





MARSUPIALS AND RODENTS OF THE ADMIRALTY ISLANDS, PAPUA NEW GUINEA

Front cover: A recently killed specimen of an adult female *Melomys matambuai* from Manus Island. Photograph courtesy of Ann Williams.

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Abstract

We provide the first account of all non-volant, non-marine mammals recorded, whether reliably, questionably, or erroneously, from the Admiralty Islands, Papua New Guinea. Species recorded with certainty, or near certainty, are the bandicoot *Echymipera* cf. *kalubu*, the wide-spread cuscus *Phalanger orientalis*, the endemic (?) cuscus *Spilocuscus kraemeri*, the endemic rat *Melomys matambuai*, a recently described species of endemic rat *Rattus detentus*, and the commensal rats *Rattus exulans* and *Rattus rattus*. Species erroneously reported from the islands or whose presence has yet to be confirmed are the rats *Melomys bougainville*, *Rattus mordax*, *Rattus praetor*, and *Uromys neobrittanicus*. Included additional specimens to those previously reported in the literature are of *Spilocuscus kraemeri* and two new specimens of *Melomys matambuai*, previously known only from the holotype and a paratype, and new specimens of *Rattus exulans*. The identity of a specimen previously thought to be of *Spilocuscus kraemeri* and said to have been taken on Bali, an island off the coast of West New Britain, does appear to be of that species, although this taxon is generally thought of as occurring only in the Admiralties and vicinity. Summaries from the literature and new information are provided on the morphology, variation, ecology, and zoogeography of the species treated.

Key words: Austro–Papuan region, biogeography, Bismarck Archipelago, *Echymipera kalubu*, marsupial dentition, morphology, *Phalanger orientalis*, Phalangeridae, *Rattus detentus*, taxonomy

INTRODUCTION

The Admiralty Islands, a group of 18 islands of low elevation and located 275-300 km north of the island of New Guinea, and politically part of Papua New Guinea, have a poorly known mammal fauna. Manus Island is the largest of the Admiralties and it has been designated by the World Wildlife Fund as an area of high biological importance (WWF 2014). Some four-fifths of Manus remained forested at least until the mid-1990s, but many of the smaller adjacent islands have been converted into coconut plantations (Rannells 1995). The original vegetation of the Admiralty Islands is evergreen forest, including tropical and subtropical moist broadleaf forest (Wikramanayake et al. 2002); however, the only significant forests remain on Manus. The need to study the Tropical and Subtropical Moist Broadleaf Forests, especially in central Manus, from Mt. Dremsel to the northern coast, in order to protect the Calophyllum and Sararanga forests as an area of

high biological importance, has been highlighted by Johns (1993) and Wikramanayake et al. (2002).

The Admiralties have a number of vertebrates that are endemic or of limited distribution elsewhere, including the cuscus *Spilocuscus kraemeri* (Schwarz, 1910) (Phalangeridae); the bats: *Dobsonia anderseni* Thomas, 1914 (Pteropodidae), *Pteropus admiralitatum* Thomas, 1894 (Pteropodidae), and *Emballonura serii* Flannery, 1994 (Emballonuridae); and the rats: *Melomys matambuai* Flannery, Colgan, and Trimble, 1994 (Muridae) and the recently described endemic species *Rattus detentus* Timm, Weijola, Aplin, Flannery, and Pine, 2016 (Muridae). Three of the six bird species endemic to the Admiralties have been listed as Vulnerable on the IUCN Red List—Manus Fantail (*Rhipidura semirubra*), Superb Pitta (*Pitta superba*), and Manus Masked Owl (*Tyto manusi*). The large, brightly-colored land snail *Papustyla pulcherrima* is listed as endangered owing to over-collecting for the commercial trade. The recent description of the endemic Admiralties Rat *Rattus detentus* adds further weight to calls for continued study and protection of the unique flora and fauna of these islands.

Our goals herein are to document what is known about the marsupials and rodents of the Admiralty Is-

lands, summarize and comment on the widely scattered and sometimes obscure and/or misleading published literature, and to report on newly acquired specimens. In particular, we provide: new information on coat color and dentition; cranial images of certain species; the first color photograph of the skin of a female *Spilocuscus kraemeri*; and the first such photograph of the skin of a *Melomys matambuai* and a comparison of that species with *M. rufescens*.

MATERIALS AND METHODS

English names.—English names follow Flannery (1995b), except for that of *Rattus detentus*, which follows Timm et al. (2016). Not all English names are in keeping with the principles recommended for their construction by Duckworth and Pine (2003).

Taxon sampling.—Specimens were examined at and/or on loan from the following museums (acronyms for U.S. institutions follow Hafner et al. 1997): American Museum of Natural History (AMNH), New York, New York; Bernice P. Bishop Museum (BPBM), Honolulu, Hawaii; Field Museum (FMNH), Chicago, Illinois; Los Angeles County Museum (LACM), Los Angeles, California; Natural Science Research Laboratory at the Museum of Texas Tech University (TTU), Lubbock, Texas; Papua New Guinea National Museum & Art Gallery (PNGMAG), Port Moresby; University of Kansas Natural History Museum (KU), Lawrence, Kansas; and University of Wisconsin Zoological Museum (UWZM), Madison, Wisconsin.

Morphologic evaluations.—All linear measurements presented herein are in millimeters, and masses are given in grams. Skull/dental measurements were taken with dial calipers to the nearest 0.1 mm. Those for specimens of *Rattus* are as defined by Taylor et al. (1982); those for *Melomys* follow those of Thomas (1905) and Hershkovitz (1962) or are self-explanatory. External measurements are given as recorded on the tags by collectors.

Tooth terminology in Phalangeridae.—For the purposes of this paper, adult phalangerids will be treated as having no more than three premolars and four molars in the maxilla and the last upper premolar above and below will be designated as the third. If there are three

premolars in the maxilla, the first two will be designated as P1 and P2. The minute, functionless teeth in the mandible, posterior to the large procumbent anterior incisors, which might be interpreted as constituting one or more other incisors, possibly a canine, and one or more premolars, will simply be referred to as "unicuspids." The first tooth after the "unicuspids" will be designated as p3 and the teeth posterior to this tooth will be designated as m1, m2, m3, and m4. This clarification is given here because various hypothetical schemes as to the homologies and "actual identity" of various teeth in marsupials have caused inconsistency resulting in various conflicting, confusing, and misleading treatments. Our scheme of terminology is not intended to involve hypothetical considerations in regard to homology and phylogeny but is adopted purely for effective communication, convenience, and comprehensibility. An example of what we are trying to avoid can be found in Nowak (1999:89), in which he presents the dental formula of Phalangeridae as "i 3/1-2, c 1/0-1, pm 2-3/3, m 5/5," and gives the total number of teeth as 40-46, citing Archer (1984a) as his authority. No more than 40 teeth, however, are normally present in a phalangerid skull. The discrepancy is caused by Nowak believing that both a lower canine and a lower second incisor can exist in the same dentary, although actually only one tooth is involved, and it is uncertain whether to call it an incisor or a canine. Also, Archer (1984a, b) regarded the deciduous teeth, above and below, which are displaced by P3 and p3, as representing an M1 and m1. Thus, Archer maintained that there were, in fact, five teeth above and below which could be regarded as molars, but all five would not be present after the putative "M1" and "m1" were replaced by the P3 and p3, but Nowak erroneously counted them in the adult dentition. Although they did not explicitly say so, it appears that Lidicker and Ziegler (1968) reported all of the teeth that we treat as "unicuspids" as being premolars, because they treat the deciduous teeth and permanent

last premolars as fourth premolars, apparently believing that the "missing" most anterior premolar should be numbered premolar number 1.

SPECIES ACCOUNTS

PERAMELEMORPHIA Peramelidae *Echymipera* cf. *kalubu* (Fischer, 1829)

Fischer (1829:68) named "*P*[*erameles*].? *Kalubu*" from "insula Waigiou" (= Waigeo) and attributed the name to Lesson ("Less. in Dict. class. XIII. P. 200"). We follow Husson (1955) in regarding Fischer as the author of the name.

Thomas (1914) reported a specimen of "*Echymipera cockerelli* [sic] from "Admiralty Island," presumably meaning Manus.

