On the cover: Dense, long, and silky-soft fur, brownish-gray upperparts, grayish-white underparts, gray ears, white feet, and a bicolored tail characterize *Bunomys penitus,* one of eight documented species of *Bunomys,* all endemic to forested landscapes on the Indonesian island of Sulawesi. Nocturnal and terrestrial, *B. penitus* lives only in mountain forests where the ambience is cool and wet, the trees and ground covered with thick moss and epiphytes; its diet includes invertebrates, fungi, and fruit.

MUSSER: SULAWESI *BUNOMYS*

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A Systematic Review of Sulawesi *Bunomys* (Muridae, Murinae) with the Description of Two New Species

GUY G. MUSSER

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

A SYSTEMATIC REVIEW OF SULAWESI *BUNOMYS* (MURIDAE, MURINAE) WITH THE DESCRIPTION OF TWO NEW SPECIES

GUY G. MUSSER

Division of Vertebrate Zoology (Mammalogy)
American Museum of Natural History

DEDICATION

I dedicate this review of *Bunomys* to the memories of two men of great intelligence and abilities whose sustained sponsorship and unflagging support of my research made possible my survey of endemic murines in the northern part of the west-central region of Sulawesi. Dr. Sampurno Kadarsan, a parasitologist specializing in tick taxonomy, was Director of the Museum Zoologicum Bogoriense during the period I lived in Indonesia. In addition to representing the museum as my sponsor in his country, Dr. Kadarsan (''please call me Sam,'' he asked) provided access to the Museum's resources, a place in the Bogor gardens to stay when not in the field, the frequent hospitality of his home, and lively conversations covering a range of topics from science to Indonesian history (see my tribute in the etymology of *Kadarsanomys*, a Javan endemic murine; Musser, 1981: 32).

Dr. P.F. Dirk Van Peenen, a Navy physician and epidemiologist, was in charge of Naval Medical Research Unit No. 2 (NAMRU-2), Jakarta Detachment. We first met at the American Museum of Natural History when Dirk visited to examine Southeast Asian mammal specimens for a handbook on Vietnamese mammals he was preparing. I helped with some of the taxonomic problems, and later identified mammalian hosts collected on epidemiological surveys made in Indonesia by Dr. Van Peenen and his team. Knowing of my desire to begin fieldwork on Sulawesi, Dirk invited me to use the research facilities NAMRU-2 had organized in the village of Tomado, on the shore of Danau Lindu in central Sulawesi, as the starting point for my fieldwork and provided logistical and other kinds of assistance whenever needed, an arrangement heartily condoned by Sam Kadarsan.

Through circumstances I could not have anticipated when I joined the Department of Mammalogy at the American Museum of Natural History, a Javanese native and Indonesian scientist united with an American physician and dedicated epidemiologist to facilitate my journey into the tropical rain forests of Sulawesi.

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Fig. 1. The island of Sulawesi showing its four peninsulas and core or central region. Highlighted are four mountainous regions that support suites of endemic mammals discussed here. Boundaries separating other relevant areas of endemism are indicated by dashed lines: **SM-D** = lowland reaches of the Sungai Onggak Mongondaw and Sungai Onggak Dumoga; **SB-DL** = lowlands of the Sungai Bone and Danau Limboto; **TD** = Tempe Depression.

ABSTRACT

Two new species of of *Bunomys* are described, *B. karokophilus* and *B. torajae*, both from the west-central mountain region of central Sulawesi. The descriptions are presented within the context of a systematic review of *Bunomys* in which are provided characteristics of the genus and species (external form, secondary sexual traits, spermatozoa, stomach morphology, skull, dentition, chromosomes); diagnoses, geographic and elevational distributions; sympatric, syntopic, and parapatric distributional relationships; morphological, distributional, and in some cases ecological comparisons among the species; natural histories for certain species derived from field observations; parasites; allocation of generic and specific synonyms; and documentation of subfossils for two of the species.

Eight species are recognized; all are nocturnal, terrestrial, and endemic to the island of Sulawesi. *Bunomys chrysocomus* has been collected from most regions of the island and inhabits both lowland tropical evergreen and montane rain forests (elevational range = 250–2200 m). *Bunomys coelestis* is endemic to montane forests on Gunung Lompobatang, the high volcano at the southern end of the southwestern peninsula (1829–2500 m). *Bunomys prolatus* has been reported only from mountain forest on Gunung Tambusisi at the western end of the eastern peninsula (1829 m). *Bunomys torajae,* n. sp., is described from a small sample collected in montane forest on Gunung Gandangdewata at the southern end of the west-central mountain block (2500–2600 m). *Bunomys fratrorum* is currently documented only from the northeastern area of the northern peninsula where it occupies habitats in lowland tropical evergreen and montane rain forests (coastal plain to 1982 m). *Bunomys andrewsi* has been collected primarily in lowland tropical evergreen rain forests in the core of Sulawesi and on the eastern, southeastern, and southwestern peninsula (coastal plain to 1600 m). *Bunomys penitus* is strictly montane and recorded only from the west-central mountain block and Pegunungan Mekongga on the southeastern peninsula (1285–2287 m). *Bunomys karokophilus,* n. sp., is currently known only from lowland tropical evergreen rain forest in the northern portion of the west-central mountain block (823–1150 m).

Analyses of morphometric traits (cranial and dental measurements) results in a phenetic relationship among the species in which *B. chrysocomus*, *B. coelestis*, *B. prolatus*, and *B. torajae,* n. sp., form one group characterized by small physical size and small molars, and *B. fratrorum*, *B. andrewsi*, *B. penitus*, and *B. karokophilus* another group in which larger physical size and heavier molars are the phenetic definers. Whether or not the integrity of this phenetic pattern will withstand testing by analyses of DNA sequences, it remains a convenient arrangement in which to present and define the eight species.

The morphological, elevational, and ecological relationships among the four species of *Bunomys* (*B. chrysocomus*, *B. andrewsi*, *B. penitus*, and *B. karokophilus,* n. sp.) collected along my transect area in the northern portion of the west-central mountain block (presently known as Lore Lindu National Park) and comparison between them and the elevational distributions of the other murids encountered along the transect are described.

Finally, a brief introduction to the species of murid rodents that have been recorded from mainland Sulawesi and nearby islands is provided, which defines the murine faunal context for the species of *Bunomys*.

The treatment of *Bunomys* offered here focuses on definitions of the species as outlined by phenetic traits, elevational and geographic distributions, and the natural history characteristics that are available for some of the species, and does not cover an analysis of the phylogenetic relationships between *Bunomys* and other Indoaustralian murines.

INTRODUCTION

"*Apa saja mencari* ("what am I searching for")?" Aminudi's question floated on the breeze across the narrow stream. He did not know what he was seeking and neither did I. "*Saya belum tahu, tetapi kapan kita melihat itu, kita akan tahu* ("I don't know, but when we see it, we will know")," I answered hopefully. On hands and knees we crawled along the stream terraces, Aminudi on one bank, me on the opposite, sinking into clinging mud, scraping knees on rocks, pushing aside ginger stems and spiny rattan rosettes. Wet leafy branches slapped our faces as we clambored over slick palm fronds

and decaying tree limbs. Alarmed at our advance, a kingfisher fled its perch and raced downstream, a bright azure streak tinting the humid air. Sun rays pierced the streamside canopy, shattering into glittering shards on wet rocks and burbling current. Dragonflies darted above the sparkling surface, their translucent wings shimmering in the yellow shafts; iridescent green tiger beetles sprang from one mossy rock to the other. Bridging the stream from each terrace, a large and decaying tree trunk partially concealed by tall ginger plants blocked our progress. Crawling closer, we spotted a clump of rubbery purplish lobes attached to the rough bark, a cluster that Aminudi directly recognized as ''*karoko*'' in his Kulawi language. We found what we had been seeking.

Fungal specialists know *karoko* as *Auricularia delicata*, an ''ear fungus'' in the Auriculariaceae (order Auriculariales, class Agaricomycetes, division Basidiomycota). *Karoko* grows on decaying wood lying in protected wet pockets of forest on hillsides just above streams, in wet ravines, and on canopied stream terraces—areas that remain wet and cool between rains. These are also the microhabitats of *tikus abu-abuan*, the gray rat. Before our streamside crawl, we found purplish rubbery segments in two stomachs of the gray rat, and after discovering the rubbery purplish cluster on the decaying trunk, we confirmed the stomach contents as ingested *karoko.* With the acquisition of more rats and more stomachs surveyed, and after feeding different foods to live rats, we established that the gray rat's diet consists mostly of *Auricularia delicata.*

This rat of medium body size with steelgray upperparts and gray underparts is an undescribed member of the genus *Bunomys*, a cluster of species endemic to the forested landscapes of Sulawesi. To name and describe the gray rat requires that it be compared with the other species of *Bunomys*, which in turn dictates a study to determine definitions of those other species, limits outlined primarily by the morphological and distributional boundaries of each as derived from study of voucher specimens. The present systematic review of species in the genus *Bunomys* forms the context in which I characterize morphological, distributional, and natural history attributes of *tikus abu-abuan*.

Three sets of data underpin my knowledge of *Bunomys*. One derives from study of specimens stored in collections of museums in the United States, Europe, Asia, and Australia; this material was obtained by collectors other than me. The second was gathered during the 1970s when I worked in the forests of central Sulawesi focusing on an inventory of murid rodents along a transect extending from lowland forest environments into montane habitats. In addition to acquiring material for taxonomic study, I obtained habitat and other biological information for most of the specimens collected. The third results from samples of three species of *Bunomys*, one undescribed, collected in 2011 by A.S. Achmadi and K.C. Rowe on Gunung Gandangdewata in the southern portion of the west-central mountain block.

For various reasons I have not included all the material of *Bunomys* that might be available for study. Over the last two decades, parts of Sulawesi have been and are actively being inventoried for its small mammal fauna by investigators from several research institutions. Some of the collections contain representatives of *Bunomys*, which I have examined, and these results are recorded in this revision. Of the other collections I have not seen, that made by Ibnu Maryanto and other members of the Museum Zoologicum Bogoriense (Indonesian National Museum of Natural History) in Lore Lindu National Park stands out. Their published results (Maryanto and Yani, 2003; Maryanto et al., 2009) include specimens identified as *Bunomys*; their samples likely augment those in my collections because I obtained them in what is now Lore Lindu National Park.

Materials and methods follow this introduction, after which my review of *Bunomys* begins with an exhibition of the mostly phenetic characteristics of the genus (external form, spermatozoa, stomach morphology, skull, dentition, chromosomes), in which an emended generic diagnosis is included. An exposition of the species is next presented, divided into two sections, the *B. chrysocomus* group and the *B. fratrorum* group. Each account covers the species's geographic and elevational distributions; its cooccurrence

with other species of *Bunomys*; morphological description; comparisons with other species; natural history (available for only a few species); ectoparasites, endoparasites, and pseudoscorpions (not all species of *Bunomys* have been surveyed); reasons behind allocations of any synonyms; and subfossils (samples for only two of the species). The various relationships (morphological, elevational, and ecological) among the four species of *Bunomys* collected along my transect area in the west-central mountain block, and a comparison between them and the elevational distributions of the other murids encountered on the transect follows. A penultimate segment provides a brief introduction to the species of murid rodents that have been recorded from mainland Sulawesi and nearby islands, which sets a murine faunal context for the species of *Bunomys*. Endnotes conclude the report.

That the species described and contrasted in the following pages represent a phylogenetic radiation unique to the island of Sulawesi is my bedrock hypothesis, and all the information covering the species is presented within that context. I declare this upfront because one geographic region outside of Sulawesi is claimed to harbor another species of *Bunomys*. Some researchers regard the Flores endemic *Paulamys naso* (Musser, 1981b; Musser et al., 1986) to be a member of *Bunomys* (Kitchener et al., 1991, 1998; Corbet and Hill, 1992; Kitchener and Yani, 1998). But *Paulamys naso* is part of a *Rattus*-like fauna endemic to Flores and some nearby islands that includes yet another undescribed species of *Paulamys*; *Komodomys rintjanus* and several undescribed species of that genus; "*Rattus*" *hainaldi*, a close relative of *Komodomys* as revealed by DNA sequences; and three species of *Papagomys*, one of which has yet to be named and described (Musser et al., MS). I suspect *Paulamys naso* is a phylogenetic component of this endemic Flores radiation and is not more closely related to either Sulawesian *Bunomys*, or to species of Moluccan, New Guinea, and Australian *Rattus*. Three hypotheses that require testing can be drawn from that supposition:

(1) *Paulamys naso* and the undescribed species in *Paulamys* is part of the *Rattus*-like radiation

of species endemic to Flores and nearby islands.

(2) The two species of *Paulamys* are phylogenetically more closely related to Sulawesian *Bunomys* than to the endemic Flores cluster.

(3) *Paulamys naso* and its close relative share closer kinship with species of endemic Moluccan, New Guinea, and Australian *Rattus* than with *Bunomys*.

Results derived from analyses of DNA sequences representing multiple genes combined with those obtained by careful examination of cranial and dental morphologies would identify the hypotheses to be rejected. For now, the relationship between *Bunomys* and the murine fauna endemic to Flores and other islands in the Lesser Sunda chain is unresolved.

My review of *Bunomys* spotlights the species as they are defined by distinctions in morphological traits, elevational and geographical distributions, sympatry or parapatry, and natural histories. The phylogenetic alliance between *Bunomys* and other Indo-Australian murines is referenced in only tangential fashion. Results from recent analyses of mitochondrial and nuclear DNA sequences reveals *Bunomys* forms a clade with Sulawesian species of *Taeromys* and *Paruromys*. That phylogenetic cluster is most closely related to *Halmaheramys bokimekot*, a newly discovered Moluccan endemic. Both of those clades connect phylogenetically to an assemblage containing Philippine *Bullimus* and Sundaic *Sundamys* (Fabre et al., 2013). The alliance of *Bunomys* with *Paruromys*, *Sundamys*, and *Bullimus* is also substantiated by Fabre et al. (2012) and Schenk et al. [2013] using DNA sequences, and the association of *Bunomys* with *Taeromys*, *Paruromys*, and *Sundamys* was earlier postulated by Misonne (1969: 140) based on molar cusp patterns.

Materials and Methods

INSTITUTIONS AND SPECIMENS: The definitions of species documented here are determined from my examination of specimens stored in the following institutions: the American Museum of Natural History, New York (**AMNH**); Natural History Museum, London (**BMNH**); field number of Chris H.S. Watts, South Australian Museum, Adelaide (**CHSW**); field number of Lance A. Durden,

Georgia Southern University, Statesboro (**LAD**); Museum Zoologicum Bogoriense, Cibinong, Java (**MZB**; now the Indonesian National Museum of Natural History; also known as the Research Center in Biology–Lembaga Ilmu Pengetahuan Indonesia); Museum of Vertebrate Zoology, Berkeley, California (**MVZ**); Nationaal Natuurhistorisch Museum, Leiden (**RMNH**); South Australian Museum, Adelaide (**SAM**); Staatliches Naturhistorische Sammlungen Dresden, Museum für Tierkunde (**SNSD**); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (**USNM**). Specimens referenced by catalog or field number in gazetteers, tables, text, and figure captions are preceded by one of these acronyms.

Many of the generic and specific traits described here are those associated with a skin and associated skull—one of the standard museum preparations. Color descriptions of fur, ears, feet, and tail of three species (*B. coelestis*, *B. prolatus*, *B. torajae,* n. sp., and *B. fratrorum*) are derived from those museum specimens—my fieldwork never took me to the geographic regions where those species reside. Color descriptons of four other species (*B. chrysocomus*, *B. andrewsi*, *B. penitus*, and *B. karokophilus,* n. sp.) come from my field journals (stored in Mammalogy Archives, AMNH) where I recorded coloration and other details of freshly caught rats, and from the specimens themselves. My collection also includes fluid-preserved whole specimens or skinned carcasses that were initially fixed in 10% formalin, soaked for several days in water, and finally stored in 70% ethanol. I used this material to describe stomach morphology and topography of palmar and plantar surfaces, and to measure length of testes.

MEASUREMENTS: Values for external dimensions are from two groups of specimens. One consists of samples I collected in central Sulawesi. For each of these specimens I measured total length; length of tail (**LT**), as well as length of the distal white tail tip (**LWT**); length of hind foot, including the claw (**LHF**); and length of ear, from notch to crown (**LE**). I took these measurements soon after the rat was caught, and also weighed it at that time to obtain a value for body mass or weight (**WT**, in grams).

The second group contains specimens in museums obtained and prepared by other collectors. They recorded total length, length of tail, length of hind foot, sometimes length of ear, but rarely weight. I used their value for length of tail, and measured length of the distal white tail segment on the dry study skin. I often ignored any value for length of ear because I did not know how preparators measured that dimension, and did not use collector's value for length of hind foot but measured that distance (including claws) myself on the dry skin. I also did not use total length from either group in any analyses, but subtracted length of tail from it to obtain a value for length of head and body (**LHB**).

In the laboratory, several measurements were made on specimens from both groups. I counted number of scale rings per centimeter (**TSR/CM**) on the tail about one-third the distance from its base. To measure lengths of overfur and guard hairs on the dorsum, I placed a ruler at a right angle to the skin surface on the back near the rump and recorded the approximate mark where ends of the bunched hairs rested; the technique is unsophisticated and the results imprecise, but provides a descriptive estimate of lengths for those pelage constituents.

Using dial calipers graduated to tenths of a millimeter, I measured the following cranial and dental dimensions; limits of most are illustrated in figure 2 (measurements are identified by acronyms in tables and ratio diagrams):

ONL occipitonasal length (= greatest length of skull; distance from tip of the nasals to posterior margin of the occiput)

ZB zygomatic breadth (greatest breadth across the zygomatic arches)

IB interorbital breadth (least distance, as viewed dorsally, across the frontal bones between the orbital fossae)

LR length of rostrum (from tip of the nasal bones to the posterior margin of the zygomatic notch)

BR breadth of rostrum (greatest breadth across the rostrum, including the bony nasolacrimal capsules)
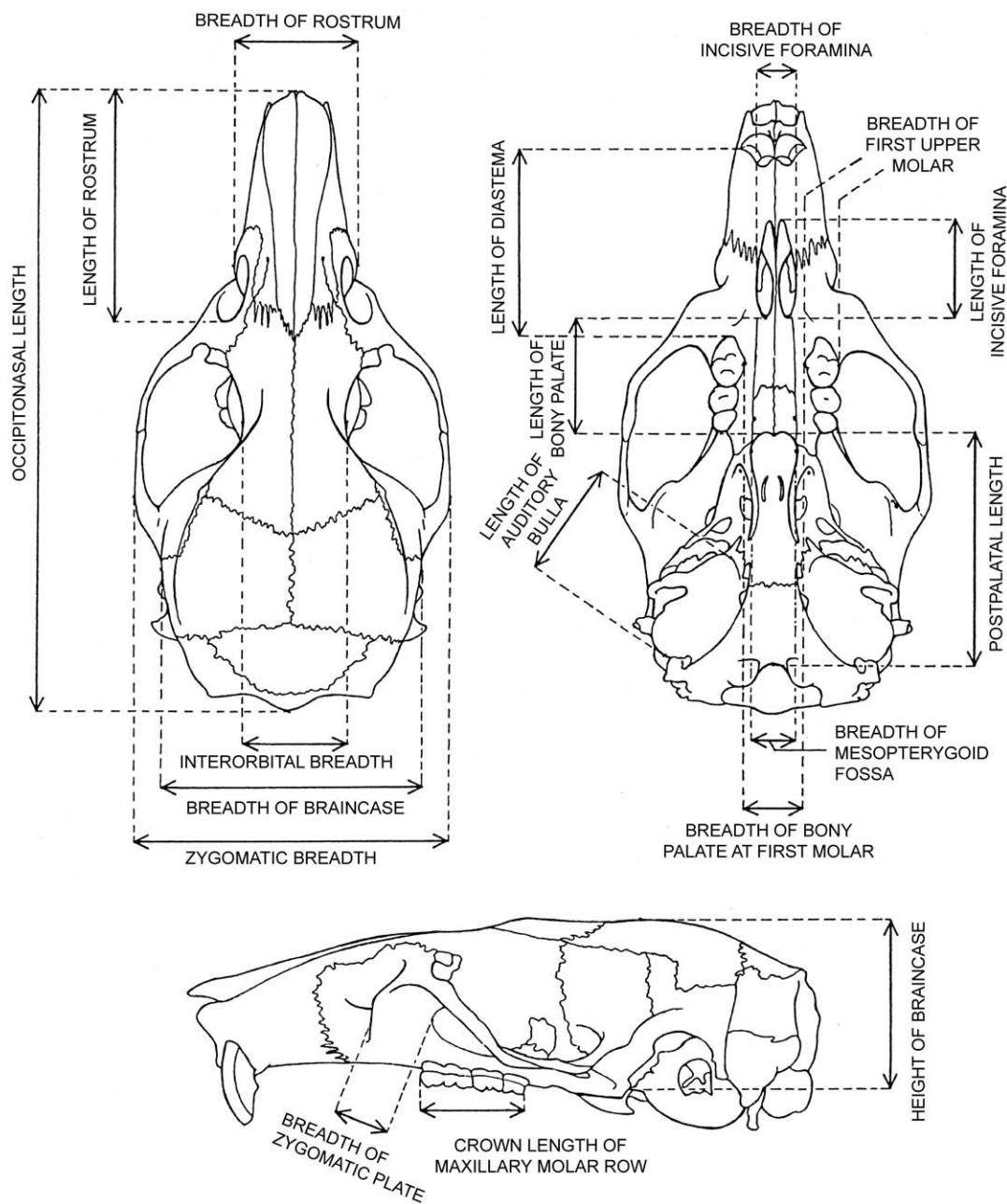
Fig. 2. Skull of an adult *Bunomys chrysocomus* illustrating limits of cranial and dental measurements I employed. Definition details are provided in the text.

BBC   breadth of braincase (measured from just above the squamosal root of each zygomatic arch)

HBC   height of braincase (from top of the braincase to the ventral surface of the basisphenoid)

BZP   breadth of zygomatic plate (distance between the anterior and posterior edges of the zygomatic plate)

LD   length of diastema (distance from posterior alveolar margins of upper incisors to anterior

PPL   alveolar margins of first upper molars)

PPL   postpalatal length (distance from the posterior margin of the palatal bridge to posterior edge of the basioccipital)

LBP   length of bony palate (distance from posterior edge of incisive foramina to posterior margin of the bony palate)

BBP   breadth of bony palate at first molar (least distance between lingual alveolar margins of first molars)

LIF   length of incisive foramina (distance from anterior to posterior margins of one of the foramina)

BIF   breadth across incisive foramina (greatest distance across both foramina)

BMF   breadth of mesopterygoid fossa (distance from one edge of mesopterygoid fossa to the other)

LB   length of ectotympanic (auditory) bulla (greatest length of the bullar capsule, excluding the bony eustachian tube)

CLM1–3   crown length of maxillary molar row (from anterior enamel face of M1, excluding the root, to posterior enamel face of M3)

clm1–3   crown length of mandibular molar row (from anterior enamel face of m1 to posterior enamel face of m3)

alm1–3   alveolar length of mandibular molar row (from anterior alveolar rim of m1 to posterior alveolar rim of m3)

BM1, BM2   breadths of M1 and M2, respectively (taken across widest part of molar)

bm1, bm2, bm3   breadths of m1, m2, and m3, respectively (measured across widest part of the tooth).

AGE AND SEX: I could consistently sort specimens into one of five relative age groups: (1) old adult (body size among the largest in a sample, clothed in full adult pelage, molars worn nearly to tops of roots so cusps are obliterated or nearly so, the crowns usually worn into shallow basins); (2) adult (body size among the largest in a sample, covered in full adult pelage, molars obviously worn, occlusal surfaces retain pattern of major cusps, but their enamel margins are worn low, so the dentine is broadly exposed with some of the cusp rows coalesced at their labial and lingual margins, labial cusplets nearly obliterated); (3) young adult (body size usually smaller than older adults, covered in fresh adult fur, molars slightly worn, enamel borders of cusps much higher than the enclosed dentine with its restricted exposure, cusps and labial cusplets discrete, either not coalesced or only slightly so); (4) juvenile-adult (body size usually smaller than young adults, all molars erupted and slightly worn, clothed mostly in juvenile fur that conceals underlying replacement hairs of partially proliferated adult coat, older specimens retain juvenile pelage along back and rump but possess fresh adult fur on venter and sides of body); (5) juvenile (body size among smallest in a sample; covered in juvenile pelage that is easily recognizable compared to the adult coat, upper and lower third molars unerupted or if erupted usually unworn).

These roughly defined age groups are unequally represented among samples: old adults and juveniles are scarce, adults and young adults are most common. Old adults, adults, and young adults were combined into samples from which cranial and dental measurement values were obtained for multivariate analyses and univariate descriptive statistics. Recognition of relative age classes was important for identifying relative age of holotypes and subfossils as well as gauging the position of particular specimens showing incongruous distributions in principal-components and canonical-variate ordinations.

Males and females were not separated in any of the statistical analyses. Examined side by side, size differences in adult skulls of males and females within a single species collected from the same area appeared negligible. This observation was reinforced by results from determining significance of differences between means for cranial and dental variables of each sex (t-test) in samples of *Bunomys chrysocomus* (a member of the small-bodied *B. chrysocomus* group), *B.*

TABLE 1
Differences in Means of Cranial and Dental Variables between Sexes in Samples of *Bunomys chrysocomus*,
B. penitus*, and *B. fratrorum
(Mean ± 1 SD are listed; samples consist of young to old adults. Probability values [P] are derived from t-tests; significant P values [≤ 0.05] are in boldface.)

Variable	*B. chrysocomus* Sungai Sadaunta[a]			*B. penitus* Gunung Nokilalaki[b]			*B. fratrorum* Teteamoet[c]		
	♀N = 54	♂N = 54	P	♀N = 36	♂N = 46	P	♀N = 15	♂N = 18	P
ONL	38.0 ± 1.05	38.5 ± 1.00	**0.017**	42.6 ± 1.12	43.1 ± 1.25	**0.049**	44.5 ± 1.05	43.9 ± 0.96	0.060
ZB	18.0 ± 0.66	18.0 ± 0.57	0.619	19.8 ± 0.57	19.8 ± 0.67	0.593	21.2 ± 0.72	20.8 ± 0545	0.056
IB	6.3 ± 0.18	6.4 ± 0.23	0.575	6.8 ± 0.14	6.8 ± 0.29	0.455	6.1 ± 0.40	6.1 ± 0.31	0.813
LR	13.4 ± 0.53	13.7 ± 0.51	**0.005**	15.9 ± 0.59	16.1 ± 0.63	**0.047**	15.2 ± 0.50	14.9 ± 0.47	0.074
BR	6.8 ± 0.32	6.8 ± 0.26	0.869	7.9 ± 0.34	7.9 ± 0.36	0.862	8.2 ± 0.30	7.9 ± 0.34	**0.015**
BBC	15.5 ± 0.39	15.3 ± 0.35	0.131	16.7 ± 0.37	16.7 ± 0.42	0.995	16.3 ± 0.59	16.2 ± 0.35	0.779
HBC	10.7 ± 0.32	10.7 ± 0.34	0.664	11.9 ± 0.37	11.9 ± 0.42	0.964	12.3 ± 0.50	12.2 ± 0.36	0.361
BZP	3.3 ± 0.24	3.3 ± 0.29	1.000	3.0 ± 0.19	3.0 ± 0.22	0.238	3.9 ± 0.31	4.0 ± 0.28	0.659
LD	10.1 ± 0.52	10.3 ± 0.47	**0.020**	11.2 ± 0.50	11.4 ± 0.54	0.128	11.5 ± 0.46	11.2 ± 0.34	0.093
PPL	13.4 ± 0.56	13.6 ± 0.60	**0.044**	14.4 ± 0.48	14.4 ± 0.53	0.906	15.8 ± 0.46	15.5 ± 0.41	**0.026**
LBP	7.4 ± 0.39	7.5 ± 0.38	0.127	8.8 ± 0.38	8.9 ± 0.38	0.689	7.8 ± 0.30	7.9 ± 0.35	0.851
BBP	3.7 ± 0.25	3.8 ± 0.21	0.095	3.7 ± 0.24	3.7 ± 0.26	0.782	3.7 ± 0.25	3.7 ± 0.18	0.908
BMF	2.9 ± 0.24	2.9 ± 0.21	0.577	3.8 ± 0.27	3.7 ± 0.27	0.104	3.5 ± 0.21	3.4 ± 0.19	0.417
LIF	6.2 ± 0.32	6.3 ± 0.39	**0.051**	8.0 ± 0.53	8.1 ± 0.45	0.580	7.4 ± 0.36	7.3 ± 023	0.423
BIF	2.5 ± 0.14	2.5 ± 0.15	0.264	3.0 ± 0.20	2.9 ± 0.22	0.336	2.9 ± 0.11	2.8 ± 0.15	0.298
LB	6.4 ± 0.22	6.5 ± 0.23	0.298	6.8 ± 0.24	6.8 ± 0.22	0.915	6.4 ± 0.14	6.4 ± 0.18	0.937
CLM1–3	6.1 ± 0.20	6.1 ± 0.19	0.207	7.8 ± 0.24	7.8 ± 0.22	0.608	7.6 ± 0.24	7.6 ± 0.22	0.784
BM1	2.0 ± 0.08	2.0 ± 0.08	0.328	2.5 ± 0.12	2.5 ± 0.10	0.936	2.4 ± 0.07	2.4 ± 0.08	0.863

[a] Specimens were collected on stream terraces and adjacent wet hillsides along the Sungai Sadaunta in continuous primary tropical lowland evergreen rain forest between 675 and 960 m.

[b] The sample was obtained in primary montane forest covering upper slopes and summit of Gunung Nokilalaki between 1768 and 2287 m.

[c] Collected in tropical lowland evergreen rain forest on coastal plain near tip of northern peninsula.

penitus, and *B. fratrorum* (both belonging to the large-bodied *B. fratrorum* group), the only three species for which large samples were available (table 1). Within each of the species, differences between means were not significant across most variables—sex is a trivial contribution to intrasample nongeographic variation of cranial and dental variables.

Results of principal-components analysis of the three species (not illustrated here) did not reveal a different pattern in morphometric variation among the cranial and dental variables due to sex. The distribution of specimen scores projected onto first and second components for each species produced a single cloud of thoroughly intermixed points for males and females—polygons enclosing maximum dispersion of scores representing each sex, and ellipses outlining 95% confidence limits for cluster centroids broadly overlapped.

Weak sexual dimorphism in cranial and dental variables generally characterizes nongeographic sexual variation among muroid rodents. For examples of sigmodontines, see Carleton and Musser (1989, 1995 [*Microryzomys* and *Oligoryzomys*], Carleton et al. (1999 [*Sigmodon*]; 2009 [*Oecomys*]), Myers and Carleton (1981 [*Oligoryzomys*]), Voss (1991 [*Zygodontomys*]), Emmons and Patton (2012 [*Juscelinomys*]), and Percequillo et al. (2011 [*Drymoreomys*]); for murine examples, see Carleton and Robbins (1985 [*Hybomys*]), Carleton and Martinez (1991 [*Dasymys*]) Carleton and Van der Straeten (1997 [*Lemniscomys*]), Carleton and Byrne (2006 [*Otomys*]), Carleton and Stanley (2005, 2012 [*Hylomyscus* and *Praomys*]), Helgen and Helgen (2009 [*Pseudohydromys*]), Musser (unpublished data [*Margaretamys*, *Rattus facetus*, and *Coccymys*]), Musser and Durden (2014 [*Echiothrix*]), Van der Straeten and Verheyen (1982 [*Hybomys*]), Heaney et al.

TABLE 2
Population Samples Employed in Univariate and Multivariate Analyses of Cranial and Dental Variables for Species of *Bunomys*
Localities, along with elevations and geographic coordinates, are referenced in the gazetteers and marked on the distribution maps. Brackets enclose total number of specimens for each species. Specimens measured are identified in footnotes.

Species and sample	N	Locality
Bunomys chrysocomus[a]	[232]	
Northern peninsula	10	Bogani Nani Wartabone National Park (Toraut Danmi, Gunung Mogogonipa)
Bumbarujaba	7	
Sungai Oha Kecil + Sungai Sadaunta	146	
Danau Lindu Valley + Gunung Kanino	42	Tomado, Sungai Tokararu, Gunung Kanino
Gimpu	3	
Bakubakulu	1	Puro Valley
Gunung Balease	3	
Gunung Tambusisi	6	
Pegunungan Mekongga	10	Tanke Salokko
Lalolei	3	
Bunomys coelestis[b]	[18]	
Gunung Lompobatang	18	
Bunomys prolatus[c]	[8]	
Gunung Tambusisi	8	
Bunomys torajae[d]	[3]	
Gunung Gandangdewata	3	Mamasa region
Bunomys fratrorum[e]	[100]	
Teteamoet	33	
Kuala Prang	27	
Gunung Klabat	2	
Rurukan	1	
Temboan	33	
Gunung Maujat + Gunung Mogogonipa	4	Gunung Maujat, Gunung Mogogonipa (1 km north)
Bunomys andrewsi[f]	[98]	
Northeast-central region	32	Labuan Sore, Kuala Navusu, Pinedapa
South-central region	16	Gunung Balease, Malili area (Desa Lawaki Jaya), Sukamaju
Eastern + southeast peninsulas	9	Sungai Ranu, Wawo, Masembo
Northern west-central region	16	Puro-Sungai Miu (Tanah Harapan, Pakuli, Sungai Oha Kecil, Sungai Sadaunta), Tamalanti, Tuare
Southern west-central region	16	Mamasa area (Lambanan, Mambulillin, Sumarorong, Gunung Gandangdewata)
Southwest peninsula	7	Lombasang
Pulau Buton	2	
Bunomys penitus[g]	[185]	
Gunung Kanino	74	(1285–1616 m)
Gunung Nokilalaki	82	(1754–2287 m)
Rano Rano	3	
Gunung Lehio	5	
Mamasa Area	7	Lambanan, Gunung Gandangdewata
Pegunungan Latimojong	3	
Pegunungan Mekongga	11	Tanke Salokko
Bunomys karokophilus[h]	[17]	
Sungai Sadaunta + Danau Lindu Valley	17	Sungai Sadaunta, Tomado, Sungai Tokararu

[a] Bogani Nani Wartabone National Park: AMNH 256885–89; LAD 18; SAM 12617, 12621, 12627, 12629. Bumbarujaba: USNM 218127, 218128, 218132–35, 218140 (holotype of *Rattus nigellus*). Sungai Oha Kecil + Sungai

TABLE 2

(*Continued*)

Sadaunta: AMNH 224054, 224078, 224079, 224081–086, 224088–091, 224093, 224095, 224096, 224099–105, 224109–14, 224118–26, 224128–35, 224137–40, 224143, 224647, 224649–60, 224662–71, 224673–88, 224692–94, 224696–703, 224706, 224709, 224711, 224713–15, 224717, 224719–25, 224728, 224729, 224731, 224733–47, 224750, 224752, 224755–58, 224762–65, 224767–69, and 227730. Danau Lindu Valley + Gunung Kanino: AMNH 223040, 223044, 223050–053, 223055, 223057, 223059, 223062, 223064, 223065, 223069, 223078, 223079, 223081, 223082, 223292, 223297–300, 223302, 223303, 223308, 223310, 223312, 223314, 223317, 223319, 223468, 223567, 223568, 224154–56, 225148; USNM 218691, 218692, 218702, 218704. Gimpu: USNM 219580, 219595 (holotype of *Rattus rallus*), 219713. Bakubakulu: AMNH 229519. Gunung Balease: MVZ 225697, 225714, 225810. Gunung Tambusisi: AMNH 265077, 265078; MZB 12181, 12183, 12185; SAM 15588. Pegunungan Mekongga: AMNH 101195, 101197, 101200, 101202, 101211, 101217, 101220, 101223, 101224, 101234, 101236 (holotype of *Bunomys coelestis koka*). Lalolei: AMNH 101052, 101055 (holotype of *Rattus lalolis*), 101288.

[b] Gunung Lompobatang: AMNH 101132, 101133, 101135, 101137, 101138, 101141–44, 101149, 101150, 101152, 101153, 101155, 101157, 101158; BMNH 97.1.3.12 (holotype of *Mus coelestis*).

[c] Gunung Tambusisi: AMNH 265074–076; MZB 12187, 12188, 12190 (holotype of *Bunomys prolatus*), 12191, 12193.

[d] Gunung Gandangdewata: MZB 34730 (holotype of *B. torajae* n. sp.), 34733, 34734.

[e] Teteamoet: USNM 216836, 216837, 216839, 216841, 216843, 216887–89, 216892, 216894, 216895, 216897, 216899, 216902–904, 216906, 216907, 216909–15, 216919, 216920, 216922–26. Kuala Prang: USNM 217587, 217589–91, 217594, 217596–600, 217602, 217603, 217605, 217606, 217609, 217611, 217613, 217614, 217827–29, 217831, 217832, 217834, 217835, 217837. Gunung Klabat: USNM 217581, 217585. Rurukan: BMNH 97.1.2.28 (holotype of *Mus fratrorum*). Temboan: USNM 217624, 217635, 217638, 217639, 217643, 217648–51, 217653, 217655, 217656, 217659, 217661, 217662, 217666, 217668, 217670, 217854, 217856–58, 217866, 217868, 217876, 217880, 217881, 217887, 217896, 217898, 217900, 217902 Gunung Maujat + Gunung Mogogonipa: SAM 12616, 12619, 12623, 12644.

[f] Pulau Buton: AMNH 31294; USNM 175899 (holotype of *Mus andrewsi*). Labuan Sore: USNM 218115, 218138. Kuala Navusu + Pinedapa: AMNH 225647–49, 225651–58, 225661–63; USNM 219581, 219587, 219589, 219591, 219593, 219594, 219596, 219600, 219601, 219602 (holotype of *Rattus adspersus*), 219603, 219605, 219606, 219619, 219620, 219622. Sungai Ranu: AMNH 249942–45; CHSW 36. Sukamaju: AMNH 229720. Gunung Balease: MVZ 225683, 225685, 225688, 225689, 225695, 225708, 225710, 225812. Desa Lawaki Jaya: MVZ 225691, 225698, 225699, 225702, 225719–21. Wawo + Masembo: AMNH 101059 (holotype of *Rattus penitus inferior*), 101061, 101069, 101072. Puro-Sungai Miu: AMNH 257187, 257189, 224630–33, 224107, 224116. Tamalanti: BMNH 40.446–40.448, 40.450–40.452. Tuare: USNM 219598, 219599. Mamasa area: AMNH 267796–98, 267800–804, 267806, 267807; MZB 34912, 34913, 34916, 34917, 34926, 34955. Lombasang: AMNH 100996–98, 101004, 101006 (holotype of *Rattus penitus heinrichi*), 101009, 101010.

[g] Gunung Kanino: AMNH 223805, 223806, 223809, 223811, 223814, 223815, 223819–22, 223826, 223828, 223829, 223831–33, 223835, 223836, 223829, 223840, 223842, 223845–850, 223852, 223904–907, 225251, 225253, 225254, 225256, 225257, 225260, 225262, 225264, 225265, 225267, 225269, 225271–273, 225275, 225276, 225278–85, 225287, 225288, 225290–93, 225295–302, 225304–306, 225376. Gunung Nokilalaki: AMNH 223853, 223855, 223857, 223859, 223861–66, 223868, 223870–75, 223878–82, 223885–88, 223892, 223895–97, 223899–902, 225307, 225308, 225310–15, 225317–25, 225328–33, 225335, 225336, 225338, 225340–42, 225344–46, 225348–54, 225359, 225361–65, 225368, 225369. Rano Rano: USNM 219627 (holotype of *Rattus sericatus*), 219630, 219631. Gunung Lehio: USNM 218682–684, 218686 (holotype of *Rattus penitus*), 218687. Mamasa area: AMNH 267790, 267793, 267794; MZB 34845, 34848–50. Pegunungan Latimojong: AMNH 196587, 196588, 196590. Pegunungan Mekongga: AMNH 101193, 101196, 101209, 101210, 101213, 101216, 101222, 101227, 101231, 101235, 101237.

[h] Sungai Sadaunta + Danau Lindu: AMNH 223046, 223056, 223058, 223060, 223072, 223305, 223316, 224153, 225027–029, 225031, 225033, 225035–037, 225038 (holotype of *Bunomys karokophilus* n. sp.).

(2006 [*Apomys, Batomys,* and *Linnomys*]), and Balete et al. (2012 [*Soricomys* and *Archboldomys*]). The sigmodontine *Oryzomys couesi* is a noteable exception (Carleton and Arroyo-Cabrales, 2009).

STATISTICAL ANALYSES: Standard univariate descriptive statistics (mean, standard deviation, and observed range) were calculated for population samples (identified in table 2) and for species and are listed in tables scattered through the text.

Principal-component and discriminant-function analyses were computed using original cranial and dental measurements transformed to natural logarithms. Principal components were extracted from a variance-covariance matrix, and canonical variates were extracted from the discriminant-function analyses;

loadings (correlations) of the variables are given as Pearson product-moment correlation coefficients between the extracted principal components or canonical variates and the log-transformed input variables. Probability levels denoting the significance of the correlations in both kinds of analyses are unadjusted. Individual specimen scores were projected onto scatter plots usually bounded by two axes representing the first two factors extracted. Most analyses are based on 16 cranial and two dental measurements from intact skulls of adults (young to old); some scatter plots were generated using fewer variables because only damaged skulls or subfossil fragments were available for analysis; a few comparisons utilized lengths of head and body, tail, hind foot, and ear.

Plottings of cluster analyses (UPGMA) provide visual patterns that reflect similarity or contrast in the combination of cranial and dental dimensions among geographic samples of a single species or among samples of separate species. UPGMA clusters of population samples were derived from Mahalanobis distances (squared) among population sample centroids and produced by the unweighted pair-grouup method employing arithmetic averages.

The statistical packages in SYSTAT 11 for Windows, Version 11 (2005), were used for all analytical procedures.

RATIO DIAGRAMS: Data used in constructing the ratio diagrams in figures 19, 56, 91, 93, and 95 were derived from values for mean, standard deviation, and sample size of variables listed in table 42. 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. Straight or dashed lines connect sample means, and bracketing symbols represent ±2 SE of the mean. A sample having the same proportions as the standard are 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.

ANATOMY: Terminology follows Brown (1971) and Brown and Yalden (1973) for particular external features of the head and limbs; Bugge (1970) for cephalic arteries; Carleton (1980), Musser and Newcomb (1983), Carleton and Musser (1984), Wahlert (1985), Musser and Heaney (1992), Voss (1988), and Carrasco and Wahlert (1999) for cranial foranima and cranial morphology. Names of cusps and cusplets of maxillary (upper) and mandibular (lower) molars are indicated in figure 11; sources for the terminology are explained in the legend.

CHROMOSOMES: I prepared karyotypes in the field from chromosomes of cells in bone marrow tissue, and processed them by employing colchicine, hypotonic citrate, and flame drying, procedures that were outlined by Patton (1967). The slides were made and stained at my camps in the forests.

Four terms describe the shape of each chromosome relative to position of the centromere: *metacentric* (the chromosome is biarmed, one arm being about the same length as the other); *submetacentric* (one arm is shorter than the other, about a third of its length); *subtelocentric* (one arm is very short relative to the long arm on the other side of the centromere); and *acrocentric* (the centromere is at the tip of the chromosome or near enough that any portion on the other side of the centromere is so short as to be indistinguishable or nearly so).

The fundamental numbers listed in table 12 and text are broken into the number of autosomal arms (FNa) and the total number of arms (FNt, including XX for females and XY for males). Jim Patton (in litt., 2013) suggested using these two categories and his reasoning stems "from the independent evolutionary trajectories typically operating on autosomes and sex chromosomes—the combination of 2N + FNa and/or FNt thus provides quick insight into mechanisms that might underlie evolutionary change."

STOMACH CONTENTS: I recorded in my field journals the contents found in stomachs

of some freshly caught rats. Sometimes only a general description was possible—presence of fruit, seeds, fungi, and arthropods, for example—but often freshly ingested and masticated fruit, seeds, and fungi could be easily identified to at least genus by color, shape, and texture; oligochaete earthworm pieces were obvious; and some arthropod remains could be identified to order. Many samples were preserved in ethanol, which I examined later in the laboratory under a dissecting microscope, and found additional arthropod particulates—termites especially—not seen in the field. I supplemented this material by extracting stomachs from undissected rats. Stomachs were removed by severing the posterior end of the esophagus and the anterior section of the duodenum. I bisected the isolated stomach along the midfrontal plane, transferred the contents to a white ceramic dish, and examined them with a dissecting microscope. In addition to remains of ingested foods, stomachs contained strands of hair, likely ingested during grooming. Stomachs emptied in the field are still attached to the gasterointestinal tract of carcasses preserved in fluid at AMNH. Those stomachs extracted in the laboratory are stored, with their contents, in leakproof vials in the fluid collection at AMNH.

My survey of stomach contents is not exhaustive. I did not extract the stomach of every specimen collected, and did not attempt to identify every tiny arthropod fragment. Chewed pieces of fungi were easily recognized and I was able to locate in the forest some of the fungal species; I relied on gross evidence for fungal remains, without surveying stomach contents for spores or other microscopic remains.

Most species of *Bunomys* readily enter live traps, quickly adapt to a cage environment, and can be kept healthy for some time. I supplied captives with a range of forest foods to determine what would be accepted or rejected.

The problem of identifying arthropod remains, particularly insects, found in the stomachs of *Bunomys* was solved by tapping David Grimaldi's (AMNH) wide-ranging knowledge of insects in particular and arthropods in general. Several times he unselfishly diverted his own research efforts to examine vials containing a range of different insects and to provide me with identifications along with ecological insights relating to these invertebrates. I also consulted various general publications covering insects, but found Grimaldi and Engel's (2005) *Evolution of the Insects* to be the most rewarding not only for the information it contained in text and illustrations but for the intellectual satisfaction derived from learning about different insect groups of interest to me and their evolutionary origins.

GEOGRAPHY (fig. 1): The island of Sulawesi consists of a central region from which four arms or peninsulas radiate: the northern peninsula, which ends in a northeastern jog; the eastern peninsula; the southeastern peninsula; and the southwestern peninsula. I use these informal labels when describing distributions of the species of *Bunomys* over the island, and refer to the cenral portion as Sulawesi's core, or simply "core."

In figure 1 and the text I refer to four mountainous regions that support suites of endemic mammals discussed here. The west-central highlands or west-central mountain block, which forms the western portion of Sulawesi's core. It is the region of foothills, peaks, and interior valleys situated above 100 m and lying roughly west of Danau Poso and extending from the Palu area in the north to Pegunungan Latimojong in the south. Pegunungan Mekongga is at the center of a less expansive highland region on the southeastern peninsula. Gunung Tambusisi is at the western end of the mountain chain forming the backbone of the eastern peninsula. The volcano Gunung Lompobatang forms the highest landscape on the southwestern peninsula. Other regional areas of endemicity relevant to distributions of the species in *Bunomys* are highlighted in figure 1 and discussed in the text.

Throughout the report I use the Indonesian terms *sungai* (stream or small river), *kuala* (stream discharging directly into the sea), *gunung* (mountain), *pegunungan* (mountain range), *pulau* (island), *kepulauan* (archipelago), *selat* (strait), *tanjung* (cape), and *teluk* (bay).

BUNOMYS AND MY COLLECTING AREAS: During 1973–1976, I lived and worked in the forests of central Sulawesi focusing on an inventory of murid rodents, of which a
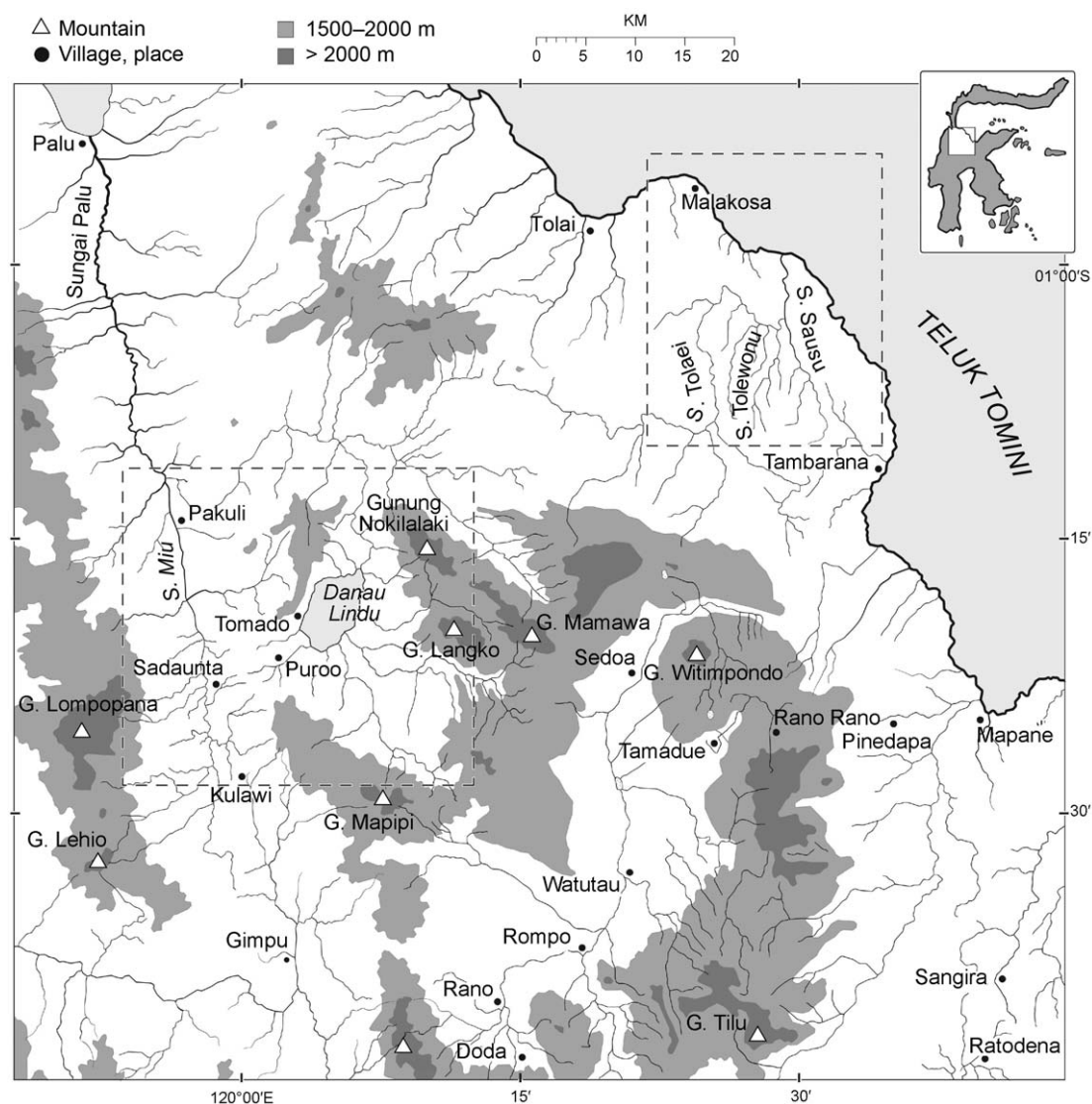
Fig. 3.   The northern portion of Sulawesi's core showing the two regions where I worked: the Sungai Miu–Danau Lindu (left dashed square) and Malakosa (right dashed square) areas. Three of H.C. Raven's collection sites are also indicated on the map: Gunung Lehio, southwest of Kulawi; Pinedapa, west of Mapane; and Rano Rano, in the mountains west of Pinedapa. Enlargements of the Danau Lindu and Malakosa areas are shown in figures 4 and 5, respectively.

significant portion consisted of samples containing four species of *Bunomys.* I worked in two regions (fig. 3). One included low-to-middle elevations along tributaries of the Sungai Miu and to the east in the drainage basin of Danau Lindu; and higher elevations from Gunung Kanino, a ridge descending from Gunung Nokilalaki, all the way to the

summit of the latter (fig. 4); this comprised a transect extending from 290 m where the small Sungai Oha Kecil joins the Sungai Miu to the summit of Gunung Nokilalaki at 2280 m (which in this review I refer to as *my transect*) and included habitats in lowland tropical evergreen rain forests and montane forests in the northern portion of the west-
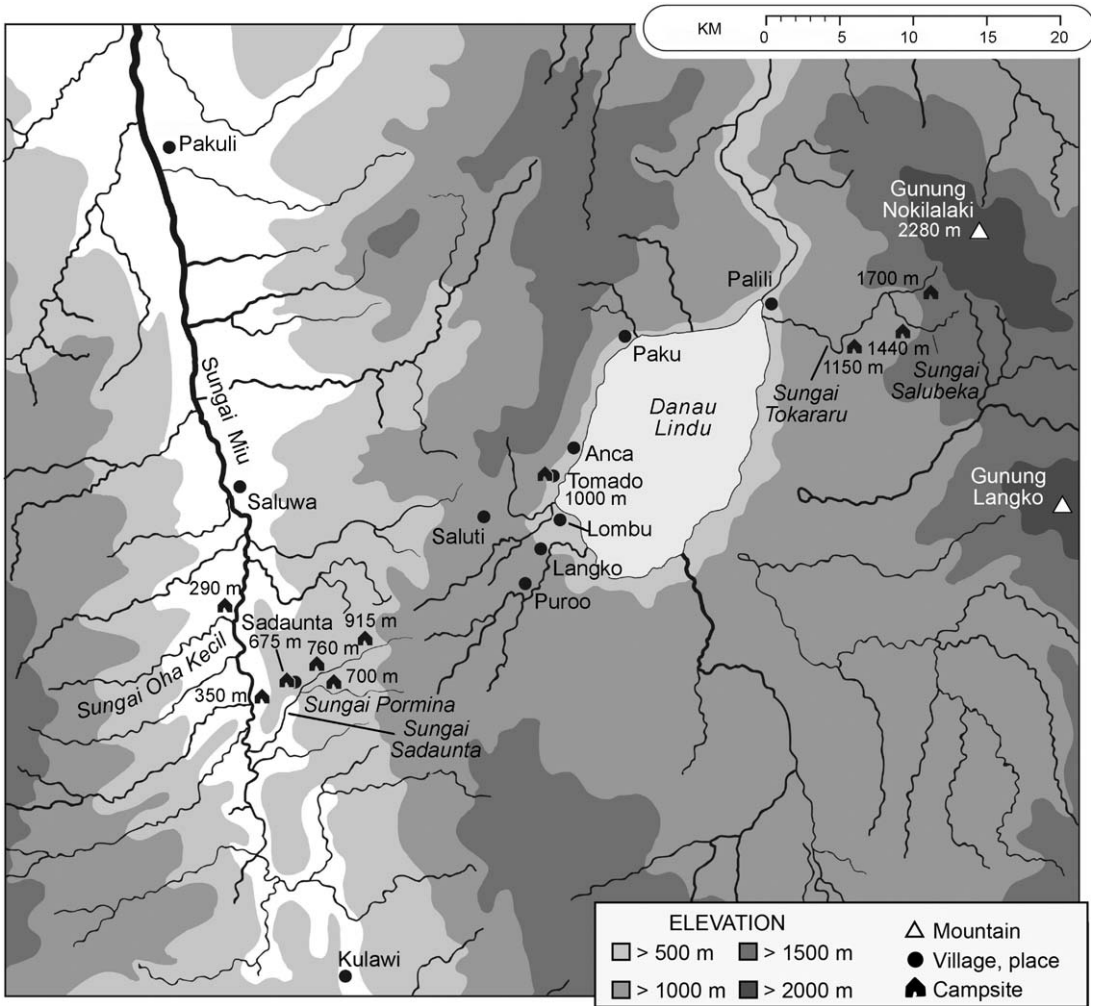
Fig. 4.   The Sungai Miu–Danau Lindu area in the west-central mountain block. Where the Sungai Oha Kecil flows into the Sungai Miu at 290 m was my lowest camp, the summit of Gunung Nokilalaki the highest place I worked. Tropical lowland evergreen rain forest embraces the area from the Sungai Oha Kecil to the camp along the Sungai Tokararu at 1150 m. The camp at 1440 m was on a ridge, part of Gunung Kanino, in lower montane rain forest. The lower camp at 1150 m (Sungai Tokararu) was at the western end and base of the Kanino highland. The highest camp at 1700 m was situated on the flanks of Gunung Nokilalaki, which at altitudes above about 2000 m was covered with upper montane rain forest. Ambient air temperatures, relative humidities, and rainfall recorded at the camps are provided in table 3.

central mountain block. The other region was east of the west-central block in the lowlands of the Malakosa area in the northeastern portion of Sulawesi's core bordering Teluk Tomini (fig. 4) where the elevations covered ranged from near sea level at Kuala Navusu to ridges behind Sungai Tolewonu at about 1000 m (fig. 5); lowland tropical evergreen rain forest covered the area. The Sungai Miu-

Danau Lindu-Gunung Nokilalaki transect was intended to explore habitats in both lowland tropical evergreen and montane rainforest formations. Work in the Malakosa region concentrated on surveying lowland habitats, particularly at elevations below 290 m.

Ambient air temperatures, relative humidity, and rainfall patterns recorded at the
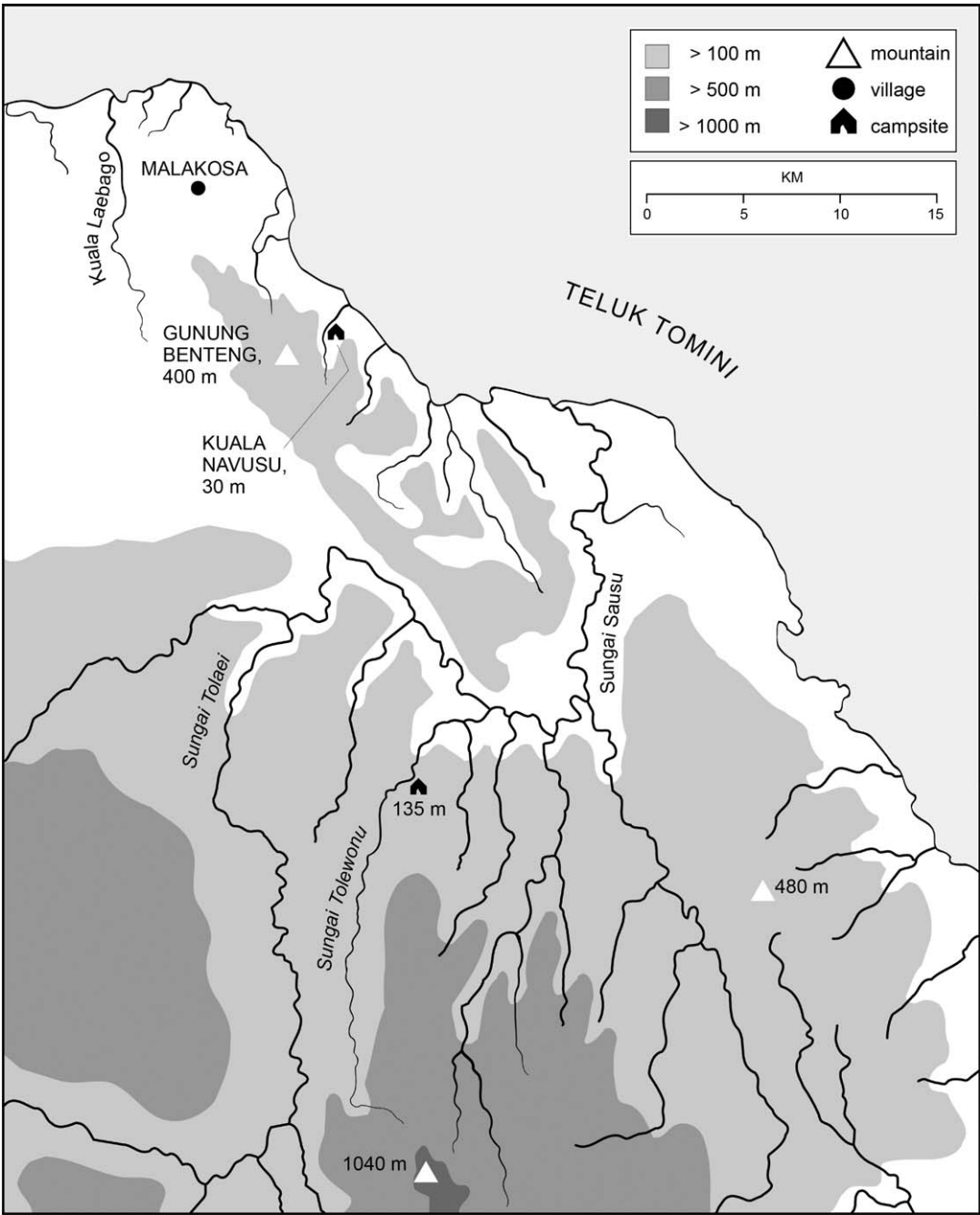
Fig. 5.   The region south of Malakosa in Sulawesi's northeastern core. My two lowland camps in tropical lowland evergreen rain forest are indicated. The area lies east of the west-central mountain block. See table 3 where ambient air temperatures, relative humidities, and rainfall recorded at the two camps are summarized.

TABLE 3
Ambient Air Temperature, Relative Humidity, and Rainfall Pattern at Camps in Central Sulawesi[a]

Elevation (m) at thermometer site	Place	Temperature (°F) (mean, ranges in parentheses)		Relative humidity (%)			Days			Recording period
		Minimum	Maximum	Morning	Midday	Evening	Recording	Rainfall	Recording/ rainfall (%)	
2275	Gunung Nokilalaki	51.0 (48–54)	56.6 (52–63)	—			60	40	67	Mar. 4–May 2, 1975
2060	Gunung Nokilalaki	54.7 (51–58)	60.4 (54–65)	86–100	68–98	86–100	60	40	67	Mar. 4–May 2, 1975
1730	Gunung Nokilalaki	57.5 (55–66)	64.8 (61–69)	70–97	—		30	—	—	Dec. 6, 1973–Jan. 4, 1974
1440	Gunung Kanino	58.4 (52–61)	68.9 (63–76)	90–98	58–98	85–98	32	20	63	Jan. 16–Feb. 16, 1975
1150	Sungai Tokararu	61.1 (56–64)	73.9 (69–83)	73–96	—		32	—	—	Sept. 12–Oct. 13, 1973
1000	Tomado	65.0 (56–67)	80.9 (70–94)	—			24	—	—	Aug. 7–Sept. 3, 1973
758	Sungai Sadaunta	66.9 (62–70)	75.2 (70–86)	92–100	60–98	88–100	92	56	61	Sept. 16–Dec.16, 1974
290	Sungai Oha Kecil	70.1 (66–73)	78.8 (75–83)	86–100	64–99	87–100	37	21	57	July 31–Sept. 5, 1974
136	Sungai Tolewonu	69.8 (67–72)	77.3 (72–81)	96–99	87–99	95–99	57	36	63	Jan.3–Feb. 28, 1976
30	Kuala Navusu	73.6 (72–76)	80.9 (74–87)	94–100	78–100	94–100	95	64	67	Aug. 28–Nov. 30, 1975

[a] Minimum and maximum recordings were collected during a 24-hour period. Thermometers were placed just above the ground beneath the canopy in primary forest; 2275 m is the summit of Gunung Nokilalaki. Intensity of rainfall ranged from sprinkles to rain falling day and night. At Tomado the thermometer was placed in a shaded guest house in a meadow adjacent to forest. Data are from my field journals (stored in Mammalogy Archives, AMNH).

Ten to 12 consecutive wet months and two or less consecutive dry months are the rainfall patterns for the drainage basins of the Sungai Miu (Sungai Sadaunta and Sungai Oha Kecil), Danau Lindu (Tomado and Sungai Tokararu), and surrounding mountains (Gunung Kanino and Gunung Nokilalaki), which places these areas in a "permanently humid" zone. Five to six consecutive wet months and three or less consecutive dry months are usual for Kuala Navusu and Sungai Tolewonu on the eastern coastal plain, a "slightly seasonal" region (see Whitten et al., 1987: 22). Mean annual rainfall in both areas is about 3000 mm (Whitten et al., 1987: 25).

camps and other elevations are summarized in table 3.

All the kinds of data derived from inventories of small mammals obtained by trapping originate not only from the animal caught in the trap but also from the spot where the trap was placed: for example, on the ground or at levels in the forest above the ground, in the open or beneath cover, on hillsides or ridgetops, on stream terraces or decaying tree or palm trunks and limbs bridging streams, in primary forest or disturbed forest at various stages of reforestation. I needed to know where each animal was trapped, so during my first year I set my own traplines, ran them myself, and recorded the habitat at the spot where each small mammal had been taken. During the second and third years I was aided by two excellent helpers, Aminudi and Usma, both from a village near Sadaunta in the drainage of the Sungai Miu. At each of the camps, the three of us set three different traplines, each consisting of 100–150 traps, and each of us would check his own line. When Aminudi and Usma first set their lines, I accompanied them so I would know the location of their traps and could record habitat and elevation at any site of capture. None of our specimens came from local trappers.

We used a variety of traps: cage live traps fabricated in Taiwan, Sherman live traps (both 6 inch and 10 inch models), Victor rat snap traps, the smaller Museum Special snap traps, and Conibear body-gripping traps (single spring #110). Bait consisted of a combination of peanut butter, rolled oats, raisins, and bacon ground to a firm paste.

We concentrated our trapping efforts in old-growth (primary) forest. For the most part we avoided second-growth and anthropogenic habitats associated with village houses and gardens, rice fields, and other kinds of croplands. Exceptions were places in primary forest where a large tree had been removed for building materials; small areas of coffee groves situated in the primary forest where the canopy trees remained intact, but the understory had been partially cleared for coffee trees; and clearings deep in the primary forest caused by fallen canopy trees, landslips, and stream flooding due to nonanthropogenic causes.

I provide this brief description of the regions in which we worked and collected examples of *Bunomys* and the note on trapping protocol because along with acquiring material for taxonomic study, I also obtained habitat and other biological information that are attached to the specimens collected. These natural history data are summarized for four species of *Bunomys*, and constitute the only firsthand natural history information I had available for this review.

GAZETTEERS AND MAPS: Localities from which samples were collected, along with the institutional acronym and catalog number of each specimen examined, are listed in a gazetteer of collection localities for each species. No specimen is listed that I did not personally examine. Descriptions of locality and elevations (recorded in meters or feet, depending on the convention used by the collector) were taken from labels attached to skins. These basic data were enhanced where necessary by relevant information from field journals, other archival material, and published expeditionary accounts and gazetteers; sources are cited in the locality entry.

Spelling of locality names are those approved by the United States Board on Geographic Names in the Gazetteer of Indonesia (3rd ed.), volumes 1 and 2, published by the Defense Mapping Agency, Washington, D.C., in 1982 (referenced as USBGN Indonesia, 1982). Some localities could not be located in that gazetteer but were found on the topographic map sheets described below; other spellings come from my field notes.

Coordinates for some collection localities were found in USBGN Indonesia (1982) or the Gazetteer of Celebes published in 1944 through the Hydrographic Office of the United States Navy Department (HOUSND Celebes, 1944). Coordinates for most of Harry C. Raven's collection localities were estimated from his personal copy of a Dutch map of Celebes on which he had marked his camp sites and travel routes (Overzichtskaart van het eiland Celebes, Schaal 1:1,250,000, ''met aanduiding van de politieke indeeling, de organisatie van het bestuur, de bestaande en nog aan te leggen verkeerswegen en van de

groote cultuur- en industrieele centra. Sa-
mengesteld op last van de N.I. Regeering"
("indicating the political divisions, the orga-
nization of the administration, the existing
and the still to be built road system, and the
large cultural and industrial centers. Created
at the request of the N.I. [Nederlands Indië =
Dutch East Indies] Government"), published
in 1909), and referred to in the text as
"Raven's map." Coordinates for my collec-
tion localities, as well as height above sea
level for places for which altitudes were
not recorded by collectors, were estimated
from "JOINT OPERATIONS GRAPHIC-
GROUND" topographic maps, scale 1:250,000,
compiled by Mapping and Charting Estab-
lishment RE, 1969, and published by the
Director of Military Survey, Ministry of
Defence, United Kingdom, 1970, or by the
Army Map Service, Washington, D.C.
(Sheets NA 51-9 [1967], NA 51-12 [1967],
NA 51-14 [1967], SA 50-8 [1971], SA 51-1
[1970], SA 51-5 [1967], and SA 51-14 [1967],
SB 50-8 [1966], SB 51-1 [1970]). Coordinates
for localities trapped by personnel associated
with the Navy Medical Research Unit
(NAMRU) stationed in Jakarta were ob-
tained from their archival records.

FORESTS AND PLANTS: The tropical rain
forests embracing the habitats of Sulawesi's
species of *Bunomys* will be described broadly
in the accounts of species by applying three
of the forest formations categorized by
Whitmore (1984): tropical lowland evergreen
rain forest, tropical lower montane rain
forest, and tropical upper montane rain
forest. Whitmore's descriptions of these
different forest landscapes are illuminating
and, as he notes, an extension and elabora-
tion of P.W. Richards's (1952) classic "Trop-
ical Rain Forest," which readers will also
find informative (a second edition was
published in 1996).

We collected botanical samples at the
various camps and had some examined by
specialists who identified most of the material
to either genus only or to genus and species.
Because some of those scientific names are
now synonyms or were found to be invalid, I
checked the names against those compiled in
The Plant List (2013), version 1.1 (http://
www.theplantlist.org/).

HISTORICAL SUMMARY

In October of 1895, A.H. Everett, a
collector for the Natural History Museum in
London, worked in the southern portion of
Sulawesi's southwestern peninsula with the
purpose "to obtain for our National Museum
specimens of the numerous small mammals
that have been described of late years from
the island of Celebes and have hitherto been
unrepresented in the British Museum," wrote
Thomas (1896: 241), who reported on Ever-
ett's collection. Among Everett's material was
a rat collected from high forest on "Bonthain
Peak" (= Gunung Lompobatang), which
Thomas (1896: 248) described under the name
"*Mus coelestis*," a taxon that would eventu-
ally form the type species of *Bunomys*.
Thomas enthusiastically wrote that this

> remarkable species differs so much in its
> external characters from ordinary rats that I
> have had great doubts whether a special genus
> or subgenus ought not to be made for its
> reception. As, however, there do not seem to be
> any very definite cranial or dental characters, I
> feel justified in leaving it for the present in the
> genus *Mus*.

Fourteen years later, Thomas (1910: 506)
changed his mind and wrote that

> on attempting to arrange the Australasian Muridae
> hitherto referred to "*Mus*" in genera of a more
> modern character, I find that certain peripheral
> species stand out at once as so different from all
> others as to need removal from *Mus* or *Epimys*
> before any idea of the characters of the great
> majority of the species can be gained.

Thomas (1910: 508) then described *Bunomys*
with *Mus coelestis* as the type and
only species, and compared it with *Stenomys*
(originally based on a New Guinea species):

> Fore claws elongated, fossorial. Clitoris ex-
> tremely long, as long as the penis of an ordinary
> murine. Mammae 0–2=4.

> Interparietal much smaller. Palatine foramina
> rather short.

> Second molar with a small antero-external cusp.
> Upper incisors quite flat in front; lower incisors
> very slender, the gnawing section of unusual length.

Bunomys, noted Thomas (1910: 508), "is
no doubt the Celebean representative of

Stenomys," a genus he had described on the previous page in the same publication. *Stenomys* is currently treated as a synonym of *Rattus,* its former contents have been subsumed within a "*Rattus leucopus* species group" containing species endemic to the Moluccas and the Australia–New Guinea region (Musser and Carleton, 2005; Rowe et al., 2011), and DNA sequences place those species in a clade separate and distant from a *Bunomys-Paruromys-Taeromys* clade (Fabre et al., 2013).

Following Thomas's (1910) description, *Bunomys* retained its generic status in publications dealing with taxonomy of murids until 1941 when it was incorporated into *Rattus,* but by the 1980s was revitalized as a separate genus. During that interval between 1910 and 1941, Tate (1936), in his presentation of some Muridae of the Indo-Australian region, recognized *Bunomys* but doubted the close relationship between it and *Stenomys* claimed by Thomas. Tate (1936: 580–581) suggested that *Bunomys*

> seems to comprise merely offshoots of the *Rattus chrysocomus* group which have become slightly fossorial, as indicated by their lengthened claws. The adult skull possesses the lengthened rostrum with tendency to expansion at its anterior end and the widened posterior portion of the braincase as well as a sloping zygomatic plate, all of which characters appear in the *chrysocomus* rats… . it appears that the Mengkoka form *koka* [described by Tate and Archbold, 1935b, as a subspecies of "*Bunomys caelestis*" but the sample on which the name is based is a geographic population of *B. chrysocomus* as I will document in the account of that species] constitutes a geographical race differing from true *caelestis* in being smaller, with a smaller hindfoot, and shorter claws (thus becoming annectant with the *chrysocomus* group of *Rattus*)….

Besides *coelestis* and *koka,* Tate arranged the other taxa that would become associated with *Bunomys* into "large-toothed rats" (*Rattus penitus*—with *sericatus, heinrichi, inferior, and adspersus* as subspecies—*R. andrewsi,* and "possibly *R. fratrorum*") and "small-toothed rats" (*R. nigellus, R. rallus, R. brevimolaris,* and "possibly *R. chrysocomus*" within a "*Rattus chrysocomus* Group" that was part of his "*Rattus rattus* Division" (table 4).

In 1941, Ellerman (1941: 160) endorsed Tate's observation by merging *Bunomys* with *Rattus,* and recognizing a "*coelestis* Group" containing *R. coelestis coelestis* and *R. coelestis koka* (1941: 191). The other taxa he gathered together in a "*Rattus chrysocomus* Group" under subgenus *Rattus* of genus *Rattus* and, except for listing *adspersus* as a species, copied Tate's allocation of taxa to species and subspecies, but offered this reservation (1941: 217): "All described members of this group appear to represent one species only, or very probably so."

Bunomys was one of many genera that Simpson (1945: 89) treated as a synonym of *Rattus* in his classification of mammals.

By 1949, Ellerman (1949: 66–67, 70) had reassigned the taxa into two subgenera of *Rattus.* Subgenus *Maxomys* contained *Rattus chrysocomus* (with *fratrorum* as a subspecies), and all the other taxa were arranged in the *coelestis* Group of subgenus *Rattus.* While now recognizing the distinctness of *chrysocomus,* Ellerman retained his view of the taxa in the *coelestis* Group as representing a single species, but with less certainty:

> I assume that all the Mid Celebes forms will be races of this [*coelestis*], which appears to be the first name, but my knowledge of them is not extensive. *Adspersus* seems to be distinct from *coelestis. R. chrysocomus,* which has been placed in the neighbourhood of these rats, proves on re-examination to have small bullae, and on that account is placed in a different subgenus in the present classification.

Between 1949 and the late 1970s, the morphological traits associated with *Bunomys* continued to be viewed as part of the range of variation defining *Rattus,* and taxonomists either followed Ellerman's arrangement of taxa published in 1949 or provided a different listing (table 4). Laurie and Hill (1954), in their list of land mammals of New Guinea, Celebes, and adjacent islands, accepted Ellerman's 1949 arrangement in total. Fifteen years later, Misonne's (1969) view of evolutionary trends among African and Indo-Australian Muridae was published, wherein he retained *Bunomys* as a synonym of *Rattus* and placed *coelestis* in the subgenus *Bullimus* (1969: 140), a category containing, in his opinion, species "fairly

TABLE 4
Past and Present Arrangements of Scientific Names Associated with *Bunomys*[a]

Tate, 1936	Ellerman, 1941	Sody, 1941	Ellerman, 1949	Corbet and Hill, 1992	Musser and Carleton, 2005	Present report
Rattus	*Rattus*	*Frateromys*	*Rattus*	*Bunomys*	*Bunomys*	*Bunomys*
Rattus rattus Division, *R. chrysocomus* Group	subgenus *Rattus, R. chrysocomus* Group	—	subgenus *Rattus, coelestis* Group	—	—	—
Large-toothed rats						**Bunomys fratrorum Group**
R. penitus penitus	R. penitus penitus	F. penitus penitus	R. adspersus penitus	B. penitus	B. penitus	B. penitus
R. penitus sericatus	R. penitus sericatus	—	R. adspersus sericatus	B. penitus	B. penitus	B. penitus
R. penitus inferior	R. penitus inferior	F. penitus inferior	R. adspersus inferior	B. andrewsi	B. andrewsi	B. andrewsi
R. penitus heinrichi	R. penitus heinrichi	F. penitus heinrichi	R. adspersus heinrichi	B. heinrichi	B. andrewsi	B. andrewsi
R. penitus adspersus	R. adspersus	—	R. adspersus adspersus	B. andrewsi	B. andrewsi	B. andrewsi
R. andrewsi	R. andrewsi	—	R. andrewsi	B. andrewsi	B. andrewsi	B. andrewsi
Possibly R. fratrorum	R. fratrorum	F. fratrorum	Synonym of R. chrysocomus (in subgenus Maxomys)	B. fratrorum	B. fratrorum	B. fratrorum
—	—	—	—	—	—	B. karokophilus
Small-toothed rats	**Rattus coelestis Group**	—	subgenus **Rattus, coelestis Group**			**B. chrysocomus Group**
R. nigellus	R. nigellus	—	R. adspersus (?) nigellus	B. chrysocomus	B. chrysocomus	B. chrysocomus
R. rallus	R. rallus	—	R. adspersus (?) rallus	B. chrysocomus	B. chrysocomus	B. chrysocomus
R. brevimolaris	R. brevimolaris	F. brevimolaris	R. adspersus (?) brevimolaris	B. chrysocomus	B. chrysocomus	B. chrysocomus
Possibly R. chrysocomus	R. chrysocomus	—	R. chrysocomus (in subgenus Maxomys)	B. chrysocomus	B. chrysocomus	B. chrysocomus
Bunomys	—	—	**coelestis Group (in subgenus Rattus)**			
B. coelestis coelestis	R. coelestis coelestis	—	R. coelestis coelestis	B. coelestis	B. coelestis	B. coelestis
B. coelestis koka	R. coelestis koka	—	R. coelestis koka	B. coelestis	B. chrysocomus	B. chrysocomus
—	—	—	—	B. prolatus	B. prolatus	B. prolatus
—	—	—	—	—	—	B. torajae

[a] Only some landmark sources are summarized in this table. I omitted three references. In their checklist of mammals from New Guinea, Sulawesi, and adjacent islands, Laurie and Hill (1954) simply followed the arrangement of species and their synonyms presented by Ellerman (1949). Misonne (1969) subsumed *Bunomys* in the genus and subgenus *Rattus* but placed *chrysocomus*, *coelestis*, and *adspersus* in subgenus *Bullimus* of *Rattus*. And except for listing *heinrichi* as a species of *Bunomys*, the species and synonyms recognized by Musser and Carleton in 1993 match their 2005 accounts.

closely related to one another'' and ''repre-
sented by at least five species or groups of
species, from Celebes, by four Bornean and
Malayan species, and by at least two
Philippine species.''

By the early 1980s, *Bunomys* had been
revalidated as a genus separate from *Rattus*
in various discussions covering taxonomy
of Indo-Australian murines (Musser, 1981b,
and Musser and Newcomb, 1983, are exam-
ples) and since that time has been acknowl-
edged in regional faunal treatises (Corbet and
Hill, 1992; Pavlinov et al., 1995) and broader
compendia of taxa (Carleton and Musser,
1984; Corbet and Hill, 1991; McKenna and
Bell, 1997; Musser and Carleton, 1993, 2005).

THE GENUS

Bunomys Thomas, 1910

Frateromys Sody 1941: 260.

TYPE SPECIES: *Mus coelestis* Thomas,
1896: 248.

EMENDED DIAGNOSIS: A genus in Rattini
(Lecompte et al., 2008; Aplin and Helgen,
2010) or *Rattus* Division (Musser and Carle-
ton, 2005) of Murinae within Muridae (as
delimited by Musser and Carleton, 2005) that
is distinguished from all other described
murine genera by the following combination
of traits: (1) all species terrestrial in habitus;
(2) dorsal pelage covering head and body
dense and soft, with guard hairs only slightly
longer than overhairs, so coat has an even
surface, dorsal coat dark gray, dark blue-
gray, brownish gray or brown speckled with
buff and black; (3) ventral coat soft and
dense, whitish gray, dark grayish white, blue-
gray lightly speckled with white, grayish pale
buff to ochraceous gray, demarcation be-
tween upperparts and underparts inconspic-
uous; (4) muzzle elongate in most species,
ears rubbery in texture, gray to brown; (5)
tail shorter than combined length of head
and body, coequal or slightly longer (mean
values of LT/LHB range from 79% to 102%),
scales small, their annuli overlapping, three
short hairs associated with each scale, dorsal
surface grayish bown to brown, ventral
surface ranges from white (tail is bicolored)
to brown (tail is monocolored), a white tip

occurs infrequently or is usual, depending
upon the species; (6) digits white, dorsal
surfaces of carpal and metacarpal regions
white to brown, palmar surface adorned with
usual number of tubercles found in murines
(three interdigitals, a thenar, and a hypothe-
nar), hind foot elongate with full complement
of plantar tubercles (four interdigitals, a
thenar, and a hypothenar), front claws
elongate in three species; (7) two pairs of
inguinal teats; (8) testes of adults large
relative to length of head and body (22%)
or smaller (8%–15%); (9) rostrum of adults
elongate and either narrow or broad, inter-
orbital and postorbital margins bounded by
low ridges, zygomatic arches flare from sides
of skull, posterior zygomatic root situated
low on braincase, braincase boxlike (moder-
ately wide and deep), occiput deep, no cranial
flexion; (10) zygomatic plate wide or narrow,
its anterior margin either barely projecting
beyond dorsal maxillary root of zygomatic
arch or bowed beyond it, its posterior edge
even with the anterior third of the first molar;
(11) squamosal intact (not perforated by a
subsquamosal foramen); (12) alisphenoid
struts absent; (13) incisive foramina long in
most species and moderately wide, their
posterior margins ending well anterior to
front faces of first molars; (14) molar rows
diverge slightly posteriorly, bony palate short
with its posterior margin even with back
faces of third molars or extending slightly
beyond them, palatal surface with moderate-
ly deep palatine grooves, posterior palatine
foramina at level where second and third
molar touch; (15) moderately long and narrow
sphenopalatine vacuities; (16) wide pterygoid
plates with moderately deep pterygoid fossa,
small sphenopterygoid openings; (17) medium
or large ectotympanic (auditory) bulla relative
to skull size, capsule incompletely covering
periotic, posterodorsal wall of carotid canal
formed by periotic and not bullar capsule; (18)
large stapedial foramen, no sphenofrontal
foramen or squamosal-alisphenoid groove,
indicating a carotid arterial pattern wide-
spread within Murinae (char. state 2 of
Carleton, 1980; pattern 2 described by Voss,
1988); (19) dentary somewhat elongate, low
ramus between incisor and molar row, mod-
erately high ascending ramus, large coronoid
and condyloid processes, end of alveolar

capsule forming modest labial swelling level with base of coronoid process; (20) upper and lower incisors with orange enamel and ungrooved anterior faces, uppers emerge from the rostrum at a right angle (orthodont) or curve slightly caudad (opisthodont), each lower incisor awl shaped with elongate wear facets; (21) each first upper (maxillary) molar with five roots, the second with four, and the third with three, each first lower (mandibular) molar with four, the second and third molars each with three; (22) molars brachydont, cusp rows forming simple cuspidate occlusal patterns, third molar small relative to others in toothrow; (23) first and second rows of cusps on first upper molars laminarlike or gently arcuate because cusp t3 on the first row and cusp t6 on the second row are oriented horizontally and broadly coalesced with the respective central cusp t2 and cusp t5, anterior row of second molar shaped like second row of first molar; (24) no cusp t7 or posterior cingulum on upper molars, and no other occlusal embellishments (such as an enamel ridge projecting from anterolingual surface of cusp t8 anteriorly to posterior margin of lingual cusp t4, a labial enamel ridge connecting anterolabial margin of cusp t9 with posterolabial margin of cusp t6, or a comparable but shorter ridge projecting from the anterior surface of cusp t5 to meet the posterior margin of cusp t3 near the cingulum, all typical of some other murines with more complicated enamel occlusal patterns; the New Guinea *Coccymys* is an example [Musser and Lunde, 2009]), cusp t3 typically missing from second molars in all but two species and from third molar in most specimens; (25) anteroconid formed of large anterolingual and anterolabial cusps, anterocentral cusp absent, anterolabial cusp present or missing from second and third lower molars depending upon the species, anterior labial cusplets typically not present on first and second lower molars, but posterior labial cusplet present on each tooth, posterior cingulum round or elliptical; (26) stomach unilocular-hemiglandular; (27) sperm head asymmetrical and falciform in shape, with single apical hook lacking ventral processes, spermatozoal tail short to moderately long; and (28) karyotype, $2N = 42$, FNa = 56 or 58, FNt = 58, 60, or 61.

CONTENTS: *Bunomys chrysocomus*, *B. coelestis*, *B. prolatus*, *B. torajae,* n. sp., *B. fratrorum*, *B. andrewsi*, *B. penitus*, and *B. karokophilus,* n. sp.; all are endemic to Sulawesi.

GEOGRAPHIC AND ELEVATIONAL DISTRIBUTIONS: One species is spread over the island, the others restricted to certain regions (table 5; also see the maps showing collection localities in figs. 22, 50, and 51). *Bunomys chrysocomus* is the most widespread (as documented by voucher specimens): samples are from the central core and most of the peninsulas and were collected through an elevational range bracketed by lowland to montane habitats. *Bunomys coelestis* is known only from montane forest on Gunung Lompobatang, the highest landform in the southwestern peninsula; the montane *B. prolatus* has been taken to date only from Gunung Tambusisi at the western terminus of the eastern peninsula; and *B. torajae,* n. sp., has been collected so far only from montane habitat on Gunung Gandangdewata in the southern section of the west-central mountain block. *Bunomys fratrorum* is endemic to the northern peninsula east of the Gorontalo area where it occupies tropical lowland evergreen and montane rainforest habitats. *Bunomys andrewsi* occurs primarily in tropical lowland evergreen rain forests and is represented by voucher material from the Sulawesi's core, the western end of the eastern peninsula, and the southeastern and southwestern peninsulas. *Bunomys penitus* is strictly montane, found so far only in the west-central mountain block and in Pegunungan Mekongga on the southeastern peninsula. The only samples of *B. karokophilus,* n. sp., come from tropical lowland evergreen rain forest at middle elevations in the northern portion of the west-central region.

COOCCURRENCE AMONG THE SPECIES: The patterns of sympatric or parapatric geographic distributions as well as syntopic occurrences among the species of *Bunomys* is summarized in table 6 and elaborated in the accounts of species.

DESCRIPTION: Morphological variation categorizing the species of *Bunomys* reflects rats of medium body size (fig. 6; table 7) adapted to terrestrial habitats. The general character variation as expressed in live animals and preserved specimens is described below under external form (fur, ears, tail,

TABLE 5
Summary of Elevational Distributions (m) over Mainland Sulawesi for Species of *Bunomys* derived from Voucher Specimens
See the maps showing collection localities in figures 22, 50, and 51.

Species	Northern Peninsula	Core	Eastern peninsula	Southeastern peninsula	Southwestern peninsula	Tropical forest formation
B. chrysocomus	250–800	320–2200	1372–1829	300–2000	coastal plain[a]	lowland evergreen and montane
B. coelestis	—	—	—	—	1829–2500	Montane
B. prolatus	—	—	1829	—	—	Montane
B. torajae	—	2500–2600	—	—	—	Montane
B. fratrorum	coastal plain to 1982	—	—	—	—	lowland evergreen and montane
B. andrewsi	200	30–1600	50–100	50–550	coastal plain to 1100	lowland evergreen
B. penitus	—	1285–2287	—	1500–2000	—	Montane
B. karokophilus	—	823–1150	—	—	—	Lowland

[a] Based on subfossils excavated from cave deposits; actual elevation of the living population in which the subfossils were components is unknown.

feet, teats, and testes), gross spermatozoal morphology, gross stomach structure, skull, and teeth. Each species is characterized by its own combination of traits and these will be addressed in the accounts of species.

External Form

Fur: In adults of all species, the glossy dorsal coat is soft and silky to the touch, dense, and moderately long (12–25 mm). It is composed of long, soft, and fine underhairs (or ''wool'' hairs; Voss, 1988) that form the underfur layer; overhairs (also called awns; Voss, 1988) comprising the overfur; and short, glossy guard hairs scattered throughout the overfur layer. Most underhairs are gray their entire lengths; some are tipped with a short, pale buffy band. Intermixed with the underfur and projecting slightly beyond it are the overhairs; each hair is gray for most of its length, but ends with a subterminal dark-brown band and capped by a bright buffy band. Guard hairs are inconspicuous because they are scattered through the coat and barely extend beyond the layer of overfur; each is thin and soft, gray along its basal two-thirds and either pale buff or glossy black at the tip. Because underhairs are nearly as long as the overhairs, and guard hairs are soft and barely project beyond the overfur layer, the dorsal fur appears to form an even, soft, and dense covering over upperparts of the head and body. In seven species, the dorsal coat of

most specimens is a lustrous, rich brown with some gray highlights, a tone influenced by the wide buffy tips of the overhairs. The upperparts are much darker in a seventh species where the hairs are dark gray for most of their lengths. Soft and fine underhairs and overhairs, but not guard hairs, form the ventral coat of adults, which is 8–15 mm long. The hairs are gray for most of their lengths and have unpigmented (appearing white or silvery) or buffy tips. Depending upon lengths of tips and density of pigment, overall color of the venter is whitish gray, dark grayish white, buffy dark gray, or ochraceous dark gray. Countershading is evident but weakly expressed in examples of seven species (rich brown or grayish-brown upperparts, grayish-white to to grayish-buff underparts), but inconspicuous in an eighth species where a dark blue-gray dorsum hardly contrasts with a dark gray venter.

Fur covering the head of adults is pigmented like that clothing the body; throat is chromatically indistinguishable from chest and abdomen. The only obvious facial pattern is formed by blackish brown eyelids and a circle of darker hairs around each eye. All species have an array of mystacial, submental, superciliary, subocular, genal, and interramal vibrissae adorning the head; the mystacial barely extend beyond the ears when laid back over the head (see Brown, 1971, for descriptions of these sensory hairs and terminology). Some of the hairs lack

TABLE 6
Summary of Sympatry over the Mainland of Sulawesi for Species of *Bunomys* derived from Voucher Specimens

Species	Northern peninsula (east of Gorontalo)	Core	Eastern peninsula	Southeastern peninsula	Southwestern peninsula
B. chrysocomus	*B. fratrorum* (syntopic)	*B. andrewsi*, *B. karokophilus*, *B. penitus* (syntopic with all three); sympatric with *B. torajae*	*B. prolatus* (elevationally parapatric)	*B. andrewsi* (sympatric), *B. penitus* (syntopic)	*B. andrewsi* (syntopic as subfossils)
B. coelestis	—	—	—	—	Only species recorded between 1800 and 2500 m
B. prolatus	—	—	*B. chrysocomus* and *B. andrewsi* (elevationally parapatric with each)	—	—
B. torajae	—	*B. chrysocomus* (sympatric); elevationally parapatric with *B. penitus* and *B. andrewsi*	—	—	—
B. fratrorum	*B. chrysocomus* (syntopic)	—	—	—	—
B. andrewsi	—	*B. chrysocomus* (syntopic and sympatric); elevationally parapatric with *B. penitus* and *B. torajae*	*B. chrysocomus* and *B. prolatus* (elevationally parapatric with each)	*B. chrysocomus* (sympatric)	*B. chrysocomus* (syntopic as subfossils)
B. penitus	—	*B. chrysocomus* (syntopic); elevationally parapatric with *B. andrewsi* and *B. torajae*	—	*B. chrysocomus* (syntopic)	—
B. karokophilus	—	*B. chrysocomus* (syntopic); elevationally parapatric with *B. andrewsi* and *B. penitus*	—	—	—

pigment (appear silvery), others are brown, but most are black; all have glossy surfaces.

Ears: Pinnae are moderately large relative to size of head and body in all of the species (table 7). In life, the pinnae feel and appear rubbery, and while seemingly naked are scantily covered on inner and outer surfaces by short, fine, and dark hairs that are too short to form a fringe along the dorsal internal rim of each ear. Color of the ears is variable, ranging from shiny gray through dark gray, dark grayish brown or grayish black, to blackish gray. Some species, such as *B. chrysocomus*, exhibit this full range of shades; other species, *B. penitus*, for example, tend to have grayish ears. The dried ears of museum puppet skins are stiff, dark brown, and lack the rubbery texture of the live animal.

Fig. 6.   Four species of Sulawesian *Bunomys* drawn from photographs of live animals: *B. andrewsi* (upper left), *B. penitus* (upper right), *B. chrysocomus* (lower left), and *B. karokophilus,* n. sp. (lower right). All occur in forests somewhere along my transect extending from the lowlands at Sungai Oha Kecil to the summit of Gunung Nokilalaki; only *B. andrewsi* was found in the Malakosa area.

Tail: In samples of adults, length of tail is typically as long as the combined head and body length in *Bunomys fratrorum* and *B. penitus*, but shorter in the other six species (table 7). In all species, the tail is squarish in cross section, covered with slightly overlapping rings of thin small scales (13–18 scale annuli per cm). Three fine, short hairs (as long as one or two scales) emerge from beneath each scale. Because the hairs are so fine and short, the scutellation is exposed all along the tail. Distribution of pigmented scales and hairs along the tail varies both within a species and among species, producing several chromatic patterns: (1) solid brown on all surfaces (monocolor tail); (2)

TABLE 7
Contrasts in Physical Size among Species of *Bunomys*
Listed are ranges for lengths of head and body (LHB), tail (LT), hind foot (LHF), ear (LE), skull (ONL) and maxillary molar row (CLM1–3) in millimeters; LT/LHB (%); and weight (WT) in grams. Data are summarized from univariate descriptive statistics presented in tables scattered throughout the text.

Species	LHB	LT	LT/LHB	LHF	LE	WT	ONL	CLM1–3
B. chrysocomus	97–180	90–180	85–98	31–40	17–28	55–175	35.8–41.1	5.7–6.8
B. coelestis	147–179	136–165	95	35–39	21–25	—	37.6–41.8	5.7–6.6
B. prolatus	156–179	125–142	79	33–35	24–26	—	40.4–43.2	6.3–6.8
B. torajae	156–210	160–170	93	36–39	26–28	98–128	41.2–41.8	6.5–6.6
B. fratrorum	157–190	150–200	87–101	36–44	26–28	175	41.5–46.5	6.8–8.1
B. andrewsi	137–195	110–167	75–92	35–44	22–27	88–222	37.1–45.5	6.5–8.0
B. penitus	155–242	138–198	88–102	38–45	23–29	95–212	39.3–46.1	7.0–8.4
B. karokophilus	155–190	150–205	95	36–42	22–25	105–175	39.0–42.4	6.8–7.3

solid brown, grayish brown, or brownish gray over the dorsal surface, lightly to heavily mottled brown on the ventral surface; (3) heavily mottled brown over both dorsal and ventral surfaces; (4) solid brown or grayish brown above except for the tip, white (unpigmented) along entire ventral surface and tip of tail (bicolored tail); (5) solid brown over all surfaces except for a distal white segment of variable length (see table 8).

Feet: Each front foot has four slender digits ending in ivory-colored claws and a stubby thumb (pollex) bearing a nail (fig. 7). Digits and dorsal surface of the metacarpal region are covered with either silvery or brown hairs, depending on the species. Ungual tufts are short, sparse, and inconspicuous. Three interdigital pads are set close together and the large paired thenar and hypothenar mounds form much of the naked palmar surface.

All the species have long and narrow hind feet and slender digits (fig. 7). Depending on the species, dorsal surfaces of the metatarsal region are brown, white, or a combination of brown and white; digits are typically white. Silvery ungual tufts cover the ivory-colored claws in all species and project beyond the claws in two of the eight species. The first (hallux) and fifth digits are much shorter than the three longer middle digits, which are all about the same length. Claw of the hallux barely reaches beyond base of the second digit, and claw of the fifth extends to about middle of the second digit. The naked plantar surfaces are adorned by six moderately fleshy pads: four interdigital mounds (forming a cluster at

bases of the digits), a very small (relative to sizes of the interdigitals) hypothenar, and an elongate thenar. The hypothenar pad does not occur on some individuals of certain Sulawesian murines (*Maxomys musschenbroekii*, for example; see Musser, 1991), but it is present on every specimen of *Bunomys* examined. Six specimens of *B. andrewsi* from Pinedapa show an extra small pad on the right foot (USNM 219622), the left foot (USNM 219599, 21966), or both feet (USNM 219587, 219589, 219606).

Teats: Two pairs of inguinal teats are characteristic of all females surveyed.

Testes: *Bunomys chrysocomus* has large testes relative to body size (length of testes/length of head and body = 16%–26%). Other species for which this information is available have relatively smaller testes (7%–18% is the range for samples of *B. torajae,* n. sp., *B. fratrorum*, *B. andrewsi*, *B. penitus*, and *B. karokophilus,* n. sp.); table 9.

Spermatozoa

Gross morphology of the spermatozoa of *Bunomys chrysocomus*, *B. andrewsi*, *B. penitus*, and *B. karokophilus,* n. sp. (as "*Bunomys* sp.''), has been described by Breed and Musser (1991); electron microscopic description that includes ultrastructure of the sperm head of *B. fratrorum* and *B. chrysocomus* is provided by Breed (2004). All consist of an asymmetrical head that is falciform in shape, terminates in a long or short apical hook, and lacks ventral hooks. The tail is attached to the ventrocaudal surface of the head in four

TABLE 8
The White Tail Tip in Geographic Samples of *Bunomys*[a]
Frequency of occurrence of white tip (WT), its absolute length (LWT), and its length relative to length of tail (LWT/LT) are listed. Mean and observed range (in parentheses) is indicated for LWT and for the percentages derived from LWT/LT.

Species and sample	N	% of sample with WT (N with white tip)	LWT (mm)	LWT/LT (%)
B. chrysocomus				
Northern peninsula	10	0	—	—
Bumbarujaba	10	10 (1)	3	3
Sungai Oha Kecil	41	27 (11)	13.7 (2–35)	10 (1–25)
Sungai Sadaunta	193	28 (54)	9.4 (1–26)	7 (1–25)
Tomado	60	12 (7)	11.1 (2–24)	8 (1–15)
Sungai Tokararu	26	4 (1)	4	3
Gunung Kanino	10	10 (1)	5	4
Gimpu	2	0	—	—
Pegunungan Latimojong	7	0	—	—
Gunung Tambusisi	6	0	—	—
Gunung Balease	3	33 (1)	8	5
Pegunungan Mekongga	21	10 (2)	7.5 (5–10)	6 (4–8)
Lalolei	7	14 (1)	5	4
B. coelestis				
Gunung Lompobatang	29	0	—	—
B. prolatus				
Gunung Tambusisi	7	14 (1)	2	2
B. torajae				
Gunung Gandangdewata	4	50 (2)	10.0 (3–17)	7 (2–11)
B. fratrorum[b]				
Teteamoet	43	79 (34)	33.2 (10–129)	19 (6–75)
Gunung Klabat	3	67 (2)	24.0 (23–25)	15 (14–15)
Tonsealama	20	86 (18)	27.4 (10–45)	16 (6–25)
Temboan	33	94 (31)	36.0 (6–90)	22 (4–53)
B. andrewsi[c]				
Pulau Buton	1	0	—	—
Labuan Sore	2	0	—	—
Kuala Navusu	20	2 (4)	2.3 (1–5)	12 (1–3)
Sungai Ranu	4	25 (1)	20	13
Gunung Balease	18	33 (6)	9.2 (4–15)	6 (3–11)
Malili Area	16	38 (6)	6.8 (2–12)	5 (2–8)
Wawo + Masembo	9	0	—	—
Puro-Sungai Miu[d]	15	47 (7)	5.9 (2–10)	5 (1–10)
Tamalanti	8	0	—	—
Mamasa Area	18	17 (3)	7.3 (2–12)	5 (1–8)
Lombasang	22	0	—	—
B. penitus				
Gunung Kanino	130	99 (129)	39.4 (7–118)	23.8 (4–68)
Gunung Nokilalaki	131	99 (130)	38.8 (6–80)	24.4 (4–46)
Rano Rano	3	100 (3)	20.0	12.3 (12–13)
Gunung Lehio	3	100 (3)	55.7 (53–61)	30.7 (29–32)
Pegunungan Quarles	6	83 (5)	39.2 (15–85)	22.6 (10–47)
Pegunungan Mekongga	20	85 (17)	20.2 (5–45)	12.4 (3–28)

TABLE 8
(*Continued*)

Species and sample	N	% of sample with WT (N with white tip)	LWT (mm)	LWT/LT (%)
B. karokophilus[e]				
Sungai Sadaunta	15	100 (15)	31.1 (4–50)	21.0 (3–31)
Tomado	7	100 (7)	16.1 (4–27)	9.7 (2–16)
Sungai Tokararu	2	100 (2)	39.0 (35–43)	24.0 (22–26)
Totals				
B. chrysocomus	396	20 (79)	7.4 (1–35)	5.5 (1–25)
B. coelestis	29	0	—	—
B. prolatus	7	14 (1)	2	2.0
B. torajae	4	50 (2)	10.0 (3–17)	7.0 (2–11)
B. fratrorum	99	86 (85)	30.2 (6–129)	18.0 (4–75)
B. andrewsi	133	20 (26)	8.6 (1–20)	7.7 (1–13)
B. penitus	293	98 (287)	35.6 (5–118)	21.0 (3–68)
B. karokophilus	24	100 (24)	28.7 (4–50)	18.2 (2–31)

[a] In the field, I measured length of tail and length of the white segment at the tip on specimens from Sungai Oha Kecil, Sungai Sadaunta, Tomado, Sungai Tokararu, Gunung Kanino, and Gunung Nokilalaki. For material from all the other localities, I measured lengths on dry skins or fluid-preserved animals.

[b] Of the 34 specimens from Teteamoet with a tail pattern, the distal portion of the tail is white in 19 (56%) but white with slight to moderate brownish speckling in 15. In the Temboan sample, the distal portion of the tail is white in 25 (81%) of the 31 individuals, the other six have white tips that are moderately speckled with brown. The end of the tail is white on specimens in the other samples of *B. fratrorum* listed here. The comparable contrasting distal tail segment is white on specimens in samples of all the other species.

[c] I omitted the sample from Pinedapa (the type-series of *Rattus adspersus*; see gazetteer) collected by H.C. Raven because the tail tip is missing from more than half of the specimens. Of the two skins from Pulau Buton, one (AMNH 31294) has a complete tail, which lacks a white tip; half the tail is missing from the other (the holotype, USNM 175899), but was intact when Allen (1911: 336) described it because he noted that the tail was "dark brown above and on sides, flesh color below and all around at the extreme tip."

[d] Includes all specimens from collection localities 4–12 in the gazetteer for *B. andrewsi*.

[e] The entire sample of the species consists of 27 specimens, but the distal portions of the tails in three are missing.

species, to the middle of the head in another. The variation among the five species involves length and breadth of sperm head, length of apical hook, length of sperm tail, and site of attachment of tail to head; the relevance of this variation in discriminating among different species is highlighted in the appropriate account of species where different combinations of the five species are contrasted.

Stomach Morphology

Stomachs of *Bunomys chrysocomus, B. fratrorum, B. andrewsi, B. penitus,* and *B. karokophilus,* n. sp., are similar in their gross morphology, which matches the design Carleton (1973: 10) has described as unilocular-hemiglandular, a stomach that is:

single-chambered with a shallow incisura angularis that scarcely extends beyond the esophageal opening… the corpus is spacious, with a broad fornix ventricularis. Distribution of cornified and glandular linings coincides closely with the basic stomach divisions: cornified epithelium is found in the corpus while glandular epithelium is limited mainly to the antrum. The bordering fold crosses the lesser curvature at the apex of the incisura angularis and the greater curvature at a locus opposite the incisura angularis.

Stomachs of the *Bunomys* sampled (I did not have stomachs for *B. coelestis, B. prolatus,* and *B. torajae,* n. sp.) are not illustrated here for they closely resemble the fully distended stomach of *Rattus hoffmanni* portrayed by Musser and Durden (2002: 32). This single-chambered hemiglandular morphology, in which the glandular zones are separated by a smooth bordering fold and the incisura angularis is shallow, forms the gastric conformation that Carleton (1973,
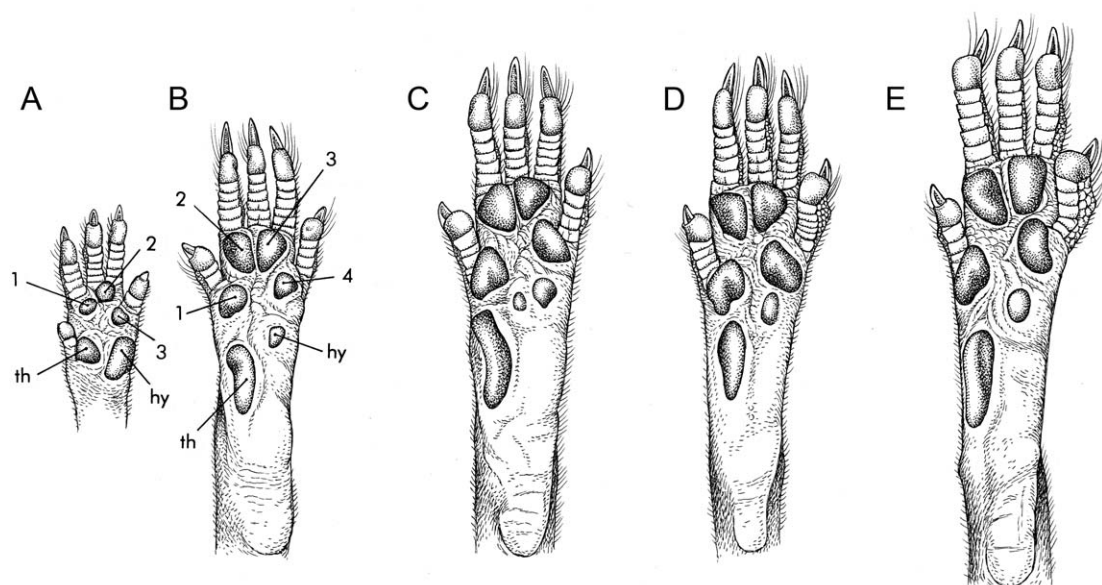
Fig. 7.   Views of left feet in adult examples of *Bunomys*. **A-B**: palmar and plantar surfaces of *B. chrysocomus* (AMNH 224166, Sungai Sadaunta); pattern and relative size of pads are similar in *B. coelestis* and *B. torajae*; feet of *B. prolatus* are portrayed in Musser, 1991: 10). **C-E**: plantar views of *B. andrewsi* (AMNH 225665, Kuala Navusu), *B. karokophilus,* n. sp. (AMNH 224833, Sungai Sadaunta), and *B. penitus* (AMNH 223924, Gunung Kanino), respectively. Topography of palmar surfaces resembles that depected in **A**. Abbreviations: **hy**, hypothenar pad; **th**, thenar pad; **1–4**, interdigital pads. All views are drawn from specimens preserved in formalin at camp and later transferred to a 70% ethanol solution.

1980) suggested represents the primitive evolutionary state among muroid rodents. The general unilocular-hemiglandular design is common to Sulawesian species in which the diets are composed of insects and fruit (*Margaretamys*); seeds (*Haeromys*); fruit, vegetative and flowering plant parts, and insects (*Lenomys* and *Eropeplus*); small vertebrates, arthropods, snails, earthworms, fruit, and fungi (*Bunomys*); primarily fruit, some insects (*Taeromys*); and primarily fruit (*Rattus*); see table 79. In these species, the extent of glandular epithelium lining the antrum relative to the area of cornified epithelium of the corpus resembles the pattern in *Rattus hoffmanni* with a range of variation in which the the glandular portion does not extend beyond the level of the esophageal orifice to a configuration where the glandular lining penetrates the corpus well past the esophageal opening.

Skull

The basic cranial configuration shared by all seven species of *Bunomys* is illustrated in the portraits of skulls throughout the text (figs. 16, 17, 37–39, 52–54, 84–86, and 99–101); osseous and foraminal landmarks described below are labeled on images of a skull of *B. chrysocomus* in figures 8 and 9. The gradually tapered rostrum is wide and moderately long (34% to 38% of occipitonasal length, depending on the species) in all the species but one. The smooth sides are broken near the base of the rostrum by low nasolacrimal capsules that barely bulge beyond the rostral walls (and are hardly evident in dorsal or ventral view). Tips of the nasals are pointed and overhang the external nares, and their posterior margins are either even with ends of the rostral processes of the premaxillae or extend slightly posterior to the premaxillary-frontal suture. From its maxillary root originating posterior to the nasolacrimal bulge and above the first molar, the zygomatic plate is moderately wide or narrow, depending on the species, its anterior margin is either straight or convex, but is always inclined and joins the dorsal maxillary

TABLE 9
Descriptive Statistics for Lengths of Head and Body (LHB) and Testis (LTe), in mm, derived from Samples of *Bunomys*[a]

Mean ± 1 SD and observed range (in parentheses) is listed. Mean values were used to compute LTe/LHB.

Species and sample	N	LHB	LTE	LTe/LHB (%)
B. chrysocomus				
Sungai Oha Kecil, Sungai Sadaunta, Tomado, Sungai Tokararu, and Gunung Kanino	75	164.6 ± 6.95 (150–180)	35.2 ± 2.83 (28–42)	22
B. torajae				
Gunung Gandangdewata	2	159.5 ± 14.85 (149–170)	21.0 ± 1.41 (20–22)	13
B. fratrorum				
Teteamoet USNM 217084	1	168	13	8
B. andrewsi				
Kuala Navusu	7	183.1 ± 11.41 (160–195)	27.9 ± 4.78 (20–33)	15
Gunung Balease	4	173.3 ± 3.78 (168–177)	13.8 ± 2.99 (10–17)	8
Malili Area	5	175.0 ± 10.58 (158–186)	19.4 ± 3.65 (15–25)	11
Sungai Oha Kecil and Sungai Sadaunta	4	165.3 ± 8.73 (156–177)	20.8 ± 0.96 (20–22)	13
Gunung Gandangdewata	3	159.7 ± 3.79 (157–164)	17.0 ± 2.65 (14–19)	11
B. penitus				
Gunung Kanino and Gunung Nokilalaki	44	181.5 ± 9.17 (161–199)	16.6 ± 1.85 (12–21)	9
Gunung Gandangdewata	1	195	25	13
B. karokophilus				
Sungai Sadaunta, Tomado, and Sungai Tokararu	11	175.9 ± 9.85 (155–190)	17.6 ± 2.20 (13–21)	10

[a] Measurements are of testes (including the epididymis) on the fluid-preserved carcasses of mature adults. I collected and measured length of head and body of all the *B. chrysocomus*, the *B. andrewsi* from Kuala Navusu and Sungai Oha Kecil + Sungai Sadaunta, the *B. penitus*, and the *B. karokophilus*. Specimens of *B. andrewsi* from Gunung Balease, Malili Area, and Gunung Gandangdewata were either measured by the collectors in the field or by me. The example of *Bunomys fratrorum* was collected by H.C. Raven. I measured the testes of this intact specimen, the only one I have seen preserved in fluid. The specimens of *B. torajae* and *B. penitus* from Gunung Gandangdewata were measured by the collectors. Fluid-preserved specimens of *B. coelestis* and *B. prolatus* were not available. I used length of head and body as a measure of body size.

root to form a shallow notch between the anterior edge and side of the skull (as seen from dorsal perspective). The posterior edge of the zygomatic plate sits above the anterior one-third or one-fourth of the first molar. A tall and narrow infraorbital foramen is the usual configuration. Zygomatic arches bow appreciably outward in most of the species, but are only moderately spread in others; the maxillary and squamosal roots of each arch are united by a moderately long jugal. The squamosal root of each zygomatic arch originates low on the outer braincase wall and its posterior margin extends along the braincase to the occiput as an inconspicuous ridge.

An interorbit that ranges from moderately narrow to wide is usual. Its dorsolateral borders are defined by low ridges that extend along dorsolateral margins of the postorbital
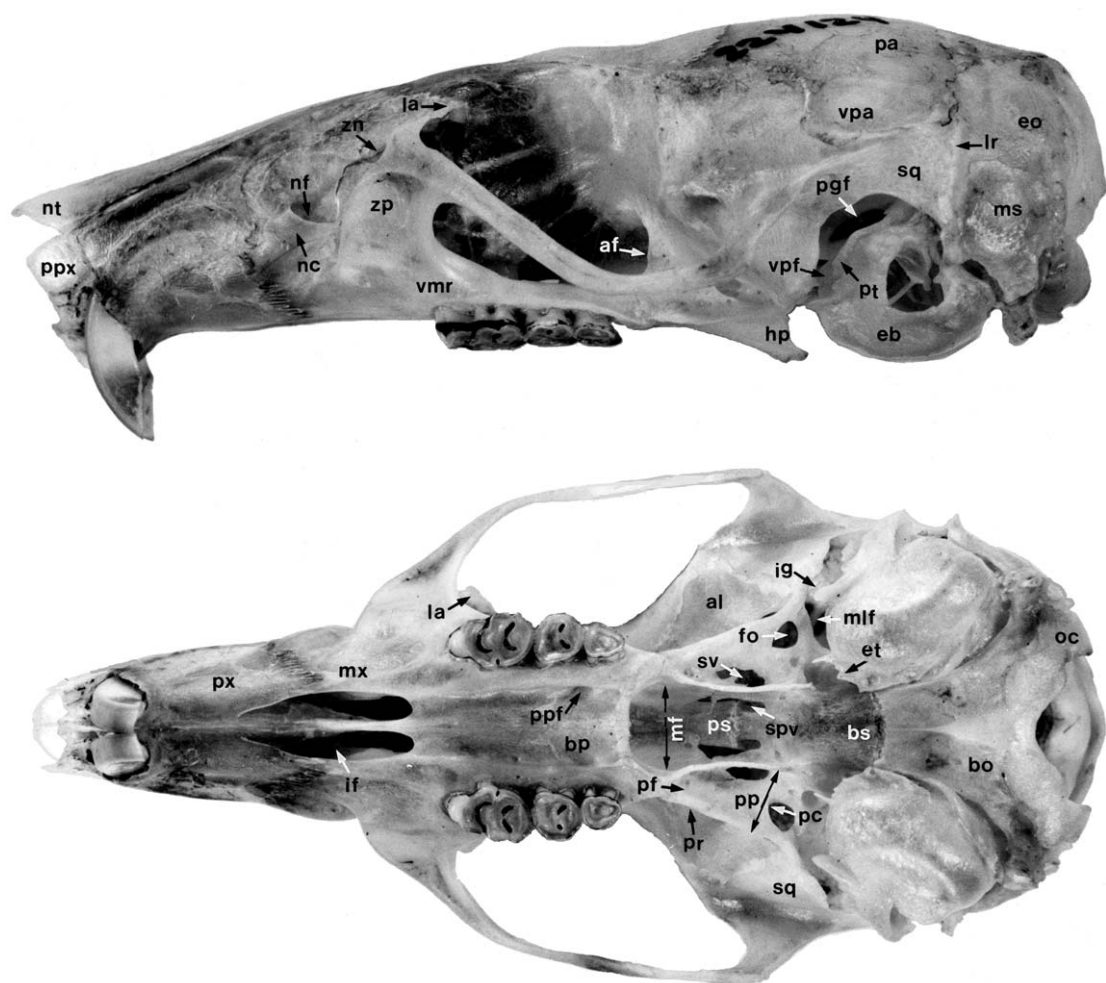
Fig. 8.   Lateral (top) and ventral (bottom) cranial views of *Bunomys chrysocomus* (AMNH 224124) identifying osseous and foraminal landmarks discussed in the text. Abbreviations: **af,** anterior alar fissure; **al,** alisphenoid; **bo,** basioccipital; **bp,** bony palate; **bs,** basisphenoid; **eb,** ectotmpanic (auditory) bulla; **eo,** exoccipital; **et,** very short bony eustachian tube; **fo,** foramen ovale; **hp,** hamular process; **if,** one of the paired incisive foramina; **ig,** groove for the infraorbital branch of the stapedial artery; **la,** lacrimal; **lr,** lamboidal ridge; **ms,** mastoid portion of the petromastoid; **mf,** mesopterygoid fossa; **mlf,** middle lacerate foramen; **mx,** maxillary; **nc,** nasolacrimal capsule; **nf,** nasolacrimal foramen; **nt,** nasal tips overhang the projecting premaxillaries to form a short tube anterior to the incisor faces; **oc,** occipital condyle; **pa,** parietal; **pc,** posterior opening of the alisphenoid canal (the infraorbital branch of the stapedial artery enters the braincase—where the arrow points—dorsal to the pterygoid plate); **pf,** pterygoid fossa, the site of muscle attachment on the pterygoid plate; **pgf,** postglenoid foramen; **pp,** pterygoid plate; **ppf,** left posterior palatine foramen; **ppx,** projection of the premaxillary beyond anterior faces of the upper incisors; **pr,** pterygoid ridge; **ps,** presphenoid; **pt,** periotic; **px,** premaxillary; **spv,** one of the paired sphenopalatine vacuities; **sq,** squamosal; **sv,** spenopterygoid foramen; **vmr,** ventral maxillary root of the zygomatic arch; **vpa,** ventral extension of the parietal to form the braincase wall above the squamosal root of the zygomatic arch; **vpf,** ventral postalar fissure, which is confluent dorsally with the postglenoid foramen, and ventrally with the middle lacerate foramen; **zn,** zygomatic notch; **zp,** zygomatic plate.
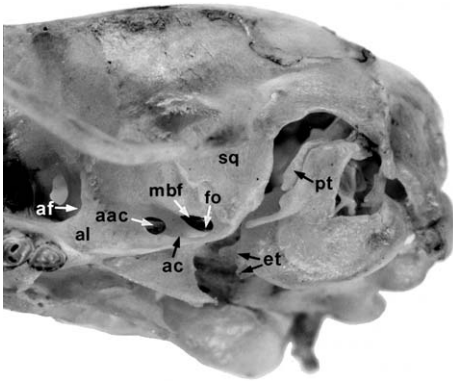
Fig. 9. Lateral view of the same specimen of *Bunomys chrysocomus* depicted in figure 8 showing details of the alisphenoid region. No strut of alisphenoid bone conceals the alisphenoid canal (**ac**) so the anterior opening of the alisphenoid canal (**aac**) is exposed, and the foramen ovale (**fo**) is confluent with the masticatory-buccinator foramen (**mbf**), the configuration common to all species of *Bunomys*. Also shown is the narrow periotic (**pt**), the short bony eustachian tube (**et**), the anterior alar fissure (**af**), squamosal (**sq**) and alisphenoid (**al**).

region (but never wide enough to form narrow shelves) and finally on to the braincase to form low temporal ridges. The braincase is otherwise smooth; it is also deep and either oval or squarish from a dorsal perspective. A triangular portion of the parietal drops below the dorsolateral margin of the braincase almost to the top of the zygomatic root; this projection and the squamosal form the wall of the braincase. The inner walls of the braincase are smooth, without squamosal-alisphenoid grooves. Depending on the species, sides of the braincase are generally vertical or nearly so from the temporal beading to squamosal roots of the zygomatic arches. The occipital region is moderately deep and roofed by the interparietal in the middle and dorsal segment of the exoccipital on either side. The boundary between squamosal and exoccipital is marked by low or moderately prominent lamboidal ridges. Posterior wall of the occiput is either vertical or gently convex (in lateral view) and either slightly overhangs the occipital condyles or is even with them, depending on the species. The squamosal above each auditory (ectotympanic) capsule and just anterior to

the lamboidal ridge is complete (not penetrated by a subsquamosal foramen).

The incisive foramina are long (58% to 73% of diastemal length), narrow or moderately wide, and their posterior borders are located anterior to the first molars. Except for a pair of shallow or moderately deep grooves, the bony palate is smooth; its posterior margin is even with backs of the third molars in some specimens, but projects slightly past the molars in others. A pair of posterior palatine foramina penetrates the palate at the maxillopalatine suture opposite the anterolingual root of each third molar. The maxillary molar rows diverge slightly toward back of the bony palate. Dorsolateral walls of the broad mesopterygoid fossa are perforated by two short and narrow slits (sphenopalatine vacuities) that expose the medial borders of the presphenoid and basisphenoid. The pterygoid plates adjacent to the mesopterygoid fossa are slightly or moderately excavated and each is pierced by a large or small sphenopterygoid vacuity. The posterolateral and posterior edges of each plate converge behind the foramen ovale to form a wide and smoothly rounded ridge, which defines the anterolateral border of the spacious medial lacerate foramen that separates the pterygoid plate from the ectotympanic bullar capsule. Just medial to this pterygoid ridge is a deep groove for the infraorbital branch of the stapedial artery. The point where the artery leaves the groove and passes to the dorsal surface of the pterygoid plate defines the posterior opening of the alisphenoid canal.

Each ectotympanic bulla (= auditory or bullar capsule) is slightly inflated, and bears a short bony eustachian tube. The medial sagittal plane of each bullar capsule is oriented ventromedially, so it appears to rest on the basicranium and project toward the midline rather than more nearly vertical, and the capsule does not cover the entire surface of the enclosed periotic bone, leaving exposed a posteromedial segment and a narrow flange extending forward between ectotympanic and basioccipital. The carotid canal is bounded by the periotic and adjacent ectotympanic. All specimens of each species possess a large stapedial foramen penetrating the crevice (the petromastoid fissure) between the bullar

capsule and the periotic. A spacious middle lacerate foramen separates the bullar capsule from the posterior margin of the pterygoid plate.

In lateral view, a flange of periotic is exposed along the anterodorsal margin of the bullar capsule. The capsule and periotic are separated from most of the squamosal by a broad postglenoid foramen that is confluent with a spacious ventral middle lacerate foramen. The mastoid portion of the periotic is slightly inflated, its outer wall complete.

Within the orbit the ethmoid foramen is small and the optic foramen moderately large. Orbitosphenoid, alisphenoid, and frontal bones join to form a solid section of the braincase wall, unbroken by a sphenofrontal foramen. Sphenopalatine and dorsal palatine foramina are separate, a pattern similar to that found in species of *Rattus* (Musser, 1982: 22). In the alisphenoid region posterior to the orbit (seen in lateral view), a bony alisphenoid strut is not present, resulting in coalescence of foramen ovale accessorius and masticatory-buccinator foramina. Exposed to view is the anterior opening of the alisphenoid canal, the open canal itself, and the foramen ovale.

All specimens of *Bunomys* possess a carotid arterial plan that is derived for muroid rodents in general but primitive for members of subfamily Murinae (char. state 2 of Carleton, 1980; pattern 2 described by Voss, 1988; conformation diagrammed for *Oligoryzomys* by Carleton and Musser, 1989). In this pattern, no sphenofrontal foramen penetrates the bony 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; but there is a large stapedial foramen in the petromastoid fissure, and a deep groove extending from the middle lacerate foramen to the foramen ovale on the ventral posterolateral surface of each pterygoid plate. This disposition of foramina and grooves indicates that the stapedial artery branches from the common carotid, enters the periotic region through a large stapedial foramen, the infraorbital branch of the stapedial artery exits the pteriotic through

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

Each dentary is somewhat elongate, particularly the portion between incisor and anterior margin of the first molar (diastema), and overall either moderately robust or gracile. The delicate coronoid process projects dorsally to height of the elongate condyloid (articular) process; the sigmoid notch is deep and the angular notch (outline of posterior dentary margin between articular and angular processes) is deep and broadly concave. Capsular projection of the lower incisor is indistinct in most specimens but forms a low bulge in others, and generally teminates at a level below the coronoid process. Masseteric ridges on the lateral surface of each dentary are low.

Teeth

The ungrooved enamel of upper and lower incisors is orange in all species of *Bunomys*; lower incisors are slightly paler. Upper incisors emerge from the rostrum at a right angle or nearly so (orthodont in form) in some specimens, or curve slightly caudad (opisthodont in configuration) in others (see Thomas, 1919, for definitions of these incisor configurations). Each lower incisor is awl shaped—the ends are sharper in some specimens—with elongate wear (occlusal) facets.

Molars of *Bunomys* have multiple roots. The alveolar patterns illustrated for *B. prolatus* in figure 10 are common to all the species. Five roots anchor each first upper
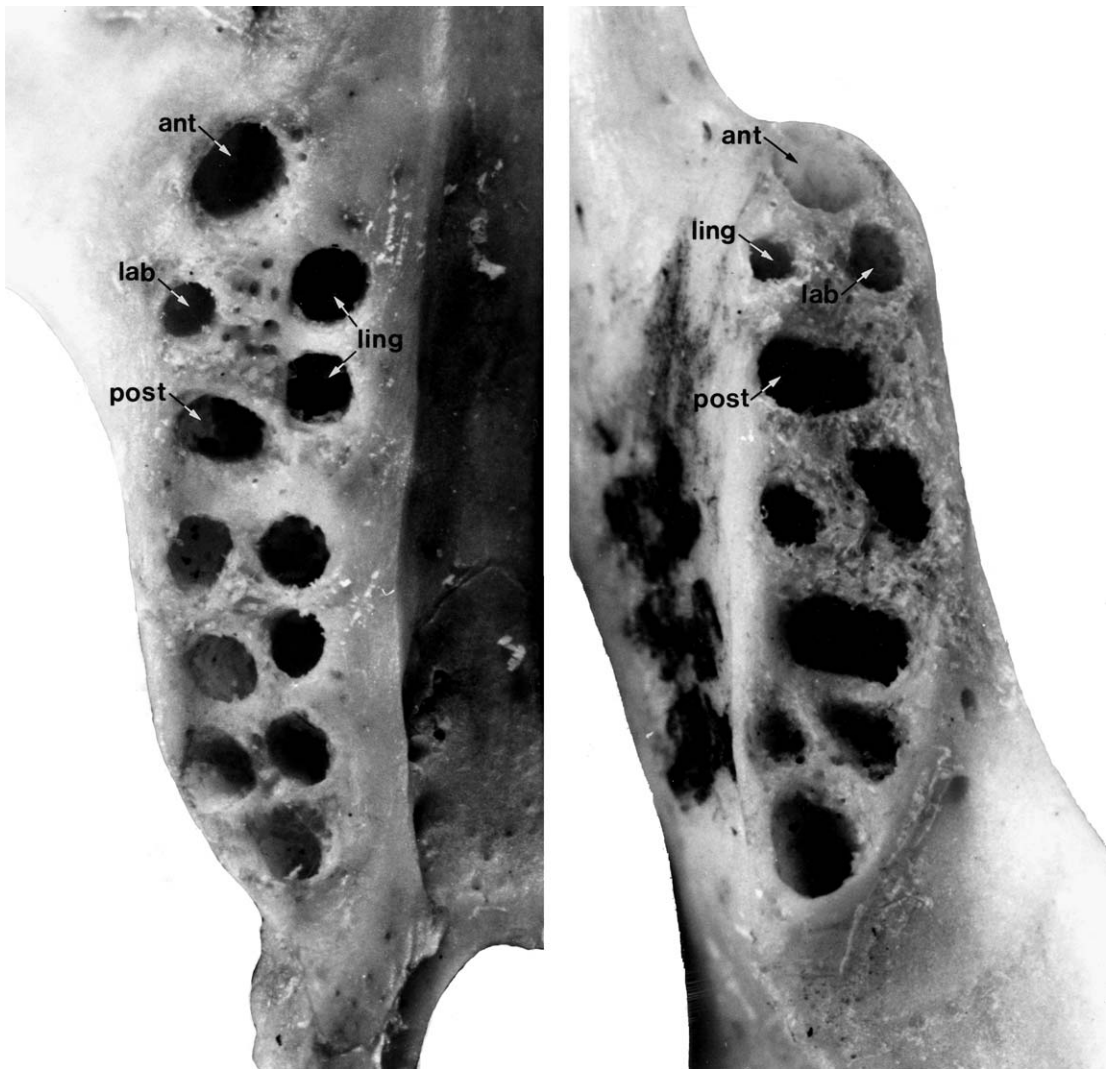
Fig. 10. Views of alveoli for right molar roots in *Bunomys prolatus* (AMNH 265076). **Left**, ventral view of maxillary alveoli (number of sockets per molar is, from top to bottom, 5, 4, and 3, respectively). **Right**, dorsal view of mandibular alveoli (number of sockets per molar is, from top to bottom, 4, 3, and 3, respectively). Abbreviations: **ant**, alveolus for anterior root; **lab**, labial socket; **ling**, lingual; **post**, posterior. ×12. These alveolar patterns are common to all species of *Bunomys*.

molar: a large anterior, two smaller lingual (that are fused to form a large single root in some specimens of two species), a large posterolabial holdfast, and a small labial. Four roots of about equal size are under the second upper molar (the two lingual roots are fused to form a single holdfast in a few specimens). Two anterior roots of medium size and a large posterior one hold each third upper molar in place. There are four roots beneath the first lower molar and three beneath the second molar as well as the third. The anterior root on the first molar is large and sturdy, the labial and lingual roots are small, and the posterior anchor is thick and wide, slightly narrower than the breadth of the tooth. A similar wide and chunky posterior root and two smaller, round anterior holdfasts anchor the second molar. Two anterior roots and a single posterior
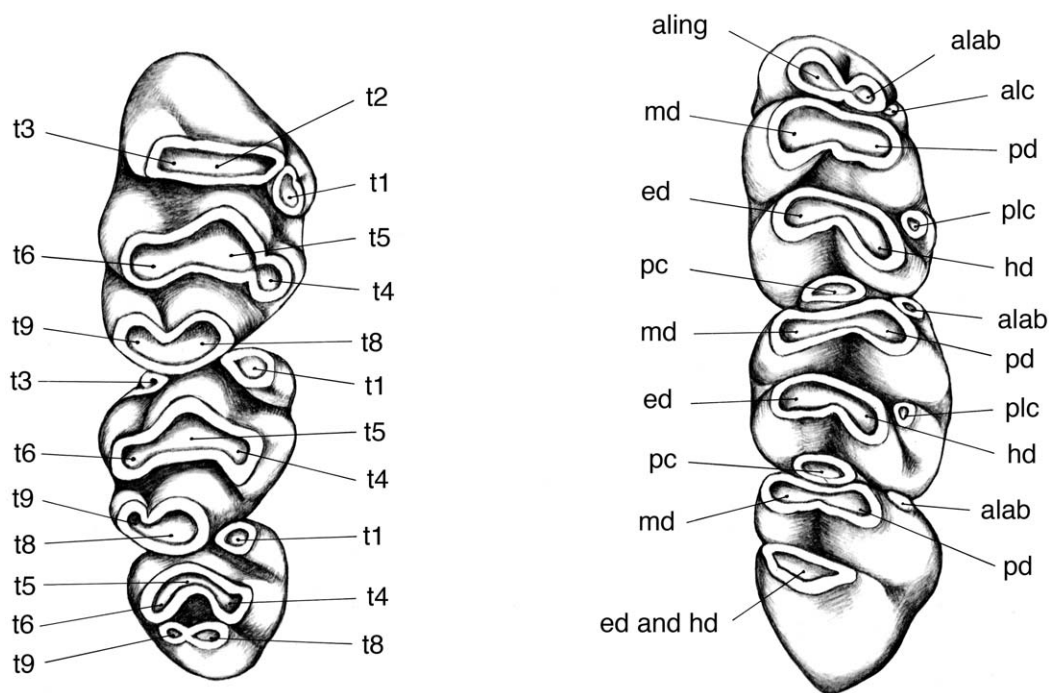
Fig. 11. Diagram of right maxillary (left) and mandibular (right) molar rows of *Bunomys chrysocomus* illustrating structural terms. Maxillary molars: cusps are numbered according to Miller's (1912) scheme and referred to in the text with the prefix "t." Mandibular molars (nomenclature is adapted from van de Weerd, 1976: 44): **alab**, anterolabial cusp; **aling**, anterolingual cusp; **alc**, anterior labial cusplet; **ed**, entoconid; **hd**, hypoconid; **md**, metaconid; **pc**, posterior cingulum (also identified as the talonid or Z [= hypoconulid] cusp by Misonne, 1969: 38); **pd**, protoconid; **plc**, posterior labial cusplet. See Misonne (1969) for a different terminology applied to cusps and cusplets in murines.

anchor project from beneath each third molar.

Molar rows are moderately long relative to size of skull (16%–18% of occipitonasal length). Molars are brachydont and grade in size within each row: the first is the largest, the third the smallest, which is the usual configuration observed in most species of murine rodents (Carleton and Musser, 1984). And like many murines, the cusp rows incline caudad, so that within each upper row the first molar overlaps the second and the second leans slightly against the third; the third molar in each mandibular row inclines against the second and that tooth slightly overlaps the first. In most of the teeth, the rows of cusps are moderately close to one another, rather than being widely separated; the former is usually associated with inclined rows of cusps, the latter with erect cusps.

Relatively simple occlusal patterns characterize upper (maxillary) and lower (mandibular) molars (figs. 12, 40, 41, 61, 74, 75, 87, 88). The uncomplex patterns of the maxillary molars reflect several conditions. First, cusp t3 (the anterolabial cusp) of each first upper molar is fused with the central cusp t2 to such a degree that the two form a single structure (outlines of each cusp remain in some specimens but are lost in most others); the front row of cusps takes the form of a simple bowed or tranverse lamina with a caudally directed large lingual projection representing cusp t1. Cusps in each of the other rows on all the upper molars are also broadly coalesced, which imparts to the occlusal plane of adults a serial pattern of chewing surfaces that are laminar, gently arcuate, or chevron shaped. Second, there is no enamel ridge or cusp (cusp t7) on the lingual margin
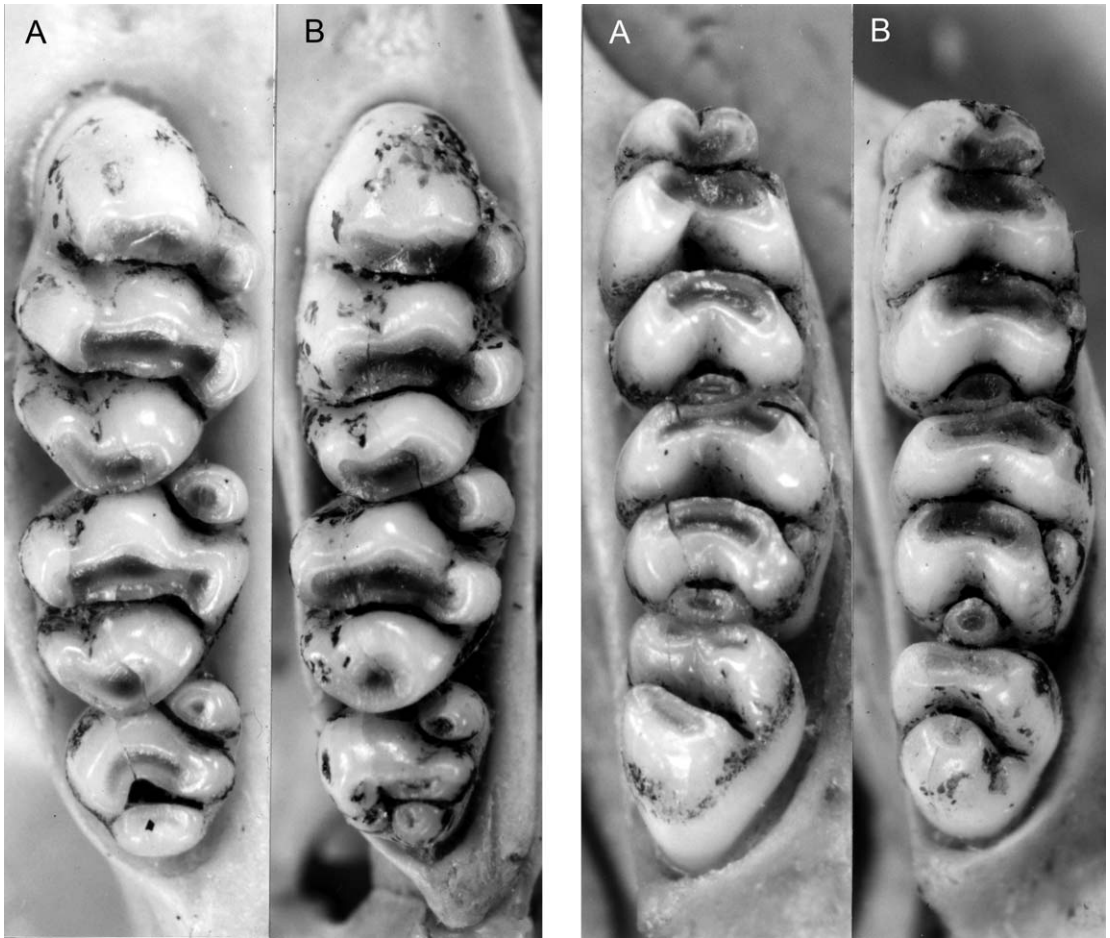
Fig. 12.   Occlusal views of right maxillary (left pair) and mandibular (right pair) molar rows from *Bunomys chrysocomus* (**A**, AMNH 224726; CLM1–3 and clm1–3 = 6.0 mm) and *B. fratrorum* (**B**, USNM 217644; CLM1–3 = 7.5 mm; clm1–3 = 7.7 mm). See figure 11 for names of cusps and cusplets.

of each molar between cusps t4 and t8 (a cusp t7 is a prominent feature of the occlusal surface in certain genera of murines—*Lenothrix*, for example; see Musser and Newcomb, 1983). Although close to one another, cusps t4 and t8 do not coalesce along their lingual margins until they are worn to the cingulum. Third, cusp t3 is absent from the anterolabial margin of each second molar in either all (*B. prolatus*) or the majority of specimens representing seven of the eight species (the cusp occurs at a higher frequency in *B. coelestis*, *B. penitus*, and the sample of *B. andrewsi* from the southwestern peninsula), and is not a part of the anterolabial margin of each third molar in the majority of

specimens of all eight species (table 10). Even when present, cusp t3 is often represented by only a slight vertical enamel projection from the lingual border that hardly modifies the simple rounded form of the tooth outline (fig. 41) or a very small inconspicuous pimplelike structure (fig. 75). Fourth, an element adding structural complexity to the second and third molars in some murine genera but not present in specimens of *Bunomys* is a posterior cingulum. This structure springs from the back of cusp t8 either in the form of a ridge, a triangular projection, or a large cusp projecting labially to form a significant portion of the occlusal surface (as exemplified by the occlusal pattern of *Lenothrix*; see

TABLE 10

Presence (+) or Absence (−) of Cusp t3 on Second (M2) and Third (M3) Maxillary Molars in Samples from Species of *Bunomys*

Number of individuals with or without the cusp is expressed as a percentage of the entire sample of a species; total number of specimens surveyed is in parentheses. Data are derived from juveniles, young adults, and adults with molars showing moderate wear. Geographic origins of samples are identified in footnotes.

	M2		M3	
	+	−	+	−
B. chrysocomus[a]	17 (33)	83 (164)	5 (10)	95 (187)
B. coelestis[b]	89 (25)	11 (3)	18 (6)	82 (23)
B. prolatus[c]	—	100 (4)	—	100 (4)
B. torajae[d]	50 (1)	50 (1)	—	100 (2)
B. fratrorum[e]	11 (7)	89 (67)	9 (6)	91 (68)
B. andrewsi				
Pulau Buton	—	100 (1)	—	100 (1)
Sulawesi's core + southeast peninsula[f]	17 (12)	83 (58)	4 (3)	96 (67)
Southwest peninsula[g]	78 (14)	22 (4)	17 (3)	83 (15)
B. penitus[h]	62 (120)	38 (73)	5 (10)	95 (183)
B. karokophilus[i]	33 (6)	67 (12)	22 (4)	78 (14)

[a] West-central mountain block (Sungai Oha Kecil, Sungai Sadaunta, Sungai Pormina, Tomado, Sungai Tokararu, and Gunung Kanino).

[b] Southwestern peninsula (Gunung Lompobatang).

[c] Eastern peninsula (Gunung Tambusisi).

[d] West-central mountain block (Gunung Gandangdewata).

[e] Northern peninsula (Temboan).

[f] Sulawesi's core (Kuala Navusu, Pinedapa, Gunung Balease, Puro-Sungai Miu region, Mamasa area) and southeastern peninsula (Desa Lawaki Jaya, Wawo, Masembo).

[g] Lombasang

[h] West-central mountain block (Gunung Kanino and Gunung Nokilalaki).

[i] West-central mountain block (Sungai Sadaunta, Tomado, and Sungai Tokararu).

Musser and Newcomb, 1983). Fifth, the anterior cingular face on each first upper molar is smooth in all specimens of *Bunomys*, without a shelflike ridge or small cusp (a cingular ridge, often bearing a small cusp, is a usual component of the first molar in *Rattus hoffmanni*, for example; Musser and Holden, 1991: 348). Finally, cusp rows stand free, unconnected by labial or lingual enamel bridges (stephanodont crests as described by Misonne, 1969: 55).

The occlusal topography of each mandibular toothrow consists primarily of chunky straight or slightly bowed laminae, each representing the complete merging of two cusps. A large posterior cingulum, circular or elliptical in cross section, sits at the back of each first and second molar. Located at the front of the first molar is a chunky anteroconid composed of large anterolabial and anterolingual cusps (I did not see an anterocentral cusp on any specimen of *Bunomys*)

that have merged to form a large oblong lamina (without discernable cusp boundaries in some specimens, but clearly formed from two cusps in others) either slightly or much narrower than the lamina behind it. Various combinations of anterior and posterior labial cusplets along with an anterolabial cusp on second and third molars of some specimens comprise minor components of the occlusal surface (table 11).

CHROMOSOMES: Metaphase chromosomal spreads are available from *Bunomys chrysocomus*, *B. andrewsi*, *B. penitus*, and *B. karokophilus,* n. sp. (table 12); no karyotypes have been published for *B. coelestis*, *B. prolatus*, *B. torajae,* n. sp., or *B. fratrorum*.

