	4.8 ± 0.01	0.28	3.9–5.8
Alveoli m^{1-3} length	5.2 ± 0.01	0.28	4.3–6.2
Crowns m^{1-2} length	3.9 ± 0.01	0.29	3.0–4.8

tral pelage contrasts sharply with the dorsal, is spinous in individuals with abundant dorsal spines, and measures 5–10 mm. in length. Ventral coloration on regular hairs is gray basally with a yellow-white (or occasionally, cinnamon) tipping of 1–2 mm. and the spines, if present, are translucent. The plain tail is medium brown and has short brown hairs measuring 1–2 mm. There are 13–18 scale rows per cm. The feet are covered dorsally by white hair or a mixture of light brown mid-dorsally blending to white laterally. Juvenile pelage is very similar to that of the adult except it is shorter, grayer dorsally, lacks guard hairs or spines, and the ventral fur is tipped in white rather than in yellow-white.

The mammary formula is 2 + 2 = 8.

The skull is small and delicate and is the shortest in occipitonasal length of any *Rattus* in New Guinea (fig. 38). It has well differentiated supraorbital-temporal ridging that rises up to 0.7 mm. above the cranium on large skulls. The incisive foramina are bowed at midlength and extend posteriorly to the commencement of the molar row. The palate terminates 1 mm. posterior to the molar row. The nasals are slightly flared anteriorly and project well beyond the anterior face of the upper incisors. The bulla is inflated and conspicuously large relative to skull size.

The juvenile skull lacks distinct supraorbital ridging, the incisive formina are less bowed, and the cranium is inflated.

Diagnostic Characters: This is the only small *Rattus* that has a mammary formula of 2 + 2 = 8. *Rattus niobe,* the only other species that approaches *R. e. browni* in adult size, has a mammary formula of 1 + 2 = 6. *Rattus e. browni* is also the only small *Rattus* that may possess conspicuous spines.

The skull averages smaller than that of any other *Rattus* in New Guinea. It is the only small *Rattus* skull that has conspicuous supraorbital-temporal ridging. *Rattus exulans browni* has large bullae, for the ratio of bulla

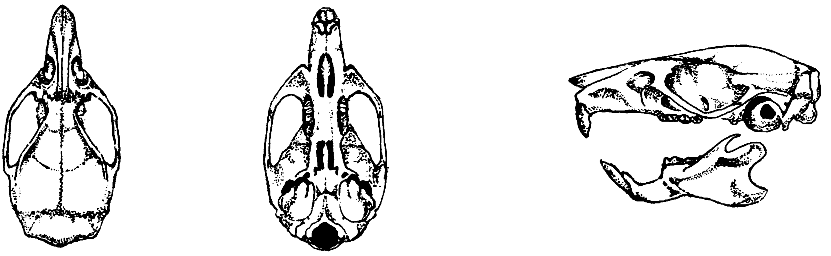

FIG. 38. Dorsal, ventral, and lateral views of skull of adult *Rattus exulans browni,* BBM 61041, from Wau. Occipitonasal length 32.2 mm.

length to basal skull length is 20.8 percent. Only *R. sordidus aramia* (21.9 percent) and *R. s. gestri* (21.8 percent) exceed *browni* in this ratio. All other native *Rattus* have a ratio less than 19.5 percent.

Rattus exulans browni is occasionally misidentified as young *R. rattus,* presumably due to its relatively long tail, prominent supraorbital-temporal ridging, or semi-commensal habits. It has also once been misidentified and designated paratype material of *R. owiensis* (see Taxonomic History of *R. jobiensis*). Both types of misalliance are the result of a failure to distinguish between adult and juvenile skulls, for in neither case does *R. e. browni* show close morphological affinity to these other species.

PREVIOUS DESCRIPTIVE ACCOUNTS: The first account was that of Alston (1877) when he proposed *Mus browni*. The type locality, Duke of York Island (or alternates, as listed), is presumably near sea level and the description of the skin included an account of the spinous quality of the fur of adults and the softer pelage of immature specimens. It also included skin measurements of two specimens and the correct mammary formula. In the same year, Ramsay (1877) described *Mus*? *echimyoides* from the same locality and again noted the spinous quality of the pelage. He made no mention of *M. browni*. Jentink (1907b) provided further measurements of specimens from other localities, a brief skin description, and noted that the tail was variable in length. Sody (1933) was so struck by the quality of the fur of specimens from Anggi Guyi Mountain (1800 m.) that he proposed a new subspecies, *R. concolor lassacquèrei* and provided a description of the soft pelage. He, too, specified the mammary formula and gave both skin and skull measurements of the holotype. Sody (1934) then described another subspecies, *R. concolor manoquarius,* largely on the basis of its shorter tail and grayer pelage. It is a lowland form and he provided skin and skull measurements of the holotype.

Tate (1935, fig. 3) illustrated the right upper molars of *browni* and characterized it as a short-tailed, harsh-furred species with an extra cusp in m^2 and a distinct anterior cingular tubercle on m^1. He acknowledged, however, that such cusp differences are not constant and usually represent individual variation. Tate (1936) discussed at length pelage differences in the *R. concolor* Group of New Guinea, in which he included both *browni* and *manoquarius* and provided measurements of skins and skulls of 19 specimens.

Troughton (1937) gave a brief description and measurements of the skins and skulls of the four subspecies that he proposed: *R. browni praecelsus,* a soft-furred highland form, *R. b. aitape,* a more spinous form from a lowland locality, *R. b. suffectus,* another spinous lowland rat, and *R. b. tibicen* from the eastern tip of Papua. Rümmler (1938), who synonymized Sody's subspecies with *browni,* gave a few measurements and an extended description of skin and skull features. He also illustrated the dorsal, ventral, and lateral views of the skull (Rümmler, 1938, Pl. VI, Illus. 8), and pointed out that the molars figured by Tate (1935) are atypical. Sody (1941) divided *R. concolor* into highland and lowland forms and included a brief description of pelage differences. He viewed the transition zone at approximately 1500 m. altitude, an approximation that our own much more extensive series supports.

Troughton (1945) provided brief further descriptions when he proposed *R. rennelli* and *R. b. gawae*. The holotype of the latter is a juvenile which Troughton apparently did not recognize. Tate (1951) gave brief descriptions of the various subspecies of *R. exulans* that had been described from New Guinea, and skin and skull measurements of the holotypes. Hill (1956), who viewed *rennelli* as a subspecies of *R. exulans,* supported his assessment with skin and skull measurements of several specimens that showed its close affinity to *R. e. exulans*.

Lidicker (1968, fig. 9) described and illustrated the male phallus of *R. exulans* of the eastern mainland of New Guinea and concluded, on the basis of phallic morphology, that *R. exulans* was the first of four invasions to New Guinea of modern species of *Rattus* that evolved elsewhere. The sample of *R. e. browni* taken by Lidicker and Ziegler (1968) was measured and summarized by altitude (*ibid.,* table 5), and they noted the gradual loss of spines from the pelage with an increase in altitude. They also provide information and mensural data on reproductive status over a one-month period.

Dwyer (1975) recorded mean weights and breeding information for *R. exulans* from the Eastern Highlands over a 10-month interval. *Rattus exulans* had the greatest mean litter size of any of the species he studied. Dennis and Menzies (1978) have described the karyotype and found it to be identical with that of *R. exulans* from southeast Asian countries, as reported and illustrated by Yong (1969, fig. 6) and Yosida (1973, fig. 2).

HABITS AND HABITAT: A number of workers (Lidicker, 1968; Lidicker and Ziegler, 1968; Gressitt and Ziegler, 1973; Dwyer, 1975, 1978) have demonstrated that *R. e. browni* is fundamentally an occupant of man-modified environments. It lives in a wide spectrum of habitats, such as grasslands and forest situations, including *Pandanus* and moss forests, and human habitations. It invades secondary forests, plantations of coffee, sweet potato, cocoa, cocoanut, and other cultivated crops, as well as native villages. This rat is both a ground dweller and arboreal, climbing in vegetation and occupying roofs in dwellings. Menzies and Dennis (1979) state that it is mainly terrestrial and normally lives in holes in the ground. They also state that it is a pest and village food stores often have to be protected by being raised on smooth posts. From sea level upward to almost 3000 m., the rat makes use of almost any type of cover available to it. Its limitations appear to be subalpine and alpine habitats and the vast southern portion of New Guinea west of 146° E longitude. The strength of these barriers is undoubtedly ecological rather than geographical, and the ecological factor may account also for its lack of establishment in Australia. Taylor and Horner (1973) have suggested that the northern Australian climate may be seasonally too dry for *exulans* and excludes it from that continent.

The above habitat accounts have largely been taken from notations on specimen labels. Rümmler (1938), who was the first to describe the mode of life of this subspecies, also derived his information from skin labels.

Johnson (1946) gave a graphic description of the commensal habits of *R. e. browni* following establishment of military camps on Bougainville Island during World War II. These small rats were successful in association with both *R. praetor* and *R. rattus,* each of which is a considerably larger species. On the other hand, Menzies and Dennis (1979) state that *R. exulans* is being displaced in many coastal villages by *R. rattus*. A label notation on specimens from Rennell Island indicates that the rats were taken in a sandy grass plain near the shore (Hill, 1956). Although the natural colonizing abilities of *R. exulans* are extraordinary, their commensal relationship with human beings and their general lack of regional distinctiveness led Braestrup (1956) to suggest that *R. e. rennelli,* the only non-flying mammal of Rennell Island, is a poor zoogeographic marker.

SYMPATRY: *Rattus exulans browni* is sympatric with *Rattus sordidus gestri, Rattus jo-*

biensis, Rattus leucopus dobodurae, Rattus novaeguineae, Rattus mordax mordax, Rattus mordax fergussoniensis, Rattus niobe niobe, Rattus niobe arrogans, Rattus nitidus, Rattus praetor praetor, Rattus praetor coenorum, Rattus rattus, Rattus steini hageni, Rattus steini foersteri, Rattus verecundus verecundus, Rattus verecundus mollis, Rattus verecundus unicolor, and *Rattus argentiventer* (at Tanah Merah on the north coast).

TAXONOMIC HISTORY: Alston (1877) described *Mus browni* from three adults and four presumed juveniles, but he did not designate a holotype. In the same year, Ramsay (1877) proposed the name *Mus? echimyoides* for an adult rat from the same locality, Duke of York Island. It must be assumed that he was not aware of Alston's paper. Peters and Doria (1881) recognized the synonymy but did not realize that *browni* had nomenclatorial priority for they used the name *M. echimyoides* for material from Humboldt Bay and Hatam. In referring to species of mammals from Duke of York Island, Thomas (1889) used *M. browni* rather than *M. echimyoides* and thus must have been aware that it was the earlier published name.

Thomas (1896, 1897) was the first to suggest that *M. browni* was a close ally of *M. exulans* and other forms now included in that species. In consequence, he used the name *browni* provisionally when he wrote a brief account of its widespread occurrence throughout the Papuan Archipelago and southeastern mainland of Papua. Jentink (1907a, 1907b), in listing further specimens of this rat from New Guinea, made reference to the synonymy first recognized by Peters and Doria (1881), but correctly acknowledged the priority of *browni*. Jentink (1908) was disturbed by Trouessart's (1904) inclusion of *Mus exulans* in the New Guinean fauna and rejected the possibility.

In his rationalization of the large genus *Mus*, Thomas (1916) transferred *browni* to *Rattus*, and in 1921 designated BMNH 77.7.18.26 female as lectotype of *R. browni*.

Dollman (1930) identified a specimen from the Arfak Mountains, Irian Jaya, as *R. browni*, yet Sody (1933) described a series of four rats from the same area as a new subspecies of highland *R. concolor, R. c. lassacquèrei*. He viewed *concolor* as a species distinct from either *R. exulans* or *R. browni*. Sody (1934) then described a new lowland subspecies from the same general area as *R. c. manoquarius*. Tate (1935) retained *browni* as a species distinct from *concolor*, primarily on the basis of an extra cusp on m^2, shorter tail, and spinous fur, although he included it in his "*concolor* Group." Tate (1936) suggested that *browni* may be only subspecifically distinct from *R. concolor*. Both Sody (1933, 1934) and Tate (1935, 1936) placed considerable importance on relative tail length in distinguishing their groups.

Troughton (1937) was the first to describe subspecies of *R. browni*. Largely on the basis of pelage color and quality and on relative length of the tail, he proposed four subspecies: *R. b. praecelsus, R. b. aitape, R. b. suffectus,* and *R. b. tibicen,* all from the eastern half of mainland New Guinea. Two of them, *aitape* and *tibicen,* are apparently based on single specimens. Rümmler (1938) appreciated that *R. exulans* was common and widespread throughout New Guinea and synonymized the named forms of *concolor* from New Guinea under *R. e. browni*. He was the first to recognize the variable nature of both external and skull features of this subspecies, and to point out that the molar features used by Tate (1935) to characterize *browni* were atypical. Sody (1941) continued to regard *lassacquèrei* and *manoquarius* as subspecies of *R. concolor* and now suggested that *browni* might also be a race of *concolor*. Ellerman (1941, 1949), however, followed Rümmler's synonymy, yet Troughton (1945) continued to subscribe to the older view and proposed another race of *browni, R. b. gawae,* based upon a single juvenile female that he apparently did not recognize as immature. He also proposed a new species, *Rattus rennelli,* related to, but larger than, *R. browni*. Frechkop (1948) chose Rümmler's synonymy. Tate (1951) accepted Troughton's and Sody's subspecies provisionally, and as a result treated *browni* in a very restricted sense by confining its distribution to the type locality, the Bismarcks, and western Solomon Islands. He supported Troughton's proposal of *rennelli* as a distinct species. Laurie (1952) and Laurie and Hill (1954) placed *echimyoides, lassacquèrei, manoquarius, praecelsus, aitape, suffectus, tibicen,* and *gawae* in synonymy under *R. e. browni,* but regarded *rennelli* as a full species. Wolff (1955) referred to the Rennell Island rat simply as *R. exulans,* while Hill (1956, 1968) was the first to formally list this rat as *R. e. rennelli.* He provided skin and skull measurements of four specimens and compared them to those of *R. e. exulans,* but unfortunately did not compare them also with *browni.* Both Braestrup and Hill (Braestrup, 1956) regarded the racial distinction of *rennelli* as very slight, however, they retained its subspecific designation.

Although earlier investigators had commented upon the similarity of *R. exulans* to *R. rattus,* Schwarz (1960) and Schwarz and Schwarz (1967) formalized it by treating all subspecies of *exulans,* including those of New Guinea, under the "*exulans* series" of *R. rattus.* Those from New Guinea are placed in *R. rattus vitiensis* of that series, and the tail length ratio was described as highly variable. These authors suggest that *vitiensis* has dispersed from Flores, a dispersal point of the ancestral *R. r. wichmanni,* along the north coast of New Guinea and from there to the Bismarck Archipelago and the Solomon Islands to as far east as the Samoan Islands. No other authors have supported the inclusion of *exulans* under *R. rattus.*

Lidicker (1968) quotes the view that *R. exulans* arrived in New Guinea a few thousand years ago with "Polynesian man," and states that it has attained some subspecific differentiation there despite its continued dependence upon a primary habitat of "kunai" grasslands, a presumably man-modified habitat. His analysis falls short of subspecific nomenclatorial designations. Lidicker and Ziegler (1968) assigned their collection of *exulans* from the Wau-Bulolo area to *R. e. browni,* following Laurie and Hill (1954) as their authoritative reference. External differences between high and lower altitude forms were discussed with new examples from their collection, and they were cognizant of the fact that the naming of races of *exulans* from New Guinea generally reflected this tendency.

RECENTLY INTRODUCED *RATTUS*

Four species of *Rattus, R. nitidus, R. rattus, R. norvegicus,* and *R. argentiventer,* are relatively recent arrivals to New Guinea, although it is not possible to date these introductions. When European voyagers first visited the eastern Indonesian region in the sixteenth century, they found a flourishing trade between the islands that had presumably been going on for many centuries. The trading stations included the Moluccas and the Vogelkop Peninsula. Food was of particular importance in the trade; rice was brought eastward from Java and perhaps other sources, and New Guinea supplied sago, skins of colorful birds, and slaves. The traders' substantial prahus and junks laden with food were no doubt ideal homes for commensal rats, and it is possible, and even likely, that *R. nitidus, R. rattus, R. argentiventer,* and further stocks of *R. exulans,* were unwitting immigrants during this early trade period. In eastern New Guinea most contact by sea in historical times has been with Australia and Europe, and it is probable that *R. rattus* in eastern New Guinea and *R. norvegicus* came from those sources.

These species warrant only brief review since our revision of New Guinea *Rattus* is directed solely to the native species.

Rattus nitidus (Hodgson)

Mus nitidus Hodgson, 1845, p. 267.
Mus ruber Jentink, 1880, p. 18.
Rattus nitidus: Hinton, 1918, p. 59.
Rattus vanheurni Sody, 1933, p. 435.
Rattus gestri vanheurni: Rümmler, 1938, p. 209.
Rattus sordidus vanheurni: Ellerman, 1949, p. 67.

HOLOTYPE: Skin and skull, BMNH 79.11.21.415, Nepal (not examined). [Hinton (1919) states that this is the type.]

DISTRIBUTION: *Rattus nitidus* in New Guinea is known only from the Vogelkop Peninsula, Irian Jaya Province, Indonesia, at Manokwari (=Doreh), Kebar Valley, and

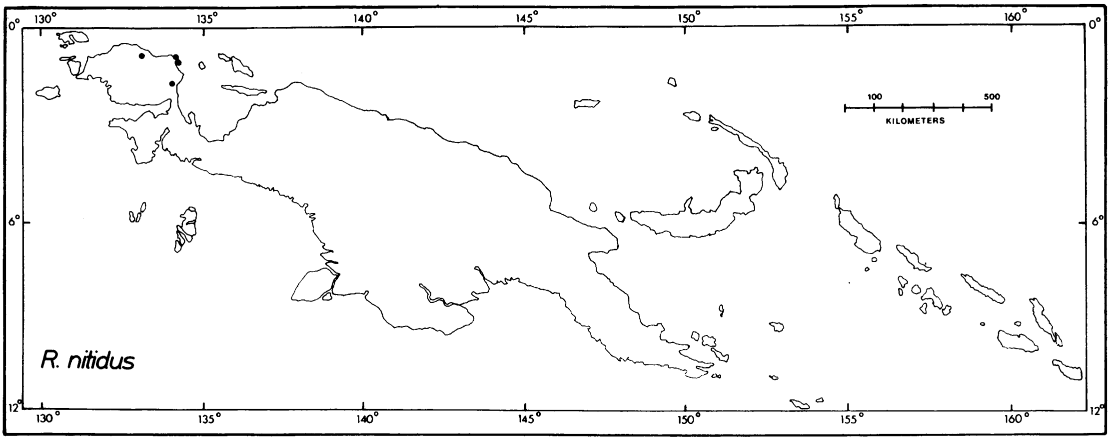

FIG. 39. Distribution map of *Rattus nitidus*. Locality records are indicated by dots.

Siwi at altitudes ranging from sea level to 800 m. (fig. 39).

MEAN MEASUREMENTS (IN MM.): External: head and body 166; tail 130; hind foot (s.u.) 34.9. Skull: occipitonasal length 41.3; braincase width 16.6; bulla length 6.9; crowns m^{1-3} length 6.4. (See table 27 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 36.5 or less.

DESCRIPTION: The pelage is without spines, and the dorsal fur is 14–15 mm. long, of which the last 2 mm. is tipped in rust color. The color of one of the specimens we examined (holotype of *M. ruber*) was so faded from the rusty brown color described by Jentink (1880) that accurate definition of color from this specimen is today impossible. According to Musser (1977) the dorsal pelage of *R. nitidus* is dark and slightly woolly. The ventral pelage is lighter than that of the dorsal side and measures 9–10 mm. in length. Musser (*ibid.*) states that it is consistently gray. There are seven rows of tail scales per cm., and the tail is shorter than the head and body length. The feet of the *R. ruber* holotype are covered dorsally by sparse hair that is now fawn color. Musser (*ibid.*) describes the feet of *nitidus* as pearly white.

The mammary formula of southeast Asian *R. nitidus* is 3 + 3 = 12 (Schwarz and Schwarz, 1967). Tate (1951) stated that it was 2 + 2 = 8 for the holotype of *M. ruber,* and Sody (1933) said that it was 3 + 2 = 10 for the holotype of *R. vanheurni,* but he was uncertain of this count. We located two pectoral and two inguinal teats on the right and two pectoral teats on the left, but no left inguinal teats on the holotype of *M. ruber*. The mammary count was 12 in the specimens that Musser (1977) examined, which includes those from New Guinea.

The skull of *R. nitidus* of New Guinea has been illustrated in dorsal, ventral, and lateral views (Calaby and Taylor, 1980, fig. 1). It has a strong resemblance to that of *R. rattus*. The features that most readily distinguish *R. nitidus* from the latter in New Guinea are the greater length of the nasals (40 percent or more of the condylobasal length in *nitidus*) and the anterior labial cusp that is either absent or very minute in *R. nitidus* whereas it is conspicuous in *R. rattus* (Musser, 1977).

HABITS AND HABITAT: Nothing is known about the habits or habitat of *R. nitidus* in New Guinea except that it is found in association with human occupation, both in houses and in gardens, and has not been found in primary forest (Musser, 1977).

SYMPATRY: *Rattus nitidus* is sympatric with *Rattus exulans browni* and *Rattus rattus* in New Guinea.

TAXONOMIC HISTORY: Presence of *R. nitidus* in New Guinea is of particular significance since a specimen of it had been described as the holotype of *M. ruber,* a rat

TABLE 27
Measurements (in Millimeters) of Adult *Rattus nitidus*
(N = 6 for skin measurements; N = 3 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	165.7 ± 9.87	24.18	150.0–214.0
Tail length	130.0 ± 3.42	8.37	120.0–140.0
Hind foot (s.u.) length	34.9 ± 0.54	1.32	33.5–37.0
Occipitonasal length of skull	41.3 ± 2.46	4.25	38.0–46.1
Condylobasal length	38.6 ± 2.50	4.33	35.2–43.5
Basal length	36.1 ± 2.76	4.77	32.2–41.4
Zygomatic width	19.2 ± 1.30	2.25	17.0–21.5
Interorbital width	6.0 ± 0.46	0.79	5.4–6.9
Interparietal length	5.5 ± 0.39	0.68	5.0–6.3
Interparietal width	10.8 ± 0.40	0.69	10.4–11.6
Braincase width	16.6 ± 0.94	1.63	15.2–18.4
Mastoid width	14.2 ± 0.95	1.65	12.8–16.0
Nasal length	15.3 ± 1.47	2.55	13.1–18.1
Nasal width	4.5 ± 0.29	0.50	4.0–5.0
Palatal length	22.0 ± 1.32	2.29	20.2–24.6
Incisive foramen length	8.0 ± 0.44	0.76	7.3–8.8
Incisive foramina width	2.8 ± 0.03	0.06	2.8–2.9
Inside m$^{1-1}$ width	4.0 ± 0.43	0.74	3.4–4.8
Outside m$^{1-1}$ width	8.2 ± 0.46	0.80	7.4–9.0
Bulla length	6.9 ± 0.15	0.25	6.7–7.2
Crowns m$^{1-3}$ length	6.4 ± 0.03	0.06	6.4–6.5
Alveoli m$^{1-3}$ length	7.0 ± 0.09	0.15	6.9–7.2
Crowns m$^{1-2}$ length	5.1 ± 0.06	0.10	5.0–5.2

from Irian Jaya that was regarded as native to New Guinea (Jentink, 1880). For a century the holotype remained misidentified until, in the course of our present study, we detected the error. The consequences of its description as *M. ruber,* a name that has been applied to several species of *Rattus* of New Guinea in recent publications, are so extensive that separate publication of the problem was warranted (Calaby and Taylor, 1980). Discussion of this problem is also given in this revision as it relates to the Taxonomic History of *R. praetor, R. s. hageni, R. jobiensis, R. giluwensis,* and *R. mordax.*

Rattus nitidus was first described from Nepal (Hodgson, 1845) and not until Musser (1973, 1977) identified specimens of it from Irian Jaya was its presence recognized in New Guinea. He discovered that *R. vanheurni,* a species described from Irian Jaya (Sody, 1933), was also *R. nitidus.* Earlier, Tate (1951) had suggested that *vanheurni* might be a young *ruber,* but since he had not recognized *ruber* as *nitidus,* the synonymy now recognized by Musser had escaped his detection. Laurie and Hill (1954) had also viewed *vanheurni* as a possible synonym of another species of *Rattus* from the Vogelkop Peninsula, but offered no suggestions. The species *R. nitidus* is currently being re-evaluated by Musser and its subspecific determination in New Guinea awaits his analysis.

Rattus rattus (Linnaeus)

Mus rattus Linnaeus, 1758, p. 61.
Mus beccarii Peters and Doria, 1881, p. 700.
Mus doriae Trouessart, 1897, p. 472.
Mus doboensis de Beaufort, 1911, p. 112.
Rattus rattus: Hollister, 1916, p. 126.

HOLOTYPE: None known. Sweden.

DISTRIBUTION: *Rattus rattus* has followed human European settlement of New Guinea and adjacent islands and has established it-

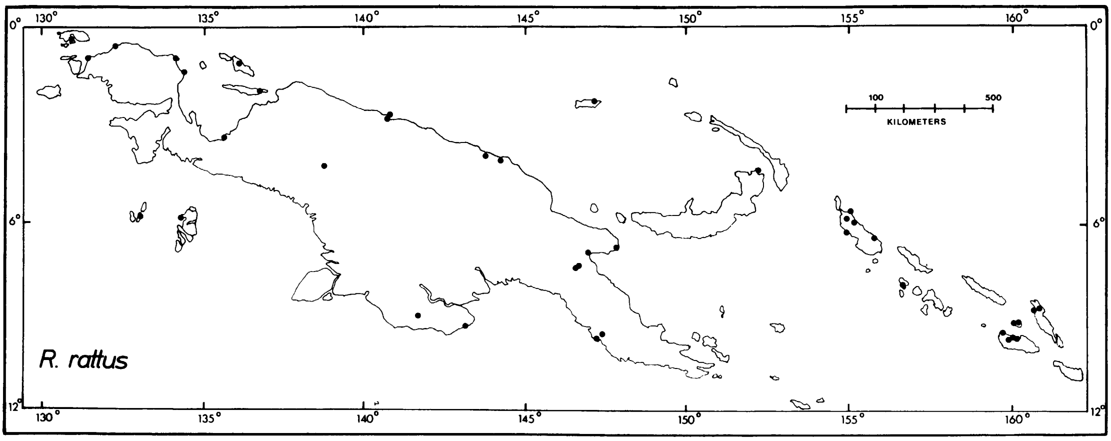

FIG. 40. Distribution map of *Rattus rattus*. Locality records are indicated by dots.

self in almost every lowland European colonization. It is mainly distributed in and near seaports and in the lowlands below 750 m. (fig. 40). There is at least one record, the Ibele River of 2200 m., from which it has been taken, but we know of no records above this altitude in New Guinea.

MEAN MEASUREMENTS (IN MM.): External: head and body 175; tail 198; hind foot (s.u.) 35.9. Skull: occipitonasal length 41.7; braincase width 16.6; bulla length 6.9; crowns m^{1-3} length 6.0. (See table 28 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 36.0 or less.

HABITS AND HABITAT: This species is a commensal in human dwellings and cultivated areas.

SYMPATRY: *Rattus rattus* is sympatric with *Rattus norvegicus, Rattus jobiensis, Rattus exulans browni, Rattus steini steini* (Ibele River), *Rattus steini hageni, Rattus leucopus dobodurae, Rattus leucopus ratticolor, Rattus mordax mordax, Rattus praetor praetor, Rattus praetor coenorum, Rattus niobe arrogans* (Ibele River), *Rattus nitidus, Rattus sordidus aramia, Rattus sordidus gestri,* and, undoubtedly, *Rattus argentiventer* (Tanah Merah on north coast).

TAXONOMIC HISTORY: It is not our intention to treat this species in any detail, although it warrants brief mention of our inclusion of *Mus doboensis* as a junior synonym of *R. rattus. Mus doboensis* was described and illustrated by de Beaufort (1911) in his review of mammals of the Aru and Kei Islands. We have re-examined the single specimen from Dobo, Aru Island, from which this new species was described, and it is a young adult of *R. rattus*. Earlier, Tate (1951) suggested that *doboensis* might be a subspecies of *R. leucopus* but he never examined the holotype, and Laurie and Hill (1954) suggested that it might be a subspecies of *ruber*. Rümmler (1938), however, regarded *doboensis* as a *R. rattus,* even though he, too, never examined the holotype. Ellerman (1941, 1949) placed *doboensis* in his *rattus* Group although, not having examined the holotype, he was unsure of its status and retained it as a full species.

Rattus rattus from Port Moresby has a diploid chromosome number of 38 which is said to be identical with that of Australian and New Zealand members of this species (Yosida et al., 1969, 1971; Yosida, Tsuchiya, and Moriwaki, 1971), and those authors claim that the several subspecies of *R. rattus* from eastern and Southeast Asia have 42 chromosomes. On the basis of these differences, Yosida, Tsuchiya, and Moriwaki (1971) recognize two subspecies in New Guinea. They maintain that the one in the eastern portion of New Guinea is *Rattus rattus rattus* with

TABLE 28
Measurements (in Millimeters) of Adult *Rattus rattus*
(N = 71 for skin measurements; N = 78 for skull measurements)

Measurement	Mean ± SE	SD	Range
Head and body length	175.0 ± 1.94	16.36	142.0–212.0
Tail length	198.0 ± 2.86	24.14	146.0–247.0
Hind foot (s.u.) length	35.9 ± 0.30	2.52	29.0–41.0
Occipitonasal length of skull	41.7 ± 0.31	2.70	36.4–47.5
Condylobasal length	39.2 ± 0.31	2.70	33.3–44.8
Basal length	36.4 ± 0.31	2.70	30.4–41.9
Zygomatic width	19.4 ± 0.14	1.22	16.8–22.4
Interorbital width	5.7 ± 0.04	0.35	5.0–6.6
Interparietal length	5.6 ± 0.07	0.58	4.3–7.0
Interparietal width	10.7 ± 0.08	0.74	9.1–12.5
Braincase width	16.6 ± 0.08	0.69	15.3–18.2
Mastoid width	14.1 ± 0.08	0.67	12.2–15.4
Nasal length	14.8 ± 0.14	1.24	12.3–17.0
Nasal width	4.3 ± 0.05	0.47	3.4–5.9
Palatal length	22.0 ± 0.18	1.58	18.9–25.2
Incisive foramen length	7.4 ± 0.08	0.70	5.5–8.8
Incisive foramina width	2.6 ± 0.04	0.38	1.9–3.4
Inside m^{1-1} width	3.4 ± 0.05	0.45	2.3–4.6
Outside m^{1-1} width	7.8 ± 0.06	0.51	6.6–8.9
Bulla length	6.9 ± 0.06	0.49	5.9–7.8
Crowns m^{1-3} length	6.0 ± 0.03	0.30	5.3–6.6
Alveoli m^{1-3} length	6.5 ± 0.04	0.32	5.8–7.2
Crowns m^{1-2} length	4.8 ± 0.04	0.35	3.9–5.7

a diploid number of 38 chromosomes and that it has been introduced from Europe. They identify the other subspecies, the one occupying the western portion of New Guinea, as *Rattus rattus argentiventer,* bearing a diploid number of 42 chromosomes and of southeast Asian origin. This interpretation suffers from inadequate documentation as it pertains to the New Guinean situation, for *argentiventer* is currently known here from only one locality and one date of collection (see section on *Rattus argentiventer*). Furthermore, now it is more commonly treated not as a subspecies of *R. rattus* but as a full species (Harrison, 1961; Yong, 1969; Musser, 1973).