Flannery (1995b:68) wrote "Two specimens are known from Manus: BMNH 14.4.1.24, a male collected by Meek and Eichhorn on 23 September 1913 [the specimen reported by Thomas (1914)]; and BZM [apparently a lapsus for MZB = Museum Zoologicum Bogoriense] 15061, a male collected by H. Schodde [apparently a lapsus for H. Schoede, see Aplin et al. (2015), and earlier authors] at Seeadlerhafn. There is also a specimen (unregistered) held in the collections of the Museum für Naturkunde, Berlin, from the nearby island of Lou. [Aplin et al. (2015) misquote Flannery in regard to these specimens]. Preliminary investigations of archeological sites on Manus suggest that it has been introduced there" Earlier, Fredericksen et al. (1993) had written, in regard to evidence from the Pamwark archaeological site, that their findings suggested that the bandicoot had first appeared there at about 11,000 BP, when the inhabitants had shifted from flaked "stone" to obsidian artifacts, and that the animal had presumably been introduced by humans, from the mainland of New Guinea. Flannery et al. (1994:29) further stated that evidence suggested that E. kalubu had "been introduced by humans during the Holocene." Flannery (1995b) would apparently have classified the Admiralty Echymipera as E. k. cockerellii Ramsay, 1877, which Flannery consistently, and apparently inadvertently, referred to as "Perameles cockerellii." Laurie and Hill (1954) and others spelled this Perameles cockerelli [see also Thomas (1914)]. The correct spelling is cockerellii (see Ramsay 1877). Echymipera kalubu cockerelli [sic] is also one of the three subspecies recognized by Groves (2005b), who did not mention the Admiralties as within the species' range. Williams (1999) reported E. kalubu as dating back to "12400 +/- 480 BP" (also given as "at approx 12,000 BP") at the Pamwak archeological site on Manus. This corresponds in time with archeological evidence that would mean that the inhabitants had become more seafaring. Williams wrote (p. 248) that "The implication of the bandicoot presence is that it was brought to the island by people accidentally or as a food source." Helgen and Flannery (2004:831), however, wrote "... Echymipera kalubu is common at all levels throughout the Pamwak deposit ["a rockshelter site in southern Manus"] back to about 12,400 years ago; it could be native to Manus ... and its taxonomic status deserves study." Aplin et al. (2015:56) wrote that clarification of the identity of this animal "is a high priority for future research." However, Dickman (2015) seems to have little doubt as to the specific identity of the Manus bandicoot, because he assigns it the subspecies E. k. cockerelli [sic] Ramsay, 1877. He hypothesized that it reached the Admiralties by human agency in the late Pleistocene.

Timm et al. (2016) reported that snares are set by local trappers on Manus, around Kawaliep Village, in hopes of catching these bandicoots and rats and that both are eaten. However, Aplin et al. (2015) indicated that this species appears to be scarce on Mt. Sobomu, stating that landowners in 2014 claimed that they are present in the forest, primarily in rocky areas and only in low numbers, such that they were not worth trying to hunt or set snares for. Aplin et al. however stated that locals at their Yeri River site in 2014 said that bandicoots were plentiful and could be snared along runways. Efforts by Aplin et al. at spotlighting, looking for sign, and camera trapping that year also produced no evidence of the presence of this species.

DIPROTODONTIA Phalangeridae *Phalanger orientalis* (Pallas, 1766) Northern Common Cuscus

It is clear that Tate (1945:13) knew of no Phalanger orientalis from the Admiralties, for he wrote: "If orientalis is represented on the Admiralty Islands and St. Matthias it may be expected to conform to this general type [like animals from 'Long Island and Ruk,' etc.]." Kisokau (1974), however, recorded both "Pha*langer maculata*" (presumably = *Spilocuscus kraemeri*) and *Phalanger orientalis* from "Rambutso Island" [= Rambutyo Island] and "Phalanger maculata" (again, presumably = S. kraemeri) from Lou. Menzies and Pernetta (1986) seem to be the only authors who have taken note of Kisokau's report. They wrote that they had seen no specimens of P. orientalis from the Admiralties but that they would expect them to be of the "subspecies" P. o. intercastellanus Thomas, 1895 (now regarded as a species in its own right-see Colgan et al. 1993). One might wonder if some or all of the animals reported by Kisokau, as Phalanger orientalis, might be misidentified Spilocuscus kraemeri-young individuals and/or adult females, and/or individuals of the nearly uniformly silver gray color phase mentioned by Cohn (1914). However, as a native of Manus (see Flannery 2011), Kisokau is one to be expected to know how to tell Spilocuscus kraemeri from Phalanger orientalis, and so we are inclined to accept his having regarded the two as sympatric on Rambutyo. In this regard, Helgen and Flannery (2004), who think that Spilocuscus kraemeri may occur on New Britain, explained its rarity there, if it is found there, as possibly owing to competitive interactions with Phalanger orientalis on that island. Accordingly, Helgen and Flannery also hypothesized that the commonness of S. kraemeri on Manus could be explained by the absence of P. orientalis. However, Helgen and Jackson (2015) listed P. o. breviceps Thomas, 1888, for Manus, and assumed that it had been introduced. We know of no evidence, however, that it has ever occurred there. They did not list Rambutyo as an island occupied by this species.

Spilocuscus kraemeri (Schwarz, 1910) Admiralty Cuscus

The literature on this species is complex, confusing, widely scattered, and in various languages; thus we thought it useful to summarize, analyze, and annotate the published pertinent information on the species. Schwarz (1910) named "Phalanger maculatus krämeri" from the "Admiraltäts- und Hermit-Inseln" and on the basis of 35 skins and 7 skulls in the Berlin Museum [given as "32 specimens" by Aplin et al. (2015:50)] and collected by "... THILENIUS, SCHOEDE und ... KRÄMER." The new taxon was said to be most closely related to "Ph[alanger]. m[aculatus]. papuensis" [now generally regarded as a full species, Spilocuscus papuensis (Desmarest, 1822)] "from Waigeoe" (= Waigeo). The male of the new species was described as having a white to yellowish ground color with moderately large blackish-brown spots with faded borders. The snout, cheeks, and forehead were said to be mostly a paler rusty brown; the limbs spotted, (the spots?) somewhat paler than [on?] the back; the tail with large brown spots. The chin and throat white, the chest and belly yellowish. The female was described as unspotted with the snout and forehead reddish brown, the top of the head, nape of the neck, and the back blackish brown, not shiny. The rear part of the back was described as reddish brown, the tail somewhat darker, the limbs reddish brown, the chin white, the throat and upper part of the chest blackish brown, the ventral portion of the chest and belly yellowish, the underside of the base of the tail dark brown. Skull measurements were given for the holotype, an old male, variously identified as "Berl. Mus. A. 12.6.09" and "A. 126 09", "gesammelt von Schoede;" and for a subadult female, "Berl. Mus. A. 19.07.2." No definite localities, even to island or island group, were given for any specimen. Although earlier in the description Schwarz had stated that the specimens were from both the Admiralties and the Hermit Islands (p. 406), he later (p. 408) wrote "Hab.: Admiralitäts-Inseln." The skull and dentition were described and the former compared with those of specimens of Spilocuscus maculatus (sensu lato?) that Schwarz had seen from other localities. Although Schwarz did not indicate a type locality, Feiler (1978) provided a color drawing of an individual identified as Berlin Museum "12609" and from Manus, presumably the holotype.

Thomas (1914) listed four specimens of "*Phalan-ger maculatus krämeri*, Schwarz" from Manus. Two in the BMNH were collected by Meek and Eichhorn and two were listed as being in the Tring Museum.

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Cohn (1914), unaware of Schwarz's (1910) description of S. kraemeri, redescribed his animal as Phalanger maculatus minor, on the basis of at least 80 specimens from Manus. These specimens presumably are or were housed in Bremen. However, our attempts to confirm this have not met with success. He also stated that over 60 living individuals from Manus had passed through his hands. No type specimen was designated, no catalog numbers or museum(s) of deposition were mentioned, and no localities, other than the names of islands, were given. In addition to Manus, Cohn stated that he had seen this species on Ponam, and on Lou, where he found it to be quite common. He attributed its presence on these islands to the persistence of primary forest, although Flannery (1995b:105) found this species to be "common in all vegetation types, from gardens to almost undisturbed forest" on Manus. Cohn stated that on smaller, more heavily populated islands, the species had been extirpated, but mentioned only Baluan as being one of these islands (see also Helgen and Jackson 2015). It is unclear whether Cohn actually had any evidence of the former occurrence of S. kraemeri on any of these islands or merely surmised that it had once occurred there. The latter seems more likely, although Flannery (1995b) accepted the former presence of S. kraemeri on Baluan, based on Cohn's statement (see also Helgen and Jackson 2015). Cohn found S. kraemeri to be very common on Manus and to be the most important game animal for the locals. Cohn was on Manus from September until December of 1912. During this time, he examined many pouch young ranging in size down to 95 mm head plus body length and 80 mm tail length. These smallest ones were blind and hairless. Cohn concluded that this species did not breed all year long. He stated that the heavy rains began in November (with the dry season starting around March/April) and it appeared to him that breeding must have ceased a short time before this. He concluded that a second breeding season must exist early in the year, making the species diestrous, because in September he found numerous already half-grown animals. Flannery (1995b), in discussing Cohn's findings, apparently thought that all of the small September-December young were around the minimum size given and omitted the evidence for a second breeding season. Aplin et al. (2015:56) reported a "fully furred pouch young" during the period 2-6 October 2014. According to Helgen and Jackson (2015:496), "Limited observations [unspecified] suggest the Admiralty Spotted Cuscus breeds seasonally, giving birth generally to a single young in July–August, with pouch young observed in September–December (then carried by mothers on their backs); young achieve independence in June."

According to Cohn, the females are more numerous and larger than the males. The males were described as having dark brown legs with little white on them, the belly white with very small brown spots, the tail as a rusty-brown. In these respects, Cohn's description differed somewhat from that of Schwarz (1910). Two male specimens out of considerably more than 20 were a uniform silver gray with small dark dots on the back; the base of the tail with a faint brownish wash. Both of these males were half grown and were taken to Cohn at the same time and he speculated that they might have been from the same litter.

