AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3001, 41 pp., 22 illustrations, 7 tables March 7, 1991

Sulawesi Rodents: Descriptions of New Species of *Bunomys* and *Maxomys* (Muridae, Murinae)

GUY G. MUSSER[1]

ABSTRACT

Bunomys prolatus, new species, and *Maxomys wattsi,* new species, are described and contrasted with their Sulawesian relatives. The two new rats were collected in montane forest on Gunung Tambusisi (1°38′S, 121°23′E), which is part of the highlands at the western end of the eastern peninsula of central Sulawesi. Morphology of the new *Bunomys* resembles that of *B. chrysocomus* (which occurs throughout the island except on the southwestern peninsula) as well as *B. coelestis* (known only from the southwestern arm of Sulawesi). The new *Maxomys* is characterized by a distinctive suite of characters and is morphologically unlike any other described species in the genus that is endemic to Sulawesi. It is sympatric with *M. musschenbroekii.* Cladistic associations of each species will be examined in a report now being prepared describing the species diversity and phylogenetic relationships within both *Bunomys* and *Maxomys.*

INTRODUCTION

About 30 percent of the total Sulawesian mammalian fauna and about 52 percent of all the endemics consist of species in the rodent subfamily Murinae (of the family Muridae, as defined by Carleton and Musser, 1984). Descriptions, of varying utility, are available for most of the murine fauna (see the references in Musser, 1987), but some species, discovered within the last 10 to 15 years, have yet to be described and diagnosed. Documenting a new species of *Bunomys* and a new kind of *Maxomys,* both of which are known by small samples collected from only one small highland region in central Sulawesi, is my purpose in this report. I had originally intended to include these ac-

[1] Archbold Curator, Department of Mammalogy, American Museum of Natural History.

 ISSN 0003-0082 / Price $5.40

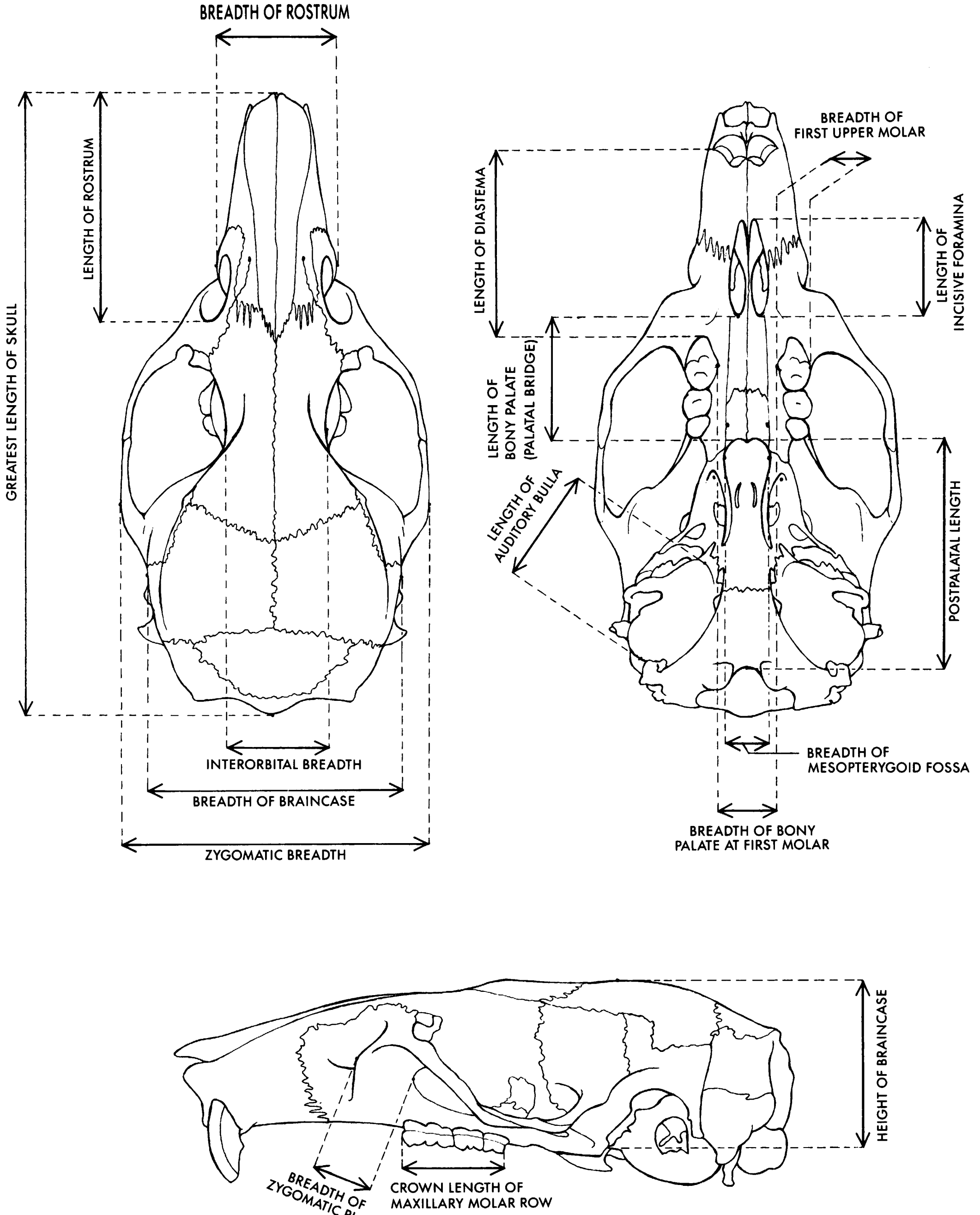

Fig. 1. Views of cranium and molars of an adult *Bunomys chrysocomus* showing limits of cranial and dental measurements. See text for abbreviations and additional information.

counts in a systematic revision of those two genera but that project is taking longer than I had anticipated and the descriptions of the two new rats have to be published now because they are host species of ectoparasites that are also being described as new taxa (Durden and Musser, 1991).

In the following pages, I describe and diagnose the new species of *Bunomys*, then the new *Maxomys*. Cladistic relationships of each

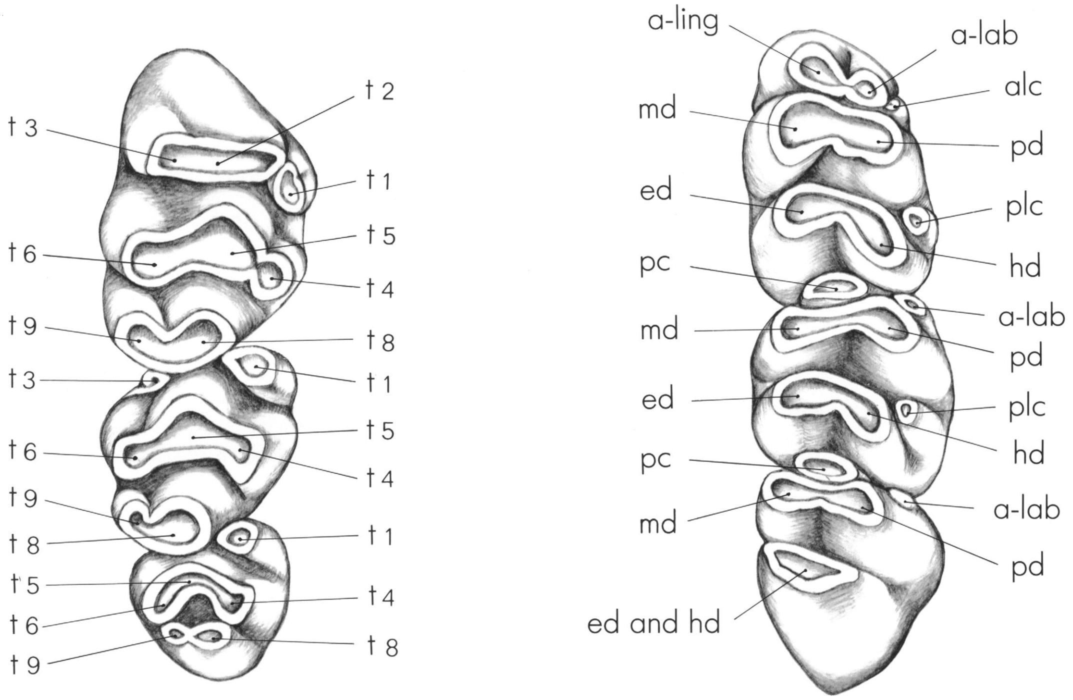

Fig. 2. Diagram of upper (left) and lower (right) molars from right side of *Bunomys chrysocomus* illustrating structural terms. **Upper molars:** cusps are numbered according to Miller's (1912) scheme and referred to in the text with the prefix t. **Lower molars: a-lab,** anterolabial cusp; **a-ling,** anterolingual cusp; **hb,** hypoconid; **md,** metaconid; **ed,** entoconid; **pc,** posterior cingulum; **alc,** anterior labial cusplet; **plc,** posterior labial cusplet.

species relative to the other members within each of the genera will be presented in another document (Musser, in prep.).

ABBREVIATIONS AND METHODS

INSTITUTIONS AND SPECIMENS: Specimens I cite by catalog number are stored in collections of the American Museum of Natural History, New York (AMNH); the Museum Zoologicum Bogoriense, Bogor (MZB); the South Australian Museum, Adelaide (SAMA); the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); and the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM).

Morphologies of specimens described in this report are based primarily on stuffed museum skins and associated skulls. Illustrations of palmar and plantar regions were drawn from material initially preserved in a formalin solution and later stored in 70 percent ethanol.

MEASUREMENTS: Values for total length, length of tail (LT), and length of ear (LE) are those recorded by collectors on labels attached to skins; subtracting length of tail from total length produced a value for length of head and body (LHB). Values for length of hind foot, including claw (LHF), were either taken from skin labels (samples I collected on the Archbold Sulawesi Expedition) or from my measurements of dry study skins (all other museum specimens).

Using dial calipers graduated to tenths of mm, I took the cranial and dental measurements listed below (arranged in the sequence they appear in the tables); their limits are illustrated in figure 1 and verbally defined in Musser and Newcomb (1983).

GLS	greatest length of skull
ZY	zygomatic breadth
IB	interorbital breadth
LR	length of rostrum
BR	breadth of rostrum

BZP	breadth of zygomatic plate
BBC	breadth of braincase
HBC	height of braincase
LD	length of diastema
PPL	postpalatal length
LIF	length of incisive foramina
BIF	breadth of incisive foramina
LBP	length of bony palate
BBPM1	breadth of bony palate at first molar
BMF	breadth of mesopterygoid fossa
LB	length of bulla
CLM1-3	crown length of maxillary molar row
BM1	breadth of first upper molar

Values of all external and craniodental measurements are provided in millimeters.

DENTAL TERMINOLOGY: The names used throughout the text for cusps and cusplets of upper and lower molars are indicated in figure 2.

GEOGRAPHY: A simplified reference map of Sulawesi and nearby islands is shown in figure 3. Throughout the report I use the Indonesian sungai (stream or small river), kuala (stream discharging directly into the sea), gunung (mountain), Pegunungan (mountain range), pulau (island), kepulauan (archipelago), selat (strait), and teluk (bay). Spelling for locality names and some coordinates were obtained from Gazeteer of Indonesia, Third Edition (names approved by the United States Board on Geographic Names, published by the Defense Mapping Agency, September, 1982).

CREDITS

The specimens discussed here were obtained by Dr. C. H. S. Watts, Chief Scientist, Division of Natural Science of the South Australian Museum in Adelaide. In 1980 Watts worked in Sulawesi as a member of an expedition organized by the British Scientific Exploration Club (Operation Drake) to survey a region near Morawali in the eastern part of central Sulawesi. Among the material he sent me to identify were samples of the new *Bunomys* and *Maxomys*. I appreciate his collecting efforts and his willingness to allow me to report on these new additions to the Sulawesi fauna. I apologize for the long period of time between my receipt of the specimens and their published descriptions.

In addition to Dr. Watts, Drs. Gordon B. Corbet, Colin P. Groves, and Lance A. Durden read early versions of the manuscript and provided intelligent evaluations and suggestions for change that added clarity to the report. I am indebted to them for their competent efforts.

The map (fig. 3) and drawings of the skull (fig. 1), teeth (fig. 2), and feet (figs. 4 and 13) are the work of Patricia Wynne. Peter Goldberg is responsible for the photographs of skulls and dentitions. These excellent products reflect their talent and high standards of craftmanship.

I am grateful for the continued support of curators and support staff at those institutions where I worked and borrowed specimens.

This report is No. 121 in Results of the Archbold Expeditions.

THE NEW SPECIES OF *BUNOMYS*

There are at least eight species of *Bunomys* (Musser and Holden, MS) and all of them occur in the forests on Sulawesi and nowhere else (Musser and Newcomb, 1983; Musser, 1987). The distinctive population living in moss forest on Gunung Tambusisi was listed by me as "*Bunomys* sp. A" (Musser, 1987: table 7.3, p. 79); it is named, diagnosed, and described in the following pages.

***Bunomys prolatus*, new species**

HOLOTYPE: MZB 12190, an adult male collected by C. H. S. Watts (original number 25) from Gunung Tambusisi (1°38′S, 121°23′E) at 6000 ft, on March 9, 1980. The skin is dried on a cardboard insert. Most of the right side and abdominal region are missing. The cranium is mostly intact: sections of the right zygomatic arch and hamular process are not present (fig. 5). A small piece of angular process of the left dentary is missing from an otherwise complete mandible (fig. 5). All teeth are present (figs. 9 and 10). Measurements of the holotype are listed in table 1.

REFERRED SPECIMENS: Seven individuals that were trapped at 6000 ft on a ridge of Gunung Tambusisi (also spelled Tambasisi and Tamboesisi) during the period March 9–11, 1980: AMNH 265074, old adult male; SAMA M15586, adult male; MZB 12188, adult female; AMNH 265075, young adult

Fig. 3. Mainland Sulawesi, offshore islands, and nearby archipelagos. The large black dot indicates Gunung Tambusisi (1°38′S, 121°23′E).

female; MZB 12191, adult female; AMNH 265076, adult male; and SAMA M15587, old adult female. All consist of flat skins dried on cardboard inserts, and associated skulls.

DISTRIBUTION: Known only from 6000 ft on Gunung Tambusisi, which is part of the highland mass at the western end of the eastern peninsula of central Sulawesi (fig. 3).

ETYMOLOGY: The Latin *prolatus* means elongate and I use it to express the head conformation of the new *Bunomys* from Tambusisi.

DIAGNOSIS: *Bunomys prolatus* is distinguished from other species in *Bunomys* by the following combination of characters: (1) very short tail that is much shorter than combined lengths of head and body; (2) darkly pigmented epidermal scales on dorsal surfaces of front and hind feet as well as digits; (3) large, elongate claws with curved and sharp tips; (4) long, dense, and very soft fur; (5) a long and tapered rostrum; (6) elongate cranium; (7) gracile and weakly flaring zygomata; (8) long and narrow incisive foramina, which end anterior to the molar rows; (9) an elongate dentary, especially that part of the ramus between molar row and edge of incisor alveolus; (10) cusp t3 absent from second and third molars; (11) no anterior labial cusplet on first lower molar, but posterior labial cusplet present on that tooth, and full array of labial cusplets occurring on second and third molars.

DESCRIPTION AND COMPARISON: Descriptions of pelage and other features associated with the skin are incomplete because each of the eight pelts is mounted on a flat piece of cardboard, which distorts the body outline. Large chunks of skin and fur are missing from the venter and sides of each specimen, and the tail was lost from one. No examples of the species were preserved in fluid.

Traits of the new *Bunomys* most closely resemble the morphology of *B. chrysocomus*, and it is with samples of that species that I contrast *B. prolatus* in this section. I compared the new species with samples of *B. chrysocomus* that were obtained from northern and central Sulawesi, as well as the southeastern peninsula (tables 1 and 2), but I paid closest attention to the specimens collected by Watts from Gunung Tambusisi. One (MZB 12181, an adult female) from there was trapped 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 period, March 6–27, 1980 (AMNH 265077, adult; SAMA M15588, old adult male; AMNH 265078, old adult male; MZB 12183, adult; MZB 12184, adult; and MZB 12185, adult female).

I am confident that the small sample from the mountain represents *B. chrysocomus* because chromatic and morphological features of the specimens do not differ in any significant or noticeable way from those in samples of the species from other regions of Sulawesi, including the northeastern arm, the region where the holotype was collected (Musser, 1970; also see tables 1 and 2).

Bunomys prolatus is a medium-size rat (table 1) that, as its name indicates, has a protracted face between eyes and nose, a short tail, and brownish gray fur that is long, dense, and soft. Two color phenotypes are present in the small sample before me. Whether a real chromatic dimorphism exists in the species or my sample represents two classes in a continuous variation from one phenotype to the other is unknown. Also, I could not correlate either morph with any other traits reflecting body size, age, or morphology. Five of the specimens have tawny, brownish gray dorsal pelage; the other three are burnished dark brownish gray, an effect that borders on chestnut. The color is uniform over the head and body, and is formed by the long hairs of the overfur, which are dark gray for most of their lengths and either tipped with black bands, with dark buff bands, or end in a subterminal black band and a buffy tip. The underfur is especially thick, long, and dark gray—a few hairs are tipped with pale buff. The hair over the back and rump reaches 20–25 mm and the whole coat is very dense and soft to the touch. Guard hairs, which have black terminal bands, are scattered through the pelage; all are short, extending only 5–10 mm beyond the overfur.

