Zootaxa 913: 1–20 (2005)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)
913

The amphibious murines of New Guinea (Rodentia, Muridae): the generic status of *Baiyankamys* and description of a new species of *Hydromys*

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Abstract

The amphibious murine rodents of New Guinea have traditionally been classified in three genera: *Hydromys* E. Geoffroy, 1804, *Parahydromys* Poche, 1906, and *Crossomys* Thomas, 1907. Species currently classified in *Hydromys* can be further divided into two cladistic groups: species distributed in lowland habitats (below 2000 m) with glossy, dark brown dorsal pelage, and species restricted to upper montane rivers and lakes (generally above 2000 m) with soft, silvery grey dorsal pelage. These two groups differ not only in pelage traits and habitat association but also in craniodental and phallic anatomy. The generic-level name *Baiyankamys* Hinton, 1943, is resurrected for the latter cluster (which includes two species, *B. shawmayeri* of eastern New Guinea and *B. habbema* of west-central New Guinea). Additionally, a new species of *Hydromys* (*H. ziegleri* n. sp.) is described from the southern foothills of the Prince Alexander Range of Papua New Guinea. Mammalian zoogeography in the North Coast Ranges, an area of considerable geographically-restricted mammalian endemism, is reviewed.

Key words: *Hydromys, Baiyankamys,* New Guinea, taxonomy, North Coast Ranges, amphibious rat

Introduction

The murine tribe Hydromyini comprises the amphibious “water-rats” and the terrestrial “moss-mice” of the Australo-Papuan region, a group of species currently classified in 10 genera (Ellerman 1941; Menzies and Dennis 1979; Flannery 1995), with greatest diversity in the mid-montane forests along the Central Dividing Ranges of New Guinea (Flannery 1995). In each of these genera the cranium is dorsally 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 or grossly reduced—a combination of charac-

Accepted by G. Veron: 1 Mar. 2005; published: 21 Mar. 2005

ters unique among Australo-Papuan rodents. Monophyly of the Hydromyini is arguably supported further by studies of phallic anatomy and sperm morphology (Lidicker 1968; Breed and Aplin 1995), though results of early genetic studies, such as those drawing from albumin immunology, do not so far support the monophyly of hydromyins as a group (e.g. Watts and Baverstock 1994). Comprehensive genetic comparisons, ideally based on sequence data from multiple nuclear genes, are needed to confirm the interrelationships of hydromyin genera in the broader context of Australian and New Guinean rodent diversification.

The rivers, lakes, and streams of the large tropical island of New Guinea support three highly-derived amphibious hydromyin genera—the murids *Parahydromys* Poche, 1906, *Crossomys* Thomas, 1907, and *Hydromys* E. Geoffroy, 1804. These three genera share a broadened muzzle, extremely long vibrissae, large, basin-shaped molars, and an enlarged hindfoot entirely or partially webbed between the toes, and are assumed to form a natural group, though rigorous cladistic assessments are still lacking (Musser and Carleton 2005). Two of these genera, *Crossomys* and *Parahydromys,* occur almost exclusively in and along (respectively) montane lakes, rivers, and streams (usually at and above 1200 m, though occasionally much lower for *Parahydromys*), but the genus *Hydromys* includes species adapted to life both in montane waterways and in lowland rivers and coastal habitats. *Parahydromys* is represented by a single species, *P. asper*—a dark brown, medium-sized rat with a greatly swollen muzzle and lips, and extremely large teeth. *Parahydromys* has a relatively wide range in montane New Guinea, including the entire breadth of the Central Dividing Ranges, the outlying North Coast Ranges (records are from the Torricelli and Cyclops ranges and the upper Mamberamo River) and the mountains of the Vogelkop Peninsula (Flannery 1995; Aplin *et al.* 1999). *Crossomys* is likewise monotypic, comprising the single species *C. moncktoni*. *Crossomys* is the most derived of New Guinean rodents, and the world’s most highly-specialized amphibious murid (Thomas 1907; Voss 1988; Peterhans and Patterson 1995). Its extremely large hindfeet are completely webbed to the ends of the toes between all digits, its forelimbs are strongly reduced relative to *Parahydromys* and *Hydromys*, its external ears are absent or reduced to very small nubs of skin in the fur, its eyes are extremely small, and its long tail bears a divided mid-ventral fringe of hairs along its underside (Ellerman 1941; Tate 1951a, 1951b; Voss 1988). (In each of these traits, it is convergent to remarkable extent upon the East Asian montane water-shrew *Nectogale*.) *Crossomys* is found only in montane lakes, rivers, and streams in the Central and Eastern Highlands regions of Papua New Guinea, where it is known to occur from the vicinity of Mt. Sisa (= Mt. Haliago) in the west to the Astrolabe Range in the east (Flannery 1995).

The zoogeography and biology of *Parahydromys* and *Crossomys* will be reviewed in a forthcoming account; the remainder of the present report concerns the taxonomy and zoogeography of amphibious murines currently classified in the third, more widespread genus *Hydromys*.

The generic limits of *Hydromys* E. Geoffroy, 1804

In 1941 George Tate and Richard Archbold of the American Museum of Natural History in New York reported the discovery of a small aquatic rodent from the vicinity of Lake Habbema, collected high in the mountains of western New Guinea by the 1938 Archbold Expedition, which they named *Hydromys habbema* (Tate and Archbold 1941). *Hydromys habbema* differed markedly in morphology from both species of *Hydromys* known at that time (*H. chrysogaster* from lowland New Guinea and Australia and *H. neobrittanicus* from the lowlands of the island of New Britain in the Bismarck Archipelago) in its relatively small size and greatly reduced pinnae; soft, woolly, grey pelage; and long, narrow rostrum.

Soon after, Martin Hinton of the British Museum (Natural History) of London (now the Natural History Museum, London) reported the discovery of another small amphibious rat from the mountains of eastern New Guinea, for which he erected the new genus and species *Baiyankamys shawmayeri* (Hinton 1943). This new taxon was extremely similar in external and cranial appearance to *Hydromys habbema*, but Hinton (1943) noted that it could be distinguished both by its unreduced pinnae and by its mandibular dentition, which included three lower molars in both quadrants of the lower jaw, as opposed to two in all other amphibious murines of New Guinea. However, Mahoney (1968) later realized that the holotype of *B. shawmayeri* was a composite specimen, consisting of the skull and cranium of a small water-rat and an incorrectly-associated mandible from a specimen of *Rattus niobe*. Mahoney (1968) chose the skin and cranium of the "holotype" as the lectotype of *Baiyankamys shawmayeri*, thereby restricting this name to the water-rat (rather than the misallocated *Rattus* mandible), and found the correct mandible for this specimen within the BMNH collections, likewise mismatched with the cranium of a specimen of *Rattus niobe*. On the basis of its overall similarity to *H. habbema* of western New Guinea, Mahoney (1968) proposed that *shawmayeri* should be recognized as a synonym of that species, but Musser and Carleton (1993, 2005) and Flannery (1995) have since argued that *H. habbema* and *H. shawmayeri* are best recognized as closely-related but distinct allopatric species. Indeed, the two are easily distinguished by external and cranial traits (a point reviewed in further detail below).