Cabrera (1919) synonymized *Phalanger maculatus krämeri* Schwarz with *Phalanger maculatus minor* Cohn and placed [*Phalanger*] "*minor* y *fusca*" Oken, 1821 in the synonymy of *Phalanger orientalis* (Pallas, 1766). In this, he seems to have been following Thomas (1888:201), who had placed "Phalangista minor and fusca (*Oken*) Schinz, Cuv. Thierr. ... (1821)" in "*Phalanger orientalis*."

According to Schwarz (1934:90), in the course of his idiosyncratic, essentialistic speculations concerning the phylogeny of and also supposedly directly environmentally-induced color patterns in cuscuses, certain spotted patterns belong "to the segmental type, being homologous to the rosettes of a leopard, and representative of the 'English' type [undefined] of piebald pattern ... these spots evolve a tendency to spread, thus in the end producing a true piebald pattern, such as is found in the males of Ph. maculatus. [new paragraph] That the very distinct markings found in this species are derived from the ones just described is shown by the females of Ph. m. papuensis Desmarest from Waigen and of Ph. m. krämeri Schwarz from the Admiralty Islands, some of which develop spots, but of a less progressive type than is found in the males, and more resembling that of the male Ph. o. ornatus." Schwarz (1934:90-91) went on to write "Males which are nearly or perfectly white are ... found in Ph. macu*latus*, although in that species perfect albinism is rare, and a stage similar to the 'Siamese' or 'Marten' type of cats and rabbits is the rule ... the individuals show the normal piebald pattern earlier in life."

Tate and Archbold (1937:381) noted that "Minor Cohn from Admiralty Islands would appear to be a synonym of krämeri Schwarz ..." and stated that the Archbold collection held topotypes of "krämeri." They figured the skull, minus the mandible, of AMNH 99900, seen from below. Concerning "krämeri" they wrote (p. 383) that the pelage "... appears to be thoroughly and consistently distinct from that of our Arfak and south New Guinea specimens ... A striking characteristic of krämeri in both sexes is the nearly black head on which the cinnamon-colored ears stand out contrastingly, and the deep chestnut-colored fore limbs." The Archbold holdings were listed (p. 384) as "Admiralty Islands (Manus Isl.): 1 y. ad. 3; 3 y. ad. 9s (all except one 9skins only); 3 y. \Im s, 1 y. \Im (skulls only); 1 ad. albino Q." Concerning the last, Tate and Archbold wrote (p. 384) "The muzzle and the insertions of the superciliary and labial vibrissae are reddish brown ... and the skin and hairs of the hands and feet are yellowish" The supposed "albino" is presumably AMNH 99749, which was recorded as having a brown iris, apparently the normal color-the collector, W. F. Coultas, also recorded a brown iris for specimens with normally colored pelage. Our notes on this specimen state "All white dorsally except some very faint buffy areas on rump and base of tail. Ventrally, base of tail and adjacent area faint buffy. Some buffy toward end of tail. Grayish around pouch area and posterior to that but maybe soiled." In their tables of measurements (pp. 448-449), the following specimens are listed: "A.M. 99832 juv. and ... Manus", "A.M. 99831 juv. ♂ ... Manus", "A.M. 99829 y. ad. ♀ ... Admiralty Is.", "A.M. 99900 y. ad. Q ... Admiralty Is.", "A.M. 99749 ad. ♀ (albino) ... Admiralty Is."

Tate (1945:27) mentioned "Our [AMNH] original small series of skins and skulls from Manus ... including one white female." Tate, who treated this species as "*Phalanger maculatus krämeri*," mentioned the Echiquier (Ninigo) Islands as included in its range but provided no further information. Tate also, somewhat tentatively, synonymyzed *Phalanger maculatus rufo-niger* Zimara, 1937 [= *Spilocuscus rufoniger* (Zimara)] of mainland New Guinea, with *S. kraemeri*. He (p. 19) characterized *S. kraemeri* (including *rufoniger*) as "Male with dark head, most spots dark, on white ground, female dark throughout, with reddish tail, hands, and feet. A white aberration occurs." Concerning the Ninigo Islands, Jentink (1885:117–118) had reported "*Cuscus maculatus*" from there on the basis of "Young male, Museum Godefroy, Hamburgh, 1869. Collected by Captain Alfred Tetens. Head, ears, hands, feet and spots on tail and on outerside of legs red; spots on back and nape of neck brownish red ... Adult female. Museum Godefroy, 1869. Collected by Captain Alfred Tetens. Tail injured. Crown of head, nape of neck, back and flanks sooty red; face and legs red; ears and tail yellowish red; underparts like in other females."

Laurie and Hill (1954) used the name *Phalanger* maculatus kraemeri for this form and, presumably following Tate (1945), treated it as not even subspecifically distinct from *Spilocuscus rufoniger* and listed it as occurring in the Echiquier (Ninigo) Islands and on the Huon Peninsula. They placed *Balantia minor* Oken, 1816 in the synonymy of *Phalanger orientalis* (Pallas).

Haltenorth (1958:28) wrote, concerning this animal, "Huon-F[leckenkuskus]., *P. m. krämeri* Schwarz, 1910; Huon-Halbinsel, Kaiser Wilhelms-Land, Admiralitäts- u. Echiquier-Inseln."

Collins (1973:177) gave the range of "*Phalanger* maculatus" as including "the Ninigo and Admiralty Islands, New Britain, New Ireland, and some of the Bismarck Archipelago."

Kisokau (1974) stated that he had collected "*Pha-langer maculata*" during the period 22 December 1971 to 19 January 1972 on "Rambutso Island" [= Rambutyo Island] and Lou. No information concerning where the specimens were deposited was given but it seems likely that it was in a collection that was housed in the old Department of Environment holdings at Moitaka, much of which was lost to mold, decay, and general lack of curation by the 1990s (information provided by an anonymous reviewer). All subsequent authors except for Menzies and Pernetta (1986) seem to have overlooked Kisokau's publication.

Feiler (1978) examined 32 skins and 2 skulls from Manus. These were some of the 35 skins and 7 skulls that had been the basis for Schwarz's original description of the species. Feiler gave the type locality as "Admiralitäts-Inseln." He mentioned one small white individual ("gelblichweiss oben und unten") which he thought was a young animal but said that the remainder were spotted. Feiler made it seem that the three females mentioned by Schwarz (1910), and showing the unspotted female pattern, were unavailable for some reason. Schwarz did not mention a white specimen. Feiler stated incorrectly that Schwarz had written that S. kraemeri's range reached to eastern New Guinea (the island). Feiler also mentioned two female, Berlin Museum, skins damaged by the war ("ZMB, 11. 9. 1899"), collected by Thilenius, presumably from the Admiralties, that he said that Schwarz must have seen. Feiler then divided the males into four groups on the basis of color pattern. For some reason, he listed only 30 of the 32 specimens he had examined. His first group consisted of the single whitish specimen. His second was individuals with the palest [or most pronounced?] spots, with the snout rusty red, rust-colored to reddishblack; the front feet and nape of the neck more or less paler or darker rusty (from golden yellow to reddishbrown); with only isolated white spots; pale rusty-red spots on the back, isolated darker spots between them; about 60% of its surface white, tail almost solidly rusty red with isolated pale spots.

The third group had the face until above the eyes rusty red, the neck rusty to almost black and without spots; the forefeet darker, reaching, in two cases, a blackish reddish brown, in general like in his second group. The ground color cream with pale golden reddish brown tinge, 60-80% of the surface of the back is white with large spots; the tail reddish brown more or less paler or darker and with white spots. Feiler mentioned one specimen from "12. 6. 1909" (recall that the catalog number of the holotype was variously given by Schwarz as "A. 12.6.09" and "A. 126 09") and taken by Schoede, identified to locality only by "Deutsch-Neuguinea," as having the ground coloration more yellow and with the dorsal spots not reddish-black but a deep and sharply contrasting black with 80% of its surface white.

The fourth group was made up of animals with dark skins, the forefeet a dark rusty red, large spots, with 30–50% of the skin white, intensely black spots on a yellow–white background, sometimes with isolated reddish spots in between, the tail reddish above, a pale yellowish–white underneath, the hind end above and below the same, one individual from "D.-Neuguinea" with the tail underneath also mostly reddish brown. A skin from "Hermit-Inseln," "Berlin Museum 5. 7. 1909," taken by Krämer resembled the specimens from Manus, the nape of the neck was very rusty, which is

seldom the case in specimens from Manus. The tail was said to be reddish brown as in the specimens from Manus.

Feiler discussed two skulls from what he called the "Hermit-Inseln," one from "Echiquier," "MNHL" (apparently a typo for MNHG, meaning from the Museo Civico di Storia Naturale "Giacomo Doria," Genoa) taken by Godeffroy, and a specimen in the Berlin Museum, "Agoma [?] A 19. 07." taken by Krämer.

Koopman (1979) referred to animals from the Admiralty and Ninigo Islands as *P*[*halanger*]. *maculatus*.

George (1987) treated *S. kraemeri* as belonging in the species *S. maculatus* (É. Geoffroy St.-Hilaire) and, tentatively, as constituting a recognizable subspecies.