Another interpretation about the introduction of *R. rattus,* and *R. norvegicus* as well, is based upon phallic morphology (Lidicker, 1968) and supports the earlier view expressed by both Tate (1951) and Simpson (1961) that these species represent the fourth and most recent invasion of rodents into New Guinea.

Rattus norvegicus (Berkenhout)

Mus norvegicus Berkenhout, 1769, p. 5 (not seen).
Rattus norvegicus: Hollister, 1916, p. 126.

HOLOTYPE: None known. Great Britain.

DISTRIBUTION: Specimens of *R. norvegicus* from New Guinea are poorly represented in museum collections. They have been taken in major seaports, such as Port Moresby, Hollandia (Jayapura), and Lae, but are apparently unknown away from major, lowland, former European settlements.

HABITS AND HABITAT: The paucity of museum records probably reflects its true status here and throughout the tropics. It is basically a species of more temperate climates of higher latitudes and becomes established in tropical situations only where European activities have greatly modified the environment. It does not spread into tropical forests or to any degree into cultivated areas in the tropics (Johnson, 1962). It joins both *R. nitidus* and *R. argentiventer* in being at present poorly established commensal rats of New Guinea that are sharply restricted to lowland areas of considerable human activity and former European settlement.

SYMPATRY: *Rattus norvegicus* is sympatric with *Rattus exulans browni* and *Rattus rattus*.

TAXONOMIC HISTORY: The history of the taxonomy of this species is of no significance as it relates to the distribution of this rat in New Guinea.

Rattus argentiventer (Robinson and Kloss)

Epimys rattus argentiventer Robinson and Kloss, 1916, p. 274.
Rattus argentiventer: Harrison, 1961, p. 21.

HOLOTYPE: Skin and skull, BMNH 19.11.5.89, old male, Pasir Ganting, West Sumatra (not examined).

DISTRIBUTION: Known only from Tanah Merah in its distribution in New Guinea (Musser, 1973). Sody (1941) associated this collecting site with a Tanah Merah of "S. New Guinea." Later, Musser (1973) specified a settlement called Tanah Merah on the Digoel (Digul) River in southern New Guinea as the collecting site. The history of exploration of the Digoel River does not, however, lend confirmation to this as the site. It is unlikely that in 1910, the year of collection, a settlement of that name existed here. When the Digoel River was explored in 1905, the vessel hit shoals at about the site later named Tanah Merah. The explorers camped here overnight on April 7–8. This campsite is marked Regen-kamp on a very detailed map (scale = 1 cm. : 2 km.) on which the name Tanah Merah does not appear (Koninklijk Nederlandsch Aardrijkskundig Genootschap, 1908, map VI). In the narrative of the exploration the name Tanah Merah also does not appear (Meyjes, 1908).

In 1907 the Digoel River was again navigated, this time as part of a Dutch military exploration of Dutch New Guinea (1907 to 1915). Beyond the shoal campsite used two years earlier, smaller vessels were required to reach the upper portions of the river system. In the text and in the series of maps, again the name Tanah Merah does not occur in association with this river system (Nederlandsch Indië, Departement van Oorlog, 1920). After the 1926–1927 Javanese rebellion, an internment camp was established near the shoal site, by now called Tanah Merah, on the Digoel River (Garnaut and Manning, 1974).

In the description of the military explorations of 1907–1915, however, three other localities by the name of Tanah Merah are present on a map of Dutch New Guinea (Nederlandsch Indië, Departement van Oorlog, 1920). Two are in the west (02°26′ S, 133°07′ E and 03°27′ S, 132°41′ E) and, although they cannot be dismissed as possible collecting sites for *R. argentiventer,* neither was associated with distant commercial trade. The third locality at 02°24′ S, 140°21′ E is a bay 20 km. northwest of Hollandia (Jayapura) which was at this time one of six main anchorage sites in Dutch New Guinea (Prothero, 1920).

As early as 1643, the explorer Tasman used this bay to make a detailed description of the nearby Cyclops Mountains (Wichmann, 1909). It was used by many other navigators as well during the past three centuries (Wichmann, 1910, 1912). It is this site called Tanah Merah Bay, used for hundreds of years by trading vessels of all sizes, that we deem the most likely collecting locality for *R. argentiventer,* a true commensal species.

Two specimens of *R. e. browni* (MZB 4603–4604) were collected at "Tanah Merah" on the same date, June 7, 1910, and are lodged in the same museum as the *R. argentiventer* specimens located and described by Musser (1973). Three more *browni* specimens (MZB 4605–4607), in the same museum registration sequence as those from Tanah Merah, were collected at "Hollandia" in 1910. Regrettably, the precise date is not provided for these Hollandia specimens, and no collector's name is specified on any of the above material. If, however, the Digoel River site were considered, it would place the

TABLE 29

Decreasing F-Values for 20 Skull Characters of New Guinean *Rattus* Entered into Discriminant Analyses

Subspecies Level Measurement	F-Value	Species Level Measurement	F-Value
Bulla length	132.1	Bulla length	223.7
Interorbital width	67.7	Interorbital width	115.7
Occipitonasal length	41.4	Occipitonasal length	61.9
Incisive foramen length	39.5	Incisive foramen length	61.4
Zygomatic width	33.2	Zygomatic width	45.1
Inside m^{1-1} width	30.9	Palatal length	38.5
Palatal length	27.8	Braincase width	38.2
Braincase width	27.6	Nasal length	37.5
Outside m^{1-1} width	27.0	Incisive foramina width	37.4
Incisive foramina width	24.7	Nasal width	36.2
Nasal length	24.1	Outside m^{1-1} width	33.2
Nasal width	23.1	Interparietal length	32.2
Interparietal length	21.8	Condylobasal length	19.5
Condylobasal length	16.9	Mastoid width	19.1
Mastoid width	12.5	Inside m^{1-1} width	18.2
Alveoli m^{1-3} length	12.5	Alveoli m^{1-3} length	15.4
Basal length	11.6	Basal length	13.6
Interparietal width	9.1	Interparietal width	13.2
Crowns m^{1-3} length	8.2	Crowns m^{1-3} length	12.2
Crowns m^{1-2} length	2.0	Crowns m^{1-2} length	2.1

occurrence of these *R. e. browni* specimens over 800 km. west of the known southern lowland distribution of the species (fig. 37).

Although this locality problem may never be fully resolved, we adopt the Tanah Merah Bay site near Hollandia, Irian Jaya Province, Indonesia, as the most reasonable on historical grounds, on the basis of its long service as a major anchor site for commercial trading vessels, and on the distribution of *browni* collected here on the same date.

Mean Measurements (in mm.): No specimens examined. See Musser (1973, table 1) for skull measurements of a specimen from New Guinea.

Habits and Habitat: *Rattus argentiventer* is a commensal of human beings, but no information on its habitat utilization in New Guinea is known.

Sympatry: If the northeastern Irian Jaya site of Tanah Merah is correct, this rat is sympatric with *Rattus exulans browni* and, undoubtedly, *Rattus rattus* as well. At the Digoel River site, specified by Musser, it would be sympatric with *Rattus rattus* (Musser, 1973) and *Rattus leucopus ratticolor*.

Taxonomic History: *Rattus argentiventer* was first identified as part of the New Guinean fauna by Sody (1941) who discovered a specimen from Tanah Merah in an old collection of the Zoological Museum at Buitenzorg (Bogor). His identification, which was tentatively assigned to *argentiventer,* has been confirmed by Musser (1973) who located five additional specimens from the same locality. His paper examines all that is known to date of its status in New Guinea.

MULTIVARIATE ANALYSIS

Subspecies Level—Discriminant Analysis

Skull characters are listed in table 29 by decreasing order of their F-values after each of the 20 measurements has been entered into discriminant analysis. The length of the bulla ranks considerably higher as a discriminator between subspecies than do other variables, and second is interorbital width. The remaining variables are either less effective or redundant with those of high value and all molar row length measurements have among the lowest F-values.

The classification matrix and the jackknifed classification, generated by the discriminant analysis and based on the logarithmic transformations of the 20 variables, correctly assign 87.0 percent and 85.2 percent, respectively, of the 3800 individuals to subspecies. Of the two matrices, the jackknifed classification is the more rigorous since it is identifying any given case only on the basis of information from other cases and does not include information from the case in question.

With few exceptions, in the jackknifed classification all taxa that score less than the overall average are allying primarily with conspecifics and in so doing score to as low as 50 percent correct on their own. In all cases of subspecies, they are well separated geographically from their conspecifics. One exception at the species level, *R. nitidus,* is represented by a sample of three. Of these, one allies to *R. rattus* and another to *R. l. dobodurae,* leaving the third to produce the score of 33.3 percent correct for *nitidus.* A similar problem occurs with *R. jobiensis,* known only from eight complete skulls. It scores 62.5 percent correct, one outlier residing with *R. m. fergussoniensis* and two with *R. l. ratticolor,* the two other taxa of largest body size. The final exception, *R. p. coenorum,* may reflect more biological validity. Although it is represented by 69 skulls, it scores only 27.3 percent correct. Its strongest outlying affiliation is with the conspecific, *R. p. praetor* (10 skulls), but it also allies almost as strongly to *R. l. dobodurae* (eight skulls), *R. s. steini* (seven skulls), and *R. jobiensis* (seven skulls), with smaller ties to *R. novaeguineae, R. m. fergussoniensis, R. s. hageni, R. l. ratticolor, R. s. baliemensis, R. v. verecundus, R. m. mordax,* and *R. rattus,* in descending order. Since most of these alliances are specious, they reinforce our suggestion that the subspecies *R. p. coenorum* is inadequately defined. We discussed this problem earlier under the account of this subspecies and suggested, on the basis of other types of evidence, that when material is available which provides better geographic representation of this widespread rat, it may be possible to demonstrate that it embraces more than one subspecies.

SUBSPECIES LEVEL—CLUSTER ANALYSES

The first two canonical variates, generated from group means of subspecies and produced by the discriminant analysis, account for 85.6 percent of the total between-sample variation. Each point established by the plot of the scores of Canonical Variate 1 against Canonical Variate 2 represents the group mean of a subspecies and the circle is the 95 percent confidence circumference for the mean (fig. 41). In this two-dimensional plot, *R. e. browni* is the most isolated subspecies and is followed by *R. s. gestri* and *R. s. aramia.* These last two subspecies are in close proximity and, perhaps due to the small sample size of *R. s. gestri,* their confidence circles for the mean overlap. *Rattus niobe niobe,* which is represented by almost one-third of the entire sample, is a well-differentiated group and its confidence circle is very tight. The group closest to *R. n. niobe* is *R. n. arrogans,* although *arrogans* is actually closer to three of the four subspecies of *R. verecundus.* The small sample size of *R. v. vandeuseni* may account for the inclusion of the centroids of two other subspecies of *R. verecundus* and of *R. richardsoni* within its bounds. *Rattus verecundus vandeuseni* has its closest affinity to *R. v. mollis* and *R. v. unicolor,* the two other mid-montane subspecies of *verecundus. Rattus richardsoni* joins the close association of subspecies of *R. verecundus* in this two-dimensional plot. This cluster of seven subspecies in the negative quadrant for both canonical variates and the placement of *R. e. browni* in the negative area for Canonical Variate 1 represent the smaller subspecies of New Guinean *Rattus.* Skull size, which is a major force in Canonical Variate 1, is largely responsible for the somewhat horizontal string of plots of the subspecies between *foersteri* and *baliemen-*

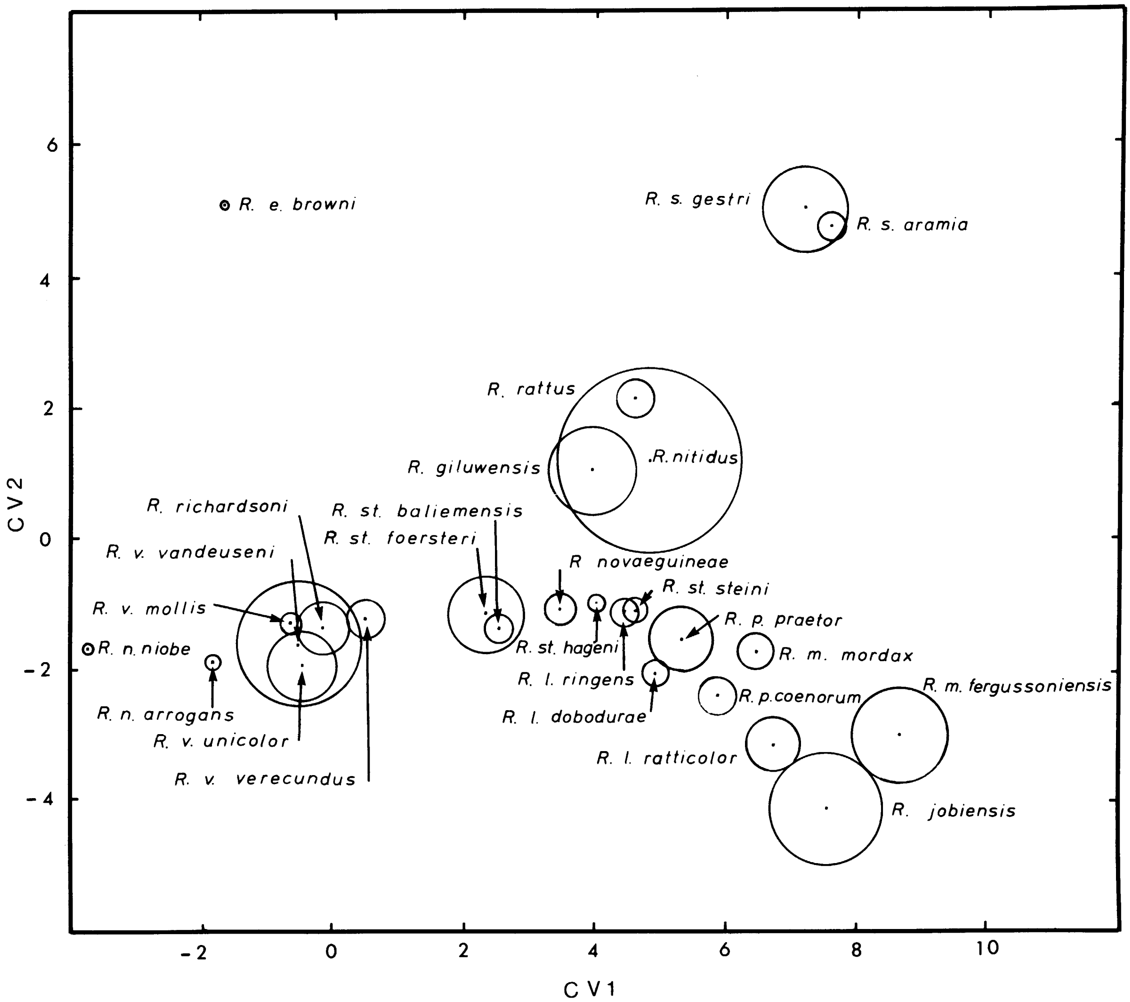

FIG. 41. Group means of subspecies of New Guinean *Rattus* plotted on scores of the first two canonical variates (CV1 and CV2). In each case, the central dot is the group sample mean and the circle represents 95 percent confidence limits for the group mean.

sis on the left and the larger *ratticolor, fergussoniensis,* and *jobiensis* on the lower right. Although most of these subspecies show little or no overlap of the confidence circles for their means, their positions are affected by this size problem. Both *foersteri,* which includes the conspecific *baliemensis,* and *nitidus,* which overlaps with the circles of two other species, are represented by extremely small sample sizes.

The three-dimensional plot, based upon scores of the first three canonical variates, pulls apart some of the groups that were spuriously allied in the two-dimensional plot (fig. 42). These three canonical variates account for 91.2 percent of the total dispersion. *Rattus exulans browni* and the two subspecies of *R. sordidus* remain distinct. *Rattus niobe niobe* and *R. n. arrogans* are now closer to each other than either is to any subspecies of *R. verecundus*. *Rattus richardsoni* appears as closely affiliated with *R. n. ar-*

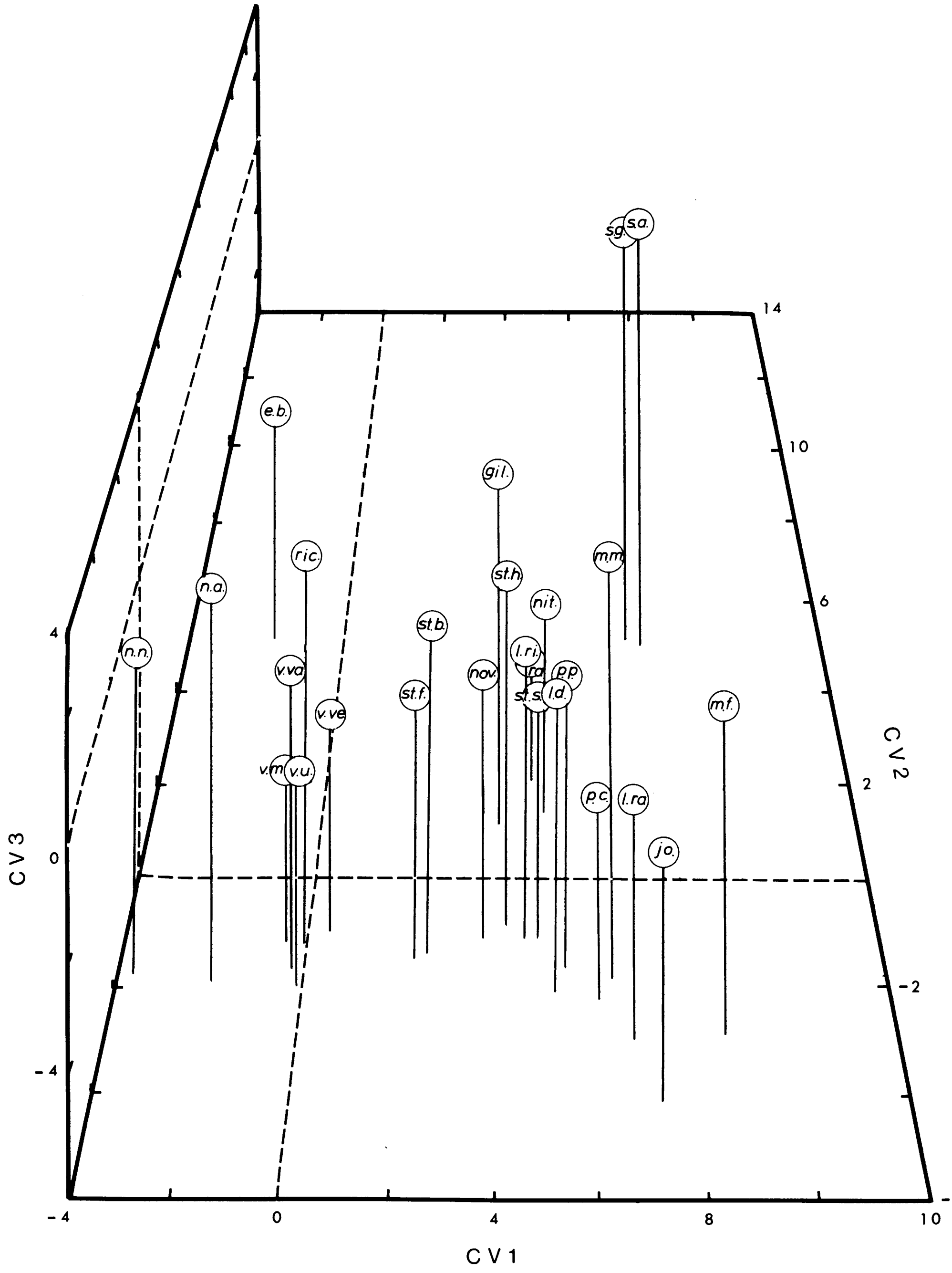

FIG. 42. Three-dimensional projection of group means of the subspecies of New Guinean *Rattus*. The plot is based on scores of the first three canonical variates (CV1, CV2, and CV3). Scientific names of the subspecies are abbreviated to first (or first two) letters of species name and first letter of subspecies name. Monotypic species are abbreviated to first two or three letters of species name.

TABLE 30
The First Eight Canonical Variates of Subspecies of New Guinean *Rattus* Evaluated at Group Means

Subspecies	CV 1	CV 2	CV 3	CV 4	CV 5	CV 6	CV 7	CV 8
R. e. browni	−1.59	5.01	−0.49	0.01	−0.12	−0.11	0.10	−0.11
R. giluwensis	4.02	1.06	1.17	−0.72	−1.01	2.78	−0.48	0.08
R. jobiensis	7.59	−3.99	−1.82	1.87	0.70	−0.59	1.64	0.10
R. l. dobodurae	4.85	−2.02	−0.69	1.47	0.41	−0.37	0.42	−0.42
R. l. ratticolor	6.71	−3.19	−1.48	2.76	0.63	−0.31	0.30	−1.11
R. l. ringens	4.49	−1.11	−0.75	1.15	0.60	0.53	0.06	−1.26
R. m. mordax	6.32	−1.84	1.33	−0.96	−0.16	0.02	1.11	0.64
R. m. fergussoniensis	8.42	−2.92	−0.18	−0.34	−0.39	−0.23	0.88	0.24
R. n. niobe	−3.75	−1.76	0.41	−0.06	0.24	0.17	−0.03	0.06
R. n. arrogans	−1.91	−1.90	1.74	1.54	−0.92	−0.87	0.26	−0.32
R. nitidus	4.80	1.21	−1.55	1.61	0.24	1.87	−0.68	0.84
R. novaeguineae	3.56	−1.21	−0.97	−0.21	1.37	−1.40	−1.52	0.22
R. p. praetor	5.42	−1.56	−0.91	−0.09	0.10	−0.70	0.58	0.36
R. p. coenorum	5.78	−2.36	−1.31	0.42	0.60	−0.38	−0.09	0.41
R. rattus	4.59	2.04	−1.19	2.41	0.87	1.21	0.73	1.06
R. richardsoni	−0.19	−1.34	1.21	3.75	−1.72	0.29	−1.24	0.20
R. s. aramia	7.55	4.74	3.92	−0.14	0.83	−0.07	−0.68	0.41
R. s. gestri	7.15	5.03	3.80	0.04	0.35	0.29	−0.27	0.78
R. s. steini	4.65	−1.09	−1.40	0.19	−1.26	0.59	−0.82	0.17
R. s. baliemensis	2.59	−1.43	0.05	−0.65	−0.75	−0.67	0.41	0.50
R. s. foersteri	2.21	−1.31	−0.90	−1.11	−0.70	−0.94	−0.30	0.94
R. s. hageni	4.04	−0.95	0.79	−1.79	−0.22	0.32	0.01	−0.64
R. v. verecundus	0.58	−1.19	−2.03	−0.09	−0.40	0.38	−0.60	0.32
R. v. mollis	−0.59	−1.36	−2.70	−1.52	0.10	−0.29	0.06	0.09
R. v. unicolor	−0.35	−1.96	−1.85	0.84	−0.26	0.08	0.29	1.42
R. v. vandeuseni	−0.52	−1.62	−0.30	−1.08	−0.67	−0.44	−0.35	1.58

rogans as it does with any of the subspecies of *R. verecundus*. All subspecies of the latter form a tight group. Both *R. rattus* and *R. nitidus* show greater affinity than either does to *R. giluwensis,* even though *giluwensis* was the closer to *R. nitidus* in the two-dimensional plot. Now *R. giluwensis* stands well apart. *Rattus mordax mordax* and *R. m. fergussoniensis* show greater alliance, while the remaining groups from *foersteri* to *jobiensis* are not appreciably better defined.

The unweighted pair-group clustering method using arithmetic averages (UPGMA) is based upon the first eight canonical variate scores for the group means (table 30). These variates account for 98.3 percent of the total between-sample variation. The cluster analysis is run on a Mahalanobis distance matrix, the cophenetic correlation coefficient for the phenogram is 0.808 (fig. 43), and the OTUs are group means of subspecies. The two subspecies, *R. s. aramia* and *R. s. gestri,* are the farthest from any other subspecies and are more closely grouped than is any other pair. This type of cluster analysis pulls these two subspecies (group 1b) farther from the remaining groups than does either of the plots just described. The next most distinct subspecies is *R. e. browni* (group 2a). It, like the above two subspecies, shows no close relationship to any other groups. Set 3b contains the remaining subspecies of small skull size that form the three groups, *R. niobe, R. verecundus,* and *R. richardsoni*. Each subspecies clusters well with its conspecifics. The other major set (3a) includes the remaining subspecies and divides into two major groups (4a and 4b). *Rattus giluwensis* has the greatest cophenetic distance (1.6) in this association and is remotely linked with *R. ni-*

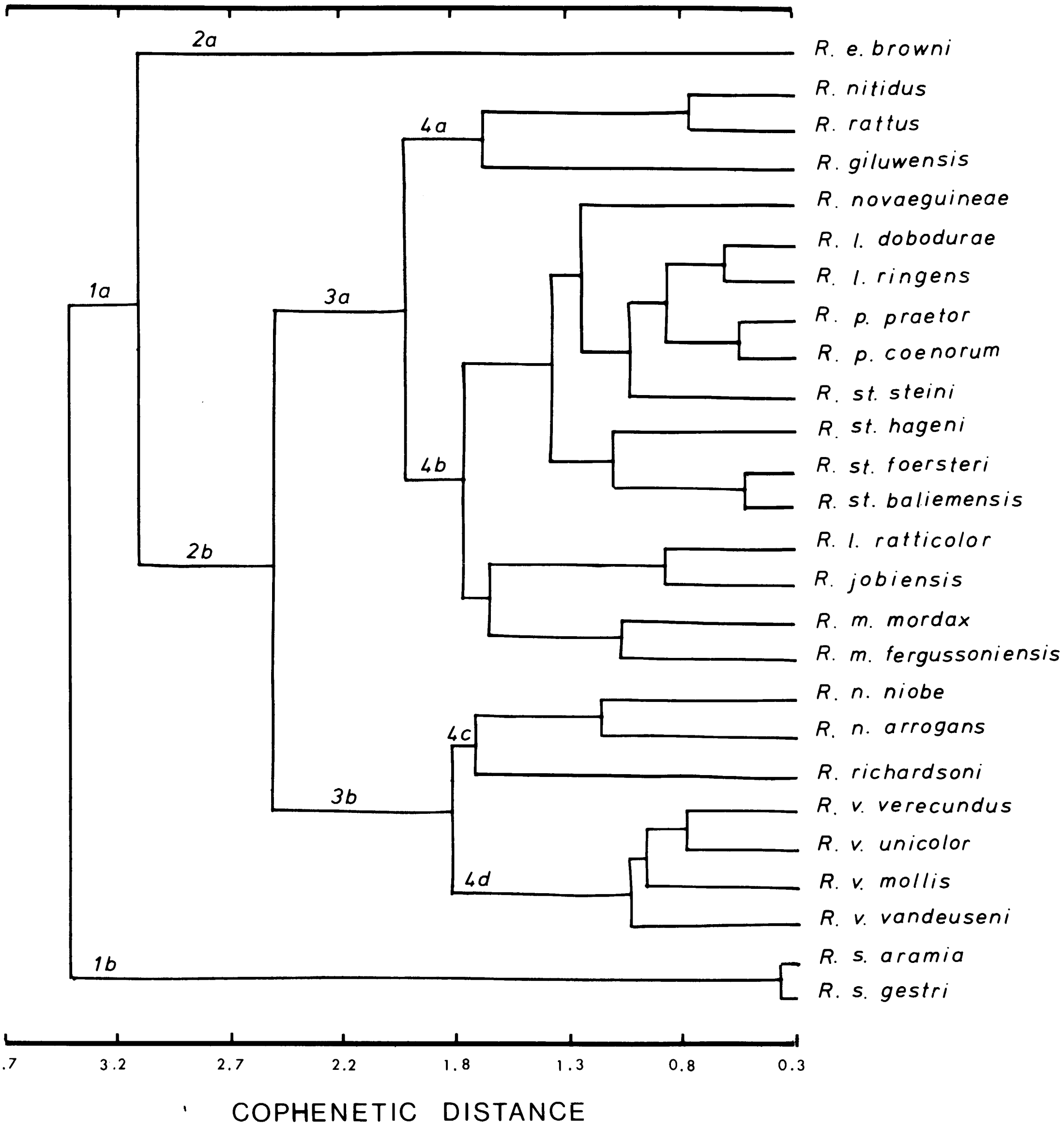

FIG. 43. Phenogram of subspecies of New Guinean *Rattus,* based on scores of the first eight canonical variates evaluated at group means, computed on a Mahalanobis D distance matrix, and clustered by UPGMA. Cophenetic correlation coefficient is 0.808.

tidus and *R. rattus*. The lower group (4b) includes most of the middle-sized subspecies. The new species *R. novaeguineae* is very distinct and the subspecies of both *R. mordax* and *R. praetor* cluster with their conspecifics. Three of the four subspecies of *R. steini* and two of the three subspecies of *R. leucopus* also cluster with their conspecifics. *Rattus steini steini,* the largest of the subspecies of *steini,* associates more closely