More recently, Musser and Piik (1982) described another species of small-bodied *Hydromys* (*H. hussoni*) from the Wissel (= Paniai) Lakes of western New Guinea (1750–1765 m) based on a large series of specimens collected during the 1939 New Guinea Expedition of the Royal Netherlands Geographic Society. Notably, in its brown, glossy pelage and overall cranial conformation *Hydromys hussoni* closely resembles both larger-bodied *Hydromys* species known from habitats in lowland Melanesia (*H. chrysogaster* and *H. neobrittanicus*), rather than the other small-bodied montane species of the genus (*H. habbema* and *H. shawmayeri*) (Musser and Piik 1982; Musser and Carleton 2005). Ziegler (1984) subsequently reported the collection of a single small-bodied water-rat specimen from the southern margins of the Prince Alexander Range in northern Papua New Guinea, which he tentatively identified as *H. hussoni*. This locality is far disjunct from (800 km distant) and situated at a much lower elevation (about 200 m) than the type and otherwise only known locality for *H. hussoni* (Figure 1). In fact, Ziegler's (1984) specimen is morphologically unique and represents a previously-undescribed species (*H. ziegleri* n. sp.; see below), similar to but distinct from *H. hussoni*—a taxonomic conclusion anticipated by Musser and Carleton (2005).

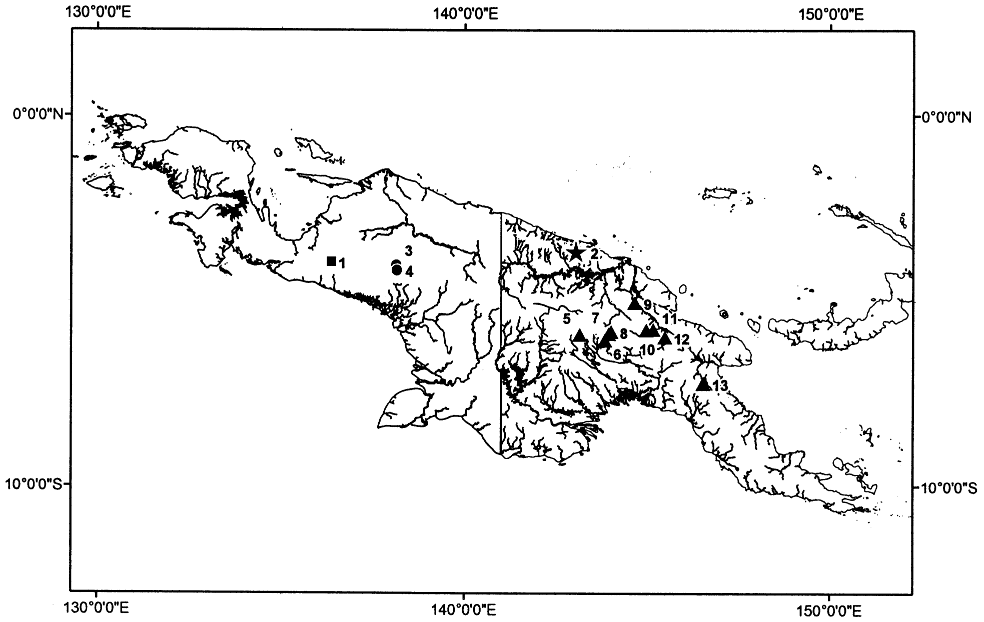

FIGURE 1. Distribution of the smaller-bodied species of *Hydromys* (*H. hussoni*, locality 1; *H. ziegleri*, 2) and the species of *Baiyankamys* (*B. habbema*, localities 3–4; *B. shawmayeri*, 5–13) in New Guinea.

This brief review of the content of *Hydromys* emphasizes that the genus, as currently defined, embraces two highly distinctive groups: a moderately diverse cluster of brownish, glossy-furred species found in coastal, lowland, and lower montane contexts (below 2000 m) throughout Australasia (*chrysogaster, neobrittanicus, hussoni, ziegleri* n.sp., and an undescribed insular species from Obi; see below), and a small group of grey, soft-furred species restricted to lakes, rivers, and streams in montane forests (generally at 2000 m and above, but occasionally to 1500 m; Table 1) in the Central Dividing Ranges of New Guinea (*habbema, shawmayeri*). These two groups differ not only in habitat association and pelage coloration and texture, but also in other anatomical aspects, and together may not form a natural (i.e. monophyletic) assemblage. For example, in studies that included *Hydromys chrysogaster, H. habbema, Parahydromys asper,* and *Crossomys moncktoni*, Lidicker (1968, 1973) found that *H. habbema* differs trenchantly in aspects of phallic anatomy not only from *H. chrysogaster,* but also from *Parahydromys, Crossomys,* and all other hydromyin rodents studied.

TABLE 1. Geographic and elevational distribution of the small species of *Hydromys* and the species of *Baiyankamys* (numbers refer to Fig. 1), with a list of specimens examined.

Hydromys hussoni Musser and Piik, 1982

1. Enarotali, Lake Paniai, and Araboe-bivak, Araboe River (03°55’40”S, 136°22’06”E), Wissel (= Paniai) Lakes area, 1750–1765 m, Papua Province, Indonesia (series at RMNH: see Musser and Piik 1982)

Hydromys ziegleri new species

2. Bainyik (03°40’S, 143°05’E), 700 ft (= 213 m), East Sepik Province, Papua New Guinea (BBM-NG 101683).

Baiyankamys habbema (Tate and Archbold, 1941)

3. Kelangurr Cave (04°01’S, 138°08’E) and adjacent West Baliem River, 2800–2950 m, Papua Province, Indonesia (see Flannery 1999: 342, 343; Flannery 1995: 238).
4. Lake Habbema (04°09’S, 138°41’E), 3225 m, and 7 km NE of the top of Mt. Wilhelmina (= Trikora) (04°15’S, 138^{o}45’E), 3560–3600 m, Papua Province, Indonesia (series at AMNH: see Tate 1951b; Musser and Piik 1982: 155).

