On the cover: Dorsal and ventral views of the cranium of *Brassomys albidens* (AMNH 150821).

MUSSER & LUNDE: NEW GUINEA COCCYMYS AND "MELOMYS" ALBIDENS   AMNH BULLETIN 329   2009

SYSTEMATIC REVIEWS OF NEW GUINEA *COCCYMYS* AND *"MELOMYS" ALBIDENS* (MURIDAE, MURINAE) WITH DESCRIPTIONS OF NEW TAXA

GUY G. MUSSER AND DARRIN P. LUNDE

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

SYSTEMATIC REVIEWS OF NEW GUINEA *COCCYMYS* AND "*MELOMYS*" *ALBIDENS* (MURIDAE, MURINAE) WITH DESCRIPTIONS OF NEW TAXA

GUY G. MUSSER

Division of Vertebrate Zoology (Mammalogy)
American Museum of Natural History
Current address: 305 Clevington Way,
Simpsonville, SC 29681
(holdenmusser@charter.net)

DARRIN P. LUNDE

Division of Vertebrate Zoology (Mammalogy)
American Museum of Natural History
(lunde@amnh.org)

The *Guba*, which means "sudden storm" in the New Guinean Motu dialect, was a model PBY 2 Catalina Flying Boat. Owned and piloted by Richard Archbold, it was used to supply the 1938–1939 New Guinea Expedition to the Snow Mountains and is here shown being unloaded on Lake Habbema with Mt. Wilhelmina in the distance. The *Guba* made it possible for the expedition to reach the remote interior and to bring back large numbers of specimens for the American Museum.

CONTENTS

ABSTRACT

A new species of the New Guinea endemic murine genus *Coccymys* is described, based on a small sample from Mt. Dayman and Mt. Simpson in the Maneau Range at the far eastern end of the Owen Stanley Ranges of eastern Papua New Guinea, and two specimens from the western portion of the Owen Stanleys, one from Smith's Gap near Mt. St. Mary, the other from Bulldog Road in the Wau area. *Coccymys kirrhos*, n. sp., is a vicariant relative of *C. shawmayeri*, which occurs in the Central Cordillera of Papua New Guinea extending from Mt. St. Mary in the east to the Telefomin region in the west. *Coccymys shawmayeri* in turn is the eastern montane vicariant of the western New Guinea *C. ruemmleri*, so far recorded only from the Snow Mountains in western New Guinea (Papua Province of Indonesia) and the eastern end of the Star Mountains over the border in the western section of Papua New Guinea. *Coccymys ruemmleri* and *C. shawmayeri* are regionally sympatric in western Papua New Guinea where the former is apparently restricted to high altitudes on the Star Mountains and the latter occurs at lower altitudes in the highlands bounding the Telefomin Valley. The ranges of *C. shawmayeri* and *C. kirrhos*, n. sp., overlap at the western section of the Owen Stanley Ranges, and both species have been caught at Bulldog Road, but in different years. This linearly distributed trio of species has been found only in the montane forests and alpine grasslands of the Central Cordillera—there are no records from mountains on Vogelkop Peninsula and the Huon Peninsula, nor from any of the north coast ranges. The new species is described within the context of rediagnosing the genus *Coccymys*, and documenting morphometric and geographic limits of *C. ruemmleri* and *C. shawmayeri* based on most specimens stored in collections of museums. This material consists primarily of museum study skins and accompanying skulls, some fluid-preserved specimens, skeletal fragments from modern samples of owl pellets, and Holocene and Late Pleistocene fossils (for *C. ruemmleri* only). All species of *Coccymys* are nocturnal and scansorial; stomach contents from samples of *C. shawmayeri* indicate the diet consists of seeds, fruit, and arthropods.

The taxon *albidens* is represented by six modern examples collected at 2800 m and 3225 m in 1938 from the northern slopes of the Snow Mountains of western New Guinea, and three Late Pleistocene fossils obtained from the same region. The species was initially described as a *Melomys* (Tate, 1951); later an alliance with *Coccymys* was suggested (Flannery, 1990; Menzies, 1990; Musser and Carleton, 1993), but restudy of anatomical traits (derived solely from stuffed skins with accompaning skulls) reveals a degree of morphological divergence not only from species in *Coccymys* but from any other "Old Endemic" New Guinea murine. A new genus, *Brassomys*, sampled by only six modern specimens and three Late Pleistocene fossils, is proposed to embrace *albidens*. Morphological attributes of that species are contrasted primarily with those characterizing *Coccymys*, and secondarily with the genera *Melomys, Paramelomys, Mammelomys, Protochromys, Abeomelomys*, and *Pogonomelomys*.

Biological aspects of *albidens* are unknown; however, particular external, cranial, and dental traits in combination strongly suggest the species is a nocturnal, arboreal/scansorial invertebrate predator.

INTRODUCTION

"A beautiful little *Pogonomelomys* was also found in this shrubby forest fringe," exclaimed Brass (1956: 129) in his summary of the mammals that were caught at the intersection of forest and grassland at 2230 m on the northern ramparts of Mt. Dayman in the Maneau Range, near the eastern end of the Owen Stanley Ranges in Papua New Guinea. Eighteen species of mammals were obtained at that locality, the "Top Camp," which were a part of the 59 species and more

than 1000 specimens collected by members of the Fourth Archbold Expedition to New Guinea in 1953 along a transect between the top camp and the northern coast at Baiawa, Moi Biri Bay (figs. 38, 39). Three individuals from the top camp represent that "beautiful little *Pogonomelomys*," with its bright tawny upperparts and whitish gray underparts, small body, and very long tail. They are not members of *Pogonomelomys*, but a sample of the endemic New Guinea *Coccymys*, which until now was thought to consist of only one species, *C. ruemmleri,* found in montane

habitats extending from the Snow Mountains in western New Guinea eastward to Mt. St. Mary in the western part of the Owen Stanley Ranges in Papua New Guinea (Musser and Carleton, 2005, for example).

To describe the new species of *Coccymys* from the Owen Stanley Ranges required that we reassess phenetic and geographic variation in samples of "*C. ruemmleri*" from throughout its known range using specimens stored in collections of museums. Through comparative inspection of skins and skulls, and univariate and multivariate analyses of cranial and dental variables, all combined with collection localities, we are able to unambiguously define the boundaries of *C. kirrhos*, n. sp. The morphometric and geographic limits of two other species of *Coccymys* are also revealed. *Coccymys ruemmleri* does not extend the length of the Central Cordillera as formerly referenced (Flannery, 1995; Menzies, 1990; Musser and Carleton, 1993, 2005), but is endemic only to that cordilleran segment in western New Guinea formed by the Snow and Star mountains. In the region of the Star Mountains and Telefomin Valley of western Papua New Guinea, *C. ruemmleri* is regionally sympatric with a different species, *C. shawmayeri*, which ranges through montane forests and alpine grasslands eastward along the Papuan segment of the Central Cordillera to Mt. St. Mary in the western part of the Owen Stanley Ranges where it overlaps the range of *C. kirrhos*, n. sp. Documenting morphological and geographical attributes of these three species is important to understanding actual species diversity within *Coccymys*, which in turn informs past evolutionary history of that monophyletic cluster and contributes to biogeographic inquiries.

Describing the *Coccymys* from the eastern Papuan peninsula as a new species within the framework of reviewing the morphological and distributional characteristics of *C. ruemmleri*, the type species of the genus, and *C. shawmayeri*, is one of our two objectives in this report. Results from our second inquiry also reveal increased diversity within the endemic New Guinea mammalian fauna, but at a higher taxonomic level. During the 1938–1939 Archbold Expedition to western New Guinea, six woolly-furred,

small-bodied, and long-tailed rats were collected at two places in upper and midmontane rain forests along the northern ramparts of the Snow Mountains. When descriptions of new species discovered in the Snow Mountains began to appear (Tate and Archbold, 1941, for example), mention of these six specimens was not included. We later discovered that three of the six had been misidentified as either "*Pogonomelomys ruemmleri*," which was described by Tate and Archbold (1941) or "*Pogonomys sylvestris*," named and described by Thomas (1920). By the late 1940s, Tate had identified the other three as a unique entity and they became his sample of *Melomys albidens*, described in 1951. Although placed in *Melomys*, which at the time contained a wide range of morphologies that would later be formally separated into several genera (Menzies, 1996), little was known about *albidens* and its phylogenetic affinities were murky. Added to its aura of mystery was the absence of additional specimens, especially in the face of several expeditions to different parts of the Snow Mountains undertaken after the Second World War. By the late 1980s, a few researchers had examined the three specimens that were the basis for Tate's description of *albidens* and all suggested a phylogenetic alliance with *Coccymys*, which at the time contained only *C. ruemmleri* (Flannery, 1990; Menzies, 1990; Musser and Carleton, 1993).

We looked again at *albidens*, wondering if it really was another member of *Coccymys*. Our fresh inquiry uncovered the three formerly misidentified specimens that could be added to the three studied by Tate, as well as three Late Pleistocene fossil fragments from Kelangurr Cave in the Snow Mountains, not too far from Lake Habbema; the inquiry also revealed a degree of morphological divergence not only from species in *Coccymys* but from any of the "Old Endemic" New Guinea murines. Based upon a unique combination of anatomical traits seen in the six skins and skulls representing *albidens*, we propose a new genus, *Brassomys*, to embrace that species. While the generic distinctiveness of *albidens* is certain, the strength of its phylogenetic ties to other endemic New Guinea murine genera remains cloudy; we sift

through possibilities here, along with a review of the postulated affinities for *Coccymys*, but cannot resolve the issue outside of a comprehensive phylogenetic analysis of all endemic New Guinea rodent taxa.

A rediagnosis of *Coccymys*, and descriptions of the three species it contains as well as comparisons among them, diagnosis of the new genus with a redescription of *albidens*, and contrasts between the new genus and other relevant genera, comprise the bulk of our report. We add summaries of habitats extracted from specimen tags and published sources, especially those presented in results of the Archbold Expeditions for 1938–1939, 1953, and 1959 (Archbold et al., 1942; Brass, 1941, 1956, 1964). We include the modest biological data available for species of *Coccymys*, and discuss sympatric relationships among the three species as well as with other species of mammals, particularly those faunal records resulting from the Archbold Expedition's transects in the Snow Mountains and Maneau Range. We provide a hypothesis about some biological aspects of *albidens* based upon certain specialized anatomical traits. In the end, we decline serious zoogeographic discussion; our results define increased diversities at species and generic levels and reflect the sort of primary taxonomic and distributional data required for subsequent and comprehensive zoogeographic analyses (see Helgen, 2007a).

In proposing the new genus, *Brassomys*, we honor the memory of Leonard J. Brass. Through his lucid published summaries of the various expeditions to New Guinea sponsored by Richard Archbold and the American Museum of Natural History, this intelligent, tough field botanist and explorer brought to us a vivid view of the tropical forests, savannas, and grasslands forming the landscapes of New Guinea. We smell the damp earth and wet moss of the high montane forests; see the magnificent stretches of beech, those great trees with mossy lower trunks, massive branches, dense foliage, and rough dark bark; hear the rustling ebb and flow of tussock grasses pushed by alpine breezes; and are chilled to the bone by the cold wind flowing down the high rocky face of Mt. Wilhelmina.

METHODS AND MATERIALS

INSTITUTIONS AND SPECIMENS: Specimens we cite by catalog number are stored in the collections of the American Museum of Natural History, New York (AMNH); the Australian Museum, Sydney (AM); fossil collection at the Australian Museum, Sydney (AMF); Bernice P. Bishop Museum, Honolulu (BBM-NG); and Natural History Museum, London (BMNH). These acronyms preface catalog numbers referring to specimens we list in the gazetteer, tables, and text. Most of the material consists of standard museum preparations: a stuffed study skin and accompanying cranium and mandible. A few series are stored in fluid preservative and from some of these we extracted skulls. The specimens identified by AMF are Late Pleistocene fossilized fragments of dentaries from Kelangurr Cave on the northern slopes of the Snow Mountains in western New Guinea (see Flannery, 1999).

MEASUREMENTS: Values (in millimeters) for total length and length of tail (abbreviated LT) are those recorded by collectors on labels attached to skins; subtracting length of tail from total length produced a value for length of head and body (LHB). The tail is appreciably longer than head and body in all samples of *Coccymys* as well as *albidens*, and that proportion is expressed as a percentage by the ratio LT/LHB. The terminal portion of the tail is white in many examples of *Coccymys shawmayeri*, and we measured length of that white segment (LWTT) on the dry study skins and some fluid-preserved specimens or transcribed the values recorded on skin tags (Hobart Van Deusen measured white tips in the field for many specimens from Mt. Wilhelm and an individual from Mt. Otto). Values for length of hind foot, including claws (LHF), were either transcribed from skin labels or derived from measuring the dry hind foot of study skins. Length of ear (LE) is noted on labels attached to skins for most specimens; while we summarized those values in univariate statistics (table 2), we did not unduly emphasize the significance of any differences recorded among samples of *Coccymys*, noting only the size difference between that genus and *albidens*. Of all external measurements,

length of ear is most subject to variable measure by collectors because rarely do they indicate whether the value represents total length of the external pinna or length from notch to outer margin of the crown (except for A.B. Mirza, who measured both dimensions and recorded the values on skin tags).

We used digital calipers to measure (recorded to the nearest 0.01 mm) the following cranial and dental dimensions (listed in their order of appearance in the tables):

ONL	occipitonasal length (= greatest length of skull)
ZB	zygomatic breadth
IB	interorbital breadth
LR	length of rostrum
BR	breadth of rostrum
BBC	breadth of braincase
HBC	height of braincase
BZP	breadth of zygomatic plate
LD	length of diastema
PPL	postpalatal length
LBP	length of bony palate
BBPM1	breadth across bony palate at first molars
BMF	breadth of mesopterygoid fossa
LIF	length of incisive foramina (= anterior palatine foramina)
BIF	breadth of incisive foramina (= anterior palatine foramina)
LB	length of auditory (ectotympanic) bulla
CLM1–3	crown length of maxillary molar row
BM1	breadth of first upper molar
clm1–3	crown length of mandibular molar row
alm1–3	alveolar length of mandibular molar row
bm1	bm2, bm3, breadths of first, second, and third lower molars

Limits of most of these dimensions are illustrated in figure 1 and most are spelled out in Musser and Newcomb (1983). The following dimensions are not illustrated in figure 1: BIF, the greatest distance across both incisive foramina; clm1–3, greatest distance between the anterior enamel margin of the first lower molar and the posterior enamel margin of the third; alm1–3, the distance between the anterior margin of the alveolus of the first molar and the posterior alveolar lip of the third molar; bm1, bm2, bm3, the greatest distance across each molar.

Only the values for cranial and dental measurements were used in multivariate analyses. Values from external measurements provided an appreciation of general body size and lengths of appendages but were excluded from the multivariate analyses.

AGE AND SEX: Only measurements from adults were used in the multivariate analyses and tables of descriptive statistics for external, cranial, and dental variables. This category embraces three rough age classes separated primarily by wear of molars—old adults, adults, and young adults (as defined by Musser and Heaney, 1992: 5).We combined males with females in the samples, which provided reasonably large sample sizes for the univariate and multivariate analyses.

STATISTICAL ANALYSES: We calculated standard univariate descriptive statistics (mean, standard deviation, and observed range) for the population samples listed in the tables.

Cluster 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. Measurements from complete skulls of adults (young to old) were used in the analyses. Discriminant-function and principal-components analyses were computed using the combination of cranial and dental variables indicated in various tables throughout the text. All measurements were transformed to natural logarithms. Canonical variates were extracted from the discriminant function analyses. UPGMA clusters employed the squares of Mahalanobis distances to the group centroids. Principal components were extracted from a covariance matrix and projected on three axes, but usually significant structure was revealed only in the ordination of first and second principal components factors, which are illustrated (the pattern of specimen scores in plots employing first and third principal components were usually similar to those bounded by first and second axes). SYSTAT 11 for Windows (2004 edition) was used for all analytical procedures.
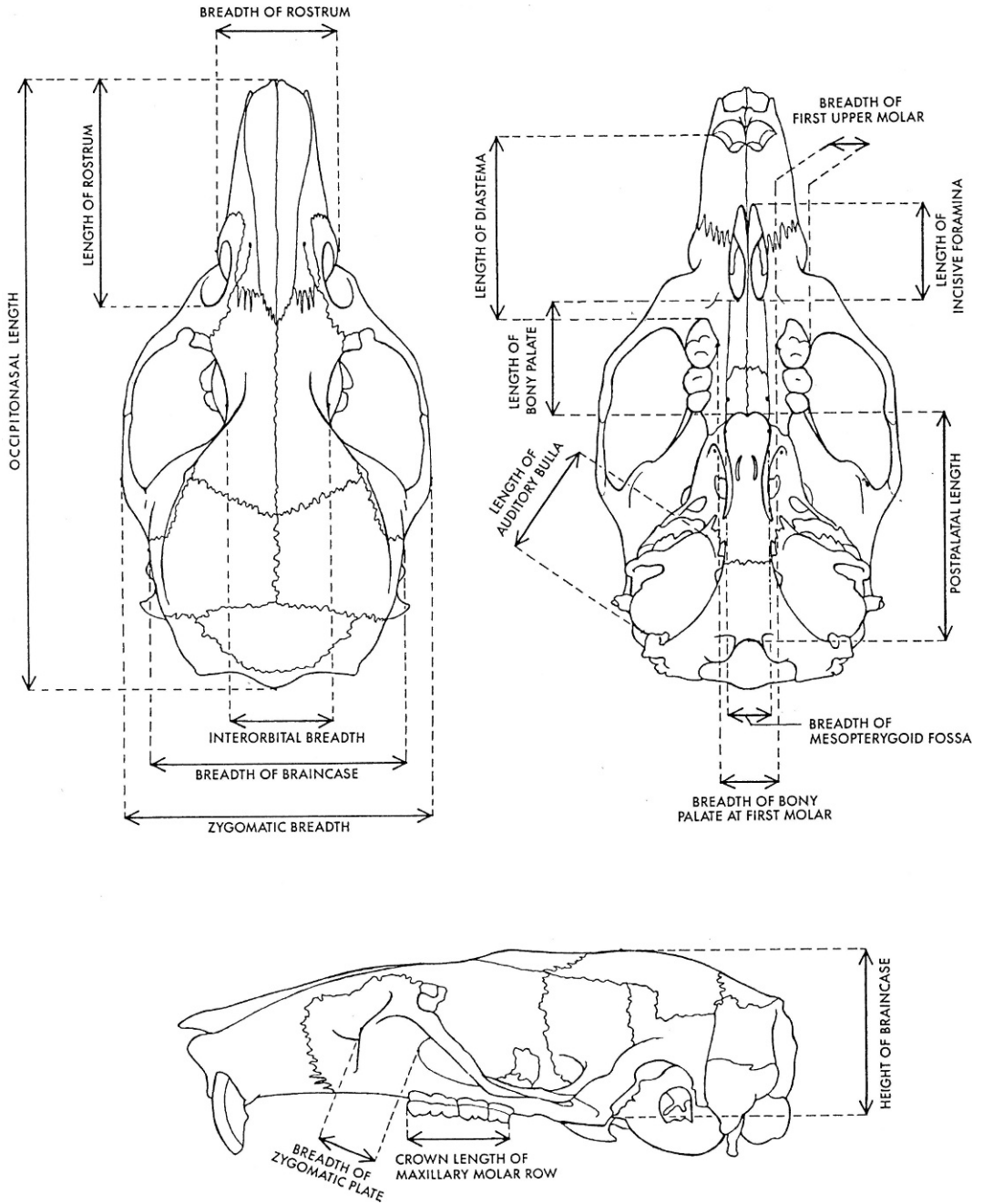
Fig. 1. Diagram of the cranium of an adult *Bunomys chrysocomus* (from Sulawesi) showing limits of cranial and dental measurements.

MORPHOLOGICAL DEFINITIONS: 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), Musser and Heaney (1992), and Voss (1988) for

cranial morphology. Names of cusps and cusplets of maxillary (upper) and mandibular (lower) molars are noted in figure 13; sources of this terminology are explained by Musser and Newcomb (1983: 332).

STOMACH CONTENTS: From fluid-preserved specimens representing all three species of *Coccymys* and *Protochromys fellowsi* we removed stomachs by severing the posterior end of the esophagus and the anterior section of the duodenum. We bisected the isolated stomach along the midfrontal plane, transferred the contents to a white ceramic dish, examined them with a Wild stereoscopic microscope, and were able to sort the contents into gross categories of fruit, seeds, other plant material, and insects. Every stomach also contained isolated strands of hair, likely ingested during grooming, and a few stomachs held tiny nematodes. We saved the contents in a leak-proof vial to be stored with the specimen from which it was extracted. Except for BBM-NG 184493, specimens examined are AMNH; stomachs and their contents are stored in the mammal collections at AMNH and BBM.

Anatomical terms describing gross stomach structure are those employed by Carleton (1973).

GAZETTEER: Collection sites are in Papua Province of Indonesia (western New Guinea) and Papua New Guinea (eastern New Guinea). We refer to the sites in Papua Province by the names used before the political transfer of Netherlands New Guinea to Indonesia (the Snow Mountains, for example, are now Pegunungan Maoke). These pre-Indonesian colonial names, many of which refer to well-known type localities and places visited during famous biological surveys, are embedded in the taxonomic literature and familiar to researchers toiling with taxonomy of New Guinea mammals. Those readers interested in the Indonesian versions of the locality names we use can consult USBGN Indonesia (1982) or current maps and gazetteers.

PHOTOGRAPHS: The photographs illustrating habitats at various camps on the northern slopes of the Snow Mountains in western New Guinea were taken by members of the 1938–1939 Archbold Expedition; habitats in localities on the northern slopes of Mt. Dayman were photographed by L.J. Brass in 1953 during the Fourth Archbold Expedition to New Guinea. Brass also photographed the habitats reproduced here during the survey on the Sixth Archbold Expedition to New Guinea in 1959. All negatives and prints are stored in the Department of Mammalogy Archives at the American Museum of Natural History.

GAZETTEER AND SPECIMENS

Names of collection localities and altitudes were taken from skin tags, field journals, or published expedition summaries. Cole et al. (1997), Flannery (1995), Flannery and Seri (1990), Leary and Seri (1997), Taylor et al. (1982), Laurie and Hill (1954), HOUSND (1944), and USBGN (1982) were the sources consulted for most geographic coordinates. The number preceding each place corresponds to the numbered locality on the map in figure 2 for *Coccymys* and figure 3 for *Brassomys*, n. gen. We personally examined all the specimens of *Coccymys* stored in AMNH, and Musser studied the holotype of *Rattus shawmayeri* and other specimens at BMNH, as well as fossil material from Kelangurr Cave. The samples of *C. ruemmleri* from the Star Mountains and all the specimens of *C. shawmayeri* from Papua New Guinea that are stored in BBM were initially identified by Kris Helgen, who graciously provided us with his determinations and collection data associated with the specimens. We borrowed some of those BBM samples, as well as specimens from AM, that we considered to be critical to providing comprehensive morphological and geographic definitions for the species of *Coccymys*. We have personally studied all the material attributable to *C. kirrhos*, n. sp. The material documented here constitutes most of the specimens of *Coccymys* stored in museums. Examples in the Papua New Guinea National Museum and University of Papua New Guinea included by Menzies (1990) in his revision of *Coccymys*, and most of the specimens at the Australian Museum referenced by Flannery (1990) comprise the few series we have not personally studied.
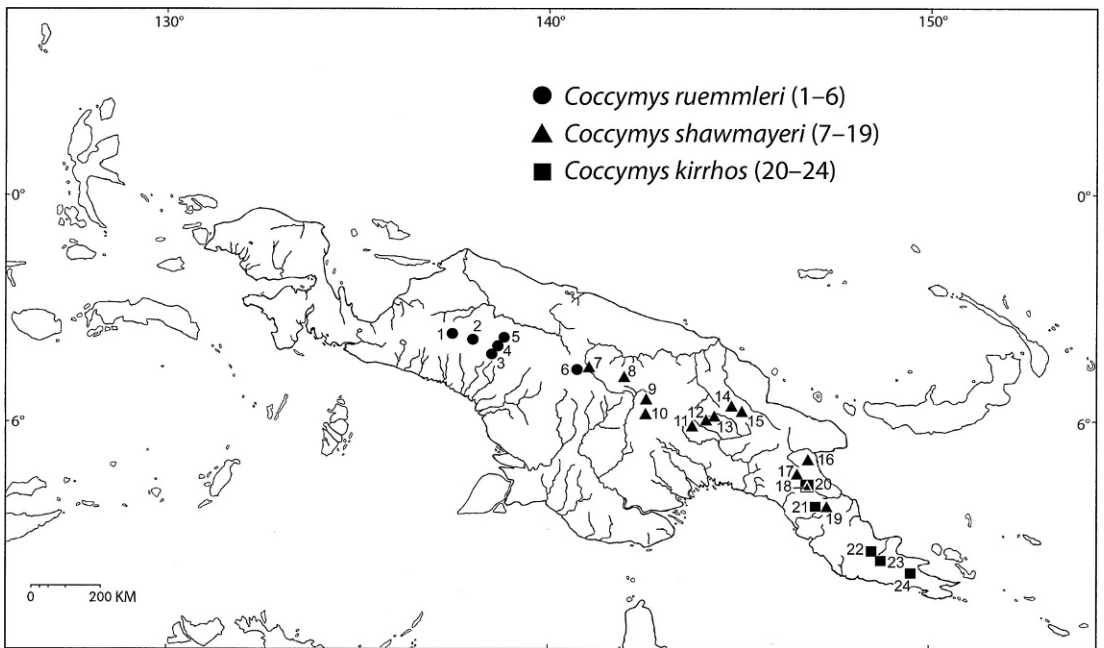
Fig. 2.   Collection localities for specimens of *Coccymys ruemmleri*, *C. shawmayeri*, and *C. kirrhos*. Numbers key to localities described in the gazetteer where specimens are also identified by museum initials and catalog numbers. Localities 1 and 2 are based on Holocene and Late Pleistocene fossils, respectively; modern specimens come from all other places of collection.

We document here all known specimens of *Brassomys*, n. gen., *albidens*, six skins and skulls held in AMNH, and three Pleistocene fossils stored in AMF. During his visits to some European museums, Musser has searched for additional examples of *albidens*, and Kris Helgen has surveyed New Guinea mammals in all of the world's museums; neither one of us has located any other samples of *albidens*.

Coccymys ruemmleri

INDONESIA, PAPUA PROVINCE

1. **Snow Mountains, northern slopes of the Carstensz Massif (Mt. Jaya), Asair Fissure,** "about 15 km northeast of the Northwall and 1 km south of the Kemabu River," (J. H. Hope, 1976: 211; also see map on p. 213), (04°04′S, 137°11′E) 3450 m: AMF 54858, 54866–69, 54875, 54876. These specimens consist of Holocene cranial and mandibular fragments found in a limestone fissure and were reported by J. H. Hope (1976). We have not examined this material but agree

with Hope's determination as the values for the cranial and dental measurements she provided fall within the range of variation for our modern samples from Mt. Wilhelmina, Lake Habbema, and Bele River valley.

2. Northern ramparts of the **Snow Mountains, Kelangurr Cave** (04°01′S, 138°08′E), 2950 m (about 60 km west of Lake Habbema), in a valley confluent with the valley of the West Baliem River (see map and description in Flannery, 1999): AMF 134109, 134052–70, 134073, 134078, 134079, 134081–95, 134097–102, 134104–108, 134110, 134112, 134113, 134115–24, 134128. These 63 specimens consist of dentary fragments extracted from Pleistocene sediments excavated in Kelangurr Cave and were studied and identified by Musser; about half of the sample was initially identified by Flannery (1999) as *Coccymys ruemmleri*.

3. Papua Province, **Snow Mountains, Mt. Wilhelmina** (Gunung Trikora on modern maps), **7 km northeast of top** (04°15′S, 138°45′E), 3560 m: AMNH 110326, 110382, 110392, 110407, 110431, 110445, 150455, 150461, 150466, 150467, 150481, 150182. **Mt. Wilhelmina, 2 km east of top** (04°16′S, 138°40′E)
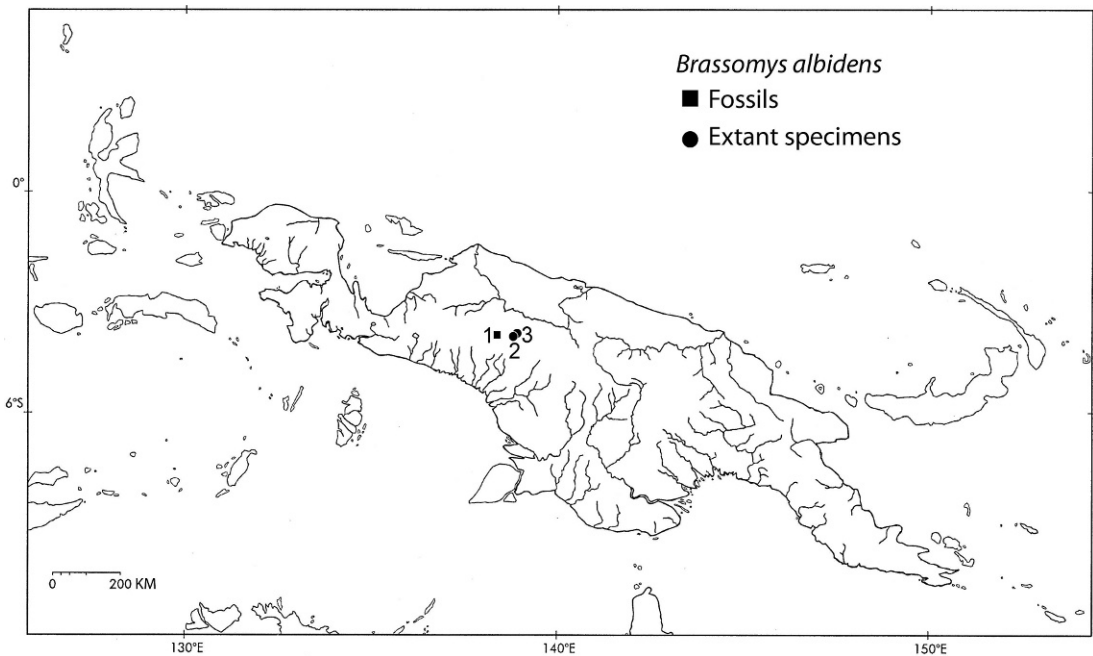
Fig. 3. Collection localities for specimens of *Brassomys albidens*. Numbers key to localities described in the gazetteer where specimens are also identified by museum initials and catalog numbers.

3800–4050 m: AMNH 110151 (3800 m), 110183 and 110184 (3950 m), 110188 (4050 m). In addition to these skins and skulls, we identified 12 specimens (AMNH 276455–66) consisting of fragmentary dentaries and crania extracted from owl pellets that were gathered by members of the Archbold Expedition at or above the 3800 m camp during September 1938.

4. **Snow Mountains, Lake Habbema** (04°49′S, 138°41′E), 3225 m: AMNH 150662, 150669 (holotype of *Pogonomelomys ruemmleri*), 150696, 150700, 150709, 150771, 150811–14, 150820, 150852, 150861, 150872, 150878, 150891, 150895, 152740.

5. **Bele** (also spelled Ibele) **River, 18 km northeast of Lake Habbema** (04°05′S, 138°42′E), 2200 m: AMNH 151185, 151220, 151306, 151323, 151277. **Bele River valley, 9 km northeast of Lake Habbema** (04°05′S, 138°50′E), 2800 m: AMNH 150537, 150565, 150589, 150619.

All the specimens from localities 3–5 were obtained during the 1938–1939 Archbold Expedition to western New Guinea. The general region and collection stations are described by Archbold et al. (1942) and Brass (1941). See map in figure 48.

PAPUA NEW GUINEA

6. Western Province, **"Star Mountains"** (05°11′S, 141°11′E), no exact locality: 3100 m, BBM-NG 100167, 100179, 100195, 100212, 100227, 100239, 100241, 100249, 100250, 100261; 10,500 ft (3200 m), BBM-NG 98563, 98581, 98588, 98600. **Dokfuma Basin,** on the southern slopes of Mt. Capella (04°58′S, 141°05′E), which is in the Star Mountains but barely in southern Sandaun Provine, 3200 m: AM 22281 (originally recorded by Flannery and Seri, 1990).

Coccymys shawmayeri

7. Sandaun Province, **Telefomin Valley**, between Telefomin (05°08′S, 141°38′E) and Lake Louise (05°14′S, 141°24′E). **Lake Louise**, westnorthwest of Telefomin, 2800 m: BBM-NG 98492, 100147. **"NE of Telefomin,"** 8000 ft (2440 m): BBM-NG 98365, 98407. **Bafunmin** (05°06′S, 141°26′E) and 5 km south, 2300 m: BBM-NG 108076, 108166, 108233. **Upper Sol River valley,** 2600 m: AM M16745. Flannery and Seri (1990: 190) identified this last specimen as *C. ruemmleri*, and Flannery portrayed the same animal in a color plate published in his Mammals of New Guinea (Flannery, 1995: 275; T.

Flannery, in litt., 2008). Its warm brown fur over the upperparts of the body and and relatively long tail with a long white tip are typical of *C. shawmayeri.*

8. Sandaun Province, **Oksapmin** (05°15′S, 142°14′E), 1850 m: BBM-NG 55461.

9. Enga Province, **Kaijende Highlands, Porgera Area** (05°28′S, 143°11′E for Porgera): Menzies (1990: 136) examined specimens (identified as *ruemmleri*) from "Porgera" and Helgen (2007b: 60) reported remains (as *ruemmleri*) that "were found in owl pellets in alpine grassland along Waile Creek Road near the Porgera Reservoir [3010 m]."

10. Southern Highlands Province, **Tari region** (05°54′S, 142°57′E for Tari). **Tari Gap**, 2600 m, BBM-NG 105507, 105534, 105577. **Doma Peaks**, 2400 m, BBM-NG 105712, 105714. **Fringe of Lavani Valley**, 2450 m, BBM-NG 60907.

11. Southern Highlands Province, **Mt. Giluwe region. 5 km W of Mendi**, 2000 m: BBM-NG 60320. **Kagaba** (05°51′S, 143°46′E) and vicinity, at base of Mt. Giluwe, 40 road km NE of Mendi, 2800–3600 m: BBM-NG 60524, 60625, 97059, 97157, 97161, 97180, 97238A, 97238B, 97238C, 97241, 97258, 97274A, 97274B, 97280, 97298A, 97298B. **North slope of Mt. Giluwe**, 3300 m and 3500 m: BBM-NG 101844, 101890. **Southeast slopes of Mt. Giluwe**, 3600 m: BBM-NG 101924. **Southsoutheast slopes of Mt. Giluwe**, 2900 m: BBM-NG 101991, 101992, 102008, 102056.

12. Western Highlands Province, **Mt. Hagen region. Mt. Hagen** (05°45′S, 144°02′E) 7000–8500 ft (2135–2592 m): AMNH 156475, 156486, 156490, 156513, 156514, 156540, 156546–548, 156588, 156589, 156605, 156664, 156665, 156671, 156673. **Tomba, southwestern spur of the Hagen Range** (05°50′S, 144°02′E), 8000 ft (2440 m): BMNH 50.1760, 50.1761. **Yanka, eastern slopes of the Hagen Range**, BMNH 50.1759 (the examples from Tomba and Yanka were identified as *Rattus shawmayeri* by Laurie, 1952: 305). **Murmur Pass** (05°45′S, 143°56′E), 10–16 km NNE of Tambul, 2700 m: BBM-NG 60685, 60753, 97420, 97456, 97477A, 97556.

13. Western Highlands Province, **Nondugl** (05°52′S, 144°43′E): 1600 m, AMNH 222232, 222239; 6000 ft (1830 m), AMNH 183609, 183634, 183635.

14. Simbu (Chimbu) Province, **Bismarck Range. East slopes of Mt. Wilhelm** (05°40′S, 145°05′E)**, Lake Aunde**, 3570 m (AMNH 192092–97, 192100–102, 192105–107, 192109); **2 mi E Lake Aunde**, 3400 m (AMNH 192098); **Pengagl Creek** 2770 m (AMNH 192103, 192307, 192735); **Mt. Wilhelm, "E. slopes"** (AMNH 192104, 192113, 192733, 192734, 192736–40); **"Mt. Wilhelm"** (AMNH 192108, 192114, 192115); **Mt. Wilhelm, "9,000 ft"** (AMNH 156618); **Mt. Wilhelm**, "9,000–12,000 ft" (AMNH 156608). Consult Brass (1964) for descriptions of the camps at Lake Aunde and Pengagl Creek where some of these AMNH specimens were obtained. We identified an additional 56 individuals (AMNH 276640–95) that are represented by cranial fragments and dentaries extracted from owl pellets found at 3660 m beneath a boulder on the side of a ridge rising sharply beyond the Lake Aunde camp (Van Deusen's notes in AMNH archives). **High slopes of Mt. Wilhelm**: BMNH 50.1763, 50.1764. **Mt. Wilhelm**, 11,400 ft (3477 m): BBM-NG 100473–77, 100518, 100524, 100557, 100577, 100587, 100619, 100635, 100636, 100644, 100645, 100653–55, 100672, 100673, 100676, 100681, 100696, 100697, 100709. **Yandara, Bismarck Range**: BMNH 50.1758. **Bogo, south slopes of Bismarck Range**: BMNH 50.1762 (the BMNH specimens were identified as *Rattus shawmayeri* by Laurie, 1952: 305). **Baiyanka, Purari-Ramu Divide, southeastern part of the Bismarck Range** (05°46′S, 145°10′E) 8000 ft (2440 m): BMNH 1947.1155 (holotype of *Rattus shawmayeri* Hinton, 1943). **Mt. Kerigomna** (05°58′S, 145°07′E), 3400 m: BBM-NG 55607.

15. Eastern Highlands Province, **eastern end of the Bismarck Range. South slopes of Mt. Otto, Collin's Sawmill** (05°59′S, 145°25′E), 2300 m: AMNH 192116 (Brass, 1964, described and mapped this locality). **Fatima River, 5 km W of Collin's Sawmill**, 2500 m: BBM-NG 55563, 55582.

16. Morobe Province, **Kuper Range, Southern slopes of Mt. Missim** (07°14′S, 146°50′E), 2000 m: one specimen reported (as *ruemmleri*) by Willett et al. (1989).

17. Morobe Province, **Kuper Range, Mt. Kaindi region. Mt. Kaindi** (07°21′S, 146°43′E): BBM-NG 105375 (2200 m), 51129 (2300 m), 53512 (2350 m), 97718 (8000 ft [2440 m]). **Mt. Kaindi Road, vicinity of Wau**, 1900 m: BBM-NG 97657. **Edie Creek, Mt. Kaindi**: USNM 357491.

18. Morobe Province, **Wau area. Bulldog Road, "12 mi S" of Edie Creek** (07°31′S, 146°40′E), 2500 m: BBM-NG 101267, 101502. **Bulldog Road, "12 mi from" Edie Creek** (07°31′S, 146°40′E), 2400 m: BBM-

NG 61669, 96646, 96802. **Bulldog Road, "32 road km S Wau"** (07°31′S, 146°40′E), 2400 m: BBM-NG 29140.

19. Central Province, **SSW of Mt. St. Mary** (08°10′S, 146°58′E), 3000 m: BBM-NG 96863, 96864, 96895–97, 96909, 96913 *Coccymys kirrhos*, n. sp.

20. Morobe Province, **Wau area, Bulldog Road, "12 mi from" Edie Creek** (07°31′S, 146°40′E), 2500 m: BBM-NG 55824.

21. Central Province, **Smith's Gap** (08°03′S, 146°53′E), "in the vicinity of Guari," 2500 m: BBM-NG 96950. Kris Helgen wrote us that "From my understanding, Smith's Gap is a locality in the border area between Central and Northern Province and is situated at 2500 m. Taylor et al. (1982) gave the elevation of Smith's Gap as 762 m [2500 ft], which is not correct, and in doing so provided the (artificially) lowest record of occurrence of *Rattus niobe*, which has been cited since."

22. Milne Bay Province, eastern region of the Owen Stanley Ranges, Maneau Range (also spelled "Maneao"), **north slopes of Mt. Dayman** (top camp; 09°49′ S, 149°16′E), 2230 m: AMNH 158173 (2300 m is noted on the skin tag of this specimen, but 2230 was written in Hobart Van Deusen's field catalog), 158174,158175 (holotype of *Coccymys kirrhos*). The locality was described and mapped by Brass (1956; also see fig. 38).

23. Milne Bay Province, **southeastern ramparts of Mt. Dayman on the Garatin Ridge in the Agaun Region of the Maneau Range, Dumae Creek,** 2.3 km N, 0.4 km W of Agaun (09°53′S, 149°23′E; Dumae Creek, the base camp for the expedition recounted by Cole et al. [1997], is below Garitin Pass, on the road from Agaun to Bonenau), 1525 m: BBM-NG 109165.

24. Milne Bay Province, Maneau Range, **North slopes of Mt. Simpson**, **0.5 km S of Bunisi Village** (10°01′S, 149°35′E)**, "Camp 5,"** 1490 m: BBM-NG 184493.

Brassomys, n. gen., *albidens*

INDONESIA, PAPUA PROVINCE

1. Northern ramparts of the **Snow Mountains, Kelangurr Cave** (04°01′S, 138°08′E), 2950 m, in a valley confluent with the valley of the West Baliem River (see map and description in Flannery, 1999): AMF 134074, 134096, 134126. These three specimens are dentary fragments extracted from

Pleistocene sediments excavated at Kelangurr Cave and were identified by Musser.

2. **Snow Mountains, Lake Habbema** (04°49′S, 138°41′E), 3225 m: AMNH 150821 (holotype of *Melomys albidens*).

3. **Snow Mountains, Bele River valley, 9 km northeast of Lake Habbema** (04°05′S, 138°50′E), 2800 m: AMNH 150531, 150541, 150607, 150618, 150923.

CHARACTERISTICS OF *COCCYMYS*

The type species of *Coccymys* is *ruemmleri*[1], described as a species of *Pogonomelomys* by Tate and Archbold (1941: 6) who, under the heading "General Characters," characterized it as a "small dark brown rat with *Melomys*-like dentition, feet unmodified for climbing… but with dorsal 3 cm. of tail provided with tactile surface for prehension." They followed with this description:

Skin with rather long fur (12 mm.), colored above near Bone Brown, becoming Clove Brown along the back, the face with a grayish cast; underparts grayish white, the long pelage with fuscous bases which show through. Hands and feet clothed with light yellow-brown hairs. Ears fuscous. Tail brown; the scales small and lacking the prominent keeled structure of true *Melomys,* their scale-hairs blackish, 3 per scale and from 2 to 3 scale-lengths. … Skull much smaller than that of *P. mayeri*, the rostrum much compressed and less shortened; supraorbital ridges undeveloped; braincase fuller; zygomatic plate much narrower, and nearly straight as in *Macruromys*; palate with posterior foramina; back of palate even with back of M^3; bullae small; angular process of mandible quite short. Incisors narrow, unbroadened, orange. Molars very small and of characteristically simple *Melomys* type.

Tate (1951: 316) was uneasy about the generic allocation of *ruemmleri*, noting that

---

[1]The name is spelled "*rümmleri*" in Tate and Archbold's (1941) original description, a patronym honoring Hans Rümmler's contribution to systematics and evolution of New Guinea rodents (Rümmler, 1938). Except where we quote authors using the original spelling, we use "*ruemmleri*," thus conforming to the edict promulgated in Article 35.5.2.1 of the International Code of Zoological Nomenclature (fourth edition, 1999: 40): "In the case of a diacritic or other mark, the mark concerned is deleted, except that in a name published before 1985 and based upon a German word, the umlaut sign is deleted from a vowel and the letter 'e' is to be inserted after that vowel."

Pogonomelomys "remains an unsatisfactory genus due to the fact that it seems to be diphyletic or even triphyletic." He recognized two subdivisions within the genus, the "*mayeri-bruijnii* group," which contains the only two species that now constitute *Pogonomelomys* (Menzies, 1990; Musser and Carleton, 2005), and the "*sevia-rümmleri* group." Laurie and Hill (1954: 127) simply listed *ruemmleri* as a species of *Pogonomelomys* without question in their list of the land mammals of New Guinea, and before that Ellerman (1949: 88) had suggested a relationship between *Pogonomelomys ruemmleri* and *P. tatei*, a form named and described by Hinton (1943).

Tate's separation of *ruemmleri* from the other species of *Pogonomelomys* was later supported by data from study of phallic morphology of endemic New Guinea murines by Lidicker (1968: 641) who noted that it "is evident from phallic morphology that *P. ruemmleri* and *P. mayeri* are not especially closely related, although both fall in the *Uromys* group. … The latter is close to *Melomys*, whereas the former is a highly specialized type most closely allied to *Uromys* and *Hyomys*. More species of this genus obviously need to be examined, but at least the genus as now constituted seems to be polyphyletic."

At about the same time Lidicker's report was published, Dr. Jack Mahoney at the University of Sydney was studying endemic New Guinea murines with the intention of revising several groups, *Pogonomelomys* among them. During Musser's visit to Australia in 1976, Mahoney described his progress with the revision and showed Musser the external, cranial, and dental characters of *ruemmleri* that set it apart from the other species in *Pogonomelomys*, features that in combination were not repeated in any other described New Guinea endemic and were going to be used by him to place *ruemmleri* in its own genus. Mahoney died before completing his revisionary work.

Other systematists working with New Guinea murines were aware of *ruemmleri*'s distinct morphology compared to the other species of *Pogonomelomys*. Ziegler (1982: 880), for example, citing Menzies (1973: 4), indicated that *ruemmleri* probably merited generic status. Later, Flannery (1990: 239) commented that "Studies currently underway suggests that "*P.*" *ruemmleri* is the most derived member of a clade containing "*P.*" *sevia* and "*M.*" *albidens*." Ultimately, Menzies (1990: 132) revised *Pogonomelomys*, excluding *ruemmleri* from it and making it the type-species for the new genus *Coccymys* ("from the Greek *coccyx* and *mys*, 'cuckoo-mouse' with reference to spending its early taxonomic life in a place not its own"), with this diagnosis:

> a combination of very long incisive foramina; large 3rd upper molar; incipient division of 1st and 2nd upper molar lophs into separate cusps; very broad interparietal; long palate with deep longitudinal grooves, tail with overlapping scales subtending 3 hairs each, grey-based ventral fur and mammary formula of 1+2=6.

Menzies provided a description of certain external, cranial, and dental features of *C. ruemmleri* and compared it with other murines, particularly species of *Paramelomys* and *Pogonomelomys*. *Pogonomelomys sevia*, the other member of Tate's (1951) "*sevia-rümmleri* group" and Flannery's (1990) suggested *ruemmleri-sevia-albidens* clade, was extracted from *Pogonomelomys* by Menzies (1990: 133) and made the type species of *Abeomelomys* ("from the latin *abeo,* to go away from").

The characterization of *ruemmleri* by Tate and Archbold and the diagnosis of *Coccymys* by Menzies were presented in the context of comparisons with other New Guinea murines, primarily species of *Melomys* and *Pogonomelomys*, but neither is diagnostic within Indo-Australian Murinae or the geographically broader Murinae. Tate and Archbold's description of *ruemmleri* is actually more satisfactory as a diagnosis for *Coccymys* than is Menzies's. We expand on their exposition by providing an emended generic diagnosis, and a detailed description of the type species *ruemmleri* based primarily upon anatomical attributes of dry study skins, cleaned skulls, and some material preserved in fluid.

Coccymys Menzies, 1990

TYPE SPECIES: *Pogonomelomys ruemmleri* Tate and Archbold, 1941: 6.

EMENDED DIAGNOSIS: A genus in the *Pogonomys* Division (Musser and Carleton, 2005) of subfamily Murinae, family Muridae (as delimited by Carleton and Musser, 1984, and Musser and Carleton, 2005) that is distinguished from all other described murine genera by the following combination of traits: **(1)** dorsal pelage covering head and body thick and soft, very dark brownish with blackish infusion through brownish gray to bright tawny-russet, ventral coat soft and thick, whitish gray to dark grayish white, some individuals washed with buff; **(2)** short muzzle, gray face, and prominent blackish region around each eye and extending along each side of the muzzle; **(3)** tail slender and much longer than head and body (LT/LHB ranges from 140% to 181%), scales small and slightly swollen, their annuli abutting each other (not overlapping), three short hairs associated with each scale, dorsal surface near tip with thickened epidermis and lacking scales and hairs, indicating some degree of prehensility, entire tail brownish gray, some individuals with a white tip; **(4)** dorsal surfaces of front and hind feet whitish or pale tan, hallux with claw, hind foot elongate with full complement of plantar tubercles; **(5)** three pairs of teats, one postaxillary and two inguinal; **(6)** rostrum narrow and moderately long, interorbital and postorbital margins smooth, interorbit hourglass-shaped in dorsal view, zygomatic arches flare from sides of skull, braincase smooth and globular, interparietal wide, occiput deep, evident cranial flexion; **(7)** zygomatic plate narrow, its anterior margin straight and barely projecting beyond dorsal maxillary root of zygomatic arch, its posterior edge set just in front of the first molar, superficial masseter inserts on a rugose bump at base of ventral zygomatic root; **(8)** vertical ridge marking frontal-squamosal suture at back of postorbital region, section of parietal projects ventrad beyond temporal beading to form part of lateral braincase wall, squamosal intact except for large subsquamosal foramen; **(9)** wide, bony alisphenoid struts; **(10)** moderately wide and long incisive foramina, their posterior margins ending slightly anterior to front faces of first molars, even with them or, projecting slightly between; **(11)** molar rows diverge slightly, bony palate short with its posterior margin even with back faces of third molars or extending slightly beyond them, palatal surface with deep palatine grooves, posterior palatine foramina level with middle of second molar; **(12)** elongate and spacious sphenopalatine vacuities; **(13)** wide pterygoid plates with moderately deep pterygoid fossa, small to moderate sphenopterygoid openings; **(14)** small ectotympanic (auditory) bulla relative to skull size, capsule incompletely covering periotic, posterodorsal wall of carotid canal formed by periotic and not bullar capsule; **(15)** large stapedial foramen, no sphenofrontal foramen or squamosal-alisphenoid groove, indicating a carotid arterial pattern widespread within Murinae (character state 2 of Carleton, 1980; pattern 2 described by Voss, 1988); **(16)** dentary stocky, high ramus between incisor and molar row, high ascending ramus, large coronoid and condyloid processes, end of alveolar capsule forming prominent labial projection at level of sigmoid notch between coronoid and condyloid processes; **(17)** upper incisor enamel orange, lowers slightly paler; **(18)** each upper molar (maxillary) with three roots, each lower (mandibular) with two; **(19)** molars brachydont, cusp rows forming moderately complicated cuspidate occlusal patterns, third molar large relative to others in toothrow; **(20)** first and second upper molars of most specimens with some form of an enamel ridge projecting from anterolingual surface of cusp t8 anteriorly to posterior margin of lingual cusp t4, a labial enamel ridge connects anterolabial margin of cusp t9 with posterolabial margin of cusp t6, a comparable but shorter ridge projects from the anterior surface of cusp t5 to meet the posterior margin of cusp t3 near the cingulum, and with conspicuous posterior cingulum on first molars, also present on second molar in a few specimens; **(21)** no cusp t7; **(22)** anteroconid formed of chunky anterolingual and anterolabial cusps, anterocentral cusp absent, anterolabial remnant on second lower molar, no anterior labial cusplets on first and second lower molars, but posterior labial cusplet present on each tooth, posterior cingulum elongate; **(23)** phallic morphology highly divergent from other endemic New Guinea murines surveyed (Lidicker, 1968); **(24)** sperm head falciform

in shape, with single and long apical hook and lacking ventral processes, spermatozoal tail moderately long (Breed and Aplin, 1994).

THE SPECIES OF *COCCYMYS*

Most lists, faunal studies, and taxonomic revisions published since Tate's 1951 treatise recognized only *ruemmleri*, whether as a species of *Pogonomelomys* (Tate, 1951; Laurie and Hill, 1954; Menzies and Dennis, 1979; Willett et al., 1989; Flannery, 1990) or *Coccymys* (Menzies, 1990; Musser and Carleton, 1993; Flannery, 1995). This view of a single species was championed in Menzies's (1990: 133) revision in which *C. ruemmleri* was recorded as occurring "throughout the central mountain ranges of New Guinea from Lake Habbema in the west to the Wau-Bulolo area in the east, possibly further east, usually over 1500 asl and up to 2500 or higher." By 2005, Musser and Carleton (2005) had accepted the Central Cordilleran distribution of *ruemmleri* previously outlined by Menzies but also announced the presence of a second undescribed species in the Maneau Range of New Guinea's eastern peninsula.

The present report on *Coccymys* was sparked by our intention to describe that eastern peninsular species, and was not meant to comprise a revision of the genus. But this simple goal could not be achieved without comparing the sample from the Maneau Range with material collected from the Central Cordillera in western and central New Guinea, an undertaking that has resulted in a revision of species diversity in *Coccymys*. Through those comparisons, we could demonstrate the distinctiveness of the new form and in the process reject the notion that a single species occurred from the Lake Habbema region in the west to the Wau-Bulolo area in the east. The reality is different—two species are found throughout this Cordilleran backbone, generally replacing one another in a linear pattern but with regional sympatry in western Papua New Guinea. True *C. ruemmleri* is documented by specimens from the Snow Mountains and Star Mountains in the western half of New Guinea. *Coccymys shawmayeri* replaces *C. ruemmleri* in the montane forests and alpine grasslands of the Central Cordillera from the

Telefomin area in the west eastward beyond the Wau-Bulolo region to Mt. St. Mary in the east, the western region of the Owen Stanley Ranges. From the Wau-Bulolo area eastward to the Maneau Range is the territory of the new species, *C. kirrhos*, which is sympatric with *C. shawmayeri* in the Wau-Bulolo area and farther east in the western portion of the Owen Stanley Ranges.

We arrived at this view of three species occurring along the mountainous backbone of New Guinea by first analyzing phenetic variation in external, cranial, and dental traits among AMNH samples of *Coccymys* only. The results were later tested against data derived from AM, BBM, and BMNH samples. We organized the AMNH specimens into six population samples, three from the Snow Mountains in western New Guinea, one of which contains the holotype and type series of *ruemmleri*; two from the eastern Cordillera, Mt. Hagen, and Mt. Wilhelm; and the three examples from Mt. Dayman in the Maneau Range at the far end of the Owen Stanley Ranges (table 1). Variation among these samples in external traits (lengths of head and body, tail, and hind feet) is summarized by univariate means (tables 4–6). Multivariate approaches in the form of discriminant function analyses allowed us to assess the significance of morphometric variation in cranial and dental variables among the six AMNH samples.

Morphometric differences among the six population samples are summarized in the patterns of covariation in cranial and dental variables reflected in graphs of specimen scores projected onto the first and second canonical variates extracted from discriminant-function analysis (fig. 4). Three patterns in multivariate space are revealed. First, two slightly overlapping clusters of scores are aligned along the first axis. The left cluster identifies specimens from the Snow Mountains (Mt. Wilhelmina, Lake Habbema, and Bele River valley), the right encompasses specimen scores from eastern New Guinea samples (Mt. Hagen and Mt. Wilhelm). Covariation in breadth of mesopterygoid fossa; height of braincase; and lengths of bony palate, rostrum, and maxillary molar row are principally responsible for this scatter of scores along the first axis, partic-

TABLE 1
Population Samples of the Species of *Coccymys* and *Brassomys* Employed in Univariate and Multivariate Analyses of Cranial and Dental Variables
(Number in parentheses after each locality keys to numbered collection locality in gazetteer and distribution maps in fig. 2 for *Coccymys* and fig. 3 for *Brassomys*. Number in brackets indicates total number of specimens for each species. Specimens measured are identified by museum initials and catalog numbers in footnotes.)

Species and sample	N	Locality
Coccymys ruemmleri[a]	[47]	
Mt. Wilhelmina	13	Snow Mountains, 3560–4050 m (3)
Lake Habbema	15	Snow Mountains, 3225 m (4)
Bele River area	6	Snow Mountains, 9, 18 km NE Lake Habbema, 2800 m and 2200 m (5)
Star Mountains	13	3100 m and 3200 m (6)
Coccymys shawmayeri[b]	[54]	
Telefomin Valley	6	2300 m, 2594 m, and 2300 m (7)
Mt. Hagen	14	2121–2576 m (12)
Mt. Wilhelm	25	Lake Aunde, Pengagl Creek, east slopes; 2770, 3400 and 3570 m (14)
Wau area, Bulldog Road	2	South of Edie Creek, 2400 m and 2500 m (18)
Mt. St. Mary	7	3000 m (19)
Coccymys kirrhos[c]	[3]	Mt. Dayman, 2230 m (22)
Brassomys albidens[d]	[3]	Lake Habbema, 3225 m, and 9 km NE, 2800 m (2, 3)

[a]Mt. Wilhelmina: AMNH 110151, 110183, 110184, 101188, 110325, 110382, 110392, 110407, 110431, 110445, 150455, 150461, 150466. Lake Habbema: AMNH 150669 (holotype of *ruemmleri*), 150700, 150709, 150771, 150811–813, 150820, 150852, 150861, 150872, 150878, 150891, 150895, 151559. Bele River valley: AMNH 150565, 150619, 151185, 151277, 151306, 151323. Star Mountains: BBM-NG 98563, 98581, 98588, 98600, 100167, 100177, 100195, 100212, 100227, 100239, 100241, 100250, 100261.
[b]Telefomin Valley: BBM-NG 98365, 98407, 98492, 100147, 108076, 108233. Mt. Hagen: AMNH 156475, 156486, 156513, 156514, 156540, 156547, 156548, 156589, 156605, 156646, 156664, 156665, 156671, 156673. Mt. Wilhelm: AMNH 192092–098, 192100–102, 192104–109, 192114, 192115, 192733–736, 192738, 192740. Bulldog Road: BBM-NG 101267, 101502. Mt. St. Mary: BBM-NG 96863, 96864, 96895–897, 96909, 96913.
[c]Mt. Dayman: AMNH 158173, 158174, 158175 (holotype of *kirrhos*).
[d]Lake Habbema and Bele River valley : 150541, 150531, 150821 (holotype of *albidens*).

ularly rostral length—breadth of first upper molar also contributes but with less force (see table 2, and diagram of factor loadings in fig. 4). Compared with the three series of *C. ruemmleri* from the Snow Mountains, samples from Mt. Hagen and Mt. Wilhelm have a relatively wider mesopterygoid fossa; shallower braincase (less bulbous); noticeably shorter bony palate, rostrum, and maxillary toothrow; and somewhat narrower first upper molar.

