

Chapter 8

Biodiversity and Biogeography of the Moss-Mice of New Guinea: A Taxonomic Revision of *Pseudohydromys* (Muridae: Murinae)

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ABSTRACT

Morphological investigations involving nearly all available museum material representing New Guinea “moss-mice” (rodents traditionally classified in the genera *Pseudohydromys*, *Neohydromys*, *Mayermys*, and *Microhydromys*) reveal outstanding undiagnosed taxic diversity (a minimum of 16 species, versus the eight species previously described) and allow for redefinition of generic boundaries among these little-studied rodents. Apart from *Microhydromys* Tate and Archbold, 1941 (comprising two species, as recently revised by Helgen et al., in press), herein we recognize two genera of New Guinea moss-mice: *Pseudohydromys* Rümmler, 1934 (now incorporating *Neohydromys* Laurie, 1952, *Mayermys* Laurie and Hill, 1954, and “*Microhydromys*” *musseri* Flannery, 1989) and a newly described genus, *Mirzamys*. Species of *Pseudohydromys* are recorded from montane areas throughout New Guinea (elevations spanning 600 to at least 3800 meters), including the mountain ranges of the Central Cordillera, the Huon Peninsula, and the North Coastal ranges. We diagnose and review 12 species of *Pseudohydromys*, including six species described as new. The new genus *Mirzamys* is erected to accommodate two newly described species of small terrestrial rodents from middle and upper montane forests and subalpine grassland edges (1900–3450 m) in the mountains of central New Guinea. Together these two new species represent a distinctive hydromyine lineage that resembles the terrestrial New Guinea hydromyine genera *Pseudohydromys* and *Paraleptomys* in various traits. Ecological attributes of all recognized moss-mice taxa, both previously and newly described, are reviewed in light of all information currently available about their biology.

INTRODUCTION

For 12 months during 1932–1933, Herbert Stevens, a museum collector engaged by Harvard’s Museum of Comparative Zoology (MCZ), camped and worked in the vicinity of Wau, a village community in eastern New Guinea’s Morobe District (today Papua New Guinea’s Morobe Province), shooting birds, collecting insects, and preparing museum specimens (Greenway, 1935). His large bird collection, meticulously prepared, is the most complete made in the vicinity to date (Beehler, 1978). Presumably at the urging of Harvard’s then Curator of Mammals, Professor Glover M. Allen, Stevens also collected

mammals for the MCZ during his stay in New Guinea. During March and April of 1933, Stevens preserved small mammals trapped and hunted in montane forest habitats on Mt. Missim, amassing an important collection (Helgen and McFadden, 2001). On 8 March 1933, Stevens collected and prepared the study skin and skull of a mouse, small and blackish, with soft dense fur and tiny eyes. This was the first documented encounter between a zoologist and a New Guinean “moss-mouse”—a group of small, dark-colored terrestrial insectivorous rodents now known to occur throughout montane forest formations across much of New Guinea, the world’s largest tropical

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island. Soon after, following a visit to study Stevens' deposited collections at Harvard, the German mammalogist Hans Rümmler published a description of this then unique specimen, designating it the holotype of a new genus and species, *Pseudohydromys murinus* (Rümmler, 1934, 1938).

Discoveries of other species of New Guinea moss-mice followed over the next decades. After extensive collecting in western New Guinea under the banner of the Third Archbold Expedition to New Guinea (Brass, 1941; Archbold et al., 1942; Cookson, 2000), George Tate and Richard Archbold reported the discovery of another new genus and species of moss-mouse, *Microhydromys richardsoni*, collected not in montane forest but in lowland hill forest, along the Idenburg River on the northern slopes of the Snow Mountains (Tate and Archbold, 1941). Tate (1951) later reported another new species, described as *Pseudohydromys occidentalis*, collected during the same expedition in upper montane forests around Lake Habbema, high in the Snow Mountains. The following year, Eleanor Laurie of the British Museum described a further new genus and species, *Neohydromys fuscus*, based on a series of specimens collected by Fred Shaw-Mayer on Mt. Wilhelm in the Bismarck Range, today in central Papua New Guinea (Laurie, 1952). This was followed by Laurie's announcement of a fifth species of moss-mouse, also discovered by Shaw-Mayer on Mt. Wilhelm, which was described as *Mayermys ellermani*—the type species of yet another nominal genus (Laurie and Hill, 1954; Peckover and George, 1992). The discovery of *Mayermys* elicited particular excitement among zoologists at the time (e.g., Van Deusen, 1955), as it was the only rodent then known, living or fossil, with only four molars in the dentition (i.e., only a single molar in each quadrant of the jaw—each represented by a tiny peg). Previously discovered New Guinean moss-mice had two molars in each jaw quadrant, while the overwhelming majority of rodents worldwide have three.

Only rather recently have further species of New Guinea moss-mice been discovered and described. Flannery (1989) introduced a new taxon, *Microhydromys musseri*, on the basis of a single specimen collected in the Torricelli

Mountains of northern Papua New Guinea. While there is no doubt that *musseri* is a distinctive species, various authors have queried its classification within *Microhydromys* (e.g., Musser and Carleton, 2005; Helgen, 2005b), a point we review in this paper. Helgen (2005a) described a second species of *Mayermys*, *M. germani*, based on a single specimen trapped in the Maneau Range of far southeastern New Guinea in 1992. Most recently, Helgen et al. (2009) described another species of *Microhydromys*, *M. argenteus*, distributed along the southern slopes of the Central Cordillera in Papua New Guinea.

Taxonomic descriptions of these eight species were each originally founded on a single specimen or a small series of specimens. Today natural history museums around the world hold about 200 examples of moss-mice collected in New Guinea. No previous investigation has made use of most of this available museum material, with the result that no serious taxonomic overview of New Guinea moss-mice has ever been undertaken. The bulk of this material was collected in highland forests along the eastern part of New Guinea's Central Cordillera, from the Star Mountains to the Eastern Highlands in Papua New Guinea, though a handful of samples also originate from other localities situated in the western Central Cordillera, in southeastern New Guinea, in the disjunct mountains of the Huon Peninsula, on mountains in the Kikori River Basin of south-central New Guinea, and in the isolated North Coastal Range of northern New Guinea. Our study draws on nearly all of this material. In the present account we concern ourselves primarily with species limits among museum samples previously identified as representatives of the genera *Pseudohydromys*, *Neohydromys*, or *Mayermys*. Species limits in the other New Guinea moss-mouse genus, *Microhydromys*, were treated in another recent revision (Helgen et al., in press).

Taxa discussed here (*Pseudohydromys*, *Neohydromys*, *Mayermys*, *Microhydromys*, and *Mirzamys*, n. gen.) have generally been referred to as "shrew mice" in past literature (Flannery, 1995a; Musser and Carleton, 2005; Helgen, 2005a). In this account we

prefer to use the vernacular term “moss-mouse” for these genera (or more appropriately “moss-rat” in the case of *Mirzamys*, n. gen.). Though simply a matter of preference, this vernacular distinction serves to differentiate these Melanesian genera from particular taxonomic assemblages of terrestrial murines from the Philippines (e.g., the genera *Crunomys*, with three Philippine species, *Archboldomys*, with three species, and *Rhynchomys*, with four species; Rickart et al., 1998; Musser and Carleton, 2005; Balet et al., 2006, 2007), and from Sulawesi (*Crunomys*, with one Sulawesi species, *Melasmothrix*, with one species, *Tateomys*, with two species, *Echiothrix*, with two species, and *Sommeromys*, with one species; Musser, 1982; Musser and Durden, 2002; Musser and Carleton, 2005) that are also generally dubbed “shrew rats” or “shrew mice” (e.g., Musser, 1982; Musser and Carleton, 2005). These Sulawesian and Philippine taxa, though broadly similar in ecology and appearance to New Guinea’s moss-mice, share no special phylogenetic relationship with them. Moss-mice instead comprise part of an adaptive radiation of terrestrial and amphibious animalivores that also includes the genera *Hydromys* E. Geoffroy, 1804, *Parahydromys* Poche, 1906, *Crossomys* Thomas, 1907, *Baiyankamys* Hinton, 1943, *Leptomys* Thomas, 1897, *Paraleptomys* Tate and Archbold, 1941, and *Xeromys* Thomas, 1889, all of which occur in New Guinea and are endemic to the broader Australo-Papuan region (Flannery, 1995a, 1995b; Helgen, 2005b; Hitchcock, 1998). In each of these genera the cranium is typically constricted behind (rather than between) the orbits, the occlusal patterns of the molars are simplified or obliterated, and the third upper and lower molars are absent (in the majority of genera) or grossly reduced (in *Leptomys* alone)—a distinctive combination of characters unique among Australo-Papuan murines (see below). This taxonomic grouping has in the past often been recognized at tribal level as the Hydromyini (e.g., Flannery, 1995a). Though the most recent comprehensive taxonomic overview of murine rodents recognizes only suprageneric “divisions” rather than tribes (Musser and Carleton, 2005), we continue to employ the informal tribal label “hydromyin” throughout this paper as a

term of convenience that also conveys our understanding that these selected New Guinean genera together comprise a monophyletic group among murine rodents.

Vernacular usage of the term *moss-mouse* for this group of rodents is not without potential confusion, as this term has been used by some authors to designate still other Philippine murids (species in the genera *Tarsomys*, *Limnomys*, and *Bullimus*; e.g., Heaney et al., 1999; Rickart et al., 2003). However, use of the term for New Guinea murines (e.g., by Menzies and Dennis, 1979) apparently antedates the usage for these Philippine taxa, and the most recent comprehensive delineation of common names for murine rodents (Musser and Carleton, 2005) employs alternate vernacular names within *Tarsomys*, *Limnomys*, and *Bullimus*. We advocate limitation of the term *moss-mice* to the New Guinea genera *Pseudohydromys* and *Microhydromys* in future literature.

MATERIALS AND PROCEDURES

Specimens discussed here by catalog number are stored in the collections of the Australian Museum, Sydney, Australia (AM); the American Museum of Natural History, New York, USA (AMNH); the Bernice P. Bishop Museum, Honolulu, Hawaii, USA (BBM, with the museum’s prefix BBM-NG designating holdings from Papua New Guinea); the Natural History Museum, London, U.K. (BMNH); the Australian National Wildlife Collection, Canberra, Australia (CSIRO); the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ); the Museum of Vertebrate Zoology, University of California, Berkeley, California, USA (MVZ); the Swedish Museum of Natural History, Stockholm, Sweden (NMS); the Papua New Guinea National Museum and Art Gallery, Port Moresby, Papua New Guinea (PNGNM); the University of Papua New Guinea, Port Moresby, Papua New Guinea (UPNG); the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM); and the Western Australian Museum, Perth, Australia (WAM). These institutional abbreviations preface catalog numbers referring to speci-

mens listed in the tables, text, and figure legends. Most of this material consists of standard museum preparations, either a study skin and accompanying cranium and mandible, or specimens stored whole in fluid preservative (in particular at AM and BBM), from some of which we extracted and cleaned skulls. A few specimens that we have examined (AM and BBM) are prepared as largely or wholly complete skeletons.

Terminology and definitions of cranial, dental, and external traits follow standards established by Musser (1982), Voss (1988), and Musser and Heaney (1992). Anatomical terminology follows Brown (1971) and Brown and Yalden (1973) for external features of the head and limbs; Bugge (1970) for the cephalic arteries; Wahlert (1985) for the cranial foramina; and Carleton (1980), Carleton and Musser (1984, 1989), Musser and Heaney (1992), and Musser et al. (1998) for cranial morphology. Names of cusps and cusplets of maxillary (upper) and mandibular (lower) molars follow the terminology employed by Musser and Newcomb (1983: 332).

We used digital calipers to measure (and record to the nearest 0.01 mm) the following cranial and dental dimensions for each specimen, under a magnifying lens when necessary:

CIL	condyloincisive length
ZB	zygomatic breadth
POB	postorbital breadth
BBC	breadth of braincase
HBC	height of braincase
LN	length of nasals
LD	length of diastema
PL	palatal length
LBP	length of bony palate (palatal bridge)
BBP	breadth across bony palate at second molars
BMF	breadth of mesopterygoid fossa
BIT	breadth across upper incisors at tips
BIR	breadth across upper incisors at roots
BR	breadth of rostrum
LIF	length of incisive foramina
CLM	crown length of maxillary molar row

LM1	length of first upper molar (crown)
BM1	breadth of first upper molar (crown)
BM2	breadth of second upper molar (crown)

Limits of these measurements are defined by Musser and Newcomb (1983), Voss (1988), and Musser et al. (2008). Molars were measured across their crowns.

Unless explicitly noted, all reported metrics (and resulting statistical and multivariate comparisons) refer only to fully mature (adult) specimens, as judged in most cases by direct examination of skulls. The classification of "adult" was applied generally only to skulls in which the full dentition is completely erupted, and in which the basilar (basioccipital-basisphenoid) suture in particular is obliterated via ossification. Old adults, adults, and young adults (as defined by Musser and Heaney, 1992: 5) were all pooled as "adults" in statistical compilations and multivariate comparisons. Our data demonstrate no consistent patterns of sexual size dimorphism within available samples of any species or sample of moss-mouse, such that our descriptive statistics and morphometric analyses include both sexes.

Standard descriptive statistics (mean, standard deviation, and observed range) were calculated for the samples of populations and species listed in the tables. Only cranial and dental measurements were incorporated in the multivariate analyses. Plottings of specimen scores in principal component analyses provided visual patterns that reflect similarity or contrast in the combination of cranial and dental dimensions among geographic samples of a single species or among samples of different species. Principal component analyses were computed using the combination of cranial and dental measurements indicated in various tables and in the text. All measurement values were transformed to natural logarithms prior to multivariate analysis. Principal components were extracted from a covariance matrix. Variables for multivariate analyses were selected judiciously to maximize sample sizes for comparison by allowing for inclusion of partially broken skulls in some cases. The software program Statistica

8.0 (Statsoft Inc., Tulsa, Oklahoma, USA) was used for all analytical procedures.

Values from external measurements are presented to provide an appreciation of general body size and lengths and proportions of appendages. Values (in mm) for total length and length of tail are usually those recorded by collectors on labels attached to skins; subtracting length of tail (abbreviated TV) from total length produced a value for length of head and body (HB). Values for length of hind foot (HF), which includes claws, were either obtained from skin labels or from our measurements of dry study skins; those for length of external ear (E), or pinna, come from collector's measurements recorded on skin labels or in field journals (we assume, but are not certain for all specimens, that ear-length measurements represent the greatest length from the notch to the distal margin of the pinna). In a few cases where no original field measurements had been recorded, values for external measurements were obtained by measuring specimens preserved in fluid.

Locality names and elevations provided here are taken primarily from specimen tags, field journals, or published expedition summaries. Geographic coordinates (in degrees and minutes of latitude and longitude) and map plottings provided in our account reflect our best understanding of the geographic provenance of the specimens that we have studied in world museums. Bonaccorso (1998), Flannery (1995a), Taylor et al. (1982), Tate (1951), Laurie and Hill (1954), HousND (1944), and USBGN Indonesia (1982) were the sources usually consulted for information on New Guinea collecting localities.

THE GENERIC SCOPE OF *PSEUDOHYDROMYS*

Each of the four moss-mouse genera named to date (*Pseudohydromys*, *Microhydromys*, *Neohydromys*, and *Mayermys*) is very distinctive phenetically (figs. 1, 2). Species of *Microhydromys* (excluding the unrelated "*M.*" *musseri*; see below) are the smallest, with the skull measuring absolutely smaller than in other moss-mice (CIL < 20.5 mm); they are also immediately identifiable by their

grooved upper incisors and relatively very large auditory bullae. The species of *Mayermys* are instantly recognizable by their reduced number of molars and also by their relatively flattened skulls, stout zygomata, crania laterally constricted behind the zygomata, excessively reduced interparietals, extremely narrowed mesopterygoid fossae, and proodont incisors. In *Neohydromys fuscus* (the type and only species referred to *Neohydromys*), two molars are retained in each jaw quadrant, but these teeth are extremely tiny (maxillary tooth row averaging 2.0 mm, shorter even than in the much smaller-skulled *Microhydromys*). The skull of *Neohydromys fuscus* uniquely features a combination of widely splayed zygomatic arches, a much narrowed mesopterygoid fossa, markedly proodont incisors, and bright red enamel on the faces of the upper incisors (yellow-orange in other moss-mice), among other diagnostic traits (Laurie, 1952); its tail is also shorter than in other moss-mice. Skulls of the two species traditionally classified in *Pseudohydromys* (*P. murinus* and *P. occidentalis*) feature two molars in each quadrant of the jaw, each relatively unreduced in size relative to other moss-mice, plus a less constricted mesopterygoid fossa, weakly flared zygomata, and a longer rostrum. It is unsurprising that a principal component analysis comparing adult skulls on the basis of commonly employed craniometric landmarks for rodents (table 1) recovers these traditional generic groupings in a plot of the first and second principal components, segregating specimens based on cranial size and on several of the phenetic distinctions highlighted above (fig. 2). Notably, these morphometric comparisons phenetically ally "*Microhydromys*" *musseri* with specimens of *Pseudohydromys*, not with other *Microhydromys*, as we review below. These preliminary comparisons also highlight the morphometric distinctness of an additional taxonomic lineage, considerably larger and readily distinguished on the basis of qualitative anatomy from other moss-mice (fig. 2; table 1), which is described below as a new genus.

In our view *Microhydromys* (as represented only by *M. richardsoni* and *M. argenteus*) is the least derived in morphology of the New Guinea moss-mice genera. It differs from the



Fig. 1. Skulls representing the four previously described nominal genera of New Guinea moss-mice, adapted from Flannery (1995a: 523–524). In rows, from top to bottom: *Neohydromys* Laurie, 1952 (*Pseudohydromys fuscus*, type species of *Neohydromys*, AM M14170, Mt. Elimbari), *Pseudohydromys* Rümmler, 1934 (*Pseudohydromys murinus*, type species of *Pseudohydromys*, AM M14161, Mt. Kaindi), *Mayermys* Laurie and Hill, 1954 (“*Mayermys ellermani*” of Flannery (1995a) [= *Pseudohydromys pumehanae*, n. sp.; see below], AM M15342, Mt. Karimui), and *Microhydromys* Tate and Archbold, 1941 (“*Microhydromys richardsoni*” of Flannery (1995a) [= *Microhydromys argenteus* Helgen et al., in press], AM M14166, Mt. Sisa). Scale bar = 10 mm.

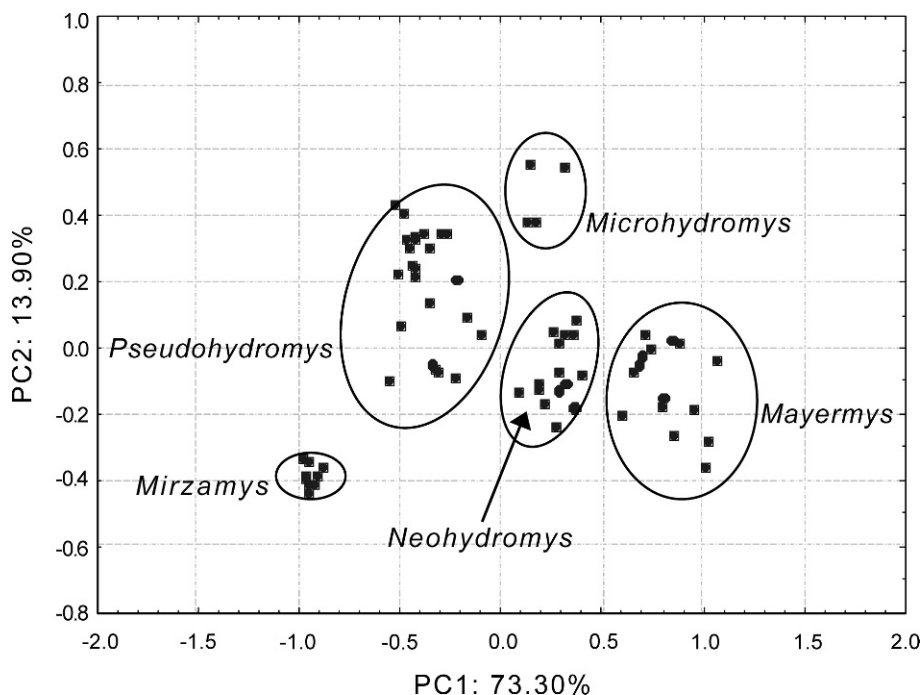


Fig. 2. Morphometric separation (principal component analysis) of intact crania representing New Guinea moss-mice. Principal components extracted from a covariance matrix of 10 log-transformed craniodontal variables (table 1) separate five highly distinctive phenetic groupings of New Guinea rodents, corresponding to the generic concepts of *Pseudohydromys*, *Neohydromys*, *Mayermys*, *Microhydromys* (minus "*M.*" *musseri*"; see Helgen et al. [in press] and account in this paper), and a newly diagnosed genus (*Mirzamys*). The x -axis (PC1) is largely a shape factor that portrays a decrease in relative size of both M1 and mesopterygoid fossa width from left to right; the y -axis (PC2) is largely a size factor that portrays an overall increase in skull size from top to bottom. In this plot, as in other morphometric plots figured in this paper, ellipses surrounding each cluster are fitted by eye to indicate cohesion, and do not reflect statistical confidence intervals.

other genera in its less expansive postglenoid and middle lacerate foramina, less reduced interparietal, unreduced bullae, and in its retention of the primitive murine cephalic arterial pattern (see below). It is united morphologically with other moss-mice genera only by its small size and dusky pelage, and may not be closely related to *Pseudohydromys* (Musser and Carleton, 2005; Helgen et al., in press). The phylogenetic remoteness of *Microhydromys* relative to other moss-mice genera is apparent not only in morphological contrasts, but also in ecological associations, with the species of *Microhydromys* generally inhabiting lower elevation forests than the high montane species of *Pseudohydromys*, *Neohydromys*, and *Mayermys*.

Studies of spermatozoal conformation (Breed and Aplin, 1994) and phallic anatomy (Lidicker, 1968, 1973; Lidicker and Brylski, 1987) complement impressions based on cranial morphology (e.g., Tate, 1951; Laurie, 1952; Laurie and Hill, 1954; Musser and Carleton, 2005) in suggesting a close relationship between *Pseudohydromys*, *Neohydromys*, and *Mayermys*. Indeed, immunological studies presented by Watts and Baverstock (1994, 1995, 1996) suggest that members of these three nominal genera are indistinguishable in comparisons drawing from micro-complement fixation of albumin, indicating close genetic similarity. Based in part on these data, Musser and Carleton (2005: 1452) opined that "species in [these] three genera

TABLE 1
Results of a Principal Component Analysis
Comparing Crania of All New Guinea Moss-mice
(factor loadings and percentage variance)

Principal components are extracted from a covariance matrix of 10 log-transformed cranial and dental variables (see fig. 2). Many specimens have slightly damaged crania; craniometric variables were selected to maximize sample size across all taxa.

	PC1	PC2
POB	-0.7173	-0.5040
ZB	-0.2486	-0.8008
LD	0.5639	-0.6507
LBP	0.0690	-0.7118
BBP	-0.7145	-0.3771
BMF	-0.9042	-0.0801
BR	-0.3225	-0.8101
LIF	-0.4727	-0.7308
LM1	-0.9684	0.1222
BM1	-0.9868	0.0515
% variance	73.30	13.90

clearly form a tight monophyletic group that should be taxonomically expressed by uniting *Neohydromys* and *Mayermys* with *Pseudohydromys*.” These authors observed that these three nominal genera share a number of distinctive and/or derived morphological traits including “dense, velvety fur, generally similar cranial conformation, spacious postglenoid and middle lacerate foramina, derived configuration of cephalic arterial pattern, loss of third molars, or second and third molars (*Mayermys*), dentary shape and degree of penetration of incisor alveolus, [and] extent of enamel relative to dentine on upper and lower incisors.” (The distribution and significance of these and other anatomical traits are reviewed in the accounts below.) Though the first author of this account has recently maintained *Pseudohydromys*, *Neohydromys*, and *Mayermys* as distinct genera (Helgen, 2005a), we agree with Musser and Carleton (2005) that these nominal generic-level taxa can be conveniently united on account of their clear and intimate morphological and genetic affiliation relative to all other murines, despite the striking variation in dental formulae and craniodental conformations evident within this assemblage. With the discovery and characterization of many additional allied species, reported here, it is now evident that the type species of *Neohydromys* and

Mayermys are simply two of the more phenetically distinctive taxa within a diverse but likely monophyletic radiation of moss-mice that also incorporates species traditionally classified in *Pseudohydromys* (*P. murinus* and *P. occidentalis*) and one previously classified in *Microhydromys* (“*M.*” *musseri*).

In our assessment, the newly envisioned boundaries of a more expansive genus *Pseudohydromys* comprise 12 species, as diagnosed and documented in this revision. Our delineations of species boundaries rely especially on discrete, covarying character states of the skin and skull; consistent distinctions in size and shape as revealed by cohesion of specimens in morphometric space; and combinations of sympatric occurrence demonstrated among distinct phen. Available museum samples also reveal the existence of a third distinctive moss-mouse lineage in New Guinea, generically distinct from both *Pseudohydromys* and *Microhydromys*. This lineage, represented by two newly described species from mountain ranges in western Papua New Guinea, is described below as the new genus *Mirzamys*.

Pseudohydromys Rümmler, 1934

Pseudohydromys Rümmler, 1934: 47.

Neohydromys Laurie, 1952: 311.

Mayermys Laurie and Hill, 1954: 133.

TYPE SPECIES AND CONTENT: The type species of *Pseudohydromys* is *P. murinus* Rümmler, 1934. Synonyms of *Pseudohydromys* Rümmler, 1934, are *Neohydromys* Laurie, 1952 (type species *Neohydromys fuscus* Laurie, 1952), and *Mayermys* Laurie and Hill, 1954 (type species *Mayermys ellermani* Laurie and Hill, 1954). Current taxonomies recognize a total of five species of *Pseudohydromys*—*P. murinus*, *P. occidentalis*, *P. fuscus*, *P. ellermani*, and the recently discovered *P. germani*, originally described within the genus *Mayermys* (Flannery, 1995a, Musser and Carleton, 2005; Helgen, 2005a). The 12 species of *Pseudohydromys* characterized here more accurately portray biodiversity within the genus as represented by current holdings in natural history museum collections (recognized species, in alphabetical order): *P. berniceae*, n. sp.; *P. carlae*, n. sp.; *P. eleanorae*, n. sp.; *P. ellermani*

(Laurie and Hill, 1954); *P. fuscus* (Laurie, 1952); *P. germani* (Helgen, 2005a); *P. murinus* Rümmler, 1934; *P. musseri* (Flannery, 1989); *P. occidentalis* Tate, 1951; *P. patriciae*, n. sp.; *P. pumehanae*, n. sp.; *P. sandrae*, n. sp.

DIAGNOSIS: The genus *Pseudohydromys* comprises a group of small-bodied brownish or grayish terrestrial murine species endemic to montane habitats in New Guinea. The genus can be distinguished from all other murines by the following combination of characters: (1) small body and cranial size, with condyloincisive length measuring 21.5–25.6 mm, absolutely larger than in *Microhydromys* (CIL \leq 20.5 mm) and absolutely smaller than in *Mirzamys*, n. gen. (CIL \geq 26 mm); (2) soft, dense, dark brown or gray-brown pelage; (3) a tail that ranges in length from about 15% shorter than the head and body length (in *P. fuscus*) to about 10% longer (in *P. berniceae*, n. sp.); (4) upper incisors varying in configuration from very slightly opisthodont to strongly proodont (incisor configurations as defined by Thomas, 1919), and lower incisors long and strongly upcurved, with yellow-orange enamel faces; (5) either one or two small molars in each quadrant of the jaw; (6) large postglenoid and middle lacerate foramina, sometimes confluent with one another, and sometimes with the middle lacerate foramen confluent with the foramen ovale (in which case the foramen ovale accessorius remains discrete); (7) a reduced interparietal bone, strongly shortened anteroposteriorly; (8) osseous reflections in the basicranium denoting a derived cephalic arterial configuration (see Musser and Heaney, 1992: 87; confirmed here for all species of the genus); and (9) short incisive foramina (measuring 7%–12% of CIL).

SPECIES GROUPS: In the accounts below we characterize 12 species of *Pseudohydromys*. For diagnostic efficiency we have divided these species into five species groups according to our impressions of their anatomical features. These phenetic clusters, two of which are monotypic, are useful for diagnosing and contrasting the various members of this diverse genus, but for now we regard these as assemblages of convenience rather than explicit indications of phyloge-

netic relationship. Immediate relationships between most species of *Pseudohydromys* are difficult to discern mainly on account of the highly distinctive craniodental morphologies evident within the genus.

- (1) The *murinus* species group: *Pseudohydromys murinus* Rümmler, 1934, *P. berniceae*, n. sp., and *P. eleanorae*, n. sp.

Included here are three species found only in eastern New Guinea—*P. murinus*, the type species of *Pseudohydromys*; a newly discovered species from southeastern New Guinea, smallest in body size within the genus (*P. berniceae*, n. sp.); and a new species occurring in sympatry with *P. murinus* and formerly confused with that species (*P. eleanorae*, n. sp.).

Traits that characterize the members of this group include: (1) two molars in each quadrant of the jaw, relatively unreduced in size compared to other *Pseudohydromys* species, with the upper molar row situated at the posterior margin of the zygomatic plate (in most congeners the molar row is deflected well behind the zygomatic plate, and the molars are markedly reduced in size and, in the *ellermani* species group, also in number); (2) upper incisors slightly opisthodont or orthodont (orthodont to strongly proodont in most other *Pseudohydromys*); (3) incipient confluence between the postglenoid and middle lacerate foramina interrupted by a bony anterior projection of the auditory bulla that extends to the alisphenoid portion of the pterygoid plate, largely or wholly separating the postglenoid foramen and the middle lacerate foramen from one another (see below; these foramina are not discrete in many other *Pseudohydromys*); (4) an interparietal bone comparatively unreduced relative to other *Pseudohydromys* (with the exception of *P. patriciae*; see below); (5) mesopterygoid fossa not markedly constricted relative to the bony palate and narrowed relative to the width of the skull (WMF/ZB generally $> 14.5\%$ in the *murinus* species group, compared to $< 14.5\%$ in other species groups, except *P. patriciae*; see below). We explicitly note that the traits that unite this assemblage, though distinctive in combination, may be symplesiomorphies.

Pseudohydromys murinus and *P. berniceae*, n. sp., are very similar in qualitative cranial and external morphology, though they differ rather markedly in average body size. They have been collected syntopically (in the same pitfall line) but have quite different overall elevational associations (the lowest recorded elevational occurrence for *P. murinus* is the same as the highest recorded elevational occurrence for *P. berniceae*, n. sp.). They are the two smallest species in the genus, each with blackish-brown fur and molars less reduced in relative size than in all other congeners, and the only two-molared species of *Pseudohydromys* in which the tail averages longer than the head-body length. Though each of these traits may be plesiomorphies, on account of their very close morphometric and phenetic resemblance we regard them as sister species, a hypothesis that must remain to be tested in future with other types of comparisons.

As discussed above, *P. eleanorae*, n. sp., is more or less equivalent in body size to *P. murinus*, and occurs sympatrically with that species in the Bismarck and Hagen ranges. Though overlooked in the past, it is morphologically very distinctive. Here we cautiously ally it with *P. murinus* and *P. berniceae* principally on the characters cited above and on the basis of morphometric affiliation (e.g., fig. 3; table 2)—a working hypothesis, based largely on phenetic indications, to be evaluated in future phylogenetic comparisons.

(2) *Pseudohydromys patriciae*, n. sp.

This species, endemic to western New Guinea, is morphologically and morphometrically remote relative to other *Pseudohydromys* (e.g., fig. 3). It shares most of the traits, outlined above, that unite the members of the *murinus* species group, but is larger than these species and stands apart from them in many aspects—for example, in its distinctively narrowed foramen magnum, its pale ventral markings, and its possibly unique mammary formula (see description, below). As reviewed below, while the skull especially recalls *P. murinus* and *P. berniceae* in certain aspects, these resemblances are generally superficial or likely to be symplesiomorphic. In the

absence of molecular or other comparisons, we regard the relationships of this species with respect to all other members of the genus as entirely uncertain.

(3) The *occidentalis* species group: *P. occidentalis* Tate, 1951, *P. musseri* Flannery, 1989, and *P. sandrae*, n. sp.

