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Systematic Review of New Guinea *Leptomys* (Muridae, Murinae) with Descriptions of Two New Species

GUY G. MUSSER¹, KRISTOFER M. HELGEN², AND DARRIN P. LUNDE³

ABSTRACT

Two new species of the endemic New Guinea rodent genus *Leptomys* Thomas, 1897, are described: *L. paulus*, indigenous to the montane forests in the Owen Stanley Range in eastern New Guinea, and *L. arfakensis*, known only from the Arfak Mountains on the Vogelkop Peninsula in western New Guinea. These descriptions are presented within a taxonomic review of *Leptomys* based on all known specimens in collections of the world's museums. In addition to the new species, the morphological attributes and geographic distributions of three others are documented. *Leptomys elegans* occurs in southcentral and southeastern New Guinea both north and south of the Central Cordillera, ranging from the Kikori River Basin in the west to the southern slopes of the Owen Stanley Range, then extending round to the north side of the Cordillera in the Maneau Range, and in the outlying highland block of Mount Victory. *Leptomys signatus* is recorded only from the Fly and Kikori River drainages south of the Central Cordillera. *Leptomys ernstmayri* is found in montane forests of the eastern Central Cordillera (Aroa River to Mt. Karimui), reaches to the outlying mountains on the Huon Peninsula and the Adelbert Range, and also occurs in the isolated Foja Mountains of far western New Guinea. Judged by variation in qualitative and morphometric external, cranial, and dental traits associated with available samples, *L. arfakensis*, n. sp., is likely more closely related to *L. elegans* and *L. signatus*, all with large bodies and relatively short tails, than to *L. ernstmayri* and *L. paulus*, n. sp., that are characterized, among other features, by smaller body size and relatively longer tails. There is significant phenetic divergence among the geographic samples identified here as *L. ernstmayri*, and additional inquiry, especially utilizing

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data from molecular sources, is required to determine whether this intersample variation reflects the presence of separate species, each endemic to the Huon Peninsula, Adelbert Range, Central Cordillera, and possibly the Foja Mountains, or instead represents montane variation within a single morphologically variable species.

INTRODUCTION

The attributes *thin*, *fine*, *small*, *slender*, and *delicate* are attached to the Greek word *leptos* and perhaps some or all of those adjectives were in the thoughts of Oldfield Thomas when he combined that prefix with *mys* (“mouse” or “rat”) to form *Leptomys*, a genus based on one specimen that was also designated as the holotype for *L. elegans* (Thomas, 1897). By 1938 two additional species had been discovered, *L. ernstmayri* (Rümmler, 1938) and *L. signatus* (Tate and Archbold, 1938), and we describe two more here. The meanings of *leptos* are certainly descriptive, for the species of *Leptomys* are fine, handsome animals with rich tawny brown or buffy gray dorsal body fur, and contrasting white or grayish white underparts, a slender head and muzzle, thin tail, dainty front and hind digits, elongate hind feet, long and slender skull, and delicate molars with simple chewing surfaces. “A most elegant animal,” wrote Peter Dwyer in his field journal after observing a captive *L. elegans*. In life, our new species, *L. paulus* (fig. 19), epitomizes the Greek attributes.

We now know that species of *Leptomys* are terrestrial, nocturnal, carnivorous, and inhabit tropical lowland and montane rain forests on New Guinea, but between 1897 and 1938 only a handful of specimens formed the basis of our meager understanding of biological diversity within the genus. Results from biological surveys, especially those made during the decades since the 1950s have generated many more samples, some of them associated with reliable ecological information, from a greater geographic range. We have studied all the specimens, which are scattered in collections of the world’s museums, and used the data derived from them to form a new estimate of the diversity of species within *Leptomys* and their geographic distributions. Our analyses of variation in quantitative and qualitative external, cranial, and dental traits reveal the presence of at least five species. We also summarize all ecological information that is presently associated with each species, discuss

possible zoogeographical significance of the geographic distributions, and suggest the nature of future inquiries needed to test our results.

Ours is strictly an alpha-level taxonomic investigation. We do not explore phylogenetic affinities between *Leptomys* and other genera traditionally regarded to be closely related: *Hydromys*, *Baiyankamys*, *Crossomys*, *Parahydromys*, *Pseudohydromys*, *Paraleptomys*, *Microhydromys*, and *Xeromys*. These, in combination with *Leptomys*, are at the heart forming the iconography of endemic Australo-Papuan murids. Identified informally as a recognizable group or formally as tribe, subfamily, or even family (Flannery, 1995; Helgen, 2005b 2007a; Musser and Carleton, 2005; Tate, 1951), members of this assemblage are primarily carnivorous and demonstrate a remarkable evolutionary radiation in geographic isolation that resulted in adaptive morphologies ranging from amphibious to shrewlike ecologies. The cladistic position of *Leptomys* within this assemblage is the subject of inquiries to be completed at a later time.

MATERIAL AND PROCEDURES

INSTITUTIONS AND SPECIMENS: Specimens cited by catalog number are stored in the collections of the Australian Museum, Sydney (AM); American Museum of Natural History, New York (AMNH); Bernice P. Bishop Museum, Honolulu (BBM-NG); Natural History Museum, London (BMNH); Australian National Wildlife Collection, Canberra (CSIRO); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); Museo Civico di Storia Naturale di Genova, Genoa (MSCN); Museum Zoologicum Bogoriense, Cibinong, Indonesia (MZB); Papua New Guinea National Museum and Art Gallery, Port Moresby, Papua New Guinea (PNGNM); University of Papua New Guinea, Port Moresby, Papua New Guinea (UPNG); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); and Museum für Naturkunde, Humboldt-

Universität, Berlin (ZMB). These acronyms preface catalog numbers referring to specimens listed in the gazetteer, tables, text, and figure legends. Most of the material consists of standard museum preparations, a stuffed skin and accompanying cranium and mandible. A few series are stored in fluid preservative (in particular at AM and BBM-NG) and from some of these we extracted skulls.

MEASUREMENTS: Values (in millimeters) for total length and length of tail are those recorded by collectors on labels attached to skins; subtracting length of tail (LTV) from total length produced a value for length of head and body (LHB). Values for length of hind foot (LHF), which includes claws, were obtained either from skin labels or from our measurements of dry study skins; those for length of ear (LE) come from collector's measurements notated on skin labels or in field journals (we assume, but are not certain, for all specimens, they represent greatest length from the notch to the distal margin of the pinnae). The distal one-tenth to one-half of the tail is white in nearly all examples of *Leptomys*. We measured the length of this white tail tip (WTT) on the dorsal surface of each tail and expressed the result as a percentage of total tail length.

We used digital calipers to measure (recorded to the nearest 0.01 mm) the following cranial and dental dimensions (listed in the sequence they appear in tables):

ONL	occipitonasal length (= greatest length of skull)
ZB	zygomatic breadth
IB	interorbital breadth
LN	length of nasals
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 (palatal bridge)
BBP	breadth across bony palate at first molars
BMF	breadth of mesopterygoid fossa
LIF	length of incisive foramina
BIF	breadth of incisive foramina
LB	length of bulla
CLM	crown length of maxillary molar row

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

Limits of these measurements are illustrated in figure 1 and verbally defined by Musser and Newcomb (1983). Only the cranial and dental measurement values obtained were incorporated in the multivariate analyses. Values from external measurements provide an appreciation of general body size and lengths of appendages, but were excluded from any multivariate analyses. Values for length of nasals (not illustrated in fig. 1) can also be used as a reasonable estimate of rostral length for samples of *Leptomys*. In specimens of other murine genera, we measure length of rostrum from tip of the nasals to posterior margin of the zygomatic notch (anterior edge of the dorsal maxillary root of the zygomatic plate). There is no zygomatic notch in examples of *Leptomys* and we could not identify a different proximal endpoint for the rostral measurement that would provide a consistent measurement from which we could obtain accurate results. Length of first upper molar (not illustrated in fig. 1) was measured across its greatest crown length. We included length of the auditory bulla (LB) in the measurements used to calculate the ratio diagram in figure 21, but omitted it from all other quantitative analyses.

AGE AND SEX: Old adults, adults, and young adults (as defined by Musser and Heaney, 1992: 5) were lumped as "adults" and measurements derived from them are used in the multivariate analyses and tables of univariate descriptive statistics. Because our data demonstrate no consistent patterns of sexual size dimorphism within available samples of any species of *Leptomys*, our univariate descriptive statistics and multivariate analyses include males combined with females.

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

Plottings of specimen scores in cluster analyses provided visual patterns that reflect similarity or contrast in the combination of all cranial and dental dimensions among geographic samples of a single species or among samples of different species. Principal compo-

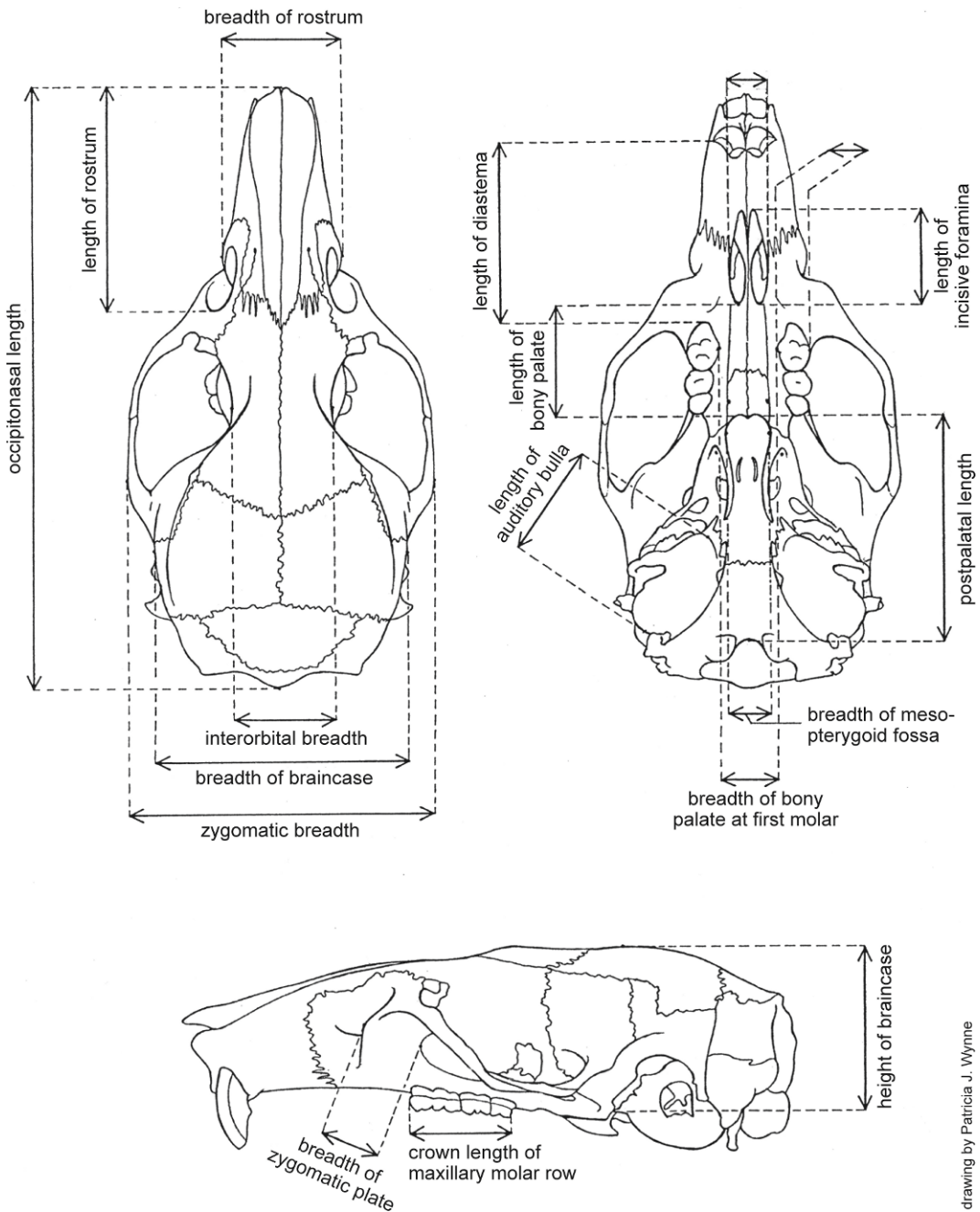


Fig. 1. Diagram of the cranium of an adult *Bunomys chrysocomus* (from Sulawesi) showing limits of cranial and dental measurements. Abbreviations are explained in the text.

nents and discriminant-function analyses were computed using the combination of cranial and dental measurements indicated in various tables in the text. All measurement values were

transformed to natural logarithms. Principal components were extracted from a covariance matrix. Canonical variates were extracted from the discriminant-function analyses. The

software program Statistica 6.0 was used for all analytical procedures.

RATIO DIAGRAM: Data used to construct the ratio diagram in figure 21 were derived from values for means, standard deviations, and sample sizes of variables listed in table 11. 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.

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 Musser et al. (1998) for cranial morphology. Names of cusps and cusplets of maxillary (upper) and mandibular (lower) molars are noted in figure 11; sources of this terminology are explained by Musser and Newcomb (1983: 332).

GAZETTEER AND SPECIMENS

Place names and altitudes were taken from skin tags, field journals, or published expedition summaries. Bonaccorso (1998), Cole et al. (1997), Flannery (1995), Leary and Seri (1997), Taylor et al. (1982), Laurie and Hill (1954), HOUSND (1944), and USBGN Indonesia (1982) were the sources consulted for most geographic coordinates. The number

preceding each place corresponds to the same numbered locality on the maps in figures 2 and 3. With the exception of two *L. signatus* that are documented by photographs (see the account of that species), only specimens we personally examined and identified are included; to our knowledge this incorporates all available examples of *Leptomys* in collections of the world's museums.

Leptomys arfakensis, n. sp.

INDONESIA

1. West Papua, Irian Jaya Barat Province, “**Arfak Mountains**” (ca. 01°09'S, 134°00'E), 1000 m (BMNH 29.5.27.22 and 29.5.27.23 [holotype of *Leptomys arfakensis*, n. sp.]).

Leptomys signatus

PAPUA NEW GUINEA

2. Western Province, **north bank of Fly River opposite Sturt Island** (Sturt Island Camp, 08°15'S, 142°15'E), near sea level (AMNH 105370, 105792 [holotype of *Leptomys signatus*], 105793, 105794). See Rand and Brass (1940) for map and description of the location.

3. Southern Highlands Province, **NNW slopes of Mount Bosavi** (06°33'S, 142°50'E), 1400 m (BBM-NG 103319, 103263).

4. Gulf Province, **Darai Plateau** (07°08'S, 143°37'E), 380 m (two voucher specimens deposited at UPNG). See Leary (2004) for additional information.

Leptomys elegans

PAPUA NEW GUINEA

5. Southern Highlands Province, Kikori River Basin, **Mount Sisa** (ca. 06°09'S, 142°45'E): “**Mount Sisa**” (AM 14167; PNGNM 23932–34); **Mount Sisa**, 1500 m (AM M15457); **Bobole**, 1100–1450 m (AM M15573, 17129); **Fau**, 750 m (AM M17132, 17321); **Magidobo**, 1450 m, southern slopes of Mount Sisa (AM M18618); **Namosado**, 750–1000 m (AM M17130), 800 m (AM M14171). Leary and Seri (1997) provide a map and other

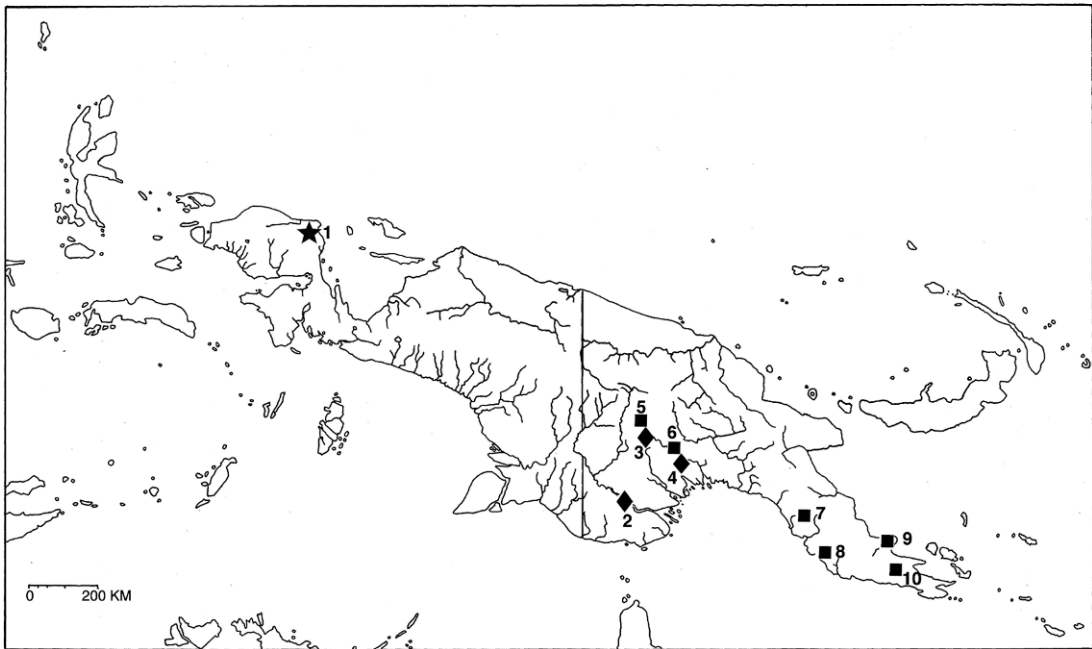


Fig. 2. Collection localities for specimens representing the *Leptomys* with larger body size: *L. arfakensis* (locality 1), *L. signatus* (localities 2–4), and *L. elegans* (localities 5–10). Numerals refer to numbered localities in the gazetteer where locality information is provided and specimens are identified by museum acronyms and catalog numbers.

relevant information for Mount Sisa and environs; Plowman (1983) presents floristic, climatic, and other information for Magidobo; see also Dwyer (1984).

6. Southern Highlands Province, **Wassi Falls**, (06°44'S, 143°36'E), 490 m (AM M32103). See Leary and Seri (1997) for map and additional information.

7. Central Province, Wharton Range, **Mafulu** (08°31'S, 147°00'E), 1253 m (AMNH 104199, 104200). See Archbold and Rand (1935) for map and description of the locality.

8. Central Province, **Astrolabe Range**: “**behind Port Moresby**” (MSCN 32988); **Sogeri** (09°25'S, 147°26'E), 410 and 450 m (AMNH 108449, 108450); “**Karema, Brown River Forest Station, 40 km NW Port Moresby**” (09°12'S, 147°14'E, for Karema), about 20 m (see Zweifel, 1972) (BBM-NG 60171); **Baruari Rest House** (09°30'S, 147°20'E), 520 m (AMNH 108447, 108448); “**Astrolabe Gebirge**” (ZMB 31782).

9. Northern (= Oro) Province, **Mount Victory, Kwin River** (09°12'S, 149°05'E), 800 m (AM M29378).

10. Milne Bay Province, Maneau Range, **north slopes of Mount Dayman** (Number 3 camp, 09°49'S, 149°16'E), 700 m (AMNH 158203, 158204). See map and description of the locality in Brass (1956).

Leptomys ernstmayri

INDONESIA

11. West Papua, Papua Province, Mamberamo Basin, **Foja Mountains, near Bog Camp** (02°35'S, 138°35'E), 1150 m: (MZB, uncataloged, field number KMH 1959).

PAPUA NEW GUINEA

12. Madang Province, **Schrader Range** (ca. 05°04'S, 144°14.5'E), **Hagahai**, altitude unrecorded (UPNG 3600, 3619; M. Yaroo, in litt., 2005).

13. Chimbu Province, **Mount Karimui** (06°35'S, 144°48'E): upper east face, 1750 m (AM M14862); northeastern slopes, 2200 m (BBM-NG 105313).

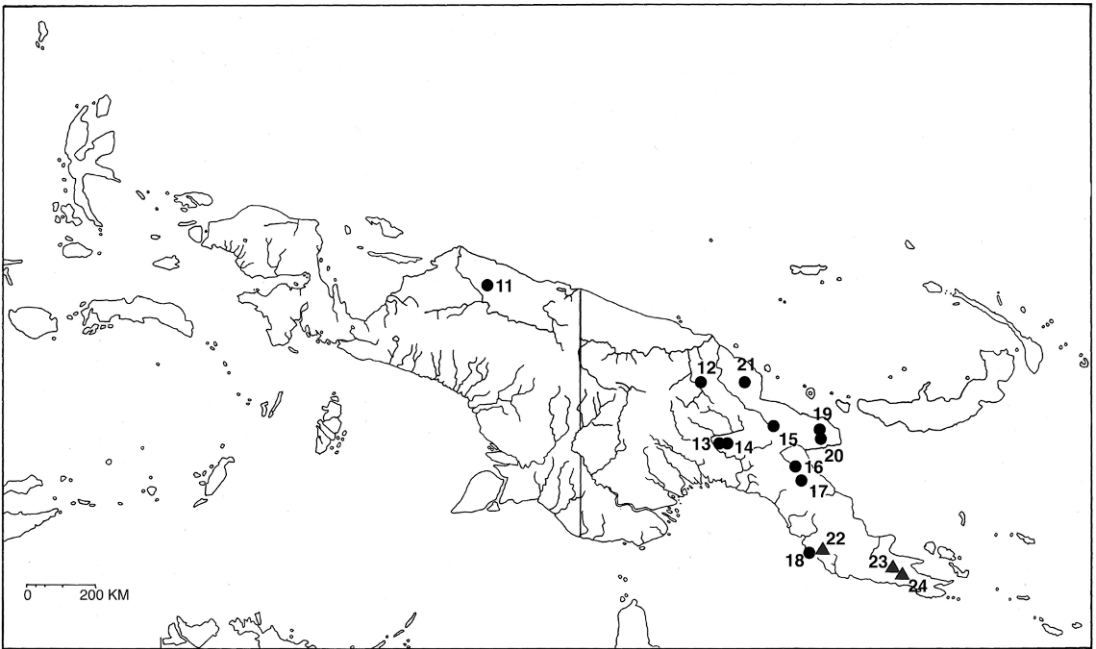


Fig. 3. Collection localities for specimens representing the *Leptomys* with smaller body size: *L. ernstmayri* (localities 11–21) and *L. paulus* (localities 22–24). Numerals refer to numbered localities in the gazetteer where locality information is provided and specimens are identified by museum acronyms and catalog numbers.

14. Eastern Highlands Province, **Okapa area** (06°36'S, 145°01'E): **Kamila**, 1900 m (AMNH 191405–407); **Purosa**, 1970 m (AMNH 191408). See Brass (1964) for map and descriptions of localities.

15. Eastern Highlands Province, **Kratke Range** (ca. 06°13'S, 146°01'E): **Arau District**, 4000–5000 ft (= 1220–1524 m) (BMNH 50.1256); **Kassam**, 1350 m (AMNH 191409; see Brass, 1964, for map and locality description), 1400 m (BBM-NG 54966, 54995); **Kambaidam**, 4000 ft (= 1220 m) (BMNH 50.1252–55).

16. Morobe Province, **Mount Missim** (07°13'S, 146°49'E), 1980 m (BBM-NG 160978); see Rudd and Stevens (1994, 1996) and Willett et al. (1989); 6700 ft (= 2030 m) (MCZ 29903). Two additional specimens at PNGNM (PNGNM 24878, 24880) without collection localities probably originate from the Wau Ecology Institute (07°21'S, 146°43'E) in Morobe Province.

17. Morobe Province, Bowutu Mountains, **Lake Trist** (07°29'S, 146°58'E), 1600 m (USNM 357412, 357418).

18. Central Province: **Aroa River: Head of Aroa River**, above 1200 m, (9°05'S, 146°48'E) (BMNH 5.11.28.22); **Avera**, on the Aroa River, 08°57'S, 146°57'E, ca. 1200 m (see Tate, 1947; Heron, 1975) (BMNH 3.12.1.5, 3.12.1.9).

19. Morobe Province, Huon Peninsula, **Ogeramnang** (06°26'S, 147°22'E), 1785 m: ZMB 42400 (holotype of *Leptomys ernstmayri*). See Van Deusen (1978), where this locality is mapped.

