



Journal of Mammalogy, 91(5):861–870, 2010

DOI:10.1093/jmammal/gyw034

Published online April 12, 2016

Version of Record, first published online April 12, 2016, with fixed content and layout in compliance with Art. 8.1.3.2 ICZN.

## A new species of *Rattus* (Rodentia: Muridae) from Manus Island, Papua New Guinea

ROBERT M. TIMM,\* VALTER WEIJOLA, KEN P. APLIN, STEPHEN C. DONNELLAN, TIM F. FLANNERY, VICKI THOMSON, AND RONALD H. PINE

Department of Ecology and Evolutionary Biology & Biodiversity Institute, University of Kansas, Lawrence, KS 66045, USA (RMT)

Zoological Museum, University of Turku, Turku 20014, Finland (VW)

Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013, USA (KPA)

Wildlife Conservation Society, Goroka, Papua New Guinea (KPA)

South Australian Museum and Australian Centre for Evolutionary Biology and Biodiversity, University of Adelaide, Adelaide 5005, Australia (SCD)

Climate Council of Australia, P.O. Box 1267, Potts Point, New South Wales 2011, Australia (TFF)

School of Biological Sciences, University of Adelaide, Adelaide 5005, Australia (VT)

Biodiversity Institute, University of Kansas, Lawrence, KS 66045, USA (RHP)

\* Correspondent: [btimm@ku.edu](mailto:btimm@ku.edu)

We describe a new species of *Rattus*, from 3 modern specimens collected on Manus Island in the Admiralty Group, Papua New Guinea, between 2002 and 2012. Subfossil specimens of early to late Holocene age from the Pamwak archaeological site on Manus Island are referred to the new species on morphological criteria; these confirm the species as a long-term resident of Manus Island. The new species is distinguished by its combination of large size; short tail; dorsal pelage that is coarse, spiny, and dark, with prominent black guard hairs; and sharply contrasting cream ventral pelage. Based on its overall body form, the species is almost certainly terrestrial. The dentition combines robust incisors with relatively small molars and the cranium displays a distinctive mélange of characters—including an elongate and anteriorly expanded rostrum and a mesopterygoid fossa that is narrow anteriorly and broadens to the rear. Sequence data from the mitochondrial *control region* and 3 nuclear genes place the new species as a highly divergent member of the Australo–Papuan *Rattus* radiation, with no identified close relative among sampled taxa. Morphological comparisons are made between the new species and other pertinent species of *Rattus* from the region, including *R. sanila*, a species known only from Late Pleistocene fossil to Late Holocene subfossil remains from an archaeological site on New Ireland. The conservation status of the new species is discussed in the light of a recent survey that failed to locate surviving populations in 2 areas of natural forest on Manus Island. Further survey work is urgently needed to identify any surviving populations and to assess the role of potential threats to the species.

Key words: Admiralty Islands, Australo–Papuan Region, biogeography, Bismarck Archipelago, conservation, mitochondrial control region, molecular phylogeny, morphology, nuclear genes, *Rattus sanila*

© 2016 American Society of Mammalogists, [www.mammalogy.org](http://www.mammalogy.org)

The rodent genus *Rattus* Fischer, 1803, currently comprises 67 recognized species (Musser and Carleton 2005; Maryanto et al. 2010), of which 3 appear to have become extinct in historical times. The genus shows its greatest disparity on mainland Asia and almost certainly arose there (Pagès et al. 2011; Fabre et al. 2013). However, the highest species diversity is present in insular Southeast Asia, Melanesia, and in Australia, each of which supports rich local radiations (Musser and Heaney 1985; Musser and Holden 1991; Rowe et al. 2011). Melanesia, which

comprises the island of New Guinea and its satellites, has 17 native species currently recorded (Flannery 1995a, 1995b; Musser and Carleton 2005; Maryanto et al. 2010), though a recent genetic survey points to additional cryptic diversity, especially among the small montane species (Robins et al. 2014). Most Melanesian islands also support populations of 2 or more introduced species of *Rattus* that have spread as commensals of humans in prehistoric to colonial times (Flannery 1995b; Matisoo-Smith and Robins 2004; Aplin et al. 2011).

Here we describe a new species of *Rattus* from Manus Island in the Admiralty Group, Bismarck Archipelago, Papua New Guinea, based on 3 specimens, 2 obtained in 2002 and 1 in 2012. We also refer subfossil specimens of *Rattus* from an Early to Mid-Holocene archaeological site on Manus Island to the new species, thereby confirming the new species as a long-term resident of the island.

The Admiralty Group lies about 2 degrees south of the equator and some 275–300 km north of the island of New Guinea. It comprises 18 islands with a total land area of 2,100 km<sup>2</sup>. Manus is the largest island of the group (approximately 1,900 km<sup>2</sup>) and reaches a maximum elevation of 720 m on Mt. Dremmel. The islands arose along a volcanic arc during the mid-Tertiary to late Tertiary (Davies 2012) and were not connected to New Guinea or any other landmass during Quaternary glacial cycles (Voris 2000). Mussau Island in the St. Matthias Group lies some 260 km to the east, while Lavongai Island (formerly New Hanover; located northwest of New Ireland) and New Britain are 300 km and 390 km away, to the east and southeast, respectively. The dominant natural vegetation of the Admiralty Group is primary evergreen forest, including tropical and subtropical moist broadleaf forests (Wikramanayake et al. 2002). On floristic criteria, these communities have been identified as being of high regional biological significance (Johns 1993; Wikramanayake et al. 2002).

Prior to the collection of the new *Rattus* species, only 4 species of rodents were recorded in the modern fauna of the Admiralty Group. Taylor et al. (1982) reported *R. praetor* (Thomas, 1888) from Bat Island, which lies approximately 70 km southwest of Manus Island, and identified museum specimens of 2 species of *Rattus* from the Admiralty Group, with both occurring on Manus—*R. exulans* (Peale, 1848) [see also (Thomas 1914)] and *R. rattus* (Linnaeus, 1758). Both are widespread commensals of humans. The 4th species was collected in 1988 on Manus Island, the endemic Manus Melomys *Melomys matambuai* Flannery, Colgan, and Trimble, 1994. Two other species of rodents listed for Manus by Menzies and Dennis (1979)—*Rattus ruber* (Jentink, 1879) [= *R. praetor*], followed by Flannery (1995b), and *Uromys neobritannicus* Tate and Archbold, 1935—are unsubstantiated to our knowledge, either by literature references or by vouchers. In their discussion of *M. matambuai*, Musser and Carleton (2005:1379), in an apparent lapsus, erroneously gave the range of *M. bougainville* Troughton, 1936, as “Manus Isl.”

Archaeological samples from Manus Island have been cited as evidence of a formerly more diverse rodent fauna. Williams (1997, 1999) reported examples of *R. mordax* (Thomas, 1904a), cf. *R. mordax*, *R. praetor*, *R. rattus*, and *Rattus* sp., but not *R. exulans*, in a large assemblage of latest Pleistocene fossils and remains of more recent age, from the Pamwak archaeological site (see Fredericksen et al. 1993 for site details). White et al. (2000) mentioned Williams’s (1997, 1999) determinations in their review of the historical and present distribution of the semicommercial *R. praetor*. However, Flannery (1995b:38) had earlier reexamined the Pamwak rodents and found only *M. matambuai* and a “large species of *Rattus*, probably representing an undescribed species, (that) persists into the most recent levels.”

Flannery’s assessment was confirmed by Aplin who restudied the Pamwak rodent assemblage as part of the present study.

In August 2002, Ann Williams, working on a biotic survey of Manus for Conservation International, obtained 2 specimens of a large *Rattus*—a nearly complete skeleton and an isolated mandible—from hunters at the village of Tulu No. 1 along the northwestern coast. A full decade later, in August 2012, Weijola obtained a complete adult female specimen of the same large, distinctive species while conducting fieldwork on monitor lizards in the central hill forests of Manus Island.

Here we 1) describe the new species of *Rattus* from Manus Island, based on the available modern and archaeological specimens; 2) assess the distinctiveness of this species in comparison with other *Rattus* in the region, using molecular genetic and morphological data; 3) relate our new observations to current views regarding the biogeography of Australo-Papuan *Rattus* and of the Admiralty Group; and 4) discuss the conservation status of the new species.

## MATERIALS AND METHODS

*Taxon sampling.*—Taxonomic assessment of the Manus *Rattus* was aided by the extensive morphological reviews of Australian and Melanesian *Rattus* by Taylor and coworkers (Taylor and Horner 1973; Taylor et al. 1982) and by subsequent work in the field (Flannery 1995a, 1995b) and in collections (Musser and Carleton 2005). Taylor et al. (1982) included a critical assessment of all of the available names applied to Melanesian *Rattus*. We follow their assessments of synonymy. For the molecular genetic study, we compared sequences obtained for the new species, with all available data from Australo-Papuan *Rattus* (Robins et al. 2010, 2014; Rowe et al. 2011) and from a range of other *Rattus* species representing other geographic radiations. Three of the currently recognized extant species of *Rattus* in Melanesia are unrepresented in the genetic taxon sampling—*R. jobiensis* Rümmler, 1935; *R. omichlodes* (Misonne, 1979); and *R. richardsoni* (Tate, 1949). Also missing from our sampling is the Gag Island population described recently as a new species—*R. nikenii* Maryanto et al., 2010—but which in our view may be an insular variant of *R. steini*. Of these, only *R. jobiensis* is a serious candidate for identity with the Manus rat, as *R. omichlodes* and *R. richardsoni* are both small species of subalpine habitats of the central ranges of New Guinea.

*Morphological techniques.*—Craniodental measurements were taken with dial calipers; the majority of mensural points follow Taylor et al. (1982) to facilitate comparison with their tables of measurements. Percentages given of head + body length, as compared to total length, in species other than the new *Rattus* from Manus are calculated from figures given in tables by Taylor et al. (1982). Descriptive terminology for the skull and teeth follows that used in many publications on murine rodents by Musser (e.g., Musser 1982; Musser and Lunde 2009). Upper and lower molars are designated by “M” and “m,” and upper and lower incisors are designated by “I” and “i,” respectively. Length of hind foot does not include claw.

Specimens from the following institutions (acronyms in parentheses) are used for comparisons: Australian Museum (AMS), Sydney, New South Wales; Australian Biological Tissue Collection (ABTC), South Australian Museum (SAM), Adelaide, South Australia; National Museum & Art Gallery, Port Moresby, Papua New Guinea (PNGMAG); American Museum of Natural History (AMNH), New York; Bernice P. Bishop Museum (BPBM), Honolulu, Hawaii; Field Museum (FMNH), Chicago, Illinois; Natural History Museum of Los Angeles County (LACM), Los Angeles, California; United States National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.; University of Kansas Natural History Museum (KU), Lawrence, Kansas; and University of Wisconsin Zoological Museum (UWZM), Madison, Wisconsin. Specimens used in craniodental comparisons are listed in [Supporting Information S1](#).

The archaeological specimens were compared with the modern specimens, for consistency of dental and bony structures. Whenever possible, measurements of molar lengths and widths and incisor widths and depths were taken. Bivariate plots were examined to identify possible outliers that might indicate the presence in the sample of more than 1 species.

**Molecular genetic techniques.**—DNA was extracted from tissue samples, using a Puregene DNA Isolation Kit (Gentra Systems, Minneapolis, Minnesota), following the manufacturer's protocol for 5–10 mg of fresh or frozen tissue. The mitochondrial *control region* (*CR*) and 3 nuclear genes—*ATP5A1*, *DHFR*, and *FGB* were amplified with the following sets of primers: mt15996L (5'-CTCCACCATCAGCACCCAAAGC-3') and mt16502H (5'-TTTGATGGCCCTGAAGTAAGAACCA-3') for the *CR* ([Houlden et al. 1999](#)); Atp5A1\_F (5'-TTATCCCCGAATCTCTGTG-3') and Atp5A1\_R (5'-TGCAAACAAACGGTTGTAA-3') for *ATP5A1*; Fgb\_F (5'-GGGGAGAACAGAACCATGACCATCCAC-3') and Fgb\_R (5'-ACCCAGTAGTACTGCCATTCGGATT-3') for *FGB*; and DHFR\_F (5'-GTCCC AAAATATGGGCATTG-3') and DHFR\_R (5'-TGCCCAG GTTTTTATTCTGG-3') for *DHFR* ([Rowe et al. 2011](#)). PCRs were set up in 25  $\mu$ L volumes containing a final concentration of 1 Unit Immolase DNA Polymerase (Bioline), 2  $\times$  PCR Buffer (Immolase, Bioline), 7.5 mM MgSO<sub>4</sub>, 1 mM each dNTP, 0.24  $\mu$ M forward and reverse primers, and 2–3  $\mu$ L of template DNA. PCRs were performed on an Eppendorf PCR machine (Thermo Fisher Scientific Australia Pty Ltd, Scoresby, Victoria, Australia), according to the following protocol: 95°C for 10 min, 35 cycles at 94°C for 45 s, 60°C for 45 s, 72°C for 1 min, and a final extension of 6 min at 72°C (the annealing temperature of each primer set was optimized independently—57°C for mt15996L/mt16502H and Fgb\_F/Fgb\_R, 60°C for LM1268/LM1269, and 50°C for Atp5A1\_F/Atp5A1\_R and DHFR\_F/DHFR\_R). We included negative controls in all experiments, to monitor contamination. PCR products were separated by electrophoresis on a 1.5% agarose gel. Successful PCR products (20  $\mu$ L) were purified using Multiscreen PCR cleanup plates (EMD Millipore Corporation,

Billerica, Massachusetts). The purified PCRs were sent to the Australian Genome Research Facility for cycle sequencing in both directions, using Big Dye Terminator v3.1 reagents and subsequent capillary sequencing.

We produced new sequences from 2 specimens of *R. mordax* and from the holotype of the new species and aligned our sequences with data from [Rowe et al. \(2011\)](#) for the remaining Australo-Papuan *Rattus* and outgroups, using Geneious version 5.5.6 (Biomatters Limited, Auckland, New Zealand). GenBank accession numbers for all sequences used are presented in [Supporting Information S2](#).

We conducted phylogenetic analyses on the concatenated, mitochondrial, and nuclear alignments, using Bayesian (MrBayes) and maximum likelihood (PhyML) algorithms after use of PartitionFinder version 1.0.1 ([Lanfear et al. 2012](#)) to determine the best partitioning strategy and models of nucleotide substitution (HKY for *FGB*, and HKY+G for the *CR*, and *DHFR* and *ATP5A1*). MrBayes v.3.2 ([Ronquist et al. 2012](#)) was run using 4 chains for 2.5 million generations, with trees and parameters recorded every 250 generations, and with unlinked parameters for each partition and branch lengths allowed to vary proportionally across partitions. PhyML ([Guindon et al. 2009](#)) was used to compute the best maximum likelihood tree using both the Nearest Neighbor Interchange (NNI) algorithm to improve the starting tree and Subtree Pruning and Regrafting (SPR) topological moves to efficiently sample tree space with 3 random starting trees. One hundred bootstrap pseudoreplications were performed on the best tree. RAxML ([Stamatakis 2014](#)) was used to compute the best maximum likelihood tree for the extended mtDNA *CR* dataset, using a GTR + gamma model of nucleotide substitution with a rapid bootstrap analysis.

## RESULTS

### *Rattus detentus*, new species Timm, Weijola, Aplin, Flannery, and Pine

Admiralties Rat

[Figs. 1, 2, 4, 5](#)

*Rattus praetor*: [Williams 1999:244](#); not *Mus praetor* [Thomas, 1888](#).

*Rattus mordax*: [Williams 1999:244](#); not *Mus mordax* [Thomas, 1904a](#).

**Holotype.**—Adult female obtained by Valter Weijola on 24 August 2012. Voucher specimen fixed in formalin, preserved in spirit, and registered as PNGMAG 274363 (and AMS M45608) in the National Museum & Art Gallery, Port Moresby, Papua New Guinea ([Figs. 1A, 1C, and 1D](#)). Tissue sample preserved in ethanol and registered as ABTC 125036 in the Australian Biological Tissue Collection, South Australian Museum, Adelaide. Extracted skull is in excellent condition, all teeth fully erupted and moderately worn, cranium with advanced fusion of basicranial synchondroses ([Fig. 2](#)).

**Type locality.**—Vicinity of a small stream near western end of Kawaliap Village, el. 200 m (2°6'40"S, 147°3'40"E), Manus Island, Admiralty Islands, Manus Province, Papua New Guinea.



**Fig. 1.**—A) Adult female *Rattus detentus* (PNGMAG 274363—holotype) from Manus Island. B) Nuts from *Canarium indicum* (Burseraceae) with gnawing marks most likely made by *R. detentus*. C) Adult female *R. detentus* (PNGMAG 274363—holotype), dorsal view. D) Adult female *R. detentus* (PNGMAG 274363—holotype), ventral view. E) Collection site of the *R. detentus* holotype, a traditional subsistence garden and grove of *Metroxylon* near Kawaliap Village. F) Elevated view of the forest where *R. detentus* is found.

*Paratypes.*—KU 163723: skull and almost complete postcranial skeleton of a young adult of unknown sex. The animal had been killed by local villagers, its carcass buried and the skeleton retrieved and given to Ann Williams on 3 August 2002. All teeth are fully erupted but little worn, and the basicranial synchondroses are not fused (Fig. 2). The skull is missing both jugals and the hamuli of both pterygoids; mandibular rami are separated. KU 163724: mandible only of an adult of unknown sex, dug up from the same hole as KU 163723 and at the same time (Andrew L. Mack, field number 1573). Both specimens were obtained from the villagers at the village of Tulu No. 1, elevation 34 m, Manus Island, Admiralty Islands, Manus Province, Papua New Guinea (01°57'37"S, 146°50'28"E).

Associating the correct mandible with the cranium was possible because the 2 individuals are of different ages and sizes.