The three species in this group include a species traditionally classified in the genus *Pseudohydromys* (*P. occidentalis*), a species formerly classified in the genus *Microhydromys* (*P. musseri*), and a newly described species (*P. sandrae*, n. sp.).

Characteristics that unite the members of this group include: (1) two molars in each quadrant of the jaw, reduced in size relative to the *murinus* and *patriciae* species groups, and with the upper molar row situated well behind the zygomatic plate; (2) rostrum relatively short, stout, and more or less parallel sided, with the nasolacrimal capsules clearly bulging beyond the sides of the rostrum in dorsal view, and with the nasals moderately retracted, usually not projecting beyond the upper incisors; (3) upper incisors orthodont or proodont; (4) braincase wide and relatively high domed; (5) zygomata relatively robust, jutting well beyond the margins of the braincase; (6) middle lacerate foramen entirely confluent with the postglenoid foramen; and (7) tail shorter than the head-body length.

These species also share a close craniometric resemblance relative to other New Guinea moss-mice (fig. 3). Two of these species, *P. musseri* and *P. sandrae*, n. sp., both have short pelage, molars that are relatively narrower than in other two-molared species of *Pseudohydromys*, and chromatic patterning unique in the genus, such that coloration of the dorsum and venter contrast markedly.

(4) *Pseudohydromys fuscus* (Laurie, 1952).

Apart from its excessively reduced molars, unique in the genus among two-molared species, *Pseudohydromys fuscus* is craniometrically most similar to the species of the *occidentalis* species group, and shares with that group its distinctive combination of traits, tallied above. It shares important apomorphic traits (a posteriorly shifted

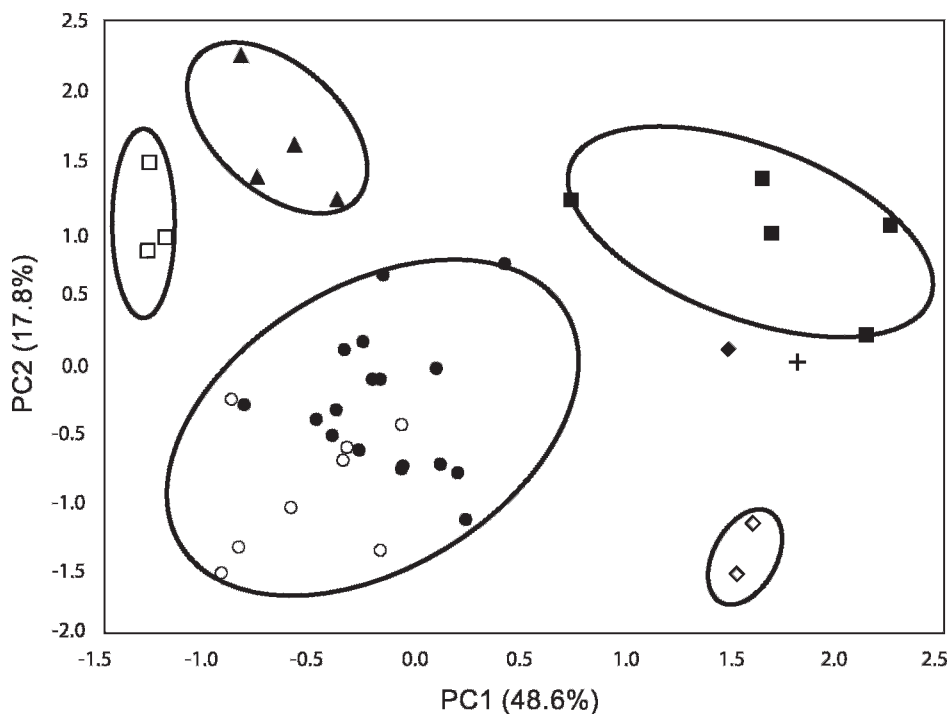


Fig. 3. Morphometric dispersion (principal component analysis) of the two-molared species of *Pseudohydromys* (i.e., excluding *P. fuscus*, which forms a tight cluster far removed in morphospace from other species in all multivariate craniometric comparisons; e.g., fig. 2). Principal components extracted from a covariance matrix of 12 log-transformed craniodental variables (table 2). Separation on the x -axis (PC1) especially reflects cranial size (increasing left to right), while separation on the y -axis (PC2) especially reflects relative differences in molar size, braincase breadth, and postorbital breadth (in each case increasing from bottom to top). Taxa and symbols: *Pseudohydromys murinus* (open circles: samples from eastern Papua New Guinea; closed circles: samples from central Papua New Guinea [see text and fig. 6]); *P. berniceae*, n. sp. (open squares); *P. eleanorae*, n. sp. (triangles); *P. occidentalis* (squares); *P. musseri* (filled diamond); *P. sandrae*, n. sp. (cross); and *P. patriciae*, n. sp. (open diamonds).

molar row, confluence of the postglenoid and middle lacerate foramina) with both the *occidentalis* species group and the *ellermani* species group. We suspect that *P. fuscus* is the sister lineage to the *ellermani* species group, with which it shares a number of apparently derived traits not seen in other members of the genus, including markedly proodont incisors, a molar row both excessively shortened and posteriorly shifted, an extremely narrowed mesopterygoid fossa, and the presence of cartilage in the lateral bacular mounds in the phallus (the last trait documented to date only in one member of the *ellermani* species group, *P. ellermani*; Liddicker, 1968, 1973). This is a hypothesis that requires further scrutiny in more formal

morphological and molecular phylogenetic comparisons.

- (5) The *ellermani* species group: *P. ellermani* (Laurie and Hill, 1954), *P. germani* (Helgen, 2005a), *P. carlae*, n. sp., and *P. pumehanae*, n. sp.

This is the most phenetically distinctive subdivision within the genus, and there is no doubt that the species included in this assemblage, with characters noted below, are immediately related and comprise a monophyletic lineage. The four species classified in the *ellermani* species group (two of which are newly described here) are the only rodents with only one molar in each quadrant of the jaw.

TABLE 2

Results of a Principal Component Analysis Comparing Crania of All *Pseudohydromys* Taxa without Markedly Reduced Molars—i.e., the *murinus*, *patriciae*, and *occidentalis* Species Groups (factor loadings, eigenvalues, and percentage variance)

Principal components are extracted from a covariance matrix of 13 log-transformed cranial and dental variables (see fig. 3). Many specimens have slightly damaged crania; craniometric variables were selected to maximize sample size across all taxa.

	PC1	PC2	PC3
POB	0.6583	-0.5327	0.1295
BBC	0.6209	-0.5639	0.0741
HBC	0.5951	-0.5283	0.0659
LN	0.5744	-0.2370	0.2527
ZB	0.8643	-0.2386	-0.0116
PL	0.9153	0.2552	-0.0787
LBP	0.9658	0.0413	0.0204
BBP	0.8983	-0.1562	0.1218
BMF	0.6139	-0.1078	-0.3323
LIF	0.1005	-0.1597	-0.9325
CLM	-0.3357	-0.8802	0.0570
LM1	-0.2836	-0.7770	-0.1203
BM1	-0.3570	-0.6870	0.0011
Eigenvalue	0.045	0.016	0.009
% variance	48.57	17.82	10.01

In most species of *Pseudohydromys*, the first and second upper molars are both anchored by three large roots (one large anterior, one large posterior, and one lingual root), and each lower molar is anchored by two roots. In the *ellermani* species group, however, in which the molars are reduced greatly in size as well as in number, the single molar in each quadrant of the jaw (including the upper molars) is anchored by two roots.

Characteristic traits of the *ellermani* species group include the following: (1) only one double-rooted molar in each quadrant of the jaw, each excessively reduced in size and simplified to a simple peg, with the upper molar situated well behind the zygomatic plate; (2) rostrum short, stout, and more or less parallel sided, with the nasals strongly retracted, not extending forward to project beyond the upper incisors; (3) upper incisors proodont; (4) cranium relatively flat topped and dorsoventrally flattened relative to other species groups; (5) zygomata jutting beyond the margins of the braincase; (6) cranium laterally constricted behind the squamosal roots of the braincase, behind which the walls of the braincase diverge laterally; (7) interparietal excessively reduced in size to form a narrow linear bar behind the parietals; (8)

auditory bullae flattened and reduced in size; (9) mesopterygoid fossa conspicuously narrowed; (10) middle lacerate foramen expansive but separated from the postglenoid foramen by a bony anterior projection of the auditory bulla that extends to the alisphenoid portion of the pterygoid plate; (11) tail ranging from slightly shorter to slightly longer than the head-body length; and (12) pelage smoky gray above and below. (Of these, we interpret traits 1, 2, 6, and 7 to be uniquely shared synapomorphies within the genus, clearly indicative of a close phylogenetic relationship among these four taxa.) The trends toward molar reduction and interparietal obliteration that characterize the genus *Pseudohydromys* as a whole thus reach their greatest development in this species group, and most markedly of all in *P. germani* and *P. pumehanae*, n. sp.

The traits that differentiate the four allopatric species recognized in this group are subtle, but seem clear and consistent in light of the small samples currently available. We have considered in detail whether this group might be more profitably characterized as a single species with marked geographic variability, or recognized as multiple species (the arrangement employed here). In the

future, we hope the chance arises to evaluate the classification advanced here in the light of additional specimens from additional localities.

Rigorous testing of phylogenetic relationships among the species of *Pseudohydromys*, and of *Pseudohydromys* relative to other hydromyine genera, will ultimately require molecular comparisons. These are now beginning, albeit with very limited taxonomic sampling (Rowe et al., 2008). Because the various lineages of *Pseudohydromys* are closely related genetically (Watts and Baverstock, 1994, 1995, 1996), molecular investigations using a common mitochondrial gene for mammals (such as cytochrome *b* or cytochrome oxidase 1) drawing from sufficient samples would likely provide considerable insight into species limits, interspecific relationships, and relative timing of diversification within *Pseudohydromys* and *Mirzamys*, as of course would more intensive molecular comparisons involving multiple markers with different patterns of inheritance. These types of studies, now commonly used to investigate evolutionary relationships and patterns of diversification for mammals in essentially all other tropical and temperate areas worldwide, have unfortunately barely begun in New Guinea mammalogy. Within the tentative framework of the species groups sketched above, we concern ourselves in this report with alpha taxonomy—documenting the full taxic diversity of *Pseudohydromys* as evidenced by specimens stored in the collections of the world's natural history museums. In our view, this approach takes priority at present, both because diversity at this taxic level remains (or has remained until recently) markedly underestimated in most groups of mammals from New Guinea and adjacent islands (e.g., Flannery and Groves 1998; Helgen and Flannery, 2004a, 2004b; Woolley, 2005; Westerman et al., 2006; Helgen, 2003; 2005c, 2007a; Musser and Carleton, 2005; Reeder et al., 2007; Musser and Lunde, 2009; Musser et al., 2008; Helgen et al., in press), and because more comprehensive overviews of taxonomic diversity in inadequately studied mammal lineages are ideally requisite to direct future studies aimed toward better discerning, refining, and testing mammalian patterns of historical biogeogra-

phy, phylogenetic and ecomorphological diversification, and conservation prioritization in the Melanesian region (e.g., Flannery, 1995a; Heads, 2001a, 2001b, 2002a, 2002b; Helgen, 2007a; Amori et al., 2008; Schipper et al., 2008).

AN OVERVIEW OF THE SPECIES OF *PSEUDOHYDROMYS*

Pseudohydromys murinus Rümmler, 1934

TYPE MATERIAL AND LOCALITY: The holotype of *murinus* is MCZ 29904, adult male, skin and skull, from Mt. Missim (07°13'S, 146°49'E, Morobe Province, Papua New Guinea: locality 11 in fig. 6), 7000 ft (= 2134 m), collected 8 March 1933 by H. Stevens (Rümmler, 1934; Tate, 1951; Helgen and McFadden, 2001).

DIAGNOSTIC AND DESCRIPTIVE NOTES: *Pseudohydromys murinus* is one of the smaller New Guinean moss-mice (head-body length ≤ 105 mm; mass ≤ 20 grams; table 3). Dorsally it is dark brownish gray, usually with faint pale dorsal flecking (especially on the rump); ventrally it is slightly paler brownish gray (fig. 4). The head and body appear narrow and elongate in life and in fluid preserved specimens, giving the animal a rather slender, slight appearance. The tail is dark brown to blackish (darker than most other moss-mice), sometimes with paler mottling along part of its length. The tail is usually subcircular in dorsoventral cross-section, approximately subequal to head-body length (TV averaging 102% of HB), and often bears a minuscule terminal white tip. There are 17–23 tail rings per centimeter in the midsection of the tail, and the tail hairs measure about 2 tail rings in length. The ear is dark gray, the eye is very small, and the dorsal surfaces of the manus and pes are dark (grayish or blackish) rather than white.

The skull is delicate, with the zygomata very weakly flared (with ZB averaging only 1.5% greater than BBC). The upper incisors are narrow, with an orthodont or slightly opisthodont configuration. The maxillary tooth row consists of two molars, which are located just behind the zygomatic plate and are relatively large (CLM/CIL = 12.5%–15%). The diastema and incisive foramina

TABLE 3
Selected External Measurements for the Species of *Pseudohydromys* (mean \pm standard deviation, with observed range in parentheses, followed by sample size)

Sample	HB	Tail	Mean T/HB	HF	Ear	Weight (g)
<i>murinus</i>	91.4 \pm 7.5 (70–105) 43	92.2 \pm 5.0 (81–102) 43	102% 86–133%	19.9 \pm 1.0 (18–22) 43	11.2 \pm 0.9 (9–13) 43	16.8 \pm 1.6 (15–19.9) 8
<i>berniceae</i> , n. sp.	75.0 \pm 3.5 (70–80) 5	83.1 \pm 3.5 (79–88) 5	111% 101–117%	18.7 \pm 0.9 (18–20) 5	10.0 \pm 0.7 (9–11) 5	–
<i>eleanorae</i> , n. sp.	98.3 \pm 3.8 (94–103) 4	90.5 \pm 1.3 (89–92) 4	92% 88–96%	18.9 \pm 0.5 (18.5–19.5) 4	10.5 \pm 1.3 (9–12) 4	–
<i>patriciae</i> , n. sp.	99.5 (99–100) 2	85.5 (85–86) 2	86% 85–87%	20.5 (20–21) 2	11.8 (11.6–12) 2	22.3 (20.5–24) 2
<i>fuscus</i>	95.8 \pm 4.9 (80–110) 41	80.5 \pm 4.4 (72–90) 41	84% 73–100%	21.6 \pm 1.1 (20–25) 41	12.2 \pm 0.6 (11–14) 40	19.2 \pm 3.4 (14.2–25.5) 11
<i>occidentalis</i>	101.6 \pm 8.8 (87–115) 7	89.9 \pm 3.2 (85–95) 7	89% 78–100%	20.5 \pm 0.9 (19–21.5) 7	10.3 \pm 1.5 (8–12) 7	–
<i>sandrae</i> , n. sp. (n = 1)	102	95	93%	21	10.5	20
<i>musseri</i> (n = 1)	108	101	94%	22	13	–
<i>ellermani</i>	96.4 \pm 5.3 (85–103) 24	102.4 \pm 5.4 (90–113) 23	106% 95–120%	21.4 \pm 1.1 (19–23) 23	10.9 \pm 0.7 (10–12) 23	17.3 \pm 2.9 (13–21) 17
<i>germani</i>	94.0 \pm 9.6 (87–105) 3	97.7 \pm 4.6 (95–103) 3	104% 98–103%	21.0 \pm 1.0 (20–22) 3	11.9 \pm 0.8 (11–12.6) 2	25.8 (22–29.5) 2
<i>pumehanae</i> , n. sp.	99.0 \pm 2.6 (96–101) 3	101.0 \pm 1.7 (100–103) 3	102% 99–104%	21.7 \pm 1.2 (21–23) 3	11.3 \pm 0.6 (11–12) 3	18.5 (17–20) 2
<i>carlae</i> , n. sp.	95.7 \pm 7.0 (89–103) 3	88.3 \pm 4.0 (84–92) 3	93% 86–103%	21.3 \pm 0.6 (21–22) 3	10.7 \pm 1.5 (9–12) 3	15 (15–15) 2

are short (LIF/CIL = 8%–12%), though the diastema in particular varies somewhat in length geographically (see below). The braincase is relatively high domed and wide, and the mandible is long and delicate, with the lower incisors relatively slender and moderately long and upcurved (fig. 5). The nasals extend anteriorly to or slightly beyond the anterior margin of the premaxillae. In lateral profile there is usually a slight depression above the orbit between the flat-topped rostrum and the more globular braincase.

DISTRIBUTION: A Papua New Guinean endemic, *Pseudohydromys murinus* is the most commonly trapped moss-mouse in east-central New Guinea. World museums hold specimens from localities situated in montane forests (including forests fringing subalpine grasslands) at elevations between 1570 and 3400 m throughout the Central and Eastern Highlands regions of the Central Cordillera, extending east into the Owen Stanley Range. The westernmost record of the species is from the Doma Peaks (South-

ern Highlands Province) and the easternmost is from Mt. Obree (Central Province) (fig. 6). In total, vouchered records originate from Central, Northern (= Oro), Morobe, Eastern Highlands, Chimbu, Western Highlands, and Southern Highlands provinces of Papua New Guinea. Previous reviews (e.g., Flannery, 1995a; Musser and Carleton, 2005) have recorded this species only from Mt. Wilhelm in the west to the neighborhood of Wau in the east, a considerably smaller geographic range than that documented here (fig. 6).

Pseudohydromys murinus is known by about 70 museum specimens (AM, AMNH, BBM, BMNH, MCZ, MVZ, NMS, PNGNM, USNM, and WAM). Most specimens associated with explicit habitat data (located especially at BBM) record their collection from mossy montane forests situated between 2100 and 3000 m, habitats corresponding to both “lower montane forest” and “upper montane forest” as delineated by Grubb and Stevens (1985), Paijmans (1976), and Flannery (1995a). The



Fig. 4. Dorsal and ventral views of a study skin of *Pseudohydromys murinus* (AMNH 191414, adult female, Mt. Wilhelm, Chimbu Province, Papua New Guinea).

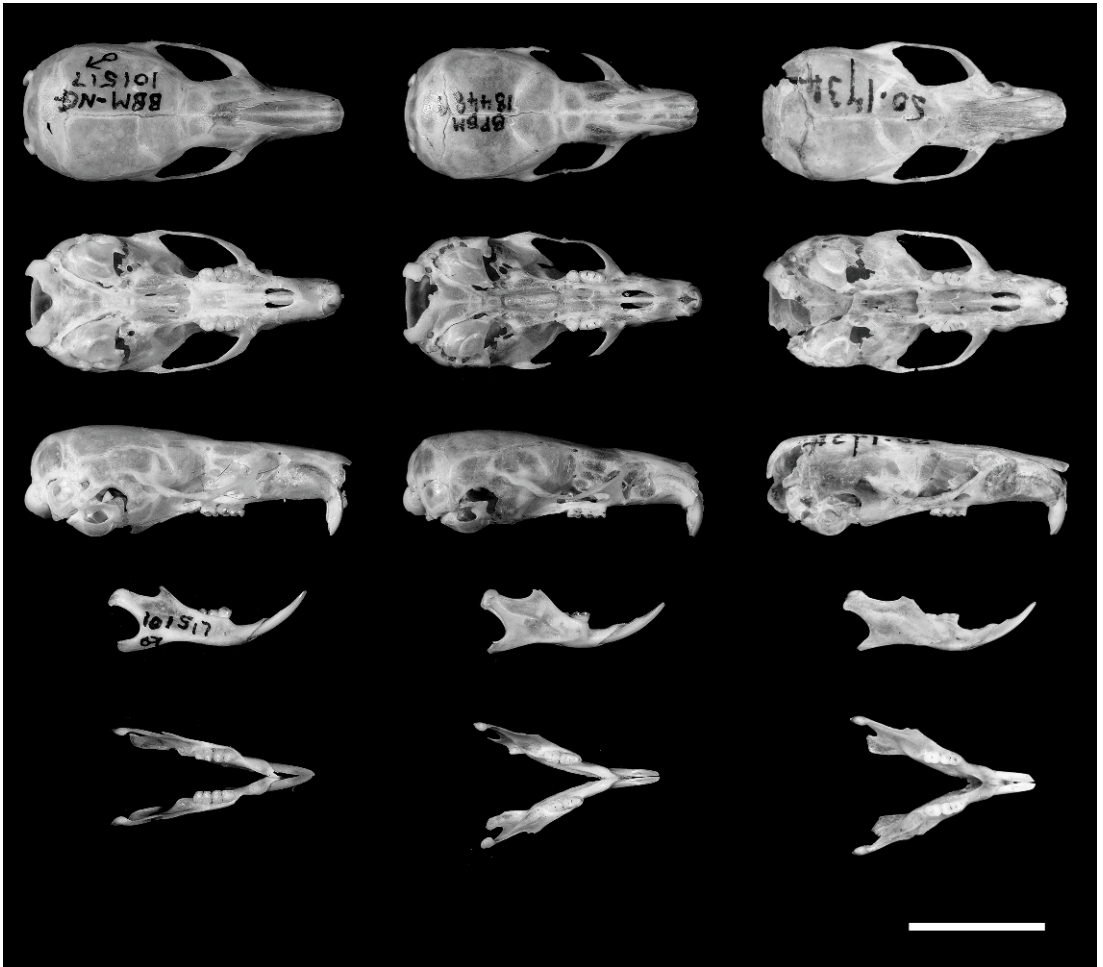


Fig. 5. Selected views of skulls of species in the *murinus* species group: (left column) *Pseudohydromys murinus*, (BBM-NG 101517, adult male, Bulldog Road, Morobe Province, Papua New Guinea); (middle column) *P. berniceae*, n. sp. (holotype, BBM-NG 184489, adult female, Mt. Simpson, Milne Bay Province, Papua New Guinea); and (right column) *P. eleanorae*, n. sp. (holotype, BMNH 50.1734, adult female, Mt. Wilhelm, Chimbu Province, Papua New Guinea). Scale bar = 10 mm.

lowest elevational record for this species (the only record below 2100 m) is a specimen collected in a pitfall trap in forest at 1570 meters on Mt. Obree (BBM-NG, unregistered); the highest (and only record above 3000 m) is a specimen snap-trapped in mossy upper montane forest at 3400 meters on Mt. Giluwe (see below). The average elevation of 20 voucher trapping sites for this species is 2432 m (median 2424 m, SD 359 m).

LOCALITIES (WITH SPECIMENS EXAMINED AND USEFUL LITERATURE REFERENCES): Baiyanka (fig. 6: locality 7), Bismarck Range,

2300–2600 m (fide Laurie, 1952: 317), Eastern Highlands Province (USNM 297609, 297610); Bulldog Road (fig. 6: locality 10), 2500–2800 m, Morobe Province (BBM-NG 101350, PNGNM 22813); Doma Peaks (fig. 6: locality 1), 2400 m, Southern Highlands Province (BBM-NG 105648); Edie Creek (fig. 6: locality 8), 2100–2500 m, Morobe Province (BBM-NG 100949, 100970, 101005, 101517; MVZ 129729; Lidicker and Ziegler, 1968); Mt. Giluwe (fig. 6: locality 2), 3400 m, Southern Highlands Province (BBM-NG 97306); Mt. Kaindi (fig. 6: local-

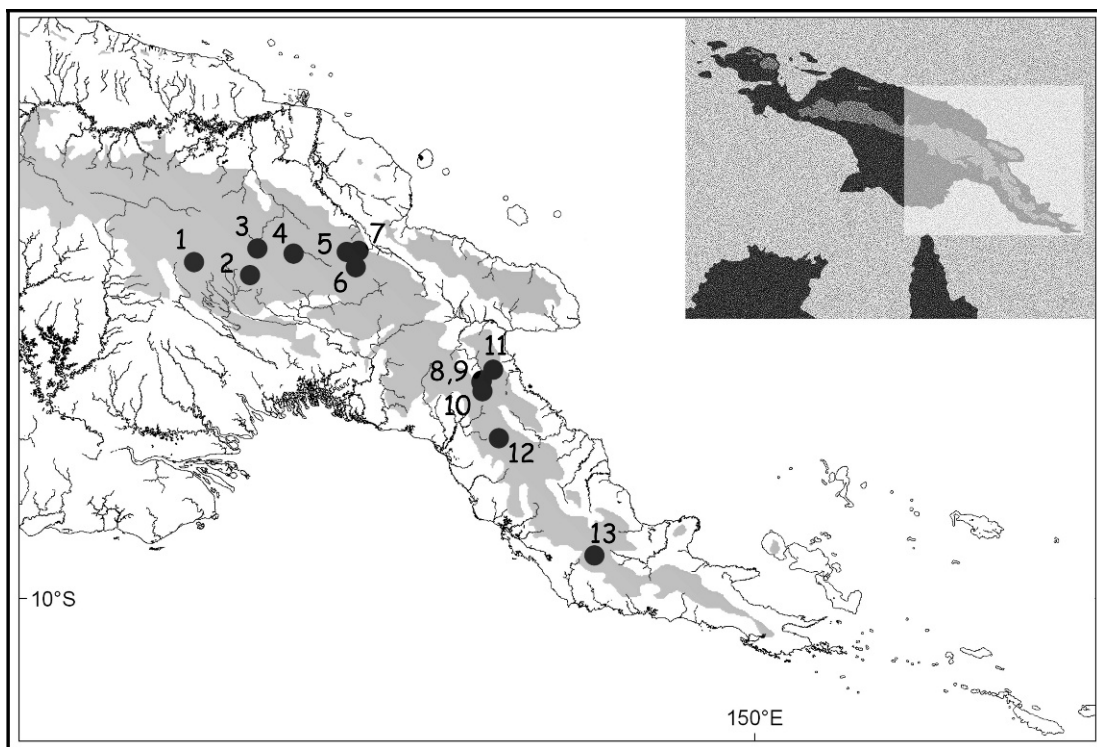


Fig. 6. Recorded distribution (vouchered localities) of *Pseudohydromys murinus*, endemic to eastern New Guinea. Areas above 1000 m in elevation are shaded in gray. See text for numbered localities.

ity 9), 2250–2360 m, Morobe Province (AM M14161, 14403–14409, 14545–14548; BBM-NG 29194, 53283, 53382, 53803, 53629, 56592, 56596, 98841, 98873, 98874, 99086; CSIRO 29764; PNGNM 24228; Gressitt and Nadkarni, 1978; additional specimens at WAM—see Jackson and Woolley, 1993); Marafunga-Goroka (fig. 6: locality 6), 2500 m, Eastern Highlands Province (BBM-NG 55564); Mt. Missim (fig. 6: locality 11), ca. 2100 m, Morobe Province (MCZ 29904; Rümmler, 1934); Mt. Obree (fig. 6: locality 13), western slopes, 1570 m, Central Province (BBM-NG, unregistered); Smith's Gap (fig. 6: locality 12), 2500 m, Northern (= Oro) Province (BBM-NG 96942); Weiga (fig. 6: locality 4), ca. 2300 m, Wahgi Mountains, Western Highlands Province (NMS 149); Welya (fig. 6: locality 3), 2400–2700 m, Western Highlands Province (BMNH 53.281, 53.283, 53.284, 53.286–53.290); Mt. Wilhelm (fig. 6: locality 5), 2400–3000 m, Chimbu Province (AMNH 191410–191414; BMNH

50.1733, 50.1735, 53.291; Laurie, 1952; Brass, 1964).

A published record of this species from Mt. Karimui (Flannery, 1995a: 524) is in error, referring instead to a specimen from Mt. Kaindi (AM M14161).

GEOGRAPHIC VARIATION: Multivariate morphometric and other comparisons reveal that at least two morphologically and geographically disjunct clusters can be identified within the taxonomic boundaries of this species as envisioned here. Specimens of *P. murinus* from the eastern portion of the species' range—samples from Mt. Obree and Smith's Gap in the Owen Stanleys (Northern and Central provinces), and Mt. Missim (the type locality of *murinus*) and Mt. Kaindi in the Eastern Highlands region (Morobe Province) (fig. 6: localities 8–13)—have, on average (and with statistical significance at $p < 0.05$ in Student's *t*-test comparisons) larger skulls, wider rostra and longer nasals, and a longer maxillary diaste-

TABLE 4
Selected Craniodental Measurements for the Species (and selected populations) of the *Pseudohydromys murinus* Species Group (*P. murinus*, *P. eleanorae*, and *P. berniceae*) and *P. patriciae* (mean \pm standard deviation, with observed range in parentheses)

Variable	<i>murinus</i> Eastern PNG (<i>n</i> = 9)	<i>murinus</i> Central PNG (<i>n</i> = 10)	<i>eleanorae</i> Central PNG (<i>n</i> = 4)	<i>berniceae</i> Owen Stanleys (<i>n</i> = 3)	<i>patriciae</i> Snow Mountains (<i>n</i> = 2)
CIL	23.29 \pm 0.47 (22.61–23.77)	22.62 \pm 0.24 (22.22–22.94)	22.20 \pm 0.33 (21.96–22.64)	21.95 \pm 0.43 (21.48–22.33)	24.77 (24.50–25.04)
ZYG	10.69 \pm 0.30 (10.33–11.22)	10.62 \pm 0.21 (10.31–10.92)	10.37 \pm 0.53 (9.63–10.87)	10.10 \pm 0.16 (9.94–10.26)	12.01 (12.00–12.02)
POB	4.68 \pm 0.14 (4.46–4.88)	4.84 \pm 0.15 (4.52–5.05)	4.29 \pm 0.17 (4.06–4.46)	4.48 \pm 0.06 (4.43–4.55)	5.59 (5.50–5.68)
BBC	10.49 \pm 0.24 (10.25–10.95)	10.50 \pm 0.20 (10.30–10.88)	9.91 \pm 0.26 (9.58–10.16)	9.71 \pm 0.17 (9.56–9.90)	11.65 (11.50–11.80)
HBC	6.70 \pm 0.18 (6.37–6.91)	6.79 \pm 0.22 (6.48–7.02)	5.84 \pm 0.16 (5.73–6.08)	6.54 \pm 0.26 (6.38–6.84)	7.58 (7.45–7.70)
BR	4.61 \pm 0.15 (4.42–4.94)	4.41 \pm 0.15 (4.11–4.59)	4.33 \pm 0.18 (4.09–4.51)	4.16 \pm 0.08 (4.07–4.23)	4.97 (4.90–5.04)
ML1	2.02 \pm 0.11 (1.80–2.14)	2.15 \pm 0.11 (1.94–2.32)	1.84 \pm 0.08 (1.75–1.94)	1.97 \pm 0.09 (1.87–2.03)	2 (2.00–2.01)
BM1	1.06 \pm 0.04 (1.00–1.10)	1.11 \pm 0.04 (1.06–1.18)	0.99 \pm 0.06 (0.91–1.05)	1.08 \pm 0.06 (1.02–1.14)	1.16 (1.12–1.20)
LIF	2.08 \pm 0.15 (1.80–2.25)	2.27 \pm 0.21 (1.90–2.65)	2.10 \pm 0.15 (1.89–2.22)	2.29 \pm 0.08 (2.23–2.38)	2.42 (2.03–2.80)
LN	7.96 \pm 0.44 (7.30–8.63)	7.56 \pm 0.47 (6.96–8.21)	7.90 \pm 0.32 (7.68–8.37)	6.37 \pm 0.06 (6.31–6.43)	9.68 (9.65–9.70)
LD	6.24 \pm 0.39 (5.54–6.83)	5.71 \pm 0.20 (5.40–6.02)	5.88 \pm 0.16 (5.67–6.01)	6.06 \pm 0.32 (5.69–6.25)	6.86 (6.80–6.92)
BMF	1.93 \pm 0.17 (1.66–2.10)	1.82 \pm 0.11 (1.61–1.96)	1.62 \pm 0.12 (1.46–1.75)	1.85 (<i>n</i> = 2) (1.49–2.20)	2.13 (2.00–2.25)
LBP	5.71 \pm 0.25 (5.37–6.10)	5.47 \pm 0.25 (5.07–5.97)	5.36 \pm 0.20 (5.16–5.63)	4.76 \pm 0.56 (4.38–5.40)	6.44 (6.30–6.58)
BBP	2.90 \pm 0.16 (2.70–3.15)	3.00 \pm 0.20 (2.64–3.29)	2.96 \pm 0.08 (2.85–3.03)	2.65 \pm 0.11 (2.55–2.76)	3.26 (3.22–3.30)
CLM	3.04 \pm 0.15 (2.84–3.28)	3.19 \pm 0.16 (2.96–3.44)	2.61 \pm 0.05 (2.56–2.66)	2.84 \pm 0.12 (2.73–2.97)	3.07 (3.05–3.10)
BIR	2.08 \pm 0.16 (1.88–2.38)	2.05 \pm 0.20 (1.75–2.41)	2.48 \pm 0.17 (2.38–2.74)	2.24 \pm 0.20 (2.06–2.45)	2.75 (2.70–2.80)

ma, but shorter incisive foramina and smaller molars, compared to series of specimens collected from central New Guinea (i.e., samples from Baiyanka, Welya, Mt. Wilhelm, the Wahgi Mountains, Doma Peaks, and Mt. Giluwe; table 4; fig. 6: localities 1–7). Tails of eastern animals average longer in proportion to the head-body length (averaging 104% of head-body length in 27 specimens) than those from central Papua New Guinea (averaging 97% of head-body length in 20 specimens). In direct comparisons of fluid specimens (at BBM), specimens drawn from this eastern cluster also have an overall

more chunky (i.e., less gracile) appearance than those from further west.