20. Morobe Province, Huon Peninsula, Rawlinson Range, **Gang Creek**, east flank of Mount Rawlinson (06°33'E, 147°23'E), 4400 ft (= 1340 m) and 4500 ft (= 1370 m) (AMNH 194931–42). Van Deusen (1978) provided a map showing this locality.

21. Madang Province, **Adelbert Range** (ca. 04°54'S, 145°19'E): **5 km north of Wanama**, 1200 m (BBM-NG 103799); **14 km NNW of Wanama**, 1500 m (BBM-NG 103894, 103917, 103918, 104008, 104081, 104172, 104274, 104320, 104345, 104346, 104380; PNGNM 22791).

Leptomys paulus, n. sp.

PAPUA NEW GUINEA

22. Central Province, Astrolabe Range, **Kagi** (on Kokoda Road, 09°07'S, 147°36'E), 1500 m (AMNH 108451, 108452).

23. Milne Bay Province, Maneau Range, **north slopes of Mount Dayman**, (09°49'S, 149°16'E), 1370 m (**Atairo ravine**) and 1540 m (**Number 2 Camp or Middle Camp**) (AMNH 158199–201, 158202 [holotype of *Leptomys paulus*]). These localities were described and mapped by Brass (1956).

24. Milne Bay Province, Maneau Range, Agaun Region: **Mount Waruman** at Kamaya Village (09°53'S, 149°22'E), 1300 m (AM M28879, M28880, M29306, M29308); **near Munimun Village** (09°53'S, 149°23'E), 1300 m (AM M29301, M29560, M29561); **Dumae Creek**, below Garitin Pass, on the road from Agaun to Bonenau (09°53'S, 149°23'E), ca. 1400 m (CSIRO 29433), 1525 m (BBM-NG 109273); **Simun Creek**, 1.6 km north and 1.0 km east of Agaun (09°55'S, 149°24'E), 1240 m (BBM-NG 109514, 109518, 109522); **Iana River** (09°53'S, 149°21'E), 1500 m (BBM-NG 109477–109480). See Cole et al. (1997) for further details regarding BBM-NG specimens and collection localities.

CHARACTERISTICS OF THE GENUS

“By the kindness of Dr. Gestro, I have been entrusted with the examination of the large collection of Mammals made by Dr. Lamberto Loria in British New Guinea between 1890 and 1893, and presented by him to the Museo Civico, Genoa.” With this statement Thomas (1897: 606) introduced his report identifying the several hundred specimens obtained by Loria. Some of the individuals represented undescribed taxa, among these an adult female rat that Thomas used to describe a new genus, *Leptomys* (“Form murine; eyes small. Tail rather short. Hind-foot long. Mammae 0–2 = 4. Skull long, narrow and low. Anteorbital foramina scarcely broader above than below. Molars strictly *Hydromyine* in structure, but 3/3 in number” Thomas, 1897: 610), and a new species, *L. elegans* (ibid.):

Fur close, soft and velvety. General colour rufous fawn, browner on the back, especially anteriorly; shoulders, flanks and hips bright rufous. Face darker; upperside of muzzle black, extending backwards to form an indistinct ring round the eyes. Ears rather small, naked, blackish. Upper lips, lower part of cheeks, inner side of arms, and whole of undersurface from chin to anus creamy white, the hairs white to their bases. Upper surface of hands and feet thinly haired, white; pollex with a small nail; fifth hind toe reaching only to the base of the fourth. Tail little longer than the body without the head, very finely scaled (15 or 16 to the centimetre) thinly hairy, its basal three-fourths brown above, whiter below, its tip whitish all around. Skull long and low, the cranial part but little higher than the muzzle; zygomata slender, not widely expanded. Supraorbital edges parallel, not ridged. Bullae small. Incisors broad, flattened in front, pale yellow with the tips white, both above and below. Molars typically hydromyine in structure; m^3 well developed both above and below.

After listing measurements, Thomas (1897: 611) noted that the specimen “considerably” resembled “*Uromys levipes*” (= *Paramelomys levipes*), but instead represented another member of the “subfamily *Hydromyinae*” with representatives in New Guinea, Australia, and the Philippines. “Dr. Loria is much to be congratulated on the addition that this animal, externally so like an ordinary rat, has made to our knowledge of the subfamily *Hydromyinae*” (Thomas, 1897: 611).

Body conformation of *Leptomys* is “like an ordinary rat” only in comparison with its close relatives, most of which deviate from the generally perceived ratlike confirmation (typified by *Rattus norvegicus* or *R. rattus*, for examples) by exhibiting amphibious adaptations and habits (*Crossomys*, *Baiyankamys*, *Hydromys*, and *Parahydromys*) or morphologies associated with terrestrial small-bodied mice or shrews specialized for foraging in dense moss and leaf litter (*Microhydromys* and *Pseudohydromys*). Neither amphibious nor

shrewlike, *Leptomys* has short and dense fur, a bicolored tail equal to or longer than head and body length, elongate hind feet, moderately large ears, and a long slender muzzle (figs. 15, 19). This combination of traits signals adaptation to moving over the forest floor by a hopping gait and the ability to escape predators by leaping in unexpected directions. *Paraleptomys* has a similar body form (see the photograph of a live animal in Flannery, 1995: 252). The relatively meager biological data compiled for *Leptomys* indicates the species of the genus to be terrestrial, nocturnal, and largely carnivorous murines that live in underground nests dug in the forest floor of tropical lowland evergreen and tropical montane evergreen rainforests (see accounts of species). Except for samples of *Leptomys* taken in the outlying Arfak and Foja mountains of western New Guinea (figs. 2, 3), all samples of *Leptomys* have been obtained from the mountains and southern coastal plain of the eastern half of the island (Papua New Guinea).

Below we provide an emended diagnosis for *Leptomys* followed by a generic description based primarily upon anatomical features of skins, skulls, and dentitions; a few other anatomical systems are also referenced, along with chromosomal and some molecular information.

We also include a section contrasting the morphological characteristics of *Leptomys* with those of *Paraleptomys*, another hydromyine endemic to New Guinea. Among hydromyines, *Paraleptomys* most closely resembles *Leptomys* in basic cranial shape, body size and conformation, and other traits (Tate, 1951; Lidicker, 1968; Helgen, 2007b). Geographic distributions of species of *Paraleptomys* and *Leptomys* do not overlap but appear to replace each other in checkerboard fashion on mountain ranges lying north of the Central Cordillera, and in an east-west pattern along the Central Cordillera, with *Leptomys* in the eastern region of the Central Cordillera, and *Paraleptomys* in the western portion (see section on Zoogeography). The close ecomorphological resemblance between the two genera may partly explain their geographic patterning.

This general morphological and probable ecological similarity of *Leptomys* and

Paraleptomys, along with their nonoverlapping geographic ranges, prompted one reviewer of our manuscript to ask us whether we are “certain that *Leptomys* is monophyletic to the exclusion of *Paraleptomys*”. We are, and we insert comparisons between the two genera to bolster our contention. We will not address whether *Paraleptomys* is phylogenetically more closely related to *Leptomys* than to some other hydromyine (Musser and Carleton, 2005) or whether the two genera together form a monophyletic cluster separate from other hydromyine genera—these are subjects outside the scope of our present inquiry (see the Introduction).

Leptomys Thomas, 1897: 610

TYPE SPECIES: *Leptomys elegans* Thomas, 1897:610.

EMENDED DIAGNOSIS: A genus of hydromyine in the subfamily Murinae, family Muridae (as Murinae is delimited by Carleton and Musser, 1984; as the contents of Murinae and Muridae are presented by 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 moderately short, dense, and silky or velvety, upperparts tawny brown, ventral coat short and dense, ranging from white everywhere to grayish white (that is washed with buff in some specimens); (2) muzzle long and narrow; (3) narrow and short bald middorsal strip between eyes and shoulders; (4) tail slender and shorter, coequal to, or longer than head and body (LT/LHB ranges from 66% to 128% in adults), tail scales very small and slightly swollen, their annuli abutting each other (not overlapping), three short hairs associated with each scale, proximal portion of tail brownish gray above, white or mottled below, distal one-fifth to one-half of tail white; (5) dorsal surfaces of front and hind feet white, hallux with claw, hind foot long and narrow with full complement of plantar tubercles in some samples, hypothenar pad absent or reduced in size in other samples; (6) two pairs of inguinal teats; (7) rostrum long and slender, interorbital and postorbital margins smooth, zygomatic arches flare moderately from sides

of skull, braincase smooth and globular, interparietal about as long as wide (diamond-shaped), occiput deep, slight to no cranial flexion; (8) zygomatic plate narrow, its anterior margin concave and not projecting beyond dorsal maxillary root of zygomatic arch, its posterior edge set just behind front of first molar, superficial masseter inserting on pronounced tubercle at base of ventral zygomatic root; (9) squamosal intact except for large subsquamosal foramen, parietal does not project ventrad beyond temporal beading to form part of lateral braincase wall; (10) alisphenoid struts wide; (11) incisive foramina wide and moderately short, their posterior margins ending far anterior to front faces of first molars; (12) molar rows parallel, bony palate long and wide, its posterior margin projecting beyond back faces of third molars, palatal surface smooth with shallow palatine grooves, posterior palatine foramina level with contact between first and second molars; (13) roof of mesopterygoid fossa generally intact, penetrated by small irregular openings in some specimens; (14) pterygoid plates narrow and complete (no sphenopterygoid openings), with shallow pterygoid fossae; (15) ectotympanic (auditory) bulla small relative to skull size, bullar capsule incompletely covering periotic, which is exposed as an expansive medial wedge, posterior wall of carotid canal formed by periotic and posterior margin of eustachian tube; (16) derived carotid circulatory pattern (character state 3 of Carleton, 1980; pattern 3 described by Voss, 1988), as indicated by absent stapedial foramen, sphenofrontal foramen, squamosal-alisphenoid groove, and groove on pterygoid plate between middle lacerate foramen and foramen ovale; (17) dentary slim, ramus long and cylindrical between incisor and molar row, low ascending ramus, delicate coronoid process, prominent condyloid and angular processes, end of alveolar capsule hidden in body of ramus at level of condyloid processes; (18) upper and lower incisor enamel smooth (unmarked by grooves), uppers orange or pale orange, lowers paler, uppers opisthodont; (19) first and second upper molars (maxillary) each with four roots, third upper molar with three roots, lower molars (mandibular) each with two roots; (20) molars brachydont and narrow,

occlusal surfaces cuspidate in juveniles but transform into shallow basins in adults, (21) labial cusps (t3, t6, and t9) absent or undetectable on upper molars, cusp t7 present on first upper molar, cusp t7 and anterolabial cingulum present on second upper molar in different frequencies depending upon geographic sample and species, posterior cingulum absent from first and second upper molars but present on second (seen in young animals), third upper molar very small relative to others in toothrow; (22) anteroconid formed of large anterolingual and anterolabial cusps, antero-central cusp absent, anterolabial cusp absent from second and third lower molars, no anterior labial cusplet on first and second lower molars, but posterior labial cusplet present on first, posterior cingulum wide and narrow on first and second molars; (23) phallus has blood sinus in wall of glans extending into the urethral lappets (Lidicker, 1968); (24) spermatozoan with sperm head bearing three elongate processes (one apical and two ventral), spermatozoan tail long (Breed and Aplin, 1994); (25) karyotype with $2n = 48$ (Donnellan, 1989).

DESCRIPTION: Thomas's description of external traits is accurate. In all samples of *Leptomys* the adult dorsal pelage is soft, dense, and short (6–12 mm long, depending on the species), and either velvety or silky to the touch. The black-tipped guard hairs either match the overhairs in length or barely extend beyond them, which partly gives the fur its uniform velvety appearance. Upperparts are tawny brown with dark brown highlights over back and rump and buffy along sides of body, thighs, and upper arms (figs. 4–6, 15, 19). Overhairs in the dorsal pelage are mostly gray with brown or buff tips. This dorsal coloration applies to all species except *L. signatus*, which has a pale buffy gray dorsal coat without the rich buff and dark brown tones seen in the other species. The head is the same color as the back in all species except *L. signatus*, which displays a large and conspicuous white blaze (fig. 4). Some specimens of *L. elegans* have a distinct but much less pronounced pale mark on the head between the eyes (evident in AM, AMNH, and PNGNM samples). Between the eyes and shoulders the fur is permanently parted to reveal a middorsal strip

of balding skin 10–15 mm long and 1–2 mm wide. The pattern is conspicuous in species with short coats but less detectable in the longer pelage of *L. paulus*, n. sp. The moderately large and dark brown pinnae appear naked but are actually scantily covered with minute dark hairs. Long mystacial and superciliary vibrissae extend well beyond the pinnae when laid against the head, the genal vibrissae reach the base of the pinnae, and the usual murine array of facial submental and interramal sensory hairs and ulnar and tarsal vibrissae are present. A dark brown mask around the eyes extends onto the muzzle in some species but not others. The muzzle at base of the mystacial vibrissae appears unpigmented in one species (because only short scattered pale hairs cover it) but is brown or grayish brown in all the other species (due to the dense covering of pigmented hairs), and the cheeks are white.

The ventral coat is also soft, dense, and shorter (5–6 mm long) than the dorsal pelage, and the underparts vary in coloration (figs. 4–6). Many specimens of *Leptomys ernstmayri* and *L. paulus*, n. sp., are grayish white, some with a pale or dark buffy wash, or whitish gray over most of the venter; a white patch or narrow strip extends from chin to chest in some individuals and many have a white inguinal region. The grayer and buffy tones result from hairs with gray bases and short unpigmented or buffy tips; the paler tones (whitish gray) reflect hairs with gray bases and longer white tips. Underparts are white everywhere (hairs are unpigmented from base to tip) in other specimens, particularly those in samples of *L. elegans*, as Thomas described the holotype (“creamy white”), *L. signatus*, and *L. arfakensis*, n. sp.

The tail averages much longer than head and body in the species of *Leptomys* with smaller body size, *L. ernstmayri* and *L. paulus*, n. sp. Among those physically larger *Leptomys*, the tail is about coequal to length of head and body in *L. signatus* and *L. arfakensis*, n. sp., and shorter than the head and body in *L. elegans* (tables 2, 4). The tail is covered in annuli of very small, slightly swollen, and inconspicuous scales (15–20 per cm). The scale hairs (three emerge from beneath each scale) are fine and laid flat

against the tail so it appears naked. From about one-fifth to one-half of the distal portion of the tail is all white (depending on the species and geographic sample), the dorsal proximal region is brownish gray, and the ventral surface below this brownish gray segment ranges from white to mottled.

Dorsal surfaces of front and hind feet, including digits and claws, are all white and densely covered with short silvery hairs that form sparse tufts at the base of each claw. The area proximal to ankle and wrist is brown. The second digit of the front foot is half the length of the third, which is the longest; the fourth is slightly shorter, and the fifth is the shortest, extending just beyond the base of the adjacent digit. The hind foot is long and narrow, 25%–28%, on average, of head and body length, depending upon the species (Tate, 1951: 222, considered *Leptomys* to be “specialized through the considerable elongation of the hind foot, which may function as an incipiently hopping organ”). The first digit is very short, its claw barely or not quite reaching base of the adjacent digit; the three middle digits are longest and subequal in length; the fifth digit is short but longer than the first, its claw reaching to proximal third of second phalanx. Palmar surfaces are naked and brown, and possess the usual complement of five pads (three metacarpals, a thenar, and smaller hypothenar). A naked plantar surface, which is partially brown and adorned with four conspicuous interdigital pads, is common to all species of *Leptomys*, but presence or absence along with size of the hypothenar is variable among samples. In all species, the thenar is elongate and conspicuous. By contrast, the hypothenar is either absent or ranges from a tiny nubbin (not always evident on dry skins and best detected in fluid-preserved material) to a moderately large pad (but always smaller than the thenar), depending upon the species and geographic samples.

In all the material we have examined, females have two pairs of teats, both inguinal in position, as previously noted by Thomas (1897: 610) and others (Tate, 1951, and Flannery, 1995, for example).

The skull in all species of *Leptomys* is elongate (figs. 7–10). The rostrum is long and slender as viewed from a dorsal perspec-



Fig. 4. **Left:** *Leptomys elegans* (AMNH 158204), an adult male from north slopes of Mount Dayman, 700 m, in the Maneau Range. External measurements: LHB = 160 mm, LTV = 164 mm, LHF = 43 mm, LE = 22 mm. **Right:** Holotype of *Leptomys signatus* (AMNH 105792), an adult female from north bank of the Fly River opposite Sturt Island. External measurements: LHB = 144 mm, LTV = 151 mm, LHF = 38 mm, LE = 19 mm. See table 1 for cranial and dental measurements.

tive, its lateral margins broken only by the slight bulge of each nasolacrimal canal. Dorsolateral outlines of the interorbital and postorbital regions are smooth, without ridging. The cranium is smooth and oval in

outline: the temporal ridges are indicated only by indistinct roughened places along the squamosal-parietal sutures, each lamboidal ridge forms an inconspicuous linear beading, and each mastoid is only slightly inflated.



Fig. 5. **Left:** *Leptomys ernstmayri* (AMNH 194931), an adult female from Gang Creek, 1340 m, east flank of Mount Rawlinson, Huon Peninsula. External measurements: LHB = 146 mm, LTV = 166 mm, LHF = 39 mm. **Right:** Holotype of *Leptomys paulus* (AMNH 158202), an adult female from north slopes of Mount Dayman, 1370 m, in the Maneau Range. External measurements: LHB = 127 mm, LTV = 163 mm, LHF = 36 mm, LE = 21 mm. See table 1 for cranial and dental measurements.



Fig. 6. Holotype of *Leptomys arfakensis* (BMNH 29.5.27.23), an adult female, from the Arfak Mountains, 1000 m. External measurements: LHB = 151 mm, LTV = 146 mm, LHF = 36 mm, LE = 21 mm. See table 1 for cranial and dental measurements.

The interparietal is roughly diamond-shaped, slightly wider than long. Thin zygomatic arches gently bow outward from sides of the skull, the jugal component of each one is short.

From a lateral view, the convex dorsal outline of the cranium arches above the dorsal plane of the rostrum, and continues back to define the arcuate posterior outline of a deep

occiput, which overhangs the occipital condyles. The rostrum is deep and somewhat rectangular in outline, the nasals and premaxillaries project as a short tube well beyond the incisor faces, and the nasolacrimal capsules are only slightly inflated. The concave anterior margin of the narrow zygomatic plate does not project anterior to the dorsal maxillary root of the zygomatic arch (no zygomatic notch). Most of the ventral maxillary root of the zygomatic plate originates anterior to the first molar, but the posterior third of the root is situated above the front third of the molar. The squamosal root of the zygomatic arch is located low on the side of the braincase. Dorsal to the squamosal root the wall of the braincase is formed entirely by the squamosal (without the contribution of a ventrally projecting extension of the parietal). Posterior to the squamosal zygomatic root and dorsal of the auditory bulla, the squamosal is intact and forms a seamless union with the exoccipital in most specimens, but in a few others the squamosal-exoccipital suture is perforated by a small or minute subsquamosal foramen. 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 the texture associated with 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 dorsal postglenoid foramen and ventral postalar fissure, each ranging from small to spacious, separates the dorsal and anterior margins of the auditory (ectotympanic) bulla from the adjacent squamosal. The periotic exposed along the dorsal 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 anteriorly as a tegmen tympani to overlap the squamosal. Projecting from the anterodorsal margin of the bullar capsule into the postglenoid space is a bony triangular process.

The short and wide incisive foramina are conspicuous when the skull is viewed from a ventral perspective, and are located about midway between incisors and anterior margins

of the first molars, occupying about 55% of the diastemal length. The wide bony palate is much longer than each molar row, a reflection of the short incisive foramina, and projection of the palate beyond posterior margins of the third molars. Its surface is mostly smooth, the pair of palatal grooves shallow and inconspicuous; posterior palatine foramina are even with the contact between first and second molars. The roof of the mesopterygoid fossa is intact in some specimens, pierced by small irregular openings or larger but still modest sphenopalatine vacuities in others. The adjacent narrow pterygoid plates (= parapterygoid plates) are also intact (no sphenopterygoid vacuities) except where each is pierced by the ventral opening of the foramen ovale, and no groove scores the posterolateral area of the ventral surface. The posterolateral margin of the pterygoid, which forms a ridge lateral to the foramen ovale in many murines (see the illustrations in Musser and Newcomb, 1983, for examples), is reduced to a delicate threadlike bone, which is often lost when skulls are cleaned. Long and narrow bony eustachian tubes project from the ectotympanic bullae, which are very small relative to size of the skull (length of bulla is about 12% of occipitonasal length). The bullar capsule does not cover the entire surface of the periotic, leaving exposed a broad wedge of that element separating the capsule from the basioccipital; the anteriomedial margin of the periotic and anteodorsal surface of the base of the eustachian tube form the posterior wall of the carotid canal (a reflection of the small ectotympanic capsule and broadly exposed periotic). The middle lacerate foramen separates the bullar capsule from the posterior margin of the pterygoid plate. None of the specimens we surveyed exhibited any trace of a stapedia foramen. When present, this opening penetrates the fissure between the bullar capsule and periotic (the petromastoid fissure), but these two elements join seamlessly in our examples of *Leptomys*.

All species of *Leptomys* possess a derived carotid circulatory pattern (character state 3 of Carleton, 1980; pattern 3 described by Voss, 1988; and the plan diagrammed for *Oryzomys palustris* by Carleton and Musser, 1989). Although this assertion is not based

upon dissection of soft tissue, the disposition of certain cranial foramina and osseous landmarks evident on cleaned skulls clearly point to such a specialized arterial circulation. A stapedia foramen is absent, as is a sphenofrontal foramen at the junction of orbitosphenoid, alisphenoid, and frontal bones. There is no squamosal-alisphenoid groove scoring the inner surface of each wall of the braincase, and no groove extending from the middle lacerate foramen to the foramen ovale on the ventral posterolateral surface of each pterygoid plate. There is a shallow trough running diagonally over the dorsal (inner) surface of each pterygoid plate. These landmarks and the circulatory pattern they reflect are similar to the derived arterial configurations described for Sulawesi *Crunomys* and *Sommeromys* (Musser and Durden, 2002), and a suite of Philippine (Musser and Heaney, 1992; Musser et al., 1998) and Sundaic (Musser and Newcomb, 1983) murines, as well as North and South American cricetids (Carleton, 1980; Steppan, 1995; Voss, 1988; Weksler, 2006). In this configuration, the stapedia artery is either absent or minute and serves only the periotic region. The supraorbital and infraorbital arteries, normally branches of the stapedia, are absent with the result that the ophthalmic and internal maxillary circulation is supplied by a secondary arterial connection branching from the internal carotid artery and coursing obliquely across the dorsal surface of the pterygoid plate. This derived carotid arterial circulatory pattern is contrasted with the other two found within muroid rodents particularly clearly through the descriptions and diagrams provided by Bugge (1970), Carleton (1980), Carleton and Musser (1989), and Voss (1988).

The dentary is slim, especially that portion of the ramus anterior to the molar row, and its labial and lingual surfaces are moderately smooth (figs. 8–10). A deeply concave posterior margin separates large and projecting condyloid and angular processes, and the smaller and more delicate coronoid process is isolated from the condyloid by a wide and deep sigmoid notch. The alveolus for the lower incisor terminates at the base of the condyloid process but is unmarked by any external swelling or lateral projection.