*Referred material.*—One hundred and ninety-one subfossil specimens from Pamwak archaeological site, located in the vicinity of Piterait Village, at elevation 30 m, 4 km inland of the south coast of Manus, Admiralty Islands, Manus Province, Papua New Guinea (Fredericksen et al. 1993). The subfossil sample includes 5 dentaries with m1–3; 11 dentaries with 1 or 2 molars retained; 26 examples of m1; 23 examples of m2; 13 examples of m3; 79 examples of the lower incisor; and 34 examples of the upper incisor. The subfossil series is consistent in both morphological and metric attributes with the modern specimens and there is no indication that the



**Fig. 2.**—Dorsal, ventral, and lateral views of the crania and lateral views of dentaries of adult *Rattus detentus*: A) PNGMAG 274363—holotype; B) KU 163723—a paratype. Scale bar represents 10 mm.

sample contains any additional species. The earliest levels of Pamwak date to approximately 14,000 years ago, but the faunal remains including the *Rattus* specimens are derived from contexts younger than approximately 9,000 years ago. These specimens are the property of the National Museum & Art Gallery, Port Moresby, Papua New Guinea (PNGMAG), and form part of its Archaeology Collection.

**Distribution.**—Currently known as a living animal from 2 localities on Manus and from subfossil remains from the Pamwak archaeological site (Fig. 3).

**Etymology.**—*detentus* (Latin for detained), in reference to the isolation of this Melanesian *Rattus* lineage on Manus Island and to the recent use of the island to detain people seeking political and/or economic asylum in Australia.

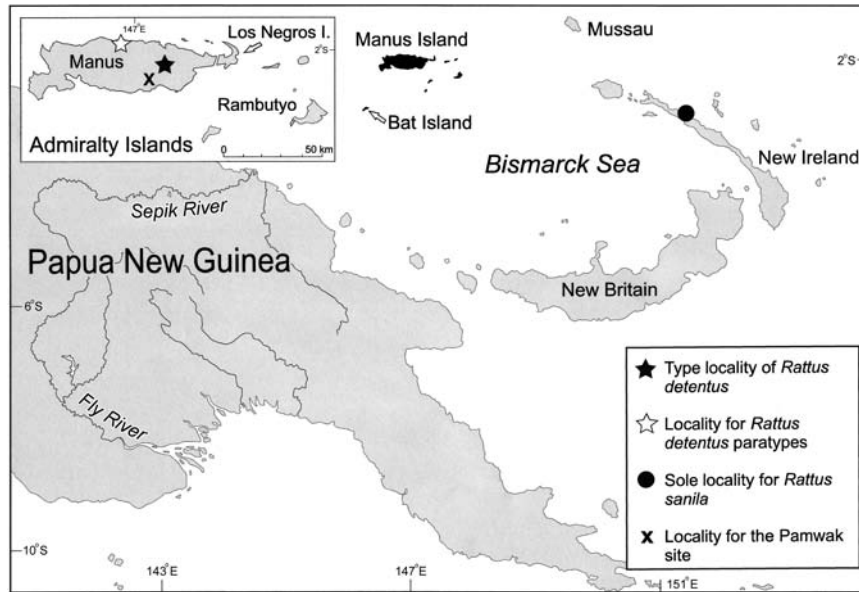
**Nomenclatural statement.**—A life science identifier (LSID) number was obtained for the new species (*R. detentus*): urn:lsid:zoobank.org:pub:E855E9C8-F224-4B3F-A5E9-47D154DAF06F.

**Diagnosis.**—A large, short-tailed (approximately 58% of head + body length) species of *Rattus* with mammary formula: 1 pectoral + 1 postaxillary + 2 inguinal. Pelage exceptionally coarse and spiny, with prominent black guard hairs. The animal's size exceeds that attained by all other Melanesian *Rattus* except *R. jobiensis*, and possibly some eastern Melanesian populations of *R. praetor coenororum* Thomas, 1922. Tail at 58% of body length is proportionally shorter than in all other New

Guinean *Rattus* species, including the 5 species that approach *R. detentus* in size [i.e., *R. jobiensis* (averaging 92.0% of head + body length), *R. leucopus* (Gray, 1867) (averaging 84.7–89.9% of head + body length in the 3 New Guinean subspecies), *R. mordax* (averaging 83.5% of head + body length in *R. m. mordax* and 82.1% in *R. m. fergussoniensis* Laurie, 1952), *R. praetor* (averaging 78.1% of head + body length in *R. p. praetor* and 89.4% in *R. p. coenororum*), and *R. steini* Rümmler, 1935 (averaging 86.0–101.5% of head + body length in the 4 recognized subspecies)].

*Rattus detentus* may be distinguished cranially from all other species of *Rattus* by the following combination of characters: rostrum elongate and anteriorly broadened; incisive foramina short, terminating anterior to the molar rows; interorbital region broad; auditory bullae relatively small, weakly inflated; mesopterygoid fossa with narrow, U-shaped anterior margin, then widening posteriorly; pterygoid fossa narrow. Distinguished dentally by combination of relatively small, simple molars (i.e., lacking accessory ridges or posterior cingula on upper molars and accessory cusps on lower molars) and broad, heavy incisors.

**Description.**—A large (mass 430 g; head + body length 260 mm), heavily built, terrestrial rat with harsh pelage (Figs. 1A, 1C, 1D, and 4). Dorsum dark gray overall but heavily flecked with pale gray and bearing numerous translucent spines (some with rufous or dark tips) and coarse, conspicuous,



**Fig. 3.**—Map of the Bismarck Archipelago, Admiralty Islands (in black), and eastern New Guinea, showing the records of *Rattus detentus* on Manus and of the apparently extinct *R. sanila* on New Ireland. All known localities of *R. detentus* are plotted. The closed star represents the type locality, the open star represents the locality of the 2 paratypes, and “X” represents the Pamwak archaeological site. The closed circle represents the Late Pleistocene–Late Holocene Balof 2 archaeological site on New Ireland, the only known locality for *R. sanila*. Manus and Los Negros are separated by a very narrow channel (indicated by a gap).

black guard hairs that are longest posteriorly to a maximum of 55 mm on lower back. Underfur of dorsum and flanks fine and pale gray. Outer surfaces of fore- and hindlimbs paler gray. Ventral fur white to roots and lacks spines—white zone extending from lip to base of tail and 40 mm wide at mid-body, lateral demarcation sharp. Rhinarium white, sides of muzzle with short, dark hairs (Fig. 4). Ears 23.4 mm from notch to rim, clothed in extremely fine hairs, their skin mottled but whiter overall at base, grayer at margin. Mystacial vibrissae stout and black, reaching 60 mm in length (Fig. 4). Skin on dorsal surface of manus and pes speckled with dark pigment, thinly clothed with short, dark hairs. Skin on dorsal surface of all digits white. Palmar surface of manus ivory with irregular gray patches on pads. Pes broad and heavy, 43.2 mm in length (su). Plantar surface dark gray from proximal extremity of heel to proximal edges of plantar pads and then mottled gray and ivory distally onto digits (Fig. 5). Plantar pads broad, flat, and smooth, lacking any trace of striae (Fig. 5). Claws on manus and pes robust, ivory-colored. Tail length 150 mm (57.7% of head + body length), overall color dark gray with paler mottling at very base. Tail scales large, subrectangular, weakly overlapping, dark gray with white skin showing between each row; 6–7 scale rows per cm midway along tail. Three stout bristles emerge from rear of each scale, central bristle longest. Midway along tail, central bristle approximately 1.5 times as long as a scale and outer bristles slightly shorter than scales; near tail tip, central bristles 2–3 times length of scales.

General anatomy of skull and dentition in *R. detentus* (Fig. 6) conforming in all major features with that in other species of *Rattus* (e.g., Greene 1935). Noteworthy features are rostrum elongate and broadened anteriorly; relatively short and bowed incisive foramina that terminate anterior to the molar rows;



**Fig. 4.**—Anterior portion of *Rattus detentus* (PNGMAG 274363—holotype), showing the coarse dorsal hair; white venter; ear appearing nearly naked; white rhinarium and forefoot; robust, ivory-colored claws; and details of the vibrissae.

interorbital region broad; zygomatic plates broad and tall; palate narrow due to slight outward flexion of molar rows, especially posteriorly; mesopterygoid fossa with narrow, U-shaped anterior margin and broadening to the rear; pterygoid fossa correspondingly narrow; auditory bullae short and uninflated; middle lacerate foramen capacious but separated from postglenoid vacuity by anterior process of ectotympanic; arrangement of stapedial and carotid foramina conforms to inferred primitive murine pattern (described and illustrated by Musser



**Fig. 5.**—A) Central portion of the tail of *Rattus detentus* (PNGMAG 274363—holotype), showing the large, subrectangular, weakly overlapping scales, with 3 stout bristles emerging from rear of each scale, central bristle longest. B) Right hindfoot of *R. detentus* (PNGMAG 274363—holotype), showing the broad, heavy pes and broad, flat, and smooth plantar pads lacking any trace of striae. Claws on both manus and pes robust and ivory-colored.

1982:5, figure 2D); dentary robust and with prominent capsular process (Fig. 2). Dentition noteworthy for combination of robust incisors with relatively small molars. Upper M1s lacking anterior cingula or accessory cuspules, all upper molars lacking posterior cingulum; cusp t3 weakly developed or absent on M2–3s (Fig. 7). The m1s with 2 cuspids on anteroconid and well-developed posterolabial cusplet; m2s with small anterolabial cuspid and well-developed posterolabial cusplet; m3s with small anterolabial cuspid only (Fig. 7). Upper and lower incisors broad and deep. Ratio of depth to breadth (D/B) of lower incisors 1.67–1.83 ( $n = 3$ ) and of upper incisors 1.58–1.65 ( $n = 2$ ).

Measurements of skull and teeth of the 2 most complete modern specimens of *R. detentus* are shown in Table 1. Measurements of the large sample of jaws and teeth of the archaeological specimens from Pamwak are shown in Supporting Information S3. The lower incisor D/B ratio in the archaeological sample ranges 1.44–2.0 ( $n = 77$ ,  $\bar{X} = 1.76$ ,  $SD = 0.122$ ).

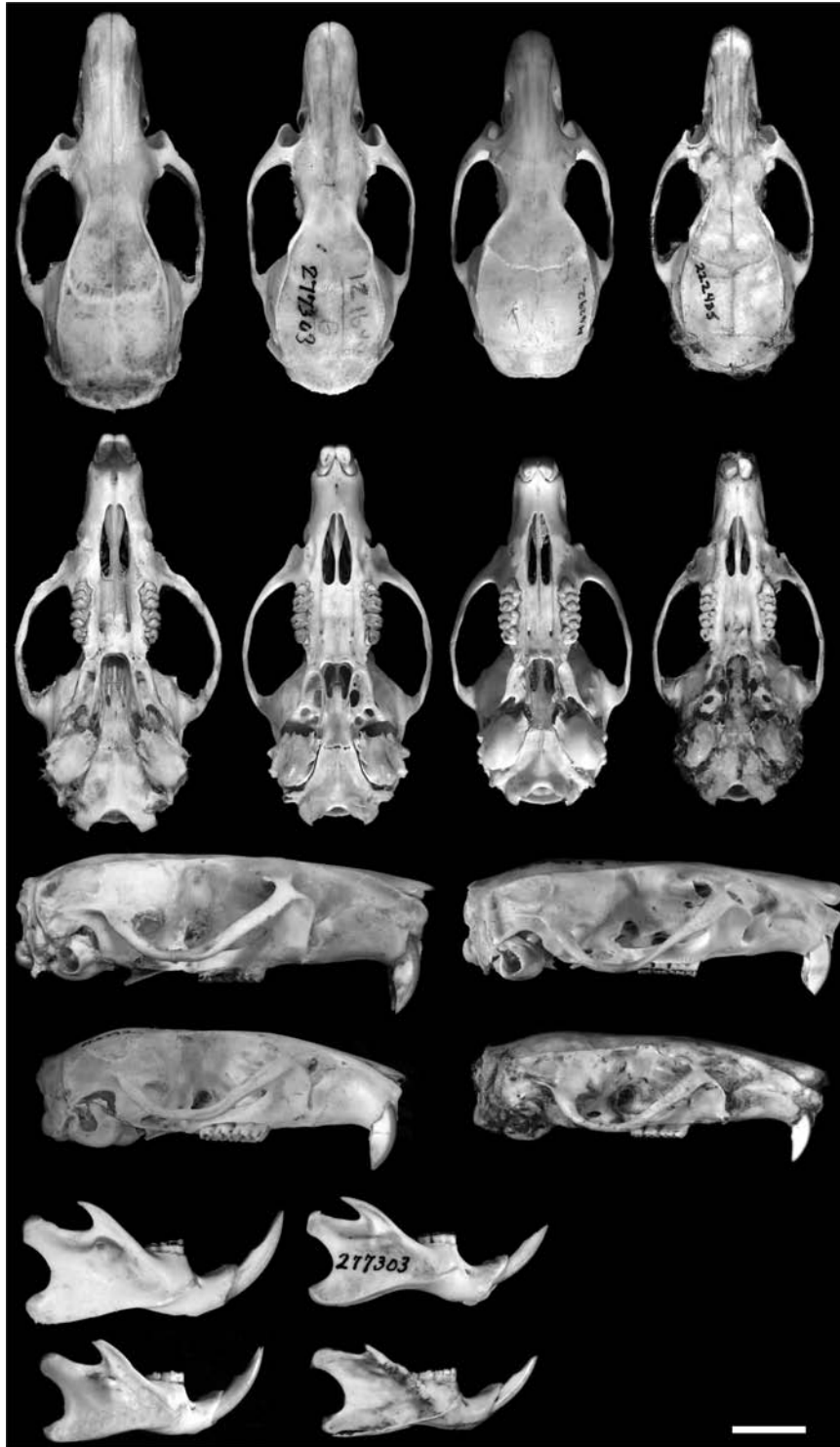
The holotype carried 2 fetuses in the uterus, each approximately 1 cm long (crown–rump length).

**Morphological comparisons.**—*Rattus detentus* is an exceptionally large and heavy-bodied member of its genus, exceeded in bulk only by mature adult specimens of *R. norvegicus* (Berkenhout, 1769), of *R. everetti* (Günther, 1879) from the Philippine Archipelago, and of *R. jobiensis* from the islands of Cenderawasih (formerly Geelvinck) Bay in northwest New Guinea. Four other species within the Australo–Papuan *Rattus* fauna approach *R. detentus* in size—*R. praetor* of the northern lowlands of New Guinea and the Bismarck Archipelago and Solomon Islands, *R. mordax* of southeast New Guinea and the D’Entrecasteaux Islands and Louisiade Archipelago, *R. leucopus* of the southern lowlands of New Guinea and northeast Australia, and *R. steini* of the central and northern ranges of New Guinea. The recently described *R. nikenii* of Gag Island is comparable to *R. steini* in size. *Rattus sanila* Flannery and White, 1991, a large-toothed species described from Late Pleistocene to Late Holocene contexts on New Ireland and now possibly extinct (see White et al. 1991), also warrants comparison with *R. detentus*. All other Melanesian *Rattus* species are considerably smaller, with adults typically not exceeding 100 g (Taylor et al. 1982; Flannery 1995a). Body proportions also distinguish this suite of smaller Melanesian *Rattus* from *R. detentus*, especially tail length that exceeds 70% of head + body length in all but 1 of the remaining species. The exception is the vole-like *Rattus giluwensis* Hill, 1960, a small (approximately 50–60 g), short-tailed (65% of head + body length) species found in subalpine grasslands of the central ranges of New Guinea (Taylor et al. 1982; Flannery 1995a). Apart from the almost 10-fold disparity in mass, *R. detentus* differs from *R. giluwensis* in numerous cranial features including its proportionally longer rostrum, its short and bowed (versus more elongate and parallel-sided) incisive foramina, and its less inflated auditory bullae (for cranium of *R. giluwensis* see Taylor et al. 1982, figure 28).

*Rattus jobiensis* has a relatively longer tail (averaging 92.0% of head + body length) and longer, narrower hindfoot (pes length 44.0–51.0 versus 43.2 mm) than *R. detentus*. Its mammary formula is 0 + 1 + 2 = 6 (Yapen and Owi Islands) or 1 + 1 + 2 = 8 (Biak Island). The ventral fur is various hues of yellow to buff but never white. The cranium of *R. jobiensis* (Fig. 6) is elongate and narrow, the nasals are narrower anteriorly than in *R. detentus* (4.8–6.0 versus 6.6–6.9 mm), the auditory bulla is more inflated, the interorbital region is narrower (6.2–7.3 versus 8.1–8.2 mm), the mesopterygoid fossa is narrower and parallel-sided (Fig. 6), and cusp t3 is larger on M2–3s (Fig. 7).

*Rattus leucopus* is a smaller rat (maximum mass 315 g—Flannery 1995a) with a narrower hindfoot and longer tail (tail length averaging 84.7–89.9% of head + body length in the 3 New Guinean subspecies). The mammary formula is 0 + 1 + 2 in all subspecies. The cranium has a more slender rostrum (Fig. 6) with narrower nasals (anterior width 3.9–6.3 mm across all subspecies), a narrower interorbital region (5.5–8.2 mm), less robust zygomatic plate, and a parallel-sided mesopterygoid fossa (for cranium of *R. leucopus* see Taylor et al. 1982, figure 19 and Flannery 1995a, Plate 36).

