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Authors: MUSSER, GUY G., and DURDEN, LANCE A.

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Sulawesi Rodents: Description of a New Genus and Species of Murinae (Muridae, Rodentia) and Its Parasitic New Species of Sucking Louse (Insecta, Anoplura)

GUY G. MUSSER[1] AND LANCE A. DURDEN[2]

ABSTRACT

The murine rodent, *Sommeromys macrorhinos*, new genus and species, is described from a single specimen collected at 2400 m near the summit of Gunung Tokala in central Sulawesi. The species is insectivorous and a member of the tropical upper montane rain forest fauna of the island. With its small body, elongate rostrum, long and slender hind feet, very long tail, and brownish gray fur, *S. macrorhinos* superficially resembles the long-tailed and small-bodied shrew rat, *Tateomys macrocercus*, another Sulawesian upper montane forest endemic. *Sommeromys macrorhinos*, however, possesses a combination of derived external, cranial, and dental traits, along with a unique rostral shape, that dissassociates it from any relationship with not only *T. macrocercus* and its close allies *T. rhinogradoides* and *Melasmothrix naso*, but with also the large-bodied shrew rats of Sulawesi (*Echiothrix*) and those indigenous to the Philippines (*Archboldomys*, *Rhyncomys*, *Chrotomys*, and *Celaenomys*) and New Guinea (*Neohydromys*, *Pseudohydromys*, *Microhydromys*, and *Mayermys*). The rostral configuration of *Sommeromys* is unlike the architecture found in any other of the more than 1300 species in the entire Muridae. The new species has a derived cephalic arterial circulation, a pattern otherwise found only in *Crunomys celebensis* among Sulawesian murines. That species, although usually regarded as a shrew rat, also does not possess any of the external and cranial specializations defining the species of *Melasmothrix, Tateomys,* and *Echiothrix*. *Crunomys* and *Sommeromys* share a similar conformation of the zygomatic plate that is not found in any other Sulawesian murine, but this is a shared primitive feature. Whether the shared cephalic

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[1] Archbold Curator, Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History.
[2] Associate Professor and Associate Curator, Institute of Arthropodology and Parasitology, Georgia Southern University, Statesboro, Georgia.

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arterial circulation indicates a closer relationship between *Crunomys celebensis* and *Sommeromys macrorhinos* than to any other native Sulawesi species, despite the striking contrast between the two in body form and a combination of cranial and dental traits, or independent derivation in each species will have to be determined by phylogenetic analysis of all the Sulawesi species as well as pertinent samples from the Sunda Shelf and Indochina.

A new species of sucking louse, *Hoplopleura sommeri* (Insecta, Anoplura, Hoplopleuridae), is also described from the new murine. A brief discussion on related species of *Hoplopleura* is included with emphasis on those species parasitizing hosts in the subfamily Murinae of family Muridae.

INTRODUCTION

This report is another in a series describing the morphological and ecological diversity seen in the species of endemic Sulawesian murine rodents, which form about 30% of the total mammalian fauna and approximately 52% of all the endemic species found on the island. Here we describe a new genus and species, a member of subfamily Murinae (of the family Muridae, as delimited by Carleton and Musser, 1984), but one possessing a a combination of specialized morphological traits that is startlingly unlike the other species known from Sulawesi, any of the species in the subfamily, or even any of the more than 1300 species in Muridae.

As part of our continuing research on the systematic and coevolutionary relationships between Sulawesian rodents and their ectoparasites, we also describe here a new species of sucking louse (Insecta, Anoplura) that parasitizes the new murine. This new louse species highlights the rich fauna of host-specific parasites (most of them undescribed) associated with the native murines of Sulawesi. Because cospeciation between permanent host-specific parasites and their hosts (Fahrenholz's rule) is widespread, analysis of the systematic relationships among parasites such as sucking lice can often provide supplementary data sets for analyzing the systematic relationships among their hosts. Phylogenetic analyses of certain groups of mammals and their characteristic lice indicate that cospeciation can account for the observed host associations of 79% of 350 species of trichodectid lice (Lyal, 1985) and for about two-thirds of the associations between pocket gophers and their trichodectid lice (Huelsenbeck et al., 1997). However, DNA sequence analyses show that hosts and parasites have disparate rates of molecular evolution, with the overall rate of nucleotide substitution being about three times greater in the lice than in their rodent hosts, which correlates with a similar difference in generation time between these two groups of interacting organisms (Hafner et al., 1994; Page and Hafner, 1996). Nonphyletic host tracking appears to account for about 21–33% of the observed host–louse associations (Lyal, 1985; Huelsenbeck et al., 1997).

ABBREVIATIONS AND PROCEDURES

RODENTS: Specimens we cite by catalog number are stored in collections of the American Museum of Natural History, New York (AMNH).

We used digital calipers to measure (recorded to the nearest 0.1 mm) the following cranial and dental dimensions (listed in the sequence they appear in the tables):

ONL	occipitonasal (greatest) length
ZB	zygomatic breadth
IB	interorbital breadth
LR	length of rostrum
BR	breadth of rostrum
BBC	breadth of braincase
HBC	height of braincase
BZP	breadth of zygomatic plate
LD	length of diastema
LBP	length of bony palate (palatal bridge)
BBP	breadth across bony palate at first molar
PPL	postpalatal length
BMF	breadth of mesopterygoid fossa
LIF	length of incisive foramina
BIF	breadth of incisive foramina
LB	length of bulla
CLM1–3	crown length of maxillary molar row
BM1	breadth of first upper molar
clm1–3	crown length of mandibular molar row

Limits of most of these measurements are illustrated in figure 3 and verbally defined by Musser and Newcomb (1983). Some additional dimensions were measured on the holotype of the new genus and species and their limits are explained in the footnote to table 1.

Anatomical terminology follows Brown (1971) and Brown and Yalden (1973) for external features of the head and limbs; Bugge (1970) for the cephalic arteries; Wahlert (1985) for the cranial foramina; and Carleton (1980), Musser and Newcomb (1983), Carleton and Musser (1984), and Musser and Heaney (1992) for cranial morphology. Names of cusps and cusplets of upper and lower molars are noted in figure 14; sources of this terminology are explained by Musser and Newcomb (1983: 332).

Stomachs (most of them fully distended with food) from adults of the following species from Sulawesi were studied and their gross gastric morphology compared.