Bunomys chrysocomus ($N = 33$) and *B. andrewsi* ($N = 5$) express the same chromosomal complement: $2N = 42$, FNa = 56, FNt = 58 (fig. 13). The autosomal set consists of one pair of large subtelocentrics, 11 pairs of acrocentrics that range from a large first pair

TABLE 11

Presence (+) or Absence (−) of Anterolabial Cusps (alab), Anterior Labial Cusplets (alc), and Posterior Labial Cusplets (plc) on Mandibular Molars (m1–m3) in Species of *Bunomys*[a]

Number of individuals with or without a particular cusp or cusplet is expressed as a percentage of entire sample of each species; total number of specimens surveyed is in parentheses. Data are derived from juveniles, young adults, and adults with molars showing moderate wear.

| | m1 | | | | m2 | | | | m3[b] | |
| | alc | | plc | | alab | | plc | | alab | |
Species	+	−	+	−	+	−	+	−	+	−
B. chrysocomus	52 (62)	48 (58)	97 (116)	3 (4)	90 (108)	10 (12)	98 (117)	2 (3)	65 (78)	35 (42)
B. coelestis	—	100 (24)	96 (23)	4 (1)	100 (24)	—	92 (22)	8 (2)	25 (6)	75 (18)
B. prolatus	—	100 (4)	100 (4)	—	100 (4)	—	100 (4)	—	75 (3)	25 (1)
B. fratrorum	—	100 (58)	42 (27)	53 (31)	12 (7)	88 (51)	78 (45)	22 (13)	—	100 (58)
B. andrewsi	—	100 (76)	100 (99)	—	94 (71)	—	100 (76)	—	18 (12)	82 (54)
B. penitus	8 (11)	92 (130)	100 (141)	—	55 (77)	45 (64)	97 (136)	3 (5)	—	100 (141)
B. karokophilus	—	100 (11)	55 (6)	45 (5)	27 (3)	73 (8)	64 (7)	36 (4)	27 (3)	73 (8)

[a] Specimens examined are from the same localities indicated in the footnotes for table. The three specimens of *B. torajae* n. sp., are not included because their occlusal surfaces are too worn to determine presence or absence of anterolabial cusps and cusplets.

[b] The primary occlusal surface of each third molar consists of an anterior lamina formed from a metaconid and protoconid, and an oblong posterior lamina that is without cusp boundaries in most specimens (see figures 11 and 12) except for a few very young juveniles in which the lamina is clearly formed from a fusion of the entoconid and hypoconid. An anterolabial cusp is detectable on many specimens, even those exhibiting more than moderate molar wear, and I record its frequency of occurrence here. I could detect a posterior labial cusplet on the labial margin of the posterior lamina in only 13 of the 422 specimens (3%) surveyed representing all species, but have not listed the frequencies for each species in the table.

to succeeding pairs of smaller chromosomes in a graded series, and seven pairs of small metacentrics. The presumed X chromosome of the males (the largest chromosome of the heteromorphic pair) is biarmed and the small Y chromosome is acrocentric.

Each female has a pair of large acrocentrics, which I assume to be the X chromosomes; the remaining chromosomes in the karyotype are similar to those of the males, both in number of kinds and gradations in size.

TABLE 12

Summary of Karyotypic Data for Samples from Four Species of *Bunomys*[a]

See figures 13–15.

| | Autosomes | | | | | Sex | | | | |
Species	2N	M	SM	ST	A	X	Y	FNa	FNt	*N*
B. chrysocomus ♂, ♀	42	7	0	1	12	A	A	56	58	33
B. andrewsi ♂, ♀	42	7	0	1	12	A	A	56	58	5
B. penitus ♀	42	7	0	2	11	A	A	58	60	5
B. penitus ♂	42	7	0	2	11	SM	A	58	61	4
B. karokophilus ♂	42	6	0	2	12	SM	SM	56	60	1

[a] Voucher specimens. *B. chrysocomus*: AMNH 223039, 223041, 223042, 223050, 223053–055, 223067, 223068, 223076–078, 223082–084, 223090, 223292, 223308, 223476, 223477, 223568, 223570, 224140, 224142, 224143, 224160, 224162–64, 224166, 224762, 224773, 226926. *B. andrewsi*: AMNH 225652, 225656, 225657, 225665, 225666. *B. penitus*: AMNH 223806, 223822, 223917, 223921, 223922, 223924, 223926, 223927, 223955. *B. karokophilus*: AMNH 225041.

Abbreviations. A = acrocentric; FNa = number of autosomal arms; FNt = total number of chromosome arms (including XX for females and XY for males); M = metacentric; SM = submetacentric; ST = subtelocentric. *N* = number of specimens surveyed.
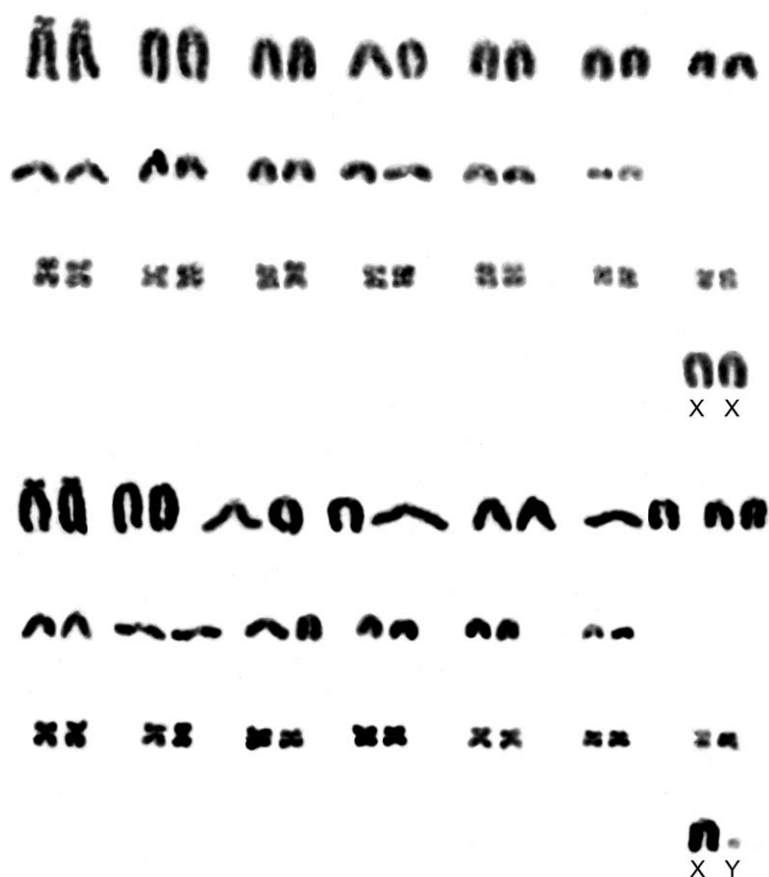
Fig. 13.   Karyotypes from a female (upper set; AMNH 223077) and a male (lower set; AMNH 223292) *Bunomys chrysocomus*: 2N = 42; FNa = 56, FNt =58. The gross chromosomal complement of *B. andrewsi* (not illustrated) is similar to this karyotype. Additional information is provided in table 12 and the text.

Bunomys penitus ($N = 9$) has a diploid number of 42, an FNa of 58 for both sexes, FNt of 60 for females and 61 for males (fig. 14). The autosomal set consists of two pairs of large subtelocentrics (only one pair in *B. chrysocomus* and *B. andrewsi*), 11 pairs of acrocentrics, and seven pairs of small metacentrics. As in *B. chrysocomus*, the presumed X chromosome of the males (the largest chromosome of the heteromorphic pair) and the small Y chromosome are acrocentrics. Each female has a pair of large acrocentrics, which I have identified as the X chromosomes; the remaining chromosomes in the karyotype are similar to those of the males.

The single male karyotyped of the new species, *B. karokophilus*, has a diploid number of 42, an autosomal fundamental number of 56, and total fundamental number of 60 (fig. 15). The autosomal set resembles that of *B. penitus*, except it has one additional acrocentric and one less metacentric. Unlike *B. chrysocomus*, *B. andrewsi*, and *B. penitus*, the presumed X chromosome of the male *B. karokophilus*, n. sp. (the largest chromosome of the heteromorphic pair), and the small Y chromosome are submetacentrics. I do not have the karyotype of a female.

NATURAL HISTORY: Based on my trapping experience, *B. chrysocomus*, *B. andrewsi*, *B. penitus*, and *B. karokophilus*, n. sp., are terrestrial and nocturnal. There is nothing in the morphology of *B. coelestis*, *B. fratrorum*, *B. prolatus*, and *B. torajae*, examples of which I have not collected, to indicate that these
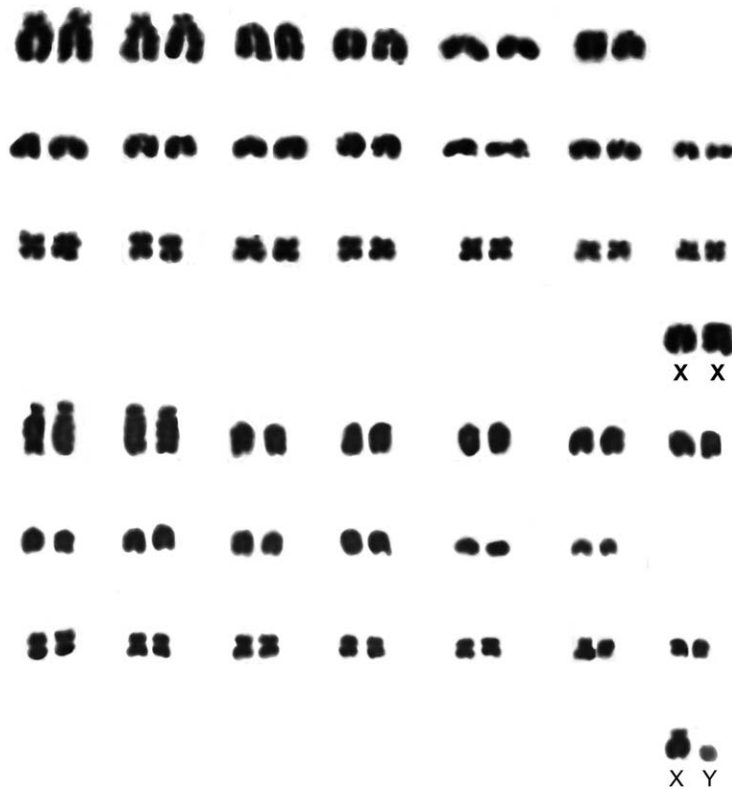
Fig. 14.   Karyotypes from a female (upper set: AMNH 223927) and a male (lower set; AMNH 223924) *Bunomys penitus*: 2N = 42; FNa = 58 for both sexes, FNt = 60 for the female and 61 for the male. Two large subtelocentric pairs are present instead of one, which is the typical number in the karyotypes of *B. chrysocomus* and *B. andrewsi* (fig. 13). Additional information is provided in table 12 and the text.

species are not also terrestrial and active during the night rather than during the day. Like other murines endemic to Sulawesi, the species of *Bunomys* live in forests. Most of my samples were collected from habitats in primary forest formations but a few were obtained in second-growth forest and coffee groves shaded by old-growth canopy and emergent trees; a few were collected near villages. Judged by recent samples obtained by other collectors, *Bunomys andrewsi* is common in second-growth forests. The species I encountered were usually encountered in wet and shaded habitats in tropical lowland evergreen rainforest formations and nearly everywhere in montane forest where the habitats remain cool and wet for most of the year. One species, *B. karokophilus,* n. sp., may be restricted to wet and shaded streamside sites.

Composition of diets is available for five of the eight species. Fruit, invertebrates, and small vertebrates comprise the diet of *B. chrysocomus*, *B. fratrorum*, and *B. andrewsi*, but *B. chrysocomus* and *B. andrewsi* are especially fond of invertebrates (insects, arachnids, centipedes, snails, and oligochaete earthworms). *Bunomys penitus* also consumes fruit and invertebrates as well as a variety of different fungi in its diet. *Bunomys karokophilus,* n. sp., is a fungal specialist, and its primary dietary component is the ear fungus *Auricularia delicata*. Diets of *B. coelestis*, *B. prolatus*, and *B. torajae* have yet to be documented. A summary of the different foods consumed, derived from examining contents of stomachs and survey of food accepted or rejected by captive rats, is presented in table 13. Details are provided in the individual accounts of species.

Fig. 15.   Karyotype from a male (AMNH 225041) *Bunomys karokophilus*, n. sp.: 2N = 42; FNa = 56, FNt = 60. The presumptive sex chromosomes are submetacentrics, which contrasts with the acrocentrics characterizing the other three species, and six pairs of metacentrics are present instead of seven (figs. 13, 14). Additional information is provided in table 12 and the text.

One or two young in litters are usual for those species for which this information is available—*B. chrysocomus*, *B. andrewsi*, *B. penitus*, and *B. karokophilus,* n. sp.

ECTOPARASITES, PSEUDOSCORPIONS, AND ENDOPARASITES: Sucking lice (*Hoplopleura*), fleas (Leptopsyllidae, Pygiopsyllidae, and Ceratophyllidae), ticks (Ixodidae), chiggers (Trombiculidae), and mites (Laelapidae) have been recorded as parasitizing seven of the eight species of *Bunomys* (no records from *B. torajae*). The combination of ectoparasites associated with the different hosts is summarized in table 14. Noted also in that table are pseudoscorpions (Chernetidae) found in the fur of *Bunomys*. "Pseudoscorpions in rodent fur are commensals that prey on ectoparasitic mites, lice and fleas. Also, large numbers of tiny phoretic (non-feeding) deutonymphal stages of histiostomatid mites [phoretomorphs] have been recorded attached to the posterior body (idiosoma) of many of the large laelapid mites removed from Sulawesi rodents (Whitaker and Durden 1987). "Combined, the ectoparasites, pseudoscorpions, and phoretomorphs can be called *epifauna* or *epifaunistic arthropods*" (L. Durden, in litt., 2013; see also Muchmore, 1972: 431; Eric Rickart kindly reminded me that pseudoscorpions are predators and not ectoparasites).

Table 14 also references the few endoparasites recovered from specimens of *Bunomys*: human blood fluke, liver fluke, and nematodes.

Details and published sources of the ectoparasite and endoparasite records as well as those of the pseudoscorpions are provided in the account of each species.

SYNONYMS: *Frateromys* (Sody, 1941), with *Mus fratrorum* as the type species, is the only generic synonym. More than one scientific name attaches to samples of *Bunomys chrysocomus*, *B. andrewsi,* and *B. penitus*, and reasons for their specific allocations are documented in the appropriate accounts of these three species. *Bunomys coelestis*, *B. prolatus*, and *B. fratrorum* have never been encumbered with synonyms; *B. karokophilus,* n. sp., and *B. torajae,* n. sp., are virginal.

SUBFOSSILS: Fragments of *Bunomys chrysocomus* and *B. andrewsi* excavated from cave deposits at the southern end of the southwestern peninsula constitute the only subfossils I have personally studied that can be attributed to *Bunomys*; all are from Holocene deposits. Some samples come from Ulu Leang I, a cave in the Maros region on the coastal plain of the southwestern peninsula where the sediments were dated as between about 9500 and 3500 B.P. Others are from a shallow deposit forming the floor of Batu Edjaja II, a small rock shelter (also at the tip of the southwestern peninsula) where age of the sediments range from about 4300 B.P. to modern (Bulbeck, 2004). The pieces in both samples are partially fossilized, that is, the organic materials have not been completely replaced by inorganic minerals, and I refer to them as subfossils. The descriptions of these fragments and data supporting their identifications are provided in the appropriate accounts of species.

Additional mammalian samples of subfossils collected on the southwestern peninsula exist and may contain examples of *Bunomys*. Ian Glover, who gave me the material referred to above, had earlier excavated more than 1000 mammalian cranial and postcranial fragments from Ulu Leang I and turned them over to the late A.T. Clason who tabulated 65 pieces representing murid rodents (Clason, 1976: 66) but did not identify them beyond family category—I have not seen the material.

Subfossil *Bunomys* have been collected from a cave (Gua Mo O'Hono) on the southeastern peninsula in the northern lowlands of the southeastern peninsula, north of the lakes district (Danau Matana, Mahalona, and Towuti). I have been helping Philip Piper and Sue O'Connor identify the excavated murid remains and those determinations will eventually be published elsewhere; Philip generously allowed me to list the species identified so far in table 81.

THE SPECIES

Seventy-two years ago, Tate (1936: 551–553) brought together a collection of Sulawesian species, proclaimed they formed a ''*Rattus chrysocomus* Group'' and arranged the taxa into two subgroups: ''Large-toothed rats'' consisting of *R. penitus penitus, R. penitus sericatus, R. penitus inferior, R. penitus heinrichi, R. penitus adspersus, R. andrewsi*, and ''Possibly *R. fratrorum*''; and ''Small-toothed rats'' containing *R. nigellus, R. rallus, R. brevimolaris*, and ''Possibly *R. chrysocomus*.'' He added: ''There is little doubt that *Bunomys* … is derived directly from the *chrysocomus* group. It differs from that group only by the apparently fossorial adaptation of the claws …, for enlargement of the muzzle can be seen also in old specimens of the *chrysocomus* group.'' At the time, Tate recognized the montane *coelestis* with its elongate claws and protracted muzzle as the only species of *Bunomys*, with *coelestis* confined to Gunung Lompobatang in the southwestern Sulawesian peninsula and the subspecies *koka* endemic to Pengunungan Mengkoka on the southeastern arm of the island.

After studying qualitative characteristics of specimens, along with results from univariate and multivariate analyses of cranial and dental variables, I can also separate the species into two clusters that are generally concordant with Tate's format (table 4). *Bunomys chrysocomus*, *B. coelestis* (but excluding *koka*), *B. prolatus*, and *B. torajae,* n. sp. (the latter two unknown to Tate), form a small-toothed assemblage, which for expository purposes I label the *B. chrysocomus* group. *Bunomys fratrorum*, *B. andrewsi*, *B. penitus*, and *B. karokophilus,* n. sp. (also unknown to Tate), comprise a large-toothed cluster I refer informally to as the *B. fratrorum* group. As Tate perceived, members of the *B. chrysocomus* cluster have small molars (CLM1–3 = 6.1–6.5 mm and BM1 = 2.0–2.3 mm are the ranges of univariate means for 261 specimens; see table 31) compared with the larger molars typical of species in the *B. fratrorum* assemblage (CLM1–3 = 7.0–7.8 mm and BM1 = 2.3–2.5 mm are the ranges of univariate means for 400 specimens; see table 42).

Paralleling the difference in molar dimensions is a contrast in body size between the two groups. Specimens in most samples of the *B. fratrorum* group are physically larger animals, as can be appreciated by the univariate means for external measurements and weights for the two groups summarized in tables 19 and 41, and for cranial and dental measurements in tables 15, 31, and 42.

The difference between the two clusters is also captured in the images of skulls portrayed in figures 16 and 17 where the smaller and gracile skull of *B. chrysocomus*, the first species to be described in the *chrysocomus* group is contrasted with the much larger and robust skull of *B. fratrorum*, the namesake and first described species of the *fratrorum* group.

The univariate mensural differences and visual cranial and dental dissimilarities are reinforced by results from multivariate analyses. The distribution of specimen scores for all population samples of *B. chrysocomus* and *B. fratrorum* projected onto first and second principal components form two discrete clusters representing the small-bodied *B. chrysocomus* to the left along the first axis of the scatter plot, and the larger-bodied *B. fratrorum* to the right (fig. 18). Size is the

TABLE 13
Summary of Foods Eaten by Species of *Bunomys*
Determined by surveying contents of stomachs from preserved animals, and recording the foods accepted or rejected by captive rats.

Species	Fungi	Fruit	Insects and other arthropods	Other invertebrates	Vertebrates
B. chrysocomus	—	Figs (from several species of strangler and understory trees); fruit from the palm, *Pigafetta filaris*; native bananas (soft pulp); ginger (pulp only); a narrow range of species recorded by unidentified fruit pulp, seeds, and rind found in stomachs	Moths, macrolepidopteran caterpillars, orthopterans (cicadids, katydids, grasshoppers, crickets), preying mantises, cockroaches, rhinotermitid termites, several kinds of adult and larval beetles (including legless and cursorial beetle larvae), margarodid scale insects, ants, wasps; spiders; geophilomorph centipedes	Snails, earthworms (oligochaetes)	Small frogs and lizards
B. coelestis	?	?	?	?	?
B. prolatus	?	?	?	?	?
B. torajae	?	?	?	?	?
B. fratrorum (USNM 217084)	?	Small unidentified fruit	Adult beetle	Earthworms	?
B. andrewsi	—	Figs (from several species of strangler trees, canopy nonstrangler species, and understory trees); fruit from understory palms (*Pinanga* sp.); fruit from the trees *Sandoricum* sp., *Sapium* sp., *Palaquium* sp., and another member of Sapotaceae; large seeds from the tree *Hydnocarpus sumatrana*, and fruit from the vine *Gnetum cuspidatum*; pulp from several unidentified fruits found in stomachs	Moths, orthopterans (mole and camel crickets, grasshoppers), praying mantises, rhinotermitid termites, adult and larval beetles (carabids, cerambycids, and other families), adult ants, ant pupal cases, a variety of other unidentified small insect remains found in stomachs; geophilomorph centipedes	Snails, earthworms	Lizards (small-bodied geckos)

TABLE 13
(*Continued*)

Species	Fungi	Fruit	Insects and other arthropods	Other invertebrates	Vertebrates
B. penitus	Fungi growing on decaying wood: ear fungi in Order Auriculariales (the white *Auricularia fuscosuccinea* and purplish *karoko A. delicata*; an unidentified large, dark brown jelly fungus, similar to *A. delicata* but tougher); Order Tremellales (a small yellow jelly fungus); Order Agaricales (*Panellus pusillus*, growing on stems of decaying rattan); at least 7 kinds of cap-and-stem gilled fungi growing on the forest floor	Small unidentified seeds and stems in some stomachs; fruit mash found in stomachs; seed and pulp of *Lithocarpus* sp. (acorns) consumed by some rats but rejected by others	Moths, macrolepidopteran caterpillars, large adult and larval carabid beetles, smaller beetles, cockroach nymphs; geophilomorph centipedes	Snails, earthworms	Flesh from rodent carcasses
B. karokophilus	The purplish *karoko, Auricularia delicata*, found in most stomachs to the exclusion of any other items; bits of different kinds of unidentified shelf fungi found in a very few stomachs	Small fruit of understory fig (*Ficus minahassae*), fruit of different fig found in stomach; hard orange seeds from an unidentified fruit found in two stomachs	Bits of unidentified insect found in one stomach, small adult beetle in another; an occasional ant; remnants of large orthopteran in one stomach, cicadid eaten by captive, pieces of centipede in a stomach	Captive ate a snail (rejected the muscular foot); earthworms (eaten by captive, segments found in stomach of two other rats)	Captive ate half a small frog (1 inch long)

TABLE 14
Summary of Ectoparasite and Pseudoscorpion Records for Species of *Bunomys*[a]
(Published sources are referenced under Ectoparasites and Pseudoscorpions in the accounts of hosts.)

Host	Sucking lice: Anoplura (Hoplopleuridae, *Hoplopleura*)	Fleas: Siphonaptera (Leptopsyllidae, Pygiopsyllidae, Ceratophyllidae)	Acari: ticks (Ixodidae); chiggers (Trombiculidae); and mites (Atopomelidae, Laelapidae and Histiostomatidae)[c]	Pseudoscorpions Pseudoscorpionida (Chernetidae)
		Ectoparasites		
B. chrysocomus	*Hoplopleura chrysocomi*,[b] *Polyplax wallacei*	*Sigmactenus alticola pilosus, Stivalius franciscae, Musserella,* n. gen. (species #1 and #4), *Gymnomeropsylla bunomydis, Nestivalius sulawesiensis*	**Ticks:** *Amblyomma* sp., *Dermacentor atrosignatus, Dermacentor* sp., *Haemaphysalis psalistos, Haemaphysalis* sp.; **Chiggers:** *Walchiella oudemansi, Leptotrombidium deliense*; **Other Mites:** *Histiostoma* sp., *Laelaps* sp.	*Megachernes* sp.
B. coelestis	?	?	**Mite:** *Listrophoroides (Marquesania) cucullatus*	?
B. torajae	?	?	?	?
B. prolatus	—	*Sigmactenus alticola pilosus*	—	—
B. fratrorum	*Hoplopleura sembeli, Polyplax wallacei*	*Sigmactenus sulawesiensis, Sigmactenus alticola crassinavis, Musserella,* n. gen. (species #4), *Macrostylophora theresae, Nestivalius sulawesiensis*	**Ticks:** *Amblyomma* sp., *Dermacentor* sp., *Haemaphysalis hystricis, Haemaphysalis* sp.; **Chiggers:** *Schoengastia sulawesiensis, Walchiella oudemansi, Gahrliepia lupella, Leptotrombidium deliense*	—
B. andrewsi	*Hoplopleura* sp.[d]	—	**Ticks:** *Haemaphysalis* sp., *Dermacentor* sp. **Mites:** *Laelaps* "near *ornatus*," *Laelaps* "near *thamnomys*"	*Chiridiochernes platypalpus*[b]
B. penitus	—	*Sigmactenus sulawesiensis, Sigmactenus alticola pilosus, Stivalius franciscae, Musserella,* n. gen. (species #1), *Neopsylla musseri Macrostylophora* sp. *Dasypsyllus gallinulae klossi*	**Ticks:** *Rhipicephalus pilans*	*Megachernes* sp., *Chiridiochernes* sp.
B. karokophilus	—	*Sigmactenus alticola pilosus, Stivalius franciscae*	—	—

[a] Lance Durden wrote me (in litt., 2013) that "Pseudoscorpions in rodent fur are commensals that prey on ectoparasitic mites, lice and fleas. Large numbers of tiny phoretic (non-feeding) deutonymphal stages of histiostomatid mites [phoretomorphs] have been recorded attached to the posterior body (idiosoma) of many of the large laelapid mites removed from Sulawesi rodents. Combined, the ectoparasites, phoretomorphs, and pseudoscorpions can be called 'epifauna' or 'epifaunistic arthropods.'"

Bunomys chrysocomus, B. andrewsi, and *B. penitus* are also parasitized by trematode and/or nematode endoparasites, and these are documented and discussed in the accounts of species.

[b] Recorded only from the host.

[c] Larvae and/or nymphs of the ticks *Amblyomma* sp., *Haemaphysalis* sp., and *Dermacentor* sp. collected from Sulawesi mammals can be currently identified only to genus (Durden et al., 2008).

[d] A new species of *Hoplopleura* found so far only on *Bunomys andrewsi* is being described by Durden and Musser (MS.).

primary force dispersing the scores, as indicated by the positive and moderate to high correlations on that axis for nearly all variables (r = 0.21–0.97; table 16). Compared with *B. fratrorum*, the skull of *B. chrysocomus* is overall appreciably smaller with lesser internal dimensions and markedly smaller molars. At the same time, despite its overall smaller skull, *B.chrysocomus* has a relatively wider interorbit than *B. fratrorum*, as signified by the negative loading for interorbital breadth (−0.23).

A suite of proportional dissimilarities between the two species are depicted in a ratio diagram (fig. 19). Compared with the sample of *B. fratrorum*, that of *B. chrysocomus* has a wider interorbit relative to skull size (indexed by occipitonasal length and zygomatic breadth), narrower rostrum relative to its length; a wider braincase relative to its height and to overall size of the skull; narrower zygomatic plate but longer diastemal region, longer and wider bony palate relative to skull length; shorter and narrower incisive foramina relative to length of diastema; larger bullae relative to most other cranial dimensions and smaller molars relative to length of bony palate.

Results of discriminant-function analysis of cranial and dental variables in population samples from all the species of *Bunomys* are summarized in a scatter plot of individual specimen scores projected on first and second canonical variates (fig. 20) and a cluster diagram based on squared Mahalanobis distances (fig. 21). In the canonical-variate ordination, the four clumps of scores to the left of center identify samples in the *B. chrysocomus* group (*B. chrysocomus*, *B. coelestis*, *B. prolatus*, and *B. torajae,* n. sp.), the four groups to the right of center represent samples in the *B. fratrorum* group (*B. fratrorum*, *B. andrewsi*, *B. penitus*, and *B. karokophilus,* n. sp.). Nearly all loadings are positive on the first axis and correlations for most variables range from moderate to high (r = 0.46–0.96; table 17) signaling that size is primary in scattering the two primary groups of scores along the first canonical variate, a quantitative testament to the larger and blocky skulls possessed by members of the *B. fratrorum* group with their greater internal

dimensions compared with the smaller and elongate skulls typical of members in the *B. chrysocomus* group (tables 31 and 42). The highest loadings for any of the variables are those for length of molar row (0.96) and breadth of the first upper molar (0.92), which translates to a contrast mirroring Tate's (1936: 551–552) division of the species with which he was familiar into two groups based on molar robustness.

Along the second canonical variate, scores for *B. fratrorum* form a discrete cloud in the upper half of the scatter plot clearly separated from the clumps in the lower half. Position of the scores along with the positive or negative sign and magnitude of loadings (table 17) document the relatively longer skull of *B. fratrorum*, its more flared zygomatic arches, narrower interorbit, higher braincase, wider zygomatic plate, greater postpalatal length, and smaller bullae compared with all the other species of *Bunomys*. The location of scores denoting *B. karokophilus,* n. sp., relative to those symbolizing *B. chrysocomus*, *B. coelestis*, and *B. penitus* attests to the relatively narrow interorbital region, long postpalatal area, and small bullae in *B. karokophilus,* n. sp., proportions similarly held by *B. fratrorum.* At the bottom of the ordination lie scores for *B. prolatus* and *B. torajae,* n. sp., and their partially isolated position is stongly influenced by the relatively narrower breadth across their zygomatic arches (less flared), their wide interorbits, very narrow zygomatic plates, and shorter postpalatal regions compared with the other species.

The cluster diagram based on the squared Mahalanobis distances (fig. 21) describes a pattern of phenetic relationships among population samples that recognizes two primary groups of species, one consisting of *B. chrysocomus*, *B. coelestis*, *B. prolatus,* and *B. torajae,* n. sp., the other containing *B. fratrorum*, *B. andrewsi*, *B. penitus*, and *B. karokophilus,* n. sp. Within the former assemblage, *B. prolatus* and *B. torajae* are phenetically the most divergent; within the latter group, *B. penitus* and *B. andrewsi* form a subgroup with the cluster containing *B. fratrorum* and *B. karokophilus* joining it at a much greater Mahalanobis distance.
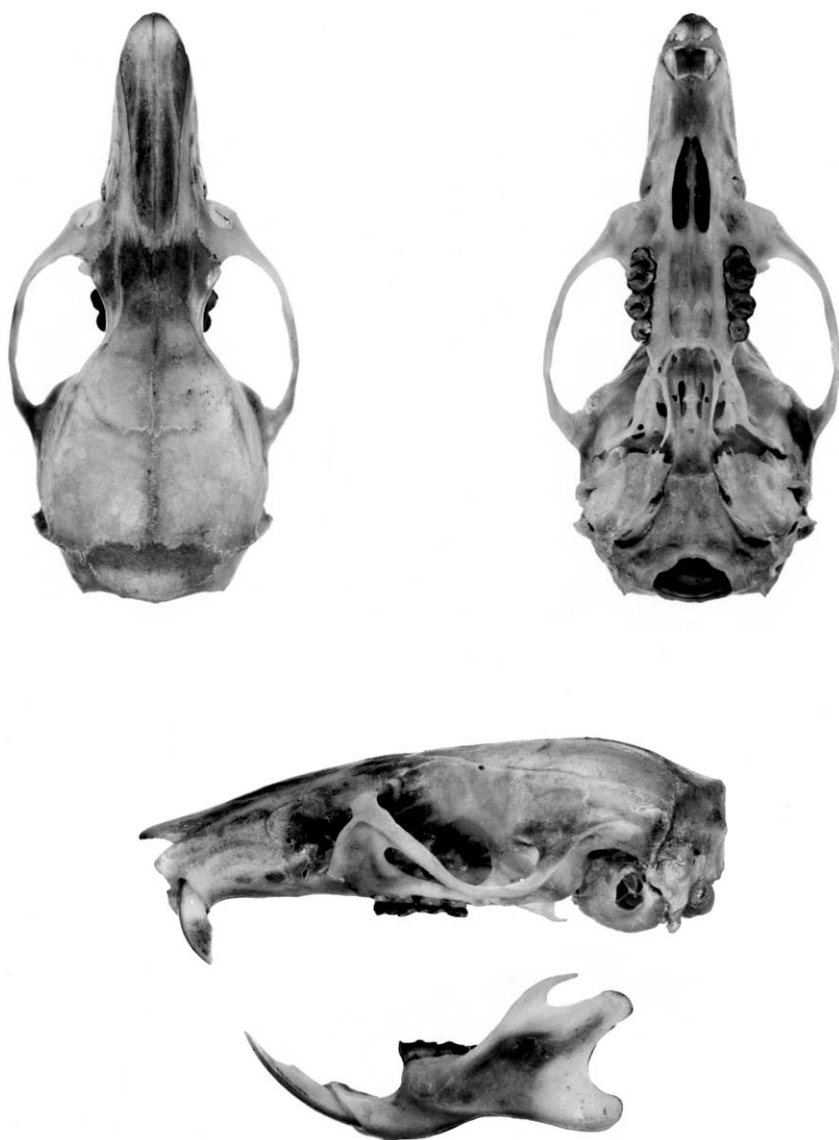
Fig. 16.   The cranium and left dentary of *Bunomys chrysocomus* (AMNH 256886), an adult male from Bogani Nani Wartabone National Park, 3 km northeast of Toraut Danmi, 250 m, northeastern segment of the northern peninsula. ×2.

Sketched here is a hypothesis of phenetic relationships among the Sulawesian species of *Bunomys*, which is based on measurements of cranial and dental variables. Whether the diagrammed alliances reflect only phenetic similarity in overall skull and molar size along with dimensional proportions or actual genetic liaison mirroring phylogenetic relationships will have to be tested by results derived from analyses of DNA sequences of multiple genes. Several testable hypotheses come to mind.

(1)   The phenogram in figure 21 does indicate genetic relationships among the population samples and the species, and is a viable reconstruction of phylogenetic relationships.

(2)   In physical size, magnitude of cranial and dental dimensions, and overall conforma-
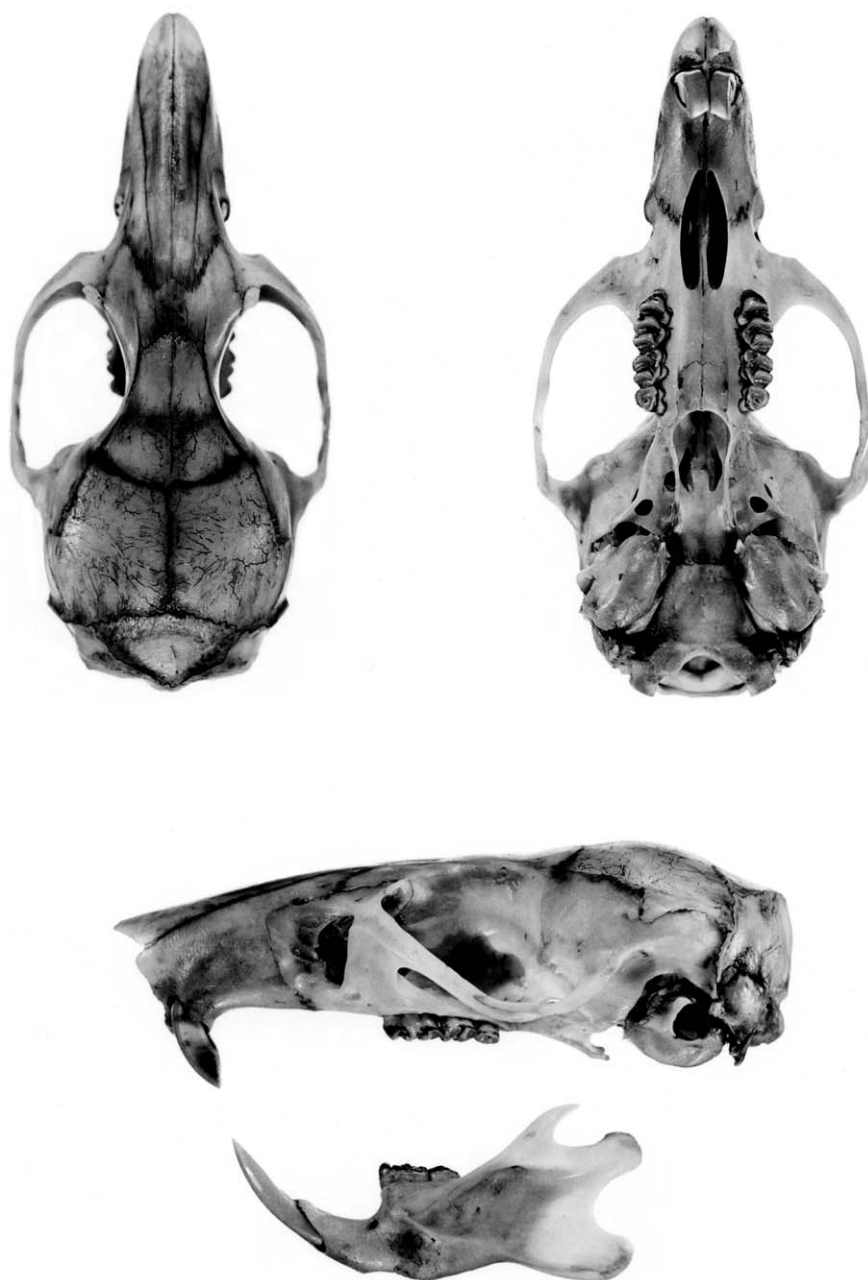
Fig. 17. The cranium and left dentary of *Bunomys fratrorum* (USNM 217650), an adult female from Temboan, 500 m, in the northeastern tip of the northern peninsula. ×2.

tions of head skeleton and molars, *B. prolatus* and *B. torajae,* n. sp., are similar and together phenetically more nearly allied to *B. chrysocomus* and *B. coelestis* than to *B. fratrorum*, *B. andrewsi*, *B. penitus*, or *B. karokophilus,* n. sp. At the same time, *B. prolatus* and *B. torajae,* n. sp., are the largest in body size among members of the *B. chrysocomus* group and are restricted to habitats in montane forests. Is either one or

TABLE 15
Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from Population Samples of *Bunomys chrysocomus* and *B. fratrorum*
Mean $\pm$ 1 SD and observed range (in parentheses) are listed.

Variable	*B. chrysocomus*	*B. fratrorum*
N	232	100
ONL	38.3 ± 1.12	44.0 ± 1.14
	(35.8–41.1)	(41.5–46.5)
ZB	18.1 ± 0.64	20.9 ± 0.90
	(16.3–19.8)	(18.2–22.9)
IB	6.4 ± 0.23	6.2 ± 0.31
	(5.8–7.2)	(5.5–7.0)
LR	13.5 ± 0.59	15.2 ± 0.56
	(12.0–15.1)	(13.9–16.6)
BR	6.8 ± 0.36	8.0 ± 0.38
	(5.6–7.7)	(7.2–9.0)
BBC	15.5 ± 0.41	16.3 ± 0.41
	(14.2–16.8)	(15.3–16.3)
HBC	10.8 ± 0.38	12.2 ± 0.43
	(10.0–12.1)	(11.3–13.1)
BZP	3.2 ± 0.26	3.9 ± 0.32
	(2.6–3.9)	(3.1–4.6)
LD	10.2 ± 0.54	11.4 ± 0.51
	(8.8–12.0)	(10.2–13.1)
PPL	13.5 ± 0.58	15.4 ± 0.60
	(12.2–15.0)	(13.9–16.8)
LBP	7.5 ± 0.40	8.0 ± 0.46
	(6.2–8.4)	(6.9–9.8)
BBP	3.8 ± 0.26	3.8 ± 0.27
	(3.1–4.5)	(3.3–4.5)
BMF	2.9 ± 0.24	3.5 ± 0.26
	(2.4–3.7)	(3.0–4.3
LIF	6.3 ± 0.37	7.3 ± 0.42
	(5.2–7.2)	(6.2–8.3)
BIF	2.5 ± 0.17	2.9 ± 0.16
	(2.0–3.1)	(2.5–3.3)
LB	6.4 ± 0.24	6.5 ± 0.20
	(5.7–7.0)	(6.1–7.0)
CLM1–3	6.2 ± 0.23	7.6 ± 0.26
	(5.7–6.8)	(6.8–8.1)
BM1	2.0 ± 0.09	2.4 ± 0.10
	(1.8–2.3)	(2.2–2.7)

both genetically more closely related to the large-bodied *B. penitus*, which is also tied to montane habitats?

(3) *Bunomys coelestis* is another montane obligate and in morphology is closely similar to *B. chrysocomus*. Is it genetically allied to that species or more tightly linked to *B. prolatus* and *B. torajae,* n. sp., essentially another affiliate of a monophyletic cluster found only in wet and cool mountain forests?

(4) Although cranial and dental morphometric traits assign *B. chrysocomus* to the small-bodied group of species in *Bunomys* and *B. andrewsi* to the larger-bodied cluster, and *B. chrysocomus* averages physically smaller than *B. andrewsi* (compare values on tables 19 and 41), they share phenetic and ecological traits that may counteract the morphometric phylogenetic indication and instead reflect a close genetic link. Range in coloration and texture of fur are similar, as is the range of chromatic patterning of the tail along with relative length and frequency of occurrence of a white tail tip (table 8). Both have a similar diet (fruit, arthropods, snails, oligochaete earthworms, small vertebrates, but no fungi) and gross chromosomal composition, and both are found predominantly in tropical lowland evergreen rain forests (*B. chrysocomus* does ascend into lower and upper montane habitats, and *B. andrewsi* in places occurs in the transition between lowland and montane forests). Is *B. chrysocomus* actually a small-bodied close relative of the large-bodied *B. andrewsi*, and the alliances indicated by cranial and dental morphometric characteristics misleading?

(5) Morphometric qualities of *B. fratrorum* tie it to the other large-bodied species, *B. andrewsi*, *B. penitus*, and especially *B. karokophilus,* n. sp. There is nothing about its external characteristics (color and texture of fur, patterns of the tail formed by pigmented and unpigmented regions, relative lengths of appendages) that depart from the range in these traits seen among the other species of *Bunomys*. At the same time *B. fratrorum* stands apart from all the other species in particular aspects: it is the only member of the genus that is endemic to the northeastern region of the northern peninsula; it occupies habitats in both tropical lowland and montane rain forests; and compared with all the other species, it has a relatively longer skull, more flared zygomatic arches, narrower interorbit, higher braincase, wider zygomatic plate, greater postpalatal length, and smaller bullae (fig. 20; table 17). While neither *B. andrewsi* nor *B. penitus* are southern phenetic counterparts of *B. fratrorum*, as judged by multivariate analyses of cranial and dental measurements, the mycophagous *B. karokophilus,* n. sp., might fit that role. Analysis of DNA sequences of multiple genes would clarify the relationship of *B. fratrorum* to all the other species of *Bunomys* and either confirm or disengage the present documented phenetic link to *B. karokophilus,* n. sp.

In the following section I review species in my informal *Bunomys chrysocomus* group, then those in the equally casual *B. fratrorum* group. Each account of a species covers the following information: (1) description of the holotype; (2) specification of the type locality; (3) original or emended diagnosis; (4) identification of specimens referred to a new species (applies to *B. torajae,* n. sp., and *B. karokophilus,* n. sp.); (5) summary of geographic and elevational distributions; (6) sympatry with other species of *Bunomys*; (7) description; (8) karyotype (available for *B. chrysocomus, B. andrewsi, B. penitus*, and *B. karokophilus,* n. sp.); (9) comparisons with other species; (10) geographic variation in phenetic characters; (11) natural history; (12) summary of ectoparasites, pseudoscorpions, and endoparasites (unavailable for *B. coelestis* and *B. torajae,* n. sp.); (13) allocation of synonyms (relevant to *B. chrysocomus, B. andrewsi*, and *B. penitus*); and (14) identification of subfossil samples (available for *B. chrysocomus* and *B. andrewsi*).

Gazetteers of collection localities, which include all specimens examined, are presented at the beginning of each primary group of species.

The *Bunomys chrysocomus* Group

Gazetteers and specimens examined: Collection localities for 487 specimens of *B. chrysocomus*, 30 examples of *B. coelestis*, eight *B. prolatus,* and seven *B. torajae,* n. sp., are listed below. The number preceding each locality keys to a symbol on the map in figure 22.

Bunomys chrysocomus

1. **Amurang**, 01°11′N, 124°35′E, coastal plain near sea level: SNSD B 612 (1707 = skin; 1727 = skull; holotype of *Mus chrysocomus*); likely collected at a higher elevation—see species account).

2. **Langgon** (also spelled ''Langowan''), 01°09′N, 124°50′E, 700–800 m: RMNH 21283–85 (originally specimens ''*d*,'' ''*i*,'' and ''*l*'' that were considered to be cotypes of *Mus callitrichus* by Jentink [1879], but reidentified as *B. chrysocomus* [Musser, 1970]).

3. **Bogani Nani Wartabone** (formerly Dumoga-Bone**) National Park, 3 km northeast of Toraut Danmi**, 00°34′N, 123°54′E, 250 and

300 m: AMNH 256885–89; LAD 18; SAM 12627, 12629. See map in Bergmans and Rozendaal (1988: 6).

4. **Bogani Nani Wartabone National Park, 1 km north of Gunung Mogogonipa**, 00°27′N, 123°57′E, 250 m: SAM 12617, 12621.

5. **Bumbarujaba** (spelled ''Bumbaroedjaba'' on specimen labels), on highway across peninsula between Tawaeli and Toboli, 00°43′S, 120°04′E (estimated from Raven's map), 915 m (according to Riley, 1924: 2): USNM 218084–86, 218127, 218128, 218131–37, 218139, 218140 (holotype of *Rattus nigellus*).

6. **Puro Valley, Bakubakulu**, 01°07′S, 120°00′E, 600 m: AMNH 229519, 229522.

7. **Valley of Sungai Miu, Sungai Oha Kecil** (small tributary on left side of Sungai Miu), 01°22′S, 119°57′E (near confluence with Sungai Miu; estimated from Sheet SA 50-8): 1050 ft (320 m), AMNH 224647–52; 1100 ft (335 m), 224653.

8. **Sungai Oha Kecil**, 1300 ft (396 m): AMNH 224654–65, 224689, 224690.

9. **Sungai Oha Kecil**, 1400 ft (427 m): AMNH 224666, 224667.

10. **Sungai Oha Kecil**, 1500 ft (457 m): AMNH 224668–80, 224691.

11. **Sungai Oha Kecil**, 1600 ft (488 m): AMNH 224681–88.

12. **Valley of Sungai Miu, Sungai Sadaunta** (also spelled ''Sidaonta'' or ''Sidaunta''; tributary on right side of Sungai Miu), 01°23′S, 119°58′E (estimated from Sheet SA 50-8), 675 m: AMNH 224078–106, 224108–15, 224117–44, 224157–66. **Sungai Pormina** (left tributary of Sungai Sadaunta), 700 m: AMNH 224146–52, 224167–69.

13. **Sungai Sadaunta**, 2500 ft (763 m): AMNH 224692–707, 224774, 224775.

14. **Sungai Sadaunta**, 2600 ft (793 m): AMNH 224708–16, 224776.

15. **Sungai Sadaunta**, 2700 ft (823 m): AMNH 224717–49, 224777–85, 226821, 226922.

16. **Sungai Sadaunta**: 2800 ft (854 m), AMNH 224750–54, 224786–90; 2850 ft (869 m), AMNH 224755–60.

17. **Sungai Sadaunta**: 2900 ft (884 m), AMNH 224761–65, 224791–94; 2950 ft (899 m): AMNH 224766–68, 224795.

18. **Sungai Sadaunta**: 3000 ft (915 m), AMNH 224796–99, 226819; 3050 ft (930 m), AMNH 226820.

19. **Sungai Sadaunta**: 3150 ft (960 m), AMNH 224769; 3200 ft (976 m), AMNH 224770, 224771, 224800–02.

20. **Sungai Sadaunta**, 3400 ft (1037 m): AMNH 224773.
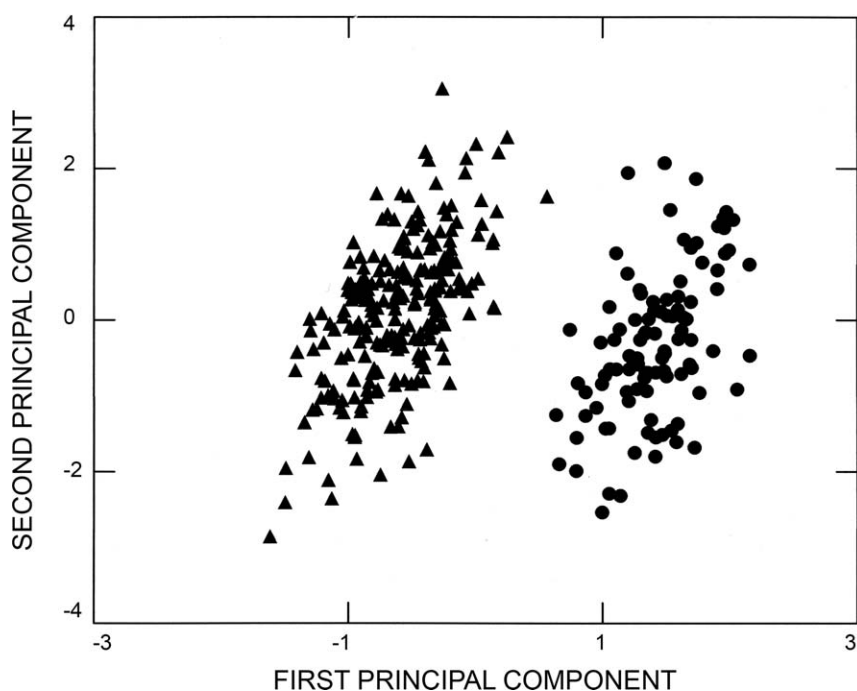
Fig. 18.   Specimen scores representing samples of *Bunomys chrysocomus* (filled triangles; $N = 232$) and *B. fratrorum* (filled circles; $N = 100$) projected onto first and second principal components extracted from principal-components analysis of 16 cranial and two dental log-transformed variables. An ordination bounded by first and second canonical variates extracted from discriminant-function analysis of the same log-transformed measurements exhibits a similar pattern of scores (not illustrated). See table 16 for correlations (loadings) of variables with extracted components and for percent variance explained.

21. **Valley of Danau Lindu, Lombu** (also spelled "Lembo"), a village southwest of Danau Lindu, 01°20′S, 120°03′E, 960 m: AMNH 223069, 223090.

22. **Valley of Danau Lindu, forest near Tomado** (a village on western shore of Danau Lindu), 01°19′S, 120°03′E (estimated from Sheet SA 50-8), 1000 m: AMNH 223035–44, 223047–55, 223057, 223059, 223061–68, 223070, 223071, 223073–89, 223093, 223094, 223292, 223320, 223468, 223469, 223476, 223477, 224154–56, 224170, 223569, 226924–26, 267795; USNM 218691, 218692, 218702, 218704.

23. **Valley of Danau Lindu, Olu** (abandoned village site just west of Danau Lindu), 01°19′S, 120°06′E, 955 m: AMNH 223091, 223092.

24. **Valley of Danau Lindu, Sungai Tokararu**, 12 km east-northeast of Palili (an abandoned village on northeast shore of Danau Lindu), 01°17′S, 120°07′E (estimated from Sheet SA 50-8), 1150 m: AMNH 223293–304, 223306–15, 223321–25, 223327, 223329.

25. **Gunung Kanino**, 01°17′S, 120°08′E (estimated from Sheet SA 50-8), 3900 ft (1189 m): AMNH 223328.

26. **Gunung Kanino**, 3920 ft (1195 m): AMNH 223317.

27. **Gunung Kanino**, 3940 ft (1201 m): AMNH 223326.

28. **Gunung Kanino**, 4000 ft (1220 m): AMNH 223318.

29. **Gunung Kanino**, 4180 ft (1274 m): AMNH 223319.

30. **Gunung Kanino**, 4520 ft (1378 m): AMNH 223567, 223570.

31. **Gunung Kanino**, 4620 ft (1409 m): AMNH 223568.

32. **Gunung Kanino**, 5040 ft (1537 m): AMNH 225148.

33. **Gunung Kanino**, 5100 ft (1555 m): AMNH 223566.

34. **Gunung Lehio, Sungai Supoi**, 01°33′S, 119°53′E, 6166–7166 ft (1880–2185 m): USNM 218673, 218681.

35. **Gimpu**, 01°36′S, 119°53′E, 400 m: USNM 219595 (holotype of *Rattus rallus*), 219713, 219580 (2000–3000 ft is written on skin label of this specimen, which is 610–915 m).

36. **Gunung Tambusisi** (also spelled "Tambasisi" or "Tamboesisi"), 01°38′S, 121°23′E: 4500–

TABLE 16
**Results of Principal-Components Analysis
Comparing All Population Samples of *Bunomys
fratrorum* and *B. chrysocomus***
Correlations (loadings) of 16 cranial and 2 dental
log-transformed variables are based on 332
specimens; see figure 18.

Variable	Correlations	
	PC1	PC2
ONL	0.97***	0.02
ZB	0.94***	0.07
IB	−0.23***	0.36***
LR	0.89***	0.13*
BR	0.92***	0.14**
BBC	0.73***	−0.01
HBC	0.87***	−0.09
BZP	0.83***	−0.15***
LD	0.81***	0.29***
PPL	0.90***	0.10
LBP	0.58***	0.19***
BBP	0.21***	0.83***
BMF	0.81***	−0.01
LIF	0.80***	−0.13**
BIF	0.84***	−0.11*
LB	0.21***	0.17**
CLM1–3	0.91***	−0.28***
BM1	0.85***	−0.36***
Eigenvalue	0.079	0.007
% Variance	68.2	6.0

*** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

Fig. 19. Ratio diagram illustrating some proportional relationships in cranial and dental variables between *Bunomys fratrorum* (the standard, $N = 100$) and *B. chrysocomus* ($N = 232$). Data were derived from values for mean, standard deviation, and sample size of the variables listed in table 15. How these diagrams were constructed and how to read them are explained in Materials and Methods.

4700 ft (1372–1433 m), AMNH 265077, 265078, SAM m15588; MZB 12183–85; 6000 ft (1830 m), MZB 12181.

37. **Pegunungan Mekongga** (also spelled "Mengkoka"), **Tanke Salokko** (the highest spot in Pegunungan Mekongga; see the maps and discussion in Heinrich [1932] and Stresemann [1940]), 03°35′S, 121°15′E (for the Pegunungan): 1500 m, AMNH 101215, 101217, 101220, 101221, 101223, 101224, 101226, 101229, 101232, 101234, 101236 (holotype of *Bunomys caelestis koka*); 2000 m, AMNH 101194, 101195, 101197, 101198, 101200, 101202–05, 101211.

38. **Lalolei** (spelled "Lalolis" on specimen tags and some maps), 03°57′S, 122°03′E, 300 m: AMNH 101051, 101052, 101054, 101055 (holotype of *Rattus brevimolaris*), 101288; MZB 4074, 4075; RMNH 21256.

39. **Pulau Buton**: RMNH 21256. I do not know where on the island this specimen was collected and simply placed a dot randomly within the island's outline. Sody (1941: 317) collected the animal ("Sody No. 4") and initially identified the skin and skull as *brevimolaris*, but provided

no provenance data other than "Boeton." I verified Sody's identification, but could not locate more precise locality information.

40. **Mamasa**, 02°56′S, 119°22′E, 1000 m: BMNH 21.2.9.12. Thomas (1921: 111) identified BMNH 21.2.9.12 and another example from Mamasa that is currently stored in MZB as "*Rattus chrysocomus*," but Sody (1941: 315) correctly reidentified the latter as an example of *Rattus hoffmanni*, which I was able to verify during my study of material at Bogor in the 1970s.

41. **Pegunungan Latimojong**, 03°30′S, 120°05′E, 2200 m: AMNH 196578–84.

42. **Ulu Leang I** (a cave about 40 km northeast of Ujung Pandang in the Maros region; see map and description in Glover, 1976), 0–100 m: AMNH 266973, 266975, 269954 (subfossil fragments; see table 27).

43. **Gunung Balease**, 2.499533333°S, 120.4873833°E, 980–1240 m: MVZ 225696, 225697, 225714, 225810.
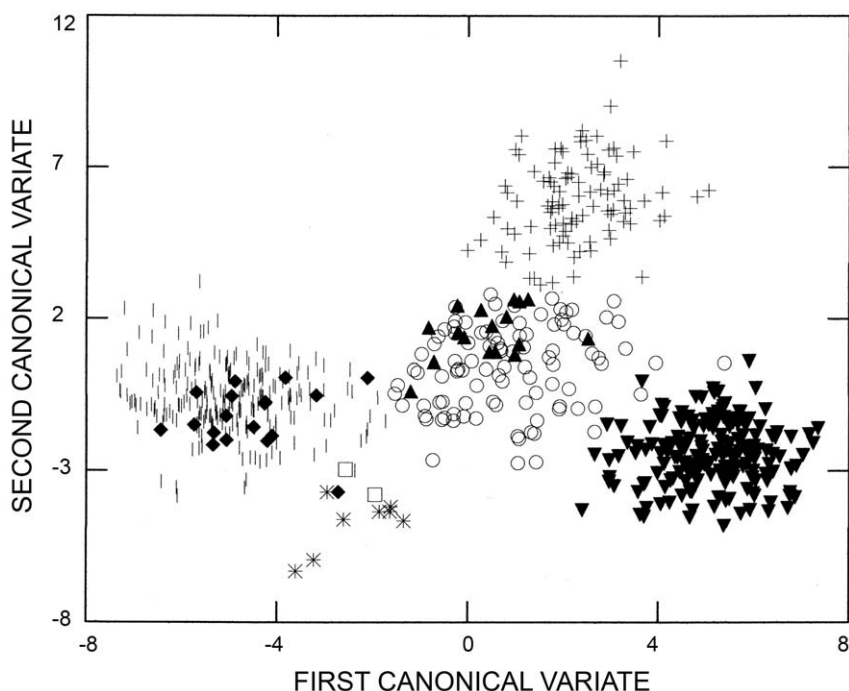
Fig. 20. Specimen scores representing samples of *Bunomys chrysocomus* (vertical lines; $N = 232$), *B. coelestis* (filled diamonds; $N = 18$), *B. prolatus* (asterisks; $N = 8$), *B. torajae,* n. sp. (empty squares; $N = 2$), *B. fratrorum* (crosses; $N = 100$), *B. andrewsi* (hollow circles; $N = 98$), *B. penitus* (inverted filled triangles; $N = 185$), and *B. karokophilus,* n. sp. (filled triangles; $N = 17$), projected onto first and second canonical variates extracted from discriminant-function analysis of 16 cranial and two dental log-transformed variables. Correlations (loadings) of variables with extracted canonical variates and percent variance are listed in table 17.

Bunomys coelestis

1. **Wawokaraeng** (also spelled Wawa Karaing; see Tate and Archbold [1935b]), **Gunung Lompobatang** (also spelled Lampobatang or Lompobattang; see Tate and Archbold [1935b] and Fraser and Henson [1996], for examples; an extinct volcanic mountain near the tip of the southwestern peninsula), 05°20′S, 119°55′E: 2000 m, AMNH 101143–59; 2200 m, AMNH 101016, 101138–40; 2300 m, AMNH 101130; 2500 m, AMNH 101131–33, 101135–37. **Piek van Bonthain**, or **Banta Eng** (Gunung Lompobatang), 6000 ft (1830 m): BMNH 97.1.3.12 (holotype of *Mus coelestis*), 97.1.3.27.

Bunomys prolatus

1. **Gunung Tambusisi** (a mountain that is part of the highlands at the western margin of the eastern peninsula), 01°38′S, 121°23′E, 6000 ft (1830 m): AMNH 265074, 265075, 265076; MZB 12188, 12190 (holotype of *Bunomys prolatus*), 12191; SAM 15586, 15587.

Bunomys torajae, n. sp.

1. **Gunung Gandangdewata** (also spelled "Ganda Dewata" and "Gandadiwata" on some maps), the highest mountain in the Quarles Range, which is in the Mamasa area), 2.748253°S, 119.368536°E: 2500 m, MZB 34904, 34735; 2600 m, MZB 34730–34.

Bunomys chrysocomus (Hoffmann, 1887)

Mus chrysocomus Hoffmann, 1887: 17.
Rattus nigellus Miller and Hollister, 1921a: 72.
Rattus rallus Miller and Hollister, 1921a: 73.
Rattus brevimolaris Tate and Archbold, 1935a: 7.
Bunomys caelistis koka Tate and Archbold, 1935b: 1.

HOLOTYPE: SNSD B 612, the skin and skull of an adult male (original numbers are

TABLE 17
Results of Discriminant-Function Analysis Comparing Samples of *Bunomys chysocomus, B. coelestis, B. prolatus, B. torajae* n. sp., *B. fratrorum, B. andrewsi, B. penitus*, and *B. karokophilus* n. sp.
Correlations (loadings) of 16 cranial and 2 dental log-transformed variables are based on 660 specimens; see figure 20.

Variable	Correlations	
	CV1	CV2
ONL	0.83***	0.29***
ZB	0.67***	0.50***
IB	0.31***	−0.57***
LR	0.82***	−0.08*
BR	0.80***	0.25***
BBC	0.75***	0.02
HBC	0.74***	0.32***
BZP	−0.04	0.73***
LD	0.59***	0.10*
PPL	0.60***	0.43***
LBP	0.71***	−0.25***
BBP	−0.15***	0.19***
BMF	0.77***	0.10**
LIF	0.85***	−0.08*
BIF	0.78***	0.14***
LB	0.46***	−0.29***
CLM1–3	0.96***	0.14***
BM1	0.92***	0.05
Canonical correlation	0.975	0.946
Eigenvalue	18.904	8.444
% Variance	55.6	24.9

*** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

1707 for the skin and 1727 for the skull) obtained by F. von Faber in 1876. External, cranial, and dental measurements, along with other data, are listed in table 18.

Until the advent of World War II, the holotype was in the collection at the Staatliches Naturhistorische Sammlungen Dresden, Museum für Tierkunde. It was apparently lost or misplaced for some time after the War (see Musser, 1970: 14), but fortunately has been found (Feiler, 1999: 409) and was loaned to me by A. Feiler, the retired curator of the mammal collection at Dresden.

The stuffed skin is intact (fig. 23), but parts of the pelage are discolored. The dorsal coat is dark brownish gray and has a slight rusty sheen due to color alteration: bands of the overhairs that are normally brown in recently collected specimens have altered to rust or yellowish brown. The appendages are dark brown, which is unusual, and are likely discolored. The dark brown ears are bent and fragile. The ventral coat is brownish buff and its color is not sharply demarcated from that of the upperparts. Except for the slight chromatic alteration of the dorsal coat and appendages, pelage color of the holotype falls within the range of variation present in the large series of *B. chrysocomus* I collected during the 1970s in the forests around Sadaunta, Danau Lindu, and Gunung Kanino (localities 7–33 in the gazetteer). Compared with a series of *B. chrysocomus* collected by C.H.S. Watts during the 1980s in the northeastern peninsula (localities 3 and 4 in the gazetteer), the holotype has a paler dorsal coat with rusty highlights (dark brownish gray with scatter of buff through the coat in the fresher specimens) and a duller ventral coat that appears soiled (contrasted to bright, buffy brown venters).

The skull is incomplete (fig. 24). Most of the left zygomatic arch, the entire occipital region, and pieces from the roof of the mesopterygoid region are missing, and the basioccipital is cracked. The mandible is intact, as are the upper and lower incisors and maxillary and mandibular molar rows (fig. 25).

TYPE LOCALITY: Amurang (01°11′N, 124°35′E), locality 1 in the gazetteer and on the map in figure 22, the northeastern arm of Sulawesi, Propinsi Sulawesi Utara, Indonesia. Hoffmann (1887: 17) indicated the region of "Minahassa, Nord Celébes" to be the origin of the holotype and that is notated on the original skin tags. Feiler (1999: 409; and in a letter to me [quoted in Musser, 1970: 15]) narrowed the locality to Amurang, a town on the coastal plain near sea level. Minahassa is an expansive administrative region within the province of Sulawesi Utara (northern Sulawesi) between 0.8°–1.8°N and 124.3°–125.3°E on the northeastern peninsula of the island (coordinates are from Fooden, 1969: 134; also see the map in Whitten et al., 1987: xiv). Amurang is unlikely the actual collection site of the holotype because no other specimens to which reliable elevational data are attached have been encountered in coastal plain habitats (see below). F. von Faber, who presented the holotype to the Dresden Museum, stayed at Amurang during 1876
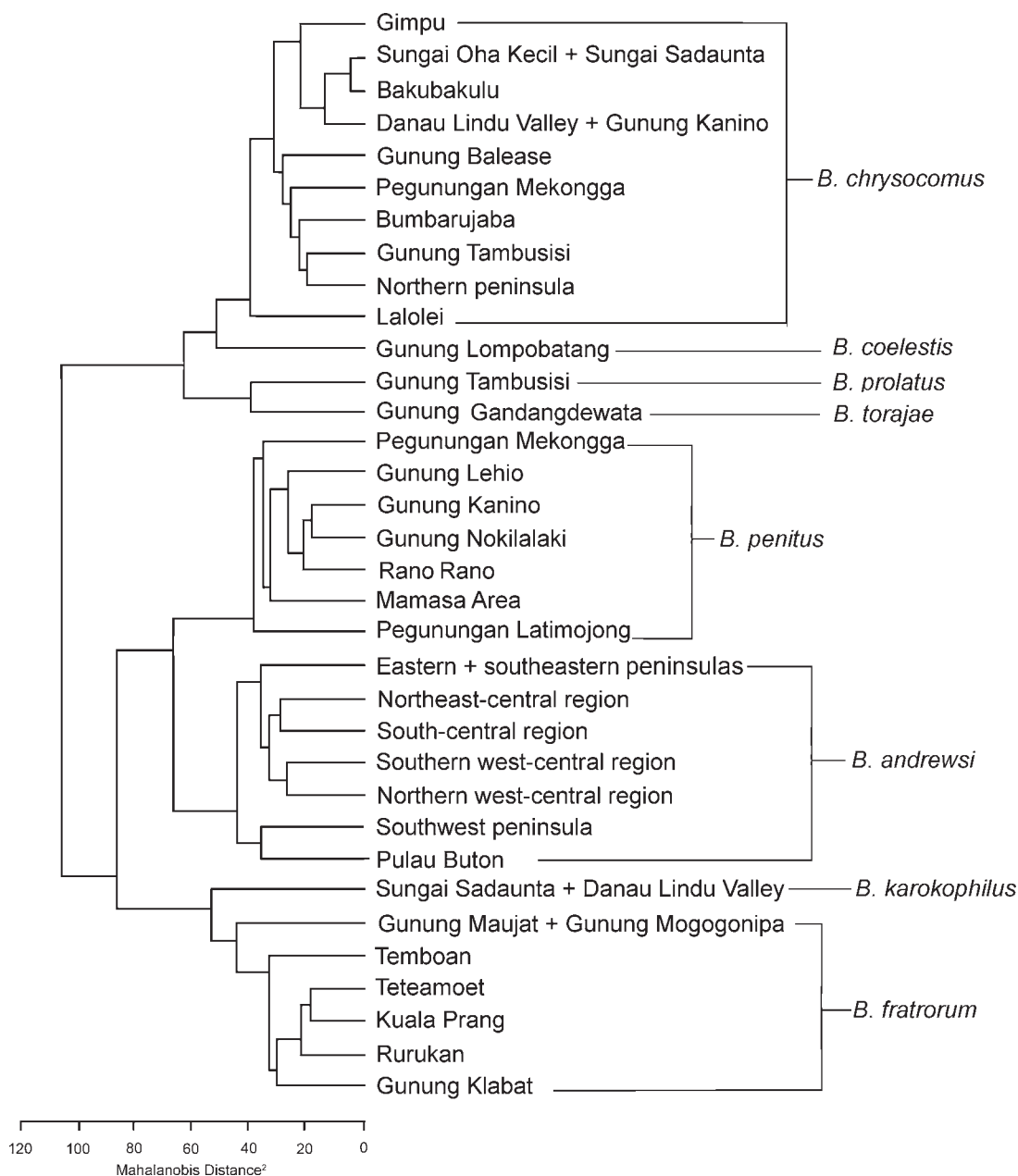
Fig. 21.   Phenetic relationships among population samples of *Bunomys*, based on UPGMA clustering of Mahalanobis distances (D^2) among group centroids derived from discriminant-function analysis using log-transformed values of 16 cranial and 2 dental variables. *Bunomys chrysocomus, B. coelestis*, *B. prolatus*, and *B. torajae*, n. sp. I refer to as the *B. chrysocomus* group; *B. fratrorum, B. andrewsi B. penitus*, and *B. karokophilus*, n. sp., constitute the *B. fratrorum* group.

while he collected birds in the broader Minahassa region (Meyer and Wiglesworth, 1898: 7). The holotype was probably obtained beyond the coastal plain at a higher elevation somewhere in "Minahassa."

EMENDED DIAGNOSIS: Among the smallest in physical size (LHB = 97–180 mm, WT = 55–175 g, ONL = 35.8–41.1 mm) of the Sulawesian species in *Bunomys* and further characterized by the following combination of traits: (1) a long muzzle, small eyes, and long external pinnae; (2) dark brown to brownish gray upperparts speckled with buff, grayish white underparts with some individuals washed with buffy, ochraceous, or rusty hues, dorsal surfaces of feet range from grayish white to brownish gray; (3) front claws moderetly long and robust; (4) tail averages shorter than length of head and body (85%–98%), brown or grayish brown on the dorsal surface, white, mottled brown, or brown along the ventral surface (5) white tail tip infrequent (20% of 396 specimens in 13 samples) and when present is short relative to tail length (mean = 5.5%, range = 1%–25%); (6) testes large relative to body size (22%); (7) sperm head long, thin, asymmetrical and falciform in outline, tail long; (8) skull gracile with a moderately long and narrow rostrum, wide upright or backward sloping zygomatic plate, bony palate projecting slightly beyond posterior margins of third molars, and large ectotympanic bulla relative to skull size; (9) molars small relative to size of skull and mandible; (10) cusp t3 occurs infrequently on second upper molar (17%) and third upper molar (5%); (11) anterior labial cusplets on first lower molar present in about half of sample, posterior labial cusplets typically present on first and second lower molars; (12) anterolabial cusp present on second lower molar in 90% of sample and on third lower molar in 65% of sample; and (13) karyotype, 2N = 42, FNa = 56, FNt = 58.

GEOGRAPHIC AND ELEVATIONAL DISTRIBUTIONS: Collection localities appear as a spotty pattern compared to Sulawesi's land area (fig. 22), but the scatter suggests *B. chrysocomus* to range throughout much of the island wherever lowland and montane evergreen rainforest formations persist. All samples of *B. chrysocomus* describe an altitudinal range from 250 m (in the Bogani

Nani Wartabone National Park on the northern arm) to 2200 m (on Pegunungan Latimojong at the southern margin of the west-central mountain block). Modern specimens with reliable provenence data have not been collected in habitats below 250 m, strongly suggesting *B. chrysocomus* to be a denizen of forested hills, mountains, and intermontane valleys. The only sample from a coastal plain (0–100 m) consists of subfossil fragments from a cave on the southwestern peninsula; whether the specimens were obtained by mammalian or avian predators near the cave or at higher elevations is unknown.

The species is either uncommon or infrequently encountered by collectors in the northern peninsula and the few records from there are in the zone of tropical lowland evergreen rain forest. Besides the holotype, obtained somewhere in the Minahassa Region, three individuals come from Langgon at 700–800 m (locality 2 in the gazetteer and map in fig. 22) and 10 were taken at 250 and 300 m in the Bogani Nani Wartabone National Park (localities 3 and 4), where it appears to be relatively abundant. The northeastern peninsula of Sulawesi has been a focus for collecting mammals and birds since the 1800s, and why *B. chrysocomus* is not represented in museum collections by large samples from more localities is inexplicable.

H.C. Raven, who collected birds and mammals for the Smithsonian Institution, was one of the more successful of the early mammal trappers to have worked in the northeastern arm of Sulawesi, and his results are illustrative. He arrived in Menado in January of 1916 and remained in the northeast until the end of August with the intention of beginning his survey at the extreme end of the peninsula and working west toward Gorontalo (Miller, 1917: 29). Raven collected in primary forest habitats in lowlands and mountains where he garnered large samples of *B. fratrorum* (see gazetteer for that species) along with other species of murines, but never encountered *B. chrysocomus*. After August, he moved south to where the northern peninsula joins the central body of the island, planning to use either Palu or Parigi as a base and working north from there until he had surveyed all of the northern peninsula. His stations were scat-
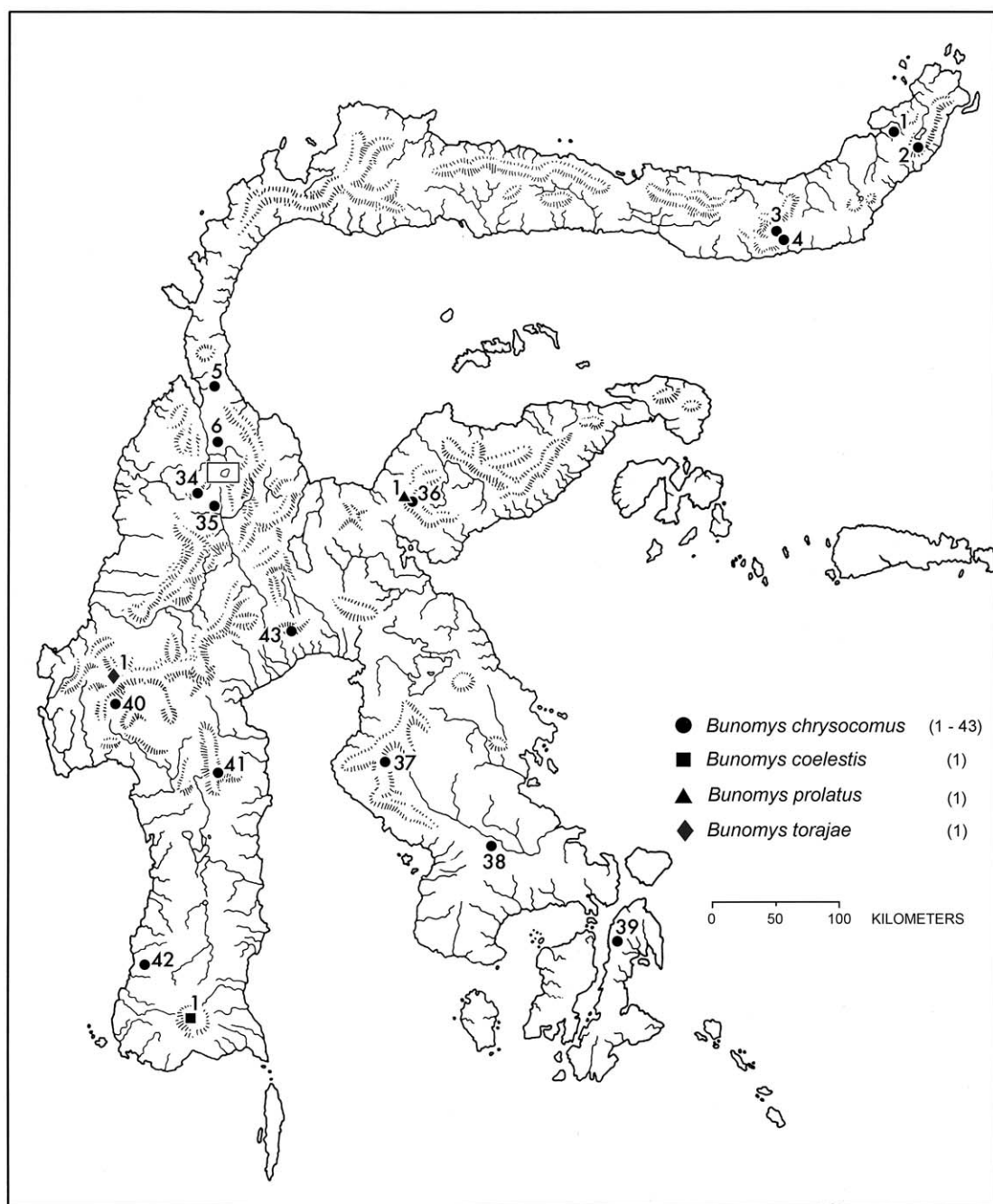
Fig. 22.   Collection localities for samples of *Bunomys chrysocomus*, *B. coelestis*, *B. prolatus*, and *B. torajae*, n. sp. Numbers key to localities described in the gazetteer. The inset map (small rectangle above and in full on opposite page) contains collection localities (7–33) for *B. chrysocomus* only, and are scattered along my transect line from the Sungai Oha Kecil to Gunung Kanino. Dashed contour line at 1300 m marks the approximate boundary between tropical lowland evergreen and lower montane rain forests.
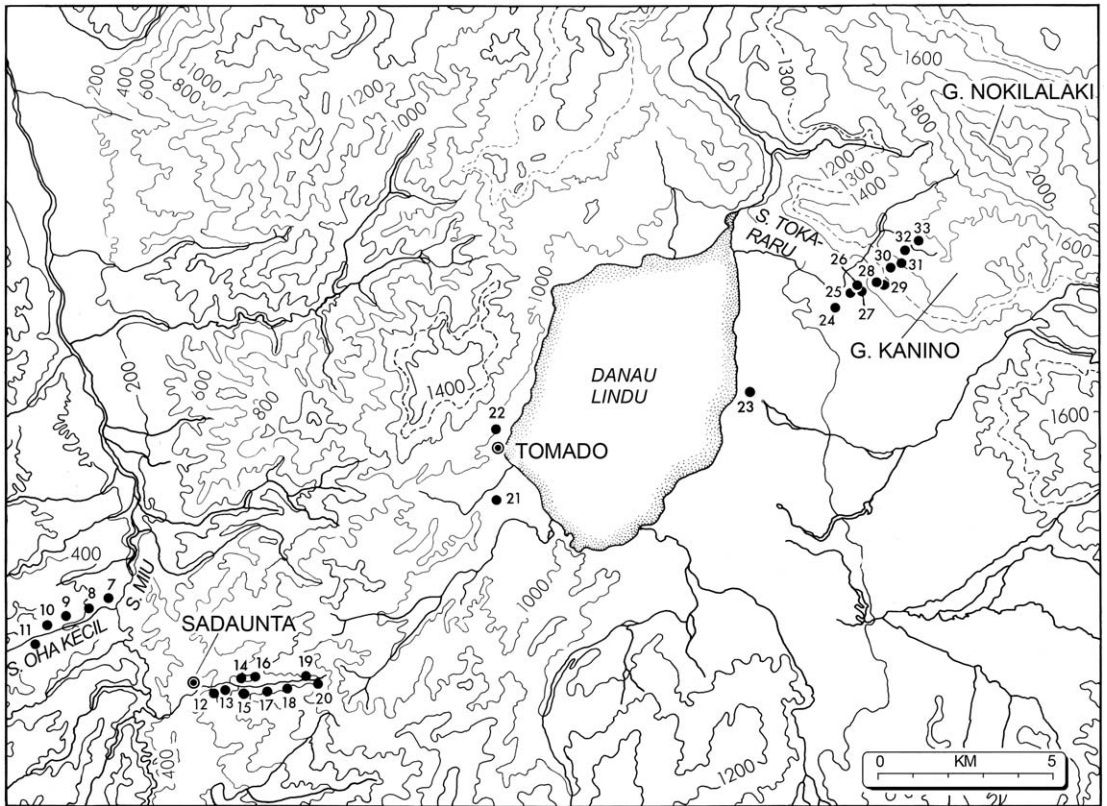
Fig. 22. Continued.

tered from west of Gorontalo in the north to the base of the peninsula in the south, and it is only there, at Bumbarujaba (locality 5), that he came upon *B. chrysocomus*.

Except for a specimen from the Mamasa area, seven specimens from Pegunungan Latimojong, and four individuals obtained on Gunung Balease, all three places in Sulawesi's west-central mountain block, most of the material I have studied came from highlands south of the Palu Valley in the northern part of the west-central region. Small samples are from south of the Palu Valley at Bakubakulu (600 m) in the Puro Valley, Gunung Lehio (1880–2185 m), and Gimpu. The bulk of the material was collected on my transect extending from 320 m along the Sungai Oha Kecil to 1555 m on Gunung Kanino, which includes the range from tropical lowland evergreen rain forest to lower montane forest. Apart from

these localities are vast stretches of forested hills, mountains, and valleys unsurveyed for small mammals, so the actual distribution of *B. chrysocomus* throughout the west-central region remains to be discovered.

Available samples of *B. chrysocomus* from the core of Sulawesi come only from the west-central region (see the map in fig. 22), which suggests to me that the range of the species does not extend into coastal lowland habitats and that its absence from mountains east of the west-central mountain block (generally between Danau Poso and the coast rimming Telok Tolo) may reflect the lack of adequate surveys for small nonvolant mammals there. East of Danau Poso lie mountainous terrain (Pegunungan Pompangeo, for example) that has yet to enjoy surveys for small mammals. There seems no reason why *B. chrysocomus* does not occur in these eastern highlands—providing, of course, that

TABLE 18
Age, Sex, Weight (g), and External, Cranial, and Dental Measurements (mm) for Holotypes Associated with
***Bunomys chrysocomus, B. coelestis, B. prolatus*, and *B. torajae* n. sp.**
(Unless otherwise indicated, I transcribed from skin tags the values for external measurements and measured
the cranial and dental dimensions.)

	Bunomys chrysocomus							
	Mus chrysocomus[a] SNSD 1707/1727	*Rattus nigellus* USNM 218140	*Rattus rallus* USNM 219595	*Bunomys caelestis koka* AMNH 101236	*Rattus brevimolaris* AMNH 101055	*Bunomys coelestis* BMNH 97.1.3.12	*Bunomys prolatus* MZB 12190	*Bunomys torajae* MZB 34730
Age	adult	adult	adult	adult	old adult	old adult	adult	adult
Sex	♂	♂	♀	♀	♂	♀	♂	♂
LHB	175	160	145	147	157	148	—	170
LT[b]	125	131	130	138	123	148	—	170
LHF[c]	34	35	32	35	35	36	—	38
LE	—	—	—	22	20	26	—	27
WT	—	—	—	—	—	—	—	124
ONL	—	37.2	38.3	38.6	39.6	40.0	42.7	41.8
ZB	—	17.5	18.5	18.2	18.9	18.7	18.3	18.3
IB	6.2	6.4	6.4	6.4	6.5	7.0	7.3	6.9
LR	13.5	12.7	13.6	13.9	13.6	13.7	16.1	16.0
BR	6.5	6.8	7.0	6.6	6.9	7.3	6.8	7.4
BBC	15.8	15.6	15.4	15.6	15.1	15.7	16.9	16.0
HBC	—	11.0	10.3	11.6	11.8	11.7	11.4	10.8
BZP	3.1	3.0	2.7	2.7	2.9	3.6	2.9	3.1
LD	10.2	10.2	10.2	10.8	10.7	11.8	11.7	11.5
PPL	—	13.9	14.0	13.3	13.9	13.8	15.2	14.5
LBP	8.0	7.4	7.2	7.8	7.7	8.8	8.4	8.7
BBP	3.3	3.6	3.8	4.0	3.9	4.0	3.7	4.4
BMF	2.5	2.6	2.9	2.6	2.6	3.0	3.0	3.1
LIF	6.0	6.4	6.2	6.2	6.7	6.7	7.0	6.2
BIF	2.2	2.3	2.6	2.4	2.2	2.2	2.5	3.0
LB	6.9	6.5	6.3	6.8	6.9	5.8	7.3	6.5
CLM1–3	6.6	6.5	6.0	6.1	6.1	6.3	6.8	6.6
BM1	2.1	2.1	1.9	2.0	2.0	2.0	2.3	2.3

[a] In the interval between publication of Hoffman's description and my examination, only two other researchers provided information about the holotype of *chrysocomus*, which had been displaced after the World War II and was relocated only recently. During a tour of European museums in the late 1800s, Oldfield Thomas studied the holotype of *chrysocomus* at Dresden and recorded his observations and measurements in a journal (the original is at the British Museum; a photographed copy made by G.H.H. Tate in 1937 is stored in Mammalogy Archives at AMNH). Thomas's values for length of tail and hind foot are 125 and 32 mm, respectively, the same as presented by Hoffmann (1887) in the original description, but Thomas recorded 165 mm for length of head and body (Hoffman gave 175 mm).

H.J.V. Sody studied the holotype in the 1930s and recorded his observations in unpublished notes (filed in Mammalogy Archives at RMNH) and a published account (Sody, 1941: 317) where he used Hoffmann's (1887) figures for external measurements, but listed his own values for cranial and dental dimensions.

I measured the tail of the holotype and obtained 125 mm, and have entered this value in the table along with Hoffmann's 175 mm for length of head and body (which could not be remeasured accurately on the dry skin). My value for length of the hind foot, is 34 mm (which includes the claws) and explains the difference from Hoffmann's value (which excludes the claws).

Sody (1941: 317) listed the holotype as a female, and ''fem.'' is printed on the original label tied to the skin, but the large scrotal sac (see fig. 23) clearly indicates otherwise.

The value for CLM1–3 in the table is mine, the same figure reported by Hoffmann. Sody (1941: 317) listed 6.8 mm but on a page of manuscript (stored in Mammalogy Archives at RMNH) where he recorded his description of the holotype of *chrysocomus*, he also indicated his measurement for ''upper toothrow'' to be 6.8 and noted that ''Hoffmann gives 6.6, but the alveolar l[ength] certainly reaches 6.8.'' In his journal, Thomas noted 6.5 mm for crown length.

[b] I measured the dry tail on the skins of *chrysocomus, koka, brevimolaris*, and *B. coelestis*.

[c] Length of hind foot for all holotypes except *nigellus* are my values from the dry hind foot (including claws); 35 mm for *nigellus* was recorded by H.C. Raven in the field and is the value I got after measuring the dry specimen. All external measurements for *torajae* were obtained by collectors in the field.

TABLE 19
**Descriptive Statistics for Measurements (mm) of Lengths of Head and Body, Tail, Hind Foot, and Weight (g),
Derived from Samples of *Bunomys chrysocomus*, *B. coelestis*, *B. prolatus*, and *B. torajae*, n. sp.**
Mean ± 1 *SD*, observed range (in parentheses), and size of sample are provided. Mean values were used to
compute LT/LHB. Specimens measured are listed in footnotes.

Species and sample	LHB	LT	LHF	LE	WT	LT/LHB (%)
B. chrysocomus[a]						
Northern peninsula	157.3 ± 15.76 (135–178) 7	138.7 ± 9.43 (131–158) 7	34.1 ± 1.07 (33–35) 7	22.3 ± 1.25 (20–24) 7	102.1 ± 18.00 (75–120) 7	88
Bumbarujaba	147.8 ± 7.01 (140–160) 9	133.6 ± 7.03 (122–145) 8	34.0 ± 1.00 (33–36) 9	—	—	90
Sungai Oha Kecil + Sungai Sadaunta	161.5 ± 8.23 (133–180) 147	137.4 ± 10.75 (90–165) 139	35.9 ± 1.25 (33–39) 147	23.3 ± 0.96 (21–26) 146	93.3 ± 15.09 (55–135) 147	85
Danau Lindu Valley + Gunung Kanino	154.8 ± 16.44 (97–176) 38	142.0 ± 14.64 (107–180) 38	35.8 ± 1.71 (32–40) 38	24.5 ± 1.22 (23–28) 38	98.8 ± 17.23 (69–135) 38	92
Gimpu	152.5 ± 10.61 (145–160) 2	127.5 ± 3.54 (125–130) 2	33.5 ± 2.12 (32–35) 2	—	—	84
Gunung Balease	147.3 ± 12.63 (129–158) 4	142.7 ± 8.02 (135–151) 3	34.8 ± 0.96 (34–36) 4	22.5 ± 1.00 (22–24) 4	96.5 ± 17.08 (72–110) 4	97
Pegunungan Mekongga[b]	141.7 ± 5.24 (134–150) 17	139.4 ± 9.58 (120–151) 17	33.3 ± 1.21 (31–35) 17	20.6 ± 0.80 (20–22) 17	—	98
Lalolei[b]	152.0 ± 5.25 (147–160) 6	132.6 ± 10.72 (123–145) 5	34.3 ± 1.51 (33–36) 6	—	—	87
Pulau Buton	134	120	33	23		90
B. coelestis[c]						
Gunung Lompobatang[b]	159.3 ± 8.31 (147–179) 23	151.6 ± 6.72 (138–165) 23	36.9 ± 0.85 (35–39) 23	23.3 ± 1.13 (21–25) 20	—	95
B. prolatus[d]						
Gunung Tambusisi	167.2 ± 10.38 (156–179) 6	132.4 ± 5.91 (125–142) 7	33.9 ± 0.69 (33–35) 7	25.7 ± 0.82 (24–26) 6	—	79
B. torajae[e]						
Gunung Gandangdewata	177.8 ± 22.96 (156–210) 4	165.3 ± 5.03 (160–170) 3	37.6 ± 1.14 (36–39) 5	26.8 ± 0.84 (26–28) 5	116.8 ± 12.05 (98–128) 5	93

[a] Northern peninsula: AMNH 265885–887; Watt's numbers 12617, 12621, 12627, 12629 (measured and weighed by C.H.S. Watts in the field; I remeasured lengths of hind feet. Bumbarujaba (measured by H.C. Raven in the field, who ignored ear length): USNM 218127, 218128, 218131–35, 218139, 218140 (holotype of *Rattus nigellus*). Sungai Oha Kecil + Sungai Sadaunta (measured by me in the field): the same specimens identified in appendix 1. Danau Lindu + Gunung Kanino (measured by me in the field): The same specimens identified in appendix 1 but excluding the four USNM examples. Gimpu (measured by H.C. Raven in the field): USNM 219580, 219595 (holotype of *Rattus rallus*). Gunung Balease (measured by J.L. Patton or K.C. Rowe in the field): MVZ 225696, 225697, 225714, 225810. Pegunungan Mekongga: AMNH 101195, 101197, 101198, 101200, 101202, 101204, 101205, 101211, 101215, 101217, 101220, 101221, 101223, 101226, 101229, 101234, 101236. Lalolei: AMNH 101051, 101052, 101055, 101288; MZB 4074, 4075. Pulau Buton: RMNH 21256 (measured by H.J.V. Sody).

[b] G. Heinrich collected these specimens and measured lengths of head and body, tail, ear, and tail but not total length (head and body plus tail). His value for length of tail is exaggerated because he incorporated part of the rump (other collectors did not), which also underestimates length of head and body. I remeasured lengths of tails and hind feet on the dry skins, and used those values for computing the descriptive statistics. I could not remeasure lengths of head and body as well as ear because the bodies are overstuffed and the ears are dry and distorted. I don't know if Heinrich measured each ear from crown to base or crown to notch (my endpoints); the former produces a smaller value than the latter. I use Heinrich's values for head and body as well as ear but cannot vouch for their accuracy.

[c] AMNH 101016, 101131–33, 101135–39, 101141–46, 101149, 101150, 101152–56, 101158.

[d] All specimens were measured by C.H.S Watts in the field. AMNH 265074–076; SAM M15588, MZB 12181, 12183, 12185.

[e] MZB 34730, 34733–35, 34904 (measured by A.S. Achmadi and K.C. Rowe in the field).
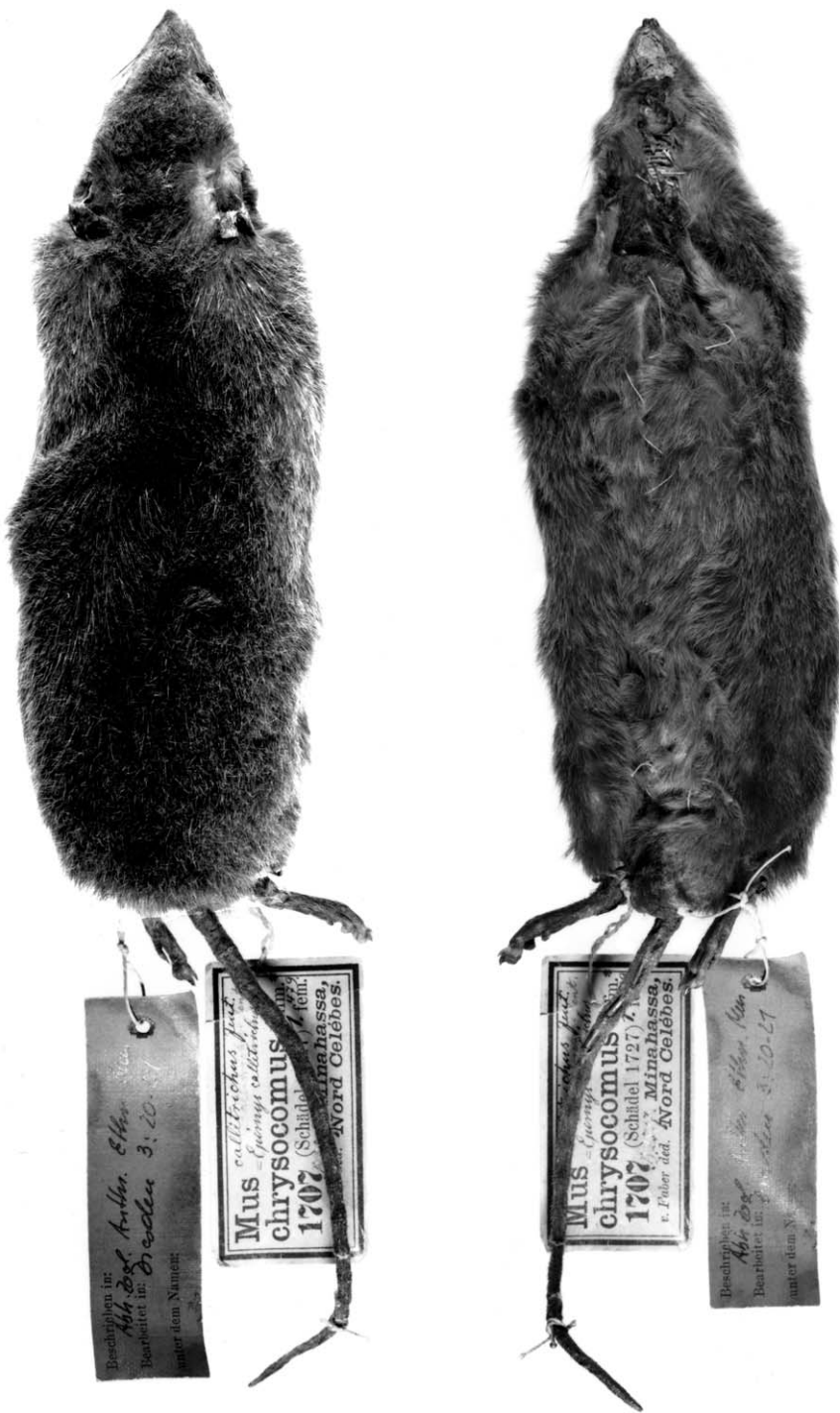
Fig. 23.   Holotype of *Mus chrysocomus*, an adult male (SNSD 1707 = SNSD B 612). Measurements are listed in table 18.
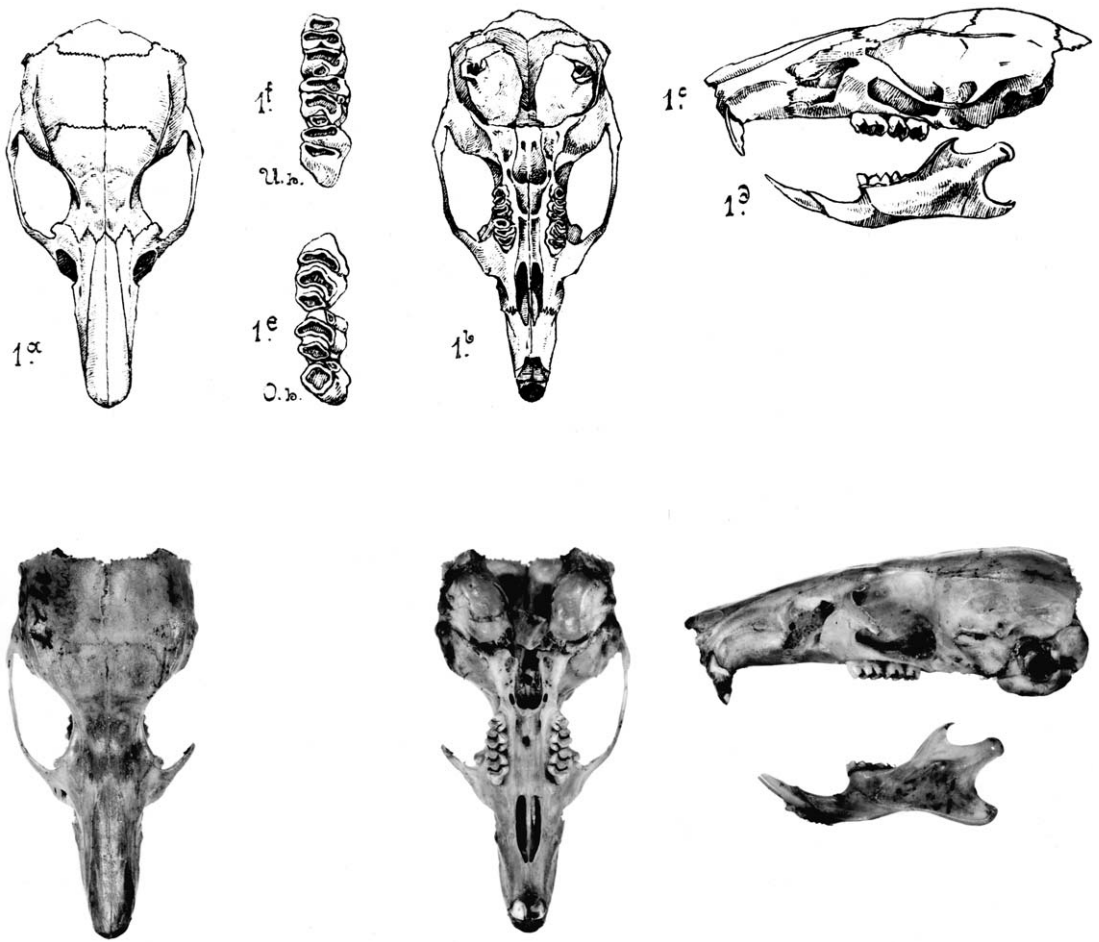
Fig. 24. Holotype of *Mus chrysocomus*, an adult male (SNSD 1717 = SNSD B 612). Upper set: Reproductions of the drawings published in Hoffmann's (1887) original description. Lower set: Photographic images of the actual skull. Measurements are listed in table 18.

forest has not been removed—because the species has been taken on the slopes of Gunung Tambusisi to the northeast at the western margin of the eastern peninsula.

Trapping efforts bolster the hypothesis that *B. chrysocomus* is absent from very low elevations. Along my transect in the northern part of the west-central mountain block, I did not encounter the species below 320 m—only *B. andrewsi* was caught at lower elevations (see fig. 103 and the gazetteer for *B. andrewsi* and map in fig. 50). Nor did I collect *B. chrysocomus* in the northern part of the eastern portion of the central core at Kuala Navusu and Sungai Tolewonu, lowlands and

ridges just back of the northeastern coast (see the map in fig. 5). I trapped only *B. andrewsi* at Kuala Navusu (31–122 m), but did not encounter either species of *Bunomys* at Sungai Tolewonu (136–366 m). Farther south in the eastern coastal lowlands, H.C. Raven collected a large sample of *B. andrewsi* from the forest by Pinedapa at 31 m but no *B. chrysocomus*.

The eastern peninsula of Sulawesi is another region receiving little exploration for small mammals, and the range of *B. chrysocomus* throughout that area is unknown. My only sample comes from 1372–1829 m on the flanks of Gunung Tambusisi,

Fig. 25.   Occlusal views of right maxillary (left image) and mandibular (right image) molar rows of the holotype of *Mus chrysocomus* (SNSD 1727 = SMT 612). See table 18 for measurements.

located at the southwestern margin of the peninsula. Mammal surveys in the eastern arm have been few, and sampling macaques has been the focus of most research trips. One exception is a collection of rodents and bats made by Luis Ruedas in 1998 from lowlands in the eastern Poso and Banggai districts of the peninsula, and another is a collection made by Jake Esselstyn and Anang Achmadi from Gunung Tompotika at the eastern end of the peninsula, neither of which contained examples of *B. chrysocomus*. What

species occur at middle and high elevations along the mountainous backbone of the eastern peninsula has yet to be determined.

Tropical lowland evergreen rain forest to lower montane forest is the broad habitat range in which samples of *B. chrysocomus* have been obtained from the southeastern peninsular arm of the island. A specimen from Pulau Buton, the small sample from Lalolei at 300 m, and the material from Pegunungan Mekongga collected at 1500 and 2000 m embody the material I have included in this report, nearly all obtained by G. Heinrich in the 1930s. Additional specimens of *B. chrysocomus* from the Mekongga highlands are reported by Mortelliti et al. (2012).

Three subfossil fragments from cave deposits in the Maros region (below 100 m), about 40 km northeast of Ujung Pandang, provide the only record of *B. chrysocomus* from the southwestern peninsula (table 27). The species apparently lived in forest habitats at low and moderately high elevations because montane forests between 1800 and 2500 m on Gunung Lompobatang, south of the caves, support populations of *B. coelestis*, the mountain counterpart of *B. chrysocomus* in this region. Much of the lowlands in the southwestern peninsula are deforested and converted to agriculture (Whitten et al., 1987: 93, 102; Bernard and De Koninck, 1996: 3), but low forest cover still exists in limestone regions, especially in the Maros hills (personal obs.; Whitten et al., 1987), which are difficult to traverse and have never been surveyed for small mammals, and possibly *B. chrysocomus* still lives in those places.

SYMPATRY WITH OTHER *BUNOMYS*: Throughout Sulawesi, *B. chrysocomus* is broadly sympatric with all the other species of *Bunomys* (tables 6, 20; also see gazetteers), but samples documenting its occurrence at the same locality and taken in the same trapline are few. Among the two other species in the *B. chrysocomus* group, *B. prolatus* and *B chrysocomus* have been collected on the slopes of Gunung Tambusisi. The eight known specimens of *B. prolatus* were trapped on a ridge at 1830 m in upper montane forest. One *B. chrysocomus* was taken ''just below the same ridge, at about the same altitude (6000 ft) but a few meters downslope, and on the same day

(March 9) as were four examples of *B. prolatus.* Six specimens of *B. chrysocomus* were collected at 4500 and 4700 ft during the same period, March 6–27, 1980'' (Musser, 1991: 6). Samples of both species are small—whether the altitudinal ranges of each narrowly overlap or the two are truely altitudinally parapatric can only be determined by future elevational surveys on Gunung Tambusisi.

No modern samples of *B. chrysocomus* are available from the lower slopes of Gunung Lompobatang at the tip of the southwestern arm of Sulawesi. It is represented there only by subfossil fragments collected on the western coastal plain. Its original altitudinal distribution on the volcano and throughout the southwestern peninsula in general is unknown. Forests above 1800 m contain *B. coelestis*, the montane relative of *B. chrysocomus.*

On the northeastern peninsular arm of Sulawesi, *B. chrysocomus* and the larger-bodied *B. fratrorum* are recorded at two localities (see gazetteers). One is Rurukan, but the samples were obtained during different years and the actual collection sites are unknown. The second place is in the Bogani Nani Wartabone National Park, 1 km north of Gunung Mogogonipa at 250 m. There during August 2–8, 1985, C. Watts collected two *B. chrysocomus* and three *B. fratrorum.* Thus, in this northeastern arm the two species are regionally sympatric and apparently syntopic at one collection site.

Bunomys chrysocomus and *B. andrewsi* have been recorded from the same places in four regions of Sulawesi. Both species come from the PuroValley at Bakubakulu, 600 m, in the northern portion of the west-central mountain block, where on July 30, 1973, NAMRU-2 personnel trapped two *B. chrysocomus* and two *B. andrewsi.*

I collected the two species along a portion of my transect that extended from the Sungai Oha Kecil at 290 m to the Sungai Sadaunta at 675 m in the valley of the Sungai Miu. At 457 m on the Oha Kecil, both species were taken in the same trapline on the same days during August, 16 and 17, 1974; along the Sungai Sadaunta at 675 m, both species were collected in the same trapline on February 10 and 12, 1974 (at the latter locality an example of *B. andrewsi* [AMNH 224107] was trapped

TABLE 20
Summary of Elevational Relationships between *Bunomys chrysocomus* and Other Species of *Bunomys* Derived from Voucher Specimens

Locality	Pairs of species	Elevation (meters)
Northeast peninsula: 1 km north of Gunung Mogogonipa	*B. chrysocomus*	250
	B. fratrorum	250
Gunung Tambusisi	*B. chrysocomus*	1372–1828
	B. prolatus	1830
Gunung Balease	*B. chrysocomus*	980–1240
	B. andrewsi	830–925
Puro Valley, Bakubakulu	*B. chrysocomus*	600
	B. andrewsi	600
My transect: Sungai Oha Kecil to Gunung Nokilalaki	*B. chrysocomus*	290–1555
	B. andrewsi	290–675
Southwest peninsula: Ulu Leang I (subfossils)	*B. chrysocomus*	0–100 m
	B. andrewsi	0–100 m
Gunung Lehio	*B. chrysocomus*	1880–2185
	B. penitus	above 1830
My transect: Sungai Oha Kecil to Gunung Nokilalaki	*B. chrysocomus*	290–1555
	B. penitus	1285–2287
Pegunungan Latimojong	*B. chrysocomus*	2200
	B. penitus	2200, 2300
Pegunungan Mekongga	*B. chrysocomus*	1500, 2000
	B. penitus	1500, 2000
My transect: Sungai Oha Kecil to Gunung Nokilalaki	*B. chrysocomus*	290–1555
	B. karokophilus	823–1150

in a runway beneath a rotting tree trunk laying in shrubby understory of streamside forest; during the next night a *B. chrysocomus* [AMNH 224108] was trapped in the same spot). *Bunomys andrewsi* was rare in this overlap zone, but *B. chrysocomus* was relatively abundant (see the elevational distribution of specimens in fig. 103).

Bunomys chrysocomus and *B. andrewsi* are sympatric, but may not be syntopic, on Gunung Balease in the southeastern portion of the west-central mountain block (table 20). During 2010, four examples of *B. chrysocomus* were caught between 980 m and 1240 m, a range through the upper limit of tropical lowland evergreen rain forest and into lower montane rain forest, on October 25, 28, and 29, and Nov 1. Downslope between 830 m and 925 m, 18 specimens of *B. andrewsi* were trapped in tropical lowland evergreen rain forest during the period, October 18–29. No *B. chrysocomus* were encountered below 980 m and no *B. andrewsi* above 925 m (elevational data was kindly provided by J.L. Patton and K.C. Rowe).

Finally, *B. chrysocomus* and *B. andrewsi* are represented by subfossil fragments extracted from sediments at Ulu Leang I, a cave in the Maros region on the western coastal plain of the southwestern peninsula. The pieces may have been originally packaged in owl pellets or scat from the civet, *Macrogalidia*. If so, we know nothing of the ranges of these predators or habitats in which they hunted and cannot now determine whether the two species of *Bunomys* lived together on the coastal plain or came from different elevations.

Except for the few places of syntopy, the ranges of *B. chrysocomus* and *B. andrewsi* are generally mutually exclusive. Places yielding large samples of *B. andrewsi*—such as Pinedapa, Kuala Navusu, Gunung Balease, and the coastal plain west of Pegunungan Mekongga—are either devoid of *B. chrysocomus*, the species is rarely encountered, or its microhabitat in those places was never or inadequately sampled. The interplay of environmental factors related to elevation and competition for food (insects, oligochete

earthworms, snails, and some fruit form the diet of both species, judged by my field observations and examination of stomach contents; see table 13) may partly explain the checkerboard pattern. Reliable altitudinal measurements indicate that modern samples of *B. chrysocomus* have yet to be encountered below 250 m. In more or less continuous intact forest, which characterized the landscape along my transect in the west-central region, I collected *B. chrysocomus* from 320 m at Sungai Oha Kecil to 1555 m on Gunung Kanino. Elsewhere in the central core of Sulawesi, the species occurs in montane forests up to 2200 m. With a few exceptions, most collection sites for *B. andrewsi* are below 600 m, and many between 30 and 300 m; 1000–1600 m seems to bracket the upper limit of its elevational range. In primary forest at Pinedapa, H.C. Raven collected 22 *B. andrewsi* during about a month, but no *B. chrysocomus.* At 30 m, that place is likely too low and the environmental conditions unsuitable for *B. chrysocomus.* West of Pinedapa, in the Malakosa region, I worked along the Kuala Navusu for three months and the nearby Sungai Tolewonu for another two months and caught *B. andrewsi* between 30 and 122 m in the Navusu area but no *B. chrysocomus.* Work in the Tolewonu drainage extended from 137 m to 366 m, but neither one of the species was encountered in forest seemingly no different than that covering the Navusu drainage basin.

Samples from four mountains provide records of syntopy between *B. chrysocomus* and the montane *B. penitus.* During June 13–14, 1930, G. Heinrich collected both species at 2200 m on Pegunungan Latimojong, the highlands on the northern margin of the southwestern peninsula. His survey on Pegunungan Mekongga in the southeastern arm of the island garnered both species from 1500 m during January 3–13, 1932, and from 2000 m during December 18–30, 1931.

Samples of the two species come from Gunung Lehio, just northwest of Gimpu. Above 1800 m, H.C. Raven collected *B. chrysocomus* on January 13 and 16, 1917, and *B. penitus* a few days later, during January 18–21.

From the end of October to the last part of November, 1973, I trapped five *B. chrysoco-mus* and 60 *B. penitus* in lower montane rain forest between 1265 and 1555 m on the slopes and top of Gunung Kanino, a high ridge leading to the higher Gunung Nokilalaki; during one night, an example of each species was taken in the same runway beneath a rotting, moss-covered tree trunk on the forest floor (fig. 32). Below 1265 m, *B. chrysocomus* ranges down through tropical lowland evergreen rain forest to 320 m along my Sungai Miu–Danau Lindu–Gunung Nokilalaki transect, and occurs with *B. andrewsi* and *B. karokophilus,* n. sp.; above 1555 m, *B. penitus* was the only *Bunomys* encountered during the period in which I trapped, and was common in lower and upper montane rain-forest formations, all the way to the summit of Gunung Nokilalaki.

Bunomys chrysocomus and *B. karokophilus,* n. sp., are sympatric and syntopic in distribution. I trapped examples of each species along my transect between 823 and 1006 m in the streamside forest along the Sungai Sadaunta (both were taken at 823 m in the same trapline on September 25 and 28, 1974; and at 854 m on October 1, 1974); at Tomado, 1000 m (taken in same trapline on July 26 and 27, and August 2–4, 10, and 14, 1973); and at 1150 m near the Sungai Tokararu (both were caught in the same trapline on October 8, 1973).

DESCRIPTION: Hoffman (1887: 17) joined *chryso,* from the Greek meaning "gold," to the Latin *coma,* referring to "hair" of the head, to produce *chrysocomus,* the combination meaning "golden haired," which emphasized, in Hoffmann's eyes, the "gold-yellow" luster highlighting the dark brown dorsal coat of the new rat presented to the Dresden Museum by F. von Faber. His description follows (translated by E. Brothers; the original German version is provided in appendix 1):

> This rat from north Celebes is yet another that is just a bit smaller than our own house rat; its coloring tallies so well with *Mus rattus* that at first glance, one might think that it was a juvenile of that species. The fundamental distinction is in the nature of the skull and of the pelt. Craniology: The rear of the skull is damaged, so I present here the range from bony nasal tips to the back edge of the parietals; this distance amounts to 3.4 cm. The rostrum is very

pointy; this is because the nasals are long and the front end of the rostrum is very narrow; at the other end the zygomatic plate is shifted back, while its forward edge is oblique, rising toward the back. Behind that lies the rudimentary upper base of the zygomatic arch, and thus also the site of the smallest width of the skull between the orbital concavities, more distant from the nose-tip than in all other rats [Hoffmann's description of *chrysocomus* was one of six accounts describing Indo-Australian species of murines]. This distance amounts to 2.07 cm; in a *M. rattus* of the same size it is only 1.75 cm. The parietals have the breadth of the aforementioned *M. rattus*, measuring 1.09 cm at the anterior suture. This forms a twice broken line, of which the front middle part is straight. The lateral parts both rise anteriorly. The orbital ridges are extremely slightly developed, yet can be discerned up to the occipitals. The interparietal is very small, its width approximately 3/5 the width of both parietals. The incisive foramina terminate about 1 mm anterior to the bases of the first molars. The bony palate terminates just behind the last molars. The molar tooth row is 0.66 cm long; the teeth themselves are wide, extend farther back and are taller than those of *M. rattus*. The distance between toothrows is 0.34 cm at the front, and both toothrows diverge, so that the distance between them is 0.41 cm at the back. The osseous bullae are 0.68 cm long. In the mandible the roots of the incisors travel outward and exactly under the forward projection of the crown; the condyle and the angular process are very weak. In general, the upper teeth, as well as those of the mandible, are comparable to those of *Mus decumanus*. A significant characteristic is that the inner cusp of both first upper teeth are displaced backward relative to *M. decumanus*. The shape of the small lateral cusp of the mandible is similar to that of *M. rattus*, only it is a bit smaller in general and those of the first lamella of the third tooth lie more to the inside of the top of the front surface of the lamella. External Characteristics: Head and body measure 17 ½ cm, tail 12 ½ cm long with about 190 scale rows. Forefoot including underarm 4 cm, hind foot 3.2 cm long. Sole of the hind foot small, callosities rather long, with a point at the back, one at the base of the middle toe, one under the first toe, and two under the fifth toe; in the center of the sole there is a small wide projecting callosity. The fur is long, thick, very soft and smooth lying. The back has a beautiful light brown color, a little darker than that of *Mus rattus*, with a gold-yellow luster; at the base it becomes a brown, nearly black color, which in most other rats and mice is not as prominent, but is here a bit more pervasive. The blackish color disappears at the sides; it merges with the lighter brown in a somewhat stronger tone, uniting to supplant it with a brownish to pure neutral gray color, which however is not as extensive as the dark color of the back–-rather it is very constrained. The underside of the body is pale yellow, paler at the back than at the front and not sharply set off from the color of the flanks. The light gray color of the bases of the hairs often asserts itself. The specimen before me presents on its underside several irregularly scattered rust-brown patches with yellow edges. The head is brown like the back, fading a bit to pale yellow at the front and sides. Fore and hind feet are dark gray-brown, and covered with whitish glossy little hairs. The very fine woolly hair is, at the midline of the back, colored dark neutral gray in the lower 2/3, the upper portion is slightly more than a third and almost completely dark brown-black, with only the outermost tip, approximately ½–1mm, a light brown. For the great length of the woolly hairs (between 1.6 and 1.8 cm) the tips are very conspicuous, thereby explaining the overall color of the back fur. Entirely spiny hairs are absent in this mouse. The bristly hairs [guard hairs] are difficult to separate from the woolly hairs. They are small in number, and distinguish themselves only in that they are completely straight and in the front part [of the dorsum] the outermost tips are colored dark brown-black. In the remaining areas they are very similar to the woolly hairs; their lengths are barely different, such that no bristle-hairs greater than 1.9 cm in length are encountered. Toward the flanks the woolly hairs become lighter next to the very dark part and mix to gray. On the other hand the light brown tips become more prominent and extensive. The bristly hairs gradually diminish altogether. The roughly 12 ½ cm long tail contains about 190 scale rows, between them stand quite a lot of dark little hairs, which are of uniform length over the entire tail.

A compact body and moderately long head, relatively short tail, dark brown, lustrous fur, and medium body size (LHB = 97–180 mm, LT = 90–180 mm, LHF = 31–40 mm, LE = 17–28 mm, W = 55–175 g, ONL = 35.8–41.1 mm) describes *Bunomys chrysocomus* (see the rendition of *B. chrysocomus* presented in fig. 6), which among members of the *B. chrysocomus* group is

physically similar to *B. coelestis*, but smaller than *B. prolatus* and *B. torajae,* n. sp. (tables 7, 19). The dorsal coat is dense, smooth, and soft to the touch; it is 12–15 mm long over the back on rats from lowlands, but reaches 20 mm on those from middle and high elevations. Dark brown with buffy speckling (produced by the combination of dark brown and buffy bands of the overhairs) describes the typical coloration of the dorsal coat covering most of the the head and body; sides of the body are paler, a grayish brown (because the brown and buffy bands are reduced in lengths or absent, more of the gray bases of the underhairs and overhairs dominate). A few individuals exhibit a darker coat, brownish black with only slight speckling. Because guard hairs and overhairs are about the same length, the surface of the coat is smooth, and the glistening guard hairs impart sheen to the fur. The rhinarium and sides of the muzzle are brown.

Fur covering the underparts of the head and body is also soft and dense, but shorter (8–10 mm long) than the dorsal fur, which is the usual pattern in murids. The contrast in color between upperparts and underparts is evident but not sharply marked. Grayish white (bases of the hairs are gray, tips are unpigmented), gray tinged with pale buff (tips of the hairs are pale buff), or dark gray washed or saturated with buff or ochraceous (hairs with long gray bands and short buffy or ochraceous tips) illustrate the predominant variation in color within the samples, although grayish white is most common; chestnut overlays the chin, neck, and chest in some specimens, pigmentation similar to that seen in many examples of *B. andrewsi*. In the west-central mountain block, deeply pigmented underparts (buffy gray or ochraceous-gray) predominate in samples from lower montane forest (Gunung Kanino and Gunung Balease) but are seen in only a few specimens from tropical lowland evergreen rain forest.

In life, the ears (external pinnae) feel and appear rubbery to me; they seem to be naked but are sparsely covered by short hairs. Their color is variable, ranging from shiny gray through dark gray, dark grayish brown, and grayish black to blackish gray. The stiff dried ears of stuffed museum skins lack the rubbery texture of the live animal and have dried to a dark brown.

Averaging shorter than the combined length of head and body (LT/LHB = 85%–98%), the tail's dorsal surface is some shade of brown, the ventral surface ranges from white to brownish; a white tail tip is infrequent (20% of 396 specimens in 13 samples; table 8) and when present is short relative to tail length (mean = 5.5%, range = 1%–25%). The following color patterns (ignoring any white tip) are present in any large sample of *B. chrysocomus*: (1) mottled brown on the dorsal surface, white for the full length of the ventral surface (a rare bicolored variant); (2) dark brownish gray along the dorsal surface, white below but very lightly speckled—still appears sharply bicolor, dark above and whitish below; (3) dark grayish brown or dark brown on dorsal surface, white on ventral surface and moderately to densely speckled grayish brown—no clear demarcation between dorsal and ventral surfaces; (4) densely speckled grayish brown on dorsal surface, slightly less speckled on ventral surface—appears grayish brown all over; (5) dark brown above, slightly paler below—appears monocolored.

Carpal and metacarpal along with tarsal and metatarsal surfaces vary in color, ranging from grayish white (skin is unpigmented and covered with short gray and silvery hairs), through whitish brown (sparsely covered with brown hairs) to brownish white and then dark brown (denser cover of brown hairs). Digits of front and hind feet are typically unpigmented and sparsely covered with short silvery hairs; in some individuals, the bases of the digits are gray, in a few others the digits are white and sparsely covered with brown hairs. The moderately long front claws are not concealed by ungual tufts, but thin tufts of silvery hairs lay over the hind claws. Palmar and plantar surfaces are typically unpigmented except for near the heel and over the tubercles, which are gray; specimens from Gunung Balease have dark brown palmar and plantar regions, the darkest I have seen.

Females exhibit the number of teats usual for all Sulawesian species of *Bunomys*—four, arranged in two inguinal pairs. Males have

large testes relative to body size, as measured by lengths (table 9) and weights (Breed and Taylor, 2000). Gross and ultrastructural spermatozoal descriptions are provided by Breed and Musser (1991) and Breed (2004).

Juveniles have a distinctly different pelage than that of adults. It is shorter, has a velvety texture, and is very dark compared with the brownish adults—brownish black with a flat tone (lacking the glossy sheen of the adult fur). Underparts are dark grayish white. Coloration of ears, feet, and tail ranges through the same patterns seen in any large series of adults.

The small gracile cranium and mandible of *B. chrysocomus* is depicted in figures 16 and 37–39. Their conformation and internal structure epitomizes the description of the *Bunomys* skull provided in the introduction to the morphological characteristics of the genus. Noteworthy features of the cranium are its wide interorbit, deep and boxy braincase, moderately long and tapered rostrum, low postorbital ridging, sloping anterior edge of the zygomatic plate in most specimens, relatively short incisive foramina, short projection of the bony palate past posterior faces of the third molars, and relatively large bullar capsules. Each dentary is gracile and somewhat elongate, especially that slim portion of the ramus between incisor and first molar (diastema).

Molars are small relative to size of the cranium and mandible, and the occlusal patterns of cusps (figs. 12, 25) mirror the general patterns already described for the genus. I point out here only the frequencies of certain cusps and cusplets. Cusp t3 occurs on the second upper molar in only 17% of the sample, and on the third upper molar in only 5% of all specimens examined (table 10). About half of all specimens surveyed support an anterior labial cusplet on the first lower molar, and posterior labial cusplets are typically present on the first and second lower molars; an anterolabial cusp is present on the second lower molar in 90% of the sample and on the third lower molar in 65% of all specimens surveyed (table 11).

KARYOTYPE: $2N = 42$, FNa = 56 and FNt = 58, comprised of seven pairs of metacentric chromosomes, one pair of subtelocentrics, and 12 pairs of acrocentrics; the sex chromosomes are acrocentrics (fig. 13, table 12).

COMPARISONS: In its morphology, *Bunomys chrysocomus* most closely resembles the other members of the *B. chrysocomus* group—*B. coelestis*, *B. prolatus*, and *B. torajae,* n. sp.—and is compared with them in those three respective accounts. *Bunomys chrysocomus* is also contrasted with each of the species in the *B. fratrorum* group in the accounts of *B. fratrorum*, *B. andrewsi*, *B. penitus*, and *B. karokophilus,* n. sp.

GEOGRAPHIC VARIATION: Morphological variation among available samples is estimated primarily from characters of dry museum skins along with qualitative and morphometric traits of the skull and dentition. In traits related to general body size, relative lengths of hind feet and tail, as well as fur and skin pigmentation, adult examples of *B. chrysocomus*, to my eyes, look similar whatever the geographic provenance of the specimen. I did not detect any noteworthy variation among population samples in dimensions of head and body, tail, hind foot, and ear; in texture and coloration of fur; in color of feet and ears; or in pigmentation patterns on the tail. In any large sample (the 146 from Sungai Oha Kecil and Sungai Sadaunta, for example), the range in chromatic tones of body fur and the range of patterns formed by brown and unpigmented regions of the tail is greater than the range of variation in these features I saw among most other geographic samples.

Some specimens are darker than most others. The four adults from Gunung Balease and the rats from Gunung Kanino have darker dorsal and ventral coats, feet, and tails than is typical of the individuals comprising most samples.

My assessment of variation in color of the fur, skin, and pattern of the tail revealed by its dorsal and ventral pigmentation is not quantified and derives from simple observation of skins. Coloration of the distal portion of the tail is an exception and I quantified the frequencies of a white tip and its length in samples (table 8). The results did not reveal a pattern among the samples that bore significant concordance with their geographic origins.

Lengths of head and body, tail, hind foot, and ear are statistically summarized by sample but I did not treat the data in any

rigorous comparative way for several reasons. Samples are uneven in composition of adult classes (young to old). Except for the material from my transect most samples are small (table 19). And there is always the problem of comparing measurements obtained by different collectors. Was length of head and body measured separately from length of tail? Was the tail measured on the dorsal side from the rump to the tip or ventrally from the anus to the tip? Did the collector include or omit claws in obtaining values for length of hind foot? Is length of pinna (if obtained; H.C. Raven, for example, did not measure the ear) measured from notch to crown or from base of the pinna to crown?

Morphometric variation in cranial and dental variables among the population samples does exist (tables 21, 22), detectable not so much by side-to-side comparison of skulls of comparable age classes, but by multivariate analyses, and I relied on those results to reveal possible patterns of variation in morphometric traits over Sulawesi's landscape. Intersample geographic variation is less apparent in the ordination of specimen scores for all population samples of *B. chrysocomus* projected on first and second principal components (fig. 26). Scores representing the two large samples from my transect (Sungai Oha Kecil + Sungai Sadaunta, Danau Lindu + Gunung Kanino) are diffused along the lengths of both axes, and that cloud also embraces nearly all scores representing the other eight population samples, including scores for the holotypes of *nigellus, rallus, koka*, and *brevimolaris* (fig. 26, upper graph) as well as *chrysocomus* itself (fig. 26, lower graph). The positive and high loadings for most variables on the first component, along with significant correlations among all of them (table 23), point to size as primarily responsible for the spread of scores along the first axis with covariation in overall size of skull (occipitonasal length and zygomatic breadth), interorbit, rostrum (length and breadth), zygomatic plate, and palatal region (length of diastema, breadth of incisive foramina, length and breadth of bony palate, postpalatal length, and breadth of mesopterygoid fossa) being the most influential ($r = 0.43$–0.78 for upper graph). Covari-

ation among other variables (size of the braincase, lengths of incisive foramina and ectotympanic bulla) exert moderate force in the dispersion of scores, and size of molars express the smallest loadings and the least pressure. After full eruption the molars do not increase in dimensions and the braincase reaches nearly full size early in ontogeny, so the dispersion of scores along the first axis partly signals variation in the facial skeleton due to different stages of postweaning growth within adults (young to old) as well as some variation associated with geographic origin of the samples.

Plotted results of discriminant-function analysis provide a sharper resolution of geographic variation in morphometric traits among samples. Individual specimen scores projected on first and second canonical variates form two slightly overlapping constellations in the scatter plot that include holotypes of *brevimolaris, koka, nigellus*, and *rallus* (fig. 27, upper graph) and the plot incorporating those holotypes as well as that for *chrysocomus* (fig. 27, lower graph). The largest and densest cluster of scores in the right half of both scatter plots represents the 188 specimens from my transect in the northern part of the west-central mountain block (Sunga Oha Kecil + Sungai Sadaunta combined with Danau Lindu + Gunung Kanino), the rat from Bakubakulu just north of my transect, and the three individuals from Gimpu, south of the transect and also in the west-central region. Specimens from along the transect were collected at sites in mostly unbroken forest extending from Sungai Oha Kecil at 320 m to Gunung Kanino at 1524 m, an elevational range embracing habitats in tropical lowland evergreen rain forest and lower montane forest. It is not surprising that their scores form a single cluster, and one that also embraces scores of the specimen from Bakubakulu and the three from Gimpu.

Slightly separated from the dense cluster of points representing specimens from the west-central region are those scores for samples from the northern peninsula (Bogani Nani Wartabone National Park); Bumbarujaba, near the southern end of the northern peninsula; Gunung Tambusisi, at the western margin of the eastern peninsula; part of the

TABLE 21
Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from Population Samples of
Bunomys chrysocomus
Mean ± 1 SD and observed range (in parentheses) are listed. Compare with statistics summarized in table 22.

Variable	Northern peninsula		Eastern peninsula	Southeastern peninsula	
	Northern peninsula	Bumbarujaba	Gunung Tambusisi	Pegunungan Mekongga	Lalolei
N	10	7	6	11	3
ONL	38.8 ± 1.36	37.5 ± 0.69	38.3 ± 1.34	38.4 ± 0.90	38.5 ± 1.28
	(37.0–40.5)	(36.7–38.7)	(35.8–39.5)	(37.3–39.8)	(37.1–39.6)
ZB	18.8 ± 0.68	17.7 ± 0.38	17.8 ± 0.61	18.0 ± 0.53	18.6 ± 0.46
	(17.7–19.7)	(17.4–18.4)	(17.1–18.4)	(16.8–18.8)	(18.1–18.9
IB	6.4 ± 0.18	6.3 ± 0.27	6.5 ± 0.25	6.5 ± 0.28	6.3 ± 0.17
	(6.1–6.7)	(5.9–6.6)	(6.1–6.8)	(6.1–6.9)	(6.2–6.6)
LR	13.6 ± 0.77	12.8 ± 0.48	13.3 ± 0.70	13.7 ± 0.56	13.5 ± 0.61
	(12.4–14.7)	(12.3–13.8)	(12.4–14.1)	(12.6–14.3)	(12.8–14.0)
BR	6.8 ± 0.48	6.7 ± 0.11	6.5 ± 0.48	6.4 ± 0.42	6.6 ± 0.55
	(6.1–7.5)	(6.5–6.8)	(5.6–6.9)	(5.7–7.1)	(6.0–7.0)
BBC	15.9 ± 0.34	15.9 ± 0.34	15.6 ± 0.42	15.8 ± 0.41	15.7 ± 0.40
	(15.5–16.6)	(15.5–16.6)	(15.1–16.2)	(15.5–16.8)	(15.3–16.1)
HBC	10.9 ± 0.36	10.9 ± 0.18	10.14 ± 0.26	11.3 ± 0.32	11.5 ± 0.49
	(10.4–11.6)	(10.7–11.2)	(10.3–11.0)	(10.8–11.8)	(10.9–11.8)
BZP	3.1 ± 0.36	3.0 ± 0.16	2.9 ± 0.08	2.9 ± 0.18	2.9 ± 0.00
	(2.7–3.9)	(2.8–3.3)	(2.8–3.0)	(2.7–3.3)	
LD	11.0 ± 0.73	10.2 ± 0.29	10.5 ± 0.55	10.6 ± 0.33	10.5 ± 0.17
	(9.8–12.0)	(9.8–10.7)	(9.6–11.1)	(10.0–11.0)	(10.4–10.7)
PPL	13.5 ± 0.69	13.4 ± 0.35	13.2 ± 0.49	13.4 ± 0.29	13.6 ± 0.30
	(12.4–14.4)	13.0–13.9)	(12.3–13.6)	(12.7–13.7)	(13.3–13.9)
LBP	7.8 ± 0.24	7.7 ± 0.35	7.6 ± 0.48	7.5 ± 0.41	7.6 ± 0.27
	(7.4–8.1)	(7.3–8.3)	(6.7–8.1)	(6.8–8.0)	(7.3–7.8)
BBP	3.8 ± 0.43	3.7 ± 0.27	3.5 ± 0.22	3.7 ± 0.21	4.0 ± 0.36
	(3.2–4.5)	(3.2–4.0)	(3.2–3.8)	(3.3–4.0)	(3.7–4.4)
BMF	2.8 ± 0.25	2.9 ± 0.21	2.7 ± 0.21	2.8 ± 0.18	2.7 ± 0.23
	(2.4–3.2)	(2.6–3.2)	(2.4–2.9)	(2.5–3.1)	(2.6–3.0)
LIF	6.3 ± 0.37	6.3 ± 0.21	6.7 ± 0.26	6.6 ± 0.27	7.0 ± 0.32
	(5.9–6.8)	(6.1–6.8)	(6.5–7.2)	(6.2–7.0)	(6.6–7.2)
BIF	2.4 ± 0.22	2.4 ± 0.11	2.3 ± 0.12	2.4 ± 0.19	2.5 ± 0.36
	(2.1–2.8)	(2.3–2.6)	(2.2–2.5)	(2.1–2.6)	(2.2–2.9)
LB	6.5 ± 0.21	6.4 ± 0.21	6.5± 0.19	6.7 ± 0.14	6.7 ± 0.32
	(6.2–6.7)	(6.2–6.8)	(6.2–6.7)	(6.5–7.0)	(6.3–6.9)
CLM1–3	6.5 ± 0.21	6.3 ± 0.21	6.3 ± 0.21	6.2 ± 0.24	6.3 ± 0.29
	(6.2–6.8)	(5.9–6.5)	(5.9–6.5)	(5.8–6.6)	(6.1–6.6)
BM1	2.1 ± 0.08	2.1 ± 0.05	2.0 ± 0.12	2.0 ± 0.12	2.0 ± 0.25
	(2.0–2.2)	(2.0–2.1)	(1.8–2.1)	(1.8–2.2)	(18–2.3)

sample from Gunung Balease on the eastern margin of the west-central mountain block; Pegunungan Mekongga in the southeastern peninsula, and Lalolei in lowlands adjacent to the Mekongga highlands. The position of scores along the first canonical variate representing these samples reflects their slightly larger braincase and bulla; longer diastema, incisive foramina, and molar row; and narrower rostrum, zygomatic plate, and mesopterygoid fossa (see moderate to large positive and negative loadings in table 24) compared with those samples from the west-central mountain block, distinctions reflected in univariate summary statistics (tables 21, 22).

The association of four of these five population samples relative to the four from the west-central region in the scatter plot is also portrayed in the clustering pattern based on Mahalanobis distances squared as a measure of phenetic resemblance (fig. 28).

TABLE 22
Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from Population Samples of
***Bunomys chrysocomus* from the West-Central Region[a]**
Mean ± 1 SD and observed range (in parentheses) are listed. Compare with statistics summarized in table 21.

Variable	Sungai Oha Kecil + Sungai Sadaunta	Danau Lindu Valley + Gunung Kanino	Gimpu	Bakubakulu	Pegunungan Latimojong	Gunung Balease
N	147	42	3	1	1	3
ONL	38.2 ± 1.07 (35.8–40.8)	38.3 ± 1.20 (36.1–41.1)	38.5 ± 0.92 (37.7–39.5)	37.9	38.5	40.2 ± 0.23 (40.1–40.5)
ZB	18.0 ± 0.62 (16.3–19.7)	18.3 ± 0.62 (17.3–19.8)	18.4 ± 0.40 (18.0–18.8)	17.7	17.1	18.8 ± 0.17 (18.7–19.0)
IB	6.4 ± 0.22 (5.9–6.9)	6.4 ± 0.24 (5.8–6.8)	6.3 ± 0.17 (6.1–6.4)	6.3	6.6	6.9 ± 0.27 (6.7–7.2)
LR	13.6 ± 0.53 (12.3–15.1)	13.6 ± 0.71 (12.0–15.1)	13.6 ± 0.15 (13.4–13.7)	13.3	13.6	14.2 ± 0.45 (13.7–14.6)
BR	6.8 ± 0.30 (6.0–7.5)	6.8 ± 0.45 (5.8–7.7)	7.1 ± 0.27 (6.9–7.4)	6.8	6.1	7.0 ± 0.20 (6.8–7.2)
BBC	15.4 ± 0.38 (14.2–16.7)	15.6 ± 0.43 (14.6–16.5)	15.2 ± 0.25 (14.9–15.4)	15.2	15.8	16.2 ± 0.21 (16.0–16.4)
HBC	10.8 ± 0.33 (10.0–11.8)	10.7 ± 0.38 (10.1–11.7)	10.4 ± 0.17 (10.3–10.6)	10.2	10.9	11.5 ± 0.55 (11.0–12.1)
BZP	3.2 ± 0.23 (2.6–3.8)	3.2 ± 0.25 (2.7–3.7)	2.9 ± 0.25 (2.7–3.2)	3.0	3.0	3.0 ± 0.30 (2.7–3.3)
LD	10.2 ± 0.52 (8.8–11.6)	10.2 ± 0.53 (8.8–11.6)	10.2 ± 0.40 (9.8–10.6)	10.2	10.7	10.8 ± 0.20 (10.6–11.0)
PPL	13.5 ± 0.59 (12.2–14.8)	13.7 ± 0.58 (12.3–15.0)	14.2 ± 0.49 (13.9–14.8)	13.3	12.6	13.9 ± 0.27 (13.7–14.2)
LBP	7.5 ± 0.39 (6.2–8.4)	7.4 ± 0.42 (6.6–8.2).	7.2 ± 0.15 (7.1–7.4)	7.6	8.2	8.2 ± 0.06 (8.1–8.2)
BBP	3.8 ± 0.24 (3.1–4.5)	3.8 ± 0.27 (3.2–4.4)	3.9 ± 0.12 (3.8–4.0)	3.9	3.0	3.9 ± 0.21 (3.7–4.1)
BMF	2.9 ± 0.22 (2.5–3.7)	3.0 ± 0.26 (2.7–3.7)	2.9 ± 0.06 (2.9–3.0)	2.9	2.5	3.0 ± 0.21 (2.8–3.2)
LIF	6.2 ± 0.36 (5.2–7.2)	6.1 ± 0.34 (5.4–6.9)	6.6 ± 0.35 (6.2–6.9)	5.8	5.7	6.0 ± 0.35 (5.7–6.4)
BIF	2.5 ± 0.16 (2.0–3.1)	2.4 ± 0.13 (2.1–2.7)	2.6 ± 0.25 (2.4–2.9)	2.4	2.4	2.4 ± 0.00
LB	6.4 ± 0.22 (5.7–7.0)	6.3 ± 0.24 (5.9–6.8)	6.6 ± 0.31 (6.3–6.9)	6.3	6.6	6.6 ± 0.27 (6.4–6.9)
CLM1–3	6.2 ± 0.22 (5.7–6.7)	6.2 ± 0.23 (5.7–6.8)	6.1 ± 0.23 (6.0–6.4)	6.3	6.1	6.2 ± 0.10 (6.1–6.3)
BM1	2.0 ± 0.09 (1.8–2.3)	2.0 ± 0.09 (1.8–2.2)	1.9 ± 0.06 (1.9–2.0)	2.0	2.1	2.1 ± 0.00

[a] The specimen from Pegunungan Latimojong is not included among the population samples used for multivariate analyses of cranial and dental variables. It is one of seven specimens: one is an old adult, two are adults, one is young adult, another is a very young adult, and two are juveniles. I could obtain a complete set of measurements only from one of the young adult skulls; two from the other adults are in fragments and one skull is missing. The juvenile and the very young adult skulls, although complete, are too young to include in the analyses. Crown lengths of maxillary molar rows (6.1 ± 0.05, 6.1–6.2 mm) and breadths of first upper molars (2.1 ± 0.05, 2.0–2.1 mm) could be measured on five of the skulls.

Samples from the northern peninsula, Bumbarujaba, Gunung Tambusisi, and Pegunungan Mekongga form a cluster separate from that containing the samples from Danau Lindu + Gunung Kanino, Sungai Oha Kecil + Sungai Sadaunta, Bakubakulu, and Gimpu. This pattern of phenetic relationships among population samples also appears in the cluster diagrams where samples of all phenetic members of the *B. chrysocomus*

Fig. 26.   Specimen scores representing 10 population samples of *Bunomys chrysocomus* projected onto first and second principal components extracted from principal-components analysis of 16 cranial and two dental log-transformed variables. Upper graph: All variables are represented and scores for four of the five holotypes associated with *B. chrysocomus* are present. Lower graph: The holotype of *chrysocomus* is added; because the skull is incomplete, four variables had to be excluded (occipitonasal and postpalatal lengths, zygomatic breadth, and height of braincase could not be measured; fig. 24). Symbols: filled triangles = northern peninsula (*N* = 10); empty triangles = Bumbarujaba (*N* = 7); empty circles = Sungai Oha Kecil + Sungai Sadaunta (*N* = 146); filled circles = Danau Lindu + Gunung Kanino (*N* = 42); empty squares = Gimpu (*N* = 3); left-pointing empty triangles = Gunung Tambusisi (*N* = 6); asterisks = Pegunungan Mekongga (*N* = 11); empty diamonds = Lalolei (*N* = 3); filled squares = Gunung Balease (*N* = 3); star = single specimen from Bakubakulu. Arrows and abbreviations identify scores for holotypes: **b** = *brevimolaris*; **c** = *chrysocomus*; **k** = *koka*; **n** = *nigellus* (empty triangle); **r** = *rallus*. See table 23 for correlations (loadings) of variables with extracted components and for percent variance.

group are compared (fig. 49) as well as the phenetic alliances among all species of *Bunomys* diagrammed in figure 21. The two clusters for *B. chrysocomus* describe a distributional pattern in which one group of

samples is from a region extending from the northern peninsula onto the western end of the eastern peninsula and ending on the southeastern peninsula (population samples are from thenorthern peninsula, Bumbaru-

TABLE 23
Results of Principal Components Analysis of All Population Samples of *B. chrysocomus*
Upper graph: correlations (loadings) of 16 cranial and two dental log-transformed variables are based on 232 specimens; includes all holotypes (*Rattus nigellus, R. rallus, R. brevimolaris,* and *Bunomys coelestis koka*) except *Mus chrysocomus*. **Lower graph**: correlations (loadings) of 12 cranial and two dental log-transformed variables are based on 233 specimens; includes the holotype of *Mus chrysocomus* (its skull is incomplete); see figure 26.

| | Correlations | | | |
| | Upper graph | | Lower graph | |
Variable	PC1	PC2	PC1	PC2
ONL	0.78***	0.26***	—	—
ZB	0.72***	0.18**	—	—
IB	0.43***	0.17**	0.40***	0.16**
LR	0.73***	0.24***	0.68***	0.22***
BR	0.74***	−0.09	0.73***	−0.05
BBC	0.32***	0.21***	0.26***	0.16*
HBC	0.27***	0.23***	—	—
BZP	0.50***	−0.85**	0.56***	−0.80***
LD	0.71***	0.28**	0.65***	0.23***
PPL	0.71***	0.18	—	—
LBP	0.46***	0.17**	0.41***	0.12
BBP	0.69***	0.01***	0.69***	0.05
BMF	0.58***	0.18**	0.62***	0.37***
LIF	0.28***	0.26***	0.25***	0.20**
BIF	0.46***	0.17**	0.49***	0.28***
LB	0.28***	0.11	0.22***	0.04
CLM1–3	0.20***	0.12	0.17**	0.12
BM1	0.15*	0.00	0.14*	0.01
Eigenvalue	0.015	0.007	0.013	0.006
% Variance	30.2	13.6	29.3	14.7

*** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

jaba, Gunung Tambusisi, and Pegunungan Mekongga), and the other samples are from mountains and valleys in the west-central region (Danau Lindu + Gunung Kanino, Sungai Oha Kecil + Sungai Sadaunta, Bakubakulu, and Gimpu).