Flannery and Calaby (1987) discussed one young female (AM 3693) and two male specimens (AM 3563, 5117). AM 5117 was labeled as from New Britain (which Flannery and Calaby thought was an extremely unlikely provenance) and the other two were Taronga Zoo (in Mosman, New South Wales) specimens of unknown origin. These specimens were identified as of S. kraemeri because they "conform closely to the morphology of kraemeri as described by Tate (1945) [see Tate's brief statement quoted above]." In addition to there being these Australian zoo specimens, the Field Museum in Chicago houses a male specimen FMNH 74914 (Figs. 1A, 2), represented by a skin and skull, from the Brookfield Zoo and labeled as from Australia, that clearly represents S. kraemeri. The history of this specimen may be tied in with that of the Australian Taronga Zoo specimens examined by Flannery and Calaby (1987). Paradiso and Fisher (1972) reported, for example, the importation of eight live "Phalanger maculatus" into the U.S. in 1970. Collins (1973) also discussed S. maculatus (including S. kraemeri?) being held in the Taronga Zoo and in at least one U.S. zoo. FMNH 7494 is discussed further in this species account under "Specimens examined." Pine has seen a specimen (apparently of S. maculatus sensu stricto) from a U.S. pet store and now housed in the Los Angeles County Museum.

Flannery and Calaby (1987) also mentioned a specimen from Mussau Island in the St. Matthias group as possibly belonging to *S. kraemeri*, but Flannery and



Figure 1. Skins of male *Spilocuscus kraemeri*. A—Stuffed skin of immature male (FMNH 74914), specific locality unknown. B—Incomplete skin of adult male (UWZM M27790) said to be from the island of Bali, off the north coast of New Britain (see text for additional details).



Figure 2. Dorsal, ventral, and lateral views of the skull of an immature male *Spilocuscus kraemeri*, specific locality unknown (FMNH 74914—see Fig. 1A). Condyloincisive length of skull = 75 mm.

White (1991), Flannery (1995b), Helgen and Flannery (2004), and Helgen and Jackson (2015) reported only *S. maculatus* from there. This last publication's treatment of the cuscuses on Mussau is odd, considering that Helgen (2007) treated the cuscus on Mussau as belonging to an unnamed introduced species.

Flannery and Calaby (1987:555) wrote "... we consider it extremely unlikely that kraemeri reached Manus with the aid of man, as it is a highly distinctive form, and given the lack of distinctive species to have evolved on islands isolated since the end of the Pleistocene in Australia, it appears to have been isolated on Manus for a considerably longer period." Nonetheless, Flannery and Calaby continued to treat kraemeri as a subspecies of S. maculatus. They noted (p. 555) that "Two color morphs have been recorded for adult female Spilocuscus from Manus. Feiler (1978) mentions a single white female from Manus. [In fact, Feiler indicated that the specimen was of a male—Tate (1945) mentioned a white female.] However, most individuals seem to be very dark-colored, with a large black saddle area on a reddish background." Although Flannery and Calaby (1987) provided color photographs of a skin of a typically spotted adult male [AM 3563] and a living juvenile male from an unknown locality, and Flannery (1995b) published a color photograph of a living adult and typically spotted male from Manus, we have found no photographs of an animal identified as an adult female. Feiler (1978) and Flannery (1994), however, provided colored drawings of adult males and females. Feiler's figured female from "Admiralitätsinseln" was Berlin Museum 11. 9. 1899, the male, Berlin Museum 12609 from Manus. Although Flannery (1994:218) stated that "The male [of the species] has small blackish spots on a white background ...," the spots on the male figured do not appear small and the earlier literature reports size of the spots as ranging from small to large. Flannery and Calaby (1987:554) wrote "It is possible that the white females from Manus and Mussau represent a distinct species related to the mainland S. maculatus and that the highly coloured kraemeri represents a separate species." Singadan (1996), however, assumed that white specimens of both sexes were only color variants in animals of the S. maculatus species group on the mainland of New Guinea, the Admiralties, and "the St. Matthais Islands." Flannery and Calaby (1987) provided descriptions of the color patterns of the specimens available to them. Their photograph of the juvenile male shows a gray animal with a white cheek. Singadan (1996) wrote that juvenile males are normally gray with grayish brown spots and patches. The two more-or-less adult males described by Flannery and Calaby are said to be (p. 554) with "limbs and tail ... brownish-red. The crown ... a darker shade of brown ... base coloration ... white ... dark mottling ... the same colour as the dark area of the crown over the shoulders ... becomes darker, almost black over ... lower back. Near ... base of ... tail ... spots lighten again [this variation in darkness of dorsal spots not evident in their published color photo]. Ventrally ... white, with brown hairs on ... lower sides of ... neck." They described (p. 554) a juvenile female as "... ventral surface has a white patch on the chest with a longer white patch over the belly. A darker line ... surrounds these light patches. Overall ... dark reddish-brown, with silvery red guard hairs. On ... base of ... tail ... lighter patch of fur ... under fur ... lighter coloured." Although Singadan (p. 78) wrote that the tail in both male and female S. kraemeri is "white with shades of brown or yellow," the specimens and figures we have seen show warm pale brown or more or less tan tails, although some white may be on the tails of some. Singadan gave body mass as 2.2-3.2 kg. Being unaware of the later archaeological discoveries to be made on Manus, Singadan hypothesized that the Admiralties cucuses had been introduced from the mainland about 3,000 years ago and had acquired their distinguishing characteristics since then.

Menzies (1991) provided a map indicating the range of S. m. kraemeri to consist of Manus and an unidentified dot in the ocean which is probably intended to represent Wuvulu, an island that is questioned as a habitat for S. kraemeri by Flannery (1995b), although it is listed from there by Helgen and Jackson (2015). Menzies gave "Admiralty Islands" as the type locality. He stated (p. 68) that isolated populations of Spilocuscus maculatus occur on "Wuvulu, Manus Islands [sic] but not New Britain." Writing of S. maculatus in general and presumably including S. kraemeri, Menzies stated (p. 69) that "Male spotted cuscuses are bigger than females" Helgen and Jackson (2015) stated the opposite, as had Jentink (1885), Cohn (1914), and Helgen and Flannery (2004). According to Helgen (2007), females average 14% heavier than males.

Flannery (1995b:104) treated *kraemeri* as a full species, stating "These species [*kraemeri* and *maculatus*] differ in dentition and skull features and are probably not closely related." The animal from Mussau Island was then apparently treated as *S. maculatus maculatus*. It was unequivocally treated as *S. m. maculatus* by Flannery (1994), apparently, also by Helgen and Flannery (2004), and definitely by Helgen and Jackson (2015).

Flannery (1994, 1995b) made no mention of the existence of white female individuals. He stated (1995b:105) "... archeological evidence suggests that it [S. kraemeri] has reached Manus recently, perhaps in the last one or two thousand years" Flannery (1994) and Flannery et al. (1994) had earlier expressed this same view. Helgen and Flannery (2004:831), however, wrote that at "Pamwak, a rockshelter site in southern Manus ... S. kraemeri is represented erratically in the record at least as far back as about 11,000 years ago. This ... suggests to us that S. kraemeri might be a natural element in the Manus fauna." In addition to Manus, Flannery (1995b:105) listed Lou and Luf (Hermit Islands) as places where S. kraemeri occurs and "Ninigo" and Wuvulu Island as places where it possibly occurs. Flannery (1994, 1995b) cited Cohn (consistently misspelled "Kohn" in 1994) (1914) as the authority for the species having been extirpated on Baluan and other, unspecified, islands. Groves (2005a) listed it only for Manus and Lou, as had Flannery (1994).

As late as 1988, Flannery (1995b:105) found *S. kraemeri* to be common on Manus "in all vegetation types, from gardens to almost undisturbed forest." The IUCN Red List of Threatened Species lists it as "Near Threatened" (see Helgen et al. 2008). Helgen and Jackson (2015:480) wrote that this species "... appears still to be common in all parts of its limited distribution"

Flannery (1994, 1995b) gave "Yowat" as the Nali language name ("South Manus") for this animal.

The colored drawing of the male, in Flannery's 1994 book, is based on AM M20925, from Polomou, Manus. The female depicted was acquired at the Lorengau Market on Manus. The specimen from Polomou is the only one of which we are aware which has had a

fairly precise field locality published for it. Flannery (1994) provided measurements from at least two males and two females from Manus. Natural history information is provided by Flannery (1994, 1995b).

Singadan (1996) noted that *S. kraemeri* is a lowland animal, usually occupying lowland rainforests, usually below 1,000 m. However, the maximum elevation of Manus is only about 720 m and no other island inhabited by this species is even that high. Singadan also noted that there were at least 52 specimens held in the collections of the University of Papua New Guinea and PNGMAG. Assuming that the 80 or so specimens seen by Cohn are still in existence, then the number of available specimens is indeed impressive.

Williams (1999) reported *S. kraemeri* remains from as far back as ca. 11,000 ybp, at the Pamwak archeological site on Manus.

Anthony (2001) discussed the purchase, in a market in Kimbe, New Britain, of a skin of a cuscus which had reportedly been speared on the small island of Bali off the north coast of New Britain. (Bali is an alternative name for the island generally known as Unea or Uneapa in West New Britain.) Judging from the photograph provided of this skin and our direct examination of the specimen (UWZM M27790; Fig. 1B), it is that of a male *S. kraemeri*, although Anthony identified it as that of an *S. maculatus*.