Rattus hoffmanni: AMNH 224965–224967, 224975, 224980, 226029, 226034, 225037, 226038, and 226041.
Maxomys hellwaldii: AMNH 224936, 224939, and 224942.
Paruromys dominator: AMNH 223334, 223338, 223605, 223606, 223609, 223611, 223613, 224826–224829, 224831, and 224840.
Sommeromys macrorhinos, n. gen., n. sp.: AMNH 226956.
Crunomys celebensis: AMNH 224316 and 225042.
Tateomys macrocercus: AMNH 225072, 225075, and 225077.
Echiothrix centrosa: AMNH 225043, 225044, and 226815.

After severing the posterior end of the esophagus and the anterior section of the duodenum, we removed the stomach and bisected it along the midfrontal plane, washed out the contents and saved them (unless it was bait). Observations were made with a Nikon stereoscopic microscope (SMZ-U). Anatomical terms are those used by Carleton (1973).

Illustrations of molar rows and pterygoid regions in figures 18, 19, and 26 were generated by a scanning electron microscope from uncoated specimens.

SUCKING LICE: Specimens examined and referred to here are deposited in the collections of the American Museum of Natural History, New York (AMNH); the Natural History Museum, London (BMNH); Museum Zoologicum Bogoriense, Bogor, Indone-

TABLE 1

Measurements (mm) of the Holotype of *Sommeromys macrorhinos*

Measurement	AMNH 226956
BODY AND APPENDAGES [a]	
Length of head and body	99
Length of tail	186
Length of hind foot (including claw)	31
Length of ear (from notch)	16
CRANIUM AND UPPER MOLARS	
Occipitonasal length	31.9
Zygomatic breadth	13.3
Interorbital breadth	5.5
Length of rostrum [b]	11.2
Breadth of rostrum at nasolacrimal capsule	5.3
Distal breadth of rostrum [c]	3.9
Projection of rostrum beyond incisors	4.3
Breadth of braincase	12.7
Height of braincase	8.9
Breadth of zygomatic plate	1.4
Length of diastema	6.8
Length of bony palate	6.4
Breadth of bony palate at M1	3.2
Postpalatal length	9.3
Breadth of mesopterygoid fossa	2.0
Length of incisive foramina	3.3
Breadth of incisive foramina	1.8
Length of bulla	4.5
Crown length of maxillary molar row	4.3
Breadth of M1	1.4
Breadth across tips of incisors	1.3
MANDIBLE AND LOWER MOLARS [d]	
Length of dentary including incisor	16.3
Length of dentary excluding incisor	13.2
Depth of dentary	6.4
Crown length of mandibular molar row	4.3
Breadth of m1	1.1

[a] Obtained by Musser from the fluid-preserved body.

[b] From tip of nasals to middle point on the slightly concave anterior margin of the zygomatic plate.

[c] Taken near to where the nasals are widest.

[d] Taken, respectively, as follows: from tip of incisor to posterior margin of condyle; from dorsoanterior tip of dentary to posterior margin of condyle; greatest distance between tips of coronoid and angular processes; from anterior face of first molar to posterior margin of third molar; greatest breadth of first molar.

Fig. 1. *Sommeromys macrorhinos*, new genus and species. Drawn from the holotype.

sia (MZB); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Other abbreviations used in the lice descriptions are as follows:

AnMHS	anterior marginal head setae
ApHS	apical head setae
DAcHS	dorsal accessory head setae
DAnHS	dorsal anterior head setae
DCAS	dorsal central abdominal setae
DLAS	dorsal lateral abdominal setae
DMHS	dorsal marginal head setae
DPHS	dorsal principal head setae
DPTS	dorsal principal thoracic setae
DPtS	dorsal prothoracic setae
PrS	paratergal setae
SHS	sutural head setae
StAS	sternal abdominal setae
TeAS	tergal abdominal setae
VPHS	ventral principal head setae

Descriptive terminology follows Kim and Ludwig (1978) and Durden and Musser (1991). Drawings of entire lice depict dorsal morphological features to the left of the midline and ventral features to the right. Measurements were made using a calibrated eyepiece micrometer attached to a high-power phase-contrast microscope.

THE NEW GENUS AND SPECIES OF RAT

Sommeromys, new genus

TYPE SPECIES: *Sommeromys macrorhinos*, the new species described below.

DIAGNOSIS: A genus of Muridae in the subfamily Murinae (as delimited by Carleton and Musser, 1984, and Musser and Carleton, 1993) that is set apart from all other described murid genera by the following combination of morphological traits: small body size; long muzzle; an extremely long tail both absolutely and relative to length of head