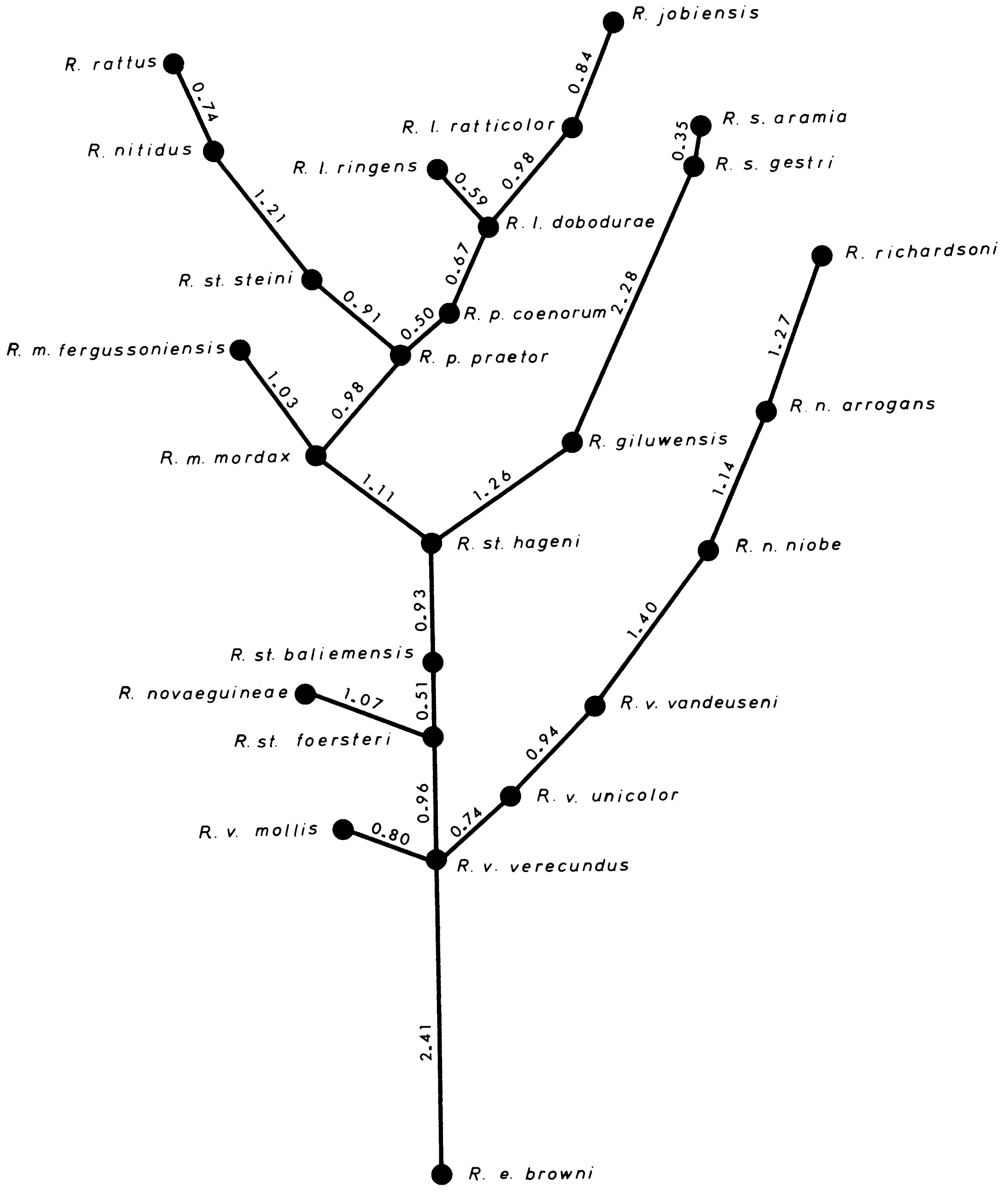

FIG. 44. Minimum spanning tree of subspecies of New Guinean *Rattus,* based on scores of the first eight canonical variates evaluated at group means, and computed on a Mahalanobis D distance matrix. Relative distances between OTUs are specified next to the linkages.

with others of similar size than to its own group. *Rattus l. ratticolor* and *R. jobiensis,* the two of largest body size, are joined and connect distantly with the two large subspecies of *R. mordax.*

The phenogram suffers from some distortion (cophenetic correlation coefficient = 0.808) in its construction and, for certain groups, a somewhat different picture of spatial relationships of subspecies is provided

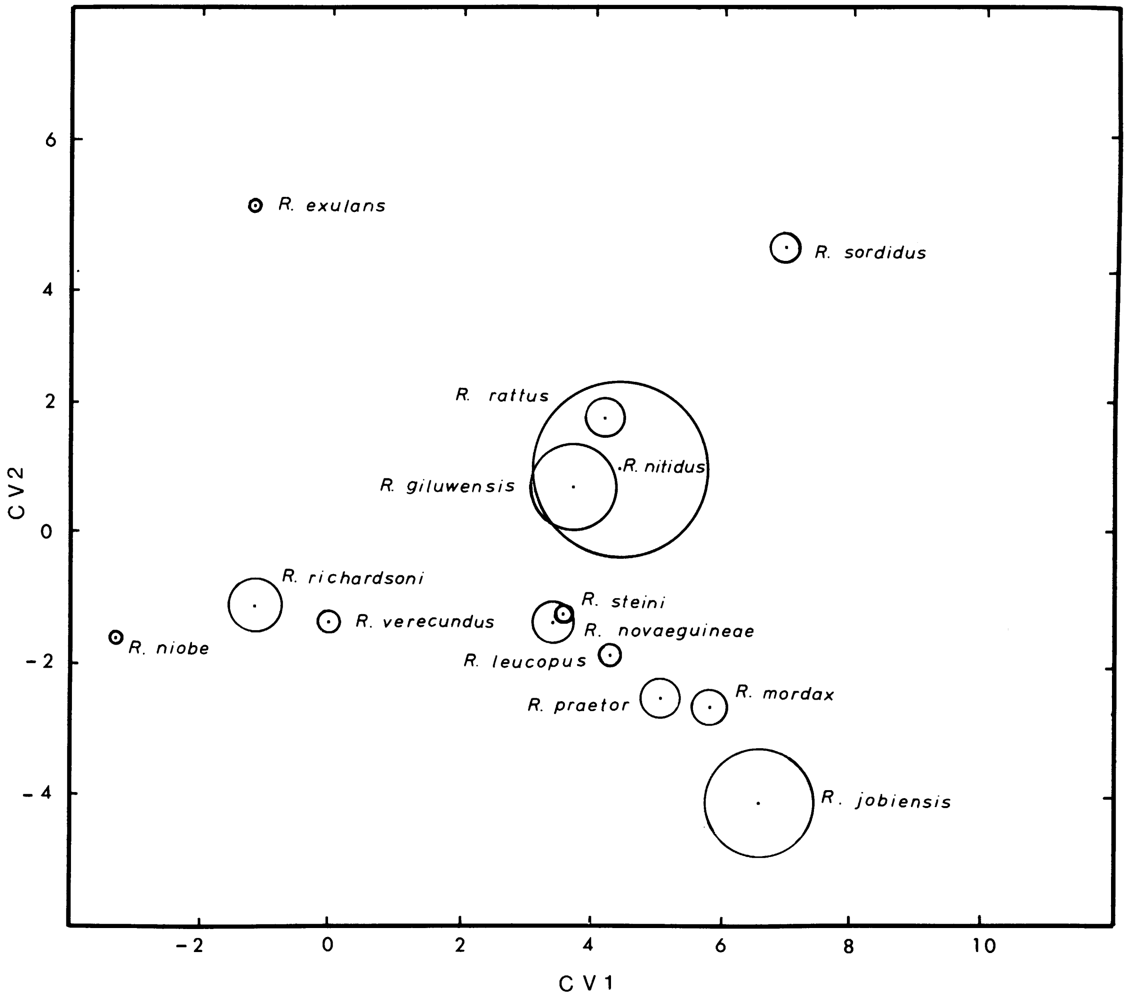

FIG. 45. Group means of species of New Guinean *Rattus* plotted on scores of the first two canonical variates. Dot and circle symbols are the same as for figure 40.

by a minimum spanning tree (fig. 44). This measure of neighborliness among OTUs, based also upon scores of the first eight canonical variates of group means and the same distance matrix, differs from the phenogram representation particularly as follows. *Rattus novaeguineae* is now associated more closely with the three subspecies of *R. steini* that were clustered in the phenogram, whereas *R. s. steini,* although maintaining affinity with *R. p. praetor* and *R. p. coenorum,* also associates with *R. nitidus*. *Rattus l. ratticolor* is in proximity both to its conspecifics as well as to *R. jobiensis*.

SPECIES LEVEL—DISCRIMINANT ANALYSIS

Effectiveness of the skull characters to operate as discriminators at the species level, after all 20 characters have been entered, is listed by F-value in table 29. The length of the bulla is once again a much stronger discriminator than are any of the rest, second is interorbital width, and third, but much weaker, is occipitonasal length. This order is the same for both species and subspecies and that of the remaining variables is also similar.

The classification matrix and the jack-

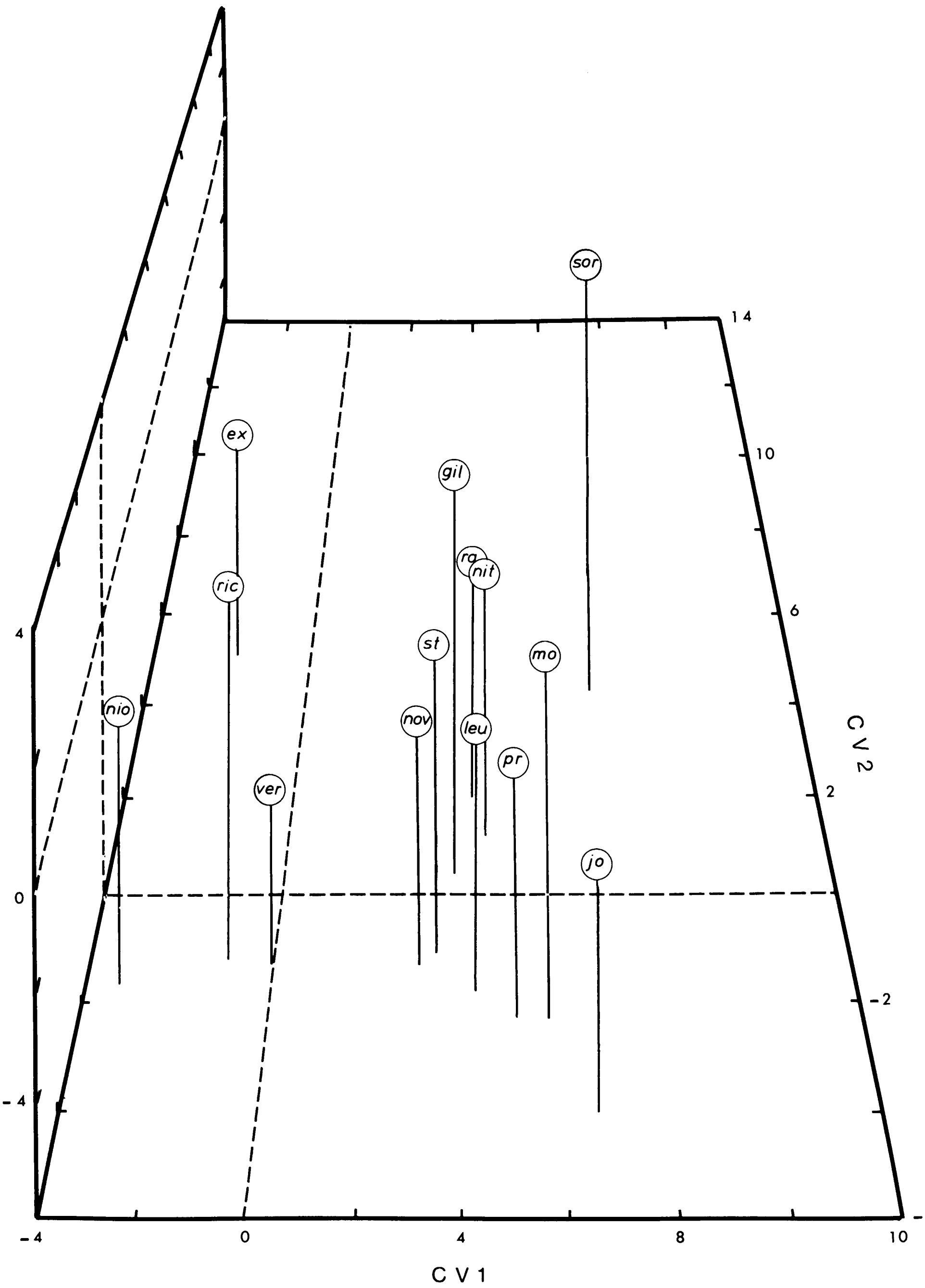

FIG. 46. Three-dimensional projection of group means of the species of New Guinean *Rattus*. Plot is as in figure 41. Species names are abbreviated to first two or three letters.

knifed classification, based on the logarithmic transformations of the 20 variables, correctly designate 89.6 percent and 89.2 percent of the 3800 cases, respectively, to

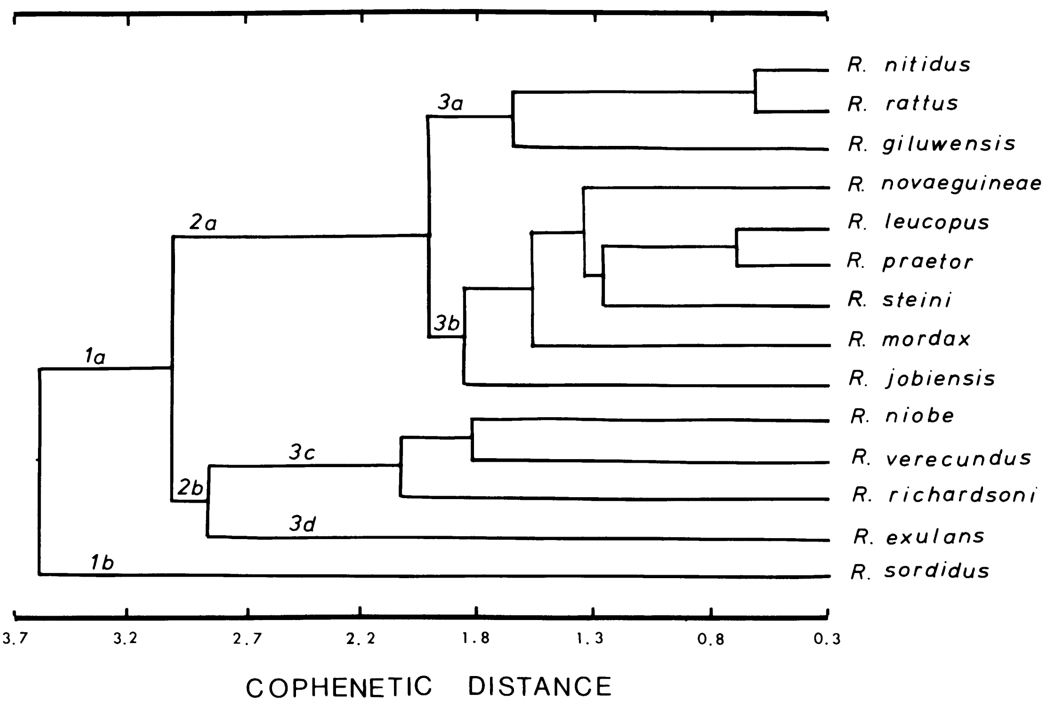

FIG. 47. Phenogram of species of New Guinean *Rattus*, based on scores of the first six canonical variates evaluated at group means, computed on a Mahalanobis distance matrix, and clustered by UPGMA. Cophenetic correlation coefficient is 0.807.

species. In this analysis, three species are assigned scores below 75 percent and thus deserve comment. *Rattus leucopus*, which scores 67.2 percent correct, loses 62 of its 244 members to *R. jobiensis*, *R. praetor*, and *R. steini*, in descending order. These extraneous alliances are mainly attributable to the larger skulls within the sample of *leucopus*.

TABLE 31

The First Six Canonical Variates of Species of New Guinean *Rattus* Evaluated at Group Means

Species	CV 1	CV 2	CV 3	CV 4	CV 5	CV 6
R. exulans	−1.08	4.98	−0.47	0.07	0.05	0.00
R. giluwensis	3.61	0.70	1.24	0.68	1.98	−0.46
R. jobiensis	6.44	−4.05	−1.46	−2.04	0.06	1.48
R. leucopus	4.17	−1.94	−0.69	−1.72	−0.01	0.09
R. mordax	5.78	−2.22	1.08	0.78	0.44	1.20
R. niobe	−3.30	−1.59	0.50	−0.09	−0.04	0.07
R. nitidus	4.24	1.03	−0.81	−1.59	0.67	0.12
R. novaeguineae	3.23	−1.32	−0.89	−0.23	−2.33	−0.86
R. praetor	5.00	−2.30	−0.99	−0.47	−0.51	0.15
R. rattus	4.11	1.91	−0.88	−2.64	0.81	0.45
R. richardsoni	−0.92	−1.13	1.36	−2.51	1.21	−2.25
R. sordidus	6.87	4.31	3.79	0.05	−0.81	0.17
R. steini	3.37	−1.30	−0.06	0.99	0.36	−0.39
R. verecundus	−0.09	−1.35	−2.23	0.77	−0.22	0.25

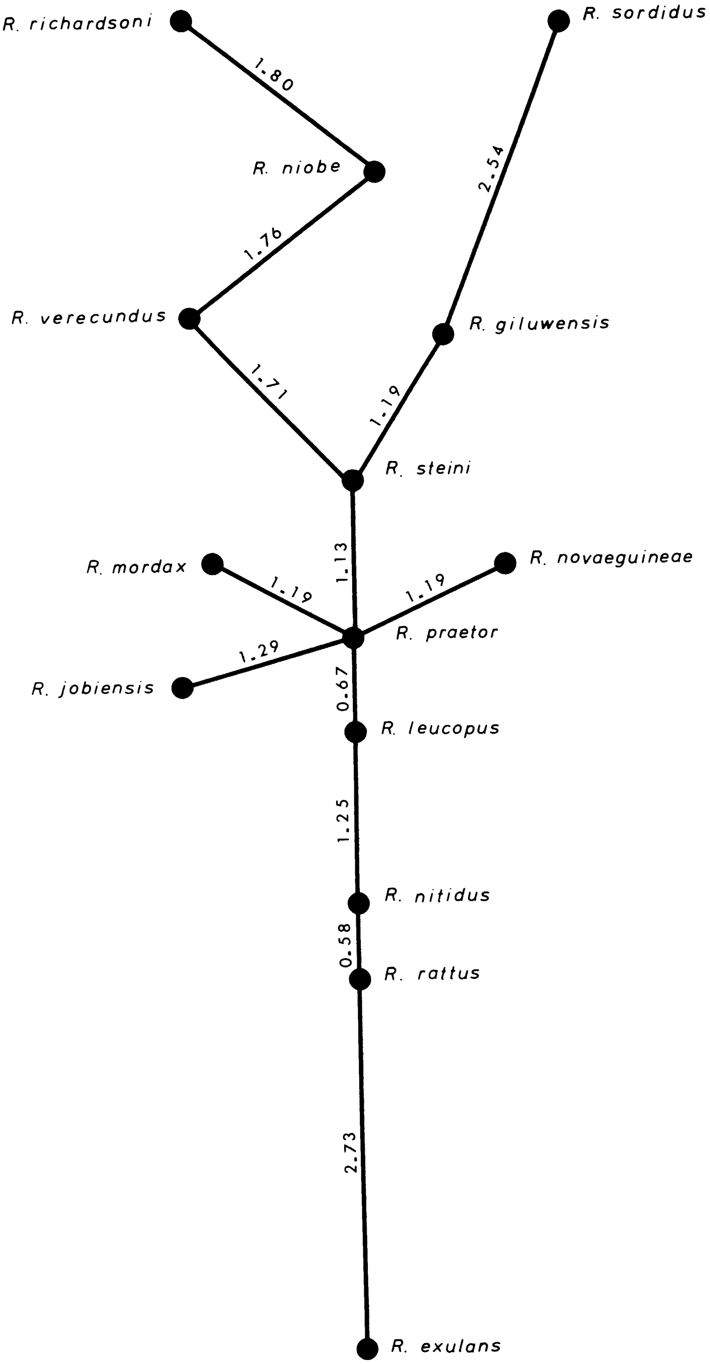

FIG. 48. Minimum spanning tree of species of New Guinean *Rattus*, based on scores of the first six canonical variates evaluated at group means, and computed on a Mahalanobis D distance matrix. Relative distances between OTUs are specified next to the linkages.

The second poor score is that of *R. praetor* (48.4 percent). It loses almost equal numbers to *R. leucopus, R. jobiensis,* and *R. steini,* largely from the *R. p. coenorum* component of this species, a problem that was also reflected in the subspecies analysis. Least in the rank of correct scores is *R. nitidus* which holds only one of the three specimens into its own sphere and loses one each to *R. leucopus* and *R. rattus*. On the other hand, *R. jobiensis,* which scored poorly in the subspecies treatment, scores 87.5 percent in the species grouping.

SPECIES LEVEL—CLUSTER ANALYSES

The first two canonical variates generated by the discriminant analysis account for 88.6 percent of the total between-sample variation, a slightly higher percentage than that at the level of subspecies. The centroids plotted from scores of these pairs of variates and the confidence circles for these means are presented in the same way as for the subspecies (fig. 45). The pattern is that of four major groups, three of which are sharply defined. These three are *R. exulans, R. sordidus,* and a grouping of *R. niobe, R. verecundus,* and *R. richardsoni*. The fourth group is more scattered, with *R. jobiensis* and a grouping of *R. rattus, R. nitidus,* and *R. giluwensis* forming the end points of a pattern that descends somewhat linearly from the center of the graph well into the negative area of Canonical Variate 2. The four species at the extremities are poorly represented in number and their confidence circles are large. In the case of *R. nitidus* (sample size = 3), the circle includes all of the *R. rattus* circle and most of that of *R. giluwensis*. The more medially positioned species are reasonably well represented (sample sizes = 78–591) but, even so, *R. steini* overlaps strongly with *R. novaeguineae*. As in the subspecies plot, spread of the taxa along the axis of Canonical Variate 1 from *R. niobe* through *R. jobiensis* is primarily an expression of progression in mean skull sizes of these species. It is necessary to turn to a three-dimensional plot to focus particularly upon the problem of species that overlapped in the two-dimensional view.

The first three canonical variates account for 93.7 percent of the total dispersion (fig. 46), which is again a slightly higher percentage than that of the subspecies three-dimensional plot. The species become considerably better defined with the inclusion of the third vector. *Rattus giluwensis* pulls away from *R. rattus* and *R. nitidus, R. steini* and *R. novaeguineae* also pull apart, and *R. praetor* becomes more distinct from *R. mordax*.

The first six canonical variates of group means, upon which the unweighted pair-group clustering method using arithmetic averages is based, account for 98.4 percent of the between-group variance (table 31). The cophenetic correlation coefficient is 0.807 for this phenogram (fig. 47), and, like that of the subspecies, is based on a Mahalanobis distance matrix. *Rattus sordidus* is the most distant species in the phenogram (lb) and next is *R. exulans* (3d). *Rattus niobe, R. verecundus,* and *R. richardsoni* are clustered (group 3c), with the first two of these in closer proximity. *Rattus giluwensis* is distantly clustered with the pair group *R. nitidus* and *R. rattus,* and lastly the six species, *R. leucopus, R. praetor, R. steini, R. novaeguineae, R. mordax,* and *R. jobiensis,* are grouped under 3b. *Rattus leucopus* and *R. praetor* form the tightest cluster of this group and *R. jobiensis* the most distant.

A minimum spanning tree, generated from scores of the first six canonical variates of the group means of species, provides a somewhat different perspective of affinities among OTUs (fig. 48). *Rattus exulans* is the most distant group and relates to two more recently introduced species, *R. rattus* and *R. nitidus*. A central cluster is formed by *R. leucopus, R. praetor, R. novaeguineae, R. jobiensis, R. mordax, R. steini,* and a more distant *R. giluwensis* that has its greatest affinity to *R. steini*. The fourth group is *R. richardsoni, R. niobe,* and *R. verecundus,* the last being the closest to the second group by way of *R. steini*. Lastly, *R. sordidus* forms a fifth group which is almost as distant from any other OTU as is *R. exulans*.

DISCUSSION

EVALUATION OF NUMERICAL RELATIONSHIPS

Decision to use multivariate morphometrics in conjunction with our facies assessment was made to obtain quantified measures of similarities among taxa based on an alternative data set, namely, craniometric observations. The numerical methods provided more objective perspectives of structural relationships that enforced, or caused us to reconsider, our non-numerical evaluations. Another factor was that these observations can be repeated, or our data base can be reassessed, by future investigators. Furthermore, one of the multivariate procedures, the discriminant analysis, provides a foundation that facilitates identifications of new *Rattus* specimens from New Guinea, a matter of economic consideration for those species of health or agricultural concern.

The two types of approaches have been compatible except for the groupings of a few taxa. Results that are mutually supportive in the two kinds of assessment and our resolutions of problem areas are now discussed.

Use of pilot runs of the discriminant analysis to explore the numerical assignments of different subdivisions of the taxa that we designated by facies assessment alone has already been noted in the methodology section. The groups most subject to this were those of widespread geographical distribution. These exploratory runs tempered our tentative assignments to certain *a priori* groupings, particularly those of *R. e. browni* and subspecies of *R. niobe* and *R. leucopus*.

The most distinct taxa in all the numerical analyses are *R. e. browni* and *R. sordidus*. All other kinds of evidence also amply demonstrate their status as that of species remote in similarity to other *Rattus* in New Guinea. Both their distinct status and their occurrences beyond New Guinea suggest that, apart from their congeneric affiliations, their evolutionary histories are generally dissociated from those of the endemic species. The two subspecies of *sordidus, R. s. aramia* and *R. s. gestri,* are assigned strong numerical affinity in all multivariate analyses and, by this criterion alone, justification of their independent status as separate subspecies would be untenable. Non-craniometric evidences presented in the accounts of species, that include differences in adult body size, pelage, and chromosome number, are together powerful discriminators and, in our appraisal, override the close numerical scores. Recognition of these taxa as separate subspecies is warranted.

The three species, *R. niobe, R. verecundus,* and *R. richardsoni,* are brought into a common major assemblage in all multivariate analyses, and their conspecific affinities become more finely tuned numerically once the third canonical variate is introduced. Analyses based upon sufficient canonical variates to account for over 98 percent of the total between-sample variation place *R. verecundus,* at both species and subspecies levels, as the most distinct in this congregation. These multivariate assignments are fully compatible with our facies assessments and, even when comparisons between allopatric taxa within this assemblage are made, the magnitude of differences between levels of species and subspecies that we recognize is sharply defined.

Relative newcomers to New Guinea that arrived by human agency, *R. rattus* and *R. nitidus,* are close neighbors in all numerically generated representations. *Rattus nitidus* of Indo-Malaysia has, on occasion, even been treated as a subspecies of *R. rattus* (Schwarz and Schwarz, 1967), but the occurrence sympatrically of both species in New Guinea and elsewhere precludes such taxonomic propinquity. All evidence that we gathered for the three specimens of *nitidus* known from New Guinea enforces its close relationship to *rattus*. The problem that emerges in most of the multivariate analyses is the inclusion of *R. giluwensis* as a distant neighbor of this pair. This is one instance in which the small sample sizes of complete skulls for *giluwensis* (12) and *nitidus* (3) may be producing aberrant results. Only in the minimum spanning tree structure (figs. 44 and 48), a representation that diminishes the distortions of a reduced dimensional plot (Neff and Marcus, 1980), is *giluwensis* removed from the *rattus-nitidus* cluster and brought into a position that is acceptable on the basis of other types of evidence. *Rattus giluwensis* is highly distinctive morphologically from all other species, all but two of which are allopatric. For example, no other *Rattus* of this size in New Guinea has such straight-sided, long incisive foramina.

Among the remaining assemblage of species, *R. mordax, R. novaeguineae, R. leucopus, R. praetor, R. steini,* and *R. jobiensis,* all but *R. mordax* and *R. novaeguineae* contain problems of reconciliation between the facies and cluster analyses. The least complicated is *R. mordax,* which is distinct in both types of analyses. Once more than three canonical variates are used in structural representation, *R. novaeguineae* is also clearly demarcated from all other taxa in everything but the minimum spanning tree of subspecies (fig. 44). Its neighbor in that tree, *R. s. foersteri,* is an allopatric form that is readily separable by its appreciably smaller size, relatively longer tail, and more delicate skull. The most difficult problems occur in the cluster of *R. l. ratticolor* with *R. jobiensis,* of *R. s. steini* with subspecies of *R. praetor* and *R. leucopus,* and of the latter to each other.

The small sample of only eight complete skulls for *jobiensis* may be affecting the resolution of its numerical alliances with *R. l. ratticolor* as, in all four multivariate analyses at the subspecies level, this affinity persists. It becomes least overpowering in the minimum spanning tree (fig. 44) where *R. l. ratticolor* is almost as strongly allied to its conspecific, *R. l. dobodurae,* as it is to *R. jobiensis*. Both *R. l. ratticolor* and *R. jobiensis* are large lowland rats and they converge morphologically in certain skull and skin features that have a propensity to be expressed in lowland species, as discussed later. *Rattus jobiensis,* however, has a more elongated appearance to the skull than does any subspecies of *R. leucopus*. This feature does not surface effectively in the multivariate analyses to create greater distance from *R. l. ratticolor,* the largest of the subspecies of *R. leucopus*. The skull of *R. jobiensis* has a narrower interorbital width, narrower cranial width, longer incisive foramina, and smaller bullae, all relative to occipitonasal length, than does any subspecies of *R. leucopus*. Furthermore, the skull of *R. jobiensis* has more delicate supraorbital-temporal ridging than does that of *R. l. ratticolor,* the largest subspecies. Together, these features distinguish the shape of the skull of *R. jobiensis* from that of *ratticolor*. These observations, in conjunction with differences in skin features outlined in the species accounts, have contributed to our conclusion that *R. jobiensis* is not conspecific with *R. leucopus*. Similarity in magnitude of skull size between *ratticolor* and *jobiensis,* plus the sparse representation of the latter, may have caused distortion in the multivariate analysis that resulted in allying the two taxa so strongly. *Rattus l. ratticolor* is, on the other hand, a large mottle-tailed subspecies of *R. leucopus* that is closer in body size to *R. l. dobodurae* than to *R. l. ringens* and its tail is relatively shorter than that of either of the other two subspecies. Otherwise, their morphological similarity is strong.

A somewhat different kind of problem occurs with *R. s. steini*. It remains a near neighbor of *R. p. praetor* and of *R. l. ringens* in the two- and three-dimensional multivariate representations, and in the minimum spanning tree *R. p. praetor* becomes its closest associate. All lines of evidence except the multivariate analyses indicate that *R. s. steini* does not closely resemble either of the above subspecies. The skull of adult *R. s. steini* is only lightly ridged, whereas typically such ridging in adult skulls of both subspecies of lowland *R. praetor* and in those of *R. leucopus* is moderately to well developed. Although *R. s. steini* shares the feature of somewhat bowed incisive foramina and general skull shape with both of the other taxa, it is smaller. It also has a more abrupt interorbital constriction of the skull compared to that of *R. leucopus* or the constriction is more anteriorly positioned in the orbitotemporal fossa compared to that of *R. praetor*.

This is a useful diagnostic character. The minimum spanning tree clearly demonstrates that *R. s. steini* is sharing closer neighborliness to the *R. praetor* subspecies than to *R. leucopus*. This affinity reflects one of the problems that has already been discussed, that of adequate depiction of membership in *R. p. coenorum*. *Rattus s. steini* and *R. p. coenorum* are, however, sympatric at a high elevation site in the distribution of the latter. Their sympatry is evidence of their differentiation at the level of species. *Rattus steini steini* most closely resembles the conspecific *R. s. baliemensis* and differs primarily from all three other subspecies only in its larger size. It is this size factor that may draw it closer in multivariate treatments to other larger species.

The association of *R. leucopus* with *R. praetor* in results of the numerical analyses is specifically that of *R. l. dobodurae* with the subspecies of *R. praetor*. Nowhere in their distributions are the two species known to be sympatric. Again, inadequate definition of the limits within subspecies of *R. praetor* may be the problem that creates this neighborliness. The skulls of the two species, which are of similar size, differ in several features that permit their distinction. *Rattus leucopus* has a less massive skull and it gives the impression of being more elongated due to the shape of the supraorbital-temporal ridging and the greater extension of the nasal bones anterior to the face of the incisors. The bow of the incisive foramina is less angled in *R. leucopus*. The mammary formula of the two species is different, and only in *R. praetor* is the ventral coloration frequently marked by a pectoral white patch. The tail of *R. leucopus* is usually mottled or tipped in white, whereas that of *R. praetor* is plain, and only in the former are the dorsal hairs of the feet white. The distribution of *R. praetor* includes insular situations, whereas that of *R. leucopus* is strictly mainland, even though insular situations contiguous to its distribution exist. They are both large lowland species that show similar convergent features, but together the distinctions just described warrant their recognition as full species.