Baiyankamys shawmayeri Hinton, 1943

5. Doma Peaks (05°54’S, 143°09.5’E), 2400 m, Southern Highlands Province, Papua New Guinea (BBM-NG 105734).
6. Mt. Giluwe (06°03’S, 143°53’E), 2800 m, Southern Highlands Province, Papua New Guinea (BBM-NG 97086, 97104, 97173, 97192).
7. Murmur Pass (05°45’S, 143°56’E), 2700 m (PNGM 22819, BBM-NG 97427); 18 km NNE Tambul, 5 km junction Mendi and Hagen Road, 2700 m (BBM-NG 97502, 97532), Western Highlands Province, Papua New Guinea.
8. Mt. Hagen (05°35’S, 144°04’E), 5000 – 8000 ft [1524 – 2438 m] (AMNH 156431 – 156433); Tomba (05°50’S, 144°02’E), south spur of Hagen Range, 8000 ft [= 2438 m] (BMNH 55.309), Western Highlands Province, Papua New Guinea.
9. Aunjang Valley (05°02’S, 144°40’E), Schrader Range, Madang Province, Papua New Guinea (AM M8661).
10. Mt. Wilhelm (05°46’S, 144°59’E): Pengagl Creek, 8500 ft [= 2591 m] (AMNH 191441 – 191444); Lake Aunde, 11800 ft [= 3597 m] (CSIRO 15691), Western Highlands Province, Papua New Guinea.
11. Baiyanka (05°46’S, 145°10’E), Purari-Ramu Divide, SE Bismarck Range, 6500 ft [= 1980 m], Eastern Highlands Province, Papua New Guinea (BMNH 1947.1143).
12. Collins’s Sawmill, Mt. Otto (05°59’S, 145°25’E), 2215–2275 m, Eastern Highlands Province, Papua New Guinea (AMNH 191445–191448).
13. Slate Creek (07°13’S, 146°33’E), 1 mile W Mt. Kaindi, 2000 m, Morobe Province, Papua New Guinea (AMNH 191440).

Despite its confused introduction, Hinton’s (1943) generic name *Baiyankamys* remains available (see Mahoney 1968), and here I utilize it at generic level for *shawmayeri* Hinton, 1943 and *habbema* (Tate and Archbold, 1941), formally removing these two species from

Hydromys. In addition to differences in phallic anatomy (Lidicker 1968, 1973), species of *Baiyankamys* differ from species of *Hydromys* in many external and craniodental traits. For example, the two species of *Baiyankamys* have tails much longer than their head-body length (tail sub-equal to or shorter than the head-body length in *Hydromys*), soft, dense, frosted grey upperparts (dorsal pelage more glossy, less dense, and dark brown to blackish in *Hydromys*), long, narrow rostra that taper strongly antero-laterally (broader, more parallel-sided rostra in *Hydromys*), extremely narrow incisors (relatively broader in *Hydromys*), very strong indentations between the masseteric tubercles on either side of the anterior palate (lacking or much less pronounced in *Hydromys*), mesopterygoid fossae proportionately much narrowed, measuring much less across than the width between the first upper molars (less reduced, sub-equal to this molar distance in *Hydromys*), and zygomata that are slender and delicate, especially along the posterior third, with the maxillary roots situated much higher than the squamosal roots, giving them a well-pronounced downcurve (thicker, less downcurved zygomata in *Hydromys*). Interestingly, all of these traits are shared by both *Baiyankamys* and *Crossomys* (Figure 2), which may suggest either a sister relationship between these two genera (i.e. if these character states are synapomorphic), or a basal divergence for both genera among New Guinean amphibious rats (if symplesiomorphic). Notably, the pinnae of one of the two species of *Baiyankamys* (*B. habbema*) are strongly reduced, a distinctive trait otherwise seen among New Guinea rodents only in *Crossomys moncktoni* (Thomas 1907; Tate 1951a). The species of *Hydromys* and *Parahydromys,* on the other hand, more closely resemble one another in most of these traits, including the quality and overall colour of their dorsal pelage as well as their broader rostra, less strongly emarginated anterior palates, proportionately wider mesopterygoid fossae, and robust, less down-curved zygomata (Figure 2). Voss (1988: 466–468) previously discussed a number of other size-independent shape differences that distinguish *Baiyankamys habbema* (and *shawmayeri*) from true *Hydromys*, including relatively larger hindfeet, larger molars, a broader palate, a narrower zygomatic plate, a more inflated braincase, and a broader occiput.

In summary, selected morphological traits of the skin and cranium phenetically link *Crossomys* and *Baiyankamys* on one hand, and *Hydromys* and *Parahydromys* on the other. Though phylogenetic relationships among these genera remain formally untested, it is now clear that the species of *Baiyankamys* (*B. shawmayeri* and *B. habbema*) comprise a morphological unit distinct from a monophyletic cluster of species that can be classified in *Hydromys sensu stricto* (*H. chrysogaster, H. neobrittanicus, H. hussoni,* and *H. ziegleri*). Hence I suggest that *Hydromys* and *Baiyankamys* are more usefully and more appropriately recognized as separate genera—a hypothesis that should be tested in the future by a careful phylogenetic analysis ideally incorporating both morphological and molecular information.

FIGURE 2. Skulls of the four amphibious murine rodent genera of New Guinea. From top to bottom: *Parahydromys asper, Hydromys hussoni, Baiyankamys shawmayeri,* and *Crossomys moncktoni*. Adapted from Flannery (1995:525–526).