*Rattus mordax* is a smaller rat (maximum recorded mass 255 g—Flannery 1995b) with tail length averaging 83.5% of head +

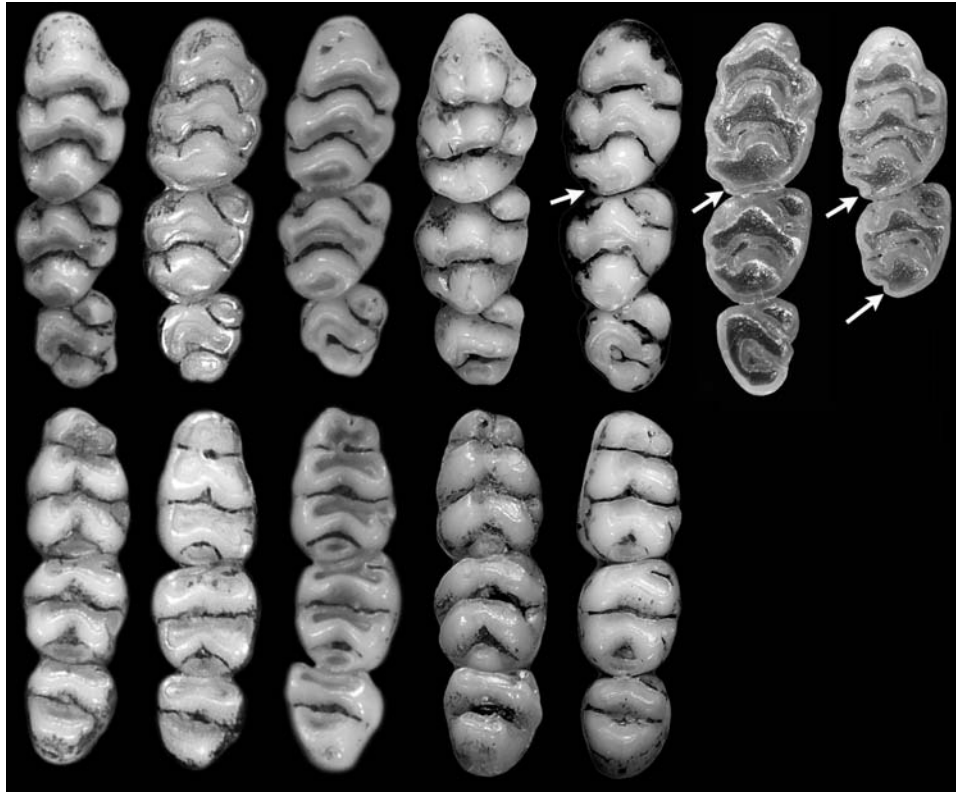


**Fig. 6.**—Crania and dentaries of 4 species of *Rattus* from Melanesia. Crania (dorsal and ventral) from left to right = *R. detentus* (PNGMAG 274363—holotype), *R. praetor* (USNM 277303), *R. mordax* (AMS M4292), and *R. jobiensis* (AMNH 222435). Lateral views of crania: upper row, left to right, *R. detentus* and *R. praetor*; lower row, left to right, *R. mordax* and *R. jobiensis*. Dentaries: upper row, left to right, *R. detentus* and *R. praetor*; lower row, left to right, *R. mordax* and *R. jobiensis*.

body length in *R. m. mordax* and 82.1% in *R. m. fergussoniensis* (Taylor et al. 1982). Its dorsal fur is less spiny than that of *R. detentus* and is “yellowish ivory with the medium gray underfur showing beneath” (Taylor et al. 1982:228). The cranium of *R. mordax* (Fig. 6) has straight-sided incisive foramina; a short and narrower

rostrum with anterior nasal width of 3.8–6.0 mm (across both subspecies); a wide, parallel-sided mesopterygoid fossa with a square rather than rounded anterior margin; larger and more inflated auditory bulla; a narrower interorbital region (5.2–7.1 mm); strongly flared temporal ridges; and M2–3s with a larger cusp t3 (Fig. 7).





**Fig. 7.**—Top: upper right molar tooththrows, from left to right, of *Rattus detentus* (KU 163723—a paratype), *R. detentus* (PNGMAG 274363—holotype), *R. praetor* (USNM 277303), *R. mordax* (AMS M4292), *R. jobiensis* (AMNH 222435); upper left tooththrows (image reversed), from left to right, of *R. sanila* (AMS F82021—holotype), *R. sanila* (AMS F89058). Arrows point to posterior cingula present only on upper molars of *R. jobiensis* and *R. sanila*. Bottom, left to right: lower right tooththrows of *R. detentus* (KU 163723—a paratype), *R. detentus* (PNGMAG 274363—holotype), *R. praetor* (USNM 277303), *R. mordax* (AMS M4292), *R. jobiensis* (AMNH 222435). Anterior is at the top. Images not to scale but made to be of similar size for ease of comparison.

*Rattus praetor* is a smaller rat (maximum recorded mass 240 g—[Flannery 1995a, 1995b](#)) with a longer tail (averaging 78.1% of head + body length in *R. p. praetor* and 89.4% in *R. p. coenorom* ([Taylor et al. 1982](#)). Its dorsal fur is less spiny than that of *R. detentus* and it has yellowish or gray rather than white ventral fur. The cranium of *R. praetor* ([Fig. 6](#)) typically has incisive foramina that are more broadly rounded at the rear; a wider, parallel-sided mesopterygoid fossa with a square rather than rounded anterior margin; larger and more inflated auditory bulla; a narrower interorbital region (5.4–7.3 mm across both subspecies); M1s with less distinct labial cusps t3 and t6; and M2s with a larger cusp t3 ([Fig. 7](#)). *R. praetor* resembles *R. detentus* in the degree of anterior widening of the rostrum ([Fig. 6](#)).

*Rattus steini* is a smaller rat (maximum recorded mass 220 g—[Flannery 1995a](#)) with shorter hindfoot (maximum recorded pes length of 38 mm—[Taylor et al. 1982](#)) and a longer tail (averaging 86.0–101.5% of head + body length in the 4 recognized subspecies—[Taylor et al. 1982](#)). Its dorsal fur is less spiny than that of *R. detentus* and it has yellowish or gray rather than white ventral fur. Its mammary formula is  $0 + 1 + 2 = 6$  (*R. s. steini* and *R. s. baliemensis* [Taylor, Calaby, and Van Deusen, 1982](#)) or  $1 + 1 + 2 = 8$  (*R. s. foersteri* [Rümmeler, 1935](#) and *R. s. hageni* [Troughton, 1937](#)). The cranium of *R. steini* (see [Taylor et al.](#)

[1982](#), figure 23 and [Flannery 1995a](#), Plate 34) has less robust zygomatic plate, a wider, parallel-sided mesopterygoid fossa with a square rather than rounded anterior margin, and a narrower interorbital region (4.9–7.2 mm across all subspecies).

The rats of Gag Island, described as *R. nikenii*, are even smaller (maximum recorded mass 175 g, maximum recorded pes length 36.5 mm), and have a tail that approaches head + body length ([Maryanto et al. 2010](#)). Based on our examination of the published images, the cranium closely resembles that of *R. steini*.

*Rattus sanila* has larger molars (length of M1 = 4.3–4.8 mm;  $n = 3$ ; width of M1 = 2.6–2.7 mm;  $n = 3$ ) than *R. detentus* and a more complex molar morphology that features an anterior cingular ridge on M1s, prominent posterior cingula on M1–2s, larger cusp t3 on M2–3s and more prominent posterior longitudinal ridges on cusps t1 and t4 of M1s and cusp t4 of M2s ([Fig. 7](#)). The upper and lower incisors of *R. sanila* are less robust than those of *R. detentus*. No further comparisons with *R. sanila* are possible because it is known only from dentaries, partial maxillae, and isolated teeth.

Bivariate plots of posterior rostral width against condylo-basal length ([Fig. 8A](#)) show that the condition in *R. detentus* is consistent with observed intra- and interspecific allometry among other New Guinean *Rattus*. However, an equivalent plot for anterior rostral width ([Fig. 8B](#)) shows that *R. praetor* and

**Table 1.**—External, cranial, and tooth measurements (in mm) of 2 of the modern specimens of *Rattus detentus* (holotype PNGMAG 274363 and paratype KU 163723) and selected related species (means in mm).

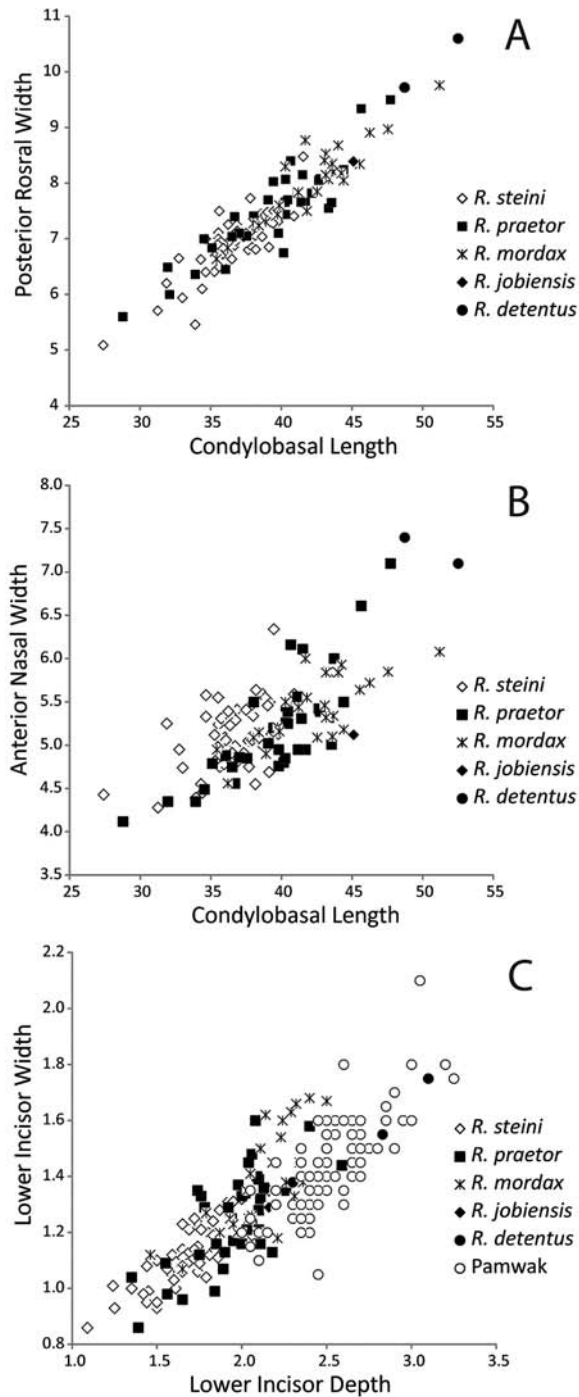
| Measurements                     | PNGMAG 274363 | KU 163723 <sup>a</sup> | <i>R. jobiensis</i>  | <i>R. leucopus</i>      | <i>R. mordax</i>       | <i>R. praetor</i>       |
|----------------------------------|---------------|------------------------|----------------------|-------------------------|------------------------|-------------------------|
| Head and body length             | 260           | —                      | —                    | —                       | —                      | —                       |
| Tail length                      | 150           | —                      | 190 ( <i>n</i> = 2)  | 157.7 ( <i>n</i> = 111) | 152.2 ( <i>n</i> = 60) | 144.4 ( <i>n</i> = 113) |
| Length of hind foot (s.u.)       | 43.2          | —                      | 45.8 ( <i>n</i> = 2) | 37.0 ( <i>n</i> = 128)  | 36.2 ( <i>n</i> = 53)  | 35.2 ( <i>n</i> = 114)  |
| Length of ear                    | 23.4          | —                      | 22.8 ( <i>n</i> = 2) | 21 ( <i>n</i> = 1)      | 19.5 ( <i>n</i> = 17)  | 19.5 ( <i>n</i> = 60)   |
| Condylbasal length               | 52.0          | 48.72                  | —                    | —                       | —                      | —                       |
| Zygomatic breadth                | 27.35         | 24.57                  | —                    | —                       | —                      | —                       |
| Lambdoidal breadth               | 19.55         | 19.93                  | —                    | —                       | —                      | —                       |
| Occipitonasal length             | 53.45         | 49.99                  | —                    | —                       | —                      | —                       |
| Length of rostrum                | 7.3           | 8.46                   | —                    | —                       | —                      | —                       |
| Breadth of rostrum               | 10.85         | 9.72                   | —                    | —                       | —                      | —                       |
| Width of zygomatic plate         | 4.9           | 5.58                   | —                    | —                       | —                      | —                       |
| Interorbital width               | 8.2           | 8.08                   | —                    | —                       | —                      | —                       |
| Nasal length                     | 20.55         | 18.99                  | —                    | —                       | —                      | —                       |
| Width across nasals              | 6.6           | 6.9                    | —                    | —                       | —                      | —                       |
| Length of bony palate            | 10.55         | 10.71                  | —                    | —                       | —                      | —                       |
| Length of upper diastema         | 15.5          | 12.84                  | —                    | —                       | —                      | —                       |
| Length of incisive foramen       | 9.65          | 8.22                   | —                    | —                       | —                      | —                       |
| Width across incisive foramina   | 3.85          | 3.25                   | —                    | —                       | —                      | —                       |
| Postpalatal length               | 7.45          | 8.81                   | —                    | —                       | —                      | —                       |
| Mesopterygoid fossa width        | 3.55          | 2.88                   | —                    | —                       | —                      | —                       |
| Length of auditory bulla         | 7.35          | 6.94                   | —                    | —                       | —                      | —                       |
| Crown length of upper tooththrow | 8.4           | 8.71                   | —                    | —                       | —                      | —                       |
| M1–3 alveolar length             | 8.6           | 9.44                   | —                    | —                       | —                      | —                       |
| Width across M1–M1 (outside)     | 5.66          | 9.2                    | —                    | —                       | —                      | —                       |
| Upper incisor width              | 2.0           | 1.7                    | —                    | —                       | —                      | —                       |
| Upper incisor depth              | 3.3           | 2.68                   | —                    | —                       | —                      | —                       |
| Width of M1                      | 2.55          | 2.57                   | —                    | —                       | —                      | —                       |
| Width of M2                      | 1.78          | 1.94                   | —                    | —                       | —                      | —                       |
| Width of M3                      | 1.95          | 1.95                   | —                    | —                       | —                      | —                       |
| m1–3 crown length                | 8.3           | 8.67                   | —                    | —                       | —                      | —                       |
| Width of m1                      | 2.15          | 2.21                   | —                    | —                       | —                      | —                       |
| Width of m2                      | 2.4           | 2.48                   | —                    | —                       | —                      | —                       |
| Width of m3                      | 2.25          | 2.2                    | —                    | —                       | —                      | —                       |
| Lower incisor width              | 1.75          | 1.38                   | —                    | —                       | —                      | —                       |
| Lower incisor depth              | 3.1           | 2.3                    | —                    | —                       | —                      | —                       |

<sup>a</sup> Because KU 163723 had the remaining soft tissues removed from it by its being buried in the ground for a period, the elements of the skull posterior to the frontals and the palatines became dissociated before and during the final cleaning. Some measurements for KU 163723 may deviate slightly from the original because some separated bones have been glued back in place but we are confident that such deviation is extremely minimal, as adjacent cranial bones fit together properly.

*R. detentus* alone have an unusual degree of anterior rostral inflation. The unusual deepening of the lower incisors in *R. detentus*, compared with the conditions in other large Melanesian *Rattus*, including *R. sanila*, is also evident from a bivariate plot (Fig. 8C). The upper incisors are similarly distinguished by their proportional depth in *R. detentus*.

**Molecular genetics.**—Concatenation of the 3 nuclear loci and the mitochondrial *CR* resulted in an alignment of 4,166 bp in length for 73 specimens comprising 24 species/subspecies. The topology of both the Bayesian and maximum likelihood trees concurred in showing the following well-supported

species groups (Fig. 9): Clade E: *R. niobe* (Thomas, 1906) + *R. mordax*; Clade F: other New Guinean *Rattus*; Clade G: *R. leucopus*; Clade H: *R. fuscipes* (Waterhouse, 1839); and Clade I: other Australian *Rattus*. *R. detentus* is placed outside of each of these well-supported clades and thus appears to be a phylogenetically isolated lineage in its own right. However, its placement on the tree as the immediate sister to all endemic New Guinean *Rattus* does not have robust support (Fig. 9). The genetic evidence thus provides strong independent support for our conclusion that the Admiralties Rat represents a very distinct species within the Australo–Papuan *Rattus* radiation.



**Fig. 8.**—Bivariate plots of selected cranial and dental dimensions in *Rattus detentus* and a range of other Melanesian *Rattus* species. A) Plot of posterior rostral width against condylbasal length. B) Plot of anterior rostral width against condylbasal length. C) Plot of lower incisor width against lower incisor depth.

The majority (72%) of parsimony informative (pi) sites (300 pi sites) were derived from the mitochondrial *CR*, compared to 28% in total among the 3 nuclear genes (*FGB*: 31 pi sites; *DHFR*: 48 pi sites; *ATP5A1*: 36 pi sites). Trees generated from the mitochondrial *CR* data only (Supporting Information S4) and from a concatenation of the 3 nuclear genes only (Supporting Information S5) differ from the tree generated

from the combined data in the following ways: nodes B and C are absent from the mitochondrial *CR* tree, whereas in the nuclear gene tree nodes B, C, E, H, I, J, and K are all absent. As might be expected from the large difference in pi sites, the mitochondrial *CR* data clearly supply much of the topology of the combined dataset tree. Nevertheless, *R. detentus* is identified as a highly divergent lineage from all other Australo-Papuan *Rattus* groups in each of the separate mitochondrial *CR* and concatenated nuclear trees.