Helgen and Flannery (2004:828) wrote, concerning Spilocuscus wilsoni, that the "adult male coat is pure white dorsally and ventrally ... as in some ... S. m. maculatus ...", taking no note of white individuals of both sexes, reported of S. kraemeri, although Flannery and Calaby (1987) had earlier mentioned white Spilocuscus from Manus and which they supposed might represent a second species there. [Somewhat incongruously, Helgen and Jackson (2015) in their discussion of S. kraemeri, mention that there are white individuals of S. rufoniger (Zimara, 1937), but make no mention of white S. kraemeri.] Helgen and Flannery (2004:830) also stated "Two species of Spilocuscus occur in the Bismarck Archipelago of eastern Papua New Guinea: S. maculatus maculatus, which occurs on the islands of Mussau ... and New Ireland; and S. kraemeri of the Admiralty group ...". They stated that the Bismarck S. maculatus apparently had been introduced from the island of New Guinea (see also Flannery and White 1991). Although Flannery et al. (1987) give the presence of a protocone on "M1" (the upper deciduous tooth in their reckoning) as a defining characteristic of Spilocuscus, Helgen and Flannery (2004) stated that the diagnostic protocone was on "P3." Citing Williams (1999), Helgen and Flannery noted that archeological remains of this species are now known from as far back as 11,000 years ago on Manus, which suggested to them that it "might be a natural element in the Manus fauna." However, they also suggested that the Admiralties populations might originally have been derived from New Britain, an island which previously had been thought to harbor no Spilocuscus. In support of the idea that S. kraemeri might inhabit New Britain, they cited the specimen (AM M5117) earlier mentioned by Flannery and Calaby (1987) as being labeled as from New Britain, and the specimen figured by Anthony (2001) and supposedly from the New Britain satellite island Bali. See our treatment of Phalanger orientalis for an account of Helgen and Flannery's ideas concerning their hypothesis as to why S. kraemeri is common on Manus and rare on New Britain (if it occurs there at all). Helgen and Jackson (2015:480) wrote, concerning the presence of S. kraemeri in the Admiralties "... may have been introduced to some or all of these islands, and have originally evolved on New Britain."

Helgen and Jackson (2015) listed S. kraemeri from the island of Los Negros, which is separated from Manus by a narrow channel, and from Pak Island in the Admiralties, in addition to the islands previously mentioned herein. They also described the ground color of the back of male S. kraemeri as being chocolate brown with creamy-white blotching or spotting. Based on specimens we have seen, however, this pattern has tended to be reversed and the dark areas often darker than chocolate brown. AMNH 99750, from Rambutyo, however, appears to have a bit more dark coloration dorsally than whitish. Aplin et al. (2015) reported that during the time spent on Mt. Sabomu (2-7 October 2014), one adult female with a fully furred pouch young was captured by a landowner and one other individual was observed sleeping in the crown of a tree (page 56), and they state that S. kraemeri has been recorded from Los Negros. It surely is there or was, but we have found no additional records of this, although AMNH 182070 (see below), a zoo-derived specimen, is labeled as from "Las [sic] Negros." A facial image of a live adult, presumably a female, was provided by Whitmore et al. (2015:xix). Aplin et al. (2015) report that Wildlife Conservation Society staff and University of Papua New Guinea students are studying the ecology of the Admiralty Cuscus at several localities (possibly only on Manus). They state further that the *Spilocuscus* from the St. Matthias Group (which includes Mussau) represents an unnamed species, and cited Helgen (2007) as their authority. As noted earlier, this is in contrast with Helgen and Jackson's (2015) account, which lists the animals from Mussau as representing *S. maculatus*.

Specimens examined.—FMNH 74914, which was referred to earlier, is represented by a stuffed skin in good condition (Fig. 1A) and a skull (Fig. 2) in which the right premaxilla is glued in place and the right maxilla and lachrymal had become loose anteriorly. The animal was an immature male received at Chicago's Brookfield Zoo on 14 July 1953 and which died in captivity on 16 December 1953. The deciduous teeth are still in place, the third molars were unerupted, and the fourth molars are undeveloped (Fig. 2). After the original skin tag was written in ink, someone added the word "Australia" to the tag in light pencil. Greatest length of skull is 75 mm. M1 is 6.9 mm in length. Only one small and nonfunctional tooth, rather than two or three such teeth, is developed on each side of the mandible, between the large incisor and the deciduous tooth. This is a common condition in S. kraemeri (see Cohn 1914; Feiler 1978) and is also the case, unilaterally, in three of the seven AMNH specimens we examined and that were collected by Maa. There can be no doubt that this specimen is of S. kraemeri. The color pattern of the pelage possesses all of the diagnostic features as seen in the most typical males of the species, as described and figured in the literature, and as also possessed by male specimens of S. kraemeri examined by us in the USNM (Fig. 3) and AMNH. This includes the very sharply contrasting dorsal and lateral pattern of whitish ground color and bold black spots, the tawny rump and tail, and the distally dark forelimbs with a chestnut suffusion (Fig. 1A).

The incomplete skin, UWZM M27790 (Fig. 1B), identified on the tag as being of an adult male, likewise appears to unequivocally belong to *S. kraemeri*. Also according to the tag, it was "Purchased from market in Kimbe, New Britain. 'Killed with spear on the Island of Bali'" just off the coast of West New Britain. The



Figure 3. Stuffed skins of adult male *Spilocuscus kraemeri* from the series of six collected in 1944 at Lorengau, Manus Island (purchased at the market?) by D. H. Johnson. A—USNM 276981; B—USNM 276978; C—USNM 276979.

reddish coloration of the rump and tail is deeper and richer than in FM 74914 and the black markings dorsally and laterally are elongated to form a somewhat striped pattern but this falls well within the range of variation in *S. kraemeri* (see, for example, Feiler's 1978 plate 2 depicting *S. kraemeri*). Here again, the dark coloration becomes more general anteriorly and what is left of the skin of the forelimbs shows a chestnut suffusion. Unfortunately, the skin of the head, the distal portions of the front limbs, of the hind limbs, and the

distalmost portion of the tail, is missing in this specimen. The apparent size of the animal that possessed this skin is consistent with that of adult *S. kraemeri*.

AMNH 193746–193752: These seven specimens, from a series also including AMNH 193753 (not seen), were collected on 15 December 1959 at Lorengau (purchased in the market?) by T. C. Maa. They were prepared as fluid-preserved heads only, but the skulls of the seven at least, have now been cleaned and the head skins—in poor condition—saved. Until examined by us, these specimens, unidentified to sex and without field measurements or notes, had been identified as of *"Phalanger orientalis intercastellanus."* They range in age from an immature with deciduous teeth, unerupted (but visible in the cleaned skull) third molars, and undeveloped fourth molars (greatest skull length = 68.8 mm) to an adult (greatest skull length = 83.3) with all adult teeth fully in place (Fig. 4A, B, C; Fig. 5A, B, C). In addition to the individuals of these two age classes, there is another with the third premolars fully erupted. All possess only two upper premolars in each maxilla, except for one which bears, unilaterally, only the third.

Additional specimens seen are: AMNH \bigcirc skin & skull 166953, "Admiralty Isl.," "Manx Zoo, N.Y. Zoo Soc.;" AMNH $\bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc$ skulls only 99829–99832 from "Manus Isl.," collected by W. F. Coultas; AMNH \bigcirc skin & skull 99900 from "Manus, Village Drabui" (coordinates?), external measurements 450, 400, 73, 25, collected by Coultas; AMNH \bigcirc skin & skeleton 182070 from "Las [sic] Negros Island; near Manus," "Gift: N.Y. Zoological Society," very large skull 94.2 mm including incisors, sutures tending to be fused;



Figure 4. Dorsal, ventral, and lateral views of crania of *Spilocuscus kraemeri*. A—AMNH 193746, condyloincisive length of skull = 65.0 mm; B—193748, condyloincisive length of skull = 76.4 mm; C—193747, condyloincisive length of skull = 78.9 mm. Specimens from a series of eight collected in 1959 at Lorengau (purchased in the market?) by T. C. Maa.



Figure. 5. Dorsal and lateral views of the corresponding mandibles from crania in Figure 4 of *Spilocuscus kraemeri* from the series of eight collected in 1959 at Lorengau, Manus (purchased in the market?) by T. C. Maa. A—AMNH 193746; B—193748; C—193747.

AMNH Q Q Q skins only 99747–99749 from "Rambutyo Is.," collected by Coultas, external measurements 480, 390, 67, 20; 500, 430, 67, 23; and 520, 440, 68, 23, respectively. A latex endocranial cast of AMNH 99749 is deposited at the Field Museum, although the skull is now missing from the AMNH. AMNH \Im skin & skull 99750 from same locality, same collector, external measurements 478, 384, 68, 21.