The species of *Baiyankamys* Hinton, 1943

Until relatively recently (Musser and Carleton, 1993; Flannery, 1995), *Baiyankamys habbema* and *B. shawmayeri* were considered conspecific (e.g. Mahoney 1968; Flannery 1990). Though now recognized as separate, geographically disjunct species (Musser and Carleton 1993, 2005), morphological distinctions between the two have not been firmly substantiated in the literature. (Musser and Carleton [2005] noted apparent differences in body size and "certain cranial proportions"; Flannery [1995] suggested differences in ventral coloration, length of the terminal white tail-tip, and a possible difference in ear length.) Having recently examined all available museum specimens of both species (Tables 1, 2), here I can confirm that while *habbema* and *shawmayeri* are craniodentally similar, they differ consistently in degree of reduction of the external ear (length 7–9 in *habbema*, 12–17 in *shawmayeri*), extent of the terminal white tail-tip (one-third to one-half of the tail in *habbema*, one-quarter or less of the tail in *shawmayeri*), in ventral coloration (dark silvery grey in *habbema*, paler slate grey in *shawmayeri*), and in size of the teeth (length of maxillary molar row generally > 5.0 in *habbema*, generally < 5.0 in *shawmayeri*). Further, *B. shawmayeri* averages smaller in most measurements, including overall length (Table 2), as intimated by Musser and Carleton (1993, 2005).

Baiyankamys habbema is currently known only from upper montane forests (2800 to 3600 m) in a relatively small geographic area situated on the southern slopes of the Snow Mountains of western New Guinea (Figure 1); *Baiyankamys shawmayeri* has a wider geographic and elevational range, being recorded from lower to upper montane forests (1500 to 3600 m, a broader altitudinal distribution than previously reported) throughout the Eastern and Central Highlands regions of Papua New Guinea, from the Doma Peaks area in the west to the vicinity of Mt. Kaindi in the east (Figure 1). (A further locality in south-eastern New Guinea mapped for this species by Flannery [1995:240] is based on an editorial error.) The mean elevation of four vouchered sites of occurrence of *B. habbema* is 3334 m (median 3393 m; SD = 306); the mean elevation of 12 vouchered sites of occurrence of *B. shawmayeri* is 2438 m (median 2492 m; SD = 516) (Table 1). Both species are recorded from streams, rivers, and lakes, and both apparently live in waterside burrows and feed on aquatic invertebrates (especially insect nymphs and larvae, but also leeches and earthworms), and small vertebrates, especially frogs (Menzies and Dennis 1979: 53; Voss 1988: 456).

No intervening populations of *Baiyankamys* are known between the geographic ranges of these two species (Fig. 1), despite the fact that two geographically-intermediate montane areas—the vicinity of Mt. Sisa in the Kikori River Basin, and the Telefomin area in the mountains of southern West Sepik (= Sandaun) Province—are among the most comprehensively studied sites for mammals in all of New Guinea (e.g. Flannery and Seri 1990a; Leary and Seri 1997). Hence the absence of *Baiyankamys* from the middle part of the New Guinean Central Cordillera may well be real, rather than an artefact of incomplete sampling efforts. A similar "drop-out" effect along the Cordillera is well-established for many avian taxa (Diamond, 1972).

TABLE 2. External metrics for the species of *Baiyankamys*. Measurements are for fully mature specimens only. For *B. habbema* n = 14 (7 males and 7 females, specimens at AMNH; see Voss, 1988); for *B. shawmayeri* n = 20 (13 males and 7 females, specimens at AMNH, BBM, BMNH, CSIRO; n = 10 for weight).

	B. habbema	***B. shawmayeri***
Length of head and body	148.6 ± 8.1 (134–160)	141.9 ± 7.0 (130–153)
Length of tail	172.3 ± 12.5 (154–187)	168.6 ± 8.8 (148–185)
Length of hindfoot	37.0 ± 1.2 (35–39)	37.5 ± 1.3 (35–39)
Length of ear	8.6 ± 0.60 (7–9)	13.8 ± 1.31 (12–17)
Weight (in grams)	—	78.4 ± 7.41 (68–88)

Methods and Materials

Specimens discussed here are deposited in the collections of the Australian Museum, Sydney (AM), the American Museum of Natural History, New York (AMNH), the Bernice P. Bishop Museum, Honolulu (BBM), the Natural History Museum, London (BMNH), the Australian National Wildlife Collection, Canberra (CSIRO), the Papua New Guinea National Museum and Art Gallery, Port Moresby (PNGM), and the Nationaal Museum van Natuurlijke Historie (formerly Rijksmuseum van Natuurlijke Historie), Leiden (RMNH). External measurements were recorded by the original collectors in the field. Craniodental measurements, except as noted, were taken by the author with hand-held callipers. Cranial measurements (Table 3), though largely self-explanatory, follow the definitions of Musser and Piik (1982) and Voss (1988). Linear measurements are in millimetres (mm), weights in grams.

A new species of *Hydromys*

Genus *Hydromys* E. Geoffroy, 1804

Type species: *Hydromys chrysogaster* E. Geoffroy, 1804.

Content: With the exclusion of *Baiyankamys*, I recognize four described species of *Hydromys* as valid: *H. chrysogaster*, with synonyms as delineated by Tate (1951b) and Musser and Carleton (2005), widely distributed in river systems and coastal areas of Tasmania, Australia, and many adjacent islands on the continental shelf, and in the lowlands of New Guinea (to 2000 m) and on immediately adjacent islands (Yapen, Biak-Supiori, Waigeo, the Aru and Kai Islands, and the D’Entrecasteaux and Trobriand Islands); *H. neo-*

brittanicus Tate and Archbold, 1935, a distinctive, large-bodied insular endemic from the large island of New Britain in the Bismarck Archipelago; *H. hussoni* Musser and Piik, 1982, known only from the Wissel Lakes of western New Guinea; and *H. ziegleri* n. sp., from foothills on the southern margins of the Prince Alexander Range in northern Papua New Guinea. There is one additional undescribed species, endemic to the island of Obi in the North-Central Moluccas (Helgen 2003; Musser and Carleton 2005).

Hydromys ziegleri **new species**

Figures 3, 4; Tables 3, 4

Holotype: BBM-NG 101683, adult female, skin (Fig. 3) and skull (Fig. 4), from Bainyik (03°40'S, 143°05'E), *circa* 5 km south of Maprik, 700 ft (= 213 m), East Sepik Province, Papua New Guinea, collected 29 October 1972 by A.B. Mirza. According to its label the holotype—the only known specimen of this species—was live-trapped in a local garden (see Ziegler 1984: 101).

Diagnosis: *Hydromys ziegleri* is the smallest species of *Hydromys*. It most closely resembles *H. hussoni*, endemic to the upland Wissel Lakes of west-central New Guinea (Figs. 3–4; Table 3–4), but differs from that species in its smaller size, broadened rostrum, shorter incisive foramina, shorter toothrow, broader first molars, lower-domed braincase, and much less densely-furred tail.