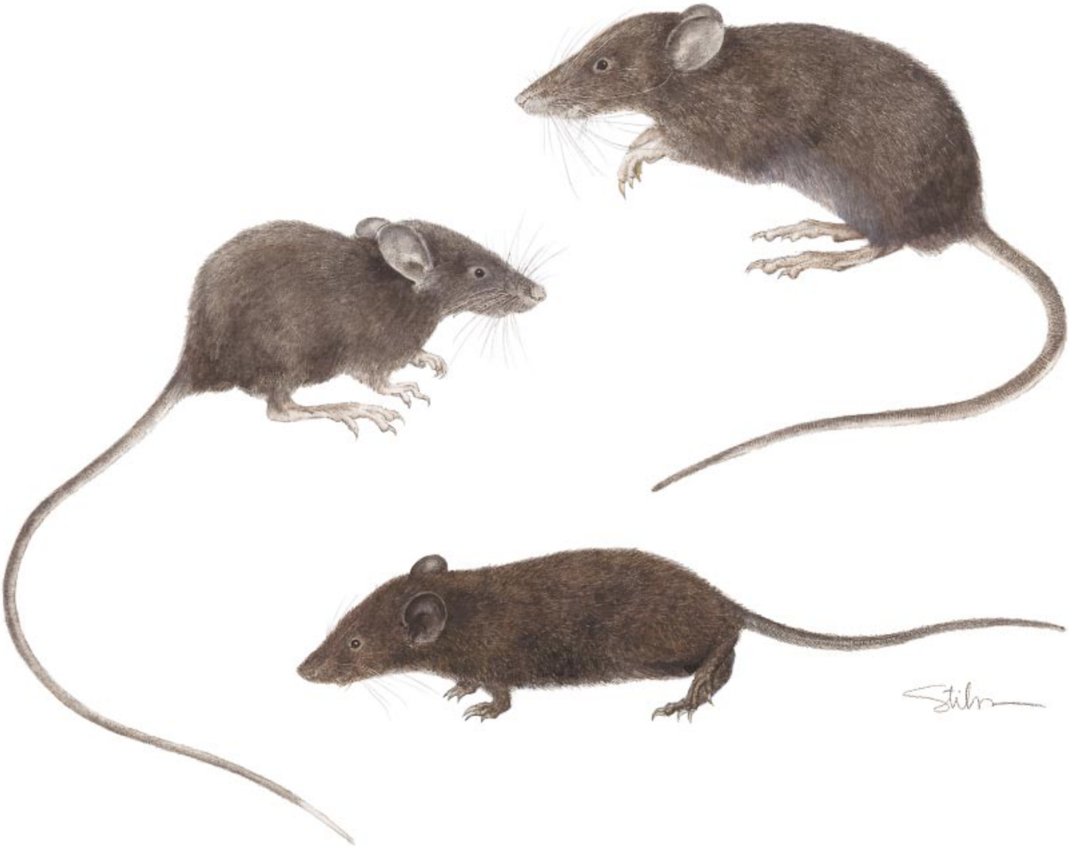

Fig. 2. Sulawesian small-bodied shrew rats. From top to bottom: the nocturnal *Tateomys rhinogradoides*, nocturnal and long-tailed *Tateomys macrocercus*, and diurnal *Melasmothrix naso*.

and body (length of tail/length of body × 100 = 188%); dorsal surface of the terminal 30 mm (one-sixth of the tail length) of the tail is hairless, scaleless, and calloused, indicating some degree of grasping capability (dorsal prehensility); large, nearly naked, mostly unpigmented, and thin external pinnae; long, fine and soft fur covering upperparts and underparts of head and body; body fur extending down over only proximal half of lower front leg and proximal two-thirds of lower hind leg (rather than reaching wrist and ankle); a short free-standing pollex; long and slender digits of manus and pes bearing long, sickle-shaped and sharp claws; elongate and thin (between dorsal and ventral surfaces) hind feet with four large and fleshy interdigital pads, and small hypothenar and thenar pads, each similar to one another in shape and size; small, gracile cranium; long and slim rostrum extending as a bony tube over top of the upper incisors and projecting appreciably beyond them; interorbital and postorbital regions smooth, without prominent ridging; braincase globular, smooth over all outer surfaces, with moderately inflated mastoid and exoccipital regions, and projecting appreciably posterior of occipital condyles; squamosal intact above auditory bulla (no subsquamosal fenestra); concave anterior margin of zygomatic plate, without anterior spine (no zygomatic notch); zygomatic arches slim and delicate, with the jugal a prominent component; anterior face of first upper molar located behind posterior border of zygomatic plate; wide and thick alisphenoid strut on each side of cranium; short and heart-shaped incisive foramina; wide,

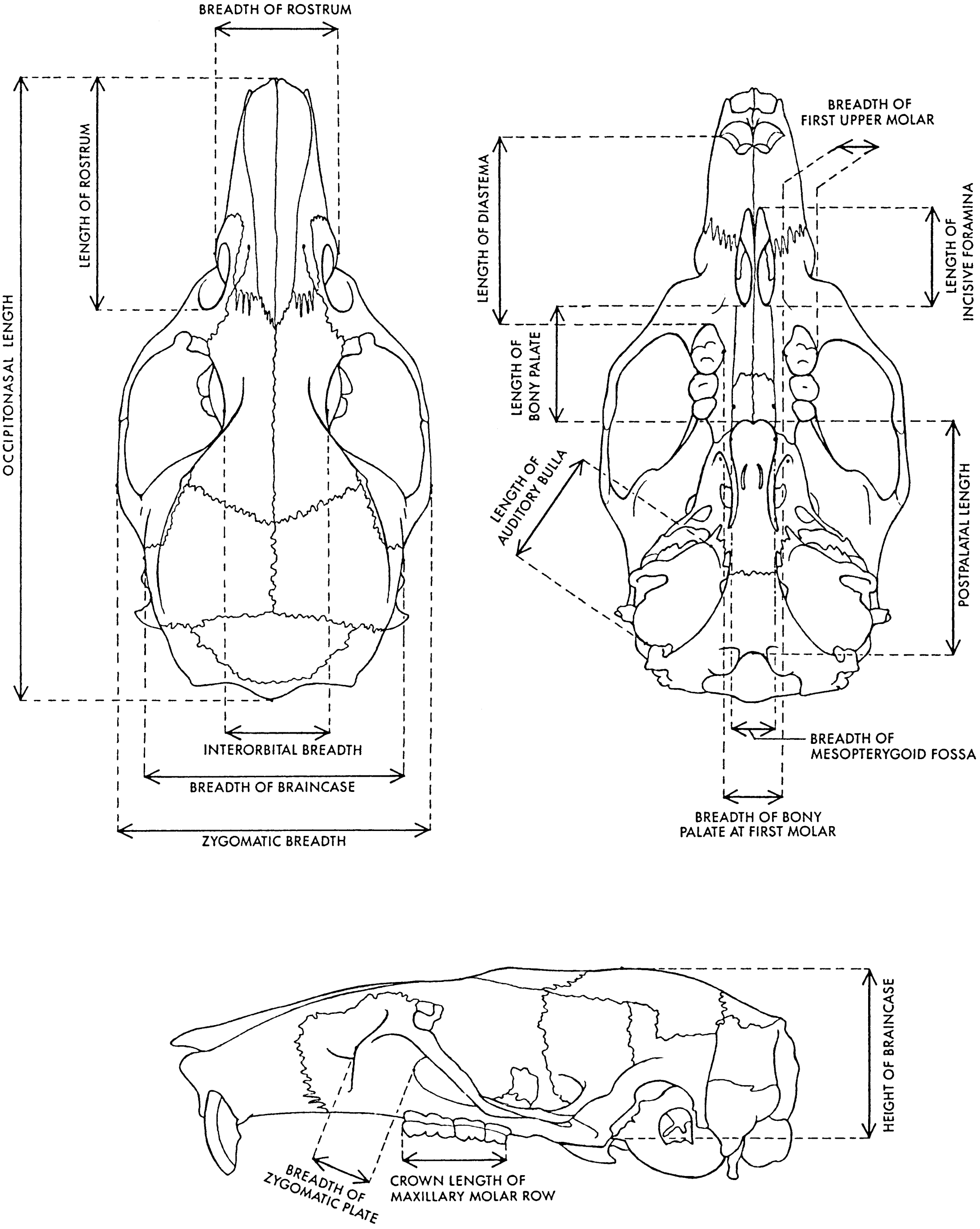

Fig. 3. Views of an adult *Bunomys chrysocomus* showing limits of most of the cranial and dental measurements we employed. See text for abbreviations and additional information.