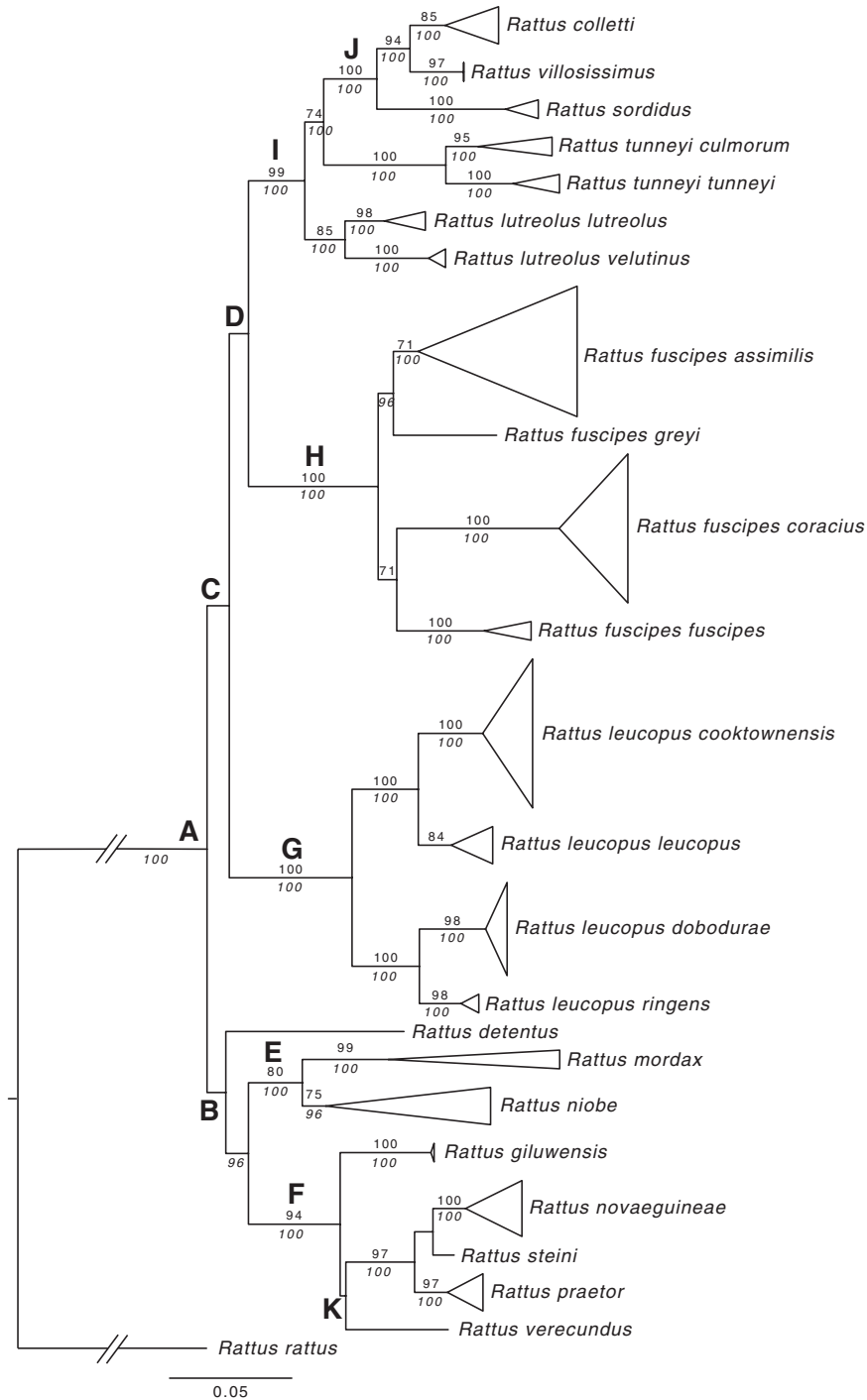
Additional mitochondrial *CR* sequences for Australo-Papuan *Rattus* are available from the studies of Rowe et al. (2011) and Robins et al. (2014). Inclusion of these sequences produces an alignment of 104 Australo-Papuan *Rattus* individuals representing 23 putative species and subspecies. As noted previously by Robins et al. (2014), phylogenetic analysis of this dataset (Supporting Information S6) identifies a number of potential cryptic species among each of the 2 montane New Guinean “species” *R. niobe* and *R. verecundus* (Thomas, 1904b). However, none of the additional *CR* lineages shows special affinity to *R. detentus*, which maintains its isolated position within the Australo-Papuan *Rattus* radiation.

**Ecology and other notes.**—In 2012, the vegetation around Kawaliap Village, in the immediate vicinity of the collection locality, was a mosaic of *Metroxylon* (sago) palms (Arecaceae), mixed tapioca (*Manihot esculenta*, Euphorbiaceae) and vegetable gardens, and secondary regrowth scrub (Fig. 1E).

The holotype was caught in a snare set by local hunters targeting bandicoots (*Echymipera* cf. *kalubu*) and rats. Both are consumed. Unbaited snares were set along visible paths made by small mammals through undergrowth and often exiting near small streams. Other evidence of rat activity in this habitat included conspicuous incisor gnawing marks on fallen nuts of *Canarium indicum* (Burseraceae)—a semidomesticated Melanesian tree species that is widely cultivated and commonly consumed by rodents (Fig. 1B).

The local language name provided to Weijola at Kawaliap Village for this rat was *Wadah* (pronunciation “Warah”). Ann Williams (in litt.) informed us that inhabitants of Tulu No. 1 identified the remains of the 2 paratypes as examples of *Musuru*; the same name is listed by Flannery (1995b; as *Musirou*) as an indigenous name for *M. matambuai*. Williams also recorded the local names *Sopol* and *Pitii* as possibly referring to rats. Manus Island supports more than 15 indigenous languages (Lynch et al. 2002) and some diversity in local names is to be expected.

In October 2014, Aplin spent 2 weeks on Manus Island as a participant in a Wildlife Conservation Society (WCS) survey (Aplin et al. 2015). Two sites were surveyed—the upper slopes of Mt. Sabomu (2°11′36″S, 146°50′00″E; the 2nd highest peak on Manus Island) at elevations ranging from 300 to 570 m, and Yeri River (2°0′06″S, 146°48′50″E) at elevations of 22–84 m. These sites were selected because they presented a mosaic of disturbed to relatively intact forest habitats but at contrasting elevations. The Yeri River locality is close to the paratype locality of Tulu No. 1 and presented comparable habitat. Both sites were sampled using a combination of trapping, camera trapping, spotlighting, and active searching for tracks and signs. Survey effort at Mt. Sabomu was 178 snap-trap nights and 44



**Fig. 9.**—Collapsed maximum likelihood tree from a concatenated analysis of Australo-Papuan *Rattus* and selected outgroups, based on the mitochondrial control region and 3 nuclear genes—*ATP5A1*, *DHFR*, and *FGB*. Nodal support is indicated by maximum likelihood bootstrap proportions above branches and Bayesian posterior probabilities values below branches. Nodes discussed in the text are labeled A–K.

camera-trap nights; and at Yeri River, 204 snaps-trap nights and 64 camera-trap nights.

Trapping produced a few individuals of *R. exulans* at each of Mt. Sabomu [1 in forest and 2 in kunai (*Imperata cylindrical*; Poaceae) grassland] and Yeri River (2 in forest and 6 in gardens) but no individuals of *R. detentus*. Camera trapping also produced images of *R. exulans* at both sites, including 1 individual in forest on Mt. Sabomu that appeared to be

occupying a burrow complex with multiple entrances, spread over an area of ca. 10 m<sup>2</sup>. Elsewhere in New Guinea, *R. exulans* typically constructs leaf or grass nests above ground but it has on occasion been found in burrows (Aplin et al. 2003), most likely excavated by other species. *Echymipera* cf. *kalubu* bandicoots do not excavate burrows but construct leaf nests in crevices or shallow depressions (Andersen et al. 1988). We suspect that the burrow complex on Mt. Sabomu

was excavated by *R. detentus* but confirmation in the form of a capture or image is required. At both sites, intensive but unsuccessful searches for other traces of a relatively large rat, such as footprints, diggings, or chewed nuts or woody endocarps, were made along stream margins, under overhanging rocks, and at the bases of buttressed trees. Elsewhere in Melanesia, large *Rattus* species are usually among the easiest of terrestrial mammals to trap and otherwise detect from footprints in areas of damp soil, and from feeding debris and feces in sheltered areas among rocks and inside logs. The lack of such signs at both survey sites suggests that *R. detentus* was either absent or present only in very low numbers during the survey period.

## DISCUSSION

*The rodent fauna of the Admiralty Group.*—With formal description of *R. detentus*, the inventory of the extant native rodents for Manus Island is most likely complete. While it is true that many parts of the island remain unsurveyed, the absence of additional taxa in the large sample of rodents from the Pamwak archaeological site makes it unlikely that any additional rodent species will be found alive on Manus Island. Even so, it is worth noting that the Pamwak mammal record spans only the last 9,000 years of a human occupation history that probably extends back 40,000 years or more, given the regional evidence of remote seafaring by early Melanesian human populations (Leavesley and Chappell 2004). In light of this still undocumented early history of human–animal interactions in the Admiralty Group, we leave open the possibility that the original rodent fauna of Manus may have included a wider range of endemic taxa, including some that fell victim to the usual threats associated with human arrival on oceanic islands.

The mammal faunas of the other islands of the Admiralty Group remain largely unstudied, and most islands are probably too small to support any native rodents. However, further survey effort is needed to determine whether any of these smaller islands support populations of either of the 2 Admiralty Island endemic rodents or any other species of rodents. The St. Matthias Group also remains poorly surveyed for mammals. However, a recent visit by Aplin as part of a WCS team failed to locate any native rodent species on Mussau Island, the largest island of the group (Aplin et al. 2015).

*Phyletic patterning in Melanesian Rattus.*—*Rattus detentus* appears to represent a deeply divergent phyletic lineage among Australo–Papuan *Rattus*. Rowe et al. (2011) estimated the initial divergence of this clade at 1.05 Ma (CI 0.85–1.28 Ma). Although we did not subject the expanded taxon set to a new divergence date estimation, the fact that inclusion of *R. detentus* in the phylogeny did not cause any other shifts in topology suggests that this molecular divergence estimate will remain largely intact. Accordingly, we regard the lineage leading to *R. detentus* to have diverged from all other sampled lineages around the transition from the Early to Middle Pleistocene. Whether or not this also represents the time of dispersal of *Rattus* to Manus Island is less certain, as consideration might be given to the alternative

scenario that divergence of this lineage was underway prior to its dispersal to the island. The latter scenario might be particularly viable if the ancestor of *R. detentus* came from the main island of New Guinea, rather than entering the Admiralties as part of an initial wave of dispersal of *Rattus* into the Melanesian region from the west. These alternatives are testable through the discovery of fossil rodents of sufficient antiquity either in the Admiralties or on the main island of New Guinea.

*Vertebrate biogeography of the Admiralty Group.*—Estimates of 8–10 million years before present (ybp) for initial subaerial emergence of Manus (Allison 1996) should probably be revised down to the early Pliocene (approximately 4–5 million ybp) in light of new dating of regional tectonic events (see Davies 2012 and references therein). Irrespective of the initial emergence time, deep water basins surrounded the Admiralties throughout the Pliocene to Recent, hence they remained isolated from other land masses through the sea-level fluctuations associated with Quaternary glacial cycles (Vorisi 2000). Thus, by whatever means, the fauna of the Admiralties must have arrived through overwater dispersal.

The Admiralties are one of a series of island groups that are located north and northeast of New Guinea and which are collectively known as the Northern Melanesian Islands. With the exception of the land-bridge island of Yapen, all of these islands are oceanic in origin.

Despite widely scattered positions, the northern Melanesian islands share striking similarities in their terrestrial vertebrate faunas. Endemic marsupial taxa include 2 species of *Spilocuscus*—*S. wilsoni* on Biak/Supiori and *S. kraemeri* in the Admiralties, and possibly 1 *Petaurus* (*P. biacensis*, see Flannery 1995b) on Biak/Supiori. Endemic subspecies (*Phalanger orientalis breviceps* and *Echymipera kalubu philipi*) have been described from New Britain and Biak/Supiori, respectively, but their taxonomic status requires confirmation.

Each island group also hosts endemic murids. The Admiralties have 2 species—*M. matambuai* and *R. detentus*. Biak Island in the Schouten Group has 2 endemic giant rats (*Uromys boeadii* Groves and Flannery, 1994, and *U. emmae* Groves and Flannery, 1994), a large *Rattus* (*R. jobiensis*), and taxonomically undifferentiated populations of a mosaic-tailed rat [*Paramelomys platyops* (Thomas, 1906)] and the widespread Australo–Papuan Water Rat (*Hydromys chrysogaster* É. Geoffroy St.-Hilaire, 1804). The same species of *Hydromys*, *Paramelomys*, and *Rattus* are present on Supiori. New Britain has an endemic water rat (*H. neobritannicus* Tate and Archbold, 1935), the highly distinctive *U. neobritannicus*, the widely distributed *M. rufescens* (Alston, 1877) and an undescribed endemic *Melomys* (Aplin and Opiang 2011), a potentially endemic *Pogonomys* tree mouse, and 2 other, undescribed, endemic species, each of an endemic genus (Aplin and Opiang 2011). New Britain also supports a *Rattus* species at least superficially similar to *R. praetor* but warranting genetic examination (Flannery 1995b; Aplin and Opiang 2011). By contrast, the murid fauna of New Ireland is depauperate, with only 2 taxa—the seemingly widespread *M. rufescens* and the endemic and apparently extinct *R. sanila*.

Manus and New Ireland stand out in lacking larger murines of the genera *Hydromys* and *Uromys*. The only clearly indigenous terrestrial mammals on these islands are the closely related species pair *M. matambuai* and *M. rufescens* (Flannery et al. 1994) and a large endemic *Rattus*. This paucity is surprising considering their size and may reflect their relative isolation (Manus) or the timing of subaerial emergence [New Ireland became emergent during the Pleistocene (see Davies 2012 and references therein)].

Levels of endemism in other groups of animals on these islands are also instructive. The herpetofauna of the Admiralties is still incompletely described, but recent surveys have documented 8 endemic species of ceratobatrachid frogs of the genus *Cornufer*, along with 2 widespread hylid frogs and 1 widespread ranid frog (Richards and Aplin 2015)—the invasive bufonid *Rhinella marina* also occurs there. The agamid *Hypsilurus schoedei*, described from Rambutyo Island in the Admiralties, is now also recorded from Mussau Island in the St. Matthias Group (Richards and Aplin 2015). The monitor lizard of the Admiralties, *Varanus cf. indicus*, differs notably from populations of northern New Guinea, with molecular studies placing it as one of the most “basal” lineages among mangrove monitors (V. Weijola, pers. obs.). Scincids and gekkonids of the Admiralties are more diverse, with 22 recorded species across the 2 families. However, only 1 gecko and 4 skinks are endemic to the Admiralties; the majority are so-called “tramp species” that seem adept at long water crossings either through natural means or accidental human transport. The situation vis-à-vis endemic status for the very few species of snakes is uncertain. The large air-breathing land snail *Papustyla pulcherrima* (Camaenidae) is a significant invertebrate endemic.

Significant endemism is seen in bats (Aplin et al. 2015; Armstrong et al. 2015) and birds (Mayr and Diamond 2001; Dutson 2011) in the northern Melanesian islands. Many species of bats are shared between Manus and the St. Matthias Group but 1 or more species are likely to be endemic to the Admiralties (Aplin et al. 2015).

Some of the nonflying species may have made the 1st part of their journey to the Admiralties via the Sepik River, which currently debouches on the north coast of New Guinea some 300 km to the southwest of Manus. However, in the Middle Pleistocene, the Sepik Basin was a shallow marine environment (Chappell 2005), and the river mouth must have been more distant from Manus. Nevertheless, it may have still been influential. While at sea between New Guinea and the Admiralties in the late 1980s, Flannery observed rafts of vegetation, some with trees still in growth position, far from land. Some rafts were large enough to provide temporary habitat for small rodents, lizards, frogs, and terrestrial snails. At various times through the Pliocene and Pleistocene, similar rafts may have been carried as far north as the Admiralties. For a more detailed account, see Flannery (2011).

The extent to which deliberate human introductions have shaped the insular distributions remains imperfectly known. New Ireland has the longest archaeological record in the region and many of the key sites contain vertebrate faunal remains (Flannery and White 1991; Leavesley and Chappell 2004). In

addition to pigs, dogs, and 2 semicommercial rats (*R. exulans* and *R. praetor*), all of which were introduced within the past 4,000 years, marsupials were also carried to New Ireland. The phalangerid *Phalanger orientalis breviceps* was introduced to the island in the early Holocene, and the macropodid *Thylogale browni* in the mid-Holocene (Flannery and White 1991). New Britain still lacks an equivalent archaeological faunal record and the status of its nonendemic marsupials and rodents is unresolved (Aplin and Opiang 2011). The same uncertainty applies also to Manus—the Pamwak site documents the presence of the bandicoot and cuscus by the early Holocene but it does not rule out their introduction at an earlier date. In spite of these uncertainties, the discovery of *R. detentus*, along with the summary of endemic insular forms, provided here, demonstrates that nonanthropogenic overwater dispersal in the northern Melanesian islands has been less difficult and more extensive than might be and has been imagined.

*Conservation.*—*Rattus detentus* is recorded with certainty from only 2 modern localities and 1 prehistoric rock shelter site on Manus. Although these records span a narrow elevational range from near sea level to 200 m, other components of the forest biota of Manus show little evidence of elevational zonation (see various chapters in Whitmore 2015). Thus, it is likely that *R. detentus* occupies or has occupied the full elevational range on Manus, as suggested also by the tentative attribution to this species of a burrow complex near the summit of Mt. Sabomu, reported herein. How much of its potential range on Manus is occupied and whether it occurs on some of the other Admiralty Islands, especially Los Negros, is unknown.

By the mid-1990s, 80% of forest on Manus was still largely intact, whereas many of the smaller adjacent islands had been converted into coconut plantations (Rannells 1995). Today, most of the lowlands on Manus are a mosaic of plantations and/or subsistence gardens and secondary forest, and logging is carried out in many areas. Intact lowland forest is confined to small patches such as those along the Yeri River, visited by Aplin in 2014. Away from the coast, steeper terrain generally supports more or less intact forest which is visited by people in search of game (chiefly the cuscus and wild pigs) and other forest products.

Local residents who were shown photographs of the holotype of *R. detentus* by Weijola claimed that the species is widespread on Manus and also occurs on adjacent Los Negros. The species does appear to possess some tolerance of habitat disturbance and human predation, as the 2 modern capture records both came from regrowth forest and gardens, and derive from the efforts of hunters. However, Aplin's recent failure to locate the species at 2 sites on Manus, with both sites sampled across a gradient of disturbance, suggests that *R. detentus* is not universally common. If it is present at the Mt. Sabomu and Yeri River sites, then it appears to survive only at low population densities. Thus, it would likely be erroneous to treat the species as secure across its range, and we urge further survey work to locate surviving populations, so as to enable study of their population dynamics, and to identify major threats to their continued existence.

Three of the most likely threats to the survival of *R. detentus* are habitat conversion and disturbance, feral cats (*Felis catus*), and the spread of introduced rodents.

Cats were introduced to Manus sometime in the 19th or 20th centuries and the occurrence of feral populations is reported from several areas by local residents. However, the WCS survey in 2014 failed to detect any sign of feral cats at its 2 survey sites (Aplin et al. 2015) and this suggests that either feral cats are not ubiquitous or that population densities are sometimes very low.