These geographic differences (table 4) may be taxonomically significant. Alternatively, these may reflect clinal distinctions owing to sampled occurrences at the eastern and western ends of a potentially continuous montane geographic distribution, or intra-specific ecomorphological patterning associated with character displacement on account of the different (and more diverse) set of congeners present in central Papua New Guinea relative to other areas where *P. murinus* is recorded (this cluster occurs

syntopically with *P. eleanorae*, n. sp., *P. ellermani*, and *P. fuscus*). Additional sampling in geographically intermediate areas (for example, in the Kratke Range) would help to assess the significance of these geographic differences. However, it is worth noting that extensive collecting in the Kratke Range by F. Shaw-Mayer (who collected the majority of available museum samples of small hydromyins from central Papua New Guinea; Laurie, 1952) failed to reveal *P. murinus*, as did collecting by the Archbold Expeditions (Brass, 1964), and later by Bishop Museum personnel, in the same area. We suggest that more integrative systematic comparisons (e.g., evaluation of these and other observed morphological differences in light of karyological or molecular data) are needed to evaluate our hypothesis that a single moss-mouse species, *P. murinus*, is distributed from the Central Highlands to the Owen Stanley Ranges.

BIOLOGICAL NOTES: Described by Rümmler on the basis of a single specimen from Mt. Missim in New Guinea's Eastern Highlands, *P. murinus* is the type species of *Pseudohydromys* and the first species of moss-mouse from New Guinea to receive a scientific name (Rümmler, 1934, 1938). When Tate (1951) published his monograph of New Guinea rodents two decades later, this species was still known only by the holotype (Helgen and McFadden, 2001). Soon after, Laurie (1952) discussed additional specimens of *P. murinus* collected at Mt. Wilhelm, but our examinations, detailed below, reveal that Laurie's series was taxonomically composite, including specimens of both *P. murinus* and *P. eleanorae*, n. sp., two small murines that occur sympatrically in the Central Highlands of Papua New Guinea (see below).

Across its geographic range, this species occurs syntopically with at least five congeners, though this sympatric assemblage varies with locality. In the Central Highlands region (e.g., at Welya and Mt. Wilhelm) *P. murinus* has been recorded in syntopy with *P. eleanorae*, n. sp., *P. fuscus*, and *P. ellermani*; in the Eastern Highlands region (e.g., at Mts. Kaindi and Missim) with *P. fuscus* and *P. ellermani*; and in the Owen Stanleys (Mt. Obree) with *P. berniceae*, n. sp., and *P. germani*.

Lidicker and Ziegler (1968) and Jackson and Woolley (1993) reported brief ecological notes on correctly identified exemplars of this species. Lidicker and Ziegler (1968) discussed an adult female *P. murinus* snap-trapped under a log in "mossy forest" at 7000 feet on Mt. Kaindi, on 23 October 1962 (the species has since been shown to be fairly common on Mt. Kaindi; Jackson and Woolley, 1993). Specimens of *Pseudohydromys ellermani* were taken under the same log. Their specimen of *P. murinus* was pregnant, with the uterus containing a single embryo (crown-rump length 8 mm).

Based on analyses of intestinal contents, Jackson and Woolley (1993) studied the diet of three syntopic moss-mice in Morobe Province (*P. murinus*, *P. fuscus*, and *P. ellermani*). They found that *P. murinus* is primarily insectivorous, and consumes less plant tissue and more oligochaete worms than both other syntopic moss-mice studied. Their specimens were collected in Elliott (= Sherman) traps, which were either unbaited or baited with sphingid moths (Jackson and Woolley, 1993: 78). Because some of their specimens (which we have examined at AM) were not fully mature, these authors reported smaller average values for head-body length and weight in *P. murinus* than those provided here (table 3).

Smales (2001) recorded three helminth parasites—*Heterakis fieldingi* Smales, 1996 (a heterakid), an unnamed species of the genus *Odilia* (a heligmonellid), and *Proto-spirura kaindiensis* Smales, 2001 (a spirurid) from the gastrointestinal tracts of two specimens of *Pseudohydromys murinus* (BBM-NG 56592 and 56596) collected on Mt. Kaindi.

Breed and Aplin (1994) described the spermatozoal morphology of *P. murinus* based on a specimen from Mt. Kaindi (BBM-NG 56596; not from the type locality, Mt. Missim, as stated in their paper).

Pseudohydromys berniceae, new species

HOLOTYPE: BBM-NG 184489, adult (pregnant) female, body fixed in formalin and stored in 70% ethanol (fig. 7), with skull extracted and cleaned (fig. 5), from the immediate vicinity of Bunisi Village



Fig. 7. Fluid specimen of *Pseudohydromys berniceae* (holotype, BBM-NG 184489, adult female, Mt. Simpson, Milne Bay Province, Papua New Guinea).

(10°01.3'S, 149°35.7'E, Milne Bay Province, Papua New Guinea; locality 6 in fig. 8), 1490 m, on the north slopes of Mt. Simpson, Maneau Range, collected 25 February 2003 by F. Kraus.

PARATYPES: Two additional specimens derive from a locality near the type locality in southeastern New Guinea: BBM-NG 184490, young adult female (collected 12 May 2002), and BBM-NG 184491, immature female (collected 15 May 2002), from the southeastern slope of Mt. Pekopekowana, along Wailahababaha Creek (a tributary of the Sagabada River), at "River Camp" (10.2826°S, 150.1548°E; locality 7 in fig. 8),

at 590–615 m (Milne Bay Province, Papua New Guinea), collected by F. Kraus. These specimens were fixed in 10% formalin and are stored in 70% ethanol, with skulls extracted and cleaned.

REFERRED SPECIMENS: Three specimens referred to this species (two males and a female), currently unregistered at BBM-NG, were collected on Mt. Obree (09°28.0'S, 148°02.8'E; locality 5 in fig. 8), at 1570 m (Central Province, Papua New Guinea), in the main body of the Owen Stanleys, by F. Kraus in January 2004.

DIAGNOSIS: This is the smallest-bodied member of the genus (tables 3–5, 7, figs. 3, 5), closely allied morphologically to *P. murinus*. Overall color is dark brownish gray, with tail length subequal to or longer than head-body length (table 3). Zygomatic breadth (< 10.3 mm) is absolutely narrower than in all other congeners except *P. eleanorae*, which has relatively smaller teeth than *P. berniceae* (table 4). In *P. berniceae* the nasals are very short and retracted relative to *P. murinus*; the braincase is relatively narrow but moderately high domed; the auditory bullae are small relative to cranial size; and the molars are relatively large (e.g., larger in absolute terms than in the larger-bodied species *P. eleanorae* or in all other congeners except *P. murinus* and *P. patriciae*, n. sp.). It is smaller than, but most closely resembles, *P. murinus*, with which it occurs sympatrically at the eastern margin (and lower elevational boundary) of that species' relatively wide range (figs. 6, 8).

DISTRIBUTION: *Pseudohydromys berniceae* is recorded from several localities situated in hill forest and lower montane forest (590–1570 m) in the Owen Stanley Ranges (including the far southeastern Maneau Range) of eastern Papua New Guinea (Milne Bay and Central provinces). The average elevation of the three known trapping localities for *P. berniceae* is 1221 meters (median 1490 m, SD 537 m), demonstrating a considerably lower elevational occurrence than that established for *P. murinus* (1570–3400 m) and for most other moss-mice of the Central Cordillera (table 11).

ETYMOLOGY: The specific epithet *berniceae* acknowledges the collective assistance and kindness of the scientific staff of the

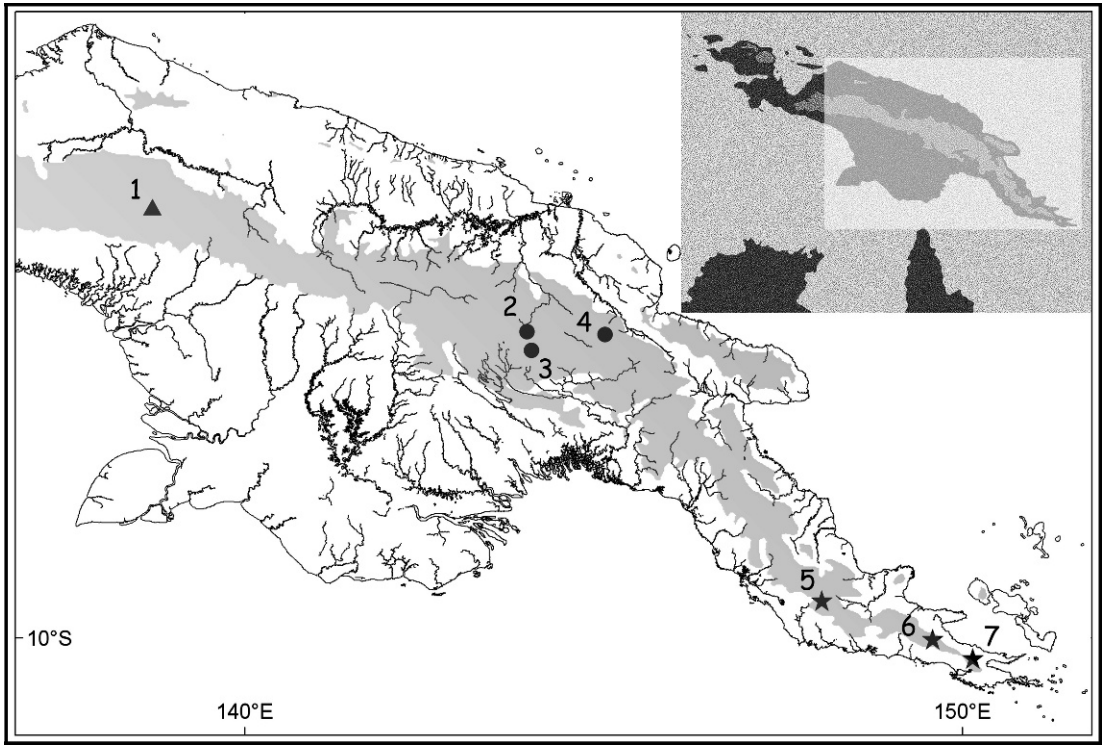


Fig. 8. Recorded distribution (vouchered localities) of three newly described species of *Pseudohydromys*: *Pseudohydromys patriciae*, n. sp. (triangle), *P. eleanorae*, n. sp. (circles), and *Pseudohydromys berniceae*, n. sp. (stars). Areas above 1000 m in elevation are shaded in gray. See text for numbered localities.

TABLE 5
Selected Craniodental Measurements for the Species of *Pseudohydromys fuscus* and the *P. occidentalis* Species Group (*P. occidentalis*, *P. musseri*, and *P. sandrae*) (mean \pm standard deviation, with observed range in parentheses)

Variable	<i>fuscus</i> (n = 17)	<i>occidentalis</i> (n = 7)	<i>musseri</i> (n = 1)	<i>sandrae</i> (n = 1)
CIL	24.66 \pm 0.48 (23.64–25.36)	24.77 \pm 1.00 (23.49–25.58)	23.33	23.87
ZYG	12.44 \pm 0.37 (11.45–12.80)	11.74 \pm 0.46 (11.11–12.30)	13.22	11.73
POB	5.11 \pm 0.12 (4.92–5.34)	5.17 \pm 0.19 (4.90–5.50)	5.12	4.97
BBC	10.70 \pm 0.29 (10.20–11.25)	10.87 \pm 0.33 (10.30–11.12)	10.60	10.21
HBC	7.22 \pm 0.24 (6.64–7.61)	7.36 \pm 0.32 (7.02–7.72)	7.00	7.05
BR	4.79 \pm 0.17 (4.54–5.14)	5.03 \pm 0.16 (4.82–5.29)	5.13	4.69
LM1	1.39 \pm 0.08 (1.21–1.52)	1.82 \pm 0.08 (1.70–1.90)	2.08	2.08
BM1	0.69 \pm 0.06 (0.62–0.87)	1.00 \pm 0.07 (0.92–1.05)	0.90	0.84
LIF	2.11 \pm 0.25 (1.77–2.72)	2.08 \pm 0.18 (1.86–2.32)	2.18	2.61
LN	7.90 \pm 0.38 (7.08–8.54)	8.14 \pm 0.41 (7.55–8.86)	7.80	7.97
LD	8.79 \pm 0.33 (8.22–9.34)	8.13 \pm 0.49 (7.37–8.94)	7.70	7.78
BMF	1.29 \pm 0.14 (1.10–1.71)	1.66 \pm 0.18 (1.54–1.92)	1.91	1.6
LBP	6.57 \pm 0.32 (6.06–7.16)	6.67 \pm 0.49 (5.88–7.23)	6.78	6.82
BBP	3.00 \pm 0.15 (2.75–3.26)	3.02 \pm 0.16 (2.71–3.23)	3.59	3.26
CLM	1.99 \pm 0.11 (1.72–2.17)	2.66 \pm 0.07 (2.59–2.80)	2.83	2.86
BIR	2.78 \pm 0.30 (2.14–3.21)	2.56 \pm 0.13 (2.34–2.66)	2.42	2.99

Bernice P. Bishop Museum in Honolulu, including Fred Kraus, Carla Kishinami, Pumehana Imada, and Allen Allison. All known specimens of this species were collected by Fred Kraus during biodiversity surveys sponsored by the Bishop Museum; the type series was kindly prepared and loaned to us by Carla Kishinami and Pumehana Imada, and further studied during a visit to Honolulu facilitated largely by Allen Allison. We recommend "Bishop moss-mouse" as an appropriate English common name.

DESCRIPTION: *Pseudohydromys berniceae* is the smallest species of *Pseudohydromys* and among the smallest of New Guinea murines—only the species of *Microhydromys* and *Lorentzimys* are similar in size or consistently smaller. In its coloration, subequal tail and head-body lengths, and skull conformation, it resembles a small version of *P. murinus*, to which we suggest it is most closely related.

Coloration (described from fluid specimens) is uniform dark brown gray above and below, essentially as in *P. murinus*. The fur is shorter than in most congeners, measuring only about 5 mm in length on the midback. The tail averages 11% longer than the head-body length (longer than in other moss-mice), and is dark brown apart from a terminal white tail tip variable in length. Both specimens from Mt. Pekopekowanana and one from Mt. Obree have prominent distal white tail tips (8–15 mm in length), but the holotype from Mt. Simpson and two other specimens from Mt. Obree have only very short tail tips or a very short bit of white mottling at the tip of the tail (1–3 mm). There are 15–18 tail scales per centimeter in the midsection of the tail, and the tail hairs are relatively short, measuring one to 1.5 tail scales in length. The dorsal surfaces of the manus are white, and the dorsal surfaces of the pes are dark gray, though all the digits are white. The ear is dark gray and the eye is relatively very small. Females have two pairs of inguinal mammae.

In most aspects the skull and teeth of *P. berniceae* (fig. 5) closely resemble those of *P. murinus* as described above, though the skull has a considerably more gracile cranial appearance on account of its smaller size, thin and spindly zygomata, and its rather

thin-walled braincase. The upper incisors are orthodont, the upper and lower molar rows are situated just behind the zygomatic plate, and the molars are large relative to congeners except *P. murinus* (CLM/CIL = 12.3%–13.3%). The cranium differs from *P. murinus* in featuring a blunter, less tapering rostrum with uniquely short nasals, a narrower interorbital constriction, and less inflated braincase and auditory bullae. The nasals are retracted in *P. berniceae* relative to *P. murinus* and *P. eleanorae*, n. sp., and do not project beyond the upper incisors. The interorbital region is more constricted and more nearly parallel sided in *P. berniceae* than in *P. murinus*, owing in part to the former species' less inflated frontals. The braincase is proportionately less inflated than in *P. murinus*, with the zygomatic arches of *P. berniceae* averaging 4% wider (at the squamosal roots) than the breadth of the braincase.

BIOLOGICAL NOTES: Very little is known about this newly discovered species. Though its tail is proportionately longer than in other moss-mice species (table 3), we suspect that, like its congeners, it is probably entirely or mostly terrestrial. All specimens have been collected in pitfall traps along drift-fence traplines intended for catching reptiles and amphibians (Kraus and Allison, 2005). Kraus and Allison (2005: 50) characterized the habitat at the type locality of *P. berniceae* (on Mt. Simpson) as "lower montane forest." The holotype (figs. 5, 7) was a pregnant female with enlarged teats and two well-developed embryos (weight of each ca. 0.8 grams, crown-rump length of each ca. 18.5 mm). It is notable that *P. berniceae* has been collected syntopically (in the same pitfall line) with both *P. murinus* and *P. germani* in lower montane forest on Mt. Obree.

With *Pseudohydromys germani*, *Chirromys lamia*, *Rattus vandeuseni*, *Leptomys paulus*, and *Coccymys kirrhos* (see Musser et al., 2008; Musser and Lunde, 2009), *P. berniceae* forms part of a diverse suite of endemic murines found only in the Owen Stanley Mountains of southeastern Papua New Guinea (the "Papuan Peninsula" or "Bird's Tail" of New Guinea). Two small marsupials, *Microperoryctes papuensis* and



Fig. 9. Dorsal and ventral views of a study skin of *Pseudohydromys eleanorae* (holotype, BMNH 50.1734, adult female, Mt. Wilhelm, Chimbu Province, Papua New Guinea).

Murexia rothschildi, are likewise endemic to montane forests on the Owen Stanley Mountains (Laurie, 1952; Flannery, 1995a), as are several distinctive monotreme and marsupial subspecies (Musser and Sommer, 1992; Aplin and Woolley, 1993; Flannery, 1995a; Flannery and Groves, 1998; Helgen, 2005a; Musser et al., 2008; Aplin et al., ms.).

Pseudohydromys eleanorae, new species

HOLOTYPE: BMNH 50.1734, adult female, study skin (fig. 9) and skull (fig. 5), from the "high northern slopes" of Mt. Wilhelm (ca. 05°47'S, 145°01.5'E, Chimbu Province, Papua New Guinea; locality 4 in fig. 8), between 9000 and 10,000 ft (= 2740–

3050 m), Bismarck Range, collected 13 May 1949 by F. Shaw-Mayer, hereafter FSM (original number 1146).

REFERRED SPECIMENS: BMNH 53.282, adult male, study skin and skull, from Welya ("forested spurs west of Hagen Range" (fig. 8: locality 2), ca. 05°44'S, 143°56'E, Western Highlands Province, Papua New Guinea), 8500 ft (= 2590 m) collected 30 December 1950 by FSM (original number 1287); BMNH 53.285, adult female, study skin and skull, from Welya, 8000–9000 ft (= 2440–2740 m), collected 24 December 1950 by FSM (original number 1264); BMNH 53.292, adult male, study skin and skull, from "forested ridges between Mts. Giluwe and Hagen," (ca. 06°S, 144°E, the border region between Southern Highlands and Western Highlands Provinces, Papua New Guinea; fig. 8: locality 3), 9000 ft (= 2740 m), collected 6 July 1951 by FSM (original number 1455).

DIAGNOSIS: *Pseudohydromys eleanorae* is superficially similar in appearance to *P. murinus*, a sympatric congener with which it has been confused until now. Nevertheless, it can easily be distinguished from *P. murinus* on the basis of both external and cranial features. Externally, *P. eleanorae* has paler fur, with a clear gray dorsum not infused with dark brown (grizzled, dark brownish gray in *P. murinus*), no pale spotting on the rump (typically present in *P. murinus*), and a relatively shorter tail, averaging 8% shorter than head-body length (averaging 4% longer than head-body length in sympatric populations of *P. murinus*). The skulls of *P. eleanorae* and *P. murinus* are essentially equivalent in size (averaging only slightly smaller in *eleanorae*) and agree closely in basic cranial configuration, but *P. eleanorae* has markedly smaller molars, broader upper incisors (at their bases), a shorter and more parallel-sided rostrum, a relatively narrowed mesopterygoid fossa, an absolutely narrower postorbital constriction, an absolutely narrower and much lower-domed braincase, and proportionally wider, parallel-sided zygomatics (table 4, fig. 5).

DISTRIBUTION: The four known specimens of this species, all at BMNH, document its occurrence in mossy montane forests situated between 2440 and 3050 m in the Bismarck

and Hagen ranges (Chimbu, Western Highlands, and Southern Highlands provinces) of the Central Highlands of Papua New Guinea (fig. 8: localities 2–4). The average elevation of the four known trapping localities is 2731 meters (median 2670 m, SD 191 m). *Pseudohydromys eleanorae* occurs syntopically in these high-elevation forests with a diverse assemblage of congeners, including *P. murinus*, *P. ellermani*, and *P. fuscus* (Laurie, 1952; Flannery, 1995a). No other local area of New Guinea is yet known to support so many species of moss-mice in sympatry.

ETYMOLOGY: The specific epithet honors Eleanor Mary Ord Laurie (1919–), former head of the Mammal Section at the British Museum (Natural History), describer and codescriber, respectively, of the small-bodied hydromyins *P. fuscus* and *P. ellermani* (Laurie, 1952; Laurie and Hill, 1954), both of which occur sympatrically with this new species. We recommend "Laurie's moss-mouse" as an appropriate English common name.

DESCRIPTION: The pelage of *P. eleanorae* is gray above and below—a 'clear' gray only slightly tinged with brown above—very similar to the coloration of sympatric *P. fuscus* and (to a slightly lesser extent) *P. ellermani*, but contrasting with the darker, more brownish dorsum of sympatric *P. murinus*. Unlike *P. fuscus* and *P. ellermani*, the fur of the rump is not infused with brown tones; unlike *P. murinus*, the rump is not flecked with white. The gray venter is still less tinged with brown than the dorsum. The pelage is thick, short (4–5 mm long on the midback), and straight, similar to that of *P. fuscus* and contrasting with the longer, more conspicuously woolly pelage of *P. murinus*.

The tail is relatively shorter in *P. eleanorae* than in *P. murinus* (table 3). The tail is not conspicuously mottled, and averages paler than the typically dark brown tail of *P. murinus*. There is a variably pronounced terminal white tail tip, about 9–10 mm in length. The dorsal surfaces of the hindfeet and forefeet are pale in pigmentation and are covered in small silvery hairs on the surfaces of the digits and dark gray hairs on the surfaces of the feet. The feet appear darker than in *P. fuscus* (which has white feet) but

paler than in *P. murinus*, in which the feet are darkly pigmented.

The face and muzzle are furred and are similar in color to the body. The mystacial vibrissae (25–30 mm at the longest) are relatively short—conspicuously shorter than in *P. fuscus* but similar in length to *P. murinus*, *P. ellermani*, and other species. The eyes are minute. Adult females have two pairs of inguinal mammae.

Although head-body length averages longer in *P. eleanorae* than *P. murinus* (table 3), the skull of *P. eleanorae* averages slightly smaller, suggesting a proportionally shorter head (table 4). *Pseudohydromys eleanorae* resembles *P. murinus* in overall cranial conformation (figs. 3, 5), but differs most notably in its smaller teeth and in various cranial proportions. Despite its slightly shorter cranial length, the skull of *P. eleanorae* is somewhat stouter than in *P. murinus*, with the width across the zygomatic arches averaging 5% wider than the width of the braincase. The zygomata are also more parallel in profile, contrasting with the anteriorly tapering zygomatic arches of *P. murinus* (fig. 5). The rostrum is narrower and more nearly parallel-sided than in *P. murinus*, and the nasolacrimal capsules show slight lateral expansion, bulging beyond the outline of the rostrum—in contrast to the more inflated, anteriorly tapering rostrum of *P. murinus*. The top of the cranium of *P. eleanorae* is flatter in lateral profile than in *P. murinus*, which has a more inflated (more rounded and higher-domed) braincase. Though compilations of summary statistics reveal that *P. eleanorae* is equivalent to *P. murinus* in many univariate cranial measurements, it differs strikingly in others, indicative of major cranio-proportional differences between the two species. For example, relative to *P. murinus* it has an absolutely narrower postorbital constriction (POB < 4.5 mm), smaller molars (LM1 < 1.9 mm; CLM/CIL \leq 12%), an absolutely lower-domed braincase (HBC < 6.1 mm), and a relatively much narrower braincase, but also broader incisors (BIR > 2.4 mm). The mandible is similar in shape to *P. murinus*, though the lower molars are considerably smaller. When *P. eleanorae* is contrasted against specimens of *P. murinus* from the

Bismarck and Hagen ranges, the regional population with which it occurs sympatrically, it is seen to measure absolutely smaller in postorbital width, braincase breadth, braincase height, maxillary toothrow length, and molar lengths and widths, but (almost absolutely) greater in the basal width of the upper incisors (table 4). Each of these traits offers a means for distinguishing the skulls of the two species, and in concert, these metric and proportional differences cleanly separate these two sympatric species in multivariate comparisons (e.g., fig. 3; table 2). The middle lacerate foramen is moderately expansive (larger than in *P. murinus*) and may be confluent with the foramen ovale, though this is difficult to assess in the few available skulls, which evidently bear some damage to delicate bones from their original cleaning.

BIOLOGICAL NOTES: Museum holdings from central Papua New Guinea reveal that no fewer than four species of similarly small-bodied congeneric moss-mice occur syntopically above 2000 m in the Central Highlands—*Pseudohydromys murinus*, *P. fuscus*, *P. ellermani*, and *P. eleanorae*. Judging from the respective numbers of these four species in museum collections from the Central Highlands, their natural abundance or trappability probably decreases in the same order. Unsurprisingly, the taxonomic discovery of these four species unfolded in the same sequence (Rümmler, 1934; Laurie, 1952; Laurie and Hill, 1954; this study).

Apart from its elevational and habitat associations—middle- to high-elevation montane evergreen rainforest, probably corresponding both to “lower montane forest” and “upper montane forest” as delineated by Grubb and Stevens (1985)—and its sympatric occurrence with three other moss-mice, nothing is yet recorded about the biology of this species. On the study skin of one adult female (BMNH 53.285), the ears appear to be bitten off short, perhaps suggestive of intra- or interspecific aggression.

In addition to *Pseudohydromys eleanorae*, other examples of mammals known only from Papua New Guinea’s Central Highlands region (i.e., the broad vicinity of the Kaijende, Bismarck, and Hagen ranges) include the vespertilionid *Nyctophilus microdon* and the murines *Rattus giluwensis*,

Protochromys fellowsi, and *Mirzamys nora-hae*, n. gen., n. sp. (see below; Helgen, 2007b). We anticipate that future taxonomic research on New Guinea mammals will identify further examples of Central Highlands regional endemics.

Pseudohydromys patriciae, new species

HOLOTYPE: AM M26991, adult male, study skin and skull (figs. 10, 11), from Porokma (ca. 04°00'S, 138°43'E, Papua Province, Indonesia: locality 1 in fig. 8), 2800 m, near Lake Habbema in the Snow Mountains of western New Guinea, collected 19 September 1988 by P.A. Woolley (field number MFC 26).

PARATYPE: AM M26882, adult female, in spirit (fixed in formalin and stored in 70% ethanol), with skull extracted and cleaned, collected at the type locality on 21 September 1988 by P.A. Woolley (fig. 12). The holotype and paratype are the only specimens known.

DIAGNOSIS: *Pseudohydromys patriciae* is a medium-sized moss-mouse (cranially larger than *P. murinus*, *P. berniceae*, and *P. eleanorae*), equivalent in body and skull size to *P. occidentalis* and *P. ellermani*, with which it occurs sympatrically, and with which the type series of *P. patriciae* has been confused in the Australian Museum collection until now. It has pale brownish-gray pelage (versus the darker, less brown-infused slate-gray pelage of *P. occidentalis*) and apart from occasional specimens of *P. ellermani* and *P. occidentalis* is the only moss-mouse that has pure white markings on the middle of an otherwise smoky-gray venter. The cranium is large for the genus, with weakly splayed zygomatic arches (more robust and more widely splayed zygomata in sympatric *P. occidentalis*), an elongate high-domed braincase that posteriorly overhangs the occipital condyles, relatively small molars situated directly behind the zygomatic plate, a sharply defined postpalatal spine, and a narrowed foramen magnum.

DISTRIBUTION: *Pseudohydromys patriciae* is recorded only from the type locality, situated at 2800 m in montane forest in the Snow Mountains of western New Guinea near Lake Habbema (Woolley, 1990). This is apparently the same site as one of the



Fig. 10. Skull of *Pseudohydromys patriciae* (holotype, AM M26991, adult male, Porokma, Lake Habbema, Papua Province, Indonesia), including close-up view of mandibular dentition (at bottom). Scale as noted. Photographs courtesy of Ken Aplin.

bivouacs established by the Third Archbold Expedition to New Guinea in 1938–1939—identified as “nine kilometers northeast of Lake Habbema,” which Brass (1941: 278) described as “a camp in high *Nothofagus*-forest at an altitude of 2800 m, five carrier hours from the lake” (see Woolley, 1990).

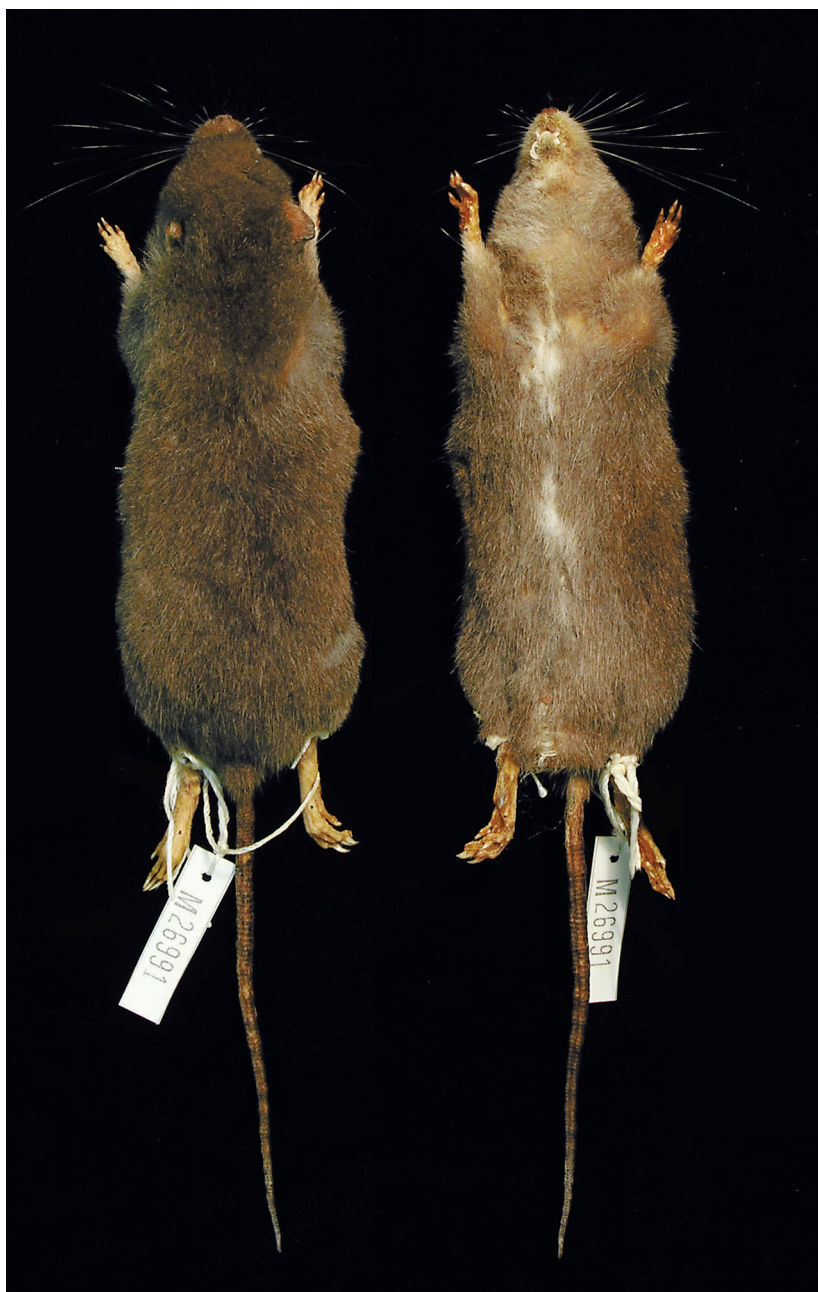


Fig. 11. Dorsal and ventral views of a study skin of *Pseudohydromys patriciae* (holotype, AM M26991, adult male, Porokma, Lake Habbema, Papua Province, Indonesia).