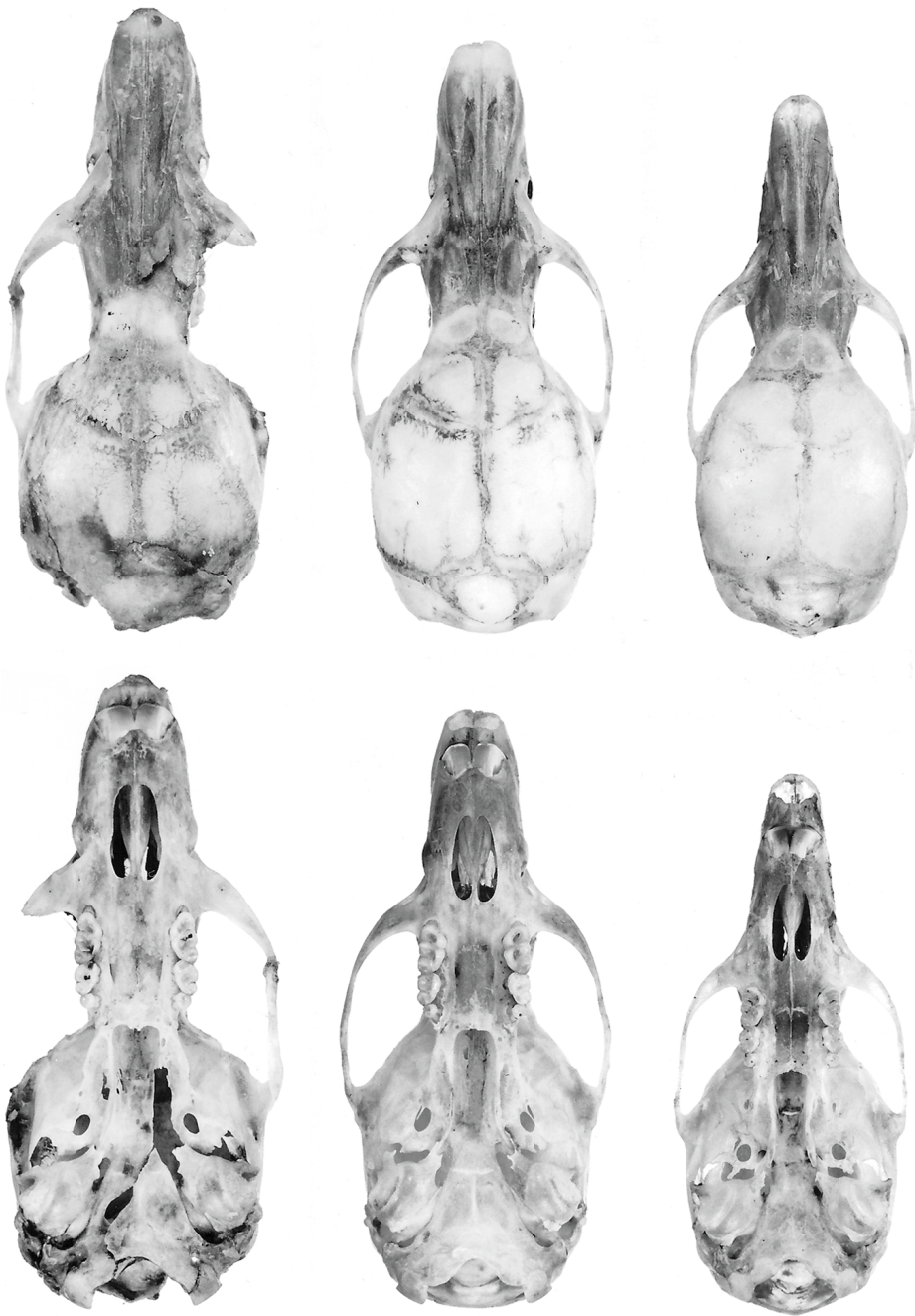


Fig. 7. Dorsal (top) and ventral (bottom) views of adult crania contrasting three species of *Leptomys*. **Left:** *L. elegans* (Mount Dayman, 700 m, Maneau Range; AMNH 158204). **Middle:** *L. ernstmayri* (Mount Rawlinson, 1370 m, Huon Peninsula; AMNH 194935). **Right:** *L. paulus* (Mount Dayman, 1370 m, Maneau Range; AMNH 158202, holotype). Approximately X2.



Fig. 8. Lateral views of crania and left dentaries of same specimens illustrated in figure 7. **Top:** *L. elegans*. **Middle:** *L. ernstmayri*. **Bottom:** *L. paulus* (holotype). Approximately X2.

Enamel layers of upper incisors are orange (diluted to pale orange in many specimens), those of the lowers are paler, even cream in many examples. The faces are smooth, lacking either grooves or shallow sulci, and the face of each upper is gently convex. The enamel face of each upper incisor does not wrap around the side, as is the pattern in the Philippine *Chrotomys*, for example, but resembles the enamel coverage seen in *Rattus* (Musser and Heaney, 1992:79). The incisors emerge from

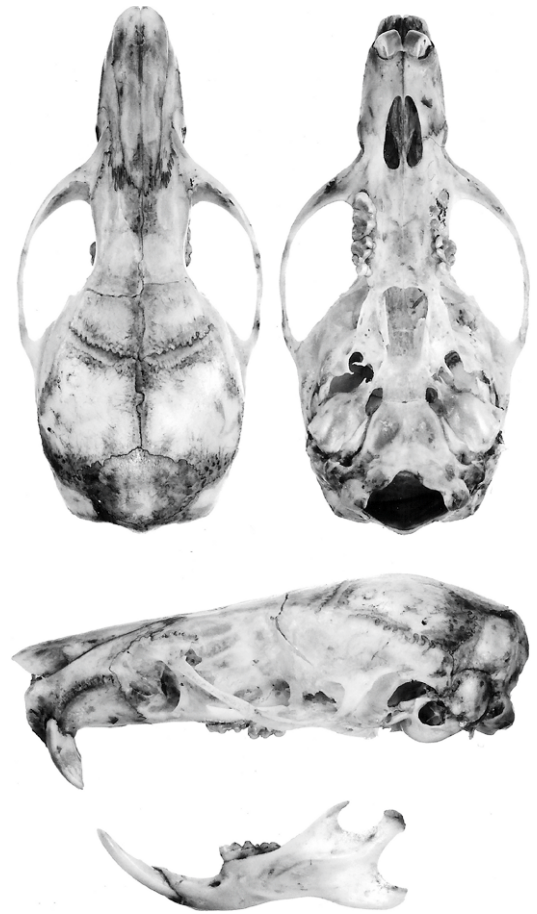


Fig. 9. Dorsal, ventral, and lateral views of cranium and dentary of AMNH 105793, an adult *Leptomys signatus* in the type series from the Fly River. Approximately X2.

the rostrum at slightly less than a right angle to the occlusal plane of the molars (slightly opisthodont). The sharp-tipped lower incisors project appreciably beyond the dentaries (figs. 8–10).

Alveolar patterns for upper and lower molar roots are similar among samples of *Leptomys*. Each first and second upper molar is anchored by four roots (one large anterior, one large posterior, and two somewhat smaller lingual roots); the third upper is anchored by three large roots coequal in size. Each of the lower molars has two roots (anterior and posterior). In their original description of *Paraleptomys* and comparisons with *Leptomys*, Tate and Archbold (1941: 2)

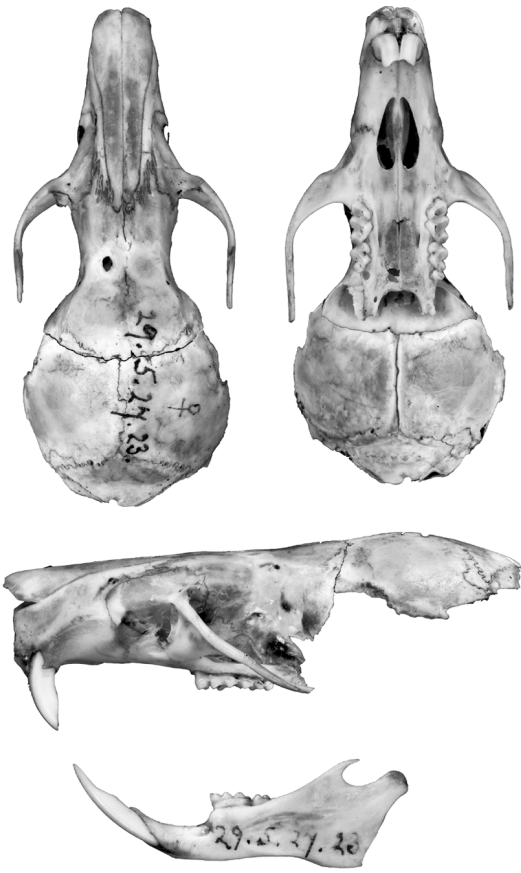


Fig. 10. Dorsal, ventral, and lateral views of cranium and dentary of BMNH 29.5.27.23 (holotype), an adult female *Leptomys arfakensis*, from the Arfak Mountains, 1000 m. Approximately X2.

correctly noted that each upper and lower third molar in *Leptomys* was anchored by three roots; later, Tate (1951: 222) incorrectly stated that each upper and lower third molar had but a single root.

Molars are brachydont and narrow. In the maxillary and mandibular rows, the elongate first molar forms about half of the row, and the second molar about a third; the round, simple third molar is very small compared with the other two, comprising about 15% of the row (figs. 11, 12). Simple occlusal surfaces are clearly cuspidate on juvenile molars but transform with age and wear into surfaces dominated by shallow basins. If our interpretation of cusp homologies is correct, the first and second upper molars in all species of

Leptomys appear to lack the series of labial cusps (t3, t6, and t9) that are present in most other murines; either they have been completely lost, or during embryonic development have coalesced so completely with the adjacent row of central cusps as to be undetectable. Occlusal surface of each first upper molar appears to consist of a diagonal anterior pair of large round cusps t1 and t2; some specimens have a slight bulge or cusplet where cusp t3 would normally occur, but that identity is impossible to verify in our material. Cusps t4 and t5 form the second row. Between them and the robust, round posterior cusp t8 is a lingual cusp or ridge that we identify as cusp t7. The second upper molar shares a similar configuration except only cusp t7 remains of the anterior row and cusp t7 is present or absent, depending upon species and geographic sample (table 6). In the large sample of *L. ernstmayri* from the Huon Peninsula (localities 19 and 20 in the gazetteer), a distinct shelflike cingulum forms the anterolabial border of each second upper molar (fig. 11); this structure occurs, in variable frequency, only in other geographic samples we identify as *L. ernstmayri* and in one example of *L. elegans* (table 6). In one specimen the anterolabial border of the second molar bears a cusplet that may represent cusp t3. A discrete posterior cingulum forms the posterior border of each second upper molar in young animals, but coalesces with cusp t8 after wear and becomes undetectable; we could not assess its frequency among our samples because most specimens are too old. We did not see a posterior cingulum on the first upper molar in any example, even juveniles. The simple round and peglike third upper molar is without significant occlusal topography in most adults. Judged from juveniles, cusp t1 and a coalesced cusp t4–t5 appear to form most of the molar.

Coronal surfaces of lower (mandibular) molars are simple but not as evidently cuspidate as are the uppers, and any cusp topography present in juveniles wears quickly down to a series of round, transverse, or oblong basins (figs. 11, 12). The anterior half of each first lower molar is basically a deep basin bounded anteriorly by anterolingual and anterolabial cusps (the anteroconid) and

posteriorly by the protoconid and metaconid. A diagonal basin consisting of coalesced hypoconid and entoconid defines the posterior half of the molar. A thin posterior cingulum forms the posterolabial border. Two transverse basins, each bounded by dentine rims, and a posterior cingulum, comprise the occlusal surface of the second lower molar. Some specimens exhibit small labial cusplets. An oblong basin forms the chewing surface of the very small, round and peglike third molar. In one species, *L. arfakensis*, n. sp., represented by the holotype and paratype, the third lower molar is excessively reduced in the latter and absent in the former (fig. 22).

Many additional anatomical systems, along with other aspects of *Leptomys*, remain to be investigated in detail, but some information on phallic anatomy, karyology, and sperm morphology is available. Phallic morphology was described by Lidicker (1968, 1973; Lidicker and Brylski, 1987; the specimens dissected, AMNH 191406 and 194940, were identified as *L. elegans*, but are actually examples of *L. ernstmayri*). Donnellan (1989) sampled the karyotype ($2n = 48$) for *L. elegans*, which differs from the postulated ancestral Australo-Papuan murine karyotype (see Baverstock et al., 1983, and references cited there), excluding *Rattus*, by the presence of a pair of submetacentrics. Spermatozoan morphology and its significance were discussed by Breed (1997, 2004) and Breed and Aplin (1994), who sampled both *L. elegans* and *L. ernstmayri*. In addition, Yrao (in litt., 2005) completed a study of gastrointestinal tract morphology in *L. ernstmayri* that is not yet published. Genetic studies that included *Leptomys* have been limited. Watts and Baverstock (1994, 1996) sampled a specimen of *L. ernstmayri* (identified as *L. elegans*) in their inquiry covering intergeneric clustering in Australo-Papuan murids based on immunological comparisons (microcomplement fixation of albumin), and *Leptomys* has been included in a phylogenetic study based on molecular data derived from a wide sampling of murines (Rowe et al., 2008).

COMPARISONS WITH *PARALEPTOMYS*: Named and described by Tate and Archbold in 1941, their diagnosis of *Paraleptomys* consisted of the short statement that it required “compar-

ison only with *Leptomys*, from which it is separated by its normal hind foot (elongated in *Leptomys*), and by the absence of $m3/3''$ (Tate and Archbold, 1941: 1). The genotype, *P. wilhelmina*, was based on two lots of specimens obtained from the northern ramparts of the Snow Mountains (Pegunungan Maoke), which form part of the massive Central Cordillera in western New Guinea (Province of Papua, Indonesian New Guinea [= Irian Jaya]). Of the 48 specimens in the first lot, 43 were collected 9 km northeast of Lake Habbema at 2800 m and five came from the Bele River Camp, 18 km northeast of Lake Habbema at 2200 m; the second lot of 30 specimens was obtained at 2150 m and 1800 m on ridges 18 km and 15 km, respectively, southwest of Bernhard Camp, near the Idenburg River (Tate, 1951: 223; the bulk of this material resides at AMNH).

True *Paraleptomys wilhelmina* comprises the samples from 2200 and 2800 m, and these remain the only record of the species. The series from 2150 m and 1800 m represents a morphologically distinct but unnamed separate biological species (“may be separable as a faintly differentiated race”, observed Tate and Archbold [1941: 2]; also see Helgen in Musser and Carleton, 2005: 1431). A single specimen identified as *P. wilhelmina* has been reported from the Tifalmin Valley at 1800 m at the eastern margin of the Star Mountains in western Papua New Guinea (Flannery, 1995), but this example, along with an unreported series collected in the Star Mountains (in BBM-NG), is a sample of a third species, yet undescribed, that is endemic to the Star Mountains of Western and Sandaun (West Sepik) provinces of Papua New Guinea (K. M. Helgen, in litt., 2007).

The only other currently recognized species of *Paraleptomys* is *P. rufilatus*, which was named and described by Osgood in 1945 and is currently recorded from montane forest formations in the North Coast Ranges—the Cyclops, Torricelli, and Bewani Mountains (Musser and Carleton, 2005: 1431). This distinctive species is larger than *P. wilhelmina* in body size and differs in pelage coloration (Flannery, 1995).

All samples of *Paraleptomys* are from high mountain forests, whether from the Central Cordillera or from the North Coastal Ranges.

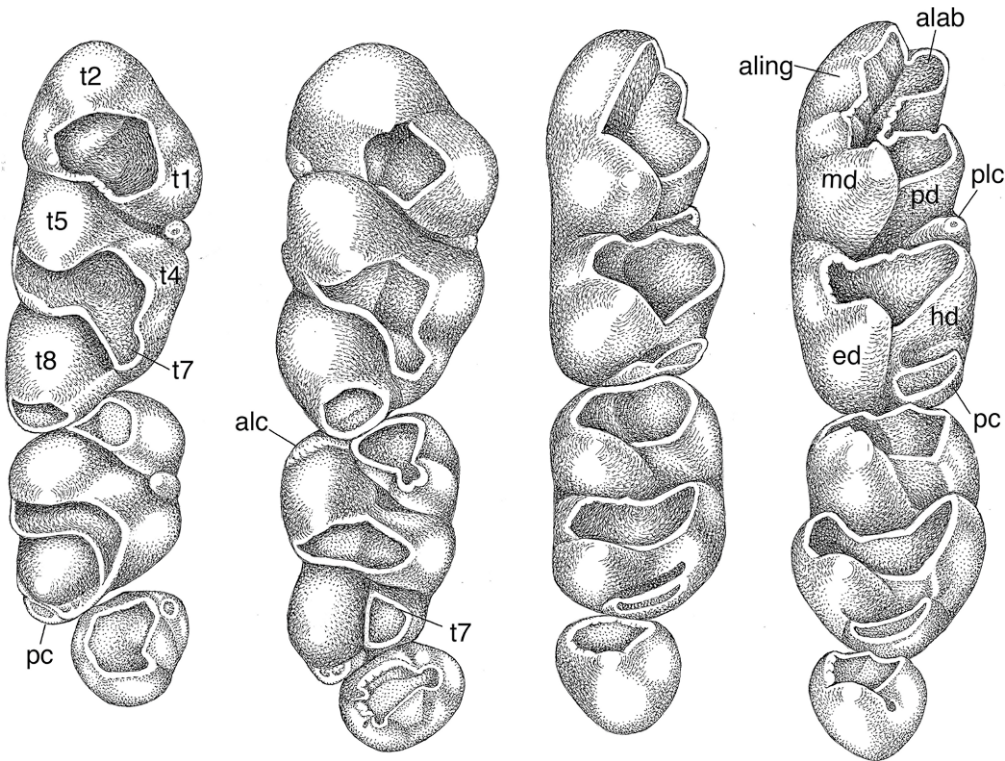


Fig. 11. Occlusal views of right maxillary (left pair) and mandibular (right pair) molar rows (X 20) drawn from juvenile examples of *Leptomys*. Left row in each pair is *L. paulus* (AMNH 158200), right row in each pair is *L. ernstmayri* (AMNH 194934). Maxillary rows: cusps are numbered according to Miller's (1912) scheme and referred to in the text with the prefix t; **alc**, anterolabial cingulum on second molar; **pc**, posterior cingulum. Mandibular rows: **alab**, anterolabial cusp; **aling**, anterolingual cusp; **hd**, hypoconid; **md**, metaconid; **ed**, entoconid; **pc**, posterior cingulum; **pd**, protoconid; **plc**, posterior labial cusplet. The basic pattern of cusps and cusplets seen here is common to all species of *Leptomys*. Two structures, however, reveal significant variation in their occurrence. Cusp t7 is absent from the second upper molar in our samples of *L. paulus* and *L. arfakensis* but generally present in samples of the other species (table 6). A conspicuous anterolabial cingulum (**alc**) on the second upper molar characterizes specimens of *L. ernstmayri* from the Huon Peninsula (and variably in samples of that species from elsewhere), but is generally lacking in the other species (table 6).

In the following comparisons between *Paraleptomys* and *Leptomys*, we generally focus on *P. wilhelmina*, the type species of the genus, as our example of *Paraleptomys*, and our observations are drawn primarily from skins and skulls stored at AMNH.

External features: Body form and lengths of appendages relative to body size resemble closely these features in *Leptomys* (compare the photograph of a live *P. rufilatus* with those of several *Leptomys* that are reproduced in Flannery, 1995). *Paraleptomys wilhelmina* is smaller in body size than any species of

Leptomys, but the larger *P. rufilatus* is about the same size as the smallest *Leptomys*, *L. paulus*, n. sp. (compare measurements in Tate, 1951, and Flannery, 1995, with those listed in tables 2 and 3). The tail is longer than length of head and body (LTV/LHB = 106%–112%) in *Paraleptomys*, which falls within the range of many *Leptomys* (tables 2, 3). Even conformation of the hind foot in *Paraleptomys*, which Tate and Archbold (1941) and Tate himself (1951) thought to be different from that of *Leptomys*, is similar in the two genera. Although the narrow hind foot of *P. wilhel-*

drawing by Patricia J. Wynne

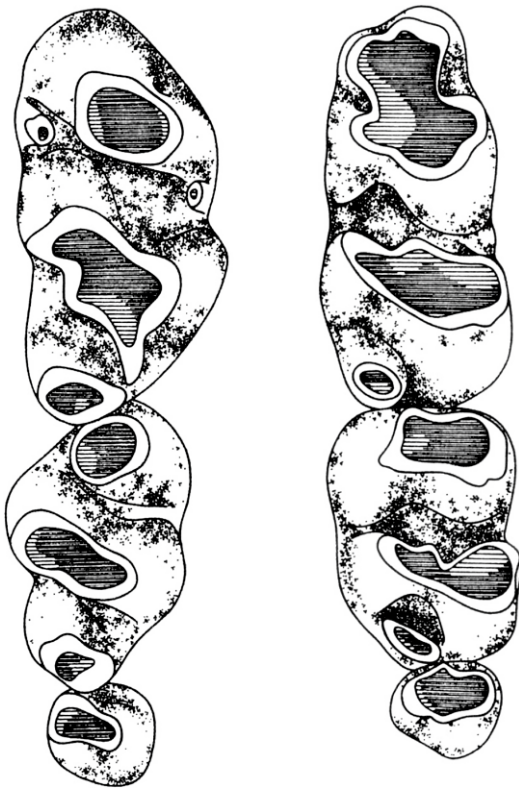


Fig. 12. Occlusal views of maxillary (left) and mandibular (right) molar rows in the paratype of *Leptomys arfakensis* (BMNH 29.5.27.22); adapted from Misonne (1969).

mina is shorter than that in any species of *Leptomys*, it is about 25% of head and body length (26% for *P. rufilatus*), a proportion falling within the average proportional range for the five species of *Leptomys* (25%–28%). Lengths of digits relative to overall length of hind foot is close: about 43% in both genera (as determined from dry study skins), as are lengths of individual digits relative to one another.

The most telling external distinction between *Paraleptomys* and *Leptomys* is pelage quality and color. The entire dorsal coat of *P. wilhelmina* is dark brown, dense (10–12 mm thick), and soft and woolly in texture (*P. rufilatus* has buffy brown sides), contrasting sharply with the bright tawny brown, short, and velvety coat common to *Leptomys*. Dark, grayish white underparts characterize *P. wilhelmina* (*P. rufilatus* has a white throat); three

species of *Leptomys* have pure white ventral coats, in samples of the other two species underparts range from white to whitish gray, some with a pale buffy wash.

Skull: *Paraleptomys* and *Leptomys* share the same general cranial shape as well as many proportional aspects: “in many respects very like *Leptomys*,” wrote Tate and Archbold (1941: 2) (see Flannery, 1995, for informative illustrations of skulls representing the two genera). *Paraleptomys*, however, diverges from that basic conformation in the following diagnostic features:

(1) The interparietal in *Paraleptomys* is much wider than long (about as wide as long in *Leptomys*).

(2) *Paraleptomys* has a shorter bony palate relative to length of skull (about 20% of occipitonasal length), which reflects the shorter molar rows due to the missing third molars (relatively longer in *Leptomys*, about 25% of occipitonasal length).

(3) The ectotympanic bulla is large in *Paraleptomys* (about 15% of occipitonasal length), and has a short bony eustachian tube relative to bullar length. The ectotympanic capsule covers much of the periotic, with its anterodorsal margin abutting the basioccipital; the back of the carotid canal is formed by capsule and basioccipital only. (*Leptomys* has a much smaller bulla, its length about 12% that of the occipitonasal dimension, and a relatively longer bony eustachian tube. The ectotympanic capsule rests on top of the periotic leaving exposed a wide and long wedge of that element that completely separates capsule from basioccipital; the rear wall of the carotid canal comprises periotic and capsule only.)

(4) *Paraleptomys* possesses a carotid circulatory pattern that is derived for murid 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 saw this pattern in certain cranial foramina and osseous landmarks in cleaned skulls, as well as dried blood vessels left on incompletely cleaned skulls. No sphenofrontal foramen exists at the junction of orbitosphenoid, alisphenoid, and frontal bones; no

squamosal-alisphenoid groove scores the inner surface of each wall of the braincase, and no shallow trough extends diagonally over the dorsal (inner) surface of each pterygoid plate. There is a large stapedia 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 stapedia artery branches from the common carotid, enters the periotic region through a large stapedia 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 run through the anterior alar fissure into the orbit. The supraorbital branch of the stapedia is absent. The circulatory pattern 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; Stepan, 1995; Voss, 1988; Weksler, 2006). *Leptomys* exhibits a carotid circulation that is derived for murines (character state 3 of Carleton, 1980; pattern 3 described by Voss, 1988; and the plan diagrammed for *Oryzomys palustris* by Carleton and Musser, 1989), as indicated by no stapedia foramen or sphenofrontal foramen, no squamosal-alisphenoid groove, no groove extending from the middle lacerate foramen to the foramen ovale on the ventral posterolateral surface of each pterygoid plate, and a shallow trough running diagonally over the dorsal (inner) surface of each pterygoid plate (see the previous section covering general description of *Leptomys*).