Two introduced rodents, *R. exulans* and *R. rattus*, are present on Manus (Taylor et al. 1982; Aplin et al. 2015). *R. exulans* may have arrived in prehistoric times, although there is no apparent evidence for this from the Pamwak site. *R. rattus* most likely arrived in colonial times or later. *R. exulans* is clearly widespread and occurs across a variety of habitats, including the remote and relatively undisturbed forest near the summit of Mt. Sabomu (Aplin et al. 2015). However, while it may be common in certain habitats, including villages, gardens, and patches of kunai grassland, it appears not to be universally abundant in forest. Given the rarity of introduced rats in the forests, inter-specific competition seems unlikely as a sufficient explanation for the apparent rarity of *R. detentus* there.

Elsewhere, the introduction of *R. rattus* has been implicated in the extinction of insular native rats. *R. macleari* (Thomas, 1887) and *R. nativitatis* (Thomas, 1889), 2 endemics of Christmas Island, became extinct around 1903 (Flannery 1990)—the proximate cause may have been a trypanosome carried by *R. rattus* which reached the island at around this time (Wyatt et al. 2008). On Manus, *R. rattus* does not yet appear to be widely invasive into rural regions and/or natural habitats. Whether the Manus population carries a pathogenic trypanosome is unknown.

A regional example of insular decline or possible extinction involves *R. sanila*, thus far known only from Pleistocene to Late Holocene rock shelter deposits on New Ireland. White et al. (1991, 2000) postulated that this species was replaced ecologically by *R. praetor*, a New Guinean species that reached the island within the last few millennia, probably with human assistance. Whether or not this view is correct, there are grounds for concern that inadvertent introduction to Manus Island of *R. praetor*, if this has not already occurred, might contribute to the decline of *R. detentus*.

#### ACKNOWLEDGMENTS

The National Research Institute (NRI) and the Department of Environment and Conservation (DEC) provided permits for our research in Papua New Guinea. Conservation International provided funding for the initial survey studies on Manus, which were undertaken by A. L. Mack and A. Williams. Weijola's fieldwork was funded in part by grants from Nordenskiöld-Samfundet, Svenska Kulturfonden, Svensk-Österbottniska Samfundet, Turun Yliopistosäätiö, and the Jenny and Antti Wihuri Foundation; and he is most grateful for the assistance, companionship, and hospitality provided by the people of Kawaliap (the Minei, Muteo, and Posakei families in particular) as well as assistance from the local government of Manus. I. Bigilale and B. Iova at the National Museum & Art Gallery, Port Moresby, and B. Wilmot (DEC) aided the export of the

holotype to Australia for examination. Aplin's fieldwork on Manus was facilitated by the Wildlife Conservation Society PNG Program and supported by funding from the Critical Partnership Ecosystem Fund; special thanks to N. Whitmore and R. Cuthbert of WCS and to the landowner communities of Peri/Mt. Sabomu and Yeri River. We thank A. Mack, A. Williams, and D. Wright for making specimens available for study, and J. A. Esselstyn, P.-H. Fabre, and K. C. Rowe for critical reviews of earlier drafts of the manuscript. J. Robins, G. Shea, J. M. Taylor, A. Williams, and C. E. Williams provided us with critical information, as did G. G. Musser, who also selected specimens to be sent to us on loan from the AMNH. S. Ingleby (AMS); E. Westwig and R. S. Voss (AMNH); L. M. Garetano, K. Imada, and C. Kishinami (BPBM); L. R. Heaney and the late W. T. Stanley (FMNH); J. Dines (LACM); L. A. Halverson and P. M. Holahan (UWZM); K. M. Helgen (USNM); and D. P. Lunde (AMNH and then USNM) made critical specimens housed in their respective museums freely available to us and/or sent them to us on loan. The molecular genetic work was funded from an ARC Discovery grant (DP0988863) to SCD and KPA. We thank A. Frost, K. Kaunisto, and V. Rinne for their outstanding assistance and expertise with the illustrations.

#### SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online ([j mammal.oxfordjournals.org](http://j mammal.oxfordjournals.org)). The materials consist of data provided by the authors that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the authors.

**Supporting Information S1.**—List of specimens analyzed for the morphological comparisons. Specimens are arranged by species, then locality information (generally as given in information currently associated with specimens). Archaeological material listed by site. Museum catalog numbers follow the institutional acronyms given in “Materials and Methods.”

**Supporting Information S2.**—Taxon, catalog number, collection depository, locality where collected, and GenBank accession numbers for sequences used in phylogenetic analyses.

**Supporting Information S3.**—Measurements of the lower and upper dentitions, mandibular ramus, and maxilla of specimens of *Rattus detentus* from the Pamwak archaeological site.

**Supporting Information S4.**—Collapsed Bayesian tree of Australo-Papuan *Rattus*, based on the mitochondrial *control region* and using *Rattus rattus* as the outgroup. Nodal support is indicated by maximum likelihood bootstrap above branches and Bayesian posterior probabilities values below branches. Nodes are labeled A–K as per Fig. 9. Data associated with specimens of *R. fuscipes assimilis* are from Rowe et al. (2011) and Robins et al. (2014), from whence the numbers associated with the specimens were obtained.

**Supporting Information S5.**—Collapsed Bayesian tree of Australo-Papuan *Rattus*, based on concatenated sequences of 3 nuclear genes—*ATP5A1*, *DHFR*, and *FGB*—and using *R. rattus*

as the outgroup. Nodal support is indicated by maximum likelihood (ML) bootstrap above branches and Bayesian posterior probabilities values below branches. Nodes are labeled A–K as per Fig. 9. The stars represent branches not present in the ML tree (i.e., these branches collapse to a polytomy). Data are from Rowe et al. (2011) and Robins et al. (2014), from whence the numbers associated with the specimens were obtained.

**Supporting Information S6.**—Maximum likelihood tree of relationships among mitochondrial *CR* sequences from a more extensive sampling of Australo–Papuan *Rattus*, drawn from combining data from this study with that of Rowe et al. (2011) and Robins et al. (2014). Numbers associated with the specimens include GenBank number and institution acronym. *Sundamys muelleri* (Jentink, 1879) and selected species of *Rattus* are used as outgroups.

### LITERATURE CITED

- ALLISON, A. 1996. Zoogeography of amphibians and reptiles of New Guinea and the Pacific region. Pp. 407–436 in *The origin and evolution of Pacific island biotas, New Guinea to eastern Polynesia: patterns and processes* (A. Keast and S. E. Miller, eds.). SBP Academic Publishing, Amsterdam, The Netherlands.
- ALSTON, E. R. 1877. On the rodents and marsupials collected by Rev. G. Brown in Duke-of-York Island, New Britain, and New Ireland. *Proceedings of the Zoological Society of London* 1877:123–127.
- ANDERSEN, T. J. C., A. J. BERRY, J. N. AMOS, AND J. M. COOK. 1988. Spool-and-line tracking of the New Guinea spiny bandicoot *Echymipera kalubu* (Marsupialia, Peroryctidae). *Journal of Mammalogy* 69:114–120.
- APLIN, K. P., P. R. BROWN, J. JACOB, C. KREBS, AND G. R. SINGLETON. 2003. Field methods for rodent studies in Asia and the Pacific. ACIAR Monograph No. 100. Australian Centre for International Agricultural Research, Canberra, Australia.
- APLIN, K. P., J. NOVERA, AND K. N. ARMSTRONG. 2015. Mammals of Manus and Mussau Islands. Pp. 50–68 in *A rapid biodiversity survey of Papua New Guinea's Manus and Mussau Islands* (N. Whitmore, ed.). Wildlife Conservation Society Papua New Guinea Program, Goroka, Papua New Guinea.
- APLIN, K. P., AND M. OPIANG. 2011. Mammals of the Nakanai Plateau, West New Britain, Papua New Guinea. Pp. 85–103 in *Rapid biological assessments of the Nakanai Mountains and the upper Strickland Basin: surveying the biodiversity of Papua New Guinea's sublime karst environments*. RAP Bulletin of Biological Assessment 60 (S. J. Richards and B. G. Gamui, eds.). Conservation International, Arlington, Virginia.
- APLIN, K. P., ET AL. 2011. Multiple geographic origins of commensalism and complex dispersal history of black rats. *PLoS One* 6:e26357.
- ARMSTRONG, K. N., J. NOVERA, AND K. P. APLIN. 2015. Chapter 7. Acoustic survey of the echolocating bats of Manus and Mussau Islands. Pp. 69–85 in *A rapid biodiversity survey of Papua New Guinea's Manus and Mussau Islands* (N. Whitmore, ed.). Wildlife Conservation Society Papua New Guinea Program, Goroka, Papua New Guinea.
- BERKENHOUT, J. 1769. *Outlines of the natural history of Great Britain and Ireland: containing a systematic arrangement and concise description of all the animals, vegetables, and fossiles which have hitherto been discovered in these kingdoms, Vol. I. Comprehending the animal kingdom*. Elmsly, London, United Kingdom.
- CHAPPELL, J. 2005. Geographic changes of coastal lowlands in the Papuan past. Pp. 525–539 in *Papuan pasts: cultural, linguistic and biological histories of Papuan-speaking peoples* (A. Pawley, R. Attenborough, J. Golson, and R. Hide, eds.). Pacific Linguistics, RSPAS, Australian National University, Canberra, Australia.
- DAVIES, H. L. 2012. The geology of New Guinea – the cordilleran margin of the Australian continent. *Episodes* 35:87–102.
- DUTSON, G. 2011. *Birds of Melanesia: Bismarcks, Solomons, Vanuatu, and New Caledonia*. Princeton University Press, Princeton, New Jersey.
- FABRE, P. H., ET AL. 2013. A new genus of rodent from Wallacea (Rodentia: Muridae: Murinae: Rattini) and its implication for biogeography and Indo-Pacific Rattini systematics. *Zoological Journal of the Linnean Society* 169:408–447.
- FISCHER, G. 1803. *Das Nationalmuseum der Naturgeschichte zu Paris. Von ersten Ursprunge bis zu seinem jetzigen Glanze*. Friedrich Esslinger. Schilderung der naturhistorischen Sammlungen mit Kupfern, Frankfurt am Main, Federal Republic of Germany. Vol. 2.
- FLANNERY, T. 2011. *Among the islands*. HarperCollins Publishers Ltd., Toronto, Ontario, Canada.
- FLANNERY, T., D. COLGAN, AND J. TRIMBLE. 1994. A new species of *Melomys* from Manus Island, Papua New Guinea, with notes on the systematics of the *M. rufescens* complex (Muridae: Rodentia). *Proceedings of the Linnean Society of New South Wales* 114:29–43.
- FLANNERY, T. F. 1990. The rats of Christmas past. *Australian Natural History* 23:394–400.
- FLANNERY, T. F. 1995a. *Mammals of New Guinea*. Reed Books, Chatswood, New South Wales, Australia.
- FLANNERY, T. F. 1995b. *Mammals of the south-west Pacific & Moluccan Islands*. Reed Books, Chatswood, New South Wales, Australia.
- FLANNERY, T. F., AND J. P. WHITE. 1991. Animal translocation (zoogeography of New Ireland mammals). *National Geographic Research and Exploration* 7:96–113.
- FREDERICKSEN, C., M. SPRIGGS, AND W. AMBROSE. 1993. Pamwak Rockshelter: a Pleistocene site on Manus Island, Papua New Guinea. Pp. 144–152 in *Sahul in review: Pleistocene archaeology in Australia, New Guinea and Island Melanesia* (M. A. Smith, M. Spriggs, and B. Fankhauser, eds.). *Occasional Papers in Prehistory* 24, Department of Prehistory, Research School of Pacific Studies, The Australian National University, Canberra, Australia.
- GEOFFROY ST.-HILAIRE, É. 1804. Note sur un nouveau genre de mammifères, de l'ordre des rongeurs, sous le nom d'hydromys [sic]. *Bulletin des Sciences, par la Société Philomathique* 3:253–254.
- GOULD, J. 1857 [1858]. On four new species of *Mus* and one of *Haplotis* from Australia. *Proceedings of the Zoological Society of London* 25:241–243.
- GRAY, J. E. 1841. Contributions towards the geographical distribution of the Mammalia of Australia, with notes on some recently discovered species. Pp. 397–414 (Appendix C) in *Journals of two expeditions of discovery in North-West and Western Australia, during the years 1837, 38, and 39* (G. Grey, ed.). T. & W. Boone, London, United Kingdom. Vol. 2.
- GRAY, J. E. 1867. Notes on the variegated or yellow-tailed rats of Australia. *Proceedings of the Zoological Society of London* 1867:597–600.
- GREENE, E. C. 1935. Anatomy of the rat. *Transactions of the American Philosophical Society, New Series* 27:1–370.
- GROVES, C. P., AND T. F. FLANNERY. 1994. A revision of the genus *Uromys* Peters, 1867 (Muridae: Mammalia) with descriptions of two new species. *Records of the Australian Museum* 46:145–169.



- GUINDON, S., F. DELSUC, J.-F. DUFAYARD, AND O. GASCUEL. 2009. Estimating maximum likelihood phylogenies with PhyML. Pp. 113–137 in *Bioinformatics for DNA sequence analysis* (D. D. Posada, ed.). Humana Press, Totowa, New Jersey. No. 537.
- GÜNTHER, A. 1879. List of the mammals, reptiles, and batrachians sent by Mr. Everett from the Philippine Islands. *Proceedings of the Zoological Society of London* 1879:74–79.
- HILL, J. E. 1960. Renaming of *Rattus ruber melanurus* Laurie and Hill, 1954. *Journal of Mammalogy* 41:277.
- HOULDEN, B. A., P. R. ENGLAND, A. C. TAYLOR, W. D. GREVILLE, AND W. B. SHERWIN. 1999. Phylogeographic differentiation in the mitochondrial control region in the koala, *Phascolarctos cinereus* (Goldfuss 1817). *Molecular Ecology* 8:999–1011.
- JENTINK, F. A. 1879. On some hitherto undescribed species of *Mus* in the Leyden Museum. *Notes from the Leyden Museum* 2:13–19.
- JOHNS, R. J. 1993. Biodiversity and conservation of native flora of Papua New Guinea. Pp. 15–75 in *Papua New Guinea conservation needs assessment* (B. M. Beehler, ed.). Biodiversity Support Program, Washington, D.C. Vol. 2.
- LANFEAR, R., B. CALCOTT, S. Y. W. HO, AND S. GUINDON. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 29:1695–1701.
- LAURIE, E. M. O. 1952. Mammals collected by Mr. Shaw Mayer in New Guinea 1932–1949. *Bulletin of the British Museum (Natural History), Zoology Series* 1:269–318.
- LEAVESLEY, M. G., AND J. CHAPPELL. 2004. Buang Merabak: additional early radiocarbon evidence of the colonisation of the Bismarck Archipelago, Papua New Guinea. *Antiquity* 78:301. <http://antiquity.ac.uk/projgall/leavesley/index.html>. Accessed 5 January 2015.
- LINNAEUS, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Holmiae: Laurentii Salvii* 1:1–824.
- LYNCH, J., M. ROSS, AND T. CROWLEY. 2002. *The Oceanic languages*. Curzon Press, Richmond, United Kingdom.
- MARYANTO, I., M. H. SINAGA, A. S. ACHMADI, AND MAHARADATUNKAMSI. 2010. Morphometric variation of *Rattus praetor* (Thomas, 1888) complex from Papua, with the description of new species of *Rattus* from Gag Island. *Treubia* 37:25–48.
- MATISOO-SMITH, E., AND J. H. ROBINS. 2004. Origins and dispersals of Pacific peoples: evidence from mtDNA phylogenies of the Pacific rat. *Proceedings of the National Academy of Sciences* 101:9167–9172.
- MAYR, E., AND J. M. DIAMOND. 2001. *The birds of northern Melanesia*. Harvard University Press, Cambridge, Massachusetts.
- MENZIES, J. I., AND E. DENNIS. 1979. *Handbook of New Guinea rodents*. Wau Ecology Institute Handbooks No. 6, Wau, Papua New Guinea.
- MISONNE, X. 1979. Muridae collected in Irian Jaya, Indonesia. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique Biologie* 51:1–16.
- MUSSER, G. G. 1982. Results of the Archbold Expeditions. No. 108. The definition of *Apomys*, a native rat of the Philippine Islands. *American Museum Novitates* 2746:1–43.
- MUSSER, G. G., AND M. D. CARLETON. 2005. Superfamily Muroidea. Pp. 894–1531 in *Mammal species of the world: a taxonomic and geographic reference* (D. E. Wilson and D. M. Reeder, eds.). 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.
- MUSSER, G. G., AND L. R. HEANEY. 1985. Philippine *Rattus*: a new species from the Sulu Archipelago. *American Museum Novitates* 2818:1–32.
- MUSSER, G. G., AND M. E. HOLDEN. 1991. Sulawesi rodents (Muridae, Murinae) morphological and geographical boundaries of species in the *Rattus hoffmanni* group and a new species from Pulau Peleng. *Bulletin of the American Museum of Natural History* 206:322–413.
- MUSSER, G. G., AND D. P. LUNDE. 2009. Systematic reviews of New Guinea *Coccyzus* and “*Melomys*” *albidens* (Muridae, Murinae) with descriptions of new taxa. *Bulletin of the American Museum of Natural History* 329:1–139.
- PAGÈS, M., G. CORBET, A. ORTH, V. VOLOBOUEV, J. MICHAUX, AND F. CATZEFLIS. 2011. Morphological, chromosomal, and genic differences between sympatric *Rattus rattus* and *Rattus satarae* in South India. *Journal of Mammalogy* 92:659–670.
- PEALE, T. R. 1848. United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U. S. N. Vol. 8. Mammalia and ornithology. C. Sherman, Philadelphia, Pennsylvania.
- PETERS, W., AND G. DORIA. 1881. Enumerazione dei Mammiferi raccolti da O. Beccari, L. M. d'Albertis ed A. A. Bruijn nella Nuova Guinea propriamente detta. *Annali Museo Civico di Storia Naturale di Genova* 16:665–707.
- RANNELLS, J. 1995. PNG: a fact book on modern Papua New Guinea. 2nd ed. Oxford University Press, Oxford, United Kingdom.
- RICHARDS, S. J., AND K. P. APLIN. 2015. Herpetofauna of Manus and Mussau Islands. Pp. 31–37 in *A rapid biodiversity survey of Papua New Guinea's Manus and Mussau Islands* (N. Whitmore, ed.). Wildlife Conservation Society Papua New Guinea Program, Goroka, Papua New Guinea.
- ROBINS, J. H., P. A. MCLENACHAN, M. J. PHILLIPS, B. J. MCCOMISH, E. MATISOO-SMITH, AND H. A. ROSS. 2010. Evolutionary relationships and divergence times among the native rats of Australia. *BMC Evolutionary Biology* 10:375.
- ROBINS, J. H., ET AL. 2014. Phylogenetic species identification in *Rattus* highlights rapid radiation and morphological similarity of New Guinean species. *PLoS One* 9:e98002.
- RONQUIST, F., ET AL. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61:539–542.
- ROWE, K. C., K. P. APLIN, P. R. BAVERSTOCK, AND C. MORITZ. 2011. Recent and rapid speciation with limited morphological disparity in the genus *Rattus*. *Systematic Biology* 60:188–203.
- RÜMMLER, H. 1935. Neue Muriden aus Neuguinea. *Zeitschrift für Säugetierkunde* 10:105–118.
- SODY, H. J. V. 1941. On a collection of rats from the Indo-Malayan and Indo-Australian regions (with descriptions of 43 new genera, species and subspecies). *Treubia* 18:255–325.
- STAMATAKIS, A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics Applications Note* 30:1312–1313.
- TATE, G. H. H. 1949. Results of the Archbold Expeditions. No. 61. A new species of *Rattus* from the Snow Mountains of Netherlands New Guinea. *American Museum Novitates* 1421:1–3.
- TATE, G. H. H. 1951. Results of the Archbold Expeditions. No. 65. The rodents of Australia and New Guinea. *Bulletin of the American Museum of Natural History* 97:183–430.
- TATE, G. H. H., AND R. ARCHBOLD. 1935. Results of the Archbold Expeditions. No. 3. Twelve apparently new forms of Muridae (other than *Rattus*) from the Indo-Australian region. *American Museum Novitates* 803:1–9.
- TAYLOR, J. M., J. H. CALABY, AND H. M. VAN DEUSEN. 1982. A revision of the genus *Rattus* (Rodentia, Muridae) in the New Guinean