ETYMOLOGY: The species epithet honors Patricia A. Woolley of La Trobe University in Melbourne, collector of the type series, and authority on New Guinea mammals. We

recommend “Woolley’s moss-mouse” as an appropriate English common name.

DESCRIPTION: The dorsal pelage of *P. patriciae* is uniformly pale brownish gray (a

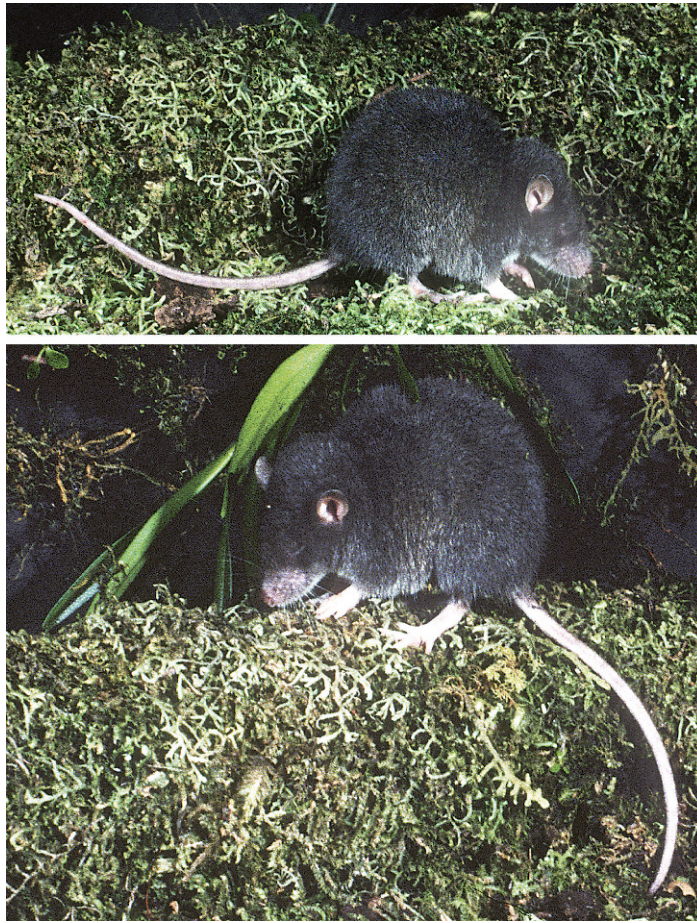


Fig. 12. *Pseudohydromys patriciae* in life (AM M26882, adult female, taken at Porokma, Lake Habbema, Papua Province, Indonesia). Photographs courtesy of the collector, Pat Woolley.

‘smoky’ gray), not flecked with white or pale gray markings—similar to the coloration of *P. ellermani* (sympatrically occurring). The fur is more infused with pale brown than the darker, more slate-gray pelage of sympatric *P. occidentalis*, and markedly paler than the darker brown fur of *P. murinus*. The pelage is thick and measures 8–10 mm in length on the midback. The venter (below the lateral level of the limbs) has fewer brown tones than the dorsum, rendering it a paler, more even gray color, and the underside of the head (i.e., the chin and lower sides of the face) is paler still, entirely lacking brown tones and appearing silvery gray. *Pseudohydromys patriciae* has pure white midventral markings (i.e., a pale chest and belly “flash”) that extend antero-

posteriorly in a narrow median line from the base of the throat over the breast and belly to terminate just anterior to the inguinal region, contrasting conspicuously with the otherwise gray venter (figs. 11, 12)—a rare feature in the genus. Less extensive white ventral markings on an otherwise dark venter are seen elsewhere in the genus only in occasional specimens of *P. ellermani* (see Lidicker and Ziegler, 1968) and *P. occidentalis* (e.g., BBM-NG 98485). The face and muzzle are furred, and similar in color to the body. The mystacial vibrissae (25–30 mm at the longest) are relatively short—conspicuously shorter than in *P. fuscus* but similar in length to *P. murinus*, *P. ellermani*, and other species. The eyes are minute.

The tail is relatively shorter in *P. patriciae* (averaging 86% of head-body length) than in all congeners apart from *P. fuscus* (table 3). The tail is rather pale, but still shows weak mottling across its length. In the holotype, there are 13 tail rings per centimeter in the midsection of the tail, and there is no obvious pale terminal tail tip. The tail hairs measure about two tail scales in length. The claws are white and less elongate than the clear claws of sympatric *P. occidentalis*. The dorsal surfaces of the hindfeet and forefeet are pigmented pale and are covered in small silvery hairs on the surfaces of the digits and the feet.

The field notes that accompany the type series of *P. patriciae*, prepared by Woolley, indicate that the adult female paratype had only a single pair of inguinal teats (i.e., the formula $0 + 1 = 2$), a point confirmed via discussion with Woolley (in litt., 2007). All other hydromyins usually have two pairs of inguinal mammae ($0 + 2 = 4$), though a single pair of mammae has been reported on specimen tags for individual specimens of *Mirzamys* and *Hydromys* (see account of *Mirzamys louiseae*, n. sp., below). More specimens of this newly described species will be needed to assess whether a single pair of mammae is the normal condition in *P. patriciae*, or whether the paratype of *P. patriciae* simply reflects an individual exception to the normal hydromyine teat conformation.

The skull of *P. patriciae* is equivalent in overall cranial size (both absolute length and width) to that of sympatric *P. occidentalis* (tables 4, 5). In many aspects the skull and mandible could be considered enlarged replicas of those of *P. murinus* of eastern New Guinea (CIL averaging 8% longer than in *P. murinus*), although the upper incisors are slightly broadened proportionately and the molars are relatively smaller than in either *P. murinus* or the much smaller *P. berniceae*. In fact, the molars of *P. patriciae* are equivalent in absolute size to the molars in these smaller-bodied species (table 4). As in *P. murinus* and *P. berniceae*, the zygomatic arches are relatively delicate and weakly splayed, averaging only 3% wider than the width of the braincase, and the braincase is globose, lending the posterior cranium a rounded

(rather than flat) aspect in lateral profile. As in most specimens of *P. murinus*, there is a dorsal depression in the cranium where the rather flat-topped rostrum meets the rounded, high-domed braincase (fig. 10).

Despite its overall similarity in cranial conformation to *P. murinus* and *P. berniceae*, the skull of *Pseudohydromys patriciae* differs both from these species and all (or most) other congeners in a handful of distinctive cranial traits. The braincase is unusually elongate, such that the interparietal is less reduced than in other species and the supraoccipital projects posteriorly to overhang the occipital condyles (fig. 10). The stapedia foramen is less reduced than in other members of the genus. The foramen magnum, typically very large in *Pseudohydromys*, is less expansive in *P. patriciae* than in all congeners, particularly in its proportionally narrowed breadth. The posterior margin of the palate bears a well-developed palatal spine, more pronounced than in other *Pseudohydromys* except *P. occidentalis* and *P. musseri* (fig. 10).

BIOLOGICAL NOTES: Little is yet known of the biology of *P. patriciae*, apart from its occurrence in montane forests in the Snow Mountains and its regionally sympatric occurrence with two congeners (*P. ellermani* and *P. occidentalis*).

Pat Woolley collected the two known specimens of *P. patriciae* in September 1988 (fig. 12). Based on a visit to the site in October–November 50 years prior, in 1938, Brass (1941: 312–316) provided excellent descriptions of tree diversity and other aspects of vegetational and ecological context in the vicinity of the type locality, and sketched an evocative picture of the montane rainforest home of this newly described species:

The camp was in the bottom of the rather steep-falling little valley of one of the headwater streams of the Bele River. Sharp spur ridges, considerably lower than those that hemmed in the river basin, rose 50 to 100 m. from the bed of the stream on both sides. The country was entirely forested except for landslips along the streams, a few small clearings planted with *Pandanus* and containing native huts, and occasional wet shrubby openings which had probably been enlarged by the natives who used

them for resting places when hunting and traveling in the mountains. Although well up in the cloud belt, weather conditions were variable, and mists not very frequent or regular in occurrence in the immediate neighborhood. The tradewinds appeared to carry less moisture than at lower altitudes, and when they were in operation the clouds tended to mass on the high spurs, so that valley conditions prevailed in the river basin. Dull, overcast, and showery weather was nevertheless the rule (Brass, 1941: 312).

Like *P. patriciae*, many mammal species are known only from western New Guinea's Snow Mountains, defined here geographically as the ranges extending from the Baliem Valley to the Paniai (= Wissel) Lakes (see Helgen, 2007a). This assemblage includes the rodents *Baiyankamys habbema*, *Hydromys hussoni*, *Mallomys gunung*, *Brassomys albicans*, *Melomys frigidicola*, and *Rattus richardsoni* (Musser and Pliik, 1982; Flannery et al., 1989; Flannery, 1995a; Helgen, 2005b; Musser and Carleton, 2005) and the macropodids *Thylogale christensenii* (known from Holocene remains—Hope, 1976) and *Dendrolagus mbaiso* (Flannery et al., 1995, 1996), as well as several other mammal species that remain undescribed (Musser and Carleton, 2005; Helgen, 2005b, 2007a).

Pseudohydromys occidentalis Tate, 1951

TYPE MATERIAL AND LOCALITY: The holotype of *occidentalis* is AMNH 150772, adult male, study skin and skull (figs. 13–14), from Lake Habbema (04°09'S, 138°09'E, Papua Province, Indonesia: locality 1 in fig. 16), 3225 m, in the Snow Mountains, collected 8 August 1938 by W.B. Richardson (Tate, 1951; Lawrence, 1993).

DIAGNOSTIC AND DESCRIPTIVE NOTES: *Pseudohydromys occidentalis* is one of the larger species of *Pseudohydromys*. Coloration is uniformly dark brownish gray dorsally and paler gray ventrally (fig. 13), with paler silvery-white hairs covering the dorsal surface of the manus and the area right around the lips. The pelage is dense and long, measuring ca. 8 mm in length on the midback. The tail, hindfeet, and ears are pale in pigmentation. The tail averages about 10% shorter than the head-body length, is not clearly mottled, and does not bear a pale tail tip. Tate (1951) gave

a figure of 20 tail rings per centimeter for this species, but our count is 12–16 tail rings per centimeter in the midsection of the tail for all specimens. The tail hairs are black or silvery white and measure about 1.5 tail scales in length. Adult females have two pairs of inguinal mammae.

The skull of *P. occidentalis* averages larger than most congeners (equivalent in overall size to the various larger-skulled taxa, e.g., *P. patriciae*, *P. fuscus*, and *P. germani*) and the zygomatics flare slightly beyond the lateral margins of the braincase, lending the skull a relatively more robust appearance than in most species (this zygomatic flare is exceeded only in *P. fuscus* and *P. musseri*; table 5). There are two molars in each quadrant of the jaw, relatively reduced in size compared to *P. murinus*, *P. berniceae*, *P. eleanorae*, and *P. patriciae*, but still relatively much larger than in *P. fuscus* (table 5). The maxillary tooth row is located well behind the zygomatic plate, but not so far back as in *P. fuscus* (figs. 14, 15). The zygomatic plate is only weakly excised. The braincase is rather highly domed, the interparietal is small, and the mandible is long and delicate with long curving incisors. The upper incisors are narrow and orthodont or slightly proodont. The mesopterygoid fossa is not as strongly constricted as in *P. fuscus*, and the hamular processes of the pterygoid region proceed posteriorly from the posterior palate in a subparallel configuration. As in *P. patriciae*, the posterior margin of the palate bears a well-defined medial spine.

DISTRIBUTION: In his comprehensive review of Australo-Papuan rodents, Tate (1951) described this species based on a series of five specimens trapped in upper montane forest in the vicinity of Lake Habbema and Mt. Trikora in the Snow Mountains (localities 1 and 2, respectively, in fig. 16). Tate's original specimens remain the only correctly identified exemplars of this species discussed in the literature to date. AMNH also holds a left dentary of *P. occidentalis* (accessioned as AMNH 276468, with M1 intact), collected (like the type series of *occidentalis*) on the Third Archbold Expedition to New Guinea, from an owl pellet accumulation discovered at a site 2 km east of "Mt. Wilhelmina Top." According to the summary account of the



Fig. 13. Dorsal and ventral views of a study skin of *Pseudohydromys occidentalis* (holotype, AMNH 150772, adult male, Lake Habbema, 3225 m, Papua Province, Indonesia).



Fig. 14. Selected views of skulls of species (and representative populations) in the *occidentalis* species group: (first column) *Pseudohydromys occidentalis* from the Snow Mountains (holotype, AMNH 150772, adult male, Lake Habbema, 3225 m, Papua Province, Indonesia); (second column) *P. occidentalis* from the Star Mountains (BBM-NG 108177, adult female, Lake Louise, West Sepik Province, Papua New Guinea; upper incisors missing); (third column) *P. musseri* (holotype, BBM-NG 101737, adult male, Mt. Somoro, West Sepik Province, Papua New Guinea); and (fourth column) *P. sandrae*, n. sp. (holotype, AM M14168, adult male, Mt. Sisa, Southern Highlands Province, Papua New Guinea). Scale bar = 10 mm.

expedition, in the area “there was an owl that evidently was fairly common above timber line, judging by the pellets and feathers found in caves under boulders and in crevices among the larger fragments of talus. No specimen was secured, and but one was seen, a medium size, dark bird, probably *Tyto tenebricosa*. Comparison of feathers gathered supported this identification” (Archbold et al., 1942: 280). As Musser and Lunde (2009) have noted, this is the only reference to owl pellets in the entire report by Archbold et al. (1942). These pellets were likely collected between 3800 and 4150 m.

Most subsequent records of *occidentalis* derive from the Star Mountains, as discussed or mentioned by Menzies and Dennis (1979), Ziegler (1982, 1989), Flannery (1990), Flannery

(1995a, in part—including a skull attributed to *P. occidentalis* on p. 524), Musser and Carleton (1993), and Smales (2001). All of these subsequent accounts actually correspond to specimens, deposited at BBM and PNGNM, that are not *P. occidentalis* but actually represent a previously unnamed genus and species, described below. Similarly, a specimen from Porgera (Enga Province, Papua New Guinea) identified as “*P. occidentalis*” by Jackson and Woolley (1993) proves on examination to represent another new taxon in the same genus, also described below (Helgen, 2007b). Reported measurements, verbal descriptors, and a photograph of a study skin presented by Flannery (1995a: 205–206) in his account of “*P. occidentalis*” actually represent *Pseu-*



Fig. 15. Comparison of the skulls of (left) *Pseudohydromys occidentalis* (BBM-NG 108177, adult female, Lake Louise, West Sepik Province, Papua New Guinea; upper incisors missing) and (right) *P. fuscus* (topotype, AMNH 191422, adult female, Mt Wilhelm, Chimbu Province). Scale bar = 10 mm.

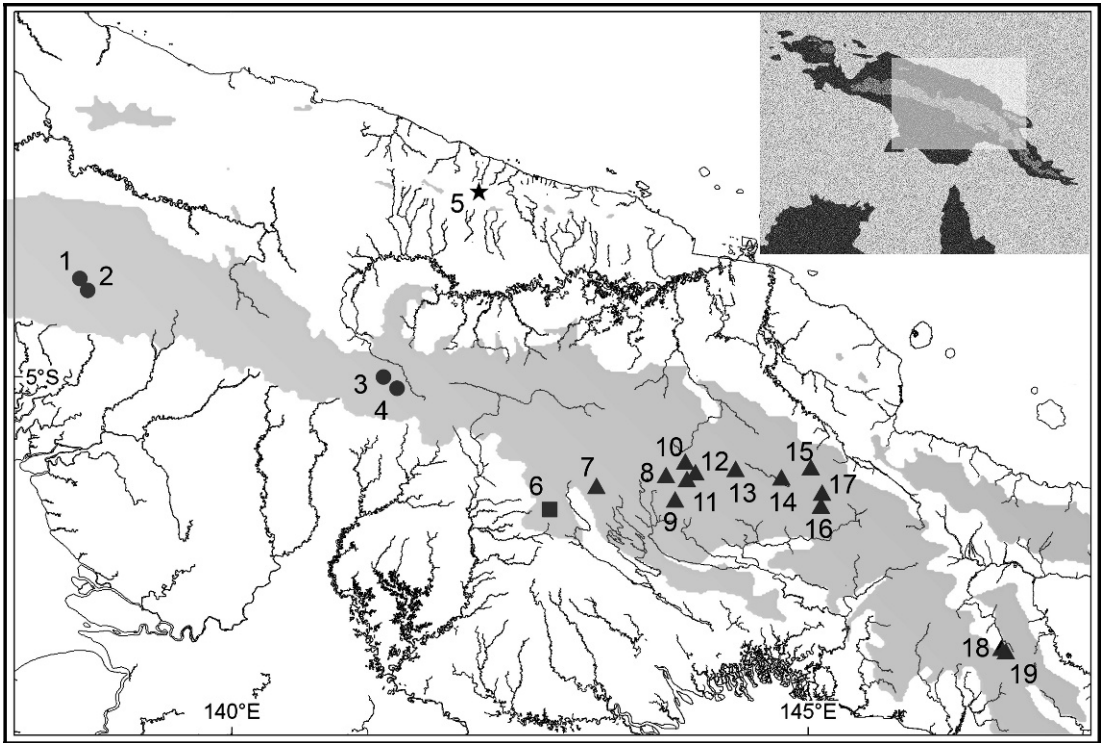


Fig. 16. Recorded distribution (vouchered localities) of selected species of *Pseudohydromys* of central New Guinea: *P. occidentalis* (circles), *P. musseri* (star), *P. sandrae* (square), and *P. fuscus* (triangles). Areas above 1000 m in elevation are shaded in gray. See text for numbered localities.

dohydromys patriciae, which occurs with *P. occidentalis* in the vicinity of Lake Habbema (see above).

Despite these previously confused identifications and published records, other specimens demonstrate that *P. occidentalis* does occur in the Star Mountains. In addition to the Snow Mountains type series in the Archbold collections, there are two other specimens of *P. occidentalis* in world museums. Both originate from the Star Mountains region in western Papua New Guinea and are deposited at BBM (see below; localities 3 and 4 in fig. 16). These were previously misidentified as *P. fuscus* by Flannery (1995a; a misidentification recently perpetuated by Musser and Carleton [2005], who cited Flannery). *Pseudohydromys fuscus* is not yet known to occur as far west as the Star Mountains, its westernmost record of occurrence being the Tari Gap in central Papua

New Guinea (see account of *P. fuscus*, below).

In summary, *P. occidentalis* has been collected to date in mossy upper montane forest habitats in two disjunct geographic areas: from the neighborhood of Mt. Trikora and Lake Habbema in the Snow Mountains at elevations from 3225 to at least 3800 m (specimens at AMNH; see above); and from the Star Mountains region of western Papua New Guinea (Western and West Sepik Provinces), at two sites situated at 2300 and 2600 m (specimens at BBM; see below). We expect that it occurs in similar habitats throughout intervening mountainous areas of West Papua and Papua New Guinea (fig. 16). The mean elevation of the five known modern trapping sites for this species is 3057 meters (median 3225 m; SD 583 m).

GEOGRAPHIC VARIATION: Our examinations of the five specimens of the type series

of *P. occidentalis* (AMNH 110326, 110344, 110366, 110391, 150772) from the Snow Mountains (3225 to 3600 m) confirm Tate's (1951) assertion that these specimens comprise a uniform morphological cluster and undoubtedly represent a single species.

No specimens have been collected from the Snow Mountains more recently than 1938 (as discussed above, more recent specimens from Lake Habbema attributed to *P. occidentalis* by Flannery [1995a] in fact represent *P. patriciae*). Of the two specimens of *P. occidentalis* collected in the Star Mountains, one (BBM-NG 108177), an adult female from Bafunmin (trapped at 2300 m; locality 4 in fig. 16), agrees with the type series in essentially all particulars, except that the rostrum is slightly longer and wider than animals from the Snow Mountains. The second specimen from the Star Mountains specimen (BBM-NG 98485), an adult female from Lake Louise (trapped at ca. 2600 m; locality 3 in fig. 16), has a smaller skull and a shorter, narrower rostrum compared to both the type series and the Bafunmin example. Despite this specimen's somewhat smaller skull, its teeth match other *P. occidentalis* in both size and shape. These seven specimens otherwise show close qualitative morphological resemblance and comprise a discrete craniometric cluster in multivariate space, which in turn shows a close morphometric affinity with the geographically outlying taxa *P. musseri* and *P. sandrae*, n. sp. (fig. 3). Collection of additional material (especially within the Star Mountains) and subsequent comparisons will be required to more robustly evaluate our hypothesis that these geographically disjunct samples from the Snow and Star Mountains represent a single species, *P. occidentalis*. If so, further collections are likely to reveal a broader and more continuous distribution for *P. occidentalis* extending over the western and central portions of New Guinea's expansive Central Cordillera.

BIOLOGICAL NOTES: *Pseudohydromys occidentalis* is an inhabitant of mossy mid- and upper montane forests, up to the subalpine interface, in the Snow and Star Mountains regions of west-central New Guinea (from 2300 to 3600 m). It co-occurs with at least three other moss-mice species across this

range. In the Star Mountains (at Bafunmin and Lake Louise) it has been collected syntopically with both *P. ellermani* and *Mirzamys louiseae*, n. gen., n. sp. (specimens at BBM and PNGNM). In the Snow Mountains, both *P. ellermani* and *P. patriciae* have also been collected in the vicinity of Lake Habbema (specimens at AM), which is the type locality of *P. occidentalis*, albeit at an elevation several hundred meters lower (2800 m) than that where the type series of *P. occidentalis* was originally trapped. Apart from basic habitat and elevational associations and geographic overlap with congeners, nothing is yet known of the basic biology of this species.

Uniquely shared distributional occurrences between the Star and Snow mountains, the pattern exhibited by *P. occidentalis*, are not uncommon in New Guinea montane mammals. Congruent mammalian examples include the murid *Coccymys ruemmleri* (Musser and Lunde, 2009), the petaurid *Dactylopsila megalura* and the dasyurid *Murexia habbema* (sensu stricto, i.e., excluding *M. hageni*) (Helgen, 2007a). If the geographically disjunct samples attributed here to *P. occidentalis* do indeed comprise a single species, this taxon should be expected to occur above 2300 meters in montane forests between the eastern Star Mountains and Lake Habbema—a broad geographic expanse (fig. 16) where very little mammal survey effort has been focused (Helgen, 2007a).

Lidicker and Ziegler (1968: 54) predicted that the disjunctly distributed *P. occidentalis* and *P. murinus*, long the only two species recognized in the genus *Pseudohydromys*, might eventually be shown to be conspecific, and Musser and Carleton (2005: 1334) cited *P. occidentalis* and *P. murinus* as a seeming example of an east-west sister species pair across the Central Cordillera. However, comparisons developed here suggest that in light of the much greater diversity now recognized within the genus, these two taxa have no special morphological, ecological, or phylogenetic affinity among the various members of the genus *Pseudohydromys*. The immediate phylogenetic affinities of *occidentalis* remain unclear, but we tentatively suggest an alliance with *P. musseri* and *P. sandrae*, n. sp., based on morphometric and

certain qualitative morphological comparisons (figs. 3, 14; see below).

Though they differ markedly in comparative molar size, *Pseudohydromys occidentalis* is similar to *P. fuscus* in external appearance, size, and proportions (table 3) and in certain quantitative and qualitative cranial aspects (table 5, fig. 15; see below). These two species have similar recorded elevational ranges (table 11) and on current evidence appear to be allopatric or parapatric, with *P. fuscus* occupying New Guinea's Eastern and Central Highlands regions, and *P. occidentalis* further west in the Snow and Star mountains. Though we do not suggest that they are immediately related phylogenetically, we suspect that these two species are ecological vicars (equivalents) that replace each other in an east-west manner across the Central Cordillera, a novel interpretation based on morphological and ecological resemblances not previously highlighted in the literature. Intensive trapping efforts in the mountainous country between Bafunmin and the Tari Gap (another little-explored area in mammalogical terms; Helgen, 2007b) will be needed to better illuminate the nature of their geographic interactions at the interface between their distributions in terms of geographical disjunction, abutment, or overlap.

Lidicker (1968: 616–620) described the baculum and phallus of this species in useful detail based on the holotype.

Pseudohydromys musseri (Flannery, 1989)

TYPE MATERIAL AND TYPE LOCALITY: The holotype of *musseri* is BBM-NG 101737, adult male, study skin and skull (figs. 14, 17), from Mt. Somoro (03°23.5'S, 142°08'E, West Sepik Province, Papua New Guinea: locality 5 in fig. 16), 1350 m, Torricelli Mountains, North Coastal Range, collected 12 November 1972 by A.B. Mirza. The holotype, snap-trapped in upper montane rainforest near the summit of Mt. Somoro, is the only known specimen.

DIAGNOSTIC AND DESCRIPTIVE NOTES: *Pseudohydromys musseri* is a medium-sized moss-mouse, equivalent or slightly larger than other congeners that have two reduced molars in each quadrant of the jaw (*P. fuscus*, *P. occidentalis*, and *P. sandrae*, n. sp.). It has

a warm brown dorsum, a sharply demarcated cinnamon-colored venter, and a distinctly mottled tail slightly shorter than the head and body (94% of head-body length) (fig. 17). The pelage is relatively short. The ears are dark gray, and the dorsal surfaces on the manus and pes are white. The coloration of the dorsum and venter in *P. musseri* is unlike the pelage patterning of any other moss-mouse (Flannery, 1989). Its uniquely wide zygomatic breadth (table 5) would give this species' head a remarkably broadened appearance in life, contrasting strongly with the comparatively slim skulls of most species of *Pseudohydromys*.

Flannery (1989) described the holotype skull of *musseri* in some detail. Though he introduced *musseri* as a second species in the genus *Microhydromys*, he expressed uncertainty as to its true relationship with respect to *Microhydromys richardsoni*, recognizing its morphological isolation. Certainly *musseri* lacks the two most distinctive autapomorphies that characterize *M. richardsoni* and the recently described *M. argenteus*—very small body size (CIL < 20.5 mm) and vertical grooves in the enamel faces of the upper incisors (see account of *Microhydromys*, below). Recently, Musser and Carleton (2005: 1353) suggested that “a new genus will likely have to be erected” for *musseri*. Morphometric comparisons developed here reveal that *musseri* closely resembles species of *Pseudohydromys* in the *occidentalis* species group (fig. 3), both in size and in intimate aspects of craniodental shape. This phenetic affiliation is further bolstered by implications of this species' cephalic arterial conformation. In contrast to *Microhydromys richardsoni* (and *M. argenteus*), the stapedia foramen in *musseri* is exceedingly minute, the foramen ovale is relatively smaller, and the pterygoid plate lacks a conspicuous groove for the passage of the infraorbital branch of the stapedia artery. These are bony reflections of a derived cephalic arterial configuration (Musser and Heaney, 1992), shared with species of *Pseudohydromys* but not with *Microhydromys*. *Pseudohydromys musseri* also differs from *M. richardsoni* (and *M. argenteus*) in having the interparietal and auditory bullae markedly reduced in relative size—further traits, probably derived relative



Fig. 17. Dorsal and ventral views of the holotype study skin of *Pseudohydromys musseri* (holotype, BBM-NG 101737, adult male, Mt. Somoro, Torricelli Range, West Sepik Province, Papua New Guinea).

to the primitive condition in hydromyins, that unite the species of *Pseudohydromys* (Helgen et al., in press). In combination, we suggest that these morphometric and qualitative morphological comparisons reject a sister relationship between *musseri* and the species of *Microhydromys* and suggest instead that *musseri* is more appropriately recognized as a member of *Pseudohydromys*.

The holotype of *Pseudohydromys musseri* shows morphological similarities to other species in the genus that have two molars that are strongly reduced in size in each quadrant of the jaw (*P. fuscus*, *P. occidentalis*, and *P. sandrae*, n. sp.), including a blunt untapered rostrum, long narrowed molars, and confluence between the postglenoid and middle lacerate foramina (fig. 14). Though highly distinctive, many of its more distinctive traits as delineated by Flannery (1989) are seen in these other species, especially *P. sandrae*, n. sp. (see below). Notably, its short pelage and contrasting dorsal and ventral coloration are external traits that also characterize *P. sandrae*, n. sp., and its elongate and narrow posterior palatine foramina approach the conformation seen in *P. fuscus*. The remarkably broadened bony palate of *P. musseri* is, however, unique in the genus (fig. 14). The posterior margin of the palate bears a moderately developed spine.

DISTRIBUTION: *Pseudohydromys musseri* is known only from the type locality (fig. 16), situated in mossy upper montane forest near the summit of Mt. Somoro, the highest peak in the Torricelli Mountains, part of the North Coastal Range, which incorporates the Prince Alexander, Torricelli, Bewani, and Menawa ranges and other smaller mountain blocks. These relatively small mountain ranges are far isolated from the expansive mountainous Central Cordillera. *Pseudohydromys musseri* is usually presumed to be endemic to the North Coastal Ranges, a zone of considerable geographically restricted vertebrate endemism (Flannery, 1989; Helgen, 2005b), but the single specimen collected offers little insight and this species might well turn up with targeted snap-trapping and pitfall trapping in other hill and montane forest areas throughout northern New Guinea, such as the Cyclops, Foja, and Adelbert ranges, the mountain ranges of the Huon

Peninsula, and even perhaps middle elevation localities on the northern slopes of the Central Cordillera (see below).

BIOLOGICAL NOTES: Apart from the fact that the holotype was snap-trapped in upper montane forest in the Torricelli Mountains, nothing is known of the biology of this species. The skull and mandible of *P. musseri* are markedly more robust than in other moss-mice, suggesting a more powerful jaw apparatus and possibly a different diet relative to other species in the genus.

Together with the Cyclops Range of northern New Guinea, these mountains lie far disjunct from all other montane areas of New Guinea, and support distinctive montane mammal assemblages, different in membership to mammal communities in montane forests along the Central Cordillera and featuring many unique taxa. In addition to *P. musseri*, other endemic mammals of the Cyclops and North Coastal ranges include the echidna *Zaglossus attenboroughi*, the tree kangaroo *Dendrolagus scottae*, the glider *Petaurus abidi*, the murines *Paraleptomys rufilatus* and *Hydromys zieglerei*, and the horseshoe-bat *Hipposideros edwardshilli* (Osgood, 1945; Ziegler, 1981; Flannery and Seri, 1990b; Flannery and Colgan, 1993; Flannery and Groves, 1998; Helgen, 2005b). One other moss-mouse species, *Microhydromys richardsoni*, is also known from the North Coastal Range, albeit only on the basis of subfossil material thus far (Helgen et al., in press). The isolated Foja and Adelbert mountain blocks, lying respectively to the southwest and east of the North Coastal and Cyclops ranges, support additional endemic mammal taxa that await formal taxonomic description (K. Helgen, personal obs.), but no moss-mice have yet been collected in these mountains.

Pseudohydromys sandrae, new species

HOLOTYPE: AM M14168, adult male, flat skin and skull (figs. 14, 18), from Namosado, Mt. Sisa (= Mt. Haliago, 06°12'S, 142°46'E, Southern Highlands Province, Papua New Guinea: locality 6 in fig. 16), between 800–850 m, in the Kikori River Basin, collected 27 September 1979 by P. Dwyer (field number 1205). The holotype is the only known specimen.