Both our facies assessment and the structural representations by multivariate procedures, based on the number of canonical variates that account for over 98 percent of the between-group variation, recognize five major groupings: *exulans, sordidus, rattus-nitidus, niobe-richardsoni-verecundus,* and the assemblage of remaining species. They are visually summarized with reasonable congruence in the minimum spanning tree cluster analysis (fig. 48). Both *R. praetor* and *R. steini* are central to the framework. The species *R. leucopus, R. novaeguineae, R. mordax, R. steini,* and the more distant *R. jobiensis* all pivot about *R. praetor*. From *R. steini* a link to *R. giluwensis* is established in the tree, a connection that backs up our suggestion, made later in this Discussion, that *giluwensis* may share more immediate evolutionary history with *steini*. Linked to *steini,* but more distantly, are the three species, *verecundus, niobe,* and *richardsoni*. Each of these species is well separated, but nonetheless together they form a distinct congregation. *Rattus sordidus* and, at the opposite end of the tree, *R. exulans,* show little affinity to any other species and both have presumably evolved to species status extralimitally. Finally, *R. rattus* is distantly linked with *R. exulans* and is closely joined by another introduced species, *R. nitidus*. They intercept the connection between *R. exulans* and the endemic species in the tree. Their proximity to the endemic species is not, however, phylogenetic for in the arena of evolution in New Guinea both are newcomers. The remainder of this Discussion is focused on our interpretation of speciation in *Rattus* of New Guinea based upon this taxonomic framework.

RECOGNITION OF TAXA

SAMPLING PROBLEMS

That we bring forth a distinctly different interpretation of the systematics of *Rattus* in New Guinea is in part the result of having considerable advantages over predecessors. These advantages are the availability of sophisticated computer facilities to aid in ma-

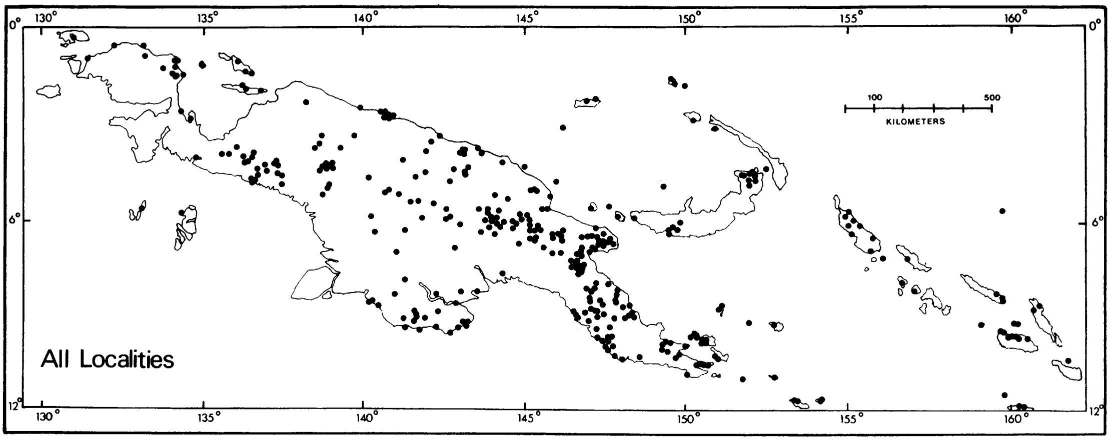

FIG. 49. Collecting sites of museum specimens of all species of *Rattus* in New Guinea except *R. argentiventer* and *R. norvegicus*. The sites are indicated by dots.

nipulations of a large data base and that of a greater quantity of specimens from an increased number of geographical sites.

Many areas remain uncollected, however, and major gaps persist in knowledge of the distribution of species. A map showing each site of collection of *Rattus* portrays a visual representation of the localities that are currently recorded (fig. 49). Examination of such fundamental problems as morphometric diversity within and between populations, evidence for clines, convergence, and competitive exclusion are largely premature with the material at hand. Interpretations on a broader level must currently be based upon certain assumptions regarding distribution and are founded upon a general grasp of the biology of this group. We readily acknowledge use of this element of subjectivity in discussing trends of evolution, as we do also the tendency to lean toward the "lumper" route in taxonomic assessments. Inadequate representation is a fundamental problem in this study, and it has reached an extreme in some taxa. Some specific examples are detailed below.

Rattus praetor praetor is known only from about a dozen localities in the extensive archipelagos of Bismarck and the Solomons, a system of islands 1850 km. long. In most cases, this rat is known from only one to three specimens per locality. It is a very large rat and the size range and concomitant morphological changes in adults are substantial. Lack of regional differentiation prevented recognition of further division within this subspecies. Although large expanses of water separate many adjacent islands and great opportunity exists for clinal evolution, on the basis of the material at hand we have treated this group as a single subspecies. The antithesis of this treatment, that each island harbors its own subspecies, may be appealing zoogeographically, but is at present statistically untenable. *Rattus praetor praetor* is apparently not an efficient commensal traveler like either *R. exulans* or *R. rattus,* the other two species that inhabit these archipelagos. Thus, if any of these were to undergo speciation along this island chain, it would be *R. p. praetor* because of its relative immobility. Sufficient material may some day be available to test or look for differentiation. A similar situation occurs on the mainland with *R. praetor coenorum*. This large lowland rat extends across all of northern New Guinea but again the sample sizes and geographical representation are inadequate to detect more than one morphological entity, if such are present.

The case of *R. niobe* is a second example of this type of problem. This is the smallest of the endemic *Rattus* and occurs from east to west along the central cordillera and into the Huon and Vogelkop peninsulas. No significant morphometric differences emerge from our criteria in material now in collections made east of 140° E, even in the Huon Peninsula that is certainly an island for montane species. The large collections of *R. n. arrogans* obtained west of 140° E by the Archbold Expedition of 1938–1939 at the Ibele River, Lake Habbema, and Mt. Wilhelmina (=Mt. Trikora) are demonstrably different from the eastern *R. n. niobe,* and included with them are those few specimens from the Carstensz Mountains, the Weyland Mountains, and the Arfak Mountains that fall well within the statistical limits of *arrogans*. With *R. niobe,* it is not only a sampling problem, but probably also one of sensitivity of the criteria used. Their small skulls vary so little in terms of millimetric scores that the measure of variation may have been inadequate to distinguish subspecies groups. However, rather than recognize most of the subspecies proposed for *R. niobe,* all of which are poorly documented and have no statistical support, we acknowledge only those two that can be readily and repeatedly recognized on the basis of the craniometric variables that we employed.

ALLOMETRIC GROWTH

A problem that has led to erroneous interpretations, and even to proposals of new taxa, relates to recognition of age groups and allometric growth of the skull. As the skull of a rat grows, the proportion between the cranium and the rostrum changes. Juveniles have a greatly inflated cranium relative to rostral development and with growth of the rat the rostral region becomes both longer and wider while the cranium grows relatively little. By the time some evidence of reproductive activity is detectable, the proportions have usually stabilized to a considerable degree. For this reason it has been necessary to estimate the size at sexual maturity for each subspecies and to eliminate juveniles from statistical analyses between taxa. This separation removes part of the problem and, by examining seriatum size differences of skulls of each subspecies, the likelihood of identifying the remarkably different juvenile skull as that of a different or new species becomes more remote.

Examples of misidentifications due to age differences are common, however, in assessment of New Guinean *Rattus*. Thomas (1922a) proposed two species, *Rattus coenorum* and *R. bandiculus,* from the same locality. Rümmler (1938) finally recognized that they were but a young and an adult of the same species. Jentink (1908) described *Mus ratticolor* as a new species on the basis of a single juvenile specimen, and identified adults of this rat from the same locality as *Mus ringens*. More recently, Troughton (1945) failed to distinguish juveniles from adults when, from a single juvenile specimen, he described *Rattus browni gawae* as a new subspecies. Furthermore, he named as paratypes of his new species, *Rattus owiensis* (=*R. jobiensis*), two adult specimens of *Rattus exulans* that he thought were juvenile *owiensis*. The most recent example is the proposal of a new species, *Rattus omichlodes,* by Misonne (1979) who failed to recognize his series as young adult examples of *R. richardsoni*.

The problem of allometric growth of the skull diminishes but does not cease in the adult category. It is of minimal consequence in the smaller species, in part because actual growth increments are small and in part because the cranium does not develop substantial supraorbital-temporal ridges or supraoccipital crests. Even in these species, however, the molars wear and change shape with use and this alters craniometric ratios in adult series. The large lowland species, *R. leucopus* and *R. praetor,* present the greatest within-species size ranges in the adult category and the greatest problems of changes in adult skull shape. The larger adult skulls develop thickened supraorbital-temporal ridging, the supraoccipital crests develop substantially and result in an elongation of the total skull length (particularly in males), the terminal portion of the nasal bones widens to form a nasal flare, and the incisive foramina also widen. These enlarging processes occur concomitantly with a gradual wearing of the molar rows that diminishes their size.

Statistical treatment of these allometric changes is feasible only if the relative magnitude of each can be related to more stable portions of the adult skull, and at such time as overall adult growth changes in an ever-growing mammal like *Rattus* are calculated species by species. Currently, this type of assessment is not feasible in New Guinean species due to lack of appropriate material and presents difficulty when numerical methods of taxonomy are applied.

ZOOGEOGRAPHY

Physiography of New Guinea

Radiation of *Rattus* is taking place on one of the largest islands in the world. New Guinea extends from the equator to 11° S latitude, and from 131° to 151° E. longitude, and is 2400 km. long. The Bismarck Archipelago and the Solomon Islands extend eastward for another 1850 km., and the Louisiade Archipelago stretches southeastward for 400 km. New Guinea is within 160 km. of Australia across Torres Strait, which was a land bridge during glacial periods until about 8000 years B.P. The extensive Indonesian archipelagos reach to the western flank of New Guinea and mark the presumed route by which all murid rodents have gained access to Australia as well as to New Guinea.

In addition to its geographical situation, the topographical features of New Guinea that provide such a unique insular setting for diversification and specialization of its biota are the spectrum of altitudes that range from sea level to the highest mountain of the southwest Pacific (Mt. Jaya, 4884 m.) and the orientation of these mountain systems (fig. 50). The most extensive cordillera is 1600 km. long and forms the backbone of New Guinea from 135° E to the southeastern tip. The Louisiade Archipelago is a partly submerged extension of this range. This central range presents a formidable barrier to faunal exchange and modifies the climate extensively on both sides. The Vogelkop Peninsula forms the western limit of the island and is mountainous to 3050 m. A chain of mountains, some of which are partially submerged, extends from Waigeo Island, the Schouten Islands of Geelvinck Bay, across the north coastal region of the mainland as isolated peaks and ranges, and emerges as New Britain on the eastern ocean side. These mountains and ranges are viewed as geologically distinct from, and of greater antiquity than, the central range. The Finisterre Mountains of the Huon Peninsula may be part of this same system (Cheesman, 1940). The Huon Peninsula is today separated from the remainder of the mainland by the valleys of the Markham and Ramu rivers. This valley system effectively severs the mountainous Huon Peninsula from the rest of the mainland into a biologically insular land mass. The relationship of this peninsula to the adjacent mainland biota west of this rift valley was the impetus of the most recent Archbold Expedition (Van Deusen, 1966, 1978). New Guinea is deeply carved into valley systems between mountains and into bays, and contains one of the most extensive swampy lowlands in the world.

The New Guinean region offers unparalleled opportunities for population fragmentation and speciation. The topography is associated with both sea level changes and with fluctuations of climate and consequent altitudinal movements of vegetation zones in the climatically sensitive highlands during the Quaternary. There is a horizontal aspect across land masses and islands and a vertical one from sea level to the edge of glacial influence. At the present day the tree line ranges from 3700–4050 m. and the snow line is about 4700 m. There is a small icecap of 8 km.^{2} on Mt. Jaya. At the maximum extent of the last glaciation about 17,000 years B.P., approximately 2000 km.^{2} were glaciated, the snow line was about 3500 m. and the tree line was as low as 2200 m. (Bowler et al., 1976; Hope and Hope, 1976; Walker, 1978).

Species of *Rattus* now occupy all regions of the mainland, adjacent islands, across the Bismarck Archipelago and the Solomon Islands to their eastern extremity, and perhaps beyond. *Rattus* has evolved into lowland species, mid-montane species, subalpine species, and within the past few decades has come to occupy the substrate bared by re-

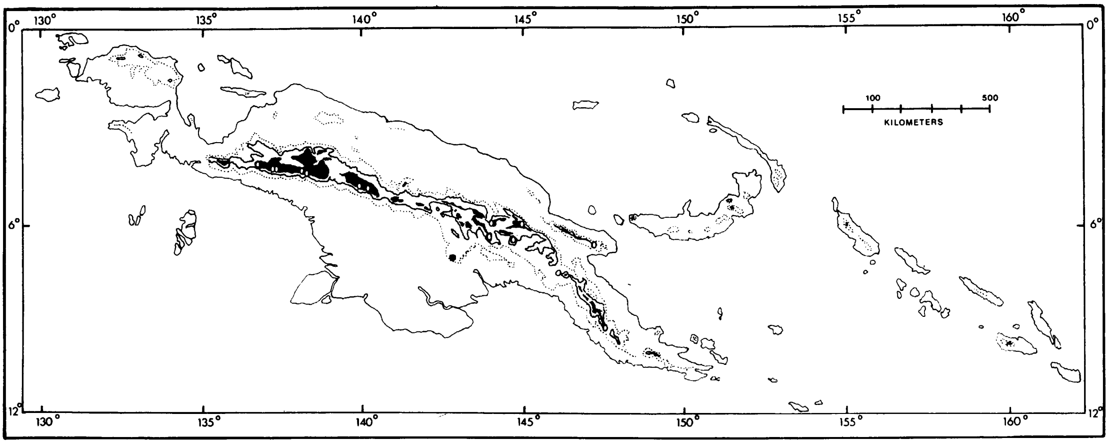

FIG. 50. Altitude map of New Guinea, Bismarck Archipelago, and the Solomon Islands. Dotted line is 1000 m. level, solid line is 2000 m. level, black areas are 3000–4000 m., and white ovals in black areas are over 4000 m.

ceding glaciers at altitudes up to 4500 m. where glacial retreat is estimated at 80 m. per century (Allison and Kruss, 1977).

Altitudinal Zonation and Distributional Patterns of Ecotypes and Species

Tabulation of mean occipitonasal length and mean altitude is given for each subspecies of *Rattus* (table 32), and a table at the species level is derived by simple arithmetic means that gives equal weight to each contributing subspecies (table 33). These tables illustrate that with increase in altitude there is a decrease in body size, using occipitonasal length as an estimate of size. Although our presentation is new and much more extensive, this observation is not entirely new. Rümmler (1938) described it in various genera of murid rodents of New Guinea and commented that it countered the predictions of Bergmann's Rule. Rümmler explained this variance on the grounds that the increase in fur length of murids at higher elevations is sufficient to compensate for the lower ambient temperature that would otherwise impose physiological stress.

A second aspect that is shown in the tables is that the two species which occur at the highest elevations, *R. giluwensis* and *R. richardsoni,* are not the smallest and are actually closer in size to the mid-montane species, *R. verecundus* and *R. steini,* than to the smallest, *R. niobe*. A lowland species, *R. sordidus,* also falls into the mid-montane size group.

Altitude is, of course, associated with zonation of major plant communities. Rümmler (1938) attempted to correlate the vertical distribution of New Guinean murids on the basis of three vegetational zones: coastal and hill forest zone 0–600/1000 m., mountain forest zone 600/1000–1400/1800 m., and mist forest zone 1400/1800–2400/2600 m. Although it is grossly oversimplified, it represents the only real attempt to make this type of classification in conjunction with rodent distribution on this island. Brass (1941, 1956) has proposed eight altitudinal zones of major plant communities in New Guinea, a classification based upon his assessment in both eastern and western New Guinea. It includes some fundamental differences in zonations of vegetation in the eastern and western sectors and in the extent to which altitudinal parameters vary with local topography. Ziegler (1977) offers a simpler version by recognizing six vegetational types. It is unfortunate that more is not known about the

TABLE 32
Vertical Distribution of Subspecies of New Guinean *Rattus* by Skull Length

	Occipitonasal Length (mm.)		Altitude (m.)	
Subspecies	Mean	Range	Mean	Range
R. n. niobe	32.6	30.0–35.8	2412	762–4000
R. n. arrogans	34.2	30.6–37.0	2768	1500–4050
R. v. vandeuseni	35.5	34.5–36.4	1540	1540
R. v. mollis	36.1	33.6–38.7	1809	1150–2750
R. giluwensis	36.4	34.8–37.8	3023	2195–3600/3660
R. richardsoni	37.2	33.9–39.8	3809	3225–4500
R. s. hageni	37.6	33.3–42.5	1643	20–2800
R. v. verecundus	37.6	33.6–41.8	877	152–1829
R. v. unicolor	38.1	35.4–40.2	1725	1000–2500
R. s. foersteri	38.1	35.2–41.9	1530	1160–1800/2000
R. s. gestri	38.2	35.6–40.8	123	sea level–670
R. s. baliemensis	38.5	34.8–42.0	1739	850/1200–2800
R. s. aramia	38.7	34.8–43.6	26	sea level–100
R. s. steini	40.9	36.9–44.9	1702	1400/1800 and 1765
R. novaeguineae	41.1	36.2–45.0	1138	740–1524
R. l. ringens	41.6	37.5–48.4	112	sea level–900
R. m. mordax	42.0	37.4–48.7	426	sea level–2750
R. p. praetor	43.3	39.0–49.4	605	sea level–1900
R. l. dobodurae	43.7	38.1–50.4	303	sea level–600
R. p. coenorum	44.6	37.4–54.9	382	sea level–1524
R. m. fergussoniensis	46.7	41.0–51.9	314	sea level–900
R. l. ratticolor	48.5	39.6–54.2	67	sea level–213
R. jobiensis	50.8	45.9–53.1	164	sea level–610
R. e. browni (introduced)	31.9	28.3–38.2	748	sea level–2880

habitats of New Guinean *Rattus* in order to make full use of these vegetational classifications.

One aspect of particular importance in this regard concerns food resources for the rats. Vegetational growth becomes reduced with increase in altitude and concomitant decrease in temperature. Rats are opportunistic feeders and will utilize almost any nutritional source. As productivity declines with colder climates, so does the availability of vegetation as well as that of other organisms which depend upon it. This factor may represent a strong selective force on body size. From an evolutionary standpoint *Rattus,* that are presumably active throughout the year, cannot sustain a large body size in situations where food resources are restricted.

Cold stress would theoretically impose a powerful force on body size in the opposite direction, as Bergmann's Rule suggests. However, all species of *Rattus* native to New Guinea are burrowers and can thus create a subterranean microclimate that circumvents periods of temperature stress, either cold or hot. At high elevations, the pelage becomes modified to a soft dense fur without spines and becomes an excellent insulator. The pelage is not necessarily longer, as Rümmler (1938) suggests, but rather is more dense and has a greater amount of underfur. The fur of *R. richardsoni* is the best example of this type of pelage, although both *R. giluwensis* and *R. niobe* are also extremely soft-furred.

The lability of the change from a pelage with spines to soft dense fur is undocumented. *Rattus exulans browni,* a species that has presumably been in New Guinea only since the arrival of indigenous people, has soft

TABLE 33
Vertical Distribution of Species of New Guinean *Rattus* by Skull Length

Species	Occipitonasal Length (mm.)		Altitude (m.)	
	Mean	Range	Mean	Range
R. niobe	33.4	30.0–37.0	2472	762–4050
R. giluwensis	36.4	34.8–37.8	3023	2195–3600/3660
R. verecundus	36.8	33.6–41.8	1523	152–2750
R. richardsoni	37.2	33.9–39.8	3809	3225–4500
R. sordidus	38.5	34.8–43.6	61	sea level–670
R. steini	38.7	33.3–44.9	1643	20–2800
R. novaeguineae	41.1	36.2–45.0	1138	740–1524
R. praetor	44.0	37.4–54.9	454	sea level–1900
R. mordax	44.4	37.4–51.9	411	sea level–2750
R. leucopus	44.6	37.5–54.2	171	sea level–900
R. jobiensis	50.8	45.9–53.1	164	sea level–610
R. exulans (introduced)	31.9	28.3–38.2	748	sea level–2880

non-spinous fur at high elevations (1500 m. and above) and harsher fur with abundant spines in the lowlands. The pelage of the endemic mid-montane species, *R. steini* and *R. verecundus*, and of the lowland *R. mordax*, also varies comparably with altitude.

The trend of large body size in the lowlands and smaller size at higher altitudes, a trend that generally runs counter to Bergmann's Rule, may be of selective advantage on the basis of food availability. The burrowing habit and the shift in quality of the pelage together counter to a large degree the potential problem of temperature stress. This pertains equally well to lowland species that are subject to a threat of heat stress but where the growing season of vegetation is continuous, as to high-altitude forms inhabiting a cold climate with restricted food resources.

The observation that the two species which occupy the highest mean elevations, *R. richardsoni* and *R. giluwensis*, are not the smallest species suggests that cold stress may become an important factor in these subalpine-alpine habitats and overrides to some extent the advantages of a burrow system and very thick body insulation. It may be critical metabolically that the body size be larger than that of *R. niobe*, an occupant of somewhat lower elevations. No plausible explanation appears evident for the smaller size of the two lowland *R. sordidus* subspecies unless it involves character displacement in association with a potentially strong competitor.

Similarities in external morphology between species occupying similar habitats that are widely separated suggest that the species have evolved as ecological counterparts. A highland example is *R. richardsoni* in Irian Jaya and *R. giluwensis* of the Southern Highlands Province of Papua New Guinea. Both are primarily alpine grassland inhabitants and show convergence in external features, such as size, pelage quality, and color, although not in skull morphology. In both geographical areas they are sympatric at lower elevations with *R. niobe* and *R. steini*.

Rattus steini, *R. verecundus*, and *R. niobe* are all mid-montane inhabitants at least to a large extent, and, of these, *R. niobe* is the most widely distributed. *Rattus niobe* also inhabits the broadest range of altitudes, including higher regions from which the other two are excluded, and is the smallest of all the endemic species. *Rattus verecundus* is a sleek rat and is larger than *niobe*. Where it is sympatric with *R. s. hageni*, the subspecies *R. v. mollis* is smaller. Although two other subspecies, *R. v. unicolor* and *R. v. verecundus*, are larger than *hageni*, in each case they are smaller than their sympatrics, *R. s. steini* and *R. m. mordax,* respectively. The biological significance of this size stratification among these mid-montane species is untested but is perhaps an example of character displacement between sympatrics.

Rattus steini is replaced in montane habitats of the Owen Stanley Range by *R. mordax,* a primarily lowland species that has extended into this southeastern montane system. *Rattus verecundus* is absent from the Huon Peninsula and appears to have no replacement there. *Rattus steini* has never been collected in the Vogelkop Peninsula and no evidence exists for an ecological replacement there.

Rattus novaeguineae occupies a restricted altitudinal range of 785 m. in vertical distribution and in a position that intervenes between the mid-montane species and those of the lowlands. It is broadly sympatric with *R. s. hageni* and, to a lesser extent, with *R. n. niobe* and *R. v. mollis*. It is not known to be sympatric with the lowland *R. m. mordax* although this absence of record may only reflect inadequate sampling.

The northern lowlands of New Guinea are occupied by *R. praetor* that extends eastward into the archipelagos of Bismarck and the Solomons. It is the only endemic species to occupy these vast chains of islands. Its mode of colonization is unclear for it does not appear to accompany human excursions, even though it readily invades gardens and buildings. Its southern counterpart in the lowlands is *R. mordax*. It, too, has become insular to the extent that it occupies the Louisiade Archipelago and the D'Entrecasteaux Islands. In this case, these may be refugia islands where these rats became isolated as the sea level rose at the end of the Pleistocene.

Rattus leucopus and *R. sordidus* are both sympatric with *R. mordax* on the mainland. Their ecological partitioning in these lowlands is unclear except that *R. sordidus* here, as well as in Australia, tends to occupy grasslands and open forests that permit extensive grass cover beneath. *Rattus leucopus* is more of a rain forest inhabitant. Neither is known as far west as Etna Bay where once again *R. praetor* is established. Etna Bay is west of the limit of the central cordillera which farther east is a major barrier to the spread of these lowland species.

Rattus jobiensis has a very restricted distribution in New Guinea since it is confined to the Schouten Islands of Geelvinck Bay. It is not only lowland in its insular distribution, but it is among the largest of the endemic rats. It shares the features of large size and harsh spinous pelage with *R. praetor coenorum, R. mordax fergussoniensis,* and *R. leucopus ratticolor*. This convergence in morphological features that typify lowland species has in past assessments led to allying *jobiensis* with one of these other species.

Influences of immeasurable consequence on the distribution of *Rattus* in New Guinea are deforestation and cultivation. The indigenous people have cleared vast areas of montane forest for cultivation and use fire to keep grasslands from reverting to forests. Brass (1941) provides a vivid description of the deforestation of the Baliem Valley up to elevations of 2400 m. where entire mountain ridges have been converted to grass. Access to higher elevations is provided for lowland species by such clearing procedures. *Rattus praetor coenorum* has been recorded here to 1500 m. and *R. rattus* has been collected at 2200 m.

The massive central cordillera divides New Guinea into northern and southern sections. For *Rattus* it is an effective geographical barrier east of the isthmus of the Vogelkop Peninsula to the southeastern extremity of New Guinea. There are no north–south passes through it below 1525 m. and few below 2000 m. Mountain peaks exceeding 4000 m. occur throughout the length of this range. Its effect on the evolution and distribution of most native *Rattus* has been to partition them into northern and southern species. Only the montane forms are less affected. *Rattus praetor* is strictly northern in its coastal distribution east of Etna Bay, even in its extensive insular distribution, and *R. novaeguineae* is known only from the northeast side. Except for *R. jobiensis,* which is solely insular in distribution, these two are the only primarily northern native species. The southern side is richer. Lowland species, such as *R. mordax, R. sordidus,* and *R. leucopus,* are distributed on both sides of the Owen Stanley Range, a southeastern portion of the central cordillera where, south of Collingwood Bay, the range loses altitude and lower passes are available. *Rattus sordidus* and *R. leucopus* also occur in northern Australia. In New Guinea both species extend across the southeastern portion and *leucopus* continues westward in the lowlands to just east of Etna Bay. *Rattus mordax* is confined to the southeastern region but, unlike the other two, has an insular distribution as well.

Only *R. niobe, R. verecundus,* and *R. steini* straddle the greater length of the central cordillera and can be included in both northern and southern components of the *Rattus* fauna. *Rattus richardsoni* and *R. giluwensis* do not have real membership here for they are both apical and very restricted in their distributions.

Rattus exulans, a more recent arrival, is primarily a northern species. Only in the southeastern portion has it gained access to the south side of the cordillera where even there it extends westward only to the east side of the Gulf of Papua. It is *R. exulans,* along with *R. rattus,* that has joined *R. praetor* in its extensive insular distribution in the Bismarck Archipelago and Solomon Islands. *Rattus exulans* and *R. rattus* also accompany *R. mordax* in its insular distribution.

EXTENT OF SYMPATRY

Division of the lowland native *Rattus* into northern and southern species may influence the extent of sympatry. No locality is known to us from museum specimens in which more than four native species occur sympatrically, and at only two localities out of 546 are there even four sympatric members. At the 1200 m. level at Wau these are *R. verecundus mollis, R. n. niobe, R. steini hageni,* and *R. novaeguineae.* In the southeast, *R. m. mordax, R. v. verecundus, R. leucopus dobodurae,* and *R. sordidus gestri* occur together at the 450 m. level at Sogeri. Seventeen cases, or 3 percent, have three sympatric species. Of these, nine cases involve *R. verecundus mollis, R. steini hageni,* and *R. n. niobe* between the altitudes of 1925 and 2530 m., three involve *R. leucopus dobodurae, R. m. mordax,* and *R. v. verecundus* between 350 and 520 m. altitude, and two involve *R. sordidus gestri, R. leucopus dobodurae,* and *R. m. mordax* between 10 and 450 m. altitude. All 17 cases are east of 143°30′ E and south of 05°00′ S. Eighty-five cases, or 15.8 percent, involve sympatric pairs and, of these, 6.5 percent are pair combinations of *R. steini hageni, R. verecundus mollis,* and *R. n. niobe* in almost equal numbers.

If the collections of *Rattus* over the past century can be regarded collectively as a reasonable portrayal of real distributional patterns, several conclusions can be drawn from these sympatric associations. An association of four species of *Rattus* that are native to New Guinea appears to be maximum. Known distributional patterns of the species, both vertical and horizontal, indicate that this association could take place only within the ranges of *R. novaeguineae, R. giluwensis,* or *R. m. mordax.* Either of the first two species may associate with *R. verecundus mollis, R. steini hageni,* and *R. n. niobe. Rattus mordax mordax* can associate with *R. leucopus dobodurae, R. v. verecundus,* and *R. n. niobe.* The Wau collection verifies the *novaeguineae* sympatry and the Sogeri one the *mordax* association. There are no other regions in New Guinea, according to the distributional records, where four different species could meet.

Records of the sympatric association of three species, known only from the southeastern segment of New Guinea, seem too geographically restricted and may in part reflect inadequate collecting at other potential sites. The association of *R. steini hageni, R. verecundus mollis,* and *R. n. niobe* should persist much farther west along the central cordillera and possibly even to the Star Mountains. In Irian Jaya, *R. s. steini, R. verecundus unicolor,* and *R. niobe arrogans* should be sympatric in the Snow Mountains at altitudes between 1600 and 1800 m., and *R. v. unicolor* should associate with *R. steini* *baliemensis* and *R. n. arrogans* farther east on the north slope of this mountain system.

In both the Huon Peninsula and the Vogelkop Peninsula there is evidence to support the existence of only two sympatric species, *R. steini foersteri* with *R. n. niobe,* and *R. niobe arrogans* with *R. verecundus unicolor,* respectively. Throughout the extensive lowlands, both north and south of the central cordillera and west of 145° E, distributional records indicate that opportunity exists for no more than pairs of sympatric species. It is largely flat, swampy country that floods seasonally in the monsoon period with up to several meters of water for 2–3 months continuously (Brass, 1941). It is generally avoided by indigenous human settlers and much of it is inhospitable terrain for a burrowing rodent like *Rattus* that must take refuge in higher ground during these periods.

Although the representation has to be regarded as oversimplified due to the amount of data at hand, we have constructed six stratifications of *Rattus* species according to major regional divisions. It provides, not necessarily a sympatric association, but rather a regional vertical distribution. This type of construction reveals several trends. First of all, except for the peninsulas, there are about the same number of species in each of the major regional stratifications (table 34). Secondly, except where *richardsoni* and *giluwensis* are present, *R. niobe* is the highest rat altitudinally in each case and *R. verecundus* is next everywhere but in the Huon Peninsula where the latter is absent. In the southeastern region where *R. steini* is absent, *R. m. mordax* occupies not only its typical lowland stratum but also extends to the mid-montane altitudes otherwise occupied by *steini.* Also, it is only in this region that *R. verecundus* extends from middle altitudes to sea level and here is larger than its conspecifics.