Samples from Laolei and Gunung Balaese, not mentioned above, deserve highlighting. The three Laolei animals are from lowlands (300 m) adjacent to Pegunungan Mekongga. Their individual scores in the canonical variate ordinations group with those representing specimens in samples from the northern peninsula, Bumbarujaba, Gunung Tambusisi, and Pegunungan Mekongga (fig. 27). Close association with Pegunungan Mekongga should be expected considering the near geographic proximity of Lalolei to that highland region, but in the Mahalanobis diagram, the sample forms an independent link to both that cluster and the one containing samples from the west-central region (figs. 28, 49). In different iterations of the Mahalanobis diagram where small samples of *B. chrysocomus* were subtracted or samples of other species of *Bunomys* were added (not illustrated here), the Lalolei sample either remains isolated or links with the group of population samples containing Pegunungan Mekongga. A larger sample from the lowlands adjacent to the Mekongga massif is needed to obtain a better estimate of the population mean and more reliable assessment of its phenetic affinity to other population samples.

Results of the multivariate analyses of cranial and dental variables described above suggest some interruption of gene flow between populations in the west-central region and those on the northern and southeastern peninsulas (geographic variation within a single species) but not complete genetic isolation (two species very similar in morphological attributes). In this context, the samples from Gunung Balease and Bakubakulu provide insights. Gunung Balease lies on the eastern margin of the west-central mountain block (locality 43 on the map in fig. 22). Collecting efforts there during October, 2010, produced four adult *B. chrysocomus*, but only three have intact skulls and these three form the population sample used in the multivariate analyses (see table 2). Mitochondrial cytochrome-*b* sequences were obtained from three specimens and analyzed in Jim Patton's laboratory. One rat was collected at Bakubakulu (locality 6 on the map in fig. 22) in the Puro Valley, which is just north of my transect; no DNA sequences are available for it.

In the canonical variate ordinations (fig. 27), scores for two of the animals from Gunung Balease cluster with scores representing the northern and eastern population samples (northern peninsula, Bumbarujaba, Gunung Tambusisi, Pegunungan Mekongga, and Lalolei), but the third score falls in the constellation formed by points identifying samples from the west-central mountain block (Sungai Oha Kecil + Sungai Sadaunta, Danau Lindu + Gunung Kanino, Bakuba-
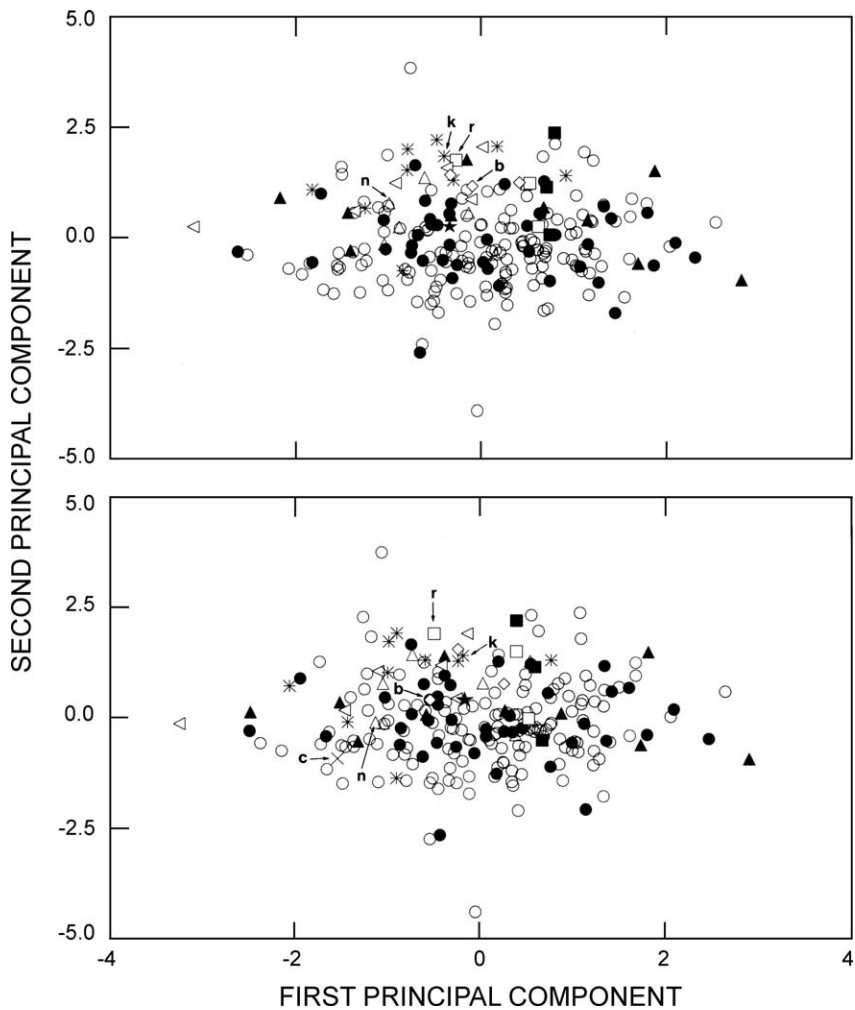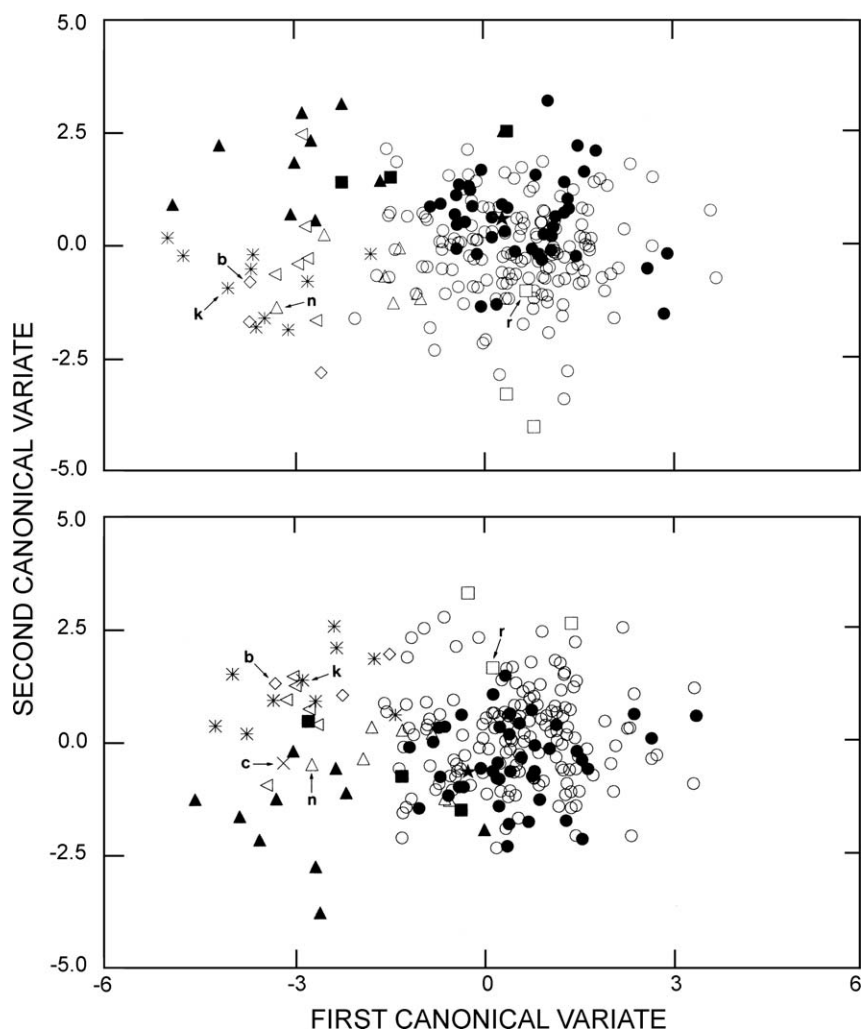
Fig. 27.   Specimen scores representing 10 population samples of *Bunomys chrysocomus* projected onto first and second canonical variates extracted from discriminant-function analysis of 16 cranial and two dental log-transformed variables. Upper graph: All variables are represented and scores for four of the five holotypes are present. Lower graph: The holotype of *chrysocomus* is added, but its skull is incomplete so four variables are omitted (occipitonasal and postpalatal lengths, zygomatic breadth, and height of braincase could not be measured; fig. 24). Symbols: filled triangles = northern peninsula (N = 10); empty triangles = Bumbarujaba (N = 7); empty circles = Sungai Oha Kecil + Sungai Sadaunta (N = 146); filled circles = Danau Lindu + Gunung Kanino (N = 42); empty squares = Gimpu (N = 3); left-pointing empty triangles = Gunung Tambusisi (N = 6); asterisks = Pegunungan Mekongga (N = 11); empty diamonds = Lalolei (N = 3); filled squares = Gunung Balease (N = 3); star = single specimen from Bakubakulu. Arrows and abbreviations identify scores for holotypes: **b** = *brevimolaris*; **c** = *chrysocomus*; **k** = *koka*; **n** = *nigellus*; **r** = *rallus*. Correlations (loadings) among variables with extracted canonical variates and percent variance are listed in table 24.

kulu, and Gimpu). In the Mahalanobis distance (squared) cluster, the sample from Gunung Balease either links with the sample from Pegunungan Mekongga (figs. 21, 28) or is independent, without a discrete link to either of the two primary clusters of population samples (fig. 49) depending on what species are used in the analyses.

TABLE 24
Results of Discriminant-Function Analysis of All Population Samples of *B. chrysocomus*
Upper graph: correlations (loadings) of 16 cranial and two dental log-transformed variables are based on 232 specimens; includes all holotypes (*Rattus nigellus, R. rallus, R. brevimolaris*, and *Bunomys coelestis koka*) except *Mus chrysocomus*. **Lower graph**: correlations (loadings) of 12 cranial and two dental log-transformed variables are based on 233 specimens; includes the holotype of *Mus chrysocomus* (its skull is incomplete); see figure 27.

	Correlations			
	Upper graph		Lower graph	
Variable	CV1	CV2	CV1	CV2
ONL	−0.10	0.24***	—	—
ZB	−0.12	0.37**	—	—
IB	−0.11	0.24***	−0.14*	−0.06***
LR	0.05	0.14*	0.03	0.34***
BR	0.26***	0.10	0.24***	−0.66*
BBC	−0.38***	0.37***	−0.42***	−0.57***
HBC	−0.43***	0.04	—	—
BZP	0.47***	0.20**	0.48***	−0.33
LD	−0.39***	0.24***	−0.42***	−0.13
PPL	0.12	0.02	—	—
LBP	−0.19**	0.22***	−0.23***	−0.23
BBP	0.12	0.04	0.14*	−0.04
BMF	0.34***	0.11	0.36***	−0.19
LIF	−0.40***	−0.31***	−0.38***	0.40*
BIF	0.19**	−0.22***	0.22***	0.14***
LB	−0.36***	−0.20**	−0.37***	0.34**
CLM1–3	−0.29***	0.23***	−0.33***	−0.33***
BM1	−0.07	0.38***	−0.10***	−0.44
Canonical correlation	0.791	0.561	0.765	0.520
Eigenvalue	1.669	0.460	1.414	0.370
% Variance	52.6	14.5	57.6	15.1

*** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$.

Both principal-components and canonical variate ordinations place the score for the specimen from Bakubakulu in the heart of the cloud of scores representing the samples from the west-central mountain block (figs. 26, 27). In the Mahalanobis cluster diagrams, no matter the composition of the species, the specimen always links with the sample from Sungai Oha Kecil + Sungai Sadaunta (figs. 21, 28, 49). This placement is significant in that Bakubakulu (01°07′S, 120°00′E) is not far from Tangoa (01°10′S, 120°05′E), also in the Puro Valley, where Chris Watts collected specimens and preserved tissues from which DNA sequences could be extracted. Attached to the Tangoa specimen is a cytochrome-*b* sequence available from GenBank (ABTC 65755; I have not seen the voucher or any of Watts's material from the Puro Valley), and I am assuming it could easily represent cytochrome-*b* sequences for the population of *B. chrysocomus* in the Puro Valley, including the sample from Bakubakulu.

Placements of the scores for three specimens from Gunung Balease and the animal from Bakubakulu in multivariate space are summarized in the lower canonical-variate scatter plot in figure 28. The left cloud contains scores for the northern and eastern population samples combined, the right assemblage represents combined samples from the west-central region. The two constellations marginally overlap, the sample from Gunung Balease overlaps each large cluster, and the score for the Bakubakulu rat is nestled among those for the animals collected in the west-central region. The molecular distance between the cytochrome-*b* sequence from the Tangoa animal (which I use as a stand-in for the Bakubakulu rat, that is, drawn from the same population) and those from Gunung Balease is about 1% (the molecular trees were provided by Jim Patton and Kevin Rowe), "which is well within what might be viewed as a 'typical' intraspecific range" (J.L. Patton, in litt., 2011; see also Baker and Bradley, 2006). The meager genetic data combined with the larger set of information revealing morphometric variation among samples suggests that samples available to me represent a single species. There are homogeneous populations in some areas (the west-central mountain block, for example) that are somewhat different in their genetic and morphometric attributes from populations in other regions of the island, but the geographic variation seems to be contained within *B. chrysocomus*. This is a reasonable hypothesis but certainly one that requires testing by analyzing DNA sequences from multiple genes (mitochondrial and nuclear) derived from far more geographic samples, and also looking at variation in cranial and dental variables in large samples from currently unsampled geographic regions. Expansive stretches of the island have not been surveyed for the species: most of the northern peninsula, the Pompango
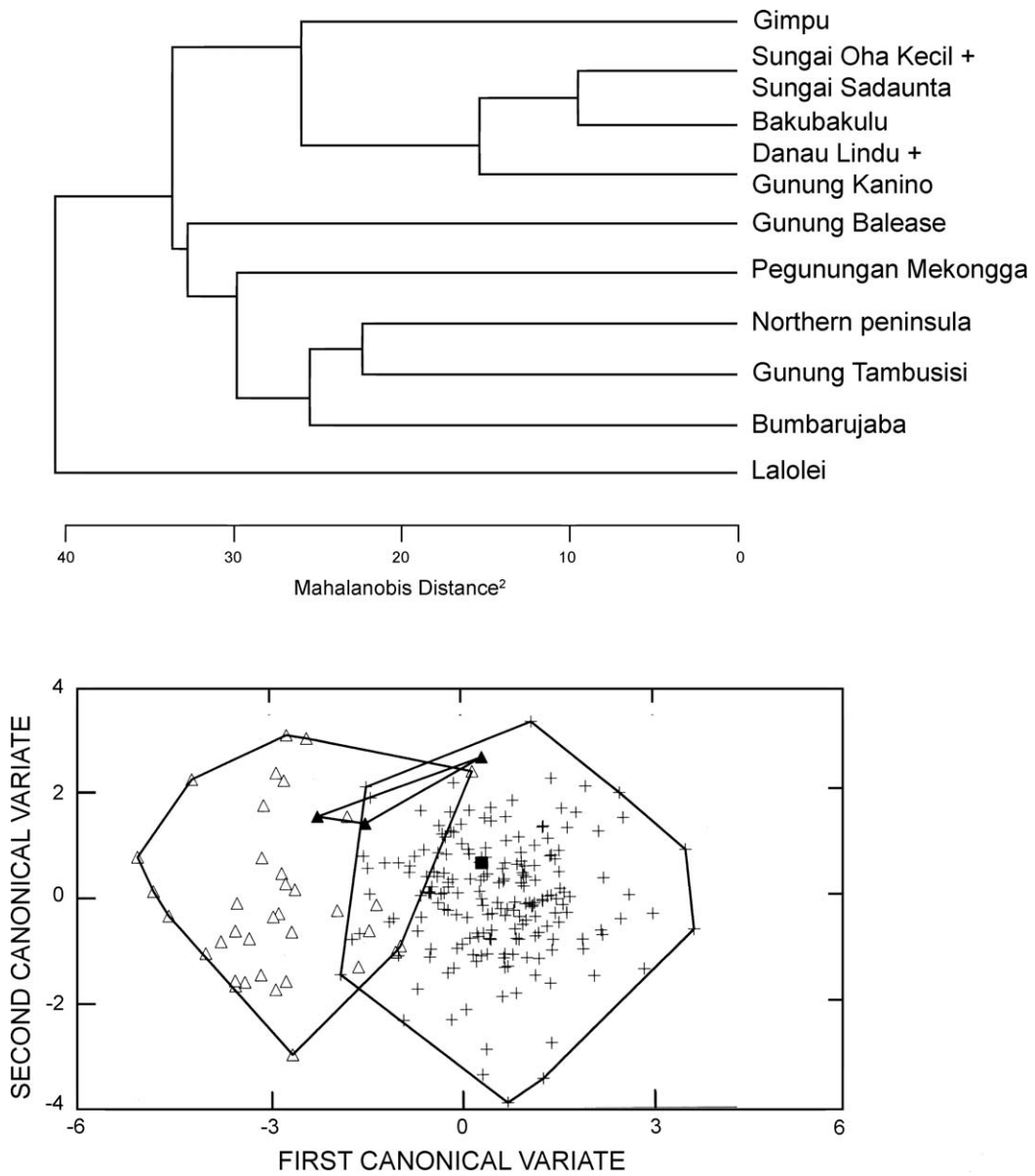
Fig. 28.   Upper diagram: Phenogram generated from UPGMA clustering of squared Mahalanobis distances among 10 population sample centroids for *Bunomys chrysocomus*, as derived from discriminant-function analysis. Lower diagram: Specimen scores representing *B. chrysocomus* projected onto first and second canonical variates extracted from discriminant-function analysis of 16 cranial and two dental log-transformed variables. Scores represent four samples: (1) combined population samples from northern peninsula, Bumbarujaba, Gunung Tambusisi, Pegunungan Mekongga, and Lalolei (empty triangles; $N = 36$); (2) series from Sungai Oha Kecil + Sungai Sadaunta, Danau Lindu + Gunung Kanino, and Gimpu (crosses; $N = 192$); (3) Gunung Balease (filled triangles; $N = 3$); (4) Bakubakulu (filled square; $N = 1$). The upper graph in figure 27 shows the same overall distribution of scores but with separate population samples identified. See table 24 for correlations (loadings) among variables and percent variance explained.

mountains east of Danau Poso, the entire eastern peninsula, most of the west-central mountain block south of the Danau Lindu area, and the remnants of forest on the southwestern arm require focused survey efforts. Current samples are unequal in size (available series of specimens from Bogani Nani Wartabone National Park, Bumbaru-jaba, Gunung Tambusisi, Pegunungan Mekongga, and Lalolei are small, ranging from 3 to 11 specimens for a total of 37) and univariate mean differences among all the population samples are not great (tables 21 and 22). Available samples are unequal in composition of adult age categories and future inquiries into patterns of geographic variation should be based on comparisons among similar adult age classes.

Of course, analyses of gene sequences in samples from the same regions from which my samples were obtained, and analysis of morphometric traits in samples from regions where specimens are now not available, may produce a different pattern of phenetic and genetic alliance among regional populations that is not revealed by my present analyses.

From my study of variation in cranial and dental variables emerged another pattern of phenetic relationships among some of the population samples that are instructive with-in the context of contrasting samples from montane habitats in different regions of Sulawesi. Are montane populations in differ-ent areas isolated by stretches of lowland forest closely related to one another or is a particular population in montane forest more closely related to the population inhabiting the adjacent lowlands covered by tropical lowland evergreen rain forest? My analyses points to a closer tie (phenetically and presumably genetically) between highland and immediately adjacent lowland popula-tions than among distant montane regions, at least in comparison between samples from the core of the island and those from the southeastern peninsula. In the west-central region, the specimens from along my transect come from lowlands and middle elevations along the Sungai Oha Kecil, Sungai Sa-daunta, and in the valley of Danau Lindu in tropical lowland evergreen forest, and from higher elevations on nearby Gunung Kanino in lower montane forest. Scores for

these specimens are tightly packed in mutil-variate space as reflected by first and second canonical variates and phenetic clustering based on squared Mahalanobis distances among centroids (figs. 27, 28), which suggests uninhibited gene flow between the lowland to middle-elevation populations (Sungai Oha Kecil, Sungai Sadaunta, and Danau Lindu) and the one in the adjacent highlands (Gunung Kanino).

None of the scores for the specimens in "Danau Lindu + Gunung Kanino" are close to the scores representing the sample from Pegunungan Mekongga on the southeastern peninsula. In the canonical-variate ordina-tions, scores for individuals from that moun-tain range fall closer to the points represent-ing the sample from Lalolei, located in the lowlands south of Pegunungan Mekongga. The samples from the southeastern peninsula are small and none come from a transect linking samples from lowland tropical ever-green rain forest with montane forest habitats on the Mekongga range, but the analysis suggests a stronger phenetic (and inferentially genetic) link between lowland and highland populations on the southeastern arm than between the Pegunungan Mekongga popula-tion and those in montane habitats of the west-central region.

In this context of montane samples one other small group of specimens deserves attention. The highest point from which a sample of *B. chrysocomus* has been collected is 2200 m on Pegunungan Latimojong, the highlands forming the southern margin of the west-central mountain block. That series is not included in the multivariate analyses of cranial and dental measurements. Of the seven specimens available to me, one is an old adult, two are adults, one is a young adult, another is a very young adult (in fresh adult coat), and two are juveniles. I could obtain a complete set of measurements from only one of the young adult skulls (table 22); two from the other adults are in fragments and one skull is missing. The juvenile skulls and that from the very young adult, although complete, are too young to include in the multivariate analyses. Values for cranial and dental measurements from the intact young adult skull fall within the range of variation seen in the other geographic samples of *B.*

chrysocomus from the mountain block (tables 21, 22). Crown lengths of maxillary molar rows and breadths of first upper molars, which could be measured in five of the seven skulls, range from 6.1 to 6.2 mm and 2.0 to 2.1 mm, respectively, also well within the range of variation for these two variables in the other three population samples from the west-central region. Dorsal and ventral coats of the five adults are long (15–20 mm), and browner than in most other population samples, but with a sheen and silky texture resembling most other examples of *B. chrysocomus.*

In summary, geographic variation in qualitative traits associated with the skull and molars, or with any aspects of fur traits (texture, thickness, and coloration), tail pattern, or dimensions of combined head and body, ears, feet, or tail is not readily apparent or lost within the variation seen in any large single sample. By contrast, intersample variation in measured dimensions of crania and molars is present, as shown by discriminant-function analyses. Revealed are two primary sets of samples: one is from the west-central mountain block, the other contains samples from the northern peninsula, western margin of the eastern peninsula, and the southeastern arm of the island. Absolute and proportional differences among univariate means responsible for the geographic patterns are modest and usually undetectable by visually comparing skulls and dentitions (using specimens of relative comparable age). The degree of difference between the two geographic clusters in Mahalanobis distance units is far less than the magnitude separating the morphologically similar and montane *B. coelestis*, *B. prolatus*, and *B. torajae,* n. sp., from the population samples representing *B. chrysocomus* (fig. 49).

NATURAL HISTORY: Information presented here is organized under habitat, diet, burrows, nests, development of young, testes and sperm, and forest pathways.

Habitat: *Bunomys chrysocomus* was commonly encountered along the transect area extending from Sungai Oha Kecil to Gunung Kanino in forest formations embracing environs in tropical lowland evergreen rain forest (figs. 29–31, 96–98) and lower montane forest (figs. 32, 79) through the elevational range from 320 m to 1555 m (fig. 103). More specimens of *B. chrysocomus* (323 examples) were collected than any other murid, all but five were taken in lowland tropical evergreen rainforest habitats, and those five were trapped in lower montane forest (fig. 103). Only *Paruromys dominator* (306 specimens) came close to the dominance of *B. chrysocomus* along the transect line, followed by *Rattus hoffmanni* (201 examples) and *Rattus facetus* (161 specimens).

Nocturnal and terrestrial, all but two specimens were caught on the ground. The exceptions are one taken on a woody vine about 2 ft above ground, another on a vine 3 ft above ground; both places were easily accessible from ground level.

Examples of the microhabitats in which we trapped *B. chrysocomus* are described in table 25 (the descriptions are selected to cover the range of habitats trapped and not to document where every rat was trapped). Mean ambient air temperatures ranged from 61.1° to 80.9° F in the lowland forest from Sungai Oha Kecil (290 m) to Sungai Tokararu (1150 m), with high relative humidity; 58.4° to 68.9° F and comparable relative humidity characterized lower montane forest on Gunung Kanino (table 3).

Mature tropical lowland evergreen rainforest habitats where we encountered most of the *B. chrysocomus* along the transect is floristically species rich. While our floristic survey was not exhaustive, we either collected samples of or identified approximately 350 species of trees (canopy species, emergents, and understory trees), nine species of solitary palms (in *Areca, Pinanga, Pigafetta, Arenga, Caryota,* and *Licuala*), a dozen species of rattan (*Calamus Korthalsia,* and *Daemonorops*), half a dozen species of terrestrial pandans (*Pandanus*) and climbing pandans (*Freycinetia*), several kinds of gingers, a few lilies, two species of native bananas (*Musa*), dozens of shrubs, two kinds of bamboo, and some woody and herbaceous vines.

Most *B. chrysocomus* were encountered in steep and wet hillside forest, on forested terraces bordering streams and rivers, along streams at the waters edge, and occasionally on decaying tree trunks and limbs spanning streams (figs. 29, 30).

TABLE 25
Selected Examples of Microhabitats at Trap Sites in Which Some of the Specimens of *Bunomys chryscomus*
Were Collected on My Transect in Central Sulawesi, 1973–1974
Descriptions of the collection sites are summarized from my field journals (in Mammalogy Archives at
AMNH). See habitats in figures 29–32.

Place and date	Microhabitat
Sungai Oha Kecil	**Primary tropical lowland evergreen rain forest (320–488 m)**
	Streamside or just above stream at base of steep hillside
(July 30– Sept 5, 1974)	On ground 1–3 ft above stream alongside partly cut bank in understory—very damp, good cover of shrubs, ground blanketed by debris and leaf litter.
	Ground at base of cut bank among large, open roots of strangler fig growing 10 ft higher on bank. *B. chrysocomus* also taken nearby on ground under roots of small tree growing from undercut bank away from stream, undergrowth densely shrubby.
	On damp ground beneath overturned rotting base of a large tree that was laying downslope and over the stream; good runways, very damp; dense streamside vegetative cover.
	Alongside rotting tangle of trunk and limbs on steep rocky slope just above stream, all covered, including the trunk and limbs, by dense streamside vegetation; 5 ft away a limb from this tangle lay across the stream and on it I caught three *B. andrewsi.*
	On wet, decaying trunk (not mossy) across stream (two other *B. chrysocomus* and a *Maxomys muschenbroekii* were taken at same spot); on nearby terrace caught *B. chrysocomus* at base of rocks
	Above stream in moss-covered cleft 5 ft from ground in damp, moss-encrusted rock cliff face; other *B. chrysocomus* were trapped nearby on ground in dense low shrubbery above stream in upper streamside forest—no special rock, trunk or other cover, just dense undergrowth.
	Open ground beneath base of decaying trunk where upturned roots are resting on the ground, on very steep, short steamside forest; three other *B. chrysocomus* were taken at same spot.
	On steep, wet upper streamside slope; trap set at base of boulder that is part of a jumble of rocks densely covered with understory shrubs and vines; many cavities among large and small rocks; probably washed by water during high runoffs, but used by rats when stream is lower and not flooding.
	In runway beneath roots on cut bank above stream; one *Rattus hoffmanni*, *Rattus facetus*, and another *B. chrysocomus* were caught in same spot.
	On ground at end of huge, wet, rotting trunk laying in dense shrubby understory of streamside forest; adjacent slopes are steep.
	On wet ground beneath pile of rotting limbs draped over tree roots on stream terrace, very dark and damp—upper streamside forest.
Sungai Sadaunta	**Primary tropical lowland evergreen rain forest (762–1037 m)**
	Steep hillside forest
(Feb 5–March 8, 1974)	On forest floor beneath dense undergrowth.
	On ground among tall roots of large *Ficus* on steep hillside; caught other *B. chrysocomus* here.
	On gound inside base of trunk remnant of huge tree decaying on ground—only skeleton of outer trunk remains.
	On leaf litter alongside rocks, underbrush is dense, patch of ferns and shrubs, probably regenerating vegetative cover over landslip or clearing made by old treefall.
	On ground beneath base of decaying trunk lying down hillside; caught other *B. chrysocomus* here.
	On wet, leaf-littered forest floor in open part of understory below large pangi (*Pangium edule*) and torode (*Pterospermum celebicum*) trees, no undergrowth here, only open space in understory.
	Trap set in runway under and alongside root of tall strangler fig, this and an adjacent strangler fig are well developed and enclose living canopy tree host.
	On ground beneath decaying trunk bridging damp, leaf-littered ravine in forest on hillside terrace above stream.
	On steep hillside beneath tangle of rotten branches and twigs that are part of an old treefall.
	Terrace above stream near camp
	On damp ground at end of rotting limb in thick shrubbery on terrace above a small tributary of Sungai Sadaunta.
	On ground among rocks covered with a dense undergrowth of epiphytes, small shrubs, moss, and ferns.
	In wet and damp forest above gully joining main stream; understory of saplings, gingers, shrubs, palms (*Caryota*, *Pinanga, Areca*), and much rattan; caught another *B. chrysocomus* on the forest floor here.

TABLE 25
(Continued)

Place and date	Microhabitat
	On wet ground in front of large angular opening into rock pile; caught several *B. chrysocomus* here.
	On leaf litter in open space in understory; *Maxomys muschenbroekii* was taken nearby.
	On wet ground beneath jumble of rotting, wet limbs on steep hillside in dense underbrush above terrace. *B. chrysocomus* was also trapped nearby on damp ground at base of moss and fern-covered rocks in dense cover of shrubs and ferns on stream terrace.
	On ground in front of burrow entrance at base of medium-sized tree (bole 1–1.5 ft diameter near ground) at junction of hillside and terrace above stream, between short buttress roots (2 ft high, 1 ft from bole); leaf litter and debris has accumulated and been nearly incorporated with earth; burrow entrance 2 in. wide in one of these alcoves; typical hillside forest understory.
	On wet ground beneath tangled understory of rattan and shrubs on terrace of small tributary to Sungai Sadaunta, undergrowth is thick, mostly tall shrubs, tall gingers, and rattan, along with woody and monocot vines, good cover for small mammals, very wet, much leaf litter.
	On leaf litter in open place in very steep hillside, relatively dry (drier than along stream), good forest, about 50 ft above stream.
	On wet ground beneath rotten, moss-covered trunk leaning from cut bank to ground. High (15 ft) terrace above stream; dense underbrush of shrubs and ferns; ground muddy, rocky, eroded but still partly covered with leaf litter.

Mixture of primary forest, disturbed forest, coffee grove, and garden near house (675 m)

Intact primary forest

Rats were taken on ground in underbrush alongside dry creek; under rocks in open understory of streamside forest; runway among roots of giant strangler fig; beneath rotting trunk in shrubby understory of streamside forest; on ground beneath rotting roots and stump in understory of steamside forest; along earth bank beneath overhang in shrubby understory; on ground under rotting trunk of huge tree, nearly covered by shrubby and viney understory; on ground beneath boulder in boulder-strewn streamside forest.

On large woody vine growing from steep hillside and into canopy from where it hangs down 2–3 ft from ground; two traps were placed back to back, rat caught in trap with opening facing ground.

Trap above ground on tree (8–10 ft diameter) that grows from steep slope and out through the understory (of saplings, small trees, thin shrubs, rataan, leafy and woody vines) in a low arc, so it forms a long (40 ft) limb platform in the understory above the ground; two *Rattus facetus* also taken here.

Slightly thinned forest along stream

B. chrysocomus was caught on clear ground underneath boulder in dense undergrowth; runway along rocks beneath dense undergrowth; damp ground underneath limbs next to creek; at base of rocks in dense undergrowth; on top of trunk and vine about 1 ft off ground in understory; on leaf litter at base of young tree in understory of forest; on ground under boulder and roots; base of emergent strangler fig.

Three feet above ground on thick woody vines at base of giant canopy carmel-barked tree—the vines twirl and twist from the crown down the trunk of the tree to a mass of loops on the ground around the base of the tree; caught one *Rattus facetus* in same spot and another *B. chrysocomus* on ground beneath the tangle of woody vines.

Two *chrysocomus* 4 feet off ground on top of large rotten stump covered with vines.

Coffee grove

B. chrysocomus were encountered among interstices of rocks next to stream; in scub adjacent to coffee trees; runway along rocks and tree limbs in dense undergrowth beneath coffee trees; on ground beneath roots of large emergent strangler fig shading coffee trees; beneath decaying trunk lying in dense undergrowth next to newly planted coffee grove; along base of rocks in dense undergrowth between coffee grove and stream.

Disturbed habitat

Two *B. chrysocomus* in a garden between a house and dense scrub (caught one *Rattus tanezumi* here); two *B. chrysocomus* in cut-over forest next to a house.

TABLE 25
(Continued)

Place and date	Microhabitat
Tomado	**Deep intact forest, slightly disturbed areas, coffee grove (1000 m).**
	Intact primary forest
(July 21– September 11, 1973; Jan 15–21, 1974; May 12–28, 1974)	Several *B. chrysocomus* trapped on ground beneath understory in deep forest; runway beneath rotting trunk covered with moss and vines; beneath moss-covered jumble of large branches and smaller limbs from old tree-fall; on moss-covered rotting trunk (1 ft diam) lying across stream 6 ft from water surface; open ground underneath tangle of rattan on steep slope (caught *Taeromys celebensis* in same spot, *Maxomys hellwaldii* and *Rattus hoffmanni* nearby on terrace).
	Stream and meadow
	In dense scrub alongside stream, and dense scrub on other side adjacent to meadow; on ground beneath shrubs, ferns, and vines bordering forest on one side and large meadow on the other.
	Slightly thinned forest
	On ground in undergrowth of slightly thinned forest; among roots of large strangler fig; alongside large trunk lying on ground; beneath tree trunk and tangle of rattan and shrubs.
	Coffee grove
	Beneath trunk lying in scrub next to coffee grove; caught *Rattus hoffmanni* on top of trunk.
Sungai Tokararu	**Primary tropical lowland evergreen rain forest (1150 m)**
(September 12– October 11, 1973)	On matted leaves, twigs, and soil deep beneath jumble of rotting tree limbs in clearing caused by huge treefall; caught *Taeromys celebensis* two other *B. chrysocomus*, and two *Rattus hoffmanni* in same spot.
	On wet leaf litter beneath huge (house-size) jumble of decaying branches, larger limbs and trunks of old treefall.
	Rats taken beneath rotting stump and nearby under moss-covered decaying trunk on ground.
	On top of moss-covered rotting trunk in open understory of forest.
	On large limb 3 ft from ground, part of a large, old treefall; caught *Rattus facetus* in same spot and *Taeromys callitrichus* on ground next to the trunk.
	On large, moss-covered woody vine 1 ft from forest floor; vine drapes down from canopy through understory.
	In runway alongside high walllike root of huge emergent strangler fig; vines and shrubs grow around the base of the tree and over the roots, leaf and rotting twigs form a deep carpet and fill spaces between the high shouldered roots; five other *B. chrysocomus* were taken here along with a *Rattus hoffmanni*.
	On ground at base of emergent strangler fig; within the interstices of same tree and about 10 ft from ground caught two *Paruromys dominator*.
	On ground in hollow base of huge emergent strangler fig; trapped three *B. chrysocomus*.
	In runway alongside decaying, moss-covered trunk lying on forest floor; two *Paruromys dominator* were caught in same spot.
	At base of tree on leaf litter in open part of the forest understory.
Gunung Kanino	**Primary forest: upper band of lowland evergreen rain forest-lower montane forest (1190–1555m; lower montane begins about 1285 m)**
(October 5–November 20, 1973)	On leaf litter of forest floor at base of small tree in understory.
	Runway along clump of exposed roots on steep slope in dense understory consisting of rattan, shrubs, woody and herbaceous vines, some covered with moss.
	On ground among roots at base of small tree on steep slope; understory dense, forest like at 1150 m; two *Rattus hoffmanni* also taken here.
	Beneath decaying, moss-covered trunk on leaf-carpeted forest floor near large strangler fig; relatively open understory in tall forest.
	In runway beneath roots, vines, rotting limbs, leaf and stem litter, and rattan rosettes in very dense understory on hillside forest; *Taeromys hamatus* caught just above this spot; this is part of dense second-growth between 1220 and 1311 m that is covering an old landslip and tree-fall area; undisturbed tropical lowland forest just below and lower montane forest above; on either side of this regrowth the transition between intact lowland and lower montane formations is sharp.
	On forest floor in tunnel-like runway beneath dense tangle of rattan fronds, tree branches, and woody and herbaceous vines in open part of forest.
	In runway beneath decaying moss-covered trunk lying on ground in chestnut forest; caught *Bunomys penitus* and *Rattus hoffmanni* in same spot (see figure 32).

Fig. 29.   Tropical lowland evergreen rain forest along the Sungai Sadaunta, 750–850 m (in 1974). Typical forest composition on terraces just above the stream: dense undergrowth of shrubs and tree saplings, woody vines looping through the understory. Beneath the dense cover, the ground is wet, the air cool. Most *Bunomys chrysocomus* were trapped in this kind of stream terrace habitat, either on the ground beneath the shrubs, alongside decomposing, moss-covered trunks and limbs lying on the terrace, or among moss-covered rocks. *Bunomys karokophilus,* n. sp., was encountered in similar habitat.

Vegetation bordering streams the size Sadaunta and its tributary Pormina at about 700 m (fig. 31) form good examples of bank and terrace habitats. The waterways may be open in spots but usually have a broken or partial canopy shading them. A low partial or complete canopy over the stream is provided by half a dozen species of understory figs (which include *Ficus lepicarpa, F. minahassae, F. adenosperma, F. obscura, F. nervosa, F. geocarpa* among others) that line the banks. These figs are the most common small tree along the streams and a few of them also grow back on terraces and hillsides. Their crowns, coming from each side of the stream sometimes intertwine over it and in places are connected by looping and coiling woody vines. Growing up through the figs as tall emergents are *Wanga* palms (*Pigaffetta filaris*), some *Lekotu* (*Duabanga moluccana*), the common *Leutu* (*Pometia pinnata*), and scattered *Leda* (*Eucalyptus deglupta*). At spots, the *Wanga* palms are dense enough to form a high canopy. Beneath the *Wanga* palms and tall trees are scattered ground and tree ferns; the palms *Korthalsia celebica, Arenga undulatifolia, Areca vestiaria, Caryotis mitis*, and the occasional *Pinanga* sp.; bananas (two species of *Musa*) that form groves in forest openings; the understory tree *Semecarpus* sp.; dense shrubs mixed with tall waist-high ground ferns, gingers, *Pandanus* sp., and a variety of broad-leaved monocots. Decaying wet tree trunks and limbs clutter the banks, here and there bridging the stream.

Mature forest at the level where Sungai Pormina joins the Sungai Sadaunta, about 700 m, is comprised of many species of large

Fig. 30.   Traps set (1974) below the stream terrace on wet and rocky banks of the Sungai Sadaunta beneath dense streamside vegetation yielded *Bunomys chrysocomus*. Rats were caught along the margin of the terrace (upper part of the photograph); on rocks beneath the ferns, rattan rosettes, and broad-leafed monocots; and on rocks only a few inches from the water's edge.

and old trees, some forming the high canopy, others emerging above it, and is characteristic of lowland and middle elevation forest along the transect. On the higher terraces back of the streams and base of the steep hills, for example, *Dysoxylum densiflorum*, *Magnolia vrieseana* (with boles 6 ft in diameter at waist level), *Ficus magnifolia* (4 ft diameter near base), *Ficus cordatula*, *Octomeles sumatrana*, *Pterospermum celebicum*, *Aglia argentia*, *Canarium* sp., and *Palaquium obovatum* are some of the common big trees, along with scattered strangler figs (*Ficus* sp.). Commonly encountered understory trees are *Dillenia serrata*, *Pangium edule*, *Macaranga* sp., *Siphonodon* sp., and the laurels *Litsea* and *Alseodaphne*. Most of the terrace species extend onto the hillsides, but there the most common high-canopy former is usually *Mussaendopsis beccariana*. Scattered oaks (*Lithocarpus* sp.), walnut (*Engelhardtia serrata*), *Calophyllum* sp., the occasional ebony (*Diospyros macrophylla*), old strangler and solitary figs also contribute to the canopy. Recognizable understory trees are *Nauclea puberla*, *Timonius koordersii*, *Pouteria maclayana*, *Elaeocarpus* sp., nutmegs (*Knema*, *Myristica*), *Artocarpus* sp., and *Cinnamomum* sp. The sugar palm *Arenga pinnata* is scattered through the forest as are the palms *Areca vestiaria*, *Pinanga* sp., and *Caryota* sp. Here and there are clumps of pandans and groves of *Casurina* in open spots.

Bunomys chrysocomus, although commonly found in wet and shaded parts of the forest, is also one of the few murids found in the drier steep hillside forest and ridgetops well away from streams. For example, we set a trapline in steep hillside forest away from any streams or wet ravines from 763 to 1068 m above one of our camps and caught 40 *B. chrysocomus* and three *Paruromys dominator*. Other murid species were in these hillside forests but only in damper situations along small tributary brooks and the sides of wet ravines.

Fig. 31.   Tropical lowland evergreen rain forest along the Sungai Sadaunta, 700 m (in 1976). Examples of *Bunomys chrysocomus* were caught amid the rocks in the foreground, deep within the forest, and occasionally on trunks and branches spanning the stream. Similar dense streamside forest and bridging trunks and limbs from old treefalls characterize much of the habitat along the Sungai Sadaunta where *B. chrysocomus* as well as *B. karokophilus,* n. sp., were encountered (see Natural History in account of *B. chrysocomus*).

Fig. 32. Lower montane rain forest on Gunung Kanino, 1556 m, 1973. During different nights, *Bunomys chrysocomus*, *B. penitus*, and *Rattus hoffmanni* were trapped in a damp runway beneath the large decomposing and moss-covered chestnut trunk shown here. This is the highest spot where I encountered *B. chrysocomus*, which proved to be rare in this lower montane habitat as compared with the higher concentrations at lower elevations in tropical lowland evergreen rain forest (see fig. 103). *Bunomys penitus*, which extends down to the lower limit of lower montane rain forest at 1285 m, was common in the forest here and the only species of *Bunomys* found at elevations above 1556 m and all the way to the summit of Gunung Nokilalaki (see fig. 103). *Paruromys dominator* was frequently encountered in the forest surrounding the decaying trunk, *Maxomys musschenbroekii* and *Rattus facetus* were trapped nearby. *Prosciurillus topapuensis* and *P. murinus* were the squirrels usually seen, but the large reddish *Rubrisciurus rubriventer* was rarely encountered.

Most of the *B. chrysocomus* came from intact primary forest, but we did trap a few in other habitats. One was scrubby secondary growth on landslips and clearings made by tree-falls in intact old-growth forest. An example was a place on a high terrace along the Sungai Sadaunta where the mature forest was interrupted by a 40–50 ft square area covered by regenerating growth 10–20 ft high concealing a fallen canopy tree, now shattered into decaying limbs and trunk partly covered with moss. Low ground shrubs, bananas, clumps of ginger, dense thickets of ground ferns and spiny rattan rosettes, young solitary palms and pandans, tree seedlings and saplings, all threaded by herbaceous and woody vines, are typical elements of this secondary growth.

Another was a patch in tall mature forest near the village of Tomado where the understory had been thinned by villagers to plant coffee trees. Huge, tall canopy and emergent trees were left from the old-growth forest to shade the coffee. Among the most prominent of these were strangler and nonstrangler figs (*Ficus* sp.), Uru (*Magnolia vrieseana*), Kume (*Palaquium obtusifolium*), Torode (*Pterospermum celebicum*), Benoa (*Octomeles sumatrana*), Lekotu (*Duabanga moluccana*), and Tahiti (*Dysoxylum densiflorum*).

A third place was scrubby ecotone between high forest and meadow or garden (table 25).

Diet: *Bunomys chrysocomus* consumes invertebrates, small vertebrates, and some fruit, but not fungi (table 13). At several camps I kept a few adults captive (each for 3–4 weeks) and offered them a variety of foods gathered from the forests. Invertebrates and vertebrates were the items most voraciously consumed. All were very selective about fruits, accepting only a very few of the wide range offered. Below I present the foods eaten by *B. chrysocomus* drawn from my observations of captive animals and study of contents extracted from stomachs.

Earthworms (oligochaetes)—A rat aggressively yanked an earthworm from my fingers with its incisors before transferring the worm to its front feet. The rat placed one end of the worm in its mouth, cutting it into segments and pulled the worm through its paws until entirely consumed (the remains of earthworms in most of the stomachs surveyed consisted of short unchewed pieces); the action is to pull, bite off a piece, chew it, swallow, then bite off another segment. No attempt was made to seek the anterior end of the worm (specialized Sulawesi murid vermivores such as *Echiothrix* manipulate the earthworm so it could ingest the anterior portion first and hold the body tight so most of the gastrointestinal contents are forced out of the worm's anus onto the ground; see Musser and Durden, 2014), which resulted in the worm's gastrointestinal contents covering the muzzle and front feet.

All sizes of earthworms were offered and accepted. I had been feeding one captive male small earthworms (2–3 inches long) and one day placed a very large worm (6 inches long, about 3/8 inches in diameter) in the cage. He promptly jumped on the worm but could not initally subdue it, attacking one end and then the other. Repeated attacks caused the worm to eject a clear fluid 8–12 inches into the air from pores along its body. At first irritated, the rat left the worm, cleaned its muzzle, but quickly renewed its attack. Finally he sank his incisors into the last 2 inches of the worm and managed to separate and eat that short segment. Although captive rats ate large earthworms, I found only segments of small worms in stomachs. Smaller earthworms are likely more commonly taken and can be eaten quickly with less exposure of the rat to predators. Earthworms averaging 2 inches long and 1/8 inch in diameter were consumed in 3 to 14 seconds by captive rats; worms 4–5 inches long and 1/8 to 3/16 inches diameter were completely ingested by the rats after 57 to 145 seconds. One rat used 5 minutes to eat a 6 inch long earthworm that it first had to bite into several pieces.

Snails—Managing snails followed a typical behavior by all captive *B. chrysocomus*. Each snail was grabbed with the incisors and transferred to the front feet. The rat usually used 30–60 seconds to turn the shell over and over, trying several spots with the incisors, all the while sniffing the shell. Eventually it began biting off pieces from around the aperature until enough shell had been removed to expose the snail's body; sometimes the rat turned the shell and bit into the side, removing bits of shell until the enclosed body

was exposed. Once accessible, the rat pulled away a bit of the flesh, ingested it, bit away more shell, pulled and ingested more of the tissue, and proceeded in this manner until the entire snail was consumed. After the snail's body was extracted the remainder of the shell was discarded. Sometimes after removing just a few pieces of shell, a rat managed to extract the entire snail. The shell fragments were not ingested, and I never found pieces in the stomachs I surveyed; I did find an operculum along with the partly digested remains of the snail in a few stomachs.

Most of the snails accepted by the rats were small, ½ to 1 inch in diameter and a quarter of an inch thick. I often encountered empty shells this size and some up to 1.5 inches in diameter lying among the leaf litter and debris on stream banks and terraces; all were breached.

Insects and other arthropods—Moths, cicadids, grasshoppers, katydids, crickets, praying mantises, cockroaches, and wasps were provided and all consumed by captive adult rats. Each rat used its incisors to pull the insect from my fingers, transfered it to the front feet and manipulated it until the head was up. It then bit the insect's head and proceeded to voraciously consume head, thorax, and abdomen—wings and legs were discarded. Only heads of the wasps were eaten. Larger insects, such as praying mantises, were propped against the cage floor and consumed beginning with the head.

One particular rat never seemed satisfied with the number of insects provided. One morning I gave it 12 large crickets (up to 2 in. long), which were quickly dispatched and eaten; afterward it kept probing the mesh with its muzzle seeking more. Another rat ate 17 cockroach nymphs (1–1.5 in. long, half an inch wide) at one feeding, consuming one after the other, averaging 90 seconds per nymph. A different rat ate five large katydids (3–4 in. long) in one evening, taking 6–8 minutes to consume each insect. The head, thorax, abdomen, and thicker portions of the hind legs were ingested, wings and other legs were discarded.

A juvenile given small grasshoppers and crickets ate them in much the same way as did the adult rats. Often, however, the young rat fumbled about trying to catch and dispatch a grasshopper by the head in which case the insect would escape and hop about the cage with the little rat in hot pursuit. Once caught and eventually killed the grasshopper was eaten beginning at the head and finishing with the abdomen; only wings and legs were discarded, the typical feeding behavior of adult rats.

Contents of the stomachs I surveyed record additional kinds of insects and other arthropods consumed by *B. chrysocomus*: macrolepidopteran caterpillars, rhinotermitid termites, adult and larval beetles, ants, spiders, and geophilomorph centipedes (table 13).

Other invertebrates—I offered small freshwater crabs found near streams to *B. chrysocomus*—all were ignored.

Vertebrates—I gave small frogs and a small lizard to the captive adult *B. chrysocomus*. One rat was satisfied with three small frogs (1 to 1.5 inches long) at any single feeding bout. The rat grabbed the head, bit it, which immobilized the frog, then turned the frog around and began eating the legs. Both legs were usually eaten first, sometimes the body, but the head was discarded. Sometimes the rat would begin chewing on the head, stop and turn to the legs, ignoring the head. A different rat consumed all but a few foot bones of a frog 2.5 inches long. A juvenile rat seemed less familiar with frogs and those placed in its cage often escaped. Once the frog was subdued, the rat chewed on the hind legs without any attempt to first bite the head to immobilize the frog.

Small frogs are likely one of the most common small vertebrates encountered in the wet forests along streams and sheltered hillsides, the habitats where *B. chrysocomus* was commonly trapped. It was in those places that I collected the frogs fed to the rats.

In another rat's cage I placed a small lizard (head and body 2 in. long, tail about 4 in. long). The rat immediately pounced on the lizard, bit the head, and consumed the entire animal, proceeding from head to tip of the tail, leaving nothing.

Fruit—I offered captive rats a variety of fruits. Those from the following species of canopy and understory trees were rejected: *Chisocheton*, *Garcina*, *Planchonella*, *Knema*,

Aglia, *Palaquium*, *Magnolia*, *Myristica*, *Eleocarpus*, *Siphonodon*, *Lithocarpus*, and some *Ficus*. Fruit from several species of woody vines were consistently rejected as well as fruits from three species of common understory palms, *Areca vestiaria*, *Pinanga ceasia*, and *Pinanga* sp.

Only a few fruits were eaten by the rats. Two species of wild bananas (*Musa*) occur in tropical lowland evergreen rain forest throughout my transect area; the white, sticky pulp of both species was readily accepted and consumed by all captive *B. chrysocomus*; the skin along with the large and hard seeds were rejected. Pulp surrounding seeds of fruit from the canopy tree *Himantandra belgraveana* was eaten, as were small red berries from an understory shrub, and large and small figs from different species of understory *Ficus*. Remains of fig were the most common fruit found in contents of stomachs. Fruit from the *wanga* palm *Pigafetta filaris* was always accepted. The rats neatly removed the scaly covering, ate the transparent jellylike pulp and discarded the single hard black seed. One rat ate the gelatinous pulp that encloses the seeds of a ginger.

Stomachs examined rarely contained only fruit. The content of stomachs from two rats trapped at Tomado is illustrative. One full stomach contained remains of a fig with large seeds and seeds from another kind of fruit; several moderately large cursorial beetle lavae, pieces of a cockroach numph, and one geophilomorph centipede were mixed with the masticated fruit. Another stomach was distended with reddish-brown fruit pulp, remains from two kinds of figs, a fruit with hard orange oblong seeds, and a different fruit with small striped seeds; one well-chewed earthworm, fragments of a young cockroach instar, and remains of a few rhinotermitid soldiers constituted the invertebrate remains.

Stomachs from two rats illustrate contents consisting of primarily invertebrates and little fruit. An animal from Tomado had a stomach packed with rhinotermitid soldiers and workers, and also held remains of a few small adult beetles, a cockroach nymph, geophilomorph centipede, and pulp from figs. The stomach from a rat trapped on the Sungai Sadaunta was distended with remains of arthropods: many rhinotermitid termites and small adult beetles, pieces of larger adult beetles, two kinds of small beetle larvae, one geophilomorph centipede, one macrolepidopteran caterpillar, orthopterans, several cockroach nymphs, and a few ants; a bit of tan-orange pulp and some small pieces of tough rind comprised the meager remains of fruit.

Fungi—I offered captive rats samples of the two kinds of shelf or ear fungi so readily consumed by *Bunomys karokophilus*, n. sp. (see that account), the purplish *Auricularia delicata* and white *A. fuscosuccinea*. Both were consistently rejected. Offerings of cap-and-stem fungi were also ignored.

Overview—*Bunomys chrysocomus* is an aggressive, quick and agile predator of arthropods, earthworms, snails, and small vertebrates. Any insect or frog loose in a cage was immediately chased and caught in a blur of movement; usually a rat grabbed the prey with its incisors, occasionally pinning it to the cage floor with its front feet. The animals are also adept at nosing through leaf litter and debris on the forest floor. I watched a released male nose about in the leaf litter until only half the body was visible, and occasionally dig, then nose about again, dig, and when he located something stop and eat. Most of the work was done with his head and nose, pushing into the litter and sniffing about, sometimes digging or pulling back debris with the front feet. He also ambled over the litter, sometimes making quick jumps of a foot or so. *Bunomys chrysocomus* has access to prey living on the surface of the forest floor (leaf litter, exposed soil surface); within the leaf litter and ground debris; in decaying trunks and limbs of treefalls; on the surface of green leaves attached to stems and branches freshly detached from trees during storms and lying on the forest floor; and on the basal stems of forbs, shrubs, trees, and palms. See the account of *B. andrewsi* for an inventory of the range of invertebrates and small vertebrates found in these places.

The contents of a stomach from a rat trapped at Tomado summarize the range of foods ingested by *B. chrysocomus*. The distended stomach contained pulp and skin

from an unidentified fruit; several earth-worms chopped into segments (contents of the gastrointestinal tract present within each segment, unlike remains found in stomachs of *Echiothrix* in which the worm segments are hollow); several ants; at least one cockroach nymph; one ''hairy spider'' (long hairy legs and part of thorax); at least four kinds of beetle larvae (one small with rows of markings and ''proleg'' type feet, many that are small and intact [5–8 mm long], a few small legless larvae, and thoracic remains from long-legged cursorial larvae); several large margarodid scale insects; small adult staphylinid beetle; skin fragments from a macrolepidopteran caterpillar; and a few rhinotermitid workers. The combination of invertebrates would have been found in leaf litter, decaying wood, beneath rocks, and in soil beneath moss and decaying wood.

I insert a final statement about the reaction by captives to food. All the captive adult *B. chrysocomus* (as well as the examples of *B. andrewsi*, *B. penitus*, and *B. karokophilus,* n. sp.) unambiguously either accepted or reject-ed different foods I offered. Of those rejected, particular items were especially distasteful to the rats (some fruits and fungi) and their first response was to run about the cage rubbing their lips and chin on pieces of wood, leaves, or even the cage floor. Then a rat would use its tongue to moisten its palms to clean the lips and chin.

Burrows, nests, and young: *Bunomys chry-socomus* nests in burrows below ground. I have seen burrow openings in the alcove between buttresses of a tree growing on the terrace of a stream; runways and entrances to burrows along a 6 inch high tree root growing above ground; and under jumbles of rocks lying on a stream terrace just above water level. At about 8:00 A.M. on a ridge terrace at about 1000 m I saw an adult *B. chrysocomus* with two young running around the base of a tree. They heard me. The adult female stopped by a raised root and sat there. The two young ran, each in a different direction, about 2 ft from the root and froze, looking at me. Eventually the juveniles ran off into the undercover and the adult disappeared down a burrow beneath the root. At another time I captured a rat in a live trap that had been placed on the mud

and leaves just above a stream; when released, it peered out of the trap, finally ambled away, then slowly ran uphill about 4 ft to disappear into a burrow beneath a pile of small rocks partially covered with soil and vegetation.

My notes recording construction of nests are summarized here. I placed dry leaves in a small cage with an adult male caught along the Sungai Sadaunta. He arranged these into a globular nest with a deep cup-shaped depression in which he slept. None of the leaves were folded or cut, simply arranged to form the nest. Another rat kept in a small cage on the ground reached between the mesh to pull in pieces of dry stems and leaves of grass and sedges, small forbs, and plant debris. The green, growing plants would be pulled through the mesh, cut and placed on the growing pile of vegetation on which it slept in a depression during the day. At night the rat shoved the debris around with its nose, often burrowing into the pile, and occasionally flushing an insect, which it quickly pounced on and ate.

One captive female kept constructing a nest using dry leaves in much the same way as described above. After about a week, she gave birth to two young. Their growth and interac-tions with the mother are summarized in table 26. One or two young is standard for *B. chrysocomus* and all the other species of *Bunomys* for which I have data covering litter size.

Testes and sperm: Body and testes weights (mass) along with sperm size was derived from two *B. chrysocomus* by Breed and Taylor (2000) and employed in an investiga-tion of murines designed ''to test the hypoth-esis that differences in relative testes mass, and perhaps sperm size, relate to interspecific differences in the amount of intermale sperm competition and in breeding systems.''

Forest pathways: Along my transect in the west-central region and in the Malakosa area, we always set traps on decaying tree trunks and limbs, and palm trunks bridging streams, creeks, and ravines. Traps were also placed on leafy limbs growing across streams. Squirrels used these live bridges as well as rotting and wet trunks and limbs spanning streams, but we caught rats only on the latter, not on the live limbs. By using the trunks and limbs, rats can

TABLE 26
**Ontogenetic Development from Nestling to Juvenile Stages of Young in Litter of *Bunomys chrysocomus*
Captured at Sungai Oha Kecil in Sulawesi's West-Central Region, August–September, 1974**

Date	Developmental progression of young
Aug. 20	Two pups born, each 30 mm long, naked, unpigmented (pink), eyes sealed, little puffy outgrowths for ears, tiny claws, digits webbed, mouth sealed except for pinhole opening. Both squeal when uncovered and detached from mother's teats; easily crawl over leaf litter; nest a depression in pile of dry leaves.
Aug. 21	Pups a few millimeters longer, but have increased in bulk; eyes still shut, digits remain webbed, back and top of head pale gray; silver mustacial vibrissae 3 mm long. Mother modified nest, surrounded herself with dry leaves, is more wary and watches over young more intensely; she will leave nest to grab an insect, but then rushes back and consumes it in the nest.
Aug. 22	Pups 38 mm long, eyes gray and still shut; ears gray, still sealed on one pup, the external pinnae erect on the other; top of back and neck gray; digits beginning to separate distally. Pups pull themselves over the nest with front feet, hind legs still weak; both emit loud squeaks.
Aug. 23	Both pups 42 mm long; solid gray over the back and head; external pinnae gray and erect on both pups; ankles gray, but remainder of feet unpigmented. Bodies covered with fine fuzz. Digits still fused for ¾ their lengths. Eyes still shut.
Aug. 24	Pups about 50 mm long; heads and back solid gray; dorsal surface of tail pale gray; pinnae, forearms, heel, and instep are gray. Eyes still closed. Pups crawl but can almost stand on all legs and move about.
Aug. 25	Pups a bit fatter, more darkly pigmented. Vocalizations beginning to have tone and timber of adult rather than the squeaks and squeals when younger.
Aug. 26	Pups appear strong and bulky, still about 50 mm long; no longer resemble inflated bag with short appendages, but are taking on form of a young rat. Fur thick but still fuzzy, growing towards midline where it is forming a ridge; upperparts of head and body intense solid dark gray, dorsal surface of tail gray, ventral surface unpigmented; pinnae, legs, and plantar surfaces gray. Claws long and conspicuous; digits fully separated; mustachial region prominent. Eyes still shut. Mouths open and pups often yawn. Pups crawl about and burrow into the leaf litter. When left by the mother pups lay together in nest with minor vocalizing.
Aug. 27	Pelage thicker, black and gray hairs give speckled appearance; basic adult outline of pelage covering evident. Eyes still closed. Pups yawn frequently. Periodically, mother grooms back of each pup by vibrating her incisors over the back.
Aug. 28	Pups fatter. Fur covering thicker, forming high middorsal ridge where tips of hairs meet as they grow from each side of body. Tops of ears gray but still appear naked. Pups able to stand for nearly a minute. Mother occasionally drags them from nest until they become disengaged from the teats. Then she returns to the nest, grabs the pup's skin on head or back with her incisors, pulls it back into the nest, then grooms each pup and tucks it beneath her body.
Aug. 29	Pups 65–75 mm long; pelage thicker, upperparts gray and speckled black; underparts grayish white. Eyes remain shut, but membrane gone.
Aug. 30	Pelager thicker and darker; pups actually look like small furry mice. Eyes still shut. Mother extremely protective and responsive to pups, grooms them frequently, licking them over head and body, around genitals and anus, and over feet and tail. Between lickings, she changes into her vibrating motion, going over the body with her incisors, then returns to licking.
Aug. 31–Sept. 1	Pups stronger, tails longer; feet, ears, and head larger. Pelage thicker, upperparts darker. Eyes still shut. Both walk clumsily around cage, scream less when left alone. One pup can scratch itself with its hind foot. Mother protective, leaves nest only to accept insects, then rushes back and eats them at nest.
Sept. 3	Nestlings about 75 mm long; now covered in thicker juvenile pelage. Young are aggressive, strong, and spend more time sleeping than before. Eyes still shut. Pups are large enough now that mother has to lie on her side so they can nurse.
Sept. 4	Young exploring cage; when they bump into the mother they don't try to nurse but amble off erratically in another direction. They stand but still tremble, move erratically, plunging ahead quickly only to topple when they reach their goal; clearly coordination still developing. Grooming behavior much like that of mother: lick front feet, wash their face, scratch with hind feet and lick digits after scratching. Eyes still closed. Vocalizations resemble adult sounds but still higher-pitched.
Sept. 5	Eyes still closed. Pups move about quicker, less erratically; vocalizations becoming more like adult; now yell when mother steps on them, but not when she leaves the nest.
Sept. 6	Eyes have opened. Pups can stand without the body trembling, the tail held straight out with the distal half moving up and down. Both are better coordinated, although they often still fall over when grooming.

TABLE 26
(*Continued*)

Date	Developmental progression of young
Sept. 9	Both young in full, fluffy juvenile pelage. Both still suckling, both run quickly about in the cage and only occasionally stumble or vibrate their tails.
Sept. 12	Young very active and have achieved full body coordination. They run around in the cage, burrow beneath the dry leaves and debris, and occasionally squeeze through the mesh and run around outside the cage. Both are still nursing, but sometimes will grab a piece of cockroach with their front feet, sit back and take tentative bites, only to then discard the piece. Pelage is thick and fluffy, darker and grayer than the adult, the banded hairs pale buffy yellow rather than buffy brown. Ears are shiny dark gray; feet pigmented as in the adult; tail solid tan on the dorsal surface and unpigmented below, covered with tiny silver hairs. Mother still grooms young by licking fur and biting the skin; she turns each over and licks the genital region.
Sept. 14	Still nursing, but active in cage. One squeezed through mesh in the afternoon but returned during the night.
Sept. 16	Young very active, run around the cage chasing cockroach nymphs. They grab the nymph then sit back like the adult and hold the insect with their front feet and start to eat it, head first; still slow and awkward handling the nymph. Beginning to compete with the mother for cockroaches, although cannot quite handle a living, adult cockroach, but will accept a dead or live nymph from my fingers. The young still nurse between bouts of chewing on nymphs.
Sept. 19	Both still nursing, and actively bother the mother as she eats. Young can consume cockroach nymphs much quicker than on previous days. Each night both young leave the cage, wander around in the tent and outside of it, then return to the cage. Mother devours small earthworms in seconds, but young show no interest in either earthworms or snails.
Sept. 23	One young left cage night of 22nd and did not return; other young left next night without returning; mother released same evening. Young were still nursing but also eating insects and aggressively competing with mother for food. Both had shiny, dark gray ears and were in full juvenile pelage that was soft, fluffy, and thick—a pale bluish gray and contrasting with the stiffer, brown adult coat.

scamper across streams and narrow rivers without getting wet. Wet fur is life threatening. Mist and fine droplets of water adhering to the end of the hairs can be shaken off without compromising the insulative capacity of the coat—the fur between hair tips and skin remains dry. If the rats accidentally fall into water or are forced to run through shallow parts of the stream the fur may become soaked and difficult to dry in an environment where the relative humidity is between 90% and 100%.

We saw firsthand the importance of keeping fur dry when occasional intense storms knocked over tents and cages in which we kept some *B. chrysocomus*. The rats were soaked, appeared to be stunned and made no attempt to dry their fur until hours later when the coat had partially dried. Then each rat tried to fluff the fur, but most of the coat remained matted and difficult to groom. Rats taken in live traps unprotected from nightly rains were sickly when we found them in the morning and did not recover.

Rats might scramble over rocks jutting above the water surface in shallow streams.

We placed traps on such exposed rats but invariably caught only toads—no rats. This type of potential crossing is useless when the stream floods during heavy rains, which was usual during the time I worked in forests along the transect. Dead trunks and limbs connecting higher stream terraces usually were higher than flood level.

ECTOPARASITES, PSEUDOSCORPIONS, AND ENDOPARASITES: Sucking lice, fleas, ticks, chiggers, and mites are the groups of ectoparasites utilizing *Bunomys chrysocomus* as a host (table 14). Of the two species of sucking lice (Anoplura), *Hoplopleura chrysocomi* has been found only on *Bunomys chrysocomus* (Durden, 1990), but *Polyplax wallacei* also parasitizes *Bunomys fratrorum* and a species of *Taeromys* (Durden, 1987; Durden and Musser, 1991, 1992).

Six species of fleas (Siphonaptera) in five genera are recorded from *Bunomys chrysocomus*. In addition to *B. chrysocomus*, *Sigmactenus alticola pilosus* (Leptopsyllidae) also infests 14 other species of endemic Sulawesi murine rodents (*Bunomys penitus*, *B. prolatus*,

and *B. karokophilus,* n. sp.; *Margaretamys elegans*; *Maxomys hellwaldii*, *M. wattsi*, and *Maxomys* sp.; *Melasmothrix naso* and *Tateomys rhinogradoides*; *Paruromys dominator*; *Taeromys celebensis* and *Taeromys* sp.; *Rattus hoffmanni* and *R. facetus* [recorded as *R. marmosurus*]), and the nonnative *Rattus exulans* (Durden and Beaucournu, 2000). Besides *Bunomys chrysocomus*, five endemic Sulawesi murids (*Rattus hoffmanni*; *Bunomys penitus* and *B. karokophilus,* n. sp.; *Maxomys* sp.; *Paruromys dominator*) and two nonnative rats (*Rattus exulans* and *R. nitidus*) are also hosts for *Stivalius franciscae* (Stivaliidae; Beaucournu and Durden, 2001). *Gymnomeropsylla bunomydis* (Pygiopsyllidae) parasitizes the Sulawesi endemic rat *Maxomys wattsi* as well as *Bunomys chrysocomus*. (Durden and Beaucournu, 2002). *Nestivalius sulawesiensis* (Pygiopsyllidae) is recorded from *Bunomys chrysocomus* and from *Bunomys fratrorum*, *Maxomys hellwaldii* and *M. musschenbroekii,* and *Rattus facetus* and *R. hoffmanni* (Mardon and Durden, 2003). Finally, *Musserella,* n. gen., species #1 and #4 (Pygiopsyllidae) resides not only on *Bunomys chrysocomus*, but also parasitizes eight other Sulawesi endemic murids (*Bunomys penitus* and *B. fratrorum, Rattus hoffmanni* and *R. facetus, Paruromys dominator, Maxomys hellwaldii* and *M. muschenbroekii,* and *Taeromys celebensis*) and the nonnative *Rattus exulans* and *R. tanazumi* (Durden, in litt., 2008).

Bunomys chrysocomus is host to immature stages (larvae and nymphs) of species in three genera of ticks (Acari: Ixodoidea): *Amblyomma* sp., *Dermacentor atrosignatus* and *Dermacentor* sp., and *Haemaphysalis psalistos* and *Haemaphysalis* sp. (Durden et al., 2008). Collectively, in addition to *B. chrysocomus*, members of these three tick genera have been collected from a suite of other mammal hosts living in Sulawesi: immature stages from shrews (the endemic *Crocidura* sp. and *Crocidura elongata*, and the commensal *Suncus murinus*), two species of bat (*Nyctimene minutus* and *Rousettus celebensis*), three endemic squirrels (*Rubrisciurus rubriventer, Hyosciurus heinrichi,* and *H. ileile*), 12 species of endemic murid rodents (*Bunomys fratrorum* and *B. andrewsi; Margaretamys beccari; Echiothrix centrosa; Maxomys hellwaldii, M. musschenbroekii*, and *M. wattsi; Parur-*

omys dominator; Taeromys sp.; *Rattus hoffmanni*, *R. xanthurus*, and *R. facetus* [recorded as *R. marmosurus*]), four nonnative murines (*Mus musculus; Rattus tanezumi* [recorded as *R. rattus*], *R. argentiventer*, and *R. exulans*), and adults from pigs (*Sus celebensis* and *Babyrousa babyrussa*, both endemics, and the domestic *Sus scrofa*), rusa (*Rusa timorensis*, nonnative), water buffalo (*Bubalus bubalis*, nonnative), humans, and domestic dog (nonnative) (Durden et al., 2008; Musser and Durden, 2014).

Two species of chiggers (Acari: Trombiculidae) are known to parasitize *Bunomys chrysocomus*. *Walchiella oudemansi* also parasitizes *Bunomys fratrorum* and the nonnative *Rattus exulans* (Goff and Durden, 1987; Whitaker and Durden, 1987). *Leptotrombidium deliense* has also been recorded from the endemic rats *Bunomys fratrorum*, *Maxomys musschenbroekii*, *Paruromys dominator*, *Rattus hoffmanni*, and *Rattus xanthurus*. Phoretic deutonymphs of one species of mite (Acari: Histiostomatidae), *Histiostoma* sp., have also been recorded as being attached to laelapid mites (*Laelaps* spp.) parasitizing *Maxomys hellwaldii, M. musschenbroekii*, and *Rattus hoffmanni* (Whitaker and Durden, 1987); as noted above, *Laelaps* sp. have also been recorded from *B. chrysocomus* (L.A. Durden, personal commun.).

The pseudoscorpion, *Megachernes* sp., has been found on *Bunomys chrysocomus* (W.B. Muchmore, in litt., 1986).

A trematode (Trematoda) and nematodes (Nematoda) constitute the endoparasitic records. The human blood fluke, *Schistosoma japonicum* (Strigeidida, Schistosomatidae), is a trematode that requires in its life cycle an oncomelanid snail as intermediate host, and a mammal as the definitive or reservoir host. In the valley of Danau Lindu, humans, along with their dogs and domestic livestock, are reservoirs for the parasite as are the native murid rodents *Bunomys chrysocomus*, *Rattus facetus* [recorded as *R. marmosurus*], *Rattus hoffmanni*, and *Taeromys celebensis*, and the nonnative *Rattus exulans* (Sudomo and Carney, 1974; W.P. Carney, in litt., 1974; see also Clarke et al., 1974; I identified the hosts).

Several reports record nematodes parasitizing "*Bunomys chrysocomus*" and "*Bunomys prolatus,*" but identifications of the hosts have

to be verified (I have not seen the specimens). Specimens from Kabubaten Donggala identified as "*Bunomys chrysocomus*" and series from Lore Lindu said to be "*B. prolatus*" were found to be parasitized by the nematode, *Syphacia rifaii* (Oxyurida, Oxyuridae), which is presumed to infect only species of *Bunomys* (Dewi and Hasegawa, 2010). The sample of "*B. chrysocomus*" was collected at Kampong Simoro, Gunung Watu (01°15′45.8″S, 119°58′40.9″E), 559 m (K. Dewi, in litt., 2012), which lay in the northwestern portion of Lore Lindu not far south of Bakubakulu in Puro Valley, (01°07′S, 120°00′E), 600 m, where *B. chrysocomus* and *B. andrewsi* occur together (table 20). In this region, the two species are closely similar in physical size and color of fur, and the host specimens could be either *B. chrysocomus* or *B. andrewsi*. The other host sample, "*B. prolatus,*" does not reside in the Lore Lindu region and those specimens are likely misidentified *B. chrysocomus* (see my account of *B. prolatus*).

"*Bunomys chrysocomus*" and "*Bunomys prolatus*" from Lore Lindu have also been reported as hosts for the nematodes *Subulura andersoni* (Ascaridida, Subuluridae), *Heterakis spumosa* (Ascaridida, Ascarididae), and *Syphacia muris* (= *S. rifaii*, see Dewi and Hasegawa, 2010); "*Bunomys chrysocomus*" from Lore Lindu is host to *Protospirura muris* (Spirurida, Spiruridae) and *Trichurus muris* (Trichurida, Trichuridae); and "*Bunomys prolatus*" hosts *Molinacuaria indonesiensis* (Spirurida, Acuariidae) (Purwaningsih and Dewi, 2007). Again, *Bunomys prolatus* has been found only on Gunung Tambusisi at the western margin of the eastern peninsula and does not occur in Lore Lindu and I suspect the voucher specimens represent *B. chrysocomus*. The hosts identified as "*Bunomys chrysocomus*" are either *B. chrysocomus* or *B. andrewsi*, which in Lore Lindu are very similar in their external traits.

Finally, Dewi (2008, 2011) reported the nematodes *Subulura andersoni*, *Heterakis spumosa*, *Syphacia rifaii*, and *Gongylonema neoplasticum* (Spirurida, Gonglonematidae) were found in "*Bunomys chrysocomus*" collected at Pakuli, a village in the valley of Sungai Miu at 110 m (01°14′S, 119°56′E; see locality 7 in the gazetteer for *Bunomys*

andrewsi). But 250 m is the lowest *B. chrysocomus* has been collected anyplace in Sulawesi where surveys for small mammals have been conducted (table 6), and 320 m is the lowest point in the valley of Sungai Miu where *B. chrysocomus* was encountered (see gazetteer for *B. chrysocomus*). The only accurately identified *Bunomys* from Pakuli represent *B. andrewsi* (see that account), and that may be the host species for the nematodes reported by Dewi.

SYNONYMS: Information about holotypes of the four taxa that are associated with *Bunomys chrysocomus* and reasons why the name attached to a particular holotype is a synonym is summarized below.

Rattus nigellus Miller and Hollister, 1921a: 72. HOLOTYPE: USNM 218140 (skin and skull; measurements are listed in table 18), an adult male collected November 8, 1916, by H.C. Raven (original number 2936). TYPE LOCALITY: Indonesia, Propinsi Sulawesi Tengah, Bumbarujaba (00°43′S, 120°04′E), 915 m (locality 5 in gazetteer and the map in fig. 22).

Of the four names I synonymize with *chrysocomus*, two of them were proposed by Miller and Hollister. The first, *Rattus nigellus*, Miller and Hollister (1921a: 72) diagnosed as:

a small dark member of the *chrysocomus* group with long, soft pelage. Flanks as dark as back, median area of underparts cinnamon drab. Flecking of upperparts brown, not yellowish; wrist and heel blackish; toes whitish. Tail short, almost entirely blackish, with only a slight indication in a few specimens of light color on underside. Skull smaller than that of *Rattus adspersus*.

The authors remarked of *nigellus* that "this small species is related to *R. adspersus* rather than to *R. chrysocomus* of northern Celebes. It is easily distinguished from *adspersus* by its lesser external measurements; longer, softer pelage; and small skull." Twelve specimens were identified as *nigellus*, 11 from Bumbarujaba, the type locality, and one from Labuan Sore. I located three additional examples of *nigellus* that Raven had trapped at Bumbarujaba (see locality 5 in the gazetteer); the individual from Labuan Sore (USNM 218138) is an example of what Miller and Hollister (1921a: 71) described, on a page

preceeding their description of *nigellus*, as *Rattus adspersus* (= *B. andrewsi*; see that account).

I understand why Miller and Hollister thought the specimens from Bumbarujaba represented an undescribed species. The authors had never examined the holotype of *chrysocomus* and Raven did not encounter it in northern Sulawesi. He trapped 176 specimens of a *Bunomys* at Teteamoet, Kuala Prang, Gunung Klabat, and Temboan on the northeastern peninsula of the island (see the gazetteer for *B. fratrorum* and the map in fig. 50), which were subsequently identified by Miller and Hollister as *B. chrysocomus*. All, however, are examples of the larger-bodied *B. fratrorum*. Fur coloration and tail patterning as well as small size of skull and molars typical of the specimens from Bumbarujaba are strikingly unlike comparable traits in Raven's series from the northeast peninsula, which have somewhat paler fur, different tail patterns, and significantly greater external (compare the values in tables 19 and 41) as well as cranial and dental dimensions (table 42). And specimens in the sample from Bumbarujaba, although appreciably smaller in body size and cranial and dental dimensions than *adspersus*, as Miller and Hollister noted, closely resemble the larger-bodied *adspersus* in fur coloration and tail patterning. Without examples of true *chrysocomus* at hand for comparison, coupled with their misidentification of Raven's material from the northeast peninsula as *chrysocomus*, Miller and Hollister correctly noted that the specimens from Bumbarujaba were appreciably different not only from Raven's peninsular samples but from the central Sulawesian *adspersus*, and looked on them as representing an undescribed species.

In their cranial and dental measurements and proportions, Miller and Hollister's sample of *nigellus* clusters with population samples from the northern peninsula, Gunung Tambusisi, and the southeastern peninsula (see Geographic Variation).

Rattus rallus Miller and Hollister, 1921a: 73. HOLOTYPE: USNM 219595 (skin and skull; measurements are listed in table 18), an adult female collected September 7, 1917, by H.C. Raven (original number 3233). TYPE

LOCALITY: Indonesia, Propinsi Sulawesi Tengah, Gimpu (01°36′S, 119°53′E), 400 m (locality 35 in gazetteer and the map in fig. 22).

Rattus rallus, the second species to be named in the same publication as *nigellus,* was diagnosed by Miller and Hollister (1921a: 73–74) as:

> A member of the *chrysocomus* group resembling *Rattus nigellus*, but smaller, with shorter hind foot, and much smaller teeth. Tail dark above, light below. Skull with flatter, less arched braincase, longer rostrum, and smaller auditory bullae. This species differs conspicuously from the other member of the *chrysocomus* group inhabiting the same district (*Rattus penitus*), and externally resembles very closely *Rattus nigellus* from northern Middle Celbes. From *R. nigellus* it is chiefly distinguished by the smaller foot, more sharply bicolored tail; more slender skull with less inflated braincase; and smaller teeth. Two specimens out of the eight examined have the tip of the tail for 12 mm. whitish.

Miller and Hollister assigned eight specimens to *rallus*: two from Gimpu, four from the valley of Danau Lindu, and two from Gunung Lehio. They overlooked an additional example collected by H.C. Raven from Gimpu that is represented by only a skull (see the gazetteer).

The holotype of *rallus* along with two additional specimens from Gimpu, the type locality, form one of the 10 population samples used in my multivariate analysis (table 2). In the scatter plots defined by first and second principal components and first and second canonical variates (upper and and lower graphs in figs. 26 and 27), scores representing the three specimens of *rallus* fall within or near the large cloud of points for specimens in the two population samples from along my transect in the west-central mountain block (Sungai Oha Kecil + Sungai Sadaunta and Danau Lindu + Gunung Kanino) and the animal from Bakubakulu just north of my transect. Scores for the seven specimens from Bumbarujaba, the type locality of *nigellus*, lay at the edge and to the left of the large west-central constellation. Among the variables influencing the position of the seven *nigellus* along the first canonical axis is their slightly higher braincase and larger bullae compared with the specimens of

rallus from Gimpu (see Geographic Variation) and highlights two of the traits Miller and Hollister used to distinguish *rallus* from *nigellus*: ''less arched braincase'' and ''smaller auditory bullae'' (higher braincase and larger bullae in *nigellus*). Scores for *nigellus* from Bumbarujaba are more closely positioned near those for samples from the northern peninsula, Gunung Tambusisi at the western margin of the eastern peninsula, and Pegunungan Mekongga on the southeastern peninsula than to the points representing *rallus* from Gimpu, which is also reflected by the cluster configuration in the diagram of Mahalanobis distance as a phenetic measure of resemblance (fig. 28).

These multivariate analytical results described above pertain only to cranial and dental variables. The range of variation in fur coloration, color and pattern of the tail, ears, and feet, along with dimensions of the combined head and body, tail, and hind feet typical of the series of *nigellus* fall within that range of variation seen in the large sample obtained from my transect, which also embraces the range of variation in these external traits present among the three specimens of *rallus*. Miller and Hollister thought the smaller foot and more sharply bicolored tail of *rallus* distinguished it from *nigellus*, but neither trait is diagnostic. Length of hind foot varies within any large sample (table 19), and the extremes of a sharply bicolored tail and a monocolored tail connected by intermediate patterns is also usual in large samples (see the range of patterns enumerated in the description of *B. chrysocomus*).

There appears to be detectable geographic variation in cranial and dental variables among population samples of *B. chrysocomus*, which is reflected in the different spatial distribution of scores for the samples of *nigellus* and *rallus* in the discriminant-function ordinations, and the observations recorded by Miller and Hollister. The population samples defined here form two clusters, one from the west-central region, and the other from peninsulas east of there. Should analyses of DNA sequences and morphometric data from future samples demonstrate the populations living in the valleys and mountains in the west-central

region to be genetically isolated from populations occurring elsewhere on Sulawesi, *rallus* would be the name to apply to the west-central form.

Rattus brevimolaris Tate and Archbold, 1935a: 7. HOLOTYPE: AMNH 101055 (skin and skull; measurements are listed in table 18), an adult female collected January 6, 1932, by G. Heinrich (original number 891). TYPE LOCALITY: Indonesia, Propinsi Sulawesi Tenggara (southeastern peninsula of Sulawesi), Lalolei (03°57′S, 122°03′E), 300 m (locality 38 in gazetteer and the map in fig. 22).

Tate and Archbold proposed the two other scientific names that turn out to be synonyms of *B. chrysocomus*, one as a species of *Rattus*, the other as a subspecies of *Bunomys coelestis*. *Rattus brevimolaris* was characterized by Tate and Archbold (1935a: 7) as ''A rather small member of the *chrysocomus* group with somewhat thin pelage, a skull with small palatal foramina, narrowly pointed anteriorly and quite small molars.'' The holotype was described as follows:

> Pelage of type rather thin, thinner than that of *andrewsi*, approximating the condition in the larger sized *inferior*. Dorsal color, as in allied forms, near natal brown, but not uniformly so because of dulling effect of gray under-color. Ventral color dirty buff, becoming clay color on breast and russet just anterior to scrotum. No clear line of demarcation along sides. Feet dull grayish-white. Tail short, white beneath.

> Skull small and delicate, the palatal foramina well pointed in front, only slightly exceeding length of tooth row (110 per cent); bulla large to medium (in type 7.0 mm., in another specimen, female, only 6.1 mm.). Molars quite small . . . .

> Besides the type, 3 males and 3 females, all topotypes [see specimens listed under locality 38 in gazetteer] have been studied. At first sight this species looks like *andrewsi*. The latter, however, has crown of m^1 at least 3.8 × 2.2. When the type of *chrysocomus* is restudied it may be found that our *brevimolaris* will fit in with it. Meanwhile, we consider the closests allies of *brevimolaris* to be *nigellus* and *rallus*.

Tate and Archbold had never examined the holotype of *Mus chrysocomus*, but they correctly assessed the taxonomic affinities of *brevimolaris* (which Tate [1936: 554] repeated in his survey of ''Some Muridae of the Indo-

Australian Region": *brevimolaris* "is intermediate in size and locality between *inferior* of the Mengkoka Mts. and *andrewsi* of Buton Island, southeast of Celebes. Its nearest relatives, however, on account of its small skull and teeth, should be sought in *nigellus* and *rallus* of Middle Celebes."). Sody (1941: 317), who had actually examined the holotype of *chrysocomus*, noted that tail coloration was the only difference he could find between *brevimolaris* (known to Sody by the specimen listed in the gazetteer from locality 39 [Pulau Buton], the original description by Tate and Archbold, and two AMNH specimens from Lalolei that had been sent to Bogor [MZB 4074 and 4075, both with incomplete skulls]) and the holotype of *chrysocomus*. The tail of the latter is monocolor, those of *brevimolaris* bicolored; these extremes, however, are found within any large sample of *B. chrysocomus* collected from a single locality. The slightly higher braincase possessed by the holotype of *brevimolaris*, and the other two specimens from Lalolei (where the type was also collected), is one of several cranial variables that are responsible for clustering the scores representing the Lalolei specimens closely with those for the sample from Pegunungan Mekongga and more broadly with scores for the samples from the northeastern end of the northern peninsula, Bumbarujaba at the base of the northern peninsula, and Gunung Tambusisi at the western margin of the eastern peninsula as reflected in the ordination bounded by first and second canonical variates (fig. 27; see Geographic Variation).

Bunomys caelestis koka Tate and Archbold, 1935b: 1. HOLOTYPE: AMNH 101236 (skin and skull; measurements are listed in table 18), an adult female collected January 11, 1932, by G. Heinrich (original number 753). TYPE LOCALITY: Indonesia, Propinsi Sulawesi Tenggara (southeastern peninsula of Sulawesi), Pegunungan Mekongga (03°35′S, 121°15′E), Tanke Salokko, 1500 m (locality 37 in gazetteer and the map in fig. 22).

Tate and Archbold (1935b: 1) characterized "*Bunomys caelestis koka*" as "Smaller than true *caelestis* and with smaller hind foot, shorter claws, and shorter nasal bones … ," and provided the following description:

Pelage soft and fine, dorsally fuscous-based, tipped with Mars brown which pales to Prout's brown on sides. Under parts with bases of hairs fuscous, their tips tawny, the tawny becoming pale russet on chest and throat. Hands and feet with backs light fuscous, digits flesh-colored. Tail fuscous above, flesh-colored beneath. Ears light fuscous. Claws, though decidedly more elongate than those of the *R. chrysocomus* rats (of which we consider *Bunomys* a derivative), shorter than those of *B. c. caelistis*.

Skull with the long rostrum and full occipital region of *Bunomys*. Zygomatic plate sloping; palatal foramina short; bullae moderate in length; back of palate level with back of m³; molar teeth small. No inflation of muzzle (which, however, probably occurs as a manifestation of age and growth).

The authors described and provided measurements for only the holotype; that specimen is one from a series of 21 collected by G. Heinrich from Pegunungan Mekongga (see locality 37 in the gazetteer).

The holotype and other specimens of *koka* do contrast with examples of *Bunomys coelestis*, which is known only by voucher samples from Gunung Lompobatang on the southwestern peninsula of Sulawesi (fig. 22), in the way that Tate and Archbold characterized *koka*. Those differences are part of the suite of phenetic external and and morphometric traits that distinguish examples of *B. chrysocomus* from specimens of *B. coelestis* (see Comparisons in the account of *B. coelestis*).

Coloration of the tail is an example of a chromatic trait linking *koka* with *B. chrysocomus* and not *B. coelestis.* Typically, specimens of *B. coelestis* have a sharply bicolored tail: from base to tip, the dorsal surface is dark brown and the ventral surface white (unpigmented). Dorsal surfaces of the tails are dark brown in the sample of *koka,* but the ventral surfaces range from all white (tail bicolored) to all brown (tail monocolored), and a range of brown speckling between those extremes, variation that is typical of the ventral tail pigmentation found in any large sample of *B. chrysocomus*.

Results of multivariate analyses of cranial and dental variables cement the identity of *koka* with *B. chrysocomus* rather than *B. coelestis.* In the discriminant-function analy-

sis of population samples for *B. chrysocomus*, the points representing specimens of *koka* overlap those of the three scores for *brevimolaris* from the lowlands adjacent to the Mekongga highlands and *nigellus* from the southern tip of the northern peninsula (fig. 27). Furthermore, in a canonical variate ordination where the sample of *B. coelestis* from Gunung Lompobatang is compared with all 10 population samples of *B. chrysocomus*, the specimen scores for *koka* fall within the cluster of scores representing *B. chrysocomus* and well outside the cloud of points for *B. coelestis* (fig. 42). Clustering based on Mahalinobis distance (squared) also aligns the sample of *koka* (from Pegunungan Mekongga) with the rest of the population samples of *B. chrysocomus*, not with the sample of *B. coelestis* (figs. 21, 49).

Although originally described as a subspecies of *B. coelestis*, the specimens identified as *koka* from Pegunungan Mekongga are actually examples of *B. chrysocomus* and are phenetically more similar in their cranial and dental dimensions to *brevimolaris* of the nearby lowlands than to other geographic samples of *B. chrysocomus*.

SUBFOSSILS: Two right dentary fragments (fig. 33) and an isolated right lower incisor (tables 27, 28) were found in sediments excavated from Ulu Leang I, a cave in the Maros region on the coastal plain of the southwestern peninsula (locality 42 in the gazetteer and map in fig. 22; also mapped by Simons and Bulbeck, 2004: 168).

Excavations in the cave were described by Glover (1976), who provided me with 10,000–3500 years B.P. as the age of the dated sediments (Glover, in litt., 1989; Bulbeck, 2004, reported 9500–3470 years B.P.). More precise dates associated with the particular site ("Trench J") at which the pieces were uncovered are unavailable.

Two other species of *Bunomys* occur on the southwestern peninsula: *B. coelestis* inhabits mountain forest on Gunung Lompobatang and *B. andrewsi* has been collected at lower elevations on the flank of the volcano and is represented in the lowlands by subfossils (see accounts of those species).

I compared the two jaw fragments with dentaries in samples of the three species. No modern samples of *B. chrysocomus* exist from the southwestern peninsula, so I first compared the subfossils with specimens of *B. chrysocomus* from the west-central region. Shape of the dentary fragments and sizes of the molars remaining in those pieces qualitatively and quantitatively closely resemble dentaries and molars in the sample of modern *B. chrysocomus* (table 28).

Bunomys coelestis is a close montane relative of *B. chrysocomus*, so my second set of comparisons set the subfossils against the sample of *B. coelestis* from Gunung Lompobatang to test the possibility that the subfossils actually represent a lowland sample of *B. coelestis*. In side-by-side comparisons of specimens of comparable age (judged by degree of molar wear), the fragmentary ramus of each subfossil is qualitatively more robust and the portion anterior to the first molar is shorter than the gracile *B. coelistis* with its more delicate ramus and elongate incisor sheath; the ramal remnants fit better with the morphology characteristic of *B. chrysocomus*.

Sizes of the molars associated with the fragments are more typical of the range of variation seen in *B. chrysocomus* than in *B. coelestis* (table 28). These qualitative observations of molar size were quantitatively verified by results from principal-components analyses that associate the subfossils with the sample of *B. chrysosomus* and not *B. coelestis* (fig. 34). In both ordinations containing specimen scores projected onto first and second principal components, size of molars is primarily responsible for the separation of scores for *B. chrysocomus* (right side of each graph) from the constellation representing *B. coelestis* with smaller molars (table 29).

The curvature of the subfossil incisor, the third subfossil fragment from Ulu Liang I, along with its width and shape of wear facet, matches examples of *B. chrysocomus*.

The two dentary fragments and lone incisor are not lowland samples of the montane *B. coelestis*.

Finally, I contrasted the two dentary fragments from Ulu Leang I with dentaries of *B. andrewsi* from Lombasang on the flanks of Gunung Lompobatang, and included the subfossil fragment of that species found in Batu Ejaya II. Compared with *B. chrysocomus*, examples of *B. andrewsi* are physically
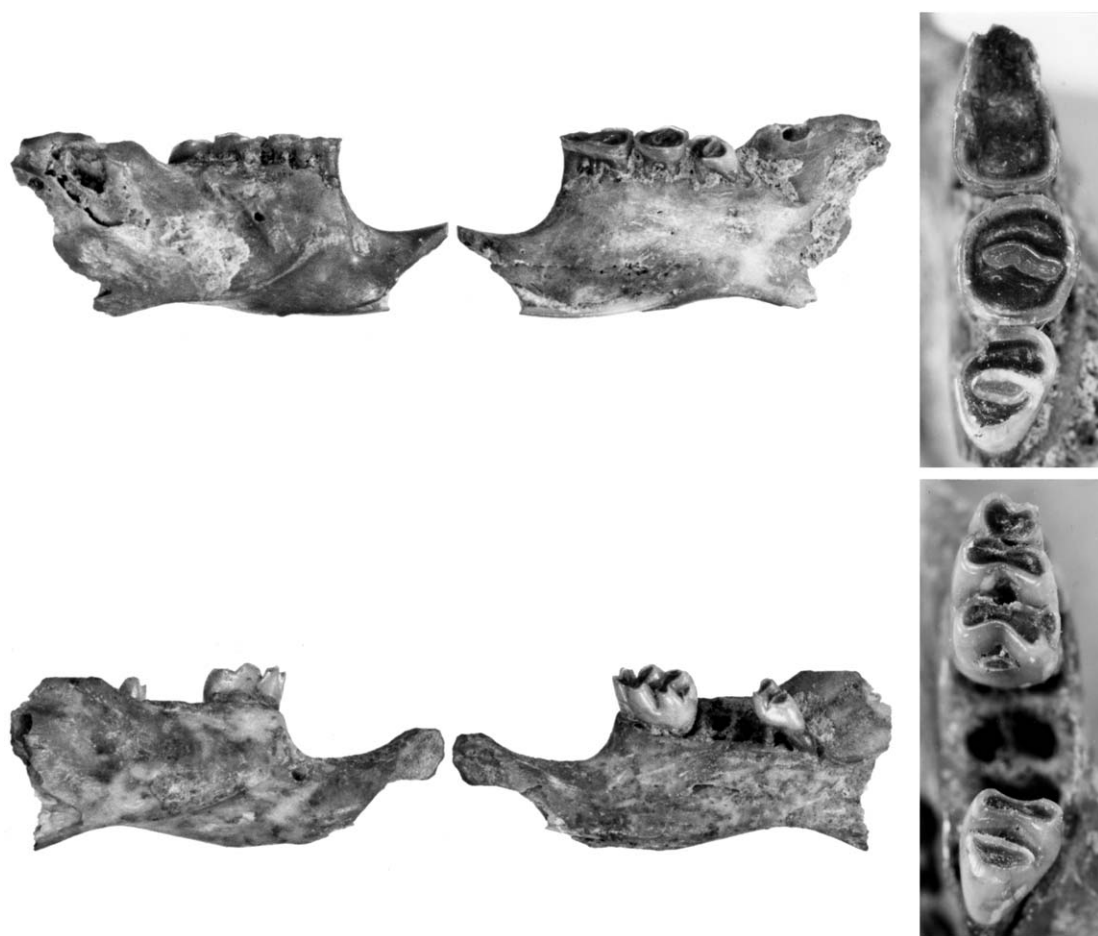
Fig. 33.   Subfossil right mandibular fragments of *Bunomys chrysocomus* from Ulu Leang I, a cave about 40 km northeast of Ujung Pandang in the Maros region near the tip of Sulawesi's southwestern peninsula (see gazetteer and the map in fig. 22). Upper set: partial dentary (×4) and accompanying molar row (×10) of AMNH 269954, an old adult. Lower set: comparable elements (×4) representing AMNH 266975, a young adult. Additional information is presented in the text and tables 27 and 28.

larger (see external measurements seen in tables 19 and 41, and cranial and dental measurements in table 42), and this size distinction is reflected in the dentaries. *Bunomys andrewsi* typically has more robust dentaries, a longer toothrow, and wider molars (tables 28, 42). Inspected side by side, the dentary fragments and molars from Ulu Liang I are smaller than those elements in the series of specimens from Lombasang, and this difference is quantitatively reinforced by results of principal-components analyses. Specimen scores projected on first and second axes (fig. 35) form two clusters along the first

component, those for *B. chrysocomus* on the left and *B. andrewsi* on the right, a function of the larger molars in the latter (table 30).

The subfossil from Batu Ejaya II is associated with the aggregation of points representing the sample from Lombasang (*B. andrewsi*), and the two subfossils from Ulu Leang I nest with the cluster of scores denoting *B. chrysocomus.*

The three subfossil fragments from Ulu Liang I are the only representatives of *B. chrysocomus* found to date in lowlands of the southwestern peninsula. I would like to see more complete specimens but until any are

TABLE 27
Subfossil *Bunomys chrysocomus* from the Southwestern Peninsula of Sulawesi

Cave and specimen	Age	Description
ULU LEANG I		
AMNH 266975	young adult	Fragment of right ramus with intact first and third molars; inferior masseteric ridge and mental foramen present; piece of incisor in alveolus (fig. 33).
AMNH 269954	old adult	Fragment of right ramus with molar row in which occlusal patterns of cusps are nearly obliterated by extreme wear and some margins are eroded; mental foramen evident; masseteric ridges intact; section of incisor within alveolus (fig. 33).
AMNH 266973	adult	Isolated lower right incisor.

encountered, either as fossils or members of living populations, my identification is a hypothesis, and one that is reasonable considering the morphology of the fragmentary remains and the known altitudinal distribution of *B. chrysocomus* elsewhere in Sulawesi. The species does occur in high mountain forests but has been more commonly encountered at intermediate and moderately low elevations. The montane forests on Gunung Lompobatang are inhabited by *B. coelestis*,

which has not been collected below 1830 m (see gazetteer for *B. coelestis*). *Bunomys andrewsi* is the only other member of the genus recorded from lower altitudes in the southwestern peninsula, where it is represented by modern specimens at 1100 m on the flank of Gunung Lompobatang, and subfossils excavated from cave deposits in the lowlands (see account of that species).

The next account describes a strictly montane member of the *Bunomys chrysocomus*

TABLE 28
Measurements (mm) of Mandibular Molars from Subfossil and Modern Samples of *Bunomys chrysocomus* and *B. andrewsi,* and Modern Samples of *B. coelestis*

Mean ± 1 SD and observed range (in parentheses) is listed for the modern specimens, which are identified in footnotes. The subfossil fragments are described in tables 27 and 56. Subfossils are from the southwestern peninsula as are the modern samples of *B. coelestis* and *B. andrewsi*. The west-central region is the source for the sample of modern *B. chrysocomus*.

Locality and specimen	N	clm1–3	bm1	bm2	bm3
B. chrysocomus					
AMNH 269954 (subfossil)[a]	1	—	1.7	1.7	1.4
AMNH 266975 (subfossil)	1	6.4	1.7	—	1.6
Sungai Sadaunta (modern)[b]	20	6.2 ± 0.17	1.8 ± 0.05	1.9 ± 0.06	1.6 ± 0.10
		(5.9–6.5)	(1.7–1.8)	(1.7–1.9)	(1.4–1.9)
B. coelestis					
Gunung Lompobatang[c]	20	6.1 ± 0.19	1.6 ± 0.09	1.7 ± 0.06	1.4 ± 0.06
		(5.8–6.5)	(1.4–1.7)	(1.6–1.8)	(1.3–1.5)
B. andrewsi					
Lombasang[d]	18	6.9 ± 0.23	1.8 ± 0.08	2.0 ± 0.09	1.6 ± 0.06
		(6.5–7.2)	(1.7–2.0)	(1.9–2.2)	(1.5–1.7)
Batu Ejaya II (subfossil)[e]	1	7.0	1.9	2.1	1.8

[a] All three molars are present, but length of the molar row could not be measured because the anterior margin of the very worn first molar is eroded (see fig. 33).
[b] AMNH 224102, 224105, 224108, 224126, 224130, 224131, 224136, 224139, 224141, 224143, 224694, 224697, 224702, 224706, 224710, 224733, 224734, 224740–742.
[c] AMNH 101016, 101130–33, 101135–39, 101141–49, 101152.
[d] AMNH 100996, 100998–1006, 101008–015.
[e] AMNH 265013.

Fig. 34. Specimen scores representing *Bunomys chrysocomus* from Sungai Sadaunta (filled triangles; N = 20), *B. coelestis* from Gunung Lompobatang (empty diamonds; N = 20), and two subfossils from Ulu Leang I projected onto first and second principal components extracted from principal-components analysis of four dental log-transformed variables. Upper graph: AMNH 266975 is the subfossil (asterisk). Lower graph: AMNH 269954 is the subfossil (cross). Factor scores that denote subfossils fall within the huddle of specimen scores for *B. chrysocomus* and not those designating *B. coelestis*. See table 29 for correlations (loadings) of variables with extracted components and for percent variance explained.

group, one found only on the high volcano Gunung Lompobatang at the southern end of the southwestern peninsula of Sulawesi.

Bunomys coelestis (Thomas, 1896)

Mus coelestis Thomas, 1896: 248.

Fourteen years after naming and describing *Mus coelestis*, Thomas (1910) used it as the type species for the genus *Bunomys*. In the years to follow, *coelestis* was shuttled between *Bunomys* and *Rattus* (table 4): it was retained in *Bunomys* by Tate (1936), later transferred to subgenus *Rattus* of *Rattus* (Ellerman, 1941, 1949; Laurie and Hill, 1954), placed in subgenus *Bullimus* of *Rattus* (Misonne, 1969), returned to *Bunomys* in the early 1980's (Musser, 1981b; Musser and

TABLE 29
Results of Principal-Components Analysis of
Bunomys chrysocomus* and *B. coelestis
The sample of *B. coelestis* from Gunung
Lompobatang (southwestern peninsula), *B.
chrysocomus* from Sadaunta (west-central region),
and two subfossils from Ulu Leang I (southwestern
peninsula) are compared. **Upper graph:** AMNH
266975 is the subfossil (m2 is missing). **Lower graph:**
AMNH 269954 is the subfossil (clm1–3 could not be
measured). Correlations (loadings) of four dental
log-transformed variables are based on 41
specimens; see figure 34.

| | Correlations | | | |
| | Upper graph | | Lower graph | |
Variable	PC1	PC2	PC1	PC2
clm1–3	0.45**	0.47**	—	—
bm1	0.90***	0.42**	0.91***	−0.01
bm2	—	—	−0.43**	0.89***
bm3	0.93***	0.28	0.91***	0.08
Eigenvalue	0.009	0.002	0.009	0.003
% Variance	74.1	13.8	66.1	22.9

*** P ≤ 0.001; ** P ≤ 0.01.

Newcomb, 1983), and eventually renewed as a distinct species of *Bunomys* endemic to Gunung Lompobatang on the southwest peninsula of Sulawesi (Corbet and Hill, 1992; Musser, 1991; Musser and Holden, 1991; Musser and Carleton, 1993, 2005).

HOLOTYPE: BMNH 97.1.3.12, the skin and skull of an old adult female collected sometime during October, 1895, by A.H. Everett. Measurements (external, cranial, and dental) and other relevant data are listed in table 18. The skin, a conventional museum preparation, is intact and the pelage coloration is not noticeably altered. The cranium and mandible are whole, all incisors and molars are present.

TYPE LOCALITY: "Piek van Bonthain" (the volcano, Gunung Lompobatang [see fig. 1], 05°20′S, 119°55′E), 6000 ft (1830 m; locality 1 in the gazetteer and map in fig. 22), southwestern arm of the island, Propinsi Sulawesi Selatan, Indonesia (*cælestis* means "belonging to heaven or of the sky/skies," and presumably Thomas was referring to the high collection site on the flank of Gunung Lompobatang).

EMENDED DIAGNOSIS: A montane member of *Bunomys* with long, dark brown fur that among species of *Bunomys* is morpho-logically most similar to *B. chrysocomus*, but is distinguished from it by the following traits: (1) longer head and body, tail, and hind feet, longer claws on the front feet; (2) darker brown upperparts, brownish gray underparts; (3) dorsal coat averages longer (18–22 mm; lowland samples of *B. chrysocomus* have a shorter coat [12–15 mm], those from middle elevations and mountains have slightly longer coats [15–20 mm]) with more of a woolly texture (smooth and silky in *B. chrysocomus*); (4) most specimens with a bicolor tail, brown over the dorsal surface and unpigmented ventral surface from base to tip (the range extends from monocolor brown through various degrees of ventral speckling and mottling to bicolored in *B. chrysocomus*), and all specimens in the sample lack white tail tips (of the 393 *B. chrysocomus* surveyed, 77 [20%] have a white tip); (5) average larger cranium with an appreciably longer rostrum, longer and narrower incisive foramen, longer diastema, wider zygomatic plate, and higher braincase; (6) more elongate dentary and longer, more slender lower incisors; (7) cranial and dental proportional distinctions that are mirrored in the scatter plots derived from multivariate analyses; (8) cusp t3 present on second upper molar in 89% of sample (only in 17% of sample of *B. chrysocomus*); (9) anterior labial cusplets absent from first lower molar of all specimens examined (present in half the sample of *B. chrysocomus*); and (10) anterior labial cusp typically present on second lower molar but infrequent on third lower molar (present in 25% of the sample; found in the third molars in 65% of the sample of *B. chrysocomus*).

GEOGRAPHIC AND ELEVATIONAL DISTRIBUTIONS: All material of *B. coelestis* preserved in collections of museums was obtained at sites between 1800 and 2500 m on Gunung Lompobatang, and the species is likely restricted to montane rainforest formations there. Support for this supposition comes from collections made on the volcano in 1931 by G. Heinrich. He obtained 28 of the 30 documented specimens of *B. coelestis* in montane evergreen forest between 2000 and 2500 m. Heinrich also had a lower camp at Lombasang (05°16′S, 119°55′E), 1100 m, in the northwestern foothills of Gunung Lom-
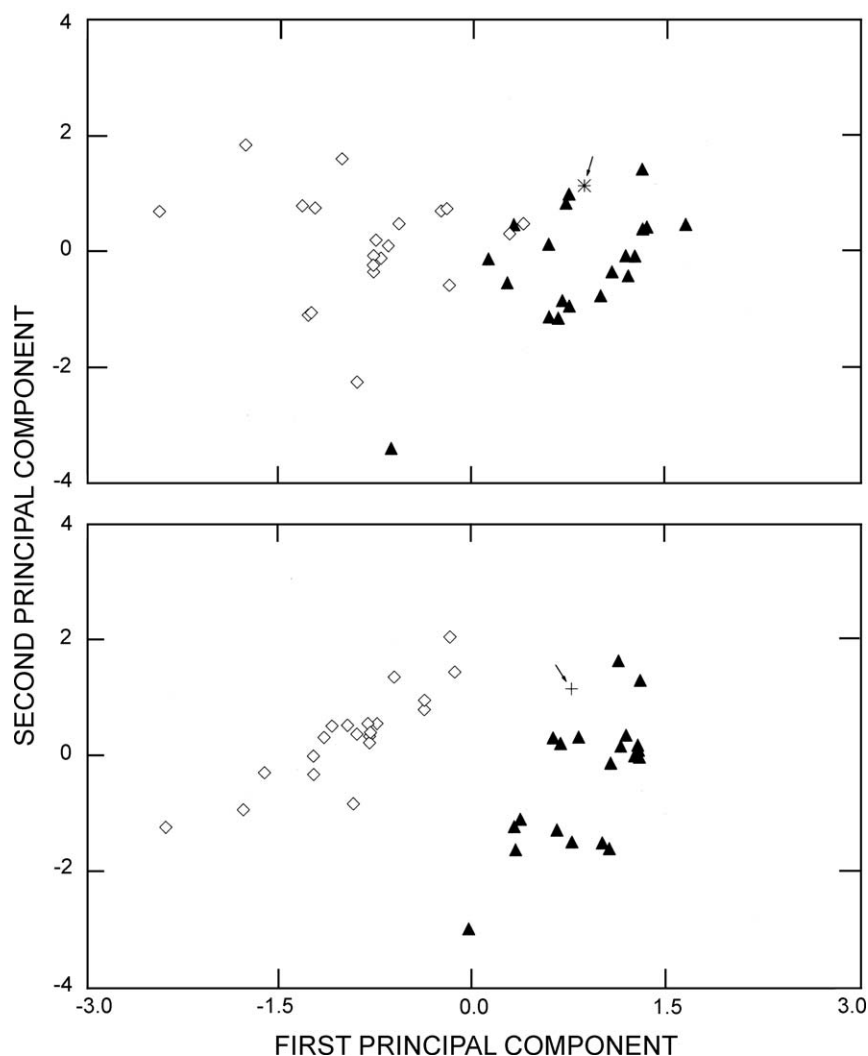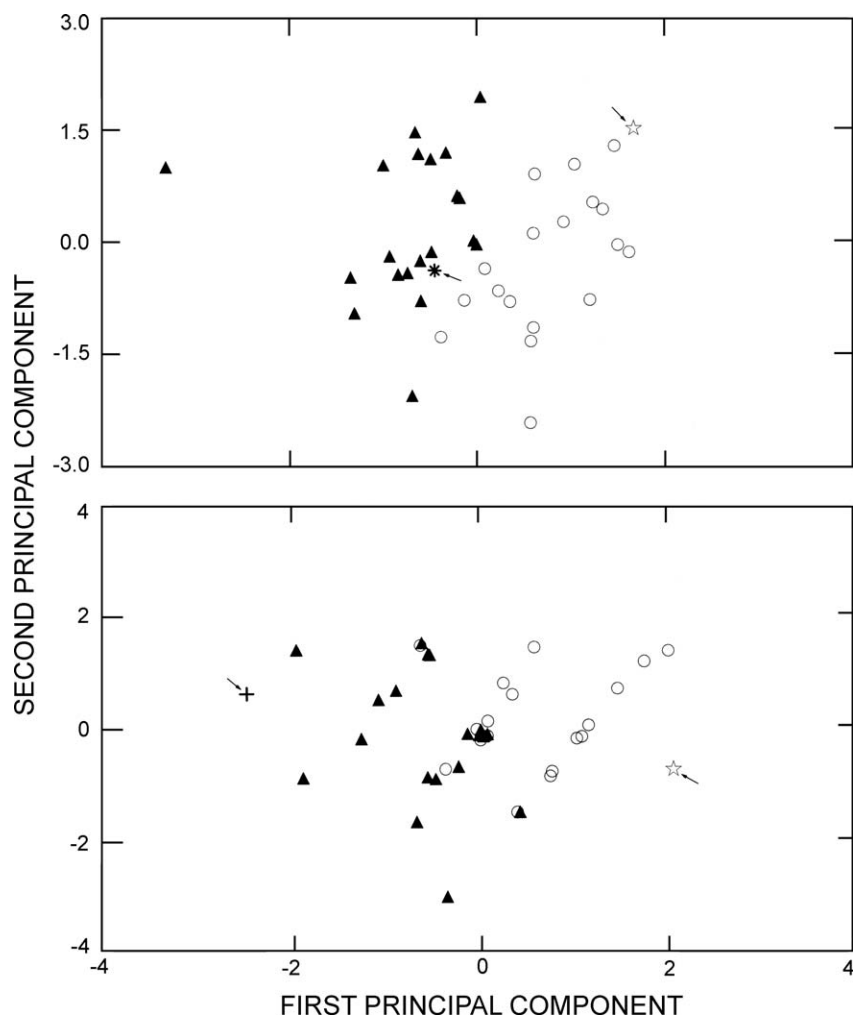
Fig. 35.   Specimen scores representing *Bunomys chrysocomus* from Sungai Sadaunta (filled triangles; *N* = 20), *B. andrewsi* from Lombasang (empty circles; *N* = 18), two subfossils from Ulu Leang I, and one subfossil from Batu Ejaya II projected onto first and second principal components extracted from principal-components analysis of four dental log-transformed variables. Upper graph: AMNH 266975 is the subfossil (asterisk) from Ulu Leang I. Lower graph: AMNH 269954 is the other subfossil (cross) from Ulu Leang I. The subfossil from Batu Ejaya II (AMNH 265013) is represented in both scatter plots (hollow stars). Scores symbolizing the two subfossils from Ulu Leang I fall within the group of scores signifying *B. chrysocomus* and not *B.andrewsi*; the score for the subfossil from Batu Ejaya II is closely associated with the aggregation denoting *B. andrewsi*. See table 30 for correlations (loadings) of variables with extracted components and for percent variance explained.

pobatang (see the maps in Heinrich, 1932, and Stresemann, 1940) where he trapped a large sample of *B. andrewsi* but no *B. coelestis*; Biror, which is near Lombasang, is the site of a more recent survey that yielded one example of *B. andrewsi*. Lowland tropical evergreen rainforest usually occurs at that elevation and constitutes the formation from

which nearly all samples of *B. andrewsi* have been collected. *Bunomys coelestis* seems to be a montane species endemic to Gunung Lompobatang, the only highland massif with appreciable height on the southwestern peninsula of the island, but how low it once occurred will probably never be known. Except for steep slopes at 1000 m, former

TABLE 30
Results of Principal-Components Analysis of
Bunomys andrewsi* and *B. chrysocomus

Comparisons are among the sample of *B. andrewsi* from Lombasang (southwestern peninsula), *B. chrysocomus* from Sadaunta (west-central region), two subfossils from Ulu Leang I, and one subfossil from Batu Ejaya II (southwestern peninsula). **Upper graph:** AMNH 266975 is the subfossil from Ulu Leang I (m2 is missing). **Lower graph:** AMNH 269954 is the other subfossil from Ulu Leang I (clm1–3 could not be measured). AMNH 265013 is the subfossil from Batu Ejaya II and is compared in both ordinations. Correlations (loadings) of four dental log-transformed variables are based on 39 specimens; see figure 35.

| | Correlations | | | |
| | Upper graph | | Lower graph | |
Variable	PC1	PC2	PC1	PC2
clm1–3	0.95***	−0.30	—	—
bm1	0.70***	−0.35*	0.80***	0.32
bm2	—	—	0.91***	0.30
bm3	0.84***	0.43**	0.89***	−0.46**
Eigenvalue	0.007	0.001	0.006	0.001
% Variance	77.3	12.4	77.4	14.0

*** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

forest cover has been converted to farms and tree plantations below about 1700 m (Fraser and Henson, 1996), and the upper forested slopes of the volcano form an island ''in a sea of densely-populated agricultural land east of Ujung Pandang'' (Whitten et al., 1987: 519). The only lowland records of *Bunomys* from the southwestern peninsula consist of subfossil fragments I identify as *B. andrewsi* and *B. chrysocomus* (see those accounts) found in cave sediments near sea level. Except for the sites at Lombasang and Biror, no extant specimens of any species of *Bunomys* are known from altitudes between 1100 m and sea level, a zone now mostly deforested. Unless archaeological or fossil remains are discovered within this interval, the upper altitudinal limits of *B. chrysocomus* and the actual lower boundary of its close montane relative, *B. coelestis* will remain unclear.

SYMPATRY WITH OTHER *BUNOMYS*: No other species of *Bunomys* has ever been collected within the elevational range on Gunung Lompobatang in which *B. coelestis* is documented by specimens (table 4). Samples of *B. chrysocomus* and *B. andrewsi* come from lower elevations either on the volcano or elsewhere on the southwestern peninsula (see those two accounts of species).

DESCRIPTION: Here is Thomas's (1896: 248) original description of *Mus coelestis*:

Size rather less than *Mus fratrorum*. Fur long and soft, hairs of back about 18 millim. in length; no longer bristles intermixed. Muzzle unusually long, cylindrical. Eyes small. Ears large, rounded, laid forward in a spirit-specimen they reach to the anterior canthus of the eye. Palate-ridges 3–5. General colour above rich rufous brown (perhaps, in a bright light, nearest to Ridgway's 'hazel'), the hairs dark slate for the greater part of their length and just tipped with rufous. The belly is also of much the same colour, only lighter, and the line of demarcation on sides is quite imperceptible. Fore feet with the dark colour extending on to the metacarpals, fingers white; claws exceptionally long and strong, little curved, quite different to those of ordinary rats. Hind feet similarly coloured to the fore; claws long and strong; fifth hind toe without claw reaching to the end of the first phalanx of the fourth; pads, as usual, six in number, large and rounded. Mammae 0–2 = 4; clitoris very long and slender. Tail about equal in length to the head and body, finely scaled (about 14 scales to the centimetre), uniformly thinly haired, blackish above, white below, the two colours intergrading on the sides. Skull less different from that of ordinary rats than the very peculiar external characters would lead one to expect. Muzzle long and cylindrical, slightly concave upwards near the middle of the nasals. Interorbital region very broad, rounded above, its edges slightly beaded. Interparietal narrow antero-posteriorly. Projection of anterior zygoma-root medium. Anterior palatal foramina about the length of the molar series, and narrow, little open, not reaching backwards nearly to the level of [first upper molar]. Bullae small.

Thomas aptly captured the essence of *B. coelestis.* It has a compact body, long muzzle, dark and thick fur, tail slightly shorter than the combined length of head and body, long front claws, and is one of the physically smaller species of *Bunomys* (LHB = 147–179 mm, LT = 136–165 mm, LHF = 35–39 mm, LE = 21–25 mm, ONL = 37.6–41.8 mm), more similar in size to *B. chrysocomus* rather than the larger *B. prolatus* or *B. torajae,* n. sp. (table 19). The dorsal coat is very long (18–25 over the back), soft to the touch, and woolly in appearance. It is a

rich dark brown highlighted by buffy speckling (produced by the combination of dark brown and buffy bands of the overhairs) over most of the head and body; sides of the body are slightly paler. Because guard hairs and overhairs are about the same length, the surface of the coat is smooth.

Fur covering the underparts of the head and body is also long (8–15) and soft. Dark grayish white pelage predominates in the sample, which characterizes 17 of the 27 adults in AMNH. Four have dark grayish-white coats tinged with buff (tips of the hairs are unpigmented or pale buff), and six express a rich buffy dark gray or ochraceous-gray ventral fur; the contrast between upperparts and underparts is evident but not sharply marked.

The ears (external pinnae) appear naked, but are scantily covered by short hairs. The dried ears on the stuffed museum skins are dark brown (I have not seen freshly caught animals).

Typically, the tail is slightly shorter than the combined length of head and body (LT/LHB = 95%). Of the 30 specimens (adults and juveniles) stored in AMNH, 28 have sharply bicolored tails (as does the holotype): dorsal surface of the tail, from its base to its tip, is dark brown; the ventral surface, from base to tip, is unpigmented (white). In two specimens, the ventral surface is speckled brown (both scales and hairs are brown). None of the specimens exhibit a white tail tip.

Tarsal and metatarsal surfaces are typically brown and covered by unpigmented (silvery) hairs, all digits are white. The front claws are long and sharp, their lengths relative to lengths of the front digits exceeded only by the elongate claws of *B. prolatus* (fig. 36), and are not concealed by the short ungual tufts; comparable tufts of silvery hairs sparsely cover the hind claws. Palmar and plantar surfaces are typically unpigmented except for gray near the heel.

Females exhibit the number of teats usual for all species of *Bunomys* (four, arranged in two inguinal pairs). Testes are likely large relative to body size, as in the close relative *B. chrysocomus* (table 9), but I have not seen fluid-preserved material to verify this possible proportion in *B. coelestis*.

Juveniles have soft and woolly dorsal pelage that is darker brown than the adult coat and slightly shorter (overhairs reach 18 mm). Underparts are dark grayish white. Coloration of the ears and feet match those of adults, and the tail is bicolored (dark brown on the dorsal surface, white along the ventral surface) and without a white tip.

The gracile skull is marked by a long rostrum, moderately wide interorbit, and deep braincase; each dentary is elongate, particularly that part of the ramus between incisor and first molar (figs. 37–39). Molars are smaller relative to size of cranium and mandible than is typical of *B. chrysocomus*, but the basic occlusal patterns formed by cusp rows are similar in the two species (compare the occlusal views of molar rows from *B. chrysocomus* in fig. 12 with those of *B. coelestis* in fig. 40); the primary distinction between the two species lies in different frequencies of certain cusps and cusplets, as I describe below.

KARYOTYPE: Not yet determined.

COMPARISONS: Among species of *Bunomys*, the montane *B. coelestis* is phenetically most similar to *B. chrysocomus* in traits associated with skins, skulls, and dentitions. While the two species bear a general resemblance to each other in body size and coat color, there are conspicuous differences between them. Compared with all samples of *B. chrysocomus* I examined, *B. coelestis* typically has a longer head and body, tail, and hind foot (table 19), and darker and longer fur (mean = 20.1 mm, range = 18–23 mm, for 23 adult *B. coelestis*; mean = 15.5, range = 13–18 mm in 41 adult *B. chrysocomus* from Sungai Sadaunta, 675 m). *Bunomys coelestis* has a darker brown dorsal coat that appears somewhat woolly in texture (dark brown with buff and gray highlights in *B. chrysocomus*, and sleek, silky fur), underparts are dark grayish brown (the range is grayish white to gray tinged or washed with pale or rich buff in most examples of *B. chrysocomus*). All individuals of *B. coelestis* lack a white tail tip (20% of the 396 *B. chrysocomus* surveyed exhibit a white tip; table 8); most have bicolored tails, brown along the dorsal surface, white ventrally from base to tip (in *B. chrysocomus*, tails range from bicolor to monocolor brown with
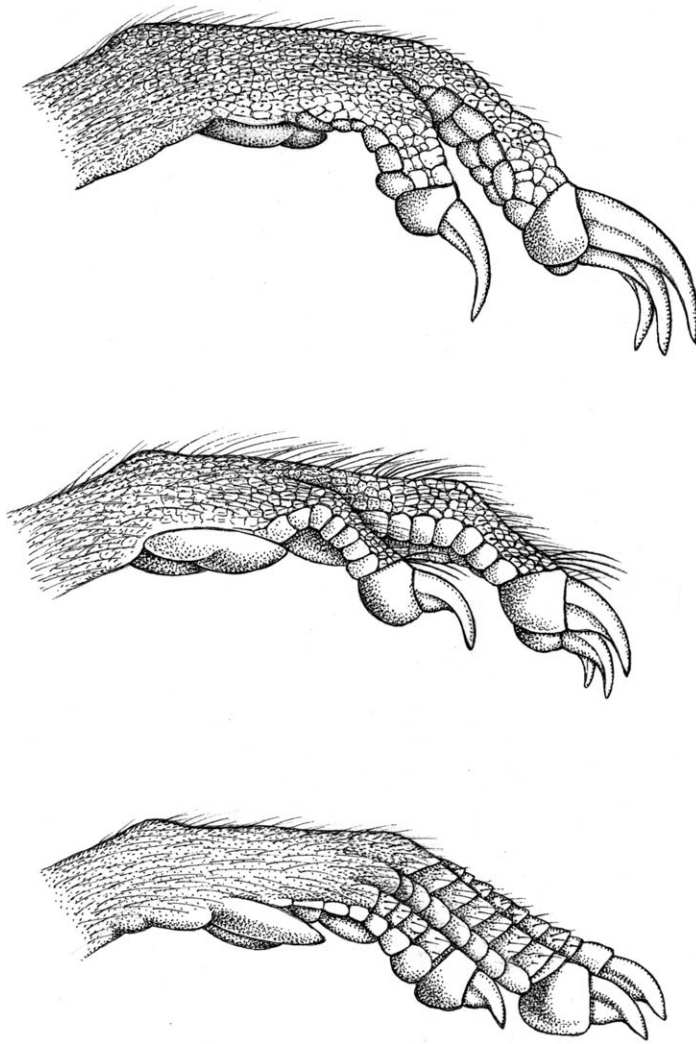
Fig. 36. Views of right front foot in three species of *Bunomys* showing relative lengths of claws in adults. Upper: *B. prolatus* (MZB 12187, Gunung Tambusisi), longest claw = 6.5 mm. Middle: *B. coelestis* (AMNH 101141, Gunung Lompobatang), longest claw = 5.1 mm. Lower: *B. chrysocomus* (AMNH 265077, Gunung Tambusisi), longest claw = 3.2 mm. Claw length in *B. torajae,* n. sp., is similar to that of *B. chrysocomus.*

intermediate patterns consisting of brown above and white below patterned by a range of mottling or speckling); and have appreciably longer claws on the four digits of each front foot than do specimens of *B. chrysocomus* (fig. 36).

Differences in absolute size and proportions of cranial and dental dimensions provide noticeable contrasts between *B. coelestis* and *B. chrysocomus*, which is evi-denced by illustrations of skulls (figs 37–39), univariate summary statistics (table 31), and results of multivariate analyses. Specimen scores projected on first and second principal components form two parallel elliptical clouds, one identifying specimens of *B. chrysocomus*, the other representing *B. coelestis* (fig. 42, upper graph). Axes of these clusters are phenetically distinct: their Y-intercepts are significantly different between

Fig. 37.   Dorsal views of adult skulls from four species of *Bunomys*. Upper pair, left to right: *B. chrysocomus* (AMNH 224719, Sungai Sadaunta) and *B. coelestis* (AMNH 101132, Gunung Lompoba-tang). Lower pair, left to right: *B. prolatus* (MZB 12190, holotype, Gunung Tambusisi) and *B. torajae,* n. sp. (MZB 34730, holotype). ×2.

Fig. 38.   Ventral views of the same skulls shown in figure 37. Upper pair, left to right: *B. chrysocomus* and *B. coelestis*. Lower pair, left to right: *B. prolatus* and *B. torajae,* n. sp. ×2.
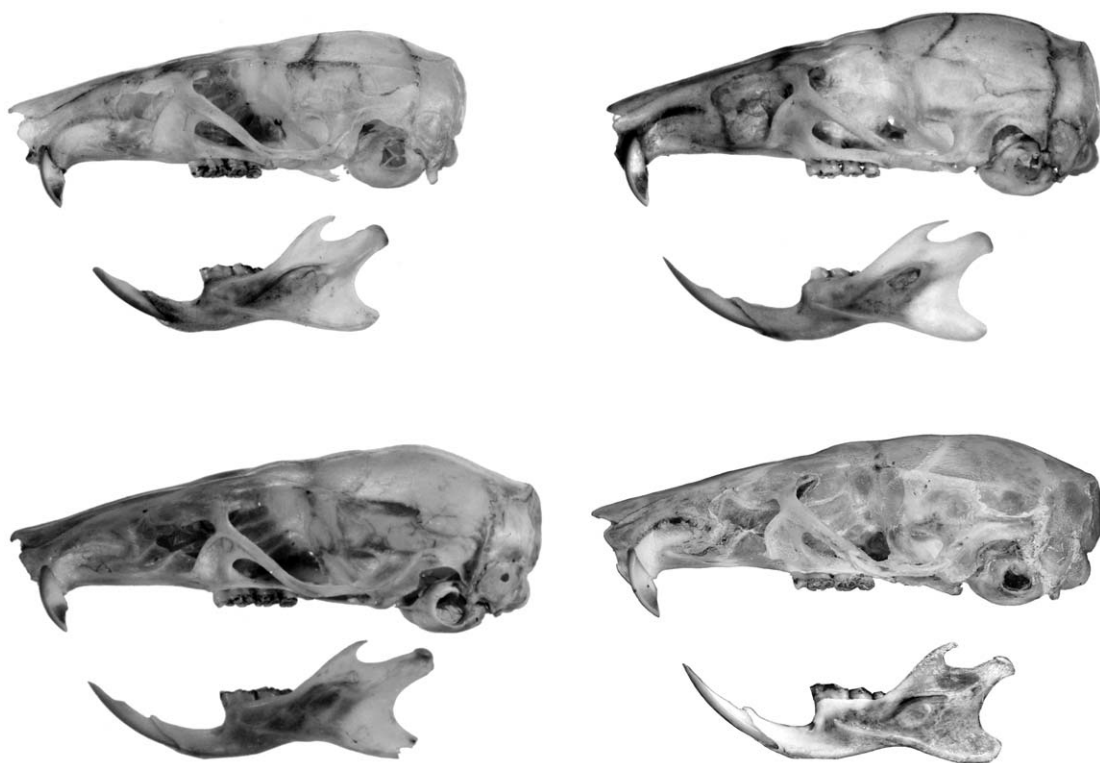
Fig. 39. Lateral views of the cranium and dentary from the same specimens presented in figures 37 and 38. Upper pair, left to right: *B. chrysocomus* and *B. coelestis*. Lower pair, left to right: *B. prolatus* and *B. torajae,* n. sp. ×2.

the two species (-0.189 versus $+2.746$; F = 10.94, P = 0.001), but not their slopes (-0.279 versus -0.255; F = 0.47, P = 0.384). The spread of scores along the first axis is influenced by the positive and moderate to high loadings for cranial variables that highlight the overall larger skull of *B. coelestis* (indexed by occipitonasal length and zygomatic breadth); its longer facial skeleton (lengths of rostrum, diastema, incisive foramina, and bony palate) and postpalatal region; wider zygomatic plate, rostrum, bony palate, and incisive foramina; wider and deeper braincase, and larger bulla ($r = 0.24$–0.86; table 32) compared with the bulk of specimens forming the sample of *B. chrysocomus*.

Dispersion of scores along the second axis and the moderate to high positive and negative correlations (table 32) point to the relatively higher braincase, longer diastema

and incisive foramina, but more slender anterior cranial region of *B. coelestis* (indexed by breadths of rostrum, bony palate, mesopterygoid fossa, and incisive foramina), and weaker molars (shorter molar rows and narrower molars) compared to those variables in most examples of *B. chrysocomus*.

Specimen scores for samples of the two species projected on first and second canonical variates segregate into two discrete clusters along the first axis, a large one formed by combined population samples of *B. chrysocomus*, and a smaller group representing specimens of *B. coelestis* (fig. 42, lower graph). The dispersal is influenced by moderate to high negative correlations ($r = -0.25$ to -0.76; table 32) reflecting the generally larger skull and greater internal dimensions of *B. coelestis* (revealed also in univariate means; table 31) as compared with *B. chrysocomus*; covariation in lengths of

diastema and incisive foramina, along with height of braincase, exerts the most force (table 32). In contrast, *B. coelestis* has a narrower incisive foramina and mesopterygoid fossa compared to *B. chrysocomus.*

The high positive loading on the second axis for breadth of zygomatic plate ($r = 0.74$) and lesser negative values for lengths of bulla and molar row, and molar breadth ($r = -0.43, -0.27,$ and -0.14, respectively) reflect the relatively wider plate of *B. coelestis* and its relatively smaller bullae and weaker molars compared to most specimens in the sample of *B. chrysocomus.*

In summary, *B. coelestis* has an overall larger cranium than *B. chrysocomus*, in which the rostrum is especially longer and thinner, the incisive foramina longer and narrower, the zygomatic plate wider, and the braincase higher. The mesopterygoid fossa and first upper molar are narrower, and bulla and molar row shorter relative to overall cranial size as compared with *B. chrysocomus.*

Results of UPGMA cluster analysis derived from Mahalanobis distances among centroids as a phenetic measure of resemblance also highlights the separation of *B. coelestis* from all population samples of *B. chrysocomus* (fig. 49).

Cranial contrasts between the two species are mirrored by mandibular distinctions (fig. 39). Compared with *B. chrysocomus*, the region between anterior margin of first molar and the incisor alveolus (diastema) is longer in *B. coelestis* and body of the ramus is not as high, resulting in a lower and more elongate structure. *Bunomys coelestis* also has appreciably longer and more slender lower incisors.

Occlusal patterns of molars are similar in *B. chrysocomus* and *B. coelestis* except for frequency of small cusps and cusplets found on certain molars. Nearly all specimens (25 of 28) in the sample of *B. coelestis* have a small cusp t3 on the second upper molar, but t3 is lost in most examples (164 of 197) of *B. chrysocomus* (table 10). Anterior labial cusplets could not be identified on first lower molars of any of the 24 specimens of *B. coelestis* surveyed, and occurred on the third lower molars only in 8 of the 24 examples. By contrast, first lower molars in about half of the sampled *B. chrysocomus* (62 of 120

specimens) exhibit anterior labial cusplets, and third lower molars in appreciably more than half of the sample (78 of 120) have such cusplets (table 11).

The morphological external, cranial, and dental configuration of *B. coelestis* is basically a slight but distinguishable modification of the anatomy seen in *B. chrysocomus.* Samples of the latter collected in montane forest habitats come from Gunung Kanino (1189–1555), Gunung Lehio (1880–2185 m), and Pegunungan Latimojong (2200 m) in the west-central mountain block; Gunung Tambusisi (1372–1830 m) at the western margin of the eastern peninsula; and Pegunungan Mekongga (2000 m) on the southeastern peninsula. Except for their long fur, none of these specimens exhibit the traits diagnostic of *B. coelestis*, and closely resemble the external, cranial, and dental features in samples of *B. chrysocomus* collected from lower elevations in the west-central region and southeastern peninsula (see account of *B. chrysocomus*).

GEOGRAPHIC VARIATION: There is no evidence that *B. coelestis* occurs anywhere else than above 1800 m on the forested slopes of Gunung Lompobatang, the high volcano that looms over the tip of the southwest peninsula (fig. 1). The specimens listed here constitute a single population sample of the species, and is large enough to be composed of age categories ranging from young to old adults. What intrasample variation I detected is expressed as differences in external, cranial and dental measurements reflecting age composition as well as individual differences among specimens of comparable ages. The extent of morphometric variation, for example, is indicated in summary statistics (table 31) and the generally tight cluster of specimen scores in the ordinations derived from principal-components and discriminant-function analyses (fig. 42).

NATURAL HISTORY: I lack firsthand experience with *B. coelestis* in its natural habitat, and field journals of collectors are devoid of useful ecological information. Long, thick, and dark fur, long claws on the forefeet, elongate rostrum and mandible, and protracted lower incisors, which are characteristic of *B. coelestis*, are traits associated

Fig. 40.   Occlusal views of right molar rows. Left pair: maxillary (left image; CLM1–3 = 5.9 mm) and mandibular (right image; clm1–3 = 6.1 mm) rows of *Bunomys coelestis* (AMNH 101151). Right pair: maxillary (left image; CLM1–3 = 6.6 mm) and mandibular (right image; clm1–3 = 6.7 mm) rows of *Bunomys prolatus* (AMNH 265075).

with murine species living in cool and wet habitats of montane evergreen rain forests, at least in Sulawesi. Because in its morphology, *B. coelestis* appears to be a montane relative of *B. chrysocomus*, I suspect it to be terrestrial and have a similar diet—primarily earthworms, snails, arthropods, small vertebrates, along with some fruit. Its reproductive traits are also probably similar to those of *B. chrysocomus*. Results of extended fieldwork in patches of montane forest remaining on the volcano would test these suppositions.

ECTOPARASITES: *Bunomys coelestis* is parasitized by the tiny fur mite *Listrophoroides* (*Marquesania*) *cucullatus* (table 14), which is also found on Sulawesian *Rattus hoffmanni* and *R. xanthurus* as well as a variety of murines from the Indoaustralian region and Philippines (Bochkov and Fain, 2003: 577).

SYNONYMS: None.

A species so far known only from montane habitats on Gunung Tambusisi at the western end of the eastern peninsula is the subject of the following account.

Bunomys prolatus Musser, 1991

Bunomys prolatus Musser, 1991: 4.

HOLOTYPE: MZB 12190, the skin and skull of an adult male (original number 25) collected March 9, 1980, by C.H.S. Watts. External, cranial, and dental measurements, along with other data, are listed in table 18. Pieces are missing from both skin and skull; I

Fig. 41. Occlusal views of right maxillary (left image; CLM1–3 = 6.5 mm) and mandibular (right image; clm1–3 = 6.7 mm) molar rows of *Bunomys torajae*, n. sp. (MZB 34733).

have already described the extent of this damage (Musser, 1991: 4).

TYPE LOCALITY: Gunung Tambusisi ("Tambusisi Ridge") (01°38′S, 121°23′E), 6000 ft (1830 m; locality 1 in gazetteer and the map in fig. 22), near the western end of the eastern peninsula of the island, Propinsi Sulawesi Tengah, Indonesia (see fig. 1).

EMENDED DIAGNOSIS: One of the largest in physical size among members of the *Bunomys chrysocomus* group (LHB = 156– 179 mm, ONL = 40.4–43.2 mm) and further distinguished from members in that assemblage by the following combination of traits: (1) long, dense, and very soft fur; (2) tail that is much shorter than combined lengths of head and body (LT/LHB = 79%), dorsal surface brown, ventral surface grayish brown, white, or white speckled with brown; (3) white tail tip typically absent (a 2 mm

white tip present on one of seven specimens); (4) short hind foot relative to body size; (5) large, darkly pigmented epidermal scales on dorsal surfaces of fore- and hind feet as well as digits; (6) large and strong elongate claws with curved and sharp tips; (7) elongate cranium and mandible, long and tapered rostrum (with an associated long diastema and incisive foramina), wide interorbital region, and large braincase and auditory bulla; (8) narrow across zygomatic arches and narrow zygomatic plates; (9) long molar rows and wide molars; (10) cusp t3 absent from second and third upper molars; and (11) no anterolabial cusp on first lower molar and most specimens with anterolabial cusp on third molar.

GEOGRAPHIC AND ELEVATIONAL DISTRIBUTIONS: The sample of *B. prolatus* was collected at 1830 m, an elevation that Whitten et al. (1987: 521) surmise is in the zone of upper montane forest on Gunung Tambusisi ("between 1700 and 2500 m"). Trapping efforts by members of the expedition did not extend higher. Presumably the species occurs in suitable habitat elsewhere on the mountain, possibly up to the summit (which is at 2422 m according to Whitten et al., 1987: 521). I suspect *B. prolatus* to be confined to montane evergreen rainforest formations—its actual altitudinal limits can be determined only by future survey.

Maryanto and Yani (2003) and Maryanto et al. (2009) have recorded *B. prolatus* from Lore Lindu National Park in central Sulawesi, which is certainly based on a misidentification (DNA has recently been extracted from a voucher specimen in Maryanto's Lore Lindu collection that was labeled "*Bunomys prolatus*," but the DNA sequence identifies it as *B. chrysocomus*; Ken Aplin, personal commun., 2011). My transect was in what is now Lore Lindu National Park, and I never encountered the species, even during the months camped in montane forests on Gunung Kanino and Gunung Nokilalaki. Highland regions surveyed by other collectors outside but adjacent to the Park boundaries, and those sampled farther south in the west-central mountain block have never yielded *B. prolatus*; the species is recorded only from Gunung Tambusisi, which is at the western part of the eastern

TABLE 31
Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from All Population Samples for
***Bunomys chrysocomus*, *B. coelestis*, *B. prolatus*, and *B. torajae* n. sp.**
Mean ± 1 SD and observed range (in parentheses) are listed.