In addition to the above specimens, we are fortunate to have examined five specimens in the Papua New Guinea National Museum & Art Gallery. These consist of four adult females and an immature male for which developmental information is available. Also, all five are provided with locality data. Previously, only one locality had ever been published. Our figured color photograph (Fig. 6) of a skin of an adult female is the first such photo to be published either in color or black and white. Whitmore (2015:xix) provided a photograph of a head and part of a forelimb of a living animal, however, which might very well be that of an adult female, perhaps the one mentioned by Aplin et al. (2015:56). The immature male, PNGMAG 22552 (Fig. 7), was shot in "Tall Lowland Canopy" at Kabuli on 17 November 1974. Total length was 447, head plus body length 239, tail length 208, mass 250 g. The milk premolars are still in place, the first molars the only ones erupted. The coloration of this immature is unlike that of any specimens, of any age, reported previously, being a uniform dark drabby brown dorsally and laterally, creamy midventerally and on the lower jaw. Additional data dealing with measurements and dates of collection will be necessary in order to evaluate Cohn's (1914) conclusion that this species is diestrous.

The four females (PNGMAG 22430, 22550, 22551, 22553) are all age-ranked as old adults, except for 22553, which is ranked as a young adult. All were shot in "Lowland Rainforest" or "Lowland Canopy" or "Tall Lowland Canopy" at "Kabuli Base Camp, SW Manus I." or at "Kabuli (2°7′50″S, 146°40′0″ or 10″E or 2.1305S, 146.6695E)." Measurements of the three old adults are: condylobasal length 82.1–90; total length (for 2) 880, 915; head plus body length 462–498; tail length 417–425; hind foot without claw 58–60; ear from



Figure 6. Skin of adult female *Spilocuscus kraemeri* (PNGMAG 22550) from Kabuli, Manus Island. Total length = 892 mm; mass = 2.8 kg; condylobasal length = 82.1 mm.



Figure 7. Skin of an immature male *Spilocuscus kraemeri* (PNGMAG 22552) obtained at Kabuli, Manus Island, on 17 November 1974. Total length = 447 mm.

notch 22–26; mass 2.8–3.2 kg. None of the dimensions of the young female exceeded the greatest ones for the older animals and some were smaller than them all. Its mass was 2.2 kg. Coloration in these females was more or less similar. The dorsum anterior to the rump ranged from dark chocolate brown sometimes suffused with chestnut, especially anteriorly and on the crown. The rump and tail fur are contrastingly bright pale golden brown. The legs tend toward chestnut. The cheeks and lower jaw and a midventral stripe are cream-colored, with this stripe sometimes bordered with black or near-black (see Fig. 6).

Eight specimens, all from 1944, were briefly examined at the (U.S.) National Museum of Natural History. These were USNM 276975-2769781, 277034. USNM 276975 was taken on "Ponam Islet." The rest were labeled as from "Lorengau on Manus (purchased in market?), except for 277034, labeled as from "Admiralty Islands." The specimen from "Ponam Islet," represented by a skin and skull, had a very large, robust skull with the supraorbital region much elevated, as is typical for Spilocuscus maculatus. Only one of the anterior minute lower premolars was present on each side. USNM female 276976 and 277634, provided with both skins and skulls, had skins with color patterns similar to those of females in PNGMAG (see Fig. 6), although no sex determination was provided for 277034. USNM female 276977 was cataloged as a skin plus skull specimen but only the skull was found. Both initial upper premolars were absent. USNM males 276978, 276999, 276981, skins with skulls, had pelage pattern and coloration (see Fig. 3) similar to that of FMNH 74914 (see Fig. 1A). USNM 276979 had only one of the minute initial lower premolars present on each side. USNM 276981 lacked the initial right upper premolar. USNM 276980, an immature, supposedly a skin plus skull specimen, had only the skull at hand. USNM 277003, a female immature in fluid, was not examined.

The Australian Museum (Sydney, New South Wales) has 21 specimens of *S. kraemeri* that were obtained from markets on Manus and 6 specimens obtained from the Taronga Park Zoo.

RODENTIA Muridae Melomys matambuai Flannery, Colgan, and Trimble, 1994 Manus Melomys

Flannery, Colgan, and Trimble (1994) named Melomys matambuai and placed it in the Melomys rufescens (Alston, 1877) complex, an assigned affinity with which we agree. They regarded it as the only known non-volant, endemic mammal inhabiting Manus. Judging from the literature, other members of the complex are M. arcium (Thomas, 1913); M. bougainville Troughton, 1936; M. caurinus (Thomas, 1921); M. cooperae Kitchener, 1995; M. dollmani Rümmler, 1935; M. fulgens (Thomas, 1920); M. gracilis (Thomas, 1906); M. leucogaster (Jentinck, 1908); M. paveli Helgen, 2003; and M. talaudium (Thomas, 1921). Various members of this group have been unusually successful in colonizing far-flung islands. (One wonders if their apparent semi-arboreality has made it more likely that they would be transported and survive on floating masses of woody vegetation.) Flannery et al. (1994) noted that Rattus exulans, Spilocuscus kraemeri, and Echymipera kalubu had been recorded from Manus, but they regarded these species as having been introduced by human agency during the Holocene. Helgen and Flannery (2004), however, concluded that S. kraemeri and E. kalubu might be native to the island. In 1995(b), Flannery mentioned Rattus praetor (Thomas, 1888) as an additional species occurring on Manus (where it is not actually known to occur), but he probably regarded this animal as also having been introduced by humans, because he wrote (p. 199) "It has been introduced prehistorically into most of its insular distribution " Musser and Carleton (2005), in their account of Melomys matambuai, referred to "M[elomys]. bougainville on Manus Isl," but they did not list Manus in their account of Melomys bougainville and we know of no records from there.

The original description was based on two specimens, with the holotype being of an adult female taken 15 June [non-lactating according to Flannery (1995b)] and consisting of a damaged and incomplete skin, undamaged skull, spirit-preserved carcass, and a frozen liver sample. This specimen was taken at "200 m near Polomou DPI Station, south-central Manus (2°08'S, 147°05'E)." The paratypic specimen is also of a female, variously referred to in the description as an "adult" and "subadult," and consists of a skin, "fragmented skull," and a carcass in spirit, and was taken "at the western end of Manus Island."

Both the holotype and paratype were shot, the holotype in low secondary growth about 1.5 m above the ground at the edge of a cacao plantation "climbing on a cacao bush" according to Flannery (1995b:140). The paratype was shot in a "sago palm." Trapping efforts on the ground failed to capture this species, which led its describers to suggest that the animal is largely arboreal, as is also suggested to us by its morphology and coloration, and is in keeping with the habits of its nearest relatives (see Flannery 1990, 1995a, b). Aplin et al. (2015) also failed to obtain specimens or images of this animal by means of both live traps and camera trapping on the ground. By contrast, they noted that camera trap images had been obtained of it in trees in 2013 and 2014.

The University of Kansas has now acquired, from Manus, the third and elements of the fourth known specimens of this species, and the Papua New Guinea National Museum & Art Gallery also a portion of the fourth, allowing us to provide additional details concerning its morphology and natural history, beyond what Flannery et al. (1994) provided. The specimens are KU 163717, adult female, well-prepared skin (Fig. 8) with intact skull and first two cervical vertebrae and part of the third, taken 9 August 2002 by Ann Williams; KU 163722/PNGMAG 28051, an adult female, intact skull and first three cervical vertebrae (KU), well-prepared skin (PNGMAG), and taken on 6 August 2002 by Williams at "Tulu No 1," at 1°57.371' S, 146°50.282' E. KU 163717 was acquired at "Sokai Camp" at 1°58.267'S, 146°47.773'E, "captured in live trap on ground—in base of large tree" according to the skin tag but in "trap set in large dead tree buttress/hole" and "foetus preserved" according to the field catalog. KU 163722/PNGMAG 28051 was taken in trap "set on ground under rattan in sparse undergrowth" "foetus inside." One of these individuals, freshly killed, is shown in Fig. 9. Its pelage, as it appears in the photograph, is much more reddish than in the KU skin.



Figure 8. Dorsal and ventral views of a stuffed skin of an adult female *Melomys matambuai* from "Sokai Camp," Manus (KU 163717). Total length = 342 mm.



Figure 9. A recently killed specimen of an adult female *Melomys matambuai* from Manus Island (either KU 163717 or KU 163772/PNGMAG 28051). Photograph courtesy of Ann Williams.