(5) The dentary in *Paraleptomys* has a large coronoid process relative to area of the dentary surface (relatively smaller and more delicate in *Leptomys*).

Dentition: Shapes of the upper and lower incisors, coloration of enamel, and the right-angle projection of the uppers from the rostrum (opisthodont configuration) are similar in *Paraleptomys* and *Leptomys*. They also share brachydont molars, with the first and second each anchored by four roots (large anterior and posterior roots, two smaller

lingual holdfasts). Outside of these similarities the dentitions are quite different. Basically, *Paraleptomys* has fewer molars and those present have less complex occlusal surfaces, which take the form of a series of enamel basins very early in the animal's life (comparable formation of basined laminae occurs much later in the life of *Leptomys*). The morphology is similar to other hydromyins with no third molars and basined occlusal surfaces, such as the species of *Hydromys*, *Baiyankamys*, *Parahydromys*, and *Crossomys*, for example.

(1) *Paraleptomys* lacks upper and lower third molars (present in *Leptomys*; one of two known examples of *L. arfakensis*, n. sp., is without lower third molars).

(2) No discernable cusp t7 exists on either the first or second upper molar in *Paraleptomys* (present on the first molars in *Leptomys* and also on the second molars in some samples; see table 6).

(3) The second upper molar in *Paraleptomys* is without an anterolabial cingular shelf or cusp (an anterolabial cingular shelf is present in some samples of *Leptomys*; see table 6).

(4) *Paraleptomys* has a second upper molar consisting of only two basined laminae—cusp t8 and a posterior cingulum is not present. The second lamina is oriented toward the vertical, about 30° from the midline of the bony palate (cusp t8 is present and forms about a third of the occlusal surface of the second molar in *Leptomys*; a posterior cingulum is evident in young dentitions but generally loses its identity with wear; and the second lamina is oriented toward the horizontal, about 70° from the midline of the palate).

(5) The first lower molar of *Paraleptomys* has a very small posterior cingulum relative to overall size of tooth; the posterior cingulum is either not present on the second lower molar or represented by an indistinct, minute bump (the posterior cingulum is large and conspicuous on both first and second lower molars in *Leptomys*).

Disappearance of the third upper molars in all hydromyins genera except *Leptomys* is apparently attended by loss of the posterior lamina (the large cusp t8) and posterior cingulum on each second upper molar ("Assumption of m² of the terminal position

in the toothrow has so modified its form that the postero-external tubercle has been eliminated", opined Tate and Archbold [1941: 2]), and in *Paraleptomys* a reorientation of the second lamina from the horizontal toward a nearly vertical position. Attending the absence of third lower molars is a reduction in size of the posterior cingulum on each first molar (at least in *Paraleptomys*) and diminution to a minute remnant, or actual loss, of the posterior cingulum on each second molar. This generalization does not apply to the holotype of *Leptomys arfakensis*, n. sp., which does not have lower third molars, yet exhibits a prominent posterior cingulum on each first and second lower molar (fig. 22).

Tate and Archbold (1941: 2) noted that the first upper molar in *Paraleptomys* was "slightly broader" than its counterpart in *Leptomys*, and the fissures separating the laminae deeper, differences we cannot verify and do not appreciate.

Phallus and spermatozoa: These contrasts are extracted from the literature; we have not verified them by direct observation of specimens.

(1) *Paraleptomys* has a simple phallus compared with that of *Leptomys* (comparisons based on *L. ernstmayri* and *P. wilhelmina*; Lidicker, 1968). In both genera, the wall of the glans contains a conspicuous blood sinus extending into the bases of the urethral lappets, but in *Paraleptomys*, the primary blood sinus is medial to the inner crater (situated between inner and outer craters in *Leptomys*). *Paraleptomys* has few or no tiny papillae and no denticles adorning the rim of the outer crater wall (large papillae and tiny denticles along the rim in *Leptomys*), no dorsal groove extending from the dorsal notch in the rim of the outer crater wall (prominent dorsal groove in *Leptomys*), a proximal baculum in which the shaft is bowed ventrally and its base strongly notched (straight shaft without a notch in the base in *Leptomys*), and tips of lateral bacular processes oriented ventrally (point distally in *Leptomys*).

(2) *Leptomys* and *Paraleptomys* share a similar spermatozoan morphology, differing primarily in the shorter tail of the latter (Breed and Aplin, 1994; *L. elegans*, *L. ernstmayri*, and *P. rufilatus* were sampled).

Summary: Like the species of *Leptomys*, those of *Paraleptomys* are clearly terrestrial. The two genera also resemble each other in external body form and proportions. Their crania and mandibles are similar in overall shape and dimensional proportions—these elements appear much less highly derived than those in most other hydromyins. But *Paraleptomys* is characterized by a unique combination of traits relative to *Leptomys*: dark, thick, and woolly pelage; differently shaped interparietal and relatively shorter bony palate; large bullae relative to skull size, with more of the periotic cloaked by the ectotympanic capsule; a cephalic arterial circulation that is primitive for murines; larger coronoid process relative to area of dentary; no third molars; first and second upper molars with simple (compared to *Leptomys*) and basined occlusal surfaces (no cusp t7 or anterolabial cingulum), second upper molar without cusp t8 and posterior cingulum; lower molars also exhibiting simple and highly basined chewing surfaces, and very small or no posterior cingula; and differences from *Leptomys* in phallic and spermatozoal features. This suite of traits does not characterize any of the specimens we examined representing the five species of *Leptomys*. Our observations, derived primarily from dry museum skins with accompanying cleaned skulls, do not support the notion that either *Paraleptomys* or *Leptomys* is polyphyletic, rather just the opposite: the species in each form separate monophyletic clusters.

THE SPECIES OF *LEPTOMYS*

Most lists and faunal studies published since 1951 recognized only one species of *Leptomys* (Flannery, 1990; Laurie and Hill, 1954; Menzies and Dennis, 1979; Tate, 1951), but Rümmler's (1938) revision in which he identified two species (*L. elegans* and *L. ernstmayri*), Tate and Archbold's (1938) description of a third (*L. signatus*), and the two we name and describe below more accurately reflect the known diversity.

The first three accounts present species already described and the first is the large-bodied *L. elegans*, followed by *L. signatus*, also with large body size, then the small-

TABLE 1
Measurements (mm) for Holotypes of *Leptomys*

Measurement	<i>L. signatus</i>	<i>L. elegans</i> ^a	<i>L. ernstmayri</i> ^b	<i>L. paulus</i>	<i>L. arfakensis</i>
	AMNH 105792	MCSN 32988	ZMB 42400	AMNH 158202	BMNH 29.5.27.23
LHB	144	162	133	127	151
LTV	151	154	151	163	146
LHF	38	40	39	36	36
LE	19	20	21	21	21
ONL	38.29	40.07	36.3	34.16	—
ZB	16.14	18.32	15.5	14.48	16.00
IB	6.17	5.80	6.2	5.85	6.38
LN	13.47	14.53	12.5	12.44	13.84
BR	6.70	7.11	—	5.58	6.69
BBC	14.60	15.36	14.6	13.30	14.7 ^c
HBC	10.64	10.81	10.7	9.97	—
BZP	2.11	2.24	—	1.55	2.4
LD	9.83	10.66	8.5	8.03	9.85
PPL	12.72	14.34	—	11.59	—
LBP	9.54	9.37	—	6.99	8.62
BBP	3.52	—	—	3.20	—
BMF	3.11	2.87	—	2.09	3.00
LIF	4.69	5.63	4.8	4.76	5.25
BIF	2.48	2.98	2.5	2.30	3.11
LB	4.72	5.20	—	4.15	5.12
CLM1-3	6.18	6.01	5.5	5.04	5.79
BMI	1.71	1.65	1.7	1.53	1.44

^a Values for lengths of body and appendages are from Thomas's (1987) original description; Helgen measured carefully the skull and molars.

^b Most values are from Rümmler (1932); Musser obtained values for the length of hind foot and some cranial and dental measurements.

^c The braincase is slightly damaged, the value is approximate.

bodied *L. ernstmayri*. The last two accounts cover descriptions of the new species, one of small body size, the other larger. The larger-bodied species are separated from the smaller-bodied in tables and figures where univariate summaries of morphometric data are presented. While convenient for expository purpose, the groupings may also reflect phylogenetic kinship for in their overall morphologies those species with large body size (*L. elegans*, *L. signatus*, and *L. arfakensis*, n. sp.) appear to have more affinity to each other than to the species of small body size (*L. ernstmayri* and *L. paulus*, n. sp.), which seem closely related.

Each of the following accounts carries several subjects indicated by appropriate subheadings. "Habitat and Biology" is one of these. Our attempts to tie specimens we examined to habitats remain unsatisfactory. Consulting field journals, published faunal reports, and expedition summaries allowed us

to associate some specimens with descriptions of forest formations at or near collection sites; the link, however, is explained within a broad picture of different forest formations and lacks focus on microhabitats in which the animals were trapped. Most other kinds of biological information remain unavailable.

Leptomys elegans Thomas, 1897

HOLOTYPE AND TYPE LOCALITY: The holotype of *L. elegans* is MSCN 32988, an intact skull and study skin of an adult female, collected by Dr. Lamberto Loria between 1890 and 1893 in the Astrolabe Range behind Port Moresby (Central Province, Papua New Guinea); measurements are listed in table 1. The tag of the holotype bears no definite locality other than "British N.G.", and no exact provenance was published in the original description of *L. elegans*, although Thomas

(1897: 607) wrote that Loria's localities "are mostly between the Owen Stanley Range and the sea, in or near the watershed of the Kemp Welch river", an area that would include the Astrolabe Range and adjacent Sogeri Plateau. Tate (1951: 223) observed that "Loria collected in the Astrolabe Range behind Port Moresby", and we regard specimens from the Astrolabe Range (available at AMNH and ZMB) as toptypical.

DIAGNOSIS AND CONTRASTS: Of the known species in the genus, *L. elegans* is the largest in body size (as indexed by length of head and body along with mass), but has the shortest tail relative to body length (tables 2, 3). On average, the tail is shorter than head and body in *L. elegans*, about coequal in *L. signatus* and *L. arfakensis*, n. sp., and appreciably longer in *L. ernstmayri* and *L. paulus*, n. sp. The coat covering upperparts of head and body is moderately long, soft, dense, velvety in texture, overall tawny brown, and usually without decoration (some specimens in AM, AMNH, and PNGNM series have a discernable but small, pale marking on the head between the eyes). This coloration and texture is shared with all the other species of *Leptomys* except *L. signatus*, which has shorter, buffy gray dorsal pelage marked by an expansive white blaze on the head (fig. 4), and *L. paulus*, n. sp., which has longer and softer pelage that is silky to the touch. Pure white underparts are characteristic of *L. elegans* (also *L. signatus* and *L. arfakensis*, n. sp., figs. 4, 6); the fur covering the venter in most examples of the smaller-bodied *L. ernstmayri* and *L. paulus*, n. sp., is white suffused with varying intensities of gray or buff (fig. 5).

Most cranial and dental dimensions characterizing *L. elegans* are, on average, appreciably greater than those associated with *L. ernstmayri* and *L. paulus*, n. sp., the species of smaller body size (see skulls compared in figs. 7, 8), and more equitable with those of *L. signatus* and *L. arfakensis*, n. sp. (tables 4, 5). But significant proportional contrasts shown by *L. signatus* (relatively short nasals, narrow zygomatic plate, and larger molars), along with an absolutely narrower rostrum, highlight its morphometric distinction from *L. elegans*, and the much smaller molars in *L. arfakensis*, n. sp., help mark its clear

separation from *L. elegans* (tables 4, 7; figs. 13, 14).

Most specimens in our sample of *L. elegans* have a small cusp t7 on the second upper molar but lack an anterolabial cingulum (table 6). That latter structure is absent in all but one of the 17 specimens we surveyed, and in that individual (AM M32103) it is very small. Occurrence of cusp t7 in *L. ernstmayri* and *L. signatus* is comparable to its frequency in *L. elegans*, but the cusp is not present in all specimens examined representing the two new species, *L. paulus* and *L. arfakensis*. The low frequency of occurrence of the anterolabial cingulum in *L. elegans* is comparable to that seen in samples of all the other species except *L. ernstmayri* (found in only one of 38 examples of *L. elegans*, *L. signatus*, *L. arfakensis*, n. sp., and *L. paulus*, n. sp.; occurs in about half of the total samples for *L. ernstmayri*).

GEOGRAPHIC DISTRIBUTION: *Leptomys elegans* is recorded from localities scattered throughout the Papuan Peninsula of southeastern New Guinea (along the slopes of the Astrolabe, Wharton, and Maneau ranges, as well as the outlying peak of Mount Victory) and along the southern slopes of the Central Cordillera in the Kikori River Basin (see gazetteer and map in fig. 2). The altitudinal range of the species, as documented by voucher specimens, extends from lowlands near sea level to uplands at 1500 m. The average altitude of 16 trapping sites, from which specimens of *L. elegans* were preserved, is 840 m (median = 775 m, SD = 426 m).

GEOGRAPHIC VARIATION: *Leptomys elegans* is recorded by specimens from two broad regions in New Guinea. One is the Papuan Peninsula, basically southeastern New Guinea. The other is the Kikori River Basin on the southern slopes of the Central Cordillera in east-central New Guinea (fig. 2). Some consistent morphological differences are apparent between these two geographically disjunct populations. In the discriminant-function analysis depicted in figures 13 and 14, for example, the dispersion of specimen scores along the first canonical variate indicates narrow separation between samples from the Papuan Peninsula and Kikori River Basin that is influenced primarily by the Papuan specimens' possession of smaller molars but

TABLE 2

Descriptive Statistics for External Measurements (mm), Mass (grams), and Proportions of Adult *Leptomys* with Larger Body Size: *Leptomys elegans*, *Leptomys signatus*, and *Leptomys arfakensis*
(Mean plus or minus one SD, observed range in parentheses, and size of sample are provided.)

Measurement	<i>L. elegans</i>	<i>L. elegans</i>	<i>L. signatus</i>	<i>L. arfakensis</i>
	Papuan Peninsula	Kikori River Basin	Southcentral Lowlands	Arfak Mountains
LHB	160 ± 14.3 (143–190) 9	163 ± 17.7 (142–194) 11	148 ± 6.3 (140–155) 6	145 (138–151) 2
LTV	151 ± 11.4 (125–164) 9	152 ± 5.9 (144–163) 11	148 ± 4.4 (143–155) 6	146 (146–146) 2
LHF	40.2 ± 1.71 (37–42) 9	38.3 ± 2.72 (36–43) 7	39.6 ± 3.10 (36–45) 6	37.5 (36–39) 2
LE	21.0 ± 1.63 (18–23) 9	21.2 ± 2.97 (19–26) 5	20.1 ± 1.20 (19–21.5) 6	21 (21–21) 2
Mass	101 (81–120) 2	91.8 ± 17.3 (66–120) 6	80 (80) 1	— —
LTV/LHB (%)	95 (66–110) 9	94 (79–108) 11	101 (92–111) 6	101 (97–106) 2
WTT/LTV (%)	32 (21–40) 9	38 (36–42) 3	49 (44–54) 4	30 (27–33) 2

broader incisive foramina relative to specimens from the Kikori River Basin (see table 7), a difference also reflected in means of measurements listed in table 4. Scatter of specimen scores along the second canonical axis forms two barely overlapping groups, affected mostly by the relatively longer nasals in the Kikori sample, its narrower zygomatic plate, and longer molar rows but narrower first upper molars. If the morphological traits expressed in our samples reflect variation present in the populations from which they were derived then the population occurring on the Papuan Peninsula is distinguished from that in the Kikori River Basin by its relatively smaller molars, broader incisive foramina and zygomatic plate, and shorter nasals (indicating a shorter rostrum). We currently regard these distinctions to reflect geographic variation between conspecific populations. Should they become available, series of *L. elegans* from intermediate localities (such as from Gulf Province) might demonstrate these contrasts to be clinal.

The single specimen collected at 800 m on Mount Victory (on the Papuan Peninsula; locality 9 in fig. 2) differs from all other examples of *L. elegans* in having longer and narrower incisive foramina and a broader braincase. Mount Victory is an isolated peak entirely separated from the montane forests of

the Central Cordillera by lowland tropical rainforest, the biota of which remains poorly surveyed (Diamond, 1985). Series from this outlying mountain block will be needed to assess patterns of morphological covariation in *Leptomys* from Mount Victory compared to samples of *L. elegans* collected along the margin of the Central Cordillera. However, because *L. elegans* is known from several lowland localities (see gazetteer), it may range throughout the lowland rainforest corridor between the two lower montane regions.

HABITAT AND BIOLOGY: Information gleaned from collection sites indicates that *L. elegans* inhabits tropical lowland and lower montane evergreen rain forests, including both mature and secondary forested habitats. All collection localities for this species lie on mountain slopes, and all of the specimens were collected between 20 m and 1500 m, which would seem to be the core altitudinal distribution of *L. elegans*.

The lowest record is BBM-NG 60171, collected at “Karema, Brown River Forest Station” (locality 8 in gazetteer and fig. 2). The tag of this specimen bears the annotation “lowland evergreen rainforest”. Although the altitude of the trapping locality is unrecorded, Zweifel (1972) gave the altitude in the vicinity of Karema as ca. 20 m. Additional records in the vicinity of the Brown River include

TABLE 3
Descriptive Statistics for External Measurements (mm), Mass (grams), and Proportions of Adults in Samples of *Leptomys* with Smaller Body Size: *Leptomys ernstmayri* and *Leptomys paulus*.
 (Mean plus or minus one SD, observed range in parentheses, and size of sample are provided.)

Measurement	<i>L. ernstmayri</i> Huon Ranges	<i>L. ernstmayri</i> Adelbert Range	<i>L. ernstmayri</i> Central Cordillera	<i>L. ernstmayri</i> Foja Mountains	<i>L. paulus</i> Owen Stanley Range
LHB	138 ± 5.27 (129–145) 13	139 ± 7.08 (126–150) 11	140 ± 8.55 (124–156) 20	129 (—) 1	125 ± 4.85 (117–132) 15
LTV	162 ± 7.35 (150–171) 13	144 ± 7.80 (132–144) 11	151 ± 8.80 (134–168) 20	126 (—) 1	148 ± 5.03 (138–163) 15
LHF	38.9 ± 1.12 (37–41) 13	37.3 ± 1.49 (36–40) 11	38.2 ± 1.92 (33–42) 23	38 (—) 1	34.4 ± 1.60 (31–36) 12
LE	20.1 ± 0.51 (19–21) 12	21.5 ± 0.69 (20–22) 11	20.5 ± 1.83 (15–24) 22	23 (—) 1	20.6 ± 1.56 (18–23) 11
Mass	57.3 ± 6.28 (48–68) 12	—	61.3 ± 5.09 (54–69) 17	70 (—) 1	41.8 ± 3.73 (34–52) 13
LTV/LHB (%)	117 (114–122) 13	104 (94–112) 11	108 (93–117) 20	98 (—) 1	118 (108–128) 15
WTT/LTV (%)	29 (13–27) 12	24 (15–37) 11	20 (11–32) 12	24 (—) 1	26 (19–29) 14

specimens taken on the Sogeri Plateau (410–450 m) and in the Astrolabe Range (520 m), localities associated with lowland evergreen rainforest (K. P. Aplin, personal commun.). Other specimens collected nearby came from the Wharton Range at Mafulu (1253 m), situated in lower montane forest (Archbold and Rand, 1935).

The highest records, 1400–1500 m, come from Mount Sisa, situated along the southern slopes of the Kikori River Basin (locality 5 in fig. 2 and gazetteer). Dwyer (1984) recorded the distribution of New Guinea rodents according to successional phases in the transition from gardens to forest over 20 years on the southern slope of Mount Sisa. Examples of *L. elegans* were taken in second-growth formations estimated at 10 and 12.5 years regrowth from garden environments, 25-year-old secondary forest, and primary forest, but not in any of the environments representing the transition from gardens and grassy stages through to early regrowth and very low secondary forest, an estimated period of five to seven years. Flannery (1990: 177; 1995: 241) portrayed a living individual that was trapped on Mount Sisa.

Leary and Seri (1997) reported additional specimens of *L. elegans* from the Kikori River Basin. Within that expansive area, the species has now been recorded at several sites,

including those on Mount Sisa, situated between 450 and 1500 m (see gazetteer). Habitats at these various places correspond to lowland evergreen rainforest, lower montane forest, and the transition between the two (K. P. Aplin, personal commun.). *Leptomys signatus* is also represented by specimens from the Kikori River Basin, on the north-northwestern slopes of Mount Bosavi and on the Darai Plateau (localities 4 and 5, respectively, on the map in fig. 2); whether the distributions of these two species closely abut or overlap within the region remains unknown.

The single specimen trapped in the Maneau Range in far southeastern New Guinea (AMNH 158204) was caught at 700 m (“Number 3 Camp” or “Bottom Camp”) on the north slopes of Mount Dayman by H. M. Van Deusen, a member of the Fourth Archbold Expedition to New Guinea. This camp, as described by Brass (1956: 133),

was situated close below the junction of the mixed rain forests of the lower slopes and the oak and *Castanopsis* forest of the middle slopes. As evidenced by second-growth rain forest beginning immediately below the camp, we were at the exact upper limit of former cultivation on this part of the mountain by the Daga people who now live in the Biniguni group of

TABLE 4
Descriptive Statistics for Cranial and Dental Measurements (mm) of Adults in Samples of *Leptomys* with larger body size: *Leptomys elegans*, *Leptomys signatus*, and *Leptomys arfakensis*
 (Mean plus or minus one SD, observed range in parentheses, and size of sample are listed.)

Measurement	<i>L. elegans</i>	<i>L. elegans</i>	<i>L. signatus</i>	<i>L. arfakensis</i>
	Papuan Peninsula	Kikori River Basin	Southcentral Lowlands	Arfak Mountains.
ONL	38.7 ± 0.90 (37.62–40.07) 8	39.3 ± 1.49 (37.44–42.71) 9	37.9 ± 0.53 (37.26–38.55) 5	— —
ZB	17.6 ± 1.41 (15.63–20.30) 9	16.9 ± 1.05 (15.50–18.93) 9	16.8 ± 0.78 (15.97–17.79) 5	16.0 (16.00) 1
IB	6.0 ± 0.22 (5.68–6.31) 10	6.3 ± 0.25 (5.97–6.79) 9	6.1 ± 0.15 (5.84–6.18) 5	6.2 (6.08–6.38) 2
LN	14.2 ± 0.69 (12.89–15.60) 8	14.7 ± 0.87 (13.66–16.69) 9	13.7 ± 0.29 (13.47–14.20) 5	14.1 (14.84–14.42) 2
BR	7.2 ± 0.47 (6.59–7.83) 9	7.0 ± 0.54 (6.10–7.92) 9	6.5 ± 0.36 (5.88–6.71) 5	6.5 (6.35–6.69) 2
BBC	15.2 ± 0.43 (14.42–15.63) 7	14.9 ± 0.46 (14.29–15.52) 9	14.9 ± 0.37 (14.53–15.36) 5	14.5 (13.30–14.70) 2
HBC	11.0 ± 0.41 (10.48–11.60) 8	11.0 ± 0.29 (10.54–11.34) 9	10.9 ± 0.25 (10.64–11.29) 5	10.3 (10.30) 1
BZP	2.2 ± 0.23 (1.75–2.51) 9	1.9 ± 0.31 (1.45–2.50) 9	2.0 ± 0.13 (1.81–2.11) 5	2.4 (2.31–2.40) 2
LD	10.0 ± 0.51 (9.26–10.73) 9	9.3 ± 0.26 (9.09–9.80) 6	9.5 ± 0.28 (9.19–9.83) 5	9.6 (9.38–9.85) 2
PPL	13.6 ± 0.56 (12.85–14.34) 8	13.2 ± 0.83 (11.70–14.43) 9	12.7 ± 0.38 (12.39–13.23) 5	— —
LBP	9.1 ± 0.49 (8.36–9.81) 9	9.4 ± 0.39 (8.80–10.16) 9	9.2 ± 0.22 (8.98–9.54) 5	8.5 (8.46–8.62) 2
BBP	3.9 ± 0.52 (3.57–4.92) 7	3.6 ± 0.18 (3.40–3.90) 5	3.4 ± 0.28 (3.10–3.62) 3	— —
BMF	2.9 ± 0.14 (2.62–3.17) 9	3.1 ± 0.19 (2.70–3.32) 9	3.3 ± 0.20 (3.01–3.54) 5	2.9 (2.82–3.00) 2
LIF	5.3 ± 0.38 (4.61–5.63) 10	5.3 ± 0.30 (4.80–5.65) 9	4.8 ± 0.28 (4.51–5.15) 5	5.1 (4.98–5.25) 2
BIF	2.9 ± 0.13 (2.72–3.10) 10	2.7 ± 0.22 (2.40–3.09) 9	2.5 ± 0.10 (2.37–2.63) 5	3.0 (2.82–3.11) 2
CLM	6.0 ± 0.17 (5.86–6.30) 10	6.2 ± 0.26 (5.81–6.61) 9	6.1 ± 0.15 (5.96–6.34) 5	5.7 (5.58–5.79) 2
LM1	3.3 ± 0.12 (3.03–3.45) 10	3.5 ± 0.15 (3.28–3.75) 11	3.5 ± 0.10 (3.35–3.60) 5	3.0 (2.99–3.08) 2
BM1	1.7 ± 0.09 (1.59–1.83) 10	1.7 ± 0.05 (1.56–1.73) 9	1.7 ± 0.04 (1.70–1.79) 5	1.5 (1.44–1.56) 2

villages on the lowlands. ...With great regularity in late morning or early afternoon a pall of heavy dark cloud enveloped the slopes above us, its lower edge often resting in the treetops of the oak-*Castanopsis* forest only 50 meters higher on the slopes, but we were below the zone of regular mists and seldom had any in camp. A brown haze obscured the lowlands and the coast nearly always, and at no time were the mountains of the Cape

Nelson Peninsula visible, though distant less than 40 miles to the north.