Variable	*B. chrysocomus*	*B. coelestis*	*B. prolatus*	*B. torajae*
N	232	18	8	N = 2 or 3[a]
ONL	38.3 ± 1.12	40.2 ± 0.92	41.8 ± 1.03	41.5 ± 0.42
	(35.8–41.1)	(37.6–41.8)	(40.4–43.2)	(41.2–41.8) 2
ZB	18.1 ± 0.64	18.7 ± 0.64	17.8 ± 0.38	18.3 ± 0.15
	(16.3–19.8)	(17.2–20.4)	(17.2–18.3)	(18.2–18.5)
IB	6.4 ± 0.23	6.6 ± 0.24	7.1 ± 0.23	7.2 ± 0.23
	(5.8–7.2)	(6.2–7.2)	(6.9–7.4)	(6.9–7.3)
LR	13.5 ± 0.59	14.7 ± 0.56	15.7 ± 0.61	15.6 ± 0.36
	(12.0–15.1)	(13.6–15.7)	(14.7–16.4)	(15.3–16.0)
BR	6.8 ± 0.36	6.8 ± 0.47	6.7 ± 0.36	7.1 ± 0.31
	(5.6–7.7)	(5.7–7.6)	(6.1–7.1)	(6.8–7.4)
BBC	15.5 ± 0.41	15.7 ± 0.41	16.3 ± 0.37	16.1 ± 0.61
	(14.2–16.8)	(14.9–16.3)	(15.7–16.9)	(15.6–16.8)
HBC	10.8 ± 0.38	11.6 ± 0.24	11.4 ± 0.19	11.0 ± 0.49
	(10.0–12.1)	(11.1–12.1)	(11.0–11.6)	(10.7–11.6)
BZP	3.2 ± 0.26	3.6 ± 0.19	2.8 ± 0.10	2.8 ± 0.23
	(2.6–3.9)	(3.3–4.0)	(2.6–2.9)	(2.7–3.1)
LD	10.2 ± 0.54	12.1 ± 0.54	11.5 ± 0.56	11.4 ± 0.23
	(8.8–12.0)	(11.0–13.1)	(10.7–12.3)	(11.1–11.5)
PPL	13.5 ± 0.58	14.3 ± 0.53	14.6 ± 0.51	14.2 ± 0.50
	(12.2–15.0)	(13.1–15.2)	(13.8–15.2)	(13.8–14.5) 2
LBP	7.5 ± 0.40	8.1 ± 0.39	8.7 ± 0.35	8.8 ± 0.15
	(6.2–8.4)	(7.5–8.8)	(8.3–9.20)	(8.7–9.0)
BBP	3.8 ± 0.26	3.7 ± 0.20	3.7 ± 0.15	4.0 ± 0.36
	(3.1–4.5)	(3.3–4.0)	(3.4–3.9)	(3.7–4.4)
BMF	2.9 ± 0.24	2.8 ± 0.18	2.8 ± 0.14	2.9 ± 0.21
	(2.4–3.7)	(2.5–3.2)	(2.6–3.0)	(2.7–3.1)
LIF	6.3 ± 0.37	6.9 ± 0.36	6.7 ± 0.29	6.1 ± 0.15
	(5.2–7.2)	(6.5–7.7)	(6.3–7.1)	(5.9–6.2)
BIF	2.5 ± 0.17	2.2 ± 0.15	2.3 ± 0.13	2.8 ± 0.21
	(2.0–3.1)	(1.9–2.5)	(2.1–2.5)	(2.6–3.0)
LB	6.4 ± 0.24	6.3 ± 0.22	6.9 ± 0.30	6.4 ± 0.23
	(5.7–7.0)	(58–6.8)	(6.5–7.3)	6.1–6.5
CLM1–3	6.2 ± 0.23	6.1 ± 0.23	6.5 ± 0.17	6.5 ± 0.06
	(5.7–6.8)	(5.7–6.6)	(6.3–6.8)	6.5–6.6
BM1	2.0 ± 0.09	2.0 ± 0.10	2.2 ± 0.09	2.3 ± 0.06
	(1.8–2.3)	(1.8–2.1)	(2.0–2.3)	(2.2–2.3)

[a] ONL and PPL are based on two specimens; statistics for all the other variables are derived from three skulls (one of the three skulls is damaged and ONL and PPL could not be measured).

peninsula (fig. 1). Outside of Gunung Tambusisi, the places to expect *B. prolatus* are in the other highland regions of the eastern arm: Pegunungan Tokala to the east of Gunung Tambusisi; Gunung Katopasa to the north; and Pegunungan Balinggara (containing Gunung Bulutumpu) farther out on the peninsula (see the map in Whitten et al., 1987: 498). These mountains and stretches of highlands connecting them are high enough to support montane forest, and all, including Gunung Tambusis, are isolated from the expansive west-central mountain block in the central core of the island. Except on Gunung Lompobatang in the southwestern peninsula, and on the northern peninsula, *B. penitus* is the common *Bunomys* occurring in all montane forests surveyed outside of the eastern peninsular highlands. *Bunomys prolatus* may represent its ecological replacement
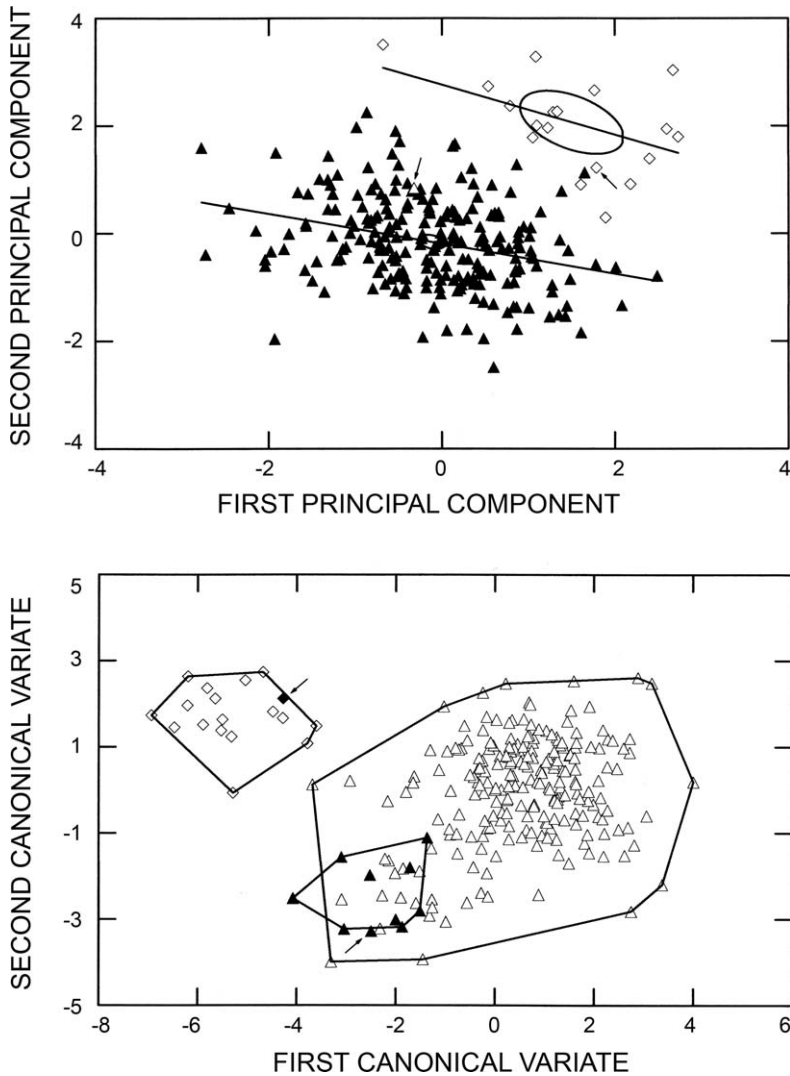
Fig. 42.   Upper graph: Specimen scores representing the sample of *Bunomys coelestis* (empty diamonds; $N = 18$) and all population samples of *B. chrysocomus* (filled triangles; $N = 232$) projected onto first and second principal components extracted from principal-components analysis of 16 cranial and two dental log-transformed variables. Arrows point to scores for holotypes of *Bunomys coelestis* (empty diamond) and *Bunomys caelestis koka* (empty triangle). Ellipses outline 95% confidence limits for cluster centroids. Equations for the regression lines are: *B. chrysocomus*, $Y = -0.279 \times -0.189$ ($F = 24.10$, $P = < 0.000$); *B. coelestis*, $Y = -0.479 \times +2.746$ ($F = 4.74$, $P = 0.045$). Lower graph: Scores for the same samples of *B. coelestis* (empty diamonds) and *B. chrysocomus* (empty triangles) projected onto first and second canonical variates extracted from discriminant-function analysis of the 16 cranial and two dental log-transformed variables. Included are scores for the holotype of *Bunomys coelestis* (filled diamond marked by arrow) and sample of *Bunomys caelestis koka* (filled triangle, arrow identifies holotype). Scores for the specimens of *koka*, including the holotype, mostly nest within the polygon bounding scores for *B. chrysocomus* and nowhere near the cluster marking *B. coelestis*. See table 32 for correlations (loadings) of variables with extracted components or canonical variates and for percent variance explained for both ordinations.

TABLE 32
Results of Principal-Components and Discriminant-function analyses Comparing All Population Samples of
Bunomys chrysocomus* with the Sample of *B. coelestis
Correlations (loadings) of 16 cranial and two dental log-transformed variables are based on 232 *B. chrysocomus* and 18 *B. coelestis*; see figure 42.

Variable	Correlations			
	PC1	PC2	CV1	CV2
ONL	0.86***	0.18*	−0.44***	0.23***
ZB	0.75***	−0.02	−0.30***	0.10
IB	0.49***	0.06	−0.30***	0.13*
LR	0.81***	0.14*	−0.40***	0.38***
BR	0.67***	−0.26***	0.10	0.22***
BBC	0.35***	0.05	−0.33***	−0.16**
HBC	0.43***	0.33***	−0.66***	0.04
BZP	0.60***	0.13**	−0.13*	0.74***
LD	0.82***	0.40***	−0.76***	0.21***
PPL	0.76***	−0.01	−0.25***	0.29***
LBP	0.57***	0.21**	−0.45***	0.14*
BBP	0.58***	−0.29***	0.11	0.05
BMF	0.39***	−0.74***	0.30***	0.20***
LIF	0.48***	0.41***	−0.57***	−0.07
BIF	0.25***	−0.64***	0.35***	−0.08
LB	0.24***	0.03	−0.05	−0.43***
CLM1–3	0.15*	−0.20***	−0.08	−0.27***
BM1	0.02	−0.33***	0.17**	−0.14**
Canonical correlation			0.875	0.708
Eigenvalue	0.017	0.008	3.270	1.003
% Variance	31.4	15.7	58.6	18.0

*** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$.

on Gunung Tambusisi, as well as the other nearby mountain expanses; those highlands have yet to be surveyed for their small mammal faunas.

SYMPATRY WITH OTHER *BUNOMYS*: *Bunomys prolatus* and *B. chrysocomus* have been collected on the slopes of Gunung Tambusisi (see Musser, 1991, and tables 6, 20). The eight known specimens of *B. prolatus* were trapped on a ridge at 1830 m in upper montane forest. One *B. chrysocomus* was taken "just below the same ridge, at about the same altitude (6000 ft [1830 m]) but a few meters downslope, and on the same day (March 9) as were four examples of *B. prolatus*. Six specimens of *B. chrysocomus* were collected at 4500 [1372 m] and 4700 ft [1433 m] during the same period, March 6–27, 1980" (Musser, 1991: 6). C.H.S. Watts, the collector, wrote me (Musser, 1991: 40) that he "recalls catching the *B. prolatus* in traps set in short and very mossy forest along a ridgetop and the example of *B. chrysocomus*

about 10 m below the ridge itself. He clearly remembers being impressed by the sharp and sudden vegetative transition between the ridgetop and just below it, and the concordant change in species of *Bunomys*." Watts' samples of both species are small and whether the altitudinal ranges of each narrowly overlap or the two are truely altitudinally parapatric can only be determined by careful trapping efforts during future surveys.

DESCRIPTION: *Bunomys prolatus* is the largest in physical size among species in the *B. chrysocomus* group (LHB = 156–179 mm, LT = 125–142 mm, LHF = 33–35 mm. LE = 24–26 mm, ONL = 40.4–43.2 mm), has a protracted face between eyes and nose, short tail and hind feet relative to combined lengths of head and body (LT/LHB = 79%, LHF/LHB = 20%), and brownish-gray fur that is long, soft, and dense. The elongate skull and mandible are portrayed in figures 37–39, and occlusal patterns of the molars in figure 40. I have elsewhere provided a full description of

the skin, skull, and dentition of the species (Musser, 1991).

The Latin *prolatus* means "elongate" and is an appropriate name for this species of *Bunomys* characterized by its elongate face, skull, and front claws.

KARYOTYPE: No information.

COMPARISONS: Among species of *Bunomys*, *B. prolatus* is morphologically (and phenetically) most similar to *B. chrysocomus*, *B. coelestis*, and *B. torajae,* n. sp. Here I compare *B. prolatus* with the first two species; contrasts between *B. prolatus* and *B. torajae,* n. sp., will be presented in the following account where that new species is described. *Bunomys prolatus* will be compared with certain population samples of *B. andrewsi* and *B. penitus*—members of the *B. fratrorum* group—in each of those respective accounts.

Bunomys prolatus and B. chrysocomus: Elsewhere I detailed contrasts and similarities between the two species (Musser, 1991), and here will only summarize major differences. Compared with samples of *B. chrysocomus* from throughout its documented geographic range (see the map in fig. 22), the sample of *B. prolatus* averages larger in body size (indicated by combined length of head and body), has shorter hind feet and tail (absolutely and relative to length of head and body; table 19), longer pelage, strikingly more robust and longer claws on the forefeet (fig. 36), and more extensive brown epidermal scutellation on dorsal surfaces of feet and digits.

Differences in absolute size and proportions summarize the primary morphometric cranial and dental contrasts between the two species: *B. prolatus* has a larger skull and molars and differs in proportions of internal cranial dimensions. The contrast is evident in the cranial illustrations of *B. prolatus* and *B. chrysocomus* (figs. 37–39), univariate descriptive statistics (table 31), and the ordination of specimen scores for samples of *B. prolatus* and *B. chrysocomus* projected on first and second principal components (fig. 43). Size is the primary factor dispersing the spread of scores along the first axis with scores for *B. prolatus* and the larger specimens of *B. chrysocomus* falling in the right half of the scatter plot; positive and moderate to high loadings for nearly all variables are respon-

sible for this distribution ($r = 0.19$–0.81; table 33). Univariate means of most measurements are greater in the sample of *B. prolatus* than in samples of *B. chrysocomus* (table 31). The isolation of the *B. prolatus* cluster along the second axis (shape factor) underscores its relatively wider interorbit; larger braincase; and longer rostrum, diastema, bony palate, incisive foramina, bullar capsule, and molar row compared with *B. chrysocomus* (table 33). Also predominant in isolating the scores for *B. prolatus* at the top of the scatter plot is its relatively narrower skull (breadth across the zygomatic arches) and rostrum compared with the conformation in *B. chrysocomus*, its relatively much narrower zygomatic plate, and relatively slightly narrower bony palate, mesopterygoid fossa, and incisive foramina; univariate mean values for these measurements are similar in the two species, indicating that the dimensions are relatively smaller in *B. prolatus* compared with *B. chrysocomus*. This quantification reinforces the visual contrast between the two species when skulls are compared side by side: *B. prolatus* has larger molars than *B. chrysocomus*, a cranium that is about as wide (except for interorbit and braincase) but significantly longer—protracted by comparison with the skull of *B. chrysocomus*—with a relatively narrower zygomatic plate, rostrum, and bony palate (figs. 37–39).

The primary mandibular difference between the two species mirrors the cranial contrasts. *Bunomys prolatus* has longer dentaries, particularly in the more elongate bony stretch between incisor alveolus and anterior margin of the molar row (fig. 39).

Frequency of some cusps and cusplets differ. A cusp t3 is not present on any example of *Bunomys prolatus*, but is part of the occlusal surface on the second molar in 17% of the *B. chrysocomus* sample, and on the third molar in 5% of the sample (table 10). All specimens of *B. prolatus* lack an anterior labial cuspet on the first lower molar; such a cusp occurs in 52% of the sample of *B. chrysocomus* (table 11).

Bunomys prolatus and B. coelestis: These two species have been collected only from montane forest habitats. Both have dark,
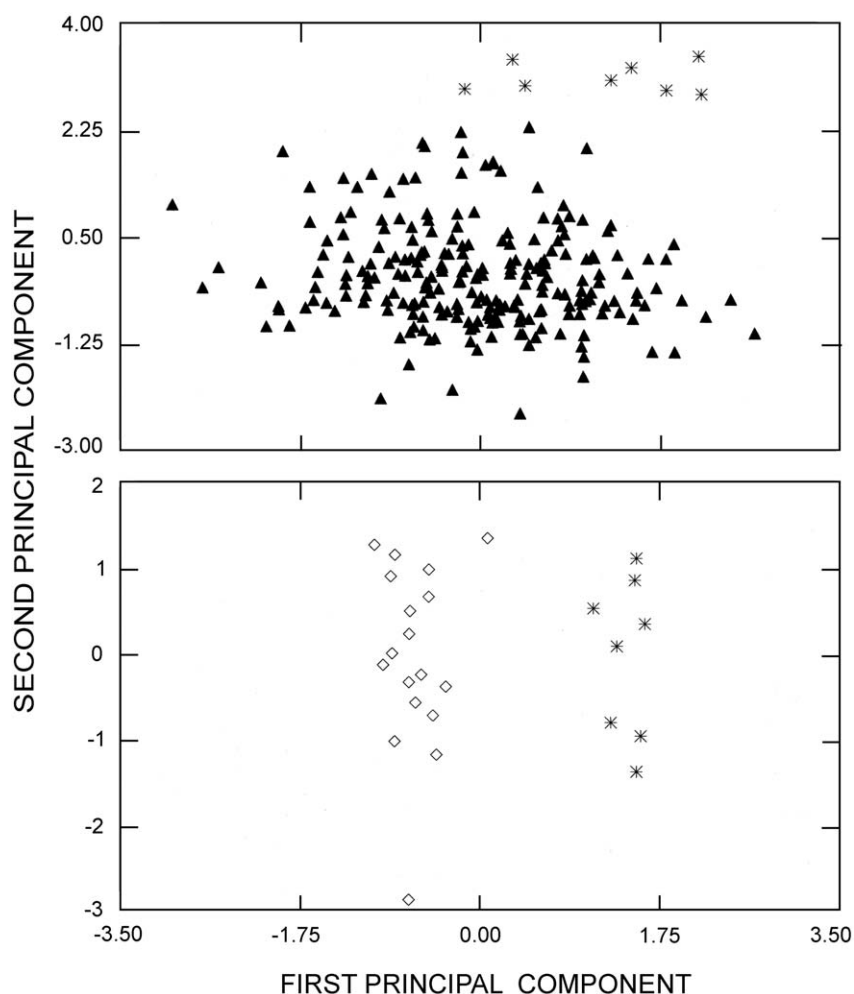
Fig. 43.   Specimen scores representing *Bunomys prolatus* (asterisks; $N = 8$), all population samples of *B. chrysocomus* (filled triangles; $N = 232$), and *B. coelestis* (empty diamonds; $N = 18$) projected onto first and second principal components extracted from principal-components analysis of 16 cranial and two dental log-transformed variables. Upper graph: *B. prolatus* compared with *B. chrysocomus*. Lower graph: *B. prolatus* contrasted with *B. coelestis*. Correlations (loadings) of variables with extracted components and percent variance explained for both scatter plots are listed in table 33.

soft, and long fur, long front claws (fig. 36), a large cranium with an elongate rostrum, and long and gracile mandible (figs. 37–39). *Bunomys prolatus* is larger than *B. coelestis*, as indexed by its average longer head and body, hind foot, and ears, but has a shorter tail (absolutely relative to length of head and body; LT/LHB = 79% for *B. prolatus*, 95% for *B. coelestis*). The Tambusisi rat has larger, longer, and more robust claws on digits of the front feet (fig. 36) as well as

more extensive brown epidermal scutellation on dorsal surfaces of the feet and digits.

Bunomys prolatus has a larger skull than *B. coelestis*, as indicated by the greater size of most of its cranial and dental dimensions; however, a few other cranial variables are of lesser magnitude than comparable dimensions in *B. coelestis* (table 31). These two sets of contrasts are quantitatively summarized through principal-components analysis. Specimen scores for *B. coelestis* and *B. prolatus*

| | Correlations | | | |
| | *B. prolatus* and *B. chrysocomus* | | *B. prolatus* and *B. coelestis* | |
Variable	PC 1	PC 2	PC1	PC2
ONL	0.81***	0.43***	0.59**	0.66***
ZB	0.70***	−0.02	−0.60***	0.62***
IB	0.50***	0.37***	0.73***	0.31
LR	0.76***	0.40***	0.57**	0.54**
BR	0.70***	−0.22***	−0.12	0.83***
BBC	0.40***	0.34***	0.63***	0.26
HBC	0.34***	0.36***	−0.46*	−0.27
BZP	0.35***	−0.78***	−0.96***	0.21
LD	0.77***	0.40***	−0.54**	0.72***
PPL	0.75***	0.19**	0.21	0.78***
LBP	0.54***	0.44***	0.59**	0.38*
BBP	0.64***	−0.20**	−0.04	0.48**
BMF	0.50***	−0.35***	−0.14	0.59***
LIF	0.35***	0.34***	−0.34	0.46*
BIF	0.41***	−0.23***	0.23	0.74***
LB	0.37***	0.37***	0.77***	0.33
CLM1–3	0.27***	0.27***	0.66***	0.30
BM1	0.19**	0.13*	0.73***	0.26
Eigenvalue	0.024	0.015	0.025	0.015
% Variance	40.7	25.7	42.7	24.7

*** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

projected onto first and second principal components form two widely separated clusters along the first axis (fig. 43). Their positions are determined primarily by the large and positive loadings for skull length; breadths of interorbit and braincase; lengths of rostrum, bony palate, bullar capsule; and size of molars ($r = 0.57$–0.77; table 33). Compared with *B. coelestis*, the Tambusisi species has a longer skull, wider interorbital region and braincase, longer rostrum and bony palate, larger bullar capsule, and heavier molars. The negative loadings associated with the first principal component points to the less-flared zygomatic arches (narrower zygomatic breadth) of *B. prolatus* compared with *B. coelestis*, along with its shallower braincase, much narrower zygomatic plate, and shorter diastema (the counterpoint to the longer bony palate and molar rows in *B.*

prolatus). These dimensional contrasts between the two species are reflected in univariate means for the variables (table 31) and can be visually appreciated in the illustrations of skulls (figs. 37–39).

Frequency of particular cusps and cusplets differ. Cusp t3 is absent from second and third upper molars of all examples of *B. prolatus*, but in *B. coelestis* is present on the second upper in 89% of the sample and on the third molar in 5% (table 10). An anterolabial cusp is present on the third lower molar in 75% of the *B. prolatus* sample but only in 25% of the sample of *B. coelestis* (table 11).

GEOGRAPHIC VARIATION: Because all the specimens of *B. prolatus* were taken in one trapline at a single locality, I cannot assess variation associated with geography. The differences in coat color among the specimens I have already described (Musser, 1991) and the range in measurements for each variable reflect individual variation and variation attributable to age among the adult specimens. Age-related size differences among crania, ranging from old adult (the largest) to adult and finally young adult (the smallest) individuals, is illustrated elsewhere (Musser, 1991: 20).

NATURAL HISTORY: All information concerning *B. prolatus* comes from the collector, C.H.S. Watts (in litt., 1980). The specimens were trapped on a ridgetop at 1830 m in forest where the trees were short (4 m) and gnarled, and on exposed areas the vegetation was heathlike. Pitcher plants (*Nepheris*) abounded and the ground was deeply covered in moss. On Gunung Tambusisi, 1830 m is in the zone of upper montane forest (Whitten et al., 1987: 521). One individual was caught in deep moss during the day between 10 and 11 A.M.; all the others were taken during the night.

A female had one recent placental scar.

The external morphology of *B. prolatus* is that of a terrestrial rat. Its long muzzle, very long and strong claws, and overall skull conformation suggests a diet consisting primarily of invertebrates, likely containing a range of items similar to those eaten by *B. chrysocomus* (see that account and table 13).

ECTOPARASITES: *Bunomys prolatus* is host to the flea *Sigmactenus alticola pilosus*

(table 14), and that ectoparasite has also been recorded from 14 other species of endemic Sulawesi murine rodents (*Bunomys penitus*, *B. chrysocomus*, and *B. karokophilus,* n. sp.; *Margaretamys elegans*; *Maxomys hellwaldii*, *M. wattsi*, and *Maxomys* sp.; *Melasmothrix naso* and *Tateomys rhinogradoides*; *Paruromys dominator*; *Taeromys celebensis* and *Taeromys* sp.; *Rattus hoffmanni* and *R. facetus* [recorded as *R. marmosurus*]) and the nonnative *Rattus exulans* (Durden and Beaucournu, 2000).

The nematode, *Syphacia rifaii* (Oxyuroidea, Oxyuridae), was extracted from host specimens identified as *B. prolatus* that were collected in Lore Lindu (Dewi and Hasegawa, 2010), but the host rats are likely examples of *B. chrysocomus* and not *B. prolatus.*

SYNONYMS: None.

The next account also deals with another montane isolate, one phenetically closely allied with *Bunomys prolatus* but occurring far to the south of Gunung Tambusisi in the high mountainous landscape of the Quarles Range in the southern part of the west-central mountain block. The species is named and described here by the four authors listed and they should be cited as the authorities for the name.

Bunomys torajae, new species, G.G. Musser, A.S. Achmadi, J.A. Esslestyn, and K.C. Rowe

HOLOTYPE: MZB 34730, the skin, skull, fluid-preserved carcass, and tissue for extraction of DNA of an adult male (original number KCR 1294) collected October 26, 2011, by A.S. Achmadi and K.C. Rowe. Standard external measurements, weight, and other data, and measurements of the skull and dentition are listed in table 18. The stuffed skin is complete, the cranium and mandible are intact (figs. 37–39).

TYPE LOCALITY: Tropical lower montane rain forest at 2600 m (trapline GD01, −2.84467° S, 119.38295° E) near Gunung Gandangdewata (−2.748253° S, 119.368536° E for the peak, Rano Rano, Kampung Rantepangko, desai Tondok Bakaru, Kabatuan Mamasa), which is the highest peak in Pegunungan Quarles in the southern portion of the west-central mountain block of the island's core, Kabupaten Mamasa, Propinsi Sulawesi Barat, Indonesia. The trapping area is on a large plateau and some distance from the peak.

DIAGNOSIS: On average, in physical size the largest member of the *B. chrysocomus* group (LHB = 156–210 mm, W = 98–128 g, ONL = 41.2–41.8 mm) and further characterized by the following combination of traits: (1) a protracted muzzle and large external pinnae; (2) dorsal fur luxuriant, soft, long, somewhat woolly in appearance, and dark brown speckled with buff, ventral fur also soft and thick and buffy dark gray; (3) dorsal carpal and metacarpal surfaces brown, digits and claws unpigmented, front claws slender but short and delicate relative to body size, hind foot short in relation to head and body length; (4) tail averages slightly shorter than length of head and body (LT/LHB = 93%), dark brownish gray on dorsal surface, white or lightly mottled grayish brown over ventral surface; (5) white tail tip characterizing half the specimens in sample, short to moderately long relative to length of tail (mean = 7.0%, range = 2%–11%); (6) testes moderately small in relation to length of head and body; (7) moderately large cranium with a long, wide, and tapered rostrum (with an associated long diastema); (8) wide and smooth interorbital region; (9) gracile and weakly flaring zygomatic arches; (10) large braincase, moderately small auditory bulla, narrow zygomatic plates, long and wide bony palate, short and wide incisive foramina; (11) an elongate dentary, especially that section of the ramus between molar row and edge of incisor alveolus; (12) long molar rows and wide molars; and (13) cusp t3 absent from second molar in half the sample, absent from third upper molars in entire sample.

REFERRED SPECIMENS: Total 7 with the holotype; MZB 34730–35, 34904. All were collected during the interval, October 26 to November 3, 2011.

GEOGRAPHIC AND ELEVATIONAL DISTRIBUTIONS: The only known sample of *Bunomys torajae* consists of the specimens collected in tropical lower montane forest at 2500 and 2600 m on Gunung Gandangdewata in the Quarles Range, part of the southern highlands of the west-central mountain block (see gazetteer and the map in

fig. 22). No specimens exist in older collections stored in the world's museums.

No present evidence indicates the range of *B. torajae* to extend beyond the western mountainous region of central Sulawesi and outside the high elevations in the Mamasa area. None of the collections of *Bunomys* from other west-central mountains sampled (Gunung Nokilalaki, Gunung Lehio, Rano Rano, Gunung Latimojong, Gunung Balease) contain examples of *B. torajae*. Whether the new species is endemic to Pegunungan Quarles or occurs at high elevations elsewhere in the west-central mountain block will have to be determined by results of additional surveys of the many currently unexplored montane habitats in the core of Sulawesi.

SYMPATRY WITH OTHER *BUNOMYS*: *Bunomys torajae* is regionally sympatric with three other species of *Bunomys* in the Mamasa highlands. A single specimen (BMNH 21.2.9. 12) documents the presence of *B. chrysocomus*. It was obtained by the Dutch "Controleur" on May 19, 1916, with the provenance noted as "Mamasa, Toradjalander." On the back of the tag attached to the skin is written "*Rattus chrysocomus* Hoffm." in Oldfield Thomas's handwriting. The skin is misshapen and the fur discolored; only an anterior segment of the rostrum and a piece of the mandible remains of the skull. Breadth across both upper incisor tips is 1.9 mm, which is within the range of measurements from a sample of 22 *B. chrysocomus* that Musser collected along the Sungai Sadaunta (mean = 1.8 mm, range =1.7–2.1 mm); each of the three skulls of *B. torajae* measure 2.0 mm. Ranges for the six specimens of *B. andrewsi* (2.0–2.5 mm) and four examples of *B. penitus* (2.2–2.3 mm) collected by Achmadi and Rowe from Gunung Gandangdewata are typical for those two species, which have larger skulls and teeth (for example, the range is 2.0–2.3 mm for 27 *B. andrewsi* from Kuala Navusu and Pinedapa and 2.1–2.6 mm for *B. penitus* from several places in the west-central mountain block). There are no recent records of *B. chrysocomus* from the Mamasa area and its distribution there remains unknown.

Of the other two *Bunomys* from the Mamasa district, *B. andrewsi* has been obtained near Sumarorong, south of Mamasa at 970 m, near Lambanan and Mam-

bulillin at about 1500 m, northeast of Mamasa, and Gunung Gandangdewata at 1600 m, north of Mamasa (see gazetteer). Samples of *B. penitus* come from near Lambanan and at 2000 m on Gunung Gandangdewata. On the latter highland, Achmadi and Rowe collected *B. torajae* (2500–2600 m), *B. penitus* (about 2000 m), and *B. andrewsi* (1600 m) during the period, October 26-November 11, 2011; the distribution of the three species as indicated by samples at hand reflects local sympatry but not syntopy.

ETYMOLOGY: Gunung Gandangdewata is part of the southern mountains in central Sulawesi known in *Bahassa Indonesia* as *Tana Toraja*, land of the indigenous Toraja people. "Belonging to" is one of the meanings of the Latin feminine genitive case ending -*ae* and by combining it with Toraja we signify that *Bunomys torajae* belongs to Tana Toraja. The scientific name will always identify Tana Toraja as the place where *B. torajae* was first discovered should future surveys find the species elsewhere in the west-central mountain block.

DESCRIPTION: (based primarily on four adult skins and three skulls) in body size, *Bunomys torajae* is the largest of the species in the *B. chrysocomus* group (LHB = 156–175 mm, LT = 160–170 mm, LHF = 36–39 mm, LE = 26–28 mm, W = 98–128 g, ONL = 41.2–41.8 mm), with dark-brown upperparts, buffy dark-gray underparts, and a moderately long tail. Soft, dense, and long (coat 20–25 mm) to the touch, and somewhat woolly to the eye, fur covering the upperparts is dark brown from muzzle to rump with buff and black speckling (produced by the combination of dark gray underfur, overhairs that are dark gray for most of their lengths with subterminal and terminal buffy or black bands, all intermixed with black guard hairs); sides of the body are slightly paler, brown rather than dark brown. Because the guard hairs are only slightly longer than the overhairs, the surface of the coat is smooth. Fur over the forearms and legs is the same color as the sides of the body, and the muzzle, cheeks, and around the eyes match the dark brown of the back.

Fur covering the underparts of the head and body is also soft and thick, but shorter

(10–15 mm thick) than the dorsal fur, which is usual in murids. Underparts of three of the four skins at hand are covered with buffy dark gray fur from the chest to inguinal region (hairs are dark gray for most of their lengths and end in long bright buffy tips); throats are dark gray. One specimen is paler, the background is dark gray, but the wash is pale buff. The contrast between dorsal and ventral coats is inconspicuous.

The large dark brown ears (pinnae) appear to be naked, but are scantily covered by short hairs.

The tail is nearly equal to or shorter than the combined length of head and body (LT/LHB = 93%). Tail patterning is individually variable: dorsal surface and sides are dark brownish gray in all four rats; the ventral surface is white from base to tip in three specimens and white mottled with grayish brown in the fourth. Two specimens show a distal white segment (unpigmented on all surfaces) ranging from 2% to 11% of the tail length (mean = 7.0%; table 8). The rat with the longer white tip also has a sharply bicolored tail throughout its length, the overall pattern similar to that common to *B. penitus* (see that account).

Metacarpal and metatarsal surfaces range from gray to brownish gray (the integument is white but densely covered with unpigmented and brown hairs), with silvery highlights in some specimens. Palmar pads are gray, the rest of the palmar surface ranges from pale gray to unpigmented; all the plantar surface ranges from gray to dark gray. Digits of front and hind feet are typically unpigmented. All claws are unpigmented, those on the front digits are moderately long and sharp and not concealed by ungual tufts, but comparable tufts of silvery hairs cover and extend beyond the hind claws. Size of the claws in relation to body size is closely similar to the proportion seen in *B. chrysocomus* (see fig. 36).

Females exhibit the number of teats usual for all species of *Bunomys* (four, arranged in two inguinal pairs). Testes are relatively small in relation to length of head and body (table 9).

The specimens available are in adult pelage; the juvenile coat will have to be described after examples of that age group are collected. However, the fur is probably similar to that in juveniles of other species of *Bunomys*: dense, woolly, and very dark gray upperparts with a flat tone (lacking the glossy sheen of the adult fur); dark grayish white or buffy gray underparts.

In size and shape, the skull of *B. torajae* is similar to that of *B. prolatus* (figs. 37–39; table 31). Smooth sides of the long and tapered rostrum are interrupted by slight bulges of the nasolacrimal capsules. Frontal bones forming the dorsal surface of the broad interorbit are slightly inflated into two low mounds. Dorsolateral margins of the interorbit are smooth, without ridging, but postorbital edges are outlined by slight ridges that extend back along dorsolateral margins of the domed braincase but not all the way to the lamboidal ridges. The occiput, as in other species of *Bunomys*, is moderately deep and mostly roofed by the interparietal. The short and wide incisive foramina end well anterior to front surfaces of the first molars (with a correspondingly long bony palate), and each zygomatic plate is narrow with its concave anterior margin projecting beyond the dorsal zygomatic root. The ectotympanic bullae are small relative to skull size.

Configuration of each dentary resembles the shape of this element in other members of the *B. chrysocomus* group, particularly *B. prolatus* (fig. 39). Elongate and gracile describe the configuration. Musser's (1991: 15) original description of the dentary of *B. prolatus* could stand in for that element in *B. torajae*.

Enamel layers of the narrow upper and lower incisors are pigmented orange, the lowers paler than the uppers. Uppers emerge from the rostrum at either a 90° angle to the ventral surface of the rostrum (orthodont configuration) or curve back (opisthodont). The lower incisors have narrow sharp tips and elongate wear facets.

Size and occlusal topography of maxillary and mandibular molars are similar in *B. torajae* and *B. prolatus* (figs. 40, 41; table 31). Long molar rows and wide molars characterize both species. Cusp patterns forming the occlusal surfaces are unelaborate and after even moderate use the cusp rows wear to irregular basins surrounded by dentine. The lack of occlusal complexity and the cusp morphology that contributes to it as is

portrayed in the original description of *B. prolatus* (Musser, 1991: 17) also fits the cusp patterns possessed by *B. torajae*. Presence or absence of most accessory cusps cannot be determined for *B. torajae*, especially on the mandibular molars, because the teeth are too worn in the three specimens at hand. Of the two rats in which the uppers are not excessively worn, cusp t3 is present on the second molar in one individual but absent in the other, and the comparable cusp is absent from the third molar in both specimens (table 10).

KARYOTYPE: No information.

COMPARISONS: *Bunomys torajae* requires comparison with two sets of species. The first comprises *B. prolatus*, *B. coelestis*, and *B. chrysocomus*, the three phenetically (but not necessarily genetically) most closely allied to the Gandangdewata rat (see cluster diagrams in figs. 21 and 49). *Bunomys andrewsi* and *B. penitus* constitute the second set; both are sympatric with *B. torajae* on Gunung Gandangdewata and all three appear superficially similar in their external characteristics. The sample of *B. torajae* used in the analyses is small (three adults) so outcome of the following comparisons should be tested in the future with more examples of that species.

Bunomys torajae and B. prolatus: Of all the described species of *Bunomys*, *B. torajae* is phenetically most similar to *B. prolatus*. Both occupy isolated montane habitats and resemble one another in physical body size, most cranial and dental dimensions, and overall conformation of skulls and dentitions. Both species have luxuriant, soft, and thick brown fur covering the upperparts and dark gray underparts washed with buff, except that the buffy suffusion is more intense in *B. torajae*.

Although similar in some external traits, they do differ in others. *Bunomys torajae* averages greater in lengths of head and body, tail, hind feet, and ears, but the most spectacular difference is relative length of tail. Not only does *B. torajae* have an absolutely much longer tail than *B. prolatus* (see below) but it is also longer relative to length of head and body (LT/LHB = 93% in *B. torajae* versus 79% for *B. prolatus*). Relative to length of head and body, lengths of feet and ears are not dissimilar in the two

species—those dimensions scale to body size, averaging larger in *B. torajae*, which also averages greater in head and body length (table 19). The front claws of *B. torajae* are moderately long with slender tips and their size relative to body size is similar to the proportions seen in *B. chrysocomus* (see fig. 36); they diverge sharply from the strikingly more robust and appreciably longer claws on the forefeet of *B. prolatus* (fig. 36) that are huge in relation to body size as compared with the shorter and gracile configuration in *B. torajae*. The Gandangdewata species also lacks the extensive brown epidermal scutellation on dorsal surfaces of feet and digits that is so characteristic of *B. prolatus* (Musser, 1991).

Size differences of appendages is graphically portrayed in the ordination of specimen scores for samples of *B. torajae* and *B. prolatus* projected onto first and second principal components where the scores form two discrete clumps along the first axis, those on the right signal the larger *B. torajae*, those on the left *B. prolatus* (fig. 44, upper graph). Correlations for lengths of tail and hind foot ($r = 0.97$ and 0.91, respectively; table 34) are the most influential in spreading the scores along the first component and these variables show the greatest univariate mean differences between the two species (LT = 165.3 mm, LHF = 37.6 mm for *B. torajae*; 132.4 mm and 33.9 mm, respectively, for *B. prolatus*).

Both species are generally similar in overall conformation of their skulls along with the magnitude of many cranial and dental measurements (figs. 37–39; table 31). The notable morphometric distinctions are displayed in a scatter plot where specimen scores for *B. torajae* and *B. prolatus* are projected onto first and second principal components (fig. 44, lower graph). The spread of scores along the first axis is primarily influenced by the positive and large loadings for several cranial variables that distinguish the two species ($r = 0.67$–0.98; table 34). Compared with *B. prolatus*, the Gandangdewata species has more flaring zygomatic arches and a wider rostrum, bony palate, mesopterygoid fossa, and incisive foramina; *B. torajae* also has a shallower braincase ($r = -0.69$). These contrasts are reflected in univariate descrip-

Fig. 44.   Specimen scores representing samples of *Bunomys torajae* (empty squares) and *B. prolatus* (asterisks) projected onto first and second principal components extracted from principal-components analysis. Upper graph: derived from log-transformed values for lengths of head and body, tail, hind foot, and ear (*N* = 3 *B. torajae*, 6 *B. prolatus*). Lower graph: based on log-transformed values for 14 cranial and 2 dental variables (*N* = 3 *B. torajae*, 8 *B. prolatus*). See table 34 for correlations (loadings) of variables with extracted components and for percent variance explained for both scatter plots.

tive statistics (table 31) and images of skulls (figs. 37–39).

Noteworthy among the loadings on the second component is that for bullar length (*r* = 0.82; table 34), reflecting *B. torajae*'s much smaller bullae compared with *B. prolatus.*

Coronal patterns of the primary cusps on molars are closely similar in the two species (figs. 41, 42) as is length of the molar row

(mean is 6.5 mm for each sample). Similarities or differences between the two species in presence or absence of accessory cusps and cusplets cannot be reliably assessed because the sample of *B. torajae* is small and the molars too worn.

Bunomys torajae and B. coelestis: These two species need to be compared because both have been collected only from southern

Upper graph: Correlations (loadings) of log-transformed values for lengths of head and body, tail, hind foot, and ear derived from three *B. torajae* and six *B. prolatus*. **Lower graph**: Correlations (loadings) of 14 cranial and two dental log-transformed variables are based on three *B. torajae* and eight *B. prolatus*. Occipitonasal and postpalatal lengths are omitted because they could not be measured on one damaged specimen of *B. torajae*. See figure 44.

Variable	Correlations			
	Upper graph		Lower graph	
	PC1	PC2	PC1	PC2
LHB	0.54	−0.85**	—	—
LT	0.97***	0.34	—	—
LHF	0.91***	0.33	—	—
LE	0.60	0.23	—	—
ZB	—	—	0.79**	0.17
IB	—	—	0.15	0.21
LR	—	—	0.42	0.86***
BR	—	—	0.74**	0.46
BBC	—	—	−0.09	0.33
HBC	—	—	−0.69*	0.10
BZP	—	—	0.59	−0.54
LD	—	—	0.36	0.82**
LBP	—	—	0.39	0.32
BBP	—	—	0.87***	0.02
BMF	—	—	0.67*	0.05
LIF	—	—	−0.52	0.56
BIF	—	—	0.98***	−0.09
LB	—	—	−0.34	0.82**
CLM1–3	—	—	0.05	0.03
BM1	—	—	0.41	−0.34
	—	—	—	—
Eigenvalue	0.018	0.008	0.020	0.007
% Variance	67.3	28.9	49.8	18.3

*** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

montane forest habitats, their dorsal coat is dark brown, soft, and thick, and both have a large cranium with a long and narrow rostrum and an elongate and gracile mandible (figs. 37–39) with slender and sharp lower incisors.

Bunomys torajae is physically larger than *B. coelestis*, as indexed by its average longer head and body, tail, hind feet, and ears (table 19). However, tail length relative to length of head and body is similar (LT/LHB = 93% for *B. torajae*, 95% for *B. coelestis*) as is pelage length (up to 25 mm long for the

dorsal coat, 10–15 mm for the ventral fur). While color of the dorsal fur is similar in the two species, there is a difference in the range of chromatic expression of the ventral coat. Most specimens of *B. coelestis* have dark grayish-white underparts, a few show a pale or dense buffy wash (see that account); all four skins of *B. torajae* have buffy dark gray ventral coats (whether these four skins represent the usual coloration or the range is similar to that seen in *B. coelestis* will have to be determined from a larger sample of *B. torajae*). Finally the front claws of *B. torajae* are shorter than the elongate claws typical of *B. coelestis*, their shape and bulk relative to body size similar to the proportion in *B. chrysocomus* rather than *B. coelestis* (see fig. 36).

The ordination of specimen scores for samples of *B. torajae* and *B. coelestis* projected onto first and second principal components (fig. 45, upper graph) summarizes difference in size of external variables between the two species. Positive moderate to high loadings for all four variables sort the scores into two marginally overlapping clumps along the first axis, the larger-bodied *B. torajae* on the right, and the physically smaller *B. coelestis* to the left, with loadings for lengths of head and body, tail and ear (r = 0.88, 0.80, and 0.65, respectively; table 35) the most forceful in scattering the scores. These three variables show the greatest univariate mean differences between the two species (table 19).

Bunomys torajae has a larger skull and much heavier molars than *B. coelestis*, along with some greater internal measurements (table 31); a few other cranial variables are of lesser magnitude than comparable dimensions in *B. coelestis*, and there is essentially no significant difference between the two samples in postpalatal length and length of bulla. These sets of dimensional contrasts and similarities are summarized by specimen scores for *B. torajae* and *B. coelestis* projected onto first and second principal components where they form two widely separated clusters along the first axis (fig. 45, lower graph), the scatter determined primarily by the large and positive correlations (r = 0.49–0.90; table 35) for most cranial and dental dimensions. Compared with *B. coelestis*, the
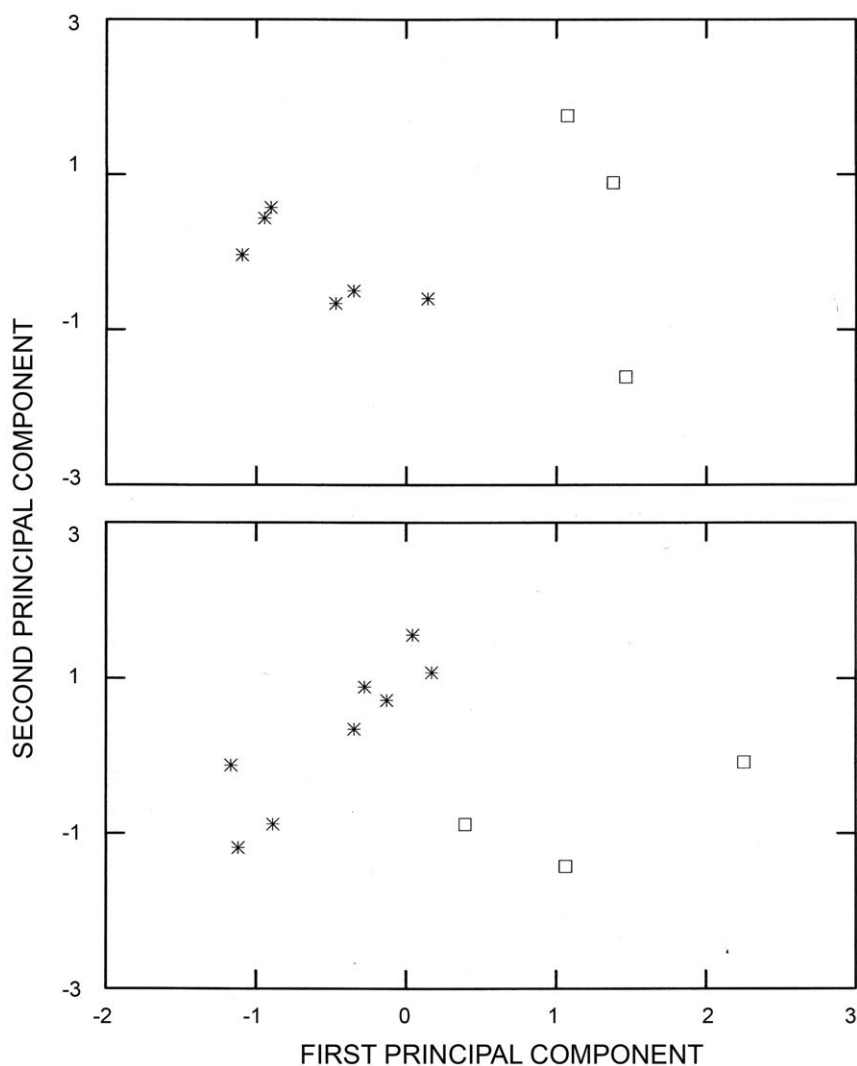
Fig. 45. Specimen scores representing samples of *Bunomys torajae* (empty squares) and *B. coelestis* (filled diamonds) projected onto first and second principal components extracted from principal-components analysis. Upper graph: derived from log-transformed values for lengths of head and body, tail, hind foot, and ear ($N = 3$ *B. torajae*, 20 *B. coelestis*). Lower graph: based on log-transformed values for 14 cranial and 2 dental variables ($N = 3$ *B. torajae*, 18 *B. coelestis*). See table 35 for correlations (loadings) of variables with extracted components and for percent variance explained for both ordinations.

Gandangdewata species has a wider interorbital region and braincase, longer and wider rostrum, longer and wider bony palate, wider mesopterygoid fossa and incisive foramina, and heavier molars. The high negative loadings associated with the first principal component ($r = -0.57$, -0.61, and -0.72) points to *B. torajae*'s shallower braincase, much narrower zygomatic plate, and notably shorter incisive foramina compared with these variables in *B. coelestis*. These differences between the two species are reflected by univariate means (table 31) and in the images of skulls (figs. 37–39).

Occlusal patterns of primary molar cusps are similar in the two species (figs. 41, 42). The sample of *B. torajae* is too small and the molars too worn to detect potential similarities or differences in presence or absence of accessory cusps and cusplets.

Upper graph: Correlations (loadings) of log-transformed values for lengths of head and body, tail, hind foot, and ear derived from three *B. torajae* and 20 *B. coelestis*. **Lower graph**: Correlations (loadings) of 14 cranial and two dental log-transformed variables are based on three *B. torajae* and 18 *B. coelestis*. Occipitonasal and postpalatal lengths are omitted because they could not be measured on one damaged specimen of *B. torajae*. See figure 45.

| | Correlations | | | |
| | Upper graph | | Lower graph | |
Variable	PC1	PC2	PC1	PC2
LHB	0.88***	−0.44*	—	—
LT	0.80***	0.13	—	—
LHF	0.39	0.09	—	—
LE	0.65***	0.73***	—	—
ZB	—	—	0.07	0.71***
IB	—	—	0.67***	−0.07
LR	—	—	0.55**	0.37***
BR	—	—	0.49*	0.69***
BBC	—	—	0.44*	−0.05
HBC	—	—	−0.61**	−0.08
BZP	—	—	−0.72***	0.63**
LD	—	—	−0.25	0.84***
LBP	—	—	0.68***	0.04
BBP	—	—	0.62**	0.29
BMF	—	—	0.50*	0.50*
LIF	—	—	−0.57**	0.64**
BIF	—	—	0.90***	0.25
LB	—	—	0.19	0.38
CLM1–3	—	—	0.62**	0.16
BM1	—	—	0.85***	−0.01
	—	—	—	—
Eigenvalue	0.008	0.004	0.027	0.013
% Variance	60.9	25.4	46.4	21.8

*** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

***Bunomys torajae* and *B. chrysocomus*:** With its long muzzle and fur color, *B. torajae* conveys the physical impression of a high-mountain population of *B. chrysocomus*, which it is not, and the reason behind documenting here the specific integrity of the Gandangdewata rat relative to the more widespread *B. chrysocomus*. Compared with samples of *B. chrysocomus* from throughout its documented geographic range (see the map in fig. 22), the sample of *B. torajae* contains much larger rats that have greater average lengths of head and body size, tail, hind feet, and ears as well as mass (table 19);

length of tail relative to length of head and body in *B. torajae* (LT/LHB = 93%) falls wihin the range derived from the samples of *B. chrysocomus* (84%–98%). The size disparity in external variables is visualized in the ordination of specimen scores for samples of *B. torajae* and *B. chrysocomus* projected onto first and second principal components (fig. 46, upper graph; here the scores for *B. chrysocomus* are represented by a sample collected and measured by Musser from Sungai Sadaunta, Tomado, and Sungai Tokararu—univariate statistics are tabulated in table 68). The larger external variables in *B. torajae* as indicated by the moderate to large and positive loadings (r = 0.37–0.94; table 36) separate the three scores for that species to the right of the cluster signifying *B. chrysocomus* along the first component.

In addition to the dimensional dissimilarities noted above, *B. torajae* has a thicker coat than specimens in samples of *B. chrysocomus*, even those from high elevations (see that account), and smaller testes relative to length of head and body (table 9). Range of size of the front claws is similar in the two species, but because *B. torajae* is physically larger its claws are relatively smaller.

Absolute size and proportions summarize the primary morphometric cranial and dental contrasts between the two species: *B. torajae* has a larger skull and molars and differs in proportions of internal cranial dimensions. The contrast is evident in the cranial illustrations of *B. torajae* and *B. chrysocomus* (figs. 37–39), univariate descriptive statistics (table 31), and the ordination of specimen scores for samples of *B. torajae* and all 10 population samples of *B. chrysocomus* projected onto first and second principal components (fig. 46, lower graph; all population samples of *B. chrysocomus* are employed—the pattern of scores is similar when *B. torajae* is compared with only samples of *B. chrysocomus* from the west-central mountain block, which is not illustrated here). Size is the primary factor affecting the spread of scores along the first axis with those indicating *B. torajae* and the larger specimens of *B. chrysocomus* falling in the right half of the scatter plot. Significant covariation among all variables, as indicated by the moderate to
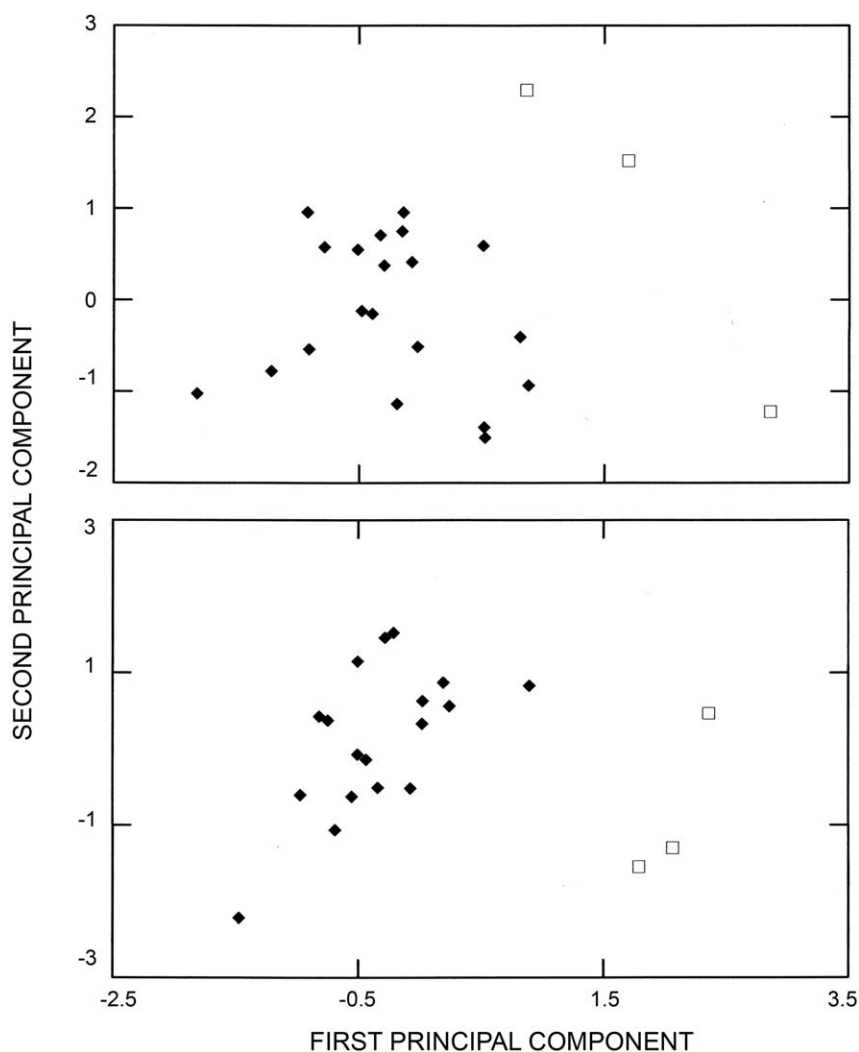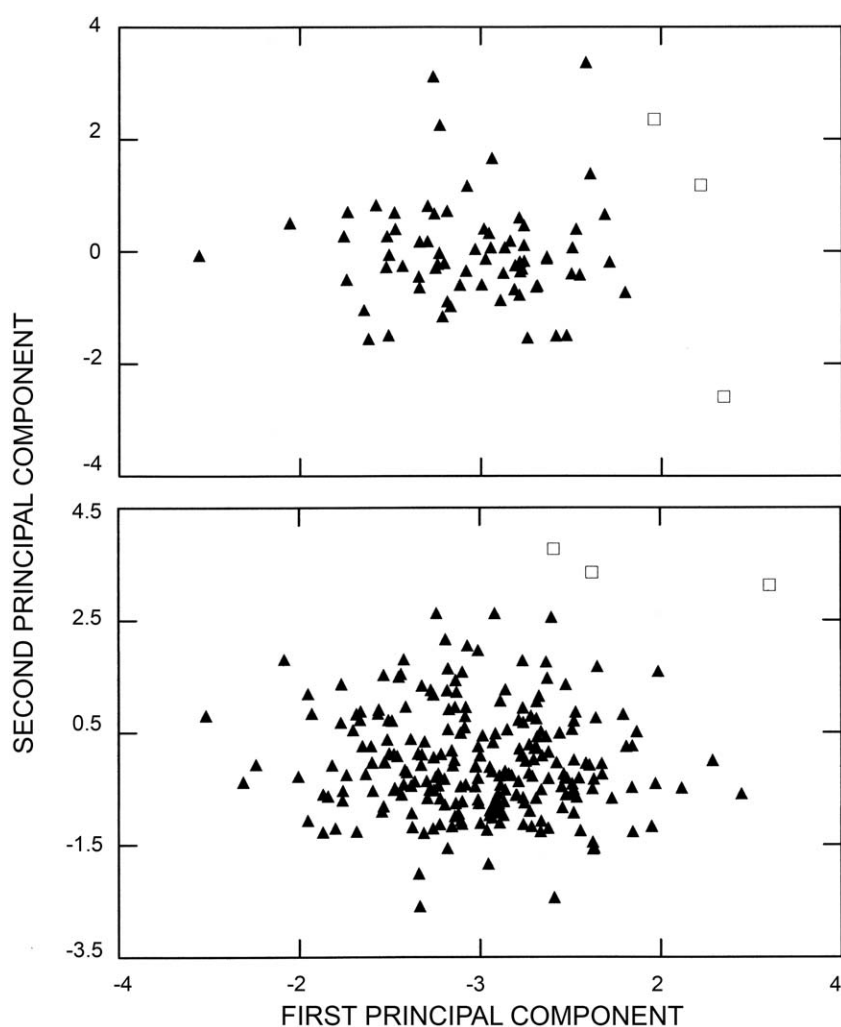
Fig. 46.   Specimen scores representing samples of *Bunomys torajae* (empty squares) and *B. chrysocomus* (filled triangles) projected onto first and second principal components extracted from principal-components analysis. Upper graph: derived from log-transformed values for lengths of head and body, tail, hind foot, and ear ($N = 3$ for *B. torajae*; $N = 71$ for *B. chrysocomus* from Sungai Sadaunta, Tomado, and Sungai Tokararu). Lower graph: based on log-transformed values for 14 cranial and 2 dental variables ($N = 3$ *B. torajae*; $N = 232$ for all 10 population samples of *B. chrysocomus*). See table 36 for correlations (loadings) of variables with extracted components and for percent variance explained for both ordinations.

large positive loadings (r = 0.25–0.73), influences the spread of points—especially forceful is zygomatic breadth, length and breadth of rostrum, length of diastema, and breadths of bony palate and mesopterygoid fossa (table 36); univariate means of most cranial and dental measurements are greater in the smaller sample of *B. torajae* than in the much larger sample of *B. chrysocomus* (table 31). The isolation of scores denoting *B.*

torajae from those signifying *B. chrysocomus* along the second axis underscores the relatively wider interorbit of *B. torajae*, its longer rostrum, larger braincase, narrower zygomatic plate, longer diastema and bony palate, more spacious incisive foramina, and heavier molars compared with *B. chrysocomus* (see the correlations in table 36). The relatively narrower zygomatic plate of *B. torajae* is most forceful (r = -0.80) in isolating the

TABLE 36
Results of Principal-Components Analyses Comparing Samples of *Bunomys torajae* and *B. chrysocomus*

Upper graph: Correlations (loadings) of log-transformed values for lengths of head and body, tail, hind foot, and ear derived from three *B. torajae* and 71 *B. chrysocomus* from my transect sample (Sadaunta, Tomado, Sungai Tokararu). **Lower graph**: Correlations (loadings) of 14 cranial and two dental log-transformed variables are based on 3 *B. torajae* and 232 *B. chrysocomus* (all population samples). Occipitonasal and postpalatal lengths are omitted because they could not be measured on one damaged specimen of *B. torajae*. See figure 46.

	Correlations			
	Upper graph		Lower graph	
Variable	PC1	PC2	PC1	PC2
LHB	0.63***	−0.73***	—	—
LT	0.94***	0.19	—	—
LHF	0.68***	0.07	—	—
LE	0.37***	0.48***	—	—
ZB	—	—	0.70***	0.16*
IB	—	—	0.45***	0.32***
LR	—	—	0.72***	0.29***
BR	—	—	0.73***	−0.06
BBC	—	—	0.34***	0.33***
HBC	—	—	0.26***	0.30***
BZP	—	—	0.46***	−0.80***
LD	—	—	0.70***	0.33***
LBP	—	—	0.49***	0.38***
BBP	—	—	0.70***	−0.06
BMF	—	—	0.60***	−0.15*
LIF	—	—	0.25***	0.20**
BIF	—	—	0.52***	0.19**
LB	—	—	0.26***	0.13*
CLM1–3	—	—	0.25***	0.34***
BM1	—	—	0.28***	0.31***
	—	—		
Eigenvalue	0.009	0.003	0.014	0.007
% Variance	56.1	19.9	29.2	13.7

*** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

scores for *B. torajae* at the top of the scatter plot. These results from the principal-components analysis reinforce the visual contrast between the two species when skulls are compared side by side: *B. torajae* typically has larger molars than *B. chrysocomus*, and a larger skull with a relatively much narrower zygomatic plate (figs. 37–39).

The primary mandibular difference between the two species mirrors the cranial contrasts. *Bunomys torajae* has longer dentaries, particularly in the more elongate stretch between incisor alveolus and anterior margin of the molar row (fig. 39).

Occlusal patterns of primary molar cusps are similar in the two species (figs. 41, 42), but the molars too worn in the sample of *B. torajae* to detect potential similarities or differences between *B. torajae* and *B. chrysocomus* in presence or absence of accessory cusps and cusplets.

***Bunomys torajae*, *B. andrewsi*, and *B. penitus*:** Comparisons here are between the few examples of *B. torajae* and samples of *B. andrewsi* and *B. penitus* from localities in the west-central mountain block, which include specimens from Gunung Gandangdewata where *B. torajae* and the other two species are sympatric but elevationally discrete (specimens of *B. torajae* comes from 2500 and 2600 m, those of *B. penitus* from 2000 m, and the sample of *B. andrewsi* from 1600 m).

In snare or trap, in hand, and as study skins, examples of the three species from Gunung Gandangdewata appear to the collector nearly indistinguishable from one another in external traits—adults of *B. torajae* and *B. andrewsi* are especially difficult to separate. *Bunomys torajae* is larger but not heavier; it typically has a longer head and body, tail, hind foot, and ear than *B. andrewsi* (tables 19, 41), but length of tail relative to length of head and body is similar (93% versus 92%) and mass is not so different (116.8 g versus 111.7 g). Both species have soft and long, dark brown dorsal coats and buffy dark gray underparts, but the coat appears woolly in texture and is slightly longer in *B. torajae* (dorsal coat up to 25 mm in *B. torajae*, up to 20 mm in *B. andrewsi*). The dorsal coat of *B. andrewsi* has stronger yellow and buff highlights because the speckling appears more intense due to the longer buffy tips; *B. torajae* shows a denser dark brown—a subtle but noticeable difference. Finally, patterning of the tail differs. Tails of *B. andrewsi* are typically monocolor brown with some specimens showing a mottled underside but usually so intensely mottled that it appears monocolored. Tails of *B. torajae* are bicolored: brown on the upper surface and either white or only slightly mottled with gray or pale brown along the underside.

TABLE 37
Descriptive Statistics for Cranial and Dental Measurements (mm) derived from Samples of *B. andrewsi*, *B. penitus*, and *B. torajae*
Mean ± 1 SD and observed range (in parentheses) are listed.

| Variable | West-central mountain block | | Gunung Gandangdewata | | |
	B. andrewsi	*B. penitus*	*B. andrewsi*	*B. penitus*	*B. torajae*
N	40	170	6	4	N = 2 or 3[a]
ONL	40.5 ± 1.84	43.0 ± 1.18	39.3 ± 0.72	44.7 ± 0.92	41.5 ± 0.42
	(38.0–44.8)	(40.1–46.1)	(38.2–40.0)	(43.8–46.0)	(41.2–41.8) 2
ZB	19.7 ± 1.02	19.7 ± 0.67	19.1 ± 0.74	19.7 ± 0.50	18.3 ± 0.15
	(18.3–21.9)	(18.0–21.4)	(18.4–20.0)	(19.0–20.2)	(18.2–18.5)
IB	6.7 ± 0.27	6.8 ± 0.24	6.4 ± 0.25	6.8 ± 0.33	7.2 ± 0.23
	(6.1–7.3)	(6.1–8.3)	(6.2–6.9)	(6.5–7.2)	(6.9–7.3)
LR	14.5 ± 0.98	16.1 ± 0.66	14.3 ± 0.42	16.5 ± 0.55	15.6 ± 0.36
	(12.5–17.2)	(14.6–18.1)	(13.7–14.8)	(16.0–17.2)	(15.3–16.0)
BR	7.5 ± 0.46	7.9 ± 0.34	7.1 ± 0.26	8.5 ± 0.51	7.1 ± 0.31
	(6.7–8.9)	(7.0–8.9)	(6.7–7.5)	(7.0–9.0)	(6.8–7.4)
BBC	16.2 ± 0.47	16.6 ± 0.40	16.0 ± 0.45	16.7 ± 0.29	16.1 ± 0.61
	(15.3–17.2)	(15.4–17.7)	(15.5–16.7)	(16.4–17.1)	(15.6–16.8)
HBC	11.4 ± 0.44	11.9 ± 0.35	11.1 ± 0.66	11.6 ± 0.30	11.0 ± 0.49
	(10.6–12.4)	(10.9–12.7)	(10.6–12.4)	(11.2–11.9)	(10.7–11.6)
BZP	3.5 ± 0.45	3.0 ± 0.21	3.3 ± 0.23	3.3 ± 0.35	2.8 ± 0.23
	(2.9–4.5)	(2.4–3.6)	(2.9–3.5)	(2.9–3.6)	(2.7–3.1)
LD	10.8 ± 0.66	11.3 ± 0.50	10.3 ± 0.38	12.3 ± 0.37	11.4 ± 0.23
	(9.7–12.2)	(10.2–12.8)	(9.9–10.8)	(11.8–12.7)	(11.1–11.5)
PPL	14.2 ± 0.84	14.6 ± 0.50	13.6 ± 0.71	15.2 ± 0.40	14.2 ± 0.50
	(12.5–16.0)	(13.4–16.1)	(12.5–14.5)	(14.8–15.7)	(13.8–14.5) 2
LBP	7.7 ± 0.43	8.8 ± 0.43	7.8 ± 0.27	8.7 ± 0.49	8.8 ± 0.15
	(7.0–8.7)	(7.4–9.8)	(7.3–8.0)	(8.3–9.4)	(8.7–9.0)
BBP	3.8 ± 0.32	3.6 ± 0.27	3.7 ± 0.29	4.1 ± 0.24	4.0 ± 0.36
	(3.2–4.5)	(3.0–4.3)	(3.3–4.1)	(3.8–4.3)	(3.7–4.4)
BMF	3.2 ± 0.27	3.7 ± 0.27	3.3 ± 0.20	3.3 ± 0.31	2.9 ± 0.21
	(2.7–4.0)	(2.9–4.4)	(3.0–3.6)	(3.0–3.7)	(2.7–3.1)
LIF	7.8 ± 0.51	8.1 ± 0.45	7.6 ± 0.39	8.8 ± 0.27	6.1 ± 0.15
	(6.8–9.3)	(7.0–9.2)	(7.2–8.3)	(8.5–9.1)	(5.9–6.2)
BIF	2.9 ± 0.21	3.0 ± 0.19	2.9 ± 0.12	2.8 ± 0.21	2.8 ± 0.21
	(2.5–3.4)	(2.5–3.4)	(2.7–3.0)	(2.6–3.1)	(2.6–3.0)
LB	6.5 ± 0.26	6.8 ± 0.28	6.6 ± 0.16	6.7 ± 0.22	6.4 ± 0.23
	(5.9–7.0)	(6.0–8.2)	(6.3–6.8)	(6.5–7.0)	6.1–6.5
CLM1–3	7.1 ± 0.37	7.8 ± 0.25	7.0 ± 0.25	7.7 ± 0.29	6.5 ± 0.06
	(6.5–8.0)	(7.0–8.4)	(6.6–7.3)	(7.4–8.0)	6.5–6.6
BM1	2.3 ± 0.10	2.5 ± 0.11	2.3 ± 0.10	2.5 ± 0.05	2.3 ± 0.06
	(2.1–2.5)	(2.2–2.8)	(2.2–2.4)	(2.4–2.5)	(2.2–2.3)

[a] ONL and PPL are based on two specimens; statistics for all the other variables are derived from three skull (one skull is damaged and ONL and PPL could not be measured).

Bunomys torajae is similar to *B. penitus* in length of head and body (comparing adults of comparable age), but *B. torajae* has, on average, a shorter tail and hind foot than *B. penitus*, and lesser mass (tables 19, 41). Mean length of ear is about the same (26.8 mm versus 26.0 mm), which indicates the ears to be larger relative to body size in *B. torajae*. Tail length in relation to length of head and body also differs with *B. torajae* possessing a relatively shorter tail (LT/LHB = 93% versus 102%). Both species have soft and dense fur, but compared with *B. torajae* the dorsal coat of *B. penitus* is more intensely flecked with buff (the pigmented hair tips are longer), the guard hairs extend farther beyond the over-hair layer (inconspicuous in *B. torajae*), and the underparts are grayish white (buffy dark

gray in *B. torajae*). *Bunomys penitus* typically has a bicolored tail, brownish gray along the dorsal surface and white along the entire ventral surface; a white tip is usual (table 8). Tail pattern in three of the *B. torajae* is similar to that seen in *B. penitus*, but the fourth specimen is lightly mottled with gray along the underside of the tail; a white tail tip occurs less frequently than in *B. penitus.*

Differences in magnitudes of cranial and dental dimensions between *B. torajae* and *B. andrewsi* and between the former and *B. penitus* are documented by univariate means (table 37) and images of skulls (fig. 48).

Bunomys torajae has a longer but narrower skull (as indexed by occipitonasal length and zygomatic breadth) than *B. andrewsi*; overall it is less robust and more gracile in conformation, but some of its internal dimensions are greater, others lesser. For example, *B. torajae* has a wider interorbit, longer but narrower rostrum, shallower braincase, longer diastema, and longer and wider bony palate, but notably narrower zygomatic plates and mesopterygoid fossa, much shorter incisive foramina, smaller bullae, and shorter molar rows. Proportional (shape) distinctions between *B. torajae* and *B. andrewsi* are summarized by specimen scores designating each species projected onto first and second principal components (fig. 47, upper graph). Along the second component, the scores form two discrete clusters, the spread influenced by several cranial variables (table 38): *Bunomys torajae* has a relatively wider interorbital region, longer rostrum and diastema, more expansive bony palate (r = 0.33–0.84), and appreciably shorter incisive foramina (r = −0.55) compared with *B. andrewsi.*

Bunomys torajae has a smaller skull than *B. penitus*, and nearly all of its cranial and dental dimensions are less (as indicated by univariate means). The exceptions are breadths of the interorbit and bony palate, which exceed, on average, those dimensions in the sample of *B. penitus*. This size disparity among the variables is reflected by the specimen scores representing each species projected onto first and second principal components (fig. 47, lower graph). The distribution of scores along the first axis, signifying variation in size, is influenced by nearly all variables as denoted by the

moderate to high positive loadings listed in table 37 (r = 0.25–0.75), and explains the position of the three scores for *B. torajae* that lay to the left (smaller) of most scores representing the larger *B. penitus* (and without overlapping the scores signifying the four Gandangdewata *B. penitus*). Along the second axis, scores for *B. torajae* and *B. penitus* form two separate clusters, revealing noteworthy proportional contrasts. Compared with *B. penitus*, the Gandangdewata species has a relatively wider interorbit, shallower braincase, longer diastema, wider bony palate, narrower mesopterygoid fossa, shorter incisive foramina, smaller bullae, and smaller molars (see the positive and negative loadings in table 38).

Assuming that specimens of comparable age are compared, the gracile skull of *B. torajae* with its small molars is at once distinguished from the robust skull of *B. andrewsi* and larger skull of *B. penitus* with its heavier molars, whether specimens of the latter two species are from Gunung Gandangdewata or elsewhere in the west-central mountain block (fig. 48).

Geographic Variation: Because all the samples of *B. torajae* come from a single locality, color and morphometric variation associated with geography will have to wait for additional material if the species proves to occur in montane forests beyond the Mamasa region.

Natural History: Examples of *Bunomys torajae* were caught on the ground and during the night in montane forest at 2500 and 2600 m. Fourteen other murids were collected at those elevations during the same survey: *Tateomys rhinogradoides* and *T. macrocercus*, *Melasmothrix naso*, *Sommeromys macrorhinos*, *Margaretamys elegans* and *M. parvus*, *Haeromys* sp., *Taeromys* sp., *Paruromys dominator*, *Eropeplus canus*, *Eropeplus*-like new genus and species, *Maxomys musschenbroekii*, and *Rattus hoffmanni* and *R. facetus.*

Litter size is unknown, but one or two young is usual for the species of *Bunomys* for which that kind of information is available—*B. torajae* is probably no different.

Like *B. prolatus*, the external morphology of *B. torajae* is that of a terrestrial rat. Its long muzzle, sharp lower incisors, and overall skull conformation suggests a diet consisting
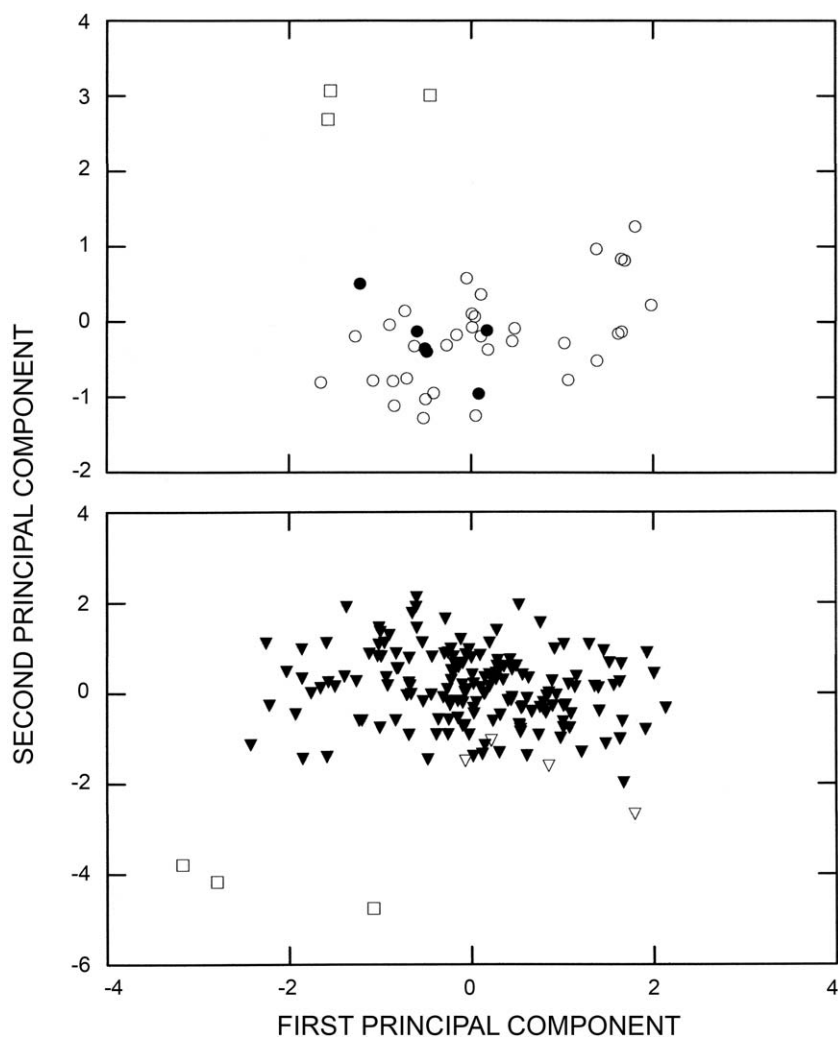
Fig. 47.   Specimen scores representing samples of *Bunomys torajae* (empty squares) compared with samples of *B. andrewsi* (empty circles) and *B. penitus* (filled inverted triangles) from the west-central mountain block projected onto first and second principal components extracted from principal-components analysis of log-transformed values for 14 cranial and 2 dental variables. Upper graph: *B. torajae* ($N = 3$) contrasted with *B. andrewsi* ($N = 40$; filled circles = scores for six specimens from Gunung Gandangdewata). Lower graph: the same specimens of *B. torajae* compared with *B. penitus* ($N = 170$; empty inverted triangles = scores of four specimens from Gunung Gandangdewata). See table 38 for correlations (loadings) of variables with extracted components and for percent variance explained for both ordinations.

primarily of invertebrates, likely containing a range of items similar to those eaten by *B. chrysocomus* and even *B. andrewsi*; also, a partially mycophagous diet cannot be ruled out (see those accounts and table 13).

ECTOPARASITES, PSEUDOSCORPIONS, AND ENDOPARASITES: No records.

SYNONYMS: None.

Summary of Contrasts among Members of the *Bunomys chrysocomus* Group

Bunomys coelestis, *B. prolatus*, and *B. torajae* are mountain endemics: *B. coelestis* is isolated in montane forest on Gunung Lompobatang at the southern tip of the southwestern peninsula of Sulawesi, *B. pro-*

TABLE 38
Results of Principal-Components Comparing the Sample of *Bunomys torajae* with Those of *B. andrewsi* and *B. penitus* from the West-Central Mountain Block
Correlations (loadings) of 14 cranial and two dental log-transformed variables are based on three *B. torajae*, 40 *B. andrewsi* and 170 *B. penitus*; see figure 47. Occipitonasal and postpalatal lengths are omitted because they could not be measured on one damaged specimen of *B. torajae*.

	Correlations			
	B. torajae and *B. andrewsi*		*B. torajae* and *B. penitus*	
Variable	PC1	PC2	PC1	PC2
ZB	0.92***	−0.04	0.73***	−0.03
IB	0.26	0.33*	0.16*	−0.25***
LR	0.61***	0.62***	0.59***	−0.01
BR	0.79***	0.05	0.75***	−0.04
BBC	0.50***	0.10	0.31***	0.07
HBC	0.57***	−0.13	0.34***	0.29***
BZP	0.92***	−0.16	0.56***	−0.12
LD	0.67***	0.54***	0.68***	−0.29***
LBP	0.18	0.84***	0.26***	−0.12
BBP	0.67***	0.51***	0.55***	−0.71***
BMF	0.44**	−0.13	0.64***	0.45***
LIF	0.70***	−0.55***	0.61***	0.33***
BIF	0.61***	−0.03	0.65***	0.01
LB	0.50***	−0.15	0.41***	0.30***
CLM1–3	0.69***	−0.12	0.25***	0.59***
BM1	0.46**	0.01	−0.03	0.38***
Eigenvalue	0.037	0.011	0.014	0.006
% Variance	49.2	14.6	31.2	13.8

*** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$.

latus is recorded only from Gunung Tambusisi at the western end of the eastern arm of Sulawesi, far to the north of Gunung Lompobatang, and *B. torajae* is known so far only from high elevations on Gunung Gandangdewata, part of Pegunungan Quarles in the southern part of the west-central mountain block. *Bunomys chrysocomus* apparently occurs throughout much of Sulawesi in suitable habitat, including slightly lower altitudes on Gunung Tambusisi and in the Mamasa area. At one time *B. chrysocomus* also lived (and may still occur) in the lowlands on the southwest peninsula where currently only subfossil fragments document its presence.

Among the four species, *B. prolatus* and *B. torajae* are the largest in physical size, but *B.*

prolatus has the shortest tail relative to head and body length (LT/LHB = 79% for *B. prolatus*, 84%–98% for nine samples of *B. chrysocomus*, 95% for *B. coelestis*, and 93% for *B. torajae*). *Bunomys coelestis* is closest to *B. chrysocomus* in physical size, but has, on average, a longer tail and hind foot (table 19). Both *B. coelestis* and *B. prolatus* have long front claws—absolutely and relative to body size—compared to the short claws in *B. chrysocomus* and *B. torajae*, and the claws are even more robust and longer in *B. prolatus* (fig. 36). The deeply pigmented scutellation over dorsal surfaces of the feet in *B. prolatus* is diagnostic.

Similarities and contrasts in magnitude of cranial and dental dimensions between sets of the four species have been visually quantified by the results from principal components and discriminant-function analyses previously described (figs. 42–46). A graphic summary of the morphometric distinctions among the four species is portrayed by individual specimen scores projected onto first and second canonical variates (fig. 49). Position of the large cluster representing *B. chrysocomus* to the right of the smaller clouds of points for *B. coelestis*, *B. prolatus*, and *B. torajae* along the first axis reflects covariation among variables that signal the overall larger size of the skull in *B. coelestis*, *B. prolatus*, and *B. torajae* as compared with *B. chrysocomus*. Those three species have a longer skull; wider interorbit; wider and higher braincase; longer rostrum, diastema, bony palate, and postpalatal region (all correlated with the longer skull); and more spacious incisive foramina than *B. chrysocomus* (r = −0.20 to −0.80; table 39), but a narrower mespopterygoid fossa and incisive foramina (r = 0.22 and 0.31, respectively).

The distribution of scores along the scond variate highlights the close position of *B. prolatus* and *B. torajae* as a clump at the top of the ordination isolated from the clusters representing *B. coelestis* and *B. chrysocomus*. Covariation among several variables shows that *B. prolatus* and *B. torajae* have a relatively longer skull than either *B. coelestis* or *B. chrysocomus*, less-flaring zygomatic arches, wider interorbit, longer rostrum, wider braincase, appreciably narrower zygo-
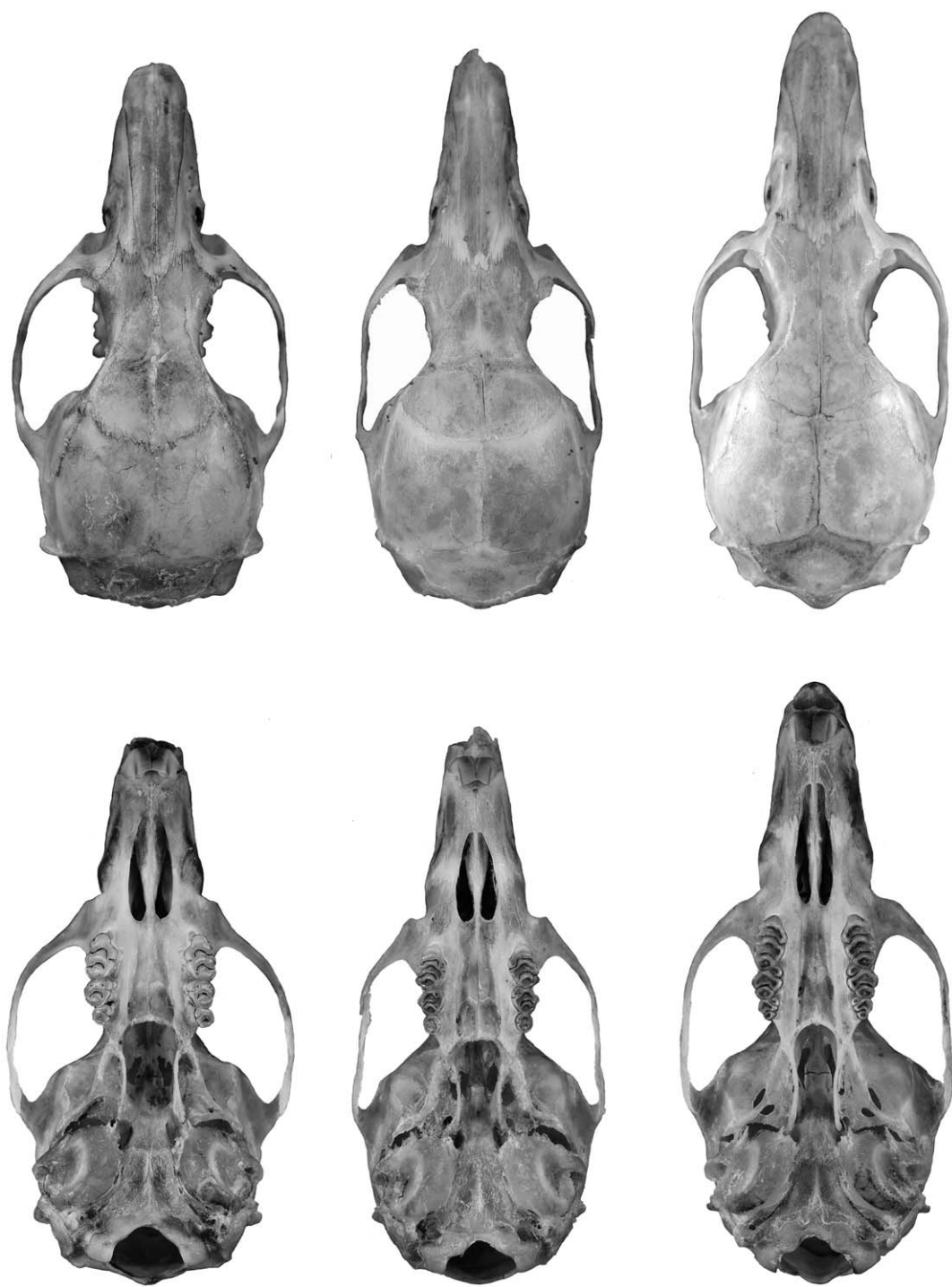
Fig. 48.   Dorsal (top) and ventral (bottom) views of adult skulls representing three species of *Bunomys* collected on Gunung Gandangdewata. Left to right: *B. andrewsi* (MZB 34917, 1600 m), *B. torajae* (MZB 34730, holotype, 2600 m), and *B. penitus* (MZB 34850, 2000 m). ×2.

matic plate, longer bony palate, larger bullae, and heavier molars.

Results of cluster analysis based on Mahalanobis distances (squared) among centroids reveals a pattern of phenetic resemblance among the four species (fig. 49). *Bunomys coelestis* is the first to separate from the 10 population samples of *B. chrysocomus*, then *B. prolatus* and *B. torajae*, which are linked together. In this phenetic context, *B. coelestis* appears to be a close relative of *B. chrysocomus* that is isolated in montane habitats on Gunung Lompobatang at the south end of the southwestern peninsula. The strong morphometric link between *B. chrysocomus* and *B. coelestis* appeared in several Mahalanobis distance cluster analyses that I generated when samples from all species of *Bunomys* were compared (fig. 21), and when samples of all species of *Bunomys* were compared with samples of *Paruromys dominator* and all species of *Taeromys* (not illustrated)—the latter two genera and *Bunomys* are part of the same Sulawesian clade as indicated by analyses of DNA sequences (Fabre et al., 2013). The large-bodied *B. prolatus* and *B. torajae* are phenetically closely related montane isolates. If this liaison is reinforced by results derived from analyses of DNA sequences, the two species may be montane relicts of a separate evolutionary pulse within *Bunomys*.

The phenetic pattern of relationships among the four species requires testing by analyses of DNA sequences from multiple genes. Would those results confirm the phenetic pattern illustrated here by the scatter plot of scores and cluster diagram? Or would the following different associations be uncovered?

(1) *Bunomys coelestis*, rather than a close phylogenetic relative of *B. chrysocomus* as the morphometric data analyzed here suggests, is instead another mountain isolate evolved from the same ancestral stock from which *B. prolatus* and *B. torajae* possibly sprang.

(2) Body size is possibly an unreliable index of genetic alliance, and *B. prolatus* may be cladistically more closely related to *B. penitus* or some other large-bodied member of the *B. fratrorum* group. It could even be a phylogenetic outlier to all the other known species of *Bunomys*, although its overall morphology, especially cranial and dental conformations and the long front claws, seem an elaboration of the *chrysocomus* morphotype.

(3) The montane *B. torajae*, despite its phenetic alliance with *B. prolatus* documented here, may be in its genetic history more closely allied to *B. penitus*, the strictly montane large-bodied member of the *B. fratrorum* group.

(4) *Bunomys andrewsi*, phenetically a member of the *B. fratrorum* group, may genetically be more closely tied to *B. chrysocomus* than to any species in the *B. fratrorum* group. Although *B. andrewsi* is much larger in body size than *B. chrysocomus*, the two are similar in pelage coloration, relative tail length, range of variation in chromatic patterning of the tail, frequency of occurrence of a white tail tip, and diet.

The *Bunomys fratrorum* Group

Gazetteers and specimens examined: Collection localities for 330 specimens of *Bunomys fratrorum*, 146 examples of *B. andrewsi*, 339 specimens of *B. penitus*, and 28 *B. karokophilus,* n. sp., are listed below. The number preceding each locality keys to a symbol on the maps in figures 50 and 51.

Bunomys fratrorum

1. **Teteamoet** (several miles southeast of Likupang; see Raven's brief description of the place in Miller, 1917: 29), 01°40′N, 125°05′E (estimated from Raven's map), on coastal plain near sea level: USNM 216836–46, 216883–909, 216911–26, 216929, 216979, 216981, 216983–86, 217084.

2. **Mapanget**, 01°32′N, 124°56′E, less than 100 m: MZB 4065.

3. **Manado** ("Menado" is the common alternative spelling), 01°30′N, 124°50′E, coastal plain near sea level: BMNH 21.2.9.9, 97.1.2.29; MZB 2448.

4. **Lota** (also spelled ''Lotta''), 01°25′N, 124°49′E (from HOUSND, Celebes, 1944: 100), 200–300 m (estimated from sheet NA 51-12): SNSD B.2511, B.2515, B.2516, B. 2517.

5. **Kuala Prang**, 01°28′N, 125°14′E (estimated from Raven's map), coastal plain near sea level: USNM 217586–614, 217827–29, 217831–39.
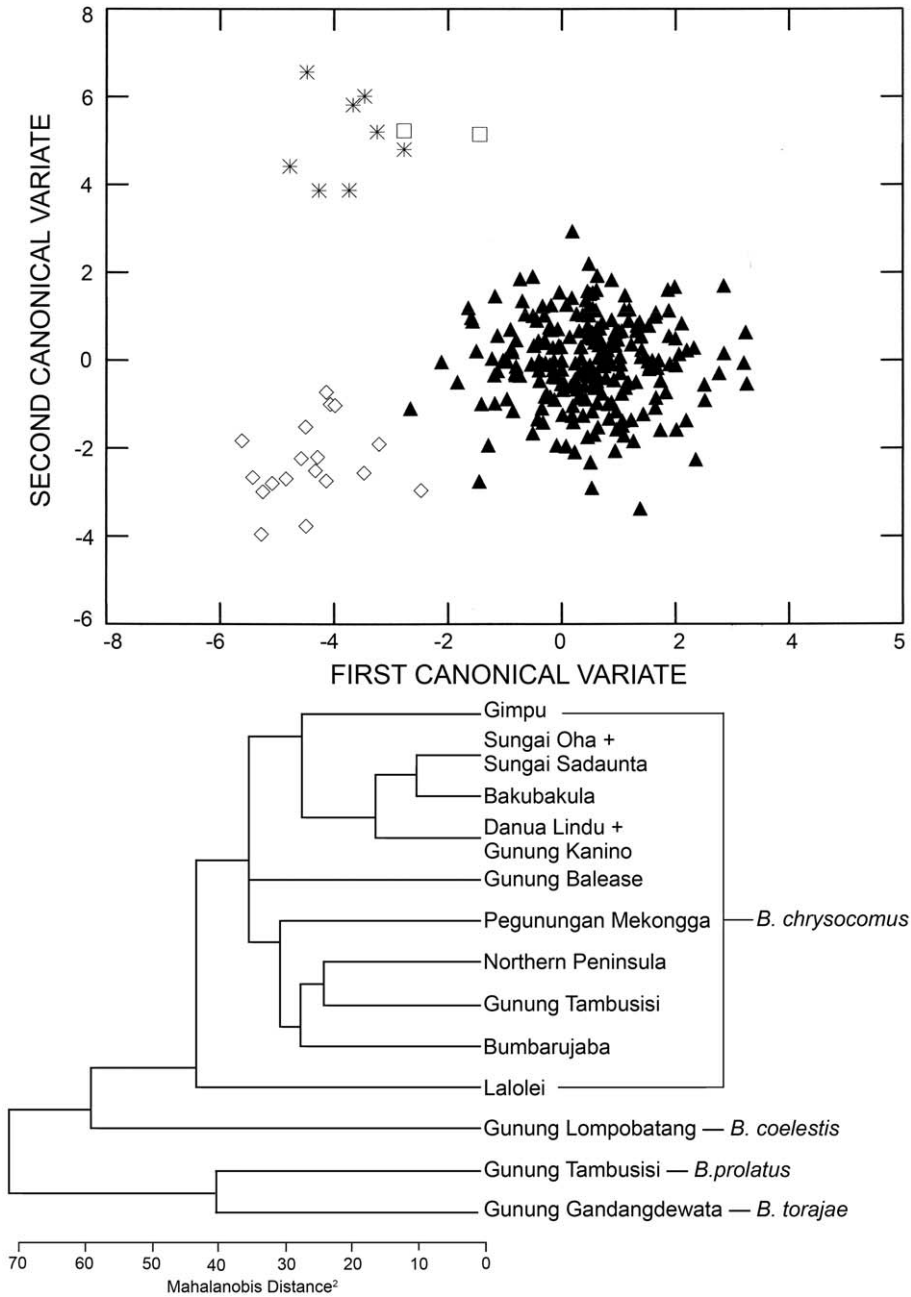
Fig. 49.   Upper graph: Specimen scores representing all population samples of *Bunomys chrysocomus* (filled triangles; $N = 232$), and the samples of *B. coelestis* (empty diamonds; $N = 18$), *B. prolatus* (asterisks; $N = 8$), and *B. torajae* (empty squares; $N = 2$) projected onto first and second canonical variates extracted from discriminant-function analysis of 16 cranial and two dental log-transformed variables. See table 39 for correlations (loadings) of variables with extracted canonical variates and for percent variance explained. Lower diagram: Phenetic relationships among 13 population samples representing *Bunomys chrysocomus*, *B. coelestis*, *B. prolatus*, and *B. torajae* generated from UPGMA clustering of squared Mahalanobis distances among group centroids as derived from discriminant-function analysis.

TABLE 39
Results of Discriminant-Function Analysis Comparing Samples of *Bunomys chrysocomus*, *B. coelestis*, *B. prolatus*, and *B. torajae*
Correlations (loadings) of 16 cranial and two dental log-transformed variables are based on 232 *B. chrysocomus*, 18 *B. coelestis*, *B. prolatus*, and two *B. torajae*; see figure 49.

Variable	Correlations	
	CV1	CV2
ONL	−0.64***	0.33***
ZB	−0.23***	−0.23***
IB	−0.50***	0.42***
LR	−0.68***	0.36***
BR	−0.03	0.01
BBC	−0.33***	0.32***
HBC	−0.64***	−0.04
BZP	−0.20**	−0.54***
LD	−0.80***	−0.05
PPL	−0.50***	0.14
LBP	−0.60***	0.31***
BBP	0.07	0.02
BMF	0.22***	−0.04
LIF	−0.54***	−0.08
BIF	0.31***	0.13*
LB	−0.08	0.45***
CLM1–3	−0.09	0.38***
BM1	0.09	0.45***
Canonical correlation	0.823	0.766
Eigenvalue	2.105	1.419
% Variance	57.4	38.7

*** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$.

6. **Gunung Klabat** ("Goenoeng Kalabat" on specimen tags), 01°28′N, 125°02′E: 6000 ft (1830 m), USNM 217581, 217582; 6500 ft (1982 m), USNM 217585. These specimens were collected by H.C. Raven, who provided this note (quoted in Riley, 1924: 1): "My camp was at about 1,700 meters (5,600 feet), where the forest is only semitropical in appearance. Practically all the trees are heavily coated with moss and are not tall. Kalabat is the highest mountain in Minahassa, having an altitude of 2,020 (6,617) feet."

7. **Rurukan**, 01°21′N, 124°52′E: AMNH 196620 (800 m); BMNH 97.1.2.28 (holotype of *Mus fratrorum*), 97.1.2.31, 3500 ft (1068 m); SNSD B.3384, B.3386.

8. **Gunung Masarang**, 01°19′N, 124°51′E, 3500 ft (1068 m): BMNH 97.1.2.30.

9. **Tonsealama** (also known as "Tonsea"), 01°19′N, 124°55′E, 600–700 m (estimated from sheet NA 51-12): BMNH 40.395–40.439; MZB 4052–57, 4059–63, 4068.

10. **Tomohon**, 01°19′N, 124°49′E, 700–800 m (estimated from sheet NA 51-12): BMNH 99.10.1.27; MZB 4066–68, 4070, 4071.

11. **Tumaratus** (north lower slope of Gunung Soputan; spelled "Toemaratas" on specimen labels as well as old maps and gazetteers), 01°09′N, 124°48′E, 700–800 m (estimated from sheet NA 51-12): USNM 217615.

12. **Tumaluntung** (north lower slope of Gunung Soputan; "Lekoean, Toemaloentoeng, Gng. Sapoetan" is the designation associated with the specimens; not the "Toemaloentoeng" at 01°24′N, 124°58′E listed in HOUSND Celebes [1944: 192], but the other "Toemaloentoeng" listed in that gazetteer with the coordinates 01°12′N, 124°42′E), 700–800 m (estimated from sheet NA 51-12): RMNH 21089, 21090.

13. **Gunung Soputan** (spelled Sapoetan on old maps; "Toenan, Tombasian atas, Gng. Sapoetan" is the locality designation associated with the specimens), 01°07′N, 124°45′E: RMNH 21087, 21088.

14. **Kakas**, 01°11′N, 124°53′E, 600–700 m (estimated from sheet NA 51-12): RMNH 21278 (originally specimen "*b*" that had been regarded as a cotype of *Mus callitrichus* by Jentink, 1879; see Musser, 1970).

15. **Langoon** (also spelled "Langowan" or "Langowen" on specimen labels and old maps), 01°09′N, 124°50′E, 700–800 m (estimated from sheet NA 51-12): RMNH 21279–81 (originally specimens "*g*," "*h*," and "*j*," which Jentink, 1879, considered to be cotypes of *Mus callitrichus*; see Musser, 1970).

16. **Amurang**, 01°11′N, 124°35′E, coastal plain near sea level: MZB 407.

17. **Temboan** (on Kuala Kalait, "is a new clearing of eight houses and lies from Mt. Sapoetan south, 55° west and about six miles from Loboe," noted Raven in his field journal, which is stored in the Mammal Division Library, USNM), 01°03′N, 124°33′E (estimated from Raven's map), 500 m (estimated from sheet NA 51-12): USNM 217616, 217620–26, 217628–71, 217682, 217850, 217854, 217857, 217858, 217864–69, 217876–81, 217883, 217884, 217886–88, 217895, 217896–902.

18. **Gunung Maujat** (15 km east of Kotambogan; mapped in Bergmans and Rozendaal, 1988: 6), 00°45′N, 124°25′E, 1780 m: SAM 12644, 12636.

19. **Bogani Nani Wartabone National Park, 1 km north of Gunung Mogogonipa**, 00°27′N, 123°57′E, 250 m: SAM 12616, 12619, 12623.

In 1932, H.J.V. Sody collected 48 specimens of *B. fratrorum* (RMNH 21091–39), each
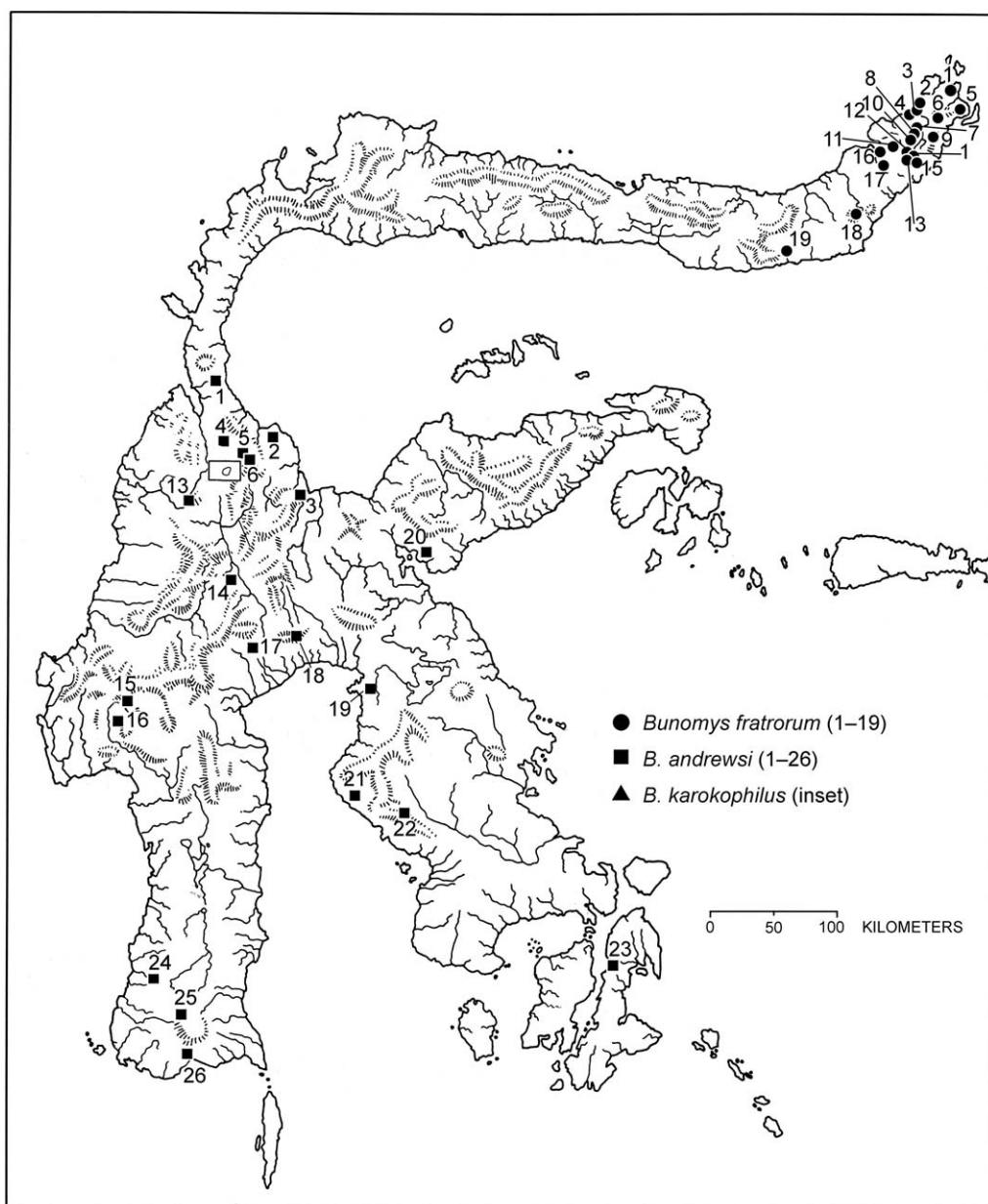
Fig. 50.   Collection localities for samples of *Bunomys fratrorum*, *B. andrewsi*, and *B. karokophilus*, n. sp. Numbers key to localities described in the gazetteer. The inset map (small rectangle above and in full on opposite page) contains some of the localities where *B. andrewsi* was obtained (7–12) and all the places where we trapped *B. karokophilus*, n. sp., along Sungai Sadaunta, the area around Danau Lindu, and near Sungai Tokararu (localities 1–10). The dashed contour line at 1300 m marks the approximate boundary between tropical lowland evergreen rain forest and tropical lower montane forest. The filled circle (highlighted by arrow) on that dashed line is the lowest spot (1285 m in lower montane forest) where we encountered *B. penitus*, a species trapped at higher elevations all the way to the summit of Gunung Nokilalaki (see the map in fig. 51, and discussion in the account of *B. karokophilus*, n. sp., where that species and *B. penitus* are compared).
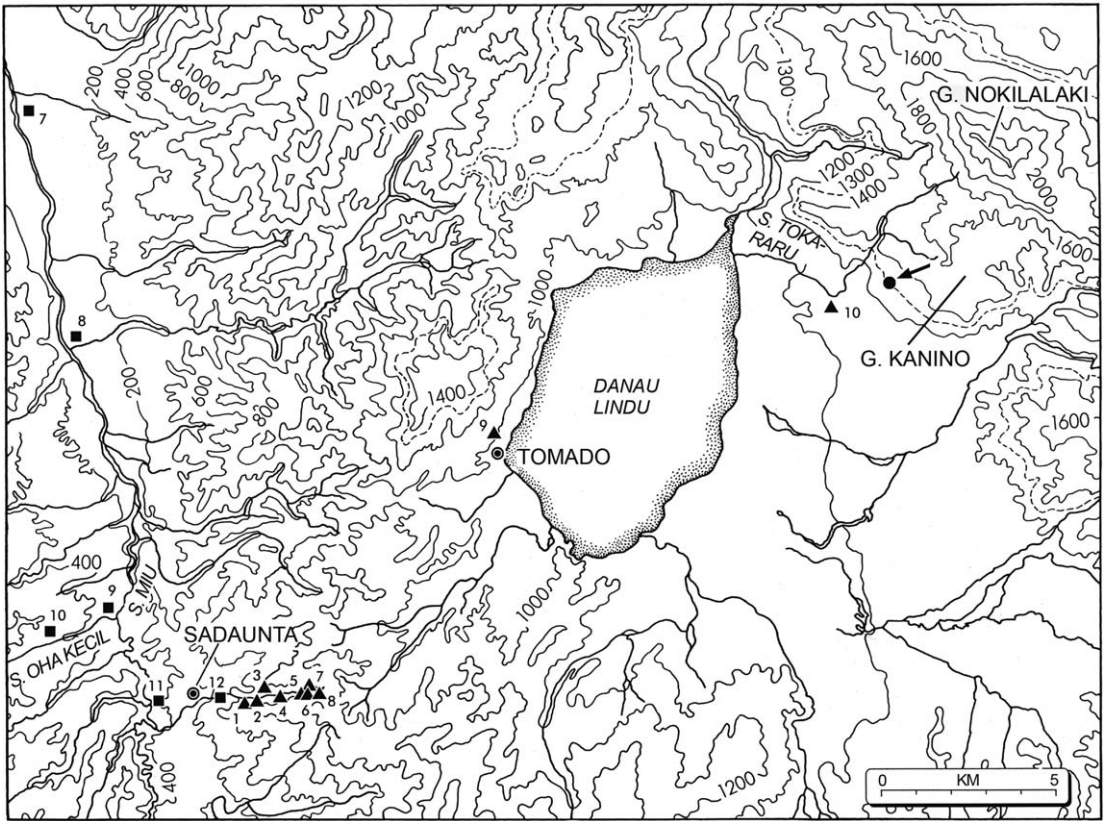
Fig. 50. Continued.

with one of his field labels attached on which is recorded his collection number that keys to records in his field journal. Unfortunately, that particular notebook was apparently lost and the only provenance data associated with the specimens is "N.E. Celebes, Minahassa District, 1932."

Bunomys andrewsi

1. **Labuan Sore** (spelled "Laboea Sore" on specimen labels and "Laboean Sore"on Raven's map), on east coast just north of Marantate, about midway between Towera and Toboli, 00°37′S, 120°03′E (estimated from Raven's map; see Bynum et al., 1997, who discussed the location of Raven's collection locality), 200 m (estimated from sheet SA 51-1: USNM 318114, 218115, 218138.

2. **Malakosa, Kuala Navusu**, 00°58′S, 120°27′E (estimated from sheet SA 51–1): 100 ft (31 m),

AMNH 225646; 150 ft (46 m), AMNH 225647, 225648, 225665; 175 ft (54 m), AMNH 225649–56; 180 ft (55 m), AMNH 225657, 225666; 200 ft (61 m), AMNH 225658; 400 ft (122 m), AMNH 225659–64.

3. **Pinedapa**, 01°25′S, 120°35′E (estimated from Raven's map), 100 ft (31 m):USNM 219573–75, 219581, 219587, 219589, 219591, 219593, 219594, 219596, 219597, 219600, 219601, 219602 (holotype of *Rattus adspersus*), 219603–606, 219616, 219619, 219620, 219622, 219723. Raven penned in his field journal (p. 125; January, 1918) that "Pinedapa is a new kampong [village] at the base of the main mountains of central Celebes. The kampong is on the level but some of the clearings are on the slopes to the northwest of the kampong. The immediate kampong is surrounded by heavy forest. The distance to the sea is about five miles."

4. **Puro Valley, Bakubakulu**, 01°07′S, 120°00′E, 600 m: AMNH 229520, 229521.
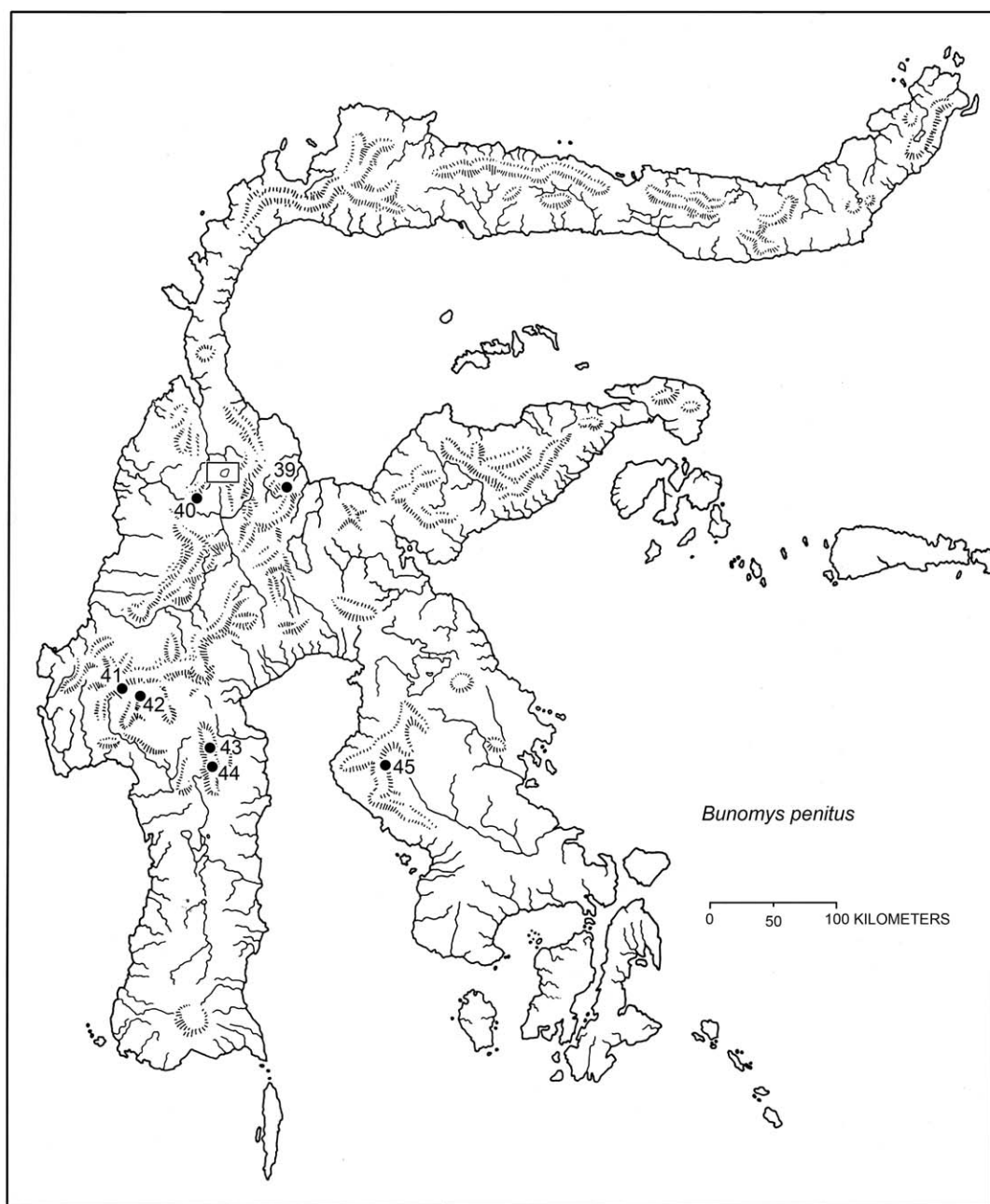
Fig. 51.   Collection localities for samples of *Bunomys penitus*. Numbers key to localities described in the gazetteer. The inset map (small rectangle above and in full on opposite page) records collection sites on Gunung Kanino and Gunung Nokilalaki in lower and upper montane forest. The dashed contour line at 1300 m marks the approximate boundary between tropical lowland evergreen rain forest and lower montane forest. The filled triangle (highlighted by arrow) is the highest place (1150 m in lowland tropical evergreen rain forest) where we trapped *B. karokophilus,* n. sp. (see discussion in the account of *B. karokophilus,* n. sp., where it and *B. penitus* are compared).
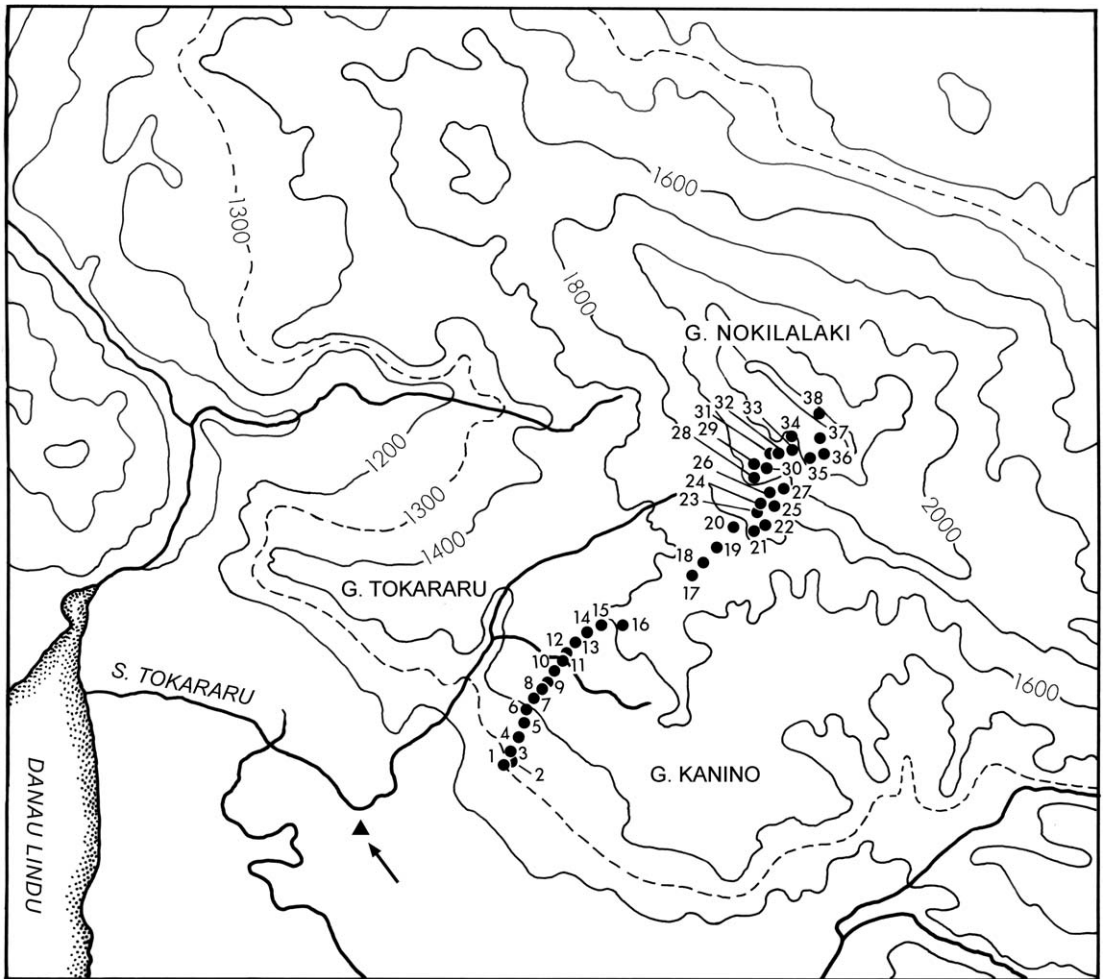
Fig. 51.   Continued.

5. **Puro Valley,** 01°07′S, 120°02′E. **Kapiroe**, 350 m: AMNH 229523. **Makmur**, 600 m: AMNH 229524.

6. **Puro Valley, Tanah Harapan**, 01°08′S, 120°04′E, 600 m: AMNH 257187.

7. **Valley of Sungai Miu, Pakuli**, 01°14′S, 119°56′E, 110 m: AMNH 257189.

8. **Valley of Sungai Miu, Omu,** 01°18′S, 119°57′E, 130 m: AMNH 257188.

9. **Valley of Sungai Miu, Sungai Oha Kecil** (tributary on left side of Sungai Miu), 01°22′S, 119°57′E (near confluence with Sungai Miu; estimated from Sheet SA 50-8), 290 m: AMNH 224630.

10. **Sungai Oha Kecil**, 1500 ft (457 m): AMNH 224631–33.

11. **Valley of Sungai Miu, terrace on right bank of Sungai Miu**, 01°23′S, 119°58′E (estimated from sheet SA 50-8), 350 m: AMNH 224145.

12. **Valley of Sungai Miu, Sungai Sadaunta** (tributary on right side of Sungai Miu), 01°23′S, 119°58′E (estimated from sheet SA 50-8), 675 m: AMNH 224107, 224116.

13. **Tamalanti**, 3300 ft (1006 m): BMNH 40.446–453. Laurie and Hill (1954: 156) noted that Tamalanti is a "Plantation between Rante-karoa [02°50′S, 119°50′E] and Koelawi [01°27′S, 119°59′E]," which was also the only information I found when searching through field notes and other documents at the Natural History Museum in London. Berg-mans and Rozendaal (1988: 72) found the

locality in a gazetteer with the coordinates, 01°20′S, 119°46′E.

14. **Tuare** (also spelled "Toware," "Toare," or "Toware, Bada" on old maps and some specimen labels), 01°54′S, 120°10′E, 800 m (estimated from sheet SA 50-8): USNM 219598, 219599.

15. **Mamasa Area**, 02°56′S, 119°22′E (for Mamasa). **Lambanan**, 1500 m: AMNH 267807. **Mambulillin**, 1500 m: AMNH 267803, 267804. These two places are a few kilometers northeast of the town of Mamasa, which is at about 1000 m. Local farmers trapped the rodents and brought them to members of the expedition, who later determined that the two places are at approximately 1500 m (H. Hasegawa, personal commun.). **Gunung Gandangdewata**, −2.748253° S, 119.368536° E (for the peak), 1600 m: MZB 34780, 34912, 34913, 34916, 34917, 34926, 34955.

16. **Sumarorong** (a small village 35 road km south of Mamasa), 03°11′S, 119°20′E, 970 m: AMNH 267796–802, 267805, 267806, 269956.

17. **Sukamaju (Masamba region)**, 02°38′S, 120°28′E, less than 100 m: AMNH 229720.

18. **Gunung Balease**, 2.499533333S, 120.4873833E, 830–925 m: MVZ 225683–689, 225692–95, 225707–13, 225812.

19. **Malili area, Desa Lawaki Jaya**, 2.795178S, 121.055763E, 450 m: MVZ 225690, 225691, 225698–706, 225715–21.

20. **Sungai Ranu region**, 01°51′S, 122°30′E. **20 km north of Ranu Camp,** 50 m: AMNH 249942–45; CHSW 36. **Ranu Ridge,** 100 m: CHSW 102. See the map in Bergmans and Rozendaal (1988: 4).

21. **Wawo** (on the plain between the coast and western foothills of Pegunungan Mekongga (also spelled "Mengkoka"), 03°41′S, 121°02′E, 50 m: AMNH 101057, 101059 (holotype of *Rattus penitus inferior*), 101061; MZB 5821, 5822.

22. **Masembo** (southeast of Wawo and the highest place in the southern portion of Pegunungan Mekongga; see the maps and discussion in Heinrich [1932] and Stresemann [1940]), 03°35′S, 121°15′E (for the Pegunungan), 550 m: AMNH 101069–73.

23. **Pulau Buton,** 05°00′S, 122°55′E: AMNH 31294; USNM 175899 (holotype of *Mus andrewsi*; formerly AMNH 31293). The exact collection site of these specimens is unknown; I simply placed a dot randomly within the island's outline on the distribution map.

24. **Ulu Leang I,** (a cave about 40 km northeast of Ujung Pandang in the Maros region; see map and description in Glover, 1976), less than 100 m: AMNH 266974 (subfossil fragments).

25. **Lombasang** (in northwestern foothills of Gunung Lompobatang), 05°16′S, 119°55′E, 1100 m: AMNH 100996–101005, 101006 (holotype of *Rattus penitus heinrichi*), 101007–015; MBZ 5819, 5820. **Biror**, south of Malino in northwestern foothills of Gunung Lompobatang: USNM 359791. This is the specimen identified as "*Rattus penitus*" from which the holotype of a new genus and species of pseudoscorpion was collected and later described by Muchmore (1972).

26. **Batu Ejaya II** (a small rock shelter at the southern tip of the southwestern peninsula; see map, description, and references in Mulvaney and Soejono, 1970), 275 m: AMNH 265013–15, 265020, 269963 (subfossil fragments).

Bunomys penitus

1. **Gunung Kanino**, 01°17′S, 120°08′E (estimated from Sheet SA 50-8), 4200 ft (1285 m): AMNH 223904.

2. **Gunung Kanino**, 4300 ft (1311 m): AMNH 223955.

3. **Gunung Kanino**, 4400 ft (1342 m): AMNH 223370.

4. **Gunung Kanino**, 4500 ft (1372 m): AMNH 223905.

5. **Gunung Kanino**, 4540 ft (1384 m): AMNH 226941.

6. **Gunung Kanino**: 4600 ft (1402 m), AMNH 223906, 223907, 225251–53; 4650 ft (1418 m), AMNH 225254, 225255.

7. **Gunung Kanino**, 4700 ft (1433 m): AMNH 223908.

8. **Gunung Kanino**, 4750 ft (1448 m): AMNH 225256–62.

9. **Gunung Kanino**, 4800 ft (1463 m): AMNH 223805–22, 223909–13, 223976, 225263–77, 225279.

10. **Gunung Kanino**: 4880 ft (1488 m), AMNH 225278, 225280; 4900 ft (1494 m), AMNH 225281–93, 225306.

11. **Gunung Kanino**, 4960 ft (1512 m): AMNH 225294, 225295, 225377, 225378.

12. **Gunung Kanino**, 5000 ft (1525 m): AMNH 223823–34, 223914–18, 225296–300.

13. **Gunung Kanino**, 5040 ft (1537 m): AMNH 225374.

14. **Gunung Kanino**: 5100 ft (1555 m), AMNH 223919–24, 223835–40, 225301, 225375; 5150 ft (1570 m), AMNH 225376.

15. **Gunung Kanino**, 5200 ft (1585 m): AMNH 223841–52, 223925–28.

16. **Gunung Kanino**, 5300 ft (1616 m): AMNH 225302–05, 225379.

17. **Gunung Nokilalaki**, 01°13′S, 120°08′E, 5700 ft (1739 m): AMNH 225307, 223977.

18. **Gunung Nokilalaki**, 5750 ft (1754 m): AMNH 225308.
19. **Gunung Nokilalaki**, 5800 ft (1768 m): AMNH 223854, 223855.
20. **Gunung Nokilalaki**, 5900 ft (1799 m): AMNH 225309.
21. **Gunung Nokilalaki**, 5950 ft (1814 m): AMNH 223856.
22. **Gunung Nokilalaki**: 6000 ft (1830 m), AMNH 223857, 223858, 225310, 225311; 6050 ft (1845 m), AMNH 225312–14.
23. **Gunung Nokilalaki**: 6100 ft (1860 m), AMNH 223859, 223860, 223929; 6150 ft (1875 m), AMNH 225315.
24. **Gunung Nokilalaki**, 6200 ft (1890 m): AMNH 223861.
25. **Gunung Nokilalaki**, 6300 ft (1921 m): AMNH 223862.
26. **Gunung Nokilalaki**, 6400 ft (1951 m): AMNH 223863–68, 223930–33.
27. **Gunung Nokilalaki**, 6500 ft (1982 m): AMNH 223853, 223869, 223934, 223935, 225316, 225317.
28. **Gunung Nokilalaki**, 6700 ft (2043 m): AMNH 223870, 223871, 223936, 223967.
29. **Gunung Nokilalaki**: 6800 ft (2073 m), AMNH 223872–75, 225318–20; 6850 ft (2091 m), AMNH 225329, 225330.
30. **Gunung Nokilalaki**, 6900 ft (2104 m): AMNH 223876, 225331–37.
31. **Gunung Nokilalaki**, 6950 ft (2119 m): AMNH 223877, 223938.
32. **Gunung Nokilalaki**, 7000 ft (2134 m): AMNH 223939, 225338–42.
33. **Gunung Nokilalaki**, 7200 ft (2195 m): AMNH 223878–83, 223940–42, 225341, 225342.
34. **Gunung Nokilalaki**, 7250 ft (2210 m): AMNH 225321–25.
35. **Gunung Nokilalaki**, 7300 ft (2226 m): AMNH 223884, 225326, 225327.
36. **Gunung Nokilalaki**, 7400 ft (2256 m): AMNH 223885, 225328, 225343–60.
37. **Gunung Nokilalaki**, 7450 ft (2271 m): AMNH 223866, 223943.
38. **Gunung Nokilalaki**, 7500 ft (2287 m): AMNH 223887–903, 223944–54, 225361–73.
39. **Rano Rano** 01°30′S, 120°28′E, 6000 ft (1829 m): USNM 219627 (holotype of *Rattus sericatus*), 219628–31.
40. **Gunung Lehio**, 01°33′S, 119°53′E, above 6000 ft (1830 m): USNM 218682–84, 218686 (holotype of *Rattus penitus*), 218687.
41. **Mamasa Area, Lambanan**, 02°56′S, 97°47′E (for Mamasa), 1500 m: AMNH 267790–94. Lambanan is a few kilometers northeast of the town of Mamasa, which is at about 1000 m. Local farmers trapped the rodents and brought them to members of the expedition, who later determined that Lambanan is at about 1500 m

(H. Hasegawa, personal commun.). **Pegunungan Quarles, Gunung Gandangdewata**, −2.748253° S, 119.368536° E (for the peak), 1600 and 2000 m: MZB 34845, 34848, 34849, 34850.
42. **Pegunungan Quarles, Bulu (Gunung) Karua** (referred to as ''Rantekaroa, Quarles Mt.'' on specimen tags), 02°56′S, 119°39′E, 6000 ft (1830 m): BMNH 40.440–40.445.
43. **Bulu (Gunung) Rantemario**, 03°23′S, 120°02′E, 3250 m: plate 50b in Whitten et al. (1987) portraying a specimen identified by me, which is now in the collection at MZB.
44. **Pegunungan Latimojong**, 03°30′S, 121°23′E: 2200 m, AMNH 196585–89; 2300 m, AMNH 196590.
45. **Pegunungan Mekongga** (also spelled ''Mengkoka''), **Tanke Salokko** (the highest spot in Pegunungan Mekongga; see the maps and discussion in Heinrich [1932] and Stresemann [1940]), 03°35′S, 121°15′E (for the Pegunungan), 1500 m, AMNH 101213, 101216, 101222, 101225, 101227, 101230, 101231, 101233, 101235, 101237, 101239, 101240; 2000 m: 101193, 101196, 101199, 101201, 101206–10.

Bunomys karokophilusn, n. sp.

1. **Valley of Sungai Miu, Sungai Sadaunta** (tributary on right side of Sungai Miu), 01°23′S, 119°58′E (estimated from Sheet SA 50-8), 2700 ft (823 m): AMNH 225027–33.
2. **Sungai Sadaunta**, 2850 ft (869 m): AMNH 225034, 225039.
3. **Sungai Sadaunta**, 2900 ft (884 m): AMNH 225035.
4. **Sungai Sadaunta**, 3000 ft (915 m): AMNH 225040.
5. **Sungai Sadaunta**, 3200 ft (976 m): AMNH 224772, 226833.
6. **Sungai Sadaunta**, 3250 ft (991 m): AMNH 225036, 225037.
7. **Sungai Sadaunta**, 3275 ft (999 m): AMNH 225041.
8. **Sungai Sadaunta**, 3300 ft (1006 m): AMNH 225038 (holotype).
9. **Valley of Danau Lindu, forest near Tomado** (a village on the western shore of Danau Lindu), 01°19′S, 120°02′E (estimated from Sheet SA50-8), 1000 m: AMNH 223045, 223046, 223056, 223058, 223060, 223072, 224153, 226931, 257190.
10. **Valley of Danau Lindu, Sungai Tokararu, 12 km (by air) ENE Palili** (an abandoned village on the northeast shore of Danau Lindu), 01°17′S, 120°07′E (estimated from sheet SA 50-8), 1150 m: AMNH 223305, 223316.

TABLE 40
Age; Sex; External, Cranial, and Dental Measurements (mm); and Weight (g) for Holotypes Associated with
***Bunomys fratrorum, B. andrewsi, B. penitus*, and *B. karokophilus* n. sp.**
(Unless otherwise indicated, I copied from skin tags the values for external measurements and measured cranial and dental dimensions.)

	Bunomys fratrorum	*Bunomys andrewsi*				*Bunomys penitus*		
	Mus fratrorum BMNH 97.1.2.28	*Mus andrewsi* USNM 175899	*Rattus adspersus* USNM 219602	*Rattus penitus inferior* AMNH 101059	*Rattus penitus heinrichi* AMNH 101006	*Rattus penitus* USNM 218686	*Rattus sericatus* USNM 219627	*Bunomys karokophilus* AMNH 225038
Age	young adult	old adult	adult	adult	adult	adult	adult	adult
Sex	♀	♂	♂	♂	♂	♂	♂	♂
LHB	–	147	163	177	162	172	175	190
LT[a]	145	113	147	153	131	190	170	160
LHF[b]	40	39	39	42	36	41	40	40
LE	–	24	–	23	20	–	–	24
WT	–	–	–	–	–	–	–	165
ONL	44.3	42.2	41.3	44.2	39.4	43.0	44.8	42.4
ZB	21.0	19.9	19.8	29.4	19.9	18.9	19.7	20.4
IB	6.4	6.5	6.7	6.6	6.3	6.9	7.0	6.8
LR	15.0	14.5	14.4	16.7	14.4	16.5	17.2	14.5
BR	8.4	8.0	7.2	8.6	6.7	8.1	8.5	7.9
BBC	16.2	15.6	16.0	16.6	15.6	16.4	16.8	16.3
HBC	12.3	11.2	11.5	11.8	11.8	11.8	11.9	11.7
BZP	3.5	3.8	4.0	4.1	3.8	3.0	3.1	3.3
LD	11.8	11.3	11.3	12.4	10.4	11.4	11.8	11.0
PPL	15.0	15.0	15.1	15.6	14.1	15.1	14.9	15.2
LBP	8.2	8.6	8.4	8.3	7.9	9.3	9.4	8.8
BBP	3.9	4.0	4.1	4.2	2.9	3.7	3.6	4.0
BMF	3.5	3.0	3.0	3.7	2.7	3.8	3.5	3.2
LIF	7.4	7.3	7.6	9.5	7.9	7.8	8.1	6.5
BIF	3.3	3.0	2.9	3.6	2.7	3.1	3.0	3.0
LB	6.3	7.4	6.5	7.0	6.5	6.6	6.9	6.2
CLM1–3	7.9	7.0	7.4	7.9	7.3	7.9	8.0	7.3
BM1	2.5	2.1	2.3	2.5	2.3	2.5	2.6	2.5

[a] I measured the dry tail on the skins of *fratrorum, inferior*, and *heinrichi*. I cannot vouch for the accuracy of the other measurements made by the collectors.

[b] I measured the hind foot (including claws) on the dry skins of all holotypes except for *karokophilus*, which I measured in the field on the freshly caught rat.

The first account covering members of the *B. fratrorum* group is for *B. fratrorum* itself, which is endemic to the northern peninsula east of the Gorontalo region.

Bunomys fratrorum (Thomas, 1896)

Mus fratrorum Thomas, 1896: 246.

HOLOTYPE: BMNH 97.1.2.28, the skin and skull of a young adult female collected October 8, 1895, by C. Hose and E. Hose. Measurements (external, cranial, and dental), along with other information, are listed in table 40. The skin is stuffed in the conventional museum fashion and shows no significant alteration in color of fur. The cranium and mandible are intact, and all incisors and molars are present.

TYPE LOCALITY: Rurukan (01°21′N, 124 52′E), 3500 ft (1068 m; locality 7 in gazetteer and on the map in fig. 50), northeastern tip of the northern peninsula of Sulawesi, Propinsi Sulawesi Utara, Indonesia.

EMENDED DIAGNOSIS: One of the larger-bodied members of the *B. fratrorum* group (LHB = 157–190 mm, WT = 175 g, ONL =

41.5–46.5 mm) and further set apart by the following combination of traits: (1) dorsal fur brownish gray speckled with buff, ventral coat grayish white tinged with pale buff; (2) tail typically equal to combined length of head and body (99%–101%), brown on dorsal surface, white or mottled brown on ventral surface, most with a white or speckled tip (86% of the 99 specimens surveyed) that is moderately long relative to tail length (mean = 18.0%, range = 4%–75%); (3) testes small relative to body size (8%); (4) sperm head short, asymmetrical and gently curved in outline, with a short tail attached near the middle of its concave surface; (5) cranium and mandible robust (6) rostrum and zygomatic plate wide, interorbit narrow, braincase deep, postpalatal region (basicranium) short, and ectotympanic bulla small relative to size of cranium; (7) molar row relatively long; (8) cusp t3 absent from second and third upper molars in most of sample (89% and 91%, respectively); (9) anterolabial cusp rare on second lower molars (12%) and absent from third lower molars; and (10) posterior labial cusplet present on first lower molar in about half of sample and on third lower molar in three-fourths of sample.

GEOGRAPHIC AND ELEVATIONAL DISTRIBUTIONS: *Bunomys fratrorum* is endemic to the northeastern section of the northern peninsula where it is documented by voucher specimens collected at localities scattered from Teteamoet, near the tip of the peninsula, west to near Gunung Mogogonipa (see the map in fig. 50). This region is on the peninsular mainland east of Gorontalo (00°31′N, 123°03′E) where the distribution of *B. fratrorum* is concordant with that of several other mammals: the macaques *Macaca nigra* and *M. nigrescens* (Fooden, 1969; Groves, 1980, 2005); and the murids, *Echiothrix leucurus*, *Taeromys taerae*, *Rattus xanthurus*, and *R. marmosurus* (Musser and Carleton, 2005; also see table 81). *Bunomys fratrorum* has not been collected from islands adjacent to the Sulawesi mainland.

Known elevational range extends from lowlands near sea level (Teteamoet, for example) to about 2000 m on Gunung Klabat (table 5).

SYMPATRY WITH OTHER *BUNOMYS*: *Bunomys fratrorum* is the only member of the *B. fratrorum* group found on the northern arm east of the Gorontalo region. There it is sympatric with *B. chrysocomus*, which also occurs elsewhere on Sulawesi (see that account and table 6). C.H.S. Watts collected examples of both species 1 km north of Gunung Mogogonipa at 250 m during August 2–8, 1985 (table 20). *Bunomys fratrorum* and *B. chrysocomus* are the only species in the genus recorded from the northeastern tip of the northern peninsula east of the Gorontalo region.

DESCRIPTION: As is usual in his descriptions of new taxa, Thomas (1896: 246) captured the essence of *Mus fratrorum*:

Size about as in *Mus rattus*. Fur of medium length, soft, without longer bristles intermixed. Ears large, evenly rounded. General colour above brownish grey, finely sprinkled with dull yellowish. Head rather paler, but the circumference of each eye slightly darker. Under surface dirty greyish yellow, the bases of the hairs slaty grey, their tips dull yellowish; line of demarcation on sides little marked. Hind feet rather elongate; fifth hind toe reaching to the middle of the first phalanx of the fourth; upper surface of hands and feet silvery white. Tail somewhat shorter than head and body, finely scaled (about 11scales to the centimetre), its proximal two thirds above brown, its end and the whole of its under surface white. Skull with rather a small cranial and long facial portion. Subraorbital beads distinct, although not strong. Front of zygoma-root little projected forwards. Anterior palatal foramina of medium length, not reaching back to thelevel of [first upper molar]. Molars large and heavy. Bullae small.

After providing measurements, Thomas noted (1896: 247) that besides "the type, there are several other specimens from Rurukan, two from Menado, and one from Mount Masarang. This species is apparently most closely allied to *M. chrysocomus*, Hoffm., also a native of Celebes, but differs from it by its larger size, beaded supraorbital edges, and much heavier molars." Apparently Thomas's perception of the close morphological relationship between *fratrorum* and *chrysocomus* prompted him to propose "*fratrorum*," which is derived from the Latin *frater* meaning "brother."

TABLE 41
Descriptive Statistics for Measurements (mm) of Lengths of Head and Body, Tail, Hind Foot, and Ear, and for Weight (g), Derived from Samples of *Bunomys fratrorum*, *B. andrewsi*, *B. penitus*, and *B. karokophilus* n. sp.
Mean ± 1 SD, observed range (in parentheses), and size of sample are listed. Mean values were used to compute LT/LHB. Specimens measured are listed in footnotes.

Species and sample	LHB	LT	LHF	LE	WT	LT/LHB (%)
B. fratrorum[a]						
Teteamoet	155.0 ± 5.91	178.5 ± 11.64	39.9 ± 1.24	—	—	101
	(165–187) 40	(150–200) 39	(38–44) 40			
Kuala Prang	177.3 ± 6.99	179.0 ± 12.86	40.4 ± 1.27	—	—	101
	(165–190) 21	(155–195) 21	(38–43) 21			
Temboan	165.8 ± .86	167.5 ± 8.06	39.6 ± 0.99	—	—	99
	(157–182) 34	(150–180) 33	(36–41) 34			
Gunung Maujat	183.5 ± 3.54	159.0 ± 1.41	39.5 ± 0.71	27.0 ± 1.41	175.0 ± 0.00	87
	(181–186) 2	(158–160) 2	(39–40) 2	(26–28) 2	2	
B. andrewsi[b]						
Pulau Buton	148.5 ± 2.12	111.5 ± 2.12	37.5 ± 2.12	24	—	75
	(147–150) 2	(110–113) 2	(36–39) 2			
Wawo + Masembo[c]	170.1 ± 15.20	148.6 ± 7.02	39.3 ± 2.25	—	—	87
	(153–186) 8	(144–160) 7	(36–41) 8			
Kuala Navusu	177.4 ± 11.62	150.1 ± 9.92	40.5 ± 1.33	24.7 ± 1.00	154.6 ± 33.43	85
	(157–195) 17	(130–161) 15	(38–42) 17	(23–26) 17	(98–222) 17	
Pinedapa	163.1 ± 8.59	145.8 ± 8.93	37.1 ± 1.62	—	—	89
	(145–175) 17	(130–165) 17	(35–40) 17			
Gunung Balease	171.9 ± 7.54	156.8 ± 5.96	40.2 ± 1.75	26.6 ± 1.93	149.6 ± 21.60	91
	(157–181) 11	(148–165) 12	(37–44) 12	(24–30) 12	(121–177) 11	
Malili Area	169.9 ± 9.81	153.0 ± 6.19	40.4 ± 1.08	27.1 ± 1.51	145.0 ± 19.22	90
	(155–186) 12	(145–167) 12	(39–42) 12	(24–29) 11	(120–179) 12	
Puro-Sungai Miu	163.1 ± 8.24	146.4 ± 10.86	38.1 ± 1.27	24.4 ± 1.24	113.7 ± 11.50	89
	(151–177) 9	(130–165) 9	(36–40) 9	(23–27) 9	(95–135) 9	
Tamalanti	162.5 ± 4.18	139.2 ± 5.85	36.0 ± 1.10	24.5 ± 1.23	—	86
	(160–170) 6	(130–145) 6	(35–38) 6	(22–25) 6		
Tuare	147.5 ± 3.54	135.0 ± 0.00	35.0 ± 0.00	—	—	92
	(145–150) 2	2	2			
Gunung Gandangdewata	156.1 ± 5.15	142.9 ± 5.52	35.4 ± 0.55	23.3 ± 0.76	111.7 ± 19.48	92
	(149–164) 7	(134–150) 7	(35–36) 7	(22–24) 7	(88–144) 7	
Lombasang[c]	148.8 ± 7.74	137.4 ± 8.19	35.8 ± 0.80	—	—	92
	(137–162) 14	(129–153) 13	(35–37) 14			
B. penitus[d]						
Gunung Lehio	168.0 ± 2.92	171.8 ± 19.47	40.4 ± 0.89	—	—	102
	(165–172) 5	(140–190) 5	(39–41) 5			
Rano Rano	170.8 ± 7.89	161.3 ± 8.54	38.8 ± 1.89	—	—	94
	(160–178) 4	(150–170) 4	(36–40) 4			
Gunung Kanino	182.6 ± 7.34	169.1 ± 8.24	41.8 ± 1.40	26.2 ± 1.03	132.3 ± 14.47	93
	(167–199) 74	(153–188) 71	(38–45) 74	(24–29) 74	(100–170) 74	
Gunung Nokilalaki	184.0 ± 10.45	162.5 ± 8.63	41.4 ± 1.30	26.1 ± 0.91	133.3 ± 15.42	88
	(155–242) 82	(138–185) 76	(38–44) 82	(23–28) 82	(95–170) 76	
Pegunungan Quarles	179.2 ± 10.21	171.7 ± 11.26	39.7 ± 1.37	25.0 ± 0.00	—	96
	(160–190) 6	(155–175) 6	(38–41) 6	6		
Gunung Gandangdewata	176.8 ± 14.34	180.5 ± 14.48	42.0 ± 0.82	26.0 ± 0.82	169.3 ± 31.38	102
	(160–195) 4	(164–198) 4	(41–43) 4	(25–27) 4	(137–212) 4	
Pegunungan Latimojong[e]	167.8 ± 10.21	159.8 ± 10.26	39.8 ± 0.45	—	—	95
	(154–179) 5	(143–171) 5	(39–40) 5			
Pegunungan Mekongga[e]	159.3 ± 7.79	160.9 ± 8.29	37.8 ± 1.44	—	—	101
	(145–173) 19	(146–179) 18	(36–40) 19			

TABLE 41
(*Continued*)

Species and sample	LHB	LT	LHF	LE	WT	LT/LHB (%)
B. karokophilus[f]						
Sungai Sadaunta + Danau Lindu Valley	173.8 ± 8.74 (155–190) 22	164.4 ± 11.85 (150–205) 22	39.3 ± 1.39 (36–44) 22	23.3 ± 0.78 (22–25) 24	133.2 ± 17.22 (105–175) 22	95

[a] All specimens from Teteamoet, Kuala Prang, and Temboan were measured by H.C. Raven in the field. Teteamoet: USNM 216836–34, 216883, 216887–89, 216891–97, 216899, 216902–15, 216919, 216920, 216922–26, 216929, 216979. Kuala Prang: USNM 217588–91, 217593–600, 217602, 217603, 217605, 217606, 217608, 217609, 217611, 217613, 217614. Temboan: 217616, 217622–25, 217627–30, 217635, 217637–43, 217645, 217648–51, 217653, 217655, 217656, 217659, 217661–63, 217665, 217666, 217668, 217670, 217671, 217896. Gunung Maujat (measured by C.H.S. Watts in the field): SAM 12636, 12644.

[b] *B. andrewsi*—Pulau Buton (measured by R.C. Andrews in the field): AMNH 31294; USNM 175899 (holotype of *Mus andrewsi*). Kuala Navusu (measured by me in the field): AMNH 225652, 225654–58, 225661–63, 225666. Pinedapa (measured by H.C. Raven in the field): USNM 219581, 219587, 219589, 219591, 219593, 219594, 219596, 219597, 219600, 219601, 219602 (holotype of *Rattus adspersus*), 219603, 219605, 19606, 219619, 219620, 219622. Gunung Balease (measured by J.L. Patton, K.C. Rowe, and J.A. Esselstyn in the field): MVZ 225683, 225685, 225688, 225689, 225692, 225693, 225695, 225708–12, 225812. Malili Area, Desa Lawaki Jaya (measured by J.L. Patton, K.C. Rowe, and J.A. Esselstyn in the field): MVZ 225690, 225691, 225698, 225699, 225701, 225702, 225705, 225706, 225715, 225717, 225719–21. Wawo + Masembo: AMNH 101059 (holotype of *Rattus penitus inferior*), 101061, 101069, 101071, 101072. Puro-Sungai Miu (measured by me in the field): AMNH 224107, 224116, 224145, 224630–33, 257187, 257189. Tamalanti (measured by W.J.C. Frost in the field): BMNH 40.446–40.452. Gunung Gandangdewata: MZB 34780, 34912, 34913, 34916, 34917, 34926, 34955 (measured by K.C. Rowe and A. Setiawan A. in the field). Lombasang: AMNH 100996–98, 101003–05, 101006 (holotype of *Rattus penitus heinrichi*), 101007, 101009, 101010, 101014.