Fig. 18. Flat skin of *Pseudohydromys sandrae* (holotype, AM M14168, adult male, Mt. Sisa, Southern Highlands Province, Papua New Guinea).

DIAGNOSIS: *Pseudohydromys sandrae* is a medium-sized moss-mouse bearing the characteristic features of the *occidentalis* species group, probably most closely allied to *P. musseri*. This species' entirely white underside (fig. 18) is unique in the genus. The tail measures 93% of head-body length in the sole available specimen (equivalent to *musseri*; table 3). Its skull resembles that of *P. occidentalis* and *P. musseri* in certain aspects (fig. 3), but differs in its considerably longer incisive foramina, narrower rostrum, narrower molars, and less laterally tapering upper incisors (fig. 14). It differs especially from *P. musseri* in having more slender zygomatic arches, much weaker zygomatic spread, and a narrower bony palate (fig. 14).

DISTRIBUTION: *Pseudohydromys sandrae* is known to date by a single specimen trapped on Mt. Sisa (locality 6 in fig. 16), a peak situated along the southern margin of the Central Cordillera in the Kikori River Basin of Southern Highlands Province, Papua New Guinea (see Dwyer, 1982, 1983a, 1984; Leary and Seri, 1997; Plowman, 1983). The trapping locality is situated in lowland hill forest (*sensu* Pajmans, 1976), approximately 200–300 m below the local transition to lower montane tropical evergreen forest, an unusually low-elevation habitat compared to that documented for most other species of *Pseu-*

dohydromys (K. Aplin, in litt.). Among all New Guinea moss-mice, only *Pseudohydromys berniceae* and the species of *Microhydromys* extend to lower absolute elevations (table 11).

ETYMOLOGY: This species is named for Sandra Ingleby of the Mammal Section at the Australian Museum in Sydney, in recognition of her friendship and kind assistance to us in our studies of Melanesian mammals. We recommend “White-bellied moss-mouse” as an appropriate English common name.

DESCRIPTION: *Pseudohydromys sandrae* is a medium-sized moss-mouse (table 3), equivalent in body size to *P. occidentalis*, *P. musseri*, and *P. fuscus*, but larger than members of the *murinus* species group, including *P. murinus*, the identification associated with this specimen in the Australian Museum collection until now. However, we must certainly credit Peter Dwyer, the collector of the holotype of *P. sandrae*, for his published observation that this specimen “does not fit any described forms of *Pseudohydromys*” (Dwyer, 1990: 210).

An immediately striking feature of *Pseudohydromys sandrae* is its wholly white belly, chin and throat—a pelage coloration pattern unique among New Guinea moss-mice. (Walker (1964: 972) figured a photograph from the AMNH Archbold Expedition ar-

chives of a pale-bellied rodent from New Guinea attributed to the genus *Pseudohydromys*, but this photograph does not depict a moss-mouse. Its large ears, unreduced eye, long feet, buff belly, pale underside to the tail, and white terminal tail tip indicate that this is a specimen of *Paraleptomys*.)

In *Pseudohydromys sandrae* the dorsum and the sides of the body are dull gray-brown from nose to tail (recalling the dorsal coloration of *Microhydromys argenteus*, which occurs in the same region; Helgen et al., in press). The transition between gray-brown above to white below is sharply demarcated rather than grading. The dorsal surfaces of the manus and pes are white, and the ear is gray. The pelage is short over the entire body, in strong contrast to most other species of the genus, which live in higher-elevation forests and have thick pelage with a velvety or woolly texture. Only in *P. musseri* is the pelage similarly short. External measurements of the holotype are as follows: head-body 102 (from skin label), tail length 95 (original measurement from skin label; the tail is now broken off and part is missing); hindfoot length ca. 21 (measured from the flat skin), ear ca. 10.5 (measured from the flat skin), and body mass 20 grams (from the skin label). There are 17 tail rings per centimeter in the midsection of the tail, and the tail hairs are short, measuring only about one tail ring in length. The unbroken portion of the tail appears to be relatively pale overall, though somewhat darker above than below and with some suggestion of mottling.

The skull of the holotype closely matches that of *musseri* in condyloincisive length and falls within the range of variation in condyloincisive length seen in both *P. fuscus* and *P. occidentalis*. Relative to other members of the *occidentalis* species group and to *P. fuscus*, the zygomatic arches are more slender and delicate, and rather weakly splayed (figs. 14, 15), though still they show greater lateral expansion than in *P. patriciae* and in members of *murinus* species group, jutting laterally well beyond the margins of the braincase (ZB/BBC = 115%). The braincase is high domed and relatively wide. In lateral profile the top of the cranium slopes linearly downward from the high-domed braincase to the front of the nasals. As in *P. musseri*, the

upper and lower incisors are relatively much broadened, and the nasolacrimal capsules bulge slightly beyond the sides of the rostrum, which is relatively blunt and not strongly tapered. The tooth row is situated well behind the zygomatic plate. The mesopterygoid fossa is similar in conformation to *P. occidentalis*, not excessively narrowed as in *P. fuscus* or with the hamular processes so posteriorly convergent as in *P. musseri*. There are two paired, well-developed foramina in the presphenoid, anterior to the sphenopalatine vacuities. The palatal spine is weakly developed. The molars are narrow relative to their lengths. Dental measurements in the holotype are as follows: M1 length 2.08, M1 width 0.84, M2 length 0.95, M2 width 0.78, m1 length 1.72, m1 width 0.80, m2 length 1.13, m2 width 0.70. The first molars are equivalent in absolute size to molars in the holotype of *P. musseri*, but the second molars of *P. musseri* are reduced in size relative to *P. sandrae* (cf. Flannery, 1989: 221). Molar characteristics described as distinctive attributes of *musseri* (e.g., M1 with a largely unbroken raised lingual ridge and posterior cingulum) characterize the holotype of *P. sandrae*. As in other members of the *occidentalis* species group and in *P. fuscus*, the postglenoid foramen is very large and confluent with the middle lacerate foramen, though in *P. sandrae* a blunt claw-shaped extension of the pterygoid plate partially infringes the area between these foramina. The middle lacerate foramen appears to be confluent with the foramen ovale.

A close relationship is apparent between *P. sandrae* and *P. musseri*. They are the only two species in which the color of the venter contrasts strongly with the dorsal fur coloration, and both have short (rather than long velvety) fur. In these species the molars are relatively narrower than in other two-molared species of *Pseudohydromys*, and the first molars appear to be equivalent in size and shape. The holotypes of the two species (the sole available specimens) match one another closely both in external measurements and proportions (table 3) and in many craniodental measurements (table 5; though *P. sandrae* departs notably from *P. musseri* in its much weaker zygomatic spread, narrower bony palate, longer incisive foramina, wider

incisors, and narrower rostrum). This dimensional and proportional resemblance is reflected in their morphometric alliance in principal component analyses (e.g., fig. 3).

BIOLOGICAL NOTES: Mount Sisa, the type locality of *P. sandrae*, is one of the most comprehensively inventoried sites for rodents in New Guinea. At least 31 rodent species are recorded from Mt. Sisa at elevations between 800 and 1500 m—the 31 species reported from Sisa by Leary and Seri (1997), minus both reported species of *Pogonomelomys* (our reidentifications of material at PNGNM), plus *Melomys dollmani* (recorded from Mt. Sisa as *M. gracilis* by Flannery et al., 1994; see Musser and Carleton, 2005) and *Pseudohydromys sandrae*, newly described and recorded here. Six hydromyines are known from Mt. Sisa (*P. sandrae*, *Hydromys chrysogaster*, *Parahydromys asper*, *Crossomys moncktoni*, *Leptomys elegans*, and *Microhydromys argenteus*). Given that most moss-mice occur only in montane forests well above 1000 m elevation, it is especially interesting that *P. sandrae* has been collected only at the lower boundary of extensive trapping efforts (at circa 800 m) on Mt. Sisa.

The holotype of *P. musseri* is the only *Pseudohydromys* specimen collected to date north of the Central Cordillera, while the holotype of *P. sandrae* is one of the few moss-mice yet collected on the cordillera's southern margin. In our view these two well-marked species may represent a north-south species pair, together representing a distinctive lineage within the genus that is specialized for life on lower-elevation mountain slopes rather than in high montane forests. As discussed by Helgen et al. (in press), several groups of vertebrates inhabiting the lowlands of New Guinea show examples of sibling species pairs (or strong intraspecific phylogeographic structure) divided by the Central Cordillera (Pratt, 1982; Aplin, 1998; Austin, 2000; Dumbacher and Fleischer, 2001; Dumbacher et al., 2003; Rawlings and Donnellan, 2003; Helgen, 2007a; Norman et al., 2007); other apparent mammalian examples include lowland cuscuses (*Phalanger orientalis* in the north, *P. intercastellanus* and *P. mimicus* in the south), forest wallabies (*Dorcopsis hageni* in the north, *D. luctuosa* in the south), pademelons (*Thylogale browni* in the north,

T. brunii in the south), lowland rats (*Rattus praetor* in the north, *R. leucopus* in the south), and *Microhydromys* moss-mice (*M. richardsoni* in the north, *M. argenteus* in the south) (Helgen et al., in press).

Extensive trapping efforts are needed to better understand the nature of the distributions of *P. musseri* and *P. sandrae*. Does the distribution of *P. musseri* extend to other outlying mountain ranges in northern New Guinea (e.g., the Foja, Cyclops, Adelbert, or Huon ranges) or to the northern slopes of the Central Cordillera? Is *P. sandrae* restricted to peaks in the Kikori River Basin, or does it have a more extensive distribution along the southern slopes of the Cordillera? Will different montane areas prove to support additional distinctive species within this lineage? The type localities of both *musseri* and *sandrae* (Mt. Somoro and Mt. Sisa, respectively) are areas that have received extensive trapping attention in past mammalogical surveys. That these two species remain known by single specimens suggests that they are naturally rare or exceedingly difficult to trap by snap-trapping. Recovery of excellent comparative series would probably require large-scale or long-term pitfall trapping efforts in appropriate hill forest areas along the Cordilleran slopes and in montane forests on outlying ranges.

Dwyer (1990: 210) noted that Etolo speakers from Mt. Sisa used the name *Ebele Ebele Mano* for this species, a designation that indicated their impression that it was a “baby rat or a baby *Leptomys elegans*” (cf. Musser et al., 2008). The same Etolo term was also applied to another species of moss-mouse from the same area, *Microhydromys argenteus* (Dwyer, 1990; Helgen et al., in press).

Pseudohydromys fuscus (Laurie, 1952)

TYPE MATERIAL AND LOCALITY: The holotype of *fuscus* is BMNH 50.1736, adult female, skin and skull, from the “high northern slopes” of Mt. Wilhelm (ca. 05°47'S, 145°01'E, Chimbu Province, Papua New Guinea: locality 15 in fig. 16), 9000 to 10,000 feet (=2727–3030 m), Bismarck Range, collected 19 June 1949 by F. Shaw-Mayer.

DIAGNOSTIC AND DESCRIPTIVE NOTES:

Pseudohydromys fuscus is a medium-sized moss-mouse (tables 3, 5). The dorsal coloration is uniform clear gray above and slightly paler gray below, with the dorsum sometimes infused with russet-brown tones (fig. 19) and occasionally bearing faint pale flecking, especially on the rump. The dorsal surfaces of the manus and pes are white, and the ear is pale gray. Judging from direct comparisons of fluid material, the eye also appears to be slightly less reduced in *P. fuscus* than in other *Pseudohydromys* (at least in sympatric taxa), and the mystacial vibrissae are longer than in other species. It can easily be distinguished from the three other congeners with which it occurs sympatrically (*P. murinus*, *P. eleonorae*, and *P. ellermani*) by the size of its head, which is noticeably wider relative to these species in life, reflecting its wider zygomatic spread and heavier jaw musculature.

Pseudohydromys fuscus has the shortest relative tail length in the genus (averaging 84% of head-body length). The tail is pale overall, with vague light and dark mottling over much of its length, and often bears a long and prominent white tail tip (about one-fifth to one-third the length of the tail). Though the tails of most *Pseudohydromys* species show a tendency toward a quadrilateral shape in dorsoventral cross-section, this trend reaches its greatest development in *P. fuscus*, in which the tail is seemingly always subrectangular in cross-section. There are 16–17 tail rings per centimeter in the midsection of the tail, and the tail hairs measure less than 1 tail ring in length, shorter than in other *Pseudohydromys*.

This species is extremely distinctive craniodentally (figs. 3, 15), the reason for its former taxonomic isolation in the monotypic genus *Neohydromys* (Laurie, 1952; Flannery, 1995a; Musser and Carleton, 1993). The incisors are strongly proodont and broadened relative to all other species except *P. occidentalis* and *P. sandrae* (table 5). The lower incisors are correspondingly broadened, very elongate, strongly upcurved, and separated from the lower molar row by an expansive diastema; they match the lower incisors of *P. occidentalis* in both length and arc shape, but are relatively more elongate

than in other congeners. The roots of the lower incisors extend farther posteriorly in the alveolus of the jaw than in other taxa, nearly reaching the articular surface of the articular process (cf. Musser and Heaney, 1992: 89). The enameled faces of both the upper and lower incisors are more intensely red-orange than in all other species of *Pseudohydromys*. The cranium is robust compared to most congeners (the notable exception being *P. musseri*) and very wide relative to its length, with the zygomata very strongly splayed laterally relative to other *Pseudohydromys* species, surpassed in relative width only by the holotype of *P. musseri*. The posterior palatine foramina are elongate and deeply incised, a trait seen elsewhere in the genus only in *P. musseri*. The nasals are very strongly retracted, not overhanging the premaxillae or incisors. As in *P. occidentalis*, *P. sandrae*, and *P. musseri*, there are two molars in each quadrant of the jaw, and the maxillary tooth row is situated well behind the zygomatic plate, which is barely excised, being almost vertical (fig. 15). The molars are strongly reduced in size relative to all species of *Pseudohydromys* except members of the *ellermani* species group (table 5). The mesopterygoid fossa is markedly constricted, a feature developed to similar extent elsewhere in the genus only in the *ellermani* species group. The masseteric tubercle is weakly developed, and the incisive foramina are relatively short—similar in length to *P. murinus*, but situated relatively farther back in the diastema, extending back beyond the zygomatic plate (as in *musseri*).

DISTRIBUTION: In total, natural history museums hold approximately 45 specimens of *P. fuscus* (at AM, AMNH, BBM, BMNH, NMS, and WAM) collected from montane forests throughout the Central and Eastern highlands regions of eastern New Guinea, from Porgera and the Tari Gap in the west to Mt. Kaindi in the east, at elevations between about 1600 and 3660 m (fig. 16; localities 7–19). Vouchered records originate from Morobe, Eastern Highlands, Chimbu, Western Highlands, Southern Highlands, and Enga provinces of Papua New Guinea.

Most specimens of *P. fuscus* with associated habitat data (located especially at BBM) record their collection in mossy montane



Fig. 19. Dorsal and ventral views of a study skin of *Pseudohydromys fuscus* (BBM-NG 55613, adult female, Mt. Kerigomna, Eastern Highlands Province, Papua New Guinea).

forests, corresponding to both "lower montane forest" and "upper montane forest" as delineated by Grubb and Stevens (1985) and Pajmans (1976), including forests at the subalpine grassland ecotone. The lowest elevational record for this species is a specimen collected at Big Wau Creek, apparently at 1600 m (WAM M25386; elevation reported by Jackson and Woolley, 1993); the highest records are of a specimen snap-trapped in mossy upper montane forest at 3600 meters on Mt. Giluwe (BBM-NG 56440) and specimens extracted from an owl pellet deposit on Mt. Wilhelm at circa 3660 m (AMNH 276598–276599, see below). All other specimens originate from montane forests between 1800 and 3450 meters. The average elevation of 22 vouchered localities for this species (represented by specimens at AM, AMNH, BBM, BMNH, NMS, USNM, and WAM) is 2691 m (median 2780 m, SD 478 m).

LOCALITIES (WITH SPECIMENS EXAMINED AND USEFUL REFERENCES): Big Wau Creek (fig. 16: locality 19), 1600 m, Morobe Province (specimen at WAM—see Jackson and Woolley, 1993); Mt. Elimbari (= Mt. Erimbari, fig. 16: locality 16), ca. 2400 m, Eastern Highlands Province (AM M14170; Dwyer, 1983b); Mt. Giluwe (fig. 16: locality 8), 2400–3600 m, Southern Highlands Province (BBM-NG 56440, 97183, 97239; BMNH 53.302–305); Mt. Kaindi (fig. 16: locality 18), 2250–2350 m, Morobe Province (AM M14400–14402, BBM-NG 56591, 56593, 99085; Gressitt and Nadkarni, 1978; additional specimens at WAM—see Jackson and Woolley, 1993); Mt. Kerigomna (fig. 16: locality 17), 3050 m, Chimbu Province (BBM-NG 55613); Lamende Range, NW of Mt. Giluwe (fig. 16: locality 9), 2400–3000 m, Southern Highlands Province (BMNH 53.306–53.308); Nondugl (fig. 16: locality 14), 1800 m, Western Highlands Province (AMNH 183460); Tambul (fig. 16: locality 11), Murmur Pass, 2800 m, Western Highlands Province (BBM-NG 60864); Tari Gap (fig. 16: locality 7), 2600 m, Southern Highlands Province (BBM-NG 105506); Tomba (fig. 16: locality 12), 2400–2700 m, Western Highlands Province (BMNH 53.301); Weiga (fig. 16: locality 13), ca. 2300 m, Wahgi Mountains, Western Highlands Province

(NMS 158); Welya (fig. 16: locality 10), 2400–2700 m, Western Highlands Province (BMNH 53.295–53.300); Mt. Wilhelm (fig. 16: locality 15), 2700–3660 m, Chimbu Province (AMNH 191415–191422, 276598–276599; BBM-NG 100637; BMNH 50.1736; Laurie, 1952; Brass, 1964).

Most recently, the first author extracted a *P. fuscus* mandible from an owl pellet accumulation at a cave entrance at Waile Creek (circa 05°34'S, 143°04'E), 3000 m, Enga Province (USNM 586242), the first record of this species from Enga Province and one of the westernmost records for this species to date (not mapped in fig. 16).

A specimen of *P. fuscus* (BBM-NG 56591) attributed to Mt. Missim (Morobe Province) by Breed and Aplin (1994: 30) originated from Mt. Kaindi (see also Breed, 1997); we know of no records to date of this species from Mt. Missim (though we expect it occurs there).

BIOLOGICAL NOTES: *Pseudohydromys fuscus* is one of the more widely distributed species of *Pseudohydromys* (see above). Its recorded geographic distribution is nearly congruent to that of *P. murinus*, except that *P. fuscus* is not yet recorded east of Mt. Kaindi. It has the widest elevational range yet recorded for any New Guinea moss-mouse species, spanning more than 2000 meters, from 1600 to 3660 m (table 11). In the Hagen and Bismarck ranges it co-occurs with three congeners in forests between 2400 and 2800 m (*P. murinus*, *P. eleanorae*, and *P. ellermani*), making this the most diverse local community of moss-mice recorded anywhere in New Guinea. Critical examinations of all available specimens suggest to us that *P. fuscus* is morphologically and craniometrically homogeneous across its known geographic range.

Pseudohydromys fuscus is terrestrial and insectivorous. Judging from specimen labels, it has usually been taken in snap-traps set on the ground but is sometimes captured in live traps. Jackson and Woolley (1993: 78) reported specimens collected in Elliott (= Sherman) traps, which were either unbaited or baited with sphingid moths. Intestinal content studies have shown that *P. fuscus* is largely insectivorous, and consumes a greater percentage of adult lepidopterans (judging

from relative surface area of lepidopterans in the intestinal contents) than sympatric congeners (Jackson and Woolley, 1993). The larger eyes, longer vibrissae, more procumbent incisors, and heavier jaw musculature of *P. fuscus* relative to most other *Pseudohydromys* species could be correlates of a lifestyle more specialized than other moss-mice for catching and eating moths and other flying insects.

Owls prey on moss-mice. Van Deusen collected maxillary and mandibular fragments representing *P. fuscus* (accessioned as AMNH 276598–276599) from an owl pellet accumulation on Mt. Wilhelm; feathers of the sooty owl (*Tyto tenebricosa*) were found at the roost. These pellets were found under a boulder high up on the ridge that rises sharply beyond the Lake Aunde camp; Van Deusen recorded an altitude of 12,000 ft for the pellet site (Brass, 1964; G. Musser, in litt.). In 2008 the first author collected a jaw of *P. fuscus* from an owl pellet accumulation in a cave adjacent to Waile Creek in the Kaijende Highlands, also apparently accumulated by sooty owls (specimen at USNM, see above).

Smales (2006) recorded the rictulariid helminth parasite *Rictularia mackerrasae* Mawson, 1971, from specimens of *P. fuscus* collected at Mt. Kaindi and at Tari Gap.

Based on a specimen collected on Mt. Wilhelm, Lidicker (1968) described the phallus and baculum of this species in useful detail, and Breed and Aplin (1994) described its spermatozoal morphology based on a specimen from Mt. Kaindi (see above). According to Lidicker (1968: 620), of all New Guinean rodents studied (including representatives from the great majority of Melanesian genera), “this species and *Mayermys ellermani* are the only forms observed in which the lateral bacular mounds have a cartilaginous core ... these two are also unique among the hydromyines in having the lateral bacular mounds extending farther distally than the tip of the distal bacular cartilage.” Despite its closer phenetic resemblance to other two-molared congeners, these phallic traits comprise part of a suite of morphological synapomorphies that seem to unite *P. fuscus* as the sister lineage to species of the *ellermani* species group (see above).

However, it is important to note that Lidicker’s studies of phallic anatomy included only a few species of *Pseudohydromys* (*murinus*, *occidentalis*, *fuscus*, and *ellermani*, which nevertheless represent most of the morphological “species groups” recognized here). We recommend that future studies of variation in phallic and other anatomical character systems (for example, gastric or female reproductive anatomy) should ideally sample more broadly across the taxonomic and ecomorphological breadth of the genus.

Pseudohydromys ellermani (Laurie and Hill, 1954)

TYPE MATERIAL AND LOCALITY: The holotype of *ellermani* is BMNH 53.277, adult male, skin and skull, from the northern slopes of Mt. Wilhelm (ca. 05°47’S, 145°01’E, Chimbu Province, Papua New Guinea; locality 7 in fig. 20), 8000 feet (= 2424 m), Bismarck Range, collected 22 May 1950 by F. Shaw-Mayer.

DIAGNOSTIC AND DESCRIPTIVE NOTES: *Pseudohydromys ellermani* is a medium-sized moss-mouse bearing the characteristic traits of the *ellermani* species group. It is similar to other members of the species group in head-body length (table 3) but is lighter in body mass and more gracile in overall appearance compared to *P. germani* and *P. pumehanae*, n. sp. The fur is soft, dense, and smoky gray above (the fur is gray with brown tips) and slightly paler below, occasionally with white markings on the breast (fig. 23). The tail averages slightly longer than the head-body length (averaging 106% of head-body length) and averages longer than in other species of the *ellermani* species group (table 3). The tail is brown, often mottled with paler markings over its length, and usually bears a short white tail tip. There are 15 to 18 tail scales per centimeter in the midsection of the tail, and the tail hairs measure 1.5 to 2 hairs in length. The ears and dorsal surfaces of the manus and pes are usually pale (buff to pale gray).

The skull of *P. ellermani* is relatively long and narrow, and distinctly flattened dorsoventrally relative to all congeners apart from its relatives in the *ellermani* species group. The incisors are strongly proodont. The skull averages slightly shorter and relatively nar-

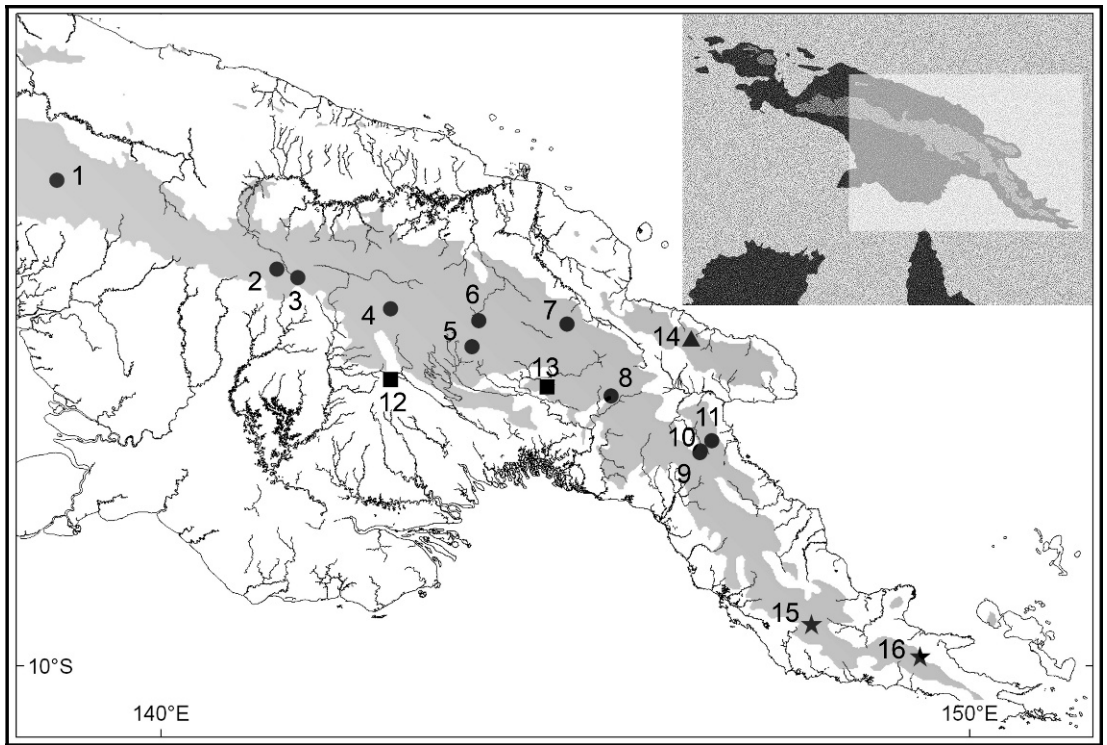


Fig. 20. Recorded distribution (vouchered localities) of species in the *ellermani* species group: *Pseudohydromys ellermani* (circles), *P. pumehanae*, n. sp. (squares), *P. carlae* n. sp. (triangle), and *P. germani* (stars). Areas above 1000 m in elevation are shaded in gray. See text for numbered localities.

rower than in *P. germani* and *P. pumehanae*, n. sp., and is equivalent in size to that of *P. carlae*, n. sp., but the interorbital region is more greatly constricted (table 7). When the skull is held with the palate in the horizontal plane, the top of the skull slopes linearly from the posterior braincase to the nasals. The molars are relatively larger than in *P. germani* and *P. pumehanae*, n. sp. (figs. 21, 22; Helgen, 2005a), but relatively smaller than in *P. carlae*, n. sp. (table 7). One specimen retaining M2 on the right side of the jaw (measuring 0.2×0.2 mm) has been reported from Mt. Kaindi (Lidicker and Ziegler, 1968: 57); another skull from Porokma in the Snow Mountains retains a minuscule M2 in the left side of the jaw. All other museum specimens have only one molar in each jaw quadrant.

DISTRIBUTION: *Pseudohydromys ellermani* inhabits forests throughout the mountain ranges of the central portion of New Guinea's extensive Central Cordillera, including the Snow Mountains, the Star Mountains,

and the Central and Eastern highlands regions, from 1400 to 2800 meters (fig. 20: localities 1–11), with the great majority of records originating from above 1900 m. Vouchered records from Papua New Guinea include localities in Morobe, Eastern Highlands, Chimbu, Western Highlands, Southern Highlands, Enga, and West Sepik (= Sandaun) provinces. The westernmost record is from Porokma, near Lake Habbema in the Snow Mountains; the easternmost record is from the neighborhood of Wau in Morobe Province, Papua New Guinea.

Most specimens of *P. ellermani* with associated habitat data (located especially at BBM) record their collection from mossy montane forests—in this case, a habitat in New Guinea often characterized as “mid-montane forest” and corresponding to “lower montane forest” as delineated and described by Grubb and Stevens (1985). The mean elevation of collection for 15 trapping localities with explicit elevational data is 2207 m



Fig. 21. Selected views of skulls of three of the four species in the *ellermani* species group: (left column) *Pseudohydromys ellermani* (BBM-NG 100357, adult female, Feramin, West Sepik Province, Papua New Guinea); (middle column) *P. pumehanae*, n. sp. (BBM-NG 103485, adult female, Mt. Bosavi, Southern Highlands Province, Papua New Guinea); and (right column) *P. germani* (holotype, AM M29245, adult male, Munimun, Milne Bay Province, Papua New Guinea). Scale bar = 10 mm.

(median 2200 m, SD 458 m). Unlike most congeners that occur in the middle portion of the Central Cordillera (i.e., *P. murinus*, *P. occidentalis*, *P. fuscus*, and *P. eleanorae*), the elevational range of this species is not known to extend to or above 3000 m.

LOCALITIES (WITH SPECIMENS EXAMINED AND USEFUL REFERENCES): 5 km south of Bafunmin (locality 2 in fig. 20), 1600–2300 m, West Sepik (= Sandaun) Province (BBM-NG 107905, 108176); Big Wau Creek (locality 10 in fig. 20), 1600 m, Morobe Province (specimen at WAM—see Jackson and Woolley, 1993); Edie Creek (locality 9 in fig. 20), ca. 2100 m, Morobe Province (MVZ 129794–129796, 129798; Lidicker and Ziegler, 1968); Mt. Elimbari, (= Mt. Erimbari), between 1900 and 2700 m, Chimbu Province (AM M24312; Dwyer, 1976); Feramin (lo-

cality 3 in fig. 20), 1400 m, West Sepik (= Sandaun) Province (BBM-NG 100357); Mt. Giluwe (locality 5 in fig. 20), 2700–2800 m, Southern Highlands Province (BBM-NG 91734; BMNH 53.280); Mt. Kaindi (locality 10 in fig. 20), 2350 m., Morobe Province (AM M14399; PNGNM 24661; Gressitt and Nadkarni, 1978; other specimens at WAM—see Jackson and Woolley, 1993); Mt. Missim (locality 11 in fig. 20), 1980 m, Morobe Province (BBM-NG 160959, 161196); Purosa (locality 8 in fig. 20), 1970 m, Eastern Highlands Province (AMNH 191424; Brass, 1964); Lake Tawa (locality 4 in fig. 20), ca. 2200 m, Enga Province (AM unregistered); Porokma (locality 1 in fig. 20), 2800 m, Papua Province [Indonesia] (AM M26880, 26881, 26984, 26987); “Wau,” no altitude given, Morobe Province (PNGNM 24667);

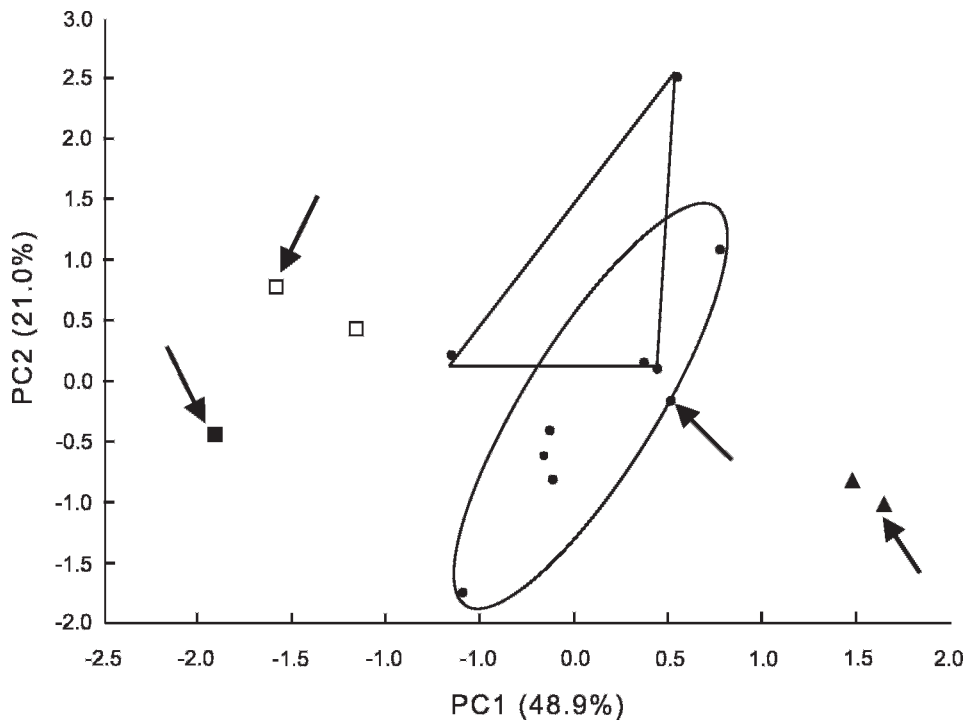


Fig. 22. Morphometric dispersion (principal components analysis) comparing crania representing species of the *Pseudohydromys ellermani* species group. Principal components extracted from a covariance matrix of 10 log-transformed craniodental variables measured from sufficiently intact skulls; the first component is most heavily influenced by molar dimensions (increasing left to right), while the second component is especially influenced by the length of the incisive foramina (increasing from bottom to top) (table 6). Taxa and symbols: *P. pumehanae*, n. sp. (solid square); *P. germani* (open squares); *P. carlae*, n. sp. (solid triangles); *P. ellermani* (dots). Western (Snow Mountains, dots joined in a triangle) and eastern (dots encompassed by oval) samples of *P. ellermani* are denoted (see text). Holotypes of the four recognized species in the group are designated with arrows.