In both morphs, coloration of the dorsal coat grades imperceptibly into the slightly paler tone of the ventral pelage, which is also soft and thick but shorter (rarely longer than 10 mm) than the dorsal coat. The tawny

TABLE 1

Measurements (in millimeters) of Adult *Bunomys prolatus* and *Bunomys chrysocomus* from Northern Sulawesi

(The mean plus or minus one standard deviation, number of specimens, and range in parentheses are listed for each measurement)

	B. prolatus		*B. chrysocomus*		
	Holotype[a]	Gunung Tambusisi[b]	Gunung Tambusisi[c]	Northern peninsula[d]	Northern peninsula[e]
LHB	—	167.2 ± 10.4, 6 (156–179)	155	—	147.8 ± 7.0, 9 (140–160)
LT	—	132.4 ± 5.9, 7 (125–142)	130	135	133.6 ± 7.0, 8 (122–145)
LHF	—	33.9 ± 0.7, 7 (33–35)	32.3 ± 0.6, 3 (32–33)	36	33.9 ± 0.9, 9 (33–36)
LE	—	25.7 ± 0.8, 6 (24–26)	25	— —	—
GLS	42.7	41.8 ± 1.0, 8 (40.4–43.2)	38.3 ± 1.3, 6 (35.8–39.5)	40.5	37.6 ± 0.7, 9 (36.7–38.7)
ZB	18.3	17.8 ± 0.4, 8 (17.2–18.3)	17.8 ± 0.6, 6 (17.1–18.4)	18.5	17.9 ± 0.4, 6 (17.4–18.4)
IB	7.3	7.1 ± 0.2, 8 (6.9–7.4)	6.5 ± 0.3, 6 (6.1–6.8)	6.4	6.4 ± 0.3, 10 (5.9–6.9)
LR	16.1	15.7 ± 0.6, 8 (14.9–16.4)	13.3 ± 0.7, 6 (12.4–14.1)	14.7	12.8 ± 0.5, 10 (12.3–13.8)
BR	6.8	6.7 ± 0.4, 8 (6.1–7.1)	6.5 ± 0.5, 6 (5.6–6.9)	7.0	6.7 ± 0.2, 10 (6.5–7.1)
BZP	2.9	2.8 ± 0.1, 8 (2.6–2.9)	2.9 ± 0.1, 6 (2.8–3.0)	3.3	3.0 ± 0.2, 10 (2.8–3.3)
BBC	16.9	16.3 ± 0.4, 8 (15.7–16.9)	15.6 ± 0.4, 6 (15.1–16.2)	16.1	15.6 ± 0.4, 9 (15.0–16.5)
HBC	11.4	11.4 ± 0.2, 8 (11.0–11.6)	10.8 ± 0.3, 6 (10.3–11.0)	10.9	11.0 ± 0.3, 9 (10.7–11.8)
LD	11.7	11.5 ± 0.6, 8 (10.7–12.3)	10.5 ± 0.6, 6 (9.6–11.1)	11.3	10.2 ± 0.3, 10 (9.8–10.7)
PPL	15.2	14.6 ± 0.5, 8 (13.8–15.2)	13.2 ± 0.5, 6 (12.3–13.6)	14.2	13.4 ± 0.3, 7 (13.0–13.9)
LIF	7.0	6.7 ± 0.3, 8 (6.3–7.1)	6.7 ± 0.3, 6 (6.5–7.2)	6.6	6.3 ± 0.3, 10 (5.9–6.6)
BIF	2.5	2.3 ± 0.1, 8 (2.1–2.5)	2.3 ± 0.1, 6 (2.2–2.5)	2.4	2.4 ± 0.1, 10 (2.3–2.6)
LBP	8.4	8.7 ± 0.4, 8 (8.3–9.2)	7.6 ± 0.5, 6 (6.7–8.1)	8.0	7.7 ± 0.3, 10 (7.3–8.3)
BBPM^{1}	3.7	3.7 ± 0.2, 8 (3.6–3.9)	3.5 ± 0.2, 6 (3.2–3.8)	3.7	3.8 ± 0.3, 10 (3.2–4.3)
BMF	3.0	2.8 ± 0.1, 8 (2.6–3.0)	2.7 ± 0.26, 6 (2.4–2.9)	3.0	3.0 ± 0.2, 10 (2.6–3.2)
LB	7.3	6.9 ± 0.3, 8 (6.5–7.3)	6.5 ± 0.2, 6 (6.2–6.7)	6.7	6.3 ± 0.1, 8 (6.2–6.5)
CLM$^{1-3}$	6.8	6.5 ± 0.2, 8 (6.3–6.8)	6.3 ± 0.2, 6 (5.9–6.5)	6.5	6.4 ± 0.2, 11 (5.9–6.6)
BM^{1}	2.3	2.2 ± 0.1, 8 (2.0–2.3)	2.0 ± 0.1, 6 (1.8–2.1)	2.1	2.1 ± 0.1, 10 (2.0–2.2)

[a] MZB 12190.

[b] AMNH 265074–265076; SAMA M15586 and M15587; MZB 12188, 12190, and 12191.

[c] AMNH 265078 and 265077; SAMA M15588, MZB 12181, 12183, and 12185.

[d] Dumoga-Bone National Park, Sulawesi Utara, 230 m; Lance A. Durden Field No. 18.

[e] Bumbarujaba, lowlands: USNM 218025, 218127, 218128, 218131–218135, 218139, and 218140 (holotype of *Rattus nigellus* Miller and Hollister, 1921: 72).

TABLE 2

Measurements (in millimeters) of Adult *Bunomys prolatus, Bunomys chrysocomus* from Central and Southeastern Sulawesi, and *B. coelestis*

(The mean plus or minus one standard deviation, range in parentheses, and number of specimens are listed for each measurement)

	Bunomys prolatus	*B. chrysocomus*			*B. coelestis*
	Gunung Tambusisi[a]	Central region[b]	Southeastern highlands[c]	Southeastern lowlands[d]	Southwestern peninsula[e]
LHB	167.2 ± 10.4, 6 (156–179)	154.7 ± 15.5, 34 (97–176)	149.2 ± 6.2, 17 (140–161)	149.6 ± 10.2, 5 (134–160)	158.9 ± 6.9, 23 (147–179)
LT	132.4 ± 5.9, 7 (125–142)	140.9 ± 14.4, 34 (107–180)	139.3 ± 9.6, 17 (120–151)	131.0 ± 10.4, 5 (120–145)	153.3 ± 7.6, 23 (138–171)
LHF	33.9 ± 0.7, 7 (33–35)	36.0 ± 1.5, 34 (32–40)	33.2 ± 1.1, 7 (31–35)	33.4 ± 0.9, 9 (33–35)	35.8 ± 0.7, 23 (35–38)
LE	25.7 ± 0.8, 6 (24–26)	24.5 ± 1.2, 34 (23–28)	— —	— —	— —
GLS	41.8 ± 1.0, 8 (40.4–43.2)	38.2 ± 1.1, 34 (36.1–40.3)	38.6 ± 1.0, 11 (37.3–39.9)	38.1 ± 1.3, 4 (36.0–39.6)	40.2 ± 0.6, 18 (39.4–41.4)
ZB	17.8 ± 0.4, 8 (17.2–18.3)	18.3 ± 0.6, 33 (17.3–19.8)	18.2 ± 0.5, 10 (17.7–18.9)	18.9	19.0 ± 0.5, 14 (18.5–20.6)
IB	7.1 ± 0.2, 8 (6.9–7.4)	6.4 ± 0.3, 34 (5.8–6.8)	6.4 ± 0.3, 13 (6.0–6.9)	6.2 ± 0.2, 5 (6.0–6.5)	6.6 ± 0.2, 21 (6.2–7.2)
LR	15.7 ± 0.6, 8 (14.9–16.4)	13.6 ± 0.7, 34 (12.0–15.1)	13.9 ± 0.4, 16 (13.1–14.6)	13.4 ± 0.5, 4 (12.8–14.0)	14.9 ± 0.4, 23 (14.2–15.7)
BR	6.7 ± 0.4, 8 (6.1–7.1)	6.7 ± 0.5, 34 (5.8–7.7)	6.4 ± 0.4, 16 (5.8–7.3)	6.5 ± 0.5, 4 (6.0–7.0)	6.7 ± 0.4, 22 (6.3–7.7)
BZP	2.8 ± 0.1, 8 (2.6–2.9)	3.2 ± 0.3, 34 (2.7–3.7)	2.8 ± 0.2, 17 (2.5–3.2)	2.8 ± 0.2, 6 (2.5–2.9)	3.4 ± 0.2, 22 (3.2–3.8)
BBC	16.3 ± 0.4, 8 (15.7–16.9)	15.5 ± 0.4, 34 (14.6–16.5)	15.6 ± 0.4, 13 (14.8–16.8)	15.6 ± 0.4, 5 (15.0–16.1)	15.5 ± 0.4, 18 (14.7–16.0)
HBC	11.4 ± 0.2, 8 (11.0–11.6)	10.7 ± 0.4, 34 (10.1–11.7)	11.2 ± 0.3, 9 (10.9–11.6)	11.2 ± 0.6, 5 (10.5–11.8)	11.6 ± 0.3, 20 (11.0–12.0)
LD	11.5 ± 0.6, 8 (10.7–12.3)	10.5 ± 0.6, 34 (8.2–11.6)	10.6 ± 0.4, 16 (10.1–11.5)	10.3 ± 0.4, 6 (9.5–10.7)	11.8 ± 0.4, 23 (11.1–12.8)
PPL	14.6 ± 0.5, 8 (13.8–15.2)	13.7 ± 0.6, 34 (12.3–15.0)	13.9 ± 0.4, 9 (12.7–14.2)	13.5 ± 0.3, 4 (13.1–13.9)	14.4 ± 0.4, 16 (13.8–15.4)
LIF	6.7 ± 0.3, 8 (6.3–7.1)	6.1 ± 0.3, 34 (5.4–6.8)	6.8 ± 0.3, 16 (6.3–7.4)	6.8 ± 0.4, 5 (6.3–7.2)	7.1 ± 0.2, 22 (6.6–8.0)
BIF	2.3 ± 0.1, 8 (2.1–2.5)	2.4 ± 0.1, 34 (2.1–2.7)	2.4 ± 0.2, 16 (2.0–2.7)	2.4 ± 0.3, 5 (2.1–2.8)	2.29 ± −0.0, 22 (2.1–2.6)
LBP	8.7 ± 0.4, 8 (8.3–9.2)	7.4 ± 0.4, 34 (6.6–8.2)	7.2 ± 0.4, 15 (6.7–7.8)	7.5 ± 0.3, 4 (7.1–7.8)	8.0 ± 0.3, 21 (7.5–8.6)
BBPM[1]	3.7 ± 0.2, 8 (3.6–3.9)	3.8 ± 0.3, 34 (3.3–4.4)	3.7 ± 0.3, 16 (3.3–4.1)	3.7 ± 0.5, 5 (3.3–4.4)	3.6 ± 0.3, 23 (3.1–4.1)
BMF	2.8 ± 0.1, 8 (2.6–3.0)	3.0 ± 0.3, 33 (2.7–3.7)	2.7 ± 0.1, 13 (2.5–3.0)	2.7 ± 0.4, 4 (2.2–3.0)	2.8 ± 0.2, 21 (2.6–3.1)
LB	6.9 ± 0.3, 8 (6.5–7.3)	6.3 ± 0.2, 34 (5.9–6.8)	6.7 ± 0.2, 15 (6.4–6.9)	6.7 ± 0.3, 5 (6.3–6.9)	6.3 ± 0.2, 18 (6.0–6.9)
CLM1-3	6.5 ± 0.2, 8 (6.3–6.8)	6.1 ± 0.2, 34 (5.7–6.5)	6.1 ± 0.3, 20 (5.7–6.7)	6.2 ± 0.2, 6 (5.9–6.6)	6.1 ± 0.3, 22 (5.7–6.7)
BM1	2.2 ± 0.1, 8 (2.0–2.3)	2.0 ± 0.1, 34 (1.8–2.2)	2.0 ± 0.1, 20 (1.8–2.2)	2.1 ± 0.2, 6 (1.8–2.3)	1.0 ± 0.8, 21 (1.8–2.0)

[a] See table 1 for specimen numbers.

[b] Danau Lindu Valley, Tomado and Sungai Tokararu: AMNH 223040, 223044, 223050–223053, 223055, 223057–223969, 223062, 223064, 223065, 223069, 223079, 223081, 223082, 223292, 223297–223300, 223302, 223303, 223308, 223312, 223314, 223315, 223317, 223319, and 224154–224156.

brown morph has pale, buffy gray underparts, the ventral fur appears as tan suffused with gray. The darker phenotype has dark gray fur tinged with pale buff in two examples, and washed with a brighter buff in the third specimen. The overall impression of the three darkly furred rats is of burnished brown (slightly chestnut) upperparts and dark gray underparts with some buff overlay. The paler specimens in the sample appear tawny brown above and tannish gray below. A large piece of the venter is missing in all of these skins, but the part that is present is sufficiently intact to indicate that the underparts are basically dark gray with either a silver frosting or a whitish buff overlay. The effects are due to long gray hairs tipped with either silver or whitish buff bands.

There is the array, usual for Sulawesian murines, of mystacial, submental, superciliary, genal, and interramal vibrissae (see Brown, 1971, for descriptions of these sensory hairs and terminology) adorning the head. The interramal and submental hairs lack pigment; vibrissal clumps in the other sets are either glossy dark brown with silvery tips or entirely unpigmented. Eyelids are blackish. Ears are brown in the tannish gray morph, dark brown in the darker animals, and covered inside and out with soft and short hairs in all specimens.

Compared with individuals of *B. prolatus* of comparable age, *B. chrysocomus* is a smaller animal (tables 1 and 2). It also has soft and dense fur, but the coat is shorter, 15–20 mm long. In overall coloration, most specimens of *B. chrysocomus* are like the three examples of the dark form of *B. prolatus* and nearly inseparable from them except for hair length. A few examples in any large sample of *B. chrysocomus* are tannish gray, which is one end of the range of variation in the species, and thus resemble the paler morph of *B. prolatus*. Chromatic features of the fur are very similar in both species.

The sample of *B. prolatus* contains adults only. Juvenile pelage will have to be described when specimens of that age group are collected and studied.

Because of the pieces of skin missing from the poor preparations, I cannot determine the mammary count of *B. prolatus*. Two inguinal pairs of mammae are common to *B. chrysocomus* and all the other species of *Bunomys*, at least those which have been described, and I suspect that four teats will be found in *B. prolatus* if better preserved material of that species is ever obtained.

The tail in *B. prolatus* is shorter than combined lengths of head and body (table 1) and very short relative to body length (79% of head and body). It is covered by short hairs that are either dark brown or unpigmented, which arise from beneath overlapping rings of epidermal scales. Three hairs extend from each scale and their lengths cover three to four scale rings. Tail coloration varies within the sample. In one specimen, all surfaces are dark brown except for 2 mm of the tip, which is white. Among six specimens, the dorsal and lateral surfaces of each tail are dark brown; the ventral surface of one is grayish brown and only slightly paler than the rest of the tail; and the ventral surfaces of the others are either mostly white but speckled over the distal two-thirds, or all white and contrasting sharply with dorsal and lateral surfaces. No diagnostic bicoloration or monocoloration seems fixed in the population if my sample reliably indexes the range of variation in chromatic tail patterns. And no correlation exists between tail pigmentation and color of body pelage.

The tail is also shorter than combined lengths of head and body in samples of *B. chrysocomus* (tables 1 and 2), but propor-

---

←

[c] Gunung Tanke Salokko, 1500–2000 m: AMNH 101195, 101197, 101198, 101200, 101202–101205, 101211, 101215, 101217, 101220, 101221, 101223, 101226, 101229, 101234, and 101236 (holotype of *Bunomys coelestis koka* Tate and Archbold, 1935: 1).

[d] Lalolis, 300 m: AMNH 101051, 101052, 101054, 101055 (holotype of *Rattus brevimolaris* Tate and Archbold, 1935, p. 7). Pulau Buton: RMNH 21256.

[e] Gunung Lompobatang, 2000–2500 m: AMNH 101016, 101131–101133, 101135–101139, 101141–101146, 101149, 101150, 101152–101156, and 101158.

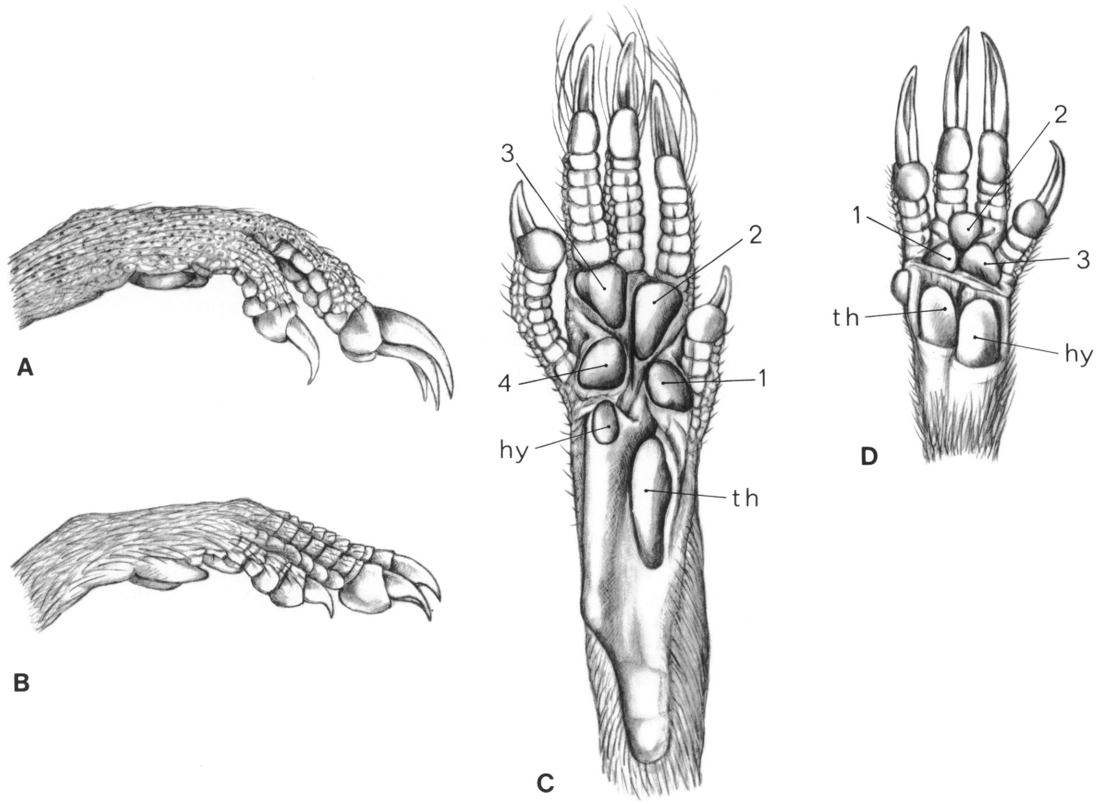

Fig. 4. Views of front and hind feet in species of *Bunomys* from Gunung Tambusisi. **A,** right front foot of *B. prolatus* (MZB 12187). **B,** right front foot of *B. chrysocomus* (AMNH 265077). Note the contrast in claw size between the species. **C,** plantar view of right hind foot of *B. prolatus* (MZB 12187). **D,** palmar view of left front foot of the same specimen as C. **hy,** hypothenar pad; **th,** thenar pad; **1–4,** first through fourth interdigital pads.

tionally, it is longer relative to body length (88 to 93% of head and body) than in *B. prolatus*. However, pilosity and the range in color variation and pattern match the conditions in the small series of the new species. In any large series of *B. chrysocomus,* the two extremes are represented by a monocolored tail and a sharply bicolored one, with most specimens reflecting all degrees of intermediate expressions between those boundaries; a very few specimens will also have unpigmented tail tips (the last 1–5 mm).

Front and hind feet of both *B. prolatus* and *B. chrysocomus* are long and slender. Palmar and plantar surfaces are naked and range in tone from pale to dark brown. In each species, the palmar surface is adorned with three small interdigital mounds and two large and tough metacarpal mounds—a medial thenar and lateral hypothenar (fig. 4D). Six pads are usual on each plantar surface: four interdigital mounds, one small hypothenar, and an elongate thenar (fig. 4C; see Brown and Yalden, 1973, for discussion of foot structures and their terminology).