[c] G. Heinrich collected these specimens and measured lengths of head and body, tail, hind foot, and ear but not total length (head and body plus tail). His value for length of tail is exaggerated because he incorporated part of the rump (which other collectors did not), which also underestimates length of head and body. I measured lengths of tails and hind feet on the dry skins, and used those values for computing the descriptive statistics. I could not measure lengths of head and body as well as ear because the bodies are overstuffed and the ears are dry and distorted; I used Heinich's values to derive the statistics for length of head and body, but cannot vouch for the accuracy of his measurement. I have excluded his ear measurements; they clearly reflect a shorter dimension (probably base of the pinna to its crown) than distance from notch to crown (my measurement).

[d] Gunung Lehio (measured by H.C. Raven in the field): USNM 218682–84, 218686 (holotype of *Rattus penitus*), 218687. Rano Rano (measured by H.C. Raven in the field): USNM 219627 (holotype of *Rattus sericatus*), 219629–31. Gunung Kanino (measured by me in the field): AMNH 223805, 223806, 223809, 223811, 223814, 223815, 223819–22, 223826, 223828, 223829, 223831–33, 223825, 223839, 223840, 223842, 223845–50, 223852, 223904–907, 225251, 225253, 225254, 225256, 225257, 225260, 225262, 225264, 225265, 225267, 225269, 225271–73, 225275, 225276, 225278–85, 225287, 225288, 225290–93, 225295–302, 225304–306, 225376. Gunung Nokilalaki (measured by me in the field): AMNH 225853, 223855, 223857, 223859, 223861–66, 223868, 223870–75, 223878–82, 223885–88, 223892, 223893, 223895–97, 223899–902, 225307, 225308, 225310–15, 225317–25, 225328–33, 225335, 225336, 225338, 225340–42, 225344–46, 225348–54, 225359, 225361–65, 225368, 225369. Pegunungan Quarles: BMNH 40.440–40.445 (measured by W.J.C. Frost in the field).

Gunung Gandangdewata: MZB 34845, 34848–50 (measured by K.C. Rowe and A. Setiwan A. in the field). Pegunungan Latimojong: AMNH 196585–88, 196590. Pegunungan Mekongga: AMNH 101193, 101196, 101206–10, 101213, 101216, 101222, 101225, 101227, 101230, 101231, 101233, 101235, 101237, 101239, 101240.

[e] G. Heinrich collected and measured these specimens. The statistics are derived from his values for lengths of head and body as well as tail; however, I cannot vouch for their accuracy (see preceeding footnote). I measured length of the hind foot on each dry skin. Heinrich's values for length of ear are excluded because he probably measured from the base of the pinna to the crown instead of from the notch to the crown; his values are much smaller than those I obtained from the specimens I collected.

[f] All specimens were measured by me in the field. AMNH 223046, 223056, 223058, 223060, 223072, 223305, 223316, 224153, 225027–37, 225038 (holotype of *Bunomys karokophilus*), 225039, 225041, 226833, 226931.

Fig. 52.   Dorsal views of adult skulls from species of *Bunomys*. Left to right: *B. fratrorum* (USNM 217650, Temboan, northeastern peninsula); *B. andrewsi* (AMNH 225652, Kuala Navusu, central Sulawesi), and *B. penitus* (AMNH 225275, Gunung Kanino, west-central mountain block). ×2.

Thomas knew the characteristics of *chrysocomus*, at least as reflected in the type specimen, because during a tour of several European museums in the late 1800s, he examined the holotype of *chrysocomus* at Dresden during October, 1887, and recorded his observations and measurements in a journal, which is in the library of the mammal section at BMNH (a photographic copy was made by G.H.H. Tate in 1937 and is stored in the Mammalogy Archives at AMNH). It was clear to Thomas that *fratrorum* was a species distinct from *chrysocomus* and that both occurred on the northeastern region of the northern peninsula of Sulawesi.

The large-bodied *B. fratrorum* (LHB = 157–190 mm, LT = 150–200 mm, LHF = 36–44 mm; ONL = 41.5–46.5 mm) has soft, long (12–15 mm long), and glistening brownish-gray dorsal fur brightly speckled with buff ("finely sprinkled with dull yellowish," as Thomas wrote). In a large sample, the tonal range extends from brownish gray to a dark brownish gray with blackish highlights. Fur covering the underparts is dark gray and either speckled with buff (Thomas's "dirty greyish yellow"), which is usual, or heavily washed with buffy tones. Ears are brownish gray, rubbery in texture (noted in a fluid-preserved example), their inner and outer surfaces covered with short, fine hairs.

Dark brown above, white or speckled below, and around the tip is the basic coloration of the relatively long tail, which is typically as long as the head and body in most samples (LT/LHB = 99%–101%). Most specimens (86% of the 99 specimens surveyed) exhibit a white or speckled tip that is moderately long (mean = 18.0%, range = 4%–75% of tail length in 85 specimens; table 8). Color pattern varies in any large sample. The dorsal surface and sides of the tail are brown in all specimens, the ventral surface is either glistening white the entire tail length or lightly to heavily speckled with tan; the tail tip is either white or speckled to some degree. Thirty-three males and females from

Fig. 53.   Ventral views of the same skulls shown in figure 52. From left to right: *B. fratrorum*, *B. andrewsi*, and *B. penitus*. ×2.

Temboan (locality 17) illustrate the variation. The dorsal surface and sides of the tail range from brown to dark brown, the ventral surface is white in 16 specimens and lightly to heavily speckled in the other 17; 31 have a whitish tip that is entirely white in 25 rats, but speckled in six.

Dorsal surfaces of front and hind feet are white and covered with short, fine silvery hairs (some specimens are brown from grease stains). Claws are short and unpigmented, and not concealed by the meager silvery ungual tufts. Palmar and plantar surfaces are naked and gray.

Females possess four teats configured in two inguinal pairs. Males have small testes relative to body size (8%; see table 9). Gross morphology and ultrastructural anatomy of the spermatozoa are described by Breed (2004).

Bunomys fratrorum has a large skull, its overall dimensions matched only by *B. penitus*, with a moderately long and narrow rostrum and a wide zygomatic plate (figs. 52–54; tables 42, 45). The interorbit is narrow and its dorsolateral margins framed by moderately high ridges, the braincase wide and deep, the incisive foramina short and wide, and the bullae small. Each dentary is robust and similar in shape to those of the other species in the *B. fratrorum* group.

Large molars with simple occlusal patterns are typical of *B. fratrorum* (fig. 12). Contributing to this simplicity is the absence of cusp t3 from the second and third upper molars in 89%–91% of the sample (table 10). As in most other species of *Bunomys*, an anterior labial cusplet is absent from the first lower molar, but a posterior labial cusplet typically forms part of the chewing surface on the first lower molar in about half of the sample and on the third lower molar in 78% of the sample (fig. 12; table 11). An anterolabial cusp is absent from the second lower molar in most specimens (present on only 12 of 58 individuals) and was not detected on any third lower molar.

Karyotype: No information.

Comparisons: *Bunomys fratrorum* first requires comparison with *B. chrysocomus*.

Fig. 54.   Lateral views of the cranium and dentary of the same specimens presented in figures 52 and 53. Upper pair: *B. fratrorum* and *B. andrewsi*. Lower image: *B. penitus.* ×2.

TABLE 42
Descriptive Statistics for Cranial and Dental Measurements (mm) derived from Population Samples for
***Bunomys chrysocomus* and the Four Species in the *B. fratrorum* Group**
Mean ± 1 SD and observed range (in parentheses) are listed.

Variable	B. chrysocomus Group	B. fratrorum Group			
	B. chrysocomus	B. fratrorum	B. andrewsi	B. penitus	B. karokophilus
N	232	100	98	185	17
ONL	38.3 ± 1.12	44.0 ± 1.14	41.0 ± 2.04	43.0 ± 1.24	40.5 ± 1.13
	(35.8–41.1)	(41.5–46.5)	(37.1–45.5)	(39.3–46.1)	(39.0–42.4)
ZB	18.1 ± 0.64	20.9 ± 0.90	20.0 ± 1.04	19.6 ± 0.70	19.2 ± 0.89
	(16.3–19.8)	(18.2–22.9)	(17.9–22.2)	(17.0–21.4)	(18.3–21.0)
IB	6.4 ± 0.23	6.2 ± 0.31	6.6 ± 0.24	6.8 ± 0.25	6.3 ± 0.27
	(5.8–7.2)	(5.5–7.0)	(6.1–7.3)	(6.1–8.3)	(6.0–6.8)
LR	13.5 ± 0.59	15.2 ± 0.56	14.6 ± 1.02	16.1 ± 0.66	13.9 ± 0.62
	(12.0–15.1)	(13.9–16.6)	(12.2–17.2)	(14.6–18.1)	(13.1–15.1)
BR	6.8 ± 0.36	8.0 ± 0.38	7.4 ± 0.50	8.0 ± 0.37	7.6 ± 0.44
	(5.6–7.7)	(7.2–9.0)	(6.5–8.9)	(7.0–9.0)	(6.8–8.6)
BBC	15.5 ± 0.41	16.3 ± 0.41	16.2 ± 0.48	16.5 ± 0.45	15.9 ± 0.39
	(14.2–16.8)	(15.3–16.3)	(15.0–17.9)	(15.1–17.7)	(15.2–16.6)
HBC	10.8 ± 0.38	12.2 ± 0.43	11.6 ± 0.46	11.8 ± 0.36	11.1 ± 0.41
	(10.0–12.1)	(11.3–13.1)	(10.6–13.0)	(10.9–12.7)	(10.5–11.8)
BZP	3.2 ± 0.26	3.9 ± 0.32	3.7 ± 0.42	3.0 ± 0.22	3.1 ± 0.20
	(2.6–3.9)	(3.1–4.6)	(2.9–4.6)	(2.4–3.6)	(2.7–3.5)
LD	10.2 ± 0.54	11.4 ± 0.51	10.9 ± 0.76	11.3 ± 0.53	10.7 ± 0.46
	(8.8–12.0)	(10.2–13.1)	(9.5–12.6)	(10.0–12.8)	(10.0–11.6)
PPL	13.5 ± 0.58	15.4 ± 0.60	14.5 ± 0.87	14.6 ± 0.54	14.3 ± 0.63
	(12.2–15.0)	(13.9–16.8)	(12.5–16.2)	(12.9–16.1)	(13.2–15.2)
LBP	7.5 ± 0.40	8.0 ± 0.46	7.8 ± 0.51	8.8 ± 0.43	8.2 ± 0.37
	(6.2–8.4)	(6.9–9.8)	(6.8–9.9)	(7.4–9.8)	(7.6–9.0)
BBP	3.8 ± 0.26	3.8 ± 0.27	3.8 ± 0.33	3.6 ± 0.28	3.8 ± 0.28
	(3.1–4.5)	(3.3–4.5)	(2.9–4.6)	(2.9–4.3)	(3.3–4.3)
BMF	2.9 ± 0.24	3.5 ± 0.26	3.2 ± 0.27	3.6 ± 0.28	3.3 ± 0.21
	(2.4–3.7)	(3.0–4.3	(2.6–4.0)	(2.8–4.4)	(3.0–3.7)
LIF	6.3 ± 0.37	7.3 ± 0.42	8.0 ± 0.57	8.1 ± 0.47	6.5 ± 0.32
	(5.2–7.2)	(6.2–8.3)	(6.8–9.5)	(7.0–9.2)	(6.0–7.1)
BIF	2.5 ± 0.17	2.9 ± 0.16	3.0 ± 0.23	3.0 ± 0.20	2.8 ± 0.19
	(2.0–3.1)	(2.5–3.3)	(2.5–3.6)	(2.5–3.4)	(2.6–3.2)
LB	6.4 ± 0.24	6.5 ± 0.20	6.5 ± 0.34	6.8 ± 0.30	6.3 ± 0.25
	(5.7–7.0)	(6.1–7.0)	(5.7–7.4)	(6.0–8.0)	(5.9–6.7)
CLM1-3	6.2 ± 0.23	7.6 ± 0.26	7.2 ± 0.31	7.8 ± 0.26	7.0 ± 0.15
	(5.7–6.8)	(6.8–8.1)	(6.5–8.0)	(7.0–8.4)	(6.8–7.3)
BM1	2.0 ± 0.09	2.4 ± 0.10	2.3 ± 0.10	2.5 ± 0.11	2.4 ± 0.07
	(1.8–2.3)	(2.2–2.7)	(2.0–2.5)	(2.2–2.8)	(2.3–2.6)

The two species occur sympatrically on the northern peninsula east of Gorontalo, and *fratrorum* for a while was regarded as a synonym of *B. chrysocomus* (Ellerman, 1949; Laurie and Hill, 1954; table 4).

Demonstrating that *B. fratrorum* is not just a geographic population of one of the members of the large-bodied *B. fratrorum* group found on Sulawesi south of the northern peninsula demands its contrast with *B. penitus*, *B. andrewsi*, and *B. karokophilus,* n. sp. Here I will contrast the characteristics of *B. fratrorum* first with *B. chrysocomus,* then with *B. andrewsi* followed by *B. penitus.* Comparisons between *B. fratrorum* and *B. karokophilus,* n. sp., will be entertained in the account in which the new species is described.

Bunomys fratrorum and B. chrysocomus: In the years between 1896 and 1941, *fratrorum* was recorded in the scientific literature by most taxonomists as a distinct species and first placed in *Mus* (Trouessart, 1897: 485; Matschie, 1900: 286), then either *Rattus* (Tate, 1936: 551; Ellerman, 1941: 190) or *Frateromys* (Sody, 1941: 316).

Two reports during this period provided different allocations of *fratrorum*. Meyer (1899: 24) listed *Mus fratrorum*, as well as *Mus chrysocomus*, as synonyms of *Mus callitrichus*, and Miller and Hollister (1921a: 72) "included" *fratrorum* in "*Rattus chrysocomus*." The reasoning behind Meyer's action is explained in the first paragraph of his account of "*Mus callitrichus*" (Meyer, 1899: 24; translated from the German by E.M. Brothers; the German text is reproduced in appendix 2):

> As Hoffmann described for *M. chrysocomus*, the Dresden Museum possesses no examples of *callitrichus*, as had been indicated in Jentink's account. However, four specimens were uncovered in 1894, which the good Doctor Jentink was kind enough to compare with his types and thus one can determine their identity with certainty, even though the description of the species (NLM 1879 I, 12) is not comprehensive enough for one using it alone to know how to identify them with complete confidence. Between the sole available *chrysocomus* (the type) and the examples of *callitrichus* now before me, I can in some fashion diagnose essential differences, which are as few as exist between *M. fratrorum* <u>Thos</u>. (two in the Dresden Museum which Thomas identified) and *callitrichus*. [The two identified by Thomas were collected by Charles and Ernest Hose in 1895 from Rurukan—see locality 7 in gazetteer—and formed part of the series upon which Thomas based his original description of *Mus fratrorum*. Thomas noted that in addition to the holotype, which had been obtained at Rurukan, he had studied several other specimens from the same place. Two of these had been sent to Dresden and are now cataloged as B.3384 and B.3386. Written on the skin label of each is "<u>fratrorum</u> Thos." in Thomas's handwriting.] Of these he said (AMNH XVIII, 247) that *fratrorum* [and] *M. chrysocomus* are very closely allied, but [*fratrorum*] is distinctive on the basis of overall size, a beaded supraborbital rim, and enormous molars. However, the two skulls available to me do not exhibit these beadings, and they have rather sharp rims as is customary. Overall size and huge molars can not be regarded as species differences, these notable differences arise with regard to age and sex.

I borrowed eight specimens that Meyer had identified as "*Mus callitrichus*," which are stored in the Staatliches Naturhistorische Sammlungen Dresden, Museum für Tierkunde. Two are from Rurukan (locality 7 in the gazetteer) and were part of Thomas's original series of *fratrorum*; the rest were collected at Lota (locality 4 in the gazetteer). All are examples of *Bunomys fratrorum*. Meyer was able to contrast the holotype of *chrysocomus* with specimens that Thomas had identified as *fratrorum*, but the distinctive size differences in cranial and dental dimensions between specimens in the two samples that had stimulated Thomas to name the larger animal as a new species (remember that Thomas had also studied the holotype of *chrysocomus*) were interpreted by Meyer as the kind of differences related to age and sex found in a sample of a single species. Furthermore, Meyer considered *chrysocomus* and *fratrorum* to be synonyms of Jentink's (1879) *Mus callitrichus*.

Meyer had accepted Jentink's identification of the four specimens sent to him (presumably four of the examples identified here as *fratrorum*). Jentink compared Meyer's material with the type series of *Mus callitrichus*, which was stored in the museum at Leiden, and found no noteworthy differences. This is not surprising. The original types associated with *M. callitrichus* consisted of 12 specimens and represented not one species but five: three specimens of *Taeromys callitrichus*, one example of *Paruromys dominator*, three specimens of *Bunomys chrysocomus*, four *Bunomys fratrorum*, and a single example of *Rattus hoffmanni* (Musser, 1970). To Jentink, the characteristics of Meyer's specimens fit within the range of variation exhibited by the type material of *M. callitrichus*.

In 1921, Thomas (1921: 111) rebutted Meyer's (1899) synonymy: "In his large paper on the mammals of Celebes … Dr. A.B. Meyer has placed both *chrysocomus* and *fratrorum* as synonyms of *R. callitrichus*, Jent., but all these are perfectly distinct differing considerably in size and having

quite appreciable diagnostic skull characters.'' The statement was quoted 20 years later by Sody (1941: 316), who also noted that ''This certainly is correct (as I was able to control when studying the type of *Mus chrysocomus* at the Dresden Museum).'' In addition to Thomas (1896) and Meyer (1899), Sody was the only other researcher who had actually studied the holotype of *Mus chrysocomus*, contrasted it with examples of *fratrorum*, and published their observations.

In the same year that Thomas (1921) reasserted the distinctness of *fratrorum* as compared with *chrysocomus*, Miller and Hollister (1921a) ''included'' (their word) *fratrorum* within *chrysocomus*, but did not explain why. I suspect their view derived from study of the mammals collected in northeastern Sulawesi by H.C. Raven during the early 1900s. Raven obtained large samples of a species from Teteamoet, Kuala Prang, Gunung Klabat, and Temboan (localities 1, 5, 6, and 14 in the gazetteer and on the map in fig. 50) that were idenfitifed by Miller and Hollister as ''*Rattus chrysocomus.*'' These are the only examples of a species in what has been called the *Rattus chrysocomus* group (see Tate, 1936, for example, and table 4), now recognized as *Bunomys*, that were collected by Raven during his survey in northeastern Sulawesi. Neither Miller nor Hollister had ever seen an actual *chrysocomus* from the northeastern end of the northern peninsula. At the time none were present in collections of museums in the United States, and the species was represented only by specimens collected during the late 1800s in institutions outside that country: the holotype in Dresden (Hoffmann, 1887) and three of the 12 specimens at Leiden that had been designated cotypes of *Mus callitrichus* by Jentink in 1879 (Musser, 1970). It would not be until 1985 that *chrysocomus* would again be encountered by collectors from northeastern Sulawesi (at two sites in Bogani Nani Wartabone National Park, localities 3 and 4 in gazetteer for *Bunomys chrysocomus* and on the map in fig. 22). Because Raven obtained only one kind of *Bunomys* in the northeastern peninsula, a species which seemed to be common, Miller and Hollister apparently assumed it was *chrysocomus* (the older name) and the

same animal that Thomas had described as *Mus fratrorum*. Thomas's description of *fratrorum* does match all of Raven's specimens, and most external, cranial, and dental dimensions of the holotype of *fratrorum*, but not the holotype of *chrysocomus*, fall within the range of variation shown by Raven's samples (tables 19, 40–42). Raven had collected examples of the large-bodied *fratrorum* and surprisingly had not encountered the smaller-bodied *chrysocomus*.

Influential checklists published after 1941, and originating primarily from the Natural History Museum in London, treated *fratrorum* as a synonym of *Rattus chrysocomus* (Ellerman, 1947: 265, 1949: 52; Laurie and Hill, 1954: 118). But by 1970 its separate status as a distinct species, and reaffirmation of Thomas's observations, was promulgated by Musser (1970, 1981b, 1991), Musser and Newcomb (1983: 393), Musser and Holden (1991: 406), and accepted by Corbet and Hill (1991, 1992) in their world list of mammalian species and systematic review of Indomalayan mammals, and cemented in place by Musser and Carleton (1993: 582; 2005: 1300).

Bunomys fratrorum and *B. chrysocomus* are easily distinguished by body size alone and that this dimensional contrast could be interpreted as variation within a single species as Meyer did is remarkable. *Bunomys fratrorum* is physically larger than *B. chrysocomus* with longer head and body, tail, and hind foot (values for *B. chrysocomus* in table 19 and those for *B. fratrorum* in table 41). The tail in *B. fratrorum* is about equal to length of head and body (LT/LHB = 99%–101%), while *B. chrysocomus* has a relatively shorter tail (LT/LHB = 84%–98%). Color pattern of the tails also differ. In both species, tails are brown or brownish gray over their dorsal surfaces. Tails end in a moderately long white tip relative to tail length (mean = 18.0%, range = 4%–75%) in most specimens of *B. fratrorum* (86% of total specimens surveyed), and the ventral surface of the tail is white or mottled with brown (the pigment is contained in the scales and tail hairs). By contrast, a short white tail tip occurs in only 20% of all specimens of *B. chrysocomus* surveyed and is short relative to tail length (mean = 5.5%, range = 1%–25%). The undersurface of the tail ranges from

brown to heavily mottled brown in most samples—a white ventral surface is uncommon.

Testes size provides a strong contrast between the species (table 9). Relative to length of head and body, the testes of *B. chrysocomus* are longer (22%), those of *B. fratrorum* much shorter (8%), a difference also indicated by relative testes mass. Testes mass relative to body mass was measured by Breed and Taylor (2000) and reported as 3.02% in *B. chrysocomus* ($N = 2$) and 0.28% in *B. fratrorum* ($N = 2$).

The two species also differ in spermatozoan morphology. In *B. chrysocomus*, the falciform sperm head is long and thin with a long tail attaching near the end of the head, but in *B. fratrorum*, the sperm head is shorter and gently curved, with the tail (which is much shorter than in *B. chrysocomus*) attached near the middle of its concave surface (Breed and Musser, 1991; Breed and Taylor, 2000).

With the exception of three variables, all cranial and dental dimensions measured are absolutely much greater in *B. fratrorum* than in *B. chrysocomus*, a distinction qualitatively marked in illustrations of skulls (figs. 16, 17) and quantitatively expressed by univariate means for 232 *B. chrysocomus* and 100 *B. fratrorum* (table 42). Among the three dimensional exceptions, the interorbit is absolutely wider in *B. chrysocomus* (M = 6.4 mm) than in *B. fratrorum* (M = 6.2 mm), and breadth of the bony palate (M = 3.8 mm in both species) and length of bulla (M = 6.4 mm for *B. chrysocomus*, 6.5 mm for *B. fratrorum*) are statistically identical in the two species. Set against the absolute size contrast between the two, *B. chrysocomus* has a conspicuously wider interobital region and bony palate, and a longer bulla relative to all other cranial and dental dimensions measured, proportional distinctions diagrammed previously (fig. 19).

Lower molars of *B. fratrorum* have a somewhat simpler occlusal topography than do those of *B. chrysocomus* judged by frequencies of certain cusps and cusplets (table 11). An anterolabial cusp is present on the second molar in only 12% of the sample and all the specimens lack the cusp on the third molar; this cusp is part of the occlusal surface of the second molar in 90% of the sample of *B. chrysocomus* and occurs on the third molar in 65% of the sample. An anterior labial cusplet is not found on the first molar of all examples of *B. fratrorum* surveyed, but is usual in about half the sample of *B. chrysocomus*. The posterior labial cusplet of the first molar occurs in about half the sample of *B. fratrorum*, but is present in 97% of the series of *B. chrysocomus*.

Thomas was impressed by the prominent ("beaded") supraorbital ridges in *B. fratrorum* compared to *B. chrysocomus*. Interorbital and postorbital margins are delimited by low ridges on the skulls of both species, and those in *B. chrysocomus* are not as prominent as in *B. fratrorum* (figs. 16, 17). The absolute difference is related to size, the much larger skull of *B. fratrorum* carries with it heavier ridging than does the smaller skull of *B. chrysocomus*; relative to size of skull, however, prominence of the interorbital and postorbital borders is similar.

The conspicuous contrasts between *B. fratrorum* and *B. chrysocomus* in body size, relative length of tail, length of the white tail tip and its frequency in populations, cranial and dental dimensions in absolute and proportional terms, frequencies of cusp and cusplets on lower molars, structure of spermatozoa, relative testes size, and sympatry should dispel any notion that the samples of each represent a single species.

***Bunomys fratrorum* and *B. andrewsi*:** *B. andrewsi* has never been collected on the northern peninsula of Sulawesi. It ranges from the southern end of the northern peninsula over the lowlands and highlands of Sulawesi's core, through the southeastern peninsula and on Pulau Peleng at the end of that arm, and into the southwestern peninsula (see the map in fig. 50). *Bunomys andrewsi* and *B. fratrorum* are similar in some phenetic characteristics. Both have brownish-gray upperparts lightly speckled with buff and black and grayish-white underparts tinted or washed with a range of buffy tones. *Bunomys fratrorum* is comparable in lengths of head and body and hind foot to *B. andrewsi* (table 41). The most conspicuous external difference is expressed in length of tail and its color pattern. The tail is long

(means = 167.5–179.0 mm in six population samples), coequal to length of head and body in samples of *B. fratrorum* (LT/LHB = 99%–101%), and most individuals (86% of the sample) show a long and white terminal portion (mean = 18.0%, range = 4%–75% of tail length). By contrast, the tail is absolutely shorter in *B. andrewsi* (mean = 111.5–156.8 for all population samples; table 41), much shorter relative to length of head and body (LT/LHB = 75%–92%), a white tip occurs infrequently in the samples (20% of 133 specimens), and when present is short relative to length of tail (mean = 7.7%, range = 1%–13%; table 8).

Relative testes size and spermatozoal morphology differ (table 9). Size of testes relative to body size is less in *B. fratrorum* (8%) compared with the range in *B. andrewsi* (8%–15%). Spermatozoa of *B. fratrorum* have a short and gently curved sperm head to which a short tail is attached near the middle of its concave surface (Breed and Taylor, 2000) while *B. andrewsi* resembles *B. chrysocomus*is in having a falciform sperm head that is long and thin with a moderately long tail attaching near the base of the head (Breed and Musser, 1991).

Most of the cranial and dental measurements derived from the samples of *B. fratrorum* average greater than in the combined population samples of *B. andrewsi* (table 42). Interorbital breadth and expanse of the incisive foramina are exceptions. *Bunomys fratrorum* has a narrower interorbit (mean = 6.2 mm) compared with *B. andrewsi* (mean = 6.7 mm) and shorter incisive foramina (mean = 7.3 mm for *B. fratrorum*, 8.0 mm for *B. andrewsi*), contrasts evident when skulls of comparable adult age classes are compared (figs. 52–54).

A scatter plot of specimen scores representing *B. fratrorum* and *B. andrewsi* projected on first and second principal components summarizes the morphometric distinctions between the two species (fig. 55, upper graph). The major axes of the two elliptical clouds of scores are phenetically discrete: the regression lines of the second principal component on the first are parallel, their Y-intercepts are significantly different between the two species (+0.951 versus −0.951; F = 73.62, P = 0.000), but their slopes are statis-

tically equivalent (−0.406 versus −0.407; F = 0.00, P = 0.998). Although there is marginal overlap between the two ellipsoidal clusters of scores along the second axis, there is enough separation to indicate that *B. andrewsi* has a relatively wider interorbit, narrower rostrum, narrower braincase, shorter but wider bony palate, narrower mesopterydoid fossa, markedly longer and wider incisive foramina, larger bulla and smaller molars compared with *B. fratrorum* (see the correlations in table 43). The ratio diagram in figure 56 presents most of these same proportional contrasts in graphic form but also shows the braincase of *B. andrewsi* to be wider relative to its height compared with *B. fratrorum*, and the molars smaller relative to expanse of the palatal bridge.

Frequencies of two structures on the mandibular molars differs betwen samples of *B. fratrorum* and those representing *B. andrewsi* (table 11). An anterolabial cusp is present on the second molar in only 12% of the sample of *B. fratrorum*, but occurs in 88%–100% of the combined samples of *B. andrewsi*. About half of the sample of *B. fratrorum* has a posterior labial cusplet on the first molar, but nearly all specimens of *B. andrewsi* bear this structure (97%–100% of all specimens surveyed).

The morphometric distinctiveness of *B. fratrorum* relative to *B. andrewsi* is reinforced by a phenogram based on squared Mahalanobis distances among centroids for all population samples representing *Bunomys* (fig. 21). The cluster of samples identifying *B. fratrorum* unites with that of *B. karokophilus,* n. sp., and those samples link with the clusters of population samples for *B. andrewsi* and *B. penitus*. There is no evidence from morphology of skin and skull suggesting that *B. fratrorum* is a fragment of *B. andrewsi* isolated in the northeastern segment of the northern peninsula.

Bunomys fratrorum and Bunomys penitus: Within the forests mantling the northeastern end of the northern peninsula, the altitudinal distribution of *B. fratrorum* stretches from lowlands into mountains. *Bunomys penitus* inhabits only mountain forests clothing highlands in the west-central mountain block of the island and on the southeastern peninsula. The two species are smililar in
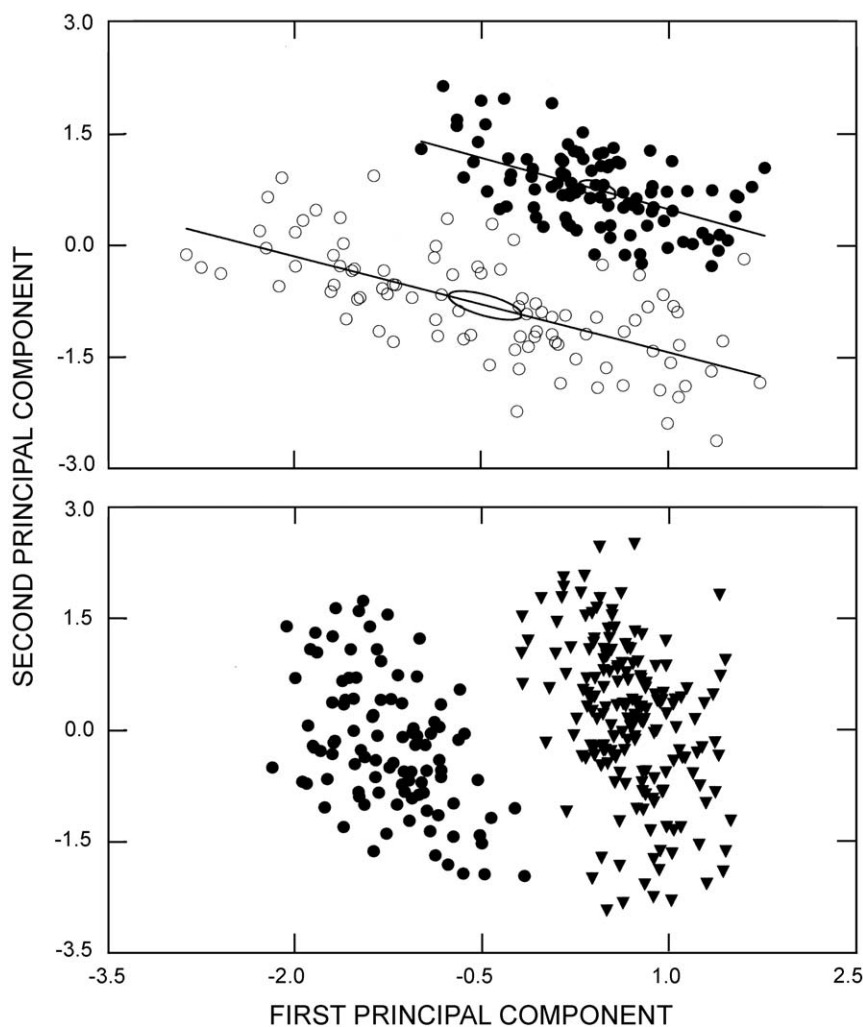
Fig. 55.   Specimen scores representing all population samples of *Bunomys fratrorum* (filled circles; $N = 100$), *B. andrewsi* (empty circles; $N = 98$), and *B. penitus* (filled inverted triangles; $N = 181$) projected onto first and second principal components extracted from principal-components analysis of 16 cranial and two dental log-transformed variables. Upper graph: Samples of *B. fratrorum* are contrasted with all population samples of *B. andrewsi*. Ellipses outline 95% confidence limits for the cluster centroids. Equations for the regression lines are: *B. fratrorum*, $Y = -0.406 \times 0.951$ ($F = 34.30$, $P = 0.000$); *B. andrewsi*, $Y = -0.407 \times -0.951$ ($F = 60.46$, $P = 0.000$). Lower graph: samples of *B. fratrorum* are contrasted with all population samples of *B. penitus*. See table 43 for correlations (loadings) of variables with extracted components and for percent variance explained for both ordinations.

body size, but the tail averages slightly longer and is generally longer relative to head and body length in *B. fratrorum* compared with *B. penitus* (table 41).

The dorsal pelage of *B. penitus* is dense and long (up to 25 mm), soft to the touch, silky in appearance, and brownish gray tending toward grayish tones (coat is not as long in *B. fratrorum,* not longer than 12 mm in most specimens, somewhat courser in texture and not silky, and brownish gray tending toward darker tones). Underparts are dark grayish white (underparts are also grayish white in *B. fratrorum* but tinged or washed with buffy tones in many specimens). The tail ends in a long white segment, behind it the dorsal

TABLE 43
**Results of Principal-Components Analysis
Comparing All Population Samples of *Bunomys
fratrorum* with Those of *B. andrewsi* and *B. penitus***
Correlations (loadings) of 16 cranial and two dental
log-transformed variables are based on 100 *B.
fratrorum*, 98 *B. andrewsi*, and 185 *B. penitus*; see
figure 55.

| | Correlations | | | |
| | *B. fratrorum* and *B. andrewsi* | | *B. fratrorum* and *B. penitus* | |
Variable	PC1	PC2	PC1	PC2
ONL	0.90***	0.28***	0.48***	0.61***
ZB	0.87***	−0.03	−0.70***	0.45***
IB	−0.14*	−0.62***	0.65***	0.31***
LR	0.82***	0.04	0.43***	0.60***
BR	0.80***	0.24***	−0.29***	0.68***
BBC	0.39***	−0.04	0.18**	0.36***
HBC	0.68***	0.30***	−0.48***	0.26***
BZP	0.78***	−0.11	−0.99***	0.07
LD	0.85***	−0.06	−0.17**	0.71***
PPL	0.85***	0.08	−0.63***	0.38***
LBP	0.47***	0.27***	0.55***	0.29***
BBP	0.57***	−0.48***	−0.39***	0.59***
BMF	0.56***	0.37***	0.17**	0.60***
LIF	0.19**	−0.85***	0.55***	0.54***
BIF	0.41***	−0.65***	0.14*	0.63***
LB	0.41***	−0.24***	0.43***	0.41***
CLM1–3	0.53***	0.33***	0.33***	0.18**
BM1	0.23***	0.36***	0.50***	−0.02
Eigenvalue	0.029	0.012	0.032	0.013
% Variance	40.8	17.0	43.7	18.1

*** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

surface is glossy grayish brown or brownish gray, and the ventral surface is pure white (dorsal surface is brown in *B. fratrorum* except for a white terminal segment, the ventral surface ranges from pure white to white speckled with brown to mottled white and brown). Although a white-tipped tail is characteristic of both species (table 8), the white segment is longer relative to tail length in *B. penitus* (means = 12.3%–30.7% for six samples of *B. penitus*; 15.0%–22.0% for four samples of *B. fratrorum*) and never speckled—some portion of specimens in most samples of *B. fratrorum* exhibit a speckled distal tail segment. Dorsal surfaces of the feet are white or white suffused with gray; the claws are delicate and nearly concealed by long, dense, and silvery ungual tufts (metatarsal and metacarpal surfaces range from white to brownish white in *B. fratrorum*, the claws are sturdy and not concealed by ungual tufts.

Testes size relative to head and body is similar in the two species (table 9). Sperm morphology is different. Spermatozoa of *B. fratrorum* have a short and gently curved sperm head to which a short tail is attached near the middle of its concave surface (Breed and Taylor, 2000) while *B. penitus* has a falciform sperm head that is long and thin with a moderately long tail attaching near the base of the head (Breed and Musser, 1991).

The skull in the sample of *Bunomys penitus* averages overall somewhat smaller (indicated by means for occipitonasal length and zygomatic breadth) than that of *B. fratrorum*, the braincase is not as deep, the zygomatic plate startlingly narrower, the bony palate narrower, and the postpalatal region (basicranium) shorter, as reflected by absolute differences in univariate means (table 42). Means for three internal dimensions are not significantly different between the two species (breadths of rostrum and braincase, and length of diastema), but the interorbit of *B. penitus* is wider, the rostrum and bony palate longer, the mesopterygoid fossa more spacious, the incisive foramina longer and broader, the ectotympanic bulla larger, and the molars heavier (longer molar row, wider molars).

Separate clouds of specimen scores for *B. penitus* and *B. fratrorum* projected on first and second principal components provide a multivariate summary of the contrast between the two species in cranial and dental variables (fig. 55, lower graph). Covariation in interorbital breadth, along with lengths of rostrum, bony palate, incisive foramina, bullar capsule, and molar size (large positive loadings for these variables, r = 0.33–0.65; table 43) strongly influence the spread and separation of scores along the first axis, and highlights the greater magnitude of these dimensions in *B. penitus* as compared to *B. fratrorum*, measurement contrasts reflected by univariate means (table 42).

There are striking proportional differences between *B. penitus* and *B. fratrorum* in cranial and dental variables, which are revealed in a ratio diagram (fig. 56). The most conspicuous contrasts involve magni-
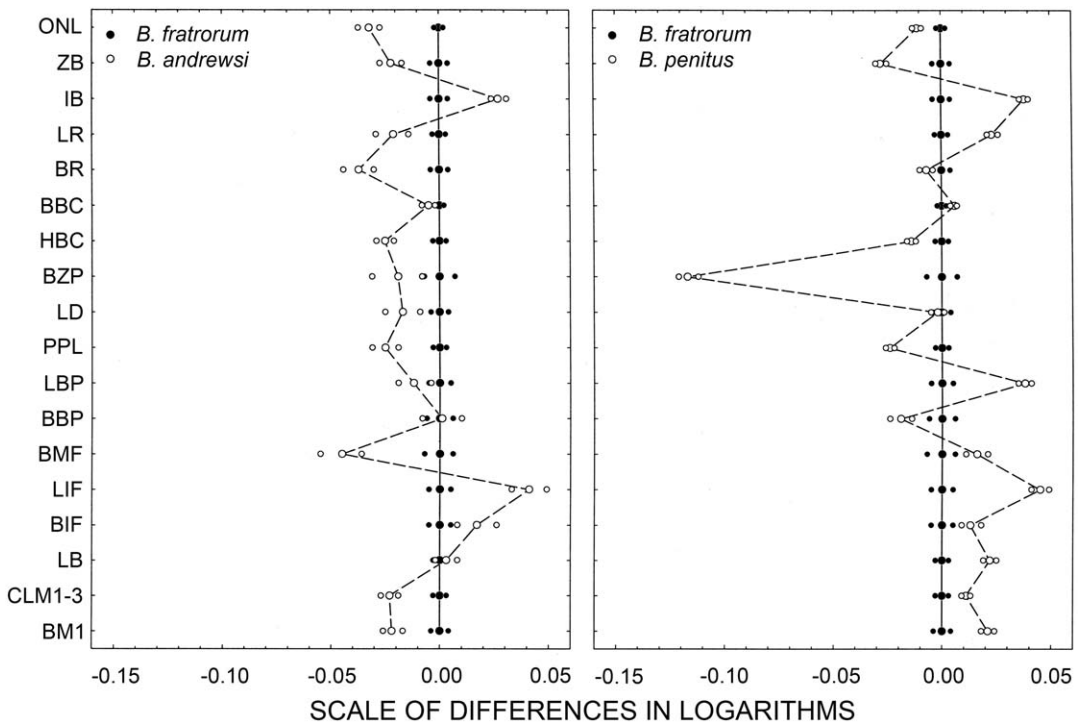
Fig. 56.   Ratio diagrams illustrating some proportional relationships in cranial and dental dimensions between *Bunomys fratrorum* (the standard, $N = 100$) and *B. andrewsi* ($N = 98$), and between *B. fratrorum* and *B. penitus* ($N = 185$). Data were derived from values for mean, standard deviation, and sample size of variables listed in table 42. How the diagram was constructed and how to read it is explained in Materials and Methods.

tudes of certain cranial dimensions relative to size of skull (indexed by occipitonasal length): *B. penitus* is relatively narrower across the zygomatic arches but has a much broader interorbit, the facial region is relatively longer (longer rostrum, incisive foramina, and diastema), the zygomatic plate strikingly narrower, the bony palate longer, the mesopterygoid fossa wider, the bullar capsule larger, and the molars more massive. The elongate facial region is also proportioned differently in that *B. penitus* has a narrower rostrum, incisive foramina, and bony palate relative to their respective lengths.

Frequencies of certain cusps and cusplets forming parts of the coronal surfaces of molars differ between the two species. No specimen of *B. fratrorum* I examined shows a large labial cusplet adjacent to or merging with cusp t6 on the first upper molar (such a cusplet is present in 30% of the sample of *B.*

penitus; fig. 75). Cusp t3 is absent from the third upper molar on most examples of both species, is part of the second molar in only 11% of the sample of *B. fratrorum*, but is present in 62% of the sample of *B. penitus* (table 10). A posterior labial cusplet is present on the first lower molar in nearly half of the sample of *B. fratrorum* but in every specimen of *B. penitus*, and an anterolabial cusp occurs infrequently on the second lower molar in the sample of *B. fratrorum* (12%) but is present in about half of the sample of *B. penitus* (55%); see table 11.

Summary of contrasts between population samples of *Bunomys fratrorum* and those of *B. andrewsi* and *B. penitus*: *Bunomys fratrorum* is found only on the northern peninsula east of the Gorontalo region and inhabits tropical lowland evergreen and montane rain forests; *B. andrewsi* occurs primarily in tropical

lowland evergreen rain forest in Sulawesi's core and the southeastern and southwestern peninsulas; *B. penitus* is strictly montane, found so far only in the west-central mountain block and Pegunungan Mekongga on the southeastern peninsula. Body size is similar among the species.

Bunomys andrewsi has a shorter tail (both absolutely and relative to combined length of head and body), and a short, white tail tip is present in only a small portion of the sample; tails are longer and often coequal with length of head and body in *B. fratrorum* and *B. penitus*, and a long, white tip is usual in both species (tables 8, 41). *Bunomys penitus* has a longer dorsal coat and grayer underparts; dorsal surfaces of the front and hind feet are typically white rather than white- to brownish gray, the range in the other species; front claws are more robust and ungual tufts are sparse at the bases of front and hind claws in *B. andrewsi* as well as *B. fratrorum* compared with the smaller, gracile front claws of *B. penitus* and its longer ungual tufts.

Absolute and proportional similarities and contrasts in cranial and dental variables between *B. fratrorum* and the other two species have been presented in the images of skulls (figs 52–54), univariate summary statistics (table 42) results from principal-components analyses (fig. 55, table 43) and ratio diagrams (fig. 56) previously described. A graphic summary of the morphometric distinctions among the species is portrayed by individual specimen scores projected onto first and second canonical variates (fig. 57). Scores for the three species fall into three discrete clusters. Along the first axis, the group of points representing *B. fratrorum* is isolated from the other two aggregations by covariation in several cranial and dental variables (moderate to high loadings; table 44) that, compared with *B. andrewsi* and *B. penitus*, reflect its more greatly flared zygomatic arches, narrower interorbit, shorter rostrum (compared with *B. penitus*), higher braincase, much wider zygomatic plate, longer basicranium (measured by postpalatal length) shorter bony palate and incisive foramina, smaller bulla, and smaller molars (compared with *B. penitus*).

Along the first canonical axis, scores for *B. penitus* form a cluster opposite the clump representing *B. fratrorum*, which emphasizes the wider interorbit of *B. penitus* compared with *B. fratrorum*, its longer rostrum, wider but shallower braincase, much narrower zygomatic plate (which is diagnostic for *B. penitus*), longer bony palate and incisive foramina, larger bulla, and heavier molars (see the loadings in table 44). The separation of scores denoting *B. andrewsi* from the aggregations for *B. fratrorum* and *B. penitus* along the second axis reflects proportional contrasts and is influenced primarily by the relatively smaller skull of *B. andrewsi* compared with the other two species, its relatively shorter and narrower rostrum, smaller braincase, wider zygomatic plate, shorter diastema, shorter but wider bony palate, narrower mesopterygoid fossae, and less robust molars (table 44).

The isolation of *B. fratrorum* from *B. andrewsi* and *B. penitus* by morphometric attributes is reinforced by a phenogram derived from squared Mahalanobis distances among centroids for population samples (fig. 21). Population samples for *B. andrewsi* and *B. penitus* join in a monophyletic group before linking with those representing *B. fratrorum.* This picture, along with the phenetic distinctions among the sets of samples evident from inspection of skins and skulls, absolute and proportional contrasts in dimensions, results of other multivariate analyses, and different geographic and altitudinal relationships support the hypothesis that *B. fratrorum* is a distinct entity with a different genetic history (species) from *B. andrewsi* and *B. penitus*. Neither the montane *B. penitus* nor the lowland and middle-elevation *B. andrewsi* can be viewed as simply geographic or altitudinal variants (subspecies) of the northern peninsular *B. fratrorum.* Its closest phenetic relative, judged by the pattern seen in the Mahalanobis distance cluster, may be the central Sulawesian *B. karokophilus,* n. sp. (see that account).

GEOGRAPHIC VARIATION: Variation in external traits among samples of *B. fratrorum* does not conform to any obvious geographic pattern. The range of variation of coat color and thickness, tail pattern, and external dimensions within any one of the three
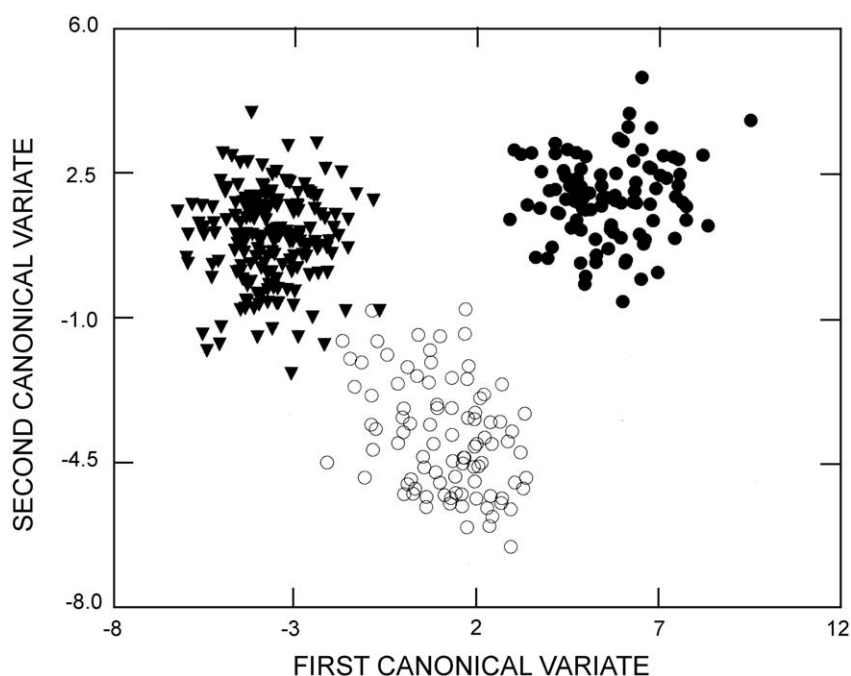
Fig. 57.   Specimen scores representing all population samples of *Bunomys fratrorum* (filled circles; N = 100), *B. andrewsi* (empty circles; N = 98), and *B. penitus* (inverted filled triangles; N = 185) projected onto first and second canonical variates extracted from discriminant-function analysis of 16 cranial and two dental log-transformed variables. See table 44 for correlations (loadings) of variables with extracted canonical variates and for percent variance explained.

largest samples of *B. fratrorum* I studied (those from Teteamoet, Kuala Prang, and Temboan; see table 41) matches the extent of variation in these variables present among all the population samples except one. The three specimens collected above 1800 m in montane forest on Gunung Klabat have slightly longer and darker fur covering the upperparts of head and body.

Morphometric variation in cranial and dental variables does exist among population samples as results of principal-components and discriminant-function analyses illustrate. A scatter plot defined by first and second principal components encloses specimen scores scattered along the two axes generally without forming perceptible patterns (fig. 58). Scores for the Teteamoet and Temboan samples fill the multivariate space, overlapping points for nearly all the other samples. The spread along the first component is influenced primarily by size, as signified by the moderate to high positive

correlation coefficients (r = 0.32–0.78) of most cranial variables (table 46) and likely mostly reflects age and individual variation within the range of adult cohorts from young to old. The filled square at the top of the scatter plot along the second axis denotes an adult from Gunung Mogogonipa with an exceptionally long bony palate and short incisive foramina (r = 0.72 and −0.53, respectively; table 46).

A different view of covariation in cranial and dental variables among population samples is provided by individual specimen scores projected on first and second canonical variates in which scores for the larger samples form a pattern related to geographic provenance (fig. 59; table 46). Points identifying specimens from Teteamoet and Kuala Prang, located at the northeastern tip of the northern peninsula (localities 1 and 5 on the map in fig. 50), form a cluster in the right half of the ordination along the first axis that marginally overlaps the cloud of scores in the

	Correlations	
Variable	CV1	CV2
ONL	0.18***	0.65***
ZB	0.54***	0.10*
IB	−0.68***	−0.18***
LR	−0.41***	0.57***
BR	0.06	0.54***
BBC	−0.22***	0.28***
HBC	0.32***	0.46***
BZP	0.79***	−0.32***
LD	−0.01	0.34***
PPL	0.44***	0.28***
LBP	−0.54***	0.51***
BBP	0.24***	−0.21***
BMF	−0.20***	0.59***
LIF	−0.58***	−0.22***
BIF	−0.17***	−0.14**
LB	−0.45***	0.18***
CLM1–3	−0.28***	0.66***
BM1	−0.41***	0.59***
Canonical correlation	0.960	0.900
Eigenvalue	11.603	4.273
% Variance	73.1	26.9

*** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$.

left half of the scatter plot designating specimens from Temboan (locality 17 on the map in fig. 50), which lies far to the southwest of Kuala Prang and Teteamoet, and Maujat + Mogogonipa, highlands west of Temboan (localities 18 and 19 on the map in fig. 50). Scores for the holotype from Rurukan clusters with the Teteamoet sample, the two representing Gunung Klabat are contained in the Temboan cluster. Pattern of the scores reflects the slightly larger skulls (indexed by occipitonasal length and zygomatic breadth) in the Kuala Prang and Teteamoet samples, their deeper braincase, longer postpalatal region and incisive foramina but shorter bony palate compared with the Temboan and Maujat + Mogogonipa samples as signified by the larger positive and negative loadings for these variables on the first axis listed in table 46 (and reflected by univariate means in table 45). Intersample

variation summarized in the canonical variates ordination suggests a gradient in skull size from east to west within the range of *B. fratrorum*.

Cluster analysis derived from average Mahalanobis distances (squared) among centroids for population samples also illustrate a close relationship between samples from Teteamoet and Kuala Prang, the localities close to one another, and these link to Temboan. Samples from Gunung Klabat and Rurukan cluster, and these places are geographically near one another (see the map in fig. 50). The westernmost sample from Gunung Maujat and Gunung Mogogonipa is distant from the other five population samples in the cluster diagram, an arrangement suggested by the position of scores in the canonical variate scatter plot where scores identifying the four specimens from Maujat and Mogogonipa lay at the far left margin of the total scatter of scores.

The population samples for *B. fratrorum* come from two regions of the northern peninsula that are deemed areas of endemism as illustrated by macaques (Fooden, 1969), toads (Evans et al., 2003a), and fanged frogs (Evans et al., 2003a, 2003b). The northeastern end of the peninsula from the tip west to approximately the drainages of the Sungai Onggak Mongondaw and Sungai Onggak Dumoga describes one endemic region (''northeast'') and it is where the specimens of *B. fratrorum* from Teteamoet, Kuala Prang, Gunung Klabat, Rurukan, and Temboan were obtained. Those samples are closely linked (in Mahalanobis distance units) compared with the distant position of the samples from Gunung Maujat and Gunung Mogogonipa, which were collected to the west in the ''north central'' endemic region, approximately between Sungai Onggak Dumoga and the Gorontalo area (see fig. 1). But the Maujat and Mogogonipa samples are small, consisting of two adults, a young adult, and very young adult. Study of larger samples from the ''north central'' segment along with collections from the region between Gunung Maujat-Gunung Mogogonipa and the eastern site of Temboan will be required to determine whether the populations living between Sungai Onggak Dumoga and the Gorontalo area are a separate species, a morphometrically

TABLE 45
Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from Population Samples of
Bunomys fratrorum
Mean ± 1 SD and observed range (in parentheses) are listed.

Variable	Teteamoet	Kuala Prang	Gunung Klabat	Rurukan	Temboan	G. Maujat + G. Mogogonipa
N	33	27	2	1	33	4
ONL	44.2 ± 1.05	44.4 ± 1.17	43.9 ± 0.57	44.3	43.5 ± 1.07	44.7 ± 1.52
	(42.0–46.4)	(42.1–46.5)	(43.5–44.3)		(41.5–45.3)	(43.3–46.4)
ZB	21.0 ± 0.66	21.5 ± 0.72	20.8 ± 0.28	21.0	20.4 ± 0.96	21.1 ± 1.31
	(19.7–22.2)	(20.0–22.5)	(20.6–21.0)		(18.2–22.3)	(19.8–22.9)
IB	6.1 ± 0.35	6.2 ± 0.22	5.8 ± 0.00	6.4	6.2 ± 0.30	6.6 ± 0.35
	(5.5–6.8)	(5.8–6.8)			(5.7–7.0)	(6.2–6.9)
LR	15.0 ± 0.50	15.4 ± 0.54	15.3 ± 1.06	15.0	15.3 ± 0.58	15.4 ± 0.61
	(13.9–15.9)	(14.3–16.5)	(14.5–16.0)		(13.9–16.6)	(14.9–16.3)
BR	8.0 ± 0.35	8.2 ± 0.40	7.9 ± 0.57	8.4	7.9 ± 0.38	7.9 ±0.13
	(7.4–8.6)	(7.3–9.0)	(7.5–8.3)		(7.2–8.7)	(7.7–8.0)
BBC	16.2 ± 0.46	16.4 ± 0.28	15.8 ± 0.14	16.2	16.3 ± 0.43	16.6 ± 0.30
	(15.3–17.2)	(15.9–17.1)	(15.7–15.9)		(15.4–17.5)	(16.2–16.8)
HBC	12.2 ± 0.43	11.7 ± 0.39	11.7 ± 0.21	12.3	12.1 ± 0.38	11.8 ± 0.52
	(11.4–13.1)	(11.7–13.1)	(11.5–11.8)		(11.3–12.8)	(11.3–12.3)
BZP	4.0 ± 0.29	3.8 ± 0.23	3.8 ± 0.07	3.5	3.9 ± 0.37	3.6 ± 0.46
	(3.3–4.6)	(3.5–4.4)	(3.7–3.8)		(3.2–4.6)	(3.1–4.2)
LD	11.3 ± 0.46	11.4 ± 0.47	11.5 ± 0.28	11.8	11.3 ± 0.51	12.0 ± 0.92
	(10.3–12.4)	(10.5–12.4)	(11.3–11.7)		(10.2–12.2)	(11.0–13.1)
PPL	15.6 ± 0.46	15.6 ± 0.60	14.6 ± 0.71	15.0	15.0 ± 0.54	15.4 ± 0.42
	(14.6–16.6)	(14.1–16.8)	(14.1–15.1)		(13.9–16.0)	(14.8–15.8)
LBP	7.9 ± 0.32	7.8 ± 0.43	8.5 ± 0.14	8.2	8.2 ± 0.35	9.0± 0.70
	(6.9–8.5)	(7.2–8.8)	(8.4–8.6)		(7.5–9.0)	(8.2–9.8)
BBP	3.7 ± 0.21	3.9 ± 0.30	3.5 ± 0.14	3.9	3.8 ± 0.28	3.9 ± 0.29
	(3.4–4.2)	(3.4–4.5)	(3.4–3.6)		(3.3–4.4)	(3.5–4.1)
BMF	3.4 ± 0.20	3.6 ± 0.28	3.8 ± 0.07	3.5	3.5 ± 0.26	3.2 ± 0.13
	(3.1–3.9)	(3.2–4.3)	(3.7–3.8)		(3.0–4.2)	(3.0–3.3)
LIF	7.3 ± 0.29	7.6 ± 0.38	7.2 ± 0.50	7.4	7.0 ± 0.31	6.6 ± 0.40
	(7.0–8.3)	(7.0–8.3)	(6.8–7.5)		(6.4–7.6)	(6.2–7.1)
BIF	2.9 ± 0.14	2.9 ± 0.14	3.1 ± 0.35	3.3	2.8 ± 0.15	2.8 ± 0.21
	(2.6–3.2)	(2.6–3.2)	(2.8–3.3)		(2.5–3.2)	(2.6–3.0)
LB	6.4 ± 0.16	6.5 ± 0.20	6.4 ± 0.28	6.3	6.4 ± 0.22	6.7 ± 0.22
	(6.1–6.9)	(6.1–7.0)	(6.2–6.6)		(6.1–6.8)	(6.4–6.9)
CLM1–3	7.6 ± 0.23	7.6 ± 0.25	7.7 ± 0.35	7.9	7.5 ± 0.31	7.7 ± 0.19
	(7.1–8.1)	(7.0–8.0)	(7.4–7.9)		(6.8–8.1)	(7.4–7.8)
BM1	2.4 ± 0.07	2.4 ± 0.12	2.5 ± 0.21	2.5	2.4 ±0.09	2.4 ± 0.06
	(2.3–2.5)	(2.2–2.7)	(2.3–2.6)		(2.2–2.5)	(2.3–2.4)

definable geographic variant of *B. fratrorum* inferring some degree of genetic isolation, or simply another geographic sample of that species genetically connected to populations occurring to the east. In the context of such an inquiry the use of DNA sequences would be most welcome.

Most examples of *B. fratrorum* come from altitudes below 1000 m in tropical lowland evergreen rainforest habitats. A few were collected at higher elevations in lower montane forest on Gunung Maujat (at 1780 m) and Gunung Klabat (at 1829 and 1982 m). It is significant that study of skin and skulls along with results of multivariate analyses place these specimens with other population samples of *B. fratrorum* and not with any other species of *Bunomys* (see particularly the cluster diagram in fig. 21, showing phenetic relationships among all species of *Bunomys* based on squared Mahalanobis distances among centroids for population samples). Within its range, *B. fratrorum* is not replaced in montane forest formations by another

species of *Bunomys*. This elevational distribution contrasts with the pattern demonstrated by other species in the *B. fratrorum* group occurring elsewhere on Sulawesi. In the northern part of the west-central region of Sulawesi's core, for example, tropical lowland evergreen rainforest habitats are occupied by *B. andrewsi* and *B. karokophilus,* n. sp., and these two species are replaced by *B. penitus* at higher elevations in lower and upper montane forests. *Bunomys andrewsi* also inhabits lowland habitats on the southeastern peninsula and is replaced by *B. penitus* at higher elevations there in montane forest habitats. That *B. fratrorum* is the only large-bodied species of *Bunomys* found in both lowland and montane evergreen rain forests on the northern peninsula of Sulawesi may be related to past periodic fluctuations in sea level and tectonic activity that isolated the region east of Gorontalo as one or more islands (Fooden, 1969). One of those islands may have supported a population of ancestral *Bunomys* from which *B. fratrorum* evolved in isolation from populations on mainland Sulawesi. Modern samples of *B. chrysocomus* represent the only other species of *Bunomys* currently recorded from the northeastern tip east of Gorontalo and may be a relatively recent immigrant to that region.

NATURAL HISTORY: I have no first-hand experience with *B. fratrorum* and no information from the collector's field journals. The species occupies habitats in tropical lowland evergreen and montane rain forests and, as is usual with the other species of *Bunomys*, is likely terrestrial and nocturnal.

I can provide a bit of data about diet. Fortunately, H.C. Raven preserved an adult male in fluid (USNM 217084) that he caught at Teteamoet on the coastal plain (locality 1 in the gazetteer and on the map in fig. 50). The stomach contains remains of up to five small earthworms, fragments of a small adult beetle, head of a termite, and pieces of a small unidentified fruit. The composition of items is similar to that constituting the diet of *B. chrysocomus* and *B. andrewsi* (see those accounts and table 13).

Spermatozoa of *B. fratrorum* have been used in several inquiries. Body and testes weights (mass) along with sperm size was derived from two *B. fratrorum* by Breed and Taylor (2000) and employed in an investigation of murines designed "to test the hypothesis that differences in relative testes mass, and perhaps sperm size, relate to interspecific differences in the amount of intermale sperm competition and in breeding systems." Related studies in which spermatozoa of *B. fratrorum* was included investigate morphometry, competition, cooperation, and sociality in rodent sperm (Immler et al., 2007; Pizzari and Foster, 2008).

ECTOPARASITES: *Bunomys fratrorum* is parasitized by sucking lice, fleas, ticks, and chiggers (table 14). Of the sucking lice, *Hoplopleura sembeli* has also been recorded from the endemic Sulawesi rats *Maxomys hellwaldii* and *Rattus hoffmanni* (Durden, 1990; Durden and Musser, 1991), and *Polyplax wallacei* also parasitizes *Bunomys chrysocomus* and a species of *Taeromys* (Durden, 1990; Durden and Musser, 1991).

Of the species in the four genera of fleas (Siphonaptera) that parasitize *B. fratrorum*, *Sigmactenus sulawesiensis* (Leptopsyllidae) also parasitizes four other endemic Sulawesi murines (*Bunomys fratrorum*, *Eropeplus canus*, *Maxomys musschenbroekii*, and *Paruromys dominator*) and the endemic tree squirrel *Prosciurillus topapuensis* (Durden and Beaucournu, 2000). *Sigmactenus alticola crassinavis* also infests a native shrew (*Crocidura* sp.) and the endemic murines, *Maxomys musschenbroekii*, *Paruromys dominator*, *Rattus hoffmanni*, and *R. xanthurus* (Durden and Beaucournu, 2000). *Musserella,* n. gen. and species #4 (Pygiopsyllidae), infests not only *Bunomys fratrorum*, but also five other Sulawesi endemic murids (*Bunomys chrysocomus, Rattus hoffmanni, Paruromys dominator, Maxomys hellwaldii*, and *M. musschenbroekii*) and the nonnative *Rattus tanezumi* (Durden, in litt., 2008). *Nestivalius sulawesiensis* (Pygiopsyllidae) is recorded from *Bunomys fratrorum* and *B. chrysocomus*; *Maxomys hellwaldii* and *M. musschenbroekii*; and *Rattus facetus* (recorded as *R. marmosurus*) and *R. hoffmanni* (Mardon and Durden, 2003). Finally, *Macrostylophora theresae* also infests *Paruromys dominator* and *Rattus xanthurus* (Durden and Beaucournu, 2006).

Bunomys fratrorum is host to the immature stages of species in three genera of ticks (Acari: Ixodoidea): *Amblyomma* sp., *Derma-*
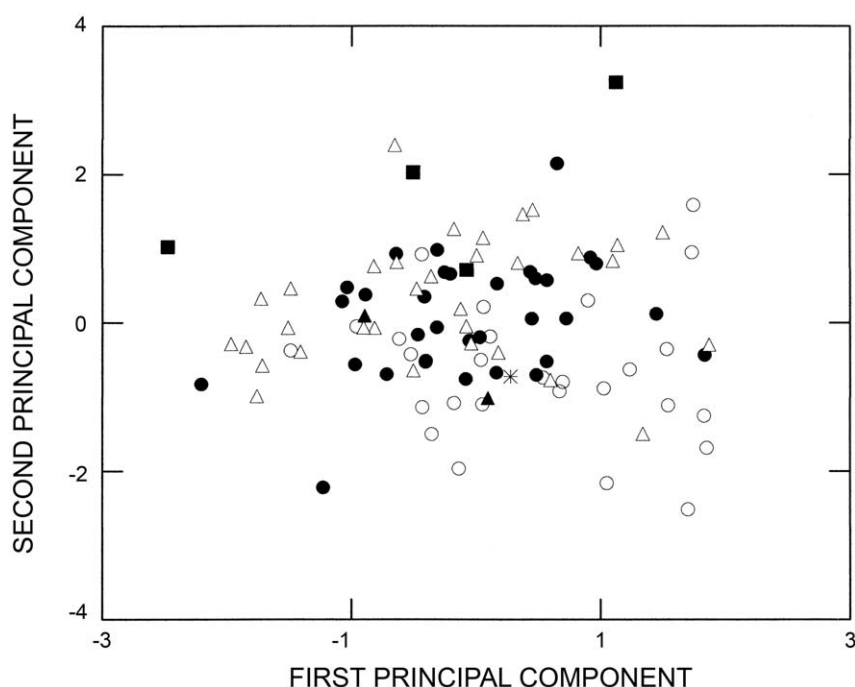
Fig. 58. Specimen scores representing six population samples of *Bunomys fratrorum* projected onto first and second principal components extracted from principal-components analysis of 16 cranial and two dental log-transformed variables. Symbols: filled circles = Teteamoet ($N = 33$); empty circles = Kuala Prang ($N = 27$); filled triangles = Gunung Klabat ($N = 2$); asterisk = Rurukan ($N = 1$; holotype of *Mus fratrorum*); empty triangles = Temboan ($N = 33$); filled squares = Gunung Maujat + Gunung Mogogonipa ($N = 4$). Correlations (loadings) of variables with extracted components and percent variance explained are listed in table 46.

centor sp., *Haemaphysalis hystricis*, and *Haemaphysalis* sp. (Durden et al., 2008). In addition to *Bunomys fratrorum*, immatures of members of these three tick genera have been collected from a suite of other mammal hosts living in Sulawesi: shrews (the endemic *Crocidura* sp. and *Crocidura elongata*, and the commensal *Suncus murinus*), pigs (*Sus celebensis*, endemic, and the domestic *Sus scrofa*), rusa (*Rusa timorensis*, nonnative), water buffalo (*Bubalus bubalis*, nonnative), domestic dog (nonnative), three endemic squirrels (*Rubrisciurus rubriventer*, *Hyosciurus heinrichi* and *H. ileile*), 12 species of endemic murid rodents (*Bunomys chrysocomus* and *B. andrewsi*; *Margaretamys beccarii*; *Echiothrix centrosa*; *Maxomys hellwaldii*, *M. musschenbroekii*, and *M. wattsi*; *Paruromys dominator*; *Taeromys* sp.; *Rattus hoffmanni*, *R. xanthurus*, and *R. facetus* [recorded as *R. marmosurus*]), and four nonnative murines

(*Mus musculus*; *Rattus tanezumi* [recorded as *R. rattus*], *R. argentiventer*, and *R. exulans*); whereas adults have been recorded from pigs (*Sus celebensis*, *Sus scrofa*), rusa (*Rusa timorensis*), water buffalo (*Bubalus bubalis*), and domestic dog (Durden et al., 2008).

Four species of chiggers (Acari: Trombiculidae) are known to parasitize *Bunomys fratrorum* (Goff et al., 1986; Goff and Durden, 1987; Whitaker and Durden, 1987). *Schoengastia sulawesiensis* is also found on *Maxomys musschenbroekii* and *Rattus hoffmanni*. *Walchiella oudemansi* also parasitizes *Bunomys chrysocomus* and the nonnative *Rattus exulans*). *Leptotrombidium deliense* has also been recorded from the endemic rats *Bunomys chrysocomus*, *Maxomys musschenbroekii*, *Paruromys dominator*, *Rattus hoffmanni*, and *Rattus xanthurus*. Finally, *Gahrliepia lupella* infests *Maxomys musschenbroekii* in addition to *Bunomys fratrorum*.

TABLE 46
Results of Principal-Components and Discriminant-Function Analyses Performed on All Population Samples of *Bunomys fratrorum*
Correlations (loadings) of 16 cranial and two dental log-transformed variables are based on 100 *B. fratrorum*; see figures 58 and 59.

	Correlations			
Variable	PC1	PC2	CV1	CV2
ONL	0.71***	0.18	0.26**	−0.03
ZB	0.78***	0.04	0.39***	−0.26**
IB	0.13	0.29**	−0.23*	−0.11
LR	0.54***	0.15	−0.20*	−0.27**
BR	0.74***	0.02	0.24*	−0.31***
BBC	0.32***	0.09	−0.05	−0.17
HBC	0.55***	−0.11	0.31**	−0.33***
BZP	0.68***	0.40***	0.12	0.10
LD	0.65***	0.30**	−0.07	0.01
PPL	0.62***	0.02	0.51***	0.06
LBP	0.06	0.72***	−0.62***	0.24*
BBP	0.68***	−0.000	−0.01	−0.28**
BMF	0.38***	−0.66***	0.01	−0.57***
LIF	0.49***	−0.53***	0.62***	−0.52***
BIF	0.48***	−0.37***	0.18	−0.34***
LB	0.34***	0.17	−0.02	−0.17
CLM1–3	0.04	0.13	0.13	0.01
BM1	−0.13	−0.18	0.25**	−0.27**
Canonical correlation			0.865	0.693
Eigenvalue	0.013	0.007	2.960	0.924
% Variance	28.8	15.7	52.2	17.3

*** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

SYNONYMS: No other scientific names have been proposed that apply to *B. fratrorum*.

Bunomys andrewsi, the next species to be discussed, is not all that different from *B. fratrorum* in fur color and physical size, but judged by dimensions of the skull and molars is phenetically more like the montane *B. penitus* than *B. fratrorum* (see fig. 21), and has been recorded only from the southern half of Sulawesi where it occurs primarily in tropical lowland evergreen rain forest.

Bunomys andrewsi (Allen, 1911)

Mus andrewsi Allen, 1911: 336.
Rattus adspersus Miller and Hollister, 1921a: 71.
Rattus penitus inferior Tate and Archbold, 1935a: 6.
Rattus penitus heinrichi Tate and Archbold, 1935a: 6.

HOLOTYPE: USNM 175899, the skin and skull of an old adult male (original

number 25) collected December 13, 1909, by R.C. Andrews. In the original description, Allen (1911: 336) referred to the holotype as 32193. That is a misprint for 31293, which is the number given to the specimen by staff at the American Museum of Natural History, where it was initially deposited and cataloged. Standard external measurements, other relevant data, and measurements of the skull and dentition are listed in table 40. The skin is overstuffed but intact, the cranium and mandible are complete except for missing hamular processes in the pterygoid region, all incisors and molars are present (fig. 60).

TYPE LOCALITY: Pulau Buton (05°00′S, 122°55′E; locality 23 in the gazetteer and on the map in fig. 50) southeastern region of Sulawesi, Propinsi Sulawesi Tenggara, Indonesia.

EMENDED DIAGNOSIS: A member of the *B. fratrorum* group resembling the other species in that assemblage in body size (LHB = 137–195 mm, WT = 95–222 g, ONL = 37.1–45.5 mm) and further characterized by the following combination of traits: (1) a relatively long muzzle and broad face, and stocky body; (2) dorsal fur dense, lustrous, dark brown speckled with buff and black, ventral fur grayish white to buffy gray or ochraceous gray, digits white, dorsal surfaces of carpal and metacarpal regions typically white, range from grayish white to grayish buff in some samples; (3) claws on front feet short but not as short and delicate as in *B. penitus*, scanty ungual tufts at bases of front and hind claws; (4) tail shorter than length of head plus body (LT/LHB = 75%–92%), dark brown on dorsal surface, white through mottled brown to solid brown on ventral surface (5) white tail tip uncommon (characterizes 20% of 127 specimens) and when present is short relative to tail length (mean = 7.7%, range = 1%–13%); (6) testes moderately small relative to body size (8%–15%); (7) shape of sperm head similar to that of *B. chrysocomus* but shorter and slightly wider; (8) robust skull with a moderately long and narrow rostrum, wide upright zygomatic plate, long incisive foramina (actually and relative to length of skull), and moderately large ectotympanic bulla relative to skull size; (9) molars moderately large relative to size of skull and mandible; (10) cusp t3 occurs frequently on second upper molar (78%) in
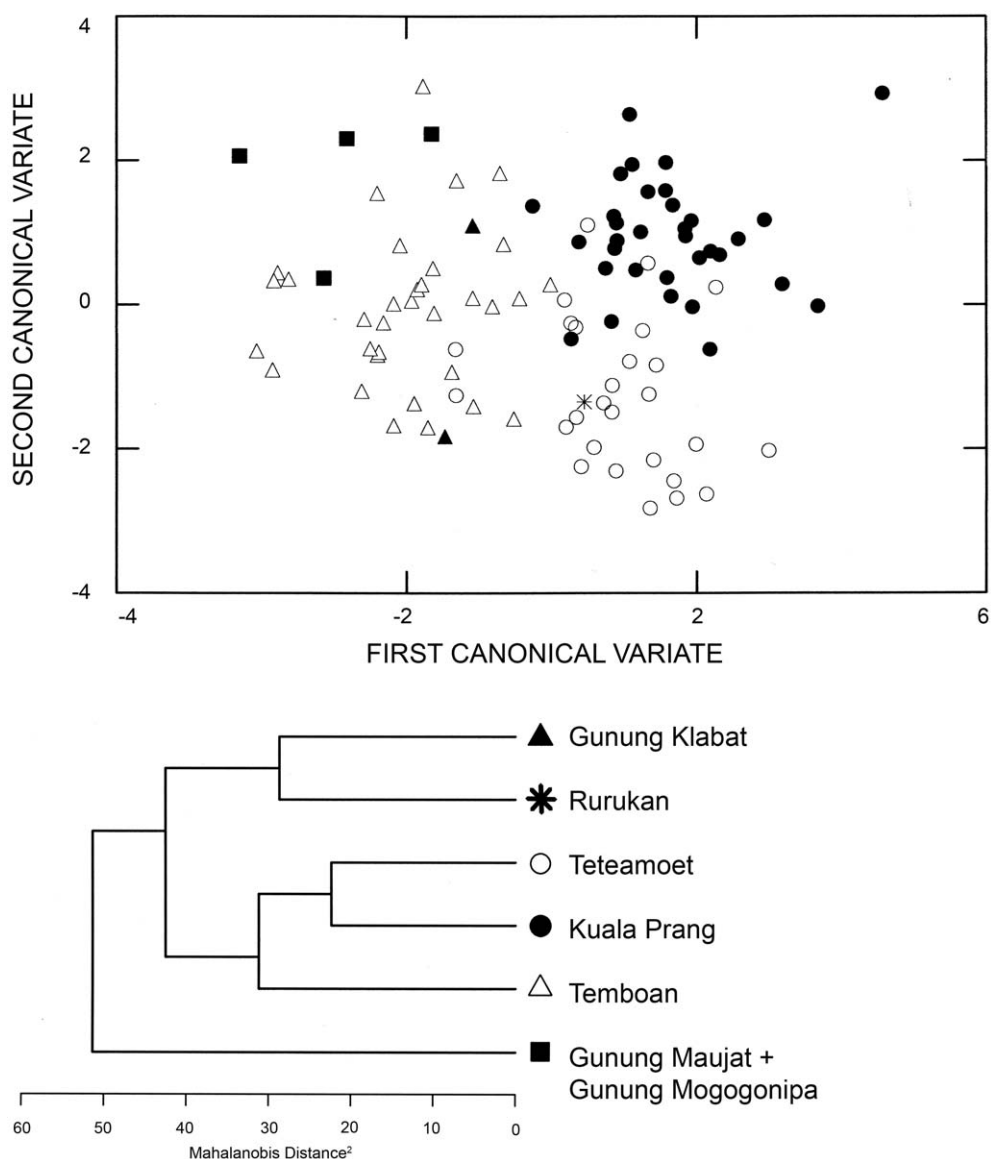
Fig. 59. Upper graph: Individual specimen scores projected onto first and second canonical variates extracted from discriminant-function analysis of of 16 cranial and two dental log-transformed variables derived from six population samples of *B. fratrorum*. Symbols: filled circles = Teteamoet (*N* = 33); empty circles = Kuala Prang (*N* = 27); filled triangles = Gunung Klabat (*N* = 2); asterisk = Rurukan (*N* = 1; holotype of *Mus fratrorum*); empty triangles = Temboan (*N* = 33); filled squares = Gunung Maujat + Gunung Mogogonipa (*N* = 4). See table 46 for correlations (loadings) of variables with extracted canonical variates and for percent variance explained. Lower diagram: Pattern of phenetic relationships among six population samples of *Bunomys fratrorum* derived from UPGMA clustering of squared Mahalanobis distances among group centroids that was derived from discriminant-function analysis.

sample from southwestern peninsula but infrequently (17%) elsewhere; (11) anterolabial cusp characteristically present on second lower molar (94% of sample) but occurs infrequently on third lower molar (18%); (12) anterior labial cusplets typically absent from first lower molars, posterior labial cusplets typically present on first and second molars;

Fig. 60.   The holotype of *Bunomys andrewsi* (USNM 175899), an old adult male from Pulau Buton, off the southern coast of the southeastern peninsula. ×2.

and (13) karyotype, 2N = 42, FNa = 56, FNt = 58.

GEOGRAPHIC AND ELEVATIONAL DISTRI-BUTIONS: Labuan Sore (00°37′S, 120°03′E) at the southern terminus of the northern penin-sula is the northernmost record of *B. andrewsi*. South of there voucher specimens indicate the species occurs in lowlands and

mountains of Sulawesi's core, on the eastern peninsula, the two southern peninsulas, and on Pulau Buton off the coast of the southern margin of the southeastern peninsula (see the map in fig. 50).

Reliable elevations associated with each specimen document 30 m to 1600 m as the range in which most collections have been

made. The upper limit is anchored by animals recently collected by Kevin Rowe (Museum Victoria) and Anang Achmadi (Museum Zoologicum Bogoriense) from the Mamasa area on Gunung Gandangdewata (see the gazetteer and table 6). Most of the specimens reported from there are from tropical lowland evergreen rain forest, but some were taken in the transition between lowland evergreen and montane forest habitats.

Collections of small mammals from the northern peninsula north of Labuan Sore (at the base of the peninsula) do not contain examples of *Bunomys andrewsi*. The narrow stretch of coastal lowlands and mountains between Labuan Sore and the northwest curve of the peninsula has not been adequately (if at all) surveyed for small mammals; whether *B. andrewsi* occurs there is unknown. The remainder of the northern peninsula, however, has been surveyed periodically by different collectors dating from the late 19th century and into the 20th century (the Sarasins, G. Heinrich, H.C. Raven, and J.J. Menden, for example), but no collections made then, some of which are large in number of specimens and diversity of taxa, include *B. andrewsi*. The northeastern section of the northern peninsula, that stretches east of the Gorontalo region, has been the focus of relatively intense collecting efforts by Dutch, English, German, Indonesian, and North American naturalists, and only *B. fratrorum* and *B. chrysocomus* have been documented from this region (see the gazetteers and distribution maps for these species).

The peninsular neck between Palu and Parigi, where Labuan Sore is located, may approximate the natural northern range boundary for *B. andrewsi*. That region is the southern limit for the geographic distribution of the tree squirrel, *Prosciurillus leucomus* (at Bumbarujaba, 00°43′S, 120°04′E; Musser et al., 2010) and confluence of the ranges for the northern peninsular *Macaca hecki* and southern Sulawesi *Macaca tonkeana* (Fooden, 1969; Watanabe et al., 1991; Bynum et al., 1997; Groves, 2001). Results of future surveys for small mammals in this southern region of the northern peninsula would be most revealing.

SYMPATRY WITH OTHER *BUNOMYS*: Except for *B. fratrorum*, which is restricted to the northeastern end of the northern peninsula and is sympatric only with *B. chrysocomus* (see that account), the ranges of all other species of *Bunomys* fall within the broad geographic distribution for *B. andrewsi* (table 6). But little or no overlap (syntopy) characterizes the ranges of *B. andrewsi* and the other species. The usual pattern has populations of *B. andrewsi* occurring in lowlands and those of other species existing at higher elevations (elevationally parapatric). Three pairs of distributions form examples. At the western margin of the eastern peninsula, *B. andrewsi* has been collected in the lowlands (Sungai Ranu, 50–100 m) and *B. chrysocomus* and *B. prolatus* only much higher on the adjacent Gunung Tambusisi (1372–1830 m). On the western side of the southeastern peninsula, *B. andrewsi* is documented from Wawo and Masembo in lowlands (50–550 m) adjacent to Pegunungan Mekongga, and *B. penitus* and *B. chrysocomus* are found in montane forest on that mountain (1500–2000 m). *Bunomys andrewsi* and *B. coelestis* are found on Gunung Lompobatang at the southern end of the southwestern peninsula where *B. andrewsi* was collected on the lower flanks up to 1100 m and *B. coelestis* higher on the volcano between 1830 and 2500 m.

Certain collections of *B. andrewsi* and *B. chrysocomus* provide the only reliable syntopic distributional records between the former and any other species of *Bunomys* (table 20). Both species were collected in the northern part of the west-central mountain block at Bakubakulu, 600 m, in the Puro Valley. Along my transect between 290 and 675 m I collected examples of each in the same trapline. I did not encounter *B. andrewsi* at higher elevations where *B. chrysocomus* was common. Subfossil remains of both species have been excavated from Ulu Leang I, a cave on the coastal plain at the southern end of the southwestern peninsula (see the account of *B. chrysocomus* for additional information covering distributional sympatry or overlap between that species and *B. andrewsi*).

Bunomys andrewsi and *B. penitus* are regionally sympatric in the west-central mountain block but generally occur at

contrasting elevations and forest formations. Most samples of *B. andrewsi* were obtained through an elevation range extending from about 100 to 1000 m and were caught in habitats associated with tropical lowland evergreen rain forest. *Bunomys penitus* is tied to montane forests: 1285–2287 m brackets the elevations at which samples were collected. There are no reliable records that document collection of the two species at the same place (syntopic).

Bunomys andrewsi is locally sympatric with *B. penitus* and *B. torajae* on Gunung Gandangdewata in the Quarles Range in the southern part of the west-central mountain block. *Bunomys penitus* and *B. torajae* were encountered in montane habitats between 2000 m and 2600 m, *B. andrewsi* was collected at 1600 m in tropical lowland rain forest.

DESCRIPTION: The original description of *Mus andrewsi*, obviously named after the collector, is based on two specimens, an old adult and a young adult. The older one is the holotype and Allen (1911: 336) described it as follows:

> Fur long and soft, without spines. General color of the whole dorsal region cinnamon rufous finely grizzled with black-tipped and white-tipped hairs, the former prevailing, the hairs being grayish plumbeous at base darkening to blackish and broadly ringed subapically with pale rufous, and for the most part tipped narrowly with black, mixed with many wholly black-tipped hairs and a few light-tipped hairs; sides of the body similar in color to the back but much lighter; ventral surface whitish gray, the hairs darker but still light gray basally; top of head to nose like the back or slightly lighter; limbs like the sides of the body; feet flesh-colored, scantily clothed with short glistening white hairs; ears large, naked, much longer than broad, dark brown above and on sides, flesh color below and all around at the extreme tip.

Allen then provided some measurements, noted a few features of the younger specimen and remarked that

> This species has many points of resemblance to *Mus luzonensis* Thomas, not only in coloration and proportions but in cranial characters. The type shows a tendency to albinism through the presence of scattered white hairs and one or two small bunches of white hairs on the back, and

an irregular submedian line of wholly white hairs on the ventral surface.

Adult *Bunomys andrewsi* has a broad head, unpigmented rhinarium and lips, a stocky body, and in physical size (LHB = 137–195 mm, LT = 110–167 mm, LHF = 35–44 mm, LE = 22–30 mm, W = 95–222 g, ONL = 37.1–45.5 mm) resembles the other members of the *B. fratrorum* group (see the portrait of *B. andrewsi* in fig. 6). The dorsal coat is soft and moderately long (12–15 mm long on specimens taken in lowlands, up to 20 mm on rats from higher elevations). Guard hairs barely project beyond the over-hair layer so the surface of the coat appears smooth; the texture is similar to that in *B. chrysocomus*. Overall color is a rich dark brown or brownish gray speckled with buff and black (underfur is gray and tipped with pale buff, overhairs are gray basally and tipped with buff, guard hairs provide the black peppering). Sides of the body are slightly paler but show more rusty and buffy highlights. Forearms are the same color as sides of body, except for a grayish brown to dark brown area 8–10 mm behind the wrist that contrasts with the metacarpal surfaces and grayish underparts.

The demarcation between coloration of dorsal and ventral coats is subtle in some animals where the underparts are dark buffy or ochraceous gray, but conspicuous in others where the ventral coat is primarily grayish white. Coloration of underparts is individually variable, but a similar chromatic range can be found in all large samples. At one end of the range is the darkest, dark grayish white (hairs are dark gray for most of their lengths, unpigmented at their tips) or dark grayish buff (hairs have buffy tips), which occurs most frequently in highland samples. The other extreme is pale grayish white or pale grayish-buff underparts (hairs are pale gray with either unpigmented or buffy tips), and predominates in lowland samples. In any large lowland series, the venter coloration is broken by white or buff strips on the chest, along the midventral region in some specimens, at the inguinal area in others. Two specimens from Lombasang are brighter than any of the total specimens I have studied, one has bright

buffy gray underparts, the other bright ochraceous-gray ventral fur. On many specimens in samples from low elevations (Pinedapa, Kuala Nausu, Sungai Ranu, Masembo, and Wawo) there are dense orange or rusty patches or strips on the throat and chest, or the inguinal region, or scattered over the abdomen. One adult from Kuala Navusu has a cream venter slightly suffused with pale gray and is rusty around the chin and throat and pale rusty over the neck and chest.

Two samples from about 1000–1500 m deserve additional attention. Except for two specimens, underparts in the sample from Lombasang on the southwestern peninsula show the range in coloration typically seen in series from other places and lower elevations, but just darker: dark grayish white to grayish buff. Two rats have brighter coats, one is buffy gray everywhere, the other ochraceous gray. No specimen in the sample has rusty patches. Specimens in the sample from the Mamasa region (locality 19 in the gazetteer and on the map in fig. 50) have a thicker dorsal coat (15–20 mm) that is darker than lowland samples (the overhairs and their gray segments are longer, imparting a darker tone to the pelage) and darker than the Lombasang series. Underparts are also dark, ranging from dark grayish white to dark grayish buff, and two rats exhibit rusty patches on the neck and chest, similar to the pattern in lowland samples; otherwise, the only difference between this series and those from lower altitudes is the longer, darker pelage.

Ears (external pinnae) are moderately large and appear naked but are covered in short, fine, and unpigmented hairs. In life, the ears have a rubbery texture and are pigmented with gray and brown hues—the range extends from dark gray through brownish gray to dark brownish gray. The dried ears of stuffed museum skins have lost the rubbery texture of the live animal and dried to dark brown with no hint of the actual range in hue and tone.

A tail shorter than the combined length of head and body (LT/LHB = 75%–92%) is typical for *B. andrewsi*, and the tail is relatively shorter than in samples of the other three species in the *B. fratrorum* group (table 41). Grayish brown to very dark brown is the range over the dorsal surface of the tail. The ventral surface exhibits the range from all white (from base to tip, and the tail appears conspicuously dorsoventrally bicolored) to monocolored brown or brownish gray. Intermediate variations range from tails that are gray or tan along the ventral surface to surfaces that are mottled pale grayish brown (all of each scale with brown pigment) or speckled with brown (pigment in center of scale). In most samples, the brown on the dorsal surface extends to the tail tip and individuals showing a white tip are uncommon (20% of 133 specimens), and when present the white tip is short relative to length of tail (mean = 7.7%, range = 1%– 13%; see table 8). The gray cast to the dorsal surface of the tail is evident in freshly caught rats, but is lost in the dry study skins where the dorsal surfaces appear brown.

Front and hind feet are long and slender. Front and hind digits are white, dorsal carpal and metacarpal surfaces are white, white lightly speckled with brown (hairs are brown at tips), or white speckled with brownish orange. The naked palmar and plantar surfaces are either unpigmented or show gray or pale brown tones. Claws are unpigmented, those on the front digits are, relative to lengths of the digits, about the same size as in *B. fratrorum* and larger than the delicate claws of *B. penitus*; a sparse ungual tuft springs from the base of each front and hind claw.

Females have four teats, arranged in two inguinal pairs, the number of teats common to all species of *Bunomys*. The scrotal sac of males is gray and sparsely haired (appears naked), and the testes are small relative to body size (8%–15%; see table 9). Description of gross spermatozoal morphology is provided by Breed and Musser (1991).

The dorsal coat of juveniles is shorter (up to 10 mm long) than that of adults, the hairs are finer, and the overall color is darker, without the buffy highlights of the adult coat. Underparts are grayish white. The range in coloration of the feet and tail matches that seen in samples of adults.

Bunomys andrewsi typically has a large skull with a long and narrow rostrum and a wide zygomatic plate (figs. 52–54, 60; tables 42, 51). The interorbit and braincase is moderately wide, the incisive foramina very

long (but their posterior rims remain anterior to front surfaces of the first molars), as is the wide bony palate. Each dentary is robust and similar in shape to those of the other species in the *B. fratrorum* group.

Moderately large molars with simple occlusal patterns are typical of *B. andrewsi* (fig. 61). The frequencies of cusp t3 are geographically variable. It is present on the second upper molar in only 17% of 70 specimens from the central core and rarely occurs on the third molar in that sample (4%). By contrast, cusp t3 is present on the second molar in 78% of 18 specimens from Lombasang on the southeastern peninsula and exists on the third molar in 22% of that sample (table 10). As in most other species of *Bunomys*, an anterior labial cusplet is absent from the first lower molar, but a posterior labial cusplet typically forms part of the chewing surfaces of both the first and second lower molars (fig. 57; table 11). An antero-labial cusp is present on the second lower molar in most specimens (94% of 71 individuals) but is less prevalent on the third molar (18% of 66 specimens).

KARYOTYPE: 2N = 42, FNa = 56 and FNt = 58, comprised of seven pairs of metacentric chromosomes, one pair of subtelocentrics, and 12 pairs of acrocentrics; the sex chromosomes are acrocentrics (table 12).

COMPARISONS: *Bunomys andrewsi* resembles the northeastern peninsular *B. fratrorum* in color of body fur, but the dissimilarities in the two species, as described in the account of *B. fratrorum*, are otherwise trenchant and no data suggests that samples of *B. andrewsi* are simply southern Sulawesi variants of *B. fratrorum*. In the Mamasa region, *B. andrewsi* and *B. torajae* are sympatric but elevationally separated, and morphologies of the two were contrasted in the account of *B. torajae*.

Outside of *B. fratrorum* and *B. torajae*, *B. andrewsi* requires comparison with three members of the *B. chrysocomus* group, and with *B. penitus* and *B. karokophilus,* n. sp., in the *B. fratrorum* group. Contrasts between *B. andrewsi* and *B. karokophilus,* n. sp., will take place in the account of the new species. Here I compare *B. andrewsi* first with *B. penitus*, then with *B.chrysocomus, B. coelestis,* and *B. prolatus*.

Bunomys andrewsi and B. penitus: The distribution of *B. penitus* takes in Pegunungan Mekongga on the southeastern peninsula and the montane forests in the west-central mountain block in Sulawesi's core (see the map in fig. 51). Samples of *B. andrewsi* describe a more expansive range: lowlands on the southeastern peninsula and Pulau Buton, lowlands at the western end of the eastern peninsula, low and middle elevations in the mountains of Sulawesi's core, and middle elevations at the southern end of the southwestern peninsula (see the map in fig. 50). I compare all these samples with those of *B. penitus*. Of the four taxa associated with *B. andrewsi*, two were described as subspecies of "*Rattus penitus.*" On the southeastern peninsula, the samples of *B. andrewsi* from Wawo and Masembo in lowlands immediately adjacent to Pegunungan Mekongga are geographically closest to the Mekongga population of *B. penitus*. This sample of *B. andrewsi* was described as "*Rattus penitus inferior*" by Tate and Archbold (1935a), "*inferior*" referring to what they viewed to be a lowland population of the montane *B. penitus.* "*Rattus penitus heinrichi*" was applied by Tate and Archbold (1935a) to the sample of *B. andrewsi* from the flanks of Gunung Lompobatang at the southern end of the southwestern peninsula. *Bunomys penitus* does not occur in montane habitats on that arm of Sulawesi; presumably, Tate and Archbold thought of "*heinrichi*" as a geographic form of the central Sulawesi *penitus*. Miller and Hollister's (1921a) "*Rattus adspersus*" is based on a sample of *B. andrewsi* from the northern lowlands of Sulawesi's core; *B. penitus* is common in montane habitats of that region. The two specimens on which "*Mus andrewsi*" (Allen, 1911) is based were collected on Pulau Buton where *B. penitus* does not occur.

Bunomys penitus is physically similar to *B. andrewsi*, averaging slightly longer in lengths of head and body and hind foot, but broadly overlapping in length of ear and mass (table 41). The greatest dimensional contrast between the two species involves tail length, which is absolutely longer in *B. penitus* (M = 159.8–171.8 mm) compared with *B. andrewsi* (mean = 111.5–156.8 mm) and longer relative to length of head and body (LT/
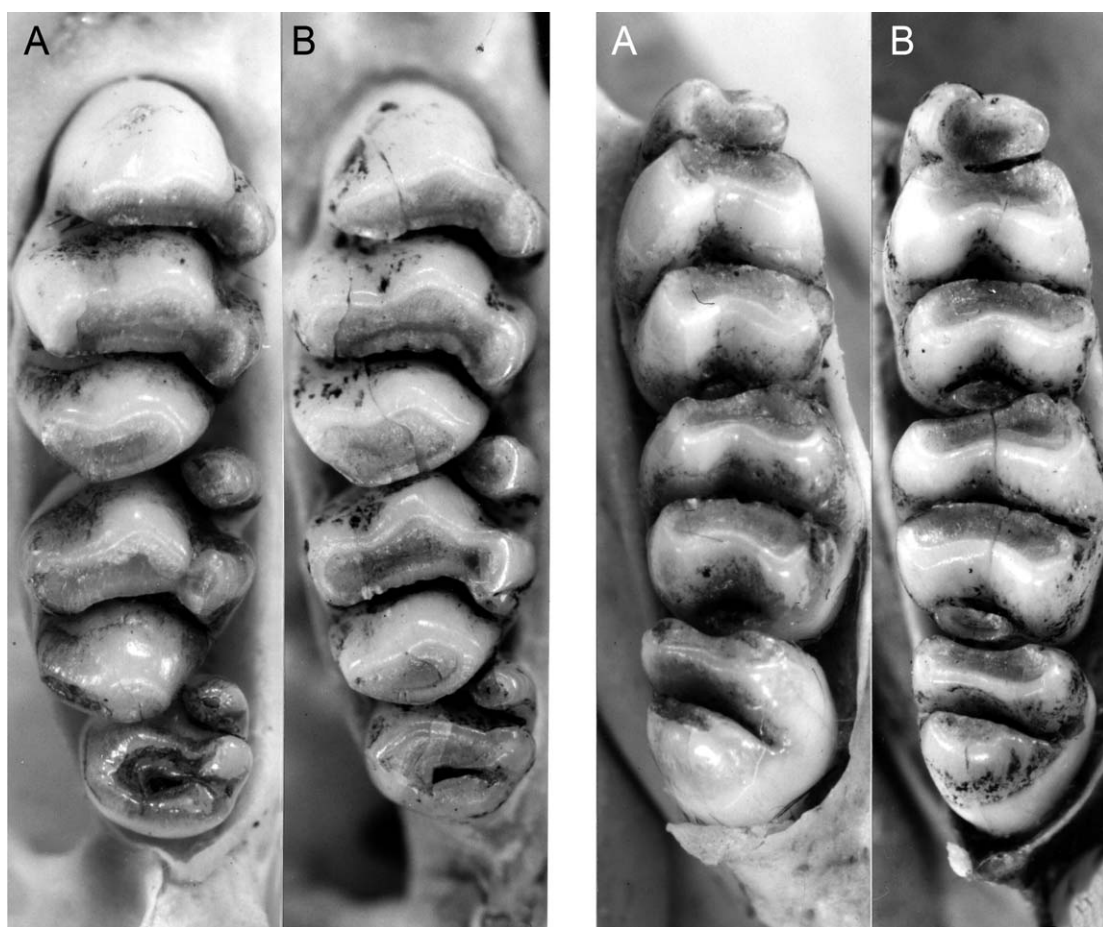
Fig. 61.   Occlusal views of right maxillary (left pair) and mandibular (right pair) molar rows from two specimens of *Bunomys andrewsi* collected at Kuala Navusu. **A**, very young adult showing slight wear (AMNH 225660; CLM1–3 = 7.1 mm, clm1–3 = 7.5 mm). **B**, typical degree of wear in an adult (AMNH 225659; CLM1–3 = 7.1 mm; clm1–3 = 7.4 mm). Note the absence of cusp t3 from the second upper molar, a configuration present in 83% of the specimens from Sulawesi's core (where Kuala Navusu is located) and southeastern peninsula, but not for the sample from the southwestern peninsula where cusp t3 occurs in 78% of the sample; cusp t3 typically occurs at a low frequency on the third upper molar in all samples (table 10).

LHB = 88%–102% for *B. penitus*, 75%–92% for *B. andrewsi*). The montane species clashes with the lowland form in its soft, long (up to 25 mm) and silky brownish-gray to grayish-brown dorsal pelage (dorsal coat up to 12 mm thick in most examples of *B. andrewsi*, soft but not silky, dark brownish gray tinged with bright buff); grayish white ventral coat (underparts in *B. andrewsi* are dark grayish white, grayish buff, or gray washed with brighter ochraceous hues); its tail that is grayish brown to brownish gray on the dorsal surface behind a white tip, and pure white over the ventral surface (brownish gray on top, ranges from white to brown below in *B. andrewsi*); and a white tail segment present in 98% of the sample that is long relative to tail length (mean = 21%, range = 3%–68%; a white tip is present in only 20% of the combined samples of *B. andrewsi* and when present is short relative to length of tail, mean = 7.7%, range = 1%–13%; table 8).

Size of testes relative to head and body (table 9) and gross spermatozoa morphology (Breed and Musser, 1991) differ between the two species. *Bunomys andrewsi* averages larger testes relative to body size (8%–15% for four samples) than does *B. penitus* (9%; the sample is from the west-central mountain block; I have not seen fluid-preserved material from Pegunungan Mekongga). Both have an asymmetrical sperm head falciform in outline and a tail; the head is slightly longer, the apical hook much shorter, and the tail shorter in *B. penitus* (specimens from Gunung Kanino) than in *B. andrewsi* (an example from Kuala Navusu).

Both species have a 2N of 42, but different fundamental numbers (FNa = 56 and FNt = 58 for *B. andrewsi*, FNa = 58 and FNt = 60–61 for *B. penitus*; table 12).

The skull averages longer in samples of *Bunomys penitus* compared with population samples of *B. andrewsi*, and univariate means for all but six cranial and dental dimensions are also greater in *B. penitus* (table 42). By contrast, breadth across the zygomatic arches is less in *B. penitus* than in *B. andrewsi*, and its zygomatic plate is appreciably narrower. Postpalatal length and length and breadth of the incisive foramina are the same in the two species. See the skull illustrations for visual appreciation of these dimensional similarities and differences (figs. 52–54).

Specimen scores projected on first and second principal components provides a graphic quantitative summary of differences among the cranial and dental variables (fig. 62, upper graph). Covariation in nearly all variables, as expressed by their high and positive correlation coefficients (r = 0.42–0.79; table 47), is responsible for the presence of two clusters with very narrow overlap situated along the first axis, scores for the larger skulls of *B. penitus* to the right, scores for the smaller *B. andrewsi* to the left. Particularly influential values reflect the appreciably longer and wider rostrum of *B. penitus*, its longer bony palate, wider mesopterygoid fossa, larger bullae, and heavier molars. Negative loadings for breadths of zygomatic plate and bony palate indicate how much narrower, absolutely and relative to skull size, are these dimensions in *B. penitus* compared with *B. andrewsi*.

The distribution of scores in the ordination affirms identities of the holotypes (and by extension the sample of which each is a part) associated with each species. Scores for holotypes of ''*Rattus penitus inferior*'' and ''*Rattus penitus heinrichi*'' fall within the constellation representing all population samples of *Bunomys andrewsi*, as are the points for holotypes of ''*Rattus adspersus*'' and ''*Mus andrewsi*.'' Holotypes of ''*Rattus penitus*'' and ''*Rattus sericatus*'' are indicated by two scores in the center of the cloud of points defining *B. penitus*.

There are three qualitative dental distinctions between *B. andrewsi* and *B. penitus*. The first is the absence of a large labial cusplet adjacent to cusp t6 on the first upper molar in all examples of *B. andrewsi* I examined; such a cusp is found in 30% of the sample of *B. penitus* (fig. 75). Second is the frequency of occurrence of cusp t3 on the second upper molar (table 10), which is rare in most samples of *B. andrewsi* (17%; fig. 61) but relatively common in the sample of *B. penitus* (62%; fig. 75). Third is frequency of the anterolabial cusp on the second and third lower molars (table 11). That cusp forms part of the anterolabial margin of the second molar in most examples of *B. andrewsi* (94%) but is pesent in only about half the sample of *B. penitus* (55%); it is found infrequently on the third molar in the sample of *B. andrewsi* (18%) but is absent from all specimens surveyed of *B. penitus*.

***Bunomys andrewsi* and *B. chrysocomus*:** As documented by modern samples, both species are regionally sympatric at the southern end of the northern peninsula, the western margin of the eastern peninsula, the southeastern peninsula and Pulau Buton, and Sulawesi's core (see tables 6 and 20). Each has been taken in the same trapline in three places: the PuroValley at Bakubakulu, 600 m, and the valley of the Sungai Miu along Sungai Oha Kecil at 290 m and Sungai Sadaunta at 675 (see the account of *B. chrysocomus*). Both species are also recorded from the southern end of the southwestern peninsula where the comparative material consists of subfossils and modern specimens representing *B. andrewsi* and subfossils only for *B. chrysocomus*; no modern examples of *B. chrysocomus* have been collected anywhere on the south-
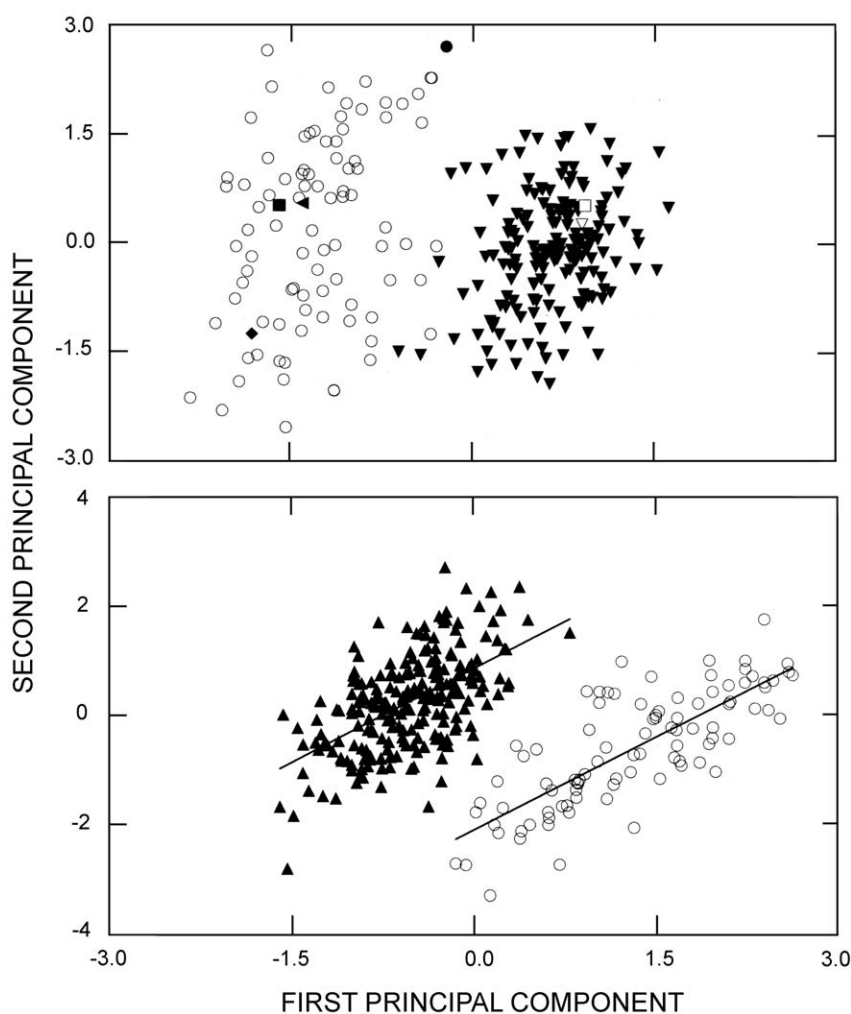
Fig. 62.   Specimen scores representing all population samples of *B. andrewsi* (empty circles; $N = 98$), *Bunomys penitus* (filled inverted triangles; $N = 185$), and *B. chrysocomus* (filled triangles; $N = 232$) projected onto first and second principal components extracted from principal-components analysis of 16 cranial and two dental log-transformed variables. Upper graph: *B. andrewsi* contrasted with *B. penitus*. Scores for holotypes associated with *B. andrewsi*: "*Rattus adspersus*" (filled square), "*Mus andrewsi*" (filled left-pointing triangle), "*Rattus penitus heinrichi*" (filled diamond), "*Rattus penitus inferior*" (filled circle). Scores for holotypes linked to *B. penitus*: "*Rattus penitus*" (hollow inverted triangle), "*Rattus sericatus*" (hollow square). Lower graph: *B. andrewsi* compared with *B. chrysocomus*. Equations for the regression lines are: *B. chrysocomus*, $Y = 1.140 \times 0.873$ ($F = 107.32$, $P = 0.000$); *B. andrewsi*, $Y = 1.075 \times -1.984$ ($F = 145.31$, $P = 0.000$). See table 47 for correlations (loadings) of variables with extracted components and for percent variance explained for both ordinations.

western peninsula south of the Tempe Depression (identified in fig. 1). Identity of the subfossils and their comparisons with *B. andrewsi* and subfossil examples of *B. chrysocomus* are discussed in a later section (see Subfossils).

Bunomys chrysocomus is physically smaller than *B. andrewsi*, averaging less in lengths of head and body, hind foot, ear, and mass (tables 19, 41). The tail of *B. chrysocomus* is typically shorter than that of *B. andrewsi* (mean range of population samples = 120.0–

TABLE 47
Results of Principal-Components and Analyses Comparing All Population Samples of *Bunomys andrewsi* with Those of *B. penitus* and *B. chrysocomus*
Correlations (loadings) of 16 cranial and two dental log-transformed variables are based on 98 *B. andrewsi*, 185 *B. penitus*, and 232 *B. chrysocomus*; see figure 62.

	Correlations			
	B. andrewsi and *B. penitus*		*B. andrewsi* and *B. chrysocomus*	
Variable	PC1	PC2	PC1	PC2
ONL	0.68***	0.63***	0.90***	0.23***
ZB	−0.00	0.82***	0.91***	0.10
IB	0.29***	0.26***	0.55***	0.06
LR	0.79***	0.42***	0.81***	0.30***
BR	0.63***	0.52***	0.81***	0.24***
BBC	0.47***	0.26***	0.68***	−0.09
HBC	0.41***	0.37***	0.73***	−0.10
BZP	−0.71***	0.64***	0.77***	0.19***
LD	0.48***	0.73***	0.75***	0.37***
PPL	0.22***	0.76***	0.80***	0.31***
LBP	0.78***	0.15**	0.48***	0.32***
BBP	−0.18**	0.72***	0.41***	0.69***
BMF	0.80***	0.26***	0.60***	0.26***
LIF	0.20***	0.65***	0.90***	−0.30***
BIF	0.09	0.63***	0.88***	−0.21***
LB	0.51***	0.27***	0.35***	0.13*
CLM1–3	0.73***	0.10	0.84***	−0.34***
BM1	0.70***	−0.12*	0.73***	−0.38***
Eigenvalue	0.031	0.023	0.061	0.009
% Variance	37.8	28.5	60.3	9.2

*** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

142.7 mm for *B. chrysocomus*, mean range = 111.5–156.8 mm for *B. andrewsi*) but at the same time averages longer in relation to length of head and body (LT/LHB = 84%–98% for *B. chrysocomus*, 75%–92% for *B. andrewsi*).

Bunomys chrysocomus and *B. andrewsi* are not easily separated by color of fur and appendages, particularly in those places where examples of each were taken in the same trapline. Texture and length of the fur covering upperparts of head and body is similar in the two species. The coat is dark brownish gray in most examples of *B. chrysocomus* and only lightly speckled (buffy bands of the hairs are dull and short) while the pelage of *B. andrewsi* is brighter with more intense buffy and yellowish speckling (buffy bands are bright and wide); ears and tops of

the front and hind feet are similarly pigmented in both species. Some examples of *B. chrysocomus*—from Gunung Balease and Gunung Nokilalaki, for example—have very dark, brownish-black dorsal fur with muted speckling and are unlike nearly all examples of the brighter *B. andrewsi* (exceptions are the specimens from the Mamasa area that were trapped at 1500–1600 m and have much darker upperparts than is usual in most samples of *B. andrewsi*). Variation in color pattern of the tail is similar in the two species, a low percentage of specimens in samples of each have a white-tipped tail, and in both species that unpigmented segment is short relative to length of tail (table 8). *Bunomys chrysocomus* has longer, more gracile claws on the front feet.

While preserved specimens of each species can be difficult to distinguish, the living animals are easier: *B. chrysocomus* has a longer muzzle with an upturned snout in contrast to the broad face of *B. andrewsi* without an upturned rhinarium.

Sexually mature males can be separated by size of testes (table 9), which in *B. chrysocomus* are large relative to body size (mean length of testes/length of head and body = 22%), but in *B. andrewsi* are relatively smaller (8%–15%). This relative size disparity is strikingly evident in freshly caught animals where sexually mature examples of each species are taken at the same place.

Configuration of spermatozoa is similar in the two species, but the sperm head is shorter and wider in *B. andrewsi* (Breed and Musser, 1991).

Bunomys chrysocomus has a small skull and weak molars compared with *B. andrewsi*. Univariate mean values for all cranial and dental variables in combined population samples of *B. andrewsi* exceed univariate means for those dimensions in all the combined samples of *B. chrysocomus* (table 42). Similar metric distinctions exist in samples of each species obtained from most places where the two are regionally sympatric (table 48). The dimensional contrasts can be appreciated in the images of skulls of *B. chrysocomus* arranged in figures 16 and 99–101 with those of *B. andrewsi* portrayed in figures 52–54 and 99–101. Samples from the northern part of the west-central mountain

TABLE 48
Descriptive Statistics for Cranial and Dental Measurements (mm) Contrasting Particular Samples of *Bunomys chrysocomus* with Samples of *B. andrewsi*
Mean ±1 SD, and observed range (in parentheses) are listed.

| Variable | Pulau Buton | | Eastern peninsula | | Gunung Balease | |
	B. andrewsi	*B. chrysocomus* RMNH 21256	*B. andrewsi* Sungai Ranu	*B. chrysocomus* Gunung Tambusisi	*B. andrewsi*	*B. chrysocomus*
N	2	1	5	6	8	3
ONL	40.4 ± 2.62 (38.5–42.2)	36.9	44.0 ± 1.27 (41.9–45.0)	38.3 ± 1.34 (35.8–39.5)	42.8 ± 1.33 (40.3–44.8)	40.2 ± 0.23 (40.1–40.5)
ZB	19.5 ± 0.64 (19.0–19.9)	—	20.9 ± 0.16 (20.7–21.1)	17.8 ± 0.61 (17.1–18.4)	21.1 ± 0.74 (19.7–21.9)	18.8 ± 0.17 (18.7–19.0)
IB	6.6 ± 0.07 (6.5–6.6)	6.0	6.5 ± 0.13 (6.3–6.6)	6.5 ± 0.25 (6.1–6.8)	7.0 ± 0.19 (6.7–7.3)	6.9 ± 0.27 (6.7–7.2)
LR	13.8 ± 1.06 (13.0–14.5)	—	15.7 ± 1.05 (14.3–17.1)	13.3 ± 0.70 (12.4–14.1)	15.4 ± 0.60 (14.6–16.1)	14.2 ± 0.45 (13.7–14.6)
BR	7.6 ± 0.64 (7.1–8.0)	6.1	8.0 ± 0.46 (7.4–8.7)	6.5 ± 0.48 (5.6–6.9)	7.9 ± 0.46 (7.5–8.9)	7.0 ± 0.20 (6.8–7.2)
BBC	15.8 ± 0.21 (15.6–15.9)	15.0	16.5 ± 0.34 (16.1–16.8)	15.6 ± 0.42 (15.1–16.2)	16.6 ± 0.39 (15.8–17.1)	16.2 ± 0.21 (16.0–16.4)
HBC	11.0 ± 0.28 (10.8–11.2)	11.0	11.8 ± 0.29 (11.5–12.2)	10.14 ± 0.26 (10.3–11.0)	11.7 ± 0.48 (11.1–12.2)	11.5 ± 0.55 (11.0–12.1)
BZP	3.5 ± 0.42 (3.2–3.8)	2.7	4.1 ± 0.29 (3.9–4.6)	2.9 ± 0.08 (2.8–3.0)	4.2 ± 0.34 (3.4–4.5)	3.0 ± 0.30 (2.7–3.3)
LD	10.6 ± 1.06 (9.8–11.3)	9.5	12.0 ± 0.46 (11.5–12.5)	10.5 ± 0.55 (9.6–11.1)	11.4 ± 0.67 (10.1–12.2)	10.8 ± 0.20 (10.6–11.0)
PPL	14.3 ± 0.99 (13.6–15.0)	13.5	15.2 ± 0.60 (14.4–16.0)	13.2 ± 0.49 (12.3–13.6)	15.0 ± 0.79 (13.7–16.0)	13.9 ± 0.27 (13.7–14.2)
LBP	8.1 ± 0.71 (7.6–8.6)	7.1	8.9 ± 0.78 (7.8–9.9)	7.6 ± 0.48 (6.7–8.1)	8.1 ± 0.34 (7.7–8.7)	8.2 ± 0.06 (8.1–8.2)
BBP	3.8 ± 0.35 (3.5–4.0)	3.1	3.9 ± 0.35 (3.6–4.1)	3.5 ± 0.22 (3.2–3.8)	4.1 ± 0.22 (3.8–4.5)	3.9 ± 0.21 (3.7–4.1)
BMF	2.9 ± 0.21 (2.7–3.0)	2.6	3.5 ± 0.28 (3.2–3.8)	2.7 ± 0.21 (2.4–2.9)	3.1 ± 0.18 (2.9–3.4)	3.0 ± 0.21 (2.8–3.2)
LIF	7.3 ± 0.00	6.3	8.5 ± 0.66 (7.8–9.5)	6.7 ± 0.26 (6.5–7.2)	8.2 ± 0.41 (7.6–8.6)	6.0 ± 0.35 (5.7–6.4)
BIF	2.8 ± 0.28 (2.6–3.0)	2.4	3.1 ± 0.15 (2.9–3.3)	2.3 ± 0.12 (2.2–2.5)	3.0 ± 0.11 (2.8–3.1)	2.4 ± 0.00
LB	7.3 ± 0.21 (7.1–7.4)	6.9	6.6 ± 0.23 (6.3–6.9)	6.5 ± 0.19 (6.2–6.7)	6.6 ± 0.24 (6.3–6.9)	6.6 ± 0.27 (6.4–6.9)
CLM1–3	7.2 ± 0.28 (7.0–7.4)	5.9	7.4 ± 0.22 (7.1–7.6)	6.3 ± 0.21 (5.9–6.5)	7.6 ± 0.24 (7.3–8.0)	6.2 ± 0.10 (6.1–6.3)
BM1	2.2 ± 0.21 (2.0–2.3)	2.1	2.3 ± 0.06 (2.2–2.3)	2.0 ± 0.12 (1.8–2.1)	2.4 ± 0.08 (2.3–2.5)	2.1 ± 0.00

block are an exception because the *B. andrewsi* from there are smaller in body size and the range of variation in some of the cranial variables overlaps in samples of the two species; this contrast will be amplified in a later section.

Morphometric distinctions between *B. chrysocomus* and samples of *B. andrewsi* are summarized by a scatter plot containing specimen scores projected onto first and second principal components where they form two oblique elliptical clouds, one representing *B. chrysocomus*, the other *B. andrewsi* (fig. 62, lower graph). Major axes of the elliptical spreads of scores are parallel, phenetically distinct: their Y-intercepts are significantly different between the two species (+0.873 versus −1.984; F = 117.57, P = 0.000), but their slopes are comparable (1.140 versus 1.075; F = 0.20, P = 0.652). Moderate to high

positive loadings for nearly all variables ($r = 0.42–0.91$; table 47) on the first component reflect size, scores representing *B. andrewsi* with the larger skulls and molars to the right, those for *B. chrysocomus* with the smaller skulls and molars to the left with overlap in the center of the scatter plot. Loadings for skull size (occipitonasal length and zygomatic breadth), length and breadth of the rostrum, size of braincase, breadth of zygomatic plate, lengths of diastema and the postpalatal region, expanse of the incisive foramina, and size of molars are especially influential in dispersing scores along the first axis. All these dimensions are less in *B. chrysocomus* (table 42), especially overall size of the skull, width of the zygomatic plate, size of the rostrum along with extent of the incisive foramina, and molar robustness, which form salient distinguishing landmarks readily appreciated in the images of skulls portrayed in the figures as well as in side-by-side comparisons of actual skulls.

Frequencies of a cusp and cusplet on lower molars differ between the two species (table 10). An anterior labial cusplet occurs on the first molar in half of the *B. chrysocomus* examined but is absent from all the specimens of *B. andrewsi* surveyed. The third molar bears an anterolabial cusp in 65% of the sample of *B. chrysocomus* but is present at a much lower frequency in the specimens of *B. andrewsi* (18% of the sample).

***Bunomys andrewsi* and *B. coelestis*:** *Bunomys coelestis* inhabits montane forests on Gunung Lompobatang where samples were collected between 1800 and 2500 m; *B. andrewsi* is found in tropical lowland evergreen rainforest at lower elevations on the volcano with the only large sample coming from Lombasang at 1100 m; the species is also documented by subfossils excavated from deposits in caves on the western coastal plain. *Bunomys andrewsi* and *B. coelestis* are contrasted here because individuals in the peninsular population of *B. andrewsi* on average are smaller in body size than those in other geographic samples of the species, and many cranial dimensions, compared to samples of *B. andrewsi* from elsewhere on the island are more similar to *B. coelestis* (tables 49, 51).

Bunomys coelestis is physically larger than animals in the peninsular sample of *B. andrewsi*, a difference reflected in its greater univariate means for lengths of head and body, tail, hind foot, and ear (compare the values for *B. coelestis* listed in table 19 with those for the sample of *B. andrewsi* from Lombasang in table 41). *Bunomys coelestis* has darker upperparts, a longer muzzle, and appreciably longer claws at the ends of the front digits.

Compared with *B. andrewsi* from Lombasang, *B. coelestis* typically has a longer but narrower skull (indexed by occipitonasal length and zygomatic breadth); wider interorbit; longer but narrower rostrum (elongate compared with the relatively stocky rostrum of *B. andrewsi*); wider zygomatic plate; longer diastema, longer and wider bony palate, and longer basicranial region (measured by postpalatal length); less spacious incisive foramina (shorter and narrower than the expanded foramina in *B. andrewsi*); smaller auditory bulla; and smaller molars (table 49). Size of the braincase (breadth and height) is comparable in the two species.

These contrasts in cranial and dental dimensions indicated by univariate mean values are summarized in a scatter plot where individual specimen scores are projected onto first and second principal components (fig. 63, upper graph). Two widely separated groups of scores represent *B. coelestis* in the right half of the ordination and *B. andrewsi* from Lombasang in the left, positions influenced by the longer skull of *B. coelestis* along with its longer rostrum and diastema, and longer and wider bony palate ($r = 0.42–0.76$; table 50). Moderate to high negative correlations ($r = -0.40$ to -0.88) point to the wider skull of *B. andrewsi* (indexed by zygomatic breadth) along with its broader rostrum and mesopterygoid fossa, longer and broader incisive foramina, larger bullae, and heavier molars as compared with *B. coelestis*, contrasts between the two species that are mirrored by univariate means (table 49).

***Bunomys andrewsi* and *B. prolatus*:** Samples of three species of *Bunomys* come from Gunung Tambusisi and adjacent lowlands in the western region of the eastern peninsula of Sulawesi. *Bunomys chrysocomus* and *B.*

TABLE 49
Descriptive Statistics for Cranial and Dental Measurements (mm) Contrasting Particular Samples of *Bunomys andrewsi* with Samples of *B. coelestis* and *B. prolatus*
Mean ± 1 SD and observed range (in parentheses) are listed.

	Southwestern peninsula		Eastern Peninsula	
Variable	*B. andrewsi* Lombasang	*B. coelestis* Gunung Lompobatang	*B. andrewsi* Sungai Ranu	*B. prolatus* Gunung Tambusisi
N	7	18	5	8
ONL	38.8 ± 0.82	40.2 ± 0.92	44.0 ± 1.27	41.8 ± 1.03
	(37.6–40.2)	(37.6–41.8)	(41.9–45.0)	(40.4–43.2)
ZB	19.2 ± 0.60	18.7 ± 0.64	20.9 ± 0.16	17.8 ± 0.38
	(18.1–19.9)	(17.2–20.4)	(20.7–21.1)	(17.2–18.3)
IB	6.4 ± 0.24	6.6 ± 0.24	6.5 ± 0.13	7.1 ± 0.23
	(6.2–6.9)	(6.2–7.2)	(6.3–6.6)	(6.9–7.4)
LR	14.0 ± 0.56	14.7 ± 0.56	15.7 ± 1.05	15.7 ± 0.61
	(13.0–14.8)	(13.6–15.7)	(14.3–17.1)	(14.7–16.4)
BR	7.1 ± 0.35	6.8 ± 0.47	8.0 ± 0.46	6.7 ± 0.36
	(6.7–7.6)	(5.7–7.6)	(7.4–8.7)	(6.1–7.1)
BBC	15.6 ± 0.35	15.7 ± 0.41	16.5 ± 0.34	16.3 ± 0.37
	(15.0–16.0)	(14.9–16.3)	(16.1–16.8)	(15.7–16.9)
HBC	11.7 ± 0.62	11.6 ± 0.24	11.8 ± 0.29	11.4 ± 0.19
	(11.2–13.0)	(11.1–12.1)	(11.5–12.2)	(11.0–11.6)
BZP	3.4 ± 0.24	3.6 ± 0.19	4.1 ± 0.29	2.8 ± 0.10
	(3.1–3.8)	(3.3–4.0)	(3.9–4.6)	(2.6–2.9)
LD	10.2 ± 0.30	12.1 ± 0.54	12.0 ± 0.46	11.5 ± 0.56
	(9.9–10.7)	(11.0–13.1)	(11.5–12.5)	(10.7–12.3)
PPL	13.8 ± 0.40	14.3 ± 0.53	15.2 ± 0.60	14.6 ± 0.51
	(13.2–14.3)	(13.1–15.2)	(14.4–16.0)	(13.8–15.2)
LBP	7.7 ± 0.31	8.1 ± 0.39	8.9 ± 0.78	8.7 ± 0.35
	(7.4–8.3)	(7.5–8.8)	(7.8–9.9)	(8.3–9.20)
BBP	3.3 ± 0.22	3.7 ± 0.20	3.9 ± 0.35	3.7 ± 0.15
	(2.9–3.5)	(3.3–4.0)	(3.6–4.1)	(3.4–3.9)
BMF	3.3 ± 0.22	2.8 ± 0.18	3.5 ± 0.28	2.8 ± 0.14
	(2.9–3.5)	(2.5–3.2)	(3.2–3.8)	(2.6–3.0)
LIF	7.6 ± 0.24	6.9 ± 0.36	8.5 ± 0.66	6.7 ± 0.29
	(7.2–7.9)	(6.5–7.7)	(7.8–9.5)	(6.3–7.1)
BIF	2.8 ± 0.20	2.2 ± 0.15	3.1 ± 0.15	2.3 ± 0.13
	(2.6–3.1)	(1.9–2.5)	(2.9–3.3)	(2.1–2.5)
LB	6.6 ± 0.24	6.3 ± 0.22	6.6 ± 0.23	6.9 ± 0.30
	(6.1–6.8)	(58–6.8)	(6.3–6.9)	(6.5–7.3)
CLM1–3	7.0 ± 0.27[a]	6.1 ± 0.23	7.4 ± 0.22	6.5 ± 0.17
	(6.6–7.3)	(5.7–6.6)	(7.1–7.6)	(6.3–6.8)
BM1	2.2 ± 0.08[a]	2.0 ± 0.10	2.3 ± 0.06	2.2 ± 0.09
	(2.1–2.3)	(1.8–2.1)	(2.2–2.3)	(2.0–2.3)

[a] These statistics were derived from the seven intact skulls of the 20 in the complete sample from Lombasang stored at AMNH. The molar row of 19 could be measured (6.9 ± 0.25, 6.5–7.3 mm), and all 20 could be measured for BM1 (2.2 ± 0.08, 2.0–2.3 mm).

prolatus were collected by C.H.S. Watts from slopes of the mountain (1372–1829 m), and he obtained *B. andrewsi* from adjacent lowland forest in the Sungai Ranu area (50 m). The large-bodied *Bunomys prolatus* could possibly be confused with *B. andrewsi*, which is also characterized by large body size in the Tambusisi region.

While *B. prolatus* and *B. andrewsi* are comparable in body size (estimated by length of head and body), *B. prolatus* has a much shorter tail (absolutely and relative to length

of head and body), shorter hind feet, but relatively larger ears (compare the measurements of *B. prolatus* listed in table 18 with those of *B. andrewsi* from Kuala Navusu, Pinedapa, and Wawo + Masembo listed in table 41; I lack external measurements for the sample from Sungai Ranu). As is typical of the contrast between montane and lowland populations, the lush dorsal coat of *B. prolatus* is soft and dense, 20–25 mm long; that of most *B. andrewsi*, and especially the rats from Sungai Ranu, are harsher and 12–15 mm long. The robust and very long front claws of *B. prolatus* (fig. 36) are unlike the weaker and short front claws, a conformation typical of specimens in all population samples of *B. andrewsi*.

The skull of *B. prolatus* has a gracile aspect to it compared with the stocky conformation that is usual for *B. andrewsi* (compare the images of *B. prolatus* in figs. 37–39 with those for *B. andrewsi* from Kuala Navusu portrayed in figs. 52–54). The more delicate cranial conformation in *B. prolatus*, so visually apparent in the cranial illustrations, is reinforced qualitatively by univariate means for cranial and dental variables where most dimensions average less than those for the sample of *B. andrewsi* from Sungai Ranu; exceptions are interorbital breadth and length of bullar capsule, which average greater in *B. prolatus* (table 49).

Contrasts among the cranial and dental variables are summarized in multivariate space by the scatter plot of specimen scores projected onto first and second principal components (fig. 63, lower graph). Aggregations of scores identifying the specimens of *B. prolatus* and those for *B. andrewsi* from Sungai Ranu are widely separated along the first axis, reflecting the general disparity in size as indicated by the large and positive loadings ($r = 0.45$–0.99; table 50) for all but two variables, which mirrors the contrasts in univariate means (table 49). The two high negative loadings are for interorbital breadth (-0.86) and length of bulla (-0.51), both absolutely and relatively greater in *B. prolatus* (table 49).

The long fur of *B. prolatus*, its robust and long front claws, elongate skull, wide interorbit, narrow zygomatic plate and mesopterygoid fossa, short and narrow incisive foramina, large bulla, and link to montane forest are strongly diagnostic compared with the larger-bodied *B. andrewsi* from the nearby lowlands.

GEOGRAPHIC VARIATION: There is conspicuous variation in body size among geographic samples of *B. andrewsi*. During 1974, I was trapping between 290 and 675 meters along the Sungai Oha Kecil, Sungai Miu, and Sungai Sadaunta in the northern part of the west-central region of Sulawesi and encountering mostly *B. chrysocomus*. Here and there another kind of rat showed up in the traps that in body size and fur color resembled *B. chrysocomus* but with a shorter muzzle. It was also similar to *B. andrewsi* but physically smaller than rats in samples of that species with which I was familiar. Later I worked in lowlands east of the west-central mountain block but not too distant from Pinedapa, the place where H.C. Raven collected a series of rats in 1918 that would subsequently be described by Miller and Hollister (1921a) as *Rattus adspersus*. Near my camp on Kuala Navusu, I caught what clearly looked to be *adspersus*. The rats resembled animals taken at the Sungai Oha Kecil, Sungai Miu, and Sungai Sadaunta (means for LHB = 163.1 mm and weight = 113.7 g for the Puro-Sungai Miu sample) but were larger in body size (LHB = 177.4 mm and weight = 154.6 for the sample from Kuala Navusu).

The difference registered by my two collections generally reflects the magnitude of variation in adult body size among all the samples of *B. andrewsi* I have studied (see table 41). Generally, large physical size characterizes specimens in the population samples from northeast–central core (Labuan Sore, Kuala Navusu, and Pinedapa), south–central core (Gunung Balease, Malili area, and Sukamaju), and the eastern + southeast peninsulas (Sungai Ranu, Wawo, and Masembo). Animals averaging smaller in body size form the population samples from lowlands and highlands in the west-central mountain block—northern west-central highlands (Puro-Sungai Miu, Tamalanti, and Tuare) and southern west-central highlands (Mamasa Area)—and the southwest peninsula (Lombasang).

To determine the geographic trends in body size, I relied on my measurements of
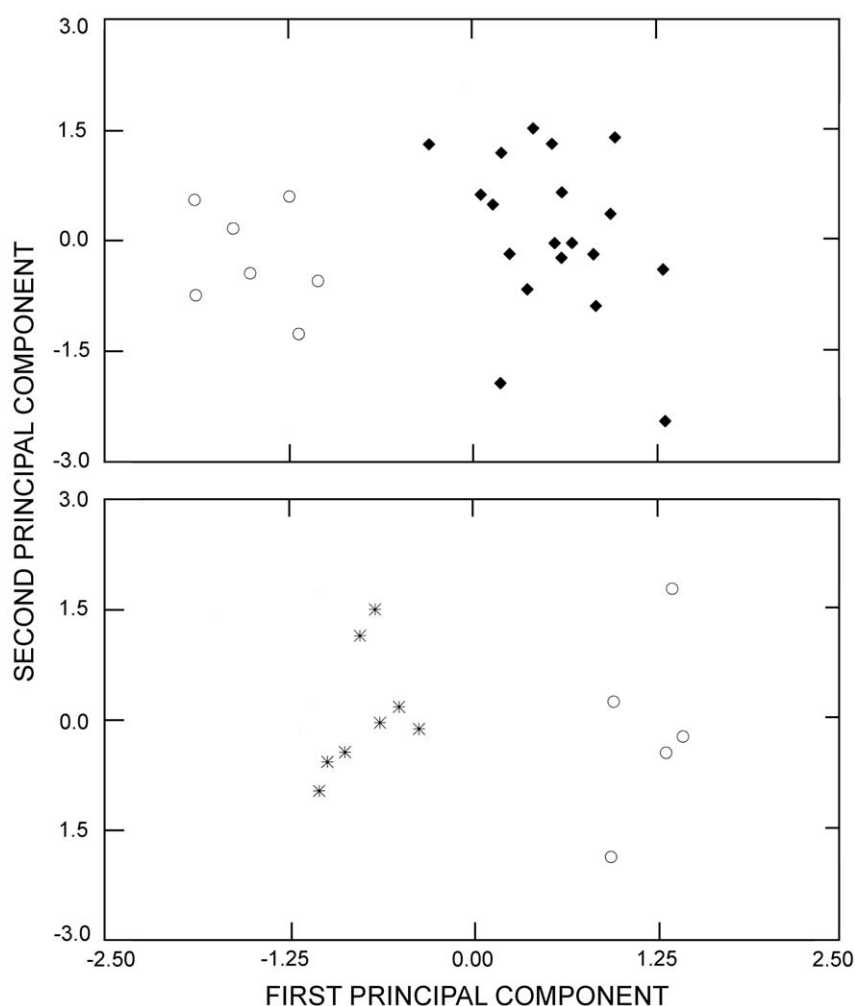
Fig. 63.   Specimen scores representing two geographic samples of *Bunomys andrewsi* and samples of *B. coelestis* and *B. prolatus* projected onto first and second principal components extracted from principal-components analysis of 16 cranial and two dental log-transformed variables. Upper graph: the sample of *B. andrewsi* (empty circles; *N* = 7) from Lombasang on the lower slopes of Gunung Lompobatang is contrasted with the sample of *B. coelestis* (filled diamonds; *N* = 19) from montane forest higher on the same volcano. Lower graph: the lowland sample of *B. andrewsi* from Sungai Ranu (empty circles; *N* = 5) at the western margin of the eastern peninsula is contrasted with the montane sample of *B. prolatus* from nearby Gunung Tambusisi (asterisks; *N* = 8). See table 50 for correlations (loadings) of variables with extracted components and for percent variance explained for both ordinations.

cranial and dental dimensions (measurements for head and body and appendages were made by different collectors who may or may not have utilized the same endpoints). Morphometric relationships among the population samples are summarized in the univariate descriptive statistics listed in table 51, results of principal-components and discriminant-function analyses (figs. 64, 65),

cluster diagram (fig. 66), and descriptive exposition in the text.

Intersample variation in cranial and dental measurements is apparent in the ordination of specimen scores for all seven population samples of *B. andrewsi* projected on first and second principal components (fig. 64); embedded in the scatter plot are results concordant with geographic differences in body size

TABLE 50
**Results of Principal-Components Analyses
Comparing Two Samples of *Bunomys andrewsi* with
Samples of *B. coelestis* and *B. prolatus***
Correlations (loadings) of 16 cranial and two dental
log-transformed variables are based on 12 *B.
andrewsi*, 19 *B. coelestis*, and eight *B. prolatus*.
Upper graph: *B. andrewsi* from lower slopes of
Gunung Lompobatang is contrasted with *B.
coelestis* from higher on the volcano. **Lower graph**:
The lowland *B. andrewsi* from Sungai Ranu is
contrasted with the montane *B. prolatus* from
Gunung Tambusisi. See figure 63.

| | Correlations | | | |
| | (*B. andrewsi* and *B. coelestis*) | | (*B. andrewsi* and *B. prolatus*) | |
Variable	PC 1	PC 2	PC 1	PC 2
ONL	0.45*	0.74***	0.82***	0.46
ZB	−0.49**	0.59**	0.99***	−0.01
IB	0.23	0.59***	−0.86***	0.23
LR	0.42*	0.65***	0.20	0.64*
BR	−0.40*	0.73***	0.92***	0.36
BBC	0.02	0.19	0.36	0.21
HBC	0.03	0.14	0.70**	0.02
BZP	0.32	0.58**	0.98***	0.07
LD	0.76***	0.56**	0.64*	0.54
PPL	0.26	0.72***	0.66*	0.61*
LBP	0.44*	0.61***	0.23	0.90***
BBP	0.58**	0.53**	0.45	0.55*
BMF	−0.59***	0.25	0.94***	−0.24
LIF	−0.75***	0.19	0.93***	−0.25
BIF	−0.87***	0.33	0.96***	−0.06
LB	−0.51**	0.07	−0.51	0.19
CLM1–3	−0.88***	−0.00	0.93***	−0.00
BM1	−0.85***	−0.00	0.57*	−0.32
Eigenvalue	0.032	0.014	0.118	0.011
% Variance	47.2	20.3	82.0	7.3

*** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

I encountered in my trapping. Moderate
to high positive loadings (r = 0.46–0.95;
table 52) among nearly all variables influence
the dispersal of scores along the first axis;
variation in size is stressed here with scores
for the smallest skulls sprinkled to the left in
the scatter plot, those for larger skulls to the
right. Reflected in the spread of points along
the first axis is individual variation and that
attached to adults of different ages (young to
old) but there is also a geographic pattern.
Scores for specimens with the largest skulls
are from eastern + southeast peninsulas
(empty triangle; Sungai Ranu, Masembo,
and Wawo) and cluster along the far right

of the entire scatter. Northern west-central
region (inverted filled triangle; Puro-Sungai
Miu, Tamalanti, and Tuare) and southwest
peninsula (empty diamond; Lombasang) are
represented by scores filling the left half of
the ordination, and these samples contain the
smallest skulls (table 51). Straddling these
outlying clumps are scores for specimens in
northeast–central region (filled circle; La-
buan Sore, Kuala Navusu, and Pinedapa),
south–central region (empty circle; Gunung
Balease, Malili area, and Sukamaju), and
southern west-central region (asterisk; Ma-
masa Area). Of the two scores representing
Pulau Buton, the very young adult aligns
with the smaller specimens, the other—the
old adult holotype—nests in the center of the
cloud of scores for northeast–central region.
Although there is a geographic trend in size
of skulls, clusters representing the population
samples greatly overlap and not one of them
is isolated within the ordination.

Shape information can be extracted from
the spread of scores along the second
component (table 52). Most specimens from
northeast-central region (filled circle in
fig. 64) have a relatively narrower zygomatic
plate, wider mesopterygoid fossa, larger
bullae, and shorter molar row compared with
animals represented by the points in the top
half of the scatter plot, especially those from
the west-central mountain block (northern
west-central region and southern west-central
region population samples).

A sharper picture of geographic trends in
intersample variation of cranial and dental
variables emerged from results of discrimi-
nant-function analysis. Among the first,
second, and fourth canonical variates ex-
tracted, the spread of scores along the first
variate (fig. 65, upper graph) is a response to
the positive moderate to high correlations (or
loadings; r = 0.32–0.68; table 53) for the
variables. Size is reflected along this axis: the
right half of the ordination contains samples
from the west-central mountain block (north-
ern west-central region and southern west-
central region) and southwest peninsula,
which are generally characterized by small
skulls; the left half holds scores for larger-
bodied animals from eastern + southeast
peninsulas and northeast–central region (east
of the west-central mountain block); scores

TABLE 51
Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from Population Samples of
Bunomys andrewsi
Mean ± 1 SD and observed range (in parentheses) are listed.