Welya (locality 6 in fig. 20), ca. 2700 m, Western Highlands Province (BMNH 53.278. 53.279); Mt. Wilhelm (locality 7 in fig. 20), ca. 2400 m, Chimbu Province (AMNH 191423; BMNH 53.277; Laurie and Hill, 1954; Brass, 1964).

GEOGRAPHIC VARIATION: In our assessment, specimens attributed here to *P. ellermani* can be clearly apportioned into two morphological groups, representing an eastern cluster (typical *ellermani*, from the Eastern Highlands, Central Highlands, and Star Mountains) and a western cluster (from the Snow Mountains).

Specimens from the eastern cluster derive from montane forests (1400 to 2800 m) in New Guinea's Eastern and Central highlands regions (Mts. Kaindi and Missim, the Purosa

and Welya areas, and Mts. Elimbari, Wilhelm [type locality of *ellermani*], and Giluwe, and the Porgera area: localities 4–11 in fig. 20) and the Star Mountains (Bafunmin, Feramin; localities 2 and 3 in fig. 20). These populations differ most notably from Snow Mountains specimens referred to *P. ellermani* (locality 1 in fig. 20) in their absolutely narrower postorbital constriction (POB < 4.5 mm), lower-domed braincase (HBC < 6.7 mm), and narrower incisors (BIR < 1.8 mm). Specimens from the western cluster (POB > 4.5 mm, HBC > 6.7 mm, BIR > 1.8 mm) were collected near Lake Habbema in the Snow Mountains (2800 m) in 1998. Additional specimens collected from intervening geographic areas (i.e., the western Star Mountains and the eastern Snow Mountains)



Fig. 23. Dorsal and ventral views of a study skin of *Pseudohydromys ellermani* (BBM-NG 97134, adult male, Mt. Giluwe, Southern Highlands Province, Papua New Guinea).

TABLE 6
Results of a Principal Component Analysis of Crania Representing Taxa in the *Pseudohydromys ellermani* Species Group

Factor loadings, eigenvalues, and percentage variance; principal components are extracted from a covariance matrix of 10 log-transformed cranial and dental variables (see fig. 22). Many specimens have slightly damaged crania; craniometric variables were selected to maximize sample size, which includes 10 specimens of *P. ellermani* and the holotype and one referred specimen for each of *P. germani*, *P. pumehanae*, n. sp., and *P. carlae*, n. sp. The third principal component (PC3) is not depicted in fig. 22.

	PC1	PC2	PC3
POB	0.1017	0.0262	-0.0477
BBC	-0.2949	0.3826	-0.2322
HBC	-0.0596	0.4490	-0.2849
LD	-0.5866	-0.2329	-0.0712
BBP	-0.0837	-0.7188	0.1957
BIR	-0.2870	0.0238	-0.2308
BR	-0.4416	0.6025	-0.0062
LIF	-0.4986	0.8286	-0.0033
LM1	0.9589	0.1292	-0.2351
BM1	0.7197	0.2688	0.6264
Eigenvalue	0.0464	0.0200	0.0092
% variance	48.86	21.01	9.71

may in the future bridge the apparent morphometric gap between these geographically disjunct clusters (fig. 20). Alternatively, further studies and new material may further illuminate their taxonomic divergence. At present we comfortably assign both of these clusters to *P. ellermani*.

BIOLOGICAL NOTES: *Pseudohydromys ellermani* has the widest recorded geographic distribution of any moss-mouse in New Guinea. Across its full geographic range, this species occurs syntopically with at least five congeners, though this sympatric assemblage varies with locality. In the Snow Mountains (near Lake Habbema), *P. ellermani* has been recorded sympatrically with *P. patriciae* and *P. occidentalis*; in the Star Mountains (at Bafunmin) with *P. occidentalis*; in the Central Highlands (e.g., at Welya and on Mt. Wilhelm) with *P. murinus*, *P. eleanorae*, and *P. fuscus*; and in eastern Papua New Guinea (at Mt. Kaindi) with *P. murinus* and *P. fuscus*. It has also been collected alongside both species of *Mirzamys*, n. gen., at localities in West Sepik and Enga Provinces, respectively (see account of *Mirzamys*, n. gen., below).

Brass (1941: 312–316) described in useful detail the vegetation and forest formations around the same site in the Snow Mountains where Pat Woolley trapped *P. ellermani* in

1988 in upper montane forest at 2800 m (Woolley, 1990; see account of *P. patriciae*, above). Takeuchi (2007) described habitat formations in the vicinity of Lake Tawa in Enga Province, where this species has been trapped in forest situated at 2200 m (Helgen, 2007b). Brass (1964: 199–200) provided a description of “mid-mountain forest” at Purosa, where *P. ellermani* was collected during the Sixth Archbold Expedition to New Guinea (see also Musser et al., 2008).

Available evidence suggests that *Pseudohydromys ellermani* is entirely terrestrial. Though not commonly trapped, it has been taken in snap-traps, Elliott/Sherman traps, and pitfall traps placed on the ground. Lidicker and Ziegler (1968) recorded the capture of four males “under two large adjacent logs in mossy forest” at about 2100 m. The first author once snap-trapped a specimen of *P. ellermani* precisely at nightfall, catching the animal less than two minutes after laying down the trap at one end of a log across a creek, baited with an earthworm (AM specimen from Lake Tawa). Jackson and Woolley (1993) apparently captured specimens in Elliott (= Sherman) traps which were either unbaited or baited with sphingid moths.

This species is insectivorous and possibly vermivorous. Jackson and Woolley (1993)

TABLE 7
Selected Craniodental Measurements for the Species (and selected populations) of the *Pseudohydromys ellermani* Species Group (mean \pm standard deviation, with observed range in parentheses)

Variable	<i>ellermani</i>		<i>ellermani</i>		<i>pumehanae</i>		<i>germani</i>		<i>carlae</i>	
	Eastern (<i>n</i> = 10)	Snow Mts. (<i>n</i> = 3)	Bosavi/Karimui (<i>n</i> = 2)	Owen Stanleys (<i>n</i> = 2)	Finisterres (<i>n</i> = 2)					
CIL	24.07 \pm 0.69 (23.04–25.10)	24.69 \pm 0.33 (24.32–24.95)	24.2 (23.92–24.51)	24.61 (23.72–25.50)	23.63 (<i>n</i> = 1)					
ZYG	10.89 \pm 0.23 (10.62–11.28)	11.07 \pm 0.11 (10.95–11.14)	11.14 (10.94–11.33)	11.32 (11.00–11.64)	10.90 (<i>n</i> = 1)					
POB	4.18 \pm 0.12 (4.04–4.43)	4.54 \pm 0.01 (4.53–4.56)	4.22 (4.19–4.24)	4.62 (4.38–4.86)	4.84 (4.68–5.00)					
BBC	10.06 \pm 0.25 (9.70–10.42)	10.42 \pm 0.06 (10.37–10.49)	10.03 (9.98–10.07)	10.61 (10.35–10.87)	10.13 (9.87–10.38)					
HBC	6.15 \pm 0.26 (5.79–6.60)	6.82 \pm 0.09 (6.72–6.88)	5.97 (5.81–6.12)	6.43 (6.08–6.77)	6.18 (6.00–6.36)					
BR	4.59 \pm 0.21 (4.15–4.97)	4.81 \pm 0.25 (4.52–4.98)	4.95 (4.94–4.96)	4.86 (4.70–5.02)	4.56 (4.51–4.60)					
LM1	0.87 \pm 0.07 (0.76–1.00)	0.90 \pm 0.10 (0.80–1.00)	0.60 (0.53–0.66)	0.69 (0.68–0.70)	1.08 (1.01–1.15)					
BM1	0.54 \pm 0.05 (0.44–0.60)	0.56 \pm 0.09 (0.46–0.63)	0.56 (0.55–0.56)	0.47 (0.44–0.50)	0.63 (0.58–0.68)					
LN	7.19 \pm 0.40 (6.51–7.83)	7.38 \pm 0.36 (7.13–7.79)	7.01 (6.75–7.26)	7.33 (7.19–7.47)	7.08 (6.85–7.26)					
LD	8.32 \pm 0.52 (7.47–9.11)	8.33 \pm 0.01 (8.32–8.34)	8.53 (8.17–8.89)	8.61 (8.27–8.94)	8.24 (8.22–8.25)					
BMF	1.20 \pm 0.12 (0.98–1.35)	1.19 \pm 0.18 (1.06–1.40)	1.28 (1.14–1.41)	1.37 (1.29–1.44)	1.40 (<i>n</i> = 1)					
LBP	6.21 \pm 0.29 (5.78–6.69)	6.13 \pm 0.21 (5.92–6.34)	6.03 (6.00–6.06)	6.14 (5.81–6.46)	6.15 (<i>n</i> = 1)					
BBP	2.55 \pm 0.23 (2.10–2.89)	2.41 \pm 0.16 (2.24–2.56)	2.50 (2.30–2.70)	2.55 (2.40–2.69)	2.79 (2.70–2.87)					
BIR	2.43 \pm 0.24 (2.04–2.87)	2.50 \pm 0.13 (2.40–2.64)	2.33 (2.20–2.46)	2.56 (2.54–2.57)	2.35 (2.30–2.39)					

studied alimentary canal contents from specimens of this species (and of two sympatric congeners, *P. murinus* and *P. fuscus*) on Mt. Kaindi (however, we note that one of the specimens attributed to this species, AM M14400, is actually a specimen of *P. fuscus*; we have not studied most of the remainder of their sample, deposited at WAM). In the nine specimens they identified as *P. ellermani*, insects other than lepidopterans occupied 45.8% of the relative surface area of the "gut" (the small and large intestines and caecum), and lepidopterans occupied 11.9%. The gut contents of their sample of *P. ellermani* were similar to those of both other congeners included in the study, especially *P. murinus*, except that *P. murinus* consumed more fungi and more oligochaete worms (notably, Jackson and Woolley found earthworms to be lacking in the diet of their sample of *P. ellermani*). Jackson and Woolley found that *Pseudohydromys fuscus* differs from both of these species in consuming a considerably higher proportion of lepidopterans (table 4b of Jackson and Woolley, 1993). In other words, all three of these sympatric moss-mice are apparently predominantly animalivorous, but *P. murinus* may eat more fungi and more worms than *P. ellermani*, and *P. fuscus* more moths and butterflies. Jackson and Woolley (1993: 81) observed that "the extreme reduction of molar teeth in *Mayermys ellermani* suggests a different diet to the other 'moss-mice'... however, dietary analysis did not reveal any difference." More detailed study of the diet in *P. ellermani* and other members of the *ellermani* species group, based on definitively identified material, is needed. The molars in these species are more reduced in number, size, and occlusal morphology than in any other rodent, which (in spite of these results reported by Jackson and Woolley) strongly indicates that species in the *ellermani* species group have a highly specialized diet. The murine genera *Rhynchomys* (Luzon) and *Echiothrix* (Sulawesi), possess convergently reduced and simplified molars (though with M2 retained), attributes that are associated with a vermivorous diet (Rickart et al., 1991; Heaney et al., 1999; Balet et al., 2007), perhaps suggestive of a similar diet for members of the *ellermani* species group.

The behavioral ecology of all moss-mice, as for essentially all Melanesian murids, remains entirely unstudied. However, in some cases data derived from museum specimens may offer potential insights into behavior. Based on their canvas of specimens known at the time, Lidicker and Ziegler (1968) commented that "it is curious that all eight reported specimens [of *P. ellermani*] are males." Flannery (1995a: 246) also took note of this bias. Though larger samples are now available, still the ratio of males to females represented in world museum collections is very strongly skewed toward males; the same is true in the small available samples of the three other species in the *ellermani* species group (table 12). A similar bias does not characterize other *Pseudohydromys* species (table 12). This may point to a sex-ratio or behavioral difference between taxa in the *ellermani* species group and other *Pseudohydromys*. If the sex ratio in *ellermani* species group taxa is not highly skewed toward males naturally, these combined trapping data suggest to us that males may have distinctive activity patterns. Because this skewed sex ratio characterizes samples obtained both from snap-trapping and pitfall trapping, males must truly be more abundant or mobile than females, rather than simply being more inclined to approach a baited trap.

Lidicker (1968) figured the baculum of *P. ellermani* and described the phallus in useful detail, based on studies of the series at MVZ from Mt. Kaindi (Lidicker and Ziegler, 1968).

Pseudohydromys germani (Helgen, 2005a)

TYPE MATERIAL AND LOCALITY: The holotype of *germani* is AM M29245, adult male, skull and study skin (figs. 21, 24), from Munimun Village (09°53'S, 140°23'E, Maneau Range, near Agaun, Milne Bay Province, Papua New Guinea; locality 16 in fig. 20), 1300 m, collected 11 August 1992 by P. German (field number FR341). We recommend "Eastern small-toothed moss-mouse" as an appropriate English common name for *P. germani*.

DIAGNOSTIC AND DESCRIPTIVE NOTES: All four species of the *ellermani* species group

are more or less equivalent in head-body length (table 3), but *Pseudohydromys germani* is heavier and has a chunkier appearance than all other species in the group. Fur coloration in *P. germani* matches that of other species in this group (soft, dense, smoky-gray pelage above, similar in color but paler below), but differs from these species in that the pinnae are somewhat darker gray (fig. 24). The pelage is long and thick, measuring ca. 10 mm on the midback. The tail is dark gray, subequal to the head-body length, occasionally mottled with pale specks across its length, and bears a distinct white tail tip 13 to 22 mm in length. There are 14–18 tail scales per centimeter in the midsection of the tail, and the tail is more sparsely furred and the tail hairs are shorter than in *P. ellermani*, *P. pumehanae*, n. sp., and *P. carlae*, n. sp., measuring only about 1 tail scale in length.

The skull of *P. germani* is slightly larger in overall size and more robust in overall appearance (zygomata, rostrum, and braincase relatively broadened) compared to other species in the *ellermani* species group. The incisors are slightly proodont, not as procumbent as in other taxa in the *ellermani* species group. The molars ($LM1 \leq 0.7$) are smaller than in *P. ellermani* and *P. carlae*, n. sp., and similar in size to *P. pumehanae*, n. sp. Compared to other *ellermani* species group taxa, the interorbital region is broader, with the frontals in particular more greatly inflated laterally, and the rostrum is more flat topped and less downward sloping when viewed in lateral profile.

DISTRIBUTION: *Pseudohydromys germani* is known only from lower montane forests in the Owen Stanley Ranges, including the far southeastern Maneau Range, from 1300 to 1570 meters (fig. 20: localities 15 and 16). Records derive from localities in Milne Bay and Central provinces of Papua New Guinea. This recorded elevational range averages considerably lower than that recorded for other species in the *ellermani* species group (table 11). The holotype from the Maneau Range remains the largest (largest condylobasal length, heaviest body weight) specimen of the *ellermani* group on record (Helgen, 2005a; fig. 21). Additional specimens from throughout the range of *P. germani* are

needed to assess whether there is appreciable intraspecific geographic variation within this species.

BIOLOGICAL NOTES: *Pseudohydromys germani* is probably terrestrial, and is presumably very similar in habits to its slightly better-known relative, *P. ellermani*. The holotype, the only specimen previously reported, was trapped on the ground in a snap-trap baited with beetle larvae (Flannery, 1995a; Helgen, 2005a). Two newly collected specimens of *P. germani* from Mt. Obree (Central Province, Papua New Guinea) extend the known distribution of this species northward beyond the Maneau Range, into the main body of the Owen Stanley Range (locality number 15 in fig. 24). These additional exemplars replicate the distinctive diagnostic features of the holotype and confirm that *P. germani* is distinguished from *P. ellermani* by its larger size and small teeth (Helgen, 2005a). These new specimens were taken in forest at 1570 m in pitfall traps placed along a drift-fence trapline intended for catching reptiles and amphibians (Kraus and Allison, 2006). Notably, specimens of both *P. berniceae* and *P. murinus* were also collected in pitfall traps at this same site and elevation. All three specimens of *P. germani* collected to date are male.

As noted above in the description of *P. berniceae*, recent field and systematic studies are increasingly highlighting the biotic distinctiveness of the Papuan Peninsula (southeastern New Guinea) relative to other montane areas of New Guinea. Forests in these mountains support a diverse and regionally unique local mammal assemblage that features a considerable number of mammalian endemics, including the bandicoot *Microperoryctes papuensis*, the dasyure *Murexia rothschildi*, and, in addition to *P. germani* and *P. berniceae*, the murids *Rattus vandeusenii*, *Chiruomys lamia*, *Leptomys paulus*, and *Coccymys kirrhos* (Brass, 1956; Helgen, 2005a; Musser et al., 2008; Musser and Lunde, 2009).

Smales (2006) reported helminth parasites, including unidentified encapsulated ascarid larvae and the heligmonellid *Odilia emanuelae* (Mawson, 1961) from the holotype of *P. germani* (as “*Mayermys ellermani*”).



Fig. 24. Dorsal and ventral views of a study skin of *Pseudohydromys germani* (holotype, AM M29245, adult male, Munimun, Milne Bay Province, Papua New Guinea).

Pseudohydromys pumehanae, new species

TYPE MATERIAL AND LOCALITY: The holotype of *pumehanae* is BBM-NG 103485, adult female, skull and study skin (figs. 21, 25), from the NNW slopes of Mt. Bosavi (= Mt. Leonard Murray; 6°33'S, 142°50'E, Southern Highlands Province, Papua New Guinea; locality 12 in fig. 20), 2100 m, in the Kikori River Basin, collected 3 July 1973 by A.B. Mirza.

REFERRED SPECIMENS: Two additional specimens are tentatively identified as *P. pumehanae* on the basis of external coloration and proportions and molar size: AM M14827 (in fluid, field number U04) and AM M15324 (skin and skull: fig. 1; field number U05), both males, from the "lower east face of Mt. Karimui" (6°35'S, 144°49'E, Chimbu Province, Papua New Guinea; locality 13 in fig. 20), 1550 m, collected 27 May 1984 by K.P. Aplin. One of these specimens is the animal in a photograph taken on Mt. Karimui by P. Wilson that was figured by Flannery (1995a: 245), which shows the pale ears and tail also characteristic of the holotype of *P. pumehanae*.

DIAGNOSIS: *Pseudohydromys pumehanae* is distinguished from *P. ellermani* and *P. carlae*, n. sp., in having a proportionally wider skull, a relatively broad rostrum and mesopterygoid fossa, and relatively smaller molars, and further from *P. carlae*, n. sp., in having a longer tail and narrower postorbital constriction. In these craniometric aspects it resembles *P. germani*, which differs from *P. pumehanae* in its slightly larger cranial size and body mass, darker gray ears (paler ears in *P. pumehanae*), and darker and less hairy tail (paler, more heavily mottled, and hairier tail in *P. pumehanae*).

DISTRIBUTION: *Pseudohydromys pumehanae* is recorded definitively only from the type locality, situated in montane forest on the north-northwestern slopes of Mt. Bosavi, an extinct volcanic peak in south-central New Guinea's Kikori River Basin, rising to about 2500 m in maximum elevation. Though Mt. Bosavi is situated immediately adjacent to the southern margin of New Guinea's extensive Central Cordillera, forest at upper reaches on the peak are fully isolated from montane forests in these cordilleran ranges by the

lower-elevation valleys of the Rentoul and Hegigio-Kikori rivers (De Boer, 2000; Diamond, 1985).

As noted above, we more tentatively refer to *P. pumehanae* two specimens from Mt. Karimui (locality 13 in fig. 20), a peak that, like Bosavi, is situated on the southern margin of the Central Cordillera in Papua New Guinea's Chimbu Province. If this identification is correct, this indicates that the distribution of *P. pumehanae* may extend more broadly across the southern slopes and southern outlying peaks of the eastern Central Cordillera.

Breed and Aplin (1994) described the spermatazoal morphology of this species (as *Mayermys ellermani*) based on the referred specimens from Mt. Karimui (see also Breed, 1997).

ETYMOLOGY: This species is named for Kathleen Pumehana Imada of the Bishop Museum in Honolulu, in recognition of her kind assistance in our research, especially in facilitating specimen loans relevant to our studies of New Guinea mammals. We recommend "Southern small-toothed moss-mouse" as an appropriate English common name.

DESCRIPTION: All four species in the *ellermani* species group are more or less equivalent in head-body length (table 3), though they differ in overall heftiness, as evidenced from cranial robustness (table 7), recorded body masses, and examinations of bodies stored in fluid. The skull of *P. pumehanae* has a more robust appearance than *P. ellermani* or *P. carlae*, n. sp., with broader zygomata and a relatively broader rostrum and broader braincase with better defined temporal lines. The molars, however, are very small, similar in size and proportion to *P. germani* (Helgen, 2005a). The lower incisors are upcurved and relatively long for the *ellermani* species group, and are stouter (greater depth) and slightly more deeply pigmented (pale orange) than in *P. ellermani*. On the basis of these comparisons, we observe that *Pseudohydromys pumehanae* is a slightly heftier mouse than *P. ellermani* and *P. carlae*, n. sp., but slightly smaller than *P. germani*.

Pelage coloration in *P. pumehanae* is similar to *P. ellermani* and *P. germani*—soft,



Fig. 25. Dorsal and ventral views of a study skin of *Pseudohydromys pumehanae* (holotype, BBM-NG 103485, adult female, Mt. Bosavi, Southern Highlands Province, Papua New Guinea).

dense, smoky-gray fur, above, and somewhat paler below, without strong brown tones (fig. 25). The surfaces of the manus and pes, ear, muzzle, and most of the tail (see below) are pale, as in *P. ellermani* (the tail and ear are darker in *P. germani*). The pelage is relatively short, measuring 4–5 mm in length on the midback (shorter than in *P. ellermani*, *P. germani*, and *P. carlae*, n. sp.). The crown and sides of the head and the midline of the anterior dorsum are conspicuously darker gray than the rest of the pelage (clear in the holotype, less contrasting in the paratypes), and some faint white flecking is apparent on the midback. The dorsal surfaces of the forefeet and hindfeet are pigmented pale and cloaked in short white hairs. The tail averages slightly longer (2% more) than the head-body length (table 3) according to recorded external measurements. A pale terminal tail tip, present in *P. ellermani* and *P. germani*, but not in the type series of *P. carlae*, n. sp., is not clearly evident. Instead, the tail of the holotype appears to be dark gray (above and below) over its proximal quarter; pale, above and below, over its central portion (comprising half the tail length); and mostly dark gray (though somewhat mottled dark and pale), above and below, over its distal quarter. The tail in the referred specimens is variably mottled dark and pale over its length. There are 16 tail scales per centimeter in the midsection of the tail. As in *P. ellermani*, the tail appears heavily haired when viewed at magnification, with the tail hairs measuring 1.5 to 2 tail scales in length (in *P. germani* the tail is more sparsely furred, with the hairs subequal in length to the tail scales). The holotype has two pairs of inguinal teats.

BIOLOGICAL NOTES: *Pseudohydromys pumehanae* is no doubt similar in habits to the slightly better known *P. ellermani*. The specimens from Mt. Karimui were taken in Elliott traps, one of which was placed on the ground among fallen timber. Intriguingly, on Mt. Karimui one other moss mouse, presumed to be this species, was observed climbing vines high up into a tree (K. Aplin, in litt.), to our knowledge the only observation of arboreal/scansorial behavior by a species of *Pseudohydromys*. Targeted pitfall or snap-trapping efforts on Mt. Bosavi, Mt.

Karimui, and on other outlying peaks along the southern margin of the Central Cordillera in south-central Papua New Guinea are needed to secure further specimens of this species in order to more fully document its geographic and altitudinal ranges of occurrence and other aspects of its basic biology.

The middle and upper forested reaches of Mt. Bosavi, still little explored mammalogically, are also known to support an endemic species of *Mallomys*, collected by Mirza on the same expedition (1973), and more recently (2009) by the first author and colleague Muse Opiang (K.M. Helgen, personal obs.). First highlighted here, the apparent uniqueness of multiple murine lineages (*Pseudohydromys* and *Mallomys*) from Mt. Bosavi and perhaps from adjacent peaks along the southern margin of the Cordillera indicates the largely unrecognized biotic significance of this region's montane forests, which seem to have fostered considerable evolution in isolation, and the need for further targeted inventory and conservation attention on their behalf. The seeming biotic significance of Mt. Bosavi as a generator of local endemism both among mammals and other animal groups (e.g., cicadas, De Boer, 2000) points to the need to survey other isolated tall peaks that support high montane forests in south-central New Guinea. Apart from Mt. Bosavi, the most significant of these are Mt. Murray (Southern Highlands Province), rising to about 2300 m, and the peaks of the Keieru Range (Gulf Province), rising to about 1900 m (Diamond, 1985). As far as we are aware, the biotas of these outlying peaks remain entirely unknown today, more than 20 years after Jared Diamond called for their biological exploration (Diamond, 1985: 68).

As noted above, *P. germani* and *P. pumehanae* resemble one another in cranial and dental proportions, but differ in subtle aspects of body size and external morphology (pigmentation in the ears and tail, hairiness of the tail). Further detailed study is needed, particularly once additional relevant museum series come available, to assess whether these taxa are not better regarded as conspecific populations sampled at several disjunct points across a continuous distribution centered on lower montane forests along the

southern side of the Cordillera—from the Kikori River Basin (Mt. Bosavi, the type locality of *pumehanae*) in the west to the Maneau Range (Agaun, the type locality of *germani*) at the far southeastern tip of New Guinea in the east (fig. 20). Several other mammal species, including the dasyurid *Myoictis leucura* (see Woolley, 2005), the macropodid *Dorcopsulus macleayi* (Flannery, 1995a), and the murids *Leptomys elegans* and *Microhydromys argenteus* (see Musser et al., 2008; Helgen et al., in press) exhibit such a distributional pattern, with western recorded limits in the Kikori Basin and eastern limit extending to the southern slopes of the Owen Stanley Range and/or to the Maneau Range at the far southeastern tip of the island (in one case, *L. elegans*, the recorded distribution extends marginally around the northern side of the Cordillera to the isolated peak of Mt. Victory; Musser et al., 2008). Although there are clearly precedents for this distributional pattern, in light of the very small number of specimens currently available, we are comfortable in our assignment of samples referred to *P. germani* (Agaun and Mt. Obree) and *P. pumehanae* (Mts. Bosavi and possibly Karimui) on the basis of morphological and morphometric distinctions. Further evaluations of the taxonomic status and distribution of these taxa relative to one another and to other members of the *ellermani* species group must await the collection and study of additional vouchered material.

***Pseudohydromys carlae*, new species**

HOLOTYPE: BBM-NG 104864, adult male, body fixed in formalin and stored in 70% ethanol, with (broken) skull extracted, from the “Teptep Patrol Post” (Teptep = 05°57.2'S, 146°33.7'E, Madang Province, Papua New Guinea: locality 14 in fig. 20), 2560 m, Finisterre Range, Huon Peninsula, collected 24 October 1975 by A.B. Mirza.

PARATYPES: Two specimens; BBM-NG 104996, adult male, in fluid, with skull extracted and cleaned, from “3 kilometers north-west of Teptep”, 3000 m, collected 23 November 1975 by A.B. Mirza; and BBM-NG 104895 (adult male, stored whole in fluid; fig. 26), with all collection details as for the holotype.



Fig. 26. Fluid specimen of *Pseudohydromys carlae* (paratype, BBM-NG 104895, adult male, near Teptep, Finisterre Range, Madang Province, Papua New Guinea).

DISTRIBUTION: *Pseudohydromys carlae* is known only by the type series of three specimens, trapped near Teptep in the Finisterre Mountains on the Huon Peninsula between 2560 and 3000 m. The mountain ranges of the Huon Peninsula (the Finisterre, Saruwaged, Cromwell, and Rawlinson ranges) lie isolated from the Central Cordillera across the dry lowland forests of the Markham River Valley (fig. 20). No moss-mouse species has previously been recorded from the Huon Peninsula.

DIAGNOSIS: *Pseudohydromys carlae* differs from other members of the *P. ellermani*

species group (*P. ellermani*, *P. germani*, and *P. pumehanae*) in its proportionally shorter tail that lacks a color-contrasting terminal tail tip, and craniodentally in its larger molars ($LM1 > 1.0$), proportionally shorter incisive foramina, and broader interorbital region (tables 3, 6, 7).

ETYMOLOGY: This species is named for Carla Kishinami of the Bishop Museum in Honolulu, in recognition of her frequent assistance in our studies of New Guinea mammals. We recommend “Huon small-toothed moss-mouse” as an appropriate English common name.

DESCRIPTION: This moss-mouse is represented by three previously overlooked specimens collected by A.B. Mirza, until recently stored together in a jar at the Bishop Museum with skulls in situ. In 2005 we removed the skulls of two of these specimens (see above), revealing just a single molar in each quadrant of the jaw, with each molar somewhat less reduced in size than in previously described taxa of the *ellermani* species group (*P. ellermani* and *P. germani*).

Pseudohydromys carlae is similar to *P. ellermani* in overall body size. It is a considerably less chunky rat than *P. germani* and *P. pumehanae*, as evidenced by differences in body weight (table 3) and by direct comparisons of intact fluid specimens. As all three specimens of *P. carlae* are stored in alcohol and were collected more than three decades ago, it is difficult to assess exactly the coloration of the pelage, but we detect no chromatic distinctions in the fur between the four species in the *ellermani* species group. The pelage is as described for other members of the *ellermani* species group (soft, dense, smoky-gray pelage above and below), and the tail, surfaces of the manus and pes, ear, and muzzle are pale, as in *P. ellermani* and *P. pumehanae* (the tail and ear are darker in *P. germani*). The pelage measures about 7 mm long on the midback. In the three available specimens the tail averages 7% shorter than the head-body length—considerably shorter in absolute and relative terms compared to other members of the *ellermani* species group (table 3). A pale terminal tail tip, present in *P. ellermani* and *P. germani*, is not evident in *P. carlae*. There are 15–17 tail scales per centimeter in the midsection of the tail. Like

P. ellermani and *P. pumehanae*, the tail appears rather heavily haired when viewed at magnification, with the tail hairs measuring 1.5 to 2 tail scales in length (in *P. germani* the tail is more sparsely furred, with the hairs subequal in length to the tail scales).

The skull of *P. carlae* is somewhat smaller than in *P. ellermani*, *P. pumehanae*, or *P. germani* (table 7), though few skulls of this new taxon are available (and condyloincisive length can be measured in only one). The skull is immediately distinguished from the more robust *P. germani* and *P. pumehanae* (see above) and bears closest resemblance to *P. ellermani*. The most striking difference between *P. ellermani* and *P. carlae* is found in the size of the molars, which, though still very small (and exhibiting the characteristic molar features of the *ellermani* species group), nevertheless measure absolutely and proportionately larger in *P. carlae* than in *P. ellermani* and *P. germani* (with $LM1 \geq 1.0$ mm a convenient diagnostic measurement in light of specimens currently available). In addition, the interorbital region is distinctly less constricted than in *P. ellermani*, *P. pumehanae*, and *P. germani*, and the incisive foramina are very short.