Between July 19 and July 26, mean maximum temperature was 25.1°C (77°F), mean minimum was 17.2°C (63°F). Brass provided additional description of the nearby forest, which indicates that Number 3 Camp was situated at the upper limits of what Whitmore (1984) designates as tropical lowland evergreen rain forest and just below tropical lower

TABLE 5
Descriptive Statistics for Cranial and Dental Measurements (mm) of Adults in Samples of *Leptomys* with Smaller Body Size: *Leptomys ernstmayri* and *Leptomys paulus*.
 (Mean plus or minus one SD, observed range in parentheses, and size of sample are listed.)

Measurement	<i>L. ernstmayri</i> Huon Peninsula	<i>L. ernstmayri</i> Adelbert Range	<i>L. ernstmayri</i> Central Cordillera	<i>L. ernstmayri</i> Foja Mountains	<i>L. paulus</i> Owen Stanley Range
ONL	36.6 ± 0.76 (33.88–36.63) 12	35.3 ± 0.87 (33.85–36.50) 9	36.2 ± 0.96 (34.62–37.90) 18	35.5 (—) 1	33.8 ± 0.71 (32.70–34.74) 12
ZB	15.6 ± 0.48 (14.75–16.10) 13	15.5 ± 0.54 (14.53–16.20) 10	15.8 ± 0.51 (15.12–17.00) 20	15.2 (—) 1	14.3 ± 0.40 (13.42–14.71) 13
IB	6.1 ± 0.13 (5.86–6.24) 13	5.7 ± 0.16 (5.49–6.05) 10	5.8 ± 0.21 (5.55–6.38) 22	5.9 (—) 1	5.6 ± 0.15 (5.35–5.86) 13
LN	12.1 ± 0.27 (11.57–12.43) 12	12.5 ± 0.47 (11.86–13.19) 10	12.9 ± 0.48 (11.95–13.70) 19	13.3 (—) 1	12.4 ± 0.28 (12.10–13.03) 12
BR	6.0 ± 0.33 (5.55–6.44) 12	5.9 ± 0.15 (5.70–6.13) 10	6.2 ± 0.25 (5.71–6.84) 21	6.1 (—) 1	5.6 ± 0.23 (5.25–6.06) 13
BBC	13.8 ± 0.37 (13.37–14.60) 13	14.1 ± 0.38 (13.19–14.62) 10	14.3 ± 0.35 (13.72–15.23) 20	13.5 (—) 1	13.3 ± 0.25 (12.85–13.72) 13
HBC	10.2 ± 0.25 (9.87–10.63) 12	10.3 ± 0.25 (9.82–10.69) 10	10.5 ± 0.32 (9.95–10.10) 20	10.3 (—) 1	10.0 ± 0.27 (9.65–10.39) 13
BZP	1.9 ± 0.12 (1.71–2.05) 13	1.8 ± 0.09 (1.71–1.99) 10	1.7 ± 0.15 (1.34–1.94) 22	1.6 (—) 1	1.6 ± 0.19 (1.30–2.00) 13
LD	8.5 ± 0.35 (8.03–9.19) 12	8.6 ± 0.27 (8.09–8.88) 9	8.9 ± 0.41 (8.20–9.99) 18	8.6 (—) 1	7.8 ± 0.27 (6.76–8.35) 11
PPL	12.9 ± 0.62 (11.76–13.83) 13	12.8 ± 0.38 (12.41–13.67) 9	12.7 ± 0.37 (11.93–13.54) 18	12.1 (—) 1	11.7 ± 0.33 (10.90–12.11) 12
LBP	7.6 ± 0.23 (7.16–8.05) 13	7.9 ± 0.18 (7.60–8.26) 10	8.5 ± 0.30 (7.95–9.00) 19	8.5 (—) 1	7.2 ± 0.23 (6.80–7.80) 11
BMF	2.5 ± 0.19 (2.13–2.81) 13	2.5 ± 0.16 (2.32–2.71) 10	2.5 ± 0.26 (2.14–3.09) 19	2.5 (—) 1	2.4 ± 0.14 (2.10–2.60) 13
LIF	4.8 ± 0.18 (4.54–5.10) 13	4.3 ± 0.19 (4.10–4.66) 10	4.6 ± 0.27 (4.35–5.45) 18	4.6 (—) 1	4.6 ± 0.14 (4.30–4.94) 11
BIF	2.6 ± 0.13 (2.43–2.93) 13	2.4 ± 0.14 (2.21–2.59) 10	2.5 ± 0.20 (2.23–2.92) 18	2.3 (—) 1	2.4 ± 0.10 (2.23–2.60) 12
CLM	5.5 ± 0.10 (5.34–5.72) 13	5.4 ± 0.13 (5.28–5.66) 10	5.6 ± 0.18 (5.16–5.86) 21	5.8 (—) 1	5.0 ± 0.25 (4.45–5.35) 13
LM1	2.9 ± 0.07 (2.82–3.03) 11	3.0 ± 0.07 (2.84–3.07) 10	3.0 ± 0.12 (2.65–3.22) 22	3.2 (—) 1	2.8 ± 0.14 (2.59–2.94) 11
BM1	1.6 ± 0.07 (1.52–1.82) 13	1.6 ± 0.10 (1.52–1.82) 10	1.6 ± 0.08 (1.46–1.71) 22	1.5 (—) 1	1.5 ± 0.09 (1.38–1.65) 13

montane rain forest (Brass's "mid-montane" forest "at once distinguished from the more mixed rain forest by its generally more open character under the canopy and the distinctive appearance of its dominant oaks and *Castanopsis*"; Brass, 1956: 134). Some interdigitation of the two formations characterized the forest near the camp (Brass, 1956: 134):

Rain-forest canopy trees entered the mid-mountain forest and extended sporadically far up the mountainside. Scattered large trees of one of the oaks,

with small acorns, grew in the upper parts of the rain forest at camp level. Many minor floristic elements such as woody and herbaceous undergrowth species, epiphytic orchids and ferns, and some large lianas occurred in both types of forest, but others did not. The lower limits of the zone of regular cloud formation on the mountainside marked, here as apparently everywhere in New Guinea where such cloud conditions prevail, the contact line of two readily distinguishable forest types.

TABLE 6
**Frequency of Cusp t7 and a Discrete Recognizable Anterolabial Cingulum on the Second Upper Molar in
 Samples of *Leptomys***
 (See fig. 13. Specimens are stored in AM, AMNH, BBM, BMNH, MCZ, MSCN, and USNM.)

Species and Provenance	Cusp t7	Anterolabial Cingulum
<i>L. ernstmayri</i>		
Huon Peninsula	13/13 = 100%	13/13 = 100%
Adelbert Range	2/10 = 20%	7/10 = 70%
Foja Mountains	0/1 = 0%	0/1 = 0%
Central Cordillera	15/18 = 83%	4/18 = 22%
Total	30/42 = 71%	24/42 = 57%
<i>L. paulus</i>		
Owen Stanley Range	0/13 = 0%	0/13 = 0%
<i>L. elegans</i>		
Papuan Peninsula	10/11 = 91%	0/11 = 0%
Kikori River Basin	3/6 = 50%	1/6 = 16%
Total	13/17 = 76%	1/17 = 6%
<i>L. signatus</i>		
Southcentral Lowlands	6/6 = 100%	0/6 = 0%
<i>L. arfakensis</i>		
Arfak Mountains	0/2 = 0%	0/2 = 0%

The smaller-bodied *Leptomys paulus*, n. sp., was encountered at Number 2 Camp, higher on Mount Dayman in tropical lower montane rain forest (see account of *L. paulus*, below).

The specimen of *L. elegans* from Mount Dayman was the only *Leptomys* that Van Deusen, its collector, had ever encountered (partial manuscript in AMNH Mammalogy archives). Of his experience, he wrote:

While jacklighting at 8:00 on the evening of July 17, I observed and then shot a large male (158204) as he was hopping on the forest floor. This individual may well have been frightened to such action by my presence. I cannot say with certainty that hopping is the normal rapid gait of *Leptomys*.

Because the tail slightly exceeds length of head and body, Van Deusen suspected "hopping may often be the preferred gait, especially to escape predators".

According to its associated field data, the single available specimen from Mount Victory, an outlying peak north of the Central Cordillera in far southeastern New Guinea (Diamond, 1985), was taken in an Elliott trap set "on mossy ground in secondary forest" at

800 m. This elevation probably marks the approximate zone of transition between lowland and lower montane evergreen rain forest on this small isolated mountain block.

Apart from habitat associations, only meager biological data is available for *L. elegans*. The only reproductive information is from two sources. Dwyer (1984) reported a mean litter size of 1.75, based on four pregnant females taken on Mount Sisa. Leary and Seri (1997: 89) noted a single young born to another pregnant female caught during March, 1995, in the Kikori River Basin.

During Dwyer's study of rodents and plant succession on the southern slopes of Mount Sisa in 1979 and 1980 (see Dwyer, 1984, and references cited there), he described behavior and diet of a juvenile male (extracted from his field notes on file at CSIRO). The animal slept in a "sitting" position, resting upright on the full extent of the hind feet with its back curled and the head inserted down between the front legs; his sketch suggested that the tail was extended rather than curled in (this sleeping position of the head and body may possibly explain the balding pattern of the fur between ears and shoulders). However, he also noted that when at rest, the tail was curled forward along the right side of the body all the way around the head to ear level on the left side.

The animal walked about “elegantly”, on its digits with most of the plantar portion off the ground, and the tail arched with the tip pointing downward.

Available evidence gleaned from published and unpublished sources indicates *Leptomys elegans* to be carnivorous. Leary and Seri (1997) captured two specimens from the Kikori River Basin in traps baited with “sago grubs” and a specimen from Mount Dayman (AMNH 158203) was taken in a live trap baited with meat. Dwyer’s observations recorded in his field notes are definitive. During one afternoon and night his captive male “had eaten 20 or so small grasshoppers” and one preying mantis (3 inches long), pouncing on each insect and attacking at the “head end first”; it also gnawed cooked flesh off a cuscus (phalanger) vertebrae. Over the following day and night the rat ate an entire carcass of a juvenile male *Rattus niobe* (weighing 26 g; the *Leptomys* weighed 39 g when caught and 2 g less when released a few days later), “leaving skin, feet and tail but chewing up smaller bones”. Dwyer’s captive also devoured the raw flesh off skulls. It ignored pawpaw (a fruit). Another of Dwyer’s specimens, a female, had “insect stuff and other [unidentified matter]” in her stomach. Although *Leptomys* has been caught in traps baited with coconut—two specimens from the Kikori River Basin (Leary and Seri, 1997: 89) and an example from Mount Victory—we suspect the rats in these instances were attracted to invertebrates that had gathered on and around the coconut bait.

Smales (2006) lists helminth parasites discovered in the digestive tract of “*L. elegans*” (taken from samples of *Leptomys* at AM and BBM), but Smales’s results are impossible to interpret as presented, because her host sample was composite, including two specimens of *L. paulus*, n. sp., from the Maneau Range, two individuals of *L. ernstmayri* from the Adelbert Range, and two examples of *L. elegans*, one from Mount Victory and the other from the Kikori River Basin.

Leptomys signatus Tate and Archbold, 1938

HOLOTYPE AND TYPE LOCALITY: The holotype of *signatus* is AMNH 105792, an adult female, represented by an intact skull and

study skin, from the “east bank” (= north bank) of the Fly River opposite Sturt Island (“Sturt Island Camp”, Rand and Brass, 1940: 361; [Papua New Guinea, Western Province]), near sea level, 08°15’S, 142°15’E, and collected October 12, 1936 by G.H.H. Tate. Skin of the holotype is shown in figure 4, a skull from the original series is illustrated in figure 9, and measurements of the holotype are listed in table 1.

GEOGRAPHIC DISTRIBUTION: We identify samples of *Leptomys signatus* that were collected from three sites in south-central New Guinea, located in Western, Southern Highlands, and Gulf provinces of Papua New Guinea. The specimens come from an altitudinal range extending from near sea level to 1400 m.

The four specimens in the type series of *L. signatus* were taken in the Trans-Fly region along the southern Fly River in Western Province (locality 2 in gazetteer and fig. 2), and until now these have been the only published records of the species. Two additional specimens, previously undocumented, originate from the north-northwestern slopes of Mount Bosavi (locality 3, gazetteer and fig. 2), where they were trapped at 1400 m by A.B. Mirza (BBM-NG 103319 and 103263); no other information is available about these Bosavi examples, which, judging from the trapping altitude, were taken in lower montane rain forest, a different type of habitat than recorded for *L. signatus* elsewhere.

Leary (2004) collected and discussed the most recent sample of *L. signatus* to have been collected, which consists of two specimens trapped on the Darai Plateau, 380 m, in Gulf Province (locality 4, gazetteer and fig. 2). We have not studied these vouchers, but Leary provided us with photographs in support of the record (see fig. 15), demonstrating that both specimens exhibit a conspicuous pale spot on the head as well as other associated biological data that we exhibit below. However, some specimens of *L. elegans* show weak to moderate white markings between the eyes, so the skulls of the Darai specimens will have to be examined to confirm their identification as *L. signatus*.

These additional specimens (Mount Bosavi, and probably Darai Plateau) replicate the

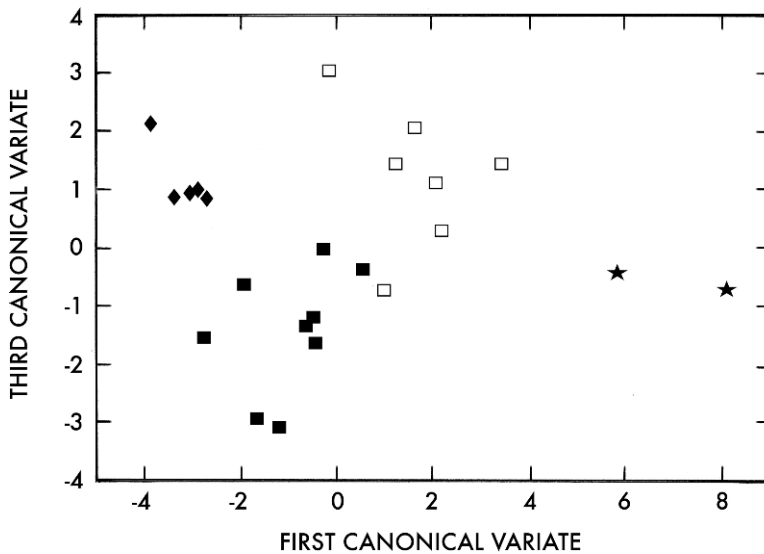


Fig. 14. Morphometric contrast (discriminant-function analysis performed on cranial and dental variables) among *Leptomys* with larger body size—*L. elegans*, *L. signatus*, and *L. arfakensis*—showing projection of specimen scores on the first and third canonical variates extracted. See table 7. Species key: *L. arfakensis*, black stars; *L. elegans* from the Papuan Peninsula, hollow squares, and from the Kikori River Basin, solid squares; *L. signatus*, diamonds.

signatus possesses cusp t7 but lacks an anterolabial cingulum (table 6). Cusp t7 is present in about three-fourths of our sample of both *L. elegans* and *L. ernstmayri*, but is absent in samples of *L. paulus*, n. sp., and *L. arfakensis*, n. sp. In addition to *L. signatus*, an anterolabial cingulum is absent in the two new species and most examples of *L. elegans*, but in only about 40% of the specimens of *L. ernstmayri*.

HABITAT AND BIOLOGY: *Leptomys signatus* is certainly terrestrial, likely nocturnal, but most other biological attributes have yet to be revealed. Although it has long been known only by the type series from the Fly River Basin, and thus considered an exclusively lowland species (Musser and Carleton, 1993, 2005; Flannery, 1995), the series from the northern slopes of Mt. Bosavi demonstrate that the altitudinal range of *L. signatus* is similar in vertical extent to that of *L. elegans* (see account of *L. elegans*). The mean altitude of the three known trapping sites is 593 m (median 380 m, SD 724 m).

According to Rand and Brass (1940:361), the type locality of *L. signatus* (the Sturt Island Camp), was:

situated in a grove of bamboos on the top of a red bluff, about 12 m. high, overlooking the river. ...Bordering the river in many places are muddy tidal terraces with tall forests dominated by a mangrove (*Bruguiera*), and a nutmeg with a highly developed system of aerial roots....The general terrain is of irregular lateritic ridges, among which are enclosed flat basins, for the most part swampy, and connected with the river by sometimes almost imperceptible water-courses which empty into muddy tidal creeks....With the exception of the wetter flats, where transitions from rain-forest to swamp-forests of tea-tree and sago and eventually open reed swamps occur, the whole area is covered with rain-forest.

Rand and Brass (1940: 361–363) provided excellent descriptive views of the different vegetative formations along with photographs of the bamboo substage of dry, open rain-forest, and different kinds of tall swamp forests in the dry season. The region around Sturt Island Camp in that part of the Fly

TABLE 7

Results of Discriminant-Function Analysis Performed on 23 Adult *Leptomys* with Larger Body Size: *Leptomys elegans*, *Leptomys signatus*, and *Leptomys arfakensis*

(Correlations, eigenvalues, and cumulative variance are explained for three canonical roots; see table 4, figs. 13, 14. We used 10 variables instead of the 17 utilized in our other multivariate analyses to accommodate both skulls representing *L. arfakensis*, neither of which is complete.)

Variable	CV1	CV2	CV3
IB	-0.0268	-0.46536	-0.0858
LN	0.0101	-0.4401	0.2359
BR	0.0296	-0.0603	0.4923
BBC	-0.0476	0.1490	0.3511
BZP	0.1803	0.3166	-0.0891
LIF	0.1033	-0.1799	0.5524
BIF	0.2740	0.0086	0.3406
CLM	-0.2493	-0.2123	0.2249
LM1	-0.3633	-0.1919	0.0591
BMI	-0.3989	0.2978	0.0260
Canonical Correlation	0.9502	0.8086	0.7341
Eigenvalue	9.2900	1.8888	1.1689
Cumulative Variance	0.7524	0.9053	1.000

River was a mosaic of rain forest; sago, *Melaleuca*, and other kinds of swamp forests; and open marsh and swamp (see their summary of habitat types and map, Rand and Brass, 1940: 372–373). According to the collectors of the type series, within this complex mosaic of habitats, *Leptomys signatus* inhabits “well-drained forests bordering the north banks of the Fly River” (Tate and Archbold, 1938: 1).

Leary (2004) noted that:

Two individuals were caught on the Darai Plateau, a sub-adult male and a pregnant female. These traps were set in a drainage line that flooded during heavy rain, but the water soon dissipated through limestone crevices after the rain ceased. The female was pregnant with a single embryo. They were both caught in small Elliot traps baited with singed coconut and set on the ground.

No other biological data are available for *L. signatus*.

Leptomys ernstmayri Rümmler, 1932

HOLOTYPE AND TYPE LOCALITY: The holotype of *ernstmayri* is ZMB 42400, adult male,

study skin and skull, from Ogeramnang (06°26'S, 147°22'E), 1785 m, Huon Peninsula, collected February 20, 1929, by Ernst Mayr; measurements are listed in table 1. Rümmler (1932) placed Ogeramnang in the Saruwaged Mountains, but the locality is not in that range. H. M. Van Deusen (partial manuscript in AMNH Mammalogy archives) noted that Ogeramnang “lies on high ground above and just north of the lower Bulum River, and looks south to the Rawlinson Range. The Saruwaged Mountains lie far to the northwest”. The geographic position of Ogeramnang is clearly portrayed in the published map showing collection sites of the Seventh Archbold Expedition to New Guinea undertaken in 1964 (Van Deusen, 1978: 19).

DIAGNOSIS AND CONTRASTS: *Leptomys ernstmayri* is a distinctive species that has usually been misidentified as *L. elegans* in museum collections and reports published prior to 1993 (Tate, 1951, and Flannery, 1990, are examples). It is distinguished from *L. elegans* by the diagnostic morphological traits and altitudinal associations that were carefully enumerated by Rümmler (1932) and illuminated in greater detail by data presented here. *Leptomys ernstmayri* is smaller in body size (as indicated by length of head and body, and mass; contrast measurements in tables 2 and 3) than *L. elegans*, but has a much longer



Fig. 15. *Leptomys* sp. cf. *signatus* in life, a young male trapped on the Darai Plateau, Gulf Province, Papua New Guinea (see fig. 2 and gazetteer). Photographed by Tanya Leary.

tail relative to length of body. This smaller size of *L. ernstmayri* is also reflected in the lesser cranial and dental dimensions compared with those characteristic of *L. elegans* (contrast values in tables 4 and 5). An anterolabial cingulum is present in more than half of the total available samples of *L. ernstmayri*, but is generally absent in our material representing *L. elegans* (table 6). In an ecological context, *L. ernstmayri* replaces *L. elegans* at high altitudes in tropical lower and upper montane rain forests.

The morphological distinctions setting *L. ernstmayri* apart from *L. elegans* are generally similar to those separating the former from *L. signatus* and *L. arfakensis*, n. sp. (see those accounts). *Leptomys signatus* has the additional combination of short, grayish upperparts broken by a white blaze on the head, which contrasts it with any specimen of *L. ernstmayri* we have studied.

Leptomys ernstmayri, in body size and ecology is more similar to a species we describe below that lives in mountain forests covering the Owen Stanley Range, but differs significantly by its larger dimensions (tables 3, 5; figs. 5, 7, 8, 16, 20) and a suite of other morphological traits that are chronicled in the account of *L. paulus*, n. sp.

GEOGRAPHIC DISTRIBUTION: The geographic distribution of *Leptomys ernstmayri* is documented by voucher specimens collected from four discrete montane populations, one in western New Guinea, all the others in eastern New Guinea (see gazetteer and map in fig. 3): (1) the Foja Mountains, an isolated north-coast range in western New Guinea, where the species is represented by one specimen collected at 1150 m; (2) the mountain ranges of the Huon Peninsula (including the Saruwaged and Rawlinson ranges), where it is recorded from 1340 m to 1785 m; (3) the isolated Adelbert Range on the northern coast, where it is documented from 1200 m to 1500 m; and (4) the eastern body of New Guinea's extensive Central Dividing Ranges (Central Cordillera), where it has been collected from Mt. Karimui (on the southern slopes) and the Schrader Range (on the northern slopes) in the west to the headwaters of the Aroa River (on the southern slopes) and Mount Missim and Lake Trist (on the northern slopes) in the east, at altitudes between 1200 m and 2200 m.