The nipples in both of the two new specimens are hypertrophied and consist of two inguinal pairs [according to Helgen (2003:169) this pattern is found in all "*Melomys* (sensu stricto) and closely related genera (excluding *Mammelomys* ...)"]. External measurements taken by the collector of KU 163717 and KU 163722/PNGMAG 28051, respectively, are: head plus body, 162, 165; tail, 180, 175; ear (from notch), 19, 19; hind foot without claw, 36, 36; hind foot with claw, 39, 39; mass, 170 g, 200 g. As noted in the original description, *M. matambuai* is the largest species in the *Melomys rufescens* species group. A cryptic note on the tag of KU 163717 and concerning the tail reads "not visible white tip." This was noted in contrast to the situation in KU 163722/PNGMAG 28051, which had a white-tipped tail according to the field catalog, but this is not apparent in a photograph of this specimen. The tail in the holotype is mostly missing, so whether it had a white-tipped tail is unknown. Compared to the skins of six specimens of mainland *Melomys rufescens* sensu Flannery (1995a) from Eastern Highlands Province, Simbu (= Chimbu) Province, and Gulf Province, at elevations ranging from 50 m to 1450 m, the fur of KU 163717 appears less dense, coarser, crisper, and less woolly. The dorsal fur at midback on KU 163717 is no longer than 10 mm, about the same as for a specimen

of M. rufescens (KU 163715) from an elevation of 50 m. Although Flannery et al. (1994) stated that the fur is shorter in M. matambuai than in M. rufescens, it is not always absolutely shorter, although it is relatively shorter. The dorsal fur length on the remaining M. rufescens ranges up to at least 15 mm. The ventral fur at midbelly on KU 163717 is very short, ca. 4 mm, again matched by that on M. rufescens KU 163715, but exceeded in length by that of M. rufescens from higher elevations. The colors and their distributions are essentially the same as in some *M. rufescens* examined. Dorsally, the fur appears to be between Snuff Brown and Buffy Brown of Ridgway (1912) and between Prout's Brown and Brussels Brown of Smithe (1975). The coloration as shown in our photographs of the skin of KU 163722/PNGMAG 28051 is variable, sometimes appearing darker than in KU 163717, sometimes redder, and sometimes about the same. Probably there is little difference between the two in this regard. In both specimens, the venter is broadly self-colored white from the lower lip, the naked palms, the ankles, and the vulva, with very little encroachment of gray-based white hairs laterally. Some M. rufescens seen have much less extent of white on the extremities. The description that follows is based mostly on KU 163717. Vibrissae of the head are long and numerous, ranging in length to at least 60 mm. The heaviest vibrissae are black, finer ones unpigmented, with a few black basally and unpigmented near the tips. Vibrissae at the wrist are few in number and unpigmented. The outside surface of the pinna is well-furred basally and provided with minute pale hairs distally. The manus is provided with sparse dark hairs dorsally grading into less-pigmented hairs on the digits. Scalation is quite evident dorsally on the digits. The palm is without pigment. The dorsal surface of the pes possesses very short, mostly unpigmented hairs. Scalation is evident on the toes. The sole is either unpigmented or very lightly so. The claws are very large, curved, and thick. Although Flannery et al. (1994) stated that the tail in their specimen is "uniformly black," in the specimen at hand it is quite definitely brown, not black, above and below, although it is somewhat paler below and proximally. The tails of the M. rufescens available for comparison are darker than that of KU 163717, although, for the most part, they are merely a darker brown, rather than being actually black, in spite of the vernacular name "Black-tailed Melomys" and statements in the literature that the tail is black. The tail scales are flatter, less raised in KU 163717 than in the *M. rufescens* at hand and many are concave within a raised outer border. Their shape ranges from roughly circular to squarish to roughly hexagonal. Dorsally and proximally, they number 14 per cm; laterally, midway along the tail, 11 per cm. Distally, there is one hair per tail scale; proximally, this number can be exceeded. Tail tip without scales.

The skulls of the two new specimens of M. matambuai, compared with those of nine mainland New Guinea M. rufescens sensu Flannery (1995a), are much larger and more massively constructed, with proportionally shorter and heavier rostra and indications of postorbital processes of the frontals, which are not present in the *M. rufescens* nor, apparently, in the holotype and paratype of *M. matambuai*. Although the describers of M. matambuai noted its relatively robust rostrum, they stated that "the parietal cresting is less well-developed." In the KU specimens, however, the lambdoidal crests, including their extension onto the parietals, are more prominent than in the specimens of M. rufescens at hand. The braincase is less inflated in M. matambuai. Otherwise, the skulls of the two species are similar (Fig. 10A, B). Because the skull of the paratype is "fragmented," only a single value has been available for many cranial measurements. Therefore, the availability of the skulls for the new specimens is especially welcome.

One additional difference between M. matambuai and *M. rufescens* is that the bone in the orbital region, and/or just anterior to that and medial to the zygomatic bridge, consists of very thin bone and one wonders if it is always bony at all or merely, at least in part, replaced by a membrane. This is because in all nine skulls of M. rufescens at the University of Kansas, there is a bilateral vacuity in this region (see Fig. 10B). This is also the case in 15 skulls labeled as being of M. rufescens at the (U.S.) National Museum of Natural History. A 16th skull, USNM 58640, so identified, but atypically small and with unusually large teeth, with body in fluid, may lack this hole or have it barely manifested on the right side. This vacant space in the bone varies in size, shape, and position and may be doubled. It appears that the cleaning process, perhaps starting with the dermestid stage, removed the very thin bone that presumably must have been there originally.



Figure 10. Dorsal, ventral, and lateral views of the crania and lateral view of the right dentaries of adult female *Melomys* from Papua New Guinea. A—*Melomys matambuai* from "Tulu No. 1," Manus Island (KU 163722/PNGMAG 28051, greatest length of skull = 39.7 mm); B—Adult \bigcirc *Melomys rufescens* from mainland New Guinea (KU 160752; Ivimka Camp, 11 km SE of Tekadu Airstrip, Gulf Province, Papua New Guinea, 120 m, 7°44′05″S, 146°29′45″E; greatest length of skull = 32.0 mm).

Cranial measurements (for KU 163717, then for KU 163722/PNGMAG 28051) are: greatest length of skull (occiput–nasals), 39.9, 39.7; condylobasal length, 37.9, 37.3; greatest nasal length, 12.3, —; palatal length, 19.5, 19.4; palatilar length, 16.9, 16.5; incisive foramen length, 5.1, 4.7; palatal bridge (left side), 9.0,

8.8; length of upper diastema, 10.1, 10.1; upper molar alveolar length, 7.3, 7.0; width of rostrum, 7.5, 7.9; least interorbital breadth, 7.2, 7.0; zygomatic breadth, 20.7, 20.5; interparietal length, 7.0, 6.2; and interparietal width, 11.5, 10.0.

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Both new specimens were pregnant with only a single fetus. This is in keeping with the very small number of young in litters of other species of *Melomys* and with the small number of mammae.

Ann Williams (in litt.; see Timm et al. 2016) writes that the local name for this animal is "murasu." This was rendered by Flannery (1995b) as "Musirou" for central Manus. C. Williams (1999) reported skeletal material identified as of "*Melomys* sp." and as of the "Manus Melomys." Flannery (1995b) noted the presence of *M. matambuai* throughout the Pamwak archaeological site sequence. Aplin et al. (2015) stated that numerous specimens are known from that site but incorrectly indicated that Flannery had not found them among the Pamwak rodents.

The IUCN Red List of Threatened Species lists *M. matambuai* as "Endangered" (Leary et al. 2008). Aplin et al. (2015) reported 397 "ground trap nights" in 2014, without catching this species.

Rattus detentus Timm, Weijola, Aplin, Flannery, and Pine, 2016 Admiralties Rat

This recently described species, so far as known endemic to Manus and probably adjacent Los Negros, is the subject of a recent description and biogeographical analysis by Timm et al. (2016).

In 1988, Tim Flannery, while on Manus (Flannery 2011), was told that there were two species of rat on the island, besides the ones he knew were introduced commensals. One was described as a red-pelaged arboreal rat and the other as a terrestrial rat with a white-tipped tail. Flannery succeeded in acquiring the first, which was *M. matambuai*.

Subsequently, archeological excavations at the Pamwak rock shelter on Manus turned up jaws and teeth of an early to late Holocene age rat that was variously identified by Williams (1999) as *Rattus praetor* and *R. mordax*. Flannery (1995b) examined these specimens and identified them as being of what he later described (2011:97) as "a formidable, hitherto unknown rat with a powerful bite." Flannery (1995b:38) wrote, concerning this rat, "A large species of *Rattus*, probably representing an undescribed species, persists into the most recent levels..." of the Pleistocene Pamwak deposits—see also White et al. (2000).

In 2002, Ann Williams acquired from local people on Manus a nearly complete skeleton and a mandible of a second specimen, which came to the University of Kansas. Although the skeleton and isolated mandible are clearly from adults of the same species, the mandible is from what must have belonged to a larger individual than the other. Measurements of greatest distance between posteriormost point of alveolus of incisor and posterior edge of coronoid process are, respectively, 26.8 and 29.7. Flannery identified these two specimens as representing the same species as the undescribed rat from the Pamwak site. In 2012, Valter Weijola acquired an entire specimen which became the holotype of Rattus detentus. This species is presumably the same animal as the large terrestrial rat with a white-tipped tail of which Flannery (2011) had written, although the holotype, the only specimen for which external anatomy is known, does not have a white-tipped tail. It should be noted that one of the two recent specimens of Melomys matambuai, which have complete tails, has a white-tipped tail. However, according to Flannery (2011), and as noted earlier, the locals distinguish between a red, arboreal rat (M. matambuai) and a large terrestrial rat, and it was the latter that was said to have the white-tipped tail.

In 2014, Aplin (see Aplin et al. 2015), who had, by this time, studied not only all three recently collected specimens, but also the specimens from the Pamwak site, made special efforts to find this rat on Manus. In this he failed, although he did find a burrow system which he thought had probably been excavated by this species. Other signs of its presence, which Aplin expected to find if the species was at all common, were not found. This apparent rarity is in contrast with what locals told Valter Weijola when they were shown pictures of the future holotype. They claimed that the species is widespread on Manus and also occurs on Los Negros (Timm et al. 2016).