TABLE 34

Regional Vertical Stratifications of Native *Rattus* from High to Low Altitudes

Southeastern New Guinea
Rattus niobe niobe
(*Rattus verecundus vandeuseni*)
Rattus verecundus verecundus and *Rattus mordax mordax*
Rattus leucopus dobodurae and *Rattus sordidus gestri*

* * * * * * *

Huon Peninsula
Rattus niobe niobe
Rattus steini foersteri
Rattus mordax mordax

* * * * * * *

Southern Irian Jaya
Rattus richardsoni
Rattus niobe arrogans
Rattus verecundus unicolor
Rattus steini steini
Rattus praetor coenorum (2 known localities)
Rattus sordidus aramia and *Rattus leucopus ringens* or
Rattus sordidus aramia and *Rattus leucopus ratticolor*

* * * * * * *

Northeastern New Guinea
Rattus giluwensis
Rattus niobe niobe
Rattus verecundus mollis
Rattus steini hageni
Rattus novaeguineae
Rattus mordax mordax or *Rattus praetor coenorum*
(southern) (northern)

* * * * * * *

Vogelkop Peninsula
Rattus niobe arrogans
Rattus verecundus unicolor
Rattus praetor coenorum

* * * * * * *

Northern Irian Jaya
Rattus richardsoni
Rattus niobe arrogans
Rattus verecundus unicolor
Rattus steini baliemensis
Rattus praetor coenorum
Rattus jobiensis (insular)

If the assumption is made that montane species of *Rattus* must be derived from lowland colonizers, this stratified series may be helpful in identifying common ancestry within the genus. All species, except *R. richardsoni, R. giluwensis, R. steini, R. novaeguineae,* and *R. niobe,* have strong lowland representation, at least over part of their distributions. The closest ally of *niobe* and *richardsoni* with lowland representation is *verecundus* and they all probably share a major ancestral lineage. Reflection of probable common lineage between *R. praetor* and *R. steini* is manifested in the difficulty of establishing a common basis for morphological separation of the two species at higher elevations. Here, *R. praetor coenorum* becomes hard to distinguish from *R. steini hageni* of the east or from *R. s. steini* or *R. s. baliemensis* of the west. *Rattus novaeguineae* shows resemblance both to the *praetor-steini* group and to *R. leucopus*; they probably all share common ancestry. *Rattus giluwensis* is the most difficult to relate directly to a lowland species but the best candidate is the *praetor-steini* line through the mid-montane *steini* ancestral branch. This leaves *R. mordax* and *R. sordidus,* the two lowland species of the mainland that have no ally in a montane situation. *Rattus mordax* does invade higher altitudes in the local absence of *R. steini,* but remains low where *steini* occurs (i.e., Markham-Ramu Valley system and adjacent mountains; Huon Peninsula) and acts as the southern counterpart of *R. praetor. Rattus sordidus,* which is the most distinctive of all the native *Rattus* of New Guinea, may have originated in Australia and secondarily gained access to southern New Guinea when the Torres Strait was a land connection, a possibility suggested in the most recent revision of the Australian *Rattus* (Taylor and Horner, 1973). That more exchange here has not taken place between the two large islands involving, for example, Papuan *mordax* or Australian *Rattus tunneyi,* poses a difficult question, and it may relate to the possibility of saturation of numbers of species on both sides.

Another problem that is difficult to reconcile is the relationship of *R. leucopus* on either side of the Torres Strait. The suggestion has been made that *R. leucopus* shares common ancestry with *R. fuscipes coracius* of northeastern Australia, established species status in New Guinea, and has subsequently re-entered Australia where it is still very limited in distribution (Taylor and Horner, 1973). Dennis and Menzies (1978) concur with the suggestion that *leucopus* is a migrant into Australia, but question its derivation from a *fuscipes*-like ancestor. Alternatively, with *leucopus* as a member, they establish a *Rattus leucopus* Group in which they include all species of *Rattus* of New Guinea, as recognized by Tate (1951), except *R. gestri* (=*R. sordidus* in our revision), *R. bunae* (=*R. sordidus gestri*), and *R. shawmayeri* [=*Pogonomelomys* according to Mahoney, in George (1979)]. Their grounds are that *R. leucopus* is most similar in karyotype to three other members of the Group, *R. verecundus, R. niobe,* and *R. "ruber"* (probably represented by *R. steini hageni, R. mordax fergussoniensis,* and possibly *R. novaeguineae,* in their samples) and differs from them by only one fusion. We have reexamined the Australian material in light of our present study and the strong similarity of the two taxa, *leucopus* and *fuscipes coracius,* especially where they occur sympatrically, is reconfirmed. That *R. leucopus* also has major alliance to certain other endemic New Guinean species, especially to *R. praetor,* is evident from our present analysis, but its affinity to the entire *R. leucopus* Group of Dennis and Menzies (1978) is refuted. The dual Australo-New Guinean affinities of *R. leucopus* probably reflect a complex evolutionary history coincident with glacially induced sea level fluctuations that established a recurrent land bridge across the Torres Strait.

COMPARISON BETWEEN *RATTUS* OF AUSTRALIA AND NEW GUINEA

Based upon mean occipitonasal lengths, only three New Guinean subspecies, *R. n. niobe, R. n. arrogans,* and *R. verecundus vandeuseni,* are appreciably smaller than the Australian subspecies (Taylor and Horner, 1973), but six are larger. Relative to these Australian species, *Rattus* of New Guinea have not decreased substantially in size at higher elevations, but rather have increased in body size in lowland environments. That such increment in size represents an adaptation to a lowland tropical environment is supported in the Australian situation. There the largest subspecies, *R. leucopus leucopus* (42.0 mm. mean occipitonasal length), *R.*

fuscipes coracius (41.9 mm.), *R. sordidus villosissimus* (41.3 mm.), and *R. leucopus cooktownensis* (41.2 mm.), are either exclusively tropical or, in the case of *villosissimus,* has the main reservoir of its permanent population in the tropics (Taylor and Horner, 1973).

The difference in mean occipitonasal lengths of the species of continental Australian *Rattus* is 6.1 mm., 42.0 mm. for *R. l. leucopus,* the largest, and 35.9 mm. for *R. tunneyi culmorum,* the smallest (Taylor and Horner, 1973). Among *Rattus* of New Guinea, however, the same measurement differs by 18.2–18.9 mm. between the largest, *R. jobiensis* at 50.8 mm., and the two smallest, *R. n. niobe* at 32.6 mm. and *R. e. browni* at 31.9 mm. This distinction between the *Rattus* faunas of the two islands indicates that Australian *Rattus* are more conservative in body size and have remained relatively small in the course of their evolution. Australia is a scoured and eroded lowland continent, half in the temperate zone and half in the tropics, and has few mountain ranges. The highest of these, the Snowy Mountains, is at its maximum only 2230 m. in altitude. New Guinea, on the other hand, is a much smaller, but mountainous, tropical island with a vertical rise to almost 5000 m. and all the central cordillera is 1525 m. or above. The native *Rattus* occupy habitats from sea level to the fringe of glaciation on peaks and associated with this tremendous span of vertical occupation are these substantial differences in body size.

Although *Rattus* has evolved in New Guinea under the influence of almost the antithesis of topographic features that occur in Australia, a strong similarity emerges from the analysis of sympatry. In both land masses sympatry rarely involves more than three species of native *Rattus* and more likely it is only a pair (Taylor and Horner, 1973, fig. 44; present study).

CONCLUSIONS

We propose that three major species groups of truly native (all subspecies are endemic) *Rattus* can be recognized in New Guinea. They are 1) *niobe-richardsoni-verecundus,* 2) *praetor-steini-leucopus-giluwensis-mordax-novaeguineae-jobiensis,* and 3) *sordidus.* Only the first group, however, is completely endemic and, presumably, autochthonous at the level of species. The second includes *jobiensis,* which may be more closely related to Indo-Malaysian species, and *leucopus,* which is represented as well by two subspecies in Australia. The third group, *sordidus,* is widespread as three subspecies in Australia and may have evolved there before gaining access to New Guinea.

The remaining species, *R. exulans, R. nitidus, R. rattus, R. argentiventer,* and *R. norvegicus,* are all immigrants that reached New Guinea by human agency. Of these, *R. exulans* appears to be the most widespread, both geographically and ecologically, and probably arrived considerably earlier than the rest.

We recognize 11 native species of *Rattus* in New Guinea and five that have been introduced with human beings. All records of sympatry suggest that no more than four species of *Rattus* share a given area and that the usual number is two or less. The native species have radiated widely throughout New Guinea in every major habitat, and range altitudinally from sea level as coarse-furred lowland species to montane habitats as soft-furred forms. One of the montane species extends to the edge of receding glaciers at elevations to 4500 m. The various species show a tendency to become smaller in body size and denser in pelage with concomitant increase in altitude.

Among the native species, we recognize two subspecies of *Rattus niobe*: *R. n. niobe* (synonyms = *Stenomys rufulus* and *Stenomys niobe stevensi*), and *R. n. arrogans* (synonyms = *Rattus niobe haymani* [=*klossi*], *Stenomys niobe arfakiensis,* and *Rattus niobe pococki* [=*clarae*]); *Rattus richardsoni* as monotypic (synonym = *Rattus omichlodes*); four subspecies of *Rattus verecundus*: *R. v. verecundus, R. v. mollis* (synonym = *Rattus verecundus tomba*), *R. v. unicolor,* and *R. v. vandeuseni,* new subspecies Taylor and Calaby; two subspecies of *Rattus praetor*: *R. p. praetor* (synonyms = *Rattus praetor mediocris* and *Rattus purdiensis*), and *R. p. coenorum* (synonyms = *Rattus mordax tramitius, Rattus bandiculus, Rattus leucopus utakwa,* and *Rattus sansapor*); two subspecies of *Rattus mordax*: *R. m. mordax* and *R. m. fergussoniensis*; three subspecies of *Rattus leucopus*: *R. l. ringens, R. l. ratticolor,* and *R. l. dobodurae*; four subspecies of *Rattus steini*: *R. s. steini, R. s. foersteri, R. s. hageni* (synonym = *Rattus rosalinda*), and *R. s. baliemensis,* new subspecies Taylor and Calaby; *Rattus giluwensis* as monotypic; *Rattus novaeguineae,* new species Taylor and Calaby as monotypic; *Rattus jobiensis* as monotypic (synonyms = *Rattus owiensis* and *Rattus biakensis*); and two subspecies of *Rattus sordidus*: *R. s. gestri* (synonyms = *Rattus brachyrhinus* and *Rattus gestri bunae*) and *R. s. aramia.*

Among the introduced *Rattus,* the only one we assessed taxonomically was *R. e. browni.* We regard it as a senior synonym of the following: *Mus? echimyoides, Rattus concolor lassacquèrei, Rattus concolor manoquarius, Rattus browni praecelsus, Rattus browni aitape, Rattus browni suffectus, Rattus browni tibicen, Rattus browni gawae,* and *Rattus rennelli.*

KEY TO ADULT *RATTUS* IN NEW GUINEA

(Excluding *Rattus norvegicus* and *Rattus argentiventer.*)

1. Tail length less than 70 percent of head and body length; pelage long and lacks spines .... *R. giluwensis*

Tail length 70 percent of head and body length or more; pelage variable 2

2(1). Tail length less than 85 percent of head and body length; inflated bulla 22 percent of basal length 3

This combination of characters not present 4

3(2). Nasal width averages 31 percent of nasal length; tail averages 74 percent of head and body length .... *R. sordidus aramia*

Nasal width averages 35 percent of nasal length; tail averages 78 percent of head and body length ... *R. sordidus gestri*

4(2). Tail longer than head and body by 10 percent or more 5

Tail subequal to or shorter than head and body length 8

5(4). Large commensal rat; basal length 5.4 times or less bulla length; mammary formula 3 + 3 = 12 or 2 + 3 = 10; tail plain .... *R. rattus*

Medium to small non-commensal rat; basal length 5.7 times or more bulla length; mammary formula 1 + 2 = 6 or 0 + 2 = 4; tail usually tipped with white . 6

6(5). Incisive foramen length 3 times incisive foramina width; mammary formula 0 + 2 = 4; occipitonasal length 11 times or more m^{1-1} inside width .... *R. verecundus vandeuseni*

Incisive foramen length 2.7 times or less incisive foramina width; mammary formula 1 + 2 = 6; occipitonasal length 9.5 to 11 times m^{1-1} inside width ... 7

7(6). Pelage soft; occipitonasal length 9.5 to 10.2 times m^{1-1} inside width .... *R. verecundus mollis*

Pelage soft or lightly spinous; occipitonasal length 10.3 to 11 times m^{1-1} inside width .... *R. verecundus verecundus*

8(4). Tail length within 15 mm. of head and body length 9

Tail length shorter by more than 15 mm. than head and body length 14

9(8). Pelage usually light to moderately spinous; bulla length 21 percent of basal length; moderate supraorbital ridging; small commensal rat .... *R. exulans browni*

Pelage variable; bulla length less than 19 percent of basal length; supraorbital ridging variable; non-commensal rat 10

10(9). Tail 8 to 15 mm. shorter than head and body length 11

Tail length and head and body length subequal to within 7 mm. 12

11(10). Long, dense, and soft pelage; dark venter; interorbital width 19 to 20 percent of basal length .... *R. richardsoni*

Harsh-furred; whitish venter; interorbital width less than 18 percent of basal length .... *R. novaeguineae*

12(11). Interorbital width 20 percent or more of basal length; nasal length equal to or less than mastoid width .... *R. niobe niobe*

Interorbital width 19 percent or less than basal length; nasal length greater than mastoid width 13

13(12). Nasal width 70 to 80 percent of interorbital width; m^1 approximately 2.5 mm. wide; mammary formula $2 + 2 = 8$ .. .. *R. steini foersteri*

Nasal width less than 70 percent of interorbital width; m^1 2 mm. wide; mammary formula $1 + 2 = 6$ .... *R. verecundus unicolor*

14(8). Coarse-furred; strong supraorbital beading, usually with lateral projection near fronto-parietal suture; straight-sided incisive foramina 15

Combination of above not present ... 16

15(14). Bulla length 83 percent or more of incisive foramen length ... *R. mordax mordax*

Bulla length less than 83 percent of incisive foramen length .... *R. mordax fergussoniensis*

16(14). Tail length less than 80 percent of head and body length 17

Tail length more than 80 percent of head and body length 18

17(16). Pelage lacks spines; bulla 18 percent or more of basal length; mammary formula $3 + 3 = 12$ .... *R. nitidus*

Spinous pelage; bulla 17 percent or less of basal length; mammary formula $2 + 2 = 8$ .... *R. praetor praetor*

18(16). Bulla length less than 15.6 percent of basal length; spinous pelage .... *R. jobiensis*

Bulla length more than 15.6 percent of basal length; pelage variable 19

19(18). Bulla length 18 percent or more of basal length; spinous pelage .... *R. leucopus ringens*

Bulla length less than 18% of basal length; pelage variable 20

20(19). Bulla length 17 to 17.8 percent of basal length 21

Bulla length 15.8 to 16.8 percent of basal length 23

21(20). Pelage very soft; no white ventral marking; interorbital width 35 percent or more of zygomatic width .... *R. niobe arrogans*

Pelage may include spines; white ventral marking common; interorbital width less than 35 percent of zygomatic width 22

22(21). Mastoid width 90 to 95 percent of nasal length; bulla length is 90 percent or more of incisive foramen length; mammary formula $1 + 2 = 6$ .... *R. steini steini*

Mastoid width and nasal length approximately equal; bulla length 85 percent or less of incisive foramen length; mammary formula $2 + 2 = 8$ .... *R. steini hageni*

23(20). Bulla length 16.6 percent or more of basal length; mastoid width less than 85 percent of cranium width .... *R. leucopus dobodurae*

Bulla length less than 16.6 percent of basal length; mastoid width 85 percent or more of cranium width 24

24(23). Pelage without coarse spines; supraorbital ridging slight and terminates anterior to parietal; hind foot usually less than 35 mm.; m^1 width 58 percent or more of nasal width .. *R. steini baliemensis*

Pelage coarsely spinous; supraorbital ridging conspicuous and confluent with parietal ridging; hind foot generally longer than 35 mm.; m^1 width 54 percent or less of nasal width 25

25(24). Tail length 85 percent of head and body length; tail usually white-tipped; m^1 width 35 percent that of interorbital width; mammary formula $1 + 2 = 6$ .. .. *R. leucopus ratticolor*

Tail length 90 percent of head and body length; tail plain; m^1 width 40 percent of that of interorbital width; mammary formula $2 + 2 = 8$ .... *R. praetor coenorum*

MUSEUM SPECIMENS EXAMINED AND LOCALITIES

Rattus niobe niobe

Albert Edward, Mt., 3680 m, 08°22′ S, 147°18′ E (AMNH 104251–104272); Baiyanka, 1829 m, 05°35′ S, 144°51′ E (BM 47.1152–47.1154); Bolan Mt., 3700 m, 06°15′ S, 146°55′ E (RMNH 292-R61); Bosavi, Mt., 1400 m, 06°34′ S, 142°51′ E (BBM 103278, 103295–103297, 103306–103309, 103317, 103352–103355, 103359, 103367); Bosavi, Mt., 1829 m, 06°34′ S, 142°51′ E (BBM 103376, 103380, 103391, 103405, 103417–103424, 103435–103437, 103439–103440, 103444–103445, 103447–103448, 103452–103458, 103479–103482, 103487–103490, 103494, 103505); Bosavi, Mt., 2100 m, 06°34′ S, 142°51′ E (BBM 103465–103467, 103475–103476, 103499–103501); Bosavi, Mt., 2300 m, 06°34′ S, 142°51′ E (BBM 103401–103404, 103410–103411, 103426, 103431–103434); Bowutu Mts., 1981 m, 07°45′ S, 147°13′ E (BBM 99068); Bulldog Road, 2625 m, 07°28′ S, 146°40′ E (AMNH 222408–222412; BBM 28953, 28962); Bulldog Road, 6 mi. from Edie Creek, 2200 m, 07°26′ S, 146°40′ E (BBM 99450–99451, 99455, 99457–99460, 99462–99465, 99471–99472, 99476, 99478, 99480–99481, 99483, 99486, 99494, 99502–99504, 99509, 99515–99518, 99540–99541, 99543–99544, 99546, 99548, 99554, 99565–99567, 99569, 99584, 99586, 99592–99594, 99603–99607, 99613); Bulldog Road, 12 miles from Edie Creek, 2400 m, 07°31′ S, 146°40′ E (BBM 52183–52185, 52229–52230, 52234, 52236, 52252, 52254–52255, 52273, 52275, 52284–52285, 52288, 52298, 52300, 52302–52305, 52318–52319, 52334–52335, 52348, 52350, 52354, 52356–52357, 52377, 52379, 52381–52382, 52401, 52408, 52426, 52447, 52449, 52474–52475, 52478, 54739–54742, 54746, 54773, 54832–54833, 54856, 54858, 54885–54886, 61676–61682, 61684, 96633–96635, 96638–96639, 96649–96654, 96681–96686, 96690, 96697, 96699–96701, 96723, 96725–96727, 96734–96739, 96744, 96749–96756, 96774–96775, 96777–96783, 96810, 96812–96816, 96881, 100467, 100471, 100857, 100860, 100869, 100890, 100950–100951, 100972, 100975, 100992–100993, 101087–101088, 101097–101098, 101342, 101344, 101351, 101382, 101432, 101447–101448, 101451, 101456, 101459, 101481–101482, 101485, 101498, 101505, 101553–101559, 101570–101573); Dayman, Mt., 1540 m, 09°49′ S, 149°16′ E (AMNH 157784–157857); Dayman, Mt., 2050 m, 09°49′ S, 149°16′ E (AMNH 157685–157696, 157761–157765, 157768–157769); Dayman, Mt., 2230 m, 09°49′ S, 149°16′ E (AMNH 157640–157679, 157683–157684, 157697–157700, 157705–157706, 157709–157757, 157760, 157766–157767, 157770–157776, 157781–157783); Dayman, Mt., summit, 2430 m, 09°49′ S, 149°16′ E (AMNH 157701–157704, 157707–157708, 157777–157780); Edie Creek, 1900 m, 07°21′ S, 146°40′ E (BBM 100366, 100372, 100377); Edie Creek, 2134 m, 07°21′ S, 146°40′ E (AMNH 191671–191676; BBM 28894; MVZ 129880–129893); Edie Creek, 2256 m, 07°21′ S, 146°40′ E (MVZ 129894, 129896, 129898); Enaena, 1219 m, 10°03′ S, 149°38′ E (BM 47.1151); Ero Creek, 2860 m, 08°29′ S, 147°22′ E (AMNH 104192, 104280–104296, 104298–104303); Erumelavava, 1900 m, 08°15′ S, 146°59′ E (BBM 96838, 96846, 96848); Garaina, 12 mi. S.W., 1829 m, 08°00′ S, 147°00′ E (BBM 98974–98975); Giluwe, Mt., 2300 m, 06°03′ S, 143°53′ E (BBM 102178, 102188, 102200–102201, 102211–102213); Giluwe, Mt., 2743 m, 06°03′ S, 143°53′ E (BBM 102128–102132, 102134–102136, 102142–102147); Giluwe, Mt., 2900 m, 06°03′ S, 143°53′ E (BM 53.244–53.245; BBM 101972, 101975, 101980, 102016–102017, 102029, 102055, 102073–102082, 102084–102088, 102090–102094, 102096, 102098–102103, 102106–102107, 102109–102112, 102115); Giluwe, Mt., 3300 m, 06°03′ S, 143°53′ E (AMNH 222426–222427; BBM 20267, 20273–20275, 101845–101846, 101856, 101858–101859, 101876–101880); Giluwe, Mt., 3600 m, 06°03′ S, 143°53′ E (BBM 101892–101893, 101897, 101913–101917, 101930–101934, 101936, 101940–101941, 101945, 101951–101952, 101954, 101956–101957); Gono, 1900 m, 06°20′ S, 145°12′ E (AMNH 191803–191804); Ialibu, Mt., 2600 m, 06°15′ S, 144°03′ E (BBM 98210); Kabwum, 2550 m, 06°13′ S, 147°03′ E (BBM 52683, 52775, 52798–52800, 52803, 52829, 52835, 52838, 52840, 52854–52855, 52866, 52885–52887, 52894, 52897); Kabwum, 2880 m, 06°13′ S, 147°03′ E (BBM 52604, 52624–52626, 52636–52639, 52647, 52744–52745, 52760); Kabwum, 3300 m, 06°13′ S, 147°03′ E (BBM 52661–52662); Kabwum, 3580 m, 06°13′ S, 147°03′ E (BBM 52652–52654, 52656–52657, 52736–52737, 52739); Kagaba, 2800 m, 05°51′ S, 143°46′ E (BBM 60377–60380, 60387–60388, 60394, 60396, 60400, 60402–60405, 60412–60413, 60419, 60423–60424, 60427, 60429–60430, 60432, 60440, 60449, 60451, 60454, 60456, 60467, 60469, 60471, 60474, 60494, 60497–60499, 60501–60502, 60543, 60546, 97064A, 97064B, 97070A, 97070B, 97079, 97120–97121, 97207, 97256); Kagaba, 3200 m, 05°51′ S, 143°46′ E (BBM 60540, 60545, 60551, 60557–60558, 60562–60563, 60565–60567, 60569–60570, 60572–60573, 60577, 60589, 60595, 60597, 60601, 60603, 60608–60609, 60617, 60621, 60623, 60634–60635, 97214); Kagaba, 3400 m, 05°51′ S, 143°46′ E (BBM 60576, 60578, 60604, 97266, 97275, 97291); Kagaba, 3600 m, 05°51′ S, 143°46′ E (BBM 97296B, 97296C, 97297, 97299); Kagi, 1433 m, 09°07′ S, 147°36′ E (AMNH 108206, 108208, 108219–108220, 108228–108229); Kaindi, Mt., 2060 m, 07°21′ S, 146°43′ E (AMNH 191657–191670, 191677–191682; BBM 28875, 28879); Kaindi, Mt., summit, 2350 m, 07°21′ S, 146°43′ E (AMNH 222413–222416, 222424; BBM 20200, 20205, 29157–29161, 29169–29170, 29173, 29177, 29192, 50693, 50696–50700, 50705–50706, 50711–50712, 51021, 51028, 51042, 51082, 51104, 51113–51114, 51125, 51132–51133, 52188, 52190–52192, 52194–52195, 52197–52199, 52201, 52208–52212, 52219, 52224, 53273, 53307, 53325, 53329, 53343–53351, 53372–53377, 53401–53403, 53405, 53425–53428, 53458, 53517–53518, 53520, 53543–53544, 61528, 61530–61535, 61537, 61546–61547, 61549–61554, 61557, 61562–61563, 61574–61581, 61586–61589, 97566–97567, 97578, 97601–97602, 97609, 97616–97618, 97682–97686, 97695–97696, 97713, 97721, 98722, 98745–98750, 98752–98753, 98758–98759, 98761–98764, 98771, 98773–98774, 98784, 98786, 98796–98808, 98815–98819, 98821–98824, 98826, 98848–98850, 98854–98860, 98875–98876, 99088–99090, 99141–99142, 99159); Keglsugl, 2438 m, 05°50′ S, 145°06′ E (AMNH 191752; BBM 100735, 100741–100742, 100744, 100784, 100792–100795, 100797–100801, 100804, 100806–100810, 100827–100832, 100834–100838, 100840–100841, 100844); Kemp, Mt., 2438 m, 07°48′ S, 147°15′ E (BBM 98001, 98022, 98024, 98031–98032); Kerigomna, Mt., 3050 m, 05°58′ S, 145°07′ E (BBM 55595, 55608); Kudiseru, 2134 m, 07°26′ S, 146°45′ E (BBM 97770–97776, 97787–97788, 97804–97806, 97813, 97826, 97828, 97845–97846, 97848–97852); Lavani Valley, 2450 m, 05°45′ S, 142°35′ E (BBM 60883–60886, 60891–60893, 60904, 60922–60924, 60931–60932, 60935–60936, 60938, 60952–60956, 60962, 60965, 60968–60974, 60983, 60986–60987, 61002, 61006–61008, 61011, 61018–61019); Louise Lake, 2591 m, 05°14′ S, 141°24′ E (BBM 98443, 98450–98451, 98453–98454, 98457, 98463–98464, 98469–98471, 98477–98479, 98495, 98506–98507, 98512, 98517, 98521, 98524–98525, 98531, 98533–98535, 98551–98553); Louise, Lake, 2800 m, 05°14′ S, 141°24′ E (BBM 98472, 99931–99942, 99956–99961, 99963–99976, 99978, 99985, 99987–99993, 100000–100005, 100017–100018, 100030–100034, 100046, 100048, 100062–100066, 100068–100069, 100071–100074, 100085–100089, 100091–100092, 100095–100099, 100102–100104, 100110–100113, 100115–100116, 100118–100123, 100126, 100128–100132, 100138–100141, 100144–100146); Maneau, Mt., 2700 m, 09°48′ S, 149°20′ E (AMNH 157680–157682, 157758–157759); Marafunga, 2400 m, 05°58′ S, 145°08′ E (BBM 55537–55539, 55545, 55549); Mendi, 2000 m, 06°10′ S, 143°36′ E (BBM 55214–55216, 55219, 55221–55222, 55225, 55227, 55233, 55240, 55243, 55300, 60313, 60315, 60317–60319, 60331, 60333, 60354–60356, 60366); Michael, Mt., 2134 m, 06°25′ S, 145°20′ E (AMNH 191806–191808, 191810–191826); Michael, Mt., summit ridge, 3627 m, 06°25′ S, 145°20′ E (AMNH 192269); Minj River headwaters, 1829 m, 06°01′ S, 144°35′ E (BM 53.232–53.236); Missim, Mt., 1900 m, 07°13′ S, 146°50′ E (BBM 29080–29081, 29098, 29102, 29106–29110, 29125, 50602–50604, 50610–50611); Missim, Mt., 2100 m, 07°13′ S, 146°50′ E (MCZ 29907, 29909–29919); Moimo, 1829 m, 07°59′ S, 147°01′ E (BBM 98050–98052, 98064, 98069, 98071, 98073, 98084, 98090–98091, 98107, 98110, 98120, 98123–98126, 98140); Mongibusu, 2600 m, 06°23′ S, 147°15′ E (ZM 45931); Murmur Pass, 2750 m, 05°45′ S, 143°56′ E (BBM 60650–60653, 60655–60656, 60658–60660, 60673, 60678, 60681, 60698, 60702–60703, 60705, 60707, 60711, 60721–60723, 60730, 60732, 60734, 60738, 60750–60752, 60762–60764, 60790, 60792–60793, 60795, 60813, 60833, 60859, 60861, 97388, 97411A, 97411B, 97469, 97472A, 97515A, 97515B, 97516A, 97516B); Nimodia, 2070 m, 08°36′ S, 147°11′ E (AMNH 104304–104314); Nondugl, 1700 m, 05°52′ S, 144°45′ E (AMNH 222607–222608, 222613–222616); Otto, Mt., Collins Sawmill, 2215 m, 05°59′ S, 145°25′ E (AMNH 191784–191793, 191795–191797); Otto, Mt., Collins Sawmill, 2275 m, 05°59′ S, 145°25′ E (AMNH 191798–191801); Owgarra, 2750 m, 08°46′ S, 147°24′ E (BM 5.11.28.7); Pengagl Creek, 3002 m, 05°40′ S, 145°05′ E (AMNH 191729–191740, 191742–191751, 191753–191781, 192181–192250); Piunde-Aunde Creek, 3570 m, 05°39′ S, 145°05′ E (AMNH 191728); Piunde-Aunde Lake, 3570 m, 05°39′ S, 145°05′ E (AMNH 191683–191727); Purosa, 1970 m, 06°36′ S, 145°34′ E (AMNH 191827–191836); St. Mary, Mt., 3000 m, 08°10′ S, 146°58′ E (BBM 96867–96870, 96899–96906, 96910–96912, 96914–96915, 96917–96918, 96924, 96926–96929, 96931–96936); Saruwaged Mts., 4000 m, 06°16′ S, 146°45′ E (BM 28.10.1.34–28.10.1.35); Schrader Mts., 2530 m, 05°10′ S, 144°26′ E (BM 69.357–69.360); Shungol, Mt., 2000–2300 m, 06°51′ S, 146°44′ E (BBM 60294A, 60295, 98294); Simbai, 1676 m, 05°10′ S, 144°26′ E (BM 69.356); Smith's Gap, 762 m, 08°03′ S, 146°53′ E (BBM 96943–96947, 96951–96954, 96958–96961, 96970–96973, 96976–96981, 96989–96992, 97002, 97004–97006, 97011–97014, 97024–97027, 97037–97040); Star Mts., 3150 m, 04°54′ S, 140°47′ E (BBM 98556–98557, 98559, 98565–98567, 98570–98575, 98578, 98585–98586, 98590, 98592–98593, 98595, 98597–98598, 98602, 98607–98608, 100149, 100151, 100157, 100159–100163, 100169, 100178–100179, 100186–100187, 100189, 100194, 100202, 100205, 100208, 100213, 100216–100218, 100223–100226, 100228–100232, 100237, 100240, 100242–100245, 100251, 100257–100260, 100263); Strong Mt., 2700 m, 07°57′ S, 146°57′ E (BBM 96605–96606); Tafa, Mt., east slope, 2070 m, 08°35′ S, 147°09′ E (AMNH 104315–104318, 104320); Tafa, Mt., west slope, 2400 m, 08°34′ S, 147°06′ E (AMNH 104142, 104322–104337, 104339, 104342–104349, 104353–104354); Tambul, 2286 m, 05°53′ S, 143°58′ E (BBM 27943); Tambul, 2438 m, 05°53′ S, 143°58′ E (BBM 27956); Tapu, 1829 m, 06°14′ S, 145°50′ E (BM 47.1149–47.1150); Telefomin, 2438 m, 05°12′ S, 141°38′ E (BBM 98346–98347, 98351–98353, 98356–98358, 98380–98382, 98397, 98409–98410); Tomba, Mt., 2530 m, 05°50′ S, 144°02′ E (AM M9592; BM 53.243; ZS 1965/30); Ulur, Mt., 2377 m, 06°14′ S, 147°24′ E (AMNH 195091–195116); Wau, 1200 m, 07°20′ S, 146°43′ E (AMNH 222418); Wau, 1925 m, 07°20′ S, 146°43′ E (BBM 101125–101126, 101134–101137, 101611–101612, 101620, 101631); Wau, 2400 m, 07°20′ S, 146°43′ E (AMNH 222417, 222606); Welya, 2438 m, 05°44′ S, 143°56′ E (BM 53.237–53.238, 53.241–53.242); Welya, 2743 m, 05°44′ S, 143°56′ E (BM 53.239–53.240); Wilhelm, Mt., 2770 m, 05°46′ S, 144°59′ E (AMNH 191783); Wilhelm, Mt., 3475 m, 05°46′ S, 144°59′ E (AMNH 222421, 222423; BM 69.1420–69.1421; BBM 20051, 20054, 100479–100483, 100486–100490, 100492, 100494–100497, 100499–100504, 100514, 100517, 100521, 100523, 100548–100552, 100554–100555, 100566–100567, 100569–100573, 100576, 100578–100579, 100582, 100590, 100593–100596, 100638, 100641, 100650–100652, 100657–100661, 100664–100667, 100682–100686, 100689–100691, 100693, 100698–100707, 100710–100711, 100714–100715, 100717, 100719); Yanca, 1981 m, 05°45′ S, 144°07′ E (BM 50.1765).