BIOLOGICAL NOTES: Essentially nothing is yet known of this species' basic biology. Judging from its closest relatives and proportionally shortened tail, it is likely terrestrial. All three known specimens were taken in snap-traps, and all are male (see account of *P. ellermani*, above). One of the paratypes of *P. carlae* was collected at a higher elevation (3000 m) than any other specimen in the *ellermani* species group (table 11).

The mountains of the Huon Peninsula are separated from the mountain ranges of New Guinea's expansive Central Cordillera by the lowlands of the Markham River Valley. These mountains support a diverse vertebrate fauna featuring a considerable number of endemic montane taxa that presumably differentiated in isolation after dispersing from the cordillera. In addition to *P. carlae*, several other mammal species (and myriad recognized subspecies) are endemic to montane habitats in the Huon, including the macropodids *Dendrolagus matschiei* and *Thylogale lanatus* (Flannery, 1992; Groves, 2005). Though *P. carlae* is recorded only

from the Finisterre Range at present, its distribution seems likely to extend throughout the other contiguous mountain ranges of the Huon Peninsula (the Saruwaged, Rawlinson, and Cromwell ranges). Still, there are indications that the Finisterres may support a murine fauna somewhat different from the other Huon ranges. For example, one of the rodents that the first author trapped most commonly during a brief visit to the Finisterres (January 2003) was a species of *Lorentzimys*, a taxon not represented in the extensive collections of murines collected in the Saruwaged, Rawlinson, and Cromwell ranges during the Seventh Archbold Expedition to New Guinea or collected during various other historical collecting efforts in these mountains (Van Deusen, 1978).

DESCRIPTION OF A NEW HYDROMYIN GENUS

Mirzamys, new genus

TYPE SPECIES AND CONTENT: The type species of *Mirzamys* is *M. louiseae*, n. sp. The genus, as recorded to date, is represented by two species from montane habitats (mountain forests and subalpine grasslands, extending from 1900 to at least 3450 m in elevation) in central New Guinea. *Mirzamys louiseae*, n. sp., is known from the Star Mountains (possibly extending to the Snow Mountains; see Distribution, below), and *M. norahae*, n. sp., is recorded only from Porgera in the Kaijende Highlands (figs. 27, 28).

DIAGNOSIS: *Mirzamys* comprises two species of small-bodied, terrestrial, brownish-gray murines. Species of *Mirzamys* appear morphologically more similar to *Pseudohydromys* than to any other murids, but are distinguished from that genus and all others by the following combination of characters (figs. 28–30): (1) larger body and cranial size than in *Pseudohydromys*, with CIL measuring ≥ 26 mm (table 8); (2) a longer, slender, tapering rostrum that features premaxillae that project well beyond the faces of the upper incisors, elongate nasals that overhang these extended premaxillae, and more elongate incisive foramina (measuring 14%–16% of CIL); (3) a relatively large stapedial

foramen, large foramen ovale, and sharply defined groove in the ventral surface of the pterygoid plate, apparently for the passage of the infraorbital branch of the stapedial artery, indicating retainment of the plesiomorphic murine cephalic arterial pattern; (4) opisthodont upper incisors with pale orange-yellow enamel, and moderately elongate lower incisors with ivory enamel; (5) a less expansive middle lacerate foramen; (6) a larger braincase, both wider and higher domed; (7) a less reduced interparietal bone, less shortened anteroposteriorly; (8) two larger molars in each quadrant of the jaw, with the upper molars bearing high cusps and more expansive t1 and t4, and the lower molars with higher cusps, especially on the anterocentral and labial cusps; (9) first and second upper molars anchored by three large roots (one large anterior, one large posterior, and one lingual root) and both lower molars anchored with two roots; and (10) more extensive (i.e., elongate) interdigital “webbing” between the middle digits of the hindfeet and forefeet compared to *Pseudohydromys* (see below). Further morphological traits are reviewed below in the species accounts of *Mirzamys louiseae*, n. sp., and *M. norahae*, n. sp.

DESCRIPTION AND COMPARISONS: Though a small rodent, *Mirzamys* is larger bodied than other previously described New Guinean moss-mice, classified here in the genera *Pseudohydromys* and *Microhydromys* (e.g., fig. 29; tables 3, 10; Helgen et al., in press). Among hydromyins *Mirzamys* is most similar in body and cranial size to *Xeromys myoides*, a swamp and mangrove dweller of northern Australia and southern New Guinea (Magnussen et al., 1976; Van Dyck, 1995; Hitchcock, 1998), but otherwise *Mirzamys* is smaller than the remainder of hydromyins, including all known species (both described and undescribed) of *Hydromys*, *Baiyankamys*, *Parahydromys*, *Crossomys*, *Leptomys*, and *Paraleptomys* (Flannery, 1995a; Helgen, 2005b; Musser et al., 2008). No weights are available, but judging from its comparative body and cranial size, we estimate that adult individuals of both species of *Mirzamys* weigh 30–40 grams.

The feet of *Mirzamys* are similar to those of *Pseudohydromys* and *Microhydromys* in

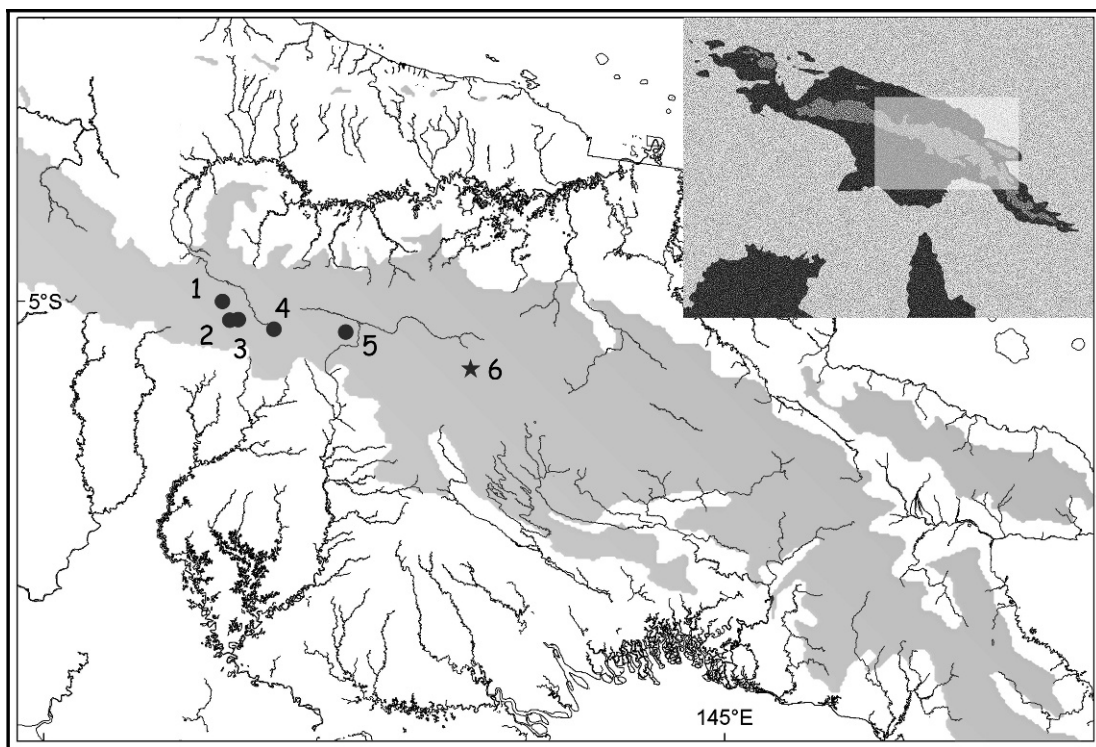


Fig. 27. Recorded distribution of the species of *Mirzamys*, *M. louiseae*, n. sp. (circles), and *M. norahae*, n. sp. (star), in central New Guinea. Areas above 1000 m in elevation are shaded in gray. See text for numbered localities.

most aspects. They are not excessively broadened as in amphibious hydromyine genera (*Hydromys*, *Baiyankamys*, *Crossomys*, *Parahydromys*) nor as comparatively elongate as in the apparently saltatorial genera *Leptomys* and *Paraleptomys* (Flannery, 1995a; Musser et al., 2008). Interestingly, *Mirzamys* seems to exhibit a more conspicuous degree of interdigital webbing between digits II–IV of the pes relative to species of *Pseudohydromys* (and *Microhydromys*), at least on average, with the interdigital membranes extending beyond the second interphalangeal joints to incorporate up to one-third of the second phalange between these digits. A similar degree of membranal interdigitation is evident between digits III and IV on the manus. In describing *Mayermys ellermani* (here *Pseudohydromys ellermani*), Laurie and Hill (1954: 134) remarked that “the feet [of *ellermani*] are very similar to those of *Pseudohydromys* and *Neohydromys* and are of a terrestrial type but, as in

Pseudohydromys and *Neohydromys*, there is a slight but definite membrane between the fingers and toes.” Although Laurie and Hill noticed these membranes in *P. ellermani* and other species of *Pseudohydromys*, interdigital membranes in these species are more trivial, usually extending no further beyond the second interphalangeal joint than about one-tenth the length of the second phalange between these digits, and in our examinations of series of various *Pseudohydromys* species preserved whole in fluid at BBM and AM (*P. fuscus*, *P. ellermani*, *P. germani*, *P. carlae*, *P. murinus*, and *P. patriciae*), we can find only the slightest trace of these membranes. The weak degree of interdigital “webbing” in *Mirzamys* is not comparable to the more pronounced foot webbing that characterizes the amphibious hydromyine genera *Hydromys*, *Parahydromys*, *Baiyankamys*, and *Crossomys* (Tate, 1951; Helgen, 2005b), and *Mirzamys* demonstrates no other anatomical specializations that are associated with an



Fig. 28. Selected views of the skulls of the species of *Mirzamys*: (left) *Mirzamys louiseae*, n. sp. (paratype, BBM-NG 98605, adult male, Star Mountains, Western Province, Papua New Guinea) and (right) *M. norahae* (holotype, WAM M21459, adult male, Porgera, Enga Province, Papua New Guinea). Scale bar for cranial images = 10 mm. Lower inset images show the enlarged maxillary molar rows of the same specimens, to scale.



Fig. 29. Study skins showing comparative mature body size of *Pseudohydromys murinus*, the type species of *Pseudohydromys* (left, AMNH 191414, adult female, Mt. Wilhelm, Chimbu Province, Papua New Guinea), and *Mirzamys louiseae*, n. sp., the type species of *Mirzamys* (right, BBM-NG 98605, adult male, Star Mountains, Western Province, Papua New Guinea).

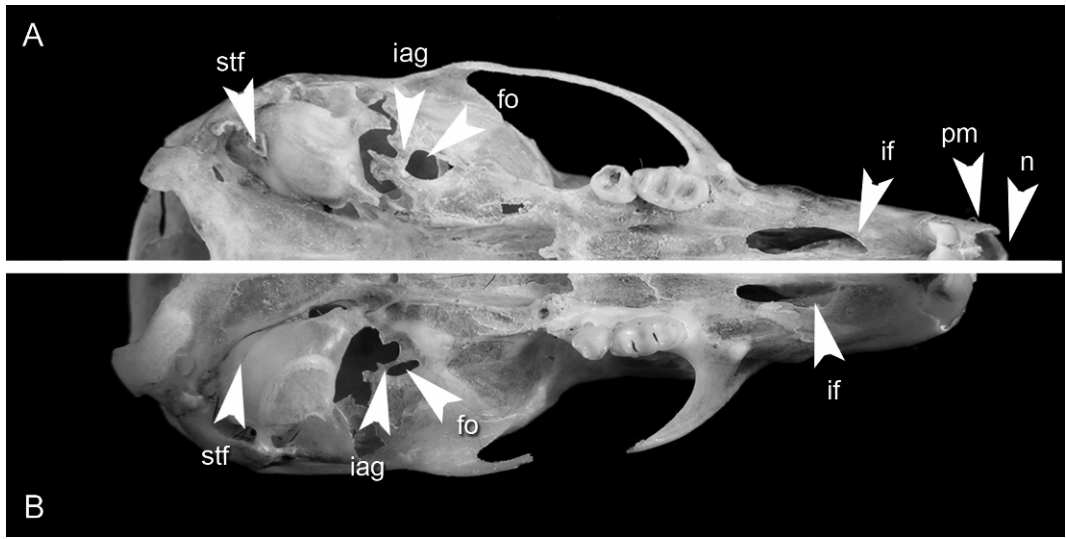


Fig. 30. Selected aspects of qualitative anatomy contrasted in the skulls of *Mirzamys* (as represented by *M. louiseae*, n. sp., half view; top), and *Pseudohydromys* (as represented by a generalized, two-molared member of the genus, *P. berniceae*, half view; bottom); scaled to the same length (*M. louiseae*, n. sp., is markedly larger than *P. berniceae*; see tables 4, 8). The figure portrays characteristic contrasts between *Mirzamys* and all species of *Pseudohydromys*, including, in *Mirzamys*, a more elongate rostrum; longer nasals (**n**) which overhang the premaxillae (**pm**); premaxillae which jut forward well in front of the upper incisors; relatively longer incisive foramina (**if**); wider molars, with expanded t1 on M1; much expanded foramen ovale (**fo**); relatively smaller auditory bullae; conspicuous (rather than indistinct) groove (**iag**) for the passage of the infraorbital branch of the stapedial artery; and larger and more obvious stapedial foramen (**stf**).

TABLE 8
Selected Craniodental Measurements for the Species of *Mirzamys* (mean \pm standard deviation, with observed range in parentheses)

Variable	<i>louiseae</i> Star Mountains (<i>n</i> = 9)	<i>norahae</i> Porgera WAM M21459	<i>norahae</i> Porgera PNGNM 25058
CIL	26.66 \pm 0.56 (26.00–27.58)	26.5	–
ZYG	12.89 \pm 0.31 (12.62–13.17)	13.3	11.7
POB	6.01 \pm 0.14 (5.73–6.20)	5.7	5.7
BBC	12.89 \pm 0.22 (12.68–13.42)	12.6	–
HBC	8.37 \pm 0.32 (7.92–8.88)	8.7	–
BR	5.40 \pm 0.27 (4.99–5.78)	5.5	4.8
LM1	2.54 \pm 0.05 (2.46–2.62)	2.4	2.4
BM1	1.38 \pm 0.05 (1.30–1.45)	1.4	1.4
LIF	4.00 \pm 0.17 (3.65–4.21)	4.1	4.1
LN	9.93 \pm 0.52 (8.80–10.54)	9.5	9.1
LD	7.07 \pm 0.21 (6.75–7.40)	6.7	–
BMF	2.37 \pm 0.11 (2.23–2.53)	2.2	2.1
LBP	6.42 \pm 0.33 (6.18–7.06)	5.5	5.7
BBP	3.55 \pm 0.18 (3.25–3.91)	3.1	–
CLM	3.82 \pm 0.13 (3.56–3.96)	3.8	3.8
BIR	2.54 \pm 0.26 (2.23–3.05)	2.8	–

amphibious lifestyle. Various external features, including its soft, dense pelage, tiny eyes, small feet, moderate tail length, small teeth, and moderately long and narrow rostrum suggest to us that it is instead probably entirely terrestrial in its habits—a composite ecomorphological impression supported by trapping data tied to museum specimens. In size, coloration, and general external conformation *Mirzamys* recalls only *Microhydromys* or *Pseudohydromys* to any extent, lacking the coppery or rufescent dorsal coloration, contrasting pale venter, and (as noted above) more elongate feet that are characteristic of the species of *Leptomys* and *Paraleptomys*, the remaining, fully terrestrial hydromyine genera.

Despite its greater overall body and cranial size relative to species of *Pseudohydromys* (table 8), in most features the skull of *Mirzamys* is no more qualitatively robust than in the species of *Pseudohydromys*. The rostrum is relatively narrow, the bones of the neurocranium are thin and translucent, and the zygomata are delicate and weakly expanded, such that the zygomatic breadth is subequal to the breadth of the braincase (e.g., averaging exactly equal in breadth in *M. louseae*, versus slightly to stoutly splayed in *Pseudohydromys*). The rostrum is longer in *Mirzamys* (e.g., $LN/CIL = 34\%–39\%$ in *M. louseae*) than in all species of *Pseudohydromys* except *P. patriciae*. The nasals slightly overhang the anterior margin of the premaxillae, which (in strong contrast to species of *Pseudohydromys*) project as lateral extensions well beyond the anterior face of the upper incisors. Among other murine genera, this conformation of the anterior rostrum (the upper incisors, premaxillae, and anterior nasals) also characterizes *Leptomys* and *Paraleptomys* (Musser et al., 2008), and is closely matched in some unrelated longer-snouted murines from other regions, such as the Sulawesi genus *Tateomys*, especially *T. macrocercus* (Musser, 1982; Musser and Durden, 2002).

The upper incisors of *Mirzamys* are slightly opisthodont and their enamel faces are pigmented a weak yellow-orange. The mandible closely resembles that of *Pseudohydromys murinus* in conformation but is of course much larger, and features a relatively longer

diastema. The lower incisors are moderately long and differ from *Pseudohydromys* in their weaker upcurve and in having ivory-colored enamel faces (yellow-orange in *Pseudohydromys*). The incisive foramina are moderately broad for their length, subparallel, and relatively long ($LIF/CIL = 14–16\%$), conspicuously longer than the characteristically short incisive foramina of *Pseudohydromys* ($LIF/CIL = 7–12\%$). The braincase is wide and long, and relatively high domed in lateral view. The interorbital region is slightly constricted behind the moderately inflated nasofrontal region. The posterior palatine foramina are short and not deeply excavated. In ventral aspect the posterior end of the palate rises gently upward, and may feature a modestly developed palatal spine. The mesopterygoid fossa is not strongly constricted and resembles the configuration in *P. murinus*.

Mirzamys has two molars in each quadrant of the jaw, with the upper molar row situated immediately behind the zygomatic plate. Compared to species of *Pseudohydromys*, the molars are less reduced in size ($CLM/CIL = 14\%–15\%$ in *M. louseae*). As in most hydromyine genera, molar cusps of the labial row ($t3$, $t6$, $t9$) are lacking or conglomerated beyond identification in *Mirzamys* (Misonne, 1969: 157). We cannot detect a $t7$ in the first upper molars. The cusps of the molars are higher crowned in *Mirzamys* (based on our examinations of *M. louseae*) than in *P. murinus*, and bear a more expansive $t1$ and $t4$. The lower molars are correspondingly larger as well, and feature much higher-crowned cusps relative to *Pseudohydromys*, especially on the anterocentral cusp of the first lower molars.

In contrast to *Pseudohydromys*, in *Mirzamys* (based on our examinations of *M. louseae*) the foramen ovale is very large, the stapedia foramen is also relatively large, and there is a distinct groove in the pterygoid plate leading from the bulla to the foramen ovale, apparently for the passage of the infraorbital branch of the stapedia artery. These are osseous reflections of the primitive murine cephalic arterial pattern (Musser and Heaney, 1992). Like most Melanesian murids, *Mirzamys* lacks the derived cephalic arterial pattern that characterizes all species of *Pseudohydromys* (in addition to a handful

of other, disparate New Guinea murine genera, including *Leptomys*, *Lorentzimys*, and *Mammelomys*).

The postglenoid foramen in *Mirzamys* (based on our examinations of *M. louiseae*) is largely or wholly separated from the middle lacerate foramen by a bony anterior projection of the auditory bulla, which extends to the alisphenoid portion of the pterygoid plate. This unspecialized configuration (cf. Musser, 1982) is shared with most species of *Pseudohydromys*, but a more derived arrangement characterizes the smaller-toothed taxa *P. occidentalis*, *P. musseri*, *P. sandrae*, and *P. fuscus* (see above). As in *Pseudohydromys*, in *M. louiseae* the postglenoid foramen is relatively large, but the middle lacerate foramen is less expansive in *M. louiseae* than in most species of *Pseudohydromys*. The foramen magnum is extremely broad in *Mirzamys*, and similar in shape to that of most *Pseudohydromys* (the narrowed foramen magnum of *P. patriciae* is an exception).

Only one cleaned postcranial skeleton of *Mirzamys* (BBM-NG 98455, a specimen of *M. louiseae*) is available in museum collections. All skeletal elements, especially the long bones of the limbs, are considerably more robust in appearance than corresponding elements in the smaller *Pseudohydromys murinus* (the only species of *Pseudohydromys* for which prepared postcranial skeletons are yet available: AM M14161, AM M14548, BBM-NG 29194, BBM-NG 53269, BBM-NG 53283, and BBM-NG 53382, all from Mt. Kaindi). In the skeleton of *Mirzamys*, there are 7 cervical vertebrae, 14 thoracic vertebrae, 7 lumbar vertebrae, 4 sacral vertebrae, and 33 caudal vertebrae. In *Pseudohydromys murinus* there are 7 cervical vertebrae, 14 thoracic vertebrae, 7 lumbar vertebrae, 4 sacral vertebrae, and 34–35 caudal vertebrae (scored in BBM-NG 29194 and 53283). On the basis of these samples it is not clear that this difference in caudal vertebrae count reflects a consistent distinction between *Mirzamys* and *Pseudohydromys*. For one, the smallest caudal vertebrae are difficult to discern and count, and may be lost in some museum specimens. Further, and perhaps more importantly, given the variability in proportional tail length across the taxonomic scope of *Pseudo-*

hydromys (table 3), we anticipate some degree of variability in numbers of caudal vertebrae within and between species in that genus.

Though osteological and external traits seem to firmly ally *Mirzamys* most closely to *Pseudohydromys*, the skull of *Mirzamys* also requires critical comparison with the larger terrestrial hydromyine genera *Leptomys* and *Paraleptomys*. Species of *Paraleptomys* (two described species, *P. wilhemina* and *P. rufilatus*) and *Leptomys* (five described species, *L. elegans*, *L. signatus*, *L. arfakensis*, *L. ernstmayri*, and *L. paulus*) are medium-sized rats (CIL 27–32 mm in *Paraleptomys*, 29–39 mm in *Leptomys*), larger than *Mirzamys*, with long, woolly coppery-brown or red-brown dorsal fur, a buffy-gray to cinnamon-colored venter, long, narrow feet, a relatively unreduced eye, and a white-tipped tail (Musser et al., 2008). Despite their dissimilar external appearances, the skulls of *Mirzamys* and *Paraleptomys*, while differing in size, agree closely in many aspects of basic cranial conformation and proportion (fig. 31). Both genera share relatively small auditory bullae, a moderately long and relatively narrow rostrum (e.g., LN/CIL = 34%–39% in *Mirzamys*, 35%–43% in *Paraleptomys*), procumbent premaxillae and nasals, slightly opisthodont upper incisors, long and relatively wide incisive foramina (LIF/CIL = 14%–16% in *Mirzamys*, 14%–17% in *Paraleptomys*), and a globular, high-domed braincase. In both genera the plesiomorphic murine cephalic arterial pattern is retained (cf. Musser and Heaney, 1992). In *Paraleptomys wilhelmina* and two other undescribed species of *Paraleptomys* from the Central Cordillera (Musser et al., 2008), as in *Mirzamys*, the skull is relatively delicate for its size, with slim zygomatic arches (fig. 31); the larger species *Paraleptomys rufilatus* (North Coast Ranges) has a considerably larger skull with more robust and more widely flared zygomata. The molars of *Paraleptomys* are larger and more prominently cusped than in *Mirzamys*, with the lingual cusps comparatively less reduced in size (fig. 31).

Cranial resemblance between *Mirzamys* and *Leptomys* is more remote, though like *Paraleptomys*, *Leptomys* shares with *Mirzamys* elongate premaxillae and nasals and long

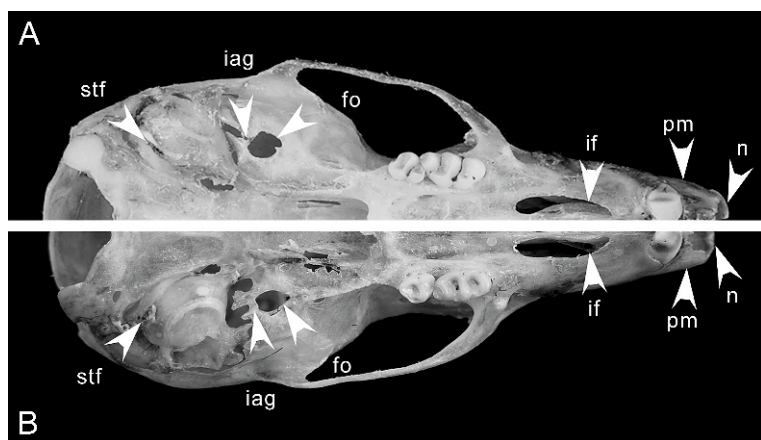


Fig. 31. Selected aspects of qualitative anatomy contrasted in the skulls of *Mirzamys* (as represented by *M. louiseae*, n. sp., BBM-NG 98605, half view; bottom) and *Paraleptomys* (*Paraleptomys* cf. *wilhelmina*, BBM-NG 98545, half view; top), scaled to same cranial size. The two genera resemble one another closely in their elongate rostrum and long nasals (**n**) which overhang the premaxillae (**pm**); premaxillae which jut forward well in front of the upper incisors; relatively long and similarly situated incisive foramina (**if**); large foramen ovale (**fo**); similarly sized auditory bullae; conspicuous (rather than indistinct) groove (**iag**) for the passage of the infraorbital branch of the stapedia artery; and prominent stapedia foramen (**stf**).

incisive foramina, a combination of traits not seen in other hydromyins. *Leptomys* diverges most outstandingly from *Mirzamys* in its considerably more complex molar surfaces, more elongate rostrum, retainment of M3, and possession of a derived cephalic arterial configuration (Musser and Heaney, 1992; Musser et al., 2008).

Whether phenetic cranial similarities between *Mirzamys* and *Paraleptomys* indicate a close phylogenetic relationship, signal ecomorphological convergence (both of these murines are terrestrial animalivores from montane forests), or simply reflect a basal position for both genera among different branches of the hydromyin radiation (cf. Musser and Carleton, 2005), must be regarded as uncertain. It is our suspicion that cranial resemblances between *Mirzamys* to *Paraleptomys* do not convey an immediate relationship between these genera. Phylogenetic relationships among various members of the hydromyin radiation remain poorly established, despite attention from various researchers employing diverse methodologies (e.g., Tate, 1951; Misonne, 1969; Lidicker, 1968, 1973; Lidicker and Brylski, 1987; Watts and Baverstock, 1994, 1995, 1996; Musser and Heaney, 1992; Rowe et al., 2008). The

most recent formal taxonomic arrangement of these rodents, introduced by Musser and Carleton (2005), divides hydromyins into two suprageneric taxonomic lineages, one dubbed the *Xeromys* Division (incorporating *Xeromys*, *Leptomys*, and *Pseudohydromys*), the other the *Hydromys* Division (incorporating *Hydromys*, *Baiyankamys*, *Parahydromys*, *Crossomys*, *Microhydromys*, and *Paraleptomys*). This provisional arrangement is based on these authors' composite impressions derived from (generally ambiguous) published evidence from spermatozoal (Breed and Aplin, 1994), phallic (Lidicker, 1968, 1973; Lidicker and Brylski, 1987), albuminological (Watts and Baverstock, 1994, 1995, 1996), and craniodental comparisons (Tate, 1951; Musser and Heaney, 1992). These hypothetical relationships await rigorous phylogenetic testing, which will require more extensive comparative data ideally derived from both anatomical and molecular comparisons. Datasets drawing from multiple nuclear genes are especially needed to generate well-supported phylogenetic topologies for the hydromyin genera, to position them within in the broader context of Australo-Papuan (and extraregional) murine evolution, and to tie these supported relationships

to hypotheses regarding biogeographic and temporal differentiation (cf. Michaux et al., 2001; Steppan et al., 2004, 2005; Jansa and Weksler, 2004; Jansa et al., 2006; Rowe et al., 2008; Lecompte et al., 2008).

ETYMOLOGY: The generic name honors Pakistani mammalogist Abid Beg Mirza, a notable collector of Melanesian mammals, formerly based at the Wau Ecology Institute in Papua New Guinea. Mirza collected the majority of available specimens representing this new genus. During his Papua New Guinea survey work in association with the Bishop Museum, Mirza collected specimens of eight of the 16 species of New Guinea moss-mice (*Microhydromys*, *Pseudohydromys*) and moss-rats (*Mirzamys*), more than any other worker, and his collections include the only known specimens of both *P. musseri* and *P. carlae*.

DISTRIBUTION: *Mirzamys* is thus far known from modern specimens collected in Enga Province (*M. norahae*) and Western and West Sepik provinces (*M. louiseae*) of west-central Papua New Guinea (fig. 27). A single subfossil mandible (accessioned in the Australian Museum's paleontological collections as AM F54877) collected at 3450 m in a fissure on Mt. Jaya (ca. 04°05'S, 137°11'E) in the Snow Mountains of West Papua (Indonesian New Guinea), reported by Hope (1976: 212, 221) as "Hydromyinae indet.," also represents *Mirzamys*, and provides an indication of a broader geographic range for the genus in high mountain landscapes across New Guinea's Central Cordillera. Hope (1976: 221) wrote: "The right mandible of one of the smaller species of hydromyines was found in the Asair fissure. Two molars are present, so the specimen is not *Mayermys*. The length of M_{1-2} is 3.7 mm." We have briefly examined this specimen; because it is represented only by a mandible and we have been unable to compare it directly to modern specimens of *M. louiseae* and *M. norahae*, the species-level identification of this specimen remains uncertain. If it represents one of these known taxa, on geographic grounds it seems more likely to be *M. louiseae*, as a number of New Guinea mammals are known only from the Star and Snow mountains (see account of *Pseudohydromys occidentalis*, above). We suspect that *Mirzamys* still occurs

in the Snow Mountains and anticipate the eventual documentation of living examples from Indonesian New Guinea.

Mirzamys louiseae, new species

HOLOTYPE: BBM-NG 98605, adult male, study skin (fig. 32) and skull, from the "Star Mountains" (i.e., apparently the Hindenburg or Blucher Range: plotted as locality 2 in fig. 27 based on our archival research at the Bishop Museum) in the "Western District, Territory of Papua" (Western Province, Papua New Guinea), at 10,500 ft (= 3180 m), collected 15 March 1970 by A.B. Mirza. The holotype was snap-trapped in mossy upper montane forest ("moss forest" on the skin tag).

REFERRED SPECIMENS: **Sandaun (West Sepik) Province, Papua New Guinea:** BBM-NG 55422A (adult male, skin only) and BBM-NG 55422A (adult male, skin only), from Oksapmin (05°13.5'E, 142°13.2'E; locality 5 in fig. 27), 1900 m, collected 19 October 1968 by R. Traub and A.B. Mirza. BBM-NG 98455 (adult female, skin, skull, and complete postcranial skeleton, collected 17 February 1970, "8500 feet" [2591 m]), BBM-NG 99986 (adult male, skin and skull, 13 April 1971, 2800 m), and BBM-NG 100117 (adult male, skin and skull, 25 April 1971, 2800 m), from Lake Louise (05°00'E, 142°19'E, "17 miles NW of Telefomin"; locality 1 in fig. 27), collected by A.B. Mirza. BBM-NG 108216 (young adult male, skin and skull), from Bafunmin (05°08'S, 141°26'E; locality 3 in fig. 27), 2300 m, collected 7 April 1980 by P.K. Wanga. BBM-NG 105241 (adult male, body fixed in formalin and stored in alcohol, with skull removed and cleaned), from Bokubet, 2850 m, "10 km east of Feramin" (05°13'S, 141°14'E; locality 4 in fig. 27), collected 8 July 1976 by T. Bukam. **Western Province, Papua New Guinea:** All specimens collected by A.B. Mirza at the type locality ("Star Mountains"; see above): BBM-NG 98584 (adult male, skin and skull, 9 March 1970, 3200 m), BBM-NG 98606 (adult male, skin and skull, collected 15 March 1970, 3200 m), BBM-NG 98610 (adult male, skin and skull, 16 March 1970, 3200 m), BBM-NG 98611 (adult female, skin and skull, 16 March 1970,



Fig. 32. Dorsal and ventral views of a study skin of *Mirzamys louiseae* (holotype, BBM-NG 98605, adult male, Star Mountains, Western Province, Papua New Guinea).