The two species contrast in color. In *B. prolatus,* dorsal surfaces of feet and digits are covered by large, dark brown epidermal scales; the upper surfaces, from either the wrist or ankle, all the way to tips of the digits, are darkly spotted giving each foot an overall dark brown tone. Long brown hairs mixed with silver strands overlay the top of the feet. From the base of each digit of the hind foot, long hairs, some of which are bicolored (brown basally and silver distally) curl over and extend beyond each claw. *Bunomys chrysocomus* has epidermal scales but either few or none of them are pigmented so the skin appears unpigmented and the brown cast over the top of each foot (from either wrist or ankle to base of digits) results primarily from a dense cover of dark brown hairs (not brown pigment in epidermal scales). Sides of each foot and the digits are unpigmented, as are the long silvery hairs covering claws on the hind feet.

Claws of both *B. prolatus* and *B. chrysocomus* are ivory in color, long, and sharply pointed, but they differ in absolute and relative size. They are larger in *B. prolatus,* which goes along with the bigger feet and greater body size of that species. However, the most striking difference is in relative lengths of claws on the front feet. *Bunomys chrysocomus* has short and stout claws (fig. 4B), but in *B. prolatus,* they are much longer relative to digital lengths, and more elongate, ending in long curved tips (fig. 4A). In both species, the rudimentary stubby pollex bears a prominent nail.

Dorsal, ventral, and lateral cranial views of *B. prolatus* are shown in figure 5; morphologies of lateral and ventral regions are enlarged in figure 7. A smoothly vaulted braincase, wide interorbit without ridged countours, and long and narrow rostrum roofed by elongate nasals express the cranial conformation when the skull is viewed from a dorsal perspective. Capsular walls of the nasolacrimal glands form slight bulges on sides of the rostrum in front of the zygomatic plates. From those slight inflations, the rostrum extends forward in an even and graceful taper. The proximal outline of the rostrum flows into the anterior margins of the zygomatic notches, which are shallow and present not because the anterior spine of each zygomatic plate projects forward but because the entire plate curves forward. The interorbital region is broad; the frontal bones forming its dorsal surface are inflated into two low mounds; and the sides are smooth, without defining beads or ridges. From the waist of the interorbit, sides of the postorbital region circle out to join the dorsolateral margins of the braincase in an hour-glass silhouette. These margins are nearly smooth, defined by inconspicuous, slight beading. The posterior sweep of the smooth braincase is truncated at low lamboidal ridges. Behind the ridges is a moderately deep occipital region in which the dorsal surface is formed mostly from the interparietal; that bone projects only slightly between the parietals, contributing very little to the dorsal shell over the brain anterior to the occiput. Sides of the braincase are vertical—they drop down from the temporal beading rather than slope outward from there to squamosal roots of the zygomatic arches. The gracile zygomata curve out slightly from the outline of the braincase.

The protracted palatal region and rostrum is evident when the cranium is seen in ventral view. Also apparent is the projection of the rostrum anterior to the incisors in the form of a short tube formed by sides of the premaxillaries and tip of the nasals. The elongated aspect of the rostrum is visually reinforced by the long and slender incisive foramina; their posterior margins project just past anterior edges of the maxillary roots of the zygomata to end in front of the molar rows (fig. 7B). The posterior half of the maxillary root of each zygomatic plate sits above the first molar.

Medial to the molars is the narrow, long, and smooth bony palate. Its anteroposterior expanse is a reflection of where the incisive foramina end rather than any significant extension of the palate past the toothrows because that posterior projection is slight; in some specimens the posterior palatal margin is nearly even with backs of the third molars. A pair of posterior palatine foramina penetrate the palate opposite the third molars (fig. 7B). The toothrows diverge slightly toward the back of the palate. The mesopterygoid fossa is narrower than the bony palate and its anterodorsal walls are slit by two short and narrow fenestrae. The pterygoid fossae are slightly to moderately excavated and a prominent sphenopterygoid vacuity forms a large opening in each pterygoid plate. The lateral margin of each plate is outlined by a beading; the posterolateral and posterior edges converge behind the foramen ovale to form a wide and smoothly rounded ridge, which defines the anterolateral border of the spacious medial lacerate foramen between pterygoid plate and auditory bulla (fig. 7B).

Medial to the ridge is a deep groove for the infraorbital branch of the stapedial artery. The point where the artery leaves the groove and

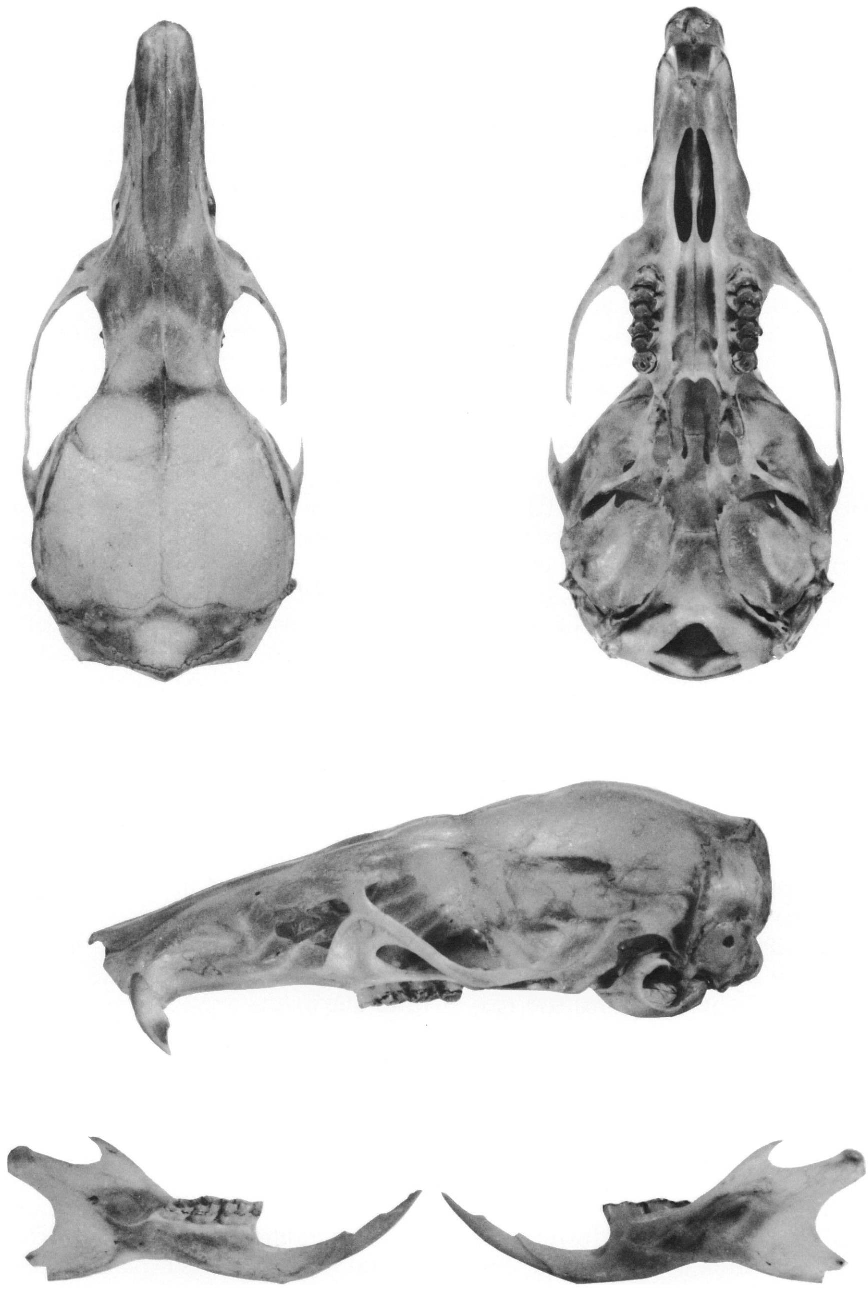

Fig. 5. Views (×2) of the cranium and dentary of the holotype of *Bunomys prolatus* (MZB 12190) from Gunung Tambusisi.

passes to the dorsal surface of the pterygoid plate defines the posterior opening of the alisphenoid canal (fig. 7B). Very short and narrow bony eustachian tubes merge with large and inflated auditory bullae. Rather than being vertical, as in species of *Rattus*, the medial sagittal plane of each bullar capsule in *B. prolatus* is oriented ventromedially so the capsules appear to rest on the basicranium and project toward the midline rather than straight

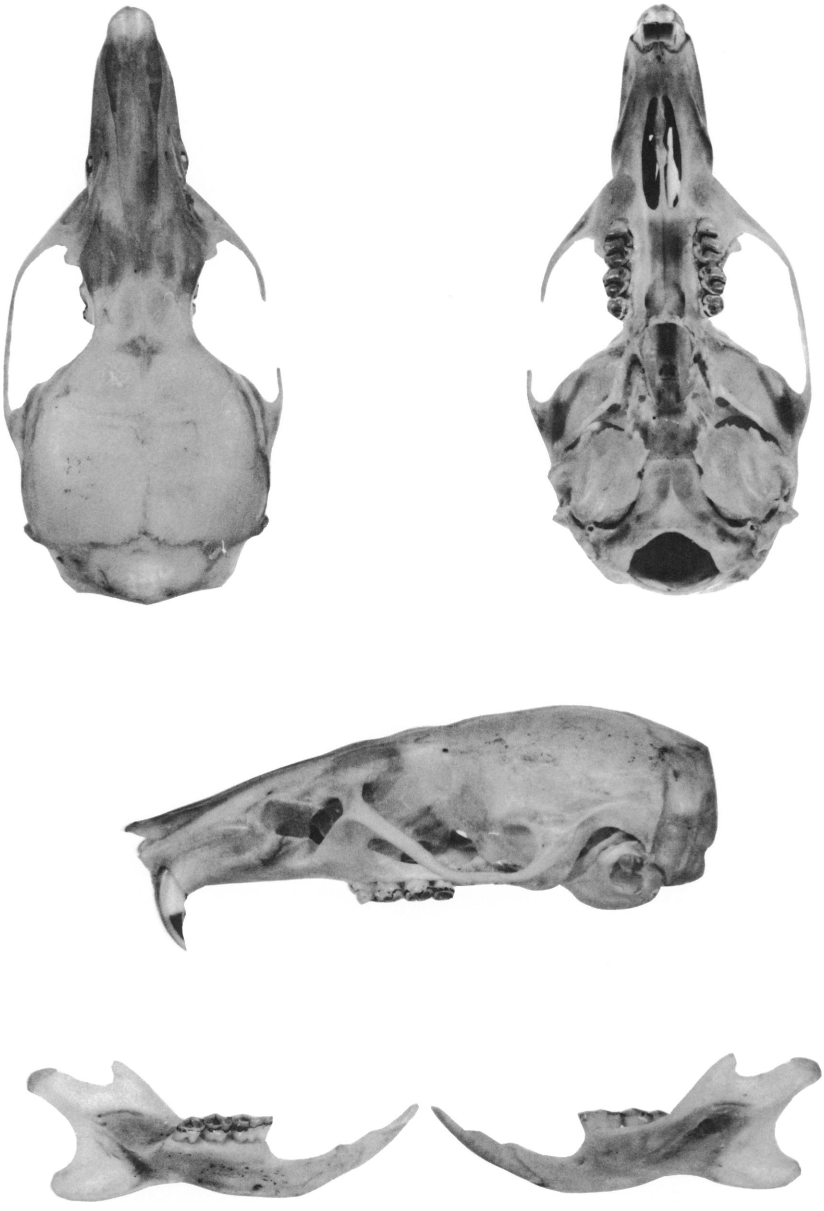

Fig. 6. Views (×2) of the cranium and dentary of an adult *Bunomys chrysocomus* (AMNH 265077) from Gunung Tambusisi.

up (seen from ventral perspective). Located between capsule and petrosal, the stapedial foramen is large but obscured in ventral view by the swollen overhang of the capsule margin. The occipital condyles are set back from the posterior rim of the braincase.

The elongation of the rostrum, the smooth interorbit, and the rounded braincase can be seen in side view (figs. 5 and 7). Gently ascending from the top of the occiput to the rounded crown of the braincase, the dorsal outline of the cranium then falls away in a long and graceful slope to the nasal tips. The rostral tube, bounded by premaxillaries and roofed with the nasal tips, is nicely illustrated in side view as it projects in front of the in-

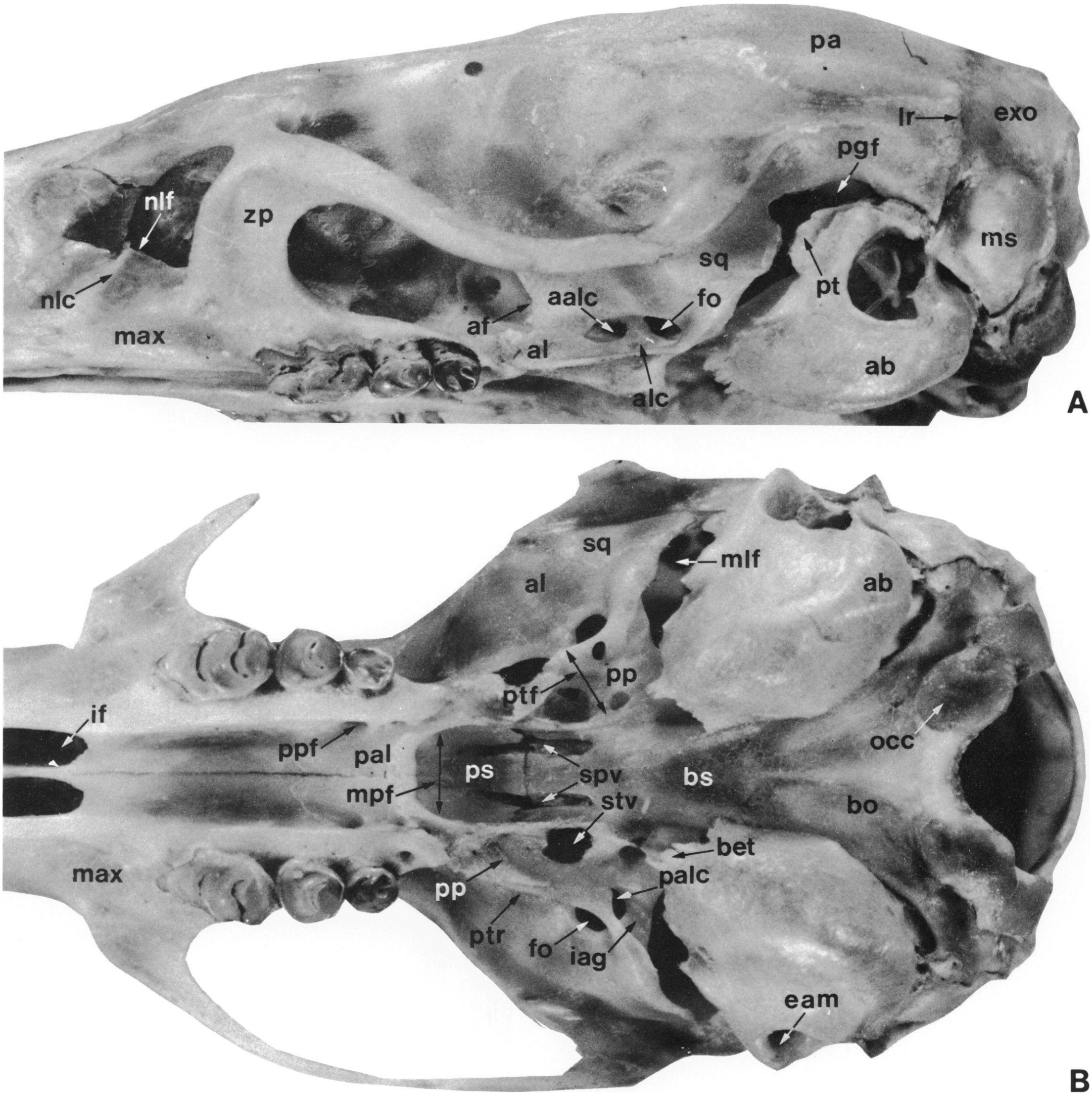

Fig. 7. Lateral (A) and ventral (B) cranial views of *Bunomys prolatus* (AMNH 265074). **aalc,** anterior opening of alisphenoid canal; **ab,** auditory bulla; **af,** anterior alar fissure; **al,** alisphenoid; **alc,** alisphenoid canal; **bet,** bony eustachian tube; **bo,** basioccipital; **bs,** basisphenoid; **eam,** external auditory meatus; **exo,** exoccipital; **fo,** foramen ovale; **iag,** groove for the infraorbital branch of the stapedial artery; **if,** incisive foramina; **lr,** lamboidal ridge; **max,** maxillary; **mlf,** middle lacerate foramen; **mpf,** mesopterygoid fossa; **ms,** mastoid portion of the petromastoid; **nlc,** nasolacrimal capsule; **nlf,** nasolacrimal foramen; **occ,** occipital condyle; **pa,** parietal; **pal,** palatine; **palc,** posterior opening of the alisphenoid canal (the infraorbital branch of the stapedial artery enters the braincase—where the arrow points—dorsal to the pterygoid); **pgf,** postglenoid foramen; **pp,** pterygoid plate; **ppf,** posterior palatine foramen; **ps,** presphenoid; **pt,** periotic; **ptf,** pterygoid fossa; **ptr,** pterygoid ridge; **sq,** squamosal; **spv,** sphenopalatine vacuities; **stv,** sphenopterygoid vacuity; **zp,** zygomatic plate.

cisors. The anterior ends of the nasals are slightly elevated dorsally, which effectively increases circumference of the nasal orifice. The position and shape of each zygomatic plate are distinctive. The maxillary root of the plate originates above the first molar (rather than anterior to it as in species of *Rattus*), and from there curves dorsad and then back, its dorsal region transforming into the graceful sweep of the zygomatic arch. Each plate is narrow and its inclination is reflected by the convex margin of the anterior edge. Anterior to the zygomatic spine is the fully exposed nasolacrimal capsule and nearly horizontal slitlike nasolacrimal foramen (fig. 7A). The squamosal root of each zygomatic arch is low on the side of the braincase and its posterior margin curves against the braincase to the occiput as a low and nearly undetectable ridge. The mastoid portion of the pteriotic complex is slightly inflated, with or without vacuities. The squamosal above each auditory capsule and just anterior to the lamboidal ridge is complete (not penetrated by a squamoso-mastoid foramen). Anteriorly, the attachment between squamosal and periotic is broken by a spacious postglenoid foramen that is confluent with the wide middle lacerate foramen; the opening forms a gulf between lateroventral margins of braincase and bulla. Those bullae are long but not deep. Below the zygomatic arch and above the beaded margin of the pterygoid plate is an alisphenoid canal. The foramen at the front of the canal is the anterior opening of the alisphenoid canal; that at the back is the foramen ovale. The infraorbital branch of the stapedial artery passes along the open canal through the anterior opening into the orbit via the anterior alar fissure (fig. 7A). An alisphenoid strut is not present, which results in the coalesence of foramen ovale accessorius and buccinator-masticatory foramina. Such a configuration of bone and cephalic arterial pattern is present in many species of muroid rodents (see the figures in Carleton and Musser, 1989). Beneath each pterygoid plate can be seen a low hamular process. Just back of each bulla is a small and inconspicuous paroccipital process, often eroded or missing in poorly cleaned skulls.