Distribution: *Hydromys ziegleri* is known only from the type locality, situated in the foothills of the southern slopes of the Prince Alexander Range, one of the North Coast Ranges of Papua New Guinea. The type locality lies in the vicinity of the Screw and Amuk Rivers, which drain from the highlands of the Prince Alexander Range and the Torricelli Range, respectively. I suspect that future collecting efforts may show it to occur more widely (and at higher altitudes) in the North Coast Ranges (see Discussion below). Two other amphibious murines (*Hydromys chrysogaster* and *Parahydromys asper*) are known from other localities in the North Coast Ranges and are thus likely to occur sympatrically with *H. ziegleri*, though only *H. chrysogaster* has been collected in the same general area to date (e.g. CSIRO 8346, adult male from Maprik).

Etymology: For the late Dr. Alan C. Ziegler (1929-2003), former head of the Vertebrate Zoology Division at the Bishop Museum in Honolulu and authority on New Guinea mammals.

Description: The holotype of *ziegleri* is smaller than most specimens of *hussoni* (Figs. 3–4; Table 3). The dorsal pelage of *ziegleri* is dark brown (somewhat darker than the rich brown of *hussoni*) tipped with paler, orange-buff hairs. The fur is considerably shorter (6–7 mm on the anterior dorsum), less dense, and conspicuously more glossy than in *hussoni*. The fur of the venter is grey-based with ochraceous-buff tipping, similar to *hussoni* (Musser and Piik 1982; Ziegler 1984), but in the holotype of *ziegleri* the lower cheeks and the underside of the throat and chin are dingy white, contrasting with the rest of the venter.

The inguinal region and ventral base of the tail are dark brown (Figure 3). As in other *Hydromys,* the hindfeet are long and broad and bear conspicuous webbing between the middle digits (II–IV). The dorsal surface of the pes is pigmented dark but covered with small pale hairs, and the claws are equal in size to those of *hussoni*, and unpigmented. The skin label gives the hindfoot length as 29, probably measured with the claw, as on the dry skin this length is closer to 27 *sans unguis* (Ziegler 1984).

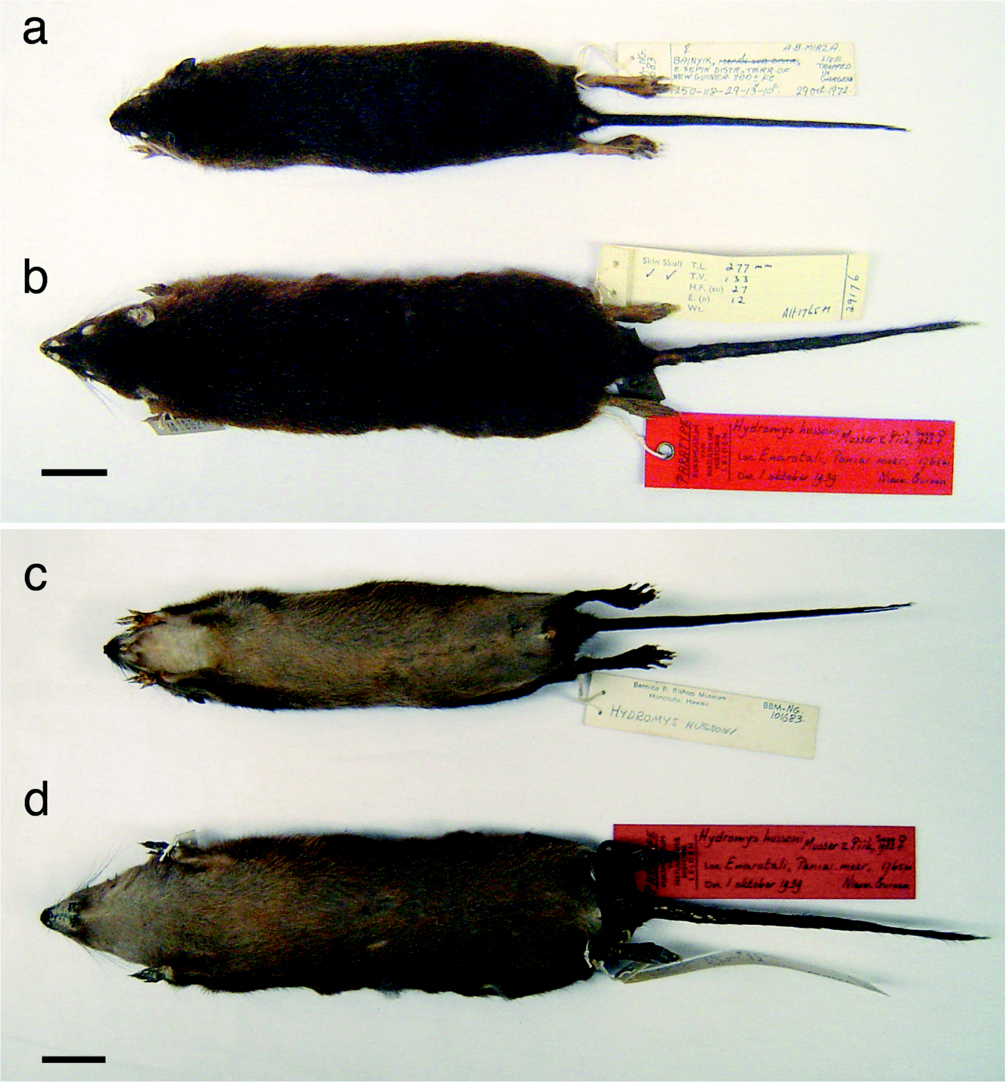

FIGURE 3. Dorsal and ventral views of the skins of *Hydromys ziegleri* (a, c; BBM-NG 101683, adult female holotype) and *Hydromys hussoni* (b, d; AM M18627; adult female paratype). Scale bar = 20 mm.

The tail of the holotype is black, and lacks a white tail-tip, which is present in 19 of 24 known specimens of *hussoni,* and always present in *Hydromys chrysogaster, Baiyankamys,* and *Parahydromys* (absent in *Crossomys*). There are 13–15 tail rings per centimetre in the mid-section of the tail. Probably the most conspicuous external difference between *ziegleri* and *hussoni* is the relative hairiness of the tail. In other *Hydromys*, including *hussoni*, the tail is extensively haired, obscuring the tail rings, and the tail hairs are long, extending for the length of many tail scales. In *ziegleri* the tail is considerably less heavily furred, lending it a much more “naked” appearance, such that the tail rings are immediately evident to the naked eye. The tail hairs measure only about 2–3 tail rings in length and lie close to the body of the tail.