smooth, and long bony palate extending slightly beyond back of third upper molars; wide mesopterygoid fossa with moderately large sphenopalatine vacuities; posterior third of pterygoid plate covered by thin bone concealing opening to the transverse canal and foramen ovale; arterial supply to orbit and upper jaw furnished by a secondary connection with the internal carotid, the very reduced stapedial artery serving only the otic region (pattern 3 in Voss, 1988); slightly inflated (in dorsoventral plane) auditory bullae; minute stapedial foramen; elongate dentary with prominent coronoid, condyloid, and angular processes; labial surface of dentary smooth, only slight masseteric ridging and no external indication of incisor capsule; incisors small, delicate, and unpigmented; upper incisors opisthodont, with broad enamel faces that are inclined medially and end in sharp lateral tips to form inverted V-shaped cutting edge; lower incisors long, with awl-shaped tips; small, cuspidate, and brachydont molars; each upper molar anchored by three roots, each lower molar by two; small cusp t3, which is discrete on second upper molar, but indistinct on first molar because most of the cusp is coalesced with cusp t2; large cusp t4 with prominent posterior projection; cusp t9 at anterolabial margin of cusp t8 and confluent with cusp t6; small, elongate posterior cingulum on first and second upper molars; no cusp t7 on any molar; X-shaped wear surface of first two rows of cusps on first lower molar; no anterior labial cusplets on first and second lower molars, but posterior labial cusplets present; each first and second lower molar with a posterior cingulum; stomach unilocular-hemiglandular.

ETYMOLOGY: We combine *mys*, Greek for mouse, with the surname, Sommer, to honor Helmut G. Sommer, retired Scientific Technician in the Department of Mammalogy at the American Museum of Natural History (fig. 4). Helmut began his employment at the museum on August 21, 1954, joined the staff of Mammalogy in February 1959, and retired March 31, 1997. The unassumingly bureaucratic title of ‘‘technician’’ belies the array of Helmut’s contributions: specimen preparator, cataloger, curator, mover, driver, plumber, electrician, mechanic, artist, researcher, field man, mentor, coauthor, and colleague are the accurate descriptors of his responsibilities and efforts during the 38 years he labored in the department. Helmut was also a member of the Archbold Sulawesi Expedition but one who worked out of the museum. Helping to obtain and pack equipment and supplies before Musser departed for Indonesia, Helmut personally resupplied him with equipment and bait during the three years Musser lived and worked in the Sulawesi rainforests, monitored specimens shipped to the museum from Indonesia, cleaned the skulls and skeletons, and cataloged the specimens. His efforts were essential to the success of Musser’s fieldwork and subsequent museum research. We are delighted to honor this friend who, through his commitment to excellence as well as his skill, integrity, and sense of responsibility and achievement, has contributed so significantly to the high quality that is associated with curation and scholarship in the Department of Mammalogy at the American Museum of Natural History.

MORPHOLOGICAL DESCRIPTION: the same as for the only known species in the genus, which is described below.

Sommeromys macrorhinos, new species[3]

HOLOTYPE: AMNH 226956, an adult male collected by a member of U. S. Navy Medical Research Unit No. 2 led by P. F. D. Van Peenen (original number NAMRU-23 S.S. 65) on August 2, 1973, at 2400 m near the summit of Gunung Tokala (02°13′S/ 120°04′E), a mountain between the Rampi and Seko valleys in the southern section of central Sulawesi (Province Sulawesi Tengah; see the map in Carney et al., 1977: 381). The specimen was initially preserved in a mixture of formalin and water and subsequently transferred to a 70% ethanol and water solution. The cranium and mandible were removed and cleaned, mostly by dermestid beetles, partly by hand (figs. 8, 9). External, cranial, mandibular, and dental measurements are listed in table 1. A portrait in possible live-pose derived from the holotype is rendered in figure 1.

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[3] This taxon was presented as ‘‘New Genus and Species’’ or ‘‘Unnamed genus’’ in the distributional lists of native Sulawesian murines found in Musser (1987: 79) and Musser and Holden (1991: 406, 408).

Fig. 4. Helmut G. Sommer. Photographed by Peter Goldberg, 1997.

REFERRED MATERIAL: Only the holotype.

GEOGRAPHIC DISTRIBUTION: Presently known only from the type locality (fig. 5), but probably occurs in upper montane forests on other highlands in central Sulawesi.

DIAGNOSIS: Because *macrorhinos* is the only known species of *Sommeromys*, generic and specific diagnoses are the same.

ETYMOLOGY: Combining the Greek *macros*, meaning long, and *rhinos*, referring to nose or snout, highlights the exceptionally long rostrum of this small-bodied rat.

MORPHOLOGICAL DESCRIPTION: The brownish gray, soft-furred, and gracile *Sommeromys macrorhinos* is further characterized by a small body, long muzzle, large ears, long and delicate front and hind legs, and extremely long tail with a dorsally prehensile tip (fig. 1). Details of external, cranial, and dental features follow. [The coloration described below is as Musser remembers and described it a few months after the specimen was preserved. Through the years, the original color has been altered to tan tones by the preservative and inadvertent overlong exposure to light.]

Pelage over head and body: Fur over upperparts is dark brownish gray, that covering the venter is grayish white. The dorsal coat is long, thick, and very soft (because the individual hairs are so fine). Overhairs are gray for about three-fourths of their length and then dark buffy brown to the tips; they extend up to 12 mm over the back and rump. Guard hairs are inconspicuous because they are so soft and fine; their tips are unpigmented and the longest extend just beyond the overhair layer. The long dorsal body fur extends down to cover only the proximal half of the lower front leg and proximal two-thirds of the lower hind leg; the remainder of each leg, as well as the dorsal metatarsal region, is sparsely covered by fine and short brown hairs. This is an exceptional pattern. In all other Sulawesian murines, body fur extends down the lower front leg nearly to the wrist, and over the lower hind leg nearly to the ankle. The muzzle is covered by shorter hairs and is paler than the body; the rhinarium is unpigmented.