Variable	Northeast-central region	South-central region	Eastern + southeast peninsulas	Northern west-central region	Southern west-central region	Southwest peninsula	Pulau Buton
N	32	16	9	16	10	7	2
ONL	41.0 ± 1.84	42.4 ± 1.41	44.0 ± 1.19	39.5 ± 1.19	40.3 ± 1.57	38.8 ± 0.82	40.4 ± 2.62
	(37.1–45.2)	(39.8–45.0)	(41.9–45.5)	(38.0–42.0)	(38.2–43.8)	(37.6–40.2)	(38.5–42.2)
ZB	20.1 ± 1.00	20.9 ± 0.80	21.0 ± 0.66	19.3 ± 0.67	19.4 ± 0.88	19.2 ± 0.60	19.5 ± 0.64
	(17.9–22.2)	(18.9–21.9)	(20.0–21.0)	(18.3–21.1)	(18.4–21.1)	(18.1–19.9)	(19.0–19.9)
IB	6.6 ± 0.21	6.9 ± 0.20	6.6 ± 0.18	6.8 ± 0.19	6.5 ± 0.25	6.4 ± 0.24	6.6 ± 0.07
	(6.2–7.0)	(6.5–7.3)	(6.3–6.8)	(6.6–7.3)	(6.1–7.0)	(6.2–6.9)	(6.5–6.6)
LR	14.4 ± 0.97	15.3 ± 0.72	15.8 ± 0.86	13.9 ± 0.67	14.7 ± 1.00	14.0 ± 0.56	13.8 ± 1.06
	(12.2–17.2)	(14.3–15.3)	(14.3–17.1)	(12.5–15.0)	(13.3–17.2)	(13.0–14.8)	(13.0–14.5)
BR	7.2 ± 0.38	7.9 ± 0.47	8.1 ± 0.41	7.4 ± 0.39	7.3 ± 0.40	7.1 ± 0.35	7.6 ± 0.64
	(6.5–8.3)	(7.2–8.9)	(7.4–8.7)	(6.9–8.4)	(6.7–8.1)	(6.7–7.6)	(7.1–8.0)
BBC	16.0 ± 0.28	16.6 ± 0.37	16.7 ± 0.52	16.2 ± 0.48	16.1 ± 0.45	15.6 ± 0.35	15.8 ± 0.21
	(15.5–16.7)	(15.8–17.2)	(16.1–17.9)	(15.3–17.2)	(15.5–17.1)	(15.0–16.0)	(15.6–15.9)
HBC	11.6 ± 0.35	11.8 ± 0.49	12.0 ± 0.38	11.3 ± 0.26	11.3 ± 0.52	11.7 ± 0.62	11.0 ± 0.28
	(10.9–12.2)	(11.0–12.6)	(11.5–12.4)	(10.8–11.7)	(10.6–12.4)	(11.2–13.0)	(10.8–11.2)
BZP	3.9 ± 0.33	3.9 ± 0.44	4.0 ± 0.26	3.3 ± 0.29	3.4 ± 0.33	3.4 ± 0.24	3.5 ± 0.42
	(3.2–4.6)	(3.1–4.5)	(3.7–4.6)	(2.9–4.1)	(2.9–4.1)	(3.1–3.8)	(3.2–3.8)
LD	10.9 ± 0.76	11.3 ± 0.57	12.1 ± 0.42	10.4 ± 0.46	10.8 ± 0.63	10.2 ± 0.30	10.6 ± 1.06
	(9.5–12.6)	(10.1–12.2)	(11.5–12.5)	(9.7–11.5)	(9.9–12.1)	(9.9–10.7)	(9.8–11.3)
PPL	14.8 ± 0.85	14.8 ± 0.73	15.4 ± 0.47	13.9 ± 0.67	14.0 ± 0.78	13.8 ± 0.40	14.3 ± 0.99
	(12.9–16.2)	(13.7–16.1)	(14.4–16.0)	(13.0–15.4)	(12.5–15.6)	(13.2–14.3)	(13.6–15.0)
LBP	7.8 ± 0.46	7.9 ± 0.40	8.4 ± 0.86	7.5 ± 0.33	7.8 ± 0.44	7.7 ± 0.31	8.1 ± 0.71
	(6.8–8.6)	(7.2–8.7)	(7.3–9.9)	(7.1–8.4)	(7.0–8.7)	(7.4–8.3)	(7.6–8.6)
BBP	3.9 ± 0.26	4.1 ± 0.23	4.0 ± 0.29	3.6 ± 0.25	3.7 ± 0.32	3.3 ± 0.22	3.8 ± 0.35
	(3.3–4.3)	(3.7–4.6)	(3.5–4.4)	(3.3–4.1)	(3.2–4.3)	(2.9–3.5)	(3.5–4.0)
BMF	3.1 ± 0.20	3.2 ± 0.17	3.5 ± 0.28	3.1 ± 0.27	3.4 ± 0.28	3.3 ± 0.22	2.9 ± 0.21
	(2.6–3.4)	(2.9–3.5)	(3.1–3.8)	(2.7–3.7)	(3.0–4.0)	(2.9–3.5)	(2.7–3.0)
LIF	8.0 ± 0.45	8.1 ± 0.43	8.8 ± 0.64	7.7 ± 0.50	7.8 ± 0.51	7.6 ± 0.24	7.3 ± 0.00
	(7.2–8.8)	(7.3–8.6)	(7.8–9.5)	(6.8–8.4)	(7.2–9.3)	(7.2–7.9)	
BIF	3.1 ± 0.19	3.1 ± 0.15	3.2 ± 0.23	2.8 ± 0.18	2.9 ± 0.26	2.8 ± 0.20	2.8 ± 0.28
	(2.7–3.5)	(2.8–3.4)	(2.9–3.6)	(2.5–3.1)	(2.5–3.4)	(2.6–3.1)	(2.6–3.0)
LB	6.4 ± 0.35	6.8 ± 0.30	6.7 ± 0.29	6.3 ± 0.25	6.5 ± 0.22	6.6 ± 0.24	7.3 ± 0.21
	(5.7–7.0)	(6.3–7.3)	(6.3–7.2)	(5.9–6.8)	(6.1–7.0)	(6.1–6.8)	(7.1–7.4)
CLM1–3	7.3 ± 0.23	7.4 ± 0.31	7.4 ± 0.26	6.9 ± 0.29	7.1 ± 0.25	7.0 ± 0.27	7.2 ± 0.28
	(6.9–7.7)	(7.0–8.0)	(7.1–7.9)	(6.5–7.4)	(6.6–7.5)	(6.6–7.3)	(7.0–7.4)
BM1	2.3 ± 0.08	2.4 ± 0.08	2.3 ± 0.09	2.3 ± 0.11	2.3 ± 0.09	2.2 ± 0.08	2.2 ± 0.21
	(2.1–2.4)	(2.2–2.5)	(2.2–2.5)	(2.1–2.5)	(2.2–2.5)	(2.1–2.3)	(2.0–2.3)

for samples from south–central region overlap the groups of scores in the left and right halves of the scatter plot. Points representing the two specimens from Pulau Buton align with those representing animals with larger skulls. The high positive loadings for overall size of skull (occipitonasal length and zygomatic breadth), breadth of braincase and zygomatic plate, length of diastema, postpalatal length, breadth of bony palate, expanse of incisive foramina, and length of

molar row indicate that these dimensions are not as great in samples from the west-central mountain block and Lombasang on the southwestern peninsula compared with series from elsewhere in Sulawesi, mainly those landscapes east of the west-central mountain block.

Shape differences are indicated by the spread of scores along the second variate in the upper graph in figure 65. High positive loadings for nearly all variables ($r = 0.27$–

0.69; table 53), along with isolation of the scores for eastern + southeast peninsulas (empty triangle) on the right margin of the ordination, and southwest peninsula (empty diamond) at the left extreme, point to the relatively overall larger cranial and dental dimensions in the former and relatively smaller dimensions in the latter compared to the other four samples clumped together in the center of the ordination, which includes the holotype of *andrewsi* (star).

The lower scatter plot in figure 65 reveals a pattern of covariation in cranial and dental measurements among the population samples similar to that in the upper scatter plot of figure 65. The large and positive loadings for breadth of rostrum (0.45) and length of bulla (0.69) on the fourth variate (see table 53) isolate scores for the two specimens from Pulau Buton from those points signifying specimens in all the other population samples. Compared with the six population samples, whether they contain small, large, or skulls of intermediate size, animals in the sample from Pulau Buton have a relatively wider rostrum and much larger tympanic bulla, particularly the holotype of *andrewsi*. A large bulla is characteristic of the small sample from Pulau Buton: 7.2 mm is the mean length of bulla for Pulau Buton, and 6.3–6.8 mm is the range of means for the other six population samples.

Cluster analysis based on squared Mahalanobis distances results in the pattern of phenetic relationships among the seven population samples portrayed in figure 66. Two primary groups of samples are apparent. The largest unites all samples from mainland Sulawesi except those at the most southern margins of the island, Pulau Buton off the south coast of the southeastern peninsula and Lombasang at the southern end of the southwestern peninsula, which form a group discrete from that containing the other five population samples.

Within the larger assemblage, the phenetic relationships among samples generally mirror geography. Specimens from lowlands at Labuan Sore, Kuala Navusu, and Pinedapa (northeast-central region) link with animals from Gunung Balease, the Malili area, and Sukamaju (south-central region), all localities east or at the margin of the west-central mountain block. Samples from the northern and southern parts of the west-central mountain block are united in the diagram and are linked (between 30 and 40 distance units) to the previous two samples from east of that mountainous region. These two sets join the sample of animals from the west end of the eastern peninsula at Sungai Ranu and Wawo and Masembo in the lowlands adjacent to Pengunungan Mekongga on the southeastern peninsula. All these samples describe a distribution covering the core of Sulawesi and the southeastern peninsula. The trend in skull size (and generally body size) extends from the west-central mountain block where populations are characterized by small skulls on average to east of the mountain block where larger-bodied animals predominate, with the largest skulls in the samples from Sungai Ranu and the southeastern peninsula. The names "*Rattus adspersus*" (Miller and Hollister, 1921a), based on the series collected at Pinedapa, and "*Rattus penitus inferior*" (Tate and Archbold, 1935a), applied to specimens from Masembo and Wawo, are associated with this large geographic block of samples.

Other traits I examined on specimens in the five population samples do not show patterns of intersample variation that accords with the geographic trend in size associated with cranial and dental variables. For example, I did not detect any geographic variation in qualitative traits of the skull or teeth. And with few exceptions, all the adults have a moderately soft and long dorsal coat that is dark brown or brownish gray speckled with buff and black; in any large sample, the ventral coat ranges from pale grayish white or pale grayish buff to dark grayish white, dark grayish buff, buffy gray, or ochraceous-gray (some specimens show rusty patches); ears are brown or brownish gray; dorsal surfaces of feet are white, gray, or buffy; the tail is shorter than combined length of head and body (LT/LHB = 85%–92%), brownish over the dorsal surface, white, mottled, or brown on the ventral surface, and either lacks or shows a relatively short white tip (see table 8).

There is variation in thickness and color of fur covering head and body that corresponds to differences in elevation, which is illustrated by samples from two regions. Specimens in
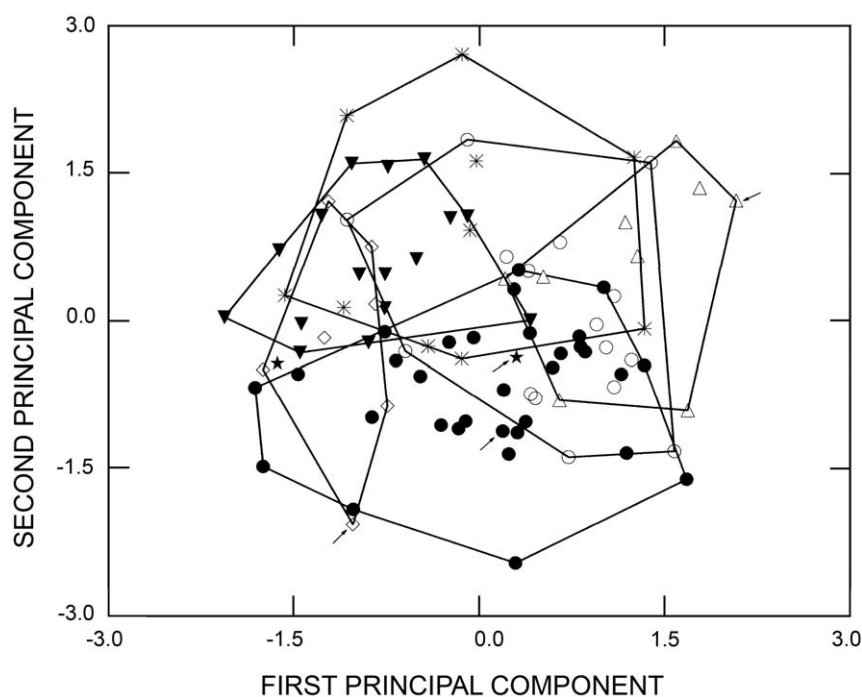
Fig. 64.   Specimen scores representing all seven population samples of *Bunomys andrewsi* projected onto first and second principal components extracted from principal-components analysis of 16 cranial and two dental log-transformed variables. Symbols: filled circles = northeast-central region (Labuan Sore, Kuala Navusu, and Pinedapa; $N = 32$); empty circles = south-central region (Gunung Balease, Malili Area, and Sukamaju; $N = 16$); empty triangles = eastern + southeast peninsula (Sungai Ranu, Wawo, and Masembo; $N = 9$); filled inverted triangles = northern west-central region (Puro-Sungai Miu, Tamalanti, and Tuare; $N = 16$); asterisks = southern west-central region (Mamasa Area; $N = 10$); empty diamonds = southwest peninsula (Lombasang; $N = 7$); stars = Pulau Buton ($N = 2$). Polygons define limits of dispersion for scores in each population sample. Arrows point to scores for holotypes: *andrewsi* (star), *adspersus* (filled circle), *heinrichi* (empty diamond), and *inferior* (empty triangle). Correlations (loadings) of variables with extracted components and percent variance explained are listed in table 52.

the Mamasa area (the southern part of the west-central mountain block) come from higher elevations (900–1600 m) than do most examples of *B. andrewsi* and have a thicker dorsal coat (15–20 mm) that is much darker than lowland samples. Underparts also average darker, ranging from dark grayish white to dark grayish buff.

The population sample of the south-central region contains specimens collected between 830 and 925 m on Gunung Balease and those obtained at 450 m in the Malili area, approximately 80 km southeast of Gunung Balease, that cannot be distinguished by cytochrome-*b* sequences (molecular trees passed to me by J.L. Patton and K.C. Rowe, in. litt., 2011), body size, cranial and dental

traits, or pelage thickness. They do show, however, slight differences in coat color that is related to elevation. Specimens from Gunung Balease have darker upperparts (dark brown to brownish black speckled with buff) than do the rats in the sample from the Malili region, which in pelage color is closely similar to the specimens from Pinedapa and Kuala Navusu and others from 400 m and lower (rich brown speckled with buff over the upperparts). Underparts of both the Balease and Malili specimens range from grayish white to grayish buff (the buff forms either a pale or intense wash over the underparts), but the mountain animals are slightly darker.

The two examples from Pulau Buton, which comprise the type series of ''*Mus*

TABLE 52
Results of Principal-Components Analysis Performed
on Population Samples of *Bunomys andrewsi*
Correlations (loadings) of 16 cranial and two dental
log-transformed variables are based on 98 *B. andrewsi*; see figure 64.

Variable	Correlations	
	PC1	PC2
ONL	0.95***	0.06
ZB	0.90***	0.01
IB	0.35***	−0.01
LR	0.86***	0.21*
BR	0.74***	0.27
BBC	0.46***	0.15
HBC	0.62***	−0.10
BZP	0.82***	−0.52***
LD	0.91***	0.13
PPL	0.90***	−0.07
LBP	0.52***	−0.10
BBP	0.77***	0.07
BMF	0.55***	0.68***
LIF	0.78***	0.11
BIF	0.71***	−0.02
LB	0.42***	0.26**
CLM1–3	0.51***	−0.26**
BM1	0.19*	0.06
Eigenvalue	0.042	0.008
% Variance	54.9	10.4

*** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

andrewsi'' (Allen, 1911) are distinguished from all other samples primarily by their relatively large ectotympanic bullae, slightly shorter but wider rostrum, short incisive foramina, and slightly average smaller skull. They also have very short tails in relation to head and body (LT/LHB = 75%; 85%–92% is the range for the other geographic samples). Color of the fur and appendages closely resembles samples from farther north in the lowlands, Kuala Navusu, Pinedapa, and the Malili area, for example. It is their average smaller skull that may be most responsible for linking the two specimens with the sample from Lombasang at the southern end of the southwestern peninsula, the type series of ''*Rattus penitus henrichi*'' (Tate and Archbold, 1935a); otherwise the animals in each sample are quite different. The Lombasang rats were collected at 1000 m and have a thicker coat (15–20 mm thick as opposed to 12–15 mm for the Buton specimens from the lowlands) that is a richer and brighter brown,

a relatively longer rostrum, longer incisive foramina (absolutely and relative to skull length), and smaller bullae (relative size is similar to specimens in samples from the center of the island and southeastern peninsula). Also, a small cusp t3 occurs on the second upper molar in 78% of the Lombasang sample; the young adult from Pulau Buton lacks a comparable cusp (molars are too worn to determine presence or absence of cusp t3 on the other Buton specimen).

To summarize, I provisionally regard the variation in coat color, body size, and the cranial and dental measurements described above to be contained within the phenetic boundary of a single species. Here are highlights of this hypothesis and suggestions for future inquiry:

(1) The core group of population samples (from the west-central mountain block and landscapes east of there in Sulawesi's core) forms a cohesive unit as measured by morphometric attributes. My data also shows appreciable variation in body size, particularly between the sample from the northern part of the west-central mountain block and those from areas to the east (Pinedapa and Kuala Navusu, for example).

(2) The small sample containing individuals from Sungai Ranu at the western end of the eastern peninsula and Masembo and Wawo in the lowlands surrounding Pegunungan Mekongga on the southeastern peninsula (the eastern + southeast peninsulas sample) diverge somewhat phenetically from the core assemblage of samples but are most likely genetically related to it. Color of fur and appendages closely resemble adults in the samples from the Malili area, Pinedapa, and Kuala Navusu (northeast-central region and south-central region). Some cranial measurements average larger than those in the latter two population samples samples, which is probably a result of sample composition—the eastern + southeast peninsulas sample is small and consists of mostly adults and old adults, while the other samples are much larger and contain the range in age from very young adults to old adults (see table 51). Comparison of much larger samples from the southeastern peninsula, ideally including analysis of DNA sequences, would likely demonstrate a strong phenetic and genetic link between populations on the mainland of the southeastern peninsula and western end of the eastern peninsula with those from the island's core.
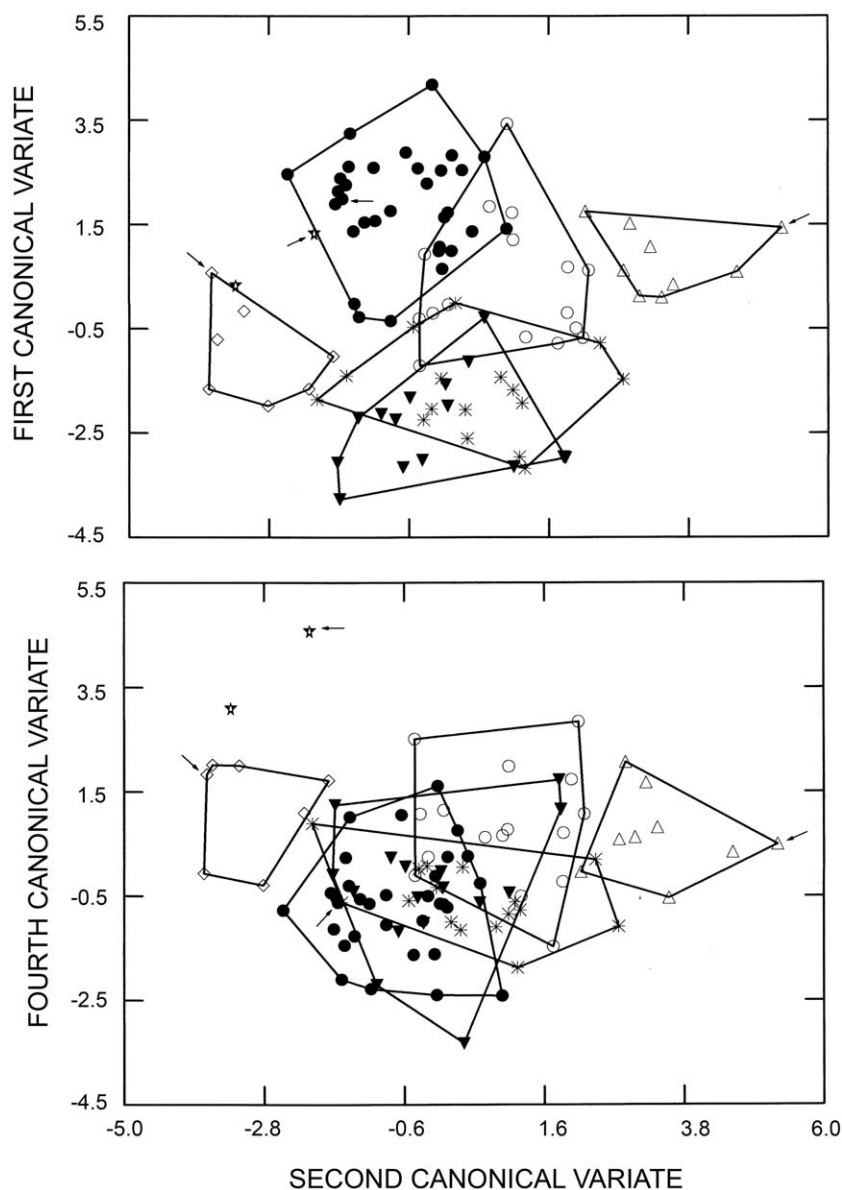
Fig. 65. Results of discriminant-function analysis of 16 cranial and two dental log-transformed variables derived from seven population samples of *Bunomys andrewsi*. Symbols: filled circles = northeast-central region (Labuan Sore, Kuala Navusu, and Pinedapa; $N = 32$); empty circles = south-central region (Gunung Balease, Malili Area, and Sukamaju; $N = 16$); empty triangles = eastern + southeast peninsula (Sungai Ranu, Wawo, and Masembo; $N = 9$); filled inverted triangles = northern west-central region (Puro-Sungai Miu, Tamalanti, and Tuare; $N = 16$); asterisks = southern west-central region (Mamasa Area; $N = 10$); empty diamonds = southwest peninsula (Lombasang; $N = 7$); stars = Pulau Buton ($N = 2$). Arrows indicate scores for holotypes: *andrewsi* (star), *adspersus* (filled circle), *heinrichi* (empty diamond), and *inferior* (empty triangle). Upper graph: Specimen scores projected onto first and second canonical variates. Lower graph: Specimen scores projected onto second and fourth canonical variates. See table 53 for correlations (loadings) of variables with extracted canonical variates and for percent variance explained for both ordinations.

TABLE 53
Results of Discriminant-Function Analysis Performed on Population Samples of *Bunomys andrewsi*
Correlations (loadings) of 16 cranial and two dental log-transformed variables are based on 98 *B. andrewsi*; see figure 65.

Variable	Correlations		
	CV1	CV2	CV4
ONL	0.43***	0.64***	0.24*
ZB	0.44***	0.47***	0.26**
IB	−0.08	0.20*	0.06
LR	0.19	0.58***	0.20*
BR	0.01	0.62***	0.45***
BBC	0.01	0.69***	0.15
HBC	0.32***	0.27**	0.17
BZP	0.68***	0.29**	0.05
LD	0.33***	0.60***	0.18*
PPL	0.54***	0.36***	0.10
LBP	0.24*	0.30**	0.27**
BBP	0.47***	0.44***	−0.03
BMF	−0.12***	0.61***	−0.10
LIF	0.40***	0.54***	0.01
BIF	0.52***	0.39***	−0.07
LB	0.12	0.19	0.69***
CLM1–3	0.51***	0.34***	0.21*
BM1	−0.11	0.44***	−0.04
Canonical correlation	0.867	0.840	0.669
Eigenvalue	3.040	2.401	0.811
% Variance	36.8	29.1	9.8

*** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$.

(3) I have examined only two specimens from Pulau Buton and do not know if they represent the chromatic and morphometric variation in the population living on that island. The nearest sample on the mainland of the southeastern peninsula is approximately 200 km northwest of Pulau Buton, leaving us ignorant about the populations of the species living in the lowland landscapes between Wawo and Pulau Buton. A much larger sample from Pulau Buton is required to fully assess the characteristics of that island population and its phenetic and genetic relationship to populations on the mainland.

(4) The distance between the Mamasa region, the provenance of the southernmost sample of *B. andrewsi* in Sulawesi's core, and Lombasang on the flanks of Gunung Lompobatang, the collection site for the type series of *heinrichi*, is approximately 300 km. No modern samples of the species are available from this stretch of lowlands and mountains. Without material from this unsampled region, I cannot determine whether the Lombasang sample represents a separate species isolated on the southwestern peninsula south of the Tempe depression (the lowlands and waterways bisecting the peninsula at the southern border of the west-central mountain block) or whether it is closely genetically tied to the core populations.
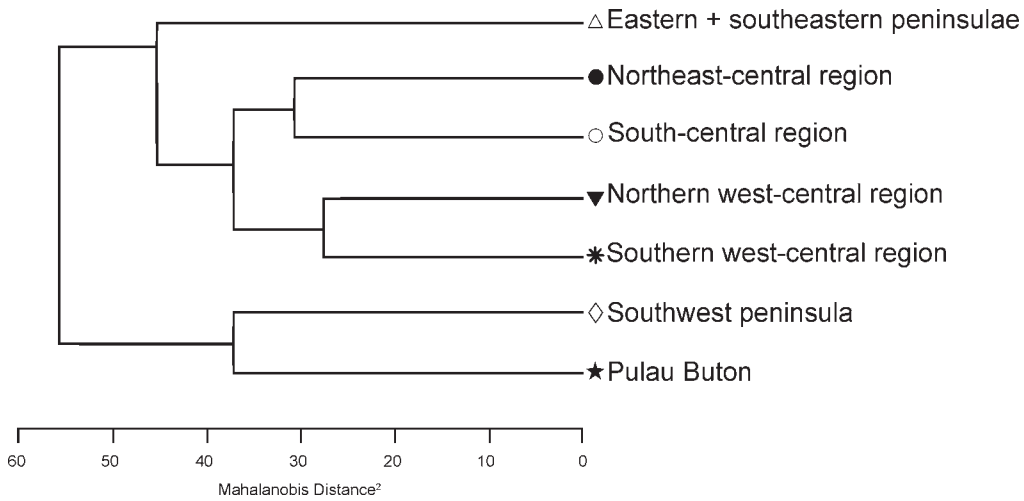

Fig. 66. Pattern of phenetic relationships among population samples of *Bunomys andrewsi* based on UPGMA clustering of squared Mahalanobis distances among group centroids and derived from discriminant function-analysis using log-transformed values of 16 cranial and 2 dental variables.

I can report that the sample from Lombasang broadly overlaps those from the west-central mountain block (northern west-central and southern west-central regions) in magnitude of many cranial and dental variables, as reflected in the scatter plots of specimen scores derived from principal-components and canonical-variate analyses (figs. 64, 65). Simply based on morphometric similarities, the southwest peninsular and west-central mountain block samples appear to be phenetically similar.

Results of cluster analysis based on squared Mahalanobis distances, however, do not link the sample from Lombasang with those from the west-central mountain block (fig. 66). In addition to the diagram in figure 66, I generated several other cluster diagrams (none are illustrated here) using different combinations of all samples, reducing the larger population samples into smaller entities for some analyses, and eliminating the two specimens from Pulau Buton for others. In each result, the configuration of population samples formed by the linked northeast-central region and south-central region connected to the linked northern west-central region and southern west-central region (west-central mountain block) retained its integrity (the island's core unit). In different iterations, the sample from Lombasang either linked with Pulau Buton or in the absence of that sample connected to the core assemblage, or to a cluster consisting of the core samples and the eastern + southeast seninsulas sample, but never directly with either of the samples from the west-central mountain block.

Morphological and genetic information derived from new material collected in the southern part of Sulawesi's core just north of the Tempe Depression as well as along the peninsula south of the depression would be most welcome and likely would resolve the present ambiguous relationship between the sample from Lombasang and those from the core of the island. Of all the samples I examined for this review, the one from Lombasang might represent a separate species, a supposition I entertained earlier (Musser, 1991; Musser and Carleton, 1993).

(5) The images of skulls portrayed in figure 67 visually summarize the variation in size of skulls among population samples. On the left is the holotype of *andrewsi* from Pulau Buton—its wider rostrum (relative to its length), shorter incisive foramina, and larger bullae are evident. On the right is the holotype of *heinrichi* from Lombasang on the southwestern peninsula. The middle skull is from Kuala Navusu and represents the typical size and conformation of many skulls in samples from Kuala Navusu, Pinedapa, and other localities on the margin of the west-central mountain block and places in the lowlands east of there and on the southeastern peninsula, and is closely similar in size and shape to the holotypes of *adspersus* and *inferior*.

NATURAL HISTORY: Included here is a summary of information covering habitat and diet, along with my few observations of nest construction.

Habitat: *Bunomys andrewsi* has been collected in primary forest, secondary growth, and village gardens. Along the Sungai Oha Kecil and Sungai Sadaunta in the northern part of the west-central region, and in the Kuala Navusu area, my helpers and I trapped *B. andrewsi* in primary forest along streams and on hillsides—all sites were shaded where the ground remained either damp or wet (descriptions of trap sites are summarized in table 54). Mean ambient air temperature ranged from 66.9° to 78.8° F along Sungai Oha Kecil and Sungai Sadaunta, and 73.6° to 80.9° F at Kuala Navusu, with relative humidities reaching 100% in all three places (table 3). Individuals were caught in traps placed on decaying tree trunks and limbs spanning streams and ravines; in runways beneath trunks and limbs that are remnants of treefalls lying on the forest floor, on wet stream terraces covered by shrubs, small trees and canopied by taller streamside forest; beneath moss-covered rocks on wet hillsides, and beneath roots of living trees. Decaying tree-falls were especially productive places to set traps because they provided excellent cover for runs beneath the trunks and limbs and are usually shaded by a dense cover of shrubs, ferns, rattan rosettes, and saplings that offered a constant damp or wet microenvironment. Examples of the typical places where we caught *B. andrewsi* are presented in figures 68 and 69. We did not encounter the rats in forest high on steep hillsides or ridgetops, areas that dry out faster than protected hillsides above streams and stream banks and terraces, which remain wet.
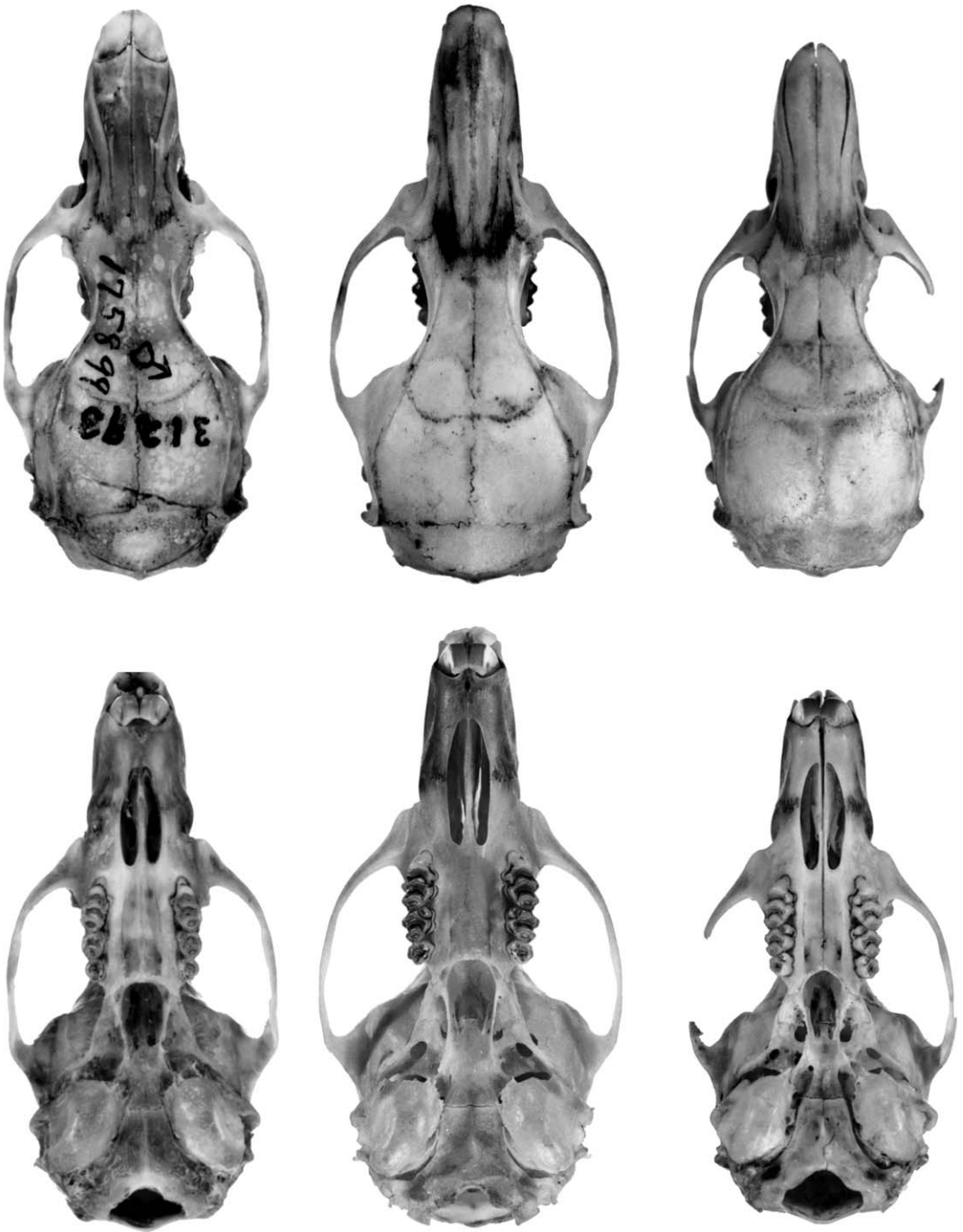
Fig. 67. Dorsal (top) and ventral (bottom) views of adult skulls representing separate population samples of *Bunomys andrewsi*. Left to right: Pulau Buton (USNM 175899, holotype of *andrewsi*), off the tip of the southeastern peninsula; Kuala Navusu (AMNH 225652), Sulawesi's core (skull is morphometrically similar to the holotypes for *adspersus* and *inferior*); and Lombasang (AMNH 101006, holotype of *heinrichi*), southwestern peninsula. ×2.

TABLE 54

Summary of Microhabitats at Trapping Sites, Stomach Contents, and other Relevant Information for Specimens of *Bunomys andrewsi* Collected in Central Sulawesi, 1974–1975

Descriptions of the trapping sites and contents of stomachs are summarized from my field journals (in Mammalogy Archives at AMNH). All collection localities are in old-growth tropical lowland evergreen rain forest; all rats were caught during the night. See habitats in figures 68 and 69.

Locality, AMNH and (ASE-field) numbers	Elevation (m)	Date	Trap site and other information
Sungai Oha Kecil			
224630 (1649)	290	July 1974	In wide runway beneath roots of trees growing along margin of ravine between the small Sungai Oha Kecil and the larger Sungai Miu. **Stomach:** nearly empty, remains of rhinotermitid termites mixed with small chunks of fruit.
224631 (1838) 224632 (1845) 224633 (1858)	457	Aug. 1974	On rotting, smooth trunk bridging Sungai Oha Kecil in streamside forest. **Stomach:** 224631 had a few pieces of fig (seeds still attached to inner wall of the rind); 224632 was full of large brown seeds (same as found in 224107 from Sungai Sadaunta), some complete (dark brown seed coat, seed roughly triangular to oblong), others partly digested, intact seeds and pieces of seed coat held in a whitish gelatinous substance; 224633 full of same fruit as found in 224632.
Sungai Miu			
224145 (1541)	350	Apr. 1974	On smooth, wet, and rotting trunk lying over narrow tributary stream; wet streamside, shrubby understory at either end of trunk, surrounded by tall river terrace forest. The rats *Taeromys celebensis*, *Rattus hoffmanni*, and *Maxomys muschenbroekii* were caught at same spot on different nights; trunk clearly used by rodents to cross stream. **Stomach:** some bait; packed with rhinotermitid workers and soldiers (mostly head capsules, body tissue, legs); fruit pulp and a few seeds; a piece that resembles snail (tissue, not shell).
Sungai Sadaunta			
224107 (1344)	675	Feb. 1974	In runway beneath rotting, wet trunk lying on wet ground in understory of streamside forest. **Stomach:** partly full of fig remains (tiny seeds, some still adhering to inside of skin, pieces of fig wall); also a few large, hard brown seeds from a different fruit; small earthworm cut into segments.
224116 (1363)	675	Feb. 1974	On damp ground beneath boulder in forest understory adjacent to Sungai Sadaunta. **Stomach:** distended with bait.
Kuala Navusu			
225666 (3199) 225667 (3247) 225657 (3247)	55	Sept. 1975	Live trap on ground beneath decaying trunk (2 ft diameter) resting on slope above a stream. Trunk is 60–70 ft long and extends down the hill, over the stream and onto the opposite bank; this old tree-fall is lying in scrubby understory, and a large, long opening persists in the canopy of the hillside forest. A *Maxomys hellwaldii* was trapped in same place. Two *Paruromys dominator* and one *Echiothrix centrosa* were trapped on same trunk but on top of that portion bridging the stream. Ate small gecko during captivity (see text).
225665 (3238)	46	Sept. 1975	On ground beneath rotting trunk (2 ft diameter) lying in dense shrubbery on terrace of stream; part of a canopy tree that fell and broke into long sections that are now decaying. Good clear run beneath trunk and dense shrubby cover on both sides. Caught *Maxomys hellwaldii* in same spot (see fig. 65) and trapped *Bunomys andrewsi* 225648 nearby. **Stomach:** 225666 was empty except for a bit of bait; 225667 empty except for unidentifiable mash and a few fragments of insect sclerites; 225657 nearly empty, unidentifiable mash, few fragments of insect sclerites.
225659 (3360)	122	Oct.1975	On rocky, wet slope above a giant *Dracontomelon dao*; here the rocks are covered with a thin layer of moss, soil and leaf litter lay among the rocks; area is shrubby; here and there vines and low understory trees grow over the rocks; clumps of tall rattan are scattered over the slope as are palms (*Licuala celebica*, *Pinanga caesia*, and *Livistona rotundifolia*); scattered understory trees form a partial canopy that shades the area;

TABLE 54
(*Continued*)

Locality, AMNH and (ASE-field) numbers	Elevation (m)	Date	Trap site and other information
			tall emergents, in addition to *D. dao*, grow upslope and downslope. Trap was placed on damp ground beneath several rocks. **Stomach:** full of fruit (not identified) and remains of small insects, mostly larvae.
225660 (3361)	122	Oct. 1975	On leaf-covered, wet ground alongside rocks on slope where 225659 was caught and about 5 ft from that rat; rocks partly covered by shrubs. A *Maxomys hellwaldii* was caught in same spot. Ate invertebrates and fruit during captivity (see text).
225661 (3371)	122	Oct. 1975	On wet ground beneath a shrub-covered group of rocks on same rocky slope where 225659 and 225660 were caught, only 3 ft from 225659. **Stomach:** crammed with mostly fruit mash from figs (large seeds, chunks of rind) and numerous rhinotermitid workers and soldiers.
225662 (3399)	122	Oct. 1975	In runway beneath rotting trunk lying on hillside above a rocky ravine; runway 6 in. wide extending length of limb (15 ft); parts of trunk covered with shrubs, leaf litter, and debris, so runway is partly concealed. Understory dense, young fan palms (*Livistona rotundifolia*), *Licuala celebica*., species of rattan, and a variety of shrubs; closed understory canopy with scattered tall trees nearby; ravine is shaded, cool, and moist, staying that way much longer than the exposed higher slopes away from the ravine. Caught a *Maxomys hellwaldii* in same spot. **Stomach:** distended with bait and unidentifiable fruit mash.
225663 (3416)	122	Oct. 1975	On ground in rocky area where 225659–225661 were caught; set trap beneath shrub and moss-covered rocks in front of burrow entrance that leads down into spaces among rocks. **Stomach:** full, mash of fig remains (seeds and skin of fruit) in which are mixed small beetle larvae.
225664 (3422)	122	Oct. 1975	On damp ground under moss-covered rocks beneath shrubs and litter; same rocky slope where 225659–225661, and 225663 were caught, a rocky area about 10 ft square in hillside forest. **Stomach:** full of fruit mixed with small insects (ant, beetle larvae)
225658 (3537)	61	Oct. 1975	On very rotten section of trunk lying across wet and deep, V-shaped, and rocky ravine that is a tributary of main stream; hillsides steep; forest uneven; canopy trees like *ula* (*Diospyros macrophylla*) and *tea* (*Artocarpus* sp.) predominate—the latter is common; same general area where 225649 was caught. **Stomach:** full of finely masticated figs with remains of adult and larval insects.
225649 (3549) 225651 (3562)	54	Nov. 1975	On top of decaying tree trunk (12 in. diameter) lying across deep rocky ravine (12 ft wide across top even with trunk, 12 ft deep from trunk to ravine bed) that is a tributary to the main stream and drains this section of the eastern-facing hillside. Generally good hillside forest, but it is open in this spot due to an old treefall that must have cleared a large area (about fourth of an acre) forming a large opening in the forest canopy; shrub and shrubby growth on slope above the ravine, and large sections of rotting trunks and limbs. The forested slopes are steep; on left side (facing up the ravine) slopes are densely covered with a field of tall (5 ft) ferns and nearby is an area of scrub consisting of palms, shrubs, saplings, euphorbs, elephant ears, and streamside figs. There are few rocks exposed on the slope along sides of the ravine. There is good cover under the rotten wood that lay in part of the scrub; a side ravine, rocky, shallow, and dry but mossy, courses down the slope and joins main ravine about where the rat was trapped; forest on right side of ravine is undisturbed; a high broken canopy surrounds the area; *ula* (*Diospyros macrophylla*), *laru* (*Myristica fasciculate*), and *tea* (*Artocarpus* sp.) are common; *Madhuca* sp. here also—the usual hillside-terrace flora; a huge (125 ft high, 4 ft diameter) pohon tea (*Artocarpus sericarpus*) towers in solitude over the scrubby area, apparently not felled by the

TABLE 54
(*Continued*)

Locality, AMNH and (ASE-field) numbers	Elevation (m)	Date	Trap site and other information
			old treefall; 225658 taken 25 ft above on trunk across main ravine; caught 225651 here at same spot. **Stomach:** 225649 full of insect remains (similar to 225648) mixed in brown fruit mash; 225651 empty.
225648 (3554)	46	Nov. 1975	On terrace of main stream, about 4 ft above stream in area of old treefall; long sections of trunks and large limbs lay rotting on hillside and portion of stream terrace; about a month ago caught a *Bunomys andrewsi* nearby beneath one of these sections; 225648 caught beneath rotting section of trunk (1.5 in. diameter, 25 ft long). This piece of trunk is covered by rotting branches, woody vines and other debris, as well as herbaceous vines and shrubs; the space beneath most of the trunk provides protected run for small animals; area stays damp even when there is little or no rain; thick debris and leaf litter cover forest floor; this part of terrace is not flooded as are washed parts nearby; understory is open, but area of treefall is surrounded by good forest; undercover is dense and shrubby as is typical of open areas that are regenerating after treefalls. **Stomach:** full of well-masticated and digested insects (legs, antennae, sclerites, larval abdomens; no termites) mixed with a little fruit, including a few hard oblong seeds.
225647 (3548)	46	Nov. 1975	In runway (6–8 in. wide) along rotting trunk (1.5 in. diameter, 20 ft long) on hillside above third tributary and main stream; good forest; trunk is from an old treefall that is shaded by two large clumps of rattan and a young fan palm (*Livistona rotundifolia*), so the ground is clear; also muddy, partly covered by leaf litter; canopy is closed overhead by mainly an emergent strangler *Ficus*; ula (*Diospyros macrophylla*) is common, understory forest intact. **Stomach:** crammed full with worker and soldier rhinotermitid termites; nothing else.
225650 (3563) 225654 (3652)	54	Nov. 1975	On damp ground that is a protected runway beneath two limbs from an *ula* that lay on hillside above main stream; good hillside forest, but here in this spot several large trees have fallen, probably within last year, so the understory is scrubby and filled with rattan, shrubs, tall gingers, short young trees, young palms, and vines. The two limbs are covered with herbaceous and woody vines that fell with the tree; they, along with the undercover, form a matlike canopy over rotting trunks and limbs, shading the ground and providing good cover. The area is usually wet, whereas farther up the hillside, the ground dries quickly; entire area for about one-eighth acre is a jumble of scrub-enclosed rotting trunks and limbs interspersed between tall canopy trees; 225652 and 225654 also caught here at same spot. **Stomach:** 225650 partly full, cut chunks of earthworm, many insect sclerites, all in an unidentifiable brownish mass; 225654 filled with orange mash containing brown globs mixed with parts of tiny insects.
225652 (3579)	54	Nov. 1975	In same area of terrace slope high above stream where 225650 was caught. Trap set beneath rotten trunk (2.5 ft diameter) lying horizontally across hillside; it is surrounded by dense undergrowth of shrubs, seedlings and debris; understory is also dense; a huge rattan winds through and over everything (probably fell with the tree), the palm *Licuala celebica*, small *Pandanus*, and short trees abound; so space beneath trunk is enclosed on sides by good, dense cover and stays relatively damp. This spot is in an area of old treefalls that are interspersed among the remaining canopy and tall understory trees, and the treefalls form large, scrubby open areas in forest canopy. **Stomach:** ate variety of invertebrates and fruit during captivity (see text).

TABLE 54
(*Continued*)

Locality, AMNH and (ASE-field) numbers	Elevation (m)	Date	Trap site and other information
225653 (3630) 225655 (3666)	54	Nov. 1975	In runway alongside 50 foot section of decaying *benoa* (*Octomeles sumatrana*) trunk (3–4 ft diameter) on terrace above main stream; two *Bunomys andrewsi* were caught just above under rotting trunks and limbs on slope; this trunk is part of an old giant that fell from hillside on other side of stream, across and onto the terrace, now broken into sections and rotting. This section of trunk surrounded by a thick cover of shrubs, gingers, young *Pandanus*, young and large rattans, and herbaceous vines, all canopied by understory trees and scattered canopy trees that were not knocked down when the tree fell; runway along trunk 8 in. wide and concealed by adjacent shrubs; 225655 also caught here on a different night. **Stomach:** 225653 full of mostly bait and fruit mash, a few pieces of earthworms, and some small insect larvae; 225655 partly full of bait.
225656 (3718)	54	Nov. 1975	Alongside end of large and long rotting trunk; a *Taeromys celebensis* was caught at the other end upslope; a few feet away is another section of the trunk beneath which 225652 was trapped; and 3 *Bunomys andrewsi* have been caught just downslope. This is an area of old treefalls that provide excellent, wet cover in the form of runs beneath decaying wood, rocks, and/or dense shrub cover. The rats seem to prefer dense undergrowth growing over damp, mossy rocks and boulders or trunks, limbs, and piles of branches; the rat is absent from steep hill forest and ridgetops, which dry out faster than hillsides just above streams and terraces; even good boulder and cliff outcrops with sufficient interstices for rats seem unsuitable for *B. andrewsi* if they are on dry hillside forest no matter how dense the canopy. Stomach: ate a variety of invertebrates and fruit during captivity (see text).
225646 (3528)	31	Oct. 1975	On ground alongside rotten section of trunk (2.5 ft diameter) lying on terrace above second tributary stream; second-growth and scrub growing over old treefall. **Stomach:** remnants of bait, nothing else.

Bunomys andrewsi has also been obtained in habitats where the original forest has been altered by human activity. The samples from Gunung Balease and the Malili area (Desa Lawaki Jaya) were trapped in secondary forest (J.L. Patton, personal commun., 2011). At Omu, a village at the lower end of my transect, a rat was "taken in a garden at edge of a swampy area (notation on the skin tag). In the Mamasa area, *B. andrewsi* was commonly encountered in second-growth forest and cacao gardens (K.C. Rowe, in litt., 2012).

We never trapped examples of *B. andrewsi* on woody vines above ground or in trees. It, like other species of *Bunomys*, is terrestrial and active during the night.

Diet: *Bunomys andrewsi* consumes a variety of invertebrates, vertebrates, and fruit, but not fungi; the categories and range of items in each are similar to those constituting the diet of *B. chrysocomus* (see that account and table 13). My dietary records derive from feeding three captive *B. andrewsi* collected at Kuala Navusu (two adults and a juvenile) and study of samples from stomachs of animals captured at Kuala Navusu, along my transect in the west-central region (Sungai, Oha Kecil, Sungai Miu, and Sungai Sadaunta), and specimens from Gunung Balease and the Malili area (obtained by J.L. Patton, K.C. Rowe, and J.A. Esselstyn); see tables 54 and 55.

All three captives aggressively attacked and consumed invertebrates. Each would instantly grab the offered earthworm or insect from my fingers, scamper to an opposite corner of the cage with the prey in its mouth, stop and watch me for a few seconds, then turn its back to me and begin eating. Even flies were chased about the cage.

Fig. 68.   Tropical lowland evergreen rain forest (in 1975) at Kuala Navusu (30 m) where in addition to *Bunomys andersoni*, we trapped *Maxomys hellwaldii*, *Rattus hoffmanni*, *Paruromys dominator*, and *Echiothrix centrosa*. Usma is siting at the base of a *Heritiera javanica*, one of the several species of large and magnificent old-growth trees that emerge above the upper canopy. We collected samples of about 160 species of trees in the Kuala Navusu area as well as woody shrubs and vines, monocots, bananas, cycads, seven kinds of palms, and eight species of rattans.

Fig. 69.　　Decaying trunk lying in dense understory on stream terrace in tropical lowland evergreen rain forest at Kuala Navusu, 46 m (in 1975). *Bunomys andrewsi*, *Maxomys hellwaldii*, and *Echiothrix centrosa* were caught in traps placed in a runway beneath the trunk (see habitat description for AMNH 225665 in table 54). *Taeromys celebensis* was taken nearby on an old treefall spanning the stream.

TABLE 55

Summary of Stomach Contents for Specimens of *Bunomys andrewsi* collected in Central Sulawesi at Gunung Balease (830–925 m) and the Malili Region (Desa Lawaki Jaya, 450 m) during October and November, 2010

Collection locality and specimen numbers are included. The two collection localities are in second-growth tropical lowland evergreen rain forest (collectors: J.L. Patton, K.C. Rowe, and J.A. Esselstyn).

Locality, MVZ and collector numbers	Contents of stomach
Gunung Balease	
225684 (JLP 25238)	Crammed; some pieces of fruit pulp and skin, but rest is mostly conglomeration of rhinotermitid termites (no soldiers, only workers and winged stages), at least one geophilomorph centipede; legs and isolated sclerites from other kinds of small insects (probably small beetles).
225687 (JAE 3474)	Full; mostly pulp and tiny seeds from figs; pulp and hard thin skin from one other kind of fruit; many fragments of rhinotermitid termites (highly fragmented, mostly workers); badly decomposed small macrolepidopteran larval skins; several segments from posterior tip of an earthworm (also some tissue that looks like internal earthworm parts); legs and sclerites from small adult beetles.
225688 (JAE 3492)	Full; small amount of fruit mash; few large hard, composite seeds that break into smaller chunks; large clumps of rhinotermitid termites (bodies of workers and soldiers, disintegrated head capsules); many larval remains from three different kinds of beetles; remains (legs, wings, pieces of elytra) of many small adult beetles; tiny bits of debris that resembles soil; fragments of moss. Clearly mostly full of insects.
225689 (JAE 3493)	Full; packed with remains of rhinotermitid termites (workers) and white spherical eggs (likely termite eggs); a bit of tan fruit mash and rind; pieces of fig rind with large seeds embedded in the inner wall; pieces of exoskeleton of a large adult insect.
225693 (JLP 25237)	Full; few macrolepidopteran larval skins; many remains (head capsules, legs, abdomen) of rhinotermitid termites; at least one large cursorial (1.5–2 in. long) beetle larva chewed into pieces; internal tissue and sclerites of legless smaller beetle larvae; few ants; a few very small intact legless beetle larvae (usually found on fruit); unidentified pulp (blackish debris eroding from blackish chunks).
225694 (JLP 25238)	Full of reddish brown fruit mash; mixed in are a few fragments of a small adult insect (probably a beetle).
225707 (KCR 1166)	Partially full; mostly brown, tan, and reddish fruit pulp; a few fragments of a small insects; one small macrolepidopteran larval skin. The insect parts are minor and fruit pulp is the main component.
225708 (KCR 1170)	Partly full; mostly tan fruit cut into small pieces; moderate amount of rhinotermitid termites (head capsules most evident); intact geophilomorph centipede; few fragments of a small adult insect.
225710 (KCR 1175)	Full, some peanut butter bait, rest fruit mash and one chewed large beetle larva (covered with setae).
225711 (KCR 1177)	Full; fruit pulp and skin; numerous fragments from small adult beetles mixed in with the pulp.
225712 (KCR 1179)	Partly full; mostly fruit pulp and skin, including coconut bait; fragments of legs and isolated sclerites of small insects.
225812 (KCR 1168)	Full; tan, somewhat fibrous fruit mash with slivers of skin; mixed in are a few fragments of small insects.
Desa Lawaki Jaya	
225690 (JAE 3539)	Partly full; contents as in 225715, remains of rhinotermitid termites and what appears to be termite nest debris; no sign of figs.
225691 (JAE 3540)	Full; dark gray claylike debris containing small white inclusions (same material as in 1198); tannish orange pulp packed with white seedlike objects, one of the figs; fragments of rhinotermitid termites (bodies, fragmented head capsules).
225700 (JLP 25308)	Full: dark brownish fruit mash in which are mixed fragments of small insects; a few rubbery blackish pieces that are probably snail.
225703 (JLP 25312)	Partially full; fruit pulp mixed with unidentified debris; numerous rhinotermitid workers and winged stages.
225705 (25325)	Partially full; chopped fruit pulp mixed with fragments of rhinotermitid termites.
225715 (KCR 1192)	Packed; black and tan debris in which are mixed fragments of many rhinotermitid termites. The debris may be part of termite nest—seen it in one other stomach (25237); pieces of fig rind and a lot of endosperm containing tiny fig seeds.

TABLE 55
(*Continued*)

Locality, MVZ and collector numbers	Contents of stomach
225716 (KCR 1197)	Full; all remains of rhinotermitid termites mixed with debris that appears to be from termite nest.
225717 (KCR 1198)	Full; a few intact adult ants, ant fragments and head capsules; many ant pupal cases; chunks of rubbery invertebrate tissue that is likely snail; tiny black "seeds" everywhere that could be fig, some larger black seeds; clay-like debris containing small elongate white particles packed together; a few rhinotermitid termites. Looks as if rat dug into or beneath in rotting wood and found a few termites and ant colony.
225719 (KCR 1202)	Full, mostly fruit pulp containing small tan seeds; also chunks of invertebrate tissue that resembles well chewed earthworms, but cannot detect external indication of segments (could be snail tissue but did not find operculum).
225720 (KCR 1203)	Full; same material as in 225715, remains of rhinotermitid termites and what appears to be termite nest debris; no sign of figs.
225721 (KCR 1204)	Packed; unidentified debris and rhinotermitid termite remains; also what appears to be pieces of fruit.

If a rat was eating fruit and offered an insect, the fruit was instantly dropped and the insect yanked from my fingers.

Items constituting the diet of *B. andrewsi* are summarized below.

Earthworms—Captives grabbed earthworms from my fingers and consumed them in less than a minute, handling the worms in the same fashion as described for *B. chrysocomus*. Cut segments of earthworms were found in stomachs of other *B. andrewsi* (tables 54, 55).

Snails—When the three captives were offered snails (half-inch to an inch in diameter), they unhesitatingly began to process them. Each rat held the shell in its front paws, made an opening with its incisors and then extracted the snail's body, all of which was consumed. The behavior was similar to that I described for *B. chrysocomus* (see that account).

Insects and other arthropods—Captives were offered moths, two kinds of large crickets (3 inches long), grasshoppers, praying mantises, several kinds of adult beetles, and large beetle larvae found in dry and rotting wood. All were quickly accepted and eaten, the behavior with these prey items was very similar to that described for *B. chrysocomus*. Contents of stomachs included rhinotermitid termites, adult ants and ant pupal cases, a variety of adult and larval beetles (including legless and cursorial larvae), macrolepidopteran larvae, and geophilo-

morph centipedes (tables 54, 55). Rhinotermitid termites were the most common insect found in stomachs, 18 of 42 stomachs contained these insects (I omitted stomachs that were empty or contained only bait); the stomach of a rat collected at Kuala Navusu was crammed with worker and soldier rhinotermitid termites and contained no other invertebrates and no fruit.

The stomach contents of a rat collected on Gunung Balease illustrates the kinds of insects procured by *B. andrewsi*. The stomach was full, containing a few macrolepidopteran larval skins, many remains of rhinotermitid termites (head capsules, legs, abdomens), at least one large cursorial beetle larva (about 2 inches long) chewed into pieces, internal tissue and sclerites of smaller legless beetle larvae, a few very small intact legless beetle larvae, a few ants, and a bit of unidentified blackish debris.

Other invertebrates—I gave an adult male a small land crab, which he quickly accepted, used his front feet to manipulate the crab, bit the carapace in several places, but then rejected it, and showed no further interest.

Vertebrates—I did not find vertebrate remains in the stomachs examined, but two of the captives readily accepted and consumed geckos. The largest offered was about 7 inches long, 4 inches of which were head and body. I held it by the body and presented it to an adult male who instantly grabbed the

gecko by the head and pulled it out of my fingers. He bit the head, chest, and abdomen several times and then manipulated the lizard until its head was between the front paws and then in his mouth. By this time the tail had come away from the body and the gecko was immobile. The rat began eating from the nose back toward the rump. Occasionally the lizard jerked, but the rat quickly placed a hind foot on the lizard's pelvis to stabilize the gecko as it chewed on the other end. Once, the rat turned the gecko's body around and ate from the rump for a bit, then returned to the head, finally consuming the entire body; the detached tail was also eaten. The process took just a few minutes and only a few pieces of breast bone remained on the cage floor. It was clear the rat recognized the gecko as prey and did not hesitate to attack and eat it. Another rat ate a smaller gecko in much the same fashion. I found the geckos inside decaying tree limbs lying on the forest floor, the same kinds of rotting wood that provides habitat for cerambycid beetle adults and larvae, rhinotermitid termites, and ant pupae, as I described in the account of *B. chrysocomus*.

Fruit—Different fruits offered the three captives were unambiguously accepted or rejected. Figs—whether from tall canopy-forming strangler *Ficus*, other nonstrangler species that contributed to the canopy, or understory species—were accepted and readily consumed by all the captives. Figs are one of the most common of the identifiable fruit remains found in contents of stomachs (tables 54, 55). Also accepted and eatern were fruit from understory palms (*Pinanga* sp.); from the trees *Sandoricum* sp., *Sapium* sp., *Palaquium obtusifolium*, and another unidentified member of Sapotaceae; large seeds from the tree *Hydnocarpus sumatrana*; fruit from the vine *Gnetum cuspidatum*; and fruit from *Pandanus*.

The captives ignored the dark green fruit from *Matthaea sanata*, a shrubby tree growing in understory; from the nutmegs, *Knema* sp. and *Myristica* sp.; the citruslike fruit from the understory tree *Dillenia serrata*; large, hard nuts from fruit of the understory tree, *Pangium edule*; and the large, green fruits from the understory tree, *Kjellbergiodendron celebicum*.

Rarely did a stomach contain only fruit. For example, one rat from Gunung Balease had a stomach full of mostly pulp and tiny seeds from figs as well as pulp and hard thin skin from one other kind of fruit. Many fragments of rhinotermitid termites, small macrolepidopteran larval skins, several segments of an earthworm, and legs and sclerites from small adult beetles were mixed with the fruit remains.

Fungi—The ear fungus *Auricularia delicata* (called "karoko" by the local people) and a few kinds of jelly fungi were broken into pieces by all three of the captives, but the fragments were eventually dropped to the cage floor and ignored. I did not find macroscopic remains of fungi in any of the stomachs examined.

Overview—Like *B. chrysocomus* (see that account), *B. andrewsi* consumes fruit, mostly figs, disdains fungi, and is an aggressive predator of invertebrates and small vertebrates. Near camp on the Kuala Navusu, my helpers and I searched for places on the forest floor where *B. andrewsi* would find invertebrates. We first looked to earthworms. During the night after a rain we found earthworms scattered on the ground surface, beneath leaf litter, or in pools of water near the stream. During the day we located them in rotting sections of tree trunks and limbs or in the soil beneath. We also found burrows, each marked by a pile of processed soil, some as tall as 2 inches. Several small worms might occupy a single burrow and were found 2–6 inches below ground. Burrows were always on well-drained slopes or stream terraces. Because the earthworms are spotty in their distribution, it is difficult to provide any meaningful estimate of worms available to *B. andrewsi* per unit area. We did find one place on a steep hillside above a wet ravine where a piece of wood had decayed into slivers. The soil was stable. We collected 21 earthworms (8 g total) in a square meter; all occurred throughout the soil from from near the surface to a depth of 6 inches.

The most common site for both large and small worms was within and beneath rotting trunks and limbs from old treefalls. At a certain stage of decomposition the wood becomes soft and is mixed at soil level with a gray or bluish gray dense claylike layer; the

worms are in this layer, and in passages within the wet and rotting pulpy wood.

Decaying sections of old treefalls lying on the forest floor also provide habitat for a variety of invertebrates in addition to earthworms that are sought and eaten by *B. andrewsi*. I tore apart a long section of rotting trunk (15 ft long, 10–12 inches in diameter) lying on a terrace about 30 ft above a stream. The pulpy wood was saturated with water in places and the underlying claylike layer nearly liquefied. Pigs had torn into the wood in two places. I extracted 30 grams of invertebrates (excluding termites—the terrestrial rhinotermitid termites, I presume—that infested the entire trunk and were too numerous to collect and weigh): 21 earthworms (some large, up to 5 inches long, most smaller, 2–3 inches), 3 mole crickets, and 6 small adult and nymphal cockroaches. From different and drier decaying trunks, I extracted scorpions, two kinds of diplopods (millipedes), several kinds of chilopods (centipedes), large adult and larval beetles, a gecko, and a legless lizard.

Small frogs and snails seemed to be most prevalent on the banks and terraces bordering streams. I found snails on top of the leaf litter and just above ground on stems of shrubs and ferns.

Nests: I placed dry leaves in the cages of two adults and a juvenile. Each formed a pile of leaves, then burrowed into the side, and came out at the top of the pile. During the day the rat slept in the top of the pile nearly concealed on all sides by the leaves. After a few days the leaves became compacted and each rat would shift them around until they again formed a deep cup-shaped sleeping chamber.

I assume that *B. andrewsi* lives in underground burrows. Near Kuala Navusu one rat was caught in a trap placed at the mouth of a burrow partially concealed by rocks on a hillside.

ECTOPARASITES, PSEUDOSCORPIONS, AND ENDOPARASITES: Sucking lice, ticks, and mites are the ectoparasites recorded to date from *Bunomys andrewsi* (table 14). An undescribed species of *Hoplopura* (Anoplura) is unique to *B. andrewsi* (Durden and Musser, MS.).

Immatures of the ticks, *Dermacentor* sp. and *Haemaphysalis* sp. (Acari, Ixodidae),

have also been collected from a variety of hosts in addition to *B. andrewsi*: shrews (the endemic *Crocidura elongata*, and the commensal *Suncus murinus*), rusa (*Rusa timorensis*, nonnative), three endemic squirrels (*Rubrisciurus rubriventer*, *Hyosciurus heinrichi* and *H. ileile*), 10 other species of endemic murid rodents (*Bunomys fratrorum* and *B. chrysocomus*; *Echiothrix centrosa*; *Maxomys hellwaldii*, *M. musschenbroekii*, and *M. wattsi*; *Paruromys dominator*; *Taeromys* sp.; *Rattus hoffmanni* and *R. facetus* [recorded as *R. marmosurus*]), and three nonnative *Rattus tanezumi* (recorded as *R. rattus*), *R. argentiventer*, and *R. exulans* (Durden et al., 2008; L.A. Durden, personal commun.). Two species of mites in the genus *Laelaps* (Acari, Laelapidae) have been documented from *Bunomys andrewsi* (Van Peenen et al., 1974).

Chiridiochernes platypalpus is a pseudoscorpion described from *B. andrewsi* that was trapped at the base of Gunung Lompobatang on the southwestern peninsula (Muchmore, 1972).

Two kinds of endoparasites are known infect *B. andrewsi*. Host specimens from the Mamasa region were found to be parasitized by the nematode *Bunomystrongylus miyagii* (Trichostrongylina, Heligmonellidae), which is host-specific (Hasegawa and Mngali, 1996). *Bunomys andrewsi* is also a host for a species of liver fluke, *Platynosomoides*, which was also recovered from the nonnative *Rattus tanezumi* (Van Peenen et al., 1974).

SYNONYMS: Three scientific names prove to by synonyms of *Bunomys andrewsi*. Data attached to the holotype and type locality, description of the taxon as originally published, and reasons for its inclusion in *B. andrewsi* are presented below, ordered by publication date.

Rattus adspersus Miller and Hollister, 1921a: 71. HOLOTYPE: USNM 219602, an adult male (skin and skull; measurements are listed in table 40) collected January 22, 1918, by H.C. Raven (original number 3427). TYPE LOCALITY: Indonesia, Sulawesi, Propinsi Sulawesi Tengah, Pinedapa (01°25′S, 120°35′N), 100 ft (30 m; locality 3 in the gazetteer and on the map in fig. 50), northeastern margin of the central core.

Miller and Hollister (1921a:71) diagnosed *Rattus adspersus* as:

Related to *Rattus chrysocomus* (Hoffmann) of North Celebes, but general coloration darker; the characteristic agouti-like flecking more brownish, less yellowish; sides and underparts especially less yellowish. Tail shorter, almost unicolor, only very slightly lighter colored on underside near base, and without light colored tip. Skull smaller.

The specimens of *adspersus*, remarked Miller and Hollister (1921a: 72),

have been compared with about 150 skins and skulls of *Rattus chrysocomus* (including for the present *Mus fratrorum* Thomas) from numerous localities in North Celebes. The specimens of *chrysocomus* vary considerably in size but average larger than examples of the new form from Middle Celebes, with much more distinctly yellowish flecking. The northern species always has the terminal portion and the whole underside of the tail whitish. The color of the upperparts in some specimens of *adspersus* approaches very closely to that of the type specimen of *Rattus andrewsi* (Allen) from Pulo Boeton, off the coast of southeastern Celebes, which proves to be a member of the *chrysocomus* group.

Miller and Hollister identified as *adspersus* 23 specimens from Pinedapa and two from Tuare. Three additional examples are from Labuan Sore (see locality 1 in the gazetteer), one had originally been determined to be *Rattus rallus* by Miller and Hollister, the other two as *Rattus hoffmanni*. Their *adspersus* is unquestionably phenetically distinct from the samples collected by Raven from the northeastern peninsula that Miller and Hollister thought were *B. chrysocomus* but are actually *B. fratrorum*. The holotype of *andrewsi* resides in USNM and was handy for comparison. While Miller and Hollister recognized a link between *adspersus* and *andrewsi* in coloration of the dorsal pelage, they presumabbly did not think the resemblance indicated attributes of a single species, which is my hypothesis based on analyses of morphometric traits as well as chromatic aspects of the pelage.

Miller and Hollister's reference of *adspersus* to a "*chrysocomus* group" was reaffirmed strongly by Tate (1936: 554) when remarking on the holotype of *adspersus* he wrote that "The skull of this form unquestionably indicates its affinity to the *chrysocomus* group." Between 1936 and 1969, *adspersus* retained its status as a species of *Rattus* in, first, a *Rattus chrysocomus* group (Ellerman, 1941), then a *Rattus coelestis* group (Ellerman, 1949), in subgenus *Rattus* (Laurie and Hill, 1954), and finally in subgenus *Bullimus* of *Rattus* (Misonne, 1969). Except for *chrysocomus*, *fratrorum*, *colestis*, *koka*, and *andrewsi*, Ellerman (1949) and Laurie and Hill (1954) relegated all the other taxa that had been associated with a *Rattus chrysocomus* group to subspecies of *R. adspersus* (see table 4).

Rattus penitus inferior Tate and Archbold, 1935a: 6. HOLOTYPE: AMNH 101059 (skin and skull; measurements are listed in table 40), an adult male collected January 23, 1932, by G. Heinrich (original nuber 808). TYPE LOCALITY: Indonesia, Propinsi Sulawesi Tenggara (southeastern peninsula of Sulawesi), Wawo (03°41′S/121°02′E), 50 m (locality 21 in gazetteer and on the map in fig. 50).

Rattus penitus inferior was characterized by Tate and Archbold (1935a: 6) as "A large member of the *chrysocomus* group with coarser pelage than either *penitus penitus* or *penitus sericatus*. Under parts irregularly suffused with hazel. Skull massive for the group, with long, broad palatal foramina." They then provided a description of the holotype:

Pelage of type with guard hairs distinct, though not longer than wool hairs; color of tips of hairs dull fawn color, the gray bases showing through and dulling the total effect. Under parts with fur mostly gray-based, tips whitish on throat, a little on sides and inside of limbs, otherwise tips hazel. Line of demarcation not sharp. Tail white beneath, not white-tipped.

Skull of type with large muzzle and sloping zygomatic plate. Length of palatal foramina exceeding length of molar crowns (118 per cent), which in turn exceeds length of bulla (110 per cent). The molar series, though short, is made up of rather heavy individual teeth (width of m^1 is 62 per cent of its length).

Their description of *inferior* was based on the holotype and nine additional specimens from southeastern Sulawesi (see localities 16 and 17 in the gazetteer and on the map in fig. 50). Both Tate (1936) and Ellerman

(1941) treated *inferior* as a subspecies of *Rattus penitus*, Sody (1941) associated *inferior* with *penitus* but arranged the latter as a species of *Frateromys*, and later Ellerman (1949) treated *inferior* as a subspecies of *Rattus adspersus*, a link accepted by Laurie and Hill (1954). By the early 1990s, *inferior* was subsumed under *Bunomys andrewsi* (Corbet and Hill, 1992) where it has remained (Musser and Carleton, 1993, 2005; see table 4). See the preceeding section on Comparisons where the identity of the holotype of *inferior* as a sample of *B. andrewsi* and not *B. penitus* is demonstrated.

Rattus penitus heinrichi Tate and Archbold, 1935a: 6. HOLOTYPE: AMNH 101006 (skin and skull; measurements are listed in table 40), an adult male collected August 31, 1931, by G. Heinrich (original number 365). TYPE LOCALITY: Indonesia, Propinsi Sulawesi Tengah, Lombasang (05°16′S, 119°55′E), 1100 m (locality 25 in the gazetteer and on the map in fig. 50), in the foothills of Gunung Lompobatang, southwestern peninsula of Sulawesi.

Rattus penitus heinrichi was characterized by Tate and Archbold (1935a: 6) as "A medium-sized member of the *chrysocomus* group with dense though rather crisp pelage." The holotype was described as follows:

> Pelage of type coarser than that of *R. p. penitus* or *R. p. sericatus*, and much denser than *R. p. inferior*. Color above, rather strong sayal brown at tips of hairs, giving a general effect of natal brown due to dark-colored hair bases showing through from below. Under parts long-haired, the hairs between pinkish buff and cream buff, with gray bases. Hands and feet thinly clothed with whitish hairs. Tail whitish beneath, the scale-hairs about one and one-half scale lengths.

> Skull of type more delicately formed than that of *p. inferior*, with narrower rostrum (? constant), smaller palatal foramina, shorter bullae, narrower mesopterygoid fossa.

Twenty-one specimens from Lombasang (locality 25 in gazetteer), in addition to the holotype, were identified as *heinrichi*.

After its description, *heinrichi* remained a subspecies of *Rattus penitus* in synoptic works published during the late 1930s and early 1940s (Tate, 1936; Ellerman, 1941); was transferred to *Frateromys*, its identity intact

as a subspecies of *penitus*, by Sody (1941); and later arranged as a subspecies of *Rattus adspersus* by Ellerman (1949) and Laurie and Hill (1954). During the 1990s, Corbet and Hill (1992) and Musser and Carleton (1993) recognized *heinrichi* as a separate species, but by the next decade it lost its identity under *Bunomys andrewsi* (Musser and Carleton, 2005) where it currently remains (table 4). Why *heinrichi* is a peninsular population of *B. andrewsi* and not a subspecies of *B. penitus* is discussed in the preceeding section covering Comparisons.

SUBFOSSILS: Two maxillary fragments, three pieces of dentaries, and an incisor fragment are the subfossils representing *B. andrewsi* that have been found in caves on the southwestern peninsula of Sulawesi.

Two maxillary fragments, two pieces of dentaries, and an isolated segment of incisor (figs. 70, 71; tables 56, 57) were excavated from a shallow deposit forming the floor of a small rock shelter, Batu Edjaja II, that has been described by Mulvaney and Soejono (1970; 167, plate V; also see locality 26 in the gazetter and on the map in fig. 50). A few artifacts were recovered (geometric microliths and pottery shards), but the deposit had been so disturbed that no reliable age could be attached to them or to the rodent remains. A sample of charcoal from near the bottom of the deposit was determined to be "modern" by C-14 dating. David Bulbeck (in litt., 1997) informed me that "Batu Ejaya 2 has abundant geometric microliths suggesting some occupation by at least 3000–2000 B.P., but the basal radiocarbon date is modern and the deposits are obviously disturbed comprehensively" (also see Bulbeck, 2004; Simons and Bulbeck, 2004).

One right dentary fragment lacking molars (fig. 71; tables 56, 57) was recovered from sediments excavated at Ulu Leang I, a cave in the Maros region of the southwestern peninsula (locality 24 in the gazetteer and on the map in fig. 50; also see the map of archaeological sites in Simons and Bulbeck, 2004: 168). Excavations in the cave were described by Glover (1976), who also provided me with 8785 ± 45 years B.P. as the date of the horizon (layer V) in which the piece was located (Glover, personal commun.); a different assessment by Bulbeck (2004: 132)

Fig. 70. Subfossil maxillary fragments (×10) of *Bunomys andrewsi* excavated from Batu Ejaya II, a cave at the southern tip of the southwestern peninsula of Sulawesi (see gazetteer and the map in fig. 50). Upper image: AMNH 266963 (arrow points to small cusp t3 on the second molar, which is also found in 78% of the modern sample from the southwestern peninsula; table 10). Lower image: AMNH 265015. Measurements and descriptive information are provided in the text and tables 56 and 57.

gives around 7500 B.P. for layer V. Specimens of *B. chrysocomus* were found in sediments from the same cave (see account of that species).

I compared all these subfossil fragments with modern samples of *B. chrysocomus* from Sadaunta in the west-central region of Sulawesi (no modern samples of *B. chryso-*
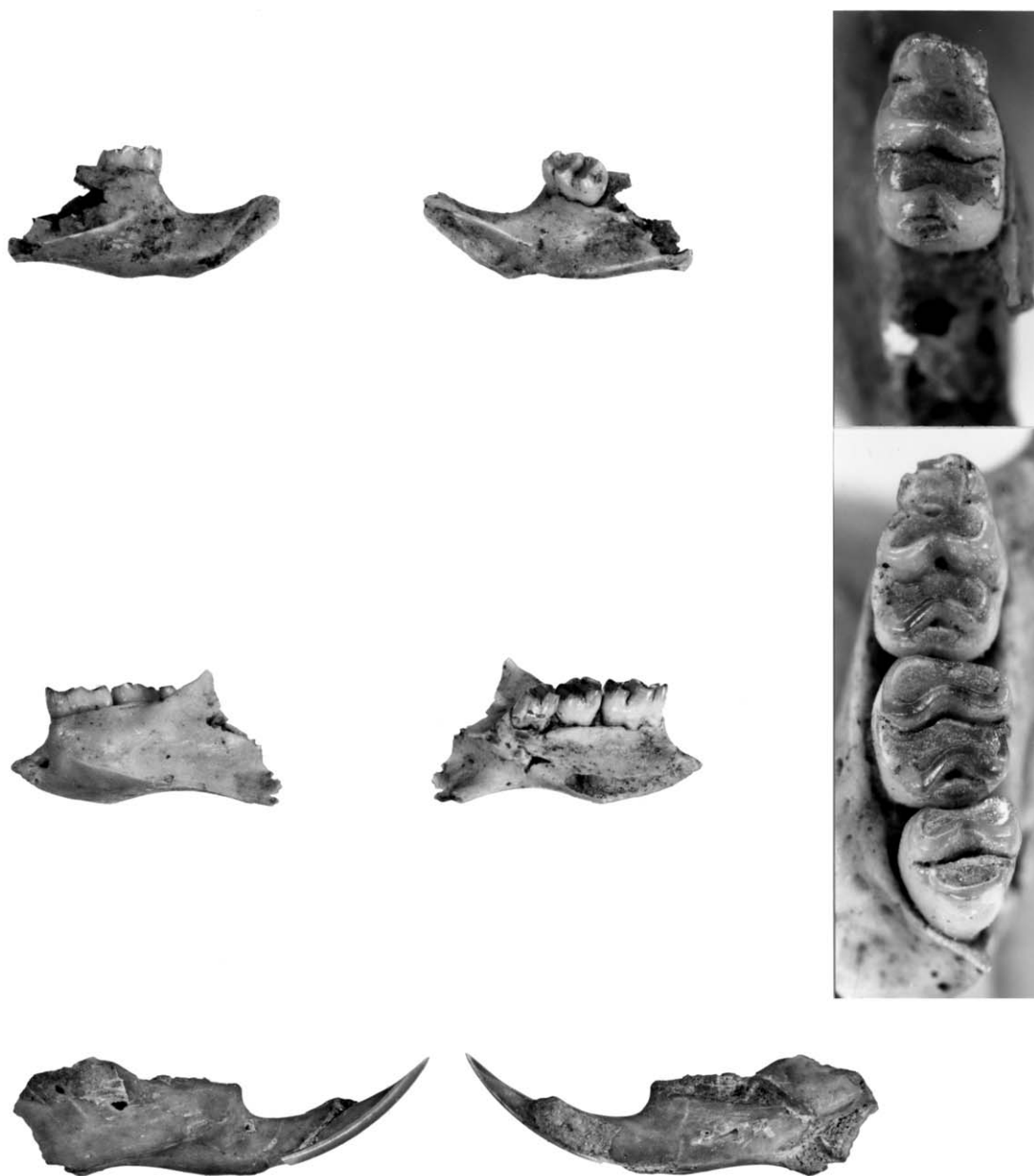
Fig. 71. Subfossil mandibular fragments of *Bunomys andrewsi*. Upper image: right dentary (×3) and first molar (×10) of AMNH 265014. Middle: left dentary (×3) and intact molar row (×10) of AMNH 265013. Both specimens were excavated from Batu Ejaya II, a cave at the southern tip of the southwestern peninsula of Sulawesi (see gazetteer and the map in fig. 50). Lower image: the right dentary (AMNH 266974; ×3) from Ulu Leang I, a cave about 40 km northeast of Ujung Pandang in the Maros region near the tip of Sulawesi's southwestern peninsula (see gazetteer and the map in fig. 50). Measurements and descriptive information are provided in the text and tables 56 and 57.

TABLE 56
Subfossil *Bunomys andrewsi* from the Southwestern Peninsula of Sulawesi

Cave and specimen	Age	Description
BATU EJAJA II		
AMNH 265015	adult	Left maxillary fragment containing partial first molar and intact second molar (fig. 70).
AMNH 265015	adult	Left maxillary fragment with intact first molar (fig. 70).
AMNH 265013	young adult	Fragment of left ramus of dentary with intact molar row; masseteric ridges and mental foramen evident; no incisor (fig. 71).
AMNH 256014	adult	Piece of anterior portion of right ramus of dentary containing intact first molar; no incisor (fig. 71).
AMNH 265020	adult	Distal fragment of right lower incisor.
ULU LEANG I		
AMNH 266974	adult	Anterior portion of right dentary with most of incisor; no molars (fig. 71).

comus are available from the southwestern peninsula), with a modern series of *B. andrewsi* collected at Lombasang on the lower flank of Gunung Lompobatang on the southwestern peninsula, and with a sample of *B. coelestis* from montane forest on Gunung Lompobatang. Whether maxillary fragments with upper molars, dentary fragments with or

TABLE 57
Measurements (mm) of Upper and Lower Molars from Subfossil and Modern Samples of *Bunomys andrewsi*, and Comparative Modern Samples of *B. chrysocomus* and B. coelestis
Mean ± 1 SD and observed range (in parentheses) is listed for the modern specimens, which are identified in footnotes. The subfossil fragments are described in table 56.

Locality and subfossils	BM1	BM2	clm1–3	alm1–3	bm1	bm2	bm3
BATU EJAJA II							
AMNH 562015	2.3	—	—	—	—	—	—
AMNH 269963	—	2.1	—	—	—	—	—
AMNH 265013	—	—	7.0	7.0	1.9	2.1	1.8
AMNH 265014	—	—	—	—	1.9	—	—
ULU LEANG I							
AMNH 266974	—	—	—	6.8	—	—	—
Modern specimens							
Bunomys andrewsi							
Lombasang[a]	2.2 ± 0.10	2.1 ± 0.09	6.9 ± 0.23	6.9 ± 0.22	1.8 ± 0.08	2.0 ± 0.09	1.6 ± 0.06
N = 18	(2.0–2.4)	(1.9–2.2)	(6.5–7.2)	(6.5–7.3)	(1.7–2.0)	(1.9–2.2)	(1.5–1.7)
Bunomys chrysocomus							
Sungai Sadaunta[b]	2.0 ± 0.05	—	6.2 ± 0.17	6.3 ± 0.21	1.8 ± 0.05	1.9 ± 0.06	1.6 ± 0.10
N = 20	(1.9–2.1)		(5.9–6.5)	(6.0–6.7)	(1.7–1.8)	(1.7–1.9)	(1.4–1.9)
Bunomys coelestis							
Gunung Lompobatang[c]	2.0 ± 0.09	—	6.1 ± 0.19	6.1 ± 0.22	1.6 ± 0.09	1.7 ± 0.06	1.4 ± 0.06
N = 20	(1.8–2.1)		(5.8–6.5)	(5.7–6.5)	(1.4–1.7)	(1.6–1.8)	(1.3–1.5)

[a] AMNH 100996, 100998–1006, 101008–015.

[b] Maxillary molars: AMNH 224079, 224081, 224085, 224086, 224089, 224096, 224099, 224100, 224102, 224113, 222118, 224119, 224121, 224126, 224130, 224135, 224138–40, 224143. Mandibular molars: AMNH 224102, 224105, 224108,224126, 224130, 224131, 224136, 224139, 224141, 224143, 224694, 224697, 224702, 224706, 224710, 224733, 224734, 224740–42.

[c] Maxillary molars: BMNH 97.1.3.12, 97.1.3.27; AMNH 101016, 101132, 101133, 101135, 101137, 101138, 101141–44, 101146, 101159, 101152, 101153, 101155, 101157, 101158. Mandibular molars: AMNH 101016, 101130–33, 101135–39, 101141–49, 101152.

without molars, or isolated incisor, all are larger than their counterparts in the samples of *B. chrysocomus* and *B. coelestis* and share conformation and tooth size with the specimens of *B. andrewsi* (table 57).

One dentary fragment I determine to be *B. andrewsi* has a complete molar row from which measurements of the individual molars could be obtained as well as crown and alveolar lengths of the molar row. I used these measurements, and those from comparable dimensions in the modern samples of *B. chrysocomus*, *B. coelestis*, and *B. andrewsi*, in a principal-components analysis to test my identity gleaned from side-by-side comparisons of specimens. The resulting specimen scores projected on first and second principal components associate the score for the subfossil with the sample of *B. andrewsi* from Lombasang (fig. 72). The high positive correlations (r = 0.84–0.96; table 58) among variables points to size as the primary factor spreading the scores along the first axis with those representing *B. chrysocomus* and *B. coelestis* with the smaller molars filling the left side of the scatter plot and those for *B. andrewsi* possessing heavier molars situated on the right. A similar pattern emerged when fewer measurements were employed in principal-components analyses using the same modern samples of *B. chrysocomus* and *B. andrewsi*, the same subfossil of *B. andrewsi*, and two subfossils of *B. chrysocomus* collected at Ulu Leang I (see the account of *B. chrysocomus*, fig. 35, and table 30).

One dental feature deserves mention. Cusp t3 occurs on the second upper molar in 78% of 18 modern specimens representing *B. andrewsi* collected at Lombasang. Within the sample the structure ranges in size from a tiny obscure bump to a large cusp defining the anterolingual border of the molar. Subfossil AMNH 269963 also has a small cusp t3 on the second upper molar. In the sample of *B. andrewsi* from Sulawesi's core and the southeastern peninsula, cusp t3 occurs on the second molar in only 17% of 70 specimens, and in 17% of 197 examples of *B. chrysocomus* from the west-central mountain block (table 10).

The next account describes a strictly montane species of *Bunomys* recorded from the west-central mountain block in the central core of Sulawesi and Pegunungan Mekongga on the southeastern peninsula.

Bunomys penitus (Miller and Hollister, 1921)

Rattus penitus Miller and Hollister, 1921a: 72.
Rattus sericatus Miller and Hollister, 1921a: 73.

HOLOTYPE: USNM 218686, the skin and skull of an adult male (original number 3109) collected January 21, 1917, by H.C. Raven. Measurements (external, cranial, and dental) and other relevant data are listed in table 40. The stuffed skin is an intact standard museum preparation. Both cranium and mandible are complete, all incisors and molars are present (fig. 73).

TYPE LOCALITY: Gunung Lehio (01°33′S, 119°43′E), 6000 ft (1830 m; locality 40 in the gazetteer and on the map in fig. 51), west-central mountain block, Propinsi Sulawesi Tengah, Indonesia.

EMENDED DIAGNOSIS: Among the largest in physical size (LHB = 155–242 mm, WT = 95–170 g, ONL = 39.3–46.1 mm) of the species in *Bunomys* and further characterized by the following combination of traits: (1) a long muzzle, broad head, and stocky body; (2) dorsal fur thick, lustrous, brownish gray speckled with buff, ventral fur grayish white, digits white, dorsal carpal and metacarpal surfaces typically white, ranging from grayish white to grayish brown in some samples; (3) claws on front feet short and somewhat delicate, long ungual tufts forming dense cover over front and hind claws; (4) tail shorter or slightly longer than length of head plus body (LT/LHB = 88%–102%), dark glossy gray to brownish gray on the dorsal surface, glossy white on the ventral surface (5) white tail tip common (98% of 293 specimens) and when present is long relative to tail length (mean = 21.0%, range = 3%–68%); (6) testes small relative to body size (range = 9%–13%); (7) shape of sperm head similar to that of *B. chrysocomus* but slightly wider with a shorter apical hook and spermatozoan tail; (8) robust skull with a long and wide rostrum, narrow and sloping zygomatic plate, long bony palate and incisive foramina, and large ectotympanic bulla relative to skull size; (9) molars large relative to size of skull and mandible; (10) large labial cusplet sits next to or partially merged with cusp t6 in
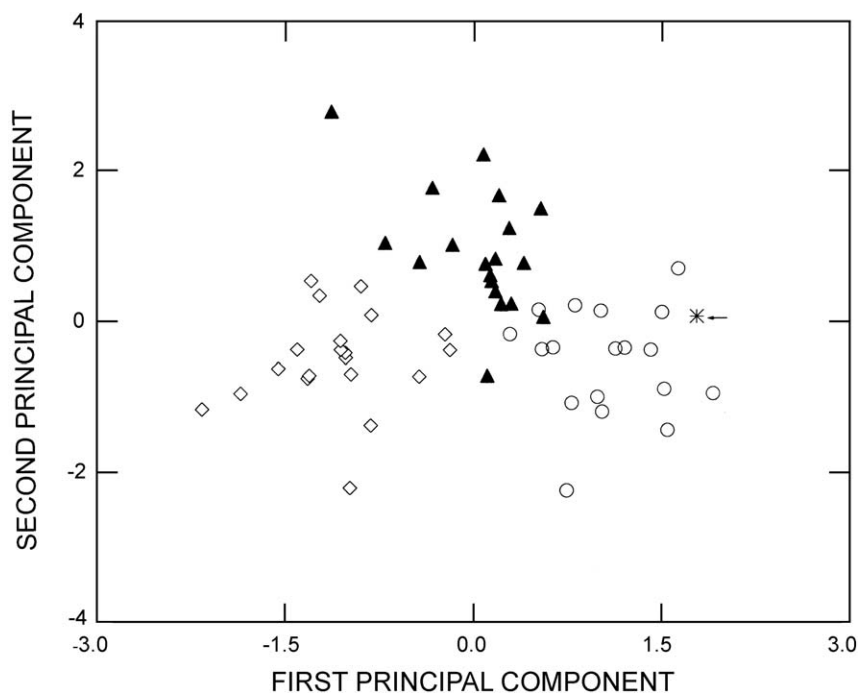
Fig. 72. Specimen scores representing *Bunomys chrysocomus* from Sungai Sadaunta in the northern part of the west-central region (filled triangles; $N = 20$), *B. coelestis* from Gunung Lompobatang at the southern end of the southwestern peninsula (empty diamonds; $N = 20$), *B. andrewsi* from Lombasang on the lower slopes of Gunung Lompobatang (empty circles; $N = 18$), and a subfossil from Batu Ejaya II (asterisk; AMNH 265013) projected onto first and second principal components extracted from principal-components analysis of five mandibular molar log-transformed variables. The factor score for the subfossil from Batu Ejaya II is closely associated with the aggregation of points representing *B. andrewsi*, not *B. chrysocomus* or *B. coelestis*. See table 58 for correlations (loadings) of variables with extracted components and for percent variance explained.

30% of sample, cusp t3 occurs frequently on second upper molar (62%) but not on third molar (5%); (11) anterolabial cusp present on second lower molar in about half of sample but absent from third lower molar; (12) anterior labial cusplets typically infrequent on first lower molars (8%), posterior labial cusplets typically present on first and second molars in all or most of sample (97%–100%); and (12) karyotype, 2N = 42, FNa = 58, FNt = 60 (females) or 61 (males).

GEOGRAPHIC AND ELEVATIONAL DISTRIBUTIONS: Samples of *Bunomys penitus* come from two major mountainous regions (see gazetteer, the map in fig. 50, and table 5). Most specimens have been collected from the west-central mountain block in Sulawesi's core where they were taken on ridges and peaks covered by lower and upper montane rainforest formations between 1285 and 2287 m: Gunung Kanino, Gunung Nokilalaki, Gunung Lehio, Rano Rano, Mamasa region (which includes Gunung Gandangdewata), Pegunungan Quarles, Gunung Rantemario, and Pegunungan Latimojong.

The other sample is from montane forest habitats between 1500 and 2000 m on Pegunungan Mekongga, the highest mountain complex on the southeastern peninsula of Sulawesi (highest point is 2500 m).

What other mountainous regions may harbor populations of *B. penitus* is unknown.

The range of *B. penitus* on the southeastern peninsula may be more expansive than is indicated by samples at hand. Northeast of Pegunungan Mekongga and south of Danau Towuti are ridges high enough (1500–2100 m) to support lower montane forests, but these

TABLE 58
Results of Principal-Components Analysis of
Bunomys andrewsi*, *B. chrysocomus*, and *B. coelestis
Samples of *B. andrewsi* from Lombasang
(southwestern peninsula), *B. chrysocomus* from
Sadaunta (west-central region), *B. coelestis* from
Gunung Lompobatang (southwestern peninsula),
and a subfossil from Batu Ejaya II (southwestern
peninsula) are compared. Correlations (loadings) of
five mandibular molar log-transformed variables
are based on 59 specimens; see figure 72.

Variable	Correlations	
	PC 1	PC 2
clm1–3	0.90***	0.31*
alm1–3	0.96***	0.07
bm1	0.92***	0.17
bm2	0.84***	−0.50***
bm3	0.88***	−0.40**
Eigenvalue	0.022	0.002
% Variance	81.8	9.4

*** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$.

highlands have not been surveyed for small mammals.

Pegunungan Pompangeo rises to more than 2500 m east of Danau Poso in the eastern sector of Sulawesi's core, and would also be a place to look for *B. penitus.*

Gunung Tambusisi, at the western end of the mountainous backbone along the eastern peninsula, has yielded *Bunomys prolatus* and *Maxomys wattsi* from its montane forests, but no *B. penitus* (see the account of *B. prolatus*). Whether *B. penitus* is absent from mountain forests covering higher elevations on Gunung Tambusisi and highlands east of there on the eastern peninsula or is replaced by *B. prolatus* or additional undescribed montane species of *Bunomys* can be determined only by careful trapping surveys.

SYMPATRY WITH OTHER *BUNOMYS*: In the west-central mountain block and on Pegunungan Mekongga, *B. penitus* is sympatric with *B. chrysocomus*; both species have been collected in the same trapline (see account of *B. chrysocomus*). With that exception, no other species of *Bunomys* has been found occupying the same montane habitat as *B. penitus* (table 5).

In addition to *B. chrysocomus*, other species of *Bunomys* occur in the west-central mountain block and on the southeastern

peninsula, but their ranges are elevationally parapatric to that of *B. penitus*. In the northern part of the west-central mountain block, *B. andrewsi* and *B. karokophilus,* n. sp., inhabit tropical lowland evergreen rain forest, but are absent from montane forest formations. In the southern portion of the block on Gunung Gandangdewata in Pegunungan Quarles, *B. penitus* is sympatric with three other *Bunomys* but not elevationally syntopic: *B. andrewsi* has been collected in tropical lowland evergreen rain forest at 1600 m, *B. penitus* in montane forest at about 2000 m, and *B. torajae* higher at 2500 and 2600 m. On the southeastern peninsula, *B. andrewsi* is found in lowland habitats adjacent to Pegunungan Mekongga, but not in montane forests.

DESCRIPTION: One of the most handsome of the species of *Bunomys*, *B. penitus* was described in 1921 by Miller and Hollister from five specimens collected at about 6000 ft on Gunung Lehio in the mountainous central region of Sulawesi (locality 40 in the gazetteer and on the map in fig. 51). The Latin, *penitus*, means "internal," "within," "inward," "inner," or "interior" (Brown, 1956: 436, 597) and the authors (who provided no etymology) were likely referring to the provenence of the sample in that it came from the core or "interior" of the island.

Defining traits of "*Rattus penitus*" were provided by Miller and Hollister (1921a: 72) in their diagnosis that was based on five specimens:

A mountain member of the *chrysocomus* group with long, soft, cinnamon-flecked fur; sides dark like upperparts; belly grayish buff; feet scantily haired with grayish or whitish, toes whiter. Entire underside and terminal third of tail above, whitish. Skull with extraordinarily enlarged rostrum, which is thickened throughout, and only very slightly tapering toward end; antorbital plate weak and sloping, without squarish angle.

Miller and Hollister (1921a: 73) remarked of "*Rattus penitus*" that "This large-snouted member of the *chrysocomus* group is very different from all the related forms …."

After 1921, Miller and Hollister's generic and specific combination was listed in most treatises and checklists published in the 1930s and early 1940s (Tate, 1936; Ellerman, 1941). An
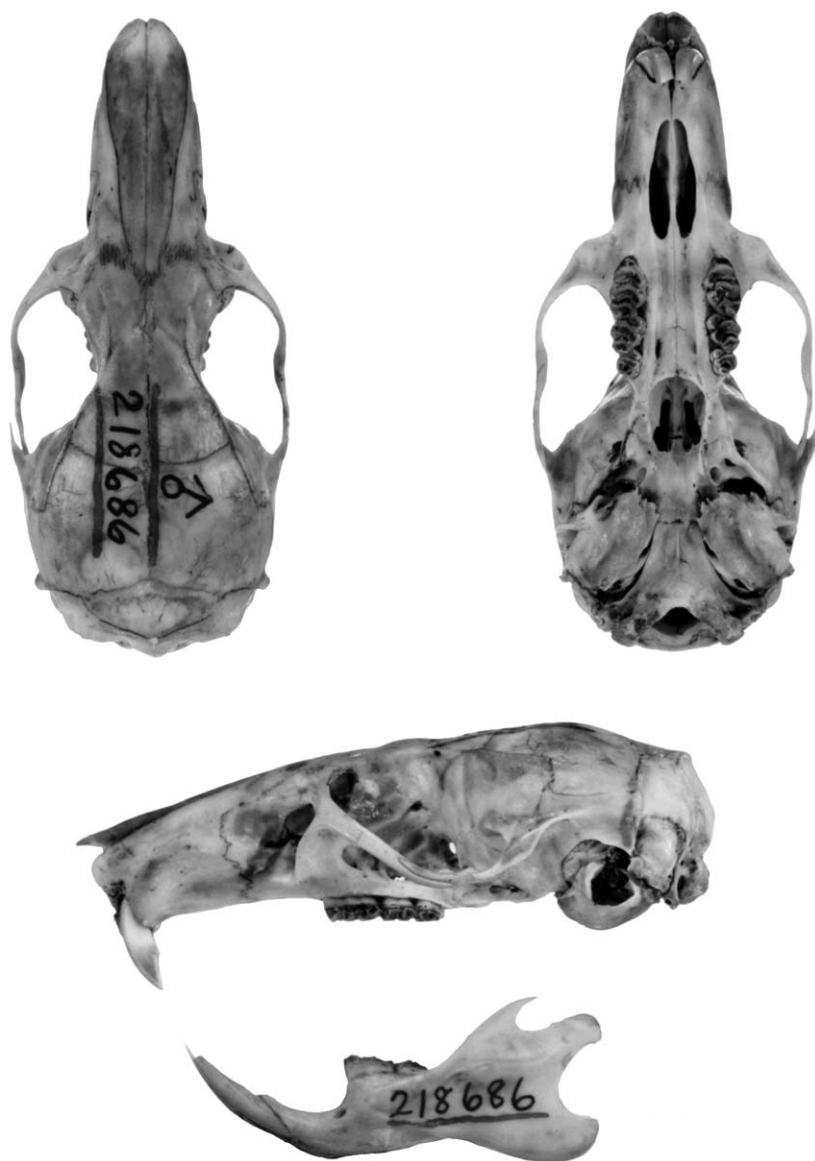
Fig. 73.   The holotype of *Bunomys penitus* (USNM 218686), an adult male from Gunung Lehio, 1829 m, in the northern portion of the west-central mountain block of Sulawesi. ×2.

exception was Sody (1941) who placed *penitus* in his newly described *Frateromys*, the genotype being *F. fratrorum*. Later, Ellerman (1949) and Laurie and Hill (1954) treated *penitus* as a subspecies of *Rattus adspersus*. By the 1980s, *penitus* had been transferred to *Bunomys* (Musser and Newcomb, 1983) and has been associated with that genus ever since (Corbet and Hill, 1992; Musser and Carleton, 2005;

the present and past nomenclatural associations of *penitus* are summarized in table 4.

Bunomys penitus is, in body size, the largest member of the *B. fratrorum* group (LHB = 155–242 mm, LT = 138–190 mm, LHF = 38–45 mm, LE = 23–29 mm, W = 95–170 g, ONL = 39.3–46.1 mm), has a broad head, long rostrum, chunky body, beautiful, soft, and luxuriant fur, and a moderately long

white-tipped tail (see the portrait of the species in fig. 6). The lustrous dorsal fur of adults is long (up to 25 mm) and very soft to the touch. Brownish gray speckled with buff is typical along the head, back, and rump (a result of the mixture of dark gray underfur, overhairs that are dark gray for most of their lengths and tipped brown and buffy bands, all intermixed with blackish guard hairs); sides of the body are paler—grayish brown. Because the guard hairs extend only slightly beyond the layer of overhairs, the surface of the fur feels smooth and looks even. The proximal portion of each forearm is encircled by dark gray. Sides of the muzzle are white.

The short (10–15 mm long) ventral coat is also soft and either grayish white or dark grayish white (tips of the gray hairs are unpigmented). On a few animals the underparts are grayish buff (the hairs are tipped with buff instead of being unpigmented) or a richer buffy gray. White patches (hairs are unpigmented for their entire lengths) occur on the chest, stomach, and inguinal region of many specimens in the sample. The contrast between dorsal and ventral coats is evident but not sharply demarcated. White tips of the hairs have altered to cream in older stuffed skins held for decades in museum collections, such as the specimens in USNM collected by H.C. Raven.

Ears (pinnae) are large and appear naked but are covered in short, fine, and unpigmented hairs. In life, the ears have a rubbery texture and are pigmented with gray and brown hues; gray, dark gray, grayish brown, and brownish gray marked the ears the freshly caught rats I examined. The dried ears of stuffed museum skins have lost the rubbery texture of the live animal and dry to dark brown with no hint of the actual range in hue and tone.

The tail ranges from slightly shorter to longer than the combined length of head and body (LT/LHB = 88%–102%; see table 41), and is bicolored except for the white tip. The entire ventral surface is glossy white in all animals I studied (best appreciated in freshly caught rats) and the white envelops all surfaces of the tail tip in 83%–100% (mean = 98%) of the specimens surveyed where the tip forms 3%–68% (mean = 21.0%) of the total tail length (table 8). Behind the white

tip, coloration of the dorsal surface and sides vary. The hues and tones I recorded from freshly caught rats are blackish gray (rare), dark glossy gray, grayish brown, and brownish gray (most common); two rats have a mottled gray dorsal covering between base of the tail and the white tip.

Front and hind feet are long and slender. Digits are white, and specimens in about 60% of the sample have white dorsal metacarpal and metatarsal surfaces; in the rest of the sample, these dorsal areas are white suffused with pale gray, dark gray, or pale brown. A few animals have white front feet and grayish or brownish hind feet. The naked palmar and plantar surfaces are either unpigmented or show gray tones. Claws are unpigmented, those on the front digits are very short relative to lengths of the digits and appear weak; a few ungual hairs spring from the base of each claw. Claws on the hind feet are longer and nearly completely concealed by long and dense tufts.

Females have four teats, arranged in two inguinal pairs. The scrotal sac of males is gray and sparsely haired (appears naked), and the testes are small relative to body size (9%–13%; table 9). Spermatozoan morphology is described by Breed and Musser (1991).

The juvenile coat covering upperparts of the head and body is duller and darker than that of the adult fur—a muted grayish brown (lacks buffy overhair tips). It is dense, fine, and very soft to the touch. Underparts are grayish white as in the adults, but the hairs are finer and shorter. White patches are prominent on the chest and inguinal region. Ears are dark gray or grayish brown. Front and hind feet are pigmented as in the adults. The tail pattern is also similar: glossy white over the ventral surface and around the tip, glossy dark gray or grayish brown on the dorsal surface and sides behind the tip.

The large skull of *B. penitus* with its long and wide rostrum and narrow zygomatic plate is distinctive (figs. 52–54, 73; tables 42, 61, 62). Among members of the *B. fratrorum* group, only *B. karokophilus,* n. sp., possesses as narrow a zygomatic plate (see table 42). Other noteworthy traits of *B. penitus* are its relatively narrow interorbital region, long and broad incisive foramina, long palatal bridge, wide mesopterygoid region, and large
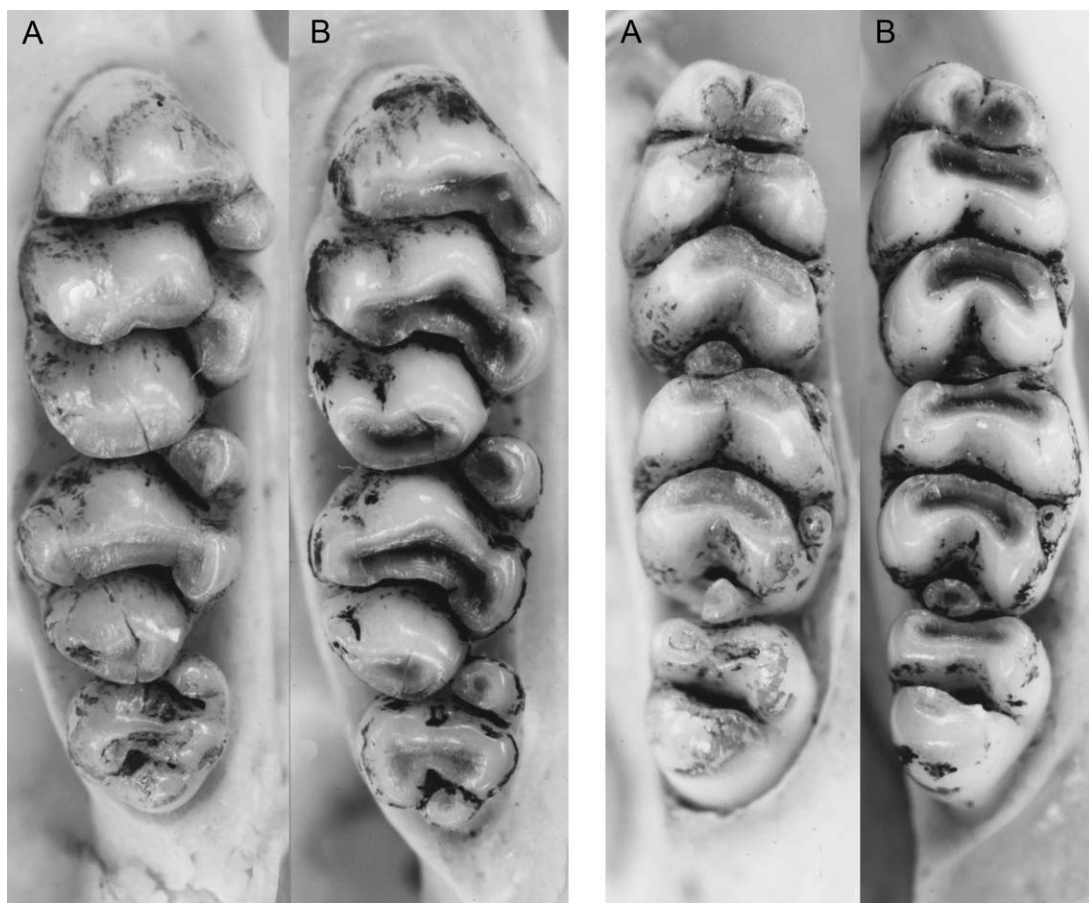
Fig. 74.   Occlusal views of right maxillary (left pair) and mandibular (right pair) molar rows from two specimens of *Bunomys penitus*. **A**, very young adult showing slight wear (AMNH 223856; CLM1–3 = 7.5 mm, clm1–3 = 7.5 mm). **B**, adult with average degree of wear (AMNH 225274; CLM1–3 = 7.6 mm; clm1–3 = 7.8 mm). Note the absence of a labial cusplet next to the large cusp t6 on the first upper molar (such a labial cusplet is shown in fig.75); of 215 specimens surveyed, 150 (70%) lacked the cusplet. An anterolabial cusp sits at the anterolabial corner of the second lower molar in about half the sample (55%) but is absent from the third molar (table 11).

ectotympanic bullae. Each dentary is similar in shape to those of other members in the *B. fratrorum* group, with the exception of its longer incisor sheath anterior to the molar row.

Large molars with simple occlusal patterns are typical of *B. penitus* (figs. 74, 75; table 10). On the first upper molar, a large labial cusplet sits adjacent to or is partially merged with cusp t6 in 30% of the sample (fig. 75), a configuration not present in other species of the *B. fratrorum* group or in members of the *B. chrysocomus* group. Cusp t3 is present on the second upper molar in

62% of the sample, but is rarely seen on the third molar (5%), although when present is often large (fig. 75). As in other species of *Bunomys*, an anterior labial cusplet is generally absent from the first lower molar, but a posterior labial cusplet typically forms part of the chewing surfaces of both the first and second lower molars (figs. 74, 75). An anterolabial cusp is present on the second lower molar in about half the sample (55%) but absent from the third molar in all specimens surveyed (fig. 74; table 11).

KARYOTYPE: 2N = 42, FNa = 58 for both sexes, FNt = 60 for females and 61 for males,

Fig. 75.   Occlusal views of right maxillary (**A, B**) and mandibular (**C**) molar rows illustrating variation in particular cusps and cusplets in the sample of *Bunomys penitus*. On the first upper molar in 65 of 215 specimens surveyed (30%), there is a large labial cusplet (short arrows) that is either separate from the adjacent cusp t6 (as in **A**) or partially merged (but still evident) with the larger cusp t6 (shown in **B**); contrast this pattern with the usual configuration shown in figure 74 where a labial cusp is not present. Cusp t3 (long and thin arrows) occurs (**B**) on the second upper molar in 62% of the sample surveyed, but is absent from the remainder of the sample (as in fig.74A), and is part of the third molar (**B**) in only 5% of the sample (table 10). All specimens surveyed exhibit a small, moderately large, or huge posterior labial cusplet (stubby arrow in **C**) on the first lower molar (as exhibited by the lower molars in figs.74 and 75); an anterior labial cusplet is rare (table 11). The second lower molars of nearly all specimens in the sample also bear posterior labial cusplets (stubby arrow in **C**) with a comparable range in size. The second lower molar in C is without an anterolabial cusp, which is absent in about half the sample (45%) and absent from the third molar in all specimens surveyed (table 11). **A**, AMNH 223818 (CLM1–3 = 7.7 mm); **B**, AMNH 223846 (CLM1–3 = 7.8 mm); **C**, AMNH 223844 (clm1–3 = 7.2 mm).

comprised of seven pairs of metacentric chromosomes, two pairs of subtelocentrics, and 11 pairs of acrocentrics; the presumed sex chromosomes of the female are acrocentrics, the male has an acrocentric and a submetacentric (table 12).

COMPARISONS: Samples of *B. penitus* were compared with those of *B. torajae, B. fratrorum,* and *B. andrewsi* in the accounts of those three species; contrasts between *B. penitus* and *B. karokophilus,* n. sp., will be addressed in the account of the latter. Here

TABLE 59
Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from All Population Samples for *Bunomys chrysocomus*, *B. penitus*, and *B. prolatus*
Mean $\pm$ 1 SD and observed range (in parentheses) are listed.

Variable	B. chrysocomus	B. penitus	B. prolatus
N	232	185	8
ONL	38.3 ± 1.12	43.0 ± 1.24	41.8 ± 1.03
	(35.8–41.1)	(39.3–46.1)	(40.4–43.2)
ZB	18.1 ± 0.64	19.6 ± 0.70	17.8 ± 0.38
	(16.3–19.8)	(17.0–21.4)	(17.2–18.3)
IB	6.4 ± 0.23	6.8 ± 0.25	7.1 ± 0.23
	(5.8–7.2)	(6.1–8.3)	(6.9–7.4)
LR	13.5 ± 0.59	16.1 ± 0.66	15.7 ± 0.61
	(12.0–15.1)	(14.6–18.1)	(14.7–16.4)
BR	6.8 ± 0.36	8.0 ± 0.37	6.7 ± 0.36
	(5.6–7.7)	(7.0–9.0)	(6.1–7.1)
BBC	15.5 ± 0.41	16.5 ± 0.45	16.3 ± 0.37
	(14.2–16.8)	(15.1–17.7)	(15.7–16.9)
HBC	10.8 ± 0.38	11.8 ± 0.36	11.4 ± 0.19
	(10.0–12.1)	(10.9–12.7)	(11.0–11.6)
BZP	3.2 ± 0.26	3.0 ± 0.22	2.8 ± 0.10
	(2.6–3.9)	(2.4–3.6)	(2.6–2.9)
LD	10.2 ± 0.54	11.3 ± 0.53	11.5 ± 0.56
	(8.8–12.0)	(10.0–12.8)	(10.7–12.3)
PPL	13.5 ± 0.58	14.6 ± 0.54	14.6 ± 0.51
	(12.2–15.0)	(12.9–16.1)	(13.8–15.2)
LBP	7.5 ± 0.40	8.8 ± 0.43	8.7 ± 0.35
	(6.2–8.4)	(7.4–9.8)	(8.3–9.20)
BBP	3.8 ± 0.26	3.6 ± 0.28	3.7 ± 0.15
	(3.1–4.5)	(2.9–4.3)	(3.4–3.9)
BMF	2.9 ± 0.24	3.6 ± 0.28	2.8 ± 0.14
	(2.4–3.7)	(2.8–4.4)	(2.6–3.0)
LIF	6.3 ± 0.37	8.1 ± 0.47	6.7 ± 0.29
	(5.2–7.2)	(7.0–9.2)	(6.3–7.1)
BIF	2.5 ± 0.17	3.0 ± 0.20	2.3 ± 0.13
	(2.0–3.1)	(2.5–3.4)	(2.1–2.5)
LB	6.4 ± 0.24	6.8 ± 0.30	6.9 ± 0.30
	(5.7–7.0)	(6.0–8.0)	(6.5–7.3)
CLM1–3	6.2 ± 0.23	7.8 ± 0.26	6.5 ± 0.17
	(5.7–6.8)	(7.0–8.4)	(6.3–6.8)
BM1	2.0 ± 0.09	2.5 ± 0.11	2.2 ± 0.09
	(1.8–2.3)	(2.2–2.8)	(2.0–2.3)

B. penitus requires comparison with two members of the *B. chrysocomus* group, *B. chrysocomus* and *B. prolatus*.

***Bunomys penitus* and *B. chrysocomus*:** Voucher specimens record the sympatry of *B. chrysocomus* and *B. penitus* on Gunung Kanino, Gunung Lehio, and Gunung Latimojong in the west-central mountain block, and Pegunungan Mekongga on the south-eastern peninsula (see table 20 and the account of *B. chrysocomus*). The two species are not difficult to distinguish. Adult *B. penitus* average larger in body size, with longer appendages (tail, hind foot, and ear) and greater mass than the smaller-bodied *B. chrysocomus* (table 74). *Bunomys penitus* is grayish, the upperparts are soft and silky, dense (up to 25 mm long), and brownish gray; underparts are grayish white; the rhinarium is unpigmented and sides of the rostrum are white; tops of front and hind feet are either solid white or tinged with gray; and the tail is glossy brownish gray along the dorsal surface until the last 5–118 mm (3%–68% of the tail length, mean = 21.0%), which is white as is the entire ventral tail surface—nearly every specimen surveyed exhibits a white tail segment (98% of 293 specimens; table 8). *Bunomys chrysocomus* is dark brown, the dorsal coat is soft and thick but not silky, and not as long (12–15 mm thick) as that in *B. penitus*, and is dark brownish gray speckled with buff; the rhinarium and sides of the rostrum are dark brown; the ventral coat is grayish white and washed with rust or buff in a few specimens; metacarpal and metatarsal surfaces are grayish white to brown; the tail is brown over its upper surface, whitish speckled or mottled with brown along the ventral surface (rarely white), and most specimens lack a white tip—when present it is short (1%–25% of the tail length, mean = 6%) and found in only 20% of the sample containing 396 specimens (table 8). *Bunomys penitus* has short, delicate claws on the front digits; *B. chrysocomus* has much longer claws, both absolutely and relative to body size.

Relative to body size, the testes are small in *B. penitus* (9%–13%) but large in *B. chrysocomus* (22%; table 9), and this contrast is obvious in freshly trapped adult males. Shape of the spermatozoa is similar in the two species, but that of *B. penitus* has a wider head, shorter apical hook, and shorter spermatozoan tail (Breed and Musser, 1991).

Both species have a 2N of 42, but different fundamental numbers (FNa = 58 and FNt = 60–61 for *B. penitus* and FNa = 56 and FNt = 58 for *B. chrysocomus*; table 12).

Bunomys penitus has a large skull and massive molars compared to *B. chrysocomus*,

but the latter has a broader zygomatic plate and bony palate. The magnitude of differences in cranial and dental dimensions tabulated in tables 59 and 74 in the form of descriptive univariate statistics can be visually examined in the cranial images (figs. 99–101), and viewed in the scatter plot of specimen scores projected onto first and second principal components (fig. 76, upper graph). In that ordination, separation of scores along the first axis for the larger *B. penitus* (the aggregation on the right side) and smaller *B. chrysocomus* (the cloud on the left) is facilitated by the large and positive correlations ($r = 0.65–0.96$) for all variables except breadths of zygomatic plate and bony palate, which are negative, reflecting the greater magnitude of most variables for *B. penitus* but its narrower zygomatic plate and bony palate as compared with *B. chrysocomus* (table 60).

The two species exhibit minor topographic differences on occlusal molar surfaces. There is no large labial cusplet adjacent to cusp t6 in all the specimens of *B. chrysocomus* I examined (present in 30% of the sample of *B. penitus*). Cusp t3 on the second upper molar occurs far more frequently (62%) in the sample of *B. penitus*, but is relatively uncommon (17%) in the large sample of *B. chrysocomus* (table 10). Just the reverse is the case for the anterior labial cusplet on the first lower molar, which is found in about half (52%) of the *B. chrysocomus* sample, but is rarely seen (8%) in the sample of *B. penitus* (table 11). On the second lower molar, an anterolabial cusp is nearly standard for *B. chrysocomus* (90%) and is also found on the third lower molar of that species in 65% of the sample; the comparable cusp occurs in only about half of the sample of *B. penitus* and is absent from the third lower molar of all specimens surveyed for this trait.

***Bunomys penitus* and *B. prolatus*:** The species of *Bunomys* living in montane habitats on Gunung Tambusisi, at the western margin of the eastern peninsula, is *B. prolatus*, not *B. penitus*, and the former may replace the latter in montane forest formations in the mountain backbone of the eastern arm. Alternatively, *B. prolatus* may occur on some highlands and *B. penitus* on others, or both may inhabit the same

montane forests—survey of those eastern peninsular highlands for small mammals has been scanty. Both species are characterized by large body size and lush gray pelage; those traits along with what may be an interesting displacement pattern of their geographic distributions warrants comparing them.

Certain external aspects of *B. penitus* and *B. prolatus* are similar. Both have brownish-gray or grayish-brown upperparts, the fur is thick, long, and soft, the underparts of both are grayish white, and each has a long muzzle and large ears. *Bunomys penitus*, however, is a physically larger animal as evidenced by its average longer head and body and longer hind foot (compare measurements for *B. prolatus* in table 19 with those for *B. penitus* in table 41). *Bunomys penitus* has a much longer tail, not only absolutely (means = 162.5–169.1 mm for two samples of *B. penitus*; mean = 132.4 mm for *B. prolatus*), but also relative to length of head and body (range of means = 88%–93% in *B. penitus*, 79% in *B. prolatus*). While the tail in nearly every specimen of *B. penitus* has a long white terminal segment, is brownish gray or paler on the dorsal surface behind that unigmented tip, and pure white along the ventral surface, only one of seven examples of *B. prolatus* has a short white tip (table 8), and the undersurface ranges from all white through white speckled with brown to brown nearly indistinguishable from the dorsal surface. Finally, the small and delicate front claws in *B. penitus* are unlike the robust and elongate front claws typical of *B. prolatus* (fig. 36).

All but two of the cranial and dental dimensions I measured average greater in the sample of *B. penitus* compared with that of *B. prolatus* (table 59). *Bunomys prolatus* has a wider interorbital region, and the ectotympanic bullar capsule is about the same length in both species, reflecting the close resemblance between the two in size of pinnae (see the values for *B. prolatus* listed in table 19 and for *B. penitus* in table 41).

Specimen scores projected on first and second principal components coalesce into two discrete aggregations along the first component (fig. 76, lower graph), providing a multivariate summary of size differences between the two species in cranial and dental
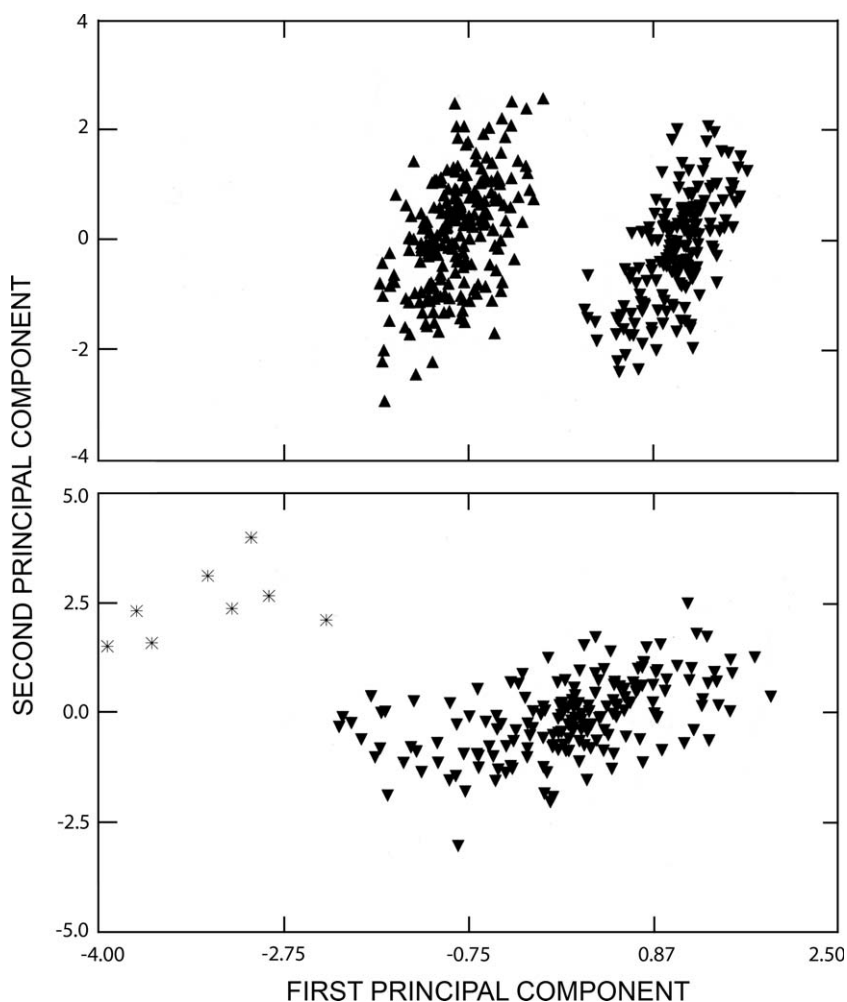
Fig. 76. Specimen scores representing all population samples of *Bunomys penitus* (inverted filled triangles; $N = 185$), *B. chrysocomus* (filled upright triangles; $N = 232$), and *B. prolatus* from Gunung Tambusisi (asterisks; $N = 8$) projected onto first and second principal components extracted from principal-components analysis of 16 cranial and two dental log-transformed variables. Upper graph: *B. penitus* contrasted with *B. chrysocomus*. Lower graph: *B. penitus* compared with *B. prolatus*. See table 60 for correlations (loadings) of variables with extracted components and for percent variance explained for both ordinations.

measurements, as indexed by the moderate to large and positive correlations among nearly all variables ($r = 0.25$–0.84; table 60). Compared with *B. prolatus*, *B. penitus* has a larger skull, more prominent rostrum, more spacious mesopterygoid fossa and incisive foramina, and larger molars, all attributes that can be seen when the cranial images of *B. prolatus* in figures 37–39 are compared with the cranial portrayals of *B. penitus* in figures 52–54.

Proportional interplay among the variables is indicated by the postion of scores along the second axis. The upper cloud of scores for *B. prolatus* separated from the lower and larger constellation for *B. penitus* reflects the relatively wider interorbit of *B. prolatus* compared with *B. penitus*; its relatively longer rostrum, diastema, and postpalatal region; wider zygomatic plate and more spacious bony palate, but weaker molars, as indicated by the moderate to high

TABLE 60
Results of Principal-Components Analysis Comparing All Population Samples of *Bunomys penitus* with Those of *B. chrysocomus*, and *B. prolatus*

Correlations (loadings) of 16 cranial and two dental log-transformed variables are based on 185 *B. penitus,* 232 *B. chrysocomus*, and eight *B. prolatus*; see figure 76.

	Correlations			
	B. penitus and *B. chrysocomus*		*B. penitus* and *B. prolatus*	
Variable	PC 1	PC 2	PC1	PC2
ONL	0.96***	0.12*	0.66***	0.43***
ZB	0.85***	0.26***	0.80***	0.10
IB	0.68***	0.13**	0.03	0.42***
LR	0.95***	0.08	0.52***	0.38***
BR	0.90***	0.22***	0.82***	0.04
BBC	0.82***	−0.02	0.33***	0.05
HBC	0.85***	−0.06	0.41***	−0.09
BZP	−0.33***	0.73***	0.49***	0.40***
LD	0.82***	0.30***	0.50***	0.64***
PPL	0.78***	0.28***	0.44***	0.44***
LBP	0.87***	0.03	0.25***	0.25***
BBP	−0.13**	0.76***	0.40***	0.68***
BMF	0.87***	0.10*	0.79***	−0.35***
LIF	0.93***	−0.05	0.70***	0.01
BIF	0.88***	0.06	0.80***	−0.20*
LB	0.65***	0.05	0.25***	0.13*
CLM1–3	0.95***	−0.18***	0.58***	−0.46***
BM1	0.91***	−0.21***	0.34***	−0.53***
Eigenvalue	0.104	0.010	0.021	0.008
% Variance	72.8	7.2	38.0	14.6

*** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

positive or negative loadings for these variables (table 60).

Frequencies of certain molar cusps differ in the two species. Every one of the four examples of *B. prolatus* lacks cusp t3 on the second upper molar (eight comprise the sample, but occlusal surfaces of four are too worn to determine presence or absence of certain cusps and cusplets), but the comparable structure characterizes 62% of the large sample of *B. penitus* (table 10). None of the examples of *B. prolatus* show a labial cusplet adjacent to cusp t6 (present in 30% of the sample for *B. penitus*; fig. 75). An anterolabial cusp is present on the second lower molar in each of the four *B. prolatus*, and is also seen on the third lower molar in three of the four specimens; only 55% of the sample of *B. penitus* exhibits the cusp on the second

molar, no specimen shows the cusp on the third molar (table 11).

GEOGRAPHIC VARIATION: Population samples of *B. penitus* come from two highland regions: the west-central mountain block in Sulawesi's core (Gunung Kanino, Gunung Nokilalaki, Gunung Lehio, Rano Rano, Mamasa Area, Pegunungan Quarles, and Pegunungan Latimojong) and Pegunungan Mekongga, the mountain complex on the southeastern peninsula of Sulawesi. In the west-central mountain block, gene exchange is likely prevalent among populations where montane habitats are continuous in particular stretches of high ridges and peaks, but interrupted among montane patches separated by tropical lowland evergreen rain forests in intermontane valleys and river gorges. Some degree of phenetic variation among samples should be expected in this extensive mountainous landscape.

In relation to samples from the west-central mountain block, that from the Mekongga range is isolated on the southeastern peninsula of the island. Certainly some phenetic differences should be expected between populations in the core and those on the southeastern peninsula. One of my aims in assessing geographic variation among population samples of *B. penitus* was to determine whether those samples from Pegunungan Mekongga represented a separate species.

There is geographic variation in some of the characters I examined, but the magnitude of difference is not great. No appreciable qualitative variation among available populations of *B. penitus* is evident in external traits, at least that I could detect. Whatever the montane provenance of a sample, individuals of comparable age are similar in physical size and look closely similar in other external traits from sample to sample: a thick, soft, and silky brownish-gray dorsal coat; dense grayish-white underparts; relatively large, rubbery grayish-brown ears; white feet, lightly suffused with gray in some individuals; a slender tail that is coequal with length of head and body, the proximal three-fourths of its dorsal surface grayish brown or paler, the distal segment and entire ventral surface pure white.

I examined skulls in all the population samples and did not detect any qualitative

TABLE 61
Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from Population Samples of
***Bunomys penitus* from the West-Central Mountain Block**
Mean ± 1 SD, and observed range (in parentheses) are listed.

Variable	Gunung Kanino	Gunung Nokilalaki	Rano Rano	Gunung Lehio
N	74	82	3	5
ONL	43.0 ± 1.14	42.9 ± 1.22	43.9 ± 0.81	43.6 ± 1.23
	(40.5–46.0)	(40.1–46.1)	(43.2–44.8)	(41.8–44.9)
ZB	19.5 ± 0.66	19.8 ± 0.63	19.4 ± 0.44	19.1 ± 0.42
	(18.0–21.0)	(18.2–21.4)	(18.9–19.7)	(18.7–19.8)
IB	6.7 ± 0.22	6.8 ± 0.23	7.0 ± 0.15	6.9 ± 0.45
	(6.2–7.5)	(6.4–8.3)	(6.9–7.2)	(6.9–7.0)
LR	16.1 ± 0.65	16.0 ± 0.63	17.0 ± 0.29	16.6 ± 0.85
	(14.6–18.1)	(14.8–17.8)	(16.7–17.2)	(15.2–17.3)
BR	7.9 ± 0.33	7.9 ± 0.35	8.1 ± 0.35	8.2 ± 0.13
	(7.1–8.9)	(7.0–8.7)	(7.9–8.5)	(8.1–8.4)
BBC	16.5 ± 0.37	17.0 ± 0.40	16.4 ± 0.35	16.3 ± 0.50
	(15.7–17.3)	(15.4–17.7)	(16.1–16.8)	(15.6–16.8)
HBC	11.8 ± 0.30	11.9 ± 0.39	11.8 ± 0.10	11.7 ± 0.30
	(10.3–12.5)	(10.9–12.7)	(11.7–11.9)	(11.2–12.0)
BZP	2.9 ± 0.18	3.0 ± 0.21	3.1 ± 0.00	2.8 ± 0.30
	(2.4–3.2)	(2.5–3.5)		(2.5–3.3)
LD	11.3 ± 0.46	11.3 ± 0.53	11.5 ± 0.29	11.6 ± 0.33
	(10.4–12.8)	(10.2–12.4)	(11.3–11.8)	(11.3–12.1)
PPL	14.7 ± 0.46	14.4 ± 0.51	14.4 ± 0.40	14.9 ± 0.31
	(13.7–16.1)	(13.4–15.5)	(14.2–14.9)	(14.4–15.2)
LBP	8.7 ± 0.43	8.9 ± 0.38	9.0 ± 0.51	9.3 ± 0.33
	(7.4–9.7)	(8.1–9.8)	(8.4–9.4)	(8.9–9.8)
BBP	3.6 ± 0.27	3.7 ± 0.25	3.4 ± 0.15	3.7 ± 0.29
	(3.0–4.3)	(3.1–4.2)	(3.3–3.6)	(3.5–4.2)
BMF	3.6 ± 0.25	3.7 ± 0.27	3.7 ± 0.49	3.7 ± 0.11
	(2.9–4.4)	(3.1–4.4)	(3.4–4.3)	(3.6–3.9)
LIF	8.0 ± 0.39	8.1 ± 0.48	7.9 ± 0.20	8.0 ± 0.35
	(7.2–9.2)	(7.0–9.1)	(7.7–8.1)	(7.6–8.4)
BIF	3.0 ± 0.17	3.0 ± 0.21	3.0 ± 0.06	3.1 ± 0.18
	(2.6–3.3)	(2.5–3.4)	(2.9–3.0)	(2.9–4.4)
LB	6.9 ± 0.31	6.8 ± 0.23	6.7 ± 0.35	6.4 ± 0.26
	(6.3–8.0)	(6.3–7.3)	(6.3–6.9)	(6.1–6.7)
CLM1–3	7.8 ± 0.26	7.8 ± 0.23	7.9 ± 0.31	7.7 ± 0.16
	(7.0–8.4)	(7.2–8.4)	(7.6–8.2)	(7.5–7.9)
BM1	2.5 ± 0.09	2.5 ± 0.11	2.6 ± 0.06	2.4 ± 0.08
	(2.3–2.7)	(2.2–2.8)	(2.6–2.7)	(2.3–2.5)

traits that were associated with particular geographic regions or any pattern indicated by descriptive statistics for cranial and dental measurements (tables 61, 62). A similar picture was generated by results from quantitative analyses of cranial and dental variables using one multivariate technique, but two other multivariate approaches produced a more revelatory pattern.

A scatter plot of specimen scores projected on first and second principal components produced no apparent pattern reflecting covariation among the variables correlated with geography (fig. 77, upper graph). Scores for specimens in the large samples from Gunung Kanino and Gunung Nokilalaki in the west-central mountain block are spread along both axes and overlap nearly every score for specimens from other collection sites in that mountain block (Rano Rano, Gunung Lehio, Mamasa Area, and Pegunungan Latimojong) as well as scores for the sample from Pegunungan Mekongga on the southeastern peninsula. Ordinations (not

TABLE 62
Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from Population Samples of
Bunomys penitus **from the West-Central Mountain Block and Southeastern Peninsula**
Mean ± 1 SD, and observed range (in parentheses) are listed.

| Variable | West-central mountain block | | | SE peninsula |
	Mamasa area	Pegunungan Latimojong	Total for mountain block	Pegunungan Mekongga
N	7	3	174	11
ONL	43.9 ± 1.51	43.4 ± 1.06	43.0 ± 1.18	41.8 ± 1.45
	(41.6–46.0)	(41.6–44.4)	(40.1–46.1)	(39.3–44.5)
ZB	19.6 ± 0.47	20.9 ± 0.64	19.7 ± 0.67	18.9 ± 0.86
	(19.0–20.0)	(20.2–21.4)	(18.0–21.4)	(17.0–20.0)
IB	6.6 ± 0.36	6.8 ± 0.06	6.8 ± 0.24	6.6 ± 0.35
	(6.1–7.2)	(6.8–6.9)	(6.1–8.3)	(6.1–7.0)
LR	16.1 ± 0.85	16.6 ± 0.35	16.1 ± 0.66	16.2 ± 0.60
	(14.7–17.2)	(16.2–16.8)	(14.6–18.1)	(15.3–17.1)
BR	8.3 ± 0.43	8.2 ± 0.35	7.9 ± 0.34	7.9 ±0.59
	(7.9–9.0)	(7.9–8.6)	(7.0–8.9)	(7.2–8.9)
BBC	16.5 ± 0.38	16.2 ± 0.12	16.6 ± 0.40	15.7 ± 0.46
	(15.9–17.1)	(16.1–16.3)	(15.4–17.7)	(15.1–16.5)
HBC	11.5 ± 0.33	11.6 ± 0.35	11.9 ± 0.35	11.6 ± 0.41
	(11.0–11.9)	(11.2–11.8)	(10.9–12.7)	(11.0–12.1)
BZP	3.2 ± 0.27	3.3 ± 0.35	3.0 ± 0.21	3.1 ± 0.29
	(2.9–3.6)	(2.9–3.6)	(2.4–3.6)	(2.5–3.5)
LD	11.9 ± 0.84	11.8 ± 0.31	11.3 ± 0.50	11.1 ± 0.69
	(10.5–12.7)	(11.5–12.1)	(10.2–12.8)	(10.0–12.6)
PPL	14.9 ± 0.52	14.9 ± 0.57	14.6 ± 0.50	14.0 ± 0.68
	(14.1–15.7)	(14.3–15.4)	(13.4–16.1)	(12.8–14.9)
LBP	8.4 ± 0.52	8.4 ± 0.31	8.8 ± 0.43	8.8 ± 0.46
	(7.7–9.4)	(8.1–8.7)	(7.4–9.8)	(8.2–9.7)
BBP	3.9 ± 0.33	3.6 ± 0.23	3.6 ± 0.27	3.6 ± 0.38
	(3.3–4.3)	(3.3–3.7)	(3.0–4.3)	(2.9–4.3)
BMF	3.3 ± 0.24	3.5 ± 0.27	3.7 ± 0.27	3.4 ± 0.33
	(3.0–3.7)	(3.2–3.7)	(2.9–4.4)	(2.8–3.8)
LIF	8.6 ± 0.36	8.9 ± 0.31	8.1 ± 0.45	7.8 ± 0.58
	(8.0–9.1)	(8.6–9.2)	(7.0–9.2)	(7.0–8.8)
BIF	2.9 ± 0.27	3.0 ± 0.27	3.0 ± 0.19	3.0 ± 0.29
	(2.6–3.4)	(2.7–3.2)	(2.5–3.4)	(2.6–3.4)
LB	6.6 ± 0.20	6.7 ± 0.06	6.8 ± 0.28	6.3 ± 0.19
	(6.4–7.0)	(6.6–6.7)	(6.0–8.0)	(6.0–6.6)
CLM1–3	7.7 ± 0.27	7.4 ± 0.21	7.8 ± 0.25	7.4 ± 0.16
	(7.4–8.0)	(7.2–7.6)	(7.0–8.4)	(7.2–7.7)
BM1	2.5 ± 0.11	2.5 ±0.17	2.5 ± 0.11	2.5 ± 0.08
	(2.3–2.6)	(2.3–2.6)	(2.2–2.8)	(2.3–2.4)

illustrated here) bounded by the combinations of first and third, and second and third components showed similar patterns of specimen scores. Covariation in most variables is responsible for the dispersal of scores along the first axis ($r = 0.31$–0.76), with breadths of zygomatic plate and mesopterygoid fossa most influential (table 63). Rather than identifying significant intraspecific geographic variation or separate clusters possibly indicating the presence of more than one species, the spread of scores, signifying both size (first component) and shape (second axis) factors, more likely reflects individual variation as well as the range of variation in variables due to age within my young to old adult categories.

A fuzzy pattern of geographic variation emerged from results of discriminant-function analysis where individual specimen scores from the population samples are projected on first and second canonical variates (fig. 77,

Fig. 77.   Specimen scores representing all population samples of *Bunomys penitus* projected onto first and second principal components extracted from principal-components analysis (upper graph) and on first and second canonical variates extracted from discriminant-function analysis (lower graph) of 16 cranial and two dental log-transformed variables. Symbols: filled circles = Gunung Kanino ($N = 74$); empty circles = Gunung Nokilalaki ($N = 82$); empty triangles = Rano Rano ($N = 3$); empty squares = Gunung Lehio ($N = 5$); empty right-pointing triangles = Mamasa area ($N = 7$); asterisks = Pegunungan Latimojong ($N = 3$); filled squares = Pegunungan Mekongga ($N = 11$). Arrows point to scores for holotypes: *penitus* (empty square) and *sericatus* (empty triangle). See table 63 for correlations (loadings) of variables with extracted components and canonical variates and for percent variance explained that apply to both ordinations.

lower graph). The large cluster of scores for Gunung Kanino and Gunung Nokilalaki also contains nearly all points for specimens collected elsewhere in the west-central moun-

tain block. Two outliers are the five specimens from Gunung Lehio, with a slightly longer postpalatal region and narrower zygomatic plate compared with the other samples from

TABLE 63
Results of Principal-Components and Discriminant-Function Analyses Performed on All Population Samples of *Bunomys penitus*
Correlations (loadings) of 16 cranial and two dental log-transformed variables are based on 185 specimens; see figures 77 and 78.

	Correlations			
Variable	PC1	PC2	CV1	CV2
ONL	0.76***	−0.17*	0.09	0.03
ZB	0.73***	0.02	0.30***	−0.46***
IB	0.32***	−0.01	0.23**	−0.12
LR	0.62***	0.13	−0.21**	0.07
BR	0.73***	−0.00	−0.24***	−0.04
BBC	0.32***	0.15*	0.60***	−0.22**
HBC	0.31***	0.22**	0.37***	−0.02
BZP	0.56***	−0.47***	−0.20**	−0.49***
LD	0.76***	−0.25***	−0.08	−0.00
PPL	0.61***	−0.15**	0.14**	0.25***
LBP	0.32***	0.10	0.01	0.05
BBP	0.67***	−0.15*	−0.00	−0.20**
BMF	0.58***	0.74***	0.32***	−0.03
LIF	0.57***	−0.27***	−0.01	−0.28***
BIF	0.60***	0.17*	−0.06	0.14
LB	0.38***	0.14*	0.66***	−0.07
CLM1–3	0.14*	0.14	0.48***	0.07
BM1	−0.15*	0.08	0.22**	−0.07
Canonical correlation			0.757	0.669
Eigenvalue	0.015	0.005	1.343	0.811
% Variance	32.7	12.0	38.7	22.4

*** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

the mountain block, and the three specimens from Pegunungan Latimojong that show an average wider skull (indicated by zygomatic breadth) and zygomatic plate along with longer incisive foramina (see tables 61 and 62). The significance of these average differences is unclear because the samples from Gunung Lehio and Pegunungan Latimojong are so small relative to the very large series from Gunung Kanino and Gunung Nokilalaki.

Scores representing the sample from Pegunungan Mekongga on the southeastern peninsula ($N = 11$) lie to the left relative to position of the scores for the other samples in the ordination, all of them from the west-central mountain block (fig. 77). An overall smaller skull, both shorter (measured by occipitonasal length) and narrower (indexed by zygomatic breadth and breadths of inter-

orbit and braincase) shorter basicranium (postpalatal length), smaller bullae, and shorter molar row characterizes the sample from Pegunungan Mekongga compared with those collected in the west-central region (see the univariate descriptive statistics in table 62); breadth of braincase and lengths of bulla and molar row are especially forceful in spacing the scores along the first canonical variate, with those for Pegunungan Mekongga at one end of the spread and the points representing Gunung Kanino and Gunung Nokilalaki at the opposite (fig. 77, table 63).

Lengths of head and body, tail, and hind foot also average shorter in the sample from Pegunungan Mekongga compared with those series collected in the west-central mountain block (table 41). The contrast in these cranial and external variables suggests underlying partial genetic isolation between populations living in the two mountainous landscapes.

Cluster analysis resulted in a pattern of montane variation that for most samples mirrored the relative position of their highland collection sites (fig. 78). The clustering pattern based on squared Mahalanobis distances unites first the samples from Gunung Nokilalaki and Gunung Kanino (which is a high ridge leading to Nokilalaki) within a cluster comprised also of Rano Rano (highlands just east of Kanino and Nokilalaki), Gunung Lehio (west of the latter three locations and across the valley of the Sungai Miu), and the Mamasa Area (to the south of those four places)—all part of the west-central mountain block. Those five are linked to Pegunungan Mekongga on the southeastern peninsula. Pegunungan Latimojong, in the southern part of the west-central mountain block, connects to the sample from Pegunungan Mekongga rather than to samples from the west-central mountain block. I do not know whether this last link reflects a real phenetic relationship or is an artifact of sample size.