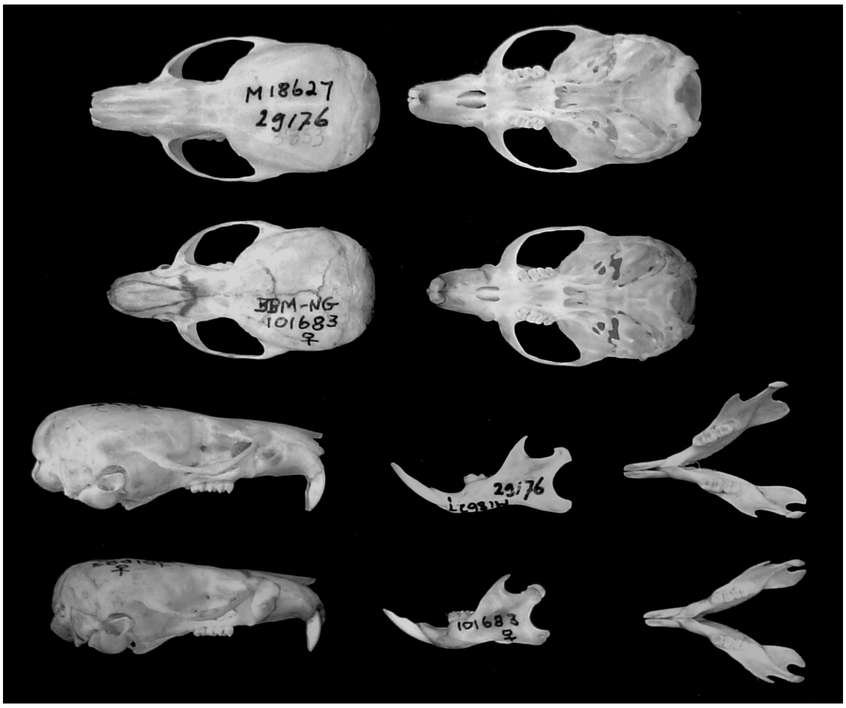

FIGURE 4. Crania and mandibles of *Hydromys ziegleri* (below, adult female holotype) and *Hydromys hussoni* (above, AM M18627, adult female paratype).

In many ways the cranial resemblance between *hussoni* and *ziegleri* is close (Ziegler 1984). However, judging from direct comparisons between the holotype of *ziegleri* and a paratype *of hussoni* (AM M18627, formerly RMNH 29162, also adult female), my notes on the type series of *hussoni* at RMNH, comparisons with the verbal and mensural descriptions of *hussoni* by Musser and Piik (1982) and Voss (1988), and illustrations of the holotype of *hussoni* figured by Musser and Piik (1982), many qualitative cranial differences between the two species are immediately apparent. The skull of *ziegleri* is noticeably shorter and stouter than that of *hussoni* (Fig. 4). The rostrum is short and broad in both species, but the nasolacrimal capsules are laterally expanded to a much greater degree in *ziegleri*, as reflected in its relatively greater rostral breadth, and the nasals are correspondingly broader (Table 3) and also more strongly retracted. The incisive foramina are more truncate in *ziegleri*, only 31% of the length of the diastema, versus 37% (in *hussoni*) or greater in all other species of *Hydromys* and *Baiyankamys* (Musser and Piik 1982: 164). The zygomatic plate is more excavated in *ziegleri* than *hussoni*, and the braincase is markedly less expanded dorso-ventrally (Table 3; braincase height is 64% of braincase breadth in *ziegleri*, versus 69% or greater in all other *Hydromys* and *Baiyankamys*; Musser and Piik 1982:164).

TABLE 3. Craniodental metrics for the adult female holotype of *Hydromys ziegleri* and for series of adult female and mixed adult *Hydromys hussoni*.

Measurements	***H. ziegleri***	***H. hussoni* ♀♀ [1]** n = 6-9	***H. hussoni* ♀♀, ♂♂ [2]** n = 20
Length of head and body	132	150.1 ± 9.4 (138-164)	147.9 ± 15.4 (122-171)
Length of tail	118	125.5 ± 14.3 (103-144)	126.4 ± 13.8 (103-152)
Length of hindfoot	29	27.4 ± 1.1 (26-29)	29.8 ± 2.0 (27-33)
Length of ear	13	12.4 ± 0.8 (12-14)	12.1 ± 0.8 (11-14)
Greatest length of skull	29.01	31.54 ± 0.87 (30.1-32.8)	—
Condyloincisive length	28.50	—	30.5 ± 1.41 (27.9-32.9)
Zygomatic breadth	14.98	15.60 ± 0.50 (14.8-16.3)	15.5 ± 0.87 (14.0-17.3)
Breadth of rostrum	6.23	5.82 ± 0.21 (5.6 - 6.1)	—
Length of nasals	8.73	10.17 ± 0.43 (9.4-10.6)	9.8 ± 0.68 (8.6-11.2)
Breadth of nasals	3.39	—	3.10 ± 0.18 (2.8-3.4)
Length incisive foramina	2.48	3.08 ± 0.13 (2.9-3.3)	3.0 ± 0.33 (2.0-3.3)
Maxillary toothrow	4.13	4.71 ± 0.15 (4.5-5.0)	4.6 ± 0.12 (4.4-4.8)
Breadth of braincase	13.09	13.44 ± 0.28 (13.1-13.8)	13.7 ± 0.36 (13.0-14.4)
Height of braincase	8.39	9.21 ± 0.19 (8.9-9.5)	—
Postorbital constriction	5.09	5.28 ± 0.14 (5.1-5.5)	5.3 ± 0.14 (5.0-5.6)
Breadth of incisor tips	1.62	1.67 ± 0.13 (1.5-1.9)	1.6 ± 0.15 (1.4-1.9)
Length of diastema	7.99	8.39 ± 0.36 (7.9-9.0)	8.5 ± 0.54 (7.6-9.3)

[1] From Musser and Piik (1982: 159).

[2] From Voss (1988: 467): 12♀♀ and 8♂♂.