These proportional distinctions are also mirrored in the univariate summaries listed in tables 4–6, and are summarized in a phenetic clustering pattern of population samples based on Mahalanobis distance squared (fig. 5). This dichotomy, based on cranial and dental variables, is accompanied by contrasts in length and coloration of fur, relative length of tail, and frequency of white tail tips in the samples. Specimens in the three samples from the Snow Mountains are typically characterized by a thicker dorsal coat along with darker upperparts, underparts, and tail than specimens from Mt. Wilhelm and Mt. Otto (we could not use most of the specimens from Mt. Hagen to assess coloration of pelage or most dimensions of appendages because in the field they were all dumped into fluid preservative and not measured beforehand; the bodies are now contorted and stiff, the fur and surfaces of appendages discolored). Relative to length of head and body, the tail is short in the samples from the Snow Mountains (LT/LHB = 140%–146%), the frequency of a white tail tip is very low (15% of 41 specimens), and when present the white portion is short (5–30 mm). By contrast, samples from Mt. Wilhelm and Mt. Otto in Papua New Guinea
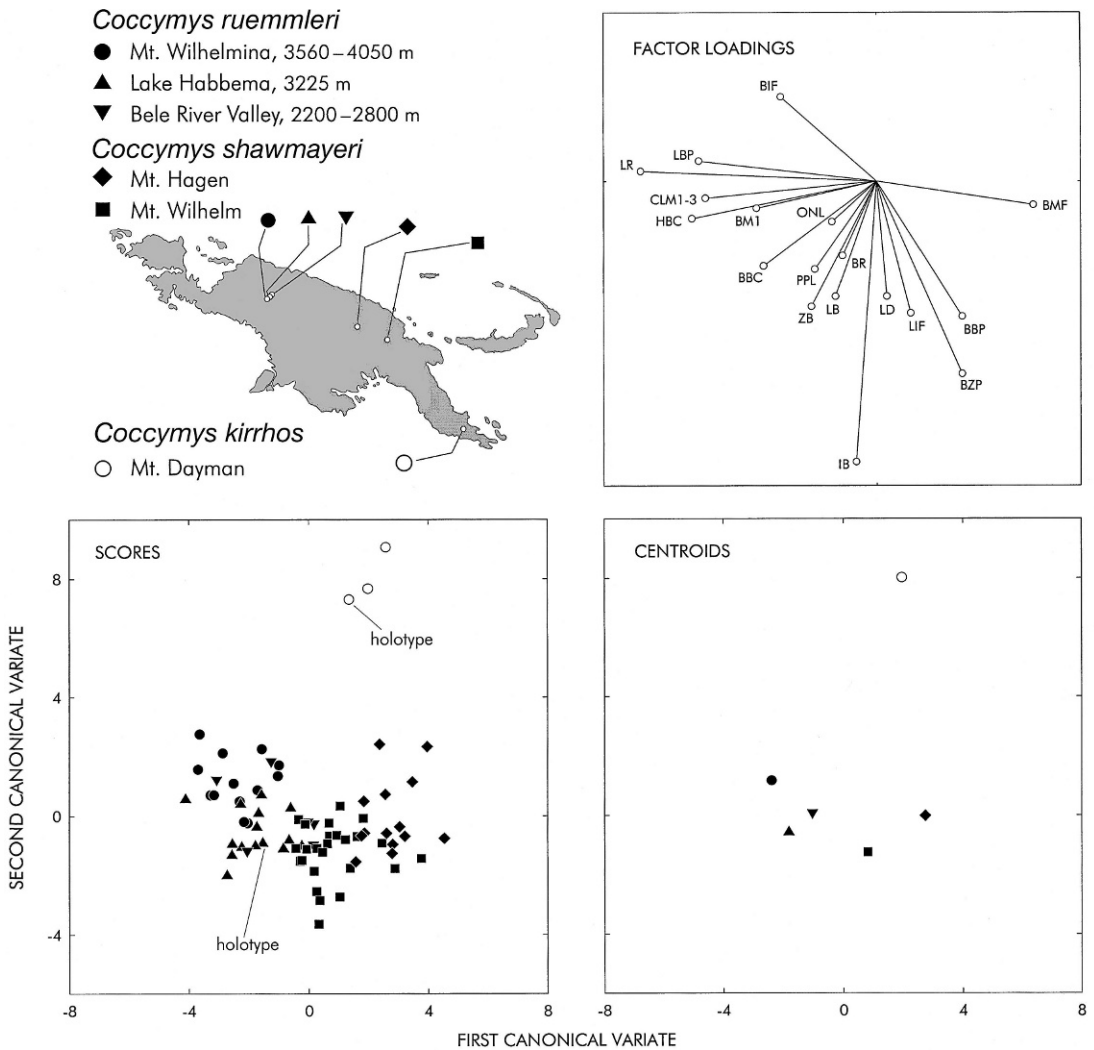
Fig. 4.   Results of discriminant function analysis. Lower left: Individual specimen scores based on log-transformed values of 16 cranial and 2 dental variables and projected onto the first and second canonical variates extracted from discriminant function analysis of six population samples representing *Coccymys ruemmleri*, *C. shawmayeri*, and *C. kirrhos*. Lower right: Plot of group centroids (population sample means) on first two canonical variates derived from discriminant function analysis of the six population samples. Upper right: Vectors of 18 cranial and dental variables corresponding to the magnitude and direction of their loadings on first and second canonical variates (also see table 2).

tend to have a relatively much longer tail (LT/LHB = 162%–170%), nearly all the tails have white tips (77% of 31 specimens), and the white segment averages longer (10–42 mm); see table 8.

These qualitative and quantitative contrasts reflect distinctions between two species: the AMNH samples from the Snow Mountains represent *Coccymys ruemmleri*; attri-

butes of the holotype of Hinton's (1943) *shawmayeri* fit with those exhibited by samples from Mt. Hagen, Mt. Wilhelm, and Mt. Otto, and that name applies to those samples.

The second pattern in the canonical ordination in figure 4 is revealed by specimen scores aligned along the second canonical variate. There the scores representing the three AMNH specimens from Mt. Dayman

TABLE 2
Results of Discriminant Function Analysis Derived from 76 Adults in Six Population
Samples of *Coccymys ruemmleri*, *Coccymys shawmayeri*, and *Coccymys kirrhos*
(Correlations, eigenvalues, and proportions of variance are explained for two canonical roots; see fig. 22.
Localities constituting each sample, and sample sizes, are listed in table 1. Mean values of measurements in
each sample are listed in tables 4–6.)

Variable	CV1	CV2	*F* (sample)	*P*
ONL	−0.013	−0.012	9.877	.000
ZB	−0.019	−0.037	7.307	.000
IB	−0.006	−0.083	25.344	.000
LR	−0.069	0.003	9.237	.000
BR	−0.010	−0.022	2.037	.084
BBC	−0.033	−0.025	13.387	.000
HBC	−0.054	−0.011	11.536	.000
BZP	0.025	−0.057	3.373	.009
LD	0.003	−0.034	10.112	.000
PPL	−0.018	−0.026	4.310	.002
LBP	−0.052	0.006	4.531	.001
BBPM1	0.025	−0.040	2.526	0.37
BMF	0.046	−0.007	3.717	.005
LIF	0.010	−0.039	7.671	.000
BIF	−0.028	0.025	2.858	.021
LB	−0.012	−0.034	8.444	.000
CLM1–3	−0.050	−0.005	10.456	.000
BM1	−0.035	−0.008	4.469	.001
Canonical correlation	0.889	0.885		
Eigenvalue	3.754	3.622		
% Variance	35.3	34.1		

are isolated from the two constellations corresponding to the samples of *C. ruemmleri* (Snow Mountains) and *C. shawmayeri* (Mt. Hagen and Mt. Wilhelm). The distribution of scores along this axis is influenced most strongly by breadths of the incisive foramina, mesopterygoid fossa, interorbit, and zygomatic plate: compared with *C. ruemmleri* and *C. shawmayeri*, the incisive foramina and mesopterygoid fossae are relatively broader in the Mt. Dayman sample, and its interorbit and zygomatic plates are relatively narrower (proportions also reflected in ratio diagrams, figs. 30, 31). Other variables responsible for the spread of scores along the second axis, but with less influence, are breadths of the bony palate and braincase, zygomatic breadth, and lengths of incisive foramina, diastema, bullae, and postpalatal region. The Mt. Dayman population has a relatively narrower bony palate, braincase, and zygomatic expanse, but shorter incisive foramina, diastema, bullae, and postpalatal region (see

table 2 and the factor loadings in fig. 4). Phenetic clustering of population samples based on Mahalanobis distances squared also reflects the broad morphometric gulf betwen the sample from Mt. Dayman and those representing *C. ruemmleri* and *C. shawmayeri* (fig. 5).

The AMNH sample from Mt. Dayman forms the type series of the new species, *C. kirrhos*, to be described in the accounts of species following this section. Coupled with the multivariate contrasts outlined here, the new species is typically smaller in some external dimensions and in most cranial and dental measurements than the other two species, and exhibits different fur thickness and coloration, and tail proportion and color pattern.

A final pattern of covariation among variables is evident in the clustering of projected scores along the first canonical axis in figure 4. Scores representing *C. kirrhos*, n. sp., are aligned with those for the samples of
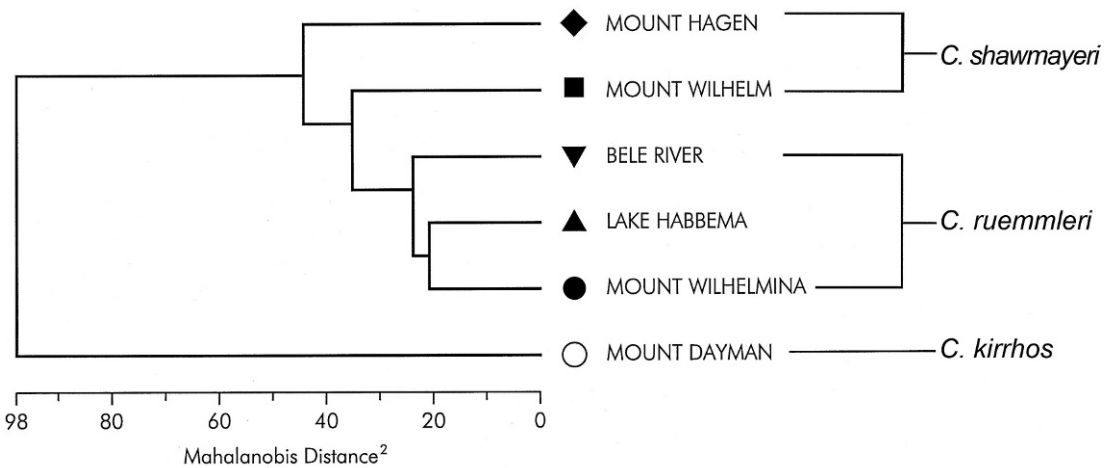
Fig. 5.   UPGMA clustering of six population samples representing *Coccymys ruemmleri*, *C. shawmayeri*, and *C. kirrhos* generated from Mahalanobis distances (D^2) among group centroids (means). Size of samples, mean values of measurements for variables, and specimens measured are listed in tables 4–6.

C. shawmayeri from Mt. Hagen and Mt. Wilhelm in the Central Cordillera west of the Owen Stanley Ranges, and not with scores for the three population samples of *C. ruemmleri* from the Snow Mountains. Covariation in breadth of mesopterygoid fossa, height of braincase, and lengths of bony palate, rostrum, and maxillary molar row are principally responsible for the dispersion of scores along the first axis, particularly rostral length and breadth of mesopterygoid fossa; breadth of first upper molar also contributes but with less impact (see table 2, and diagram of factor loadings in fig. 4). Compared with the three series of *C. ruemmleri* from the Snow Mountains, samples of *C. shawmayeri* from Mt. Hagen and Mt. Wilhelm, along with *C. kirrhos*, n. sp., from Mt. Dayman, have a relatively wider mesopterygoid fossa, narrower braincase and first upper molar, but shorter bony palate, rostrum, and maxillary molar row. This pattern supports the assumption that the population of *C. kirrhos*, n. sp., in the Maneau Range (and, as we will demonstrate below, populations elsewhere in the montane reaches of the Owen Stanley Ranges) is more closely related to populations of *C. shawmayeri* in the eastern half of the Central Cordillera than to those of *C. ruemmleri* in the western region, suggesting

past geographic isolation and subsequent morphological divergence from *C. shawmayeri* that eventually resulted in the distinctive phenetic traits now characterizing *C. kirrhos*, n. sp.

We also uncovered patterns in covariation of cranial and dental variables by employing a range of principal components analyses designed to test the significance of covariation among different sets of geographic samples. For this multivariate approach, various AMNH samples were combined in different analyses with BBM population samples from the Star Mountains, the Telefomin Valley, Bulldog Road in the Wau area, and Mt. St. Mary (table 1). Single specimens from Smith's Gap (BBM), Dumae Creek and Mt. Simpson (BBM) in the Manau Range, and the holotype of *shawmayeri* (BMNH) were also included. The patterns revealed in the principal components analyses, combined with our observations of qualitative external traits and univariate summaries of cranial and dental variables, identify the sample from the Star Mountains as *C. ruemmleri*; the material from the Telefomin area, Mt. St. Mary, and six of the seven from Bulldog Road as *C. shawmayeri*; and one individual from Bulldog Road, a specimen from Smith's Gap, one from Dumae Creek, and another

from Mt. Simpson as *C. kirrhos*, n. sp. Results of these analyses are presented in the appropriate accounts of species.

The first account consists of a detailed description of *C. ruemmleri*, the type species of the genus, and covers its morphology based on evidence primarily from skins and skulls, known geographic range, habitats, and whatever other biological information that is available in the literature. The characteristics of *C. ruemmleri* form the standard to which the other two species, *C. shawmayeri* and *C. kirrhos*, n. sp., will be compared.

Coccymys ruemmleri
(Tate and Archbold, 1941)

HOLOTYPE AND TYPE LOCALITY: The holotype of *Coccymys ruemmleri* is an adult male (AMNH 150669) collected by W.B. Richardson (original number 4523) on July 26, 1938. It consists of an intact stuffed study skin (fig. 6) and skull, which, except for the missing jugal bones, is in good condition (fig. 9). Occlusal surfaces of molars are worn, but cusp patterns are still evident. External, cranial, and dental measurements are listed in table 7.

The type locality is about 15 miles (24 km) north of Mt. Wilhelmina (Gunung Trikora on contemporary maps) at 3225 m near Lake Habbema (04°49′S/138°41′E; locality 4 in gazetteer and fig. 2), which is nestled between ridges forming northern slopes of the Snow Mountains ("Sneeuw Gebergte" on older Dutch maps; Pegunungan Maoke is the Indonesian designation on contemporary maps and in modern gazetteers), that region of the Central Cordillera in western New Guinea (Papua Province, Indonesia).

EMENDED DIAGNOSIS: Most of the traits enumerated in the generic diagnosis also characterize *C. ruemmleri*: the dorsal fur is soft, thick (11–14 mm, measured near the rump), and dark brown (suffused with black in some individuals); underparts are whitish gray to dark grayish white, with the darker tone predominating in samples (a few specimens exhibit a buffy wash resulting in grayish buff underparts); the tail is longer than length of head and body (LT/LHB = 140%–146%; table 3), brown everywhere in
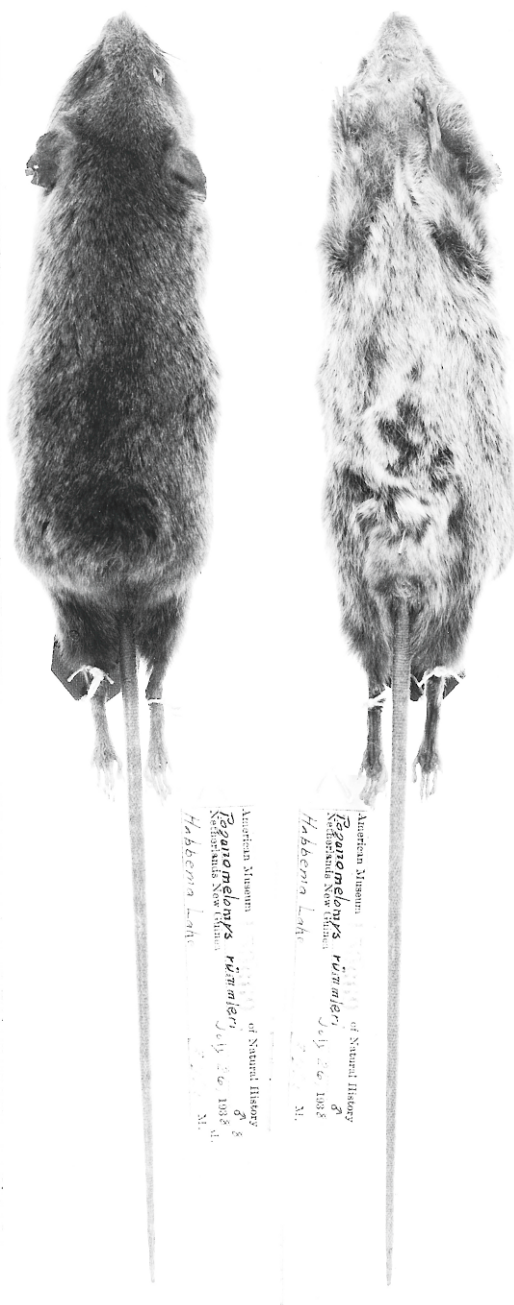

Fig. 6. Holotype of *Coccymys ruemmleri* (AMNH 150669), an adult male from Lake Habbema on north slopes of the Snow Mountains, 3225 m. Measurements are listed in table 7.

TABLE 3
**Descriptive Statistics for Measurements (mm) of Lengths of Head and Body (LHB), Tail
(LT), Hind Foot (LHF), and Ear (LE) from Population Samples of *Coccymys ruemmleri*,
Coccymys shawmayeri, *Coccymys kirrhos*, and *Brassomys albidens*[a]**
(Mean plus or minus one SD and observed range [in parentheses] are listed. Specimens measured are listed
in footnotes.)

Species and sample	N	LHB	LT	LHF	LE	LT/LHB (%)
C. ruemmleri[b]						
Mt. Wilhelmina	13	102.5 ± 3.69	143.7 ± 7.31	26.8 ± 0.38	16.5 ± 1.27	140
		(98–108)	(130–156)	(26–27)	(15–18)	
Lake Habbema	16	102.3 ± 4.68	148.4 ± 6.67	26.7 ± 0.48	16.9 ± 1.09	145
		(93–109)	(135–157)	(26–27)	(15–19	
Bele River valley	8	107.3 ± 3.92	157.0 ± 8.49	26.8 ± 1.04	16.9 ± 0.64	146
		(103–114)	(146–171)	(25–28)	(16–18)	
Star Mountains	14	100.9 ± 5.66	141.6 ± 9.54	27.5 ± 0.76	19.5 ± 1.09	140
		(89–110)	(122–154)	(26–28)	(17–21)	
C. shawmayeri[c]						
Telefomin area	6	97.5 ± 6.02	147.0 ± 6.75	25.2 ± 0.75	16.7 ± 1.03	151
		(88–105)	(140–155)	(24–26)	(16–18)	
Mt. Wilhelm	16	96.7 ± 5.89	156.9 ± 8.69	25.9 ± 0.57	17.7 ± 1.14	162
		(87–107)	(140–170)	(25–27)	(16–20)	
Mt. Otto	1	104	177	27	18	170
Bulldog Road	3	101.3 ± 0.58	149.3 ± 5.67	24.3 ± 0.58	17.7 ± 0.58	147
		(101–102)	(143–157)	(24–25)	(17–18)	
Mt. St. Mary	7	102.3 ± 2.93	148.7 ± 11.60	26.3 ± 0.76	19.3 ± 0.49	145
		(97–105)	(132–165)	(25–27)	(19–20)	
C. kirrhos[d]						
Bulldog Road	1	105	157	26	20	150
Smith's Gap	1	98	150	25	20	153
Mt. Dayman	3	92.0 ± 4.36	153.7 ± 4.73	24.0 ± 0.00	13.7 ± 0.58	167
		(87–95)	(150–159)	(—) 3	(13–14)	
Dumae Creek	1	94	142	23	20	151
Mt. Simpson	1	80	145	24	17	181
B. albidens[e]						
Bele River valley, Lake Habbema	5	116.6 ± 5.23	154.2 ± 7.76	26.2 ± 0.98	20.0 ± 1.58	132
		(111–122)	(144–162)	(25–27)	(18–22)	

[a]Data were obtained from collector's measurements recorded on skin labels except for length of hind foot (includes claws), which Musser measured on the dry skin. Length of ear was taken from notch to distal curve of pinnae for BBM specimens; we assume AMNH specimens were measured the same way but cannot be certain. The ratio, LT/LHB, was calculated using mean values.

The sample from Mt. Hagen on which cranial and dental measurements were made (table 4) consists of specimens preserved in fluid in the field, with skulls later extracted in the museum. Unfortunately, no external measurements are attached to the specimens. We could not measure the bodies because most had been eviscerated in the field and obtaining reliable measurements was not possible; the specimens are also discolored and provide no basis for any chromatic observations of the fur and tail.

[b]Mt. Wilhelmina: AMNH 110151, 110183, 110184, 110188, 110325, 110382, 110392, 110407, 110431, 110445, 150455, 150461, 150466. Lake Habbema: AMNH 150669 (holotype of *ruemmleri*), 150696, 150700, 150709, 150771, 150811–814, 150820, 150852, 150861, 150872, 150878, 150891. Bele River valley: AMNH 150565, 150589, 150619, 151185, 151220, 151277, 151306, 151323. Star Mountains: BBM-NG 98563, 98581, 98600, 100167, 100212, 100241.

[c]Telefomin area: BBM-NG 98365, 98407, 98492, 100147, 108076, 108233. Mt. Wilhelm: AMNH 192092, 192093, 192095–098, 192100–102, 192104–109, 192113. Mt. Otto: AMNH 192116. Bulldog Road: BBM-NG 55824, 101267, 101502. Mt. St. Mary: BBM-NG 96863, 96864, 96895–897, 96913, 96909.

[d]Mt. Dayman: AMNH 158173, 158174, 158175 (holotype of *kirrhos*). Dumae Creek: BBM-NG 109165. Mt. Simpson: BBM-NG 184493.

[e]Bele River and Lake Habbema: AMNH 150531, 150541, 150607, 150821 (holotype of *albidens*), 150923.

TABLE 4
Descriptive Statistics for Cranial and Dental Measurements (mm) from Population
Samples of *Brassomys albidens* and *Coccymys ruemmleri*
(Mean plus or minus one SD and observed range [in parentheses] are listed.)

Variable	*B. albidens* Bele River and Lake Habbema N = 3	*C. ruemmleri* Mt. Wilhelmina N = 13	*C. ruemmleri* Lake Habbema N = 15	*C. ruemmleri* Bele River valley N = 6	*C. ruemmleri* Star Mountains N = 13
ONL	30.16 ± 0.58 (29.49–30.55)	28.40 ± 0.59 (27.35–29.41)	27.93 ± 0.61 (27.56–28.71)	28.76 ± 0.41 (28.06–29.18)	29.21 ± 0.76 (27.9–30.1)
ZB	15.35 ± 0.31 (15.04–15.65)	15.64 ± 0.33 (15.15–16.15)	15.73 ± 0.41 (15.13–16.40)	15.45 ± 0.28 (15.11–15.89)	15.47 ± 0.42 (14.8–16.2)
IB	5.03 ± 0.39 (4.64–5.42)	4.37 ± 0.09 (4.20–4.54)	4.48 ± 0.13 (4.19–4.73)	4.44 ± 0.17 (4.14–4.63)	4.31 ± 0.11 (4.2–4.5)
LR	9.30 ± 0.49 (8.75–9.70)	8.39 ± 0.20 (8.11–8.76)	8.41 ± 0.30 (7.81–8.91)	8.54 ± 0.19 (8.21–8.73)	8.27 ± 0.35 (7.6–8.9)
BR	5.75 ± 0.27 (5.45–5.98)	4.65 ± 0.19 (4.27–5.01)	4.70 ± 0.24 (4.25–5.14)	4.83 ± 0.09 (4.70–4.93)	4.72 ± 0.15 (4.5–5.0)
BBC	13.90 ± 0.46 (13.37–14.20)	13.78 ± 0.23 (13.48–14.16)	13.84 ± 0.21 (13.35–14.12)	13.44 ± 0.15 (13.23–13.58)	13.99 ± 0.23 (13.7–14.4)
HBC	9.75 ± 0.42 (9.49–10.24)	9.65 ± 0.31 (9.13–10.24)	9.56 ± 0.18 (9.20–9.88)	9.37 ± 0.21 (8.97–9.52)	9.61 ± 0.27 (9.3–10.1)
BZP	2.18 ± 0.10 (2.06–2.25)	2.66 ± 0.15 (2.36–2.88)	2.69 ± 0.15 (2.26–2.90)	2.91 ± 0.11 (2.79–3.10)	2.81 ± 0.20 (2.5–3.2)
LD	7.26 ± 0.21 (7.07–7.49)	7.26 ± 0.23 (6.80–7.57)	7.24 ± 0.23 (6.77–7.54)	7.47 ± 0.21 (7.22–7.77)	7.10 ± 0.27 (6.6–7.5)
PPL	11.07 ± 0.55 (10.64–11.68)	10.28 ± 0.38 (9.70–10.90)	10.09 ± 0.30 (9.47–10.57)	10.46 ± 0.15 (10.25–10.62)	10.02 ± 0.37 (9.4–10.6)
LBP	5.59 ± 0.43 (5.18–6.04)	4.84 ± 0.147 (4.56–5.09)	4.68 ± 0.26 (4.25–5.19)	4.86 ± 0.26 (4.59–5.22)	4.82 ± 0.19 (4.5–5.1)
BBPM1	2.76 ± 0.18 (2.61–2.96)	2.98 ± 0.28 (2.07–3.16)	3.03 ± 0.14 (2.88–3.37)	3.08 ± 0.18 (2.97–3.44)	3.15 ± 0.11 (2.9–3.3)
BMF	2.49 ± 0.14 (2.40–2.65)	1.90 ± 0.13 (1.64–2.11)	1.97 ± 0.16 (1.65–2.24)	1.95 ± 0.20 (1.64–2.25)	1.85 ± 0.13 (1.7–2.0)
LIF	4.78 ± 0.35 (4.54–5.18)	4.95 ± 0.16 (4.70–5.20)	4.92 ± 0.16 (4.66–5.26)	4.90 ± 0.14 (4.73–5.11)	4.79 ± 0.17 (4.5–5.0)
BIF	1.88 ± 0.08 (1.84–1.97)	1.94 ± 0.14 (1.75–2.19)	1.94 ± 0.14 (1.74–2.19)	1.82 ± 0.07 (1.75–2.19)	1.95 ± 0.07 (1.9–2.1)
LB	5.35 ± 0.17 (5.20–5.53)	4.16 ± 0.12 (3.88–4.32)	4.16 ± 0.12 (3.98–4.37)	4.27 ± 0.13 (4.09–4.46)	4.23 ± 0.12 (4.0–4.4)
CLM1–3	5.11 ± 0.04 (5.09–5.16)	4.40 ± 0.13 (4.18–4.59)	4.36 ± 0.12 (4.15–4.57)	4.40 ± 0.11 (4.30–4.57)	4.63 ± 0.10 (4.4–4.7)
BM1	1.61 ± 0.04 (1.58–1.65)	1.33 ± 0.04 (1.28–1.39)	1.34 ± 0.04 (1.26–1.40)	1.32 ± 0.06 (1.22–1.37)	1.37 ± 0.05 (1.3–1.4)

most specimens, with a very few (6 out of 55; 11%) showing a short white tip (table 8); the skull has a long rostrum and bony palate, bulbous braincase, and heavy molars.

GEOGRAPHIC DISTRIBUTION: As documented by modern and fossil specimens, *C. ruemmleri* is known only from the Snow Mountains and the adjacent Star Mountains to the east, which together comprise most of the high Central Cordillera of western New Guinea (see fig. 2 and gazetteer). This mountain backbone is part of what Flannery (1995: 37) labeled the "Western Sub-Province" of the "Tumbunan Biogeographic Province" that was defined by Schodde and Calaby (1972); the Sub-Province extends from the Paniai (= Wissel) Lakes region in the west (03°55′S, 136°15′E) to the deep valley of the Strickland River in the east (06°30′S, 142°04′E). Helgen (2007c) regards the Snow Mountains region and Star Mountains region as separate zoogeographic divisions.

TABLE 5
**Descriptive Statistics for Cranial and Dental Measurements (mm) from Population
Samples of *Coccymys shawmayeri***
(Mean plus or minus one SD and observed range [in parentheses] are listed.)

Variable	Telefomin area N = 5	Mt. Hagen N = 14	Mt. Wilhelm N = 25	Bulldog Road N = 2	Mt. St. Mary N = 7
ONL	27.76 ± 0.77 (27.2–29.0)	28.46 ± 0.77 (27.50–30.16)	27.37 ± 0.98 (26.02–29.38)	28.55 ± 0.50 (28.2–28.9)	28.80 ± 0.76 (27.5–29.9)
ZB	15.0 ± 0.41 (14.5–15.5)	15.45 ± 0.36 (14.92–16.12)	15.60 ± 0.50 (14.73–16.50)	15.55 ± 0.50 (15.2–15.9)	15.66 ±0.47 (14.9–16.2)
IB	4.18 ± 0.15 (4.0–4.4)	4.45 ± 0.13 (4.20–4.65)	4.50 ± 0.13 (4.31–4.84)	4.30 ± 0.14 (4.2–4.4)	4.50 ± 0.19 (4.3–4.8)
LR	8.02 ±0.31 (7.7–8.4)	7.88 ± 0.27 (7.39–8.30)	7.95 ± 0.42 (6.76–8.67)	8.00 ± 0.00 (8.0–8.0)	7.81 ± 0.23 (7.5–8.2)
BR	4.34 ± 0.15 (4.2–4.6)	4.72 ± 0.28 (4.10–5.19)	4.60 ±0.28 (3.98–4.96)	4.55 ± 0.07 (4.5–4.6)	4.76 ± 0.29 (4.4–5.2)
BBC	13.12 ± 0.24 (12.9–13.5)	13.38 ± 0.38 (12.61–13.91)	13.55 ± 0.25 (13.08–14.07)	13.65 ± 0.50 (13.3–14.0)	13.67 ± 0.27 (13.2–13.9)
HBC	9.10 ± 0.45 (8.5–9.6)	9.14 ± 0.33 (8.83–9.77)	9.18 ± 0.27 (8.74–9.61)	9.20 ± 0.57 (8.8–9.6)	9.19 ± 0.16 (9.0–9.4)
BZP	2.82 ± 0.08 (2.7–2.9)	2.78 ± 0.27 (2.35–3.26)	2.79 ± 0.20 (2.47–3.18)	3.05 ± 0.21 (2.9–3.2)	2.89 ± 0.19 (2.7–3.2)
LD	6.92 ± 0.33 (6.6–7.3)	7.55 ± 0.34 (7.06–8.11)	7.08 ± 0.34 (6.63–7.71)	6.95 ± 0.35 (6.7–7.2)	7.07 ± 0.26 (6.7–7.5)
PPL	9.80 ± 0.51 (9.3–10.5)	10.22 ± 0.50 (9.42–11.00)	10.01 ± 0.52 (9.12–11.06)	10.50 ± 0.07 (10.0–10.1)	10.26 ± 0.47 (9.3–10.8)
LBP	4.48 ± 0.13 (4.3–4.6)	4.56 ± 0.28 (4.15–5.08)	4.55 ± 0.21 (4.15–4.97)	4.40 ± 0.00 (4.4–4.4)	4.44 ± 0.17 (4.2–4.6)
BBPM1	2.82 ± 0.08 (2.7–2.9)	3.17 ± 0.18 (2.89–3.56)	3.01 ± 0.21 2.53–3.42)	2.95 ± 0.07 (2.9–3.0)	3.03 ± 0.13 (2.8–3.2)
BMF	1.74 ± 0.06 (1.7–1.8)	1.97 ± 0.18 (1.67–2.22)	2.08 ± 0.13 (1.90–2.49)	1.90 ± 0.14 (1.8–2.0)	1.93 ± 0.15 (1.7–2.1)
LIF	4.66 ± 0.18 (4.5–4.9)	5.13 ± 0.15 (4.73–5.46)	4.88 ± 0.26 (4.37–5.54)	4.85 ± 0.07 (4.8–4.9)	4.84 ± 0.22 (4.6–5.1)
BIF	1.78 ± 0.08 (1.7–1.9)	1.91 ± 0.13 (1.70–2.11)	1.82 ± 0.13 (1.54–2.06)	1.80 ± 0.00 (1.8–1.8)	1.94 ± 0.08 (1.8–2.0)
LB	3.98 ± 0.13 (3.8–4.1)	4.20± 0.13 (3.94–4.35)	4.10 ± 0.15 (3.83–4.34)	4.04 ± 0.07 (4.0–4.1)	4.23 ± 0.16 (4.0–4.5)
CLM1–3	4.02 ± 0.08 (3.8–4.1)	4.20 ± 0.11 (4.00–4.39)	4.20 ± 0.125 (3.92–4.40)	4.10 ± 0.14 (4.0–4.2)	4.24 ± 0.08 (4.1–4.3)
BM1	1.30 ± 0.07 (1.2–1.4)	1.27 ±0.050 (1.20–1.33)	1.32 ± 0.04 (1.26–1.41)	1.30 ± 0.00 (1.3–1.3)	1.31 ± 0.04 (1.3–1.4)

A few Holocene subfossils collected at the base of the Carstensz Massif (Mt. Jaya) comprise the westernmost sample from the Snow Mountains (J.H. Hope, 1976). To the east is the source of the largest modern sample (in AMNH), collected from a transect along the northern slopes of the Snow Mountains, extending from the Bele River valley at 2200 m through the terrain around Lake Habbema at 3235 m and onto the high flanks of Mt. Wilhelmina between 3560 and 4040 m (figs. 2, 47, 48). Fossils excavated from Pleistocene sediments in Kelangurr Cave come from about 60 km west of Lake Habbema, in a valley leading into the broader valley of the West Baliem River.

The easternmost record consists of specimens from 3100 and 3200 m in the eastern section of the Star Mountains in western Papua New Guinea (in BBM; also Flannery and Seri, 1990).

Coccymys ruemmleri most likely occurs throughout the high reaches of the western Central Cordillera, but the vast montane

TABLE 6
Cranial and Dental Measurements (mm) for Samples of *Coccymys kirrhos*
(Mean plus or minus one SD and observed range [in parentheses] are listed for the sample from Mt. Dayman.)

	Wau area, Bulldog Road BBM-NG 55824 Adult	Smith's Gap BBM-NG 96950 Adult	Maneau Range, Mt. Dayman AMNH 158173–175 Young adult–adult	Maneau Range, Dumae Creek BBM-NG 109165 Adult	Maneau Range, Mt. Simpson BBM-NG 184493 Young adult
ONL	28.9	28.5	26.14 ±0.54 (25.52–26.53)	27.2	26.4
ZB	15.2	14.6	14.26 ± 0.30 (13.96–14.55)	14.1	13.6
IB	3.9	4.2	3.74 ± 0.07 (3.66–3.79)	3.9	3.8
LR	8.2	8.4	7.87 ± 0.23 (7.61–8.02)	7,9	7.7
BR	4.8	4.4	4.35 ± 0.09 (4.25–4.41)	4.2	4.3
BBC	13.4	13.2	12.71 ± 0.19 (12.56–12.92)	12.9	13.6
HBC	10.0	9.2	8.78 ± 0.02 (8.76–8.80)	8.9	8.5
BZP	2.4	2.5	2.47 ± 0.11 (2.34–2.54)	2.7	2.1
LD	7.4	6.8	6.45 ± 0.32 (6.09–6.69)	6.4	6.6
PPL	9.5	9.7	9.25 ± 0.45 (8.73–9.55)	9.6	8.6
LBP	5.2	4.4	4.48 ± 0.08 (4.40–4.56)	4.2	4.4
BBPM1	3.0	2.7	2.75 ± 0.18 (2.62–2.96)	2.4	2.5
BMF	2.1	2.0	2.13 ± 0.08 (2.05–2.20)	2.1	1.8
LIF	4.6	4.8	4.41 ± 0.32 (4.08–4.72)	4.4	4.2
BIF	2.1	2.0	1.90 ± 0.06 (1.84–1.96)	1.9	1.8
LB	3.9	4.0	3.75 ± 0.10 (3.66–3.86)	3.7	3.6
CLM1–3	4.2	4.0	4.07 ± 0.03 (4.05–4.10)	4.0	4.0
BM1	1.3	1.3	1.30 ± 0.04 (1.26–1.34)	1.3	1.3

landscape between documented collection sites in the Carstensz and Wilhelmina regions of the Snow Mountains and those localities to the east in the Star Mountains has not enjoyed any significant biological surveys focusing upon small mammals (Helgen, 2007a). Aside from activities along the transect between Mt. Wilhelmina and the Bele River valley, undertaken by the Archbold Expedition in 1938, results of only a few other attempts to obtain living small mammals in the area have been published. Patricia Woolley visited Lake Habbema in 1989 (see Woolley, 1990) where she collected several species of small mammals not taken in previous survey efforts, which included samples of *Pseudohydromys ellermani* and another species of *Pseudohydromys* that is being described (Helgen, 2007a). Her specimens are deposited in the Australian Museum at

TABLE 7
**Measurements (mm) for Holotypes (All Are Adults) of *Coccymys kirrhos*, *Coccymys ruemmleri*,
Coccymys shawmayeri, and *Brassomys albidens***

Variable	C. kirrhos AMNH 158175	C. shawmayeri BMNH 1947.1155	C. ruemmleri AMNH 150669	B. albidens AMNH 150821
Body and appendages[a]				
LHB	94	97	104	122
LT	159	159	138	162
LT/LHB (%)	169	164	133	133
LWTT	—	25	—	—
LHF	24	23.5	26	27
LE	14	16	17	22
Cranium and upper molars[b]				
ONL	26.37	27.82	27.65	30.44
ZB	14.55	15.51	16.06	15.65
IB	3.79	4.55	4.47	5.42
LR	7.99	8.23	8.36	9.16
BR	4.41	4.7	4.78	5.45
BBC	12.92	13.79	13.99	14.12
HBC	8.76	8.80	9.50	9.53
BZP	2.54	2.94	2.72	2.23
LD	6.58	6.83	7.18	7.23
PPL	9.46	9.25	10.13	10.88
LBP	4.40	4.74	4.35	5.18
BBPM1	2.96	2.57	3.08	2.70
BMF	2.13	1.53	1.94	2.40
LIF	4.72	4.18	5.04	5.18
BIF	1.89	1.88	2.05	1.97
LB	3.66	4.18	4.09	5.53
CLM1–3	4.06	4.06	4.25	5.16
BM1	1.30	1.29	1.35	1.59

[a]Except for the holotype of *C. shawmayeri*, Musser measured the dry hind foot (includes claws) on all of the other three skins; otherwise the values for *C. kirrhos* are Hobart Van Deusen's as written on the skin label, and those for *C. ruemmleri* and *B. albidens* are William B. Richardson's as recorded on the skin labels. Values for *C. shawmayeri* are from Hinton's (1943) original description.

[b]Paula Jenkins kindly measured the holotype of *C. shawmayeri* for us. We measured the other three.

Sydney. Collections have been made on the north slopes of the Carstensz area during the Carstensz Glaciers Expedition where subfossils were gathered (J.H. Hope, 1976), at a few locations on the south slope (Misonne, 1979), and in the Kwiyawagi area where Pleistocene fossils were collected at Kelangurr Cave (Flannery, 1999)—no living examples of *C. ruemmleri* were taken during any of these surveys. J.H. Hope (1976) accounted for 20 species of mammals obtained during the Carstensz Glaciers Expedition; of these only seven were observed, collected, or trapped, and 13 are represented by subfossils collected in limestone shelters. Trapping efforts yielded only eight *Rattus richardsoni*, eight *Rattus arrogans* (reported as *R. niobe*), and two

Paramelomys rubex in the way of rodents. As part of the Kelangurr Cave survey, Flannery (1999) surveyed the modern mammal fauna in the Kwiyawagi area (six days in June, 1994) and accounted for 14 species of marsupials, two species of bats, and nine species of rodents. We asked Tim Flannery why *C. ruemmleri* was not encountered and he wrote us: "As to *ruemmleri* in the Kwiyawagi area, we did limited trapping there so I'm not surprised we missed it. Local people seemed to collect specimens from around the villages at 2950 m and we only got upper montane and mostly larger mammals there."

Other collections from the Snow Mountains are the results of Dutch surveys to the Paniai Lake region and on the south slopes of

TABLE 8
**Frequency and Length of White Tail Tip in Geographic Samples of *Coccymys ruemmleri*,
Coccymys shawmayeri, and *Coccymys kirrhos*[a]**
(Totals for lengths of white tip are expressed as mean plus or minus one SD and observed range
[in parentheses].)

Species and sample	N	% of sample with white tip (actual number of specimens with white tip)	Range of white tip length in sample (mm)
C. ruemmleri			
Mt. Wilhelmina	16	13 (2)	5–12
Lake Habbema	16	6 (1)	22
Bele River valley	9	33 (3)	18–30
Star Mountains	14	0	—
C. shawmayeri			
Telefomin area	8	63 (5)	5–27
Nondugl	3	100 (3)	4–36
Mt. Wilhelm	27	74 (20)	10–42
Mt. Otto	1	100 (1)	28
Bulldog Road	5	100 (5)	10–24
Mt. St. Mary	7	86 (6)	10–36
C. kirrhos			
Bulldog Road	1	0	—
Smith's Gap	1	0	—
Mt. Dayman	3	0	—
Dumae Creek	1	0	—
Mt. Simpson	1	0	—
Totals			
C. ruemmleri	55	11 (6)	19.5 ± 9.96 (5–30)
C. shawmayeri	50	76 (38)	25.1 ± 9.14 (4–42)
C. kirrhos	7	0	—

[a]Lengths of the white segment at the end of the tail for specimens from Mt. Wilhelm and Mt. Otto were measured by Hobart Van Deusen in the field and recorded on skin tags. We measured lengths on dry skins or fluid-preserved material from other collection localities.

the Snow Mountains along the Lorentz and Utakwa rivers (Helgen, 2007c). No examples of *Coccymys* were acquired. Large samples of rodents were obtained near the Paniai Lake around 1750 m; perhaps too low for *C. ruemmleri*, judged from its lower altitudinal limit along the Archbold transect on the northern slopes of the Snow Mountains (2200 m).

Surveys for mammals in the high reaches of the Star Mountains have been spotty. Except for the especially fine efforts by A.B. Mirza, who collected the BBM sample of *C. ruemmleri* from above 3000 m, and the single record of *C. ruemmleri* from Mt. Capella at 3200 m (Flannery and Seri, 1990), the only significant mammalian inventories have focused on the lower northeastern slopes bounding the Telefomin Valley and in the Miyanmin area of the Telefomin District (Morren, 1989; Flannery and Seri, 1990; collections in BBM made by A.B. Mirza), and in the rainforests ("Foothill Rain Forest to Midmontane Rain Forest," 500–2500 m) of the OK Tedi headwaters on the southern flanks of the Star Mountains (Hyndman and Menzies, 1990). Surveys in the Telefomin area between 2300 and 2800 m have yielded only *C. shawmayeri* (see gazetteer), and no examples of *Coccymys* were collected during the study described by Hyndman and Menzies (1990). The bulk of the Star Mountains, particularly altitudes at 3000 m and above, remain unexplored for mammals (Helgen, 2007a).

Fig. 8. Holotype of *Brassomys albidens* (AM-NH 150821), an adult male from Lake Habbema, 3225, on the northern flanks of the Snow Mountains. Measurements are listed in table 7.

←

Fig. 7. Holotype of *Coccymys kirrhos*, n. sp. (AMNH 158175), an adult male from the north slopes of Mt. Dayman, 2230 m, in the Maneau Range. Measurements are listed in table 7.

The Star Mountains region, a zoogeographic entity separate from the Snow Mountains in Helgen's (2007c) view, also include the contiguous Victor Emanuel and Hindenburg ranges in western Papua New Guinea. The species of *Coccymys* that might be found in the montane reaches of those latter two ranges are unknown—whether *C. ruemmleri, C. shawmayeri,* or both.

The recorded altitudinal occurrence of *C. ruemmleri* in the Snow Mountains extends from mountain forests at 2200 m to alpine grasslands and scattered clumps of trees at 4050 m, the "Absolute tree limit" in the Mt. Wilhelm area (Archbold et al., 1942: 278); 3100–3200 m is the known range in upper montane forest on the Star Mountains (table 13).

The lowest record of 2200 m in the Snow Mountains deserves attention. The specimens were gathered during the Archbold Expedition in November and December 1938, and are from the vicinity of the Bele River, 18 km northeast of Lake Habbema. Writing about the birds collected in the area of the 2200-meter camp, Archbold et al. (1942: 262–263) cautioned that since

> many of the specimens were brought in by natives, sometimes by parties who had evidently come from a distance, records of altitudes at which some of the specimens were taken are lacking. Certainly at this 2,200-meter Camp we received some bunches of birds that had been taken on the top of the range above 3,000 meters.

The local people also influenced mammal acquisition (Archbold et al., 1942: 263):

> They followed the trappers, examined the traps and even tended the traps and brought in (expecting pay) mammals removed from them. But they were effective trappers on their own and from their deadfalls brought large numbers of specimens. One day more than 100 specimens, representing at least nine species, were purchased from them. In all nearly a thousand mammal specimens of at least eighteen species were brought from the natives.

Distressingly, from the archival records of the expedition, there is no way to separate the identities of the species trapped by W.B. Richardson (responsible for collecting mammals) from those brought in by local people.

Despite the ambiguity attached to the station at 2200 m, other mammals collected during the Archbold Expedition suggest 2200 m may be a real altitudinal lower limit for montane species, and the high point for those species restricted to lower altitudes, at least in the habitats along the transect worked by members of the expedition (fig 49). For example, the marsupials, *Phalanger sericeus, Phalanger carmelitae, Pseudochirops corinnae, Pseudochirulus mayeri,* and *Pseudochirulus caroli,* and the rodents *Paraleptomys wilhelmina, Hyomys dammermani, Mallomys istapantap, Mallomys rothschildi, Pogonomys* sp., and *Rattus arrogans* were encountered at 2200 m and higher but not at lower camps. Furthermore, below 2200 m, *Paraleptomys wilhelmina* and *Rattus arrogans* are replaced by closely related sister species, *Paraleptomys* sp. and *Rattus pococki* (fig. 49; Musser and Carleton, 2005). In this context, we accept the 2200-m record as a reasonable lower altitudinal limit for *C. ruemmleri* on the northern slopes of the Snow Mountains along the Archbold Expedition transect.

At lower elevations in the Papuan portion of the Star Mountains, and through a range of altitudes east of there, *C. ruemmleri* is replaced by *C. shawmayeri* in the montane reaches of the Central Cordillera all the way to Mt. St Mary in the western portion of the Owen Stanley Ranges. *Coccymys kirrhos,* n. sp., overlaps *C. shawmayeri* in the western Owen Stanley Ranges and extends to the Maneau Range at the eastern end of the Owen Stanley highlands.

Coccymys ruemmleri is apparently a western Central Cordilleran endemic. No modern or fossil examples have been recorded from the Tamrau, Arfak, or other mountains on the Vogelkop (Bird's Head) Peninsula (see Aplin, 1998; Aplin et al., 1999, who summarize Late Quaternary vertebrates from the Vogelkop). Most of these highlands remain unexplored for their mammalian faunas (Helgen, 2007c; Musser et al., 2008). The Arfaks have been the only highlands receiving any significant surveys. During recent decades, Tim Flannery worked there in 1992 in the Mokwam area (specimens at AM) at altitudes above 1500 m, and collectors from the Bernice P. Bishop Museum worked at the

Anggi Giji Lakes in 1963 (specimens at BBM-NG and AMNH; see Helgen and Flannery, 2004). *Coccymys* was not encountered during either inventory.

The Weyland Range, forming the western margin of the western Central Cordillera west of the Paniai Lakes and Snow Mountains, forms a distinctive zoogeographic unit in Helgen's (2007c: 737) view, "its mammal fauna appears highly distinctive in comparison with the rest of the Snow Mountains region." No *Coccymys* have been collected from the Weyland Range, even though the area has been reasonably well surveyed for small mammals.

Neither *Coccymys ruemmleri* nor any other species of the genus is a member of any montane mammalian fauna characteristic of the mountains between the Snow and Star Mountains and the northern coast: The Foja Mountains, situated between the Snow Mountains and the lowlands in western New Guinea, and the northern coastal ranges—the Cyclops Range in western New Guinea, and the Bewani, Menawa, and Torricelli Ranges in Sandaun Province of western Papua New Guinea. Older and recent mammalian inventories have not produced samples of the species (see Helgen, 2007a).

DESCRIPTION: A short, masked gray face; small body clothed in luxuriant, thick, and dark fur; a thin, brown tail (infrequently with a white tip) much longer than head and body; and slender hind feet describe the physical appearance of adult *C. ruemmleri* (generally similar to the color photograph of *C. shawmayeri* in Flannery, 1995: 275; also fig. 6). The thick coat (overhairs are 11–15 mm long, measured near the rump) covering the upperparts is dense, lax, and soft to the touch. This dorsal pelage is a rich, dark brown with burnished highlights (overhairs are dark gray for most of their lengths, tipped with dark brown) in a few specimens, but dark brown suffused with black, particularly strong over the lower back and between the ears, characterizes most animals. The dark tone and blackish wash are augmented by black guard hairs, which project slightly beyond the overfur layer but not enough to appreciably alter the even contour of the upperparts. The darker tones

over the back yield to dark gray on the thighs, upper arms, face, and muzzle. A prominent blackish brown area encircles each eye and extends onto both sides of the muzzle at the bases of the mystacial vibrissae. Those sensory hairs are mostly black with silvery tips, the longest reaching 50 mm and extending beyond the pinnae when laid against the head. The superciliary vibrissae extend to but not beyond the pinnae, the very fine genal vibrissae do not reach the base of the pinnae, and the usual murine array of facial submental and interramal sensory hairs and ulnar and tarsal vibrissae are apparent. The ears are small, dark brown, and covered inside and out with fine short hairs.

The ventral coat is also soft and dense, up to 8 mm thick, and ranges from whitish gray to very dark grayish white, from chin to inguinal region, in 36 of the 42 skins in the sample from the Snow Mountains; one of the remaining six (AMNH 150565) has a whitish gray venter with a large white chest patch, another (AMNH 151185) has dark grayish white underparts with large white chest and inguinal patches, and four (AMNH 110446, 150467, 150700, and 150811) have dark grayish white venters suffused with buff. The darker tones are produced by hairs that are dark gray for most of their lengths and have short tips, either unpigmented or buffy; relatively longer unpigmented tips result in the whitish gray venters.

The tail is slender and much longer than the head and body (the average LT/LHB ranges from 140% to 146% in 51 specimens from the Snow and Star Mountains [observed range is 140%–146%]; table 3). It is covered in annuli of small and slightly swollen scales (14–18 per cm) pressed into the epidermis. These rings of scales have been described as overlapping (Menzies, 1990: 132) and figured that way (Flannery, 1995: 263), but Tate and Archbold (1941) did not describe such a configuration, and in the specimens we examined the scale annuli do not overlap but abut against one another, an arrangement best viewed under magnification; although the rings do not overlap, the scale pattern is not the specialized arrangement seen in *Melomys* and related genera (see drawings in Flannery, 1995: 262–263). Emerging from beneath each scale are three

short and dark brown hairs (with short, unpigmented tips), as long as 2 scale lengths near the basal third of the tail, longer toward the tip; the scales decrease in size along the tail but the scale hairs increase in length (up to 3 scales long), which gives the tail a slight increase in hirsute texture from base to tip, but no tuft at the tip (tail appears somewhat hairy rather than naked). The dorsal surface over about the terminal fifth or sixth of the tail consists of a calloused strip (thickened epidermis) devoid of scales or hair ("dorsal 3 cm. of tail provided with tactile surface for prehension," as described by Tate and Archbold, 1941: 6; "terminal 20 mm white and hairless on the dorsal side also scaleless towards the apex " Menzies, 1990: 132; "with long naked gripping pad at tip on dorsal side" Flannery, 1995: 261), indicating a tactile dorsally prehensible region. Aside from this area, all surfaces of the tail are brown (scales are brown, scale hairs are brown with short, pale brown or unpigmented tips). Very few specimens exhibit a white distal portion, a pattern that has been considered characteristic of *C. ruemmleri* (Menzies, 1990; Flannery, 1995). Tate and Archbold (1941: 6), however, did not note a white tail tip in their original description, and the holotype has a completely brown tail. Of 41 specimens with intact tails at AMNH that were collected in the Snow Mountains during the 1938–1939 Archbold Expedition, only six (15%) have tails expressing white tips, and they are short (range, 5–30 mm long); none of the 14 specimens of *C. ruemmleri* we examined from the Star Mountains have a white tail tip (table 8).

Dorsal surfaces of front and hind feet, including digits, are generally unpigmented (but the range includes tan and very pale brown hues) and covered with silvery hairs. A sparse tuft of unpigmented hairs springs from the base of each unpigmented claw to cover it—a few project beyond the tip. These claws are moderately long and slightly recurved. The two middle digits of each front foot are the longest, the lateral digits slightly shorter. Palmar surfaces are naked, unpigmented to pale brown, and nearly the entire surface is adorned with three fleshy interdigital pads and posterior thenar and hypothenar mounds. Each hind foot is moderately

long but very slender for its length. The three central digits are subequal in length and longer than the much shorter hallux (which bears a claw); the fifth digit is longer than the hallux and slightly shorter than the three central ones. The unpigmented or pale brown plantar surfaces are naked and bear four large and fleshy interdigital pads, a large thenar located well posterior of the interdigitals, and a small hypothenar.

Females in all samples we examined bear three pairs of teats, one postaxillary pair, and two pairs inguinal in position, as previously indicated by Menzies (1990) and Flannery (1995). The same pattern of teats is also found in *C. shawmayeri* and *C. kirrhos*, n. sp.

Juvenile pelage is nearly indistinguishable from that of adults. Juveniles have a shorter coat (10 mm) with a finer and softer texture. Fur covering head and body is brown, only slightly duller than the adult coat, and underparts are whitish gray.

Only one example of *C. ruemmleri* we examined has a weight associated with it. A specimen from Mt. Capella in the Star Mountains weighed 34 g, within the range of values for body mass available for adults of *C. shawmayeri* (see that account).

The skull of *C. ruemmleri* is small with a globular braincase that appears disproportionately large compared with the facial and orbital regions (fig. 9). The rostrum is moderately long, narrow, and slightly tapered as viewed from a dorsal perspective, its lateral margins interrupted by the moderate bulge of each nasolacrimal canal. Dorsolateral boundaries of the interorbital and postorbital regions are smooth, without ridging; the interorbit is hourglass-shaped. The back of the postorbital area is defined by a vertical ridge where the frontal and squamosal bones meet, and from dorsal view appears as an angular projection interrupting the curved outline that defines the margins of the interorbital and postorbital areas. This ridge is more pronounced in older individuals. Beyond the postorbital region, the braincase is round in outline and mostly smooth in texture: barely perceptive roughened places or low beading along the squamosal-interparietal sutures mark the temporal muscle attachment, an inconspicuous linear beading defines each lambdoidal

ridge, and each mastoid is moderately inflated. The interparietal is long (anterior-posterior plane) and wide, forming most of the dorsal occipital surface. Moderately thin zygomatic arches flare outward from sides of the skull and taper toward the rostrum where the anterior margins of the dorsal maxillary roots of the zygoma form right angles to the rostrum; the inconspicuous zygomatic notch is indicated by a shallow convex dorsal margin between rostrum and top of the zygomatic plate. The jugal component of each zygoma is short.

From a lateral view, the convex dorsal outline of the skull defines a high arch extending from tip of the nasals to the deep occiput, which overhangs the occipital condyles, reflecting significant cranial flexion (fig. 9). The rostrum is tapered, deeper near the zygomatic plates than at the incisors; the nasals and premaxillaries are either even with the incisor faces or barely project beyond them; and the nasolacrimal capsules are moderately large and inflated. The zygomatic plate is narrow, and its vertical, straight anterior edge projects only slightly beyond the dorsal maxillary root of the zygomatic arch, which results in a shallow zygomatic notch; the posterior edge of the plate is just anterior to the front surface of the first molar or even with it. Either a circular rugose spot or a low bump at the outer base of the ventral zygomatic root marks the origin of the superficial masseter muscle (fig. 41). Behind the orbit, the squamosal root of the zygomatic arch originates midway on the side of the braincase. Posterior to the squamosal zygomatic root and dorsad of the auditory bulla, the squamosal is intact except near the squamosal-exoccipital suture where it is perforated by a large subsquamosal foramen through which the periotic can be seen. A triangular portion of the parietal drops below the dorsolateral margin of the braincase almost to the top of the zygomatic root; this projection and the squamosal form the wall of the braincase. The junction of the orbitosphenoid, alisphenoid, and frontal bones forms a solid section of the braincase wall, unbroken by a sphenofrontal foramen. The inner walls of the braincase are smooth, without squamosal-alisphenoid grooves. A wide, bony alisphenoid strut (present in all

skulls surveyed) separates the foramen ovale accessorius from the combined buccinator-masticatory foramen. A spacious postglenoid foramen and ventral postalar fissure separate the dorsal and anterior margins of the auditory (ectotympanic) bulla from the adjacent squamosal. The periotic exposed along the dorsolateral margin of the bullar capsule may or may not extend anteriorly to touch the posterior margin of the squamosal but in no specimen does it project as a tegmen tympani to overlap the squamosal.

The long and wide incisive foramina are conspicuous when the skull is viewed from a ventral perspective; they occupy about 70% of the diastema, and their posterior margins end slightly before front margins of the first molars, even with them, or project slightly between the molars—one of Menzies's (1990) diagnostic traits for *Coccymys*. The wide, bony palate is not much longer than the slightly posteriorly divergent molar rows (toothrows are about 90% of the length of the bony palate), and its posterior margin is either level with the backs of the third molars or projects slightly beyond them (fig. 9). Its surface is textured by a deep pair of palatal grooves and large posterior palatine foramina set even with the middle of each second molar. The mesopterygoid fossa is wide but narrower than the bony palate and its dorsolateral margins are breached by spacious sphenopalatine vacuities (covered with thin tissue in insufficiently cleaned skulls). The adjacent pterygoid plates (= parapterygoid plates) are triangular in ventral view and mostly intact except in the middle section where each is perforated by moderately large sphenopterygoid vacuities (often covered with tissue), and at the back of each plate, which is pierced by the large ventral opening of the foramen ovale. Between the foramen ovale and middle lacerate foramen, a conspicuous groove scores the posterolateral area of the plate's ventral surface. Each pterygoid fossa is moderately deep. The posterolateral margin of the pterygoid forms a substantial ridge lateral to the foramen ovale. A short but wide bony eustachian tube projects from each ectotympanic bulla; which is small relative to size of the skull (length of bulla is about 14% of occipitonasal length). The bullar capsule does not cover the entire

Fig. 9. The cranium and dentary of the holotype of *Coccymys ruemmleri* (AMNH 150669), an adult male from the northern slopes of the Snow Mountains at Lake Habbema, 3225 m, ×3. Measurements are listed in table 7.

Fig. 10.   The cranium and dentary of the holotype of *Brassomys albidens* (AMNH 150821), an adult male from the northern slopes of the Snow Mountains at Lake Habbema, 3225 m, ×3. Measurements are listed in table 7.

surface of the periotic, leaving exposed a posteromedial segment and a narrow flange extending forward between ectotympanic capsule and basioccipital. The dorsal and lateral wall of the carotid canal is formed by the periotic, and its medial surface is formed by the basioccipital in some specimens (the configuration is similar to that illustrated for the Vietnamese murine *Tonkinomys*, Musser et al., 2006: 16); but in other skulls part of the ectotympanic, and not the periotic, forms the lateral wall of the canal (a conformation resembling that shown for the sigmodontine *Oligoryzomys* in Carleton and Musser, 1989: 33). All of the specimens we examined possessed a large stapedial foramen penetrating the crevice (the petromastoid fissure) between the bullar capsule and the periotic. A spacious middle lacerate foramen separates the bullar capsule from the posterior margin of the pterygoid plate.

All specimens of *Coccymys ruemmleri* that we examined possess a carotid arterial arrangement that is derived for muroid rodents in general but primitive for members of subfamily Murinae (character state 2 of Carleton, 1980; pattern 2 described by Voss, 1988; conformation diagrammed for *Oligoryzomys* by Carleton and Musser, 1989). We did not detect this pattern by dissecting carcasses preserved in fluid, but saw it reflected in certain cranial foramina and osseous landmarks in cleaned skulls, as well as dried blood vessels left on incompletely cleaned skulls. There is no sphenofrontal foramen at the junction of the orbitosphenoid, alisphenoid, and frontal bones, no squamosal-alisphenoid groove scoring the inner surface of each wall of the braincase, and no shallow trough running diagonally over the dorsal (inner) surface of each pterygoid plate. There is a large stapedial foramen in the petromastoid fissure, and a deep groove extending from the middle lacerate foramen to the foramen ovale on the ventral posterolateral surface of each pterygoid plate. This disposition of foramina and grooves indicates that the stapedial artery branches from the common carotid, enters the periotic region through a large stapedial foramen, and, as the infraorbital artery exits the periotic through the middle lacerate foramen, then courses in a short

groove on the outside of the pterygoid plate to disappear into the braincase through the alisphenoid canal from which it emerges to course through the anterior alar fissure into the orbit. The supraorbital branch of the stapedial is absent. This circulatory plan is widespread among murines (Musser and Newcomb, 1983; Musser and Heaney, 1992), and is also found in some North and South American cricetids (Carleton, 1980; Voss, 1988; Steppan, 1995; Weksler, 2006). This derived version of the carotid arterial supply is contrasted with the primitive configuration and a more derived pattern found within muroid rodents; it is particularly clear in the descriptions and diagrams provided by Bugge (1970), Carleton (1980), Voss (1988), and Carleton and Musser (1989).