Rattus niobe arrogans

Arfak Mts., 2000 m, 01°09′ S, 134°00′ E (BM 29.5.27.36); Baliem River, 1600 m, 04°10′ S, 138°56′ E (AMNH 110205, 110217, 110233, 110242); Bernhard Camp, 10 km southwest, 1500 m, 03°31′ S, 139°11′ E (AMNH 152117–152120); Bernhard Camp, 15 km southwest, 1500–1800 m, 03°32′ S, 139°10′ E (AMNH 152121–152127, 152130–152165, 152477–152478, 152823; MZB 8275–8276); Bernhard Camp, 18 km southwest, 2150 m, 03°33′ S, 139°09′ E (AMNH 152166–152183); Carstensz Meadow, 3630 m, 04°11′ S, 137°11′ E (ANWC CM11709); Discovery Lake, 3750 m, 04°03′ S, 137°11′ E (ANWC CM11711–CM11712); Doormanpad-bivak, 2400 m, 03°30′ S, 138°30′ E (BM 22.2.2.23–22.2.2.24; MZB 427–429); Ertsberg, 3580 m, 04°06′ S, 137°07′ E (ANWC CM11707–CM11708); Habbema, Lake, 3225 m, 04°09′ S, 138°41′ E (AMNH 150663–150668, 150670–150698, 150710–150728, 150730–150733, 150735–150763, 150765–150770, 150773–150779, 150781–150789, 150792, 150794–150809, 150816–150819, 150825–150830, 150832–150851, 150853–150858, 150862–150871, 150873–150877, 150879–150890, 150892–150894, 150897, 150899–150913, 151558, 151560); Habbema, Lake, 9 km northeast, 2800 m, 04°05′ S, 138°50′ E (AMNH 150488–150502, 150505–150509, 150514–150515, 150518–150520, 150523, 150525–150529, 150535, 150539–150540, 150543, 150547–150555, 150557–150558, 150561–150562, 150568–150570, 150572–150575, 150582–150587, 150590–150591, 150595–150596, 150599–150600, 150604–150606, 150609, 150614, 150617, 150621, 150631–150632, 150646, 150652–150656, 150921–150922); Ibele River, 2200 m, 04°05′ S, 138°42′ E (AMNH 109822, 150914–150915, 150935, 150955, 150959, 150961, 150966 (skull only; skin is *R. s. baliemensis*), 150984–150987, 150990, 150993, 150999, 151020, 151023, 151027, 151070, 151092–151095, 151118, 151145–151146, 151149–151151, 151168–151169, 151186–151187, 151189, 151240, 151280, 151289–151294, 151298, 151313–151314, 151324–151326, 151583–151587, 151710–151717, 151733–151743, 151751–151753, 151774–151775); Larson, Lake, 3980 m, 04°04′ S, 137°11′ E (ANWC CM11710); Sumuri, 2500 m, 03°50′ S, 135°30′ E (ZM 39695–39696, 45679, 91959–91961); Utakwa River, Camp No. 9, 1676 m, 04°11′ S, 137°12′ E (BM 13.6.18.82–13.6.18.85); Utakwa River, Camp No. 11, 2438 m, 04°07′ S, 137°11′ E (BM 13.6.18.86–13.6.18.88); Wilhelmina, Mt., 2 km east of top, 3850 m, 04°16′ S, 138°40′ E (AMNH 110136–110138, 110140–110143, 110145–110146, 110148–110150, 110155–110161, 110168, 110173–110174, 100176, 110178, 110181–110182, 110189–110191); Wilhelmina, Mt., 2 km east of top, 4050 m, 04°16′ S, 138°40′ E (AMNH 110169, 110172, 110177, 110192–110193); Wilhelmina, Mt., 7 km northeast of top, 3610 m, 04°15′ S, 138°45′ E (AMNH 110134, 110327–110336, 110340–110343, 110345–110350, 110352–110364, 110367–110373, 110375–110380, 110383–110390, 110393–110405, 110408–110412, 110414–110429, 110432–110439, 110441, 110443–110444, 110446–110450, 150451–150453, 150456–150460, 150463–150465, 150468–150469, 150471–150474, 150476–150480, 150483–150484; MZB 8273–8274).

Rattus richardsoni

Discovery Lake, 3640 m, 04°03′ S, 137°11′ E (ANWC CM11705); Ertsberg, 3400 m, 04°06′ S, 137°07′ E (KNMB 4030–4031); Habbema, Lake, 3225 m, 04°09′ S, 138°41′ E (BM 63.1155; AMNH 150701–150708, 150734, 150764, 150780, 150790–150791, 150793, 150810, 150815, 150822–150823, 150859–150860, 150896, 150898; MZB 8277–8278); Meren Valley, 4250 m, 04°05′ S, 137°10′ E (ANWC CM11701–CM11703); Middenspitz, 4500 m, 04°05′ S, 137°10′ E (ANWC CM11704); Wilhelmina, Mt., summit, 3900–4050 m, 04°19′ S, 138°32′ E (AMNH 110153–110154, 110162, 110165–110167, 110171, 110179–110180, 110185–110186); Wilhelmina, Mt., 2 km east top, 3800–3980 m, 04°16′ S, 138°40′ E (BM 63.1156; AMNH 110139, 110144, 110147, 110152, 110163–110164, 110170, 110187); Wilhelmina, Mt., 7 km northeast of top, 3610 m, 04°15′ S, 138°45′ E (AMNH 110324, 110351, 110365, 110381, 110406, 110413, 110430, 110440, 110442, 150454, 150462, 150470, 150475).

Rattus verecundus verecundus

Astrolabe Mt., 853 m, 09°33′ S, 147°26′ E (ZM 60107); Avera, 200 m, 08°57′ S, 146°57′ E (BM 3.12.1.1–3.12.1.2, 4.12.1.12, 5.11.28.8); Baruari, 520 m, 09°30′ S, 147°20′ E (AMNH 108314, 108315 (skull only; skin is *R. l. dobodurae*), 108320, 108355); Boneno, 1219 m, 09°54′ S, 149°25′ E (BM 47.1165–47.1166); Dayman, Mt., 700 m, 09°49′ S, 149°16′ E (AMNH 157886–157897); Dinawa, 1219 m, 08°48′ S, 147°15′ E (BM 4.4.10.1–4.4.10.2); Enaena, 1219 m, 10°03′ S, 149°38′ E (BM 47.1156 (skull only; skin is *R. m. mordax*), 47.1160–47.1164); Garaina, 800 m, 07°54′ S, 147°09′ E (MVZ 141051, 141053, 141081); Garaina, 12 mi. southwest, 1829 m, 08°00′ S, 147°00′ E (BBM 98957–98958, 98967–98968, 98984, 98992–98993); Itiki, 350 m, 10°35′ S, 150°00′ E (AMNH 108359); Kagi, 1433 m, 09°07′ S, 147°36′ E (AMNH 108202–108205, 108207, 108209–108214, 108217–108218, 108221, 108226–108227, 108230–108237, 108239–108246, 108256); Lamington, Mt., 500 m, 08°50′ S, 148°08′ E (BBM 25186, 25254, 25280); Lindon's Creek, 183 m, 08°11′ S, 147°50′ E (BM 6.1.8.7, 6.8.8.8); Mafulu, 1253 m, 08°31′ S, 147°00′ E (AMNH 104227, 104248, 104276–104277); Matsika, 950 m, 08°34′ S, 147°03′ E (AMNH 104234); Moimo, 1829 m, 07°59′ S, 147°01′ E (BBM 98130, 98133); Sogeri, 450 m, 09°25′ S, 147°26′ E (AMNH 108342, 108996); Tamata Creek, upper, 152 m, 08°21′ S, 147°52′ E (BM 6.1.8.6); Tapini, 1000 m, 08°20′ S, 147°00′ E (BBM 96826, 96832–96833).

Rattus verecundus mollis

Arabari, 2100 m, 06°08′ S, 145°15′ E (BBM 55091, 55093, 55096, 55098, 55100, 99366–99369, 99371, 99374–99375, 99400–99401); Arau, 1400 m, 06°20′ S, 146°05′ E (AMNH 191842–191853); Atitau, 1158 m, 04°48′ S, 145°20′ E (AMNH 198828); Bosavi, Mt., 1400 m, 06°34′ S, 142°51′ E (BBM 103269, 103272, 103277); Bosavi, Mt., 1829 m, 06°34′ S, 142°51′ E (ZS 1966/508–1966/513); Bowutu Mts., 1981 m, 07°45′ S, 147°13′ E (BBM 99051, 99066); Buntibasa District, 1219 m, 06°27′ S, 146°07′ E (BM 50.1203–50.1204); Edie Creek, 2134 m, 07°21′ S, 146°40′ E (BBM 28897); Gono, 1900 m, 06°20′ S, 145°12′ E (AMNH 191838–191841); Hawate, 1219 m, 07°14′ S, 146°27′ E (BBM 97863, 97895); Kaindi, Mt., 2060 m, 07°21′ S, 146°43′ E (BBM 28873); Kemp, Mt., 2438 m, 07°48′ S, 147°15′ E (BBM 98009, 98016); Kudiseru, 2134 m, 07°26′ S, 146°45′ E (BBM 97765–97766, 97789, 97800, 97818–97819, 97829); Kunai Creek, 1200 m, 07°20′ S, 146°43′ E (BBM 20092A, 20093A, 99658–99659); Mendi, 2000 m, 06°10′ S, 143°36′ E (BBM 60371); Michael, Mt., 2134 m, 06°25′ S, 145°20′ E (AMNH 191579, 191637); Minj River headwaters, 1829 m, 06°01′ S, 144°35′ E (BM 53.219–53.220); Missim, Mt., 1300 m, 07°13′ S, 146°50′ E (BBM 24635, 24640, 24642, 28377, 28383, 28401, 28408); Missim, Mt., 1900 m, 07°13′ S, 146°50′ E (MCZ 29905–29906); Murmur Pass, 2750 m, 05°45′ S, 143°56′ E (BBM 97374, 97387, 97390, 97517); Namie Creek, 1524 m, 07°20′ S, 146°43′ E (BBM 98887–98889, 98891–98892); Oksapmin, 1650 m, 05°15′ S, 142°14′ E (BBM 55382, 99785); Oksapmin, 1850 m, 05°15′ S, 142°14′ E (BBM 55420, 55465, 55484, 55493, 99852, 99911); Schrader Mts., 2530 m, 05°10′ S, 144°26′ E, (BM 69.355); Tambul, 2286 m, 05°53′ S, 143°58′ E (BBM 28051); Tambul, 2438 m, 05°53′ S, 143°58′ E (BM 53.229); Tifalmin, 1829 m, 05°10′ S, 141°24′ E (BBM 98413, 98438); Tomba, 2530 m, 05°50′ S, 144°02′ E (AM M9581–M9585; BM 50.1766, 53.227; ZS 1965/5); Wanuma, 5 km north, 1200 m, 04°48′ S, 145°19′ E (BBM 103824, 103836–103837, 103877); Wanuma, 14 km north-northwest, 1500 m, 04°45′ S, 145°14′ E (BBM 103899, 103901–103903, 103926, 103928–103929, 103936, 103940, 103958, 103960–103967, 103992, 103994, 103996, 104051–104053, 104056, 104065–104073, 104083–104086, 104088, 104105–104111, 104130, 104132–104133, 104135–104136, 104153–104156, 104158, 104181–104183, 104201–104202, 104220–104221, 104224–104235, 104266–104267, 104269, 104271–

104272, 104278, 104280–104282, 104284, 104319, 104325–104327, 104349–104353, 104363, 104365–104368); Wau, 1200 m, 07°20′ S, 146°43′ E (AMNH 222602); Wau, 1562 m, 07°20′ S, 146°43′ E (AMNH 222600–222601); Wau, 1925 m, 07°20′ S, 146°43′ E (BBM 97635–97636, 97641–97643, 97653–97654, 100363–100365, 100367–100370, 100388–100392, 101639); Wau, 2400 m, 07°20′ S, 146°43′ E (AMNH 222603); Wau Creek, 1372 m, 07°19′ S, 146°44′ E (BBM 20482, 20493–20494, 27566, 27621–27622); Welya, 2134 m, 05°44′ S, 143°56′ E (BM 53.226); Welya, 2438 m, 05°44′ S, 143°56′ E (BM 53.221–53.225); Yaiya Valley, 1676 m, 06°50′ S, 146°08′ E (BM 69.354).

Rattus verecundus unicolor

Kunupi, 1000 m, 03°50′ S, 135°30′ E (ZM 39830); Kunupi, 1400–1800 m, 03°50′ S, 135°30′ E (ZM 39694, 39820–39829, 39851–39859, 45678, 91127, 91928–91956; AMNH 103269–103270); Sumuri, 2500 m, 03°50′ S, 135°30′ E (ZM 91957–91958); Sururai, Kampong, 1950 m, 01°21′ S, 133°55′ E (AMNH 222405–222407).

Rattus verecundus vandeuseni, New Subspecies

Dayman, Mt., middle camp, 1540 m, 09°49′ S, 149°16′ E (AMNH 157899–157906).

Rattus praetor praetor

Aola, 152 m, 09°32′ S, 160°28′ E (BM 88.1.5.38–88.1.5.39); Awelkom, 600 m, 05°38′ S, 147°48′ E (BBM 95268–95269); Balbi, Mt., 1900 m, 05°55′ S, 155°00′ E (BBM 61418, 61421–61422, 61444); Bat Island, 5 m, 02°51′ S, 146°14′ E (AM M7183–M7184); Bougainville Island, 183 m, 6°00′ S, 155°20′ E (AMNH 99751); Buin, 150 m, 06°46′ S, 155°42′ E (AM M5759, M5761); Iambon, Camp 6, 1067 m, 06°00′ S, 149°40′ E (AMNH 194396, 194420); Kabakadai, 450 m, 05°38′ S, 148°25′ E (BM 81.3.28.1); Karaea, Mt., 1100 m, 05°42′ S, 154°57′ E (BBM 61248); Kar Kar, 10 m, 04°33′ S, 145°57′ E (AMNH 221190–221191); Mutahi, 1450 m, 05°42′ S, 154°57′ E (BBM 61286, 61300, 61317); Pokapa, 200 m, 05°35′ S, 155°01′ E (BBM 61081–61082, 61115); Tinputz Patrol Post, 5 m, 05°34′ S, 155°01′ E (BBM 61318–61320); Torokina, 10 m, 06°14′ S, 155°03′ E (USNM 277053–277063, 277066–277067, 278066–278067); Whiteman Range, 1400 m, 05°52′ S, 149°50′ E (AMNH 194484); Yalom, 1000 m, 04°23′ S, 151°45′ E (CZM CN14795–CN14796, CN14804, CN14806).

Rattus praetor coenorum

Apangai, 245 m, 03°38′ S, 143°04′ E (ANWC CM8175); Aupik, 245 m, 03°38′ S, 143°00′ E (ANWC CM8707); Bernhard Camp, 75 m, 03°30′ S, 139°12′ E (AMNH 152356); Bernhard Camp, 4–6 km southwest, 850–1200 m, 03°30′ S, 139°12′ E (AMNH 152357–152360; MZB 8272); Brugnowi, 60 m, 04°14′ S, 142°49′ E (BBM 22586–22587, 22589, 22596); Chambri Lake, 50 m, 04°13′ S, 143°06′ E (ANWC CM8071, CM8263); Cycloop, 150 m, 02°31′ S, 140°38′ E (AMNH 110132, 152355); Derimapa, Mt., 1524 m, 03°50′ S, 135°43′ E (BM 33.6.1.46; AMNH 101964); Doormanpadbivak, 1410 m, 03°30′ S, 138°30′ E (BM 22.2.2.11–22.2.2.15; RMNH 22502, 22504; MZB 415–420); Doromena, 762 m, 02°25′ S, 140°26′ E (FMNH 54070–54071); Etnabaai, 5 m, 03°55′ S, 134°39′ E (RMNH x2, x3, 0202, 0206 (skin) and 3809 (skull), 0207, 0213, 0225, 0227–0229, 3812–3813, 3906, 3909, 3911, 3915–3916, 3925–3926); Gebroeders, 1524 m, 03°39′ S, 135°56′ E (BM x166); Hollandia, 114 m, 02°32′ S, 140°43′ E (AM M7080–M7081; USNM 277443–277446, 277782 (skull only, skin is *R. rattus*), 277784–277785, 295114–295119, 295121; FMNH 54055–54056, 54059, 54226–54227, 56398; AMNH 110113, 110115–110116, 110118, 110120, 110124, 110126; MZB 5807, 8271); Imbia, 300 m, 03°36′ S, 143°06′ E (ANWC CM8419); Kaminibus, 275 m, 03°37′ S, 143°03′ E (ANWC CM8311–CM8312); Kandangi, 50 m, 04°20′ S, 143°07′ E (ANWC CM8385, CM8390–CM8393, CM8727); Korogo, 50 m, 04°06′ S, 143°10′ E (ANWC CM8410); Maprik, 245 m, 03°38′ S, 143°04′ E (ANWC CM8210–CM8212, CM8332, CM8349, CM8351, CM8418); May River, 122 m, 04°17′ S, 141°55′ E (ZS 1965/49–1965/51, 1965/65a; BBM 22610, 22621, 22640); Nabire, 5 m, 03°21′ S, 135°31′ E (AMNH 222445–222452); Noemfor Island, 50 m, 01°00′ S, 134°53′ E (BM 21.8.1.16); Oransbari, 5 m, 01°21′ S, 134°18′ E (AMNH 222432–222434); Paiweh, 137 m, 04°26′ S, 141°38′ E (BBM 22716–22717); Pionier-bivak, 50 m, 02°16′ S, 138°03′ E (BM 22.2.2.19–22.2.2.22; MZB 421–423); Prauen-bivak, 76 m, 03°15′ S, 138°35′ E (BM 22.2.2.16–22.2.2.18; RMNH 22489; MZB 424–425); Rotanburg, 76 m, 03°14′ S, 139°35′ E (RMNH 22490); Sansapor, 5 m, 00°29′ S, 132°05′ E (AM M7194–M7195; USNM 277021, 277257, 277264, 277279, 277301–277304; AMNH 143836–143837, 143843–143845, 143849–143851, 143868–143869, 143871); Sentani Lake, 200 m, 02°37′ S, 140°31′ E (BNM 7750; AMNH 110133); Serengwandu, 50 m, 03°48′ S, 143°04′ E (ANWC CM8671); Sina, Mt., 1067 m, 02°32′ S, 140°31′ E (BM 1938.8.3.59–1938.8.3.62); Utakwa River, Camp 3, 762 m, 04°27′ S, 137°14′ E (BM 13.6.8.72, 13.6.18.65–13.6.18.80); Utakwa River, Camp 6, 884 m, 04°24′ S, 137°12′ E (BM 13.6.18.81); Vulcan Island, 5 m, 04°08′ S, 145°02′ E (BM

15.2.18.10); Wasior, 1400 m, 02°43′ S, 134°30′ E (AMNH 100878).

Rattus mordax mordax

Baiwa, 5 m, 09°36′ S, 149°29′ E (AMNH 158033); Baroka, 5 m, 08°49′ S, 146°35′ E (AMNH 104207–104209, 104211, 104213–104214, 104217, 104221 (skin only; skull is *R. n. niobe*), 104223, 104238); Baruari, 520 m, 09°30′ S, 147°20′ E (AMNH 108312, 108319, 108349, 108357); Boneno, 1219 m, 09°54′ S, 149°25′ E (BM 47.1159); Conflict Group, 5 m, 10°45′ S, 151°45′ E (BM 4.6.7.13); Dobodura, 150 m, 08°46′ S, 148°23′ E (AM M6913–M6916, M6961, M6977); Enaena, 1219 m, 10°03′ S, 149°38′ E (BM 47.1156 (skin only; skull is *R. v. verecundus*), 47.1157); Finschhafen, 5 m, 06°34′ S, 147°51′ E (USNM 295112; BBM 27649); Gwariu River, 200 m, 09°40′ S, 149°17′ E (AMNH 158034–158038, 158040, 158047–158049); Haveri, 750 m, 09°25′ S, 147°35′ E (MCSN MSNG3494; BM 97.8.7.35); Itiki, 350 m, 10°35′ S, 150°00′ E (AMNH 108258, 108322–108323, 108360, 108364–108365); Java Rarre, 600 m, 09°25′ S, 147°26′ E (BBM 60259); Joe Landing, 5 m, 11°25′ S, 153°25′ E (AMNH 159787); Kagi, 1433 m, 09°07′ S, 147°36′ E (AMNH 108238, 108257, 108368); Kemp Welch River, 30 m, 10°03′ S, 147°47′ E (AMNH 108126–108127); Kokebagu, 30 m, 09°45′ S, 147°43′ E (AMNH 108128–108145, 108155, 108160–108161, 108163–108172, 108183, 108187–108188); Kokoda, 366 m, 08°53′ S, 147°45′ E (BM 7.2.1.3–7.2.1.4, 33.9.1.6); Kulumadau, 200 m, 09°04′ S, 152°43′ E (AMNH 159689, 159822–159839); Kumusi River, mouth, 5 m, 08°27′ S, 148°14′ E (BM 6.1.8.13–6.1.8.14); Kumusi River, middle, 172 m, 08°30′ S, 148°00′ E (BM 4.8.3.1); Lae, 10 m, 06°44′ S, 147°00′ E (AM M7087–M7089); Lamington, Mt., 500 m, 08°50′ S, 148°08′ E (AM M4292, M4685, M4687, S1862, BBM 25124, 25211, 25252, 25278); Madeu, 762 m, 08°40′ S, 146°50′ E (BM 8.10.8.3–8.10.8.6); Mafulu, 1253 m, 08°31′ S, 147°00′ E (BM 34.6.1.1–34.6.1.5; AMNH 104160, 104165, 104226, 104228–104233, 104240, 104242–104246, 104249, 104274, 104382); Maiu River, 150 m, 09°40′ S, 149°17′ E (AMNH 158039); Masba Creek, 610 m, 06°28′ S, 147°34′ E (AMNH 195118–195119); Menapi, 15 m, 09°46′ S, 149°58′ E (AMNH 158029, 158031–158032, 158043–158046); Milne's Bay, 5 m, 10°20′ S, 150°25′ E (USNM 276644); Mori River, 15 m, 10°04′ S, 148°30′ E (ANWC CM12019, CM12109); Narian, 5 m, 10°42′ S, 152°48′ E (AMNH 159801); Nowata, 610 m, 09°58′ S, 149°47′ E (ANWC CM12018, CM12026, CM12085, CM12088); Oomsis Creek, 100 m, 06°43′ S, 146°48′ E (AMNH 191620–191627); Owgarra, 2750 m, 08°46′ S, 147°24′ E (BM 5.11.28.3–5.11.28.6); Peria Creek, 50 m, 09°37′ S, 149°23′ E (AMNH 158041–158042, 158050, 158430); Popondetta, 60 m, 08°46′ S, 148°15′ E (BBM 25039, 28667, 28673–28674, 28677, 28685, 28719, 28722, 28753); Rambuso, 5 m, 11°28′ S, 153°30′ E (AMNH 159781–159786, 159788–159791); Rona, 450 m, 09°28′ S, 147°27′ E (AMNH 104001, 104014, 108347–108348, 108991); Saiko, 1829 m, 08°50′ S, 148°05′ E (BM 50.1208–50.1210); Sattelburg, 290 m, 06°30′ S, 147°43′ E (RMNH 217-R57, 217-R58); Simbang, 5 m, 06°35′ S, 147°51′ E (UNM 10, 427, 2397/I6); Simburu, 61 m, 08°46′ S, 148°15′ E (BBM 28731); Sinaeada, 10 m, 10°22′ S, 150°30′ E (BBM 24535, 24558–24560, 24578); Singawa River, 30 m, 06°40′ S, 147°09′ E (BBM 24788, 24803); Sirinumu Dam, 600 m, 09°25′ S, 147°26′ E (BBM 60203, 60208); Sisa, Mt., 350 m, 10°40′ S, 152°48′ E (AMNH 159802–159811); Sogeri, 410 m, 09°25′ S, 147°26′ E (AMNH 108293–108294, 108299–108302, 108309–108310); Sogeri, 450 m, 09°25′ S, 147°26′ E (AMNH 108273, 108276–108278, 108280–108281, 108283, 108292, 108327, 108330–108331, 108333–108334, 108338–108340); Soputa River, 30 m, 08°43′ S, 148°19′ E (BBM 25094, 29835); Tafa, Mt., west slope, 2400 m, 08°34′ S, 147°06′ E (AMNH 104225); Wanum, Lake, 305 m, 06°38′ S, 146°47′ E (BBM 28610); Wapona, 305 m, 09°44′ S, 149°18′ E (BM 47.1158); Water Rice, 450 m, 06°10′ S, 146°07′ E (AMNH 191650–191656).

Rattus mordax fergussoniensis

Agamoia, 200 m, 09°33′ S, 150°37′ E (AMNH 159812); Agamoia and Ailuluai, mountain region, 900 m, 09°36′ S, 150°37′ E (AMNH 159813–159817); Bolu Bolu, 5 m, 09°23′ S, 150°21′ E (AMNH 158051–158054); Deidei, 5 m, 09°30′ S, 150°37′ E (AMNH 159818); Faralulu, 549 m, 09°37′ S, 150°29′ E (BM 50.1211–50.1212); Iamelele, 15 m, 09°32′ S, 150°33′ E (AMNH 159819–159821); Pabinama, Mt., 820 m, 10°06′ S, 151°01′ E (AMNH 159769–159780); Waikaiuna, 20 m, 10°03′ S, 150°58′ E (AMNH 159763, 159793–159800).

Rattus leucopus ringens

Aird Hills, 230 m, 07°27′ S, 144°21′ E (ZS 1960/293, 1967/149, 1967/151); Bosavi, Mt., 700 m, 06°34′ S, 142°51′ E (BBM 102985, 102995); Bosavi, Mt., 900 m, 06°34′ S, 142°51′ E (BBM 103243–103244, 103253); Bula, 5 m, 09°07′ S, 141°20′ E (PNG 10815, 10834); Daru, 10 m, 09°04′ S, 143°13′ E (AMNH 104904 (skull only; skin is *R. s. aramia*)); Daviumbu, Lake, 25 m, 07°36′ S, 141°17′ E (AMNH 105692); Dimsisi, 20 m, 08°38′ S, 142°13′ E (PNG 10723, 10914); Dogwa, 150 m, 08°57′ S, 143°05′ E (AMNH 104552, 104582); Eramboe, 35 m, 08°01′ S, 140°59′ E (AMNH 222604–222605); Fly River, lower, 12 m, 08°06′ S, 142°14′ E (AMNH 105386–105398, 105470–105505, 105514–105517); Fly River, upper, 100 m, 06°50′ S, 141°00′ E (MCSN MSNG3460; AMNH 104931–104932); Fly River, upper, below mouth Black River, 100 m, 05°46′ S, 141°43′ E (AMNH 104933, 104934 (skull only; skin is *R. s. aramia*)); Mabaduane, 5 m, 09°16′ S, 142°42′ E (AMNH 104885–104888, 104890–104891, 104893–104896, 104921); Mari Village, 5 m, 09°12′ S, 141°43′ E (PNG 10835, 10915–10917); Morehead, 30 m, 08°43′ S, 141°38′ E (PNG 10806, 10830–10831, 10850); Old Malawatta, 5 m, 09°07′ S, 142°57′ E (AMNH 104914 (skull only; skin is *R. s. aramia*), 104915 (skin only; skull is *R. s. aramia*), 104916); Oriomo River, 6 m, 09°03′ S, 143°11′ E (BBM 29428, 29436, 29594; AM M7237–M7238); Oroville Camp, 15 m, 06°09′ S, 141°15′ E (AMNH 104917, 105611–105614); Tarara, 75 m, 08°50′ S, 141°52′ E (AMNH 105569, 105578–105584, 105586–105588, 105591–105593, 105595–105597, 105599–105602, 105604–105608, 105615–105622, 105624–105635, 105637–105654); Tonda, 10 m, 08°55′ S, 141°33′ E (PNG 10728, 10730, 10825); Wando, 15 m, 08°54′ S, 141°14′ E (PNG 10748, 10843, 10901); Wuroi, 20 m, 08°57′ S, 143°12′ E (AMNH 104519–104523, 104528–104529, 104531–104532, 104537–104539, 104547, 104575, 104918–104919).