Rümmeler (1932, 1938) and Musser and Carleton (1993) included the Arfak Mountains within the range of *L. ernstmayri*, but samples from there represent a distinct species

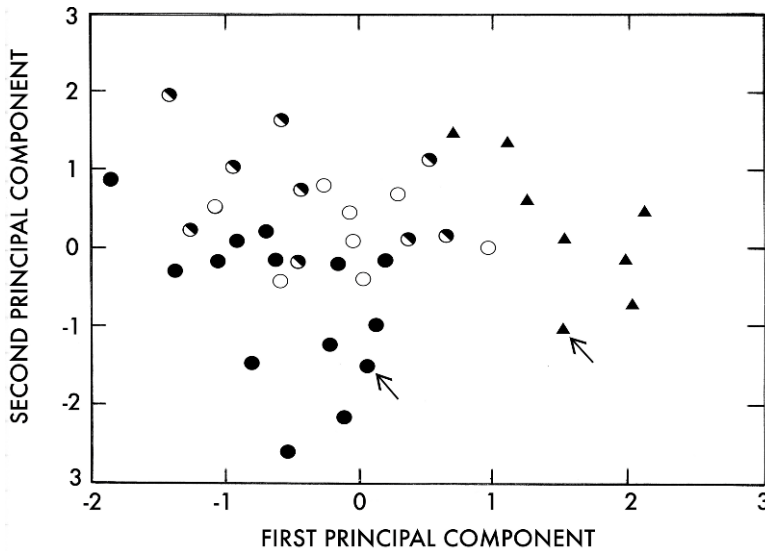


Fig. 16. Principal component analysis (performed on cranial and dental variables) showing dispersion along the first two principal components of specimen scores representing *Leptomys* of small body size. Species key: *L. paulus*, n. sp., from the Maneau Range, triangles; and *L. ernstmayri* from the Huon Peninsula, half-solid circles; Adelbert Range, hollow circles; Central Cordillera, solid circles; and Foja Mountains, solid circle signaled by arrow. The first axis is a measure of overall size (increasing from right to left), the second reflects shape. See table 8. Arrow pointing to a triangle indicates score representing the sole intact skull of *L. paulus* from the Astrolabe Range.

(*L. arfakensis*, n. sp.) that we describe in this report. Flannery (1995) and Cole et al. (1997) identified specimens from the Maneau Range of southeastern New Guinea as *L. ernstmayri*, but these likewise represent another new species (*L. paulus*, n. sp.), also described here.

GEOGRAPHIC VARIATION: Each of three geographically isolated populations that are represented by moderately large samples and identified here as *L. ernstmayri* has a combination of morphological attributes that indicate a history of diversification in isolation. This is reflected especially by divergence among populations in external proportions (table 3), qualitative dental traits (table 6), and cranial and dental morphometrics (figs. 16, 17).

Our sample from the Huon Peninsula is the most phenetically distinctive of the three in external proportions and molar architecture. It is characterized by a very long tail relative to head and body length (table 3), and the fixed presence of a cusp t7 and an anterolabial cingulum on the second upper molar (table 6).

Phenetic contrasts in external and dental traits between samples from the Adelbert Range and Central Cordillera are present but not as notable. Differences in proportions of external traits and qualitative molar structures exist but are average, not exclusive. Compared with the sample from the Adelbert Range, the tail averages longer relative to length of head and body in the Cordilleran sample, and exhibits a relatively shorter white segment (table 3). Cusp t7 on the second upper molar occurs in 15 of the 18 specimens (83%) forming the Cordilleran sample but in only 2 of the 10 animals (20%) from the Adelbert series, and the anterolabial cingulum is found in 4 of the 18 Cordilleran specimens (22%) as compared with 7 of the 10 (70%) from the Adelbert Range (table 6). In the samples from the Adelbert Range, the fur between ears and shoulders is thinner producing a more conspicuous balding pattern than seen in examples from the either the Huon Peninsula or Central Cordillera.

The morphometric structure derived from discriminant-function analyses of cranial and

TABLE 8
Morphometric Separation (Principal Components Analysis) of 39 Adult *Leptomys* with Small Body Size, *Leptomys ernstmayri* and *Leptomys paulus*
 (Principal components are extracted from a covariance matrix of 17 log-transformed cranial and dental variables; see table 5, fig. 16.)

Variable	PC1	PC2
ONL	-0.8967	-0.2392
ZB	-0.8485	-0.2586
IB	-0.3402	-0.0995
LN	-0.3339	-0.4482
BR	-0.7787	-0.3096
BBC	-0.6592	-0.4134
HBC	-0.4780	-0.4151
BZP	-0.6393	0.6526
LD	-0.8638	-0.2092
PPL	-0.7980	-0.1003
LBP	-0.7106	-0.4896
BMF	-0.2198	0.3848
LIF	-0.3125	0.0597
BIF	-0.6147	0.3937
CLM	-0.6370	-0.3739
LM1	-0.4166	-0.5512
BM1	-0.4164	-0.1052
Eigenvalue	0.0203	0.0092
Percent Variance	38.2281	17.3612

dental variables in samples of *L. ernstmayri* reflect a somewhat different pattern of geographic variation (fig. 17). The spread of specimen scores along the first canonical axis forms three clusters isolated from one another, each representing the three separate geographic regions sampled: Huon Peninsula, Adelbert Range, and Central Cordillera. Covariation in interorbital breadth, length of rostrum (as indexed by length of nasals), breadth of braincase, and length of bony palate are primarily responsible for the dispersion of scores along the first axis; lengths of diastema and first upper molar along with breadth of the incisive foramina are also influential but carry less weight (table 9).

The scattering of specimen scores along the second canonical axis reveals a different pattern of covariation in morphometric space that is mostly influenced by size as indicated by the many negative correlations (fig. 17). There the scores for specimens from the Huon Peninsula and Central Cordillera are assembled into overlapping clusters, but those

representing the sample from the Adelbert Range form a group isolated from the other two. Variation in breadths of interorbit and rostrum, length of bony palate, and spaciousness of the incisive foramina primarily influence the spread of scores along the second axis that results in the peripheral position of the Adelbert cluster; lengths of skull and molar row contribute but with less force (table 9). Proportionally, these dimensions are greater in the Adelbert sample compared to the other two geographic series.

Distribution of scores along the second axis in both the principal components and canonical variate ordinations reveals another aspect of variation among the three geographic samples (figs. 16, 17). Compared with the tight clusters of scores representing samples from the Huon Peninsula and Adelbert Range, the points within the cloud for the sample from the Central Cordillera are more widely scattered, especially within the principal components scatter plot. This pattern is not surprising. Samples from the most expansive geographic subdivision of *L. ernstmayri*, stretching from the Owen Stanley Range in the east to Mount Karimui and the Schrader Range in the west, also exhibits the greatest morphometric variability.

We have a sample from a fourth montane area. The filled circle identified by an arrow in the principal component and canonical variate scatter plots (figs. 16, 17) is the score for a young animal in adult coat, the sole specimen collected in the Foja Mountains, which is a northern outlier of the Central Cordillera in western New Guinea, far from the sources of our larger samples to the east. The specimen score is associated with the cloud of scores for the Cordilleran samples along the first and second axes in both the principal components and canonical variate (where the specimen was entered as an unknown) ordinations. Other traits we examined are unhelpful in assessing the affinities of this individual with other montane samples. It lacks a cusp t7 and an anterolabial cingulum on the second upper molar, but so do some specimens from both the Adelbert Range and Central Cordillera (table 6). Length of head and body is less than the averages for the Adelbert and Cordilleran samples, but is within the ranges of variation

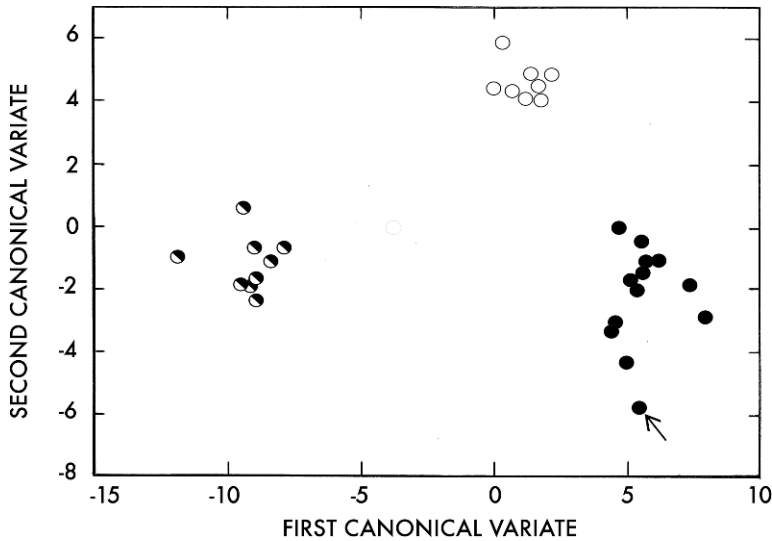


Fig. 17. Morphometric contrast (discriminant-function analysis performed on cranial and dental variables) among geographic samples of *Leptomys ernstmayri* showing projection of specimen scores on the first and second canonical variates extracted. See table 9. Key to geographic samples: Adelbert Range, hollow circles; Central Cordillera, solid circles; and Huon Peninsula, half-solid circles. Arrow identifies score for single *L. ernstmayri* from the Foja Mountains, which was entered as an unknown in the analysis.

observed for those series (table 3). The tail is shorter and outside the scope of recorded variation, but its length relative to length of head and body is not. All cranial and dental measurements are within the latitude of variation recorded for these measurements in the Cordilleran sample (table 5). The external contrasts may simply reflect the young age of the specimen. Its weight of 70 g, however, might be significant. That figure is outside the range, although not by much, of values recorded for samples from the Adelbert Range and Central Cordillera, and even the Huon Peninsula (table 3). If that body mass is typical of young adults, older animals may weigh more and the population on the Foja Mountains could be characterized by, among other traits, significantly larger body size than found in populations occurring elsewhere.

Different combinations of qualitative and quantitative morphological traits indicate phenetic divergence among samples from the Central Cordillera, Adelbert Range, and Huon Peninsula, each a discrete geographic entity. Examining morphological attributes in larger series from more places in all three regions may help confirm or dispel the pattern of geographic variation we have documented

here. Additional material from now unsampled portions of the Central Cordillera, the most expansive of all highland areas surveyed, would be of special interest for providing insight into the significance of the morphometric variation we described among our specimens from Cordilleran localities, including the Foja Mountains, which are isolated from the Central Cordillera. The addition of molecular data would be especially helpful. That critical component would help us assess whether the distinctive discriminating phenetic traits associated with samples from the Huon Peninsula, Adelbert Range, and Central Cordillera represent the outcome of prolonged genetic and ecomorphological divergence rather than a product of genetic drift among recently subdivided montane populations of a single species. For now we regard the available samples from the three montane regions to represent populations of *L. ernstmayri* based on their equivalence in overall size and similarity in pelage coloration and qualitative cranial features.

To us, the single specimen from the Foja Mountains also represents another population of *L. ernstmayri*. In overall size, texture, and coloration of pelage, and cranial traits, it is

TABLE 9
Results of Discriminant-Function Analysis
Performed on 31 Adult *Leptomys ernstmayri* from
Four Geographic Regions
 (Correlations, eigenvalues, and cumulative variance
 are explained for two canonical roots; see table 5,
 fig. 17.)

Variable	CV1	CV2
ONL	0.0451	-0.1113
ZB	0.0243	-0.0912
IB	-0.1110	-0.1905
LN	0.1262	-0.0477
BR	0.0200	-0.2322
BBC	0.1009	-0.0179
HBC	0.0531	0.0061
BZP	-0.0559	0.0800
LD	0.0644	-0.0837
PPL	-0.0218	0.0763
LBP	0.2468	-0.2274
BMF	0.0210	-0.0052
LIF	-0.0419	-0.2268
BIF	-0.0624	-0.1670
CLM	0.0251	-0.1080
LM1	0.0836	-0.0698
BM1	-0.0218	0.0487
Canonical Correlation	0.9889	0.9458
Eigenvalue	44.4826	8.4739
Cumulative Variance	0.8400	1.000

closely similar to material in all our other samples that we identify as that species. We need a larger sample from the Foja region that contains a greater range in age to evaluate the genetic and zoogeographic status of what appears to be an extremely remote montane isolate in western New Guinea. We note, however, that the Foja Mountains are emerging as an area of striking montane endemism within New Guinea, especially in birds (Diamond, 1982, 1985; Beehler et al., 2007).

HABITAT AND BIOLOGY: The specimens of *L. ernstmayri* we can tie to reliable descriptions of collection sites are all from tropical lower montane and "midmontane" rain forest formations. The AMNH series from Gang Creek (1340 and 1370 m) in the Rawlinson Range of the Huon Peninsula is the largest of this species so far collected. They were obtained by members of the Seventh Archbold Expedition to New Guinea in 1964. Hobart M. Van Deusen (partial manuscript in AMNH archival files) wrote that the credit for the fine material was

entirely due to Adion, a young native boy from the village of Zengaren, and the patience of Grierson [a member of the Expedition from the United States] who encouraged him to trap for us. A simple deadfall trap was constructed; the top was loaded with soil, and several large and active beetles, tied together with bush string, were attached to the complicated trigger. This was the only trap and trigger of this kind that we saw in use on the Huon Peninsula. The only other specimen obtained on the trip came to one of my hanging meat sets that had concealed steel traps buried beneath the bait. This method also took *Leptomys* on previous expeditions.

Except for a close view (fig. 6 in Van Deusen, 1978: 11) of the forest at the Gang Creek camp, which shows "dense, tangled vegetation with heavily mossed tree trunks", clearly indicating tropical lower montane forest (as does the altitude), no other information, either in field journals or publications, can be tied to the Gang Creek sample.

The specimen from Purosa (1970 m) and that from nearby Kamila (1900 m), collected by members of the Sixth Archbold Expedition to New Guinea in 1959, were taken in primary tropical lower montane rain forest. Brass (1964: 199–200) described this as "mid-mountain forest" (p. 208) and chronicled the rich diversity of canopy trees near camp, the great variety of subcanopy species, and the lush floristic wealth of the undergrowth, especially in ravines and shallow gullies. Purosa is at the head of a grassy valley in deep forest covering a divide over which about 2 km away was the Kamila site, also in deep forest and at the head of a smaller grassy valley. This is a common vegetational pattern in the New Guinea highlands: remnant primary forest on high divides and ridges giving way at lower altitudes to anthropogenic grasslands (Paijmans, 1976; Grubb and Stevens, 1985).

Kassam (1350 m), another camp made by the 1959 expedition but far to the northeast of Purosa and Kamila, also yielded a single example of *L. ernstmayri*. The surrounding vegetation consisted of primary tropical lower montane forest (with oak, *Castanopsis*,

Engelhardia, and a variety of laurels dominating) interdigitating with second-growth formations and anthropogenic grasslands (Brass, 1964: 203–204).

The specimen from the Foja Mountains was trapped by Helgen along the forested bank of a rushing stream at about 1200 m (fig. 18). The trap had been set on the ground 6–10 ft above the streambed. We asked Wayne Takeuchi of Harvard University, the botanist on the expedition to the Foja Mountains, to characterize the habitat at the exact site where Helgen took the rat. “The point you speak of”, wrote Takeuchi,

is where the stream starts to level off a bit and you get real alluvial debris (stream abraded rounded rocks instead of the angular colluvium higher up the bed). The forest there looked to me like a mid-stage succession; *Ficus*, *Maesa*, *Cypholophus*, stuff I would not normally associate with primary growth. However, the higher slopes bordering the bed are mainly tall growth Myrtaceae (*Syzygium*), Lauraceae (*Cryptocarya*, *Litsea*), and would count as mature growth. Like most places with unstable slopes, it’s a community mosaic, but the streambed itself is successional, and transitional to older, more shade-adapted communities.

The terrestrial habitus observed by Van Deusen was also indicated by Rudd and Stevens (1994: 45) who trapped one individual “at ground surface” at 1980 m on the southern flank of Mount Missim (then identified as “*L. elegans*”, but corresponding to BBM-NG 160978, a specimen of *L. ernstmayri*); this specimen was trapped “near the transition zone from mid-montane rain-forest to upper montane rain-forest” (Willett et al., 1989). Two specimens collected at Kassam Pass (1400 m) in the Kratke Range (BBM-NG 54966 and 54995) bear label notations indicating they were taken in a “live trap on the ground in forest” and a “snap trap on the ground in forest”, respectively. The series at BBM from the Adelbert Range (see gazetteer) and another from Mt. Karimui (BBM-NG 105313) were likewise snap-trapped, all in

“forest”, according to their labels. Another specimen (AM M14682) was taken on Mt. Karimui at 1750 m in a trap baited with sweet potato, placed below a fallen tree trunk “in lower montane forest with open understory interspersed with dense stands of climbing bamboo” (K. P. Aplin, personal commun.). A small series of specimens from the Schrader Range (at UPNG) were dug out of an underground nest by Hagahai women (Yarao, in litt., 2005).

As with all the other species of *Leptomys*, a carnivorous diet has been attributed to *L. ernstmayri*, which is certainly corroborated by Van Deusen’s observations at Gang Creek. Yarao (in litt., 2005) found that the stomach contents of animals trapped at Hagahai in the Schrader Range included only arthropods (including termites, spiders, cockroaches, and chalcid beetles) and fungal hyphae, with cockroaches and beetles predominating.

Reproductive information is meager. One of the two specimens from Lake Trist is a pregnant female that bore a single fetus (10 mm in crown-rump length) in the left horn of the uterus. Another specimen from the Schrader Range was a pregnant female carrying a single fetus (crown-rump length = 34 mm).

Leptomys paulus, new species

HOLOTYPE AND TYPE LOCALITY: The holotype is AMNH 158202, an adult female collected by Hobart M. Van Deusen (original number 12583) on July 8, 1953. The specimen consists of a stuffed museum study skin, cranium, and mandible. There is a sewn tear in the basal third of the tail; otherwise the skin is in good condition as is the skull (figs. 5, 7, 8); the teeth are intact, and although the molars are worn, the cusp patterns persist. External measurements are listed in table 1, cranial and dental measurements are included in the univariate summaries listed in tables 5 and 11.

The type locality is “Number 2 Camp” (fide Brass 1956: 130), labeled “Middle Camp” on skin tags, 1370 m, north slopes of Mount Dayman, 09°49’S, 149°16’E, in the Maneau Range (also spelled “Maneao”), at eastern end of the Owen Stanley Mountains, Milne Bay

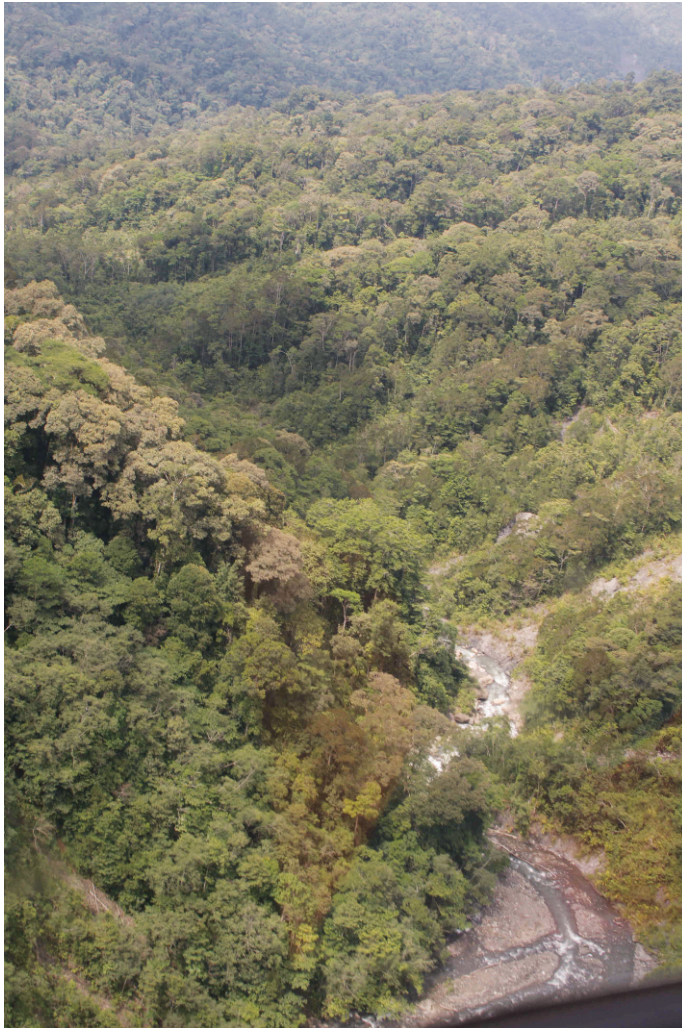


Fig. 18. Forested stream valley and ridges near Bog Camp in the Foja Mountains of western New Guinea, about 1200 m. Photographed by Bruce Beehler.

Province, eastern Papua New Guinea (locality 23 in gazetteer and fig. 3). The actual Number 2 Camp was at 1550 m “on the crest of the leading spur ridge we had followed up from lower levels” (Brass, 1956: 130). The trapping locality at 1370 m was in “the deep Atairo ravine, ...a beautiful place, very mossy, and crowded with ferns,” about an hour’s walk from the camp at 1550 m (Brass, 1956: 131). The Maneau Range is part of the Owen Stanley Range 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 Mount Dayman with its peaks, and the section of the Owen Stanley Range 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. Another perspective of the region is provided by Engilis and Cole (1997: 1) who worked there in 1985 and wrote that Mount 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: Along with the holotype, three other specimens of *L. paulus* were obtained by Van Deusen at Number 2 Camp, 1540 m: AMNH 158199, the stuffed skin, skull, and partial postcranial skeleton of a young adult male collected on June 27, 1953; AMNH 158200, the stuffed skin and skull of a juvenile male collected on June 29, 1953; and AMNH 158201, the stuffed skin, skull, and partial postcranial skeleton of an adult female collected on July 5, 1953.

An additional seven specimens were collected during August of 1992 by Pavel German at 1300 m in the Agaun region of the Maneau Range at two places: Mount Waruman and Kamaya Village (see gazetteer). These are also discussed by Flannery (1995) in his account of "*Leptomys ernstmayeri*". Cole et al. (1997) reported other specimens collected in March, 1985, from the vicinity of Agaun, which are deposited at BBM-NG (see gazetteer) as "*L. ernstmayri*"; these too represent *L. paulus*. The Australian National Wildlife Collection holds a single specimen of *L. paulus*, represented by a skull and postcranial skeleton (CSIRO 29433, adult female), obtained at Dumae Creek, Agaun (see gazetteer) in January 1986.

The northernmost record of *L. paulus* derives from Kagi, 1500 m, in the Astrolabe Range (locality 22 in gazetteer and fig. 3), where two individuals were collected by G. H. H. Tate in 1937 (AMNH 108451 and 108452).

ETYMOLOGY: The Latin, *paulus* means "little", and is used here to highlight the small body size of the species occurring in the Maneau Range and elsewhere in the eastern Owen Stanley highlands relative to all the other species of *Leptomys*, which are physically larger.

DIAGNOSIS: *Leptomys paulus* is smaller in body size than *L. elegans*, *L. signatus*, *L. arfakensis*, and *L. ernstmayri* (tables 1–5). It lacks the short buffy gray dorsal fur and white blaze on the head that is diagnostic for *L. signatus* and in pelage coloration more closely

resembles *L. elegans*, *L. arfakensis*, n. sp., and *L. ernstmayri* (figs. 4–6). Of these, *L. paulus* is ecologically and morphologically most like *L. ernstmayri*, but differs by its smaller body size, relatively longer tail (compared with samples from the Adelbert Range and Central Cordillera), rostral coloration at base of mystacial vibrissae (unpigmented to pale in *L. paulus*, dark brown in *L. ernstmayri*), longer dorsal coat that is soft and silky to the touch (shorter and velvety in *L. ernstmayri*), the part in the fur between ears and shoulders (inconspicuous because of the longer fur in *L. paulus*, a prominent feature in all the other species), missing or tiny hypothecar pad on the plantar surface (present and usually large in most examples of *L. ernstmayri*), cusp t7 and anterolabial cingulum absent from each second upper molar (table 6, fig. 11), and cranial and dental proportions (figs. 16, 20, 21).