Each dentary appears robust, with a short but high ramus between the incisor and molar row, a deep ascending ramus, and a stocky condyloid process (figs. 9, 42). The posterior margin between the condyloid and angular processes is concave, and a wide and deep sigmoid notch separates the small and delicate coronoid process from the robust condyloid. The labial surface of the ascending ramus is smooth in some specimens, but in others is sculptured by a low mound containing the incisor capsule that runs diagonally along the ascending ramus; in all specimens the incisor capsule terminates in a bony labial projection at or above the edge of the sigmoid notch between coronoid and condyloid processes.

Upper incisors curve caudad after emerging from the rostrum at less than a right angle to the occlusal plane of the molars (opisthodont conformation, as defined by Thomas, 1919). Their enamel covering is orange, and the incisor faces are smooth, lacking either grooves or shallow sulci. The enamel face of each upper incisor does not wrap around most of the labial surface, as is the pattern in the Philippine *Chrotomys*, for example, and covers about one-third of the labial side of the incisor, which resembles the enamel coverage seen in *Rattus* (Musser and Heaney, 1992: 79). Gnawing edges of the upper incisors are at right angles to the long axis of the skull, so their combined tips form a straight cutting edge (as in species of *Rattus*;

see Musser and Heaney, 1992: 79), not curved or V-shaped (as in some Philippine and Sulawesi endemics; see Musser and Heaney, 1992; Musser and Durden, 2002). Lower incisors have pale orange enamel surfaces. The lower incisors are moderately long and curve upward at about an angle of 45°; their tips form either a linear or slightly arched configuration.

Patterns of molar roots found in *C. ruemmleri* are primitive for murine rodents (Musser and Newcomb, 1983). Each upper (maxillary) molar is anchored by three roots (one large anterior, one large posterior, and a large lingual); each lower (mandibular) molar has two roots.

The cuspidate upper and lower molars are brachydont, wide, and abut against one another in each row with some overlap. The first molar in both maxillary and mandibular rows forms nearly half of the complete toothrow, and the second molar about a third; the third molar, although much smaller than the others, is relatively large (a diagnostic feature noted by Menzies, 1990), comprising about 20% of the row (figs. 11, 12).

"Molars very small and of characteristically simple *Melomys* type," noted Tate and Archbold (1941: 6) as part of their characterization of *ruemmleri*. Certainly the molars are small, but the skull is small, and their coronal cusp patterns are strikingly unlike those typical of *Melomys* (see molar rows of *Melomys rufescens* illustrated in Musser, 1982a: 39). The occlusal surface of each first upper molar is primarily formed by three broad rows of angular and oblong cusps and a posterior cingulum (figs. 11, 12). The first row consists of a large lingual cusp t1 that is offset but attached to a wide and narrow central cusp t2, which in turn is broadly fused with a much smaller cusp t3 that is either directed labially or slightly posterolabially; the elongate cusp t2 and orientation of cusp t3 impart an almost laminar configuration to them. The second row is composed of a large backward-directed lingual cusp t4 that is attached to a wide and narrow central cusp t5 and large labial cusp t6 that is smaller than cusp t4. In contrast to the first row of cusps, those in the second row are discrete, showing only narrow coalescence between each cusp. The third row is formed by a large distorted

diamond-shaped cusp t8 joined to a cusp t9 that projects straight to the labial side, not forward or backward in most specimens; in others, cusp t9 is small but evident and broadly merged with cusp t8.

Lingual and labial cingular ridges connect the rows of cusps. The second and third cusp rows on the first upper molar are joined along the lingual margin by a prominent cingular enamel ridge that in most specimens originates from the anterolingal margin of cusp t8 and projects anteriorly to the posterolingual edge of cusp t4. This projection from t8 takes several forms: (1) a solid anterolingual ridgelike extension meeting the posterior surface of t4; (2) an enamel wall topped by a pimple, which resembles an incipient cusp; (3) shallow lateral fissures in the occlusal surface of the wall, suggesting its origin from several coalesced individual cingular pieces; and (4) swollen sections of the ridge. In all its variants, the ridge structure is entirely enamel, without a dentine core (it is not a ridgelike cusp t7), and though possibly formed by more than one piece from the cingulum, clearly is associated with t8 and extends from there to t4. In a few individuals, the lingual enamel ridge is formed by a posterior projection from cusp t4 and an anterior extension from cusp t8. Along the labial cingular margin, an enamel ridge projects from the anterolabial margin of cusp t9 forward to the posterolabial margin of cusp t6. This labial ridge is about half the height of the cusps in unworn or slightly worn molars, but is transformed into a low connecting enamel wall after more wear. There is also a ridge projecting from the anterior face of cusp t6 to meet cusp t3 near its base (not present in all specimens).

A moderately large posterior cingulum forms the posterolabial margin of the first upper molar in all specimens and is recognizable even after considerable wear.

A large cusp t1 defines the anterolingual border of the second molar, and a much smaller cusp t3 sits on the anterolabial margin. Occlusal configurations of the first complete row (formed of cusps t4, t5, and t6) and the posterior row (consisting of cusps t8 and t9) are similar to those exhibited by the second and third cusp rows of the first molar. The primary difference is that cusp t4 is much

Fig. 11. Occlusal views of right maxillary molar rows. **Left**: Juvenile *Brassomys albidens* (AMNH 150618; CLM1–3 = 5.1 mm). **Middle**: Young adult *Coccymys ruemmleri* (AMNH 192737; CLM1–3 = 4.4 mm). **Right**: Adult *Coccymys kirrhos* (AMNH 158174; CLM1–3 = 4.1 mm). Cusps are numbered according to Miller's (1912) scheme and referred to in the text with the prefix t; lc, lingual enamel connection between cusps t4 and t8; lr, labial enamel ridge; pc, posterior cingulum.

narrower than its counterpart in the first molar, and cusp t8 is shaped like a regular undistorted diamond in occlusal view. The two cusp rows on the second molar are connected by enamel ridges along their lingual and labial margins, a configuration comparable to the pattern of ridges seen on the first molar.

The posterior cingulum is absent from the second molar of most specimens. When present, it is generally small and inconspicuous, much smaller than its counterpart on the first molar, and its presence is often indicated only by a ridgelike accretion at the back margins of cusps t8 and t9.

The rows of defined cusps on the first and second upper molars are wide and gently arched in occlusal view, not shaped like acuspidate chevrons (as in species of *Melomys, Paramelomys*, and *Uromys*).

A large cusp t1, arcuate anterior row formed by completely fused cusps t4, t5, and t6, and chunky, straight posterior lamina (mostly cusp t8, possibly including a small cusp t9, but difficult to discern if actually present) form the chewing surface of each third upper molar; a posterior cingulum is absent, and cusp t3 is either not present or very small.

Each first lower molar is wide and somewhat oblong in outline and its occlusal surface is formed by three rows of cusps (fig. 12). The anterior two-thirds of the molar

Fig. 12. Occlusal views of right mandibular molar rows of the specimens illustrated in figure 11. **Left**: *Brassomys albidens* (clm1–3 = 5.4 mm). **Middle**: *Coccymys ruemmleri* (clm1–3 = 4.4 mm). **Right**: *Coccymys kirrhos* (clm1–3 = 4.1 mm). Abbreviations: alab, anterolabial cusp; aling, anterolingual cusp; hd, hypoconid; md, metaconid; ed, entoconid; pc, posterior cingulum; pd, protoconid; plc, posterior labial cusplet.

(anteroconid) consists of chunky anterolingual and anterolabial cusps (the anterolingual is larger than the anterolabial, the usual conformation in murines) that are partly separate in unworn and moderately worn teeth but broadly coalesced in older adults. The triangular and large metaconid and protoconid create a nearly straight second row separated from the anteroconid (fusing with it only after much wear and usually only narrowly at the labial and lingual margins). A large and oblong entoconid and hypoconid form most of the posterior one-third of the molar, and behind that row of cusps is a wide but narrow (in the anterior-posterior plane) posterior cingulum. An anterior labial cusplet is not present (seen on the anterolabial

margin of the protoconid in other murines; see Musser and Newcomb, 1983, for examples), but a posterior labial cusplet is a prominent aspect of the labial cingulum. The occlusal surface of the nearly square second lower molar consists of two rows of cusps, an elongate posterior cingulum, and a posterior labial cusplet that in pattern and shape of cusps are similar to the posterior two-thirds of the first molar. The anterolabial margin of the molar supports an anterolabial cusp, but its opposite counterpart, the anterolingual cusp, is absent. The chunky third molar has a roughly circular outline and a simple occlusal surface created by two laminarlike cusp rows. An anterolabial cusp is absent from some specimens but present on

others, although often inconspicuous because it has nearly completely coalesced with the hypoconid. The posterior margin of the tooth is without a posterior cingulum, the usual state in most murines.

Additional anatomical systems, along with other biological aspects of *Coccymys ruemmleri*, remain generally uninvestigated, except for phallic anatomy. Morphology of the glans penis and its role in reconstructing phylogenies were presented by Lidicker (1968, 1973), who employed two specimens in the type series from Lake Habbema in the Snow Mountains. Specimens identified as *C. ruemmleri* that were used in studies of comparative sperm morphology (Breed, 1997, 2004; Breed and Aplin, 1994) and albuminological inquiries (Watts and Baverstock, 1994, 1996) are actually *C. shawmayeri*.

COMPARISONS WITH OTHER SPECIES OF *COCCYMYS*: *Coccymys ruemmleri* can be distinguished from *C. shawmayeri* and *C. kirrhos,* n. sp., by fur coloration, tail traits, and qualitative cranial and dental characters. Typically, *C. ruemmleri* has soft and thick (11–15 mm) fur, the dorsal coat is dark brown to dark brown suffused with black, the ventral coat whitish gray to dark grayish white with buffy suffusion on a few individuals; the tail is brown and longer than the head and body (LT/LHB = 140%–146%), and of the 55 specimens examined only 6 (11%) exhibit a short white tip (mean = 19.5 mm, range = 5–30 mm; table 8); the skull has a long rostrum and bony palate, bulbous braincase, and large molars. *Coccymys shawmayeri* and *C. kirrhos*, n. sp., have shorter dorsal coats (9–12 mm and 8–10 mm, respectively). The upperparts of *C. shawmayeri* are paler, a warm brownish gray with slightly burnished highlights, and without black suffusion; underparts range from whitish gray to a darker grayish white, but the paler tone—whitish gray—is usual, and no specimens examined exhibit any buffy wash. Upperparts of *C. kirrhos* are bright tawny or orange brown, underparts are whitish gray. Tails are brown in *C. ruemmleri*; both *C. shawmayeri* and *C. kirrhos*, n. sp., have paler tails—grayish brown—and the tail in each averages much longer relative to head and body length (LT/LHB = 145%–170% and

150%–180%, respectively; table 3) than in *C. ruemmleri*. Most specimens (76%) of *C. shawmayeri* have a white tail tip that averages longer (mean = 27.0 mm, range = 4–42 mm) than the white segments in the few examples of *C. ruemmleri*; all specimens of *C. kirrhos* lack a white tip (table 8).

Quantitative morphometric distinctions between *C. ruemmleri* and the other two species were summarized by the patterns of covariation in cranial and dental variables reflected in graphs of specimen scores projected onto the first and second canonical variates extracted from discriminant function analysis for AMNH samples, which we previously described. Coupled with its bright pelage and smaller body size, *C. kirrhos*, n. sp., is morphometrically distinct from *C. ruemmleri*, contrasts we will elaborate upon in the account of the new species. Here we describe the morphometric contrasts between *C. ruemmleri* and *C. shawmayeri*. As revealed in the results from discriminant function analysis (fig. 4; table 2), and in the tabulated univariate summary statistics (tables 4, 5), specimens of *C. ruemmleri* from the Snow Mountains typically have an absolutely longer rostrum and palatal bridge, deeper braincase, narrower mesopterygoid fossa, and heavier molars (indicated by the longer molar rows and wider first upper molars) than those in AMNH samples of *C. shawmayeri* from Mt. Hagen and Mt. Wilhelm. These same dimensional distinctions separate *C. ruemmleri*, including the sample from the Star Mountains, from BBM samples of *C. shawmayeri* that we measured from the Telefomin region, the Wau area, Mt. St. Mary, and the BMNH holotype of *shawmayeri* (tables 4, 5, 7).

GEOGRAPHIC VARIATION: We examined variation in external and morphometric traits and its possible significance in two ways: first, the nature of variation between the two regions where our modern samples were collected—the Snow Mountains in the west and high on the Star Mountains to the east; secondly, variation among samples along the altitudinal transect between 2200 and 4050 m on the northern flanks of the Snow Mountains.

Snow and Star Mountains: Insight into geographic variation of cranial and dental

TABLE 9
Results of Principal Components Analysis of Geographic Samples of *Coccymys ruemmleri*
Samples are from the Snow Mountains (Mt. Wilhelmina, Lake Habbema, and Bele River valley) and the Star Mountains; the holotype of *ruemmleri* is included. (Principal components are extracted from a covariance matrix of 18 log-transformed cranial and dental variables; see tables 4, 7, fig. 13)

Variable	PC1	PC2
ONL	0.016	0.005
ZB	0.001	0.013
IB	−0.005	0.011
LR	0.006	0.018
BR	0.013	0.013
BBC	−0.002	−0.006
HBC	−0.011	−0.005
BZP	0.045	0.022
LD	0.017	0.019
PPL	0.015	0.019
LBP	0.027	0.002
BBPM1	0.017	0.002
BMF	−0.039	0.064
LIF	0.001	0.012
BIF	−0.047	−0.008
LB	0.010	0.007
CLM1–3	0.004	−0.009
BM1	−0.008	−0.000
Eigenvalue	0.008	0.007
% Variance	26.601	21.788

dimensions between population samples from the Snow Mountains and Star Mountains, series we identify as *C. ruemmleri*, are summarized in the scatter plot of specimen scores projected onto the first and second principal components in figure 13. The distribution of scores along each axis is influenced by covariation in most variables, but especially breadth of zygomatic plate, length of bony palate, and breadths of mesopterygoid fossa and incisive foramina (table 9). The single cloud of points reveals no internal structure that would attach unique morphometric attributes to the Star Mountain population compared with animals from the Snow Mountains. Most scores for the specimens from the Star Mountains cluster with those identifying animals from Lake Habbema and Mt. Wilhelmina, a pattern present in other ordinations of different principal components analyses that we will present below.

Average differences in univariate means for some variables do exist between samples from the Snow and Star Mountains (tables 3, 4, 12). Compared with the Snow Mountain samples, the Star Mountain population has, on average, longer hind feet and shorter body and tail (but relative tail length is similar); greater skull length, wider bony palate, longer and wider upper and lower molars; but narrower interorbit and mesopterygoid fossa, and shorter rostrum, diastema, postpalatal region, and incisive foramina.

There is an average difference in chromatic aspects of the fur between the two sets of geographic samples. All the specimens from the Star Mountains have very dark brown upperparts, a couple with an overlay of black, and dark grayish white underparts, touched with buff in some specimens. Among the altitudinal samples from the Snow Mountains, the range extends from dark fur (matching the animals from the Star Mountains) to individuals with paler brown upperparts and whitish gray underparts.

In summary, darker pelage characterizes more animals in the Star Mountain population than in the Snow Mountain sample, the skull averages larger in the former (but some of the internal cranial dimensions are less), as do the maxillary and mandibular molars. Whether these distinctions identify a population of *C. ruemmleri* isolated in the Star Mountains is currently impossible to determine without samples from montane reaches between the Star Mountains and the northern slopes of the Snow Mountains along the Archbold transect from Mt. Wilhelmina to the Bele River valley. The two highland regions appear from maps to be connected at the 3000-m contour, certainly an altitude high enough for the continuous distribution of *C. ruemmleri*. We need to study material from this vast intermediate montane region before the significance of the distinctions we note here can be evaluated. Remember, collecting activities by members of the Archbold Expedition along the Archbold transect, A.B. Mirza's efforts on the Star Mountains, and the individual from Mt. Capella in the Star massif (see gazetteer) have produced the only specimens of *C. ruemmleri* that sample living populations.
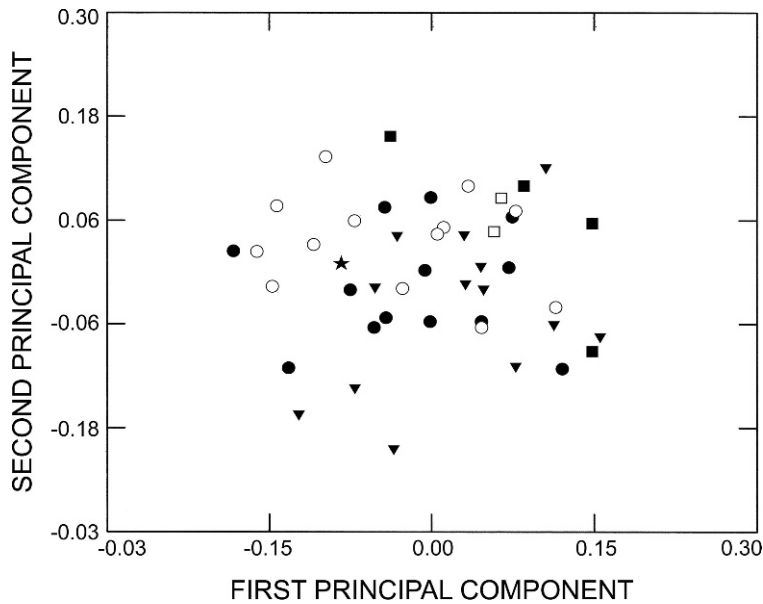
Fig. 13.   Specimen scores representing *Coccymys ruemmleri* projected on first and second components extracted from principal components analyses. Samples from the Snow Mountains (Bele River valley, 2200 m [filled square] and 2800 m [square]; Lake Habbema [filled circle]; and Mt. Wilhelmina [circle]; $N = 33$) are compared with that from the Star Mountains (inverted filled triangle; $N = 13$). A star designates the holotype of *C. ruemmleri*. See table 9 for correlations and percent variance.

Altitudinal phenetic variation: The northern slopes of the Snow Mountains have yielded the only series of *C. ruemmleri* collected along an altitudinal track extending from mid-montane forest at 2200 m to scattered clumps of trees and alpine grassland at 4050 m (see gazetteer). The samples provide an opportunity to assess altitudinal variation in qualitative and quantitative phenetic traits, and to determine if specimens collected at the lower altitudes might represent the eastern *C. shawmayeri*.

Both species occur in western Papua New Guinea where *C. ruemmleri* is represented by specimens only from upper montane forest at 3100–3200 m on the Star Mountains, and *C. shawmayeri* is found at lower altitudes, 2300–2800 m, in the Telefomin region between the upper Sol River valley and Lake Louise (see gazetteer). The contrasts in pelage and other external traits between the Star Mountain and Telefomin samples are concordant with those previously enumerated separating *C. ruemmleri* from *C. shawmayeri*. The distinction is especially striking between these two samples. All 15 *C. ruemmleri* have very dark

brown upperparts, and two are even darker owing to a black suffusion through parts of the coat; underparts are very dark grayish white, and 11 show a slight buffy wash, usually in the pectoral region and sometimes also on the abdomen; the tails are brown to their tips. Warm brown upperparts combined with bright whitish gray underparts characterize each specimen from the Telefomin area (*C. shawmayeri*); 5 out of the 8 specimens demonstrate a white tail tip (table 8).

We examined patterns of covariation in cranial and dental variables among the two sets of specimens, as summarized in the scatter plots of scores projected onto first and second principal components, by two separate principal components analyses. The first contrasts only the Telefomin and Star Mountain samples, and includes holotypes of *ruemmleri* and *shawmayeri*; the second retains those specimens and additionally embraces the type-series of *C. ruemmleri* from Lake Habbema and a subset of *C. shawmayeri* from Mt. Wilhelm, which is in the same region as the collection site for the holotype of that species (see gazetteer), and the
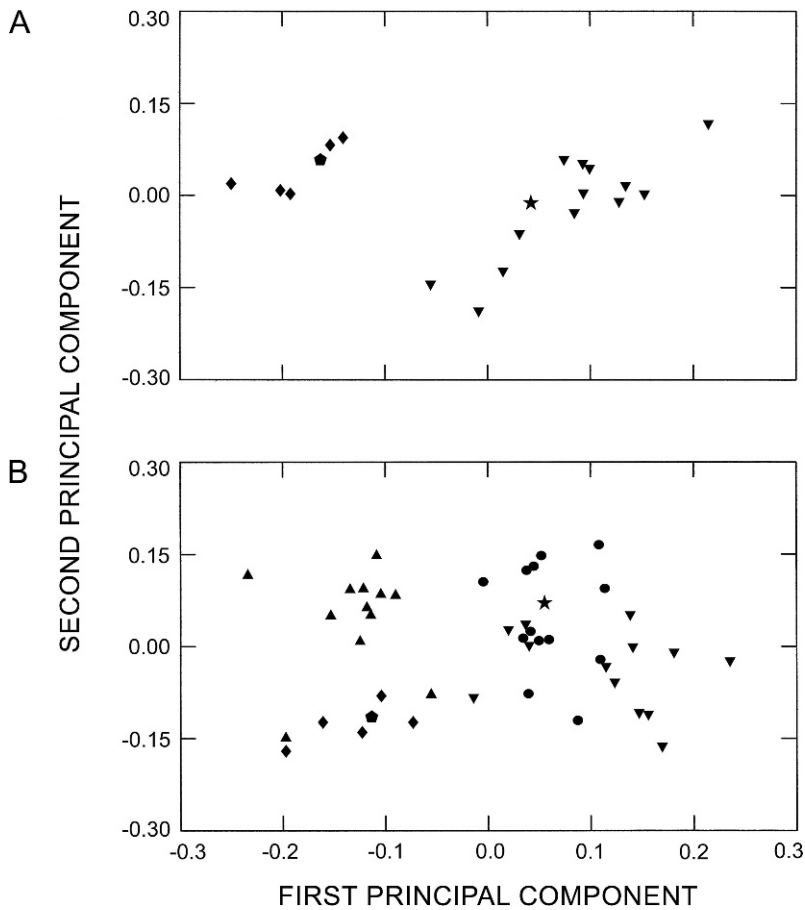
Fig. 14. Specimen scores representing two species of *Coccymys* projected on first and second components extracted from principal components analyses. **Graph A:** the sample of *C. ruemmleri* from the Star Mountains (inverted filled triangle; $N = 13$) contrasted with that of *C. shawmayeri* from the Telefomin area (filled diamond; $N = 5$). **Graph B:** samples of *C. ruemmleri* from the Star Mountains (inverted filled triangle; $N = 13$) and Lake Habbema (the type locality) in the Snow Mountains (filled circle; $N = 13$) compared to samples of *C. shawmayeri* from the Telefomin area (filled diamond; $N = 5$) and Mt. Wilhelm (filled triangle; $N = 12$). A star identifies the holotype of *C. ruemmleri*, a filled pentagon indicates the holotype of *C. shawmayeri*. See table 10 for correlations and percent variances.

holotype itself. The pattern of covariation in the first analysis is reflected by two discrete groups of scores along the first principal component (fig. 14A): those for the Telefomin individuals align with the point representing the holotype of *shawmayeri*, and specimen scores for the Star Mountain sample cluster about the score for the holotype of *ruemmleri*. Covariation in most variables scatters the scores along the first axis (table 10), reflecting a substantial size difference in cranial and dental dimensions between the samples from the Telefomin area

and Star Mountains; breadth of bony palate and length of molar row are especially influential.

A similar pattern of covariation among variables springs from the second principal components analysis where the type series of *C. ruemmleri* and specimens of *C. shawmayeri* from Mt. Wilhelm are added to the analyses (fig. 14B). Size is again the primary factor segregating the specimen scores into two clusters along the first axis, with most of the variables contributing equally, and breadth of bony palate and size of molars

TABLE 10
Results of Principal Components Analysis of Geographic Samples of Two Species of *Coccymys*
Graph A: samples of *Coccymys ruemmleri* from the Star Mountains, *C. shawmayeri* from the Telefomin area, and holotypes of *ruemmleri* and *shawmayeri*. Graph B: samples of *Coccymys ruemmleri* from Lake Habbema and the Star Mountains, and *C. shawmayeri* from the Telefomin area and Mt. Wilhelm, including holotypes of *ruemmleri* and *shawmayeri* (Principal components are extracted from a covariance matrix of 18 log-transformed cranial and dental variables; see tables 4, 5, 7, fig. 14.)

Variable	Graph A		Graph B	
	PC 1	PC 2	PC 1	PC 2
ONL	0.030	0.010	0.034	−0.014
ZB	0.020	0.011	0.018	0.006
IB	0.011	0.002	−0.002	0.018
LR	0.026	0.026	0.038	0.005
BR	0.038	0.006	0.038	−0.005
BBC	0.023	−0.012	0.018	0.003
HBC	0.023	−0.024	0.021	0.009
BZP	0.011	0.048	0.018	−0.040
LD	0.024	0.021	0.025	0.000
PPL	0.026	0.018	0.024	0.000
LBP	0.033	0.003	0.030	−0.013
BBPM1	0.060	−0.009	0.050	0.007
BMF	0.035	0.003	−0.008	0.070
LIF	0.030	0.011	0.018	0.016
BIF	0.035	−0.021	0.032	0.036
LB	0.030	0.009	0.021	−0.003
CLM1–3	0.059	−0.027	0.047	0.000
BM1	0.026	0.000	0.017	0.007
Eigenvalue	0.019	0.006	0.014	0.009
% Variance	45.238	14.802	32.339	20.153

being more forceful (table 10); two clouds of points are even more distinct as separate entities in the ordination where specimen scores are projected on first and third axes (not illustrated). Clearly, the sample from the Telefomin area is from a population of *C. shawmayeri*; specimens from the Star Mountains can be identified as *C. ruemmleri*.

Contrasts in univariate means between the two sets of samples reinforce the size distinction (tables 4, 5) revealed in the principal components analyses. Individuals in the sample of *C. ruemmleri* from high on the Star Mountains at 3100–3200 m have larger skulls and heavier molars than specimens attributable to *C. shawmayeri* occurring at 2300–2800 m in the adjacent Telefomin area.

How far *C. shawmayeri* occurs west of the Telefomin region is unknown, but if it does extend to lower altitudes along the northern slopes of the Snow Mountains, the specimens from the Bele River valley at 2200 and 2800 m might be examples of that species. But scores for the two specimens from 2800 m and the four from 2200 m form no separate cluster in the first and second principal components ordination summarizing covariation in cranial and dental variables shown in figure 15A (also see table 11) where all AMNH samples from the Snow Mountains are employed. The points are scattered among those representing individuals from Lake Habbema at 3225 m (the type series) and Mt. Wilhelmina at sites from 3560 m to 4050 m. Neither size (first axis) nor shape (second axis) isolates the specimens from the Bele River valley as a coherent group separate from samples from Lake Habbema and Mt. Wilhelmina.

The identity of the sample from Bele River valley as *C. ruemmleri* and not *C. shawmayeri* is forcefully supported in the scatter plot of specimen scores projected onto the first and

TABLE 11
Results of Principal Components Analysis of Geographic Samples of Two Species of *Coccymys*
Graph A: samples of *Coccymys ruemmleri* from Mt. Wilhelmina (3560–4050 m), Lake Habbema (3225 m), and Bele River valley (2200 m, 2800 m) in the Snow Mountains; the holotype of *ruemmleri* is included. Graph B: samples of *Coccymys ruemmleri* from Lake Habbema, Bele River valley , and the Star Mountains, and *C. shawmayeri* from the Telefomin area and Mt. Wilhelm; holotypes of *ruemmleri* and *shawmayeri* are included. (Principal components are extracted from a covariance matrix of 18 log-transformed cranial and dental variables; see tables 4, 5, 7, fig. 15.)

Variable	Graph A		Graph B	
	PC 1	PC 2	PC 1	PC 2
ONL	−0.011	0.007	0.034	−0.011
ZB	0.001	0.008	0.016	0.007
IB	0.006	0.005	−0.00l	0.014
LR	0.001	0.006	0.038	0.004
BR	−0.009	0.013	0.040	−0.005
BBC	0.004	−0.003	0.014	0.005
HBC	0.012	−0.006	0.017	0.011
BZP	−0.032	0.030	0.024	−0.035
LD	−0.017	0.013	0.029	−0.001
PPL	−0.014	0.012	0.028	−0.000
LBP	−0.026	0.002	0.033	−0.015
BBPM1	−0.012	0.003	0.048	0.010
BMF	0.049	0.056	−0.008	0.070
LIF	0.003	−0.000	0.019	0.014
BIF	0.060	−0.018	0.022	0.040
LB	−0.005	0.009	0.022	0.000
CLM1–3	0.002	0.002	0.042	0.005
BM1	0.017	0.004	0.012	0.012
Eigenvalue	0.009	0.005	0.014	0.009
% Variance	31.458	18.256	31.224	20.034

second principal components in figure 15B that again summarizes covariation in cranial and dental variables. Scores for the holotype of *C. shawmayeri*, the specimens collected between 2300 and 2800 m in the Telefomin area, and the sample from Mt. Wilhelm coalesce into a cluster distinctly separate from the clump of scores representing the holotype of *C. ruemmleri*, specimens from the Star Mountains, the type series from Lake Habbema, and the individuals from the Bele River valley collected at 2200 and 2800 m. Difference in size is primarily responsible for the separation of the two constellations along the first axis with nearly all variables contributing, but especially size of rostrum, breadth of bony palate, and length of the upper toothrow (table 11), which reflects the univariate mean differences in many of the cranial and dental dimensions summarized in the tables of descriptive statistics (tables 4, 5). These dimensions average greater in *C.*

ruemmleri, and the specimens from the Bele River valley affiliate quantitatively with that species and not with *C. shawmayeri*.

Coupled with this pattern of covariation in cranial and dental traits is the variation in external characteristics. The individuals from the Bele River valley are similar in body size, length of hind foot and ear, and relative length of tails to those *C. ruemmleri* collected at the higher sites (table 3). The range in fur color in the two samples from the Bele River valley mirrors the extent of chromatic variation seen in samples from Lake Habbema (3225 m) and Mt. Wilhelmina (3560–4050 m)—warm brown to very dark brown dorsal coat, some suffused with black, whitish gray to dark grayish white underparts. The 16 specimens in the sample from collection sites on Mt. Wilhelmina (3560–4050 m) are darker than most from lower altitudes, having dark brown upperparts with variable intensities of black wash among the
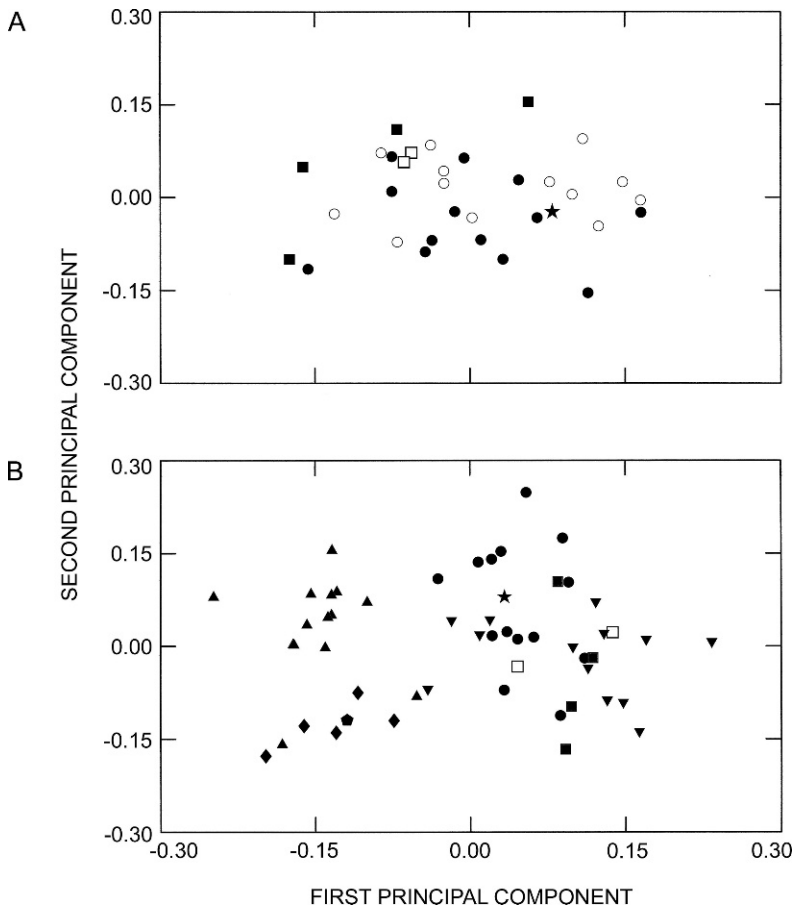
Fig. 15. Specimen scores representing two species of *Coccymys* projected on first and second components extracted from principal components analyses. **Graph A:** Comparison among samples of *C. ruemmleri* from Bele River valley at 2200 m (filled square) and 2800 m (square), Lake Habbema (filled circle), and Mt. Wilhelmina (circle) in the Snow Mountains ($N = 33$). **Graph B:** Samples of *C. ruemmleri* from the Star Mountains (filled inverted triangle; $N = 13$), Lake Habbema (the type locality; filled circle; $N = 13$), and Bele River valley at 2200 m (filled square; $N = 4$) and 2800 m (square; $N = 2$) in the Snow Mountains compared to those of *C. shawmayeri* from the Telefomin area (filled diamond; $N = 5$) and Mt. Wilhelm (filled triangle; $N = 12$) in Papua New Guinea. The star identifies the holotype of *C. ruemmleri*, the filled pentagon indicates the holotype of *C. shawmayeri*. See table 11 for correlations and percent variances.

specimens so that some appear brownish black, others even darker. The entire chromatic range occurs within the sample collected at Lake Habbema (3225 m), from warm brown dorsal fur (exemplified by AMNH 150769) to darker brownish black upperparts (AMNH 150872, for example). Among the nine individuals collected at 2800 and 2200 m in the Bele River valley, AMNH 151185 from 2200 m matches those from Mt. Wilhelmina; the rest have brown upperparts indistinguish-

able from many in the sample from Lake Habbema.

Coccymys shawmayeri is not represented in the samples collected along the Archbold transect between 2200 and 4050 m. Extensive mammalian surveys will be required to determine the limit of the range of *C. ruemmleri* both farther to the west and to the east in the Snow Mountains.

HABITAT: Descriptions of habitats at different collection sites from the Snow

Mountains in the west and the Star Mountains to the east incorporate the range of floristic associations from mid-montane forest through "mossy" or upper montane forest to subalpine forest and alpine grassland. Nowhere is this entire range of vegetative formations exemplified better than along the transect extending from the Bele River camp at 2200 m to below the summit of Mt. Wilhelmina at 4050 m, where botanical collecting and observations were an important part of the survey efforts conducted on the northern ramparts of the Snow Mountains by members of the 1938–1939 Archbold New Guinea Expedition (Brass, 1941; Archbold et al., 1942; fig. 48). The botany throughout this transect has been described by Archbold et al. (1942) and Brass (1941). Our excerpts presented below, along with photographs, are meant to convey a sense of the habitats surveyed along this transect; consult the excellent accounts in Archbold et al. (1942) and Brass (1941) for details.

Maximum and minimum ambient temperature recorded along the transect (September to December 1938) ranged from 23.0°C and 10.5°C, respectively, at the Bele River camp, through 18°C and 1.1°C at Lake Habbema, and 13.5°C and –2.0°C at 3560 m and higher.

The lowest altitude from which *C. ruemmleri* was recorded was the Bele River camp, 2200 m, which was located (Archbold et al., 1942: 260)

on the right-hand bank of the river, about ten kilometers from the mouth of the valley. … The camp was in a kind of pocket where the valley widened a little between two limestone gorges spaced less than a kilometer apart. … In parts of this pocket primary forest came down to the river banks. Other parts were deforested and grassy [fig. 16]. In it were several small villages and a number of scattered dwellings, comprising in all about fifty houses… this was the upper limit of permanent habitation in the valley. … The highest garden in the pocket, and the highest observed on the expedition, was at an altitude of 2,480 meters [fig. 17]. … The pocket between the gorges contained three more small villages and several deserted houses from which the people had moved to cultivate new land. Brush second-growth forest and grass extended up to about 2,400 meters on the camp side of the river, where the villages and producing gardens were, and up to about 2,350 meters on

the steeper slopes. Filling the gorges and completely surrounding this disturbed area were magnificent tall beech-forests [fig. 18].

The forests, recorded Archbold et al. (1942: 260),

were composed of three species of *Nothofagus* [beech], all forming great straight-stemmed rough-barked trees over forty meters high and up to a meter and one-half in diameter. One species …dominated from the river banks up to about 2,400 meters … up to about the level of daily cloud accumulation and the upper limit of cultivation on the slopes [fig. 19]. Another species … provided most of the stocking above that level. … The third … was common about 2,300 meters. Associated with these, as large subsidiary trees twenty-five meters to over thirty meters high, were oaks of four species, *Castanopsis, Engelhardtia*, several species of Cunoniaceae, Lauraceae, *Eleocarpus* and *Syzygium*. … The oaks and *Castanopsis* … were confined to the lower slopes, where, up to altitudes of about 2,350 meters, they actually attained dominance and formed isolated small patches of typical dry-appearing, mid-mountain forest on the crests of some of the broader spur ridges. … Rain-forest elements, including many large trees but for the most part small trees and undergrowth plants, were conspicuous on the river banks and, in diminishing numbers, reached far up the slopes, beyond the limit of the oaks,in ravines and hollows between the spurs.

Unfortunately, there are no data associated with the specimens of *C. ruemmleri* indicating the forest microhabitat in which they were caught. Members of the expedition trapped and hunted at the 2200-m site and were also helped by the native villagers who "followed the trappers, examined the traps and even tended the traps and brought in (expecting pay) mammals removed from them. But they were effective trappers on their own and from their deadfalls brought large numbers of specimens. One day more than 100 specimens, representing at least nine species, were purchased from them," but Archbold et al. (1942: 262–263) cautioned that since "many of the specimens were brought in by natives, sometimes by parties who had evidently come from a distance, records of altitudes at which some of the specimens were taken are lacking. Certainly

Fig. 16. View up the valley of the Bele River above the camp at 2200 m showing the combination of primary forest on hillsides, secondary growth (forest regrowth), and anthropogenic grassland. This is the lowest altitude at which *Coccymys ruemmleri* was recorded on the northern slopes of the Snow Mountains. November–December 1938.

at this 2,200-meter Camp we received some bunches of birds that had been taken on the top of the range above 3,000 meters.''

The camp 9 km northeast of Lake Habbema at 2800 m is the next station with capture records for *C. ruemmleri* (see gazetteer and figs 48, 49). Brass (1941) described the camp as surrounded by forest (see fig. 20) that included components of ''beech forest'' and ''mossy forest,'' which together fit Whitmore's (1984) designation of tropical lower and upper montane rain forest. In addition to *C. ruemmleri*, five of the six known specimens of *Brassomys albidens* are recorded from this camp at 2800 m, and we describe the environment in greater detail in the habitat section of *B. albidens*.

Mammals obtained at the 2800 m camp were trapped or hunted by the expedition members and fewer were brought in by natives compared with the camps at lower altitudes (field journal of W.B. Richardson; photocopy in AMNH archives). Presumably most of those rats trapped by Richardson were obtained in forest, but no microhabitat details describing the trap stations are available.

''Lake Habbema, 3,225 meters above sea level,'' the type locality for *C. ruemmleri*, ''lies on a shelf-like upland, trending east and west, and about nine kilometers in width at the lake. The northern edge of this upland forms the rim of the Grand Valley of the Baliem. From its southern edge rise the barren, rocky heights of the Nassau Range, and snow-capped Mt. Wilhelmina'' (Archbold et a1., 1942: 266 and pl. 23; also see fig. 21). The landscape is a mosaic of closed and open

Fig. 17.   A garden in beech (*Nothofagus*) forest at 2480 m in the Bele River valley. The trees were felled with stone axes and by burning; others were girdled but still living. This was the highest altitude at the Bele River camp where gardens were found (see text). The scene is a view of both the primary forest and its human modification at this altitude. November–December 1938.

subalpine forests on the ridges, and grasslands that "occupied, besides the broad valleys and the basal slopes of the ridges rising from them, all the lateral hollows and numerous glades in the forests" (Brass, 1941: 321; see figs. 21, 22) and alpine grassland habitats extended down through the upland valleys to about 3100 m. Archbold et al. (1942: 283) summarized the following habitats as "integral parts of the subalpine forest" in the environs about Lake Habbema: coniferous open forest, low-tree thickets, *Rhododendron* shrubberies, forest border shrubberies, mixed secondary forest, treefern stands, and lake shores.

The woody growth on the ridges behind the Lake Habbema camp

… consist of open and closed communities of subalpine forest [fig. 22]. Such closed forest as there is occurs in patches, from a few meters to a hundred meters or more across. … The closed forest is peculiar in having two tree layers, either of which may form a canopy and thus dominate the habitat. The upper layer of trees … consists of the conifers (*Podocarpus papuanus* and *Libocedrus* sp.), with which *Phyllocladus* sp. and alsoa *Schefflera* (Araliaceae) occur in quantity. The crowns of the trees are laden with bryophytes, in which grow small ferns and orchids. … As typically developed on the upland, however, the closed forest is a five to seven-meter high elfin wood of broad-leaved trees dominated by *Vaccinium dominans* and containing other *Vaccinium* spp., *Rapanea, Symplocos, Olearia* (Compositae), *Decaspermum lorentzii* and *Saurauia alpicola*, overtopped

Fig. 18.   Inside the forest on hillsides at the Bele River camp, 2200 m. See description in text. November–December 1938.

by an open stand of conifers. The broad-leaved forest develops a very dense stiff canopy, thinly draped with brown and purplish hepatics. … The crooked, leaning tree trunks are shaggy with hepatics, and a rather thin carpet of hepatics covers the ground. Shading is so heavy that normally there are few epiphytes and undergrowth plants.

Archbold et al. (1942) wrote on pp. 270–271:

Where closed forest meets grassland on the edges of glades and open hollows, it is bordered with a compact wall of erect shrubs growing to a height of one and one-half to two meters from deep moss. … The grasslands are alpine and for
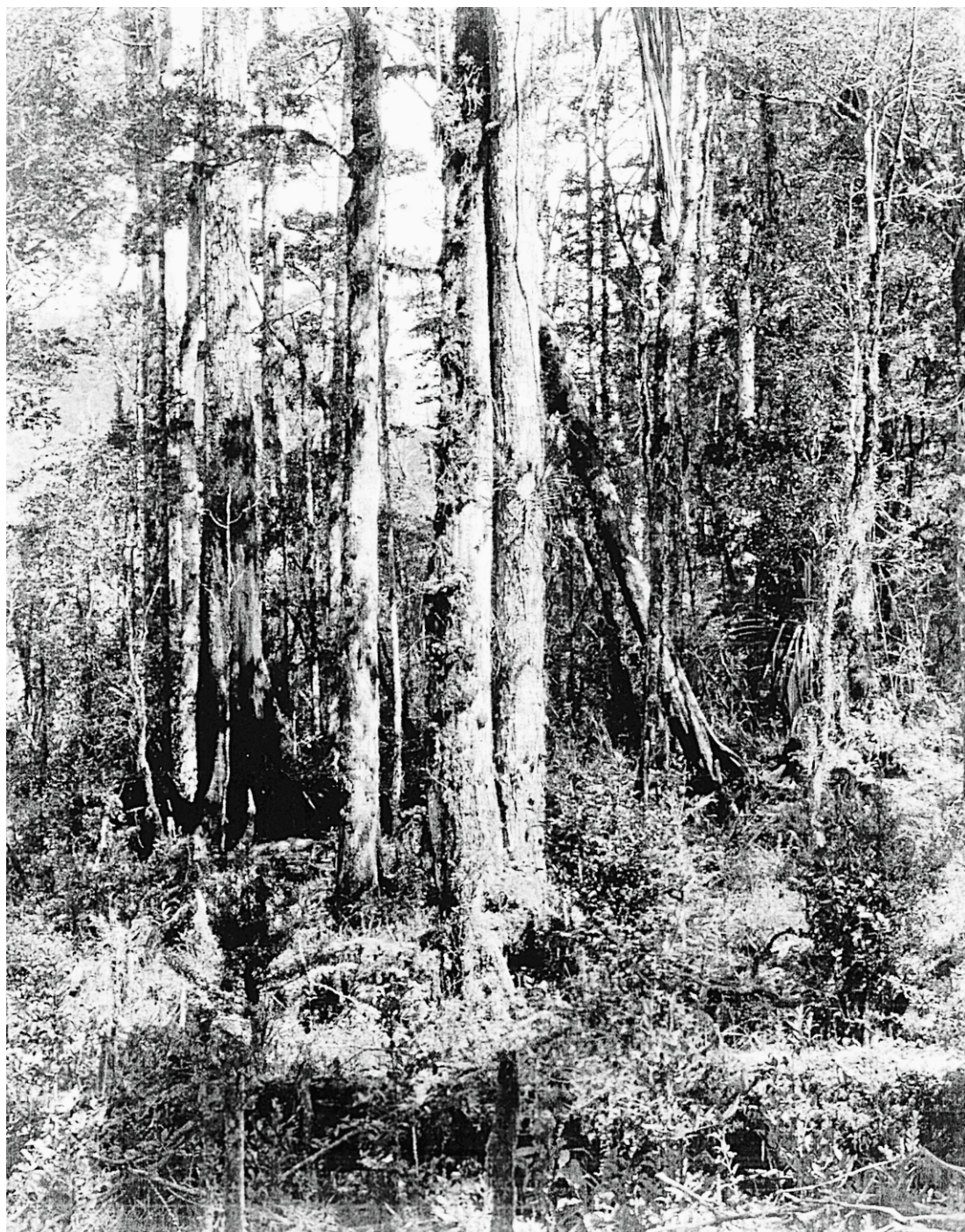
Fig. 19. Interior of the "magnificent tall" primary beech forests at 2450 m described by Archbold et al. (1942: 260), 18 km northeast of Lake Habbema above the Bele River camp (2200 m). November–December 1938.
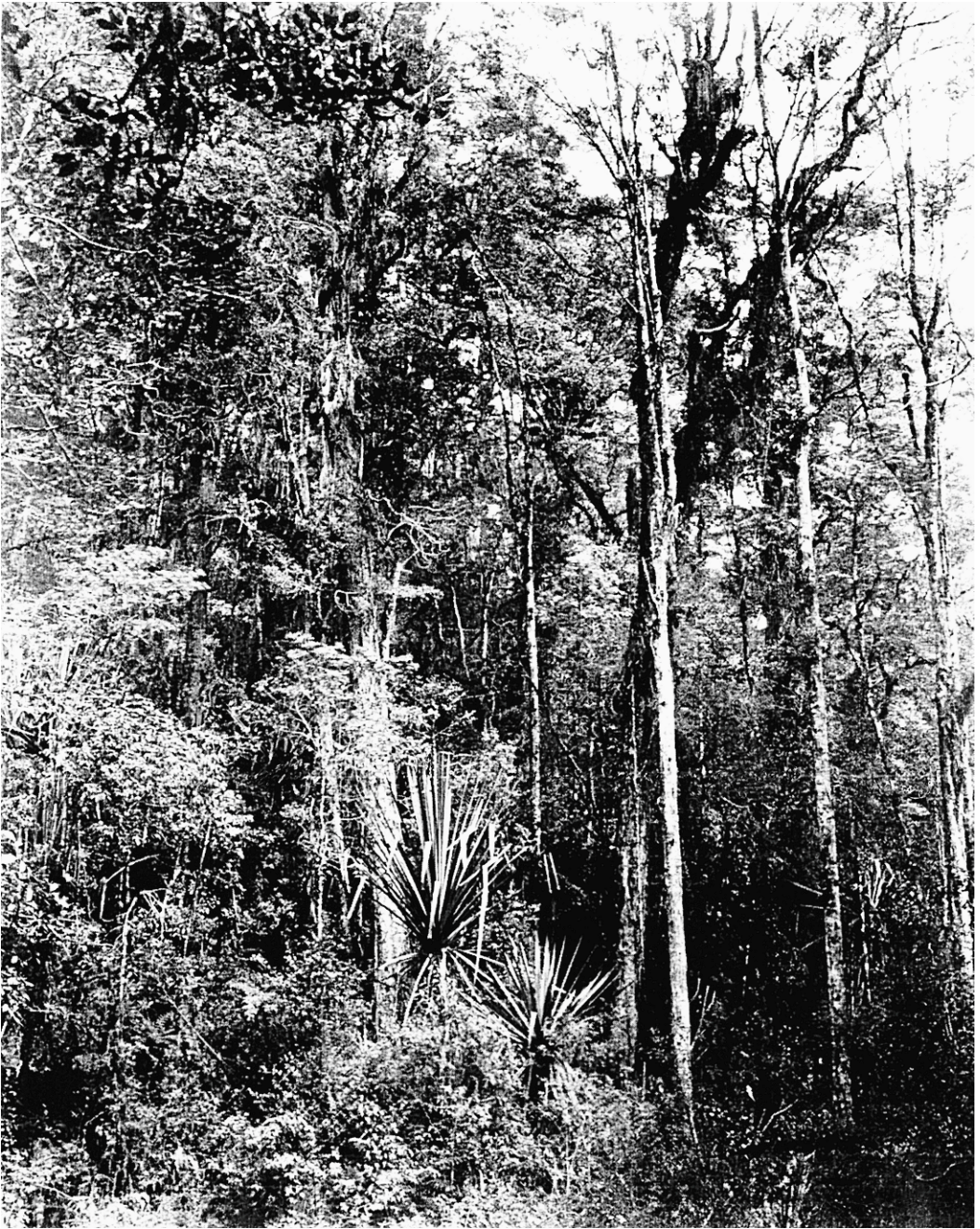
Fig. 20.   Bele River camp at 2800 m, 9 km northeast of Lake Habbema. Upper montane rain forest ("mossy forest") viewed across an open stream. "Situated high in the upper drainage basin of the Bele River beside a well-used path which led from the inhabited regions up to Lake Habbema, this camp was on a small stream. It was in heavily forested country consisting of parallel spur ridges and very narrow alleys or ravines, rising rapidly toward the highlands." Samples of *Coccymys ruemmleri* and five of the six known specimens of *Brassomys albidens* were obtained at this camp. October–November 1938.

Fig. 21. Lake Habbema, 3225 m, with Mt. Wilhelmina in the background. Closed and open upper montane rain forest ("subalpine forest," Brass, 1941) covers the ridges; grassland dominates the basal slopes of the ridges, hollows, and glades in the forest, and broad valleys; marsh rings the lake. From the environs around Lake Habbema come the holotypes of *Coccymys ruemmleri* and *Brassomys albidens.* July–September 1938.

the most part doubtless a primary condition … they contribute the ground cover to some of the open forest of the ridges. In the valleys and lateral hollows and in the numerous glades which penetrate the forests, they are treeless. The treefern (*Cyathea tomentosissima* and, to a less extent, *C. cheilanthoides*), lining the banks of streams and occurring in large numbers near forest edges, forms a characteristic feature of the grassland landscape.

Mammal trapping in the environs of Lake Habbema was productive, "and about 400 traps often yielded ten to twenty specimens a night" (Archbold et al., 1942: 273); no details are available about where the traps were placed—forest, grassland, or ecotonal margins—that yielded *C. ruemmleri.*

A large sample of *Coccymys ruemmleri* is recorded from the camp at 3560 m, approximately 7 km northeast of the summit of Mt. Wilhelmina (fig. 23). It was located in "the trough-shaped valley of one of the headwater streams of the Wamena. … The sides of the valley were occupied by low, broken forest, and its bottom was grassy" (Archbold et al., 1942: 274). Archbold et al. (1942:275) wrote that:

the forests consisted of patches and clumps separated by grassy glades and other, apparently natural, grassy spaces too broad to be called glades. By far the largest body occurred on the sheltered, steep, and, by reason of their steepness, relatively dry slopes about the cliffs. The forests were heavily mossed, very dense and rigid and often dwarfed and sheared by wind. They differed from those of Lake Habbema chiefly in the absence of conifers. *Podocarpus and Libocedrus* were abundant on the slopes up to an elevation of about 3,500 meters … but only one tree—a *Libocedrus*—was observed in the 3,560-meter Camp valley and that grew at about 3,500 meters on an east-facing slope about four kilometers below the camp. … Replacing the conifers as characteristic overtopping trees was the araliaceous 'umbrella
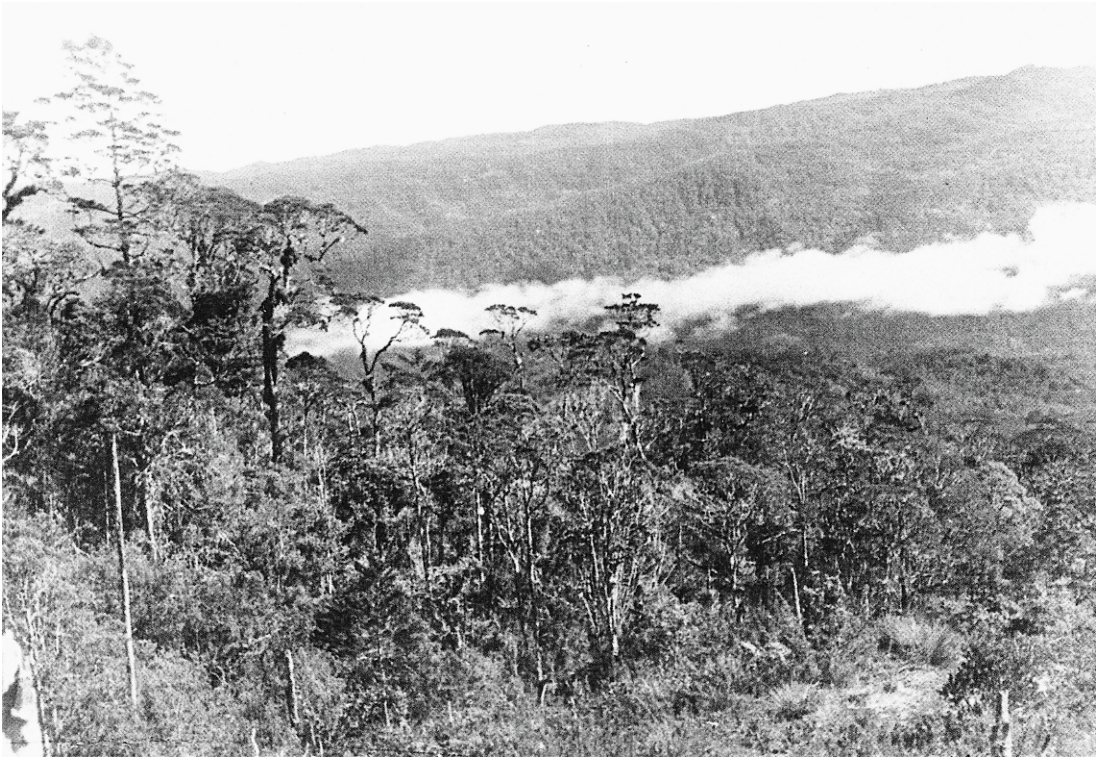
Fig. 22. Open upper montane forest at 3300 m near Lake Habbema, dominated by *Podocarpus papuanus* and *Libocedrus* sp. and a *Rhododendron* forming much of the dense undergrowth. This vegetation was described as open subalpine forest by Brass (1941: 320) who noted that closed forest "occupied but a small part of the wooded ridges in the Lake Habbema area. The prevailing tree communities of the sandstone ridges, which approached the open grasslands of the valleys and hollows in extent, were at best an open forest of smut-darkened *Libocedrus* and *Podocarpus papuanus*, and on basal slopes often no more than a low savanna stand of *Libocedrus* alone." July–September 1938.

tree" (*Schefflera*). … *Vaccinium dominans*, attaining a maximum height of five to six meters, formed the bulk of the forest. … The trees, especially those of the forest edges, were heavily cushioned with bryophytes—chiefly mosses—and wherever light entered a thick cover of mosses grew on the ground.

"Most of our collecting in the locality was done between altitudes of about 3,500 and 3,900 meters in and around the amphitheater in which we camped" (Archbold et al., 1942: 275).

The highest camp established by the expedition, 2 km east of the summit of Mt. Wilhelmina at 3800 m "was in the head of a grassy amphitheater into which a waterfall about twenty meters high dropped over a sandstone rock-step from a deep V-shaped valley … between the summit ridge of the mountain and a 4,300-meter false peak" (Archbold et al., 1942: 277). The change in vegetation between Lake Habbema and this higher camp was described by Archbold et al. (1942: 278–279): above about 3400 m,

the forests became more interrupted by grass; trees became increasingly selective as regards habitat conditions; the grasses were in the ascendant. There was still a good deal of forest at 3,700 meters, particularly on the south slopes of the range. … At 3,800 meters, the forest was reduced to about compact little clumps on the slopes, open scrubby growths scattered among rocks and a very narrow strip under the water-fall rock-step. Scattered busy tree clumps of *Rapanea* and *Drimys* were abundant up to 3,900 meters and straggled up to 4,000 meters in Scree Valley. Absolute tree limit was at

Fig. 23.   Site of the mountain base camp at 3560 m situated in a sheltered pocket in a long, grassy, north-south valley, about 7 km northeast of the summit of Mt. Wilhelmina on the northern slopes of the Snow Mountains. "The camp was on a long slope of landslip debris covered with grass tussocks. Generally, the slopes were considerably disturbed by slips and subsidences, and the soil peaty and immature" (Archbold et al., 1942: 324). The camp was surrounded by "high timbered ridges on both sides and a wet bottom in which were some open swamps to which innumerable slender grass tufts growing erect in the water gave the appearance of rice fields. Only one *Libocedrus* tree was seen after entering the valley. The limit of the conifers had been passed. The forests were getting lower, much cut by glades and the tops of nearby 3900 m. and 4000 m. peaks were without trees" (p. 324). Specimens of *Coccymys ruemmleri* are from this altitude (see gazetteer). August–September 1938.

4,050 meters under a north-facing bluff on the false peak.

Samples of *C. ruemmleri* were recorded from 3800 m, 3950 m, and 4050 m; again, no microhabitat description attends any specimen.

The eastern portion of the Star Mountains in Sandaun Province has yielded 14 specimens of *C. ruemmleri* (see gazetteer). Ten are from 3100 m and all were either "snap-trapped in grass" or in "moss forest + alpine grass." At 3200 m, four animals were "snap-trapped" in "moss forest." This information comes from notations on skin tags. The landscape at 3100 apparently consists of upper montane ("mossy") forest adjacent to alpine grassland, and that at 3200 m is upper montane forest.

Another specimen of *C. ruemmleri* was collected during a mammal survey conducted in Sandaun Province (formerly West Sepik Province) in the Dokfuma Basin of the eastern Snow Mountains (see gazetteer). "Dokfuma is a small subalpine herbfield perched on the southern slopes of Mount Capella at 3200 m" reported Flannery and Seri (1990: 178), and "The campsite was on the edge of the Dokfuma Valley, where "The valley floor is covered in subalpine herbs and ferns, with small clumps of treeferns and stunted *Rhododendron* bushes. The valley margins support an open *Dacrycarpus* woodland, with *Phyllocladus, Papuacedrus* and

Schefflera being common. In sheltered areas nearby a dense and extremely mossy Upper Montane Forest is developed.''

BIOLOGY: No first-hand observations describe biological activities of *Coccymys ruemmleri*, but some inferences are appropriately drawn from our research. The combination of dark fur, long tail relative to length of head and body, and slim hind feet suggest to us that this small-bodied, long-tailed rat is active during the night, both on the ground, particularly in alpine grassland landscapes, and at levels above ground in forest understory (terrestrial/scansorial), activities likely also characterizing *C. shawmayeri* (see that account).