Compared with samples from the west-central mountain block, that from Pegunungan Mekongga differs by its average shorter and narrower skull, shorter basicranium, smaller bullae, and shorter molar row as reflected in the tables of summary statistics
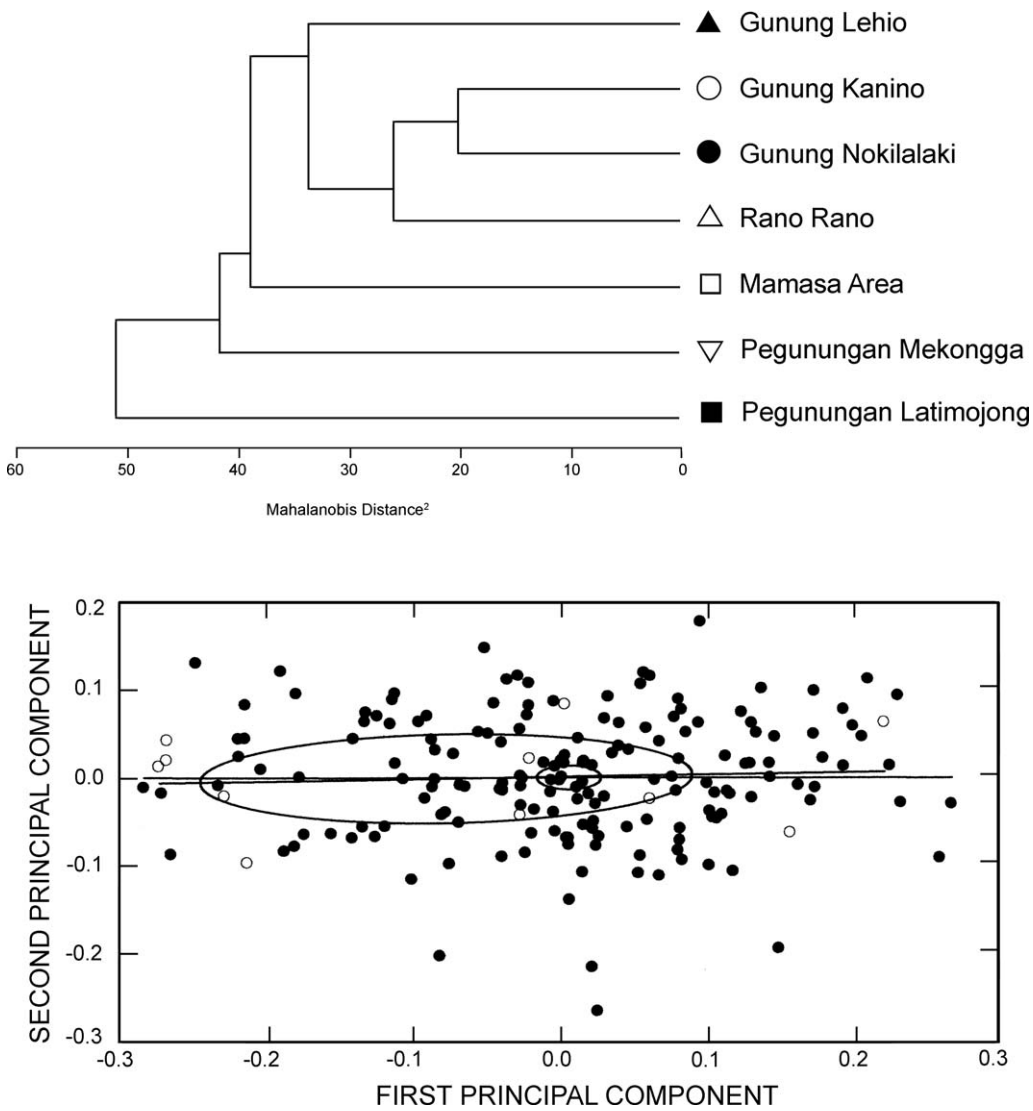
Fig. 78.   Upper diagram: Pattern of phenetic relationships among population samples representing *Bunomys penitus* derived from UPGMA clustering of squared Mahalanobis distances among group centroids as based on discriminant-function analysis. Lower diagram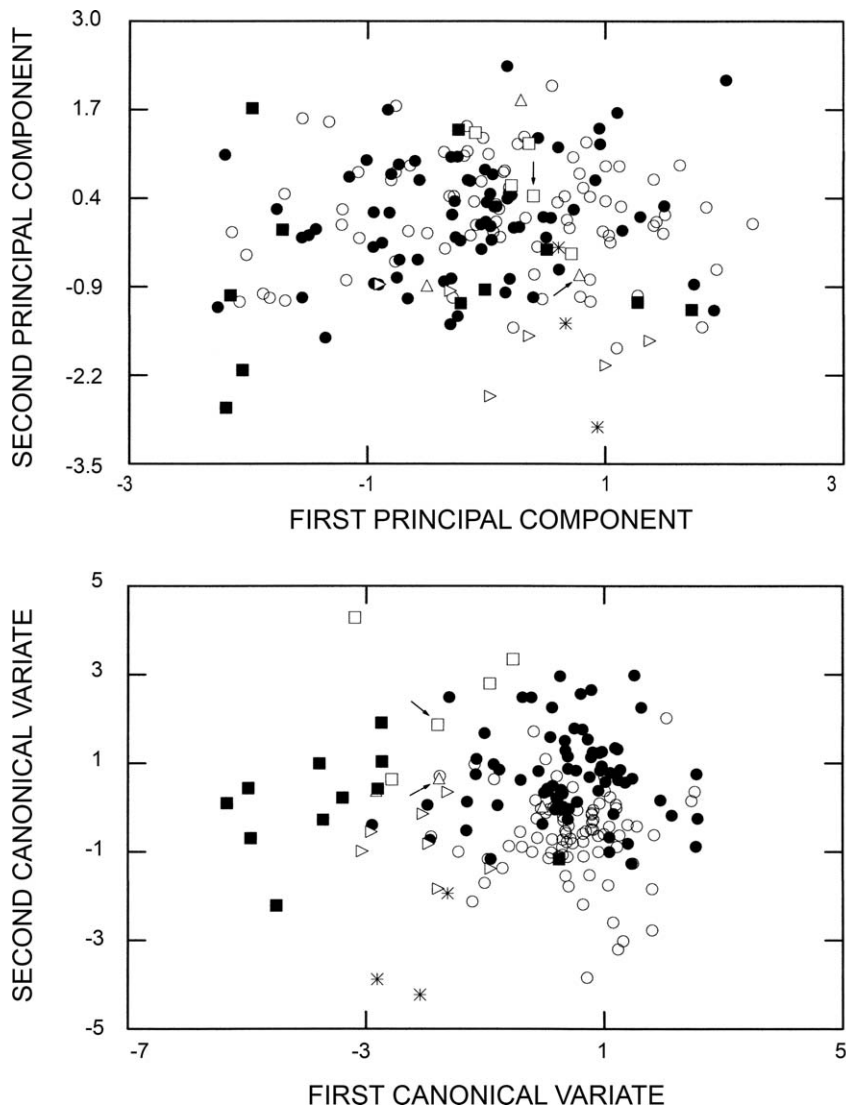: Specimen scores representing two samples of *B. penitus* projected onto first and second principal components extracted from principal-components analysis of 16 cranial and two dental log-transformed variables. Combined population samples from the west-central mountain block (Gunung Lehio, Gunung Kanino, Gunung Nokilalaki, Rano Rano, Mamasa Area, and Pegunungan Latimojong) form one sample (filled circle); the lot from Pegunungan Mekongga on the southeastern peninsula constitutes the other (empty circle). Ellipses outline 95% confidence limits for each group centroid. Equations for the regression lines are: West-central mountain block, $Y = -0.004 \times 0.000$ (F = 0.005, P = 0.941); Pegunungan Mekongga, $Y = -0.023 \times -0.001$ (F = 0.051, P = 0.826). Neither the slopes of the two regression lines or their Y-intercepts are statistically significant (see discussion in text). The ordination in figure 77 shows the same distribution of scores but with individual samples identified; correlations of variables and percent variance in table 63 apply to both principal-components diagrams.

(table 62) and results of discriminant-function analysis (fig. 77; table 63) described above. These distinctions, plus the isolated geographic position of the Mekongga population relative to those occurring in the west-central mountain block, prompted me to run an additional principal-components analysis that employed only two samples: one containing the combined six population samples from the west-central mountain block, the other consisting of the smaller sample collected on Pegunungan Mekongga. Results might reveal a sharper pattern of cranial and dental differentiation between samples from the two mountainous regions and better test whether the samples from the west-central mountain block and that from the mountain range on the southeastern peninsula represent two species rather than one.

In an ordination bounded by first and second principal components, the usual pattern of scores representing two morphologically closely related but different species consists of two slightly overlapping and obliquely oriented elliptical clouds in which the major axes (regression lines) of the spreads are phenetically discrete—the regression lines of the second principal component on the first are clearly separate and their Y-intercepts are significantly different between the two species (see Voss et al., 1990; Voss and Marcus, 1992). This is the pattern illustrated in the principal components ordination comparing samples of *B. chrysocomus* with the morphologically similar *B. coelestis* (fig. 42); other examples are provided by Carleton and Martinez (1991), Carleton and Musser (1995), Carleton et al. (1999, 2006, 2009), Carleton and Byrne (2006), Carleton and Arroyo-Cabrales (2009), Carleton and Stanley (2012), Musser et al. (1998), and Voss et al. (2002) for Mexican, Central American, South American, and African muroids; by Anderson and Gutiérrez (2009) for South American heteromyid rodents; and by Musser et al. (2010) for Sulawesi squirrels. No such dual ellipsoidal patterns characterize the distribution of scores for the two samples of *B. penitus* (fig. 78, lower graph). The two regression lines are essentially horizontal (their slopes statistically the same; −0.004 versus 0.023, F = 0.039, P = 0.844), overlap for much of their lengths, and their Y-

intercepts are not significantly different (0.000 versus 0.001, F = 0.210, P = 0.885). Statistically, there is a single major linear axis of one large assemblage of scores, reinforcing the interpretation of a single species showing geographic variation in some cranial and dental variables.

This pattern of variation contrasts with that characterizing other murid groups occurring in the Mekongga region having counterparts in the west-central mountains. *Taeromys arcuatus*, *Taeromys microbullatus*, *Maxomys* n. sp., *Margaretamys christinae*, and *Rattus salocco*, for example, are known only from Pegunungan Mekongga (see table 81), and their counterparts in the west-central mountain block are two new species of *Taeromys*, *Taeromys callitrichus*, *Maxomys dollmani*, *Margaretamys parvus* and *M. elegans*, and *Rattus facetus*, respectively (documented in manuscripts in prep.).

Present samples of *B. penitus* provide one pattern of variation in cranial and dental variables among highland populations; that picture may be altered or substantiated after study of material from unsampled highlands and larger series from some of those places recorded here. Aside from the samples from Gunung Kanino and Gunung Nokilalaki, the other population samples are small, three to seven useable intact specimens in those from Rano Rano, Gunung Lehio, Mamasa Area, and Pegunungan Latimojong, and 11 in the Pegunungan Mekongga lot (tables 61, 62). Larger series from these latter five places would allow sorting of specimens into age groups and comparing sets of similar relative age, which would provide sharper resolution of any intersample variation. The pattern revealed here does provide a hypothesis that can be tested with measurements of external and cranial variables from more and larger samples, and eventually with results from analysis of DNA sequences.

NATURAL HISTORY: Summarized here are my observations covering habitat and diet derived from the animals collected along my transect that culminated on Gunung Kanino and Gunung Nokilalaki in the cool and wet primary tropical lower and upper montane rain forests.

Habitat: Mean ambient air temperatures ranged from 58.4° to 64.8° F on Gunung

TABLE 64
Microhabitats at Trap Sites in Which a Portion of the 288 Specimens of *Bunomys penitus* Were Collected on My Transect in Central Sulawesi, 1973–1976

Descriptions of the trapping sites are summarized from my field journals (in Mammalogy Archives at AMNH). See landscapes in figures 79–83.

Place and date	Microhabitat
Gunung Kanino (October 27–November 23, 1973; January 17–February 16, 1975)	**Primary tropical lower montane rain forest (1285–1616 m)**
	On wet ground beneath decaying tree trunk that is part of an old treefall lying on forest floor and densely covered by rattan rosettes, climbing bamboo, shrubs, herbaceous vines, and rotting limbs and branches; small trees emerge above the tangle and the ground is carpeted with decaying leaves.
	Many *B. penitus* caught in traps set in damp runways beneath rotting tree trunks lying on the forest floor, on steep slopes or ridgetops, and in runways in the space beneath moss-covered tree roots, especially those of chestnut (*Castanopsis acuminatissima*).
	2 ft off ground on top of a large decaying trunk lying on a hillside next to stream.
	Damp runway beneath wet, moss-covered decaying trunk lying on terrace above stream; forest wetter here than on ridges.
	On leaf-covered ground in runway below ridgetop; trap set in open area next to a tree on a small flat.
	In front of hole in base of chestnut-trunk complex growing on terrace; chestnut base is closed, not an open hollow like so many, and has other openings to the inside, which is honeycombed with passages.
	In runway along side of huge, decaying moss-covered dammar trunk (*Agathis philippinensis*) lying in dammar area of oak-chestnut forest on ridge.
	On wet, decaying, moss-covered trunk spanning streamlet draining very wet and forested muddy hillside above Sungai Salebeka.
	In oak-chestnut forest on top of ridge; placed in runway leading to burrow under root system of short understory tree.
	On ground beneath stilt roots of chestnut cluster on ridge in oak-chestnut forest.
	Inside hollow, decaying, moss-covered base of old chestnut treefall on wet, fern-covered depression between ridges.
	On decaying trunk spanning Sungai Tokararu and 2 ft above water surface. Here the stream is about 4 ft wide, its cut bank is 8 ft wide and 2 ft high, and its terrace flat and 30 ft from slope to slope. Trunk (10–12 in. diameter) lies across terraces, is densely covered with thick moss (1 in. deep), from which are growing gingers, ferns, an oak-leaf fern, small shrubs, and tiny plants; no path is worn in moss. Terrace is wet and muddy. Caught the squirrel *Hyosciurus heinrichi* in same spot.
Gunung Nokilalaki (December 7–30, 1973; February 22–May 15, 1975)	**Primary tropical lower and upper montane rain forest (1740–2287 m)**
	In mossy runway beneath root of tree growing along top of sloping ridge.
	In wide runway beneath long, decaying and moss-covered trunk lying down slope below ridgetop. Other *B. penitus* were caught in similar microhabitat configurations—runways beneath or alongside decaying sections of trunks or large limbs lying on the forest floor, usually bordered by sedges, ferns, and monocot shrubs.
	Trap in front of burrow leading between decaying roots on hillside; extending from the roots are runways along decaying, moss-covered trunks that are lying at either side of the roots.
	On steep, washed, and muddy slopes above head of a stream. Rattans and herbaceous shrubs are the prevalent ground cover.
	In well-used runway beneath long, rotten, and moss-covered trunk lying downslope about 20 ft from top of ridge. In same spot, the ground squirrel *Hyosciurus heinrichi* was caught during the day and the rat *Rattus hoffmanni* at night.
	On ground beneath large eroded roots of live canopy tree growing next to ravine on steep slope; several *B. penitus* were caught on flats and ridges in similar situations.
	A few *B. penitus* were taken on mossy ledges that extend along vertical or steeply sloping sides of ridges just below the ridgetops.
	In runway at end of decaying, moss-covered, large trunk that is part of an old treefall. Runway extends up into main jumble of limbs and branches and connects with other passages, some of which run alongside the main trunk. Sedges and moss provide ground cover surrounding the decaying pile of moss-enclosed trunks, limbs, and branches; *B. penitus* were regularly trapped beneath other old treefalls now covered with dense moss and decaying into the wet forest floor.
	On ground beneath eroded roots of tree growing on steep slope.

TABLE 64
(*Continued*)

Place and date	Microhabitat
	Beneath pile of decaying sections of trunk and limbs lying on nearly vertical slope; entire jumble is covered with moss and surrounded by sedges, gingers, and shrubs.
	On damp ground beneath part of a rotten, moss-covered trunk lying on ridgetop in gingers, ferns, sedges, rattan rosettes, and small shrubs. The rat *Melasmothrix naso* was caught in same spot during the day.
	On ground on wet leaf litter beneath roots and rocks, all covered with thick wet moss on slope of ridge. Other *B. penitus* were encountered nearby in mossy runway along wet rocks covered with moss on steep muddy slope.
	In mossy runway beneath decaying moss-covered trunk lying on edge of summit; this runway is continuous with one in which the rat *Tateomys macrocercus* and the ground squirrel *Hyosciurus heinrichi* were caught.
	Among roots of standing trunk base (15 ft high, 4 ft diameter) of a large oak (*Lithocarpus* sp.) in which the main trunk broke and fell long ago and is now decaying on the forest floor; very wet short forest near summit.

Kanino (1440 m), and 57.5° to 64.8° F at 1730 m on Gunung Nokilalaki and 51.0° to 56.6° F on the summit (see table 3 relative humidity and rainfall patterns are also listed). A portion of the trapping sites are described in table 64 (the descriptions are selected to cover the range of microhabitats trapped and not to document where every rat was taken).

During about two months at different times camped on Gunung Kanino (October 27–November 23, 1973, and January 17–February 16, 1975) and longer on Gunung Nokilalaki (December 7–30, 1973; February 22–May 15, 1975), we collected 288 *Bunomys penitus.* This was the most frequently trapped murid in these montane habitats, followed by *Paruromys dominator* (201 examples), *Rattus hoffmanni* (92 specimens), *Maxomys musschenbroekii* (73 individuals), and *Margaretamys elegans* (40 specimens); see figure 103. And except for the lower edge of lower montane forest between 1274 and 1555 m where we trapped both *B. penitus* and *B. chrysocomus*, the former is the only representative of *Bunomys* in montane habitats on Gunung Kanino and Gunung Nokilalaki, ranging from the lower boundary of lowland montane forest at 1274–1300 m all the way to the summit of Gunung Nokilalaki at 2287 m.

Bunomys penitus is nocturnal and terrestrial; we never trapped any examples on substrates above ground level.

Gunung Kanino forms a highland mass attached to the southwestern shoulder of the higher ridge forming Gunung Nokilalaki. Its northwestern margin is defined by the Sungai Tokararu, which drains into Danau Lindu (see area at right in the distribution map in fig. 51). The base of Kanino is mantled by lowland tropical evergreen rain forest where our camp at 1150 m was located on a terrace above the Sungai Tokararu. Upslope at (1296–1311 m), the lowland forest transitions sharply into lower montane formations defined by the beginnings of chestnuts (*Castanopsis acuminatissima*) and *Calophyllum* that form extensive groves covering the slopes and terraces up to about 1800 m (fig. 79). Here the chestnuts are dominant and form most of the canopy with mature trees attaining 80–100 ft high, some reaching about 125 ft. They are spaced 15 to 20 ft apart. The ground is mossy but also thickly covered with leathery-brown chestnut leaves forming a dry litter that crackles under foot. Here *Calophyllum* is also abundant, both as young trees throughout the understory and as scattered canopy trees; they outnumber the scattered oaks (*Lithocarpus glutinosus* and *L. elegans*) and the forest could be described as a chestnut-calophyllum climax. This ratio changes with altitude and oaks become as abundant as *Calophyllum* (chestnut-oak-*Calophyllum* climax) and then exceed it in numbers as the latter and chestnuts become scattered and rare, with the oaks, primarily *Lithocarpus havilandii*, growing on higher slopes above the chestnut, where they form extensive groves in places, all the way to the summit of Gunung Nokilalaki. Stands of the

Fig. 79.   Coppice of old-growth chestnut (*Castanopsis acuminatissima*) in primary lower montane forest at 1463 m on Gunung Kanino (in 1975). Shoots growing from the base of a single tree into a cluster of trunks dominated by one or two large trunks, each reaching 2 ft in diameter, is the typical growth morphology. The base, encrusted with moss and epiphytes, may be 5–8 ft wide and as high, and hollow or honeycombed with passages. *Bunomys penitus* was trapped in and around the hollow moss-covered base. These clusters of chestnut trunks, as well as single trees with trunks 3–4 ft in diameter, contribute to the canopy (reaching 80–125 ft) along with *Calophyllum* sp. About 100 ft higher on the ridge, oak (*Lithocarpus glutinosus* and *L. elegans*) replaces *Calophyllum* and the ridges are dominated by an oak-chestnut forest. This lower montane region is shared by species of *Eugenia* and *Syzygium*; *Symplocos*; the laurels *Cryptocarya*, *Litsea*, *Endiandra*, and *Cinnamomum*; the nutmeg *Knema*; magnolias (*Magnolia* spp.); the maple *Acer caesium*; walnut (*Engelhardtia serrata*); the conifers *Agathis philippinensis*, *Dacrycarpus imbricatus*, *Podocarpus neriifolius P. rumphii*; the canopy figs *Ficus sumatrana* and *F. crassiramea*; *Madhuca malaccensis* in Sapotaceae; *Macadamia hildebrandii* in Proteaceae; and a variety of understory tree species; rattan is common and the palm *Areca vestiaria* is scattered.

Fig. 80. Ridge-top forest between 1600 and 1700 m on Gunung Kanino (in 1975) dominated by *Tristania* sp. (with the whitish bark) and species of *Eugenia*, especially *E. cuprea*; pandans (*Pandanus* sp.) are common, as are two species of *Vaccinium*—one a canopy former, the other in the understory—and rattan is abundant; the fern *Dipteris* blankets open spaces. Canopy is 50–60 ft high with the occasional chestnut or oak, which have small trunks here, emerging to about 70 ft. *Tristania* bark appears white from a distance but up close is actually streaked with gray, tan, rusty pink, and pale orange. Around the bottoms of some trunks are piles of pandan debris and sloughed *Tristania* bark, forming mounds 1–3 ft high and 3–5 ft wide that provide excellent cover for *Bunomys penitus*.

Fig. 81.   Primary upper montane rain forest at 2256 m (in 1975) near the summit of Gunung Nokilalaki. The forest is open, lacking the closed canopy so typical of forest formations at lower elevations. Oak (*Lithocarpus havilandii*) is common and joins magnolia (*Magnolia* sp.), bayberry (*Myrica javanica*), and conifers (species of *Dacrydium* and *Podocarpus*) as the largest trees; species of *Eugenia*, *Praravinia*, *Vaccinium*, *Symplocos*, *Astronia*, *Ternstroemia*, *Elaeocarpus*, *Litsea*, *Cryptocarya*, *Melastoma*, and the occasional *Ficus* are among the many species of smaller trees. The climbing pandan (*Freycinetia*) winds through the tree crowns; here and there slender rattan stems (*Calamus* and *Daemonorops*) drape below the crowns. Sedges form much of the ground cover in this spot. *Bunomys penitus* is common in this cool and wet mossy habitat where we trapped them on wet ground within the sedge cover, and along sides of the moss-covered roots, decaying trunks lying on the ground, and rocks.

Fig. 82. A different aspect of upper montane forest at 2256 m below the summit of Gunung Nokilalaki (in 1975). These forest glades, surrounded by tall trees enveloped with dense and wet moss, support a community of small gingers, rattan rosettes, several kinds of ferns, saplings, and a variety of small shrubs. We trapped *Bunomys penitus* beneath this floral cover as well as in the surrounding forest. Twelve other species of murids were collected here in the nearby forest, with *Paruromys dominator*, *Rattus hoffmanni*, *Melasmothrix naso*, *Maxomys musschenbroekii*, and *Margaretamys parvus* being the most common next to *B. penitus* at this elevation (see fig.103).
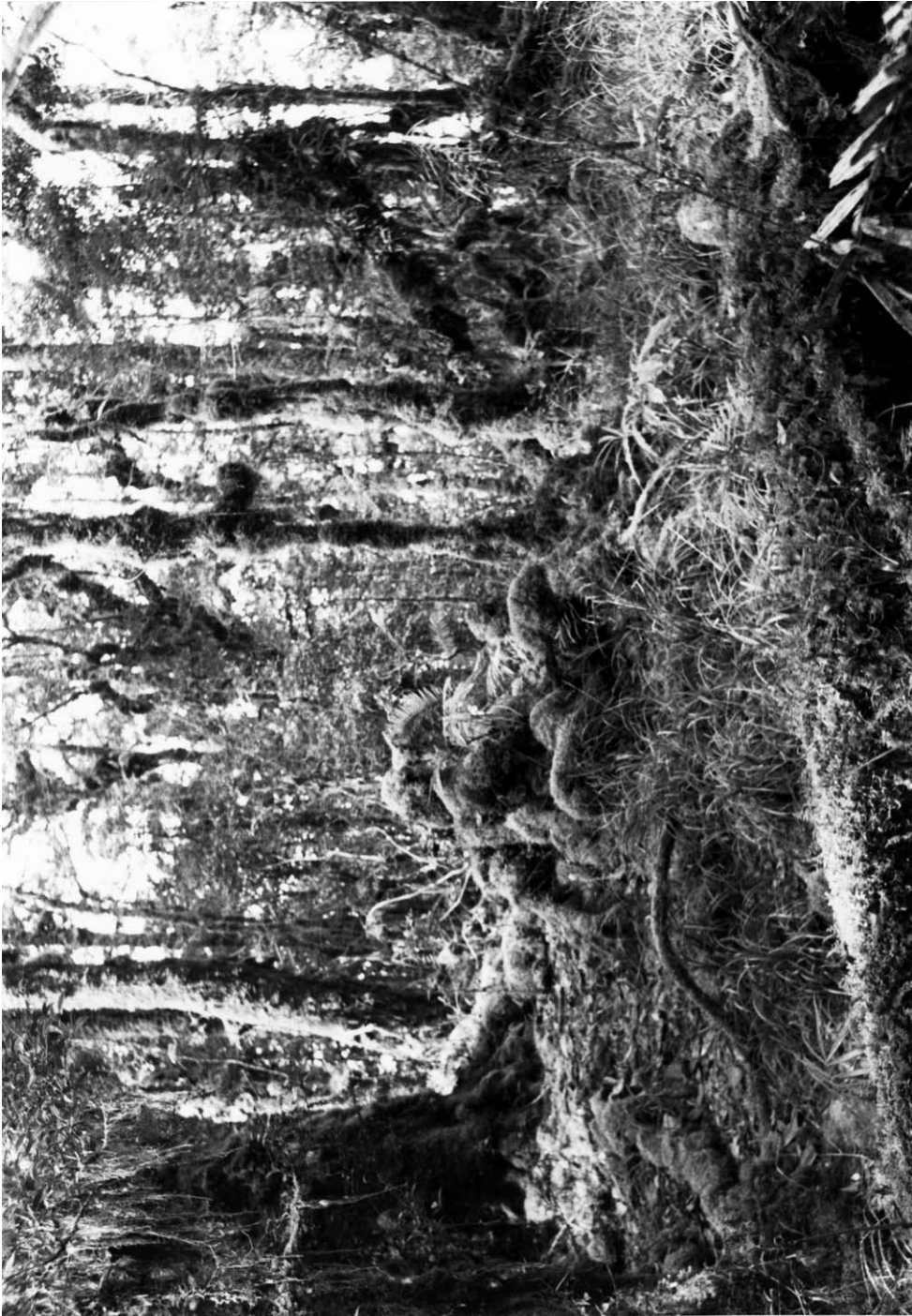
Fig. 83.   Forest margin of Gunung Nokilalaki's summit, 2287 m (in 1975). Part of the forest was opened by a fallen tree that is now decaying on the ground and completely cushioned in dense, wet moss. The jumble of trunks and branches provides superb cover for rodents, especially *B. penitus*, individuals of which were trapped beneath the pile as well as along the base of the large tree to the left, and beneath the mossy trunk in the foreground.

conifer *dammar* (*Agathis philippinensis*) along with a variety of other canopy as well as understory trees contribute to the lower montane forest composition (see legend to fig. 79). *Bunomys penitus* was frequently encountered in these chestnut-oak-*Calophyllum* groves between 1300 and 1600 m, 49% of all specimens trapped in lower and upper montane forest (see fig. 103 and the trapping sites described in table 64).

Although most *B. penitus* were caught in either chestnut-oak-*Calophyllum* forest or higher in upper montane habitats near the summit of Gunung Nokilaki, we also found them at intervening elevations, even in ridgetops covered by short forest dominated by *Tristania* and *Pandanus* (fig. 80). Generally, every line of traps set at different elevations in montane forest yielded examples of *B. penitus*.

About 39% of the 288 *B. penitus* were trapped between 2000 m and the summit of Gunung Nokilalaki in densely mossy, cool, and wet upper montane forest (see figs. 81–83, 103; also see the descriptions of this forest provided in Musser, 1982). Near and on the summit, all the rats were trapped in runways—usually damp and either muddy or carpeted with moss—beneath isolated decaying trunks, under tangles of trunks, limbs, and branches formed from old treefalls, inside rotting stumps, and within spaces among moss-covered roots of living trees (table 64).

The montane habitats in which *B. penitus* were collected lack the floristic species diversity found in tropical lowland evergreen rain forest (see Natural History in account of *B. chrysocomus*). We collected samples from about 150 species of trees, and while some of these also occur in lowland forest most are found only in montane habitats. Except for six species of rattans (*Calamus* and *Daemonorops*), only the solitary palm *Areca vestiaria* was seen scattered in the forest at high elevations. There are fewer kinds of shrubs, pandans, gingers, and ground ferns; tree ferns are scattered through the forest from the beginning of lower montane forest to the summit of Gunung Nokilalaki.

Diet: *Bunomys penitus* consumes invertebrates, small vertebrates, some fruit, and a variety of fungi (table 13) and can be viewed primarily as an invertebrate and fungal predator. I kept up to 15 adults captive for several weeks in the camps on Gunung Kanino and Gunung Nokilalaki and offered them a range of foods. Invertebrates and fungi were the items most voraciously consumed. All were picky about fruits, accepting only seeds of oaks (*Lithocarpus*). Back at the museum I extracted the contents from 97 stomachs, which fell into the following categories: (1) six were empty except for matted hair ingested during grooming; (2) one contained unidentifiable remains; (3) 16 contained only bait (ranging from stomachs distended with bait to stomachs nearly empty except for remnants of bait, usually raisin and bacon fragments); (4) four were filled with arthropods and snails but no fungi; (5) six held remains of fruit and no fungi; (6) 64 held fungal remains only or fungi mixed with bait, arthropods, snails, or fruit in different combinations.

Below I present the foods eaten by *B. penitus* drawn from my observations of captive animals and study of the contents extracted from stomachs.

Earthworms—All the captive rats consumed earthworms (2–3 inches long) and handled them in a manner similar to that described for *Bunomys chrysocomus* (see that account). Each rat would aggressively grab the worm with incisors, and quickly transfer it to the front feet. The rat placed one end of the worm in its mouth, cutting it into segments while it pulled the worm through its front feet until entirely consumed, a process taking 20–30 seconds.

Only one of the 97 stomachs contained short unchewed segments of a small earthworm and this low frequency may be related to where the earthworms occur in montane forest and the ability of *B. penitus* to obtain them. We occasionally saw an earthworm crawling over open muddy ground after a hard rain, but we found most of them living beneath thick layers of moss covering decaying trunks, limbs, and smaller branches. Some we located beneath the bark of fallen trees not yet densely mantled with moss; rotting pieces of oaks (*Lithocarpus*) provided the most abundant earthworm accumulations. Except for the occasional earthworm squirming on muddy ground, which *B.*

penitus could snatch up quickly, most would have to be excavated from beneath thick moss, which would be more difficult for the rat because its front claws are short and appear weak, at least as compared with the elongate front claws of *B. chrysocomus* and the montane species of *Melasmothrix* and *Tateomys*, all aggressive earthworm predators.

Snails—Managing snails was similar to the behavior described for *B. chrysocomus* (see that account). A snail was grabbed with the incisors, transferred to the front feet, turned over several times and eventually bitten into until enough shell was removed, so the soft body was exposed and could be extracted. Once accessible, the rat pulled away a bit of the flesh, ingested it, bit away more shell, pulled and ingested more of the tissue, and proceeded in this manner until the entire snail was consumed. The pieces of shell bitten off were always discarded. I never found fragments of the shell in stomachs, usually only an operculum along with partly digested tissue remains of the snail. Indications of snails were found in two of the 97 stomachs (semidigested tissue and operculum in one, maserated tissue, operculum, and fragment of radula in the other).

In the montane forest habitats on Gunung Kanino and Gunung Nokilalaki, snails seemed less common than in lowland rainforest environments and to average much smaller in size. I did locate snails within wet moss, sometimes crawling over wet leaf litter, here and there beneath decaying bark, and crawling up stems and onto leaves of sedges and other low ground cover.

Insects and other arthropods—Moths, cicadids, cockroaches, and beetles were provided and all consumed by the captive rats. Moths and cicadids were aggressively pulled from my fingers and quickly manipulated so the head was at the rat's mouth. It then bit the insect's head and proceeded to voraciously consume head, thorax, and abdomen—wings and legs were discarded.

Large adult beetles were always accepted, even those up to two inches long. The rats were selective, eating only the abdomen and soft parts of the thorax, and discarding everything else. Small beetles were totally ingested and were represented in the stomachs surveyed by elytra, wings, antennae, legs, along with abdominal and thoracic filamentous tissue. Beetle larvae were also consumed. A favorite were the large larvae (up to 4 inches long and ½ inch wide) I extracted from rotting wood; all the rats voraciously devoured these grubs.

Nine of the 97 stomachs held remains of insects and other arthropods: macrolepidopteran caterpillars, adult and larval beetles, cockroaches, and geophilomorph centipedes.

Remains of rhinotermitid termites, which I regularly found in stomachs of *Bunomys chrysocomus* and *B. andrewsi* that were trapped in tropical lowland evergreen rain forest, were absent from the stomachs of *B. penitus*. And I did not find any in stomachs of *B. chrysocomus* collected in lower montane forest on Gunung Kanino. The termites are either rare or may simply not occur in montane forest habitats. My helpers and I took apart many pieces of tree trunks and limbs in various stages of decay lying on the forest floor. We encountered earthworms along with adult and larval beetles but never termites (see the account of *B. andrewsi* where I provide an inventory of invertebrates, which includes termites, found in similar situations in lowland rainforest habitats).

Fruit—The meaty seeds of *Lithocarpus* were the only fruit consistently accepted by captive rats but only after I had extracted the seed from the hard shell. Of the 97 stomachs I emptied, nine contained remains of fruit, mostly fig (*Ficus*), a fruit with large oblong and dark brown seeds, and one with large flat hard and orange seeds.

Stomachs rarely contained only fruit. The content of a stomach from a rat trapped on Gunung Nokilalaki is illustrative. It was full with remains of a fig; another fruit with large, hard, and dark brown oblong seeds; fruit pulp, some bait; one small centipede, and several macrolepidopteran larvae.

Fungi—Different species of fungi form a significant part of the diet of *Bunomys penitus*, which is indicated not only by results from feeding trials but also by the prevalence of fungi in the stomachs I examined. I offered a variety of fungi to the captive animals. The two kinds of jelly or ear fungi so readily consumed by *Bunomys karokophilus,* n. sp.

(see that account), the purplish *Auricularia delicata* (identified as *karoko* by the local people) and white *Auricularia fuscosuccinea* (Class Agaricomycetes, Order Auriculariales, Family Auriculariaceae) were consistently accepted and eaten. A shelflike gilled fungus *Panellus pusillus* (Order Agaricales, Family Trichyolomataceae), which I found attached only to decaying leaf shafts and stems of rattan decaying on the forest floor, was readily accepted and consumed. Seven kinds of stalked gill fungi with caps were offered to the rats and all were eaten. These mushrooms ranged in size from delicate fruiting bodies with a stalk 2 inches long and cap ½ inch wide to larger species with caps 3 inches in diameter and stalks reaching 3 inches. Cap and stalk of the smaller mushrooms were consumed, most of the cap of the larger mushrooms were eaten (sometimes a rat would eat only the soft underside of the cap) but the tough stems were left. I also found several kinds of shelflike jelly fungi other than *Auricularia* growing on rotting and wet wood and all these were consumed by the rats.

Not all the kinds of fungi offered the rats were accepted. Woody bracken fungi were ignored, as were puffballs, and a large stalked gilled mushroom with a thick brown and yellowish cap.

Of the 97 stomachs I cut open, 64 (66%) contained either only fungi or fungi mixed with remains of invertebrates and fruit in different combinations. Of these 64, 45 (70%) contained remains of a shelf fungus resembling *Auricularia delicata* but darker in color and rubbery rather than gelatinous in texture; of those 45, 16 held only the *karoko*-like fungus and some of these stomachs were distended with it.

The fruiting bodies of *A. delicata* form small and somewhat rubbery capsules (10 mm long, 5 mm wide) or broad and thick ear-shaped lobes (up to 50 mm wide) that grow on wet and decaying wood. The top surface is smooth and purplish or purplish brown, the undersurface white and irregularly ribbed and veined. The inside is gelatinous. Individual lobes may spread across the same wet and decaying tree trunk or limb, but usually several lobes form a cluster originating from a single point of attachment (see the account of *B. karokophilus*, n. sp., for a broader description of the fungus). The *karoko*-like fungus so prevalent in the stomachs of *Bunomys penitus* is dark brown, and tougher in consistency than *A. delicata*. In most stomachs, it appears as chewed rubbery lobes attached to a thick and tough (like hard rubber) translucent core. Fragments of the woody holdfast adhering to the core were in some stomachs, and slivers of wood and bits of moss occurred along with the fungus in other stomachs. Unfortunately, I have yet to identify this *karoko*-like fungus.

The combination of the *karoko*-like fungus with other items is illustrated by a stomach from a rat collected on Gunung Kanino: few segments of a small earthworm, remains of a snail (including the operculum and fragment of radula), fragment of cockroach leg, large rubbery chunks of the *karoko*-like fungus, and a few pea-sized globular fungi.

The other 19 of the 64 fungus-containing stomachs held remains of the two species of *Auricularia*, the *Panellus*, and several kinds of pink and yellow jelly fungi that I have not identified.

Overview—*Bunomys penitus* is mycophagous, incorporating a variety of ear, jelly, and gilled fungi in its diet, and is also an aggressive and agile predator of insects, centipedes, earthworms, and snails.

ECTOPARASITES, PSEUDOSCORPIONS, AND ENDOPARASITES: Fleas and ticks comprise the ectoparasites recorded from *Bunomys penitus* (table 14). Of the species in the six genera of fleas (Siphonaptera) that parasitize *B. penitus*, *Sigmactenus sulawesiensis* (Leptopsyllidae) also parasitizes four other endemic Sulawesi murines (*Bunomys fratrorum*, *Eropeplus canus*, *Maxomys musschenbroekii*, and *Paruromys dominator*) and the endemic tree squirrel *Prosciurillus topapuensis* (Durden and Beaucournu, 2000). *Sigmactenus alticola pilosus* (Leptopsyllidae) is also recorded from 14 other species of endemic Sulawesi murine rodents (*Bunomys chrysocomus*, *B. prolatus*, and *B. karokophilus*, n. sp.; *Margaretamys elegans*; *Maxomys hellwaldii*, *M. wattsi*, and *Maxomys* sp.; *Melasmothrix naso* and *Tateomys rhinogradoides*; *Paruromys dominator*; *Taeromys celebensis* and *Taeromys* sp.; *Rattus hoffmanni* and *R. facetus* [recorded as *R. marmosurus*]) and the nonnative *Rattus exulans* (Durden and

Beaucournu, 2000). In addition to *Bunomys penitus*, five endemic Sulawesi murids (*Rattus hoffmanni*; *Bunomys chrysocomus* and *B. karokophilus,* n. sp.; *Maxomys* sp.; *Paruromys dominator*) and two nonnative rats (*Rattus exulans* and *R. nitidus*) are also hosts for *Stivalius franciscae* (Stivaliidae; Beaucournu and Durden, 2001). *Musserella,* n. gen. and species #1 (Pygiopsyllidae), resides not only on *Bunomys penitus*, but also on six other Sulawesi endemic murids (*Bunomys chrysocomus*; *Rattus hoffmanni* and *R. marmosurus*; *Paruromys dominator*; *Maxomys* sp.; *Taeromys celebensis*) and the nonnative *Rattus exulans* (Durden, in litt., 2008). *Neopsylla musseri* (Ctenophthalmidae) infests *Bunomys penitus* as well as the endemic Sulawesian *Paruromys dominator* and *Maxomys musschenbroekii* (Beaucournu and Durden, 1999). A female *Macrostylophora* sp. (Ceratophyllidae) that can not be identified to species was collected from a *Bunomys penitus* trapped on Gunung Nokilalaki (Durden and Beaucournu, 2006: 224).

Dasypsyllus gallinulae klossi (Ceratophyllidae) is a bird flea that was collected from my specimens of *Bunomys penitus* and identified by R. Traub (1983: 184), who wrote that

> The subgenus *Dasypsyllus* is probably the most catholic of all fleas in its host relationships, presumably infesting whatever warm-blooded animal comes within its reach, whether bird, man or other mammal. It undoubtedly has no peer in its geographic distribution, for one species … is not only Holarctic, but also occurs in the mountains of the Philippines, Indonesia and southern Asian mainland, and in the New World extends at least as far south as the mountains of Ecuador, Peru and Venezuela.

Lance Durden (in litt., 2010) provided me with additional information:

> Although *Dasypsyllus gallinulae* is mainly a bird flea (as borne out by its morphology and by most of the host records) it has a much wider range than most other fleas. There are three recognized subspecies of this species, *Dasypsyllus gallinulae gallinulae* in the Palearctic, *Dasypsyllus gallinulae perpinnatus* in the Americas, and *Dasypsyllus gallinulae klossi* in Southeast Asia. I have collected *D. g. gallinulae* from underground small mammal nests in England so I don't think the Sulawesi records of *D. g.*

klossi [from *Bunomys penitus*] are highly unusual. Nevertheless, morphology and most host records, tell us that this is really a bird flea.

Rhipicephalus pilans (Acari, Ixodoidea) larvae are the only tick recorded from *Bunomys penitus*. Larvae of this species also infest the native shrew, *Crocidura nigripes*; the nonnative house shrew, *Suncus murinus*; nonnative rats *Rattus exulans* and *R. tanezumi* (recorded as *R. rattus*); whereas adults parasitize a variety of domestic mammals (cattle, water buffalo, horses, goats, sheep, pigs, and dogs) as well as humans in Sulawesi (Durden et al. 2008).

Two species of pseudoscorpions, *Magachernes* sp. and *Chiridiochernes* sp. have been collected from the fur of *B. penitus* (W.B. Muchmore, in litt., 1986).

Two reports record nematodes (Nematoda) as endoparasites of *B. penitus.* Voucher hosts that I identified as *B. penitus* from the Mamasa region were found to be parasitized by the nematode *Bunomystrongylus abadii* (Trichostrongyloidea: Heligmonellidae), which is host-specific (Hasegawa and Mangali, 1996).

Bunomys penitus is listed as host for the nematode *Sibulura andersoni*, which also parasitizes a variety of other Indonesian murines (Purwaningsih and Dewi, 2007; Dewi, 2008). The provenance for the host is Kendari, in the lowlands on the eastern coast of the southeastern peninsula. *Bunomys penitus*, however, is restricted to montane habitats and on the southeast peninsula has been found only in Pegunungan Mekongga. The host record is certainly a misidentification; *B. andrewsi* would be the only *Bunomys* occurring in the Kendari area.

SYNONYMS: One synonym applies to *B. penitus.*

Rattus sericatus Miller and Hollister, 1921a: 73. HOLOTYPE: USNM 219627 (skin and skull; measurements are listed in table 41), an adult male collected December 19, 1917, by H.C. Raven (original number 3340). TYPE LOCALITY: Indonesia, Propinsi Sulawesi Tengah, Rano Rano (01°30′S, 120°28′E) in the west-central mountain block, 6000 ft (1830 m; locality 39 in gazetteer and on the map in fig. 51).

Miller and Hollister (1921a: 73) remarked of ''*Rattus penitus*'' that ''This large-snouted

member of the *chrysocomus* group is very different from all the related forms, with the exception of the species described next below, also a highland form, which it resembles in many features.''

The sample of that next species also consisted of five individuals and was named *Rattus sericatus* by Miller and Hollister (1921a: 73) who diagnosed it as ''Like *Rattus penitus*, but darker, and with still longer, softer pelage; feet more fully clothed with whitish hairs, sharply contrasted with dark brown of ankle. Skull with rostrum enlarged, but less thickened at end, more tapering, than in *penitus*.'' ''This species,'' remarked the authors, ''while obviously related to *Rattus penitus*, is readily distinguished by its much longer, softer pelage and the less thickened rostrum. Both species are large, high mountain forms of the *chrysocomus* group, with white-tipped tails.'' The name, *sericatus* means having the nature of silkiness, referring to the long, soft and silky texture of the fur, a quality common to all samples of *B. penitus*, not just the sample from Rano Rano.

Nor is the degree of white on the feet diagnostic, the entire range from pure white dorsal surfaces to white lightly suffused with gray is found in larger population samples, those from Gunung Kanino ($N = 74$) and Gunung Nokilalaki ($N = 82$), for example. The rostrum averages somewhat longer and broader in *sericatus* compared to other population samples, but not to the type series of *penitus*. In both principal-components and discriminant-function analyses, scores for the holotypes of *penitus* and *sericatus* are in the same plane along the first axis; it is the relatively longer bony palate and postpalatal region of the holotype of *penitus* (and two other specimens) that separates it from *sericatus*, as reflected by the distribution of scores along the second axis (fig. 77).

There is no phenetic trait shared among the five specimens collected by Raven at Rano Rano indicating that they represent anything other than another montane population of *B. penitus*.

SUBFOSSILS: None.

The following account describes another member of the *Bunomys fratrorum* group encountered along my transect line in the west-central mountain block, an undescribed

species that is found only in wet and cool streamside places in tropical lowland evergreen rain forest. In the field we called it *tikus abu-abuan*, the gray rat, and discovered that it eats *karoko*, an ''ear'' fungus.

Bunomys karokophilus, new species

HOLOTYPE: AMNH 225038, the skin, skull, and fluid-preserved carcass of an adult male (original number ASE 2322) collected November 6, 1974, by G.G. Musser. Standard external measurements, weight and other data, and measurements of the skull and dentition are listed in table 40. The stuffed skin is complete, the cranium and mandible are intact (figs. 84–86), and the carcass was originally preserved in formalin but is now stored in a mixture of water and ethanol.

TYPE LOCALITY: Tropical lowland evergreen rain forest along the Sungai Sadaunta (01°23′S, 119°58′E), a tributary on right side of the Sungai Miu, at 3300 ft (1007 m; locality 8 in gazetteer and on the map in fig. 50), in the northern portion of the west-central mountain block of the island's core, Propinsi Sulawesi Tengah, Indonesia.

DIAGNOSIS: A member of the *B. fratrorum* group that is moderately large in physical size (LHB = 150–190 mm, W = 95–175 g, ONL = 39.0–42.4 mm) and further characterized by the following combination of traits: (1) a short and wide muzzle and small external pinnae relative to body size; (2) dorsal fur dark gray or steel-blue speckled with pale buff, ventral fur varies from dark grayish white to dark gray or blue-gray speckled with white, dorsal carpal and metacarpal surfaces dark gray to brownish gray, digits and claws unpigmented; (3) tail typically shorter than length of head and body (LT/LHB = 94%), grayish brown to brownish gray on dorsal surface, white through mottled to brown over ventral surface (4) white tail tip characterizing all specimens in sample, short to moderately long relative to length of tail (mean = 18.2%, range = 2%–31%); (5) testes small relative to body size (10%); (6) spermatozoa head and tail length similar in shape and dimensions to spermatozoa of *B. penitus*, but the apical hook on the head is shorter and the tail is connected to middle of the concave

Fig. 84.   Dorsal views of adult skulls representing three species of *Bunomys*. Left to right: *Bunomys fratrorum* (USNM 217650, Temboan, northeastern peninsula), *B. karokophilus* (AMNH 225038, holotype, Sungai Sadaunta, west-central mountain block), and *B. andrewsi* (AMNH 225652, Kuala Navusu, central Sulawesi).   ×2.

surface; (7) chunky skull with a wide and moderately short rostrum, relatively narrow interorbit, narrow and upright zygomatic plate, short and broad incisive foramina, long bony palate (related to the short incisive foramina), and small ectotympanic bulla relative to skull size; (8) molars wide relative to lengths of maxillary and mandibular molar rows; (9) cusp t3 occurs infrequently on second upper molar (33%) and third upper molar (22%); (10) occlusal cusp pattern of third upper molar simple, cusp t1 typically not present or reduced to a low cingular ridge or pimplelike cusp on the cingular ridge in most specimens; (11) anterior labial cusplets absent from first lower molar, posterior labial cusplets present on first lower molars in half of sample and on second lower molars in three-fourths of sample; (12) anterolabial cusp present on second and third lower molars in about one-third of sample; and (13) karyotype, 2N = 42, FNa = 56, FNt = 60.

REFERRED SPECIMENS AND DATES OF COLLECTION: Total 28, including the holotype (coordinates for collection localities are provided in gazetteer; also see distribution map in fig. 50). **Sungai Sadaunta**: 2700 ft (823 m), AMNH 225027–33 (September 25–December 3, 1974); 2850 ft (869 m), AMNH 225034, 225039 (October 1, 7, 1974); 2900 ft (884 m), AMNH 225035 (October 2, 1974); 3000 ft (915 m), AMNH 225040 (October 30, 1974); 3200 ft (976 m), AMNH 224772, 226833 (November 11, 1974, March 19, 1976); 3250 ft (991 m), AMNH 225036, 225037 (November 3, 4, 1974); 3275 ft (999 m), AMNH 225041 (November 19, 1974); 3300 ft (1006 m), AMNH 225038 (holotype, November 6, 1974). **Tomado**: 1000 m, AMNH 223045, 223046, 223056, 223058, 223060, 223072, 224153, 226931, 257190 (January 25, 1972; July 26–27, 1973; August 2–14, 1973; May 14, 1974). **Sungai Tokararu:** 1150 m, AMNH 223305, 223316 (September 22, October 8, 1973).
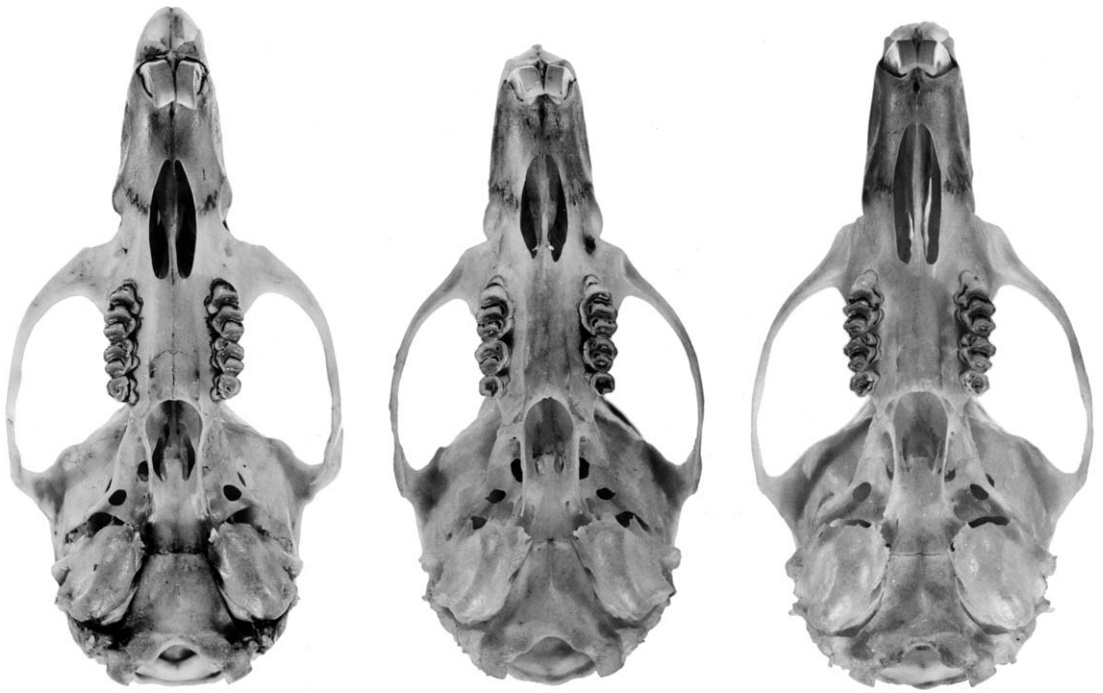
Fig. 85.   Ventral views of the same skulls shown in figure 84. From left to right: *B. fratrorum*, *B. karokophilus*, and *B. andrewsi*. ×2.

GEOGRAPHIC AND ELEVATIONAL DISTRI-BUTIONS: The only known sample of *Bunomys karokophilus* consists of the specimens collected along the Sungai Sadaunta (823–1006 m) in the drainage of the larger Sungai Miu, and in the watershed of Danau Lindu in the vicinity of Tomado (1000 m) and Sungai Tokararu (1150 m); see gazetteer and the map in figure 50. No specimens exist in older collections stored in the world's museums I have visited.

All collection sites are in the west-central mountain block of Sulawesi's core (see the map in fig. 50), and are characterized by wet and cool habitats along shaded streams and wet ravines in tropical lowland evergreen rain forest. At least three species of shrews (*Crocidura*), two or more tarsiers (*Tarsius*), a tree squirrel (*Prosciurillus topapuensis*) and ground squirrel (*Hyosciurus heinrichi*), and 20 species of rats and mice in *Crunomys*, *Maxomys*, *Bunomys*, *Sommeromys*, *Melasmothrix*, *Tateomys*, *Margaretamys*, *Taeromys*, *Paucidentomys*, *Haeromys*, *Eropeplus*, an undescribed genus related to *Eropeplus* and *Paruromys*, an undescribed shrew rat, and the amphibious rat *Waiomys* are also endemic to the west-central mountain block (table 65).

No present evidence indicates the range of *B. karokophilus* to extend beyond the western mountainous region of central Sulawesi. However, its distributional limits in that vast highland block have yet to be determined. If the collection sites along my transect reliably reflect its altitudinal range, *B. karokophilus* should be sought in tropical lowland evergreen rainforest habitats elsewhere in the west-central region and not in montane forest formations.

SYMPATRY WITH OTHER *BUNOMYS*: In addition to *B. karokophilus*, two other members of the *B. fratrorum* group are found along my transect, but neither occurs syntopically with the gray rat (fig. 103; table 6). We trapped *B. andrewsi* along the Sungai Sadaunta but only as high as 675 m; 823 m is the lowest collection site of *B. karokophilus* on the Sungai Sadaunta. The montane *B. penitus* drops to 1285 m on Gunung Kanino,
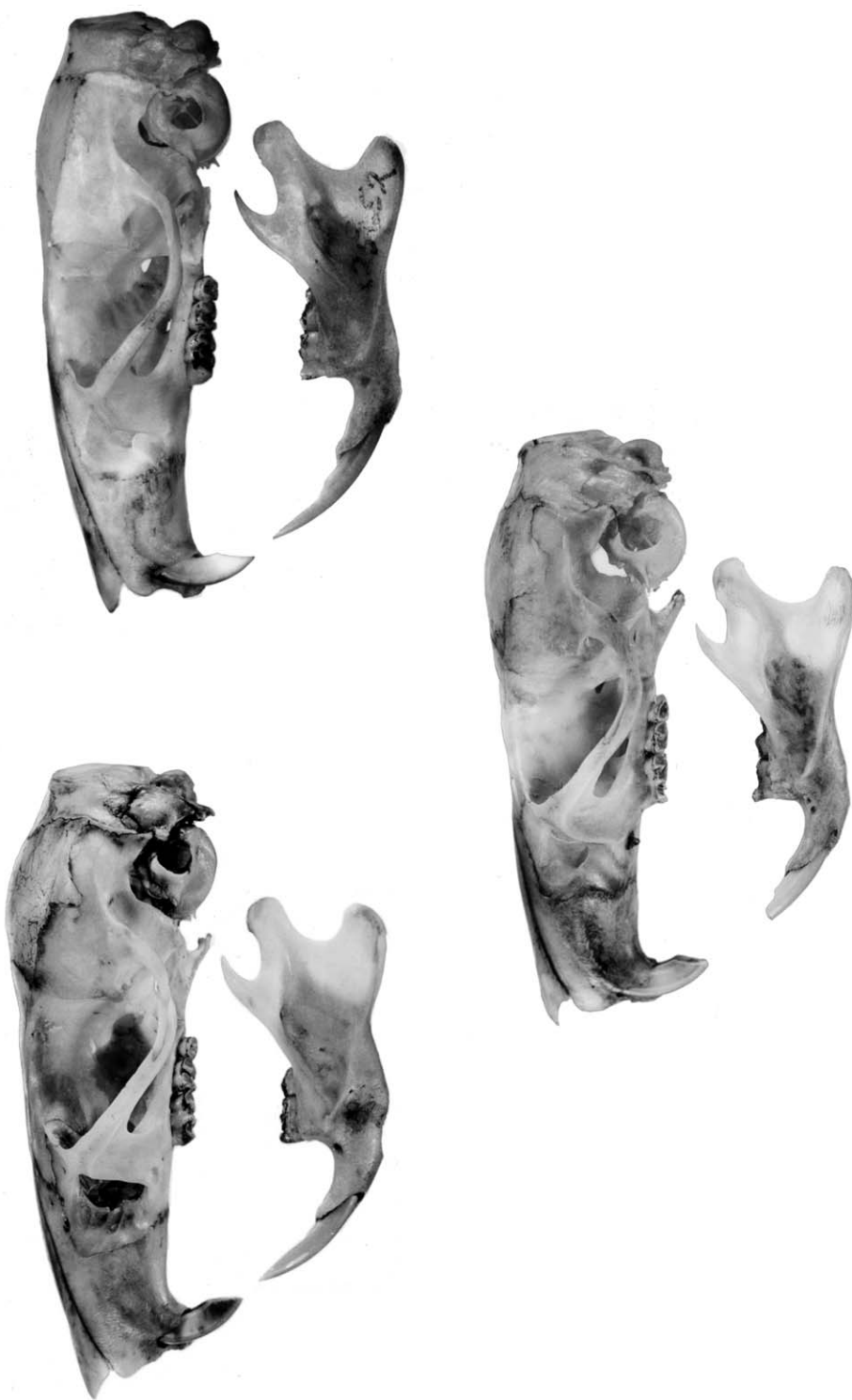
Fig. 86. Lateral views of the cranium and dentary of the same specimens presented in figures 84 and 85. Upper pair: *B. fratrorum* and *B. andrewsi*. Lower image: *B. karokophilus*. ×2.

which is the lower boundary of lower montane forest along the transect. The highest collection site for *B. karokophilus* is in tropical lowland evergreen rain forest at 1150 m (Sungai Tokararu) at the base of the high ridge forming Gunung Kanino (see the map in fig. 50).

Bunomys karokophilus lives in the same habitat as *B. chrysocomus*, the only representative of the *B. chrysocomus* group we trapped on the transect line between 823 m and 1150 m (fig. 103; tables 6, 20). We caught examples of each species between 823 m and 1006 m in streamside forest along the Sungai Sadaunta (both were taken at 823 m in the same trapline on September 25 and 28, 1974; and at 854 m on October 1, 1974); at Tomado, 1000 m (taken in same trapline on July 26 and 27, and August 2–4, 10, and 14, 1973); and at 1150 m near the Sungai Tokararu (both were caught in the same trapline on October 8, 1973).

ETYMOLOGY: ''*Karoko*,'' in the local language (*bahassa Kulawi*) in the area of central Sulawesi where I worked, refers collectively to ''ear and ear lobes'' and is also used for the gelatinous brownish-purple earlike lobes forming the fruiting body of the ear fungus *Auricularia delicata* (in the past also called a ''jelly'' fungus). This information was imparted to me by Panca, the father of Aminudi, one of my helpers, who also told me the fungus grew only on wet and decomposing wood and was sometimes eaten by the villagers. The fungus is also the primary ingredient in the diet of the gray rat, and I combine *karoko* with the Greek *philia* to indicate this gastronomic fondness.

DESCRIPTION: *Bunomys karokophilus* is of medium body size (LHB = 150–190 mm, LT = 135–205 mm, LHF = 36–44 mm, LE = 22–25 mm, W = 95–175 g, ONL = 39.0–42.4 mm) with dark gray or bluish-gray fur and a moderately long tail with a white tip (see the rendition based on a live animal in fig. 6)—a dark gray animal with a white-tipped tail. The long (15–20 mm) dorsal coat is smooth and soft to the touch. The dorsal coat of a few individuals is very dark gray speckled with pale to very pale buff (produced by the combination of dark gray underfur, overhairs that are dark gray for most of their lengths and tipped with short and pale buffy

bands, all intermixed with black guard hairs); sides of the body are paler (because of the paler gray and buffy bands). Because the guard hairs are only slightly longer than the overhairs, the surface of the coat is smooth, and the glistening guard hairs and dark gray of the underfur and overhairs produce a subdued sheen to the coat. Most specimens exhibit a darker steel-blue dorsal pelage; the buffy bands are narrower, and the combination of the long dark gray overhairs mingled with the glistening black guard hairs imparts a deep, bluish-gray cast to the fur, a tone we came to associate with ''*tikus abu-abuan.*'' An old female has unpigmented (silver) guard hairs scattered through the fur. The nose, lips, and lower half of each side of muzzle are white in some individuals, but sides of the muzzle are gray in others. Rest of the muzzle, upper cheeks, and around the eyes are darker, approaching grayish black. Forearms are dark gray, contrasting with the dorsal surfaces of the feet and rest oftops of feet and rest of the arms.

Fur covering the underparts of the head and body is also soft and dense, but shorter (8–10 mm long) than the dorsal fur, the usual pattern in murids. Four specimens out of the series have a grayish-white ventral coat with whiter areas on the throat, chest, and inguinal region (the long tips of the gray hairs are unpigmented). The rest of the specimens show very dark gray or bluish gray lightly speckled with white (the dark gray hairs have short unpigmented tips). The contrast between dorsal and ventral coats is barely evident.

In life, the ears (pinnae) feel and appear rubbery, and the color ranges from shiny dark gray through bluish gray to grayish black. They seem naked, but are scantily covered by short hairs. Ears of the stuffed voucher skins lack the rubbery texture of the live animal and have dried to brownish black.

Typically the tail is nearly equal to or shorter than the combined length of head and body (LT/LHB = 95%). Tail patterning is individually variable. All specimens show a distal white tail segment (unpigmented on all surfaces) ranging in the sample from 2% to 31% of the tail length (mean = 18.2%; table 8). Behind the white tip the top and sides of the tail range from glossy dark

TABLE 65
Nonvolant Mammal Species Currently Recorded Only from the West-Central Region in Sulawesi's Core[a]

Taxon	Lowland evergreen rain forest	Lower and/or upper montane forest
Phalangers[b]		*Strigocuscus* new species
Shrews		*Crocidura* n. sp. A
		Crocidura n. sp. B
		Crocidura musseri
Primates[c]	*Tarsius dentatus/Tarsius dianae*	
	Tarsius lariang	
		Tarsius pumilus
Squirrels[d]	*Prosciurillus topapuensis*	*Prosciurillus topapuensis*
		Hyosciurus heinrichi
Rats		*Sommeromys macrorhinos*[e]
		Tateomys rhinogradoides
		Tateomys macrocercus[e]
		Melasmothrix naso
		Paucidentomys vermidax[e]
	Shrew rat[f]	
		Waiomys mamasae
		Haeromys n. sp.[e]
		Eropeplus canus[e]
		New genus and species
		Margaretamys parvus
		Margaretamys elegans
	Crunomys celebensis	
	Maxomys dollmani[g]	*Maxomys dollmani*
	Maxomys n. sp. B[h]	
		Taeromys hamatus
		Taeromys n. sp. A
		Taeromys n. sp. B
	Bunomys karokophilus	
		Bunomys torajae

[a] The west-central region (or west-central mountain block) consists of the highlands forming the western portion of Sulawesi's core. It is that region of foothills, peaks, and interior valleys lying above 100 m and roughly west of Danau Poso, and extending from the Palu area in the north to Pegunungan Latimojong in the south (the area is outlined on the map in figure 1).

Data are derived from published (Musser, 1981a, 1982, 1987; Musser and Carleton, 2005; Musser and Dagosto, 1987; Musser and Durden, 2002; Musser and Holden, 1991; Ruedi, 1995; Merker and Groves, 2006; Esselstyn et al., 2012; Rowe et al., 2014), this report, unpublished results of my research as well as my observations made during trapping in the forests, and contributions from recent surveys (for which I am indebted to Jake Esselstyn, Kevin Rowe, and Anang Setiawan Achmadi); see also table 81. Future surveys may demonstrate that the ranges of some species extend beyond the west-central mountain block, especially some of the lowland species such as *Crunomys celebensis*, and may also uncover new species restricted to this highland landscape. Bats are excluded because I have applied only superficial taxonomic attention to this group and have yet to determine distributions on Sulawesi based upon voucher material.

[b] Specimens were collected by H.C. Raven at Besoa (01°44′S, 120°13′E; USNM) and W.J.R. Frost in Pegunungan Quarles (02°56′S, 119°39′E; BMNH). The species will be described in a review of the phalangers endemic to Sulawesi (K. Helgen, in litt., 2011).

[c] Groves (2005: 127) applied the name *dentatus* to the population of tarsiers occurring in the lowlands of central Sulawesi and regarded *Tarsius dianae* (Neimitz et al., 1991) as a synonym. Subsequently, Merker and Groves (2006) described *Tarsius lariang,* based on specimens obtained near Gimpu (01°38′S, 120°02′E, 400 m), just west of Lore-Lindu National Park in the west-central region of Sulawesi's core, and postulate the range to extend from the Palu region in the north to the Toraja highlands or Tempe depression in the south, and from the coast along the Makassar Straight in the west to the western boundary of Lore-Lindu National Park in the east (voucher specimens come only from the vicinity of Gimpu). They consider landscapes to the east of the range to be occupied by *T. dianae* (which they acknowledge may be the same as the earlier described *T. dentatus*), those to the south on the southwestern peninsula to contain *T. tarsier*, with one or more unnamed species occurring elsewhere on the island.

TABLE 65
(*Continued*)

[d] Documented in Musser et al. (2010).

[e] Nearly all records for these species come from montane forest habitats, but a few specimens of each have also been collected recently at 1600 m in the transition between tropical lowland evergreen and lower montane rainforest formations on Gunung Gandangdewata in the Quarles Range (K.C. Rowe, in litt., 2012).

[f] In lowland forest on Gunung Gandangdewata, an undescribed shrew rat (a new genus and species) was collected by Kevin Rowe and colleagues (K.C. Rowe, in litt., 2012; Esselstyn et al., 2012).

[g] The holotype of *dollmani* is from Rantekaroa (Bulu Karua), Pegunungan Quarles, in the west-central mountain block, and until the 1970s was the only specimen reported from that mountainous region. I had identified a sample of *Maxomys* collected by Gerd Heinrich from Pegunungan Mekongga on the southeastern peninsula as the same species (Musser, 1969), but that assessment is incorrect. Along my transect I collected a small series of a *Maxomys* exhibiting traits similar to the holotype of *dollmani*. Three specimens collected in 2010 by J.L. Patton and his colleagues from Gunung Balease (MVZ 225723, 225724, and 225821 also closely resemble the holotype, as does one specimen (KCR 1494) collected by K.C. Rowe and Anang Setiawan Achmadi from Gunung Gandangdewata in Pegunungan Quarles; these two samples are from the west-central mountain block. Heinrich's collection from Pegunungan Mekongga is a distinct species endemic to that range but still more closely related to *M. dollmani* than to any other Sulawesian species of *Maxomys* (Musser, MS.).

[h] This undescribed species of *Maxomys* is based on a collection I made in the forested basin of Danau Lindu, 955–1000 m. A sample from Gunung Rorekatimbo in the northern part of the west-central mountain block has been identified as an undescribed species by analysis of mtDNA (Achmadi et al., 2013); it is not included in the table because I don't know what forest formation the specimens came from.

grayish brown to brownish gray. The ventral surface varies considerably as follows: (1) same color as or only slightly paler than top and sides (monocolored); (2) basal half is the same color as the top and sides, but the distal half behind the white tip is paler or the entire ventral surface is pale brownish gray, so the tail is conspicuously bicolored; (3) white that is densely speckled with tan; (4) apparently white but is lightly speckled, usually only over basal half of tail; (5) glossy white from base to tip (so tail is bicolor except for distal white segment; this last pattern is also typical of *B. penitus*).

Metacarpal and metatarsal surfaces range from dark gray to brownish gray (the integument is white but densely covered with dark gray or brownish hairs), with silvery highlights in some specimens. Palmar pads are gray, the rest of the palmar surface ranges from pale gray to unpigmented; all the plantar surface ranges from gray to dark gray. Digits of front and hind feet are white on some specimens, on others the distal half of digits are white, the basal half speckled gray. All claws are unpigmented, those on the front digits are not concealed by ungual tufts, but comparable short tufts of silvery hairs sparsely cover the hind claws.

Females exhibit the number of teats usual for all species of *Bunomys*: four, arranged in two inguinal pairs. The scrotal sac of males is gray and sparsely haired (appears naked), and the testes are small relative to body size (10%; table 9). Spermatozoan morphology is described by Breed and Musser (1991; under *Bunomys* sp.).

Dorsal pelage of the three juveniles in the sample is denser to the touch than that of adults, appears woolly, and is dark gray with a flat tone (lacking the glossy sheen of the adult coat). Underparts are dark grayish white. The range in color of the ears and feet is similar to that of adults. All three juveniles have a white-tipped tail that is dark brown on all surfaces behind the white tip.

The stocky skull is smaller than that of most examples of other species in the *Bunomys fratrorum* group (figs. 84–86). The short and wide rostrum of *B. karokophilus* is distinctive, as is its short incisive foramina ending well anterior to front surfaces of the first molars (with a correspondingly long, bony palate). Relative to overall size of the skull, the interorbital region and zygomatic plate are narrow and the ectotympanic bullae small. Configuration of each dentary resembles the shape of this element in other members of the *B. fratrorum* group.

Compared with other members in the *B. fratrorum* group, *B. karokophilus* has a shorter molar row (indicated by the maxillary

Fig. 87.   Occlusal views of right maxillary molar rows in *Bunomys karokophilus*. Left: a very young adult (AMNH 257190; CLM1–3 = 6.8 mm) showing slight wear and no cusp t1 on the third molar (arrow). Middle: wear typical of adults; a small cusp t1 (arrow) is present on the third molar in this specimen (AMNH 223072; CLM1–3 = 7.0 mm). Right: an old adult in which most cusp rows are basined; the small cusp t1 (arrow) on the third molar is recognizable only by a bulge forming the anterolingual border of the tooth (AMNH 225027; CLM1–3 = 6.8 mm). The second molar lacks a cusp t3 (as shown in the middle image) in one-third of the sample and is less frequently present on the third molar (22% of the sample); see table 10.

molars, the row measured), but the teeth are wider relative to length of the toothrow, a proportion imparting a chunky aspect to them.

Cusp patterns forming the occlusal surfaces are also unelaborate and after much use the cusp rows wear to irregular basins surrounded by dentine (figs. 87, 88).

Another distinctive dental feature is the occlusal configuration of the third upper molar. In all species of *Bunomys* except for *B. karokophilus*, cusp t1forms the anterolingual border of the third molar and is large relative to overall size of that tooth, nearly as

relatively large as cusp t1 on the second upper molar (see the molars of *B. penitus*, for example, portrayed in figs. 74 and 75, or any of the images of maxillary molars from the other species of *Bunomys*). Cusp t1 is either missing or variable in its expression in the sample of *B. karokophilus* (fig. 87), as results of the following survey of 22 specimens demonstrate: (1) the occlusal surfaces of four individuals are too worn to discern cusp patterns; (2) there is no sign of cusp t1 on the third upper molar in five specimens, the occlusal surface is composed of an anterior lamina formed by cusps 4 and 5 and a

Fig. 88. Occlusal views of right mandibular molar rows from the same examples of *Bunomys karokophilus* that are portrayed in figure 86. The coronal patterns are uncomplicated and with age the cusp rows wear to dentine basins rimmed by enamel. Left, AMNH 257190 (clm1–3 = 7.0 mm); Middle, AMNH 223072 (clm1–3 = 7.3 mm), Right, AMNH 225027 (clm1–3 = 7.2 mm).

posterior cusp; (3) a low cingular ridge forms the anterolingual margin of the molar in one rat; (4) in four specimens, cusp t1 is very small and takes the shape of a deformed pimplelike cusp on the cingular margin, tiny compared with the normal-sized cusp t1 on the second molar; (5) seven specimens bear a definite cusp of medium size, but it is relatively much smaller than the large cusp t1 on the second molar and is distorted, configured among the seven rats as a ridge, a comma, or a ridge with two enamel bumps; (6) finally, only a single specimen has a large cusp t1 that relative to the other cusps forming the third molar is as large as cusp t1 on the second molar.

The absence of cusp t3 from second and third upper molars in a significant portion of the sample also signals an uncomplicated

chewing surface. The cusp is present on the second molar in 33% of the sample and occurs on the third molar in only 22% of all specimens surveyed (table 10).

Missing or low frequency of occurrence of particular cusps and cusplets on the lower (mandibular) molars contributes to their simple occlusal topography (fig. 88, table 11). An anterolabial cusp does not occur on the second and third molars in about three-fourths of the sample. The first lower molar does not support an anterior labial cusplet (usual for most other species of *Bunomys* except *B. chrysocomus*), but does exhibit a posterior labial cusplet in about half of the sample; this cusp occurs somewhat more frequently on the second molar.

KARYOTYPE: 2N = 42, FNa = 56 and FNt = 60, comprised of six pairs of metacentric

chromosomes, two pairs of subtelocentrics, and 12 pairs of acrocentrics; the sex chromosomes are submetacentrics (table 12).

COMPARISONS: *Bunomys karokophilus* requires comparisons with four other species of *Bunomys*, beginning with *B. fratrorum*. That species is endemic to the northern arm of Sulawesi east of the Gorontalo region; summarizing its phenetic contrasts with *B. karokophilus* is relevant to demonstrate that the latter is not just a population of *B. fratrorum* occurring in central Sulawesi. This contrast is especially relevant viewed in context of the UPGMA clustering of population samples representing all species of *Bunomys* that indicates *B. karokophilus* to be phenetically more closely related to *B. fratrorum* than to *B. andrewsi* or *B. penitus*, the other members of the *B. fratrorum* group (fig. 21).

Bunomys chrysocomus, *B. andrewsi*, and *B. penitus* are the others to be contrasted with *B. karokophilus*. The gray rat is syntopic with *B. chrysocomus* and is altitudinally parapatric with samples of *B. andrewsi* (at lower elevations) and *B. penitus* (at higher elevations) along my altitudinal transect.

Bunomys karokophilus and B. fratrorum: Both species are similar in body size, as estimated by average lengths of head and body and hind foot (because weight is unavailable for *B. fratrorum*, I cannot assess similarity or difference in mass between it and *B. karokophilus*), but differ in tail length—*B. karokophilus* has a shorter tail both absolutely and relative to length of head and body (LT/LHB = 94% as opposed to 99%–101% in the three population samples of *B. fratrorum*; table 41). *Bunomys karokophilus* also has, on average, a slightly longer white tail tip relative to tail length (mean = 18.2%, range = 2%–31% in *B. karokophilus*; mean = 17.7%, range = 6%–75% for *B. fratrorum*; table 8), and an average absolutely longer white tip (means = 35.6 mm for *B. karokophilus* and 30.2 mm for *B. fratrorum*). The dorsal fur is dark grayish brown or steel-blue and the ventral coat dark grayish white in *B. karokophilus*, but *B. fratrorum* has rich, brownish gray upperparts speckled with buff and black, and grayish white underparts speckled or washed with buff.

Testes size relative to body size is similar in the two species (table 9); spermatozoan morphology is different. In *B. karokophilus*, the falciform sperm head is long and moderately wide with a long apical hook and moderately long tail attaching near the middle of the convex surface of the sperm head. The spermatozoal tail attaches to about the middle of the sperm head in *B. fratrorum*, but the head is shorter and gently curved with a shorter apical hood, and the tail is shorter (Breed and Musser, 1991; Breed and Taylor, 2000). It may be significant that among the species of *Bunomys* surveyed for their spermatozoa morphology, in only *B. karokophilus* and *B. fratrorum* does the tail attach to the middle of the sperm head; in *B. chrysocomus*, *B. andrewsi*, and *B. penitus*, the tail attaches to the caudal portion of the sperm head. The shared spermatozoan configuration in *B. karokophilus* and *B. fratrorum* reinforces the morphometric alliance between these two species (fig. 21).

Bunomys karokophilus has a smaller skull than *B. fratrorum*, as attested by the smaller univariate mean values for almost all cranial and dental dimensions except for the interorbit and the bony palate, which are slightly wider and longer, respectively, in *B. karokophilus* (table 66); mean values for breadth of the upper molars is the same in both. Overall, *B. karokophilus* possesses a relatively wider interorbit and longer bony palate (reflecting shorter incisive foramina compared to those openings in *B. fratrorum*) relative to skull size as compared with *B. fratrorum*, and wider molars relative to length of the molar row. These absolute and proportional differences can be appreciated by examining the images of skulls portrayed in figures 84–86.

Relationships among the cranial and dental variables in the context of quantitatively discriminating between the two species are summarized by results of two multivariate analytical approaches. The first comprises a scatter plot where individual specimen scores representing the sample of *B. karokophilus* and all population samples of *B. fratrorum* are projected onto first and second principal components (fig. 89, upper graph). Along the first axis, scores for *B. karokophilus* generally cluster to the left of the cloud of

TABLE 66
Descriptive Statistics for Cranial and Dental Measurements (mm) Contrasting Samples of *Bunomys karokophilus* with Samples of *B. fratrorum* from the Northeastern Peninsula (East of Gorontalo), and *B. chrysocomus*, *B. andrewsi*, and *B. penitus* from the West-Central Mountain Block
Mean ±1 SD, and observed range (in parentheses) are listed.

| Variable | NE peninsula | West-central mountain block | | | |
	B. fratrorum	*B. karokophilus*	*B. chrysocomus*	*B. andrewsi*	*B. penitus*
N	100	17	189	40	174
ONL	44.0 ± 1.14	40.5 ± 1.13	38.2 ± 1.11	40.5 ± 1.84	43.0 ± 1.18
	(41.5–46.5)	(39.0–42.4)	(35.8–41.1)	(38.0–44.8)	(40.1–46.1)
ZB	20.9 ± 0.90	19.2 ± 0.89	18.0 ± 0.63	19.7 ± 1.02	19.7 ± 0.67
	(18.2–22.9)	(18.3–21.0)	(16.3–19.8)	(18.3–21.9)	(18.0–21.4)
IB	6.2 ± 0.31	6.3 ± 0.27	6.4 ± 0.23	6.7 ± 0.27	6.8 ± 0.24
	(5.5–7.0)	(6.0–6.8)	(5.8–7.2)	(6.1–7.3)	(6.1–8.3)
LR	15.2 ± 0.56	13.9 ± 0.62	13.6 ± 0.57	14.5 ± 0.98	16.1 ± 0.66
	(13.9–16.6)	(13.1–15.1)	(12.0–15.1)	(12.5–17.2)	(14.6–18.1)
BR	8.0 ± 0.38	7.6 ± 0.44	6.8 ± 0.34	7.5 ± 0.46	7.9 ± 0.34
	(7.2–9.0)	(6.8–8.6)	(5.8–7.7)	(6.7–8.9)	(7.0–8.9)
BBC	16.3 ± 0.41	15.9 ± 0.39	15.4 ± 0.40	16.2 ± 0.47	16.6 ± 0.40
	(15.3–16.3)	(15.2–16.6)	(14.2–16.7)	(15.3–17.2)	(15.4–17.7)
HBC	12.2 ± 0.43	11.1 ± 0.41	10.8 ± 0.36	11.4 ± 0.44	11.9 ± 0.35
	(11.3–13.1)	(10.5–11.8)	(10.0–12.1)	(10.6–12.4)	(10.9–12.7)
BZP	3.9 ± 0.32	3.1 ± 0.20	3.2 ± 0.24	3.5 ± 0.45	3.0 ± 0.21
	(3.1–4.6)	(2.7–3.5)	(2.6–3.8)	(2.9–4.5)	(2.4–3.6)
LD	11.4 ± 0.51	10.7 ± 0.46	10.2 ± 0.52	10.8 ± 0.66	11.3 ± 0.50
	(10.2–13.1)	(10.0–11.6)	(8.8–11.6)	(9.7–12.2)	(10.2–12.8)
PPL	15.4 ± 0.60	14.3 ± 0.63	13.6 ± 0.59	14.2 ± 0.84	14.6 ± 0.50
	(13.9–16.8)	(13.2–15.2)	(12.2–15.0)	(12.5–16.0)	(13.4–16.1)
LBP	8.0 ± 0.46	8.2 ± 0.37	7.5 ± 0.40	7.7 ± 0.43	8.8 ± 0.43
	(6.9–9.8)	(7.6–9.0)	(6.2–8.4)	(7.0–8.7)	(7.4–9.8)
BBP	3.8 ± 0.27	3.8 ± 0.28	3.8 ± 0.25	3.8 ± 0.32	3.6 ± 0.27
	(3.3–4.5)	(3.4–4.3)	(3.1–4.5)	(3.2–4.5)	(3.0–4.3)
BMF	3.5 ± 0.26	3.3 ± 0.21	3.0 ± 0.23	3.2 ± 0.27	3.7 ± 0.27
	(3.0–4.3)	(3.0–3.7)	(2.5–3.7)	(2.7–4.0)	(2.9–4.4)
LIF	7.3 ± 0.42	6.5 ± 0.32	6.2 ± 0.36	7.8 ± 0.51	8.1 ± 0.45
	(6.2–8.3)	(6.0–7.1)	(5.2–7.2)	(6.8–9.3)	(7.0–9.2)
BIF	2.9 ± 0.16	2.8 ± 0.19	2.5 ± 0.16	2.9 ± 0.21	3.0 ± 0.19
	(2.5–3.3)	(2.6–3.2)	(2.0–3.1)	(2.5–3.4)	(2.5–3.4)
LB	6.5 ± 0.20	6.3 ± 0.25	6.4 ± 0.23	6.5 ± 0.26	6.8 ± 0.28
	(6.1–7.0)	(5.9–6.7)	(5.7–7.0)	(5.9–7.0)	(6.0–8.2)
CLM1–3	7.6 ± 0.26	7.0 ± 0.15	6.2 ± 0.22	7.1 ± 0.37	7.8 ± 0.25
	(6.8–8.1)	(6.8–7.3)	(5.7–6.8)	(6.5–8.0)	(7.0–8.4)
BM1	2.4 ± 0.10	2.4 ± 0.07	2.0 ± 0.09	2.3 ± 0.10	2.5 ± 0.11
	(2.2–2.7)	(2.3–2.6)	(1.8–2.3)	(2.1–2.5)	(2.2–2.8)

points representing *B. fratrorum*, a positional response to the many greater dimensions typical of *B. fratrorum* as indicated by the positive moderate to high correlations ($r = 0.53–0.90$): covariation in all variables except interorbital breadth, length of bony palate, and breadth of first upper molar influence the distribution and segregation of scores along the first component (table 67). The regression lines of the second principal component on the first are phenetically distinct: their Y-intercepts are just greater than conventionally considered significantly different between the two species (+0.096 versus −0.012; $F = 3.10$, $P = 0.081$), but their slopes are not (0.130 versus 0.215; $F = 0.19$, $P = 0.667$).

Individual specimen scores for each species projected onto first and second canonical variates form another visual summary of
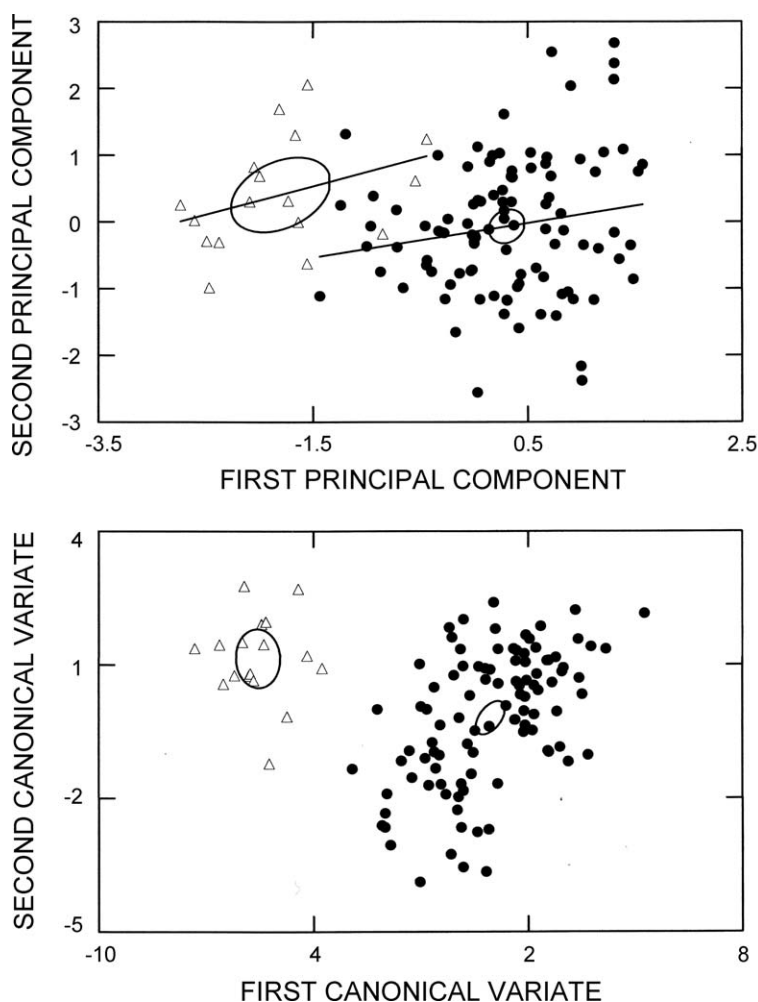
Fig. 89. Specimen scores representing *Bunomys karokophilus* (empty triangles; $N = 17$) from Sungai Sadaunta and the Danau Lindu Valley and all population samples of *B. fratrorum* (filled circles; $N = 100$) projected onto first and second principal components extracted from principal-components analysis (upper graph), and on first and second canonical variates derived from discriminant-function analysis (lower graph) of 16 cranial and two dental log-transformed variables. Ellipses outline 95% confidence limits for cluster centroids. Equations for the regression lines in the upper graph are: *B. karokophilus*, $Y = 0.215 \times 0.096$ (F = 2.12, P = 0.166); *B. fratrorum*, $Y = 0.130 \times -0.012$ (F = 2.91, P = 0.091). See table 67 for correlations (loadings) of variables with extracted components and canonical variates and for percent variance explained for both ordinations.

morphometric distinctions between the two species (fig. 89, lower graph). Two nonoverlapping clusters of scores identify each species, and their separation along the first axis is stongly influenced by correlations among the many variables in which *B. fratrorum* exceeds *B. karokophilus* in size ($r = 0.21–0.76$; table 67), along with the wider interorbit and longer bony palate of *B.*

karokophilus ($r = -0.21$ and -0.41, respectively).

The two species also differ in occlusal patterns formed by certain cusps and cusplets on maxillary molars (table 10). In the sample of *B. karokophilus*, cusp t3 occurs at a greater frequency on the second (33% in *B. karokophilus*, 11% in *B. fratrorum*) and third upper molars (22% as opposed to 9%). Cusp t1 on

TABLE 67
Results of Principal-Components and Discriminant-Function Analyses Performed on All Population Samples of *Bunomys karokophilus* and *B. fratrorum*
Correlations (loadings) of 16 cranial and two dental log-transformed variables are based on 17 *B. karokophilus* and 100 *B. fratrorum*; see figure 89.

Variable	Correlations			
	PC1	PC2	CV1	CV2
ONL	0.88***	−0.10	0.76***	−0.20*
ZB	0.87***	0.06	0.66***	0.03
IB	0.02	−0.04	−0.21*	−0.13
LR	0.75***	−0.08	0.57***	−0.48***
BR	0.72***	0.17	0.42***	0.03
BBC	0.49***	0.03	0.33***	−0.24**
HBC	0.78***	0.09	0.73***	−0.19*
BZP	0.90***	−0.30***	0.73***	−0.37***
LD	0.70***	−0.09	0.37***	−0.21*
PPL	0.77***	−0.03	0.68***	0.08
LBP	−0.06	−0.41***	−0.41***	−0.41***
BBP	0.43***	0.34***	0.09	−0.04
BMF	0.32***	0.74***	0.15	−0.08
LIF	0.70***	0.27**	0.72***	0.18*
BIF	0.47***	0.40***	0.21*	0.14
LB	0.41***	−0.09	0.22*	−0.10
CLM1–3	0.53***	−0.24**	0.61***	−0.18
BM1	−0.07	−0.05	0.01	0.35***
Canonical correlation			0.936	0.764
Eigenvalue	0.026	0.007	7.109	1.400
% Variance	43.9	11.2	68.8	13.5

***P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

the third upper molar is typically not present or reduced to a low cingular ridge or pimplelike cusp on the cingular ridge in most specimens of *B. karokophilus* (fig. 87), but takes the form of a large prominent cusp in all examples of *B. fratrorum* (fig. 12).

Coronal topography of the lower molars differs slightly between the species (table 11). An anterolabial cusp is about twice as frequent on the second molar in *B. karokophilus* (27%) as in *B. fratrorum* (12%), and occurs at the same percentage on the third molar in *B. karokophilus* (fig. 88), but is absent from the third molar in all specimens of *B. fratrorum* surveyed (fig. 12).

The combination of external, cranial, and dental traits characterizing *B. karokophilus*, along with its distinctive diet, clearly separates it from *B. fratrorum*. Although *B. karokophilus*, living in the west-central moun-

tain block, is not just a geographic population of *B. fratrorum*, which is endemic to the northern peninsula east of the Gorontalo region, the two may be more closely allied to one another than to other species of *Bunomys* if morphometric aspects of skulls and molars, along with gross conformation of spermatozoa, reliably mirror genetic alliance. The phenetic relationships among all population samples of *Bunomys* analyzed that are illustrated in the cluster diagram in figure 21, which is derived from discriminant-function analyses of covariation in cranial and dental variables, links the sample of *B. karokophilus* with those representing *B. fratrorum*. An independent test of this phenetic kinship by analyzing DNA sequences is required.

Bunomys karokophilus and *B. chrysocomus*: Samples of *tikus abu-abuan* were collected on the Sungai Sadaunta between 823 and 1006 m, and at Tomado (1000 m) and Sungai Tokararu (1150 m) in the Danau Lindu valley. *Bunomys chrysocomus* lives in the same damp forest habitats in these areas and was collected along the Sungai Sadaunta through the elevational range 823–960 m, and also at Tomado (1000 m) and Sungai Tokararu (1150 m). My comparisons are based primarily on specimens of each species representing this syntopic distribution. Descriptive univariate statistics derived from external, cranial, and dental measurements from these samples are listed in table 68. An additional comparison will contrast the sample of *B. karokophilus* with all the examples of *B. chrysocomus* collected along my transect that extended from Sungai Oha Kecil to Gunung Kanino (the two populations samples, "Sungai Oha Kecil + Sungai Sadaunta" and "Danau Lindu Valley + Gunung Kanino"; table 2); table 66 contain the relevant univariate statistics. A final contrast involves a ratio diagram pitting the sample of *B. karokophilus* against eight population samples of *B. chrysocomus* (identified in table 2).

I thought the first few specimens of *B. karokophilus* I trapped to be *B. chrysocomus* for at first glance both species appear externally much alike, with their dark dorsal coats of similar length and texture and grayish underparts. But more critical inspection reveals strong dissimilarities. *Bunomys*

TABLE 68

Descriptive Statistics for External, Cranial, and Dental Measurements (mm) derived from Samples of *Bunomys karokophilus* and *B. chrysocomus* Collected at the Same Places in Sulawesi's West-Central Region

Specimens representing each species are from Tomado (1000 m), Sungai Tokararu (1150 m) and through an overlapping elevational range along Sungai Sadaunta (823–1006 m for *B. karokophilus*; 823–960 m for *B. chrysocomus*). Mean ± 1 SD and observed range (in parentheses) are listed. Measurements (excluding WT and LT/LHB) from specimens in these two samples were used to derive the results from the principal-components analyses summarized in figure 90 and table 69.

Variable	*B. chrysocomus* (Sungai Sadaunta + Tomado + Sungai Tokararu)	*B. karokophilus* (Sungai Sadaunta + Tomado + Sungai Tokararu)
EXTERNAL	*N* = 71	*N* = 22
LHB	159.8 ± 8.91 (136–180)	173.8 ± 8.74 (155–190)
LT	139.2 ± 10.49 (107–159)	164.4 ± 11.8 (150–205)
LT/LHB (%)	87	95
LHF	35.7 ± 1.43 (32–40)	39.3 ± 1.39 (36–42)
LE	23.9 ± 1.27 (21–28)	23.3 ± 0.78 (22–25)
WT	97.0 ± 14.0 (75–135)	133.2 ± 17.22 (105–175)
CRANIAL-DENTAL	*N* = 77	*N* = 17
ONL	38.2 ± 1.03 (36.1–40.4)	40.5 ± 1.13 (39.0–42.4)
ZB	18.1 ± 0.60 (16.8–19.8)	19.2 ± 0.89 (18.3–21.0)
IB	6.3 ± 0.21 (5.8–6.9)	6.3 ± 0.27 (6.0–6.8)
LR	13.5 ± 0.56 (12.0–15.1)	13.9 ± 0.62 (13.1–15.1)
BR	6.8 ± 0.39 (5.8–7.7)	7.6 ± 0.44 (6.8–8.6)
BBC	15.4 ± 0.43 (14.3–16.7)	15.9 ± 0.39 (15.2–16.6)
HBC	10.7 ± 0.35 (10.0–11.8)	11.1 ± 0.41 (10.5–11.8)
BZP	3.3 ± 0.25 (2.6–3.7)	3.1 ± 0.20 (2.7–3.5)
LD	10.2 ± 0.51 (8.8–11.6)	10.7 ± 0.46 (10.0–11.6)
PPL	13.6 ± 0.56 (12.3–15.0)	14.3 ± 0.63 (13.2–15.2)
LBP	7.4 ± 0.39 (6.6–8.2)	8.2 ± 0.37 (7.6–9.0)
BBP	3.8 ± 0.26 (3.2–4.5)	3.8 ± 0.28 (3.4–4.3)
BMF	2.9 ± 0.26 (2.5–3.7)	3.3 ± 0.21 (3.0–3.7)
LIF	6.3 ± 0.37 (5.4–7.2)	6.5 ± 0.32 (6.0–7.1)
BIF	2.4 ± 0.56 (2.1–2.8)	2.8 ± 0.19 (2.6–3.2)
LB	6.4 ± 0.23 (5.9–7.0)	6.3 ± 0.25 (5.9–6.7)
CLM1–3	6.1 ± 0.20 (5.7–6.5)	7.0 ± 0.15 (6.8–7.3)
BM1	2.0 ± 0.09 (1.8–2.2)	2.4 ± 0.07 (2.3–2.6)

karokophilus has darker fur, the upperparts are dark grayish brown or blue-gray, the underparts are dark grayish white or blue-gray flecked with white; *B. chrysocomus* has rich, dark brownish-gray dorsal fur finely spotted with dark buff and underparts that are grayish white, or grayish white suffused with buff or ochraceous hues. The living *B. karokophilus* has a short and broad face anterior to the eyes, but that of *B. chrysocomus* is long and slender by comparison. Nose, lips, and lower half of each side of the muzzle are white in some individuals of *B. karokophilus*, the muzzle is gray in others; nose and muzzle are brownish gray in *chrysocomus*, and only the lips and very tip of the nose are unpigmented. In the living animals, ears (pinnae) of *B. karokophilus* are dark gray to blue-gray, those of *B. chrysocomus* are dark brownish gray (dried ears of specimens in museums are dark brown to blackish in both species). Dorsal surfaces of the carpal and metacarpal regions are gray and the digits unpigmented in *B. karokophilus*, while the entire dorsal surfaces of the feet are lightly to intensely speckled dark gray to brown in *B. chrysocomus*. *Bunomys karokophilus* has short and delicate front claws compared to the noticeably longer and more robust claws of *B. chrysocomus*.

In both species, the tail is typically shorter in relation to length of head and body, but *B. karokophilus* has, on average, a relatively longer tail (LT/LHB = 95%) than does *B. chrysocomus* (mean of nine samples = 90%). Length of the white tail tip relative to length

of tail is greater in *B. karokophilus* (mean = 18.2%, range = 2%–31% for *B. karokophilus*; mean = 5.5%, range = 1%–25% for *B. chrysocomus*; see table 8), and frequency of a white tip differs. All specimens of *B. karokophilus* ($N = 24$ with intact tails) exhibit a white distal segment while only 20% of the sample of *B. chrysocomus* ($N = 396$) show a white tip.

Bunomys karokophilus is physically larger than *B. chrysocomus* (comparing adults), averaging greater in body mass and in all external dimensions except length of ear, which is about the same in absolute values, making it smaller relative to body size (LE/LHB = 13% for *B. karokophilus*, 14%–16% for four samples of *B. chrysocomus*). This disparity in body size is quantified in two tables where the sample of *B. karokophilus* (table 41) is contrasted with all population samples of *B. chrysocomus* (table 19), and in table 68 where *B. karokophilus* is compared with the sample of *B. chrysocomus* from the transect where the two species overlap in range (specimens of each species are from Sungai Sadaunta, Tomado, and Sungai Tokararu). Differences in external variables for the syntopic samples are summarized by individual specimen scores projected onto first and second principal components (fig. 90, upper graph). High and positive loadings for lengths of head and body, tail, and hind foot ($r = 0.71$–0.97) power the scores along the first axis and segregate those for *B. chrysocomus* with the shorter body and appendages on the left from scores representing *B. karokophilus* with longer body and appendages on the right; length of ear is negligible in influencing the spread of points, which reflects the relatively smaller ears of *B. karokophilus* (table 69).

Relative size of testes clearly distinguishes adult males of the two species (table 9). The testes are small in relation to body size in *B. karokophilus* (length of testes/length of head and body = 10%), but conspicuously much larger in *B. chrysocomus* (22%).

External morphology of spermatozoa is also different. Breed and Musser (1991: 10) noted that compared with the spermatozoa of *B. chrysocomus*, those of *B. karokophilus* (identified as ''*Bunomys* sp. A''

in their report) have ''a wider sperm head, shorter apical hook, and shorter sperm tail.'' Also, the tail attaches to about the middle of the head in *B. karokophilus* but at the ventrocaudal portion of the head in *B. chrysocomus.*

Both species have a 2N of 42, but FNa = 56 and FNt = 60 for *B. karokophilus* and FNa = 56 and FNt = 58 for *B. chrysocomus* (table 12).

The two species do not share a similar diet. The *karoko* fungus, *Auricularia delicata*, comprises the bulk of *B. karokophilus*'s diet; *B. chrysocomus* does not consume fungi (see Natural History section in the accounts of each species). This dietary contrast proved useful in separating two juveniles I caught in live traps along the Sungai Sadaunta. They were similar in body size, color and texture of their juvenile fur, and color of ears and feet; tails of both were dark gray along their dorsal surfaces and white on the ventral surface, but one had a white tip and the other did not. They could be young of either *B. karokophilus* or *B. chrysocomus*, or the two together a sample of one of those species. I offered insects, snails, earthworms, and *karoko* to each rat. The juvenile with the white tail tip accepted and ate only *karoko*; the other juvenile rejected the *karoko* but consumed the invertebrates. Subsequent study showed the former to be *B. karokophilus*, the latter *B. chrysocomus.*

The large, robust skull of *B. karokophilus* with its stocky rostrum, narrow zygomatic plate, spacious incisive foramina, and large, chunky molars contrasts with the smaller skull of *B. chrysocomus* that is more elongate in overall shape, appearing gracile in comparison, and with weak molars (figs. 99–101). Univariate means for breadths of interorbit, zygomatic plate, and bony palate, along with length of bullar capsule are less or the same in *B. karokophilus* compared with the various samples of *B. chrysocomus*, but the means are greater for all other cranial and dental dimensions in the sample of *B. karokophilus* (tables 66, 68).

How the cranial and dental variables interact in distinguishing the two species is summarized below in results of two analyses. First, individual specimen scores from the syntopic samples (Sungai Sadaunta, To-
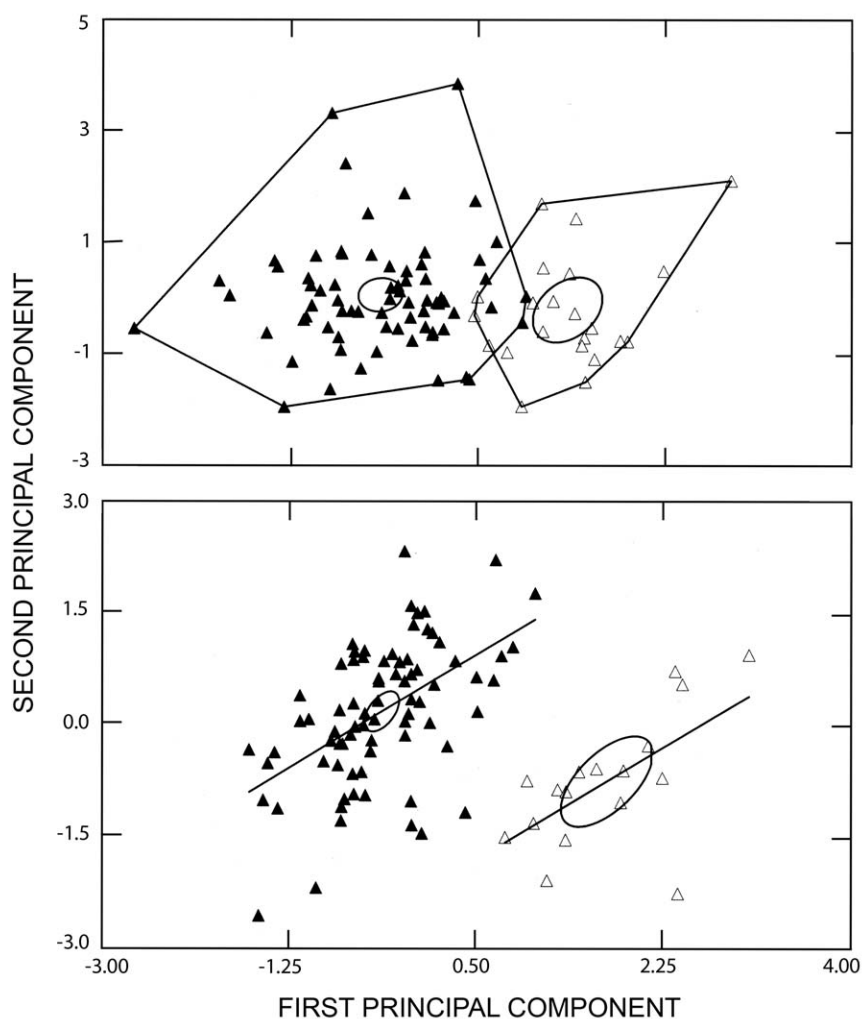
Fig. 90. Specimen scores representing samples of *Bunomys karokophilus* (empty triangles) from Sungai Sadaunta (823–1006 m), Tomado (1000 m), and Sungai Tokararu (1150 m), and samples of *Bunomys chrysocomus* (filled triangles) from Sungai Sadaunta (823–960 m), Tomado (1000 m), and Sungai Tokararu (1150 m) projected onto first and second principal components extracted from principal-components analysis. Ellipses outline 95% confidence limits for each cluster centroid in both ordinations. Upper graph: derived from a covariance matrix of log-transformed values for lengths of head and body, tail, hind foot, and ear ($N = 22$ for *B. karokophilus*; $N = 71$ for *B. chrysocomus*). Lower graph: based on a covariance matrix of log-transformed values for 16 cranial and 2 dental variables ($N = 17$ for *B. karokophilus*; $N = 77$ for *B. chrysocomus*). Equations for the regression lines are: *B. karokophilus*, $Y = 0.867X -2.254$ ($F = 9.02$, $P = 0.009$); *B. chrysocomus*, $Y = 0.873X\ 0.500$ ($F = 28.52$, $P = 0.000$). See table 69 for correlations (loadings) of variables with extracted components and for percent variance explained for both ordinations. The results illustrated here focus on samples of each species collected at Tomado, Sungai Tokararu, and within the same elevational range along the Sungai Sadaunta. The pattern of scores in the lower scatter plot, and degree of significance of the Y-intercepts of the regression lines and their slopes, is closely similar to the pattern derived from comparing the sample of *B. karokophilus* with all samples of *B. chrysocomus* from my transect ($N = 186$) and all 10 population samples ($N = 232$; table 2) of that species (neither is illustrated).

The samples of *B. karokophilus* from Sungai Sadaunta (823–1006 m), Tomado (1000 m), and Sungai Tokararu (1150 m) are compared with samples of *B. chrysocomus* from the Sungai Sadaunta (823–960 m), Tomado (1000 m), and Sungai Tokararu (1150 m). Correlations (loadings) of log-transformed values for lengths of head and body, tail, hind foot, and ear (**upper graph**); and for 16 cranial and two dental variables (**lower graph**) are based on 99 specimens; see figure 90.

| | Correlations | | | |
| | Upper graph | | Lower graph | |
Variable	PC1	PC2	PC1	PC2
LHB	0.71***	−0.63***	—	—
LT	0.97***	0.20	—	—
LHF	0.84***	0.00	—	—
LE	−0.09	0.50***	—	—
ONL	—	—	0.87***	0.18
ZB	—	—	0.79***	0.28**
IB	—	—	0.21*	0.43***
LR	—	—	0.59***	0.35***
BR	—	—	0.82***	0.28**
BBC	—	—	0.57***	0.06
HBC	—	—	0.58***	0.16
BZP	—	—	−0.04	0.76***
LD	—	—	0.63***	0.51***
PPL	—	—	0.68***	0.20*
LBP	—	—	0.69***	0.03
BBP	—	—	0.07	0.80***
BMF	—	—	0.76***	−0.17
LIF	—	—	0.38***	0.24*
BIF	—	—	0.80***	0.05
LB	—	—	0.12**	0.31**
CLM1–3	—	—	0.82**	−0.34***
BM1	—	—	0.81***	−0.37***
	—	—		
Eigenvalue	0.014	0.003	0.029	0.011
% Variance	70.1	13.2	43.4	16.2

*** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

mado, and Sungai Tokararu) are projected onto first and second principal components where they form two oblique elliptical spreads (fig. 90, lower graph). The major axes are phenetically distinct: their Y-intercepts are significantly different between the two species (−2.254 versus +0.500; F = 23.98, P = 0.000), but not their slopes (0.867 versus 0.873; F = 0.00, P = 0.988). Loadings for nearly all variables influence the distribution of scores along the first axis, reflecting

the many greater internal dimensions and overall larger skull and molars of *B. karoko-philus* compared with the smaller skull and molars of *B. chrysocomus*; loadings (correlations) for overall skull size (occipitonasal length and zygomatic breadth), breadths of rostrum, mesopterygoid fossa, incisive foramina, and first upper molar, along with lengths of bony palate, postpalatal region, and maxillary molar row, are especially high (r = 0.57–0.87; table 69). There exists but slight overlap between the two clouds of points along the first component. A principal-components analysis employing all 10 population samples of *B. chrysocomus* and the sample of *B. karokophilus* resulted in a closely similar pattern of scores (not illustrated here).

Second, relevant proportional distinctions are recorded in a ratio diagram where the sample of *B. karokophilus* is compared with all 10 population samples combined of *B. chrysocomus* (fig. 91). The interorbit of *B. karokophilus* is significantly narrower relative to overall skull size (reflected by occipitonasal length and zygomatic breadth); the rostrum is shorter relative to skull length and appreciably wider relative not only to its length, but to size of skull; the zygomatic plate is narrower relative to skull size and most other cranial and dental variables; the bony palate is longer but much narrower, and the mesopterygoid fossa is wider not only relative to skull size but to bony palate; the incisive foramina is markedly wider than long; the bulla, about the same size in univariate means, is smaller relative to size of skull; and the molar row is longer relative to many cranial variables, and the teeth are wider relative to length of molar row.

In addition to the larger molars of *B. karokophilus*, there are contrasts between it and *B. chrysocomus* in the frequencies of occurrence of several cusps and cusplets. Cusp t3 occurs at a greater frequency on the second (33% in *B. karokophilus*, 17% in *B. chrysocomus*) and third (22% as opposed to 5%) upper molars (table 10). Cusp t1 on the third upper molar is typically absent or consists of a distorted cusp, cingular ridge, or pimple in *B. karokophilus* (fig. 87), but the third molar of *B. chrysocomus* sports a prominent cusp t1 (fig. 12), which is also
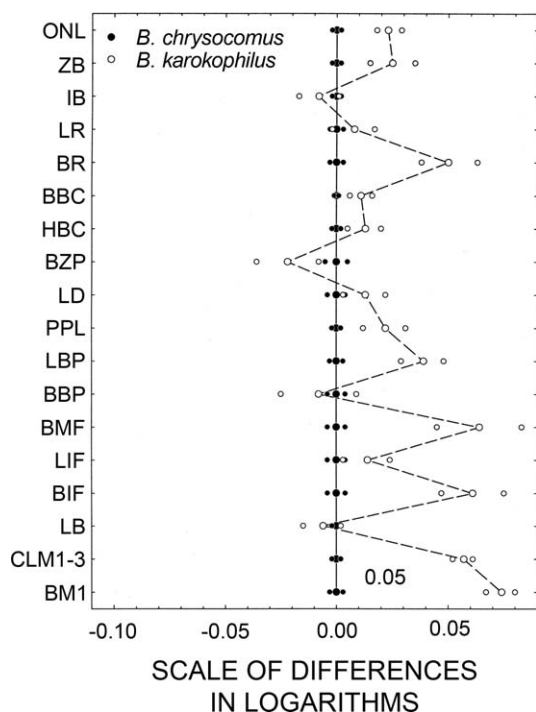
Fig. 91.   Ratio diagram illustrating some proportional relationships in cranial and dental dimensions between *Bunomys karokophilus* ($N = 17$) and all population samples of *B. chrysocomus* (the standard, $N = 232$). Data were derived from values for mean, standard deviation, and sample size of variables listed in table 41. How these diagrams were constructed and how to read them are explained in Materials and Methods.

usual in all the other species of *Bunomys* except *B. karokophilus.* In the lower molars, an anterior labial cusplet is absent from the first molar in specimens of *B. karokophilus*, but occurs in 52% of the *B. chrysocomus* sample; about half the sample of *B. karokophilus* shows a posterior labial cusplet, but nearly all specimens of *B. chrysocomus* exhibit the cusplet (table 11). On the second molar, 27% of the series of *B. karokophilus* have an anterolabial cusp, but most specimens (90%) of *B. chrysocomus* have this cusp; 64% of the sample of *B. karokophilus* show a posterior labial cusplet, but the frequency is 98% in the sample of *B. chrysocomus.* An anterolabial cusp is less frequent on the third molar in the sample of *B. karokophilus* (27%) than it is in *B. chrysocomus* (65% of the sample).

Contrasts between the two species described in the preceeding paragraphs are drawn from my observations in the forest of freshly caught animals and my study in the museum of preserved voucher specimens. The results presented here are somewhat detailed, but two approaches, one in the field, the other in the laboratory, can be used to distinguish the two species. Should one be surveying for small mammals in tropical lowland evergreen rain forest in the western mountain block of Sulawesi's core and trapping alive what may be examples of each but the identification is uncertain, find some *karoko* and offer it to the rats. In the laboratory or museum, measure the maxillary molar row and breadth of the first upper molar of the samples. *Bunomys karokophilus* has larger molars and there is little or no overlap in the range of variation within my different sets of samples. Ranges for CLM1–3 and BM1 are 6.8–7.3 mm and 2.3–2.6 mm, respectively for *B. karokophilus.* Values for *B. chrysocomus* in the syntopic samples are 5.7–6.5 mm and 1.8–2.2 mm; in the two population samples, "Sungai Oha Kecil + Sungai Sadaunta" and "Danau Lindu Valley + Gunung Kanino," the ranges are 5.7–6.8 mm and 1.8–2.2 mm; and for all 10 population samples of *B. chrysocomus* the respective ranges are 5.7–6.8 mm and 1.8–2.3 mm.

Bunomys karokophilus and B. andrewsi: These two species are generally physically similar in body size, although animals in certain geographic areas may average larger or smaller than *B. karokophilus.* For example, the samples of *B. andrewsi* from Kuala Navusu, Gunung Balease, and the Malili Area weigh more, on average, than *B. karokophilus* (mean = 131.5 g for *B. karokophilus*, range of means = 145.0–154.6 g for *B. andrewsi*), but body size is comparable (mean for length of head and body = 172.9 mm for *B. karokophilus*, range of means = 169.9–177.4 mm for *B. andrewsi*; and mean for length of hind foot in *B. karokophilus* = 39.3 mm as opposed to 40.2–40.5 mm for *B. andrewsi*); however, animals in the small sample from "Puro-Sungai Miu" weigh less (mean = 113.7 g) and average slightly smaller in lengths of head and body and hind foot (means = 163 mm and 38.1 mm, respectively).

Bunomys karokophilus has small ears (external pinnae) in relation to body size (LE/LHB = 13%) compared with the relatively larger ears of *B. andrewsi* (means = 14%–16% for four samples; see table 41). This proportional contrast is also reflected by the slightly smaller (relative to skull length) bullar capsule of *B. karokophilus* compared with the relative size of this structure in *B. andrewsi*, as seen on the ratio diagram in figure 93.

No matter their provenances, all adult examples of *B. andrewsi* can be distinguished from *B. karokophilus* by coat color and tail characteristics. Fur covering the upperparts is a rich dark brown speckled with buff in *B. andrewsi*, the ventral coat ranges from grayish white to bright buffy gray; most specimens from lowlands have a gray ventral coat washed with pale or rich buff; many have reddish stains on the chest and throat. *Bunomys karokophilus* is a dark gray rat. The dorsal coat is either dark gray speckled with pale buff or a very dark blue-gray; underparts are dark grayish white in all examples at hand.

Tails are relatively longer and white-tipped in *B. karokophilus*, shorter and mostly without white tips in *B. andrewsi*. In both species, the tail is typically shorter than length of the head and body, but it is relatively longer in *B. karokophilus* (mean = 95%) than in the samples of *B. andrewsi* (range of means = 75%–92%). All examples of *B. karokophilus* with intact tails (N = 24) have a white tail tip (mean length = 28.7 mm, range = 4–50 mm) that comprises 2%–31% of the tail length (mean = 18.2%); of the 133 specimens of *B. andrewsi*, tails of only 20% exhibit a white tip (mean length = 8.6 mm, range = 1–20 mm), and when present it is typically relatively shorter in relation to overall length of tail (mean = 7.7%, range = 1%–13%); see table 8.

Diet differs between the two species. Ear fungi, primarily *Auricularia delicata*, comprise the bulk of *B. karokophilus*'s diet; *B. andrewsi* consumes fruit, arthropods, earthworms, and small vertebrates but not fungi (table 13).

There is an average contrast in relative testes size (table 9). The testes of *B. karoko-*

philus are smaller relative to combined length of head and body (10%) compared with samples of *B. andrewsi* (8%–15%).

External morphology of spermatozoa is slightly different. Breed and Musser (1991: 10) noted that spermatozoa of *B. karokophilus* (identified as *Bunomys* sp. A) have "a wider sperm head, shorter apical hook, and shorter sperm tail" compared with those of *B. andrewsi*; also, site of attachment of tail to the sperm head differs.

Both species have a 2N of 42, but an FNa = 56 and FNt = 60 for *B. karokophilus* and FNa = 56 and FNt = 58 for *B. andrewsi* (table 12).

Comparisons in cranial and dental morphometrics are subjects of the following paragraphs. With the exception of a ratio diagram, the contrasts are between *B. karokophilus* and the samples of *B. andrewsi* from the west-central region where the two species are regionally sympatric but not syntopic in distribution (see gazetteer and the map in fig. 50). Skulls of the two species are similar in overall size (estimated by occipitonasal length) and many internal cranial and dental dimensions are equivalent (table 66). The few differences, however, are noticeable, as seen in tables of measurements and side-by-side comparisons of skulls: *B. karokophilus* typically has a narrower zygomatic breadth and interorbital region, shorter rostrum, narrower zygomatic plate, shorter incisive foramina, and longer bony palate (a reflection of the shorter incisive foramina).

The general similarity in cranial dimensions between most individuals of *B. karokophilus* compared with the specimens representing *B. andrewsi* (from Puro-Sungai Miu, Tamalanti, Tuare, Mamasa Area, and Gunung Balaese) is summarized by individual specimen scores projected onto first and second principal components where they form parallel oblique elliptical clusters (fig. 92). The major axis of each ellipsoid is phenetically discrete: their Y-intercepts are significantly different between the two species (1.493 versus −0.580; F = 12.48, P = 0.001), but not their slopes (0.573 versus 0.388; F = 0.46, P = 0.499). The high positive correlations for most cranial and dental variables (r = 0.52–0.92; table 70) spread the scores along the first axis where there is broad overlap between the
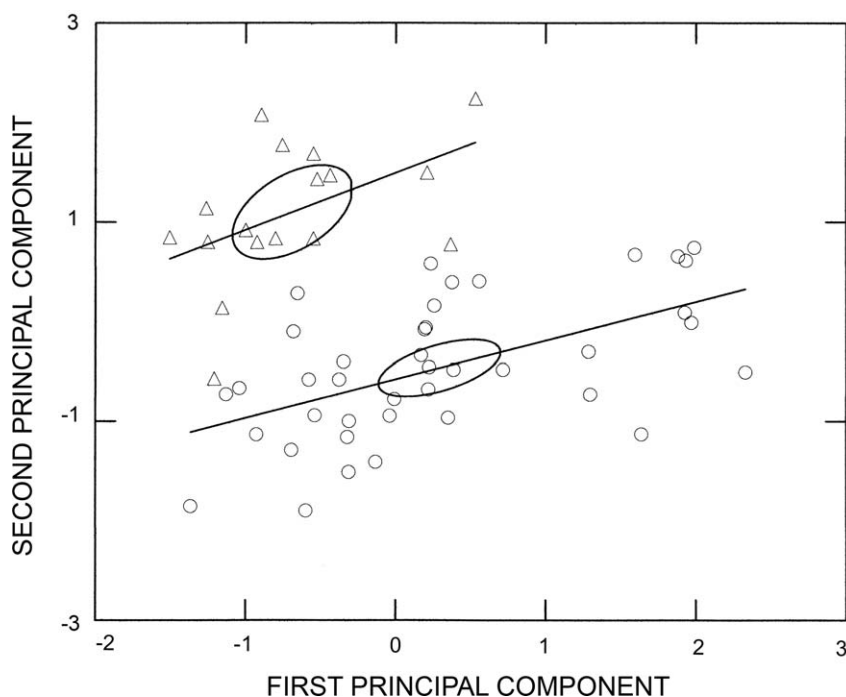
Fig. 92.   Specimen scores representing the sample of *Bunomys karokophilus* (empty triangles, $N = 17$) and the samples of *B. andrewsi* (empty circles, $N = 40$) from the west-central mountain block (Puro-Sungai Miu, Tamalanti, Tuare, the Mamasa area, and Gunung Balease) projected onto first and second principal components extracted from principal-components analysis of 16 cranial and two dental log-transformed variables. Ellipses outline 95% confidence limits for cluster centroids. Equations for the regression lines are: *B. karokophilus*, $Y = 0.573\times\ 1.493$ (F = 4.66, P = 0.048); *B. andrewsi*, $Y = 0.388\times\ -0.580$ (F = 16.91, P = 0.000). See table 70 for correlations (loadings) of variables with extracted components and for percent variance explained.

groups of scores for each species, a reflection of their similarity in magnitude of most cranial and dental variables (table 65).

Segregation of the scores into two clusters along the second component highlights shape differences (table 70). Compared with *B. andrewsi*, the gray rat has a relatively narrower interorbit ($r = -0.41$); wider rostrum, narrower zygomatic plate, longer diastema and postpalatal region, longer and wider bony palate, wider mesopterygoid fossa ($r = 0.39–0.75$); shorter incisive foramina ($r = -0.55$), and broader molars ($r = 0.47$).

Relevant proportional distinctions are recorded in a different form in a ratio diagram (fig. 93). Here, I combined all seven population samples from throughout the range of *B. andrewsi* (see table 2). Compared with this larger sample of *B. andrewsi*, the interorbit of *B. karokophilus* is significantly narrower relative to skull length (indexed by occipitonasal length); the rostrum is wider relative to its length and to length of skull; the zygomatic plate is narrower relative to skull size and most other cranial and dental variables; the bony palate is longer, and the mesopterygoid fossa is wider relative to skull length; the incisive foramina are markedly shorter than wide; and the molars are wider relative to both length of molar row and length of skull.

There are differences in occlusal cusp patterns of upper (maxillary) and lower (mandibular) molars (tables 10, 11). Compared with the sample of *B. andrewsi* from the central core of Sulawesi, cusp t3 occurs at a greater frequency on the second (33% in *B. karokophilus*, 17% in *B. andrewsi*) and third upper molars (22% as opposed to 4%). Cusp t1 on the third upper molar is typically absent

**Results of Principal-Components Analyses
Comparing the Sample of *Bunomys karokophilus*
with Those of *B. andrewsi* from the West-Central
Mountain Block**
Correlations (loadings) of log-transformed values
for 16 cranial and two dental variables are based on
17 *B. karokophilus* and 40 *B. andrewsi*; see figure 92.

Variable	Correlations	
	PC1	PC2
ONL	0.78***	0.46***
ZB	0.90***	0.18
IB	0.65***	−0.41**
LR	0.75***	0.23
BR	0.62***	0.49***
BBC	0.64***	−0.13
HBC	0.62***	−0.02
BZP	0.92***	−0.16
LD	0.74***	0.39**
PPL	0.69***	0.41**
LBP	0.12	0.75***
BBP	0.69***	0.22
BMF	0.14	0.66***
LIF	0.72***	−0.55***
BIF	0.63***	0.09
LB	0.49***	0.07
CLM1–3	0.60***	0.12
BM1	0.19	0.47***
Eigenvalue	0.037	0.012
% Variance	48.0	16.0

*** P ≤ 0.001; ** P ≤ 0.01.

or consists of a cingular ridge or distorted
pimples in *B. karokophilus*, but the third
molar of *B. andrewsi* exhibits a prominent
cusp t1, which is usual in all the other species
of *Bunomys* except *B. karokophilus*. Only
about half of the sample of *B. karokophilus*
(55%) has a posterior labial cusplet on the first
lower molar, but nearly all specimens of *B.
andrewsi* from the core of the island bear this
cusplet; 64% of the sample of *B. karokophilus*
has a posterolabial cusplet on the second
lower, but all specimens of *B. andrewsi* show
this cusplet. An anterolabial cusp occurs at a
frequency of 27% on both second and third
lower molars in *B. karokophilus*, the frequen-
cy for the second molar is 94% for *B. andrewsi*
and 18% for the third molar.

All qualitative and quantitative compari-
sons of phenetic traits attest to the distinctive
phenetic (and presumably genetic) separation
of *B. karokophilus* from *B. andrewsi*.
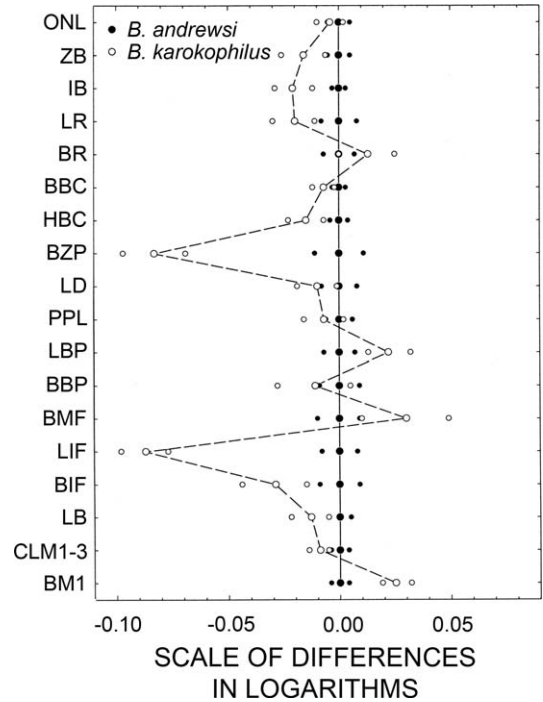
Fig. 93. Ratio diagram illustrating some pro-
portional relationships in cranial and dental
dimensions between the sample of *Bunomys
karokophilus* (N = 17) and all population samples
of *B. andrewsi* (the standard, N = 98). Data were
derived from values for mean, standard deviation,
and sample size of variables listed in table 42. How
these diagrams were constructed and how to read
them are explained in Material and Methods.

***Bunomys karokophilus* and *B. penitus*:** The
only sample of *B. karokophilus* comes from
collection localities along my transect line in
tropical lowland evergreen rainforest habitats
between 823 and 1150 m. The site at 1150 m
(locality 10 in the gazetteer and on the map in
fig. 50) is at the base of Gunung Kanino.
Upslope on that mountainous ridge at 1285 m
marks the lower boundary of lower montane
forest and the lowest spot on the transect line
where *B. penitus* was trapped (locality 1 in the
gazetteer and on the map in fig. 51). At
higher elevations on Gunung Kanino and all
the way to the summit of adjacent Gunung
Nokilalaki, *B. penitus* was common in lower
and upper montane forest habitats (see the
map in fig. 51). Most of my comparisons will
be between *B. karokophilus* and the samples
of *B. penitus* from Gunung Kanino and
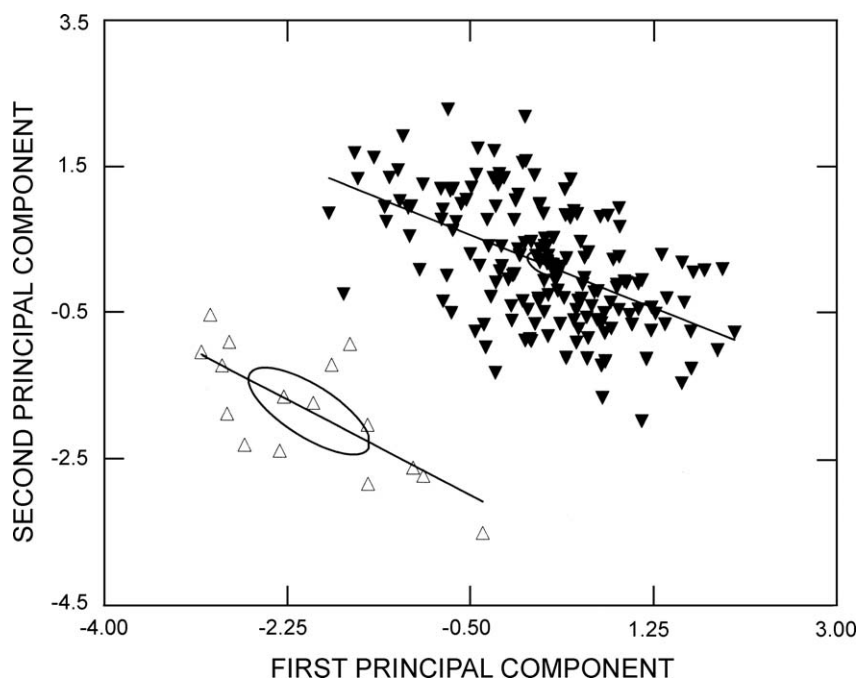
Fig. 94.   Specimen scores representing *Bunomys karokophilus* from Sungai Sadaunta and the Danau Lindu Valley (empty triangles; $N = 17$) and population samples of *B. penitus* (filled inverted triangles; $N = 174$) from the west-central mountain block (Gunung Kanino, Gunung Nokilalaki, Rano Rano, Gunung Lehio, Mamasa Area, and Pegunungan Latimojong) projected onto first and second principal components extracted from principal-components analysis of 16 cranial and two dental log-transformed variables. Ellipses outline 95% confidence limits for each group centroid. Equations for the regression lines are: *B. karokophilus*, $Y = -0.701\times -3.309$ (F = 16.04, P = 0.001); *B. penitus*, $Y = -0.564\times 0.279$ (F = 68.86, P = 0.000). See table 71 for correlations (loadings) of variables with extracted components and for percent variance explained.

Gunung Nokilalaki; one multivariate analysis and a ratio diagram are based on all population samples of *B. penitus* (identified in table 2).

Bunomys karokophilus is physically smaller than *B. penitus* (table 41). Mean values for lengths of head and body, hind foot, and ear are less in *B. karokophilus*, than in the samples of *B. penitus* from Gunung Kanino and Gunung Nokilalaki; body mass is not so different (133.2 g for *B. karokophilus*, 132.3 and 133.3 g for the two samples of *B. penitus*). Mean length of tail is similar in the two species; however, relative to length of head and body, *B. karokophilus* has a slightly longer tail (95%) than in either sample of *B. penitus* (93% and 88%). Relative size of ears also differs with *B. karokophilus* having slightly smaller ears in relation to body size

(LE/LHB = 13%) as contrasted with the larger ears of *B. penitus* (14% for two samples; table 41).

Bunomys penitus has brighter pelage than *B. karokophilus*. Its luxuriant dorsal coat is soft, long (up to 25 mm), densely silky to the touch, and dark brownish gray with buffy highlights; the soft, dense fur covering the underparts is whitish gray (*B. karokophilus* has a harsher and shorter dorsal coat—up to 15 mm long—that is dark grayish brown or dark blue gray finely speckled with buff; the ventral coat is dark grayish white or blue-gray lightly speckled with white). Ears are tan (dark gray to grayish black in *B. karokophilus*). Digits are white, dorsal surfaces of the carpal and metacarpal regions are typically white, speckled with gray in some specimens, front claws are short and appear delicate (grayish

Variable	Correlations	
	PC1	PC2
ONL	0.87***	0.10
ZB	0.69***	−0.30***
IB	0.52***	0.12
LR	0.82***	0.33***
BR	0.70***	−0.33***
BBC	0.52***	0.14
HBC	0.54***	0.21**
BZP	0.31***	−0.50***
LD	0.79***	−0.12
PPL	0.59***	−0.15*
LBP	0.46***	0.03
BBP	0.36***	−0.77***
BMF	0.59***	−0.03
LIF	0.77***	0.38***
BIF	0.63***	−0.21**
LB	0.58***	0.28***
CLM1–3	0.52***	0.53***
BM1	0.11	0.30***
Eigenvalue	0.019	0.008
% Variance	35.9	14.5

*** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$.

white to grayish brown in *B. karokophilus*, claws longer and more robust relative to body size). Glistening white below and around the tip, then tan on the proximal dorsal strip is the typical tail color pattern (tail white tipped in *B. karokophilus*, but the ventral surface ranges from glistening white through varying intensities of brown speckling and mottling to solid brown). Length of the white tip relative to length of tail averages shorter in *B. karokophilus* (mean = 18.2%, range = 2%–31%) than in *B. penitus* (mean = 21.0%, range = 3%–68%) as does actual length of the white tip (means = 28.7 mm for *B. karokophilus* and 35.6 mm for *B. penitus*).

External morphology of spermatozoa is similar in *B. karokophilus* and *B. penitus*. Each has a wide sperm head, short apical hook, and short sperm tail, but the apical hook of *B. karokophilus* is shorter than that of *B. penitus*, and the tail connects to near the middle of the head rather than at its base
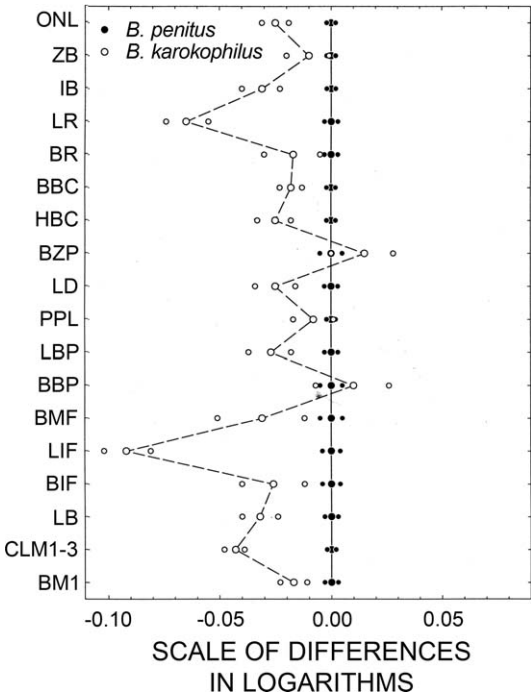
Fig. 95. Ratio diagram illustrating some proportional relationships in cranial and dental dimensions between the sample of *Bunomys karokophilus* ($N = 17$) and all population samples of *B. penitus* (the standard, $N = 185$). Data were derived from values for mean, standard deviation, and sample size of variables listed in table 42. How these diagrams were constructed and how to read them are explained in Material and Methods.

(Breed and Musser, 1991; *B. karokophilus* was reported as *Bunomys* sp. A).

Both species have a 2N of 42, but an FNa = 56 and FNt = 60 for *B. karokophilus* and FNa = 58 and FNt = 60–61 for *B. penitus* (table 12).

The smaller physical size of *B. karokophilus* compared to *B. penitus* is mirrored by the cranial and dimensions measured: except for breadths of zygomatic plate and bony palate, which are statistically the same in both species, univariate means for all the other variables average less in the sample of *B. karokophilus*, whether compared with all population samples of *B. penitus* (table 42) or only those from Gunung Kanino and Gunung Nokilalaki (table 73). Dimensional contrasts that are especially noteable are the

markedly shorter rostrum, incisive foramina, and molar row of *B. karokophilus* as compared with *B. penitus.*

The discriminating qualitative associations among the cranial and dental variables are summarized by the pattern of individual specimen scores projected onto first and second principal components (fig. 94). In this exercise, I expanded the sample of *B. penitus* to include all population samples from the west-central mountain block (Gunung Kanino, Gunung Nokilalaki, Rano Rano, Gunung Lehio, Mamasa Area, and Pegunungan Latimojong; see the univariate statistics in table 73). *Bunomys karokophilus* is represented by an elliptical group of scores in the lower-left quadrant of the ordination, *B. penitus* by a parallel elliptical cloud in the upper right. The regression lines of the second principal component on the first are phenetically distinct: their Y-intercepts are significantly different between species (-3.309 versus $+0.279$; F = 31.74, P = 0.000), but their slopes are equivalent (-0.701 versus -0.564; F = 0.18, P = 0.370). The spread and partial separation of clusters along the first component is influenced by positive and moderate to high loadings for all cranial and dental variables except breadth of first upper molar (r = 0.31–0.87; table 71) and reflects the generally greater cranial and dental dimensions of *B. penitus*, especially occipitonasal length, length and breadth of rostrum, length and breadth of incisive foramina, breadth of mesopterygoid fossa, and length of molar row.

Proportional (shape) dissimilarities are summarized in a ratio diagram (fig. 95). *Bunomys karokophilus* has an absolutely shorter and narrower rostrum than *B. penitus*, but the rostrum is significantly shorter relative to skull size (indicated by occipitonasal length and zygomatic breadth) and wider relative to rostral length, a proportion that signals the relatively chunky rostrum characteristic of *B. karokophilus* that is unlike the relatively long and narrow rostrum of *B. penitus*. Absolute average measurements are equivalent for breadth of the zygomatic plate in the two species, but the plate is much wider relative to size of skull in *B. karokophilus* compared with *B.*

penitus. The bony palate of *B. karokophilus* is wider relative to its length, the incisive foramina are relatively shorter but wider across the openings relative to their lengths, the bulla are slightly smaller in relation to skull length, and the molars are wider relative to length of the maxillary molar row.

These size and shape distinctions between *B. karokophilus* and *B. penitus* as summarized by univariate statistics for the cranial and dental variables, graphic ordinations derived from multivariate analyses, and the ratio diagram can also be detected in the illustrations where skulls of the two species are contrasted (figs. 99–101).

In addition to the difference between the two species in size of molars, the frequency of certain cusps and cusplets is variable (tables 10, 11). Cusp t3 is found on the second upper (maxillary) molar in over half the sample of *B. penitus* (62%) as opposed to a third of the sample of *B. karokophilus* (33%), but occurs infrequently on the third molar in *B. penitus* (5%) compared to *B. karokophilus* (22%). Cusp t1 on the third upper molar is typically absent or consists of a cingular ridge or pimplelike shapes in *B. karokophilus* (fig. 87), but the third molar of *B. penitus*, like all the other species of *Bunomys* excepting *B. karokophilus*, exhibits a prominent cusp t1 (figs. 74, 75). On the lower molars, a posterior labial cusplet is present on the first molar in about half of the sample of *B. karokophilus* (55%) but occurs on all specimens of *B. penitus* examined; this cusplet is present on the second lower molar in 64% of the sample of *B. karokophilus* but is more frequent in *B. penitus* (97% of the sample). About half of the sample of *B. penitus* has an anterolabial cusp on the second molar, but no specimen exhibits this cusp on the third molar; 27% of the sample of *B. karokophilus* has the cusp on both second and third molars.

GEOGRAPHIC AND ELEVATIONAL VARIATION: Because all the specimens of *B. karokophilus* come from a few localities in the northern portion of the west-central mountain block, there is nothing serious to report concerning geographic variation in external, cranial, and dental traits. The specimens comprise a single population sample; any analysis of geographic variation will have to wait until samples from else-

TABLE 72
Summary of Microhabitats at Trapping Sites, Stomach Contents, and Other Relevant Information for Specimens of *Bunomys karokophilus* Collected on My Transect in Sulawesi's West-Central Region, 1973–1976
Descriptions of the trapping sites and contents of stomachs are summarized from my field journals (in Mammalogy Archives at AMNH). All collection localities are in old-growth tropical lowland evergreen rain forest (see the habitats depicted in figures 96–98). All the rats were caught during the night in Conibear traps unless indicated otherwise. In the description of stomach contents, "*karoko*" is the local name for the purple "ear" fungus, *Auricularia delicata*.

Locality, AMNH and (ASE-field) numbers	Elevation (m)	Date	Trap site and other information
Sungai Sadaunta			
225027 (2051)	823	Sept. 1974	In a damp runway beneath crisscross of large rotting tree limbs on a narrow rocky terrace above Sungai Sadaunta. The limbs are scattered about from an old giant that lies decaying on the hillside above the stream terrace. Moss-covered rocks and limbs on the terrace are covered by leafy vines, shrubs, and ferns; the streamside environment is wet and cool. **Stomach:** packed with cut pieces of *karoko* only.
225028 (2073)	823	Sept. 1974	On wet, mossy trunk extending from one terrace of Sungai Sadaunta to the opposite terrace and resting just above water level on rocks in the stream; trunk would be inundated in high water. The tree squirrel *Rubrisciurus rubriventer* was taken on same spot during the day and the rat *Maxomys hellwaldii* on a different night. **Stomach:** stuffed with finely chopped *karoko*; in middle of the mass is a hard piece of dark brown wood (15 mm long, 10 mm wide) that probably was detached along with the fungus from the rotting trunk or limb.
225034 (2090)	854	Oct. 1974	On top of moss-covered decaying trunk lying at 30° angle across a small creek at the bottom of a steep, wet, and mossy ravine tributary to Sungai Sadaunta. Slopes above ravine covered with tall hillside forest. **Stomach:** full of *karoko*.
225035 (2100)	884	Oct. 1974	On wet, smooth, rotting trunk of a *wanga* palm (*Pigafetta filaris*) bridging the Sungai Sadaunta and resting on rocks on the stream (would be inundated after rains). The rocky, wet, and mossy stream banks are shaded by understory figs, tall shrubs, endemic banana trees (*Musa* sp.), and tall *wanga* palms. **Stomach:** full of *karoko*; also scanty remains of a large insect (a few abdominal sclerites and parts of a wing).
225029 (2116)	823	Oct. 1974	On damp ground beneath base of large, decaying tree lying on terrace above Sungai Sadaunta. Now rotten and covered with moss, shrubs, ferns, and vines, the trunk provides protected cover and pathways beneath the area where it splintered from the adjacent stump; stump and trunk are surrounded by dense and tall shrubs, tall gingers, and rattan. The rat *Paruromys dominator* was caught on same spot on a different night. Other *P. dominator*, *Bunomys chrysocomus*, *Rattus facetus*, and *Maxomys hellwaldii* were trapped on the forested hillside above the stump. **Stomach:** some *karoko*, small fig seeds and bits of rind; few chitinous segments of adult beetle abdomen and a leg.
225039 (2135)	869	Oct. 1974	On half-shredded, rotting, and slick wanga palm trunk lying across Sungai Sadaunta, extending from a low terrace (muddy, rocky, and eroded) on one side of stream across to the opposite rocky bank. *Bunomys chrysocomus* and the tree squirrels *Prosciurillus topapuensis* and *P. murinus* were caught in same spot during different days and nights. A few feet upstream a rat, *Paruromys dominator*, was trapped on a different trunk bridging the stream. **Stomach:** full of chopped *karoko*; thin flakes of the woody holdfasts are mixed with the *karoko*.

TABLE 72
(*Continued*)

Locality, AMNH and (ASE-field) numbers	Elevation (m)	Date	Trap site and other information
224933 (2250)	823	Oct. 1974	ASE 2250, a *Taeromys celebensis*, and *Rattus hoffmanni* were trapped within 10 ft of each other on trunks or limbs from an old and rotting treefall lying across Sungai Sadaunta. ASE 2250 was taken on a trunk (6–8 in. diameter) 2 ft above stream; *T. celebensis* was trapped on an adjacent branch (4–5 in. diameter) next to a trunk (12 in. diameter) on which the *R. hoffmanni* was caught; branch and trunk about 4 ft above stream surface. All three elements are wet, slightly mossy, and free of other vegetation. Terraces on either side of the stream are rocky (the rocks covered with moss), muddy, and covered with chunks and tangles of rotting tree trunks and limbs, wanga palm trunks and fronds, all nearly concealed by thick shrubbery, ferns, and vines winding through the shrubs. Gingers are common and several banana trees were emerging above the shrubs. The higher terraces above the stream support understory figs, and tall emergent trees that canopy the stream. The limbs, branches and trunks that bridge the stream also rest on the bordering terraces, providing runways across the higher terraces above the stream. **Stomach:** partly full of chopped *karoko*.
225031 (2260)	823	Oct. 1974	On moss-covered, rotting limb lying over rocky terrace next to stream and extending across the water to opposite terrace. A rat, *Rattus hoffmanni*, was taken on same spot on a different night. The limb is 20 ft upstream from the treefall on which ASE 2250 was caught during the previous evening. **Stomach:** packed with pieces of *karoko*.
225040 (2272)	915	Oct. 1974	On thick, decaying limb bridging tributary of main stream. Limb is free of vegetation and moss, extends from one high eroded bank across the stream 2 ft above water level to a lower opposite bank; stream flows through deep ravine in hillside forest. **Stomach:** full of cut pieces of *karoko*.
225036 (2302)	793	Nov.1974	On wet, moss-covered decaying limb lying across main headwater tributary of Sungai Sadaunta. The canyon is V-shaped, covered with short forest typical of steep slopes near ridgetops. Understory figs are common along stream and form canopy over the water; other components of the streamside forest are scattered fishtail palms (*Caryota mitis*) and sugar palms (*Arenga pinnata*), with wanga palms (*Pigafetta filaris*) higher on the banks; shrubs, ferns, and rattan provide a dense understory; woody and monocot vines thread through the trees and palms. **Stomach:** nearly full with *karoko*.
225037 (2307)	991	Nov. 1974	On rotting, wet and smooth trunk bridging banks of tributary stream (suspended about a foot above the water surface) and downstream from where ASE 2302 was caught the previous night. **Stomach:** distended with freshly consumed *karoko*; mouth was also full of large chunks of the fungus; looks like rat had just finished eating, then ran across trunk lying across the stream.
225038 (2322)	1006	Nov. 1974	On wet, moss-covered tree root growing across tributary creek in steep ravine; caught rats (*Taeromys celebensis*, *Rattus facetus*, and *Paruromys dominator*) and *Prosciurillus murinus* just downstream on rotten trunk lying across stream. **Stomach:** half full, chunks of karoko.
224772 (2353)	976	Nov. 1974	A juvenile caught in live trap set on wet ground beneath canopy of wanga palms on narrow terrace 4 ft above stream; little ground cover, mostly scattered ferns and shrubs. Kept captive: offered a variety of foods but accepted and consumed only pieces of *karoko* (see text).