Locals told Weijola (in litt.) that these rats often eat tapioca roots and pineapples in the gardens and fallen *Canarium indicum* (Burseraceae) nuts in the forest. The holotype was caught in an unbaited snare set by locals targeting bandicoots and rats. Unbaited snares were set along trails made by small mammals through undergrowth and often exiting near small streams. Traps set for monitors (*Varanus indicus*) and baited with fish were also sometimes raided and the lines cut off with a clean snip, which local trappers insisted was the work of rats rather than bandicoots, because the latter supposedly chew the line off. These anecdotal observations and conclusions suggest that *R. detentus*, like many other species of *Rattus*, has a rather wide dietary range. The rats themselves are said to be often hunted for food, particularly in the central parts of the island.

Timm et al. (2016) provided detailed information concerning the biogeographical features of Manus and vicinity, as they relate to the presence of R. *detentus* on Manus.

Rattus exulans (Peale, 1848) Pacific Rat

Thomas (1914:439) reported three specimens of "*Epimys browni*" from "Manus Island." Taylor et al. (1982), referring to these same three specimens, recorded them as from "Manus Is., 5 m, 02°04'S, 147°00'E," treated them as members of *Rattus exulans browni* (Alston, 1877), and gave their catalog numbers as BMNH 14.4.1.18–14.4.1.20. Owing to the known recent past and assumed present mobility of this commensal species, we do not recognize subspecies.

Williams (1999) did not report *R. exulans* as having been found at the Pamwak archeological site on Manus, but T. F. Flannery (in litt.) states that he did find this species in remains from there. Although Aplin et al. (2015:51) stated that Flannery (1995b) reported *R. exulans* from the Pamwak site, this is not the case.

Aplin et al. (2015:57) reported having caught 13 specimens in 2014, encountering this species in a variety of habitats on Manus, noting "They appeared to be most numerous in the garden and village habitats, and to be relatively scarce in the natural forest." This is not surprising in view of the commensal nature of this species. In addition to trapped individuals, visual sightings and camera trap records were also recorded.

We here report five additional trapped specimens, housed at the University of Kansas. These are KU $\stackrel{<}{\supset}$ 163725 and KU $\stackrel{<}{\ominus}$ 163726 from Manus, without more

precise known locality and taken by unidentified collectors; KU O 163727 from "Tulu 1" at 1°57.371′S, 146°50.282′E, 34 m; and KU O 163788, 163929 from Manus but from no named locality at 2°0.102′S, 146°48.634′E. Elevation for 163729 was 31 m.

In addition to the specimens at the University of Kansas, there are two specimens in the collection of PNGMAG, identified as belonging to that species and from the Admiralties. These are PNGMAG 22514 from "Airie Base Camp" with the nearest village given as Pelikawa (2°12'0"S, 146°55'59"E or 2.2°S, 146.933°E-but see locality information for next specimen), on Manus, said to be a flat skin but preserved in "75% alcohol," specimen not seen; PNGMAG 22477 from "Airie" [apparently = Aerie Camp or Airie Camp at 2°07'S, 146°42'E-see Bonaccorso (1998:427)], images of study skin and skull seen. PNGMAG 22477, on the basis of photographs, seems to have atypical coloration for R. exulans, being unusually reddish dorsally but with an apparently unremarkable gray-based venter with broadly cream-colored tips. The skull appears to be that of an R. exulans, however, in shape, size, and dentition. Taylor et al. (1982:277) stated that the quality and color of the pelage of R. e. browni are "highly variable." However, they stated unequivocally (p. 278) that the ventral fur is gray-based.

The affinities of the *exulans* on Manus might warrant further study. Although the upper toothrow lengths of the KU specimens fit within the range given by Taylor et al. (1982), there is considerable variation in tooth size in these Manus specimens. The teeth of immature 163728 are especially large, compared to those of the other specimens from there.

Rattus rattus (Linnaeus, 1758) Black Rat

Taylor et al. (1982) recorded *Rattus rattus* from "Lorengau, 10 m, 02°01'S, 147°16'E" on Manus, on the basis of AMNH 193763–193765, 193768.

Williams (1999) identified subfossils from the Pamwak archeological site as of *Rattus rattus*, going back to about 11,000 ybp, but owing to this being such an early date, expressed some uncertainty concerning the identification. Flannery (in litt.) states that he found no specimens of *R. rattus* among the Pamwak remains.

Rodents Reported Erroneously or of Dubious Occurrence in the Admiralties

Melomys bougainville Troughton, 1936

In their discussion of *Melomys matambuai*, Musser and Carleton (2005), in an apparent lapsus, gave the range of *M. bougainville* as "Manus Isl."

Rattus mordax (Thomas, 1904)

Williams (1997, 1999) identified *Rattus mordax* on the basis of subfossils of mandibles from the Pamwak archeological site on Manus. This is the sole reference that we know of to *Rattus mordax* occurring in the Admiralties. Flannery's (1995b) map shows no localities anywhere near these islands. In Williams's (1997) table of mandibular bone and lower dental measurements, some specimens are identified as of *Rattus mordax*, certain others as of cf. *Rattus mordax*, and certain others as of *Rattus detentus*. Flannery (see Timm et al. 2016), in his examination of Williams's specimens, reported only *Rattus exulans* and what is now known as *Rattus detentus*.

Rattus praetor (Thomas, 1888)

Menzies and Dennis (1979:63) listed *Rattus ruber* (= *Rattus praetor*) for "*Admiralty Islands* (Manus Island)," but gave no source for this information. Taylor et al. (1982) recorded Australian Museum specimens M7183–M7184 [the basis for Troughton's (1946) *Rattus purdiensis*] from "Bat Island, 5 m, 02°51′S, 146°14′E" but mentioned no other records in that vicinity. Flannery et al. (1994) did not list *R. praetor* from Manus, but Flannery (1995b) stated that *Rattus praetor praetor* occurs on Manus, Bat, and Blup Blup. Flannery has informed us (in litt.) that his source for *R. praetor's* supposed presence on Manus must have been Menzies and Dennis (1979).

Williams (1997, 1999) reported *R. praetor* for the Pamwak site and White et al. (2000) accepted the accuracy of these reports, but T. F. Flannery (see Timm et al. 2016) found no fossils attributable to this species, in his examination of the material. Timm et al. (2016) recently reported that many of the supposed specimens of *R. praetor* from Pamwak are best attributed to *R. detentus*.

Uromys neobrittanicus Tate and Archbold, 1935

Menzies and Dennis (1979:63) provided lists "taken from the literature" of species of rodents found on various islands in the vicinity of New Guinea. For "Admiralty Islands (Manus Island)," they listed "Uromys neobrittanicus." We have been unable to find any records of this species other than those from New Britain, in the literature that they cited, and do not know the source of Menzies and Dennis's information. Nor have we found any mention in the literature published subsequent to Menzies and Dennis's publication, of the Admiralties' harboring of this species.

Williams (1997) provided, in a table, measurements of a subfossil mandible from the Pamwak site, which was identified as of an "*Aromys* sp. [sic]", although this identification was mentioned nowhere else in that dissertation, nor was it mentioned by Williams later (1999). Flannery (in litt.) found no skeletal material that he identified as of *Uromys*, among the Pamwak specimens.

The original and consistent spelling of this animal's name was Uromys neobrittanicus (see Tate and Archbold 1935). In the same paper, Tate and Archbold also named Hydromys neobrittanicus [sic] and consistently used this spelling. Ellerman et al. (1941) simply spelled this name as Uromys neobritannicus without comment, whereas they spelled the name of the Hydromys as neobrittanicus. Laurie and Hill (1954) incorrectly emended the names of both the Uromys and the Hydromys to neobritannicus, on the basis that the original spellings were misspellings. Musser and Carleton (2005) also rendered the names as Uromys neobritannicus and Hydromys neobritannicus, and Flannery and White (1991) and Flannery (1995b) also used both these spellings.

DISCUSSION

With the discovery of *Rattus detentus*, the list of species of terrestrial, non-flying mammals of the Admiralties has probably at last been completed, at least for Manus. This is attested to by the mammal remains found and not found in the deposits of the Pamwak rock shelter, which date from the Late Pleistocene to the Late Holocene. All of the non-commensal and non-feral species which have been studied taxonomically apparently evolved there, although the specimen of Spilocuscus kraemeri from an island off the coast of New Britain raises questions in this regard. The bandicoot, Echymipera cf. kalubu, as noted in the section devoted to it above, may also prove to be an endemic form. New specimens being made available of that species would be most welcome. The extremely small numbers of non-archaeological specimens of the

two apparently endemic rodent species also invite more collection. We know of no specimens in any museum of the animals that were reported on as being on Rambutyo and identified by Kisokau (1974) as being Phalanger orientalis. Although it may very well be that there are no additional terrestrial, non-flying mammals to be reported from the Admiralties, this is apparently not the case with the bats (see Aplin et al. 2015). At any rate, additional collecting in the Admiralties is clearly needed and should be undertaken, and preferably before additional environmental degradation and introduction of additional exotic species and potential diseases take place. Aside from the native species of the Admiralties being so little known from the standpoint of ranges of variation and, in some cases, affinities, their autecology is, of course, a virtual cipher.

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