Skeletal remains in owl pellets document the nocturnal role for *C. ruemmleri*, as well as its position in the ecosystem as prey for at least one kind of avian predator. During September 1938, owl pellets were gathered by members of the Archbold Expedition on Mt. Wilhelmina, above the 3800 m camp: ''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 amongst 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). The pellets were brought back to AMNH and eventually taken apart, but the small mammal pieces extracted were never identified until now. We sorted the fragmentary remains of small-bodied rodent dentaries and crania into 302 individuals that sample five species: 12 *C. ruemmleri* (see gazetteer), 1 *Pseudohydromys occidentalis*, 1 *Baiyankamys habbema*, 93 *Rattus richardsoni*, and 195 *Rattus arrogans*. Remains of six small marsupials were also present. Three of the rodent species are strictly terrestrial, *B. habbema* is amphibious; *C. ruemmleri* is certainly part of this terrestrial cohort when found in alpine grassland. In addition to *C. ruemmleri*, living samples of the other four species were also obtained in the high reaches of the transect (fig. 49).

The sooty owl, *Tyto tenebricosa*, is about 14 in (36 cm) from head to tail and occurs throughout New Guinea from sea level to 4000 m. During the day it roosts in tree holes or forest understory, and at night preys on rodents, bats, and small marsupials in a range of forest formations, and in subalpine forests and bordering alpine grassland at high altitudes (Beehler et al., 1986: 130, pl. 26). The habitat on Mt. Wilhelmina at and above the expedition's 3800-meter camp is a mosaic of patchy subalpine forest and alpine tussock grassland (see habitat description).

We have been unable to locate reproductive information for *C. ruemmleri*. None of the specimens examined for this report are associated with notes on litter size, breeding periods, or other reproductive aspects, and the published literature is silent on this subject.

Documented dietary data for *C. ruemmleri* is equally elusive. Menzies and Dennis (1979: 40) noted that for *C. ruemmleri*, ''Limited evidence indicates that the diet consists only of vegetable matter including leaves.'' They cited no source for their evidence, and at the time the statement applied to the generally accepted view of a single species—*ruemmleri*—occurring the length of the Central Cordillera of New Guinea, from the Snow Mountains to the Owen Stanley Ranges. We located only a single specimen of *C. ruemmleri* that had been preserved in fluid, a young adult from Lake Habbema. Its stomach was empty; a fecal pellet in the intestine contained unidentifiable (at the resolution of a dissecting microscope) brown mash and a small cockroach instar. Considering the close morphological and habitat similarities between *C. ruemmleri* and *C. shawmayeri*, their diets may also be similar. We were able to survey specimens of the latter that were preserved in fluid, and their stomachs contained a range of items—insects, fruit, seeds, and vegetative fragments (table 16). We elaborate on these findings in the account of *C. shawmayeri*.

SYMPATRIC ASSOCIATIONS: We explored two views of sympatry. One is the distributional relationship between *Coccymys ruemmleri* at the eastern margin of its range and *C. shawmayeri* at its western terminus. Both species occur in western Papua New Guinea where *C. ruemmleri* is known only from montane forest at 3100–3200 m on the Star Mountains, and *C. shawmayeri* is found at lower altitudes, 2300–2800 m, in the

Telefomin region between the upper Sol River valley and Lake Louise (see gazetteer). The identity of these samples as one or the other species was discussed and defended in the section on geographic variation. Judged from present samples, the two species seem to be regionally sympatric in the Star Mountains but altitudinally parapatric. Except for the AM specimen of *C. ruemmleri* from Mt. Capella collected high in the Star Mountains, we unfortunately don't know exactly where the 14 BBM *C. ruemmleri* were collected—all are simply labeled "Star Mountains." Limits of the altitudinal distributions for the two species in the Star Mountain and Telefomin areas need to be illuminated by future surveys along appropriate altitudinal transects.

Our other look at sympatry tracks the occurrence of *C. ruemmleri* with other species of mammals collected along the Archbold transect on the northern slopes of the Snow Mountains. In figure 49 we have charted the altitudinal distributions of 2484 specimens representing 79 species of mammals obtained along a transect up the north slopes of the Snow Mountains during the 1938–1939 Archbold Expedition to western New Guinea (see the *albidens* account for details). Samples of *C. ruemmleri* are recorded at different altitudes extending from 2200 m to 4050 m (see gazetteer also). One monotreme (*Zaglossus bartoni*), 16 species of marsupials, one bat (*Murina florium*), and 21 species of murine rodents were collected from within the same altitudinal interval. Beyond this generalized summary we can offer no insights into the microhabitat associations between *C. ruemmleri* and these other nonvolant species.

Within a zoogeographic context, *C. ruemmleri* is endemic to the Central Cordillera of western New Guinea—the Snow and Star mountains—and shares this distinction with other montane mammalian endemics, most recorded only from the Snow Mountains. Among the rodents, in addition to *C. ruemmleri*, are *Brassomys*, n. gen., *albidens*, *Mallomys gunung*, *Baiyankamys habbema*, *Pseudohydromys occidentalis,* and an undescribed species of *Pseudohydromys* (see Helgen, 2007a), *Paraleptomys wilhelmina* and an undescribed species of *Paraleptomys*, an undescribed species of *Pogonomys* (Musser and Lunde, ms.), *Melomys frigicola*, *Rattus*

arrogans, and *Rattus richardsoni. Dendrolagus mbaiso* (Flannery et al., 1995) and *Dendrolagus stellarum* (often listed as a subspecies of *D. dorianus* but recognized as a separate species by Helgen, 2007c), *Murexia habbema*, *Dactylopsila megalura*, *Pseudochirulus caroli*, and two undescribed species of *Microperoryctes* (Helgen, 2007c; in litt., 2008) are the marsupial members of this group (see Helgen, 2007c).

FOSSIL SAMPLES: *Coccymys ruemmleri* is represented in two sets of fossils collected in the Snow Mountains. Cranial and dentary fragments from seven individuals were recovered from the clay filling in a limestone crevice (the "Asair fissure") at 3450 m on the south flanks of the Carstensz Massif (Mt. Jaya) at the western end of the Snow Mountains in western New Guinea (see gazetteer). According to J.H. Hope (1976: 212), who identified the material, "The bones were found at various depths in the matrix, and three small samples were taken from the top, middle and base. The same species [of marsupials and rodents] were found in all levels, but the colour of the bones varied from white at the top to red at the base, suggesting that the lower levels at least might have some antiquity." She also indicated that it was "feasible to infer a mid-Holocene age for the deposit, possibly lying within the limits of 8,000 to 2,000 years BP." Hope identified seven individuals from the sample as *Pogonomelomys ruemmleri* and provided values for interorbital breadth (4.1 mm, $N = 2$), breadth of zygomatic plate (2.6–3.1 mm, $N = 4$), length of incisive foramina (4.5–5.1 mm, $N = 5$), length of maxillary toothrow (4.5–4.7 mm, $N = 4$), and breadth of first upper molar (1.3–1.4 m, $N = 3$). Comparative values were derived from modern specimens caught on Mt. Wilhelm; J.H. Hope (1976: 221) noted that "The tooth row in the Asair specimens is slightly longer than in the modern specimens." This was an astute observation that we now know reflects one of the dimensional distinctions between the western Cordilleran *C. ruemmleri* and eastern Cordilleran *C. shawmayeri*, which occurs on Mt. Wilhelm. The maxillary molar row averages longer in modern *C. ruemmleri*, and the values from the fossils fall within the range of variation for modern samples

from both the Snow and Star mountains (table 4). Nothing in the measurement data from the fossils indicates they are fragments of anything other than Holocene counterparts of living *C. ruemmleri*.

The other lot consists of much older fossils and was gathered from Kelangurr Cave, 2950 m, situated in a valley confluent with the valley of the West Baliem River and 8 km west of the settlement of Kwiyawagi, which is 60 km or so west of Lake Habbema on the southern slopes of the Snow Mountains (see Hope and Aplin, 2007: 251 for a look inside the cave). In 1994, Flannery (1999) visited the cave and collected primary matrix and lag deposits (mostly mud and fossil bones) from the walls and floor of the first chamber in the cave (chamber 1). The deposits yielded a rich fauna of eight kinds of marsupials, one microchiropteran, and seven species of rodents (Flannery, 1999: 342). Although a few of the species were represented by material thought to be Recent, the bulk of the specimens extracted from the deposit were heavily mineralized, and two dating techniques indicated that the deposit in chamber 1 was accumulated between 25,000 and 20,000 B.P. Among the rodents, Flannery (1999: 346) identified a minimum number of 38 individuals of *Coccymys ruemmleri*, and remarked that the sample "consisted of larger individuals than those (all from Papua New Guinea) which were available for comparison" Referring to J.H. Hope's (1976) observation that her Holocene specimens from the Carstensz region were larger than modern specimens from Mt. Wilhelm, Flannery explained how the "significance of this is presently unknown, but it may indicate the presence of cryptic species within what is currently referred to as *C. ruemmleri*."

We borrowed the material from Kelangurr Cave and identified 63 individuals of *C. ruemmleri*, all represented by dentary fragments only, some still retaining molars and partial incisors, others edentulous. The pieces range from just a part of the ramus to nearly a complete dentary. Most of the specimens (53) were heavily mineralized with matrix still adhering to the dentary. A few (10) were less mineralized, discolored a dark brown, and, while not from modern animals, seem stratigraphically younger than the other batch.

We measured the intact mandibular molar rows and individual molars of the fossils, as well as molars in all our samples of modern *C. ruemmleri*, *C. shawmayeri*, and *C. kirrhos*, n. sp.; results are summarized in table 12. No appreciable differences exist between univariate means of the fossil sample and the modern samples of *C. ruemmleri* collected along the Archbold transect from Mt. Wilhelm to the Bele River valley. The notable contrast among the samples of *C. ruemmleri* is between the fossil and modern specimens from the Snow Mountains and the series from the Star Mountains—the latter have, on average, larger mandibular molars, which covary with the longer maxillary toothrows in the Star Mountain sample as compared to the modern sample from the Snow Mountains (table 4). Univariate means for lengths of molar rows average larger in the fossil sample and the modern samples of *C. ruemmleri* than those in the geographic samples of *C. shawmayeri* and *C. kirrhos*, n. sp., a size difference concordant with distinctions in certain cranial dimensions and length of maxillary toothrow described in accounts of those species (see also tables 4–6).

To us, the specimens from Kelangurr Cave sample *C. ruemmleri*, not an extinct cryptic species. Flannery (1999: 346) was aware of the need for a fresh revision of *Coccymys*, and his speculation was understandable. As J.H. Hope (1976) did, he compared the fossils with modern specimens available to him, all from Papua New Guinea, which were considered to be *C. ruemmleri* according to Menzies's (1990) study, but are actually *C. shawmayeri*, characterized in part by its average smaller molars compared with the samples from the Snow and Star mountains.

What should not be lost in the minutae of comparisons is the significance of the fossil specimens. They document the presence of *C. ruemmleri* in the Snow Mountains of western New Guinea back to the Late Pleistocene when it was a member of a rodent fauna that today still inhabits subalpine forest and alpine tussock grassland in the high reaches of the western Central Cordillera. When Flannery visited Kelangurr Cave in 1994, the area was covered with high upper montane forest, but he (Flannery, 1999: 349) noted that at the time the sediment

	N	clm1–3	bm1	bm2	bm3
C. ruemmleri					
Kelangurr Cave		4.54 ± 0.17	1.28 ± 0.07	1.31 ± 0.07	1.09 ± 0.09
		(4.3–4.8) 7	(1.2–1.4) 18	(1.2–1.4) 17	(1.0–1.2) 9
Bele River valley	7	4.49 ± 0.12	1.27 ± 0.07	1.29 ± 0.04	1.00 ± 0.06
		(4.31–4.70)	(1.19–1.37)	(1.24–1.35)	(0.91–1.1)
Lake Habbema	15	4.40 ± 0.12	1.22 ± 0.09	1.24 ± 0.09	0.97 ± 0.09
		(4.11–4.55)	(0.94–1.30)	(0.97–1.34)	(0.70–1.07)
Mt. Wilhelmina	11	4.39 ± 0.10	1.20 ± 0.08	1.29 ± 0.05	1.00 ± 0.05
		(4.26–4.58)	(1.09–1.35)	(1.22–1.39)	(0.91–1.11)
Star Mountains	14	4.71 ± 0.10	1.34 ± 0.05	1.38 ± 0.06	1.14 ± 0.05
		(4.5–4.9)	(1.3–1.4)	(1.3–1.5)	(1.1–1.2)
C. shawmayeri					
Telefomin area	6	4.08 ± 0.10	1.22 ± 0.04	1.22 ± 0.04	1.00 ± 0.05
		(4.0–4.2)	(1.2–1.3)	(1.2–1.3)	(0.9–1.0)
Mt. Hagen	14	4.26 ±0.13	1.21 ± 0.06	1.22 ± 0.08	1.01 ± 0.07
		(3.96–4.46)	(1.11–1.32)	(1.05–1.32)	(0.85–1.12)
Mt. Wilhelm	21	4.28 ± 0.12	1.25 ± 0.05	1.26 ± 0.04	1.02 ± 0.05
		(4.07–4.52)	(1.17–1.33)	(1.19–1.33)	(0.95–1.12)
Wau area, Bulldog Road	5	4.10 ± 0.10	1.26 ± 0.06	1.22 ± 0.05	1.02 ± 0.05
		(4.0–4.2)	(1.2–1.3)	(1.2–1.3)	(1.0–1.1)
Mt. St. Mary	7	4.2 ± 0.06	1.24 ± 0.05	1.21 ± 0.04	1.07 ± 0.05
		(4.1–4.3)	(1.2–1.3)	(1.2–1.3)	(1.0–1.1)
C. kirrhos					
Bulldog Road		4.3	1.2	1.2	1.0
Smith's Gap		4.2	1.2	1.3	1.0
Maneau Range	5	4.08 ± 0.04	1.23 ± 0.03	1.29 ± 0.03	1.03 ± 0.05
		(4.02–4.10)	(1.20–1.27)	(1.26–1.33)	(0.98–1.10)

containing fossils was deposited, 25,000–20,000 B.P., a "number of lines of evidence suggests that the fossil deposit preserved in Chamber 1 of Kelangurr Cave accumulated at a time when the surrounding area was vegetated with tussock grassland and some alpine scrub. Forest was almost certainly absent, as the remains of obligate forest dwelling mammals are almost entirely absent from the deposit." Alpine tussock grassland and subalpine forest characterize the terrain today at 4000–4200 m on Mt. Carstensz and Mt. Wilhelm (but see "Fossil Sample" section in the account of *Brassomys*, n. gen., *albidens*). Flannery (1999), Hope et al. (1993), Aplin and Pasveer (2005), G.S. Hope (2007), and Hope and Peterson (1975) should be consulted for the history of change in vegetation and mammal faunas in montane, especially subalpine, New Guinea during the Quaternary.

Samples of the next species of *Coccymys*, which ranges through the Central Cordillera in Papua New Guinea, consist entirely of modern specimens: skins and skulls, fluid-preserved material, and skeletal fragments from owl pellets.

Coccymys shawmayeri (Hinton, 1943)

In 1943, Hinton described *Rattus shawmayeri* (Hinton, 1943: 556) from a single specimen collected by Fred Shaw Mayer in the eastern portion of the Bismarck Range in Papua New Guinea, remarking that the taxon "represents evidently a species of *Rattus* totally unrelated to any hitherto

described from New Guinea, and superficially most like *Rattus eha* [= *Niviventer eha*] of the eastern Himalayas." It is, continued Hinton,

> characterized by very small size for the genus, … strongly elongated tail, … small bullae, very weak supraorbital ridges, palatal length less than half occipito-nasal length, but palatal foramina long. … The lower incisor root of the new species forms a noticeable knob on the outer side of the jaw, just behind the coronoid process. Molars without special peculiarity . … The frontals are strongly constricted and the brain-case is broad. … The tail is mostly dark in colour, but the terminal 25 mm is pale. There is a certain growth of hair throughout its length, and the tail is different in this character from *Melomys.* The fur is soft; back dark brown, belly whitish grey, fifth hind-toe relatively long. Approximately fourteen rings to 10 mm on the tail.

Hinton could have been describing a specimen of *ruemmleri*, but this association between that taxon and *shawmayeri* would not be formally realized until 1993 when Musser and Carleton (1993: 585) listed the latter as a synonym of *Coccymys ruemmleri.* During the two and a half decades following the publication of Hinton's description, *shawmayeri* was treated as a species of *Rattus.* Ellerman (1949: 39) placed "*Rattus shawmayeri*" in a group of *Rattus* "With *small* bullae, … with *short* palate, less than half occipitonasal length …" that also contained *niviventer, fulvescens, coxingi, chrysocomus, cremoriventer, huang, bartelsi, eha,* and *inflatus*, a conglomeration of taxa that are now associated with three genera, *Bunomys*, *Niviventer*, and *Maxomys*, none of them native to New Guinea (Musser and Carleton, 2005). In the same volume Ellerman (1949: 52–53) formally identified this cluster as the subgenus *Maxomys* and separated the species into groups. "The *eha* Group contains two very small species with extremely elongated tail and weakly ridged skull (*eha* [a distinct species of Indomalayan *Niviventer*] and *shawmayeri*)." The latter "is a remarkable species," enthused Ellerman, "even smaller than *eha* to which it comes nearest, with shorter toothrow and narrower frontals than in that species, but very reminiscent of it in most essential characters. Its tail appears to be too hairy for *shaw-*

mayeri to be referred to *Melomys.* It seems totally different from other New Guinea *Rattus* rats."

In his treatise on the rodents of Australia and New Guinea, Tate (1951: 341) recognized "*Rattus shawmayeri*," summarized Hinton's description, and commented that "Hinton distinguished *shawmayeri* from the *exulans* group but did not compare it with any relative of *niobe*. Only the type is known." Tate did not comment on the proported relationship between *eha* and *shawmayeri* suggested by both Hinton and Ellerman.

The following year, Laurie's report of the mammals collected by Shaw Mayer in New Guinea from 1932 to 1949 included an account of *Rattus shawmayeri*, which identified seven additional specimens from the Hagen and Bismarck ranges (see gazetteer). "These specimens," noted Laurie (1952: 306), "are a useful addition to our collection in which, so far, the type of the species has been the only representative."

By 1954, *shawmayeri* was still regarded as a unique species of *Rattus.* In their list of the the land mammals of New Guinea, Celebes, and adjacent islands, Laurie and Hill (1954: 118) recognized the species (in the subgenus *Maxomys*, most certainly following Ellerman's 1949 arrangement) and were vividly impressed by it: "A remarkable form, very different from other New Guinea *Rattus.* It is smaller than *Rattus eha eha* from Nepal and Sikkim, India, to which it is perhaps most closely related."

In Misonne's (1969) treatise on evolutionary trends among African and Indo-Australian Muridae, he recognized *Maxomys* as a genus and excluded *shawmayeri* from it, disagreeing with Ellerman's (1949) arrangement (*Maxomys* as a subgenus of *Rattus* and containing *shawmayeri*). Misonne still regarded *shawmayeri* as a species of *Rattus*, but placed it in the subgenus *Stenomys*, which to him was "equivalent to the *assimilis-ruber-leucopus-niobe* Division of Tate (1951), but not to the *Stenomys* group of Ellerman (1949) nor to the division adopted by Laurie & Hill (1954)" (Laurie and Hill, 1954: 136). Misonne's action disassociated *shawmayeri* from Indochinese *eha* and brought it closer to native New Guinea

murines, but still left the taxon incorrectly allocated.

Between 1969 and 1993, *Rattus shawmayeri*, with two exceptions, seems to have disappeared from the literature covering New Guinea mammals. Taylor et al. (1982) did not include it in their revision of *Rattus* from the New Guinea region, because, they noted, "A study by J.A. Mahoney of the holotype and only known specimen has shown it to be an example of *ruemmleri* Tate and Archbold, 1941, a species now listed in *Pogonomelomys*," and Menzies (1990) apparently failed to examine the holotype of *shawmayeri* or any of the BMNH specimens identified as that taxon by Laurie (1952) for his revision of *Coccymys ruemmleri*, as none are included in his list of material examined or anywhere in his report. Neither of Flannery's (1990, 1995) editions of "Mammals of New Guinea" referred to *shawmayeri* in any context, even as a synonym of *ruemmleri*. The second exception is the "Ecological check-list of New Guinea Recent mammals" by Ziegler (1982: 880) where in the account of "*Pogonomelomys ruemmleri*," he indicated that the species included *Rattus shawmayeri*. Finally, by 1993 Musser and Carleton (1993: 585) formally recognized *shawmayeri* as a synonym of *C. ruemmleri* as a result of Musser's visits to BMNH where he studied the holotype and specimens reported by Laurie (1952); this allocation was repeated in 2005 (Musser and Carleton, 2005: 1307).

As we discovered and explain below, Hinton's *shawmayeri* is not a synonym of *Coccymys ruemmleri* but the oldest name for a separate species of *Coccymys*.

HOLOTYPE AND TYPE LOCALITY: The holotype of *Coccymys shawmayeri* is an adult female (BMNH 1947.1155) collected by Fred Shaw Mayer (original number 636) during May 1940. It consists of a stuffed museum study skin and associated skull (fig. 24), both in good condition. Occlusal surfaces of the molars are worn; cusp patterns remain evident on first molars but are blurred on the second and third teeth. External, cranial, and dental measurements are listed in table 7.

The type locality is Baiyanka (05°46′S, 145°10′E), Purari-Ramu Divide, in the southeastern portion of the Bismarck Range at 8000 ft (2440 m), Eastern Highlands Prov-

ince, Papua New Guinea (locality 14 in gazetteer and fig. 2).

EMENDED DIAGNOSIS: *Coccymys shawmayeri* resembles *C. ruemmleri* in physical appearance (see measurements listed in table 3) and most morphological traits associated with the skull and teeth (compare figs. 9 and 24). It is distinguished from *C. ruemmleri* by a paler and slightly shorter coat covering upperparts of head and body, longer tail relative to length of head and body, and significantly higher frequency of white tail tips in the populations. *Coccymys shawmayeri* has an absolutely shorter rostrum and bony palate compared to *C. ruemmleri*, a lower braincase (less bulbous), shorter maxillary and mandibular molar rows, and also differs in proportions of particular cranial and dental variables, which will be reported below.

GEOGRAPHIC DISTRIBUTION: The material listed in the gazetteer describes a Central Cordilleran distribution for *C. shawmayeri* that is confined to Papua New Guinea (fig. 2). Specimens obtained in montane forests between 2300 and 2800 m in the Telefomin region in Sandaun Province define the known western limit of the range. A sample collected in upper montane ("mossy forest") at 3000 m on Mt. St. Mary in the western portion of the Owen Stanley Range is the easternmost record. Between these extremes, *C. shawmayeri* has been encountered in the high reaches of the Cordillera wherever serious mammalian inventories and ecological studies have been undertaken. The species has not been recorded from the north coastal Bewani, Torricelli, and Prince Alexander ranges in Sandaun and East Sepik provinces, in the coastal Adelbert Range of Madang Province, or in the mountains of the Huon Peninsula (Madang and Morobe provinces).

Whether the Telefomin region is the actual western limit of *C. shawmayeri*'s range is unknown. It is not present in the material collected by the Archbold Expedition on the northern slopes of the Snow Mountains far to the west of the Telefomin area. The lowest records for *Coccymys* along that transect are from the Bele River valley at 2800 and 2200 m and those samples are definitely *C. ruemmleri* (see the account of that species).

Fig. 24.   The cranium and dentary of the holotype of *Coccymys shawmayeri* (BMNH 1947.1155), an adult female from Baiyanka, Purari-Ramu Divide, in the southeastern portion of the Bismarck Range at 8000 ft (2440 m). ×3. Measurements are listed in table 7.

The Telefomin area is interesting in another distributional aspect. The highest record for *C. shawmayeri* there is 2800 m; above that contour on the Star Mountains, at least by 3100 m, the upper montane forests are occupied by *C. ruemmleri*, which is the known easternmost occurrence of that species. To the east beyond the Star Mountains, *C. shawmayeri* is alone throughout most of the Central Cordillera, ranging upward beyond 2800 m into upper montane forests and alpine grasslands.

Mt. St. Mary, in the western half of the eastern Papuan peninsula, may actually delimit, or be near, the eastern margin of *C. shawmayeri*'s geographic range. Mammal surveys in the mountains east of there, particularly of Mt. Albert Edward and other peaks in the Wharton Range, have not revealed the species (the 1933–1934 Archbold Expedition to the Wharton Range and nearby highlands is an example). It is also in the western portion of the eastern peninsula that another species of *Coccymys* is found, *C. kirrhos*, n. sp., with records from Bulldog Road in the Wau area, Smith's Gap near Mt. St. Mary (thus overlapping the range of *C. shawmayeri*), and the Maneau Range at the end of the Owen Stanley Ranges (see account of the new species). This peninsular species appears to be the sole representative of *Coccymys* beyond Mt. St. Mary. How the interplay of its present distribution and past geological and climatological events may have influenced the eastern extent of *C. shawmayeri*'s range is unknown.

The recorded extremes between 1600 m in lower montane forest at Nondugl near Mt. Hagen and 3660 m in subalpine forest and alpine grassland on the eastern slopes of Mt. Wilhelm bracket the altitudinal distribution as recorded by voucher specimens along the Central Cordillera in Papua New Guinea (table 13).

DESCRIPTION AND COMPARISONS: *Coccymys shawmayeri* and *C. ruemmleri* are physically very similar: both have soft and dense fur, a small body, much longer tail, and narrow hind feet. Average differences among all samples in fur coloration and thickness, along with cranial and dental dimensions, contrast the two species. Fur covering

upperparts is shorter (9–12 mm) in *C. shawmayeri*, compared with the thicker coat of *C. ruemmleri* (11–14 mm); the upperparts are paler, a warm brownish gray with slightly burnished highlights, and none of the individuals we studied show any degree of black suffusion (brownish gray through very dark brown to dark brown suffused with black in *C. ruemmleri*); underparts range from whitish gray to a darker grayish white, but the paler tone is more common and no specimens examined exhibit any buffy wash (underparts of *C. ruemmleri* are whitish gray to dark grayish white and dark gray washed with buff in a few individuals); the tail is typically paler, grayish brown (instead of brown or dark brown), and longer relative to length of head and body (LT/LHB = 145%–170%, as opposed to 140%–146% in *C. ruemmleri*; table 3). Most specimens of *C. shawmayeri* (76%) have a conspicuous and moderately long white tail tip (mean = 27.0 mm, range = 4–42 mm); only 6 of 55 specimens of *C. ruemmleri* (11%) show a white tip, and the length averages shorter in those six (mean = 19.5 mm, range = 5–30 mm; table 8). The animal from the Telefomin area shown in Flannery's (1995: 275) color plate demonstrates the warm brown body fur and long tail with a conspicuous white tip that is so typical of *C. shawmayeri* (Flannery referred to it as *C. ruemmleri*, but we identify the voucher as *C. shawmayeri*).

Values for mass are available for 16 adults (in AMNH) from the eastern slopes of Mt. Wilhelm. All were weighed by Hobart Van Deusen who recorded weights in ounces, which we converted to grams: mean and standard deviation = 32.9 ± 6.65 g, range = 22.7–45.4 g. The range of variation is comparable to that reported by Flannery (1995: 274) for *C. shawmayeri* (as *ruemmleri*): 26 g for an adult female and a range of 30–34.8 g for three adult males. A young adult *C. ruemmleri* caught on Mt. Capella in the Star Mountains, the only specimen of that species measured for mass, weighed 34 g, within the range of body mass recorded for *C. shawmayeri*.

Skulls in all samples of the two species are generally alike in size and shape, but contrast in certain dimensions, which is evident when skulls of each are studied side-by-side (com-

TABLE 13
Summary of Altitudes (m) and General Habitats where Samples of Fossil and Modern *Coccymys ruemmleri*, *Coccymys shawmayeri*, *Coccymys kirrhos*, and *Brassomys albidens* Were Collected

Locality	C. ruemmleri	C. shawmayeri	C. kirrhos	B. albidens
INDONESIA, PAPUA PROVINCE				
Snow Mountains				
Carstensz area	3450	—	—	—
Kelangurr Cave	2950	—	—	2950
Mt Wilhelmina	3560–4050	—	—	—
Lake Habbema	3225	—	—	3225
Bele River valley	2800	—	—	2800
Bele River	2200	—	—	—
PAPUA NEW GUINEA				
Star Mountains	3100–3200	—	—	—
Telefomin area	—	2300–2800	—	—
Oksapmin	—	1850	—	—
Kaijende Highlands	—	3010	—	—
Tari Region	—	2400–2600	—	—
Mt Giluwe region	—	2000–3600	—	—
Mt Hagen region	—	2135–2700	—	—
Nondugl	—	1600–1830	—	—
Bismarck Range				
Mt Wilhelm area	—	2440–3660	—	—
Mt Otto	—	2300–2500	—	—
Mt. Missim	—	2000	—	—
Mt. Kaindi region	—	2200–2440	—	—
Bulldog Road	—	2400–2500	—	—
Mt. St. Mary	—	3000	—	—
Bulldog Road	—	—	2500	—
Smith's Gap	—	—	2500	—
Maneau Range				
Mt Dayman	—	—	2230	—
Dumae Creek	—	—	1525	—
Mt Simpson	—	—	1490	—
SUMMARY				
Altitude	2200–4050	1600–3600	1490–2500	2800–3225
Habitat	mid montane forest to alpine grassland	lower montane forest to alpine grassland	lower to mid montane forests	mid to upper montane forests

pare figs. 9 and 24), in the graphic results of discriminant function analyses (fig. 4), and in the differences between univariate means (tables 4, 5). Generally, *Coccymys shawmayeri* has a conspicuously shorter rostrum and bony palate compared with *C. ruemmleri*, and a lower braincase (less bulbous) and smaller maxillary and mandibular molars (shorter molar rows and narrower molars). Less marked is the narrower rostrum and shorter diastema of *C. shawmayeri*.

The distinctions between *C. shawmayeri* and *C. ruemmleri* in chromatic aspect of the dorsal pelage and cranial and dental dimen-sions are most pronounced in the Star Mountains between the sample of *C. shaw-mayeri* from combined localities in the Telefomin area between 2300 and 2800 m (the westernmost recorded limit of the species) and the series of *C. ruemmleri* from higher in the Star Mountains at 3100 and 3200 m (the easternmost recorded extension of this western Cordilleran species). Every specimen of *C. shawmayeri* from those lower altitudes has warm brown upperparts and whitish gray venters, while all the *C. ruemm-leri* have very dark brown dorsal pelage, some with a weak suffusion of black, and

very dark grayish white underparts, a few suffused with buffy hues. Every cranial and dental dimension measured is less in *C. shawmayeri*, some markedly so, as reflected in the tables of univariate means and graphically in the principal components ordinations (fig. 14; tables 4, 5).

At the eastern recorded margin of its geographic range, *C. shawmayeri* overlaps the distribution of *C. kirrhos*, n. sp.; the two species clash in fur and tail coloration, absolute dimensions of the skull, and some cranial proportions. Compared with *C. shawmayeri*, the sample of the new species has bright tawny or orange brown dorsal fur, and an absolutely longer tail, on average, that is pale brown and without any white tip (tables 3, 8). *Coccymys kirrhos*, n. sp., has a smaller skull with a relatively much narrower interorbit, longer rostrum and bony palate, and smaller bullae (tables 5, 6). See the account of the new species for an extended discussion of similarities and differences between the two species.

GEOGRAPHIC VARIATION: Specimen scores projected on the first and second components extracted from principal components analyses in figure 25 illustrate covariation in cranial and dental variables among geographic samples of *C. shawmayeri* along the Papuan Central Cordillera from the Telefomin area to Mt. St. Mary. Size of braincase and breadth of first upper molar are negligible in influencing the spread of scores along the first axis, which expresses size in this case, but all other variables are to some degree responsible for the dispersion (table 14). But no obvious internal structure exists that would suggest some significant geographic pattern in covariation of cranial and dental dimensions. The large series from Mt. Wilhelm, for example, overlaps nearly every other geographic sample included in the analysis.

Scores for the five specimens from the Telefomin area form a marginal cluster along the second axis, a shape factor. Compared with other samples, the Telefomin specimens have a relatively wider zygomatic plate but narrower mesopterygoid fossa, the two variables most responsible for the dispersion of scores along the second axis (table 14). The holotype of *shawmayeri* from the Bismarck

TABLE 14
Results of Principal Components Analysis of Geographic Samples of *Coccymys shawmayeri*
Samples are from the Telefomin area, Mt. Hagen region, Bismarck Range, Wau area, and Mt. St. Mary; the holotype of *shawmayeri* is included. (Principal components are extracted from a covariance matrix of 18 log-transformed cranial and dental variables; see tables 5 and 7, fig. 25.)

Variable	PC1	PC2
ONL	0.027	−0.015
ZB	0.021	−0.002
IB	0.012	0.009
LR	0.014	−0.003
BR	0.043	−0.008
BBC	0.005	0.004
HBC	−0.000	0.000
BZP	0.033	−0.046
LD	0.043	−0.007
PPL	0.037	−0.011
LBP	0.005	0.007
BBPM1	0.055	0.019
BMF	0.015	0.079
LIF	0.034	0.006
BIF	0.031	0.013
LB	0.023	0.000
CLM1–3	0.014	0.005
BM	0.001	−0.003
Eigenvalue	0.014	0.010
% Variance	28.590	19.772

Range near Mt. Wilhelm shares these proportional traits.

The Telefomin specimens contrast with the other samples in tail patterning. Only five of the eight specimens (63%) show a white tail tip, the lowest frequency among all the samples of *C. shawmayeri* (table 8). All other physical traits—lengths of hind foot and ear, relative length of tail, and color and thickness of fur—match those features in most of the other geographic samples (table 3).

It seems improbable that significant phenetic variation in the variables we examined does not exist among the populations of *C. shawmayeri* occurring along the high central dividing range of Papua New Guinea. Our inquiry was not really designed to resolve that aspect of morphological variation. For example, although the specimens we gathered into population samples are adults, a range of ages exists within that category, from young adults to old adults, which partly explains (along with individual and possibly
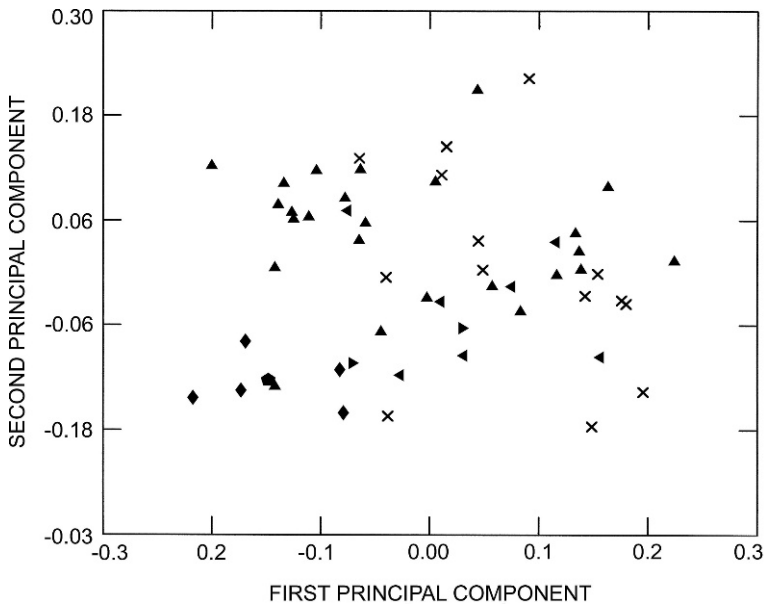
Fig. 25.   Specimen scores representing *Coccymys shawmayeri* projected on first and second components extracted from principal components analyses. Samples are from the Telefomin area (filled diamond), Mt. Hagen (reclining cross), Mt. Wilhelm (filled triangle), Bulldog Road in the Wau region (filled right-pointing triangle), and Mt. St. Mary (filled left-pointing triangle); the holotype of *shawmayeri* (filled pentagon) is included ($N = 54$). See table 14 for correlations and percent variance.

secondary sexual variations) the great spread of scores for the specimens from Mt. Wilhelm, our largest sample, along the size axis in the principal components ordination (fig. 25). A more refined sorting of age classes and analyses using only members of the same class would likely be more revealing. Therefore, larger samples from regions now represented by few specimens (the Telefomin area and Bulldog Road, for example) would be useful. We have defined *C. shawmayeri* in comparison with *C. ruemmleri* to the west and *C. kirrhos*, n. sp., to the east, but assessment of the internal geographic variation among populations of *C. shawmayeri* will require further inquiry.

HABITAT: The close physical resemblance between *C. ruemmleri* and *C. shawmayeri* is mirrored in their habitat affinities. As with that species endemic to the great dividing range in western New Guinea, *C. shawmayeri* inhabits mountain forests and grasslands, from lower montane forest formations at 1600 m through deep mossy upper montane forest to landscapes of alpine tussock grass-

land margined by clumps of subalpine forest at altitudes above 3500 m.

A large sample of *C. shawmayeri* in AMNH comes from the east slopes of Mt. Wilhelm and south slopes of Mt. Otto in the Bismarck Range, obtained during the 1959 Sixth Archbold Expedition to New Guinea. The specimen from Mt. Otto (see gazetteer) was captured a few hundred feet above a sawmill that had been operating eight years. "Below the sawmill," wrote Brass (1964: 193), "most of the original forest had been destroyed and replaced by gardens, fallow lands and *Pandanus* groves … and by forest regrowths and tall grass." From the sawmill up to 2400 m or more, the forest had been badly damaged by logging activities. Nevertheless, Brass (1964: 194) saw that "Enough remained … of [the] forest, beginning at the sawmill, to show a complex, rich, montane, mixed rain forest … of broad leaf-gymnosperm alliance, more middle altitude in appearance and floristics." It was in this zone that the *C. ruemmleri* was trapped, but there is no notation in Hobart Van Deusen's

field catalog as to whether the rat was taken on or above the forest floor.

Thirty-one examples of *C. shawmayeri* are from the eastern slopes of Mt. Wilhelm collected between 2770 and 3570 m. The specimens are simply labeled as being from ''Mt. Wilhelm,'' ''East slopes,'' ''Pengagl Creek,'' ''2 mi E Lake Aunde, 3400 m,'' and ''Lake Aunde, 3570 m.'' Floristic formations from the Pengagl camp at 2770 m to the Lake Piunde-Aunde camp at 3570 m ranged from lower montane forest through subalpine forest to alpine grassland, which is described in appreciative detail by Brass (1964).

The Pengagl camp at 2770 m was encircled by forest (Brass, 1964: 190; a fine photograph of the Pengagl camp is reproduced in Brass, 1964: pl. 7, fig. 2; also see fig. 26). Cool ambient temperatures recorded during July 3 to 31 (average maximum, 17.2°C, extremes, 13.5–21.0°C; mean minimum, 6.8°C, extremes, 5.0–9.4°C) and rain nearly every day produced a cold and wet environment. Brass (1964: 191) described the forest in the vicinity of the Pengagl camp between 2600 m and 3000 m as a broadleaf-gymnosperm formation of lower montane forest,

> a mixed, very moist forest of principally straight-boled trees 60 to 100 feet tall with fairly even, irregular, or broken canopy, scattered emergent taller trees, and where best developed in valleys and on moderate slopes, having more or less distinguishable subcanopy and substage tree layers. Bryophytes abounded in a fuzzy covering or heavier growths low on the trees and on the predominantly woody undergrowth. Under thin or broken canopy, … ''mossing'' became very heavy on trunks and branches of trees and on the ground, and a slender scrambling bamboo, present everywhere in the forest, ran rampant and formed dense tangles. In occasional small seepage areas of broken canopy through fall of trees or wetness of ground, a big stilt-rooted *Pandanus* was especially common, numerous epiphytic orchids grew close to the ground in heavy moss, *Rhododendron maius*, with big carnation-scented white flowers, was conspicuous on logs, and red-flowered *R. vandeusenii* grew low on trees.

Only three *C. shawmayeri* are labeled as being collected at ''Pengagl Creek'' but

possibly the specimens labeled ''E. slopes'' came from the vicinity of this camp, or between there and the higher camp at Lake Aunde (3650 m). Brass (1964: 192) wrote that ''Visiting natives brought specimens from probably as low as 6500 feet [2000 m] on the slopes below camp'' and remarked that ''the mammal collection from Pengagl was the largest and richest for any camp on the expedition [as opposed to the paucity of mammals collected at the higher Lake Aunde camp].'' But Brass (1964: 189) also noted that ''From levels below the subalpine [referring to the Lake Aunde camp], the Chimbu brought mammals for sale almost daily in good weather; all species so obtained were taken later at Pengagl Camp and are enumerated for that locality.'' So exactly where the *Coccymys* were trapped or caught by local people is unknown. At the Pengagl camp, Hobart Van Deusen, Brass remarked, was obliged to devote his time to preparing specimens. Hobart once related to Musser a lingering frustration at being unable to check his own traplines, and his ignorance of where many of the specimens were actually caught.

The Lake Piunde-Aunde camp at 3560 m ''was on a flat-topped, open, grassy rise at the lower end of the first of two closely adjacent, deep, alpine lakes'' (Brass, 1964: 185) surrounded by a mosaic landscape of fragmented subalpine forest, tree ferns and alpine tussock grassland (views beautifully preserved in the photographs published in Brass, 1964: pls. 10 and 11; also see figs. 27, 28). Mean maximum and minimum ambient temperatures recorded for June 14 to 28 were 13.3°C (extremes, 10–16.5°C) and 3.8°C (extremes, 2.5–5.0°C), respectively. During this period, Brass described days with light to heavy frost, occasional icing of wet ground and small pools, and snowfall during two days on the heights of Mt. Wilhelm.

Brass (1964: 187) wrote of the forest that,

> A considerable amount of fragmented, heavily mossed, low, subalpine forest occurred on slopes in the vicinity of camp, diminishing rapidly up to tree limit at 13,000 to 13,200 feet [3965–4026 m], and increasing downward until it almost completely covered the slopes and all but the cold, mostly ill-drained bottom of the U valley. … Down the mountain, the subalpine forest merged into a different forest type in a

Fig. 26.   Pengagl camp, 2770 m, east slopes of Mt. Wilhelm. This camp was "in primary forest in general little disturbed except by exploitation for timber for house frames and garden fences, and bark for house walls, by the local people, and the rootings made by pigs of the Chimbu on easily accessible ground up to several hundred feet in altitude above our camp. … Camp was so closed in by forest that the only distant views were of alpine heights up the creek and a glimpse of mountains near Bundi Gap, on the Bismarck Range at the head of the Chimbu" (Brass, 1964: 189–190). This is the lowest altitude at which *Coccymys shawmayeri* was taken on Mt. Wilhem. June 29 to July 31, 1959.

broad ecotone, with a rather definite change apparent at about 10,800 [3294 m]. Typically, the subalpine forest consisted of a dense canopy layer, 25 to 30 feet high, of generally crooked small trees with small stiff leaves and erect stiff branches. … Within the forest, a thin bryophyte layer constituted the only ground covered in very dense shade. Elsewhere an occasional herb entered from the borders to associate with a few true undergrowth plants. …

The grassland near the Lake Aunde camp also captured Brass's attention (Brass, 1964: 188):

Alpine grassland, as original primary vegetation, occupied the mountain above the forest zone, and below that ground too wet or too cold for forest. At camp level, in the valley bottom down to 10,900 feet [3325 m], and up to variously 13,000 to 13,500 feet [3965–4118 m] on open slopes, was tussock grassland. At lower to middle levels the long-grass or tussock grassland ("peaty grassland" of Hoagland) occupied mainly poorly drained or seepage-

wet peaty soils, at higher levels well-drained soils, some of which … formerly carried forest.

The grassland communities consisted not only of a great many species of grass, but a diversity of herbs, low shrubs, ground ferns, and cycadlike tree ferns resistant to frost and fire.

Of the 14 *Coccymys* obtained at "Lake Aunde," site information (taken from notations on skin tags or Van Deusen's field catalog) is associated with only 4: AMNH 192092 and 192105 were "snared in long grass," 192100 was "snared in peaty grassland," and 192107 was "snared in grass near subalpine forest."

Other associations between specimens and habitats come from published accounts or notations on tags attached to museum skins. One juvenile *C. shawmayeri* (AM 16745) was taken from the crown of a *Pandanus* at 2600 m from the upper Sol River valley during a mammal survey conducted in

TABLE 15
Summary of Habitat Information Associated with Specimens of *Coccymys shawmayeri* Stored in the Bernice P. Bishop Museum
(Nearly all specimens were collected by A.B. Mirza. Information comes from notations on skin tags.)

Locality (see gazetteer)	Altitude (m)	Habitat description of capture site ("snap-trapped" unless otherwise indicated)
Telefomin Valley	2300–2800	"moss forest"
Tari Gap	2600	"forest" and "grassland"
Doma Peaks	2400	"forest"
Lavani Valley	2450	"moss forest"
Mt. Giluwe	2000	"live trap on ground in moss forest"
"	2800	"moss forest"
"	2800	"pine forest"
"	2900	"on ground" in "forest"
"	2900	"on tree 4 feet above ground"
"	3000	"on log in moss forest"
"	3300	"in grass" in "grasslands"
"	3360	"moss forest"
"	3400	"moss forest"
"	3500	"in grass" in "grasslands"
"	3600	"grass"
"	3600	"grassland and patches of forest"
Murmur Pass	2700	"moss forest"
Mt. Wilhelm	3696	"forest," "grass," and "forest and alpine grass"
Mt. Kaindi	1900	"forest"
"	2350	"summit," "beside stump in brush and tall grass"
"	2440	"moss forest"
Bulldog Road	2400	"moss forest"
"	2500	"moss forest"
"	2500	"on tree 3 feet above ground," "moss forest"
Mt. St. Mary	3000	"moss forest"

Sandaun Province. In 1984 and 1986, Tim Flannery's base camp (Flannery and Seri, 1990: 178):

> was beside the westwards-flowing headwaters of the Sol at an altitude of between 2,200 and 2,300 m. The floor of the valley at this altitude is gardened by the inhabitants of Telefolip Village. The valley walls rise sharply to the south, north and east enclosing a relatively flat-lying basin, and gardening is restricted to its lower parts. … Away from the gardened zone, the valley is clothed in climax Lower Montane Forest. Even at altitudes of 2,600 m large fruited *Castanopsis* are common. … The forest does not become very mossy until 2,600 to 2,800 m. The lower part of the valley floor is dominated by gardens and secondary growth in various stages.

Willett et al. (1989: 11) collected a specimen in "mid-montane rain-forest" on the southern flanks of Mt. Missim at 2000 m.

They provide several views of the forest where surveys were conducted but no details describing where the specimen was caught.

The specimens of *C. shawmayeri* in the Bishop Museum collected by A.B. Mirza have short habitat notes on the skin tags, which are tabulated in table 15. The geographic coverage mirrors the Cordilleran range of *C. shawmayeri*, and the range of habitats at the collection sites extends from lower montane forest through upper montane formations to alpine grasslands.

BIOLOGY: We have been unable to locate reproductive information for *Coccymys shawmayeri*. None of the specimens we examined for this report carried any notes on litter size, breeding periods, or any other reproductive aspects, and the published literature is unhelpful. (Many of the specimens were collected by A.B. Mirza, who recorded succinct habitat notes on skin labels

TABLE 16
Contents from Stomachs of *Coccymys ruemmleri*, *Coccymys shawmayeri*, and *Coccymys kirrhos*

Species, locality, and specimen	Contents
C. ruemmleri Lake Habbema 152740	**Stomach empty:** fecal pellet in intestine consisted of unidentifiable dark brown mash and a small cockroach nymph (first or second instar)
C. shawmayeri Nondugl 183634	**Entirely insects, probably cockroaches:** very small dark brown fragments of sclerites, a few long filamentous antennae, partly digested tissue adhering to many of the larger sclerite fragments; translucent gelatinouslike pieces resembling partly digested soft tissues. Fragments are likely from early instar cockroach nymphs. Did not find mouth-parts, legs, or wings
183609	**Mostly fruit, at least one insect larva, maybe more:** very small pieces of fibrous fruit pulp; small fragments of fig with the inner lining adherent and tiny seeds embedded in it, many isolated sections of tissue filled with tiny fig seeds; a few small sclerite fragments, the larger pieces attached to partly digested tissue; and translucent sections from the body of an insect larva
183633	**Mostly insects, a little fruit:** many very small beetles (head fragments, short segmented antennae, legs, membranous wings), small cockroach nymphs, early instars (long, filamentous antennal segments, abdominal sclerites); intact early instar nymphs of katydids along with long thin antennal segments; and partly digested soft tissue mixed with translucent ventral abdominal pieces; a few small chunks of fruit pulp, some resembling outer surface of skin; no seeds
Mt. Wilhelm 192734–738, 192740, 192307	**Fruit only:** suspension of digested pulp and fragments of brown seed coats—one kind of fruit; similar to contents of 156588 and 156546 from Mt. Hagen
156618	**Fruit only:** suspension of fruit pulp
192733	**Fruit only:** finely digested pulp, many tiny black seeds that resemble fig, one fragment of possible fig skin; some larger brown seeds from a different fruit
156608	**Fruit, vegetative fragments, insect larvae:** suspension of digested pulp, fragments of brown seed coats, small wedge-shaped brown seeds, few grass seeds; plant tissue (stems, leaves, petals), and many small (5 mm long) insect larvae (probably Coleoptera)
192105	**Mostly fruit:** suspension of fruit pulp, tiny bits of seed coats, many small flat seeds; one intact flea (probably ingested during grooming)
192092	**Fruit only:** suspension of pulp, with fragments of seed coats, small pieces of skin from fruit
Mt. Hagen 156490	**Fruit only:** numerous tiny brownish black oblong seeds and partly digested fruit pulp; appears to be only one kind of fruit present; stomach greatly distended with these contents
156548	**Mostly fruit:** pulp and pieces of brown seed coat; some small (3 mm long) intact larvae (probably Diptera), the kind found infesting fruit; no other type of insect remains
156605	**Fruit only:** some digested pulp, but mostly two kinds of seeds, tiny irregularly-shaped blackish seeds, and much larger, round flat seeds (same kind as in 192733)—definitely two kinds of fruit consumed
156547	**Insects:** sclerite fragments and mouthparts from adult beetles, suspension of digested tissue; few small plant fragments; unidentifiable suspension of brown particles, either fruit pulp or insect tissue (stomach poorly preserved)
156546, 156588	**Fruit only:** stomachs full of digested pulp and tiny fragments of brownish seed coat—apparently only one kind of fruit
C. kirrhos Mt. Simpson 184493	**Fruit only:** small amount of pulp suspension, large tan and brown pieces of seed coat

but no reproductive information. His field journals, which we have not read, are stored at the Bernice P. Bishop Museum and should be consulted by those researchers planning any reports covering reproductive information for *C. shawmayeri*.)

Documented dietary data for *C. shawmayeri* is equally elusive. Menzies and Dennis (1979: 40) noted that "Limited evidence indicates that the diet [of "*C. ruemmleri*"] consists only of vegetable matter including leaves," but they cited no source for their observations. We turned to specimens preserved in fluid and stored at AMNH to extract stomachs, and surveyed the contents from 21 specimens of *C. shawmayeri* collected in Papua New Guinea at Nondugl, Mt. Wilhelm, and Mt. Hagen. Their contents are summarized in table 16. They collectively reflect a diet composed of fruit, seeds, and

Fig. 27. View of Lake Aunde and the ''Lake Piunde-Aunde Camp'' at 3560 m on the eastern slopes of Mt. Wilhelm. ''This 'Top Camp' was on a flat-topped, open, grassy rise at the lower end of the first of two closely adjacent, deep, alpine lakes encountered on the climb toward Mt. Wilhelm summit'' (Brass, 1964: 185). ''A considerable amount of fragmented, heavily mossed, low, subalpine forest occurred on slopes in the vicinity of camp, diminishing rapidly up to tree limit at 13,100 to 13,200 feet [3970 to 4000 m], and increasing downward until it almost completely covered the slopes of the U Valley'' (Brass, 1964: 187). The highest record on Mt. Wilhelm for *Coccymys shawmayeri* is near this ''Top Camp'' (see gazetteer). June 8–29, 1959.

insects, although most stomachs contained only fruit, or mostly fruit with some insect material; the remaining stomachs contained only insects, or mostly insects with some fruit. One stomach was full of fruit, small insect larvae, and bits of vegetative plant tissue. The bulk of the insects are in pieces and had been masticated, indicating active capture and chewing; some of the very small larvae are whole and may have been passively ingested with fruit.

Particular anatomical traits characteristic of *Coccymys* are consistent with a mixed diet of fruit and insects; dentition and stomach anatomy are examples. The morphology of the incisors is not specialized; their shape, pigmentation and extent of enamel cover, and size relative to the skull and mandible form a configuration common among murines. Occlusal patterns of the molars typical of *Coccymys*, especially those of the upper molars, provide rows of cuspidate and wide surfaces suitable for masticating fruit or

insects. Broadly, but not in detail, they resemble the coronal patterns seen in the species of *Margaretamys* from Sulawesi (Musser, 1981a: 284–285), particulary the upper molars. All three species of *Margaretamys* are arboreal and feed on a variety of different fruits, as well as katydids, small cicadids, camel crickets, and moths (Musser's observations in the field). Their incisor anatomy is also generalized compared with that in such highly specialized invertebrate predators as the Sulawesian and Philippine shrew rats, for example (Musser and Heaney, 1992; Musser, 1982b).

Coccymys shawmayeri (and the other two species in the genus) has a unilocular-hemiglandular type of morphology, which is described by Carleton (1973). The stomach consists of a single chamber (unilocular), and the gastric mucosa is bisected nearly equally into glandular epithelium to the right of the esophagus, lining the antrum, and cornified squamous epithelium to the left, lining the

Fig. 28. Alpine tussock grassland in valley just below Lake Aunde bordered by subalpine (upper montane) forest down the valley. "Alpine grassland, as original primary vegetation, occupied the mountain above the forest zone, and below that ground too wet or too cold for forest. At camp level, in the valley bottom down to 10,900 feet [3300 m], and up to variously 13,000 [3939 m] to 13,500 feet [4091 m] on open slopes, was tussock grassland. A short-grass community, already in evidence at camp level and below, replaced the tussock grasses at higher elevations" (Brass, 1964: 188). June 8–29, 1959.

corpus (hemiglandular); the division between the two epithelial linings is marked by a bordering fold extending from the incisura angularis (at the right of the esophagus) directly across to the greater curvature of the stomach. This single-chambered hemiglandular morphology, in which the glandular zones are separated by a smooth bordering fold, forms the gastric conformation that, as suggested by Carleton (1980: 101), represents the primitive evolutionary state among muroid rodents. The fully distended stomach of *Coccymys ruemmleri* resembles this general unilocular-hemiglandular conformation, and is similar to that of the Sulawesian *Rattus hoffmanni*, figured in Musser and Durden (2002). The design is also common to the species of Sulawesian *Margaretamys*, in which the diets consist of fruit and insects.

Being able to consume fruit, seeds, and insects is probably advantageous to species such as *C. shawmayeri* and its congeners, which we suspect to be scansorial (see discussion in account of *Brassomys albidens*). The very long tail relative to length of head and body, and moderately long and slender hind feet possessed by *C. shawmayeri* and the other two species are appendage proportions and shapes usually associated with scansorial activities. We view a scansorial animal as one that forages over the ground (partly terrestrial) and climbs into shrubs, pandans, tangles of woody vines, small trees, and lower branches of larger trees within the forest understory (partly arboreal); nests may be anywhere in that vertical range. Judged by collection data attached to some specimens of *C. shawmayeri*, individuals were trapped on the ground, on a tree trunk laying on the ground, on trees 3–4 ft above ground, and in the top of a *Pandanus* (see table 16 and "Habitat"), which describes the vertical range of scansorial activities. Opportunities for food within those horizontal and vertical habitat spaces are measurably increased when the animal is able to eat fruits, seeds, and vegetative plant parts, as well as insects.

Coccymys shawmayeri is also nocturnal and one of the species preyed upon by the sooty owl, *Tyto tenebricosa*. These assertions

are based on contents of owl pellets. Beneath a boulder on a ridge rising sharply behind the camp at Lake Aunde (3560 m, June 1959) on the eastern flanks of Mt. Wilhelm, Hobart Van Deusen uncovered a cache of owl pellets. The boulder is about 100 m above the camp; the landscape is dominated by alpine tussock grassland surrounding islands of subalpine forest (see pl. 11, fig. 2 in Brass, 1964). Feathers found at the roost, wrote Van Deusen in his notes (in Mammalogy Archives at AMNH), were collected and later identified as coming from a sooty owl; no feathers of any other kinds of birds were seen around or beneath the boulder. Back at the museum the undigested bones and teeth (no feathers were discovered) were extracted from the pellets and studied. Van Deusen identified remains from the small-bodied marsupials *Microperoryctes ornata* (8 individuals, initially determined as *M. longicauda* [see Helgen and Flannery, 2004, for the use of *ornata*]) and *Carcartetus caudatus* (5 individuals), and made provisional determinations for a few of the small rodents found. We examined all the rodent material (mostly cranial fragments and dentaries, with or without molars and incisors) and found 56 individuals of *Coccymys shawmayeri* (AMNH 276640–95), 40 *Rattus niobe* (AMNH 276600–639), 2 *Pseudohydromys fuscus* (AMNH 276598, 276599), 2 *Abeomelomys sevia* (AMNH 276596, 276597), and 3 *Pogonomys sylvestris* (AMNH 276593–95). At least during 1959, *C. shawmayeri* formed a significant component of the sooty owl's diet. *Tyto tenebricosa* ranges throughout New Guinea from coastal lowlands to treeline, nests in hollow trees and understory tangles during the day and at night preys on small marsupials and rodents in a variety of forest formations below treeline, and in subalpine forest and adjacent alpine grasslands at high altitudes. Pellets from *T. tenebricosa* from a cache high on Mt. Wilhelmina also contained *Coccymys*, in this case *C. ruemmleri*, but the number of individuals relative to other rodent prey was much lower (see the account of that species).

Other biological aspects of *Coccymys shawmayeri* have been explored, although the voucher specimens used in these studies were identified as *C. ruemmleri*. Sperm head morphology and its significance was dis-cussed by Breed (1997, 2004) and Breed and Aplin (1994). Genetic studies that included *C. shawmayeri* are represented by Watts and Baverstock (1994, 1996) who sampled one individual for their research into intergeneric clustering in Australo-Papuan murids based on albuminological comparisons (microcomplement fixation of albumin). The species has yet to be included in any published phylogenetic studies based on sequences from mitochondrial or nuclear genes.

SYMPATRIC ASSOCIATIONS: The regional sympatric relationship between the western Cordilleran *C. ruemmleri* and *C. shawmayeri* was explored in the account of the former species. Overlap of the eastern part of the geographic range of *C. shawmayeri* with the western distributional segment of *C. kirrhos*, n. sp., the eastern peninsula endemic, will be entertained in the account of the new species.

Coccymys shawmayeri also occurs sympatrically with a core of high-altitude Cordilleran marsupials and rodents. The suite of species collected by members of the Archbold Expedition from the eastern slopes of Mt. Wilhelm provides an example of the montane community. At the Lake Piunde-Aunde locality (3560 m), wrote Brass (1964: 189),

> *Rattus niobe* was trapped easily in grass and forest, and snared in large numbers on tussock grassland by visiting natives; [*Abeomelomys*] *sevia* was trapped fairly frequently on grasslands, occasionally in forest. … *Mallomys rothschildii* … was trapped only on tussock grassland but probably entered the forest. This also applies to the bandicoot [*Microperoryctes*] *longicauda* [= *ornata*]. The gentle little marsupial [*Carcartetus caudatus*] of the forest, caught by hand in old bird's nests, and trapped, and the ringtail [*Pseudochirops*] *cupreus* doubtfully ventured far from forest cover at any time. No bats were seen.