GEOGRAPHIC DISTRIBUTION: *Leptomys paulus* is documented in museum collections primarily by specimens from the Maneau Range, including the type series from the northern slopes of Mount Dayman between 1370 and 1540 m, and from several localities in the vicinity of the village of Agaun between 1240 and 1525 m (see fig. 3 and gazetteer).

Two specimens from Kagi, at 1500 m in the Astrolabe Range, along the Kokoda Trail (locality 22 in gazetteer and fig. 3) demonstrate that the geographic range of *L. paulus* extends northeast of the Maneau Range into the main body of the Owen Stanley Range. These specimens are unambiguously referred to *L. paulus* rather than to Central Cordilleran *L. ernstmayri* (which is also recorded farther to the west in the Owen Stanley Range) on the combined evidence of their small body size, lack of cusp t7 and an anterolabial cingulum in the second upper molar (table 6), proportionally long tail (115%–121% of head and body length), relative length of white tail tip (19%–29% of tail length; table 3), and their morphometric associations in principal components analysis (fig. 16).

The mean altitude of nine vouchered collecting sites for *L. paulus* (see gazetteer) is 1408 m (median = 1400 m, SD = 112 m).

DESCRIPTION AND COMPARISONS: *Leptomys paulus* is a small-bodied, long-tailed montane

representative of *Leptomys* (fig. 19). It is generally similar in external proportions as well as pelage texture and coloration to all the other species of *Leptomys* except *L. signatus*. Adult dorsal pelage is thick (up to 12 mm long) and very soft, silky to the touch (dense but slightly shorter—not more than 10 mm long—which renders coat a velvety rather than silky texture, in the other species; *L. signatus* has an even shorter coat, 5–7 mm). As a result of its longer fur, *L. paulus* is the only species of the genus in which the balding pattern on the back of the head, neck, or shoulders is not evident in study skins (however, a balding pattern similar to the other species can be found by parting the fur over the anterior dorsum manually to reveal the underfur). The upperparts are dark tawny brown over the back and rump and buffy along sides of body, thighs, and upper arms; overhairs are mostly gray with brown to dark buffy tips (dorsal coloration is similar to all other species except *L. signatus*, which has pale buffy gray upperparts without the rich buff and dark brown tones of the other species). The head is the same color as the back (all other species are similar except *L. signatus*, which has a conspicuous and large white blaze on the head; figs. 4–6). The large, dark brown pinnae appear naked but are scantily covered with minute dark hairs. The mystacial and superciliary vibrissae, 55–60 mm at longest, extend well beyond the ears when laid against the head. A dark brown mask surrounds the eyes but does not extend onto the muzzle. The muzzle at the base of vibrissae appears unpigmented because only short scattered pale hairs cover it (the muzzle is brown or grayish brown in all the other species due to the dense covering of pigmented hairs), and the cheeks are white. Coloration of the ventral coat ranges from that seen in the holotype of *L. paulus* (as well as in AMNH 158200 and BBM-NG 109478), which is grayish white over most of the venter, except for a pure white area from chin to chest and a small white patch in the inguinal region (fig. 5), to whitish gray with white chest and throat in most specimens (in the pigmented areas, the hairs are gray basally with either short unpigmented tips—producing the grayish white affect—or longer white tips, respon-

sible for the paler gray wash), to pure white throughout, except for grayish white fur on the undersides of the hind limbs (BBM-NG 109514 and 109522, AMNH 108451 and 108452). The range in ventral coloration resembles that characteristic for many specimens of *L. ernstmayri* with the exception that some individuals of that species exhibit a buffy wash over the grayish white underparts. In the sample of *L. ernstmayri* from Mount Rawlinson, for example, the underparts range from buffy gray through grayish white to whitish gray with the same white pattern on chin, chest, and inguinal area as exhibited by *L. paulus*. Specimens of *L. ernstmayri* from the Okapa region and the Kratke Range demonstrate the range from pure white venters to whitish gray underparts that are broken by the same white pattern seen in *L. paulus*.

The tail is longer than the head and body in *L. paulus* (table 3), and covered in annuli of very small flat and inconspicuous scales (18–20 per cm). The scale hairs are fine and laid flat against the tail so that it appears naked. About one-fourth (19%–29%, averaging 26%; table 3) of the distal portion of tail is all white, the dorsal proximal region is brownish gray, and the ventral surface below this brownish gray segment ranges from white to mottled. General coloration of the tail and its patterning are similar to examples of other *Leptomys*.

Dorsal surfaces of the front and hind feet, including the digits and claws, are all white and densely covered with short silvery hairs, which form short and sparse tufts at the base of each claw. The area proximal to the ankle and wrist is brown. The second digit of the front foot is half the length of the third, which is the longest; the fourth is slightly shorter, and the fifth is the shortest, reaching to only base of adjacent digit. The hind foot is very long and narrow in *L. paulus* and all the other species except in *L. signatus* where the hind foot is longer and wider relative to body size (this contrast between that species and the others is striking). In *L. paulus* and the other species, the first digit is very short, its claw barely or not quite reaching the base of the adjacent digit; the three middle digits are longest and subequal in length; the fifth digit is short but longer than the first, its claw reaching to proximal third of the second



Fig. 19. *Leptomys paulus* in life, from the vicinity of Agaun, Maneau Range (see fig. 3 and gazetteer). Photographed by P.A. Woolley and D.A. Walsh, and originally published as *L. ernstmayri* in Flannery (1995: 242).

phalanx. The configurations of manal and pedal digits are similar in all species. A naked plantar surface, which is partially brown and adorned with conspicuous interdigital pads is also common to all species of *Leptomys*, but presence or absence and size of the hypothenar is variable among samples. In all species, the thenar is elongate and conspicuous. In 14 specimens of *L. paulus* (at AM, AMNH, and BBM), the hypothenar was absent from eleven examples, present but small in two, and of normal size in one. In specimens of *L. signatus* examined for this trait (at AMNH only), three lacked a hypothenar, and one had a tiny remnant. Six of nine *L. elegans* from the Papuan Peninsula (at AMNH and MSCN) lacked the hypothenar, but a small series of fluid-preserved specimens from Mt. Sisa (at AM) all had a hypothenar. Both specimens of *L. arfakensis* appear to have a hypothenar. For specimens of *L. ernstmayri* that we scored, 11 of 13 from the Huon Peninsula (at AMNH) had a hypothenar, both Adelbert specimens in alcohol that we studied (at BBM) had a hypothenar, but all seven specimens from the Central Cordillera (at AM, AMNH, and BBM) lacked a hypothenar.

Qualitative shape of the skull and mandible of *L. paulus*, along with most dental traits,

resemble those of the other species of *Leptomys* (figs. 7–10); characteristics of skulls and dentitions were described in the section detailing generic characteristics. The primary qualitative difference we observed was in presence or absence of cusp t7, and the anterolabial cingulum, on the second upper molar. All mature *L. paulus* lack a cusp t7; it is present in incipient form on the upper left molar in one juvenile (BBM-NG 109478). In contrast, that cusp is present in all specimens of *L. ernstmayri* from the Huon Peninsula, in most of those constituting the samples from the Central Cordillera, and in two of the 10 examples from the Adelbert Range (table 6). An anterolabial cingulum is not present in any example of *L. paulus* (and is also typically absent in *L. elegans*, *L. signatus*, and *L. arfakensis*, n. sp.). Specimens of *L. ernstmayri* from the Central Cordillera usually lack an anterolabial cingulum (14 of 18), but all those from the Huon Peninsula exhibit a conspicuous cingulum, as do seven of the 10 specimens from the Adelbert Range (table 6).

The disparity in body size between *L. paulus* and specimens of *L. ernstmayri* from the Huon Peninsula, Adelbert Range, and Central Cordillera is reflected by the much shorter head and body length in *L. paulus*, its shorter

hind foot, and lesser mass (table 3). Length of tail is an exception in this comparative context. While the tail is, on average, absolutely shorter than in the sample of *L. ernstmayri* from the Huon Peninsula, it is slightly longer than the series from the Adelbert Range and only slightly shorter than the Cordilleran sample. The proportional result is a very long tail relative to body size, which, on average, is markedly greater than the proportion in samples from the Adelbert Range and Central Cordillera but closely similar to body and tail proportions in examples of the Huon sample (table 3).

The dissimilarity in cranial and mandibular dimensions between the two species is illustrated by the larger skull of an *L. ernstmayri* from the Huon Peninsula contrasted with the appreciably smaller holotype of *L. paulus* from Mount Dayman that are aligned in figures 7 and 8. Measurements of cranial and dental variables provide quantifiable univariate and multivariate (principal and discriminant-function analyses) portrayals of the size distinction. In absolute size, *L. paulus* matches *L. ernstmayri* in a few variables (lengths of nasals and incisive foramina, height of braincase) but is significantly smaller in most other metrics (table 5).

Differences in cranial and dental dimensions among all population samples of *L. paulus* and *L. ernstmayri* are summarized in the scatter plot of specimen scores projected onto the first and second principal components, where all specimens referred to *L. paulus* cluster apart from geographic samples referred to *L. ernstmayri* (table 8, fig. 16). Covariation in size of most cranial and dental variables, as indicated by the high values is responsible for the spread of scores along the first axis. This pattern, scores for *L. paulus* at one end of the plot and those for the geographic samples of *L. ernstmayri* clustered to the left, reflects the contrast in size that is apparent when skulls of the two species are compared side by side and in the table of measurements—*L. paulus* is a smaller animal than *L. ernstmayri* in nearly all variables we examined.

Patterns of covariation along the second canonical axis extracted from discriminant-function analysis clearly isolate specimen scores representing *L. paulus* from the Huon,

Adelbert, and Cordilleran samples of *L. ernstmayri* (fig. 20). Size primarily affects the spread of scores, as indicated by the positive and strong correlations of most variables with size (table 10); the analysis again quantitatively emphasizes the magnitude of the difference in most variables between the smaller *L. paulus* and larger *L. ernstmayri*.

Proportional differences between the two species can be extracted from the discriminant-function analysis (the relatively longer nasals in *L. paulus*, for example), but are better visualized in the ratio diagram that contrasts the series of *L. ernstmayri* from the Huon Peninsula (the provenance of the holotype) with the AMNH sample of *L. paulus*, which includes the holotype (fig. 21; see also table 11). Compared with the Huon sample, *L. paulus* has significantly longer nasals relative to occipitonasal length as well as any of the other measured dimensions (length of nasals is a reasonable estimate of rostral length, which we did not measure directly), a wider braincase relative to its height, longer incisive foramina relative to both their width and length of diastema, and a longer bulla relative to occipitonasal length. *Leptomys paulus* also has a significantly lesser zygomatic breadth relative to occipitonasal length or breadth of braincase; narrower rostrum relative to length of nasals or occipitonasal length; a narrower zygomatic plate relative to most of the other dimensions; a shorter diastema, bony palate, and postpalatal region relative to occipitonasal length; and a longer molar row relative to length of bony palate. These are the striking contrasts; other proportional differences and similarities are also evident in the ratio diagram.

HABITAT AND BIOLOGY: *Leptomys paulus* inhabits forests; published descriptions of collection sites correspond to definitions of tropical lower montane rainforest (Whitmore, 1984).

Two of the AMNH examples of *L. paulus* were collected at "Number 2 Camp" where members of the Fourth Archbold Expedition to New Guinea (1953) lived and worked from June 20 to July 12, 1953. Most of the mammals obtained at this elevation were trapped or shot within easy range of camp because of the unfavorable climatic condi-

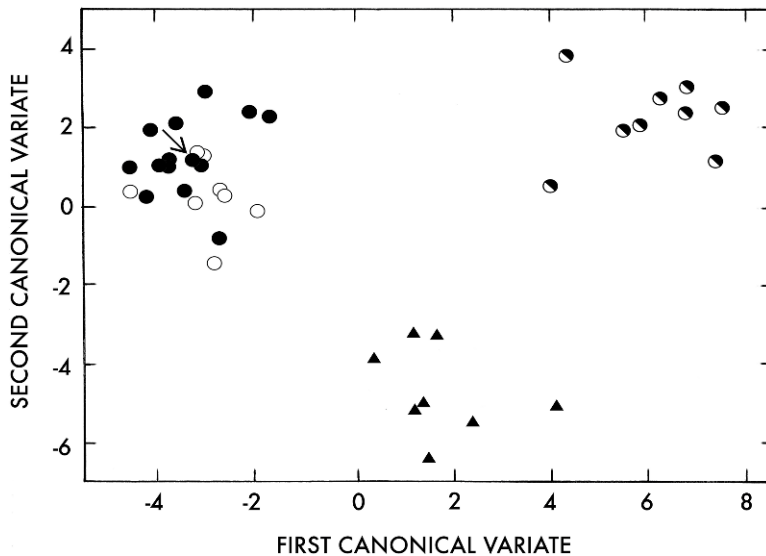


Fig. 20. Morphometric contrast (discriminant-function analysis performed on cranial and dental variables) between *Leptomys ernstmayri* and *L. paulus* showing projection of specimen scores on the first and second canonical variates extracted. See table 10. Symbol key: *L. ernstmayri*: from the Adelbert Range, hollow circles; Central Cordillera, solid circles; and the Huon Peninsula, half-solid circles; *L. paulus*, triangles. Arrow identifies score for single *L. ernstmayri* from the Foja Mountains, which was entered as an unknown in the analysis.

tions, so aptly described by Brass (1956: 130–132):

But for three of the five days following the establishment of our collecting base here and three rainless days in July, the weather can be summarized as generally dull, misty, rainy, and downright disagreeable. The climate evidently was much wetter at this altitude than at our upper camp on the mountain [at 2230 m], at least at this time of year. Many tall trees were felled to let light and wind into the camp, but for days together only rare brief bursts of sunshine would break through the clinging murk of cloud and mist and enter the clearing. On better days, by 10 A.M. often and by noon nearly always, the usual uphill air movement brought mist that turned into drizzle or was accompanied by showers. Substantial amounts of rain fell on nine days and during five nights, but as a rule the sky cleared soon after nightfall. Some of the rain was from general disturbances, for heavy falls were expe-

rienced on the lowlands at times during this period....It will be noted that owing no doubt to effects on solar radiation of the all too constant diurnal blanket of cloud and mist, maximum temperatures were slightly lower here than at the Top Camp, 680 meters higher on the mountain....Traffic on the trails soon wore through a surface layer of 5 to 10 cm. of peaty brown humus and exposed slippery yellow clay. In camp, we corduroyed the most trampled ground with sticks, between which the mire squelched and spurted as we walked in the mist. It became necessary to burn lamps in the tents all day and much of the night to dry specimens and clothing, and to have extra kerosene carried up the mountain for this purpose. Until we did this, mammal specimens pinned to drying boards remained limp, and mosses flourished on drying trays hung under the peak of my tent to take advantage of the almost non-existent heat of the sun.

Leeches, standing on end on the ground humus and waving back and

TABLE 10
Results of Discriminant-Function Analysis Derived from 39 Adult *Leptomys* with Smaller Body Size, *Leptomys ernstmayri* and *Leptomys paulus*
 (Correlations, eigenvalues, and proportions of variance are explained for two canonical roots; see table 5, fig. 20.)

Variable	CV1	CV2
ONL	-0.1007	0.3698
ZB	-0.0834	0.4387
IB	0.1559	0.2541
LN	-0.1748	-0.0225
BR	-0.0474	0.4154
BBC	-0.1956	0.3238
HBC	-0.1026	0.1780
BZP	0.0275	0.2066
LD	-0.1329	0.3650
PPL	-0.0439	0.4166
LBP	-0.3447	0.4745
BMF	-0.0342	0.0189
LIF	0.0957	0.0668
BIF	0.0972	0.2011
CLM	-0.0703	0.3925
LM1	-0.1263	0.1927
BM1	-0.0034	0.1621
Canonical Correlation	0.9720	0.9349
Eigenvalue	17.1422	6.9433
Percent Variance	61.00	24.00

forth in readiness to attach themselves to a blood supply, were active, particularly in hollows and gullies.

Mean maximum and minimum temperatures were 20.7°C (69° F) and 14.1°C (59° F), respectively (“thermometer-house temperatures in the camp clearing,” Brass, 1956: 130–131).

Brass (1956: 131) provided this description of the topography and vegetation near camp:

Except to the west where the slopes were much cut by deep ravines, the terrain about camp held some steep little gullies but for the most part consisted of fairly easy ridges. Many large trees over 30 meters tall occurred in a generally well-spaced forest dominated by a *Castanopsis* and two or three species of oaks. *Engelhardtia*, a frequent associate of these trees in New Guinea, was

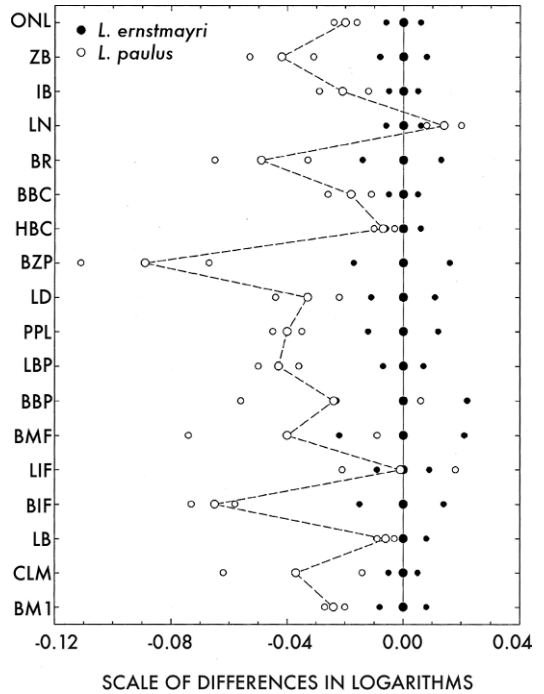


Fig. 21. Ratio diagram illustrating some proportional relationships in cranial and dental dimensions between samples of adult *Leptomys*. The standard is the AMNH sample of *L. ernstmayri* from the Huon Peninsula ($N = 11$) contrasted with the AMNH sample of *L. paulus* from Mount Dayman ($N = 3$). How the diagram was constructed and how to read it is explained in Materials and Procedures.

present, with representatives of *Goronia*, *Sloanea*, and other genera. A big, red-flowered *Metrosideros* made occasional blazes of color in ravines. Many dead trees, standing, or fallen and covered with mosses and ferns, gave parts of the forest an over-age appearance. Especially on ridge crests, the bases of the trees were mounded with a network of surface roots and covered deep with bryophytes. An abundance of leaf and twig litter lay on the ground over a carpet of mosses and hepatics. Tree trunks and branches, and a predominantly woody undergrowth were lightly to heavily mossed. Especially abundant on ridge crests and climbing to 20 meters or more, the scrambling

Table 11
Descriptive Statistics for Cranial and Dental Measurements (mm) used to derive the Ratio Diagram in Figure 21 for Adults in AMNH Samples of *Leptomys ernstmayri* and *Leptomys paulus*^a
 (Mean plus or minus one SD and observed range in parentheses are listed.)

Measurement	<i>L. ernstmayri</i> Huon Peninsula <i>N</i> = 11	<i>L. paulus</i> Mount Dayman <i>N</i> = 3
ONL	35.5 ± 0.75 (33.88–36.63)	33.9 ± 0.26 (33.65–34.16)
ZB	15.6 ± 0.50 (14.75–16.10)	14.1 ± 0.31 (13.89–14.48)
IB	6.1 ± 0.12 (5.86–6.20)	5.8 ± 0.10 (5.66–5.85)
LN	12.1 ± 0.29 (11.57–12.43)	12.5 ± 0.15 (12.35–12.64)
BR	6.1 ± 0.31 (5.57–6.44)	5.5 ± 0.17 (5.25–5.58)
BBC	13.7 ± 0.24 (13.37–14.08)	13.1 ± 0.21 (12.91–13.30)
HBC	10.17 ± 0.23 (9.87–10.63)	10.0 ± 0.07 (9.97–10.10)
BZP	1.9 ± 0.12 (1.71–2.05)	1.5 ± 0.07 (1.45–1.58)
LD	8.5 ± 0.35 (7.99–9.19)	7.9 ± 0.17 (7.70–8.03)
PPL	12.9 ± 0.60 (11.76–13.83)	11.7 ± 0.13 (11.59–11.83)
LBP	7.6 ± 0.21 (7.16–7.91)	6.9 ± 0.10 (6.80–6.99)
BBP	3.2 ± 0.27 (2.90–3.77)	3.0 ± 0.19 (2.83–3.20)
BMF	2.5 ± 0.20 (2.37–2.81)	2.3 ± 0.15 (2.09–2.38)
LIF	4.8 ± 0.17 (4.54–5.10)	4.8 ± 0.19 (4.57–4.94)
BIF	2.7 ± 0.15 (2.43–2.93)	2.3 ± 0.04 (2.23–2.30)
LB	4.2 ± 0.14 (3.98–4.41)	4.1 ± 0.02 (4.11–4.15)
CLM	5.5 ± 0.10 (5.34–5.69)	5.1 ± 0.25 (4.84–5.33)
BM1	1.6 ± 0.05 (1.52–1.71)	1.5 ± 0.01 (1.53–1.55)

^a Specimens measured: *L. ernstmayri*, AMNH 194931–194933 and 194935–194942; *L. paulus*, AMNH 158199, 158201, and 158202 (holotype).

bamboo of this altitude had larger leaves than that of the Top Camp....

These mid-mountain forests of the ridges differed almost entirely in floristics from the mossy forests and the beech forests of our Top Camp [2230 m], only a few ferns and other minor elements occurring in common. But in gullies and ravines, where mixed rain forest replaced the mid-mountain forest, a lush under-

growth contained rather numerous ferns, including *Leptopteris*, *Vandenboschia*, *Nephrolepis*, and large *Asplenium* species, and fleshy-leaved shrubs and large herbs, such as *Medinilla*, *Saurauia*, and *Begonia*, already familiar in similar habitat niches in the beech and mossy forests. The altitude was still too high or the climate too misty for palms to figure prominently, even in moist gullies in

which one species ascended as high as Top Camp, and only a *Calyptrocalyx*, a small *Linospadix*, and one other were present in addition to one or two climbing *Calamus* species. *Pandanus*, likewise, was not prominent.

Brass (1956: 131) lacked direct observations about the floristics in the deep Atairo ravine, about a one-hour walk from camp where the holotype of *L. paulus* was captured, because an injured shoulder prevented him from visiting the site and his description comes from his colleague's observations:

The deep Atairo ravine...was a beautiful place, very mossy, and crowded with ferns. My boys collected many rain-forest elements there which we did not find elsewhere on the mountain, one conspicuous plant being an *Impatiens* with large white flowers, another the fig-like *Dammaropsis kingiana*, the great leaves of which served well as bath mats in our open air 'shower room.' Of special interest as high mountain herbs descending low in this streamway were a buttercup (*Ranunculus*), *Nertera granadensis*, and *Gunnera macrophylla*. *Ranunculus*, an alpine genus in New Guinea, was not met with elsewhere on Mt. Dayman.

Members of the Fourth Archbold Expedition did not find *L. paulus* at lower camps on Mount Dayman that were situated in tropical lowland evergreen rain forest. At their 700 m "Number 3 Camp" at the upper limit of evergreen rain forest, the larger-bodied *L. elegans* was encountered (see that species account).

According to their associated field notes, specimens of *L. paulus* from Mount Waruman at Kamaya Village and near Munimun Village (deposited in AM) were collected in "primary forest" on the forest floor in snap-traps baited with beetle larvae, or dug out from a nest in the ground near a stream (apparently five individuals had been using the same nest; see Flannery, 1995).

Of the seven examples of *Leptomys paulus* obtained on the Garatin Ridge reported by Cole et al. (1997:12), one was live-trapped at

the base of a tree in primary forest. The others

were purchased with their nests from Daga hunters. All of the nests were reportedly dug up from burrow systems that contained a central nest chamber about 1 m beneath ground surface. One nest, from primary forest habitat, contained three individuals (adult female and two juvenile males); the remaining three nests, from secondary forest areas, contained one adult each. Our hunters told us that some animals escaped capture during nest excavation.