The faces of the upper and lower incisors are pigmented yellowish-orange in *ziegleri* (with pigmentation more obvious in the upper incisors), while those of *hussoni* are very weakly pigmented or almost unpigmented. In *ziegleri* the first upper molars are broader relative to their length compared to *hussoni*, and the second upper and lower molars are more reduced (e.g. Table 4). The posterior palatine foramina are lengthened into a more extensive narrow groove in the *hussoni* paratype than in the holotype of *ziegleri*, in which these foramina are essentially small ovate holes. The posterior palatal spine is extremely well-developed. Relative to *hussoni* the auditory bullae are less flattened and less elongate. The foramen ovale is distinctly larger in *ziegleri* than *hussoni*. In both species the stapedial foramen is well-developed and the foramen ovale bears a conspicuous groove for the passage of the infraorbital branch of the stapedial artery, suggesting that both possess the primitive murine cephalic arterial configuration typical of other New Guinean water-rats of the genera *Baiyankamys*, *Hydromys*, *Parahydromys*, and *Crossomys* (and the less closely-related lowland false water-rat, *Xeromys myoides*, as stated by Musser and Carleton [2005] and confirmed by my examination of specimens in the Australian Museum; cf. Musser and Heaney 1992:87).

Additional measurements of the holotype (other than those presented in Table 3) include: palatal length 13.08; breadth of mesopterygoid fossa 2.13; greatest breadth of incisive foramina 1.67; breadth of the palatal bridge between M^2–M^2 2.60; breadth of the zygomatic plate 1.54; height of upper incisor 4.58; depth of upper incisor 1.55; breadth across occipital condyles 8.37; coronoid height of mandible 7.99; alveolar length of $M_{1–2}$ 4.35; and mandible length minus incisor 14.85 (with incisor, 18.38).

TABLE 4. Comparative molar dimensions in specimens of *Hydromys ziegleri* (adult female holotype) and *Hydromys hussoni* (AM M18627, adult female paratype).

	ziegleri	***hussoni***
M^1 length x width	2.98 x 1.54	3.24 x 1.49
M^2 length x width	1.22 x 1.07	1.52 x 1.34
M^2 length / M^1 length	0.41	0.47
M^1 width / M^1 length	0.52	0.46
M_1 length x width	2.59 x 1.28	2.84 x 1.59
M_2 length x width	1.67 x 1.18	1.81 x 1.34

Zoogeography

Several isolated mountain ranges are situated along the northern coast of New Guinea, including the Adelbert, Prince Alexander, Torricelli, Bewani, Cyclops, Foya (= Gauttier), and Van Rees Mountains, collectively referred to hereafter as the North Coast Ranges. These mountain ranges are well-separated from the Central Dividing Ranges of New Guinea by large expanses of lowland forest, have distinctive geological histories (Flannery 1995), and support highly distinctive faunas.

TABLE 5. North Coast endemic mammal species recorded from the various North Coast Ranges of northern New Guinea. PA = Prince Alexander Range; T = Torricelli Range; B = Bewani Range (including Mt. Menawa); C = Cyclops Range; F = Foya Range.

	PA	T	B	C	F	Recorded elevation
Monotremes						
Zaglossus attenboroughi Flannery & Groves, 1998				x		1600 m
Marsupials						
Dendrolagus pulcherrimus Flannery, 1993	?	x			?	680 to 1120 m
Dendrolagus scottae Flannery & Seri, 1990		x	x			900 to 2000 m
Petaurus abidi Ziegler, 1981		x				800 to 1220 m
Rodents						
Hydromys ziegleri n. sp.	x					213 m
'Microhydromys' musseri Flannery, 1989		x				1350 m
Paraleptomys rufilatus Osgood, 1945		x	x	x		1200 to 1700 m
Bats						
Hipposideros edwardshilli Flannery & Colgan, 1993			x			240 m

Many endemic mammals occur in these mountain ranges (Table 5). A recently-described monotreme, the dwarf long-beaked echidna (*Zaglossus attenboroughi*), is known only by a single specimen collected in 1961 in upper montane forest (1600 m) on Mt. Rara in the Cyclops Range, behind Jayapura (Flannery and Groves, 1998). The tree-kangaroo *Dendrolagus scottae* (the "tenkile") is known from the western Torricelli Range and Mt. Menawa in the Bewanis, where it is primarily restricted to narrow bands of montane forest situated at about 1200–1500 m in the Torricellis and about 1500–2000 m on Mt. Menawa (Flannery and Seri 1990b; Flannery *et al.* 1996). Another tree kangaroo, *Dendrolagus pulcherrimus*, is recorded as a living animal from the eastern Torricellis and (on the basis of a sight record) from the Foya Range (Flannery 1993; Flannery *et al.* 1996), and is rumoured to occur in the Prince Alexander Range. The latter species (originally described as a subspecies of *D. goodfellowi* by Flannery 1993) has disappeared from much of its former range in the Torricellis in recent decades, probably as a result of unsustainable hunting practices (Flannery *et al.* 1996). In the past, *D. pulcherrimus* probably had a much more extensive distribution, as it or a very closely-related taxon is also represented in Quaternary subfossil deposits from the Vogelkop Peninsula of north-west New Guinea (Aplin *et al.* 1999). A third marsupial found only in the North Coast Ranges is the Northern glider (*Petaurus abidi*), recorded only from mid- and upper montane forest in the vicinity of Mts. Somoro and Sapau in the Torricelli Range (Ziegler 1981; Flannery 1995).

Among murine rodents, three endemic hydromyins are known from the North Coast Ranges. These are *Paraleptomys rufilatus,* a medium-sized terrestrial rat which occurs in mountaintop forests in the Cyclops, Bewani, and Torricelli Ranges (Osgood 1945; Flannery 1995; Musser and Carleton 2005); '*Microhydromys' musseri*, a small moss-mouse of uncertain phylogenetic affinity, known by a single specimen collected in 1972 in upper montane forest (1350 m) on Mt. Somoro in the Torricellis (Flannery 1989; Musser and Carleton, 2005); and now *Hydromys ziegleri*, known by a single specimen collected on the southern margin of the Prince Alexander Range. Finally, one species and one distinctive subspecies of leaf-nosed bat (*Hipposideros edwardshilli* and *Hipposideros wollastoni fasensis*) are known only from the northern and southern foothills of the Bewani range, respectively (Flannery and Colgan 1993).

During cooler climatic periods during the Late Pleistocene, montane forests extended to much lower elevations in New Guinea than they do today, and the montane-adapted species of the North Coast Ranges likely had considerably more expansive or even contiguous distributions across certain of these mountain ranges. I suspect that the seemingly haphazard distribution of endemic species recorded from the various North Coast ranges today (Table 5) reflects a combination of two factors: artefacts of geographically uneven sampling effort and, at least for some of the larger-bodied species (*Zaglossus, Dendrolagus*), historical extinctions (see Flannery *et al.* 1996; Flannery and Groves 1998).