"Containing 34 species, the mammal collection from Pengagl [2770 m and lower] was the largest and richest for any camp on the expedition," enthused Brass (1964: 192):

> The collection comprised, in marsupials, [*Murexia*] *melanurus*, … [*Microperoryctes*] *ornata*, *Phalanger* [*sericeus*], [*Carcartetus*] *caudatus*, [*Pseudochirulus*] *forbesi*, [*Pseudochirops*] *cupreus*, *P. corinnae*, *Petaurus breviceps*, *Dorcopsulus vanheurni* and a species of *Dendrolagus*.

The larger marsupials were probably kept at rather low population levels by local hunters, ranging the forests with dogs, and climbing or cutting down trees for arboreal species. … The rodents showed great dissimilarity in abundance, *Rattus niobe*, for example, being extremely common, while six of a total of 19 species were represented by only one specimen in the collection. The species, besides *Rattus niobe*, were *R.* [*steini*] (from the lower levels), *R. exulans*, *Anisomys imitator*, *Pogonomys sylvestris*, *P.* [*loriae*], *Lorentzimys nouhuysi*, [*Protochromys*] *fellowsi*, … [*Melomys rufescens*, *Paramelomys rubex*], [*Abeomelomys*] *sevia*, and *Macruromys major* in murines. Trapped and snared in the forest were the very small, very rare, shrew-like hydromyines *Pseudohydromys murinus*, [*P.*] *fuscus*, and [*P.*] *ellermani*. Taken in traps in creek-bed habitats were the big water rats *Baiyankamys shawmayeri*, *Parahydromys asper*, and the highly specialized *Crossomys moncktoni*. …

In addition to these nonvolant species, four kinds of bats were collected, species of *Pipistrellus* and *Miniopterus*, *Nyctophilus microdon*, and *Syconycteris australis*. The rendition of species collected at the two camps is certainly an incomplete survey of the mammalian species occurring with *C. shawmayeri*, but they offer an insight into the montane community.

The "beautiful little *Pogonomelomys*" that caught Brass's (1956: 129) attention on Mt. Dayman is the subject of the following species account.

Coccymys kirrhos, new species

HOLOTYPE AND TYPE LOCALITY: The holotype is AMNH 158175, an adult male collected by Hobart M. Van Deusen (original number 12256) on May 29, 1953. The specimen consists of a stuffed museum study skin, cranium, mandible, and partial postcranial skeleton. The skin and skull are in good condition (figs. 7, 29); incisors and molars are intact; the molars are worn but occlusal patterns of their cusps remain evident. External, cranial, and dental measurements are listed in table 7. Coronal patterns of maxillary and mandibular molar rows of a different specimen from Mt. Dayman are shown in figures 11 and 12.

The type locality is "Top Camp" (09°49′S,149°16′E), 2230 m, north slopes of Mt. Dayman, Maneau Range (also spelled "Maneao") at the eastern end of the Owen Stanley Ranges, Milne Bay Province, eastern Papua New Guinea (locality 22 in gazetteer and fig. 2). The camp "was on the western bank of the Atairo in a secluded grassy hollow within quarter of a mile of the head of that stream, and 1½ to 2 miles northwest of the summit of Maneau Peak" (Brass, 1956: 126). In addition to "Mount Dayman," the camp name, and altitude, recorded on specimen labels is the notation "Maneau Range," which in this case is basically synonymous with Mt. Dayman. The latter is actually a part of the Owen Stanley Ranges and, as Brass (1956: 111–112) noted, has four primary summit peaks (Maneau, Gadmarau, Mana-man, and Dayman), grouped around the head of the Gwariu Valley that are all parts of one large mountain. The entire Mt. Dayman with its peaks, and the section of the Owen Stanley Ranges dominated by the mountain was called the Maneau Range by early explorers, after Maneau Peak, which is only one, and not the highest of the four peaks. (Flannery and Groves, 1998, have also used "Nanneau Range" for this area.) Another perspective of the region is provided by Engilis and Cole (1997: 1), who worked there in 1985 and wrote that Mt. Dayman "is one of three isolated mountain peaks that dominate the extremity of the eastern peninsula of New Guinea. Viewed from the air, the summit is actually the apex of a complex series of dissected ridges. All but the summit alpine grasslands are covered in dense forest. Human settlements are in valleys below 1600 m; most are isolated by steep ridges."

REFERRED SPECIMENS: Six additional specimens. Four were collected in Milne Bay Province in the Maneau Range. Two are from the type locality and were obtained by Hobart Van Deusen at the top camp, 2330 m: the stuffed skin and the skull of an adult female (AMNH 158173) collected May 25, 1953, and the stuffed skin and nearly complete skeleton of a young adult male (AMNH 158174) collected May 28, 1953. The third specimen is an adult female (BBM-NG 109165) represented by a stuffed skin
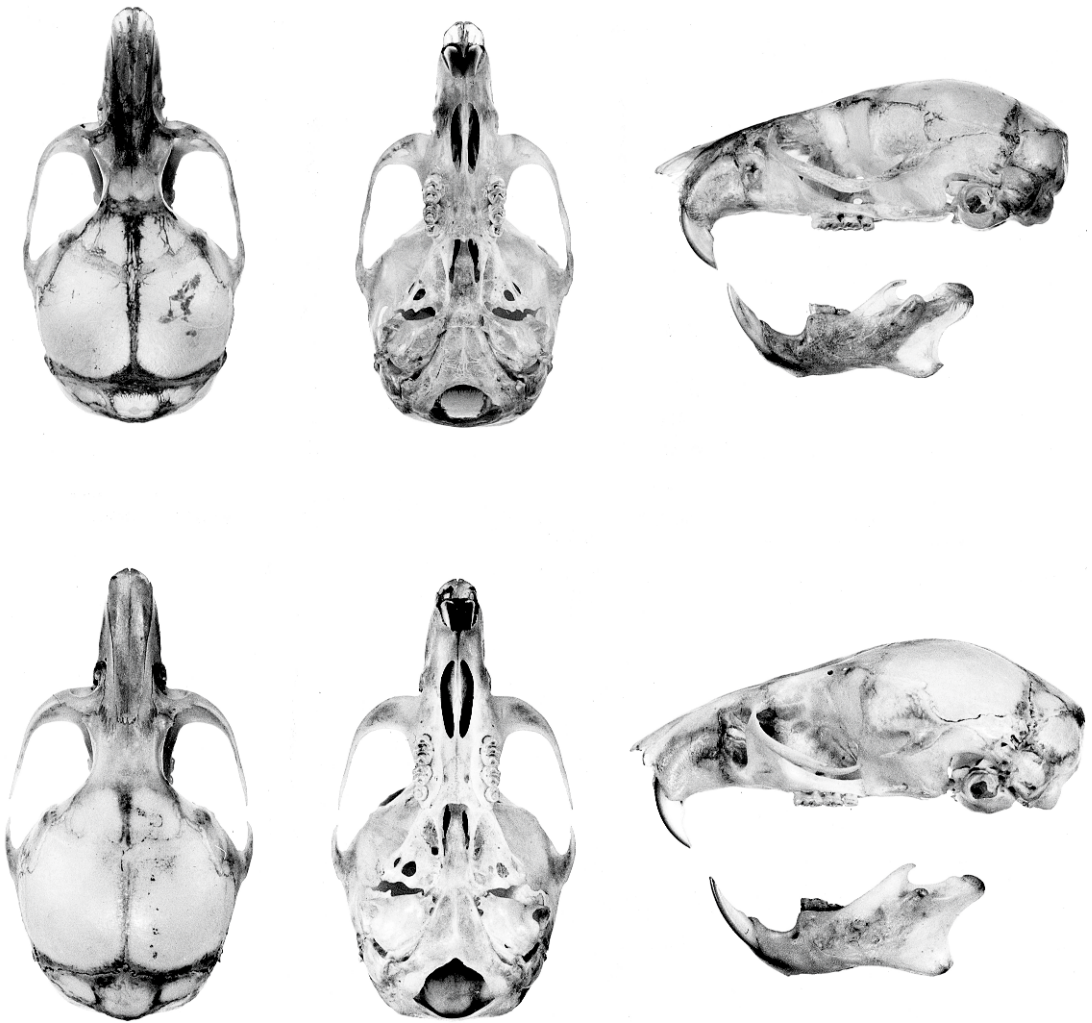
Fig. 29.   Crania and dentaries of *Coccymys* representing holotypes. **Top:** *C. kirrhos* (AMNH 158175), male from the northern slopes of Mt. Dayman, 2230 m. **Bottom:** *C. ruemmleri* (AMNH 150669), male from northern slopes of the Snow Mountains at Lake Habbema, 3225 m. ×2. Measurements are listed in table 7.

and a skull collected February 26, 1985 from the southeastern ramparts of Mt. Dayman on the Garatin Ridge in the Agaun region of the Maneau Range at Dumae Creek, 2.3 km N, 0.4 km W of Agaun (09°53′S, 149°23′E; Dumae Creek, the base camp for the expedition recounted by Cole et al. [1997], is below Garitin Pass, on the road from Agaun to Bonenau), 1525 m. The fourth specimen from the Maneau Range is a young adult (BBM-NG 184493) consisting of a body in fluid and extracted skull collected

February 25, 2003, on the north slopes of Mt. Simpson, 0.5 km S of Bunisi Village (10°01′S, 149°35′E), "Camp 5," 1490 m.

The fifth example is an adult female (BBM-NG 96950) represented by a skull and stuffed skin collected August 2, 1968, from Smith's Gap (08°03′S, 146°53′E), "in the vicinity of Guari," 2500 m, Central Province.

The sixth specimen is the skull and stuffed skin of an adult female (BBM-NG 55824) obtained November 2, 1967, from the Wau

area, Bulldog Road, "12 mi from" Edie Creek (07°31′S, 146°40′E), 2500 m, Morobe Province.

DIAGNOSIS: The small-bodied and long-tailed *Coccymys kirrhos* is physically similar to *Coccymys ruemmleri* and *C. shawmayeri*, but contrasts sharply with both of those species by the bright orange-brown or tawny fur clothing upperparts of its head and body (dark brown to blackish brown in *C. ruemmleri*, brown in *C. shawmayeri*) and by its whitish gray ventral coat (whitish gray through dark grayish white to dark buffy gray in *C. ruemmleri*, whitish gray to grayish white in *C. shawmayeri*). The very long tail of *Coccymys kirrhos* relative to head and body length, and lack of a white tip on every specimen in the sample, is distinctive. Relative length of tail is much shorter in *C. ruemmleri*, proportionally similar in *C. shawmayeri*; individuals with a white-tipped tail occur in 11% of the sample of the former and 76% of the latter (tables 3, 8). The skull and molars of *C. kirrhos* are appreciably smaller compared with *C. ruemmleri* (values for every dimension measured are less except for breadth of mesopterygoid fossa, which exceeds that in the sample of *C. ruemmleri*; tables 4, 6, 12), and only a few of the cranial and dental variables measured match or exceed those for the average larger skull of *C. shawmayeri* (tables 4–6). Significant proportional differences in cranial and dental variables also distinguish *C. kirrhos* from the other two species of *Coccymys*.

GEOGRAPHIC DISTRIBUTION: Known only from lower montane to mid-montane forests in the Central Cordillera extending through the eastern peninsula of Papua New Guinea (fig. 2). Five of the seven known specimens are from Mt. Dayman, the adjacent Agaun region, and Mt. Simpson, all part of the Maneau Range, at the eastern end of the Owen Stanley Ranges. The westernmost record is the single specimen from Bulldog Road in the Wau area on the flanks of the Kuper Range at the western end of the eastern peninsula. The only record between those geographic brackets is the individual from Smith's Gap near Mt. St. Mary, just west of the Wharton Range. *Coccymys kirrhos* likely occurs elsewhere in montane forest formations in other parts of the eastern

peninsular Cordillera, but much of that region has been poorly sampled for small mammals.

The altitudinal records for samples from the Maneau Range extend from 1490 m to 2230 m; 2500 m is the altitude at which the specimens from Bulldog Road and Smith's Gap were taken (table 13). The range of altitudes encompasses lower montane and mid-montane forest formations. Unlike the other two species of *Coccymys*, *C. kirrhos* has not been collected in upper montane habitats or alpine landscapes, and the species occurs at lower altitudes than have been recorded for either *C. ruemmleri* (2200 m) or *C. shawmayeri* (1600 m); see table 13.

ETYMOLOGY: The Greek *kirrhos* means "orange-yellow" or "tawny," which describes the bright dorsal pelage of *Coccymys kirrhos* compared with the dark and somber coat of *C. ruemmleri* and the warm brown upperparts of *C. shawmayeri*.

DESCRIPTION AND COMPARISONS: *Coccymys kirrhos*, *C. ruemmleri*, and *C. shawmayeri* have small bodies and long tails relative to length of head and body (table 3). They also agree, except for size, in their short muzzles, shapes of ears and feet, relative lengths of mystacial and other vibrissae, number of palmar and plantar pads and their extent relative to palmar and plantar areas, configuration of scale annuli on the tail, number and relative lengths of hairs emerging from beneath each tail scale, unpigmented claws, and number of teats—in these respects, *C. kirrhos* is essentially a somewhat smaller physical version of *C. ruemmleri* and *C. shawmayeri*. The two latter species contrast sharply in coloration of fur with *C. kirrhos*. The dorsal coat of *C. kirrhos* is soft and thick, much as it is in *C. ruemmleri* and *C. shawmayeri*, but averages shorter (8–10 mm long as opposed to 11–14 mm in *C. ruemmleri* and 10–12 mm in *C. shawmayeri*), and is bright orange-brown or tawny from the rump to the top of the head and cheeks, becoming more ochraceous on the sides of the body (overhairs are gray for most of their lengths, with bright buff to ochraceous buff tips); only the face between the eyes is gray (a somber dark brown and burnished highlights characterize the upperparts of most *C. ruemmleri*, with a few specimens even suf-

fused with black; brownish gray with burnished highlights is characteristic of *C. shawmayeri*). Prominent brownish black encircles each eye and covers the bases of the mystacial vibrissae, a pattern resembling that of the other two species, but their faces and cheeks are gray, while only the face between the eyes is gray in *C. kirrhos*, and its cheeks are tawny. As in the other two *Coccymys*, the dorsal surfaces of the front and hind feet as well as digits of *C. kirrhos* are scantily covered with pale brown or unpigmented hairs, but the metacarpal and metatarsal surfaces are paler. The underparts of *C. kirrhos*, from chin to base of tail, are bright whitish gray (hairs are gray basally, but the white distal segment is long, producing a denser white overlaying the gray); the range in *C. ruemmleri* extends from whitish gray through dark grayish white tones to dark grayish buff ventral coats; whitish gray to grayish white is typical in our sample of *C. shawmayeri*.

A long tail relative to length of head and body (LT/LHB = 150%–181%, N = 7) is characteristic of *C. kirrhos*, and similar proportions occur in samples of *C. shawmayeri* (145%–170%, N = 33). However, in samples of *C. ruemmleri* from the Snow and Star mountains, the tail is relatively much shorter (140%–146%, N = 33); see table 3. The tail averages paler in *C. kirrhos* (grayish brown) than in *C. ruemmleri* (brown), and generally matches *C. shawmayeri* in chromatic range. As in the other two species, *C. kirrhos* exhibits a comparable linear calloused strip devoid of hairs and scales on the dorsal surface along the terminal fifth of the tail. Not one of the seven examples of *C. kirrhos* has a white tail tip, which is more comparable to the pattern seen in most specimens of *C. ruemmleri* (6 of 55 exhibit a white segment, 11%), but unlike our samples of *C. shawmayeri* in which the majority of the specimens have a tail with some measure of white at the tip (38 of 50 individuals, 76%); see table 8.

Body mass is less in *C. kirrhos* compared to either *C. ruemmleri* or *C. shawmayeri*. The adult female *C. kirrhos* from the Garatin Ridge weighed 22.5 g. Hobart Van Deusen obtained weights for the three from Mt. Dayman as 0.75, 0.9, and 1.0 ounces, which

converts to 22, 26, and 28 g. Values for mass are available for 16 adults from the eastern slopes of Mt. Wilhelm. All were handled by Van Deusen who recorded weights in ounces, which we converted to grams: mean and standard deviation = 32.9 ± 6.65 g, range = 22.7–45.4 g. A single example of *C. ruemmleri* from the Star Mountains weighed 34 g. The mean, 24.6 ± 2.87 g, and range, 22–28 g, of the four *C. kirrhos* are much less, paralleling its average smaller body size and other variables.

Contrasts between *C. kirrhos* and the other two species of *Coccymys* in cranial and dental variables are quantitative, not qualitative, and involve differences in absolute size and proportions, which are presented as tabular and graphic results from univariate and multivariate analyses derived from the population samples listed in table 3 and the single specimens tabulated in table 6.

In absolute size, *Coccymys kirrhos* averages smaller than *C. ruemmleri* in breadth of incisive foramina and first upper molar, is markedly smaller than that species in nearly all of the other cranial and dental dimensions that were measured, and exceeds any sample of *C. ruemmleri* in breadth of mesopterygoid fossa—quantitative contrasts that are evident in tables 4 and 6 and in figure 29.

Coccymys kirrhos is closer to *C. shawmayeri* in measures of cranial and dental dimensions. Lengths of rostrum and bony palate, and breadth of first upper molar are comparable in the two species, the mesopterygoid fossa and incisive foramina average wider in *C. kirrhos*, and all the other cranial and dental variables either average less or are appreciably smaller in that species compared with *C. shawmayeri* (tables 5, 6).

Proportional morphometric differences between AMNH samples of *C. kirrhos* and the other two species have been summarized by the patterns of covariation in cranial and dental variables reflected in graphs of specimen scores projected onto the first and second canonical variates extracted from discriminant-function analysis (fig. 4) and discussed in a previous section.

These proportional contrasts—and similarities—can also be visualized in ratio diagrams. The first diagram focuses on distinctions between the type series of *C.*

kirrhos from Mt. Dayman and the population sample of *C. ruemmleri* from Lake Habbema, the type locality of that species (fig. 30; see also tables 4 and 6). Compared with the sample of *C. ruemmleri* from Lake Habbema, *C. kirrhos* is significantly narrower across the zygomatic arches relative to skull length or breadth of braincase, has a narrower interorbit relative to any other variable, longer bony palate relative to length of diastema and postpalatal region, wider mesopterygoid fossa relative to any other measured dimension, wider incisive foramina relative not only to their lengths but to many of the other variables, and wider first upper molars relative to length of molar rows (the wider molar is apparent in fig. 8 where molar rows of *C. ruemmleri* and *C. kirrhos* are compared). These are the striking contrasts; other proportional differences and similarities can be gleaned from the ratio diagram.

The second ratio diagram (fig. 31; check also tables 5, 6) contrasts the type series of *C. kirrhos* from Mt. Dayman with the AMNH population sample of *C. shawmayeri* from Mt. Wilhelm, the nearest geographic sample we have that is closest to the collection site of the holotype of *shawmayeri* (see gazetteer). Some of the proportional contrasts graphed here between *C. kirrhos* and *C. shawmayeri* also apply to *C. kirrhos* and *C. ruemmleri* (fig. 31): compared with *C. shawmayeri*, the type series of *C. kirrhos* is narrower across the zygomatic arches relative to skull length or breadth of braincase, has a narrower interorbit relative to any other variable, longer bony palate relative to length of diastema and postpalatal region, wider mesopterygoid fossa relative to any other measured dimension, and wider incisive foramina relative not only to their lengths but to many of the other variables. Other proportional distinctions apply only to *C. kirrhos* and *C. shawmayeri*: *C. kirrhos* has a longer rostrum relative to its breadth or length of skull, and smaller bullae relative to skull length or size of braincase. Finally, where *C. kirrhos* has wider first upper molars relative to length of molar rows compared with *C. ruemmleri*, no proportional difference between *C. kirrhos* and *C. shawmayeri* exists in these dental variables.
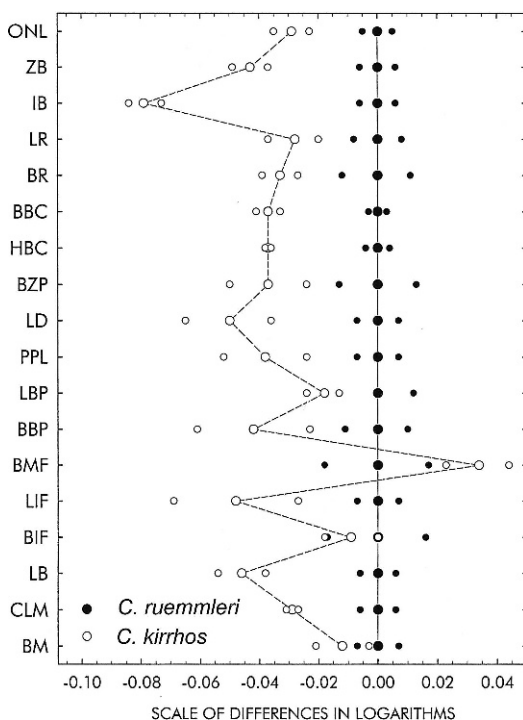

Fig. 30. Ratio diagram illustrating some proportional relationships in cranial and dental dimensions between samples of adult *Coccymys*. The standard is the type series of *C. ruemmleri* from Lake Habbema ($N = 15$; includes the holotype), which is contrasted with the sample of *C. kirrhos* from Mt. Dayman ($N = 3$; includes the holotype). Data are derived from values for mean, standard deviation, and sample size of variables listed in tables 4 and 6. For each measurement, the absolute value of the mean, and plus or minus two standard errors of the mean, were converted to logarithms. Next, the logarithm of the mean of the standard was subtracted from the logarithms of the mean, and plus or minus two standard errors, of the comparative sample. Measurements larger than the standard are thus represented by positive values, those smaller by negative values. The lines connect sample means, and the bracketing symbols represent ± 2 SE of the mean. A sample having the same proportions as the standard will be represented by mean values on a line parallel to that of the standard regardless of absolute size. Also, if values for the sample being compared with the standard are similar in absolute size, they will be close together on the diagram. If proportions between any of the measured dimensions are similar, the positions of their points relative to each other on the horizontal scale will be similar.
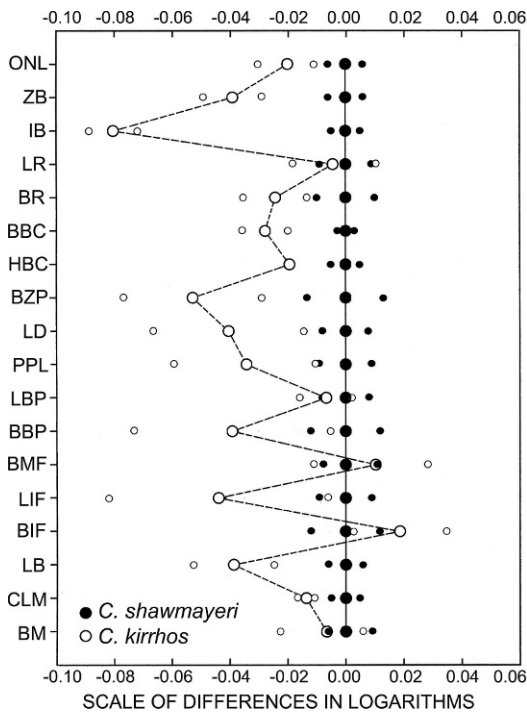
Fig. 31. Ratio diagram illustrating some proportional relationships in cranial and dental dimensions between samples of adult *Coccymys*. The standard is the type series of *C. shawmayeri* from Mt. Wilhelm (*N* = 25), which is contrasted with the sample of *C. kirrhos* from Mt. Dayman (*N* = 3; includes the holotype). Data are derived from values for mean, standard deviation, and sample size of variables listed in tables 5 and 6. See legend to figure 30.

IDENTIFICATION OF BBM SPECIMENS: We know of only seven specimens of *Coccymys* preserved in museums of the world that have tawny dorsal pelage and whitish gray underparts. Three are in the American Museum of Natural History and comprise the type series of *C. kirrhos* from the Maneau Range; four are stored in the Bishop Museum. Two of those four were collected in the Maneau Range (Dumae Creek and Mt. Simpson), the eastern ramparts of the Owen Stanley Ranges, but the other two come from the western segment of the Owen Stanley Ranges, one from Smith's Gap and the other from Bulldog Road in the Wau area. *Coccymys shawmayeri* has also been collected at Bulldog Road, and on Mt. St. Mary, which is just east of Smith's Gap. Are these two tawny

individuals *C. kirrhos* or simply examples of *C. shawmayeri* with orange-brown upperparts? If they are *C. kirrhos*, they not only document the westernmost collection localities of that species but also rather extensive sympatry between it and *C. shawmayeri*; if they are tawny *C. shawmayeri*, they demonstrate one of two chromatic expressions of the dorsal fur within that species, a dimorphism not seen in the other two species of *Coccymys*.

To answer the question, we subjected cranial and dental variables to a series of principal components analyses in which the seven tawny individuals were compared with samples of *C. shawmayeri* in different combinations. We first compared the type series of *C. kirrhos* and the four tawny BBM specimens with our samples of *C. shawmayeri*, all possessing brown dorsal pelage, from the Telefomin area, Mt. Hagen, Mt. Wilhelm (including the holotype), Bulldog Road in the Wau area, and Mt. St. Mary. The pattern of covariation in cranial and dental variables among these specimens is summarized in the scatter plot of specimen scores projected onto the first and second principal components in figure 32. The spread of scores along the first axis conforms to a group of seven specimens on the left, all with tawny dorsal fur, and a larger cluster on the right representing specimens of *C. shawmayeri*, and containing the holotype, all showing brown upperparts. Difference in size is the primary factor expressed on the first principal component with most of the variables influencing the spread of points (table 17). The tawny individuals are smaller than most of those in samples of *C. shawmayeri*, a contrast also reflected in summaries of univariate statistics (tables 5, 6) and the ratio diagram (fig. 31). The specimen from Dumae Creek, which is near Mt. Dayman, and the animal from Mt. Simpson, cluster with the type series of *C. kirrhos*, which is expected—all are from the Maneau Range. The score for the tawny specimen from Bulldog Road sits nearly on top of that representing the holotype of *C. kirrhos* and far from the two points for the brown-furred individuals also collected at Bulldog Road, which nest deep within the *C. shawmayeri* cluster (six brown-furred speci-

TABLE 17
Results of Principal Components Analysis of Geographic Samples of Two Species of *Coccymys*
Samples of *Coccymys shawmayeri* from the Telefomin area, Mt. Hagen region, Bismarck Range, Bulldog Road in the Wau area, and Mt. St. Mary are compared with samples of *Coccymys kirrhos* from the Maneau Range, Smith's Gap, and Bulldog Road in the Wau area. (Principal components are extracted from a covariance matrix of 18 log-transformed cranial and dental variables; see tables 5–7, fig. 32.)

Variable	PC1	PC2
ONL	0.027	−0.008
ZB	0.034	−0.001
IB	0.043	0.001
LR	0.010	0.002
BR	0.038	0.003
BBC	0.011	0.002
HBC	0.007	0.000
BZP	0.062	−0.041
LD	0.047	0.001
PPL	0.045	−0.004
LBP	0.010	0.005
BBPM1	0.069	0.024
BMF	0.001	0.076
LIF	0.047	0.010
BIF	0.009	0.027
LB	0.037	0.001
CLM1–3	0.015	0.008
BM1	0.001	−0.003
Eigenvalue	0.022	0.009
% Variance	38.135	15.506

mens come from Bulldog Road but only two are adults that could be used for the analysis). Of the seven tawny scores, that for the specimen from Smith's Gap is closest to the larger constellation of points, but still far from any of the of the seven scores representing the sample from Mt. St. Mary, which is geographically close to Smith's Gap. Tawny upperparts as a distinguishing trait for *C. kirrhos* seems to be supported in this analysis.

A second principal components analysis compared the seven individuals possessing tawny dorsal coats with a set of *C. shawmayeri* composed of the seven specimens from Mt. St. Mary, the two from Bulldog Road, and the holotype. Would the tawny individuals from Bulldog Road and Smith's Gap still associate with *C. kirrhos* when the effect of larger samples of *C. shawmayeri* was

removed? The pattern of specimen scores projected on the first and second principal components exhibits two discrete clusters, one consisting of all seven tawny animals, the other composed of *C. shawmayeri* (fig. 33A). Size again is the primary dividing factor, with nearly all variables spreading the scores into two clusters along the first principal component (table 18). The score for the tawny rat from Bulldog Road continues to be isolated from the two brown-furred individuals from Bulldog Road, and the point representing the rat from Smith's Gap associates more closely with *C. kirrhos* than with the sample from Mt. St. Mary.

The third analysis employed the same examples of *C. shawmayeri* but restricted the tawny-furred sample to the specimens from Bulldog Road and Smith's Gap to determine if they would separate from *C. shawmayeri* by themselves; here any effect of the five *C. kirrhos* from the Maneau Range would be eliminated. The projection of specimen scores on first and second principal components resulted, for the third time, in a large cluster containing the scores for the holotype of *shawmayeri*, the sample from Mt. St. Mary, and the two brown-furred individuals from Bulldog Road; this cluster is isolated from the two specimens with tawny upperparts (fig. 33B). The tawny animal from Bulldog Road does not clump with the other two from there, and the specimen from Smith's Gap does not nest with the sample from Mt. St. Mary. Separation of the two groups along the first axis again reflects the larger cranial and dental dimensions of *C. shawmayeri* compared with the smaller size of the two tawny individuals, and nearly all variables contribute to this dispersion of scores along the first axis (table 18).

These multivariate analyses—combined with tawny dorsal coats, whitish gray underparts, long tails relative to head and body, and tails without white tips—identify the specimen from Bulldog Road and the one from Smith's Gap as examples of *C. kirrhos*, and not *C. shawmayeri*. They document not only the westernmost records for *C. kirrhos* but also regional sympatry between that species and *C. shawmayeri*.

GEOGRAPHIC VARIATION: Our sample of *C. kirrhos* is inadequate to truly assess
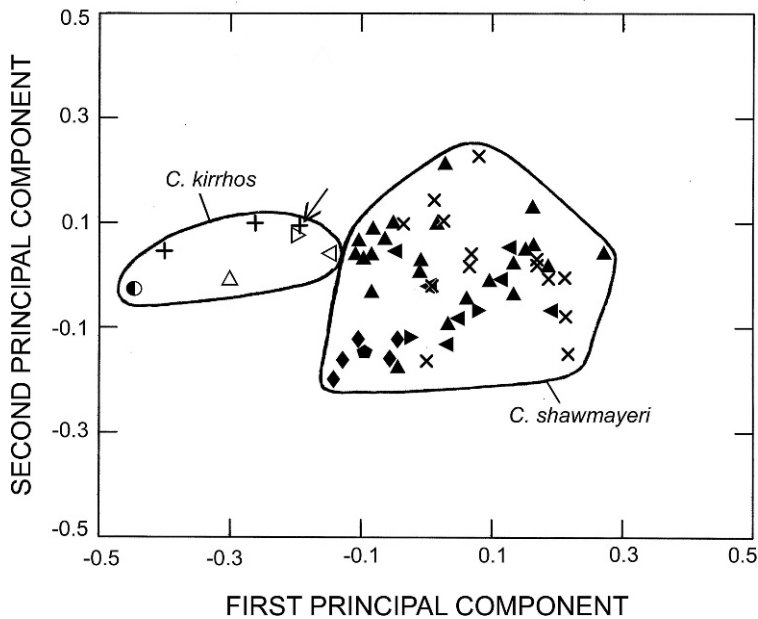
Fig. 32. Specimen scores projected on the first and second components extracted from principal components analyses. *Coccymys shawmayeri* (N = 53) from the Telefomin area (filled diamond), Mt. Hagen (reclining cross), Mt. Wilhelm (filled triangle), Bulldog Road in the Wau region (filled right-pointing triangle), and Mt. St. Mary (filled left-pointing triangle) is compared with *C. kirrhos* (N =7) from Mt. Dayman (cross) and Dumae Creek in the Maneau Range (hollow triangle), Mt. Simpson (half-filled circle), Smith's Gap (left-pointing hollow triangle), and Bulldog Road in the Wau area (right-pointing hollow triange). A filled pentagon identifies the holotype of *shawmayeri*, and an arrow points to score for holotype of *kirrhos*. See table 17 for correlations and percent variance.

geographic variation in phenetic traits. All specimens have tawny upperparts, whitish gray underparts, and a relatively long tail without patterning at the tip. The individual from Bulldog Road and the specimen from Smith's Gap have slightly thicker dorsal coats, more similar to the lengths in *C. shawmayeri*. Values for many cranial dimensions for those two specimens are also somewhat greater than recorded for the sample from the Maneau Range, and, of the two, the animal from Bulldog Road slightly exceeds the specimen from Smith's Gap in 11 of the 18 cranial and dental dimensions measured (table 6). However, in multivariate space as revealed by principal components analysis, where both skull size and shape are expressed, the specimen from Bulldog Road is closely associated with the holotype of *C. kirrhos* in most of the analyses, and among all the specimens of *C. kirrhos*, the animal from Smith's Gap, while

still part of the *C. kirrhos* cluster, is the closest to samples of *C. shawmayeri* (figs. 32, 33A, B). Larger samples of species from more localities than those currently available are required to determine geographic variation in phenetic characters and its significance.

HABITAT: During the middle of May 1953, members of the Fourth Archbold Expedition to New Guinea were ascending the northern flanks of Mt. Dayman to establish their top camp at 2230 m. From their number 2 camp at 1550 m, Brass (1956: 110–111) describes traveling along ridges through what he called mid-mountain forests (tropical lower montane rainforest in Whitmore's, 1984, terminology) of chestnut (*Castanopsis*), oaks (*Lithocarpus*), walnut (*Engelhardtia*), and species of *Gordonia, Sloanea*, and other genera. At 1800 m,

> the mid-mountain forest gave place to beech (*Nothofagus*) forest, the new dominants being easily recognizable by their large size, massive
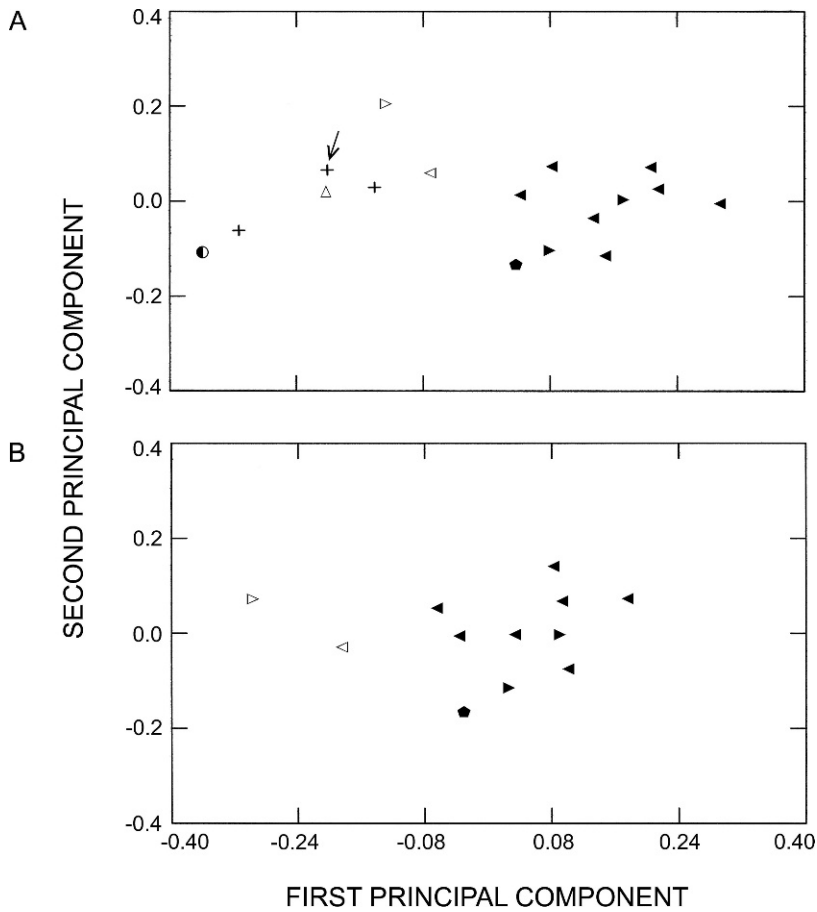
Fig. 33. Specimen scores representing two species of *Coccymys* projected on first and second components extracted from principal components analyses. Graph **A**: *C. shawmayeri* (*N* = 9) from Mt. St. Mary (left-pointing filled triangle) and Bulldog Road (right-pointing filled triangle) compared with *C. kirrhos* (*N* = 7) from Mt. Dayman (cross) and Dumae Creek in the Maneau Range (hollow triangle), Mt. Simpson (half-filled circle), Smith's Gap (left-pointing hollow triangle), and Bulldog Road (right-pointing hollow triangle). A filled pentagon identifies the holotype of *shawmayeri*, and an arrow points to score for holotype of *kirrhos*. Graph **B**: *C. shawmayeri* from Mt. St. Mary (left-pointing filled triangle) and Bulldog Road (right-pointing filled triangle) compared with *C. kirrhos* from Smith's Gap (left-pointing hollow triangle), and Bulldog Road (right-pointing hollow triangle). A filled pentagon identifies the holotype of *shawmayeri*. See table 18 for correlations and percent variance.

branches, dense foliage of small leaves, and rough dark bark. Thereafter, for two hours, the trail led through tall beech forest, usually very open underneath and with little leaf litter or moss. … At 2050 meters the first "hoop-pines" (*Araucaria*) far overtopped all other trees on the crest of the spur. … At 2060 meters we rested in especially fine tall beech forest on the first sizable bit of fairly level ground seen on the mountain [see plate 14, fig. 2 in Brass, 1956, for photograph of this spot; also fig. 34 here]. … At 2150 meters the edge of the forest was reached

after a stiff climb that took us out of the beech zone and into what I … have called mossy forest, and, coming out abruptly into intense sunshine on bracken-covered slopes, we surveyed a depressing spectacle of fire damage and destruction. The crest and upper slopes of the spur had been almost completely deforested. Gray stands of hundreds of very tall, straight *Araucaria* trees, killed by fire, edged the surviving forest in ravines on either side. … From the 2310-meter high point on the trail, where the view took in several square miles of

TABLE 18
Results of Principal Components Analysis of Geographic Samples of Two Species of *Coccymys*
Graph A: samples of *Coccymys shawmayeri* from Bulldog Road in the Wau area and Mt. St. Mary are compared to samples of *Coccymys kirrhos* from the Maneau Range, Smith's Gap, and Bulldog Road; holotypes of *shawmayeri* and *kirrhos* are included. Graph B: samples of *Coccymys shawmayeri* from Bulldog Road, Mt. St. Mary, and the holotype of *shawmayeri* is contrasted with the two *Coccymys kirrhos* from Smith's Gap and Bulldog Road. (Principal components are extracted from a covariance matrix of 18 log-transformed cranial and dental variables; see tables 5–7, fig. 33.)

Variable	Graph A		Graph B	
	PC1	PC2	PC1	PC2
ONL	0.038	0.012	0.007	0.015
ZB	0.051	0.005	0.024	0.011
IB	0.075	−0.015	0.036	−0.000
LR	0.002	0.009	−0.014	−0.004
BR	0.039	0.017	0.007	0.012
BBC	0.024	−0.005	0.012	0.001
HBC	0.019	0.028	−0.013	0.025
BZP	0.100	−0.017	0.079	−0.016
LD	0.039	0.022	0.003	0.026
PPL	0.056	0.013	0.033	0.024i
LBP	0.009	−0.018	0.020	−0.011
BBPM1	0.074	−0.011	0.075	0.030
BMF	−0.023	0.051	−0.023	0.045
LIF	0.042	0.024	0.002	0.020
BIF	0.007	0.036	−0.026	0.030
LB	0.058	0.003	0.024	0.016
CLM1–3	0.021	0.009	0.013	0.020
BM	0.006	−0.002	0.009	0.007
Eigenvalue	0.038	0.008	0.018	0.008
% Variance	57.455	11.299	40.901	18.136

terrain above the 2200-meter level, including Maneau Peak and the head of the Gwariu River Valley, … the upper parts of the whole mountain had been greatly altered by the burning of forests which must formerly have occupied all but a small fraction of the total area. Extensive forests remained, but for the most part on the more sheltered slopes and in strips in deep ravines. Grasslands of old-established appearance occupied much of the denuded ground, while bracken … and other ferns, or a mixture of fern and grass, provided the cover on slopes which at least in some instances plainly had not been so long deforested [fig. 35].

The top camp was finally established at 2230 m on a flat in a deep, sheltered, grassy hollow on the western bank of the Ataíro within a quarter of a mile of the head of that stream, and 1.5 to 2 miles (2.4−3.2 km) northwest of the summit of Maneau Peak. The flat was bounded on one side by a slope covered with grass and bracken, and on the other side by the Ataíro stream edged with mossy forest, which also covered the adjacent slope (figs. 36, 37). "Mossy forest" is the way Brass (1956: 128) described the forest formations everywhere on Mt. Dayman above the beech zone (1800–2150 m), providing a superb description of the "mossy forest" and its floristic component, both on exposed ridges and slopes of ravines, and also noted the tall lowland tropical emergents found in sheltered ravines up to the altitude of the camp.

Thirty-three days were spent at the top camp, and few "were without mist, which drifted up from lower levels very often by mid-morning and tended to clear off before nightfall" (Brass, 1956: 126). Mean maximum ambient temperature recorded for 29 days (May 22 to June 19) was 21.3°C (extremes, 18.5–24.5°C); mean minimum for 30 days (May 21 to June 19) was 5.1°C (extremes, 0–11°C).

Fig. 34. "Mossy beech (*Nothofagus*) forest" at 2060 m on the northern slopes of Mt. Dayman. May 1953. This forest zone is commonly referred to as mid-montane (for example, in Johns, 1982). Although examples of *Coccymys kirrhos* were not captured in this habitat on the northern slopes of Mt. Dayman, similar forest to the southwest on the Garatin Ridge yielded a specimen (Cole et al., 1997; Engilis and Cole, 1997).

The mosaic of grassland and mossy forest is reflected by the habitat surrounding the top camp, nestled as it was between those two botanical formations, and in notes associated with the three specimens from 2230 m. The holotype of *C. kirrhos* was trapped in "Herbaceous forest margin. Fallen trees and *Gunnera*"; of the other two, AMNH 158174 was taken along the "Forest edge," and AMNH 158173 was caught in "grassland" (notations on the skin tags and in Van Deusen's field catalog). In his summary of

Fig. 35.   Western summits of Mt. Dayman viewed from 2230 m over the Gwariu Gorge near the "Top Camp." This is the view Brass and his crew saw after emerging from primeval beech forest on the way to the "Top Camp": "From the 2310-meter high point on the trail, where the view took in several square miles of terrain above the 2200-meter level, including the head of the Gwariu River Valley, it could be seen that the upper parts of the whole mountain had been greatly altered by the burning of forests which must formerly have occupied all but a small fraction of the total area" (Brass, 1956: 111). May 17–June 19, 1953.

mammals obtained by Van Deusen, Brass (1956: 129) singled out the "beautiful little *Pogonomelomys* [= *C. kirrhos*] … that was found in the "shrubby forest fringe." Van Deusen did not record whether the three were taken near camp or farther afield. Because much of the grass- and bracken-dominated slopes are anthropogenic in origin, and, as noted by Brass (1956: 111), forest must have occurred over most of the total area on Mt. Dayman, even up to altitudes just below the summit, we can reasonably assume that *C. kirrhos* is primarily a forest inhabitant, an observation supported by data associated with the specimen from the Garatin Ridge, on the southeast ramparts of Mt. Dayman in the Agaun area.

The specimen from the Garatin Ridge (reported as *C. ruemmleri*) was encountered in primary forest, and caught "in a live trap set on the forest floor" (Cole et al., 1997: 12). "The forest on Garatin Ridge between 1,400 and 1,600 m," reported Engilis and Cole (1997: 3–4),

is transitional in nature, being composed of dominant plants and physiognomic components of both mid-montane and lower montane forest as described by Johns (1982). Some of the dominant (i.e., tallest) canopy trees documented were *Prumnopitys* (Podocarpaceae), *Lithocarpus* and *Nothofagus* (Fagaceae), *Metrosideros* (Myrtaceae), and *Garcina* (Clusiaceae). Emergent *Araucaria* (Araucariaceae), observable at long distances formed small scattered groves along the ridges. … The forest in this area [which includes the nearby base camp at Dumae Creek, 1525 m] was composed of four distinct canopy layers. … The height of the primary layer averaged 46 m. Canopy emergents uncommonly exceeded 50 m. The subcanopy was composed of two distinct layers; the upper averaged 18 m, the lower 7.4 m. The ground layer varied according to exposure but averaged 1.1 m. The surface of the canopy, as viewed from the air, revealed an uneven but continuous cover.

Fig. 36.   "Top Camp" at 2230 m on Mt. Dayman, in a deep and sheltered grassy hollow on the western bank of the Atairo near its head. Slope in lower right is covered with grass and ferns, mossy (lower montane) tall forest (see fig. 27) edges the stream, and a shrubby ecotone separates grass from forest. The three specimens of *C. kirrhos* were trapped in the "herbaceous forest margin," along the "forest edge," and in "grassland," respectively; whether near camp or elsewhere was not recorded, nevertheless the habitat around camp provides a visual appreciation of the kinds of places they were collected. May 17–June 19, 1953.

Engilis and Cole summarized these forest characteristics in a diagram of the "Typical primary rainforest phsiogonomy at Dumae Creek, 1,525 m elevation." It rained every day for the duration of the stay at the Dumae Creek camp, from February 25 to March 20. Total rainfall during this period was 333 mm with maximum rainfall (in a period of 24 hours) of 42 mm. Average high and low ambient temperatures were 21°C (extremes, 19–25°C) and 15.7° (extremes, 13–19°C).

The specimen from the north slopes of Mt. Simpson, 0.5 km S of Bunisi Village at 1490 m ("Camp 5"), was collected in a pitfall by Fred Kraus on February 25, 2003. Fred (in litt., 2008) wrote us this about his recollections of the site:

> I would call the locality primary rainforest, but it was slightly disturbed in the sense that there were a couple of footpaths running through the area and there were some gardens in the nearby vicinity. It was a short walk from this forest to more clearly secondary habitats, and it was only 0.5 km from the nearest village, but the immediate forest where the *Coccymys* came from was pretty nice itself. The forest would fit the category of lower montane forest of Paijmans. Because all the rodents I pickled from that site were collected in bucket traps set along drift fences, I can't provide you with any more specific habitat notes that would shed light on the critter's habits, other than to note that they were active at night.

BIOLOGY: *Coccymys kirrhos* certainly spends time on the ground, as the trapping records attest, and we suspect it, like *C. ruemmleri,* is also scansorial, able to scamper along limbs and woody vines in the forest understory. The rat is most likely active during the night (as Fred Kraus indicated above). Because of its close resemblance to *C. shawmayeri* in proportions of hind feet and

Fig. 37. "Tall mossy forest at camp, with bamboo undergrowth," was Brass's label for this photograph taken at the top camp, 2230 m, on the northern slopes of Mt. Dayman. This "mossy forest" is comparable to Whitmore's (1984) "tropical lower montane rainforest" and Johns's (1980) "mid montane" designation. May 17–June 19, 1953.

tail relative to body size; in cranial and mandibular conformations; in shape of incisors, their size relative to the skull and mandible, and extent of enamel; and in occlusal patterns of upper and lower molars, we infer that the diet of *C. kirrhos* is probably also similar, consisting of fruit, seeds, and insects. Stomach contents from the specimen caught on Mt. Simpson contained a suspen-sion of macerated fruit pulp and seed coats (table 16). All other aspects of its biology are unknown.

One population aspect of *C. kirrhos* requires investigation. The species may be either uncommon or difficult to trap if our sample is an indication of its relative abundance in nature. *Coccymys shawmayeri*, by contrast, seems to be common in certain

TABLE 19
Specimens of *Coccymys kirrhos* and *Coccymys shawmayeri* in the Bernice P. Bishop Museum from Bulldog Road in the Wau Area, Morobe District, Papua New Guinea[a]

C. kirrhos (tawny upperparts, no white tail tip)
  F, ad; 55824; 11–2–1967; "12 mi from Edie Creek," "2500 ± m"; P.H. Coleman

C. shawmayeri (brown upperparts, all with white-tipped tails)
  F, juv; 96646; 6–18–1968; "12 mi from Edie Creek," "2400 ± m"; A.B. Mirza
  F, juv-ya; 96802; 6–18–1968; "12 mi from Edie Creek," "2400 ± m"; A.B. Mirza
  F, ad; 61669; 9–10–1968; "12 mi from Edie Creek," "2400 ± m"; A.B. Mirza
  M, ad; 101267[b]; 7–17–1972; "12 ± mi S Edie Creek," "2500 ± m"; A.B. Mirza
  F, ad; 101502; 8–4–1972; "12 ± mi S Edie Creek," "2500 ± m"; A.B. Mirza
  M, juv; 29140; 5–19–1967; "32 road km [20 mi] S Wau," "2400 ± m"; J.L. Gressitt

[a]Sex, age, catalog number (BBM-NG), date of collection, location on Bulldog Road, altitude, and collector are provided for each specimen. Except for relative age, which we determined, all information was transcribed from labels attached to the specimens.
[b]BBM-NG 101267 is a skeleton only without notes on tail pattern.

habitats, judged by the large samples from particular mountains—Mt. Hagen and Mt. Wilhelm, for example (see gazetteer). One comparison is illustrative. Hobart Van Deusen obtained only three *C. kirrhos* during the month the Archbold Expedition worked at the "Top Camp" on Mt. Dayman in the Maneau Range, and members of the expedition (documented by Cole et al. 1997) camped for nearly a month at Dumae Creek in the Maneau Range, procuring only a single *C. kirrhos*. During a roughly similar period of time on Mt. Wilhelm, 29 specimens of *C. shawmayeri* were caught between the high Lake Aunde camp and the lower Pengagl Creek camp where the Archbold Expedition worked. The interplay of other factors—environmental, trapping techniques, and the frequency with which local people contributed to the inventories—may, of course, be responsible for the discrepancy in sample sizes, and to announce that *C. kirrhos* is uncommon in nature relative to *C. shawmayeri* (and *C. ruemmleri*, which is documented by large samples from the Snow and Star mountains; see gazetteer) is admittedly simplistic, but identifies an aspect of its population biology that should be studied.

SYMPATRIC ASSOCIATIONS: Here we discuss first the sympatry between *C. kirrhos* and *C. shawmayeri*, then the sympatric association of *C. kirrhos* with other species of mammals collected in the Maneau Range, primarily those obtained along the Mt. Day-

man transect worked by members of the Fourth Archbold Expedition.

Sympatry between the two species of *Coccymys*. Seven specimens are available from Bulldog Road, south of Edie Creek, or nearby Wau (table 19). The example of *C. kirrhos* was collected in 1967 "12 mi from Edie Creek," as was a specimen of *C. shawmayeri* obtained from 20 mi south of Wau. Other *C. shawmayeri* were taken in 1968 and 1972 from either "12 mi from Edie Creek," or "12 mi S Edie Creek," approximately the same area. Examples of the two species were collected at about the same place but at different times. Bulldog Road south of Edie Creek and Wau deserves additional surveys to determine the microhabitat and other relationships between the two species of *Coccymys* there.

The specimen of *C. kirrhos* from Smith's Gap (2500 m) provides the other record of regional sympatry. Smith's Gap is not far from the southwestern slopes of Mt. St. Mary ("SSW Mt. St. Mary," 3000 m), the source of seven *C. shawmayeri*. All were collected by A.B. Mirza who trapped the specimen from Smith's Gap in August 1968, and the series from Mt. St. Mary during July of the same year. Additional mammalian surveys in this region would certainly be welcome and might provide answers to questions unanswerable with present data. For example, are the two species separated altitudinally in this area or do they occur at the same place? Are there
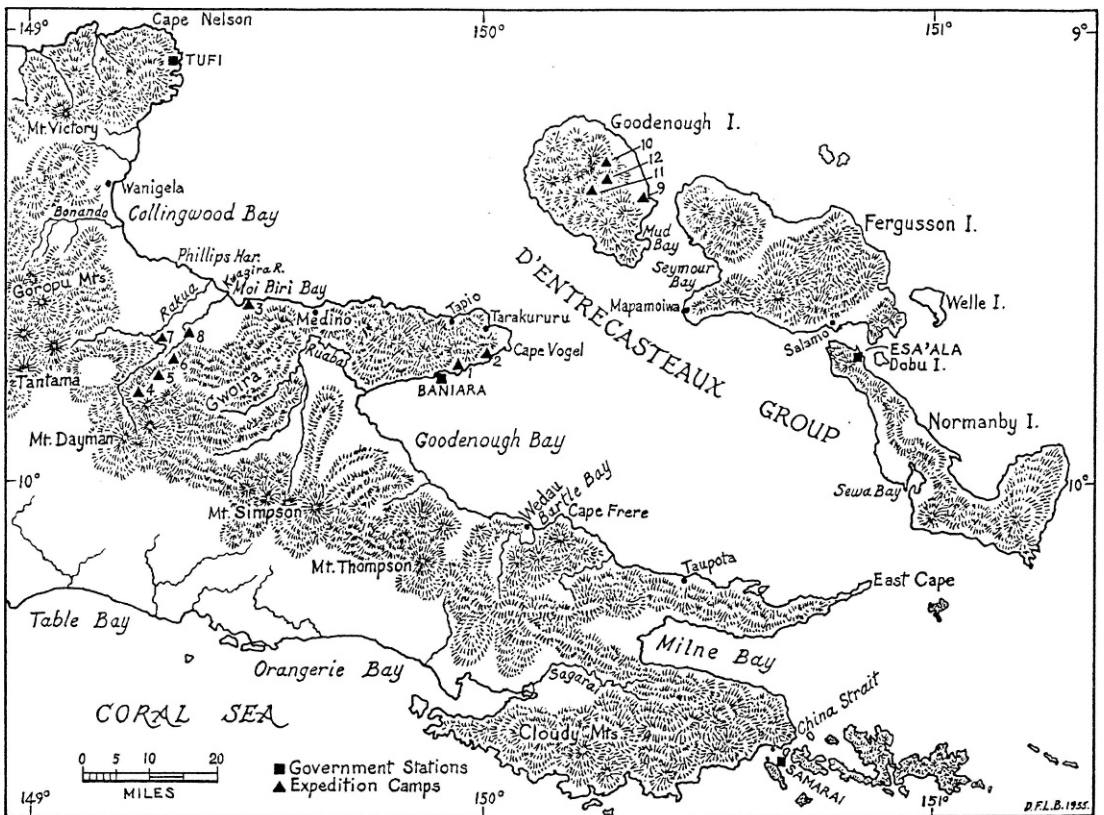
Fig. 38. Reproduction of map covering region of Mt. Dayman worked by the Fourth Archbold Expedition to New Guinea, 1953 (originally published in Brass, 1956). The holotype of *Coccymys kirrhos* was captured at locality 4, the "Top Camp," at 2230 m. This was the highest of six camps established along a transect anchored at Baiawa, Moi Biri Bay, and extending through the adjacent coastal plain on to the northern slopes of Mt. Dayman. The Cape Vogel Peninsula and Goodenough Island in the D'Entrecasteaux Archipelago were also surveyed during the same expedition, but our focus is on collections of mammals made along the transect from the coastal lowlands (beginning with camp 3) to near the summit of Mt. Dayman. The numbered camps below correspond to the numbered symbols on the map; the physical settings of the camps along with their floristic environments are reported by Brass (1956): **3,** Baiawa, 30 m: May 6–11, September 7–9; **4,** top camp, north slopes of Mt. Dayman, 2230 m, collections were made up to 2700 m, May 17 to June 19; **5,** number 2 camp, north slopes of Mt. Dayman, 1550 m, June 20 to July 12; **6,** number 3 camp "Bottom Camp," north slopes of Mt. Dayman, 700 m, July 13–26; **7,** Biniguni camp, Gwariu River, 200 m, July 27 to August 13; **8,** Peria Creek, Kwagira River, 50 m, August 14 to September 6.

any broad habitat or microhabitat distinctions between the two?

The highlands between Mt St. Mary and Mt. Victoria, an area that also embraces the Wharton Range, are one region where surveys of small mammals, particularly rodents, are sorely needed. If Mt. St. Mary is the easternmost occurrence of *C. shawmayeri*, the eastern *C. kirrhos* should be found in suitable habitats throughout the mountains.

On the other hand, *C. shawmayeri* may be the *Coccymys* living in upper montane forest and alpine grassland between Mt. St. Mary and Mt. Victoria, and *C. kirrhos* may occur syntopically with *C. shawmayeri* or be confined to lower montane forest formations at lower altitudes. Visits by biologists to the Wharton Range and surrounding highlands have largely consisted of bird collecting (for example, Archbold and Rand, 1935) and

incidental notes on a few mammals connected with a nonforest vegetation survey (Hope, 1975).

Sympatry along the Mt. Dayman transect. The three examples of *C. kirrhos* from Mt. Dayman were collected on the Fourth Archbold Expedition in 1953 (Brass, 1956). Between May and September 1953, six camps were established along a transect from the coast at Baiawa, Moi Biri Bay, to the "Top Camp," at 2230 m on the northern slopes of Mt. Dayman. Their locations and elevations are indicated in figure 38, which is a reproduction of the original map of the area published in the expedition summary (Brass, 1956).

Collection activities through this transect resulted in 1043 specimens of mammals representing 59 indigenous species of echidna, bats, marsupials, and rodents. The number of specimens of each species collected at different altitudes is summarized in figure 39. We identified all the material and employed current taxonomic designations (see Helgen, 2007c and references cited there) with a few exceptions. We do not, for example, recognize Van Dyck's (2002) genus *Murexechinus* and employ the usage of *Murexia*, following Krajewski et al. (2007). We also realize that future revisionary studies will modify some of the current names, reflecting new systematic revisionary work. Helgen (2007c), for example, notes that what is now identified as *Uromys anak* from the Owen Stanley Ranges is likely a separate species; he also suggests that some of the species currently recognized—the marsupials, *Phalanger gymnotis*, *Spilocuscus maculates*, *Petaurus breviceps*, and the bat, *Nyctimene albiventer*—may actually be species complexes. We also excluded nonnative species from the chart (one *Rattus exulans* was caught at 30 m and 24 were taken at 2230 m at the "Top Camp"), including dogs and pigs.

We are aware that members of the Archbold Expedition did not obtain samples of all the mammals living in the area. In 1952, Laurie reported on a collection of mammals made by F. Shaw Mayer in Papua New Guinea, where he worked between 1932 and 1949, and included the Maneau Range (Mt. Orian, Mt. Maneau, Mt. Mura, and Mt. Simpson) in his travels. While Shaw Mayer collected examples of some of the same species encountered by the 1953 Archbold Expedition to Mt. Dayman, he also obtained others not found by the Archbold survey, notably the marsupials *Pseudochirulus canescens*, *Microperoryctes papuensis*, *Satanellus albopunctatus*, and *Murexia rothschildi*. The Bishop Museum Expedition to Mt. Dayman, undertaken in 1985, obtained samples of the marsupials *Murexia rothschildi*, *Microperoryctes ornata* and *M. papuensis*, and *Dorcopsis macleayi*; the bats *Paranyctimene raptor* and *Rousettus amplexicaudatus*; and the rodents *Mallomys aroaensis*, *Paramelomys platyops*, *Parahydromys asper*, and *Pogonomys loriae*—none of these were collected along the Archbold Expedition's transect. Recently, two other species have been added to the fauna of the Maneau Range: the moss mouse *Pseudohydromys germani* (Helgen, 2005a), and another new species of *Pseudohydromys* (Helgen, 2007a) that is being described. Finally, Helgen (in litt., 2008) wrote us that other surveys in the general area have taken the tree kangaroo, *Dendrolagus goodfellowi*.

Compared with the total number of mammalian species recorded from the Maneau Range, the faunal representation of species documented by the Archbold survey is incomplete. However, the 59 species sampled by the Archbold Expedition do provide an altitudinal snapshot of the mammal fauna, of which *Coccymys kirrhos* is a member, along the northern slopes of Mt. Dayman and adjacent coastal lowlands in particular and in the Maneau Range generally. Seven species of marsupials, three species of bats, and seven species of rodents are recorded from 2230 m, the altitude where all three AMNH examples of *C. kirrhos* were taken.