The grayish white ventral coat is also soft, but not as thick as the dorsal pelage, and the color is not sharply demarcated from the upperparts. Overhairs are shorter (up to 8 mm long); the distal two-thirds of each is dark gray, the tip white.

Ears: Each pinna is oval in outline, thin, rubbery in texture, and large relative to size of head and body. Except for pale gray splotches on the distal curvature, both inner and outer surfaces are unpigmented and nearly naked—only a few fine tan hairs are scattered over distal inner and outer surfaces and around the margins.

Eye region: Eyes are moderate in size relative to size of head (slightly larger than in the species of shrew rats, *Melasmothrix* and *Tateomys*, but smaller than in species of *Rattus* of about the same body size) and each is surrounded by a dark eyelid and then an unpigmented wider ring.

Vibrissae: Mystacial vibrissae are extremely fine and long, the longest reaching 50 mm, and, when appressed to the head, extend well beyond the distal margin of each pinna. Each mystacial was originally black in the proximal half (fading has altered the tone to tan) and unpigmented distally (appearing silvery). The longest of the superciliary vibrissae reach to the base of the pinnae when appressed against the head. Short submental vibrissae and the longer interramal cluster are unpigmented. We could not locate genal vibrissae.

Three long ulnar carpal vibrissae (up to 10 mm long) project from behind the wrist.

Tail: The tail is whiplike, slender and nearly twice as long as head and body combined (fig. 1). It is rhomboidal in cross section (fig. 6). Dorsal surface and sides are dark brown (now bleached to tan), the ventral surface unpigmented along its entire length. Three fine and short hairs emerge from beneath each scale (there are 13 overlapping annuli of scales per centimeter counted along the basal one-third of the tail). The hair covering is so inconspicuous that the tail seems naked. Because the tail is so long relative to length of head and body, we examined it carefully to determine any sign that it might be used as a grasping appendage. The tip and dorsal surface of the distal 30 mm is calloused and devoid of either hairs or scales, indicating that region to be tactile and probably functioning as a dorsally prehensile (''. . . able to curl upon itself . . . '';

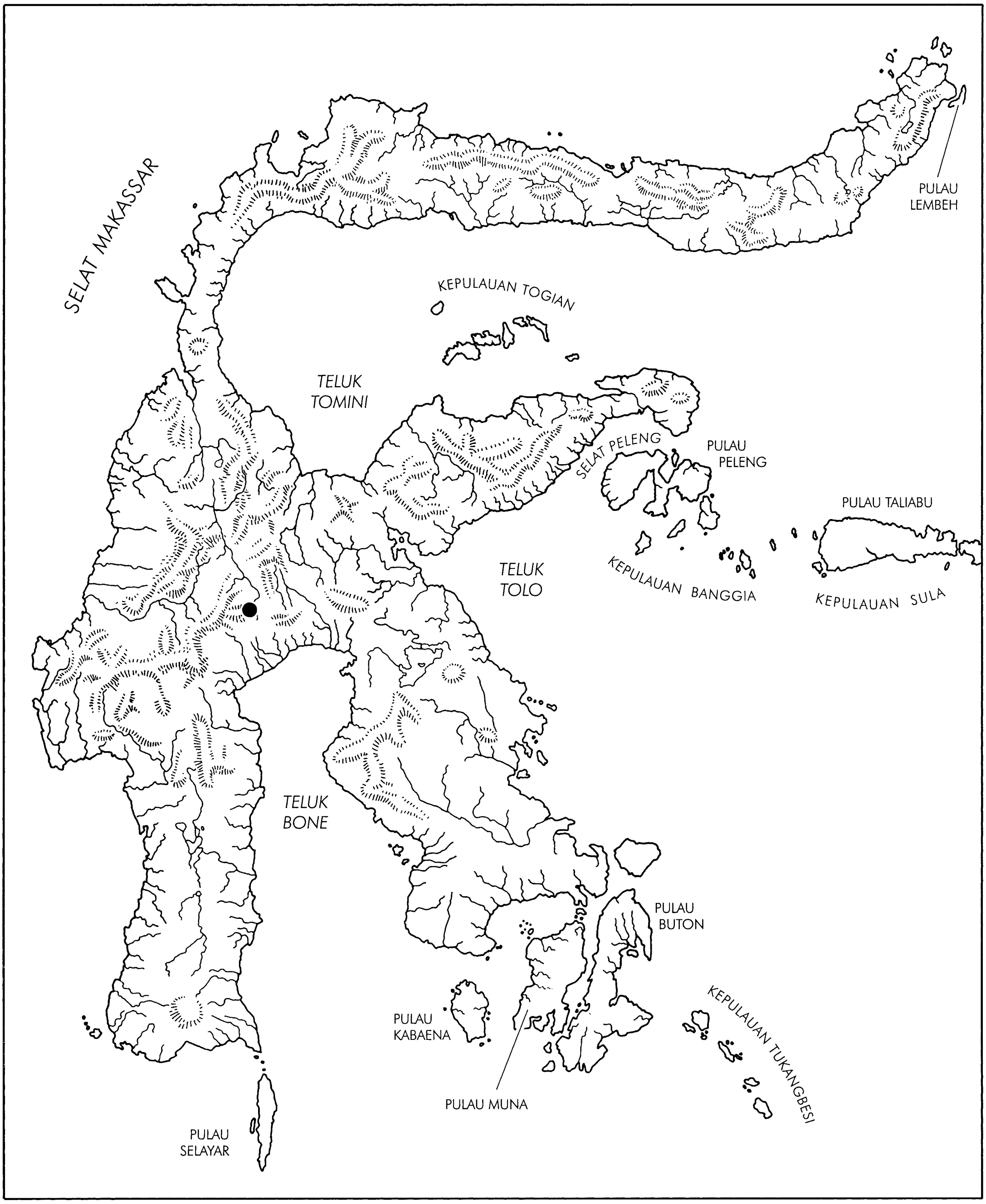

Fig. 5. Mainland Sulawesi, offshore islands, and nearby archipelagos. The large black dot indicates approximate location of Gunung Tokala (02°13′S/120°04′E), the type locality for *Sommeromys macrorhinos*.