- region. *Bulletin of the American Museum of Natural History* 173:177–336.
- TAYLOR, J. M., AND E. HORNER. 1973. Results of the Archbold Expeditions. No 98. Systematics of native Australian *Rattus* (Rodentia, Muridae). *Bulletin of the American Museum of Natural History* 150:1–130.
- THOMAS, O. 1887. Report on a zoological collection made by the officers of H.M.S. 'Flying Fish' at Christmas Island, Indian Ocean. I. Mammalia. *Proceedings of the Zoological Society of London* 1887:511–514.
- THOMAS, O. 1888. Diagnoses of six new mammals from the Solomon Islands. *Annals and Magazine of Natural History, Series 6* 1:155–158.
- THOMAS, O. 1888 [1889]. On the mammals of Christmas Island. *Proceedings of the Zoological Society of London* 1888:532–534.
- THOMAS, O. 1904a. On some mammals from British New Guinea presented to the National Museum by Mr. C. A. W. Monckton, with descriptions of other species from the same region. *Annals and Magazine of Natural History, Series 7* 14:397–403.
- THOMAS, O. 1904b. New species of Pteropus, Mus, and Pogonomys from the Australian region. *Novitates Zoologicae* 11:597–600.
- THOMAS, O. 1904c. On a collection of mammals made by Mr. J. T. Tunney in Arnhem Land, Northern Territory of South Australia. *Novitates Zoologicae* 11:222–229.
- THOMAS, O. 1906. New mammals from the Australian region. *Annals and Magazine of Natural History, Series 7* 17:324–332.
- THOMAS, O. 1914. On mammals from Manus Island Admiralty Group [sic], and Ruk Island, Bismarck Archipelago. *Annals and Magazine of Natural History, Series 8* 13:434–439.
- THOMAS, O. 1920. On small mammals from Ceram. *Annals and Magazine of Natural History, Series 9* 6:422–431.
- THOMAS, O. 1922. New mammals from New Guinea and neighbouring islands. *Annals and Magazine of Natural History, Series 9* 9:261–265.
- THOMAS, O. 1923. The Godman Exploration Fund: list of mammals from north Queensland collected by Mr. T. V. Sherrin. *Annals and Magazine of Natural History, Series 9* 11:170–178.
- THOMAS, O., AND G. DOLLMAN. 1908 [1909]. On mammals from Inkerman, north Queensland, presented to the National Museum by Sir William Ingram, Bt., and the Hon. John Forrest. *Proceedings of the Zoological Society of London* 1908:788–794.
- TROUGHTON, E. L. G. 1936. The mammalian fauna of Bouganville Island, Solomons Group. *Records of the Australian Museum* 19:341–354.
- TROUGHTON, E. L. G. 1937. Descriptions of some New Guinea mammals. *Records of the Australian Museum* 20:117–127.
- TROUGHTON, E. L. G. 1946. Diagnoses of new rats from the New Guinea area. *Records of the Australian Museum* 21:406–410.
- VORIS, H. K. 2000. Maps of Pleistocene sea levels in South East Asia: shorelines, river systems, time durations. *Journal of Biogeography* 27:1153–1167.
- WAITE, E. R. 1898. Observations on Muridae from central Australia. *Proceedings of the Royal Society of Victoria* 10:114–128.
- WATERHOUSE, G. R. 1839. Mammalia. Pp. vii–ix, 49–97, plates 25–32, 34 in *The zoology of the voyage of H.M.S. Beagle, under the command of Captain Fitzroy, R.N., during the years 1832–1836. Fascicle 10* (C. Darwin, ed.). Smith, Elder and Co., London, United Kingdom. Vol. 2.
- WHITE, J. P., G. CLARK, AND S. BEDFORD. 2000. Distribution, present and past, of *Rattus praetor* in the Pacific and its implications. *Pacific Science* 54:105–117.
- WHITE, J. P., T. F. FLANNERY, R. O'BRIEN, R. V. HANCOCK, AND L. PAVLISH. 1991. The Balof Shelters, New Ireland. Pp. 46–58 in *Report of the Lapita Homeland Project* (J. Allen and C. Gosden, eds.). *Occasional Papers in Prehistory* 20, Department of Prehistory, Research School of Pacific Studies, The Australian National University, Canberra, Australia.
- Whitmore, N. (ed.). 2015. A rapid biodiversity survey of Papua New Guinea's Manus and Mussau Islands. *Wildlife Conservation Society Papua New Guinea Program*, Goroka, Papua New Guinea. [www.wcspng.org](http://www.wcspng.org). Accessed 15 January 2016.
- WIKRAMANAYAKE, E., E. DINERSTEIN, AND C. J. LOUCKS, Jr. 2002. Terrestrial ecoregions of the Indo-Pacific: a conservation assessment. *Island Press*, Washington, D.C.
- WILLIAMS, C. 1997. Zooarchaeology of Pamwak site, Manus Island, P.N.G. Unpublished Ph.D. dissertation, Monash University, Victoria, Australia, i–vii–iv + 1–268 (with numerous gaps in pagination).
- WILLIAMS, C. 1999. Faunal composition of Pamwak site, Manus Island, PNG. Pp. 241–249 in *Le Pacifique de 5000 à 2000 avant le présent; suppléments à l'histoire d'une colonisation; actes du colloque Vanuatu, 31 juillet-6 août 1996* (J.-C. Galipaud and I. Lilleyeds, eds.). *Institut de Recherche pour le Développement*, Paris, France.
- WYATT, K. B., ET AL. 2008. Historical mammal extinction of Christmas Island (Indian Ocean) correlates with introduced infectious disease. *PLoS One* 3:e3602.

Submitted 12 October 2015. Accepted 19 January 2016.

Associate Editor was Jacob A. Esselstyn

**SI 1**  
Specimens Examined

List of specimens analyzed for morphological comparisons. Specimens are arranged by species, then locality information (generally as given in information currently associated with specimens). Archaeological material listed by site. Museum catalog numbers follow the institutional acronyms given in Materials and Methods.

*Rattus argentiventer* (Robinson and Kloss, 1916) (3).—Indonesia: Bentiang NW Borneo (109°54'E) [1♂, 1♀, AMS 11917–18]. Portugese Timor; 12 km SW Suai [1 sex ?, AMS 15287]; Betano [1♀, AMS 17813].

*Rattus detentus* (3 Recent + 191 archaeological).—Papua New Guinea: Manus Province; Admiralty Islands, Manus Island, Kawaliap Village, el. 200 m (2°6'40"S, 147°3'40"E) [1♀, AMS 45608—holotype]; Tulu no. 1, el. 34 m (01°57'37"S, 146°50'28"E) [sex ?, KU 163723–24—paratypes]; Pamwak Archaeological Site, SSE of Piterait, 4 km inland from coast, el. 30 m (Fredericksen et al. 1993), 191 unnumbered specimens, some dentaries retaining 3, 2, or 1 molars, but primarily isolated incisors and molars.

*Rattus elaphinus* Sody, 1941 (6).—Indonesia: North Moluccas; Sula Island Group, Manggole Island, Cepalulu Village (1°53'S, 125°50'E) [3♂♂, 1♀, 1 sex ?, AMS 26436, 26609–11, 26964, 26966].

*Rattus exulans* (51).—Papua New Guinea: Aitape, Sepik Div. (3°09'S, 142°21'E) [1♂, 2♀, 1 sex ?, AMS 3721–22, 6215, 6233]; Bismarck Archipelago, Duke of York Island (4°10'S, 152°28'E) [2♂♂, AMS 2364–65]; Bulolo Morobe Division (7°12'S, 146°39'E) [2♂♂, 3♀♀, AMS 6382–

86]; British New Guinea, Fife Bay (10°35'S, 150°00'E) [1♂, 1 sex ?, AMS 2483–84]; Buin District, Bougainville, 10 mi inland (6°50'S, 155°45'E) [2♂♂, 1♀, AMS 6494–96, 2♀♀, AMS 6648–49]; Dobodura North Division (8 46' S, 148 23' E) [7♂♂, 4♀♀, 6918–22, 6962–6966, 6978–6979]; Kiriwina Trobriand group NZ (8°28'S, 151°05'E) [1♂, AMS 1146]; Mt. Hagen District, Sepik Div. (5°54'S, 144°09'E) [2♂♂, 1♀, AMS 6110–6112]; Marshall Bennett Group, Gawa Is. (8°59'S, 151°58'E) [1♀, AMS 6370]; Mt. Lamington District, Northern Div. (8°50'S, 148°08'E) [4♂♂, 4♀♀, 1 sex ?, AMS 4152–4158, 4298–4299, 4688]; New Britain; Aviklo Village Mowehaffen (6°12'S, 149°30'E) [1♂, AMS 5621]; Marshall Bennett Group, Gawa Is. (8°59'S, 151°58'E) [1♀, AMS 6370]; Admiralty Group, Purdy Islands, Bat Is. (2°51'S, 146°14'E) [1♀, ASM 6976]; Indonesia: Dutch New Guinea, Sansapor Vogelkop (0°29'S, 132°05'E) [1♂, 1♀, ASM 6990–6991]; Irian Jaya (Dutch New Guinea), Schouten Island Group, Owi Island (1°15'S, 136°12'E) [2♂♂, 1 sex ?, ASM 6994, 6996–97].

*Rattus feliceus* Thomas, 1920 (2).—Indonesia: Maluku Province; Seram, South Coast, Piliانا Village (3°15'S, 129°30'E) [1♂, 1♀, AMS 30807–808].

*Rattus giluwensis* (24).—Papua New Guinea: Enga Province; Porgera area, Waili Creek [1♀, 23 sex?, AMS 37998, 37998–39116].

*Rattus jobiensis* (5).—Indonesia: Irian Jaya (Dutch New Guinea) Schouten Island Group, Owi Island (1°15'S, 136°12'E) [1♂, 1♀, AMS 6992–93]; Irian Jaya, Supiori Island, vicinity of Kampong Korido (0°50'S, 135°36'E) [1♂, 1♀, AMS 28691–92]; Papua; Japen Island [1♂, AMNH 222435].

*Rattus leucopus* (60).—Indonesia: Irian Jaya, Timika area, Namco Camp, Pt. Freeport Indonesia Company (4°47'S, 136°32'E) [1♀, AMS 31671]; Irian Jaya; Timika area, Forest at New Town Complex (4°47'S, 136°32'E) [1♂, AMS 131672]; I Irian Jaya, Etna Bay vicinity of Exploration Camp [2♀♀, AMS 37370, 32373]; Maluku Province, Aru Islands, near Namara (6°03'S, 134°22'E) [5 sex?, 45592–96]. Papua New Guinea: Imanaturu Mt. Lamington District N Div. of Papua (8°50'S, 148°08'E) [1♂, 1♀, AMS 4547, 4711]; Bulolo Morobe Division (7°12'S, 146°39'E) [6♂♂, 3♀♀, AMS 6414–6422]; Dobodura, Northern Province (8°46'S, 148°23'E) [4♂♂, 2♀♀, AMS 6917, 6960, 6973–74, 6987–88]; Oriomo R W Div. Papua (9°03'S, 143°11'E) [1♂, 1♀, AMS 7237–7238]; Motu Motu Village, Brown River [1♀, AMS 7959]; South Simbu Province, Haia Vill Pio–Tura Region (6°41'S, 145°00'E) [6♂♂, 3♀♀, AMS 13836, 13838–39, 13842, 13842, 13846–13849, 13917, 13920, 13931, 13934–35, 14685–87, 14689, 14733, 14736–37, 14739, 14741, 14743, 14810, 14826, 14829, 14850–51]; Southern Highlands Province, Waro Village (6°32'S, 143°11'E) [6♂♂, 7♀♀, 2 sex?, AMS 14868, 16280–16294]; Ioma Nth Prov. (8°22'S, 147°49'E) [1♀, AMS 16325]; Sth Highland Prov, Waro (6°32'S, 143°11'E) [1♂, AMS 17128]; Central Province; Port Moresby, Laloki [1 sex?, AMS 18862]; Central Province; Dry Forest Belt 500 m Goldie River Rd (9°21'S, 147°30'E) [1♀, AMS 21695]; Southern Highlands Province, Mt. Sisa, Bobole Village (6°12'S, 142°46'E) [1♂, AMS 24291]; Southern Highlands Province; Waro Village (6°32'S, 143°11'E) [1♀, AMS 24988]; Central Province, Goldie River Road (9°21'S, 147°30'E) [1♀, AMS 26268].

*Rattus mordax* (29).—Papua New Guinea: Mt. Lamington Dist., Div. of Papua (8°50'S, 148°08'E) [1♀, AMS M4292]; Milne Bay Province, Normanby Island, Wamla village near Guleguleu [10°30'S, 151°17'E] (3♀♀, AMS 20388–89, 20440); Fergusson Island, Kalo-kalo Village (9°25'S, 150°26'E) [11♂, AMS 28004]; German New Guinea [2 sex?, AMS 1958–59]; Dobodura North Division (8°46'S, 148°23'E) [4♂♂, 2♀♀, AMS 6913–16, 6977, 7087]; Mt. Lamington Distr. N Div. Papua (8°50'S, 148°08'E) [2♂♂, 4♀♀, AMS 4292–4293, 4685–87, 4712].

*Rattus mordax mordax* (1).—Papua New Guinea: Milne Bay, Gwariu River, 1 mi S of Biniguni [1♂, AMNH 158036].

*Rattus praetor coenorum* (15).—Indonesia: Irian Jaya (2 sex unknown, AMNH 143836–143837); Irian Jaya; The Gebroeder Weyland Range, Mt. Derimapa [1♀, AMNH 101964]; Papua; Hollandia (now Jayapura) [1♂, AMNH 110126], Bernhard Camp, 75 m [1♂, AMNH 152356], 4 km SW Bernhard Camp, 850 m (1♀, AMNH 152358), 6 km SW Bernhard Camp, 1,200 m [1♂, AMNH 152359]; West Papua; Sansapor [1♂, USNM 277303], NW Geelvink Bay [now Cenderawasih Bay], Oransbari, el. 10' [2♂♂, AMNH 222432–33], Vogelkop [1♂, AMNH 143868], Vogelkop, Sapsapore [= Sausapor?] [3♂♂, 1♀, AMNH 143843, 143849, 143851, 143871].

*Rattus sanila* (25).—Papua New Guinea: New Ireland Province; New Ireland Island, Balof 2 site; left maxillary fragment with M1–3 [AMS F82021—holotype], 7 maxillary and 17 right dentary fragments.