Coccymys kirrhos is one more addition to the seven montane and three lowland species of marsupials, bats, and rodents that occur only on the southeastern peninsula of Papua New Guinea (Helgen, 2005, 2007a; Musser et al., 2008). These species signal that region, especially the montane areas, to be a realm of mammalian endemism, possibly a reflection of the past geological history of New Guinea when the southeastern peninsula was an island separated from the emergent western portion of New Guinea until the Pliocene

(Aplin et al., 1993; Flannery, 1995). There are likely other mammals currently regarded as subspecies peculiar to the southeastern peninsula that will be recognized as distinct species after taxonomic revision (see Helgen, 2007a) and these, possibly along with new discoveries, will help define the montane habitats in the Owen Stanley Ranges in particular and that mountainous backbone and bordering coastal lowlands in general as a special faunal unit.

The account of *Coccymys kirrhos* completes our review of species diversity in *Coccymys*. The next section will compare that genus with a unique murine that is endemic to the Snow Mountains of western New Guinea and is still represented by few specimens.

RECHARACTERIZATION OF *"MELOMYS" ALBIDENS*

Melomys albidens was characterized by Tate (1951: 286) as a *"Melomys* differing sharply from all species except *M. fellowsi* by possession of white incisor teeth. From *M. fellowsi* it is distinguished by its much smaller size, and proportionately broader zygomata, larger bullae, shorter tooth row, and much narrower molars." He went on to describe the species this way:

> Pelage long and soft, above and below, the dorsal color near Wood Brown (Ridgway), with the hair bases fuscous; ventrally much paler brown, the bases of the hairs also fuscous. Ears large. Hands and feet whitish. Width of foot at base of fifth metatarsal, 4.4 mm. Tail lacking the *Melomys-Uromys* characters (which, however, are developed in the simple dentition), and instead showing the overlapping scale rings of *Rattus* and scale hairs, three per scale, about three scale lengths. Skull with full braincase and well-expanded zygomatic arches, in combination with a narrow, somewhat elongate muzzle. Interparietal wide (10 mm.). Nasals surpassed backwardly by the nasal processes of the premaxillae. Anterior part of frontals depressed. Lacrimals large, prominent. Zygomatic plate very narrow, its anterior edge vertical to the notch, which is extremely shallow. Bullae large, considerably larger than in the otherwise larger *Melomys fellowsi*. Palate extending back to middle of M3, and provided with a blunt, post-palatal spine. Pterygoid fossa rather wide
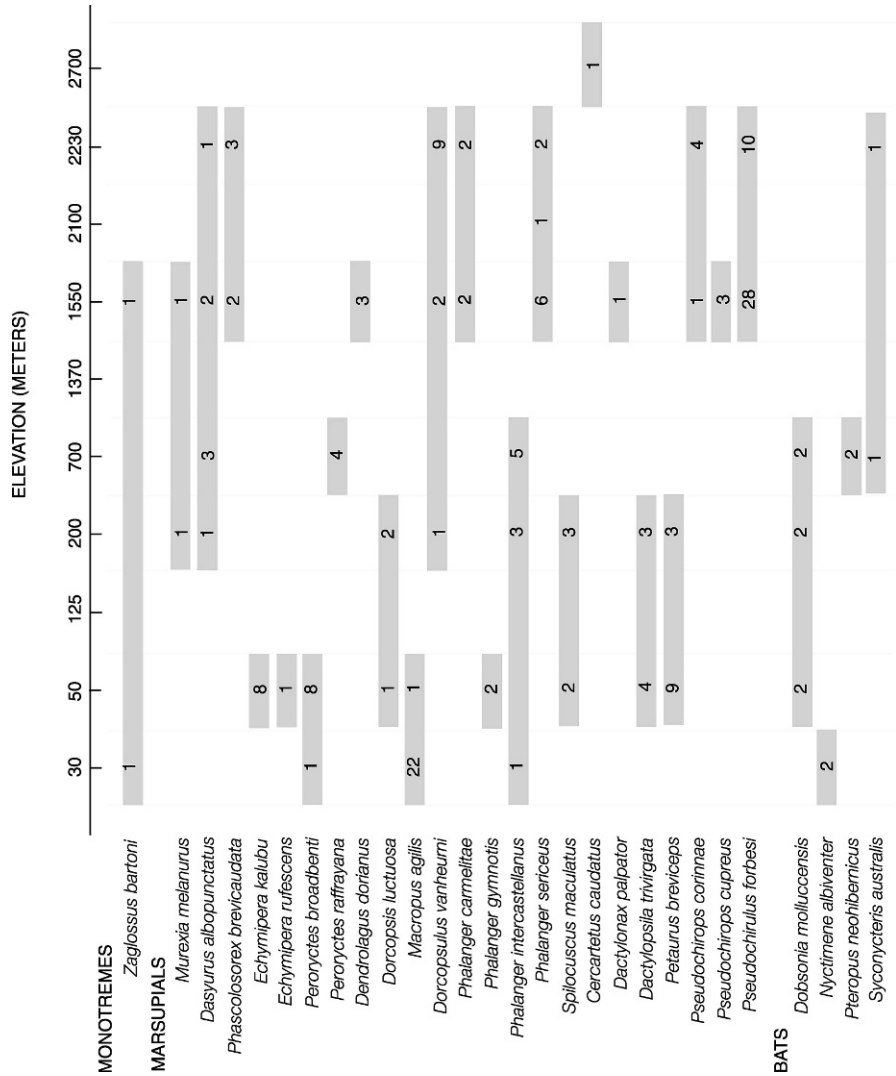
(2.8 mm). Incisive foramina, which stand well in advance of the molars, only slightly shorter than the molar rows; the tooth rows in turn shorter than the bullae.

The species *albidens* was retained in *Melomys* for several decades after Tate (1951) described it (Laurie and Hill, 1954, for example). Eventually Musser and Carleton (1993) treated *albidens* as a species of *Coccymys* simply to disassociate it from either *Melomys* or *Pogonomelomys* where it did not belong, and because so many of its anatomical traits are unlike species within those clusters, and some features more closely resemble those characterizing *C. ruemmleri*. This association had been noticed independently by other researchers. Flannery (1990: 240), for example, wrote how "Recent examination of the skull by the author suggests that it is more closely related to '*Pogonomelomys*' *ruemmleri* than to any other New Guinean murid." Menzies (1990: 127), in his revision of *Pogonomelomys*, which among other results provided a dendrogram estimating percent affinities among the taxa studied, noted that "*Pogonomelomys ruemmleri* comes out with a close affinity (90% similarity) to *Melomys albidens,* an affinity which does not appear to have been noted in the literature, while these two species together have less than 50% similarity to any others." Neither Flannery (1990) nor Menzies (1990) formally allocated *albidens* and *ruemmleri* to the same genus, but both later acknowledged this transfer (Flannery, 1995; Menzies, 1996). Our new comparisons indicate that traits associated with skins and skulls (no fluid-preserved examples of *albidens* exist) exclude *albidens* from the monophyletic cluster represented by the three species of *Coccymys*, and from any other previously identified monophyletic group of New Guinea murines. Its distinctive morphology and uncertain relationship are best expressed by placing *albidens* in its own genus.

Brassomys, new genus

TYPE SPECIES: *Melomys albidens* Tate (1951: 286).

DIAGNOSIS: A genus of subfamily Murinae, family Muridae (as delimited by Carleton and Musser, 1984, and Musser and Carleton, 2005) that is distinguished from

ELEVATION (METERS)

30 50 125 200 700 1370 1550 2100 2230 2700

MONOTREMES
Zaglossus bartoni

MARSUPIALS
Murexia melanurus
Dasyurus albopunctatus
Phascolosorex brevicaudata
Echymipera kalubu
Echymipera rufescens
Peroryctes broadbenti
Peroryctes raffrayana
Dendrolagus dorianus
Dorcopsis luctuosa
Macropus agilis
Dorcopsulus vanheurni
Phalanger carmelitae
Phalanger gymnotis
Phalanger intercastellanus
Phalanger sericeus
Spilocuscus maculatus
Cercartetus caudatus
Dactylonax palpator
Dactylopsila trivirgata
Petaurus breviceps
Pseudochirops corinnae
Pseudochirops cupreus
Pseudochirulus forbesi

BATS
Dobsonia molluccensis
Nyctimene albiventer
Pteropus neohibernicus
Syconycteris australis

Mosia nigrescens — 5, 2
Hipposideros calcaratus — 14, 4, 13
Hipposideros cervinus — 8, 157, 1
Miniopterus australis — 1
Philetor brachypterus — 21, 55
Phoniscus papuensis — 1
Pipistrellus collinus — 1, 1, 10, 5
Pipistrellus papuensis — 1, 1
Tadarida kuboriensis — 1

RODENTS

Hydromys chrysogaster — 2, 2
Leptomys elegans — 2
Leptomys paulus — 1, 3
Anisomys imitator — 4, 1
Chiruromys forbesi — 45, 61
Chiruromys lamia — 3, 17
Coccymys kirrhos — 3
Hyomys goliath — 2, 1
Lorentzimys nouhuysi — 2, 1, 1
Paramelomys mollis — 29
Paramelomys moncktoni — 5, 7, 1
Melomys rufescens — 5, 13, 1
Pogonomys macrourus — 5
Pogonomys sylvestris — 1
Uromys anak — 6
Uromys caudimaculatus — 6, 3, 1
Xenuromys barbatus — 3
Rattus leucopus — 35, 27
Rattus mordax — 1, 3, 11
Rattus niobe — 76, 147
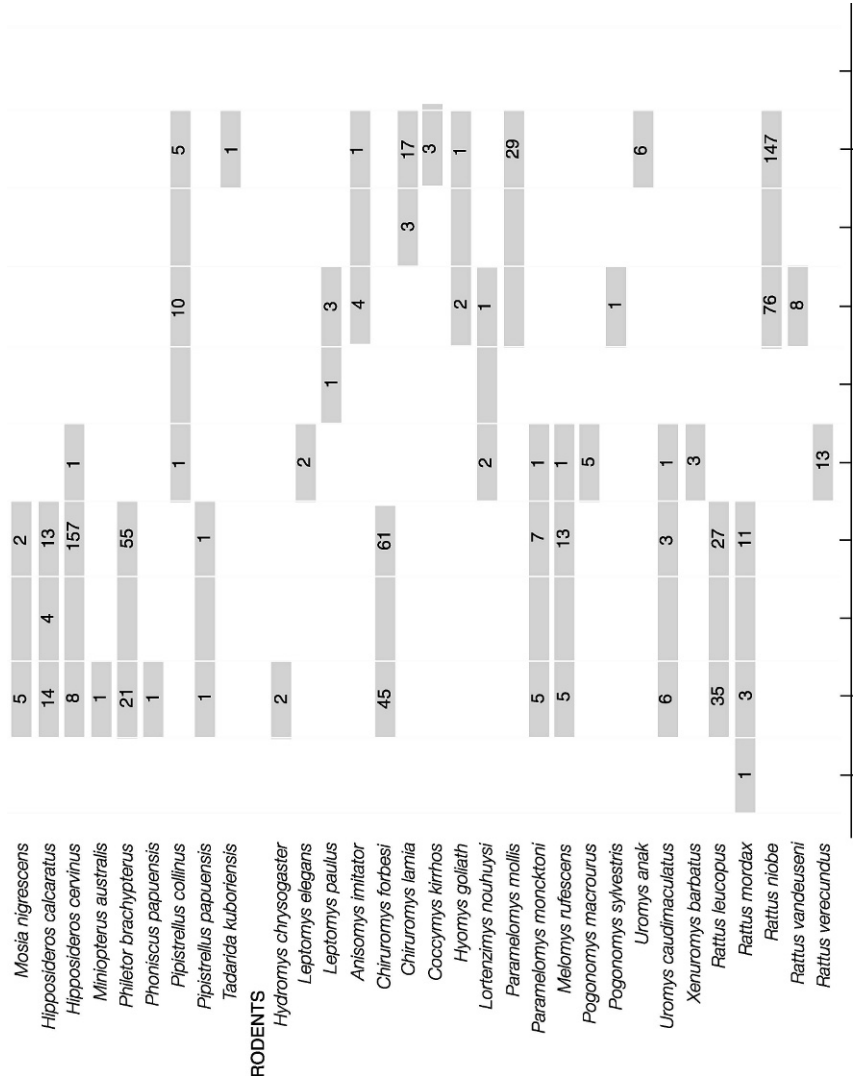Rattus vandeuseni — 8
Rattus verecundus — 13

Fig. 39. Altitudinal distribution of 1043 specimens representing 59 species of mammals obtained on the northern ramparts of Mt. Dayman during the Fourth Archbold Expedition to New Guinea in 1953. See figure 38 and text.

all other described murine genera by the following combination of morphological traits: **(1)** fur covering upperparts of head and body thick and woolly, burnished dark brown, ventral coat soft and thick, entirely whitish gray to ochraceous gray; **(2)** moderately long muzzle, brownish black mask around eyes, very long mystacial vibrissae; **(3)** tail slender and longer than head and body (LT/LHB ranges from 121% to 146%), scales small and slightly swollen, the rings of scales abutting against one another, three hairs associated with each scale, dorsal surface near tail tip covered with scales and hairs (no hairless, scaleless, calloused dorsal strip), entire tail brownish gray, one specimen with a short white tip; **(4)** dorsal surfaces of front and hind feet pale brown, hallux with claw, hind foot short and wide with full complement of plantar tubercles; **(5)** rostrum moderately long, wide, and rectangular in side view; **(6)** interorbital and postorbital dorsolateral margins smooth, interorbit hourglass-shaped in dorsal view, zygomatic arches delicate and parallel, only slightly set beyond sides of skull, braincase smooth and globular, interparietal wide and long, occiput deep; **(7)** zygomatic plate very narrow, its anterior margin straight and not projecting beyond dorsal maxillary root of zygomatic arch, its posterior edge even with anterior third of first molar, stout knoblike masseteric tubercle projecting ventrolaterally from base of ventral zygomatic root; **(8)** squamosal intact except for large subsquamosal foramen; **(9)** wide bony alisphenoid struts; **(10)** wide and moderately long incisive foramina, their posterior margins well anterior to front faces of first molars; **(11)** molar rows parallel, bony palate short with its posterior margin even with front or middle of third molars, palatal surface smooth with shallow palatine grooves, posterior palatine foramina level with anterior third of second molar; **(12)** wide mesopterygoid fossa with spacious sphenopalatine vacuities; **(13)** wide pterygoid plate with deep pterygoid fossa, sphenopterygoid openings in some specimens; **(14)** large and somewhat inflated ectotympanic bulla (relative to skull size), covering much of periotic but not touching basioccipital, dorsal wall of carotid canal formed by periotic and adjacent basioccipital; **(15)** large stapedial foramen, no sphenofrontal foramen or squamosal-alisphenoid groove, indicating a carotid arterial pattern widespread within Murinae (character state 2 of Carleton, 1980; pattern 2 described by Voss, 1988); **(16)** dentary with tubular and gently curving ramus between incisor and molar row, low and elongate ascending ramus with delicate coronoid process and elongate condyloid process, labial surface smooth without external indication of incisor capsule, that capsule terminating within the dentary at middle of base of coronoid process or just before; **(17)** upper incisor enamel white or cream, lowers with white enamel, uppers project directly down from rostrum (at a right angle) and are short and narrow (anterior-posterior plane) relative to skull size, enamel covers at least half of each labial surface, lowers thin with similar extent of enamel cover over labial surface; **(18)** each first and second upper molar (maxillary) with four roots (anterior, lingual, and two posterior) but the third with three roots, each lower (mandibular) with two; **(19)** molars brachydont, cusps rows tightly abutting one another, forming uncomplicated chevron-shaped occlusal patterns, third molar small relative to others in toothrow; **(20)** first and second upper molars with cusp rows fused at lingual margins, cusp t7 absent, enamel ridge connecting labial cusps t6 and t9, and with posterior cingulum; **(21)** anteroconid small relative to size of molar, formed by complete fusion of anterolingual and anterolabial cusps, anterolabial cusp completely coalesced with anterior lamina on second lower molar and absent from third molar, no anterior or posterior labial cusplets on any molar, posterior cingulum large and oblong.

ETYMOLOGY: "Leonard J. Brass, internationally known botanist and explorer and the world's foremost authority on the flora of New Guinea, has retired from his post as Associate Curator of the Archbold Collections at the American Museum of Natural History and leaves New York on Monday, April 18, [1966] for his native Australia. Dr. Brass was associated with the American Museum for 33 years," headlined a press release from the American Museum of Natural History. Leonard Brass left Kennedy International Airport at 10 P.M. Monday,

April 18, on Qantas Airways flight #BA506 bound for London. His ultimate destination was Queensland, Australia, where he was born in 1900 and where he would die in 1971.

Leonard wandered parts of Australia, the Solomon Islands, and Africa in his botanical explorations, but for most of his career he was associated with the six Archbold Expeditions to New Guinea sponsored by the American Museum of Natural History and financed by Richard Archbold. Brass's credentials as a superb field botanist were established between 1925 and 1933 when he led three botanical expeditions for Arnold Arboretum of Harvard University, one to Papua New Guinea, the second to Cape York in Australia, and the third to the Solomon Islands. Toward the end of this last trip, Brass received a cable from Elmer Merrill, then Director of the Bronx Botanical Garden and an internationally respected expert on botany of the Indo-Australian region, particularly the Philippines, asking if Brass would accept the position as botanist on the First Archbold Expedition. Yes, he would—and so Leonard became the official botanist for the First (1933–1934), Second (1936–1937), and Third (1938–1939) Archbold Expeditions to New Guinea, and was both leader and botanist for the Fourth (1953), Fifth (1956–1957), and Sixth (1959) Archbold Expeditions.

The biological materials gathered during those six forays into New Guinea are stored in various museums and herbaria and to this day constitute the primary source material for systematic revisions critical to understanding diversity of species on the island as well as biogeographic relationships. The specimens were collected in landscapes of forests, grasslands, savannas, rivers, and mountains, and that natural context is conveyed to us through the published expedition summaries (Archbold and Rand, 1935; Rand and Brass, 1940; Archbold et al., 1942; Brass, 1941, 1956, 1959, 1964). Although the earlier reports were coauthored, Leonard's hand is in the habitat descriptions, and it is his attention to detail and gift for description that illuminate the later reports. "Len worked hard in the field," Hobart Van Deusen once confided to Musser as we stood together in his office, "he was mild-mannered but a very tough field man, worked all day collecting botanical specimens and when not in the forest was at his work table processing the material and recording his observations [fig. 40]. Rather than moving around many times from here to there, Len insisted on staying in one place to thoroughly survey an area, which sometimes put him at odds with the more impatient members of the expedition." Van stopped speaking, his eyes drifted to a window, and whatever he saw prompted a sigh: "Len was the heart and soul of those Archbold Expeditions. I really miss him."

Brassomys albidens, new combination

HOLOTYPE AND TYPE LOCALITY: The holotype is an adult male (AMNH 150821), collected by W.B. Richardson (original number 4698) on August 14, 1938. It consists of a stuffed study skin (fig. 8) accompanied by a skull (fig. 10), all in good condition. Occlusal surfaces of the molars are worn, but cusp patterns are still evident. External, cranial, and dental measurements are listed in tables 7 and 20.

The type locality is about 15 miles (24 km) north of Mt. Wilhelmina (Gunung Trikora), at 3225 m near Lake Habbema (04°49′S, 138°41′E; locality 2 in fig. 3), which is nestled between the ridges forming northern slopes of the Snow Mountains ("Sneeuw Gebergte" on older Dutch maps; Pegunungan Maoke is the Indonesian designation on contemporary maps and in modern gazetteers) in the Central Cordillera of western New Guinea (Papua Province, Indonesia).

REFERRED MATERIAL: There are five other modern specimens, all from the Snow Mountains, captured during October 1938, in the Bele River valley, 9 km northeast of Lake Habbema at 2800 m (04°05′S, 138°50′E; locality 3 in fig. 3). Date of collection, sex, age, and measurements for each example are listed in table 20. The skulls of three specimens are intact, but those of two others are damaged. Tate had identified only two of the five as *albidens* (AMNH 150531 and 150541), one as *Pogonomys sylvestris* (AMNH 150607), and two as *Pogonomelomys ruemmleri* (AMNH 150518 and 150923).

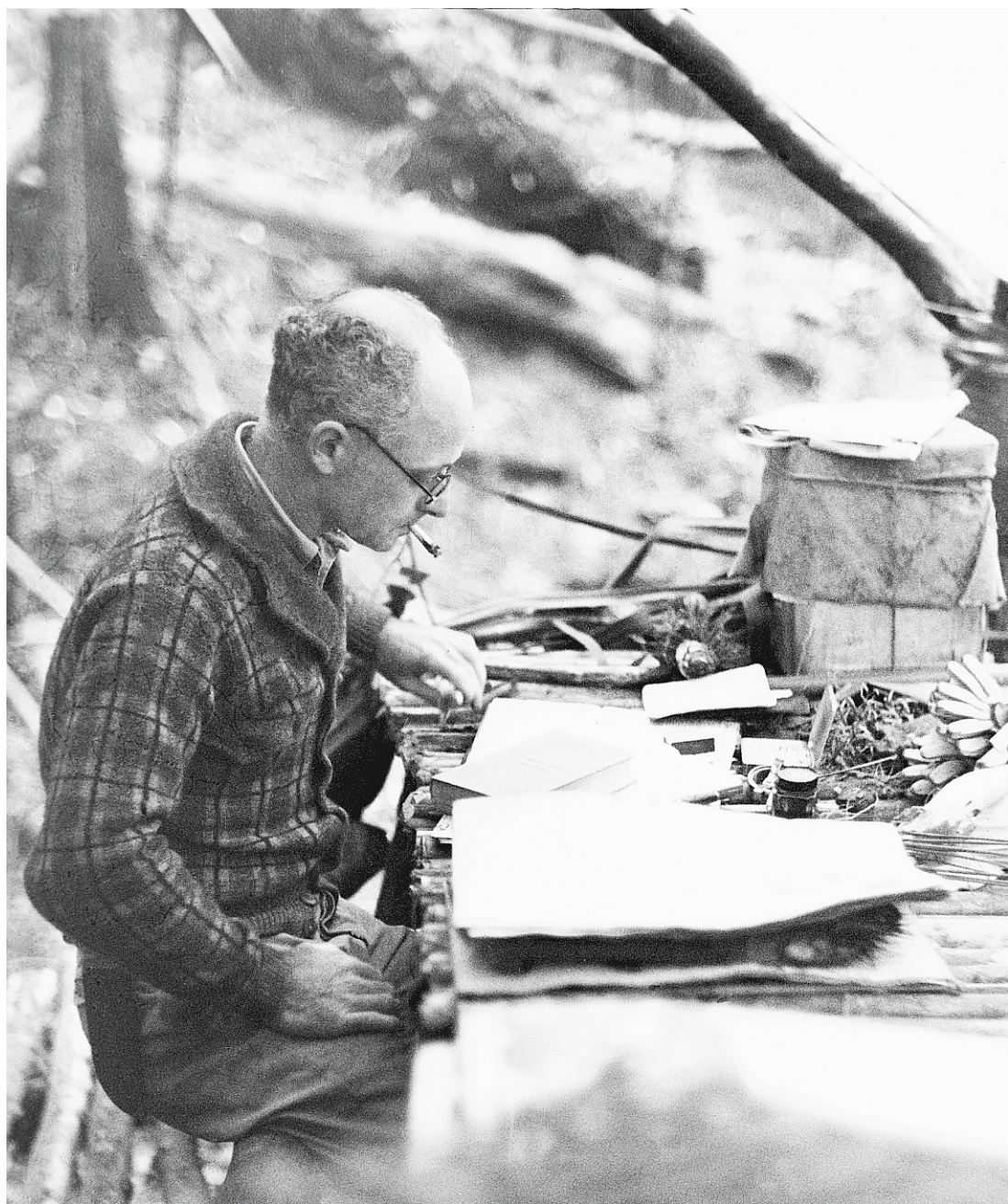In addition to the holotype and five other modern specimens, there are three dentary

Fig. 40.   Leonard J. Brass at work at the 1200-meter camp (6 km southwest of Bernhard camp) on the northern slopes of the Snow Mountains in western New Guinea, February–March 1939.

fragments (AMF 134074, 134096, 134126) that were extracted from Late Pleistocene sediments excavated in Kelangurr Cave (04°01′S, 138°08′E; locality 1 in fig. 3),

2950 m. The cave is on the northern slopes of the Snow Mountains about 60 airline km west of Lake Habbema, in a valley confluent with the valley of the West Baliem River (see

TABLE 20
Measurements (mm) of the Six Known Modern Specimens of *Brassomys albidens*

AMNH catalog number	150541	150607	150531	150821[a]	150923	150618
Locality	Bele River	Bele River	Bele River	Lake Habbema	Bele River	Bele River
Altitude	2800 m	2800 m	2800 m	3225 m	2800 m	2800 m
Date collected	19 Oct 1938	31 Oct 1938	18 Oct 1938	14 Aug 1938	28 Oct 1938	1 Nov 1938
Sex	Male	Male	Male	Male	Male	Female
Age	Old adult	Adult	Adult	Adult	Young adult	Juvenile
LHB	111	120	119	122	111	98
LT	162	152	144	162	151	130
Scale rows (per cm)	17	20	19	24	24	20
LT/LHB (%)	146	127	121	133	136	133
LHF[b]	27	26	25	27	27	25
LE	21	20	19	22	18	17
ONL	30.55	—	29.49	30.44	29.87	27.13
ZB	14.04	—	15.36	15.65	14.79	14.00
IB	4.64	—	5.04	5.42	—	5.35
LR	9.70	9.99	8.75	9.16	8.94	7.52
BR	5.83	—	5.98	5.45	5.65	5.09
BBC	13.37	—	14.20	14.12	—	13.66
HBC	9.49	—	10.24	9.53	—	9.84
BZP	2.06	2.18	2.25	2.23	1.92	1.81
LD	7.49	7.32	7.07	7.23	7.00	6.29
PPL	11.68	—	10.64	10.88	10.45	9.79
LBP	6.04	5.48	5.54	5.18	5.18	5.02
BBPM1	2.61	2.97	2.96	2.70	2.96	2.84
BMF	2.65	2.67	2.42	2.40	2.36	1.55
LIF	4.61	4.40	4.54	5.18	4.51	4.30
BIF	1.84	1.92	1.84	1.97	1.92	1.78
LB	5.33	5.21	5.20	5.53	5.13	4.97
CLM1-3	5.09	5.05	5.09	5.16	5.24	5.05
BM1	1.58	1.59	1.65	1.59	1.64	1.53

[a]Holotype.
[b]We measured length of hind foot, including claws, on the dry stuffed skins.

map and description in Flannery, 1999). Two of the fossils had been identified as *Coccymys ruemmleri*, and the third as "*C.* sp."

GEOGRAPHIC DISTRIBUTION: *Brassomys albidens* is still known by only the original six skins and skulls obtained from 3225 and 2800 m, and the three Late Pleistocene fragments collected in Kelangurr Cave on the northern slopes of the Snow Mountains, but probably occurs in montane forest formations at comparable altitudes elsewhere in the Central Cordillera of western New Guinea. If the range of *B. albidens* is concordant with that of other montane mammals that are endemic to western New Guinea (see Helgen, 2005b, 2007a, 2007c), it should be found in suitable forest habitats along the length of the Snow Mountains and possibly in the adjacent Star Mountains. This mountain backbone is part of Flannery's (1995: 37) "Western Sub-Province" of the "Tumbunan Biogeographic Province" defined by Schodde and Calaby (1972); the subprovince extends from the Wissel Lakes region in the west (03°55′S, 136°15′E) to the deep valley of the Strickland River in the east (06°30′S, 142°04′E). With very few exceptions, mammalogical surveys throughout the western Central Cordillera formed of the Snow and Star mountains have been sparse (see Geographic Distribution in the account of *C. ruemmleri*).

DESCRIPTION AND COMPARISONS: Here we describe the external form, pelage, and

characteristics of the skull and dentition of *Brassomys albidens* based on five adults and one juvenile. We note the contrasting condition in the samples of *Coccymys ruemmleri* (the type species of *Coccymys*) from the Snow Mountains at the appropriate places in the account, discuss absolute and proportional differences in cranial and dental variables, and summarize the primary trenchant distinctions between the two genera in table 21.

Adults of both *B. albidens* and *C. ruemmleri* share a short masked face; long facial vibrissae, small body clothed in luxuriant, thick, and dark brown fur; and a thin, brownish gray tail that is longer than head and body (figs. 6, 8). Upperparts of *B. albidens* are typically brighter than in *C. ruemmleri*: dorsal pelage over most of the upperparts is dense (overhairs are up to 12 mm long), soft to the touch, and woolly in appearance, and a rich buffy brown from head to rump and along back and sides (overhairs are dark gray for most of their lengths and have rich buffy brown tips). Guard hairs project slightly beyond the overfur layer but not enough to alter the even contour of the fur covering or its color. The bright buffy brown extends onto the thighs, upper arms, and cheeks. A dark brown ring encircles each eye (*C. ruemmleri* has darker, more somber upperparts, the coat is thicker, 11–14 mm, and lax instead of woolly, and the head is gray, patterned only by a blackish area around each eye that extends forward over each side of the muzzle to the bases of the mystacial vibrissae). The very long mystacial vibrissae are mostly black with silvery tips, the longest reaching 70 mm and extending well beyond the pinnae when laid against the head. The longest of the superciliary vibrissae extend to slightly beyond the pinnae, and the usual murine array of facial submental and interramal sensory hairs and ulnar and tarsal vibrissae are apparent (all except possibly the genal vibrissae, which we could not find—either they are absent or indistinguishable from overhairs in the dorsal coat). The ears are large, dark brown, and covered inside and out with fine, short hairs. *Brassomys albidens* has much larger and more expansive external pinnae than does *C. ruemmleri* (means and standard deviations are: 20.0 mm ± 1.58,

range 18–22 mm, for *B. albidens*, $N = 5$; 16.9 mm ± 1.09, range 15–19 mm for *C. ruemmleri* from Lake Habbema, $N = 16$; see table 3 for univariate summaries from other samples of *C. ruemmleri*). We compared length of ear between adults of *B. albidens* and a sample of adult *C. ruemmleri* from Lake Habbema, which were all likely measured by one collector, W.B. Richardson, so limits of the dimension would be consistent whether taken from base to crown or from notch to crown. Unfortunately, length of ear as it was measured does not convey the striking difference in size when skins are compared side-by-side.

The ventral coat of *B. albidens* is also soft and dense, and up to 10 mm thick. The entire underparts, from chin to base of tail, are pigmented and among the five adults ranges from whitish gray (AMNH 150923) through dark grayish white (AMNH 150541, 150607) and pale buffy gray (AMNH 150531) to intense and bright ochraceous gray in the holotype. The darker and buffy tones are produced by hairs that are dark gray for most of their lengths and have short unpigmented or buffy tips; relatively longer unpigmented tips result in paler expressions. Underparts of 36 of the 40 *C. ruemmleri* from the Snow Mountains that we examined are either whitish gray or a darker grayish white (the predominant tone), and only four have buffy gray underparts.

The tail is slender and longer than the head and body (LT/LHB ranges from 121% to 146% in five adults), but relatively shorter than in *C. ruemmleri* (tables 3, 7). It is covered in annuli of small, slightly swollen, and brown scales (19–24 scale rings per cm); these rings of scales abut one another near the base of the tail but appear to overlap slightly toward the tip in some specimens but not others. Three dark brown hairs, as long as three or four scales, emerge from beneath each scale, which imparts a hirsute texture to the entire tail, but no tuft at the tip (scale rows abut against each other in *C. ruemmleri*, the tail hairs are shorter relative to scale length, and while the texture is somewhat hirsute, it is slightly less hairy than in *B. albidens*). All surfaces of the tail are covered by scales and hairs, without any sign of a long and naked gripping pad (thickened

epidermis devoid of either scales or hair) over the dorsal surface of the distal fifth of the tail, indicating that the tail is not used as a dorsally prehensile organ (such a dorsal strip is prominent in *C. ruemmleri*, and the tail is used for dorsal prehensile grasping). The entire tail surface is brownish gray in all six specimens; AMNH 150607 is the only one with a short white tip (7 mm long, 5% of the tail length).

Dorsal surfaces of front feet and digits are unpigmented and densely covered with silvery hairs; metatarsal surfaces of the hind feet are pale brown, and densely covered with silvery and pale brown hairs, the digits and their covering of fine hairs are unpigmented. A tuft of silvery hairs springs from the base of each claw to cover about the basal half of each. The claws on both front and hind digits are unpigmented, large, long, and scythe-shaped (metacarpal, metatarsal, and digital surfaces are sparsely haired in *C. ruemmleri*, the ungual tufts extend from bases of the digits to the tips, and the claws are smaller). Lengths of the digits relative to one another on front and hind feet match the proportions described for *C. ruemmleri* (the two middle digits of each front foot are the longest, the lateral digits slightly shorter; the three central digits of the hind foot are subequal in length and longer than the much shorter hallux, which bears a claw). The front foot is large; its palmar surface is naked, pale brown, and most of the area is formed by three large fleshy interdigital pads and posterior thenar and hypothenar mounds set close together (the large pads are evident even in their desiccated state on each dry study skin), resembling the palmar surface in such arboreal murines as the species of *Margaretamys* from Sulawesi (Musser, 1981a: 278). (*C. ruemmleri* has smaller front feet, which reflects its smaller body size, but the pads are less expansive relative to palmar surface.) Each hind foot is moderately wide across the carpal region and short relative to length of head and body (absolute length of hind foot in *C. ruemmleri* and *B. albidens* is about the same, so the former has a longer foot relative to body size, and it is also narrower; see tables 3, 7, and 20). Plantar surfaces are naked, pale brown, and bear four fleshy interdigital pads, a moderately large thenar,

and much smaller hypothenar; the configuration is similar in *C. ruemmleri*. In both species, the pads are large but they do not occupy as much of the plantar surface as is seen in very specialized arboreal murines such as the species of Sulawesian *Margaretamys* (Musser, 1981a: 279).

No weights were recorded for the six specimens of *B. albidens* so we have no estimate of body mass. Also missing is a mammary count. All but 150618 were labeled as males in the field, do not exhibit any indication of teats, and some retain a dry scrotal sac. AMNH 150618 is in juvenile pelage and labeled as female, but there is no sign of teats on the dry skin (we cannot exclude the possibility that the specimen was incorrectly sexed in the field, which is easy to do with juveniles). A clear contrast exists between juvenile and adult coats. Juvenile pelage is slightly shorter (up to 10 mm) than that of adults and the hairs are finer, guard hairs project a bit beyond the overhairs, the texture is soft and more woolly, the upperparts are darker—a dark grayish brown—and the underparts are whitish gray. Juvenile *C. ruemmleri* (and *C. shawmayeri*; we lack juveniles of *C. kirrhos*) have a shorter coat than adults (up to 10 mm; 11–14 mm in adults) and the texture is finer and softer, but color of upperparts and underparts can hardly be distinguished from adult coverings—the underparts are whitish gray and the fur over head and body is warm brown.

The skull is small, as is that of *C. ruemmleri* (figs. 9, 10; table 4), but appears sturdy with a somewhat chunky rostrum, parallel zygomatic arches, and large, round braincase ("full braincase" as Tate, 1951: 286, described it). The rostrum is moderately long and wide, and slightly tapered as viewed from a dorsal perspective, its lateral outlines barely interrupted by the low bump of each nasolacrimal canal. Smooth dorsolateral boundaries of the interorbital and postorbital regions define an hourglass-shaped interorbit in dorsal view. The back of the postorbital area is not defined by a vertical ridge where the frontal and squamosal bones meet, the conformation exhibited by *C. ruemmleri*, so there is no angular projection (in dorsal view) breaking the curved dorsolateral outlines of

TABLE 21
Summary of Notable Chromatic and Morphological Contrasts Between Adult *Brassomys albidens* and *Coccymys ruemmleri*
(Differences are also reflected in the univariate summaries [table 4], ratio diagram [fig. 42], and illustrations of skins, skulls, and molars [figs. 6, 8–12, 40, 41].)

Trait	*Brassomys albidens*	*Coccymys ruemmleri*
Color of underparts	Fur whitish gray to ochraceous gray	Grayish white, a few suffused with buff
Tail	Shorter relative to head and body (LT/LHB = 121–146%); no dorsal scaleless, hairless, calloused strip near tip, not dorsally prehensile	Relatively longer (140–146%); dorsal scaleless, hairless, calloused strip near tip, dorsally prehensile
Hind foot	Shorter relative to head and body (LHF/LHB = 21–24%) and slightly wider	Relatively longer (26–27%) and slightly narrower
Ear	Appreciably larger	Much smaller
Rostrum	Rectangular in lateral view, as deep near incisors as near zygomatic plate	Tapered, shallower near incisors than at zygomatic plate
Zygomatic plate	Absolutely narrower and much narrower relative to skull size	Absolutely and relatively wider
Masseteric tubercle	Prominent knobby projection	Inconspicuous, oblong roughened area or low bump
Posterior edge of incisive foramina	Set well anterior to faces of M1	Usually even with faces of M1 or projects slightly between them
Posterior margin of bony palate	Even with anterior third of M3	Even with backs of M3 or extends slightly beyond them
Mesopterygoid fossa	Averages absolutely wider and much wider relative to skull size	Absolutely and relatively narrower
Ectotympanic bulla	Large and inflated, bullar capsule conceals most of periotic	Much smaller, capsule leaves exposed long wedge of periotic separating ectotympanic from basioccipital
Occiput	Shallower (anterior-posterior dimension), reflecting less cranial flexion	Deeper, greater cranial flexion
Upper incisors	White or cream enamel, uppers project from rostrum at right angle, shorter and narrower, enamel extends over half of labial surface	Orange enamel, uppers curve back from rostrum, longer and thicker, enamel covers one-third of labial surface
Maxillary molars	Absolutely larger and much larger relative to skull size	Absolutely and relatively smaller
Roots on M1, M2, and M3	4, 4, and 3	3, 3, and 3
Cusp rows on M1 and M2	Chevron-shaped occlusal patterns, with little or no cusp definition	Gently bowed, pronounced cuspidate topography
M3	Small, 16% of molar row	Larger, 20% of molar row
Anteroconid on m1	Small, anterolabial and anterolingual cusps completely fused	Large, chunky, cusps separate and fuse only after appreciable wear
Anterolabial cusp on m2	Coalesced with adjacent cusp, undetectable even in moderately worn molar	Distinct, small or large, retains identity even after much wear
Posterior labial cusplets	Small, merge early with adjacent cusp, nearly indistinguishable	Present, discrete cusplets
Shape of dentary	Long and low ramus, delicate coronoid process, elongate condyloid	High, large coronoid process, short condyloid
Lower incisor alveolus	Concealed, capsule ends within the dentary at base of coronoid process or slightly before	Alveolar capsule ends in large knobby labial projection even with dorsal margin of sigmoid notch and between coronoid and condyoid processes

TABLE 21
(*Continued*)

Trait	*Brassomys albidens*	*Coccymys ruemmleri*
Lower incisor	White or cream enamel covering half of labial surface, projects from dentary at low angle	Orange enamel covering third of labial surface, projects from dentary at higher angle

the interorbital and postorbital regions. Beyond the postorbital boundaries, the deep braincase is round in outline, and smooth in texture: the parietal joins the squamosal smoothly without any roughened places or bead marking the attachment sites for temporal muscles, an inconspicuous linear beading defines each lamboidal ridge, and each mastoid is moderately inflated. The interparietal is deep (anterior-posterior dimension) and wide. Moderately thin zygomatic arches are parallel or flare slightly toward the front, and each arch projects only slightly outward from the side of the skull (arches flare out more in *C. ruemmleri*, and are not parallel but taper toward the rostrum); anterior margins of the dorsal maxillary roots of the zygoma form right angles to the rostrum and are not indented— no zygomatic notch. (A shallow convex dorsal margin between rostrum and top of the zygomatic plate represents the zygomatic notch in *C. ruemmleri*.) The jugal component of each zygoma is short.

When the skull is viewed from a lateral perspective, the dorsal outline rises straight and even along the rostrum and interorbit to arch over the braincase down to the occiput, which barely overhangs the occipital condyles (slightly greater cranial flexion in *C. ruemmleri*, which has a relatively deeper occiput). The rostrum is rectangular in lateral view, about as deep near the incisors as at the dorsal and ventral zygomatic roots (tapered in *C. ruemmleri*, higher near the zygomatic plates than at the incisors); margins of the nasals and premaxillaries project slightly beyond the incisor faces, and the nasolacrimal capsules are large but only slightly inflated. The zygomatic plate is very narrow, and its straight, vertical, leading edge does not project anterior to the dorsal maxillary root of the zygomatic arch, so there is no zygomatic notch; the posterior margin of the

ventral maxillary root of the plate is level with the anterior third of the first molar (there is a much wider zygomatic plate in *C. ruemmleri*, both absolutely and relative to cranial dimensions [see figs. 41 and 43, table 4], with a slight zygomatic notch, the posterior edge lies in front of the first molar). The tendon for the superficial masseter muscle attaches to a robust knoblike tubercle projecting ventrolaterally from the ventral maxillary root of the zygomatic plate (the origin of the superficial masseter is simply a slightly roughened spot or low bump at the base of the plate in *C. ruemmleri*; fig. 41). Behind the orbit, the squamosal root of the zygomatic arch originates midway on the side of the braincase. Posterior to the squamosal zygomatic root and dorsad of the auditory bulla, the squamosal is intact except near the squamosal-exoccipital suture where it is perforated by a large subsquamosal foramen through which the periotic is visible. The dorsolateral margin of the braincase is mostly smooth—a slight bevel marks the temporal ridge—and formed by the union of parietal and squamosal. A small portion of the parietal drops either just below the dorsolateral margin of the braincase or about halfway between the margin and top of the zygomatic root; this short projection and the squamosal form the wall of the braincase (slight temporal beading is evident along dorsolateral margins of the braincase in *C. ruemmleri*, and a much larger portion of the parietal projects farther ventrally to form part of the lateral braincase wall). The junction of the orbitosphenoid, alisphenoid, and frontal bones forms a solid section of the braincase wall, unbroken by a sphenofrontal foramen. The inner walls of the braincase are smooth, without squamosal-alisphenoid grooves. A wide bony alisphenoid strut (present in all six skulls) separates the foramen ovale accessorius from the combined buccinator-mastica-
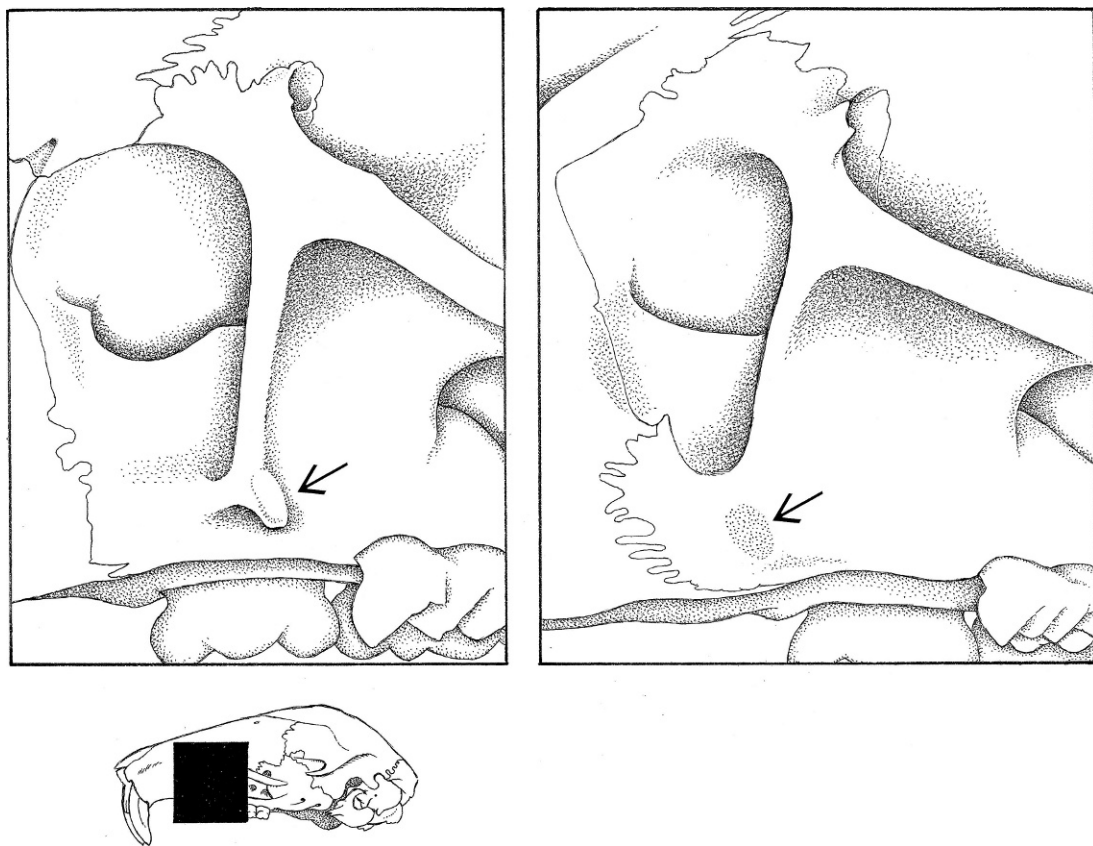
Fig. 41. Enlargements (drawn to scale) of zygomatic plates drawn from holotypes. **Left:** *Brassomys albidens* (AMNH 150821). **Right:** *Coccymys ruemmleri* (AMNH 150669). Note the contrasts in width of the zygomatic plate and origin for the superficial masseter muscle (arrows)—a knoblike projection in *B. albidens* and oblong roughened surface in *C. ruemmleri*.

tory foramen. The auditory bulla is more tightly attached to the squamosal in *B. albidens* than it is in *C. ruemmleri*: the postglenoid foramen is a slit and the ventral postalar fissure is narrow (these openings are much wider in *C. ruemmleri*); the periotic exposed along the dorsolateral margin of the bullar capsule projects forward as a thin tegmen tympani but does not overlap the squamosal. The occiput is not as deep as it is in *C. ruemmleri*—its extension beyond the occipitals is not as great, probably a reflection of the lesser degree of cranial flexion in *B. albidens*.

The wide incisive foramina are conspicuous when the skull is viewed from a ventral perspective: they occupy about 70% of the diastema, which is similar to the proportion in *C. ruemmleri*, but unlike that species, the posterior edges are anterior to front faces of the first molars (figs. 9, 10). The wide bony palate is about as long as the parallel molar rows, and its posterior margin is level with the front half of each third molar (even with backs of the third molars or projects slightly beyond them in *C. ruemmleri*). Its surface is flat and smooth except where textured by a shallow pair of palatal grooves and large posterior palatine foramina set even with the anterior third of each second molar (surface of bony palate is longitudinally indented in *C. ruemmleri*, and the palatal grooves are deeper). The very wide mesopterygoid fossa is slightly narrower than the bony palate and its dorsolateral margins are intact or breached by elongate or short sphenopalatine

vacuities. The adjacent pterygoid plates (= parapterygoid plates) are triangular in ventral view and mostly intact except where the middle section is perforated by small sphenopterygoid vacuities, and at the back of the plate where it is pierced by the large ventral opening of the foramen ovale. Between the foramen ovale and middle lacerate foramen, a shallow groove scores the posterolateral area of the plate's ventral surface. Each pterygoid fossa is moderately deep. The posterolateral margin of the pterygoid consists of either a threadlike bony ridge lateral to the foramen ovale (as in the holotype, fig. 10) or a slightly wider but still narrow and delicate ridge (the comparable ridge in *C. ruemmleri* is wider, more robust). A very short bony eustachian tube projects from each ectotympanic (auditory) bulla, and that capsule is very large and somewhat inflated relative to size of the skull—length of bulla is 18% of occipitonasal length. The bullar capsule has the same basic form as does the relatively smaller capsule in *Coccymys*, but it and the underlying periotic are just larger, and the capsule itself is deeper, not relatively wider because it shields about as much of the periotic surface as does the capsule in *Coccymys*, leaving exposed in ventral view a posteromedial wedge of that element between capsule and basioccipital and a thinner segment extending forward; the length of the medial edge of the capsule does not touch the lateral margin of the basioccipital. The dorsal wall of the carotid canal is formed by the periotic and its medial wall by the basioccipital, a configuration similar to that diagrammed for *Oligoryzomys* by Carleton and Musser (1989: 33). (the bulla is much smaller in *C. ruemmleri*, about 14% of the skull length, and not inflated, the ectotympanic does not conceal most of the periotic in ventral view, which is exposed as a posteromedial wedge and tapered flange extending forward separating the ectotympanic from the basioccipital margin). All of the specimens we examined possessed a large stapedial foramen penetrating the crevice (petromastoid fissure) between the bullar capsule and posteromedial wedge of the periotic. A slitlike or small, oval middle lacerate foramen separates the bullar capsule from the posterior margin of the pterygoid plate, a reflec-

tion of the inflated bulla (wide opening between capsule and pterygoid in *C. ruemmleri*, a result of its much smaller ectotympanic bulla).

All specimens of *Brassomys albidens* and *Coccymys ruemmleri* we studied share a carotid arterial pattern that is derived for muroid rodents in general but primitive for members of subfamily Murinae (character state 2 of Carleton, 1980; pattern 2 described by Voss, 1988; conformation diagrammed for *Oligoryzomys* by Carleton and Musser, 1989). Our sample of *B. albidens* is represented only by skulls, but they possess certain cranial foramina and bony landmarks, along with dried vessels, also apparent in skulls of *C. ruemmleri*, that signal the derived plan already described in the account of *C. ruemmleri*.

Each dentary is elongate, with a slim and long tubular ramus between incisors and molar row that gently curves upward at about 30°, a low ascending ramus, delicate coronoid process, and elongate condyloid projection (figs. 10, 42). The posterior margin between condyloid and angular processes is deeply concave, and a wide concave sigmoid notch separates the small coronoid from the projecting condyloid process. The labial surface of the ascending ramus is smooth, lacking any external indication of the incisor capsule, which is concealed within the dentary and terminates at or near the base of the coronoid process. The dentary of *C. ruemmleri* is stocky by comparison with that of *B. albidens*, the ramus between molar row and incisor is shorter and deeper and curves upward at about 45°, the ascending ramus is higher, the coronoid process more robust, and the condyloid projection wider and stocky (figs. 9, 42); the ascending ramus is smooth in some specimens of *C. ruemmleri*, but in others is sculptured by a low mound containing the incisor capsule that runs diagonally along the ascending ramus; in both textures, the capsule ends as a large, bony, labial knobby projection ending slightly below, even, or above the top of the sigmoid notch between coronoid and condyloid processes.

Enamel layers of the upper incisors are white or cream, and enamel covering the lower incisors is white (dense orange on
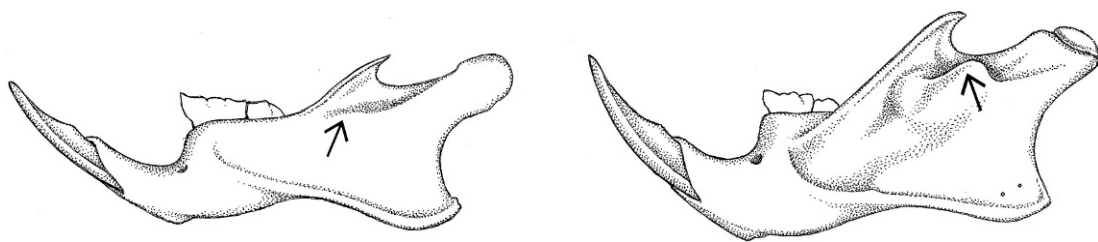
Fig. 42.   Contrasts in configuration of dentaries between holotypes. **Left:** *Brassomys albidens*. **Right:** *Coccymys ruemmleri*. Arrows indicate end of incisor capsule, which is encased within the dentary in *B. albidens* and undetectable on the labial surface, but forms a prominent labial projection in *C. ruemmleri*.

uppers and paler orange on lowers in *C. ruemmleri*). The incisor faces are smooth, lacking either grooves or shallow sulci. The incisors emerge from the rostrum at a right angle to the occlusal plane of the molars (orthodont configuration, as defined by Thomas, 1919).

The upper incisors of *B. albidens* have a distinctive shape and extent of enamel cover that are unusual among most murines, that conspicuously diverge from the incisor form in *Coccymys ruemmleri* (figs. 9, 10). The incisors of *B. albidens* project straight down from the rostrum (orthodont) rather than curve down and back (opisthodont) as they do in *C. ruemmleri*, and they are shorter and thinner (in the anterior-posterior plane). Measurements from an old adult *B. albidens* (AMNH 150541) and an old adult *C. ruemmleri* (AMNH 151277) are typical: the distance from the anterior edge of the incisor alveolus down to the incisor tip is 4.8 mm in *B. albidens* and 5.8 mm in *C. ruemmleri*, and the anterior-posterior thickness (measured near the alveolus well above the wear facet) is 1.2 mm for *B. albidens* and 1.8 mm for *C. ruemmleri*. *Brassomys albidens* has a larger skull than *C. ruemmleri* (tables 4, 7), so its incisor is both absolutely smaller and smaller relative to skull size. In side view, the white enamel covers one-third to one-half or more of the labial surface of the incisor in *B. albidens*, even though the incisor is no thicker than the orange enamel layer in *C. ruemmleri*, where it covers only one-fourth to one-third of the labial surface. Finally, the incisor tips form a gently convex cutting edge in *B. albidens*, but a straight edge in *C. ruemmleri*.

Lower incisors of *B. albidens* are slightly shorter than those in *C. ruemmleri* (5.9 mm and 6.1 mm, respectively; measured from the ventral alveolar margin to the incisor tip on the same two adults identified previously) and narrower (1.1 mm and 1.5 mm, respectively, measured in the same plane as the uppers). White enamel covers half of the labial incisor surface in *B. albidens*, but in *C. ruemmleri* the pale orange enamel covers only a third of the labial surface. The incisor tips form a convex cutting surface in *B. albidens*, but a straight edge in *C. ruemmleri*.

Numbers of roots for the first and second upper (maxillary) molars in *B. albidens* deviate from the pattern considered primitive for murines (Musser and Newcomb, 1983). Instead of three roots beneath each molar, the primitive pattern in *C. ruemmleri*, each each first and second upper molar is anchored by four roots: one large anterior, a smaller lingual, and two posterior, each about the size of the lingual. The increase from three roots to four results from a divided posterior root. In many other murines with multiple roots, especially *Rattus* and its generic allies (in the *Rattus* Division of Musser and Carleton, 2005), the posterior root is intact and it is the lingual root that becomes divided. Each third upper molar in *B. albidens* has three roots, and each lower (mandibular) molar has two holdfasts, all representing the generalized murine character state.

The upper and lower molars are brachydont, narrow relative to skull breadth, and abut against one another in each row with slight overlap (figs. 11, 12). The first upper molar forms nearly half of the maxillary

toothrow, the second molar slightly more than a third, and the third molar relatively much smaller, about 16% of the row. Proportions are similar for the lower molars. Relative to length of molar rows, size of the first and second molars in *C. ruemmleri* are similar to those in *B. albidens*, but the third lower in each jaw is relatively much larger, 20% of the respective molar row.

In contrast to the maxillary cusp rows in *Coccymys*, which are formed by discrete cusps that have not merged in young animals or only narrowly coalesced in older individuals with more worn coronal surfaces, most of the cusp rows in *B. albidens* are smooth, without clear indication of their cuspidate origin because the cusps merge early in ontogeny and even in juveniles are no longer discrete entities (a juvenile is shown in fig. 11). Also, the rows of cusps in *Coccymys* are set farther apart and not as tight as in *B. albidens.* The occlusal surface of each first upper molar of *B. albidens* is formed by three broad rows of cusps and a posterior cingulum (see figs 11, 12, where occlusal views of *Brassomys* are contrasted with those of *Coccymys*). The first two rows each conform to a chevron in occlusal view, especially in worn molars, resembling the conformation in *Melomys* (see the occlusal views of *Melomys rufescens* in Musser, 1982a: 39). Cusps t1, t2, and t3 that make up the first row are so completely coalesced that their boundaries are obliterated (such cusps are evident in the anterior lamina of *C. ruemmleri*, and the elongate central cusp t2 is broadly merged with the smaller labial cusp t3 to form a slightly bowed configuration, not a chevron). A posteriorly oriented lingual cusp t4 merged with a large triangular central cusp t5 and elongate diagonally oriented labial cusp t6 forms the second arched row; these cusps in the second row retain a bit of their definition in juveniles but lose their boundaries in older individuals (the second lamina in *C. ruemmleri* is entirely cuspidate, cusp t5 is narrow, wide, and nearly straight, and the row is gently arcuate, not chevron-shaped). A very large triangular cusp t8 joined to a labially directed much smaller cusp t9 comprises the third row (cusp t8 is compressed, from front to back, in *C. ruemmleri*, not triangular). In adults, the three cusp rows are connected at

their lingual margins where the posterior edge of cusp t1 fuses with a short and high spur projecting from the anterolingual surface of cusp t4, and the posterior edge of that cusp merges with the anterolabial edge of cusp t8; there is no lingual cusp t7 or connecting ridge between cusps t4 and t8. At the labial margin, a short ridge projects forward from the anterior surface of cusp t6 to meet the posterolabial edge of cusp t3 near its base, and the posterolabial edge of cusp t6 broadly fuses with a high enamel spur from the end of cusp t9. Between these lingual and labial connections, each cusp row forms a chevron-shaped basin bounded by enamel ridges, especially high along the lingual margins. The connections are absent or not as pronounced on molars with little wear (in *Coccymys*, the first cusp row is unattached to the second along the lingual margin; on the labial side a low ridge connects cusp t3 with the front margin of cusp t6 near the cingulum in some specimens, and a low cingular ridge extends forward from the tip of cusp t9 to fuse with the posterolabial margin of cusp t6; the first and second cusp rows do not become basined with wear). The posterior cingulum is small relative to overall occlusal surface, but remains recognizable even after considerable wear.

A large cusp t1 defines the anterolingual border of the second molar, and a much smaller cusp t3 sits on the anterolabial margin; the latter varies from a small recognizable cusp to a nubbin on the cingular margin. Occlusal configurations of the first complete row (formed of cusps t4, t5, and t6) and the posterior row (consisting of cusps t8 and t9) are similar to those exhibited by the second and third cusp rows on the first molar. Also, as in the first molar, a lingual enamel ridge connects the isolated cusp t1 with the anterior margin of cusp t4, and the posterior edge of that cusp is merged with the anterolingual margin of cusp t8; there is no cusp t7. On the labial margin, the anterior face of cusp t6 bears a vertical ridge that meets the small cusp t3 near its base if that cusp is large enough; a comparable ridge projects forward from the anterolabial edge of cusp t9 to the posterolabial margin of cusp t6 (may be absent from one molar but present on its opposite). The posterior cingulum is

present but sometimes smaller than its counterpart in the first molar.

A large cusp t1, arcuate anterior row formed by completely fused cusps t4, t5, and t6, and small, chunky posterior lamina (mostly cusp t8, possibly including a small cusp t9, but difficult to identify) form the chewing surface of each third molar. The two cusp rows are evident in the juvenile (fig. 11) but coalese after wear into dentine surrounded by an enamel ring (the anterior row is larger in *C. ruemmleri*, and the posterior lamina much larger and wider relative to occlusal surface, reflections of the relatively much larger third molar). A posterior cingulum is absent, and cusp t3 is either absent or undetectable because it has so completely merged with the anterolabial surface of the molar.