In parallel to the long and tapered anterior half of the cranium, each dentary of *B. prolatus* is elongate and gracile (fig. 5). A small and delicate coronoid projection sits anterior to the slim and long condylar process, which in turn is set off from the elongate angular process by a deep concavity that forms the posterior margin of the dentary. A low bulge slightly anterior to the falciform coronoid is a conspicuous landmark. From inside this projection, the incisor curves forward encased in the body of the ramus below the molar row and continues craniad in an elongate tubelike anterior portion of the ramus. The masseteric ridges on the lateral surface of the dentary are low. On the medial surface is a low ridge connecting the platform (in which the molars are secured) to the condyle; just dorsal to the ridge and below the back of the coronoid projection is the mandibular foramen.

The cranial conformation of *B. chrysocomus* resembles that of *B. prolatus*; primary differences between the two species are related to size and the greater rostral elongation in the Tambusisi rat, distinctions that are evident from both qualitative (tables 1 and 2) and quantitative (compare figs. 5 and 6; fig. 11) observations. On the average, samples of *B. chrysocomus* have a shorter cranium than do those of *B. prolatus*. The rostrum is also shorter but just as wide, suggesting that the more elongate configuration in *B. prolatus* represents protraction of the conformation seen in the other species. Specimens of *B. chrysocomus* also have a narrower interorbit, but wider zygomatic spread; a narrower braincase (height is about the same in the two species); wider zygomatic plates (even though the cranium is smaller overall); shorter diastema, bony palate, and postpalatal region; and smaller bullae, which is likely related to the overall smaller size of the skull. Means of length and breadth of incisive foramina, as well as breadth of bony palate and mesopterygoid fossa, are similar in the two species.

Dentaries of the two resemble each other closely in surface contour and outline. *Bunomys prolatus* has a more elongate mandible, especially in the thinner region between molar row and incisor alveolus (figs. 5 and 6).

Upper and lower incisors of *B. prolatus* are narrow, appear gracile but not weak, and their enamel is orange. The position of the uppers

Fig. 8. Views (×12) of alveoli for right molar roots in *Bunomys prolatus* (AMNH 265076). **Left,** ventral view of upper alveoli (number of alveoli per molar is, from top to bottom, 5, 4, and 3, respectively). **Right,** dorsal view of lower alveoli (4, 3, and 3, respectively). **ant,** alveolus for anterior root; **lab,** labial alveolus; **ling,** lingual; **post,** posterior.

relative to the ventral surface of the rostrum varies from being opisthodont (curving back) to orthodont (projecting from rostrum at a right angle) among the eight specimens.

Molars of *B. prolatus* have multiple roots, as is indicated by the alveoli illustrated in figure 8. Beneath each first upper molar is, clockwise, a large anterior root, two slightly smaller lingual anchors, a large posterior root, and a small labial. Four roots of about equal size anchor the second upper molar, and under the third tooth are a pair of medium-size anterior roots and a large posterior anchor. Large anterior and posterior roots coupled with smaller labial and lingual ones hold down each first lower molar. Each second and third molar is anchored by two anterior roots and a large and sturdy posterior one.

The molars themselves are wide and low-crowned (brachyodont). The four sets of three form arcuate rather than straight rows (figs. 9 and 10). In each row, the second molar lacks an anterocone/id and thus is smaller than the first, and the third is almost half the size of the second. Within the upper rows, the first molar overlaps the second and the second inclines against the third. Each third molar in the mandibular rows leans against the second and that tooth slightly overlaps the first. This configuration of partial overlap reflects the attitude of cusp rows, which are inclined rather than erect. In most of the teeth, the rows of cusps are moderately close to one another.

Occlusal patterns formed by the maxillary rows of cusps are simple in the examples of *B. prolatus* (fig. 9). Several features are responsible for this lack of surface complexity. First, cusp t3 of each first upper molar is either completely coalesced, or nearly so, with the central cusp (t2), which results in a simple tranverse lamina with a caudally directed lingual projection that represents cusp t1. Second, the lingual margin of the upper molars between cusps t4 and t8 lack a cusp (t7) or ridge. Third, the anterolabial margin of each second and third upper molar is without a cusp t3, although some specimens have an enamel pimple projecting labially from the medial cusp (t5) on second molars. Fourth, not one of the uppers has a posterior cingulum; such a cusp projects labially from the back of cusp t8 in other Indo-Australian species (see the diagram of cusps and their nomenclature in Musser and Newcomb, 1983: 333). And fifth, the cusp rows stand free, unconnected by either anterior or posterior enamel bridges—they join in various arrangements only after much wear.

Simple patterns characterize chewing surfaces of the lower molars (fig. 10). The simplicity expresses the absence of accessory structures: anterior and posterior enamel projections that would link rows of cusps; lingual cusplets; multiple labial cusplets; and an anterocentral cusp (which occurs at the front of each first molar in other murid species; see the cusp diagram in Musser and Newcomb, 1983: 333). The foundation of occlusal topography consists basically of simple laminae; a compressed elliptical posterior cingulum at the back of each first and second molar; and an anteroconid composed of anterolabial and anterolingual cusps that fuse early in the rat's life to form a large oblong lamina—without evidence of cusp boundaries—at the front of each first lower molar. Along the labial margin of each second and third molar are anterolabial and posterolabial cusplets; only a posterolabial cusplet occurs on the first molar.

Specimens of *B. chrysocomus* have shorter molar rows and tend to have narrower molars than is characteristic of *B. prolatus*; otherwise, dental traits of the two species are very similar (figs. 9 and 10). The only other distinction I detected is that about half the sample of *B. chrysocomus* has an anterior labial cusplet on the first lower molar and a small part of the sample has a cusp t3 on second and third upper molars (table 4), a difference that will have to be tested in future comparisons between that species and larger samples of *B. prolatus*.

CONTRASTS WITH OTHER SPECIES OF *BUNOMYS*: Another close relative of *B. chrysocomus* is *B. coelestis*, which occurs on the upper slopes of Gunung Lompobatang at the southern end of the southwestern peninsula of Sulawesi. Basically, *B. coelestis* is a darker-furred version of *B. chrysocomus* that also has longer claws on the front feet; a cranium that appears more delicate in build; a longer rostrum, diastema, bony palate, incisive foramina, and postpalatal region; and narrower molars (table 2). The chromatic and structural traits of *B. prolatus* differ from those of *B. coelestis* in much the same ways as they do from *B. chrysocomus* (fig. 11). The Lompobatang species has longer claws on the front feet than are seen in *B. chrysocomus*, but they are smaller and more gracile than the large and elongated claws possessed by *B. prolatus*. The rostrum in *B. coelestis*, although longer than that of *B. chrysocomus*, still tends to be shorter than rostral length in the sample of *B. prolatus* and the diastema and incisive foramina average longer in the southwestern sample. The magnitudes of differences between *B. coelestis* and *B. prolatus* in mean values of other measurements parallel the quantitative contrasts between *B. chrysocomus* and *B. prolatus* (table 2). And most specimens of *B. coelestis* have a moderately large cusp t3 on second upper molars (table 4); the comparable cusp is absent from the sample

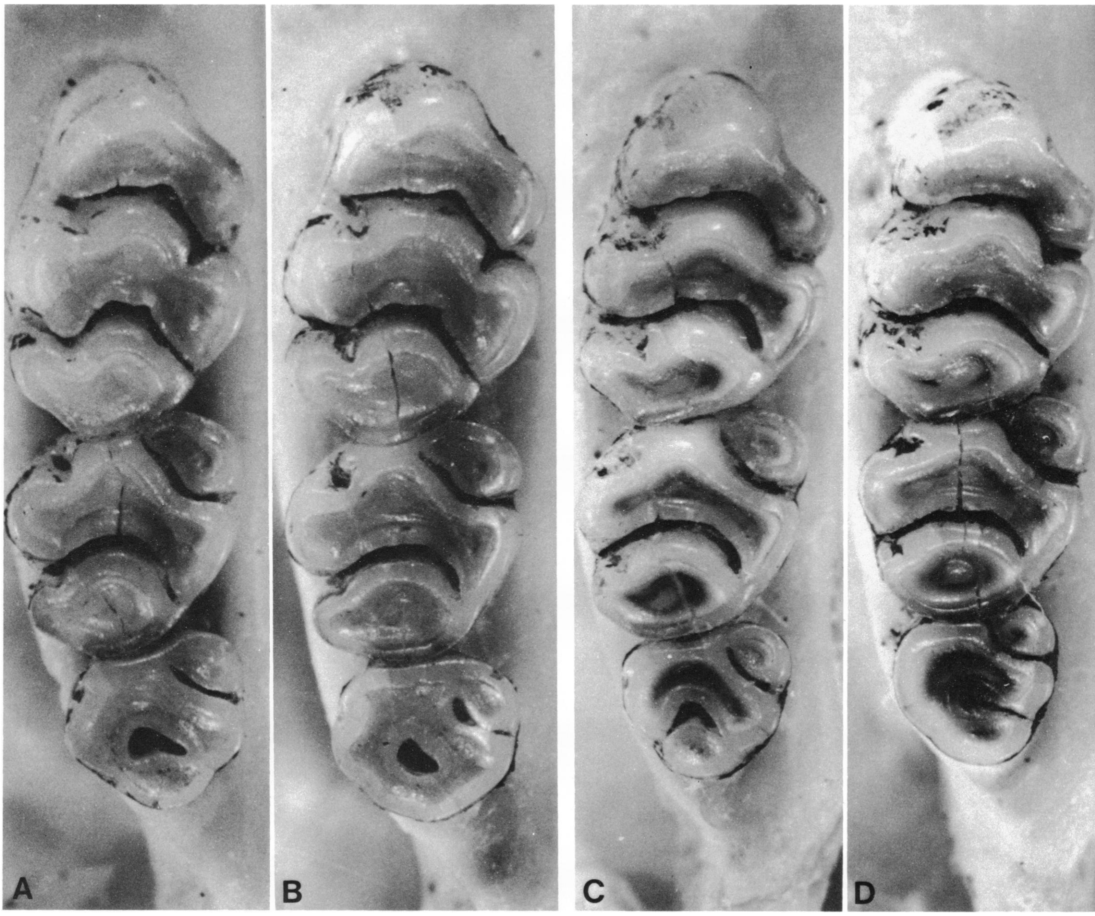

Fig. 9. Occlusal views of right upper molar rows (approximately ×14) in species of *Bunomys* from Gunung Tambusisi. **A,** *B. prolatus,* young adult (AMNH 265075). **B,** *B. prolatus,* adult and holotype (MZB 12190). **C,** *B. chrysocomus,* adult (MZB 12185). **D,** *B. chrysocomus,* adult (MZB 12183).

of *B. prolatus*. Although both *B. coelestis* and *B. prolatus* are characterized by elongate claws, cranium, and mandible, the two differ significantly in absolute dimensions, some proportions, and qualitative traits—the sample of *B. prolatus* does not represent a montane population of *B. coelestis* isolated in central Sulawesi.

Morphology of *B. prolatus* is also unlike that of any other species of *Bunomys* (table 3; fig. 12). *Bunomys andrewsi,* for example, inhabits lowland evergreen rain forest at low altitudes in central and southeastern Sulawesi and also occurs in the foothills of Gunung Tambusisi. Although similar to *B. prolatus* in body size, *B. andrewsi* has shorter and less dense fur, a robust cranium, flaring zygomatic arches, narrower interorbit, shorter rostrum but much longer incisive foramina, wider rostrum and zygomatic plates, shorter bony palate and bullae, much longer molar rows, and no anterior labial cusplets on third lower molars of most individuals in a series (table 4). Specimens of the two can be quickly separated by simple inspection.

Bunomys fratrorum is found only in the eastern and northeastern parts of the northern peninsula of Sulawesi and has been collected in both lowland evergreen and montane rain forests. It is a larger rat than *B. prolatus* (as reflected by measurements of most dimensions investigated; table 3), has a longer tail (about the same length as head and body), much narrower interorbital re-

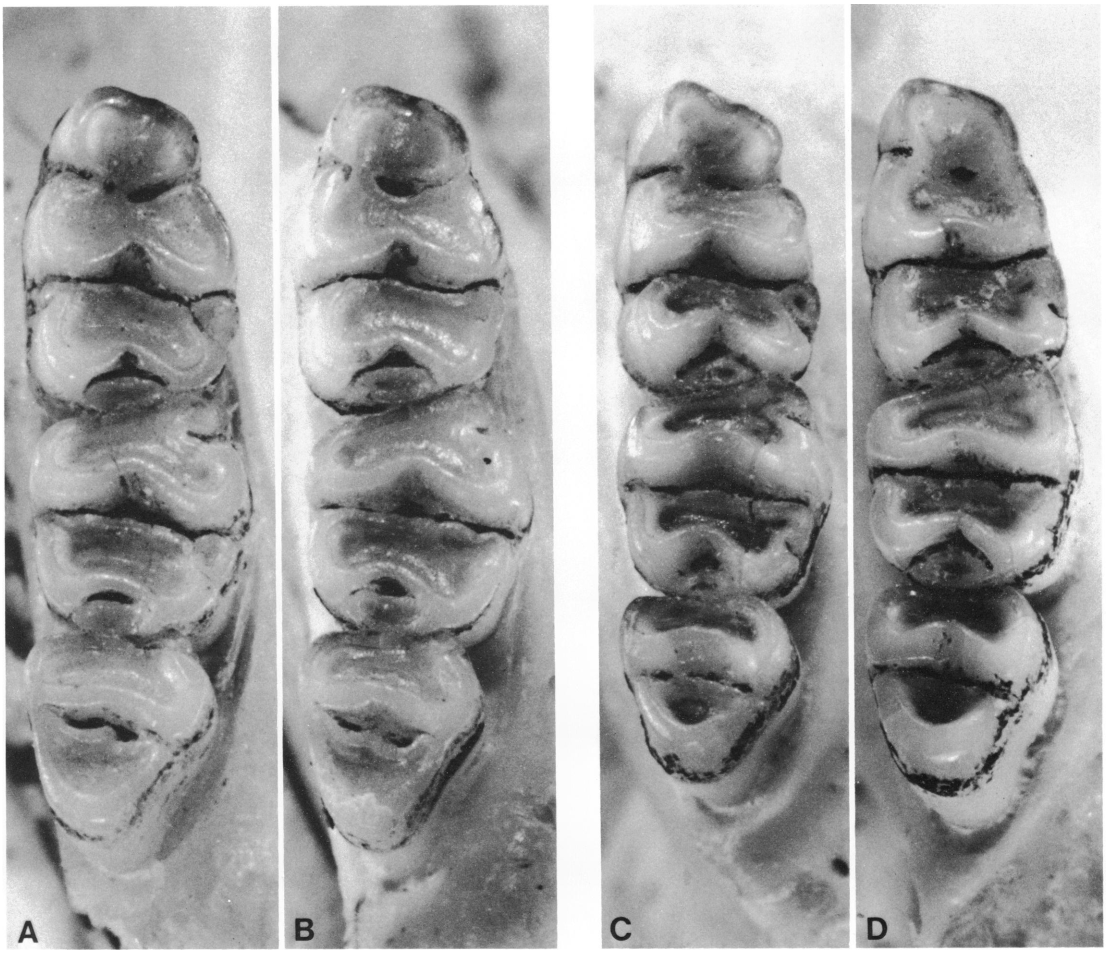

Fig. 10. Occlusal views of right lower molars (approximately × 14) of the same specimens of *Bunomys* illustrated in figure 9. **A,** *B. prolatus.* **B,** *B. prolatus,* holotype. **C,** *B. chrysocomus.* **D,** *B. chrysocomus.*

gion, shorter rostrum and bony palate, smaller bullae, appreciably larger molars, and no anterior labial cusplets on third lower molars (Table 4). Overall cranial conformation that characterizes *B. fratrorum* is unlike that typical of *B. prolatus*: the latter is not the montane central Sulawesian counterpart of the former, at least in morphology.

Bunomys penitus lives in lower and upper montane evergreen rain forest in the mountains of central and southeastern Sulawesi. It exceeds *B. prolatus* in body size; has a much longer tail, which is brown above and white below (most specimens also have a white tip); and white feet. Most cranial dimensions of *B. penitus* are greater than in the Tambusisi animal except interorbital breadth (narrower), and breadths of zygomatic plates, braincase, bony palate, and bullae (about the same). The two species also differ in frequencies of cusps and cusplets (table 4). In any sample of *B. penitus,* a cusp t3 is present on the second upper molar of most specimens (absent from *B. prolatus*), anterior labial cusplets are present on second lower molars in about half the sample (all of the sample of *B. prolatus*), and third lower molars of all individuals lack anterior labial cusplets (three out of four specimens of *B. prolatus* have them). In body size, external proportions, and cranial configuration, *B. penitus* resembles *B. fratrorum* and not the highland *B. prolatus* (table 3; fig. 11).