## SI 2

Taxon, catalog number, collection depository, locality where collected, and GenBank voucher numbers for sequences used in phylogenetic analyses. Collection acronyms are as follows: AMS = Australian Museum; KCR = Kevin C. Rowe, personal collection, Museum Victoria; SAMA = South Australian Museum; SCU = Southern Cross University, Lismore; WAM = Western Australian Museum. Acronyms for states are as follows: NSW = New South Wales; NT = Northern Territory; QLD = Queensland; SA = South Australia; TAS = Tasmania; VIC = Victoria; and WA = Western Australia; and for countries, PNG = Papua New Guinea. *CR* = mitochondrial *control region*; *ATP5A1*, *DHFR*, and *FGB3* are nuclear genes as discussed in the Methods. Rowe et al. (2011) provide phylogenetic relationships, sequences, and data on vouchers using many, but not all, of the specimens listed here. Data for new specimens incorporated herein are provided in the Specimens Examined. Rowe et al. (2011) provide phylogenetic relationships, sequences, and data on vouchers using many, but not all, of the specimens incorporated here.

| Taxon   | Specimen no. | Collection | Locality                 | State | Country   | Latitude | Longitude | <i>CR</i> | <i>ATP5A1</i> | <i>DHFR</i> | <i>FGB3</i> |
|---|--------------|------------|--------------------------|-------|-----------|----------|-----------|-----------|---------------|-------------|-------------|
| <i>Rattus colletti</i><br>Thomas, 1904c                     | ABTC51642    | SAMA       | Berrimah                 | NT    | Australia | -12.433  | 130.916   | HQ334470  | HQ334345      | HQ334788    | —           |
| <i>Rattus colletti</i>                                      | ABTC51650    | SAMA       | Fogg Dam                 | NT    | Australia | -12.566  | 131.3     | HQ334471  | HQ334346      | HQ334789    | HQ334852    |
| <i>Rattus colletti</i>                                      | ABTC51656    | SAMA       | Humpty Doo               | NT    | Australia | -12.616  | 131.25    | —         | HQ334347      | HQ334790    | HQ334853    |
| <i>Rattus detentus</i>                                      | ABTC125036   | SAMA       | Kawaliap                 | Manus | PNG       | -2.1     | 147.06    | KP702212  | KP702211      | KP702218    | KP702213    |
| <i>Rattus fuscipes</i><br><i>assimilis</i> (Gould,<br>1858) | RfaN01       | KCR        | Byfield National<br>Park | QLD   | Australia | -22.870  | 150.690   | HQ334494  | HQ334370      | HQ334811    | HQ334875    |
| <i>Rattus fuscipes</i><br><i>assimilis</i>                  | RfaN02       | KCR        | Byfield National<br>Park | QLD   | Australia | -22.838  | 150.669   | HQ334495  | HQ334371      | HQ334812    | HQ334876    |
| <i>Rattus fuscipes</i><br><i>assimilis</i>                  | RfaN05       | KCR        | Byfield National<br>Park | QLD   | Australia | -22.838  | 150.669   | HQ334496  | HQ334372      | HQ334813    | HQ334877    |
| <i>Rattus fuscipes</i>                                      | A10          | SCU        | Mount Nullum             | NSW   | Australia | -28.374  | 153.366   | HQ334446  | HQ334326      | HQ334767    | HQ334828    |

|  |              |     |                                   |     |           |         |          |          |          |          |          |
|--|--------------|-----|-----------------------------------|-----|-----------|---------|----------|----------|----------|----------|----------|
| <i>assimilis</i>                             |              |     | Nature Reserve                    |     |           |         |          |          |          |          |          |
| <i>Rattus fuscipes assimilis</i>             | C21          | SCU | Rummery Park                      | NSW | Australia | -28.599 | 153.3783 | HQ334482 | HQ334359 | HQ334799 | —        |
| <i>Rattus fuscipes assimilis</i>             | RfaS01       | KCR | Wilson's Promontory National Park | VIC | Australia | -39.017 | 146.308  | HQ334502 | HQ334376 | HQ334818 | HQ334883 |
| <i>Rattus fuscipes assimilis</i>             | RfaS05       | KCR | Wilson's Promontory National Park | VIC | Australia | -39.017 | 146.308  | HQ334503 | HQ334377 | HQ334819 | HQ334884 |
| <i>Rattus fuscipes assimilis</i>             | RfaS17       | KCR | Wilson's Promontory National Park | VIC | Australia | -39.017 | 146.308  | HQ334504 | HQ334378 | —        | —        |
| <i>Rattus fuscipes coracius</i> Thomas, 1923 | DC02R06      | KCR | Davies Creek State Forest         | QLD | Australia | -17.039 | 145.614  | HQ334486 | —        | HQ334803 | HQ334867 |
| <i>Rattus fuscipes coracius</i>              | DC08R05      | KCR | Davies Creek State Forest         | QLD | Australia | -17.039 | 145.614  | HQ334488 | HQ334364 | HQ334805 | HQ334869 |
| <i>Rattus fuscipes coracius</i>              | GI02R01      | KCR | Girringun National Park           | QLD | Australia | -18.602 | 145.812  | HQ334492 | HQ334368 | HQ334809 | HQ334873 |
| <i>Rattus fuscipes coracius</i>              | Laurance1618 | SCU | Mt. Windsor                       | QLD | Australia | -16.21  | 144.98   | HQ334445 | HQ334325 | HQ334766 | HQ334827 |
| <i>Rattus fuscipes coracius</i>              | PR06R01      | KCR | Paluma Range National Park        | QLD | Australia | -18.990 | 146.168  | HQ334498 | HQ334374 | HQ334814 | HQ334879 |
| <i>Rattus fuscipes coracius</i>              | WO04R04      | KCR | Wooroonooran National Park        | QLD | Australia | -17.646 | 145.731  | HQ334506 | HQ334380 | HQ334824 | HQ334885 |
| <i>Rattus fuscipes coracius</i>              | WO04R06      | KCR | Wooroonooran National Park        | QLD | Australia | -17.646 | 145.731  | HQ334508 | HQ334382 | HQ334822 | HQ334887 |
| <i>Rattus fuscipes coracius</i>              | WO05R04      | KCR | Wooroonooran National Park        | QLD | Australia | -17.656 | 145.714  | HQ334510 | HQ334384 | HQ334824 | HQ334889 |
| <i>Rattus fuscipes</i>                       | WO05R11      | KCR | Wooroonooran                      | QLD | Australia | -17.656 | 145.714  | HQ334512 | HQ334386 | HQ334826 | HQ334891 |



|   |           |      |                            |      |           |         |         |          |          |          |          |
|---|-----------|------|----------------------------|------|-----------|---------|---------|----------|----------|----------|----------|
| <i>coracius</i>                                 |           |      | National Park              |      |           |         |         |          |          |          |          |
| <i>Rattus fuscipes fuscipes</i>                 | ABTC08616 | SAMA | 26 km W Manjimup           | WA   | Australia | -34.25  | 116.033 | HQ334450 | HQ334330 | HQ334771 | HQ334832 |
| <i>Rattus fuscipes fuscipes</i>                 | ABTC08644 | SAMA | Greenhead                  | WA   | Australia | -30.067 | 114.967 | HQ334451 | HQ334331 | HQ334772 | HQ334833 |
| <i>Rattus fuscipes greyi</i> (Gray, 1841)       | RAT60     | SCU  | Scott Creek                | SA   | Australia | -34.933 | 138.667 | HQ334501 | HQ334375 | HQ334817 | HQ334882 |
| <i>Rattus giluwensis</i>                        | ABTC87301 | SAMA | Waile Creek Porgera        | Enga | PNG       | -5.547  | 143.073 | HQ334478 | HQ334355 | HQ334796 | HQ334861 |
| <i>Rattus giluwensis</i>                        | ABTC87305 | SAMA | Waile Creek Porgera        | Enga | PNG       | -5.547  | 143.073 | HQ334479 | HQ334356 | HQ334795 | HQ334862 |
| <i>Rattus leucopus cooktownensis</i> Tate, 1951 | ABTC51770 | SAMA | Home Rule                  | QLD  | Australia | -15.75  | 145.283 | HQ334477 | HQ334354 | HQ334804 | HQ334860 |
| <i>Rattus leucopus cooktownensis</i>            | DC07R02   | KCR  | Davies Creek State Forest  | QLD  | Australia | -17.037 | 145.61  | HQ334487 | HQ334363 | HQ334806 | HQ334868 |
| <i>Rattus leucopus cooktownensis</i>            | DC11R05   | KCR  | Dinden National Park       | QLD  | Australia | -16.980 | 145.70  | HQ334489 | HQ334365 | HQ334807 | HQ334870 |
| <i>Rattus leucopus cooktownensis</i>            | DT01R03   | KCR  | Daintree National Park     | QLD  | Australia | -16.474 | 145.327 | HQ334490 | HQ334366 | HQ334808 | HQ334871 |
| <i>Rattus leucopus cooktownensis</i>            | DT10R02   | KCR  | Daintree National Park     | QLD  | Australia | -16.042 | 145.459 | HQ334491 | HQ334367 | HQ334817 | HQ334872 |
| <i>Rattus leucopus cooktownensis</i>            | PR04R01   | KCR  | Paluma Range National Park | QLD  | Australia | -18.862 | 146.116 | HQ334497 | HQ334373 | —        | HQ334878 |
| <i>Rattus leucopus cooktownensis</i>            | WO04R05   | KCR  | Wooroonooran National Park | QLD  | Australia | -17.646 | 145.731 | HQ334507 | HQ334381 | HQ334821 | HQ334886 |
| <i>Rattus leucopus cooktownensis</i>            | WO04R09   | KCR  | Wooroonooran National Park | QLD  | Australia | -17.646 | 145.731 | HQ334509 | HQ334383 | HQ334823 | HQ334888 |
| <i>Rattus leucopus cooktownensis</i>            | WO05R09   | KCR  | Wooroonooran National Park | QLD  | Australia | -17.656 | 145.714 | HQ334511 | HQ334385 | HQ334825 | HQ334890 |

|   |           |      |                          |                    |           |         |         |          |          |          |          |
|---|-----------|------|--------------------------|--------------------|-----------|---------|---------|----------|----------|----------|----------|
| <i>Rattus leucopus doboduræ</i><br>Troughton, 1946      | M14739    | AMS  | Haia                     | Chimbu             | PNG       | -6.683  | 145     | —        | —        | HQ334774 | HQ334836 |
| <i>Rattus leucopus doboduræ</i>                         | M14741    | AMS  | Haia                     | Chimbu             | PNG       | -6.683  | 145     | HQ334454 | —        | HQ334775 | HQ334837 |
| <i>Rattus leucopus doboduræ</i>                         | M13838    | AMS  | Haia                     | Chimbu             | PNG       | -6.683  | 145     | HQ334455 | HQ334333 | HQ334776 | HQ334838 |
| <i>Rattus leucopus doboduræ</i>                         | M14743    | AMS  | Haia                     | Chimbu             | PNG       | -6.683  | 145     | HQ334456 | HQ334334 | HQ334777 | HQ334839 |
| <i>Rattus leucopus doboduræ</i>                         | M13931    | AMS  | Haia                     | Chimbu             | PNG       | -6.683  | 145     | HQ334457 | HQ334335 | HQ334778 | HQ334840 |
| <i>Rattus leucopus doboduræ</i>                         | M13849    | AMS  | Haia                     | Chimbu             | PNG       | -6.683  | 145     | HQ334480 | HQ334357 | HQ334797 | HQ334863 |
| <i>Rattus leucopus leucopus</i>                         | ABTC08493 | SAMA | Rocky River              | QLD                | Australia | -13.783 | 143.533 | HQ334449 | HQ334329 | HQ334770 | HQ334831 |
| <i>Rattus leucopus leucopus</i>                         | IR02R02   | KCR  | Iron Range National Park | QLD                | Australia | -12.674 | 143.334 | HQ334493 | HQ334369 | HQ334810 | HQ334874 |
| <i>Rattus leucopus leucopus</i>                         | SP03R01   | KCR  | Silver Plains Homestead  | QLD                | Australia | -13.834 | 143.452 | HQ334505 | HQ334379 | HQ334820 | —        |
| <i>Rattus leucopus ringens</i> (Peters and Doria, 1881) | M16281    | AMS  | Waro                     | Southern Highlands | PNG       | -6.533  | 143.183 | HQ334461 | HQ334337 | —        | HQ334844 |
| <i>Rattus leucopus ringens</i>                          | M17128    | AMS  | Waro                     | Southern Highlands | PNG       | -6.5    | 143     | HQ334481 | HQ334358 | HQ334798 | HQ334864 |
| <i>Rattus lutreolus lutreolus</i> (Gray, 1841)          | D39       | SCU  | Tyagarah                 | NSW                | Australia | -28.59  | 153.55  | HQ334483 | HQ334360 | HQ334800 | HQ334865 |
| <i>Rattus lutreolus lutreolus</i>                       | ABTC51720 | SAMA | Myall Lakes              | NSW                | Australia | -32.433 | 152.367 | HQ334475 | HQ334352 | HQ334793 | HQ334858 |
| <i>Rattus lutreolus velutinus</i> (Thomas,              | D69       | SCU  | Hobart                   | TAS                | Australia | -42.883 | 147.31  | HQ334485 | HQ334362 | HQ334802 | —        |

1882)

|   |           |      |                          |                    |           |         |         |          |          |          |          |
|---|-----------|------|--------------------------|--------------------|-----------|---------|---------|----------|----------|----------|----------|
| <i>Rattus lutreolus velutinus</i>                         | ABTC51762 | SAMA | Derwent Valley           | TAS                | Australia | -41.317 | 148.1   | HQ334476 | HQ334353 | HQ334794 | HQ334859 |
| <i>Rattus mordax</i>                                      | M27993    | AMS  | Woodlark Island          | Milne Bay          | PNG       | -9.216  | 152.933 | KP702214 | —        | —        | —        |
| <i>Rattus mordax</i>                                      | M27993    | AMS  | Fergusson Island         | Milne Bay          | PNG       | -9.416  | 150.433 | KP702216 | KP702219 | KP702220 | KP702217 |
| <i>Rattus niobe</i>                                       | M12872    | AMS  | Mt. Albert Edward        | Central            | PNG       | -8      | 147     | HQ334453 | HQ334332 | HQ334773 | HQ334835 |
| <i>Rattus niobe</i>                                       | M16311    | AMS  | near Apia River          | Southern Highlands | PNG       | -6.15   | 142.767 | HQ334459 | HQ334336 | HQ334780 | HQ334842 |
| <i>Rattus niobe</i>                                       | M17664    | AMS  | Sol River                | Sandaun            | PNG       | -5.15   | 141.633 | HQ334464 | —        | HQ334784 | HQ334847 |
| <i>Rattus novaeguineae</i><br>Taylor and Calaby<br>1982   | M14647    | AMS  | Yuro                     | Southern Highlands | PNG       | -6.533  | 144.85  | HQ334458 | —        | HQ334779 | HQ334841 |
| <i>Rattus novaeguineae</i>                                | M16318    | AMS  | Waro                     | Southern Highlands | PNG       | -6.533  | 143.183 | HQ334460 | —        | HQ334781 | HQ334843 |
| <i>Rattus novaeguineae</i>                                | M19055    | AMS  | Nokopo                   | Morobe             | PNG       | -5.95   | 146.6   | HQ334468 | HQ334343 | —        | HQ334850 |
| <i>Rattus novaeguineae</i>                                | M19056    | AMS  | Nokopo                   | Morobe             | PNG       | -5.95   | 146.6   | HQ334469 | HQ334344 | —        | HQ334851 |
| <i>Rattus praetor</i>                                     | M17484    | AMS  | Munbil                   | Sandaun            | PNG       | -4.867  | 141.217 | HQ334465 | HQ334340 | HQ334785 | HQ334848 |
| <i>Rattus praetor</i>                                     | M17461    | AMS  | Munbil                   | Sandaun            | PNG       | -4.867  | 141.217 | HQ334466 | HQ334341 | HQ334786 | —        |
| <i>Rattus praetor</i>                                     | M17459    | AMS  | Munbil                   | Sandaun            | PNG       | -4.867  | 141.217 | HQ334467 | HQ334342 | HQ334787 | HQ334849 |
| <i>Rattus rattus</i>                                      | A65       | SCU  | Nymboida                 | NSW                | Australia | -30.35  | 152.48  | HQ334447 | HQ334327 | HQ334768 | HQ334829 |
| <i>Rattus sordidus</i><br>(Gould, 1858)                   | RAT176    | SCU  | Innisfail                | QLD                | Australia | -17.517 | 146.017 | HQ334500 | —        | HQ334791 | HQ334881 |
| <i>Rattus sordidus</i>                                    | ABTC51664 | SAMA | Ingham                   | QLD                | Australia | -18.65  | 146.15  | HQ334472 | HQ334348 | HQ334816 | HQ334854 |
| <i>Rattus steini</i>                                      | M17691    | AMS  | Sol River                | Sandaun            | PNG       | -5.15   | 141.633 | HQ334462 | HQ334338 | HQ334782 | HQ334845 |
| <i>Rattus tunneyi culmorum</i> (Thomas and Dollman, 1909) | D45       | SCU  | Bundjalong National Park | NSW                | Australia | -29.333 | 153.433 | HQ334484 | HQ334361 | HQ334801 | HQ334866 |

|   |           |      |                      |         |           |         |         |          |          |          |          |
|---|-----------|------|----------------------|---------|-----------|---------|---------|----------|----------|----------|----------|
| <i>Rattus tunneyi culmorum</i>                | RAT132    | SCU  | Yarraman             | QLD     | Australia | -26.833 | 151.983 | HQ334499 | —        | HQ334815 | HQ334880 |
| <i>Rattus tunneyi tunneyi</i> (Thomas, 1904b) | M21990    | WAM  | Mitchell Plateau     | WA      | Australia | -14.767 | 125.783 | HQ334452 | —        | —        | HQ334834 |
| <i>Rattus tunneyi tunneyi</i>                 | ABTC51684 | SAMA | Edward Pellew Island | NT      | Australia | -15.5   | 136.75  | HQ334474 | HQ334351 | HQ334792 | HQ334857 |
| <i>Rattus verecundus</i> (Thomas, 1904c)      | M17628    | AMS  | Sol River            | Sandaun | PNG       | -5.15   | 141.633 | HQ334463 | HQ334339 | HQ334783 | HQ334846 |
| <i>Rattus villosissimus</i> (Waite, 1898)     | ABTC08439 | SAMA | Midway Tank          | QLD     | Australia | -24.633 | 140.95  | HQ334448 | HQ334328 | HQ334769 | HQ334830 |
| <i>Rattus villosissimus</i>                   | ABTC51675 | SAMA | Perikoola Water Hole | QLD     | Australia | -25.683 | 140.6   | HQ334473 | HQ334350 | —        | HQ334856 |

---

### S3

Measurements of specimens of *Rattus detentus* from the Pamwak archaeological site, deposited at PNGMAG. Specimens are identified by Excavation Square (Squ), Quadrant (Quad), and Spit (vertical excavation unit) (see Fredericksen et al. 1993). Isolated lower and upper incisors of *R. detentus* are distinguished from those of *Melomys matambuai* by a combination of their larger size, more extensively enameled medial surface (enamel extends at least 0.5 mm onto the medial surface vs. no more than 0.3 mm in *M. matambuai*), and presence of a beveled rather than rounded intersection between the anterior and lateral surfaces of the tooth.