Some of the larger endemic mammals of the North Coast Ranges, especially *Zaglossus attenboroughi*, *Dendrolagus scottae*, and *Dendrolagus pulcherrimus*, have minuscule global geographic ranges and are actively hunted for food (Flannery *et al.* 1996; Flannery and Groves 1998), and are probably among the most endangered of all Australasian mammals (indeed, *Z. attenboroughi* may already be extinct; Flannery and Groves 1998). All North Coast Range endemic mammals, even the smallest (such as '*Microhydromys' musseri* and *Hydromys ziegleri*), should be considered conservation priorities on account of their extremely limited geographic and altitudinal ranges, which in most cases are centred on small tracts of upper montane forest, highly susceptible to threatening processes including logging and climate change. In addition to supporting a markedly unique mammal fauna, the North Coast Ranges are also an area of considerable geographically-restricted endemism for frogs, birds, and other biotic groups (Stattersfield *et al.* 1998; Kraus and Allison

2000; Allison and Kraus 2000, 2003), ranking these mountain ranges among the most critical priorities for conservation efforts in the Melanesian region (Wikramanayake *et al.* 2002).

Of the eight endemic mammal species currently known from the North Coast Ranges, seven were described as new to science only within the last 15 years, and all eight were both discovered and described within the last 60 years (Table 5). Further, three of these remain known by a single museum specimen (*Zaglossus attenboroughi, 'Microhydromys' musseri,* and *Hydromys ziegleri*). These cursory but remarkable statistics for North Coast Range mammals aptly demonstrate how incompletely catalogued the biota of these mountains remains. While the mammal faunas of some areas in the North Coast Ranges (including the western Torricellis, Cyclops, and Bewanis) have become much better understood through recent survey efforts (e.g. Flannery 1993, 1995), others, such as the Foya and Van Rees Ranges of western New Guinea, remain almost wholly unknown mammalogically. For example, until recently the ornithologist Jared Diamond was the only westerner known to have visited the relatively expansive Foya Range, which is mostly uninhabited and largely unexplored (see Diamond 1985). Given the startling rate of new discoveries in North Coast mountain ranges in recent decades, there is no doubt that future survey efforts in this region will continue to encounter vertebrate species new to science.

The mammal fauna of the Prince Alexander Mountains is moderately well-known. Apart from *Hydromys ziegleri*, at least 23 other species are recorded from these mountains (specimens at AM, AMNH, and BBM). These include the cuscuses *Phalanger orientalis, P. gymnotis,* and *Spilocuscus maculatus,* the tree-kangaroo *Dendrolagus inustus,* the wallabies *Thylogale browni* and *Dorcopsis hageni,* the bandicoots *Echymipera clara, E. kalubu,* and *E. rufescens,* the rodents *Hydromys chrysogaster, Melomys rufescens, Rattus praetor,* and *R. exulans,* the fruit-bats *Pteropus neohibernicus, Dobsonia minor, Nyctimene aello, N. albiventer, N. cyclotis, Paranyctimene tenax, Syconycteris australis,* and *Macroglossus minimus,* the vespertilionid bat *Pipistrellus papuanus,* and the molossid bat *Mormopterus beccarii*. However, essentially all of these species (excepting *Nyctimene cyclotis,* a widespread inhabitant of New Guinean montane forests) are characteristic inhabitants of lowland habitats and are widespread in northern New Guinea. Future surveys in the Prince Alexanders should thus focus on the very highest peaks in the range, which rise to 1240 m and are likely to support unique animal assemblages unknown at lower altitudes.

As discussed above, rodent-collecting efforts in the Melanesian region have so far yielded five species of *Hydromys*—the widespread *H. chrysogaster*, the insular endemic *H. neobrittanicus,* the mid-montane Wissel Lakes endemic *H. hussoni,* the newly-described *H. ziegleri,* and an unnamed species from the Moluccan island of Obi. The three larger species (*H. chrysogaster, H. neobrittanicus,* and the Obi taxon) have all been collected in lowland rainforest, including in forest at sea level, while one of the smaller species (*H. hussoni*) is known only from forest at much higher elevations. The similarly small-bodied *Hydromys ziegleri* is thus far known only by a single specimen taken in relatively low elevation forest (213 m); given that extensive collecting efforts in other areas of lowland northern New Guinea have failed to record it elsewhere, I strongly suspect that it is a legitimate endemic of the North Coast Ranges. That the other small-bodied *Hydromys* (*H. hussoni*) and most other North Coast Range endemic mammals are restricted to higher-elevation forests suggests to me that *H. ziegleri* may be an inhabitant of montane forests, and that thus far it may be known only from the very lowest altitudinal bound of its range. Future trapping regimes targeted at streams along elevational gradients in the Prince Alexander and eastern Torricelli Mountains should serve to illuminate its real geographic and altitudinal distribution.

The ongoing discovery and description of new mammal species from throughout mainland New Guinea (e.g. Flannery and Groves 1998; Helgen and Flannery 2004; Helgen 2005), highlights how poorly-studied the biota of many areas of the island remains. Amphibious murines, which can be difficult to trap, are often especially overlooked in rapid faunal inventories. I strongly suspect that future survey efforts will identify additional small-bodied amphibious murines in outlying areas of montane New Guinea—perhaps, for example, in the mountain ranges of the Vogelkop Peninsula (the Arfaks and Tamraus), in the expansive Foya Range, or on other large mountainous islands adjacent to New Guinea, such as New Britain or Seram.

Acknowledgments

For access to specimens under their care and other assistance I thank Carla Kishinami and Allen Allison (BBM), Sandy Ingleby and Tish Ennis (AM), Chris Smeenk (RMNH), Darrin Lunde, Nancy Simmons, and Rob Voss (AMNH), Robert Palmer and Ken Aplin (CSIRO), Bulisa Iova (PNGM), and Paula Jenkins, Richard Harbord, and Daphne Hills (BMNH). I also thank Guy Musser, Tim Flannery, and Jared Diamond for useful discussion and criticism, and to Steve Donnellan and Ken Aplin for helpful discussion about murine relationships. I especially thank Carla Kishinami for assistance with loans and georeferencing and Lauren Johnston for help in preparing the figures. My research is currently supported by the U.S. National Science Foundation (Graduate Research Fellowship) and the American Society of Mammalogists (Fellowship in Mammalogy).

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