Finally, *B. heinrichi* has been collected only

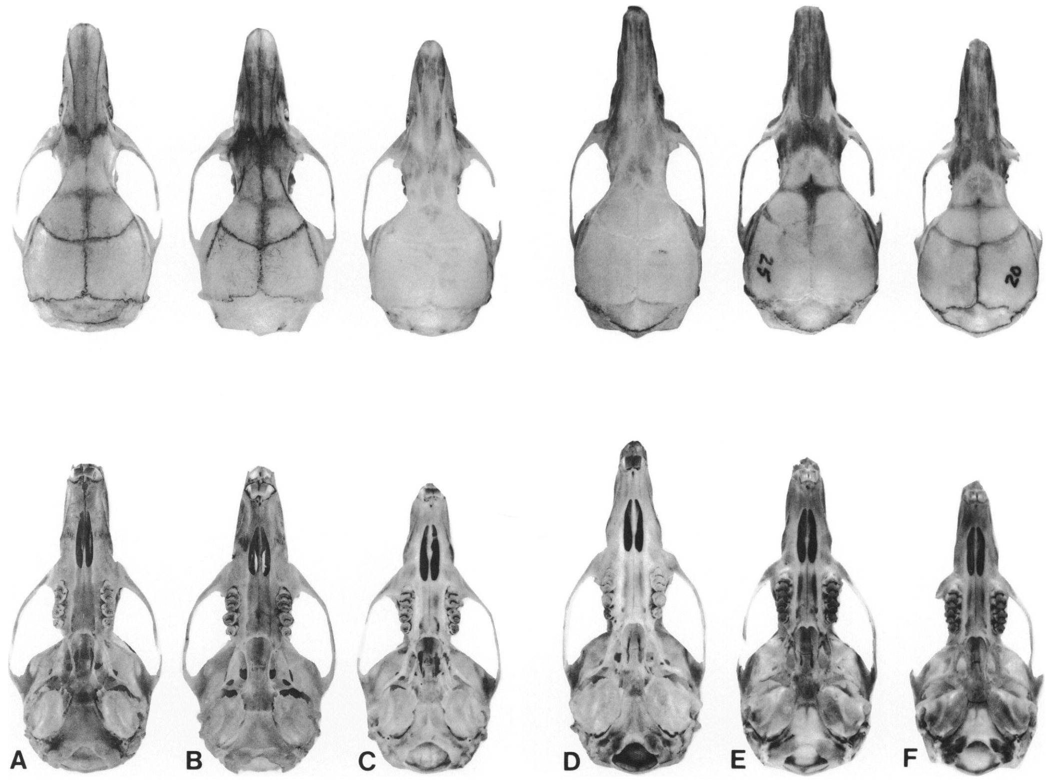

Fig. 11. Comparisons among crania (×1) from adult examples of the *Bunomys chrysocomus* group. **A,** *B. coelestis* (AMNH 101132), Gunung Lompobatang, 2500 m, southwestern peninsula. **B,** *B. chrysocomus* (AMNH 224698), Sungai Sadaunta, 2500 ft, central Sulawesi. **C,** *B. chrysocomus* (AMNH 265077), Gunung Tambususi, 4500 ft. **D–F,** *B. prolatus,* Gunung Tambususi; from left to right, AMNH 265074 (old adult), MZB 12190 (holotype, adult), and AMNH 265075 (young adult).

from 1100 m on the slopes of Gunung Lompobatang, near the tip of the southwestern peninsula of Sulawesi. It is a smaller animal than *B. prolatus,* and although the tail is shorter than head and body length, it is still relatively longer than that of the Tambusisi rat. *Bunomys heinrichi* also has a smaller skull but at the same time exhibits a wider zygoma, rostrum, and zygomatic plates, and longer incisive foramina and molar rows (table 3). About two-thirds of the specimens in any sample of *B. heinrichi* have a cusp t3 on each second upper molar (absent in *B. prolatus*), and anterior labial cusplets occur on third lower molars of approximately half the sample (three-fourths in *B. prolatus*). In color of fur, external and cranial proportions, and cranial conformation, *B. heinrichi* resembles the lowland *B. andrewsi* more closely than any other species in the genus (fig. 12).

THE NEW SPECIES OF *MAXOMYS*

There are 19 species in *Maxomys*: 13 occur on the mainland and offshore islands of Indochina as well as islands on the Sunda Shelf (Musser et al., 1979; Musser and Newcomb, 1983); six are found on Sulawesi and nowhere else (Musser, 1987). Three of the Sulawesian species have been described: *M. hellwaldii, M. dollmani,* and *M. musschenbroekii*; three have yet to be named and diagnosed. The population living on Gunung Tambusisi is one of these, which was listed by me as "*Maxomys* sp. C" (Musser, 1987: table 7.3, p. 79), and is named and described below.

Maxomys wattsi, new species

Holotype: MZB 12155, an adult male collected by C. H. S. Watts (original field number 28) from Tambusisi Damar, on the slopes

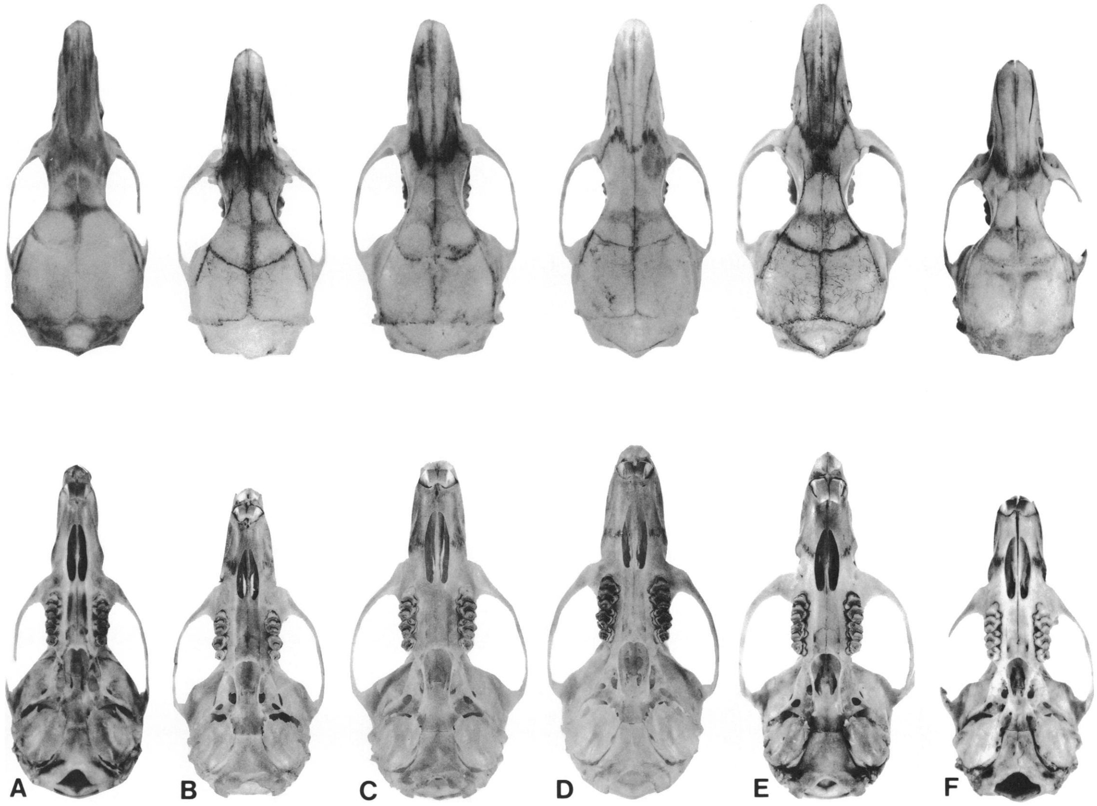

Fig. 12. Comparisons among crania (× 1) from adult *Bunomys*. **A,** *B. prolatus* (MZB 12190, holotype), Gunung Tambusisi. **B,** *B. chrysocomus* (AMNH 224698), central Sulawesi. **C,** *B. andrewsi* (AMNH 225652), central Sulawesi. **D,** *B. penitus* (AMNH 223852), central Sulawesi. **E,** *B. fratrorum* (USNM 217650), northeastern arm. **F,** *B. heinrichi* (AMNH 100996), southwestern peninsula.

of Gunung Tambusisi (1°38′S, 121°23′E), 4700 ft, in central Sulawesi on March 12, 1980. A flat study skin is supported by a piece of cardboard. Ears, feet, and tail are intact but most of the venter and pieces of the sides of the body are missing. The cranium is complete except for small pieces gone from the rostrum, left pterygoid plate, and mesopterygoid fossa (figs. 14 and 16B). The left dentary is whole, but the angular process of the right is slightly damaged (fig. 14). Molars and incisors are complete (figs. 14, 19, and 20). Measurements of the holotype are listed in table 5.

Referred Specimens: Eleven individuals trapped on the forested slopes of Gunung Tambusisi during the period March 5–15, 1980. Three come from Tambusisi Ridge, 6000 ft: SAMA M15584 (adult female, skin and skull), MZB 12158 (young adult female, skin and skull), and AMNH 265081 (young adult male, skin and skull). The rest were collected at Tambusisi Damar, 4700 ft: AMNH 265079 (adult male, skin and skull), MZB 12159 (adult male, skull only), MZB 12160 (old adult male, skull only), MZB 12161 (adult male, skull only), SAMA M15585 (adult male, skin and skull), AMNH 265080 (adult male, skin and skull), SAMA M15583 (adult, skull only), and MZB 12163 (adult, skull only).

Distribution: Known only from 4700 and 6000 ft on Gunung Tambusisi.

Etymology: The species is named after Dr. C. H. S. Watts. This action continues a tradition of using patronyms for species of *Maxomys* that are native to Sulawesi (*M. hellwaldii, M. muschenbroekii,* and *M. dollmani,* for example).

Diagnosis: *Maxomys wattsi* is distin-

TABLE 3
Comparison of Measurements (in millimeters) Between Adult *Bunomys prolatus* and Four Other Species of *Bunomys*
(The mean plus or minus one standard deviation, range in parentheses, and number of specimens are listed for each measurement)

	B. prolatus[a]	*B. fratrorum*[b]	*B. penitus*[c]	*B. andrewsi*[d]	*B. heinrichi*[e]
LHB	167.2 ± 10.4, 6 (156–179)	170.4 ± 6.4, 26 (157–182)	184.9 ± 6.1, 40 (170–199)	164.3 ± 7.4, 16 (155–175)	151.5 ± 6.1, 11 (142–162)
LT	132.4 ± 5.9, 7 (125–142)	170.0 ± 6.9, 25 (160–180)	170.3 ± 8.6, 38 (155–188)	146.8 ± 8.2, 16 (135–165)	139.6 ± 8.1, 10 (130–153)
LHF	33.9 ± 0.7, 7 (33–35)	39.6 ± 1.0, 26 (36–41)	41.9 ± 0.8, 40 (38–44)	37.3 ± 1.6, 16 (35–40)	34.6 ± 1.5, 11 (32–36)
GLS	41.8 ± 1.0, 8 (40.4–43.2)	43.8 ± 1.1, 33 (41.5–45.6)	43.3 ± 1.0, 40 (41.3–45.8)	41.0 ± 1.1, 15 (39.1–42.6)	38.8 ± 0.8, 8 (37.6–40.2)
ZB	17.8 ± 0.4, 8 (17.2–18.3)	20.9 ± 0.7, 31 (19.5–22.4)	19.6 ± 0.6, 40 (18.4–20.7)	20.0 ± 0.7, 16 (19.0–21.5)	19.1 ± 1.0, 5 (18.1–19.9)
IB	7.1 ± 0.2, 8 (6.9–7.4)	6.3 ± 0.3, 40 (5.7–7.0)	6.7 ± 0.3, 40 (6.2–7.5)	6.6 ± 0.2, 16 (6.3–7.0)	6.4 ± 0.3, 10 (6.1–6.9)
LR	15.7 ± 0.6, 8 (14.9–16.4)	15.4 ± 0.6, 38 (14.2–16.6)	16.3 ± 0.5, 40 (15.1–17.7)	14.2 ± 0.7, 16 (13.1–15.1)	14.0 ± 0.5, 10 (13.8–14.8)
BR	6.7 ± 0.4, 8 (6.1–7.1)	8.1 ± 0.4, 39 (7.0–9.0)	8.0 ± 0.3, 40 (7.3–8.9)	7.2 ± 0.3, 16 (6.8–7.9)	7.1 ± 0.3, 11 (6.7–7.6)
BZP	2.8 ± 0.1, 8 (2.6–2.9)	3.9 ± 0.4, 39 (3.0–4.6)	2.9 ± 0.2, 40 (2.4–3.2)	3.8 ± 0.3, 16 (3.4–4.4)	3.5 ± 0.3, 11 (3.1–3.9)
BBC	16.3 ± 0.4, 8 (15.7–16.9)	16.4 ± 0.5, 37 (15.4–17.5)	16.6 ± 0.4, 40 (15.7–17.3)	16.0 ± 0.3, 16 (15.7–16.7)	15.6 ± 0.4, 9 (15.0–16.0)
LIF	6.7 ± 0.3, 8 (6.3–7.1)	7.1 ± 0.3, 39 (6.4–8.0)	8.1 ± 0.3, 40 (7.4–9.1)	8.0 ± 0.4, 16 (7.3–8.8)	7.6 ± 0.2, 10 (7.2–7.9)
LBP	8.7 ± 0.4, 8 (8.3–9.2)	8.3 ± 0.4, 40 (7.5–9.1)	8.7 ± 0.4, 40 (7.4–9.6)	7.8 ± 0.4, 16 (7.3–8.6)	7.8 ± 1.0, 11 (7.3–8.4)
LB	6.9 ± 0.3, 8 (6.5–7.3)	6.4 ± 0.3, 37 (5.9–7.0)	7.0 ± 0.3, 40 (6.4–8.0)	6.4 ± 0.4, 16 (5.7–6.9)	6.7 ± 0.2, 11 (6.4–7.0)
CLM1-3	6.5 ± 0.2, 8 (6.3–6.8)	7.5 ± 0.3, 40 (6.8–8.1)	6.9 ± 0.3, 20 (6.5–7.4)	7.1 ± 0.2, 16 (6.9–7.4)	6.9 ± 0.2, 18 (6.5–7.3)

[a] See table 1 for specimen numbers.
[b] Northeastern arm, Temboan, 400–500 m: USNM 217616, 217622, 217623, 217625, 217628, 217630, 217635, 217637–217642, 217645, 217649, 217650, 217653, 217655–217659, 217661, 217662, 217665, 217666, 217670, 217671, 217868, 217869, 217880–217884, 217887, 217896, 217900, and 217902.
[c] Central region, Gunung Kanino, 4800–5000 ft: AMNH 223805, 223806, 223811, 223814, 223815, 223819–223822, 223826, 223828, 223829, 223831, 223832, 225264, 225265, 225267, 225269, 225271–225276, 225279, 225281–225285, 225287, 225288, 225290–225293, and 225296–225300.
[d] Central region, Pinedapa, 100 ft: USNM 219581, 219587, 219589, 219591, 219593, 219596, 219597, 219600–219603, 219605, 219606, 219619, 219620, and 219622.
[e] Northwestern arm, Lombasang, Gunung Lompobatang, 1100 m: AMNH 100996–101015.

guished from any other species in *Maxomys* by the following combination of traits: (1) very short tail that is much shorter than length of head and body and also shorter relative to body length; (2) very long, soft, and dense fur; (3) brownish buff upperparts, grayish white underparts; (4) a bicolored tail—dorsal surface brown, ventral surface white and lightly speckled with brown; (5) six plantar pads; (6) rostrum narrow relative to its length; (7) postorbital and temporal ridges weak and indistinct; (8) incisive foramina wide relative to lengths, their posterior margins located slightly in front of first molars; (9) posterior margin of bony palate situated anterior to back margins of third molars; (10) postpalatal length short relative to palatal length; (11) alisphenoid strut present in a few specimens;

TABLE 4

Presence (+) or Absence (−) of Certain Cusps and Cusplets on Molars in Species of *Bunomys*
(Number of cusps and cusplets are expressed as percentages; number of specimens are in parentheses)

Trait	*B. prolatus*	*B. chrysocomus*	*B. coelestis*	*B. andrewsi*	*B. penitus*	*B. fratrorum*	*B. heinrichi*
Cusp t3 on M2							
+	–	15 (3)	86 (25)	15 (3)	80 (16)	10 (12)	68 (13)
–	100 (4)	85 (17)	14 (4)	75 (17)	20 (4)	90 (8)	32 (6)
Cusp t3 on M3							
+	–	10 (2)	14 (4)	–	10 (2)	30 (6)	16 (3)
–	100 (4)	90 (18)	86 (25)	100 (20)	90 (18)	70 (14)	84 (16)
Anterior labial cusplet on m1							
+	–	55 (11)	4 (1)	–	5 (1)	–	–
–	100 (4)	45 (9)	96 (26)	100 (20)	95 (19)	100 (20)	100 (19)
Posterior labial cusplet on m1							
+	100 (4)	100 (20)	93 (25)	100 (20)	100 (20)	70 (14)	100 (19)
–	–	–	7 (2)	–	–	30 (6)	–
Anterior labial cusplet on m2							
+	100 (4)	100 (20)	100 (27)	100 (20)	45 (9)	10 (2)	100 (19)
–	–	–	–	–	55 (11)	90 (18)	–
Posterior labial cusplet on m2							
+	100 (4)	100 (20)	93 (25)	100 (20)	100 (20)	100 (20)	100 (20)
–	–	–	7 (2)	–	–	–	–
Anterior labial cusplet on m3							
+	75 (3)	65 (13)	89 (24)	15 (3)	–	–	42 (8)
–	25 (1)	35 (7)	11 (3)	85 (17)	100 (20)	100 (20)	58 (11)

(12) first upper molar with three roots; (13) cusp t4 complete on first and second upper molars, not divided into two elements; (14) cusp t3 present on second upper molar of most individuals; (15) posterior labial cusplet on second lower molar in about half the sample, on third molar in about one-fourth of sample.

DESCRIPTION: The following descriptions of pelage and other external traits are incomplete. Five specimens are represented only by skulls. Seven consist of skins and skulls. The pelts were dried on flat rectangles of cardboard, and large pieces of skin and fur—usually from the sides and venter—are missing from each specimen. One also lacks a tail. A gutted example is stored in fluid.