Two of the female *L. paulus* collected by Cole et al. (1997) in March 1997 were pregnant, one (BBM-NG 109273) with two embryos, one in each horn of the uterus, another with one embryo in the right horn (BBM-NG 109514). Engilis and Cole (1997) provided a brief description of the forest on the Garatin Ridge where the examples of *Leptomys* reported by Cole et al. (1997) were taken, and some climatological data.

Smales (2006) described a new helminth, *Labiobulura (Archeobulura) leptomyidis*, taken from the caeca of AM and BBM-NG specimens of *Leptomys paulus* from Munimun Village and Iana River, respectively (see gazetteer).

No other kinds of biological information are yet available for *L. paulus*.

Leptomys arfakensis, new species

HOLOTYPE AND TYPE LOCALITY: The holotype is BMNH 29.5.27.23, an adult female collected by Fred Shaw-Mayer (original number 11) on July 19, 1925. The specimen consists of a stuffed museum study skin, broken cranium, and mandible (figs. 6, 10). The braincase is fractured behind the maxillary portion of the zygomata (laterally), the mesopterygoid fossa (ventrally), and the anterior portion of the braincase (dorsally), but most fragments are preserved, including one large intact segment consisting of the parietals and interparietal, and another including the basioccipital, basisphenoid, intact left auditory bulla, mastoid, and occipital condyles.

External, cranial, and dental measurements are listed in table 1. Dentition from the paratype is illustrated in figure 12.

The holotype and paratype were collected in the Arfak Mountains of the Vogelkop Peninsula of western New Guinea (Papua Province, Indonesia) at an altitude of 1000 m. No more specific locality data are available.

REFERRED SPECIMENS: Only one other specimen is known: BMNH 29.5.27.22, a young adult male, represented by a study skin, similarly broken cranium, and mandible, with collection details as for the holotype. Dollman (1930) originally identified the type series as "*Melomys levipes*" (= *Paramelomys levipes* [Thomas, 1897]); subsequent authors have referred these two specimens to *Leptomys ernstmayri* (Rümmler, 1938; Mahoney, 1968; Musser and Carleton, 1993) or *L. elegans* (Flannery, 1995; Aplin et al., 1999).

ETYMOLOGY: Named after the type locality.

DIAGNOSIS: *Leptomys arfakensis* is larger in body size than *L. paulus* and *L. ernstmayri* and slightly smaller than *L. elegans* and *L. signatus* (tables 1–5). It lacks the short buffy gray dorsal fur and white blaze on the head that is diagnostic for *L. signatus* and in pelage coloration resembles the remaining species of the genus (figs. 4–6). *Leptomys arfakensis* is morphologically most like *L. elegans*, and is close to that species in cranial dimensions, but differs in its somewhat smaller body size, pronounced hypothenar pad on the hindfoot, lack of cusp t7 from each second upper molar (typically present in all other species except *L. paulus*), and small and narrow molars, in particular its excessively reduced upper and lower third molars or absent lower third molars (lacking in both dentaries in the holotype; fig. 22).

GEOGRAPHIC DISTRIBUTION: *Leptomys arfakensis* is known only by the two specimens listed above, from the Arfak Mountains, the largest mountain range on the Vogelkop Peninsula, also referred to as the Bomberai Peninsula or "Bird's Head" of New Guinea (fig. 2). Shaw Mayer's specimens are marked no more precisely than "Arfak Mountains" (see Dollman, 1930), although the altitude of collection (1000 m) is recorded on the skin tags.

DESCRIPTION AND COMPARISONS: *Leptomys arfakensis* is of medium body size, somewhat intermediate between *L. ernstmayri* and *L. elegans* (tables 1–5). Adult dorsal pelage is thick (up to 8–10 mm long) and velvety to the touch, similar to the texture in *L. elegans*. The tawny-brown upperparts are dark brown over the back and rump and buffy along sides of body, thighs, and upper arms; overhairs are mostly gray with brown to dark buffy tips (dorsal coloration is similar to all other species except *L. signatus*, which has pale buffy gray upperparts without the rich buff and dark brown tones of the other species). Like all other *Leptomys* except *L. signatus*, the head lacks a conspicuous white blaze (figs. 4, 6), and is similar in color to the back in the paratype, but conspicuously darker brown on the crown and face in the holotype. The pinnae are large, dark brown, and although they appear naked are actually scantily covered with minute dark hairs. The longest of the mystacial vibrissae reach 65–70 mm, extending well beyond the ear when laid against the head. A dark brown mask around the eyes extends onto the muzzle in the holotype but not in the paratype. The muzzle at the base of vibrissae appears unpigmented because only short scattered pale hairs cover it, a pattern similar to *L. paulus* (the muzzle is brown or grayish brown in the three other species due to dense covering of pigmented hairs), and the cheeks are white. The underparts are pure white throughout, from the chin to the anterior hind legs and inguinal region, grading into tawny brown along the lower hind legs and the base of the tail.

The tail is approximately equal to the length of head and body in *L. arfakensis* (table 2) and covered in annuli of very small flat and inconspicuous scales (17–18 per cm). The scale hairs are fine and laid flat against the tail so that it appears naked. The tail averages relatively shorter than in the long-tailed *L. paulus* and *L. ernstmayri*, similar in relative length to *L. signatus*, and slightly longer than the larger-bodied *L. elegans*. Coloration of the tail and its patterning are similar to other species of *Leptomys*. About one-third (27%–33%; table 2) of the distal portion of tail is all white, the dorsal proximal region is brownish gray, and the ventral surface below this

brownish gray segment is white with pale brown mottling.

Most attributes of the hind feet and front feet agree with other species of *Leptomys* and are as described for *L. paulus*, although the hind feet appear longer (relative to length of head and body) than in *L. elegans* but slightly shorter than in the other three species. A pronounced hypothenar plantar pad is present in both examples of *L. arfakensis*.

Overall conformation of the skull and mandible of *L. arfakensis* resemble those of the other species of *Leptomys* (figs. 7–10), but some proportional differences are clearly apparent. Morphometric analyses, for example, highlight the distinctive proportional attributes of the skull of *L. arfakensis* in relation to the two other species of similar body size, *L. elegans* and *L. signatus*. In our discriminant-function analysis performed on 10 variables (instead of 17, which allowed us to include the two damaged skulls of *L. arfakensis*), separation of the specimen scores for *L. arfakensis* from those representing *L. elegans* and *L. signatus* along the first canonical illustrates especially the small molars of *L. arfakensis* relative to cranial size, while separation from both *L. elegans* and *L. signatus* along the third canonical axis highlights the relatively wider interorbit and zygomatic plate of *L. arfakensis* (figs. 13, 14; table 7)—differences confirmed by univariate comparisons (table 4).

The molars, especially the first upper and first and second lowers, are narrower in *L. arfakensis* relative to the other species of *Leptomys*. As in *L. paulus*, both specimens of *L. arfakensis* lack a cusp t_7 on the second upper molar; this cusp is usually present in the other three species of *Leptomys* (table 6), and we consider its loss in *L. arfakensis* and *L. paulus* to be a derived trait convergently achieved in these two species that are separated by such great geographic distances, one at each end of New Guinea—the “Bird’s Head” region in the west and the “Bird’s Tail” in the east. An anterolabial cingulum is not present in either specimen of *L. arfakensis*; this structure is also absent in *L. paulus*, *L. elegans*, and *L. signatus*, but variably present in *L. ernstmayri* (table 6).

Of all the hydromyine genera, *Leptomys* has the least reduced dental formula. It is the only

hydromyine genus (cf. Helgen, 2005b) that retains third molars; all others in that group possess only first and second molars (or only first molars in *Pseudohydromys ellermani*). Within *Leptomys*, however, *L. arfakensis* demonstrates the greatest dental reduction. The paratype has very small third molars in each quadrant of the jaw. The holotype has small upper third molars but lacks any trace of the third molars in each dentary forming the lower jaw, as first noticed by Mahoney (1968: 68):

the molar formula of an female individual (B.M.29.5.27.23) of *Leptomys ernstmayri* Rümmler, 1932 from altitude 1000 meters, Arfak Mountains, west New Guinea is $3/2$ [i.e., three molars in each upper quadrant, two in each lower] while that of a male *L. ernstmayri* (B.M.29.5.27.22) with the same locality data is $3/3$ (both individuals collected by Mr. F. Shaw Mayer, July 19 th., 1928). The latter molar formula is indicated for *Leptomys ernstmayri* and *Leptomys elegans* Thomas, 1897 by Rümmler (1932...) and again by Tate (1951, p. 222) for *Leptomys elegans* within which he includes *Leptomys ernstmayri*. The absence of M_3 in B.M.29.5.27.22 supports Tate’s contention (1951, p. 222) that a tendency to lose the last molars may well be present in *Leptomys*.

Loss of the third molars has not been observed in any other sample of *Leptomys*, and reflects a trend unique to *L. arfakensis* (fig. 23).

HABITAT AND BIOLOGY: No biological information is yet available for *Leptomys arfakensis*. Within the Arfak Mountains, the transition between tropical-lowland and lower-montane forested habitats occurs at approximately 1000 m (Pasveer and Aplin, 1998; Stattersfield et al., 1998), which suggests that the type locality of *L. arfakensis* (“Arfak Mountains, 1000 meters”) lies at or near this ecotone. We are uncertain whether *L. arfakensis* can be characterized as occurring in tropical-lowland and lower-montane forest formations, as do *L. elegans* and *L. signatus*, or inhabits lower montane to midmontane



Fig. 22. Mandible from the holotype of *Leptomys arfakensis* (BMNH 29.5.27.23), showing first and second molars and absence of the third.

forests, in which *L. ernstmayri* and *L. paulus* are found. Judged from the closer anatomical resemblance of *L. arfakensis* to *L. elegans* and *L. signatus*, we suspect that its ecology is more likely to mirror those species, which are also characterized in part by large body size. This supposition is given circumstantial support by the little information that has been gleaned to date from small mammal trapping in the Vogelkop Peninsula. The most intensive trapping efforts in mid- to upper montane forests in the Arfaks (higher than 1500 m) are those

by Tim Flannery in 1992 in the Mokwam area (specimens at AM) and by collectors from the Bernice P. Bishop Museum at the Anggi Giji Lakes in 1963 (specimens at BBM-NG and AMNH; see Helgen and Flannery, 2004). Neither endeavor recovered *Leptomys*, although these undertakings are unlikely to represent a comprehensive inventory of small mammals in the region (Helgen, 2007a, 2007b). Currently, forested habitats at lower altitudes in the Vogelkop remain comparatively poorly surveyed for mammals (Aplin et al., 1999; Helgen, 2005b, 2007a, 2007b), and we suspect that, as for *L. elegans* and *L. signatus*, it is lowland and hill forest formations and the lower montane forest ecotone that will prove to be the preferred habitats of *L. arfakensis*.

ZOOGEOGRAPHY

Leptomys has a seemingly strange recorded geographic distribution (figs. 2, 3). It is known only from the mountain ranges of the eastern (but not western) portion of New Guinea's extensive Central Cordillera (as well as in the adjacent Adelbert Range and mountains on the Huon Peninsula), in the lowlands of southern (but not northern New Guinea), and in two disjunct mountain ranges in western New Guinea (the Arfak and Foja mountains). *Leptomys* is the only hydromyine retaining relatively complex occlusal molar morphology, and (with the variable exception of *L. arfakensis*) is also the only genus to possess all three molars (although the upper third molar is small). This dental morphology might identify *Leptomys* as the most primitive of the hydromyines (which was indicated by results of phallic morphologies compared among hydromyines and other endemic New Guinea murines; see Lidicker, 1968), although phylogenetic relationships within that group remain very poorly established (Musser and Carleton, 2005; Helgen, 2007b). The hydromyine genus that most closely approaches *Leptomys* in phenetic terms is *Paraleptomys*, which resembles *Leptomys* in basic cranial shape, body size, and chromatic patterning, among other traits (Tate, 1951; Lidicker, 1968; Helgen, 2007b). Whether *Paraleptomys* and *Leptomys* are phylogenetically related or not

(Musser and Carleton, 2005), we suspect that their close ecomorphological resemblance may partly explain their intriguing geographic patterning. Perhaps because of their ecological similarity, species of *Paraleptomys* and *Leptomys* appear to replace each other in checkerboard fashion on mountain ranges lying north of the Central Cordillera, with *Leptomys* in the Arfaks, Fojas, Adelberts, and Huon Ranges, and *Paraleptomys* in the Cyclops, Bewani, and Torricelli Ranges (see Helgen, 2005b, and Diamond, 1985). They also appear to replace each other in an east-west fashion along the Central Cordillera, with *Leptomys* in the Owen Stanley Range and in the eastern and central highlands in the eastern region of the Cordillera, and *Paraleptomys* in the Star and Snow mountains in the west. Unquestionably, *Leptomys* is truly absent from the western portion of the Cordillera, for within all of New Guinea, it is in the Snow and Star mountains where small mammals have been most intensively collected and studied (Archbold et al., 1942; Flannery and Seri, 1990; Hyndman and Menzies, 1990; Morren, 1989; Tate and Archbold, 1941; Tate, 1951; Helgen, 2007a). Further studies are clearly needed to assess the phylogenetic and ecological similarities between *Leptomys* and *Paraleptomys*.

Many recent taxonomic treatments of the terrestrial *Leptomys* recognize only one species, *L. elegans* (Menzies and Dennis, 1979; Flannery, 1990, are examples) or three species—*L. elegans*, *L. ernstmayri*, and *L. signatus* (Musser and Carleton, 1993, for example). The current revision documents the morphological attributes and geographic distributions of five species of *Leptomys*: *L. elegans* from southcentral New Guinea and the Papuan Peninsula (southeastern New Guinea) both north and south of the Cordillera (distributed from the Kikori River Basin in the west to the southern slopes of the Owen Stanley Range, extending round to the north side of the Cordillera in the Maneau Range, and in the outlying mountain block of Mount Victory); *L. signatus* of the Fly and Kikori River drainages; *L. ernstmayri* of the eastern Central Cordillera (Aroa River to Mt. Karimui), extending also to the outlying mountains of the Huon Peninsula and the

Adelbert Range, and isolated in the Foja Mountains of western New Guinea; *L. paulus* from lower montane forests in the Owen Stanley highlands; and *L. arfakensis* in the Arfak Mountains on the Vogelkop Peninsula.

Of particular interest in the light of these new taxonomic insights are potential ecological interactions among species of *Leptomys*. Our studies of taxonomy and geography in the genus highlight the potential for ecological interactions between species with overlapping ranges, such as *L. elegans* versus *L. ernstmayri* and *L. paulus*, or between ecomorphologically similar species with potentially abutting geographic ranges (*L. elegans* and *L. signatus*, fig. 2; or *L. ernstmayri* and *L. paulus*, fig. 3). For example, throughout the Papuan Peninsula, *Leptomys elegans* has a recorded altitudinal range of 400 to 1500 m, while *Leptomys paulus* is known to occur in the same region (the Astrolabe and Maneau ranges) at altitudes between 1200 and 1540 m, and *L. ernstmayri* is also known from overlapping elevations (1200 m and above) farther north in the Owen Stanley ranges (figs. 2, 3). Although two species have yet to be taken syntopically in the Papuan Peninsula, *L. elegans* is certainly regionally sympatric with both of these smaller highland species, and on the basis of their recorded localities and altitudes we predict that they are likely to overlap locally. Similarly, both *L. elegans* and *L. signatus* are now recorded from the Kikori River Basin, where they have similar recorded altitudinal distributions (500 m to 1500 m for *L. elegans*, 400 m to 1400 m for *L. signatus*; see Gazetteer, localities 3–6). Further study in southcentral New Guinea will be necessary to establish whether the ranges of *L. elegans* and *L. signatus* are sharply parapatric within the Kikori River Basin (as suggested by the currently known distributions; fig. 2) or whether these two morphologically similar species will prove to overlap geographically in hill forests within the Basin. Finally, both *L. ernstmayri* and *L. paulus* are recorded from montane forests in the Owen Stanley highlands; the easternmost specimens of *L. ernstmayri* originate from the Aroa River drainage (at 1200 m), while the westernmost specimens of *L. paulus* derive from the Astrolabe Range (at 1500 m). This suggests that the geographic

ranges of these two smallest-bodied members of the genus may abut or overlap somewhere in between. Like many other genera (Helgen, 2007b), including the recently documented case of the dasyurid genus *Myoictis* (see Woolley, 2005), *Leptomys* is an example of a New Guinea mammal lineage that until recently was often considered to represent a single species, but actually consists of at least five morphologically distinctive species; some of these five appear to be characterized by regional sympatry and clear-cut geographic parapatry with respect to one another, if not direct syntopy.

Leptomys arfakensis is one of many mammals endemic to the Vogelkop Peninsula, or “Bird’s Head”, of western New Guinea. The Bird’s Head region is thought to have had a long history of isolation relative to other emergent areas of New Guinea throughout the Tertiary (see Aplin, 1998), and the vertebrate fauna of the Bird’s Head exhibits considerable endemism. The Vogelkop has long been recognized as an area of endemism for mammals, but over the last decade new studies of subfossil and modern specimens from the region have further clarified the geographic discreteness of mammals of the region (Aplin et al., 1999; Helgen and Flannery, 2004). Aplin et al. (1999) described two new endemic possums from the Vogelkop, the petaurid *Dactylopsila kambuayai* and the pseudocheirid *Petauroides ayamaruensis*, both of which are still known only by Holocene subfossil remains, but likely to endure in the modern fauna. Based on modern specimens, the distinctive bandicoot *Microperoryctes aplini* has recently been described from the Arfaks (Helgen and Flannery, 2004), and a highly distinctive new species of *Mallomys* known only from the Arfaks awaits formal description (see Musser and Carleton, 2005; Helgen, 2007a, 2007b). Musser and Carleton (2005) have additionally recognized *Rattus arfakiensis* of the Arfak Mountains, phenetically similar to *Rattus niobe*, as a distinct species endemic to the Vogelkop. In addition to these newly recognized taxa, other mammal taxa endemic to the Bird’s Head region include the echidna *Zaglossus bruijnii* (see Flannery and Groves, 1998), the ringtail possums *Pseudochirops coronatus* and *Pseudo-*

schirulus schlegeli (Flannery, 1994; Flannery, 1995), and the tree kangaroo *Dendrolagus ursinus* (Flannery et al., 1996). This high number and proportion of endemic species undoubtedly reflects the Vogelkop’s long-term biotic isolation into the late Tertiary. See Helgen (2007b) for a wider review of mammalian endemism and diversity in the Vogelkop Region.

Most of the Vogelkop’s mammalian endemics (*Microperoryctes aplini*, *Pseudochirops coronatus*, *Pseudochirulus schlegeli*, *Mallomys* sp., *Rattus arfakiensis*, and *Leptomys arfakensis*) are known as living animals only from a single mountain range, the Arfak Mountains, which still remains the most intensively explored region of the peninsula. With renewed survey efforts, many of the Arfak’s seemingly unique mammal species (as well as additional, currently unknown mammals) may prove to occur in other mountain ranges in the greater Vogelkop region—especially in the expansive nearby Tamrau ranges, but also the Fakfak, Kumawa, and Wandammen ranges in the Bird’s Neck region, all of which remain poorly known as regards their mammal fauna. The Arfaks themselves, although better surveyed than other highlands on the Vogelkop, probably also support many other species that remain currently undetected. We suspect that these might include small amphibious murines and tiny terrestrial moss mice, both of which are present throughout other montane areas of New Guinea but can be challenging to collect without pitfall techniques, which have only rarely been used to collect mammals in New Guinea (Flannery, 1995; Helgen, 2005b, 2007a). Future systematic collecting of small mammals along altitudinal gradients in the Arfaks and other Vogelkop Ranges will be needed to more definitively characterize the true geographic distribution and habitat associations of *L. arfakensis*.

At the opposite end of New Guinea from the Arfak Mountains, in the far east, is the home of *Leptomys paulus*, the Owen Stanley Range, which bisect the lowlands of the Papuan Peninsula, also referred to as the “Bird’s Tail” of New Guinea. Helgen (2005a) recently provided a brief review of mammalian zoogeography in the Papuan Peninsula. In addition to *Leptomys paulus*, eight mam-

mal species are known only from the montane forests of the Papuan Peninsula, and three lowland species, the vespertilionid bat *Pharotis imogene* Thomas, 1914, the bandicoot *Peroryctes broadbenti* (Ramsay, 1879), and the murine *Chiruromys forbesi* Thomas, 1888, are endemic to the peninsula. Besides *L. paulus*, the montane endemics comprise the dasyure *Murexia rothschildi* Tate, 1938; the bandicoot *Microperoryctes papuensis* (Laurie, 1952; Aplin and Woolley, 1993); and the murines *Chiruromys lamia* (Thomas, 1897), *Rattus vandeuseni* Taylor and Calaby, 1982, *Pseudohydromys germani* (Helgen, 2005a), and as yet unnamed species of *Pseudohydromys* (see Helgen, 2007b) and *Coccymys* (Musser and Lunde, 2008; Musser and Carleton, 2005). Ongoing taxonomic studies continue to clarify the standing of these mountains as a significant zone of mammalian endemism (Flannery, 1995: 36–37; Helgen, 2007b). Like *L. paulus*, most of the montane endemics of the Papuan Peninsula extend beyond the Maneau Range to the north, to the main body of the Owen Stanley Range. The apparent exceptions are *Rattus vandeuseni* (Taylor et al., 1982; Musser and Carleton, 2005; Helgen, 2007b) and *Pseudohydromys germani* (Helgen, 2005a), each of which is recorded only from the Maneau Range.

Five of the Papuan Peninsula's eight montane endemics (all except *Pseudohydromys germani*, *Leptomys paulus*, and *Coccymys* sp.) and the lowland endemics of the Papuan Peninsula have no clear vicariant replacements outside of southeastern New Guinea (Flannery, 1995; Helgen, 2007b). This degree of faunal uniqueness represents a level of endemism similar in magnitude and depth to that exhibited by the isolated mountains of the Vogelkop Peninsula. It exists despite the modern-day geographic contiguity of the Papuan Peninsula's Owen Stanley Range with the rest of the Central Cordillera. The strikingly unique nonvolant mammal fauna of southeastern New Guinea presumably can be explained by the possible isolation of this peninsula from the rest of the emergent landmass of New Guinea until the Pliocene (Aplin et al., 1993; Flannery, 1995), but it is a true mystery why many of the Papuan Peninsula's endemic taxa, especially those

without clear vicariant replacements elsewhere, have not extended into the Eastern Highlands or to other areas along the cordillera. Interestingly, avian and bat endemism in the mountains of the Papuan Peninsula appears to be considerably less marked (Stattersfield et al., 1998; Bonaccorso, 1998), presumably because of the relatively greater vagility of these groups.

Preliminary comparisons suggest to us that more detailed studies could prompt elevation of additional taxa within this peninsular region from subspecies to species status, perhaps including such taxa as *Uromys anak* and *Phalanger* cf. *vestitus*. In fact (and as the elucidation of *Leptomys paulus* attests), further taxonomic re-evaluation of most montane mammal lineages in the Papuan Peninsula is needed (Helgen, 2007b).

Finally, our taxonomic delimitations of five species of *Leptomys* may not fully characterize biological diversity within the genus. For example, we have described the phenetic divergence among our samples representing the discrete montane populations of *Leptomys* in the Adelbert Range, Central Cordillera, Huon Peninsula, and Foja Mountains, which we refer to *L. ernstmayri*. Particularly impressive are the external and qualitative molar traits that set typical *L. ernstmayri* of the Huon Peninsula apart from the Adelbert and Central Cordillera populations. Equally interesting is the greater extent of morphometric variation seen among specimens from the Central Cordillera compared to that revealed in the Adelbert and Huon samples. Intriguing is the affinity of the population on the Foja Mountains, represented by only one specimen. Morphometric traits associate it with our material from the Central Cordillera, but not definitively so, and the actual phylogenetic affinity of that isolated population in western New Guinea, so far from the primary geographic range of *L. ernstmayri*, remains cloudy. Does the morphological variation we document among the four samples reflect montane variation within a single species or is *L. ernstmayri* actually restricted to ranges on the Huon Peninsula, and are populations on the other three mountainous areas distinct species endemic to those respective regions? These questions, along with the other aspects

discussed in this section, are the subjects we recommend for further research; such study, both of available specimens and of newly collected material, is likely to yield further surprises and insights.

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