The first lower molar in each mandibular row is relatively short and narrow, and its coronal surface is formed by three rows of cusps (fig. 12), their conformation similar to that characterizing *Melomys* (see illustration of *M. rufescens* in Musser, 1982a: 39). The front lamina, the anteroconid, is solid, small relative to surface of the first molar, with an obtuse anterior outline, and formed from the complete fusion of a large anterolingual and much smaller anterolabial cusp (no evidence of an anterocentral cusp); the two cusps are completely fused even in the juvenile example of *B. albidens* (anteroconid in *C. ruemmleri* is relatively larger and rectangularlike in occlusal outline, consisting of a chunky anterolingual cusp and only slightly smaller anterolabial cusp that are separated along most of their medial borders in unworn and moderately worn teeth but broadly coalesced in older adults where the medial borders are obliterated; fig. 12). A triangular and large fused metaconid and protoconid create the second row of cusps that is separated from the anteroconid (fusing with it only after much wear and usually only narrowly at the labial and lingual margins). A large and oblong entoconid and hypoconid form most of the posterior one-third of the molar, and behind that row of cusps is a wide and triangular posterior cingulum. Cusps forming these two rows behind the anteroconid are angled posteriorly (broad chevron shape in occlusal view) and each pair has completely

coalesced along the midline even in juveniles showing little wear (cusps forming comparable laminae in *Coccymys* display a more linear orientation and fuse only at a later stage of wear than in *Brassomys*). The occlusal surface of the somewhat rectangular second lower molar consists of two rows of cusps, each a spread chevron in occlusal view, and a large and elongate posterior cingulum (here also the chewing surfaces in *Coccymys*, especially that of the posterior lamina, are straighter and the cusps only narrowly merged). The anterolabial margin of the molar supports a small anterolabial cusp that fuses with the protoconid after only little wear; its opposite, the anterolingual cusp, is absent. The chunky third molar has a simple occlusal surface created by two laminarlike cusp rows, similar in configuration to the occlusal topography in *Coccymys*. An anterolabial cusp is absent from some specimens but present on others, although often inconspicuous because it has nearly melted into the hypoconid. The posterior margin of the tooth is without a posterior cingulum, the usual state in most murines.

Anterior and posterior labial cusplets are absent from the juvenile but can be dectected on a few of the adults where they are indicated by short projections from the anterolabial corners of the cusp rows (a relatively large and discrete posterior labial cusplet is present on each first and second molar in *C. ruemmleri*).

Differences between our samples of *Brassomys albidens* and *Coccymys ruemmleri* in absolute size of measured external, cranial, and dental variables are evident from the univariate summaries listed in tables 3 and 4. Adult *B. albidens* have larger bodies but relatively shorter tails than do the samples of *C. ruemmleri* (table 3) and exceed the latter in dental measurements and all cranial dimensions except for zygomatic breadth, breadth and height of braincase, breadth of zygomatic plate, length of diastema, and length and breadth of incisive foramina in which measurements are about the same or less (table 4).

Proportional differences in cranial and dental measurements are portrayed in a ratio diagram (fig. 43), which was constructed from the measurements taken from the

holotype and 14 other adults of *Coccymys ruemmleri* from Lake Habbema (table 4), and three adults of *Brassomys albidens*: the holotype from Lake Habbema and two from Bele River, the only adults with intact skulls (table 4). Compared with the sample of *Coccymys ruemmleri*, the smaller series of *Brassomys albidens* is proportionally significantly narrower across the zygomatic arches and has a smaller braincase relative to occipitonasal length (length of skull). *Brassomys albidens* also has a significantly wider rostrum relative to its length, a much narrower zygomatic plate relative to most other cranial dimensions, shorter diastema relative to occipitonasal length and lengths of the palatal bridge and postpalatal region, shorter incisive foramina relative to occipitonasal length, narrower bony palate relative to its length, appreciably wider mesopterygoid fossa relative to breadth of bony palate, larger bullae relative to postpalatal and occipitonasal lengths, and larger molars (as indexed by length of maxillary molar row and breadth of first upper molar) relative to occipitonasal length. Some of these proportional contrasts are easily visualized in figures 9 and 10 where skulls of the two genera are compared. There the heavier rostrum of *Brassomys* is apparent, and its narrower zygomatic plate, larger bullae, wider mesopterygoid fossa, and heavier molars are clearly evident.

HABITAT: *Brassomys albidens* is still represented only by six modern specimens, each consisting of a stuffed museum skin and skull. All were collected by members of the 1938–1939 Archbold Expedition to New Guinea during August to November 1938, along the northern ramparts of the Snow Mountains in western New Guinea. The holotype is recorded from the Lake Habbema camp at 3225 m, and the other five are labeled as originating from the Bele River camp at 2800 m (9 km northeast of Lake Habbema; see the gazetteer for *Coccymys* and map in fig. 3). The landscape in the environs of Lake Habbema is a mosaic of subalpine forest, alpine grassland, and marsh. Descriptions of the environments there were summarized in our habitat account for *Coccymys ruemmleri* and described in lucid detail by Archbold et al. (1942) and
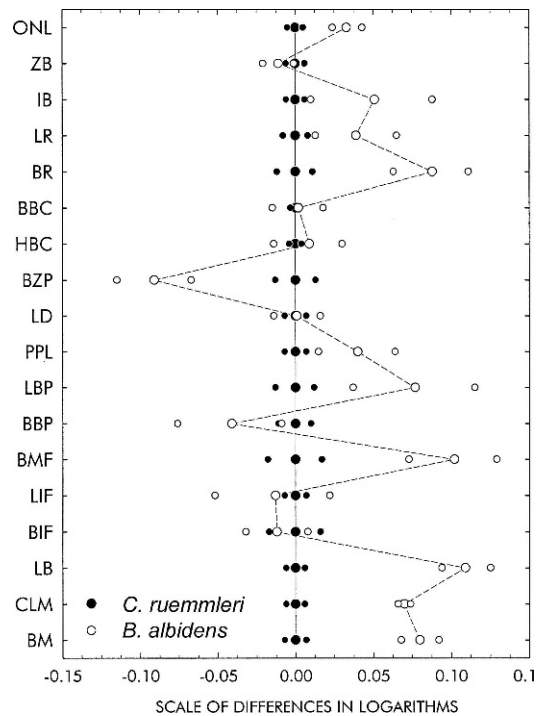

Fig. 43. Ratio diagram illustrating some proportional relationships in cranial and dental dimensions between samples of adult *Coccymys* and *Brassomys*. The standard is the sample of *C. ruemmleri* from Lake Habbema ($N = 15$; includes the holotype) contrasted with three specimens of *B. albidens* from Lake Habbema and 9 km northeast of Lake Habbema (150531; 150541; and 150821, the holotype of *albidens*). Data are derived from values for mean, standard deviation, and sample size of variables listed in tables 3 and 7. For each measurement, the absolute value of the mean, and plus or minus two standard errors of the mean, were converted to logarithms. Next, the logarithm of the mean of the standard was subtracted from the logarithms of the mean, and plus or minus two standard errors, of the comparative sample. Measurements larger than the standard are thus represented by positive values, those smaller by negative values. The lines connect sample means, and the bracketing symbols represent ± 2 SE of the mean. A sample having the same proportions as the standard will be represented by mean values on a line parallel to that of the standard regardless of absolute size. Also, if values for the sample being compared with the standard are similar in absolute size, they will be close together on the diagram. If proportions between any of the measured dimensions are similar, the positions of their points relative to each other on the horizontal scale will be similar.

Brass (1941). Here we summarize accounts of the environment at 2800 m and nearby where all but one of the six examples of *Brassomys albidens* were obtained.

Archbold and Brass (1941:265) described how the entire Bele River valley was insulated from the trade winds by high spurs: "There was therefore little air movement, and although mists frequently enveloped the more prominent local ridges and sometimes filled the little valleys, there was no very regular massing of clouds in the immediate camp locality." The camp was occupied "during a period of variable weather, with pleasant sunny mornings and showery afternoons, successions of overcast rainy days, and one dry spell in which no rain fell for four days." Between October 15 and November 9, the mean minimum ambient temperature was 7.0°C (range, 4.5°–10.0°), the mean maximum 17.5°C (range, 13.5°–21.5°).

This camp at 2800 m was erected, as described by Brass (1941: 312),

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 [fig. 44]. Although well up in the cloud belt, weather conditions were variable, and mists not very frequent or regular in occurrence in the immediate neighbourhood.

"Beech-forests continuous with those of the Bele Camp area [2200 m] and equally tall in the valleys clothed the slopes up to about 3,100 meters, where they met in a narrow ecotone subalpine coniferous forests dominated by *Podocarpus papuanus*" (Archbold et al., 1942: 263).

Brass (1941: 313) was impressed with the forests and their zonal components, particularly the magnificent beech (*Nothofagus*) zones:

The forest had many faces. In the usual splendid development, that clothed ridges and valleys alike, the dominants [mostly *Nothofagus*] grew to 35–40 m high and up to 1–1.5 m. in diameter above their spurred base, the tallest forest being found on the slopes [fig. 45]. On occasional flat seepage-wet benches in the valleys, the rather stunted forests carried a thick layer of green bryophytes on the ground and lower tree-trunks and held few of the usual ferns and orchids. On narrow ridges, especially above 2850 m., the stand degenerated into a typical open "mossy-forest" 15 m. or less in height, with a deep ground cover of brownish hepatics and matted surface roots, the trees themselves blanketed and cushioned with mosses and hepatics and hung with pendulant ferns and orchids to 5–8 m. of their length [figs 46, 47]. … In general, ground, trees and undergrowth were abundantly mossed down to 2600 m. or lower on the summits of spurs, and about 2700 m. in the valley bottoms.

All six specimens of *Brassomys albidens* lack any details indicating microhabitat, whether the rats were caught on the ground or above in the forest understory ("Brought in by Natives" is notated on the skin tag of AMNH 150923 from 2800 m). The five individuals from 2800 m were certainly caught in forest because beech and "mossy" formations dominated the landscape at the 2800-m camp. We suspect the holotype also came from the forested ridges around Lake Habbema, but no formal record corroborates that assumption.

BIOLOGY: No reproductive data are associated with any of the six specimens representing *B. albidens*, and direct evidence about diet, which could be gleaned from feeding captive animals or examining stomach contents, is unavailable. While reproductive information is impossible to extract from the dry, stuffed skins (five of the six specimens are male, the sixth is a juvenile female without any sign of teats on the skin—we don't know if the rat was correctly sexed in the field), we can infer diet drawing from morphology of the skull and dentition. We suspect that *B. albidens* is an invertebrate predator, based on architecture of the particular cranial, mandibular, and dental traits described below.

Rostrum: *Brassomys albidens* has a rectangular rostrum that is as deep near the incisors

Fig. 44. The Bele River camp, 2800 m, 9 km northeast of Lake Habbema on the northern slopes of the Snow Mountains. The camp "was in heavily forested country consisting of parallel spur ridges and very narrow valleys or ravines, rising rapidly toward the highlands but not particularly difficult to get about. A clearing about fifty meters long and twenty meters wide was hewn out of the forest on the edge of a planted *Pandanus* grove. There being very little level ground, most of the tents were set up on platforms of saplings" (Archbold et al., 1942: 263). The notation "2800 m" is on skin tags of five of the six known specimens of *Brassomys albidens*. October–November 1938.

as it is at the level of the nasolacrimal canals, and wide relative to its length, especially compared with the more usual murine configuration, such as that expressed by *Coccymys*, for example (figs. 9, 10). The relative size of this rectangular bony enclosure may reflect an increase in volume of the nasal cavity and greater expanse of nasal epithelium leading to enhanced olfactory acuity, an advantage in a wet, cool, and mossy microenvironment where the air is saturated with scents of wet moss and decaying vegetation. Most species of murine rodents that live in tropical montane forest and prey upon insects and earthworms (annelid worms) typically exhibit increased volume in the nasal cavity. Either the rostrum projects appreciably forward as a tube beyond the incisors, as in the Sulawesian *Sommeromys* (Musser and Durden, 2002); or the rostrum is elongate, whether a long and narrow tube between incisors and molar rows, the configuration in the Sulawesian species of *Melasmothrix* and *Tateomys* (Musser, 1982b), and Philippine *Rhynchomys* (Musser and Heaney, 1992; Balete et al., 2007); or the rostrum is less protracted than in those genera, but still relatively long and
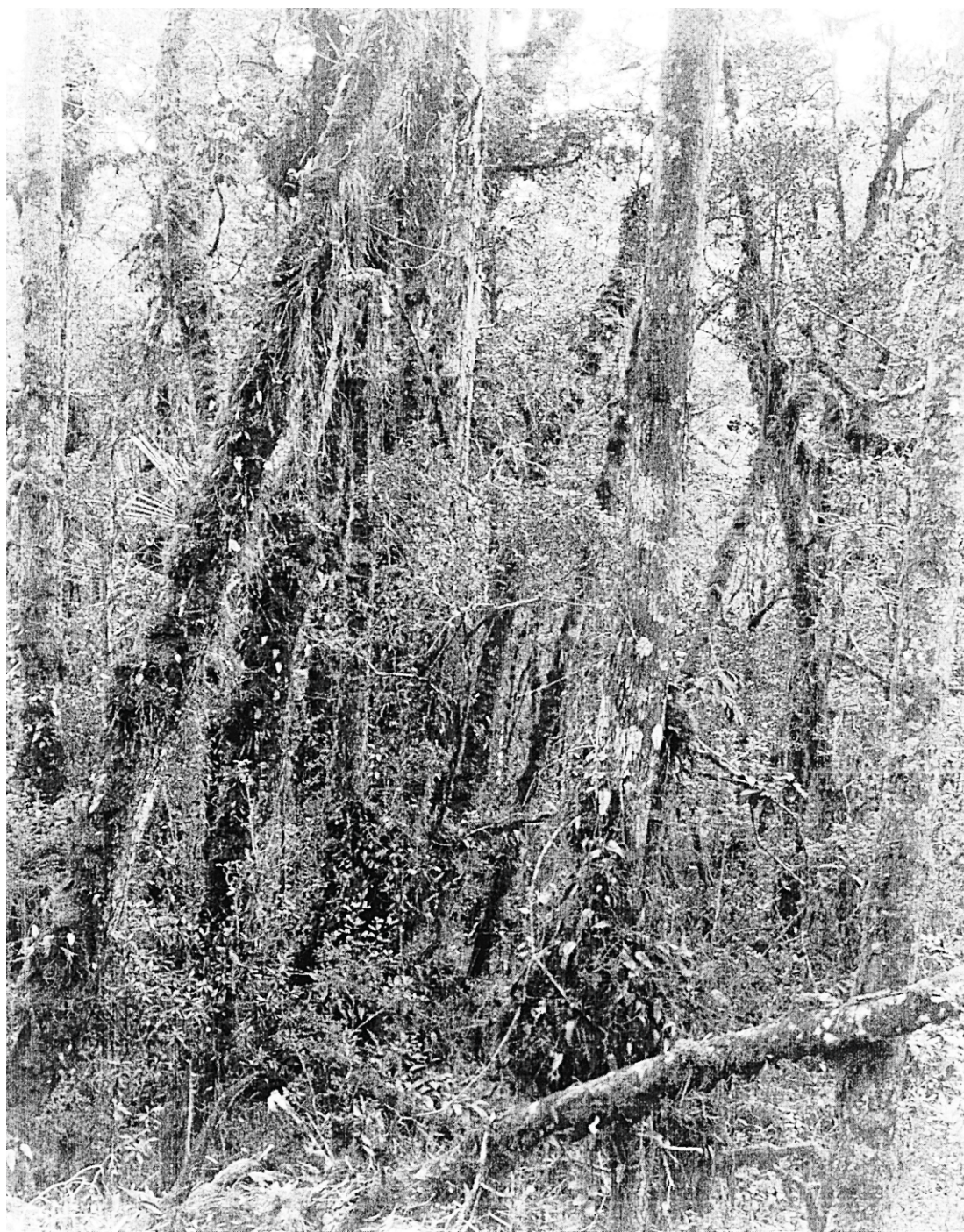
Fig. 45.   Interior of primary beech (*Nothofagus*) forest at the Bele River camp, 2800 m, 9 km northeast of Lake Habbema. October–November 1938.

Fig. 46.   Looking down into primary montane forest ("mossy forest") on a slope at 2960 m above the Bele River camp at 2800 m. "These stunted forests carried, in association with tangled wiry-stemmed orchids and a few ferns, a distinctive shrubbery undergrowth of chiefly small-leaved *Xanthomyrtus klossii, Rapanea* sp., and *Vaccinium debilescens*" (Archbold et al., 1942: 264). October–November 1938.
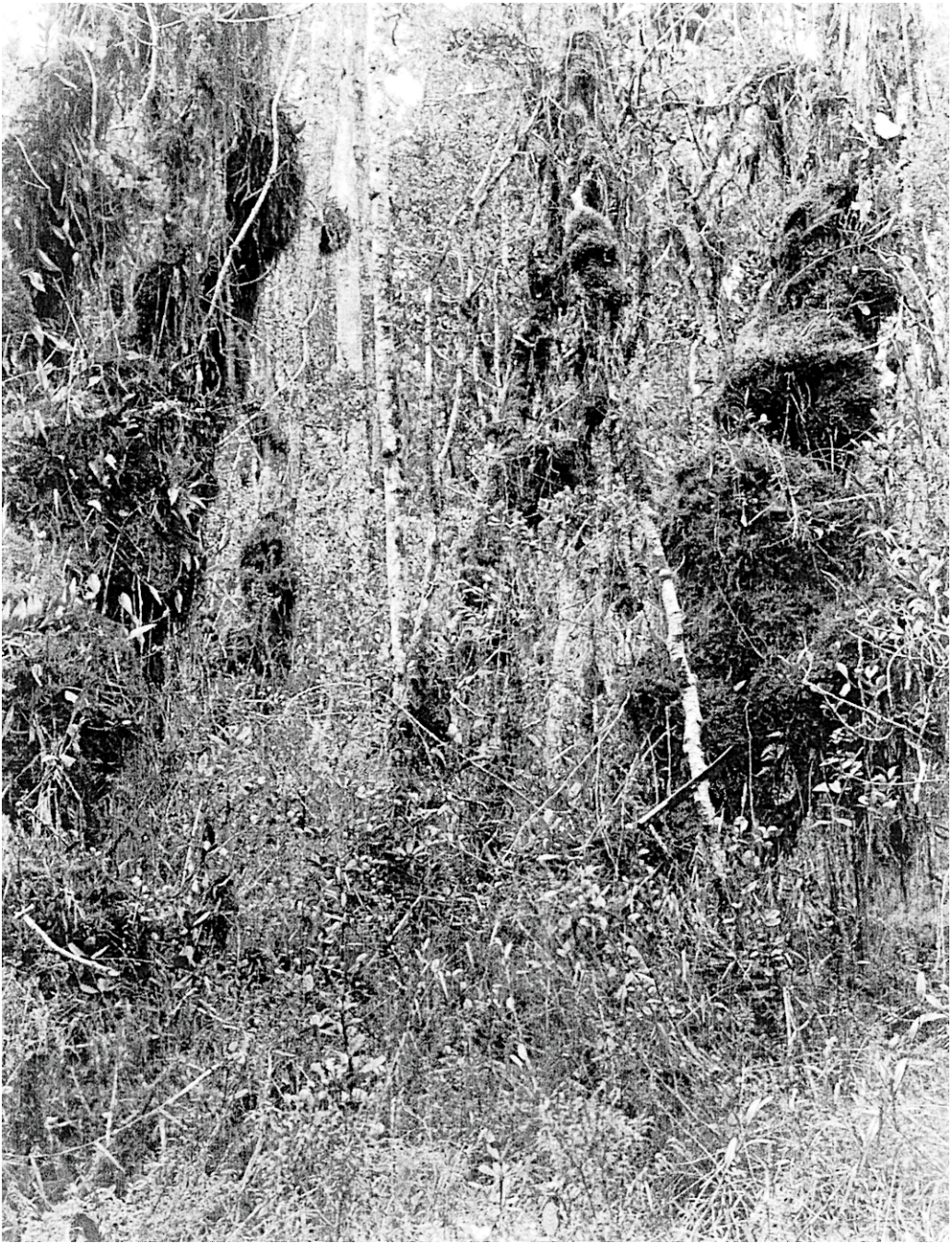
Fig. 47.   A view into the heart of heavily mossed open forest on a ridge at 3000 m above the Bele River camp at 2800 m. "A deep, springy ground cover of matted roots and brownish hepatics developed on the narrow crests of the more prominent spurs above camp level, where the forest was stunted to a height of fifteen meters or less, and open in character, and the trunks and main branches of the distorted, thick-stemmed trees were heavily blanketed and cushioned with both mosses and hepatics" (Archbold et al. 1942: 264). October–November 1938.

with the nasals and premaxillaries projecting moderately beyond the incisors, the pattern in the Philippine *Archboldomys*, for example (Musser, 1982b; Balete et al., 2006). Modifying the rostrum from the generalized slightly tapered shape seen in *Coccymys* to a rectangular box may be another solution for increasing nasal volume.

Zygomatic plate: *Brassomys albidens* has a very narrow zygomatic plate (both in absolute width and relative to size of the skull; see table 4 and fig. 43), its posterior border is directly over the first molar (the anterior third of that tooth), and the ventral zygomatic root bears a robust masseteric tubercle that projects ventrolaterally from the anteroventral edge of the plate (figs. 10, 41), the origin of the superficial masseter muscle. This combination is generally characteristic of tropical murines and Neotropical sigmodontines that feed primarily on invertebrates (some species also include small vertebrates in their diet). Among murines with a similar zygomatic architecture and knobby masseteric projection are the New Guinea hydromyins, species of *Hydromys, Parahydromys, Baiyankamys, Crossomys, Leptomys, Paraleptomys*, and *Pseudohydromys* (see cranial illustrations in Musser and Heaney, 1992: 88; Flannery, 1995: 523–526; Helgen, 2005: 7, 2007b; Flannery, 1995, summarizes diets, also see Musser et al., 2008, who provide dietary information for *Leptomys*); the Philippine *Archboldomys* (Musser, 1982b: 21; Musser and Heaney, 1992: 72; Rickart et al., 1998: 19; Balete et al., 2006; diet is documented by Rickart et al., 1991, Heaney et al., 1999, and Balete et al., 2006); *Melasmothrix naso* and species of *Tateomys*, endemics from Sulawesi (Musser, 1969: 16; Musser and Durden, 2002: 27; see Musser, 1982b, and Musser and Durden, 2007, for diet compositions); and the African *Colomys* (Dieterlen, 1983: 85–87), which preys on limnetic invertebrates and fish (Dieterlen and Statzner, 1981). Prime examples among Neotropical sigmodontines are the ichthyomyines, species of *Ichthyomys, Rheomys, Neusticomys, Anotomys,* and *Chibchanomys* (Voss, 1988, monographed the group and elaborated on diets). A narrow zygomatic plate and robust, projecting masseteric tubercle are common to all these muroids, but

position of the posterior border of the plate relative to the first upper molar varies among the genera, from just anterior to the molar, through the condition in *Brassomys albidens*, to the end of the upper molar.

Two genera of murine vermivores, the Philippine *Rhynchomys* and Sulawesian *Echiothrix*, both predators primarily of annelid worms (earthworms), are an exception to the genera summarized above. The species in each genus possess a relatively narrow zygomatic plate, but only a low, raised area or scoring on the bone identifies the anchor for the superficial masseter muscle, not a large bony projection. But little or no mastication is required by these rats to process their primary food. *Echiothrix* possesses a full complement of molars in each quadrant of the jaw, but they are very small relative to the large and robust skull (Musser, 1990). *Rhynchomys* lacks third molars and the remaining teeth are tiny—nearly vestigial—relative to the large, elongate skull (Musser and Heaney, 1992; Balete et al., 2007). Using only its incisors, *Echiothrix* cuts earthworms into sections, which are swallowed intact (Musser, 1990, and field observations); similar pieces of earthworms have been found in stomachs of *Rhynchomys* (Heaney et al., 1999; Balete et al., 2007).

Tropical Indo-Australian murines that are either primarily herbivorous or include fruit and insects in their diets exhibit a wider zygomatic plate relative to skull size and only a rugose spot or small bump (no large, knobby projecting tubercle) at the base of the ventral zygomatic root for insertion of the superficial masseter muscle (our observations). Descriptions of the zygomatic conformation in the three species of *Coccymys* are examples. Other New Guinea examples can be appreciated by viewing illustrations of skulls in Flannery (1995) of *Hyomys* (see also the figure in Musser, 1981b: 151), *Uromys, Mallomys* (see Musser, 1981b: 79), *Xenuromys,* some *Chiruromys* and *Pogonomys, Melomys, Paramelomys, Pogonomelomys, Abeomelomys*, and some *Rattus*; species in these genera, at least those with dietary information, are entirely or primarily herbivorous (see summaries in Flannery, 1995). Species of *Tarsomys, Limnomys, Batomys, Crateromys, Phloeomys,* and some *Apomys*

are Philippine endemics that are entirely herbivorous or consume fruit and invertebrates (see cranial illustrations in Musser and Heaney, 1992; dietary information is recorded by Rickart et al., 1991, 2003; Gonzales and Kennedy, 1996; Heaney et al., 1999, 2006). Endemic Sulawesian herbivores are *Lenomys meyeri* and *Eropeplus canus* (see cranial illustrations in Musser, 1981b); fruit and seeds are preferred by *Haeromys minahasae* (Musser, 1990, figured the skull); and a mixed diet of fruit and invertebrates is common to the three species of *Margaretamys* (skulls are illustrated in Musser, 1982a), along with *Bunomys chrysocomus* and *Maxomys hellwaldii* (see cranial renditions in Musser, 1991); dietary information comes from Musser's feeding in the field and survey of stomach contents. This array of species, in addition to possessing a less specialized zygomatic configuration, also lacks the specializations of the rostrum, incisors, cusp patterns of molars, and dentary configuration seen in the specialized murines described just above and in the paragraphs below.

Incisors: The conformation of the incisors in *B. albidens* suggests an invertebrate diet. The uppers are short and thin (relative to skull size) and emerge from the rostrum at a right angle. The enamel is unpigmented and wraps around the side to cover up to half of the labial surface of each incisor, and their tips form a gently convex cutting edge. Lower incisors are also relatively short and thin, with unpigmented enamel that covers a comparable extent of labial surface, and the tips are awl-shaped. They emerge from the dentary at a low angle. The positions of the upper and lower incisors relative to the rostrum and dentaries in *B. albidens*, along with unpigmented or pale incisor enamel (white to cream and pale yellow is the usual range seen in other species) that extends laterally to cover at least half of the labial surface, and a convex incisor cutting edge (whether gently convex as in *B. albidens*, convex, or markedly so as seen in *Melasmothrix* and *Chrotomys*) is common to the Sulawesian shrew rats *Melasmothrix* and *Tateomys*. *Melasmothrix naso* preys on earthworms and dipteran larvae; the two species of *Tateomys* are earthworm predators (Musser, 1982b). The Philippine *Chrotomys*

displays the extreme configuration in which the enamel covers nearly all the labial surface of the upper and lower incisors (Musser and Heaney, 1992). *Chrotomys* has an elongate rostrum and upper incisors that are procumbent with a marked convex cutting edge; invertebrates comprise the diet of those species of *Chrotomys* for which this information is available (Rickart et al., 1991; Heaney et al., 1999).

Molars: Configuration of the occlusal surfaces on the upper molars may provide supporting evidence for an invertebrate diet. The labial and lingual arms of the chevrons forming the chewing surfaces are connected at their outer margins either by their edges fusing or by a high enamel ridge. The arms of the chevrons in the first and second rows on the first molar, and the first complete row on the second tooth are transformed through wear into chevron-shaped basins bounded by labial and lingual walls; even cusp t1 on the second molar is basined. This wear pattern is not as evident in the juvenile specimen, but is already developed in very young adults (fig. 11). In our experience, basined chewing surfaces, no matter what shape the cusp row takes, are associated with diets composed primarily of invertebrates and small vertebrates. Examples are found in New Guinea hydromyins (Jackson and Woolley, 1993; Flannery, 1995; Musser et al., 2008), Sulawesi *Melasmothrix* and *Tateomys* (Musser, 1982b), Philippine *Archboldomys* and *Chrotomys* (Rickart et al., 1991; Heaney et al., 1999; Balete et al., 2006), African *Colomys* (Dieterlen, 1983; Dieterlen and Statzner, 1981), and Neotropical ichthyomyines (Voss, 1988).

Dentary: The shape of the dentary in *B. albidens* is another indicator of a specialized diet (figs. 10, 42). The ramus between molar row and the base of the incisor is tubular, and the curve made by the ramus and incisor is gently convex, not more than about 30° from the horizontal plane. The rest of the dentary is low and elongate. The overall form of the dentary and incisor resembles, but is not as extremely elongated as, the shapes of dentaries in the Sulawesian shrew rats (Musser, 1982b) and the Philippine invertebrate predators (Musser, 1982b; Musser and Heaney, 1992; Balete et al., 2006, 2007).

General conclusions: We look at *Brassomys albidens* as a nocturnal, likely arboreal, invertebrate predator. Length of the tail, which is appreciably longer than the head and body (tables 3, 7, 20), and configurations of the digits and hind feet in *B. albidens*, along with sharp and recurved claws, are consistent with arboreal activity. A wide and short hind foot relative to body size is characteristic of rats that nest and forage in the forest canopy, or nest on or below the ground but forage in trees. For example, the ratio of hind foot to head and body lengths ranges from 19% to 23% in samples of the endemic New Guinea genera of *Chiruromys* and *Pogonomelomys*, from 20% to 24% in the three arboreal species of Sulawesian *Margaretamys*, and from 17% to 18% in species of the New Guinea genus *Pogonomys* (percentages were computed from mean values of adults listed in Musser, 1981a and Flannery, 1995). The proportional range in *B. albidens* is 21% to 24% (computed from values listed in table 20). By contrast, the combined range in our population samples of *C. ruemmleri*, *C. shawmayeri*, and *C. kirrhos*, which have narrow and long hind feet relative to body size and are likely scansorial rather than arboreal, is 24% to 30% (computed from means in table 3). The range is 29% to 30% in the scansorial *Lorentzimys nouhuysi*, which nests above ground in forest understory and on the ground among rocks (Flannery, 1995). We view a scansorial species as one that forages over the ground (partly terrestrial) and climbs into shrubs, tangles of woody vines, small trees, *Pandanus* crowns, and lower branches of larger trees within the forest understory (partly arboreal); nests may be anywhere in that vertical range, as is apparently characteristic of *L. nouhuysi*. The tail is longer than the head and body in all the species in these genera, whether arboreal or scansorial (Musser, 1981a; Flannery, 1995).

Brassomys albidens certainly seems capable of moving about in the forest canopy, but also in the understory and on the ground. Whether it is wholly arboreal, nesting and foraging in the canopy (our perception of complete arboreality), which describes the behavior of *Chiruromys* and *Pogonomelomys* (Flannery, 1995) as well as the species of *Margaretamys* (Musser's field observations),

or nests in ground burrows but forages in the canopy, which is typical of species of *Pogonomys* (Flannery, 1995) and members of the Sulawesian *Rattus xanthurus* group (Musser's field observations), is of course unknown.

We lack data regarding foraging activities for *B. albidens*, but again can speculate drawn from its external traits and a cranial character. The large external pinnae and inflated ectotympanic bullae possessed by *B. albidens* likely provide sharp auditory acuity, which would certainly aid in detecting nocturnal predators, especially owls, but might also be used to listen for invertebrates moving through wet moss, beneath cracked bark on tree limbs, trunks, and woody vines, and in decaying leaf litter, whether on the ground, in the tops of *Pandanus*, or in epiphytes and ferns in the crowns of trees. Such foraging activities would also be facilitated by sharp olfaction, possibly a function of the expansive nasal cavity in the rectangular rostrum.

We are certain that *B. albidens* is nocturnal. In our experience, its pelage coloration, body form, and arboreality (if we are correct) are associated with rats that are active during the night rather than during daylight hours, at least in the Asian tropics. The species of Sulawesian *Melasmothrix* and Philippine *Archboldomys* are good examples of tropical diurnal rats. These are small-bodied murines in which the tail is shorter than length of head and body or coequal, and upperparts are dark chestnut, and underparts are chromatically similar or slightly paler; all are primarly diurnal (Musser, 1982b; Heaney et al., 1999). Within the Indo-Australian tropical murine fauna, we don't know of any arboreal or scansorial murine that is not nocturnal.

Another aspect regarding population biology of *B. albidens* is its relative abundance in the wild. Whether the few documented specimens of this unusual murine actually represent its rarity in the montane forests of the Central Cordillera, or reflect an artifact of collecting techniques is unknown. We suspect the latter. Small-bodied nocturnal, arboreal rats that are invertebrate specialists are notoriously difficult to trap or snare, and may partly explain the few specimens en-

countered during the 1938–1939 Archbold Expedition.

If our ecological description of *B. albidens* is close to reality, it would be, within the endemic murine fauna of New Guinea, the only known arboreal invertebrate specialist. All the hydromyins for which diet has been determined—species of *Hydromys, Parahydromys, Baiyankamys, Crossomys, Leptomys, Paraleptomys*, and *Pseudohydromys*—are terrestrial or amphibious, and carnivorous or primarily invertebrate specialists (Flannery, 1995; Helgen, 2005b; Musser et al., 2008). Species in the other New Guinea endemic genera for which dietary data are available, whether terrestrial, arboreal, or scansorial, are either obligate herbivores (forbs, leaves, and grasses), primarily fruit and seed consumers with invertebrates constituting only a portion of their diets (see summaries in Flannery, 1995), or fungal consumers such as *Protochromys fellowsi* (see following section).

Hopefully, future mammalogical surveys in wet, mossy montane forests of the Central Cordillera in western New Guinea may encounter *Brassomys* and provide information either bolstering or modifying our hypothesis about arboreality and diet that we propose here based on the six known modern specimens represented by stuffed museum skins and accompanying skulls.

SYMPATRIC ASSOCIATIONS: The six examples of *B. albidens* were collected during the 1938–1939 Archbold Expedition to the Snow Mountains. Base camp was at Hollandia (today the city of Jayapura) on the coast. Although most of the time there was devoted to construction and organization of the camp, some mammals were collected in the vicinity of Hollandia, in the foothills of the adjacent Cyclops Mountains, and near Sentani Lake. The major thrust of the Expedition, however, as summarized by Archbold et al. (1942: 201–102), was to survey

the north slope of the Snow Mountains. … Between the fairly well-known Weyland Mountains to the west and the mountains about the headwaters of the Sepik to the east, the north slope of the central range was practically unknown biologically and very little in any way. … It was the central part of this unknown area, between Mt. Wilhelmina and the Idenburg

River, that the expedition studied. This included collections from camps from near sea level to near the upper limit of vegetation. Specialists in mammals, birds, insects and plants spent on the average about a month at each camp.

Between June 1938 and April 1939, 11 camps had been established between the Idenburg River (Bernard camp, 50 m) and the flanks of Mt. Wilhelmina (camp 11, 3800 m). Their locations and elevations are indicated in figure 48, which is a reproduction of the original map of the area published in the expedition summary (Archbold et al., 1942).

Collection activities along the transect resulted in the most complete inventory of New Guinea mammals made at that time, and is significant to framing the faunal context for *B. albidens*. About 2484 mammals representing 79 indigenous species of echidna, bats, marsupials, and rodents were obtained between the Idenburg River and Mt. Wilhelmina. The number of specimens of each species collected at the different altitudes is summarized in figure 49.

Collections of mammals were also made in the vicinity of coastal Hollandia, adjacent foothills of the Cyclops Mountains, and nearby Lake Sentani. We excluded these specimens from the transect but listed them in a separate table (table 22). Hollandia and the other two northern coastal collection localities are separated from the wide lowland valley of the Idenburg River by "a broad tract of low mountain country, completely forested," which attains "a fairly even elevation of perhaps 800 to 1,000 meters and lay in closely parallel ridges trending east-southeast and west-northwest" (Archbold et al., 1942: 207). The northern foothills of the Snow Mountains actually begin on the southern margins of the Idenburg River valley where the mountains rise "abruptly from the plains" (Archbold et al., 1942: 234). Most of the species collected near or at Hollandia, in the foothills of the Cyclops Mountains, and near Lake Sentani were also obtained in the vicinity of Bernhard camp and the 850-meter camp, and are members of the Membrano River basin lowland fauna in the northern lowlands of New Guinea (Helgen, 2007c).
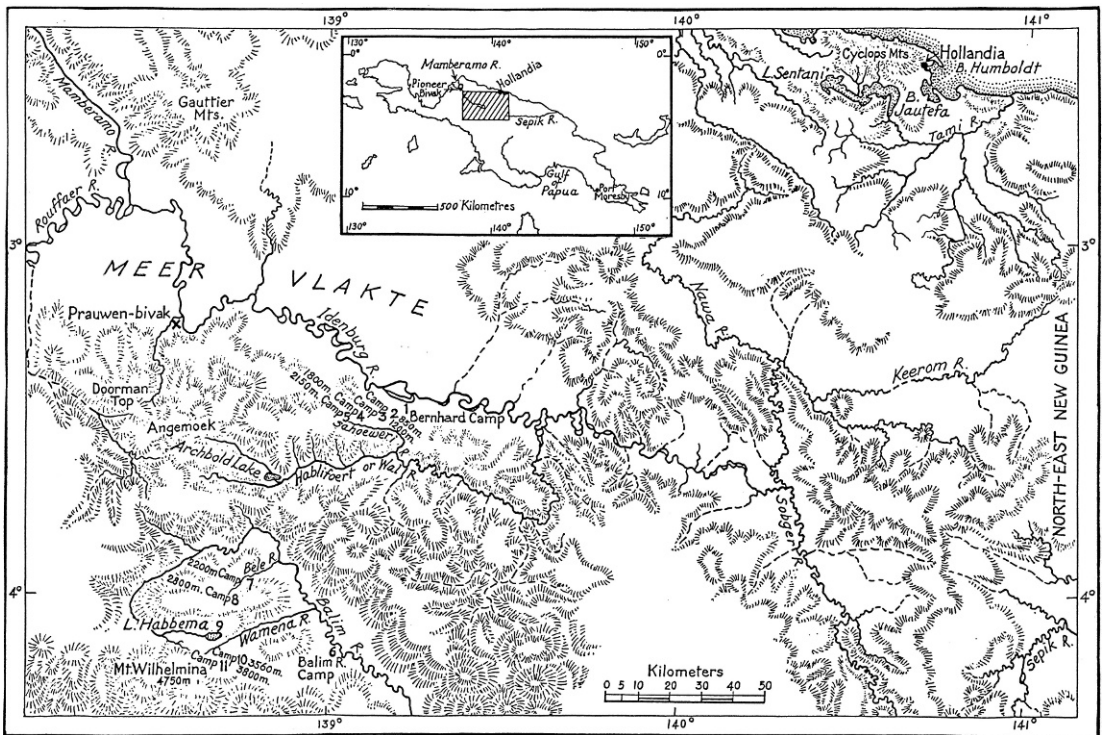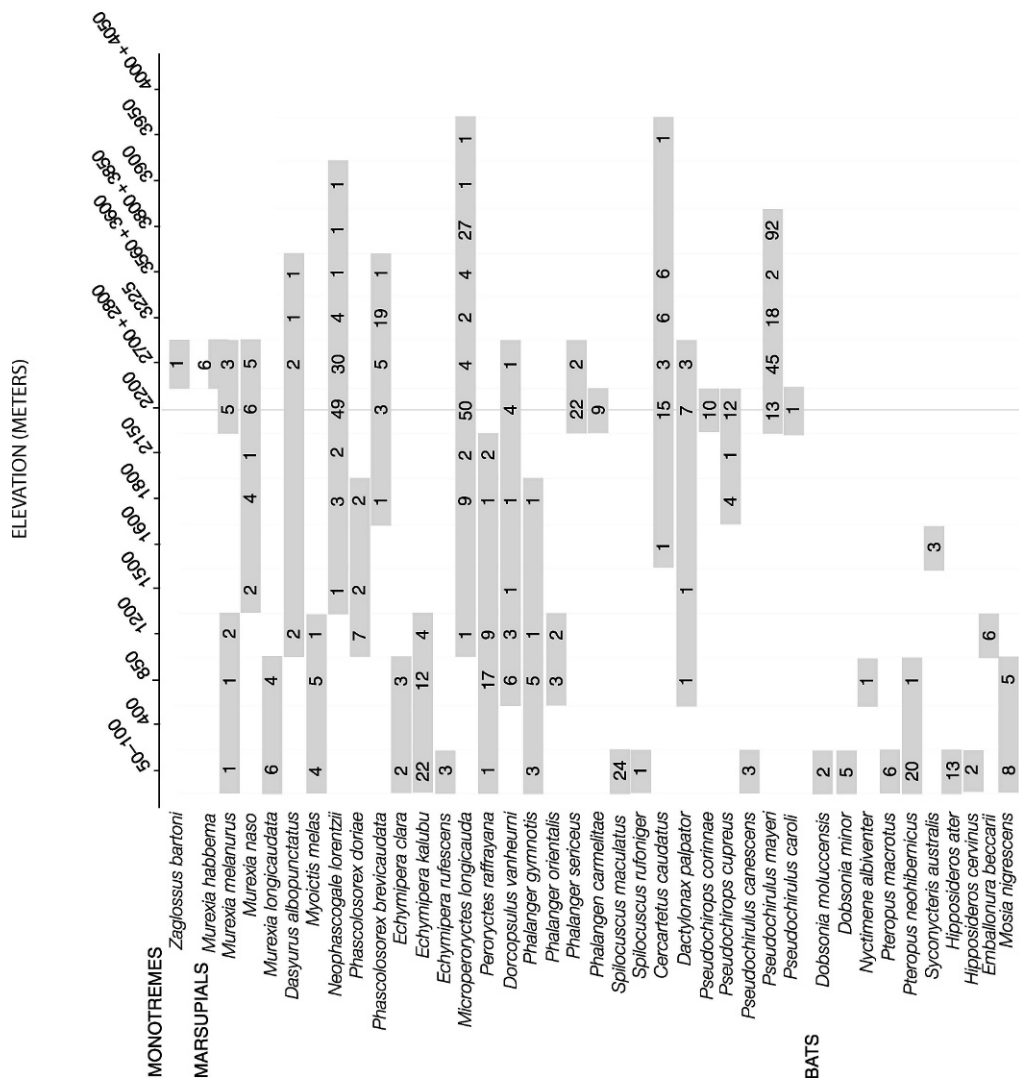
Fig. 48.   Reproduction of a map covering region of the Snow Mountains worked by the 1938–1939 Archbold Expedition (originally published in Archbold et al., 1942). Collection records extend from the valley of the Idenburg River at 50 m to the flanks of Mt. Wilhelmina (Gunung Trikora) at 4050 m. Eleven camps were established by expedition members throughout this interval; the physical settings of the camps along with their floristic environments are described by Archbold et al. (1942) and Brass (1941): **1,** Bernhard camp, 50 m, collections were made between 50 and 100 m and at 400 m, June 1938 to April 1939; **2,** 850-m camp, 4 km southwest of Bernard camp, March–April 1939; **3,** 1200-m camp, 6 km southwest of Bernard camp, February–March 1939 (Sigi Subsidiary camp, 1500 m; February 1939); **4,** 1800-m camp, 15 km southwest of Bernhard camp, January–February 1939; **5,** 2150-m camp, 18 km southwest of Bernhard camp, January–February 1939; **6,** Baliem River camp, 1600 m, December 1938; **7,** 2200-m camp, Bele River camp, 18 km northeast of Lake Habbema, November–December, 1938; **8,** 2800-m camp, 9 km northeast of Lake Habbema, October-November, 1938; **9,** Lake Habbema camp, 3235 m, July–September, 1938; **10,** 3560-m camp, 7 km northeast of Wilhelmina peak, August–September, 1938; **11,** 3800-m camp, 2 km east of Wilhelmina peak; collecting was done between 3800 m and 4050 m, September, 1938. The holotype of *Coccymys ruemmleri* is from camp 9 at 3225 m. Other examples of *C. ruemmleri* are recorded from along the transect extending from camp 7 to camp 11, 2200 m to 4050 m (see gazetteer and fig. 49). The holotype of *Brassomys albidens* was also captured at camp 9, and the other five examples are from camp 8.

We obtained the numbers for each species by counting the specimens stored in cases in the Department of Mammalogy. We either identified or verified determinations by other researchers of all the specimens and generally followed current taxonomy—published or reviews being prepared for publication (see Helgen, 2007c and references cited there) except for the following taxa. We use the marsupial genus *Murexia* for the species *habbema, melanurus,* and *naso* following Krajewski et al. (2007) rather than the genera employed by Van Dyck (2002) for these species. Two rodents indicated as "sp." in the chart are distinct species, one in *Paraleptomys*, the other in *Pogonomys*, and will be described in a coming revision of *Paraleptomys* (Helgen et al., in prep.) and a system-

Fig. 49. Altitudinal distribution of 2484 specimens representing 79 species of mammals obtained on the north slopes of the Snow Mountains during the 1938–1939 Archbold Expedition to western New Guinea. See figure 48 and text.

atic review of small-bodied, montane species of *Pogonomys* (Musser and Lunde, MS). Helgen identified the specimens of *Uromys nero* and *U.* "*caudimaculatus*" (usually lumped together as *U. caudimaculatus*), which will be supported in his forthcoming systematic revision of the genus.

Future systematic revision of particular groups will change the views of certain species listed in figure 49. Helgen (2007c), for example, provisionally recognizes *Murexia wilhelmina* as a distinct species rather than just a population of *M. melanurus* (we treat the two as the same). Helgen (2007c) also notes the existence of an undescribed species of *Microperoryctes* in the Snow Mountains, and that particular taxon, plus others now listed as species in the literature— the marsupials, *Phalanger gymnotis* and *Spilocuscus maculatus*, the rodents, *Paramelomys platyops, Paramelomys rubex*, and *Pogonomelomys mayeri*, and the bat *Nyctimene albiventer*—is each likely a complex of species.

We omitted dogs and feral pigs, along with the introduced murines, *Rattus exulans* and *R. rattus* from our list of species. Specimens of *R. exulans* were obtained at Hollandia (Taylor et al., 1982: 327) but not inland at camps along the transect. This species "is presumably native to southeast Asia, and there is no doubt that it was introduced into much of its present range along with human exploration in prehistoric times" (Taylor et al., 1982: 276). One example of *R. rattus* comes from the Bele River camp at 2200 m (Taylor et al. 1982: 330). "*Rattus rattus* has followed human European settlement of New Guinea and adjacent islands and has established itself in almost every lowland European colonization" (Taylor et al., 1982: 284).

The chart provides an altitudinal picture of the mammal fauna, however incomplete, of which *Brassomys albidens* is a part, along the northern slopes of the Snow Mountains. During the survey, one species of monotreme (*Zaglossus*), one species of bat, 12 species of marsupials, and 18 species of rodents are recorded from either 2800 m or 3225 m, or both—the altitudes from which *B. albidens* were collected. A few of these species do not occur in forest (*Rattus richardsoni*, for example, inhabits alpine tussock grassland)

but most are forest inhabitants. The lack of precise microhabitat information about where specimens were trapped, and the uncertainties tied to altitudes for the material brought in by natives (see habitat account for *Coccymys ruemmleri*) likely contribute to inaccuracies. Results of the survey also underestimate the actual number of species occurring in the habitats between the lowlands and 4050 m, particulary for bats and for nonvolant species that are usually difficult to collect, such as those moss mice (*Pseudohydromys*).

Within a zoogeographical context, *Brassomys albidens* is part of a cluster of murines so far known only from the montane forests and alpine grasslands of the Snow Mountains that includes the following: the marsupials *Murexia habbema*, an undescribed species of *Microperoryctes* (Helgen, 2007c), and *Dendrolagus mbaiso*; and the murine rodents *Coccymys ruemmleri*, *Mallomys gunung*, *Baiyankamys habbema*, *Pseudohydromys occidentalis* and an undescribed species in that genus (Helgen, 2007a, 2007b), an undescribed species of *Pogonomys* (Musser and Lunde, MS), *Paraleptomys wilhelmina* and an undescribed species of *Paraleptomys* (Helgen et al., in prep.), *Melomys frigicola*, *Rattus richardsoni*, and *Rattus arrogans.*

FOSSIL SAMPLES: *Brassomys albidens* is represented by two right dentary fragments and one left (from three individuals) extracted from primary matrix and lag deposits (mostly mud and fossil bone) collected in Kelangurr Cave, 2950 m, situated in a valley confluent with the valley of the West Baliem River and not far (8 km west) from the settlement of Kwiyawagi, which is 60 km or so west of Lake Habbema on the southern slopes of the Snow Mountains (Flannery, 1999; Hope and Apline, 2007: 251, provide a photograph of the cave). The matrix and lag sediments were obtained from the walls and floor of the first chamber in the cave (chamber 1). The deposits yielded pieces of eight kinds of marsupials, one microchiropteran, and seven species of rodents (Flannery, 1999: 342). Although a few of the species were represented by material thought to be Recent, the bulk of the specimens extracted from the deposit were heavily mineralized, and two dating techniques indicated that the

TABLE 22
The 432 Specimens Representing 35 Species of Native Mammals Obtained on the North Coast during the 1938–1939 Archbold Expedition to Western New Guinea[a]

Mammals were collected in the vicinity of Hollandia (Jayapura; 02°32′S, 140°43′E), the nearby Sentani Lake region (02°37′S, 140°31′E), and foothills of the Cyclops Mountains (Gunung Cycloop; 02°31′S, 140°38′E).

Species (* denotes species also collected inland near base of the Snow Mountains at Bernard Camp, Idenburg River; see fig. 48)[b]	Hollandia, 3–125 m	Sentani Lake and 1.5 km S Ajapo, 200 m	Cyclops Mountains, 150–300 m
Marsupials			
*Echymipera clara**	10	3	—
*Echymipera kalubu**	1	—	9
*Echymipera rufescens**	—	1	1
*Peroryctes raffrayana**	—	1	—
Dendrolagus inustus	4	—	—
Dorcopsis hageni	37	—	1
Thylogale brunii	1	—	1
*Phalanger gymnotis**	1	—	4
*Phalanger orientalis**	6	3	2
*Spilocuscus maculatus**	16	—	6
Dactylopsila trivirgata	1	—	—
Petaurus breviceps	1	1	1
Pseudochirops albertisii	—	—	1
*Pseudochirulus canescens**	1	—	—
Bats			
*Dobsonia moluccensis**	30	—	5
Nyctimene aello	—	—	2
*Pteropus neohibernicus**	4	1	2
Rousettus amplexicaudatus	—	—	1
Aselliscus tricuspidatus	55	—	—
Hipposideros calcaratus	5	—	—
*Hipposideros cervinus**	22	—	—
Hipposideros maggietaylorae	2	—	—
Rhinolophus euryotis	3	—	—
*Emballonura beccarii**	1	—	—
*Mosia nigrescens**	1	—	—
*Miniopterus australis**	24	1	—
Miniopterus tristis	—	3	—
Myotis moluccarum	10	109	—
*Pipistrellus papuanus**	1	—	—
Rodents			
*Hydromys chrysogaster**	1	—	—
Melomys leucogaster	4	—	—
*Melomys rufescens**	4	—	2
*Paramelomys platyops**	12	—	—
Pogonomys macrourus	3	—	1
*Rattus praetor**	7	1	2

[a]The landscapes in the coastal region, where expedition members worked, are described by Archbold et al. (1942: 227–231).

The scientific names listed in the table reflect currently accepted taxonomy (see Helgen, 2007c). One difference between Helgen's (2007c: 706) list of families of insectivorous bats and our table is our use of *Miniopterus tristis*. Helgen (p. 707) recognizes this species as *M. propitristis* but Simmons (2005: 522) treated *propitristis* as a subspecies of *M. tristis*, influenced primarily by Hill (1983).

Two species collected by the expedition are omitted from the table. Twenty-three specimens of the non-native *Rattus exulans* were collected at Hollandia. Two *Dugong gugon* were obtained (the only native mammal recorded from below sea level).

[b]Mammal species collected in the vicinity of Bernard camp (50 m), at the base of the Snow Mountains, and in the northern coastal Hollandia–Sentani Lakes–Cyclops Mountains localities are components of the Membrano River basin lowland fauna in the northern lowlands of New Guinea (Helgen, 2007c).

TABLE 23
Measurements of Lower (Mandibular) Molars and Alveolar Lengths in Samples from the Snow Mountains of Modern and Fossil (Late Pleistocene) *Brassomys albidens*[a]

Specimen	clm1–3	alm1–3	bm1	bm2	bm3
Modern					
150607	5.44	5.12	1.41	1.46	1.14
150541	—	5.00	—	—	—
150531	5.28	4.98	1.38	1.48	1.11
150821	5.46	5.09	1.35	1.45	1.12
150923	5.50	5.20	1.50	1.60	1.20
150618	5.30	5.17	1.29	1.37	1.11
Fossil					
134126	—	5.30	1.40	—	—
134096	—	5.00	—	—	—
134074	—	5.10	—	—	—

[a]The modern sample (AMNH) is from Lake Habbema (3225 m) and Bele River (2800 m); the holotype is included. All fossils (AMF) are from Kelangurr Cave (2950 m). We measured dimensions of molars and alveolar length in either right or left dentaries in both modern and fossil specimens.

deposit in chamber 1 was accumulated between 25,000 and 20,000 B.P. (Late Pleistocene).

All three fossils consist of the anterior portion of the ramus beneath the toothrow. In one of these, the incisor is broken off and a relatively unworn first molar is present; the other two retain intact incisors, complete alveolar sections, but no molars (table 23). The pieces are densely mineralized and the enamel covering the incisor dentine is dark gray, a discoloration from the white typical of modern specimens. The shape of the ramus fragment, conformation of the incisor and extent of its enamel covering, alveolar length of the molar row, and size plus occlusal pattern of the first molar match these traits in dentaries from the modern material collected at Lake Habbema and the Bele River valley.

When Flannery visited Kelangurr Cave in 1994, the area was covered with "high upper montane forest," but Flannery (1999: 349) noted that a "number of lines of evidence suggests that the fossil deposit preserved in Chamber 1 of Kelangurr Cave accumulated at a time [25,000–20,000 B.P.] when the surrounding area was vegetated with tussock grassland and some alpine scrub. Forest was almost certainly absent, as the remains of obligate forest dwelling mammals are almost entirely absent from the deposit." But the information we have presented in the preceding section strongly points to *B. albidens* as an obligate forest dweller. Possibly the landscape then was a mosaic of forest and tussock grassland, similar to the environment around Lake Habbema (3225 m). Another possibility is that the rats now represented by fossils were taken at lower altitudes in forest and carried by owls to the roost at the cave. Flannery purports that the accumulation of small mammal fossils in the cave sediments is the result of owl predation, whether by an extinct Pleistocene species or a Pleistocene population of the modern sooty owl (*Tyto tenebricosa*). The features of the three *B. albidens* and 63 *Coccymys ruemmleri* (see that account) from Kelangurr Cave we studied certainly resemble those of the dentary fragments extracted from modern owl pellets collected on Mt. Wilhelm that were regurgitated by a sooty owl (see the account of *C. ruemmleri*).

The three fossils document the presence of *Brassomys albidens* in the Late Pleistocene, indicate it was likely one of the prey items sought by owls, and acknowledge its membership in a montane fauna mirroring the species composition of the modern assemblage of small mammals now living in landscapes of forest and tussock grassland on the northern slopes of the Snow Mountains (see fig. 49, and Flannery, 1999).

GENERIC COMPARISONS AND OTHER OBSERVATIONS

Our discussion here derives largely from comparing the specimens of *Brassomys albidens* and examples of *Coccymys ruemmleri* (our comparative example of the species) with the large collection of endemic New Guinea murines stored at the American Museum of Natural History, focusing on samples of *Melomys, Paramelomys, Mammelomys, Protochromys, Abeomelomys*, and *Pogonomelomys.* All comparisons made are among adults.

The species *albidens* was originally described as a member of *Melomys* (Tate, 1951) but the range in anatomical variation and geographic distributions once thought to characterize that genus (Rümmler, 1938; Ellerman, 1949; Tate, 1951) has been drastically altered and is now partitioned among four monophyletic clusters, each of generic rank: *Melomys*, *Paramelomys, Mammelomys*, and *Protochromys* (Menzies, 1996; Musser and Carleton, 2005). Furthermore, *Mammelomys* is not even closely related to *Melomys* and its allies, as affirmed by morphological (Menzies, 1996; Musser and Carleton, 2005) and molecular (Rowe et al., 2008) data. This new and more accurate view does not negate the exclusion of *albidens* from the altered definition of *Melomys*, or from any of the other three genera. The combination of slightly overlapping rings of small and flat tail scales, three hairs associated with each scale, no dorsal strip near the tail tip that is devoid of hair and scales; deep and smooth braincase reflecting some cranial flexion; rectangular-shaped rostrum; very narrow zygomatic plate in which the anterior margin does not project forward past the maxillary zygomatic root, the posterior border sitting over the first molar, and the anterolabial surface bearing a projecting knoblike masseteric tubercle; large and inflated ectotympanic (auditory) bulla; generalized (for murine rodents) carotid circulatory pattern; white incisor enamel and its extent over the labial surface; small size of incisors relative to size of skull and mandible; parallel molar rows, fusion of rows along labial and lingual margins on first and second upper molars; and an elongate dentary place *albidens*

outside the range bracketed by the anatomical variation defining the generic boundaries of *Melomys, Paramelomys,* and *Mammelomys.*

Protochromys is based on *fellowsi*, which was named and described by Hinton (1943). Of medium body size and long-tailed, with dense, soft and woolly fur, and buffy gray underparts, *P. fellowsi* inhabits high montane forests at 2400–2500 m where it has been recorded from only a few places in the Central Cordillera of Papua New Guinea, primarily in the Hagen and Bismarck ranges (Flannery, 1995: 292, as *Melomys fellowsi*). When he described *Melomys albidens*, Tate (1951: 286) had suspected a close relationship between it and Hinton's *Melomys fellowsi*, because the latter was also characterized by white incisors and large bullae. Tate had borrowed two specimens of *fellowsi* (Archbold Expeditions would later acquire a large sample from Mt. Wilhelm) from the British Museum for comparison with his material. After summarizing morphological differences between the two species, which emphasized that the auditory bullae of *albidens* were even relatively larger than those in *fellowsi,* Tate wrote that "One can only conclude that these two species are not only thoroughly distinct from each other but also from any member of the three large groups of *Melomys* that form the principal part of the genus." Hinton's *fellowsi* has white or cream incisor enamel, a narrow zygomatic plate, and relatively large auditory bullae, which are among the traits used by Menzies (1996: 416) in diagnosing the genus *Protochromys* to embrace *fellowsi* and separate it from *Melomys*. Except for these features, however, external, cranial, and dental traits of *P. fellowsi* resemble those seen in most species of *Melomys* and *Paramelomys* (our observations derived from AMNH material; also compare Flannery's, 1995, illustrations of the skulls of *fellowsi*, species of *Melomys* and *Paramelomys*, and *albidens*).

In addition to physical size (*Protochromys fellowsi* is a much larger rat; see measurements in Flannery, 1995), *P. fellowsi* and *B. albidens* diverge in many anatomical traits. *Protochromys fellowsi* has larger scales on the tail. There are 11–13 annuli per cm, all pressed into the epidermis; a single hair about the length of a scale springs from each

scale; and the tail appears brown, smooth, and naked. The scales are smaller in *B. albidens*, 17–24 rings of scales per cm; proximal scale rings are pressed into the epidermis but the distal rings have their edges raised, giving the impression of overlap; there are three hairs per scale that are up to 3–4 scales long; and the tail appears somewhat hairy, definitely not naked. *Protochromys* has a large, stocky skull showing little cranial flexion so that the braincase is low and the dorsal profile (in lateral view) is nearly straight; conspicuous beading runs along dorsolateral margins of the postorbital region and onto the braincase, and the rostrum is slightly tapered in lateral view (marked cranial flexion and high braincase in *Brassomys* without postorbital or temporal beading or ridging, rostrum rectangular in lateral view). Both *Protochromys* and *Brassomys* have a narrow zygomatic plate, but in *Protochromys* the anterior border projects forward beyond the edge of the dorsal maxillary zygomatic root to form a distinct zygomatic notch, the posterior border of the plate is even with the anterior alveolar margin of the first molar, and the masseteric attachment is a small, rough circular area on the bone surface; in *Brassomys,* the plate does not project beyond the dorsal zygomatic root, there is no zygomatic notch, the posterior margin of the plate is even with the anterior half of the first molar, and there is a large, projecting knoblike masseteric tubercle—the contrasts are striking. The incisive foramina are shorter relative to diastemal length in *Protochromys* than in *Brassomys.* Large bullae relative to skull size are characteristic of *Protochromys* but only if compared with species in *Paramelomys* and *Melomys* of similar cranial dimensions. The bullae are larger in *Brassomys*, as Tate noted, not only in absolute size but strikingly larger relative to size of skull. An elongate dentary is shared by both genera, but the angular process does not project backward in *Brassomys* as far as it does in *Protochromys*, and *Brassomys* has a relatively longer coronoid process. Among the diagnostic traits Menzies (1996) described for *Protochromys* was a very narrow alisphenoid strut, but that is probably variable, for the strut is robust and wide relative to skull size—comparatively just as wide as the prominent struts in *Coccymys* and *Brassomys* in all 23 examples of *Protochromys* we surveyed in the AMNH collection.