About the size of a houserat, *Maxomys wattsi* has a stocky body (weight of five individuals ranges from 110 to 130 g), short tail, and elongate hind feet (table 5). The long (up to 20 mm), thick, and soft fur covering upperparts of head and body is composed of three kinds of hairs. Nearly filamentous in appearance, hairs comprising the underfur are very thin, soft, gray for most of their lengths, and tipped with buff. The more robust overhairs are gray for three-fourths of their lengths; the distal fourth is a rich and dark buff. Guard hairs are scattered throughout the coat but are nearly undetectable because they are about the same diameter and length as the overhairs; all are gray for about two-thirds of their length, and tipped with dark brown or black. Both overhairs and guard hairs are thin and pliable; none are wide, flattened, or semirigid. Banding patterns of the different hairs combine in the dorsal coat to produce an overall brownish buff extending from nose to rump and covering thighs, shoulders, and proximal portions of forearms and shanks. The tone alters to dark brown along the back and over the rump, and grayish brown along sides of the body. The long gray sections of the hairs

TABLE 5

Measurements (in millimeters) of Adult *Maxomys wattsi* and *Maxomys musschenbroekii* from Sulawesi
(The mean plus or minus one standard deviation, range in parentheses, and number of specimens are listed for each measurement)

	M. wattsi		*M. musschenbroekii*				
	Holotype[a]	Gunung Tambusisi[b]	Gunung Tambusisi[c]	Northeastern peninsula[d]	Gunung Nokilalaki[e]	Southeastern peninsula[f]	Southwestern peninsula[g]
LHB	–	172.4 ± 7.2, 7 (164–185)	–	137.9 ± 10.1, 18 (115–155)	145.5 ± 7.6, 22 (131–158)	138.3 ± 9.4, 18 (123–153)	136.2 ± 11.6, 5 (120–148)
LT	125	137.0 ± 9.2, 8 (125–154)	–	132.2 ± 9.3, 16 (117–148)	128.5 ± 7.0, 22 (117–142)	131.6 ± 9.5 16 (112–146)	134.2 ± 8.0, 5 (122–144)
LHF	35	36.5 ± 1.1, 10 (35–38)	–	30.3 ± 7.6, 18 (30–33)	34.5 ± 1.4, 22 (32–38)	32.6 ± 1.2, 18 (31–35)	33.0 ± 1.9, 5 (31–36)
LE	–	23.9 ± 1.8, 7 (20–25)	–	–	20.6 ± 0.7, 22 (19–22)	17.3 ± 0.7, 18 (16–18)	16.8 ± 0.8, 5 (16–18)
GLS	41.6	41.4 ± 1.5, 11 (39.8–44.1)	36.0	35.3 ± 1.2, 27 (33.2–38.0)	36.4 ± 1.1, 22 (34.5–38.7)	35.9 ± 1.3, 14 (34.3–39.4)	34.9 ± 0.2, 3 (34.8–35.1)
ZB	19.4	18.6 ± 0.5, 11 (17.7–19.4)	14.9	16.0 ± 0.6, 27 (15.1–17.7)	17.2 ± 0.4, 22 (16.5–17.7)	16.6 ± 0.5, 15 (15.6–17.6)	15.8 ± 0.2, 2 (15.6–15.9)
IB	7.5	7.3 ± 0.2, 12 (6.9–7.7)	6.0	6.0 ± 0.2, 27 (5.5–6.4)	6.1 ± 0.2, 22 (5.6–6.7)	6.1 ± 0.2, 18 (5.6–6.4)	6.0 ± 0.3, 4 (5.6–6.3)
LR	14.7	14.6 ± 0.6, 12 (13.7–15.5)	11.9	11.8 ± 0.6, 27 (10.7–12.7)	11.4 ± 0.5, 22 (10.5–12.3)	11.7 ± 0.6, 18 (10.7–13.1)	11.4 ± 0.3, 5 (11.0–11.9)
BR	7.4	7.2 ± 0.5, 12 (6.5–7.8)	2.9	6.0 ± 0.3, 27 (5.6–6.8)	6.1 ± 0.2, 22 (5.7–6.4)	6.2 ± 0.3, 18 (5.7–6.8)	6.0 ± 0.3, 4 (5.5–6.2)
BZP	3.4	3.4 ± 0.2, 12 (2.9–3.7)	2.9	2.9 ± 0.2, 27 (2.5–3.6)	3.1 ± 0.2, 22 (2.7–3.5)	3.3 ± 0.3, 18 (2.7–3.7)	2.8 ± 0.3, 5 (2.5–3.2)
BBC	16.0	15.7 ± 0.3, 11 (15.2–16.2)	14.0	14.3 ± 0.3, 27 (13.6–15.0)	14.7 ± 0.3, 22 (14.2–15.3)	14.4 ± 0.3, 14 (13.9–15.1)	14.4 ± 0.2, 3 (14.2–14.5)
HBC	11.0	11.1 ± 0.2, 11 (10.7–11.4)	9.7	9.7 ± 0.3, 27 (9.3–10.5)	10.5 ± 0.3, 22 (10.2–11.3)	10.2 ± 0.3, 14 (9.8–10.9)	9.8 ± 0.4, 3 (9.4–10.0)
LD	10.9	10.4 ± 0.6, 12 (9.3–11.2)	8.7	8.6 ± 0.5, 27 (7.7–9.4)	8.9 ± 0.3, 22 (8.1–9.5)	8.7 ± 0.6, 18 (7.7–10.3)	8.7 ± 0.5, 4 (8.2–9.3)
PPL	15.0	14.7 ± 0.7, 12 (13.8–15.7)	12.5	13.0 ± 0.7, 27 (11.7–14.4)	13.4 ± 0.5, 22 (12.6–14.4)	13.3 ± 0.6, 17 (12.5–15.2)	12.6 ± 0.6, 4 (12.0–13.1)

TABLE 5—(*Continued*)

	M. wattsi		*M. musschenbroekii*				
	Holotype[a]	Gunung Tambusisi[b]	Gunung Tambusisi[c]	Northeastern peninsula[d]	Gunung Nokilalaki[e]	Southeastern peninsula[f]	Southwestern peninsula[g]
LIF	6.3	6.1 ± 0.3, 12 (5.7–6.4)	5.4	5.1 ± 0.4, 27 (4.4–5.8)	5.4 ± 0.3, 22 (4.9–6.2)	5.2 ± 0.3, 18 (4.6–6.0)	5.0 ± 0.2, 5 (4.8–5.3)
BIF	3.6	3.5 ± 0.2, 12 (3.2–3.8)	2.9	2.6 ± 0.2, 27 (2.2–3.2)	2.6 ± 0.2, 22 (2.3–3.0)	2.5 ± 0.2, 18 (2.1–2.8)	2.5 ± 0.1, 5 (2.4–2.7)
BP	6.8	6.9 ± 0.3, 12 (2.9–3.7)	6.4	5.5 ± 0.2, 27 (5.2–6.0)	6.2 ± 0.2, 22 (5.7–6.7)	6.0 ± 0.3, 18 (5.6–6.7)	6.3 ± 0.3, 4 (5.9–6.6)
BBPM1	3.5	3.4 ± 0.2, 12 (2.9–3.7)	2.9	3.0 ± 0.3, 27 (2.6–3.6)	2.9 ± 0.2, 22 (2.6–3.3)	3.0 ± 0.2, 18 (2.6–3.2)	2.9 ± 0.2, 4 (2.6–3.1)
BMF	3.1	3.2 ± 0.2, 12 (3.0–3.7)	3.2	2.6 ± 0.3, 27 (2.1–3.2)	2.9 ± 0.3, 22 (2.2–3.7)	2.7 ± 0.2, 18 (2.5–3.0)	2.6 ± 0.2, 4 (2.3–2.8)
LB	5.1	5.1 ± 0.2, 11 (4.9–5.3)	4.8	4.7 ± 0.2, 27 (4.3–5.1)	4.7 ± 0.2, 22 (4.4–5.0)	4.5 ± 0.7, 15 (4.3–4.9)	4.8 ± 0.1, 3 (4.7–4.9)
CLM1-3	6.4	6.5 ± 0.1, 12 (6.4–6.8)	6.2	5.7 ± 0.2, 27 (5.3–6.0)	6.3 ± 0.1, 22 (6.1–6.5)	6.0 ± 0.2, 17 (5.7–6.4)	6.0 ± 0.2, 5 (5.8–6.3)
BM1	2.1	2.1 ± 0.1, 12 (2.1–2.2)	1.9	1.8 ± 0.1, 27 (1.7–1.9)	2.0 ± 0.1, 22 (1.9–2.1)	1.9 ± 0.1, 17 (1.7–2.0)	1.9 ± 0.1, 5 (1.8–1.9)

[a] MZB 12155.

[b] MZB 12155, 12158–12160, 12163, and 12164; AMNH 265079–265081.

[c] AMNH 265082.

[d] Temboan, lowlands: USNM 217709, 217711, 217721, 217726, 217728–217732, 217735–217740, 217742, 217743, 217747, 217853, 217870, 217872, 217873–217875, 217885, 217889, and 2178900.

[e] Central Sulawesi, 7400–7500 feet: AMNH 223789, 223790, 223792, 223794, 225213, 225224, 225228, 225229, 225230–225236, 225239, 225240, 225242–225245, and 225247.

[f] Gunung Masembo, 500 meters: AMNH 101065 and 101106. Gunung Tanke Salokko, 1500 and 2000 meters: AMNH 101078–101082, 101084–101086, 101090, 101093, 101095–101097, 101101, 101103, and 101104.

[g] Bantimurung, lowlands: AMNH 101293. Gunung Lompobatang (Bonthain), 1100, 2000, and 2300 meters: AMNH 101017, 101188, 101189, and 101192.

show through everywhere the fur is parted. To the touch, the coat is soft and velvety; to the eye, it appears thick and also evenly contoured because the short guard hairs do not project beyond the overfur.

The ventral coat is shorter (up to 10 mm long) than fur covering the upperparts and contains two kinds of hairs. Underfur hairs are gray for most of their lengths and have silvery or white tips. Hairs comprising the overfur are gray for two-thirds of their length and solid white along the distal third. The width of this distal white band varies among individuals: when the bands are shorter the underparts appear gray and lightly frosted; when the bands are longer the ventral coat is whitish gray. On each specimen, either the frosted gray or the whitish gray extends from chin to base of tail and undersides of limbs. Like the dorsal coat, the central pelage is soft and dense. It is not sharply delimited in tone from the upperparts.

Mystacial, submental, superciliary, genal, and interramal vibrissae project from the fur of the head region. Interramal and submental vibrissae lack pigment; clumps in the other sets are either glossy dark brown with silvery tips or entirely unpigmented. Eyelids are dark brown. The ears are also dark brown and scantily covered with soft, short hairs on both inside and outside surfaces of the pinnae.

Sample of *M. wattsi* consist only of adults. Juvenile pelage will have to be described when specimens of that age group are obtained.

I cannot determine the mammary count of *M. wattsi*; too much of the ventral integument is missing from each of the females. Most other species of *Maxomys* have eight teats (a pectoral pair, postaxillary pair, and two inguinal pairs). *Maxomys bartelsii, M. inflatus,* and *M. dollmani* have six (they lack the pectoral pair), and I suspect that one of these combinations will be found in *M. wattsi* if better preserved material of that species is ever collected.

The tail in *M. wattsi* is conspicuously shorter than combined lengths of head and body (table 5) and very short relative to body length (79% of head and body). Its dorsal surface and sides are brown, its ventral surface white from base to tip. The underpart of the tail is also speckled with brown arranged in transverse rows because the scale hairs have brown bases and unpigmented tips. Three hairs arise from the base of each epidermal tail scale, and there are 13 or 14 overlapping rings of scales per centimeter (counted about a third of the distance from the rump) on each adult tail.

The front feet of *M. wattsi* are unpigmented on both dorsal and palmar surfaces. Tops of the metacarpal region and digits are densely covered by silvery hairs; a small silver tuft occurs at the base of each short and sharp ivory-colored claw. A large nail covers the moundlike vestigial pollex. The palmar surface is formed by three large interdigital pads, a medial thenar mound about the size of an interdigital, and a larger hypothenar (fig. 13).

The hind feet are long, narrow, and whitish. A very short hallux barely projects beyond the bases of the three medial digits. The fifth digit is longer, ending at the union of second and third phalanges of the fourth digit. Claws are ivory in tone, long, sharp, and larger than those on the front feet. The integument over dorsal surfaces of the foot, including digits, is unpigmented. In most individuals, the metatarsal region and digits are densely covered by long and silvery hairs all the way to ends of the digits where the hairs spring out over the claws, nearly concealing them. Some specimens have a pale brown metatarsal stripe or patch due to short brown hairs mixed with the silvery ones. Plantar surfaces are naked and pale brown, from the heel to ends of the digits. The array of plantar pads consists of four moderately sized interdigital mounds, a very small and round hypothenar, and a long and narrow thenar (fig. 13). A hypothenar occurs on all specimens in the sample available to me.

Dorsal, ventral, and lateral cranial views of *M. wattsi* are shown in figure 14; lateral and ventral regions are enlarged in figure 16. The outlines of a moderately long and broad rostrum, parallel zygomatic arches, wide interorbital region, rounded braincase, and deep occiput provide contours of the cranium from dorsal perspective. The nasals are oblanceolate in outline and give the distal portion of the rostrum a pointed configuration. Thin capsular walls of the nasolacrimal foramina bulge slightly on sides of the rostrum anterior to the zygomatic plates. Posterior to each capsule is the shallow outline of a zygomatic

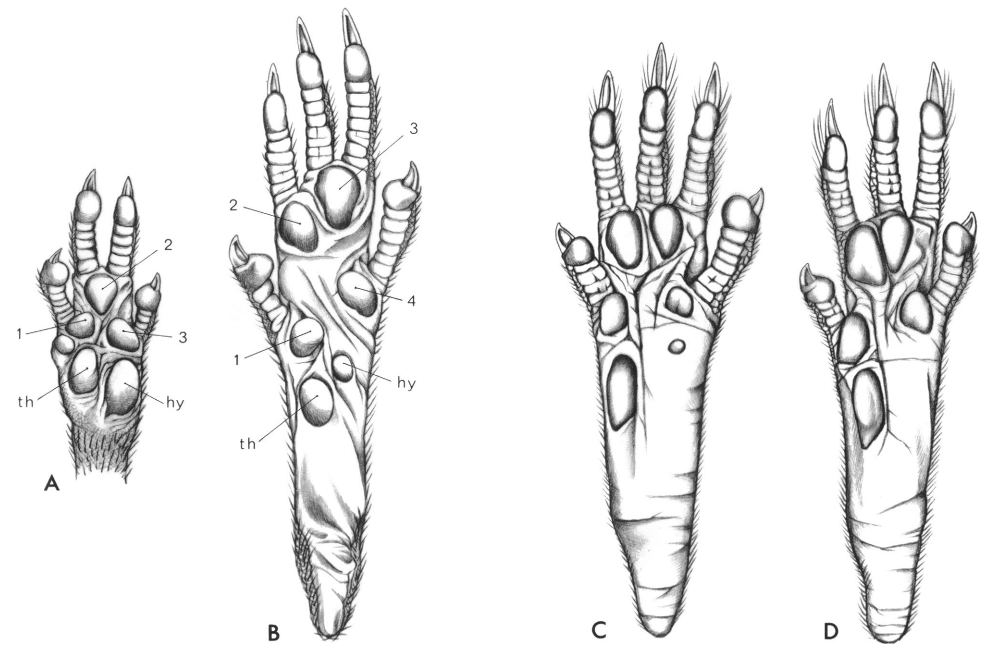

Fig. 13. Views of front and hind feet in species of *Maxomys*. **A,** palmar view of left front foot of *M. wattsi* (AMNH 249946). **B,** plantar view of left hind foot of the same individual. **C** and **D,** plantar views of left hind feet of *M. musschenbroekii* (AMNH 223802 and 223803, respectively) from Gunung Nokilalaki at 7500 ft. Note the small hypothenar pad in **C** and the absence of a comparable pad in **D.** A hypothenar pad occurs on the hind feet of all examples of *M. wattsi* but in any sampling of *M. musschenbroekii* about half of them lack such a pad. **hy,** hypothenar pad; **th,** thenar pad; **1-4,** first through fourth interdigital pads.

notch, which reflects a short anterior spine. The interorbit is broad and its dorsolateral margins smoothly rounded, undefined by ridges or beading. In contrast, the postorbital margins are marked by inconspicuous beading that sweeps caudad to form small triangular projections at the union of frontals and parietals, and then extends as indefinite temporal lines to the occiput. The anterior borders of the occiput are indicated by low lamboidal ridges behind which is a moderately deep occipital region capped almost entirely by the interparietal; that element barely projects between the parietals. Sides of the braincase are nearly vertical from the temporal beading to squamosal roots of the zygomatic arches. The zygomata are sturdy and project slightly laterally to connect braincase and rostrum in two parallel bony strands.

The characteristic outline of the cranium of *M. wattsi* is evident in ventral view (fig. 14), and several distinctive landmarks are visible. The triangular-shaped nasal tips and converging premaxillaries combine to extend the nasal aperature well anterior to the front faces of the incisors. The outline of the sturdy rostrum is broken only by the slightly swollen nasolacrimal capsules. The diastemal region is breached by short and very wide incisive foramina (mean value for the ratio, incisor breadth divided by length, is 57% for 12 specimens). The posterior margins of these openings are either even with front faces of the first molars or slightly anterior to them (the mean distance between ends of foramina and molar faces for 12 specimens is 0.26 mm, the standard deviation is 0.16, and the range is 0.0–0.5). The bony palate is wide, partly a reflection of the toothrows that diverge posteriorly, and short—its posterior edge is either even with backs of the third molars or sits just anterior to them (the mean distance between margin and molar backs for 12 specimens is 0.32 mm, the standard deviation is 0.13, and the range is 0.0–0.5). The palate is perforated by a pair of posterior palatine fo-

Fig. 14. Views (×2) of the cranium and dentary of the holotype of *Maxomys wattsi* (MZB 12155) from Gunung Tambusisi.

ramina opposite the union of second and third molars, and by nutrient foramina of various diameters near the bony posterior margin (fig. 16B). A broad mesopterygoid fossa is posterior to the bony palate; its dorsoventral walls are breached by sphenopalatine vacuities that range in size from small to medium (fig. 16B) among the crania in which that area was not destroyed by excessive cleaning. The postpalatal region (from the posterior margin of the bony palate to the ventral lip of the foramen magnum) is short relative to palatal length (mean of 78% of palatal length for the 12 specimens). The pterygoid plates on either

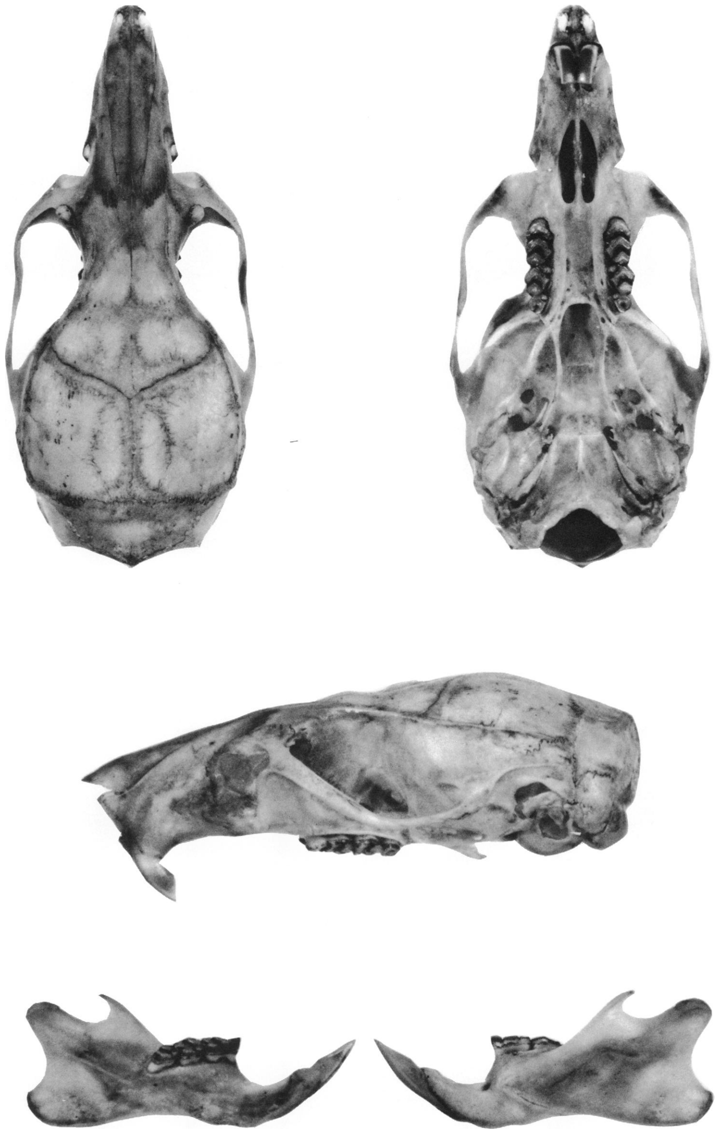

Fig. 15. Views (×2) of the cranium and dentary of an adult *Maxomys musschenbroekii* (AMNH 225213) from Gunung Nokilalaki, central Sulawesi.