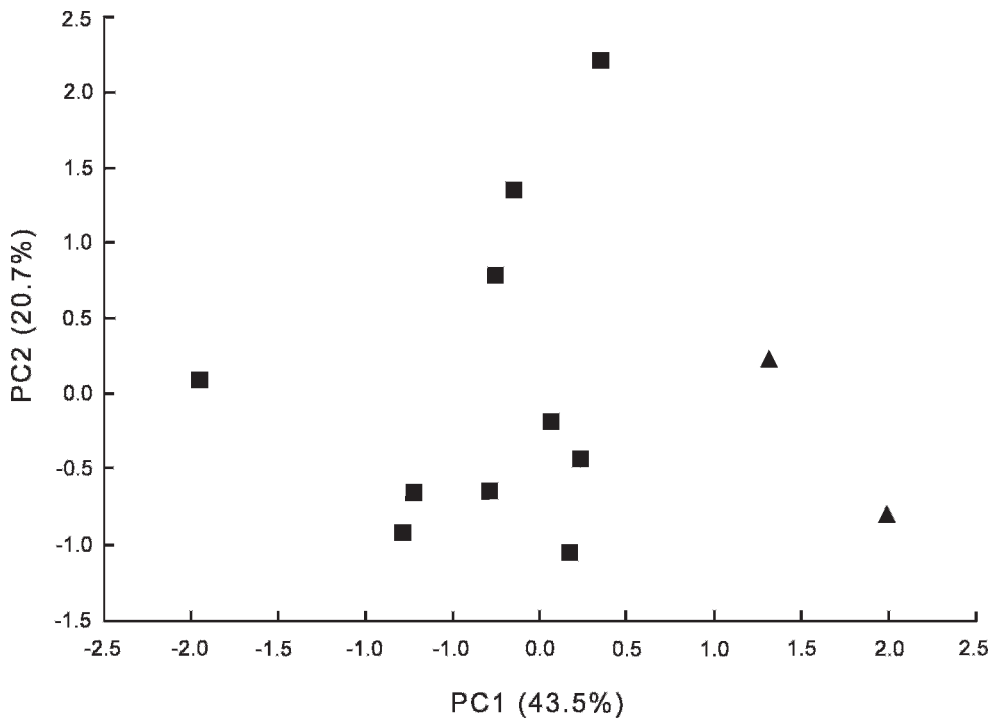


Fig. 33. Morphometric separation (principal component analysis) of crania representing the species of *Mirzamys* (*M. louiseae*, squares; *M. norahae*, n. sp., triangles). Separation along the first principal component reflects smaller values for *M. norahae* in many measured variables, especially in the length of the bony plate, coupled with high values for length of the incisive foramina and the breadth of the first molar (tables 8, 9).

3200 m), BBM-NG 100246 (adult male, skin and skull, 28 May 1971, 3100 m), BBM-NG 100248 (young adult female, skin and skull, 29 May 1971, 3100 m), and PNGNM 22812 (young adult male, skin and skull, 6 March 1970, “10,500 + feet” [ca. 3200 m]).

DIAGNOSIS: *Mirzamys louiseae* differs from *M. norahae*, n. sp. (see below), especially in having darker pelage, a proportionally longer tail, longer hind feet and ears, a longer rostrum, narrower and more slender zygomata, smaller auditory bullae, a longer and wider bony palate, and a larger foramen ovale (tables 8 and 9; figs. 28, 32–34).

DISTRIBUTION: *Mirzamys louiseae* is recorded from upper montane forests and subalpine grasslands in the Star Mountains region of central New Guinea (i.e., the Victor Emmanuel and Hindenburg ranges), just to the east of the Indonesia–Papua New Guinea border. It has been trapped at sites situated from 1900 to at least 3200 m, though it is

likely to extend to even higher elevations (fig. 27). The mean elevation of eight known trapping sites for this species is 2740 m (median 2825 m; SD = 456 m). It can be expected in similar habitats in the western Star Mountains, across the Indonesian border—mountains that remain very poorly inventoried for mammals but support a biota very similar to that in the eastern Stars (Helgen, 2007a). A subfossil mandible (accessioned as AM F54877) collected at 3450 m in a fissure on Mt. Jaya (ca. 04°05'S, 137°11'E, not mapped in fig. 27) in the Snow Mountains of western New Guinea may also represent this species, indicating the possibility of a considerably wider modern or Recent distribution for this species (see Distribution, in the generic account of *Mirzamys*, above).

This species has been collected syntopically with two smaller moss-mice, *Pseudohydromys occidentalis* (at Bafunmin, 2300 m, and Lake Louise, ca. 2600 m) and *P. ellermani* (at



Fig. 34. Fluid specimen of *Mirzamys norahae* (holotype, WAM M21459, adult male, Porgera, Enga Province, Papua New Guinea). Photograph courtesy of Claire Stevenson.

Bafunmin, 2300 m). *Microhydromys richardsoni* is also known from the vicinity of Telefomin, but at lower elevations (one record in the area at 1500 m, the highest recorded occurrence for the species [Helgen et al., in press]).

ETYMOLOGY: This species is named after Lake Louise, one of the sites where it has been collected (locality 1 in fig. 27); the name simultaneously honors Louise H. Emmons of the National Museum of Natural History at the Smithsonian Institution in Washington, D.C., friend of the authors and global authority on tropical mammals. We recommend “Mirza’s western moss-rat” as an appropriate English common name.

DESCRIPTION AND COMPARISONS: *Mirzamys louiseae* is a small murine (total length averaging 222 mm) with a dark gray-brown dorsum and venter. The fur is dark brownish gray both above and below, the hairs being gray for most of their length, with dark

brown tips. In overall pelage coloration it most closely resembles the much smaller-bodied *Pseudohydromys murinus* of eastern New Guinea (fig. 29). The fur of the dorsum is soft, long (about 12 mm on the lower back), and extremely thick. In some specimens, especially in younger animals, the underside is less strongly infused with dark brown than the dorsum, rendering it a paler gray. There is often faint pale flecking on the midback and/or rump, and in some specimens there is a pale russet-brown patch of fur on the throat. The tail is subequal to the head-body length (table 10) and is pigmented dark, appearing blackish brown, though a variable degree of somewhat paler mottling is evident along its length. A pale terminal tail tip, expressed to some extent in most *Pseudohydromys* species, is lacking in *Mirzamys*. There are 13–15 tail scales per centimeter in the midsection of the tail, and the tail hairs measure one to 1.5 tail scales in length. The eye is extremely small. The long and blackish dorsal fur is shorter on the forearms and head, and does not extend to the immediate area around the eye, creating the impression of a paler eye ring. The ears are moderately long, ovate, and dark gray. The mystacial vibrissae are fine and moderately long, the longest measuring about 50 mm and extending behind the ears when pressed to the sides of the head.

The surfaces of the manus and pes appear dark and are covered in brown hairs. The hindfoot is fairly long and relatively narrow (5–7 mm in breadth). The digits of the manus and pes are long and slender, terminate ventrally in fleshy digital pads, and bear long, sharp, sickle-shaped claws, except for the first digit of the manus, which bears an elongate nail. The palmar surfaces are composed of three fleshy interdigital pads, a large hypothenar pad, and a smaller thenar pad. The plantar surfaces feature four fleshy interdigital pads, an elongate thenar pad, and a much smaller hypothenar.

Two adult female specimens of *Mirzamys louiseae* have information on the mammae formula written on the skin tag. In one (BBM-NG 98611) the formula is given on the label as “0 : 2 = 4” (i.e., two pairs of inguinal mammae), the typical condition in hydromyins. In the other (BBM-NG 98455), it is

TABLE 9
Results of a Principal Component Analysis Contrasting the Species of *Mirzamys*

Factor loadings, eigenvalues, and percentage variance; principal components are extracted from a covariance matrix of 10 log-transformed cranial and dental variables; see fig. 33. Craniometric variables selected to maximize sample size, which includes 10 specimens of *M. louiseae*, the holotype of *M. norahae*, and the damaged cranium of the *M. norahae* paratype. Younger adult skulls tend toward higher values on PC2. The third principal component (PC3) is not depicted in fig. 33.

	PC1	PC2	PC3
POB	−0.6143	−0.3008	−0.0997
LN	−0.7597	−0.5449	−0.0855
ZB	−0.6882	−0.0141	−0.4365
LBP	−0.9251	−0.0013	0.2455
BMF	−0.5686	0.6712	0.3032
BR	−0.3421	0.5724	−0.7341
LIF	0.4284	0.5703	0.5646
CLM	−0.1908	−0.5086	0.3509
LM1	−0.6567	−0.0220	0.2069
BM1	0.5188	−0.3016	−0.2123
Eigenvalue	0.0091	0.0044	0.0034
% variance	43.50	20.73	16.33

written as “0 : 1 = 2 ?” (i.e., one pair of inguinal mammae). Both specimens were collected by A.B. Mirza, an experienced collector of hydromyins. Though it is possible that *Mirzamys louiseae* is polymorphic in its mammae formula, a more likely explanation is that the latter specimen, being a younger adult, did not have both sets of teats well developed (a supposition that probably explains Mirza’s use of the question mark). Closer inspection of the underside of the skins in question allows no clear resolution. We expect that, as in other hydromyins, the usual mammae formula in *Mirzamys* is 0 + 2 = 4, though additional specimens are needed to verify this. It has been suggested that in one other hydromyins, *Hydromys hussoni*, the mammae may number either 0 + 1 = 2 or 0 + 2 = 4 (Flannery, 1995a: 239), but our own brief investigations of skins from the type series (at the Naturalis Museum, Leiden)

suggests that 0 + 2 = 4 is the typical conformation in *H. hussoni* (see also the discussion of teat number in *Pseudohydromys patriciae*, above).

BIOLOGICAL NOTES: Little is yet recorded of this species’ habits. It is clearly terrestrial, as almost all known specimens were snap-trapped on the ground (the single exception, BBM-NG 98584, was apparently collected in a “pan trap”—possibly meaning a pitfall trap, but a denotation used by Mirza probably to refer to a type of hold trap usually used to catch larger mammals, such as wallabies). Specimen labels reveal that it has been trapped “in forest” (e.g., BBM-NG 108216, Bafunmin, 2300 m), “in moss forest” (e.g., BBM-NG 100117, Lake Louise, 2800 m), and “in grass” at the boundary of “moss forest and subalpine grassland” (e.g., BBM-NG 100248, “Star Mountains,” 3100 m). The great majority of available

TABLE 10
Selected External Measurements for the Species of *Mirzamys* (mean ± standard deviation, with observed range in parentheses, followed by sample size)

Sample	HB	Tail	Mean T/HB	HF	Ear	Weight (g)
<i>Mirzamys louiseae</i>	111.4 ± 5.9 (101–120) 14	108.9 ± 7.6 (100–124) 14	98% 83–111%	24.4 ± 0.5 (24–25) 14	14.9 ± 0.6 (14–16) 14	–
<i>Mirzamys norahae</i>	110 (105–115) 2	94.5 (89–100) 2	86% 85–87%	22.2 (22.0–22.4) 2	12.1 (11–13.2) 2	30 (<i>n</i> = 1)

TABLE 11
Elevational Associations of New Guinea Moss-mice (*Pseudohydromys* and *Microhydromys*) and moss-rats (*Mirzamys*)

Minimum and maximum elevations of trapping, recorded vertical range, mean and median elevations, and standard deviation of all known collecting sites for the 12 species of *Pseudohydromys*, two species of *Mirzamys*, and two species of *Microhydromys* (Helgen et al., 2009). All figures in meters. *n* = number of collecting sites. Only two species of *Pseudohydromys* have elevational “floors” below 1000 m elevation. All moss-mice taxa known from six or more sites have a vertical range of occurrence (i.e., maximum elevational occurrence minus minimum elevational occurrence) spanning ca. 1300 to 2000 m in total.

Species	min/max	range	mean	median	SD	<i>n</i>
<i>Pseudohydromys murinus</i> Rümmler, 1934	1570–3400	1830	2432	2424	359	> 20
<i>Pseudohydromys berniceae</i> , n. sp.	590–1570	980	1221	1490	537	3
<i>Pseudohydromys eleanorae</i> , n. sp.	2440–3050	610	2731	2670	191	4
<i>Pseudohydromys patriciae</i> , n. sp.	2800–3400	600	3100	3100	–	2
<i>Pseudohydromys occidentalis</i> Tate, 1951	2300–3800	1500	3181	3393	603	6
<i>Pseudohydromys musseri</i> (Flannery, 1989)	1350	–	1350	1350	–	1
<i>Pseudohydromys sandrae</i> , n. sp.	800/850	–	800/850	800/850	–	1
<i>Pseudohydromys fuscus</i> (Laurie, 1952)	1600–3660	2060	2691	2780	478	> 20
<i>Pseudohydromys ellermani</i> (Laurie & Hill, 1954)	1400–2800	1400	2207	2200	458	15
<i>Pseudohydromys pumehanae</i> , n. sp.	1550–2100	550	1775	1775	–	2
<i>Pseudohydromys germani</i> (Helgen, 2005)	1300–1570	270	1435	1435	–	2
<i>Pseudohydromys carlae</i> , n. sp.	2560–3600	440	2780	2780	–	2
<i>Mirzamys louiseae</i> , n. gen., n. sp.	1900–3200	1300	2740	2825	459	8
<i>Mirzamys norahae</i> , n. gen., n. sp.	2650	–	2650	2650	–	1
<i>Microhydromys richardsoni</i> Tate & Archbold, 1941	20–1500	1480	760	761	609	4
<i>Microhydromys argenteus</i> Helgen et al., in press	380–1500	1100	896	758	475	3

specimens were taken in this last habitat, the interface between mossy upper montane forest and subalpine grassland (see the excellent representative photograph figured

by Flannery, 1995a: 256), though the range of recorded elevations (ca. 1900 to 3200 m) indicates that it is likely an altitudinally versatile inhabitant of montane forests. We suspect that this species is largely if not entirely insectivorous, like its sole known congener, *M. norahae* (see below).

TABLE 12
Sex Ratios Calculated from Museum Samples of the Species of *Pseudohydromys*

Shown are species known by more than a single adult specimen (i.e., excluding *P. musseri* and *P. sandrae*). Compiled from all specimens of known sex at AM, AMNH, BBM, BMNH, MCZ, MVZ, NMS, PNGNM, and USNM. *n* = number of sexed, adult specimens.

Species	<i>n</i>	% male	% female
<i>P. murinus</i>	47	55	45
<i>P. berniceae</i>	5	40	60
<i>P. eleanorae</i>	4	50	50
<i>P. patriciae</i>	2	50	50
<i>P. occidentalis</i>	7	57	43
<i>P. fuscus</i>	40	45	55
<i>P. ellermani</i>	24	71	29
<i>P. germani</i>	3	100	0
<i>P. pumehanae</i>	3	67	33
<i>P. carlae</i>	3	100	0

Morren (1989), Flannery and Seri (1990a), and Hyndman and Menzies (1990) did not encounter *Mirzamys louiseae* during mammal-inventory efforts in appropriate habitats in the Star Mountains of Western and Sandaun Provinces of Papua New Guinea. However, these researchers also did not trap most of the other hydromyins today known to occur in the area, including *Pseudohydromys occidentalis*, *Pseudohydromys ellermani*, *Microhydromys richardsoni*, *Parahydromys asper*, and *Crossomys moncktoni* (Helgen, 2007a). We presume that these workers’ trapping efforts in higher-altitude forest were not as intensive as those of Mirza, who collected many specimens of *M. louiseae*. Either personally or through the efforts of local assistants—we do not know Mirza’s

field regimen—Mirza obtained, with snap trapping, most of the hydromyine specimens thus far known from the Star Mountains.

Smales (2001) reported a larval nematode referred to the spirurid taxon *Protospirura kairi* Smales, 2001 from BBM-NG 105241, a specimen of *Mirzamys louiseae* (then identified as “*Pseudohydromys occidentalis*”) trapped at Bokubet at 2850 m (see Referred Specimens, above).

Mirzamys norahae, new species

HOLOTYPE: WAM M21459, adult male, body fixed and stored in 70% ethanol (fig. 34) with intestines removed (see Jackson and Woolley 1993: 86) and skull extracted and cleaned (fig. 28), from the immediate vicinity of Porgera (05°28'S, 143°05'E, Enga Province, Papua New Guinea; locality 6 in fig. 27), 2650 meters, collected 12 May 1985 by P.A. Woolley (original number PAW P12).

PARATYPE: PNGNM 25058, young adult male, study skin and damaged skull, from the type locality, 2650 m, collected 23 May 1985 by P.A. Woolley (original number PAW P103).

DIAGNOSIS: *Mirzamys norahae* differs from *M. louiseae* especially in having more reddish-brown pelage, a proportionally shorter tail (averaging 86% of head-body length versus 98% in *M. louiseae*), shorter hindfoot and ear, less elongate rostrum, more robust zygomata, shorter and narrower bony palate, larger auditory bullae, and smaller foramen ovale (tables 8, 9; figs. 28, 32–34).

DISTRIBUTION: *Mirzamys norahae* is thus far known only from the type locality, Porgera, at 2650 m. Summary accounts published in the volume edited by Richards (2007) provided an overview of the ecological context in the immediate vicinity of the type locality. In particular, Takeuchi (2007) presented excellent vegetational characterizations of upper montane forests, tussock grasslands, and lower montane forests in the Kaijende Highlands (Enga Province)—expected habitats of occurrence for this little known species.

ETYMOLOGY: The specific epithet honors Norah Cooper of the Western Australian Museum in Perth, an authority on Australasian small mammals. We are most grateful

for her hospitality during visits to Perth, her efforts in loaning specimens for our use, and in particular her assistance in describing this new species. We recommend “Mirza’s eastern moss-rat” as an appropriate English common name.

DESCRIPTION: We first realized the distinctness of this species when the first author examined the specimen from Porgera designated here as a paratype (at PNGNM) in early 2003. This specimen, labeled “*Pseudohydromys occidentalis*,” consists of a partially broken skull (shattered behind the parietals above and the pterygoid region below, probably by a snap trap) accompanied by a poorly prepared and badly faded study skin. We recognized this as a moss-mouse different from any other, but one that showed affinity to *Mirzamys louiseae*, also represented in the PNGNM collection (see above). Jackson and Woolley (1993) mentioned another specimen of “*Pseudohydromys occidentalis*” from Porgera, deposited at WAM, which likewise proved upon examination to represent this new species (designated here as the holotype of *norahae*). Ken Aplin of the Australian National Wildlife Collection (CSIRO, Canberra) photographed and measured the intact skull of this specimen for us (fig. 28), and Norah Cooper and Claire Stevenson of the Western Australian Museum have very kindly provided us with descriptive notes and photographs, respectively, of the fluid body of the holotype (fig. 34); this description draws from these sources in addition to our notes on the paratype at PNGNM. Most of the general characteristics of *M. norahae* are those of *M. louiseae*, and many of these are not repeated in the description here. Despite this similarity, *M. norahae* seems to represent a second, well-marked species in the genus *Mirzamys*, sharply distinct morphologically from *M. louiseae* (e.g., fig. 33).

Mirzamys norahae is equivalent in overall size (cranially and externally) to *M. louiseae* (tables 8, 10). The tail, measuring 85%–87% of head-body length in the two available specimens, is relatively shorter than in most specimens of *M. louiseae* (in which the tail is usually subequal to the head and body), though falls within the range of variation recorded in that species (table 10). Judging from available measurements (table 8), the

holotype and paratype agree closely in external and cranial dimensions and proportions, though the paratype is a little smaller.

The dorsal pelage is soft, dense, and long, with the contour hairs measuring about 9 mm in length and fine guard hairs extending to 14 mm in length; the hairs are silvery gray with chestnut brown tips. The overall dorsal coloration can be characterized as dark chestnut (N. Cooper, in litt.), i.e., appearing reddish brown overall, in contrast to the dull, dark, brownish-gray fur of *M. louiseae*. Shorter fur of the same color extends over the nape, crown, forehead, and snout. The rhinarium and dorsal surfaces of the manus and pes are cream colored, and the muzzle bears a sparse cover of pale chestnut hairs. The pelage of the forearms and venter is slightly shorter and with duller gray hair bases than the dorsal fur. The eye is extremely small, and not highlighted by an eye ring. The ear is shorter than in *M. louiseae* (table 10), as indicated both by field measurements and direct examinations. The pinna, bearing short white hairs, is gray-brown on the distal one-third, inside and out, and white on the basal two-thirds. The tail is brown and thinly furred, with 14 scale rings per centimetre in the midsection. The surface of the tail features two silver hairs per tail scale, subequal in length to the scales.

The hindfoot is shorter in *M. norahae* than in *M. louiseae* (table 10). The palmar and plantar surfaces are smooth, cream colored, with distinct pads, the dorsal surfaces are lightly furred with chestnut hair. In the holotype the hindfoot measures 4.2 mm in breadth, narrower than in *M. louiseae* (5–7 mm).

The skull of *M. norahae* differs metrically from that of *M. louiseae* in its wider zygomatic breadth, more constricted inter-orbital region, slightly narrower braincase, shortened bony palate (not marked with a spine on the posterior margin), and slightly shorter but relatively broader first molars (table 8, fig. 28). The zygomatic arches are slightly thicker, more greatly expanded laterally at their squamosal roots, and more bowed in outline, appearing more greatly rounded and not so tapered (measuring 6% wider than the braincase breadth in the holotype of *M. norahae*, subequal to the braincase breadth in *M. louiseae*). Cusps t1

and t4 of the upper molars are larger than in *M. louiseae*, lending the molars a relatively broader appearance relative to their length. The nasals are slightly less procumbent, the hamular processes of the pterygoid region are heavier, the foramen ovale is smaller, and the auditory bullae are larger compared to *M. louiseae* (fig. 28). The upper incisors, though opisthodont, are projected backward from the premaxillae at a slightly lesser angle than in *M. louiseae*.

BIOLOGY: Like other New Guinea moss-mice, *Mirzamys norahae* is clearly terrestrial. The type series was apparently captured in Elliott traps (Jackson and Woolley, 1993). The paratype of *M. norahae* was apparently sent alive to the PNGNM, and later preserved in that museum collection after its death (P. Woolley, in litt., 2007). We observe that the brighter, more chestnut-colored fur of *M. norahae* is a possible indication of more diurnal habits relative both to *M. louiseae* and to the species of *Pseudohydromys*.

Jackson and Woolley (1993) reviewed the diets of selected New Guinea murids based on a study of intestinal contents and morphology. Their samples included one specimen of *M. norahae* (then identified as “*Pseudohydromys occidentalis*”) as well as series of *P. murinus*, *P. fuscus* and *P. ellermani* (taken at other localities). The single intestinal tract available for *M. norahae* contained spiders and various insects, including lepidopterans, but essentially no plant or fungal matter. In marked contrast, guts from *P. murinus* ($n = 24$), *P. fuscus* ($n = 7$), and *P. ellermani* ($n = 9$, but not all correctly identified; see account of *ellermani*, above) included substantial amounts of plant and fungal material; of these three species, the gut of *P. murinus* was found to contain the most insect content. Of the four species (including *M. norahae*), only *P. murinus* was found to consume earthworms; moths and butterflies comprised a much greater part of the diets of *M. norahae* and *P. fuscus* (in terms of relative gut surface area) than in other species. The extremely low ratio of total gut length to body mass in *M. norahae* (13.4, vs. 21.5 in *P. murinus*, 22.5 in *P. ellermani*, and 17.5 in *P. fuscus*) further suggests its obligate insectivory (Jackson and Woolley, 1993: 79).

Mirzamys norahae occurs sympatrically with at least two *Pseudohydromys* species; in the immediate vicinity of the type locality the first author collected a specimen of *P. ellermani* (2200 m at Lake Tawa, Helgen, 2007b) and a mandible of *P. fuscus* (at 3000 m at Waile Creek, see account above). This area, the Kaijende Highlands, remains little known biologically and is an important target area for future biodiversity surveys (Richards, 2007). Several mammal species that occur in high-altitude forests and grasslands in the Porgera area (Helgen, 2007b) are otherwise known only from Papua New Guinea's Central and Eastern highlands (e.g., *Rattus giluwensis*, *Protochromys fellowsi*, *Nyctophilus microdon*, and an undescribed species of the bandicoot genus *Microperoryctes*). Given the faunal resemblance between these two areas, it seems especially surprising that *M. norahae* has not turned up previously in hydromyine collections amassed either by Shaw-Mayer (Laurie, 1952), by Mirza, or by the collectors of the Archbold expedition efforts (Brass, 1964), from the comparatively well-explored Bismarck-Hagen-Gilwe region. This suggests that it is a naturally rare species and/or that it may be restricted to the Kaijende Highlands region.

Further study in the Porgera area may reveal that this species, like its congener *M. louiseae*, has a reasonably wide elevational range. Forests at and above the type locality of *norahae* (2650 m at Porgera) are mossy rainforest habitats that can be characterized as elfin or "upper montane forest" sensu Grubb and Stevens (1985) and Takeuchi (2007); above 2900–3000 m these forests give way to extensive *Cyathea*-dominated subalpine tussock grasslands (Takeuchi, 2007). In the Star Mountains, *Mirzamys louiseae* has been most commonly trapped in this forest-grassland ecotone, but it remains to be established whether its sole known congener, *M. norahae*, is likewise a typical inhabitant of these habitats in Enga Province.

CONCLUSION

Pseudohydromys is a diverse genus. Most montane-restricted New Guinea hydromyine genera are thought to be monotypic (*Para-*

hydromys, *Crossomys*) or show a minor tendency to speciate in geographically disjunct areas (e.g., *Baiyankamys*, with two species; *Paraleptomys*, with two named and two undescribed species; *Mirzamys*, with two species). *Pseudohydromys* is the only montane hydromyine genus that has diversified extensively both taxonomically and ecologically, such that as many as 12 species occur in the mountains of New Guinea, and up to four can occur in syntopy. Comparisons documented in this revision indicate that *Pseudohydromys* is the most diverse rodent genus in New Guinea, at least under current taxonomy (the genus *Paramelomys* Rümmler, 1936, which previously held this distinction, has nine recognized species; see Menzies, 1996; Musser and Carleton, 2005). However, we anticipate that *Paramelomys* and certain other widespread genera such as *Pogonomys* and *Rattus* will be recognized as equally or more diverse than *Pseudohydromys* pending a similarly comprehensive revision of available museum samples. As the documented distribution of the genus spans the breadth of the Central Cordillera and extends to several other outlying ranges, we suggest that species of *Pseudohydromys* are likely to occur in all montane areas in New Guinea. In the future, the number of *Pseudohydromys* species known could easily double with new discoveries stemming from targeted survey efforts in other poorly studied mountain ranges, such as the Vogelkop, Foja, Weyland, and other mountains, where *Pseudohydromys* has not been detected to date. The relatively recent discovery of *P. patriciae* in the Snow Mountains (first collected in 1988), *P. carlae* in the mountains of the Huon Peninsula (first collected in 1975), *P. germani* and *P. berniceae* in the Papuan Peninsula (first collected in 1992 and 2002, respectively), and *Microhydromys argenteus* over a relatively broad expanse of southeastern New Guinea (first collected in 1968) demonstrates that moss-mice are regularly overlooked even in areas that have received relatively intensive mammal-inventory efforts. Future discoveries of novel taxa of *Pseudohydromys* are anticipated.

Despite the outstanding array of dental morphologies within the genus, insight from albuminological comparisons (Watts and

Baverstock, 1994, 1995, 1996) suggests that the taxonomic and ecomorphological diversification of *Pseudohydromys* represents a relatively rapid adaptive radiation. For this reason, future study of the evolutionary biology of species of *Pseudohydromys* (particularly those that are more regularly trapped) could provide an illuminating natural context for exploring key topics in current biology, including, for example, signatures of directional selection acting on key phenotypic (especially molar) traits (cf. Albertson et al., 2003; Kingsolver et al., 2001; Renaud et al., 2006; Polly, 1998) or the nature of complex niche-partitioning among closely related sympatric congeners under varying habitats and circumstances (cf. Steele and Brammer, 2006; Summerville et al., 2006; Jones et al., 2001). Despite the enormous taxonomic and ecomorphological diversity of living rodents (especially Muroidea), we note that meristic, dimensional, and probably shape variability in the molar row are more extensive in *Pseudohydromys* than in any other rodent genus. Rodent models (especially *Mus musculus*) are the primary empirical avenue for studies of mammalian developmental dental biology and genetics (cf. Keranen et al., 1998; Line, 2003; Tucker and Sharpe, 2004; Kangas et al., 2004; Tucker et al., 2004; Ohazama and Sharpe, 2004; Plikus et al., 2005; Osmundsen et al., 2007; Pemberton et al., 2007; Fleischmannova et al., 2008; Caton and Tucker, 2009), and particular genes are known to simultaneously influence molar number, size, shape, and occlusal morphology in *Mus*. Genomic and developmental studies of hydromyins, particularly *Pseudohydromys* species if such research ever proves feasible, should offer key insights into the genetic control of molar development. New Guinea's moss-mice, a group of mammals regarded as highly obscure in the past, seem destined to provoke considerable biological interest into the future.

KEY TO THE SPECIES OF *PSEUDOHYDROMYS*

- 1a. One molar per quadrant; cranium relatively flat; postglenoid foramen not expanded. . . 2
- 1b. Two molars per quadrant; braincase higher domed; postglenoid foramen larger. 5

- 2a. Zygomata and rostrum proportionally narrower, molars less reduced ($LM1 \geq 0.8$ mm) 3
- 2b. Zygomata and rostrum proportionally stouter, molars more reduced ($LM1 \leq 0.7$ mm) . . . 4
- 3a. Molars smaller ($LM1 \leq 1.0$ mm); postorbital breadth narrower ($POB < 4.6$ mm); tail longer (averaging 106% of HB) *P. ellermani*
- 3b. Molars larger ($LM1 \geq 1.0$ mm); postorbital breadth broader ($POB > 4.6$ mm); tail shorter (averaging 93% of HB) . . . *P. carlae*
- 4a. Size larger (e.g., mass > 20 grams), ear dark gray; tail sparsely haired with short tail hairs (when viewed at magnification) . . . *P. germani*
- 4b. Size smaller (e.g., mass ~ 20 grams), ear pale gray; tail more heavily haired with longer tail hairs (when viewed at magnification) *P. pumehanae*
- 5a. Skull (and head) broader ($ZB > 11.1$ mm); maxillary molar row located well behind zygomatic plate; molars strongly narrowed ($BM1 \leq 1.0$ mm); postglenoid and middle lacerate foramina confluent 6
- 5b. Skull (and head) narrower ($ZB < 11.2$ mm); maxillary molar row located just behind zygomatic plate; molars less narrowed ($BM1 \geq 1.0$ mm); postglenoid and middle lacerate foramina not confluent 9
- 6a. Maxillary tooth row < 2.2 mm; upper incisors strongly proodont, with distinctly red enamel *P. fuscus*
- 6b. Maxillary tooth row > 2.2 mm; upper incisors strongly proodont, without distinctly red enamel 7
- 7a. Molars shorter ($LM1 < 2.0$ mm) and wider ($BM1 > 0.9$ mm); coloration gray above and below; pelage thick and long. *P. occidentalis*
- 7b. Molars longer ($LM1 > 2.0$ mm) and narrower ($BM1 \leq 0.9$ mm); color of venter markedly contrasting with color of dorsum; pelage short 8
- 8a. Zygomatic breadth very wide ($ZB > 13$ mm); brown above with cinnamon venter *P. musseri*
- 8b. Zygomatic breadth much less wide ($ZB < 12$ mm); brown above with white venter. *P. sandrae*
- 9a. Coloration dark blackish brown; teeth larger ($CLM > 12\%$ of condyloincisive length); tail averaging longer than head-body length . . . 10
- 9b. Coloration brownish gray; teeth smaller ($CLM < 12\%$ of condyloincisive length); tail averaging shorter than head-body length 11
- 10a. Size smaller ($ZB < 10.3$ mm); nasals shorter ($LN < 6.5$ mm) *P. berniceae*
- 10b. Size larger ($ZB > 10.3$ mm); nasals longer ($LN > 7.0$ mm) *P. murinus*

- 11a. Size larger (CIL > 24.5 mm); venter with white median markings; tail shorter (TV < 88% of HB) *P. patriciae*
 11b. Size smaller (CIL < 23 mm); venter without white median markings; tail longer (TV ≥ 88% of HB) *P. eleanorae*

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