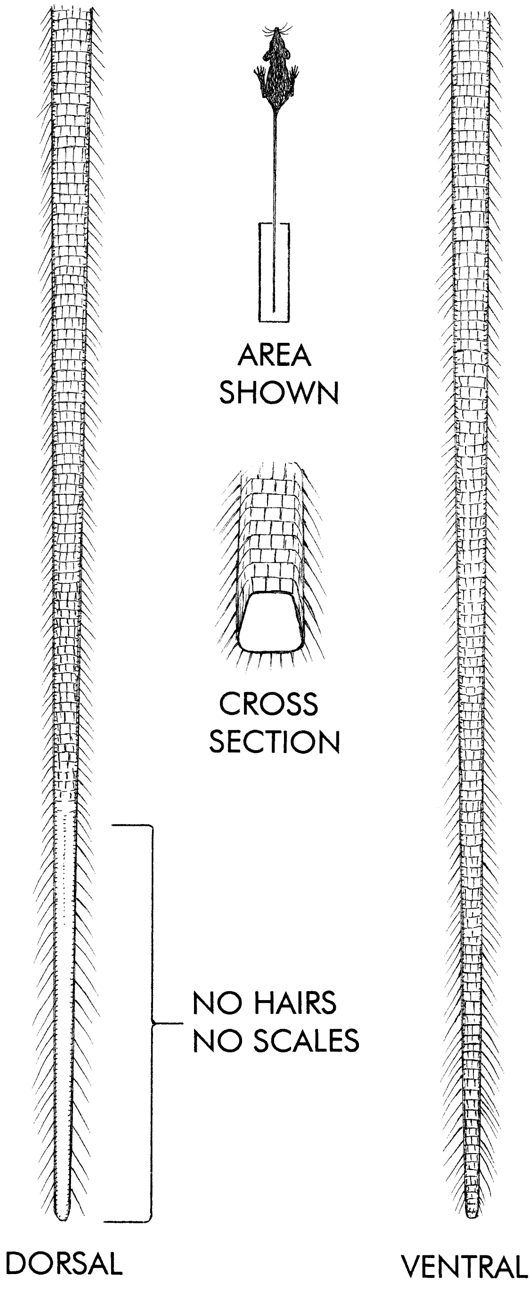

Fig. 6. Distal segment of the tail of *Sommeromys macrorhinos*. The terminal 30 mm on the dorsal surface is an elongate calloused pad devoid of hairs and scales. It is likely pressed against and curled around small-diameter twigs and branches, stabilizing the animal as it scampers and climbs in woody shrubs and tree crowns.

Hickman, 1979) organ (fig. 6). Whether the rat could actually suspend itself by the tail or used it primarily for an anchor and stabilizer is unknown. Species of *Chiruromys*, *Pogonomys*, *Pogonomelomys*, and *Abeomelomys*, as well as *Coccymys rümmleri*, and *Melomys rufescens* from New Guinea are the only other murines with dorsally prehensile long tails (both absolutely and relative to body length) in which the distal portion of the tail is hairless, scaleless, and the epidermis thickened; a "naked gripping pad" as it is called by Flannery (1995: 260–263) who provides excellent illustrations of this morphology (also see Menzies and Dennis, 1979; Menzies, 1990, 1996; we verified these reports by our survey of specimens representing all the genera in the AMNH). We know of no other Indo-Australian murine with a similar morphology. Species of the Sundaic *Pithecheir* have strongly prehensile tails but the morphology is different. The tail is not much longer than body length, the scales are squarish and do not overlap, and the entire tail is virtually naked except for a very few short hairs emerging here and there from beneath the scales (our survey of specimens in the AMNH and USNM are the basis for this observation). The tail is prehensile for most of its length and is used by the rat for support, as an anchor, and to suspend itself from a branch (Lim and Muul, 1975; Muul, personal commun.).

Feet and lower limbs: The lower front leg and lower hind leg are long and slender. Each of the slender digits of the front (manus) and hind (pes) feet end in a conspicuous and fleshy digital pad that bears a long, sickle-shaped, and sharp claw (figs. 7, 8). Dorsal surfaces of metacarpal and metatarsal regions are scantily covered with dark brown hairs, but the underlying integument, digits, claws, and the palmar and plantar surfaces are unpigmented. Short silver hairs provide a sparse cover over dorsal surfaces of the digits and sprout from the base of each claw.

Of the four digits on the front foot, the two middle ones are the longest. The pollex (thumb) is free-standing. Most of its distal segment consists of a capsule-shaped digital pad bearing a large nail, and the proximal portion is formed by a short segment of digit—the combination results in a short dig-