TABLE 72
(*Continued*)

Locality, AMNH and (ASE-field) numbers	Elevation (m)	Date	Trap site and other information
225041 (2374)	999	Nov. 1974	Adult caught in live trap set on rotting, moss-covered wet trunk (5 in. diameter) lying across headwater tributary of Sungai Sadaunta, suspended about 2 ft above water surface; ravine slopes rocky and muddy, steep hillside forest above ravine. A rat, *Paruromys dominator*, was caught in same spot about a week before; kept captive. Kept captive: accepted mostly *karoko*, and a few invertebrates (see text).
225032 (2387)	823	Nov. 1974	On rotting, clean trunk (1.5 ft diameter) extending from one terrace across the Sungai Sadaunta to the other terrace. *Karoko* usually found growing on sides of the wet trunk. About two weeks before, caught a tree squirrel, *Prosciurillus murinus* in same trap. On the wet terrace beneath the trunk caught several *Bunomys chrysocomus* and a *Rattus hoffmanni*; on limbs bridging the stream about 10 ft upstream caught a *Maxomys hellwaldii* and a *M. musschenbroekii*; and about 30 ft downstream caught two *Bunomys karokophilus*, a *Maxomys musschenbroekii*, *Rattus hoffmanni*, *Crunomys celebensis*, *Taeromys celebensis*, and the shrew *Crocidura elongata* on decaying limbs lying across the stream. Streamside terraces are rocky, mossy, wet, and densely covered with shrubs, ferns, vines, scattered banana trees, rotting, moss-covered debris from old treefalls, and palm fronds; terraces and stream shaded by understory fig trees wanga palms (*Pigafetta filaris*) with tall forest in background. **Stomach:** packed with *karoko*.
225033 (2398)	823	Dec. 1974	On same rotting trunk where ASE 2260 was caught. **Stomach:** distended with chunks of *karoko*, looks freshly consumed.
226833 (4340)	976	Mar. 1976	On large decaying trunk (2 ft diameter, 20 ft long) covered with wet moss and small plants lying across a ravine containing a tributary of the Sungai Sadaunta, and suspended about 4 ft above the water surface. Ravine sides are steep and muddy; tall wanga palms dominant in a short streamside forest; ground washed, cover sparse. **Stomach:** full of *karoko* plus one partly digested segment of an earthworm; also a few pure white fibrous pieces in which are trapped small fly larvae.
Tomado			
223045 (118)	1000	July. 1973	On ground near stream in primary forest. **Stomach:** partly full of chopped *karoko*; also a little bait.
223046 (139)	1000	July. 1973	Along wet, decaying tree trunk in understory of forest. **Stomach:** partly full of chopped *karoko*; one adult ant.
223056 (325)	1000	Aug. 1973	On ground deep in primary forest besides stream. **Stomach:** empty except for a few remnants of karoko and hairs ingested during grooming.
223058 (330)	1000	Aug. 1973	In dense undergrowth near small stream. **Stomach:** partly full of *karoko*; many oblong, flat, hard orange seeds (surrounded by translucent tissue); chewed remains of a large orthopteran (mostly semidigested tissue, parts of legs, and corregated wings).
223060 (342)	1000	Aug. 1973	In forest near small stream beneath shrubs. **Stomach:** full of *karoko*; also a few small flat, elliptical, flat orange seeds from some kind of fruit.
223072 (401)	1000	Aug. 1973	Beneath rotting, wet trunk lying on ground in tall forest partly and newly cleared of understory (preparatory to planting coffee trees). **Stomach**: partly full of *karoko*; large, long-stemmed fig seeds; remains of small spider (pedipalp, leg segments, bits of chitin).
226931 (469)	1000	Aug. 1973	On branch (8 in. diameter) that is part of a pile of branches, larger limbs, and trunk of a decaying treefall lying in understory of deep primary forest. **Stomach:** empty except for a bit of *karoko* remnants.

TABLE 72
(Continued)

Locality, AMNH and (ASE-field) numbers	Elevation (m)	Date	Trap site and other information
224153 (1606)	1000	May 1974	On trunk lying across small stream; mature undisturbed forest on one side of stream, coffee grove on the other side (mostly coffee trees shaded by emergent species of strangler figs). **Stomach:** mostly full of *karoko*, remains of fig (tiny black seeds adhering to everything in stomach); chewed remains of a centipede (antennae, legs, masticated body).
Sungai Tokararu			
223305 (623)	1150	Sept. 1973	On ground beneath rotting large trunk in primary forest. **Stomach:** full of bait only.
223316 (731)	1150	Oct. 1973	On top of large trunk lying on ground in dense understory of primary forest; ASE 1150 was caught beneath the same trunk on a different night. **Stomach:** partly full, mostly figlike skin and flesh (but no seeds from fig); a few bits of well-digested *karoko*; one intact ant and pieces of another; short posterior segment of a small earthworm.

where in the mountain block are obtained. Within the population sample I employed here the primary expression of variation in the variables measured is a reflection of the range in age from young adults to old adults.

All examples of *B. karokophilus* come from lowland tropical evergreen rain forest along the Sungai Sadaunta (823–1006 m) in the drainage of the larger Sungai Miu, and the vicinity of Tomado (1000 m) and Sungai Tokararu (1150 m), within the watershed of Danau Lindu. These voucher specimens document the known elevational range of *B. karokophilus* (table 5).

NATURAL HISTORY: This section contains the information I recorded in the field covering habitat, diet, and behavior.

Habitat: *Bunomys karokophilus* inhabits streamside forests (table 72; see description of streamside habitat under Natural History in the account of *B. chrysocomus*). Most specimens were trapped on wet and decaying tree trunks and limbs, as well as rotting palm trunks, spanning streams, narrow tributary creeks, and wet ravines in dense primary forest—the habitat images captured in figures 96 and 97 are typical. Several rats were encountered on forested terraces above streams where traps were placed beneath wet, decaying trunks and limbs from old treefalls lying on the ground and partially concealed by dense vegetation (fig. 98). Air is cool and the ground wet in these shaded environments, wet and moss-covered rocks and remains of treefalls are nestled among gingers, palm rosettes, ground and tree ferns along with a variety of tall shrubs. We never caught *B. karokophilus* in traps placed on forested ridgetops or hillsides away from stream and wet ravine terraces. Along Sungai Sadaunta, at Tomado, and Sungai Tokararu, the three areas we encountered *B. karokophilus*, mean ambient air temperatures ranged from 61.1° to 80.9° F with relative humidity reaching 100% (table 3).

All but two rats were caught in primary forest that was to my eyes undisturbed by human activities. One of those two exceptions was trapped on a decaying tree trunk lying across a small stream covered by intact forest on one bank but a coffee grove on the other. Species of large canopy and emergent trees shade the coffee trees and in their structure the groves are not unlike undisturbed forest with the coffee forming the understory beneath a tall canopy. Another animal was trapped just back from a stream flowing through forest being cleared prior to the planting of coffee trees. These groves were surrounded by tall forest. Our trapping efforts focused on undisturbed or only slightly modified forest habitats and we did not go out of our way to survey cut-over areas or secondary growth. Whether *B. karokophilus* can survive in such places is unknown. Certainly their presence would be

influenced by secondary forest tall and dense enough to provide shade and the right ambient conditions for *Auricularia delicata* (*karoko*), their primary food, to flourish.

Our trapping records indicate that *B. karokophilus* is terrestrial. We never caught it in trees or on woody vines hanging low to the ground. The few captures above ground level were on decaying tree trunks lying on the forest floor where the rats could scamper along the ground and onto the trunk (the microhabitat configuration shown in fig. 98 is an example).

Diet: *Bunomys karokophilus* is mycophagus, concentrating on one kind of ear fungus; invertebrates, vertebrates, and fruit form a minor if not insignificant part of its diet. The dietary information discussed here and summarized in tables 13 and 72 is derived from the contents of stomachs removed from preserved specimens and the range of foods I offered two captives, an adult and a juvenile.

Fungi—*Auricularia delicata* is an ''ear fungus'' (Division Basidiomycota, Class Agaricomycetes, Order Auriculariales, Family Auriculariaceae; species of *Auricularia* are also informally referred to as ''jelly fungi'' along with species in the orders Dacrymycetales and Tremellales). The fruiting bodies range in size from small rubbery and oblong capsules (10 mm long, 5 mm wide) to broad and thick ear-shaped lobes (up to 50 mm wide), rubbery to the touch. The top surface is smooth and purplish or purplish brown, the undersurface white and irregularly ribbed and veined. The inside is gelatinous. Individual small and broad lobes may occur on the same wet and decaying tree trunk or limb, but usually several lobes form a cluster originating from a single point of attachment. The North American *Auricularia auricula*, known commonly as ''tree-ear'' or ''wood-ear'' (see plate 617 in Lincoff, 1997) is very similar in morphological form to the Sulawesi *A. delicata*. In central Sulawesi, ''*karoko*'' of the Kulawi language, refers both to human ears and *A. delicata* (see etymology for *Bunomys karokophilus*).

The foods accepted by two captive *B. karokophilus* and contents of stomachs (table 72) indicate that *karoko* (*Auricularia delicata*) is the primary dietary component, at least during the seven months (March, August to January) in which my sample of *B. karokophilus* was collected. Except for one stomach containing only bait, all the other stomachs held some remains—from traces to masses—of *karoko*. *Karoko* grows only on wet and decaying tree trunks and limbs lying on the ground, usually on woody substrates free of other kinds of ear fungi, are not extensively covered in moss, and have not started to decay to the degree where soil has formed along the sides where the wood touches the wet ground supporting nurseries of small plants. Apparently the fungus requires a clear but irregular and cracked, wet, and decaying surface. *Karoko* also grows on trunks and limbs spanning streams, so the rats not only use these as bridges but also feed along them when there is a suitable fungal crop. *Karoko* is absent from wet and decomposing wanga palm trunks (*Pigafetta filaris*, the common tall palm growing on stream and river terraces), which are invariably smooth, from decaying rattan vines, and from rotting pieces of limbs and trunks that lay close to the stream surface and are inundated by periodic flooding. My two helpers and I found *karoko* to be more common after rains and located on woody substrates in protected wet pockets on streamsides, stream terraces, and hillsides that remain wet and cool between rains.

During our daily forays in the forest, we always looked for *karoko* to gain an impression of its abundance. One day we walked about 3 km along the Sungai Sadaunta from camp at 913 m up to about 1100 m looking for *karoko* on decaying and wet wood bridging the stream and resting on banks and edges of terraces above the stream. We attempted to examine all rotting and saturated wood in those areas, but did not climb away from the stream onto the hillsides; previous to our search, there had been two full days and one night without rain. The fungus was scarce. We collected enough to fill stomachs of about three adult *B. karokophilus*. Much of it was in the form of young capsules that usually appear along one side of a decaying trunk. Presumably after a rain these would have grown into clusters of larger lobes. While the fungus at times may increase in abundance after periods of heavy rains, along the stream banks and terraces it

Fig. 96. Dense streamside forest bordering a narrow section of Sungai Sadaunta, 823 m (in 1974). Rotting tree trunks and limbs from an old treefall criss-cross the channel. Shaded most of the day, the stream terraces remain wet and the air cool. During separate nights, a *Bunomys karokophilus* and *Maxomys hellwaldii* were trapped on top of the trunk in the foreground; the squirrel *Rubrisciurus rubriventer* was caught in the same spot during the day. The wet and mossy trunks provide substrate for *karoko* fungus (*Auricularia delicata*), the primary food of *Bunomys karokophilus*. This microhabitat—wet and cool, with dense cover, and source of *karoko*—seems to be optimal for *B. karokophilus*. Fifteen other murid species were trapped in the nearby forest between 800 and 900 m, with *Maxomys hellwaldii*, *Rattus hoffmanni*, *Rattus facetus*, *Paruromys dominator*, and *Bunomys chrysocomus* being the most commonly encountered (fig. 103). See description of streamside habitat in Natural History section for *B. chrysocomus*.

Fig. 97. Tropical lowland evergreen rainforest at 1150 m along the Sungai Tokararu (in 1973), which flows into Danau Lindu. The dense streamside forest shown here is a good example of similar floristic landscapes along the Sungai Sadaunta and other streams in tropical lowland evergreen rain forest that are the haunts of *Bunomys karokophilus* as well as *B. chrysocomus*. The 1150 meter site was the highest at which we encountered *B. karokophilus*, but *B. chrysocomus* ranges up into nearby lower montane forest.

Fig. 98. Decaying trunk, the remnant of an old treefall, lying in dense understory on forested flat above Sungai Tokararu at 1150 m (in 1973). We trapped one *Bunomys karokophilus* on the ground beneath the trunk; *B. chrysocomus* was also captured there on other nights. About two weeks later, We took another *B. karokophilus* in a trap set on top of the trunk; *Paruromys dominator*, *Rattus hoffmanni* and *Rattus facetus* were also caught on top of the trunk during that interval; those three, along with *Bunomys chrysocomus* are common elements of the murid community at 1150 m as contrasted with the infrequently encountered *Bunomys karokophilus* (fig. 103).

was not common during the period of our survey, and I gained the impression that *karoko* is never plentiful because when checking traplines we always looked for fungal clusters and only infrequently saw them. A crop in one place may last several nights but then disappears after sporulation (some sections of trunks and limbs where we found *karoko* just after it sporulated remained bare of fungi for several weeks), so the availability is erratic and the source shifting. It seems that during the night rats would have to hunt constantly and perhaps over long sections of streams and ravines. This may explain in part their low population density compared with other species of murids in the same areas. For example between 800–1100 m along the transect, the elevational extent in which we encountered the 27 representatives of *B. karokophilus*, we trapped 184 examples of *Bunomys chrysocomus* in the same streamside habitats, and on stream terraces and the base of hillsides we obtained 118 *Rattus hoffmanni*, 91 *Rattus facetus*, and 84 *Paruromys dominator*. We used one kind of bait for all our traps and it seemed to attract *B. karokophilus* because bait was found in the stomach of one rat and unhesitatingly consumed by a captive adult.

During subsequent surveys, we discovered *karoko* growing on wet and shaded tree trunks lying on steep hillsides 75–100 ft above stream banks and terraces, but it was uncommon compared to the density near the streams and creeks. We set traps on the hillsides near the *karoko* sites but did not capture *B. karokophilus.*

Our experience with *karoko* was primarily in habitats within tropical lowland evergreen rain forest. My helpers and I looked for it in montane forest where we found the fungus only at one spot along the transect, growing on a wet and decomposing tree trunk spanning a narrow stream (Sungai Salubeka) at 1418 m on Gunung Kanino. A small cluster was growing next to a large white *karoko* (*Auricularia fuscosuccinea*), which although possessing a similar rubbery texture and gelatinous insides, takes the form of a bracken fungus; clumps of this white *karoko* were scattered along the trunk. The narrow valley of the stream is always wetter than the adjacent upper slopes and ridgetops and the

forest mossier. During the short periods without rain (usually less than a week in my experience), the streamside environment remained wet while the higher slopes dried out. During the usual bouts of rainfall, every day or every other day during our camp on the ridge forming Gunung Kanino, the slopes remain wet and muddy and the forest constantly drips. *Bunomys karokophilus* does not live in this montane forest, but its relative, *B. penitus*, does and is also a consumer of fungus.

I watched the captive adult eat *karoko*. With its incisors the rat grasped the fungus and then transferred it to the front feet. Small capsules were held near the mouth and each piece was completely consumed. Large lobes were rested against the floor of the cage. The rat chewed around the edge of each rubbery lobe, then ate the folded whitish underside along with some of the inner gelatinous layer. Some of the larger lobes were first stripped on the underside where the skin is softer. The tougher upper skin was either discarded or folded between the front feet and then consumed in small bites. The rat ate only the firm, rubbery lobes and ignored those lobes beginning to transform into a jellylike mass (the transformation when the fungus sporulates). In most of the stomach contents I examined, the *karoko* consisted of the gelatinous insides, the cut and chewed sections of the white undersurface, and chunks of amber or purplish pieces from the lobe's margin. The same adult rat was offered two kinds of reddish bracken fungi, a brown ear fungus with a thick rubbery rind and thin gelatinous inner layer (not a *karoko*), and a white bracken fungus—all were rejected.

The captive juvenile consumed only *karoko*, ignoring all other categories of food offered.

Karoko's strong appeal to *Bunomys karokophilus* is emphasized by a rat caught in a Conibear trap that had been set on a wet and decaying section of tree trunk bridging the Sungai Sadaunta. Its mouth was crammed with large chunks of the fungus, and the stomach was distended with freshly consumed *karoko*. Apparently the rat had just finished gorging on *karoko* to the degree that it could not swallow any more pieces.

Contents of the stomach from another rat caught along the Sungai Sadaunta provide a typical example of the amount of *karoko* in relation to fruit and invertebrates seen in those few stomachs that held remains of fungus along with other items. The stomach was full of *karoko* and also contained remains of fig (rind with small black seeds adhering to inner surface of the rind) and a chewed centipede (antennae, legs, and masticated body). Only eight of the 26 stomach samples I examined held remains of *karoko* and bits of fruit and/or invertebrates; one stomach contained bait only, and remains of *karoko* was the sole constituent in 17 others.

Earthworms—Judged from stomach contents and food preferences of the adult captive, earthworms are recognized as food but are an uncommon constituent of the diet. I offered a small earthworm (2 inches long) to the adult rat. With his incisors, he grabbed the worm from my fingers, transferred it to the front feet and consumed the entire worm in less than 30 seconds. On subsequent days I offered several earthworms of about the same size, but all were rejected. One day I placed a larger worm (4–5 inches long) in the cage, which the rat chased, now and again pulling it along the cage floor; finally the rat bit the worm in several places, grasped it with his front feet, and proceeded to devour the worm, taking 2–3 minutes to do so. Biting and pulling the worm through his front feet seemed awkward and slow compared to the actions characteristic of *B. chrysocomus*, an aggressive and voracious invertebrate predator that can consume an earthworm 4–5 inches long in 10–20 seconds. I found a short, mascerated segment of an earthworm in one stomach (AMNH 226833) that otherwise contained mostly remains of *karoko* (see table 72), and a short piece from the posterior end of a worm in the stomach of another rat that also held some *karoko*, an intact ant and fragments of another, and pieces of a figlike fruit (AMNH 223316).

Snails—No stomach contained remains of snails. I offered small live snails to the captive adult. He ignored all of them. Finally I cracked open a shell and gave the extracted snail to the rat who ate only the soft portions, leaving on the cage floor the muscular foot and tougher tissue adhering to the foot. *Bunomys chrysocomus*, occurring in the same habitat and a voracious consumer of snails, not only bites open the shell but consumes the entire snail body.

Insects and other arthropods—Evidence from contens of stomachs suggests that insects and other arthropods are a minor part of *B. karokophilus*'s diet (table 72). Of the 26 stomachs examined, only four held arthropod remains: one stomach contained an ant; another a few insect sclerites and parts of a wing; the antennae, legs, and partly digested body of a centipede was in a different stomach; and another contained bits of wing, legs, and tissue from a large orthopteran. The captive adult ate an adult cicadid offered. It ignored beetle larvae placed in the cage.

Vertebrates—I did not find remains of vertebrates in stomachs. I offered a small frog (1 inch long) to the adult rat, which he grabbed with his incisors and with his front feet manipulated the frog until its head was near the rat's mouth. He began chewing on the head and consumed about half the frog, discarding the rest (part of the body and legs). The rat seemed to recognize the frog as food but handled it awkwardly and ate slowly, chewing on the frog rather than cutting it into pieces.

Fruit—Fruit, like invertebrates, is apparently not a staple in the diet of *B. karokophilus*. Of the 26 stomachs, one contained the remains of fig, two others held gelatinous-covered seeds from an unidentified fruit, and remains of a figlike fruit was found in another (table 72). I offered the captive adult the large fruits (1–2 inches long) from two species of understory streamside figs (*Ficus* sp.), and fruit from the wanga palm (*Pigafetta filaris*); all were ignored. However, the small, quarter-inch, wedge-shaped fig from *Ficus minahassae* was eaten. This is a common understory tree forming a partial understory canopy along some sections of stream banks and wet ravines. The figs are bright red and soft when ripe; the thick rind encloses a syrupy fluid filled with tiny pale orange seeds. The rat bit chunks of the rind off and discarded them, ingesting only the seeds and thick liquid in which they were suspended.

Nests and behavior: In addition to offering the captive adult different foods, I recorded the following observations. I kept the rat in a moderately large cage in which I placed dry leaves. For the first few days he would walk over the top of the leaf pile and eventually curl his body on top to sleep. Then one night he pushed the leaves into a pile at one end of the cage and burrowed into it forming a deep depression where he slept during the day. The nest was a mound of leaves 8 inches high and 10 inches wide in which there was an opening in the center and only a pink nose visible deep within. For the next few days the rat curled up in its nest with the head under the body in a vertical position rather than curled on the side so the head was lost to view and the rat became nothing more than a blue-gray furry ball nestled deeply in the leaf pile.

The adult rat, like those I observed representing other species of *Bunomys*, groomed itself by first licking the palms repeatedly, often holding the wrist of one hand with the other to steady it while it wets the palm; then he rubbed around the nose and muzzle, licked the palms again, then reached back behind the ears and with both arms brushed forward over the ears down the sides and top of the head, over the eyes to the nose, with the fore-and upper arms acting as brushes and the palms on top sweeping over the head. Then he licked sides of the body near the thighs, the back and rump, and finally licked the inguinal area and genitals. I never saw him clean his tail.

During their captivity I never heard the adult or juvenile vocalize.

ECTOPARASITES: Records include only two species of fleas (table 14). *Sigmactenus alticola pilosus* (Leptopsyllidae) is also recorded from 14 other species of endemic Sulawesi murine rodents (*Bunomys penitus*, *B. prolatus*, and *B. chrysocomus*; *Margaretamys elegans*; *Maxomys hellwaldii*, *M. wattsi*, and *Maxomys* sp.; *Melasmothrix naso* and *Tateomys rhinogradoides*; *Paruromys dominator*; *Taeromys celebensis* and *Taeromys* sp.; *Rattus hoffmanni* and *R. facetus* [recorded as *R. marmosurus*]) and one nonnative rat, *Rattus exulans* (Durden and Beaucournu, 2000).

In addition to *Bunomys karokophilus*, five endemic Sulawesi murids (*Rattus hoffmanni*; *Bunomys penitus* and *Bunomys chrysocomus*;

Maxomys sp.; *Paruromys dominator*) and two nonnative rats (*Rattus exulans* and *R. nitidus*) are also hosts for *Stivalius franciscae* (Stivaliidae; Beaucournu and Durden, 2001).

SYNONYMS: None.

SUBFOSSILS: None.

With the discussion of *Bunomys karokophilus*, exposition of the eight species of *Bunomys* is complete. The four species of *Bunomys* we sampled within the murine community along the transect in the northern portion of the west-central mountain block, the single species in the lowlands of northeast-central Sulawesi, and all eight species as elements of the total murine fauna endemic to the island are the subject of the following two accounts.

BUNOMYS AND TWO MURINE COMMUNITIES IN CENTRAL SULAWESI

This section places *Bunomys andrewsi*, *B. karokophilus*, *B. penitus*, and *B. chrysocomus* in particular faunal contexts. I use results gained from surveys in two regions. One is along the transect in the northern part of the west-central mountain block in the forested landscape stretching between the lowlands in the lower drainage of the Sungai Miu and the mountains northeast of Danau Lindu (see the map in fig. 4), the other in coastal lowlands of the northeast-central region at Kuala Navusu (see the map in fig. 5). In both areas Aminudi, Usma, and I set the traps ourselves on the ground, in the understory, and on remains of treefalls spanning streams and ravines; recorded where each rat was caught, noting, among other observations, when examples of different species were taken in the same trap set during different nights; collected ectoparasites; noted reproductive characteristics; kept rats alive to watch their behavior, particularly the differences between arboreal and terrestrial species; identified contents of stomachs from preserved animals, and offered a range of forest foods to captives and recorded what was either accepted or rejected to enhance our understanding of diets; and learned firsthand something of the diverse floristic components comprising the habitats in which the rats were encountered. Information from the

present report, published documents, and my field journals are summarized to form a general picture of the murine communities along my transect in the west-central mountain block, and east of there in the lowlands at Kuala Navusu.

Each of the other four species of *Bunomys*—*B. fratrorum*, *B. prolatus*, *B. torajae*, and *B. coelestis*—is also part of a murine community. I have not worked in the places where samples of those taxa were collected and, other than study of museum specimens, lack personal exposure in the field to their habitats and ecologies. An estimate of the species with which each is regionally sympatric can be determined from the information listed in table 81.

My Transect in the West-Central Mountain Block

Here I focus on that section of my survey between the lowlands at Sungai Oha Kecil (in the lower portion of the Sungai Miu drainage) and the summit of Gunung Nokilalaki (the highest ridge just northeast of Danau Lindu), from about 200 m to more than 2200 m, traversing habitats in tropical lowland evergreen and montane rain forests in the northern portion of the west-central mountain block. I first summarize the morphological and other distinctions among the four species of *Bunomys* collected along the transect line and then discuss those species as part of the total assemblage of the 27 species of murines encountered during the survey.

CONTRASTS AMONG FOUR SPECIES OF *BUNOMYS*: Three of the four species of *Bunomys* encountered along the transect line are of large body size. *Bunomys andrewsi* was trapped between 290 m (Sungai Oha Kecil) and 675 m (Sungai Sadaunta) in the watershed of the Sungai Miu. This is the only species of *Bunomys* that occurred below 290 m on the transect and it is recorded at lower elevations in the valley of the Sungai Miu down to 110 m at Pakuli (see gazetteer and the map in fig. 50).

At higher elevations, *B. andrewsi* is replaced by *B. karokophilus*, which is documented by specimens between 823 m and 1150 m. Elevational ranges for *B. andrewsi*

and *B. karokophilus* contain habitats within tropical lowland evergreen rain forest.

Above the transition between lowland evergreen rain forest and montane forest formations, the lowland *B. karokophilus* is replaced by the montane *B. penitus*. The latter is common in lower and upper montane forest environments from 1285 m on the lower slopes of Gunung Kanino to the summit of Gunung Nokilalaki (2287 m). Nowhere along the transect did we collect any combination of the three species from the same locality—the distributions are elevationally parapatric, *B. andrewsi* in the lowlands, *B. karokophilus* through middle elevations, and *B. penitus* on the higher slopes, ridgetops, and mountain peak.

The range of the small-bodied *B. chrysocomus* overlaps those of the other three *Bunomys*. The samples come from localities in tropical lowland evergreen and lower montane rain forests along the gradient rising from 320 m (Sungai Oha Kecil) to 1555 m (Gunung Kanino). Specimens of *B. chrysocomus* were taken in the same traplines in which examples of *B. andrewsi*, *B. karokophilus*, and *B. penitus* were trapped.

The large-bodied species: Of the three larger-bodied species, *B. andrewsi* is the smallest in body size, *B. penitus* the largest, with *B. karokophilus* averaging slightly smaller than *B. penitus* in physical dimensions but comparable to that species in mass (table 73). *Bunomys andrewsi* has larger ears than *B. karokophilus* (both absolutely and relative to body size), and although absolutely smaller than the ears of *B. penitus* its ears are slightly larger relative to body size. The dorsal coat of *B. andrewsi* is slightly shorter than that of *B. karokophilus*, and much shorter than the long, luxuriant fur of *B. penitus*. Upperparts of *B. andrewsi* are bright brown flecked with buff and black, contrasting with the dark blue-gray or grayish-brown fur of *B. karokophilus* and the brownish-gray upperparts of *B. penitus*. Similarities and differences among the three species in length of tail relative to length of head and body, color pattern of tail, and frequency of white tail tip and its length relative to tail length are tabulated in table 73. *Bunomys penitus* has long ungual tufts and relatively small front

claws, *B. karokophilus* and *B. andrewsi* have inconspicuous tufts and more robust claws.

The three species also differ slightly in spermatozoal morphology as detailed in the accounts of species, in chromosomal composition (tables 12, 73), and in presence or absence of certain molar cusps and cusplets (tables 10, 11, 73).

The difference in body size among the three species is reflected in overall skull dimensions (figs. 99–101; table 74). The smallest skull belongs to *B. andrewsi*, the largest is exhibited by *B. penitus*, and the contrasts in most cranial and dental variables conform to this pattern, but not all of them. The interorbital region, for example, is much wider in *B. andrewsi* than in *B. karokophilus*, and wider relative to skull size compared with *B. penitus* (because univariate means of interorbital breadth in *B. andrewsi* and *B. penitus* are similar, but the latter has a larger skull). The braincase is also slightly wider in *B. andrewsi* as compared with *B. karokophilus*, the zygomatic plate wider than the plate in *B. karokophilus* and *B. penitus* (absolutely and relative to size of skull), the rostrum relatively longer, tympanic bullae relatively larger and molar row longer than those variables in *B. karokophilus*. The shortest incisive foramina belong to *B. karokophilus*, and the narrowest zygomatic plate to *B. penitus*. The relatively narrow interorbit and zygomatic plate of *B. penitus* are counterpoints to the other cranial and dental measurements for this species, which reflect a large skull—the largest of the three species—with a long and wide rostrum, long and spacious incisive foramina, large bullae, and strong molars.

The morphometric contrasts in cranial and dental variables among the three large-bodied species are summarized by individual specimen scores projected on first and second canonical variates (fig. 102, upper graph). A discrete cluster of scores represents each species, and the relative positions of the three clumps along the first axis are influenced primarily by size (larger to the left, smaller to the right) as signified by the many moderate to high positive variable correlations on the first variate ($r = 0.26$–0.84; table 75). The greater loadings highlight the larger skull of *B. penitus*, its wider interorbit, larger braincase, longer rostrum, longer diastema and bony palate, appreciably longer incisive foramina, larger bullar capsule, and much longer molar row.

The separation of scores for the sample of *B. andrewsi* from the clusters representing samples of *B. karokophilus* and *B. penitus* along the second axis, along with the greater positive and negative loadings for that canonical variate emphasizes shape distinctions (table 75). *Bunomys andrewsi* has a relatively shorter skull; wider interorbit, braincase, and zygomatic plate; shorter diastema, bony palate, and postpalatal extent, but slightly longer incisive foramina; narrower mesopterygoid fossa; and slightly smaller molars contrasted with the other two species.

Bunomys chrysocomus and the large-bodied species: *Bunomys chrysocomus* overlaps the elevational ranges of *B. andrewsi*, *B. karokophilus*, and *B. penitus* along the transect (fig. 103). In physical size and mass, *B. chrysocomus* is noticeably smaller than either *B. karokophilus* or *B. penitus* but comparable to *B. andrewsi* (table 73).

When compared with samples of *Bunomys andrewsi* from places beyond my transect, *B. chrysocomus* is typically much smaller in body size (means for LHB = 134.0–161.5 mm for nine samples of *B. chrysocomus*, and 169.9–177.4 mm for samples of *B. andrewsi* from Kuala Navusu, Gunung Balease, and the Malili region). However, specimens comprising the transect *B. andrewsi* are smaller in body size compared with those in samples from other parts of Sulawesi (mean LHB = 163.1 mm and mean weight = 113.7 g mm for transect *B. andrewsi*; 169.9–177.4 mm and 145.0–154.6 g for the samples from Kuala Navusu, Gunung Balease, and the Malili region) and more closely approximates the physical size of *B. chrysocomus*.

Not only do *B. andrewsi* from the transect and *B. chrysocomus* resemble one another in physical size; texture and length of the fur covering upperparts of head and body are similar. The coat is dark brownish gray in both, but that of *B. chrysocomus* averages slightly darker (buffy bands of the hairs are shorter) while the pelage of *B. andrewsi* is somewhat brighter (buffy bands are wider); ears and tops of the front and hind feet are similarly pigmented in both species. Length

TABLE 73

Elevational Range (m), Forest Formation, Descriptive Statistics for External Measurements (mm) and Weight (g), Tail Features, Cusp t1 on M3, and Karyotype Derived from Population Samples of *Bunomys* from My Transect in the West-Central Region

Mean ± 1 SD, observed range (in parentheses), and sample size are listed; percentages for length of ear (LE) and length of tail (LT) to length of head and body (LHB) are obtained from mean values. Mean and ranges are given for length of white tail tip (LWT), ranges only for percentages derived from LWT/LT. Elevational range is based on all specimens collected, not just those measured.

	B. chrysocomus (Sungai Oha Kecil + Sungai Sadaunta)	*B. chrysocomus* (Danau Lindu Valley + Gunung Kanino)	*B. andrewsi* (Puro-Sungai Miu)	*B. karokophilus* (Sungai Sadaunta + Danau Lindu Valley)	*B. penitus* (Gunung Kanino)	*B. penitus* (Gunung Nokilalaki)
Elevation[a]	320–1037	1000–1555	110–675	823–1150	1285–1616	1739–2287
Tropical evergreen rain forest formation	lowland	lowland–lower montane	lowland	lowland	lower montane	lower–upper montane
LHB	161.5 ± 8.23 (133–180) 147	154.8 ± 16.44 (97–176) 38	163.1 ± 8.24 (151–177) 9	172.9 ± 9.68 (150–190) 24	182.6 ± 7.34 (167–199) 74	184.0 ± 10.45 (155–242) 82
LHF	35.9 ± 1.25 (33–39) 147	35.8 ± 1.71 (32–40) 38	38.1 ± 1.27 (36–40) 9	39.1 ± 1.55 (36–44) 24	41.8 ± 1.40 (38–45) 74	41.4 ± 1.30 (38–44) 82
WT	93.3 ± 15.09 (55–135) 147	98.8 ± 17.23 (69–135) 38	113.7 ± 11.50 (95–135) 9	131.5 ± 18.61 (95–175) 23	132.3 ± 14.47 (100–170) 74	133.3 ± 15.42 (95–170) 76
EAR						
LE	23.3 ± 0.96 (21–26) 146	24.5 ± 1.22 (23–28) 38	24.4 ± 1.24 (23–27) 9	23.3 ± 0.81 (22–25) 24	26.2 ± 1.03 (24–29) 74	26.1 ± 0.91 (23–28) 82
LE/LHB (%)	14	16	15	13	14	14
TAIL						
LT	137.4 ± 10.75 (90–165) 139	142.0 ± 14.64 (107–180) 38	146.4 ± 10.86 (130–165) 9	161.3 ± 13.10 (135–205) 23	169.1 ± 8.24 (153–188) 71	162.5 ± 8.63 (138–185) 76
LT/LHB (%)	85	92	89	94	93	82
% with white tail tip (N)	28 (234)	9 (96)	47 (15)	100 (24)	99 (129)	99 (130)
LWT	11.6 (1–35)	6.7 (1–26)	5.9 (2–10)	28.7 (4–50)	39.4 (7–118)	38.8 (6–80)
LWT/LT (%)	1–25	1–15	1–10	2–31	4–68	4–46
Dorsal color	brown	brown	grayish brown to dark brown	grayish brown to brownish gray	glossy gray to brownish gray	glossy gray to brownish gray
Ventral color pattern	white (bicolored) through mottling to brown (monocolored)	white (bicolored) through mottling to brown (monocolored)	white (bicolored) through mottling to brown (monocolored)	white (bicolored) through mottling to brown (monocolored)	white (bicolored)	White (bicolored)
Cusp t1 on M3	large	large	large	absent, small bump, or ridge	large	large
Karyotype (2N = 42)	FNa = 56, FNt = 58	FNa = 56, FNt = 58	FNa = 56, FNt = 58	FNa = 56, FNt = 60	FNa = 58, FNt = 60–61	FNa = 58, FNt = 60–61

[a] Note that along the transect between Sungai Oha Kecil and Gunung Kanino, the elevational distribution of *Bunomys chrysocomus* overlaps the elevational parapatric ranges of *B. andrewsi*, *B. karokophilus*, and *B. penitus*.

TABLE 74
Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from Population Samples of
B. andrewsi, B. chrysocomus, B. karokophilus, and B. penitus Collected Along My Transect in the
West-Central Region
Mean ± 1 SD and observed range (in parentheses) are listed.

Variable	B. chrysocomus (Sungai Oha Kecil + Sungai Sadaunta)	B. chrysocomus (Danau Lindu Valley + Gunung Kanino)	B. andrewsi (Puro–Sungai Miu)	B. karokophilus (Sungai Sadaunta + Danau Lindu Valley)	B. penitus (Gunung Kanino)	B. penitus (Gunung Nokilalaki)
N	147	42	8	17	74	82
ONL	38.2 ± 1.07	38.3 ± 1.20	39.3 ± 1.38	40.5 ± 1.13	43.0 ± 1.14	42.9 ± 1.22
	(35.8–40.8)	(36.1–41.1)	(38.0–42.0)	(39.0–42.4)	(40.5–46.0)	(40.1–46.1)
ZB	18.0 ± 0.62	18.3 ± 0.62	19.0 ± 0.45	19.2 ± 0.89	19.5 ± 0.66	19.8 ± 0.63
	(16.3–19.7)	(17.3–19.8)	(18.3–19.8)	(18.3–21.0)	(18.0–21.0)	(18.2–21.4)
IB	6.4 ± 0.22	6.4 ± 0.24	6.8 ± 0.13	6.3 ± 0.27	6.7 ± 0.22	6.8 ± 0.23
	(5.9–6.9)	(5.8–6.8)	(6.6–6.9)	(6.0–6.8)	(6.2–7.5)	(6.4–8.3)
LR	13.6 ± 0.53	13.6 ± 0.71	13.8 ± 0.78	13.9 ± 0.62	16.1 ± 0.65	16.0 ± 0.63
	(12.3–15.1)	(12.0–15.1)	(12.5–15.0)	(13.1–15.1)	(14.6–18.1)	(14.8–17.8)
BR	6.8 ± 0.30	6.8 ± 0.45	7.4 ± 0.28	7.6 ± 0.44	7.9 ± 0.33	7.9 ± 0.35
	(6.0–7.5)	(5.8–7.7)	(6.9–7.7)	(6.8–8.6)	(7.1–8.9)	(7.0–8.7)
BBC	15.4 ± 0.38	15.6 ± 0.43	16.3 ± 0.47	15.9 ± 0.39	16.5 ± 0.37	17.0 ± 0.40
	(14.2–16.7)	(14.6–16.5)	(15.6–17.2)	(15.2–16.6)	(15.7–17.3)	(15.4–17.7)
HBC	10.8 ± 0.33	10.7 ± 0.38	11.2 ± 0.26	11.1 ± 0.41	11.8 ± 0.30	11.9 ± 0.39
	(10.0–11.8)	(10.1–11.7)	(10.8–11.5)	(10.5–11.8)	(10.3–12.5)	(10.9–12.7)
BZP	3.2 ± 0.23	3.2 ± 0.25	3.2 ± 0.23	3.1 ± 0.20	2.9 ± 0.18	3.0 ± 0.21
	(2.6–3.8)	(2.7–3.7)	(2.9–3.5)	(2.7–3.5)	(2.4–3.2)	(2.5–3.5)
LD	10.2 ± 0.52	10.2 ± 0.53	10.2 ± 0.39	10.7 ± 0.46	11.3 ± 0.46	11.3 ± 0.53
	(8.8–11.6)	(8.8–11.6)	(9.7–10.8)	(10.0–11.6)	(10.4–12.8)	(10.2–12.4)
PPL	13.5 ± 0.59	13.7 ± 0.58	13.6 ± 0.45	14.3 ± 0.63	14.7 ± 0.46	14.4 ± 0.51
	(12.2–14.8)	(12.3–15.0)	(13.0–14.2)	(13.2–15.2)	(13.7–16.1)	(13.4–15.5)
LBP	7.5 ± 0.39	7.4 ± 0.42	7.6 ± 0.43	8.2 ± 0.37	8.7 ± 0.43	8.9 ± 0.38
	(6.2–8.4)	(6.6–8.2)	(7.1–8.4)	(7.6–9.0)	(7.4–9.7)	(8.1–9.8)
BBP	3.8 ± 0.24	3.8 ± 0.27	3.5 ± 0.18	3.8 ± 0.28	3.6 ± 0.27	3.7 ± 0.25
	(3.1–4.5)	(3.2–4.4)	(3.3–3.8)	(3.4–4.3)	(3.0–4.3)	(3.1–4.2)
BMF	2.9 ± 0.22	3.0 ± 0.26	3.0 ± 0.17	3.3 ± 0.21	3.6 ± 0.25	3.7 ± 0.27
	(2.5–3.7)	(2.7–3.7)	(2.7–3.3)	(3.0–3.7)	(2.9–4.4)	(3.1–4.4)
LIF	6.2 ± 0.36	6.1 ± 0.34	7.3 ± 0.39	6.5 ± 0.32	8.0 ± 0.39	8.1 ± 0.48
	(5.2–7.2)	(5.4–6.9)	(6.8–8.0)	(6.0–7.1)	(7.2–9.2)	(7.0–9.1)
BIF	2.5 ± 0.16	2.4 ± 0.13	2.8 ± 0.18	2.8 ± 0.19	3.0 ± 0.17	3.0 ± 0.21
	(2.0–3.1)	(2.1–2.7)	(2.5–3.1)	(2.6–3.2)	(2.6–3.3)	(2.5–3.4)
LB	6.4 ± 0.22	6.3 ± 0.24	6.4 ± 0.28	6.3 ± 0.25	6.9 ± 0.31	6.8 ± 0.23
	(5.7–7.0)	(5.9–6.8)	(6.1–6.8)	(5.9–6.7)	(6.3–8.0)	(6.3–7.3)
CLM1–3	6.2 ± 0.22	6.2 ± 0.23	6.9 ± 0.31	7.0 ± 0.15	7.8 ± 0.26	7.8 ± 0.23
	(5.7–6.7)	(5.7–6.8)	(6.6–7.4)	(6.8–7.3)	(7.0–8.4)	(7.2–8.4)
BM1	2.0 ± 0.09	2.0 ± 0.09	2.3 ± 0.07	2.4 ± 0.07	2.5 ± 0.09	2.5 ± 0.11
	(1.8–2.3)	(1.8–2.2)	(2.2–2.4)	(2.3–2.6)	(2.3–2.7)	(2.2–2.8)

of tail relative to length of head and body, frequency of white tail tip in the samples, length of tip relative to tail length, and range in color pattern of the tail is comparable in both species (table 73. Because of their close resemblance in body size and coat color, freshly caught examples of *B. chrysocomus* and *B. andrewsi* are not easily distinguished; I caught both species along the Sungai Oha Kecil but was unsure of identifications until I examined the skulls.

Coloration of the dorsal fur in *B. chrysocomus* from tropical lowland evergreen rain forest along the transect ranges from rich brown to dark brownish gray, the darker tone more similar to the fur of *B. karokophi-*

Fig. 99.   Dorsal views of adult skulls representing the four species of *Bunomys* collected along my transect extending from the Sungai Oha Kecil to Gunung Nokilalaki. Upper pair, left to right: *B. andrewsi* (AMNH 224632, Sungai Oha Kecil, 458 m) and *B. chrysocomus* (AMNH 224698, Sungai Sadaunta, 763 m). Lower pair, left to right: *B. karokophilus* (AMNH 225038, holotype, Sungai Sadaunta, 1006 m), and *B. penitus* (AMNH 225275, Gunung Kanino, 1464 m). ×2.

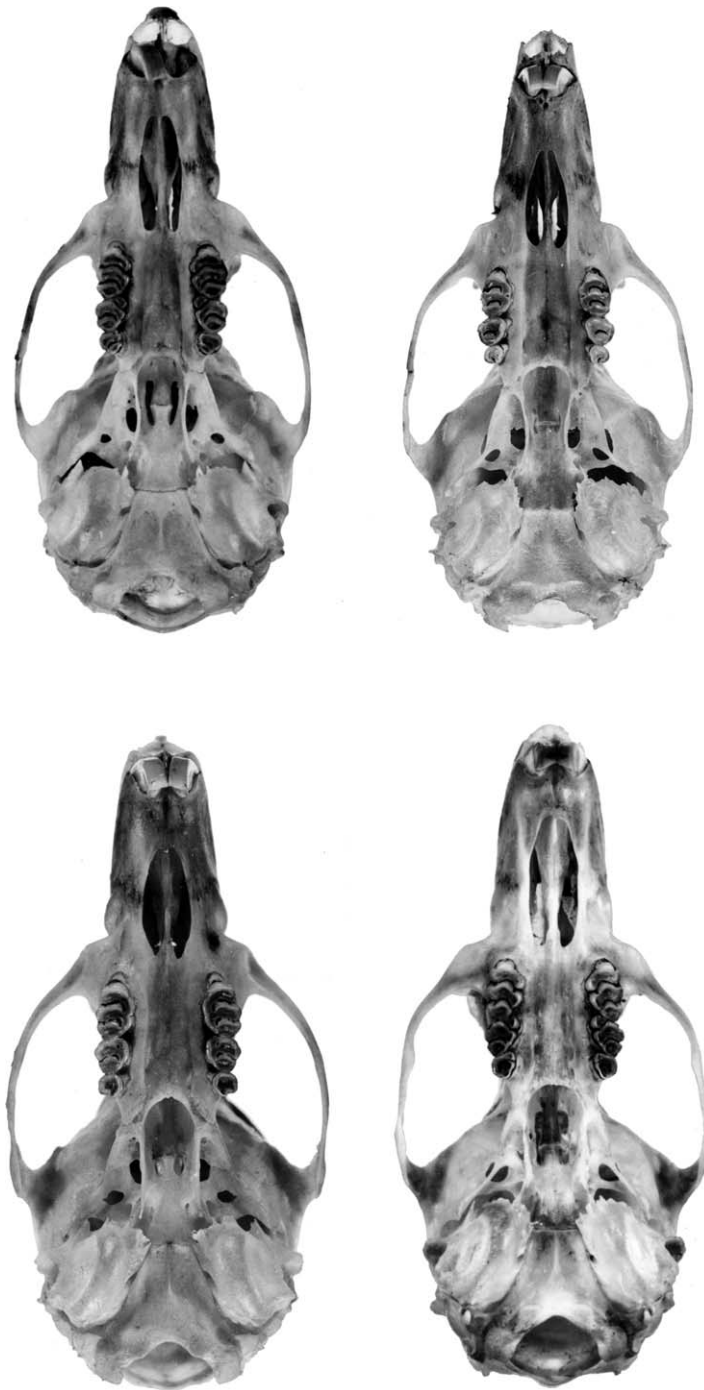Fig. 100.   Ventral views of the same skulls shown in figure 99. Upper pair, from left to right: *B. andrewsi* and *B. chrysocomus.* Lower pair, from left to right: *B. karokophilus* and *B. penitus.* ×2.
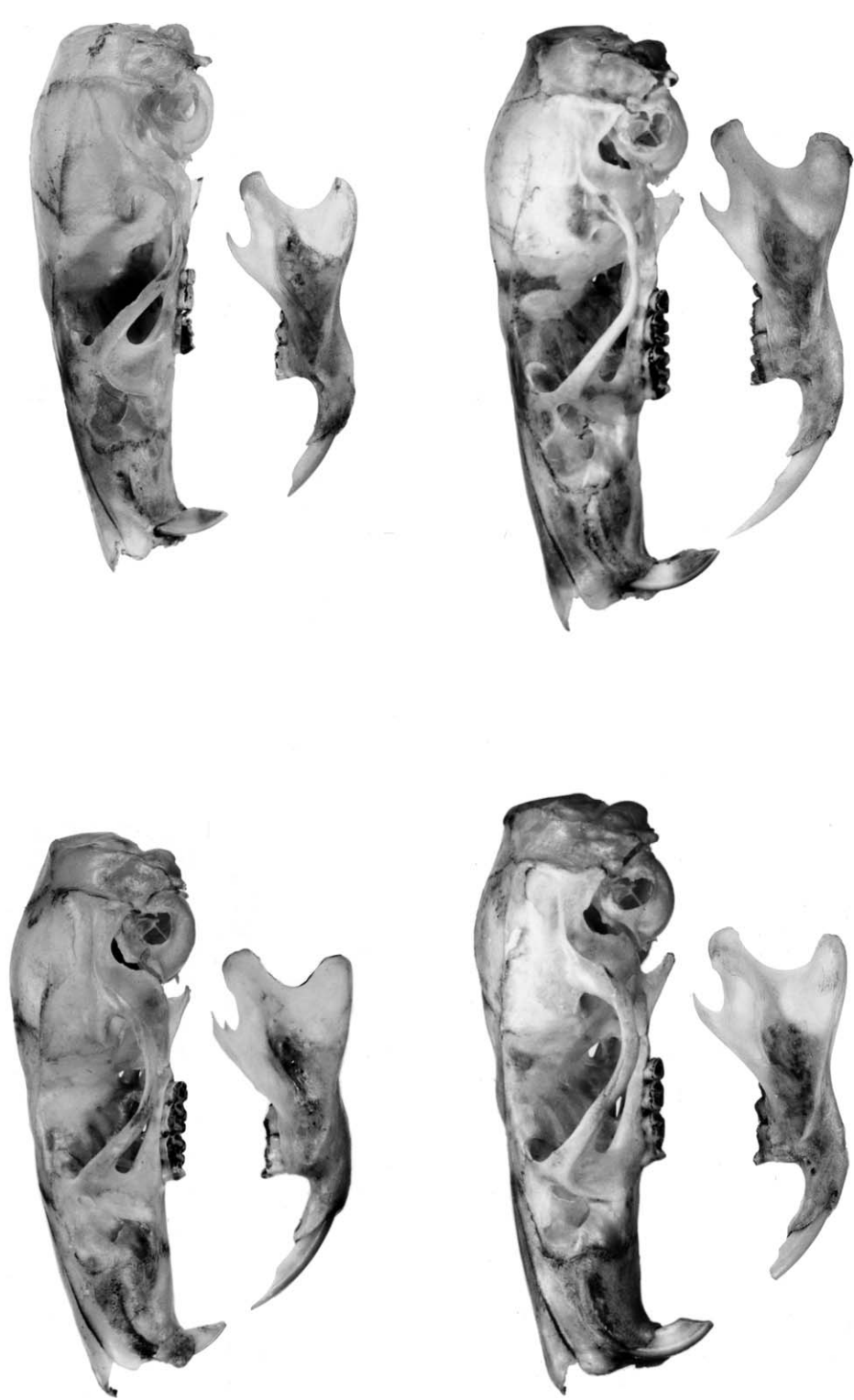
Fig. 101.   Lateral views of the the same specimens presented in figures 99 and 100. Upper pair, from left to right: *B. andrewsi* and *B. chrysocomus*. Lower pair, from left to right: *B. karokophilus* and *B. penitus*. ×2.

lus but without its dark gray or blue-gray casts. Adult examples of *B. chrysocomus* are physically smaller than adult *B. karokophilus* of comparable age, and the ears average larger in relation to body size (table 73). Ventral fur of *B. chrysocomus* is typically either grayish white or grayish white washed with buff; a few examples have richly pigmented ochraceous gray coats, contrasting with the grayish-white or dark gray underparts of *B. karokophilus.* Length of tail relative to head and body length is comparable in the two species (table 73), as is the range in dorsal-ventral tail patterning. However, the dorsal brown covering extends from base to tail tip on most examples of *B. chrysocomus,* and the tails of relatively few exhibit white tips, which are short when present; by contrast, all rats in the sample of *B. karokophilus* have a white tail tip that averages longer relative to tail length (table 73).

No contrasting ambiguity exists between *B. chrysocomus* and *B. penitus.* Both are found in lower montane forest on Gunung Kanino; *B. chrysocomus* from there has dark brown to brownish-black upperparts, *B. penitus* has longer and paler fur (grayish brown) and is much larger in physical size size (table 73). The richly pigmented ochraceous gray ventral fur found in some *B. chrysocomus* has no counterpart in the sample of *B. penitus.* Nearly all *B. penitus* from the transect have a bicolored tail with a white tip, which contrasts strongly with the range of color pattern of the tail and frequency of occurrence of a white tip in the transect sample of *B. chrysocomus* (table 73).

Other contrasts show that *B. chrysocomus* from the transect has larger testes relative to body size than do the transect samples of *B. andrewsi,* *B. karokophilus,* and *B. penitus* (table 9), differs slightly in spermatozoal morphology as detailed in the accounts of species, in gross chromosomal composition (between *B. karokophilus* and *B. penitus;* tables 12, 73), and in presence or absence of certain molar cusps and cusplets (tables 10, 11, 73).

Bunomys chrysocomus has weaker molars and a smaller, gracile skull compared with the larger and more robust skulls and dentitions of *B. andrewsi,* *B. karokophilus,* and *B. penitus* (figs. 99–101). Except for univariate means for breadths of zygomatic plate and palatal bridge, which are the same or greater in *B. chrysocomus* as compared with the other three species, all the other cranial and the dental dimensions average much less for the smaller-bodied *B. chrysocomus,* particularly when compared with *B. karokophilus* and *B. penitus,* the two largest-bodied species from the transect (table 74).

The pattern of morphometric relationships among transect samples of the four species employing cranial and dental variables is summarized by individual specimen scores projected onto first and second canonical variates (fig. 102, lower graph). The relative positions of the four discrete clusters of scores along the first axis are primarily influenced by the large and positive correlations ($r = 0.63$–0.98; table 75) for nearly all variables, reflecting the many greater cranial and dental dimensions typical of *B. andrewsi,* *B. karokophilus,* and *B. penitus* as compared with *B. chrysocomus.* Breadths of zygomatic plate and bony palate clash with this pattern ($r = -0.52$ and -0.29, respectively): the two dimensions are comparable in absolute size among the four species (table 74), thus relatively greater in *B. chrysocomus.* Along the second axis, the position of scores for *B. karokophilus* in relation to clusters representing the other three species attests to the relatively narrower interorbit in *B. karokophilus,* its relatively shorter but slightly broader rostrum, shorter incisive foramina, smaller ectotympanic bulla, and wider molars (see the loadings in table 75).

There are similarities and differences in ecological attributes among the four species. Both *B. andrewsi* and *B. chrysocomus* share a comparable diet: some fruit but primarily invertebrates and small vertebrates; both shun fungi (table 13). The ear fungus *Auricularia delicata* is the primary constituent in the diet of *Bunomys karokophilus*; fruit and invertebrates comprise a minor portion. The montane *B. penitus* also consumes fungi along with a variety of invertebrates and some fruit.

Judged by our trapping results, *Bunomys andrewsi,* *B. karokophilus,* and *B. chrysocomus* share similar habitats in the lowland
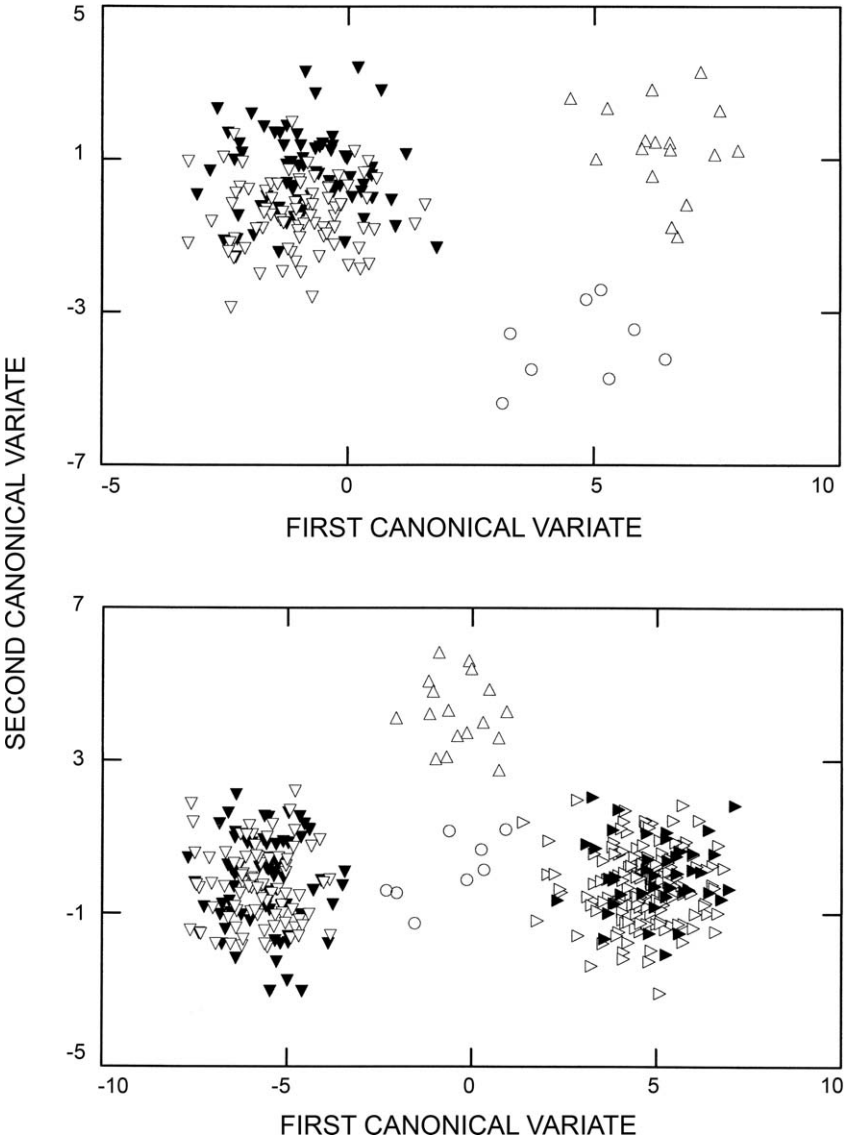
Fig. 102.   Summary of morphometric discrimination among members of *Bunomys* collected along my transect in the northern part of the west-central mountain block. Individual specimen scores are projected onto first and second canonical variates extracted from discriminant-function analysis of 16 cranial and two dental log-transformed variables. Upper graph: contrasts among samples of the large-bodied species *B. karokophilus* (empty triangles; $N = 17$), *B. andrewsi* from Puro-Sungai Miu (empty circles; $N = 8$), and *B. penitus* from Gunung Kanino (filled inverted triangles; $N = 74$) and Gunung Nokilalaki (empty inverted triangles; $N = 82$). Lower graph: discrimination among samples of the three large-bodied species of *Bunomys* and the smaller-bodied *B. chrysocomus* from Sungai Oha Kecil + Sungai Sadaunta (empty right-pointing triangles; $N = 147$) and Danau Lindu + Gunung Kanino (filled right-pointing triangles; $N = 42$). See table 75 for correlations (loadings) of variables with extracted canonical variates and for percent variance explained that apply to both ordinations.

TABLE 75
Results of Discriminant-Function Analysis Performed on Population Samples of *Bunomys karokophilus*, *B. andrewsi*, *B. penitus*, and *B. chrysocomus* Collected along My Transect in the West-Central Region
Correlations (loadings) of log-transformed values for 16 cranial and two dental variables are based on 17 *B. karokophilus*, 8 *B. andrewsi*, 156 *B. penitus*, and 189 *B. chrysocomus*; see figure 102.

	Correlations			
	B. karokophilus, *B. andrewsi*, and *B. penitus*		*B. karokophilus*, *B. andrewsi*, *B. penitus*, and *B. chrysocomus*	
Variable	CV1	CV2	CV1	CV2
ONL	0.67***	−0.31***	0.91***	0.01
ZB	0.31***	0.02	0.79***	0.11*
IB	0.51***	0.42***	0.63***	−0.29***
LR	0.84***	−0.17*	0.89***	−0.20***
BR	0.34***	−0.17*	0.85***	0.14**
BBC	0.52***	0.26***	0.84***	−0.04
HBC	0.61***	−0.02	0.86***	−0.06
BZP	0.26***	0.35***	−0.52***	−0.05
LD	0.50***	−0.30***	0.74***	−0.01
PPL	0.31***	−0.50***	0.67***	0.12*
LBP	0.54***	−0.27***	0.85***	0.06
BBP	−0.03	−0.01	−0.29***	−0.01
BMF	0.46***	−0.25***	0.81***	0.08
LIF	0.81***	0.19**	0.92***	−0.17***
BIF	0.29***	−0.05	0.83***	0.10*
LB	0.61***	−0.05	0.67***	−0.28***
CLM1–3	0.82***	−0.17*	0.98***	0.05
BM1	0.44***	−0.16*	0.94***	0.18***
Canonical correlation	0.924	0.728	0.981	0.689
Eigenvalue	5.838	1.126	22.630	0.902
% Variance	78.7	15.1	94.3	3.3

*** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

evergreen rain forest along the transect. All were collected during the night on the ground in places where the ambient environment remains cool and damp, primarily stream terraces and wet ravines protected by good forest cover. We did not trap any examples of *B. karokophilus* outside of these habitats. We did collect *B. chrysocomus* just above streams on hillsides all the way to ridgetops well above streams and the damp habitats associated with shaded ravines. *Bunomys penitus* was caught in a variety of topography in montane forest habitats—ravines, hillsides, and tops of ridges, virtually everywhere traplines were placed. Aside from short intervals of low rainfall, mainly during October in the Danau Lindu region, habitats everywhere in montane forests are wet and cool, even cold, whether deep in ravines or high on hillsides and ridgetops.

SYMPATRY BETWEEN THE FOUR *BUNOMYS* AND OTHER MURINES: In addition to the four kinds of *Bunomys*, we collected examples of 23 other species of murines between 200 m and the summit of Gunung Nokilalaki (fig. 103), a group showing an assortment of morphologies and ecologies. Information conferred here derives from data presented in tables and text in this report, in other publications cited below, and in my field journals (in Mammalogy Archives, AMNH). Only a few topics are addressed. For example, the variety of spermatozoal morphology (Breed and Musser, 1991) and chromosomal composition (Rickart and Musser, 1993) for some of the species is not included but can be appreciated by consulting those references. I also omit a summary of ectoparasites and endoparasites because that inventory is incomplete or the parasites

Species	200	300	400	500	600	700	800	900	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	2000	2100	2200
Margaretamys parvus																		4			14
Margaretamys elegans															4	3	19	7		3	4
Margaretamys beccarii					12		2	1	1												
Taeromys hamatus												3	4								7
Taeromys new species													3	7		1					
Taeromys callitrichus							1	1		1		1									1
Taeromys celebensis	1	5	1		2		4	1	15	4	3										
Maxomys dollmani							3	3	2			1	1								
Maxomys new species								4	24												
Maxomys hellwaldii	46	23			13	4	21	10	1												
Maxomys musschenbroekii	2	2			1	4	5	3	14		3		4	3		4		1	1	11	49
Rattus hoffmanni	9	6	1		17	4	20	15	56	27	7	6	21	11	1	2		5	11	6	35
Rattus facetus	11	5	1		29	4	13	3	51	24	11	3	4		3		2		2	1	7
Paruromys dominator	1	9	1		3	2	38	7	14	25	5	15	41	33	1	8	18	7	20	12	46
Crunomys celebensis							1		2												
Echiothrix centrosa							3	3													
Haeromys new species																9		1			
Haeromys minahassae							1	1													
Tateomys macrocercus																1					7
Tateomys rhinogradoides																					7
Melasmothrix naso																	2		4	4	25
Eropeplus canus																2				3	6
Lenomys meyeri							2	1													
Bunomys penitus												5	72	58	5	6	13	17	13	28	71
Bunomys chrysocomus		14	24		75	38	40	16	76	32	3	2	1	2							
Bunomys karokophilus							10	5	10	2											
Bunomys andrewsi	1	1	3		2																

ELEVATION IN METERS

Fig. 103.   The species of murine rodents (all endemic to Sulawesi) collected along my transect in the west-central region (see fig. 1). Number of specimens trapped per elevation are indicated for 27 species collected along the transect beginning in the lowlands at Sungai Oha Kecil in the valley of the Sungai Miu and ending at the summit of Gunung Nokilalaki. About 1300 m marks the transition between tropical lowland evergreen and lower montane rain forests along the transect line; 2000 m is the approximate transition between lower and upper montane forests.

have yet to be described (see Musser and Durden, 2014).

Body size and external morphology: Physical body size ranges from the very small to the very large (table 76). At one extreme are the mouse-sized species of *Haeromys* with head and body length for adults of 72–79 mm and weight 11–18 g, at the other is *Paruromys dominator* with head and body length for adults of 229–278 mm and weight 215–440 g (fig. 104, table 76). These limits currently display the stretch in physical size among endemic Sulawesian murines for no other species that are either smaller or larger in body size have so far been recorded from the island.

The collection of external morphologies is no less impressive. Anchoring one end of the range of expressions is the generalized rat conformation, using the familiar *Rattus rattus* and *R. norvegicus* as models, which on the transect is exemplified by *Rattus hoffmanni* (see images of the live rat in Musser and Holden, 1991). And the species of *Haeromys* are at once recognized as mice but with very long whiplike tails (fig. 104; Musser, 1990). The radical departure from these familiar rat and mouse designs are the shrew rats, *Echiothrix centrosa*, *Melasmothrix naso*, and the two species of *Tateomys* (Musser, 1982, 1990; Musser and Durden, 2002). Between these bookends is an array of genera containing species that are ratlike in their physical design—*Taeromys*, *Eropeplus*, *Lenomys*, *Paruromys*, *Crunomys*, *Rattus facetus*, and *Bunomys*; a nonordinary form like *Maxomys hellwaldii* with its long face, large eyes, big ears, elongate hind feet, and orange-brown fur; and the three species of *Margaretamys*, which are squirrellike with their long hirsute tails and arboreal proclivity (Musser, 1981a; Mortelliti et al., 2012).

Terrestrial species: The four species of *Bunomys* are among the 18 species, the majority, that I regard to be terrestrial (table 77); except for rare occasions we did not trap any of the species above ground in trees or clusters of woody vines suspended from tree crowns. The exceptions concerns three species. Of the 323 specimens of *B. chrysocomus* trapped on the transect, only two were taken on woody vines 2–3 ft above

the forest floor, and one of the 118 *Maxomys hellwaldii* was caught on the thick basal portion of a woody vine about 2 ft from where it was rooted in the ground. Most of the 260 specimens of *Rattus hoffmanni* were trapped on the ground, but a few were taken above ground: ''on top of a large branch 2 ft from ground level, 6 ft above the ground on the trunk of a tree growing out over a stream, in a tangle of woody vines about 6 ft above the leaf-covered floor of the forest, and 8 ft above the ground among the lattice of large aerial roots forming the trunk of a canopy strangler fig (Musser and Holden, 1991: 362). All these spots for each species were readily accessible from the forest floor. Most of the terrestrial species have moderately long and narrow hind feet (as opposed to short and wide as found in most arboreal species) along with tails that on average are equal to or shorter than length of head and body (*Taeromys hamatus*, *Taeromys,* n. sp., *Maxomys hellwaldii*, *Maxomys* n. sp., *Maxomys musschenbroekii*, *Rattus hoffmanni*, *Crunomys celebensis*, *Melasmothrix naso*, and the four species of *Bunomys*) or only somewhat longer (*Taeromys callitrichus*, *Echiothrix centrosa*, *Tateomys rhinogradoides*, and *Lenomys meyeri*); see table 77.

Two species I include as occupying terrestrial habitats are *Maxomys dollmani* and *Tateomys macrocercus*, both with very long tails relative to lengths of head and body (LT/LHB = 122% and 133%–159%, respectively) as well as long and slender hind feet. Both are capable of jumping to and scampering about on substrates above the ground but low in the understory, such as on huge jumbles of decaying trunks and limbs from old treefalls.

The terrestrial *Echiothrix centrosa* also has, on average, a long tail relative to head and body length (LT/LHB = 113%). Characteristic also are its very large ears and elongate hind feet (Musser, 1991). Specimens were trapped in runways besides decaying tree trunks on the forest floor and on decaying trunks and branches bridging streams and ravines. The morphological specializations in the body conformation reflect its ability to forage for earthworms and other soft-bodied invertebrates, run along substrates, and leap away from predators (Musser and Durden, 2014).

Fig. 104.   Extremes in body size and departure from the typical *Rattus*-like conformation (such as the species of *Bunomys* illustrated in fig. 6) among the murines encountered on the transect. Upper left: *Paruromys dominator*, the largest in body size (LHB = 229–278 mm for adults, mass = 215–440 g). Upper right: *Haeromys minahassae*, the smallest in physical size (LHB = 74–79 mm for adults, mass = 11–16 g). Lower left: *Tateomys rhinogradoides*, embodying the shrewlike physique. Lower right: *Maxomys hellwaldii*, terrestrial with long face, large eyes and ears, bright fur, and elongate hind feet, a build also similar to *Echiothrix centrosa*.

TABLE 76
Contrasts in Adult Body Size among Murines Collected Along My Transect in the the West-Central Region[a]
Listed are observed ranges for lengths of head and body (LHB), tail (LT), hind foot (LHF), and ear (LE) in millimeters; weight (WT) in grams; and LT/LHB as percentages. Data are summarized from descriptive univariate statistics derived from my measurements made in the field.

Species	LHB	LT	LT/LHB	LHF	LE	WT
Margaretamys parvus	96–114	154–184	161	23–26	19–21	23–40
Margaretamys elegans	165–197	220–286	140	35–39	23–27	85–150
Margaretamys beccarii	117–142	150–190	121–145	26–29	19–21	53–72
Taeromys hamatus	180–213	177–205	97	42–46	24–25	145–220
Taeromys n. sp.	193–240	195–232	95	47–57	33–35	220–275
Taeromys callitrichus	220–240	240–260	108	51–54	26–28	290–363
Taeromys celebensis	201–249	244–306	123	47–56	25–28	190–345
Maxomys dollmani	205–212	242–265	122	45–49	25–26	210–265
Maxomys n. sp.	155–200	155–176	91	42–45	26–30	100–170
Maxomys hellwaldii	180–220	160–200	87–89	43–49	26–30	150–270
Maxomys muschenbroekii	131–163	112–152	88–91	32–37	18–23	59–120
Rattus hoffmanni	167–211	155–200	94	36–42	21–24	95–240
Rattus facetus	178–245	222–315	119–124	40–49	21–27	120–290
Par5uromys dominator	229–278	240–326	110–114	51–60	27–36	215–440
Crunomys celebensis	115–127	80–84	66–70	25–27	14	35–55
Haeromys n. sp.	72–78	125–140	176	20–21	17–18	11–18
Haeromys minahassae	74–79	127–134	176	20	15–16	11–16
Echiothrix centrosa	210–219	230–247	113	50–55	33–35	215–270
Tateomys macrocercus	110–120	160–175	133–159	30–31	17–19	35–55
Tateomys rhinogradoides	149–156	152–170	101–110	37–38	22–24	70–98
Melasmothrix naso	111–126	81–94	74–75	27–30	18–20	40–58
Eropeplus canus	229–255	258–305	119	44–49	27–31	190–315
Lenomys meyeri	257–268	272–280	105–109	46–49	26–28	320–325
Bunomys penitus	**155–242**	**153–188**	**88–93**	**38–45**	**23–29**	**95–170**
Bunomys chrysocomus	**97–180**	**90–180**	**85–92**	**32–40**	**21–28**	**55–135**
Bunomys karokophilus	**155–190**	**150–205**	**95**	**36–42**	**22–25**	**105–175**
Bunomys andrewsi	**151–177**	**130–165**	**89**	**36–40**	**23–27**	**95–135**

[a] The use of *Maxomys hellwaldii* and *M. muschenbroekii* in this table and in tables 77–80 are provisional determinations. Whether the samples from my transect represent true *Maxomys hellwaldii* and *M. muschenbroekii*, with type localities in the northeastern end of the northern peninsula (east of the Gorontalo region), or different clades has yet to be assessed (see footnotes to table 81).

Arboreal/terrestrial species: Nine species I place in in this category (table 77). We trapped examples of the three *Margaretamys*, the two *Haeromys*, *Taeromys celebensis*, *Rattus facetus*, *Paruromys dominator*, and *Eropeplus canus* on and above ground level. These murids are much like arboreal squirrels (*Rubrisciurus rubriventer*, *Prosciurillus topapuensis*, and *Prosciurillus murinus* in the transect area; see Musser et al., 2010): they display a vertical activity zone extending from forest floor to canopy, and "enter trees habitually to forage or seek shelter" (Cartmill, 1985: 73). Our trapping results reflect active locomotion by these species on vertical, steeply sloping, horizontal, and discontinuous surfaces above ground level—woody vines, tree trunks and crowns, palms—not accidental forays into the vertical dimension as was described above for *Bunomys chrysocomus*, *Maxomys hellwaldii*, and *Rattus hoffmanni*.

The three species of *Margaretamys* are the most arboreal of the group. At ground level, the montane *M. parvus* and *M. elegans* were taken in runways alongside decaying trunks and limbs lying on the forest floor, in hollows among tree roots covered with mats of moss and soil, and on open ground at the bases of trees. In the understory we encountered them up to 25 ft above ground (about as high as we could safely climb and set traps), where the rats were trapped on tree trunks, in crowns of understory trees, and on woody vines

TABLE 77
Ecological Attributes among Murines Collected along My Transect in the West-Central Region

Species	Habitat		Active period		Tropical rain forest formation		
	Terrestrial	Arboreal/terrestrial	Nocturnal	Diurnal	Lowland evergreen	Lower and upper montane	Lowland evergreen and montane
Margaretamys parvus	—	+	+	—	—	+	—
Margaretamys elegans	—	+	+	—	—	+	—
Margaretamys beccarii	—	+	+	—	+	—	—
Taeromys hamatus	+	—	+	—	—	+	—
Taeromys n. sp.	+	—	+	—	—	+	—
Taeromys callitrichus	+	—	+	—	—	—	+
Taeromys celebensis	—	+	+	—	+	—	—
Maxomys dollmani	+	—	+	—	—	—	+
Maxomys n. sp.	+	—	+	—	+	—	—
Maxomys hellwaldii	+	—	+	—	+	—	—
Maxomys muschenbroekii	+	—	+	—	—	—	+
Rattus hoffmanni	+	—	+	—	—	—	+
Rattus facetus	—	+	+	—	—	—	+
Paruromys dominator	—	+	+	—	—	—	+
Crunomys celebensis	+	—	—	+	+	—	—
Haeromys n. sp.	—	+	+	—	—	+	—
Haeromys minahassae	—	+	+	—	+	—	—
Echiothrix centrosa	+	—	+	—	+	—	—
Tateomys macrocercus	+	—	+	—	—	+	—
Tateomys rhinogradoides	+	—	+	—	—	+	—
Melasmothrix naso	+	—	—	+	—	+	—
Eropeplus canus	—	+	+	—	—	+	—
Lenomys meyeri	+	—	+	—	+	—	—
Bunomys penitus	+	—	+	—	—	+	—
Bunomys chrysocomus	+	—	+	—	—	—	+
Bunomys karokophilus	+	—	+	—	+	—	—
Bunomys andrewsi	+	—	+	—	+	—	—

connecting crowns of canopy trees (figs. 105, 106). All the *M. beccarii* were trapped in trees or on woody vines in the understory—none were caught on the ground (fig. 108; also see Mortelliti et al., 2012).

An example of the facility with which these rats move through the trees is provided by an adult male *Margaretamys elegans* we released on the vine shown in figure 105. The rat ran along the top of the vine toward the nearby canopy tree, a species of *Eugenia*. At one point he was clinging to the underside of the vine, stopped, and looked back toward the cage trap before continuing up the vine and onto the tree trunk, running up one side of the trunk and down the other to about 15 ft from the ground. He ran down the trunk head first, just as tree squirrels do. He stopped, looked toward the ground, then toward the crown, then to the trunk of the next tree, about 2 ft away, jumped to that trunk where he ran up and onto the first large limb, continued over slender branches and twigs to the crown of an adjacent understory tree, and moved away from us in this fashion, always staying about 40 to 50 ft above ground in the crowns of the understory canopy just beneath the broken emergent canopy formed by the taller trees. About 100 ft downslope, we could mark his progress only by the movement of leafy slim branches before finally losing sight of him. His agile progression up and down trunks and along limbs, branches, and twigs were much like a squirrel—very quick, very quiet, and extremely graceful, appearing to flow over the arboreal supports.

We trapped *Haeromys* on the ground and in clumps of woody vines entangled about trunks and limbs of understory trees. We could

not locate nests of the lowland *H. minahassae,* but the montane species constructs globular nests 7–14 ft above ground within the hollow trunks of living *Eugenia* (Myrtaceae).

Rattus facetus was caught up to 12 ft above ground in tangles of woody vines, crowns of understory trees, and the hollows bounded by the lattice of aerial roots of tall strangler figs that form part of the high canopy or emerge above it. Aerial roots from the fig encircle the trunk of a host tree and over time form a constricting woody lattice-work that is eventually filled with the decaying remains of the host. The debris forms an ideal microhabitat for nests. *Rattus facetus* were also trapped on the ground but often on top of treefalls and at the bases of canopy trees and strangler figs. About half of the 174 specimens were trapped on surfaces above ground level.

Taeromys celebensis, the only arboreal member of *Taeromys*, was caught on some of the same tangles of woody vines and in the same trees as *Rattus facetus*, and was also trapped on the ground in damp runways, on vines embracing old treefalls, and on decaying branches and trunks spanning streams and ravines. Approximately one-third of the sample was taken in trees and on woody vines.

Of the more than 300 specimens of *Paruromys dominator*, most were trapped on the ground and on decaying trunks and limbs bridging streams and ravines, but a few were taken above ground in the understory on woody vines and understory trees. During the night we saw them moving about in the crowns of understory trees, and they have been photographed climbing in tall second-growth (Pangau-Adam et al., 2003).

The sample of *Eropeplus canus* is small (fig. 103). Most were trapped within large interstices of rocks bound together by tree roots and mantled in dense, wet moss, some were taken in the deep crevasse of a large rocky outcrop, and a few on a slim woody vine about 15 ft above ground level that twists through the crowns of understory trees on a hillside.

Daily activity: The majority of species are nocturnal. They were captured during the night and sometimes seen scurrying over the ground or in the crowns of understory trees. Captive representatives of many of the species slept in their cages during the day in nests constructed from dry leaves and moss and became active during the night. Only *Crunomys celebensis* and *Melasmothrix naso* were seen in the forests during the day and were trapped during daylight hours (Musser, 1982). Diurnal murids on Sulawesi tend to be small in body size with short tails relative to head and body length, have dark chestnut fur, and feed on invertebrates.

Forest formations: My transect line incorporated habitats in tropical lowland evergreen and montane rain forests (table 77). Of the 27 species, 10 were collected only in lowland environments and 10 only in montane habitats. Seven species were encountered in both lowland and mountain forests; two of these, *Taeromys callitrichus* and *Maxomys dollmani*, are represented by small samples and the extent of their distributions within the two broad forest formations are unknown although I suspect our material may accurately represent their middle-elevational range, overlapping the upper zone of lowland evergreen rain forest and lower zone of montane forest habitats. *Bunomys chrysocomus*, occurred through a wide range of lowland elevations and did not penetrate far into montane situations. Four species—*Maxomys musschenbroekii*, *Rattus hoffmanni*, *Rattus facetus*, and *Paruromys dominator*—were trapped the length of the transect extending from the lowest point at Sungai Oha Kecil to the summit of Gunung Nokilalaki.

Mammae and litter size: Six teats (one postaxillary pair and two inguinal pairs; $1 + 2 = 6$) is possessed by about half the species (table 78). Four teats (two inguinal pairs; $0 + 2 = 4$) is exhibited by nine species. Four species have eight nipples with three showing the pattern of one pectoral pair, one postaxillary pair, two inguinal pairs ($2 + 2 = 8$), and *Rattus hoffmanni* is unique with one postaxillary pair, one abdominal pair, and two inguinal pairs ($1 + 3 = 8$). Litter size ranges from one to five among the species for which number of young could be determined.

Diets: An array of diets is represented among the 27 species (table 79). Eight of them feed primarily on fruit; most of the others share a diet comprised of fruit, vegetation, fungi, arthropods, and earthworms; a few

Fig. 105.   Montane forest at 1951 m, Gunung Nokilalaki (in 1975). Usma perches below a woody vine (2–3 inches in diameter) on which two *Margaretamys elegans* were trapped about 20 ft above ground. The vine connected crowns of *Eugenia* sp. and *Lithocarpus havilandii*, which are the dominant canopy trees here with contributions from *Dacrycarpus imbricatus*. Walnut (*Engelhardtia serrata*) is abundant in the understory as seedlings and young trees. Rattans are plentiful, and *Pandanus* sp., *Podocarpus neriifolius*, and the palm *Areca vestiaria* are scattered in the understory. *Maxomys musschenbroekii*, *Rattus hoffmanni*, *Rattus facetus*, *Paruromys dominator*, *Tateomys rhinogradoides*, *Melasmothrix naso*, and *Bunomys penitus* were trapped on the ground in the forest here (see fig. 103).

Fig. 106.   Montane ridge forest at 1830 m, Gunung Nokilalaki (in 1975). *Margaretamys parvus* were taken in the Sherman traps set by Aminudi on a woody vine (1/2 in. diameter). The vine was rooted in the ground on top of the ridge, wound up a sapling and over limbs in the understory to about 10 ft, then dropped down and looped out over a steep slope in understory for 15 ft, then extended up to about 30 ft where it wound through crowns of understory trees and into the canopy. Floristic composition of the forest was similar to that noted in legend to figure 105. *Margaretamys elegans*, *Paruromys dominator*, and *Bunomys penitus* were the most frequently trapped murines at this elevation (see fig. 103).

TABLE 78
Number of Teats and Litter Sizes for the Murines Collected along My Transect in the West-Central Region

Taxa	Mammary formula[a]	Litter size[b]
Margaretamys (all three species)	1 + 2 = 6	2
Taeromys (all four species)	1 + 2 = 6	2–3 (*celebensis*)
		1 (*callitrichus*)
Maxomys hellwaldii, Maxomys n. sp.	1 + 2 = 6[c]	2–4 (*hellwaldii*)
Maxomys dollmani, M. muschenbroekii	2 + 2 = 8	?
Rattus hoffmanni	1 + 3 = 8	4–5
Rattus facetus	1 + 2 = 6[c]	1–3
Paruromys dominator	1 + 2 = 6	2–5
Crunomys celebensis	2 + 2 = 8	?
Echiothrix centrosa	0 + 2 = 4	3
Haeromys (both species)	1 + 2 + 6	2
Tateomys (both species)	0 + 2 = 4	1 (*rhinogradoides*)
Melasmothrix naso	1 + 2 = 6	1
Eropeplus canus	0 + 2 = 4	1–2
Lenomys meyeri	0 + 2 = 4	1
***Bunomys* (all four species)**	**0 + 2 = 4**	**1–2**

[a] Number of teats indicated by the formulae:

0 + 2 = 4, two inguinal pairs only;

1 + 2 = 6, one postaxillary pair and two inguinal pairs;

2 + 2 = 8, one pectoral pair, one postaxillary pair, and two inguinal pairs;

1 + 3 = 8, one postaxillary pair, one abdominal pair, and two inguinal pairs.

[b] Determined from three sources: young born during captivity, number of embryos in uterine horns, and number of discrete placental scars in uterine horns showing the same condition (fresh and old scars were not counted together).

[c] A few specimens of *Maxomys hellwaldii* and *Rattus facetus* possess a pair of pectoral nipples that are essentially small empty projections from the skin surface; subdermal mammary tissue and ducts connecting tissue to nipple—the condition in normally developed mammae—are not present.

feed only on insects or earthworms; one species takes fruit, invertebrates, and fungi; and another is largely mycophagous. Earthworms are the predominant food of the lowland *Echiothrix* and montane *Tateomys* and *Melasmothrix*. The two species of *Tateomys* and *Melasmothrix naso* occur in the same habitat, the nocturnal *Tateomys* prey on earthworms during the night, the diurnal *Melasmothrix* exploits that resource during the day.

Summary of sympatry (fig. 103): *Bunomys penitus* shares montane forest habitats with nine other species also encountered only in lower and upper montane rainforest formations: the arboreal/terrestrial *Margaretamys parvus*, *Margaretamys elegans*, *Haeromys* n. sp., and *Eropeplus canus*; the terrestrial *Taeromys hamatus*, *Taeromys* n. sp., *Tateomys macrocercus*, *Tateomys rhinogradoides*, and *Melasmothrix naso*.

Bunomys andrewsi and *B. karokophilus* are terrestrial elements of tropical lowland ever-green rain forest, which along my transect includes eight other species collected only from habitats in lowland forest: the arboreal/terrestrial *Margaretamys beccarii*, *Haeromys minahassae*, and *Taeromys celebensis*; the terrestrial *Maxomys* n. sp., *Maxomys hellwaldii*, *Crunomys celebensis*, *Echiothrix centrosa*, and *Lenomys meyeri*.

The range of *Bunomys chrysocomus* overlaps those of all the other species encountered except for seven occurring in montane forest above about 1500 meters: *Eropeplus canus*, *Melasmothrix naso*, the two species of *Tateomys*, *Haeromys* n. sp., and two species of *Margaretamys*.

Ranges of all four species of *Bunomys* cover the altitudinal distributions of four species occurring throughout my transect area. The terrestrial *Maxomys musschenbroekii* and *Rattus hoffmanni*, and the arboreal/terrestrial *Rattus facetus* and *Paruromys dominator* occupy forests extending from lowlands to the summit of Gunung Nokilalaki.

TABLE 79

Dietary Categories of Murines Collected along My Transect in the West-Central Region[a]

	Fruit	Fruit, ferns	Fruit, leaves, ferns, insects	Fruit, forbs, insects	Fruit, insects	Fruit, arthropods, snails, vertebrates	Fruit, arthropods, snails, earthworms, vertebrates	Fruit, arthropods, snails, earthworms, vertebrates, fungi	Mostly fungi	Insects	Insects, earthworms	Earthworms
Margaretamys parvus	—	—	—	+	—	—	—	—	—	—	—	—
Margaretamys elegans	—	—	—	+	—	—	—	—	—	—	—	—
Margaretamys beccarii	—	—	—	—	—	+	—	—	—	—	—	—
Taeromys hamatus	+	—	—	—	—	—	—	—	—	—	—	—
Taeromys n. sp.	+	—	—	—	—	—	—	—	—	—	—	—
Taeromys callitrichus	—	+	—	—	—	—	—	—	—	—	—	—
Taeromys celebensis	+	—	—	—	—	—	—	—	—	—	—	—
Maxomys dollmani	—	—	—	—	—	—	+	—	—	—	—	—
Maxomys n. sp.	—	—	—	—	—	—	+	—	—	—	—	—
Maxomys hellwaldii	—	—	—	—	—	—	+	—	—	—	—	—
Maxomys muschenbroekii	—	—	—	—	+	—	—	—	—	—	—	—
Rattus hoffmanni	+[b]	—	—	—	—	—	—	—	—	—	—	—
Rattus facetus	+[c]	—	—	—	—	—	—	—	—	—	—	—
Paruromys dominator	+[b]	—	—	—	—	—	—	—	—	—	—	—
Crunomys celebensis	—	—	—	—	—	—	—	—	—	+	—	—
Echiothrix centrosa	—	—	—	—	—	—	—	—	—	—	+	—
Haeromys n. sp.	+[d]	—	—	—	—	—	—	—	—	—	—	—
Haeromys minahassae	+[d]	—	—	—	—	—	—	—	—	—	—	—
Tateomys macrocercus	—	—	—	—	—	—	—	—	—	—	—	+
Tateomys rhinogradoides	—	—	—	—	—	—	—	—	—	—	—	+
Melasmothrix naso	—	—	—	—	—	—	—	—	—	—	+	—
Eropeplus canus	—	—	+	—	—	—	—	—	—	—	—	—
Lenomys meyeri	—	—	+[e]	—	—	—	—	—	—	—	—	—
Bunomys penitus	—	—	—	—	—	—	—	+	—	—	—	—
Bunomys chrysocomus	—	—	—	—	—	—	+	—	—	—	—	—
Bunomys karokophilus	—	—	—	—	—	—	—	—	+[f]	—	—	—
Bunomys andrewsi	—	—	—	—	—	—	+	—	—	—	—	—

[a] Composition of diets was determined by examining contents of stomachs and by recording the kinds of foods accepted or rejected by captive rats.

[b] *Rattus hoffmanni* and *Paruromys dominator* have been photographed visiting bird nests on the ground and in shrubby habitat and are claimed to be egg predators (Pangau-Adam et al., 2006).

[c] *Rattus facetus* shows individual variation in food preference. One captive ate fruits and voraciously consumed insects, but all other captives consumed only fruit and ignored insects and other kinds of invertebrates; only remains of fruit was found in stomachs.

[d] Diet is primarily seeds, some fruit pulp.

[e] *Lenomys meyeri* is also coprophagous, the only murid on Sulawesi with this dietary convention.

[f] While fruit, insects, earthworms, snails, and small frogs are occasionally eaten, the ear fungus *Auricularia delicata* is the primary food of *Bunomys karokophilus* (see table 13).

Small samples of *Maxomys dollmani* and *Taeromys callitrichus* were trapped in lower evergreen and lower montane rainforest formations where their ranges overlap those of *Bunomys chrysocomus* and *B. karokophilus* in lowland forest and *B. penitus* in montane habitats.

Kuala Navusu

We selected this lowland site because habitats at elevations below about 200 m along the transect in the west-central mountain block had largely been transformed from primary forest to anthropogenic landscapes: palm plantations, secondary forest, scrub, agricultural fields, and villages.

We collected 10 species of murines in primary tropical lowland evergreen rain forest on the coastal plain at Kuala Navusu between 30 and 300 m (figs. 107, 108; table 80). The assemblage includes the range in body size represented by the small *Haeromys minahassae* and large *Paruromys dominator*, both terrestrial and arboreal/terrestrial species, and the variety of diets and other natural history information similar to that recorded for the species collected in lowland forest on the transect in the west-central mountain block.

Another lowland camp was established about 25 km south of Kuala Navusu and farther inland on the Sungai Tolewonu where we trapped in primary forest between 137 and 336 m (see the map in fig. 5). We encountered the same species as found at Kuala Navusu except for *Bunomys andersoni*, *Echiothrix centrosa*, and *Haeromys minahassae.* Because the inventory of species trapped is more complete for Kuala Navusu (*B. andrewsi* was caught there and not at Sungai Tolewonu) my focus will be on that area.

My experience drawn from study of specimens from throughout central Sulawesi indicates the inventory of species from Kuala Navusu to be a realistic assessment of the murine community found in lowlands of the northeast-central region of Sulawesi's core. I had expected to collect only two others, *Taeromys punicans* and *Lenomys meyeri.* *Taeromys punicans* was taken by H.C. Raven in lowland forest at Pinedapa (30 m) south of Kuala Navusu in the northeast-central region and I was disappointed that we did not

encounter it in our survey. *Lenomys meyeri* is represented by samples obtained on the northern peninsula, the core of Sulawesi, and the southwestern peninsula, but except for the series from the southwestern peninsula, sample sizes are generally small (one or two individuals). Specimens come from lowlands and middle elevations, mostly in tropical lowland evergreen rain forest. The exception is again on the southwestern peninsula where modern material was collected in montane habitats on Gunung Lompobatang and subfossils are from the coastal lowlands. The species is not easily trapped and although I anticipated encountering it I was not surprised with the futile results of our trapping efforts.

While four species of *Bunomys* are found along my transect in the west-central mountain block, only *B. andrewsi* lives in the lowland forest habitats at Kuala Navusu. At the time I of course did not expect to trap *Bunomys penitus* in lowland forest, but did think we would encounter *B. chrysocomus* and *B. andrewsi*, and would not have been surprised to come across *B. karokophilus.* But the occurrence of only *B. andrewsi* now makes sense in light of the ranges for the different *Bunomys* documented in this report. In the core of Sulawesi, *Bunomys chrysocomus* appears to be absent from forest habitats at elevations lower than about 300 m (see that account and table 6). *Bunomys karokophilus*, judged by collection localities of samples from the current study, and its absence from older collections made in regions outside of the west-central mountain block, may be endemic to that latter region. *Bunomys andrewsi*, by contrast, ranges from 30 to 1600 m (table 5) and, based on reliable provenances of modern specimens from Sulawesi's core and the southeastern peninsula, appears to be the only species of *Bunomys* found at elevations lower than about 300 m (see account of *B. andrewsi* and table 5). Our trapping results at Kuala Navusu reflect that singular lowland occurrence.

The following and final section inserts the eight species of *Bunomys* into a discussion and tabulation of the known generic and species diversity of murines endemic to mainland Sulawesi and some nearby islands.

BUNOMYS AND SULAWESI'S ENDEMIC MURINE FAUNA

Fifty-seven species of murines in 19 genera (14 of which are unique to Sulawesi), including eight species of *Bunomys*, are currently documented, either formally diagnosed or recognized as "n. sp." but not yet described, as occurring in the Sulawesi region and nowhere else (table 81). One species is represented only by a subfossil, 10 by subfossils and modern samples, and the remainder by modern specimens. With the exception of two species endemic to Pulau Peleng in Kepulauan Banggia off the coast of the eastern peninsula (see fig. 1), and one known only from Pulau Sangihe in Kepulauan Sangihe north of the northeastern tip of Sulawesi, nearly all species are recorded only from mainland Sulawesi.

I provide this tabulation of species and general distributions, both regional and associated with forest formations, as a summary of the endemic murine fauna in which the species of *Bunomys* are a part. The list of species and number of genera will certainly be augmented, and the geographic distributions of some altered by results gained from present and future surveys of small mammals in targeted regions of Sulawesi, and by future revisionary studies incorporating anatomical and morphometric characters in concert with DNA sequences.

Particular species of *Bunomys* show restricted geographic ranges and join species in other genera equally confined to form faunal units that are characteristic of particular geographic regions. It is worthwhile to summarize those endemic units here as well as other items of interest. Relationships and distributions presented below are supported by the published results cited in table 81 and the accounts of the various species of *Bunomys* that has formed the focus of the present report.

NORTHEASTERN SEGMENT OF THE NORTHERN PENINSULA: *Bunomys fratrorum* joins *Echiothrix leucura*, *Taeromys taerae*, *Rattus xanthurus*, and *Rattus marmosurus* in a faunal cluster known only from the northeastern end of the northern peninsula generally east of the Gorontalo region (00°31′N, 123°03′E), endemic faunal regions labeled "North-east" and

"North Central" by Evans et al. (2003a). As indicated by morphometric traits, the closest phenetic relatives of *B. fratrorum* are *B. andrewsi*, *B. penitus*, and *B. karokophilus,* n. sp., which have been documented only from Sulawesi's core, and the eastern, southeastern (including Pulau Buton), and southwestern peninsulas. *Bunomys chrysocomus* is the only other *Bunomys* occurring east of Gorontalo, where it is sympatric with *B. fratrorum*, but it also ranges west of Gorontalo on the northern peninsula and south throughout much of Sulawesi (see the account of *B. chrysocomus*). Phenetic allies of *B. chrysocomus*, at least as indicated by cranial and dental morphometrics, include three montane endemics: *B. prolatus* from Gunung Tambusisi at the western margin of the eastern peninsula, *B. torajae* from Gunung Gandangdewata in the Mamasa region, and *B. coelestis* from Gunung Lampobatang on the southwestern peninsula.

The other endemic northeastern murids have allied equivalents found west of Gorontalo. *Echiothrix centrosa* extends from the northern peninsula west of Gorontalo to the core of the island (Musser and Durden, 2014). *Taeromys hamatus* is the montane relative of *T. taerae* and has been documented only from the west-central mountain block (Musser and Carleton, 2005). *Rattus facetus* is the counterpart of *R. xanthurus* and *R. marmosurus* and ranges through the northern peninsula west of Gorontalo to the core of the island and the eastern peninsula. It is the only species of the *Rattus xanthurus* group (which also includes *R. salocco* from the southern part of the southeastern peninsula, *R. bontanus* from the southwestern peninsula, and the insular *R. pelurus* and the undescribed species from Kepulauan Sangihe) found within its range (Musser and Carleton, MS.). Recent publications contend that both *R. xanthurus* and *R. marmosurus* occur together in the Lore Lindu area of the west-central region (Maryanto and Yani, 2003; Maryanto et al., 2009; Weist et al., 2010), but this view is incorrect and based on misidentifications.

EASTERN PENINSULA: *Bunomys prolatus* and *Maxomys wattsi* are montane endemics documented only from Gunung Tambusisi at the western end of the eastern peninsula

Fig. 107.   Terrestrial habitat: forest at Kuala Navusu (30 m) where in 1975 on the ground we trapped *Bunomys andrewsi*, *Maxomys hellwaldii*, *Rattus hoffmanni*, *Paruromys dominator*, and *Echiothrix centrosa*. The *Planchonia valida* shown here is among the several species of grand old-growth trees forming the upper canopy and attest to the primeval integrity of the forest. Alcoves between buttresses were productive places to trap *Maxomys hellwaldii*. The palm *Licuala celebica* with its broad frons provides contrasting shape and texture to the understory.

Fig. 108.   Arboreal habitat: woody vine on which we trapped the arboreal *Margaretamys beccarii* at Kuala Navusu (108 m) in 1975. Vine is about 15 ft above ground and part of a cluster that loops across a rocky streambed concealed by dense understory growth along each side of the stream with a few scattered canopy and emergent trees. The palms *Licuala,* young *Livistona*, *Pinanga*, and rattan are common. Slopes are steep and rocky. The forest is a mixture of primary growth along with dense secondary growth and scrub covering old landslips and streamside washouts. *Rattus facetus* and *Haeromys minahassae* were also trapped on woody vines in the understory of nearby intact forest.

TABLE 80
Bunomys andrewsi and the Other Murines Collected in the North-Central Lowlands at Kuala Navusu in Primary Lowland Tropical Evergreen Rain Forest (August-November, 1975)
The ecological and reproductive information tabulated in tables 77 and 78 also applies to the species listed here. Magnitude of external measurements and body mass listed in table 76 is similar for these species.

Species	N	Elevational range (m)	Terrestrial	Arboreal/Terrestrial
Margaretamys beccarii	4	43–122	—	+
Taeromys celebensis	3	61–152	—	+
Maxomys hellwaldii	300	30–300	+	—
Maxomys musschenbroekii	1	122	+	—
Rattus hoffmanni	18	30–214	+	—
Rattus facetus	3	122–152	—	+
Paruromys dominator	68	30–300	—	+
Echiothrix centrosa	8	30–122	+	—
Haeromys minahassae	9	76–152	—	+
Bunomys andrewsi	**21**	**30–122**	**+**	—

(Musser, 1991). Whether both range farther east in montane forest along the mountainous backbone of that peninsula is not known. Collections from surveys made elsewhere on Sulawesi have not encountered either species. Claimed exceptions are the reported identifications of specimens collected during a survey of small mammals in Lore Lindu National Park—in the northern portion of the west-central mountain block—which included supposed examples of *B. prolatus* and *M. wattsi* (Maryanto and Yani, 2003; Maryanto et al., 2009). However, the specimens upon which the identifications are based need to be reexamined. No other collector working in the Lore Lindu area has encountered either species. I lived at several camps in the forest in what is now Lore Lindu, minimally for a month at each place, and longer at other sites, and never trapped either *B. prolatus* or *M. wattsi* (see fig. 103). Chris Watts collected the samples of *B. prolatus* and *M. wattsi* and wrote me how easy they were to trap on Gunung Tambusisi; one would expect similar trapping responses in Lore Lindu if the species occurred there.

An undescribed species of *Maxomys* identified by mtDNA sequences has been discovered on Gunung Tompotika at the eastern end of the eastern peninsula (Achmadi et al., 2013) and may be another peninsular endemic found in that endemic region labeled "East Central" by Evans et al. (2003a). The Tompotika area has also yielded samples of

Maxomys muschenbroekii that prove to be a geographic haplogroup (derived from mtDNA) distinct from haplogroups identified from the southeastern peninsula and west-central mountain block (Achmadi et al., 2013).

WEST-CENTRAL MOUNTAIN BLOCK: Twenty species of murids are currently documented as occurring only in the valleys and mountains of the west-central region in Sulawesi's core (see table 65), the western portion of the what Evans et al. (2003a) define as the "West Central" endemic area, which for them embraces the entire core of Sulawesi. *Bunomys karokophilus* is one of four (*Crunomys celebensis*, an undescribed shrew rat, and *Maxomys* n. sp. are the other four) found only in tropical lowland evergreen rainforest habitats. Some of these lowland species may have a broader range in the west-central mountain block than is currently indicated by available samples. *Bunomys karokophilus*, for example, is documented by voucher material only from my transect in the Lore Lindu area, the undescribed shrew rat is represented by a sample only from the Mamasa region (K.C. Rowe, in litt., 2012). *Crunomys celebensis* has been collected in the northern and southern areas of the west-central mountain region (Musser, 1982; K.C. Rowe, in litt., 2012) and it may extend beyond this western landscape to other territory in Sulawesi covered by tropical lowland evergreen rain forest. The species of *Maxomys* may be restricted to the

drainage basin of Danau Lindu (Musser, MS.).

Five (*Sommeromys macrorhinus*, *Eropeplus canus*, *Tateomys macrocercus*, *Haeromys* n. sp., and *Paucidentomys vermidax*) are primarily montane but have been recorded from the narrow transition between lowland tropical evergreen rainforest and montane forest formations; one (*Maxomys dollmani*) ranges from middle elevations in lowland evergreen rain forest into lower montane forest habitats.

Eleven species in seven genera (*Margaretamys*, *Tateomys*, *Melasmothrix*, *Taeromys*, *Bunomys*, *Waiomys*, and one undescribed genus) are documented from habitats in montane forests. The representative for *Bunomys* is *B. torajae*, which has been recorded only from montane forest on Gunung Gandangdewata in the Mamasa region. *Bunomys penitus* is also confined to montane habitats in the west-central mountain block, but also occurs outside of that region in the Mekongga highlands on the southeastern peninsula.

The species recorded so far only in tropical lowland evergreen and montane forests in the west-central mountain block are probably not equally distributed throughout this broad region. For example, some of the species encountered in the Mamasa area in the southern portion of the west-central mountain block are not represented in material collected from other landscapes in that region. *Sommeromys macrorhinus* and *Paucidentomys vermidax* have been encountered only in the southern highlands of the west-central mountain block, as have the amphibious *Waiomys mamasae*, an undescribed shrew rat, a new genus related to *Eropeplus*, a new species of *Taeromys*, and *Bunomys torajae* (Esselstyn et al., 2012; K.C. Rowe, in litt., 2012; Rowe et al., 2014; this report). The southern ramparts of the west-central region, especially the mountain landscapes, may comprise an endemic subunit within the broader west-central mountain block.

In the northern portion of the west-central region, the distribution of *B. karokophilus* is parapatric in relation to the lower-elevation distribution of *B. andrewsi* and to the montane range of *B. penitus*, but syntopic with *B. chrysocomus* (see those four accounts of species).

PEGUNUNGAN MEKONGGA: *Margaretamys christinae*, *Maxomys* n. sp., *Taeromys microbullatus*, and *Taeromys arcuatus* are endemic to the Mekongga range in the southern portion of the southeastern peninsula, an endemic area labeled "Southeast" by Evans et al. (2003a). *Rattus salocco* has also been collected on Pegunungan Mekongga and in nearby lowlands. Of the *Bunomys*, lowlands surrounding the mountain range are occupied by *B. andrewsi*, lowland (but not below 300 m) and mountain habitats have yielded samples of *B. chrysocomus*, and montane forest on Mekongga contains *B. penitus*.

The five endemic species have counterparts elsewhere on Sulawesi. *Margaretamys christinae* is related to the montane *M. parvus* and *M. elegans* endemic to the west-central mountain block, and *M. beccarii* in the lowlands of the southeastern peninsula, the core, and northern peninsula. *Taeromys microbullatus* is the Mekongga relative of *T. callitrichus*, found elsewhere in the west-central region and northeastern tip of the northern peninsula, and *T. arcuatus* is linked to two undescribed species in that genus represented by samples from the western part of the eastern peninsula and the west-central mountain block. *Maxomys* n. sp. is a close relative of *M. dollmani* from the west-central mountain block. *Rattus salocco* is the southwestern peninsular representative of *R. facetus* on the northern peninsula west of Gorontalo and Sulawesi's core. I would have expected the Mekongga *Bunomys penitus* to diverge from populations in the west-central mountain block, but, surprisingly, none of my analyses, which are based on external features (fur color and patterning, dimensions of appendages, color pattern of tail) and measurements obtained from the skull and molars, indicates the sample of this montane *Bunomys* on Pegunungan Mekongga to be anything more than another population of *B. penitus*—DNA sequences may provide the basis for a different interpretation.

Samples of *Maxomys musschenbroekii* from the Malili area at the northern end of the southeastern peninsula prove to be a geographic haplogroup (defined by analysis of mtDNA) distinct from haplogroups iden-

TABLE 81
Provisional List of Murines (19 genera, 57 species) Endemic to Sulawesi: Their Distributions in Different Regions on the Mainland, on Nearby Islands, and within Forest Formations[a]
Symbol and abbreviations: **+** = records of modern specimens; E = endemic to the particular region; S = Holocene subfossils; F = late Pliocene-early Pleistocene fossils; — = no record; L = tropical lowland evergreen rain forest, M = lower and upper montane rain forests.

Taxon	Northeast (east of Gorontalo)	Northern peninsula (west of Gorontalo)	Core	Eastern peninsula	South-eastern peninsula	South-western peninsula	Island	Tropical rainforest formation
Crunomys celebensis[b]	–	–	+[c]	–	–	–	–	L
Sommeromys macrorhinos	–	–	+[c]	–	–	–	–	M
Melasmothri naso	–	–	+[c]	–	–	–	–	M
Tateomys macrocercus	–	–	+[c]	–	–	–	–	M
Tateomys rhinogradoides	–	–	+[c]	–	–	–	–	M
Echiothrix leucura	E	–	–	–	–	–	–	L
Echiothrix centrosa	–	+	+	–	–	–	–	L
Paucidentomys vermidax	–	–	+[c]	–	–	–	–	M
Shrew rat A[d]	–	–	+[c]	–	–	–	–	L
Shrew rat B[d]	–	+	–	–	–	–	–	M
Waiomys mamasae	–	–	+[c]	–	–	–	–	M
Lenomys meyeri	+	+	+	–	S	+, S	–	L-M
Lenomys n. sp.	–	–	–	–	E, S	–	–	L
Haeromys minahassae	+	–	+	–	–	–	–	L-M
Haeromys sp.	–	–	+[c]	–	–	–	–	M
Maxomys musschenbroekii[e]	+	+	+	+	+, S	+, S	–	L-M
Maxomys species A[f]	–	–	–	–	+[g]	–	–	M
Maxomys dollmani	–	–	+[c]	–	–	–	–	L-M
Maxomys hellwaldii [h]	+	+	+	+	+, S	+, S	–	L
Maxomys species B[i]	–	–	+[c]	–	–	–	–	L
Maxomys species C[j]	–	–	+[c]	–	–	–	–	?
Maxomys species D[k]	–	–	–	+	–	–	–	?
Maxomys wattsi	–	–	–	+[l]	–	–	–	M
Margaretamys beccarii	+	–	+	–	–	–	–	L
Margaretamys elegans	–	–	+[c]	–	–	–	–	M
Margaretamys parvus	–	–	+[c]	–	–	–	–	M
Margaretamys christinae	–	–	–	–	+[g]	–	–	M
Bunomys chrysocomus	+	+	+	+	+	+, S	Pulau Buton	L-M
Bunomys coelestis	–	–	–	–	–	E	–	M
Bunomys prolatus	–	–	–	+[l]	–	–	–	M
Bunomys torajae	–	–	+[c]	–	–	–	–	M
Bunomys fratrorum	E	–	–	–	–	–	–	L-M
Bunomys andrewsi	–	–	+	+	+, S	+, S	Pulau Buton	L
Bunomys penitus	+	–	+	–	+	–	–	M
Bunomys karokophilus	–	–	+[c]	–	–	–	–	L
Paruromys dominator	+	+	+	+	+, S	+, S, F	–	L-M

TABLE 81
(*Continued*)

Taxon	Northeast (east of Gorontalo)	Northern peninsula (west of Gorontalo)	Core	Eastern peninsula	South-eastern peninsula	South-western peninsula	Island	Tropical rainforest formation
Eropeplus canus	−	−	+[c]	−	−	−	−	M
New genus + species [m]	−	−	+[c]	−	−	−	−	M
Taeromys celebensis	+	+	+	−	+, S	S	−	L
Taeromys taerae	E	−	−	−	−	−	−	L
Taeromys hamatus	−	−	+[c]	−	−	−	−	M
Taeromys arcuatus	−	−	−	−	+[g]	−	−	M
Taeromys callitrichus	+	−	+	−	−	−	−	L-M
Taeromys microbullatus	−	−	−	−	+[g]	−	−	M
Taeromys punicans[n]	−	−	+	−	S	S	−	L
Taeromys species A[o]	−	−	+	+	−	−	−	M
Taeromys species B[o]	−	−	+[c]	−	−	−	−	M
Rattus xanthurus	E	−	−	−	−	−	−	L
Rattus marmosurus	E	−	−	−	−	−	−	L-M
Rattus facetus[p]	−	+	+	+	S	−	Pulau Kabaena	L-M
Rattus salocco	−	−	−	−	E	−	−	L-M
Rattus bontanus	−	−	−	−	−	E, S	−	L-M
Rattus pelurus	−	−	−	−	−	−	Pulau Peleng[q]	L
Rattus n. sp.	−	−	−	−	−	−	Pulau Sangihe[q]	L
Rattus koopmani	−	−	−	−	−	−	Pulau Peleng[q]	L
Rattus hoffmanni	+	+	+	+	+, S	+, S	Pulau Lembeh, Pulau Malenge	L-M
Rattus mollicomulus	−	−	−	−	−	E	−	M

[a] Data are derived from published (Musser, 1981a, 1982, 1984, 1987, 1991; Musser and Holden, 1991; Downing et al., 1998; Musser and Carleton, 2005; Musser and Durden, 2002, 2014; Esselstyn et al., 2012; Mortelliti et al., 2012; Achmadi et al., 2013; Rowe et al., 2014), unpublished results of my research (MSS. in prep.), and unpublished information provided by other researchers (I am especially indebted to Jake Esselstyn, Kevin Rowe, and Anang Setiawan Achmadi for sharing with me results of their recent survey efforts in the west-central mountain block and elsewhere in Sulawesi).

The species tabulated here represent an incomplete inventory of Sulawesi's endemic murids. The number of species and genera will certainly increase through several inquiries: (1) Current surveys in different parts of Sulawesi have yielded samples of newly discovered genera and species, some listed in this table, and other new species likely await discovery in unsurveyed regions (such as the mountainous backbone of the eastern peninsula). (2) Voucher specimens of described species are now available providing tissue samples from which DNA can be extracted. Results from analyses of mitochondrial and nuclear DNA sequences will test the genetic integrity of species currently defined by morphological traits. Interpopulation variation consistent with gene flow within a single species will be demonstrated for some, the presence of distinct genetic lineages indicating genetic isolation among geographic populations will be revealed for others, which will result in an increase in number of species endemic to the island. (3) Some species now thought to be restricted to particular geographic regions of Sulawesi may be encountered in previously unsurveyed areas. (4) Finally, the ranges of some species will be expanded or restricted as a result of future survey work.

Indications of subfossils are from Holocene deposits. Samples from the southwestern peninsula were excavated from caves and rock shelters (Musser, 1984; present report; and Musser, MS.). Subfossils from the southeastern peninsula are from a cave (Gua Mo O'Hono) in the northern lowlands of the southeastern peninsula, north of the lakes district (Danau Matana, Mahalona, and Towuti). I am indebted to Philip Piper and Sue O'Connor for allowing me to include these unpublished records.

The single fossil record documents specimens from late Pliocene–early Pleistocene strata from the Walanae Formation on the southwestern peninsula (Downing et al., 1998).

[b] I originally assigned *celebensis* to *Crunomys*, a genus previously considered a Philippine endemic, based on morphological traits, particularly those expressed in the skull and dentition (Musser, 1982). Through the years I

TABLE 81
(*Continued*)

restudied all the available samples of *Crunomys*, including new Philippine material obtained by Larry Heaney and his colleagues, but could not detect any traits of *celebensis* that might show it to be a member of a monophyletic group separate from that containing the Philippine species. Recent analyses of DNA sequences support the cladistic monophyly of Philippine *C. melanius* and *C. suncoides* with Sulawesian *C. celebensis* (Achmadi et al., 2013; Marie Pages, *in litt.*, 2014). To date, *Crunomys* is the only murine genus recorded as endemic to both Sulawesi and the main Philippine archipelago (the backbone of the archipelago extending from Luzon to Mindanao, and excluding Palawan, nearby islands, and the Sula chain).

[c] Recorded to date only from the west-central mountain block (see fig. 1 and table 65).

[d] Kevin Rowe and Anang Setiawan Achmadi collected an undescribed shrew rat in tropical lowland evergreen forest on Gunung Gandangdewata in the west-central mountain block. Jake Esselstyn and colleagues are describing a new genus and species of shrew rat collected on Gunung Dako in the Toli Toli region.

[e] Results from analysis of mtDNA sequences has revealed three "distinct and geographically structured haplotypes (Achmadi et al., 2013), which correspond to previous designations of Areas of Endemism [see Evans et al., 2003a]." Whether any of these clades represent true *Maxomys muschenbroekii* with type locality in the northeastern end of the northern peninsula (east of the Gorontalo region) has yet to be assessed.

[f] The holotype of *dollmani* is from Rantekaroa (Bulu Karua), Pegunungan Quarles, in the west-central mountain block, and until the 1970s was the only specimen reported from that mountainous region. I had identified a sample of *Maxomys* collected by Gerd Heinrich from Pegunungan Mekongga on the southeastern peninsula as the same species (Musser, 1969), but that assessment is incorrect. Along my transect I collected a small series of a *Maxomys* exhibiting traits similar to the holotype of *dollmani*, and three specimens recently collected by J.L. Patton and his colleagues from Gunung Balease also closely resemble the holotype; these samples are from the west-central mountain block. Heinrich's collection from Pegunungan Mekongga is a distinct, undescribed, species endemic to that range but still more closely related to *M. dollmani* than to any other Sulawesian species of *Maxomys* (Musser, MS.). Recently, K.C. Rowe and Anang Setiawan Achmadi obtained one *M. dollmani* (KCR 1494) from Gunung Gandangdewata in Pegunungan Quarles.

[g] Known only from Pegunungan Mekongga.

[h] Whether the samples represent true *Maxomys hellwaldii* with type locality in the northeastern end of the northern peninsula (east of the Gorontalo region) has yet to be assessed. Results from analysis of external traits and morphometric data from skull and dental measurements in population samples (Musser, MS.) coupled with analyses of mtDNA sequences (Achmadi et al., 2013) suggest that *Maxomys hellwaldii* as listed here may prove to be more diverse in geographic genetic and phenetic structure, reminiscent of the diversity uncovered in populations of *M. surifer* and *M. whiteheadi* from mainland Indochina and islands on the Sunda Shelf, each previously considered as one species (Gorog et al., 2004).

[i] This undescribed species is based on a collection I made in the forested basin of Danau Lindu, 955–1000 m.

[j] A sample from Gunung Rorekatimbo in the northern part of the west-central mountain block, and identified as an undescribed species by analysis of mtDNA (Achmadi et al., 2013).

[k] Represented by a sample from Gunung Tompotika at the end of the eastern peninsula, and identified as an undescribed species by analysis of mtDNA sequences (Achmadi et al., 2013). The phenetic traits of specimens in this sample should be compared with *M. wattsi*, endemic to highlands at the western margin of the eastern peninsula.

[l] Samples have been collected only on Gunung Tambusisi at the western end of the eastern peninsula. *Maxomys wattsi* and *Bunomys prolatus* were recorded from Lore Lindu National Park in Sulawesi's core (Maryanto and Yani, 2003; Maryanto et al., 2009), but those records represent misidentifications (see account of *Bunomys prolatus*).

[m] An undescribed genus and species collected by Kevin Rowe and Anang Setiawan Achmadi on Gunung Gandangdewata in the Quarles Range and related to *Paruromys* and *Eropeplus*.

[n] Maryanto et al. (2009) regarded *T. punicans* to prefer mountain-top habitats in Lore Lindu National Park, but all correctly identified specimens of the species have been caught in tropical lowland evergreen rain forest. I did not encounter it in montane forest habitats during my trapping (see fig. 103) and neither have Jake Esselstyn, Kevin Rowe, and Anang Setiawan Achmadi working on other mountains.

[o] Species A is a large-bodied, long-eared, and shaggy-furred *Taeromys* found in lower montane forest that is related to *T. arcuatus* from Pegunungan Mekongga. Species B is the morphological counterpart of A and represented by specimens collected by Kevin Rowe and Anang Setiawan Achmadi on Gunung Gandangdewata in the Quarles Range.

[p] In previous publications, I have referred to this species, a member of the *Rattus xanthurus* group, as *R. xanthurus* (Musser, 1984; Musser, 1987; Musser and Carleton, 1993), *R. facetus* (Musser and Holden, 1991), or *Rattus marmosurus* (Musser and Carleton, 2005), occurring on the northern peninsula east and west of the Gorontalo region and in the mountains and lowlands of Sulawesi's core. But identification of the samples collected west of the Gorontalo region has always been ambiguous to me. In body size, the rats average larger than samples of *R. marmosurus* from the northeastern

TABLE 81
(*Continued*)

segment of the northern peninsula east of Gorontalo and smaller than examples of *R. xanthurus* from east of Gorontalo. A recent review of the *R. xanthurus* group by Michael Carleton and myself (MS.) confirms the view that *R. xanthurus* and *R. marmosurus* are confined to the northeastern segment east of Gorontalo with the remainder of the northern peninsula and central Sulawesi occupied by a separate species related to *R. marmosurus* for which the earliest available name is *facetus* (described by Miller and Hollister, 1921b, and based on a juvenile). *Rattus facetus* is the only member of the *Rattus xanthurus* group found in the core of Sulawesi. The records of *R. xanthurus* and *R. marmosurus* occurring in Lore Lindu National Park in central Sulawesi (Maryanto and Yani, 2003; Maryanto et al., 2009), assuming the specimens are members of the *R. facetus* group and not misidentified *Taeromys celebensis* or *Paruromys dominator*, are most certainly based on samples of *R. facetus*.

^{q} Endemic to the particular island.

tified on the eastern margin of the eastern peninsula and in the west-central mountain block (Achmadi et al., 2013).

SOUTHWESTERN PENINSULA: *Rattus bontanus*, a member of the *R. xanthurus* group, is restricted to the southwestern peninsula south of the Tempe depression (see fig. 1), distributed in forests clothing both lowlands and Gunung Lampobatang. That high volcano comprises the range of *Bunomys coelestis*, the only recorded species of *Bunomys* endemic to montane habitats on the southwestern peninsula, and *Rattus mollicomulus*, a relative of lowland *R. hoffmanni*. Of the *Bunomys*, *B. andrewsi* and *B. chrysocomus* are documented by samples from the peninsula, the former by subfossil and modern examples and the latter by only subfossil fragments. The only other known southwestern peninsular endemic appears to be a small-bodied species of *Lenomys* that is represented by a subfossil (Musser, MS.).

Evans et al. (2003a) define the southwestern peninsula as the "South-west" endemic area.

ELEVATIONAL DISTRIBUTIONS: Scanning table 81 reveals, based on identified voucher specimens, that some species have been taken only in tropical lowland evergreen rain forest, others occur only in montane forest habitats, and a few range through both lowland and montane forests. The distributions are summarized in table 82 with the species of *Bunomys* indicated in boldface (excluded are two undescribed species of *Maxomys* because I do not know the elevations at which the samples were collected).

ISLANDS: Two islands contain endemic species. *Rattus koopmani* and *R. pelurus* are endemic to Pulau Peleng in the Kepulauan Banggia. Represented by only the holotype, the relationship of *R. koopmani* to other species of *Rattus* is unclear; possibly it is most closely allied to *R. hoffmanni* from mainland Sulawesi (Musser and Holden, 1991), but additional samples of the Peleng rat, including DNA sequences, will have to be examined to test this hypothesis.

Rattus pelurus, endemic to Pulau Peleng, is a member of the *R. xanthurus* group. Pulau Sangihe, the largest island in Kepulauan Sangihe, is the home of an undescribed species of *Rattus* also related to those comprising the *R. xanthurus* group (Musser and Carleton, MS.).

Four species found on mainland Sulawesi also occur on nearby islands. *Rattus hoffmanni* extends to Pulau Lembeh, off the coast of the northeastern tip of the northern peninsula, and islands forming Kepulauan Togian, north of the eastern peninsula. *Bunomys andrewsi* and *B. chrysocomus*, both part of the mainland fauna, are documented from Pulau Buton off the southern coast of the southeastern peninsula. Three specimens I provisionally identify as *Rattus facetus* were collected by Andy Jennings from Pulau Kabaena near Pulau Buton.

ENDNOTES

Tikus abu-abuan, *Bunomys karokophilus*, is now formally described as a member of an evolutionary radiation containing minimally eight species that are endemic to Sulawesi. *Karoko*, the ear-fungus *Auricularia delicata*, is the primary food of the gray rat, and in this dietary specialization *B. karoko-*

TABLE 82
Elevational Summary of Sulawesi Murines according to Lowland or Montane Forest Formations

Tropical lowland evergreen rain forest	Tropical lowland evergreen and montane rain forests	Lower/upper montane rain forests
Crunomys celebensis	*Haeromys minahassae*	Shrew rat sp. B
Echiothrix leucura	*Lenomys meyeri*	*Sommeromys macrorhinos*
Echiothrix centrosa	*Maxomys musschenbroekii*	*Tateomys macrocercus*
Shrew rat sp. A	*Maxomys dollmani*	*Eropeplus canus*
Lenomys sp.	**Bunomys chrysocomus**	*Haeromys* sp.
Maxomys hellwaldii	**Bunomys fratrorum**	*Paucidentomys vermidax*
Maxomys species B	*Paruromys dominator*	*Melasmothrix naso*
Margaretamys beccarii	*Taeromys callitrichus*	*Tateomys rhinogradoides*
Bunomys karokophilus	*Rattus marmosurus*	*Waiomys mamasae*
Bunomys andrewsi	*Rattus facetus*	*Maxomys* species A
Taeromys celebensis	*Rattus salocco*	*Maxomys wattsi*
Taeromys taerae	*Rattus bontanus*	*Margaretamys elegans*
Taeromys punicans	*Rattus hoffmanni*	*Margaretamys parvus*
Rattus xanthurus		*Margaretamys christinae*
Rattus pelurus		**Bunomys coelestis**
Rattus n. sp.		**Bunomys prolatus**
Rattus koopmani		**Bunomys torajae**
		Bunomys penitus
		New genus and species
		Taeromys hamatus
		Taeromys arcuatus
		Taeromys microbullatus
		Taeromys species A
		Taeromys species B
		Rattus mollicomulus

philus may be unique among endemic Sulawesian murines. The montane *B. penitus* is also mycophagous, but it consumes a wider variety of different kinds of shelf fungi as well as an assortment of cap and stem fungi and an array of insects and other invertebrates (table 13). Mycophagy is not unknown among Indoaustralian murids, having been documented for some species of Australian murids (Claridge and May, 1994) and for the Papua New Guinean endemic *Protochromys fellowsi* (Musser and Lunde, 2009: 125), but until now has not been reported in Sulawesian murids. The other three species of *Bunomys* for which dietary information is available—*B. chrysocomus*, *B. andrewsi*, and *B. fratrorum*—do not consume fungi (see table 13); whether *B. coelestis*, *B. prolatus*, and *B. torajae* include fungi in their diets has yet to be determined.

Bunomys karokophilus has been characterized within a systematic review of *Bunomys* and it is one of eight species that I define within a context constrained by morphomet-

ric traits, elevational and geographic distributions, patterns of sympatry or parapatry, and some natural history attributes. No matter how illuminating the results of my inquiries documented in this report are, they signify only a first step in understanding the diversity of species in the *Bunomys* clade and thus represent an incomplete synthesis. Results of fieldwork that is now underway by researchers from several institutions are likely to uncover not only additional species of the genus but to also enhance knowledge of the distributions and biology of the eight species discussed in this review. Data derived from analyses of DNA sequences will test the integrity of some of the species defined by the phenetic traits described here. One example concerns whether or not *B. chrysocomus* and *B. andrewsi* (both with the most expansive geographic ranges over the island) are each a single species showing geographic variation in morphometric traits, or whether each actually consists of genetically separate geographic lineages representing several distinct

species— a distinct possibility in the case of *B. andrewsi*, the most geographically variable in morphometric traits of the two. Another example involves whether *B. penitus*, presently defined by cranial and dental morphometrics derived from material collected in montane forests in the west-central mountain block and Pegunungan Mekongga, is a single genetic entity or in reality consists of separate genetically isolated montane lineages.

Applying results from analyses of DNA sequences to reconstructing phylogenetic relationships among the species of *Bunomys* will test my results of kinship based on analyses of morphometric data. Within the *B. chrysocomus* group, I suspect that molecular evidence will confirm the close relationship between *B. chrysocomus* and *B. coelestis* that is presently indicated by data from external traits along with cranial and dental measurements. But will the montane *B. prolatus* and *B. torajae* prove to be close relatives as reflected by morphometric traits, or will either one or both instead be genetically more closely related to the montane *B. penitus,* or even be cladistically isolated from all other species of *Bunomys*? Within the *B. fratrorum* group, will *B. andrewsi* continue to be phyolgenetically aligned with *B. fratrorum*, *B. penitus*, and *B. karokophilus* (see fig. 21) or instead to *B. chrysocomus*, which it resembles in pelage coloration, ecological traits, and gross chromosomal composition? Will *B. karokophilus* remain closely allied with *B. fratrorum* or will it prove to be a closer relative of *B. penitus* since both are mycophagous? Finally, where will the morphologically distinctive *B. fratrorum* fit genetically within *Bunomys*? It is the only member of *Bunomys* that is endemic to the northeastern region of the northern peninsula, an area that was an island in the Pleistocene during periods when sea level was higher than at present; it occupies habitats in both tropical lowland and montane rain forests; and, compared with all the other species, it has a relatively longer skull, more flared zygomatic arches, narrower interorbit, higher braincase, wider zygomatic plate, greater postpalatal length, and smaller bullae.

To a future expansion of my systematic review of *Bunomys* should be added ecological studies that will provide more detailed results than the observations I have recorded. I report data bearing on habitat, diet, some aspects of reproduction and behavior for only the four species I encountered along my transect in the west-central mountain block and east of there in the Malakosa area. This information is informative but still incomplete, as the dietary records are available for only portions of a season, details about burrows and their conformation is lacking, the kinds of predators can be surmised but have yet to be documented, and data regarding reproductive biology is scanty. Except that the four other species of *Bunomys* unfamiliar to me in the field are terrestrial and diurnal, and inhabit both lowland tropical evergreen rain forest and montane forest (*B. fratrorum*) or only montane forests (*B. coelestis*, *B. prolatus*, and *B. torajae*), other facets of their ecologies are unknown to us.

Discovering *tikus abu-abuan* and its primary food, *karoko*, along dense and humid streamside forest has inspired an inquiry into the taxonomy of *Bunomys* as well as the natural history for some of the species. It is hoped that the results offered here will motivate other researchers to continue the probe and ultimately provide a more complete taxonomic and ecological portrait of *Bunomys*, a phylogenetic radiation of species unique to the forested landscapes of Sulawesi.

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A systematic review is incomplete without adequate illustration, and the figures included here represent the work of highly skilled and talented artists. The four species of *Bunomys* rendered in life poses in figure 6 reflect the artistic ability of Fran Stiles and her talent for transforming the three-dimensional live animal onto a two-dimensional image. All distribution maps, drawings of feet, the molar diagram in figure 11, some of the many graphs, and figure 103 are the work of Patricia Wynne, who as she usually does provided exceptionally fine pieces (read a tribute to her talents in Velazco et al., 2014). Photographic prints of skins, skulls, molar rows, and habitats were produced by Peter Goldberg, who over the years has consistently provided me with work of high quality that has significantly enhanced communication of my research results to readers. The maps in figures 3–5 were generated by Eric Brothers.

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Two sets of samples sent to me in the last two years proved to be of special interest. The first consisted of specimens from Gunung Balease and the Malili area that were collected by Jim and Carol Patton, Jake Esslestyn, Kevin Rowe, and Anang Achmadi; their efforts were funded by Jimmy A. McGuire, herpetologist at the Museum of Vertebrate Zoology (Berkeley). McGuire's funds came from Sulawesi National Science Foundation grant number DEB 0640967; specimens were collected under permits obtained via RISTEK and LIPI. The second contained material from the Mamasa region, primarily Gunung Gandangdewata, was collected by Esslestyn, Rowe, and Achmadi. They are grateful to Papa Daud and the local people of Mamasa for assistance with fieldwork; their research was supported by grants from the Australian and Pacific Science

Tom May, mycologist at the Australian National University, Canberra, kindly examined my fungal samples and provided the most recent scientific names to apply to the material.

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APPENDIX 1

HOFFMANN'S (1887: 20–21) DESCRIPTION OF *MUS CHRYSOCOMUS* IN THE ORIGINAL GERMAN

3. *Mus chrysocomus,* n. sp. (Fig. 1).

Diese nordcelebische Ratte ist noch um ein nicht geringes Stück kleiner als unsere Hausratte; sie stimmt bezüglich der Färbung soweit mit Mus rattus von dort überein, dass man sie auf den ersten Blick für ein junges Thier genannter Art halten könnte. das wesentlich Unterschieidende ist die Beschaffenheit des Schädels und des Pelzes.

Craniologisches: Da der hintere Theil des Schädels lädert ist, so gebe ich hier die Entfernung der knöchernen Nasenspitze vom Hinterrand der Parietalia; dieselbe beträgt 3,4 cm. Der Schauzentheil des Schädels ist sehr zugespitzt; dies beruht einmal darauf, dass die langen Nasalia und der Schnauzentheil am vordersten Ende sehr schmal sind, anderseits aber sind die seitlichen Jochbogenplatten selbst sehr weit nach hinten gerückt, während ihr Vorderrand schräg nach hinten aufsteigt. In Folge dessen liegt die obere Ansatzbrücke der Jochbögen und somit auch die Stelle, welche die geringste Breite des Schädels zwischen den Orbitalhöhlen bezeichnet, weiter von der Nasenspitze entfernt als bei allen übrigen Ratten. Die letztere Entfernung beträgt 2,07 cm, bei einer gleich grossen M. rattus aber nur 1,75 cm. Die Parietalia haben dieselbe Breite wie bei der erwähnten M. rattus, sie messen an der vorderen Naht 1,09 cm. Diese bildet eine zweimal gebrochene Linie, deren mittlerer Theil frontal gerichtet ist. Die beiden seitlichen Theile verlaufen schräg nach vorn. Die Orbitalleisten sind äusserst wenig entwickelt, doch bis zu den Occipitalia zu erkennen. Das Interparietale ist sehr schmal, seine Breite beträgt ungefähr 3/5 der Breite der beiden Parietalia. Die vorderen Gaumenlöcher endigen circa 1 mm vor der Basis der vordersten Backzähne, die hintere Gaumenöffnung beginnt nur sehr wenig hinter den letzten Backzähnen. Die Backzahnreihen sind 0,66 cm lang; die Zähne selbst sind breit, nehmen aber nach hinten zu mehr an Grösse ab als bei Mus rattus. Die Entfernung der vorderen beträgt 0,34 cm, und es divergiren die beiden Zahnreihen derart, dass die hintersten 0,41 cm von einander entfernt sind. Die bullae osseae sind 0,68 cm lang. Am Unterkiefer tritt das Wurzelende des Nagezahns nach aussen hervor und zwar genau unter der Basis des Kronfortsatzes; Condylus und Eckfortsatzt sind sehr schwach. In der allgemeinen Gliederung stimmen die oberen Zähne ebenso wie diejenigen des Unterkiefers mit den Zähnen von Mus decumanus überein. Als unterscheidend kann gelten, dass die Innenhöcker der ersten beiden oberen Zähne mehr zurückliegen als bei M. decumanus. Die Bildung der Nebenhöckerchen am Unterkiefer ist wie bei M. rattus, nur sind sie im Allgemeinen etwas kleiner

und derjenige von der ersten Lamelle des dritten Zahns liegt mehr nach innen zu auf der Vorderseite der Lamelle.

Aeussere Kennzeichen: Kopf und Körper messen 17½ cm, Schwanz 12½ cm lang mit circa 190 Schuppenringen. Vorderfüsse incl. Unterarm 4cm, Hinterfüsse 3,2 cm lang. Sohle der Hinterfüsse schmal, Schwielen länglich, hinten zugespitzt, jederseits eine am Grunde der Mittelzehe, je 1 unter der ersten, je 2 unter der 5. Zehe; in der Mitte der Sohle noch eine schmale weit herabsteigende Schwiele. Der Pelz ist lang, dicht, sehr weich und glatt anliegend. Der Rücken hat schön hellbraune Färbung, wenig heller als bei Mus rattus, mit einem Schein nach Golgelb; doch gelangt auch eine tiefbraune, fast schwarze Färbung, welche bei den meisten übrigen Ratten und Mäusen mehr in den Hintergrund tritt, hier zu nicht geringer Ausdehnung. nach den Seiten zu verschwindet die schwärzliche Färbung; mit dem Hellbraun, das ebenfalls in etwas höhere Töne übergeht, verbindet sich an ihrer Statt eine bräunlich- bis rein neutralgraue Färbung, welche jedoch nicht so ausgedehnt ist, wie die dunkle des Rückens, vielmehr sehr zurücktritt. Die Unterseite des Körpers ist fahlgelb, hinten etwas heller als vorn gefärbt und gegen die Färbung der Körperseiten wenig scharf abgesetzt. Die hellgraue Färbung des Haargrundes macht sich vielfach geltend. An dem vorliegenden Examplare zeigt die Unterseite mehrere gelbumsäumte und regellos verstreute rostbraune Flecke. Kopf wie Rücken braun, nach vorn und nach den Seiten zu etwas in Fahlgelb übergehend. Vorder- und Hinterfüsse sind mit dunkelgraubraunen, weisslich glänzenden Härchen besetzt.

Die sehr dünnen Wollhaare sind in der Mittellinie des Rückens in den unteren 2/3 Theilen dunkel neutralgrau gefärbt, das obere Drittheil ist wenig verbreitet und fast völlig dunkelbraunschwarz, indem nur die äusserste Spitze auf ungefähr 1— ½ mm hellbraun ist, was einmal bei der grossen Länge der Wollhaare (zwischen 1,6 und 1,8 cm) sehr auffällt, wodurch aber zugleich die allgemeine Färbung des Rückenpelzes erklärt wird. Stachelhaare finden dieser Maus vollständig. Die Borstenhaare sind schwer von dem Wollhaaren zu trennen. Ihre zahl ist verhältnissmässig gering; sie zeichnen sich nur dadurch aus, dass sie völlig gerade und im vorderen Theil bis zur äussersten Spitze dunkel braunschwarz gefärbt sind. Im Uebrigen sind sie die Wollhaaren sehr ähnlich; auch ihre Länge ist kaum different, indem kein Borstenhaar von über 1,9 cm Länge vorkommt. Nach den Seiten zu wird an den Wollhaaren zunächst der sehr dunkle Theil heller, indem er in Grau übergeht, andreseits aber gewinnt die hellbraune Spitze bedeutend an Ausdehnung. Die Borstenhaare fallen allmählich ganz weg.

Der circa 12½ cm lange Schwanz zählt ungefähr 190 Schuppenringe, zwischen denen ziemlich viele dunkle Härchen stehen; letztere sind über den ganzen gleichmässig verbreitet.

APPENDIX 2

MEYER'S (1899:24–25) ACCOUNT OF *MUS CALLITRICHUS* IN THE ORIGINAL GERMAN

35. *Mus callitrichus* Jent.
Tafel VII Fig. 1. Nat. Grösse [1])

Mus callitrichus Jentink 1879 T. Ned. D. Ver. IV pl. LV (" 6 [0] ") und LVI (" 5 [0] " err., = meyeri) id. 1879 NLM I, 12; Thomas 1896 AMNH. (6) XVIII, 246; Trouessart 1897 Cat. Mam. 479.

Mus callithrichus (*th* laps. aut em. err.) Jentink 1887 Cat. MPB. IX 212; id. 1888 ib. XII, 65; id. 1890 Webers Zool. Erg. I, 120 Tab. X, 4—6 (*Schädel*); id. 1893 III, 78; Weber 1894 ib. 474.

Mus chrysocomus ("n. sp. 3 [0] " Jentink 1879 T. Ned. D. Ver. IV p. LVI); B. Hoffmann 1887 Abh. Ber. Dresd. 1886/7 Nr. 3 p. 20, Tafel Fig. 1 a—f (*Schädel*); Thomas 1895 AMNH. (6) XVI 163 und 1896 XVIII, 247; Trouessart 1897 Cat. Mam. 485; Thomas 1898 TZS. XIV, 403.

Mus fratrorum Thomas 1896 AMNH. (6) XVIII, 246; Trouessart 1897 Cat. Mam. 485.

   a, b. fem., in Spiritus, Tomohon, Minahassa, Nord Celébes, III und IV 94.

   c. mas juv., in Spiritus, Tomohon, III 94.

   d., e. fem. juv., in Spiritus, Tomohon, III 94.

Als Hoffmann 1887 *M. chrysocomus* beshrieb, besass das Dresdener Museum kein Exemplar von *callitrichus*, er war auf Jentinks Beschreibung angewiesen. 1894 trafen aber 4 Exemplare ein, die Dr. Jentink die Güte hatte, mit seinen Typen zu vergleichen und als solche zu bestimmen, man kann daher an ihrer Identität nicht zweifeln, trotzdem die Beschreibung der Art (NLM. 1879 I, 12) nicht so zutreffend und genügend ist, dass sie danach allein sicher erkannt werden könnte. Zwischen dem einzig vorhandenen Typus von *chrysocomus* und den mir nun vorliegenden Exemplaren von *callitrichus* kann ich aber keine irgendwie wesentlichen Unterschiede constatiren, sowenig wie zwischen *M. fratrorum Thos.* (wovon das Dresdener Museum 2 von Thomas bestimmte Exemplare besitzt) und *callitrichus*. Dieser sagt (AMNH. XVIII, 247) dass *fratrorum M. chrysocomus* sehr nahe stahe, aber durch Grösse, geperlte Supraorbitalränder und mächtigere Molaren unterschieden sei, allein die Schädel der zwei mir vorliegenden Exemplare zeigen diese Perlung nicht, sondern haben scharfe Ränder wie gewöhnlich; Grösse und mächtigere Molaren können als Artunterschiede, in Ansehung der bedeutenden Differenzen der Exemplare nach Alter und Geschlecht, nicht angesehen werden.

Jentink identificirte ferner einen Schädel ohne Unterkiefer von Parepare, Süd Celébes (Webers Zool. Erg. I, 120) mit *callitrichus* und sagt, dass es sehr leicht sei, die Art nur nach dem Schädel zu unterscheiden, unterlässt es aber die unterscheiden Charakter anzugeben; er verweist nur auf einige Abbildungen zum Vergleiche (Cat. MPB. IX Pl. 7, Zool. Erg. Tab. X), die aber hierfür, in Ansehung der beträchtlichen Unterschiede nach Alter und Geschlecht und wegen der nicht hinlänglich deutlichen Details an den Zähnen, nicht genügen. Ich halte eine solche Identificirung für unsicher und möchte erst weiteres Material von Süd Celébes abwarten, so wenig ich die Möglichkeit des Vorkommens von *M. callitrichus* in Süd Celébes in Abrede stellen will.

Endlich hat Thomas neuerdings (TZS. XIV, 403) *M. chrysocomus* vom Berge Data, Lepanto, Nord Luzon, von 8000 Fuss Höhe aufgeführt und bemerkt, dass die Art von fast allen anderen der Gattung durch das völlige Fehlen der scharfen Supraorbitalränder unterschieden sei. Ein von Thomas bestimmtes, ebenfalls männliches, ziemlich adultes Exemplar im Dresdener Museum von demselben Fundorte zeigt am Schädel ebensowenig scharfe Supraorbitalränder, während der Typus von *chrysocomus* von Nord Celébes, ein noch junges Exemplar, diese deutlich markirt hat, wie auch aus der Hoffmannschen Abbildung ersichtlich ist, und wie es der von mir angenommenen Identität mit *callitrichus* entspricht. Da nun ausserdem das Exemplar von Luzon einen viel weicheren und nicht so lebhaft gefärbten Pelz hat wie *callitrichus* (und *chrysocomus*) und noch andere kleine Unterschiede aufweist, so möchte ich, auch unter Berücksichtigung des entlegenen und hohen Fundortes, trotz notorisch vorhandener Aehnlichkeiten, die Identität nicht vertreten und nenne die Exemplare von Berge Data: **Mus datae**. Erst bei einer weit besseren Kenntniss der Mäuse dieser Gegenden, die wohl noch lange auf sich warten lassen wird, kann man zu einer klareren Einsicht, als es jetzt möglich ist, gelangen.

Was die speciellen Fundorte von *M. chrysocomus* auf Celébes angeht, so ist die Art im Norden aus der Minahassa registrirt von Manado, Langowan, Kakas (Mus. Leid.), Tomohon (Sarasins), Lotta (Mus. Dresd.), Rurukan 3500 Fuss hoch ("*fratrorum*" Brit. Mus. und Mus. Dresd.), Amurang ("*chrysocomus*" Mus. Dresd.); im Süden von Parepare, welcher letztere Fundort aber meiner Ansicht nach noch der Bestätigung bedarf.

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[1] Die goldige Ringelung der einzelnen Haare konnte auf der Abbildung (mit Handkolorit) wiedergegeben werden.