**Table 1.** Measurements of the lower dentition and mandibular ramus. Measurements are m1–3 crown length (CL), m1–3 alveolar length (AlvL), m1 crown length (CL), m1 crown width (CW), m2 crown length (CL), m2 crown width (CW), m3 crown length (CL), m3 crown width (CW), lower incisor depth (Lower I D), lower incisor width (Lower I W). Incisor depth is the least distance from the most proximal point on the occlusal facet to the opposite side (termed “antero-posterior diameter” and diagrammed by Millien-Parra and Loreau 2000).

| Squ | Quad | Spit | m1–3<br>CL | m1–3<br>AlvL | m1<br>CL | m1<br>CW | m2<br>CL | m2<br>CW | m3<br>CL | m3<br>CW | Lower I<br>D | Lower I<br>W |
|-----|------|------|------------|--------------|----------|----------|----------|----------|----------|----------|--------------|--------------|
| 4   | NW   | 12B  | 8.25       | 8.45         | 3.15     | 2.1      | 2.25     |          | 2.65     | 2.05     |              |              |
| 4   | N    | 2B   |            | 8.75         | 3.15     | 2        | 2.45     | 2.35     |          |          | 2.65         | 1.4          |
| 4   | NW   | 2B   |            |              | 3.15     | 2        | 2.45     | 2.25     |          |          | 2.6          | 1.6          |
| 2   | S    | 11B  |            |              | 3.15     | 2        | 2.5      | 2.2      |          |          | 2.55         |              |
| 4   | NEQ  | 3A   |            |              | 3.15     | 1.9      |          |          |          |          | 2.7          | 1.4          |
| 4   | NW   | 2C   | 7.7        | 7.9          | 3.2      | 2.05     | 2.2      | 2.2      | 2.25     | 1.7      |              |              |
| 2   | S    | 4A   |            | 8.9          | 3.2      | 2.1      | 2.2      | 2.45     | 2.55     | 2.1      |              |              |
| 2   | STLC | 4B   |            |              | 3.2      | 2.15     | 2.45     | 2.4      |          |          | 2.55         | 1.4          |

|   |       |     |      |      |      |      |      |      |      |      |      |  |      |
|---|-------|-----|------|------|------|------|------|------|------|------|------|--|------|
| 4 | NEQ   | 2C  |      | 8.9  | 3.25 | 2.05 |      |      |      |      |      |  | 1.5  |
| 4 | SW    | 3B  | 8.25 | 8.3  | 3.3  | 2.05 | 2.3  | 2.25 | 2.5  | 1.85 |      |  |      |
| 4 | SW    | 2B  |      | 8.75 | 3.3  | 2.1  | 2.4  | 2.5  |      |      | 3    |  | 1.6  |
| 2 | NW    | 10A |      |      | 3.3  | 2.15 | 2.5  | 2.5  |      |      |      |  |      |
| 3 | SEQ   | 3B  |      |      | 3.35 | 2.15 | 2.4  | 2.35 |      |      | 2.55 |  | 1.55 |
| 2 | MS/WA | 3   | 8.45 | 8.85 | 3.35 | 2.35 | 2.45 | 2.45 | 2.4  | 2.05 |      |  |      |
| 2 | MS/WA | 3   |      | 8.55 | 3.35 | 2.15 | 2.45 | 2.35 |      |      |      |  |      |
| 2 | N     | 5A  |      |      | 3.35 | 2.15 | 2.5  | 2.4  | 2.65 | 2    |      |  |      |
| 2 | S     | 5B  |      |      | 3.35 | 2.1  | 2.5  | 2.3  |      |      |      |  |      |
| 2 | NQ    | 4A  |      |      | 3.35 | 2    | 2.6  | 2.25 |      |      |      |  |      |
| 4 | S     | 3A  |      | 8.95 | 3.4  | 2.15 | 2.35 | 2.4  |      | 2    | 2.95 |  | 1.6  |
| 2 | MS/WA | 4   |      |      | 3.4  | 2.1  | 2.5  | 2.3  | 2.4  | 1.9  | 2.75 |  | 1.5  |
| 4 | SW    | 3B  |      | 8.5  | 3.4  | 2.15 | 2.55 | 2.25 | 2.15 | 2    |      |  |      |
| 4 | N     | 3A  |      | 8.4  | 3.45 | 2.25 | 2.5  | 2.5  |      |      |      |  | 1.35 |
| 4 | NEQ   | 2B  |      | 9.05 | 3.5  | 2.1  | 2.45 | 2.35 |      |      | 2.85 |  | 1.6  |
| 4 | SW    | 2A  |      | 8.35 | 3.5  | 2.1  | 2.5  | 2.4  | 2.4  | 1.85 |      |  |      |
| 3 | NW    | 5B  | 8.5  | 8.85 | 3.5  | 2.15 | 2.5  | 2.45 | 2.45 | 2.05 |      |  |      |
| 2 | SEQ   | 7B  |      | 8.9  | 3.5  | 2.15 | 2.5  | 2.4  | 2.45 | 2.1  | 2.85 |  | 1.65 |
| 4 | NW    | 2B  |      |      | 3.5  | 2.15 |      |      |      |      | 2.6  |  | 1.8  |
| 4 | NEQ   | 1   |      | 9.3  | 3.75 | 2.4  | 2.65 | 2.6  | 2.55 | 2.25 | 3    |  | 1.8  |
| 2 | MS/WA | 4   |      |      |      |      | 2.55 | 2.4  |      |      |      |  |      |
| 2 | S     | 3A  |      | 9    |      |      | 2.6  | 2.5  | 2.5  |      |      |  |      |
| 4 | S     | 7B  |      |      |      |      |      | 2.4  |      |      | 2.7  |  | 1.6  |
| 2 | MS/WA | 4   |      | 7.55 |      |      |      |      |      |      |      |  |      |
| 2 | SEQ   | 16A |      | 8.75 |      |      |      |      |      |      |      |  | 1.3  |
| 2 | SW    | 10A |      | 9    |      |      |      |      |      |      |      |  |      |
| 4 | SEQ   | 2C  |      | 9.3  |      |      |      |      |      |      |      |  | 1.9  |
| 2 | N     | 10A |      |      |      |      |      |      |      |      | 2.4  |  | 1.3  |
| 2 | S     | 10A |      |      |      |      |      |      |      |      | 2.45 |  | 1.35 |
| 2 | NW    | 10A |      |      |      |      |      |      |      |      | 2.15 |  | 1.2  |
| 2 | NW    | 10A |      |      |      |      |      |      |      |      | 2.65 |  | 1.5  |
| 2 | SEQ   | 10B |      |      |      |      |      |      |      |      | 2.55 |  | 1.6  |
| 2 | S     | 11A |      |      |      |      |      |      |      |      | 2.65 |  | 1.55 |
| 2 | NEQ   | 11A |      |      |      |      |      |      |      |      | 2.5  |  | 1.45 |

---

|   |     |     |      |      |
|---|-----|-----|------|------|
| 2 | N   | 11A | 2.8  | 1.5  |
| 4 | S   | 11A | 2.35 | 1.4  |
| 2 | S   | 11B | 2.35 | 1.25 |
| 2 | N   | 12B | 2.65 | 1.6  |
| 2 | SEQ | 13A | 2.5  | 1.5  |
| 2 | SEQ | 13B | 2.65 | 1.45 |
| 2 | NEQ | 13B | 2.65 | 1.55 |
| 4 | SW  | 13B | 2.4  | 1.35 |
| 2 | SW  | 14A | 2.5  | 1.4  |
| 2 | NEQ | 14A | 2.3  | 1.3  |
| 2 | NEQ | 14A | 2.2  | 1.3  |
| 4 | SW  | 14A | 2.4  | 1.4  |
| 2 | SW  | 14B | 2.45 | 1.4  |
| 2 | S   | 15A | 2.55 | 1.4  |
| 2 | SEQ | 16B | 2.05 | 1.25 |
| 1 | NEQ | 21B | 2.4  | 1.4  |
| 1 | NEQ | 22A | 2.45 | 1.45 |
| 1 | NEQ | 22A | 2.2  | 1.35 |
| 1 | SEQ | 24A | 2.35 | 1.45 |
| 4 | NW  | 2B  | 2.2  | 1.45 |
| 4 | NW  | 2B  | 3.2  | 1.8  |
| 4 | NW  | 2C  | 2.7  | 1.5  |
| 3 | SEQ | 2D  | 2.1  | 1.2  |
| 4 | NW  | 2D  | 2.15 | 1.2  |
| 4 | N   | 3A  | 3.05 | 2.1  |
| 4 | N   | 3A  | 2.7  | 1.4  |
| 2 | S   | 3B  | 2.45 | 1.05 |
| 4 | NW  | 3B  | 2.3  | 1.25 |
| 4 | NW  | 3B  | 2    | 1.2  |
| 4 | NW  | 3B  | 2.4  | 1.25 |
| 4 | NEQ | 4A  | 3    | 1.6  |
| 2 | N   | 4B  | 2.5  | 1.6  |
| 4 | NW  | 4B  | 2.5  | 1.35 |
| 4 | NW  | 4B  | 2.45 | 1.6  |

---

|   |     |    |      |      |
|---|-----|----|------|------|
| 2 | NW  | 5A |      | 1.6  |
| 4 | SEQ | 5A | 2.4  | 1.2  |
| 4 | NW  | 5A | 2.35 | 1.45 |
| 4 | N   | 5A | 2.7  | 1.55 |
| 2 | N   | 5B | 2.9  | 1.7  |
| 2 | S   | 5B | 2.9  | 1.5  |
| 2 | NW  | 6A | 2.7  | 1.55 |
| 2 | NW  | 6A | 2.05 | 1.15 |
| 3 | NEQ | 6A | 2.35 | 1.2  |
| 3 | NEQ | 6A | 2.45 | 1.3  |
| 2 | NW  | 7A | 2.6  | 1.3  |
| 2 | NW  | 7A | 2.35 | 1.5  |
| 2 | S   | 7A | 2.65 | 1.5  |
| 3 | SEQ | 7A | 3.25 | 1.75 |
| 4 | SW  | 7A | 2.5  | 1.55 |
| 4 | NW  | 7A | 2.7  | 1.5  |
| 4 | N   | 7A | 2.35 | 1.25 |
| 2 | NW  | 7B | 2.45 | 1.35 |
| 2 | NW  | 7B | 2.65 | 1.55 |
| 4 | S   | 8A | 2.1  | 1.1  |
| 2 | N   | 8B | 2.05 | 1.35 |
| 4 | S   | 8B | 2.35 | 1.3  |
| 2 | SW  | 9A | 2.4  | 1.35 |
| 2 | SEQ | 9B | 2.7  | 1.45 |
| 2 | SW  | 9B | 2.6  | 1.35 |

**Table 2.** Measurements of the upper dentition and maxilla. Measurements are M1–3 alveolar length (M1–3 Alv L), M1 crown length (M1 CL), M1 crown width (M1 CW), zygomatic plate width (Zyg Pl W), upper incisor depth (Upper I D), upper incisor width (Upper I W).

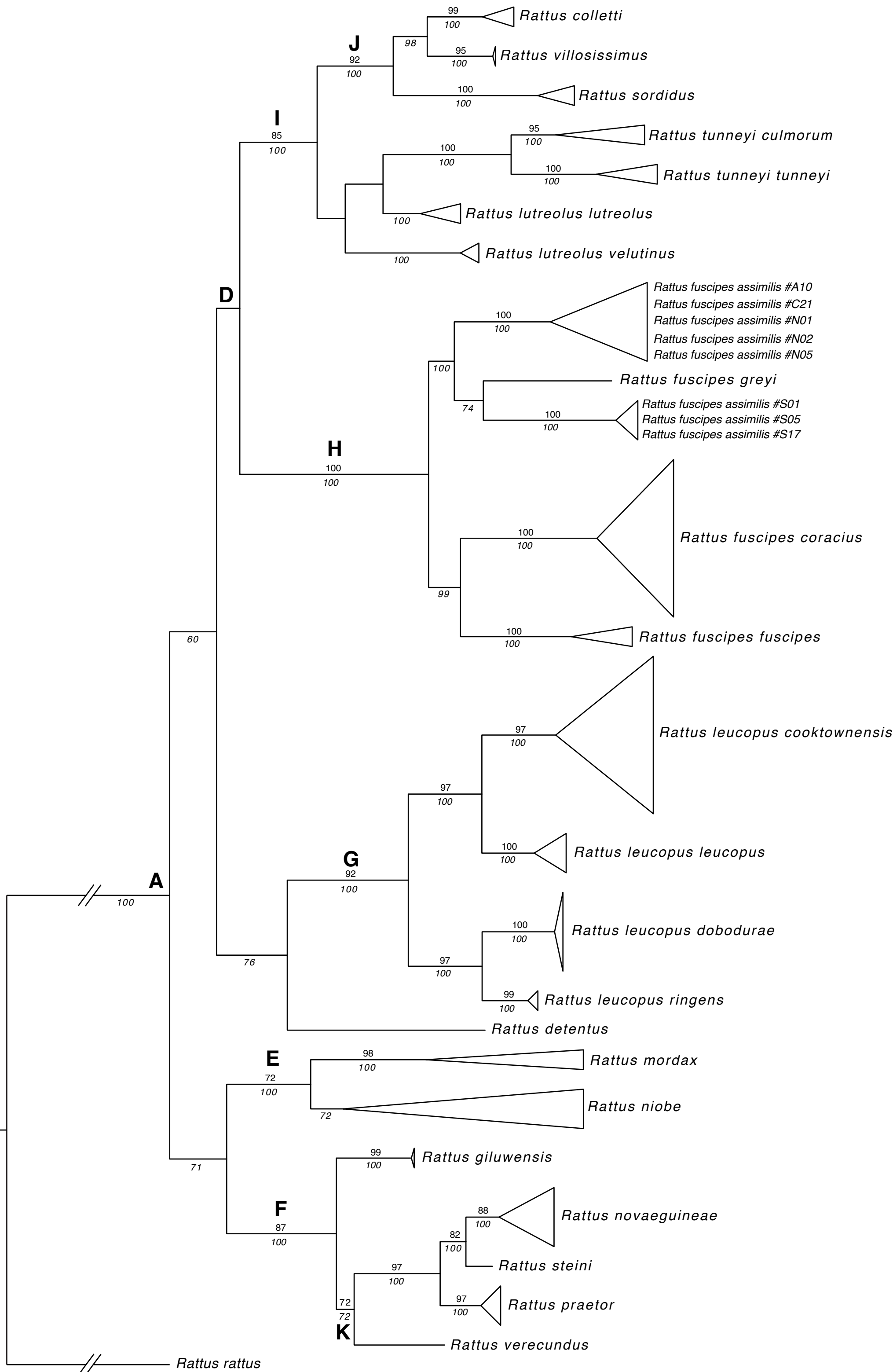


| Squ | Quad  | Spit | M1-3<br>Alv L | M1<br>CL | M1<br>CW | Zyg<br>Pl W | Upper<br>I D | Upper I<br>W |
|-----|-------|------|---------------|----------|----------|-------------|--------------|--------------|
| 2   | MS/WA | 4    |               |          |          | 5.7         |              |              |
| 2   | NW    | 8B   | 9             |          |          |             |              |              |
| 4   | NW    | 2A   |               | 4.2      | 2.65     |             |              |              |
| 4   | S     | 4A   |               |          | 2.5      |             |              |              |
| 3   | NE    | 5A   |               | 4.2      | 2.45     |             |              |              |
| 4   | SW    | 20   |               |          |          |             | 3.35         | 1.8          |
| 2   | NW    | 10B  |               |          |          |             | 3.1          | 1.7          |
| 2   | SW    | 11A  |               |          |          |             | 3.25         | 1.7          |
| 2   | N     | 12A  |               |          |          |             | 3.1          | 1.7          |
| 2   | SEQ   | 13B  |               |          |          |             | 3.05         | 1.55         |
| 4   | SW    | 13B  |               |          |          |             | 3.25         | 1.7          |
| 2   | SW    | 14B  |               |          |          |             | 2.9          | 1.65         |
| 2   | NW    | 15B  |               |          |          |             | 3.25         | 2            |
| 1   | SEQ   | 21B  |               |          |          |             | 2.7          | 1.6          |
| 1   | SEQ   | 21B  |               |          |          |             | 2.3          | 1.35         |
| 1   | SEQ   | 27A  |               |          |          |             | 3.1          | 1.75         |
| 1   | NEQ   | 28A  |               |          |          |             | 2.65         | 1.7          |
| 2   | S     | 2B   |               |          |          |             | 3.1          | 1.7          |
| 4   | SW    | 2B   |               |          |          |             | 3.1          | 1.7          |
| 4   | NEQ   | 2B   |               |          |          |             | 3.4          | 1.95         |
| 4   | NEQ   | 3A   |               |          |          |             | 3.05         | 1.65         |
| 4   | SEQ   | 3A   |               |          |          |             | 3.25         | 1.9          |
| 2   | S     | 3B   |               |          |          |             | 2.85         | 1.45         |
| 4   | SW    | 3B   |               |          |          |             | 3.35         | 1.9          |
| 4   | N     | 3B   |               |          |          |             | 3.2          | 1.85         |
| 2   | S     | 4A   |               |          |          |             | 3.65         | 2.05         |
| 4   | NEQ   | 4B   |               |          |          |             | 3.6          | 1.8          |
| 4   | NW    | 4B   |               |          |          |             | 2.9          | 1.7          |
| 2   | S     | 5A   |               |          |          |             | 3.5          | 1.95         |
| 2   | N     | 5A   |               |          |          |             | 3.15         | 1.85         |
| 3   | NEQ   | 5A   |               |          |          |             | 3.25         | 1.85         |

---

|   |     |    |      |      |
|---|-----|----|------|------|
| 4 | N   | 5A | 3.1  | 1.75 |
| 4 | SW  | 5A | 3.4  | 1.9  |
| 2 | S   | 5B | 3.45 | 1.8  |
| 3 | SEQ | 6A | 3.15 | 1.8  |
| 4 | N   | 6A | 3.05 | 1.65 |
| 2 | N   | 7B | 3.1  | 2.05 |
| 4 | N   | 8A | 3.55 | 2.1  |
| 2 | N   | 9B | 3    | 1.7  |

---



0.2