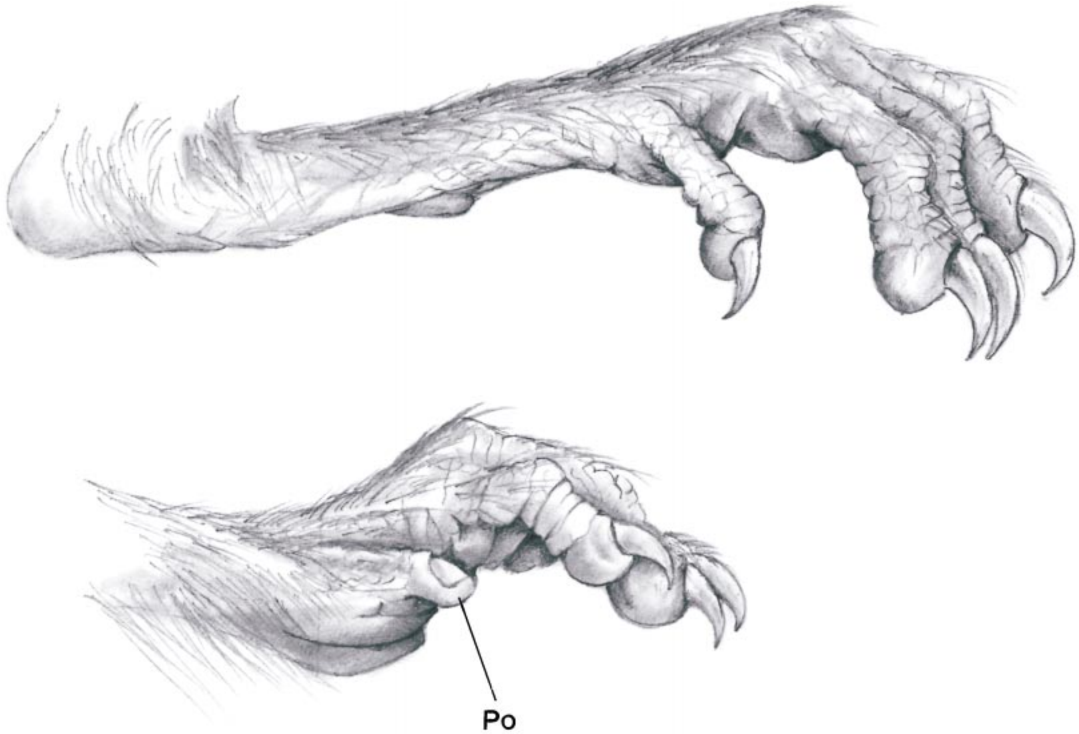

Fig. 7. Holotype of *Sommeromys macrorhinos*. **Top:** Lateral view of left hind foot. **Bottom:** Lateral view of left front foot. Note the sparse clumps of hair on dorsal surfaces of the digits and the curved, sharp claws. The pollex (thumb; **po**) is a short and discrete digit that stands free of the palmar surface, which is unlike the configuration in other murines where the pollex is a stub (as in *Crunomys celebensis*, for example; Musser, 1982: 19, 20) or mound (as exemplified by the species of *Margaretamys*; Musser, 1981b: 278) broadly fused with the palmar surface. The hind foot between heel and base of the digits is thin (between dorsal and ventral surfaces) and delicate.

itlike appendage projecting free of the palmar surface. A nail instead of a claw on the pollex is typical of murine rodents, but in nearly all other species, the pollex is represented by a nail embedded in a pad that is partially fused to the side of the palm (see, for example, fig. 26 in Musser, 1981b; figs. 11 and 12 in Musser, 1982; and figs. 1 and 13 in Musser, 1991). Each palmar surface is nearly entirely composed of three large and fleshy interdigital pads and enormous hypothenar and thenar pads (fig. 8).

Each hind foot is long, narrow, and very thin (between dorsal and ventral surfaces). The three central digits are longest and about equal in length to one another; the fifth digit is slightly shorter, and the hallux much shorter. Six conspicuous pads (tubercles) adorn the distal half of the naked plantar surface (the proximal half is smooth). Four are large and fleshy interdigitals. Just below the pad at the base of the fifth digit is a much smaller hypothenar that is elliptical in outline and only slightly raised above the plantar surface. Well separated from that tubercle, about halfway between base of digits and heel, is the thenar pad, which is closely similar to the hypothenar in shape, size, and height above the plantar surface (fig. 8).

Scrotum: The large scrotum (20 mm long) is about a fifth of the length of head and body. It is conspicuous (fig. 1), partly because of the large relative size but also because the scrotal sac is unpigmented (as is the prepuce) and the proximal two-thirds of its outer surface is covered by long, pale gray and silver hairs.