Protochromys and *Brassomys* share similar incisor configurations. In both, the uppers are small relative to skull size, and project from the rostrum at a right angle, the enamel is white or cream and forms about half of the labial surface of each tooth, and the cutting edge is gently convex. Lower incisors in each genus have white enamel that covers about half the labial surface of each tooth. In both genera, occlusal outlines of the first two rows on the first molar and anterior row on the second each take the form of a chevron (the last chunky row in each molar is also somewhat chevron-shaped) in which the cusp outlines are completely obliterated, even in young individuals, a configuration similar to the patterns seen in *Melomys* and *Paramelomys*, but here the molar similarities end. The rows are not coalesced along either their lingual or labial margins in *Protochromys*, which is unlike the configuration we described in *Brassomys*. Occlusal patterns formed by cusp rows on the lower molars are similar in both genera. A trenchant difference between the two genera not mentioned by either Tate (1951) or Menzies (1996) is the number of roots beneath each first upper molar. Both *Brassomys* and *Protochromys* possess two roots beneath each lower molar, which is the primitive pattern for murines and muroid rodents in general (Carleton, 1980; Musser and Newcomb, 1983). The first and second upper molars of *Brassomys* each has four roots, anterior, lingual, and divided posterior; the third upper molar has three roots, the primitive pattern. In *Protochromys*, however, each of the upper molars is anchored by four roots, but the third and fourth roots result from a divided lingual anchor, not a divided posterior holdfast; the pattern is specialized, but unlike the derived condition in *Brassomys*.

Set against this array of external, cranial, and dental contrasts between *Brassomys* and *Protochromys*, their shared incisor conformation and elongate dentary are likely convergent. Otherwise, traits associated with skins and skulls of *Protochromys* point to a close morphological (and likely phylogenetic) rela-

tionship with *Melomys* and *Paramelomys*, not with *Brassomys*.

We wondered if the general convergence in incisor anatomy and long and low dentary between *Protochromys* and *Brassomys* might indicate an invertebrate diet for the former. Because no dietary information has been recorded for *P. fellowsi*, we looked to fluid-preserved specimens stored in AMNH, five from Nondugl (183606, 183622, 183628, 183630, and 183632) and three from Mt. Wilhelm (192406, 192408, and 192411). Contents of all nine stomachs contained small rubbery chunks of caps and stalks from mushrooms only, not invertebrates. The pieces showed varying states of digestion. In most of the stomachs the chunks formed a solid mass difficult to break apart with forceps and severely distending the stomach. Some stomachs held only an undigested section of a bulbous stalk (the width of a little finger) and fragments of cap. Black flecks were a part of each mass. The same kinds of mushrooms, judged by texture and color, were found in each stomach, and are of the kinds that emerge from the ground as stalks and cap to produces spores. We sent samples to Tom May (mycologist at the Australian National University, Canberra) who verified the material as "definitely fungal" and noted that two different types were present, members of the phylum Basidiomycota (T. May, personal commun., 2008). Mycophagy is not uncommon among some species of Australian murids (Claridge and May, 1994) but until now has not been reported in New Guinea rodents.

Judged from our sample (which is small), presence of white incisors, in the case of *P. fellowsi*, does not point to an invertebrate diet, at least during the period when the specimens were collected. The shape of the zygomatic plate in *P. fellowsi*—its anterior spine that projects forward beyond the dorsal maxillary root to form a conspicuous notch, and position of the posterior margin relative to the first molar—is not a specialized configuration and similar to the shapes and relative position found in such genera as *Rattus* and *Melomys*, for example. This type of plate is also characteristic of two species of *Bunomys* endemic to Sulawesi that include fungi in their diet, in that case primarily rubbery shelf fungi (Musser's observations in the field). One of these *Bunomys*, an undescribed species, relies nearly exclusively on a jelly shelf fungus (*Auricularia* sp.) growing on rotten, wet tree trunks and limbs straddling shaded streams in primary forest.

Abeomelomys sevia is another New Guinea montane endemic murine bearing a superficial similarity to *Brassomys*. Two names are associated with the species: *sevia* was initially described by Tate and Archbold (1935) as a species of *Melomys*, and *tatei* was later proposed by Hinton (1943) as a species in *Pogonomelomys*. The name *sevia* was transferred to *Pogonomelomys* by Rümmler (1938). Later, Menzies (1990) separated *sevia* from both *Melomys* and *Pogonomelomys* by placing it in the new genus *Abeomelomys* and did not recognize *tatei* as a separate entity. *Abeomelomys sevia* has been recorded only from Papua New Guinea, where it is found between 1400 and 3100 m in the Central Cordillera and on the Huon Peninsula (Menzies, 1990; Flannery, 1995). A recent phylogenetic analysis of sequences for autosomal nuclear loci and mitochondrial genes linked *Abeomelomys* to *Mallomys* and *Mammelomys* in a clade separate from other New Guinea "Old Endemics" (Rowe et al., 2008).

As with *Brassomys albidens*, *A. sevia* has a thick and soft dorsal coat and ventral pelage composed of gray-based hairs, and a tail much longer than head and body (see the photograph in Flannery, 1995: 264, and description in Menzies, 1990). The upperparts of *A. sevia*, however, are reddish brown, not dark brown as in *B. albidens*, and the tail is covered in rows of large, flat, nonoverlapping rings of scales with three short hairs emerging from beneath each scale, and the dorsal surface of the terminal 5 mm at the tip of the tail is hairless and scaleless, indicating ability for dorsal prehensile grasping (see the drawing in Flannery, 1995: 263); the conformation of the tail scales is similar to that seen in species of *Melomys*, *Paramelomys*, and *Pogonomelomys* (rings of scales abut or slightly overlap in *B. albidens*, the scales are smaller, the scale hairs are relatively longer, and the dorsal surface near the tip remains covered in scales and hairs; the tail appears hairy while that of *A. sevia* is only slightly hirsute, appearing nearly naked). *Abeomel-*

Fig. 50. Views of crania and dentaries. **Top:** *Pogonomelomys mayeri* (AMNH 101954), an adult from The Gebroeders, Weyland Range, 5000 ft. **Bottom:** *Abeomelomys sevia* (AMNH 222211), an adult from Kepilam, 2400 m, in Papua New Guinea. ×2. Compare these with the skulls of *Coccymys ruemmleri* and *Brassomys albidens* pictured in figures 9 and 10, respectively.

omys sevia is physically larger than *B. albidens* (for example, range in length of head and body for five adult male *A. sevia* is 124–135 mm [Flannery, 1995: 264], that for five adult *B. albidens* is 111–122 mm [table 20], a size difference also reflected in the skull (see photographs in Flannery, 1995: 534; also compare the skull of *B. albidens* in fig. 10 with that of *A. sevia* in fig. 50).

The two species resemble each other in overall skull shape, relative length of incisive foramina, and other traits, but diverge sharply in other characters. Incisor enamel, for example, is orange in *Abeomelomys sevia*, not white as is typical of *B. albidens*, and the size of the upper and lower incisors relative to the skull and mandible, and extent of enamel covering over the labial incisor surface is like

Fig. 51.   Occlusal views of right maxillary molar rows. **Left:** *Abeomelomys sevia* (AMNH 192119; CLM1–3 = 5.8 mm) from the Okapa area, Purosa, Papua New Guinea. **Middle:** *Pogonomelomys mayeri* (AMNH 101962; CLM1–3 = 6.5 mm) from Kratke Range, Kassam, Papua New Guinea. **Right:** *Pogonomelomys bruijnii* (AMNH193306; CLM1–3 = 7.4 mm) from Eramboe, near Merauke, western New Guinea. Compare these toothrows and those in figure 52 with the molar rows of *Coccymys ruemmleri* and *Brassomys albidens* shown in figures 11 and 12.

the generalized condition in *Coccymys* and species in *Melomys, Paramelomys, Mammelomys*, and *Pogonomelomys*; the molar rows noticeably diverge posteriorly but are parallel in *B. albidens*; the auditory bullae are moderately small relative to skull size, not large and somewhat inflated; the zygomatic arches converge anteriorly, instead of being either parallel or diverging slightly posteriorly as in *B. albidens*; the zygomatic plate is broad with only a roughened site on the bone for attachment of the superficial masseter, and unlike the very narrow zygomatic plate in *B. albidens* with its knoblike masseteric tubercle; the interorbit is longer, and dorsolateral margins of interorbit and postorbital region are marked by low beading, dissimilar to the smooth borders in *B. albidens* with its hourglass-shaped interorbit (in dorsal view); and each dentary is stocky, not elongate, with a short ramus between molar row and incisor base, distinct from the slim and long ramus seen in *B. albidens*. Length of molar rows relative to skull length are equivalent in *A. sevia* and *B. albidens*, but occlusal cusp patterns on maxillary molars are somewhat less complex in *A. sevia*, more similar to those configurations in species of *Melomys, Paramelomys*, and *Pogonomelomys* where the rows of cusps take on a definite chevron shape, and its third molar is very large relative to others in the toothrow (figs. 51,

Fig. 52.   Occlusal views of right mandibular molar rows of the specimens illustrated in figure 50. **Left:** *Abeomelomys sevia* (clm1–3 = 5.8 mm). **Middle:** *Pogonomelomys mayeri* (clm1–3 = 6.8 mm). **Right:** *Pogonomelomys bruijnii* (clm1–3 = 7.5 mm).

52). Occlusal surfaces of cusp rows in *B. albidens* are somewhat chevron-shaped, but the third upper molar is relatively much smaller. In addition, cusp rows are merged at their labial borders on first and second molars in *B. albidens,* and enamel ridges join cusp rows along their lingual margins; this configuration is absent in *A. sevia*; cusp t9 projects from the central cusp t8 in a straight line, rather than diagonally as in *A. sevia*, where cusp t9 and cusp t8 coalesce to form a large triangle in occlusal outline; and of the two laminae on the third molar of *B. albidens*, the front lamina is arched, and the back lamina is small, not extending to labial and lingual margins; the counterparts in *A. sevia* are straight and wide, and reach labial and lingual margins (fig. 51). Finally, the number of roots beneath upper molars differs in the two species. In both *B. albidens* and *A. sevia*, each lower molar has two roots, a primitive pattern. The first and second upper molars of *B. albidens* are each anchored by four roots, anterior, lingual, and divided posterior holdfasts, which is specialized; three roots anchor each third upper molar. Each upper molar of *A. sevia* has three roots, anterior, lingual, and posterior, the primitive state.

Because *ruemmleri* was originally described as a species of *Pogonomelomys*, and *Brassomys albidens* has been allied with *ruemmleri* in the past, we briefly address here why *albidens* is not a member of *Pogonomelomys*. As currently documented in the published literature, *Pogonomelomys* con-

tains two white-bellied, long-tailed arboreal species: *P. mayeri*, with records from hill forests scattered over northern New Guinea, from the Weyland Range in the west to the Huon Peninsula in the east; and the larger-bodied *P. bruijnii*, which is rare in collections and recorded from a few lowland localities in western and southern New Guinea, including the Vogelkop Peninsula and the island of Salawati, the Fly River drainage, and Mt. Bosavi (Menzies, 1990; Flannery, 1995; Aplin et al., 1999; Helgen, in litt., 2008; Helgen et al., in press). Helgen (2007c), however, notes that inclusion of only two species underestimates the actual species diversity in the genus, and more than these two will be recognized after a new taxonomic review of *Pogonomelomys*. Both currently accepted species of *Pogonomelomys* are physically larger than *B. albidens* (see measurements in Flannery, 1995), have pure white underparts (whitish gray to ochraceous-gray in *B. albidens*), a mosaic pattern of tail scales (not abutting or overlapping annuli) with very short scale hairs so the tail appears naked (see drawing in Flannery, 1995: 63), and a short dorsal strip at the tip of the tail that is devoid of scales and hair, reflecting the ability for dorsal prehensility (abutting or slightly overlapping rows of small scales in *B. albidens*, with long scale hairs so tail appears somewhat hairy, no dorsal prehensile structure near tail tip). Tail anatomy typical of *Pogonomelomys* is similar to that characterizing *Abeomelomys*, which also resembles *Pogonomelomys* in other aspects of external anatomy, as well as many characteristics associated with the skull and dentition (figs. 50–52). Generally, most of the cranial differences that separate *Brassomys* from *Abeomelomys* are equivalent to the contrasts between *Brassomys* and *Pogonomelomys*. There are three clear exceptions: *Pogonomelomys* has a stockier skull, much shorter incisive foramina relative to diastemal length, and an appreciably wider zygomatic plate than in either *Brassomys* or *Abeomelomys*. Relative sizes of the maxillary molars and the coronal patterns of the cusp rows on these teeth are very similar in *Pogonomelomys* and *Abeomelomys* and diverge sharply from the configurations in *Brassomys* (compare figs. 11 and 12 with 51). Furthermore, the

first and second upper molars in *Brassomys* have four roots; those in *Pogonomelomys* and *Abeomelomys* have three roots.

How closely related *B. albidens* might be to other New Guinea "Old Endemics" is unclear, but no anatomical traits support its membership in any one of the genera to which we have compared it, or to any other New Guinea murine.

COCCYMYS: We have described the taxonomic history of *ruemmleri*, the type species of *Coccymys*, in a previous section. It was initially described as a member of *Pogonomelomys* (Tate and Archbold, 1941), a placement always considered unsatisfactory (Tate, 1951; Lidicker, 1968), and eventually Menzies (1990) designated *ruemmleri* as the type species of the new genus *Coccymys*. Menzies (1990: 133) noted that *C. ruemmleri* "differs from *Pogonomelomys* spp. in that the cranium is more rounded and less angular; the anterior palatine foramina are much longer; the zygomata are more tapering, less parallel sided; the molar crowns are more complex; the tail scales are overlapping, not mosaic, and the mammae form 3, not 2, pairs." In addition, both species of *Pogonomelomys* have pure white venters, contrasting with the whitish gray or grayish white underparts in *Coccymys*. Rows of tail scales actually abut against one another in *Coccymys* but they do not form a mosaic pattern.

Some of Menzies's cranial contrasts are evident in figures 9 and 50 where skulls of *Coccymys* and *Pogonomelomys* are presented. There are, however, other sharp cranial differences between the two genera. For example, compared with species of *Pogonomelomys*, *Coccymys* has a less robust skull with a higher and wider braincase and deeper occiput relative to overall skull size, reflecting appreciably greater cranial flexion (small braincase relative to interorbital and rostral regions of skull in *Pogonomelomys*, and shallower occiput); the interorbital and postorbital regions are short relative to the large braincase, their dorsolateral edges smooth, and the interorbit is hourglass-shaped in dorsal view (interorbital and postorbital form a long bridge, in dorsal view, connecting rostrum to braincase, its sides are either straight or diverge posteriorly, and the dorsolateral margins are marked by high

shelflike ridges in *Pogonomelomys*); the anterior margin of the zygomatic plate barely projects forward past the maxillary zygomatic root, so the zygomatic notch is slight or not present (deeper zygomatic notch in *Pogonomelomys*, reflecting greater extension of the leading edge); posterior edge of the bony palate is even with the backs of the third molars or extends slightly beyond them (margin even with anterior edges of the third molars in *Pogonomelomys*).

The molars of *Coccymys* are wide relative to their lengths, but relatively narrower in *Pogonomelomys*. Occlusal surfaces of upper molars in all three species of *Coccymys* are ''more complex'' in the sense that each row of cusps maintains its cuspidate origin even after much wear compared to the coronal surfaces of the teeth in *Pogonomelomys* where the cusp patterns are evident on unworn and slightly worn molars, but tend to disappear with wear into chunky chevrons (compare fig. 11 showing molar of *Coccymys* with fig. 51 where the upper molars of *Pogonomelomys* are illustrated). Shape of the anterior lamina on the first molar is very similar in the two genera, a posteriorly oriented cusp t1 and nearly straight segment formed by coalesced cusps t2 and t3. The second lamina on that tooth in *Coccymys* is, except for cusp t4, essentially straight and the cusps remain discrete (narrowly merged) even with significant wear. The second row in *Pogonomelomys*, by contrast, has the form of a chevron, and even with little wear cusp t4 abuts the central cusp t5, which in turn is fully fused with the labial cusp t6 (as in the young example of *P. bruijnii*); in older animals (the example of *P. mayeri*), cusp t4 is completely merged with cusp t5. In the third lamina in *Coccymys*, cusp t8 resembles a somewhat distorted diamond shape in occlusal outline, and cusp t9 projects in a straight line to the labial margin of the molar. In *Pogonomelomys*, cusp t8 is more triangular in outline partly because cusp t9 has so completely merged with cusp t8 that its boundaries are obliterated, even in young rats (as shown in the young *P. bruijnii* pictured in fig. 51); that portion of the third lamina that represents cusp t9 has a posterolabial orientation, not one straight to the labial side. Connecting cusps t4 and t8 in *Coccymys* is a high enamel

ridge (discernable even in worn molars)—no such structure is present in the species of *Pogonomelomys*.

The shape of the anterior row of cusps on the second molar is similar in both *Coccymys* and *Pogonomelomys* in that cusp t4 is long and narrow, and cusp t5 is elongate, a conformation apparent in little worn teeth (*P. bruijnii* in fig. 51) but less evident in worn molars (*P. mayeri* in fig. 51). Cusp t6, however, is discrete and much larger relative to cusp t5 in *Coccymys* and evident after much wear; cusp t6 is relatively smaller in *Pogonomelomys* and is already completely merged with cusp t5 in young animals, and in older rats the row assumes the shape of a thin, widely spread chevron. The posterior cusp row in *Pogonomelomys* is similar in occlusal outline to its counterpart on the first molar and differs from the configuration on the molar of *Coccymys* in the same ways. A strong ridge connects cusps t4 and t8 on the second molar in *Coccymys*, but not in *Pogonomelomys*. There is a low cingular extension of cusp t8 that is oriented anterolingually, but it does not form a high ridge or cusp in *Pogonomelomys*. Enamel ridges connect labial margins of the cusp rows in *Coccymys* (figs. 11, 51), but comparable structures are absent in *Pogonomelomys*.

Length of the third upper molar relative to the others in the row is similar in *Coccymys* and *Pogonomelomys*, but this tooth is more square in the latter due to the wider laminae that form it. The occlusal cusp patterns are similar, except that the anterior and posterior laminae are parallel to one other or nearly so, at least in *P. mayeri*.

Except for the relatively much larger third molar possessed by *Pogonomelomys*, its occlusal patterns formed by cusp rows on the first and second upper molars resemble those simple (no lingual or labial connecting ridges) chevron-shaped patterns characteristic of *Melomys* (see the molar row of *M. rufescens* illustrated in Musser, 1982a: 39) and *Abeomelomys*. The more complicated, gently arcuate clearly cuspidate patterns in *Coccymys* are strikingly divergent.

Coronal laminar patterns of the lower molars are generally similar in the two genera but diverge in five traits (figs. 12, 52). As with the upper (maxillary molars), cusps forming

the laminae in *Coccymys* are better defined and not as fully coalesced along the midline of each molar compared with the completely fused cusps of even young animals in *Pogonomelomys*, and the molars are wider relative to their lengths. *Coccymys* has a roughly rectangular anteroconid formed by a large anterolingual cusp and slightly smaller anterolabial cusp, which are separate in young rats but fuse completely in older individuals. The anteroconid in *Pogonomelomys* is smaller relative to the molar outline, and consists of a large anterolingual cusp fused with a very small anterolabial cusp; outlines of the two cusps can be seen in slightly worn molars (as in *P. bruijnii* in fig. 52) but are quickly lost with age. An anterolabial cusp forms the anterolabial border of the second molar in *Coccymys*, but is absent from the tooth in *Pogonomelomys*. Posterior labial cusplets are prominent along the labial margins of the first and second molars in *Coccymys*, but are not present in *Pogonomelomys*. Finally, the posterior lamina on the third molar of *Coccymys* is wider, extending from labial to lingual margins, while its counterpart in *Pogonomelomys* is narrower, its labial margin set in from the labial border.

Both genera exhibit the same number of molar roots: three beneath each upper, two anchoring each lower—the primitive configurations.

Except for overall size, the dentaries of *Coccymys* and *Pogonomelomys* are much alike (figs. 9, 50). Both are robust with a thick ramus between the molar row and incisor alveolus, expressing the same degree of curvature from the base of the ramus to the incisor tip. Both have a high ascending ramus, prominent coronoid process, and robust condyloid projection. There are two evident differences. First, the posterior concave margin of the dentary between the condyloid and angular processes is shallower in *Coccymys*. Second, the end of the incisor capsule is a large knob that projects outward from the labial surface of the ramus and its round top is about even with the margin of the sigmoid notch between coronoid and condyloid processes. The end of the incisor alveolus lies within the dentary in *Pogonomelomys*, and its terminus is indicated by a

slight swelling at about the middle of the base of the coronoid process and well below the margin of the sigmoid notch.

Lidicker's (1968) comparative analyses of phallic morphology among New Guinea murines is the only published comparative inquiry related to anatomical systems not associated with skins and skulls. He examined specimens of *Pogonomelomys mayeri* and *"Pogonomelomys" ruemmleri* and exclaimed that "The penis of *P. ruemmleri* is the most distinctive and unique of all the native forms examined" (p. 630) and did not consider *P. mayeri* and *ruemmleri* to be closely related, an estimate substantiated by comparisons of external, cranial, and dental traits.

When Tate (1951: 316) expressed his unease with the generic allocation of *ruemmleri* to *Pogonomelomys*, he thought there were two subdivisions within the genus, the "*mayeri-bruijniii* group," which are the only two species that currently constitute *Pogonomelomys* (Menzies, 1990; Musser and Carleton, 2005), and the "*sevia-rümmleri* group," which has been split into two genera, *Abeomelomys* and *Coccymys*, with the type species *sevia* and *ruemmleri*, respectively (Menzies, 1990; Musser and Carleton, 2005). Tate's grouping of *ruemmleri* and *sevia* compels us to compare *Coccymys* with *Abeomelomys*. Aside from ventral fur with gray bases and unpigmented tips clothing underparts of head and body, which is like *Coccymys*, *Abeomelomys* closely resembles *Pogonomelomys* in morphology of external traits, skull and mandible characters, and dentition, and the features associated with these different anatomies differ from comparable morphology in *Coccymys* in much the same way and degree reflected by the contrasts between *Coccymys* and *Pogonomelomys* (compare figs. 9, 11, and 12 with 50–52). There are a few exceptions, and in these traits *Abeomelomys* resembles *Coccymys*. Compared with *Pogonomelomys*, the skull of *Abeomelomys* appears less robust overall; the interorbital and postorbital regions are shorter and their dorsolateral margins smooth, without the shelflike ridges seen in *Pogonomelomys*; the anterior margin of the zygomatic plate is about even with the leading edge of the maxillary zygomatic

notch, so the zygomatic notch is barely evident; and the incisive foramina are longer relative to diastemal length, their posterior margins almost reaching the anterior alveolar edges of the first molars.

Molars of *Abeomelomys* and *Pogonomelomys* are similar (figs. 51, 52). In both, the first and second upper molars are long relative to their respective widths, and the third upper molar is large relative to size of others in the row; occlusal patterns formed by laminae on the upper molars are basically like the patterns in *Pogonomelomys*, and neither has any sign of lingual or labial connecting ridges. Lower molars are also equivalent in occlusal patterns. The posterior lamina on the third molar is relatively wider in *Abeomelomys* (extending to both labial and lingual margins), but that is the basic configurational difference. Each upper molar has three roots and each lower is anchored by two roots in both genera. As with most skull traits, contrasts between *Coccymys* and *Pogonomelomys* are also reflected in the dental dissimilarities between *Coccymys* and *Abeomelomys*.

Coccymys and *Abeomelomys* differ somewhat in sperm morphology (Breed and Aplin, 1994). The spermatozoal anatomy in *Coccymys* is "typified by a long and narrow, falciform sperm head and a long flagellum with indistinct boundary between mid- and principal pieces" (p. 24) and no accessory ventral processes, a configuration also found in *Xenuromys barbatus, Lorentzimys nouhuysi*, and both species of *Mammelomys* among the New Guinea endemics that were sampled as well as three species of endemic New Guinea *Rattus*. In contrast to these genera, *Abeomelomys sevia* "has a very distinctive sperm head, with a fairly broad lateral surface and a long apical hook" (p. 23). Sperm morphology of *Abeomelomys* is, according to Breed and Aplin (1994), somewhat intermediate between the conformation in *Coccymys* and that typical of *Hyomys* and *Anisomys*, both of which have a superficial "*Rattus*-like" spermatozoal anatomy. Neither *Coccymys* nor any of the other genera mentioned above have a sperm head with two accessory ventral hooks, which is characteristic of nearly all native Australian murines (except species of *Rattus*), Australian and New Guinea hydromyins, and the New Guinea *Mallomys, Pogonomys*, and *Chiruomys* (Breed and Aplin, 1994; Breed, 1997).

There is no question that *Coccymys ruemmleri*, along with its vicariant relatives, *C. shawmayeri* and *C. kirrhos*, are members of a generic clade different from that identified by the labels, *Pogonomelomys* and *Abeomelomys*. Morphologies associated with skins, skulls, and dentition do not support a "*sevia-rümmleri* group" (Tate, 1951) or, in combination with phallic and spermatozoal traits, inclusion in *Pogonomelomys*.

COCCYMYS AND BRASSOMYS: Although *albidens* was first described as a member of *Melomys* (Tate, 1951), and subsequent assessments of its phylogenetic affinities suggested a tie to *Coccymys ruemmleri* (Flannery, 1990; Menzies, 1990; Musser and Carleton, 1993), our comparisons between the two enumerated in a previous section contradict such a close relationship. Some traits associated with skins and skulls are shared by *Brassomys* and *Coccymys*, but these are largely primitive (see Carleton, 1980; Musser and Newcomb, 1983; Carleton and Musser, 1989; Weksler, 2006): three hairs per tail scale and thin, slightly raised tail scales; lengths of digits relative to one another; full complement of palmar and plantar pads; skull with smooth interorbital and postorbital dorsolateral margins, with the interorbit hourglass-shaped in dorsal view; cranium smooth without temporal ridging or only slight salients, and inconspicuous lamboidal beading; narrow zygomatic plate with a vertically straight anterior margin that does not project forward past the leading edge of the dorsal maxillary root or barely does so; prominent alisphenoid struts; generalized murine carotid arterial pattern; posterior cingulum on first and second upper molars; and two roots beneath each lower molar. *Brassomys* and *Coccymys* also share small body size; thick and soft fur (lax in *Coccymys*, woolly in *Brassomys*), brownish dorsal coats (in *C. ruemmleri* and *C. shawmayeri*, not *C. kirrhos*), soft and dense ventral pelage with gray-based hairs everywhere; long facial vibrissae; and a brownish tail that is longer than head and body. Polarities of these traits, however, are difficult to assess without a comprehensive

phylogenetic analysis of endemic New Guinea murines. Dark, thick, and soft fur, for example, is common to small-bodied species inhabiting cool and wet forests at high altitudes. A tail longer than head and body is possessed by many scansorial and arboreal New Guinea murines. Menzies (1990: 132) noted that *Coccymys ruemmleri* and the montane *Pogonomys sylvestris* (which also has soft and thick pelage, is small in body size, with a tail much longer than the head and body), are extraordinarily similar in external physical characteristics and fur coloration, yet cranial and dental features, along with phallic and spermatozoal traits, indicate a distant relationship. Relatively long incisive foramina and a large squamosal foramen are shared by *Coccymys* and *Brassomys* but their polarities are equivocal (see Carleton, 1980; Musser and Newcomb, 1983; Weksler, 2006). A conspicuous degree of cranial flexion characterizes skulls of both *Brassomys* and *Coccymys*, particulary compared with the flatter crania in *Pogonomelomys, Protochromys, Melomys, Mammelomys, Uromys*, and other New Guinea endemics (see skull illustrations in Flannery, 1995), which is a specialization (Carleton and Musser, 1989). The flexion is somewhat more pronounced in *Coccymys*, however, and that in *Brassomys* resembles the skull outlines (in lateral view) of other small-bodied murines such as *Pogonomys sylvestris*; so as an indicator of relationships this trait is ambiguous.

Occlusal surfaces of upper molars in *Coccymys* and *Brassomys* are derived compared with the patterns in early murines such as the late Miocene Chinese *Linomys* for example (Storch and Ni, 2002), but in strikingly divergent ways (figs. 8–10), which are reflected in the comparisons described in a previous section. Two dental characteristics are shared by *Coccymys* and *Brassomys*. Occlusal outlines of the posterior cusp rows on the first and second upper molars are alike in both genera, formed from a large cusp t8 and much smaller cusp t9 that is broadly united with cusp t8 and projects labially in a straight line. This orientation of cusp t8 relative to cusp t9 is likely primitive; it characterizes some of the earliest murines, such as the Chinese late Miocene *Linomys*

and Pakistan *Progonomys* of similar age, and even the middle Miocene *Antemus chinjiensis*, considered by most researchers to be the earliest murid (Jacobs, 1978; Storch and Ni, 2002). The other shared trait is an enamel ridge connecting the labial margins of the second and third rows on the first upper molar and comparable rows on the second along the labial margin (fig. 11). This is a derived (apomorphic) configuration, but its significance in reconstructing the degree of phylogenetic affinity between *Coccymys* and *Brassomys* is difficult to assess without a comprehensive survey of character states in "Old Endemic" New Guinea murines that would be employed in a phylogenetic analysis.

Aside from the shared cranial and dental traits described above, most of which are primitive (the polarity of others is ambiguous and the significance of a few unknown), the postulated affinity between *Brassomys* and *Coccymys* evaporates in the face of their cranial and dental divergence. The specialized morphology of the incisors and mandible, and marked degree of ectotympanic bullar inflation (and large external pinnae relative to body size) indicate that *Brassomys* is morphologically unique among endemic New Guinea murines, and not clearly a part of any previously identified monophyletic group, at least at the level of divergence we identify as generic.

Within the diversity of endemic New Guinea murines, the phylogenetic affinity of *Coccymys* is puzzling, but how *Brassomys* fits within this fauna remains a mystery. *Coccymys* "*ruemmleri*" was sampled by Watts and Baverstock (1994; their sample was actually *C. shawmayeri*) in their study of the interrelationships among species of New Guinea murines using microcomplement fixation of albumin to measure immunological distances among genera. Their results identified three groups of genera: the "*Hydromys* Clade," containing *Hydromys, Parahydromys, Leggadina, Mesembriomys, Xeromys, Crossomys, Leptomys, Pseudohydromys* (including *Mayermys* and *Neohydromys*; see Musser and Carleton, 2005), *Uromys, Solomys,* and *Melomys*; the "*Anisomys* Clade," which included *Coccymys, Chiruromys, Pogonomys, Hyomys, Macruromys,* and *Mallomys*; and a "*Lorentzi-*

mys Clade'' containing only *Lorentzimys*. According to their one-way measurements of immunological distances, ''*Coccymys* and *Hyomys* showed no clear affinities with any genus, but appear to be distinctive members of the *Anisomys* clade'' (p. 298). They also noted that ''*Coccymys ruemmleri* was available only as an antigen and its placement can only be considered indicative. It proved difficult to place but, on balance, seems to be a member of the *Anisomys* clade. … However, given the immunological distances recorded within what are currently thought of as *Uromys* and *Melomys* … this placement must remain very tentative'' (p. 301). Results generated by Watts and Baverstock are at odds with the clustering proposed by Lidicker (1968), based on phallic anatomy, in which ''*ruemmleri*'' was included in a ''*Uromys* group'' that also contained species of *Melomys, Uromys, Hyomys,* and *Pogonomelomys*. Results from a comparative study of sperm morphology that included *Coccymys* (as *ruemmleri*, but the sample was *C. shawmayeri*) were discordant with both Lidicker's arrangement and the hypothesis presented by Watts and Baverstock, as well as being ambiguous in identifying the closest phylogenetic relative of *Coccymys* (Breed and Aplin, 1994; Breed, 1997). Along with the New Guinea endemics, *Abeomelomys, Anisomys, Chiruromys, Hyomys, Macruromys, Mallomys, Mammelomys, Pogonomelomys, Pogonomys,* and *Xenuromys*, and the Timorese *Coryphomys*, Musser and Carleton (2005: 904) included *Coccymys* in a ''*Pogonomys* Division'' of Murinae, which admittedly is built on the meager phylogenetic evidence available in the literature and personal observations, but at the time seemed a reasonable proposal to test. Recent phylogenetic analysis of nuclear and mitochondrial genes breaks the ''*Pogonomys* Division'' into two separate clades, one containing *Anisomys, Macruromys, Chiruromys, Hyomys*, and *Pogonomys* (and also includes *Lorentzimys*, which Musser and Carleton, 2005, placed in its own division), the other composed of *Mammelomys, Abeomelomys*, and *Mallomys*; *Coccymys* was not sampled (Rowe et al., 2008). Currently, all data indicating that *Coccymys* is more closely related to *Melomys* and its relatives (*Uromys, Paramelomys, Protochromys*, and *Solomys*)

than to at least some members in the ''*Pogonomys* Division'' is ambiguous.

Where *Brassomys* would fit within a pattern of phylogenetic reconstruction of endemic New Guinea murines is unknown. Relative lengths of tail and hind feet suggest specializations for arboreal habits, and the long, dense, somewhat woolly fur reflects an adaptation to montane environments, but otherwise its external form does not exhibit any striking specializations. The tail, for example, lacks any anatomical indication that it can be used as a prehensile organ, and it is covered in annuli of small scales, each scale supporting three hairs, which is a primitive pattern for murines. The skull and teeth retain a constellation of primitive characteristics (see above), but the combination of a rectangular rostrum, relatively narrow zygomatic plate and its orientation relative to the first molars, knoblike masseteric tubercle, configurations of upper and lower incisors, inflated bullar capsule, and divided posterior root beneath each first and second molar is unique to *B. albidens*. Uncovering the phylogenetic affinities of *Brassomys*, as well as *Coccymys*, will require rigorous phylogenetic analyses utilizing data derived from anatomical surveys and molecular sources. Perhaps we can state that with the exception of hydromyins (*Hydromys, Baiyankamys, Microhydromys, Parahydromys, Crossomys, Leptomys, Paraleptomys, Pseudohydromys*, and *Xeromys*), all of which are terrestrial or amphibious, and invertebrate or small vertebrate predators, *B. albidens* may be one of the few arboreal invertebrate predators among the other ''Old Endemic'' New Guinea genera (which exclude endemic *Rattus*). In New Guinea ''Old Endemic'' genera, the diet, at least for those species for which dietary information is available, consists primarily of fruits, forbs, leaves, and grasses, as well as mushrooms.

ACKNOWLEDGMENTS

welcoming modest infusions of funding, and sponsoring our product through to publication in the museum publication series. Paula Jenkins at the Natural History Museum in London measured specimens for us, provided the photograph of the holotype of *shawmayeri* (fig. 24), and transmitted other helpful information. Carla Kishinami, at the Bernice P. Bishop Museum in Honolulu, loaned us important batches of *Coccymys* whenever we asked. Fred Kraus, at that institution, illuminated the site on Mt. Simpson where he collected the specimen of *Coccymys kirrhos.* Modern material housed in the Australian Museum in Sydney was made available for our use by Sandra Ingleby, and Yong Yi Zhen allowed us to borrow fossil specimens stored in the paleontological collections at the Australian Museum. Tom May, mycologist at the Australian National University, Canberra, kindly examined our fungal samples.

Three others at the American Museum have substantially aided our endeavors. Eileen Westwig routinely packed and shipped material to Musser. Dan Jacobs, in his usual meticulous fashion, sorted into vials all the many specimens extracted from owl pellets so they could be sent to Musser for identification. Pat Brunauer, with her typical good humor and sage comments, always responded quickly to our requests for publications to be photocopied, and helped with other problems that always attend the production of a large manuscript.

The photographs in figures 6–12, 29, and 50–52 are the result of Peter Goldberg's talent and expertise with a camera. Figures 1, 41, and 42 were rendered by Patricia J. Wynne, who also enhanced the four map illustrations and all the graphs illustrating results from principal components analyses, and transformed all the figures into electronic illustrations.

Two colleagues intimately familiar with New Guinea and its unique endemic mammal fauna generously shared their knowledge with us. Tim Flannery provided illuminating details about some of his survey work in the Snow Mountains and the Telefomin area. Kristofer Helgen examined specimens at the Bishop Museum and sent us the results from that survey. He also, without hesitation,

turned over to us data that will eventually be published in some of his systematic revisions. His reading of the final manuscript elicited suggestions for change and insertions that significantly enhanced our exposition. We also benefited from the critical review of the manuscript by Jim Menzies.

We applaud all the persons enumerated above, who each (in their various ways) facilitated the production of our report and helped us transfer the information residing in museum cabinets to published systematic synthesis.

REFERENCES

Aplin, K.P. 1998. Vertebrate zoogeography of the Bird's Head of Irian Jaya, Indonesia. *In* J. Miedema, C. Odé, and R.A.C. Dam (editors), Perspectives on the Bird's Head of Irian Jaya, Indonesia: 803–890. Amsterdam: Rodopi.

Aplin, K.P., P.R. Baverstock, and S.C. Donnellan. 1993. Albumin immunological evidence for the time and mode of origin of the New Guinean terrestrial mammal fauna. Science in New Guinea 19: 131–145.

Aplin, K.P., and J.M. Pasveer. 2005. Mammals and other vertebrates from late Quaternary archaeological sites on Pulau Kobroor, Aru Islands, eastern Indonesia. *In* S. O'Connor, P. Veth, and M. Spriggs (editors), Archaeology of the Aru Islands (Terra Australis 22): 41–62. Canberra: Pandanus Press, Australian National University.

Aplin, K.P., J.M. Pasveer, and W.E. Boles. 1999. Late Quaternary vertebrates from the Bird's Head Peninsula, Irian Jaya, Indonesia, including descriptions of two previously unknown marsupial species. Records of the Western Australian Museum Supplement 57: 351–387.

Archbold, R., and A.L. Rand. 1935. Results of the Archbold Expeditions. No. 7. Summary of the 1933–1934 Papuan Expedition. Bulletin of the American Museum of Natural History 68(8): 527–579.

Archbold, R., A.L. Rand, and L.J. Brass. 1942. Results of the Archbold Expeditions. No. 41. Summary of the 1938–1939 New Guinea Expedition. Bulletin of the American Museum of Natural History 79(3): 197–288.

Balete, D.S., E.A. Rickart, R.G.B. Rosell-Ambal, S. Jansa, and L.R. Heaney. 2007. Descriptions of two new species of *Rhynchomys* Thomas (Rodentia: Muridae: Murinae)from Luzon Island, Philipines. Journal of Mammalogy 88(2): 287–301.

Balete, D.S., E.A. Rickart, and L.R. Heaney. 2006. A new species of the shrew-mouse, *Archbold-omys* (Rodentia: Muridae; Murinae), from the Philippines. Systematics and Biodiversity 4(4): 489–501.

Beehler, B.M., T.K. Pratt, and D.A. Zimmerman. 1986. Birds of New Guinea. Princeton, NJ: Princeton University Press.

Brass, L.J. 1941. The 1938–1939 expedition to the Snow Mountains, Netherlands[?], New Guinea. Journal of the Arnold Arboretum 22: 271–342.

Brass, L.J. 1956. Results of the Archbold Expeditions. No. 75. Summary of the Fourth Archbold Expedition to New Guinea (1953). Bulletin of the American Museum of Natural History 111(2): [77]–152.

Brass, L.J. 1959. Results of the Archbold Expeditions. No. 79. Summary of the Fifth Archbold Expedition to New Guinea (1956–1957). Bulletin of the American Museum of Natural History 118(1): [1]–69.

Brass, L.J. 1964. Results of the Archbold Expeditions. No. 86. Summary of the Sixth Archbold Expedition to New Guinea (1959). Bulletin of the American Museum of Natural History 127(4): [145]–215.

Breed, W.G. 1997. Evolution of the spermatozoon in Australasian rodents. Australian Journal of Zoology 45: 459–478.

Breed, W.G. 2004. The spermatozoon of Eurasian murine rodents: its morphological diversity and evolution. Journal of Morphology 261: 52–69.

Breed, W.G., and K. Aplin. 1994. Sperm morphology of murid rodents from New Guinea and the Solomon Islands: phylogenetic implications. Australian Journal of Zoology 43: 17–30.

Brown, J.C. 1971. The description of mammals. 1. The external characters of the head. Mammal Review 1: 151–168.

Brown, J.C., and D.W. Yalden. 1973. The description of mammals. 2. Limbs and locomotion of terrestrial mammals. Mammal Review 3: 107–134.

Bugge, J. 1970. The contribution of the stapedial artery to the cephalic arterial supply in muroid rodents. Acta Anatomica 76: 313–336.

Carleton, M.D. 1973. A survey of gross stomach morphology in New World Cricetinae (Rodentia, Muroidea), with comments on functional interpretations. Miscellaneous Publications Museum of Zoology University of Michigan 146: 1–43.

Carleton, M.D. 1980. Phylogenetic relationships in Neotomine-Peromyscine rodents (Muroidea) and a reappraisal of the dichotomy within New World Cricetinae. Miscellaneous Publications Museum of Zoology University of Michigan 157: 1–146.

Carleton, M.D., and G.G. Musser. 1984. Muroid rodents. *In* S. Anderson and J.K. Jones, Jr (editors), Orders and families of Recent mammals of the world: 289–379. New York: Wiley.

Carleton, M.D., and G.G. Musser. 1989. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): a synopsis of *Microryzomys*. Bulletin of the American Museum of Natural History 191: 1–83.

Claridge, A.W., and T.W. May. 1994. Mycophagy among Australian mammals. Australian Journal of Ecology 19: 251–275.

Cole, R.E., A. Engilis, Jr., and F.J. Radovsky. 1997. Report on mammals collected during the Bishop Museum Expedition to Mt. Dayman, Milne Bay Province, Papua New Guinea. Occasional Papers of the Bishop Museum 51: 1–36.

Dieterlen, F. 1983. Zur systematic, verbreitung und ökologie von *Colomys goslingi* Thomas & Wroughton, 1907 (Muridae; Rodentia). Bonner Zoologische Beiträge 34: 73–106.

Dieterlen, F., and B. Statzner. 1981. The African rodent *Colomys goslingi* Thomas and Wroughton, 1907 (Rodentia: Muridae)—a predator in limnetic ecosystems. Zeitschrift für Säugetierkunde 46: 369–383.

Ellerman, J.R. 1949. The families and genera of living rodents. Vol. III. London: British Museum (Natural History).

Engilis, A., Jr., and R.E. Cole. 1997. Avifaunal observations from the Bishop Museum Expedition to Mt. Dayman, Milne Bay Province, Papua New Guinea. Occasional Papers of the Bishop Museum 52: 1–19.

Flannery, T.F. 1990. Mammals of New Guinea. Carina, Queensland: Australia: Robert Brown.

Flannery, T.F. 1995. Mammals of New Guinea. Revised ed. Ithaca, NY: Cornell University Press.

Flannery, T.F. 1999. The Pleistocene mammal fauna of Kelangurr Cave, central montane Irian Jaya, Indonesia. Records of the Western Australian Museum Supplement 57: 341–350.

Flannery, T.F., Boeadi, and A.L. Szalay. 1995. A new tree-kangaroo (*Dendrolagus*: Marsupialia) from Irian Jaya, Indonesia, with notes on ethnography and the evolution of tree-kangaroos. Mammalia 59: 65–84.

Flannery, T.F., and C.P. Groves. 1998. A revision of the genus *Zaglossus* (Monotremata, Tachyglossidae), with description of new species and subspecies. Mammalia 62: 367–396.

Flannery, T.F., and L. Seri. 1990. The mammals of southern West Sepik Province, Papua New Guinea: their distribution, abundance, human use, and zoogeography. Records of the Australian Museum 42: 173–208.

Gonzales, P.C., and R.S. Kennedy. 1996. A new species of *Crateromys* (Rodentia: Muridae) from Panay, Philippines. Journal of Mammalogy 77(1): 25–40.

Heaney, L.R., D.S. Balete, E.A. Rickart, R.C.B. Utzurrum, and P.C. Gonzales. 1999. Mammalian diversity on Mount Isarog, a threatened center of endemism on southern Luzon Island, Philippines. Fieldiana Zoology New Series 95: 1–62.

Heaney, L.R., B.R. Tabaranza, Jr., E.A. Rickart, D.S. Balete, and N.R. Ingle. 2006. The mammals of Mt. Kitanglad Nature Park, Mindanao, Philippines. Fieldiana Zoology New Series 112: 1–63.

Helgen, K.M. 2005a. A new species of murid rodent (genus *Mayermys*) from south-eastern New Guinea. Mammalian Biology 70: 61–67.

Helgen, K.M. 2005b. The amphibious murines of New Guinea (Rodentia, Muridae): the generic status of *Baiyankamys* and descriptions of a new species of *Hydromys*. Zootaxa 913: 1–20.

Helgen, K.M. 2007a. A reassessment of taxonomic diversity and geographic patterning in the Melanesian mammal fauna. Ph.D. dissertation, University of Adelaide.

Helgen, K.M. 2007b. The mammal fauna of the Kaijende Highlands, Enga Province, Papua New Guinea. *In* S.J. Richards (editor), A rapid biodiversity assessment of the Kaijende Highlands, Enga Province, Papua New Guinea. RAP Bulletin of Biological Assessment 45: 52–68. Conservation International, Arlington, VA, USA.

Helgen, K.M. 2007c. A taxonomic and geographic overview of the mammals of Papua. *In* A.J. Marshall and B.M. Beehler (editors), The ecology of Papua: 689–749. Singapore: Periplus Editions.

Helgen, K.M., and T.F. Flannery. 2004. A new species of bandicoot, *Microperoryctes aplini*, from western New Guinea. Journal of Zoology (London) 264: 117–124.

Helgen, K.M., T. Leary, G. Doria, and G. Amori. In press. Catalogue of Melanesian rodents (Mammalia: Rodentia) in the Museum of Genova. Annali del Museo Civico di Storia Naturale "G. Doria", 653–686.

Hill, J.E. 1983. Bats (Mammalia: Chiroptera) from Indo-Australia. Bulletin of the British Museum (Natural History) Zoology 45(3): 103–208.

Hinton, M.A.C. 1943. Preliminary diagnoses of five new murine rodents from New Guinea. Annals and Magazine of Natural History 11(10): 552–557.

Hope, G.S. 1975. Some notes on the non-forest vegetation and its environment. Northern flank of Mt Albert Edward, Central District, Papua New Guinea. Unpublished preliminary report: 1–21. Canberra: Department of Biogeography and Geomorphology, Australian National University.

Hope, G.S. 2007. Paleoecology and paleoenvironments of Papua. *In* A.J. Marshall and B.M. Beehler (editors), The ecology of Papua: 255–266. Singapore: Periplus Editions.

Hope, G.S., and K.P. Aplin. 2007. Paleontology of Papua. *In* A.J. Marshall and B.M. Beehler (editors), The ecology of Papua: 246–254. Singapore: Periplus Editions.

Hope, G.S., and J.A. Peterson. 1975. Glaciation and vegetation in the high New Guinea mountains. *In* R.P. Suggate and M.M. Cresswell (editors), Quaternary studies: 155–162. Wellington: Royal Society of New Zealand.

Hope, G.S., T. Flannery, and Boeadi. 1993. A preliminary report of changing Quaternary mammal faunas in Subalpine New Guinea. Quaternary Research 40: 117–126.

Hope, J.H. 1976. Fauna. *In* G.S. Hope, J.A. Peterson, U. Radok, and I. Allison (editors), The equatorial glaciers of New Guinea (Result of the 1971–1973 Australian Universities' Expeditions to Irian Jaya: survey, glaciology, meteorology, biology and palaeoenvironments): 207–224. Rotterdam: A.A. Balkema.

HOUSND. 1944. Gazetteer (No. 2), New Guinea and nearby islands. 2nd ed. United States Navy Department. Hydrographic Office Publication 882: 1–254.

Hyndman, D.C., and J.I. Menzies. 1990. Rain forests of the Ok Tedi headwaters, New Guinea: an ecological analysis. Journal of Biogeography 17: 241–273.

Jackson, K.L., and P.A. Woolley. 1993. The diet of five species of New Guinean rodents. Science in New Guinea 19: 77–86.

Jacobs, L.L. 1978. Fossil rodents (Rhizomyidae & Muridae) from Neogene Siwalik deposits, Pakistan. Museum of Northern Arizona Bulletin 52: 1–103.

Johns, R.J. 1982. Plant zonation. *In* J.L. Gressitt (editor), Biogeography and ecology of New Guinea. Monographiae Biologicae 42. Vol. 1: 309–330. The Hague: W. Junk.

Krajewski, C., R. Torunsky, J.T. Sipiorski, and M. Westerman. 2007. Phylogenetic relationships of the dasyurid marsupial genus *Murexia*. Journal of Mammalogy 88(3): 696–705.

Laurie, E.M.O. 1952. Mammals collected by Mr. Shaw Mayer in New Guinea 1932–1949. Bulletin of the British Museum (Natural History) Zoology 1(10): 271–318.

Laurie, E.M.O., and J.E. Hill. 1954. List of land mammals of New Guinea, Celebes and adjacent

islands 1758–1952. London: British Museum (Natural History), 175 pp.

Leary, T., and L. Seri. 1997. An annotated checklist of mammals recorded in the Kikori River Basin, Papua New Guinea. Science in New Guinea 23(2): 79–100.

Lidicker, W.Z., Jr. 1968. A phylogeny of New Guinea rodent genera based on phallic morphology. Journal of Mammalogy 49: 609–643.

Lidicker, W.Z., Jr. 1973. A phenetic analysis of some New Guinea rodents. Systematic Zoology 22: 36–45.

Menzies, J.I. 1973. A key to rats of the genera *Rattus*, *Melomys* and *Pogonomelomys* on the New Guinea mainland. University of Papua New Guinea Department of Biology Occasional Papers 2: 1–16.

Menzies, J.I. 1990. A systematic revision of *Pogonomelomys* (Rodentia: Muridae) of New Guinea. Science in New Guinea 16(3): 118–137.

Menzies, J.I. 1996. A systematic revision of *Melomys* (Rodentia: Muridae) of New Guinea. Australian Journal of Zoology 44: 367–426.

Menzies, J.I., and E. Dennis. 1979. Handbook of New Guinea Rodents. Wau, Papua New Guinea: Wau Ecology Institute.

Miller, G.S., Jr. 1912. Catalogue of the mammals of Western Europe (Europe exclusive of Russia) in the collection of the British Museum. London: British Museum (Natural History).

Misonne, X. 1969. African and Indo-Australian Muridae: evolutionary trends. Musée Royal de l'Afrique Centrale Tervuren Belgique Annales Serie in Octavo Sciences Zoologiques 172: 1–219.

Misonne, X. 1979. Muridae collected in Irian Jaya, Indonesia. Institut Royal des Sciences Naturelles de Belgique Bulletin Biologie 51(8): 1–16.

Morren, G.E.B., Jr. 1989. Mammals of the East Miyanmin area, Telefomin District, Papua New Guinea, with notes on folk knowledge and taxonomy. Science in New Guinea 15: 119–135.

Musser, G.G. 1969. Results of the Archbold Expeditions. No. 91. A new genus and species of murid rodent from Celebes, with a discussion of its relationships. American Museum Novitates 2384: 1–41.

Musser, G.G. 1981a. Results of the Archbold Expeditions. No. 105. Notes on systematics of Indo-Malayan murid rodents, and descriptions of new genera and species from Ceylon, Sulawesi, and the Philippines. Bulletin of the American Museum of Natural History 168(3): 225–334.

Musser, G.G. 1981b. The giant rat of Flores and its relatives east of Borneo and Bali. Bulletin of the American Museum of Natural History 169(2): [67]–175.

Musser, G.G. 1982a. Results of the Archbold Expeditions. No. 108. The definition of *Apomys*, a native rat of the Philippine Islands. American Museum Novitates 2746: 1–43.

Musser, G.G. 1982b. Results of the Archbold Expeditions. No. 110. *Crunomys* and the small-bodied shrew rats native to the Philippine islands and Sulawesi (Celebes). Bulletin of the American Museum of Natural History 174(1): 1–95.

Musser, G.G. 1990. Sulawesi rodents: species traits and chromosomes of *Haeromys minahassae* and *Echiothrix leucura* (Muridae: Murinae). American Museum Novitates 2989: 1–18.

Musser, G.G. 1991. Sulawesi rodents: descriptions of new species of *Bunomys* and *Maxomys* (Muridae, Murinae). American Museum Novitates 3001: 1–41.

Musser, G.G., and M.D. Carleton. 1993. Family Muridae. *In* D.E. Wilson and D.M. Reeder (editors), Mammal species of the world: a taxonomic and geographic reference. 2nd ed: 501–755. Washington, D.C.: Smithsonian Institution Press.

Musser, G.G., and M.D. Carleton. 2005. Family Muridae. *In* D.E. Wilson and D.M. Reeder (editors), Mammal species of the world: a taxonomic and geographic reference. 3rd ed: 894–1531. Baltimore: Johns Hopkins University Press.

Musser, G.G., and L.A. Durden. 2002. Sulawesi rodents: description of a new genus and species of Murinae (Muridae, Rodentia) and its parasitic new species of sucking louse (Insecta, Anoplura). American Museum Novitates 3368: 1–50.

Musser, G.G., and L.R. Heaney. 1992. Philippine rodents: definitions of *Tarsomys* and *Limnomys* plus a preliminary assessment of phylogenetic patterns among native Philippine murines (Murinae, Muridae). Bulletin of the American Museum of Natural History 211: 1–138.

Musser, G.G., K.M. Helgen, and D.P. Lunde. 2008. Systematic review of New Guinea *Leptomys* (Muridae, Murinae) with descriptions of two new species. American Museum Novitates 3624: 1–60.

Musser, G.G., and C. Newcomb. 1983. Malaysian murids and the giant rat of Sumatra. Bulletin of the American Museum of Natural History 174(4): 327–598.

Musser, G.G., D.P. Lunde, and N.T. Son. 2006. Description of a new genus and species of rodent (Murinae, Muridae, Rodentia) from the tower karst region of northeastern Vietnam. American Museum Novitates 3517: 1–41.

Rand, A.L., and L.J. Brass. 1940. Results of the Archbold Expeditions. No. 29. Summary of the

1936–1937 New Guinea Expedition. Bulletin of the American Museum of Natural History 77(7): 341–380.

Rickart, E.A., L.R. Heaney, and R.C.B. Utzurrum. 1991. Distribution and ecology of small mammals along an elevational transect in southeastern Luzon, Philippines. Journal of Mammalogy 72(3): 458–469.

Rickart, E.A., L.R. Heaney, and B.R. Tabaranza, Jr. 2003. A new species of *Limnomys* (Rodentia: Muridae: Murinae) from Mindanao Island, Philippines. Journal of Mammalogy 84(4): 1443–1455.

Rowe, K.C., M.L. Reno, D. Richmond, R.M. Adkins, and S.J. Steppan. 2008. Pliocene colonization and adaptive radiations in Australia and New Guinea (Sahul): multilocus systematics of the Old Endemic rodents (Muroidea: Murinae). Molecular Phylogenetics and Evolution 47: 84–101.

Rümmler, H. 1938. Die Systematik und Verbreitung der Muriden Neuguineas. Mitteilungen aus dem Zoologische Museum in Berlin 23: 1–297.

Schodde, R., and J.H. Calaby. 1972. The biogeography of the Australo-Papuan bird and mammal faunas in relation to Torres Strait. *In* D. Walker (editor), Bridge and barrier: the natural and cultural history of Torres Strait: 257–300. Canberra: Australian National University.

Simmons, N.B. 2005. Order Chiroptera. *In* D.E. Wilson and D.M. Reeder (editors), Mammal species of the world: a taxonomic and geographic reference. 3rd ed: 312–529. Baltimore: Johns Hopkins University Press.

Steppan, S.J. 1995. Revision of the Tribe Phyllotini (Rodentia: Sigmodontinae), with a phylogenetic hypothesis for the Sigmodontinae. Fieldiana Zoology, New Series 80: 1–112.

Storch, G., and X. Ni. 2002. New Late Miocene murids from China (Mammalia, Rodentia). Geobios 35: 515–521.

Tate, G.H.H. 1951. Results of the Archbold Expeditions. No. 65. The rodents of Australia and New Guinea. Bulletin of the American Museum of Natural History 97(4): 183–430.

Tate, G.H.H., and R. Archbold. 1935. Results of the Archbold Expeditions. No. 3. Twelve apparently new forms of Muridae (other than *Rattus*) from the Indo-Australian region. American Museum Novitates 803: 1–9.

Tate, G.H.H., and R. Archbold. 1941. Results of the Archbold Expeditions. No. 31. New rodents and marsupials from New Guinea. American Museum Novitates 1101: 1–9.

Taylor, J.M., J.H. Calaby, and H.M. Van Deusen. 1982. A revision of the genus *Rattus* (Rodentia,

Muridae) in the New Guinean region. Bulletin of the American Museum of Natural History 173(3): [177]–336.

Thomas, O. 1919. The method of taking the incisive index in rodents. Annals and Magazine of Natural History (9)4: 289–290.

Thomas, O. 1920. New small mammals from New Guinea. Annals and Magazine of Natural History (9)6: 533–537.

United States Board on Geographic Names. 1982. Gazetteer of Indonesia. 3rd ed. Washington, DC: Defense Mapping Agency, 2 vols.

Van Dyck, S. 2002. Morphology-based revision of *Murexia* and *Antechinus* (Marsupialia: Dasyuridae). Memoirs of the Queensland Museum 48: 239–330.

Voss, R.S. 1988. Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. Bulletin of the American Museum of Natural History 188(2): 259–493.

Wahlert, J.H. 1985. Cranial foramina of rodents. *In* W.P. Luckett and J.-L. Hartenberger (editors), Evolutionary relationships among rodents, a multidisciplinary analysis: 311–332. New York: Plenum Press.

Watts, C.H.S., and P.R. Baverstock. 1994. Evolution in the Murinae (Rodentia) assessed by microcomplement fixation of albumin. Australian Journal of Zoology 43: 105–118.

Watts, C.H.S., and P.R. Baverstock. 1996. Phylogeny and biogeography of some Indo-Australian murid rodents. *In* D.J. Kitchener and A. Suyanto (editors), Proceedings of the First International Conference on Eastern Indonesian-Australian Vertebrate Fauna, Manado, Indonesia, November 22–26, 1994: 47–50. Perth: Western Australian Museum (for Lembaga Ilmu Pengetahuan Indonesia).

Weksler, M. 2006. Phylogenetic relationships of oryzomyine rodents (Muroidea: Sigmodontinae): separate and combined analyses of morphological and molecular data. Bulletin of the American Museum of Natural History 296: 1–149.

Whitmore, T.C. 1984. Tropical rain forests of the Far East. 2nd ed. Oxford: Clarendon Press.

Willett, M.S., G.L. Stevens, and R.L. Rudd. 1989. An analysis of a small mammal community in a Papua New Guinea mid-montane rain-forest. The Wasmann Journal of Biology 47: 1–67.

Woolley, P. 1990. Wildlife over the border. Paradise Magazine 78: 5–8.

Ziegler, A.C. 1982. An ecological check-list of New Guinea Recent mammals. Monographiae Biologicae 42: 863–894.