Rattus leucopus ratticolor

Alkmaar, 55 m, 04°45′ S, 138°50′ E (RMNH 108, 113, 122, 332, 335, 341, 343–344, 436–437, 443–444); Bivak Island, 20 m, 05°01′ S, 138°39′ E (RMNH 41, 160, 408, 412, 420, 476, 483, 486, 488, 497); Canoe Camp, 6 m, 04°30′ S, 137°21′ E (BM 13.6.18.63–13.6.18.64); Digoel, near Kowageh, 150 m, 05°40′ S, 140°10′ E (RMNH 16981); Iwaka River, 122 m, 04°22′ S, 136°52′ E (BM 11.11.11.80); Kowageh, 150 m, 05°40′ S, 140°10′ E (RMNH 16978); Launch Camp, 6 m, 04°30′ S, 137°20′ E (BM 13.6.18.59–13.6.18.62); Mimika River, lower, 5 m, 04°41′ S, 136°26′ E (FMNH 35297); Mimika River, upper, 100 m, 04°18′ S, 136°36′ E (BM 11.11.11.62–11.11.11.64, 11.11.11.67, 11.11.11.81); Paramau, 10 m, 04°31′ S, 136°36′ E (BM 11.11.11.76, 11.11.11.78); Regeneiland, 30 m, 04°50′ S, 138°46′ E (RMNH 301); Setekwa River, upper, 20 m, 04°46′ S, 137°20′ E (BM 11.11.29.5–11.11.29.6); Tanah Merah, 100 m, 06°07′ S, 140°18′ E (RMNH 16982); Tiponé, 128 m, 04°35′ S, 136°25′ E (BM 11.11.11.65, 11.11.11.68); van Weel's Camp, 15 m, 04°51′ S, 138°45′ E (RMNH 67, 82–84); Wakatimi, 5 m, 04°38′ S, 136°30′ E (BM 11.11.11.66, 11.11.11.77, 11.11.11.79); Wataikwa River, 213 m, 04°10′ S, 136°50′ E (BM x3038, 11.11.11.69–11.11.11.75).

Rattus leucopus dobodurae

Baruari, 520 m, 09°30′ S, 147°20′ E (AMNH 108266, 108268–108270, 108311, 108313, 108315 (skin only; skull is *R. v. verecundus*), 108316–108318, 108350–108354, 108356, 108358); Brown River, 150 m, 09°12′ S, 147°12′ E (BBM 60053–60054, 60057, 60065–60066, 60092, 60097, 60136–60137, 60144; BM 69.350–69.353); Crystal Falls, 600 m, 09°25′ S, 147°26′ E (BBM 60231); Dabora, 5 m, 09°43′ S, 150°02′ E (AMNH 157951–157953, 157990); Dobodura, 150 m, 08°46′ S, 148°23′ E (AM M6960, M6987); Gerekanamu, 200 m, 09°31′ S, 147°22′ E (MCSN MSNG3506); Gwariu River, 200 m, 09°40′ S, 149°17′ E (AMNH 157961–157968, 157994–158005, 158007–158009); Itiki, 350 m, 10°35′ S, 150°00′ E (AMNH 108259–108265, 108321, 108361–108362, 108995); Java Rarre, 600 m, 09°25′ S, 147°26′ E (BBM 60262, 60265, 60278); Kumusi River, middle, 122 m, 08°30′ S, 148°00′ E (BM 4.8.3.3); Lamington, Mt., 500 m, 08°50′ S, 148°08′ E (AM M4711; BBM 25115–25116, 25123, 25135, 25157, 25178, 25209–25210, 25276–25277, 25279); Maiu River, 150 m, 09°40′ S, 149°17′ E (AMNH 157969–157972, 158006); Menapi, 15 m, 09°46′ S, 149°58′ E (AMNH 157948–157950, 157954–157960, 157988–157989, 157991–157993); Mori River, 15 m, 10°04′ S, 148°30′ E (ANWC CM12023, CM12064); Peria Creek, 50 m, 09°37′ S, 149°23′ E (AMNH 157973–157987, 158009–158028); Popondetta, 60 m, 08°46′ S, 148°15′ E (BBM 28687); Rona, 450 m, 09°28′ S, 147°27′ E (AMNH 104007, 104924, 104926–104928, 108251, 108253–108255, 108343, 108345–108346); Rona Falls, 275 m, 09°28′ S, 147°27′ E (AMNH 104929–104930); Sirinumu Dam, 600 m, 09°25′ S, 147°26′ E (BBM 60184, 60195, 60204–60205, 60210–60211, 60216, 60248–60249); Sogeri, 410 m, 09°25′ S, 147°26′ E (AMNH 108288, 108295–108298, 108303–108308); Sogeri, 450 m, 09°25′ S, 147°26′ E (AMNH 108271–108272, 108274–108275, 108282, 108284–108287, 108289–108291, 108328–108329, 108332, 108335–108336, 108341); Sogeri, 500 m, 09°25′ S, 147°26′ E (BBM 60181); Sogeri, 600 m, 09°25′ S, 147°26′ E (BBM 60256).

Rattus steini steini

Araboe-bivak, 1750 m, 03°51′ S, 136°26′ E (RMNH 0486, 1038–1040, 1042, 1045–1046, 1048, 1106–1107, 1112–1114, 1118, 1355, 1413, 1461, 1463, 1471, 1474, 1505, 1515–1516, 1518, 1545, 1552–1554, 1557, 1564, 1574, 1579, 1589, 1593, 1616–1617, 1621–1622, 1632, 1674, 1678–1679, 1681, 1683, 1685, 1689–1694, 1696, 1718, 1726, 1728, 1730, 1734, 1739, 1744, 1750, 1764–1765, 1788, 1795, 1802, 1806, 1817, 1822, 1824, 1837A, 1837B, 1851, 1854, 1865–1866, 1873, 1908–1909, 1926–1928, 1941–1943, 1969, 1972, 1983, 1998–1999, 3701, 3703, 3706, 3727, 3756, 3758, 3852, 3856, 3867, 3873, 3880, 3910, 3942); Enarotali, 1765 m, 03°56′ S, 136°13′ E (RMNH 0007, 0016, 0019, 0128, 0338, 0615, 0761–0762, 0772, 1115, 1203, 1208–1209, 1224, 1226, 1282–1283, 1294, 1297, 1328–1329, 1332, 1340, 1384, 1590, 1595, 1781–1782, 3702, 3704–3705, 3707–3708, 3711–3712, 3714–3715, 3717–3719, 3721–3722, 3724, 3735–3736, 3738–3741, 3744–3745, 3747, 3752–3753, 3803–3804, 3810–3811, 3816–3820, 3824–3826, 3831–3832, 3834, 3836–3837, 3839–3840, 3847, 3850–3851, 3862, 3870, 3874, 3876–3878, 3882, 3889–3890, 3893–3896, 3903–3905, 3908, 3912, 3917–3918, 3920–3924, 3930–3934, 3936–3937, 3939–3940, 3943, 3945, 3947–3948, 3950–3951, 3956–3958, 3960–3961, 3965–3970, 3973, 3976–3980, 3983, 3985–3989, 3992–3994, 3997; AMNH 222453–222454, 222455 (skin only; skull is BBM 21431), 222456–222459; BBM 21533); Jaba Kampong, 1600 m, 04°04′ S, 136°20′ E (RMNH 1192, 1357, 1443, 3835, 3844, 3848, 3865, 3868, 3872, 3879, 3892); Kunupi, 1400–1800 m, 03°50′ S, 135°30′ E (ZM 39691–39692, 45676); Majeba Tigrinem, Kampong, 1749 m, 04°05′ S, 136°16′ E (RMNH 0158–0159, 3901, 3935, 3938, 3949, 3996); Paniai Lake, 1750 m, 03°55′ S, 136°23′ E (RMNH 1230, 1233, 1235–1236, 1239, 1383).

Rattus steini foersteri

Bulung River, 1800–2000 m, 06°25′ S, 147°20′ E (RMNH 292/2, 292/5); Cromwell Mts., 1829 m, 06°15′ S, 147°15′ E (AMNH 195135); Gang Creek, 1311 m, 06°33′ S, 147°23′ E (AMNH 195120, 195130, 195133); Kulangtufu, 1520 m, 06°25′ S, 147°32′ E (ZM 45927); Numbut, 1372 m, 06°31′ S, 147°22′ E (AMNH 195131–195132); Ogeramnang, 1785 m, 06°26′ S, 147°22′ E (ZM 45928–45929); Rawlinson, Mt., 1372 m, 06°32′ S, 147°16′ E (AMNH 195134); Sevia, 1524 m, 06°18′ S, 147°36′ E (AMNH 79758, 79761); Zangaren (=Sengarin), 1160 m, 06°32′ S, 147°25′ E (AMNH 195490–195492).

Rattus steini hageni

Aiyura, 1675 m, 06°20′ S, 145°55′ E (AMNH 191854); Arabari, 2100 m, 06°08′ S, 145°15′ E (BBM 55122–55123, 55140, 55143, 99351); Arau, 1400 m, 06°20′ S, 146°05′ E (AMNH 191639–191641); Atitau, 1158 m, 04°48′ S, 145°20′ E (AMNH 198814–198827); Baiyer River, 1158 m, 05°31′ S, 144°11′ E (MVZ 140427–140429); Banz, 1680 m, 05°48′ S, 144°37′ E (BBM 20039); Bena, 1430 m, 06°08′ S, 145°30′ E (AMNH 191635–191636); Big Wau Creek, 1100 m, 07°22′ S, 146°43′ E (BBM 24491, 24505); Big Wau Creek, 1220 m, 07°22′ S, 146°43′ E (BBM 50576, 50583–50584, 50586, 53238); Big Wau Creek, 1400 m, 07°22′ S, 146°43′ E (BBM 24604); Big Wau Creek, 1650 m, 07°22′ S, 146°43′ E (BBM 50642); Bosavi, Mt., 700 m, 06°34′ S, 142°51′ E (BBM 102994, 103008, 103080, 103208); Bowutu Mts., 1981 m, 07°45′ S, 147°13′ E (BBM 99049, 99067); Bulldog Road, 2625 m, 07°28′ S, 146°40′ E (BBM 28957, 28960); Bulldog Road, 6 miles from Edie Creek, 2200 m, 07°26′ S, 146°40′ E (BBM 99514, 99531); Bulldog Road, 12 miles from Edie Creek, 2400 m, 07°31′ S, 146°40′ E (BBM 54831); Bulolo Town, 740 m, 07°11′ S, 146°39′ E (AMNH 222479; BBM 55644); Bulolo, 1 mile west, 701 m, 07°11′ S, 146°38′ E (MVZ 129903–129904); Bulolo River, 914 m, 07°12′ S, 146°39′ E (AM M6670, M6798; BBM 27888); Bulolo River, 1219 m, 07°12′ S, 146°39′ E (BBM 28479); Coviak, 1219 m, 07°21′ S, 146°47′ E (BBM 21245); Edie Creek, 2000 m, 07°21′ S, 146°40′ E (USNM 357426; AMNH 222481–222482; BBM 52578); Edie Creek, 2134 m, 07°21′ S, 146°40′ E (USNM 357427–357428); Edie Creek, 2300 m, 07°21′ S, 146°40′ E (USNM 357425); Feramin, 1400 m, 05°14′ S, 141°40′ E (BBM 100281, 100304, 100315, 100317, 100360); Garaina, 701 m, 07°54′ S, 147°09′ E (BBM 97954, 97962, 97989); Garaina, 800 m, 07°54′ S, 147°09′ E (MVZ 140430, 141046, 141049, 141066, 141082, 141092; BBM 96615, 96618); Giluwe, Mt., 2500 m, 06°03′ S, 143°53′ E (BM 53.255; MVZ 138638, 140419); Hagen, Mt., district, 1500–1800 m, 05°54′ S, 144°09′ E (AM M6102–M6104); Hawate, 1219 m, 07°14′ S, 146°27′ E (BBM 97867, 97871–97873, 97881, 97891); Hospital Creek, 1158 m, 07°20′ S, 146°43′ E (BBM 21174); Kagaba, 2800 m, 05°51′ S, 143°46′ E (BBM 60401, 60438, 97053, 97080, 97087, 97128, 97171); Kaindi, Mt., 1400 m, 07°21′ S, 146°43′ E (BBM 61592, 61610–61612, 61621, 61623–61625); Kaindi, Mt., 2060 m, 07°21′ S, 146°43′ E (BBM 28874, 54624–54625, 54632–54635, 54640, 97628, 97678); Kaindi, Mt., summit, 2350 m, 07°21′ S, 146°43′ E (BBM 29189, 52202, 52206, 53308, 53381, 53438, 53492, 97611–97612, 97705, 98845); Kalolo Creek, 1070 m, 07°17′ S, 146°41′ E (BBM 54531, 54535); Kambaidam, 1219 m, 06°19′ S, 146°05′ E (BM 50.1207); Karimui, 1100 m, 06°32′ S, 144°47′ E (BBM 20073); Kassam, 1350 m, 06°13′ S, 146°01′ E (AMNH 191642–191643, 191646–191647); Kassam Pass, 1400 m, 06°18′ S, 145°52′ E (BBM 54971, 54973, 55025); Kauli Creek, 1200 m, 07°21′ S, 146°46′ E (AMNH 222483); Keglsugl, 2300 m, 05°50′ S, 145°06′ E (BBM 20046–20047); Kemp, Mt., 2438 m, 07°48′ S, 147°15′ E (BBM 98000, 98023); Koibuga, 1585 m, 06°04′ S, 144°15′ E (BBM 28283–28284); Kopaigo, Lake, 1450 m, 05°23′ S, 142°32′ E (BBM 55511, 55516, 55526A, 55526B); Koranga, 975 m, 07°46′ S, 147°37′ E (BBM 21224); Korgua, 1494 m, 05°52′ S, 144°06′ E (BBM 28172–28173, 28197, 28211); Korn, Mt. Hagen, 1524 m, 05°50′ S, 144°19′ E (AM M9591); Koroba, 1646 m, 05°42′ S, 142°45′ E (BBM 23014); Kunai Creek, 1200 m, 07°20′ S, 146°43′ E (BBM 24620, 99666–99677, 99702, 100395–100397, 100399, 100403–100406, 100408–100411, 100413, 100416); Mageh, 450 m, 05°50′ S, 144°39′ E (AM M9589–M9590); Marafunga, 2400 m, 05°58′ S, 145°08′ E (BBM 55547A, 55547B, 55565A, 55565B, 55622); Mendi, 2000 m, 06°10′ S, 143°36′ E (BBM 55244, 60357, 60372); Michael, Mt., 2134 m, 06°25′ S, 145°20′ E (AMNH 191809); Missim, Mt., 1219 m, 07°13′ S, 146°50′ E (AMNH 222486; BBM 21102); Missim, Mt., 1300 m, 07°13′ S, 146°50′ E (BBM 24639, 28355, 28362, 28375–28376, 28381, 28409); Missim, Mt., 1600 m, 07°13′ S, 146°50′ E (BBM 21025); Mooly Creek, 1040 m, 07°20′ S, 146°43′ E (AMNH 222484–222485); Murmur Pass, 2750 m, 05°45′ S, 143°56′ E (BBM 60676, 60758, 60775, 60786, 97319, 97343, 97455, 97490, 97535); Murmur Village, 2600 m, 05°45′ S, 143°56′ E (BBM 28089, 60002); Namie Creek, 1524 m, 07°20′ S, 146°43′ E (BBM 98890, 98895); Nimdol, Bivak 36, 1676 m, 04°52′ S, 140°45′ E (RMNH 16942, 16944); Nondugl, 1700 m, 05°52′ S, 144°45′ E (ZS 1960/280–1960/281, 1960/283; AMNH 183713, 183718, 183721, 183755–183762, 183773–183774, 183776–183778, 183780–183786, 183789); Ofekomin, 1372 m, 05°12′ S, 141°38′ E (BBM 22801); Oksapmin, 1650 m, 05°15′ S, 142°14′ E (BBM 55390, 55412, 55494, 99798–99799, 99810–99811); Oksapmin, 1850 m, 05°15′ S, 142°14′ E (BBM 55435, 55497); Otto, Mt., Collins Sawmill, 2215 m, 05°59′ S, 145°25′ E (AMNH 191633–191634); Otto, Mt., Collins Sawmill, 2275 m, 05°59′ S, 145°25′ E (AMNH 191802); Purosa, 1970 m, 06°36′ S, 145°34′ E (AMNH 191638); Schrader Mts., 2316 m, 05°10′ S, 144°26′ E (BM 69.346–69.348); Shungol, Mt., 1500 m, 06°51′ S, 146°44′ E (BBM 98291); Sibil, 1830 m, 04°55′ S, 140°38′ E (RMNH 16919, 16925, 16927–16928, 16947–16948); Sibil Valley, 1250 m, 05°00′ S, 141°00′ E (AMNH 222460–222478); Sirunki Lake, 2580 m, 05°26′ S, 143°33′ E (AMNH 222596, 222598; BBM 20293, 20297); Somoro, Mt., 1219 m, 03°25′ S, 142°05′ E (BBM 101816); Somoro, Mt., 1372 m, 03°25′ S, 142°05′ E (BBM 101709, 101794); Sumsum, 579 m, 07°00′ S, 146°37′ E (BBM 21181, 21207); Tambul, 2200 m, 05°53′ S, 143°58′ E (BM 53.250–53.253; MVZ 138639); Tambul, 2286 m, 05°53′ S, 143°58′ E (BBM 27945–27946, 27974); Tambul, 2438 m, 05°53′ S, 143°58′ E (BM 53.254); Tambul, 2499 m, 05°53′ S, 143°58′ E (MVZ 140431); Tapu, 1829 m, 06°14′ S, 145°50′ E (BM 47.1141–47.1148); Tari, 1615 m, 05°54′ S, 142°57′ E (BBM 22967–22970, 22972, 22974, 22979–22981, 22984–22990, 22995, 23000, 23004, 23024, 23072, 23074–23075, 23105); Telefomin, 2438 m, 05°12′ S, 141°38′ E (BBM 22746, 22794, 22831, 22855, 22870, 22942, 98161, 98167, 98171, 98192, 99762); Tifalmin, 1829 m, 05°10′ S, 141°24′ E (BBM 98414–98415, 98419, 98430–98433, 98435, 98439); Tomba, 2530 m, 05°50′ S, 144°02′ E (AM M9586–M9588; BBM 27916, 27919; ZS 1965/1–1965/3, 1965/6–1965/10, 1965/15–1965/17, 1965/19–1965/22, 1965/25, 1965/27, 1965/31–1965/33); Uinda, 1829 m, 05°52′ S, 144°38′ E (BM 53.247–53.248); Wabag, 2000 m, 05°32′ S, 143°45′ E (AMNH 222594); Waibo Yama Valley, 1676 m, 06°50′ S, 145°53′ E (BM 69.349); Wanuma, 5 km north, 1200 m, 04°48′ S, 145°19′ E (BBM 103752, 103834); Wau, 914 m, 07°20′ S, 146°43′ E (MVZ 129912–129916); Wau, 1040 m, 07°20′ S, 146°43′ E (MVZ 129899–129902, 129905–129911; AMNH 222519–222520; BBM 20305, 21095, 28604); Wau, 1200 m, 07°20′ S, 146°43′ E (AMNH 222321, 222495–222518, 222521–222574, 222584, 222586, 222610–222611; BBM 20138–20139, 20149, 20153, 20162, 20185, 20189–20192, 24582, 28631, 29061, 52002, 56144, 61032, 61047, 61523–61524, 61598, 61609, 61628, 61635, 99621–99624, 99627–99630, 99634–99635, 99639–99641, 99645–99649, 99655–99657, 99661–99663, 99665, 100433, 100442, 100449, 100452, 100454, 100458, 100460–100462, 101143, 101162); Wau, 1562 m, 07°20′ S, 146°43′ E (BBM 50636); Wau, 1925 m, 07°20′ S, 146°43′ E (USNM 357429–357430, 357535; BBM 100362, 100378–100381, 100384); Wau Creek, 1372 m, 07°19′ S, 146°44′ E (AMNH 222487–222493; BBM 27569); Welya, 2134 m, 05°44′ S, 143°56′ E (BM 53.249); Wewak, 20 m, 03°35′ S, 143°40′ E (BBM 101657); Wilhelm, Mt., 2286 m, 05°46′ S, 144°59′ E (AMNH 191630); Wilhelm, Mt., 2770 m, 05°46′ S, 144°59′ E (AMNH 191628–191629, 191631–191632, 191782); Wurup, 1700 m, 05°53′ S, 144°18′ E (ZS 1965/36–1965/42, 1965/46–1965/47, 1965/61, 1965/67a); Yaibos, 2000 m, 05°25′ S, 143°45′ E (AMNH 222588, 222590, 222592; BBM 20283, 20285, 20287); Yanca, 1676 m, 05°45′ S, 144°07′ E (BM 50.1749–50.1750); Yandara, 1829 m, 05°46′ S, 145°09′ E (BM 50.1737–50.1748, 53.246); Yellow River, 250 m, 03°37′ S, 141°56′ E (ZS 1965/60).

Rattus steini baliemensis, New Subspecies

Baliem River, 1600 m, 04°10′ S, 138°56′ E (AMNH 110195, 110206, 110218–110219, 110234, 110241, 110243–110247, 110249–110251, 110260–110262, 110264–110273, 110277–110281, 110283–110289, 110295, 110298–110300, 110303–110306, 110312, 110320–110321; MZB 8269–8270); Bernhard Camp, 4–6 km southwest, 850–1200 m, 03°30′ S, 139°12′ E (AMNH 152361); Bernhard Camp, 10 km southwest, 1500 m, 03°31′ S, 139°11′ E (AMNH 152363); Guega, 1350 m, 03°36′ S, 138°25′ E (BBM 56510); Habbema, Lake, 9 km northeast, 2800 m, 04°05′ S, 138°50′ E (AMNH 150615–150616, 150622–150630, 150633–150640); Ibele River, 2200 m, 04°05′ S, 138°42′ E (AMNH 150929–150934, 150937–150938, 150940, 150952–150954, 150956–150958, 150962–150965, 150966 (skin only; skull is *R. n. arrogans*), 150967–150976, 150978–150983, 150989, 151000–151004, 151009–151019, 151022, 151029, 151031–151034, 151038–151057, 151067–151068, 151568, 151570–151572, 151588–151601, 151603–151616, 151646–151675); Wamena, 1700 m, 04°05′ S, 138°57′ E (RMNH 17226).

Rattus giluwensis

Giluwe, Mt., 2743 m, 06°03′ S, 143°53′ E (BBM 28072–28073); Giluwe, Mt., 3300 m, 06°03′ S, 143°53′ E (BM 53.265; BBM 101847, 101898); Giluwe, Mt., 3350–3660 m, 06°03′ S, 143°53′ E (BM 53.256–53.264; BBM 101910, 101939, 101960); Kagaba, 2800 m, 05°51′ S, 143°46′ E (BBM 97273); Kagaba, 3600 m, 05°51′ S, 143°46′ E (BBM 97296A); Kawongu, 2195 m, 05°50′ S, 143°59′ E (BBM 28130).

Rattus novaeguineae, New Species

Big Wau Creek, 1100 m, 07°22′ S, 146°43′ E (BBM 24506, 24509); Big Wau Creek, 1220 m, 07°22′ S, 146°43′ E (BBM 50571–50572, 50579–50581, 50587, 53241, 95155, 95157, 95160); Bulolo, 10 km west, 780 m, 07°11′ S, 146°34′ E (BBM 51242–51243, 51257, 51313–51315, 51344, 53642, 53661, 53683, 53965, 54004, 54006, 54014, 54016, 54021, 54046–54047, 54069, 54090, 54101–54103, 54136–54137, 54151, 54153, 54173, 54193, 54197, 54200, 54211, 54231, 54259, 54263, 54293, 54295, 54324); Bulolo River, 914 m, 07°12′ S, 146°39′ E (BBM 20317, 21179, 27858, 28459–28460); Bulolo Town, 740 m, 07°11′ S, 146°39′ E (AMNH 222480); Clear Water, 1070 m, 07°17′ S, 146°46′ E (BBM 54395, 54426–54430, 54496); Coviak, 1219 m, 07°21′ S, 146°47′ E (BBM 20344, 21253); Kaindi, Mt., 1400 m, 07°21′ S, 146°43′ E (AMNH 222429); Kalalo, 750 m, 06°04′ S, 147°11′ E (BBM 52910, 52996, 53025, 53027, 53031, 53035, 53129, 53140, 53162, 53192, 53200, 53213–53214, 53218, 53220, 53223); Kalolo Creek, 1070 m, 07°17′ S, 146°41′ E (BBM 54512, 54516–54518, 54520–54524, 54530, 54532–54534, 54536–54540, 54555–54556, 54560); Karimui, 1100 m, 06°32′ S, 144°47′ E (AMNH 222579, 222581); Kassam, 1350 m, 06°13′ S, 146°01′ E (AMNH 191644–191645, 191648–191649, 191837); Kassam Pass, 1150 m, 06°18′ S, 145°52′ E (AMNH 222582; BBM 54996, 55024); Koranga, 975 m, 07°46′ S, 147°37′ E (BBM 21222); Minava, 1400 m, 07°14′ S, 146°36′ E (BBM 97912, 97919–97920, 97924, 97938, 97942); Missim, Mt., 1219 m, 07°13′ S, 146°50′ E (BBM 21008, 21029, 21053, 21057, 21060–21061, 21073, 54714); Missim, Mt., 1300 m, 07°13′ S, 146°50′ E (BBM 28354, 28356–28361, 28363–28369, 28372–28373, 28380, 28382, 28388, 28390, 28406–28407, 50595, 54661–54663, 54685–54686); Nakata Ridge, 1524 m, 07°20′ S, 146°43′ E (BBM 27789, 27838, 28979); Nauti Village, 1400 m, 07°17′ S, 146°28′ E (BBM 99250–99251, 99284, 99286, 99288, 99301); Sandy Creek, 1067 m, 07°18′ S, 146°45′ E (AMNH 222494); Water-bung, 1143 m, 07°26′ S, 146°47′ E (BBM 97744); Wau, 1040 m, 07°20′ S, 146°43′ E (BBM 28582, 28584–28585); Wau, 1200 m, 07°20′ S, 146°43′ E (BBM 100434).

Rattus jobiensis

Biak Is., 152 m, 01°00′ S, 136°00′ E (AM M7082; AMNH 222241, 222430–222431); Dawai River, 5 m, 01°49′ S, 136°43′ E (AMNH 222435–222444); Eiori, Mt., 610 m, 01°48′ S, 136°15′ E (BM 46.633); Japen Is., 50 m, 01°45′ S, 136°10′ E (ZM 45677); Owi Is., 5 m, 01°15′ S, 136°12′ E (AM M6992–M6993).

Rattus sordidus gestri

Astrolabe Range, 670 m, 09°35′ S, 147°27′ E (ANWC CM3939); Baroka, 5 m, 08°49′ S, 146°35′ E (AMNH 104210, 104212, 104216, 104218–104219, 104222, 104239, 104381; MZB 4034–4035); Brown River, 150 m, 09°12′ S, 147°12′ E (BBM 60080, 60105); Dobodura, 150 m, 08°46′ S, 148°23′ E (AM M6910–M6912, M6975, M6989, M7072); Kapa Kapa, 10 m, 09°50′ S, 147°30′ E (BM 97.8.7.36–97.8.7.40; MCSN MSNG350/A, MSNG350/B, MSNG3260A, MSNG3260B, MSNG3501B, MSNG3501C; CZM 7665); Menapi, 15 m, 09°46′ S, 149°58′ E (AMNH 158030); Port Moresby, 5 m, 09°29′ S, 147°10′ E (AMNH 108325, 108366–108367); Rigo, 100 m, 09°48′ S, 147°34′ E (AM M4968; AMNH 108162); Rona, 450 m, 09°28′ S, 147°27′ E (AMNH 104008–104009, 104012–104013, 104015, 104925, 108252, 108324, 108326, 108344); Sogeri, 450 m, 09°25′ S, 147°26′ E (BM 88.3.16.10; AMNH 108333); Waigani, 5 m, 09°23′ S, 147°11′ E (ZS 1960/282, 1960/286, 1960/289); Yule Island, 10 m, 08°48′ S, 146°31′ E (BM 76.10.28.2).

Rattus sordidus aramia

Balimo, 9 m, 08°01′ S, 142°58′ E (BBM 50232, 50330, 50334, 50336); Bugi, 20 m, 09°09′ S, 142°15′ E (AMNH 105527–105537); Bula, 5 m, 09°07′ S, 141°20′ E (PNG 0183.1, 0184.2, 0186.3, 10906–10910); Daru, 10 m, 09°04′ S, 143°13′ E (AMNH 104853–104854, 104856–104859, 104862–104868, 104870–104884, 104902, 104904 (skin only; skull is *R. l. ringens*), 104905–104911, 104920, 105518–105519; BBM 50091); Daviumbu, Lake, 25 m, 07°36′ S, 141°17′ E (AMNH 105399–105408, 105520–105526, 105610, 105655–105691, 105693–105699, 105955–105963); Dimsisi, 20 m, 08°38′ S, 142°13′ E (PNG 10742); Fly River, upper, 1 mi. below Black River mouth, 100 m, 05°46′ S, 141°43′ E (AMNH 104934 (skin only; skull is *R. l. ringens*)); Gaima, 10 m, 08°22′ S, 142°54′ E (AMNH 105506–105513): Koembé, 10 m, 08°21′ S, 140°08′ E (RMNH 16745); Koerik, 100 m, 08°17′ S, 140°17′ E (RMNH 2–3, 17124–17127, 17129–17130, 17132–17142, 17145–17151, 17159–17165, 17167–17179, 18139); Mabaduane, 5 m, 09°16′ S, 142°42′ E (AMNH 104889, 104892, 104897–104898, 104900–104901); Mari Village, 5 m, 09°12′ S, 141°43′ E (PNG 10751, 10757, 10822, 10836); Mibini, 30 m, 08°50′ S, 141°38′ E (PNG 10867); Old Malawatta, 5 m, 09°07′ S, 142°57′ E (AMNH 104912–104913, 104914 (skin only; skull is *R. l. ringens*)), 104915 (skull only; skin is *R. l. ringens*); Oriomo River, 6 m, 09°03′ S, 143°11′ E (BBM 29400); Tarara, 75 m, 08°50′ S, 141°52′ E (AMNH 105570–105576, 105589–105590, 105594, 105598, 105603, 105609, 105623); Totani Village, 5 m, 08°00′ S, 143°30′ E (AM M4893, M4895); Uparua, 30 m, 08°38′ S, 141°38′ E (PNG 10808, 10820); Wuroi, 20 m, 08°57′ S, 143°12′ E (AMNH 104515–104517, 104524–104525, 104527, 104530, 104533–104536, 104540–104541, 104543–104546, 104548, 104550, 104574, 104578).