side of the mesopterygoid fossa are long, narrow, and their surfaces nearly horizontal, which results in shallow pterygoid fossae. Each plate is entire (not perforated by a sphenopterygoid vacuity) for most of its length. The smooth lateral edge of the plate transforms into a swollen, moundlike posterolateral margin. Medial to this swelling is a wide groove in which the infraorbital branch of the stapedial artery passes. The place where the artery leaves the groove and extends onto the dorsal surface of the pterygoid plate defines the posterior opening of the alisphenoid canal, which is part of the opening in the pterygoid plate through which the foramen ovale can be seen (fig. 16B). A spacious medial lacerate foramen separates the back of each pterygoid plate from the small, uninflated auditory bulla. Attached to the bulla is a long and bony eustachian tube. Between

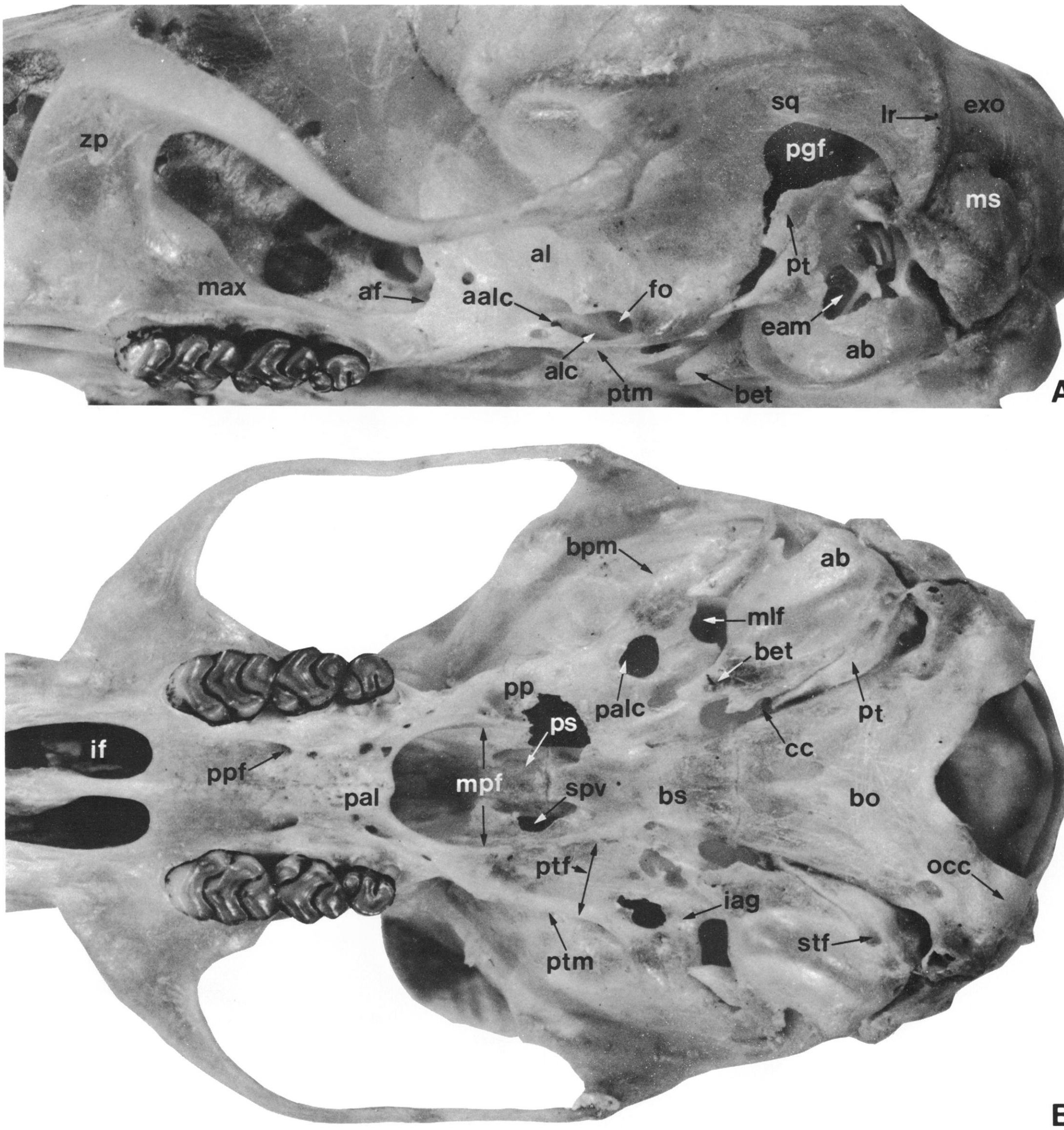

Fig. 16. Lateral (**A**) and ventral (**B**) cranial views of *Maxomys wattsi* (AMNH 12155, holotype). **aalc,** anterior opening of alisphenoid canal; **ab,** auditory bulla; **af,** anterior alar fissure; **al,** alisphenoid; **alc,** alisphenoid canal; **bet,** bony eustachian tube; **bo,** basioccipital; **bpm,** bulbous pterygoid plate margin; **bs,** basisphenoid; **cc,** common carotid canal; **eam,** external auditory meatus; **exo,** exoccipital; **fo,** foramen ovale; **iag,** groove for the infraorbital branch of the stapedial artery; **if,** incisive foramina; **lr,** lamboidal ridge; **max,** maxillary; **mlf,** middle lacerate foramen; **mpf,** mesopterygoid fossa; **ms,** mastoid portion of the petromastoid; **occ,** occipital condyle; **pal,** palatine; **palc,** 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); **pgf,** postglenoid foramen; **pp,** pterygoid plate; **ppf,** posterior palatine foramen; **ps,** presphenoid; **pt,** periotic; **ptf,** pterygoid fossa; **ptm,** pterygoid plate margin; **ptr,** pterygoid ridge; **sq,** squamosal; **spv,** sphenopalatine vacuities; **zp,** zygomatic plate.

bullar and petrosal is a large stapedial foramen near the posteroventral margin of the bulla (fig. 16B).

Visible in side view is the posterior margin of the deep occiput, which overhangs the occipital condyles; the short ascent from back of the cranium to its apex at the top of the braincase; and the long, straight dorsal contour to the nasal tips. The rostrum, from the anteroventral base of the zygomatic plate to the anterior margin of the premaxillary, is rectangular in outline. This configuration primarily reflects the even dorsal contour of the nasals and the high anterodorsal margin of each premaxillary, which nearly touches the ventral surfaces of the nasal tips. Each zygomatic plate is narrow relative to overall size of the cranium, and its anterior edge slants forward from dorsal to ventral root. The anterior spine, however, barely projects craniad of the dorsal maxillary root. Anterior to the zygomatic plate is the fully exposed nasolacrimal capsule and nasolacrimal formamen. The squamosal root of each zygomatic arch is moderately high on sides of the braincase, and its caudal margin curves against the braincase to the occiput as a nearly undetectable ridge. The mastoid portion of the periotic complex is slightly inflated and without perforations. The squamosal above each auditory capsule and just anterior to the lamboidal ridge is complete (not penetrated by a squamoso-mastoid foramen). A huge postglenoid foramen separates the periotic and bullar capsule from the squamosal; the opening is generally not confluent with the medial lacerate foramen (fig. 16A). The small size of the bullar capsule relative to cranial expanse can be appreciated in the lateral view of the cranium. Below the squamosal root of the zygomatic arch and just dorsal to the thin edge of the pterygoid plate is an alisphenoid canal. The small foramen at the front of the canal (hidden by a bony spur in some specimens) is the anterior opening of the alisphenoid canal; the hole at the back is the foramen ovale. The infraorbital branch of the stapedial artery passes along the open canal through the anterior opening into the orbit via the anterior alar fissure (fig. 16A). An alisphenoid strut is absent from both sides of the cranium in 8 of the 12 specimens. In the holotype, a strut is absent from the right side but represented on the left by a descending projection (fig. 16A). In another individual (MZB 12162), there is a threadlike strut on the right side but nothing on the left. One specimen (MZB 12158) has a wide strut on each side (fig. 17), and another (MZB 12157) has a wide strut on the right side but nothing on the left. When present, the strut defines the anterior margin of the foramen ovale accessorius and separates it from the buccinator-masticatory foramina (fig. 17); when the strut is absent, the large oval opening represents the coalescence of those foramina (fig. 16A). The configuration of bone and cephalic arterial pattern in *M. wattsi* occurs in other species of *Maxomys* and is widespread throughout murids.

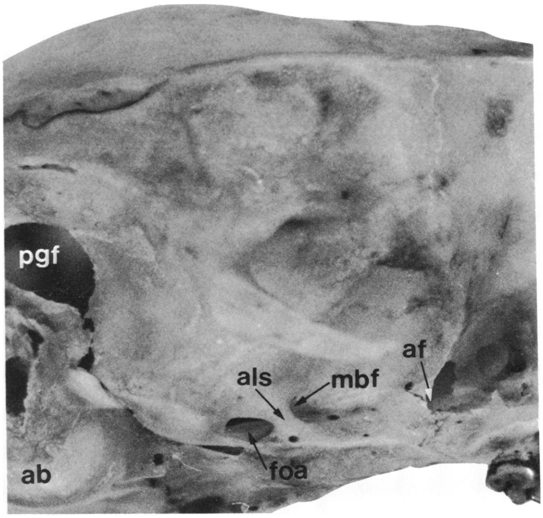

Fig. 17. Lateral view of *Maxomys wattsi* (MZB 12158) showing the alisphenoid region. An alisphenoid strut (**als**), which is not present on MZB 12155 shown in figure 16, separates a foramen ovale accessorius (**foa**) from the masticatory-buccinator foramen (**mbf**). This alisphenoid configuration is not common in the sample of *M. wattsi* (see text). **ab**, auditory bulla; **af**, anterior alar fissure; **pgf**, postglenoid foramen.

Each dentary of *M. wattsi* appears sturdy (fig. 14). As in other species of *Maxomys*, the coronoid process is small and delicate (Musser, 1981: 272; Musser et al., 1979). A deep concavity between condyloid and angular projections defines the back of the dentary. The capsule over the end of the incisor forms a slight bulge beneath the coronoid. The body

Fig. 18. Views (×12) of alveoli for right molar roots in *Maxomys wattsi* (MZB 12163). **Left,** ventral view of upper alveoli (three alveoli per molar). **Right,** dorsal view of lower alveoli (two per molar except the first which also has a labial socket). **ant,** alveolus for anterior root; **lab,** labial alveolus; **ling,** lingual; **post,** posterior.

of the ramus is deep and the masseteric ridge is weakly developed. On the medial surface of the dentary, the shelf behind the molar row extends as a ridge beneath the mandibular foramen to end just posterior to it, not at the articular surface of the condyle, which is the configuration in species of other genera (Musser, 1981: 272).

Upper and lower incisors of *M. wattsi* are not unusual (fig. 14). Both sets appear sturdy, their enamel is orange, and the uppers are mildly opisthodont in their curvature outside the alveoli.

The pattern of molar roots in the sample of *M. wattsi* is simple and primitive for murids (Musser and Newcomb, 1983). Three large roots, their positions and bulk reflected by the alveoli illustrated in figure 18, anchor each upper molar. Two large roots, their locations and size indicated by the alveoli in figure 18, fasten each lower molar to the mandible. A small labial rootlet forms an added holdfast to each first lower molar.

Molars of *M. wattsi* are robust, wide, and low-crowned (brachyodont). Within the upper rows, the first tooth inclines slightly against the anterior margin of the second, and it leans against the third. Within the lower row, the third molar leans slightly against the second, and that tooth rests on the first. The laminae and cusps of all the molars are situated closely adjacent to one another.

Coronal patterns of the molars are very simple, primarily consisting of laminae and cusps (figs. 19 and 20). For example, the pattern characteristic of each first upper molar is formed by two chevron-shaped laminae and a posterior cusp resembling the shape of a diamond with its edges rounded (fig. 19A, B). Each lamina represents the coalescence of three cusps; the bulky posterior mass is a large cusp t8 that has merged with the labial cusp t9 to the point that the latter is barely recognizable. A large cusp t1, a single chevron, and the coalesced posterior mass of cusps t8 and t9 form each second upper molar. A very small cusp t3 sits low on the anterolabial border of the tooth in 9 out of the 12 individuals; it is absent in three specimens. The small third upper molar consists of a large oblong cusp t1, a dumbell-shaped lamina composed of cusp t4 and a larger cusp t5 (cusp t6 is apparently absent from the lamina or if present is undetectable because it has so fully coalesced with cusp t5), and an oval cusp t8 that forms the back of the tooth (there is no sign of cusp t9). The anterolabial margin of the third molar is devoid of cusp t3, a configuration common to all specimens in the sample. Also absent from each of the upper molars is a cusp t7, a posterior cingulum, and enamel projections from the lamina and cusps or enamel bridges between them.

Occlusal surfaces of the first lower molars consist of an oblong anteroconid formed from the fusion of anterolabial and anterolingual cusps, and behind that two chevron-shaped laminae and an elliptical posterior cingulum plastered against the back margin of the second lamina (fig. 20A, B). Two bulky chevrons form most of the chewing surface of each second lower molar, and a round or oval posterior cingulum sits at the back of the tooth. An anterior lamina and a round-to-oblong, large posterior cusp are the simple elements of the third molar. Accessory cusps and cusplets are uncommon. For example, none of the specimens has an anterocentral cusp, an element of the anteroconid in some other murines (Musser and Newcomb, 1983). An anterior labial cusplet does not occur on any of the lower molars in any of the individuals I have examined. And of 11 rats (teeth were too worn in the 12th specimen), a posterior labial cusplet (fig. 20A) occurs on the first molar of two specimens but not on any of the others; and it also is present on the second molar of six individuals and absent from five.

COMPARISONS: The combination of characters listed in the diagnosis of *Maxomys wattsi* will distinguish this species from samples of any other species of *Maxomys*. Certain diagnostic traits are especially distinctive. The short tail (relative to head and body length) and short postpalatal length (relative to palatal length), for example, are sufficient to separate *M. wattsi* from any of the other *Maxomys*. Of the 13 species that occur outside Sulawesi (Musser et al., 1979), *M. wattsi* is larger in body size (as indexed by length of head and body and greatest length of skull; table 6) than seven of them (*alticola, bartelsii, baeodon, hylomyoides, inas, ochraceiventer,* and *whiteheadi*), smaller than three (*pagensis, panglima,* and *rajah*), and about the same size as three (*moi, inflatus,* and *surifer*).

In addition to *M. wattsi,* three other species of *Maxomys* have been described from Sulawesi. *Maxomys hellwaldii* occurs throughout the island at altitudes extending from near the coast to about 3200 ft in lowland evergreen tropical rain forest (Musser, 1969, 1987); *M. dollmani* is found in lower montane evergreen tropical forest in highlands of the southeastern peninsula and southern part of central Sulawesi (Musser, 1969, 1987); and *M. musschenbroekii* occurs in forests from coastal lowland up to mountain summits throughout Sulawesi (Musser, 1987).

The traits diagnostic for *M. wattsi* will, in combination, distinguish it from all three of the other Sulawesian species. Some traits taken individually are enough to separate the species. *M. hellwaldii* is larger than *M. wattsi* (tables 6 and 7), has a longer tail (both in absolute length and relative to head and body

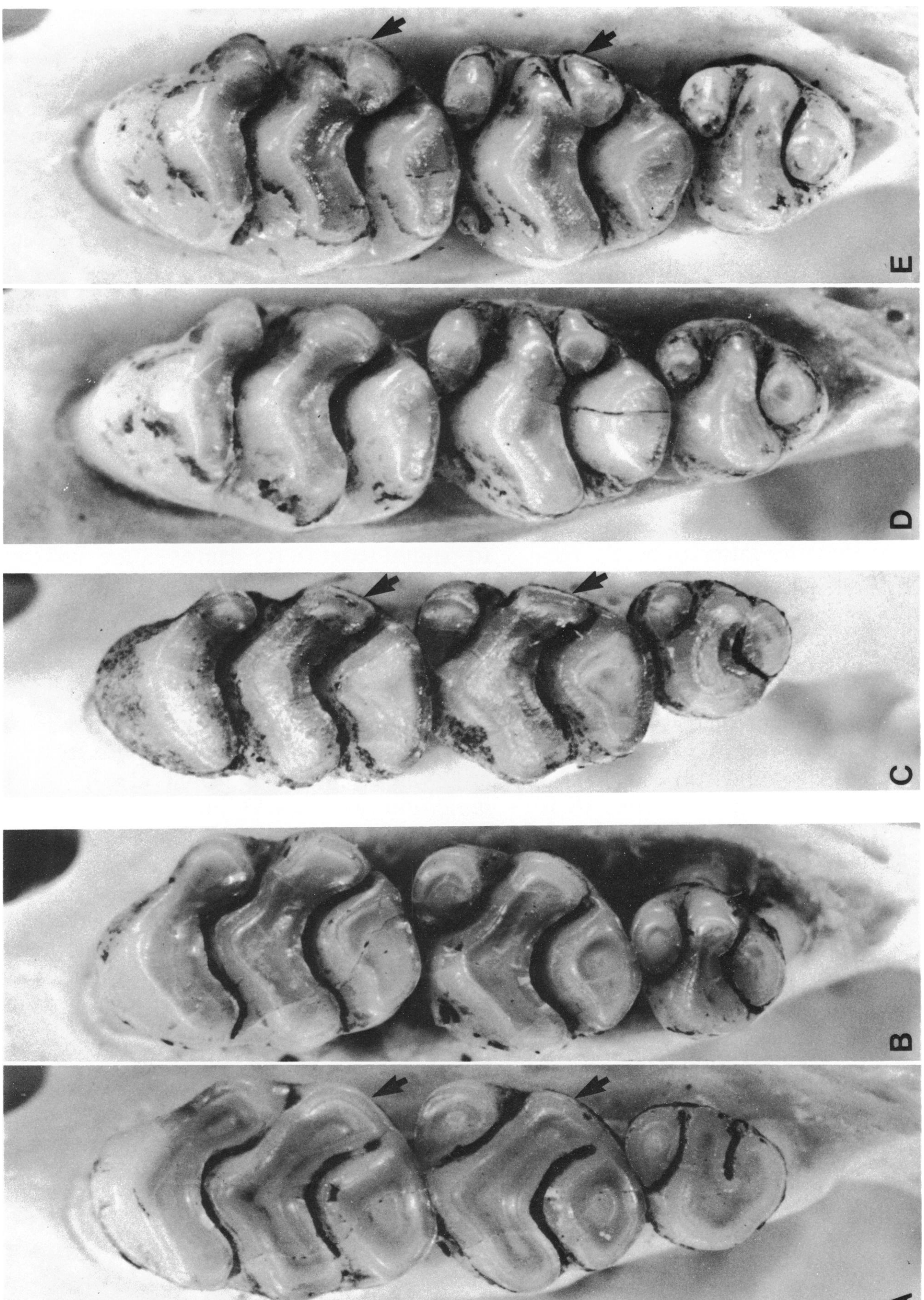

Fig. 19. Occlusal views of right upper molar rows (approximately ×14) in species of *Maxomys*. **A,** *M. wattsi*, adult (MZB 12155, holotype). **B,** *M. wattsi*, young adult (AMNH 265081). **C,** *M. musschenbroekii*, young adult (AMNH 225211). **D,** *M. hellwaldii*, juvenile (AMNH 224940). **E,** *M. hellwaldii*, juvenile (AMNH 224922). Arrows point to cusp t4, which is undivided in *M. wattsi* and *M. musschenbroekii* but completely or partially divided in *M. hellwaldii*.

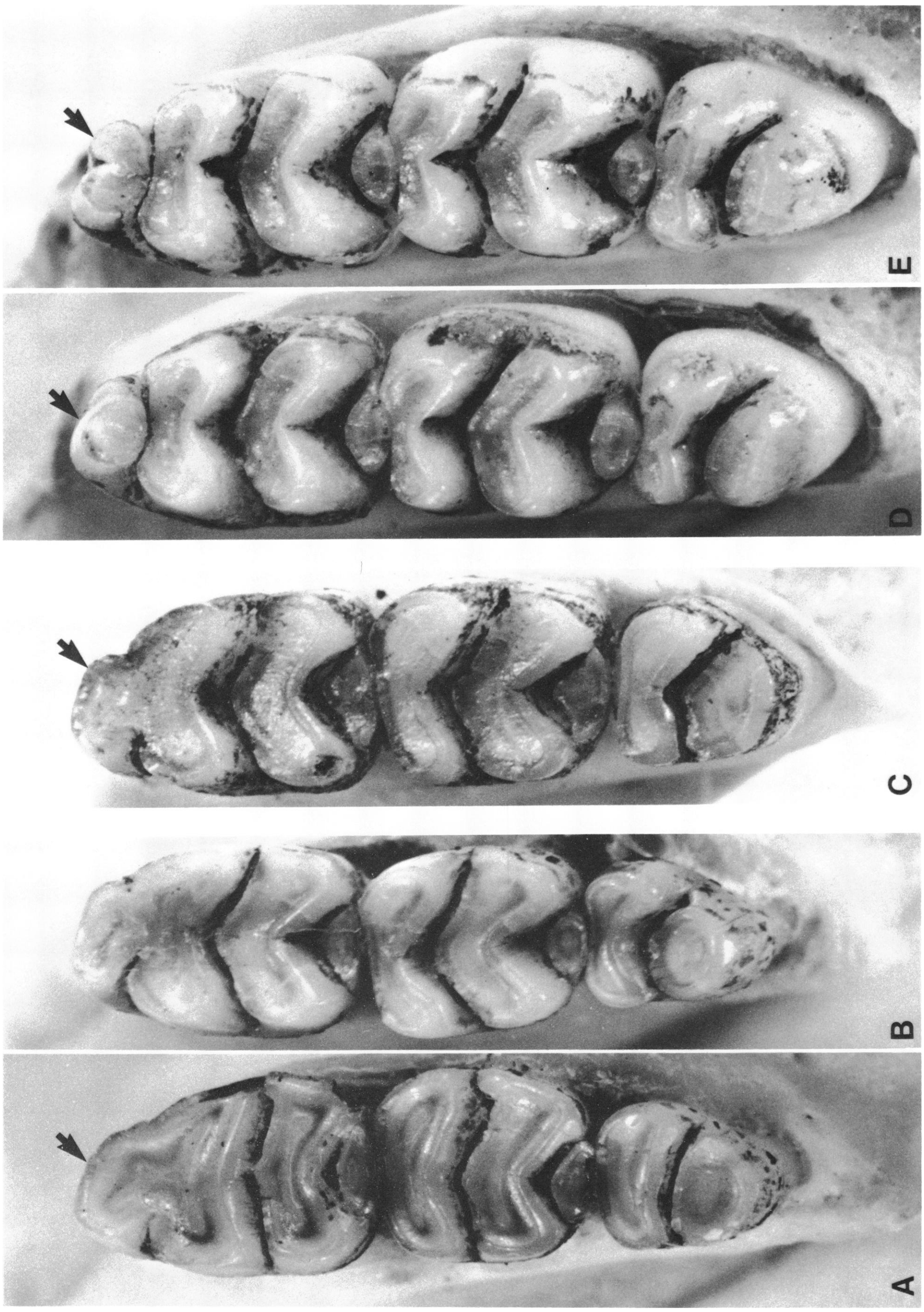

Fig. 20. Occlusal views of right lower molars (approximately ×14) of the same specimens of *Maxomys* illustrated in figure 19. **A,** *M. wattsi* (holotype). **B,** *M. wattsi.* **C,** *M. musschenbroekii.* **D,** *M. hellwaldii.* **E,** *M. hellwaldii.* Arrows point to anteroconids that are undivided or bilobed.

TABLE 6
Comparisons of Selected Measurements (in millimeters) and Ratios (in percentages) Between *Maxomys wattsi* and other Species of *Maxomys*[a]
(The mean, sample size in parentheses, and range are provided for each measurement)

Species	LHB	LT	GLS	CLM1-3	LT/LHB	BR/LR	PPL/PL	CLM1-3/GLS
Indochina								
M. moi	167.9 (26) 142–208	176.8 (24) 157–202	43.4 (26) 40.3–45.9	5.8 (22) 5.5–6.2	105	53	90	13
Sunda Shelf								
M. alticola	153.7 (23) 139–176	161.2 (21) 128–176	39.5 (23) 37.0–41.7	5.5 (20) 5.2–5.8	105	48	92	14
M. bartelsii	145.6 (27) 127–178	147.7 (26) 117–170	37.3 (17) 34.8–40.0	5.2 (24) 4.9–5.5	101	49	93	14
M. baeodon	133.8 (6) 126–140	124.0 (3) 119–133	34.1 (5) 33.2–35.2	4.5 (1)	93	—	—	13
M. hylomyoides	125.9 (8) 114–132	119.8 (8) 98–132	33.0 (6) 31.3–34.2	6.1 (8) 5.8–6.4	95	56	88	18
M. inas	147.5 (10) 124–162	149.2 (10) 135–167	37.7 (6) 36.1–40.3	6.3 (6) 6.1–6.4	101	57	99	17
M. inflatus	171.1 (35) 160–193	165.4 (34) 143–190	43.6 (31) 40.8–47.1	6.2 (6) 6.0–6.3	97	67	85	14
M. ochraceiventer	152.8 (20) 140–171	153.5 (18) 130–175	37.9 (13) 35.3–39.6	5.4 (13) 5.2–5.6	101	50	95	14
M. pagensis	196.8 (20) 170–218	179.3 (20) 163–204	47.4 (19) 44.7–49.4	7.0 (19) 6.5–7.5	91	54	91	15
M. panglima	197.9 (22) 167–222	201.9 (22) 180–226	47.6 (10) 45.5–48.6	6.8 (9) 6.5–7.1	102	55	88	14
M. rajah	192.9 (13) 166–226	184.1 (12) 162–210	45.1 (13) 40.9–48.6	6.8 (14) 6.6–7.1	95	55	82	15
M. surifer	176.8 (29) 160–191	172.9 (27) 146–148	41.9 (28) 39.4–46.1	5.8 (29) 5.3–6.8	98	55	89	14
M. whiteheadi	110.8 (22) 100–126	96.7 (21) 88–108	31.2 (21) 29.2–33.7	5.2 (20) 4.9–5.5	87	59	91	17
Sulawesi								
M. dollmani	158.9 (7) 145–175	203.3 (7) 180–221	41.4 (9) 38.7–43.7	5.9 (7) 5.7–6.1	128	51	97	14
M. hellwaldii	206.8 (48) 192–220	181.8 (41) 165–200	47.4 (48) 44.1–49.9	7.1 (48) 6.7–7.7	88	50	93	15
M. musschenbroekii	145.5 (22) 131–158	128.5 (22) 117–142	36.4 (22) 34.5–38.7	6.3 (22) 6.1–6.5	87	59	91	17
M. wattsi	172.4 (7) 164–185	137.0 (8) 125–154	41.4 (11) 39.8–44.1	6.5 (12) 6.4–6.8	79	49	77	16

[a] Ratio values for all species except *M. wattsi* are from Musser et al. (1979, table 3).

length), and a much longer postpalatal length (relative to palatal length). Furthermore, the postorbital and temporal ridges are more pronounced on *M. hellwaldii* (contrasting adults of similar ages; fig. 21), and the two species differ in form of certain cusps. In nearly every specimen examined of *M. hellwaldii*, cusp t4 on the first and second upper molar is either entirely or partially divided into two small cusps (fig. 19D, E); cusp t4 is undivided in

TABLE 7

Summary of Sizes (in millimeters), and Proportions (in percentages), Characterizing Adults in Species of Sulawesian *Maxomys*

(The mean plus or minus one standard deviation, range in parentheses, and number of specimens are recorded for each measurement)

Measurement and ratio	Species of *Maxomys*			
	M. hellwaldii[a]	*M. dollmani*[b]	*M. wattsi*[c]	*M. musschenbroekii*[d]
LHB	206.8 ± 7.7, 48 (192–200)	162.1 ± 7.3, 7 (150–175)	172.4 ± 7.2, 7 (164–185)	145.5 ± 7.6, 22 (131–158)
LT	181.8 ± 9.0, 41 (165–200)	207.2 ± 10.2, 6 (195–221)	137.0 ± 9.2, 8 (125–154)	128.5 ± 7.0, 22 (117–142)
LT/LHB	88	128	79	88
LHF	42.2 ± 1.2, 48 (44–49)	37.4 ± 0.5, 7 (37–38)	36.5 ± 1.1, 10 (35–38)	34.5 ± 1.4, 22 (32–38)
GLS	47.4 ± 1.3, 48 (44.1–49.9)	42.0 ± 1.1, 7 (40.8–43.7)	41.4 ±1.5, 11 (39.8–44.1)	36.4 ± 1.1, 22 (34.5–38.7)
BBC	18.8 ± 0.4, 48 (17.9–19.6)	16.6 ± 0.3, 7 (16.3–17.0)	15.7 ± 0.3, 11 (15.2–16.2)	14.7 ± 0.3, 22 (14.2–15.3)
LB	5.4 ± 0.2, 48 (5.1–5.8)	5.6 ± 0.2, 5 (5.3–5.8)	5.1 ± 0.2, 11 (4.9–5.3)	4.7 ± 0.2, 22 (4.4–5.0)
LB/GLS	11	13	12	13
CLM	7.1 ± 0.2, 48 (6.7–7.7)	5.9 ± 0.2, 7 (5.7–6.1)	6.5 ± 0.1, 2 (6.4–6.8)	6.3 ± 0.1, 22 (6.1–6.5)
CLM/GLS	15	14	16	17
BM	2.2 ± 0.1, 48 (2.1–2.4)	1.8 ± 0.1, 7 (1.7–1.9)	2.1 ± 0.1, 12 (2.1–2.2)	2.0 ± 0.1, 22 (1.9–2.1)

[a] Sample is from the Sungai Miu-Sadaunta region of Central Sulawesi, 960–3200 ft.
[b] Sample is from southeastern Sulawesi (Musser, 1969).
[c] Data are from table 5.
[d] Data are from Gunung Nokilalaki sample (table 5).

all specimens of *M. wattsi* (fig. 19A, B). The anteroconid in *M. hellwaldii* consists of either an oval cusp or a bifurcate structure composed of partially fused anterlabial and anterolingual cusps (fig. 20D, E); examples of *M. wattsi* possess an elongate undivided anteroconid (fig. 20A, B).

Maxomys dollmani resembles *M. wattsi* in body size (tables 6 and 7) but has a much longer tail (in absolute length as well as relative to head and body length), larger bullae, much shorter toothrows, and narrower first upper molar. Its molar coronal patterns resemble those of *M. hellwaldii,* particularly cusp t4, which is either completely or partially divided. In overall configuration, the cranium of *M. dollmani* is more like that of *M. hellwaldii* than of *M. wattsi* (figs. 21 and 22).

Maxomys wattsi and *M. musschenbroekii* are sympatric at Tambusisi Damar, 4700 ft, where two of the latter (AMNH 265082 and MZB 12167) were collected along with the other species during March 1980. In external traits as well as features of the skull and dentitions, those two specimens resemble samples of *M. musschenbroekii* collected from elsewhere on Sulawesi (table 5). To my knowledge, no other species of *Maxomys* has been collected at the same place as *M. wattsi.*

Maxomys musschenbroekii is much smaller than *M. wattsi* in body size (tables 5–7) but has a proportionally longer tail (table 7). It also has darker upperparts, and in any sam-

Fig. 21. Dorsal views (×2) comparing adult crania from the Sulawesian species of *Maxomys*. From left to right: *M. hellwaldii* (AMNH 224941), central region; *M. dollmani* (AMNH 101094), southeastern arm; *M. wattsi* (MZB 12155, holotype), Gunung Tambusisi; and *M. musschenbroekii* (AMNH 225213), central region.

Fig. 22. Ventral views (×2) of the crania shown in figure 21. From left to right: *M. hellwaldii*, *M. dollmani*, *M. wattsi*, and *M. musschenbroekii*.

ple about half the specimens lack a hypothenar pad on the plantar surface of the hind foot (fig. 13); a comparable pad is present on all examples of *M. wattsi.*

Crania and dentaries of the two species are contrasted in figures 14 and 15. Absolute size is an obvious distinguishing trait but other differences exist. For its size, *M. musschenbroekii* has more pronounced postorbital and temporal ridging, a wider rostrum relative to its length, and a longer postpalatal length relative to palatal length (tables 6 and 7).

The two species differ in number of roots anchoring upper molars. Three roots anchor each first and second upper molar in *M. wattsi.* Examples of *M. musschenbroekii* have three comparable roots but also a fourth, which represents the division of a single large labial root (as seen in *M. wattsi*) into two smaller roots.

Molar occlusal patterns of the two species are closely similar (figs. 19 and 20). Like the Tambusisi rat, *M. musschenbroekii* has an undivided cusp t4 on first and second upper molars.

Specimens of *M. wattsi* possess a distinctive suite of external, cranial, and dental features when compared with the other species of *Maxomys.* Whether used in combination or smaller sets, these traits easily distinguish the Tambusisi animal. No other species of *Maxomys* is quite like it. However, the usefulness of the diagnostic features in assessing phylogenetic relationships between *W. wattsi* and the other *Maxomys* requires resolution. Determining its cladistic position will come from a systematic revision of the genus, and an evaluation of the primitive versus derived polarities of the characters associated with each species.

A BIOGEOGRAPHIC NOTE

Bunomys prolatus was collected in upper montane forest, and *Maxomys wattsi* was found in that formation as well as lower montane forest (Watts, personal commun.). In the mountains of the central and southeastern regions of the island, the common—and usually only—species of *Bunomys* found in montane evergreen rain forest formations is *B. penitus* (Musser, 1987 and personal obs.); it is abundant in those environments on all highlands that have been sampled. However, Watts did not obtain it on Gunung Tambusisi where *B. prolatus* was the common *Bunomys* encountered.

Bunomys chrysocomus is the other species in the genus that occurs with *B. penitus* in parts of its range. It is common at low and middle altitudes in tropical lowland evergreen rain forest but also extends into lower montane formations, where it is sympatric with *B. penitus*; it does not extend all the way up into upper montane forest (Musser, MS and personal obs.). Most of Watts' specimens of *B. chrysocomus* were trapped in lower montane forest; one specimen, however, was caught at about the same elevation as the specimens of *B. prolatus.* Watts (personal commun.) 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.* So on Gunung Tambusisi, *B. chrysocomus* and *B. prolatus* apparently have a distributional relationship somewhat similar to that of *B. chrysocomus* and *B. penitus* in the central core and southeastern arm of Sulawesi.

Maxomys wattsi is not only distinctive in its morphology but it is unusual in its altitudinal distribution in that it is the only large-bodied Sulawesian species of the genus that seems to be restricted to lower and upper montane forest. *Maxomys dollmani,* of about the same body size, occurs in both lowland tropical evergreen rain forest and lower montane formations but has never been trapped in moss forest (Musser, 1987, MS and personal obs.). The small-bodied *M. musschenbroekii,* which is sympatric with *M. wattsi,* occurs throughout Sulawesi at elevations ranging from near sea level to summits of mountains. No other kinds of *Maxomys* have been recorded from montane forests on Sulawesi.

Clearly, certain small-mammal elements of the fauna in the montane forest on flanks and ridges of Gunung Tambusisi are different from those found elsewhere in Sulawesi. The Tambusisi highlands deserve further biological exploration to determine the actual number of species found there as well as their altitudinal distributions as revealed in transect studies from coastal plain to summit.

REFERENCES

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

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

Carleton, M. D., and G. G. Musser
1984. Muroid rodents. *In* S. Anderson and J. K. Jones (eds.), Orders and families of Recent mammals of the world, pp. 289–379. New York: Wiley.
1989. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): a synopsis of *Microryzomys*. Bull. Am. Mus. Nat. Hist. 191: 83 pp.

Durden, L. A., and G. G. Musser
1991. A New Species of Sucking Louse from a Montane Forest Rat in Central Sulawesi and a Preliminary Interpretation of the Sucking Louse Fauna of Sulawesi. Am. Mus. Novitates, in press.

Miller, G. S., Jr.
1912. Catalogue of the mammals of Western Europe (Europe exclusive of Russia) in the collection of the British Museum. London: British Museum (Nat. Hist.), 1019 pp.

Miller, G. S., Jr., and N. Hollister
1921. Descriptions of sixteen new murine rodents from Celebes. Proc. Biol. Soc. Washington 34: 67–76.

Musser, G. G.
1969. Results of the Archbold Expeditions. No. 92. Taxonomic notes on *Rattus dollmani* and *Rattus hellwaldii* (Rodentia, Muridae) of Celebes. Am. Mus. Novitates 2386: 24 pp.
1970. Results of the Archbold Expeditions. No. 93. Reidentification and reallocation of *Mus callitrichus* and allocations of *Rattus maculipilis, R. m. jentinki,* and *R. microbullatus* (Rodentia, Muridae). Ibid., 2440: 35 pp.
1981. Results of the Archbold Expeditions. No. 105. Notes on systematics of Indo-Malayan murid rodents, and descriptions of new genera and species from Ceylon, Sulawesi, and the Philippines. Bull. Amer. Mus. Nat. Hist. 168: 225–334.
1987. The mammals of Sulawesi. *In* T. C. Whitmore (ed.), Biogeographical evolution of the Malay Archipelago, pp. 73–93. Oxford: Clarendon Press.

Musser, G. G., and C. Newcomb
1983. Malaysian murids and the giant rat of Sumatra. Bull. Am. Mus. Nat. Hist. 174: 327–598.

Musser, G. G., J. T. Marshall, Jr., and Boeadi
1979. Definition and contents of the Sundaic genus *Maxomys* (Rodentia, Muridae). J. Mamm. 60: 592–606.

Tate, G. H. H., and R. Archbold
1935. Results of the Archbold Expeditions. No. 2. Twelve apparently new forms of *Rattus* from the Indo-Australian region. Am. Mus. Novitates 802: 10 pp.