Rattus exulans browni

Abeleti, 50 m, 11°23′ S, 154°12′ E (AMNH 159706–159710, 159712–159716); Aitape, 120 m, 03°09′ S, 142°21′ E (AM M3721, M6215, M6233); Amberbaki, 5 m, 00°32′ S, 133°02′ E (RMNH 22580–22583); Anggi Guyi, Mt., 1800 m, 01°24′ S, 133°58′ E (RMNH 22575–22578); Apouchu, 200 m, 08°00′ S, 147°54′ E (BM 6.1.8.12); Arabari, 2100 m, 06°08′ S, 145°15′ E (BBM 55088, 55192, 99352–99355, 99364–99365); Arabuka Village, 1940 m, 07°56′ S, 147°03′ E (BBM 96611); Arau, 1400 m, 06°20′ S, 146°05′ E (AMNH 191599–191609); Arfak Mts., 1000 m, 01°09′ S, 134°00′ E (BM 10.2.243, 29.5.27.20–29.5.27.21); Arfak Mts., 2000 m, 01°09′ S, 134°00′ E (BM 29.5.27.19); Aroma, 100 m, 10°08′ S, 147°59′ E (CZM 7666–7667); Astrolabe Bay, 5 m, 05°25′ S, 145°45′ E (ZM 8352, 8355, 60014, 60018–60020); Atitau, 1158 m, 04°48′ S, 145°20′ E (AMNH 198794–198801); Aviklo Village, 10 m, 06°12′ S, 149°30′ E (AM M5621); Awelkom, 600 m, 05°38′ S, 147°48′ E (BBM 95271); Baiune River, upper, 823 m, 07°03′ S, 146°29′ E (MVZ 129834–129836, 129838); Baiyanka, 1829 m, 05°35′ S, 144°51′ E (BM 47.1135); Balbi, Mt., 1900 m, 05°55′ S, 155°00′ E (BBM 61419, 61423–61431, 61437–61443, 61447–61449, 61451, 61453–61459, 61464–61471, 61476, 61480, 61482, 61509, 61511–61514); Balbi, Mt., 2100 m, 05°55′ S, 155°00′ E (BBM 61460, 61472–61475, 61477, 61481, 61483, 61505–61508, 61516–61517); Balbi, Mt., 2300 m, 05°55′ S, 155°00′ E (BBM 61484–61485, 61487–61489, 61491–61492, 61494–61495, 61499–61504, 61518–61521); Banz, 1680 m, 05°48′ S, 144°37′ E (AMNH 222383–222384; BBM 20042, 20044); Baroka, 5 m, 08°49′ S, 146°35′ E (AMNH 104220, 104236, 104375); Baruari, 520 m, 09°30′ S, 147°20′ E (AMNH 108250); Bat Is., 5 m, 02°51′ S, 146°14′ E (AM M6976, M7185, M7187); Bena, 1430 m, 06°08′ S, 145°30′ E (AMNH 191569–191577, 222390, 222392; BBM 20084, 20086–20087, 20090); Biak Is., 152 m, 01°00′ S, 136°00′ E (AM M7111–M7115); Big Wau Creek, 1100 m, 07°22′ S, 146°43′ E (BBM 24490, 24504); Big Wau Creek, 1220 m, 07°22′ S, 146°43′ E (BBM 50575, 50577); Biota, 175 m, 08°46′ S, 146°38′ E (AMNH 104237); Boliu, 5 m, 01°33′ S, 149°42′ E (CZM E1110–E1113); Bolu Bolu, 5 m, 09°23′ S, 150°21′ E (AMNH 157925–157940); Boneno, 1219 m, 09°54′ S, 149°25′ E (BM 47.1139–47.1140); Bou, 10 m, 10°19′ S, 150°43′ E (ZM 22253–22254); Bougainville Is., 183 m, 06°00′ S, 155°20′ E (AM M7121; AMNH 79814–79821); Buala, 20 m, 08°10′ S, 159°36′ E (BBM 24264); Buin, 150 m, 06°46′ S, 155°42′ E (AM M6495, M6648; KNMB 6361, 6369–6370); Bulolo, 740 m, 07°11′ S, 146°39′ E (MVZ 129800–129808, 129819–129826, 129846–129850; AMNH 222286–222287; BBM 55629, 55639–55641, 55652-A, 55652-B); Bulolo, 1 mi. W., 701 m, 07°11′ S, 146°38′ E (MVZ 129799); Bulolo, 7–8 mi. N., 579 m, 07°04′ S, 146°39′ E

(MVZ 129809–129812, 129827–129831, 129851–129856); Bulolo, 10 km. W., 780 m, 07°11′ S, 146°34′ E (BBM 51264–51265, 51267, 51324, 54005, 54070, 54089, 54125, 54196, 54198–54199, 54339); Bulolo River, 914 m, 07°12′ S, 146°39′ E (BBM 28432); Capuchin Seminary, 1670 m, 05°07′ S, 145°47′ E (MVZ 138633); Chuave, 1500 m, 06°07′ S, 145°08′ E (BBM 99309–99311, 99343); Conflict Group, 5 m, 10°45′ S, 151°45′ E (BM X25, 3.7.6.1–3.7.6.3); Cooranga, 1200 m, 07°18′ S, 146°43′ E (AMNH 222288); Coviak, 1219 m, 07°21′ S, 146°47′ E (BBM 21244, 21252); Dala, 20 m, 08°36′ S, 160°40′ E (BBM 24050, 24054, 24093, 24117, 24131); Dayman, Mt., 2050 m, 09°49′ S, 149°16′ E (AMNH 157879); Dayman, Mt., 2230 m, 09°49′ S, 149°16′ E (AMNH 157858–157870, 157872–157878, 157880); Dayman, Mt., summit, 2430 m, 09°49′ S, 149°16′ E (AMNH 157871, 157881); Deidei, 5 m, 09°30′ S, 150°37′ E (AMNH 159737–159742); Didessa, 1000 m, 06°34′ S, 142°51′ E (ZS 1967/62); Dobodura, 150 m, 08°46′ S, 148°23′ E (AM M6918–M6922, M6962–M6966, M6978–M6979, M7073); Doma Cove, 5 m, 09°19′ S, 159°48′ E (USNM 278084–278114); Doromena, 762 m, 02°25′ S, 140°26′ E (AM M7135); Duke of York Island, 5 m, 04°10′ S, 152°28′ E (AM M2364–M2365; ZM 5361; BM 77.7.18.26); Dyaul Is., 5 m, 02°56′ S, 150°54′ E (CZM CN14810–CN14814); Edie Creek, 2000 m, 07°21′ S, 146°40′ E (AMNH 222289–222290); Edie Creek, 2134 m, 07°21′ S, 146°40′ E (MVZ 129813–129814; BBM 28887); Efogi, 1219 m, 09°09′ S, 147°37′ E (BM 69.341–69.342); Emirau Is., 5 m, 01°40′ S, 150°00′ E (MVZ 109759–109763; USNM 276908–276911, 277073); Engeros, 10 m, 02°36′ S, 140°43′ E (RMNH R72, R74, 1803, 18574–18580); Erima, 10 m, 05°25′ S, 145°44′ E (UNM 2126/A5A1–2126/A5A2); Esperance, Cape, 5 m, 09°18′ S, 159°47′ E (MVZ 101682); Fife Bay, 5 m, 10°37′ S, 150°01′ E (AM M2483–M2484); Finschhafen, 5 m, 06°34′ S, 147°51′ E (ZM 45963; FMNH 54044–54045; AMNH 195090; BBM 27651, 27678); French Is., 5 m, 04°40′ S, 149°20′ E (ZM 60013); Fulakora, 10 m, 08°21′ S, 159°50′ E (MCZ 18710); Garaina, 701 m, 07°54′ S, 147°09′ E (BBM 97974, 97976, 97982, 98037–98038); Garaina, 800 m, 07°54′ S, 147°09′ E (MVZ 141043–141044, 141050, 141057–141064, 141071–141074, 141085–141091, 141093–141095; BBM 96622–96625); Garaina, 1067 m, 07°54′ S, 147°09′ E (BBM 98905–98906); Gaulim, 122 m, 04°25′ S, 152°07′ E (AMNH 222323–222326); Gawa Is., 5 m, 08°59′ S, 151°58′ E (AM M6370); Gollifer's Camp, 720 m, 08°00′ S, 156°59′ E (BBM 23339–23342, 23348–23349, 23351–23354, 23362, 23364–23365, 23367–23368, 23376, 23394–23395, 23400–23405, 23410, 23426–23427, 23429–23431, 23435–23436); Gono, 1900 m, 06°20′ S, 145°12′ E (AMNH 191578, 191589–191591, 191805); Green River, 152 m, 03°55′ S, 141°08′ E (BBM 22693, 22705, 22715); Gu Daal, 229 m, 05°37′ S, 133°02′ E (BM 23.4.3.11); Gurakor, 650 m, 06°49′ S, 146°39′ E (AMNH 191541–191542); Gwariu River, 200 m, 09°40′ S, 149°17′ E (AMNH 157916); Hagave Creek, 1980 m, 06°20′ S, 145°23′ E (AMNH 191583–191587); Hagen, Mt., district, 1500–1800 m, 05°54′ S, 144°09′ E (AM M6110–M6112); Hatam, 1200 m, 01°10′ S, 133°40′E (ZM 5684); Hawate, 1219 m, 07°14′ S, 146°27′ E (BBM 97864–97865); Hollandia, 114 m, 02°32′ S, 140°43′ E (USNM 277326–277329, 277331–277338, 277439–277440, 277461–277465, 283861–283862, 295091–295092, 295094–295096, 295098, 295100, 295103–295104, 295111; FMNH 54046, 54225, 56351, 56354, 56358, 56402–56412; AMNH 110085, 110088–110089, 110092–110103, 110107–110110, 110114, 110117, 110121–110122, 110125, 110127, 110129–110130, 150919, 152354; MZB 4605–4607, 8268); Hualil, 183 m, 06°04′ S, 149°30′ E (AMNH 194381–194383); Humboldt Bay, 5 m, 02°30′ S, 140°46′ E (ZM 5682); Hutuna, 25 m, 11°38′ S, 160°14′ E (CZM CN14520–CN14521, M14717; BM 54.904–54.906); Iambon, Camp 6, 488 m, 06°00′ S, 149°40′ E (AMNH 194384–194394); Iamelele, 15 m, 09°32′ S, 150°33′ E (AMNH 159743); Ikara, 1219 m, 10°03′ S, 149°38′ E (BM 47.1138); Ilugi, 152 m, 04°31′ S, 152°07′ E (AMNH 222327–222329, 222401); Inauavui, 20 m, 08°40′ S, 146°34′ E (AMNH 104235); Ioma, 46 m, 08°22′ S, 147°49′ E (BM 6.10.8.7–6.10.8.12); Japen Is., 50 m, 01°45′ S, 136°10′ E (AM M7119; ZM 39863–39865, 91963–91971); Jinju, 5 m, 11°19′ S, 154°14′ E (AMNH 159692–159705, 159711); Joe Landing, 5 m, 11°25′ S, 153°25′ E (AMNH 159729); Junzaing, 1370 m, 06°23′ S, 147°37′ E (ZM 45939–45961); Kabwum, 2880 m, 06°13′ S, 147°03′ E (BBM 52640, 52648–52650); Kagi, 1433 m, 09°07′ S, 147°36′ E (AMNH 108201, 108215–108216, 108222–108223, 108225); Kaindi, Mt., 1400 m, 07°21′ S, 146°43′ E (BBM 61618); Kaindi, Mt., 2060 m, 07°21′ S, 146°43′ E (AMNH 191543–191560); Kaindi, Mt., summit, 2350 m, 07°21′ S, 146°43′ E (BBM 29171–29172, 29178, 29190, 51039–51040, 51124, 52207, 53352, 53456, 54641); Kalalo, 750 m, 06°04′ S, 147°11′ E (BBM 52938, 52995, 53038–53040, 53046–53050, 53100–53102, 53115, 53117–53119, 53141, 53147, 53149–53150, 53153, 53193, 53195); Kalolo Creek, 1070 m, 07°17′ S, 146°41′ E (BBM 54505–54507, 54510, 54529, 54544, 54546, 54548, 54550, 54569–54570, 54575–54576, 54585–54586, 54597–54598, 54601–54605); Kambaidam, 1219 m, 06°19′ S, 146°05′ E (BM 50.1205–50.1206); Kandrian, 20 mi. N.E., 400 m, 06°03′ S, 149°46′ E (AMNH 194404–194406); Karaea, Mt., 1100 m, 05°42′ S, 154°57′ E (BBM 61241, 61249, 61251–61252); Karimui, 1100 m, 06°32′ S, 144°47′ E (AMNH 222388, 222404; BBM 20063, 20072); Karionk, 1707 m, 05°10′ S, 144°26′ E (BM 69.339); Karionk-Jimmi Junction, 152 m, 05°00′ S, 144°00′ E (BM 69.340); Kassam, 1350 m, 06°13′ S, 146°01′ E (AMNH 191610–191618); Kassam Pass, 1150 m, 06°18′ S, 145°52′ E (BBM 20091A); Kassam Pass, 1400 m, 06°18′ S, 145°52′ E (BBM 54951, 54953, 54964, 54975–54976, 55020, 60022, 60031); Kauli Water, 1200 m, 07°21′ S, 146°46′ E (AMNH 222291); Kebar Valley, 500 m, 00°48′ S, 133°04′ E (AMNH 222367–222381); Kiriwina Is., 10 m, 08°28′ S, 151°05′ E (AM M7150–M7151); Koibuga, 1585 m, 06°04′ S, 144°15′ E (BBM 28290); Kokoda, 366 m, 08°53′ S, 147°45′ E (BM 7.2.1.5–7.2.1.8, 33.9.1.4–33.9.1.5); Korgua, 1494 m, 05°52′ S, 144°06″ E (BBM 28175); Kotkin, 450 m, 06°34′ S, 147°27′ E (AMNH 195057); Kreeba Plantation, 20 m, 04°18′ S, 152°01′ E (BM 69.343–69.344); Kulangtufu, 1520 m, 06°25′ S, 147°32′ E (ZM 45936–45938); Kulumadau, 200 m, 09°04′ S, 152°43′ E (AMNH 159684–159688, 159690–159691); Kunai Creek, 1200 m, 07°20′ S, 146°43′ E (BBM 20094A, 99679–99681, 99689–99698, 99704, 100398, 100412, 100414–100415); Lae, 10 m, 06°44′ S, 147°00′ E (AM M7092–M7096, M7120; BBM 55660); Lamington, Mt., 500 m, 08°50′ S, 148°08′ E (AM M4153–M4156, M4299), Lau, 396 m, 04°22′ S, 151°41′ E (BM 47.1136–47.1137); Lavanggu, 75 m, 11°39′ S, 160°14′ E (CZM CN11970–CN11975); Lavongai, 10 m, 02°40′ S, 150°15′ E (ZM 60001); Liluta, 10 m, 08°24′ S, 151°06′ E (AMNH 159730–159731); Little Wau Creek, 1128 m, 07°22′ S, 146°40′ E (MVZ 129832–129833); Lunga, 10 m, 09°25′ S, 160°03′ E (BM 35.9.2.2; USNM 278073–278083); Mafulu, 1253 m, 08°31′ S, 147°00′ E (BM 34.6.1.7–34.6.1.8; AMNH 104241, 104247, 104250, 104275); Mageh, 450 m, 05°50′ S, 144°39′ E (AM M9593); Maiwara, 10 m, 10°21′ S, 150°20′ E (MVZ 138634, 140424–140426); Malangono, 10 m, 07°03′ S, 156°47′ E (BBM 23527–23529, 23538, 23551–23553, 23566–23570, 23575, 23579, 23589, 23600–23601, 23618–23621, 23623–23626, 23639, 23651–23653, 23669, 23676, 23685, 23691); Manokwari, 5 m, 00°52′ S, 134°05′ E (RMNH m, 1808, 22585); Manus Is., 5 m, 02°04′ S, 147°00′ E (BM 14.4.1.18–14.4.1.20); Marafunga, 2400 m, 05°58′ S, 145°08′ E (BBM 55600); Marienberg, 5 m, 03°58′ S, 144°15′ E (RMNH 22554–22555; MCZ 26971; FMNH 31825–31827, 31831–31838); Markham Valley, 475 m, 06°10′ S, 146°10′ E (AMNH 191619); Matafuna, 10 m, 05°21′ S, 146°59′ E (AMNH 237315); Matahenua, 10 m, 11°16′ S, 159°46′ E (CZM CN14510, E14511, CN14512); Mawes, 10 m, 02°21′ S, 139°44′ E (RMNH R67, 1807); May River, 122 m, 04°17′ S, 141°55′ E (ZS 1965/48, 1965/52–1965/54; BBM 22612, 22616, 22623–22626, 22629–22631); Menapi, 15 m, 09°46′ S, 149°58′ E (AMNH 157908–157914, 157917–157919, 157921–157924, 158195–158198); Metoe Debi, 10 m, 02°36′ S, 140°42′ E (RMNH d, e, s, R68, R70, R75, 1805); Michael, Mt., 2134 m, 06°25′ S, 145°20′ E (AMNH 191580–191582, 191588, 191592–191594); Minava, 1400 m, 07°14′ S, 146°36′ E (BBM 97911); Missim, Mt., 1219 m, 07°13′ S, 146°50′ E (AMNH 222295; BBM 21018); Moimo, 1829 m, 07°59′ S, 147°01′ E (BBM 98055–98056, 98074–98076, 98078, 98101–98102, 98106, 98131); Mongibusu, 2600 m, 06°23′ S, 147°15′ E (ZM 45962); Mooly Creek, 1040 m, 07°20′ S, 146°43′ E (AMNH 222292–222294); Mt. Hagen, town, 1707 m, 05°46′ S, 144°02′ E (AM M5622–M5628); Murmur Pass, 2750 m, 05°45′ S, 143°56′ E (BBM 97356); Mutahi, 700 m, 05°42′ S, 154°57′ E (BBM 61122–61123, 61129–61131, 61170, 61221–61222, 61306, 61313); Mutahi, 800 m, 05°42′ S, 154°57′ E (BBM 61144–61145, 61147–61149); Mutahi, 1100 m, 05°42′ S, 154°57′ E (BBM 61166, 61173, 61175, 61177, 61179, 61181–61183, 61186, 61188, 61194–61197, 61211, 61217–61218, 61234–61238, 61256, 61260); Mutahi, 1350 m, 05°42′ S, 154°57′ E (BBM 61269, 61271); Mutahi, 1450 m, 05°42′ S, 154°57′ E (BBM 61279–61285); Nalimbu River, 5 m, 09°25′ S, 160°09′ E (MVZ 101676); Narian, 5 m, 10°42′ S, 152°48′ E (AMNH 159732–159735); Nauti Village, 1400 m, 07°17′ S, 146°28′ E (BBM 99243, 99285); Nini Creek, 100 m, 09°27′ S, 160°14′ E (BBM 23809–23811, 23817, 23836, 23850–23851); Ninoa Rubber Plantation, 600 m, 09°28′ S, 147°28′ E (BBM 60230); Niupani, 25 m, 11°40′ S, 160°22′ E (CZM CN14513–CN14519); Noesi Is., 5 m, 01°18′ S, 136°24′ E (USNM 277308); Nondugl, 1700 m, 05°52′ S, 144°45′ E (ZS 1960/278–1960/279; BM 53.230); Numbut, 1372 m, 06°31′ S, 147°22′ E (AMNH 195058); Oertzen Mts., 610 m, 05°28′ S, 145°32′ E (ZM 13701, 13703, 13705); Ontong Java, 5 m, 05°33′ S, 159°44′ E (USNM 278707–278712); Oomsis Creek, 100 m, 06°43′ S, 146°48′ E (AMNH 191527–191540); Oransbari, 5 m, 01°21′ S, 134°18′ E (AMNH 222338); Otto, Mt., Collins Sawmill, 2215 m, 05°59′ S, 145°25′ E (AMNH 191564–191568, 191794); Owi Is., 5 m, 01°15′ S, 136°12′ E (AM M6994, M6996, M7201); Pepele, 10 m, 08°03′ S, 156°58′ E (BBM 23475, 23486–23489); Pindiu, 975 m, 06°27′ S, 147°33′ E (AMNH 195041–195056); Pokapa, 200 m, 05°35′ S, 155°01′ E (BBM 61077–61080, 61112–61114); Popondetta, 60 m, 08°46′ S, 148°15′ E (BBM 28726); Purosa, 1970 m, 06°36′ S, 145°34′ E (AMNH 191595–191598); Pusisama, 5 m, 07°47′ S, 156°39′ E (BBM

23166, 23171, 23175–23176, 23183–23184, 23194–23195, 23201–23203, 23235); Ralum, 5 m, 04°19′ S, 152°15′ E (ZM 9328, 9377); Rambuso, 5 m, 11°28′ S, 153°30′ E (AMNH 159717–159728, 159792); Rawlinson, Mt., 1372 m, 06°32′ S, 147°16′ E (AMNH 195059–195060); Rennell Is., 25 m, 11°37′ S, 160°15′ E (AM M4213–M4214); Riaet, 244 m, 04°33′ S, 151°59′ E (AMNH 222331–222333); Rigo, 100 m, 09°48′ S, 147°34′ E (AMNH 108182); Sandy Creek, 1067 m, 07°18′ S, 146°45′ E (BBM 21125); Sansapor, 5 m, 00°29′ S, 132°05′ E (AM M6990–M6991, M7202–M7204; RMNH 22584; AMNH 143841–143842, 143870, 143872); Sattelburg, 290 m, 06°30′ S, 147°43′ E (ZM 45932; UNM 2466/30-1, 2466/30-2); Sengarin (=Zangaren), 1219 m, 06°32′ S, 147°25′ E (BBM 27745); Sentani Lake, 200 m, 02°37′ S, 140°31′ E (BM 27.4.1.5; RMNH t, R73, R76, 1809; BNM 3201–3202); Sevia, 1524 m, 06°18′ S, 147°36′ E (AMNH 79752–79754, 79762, 79769), Simbang, 5 m, 06°35′ S, 147°51′ E (UNM 2397/17); Sinaeada, 10 m, 10°22′ S, 150°30′ E (BBM 24512); Sinewit, Mt., 853 m, 04°38′ S, 151°59′ E (AMNH 222330); Sisa, Mt., 350 m, 10°40′ S, 152°48′ E (AMNH 159736); Sitium Village, 30 m, 06°37′ S, 147°03′ E (BBM 98688–98689, 98691, 98696); Slate Creek, 762 m, 07°14′ S, 146°30′ E (BBM 20364); Sogeri, 410 m, 09°25′ S, 147°26′ E (AMNH 108248–108249); Sogeri, 450 m, 09°25′ S, 147°26′ E (AMNH 108247); Sogeri, 600 m, 09°25′ S, 147°26′ E (BBM 60191–60192); Sowata, 15 m, 09°04′ S, 159°12′ E (BM 34.5.19.2–34.5.19.3); Stephansort, 5 m, 05°27′ S, 145°45′ E (UNM 2126/A5-1, 2126/A5-8); Sumsum, 579 m, 07°00′ S, 146°37′ E (BBM 21204); Sururai, Kampong, 1950 m, 01°21′ S, 133°55′ E (AMNH 222339–222366, 222403); Tabalia, 20 m, 09°16′ S, 159°44′ E (BBM 23866–23867, 23869, 23891–23893, 23923, 23944, 23973–23974, 24014–24015, 24024); Tafa, Mt., east slope, 2070 m, 08°35′ S, 147°09′ E (AMNH 104161); Taliligap, 305 m, 04°20′ S, 152°12′ E (AMNH 222334–222336, 222400; BBM 20964); Tamata, 30 m, 08°21′ S, 147°52′ E (BM 6.1.8.10); Tambul, 2200 m, 05°53′ S, 143°58′ E (AMNH 222398; MVZ 140420, 140422; BBM 20252–20253); Tambul, 2286 m, 05°53′ S, 143°58′ E (BBM 27944); Tanah Merah Bay, 5 m, 02°24′ S, 140°20′ E (MZB 4603–4604); Tangaitutu, 50 m, 01°24′ S, 149°38′ E (CZM E1067, E1094–E1095); Tapu, 1829 m, 06°14′ S, 145°50′ E (BM 47.1131–47.1134); Tatamba, 20 m, 08°23′ S, 159°48′ E (BBM 24290–24291, 24295–24296, 24333, 24344–24345, 24350; AM M3683, M3936); Tinputz Patrol Post, 5 m, 05°34′ S, 155°01′ E (BBM 61321, 61323); Tobadi, 5 m, 02°33′ S, 140°43′ E (RMNH R66, R71, 1804); Togarau, 600 m, 05°51′ S, 155°09′ E (BBM 61333, 61342, 61344, 61415); Tolokiwa Is., 10 m, 05°18′ S, 147°36′ E (AMNH 237316–237317); Tomba, 2530 m, 05°50′ S, 144°02′ E (ZS 1965/26); Top Camp, Goodenough Is., 1600 m, 09°22′ S, 150°12′ E (AMNH 157942–157947); Torokina, 10 m, 06°14′ S, 155°03′ E (AM M7122; USNM 276824, 276833–276907, 277071, 277074, 277077–277084); Toumoa, 10 m, 06°59′ S, 156°05′ E (BBM 23729–23735); Ugi Mission, 10 m, 10°14′ S, 161°44′ E (USNM 278713); Uinda, 1829 m, 05°52′ S, 144°38′ E (BM 53.231); Ulo Crater, 10 m, 07°48′ S, 156°36′ E (BBM 23258–23260, 23265, 23267, 23273, 23282, 23293, 23303–23304, 23314–23315, 23337); Ulur, Mt. Camp, 2377 m, 06°14′ S, 147°24′ E (AMNH 195061–195071, 195073–195089); Vulcan Is., 5 m, 04°08′ S, 145°02′ E (BM 15.2.18.11–15.2.18.12); Waikaiuna, 20 m, 10°03′ S, 150°58′ E (AMNH 159744–159762, 159764–159768); Wakonai, 150 m, 09°20′ S, 150°15′ E (AMNH 157941); Wandumi, 914 m, 07°23′ S, 146°40′ E (AMNH 222296); Wanuma, 671 m, 04°51′ S, 145°19′ E (MVZ 138631–138632; AMNH 198802–198813); Wanuma, 1200 m, 04°51′ S, 145°19′ E (BBM 103857); Wau, 1040 m, 07°20′ S, 146°43′ E (MVZ 129815–129818, 129839–129845; AMNH 222310; BBM 28620); Wau, 1200 m, 07°20′ S, 146°43′ E (MVZ 129837; AMNH 222299–222309, 222311–222322, 222394, 222396; BBM 20142, 20144, 20147, 20163, 20197, 20208, 20210, 20213, 24580, 28630, 53584, 54659A, 54659B, 61036, 61038–61041, 61525–61527, 61600–61604, 61631, 96628–96629, 99625–99626, 99631, 99636–99637, 99644, 99650–99652, 99664, 100382, 100435–100440, 100443–100445, 100450, 100453, 100455–100457, 101142); Wau Creek, 1372 m, 07°19′ S, 146°44′ E (AMNH 222297–222298); Wendesi, 75 m, 02°26′ S, 134°13′ E (RMNH R63–R65, R69, 1806); Wilhelm, Mt., 2770 m, 05°46′ S, 144°59′ E (AMNH 191561–191563); Yaiya Valley, 1676 m, 06°50′ S, 146°08′ E (BM 69.345); Yalom, 1000 m, 04°23′ S, 151°45′ E (CZM 352, CN14794, CN14797, CN14799–CN14800, CN14803); Yandara, 1829 m, 05°46′ S, 145°09′ E (BM 50.1751–50.1757).

Rattus nitidus

Doreh, 5 m, 00°55′ S, 134°04′ E (RMNH a); Kebar Valley, 500 m, 00°48′ S, 133°04′ E (AMNH 222051); Manokwari, 5 m, 00°52′ S, 134°05′ E (RMNH 21704, 21706, 21709, 22425–22429, 22431–22438, 22503); Siwi, 800 m, 01°29′ S, 134°02′ E (AMNH 100879).

Rattus rattus

Ataa, 30 m, 08°32′ S, 160°54′ E (BBM 24153, 24168, 24179, 24182, 24184, 24188); Biak Is., 152 m, 01°00′ S, 136°00′ E (AMNH 222269–222273); Bulolo Town, 740 m, 07°11′ S, 146°39′ E (MVZ

129917–129936, 129939–129940; AMNH 222259–222267, 222284; BBM 20350, 21101, 55628, 55635a, 55643, 55657); Crystal Falls, 600 m, 09°25′ S, 147°26′ E (BBM 60222); Dala, 20 m, 08°36′ S, 160°40′ E (BBM 24081, 24083, 24092, 24097, 24115, 24119, 24127, 24129); Daru, 10 m, 09°04′ S, 143°13′ E (AMNH 104855, 104903; BBM 50089); Dawai River, 5 m, 01°49′ S, 136°43′ E (AMNH 222282–222283); Dobo, 10 m, 05°46′ S, 134°13′ E (BM 10.3.2.15–10.3.2.21; SMF 5555, 11553); Finschhafen, 5 m, 06°34′ S, 147°51′ E (AMNH 195117; BBM 27679); Florida Islands, 5 m, 09°05′ S, 160°15′ E (MCZ 42199); Haleta, 10 m, 09°05′ S, 160°07′ E (BBM 24395, 24414); Hollandia, 114 m, 02°32′ S, 140°43′ E (RMNH 24158–24162, 24164–24168; USNM 277322, 277453–277459, 277779–277781, 277782 (skin only; skull is *R. praetor coenorum*), 277783, 295079, 295082, 295084–295089; FMNH 54067, 54224, 56395–56396); Honiara, 10 m, 09°26′ S, 159°57′ E (BBM 23853); Ibele River, 2200 m, 04°05′ S, 138°42′ E (AMNH 151602); Kajoe Batoe, 10 m, 02°30′ S, 140°46′ E (RMNH 24163); Kieta, 10 m, 06°19′ S, 155°44′ E (AMNH 193651–193655); Lae, 10 m, 06°44′ S, 147°00′ E (AMNH 191526); Lorengau, 10 m, 02°01′ S, 147°16′ E (AMNH 193763–193765, 193768); Lunga, 10 m, 09°25′ S, 160°03′ E (BM 36.2.6.4; FMNH 54271); Manokwari, 5 m, 00°52′ S, 134°05′ E (FMNH 31842); Marienberg, 5 m, 03°58′ S, 144°15′ E (FMNH 31849); Morehead, 30 m, 08°43′ S, 141°38′ E (PNG 10819, 10868); Mutahi, 700 m, 05°42′ S, 154°57′ E (BBM 61132, 61151); Nabire, 5 m, 03°21′ S, 135°31′ E (AMNH 222274); Nini Creek, 100 m, 09°27′ S, 160°14′ E (BBM 23814, 23825, 23846); Oransbari, 5 m, 01°21′ S, 134°18′ E (AMNH 222275–222281, 222285); Passam Agricultural Station, 274 m, 03°41′ S, 143°38′ E (MVZ 138635–138637); Port Moresby, 5 m, 09°29′ S, 147°10′ E (AMNH 108199–108200); Pusisama, 5 m, 07°47′ S, 156°39′ E (BBM 23200); Rabaul, 10 m, 04°12′ S, 152°11′ E (CZM CN14815); Sansapor, 5 m, 00°29′ S, 132°05′ E (USNM 277023); Sorong, 20 m, 00°53′ S, 131°16′ E (MCSN MSNG3534); Tabalia, 20 m, 09°16′ S, 159°44′ E (BBM 23868, 23946, 23948, 24023); Tamojil, 5 m, 05°50′ S, 132°57′ E (BM 10.3.1.43); Tinputz Patrol Post, 5 m, 05°34′ S, 155°01′ E (BBM 61324); Togarau, 600 m, 05°51′ S, 155°09′ E (BBM 61331, 61334, 61340, 61343, 61406, 61408, 61410, 61412, 61414); Torokina, 10 m, 06°14′ S, 155°03′ E (AMNH 144306–144307); Tulagi, 5 m, 09°03′ S, 160°09′ E (MCZ 42188, 42190, 42203; BM 35.9.2.1); Waigeo Is., 10 m, 00°15′ S, 130°50′ E (ZM 39846–39847); Watut, 700 m, 07°14′ S, 146°36′ E (AMNH 222268).

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