Skull: The skull of *Sommeromys* is small

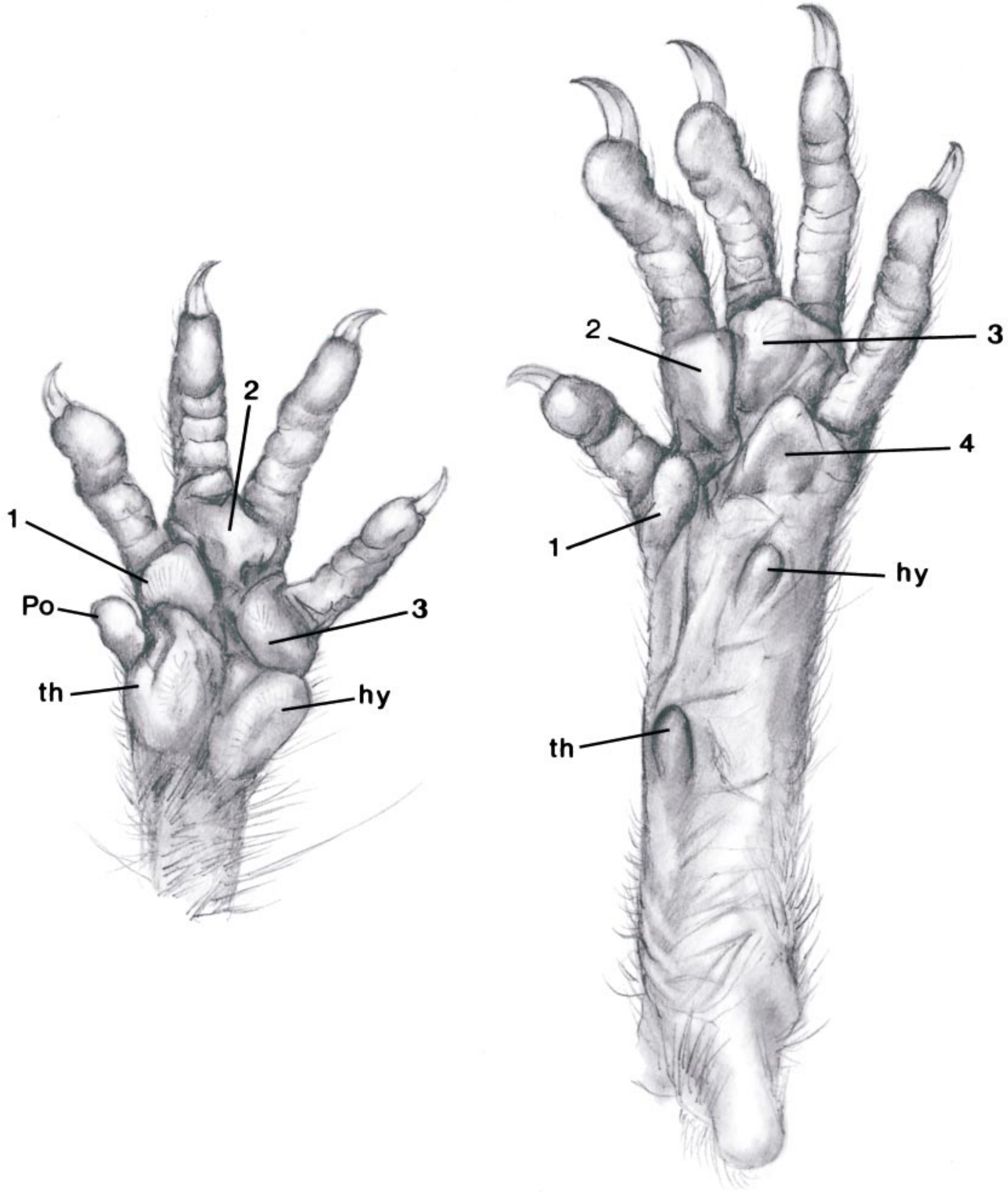

Fig. 8. Holotype of *Sommeromys macrorhinos*. **Left:** Palmar view of left front foot. **Right:** Plantar view of left hind foot. Digits of both feet are long and slender; the plantar portion is long and narrow. Note the protruding pollex (**po**) on the front foot, and the large and fleshy hypothenar (**hy**) and thenar (**th**) pads that, along with interdigital pads 1–3, form nearly all of the palmar surface. Interdigital pad 1 on the hind foot is small, pads 2–4 are large and fleshy, and hypothenar and thenar pads are coequal in size and small relative to total plantar area.

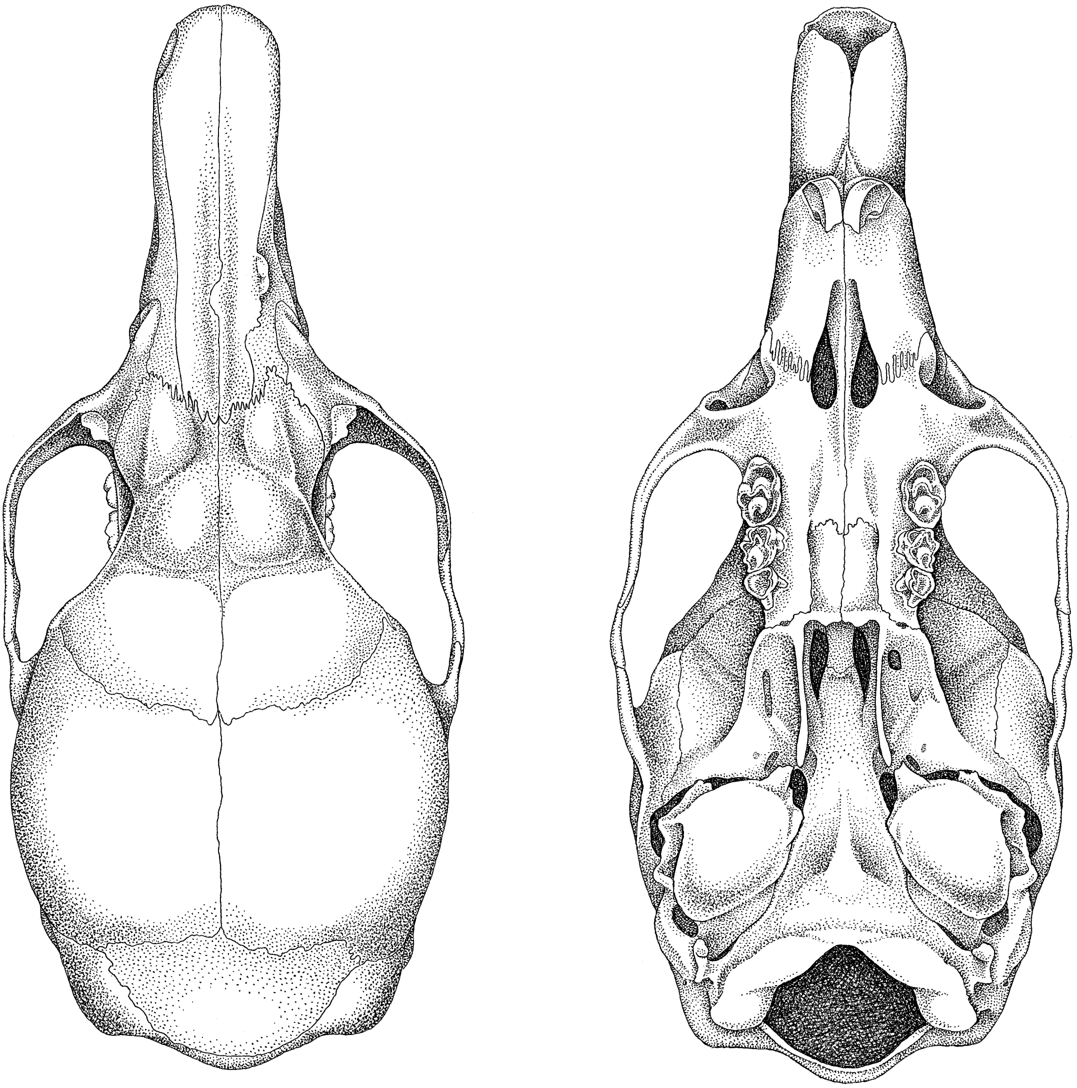

Fig. 9. Holotype of *Sommeromys macrorhinos*. Dorsal (**left**) and ventral (**right**) views of cranium. Measurements are listed in table 1.

and delicate, with a globose braincase and a long, narrow rostrum (figs. 9, 10). The most extraordinary cranial feature of *S. macrorhinos* is the conformation of the rostrum. Its length does not represent an actual elongation (stretching) of the bony rostral elements between zygomatic plates and upper incisors, which is the configuration common to species of the small-bodied Sulawesi shrew rats *Melasmothrix* and *Tateomys* (fig. 15–17; also see figs. 37 and 38 in Musser, 1982), the larger-bodied Sulawesi *Echiothrix* (see fig. 6 in Musser, 1990), and the Philippine species of *Rhynchomys* (see figs. 41–43 in Musser and Heaney, 1992). The rostral length between anterior margins of the zygomatic plates and the emergent portions of the upper incisors in *Sommeromys* is not out of proportion compared with the rest of the skull. The proportional relationship between this segment of the rostrum and the cranium posterior to it is similar to the conformation seen in other small-bodied Sulawesian rats with a short muzzle, such as *Crunomys celebensis* (figs.

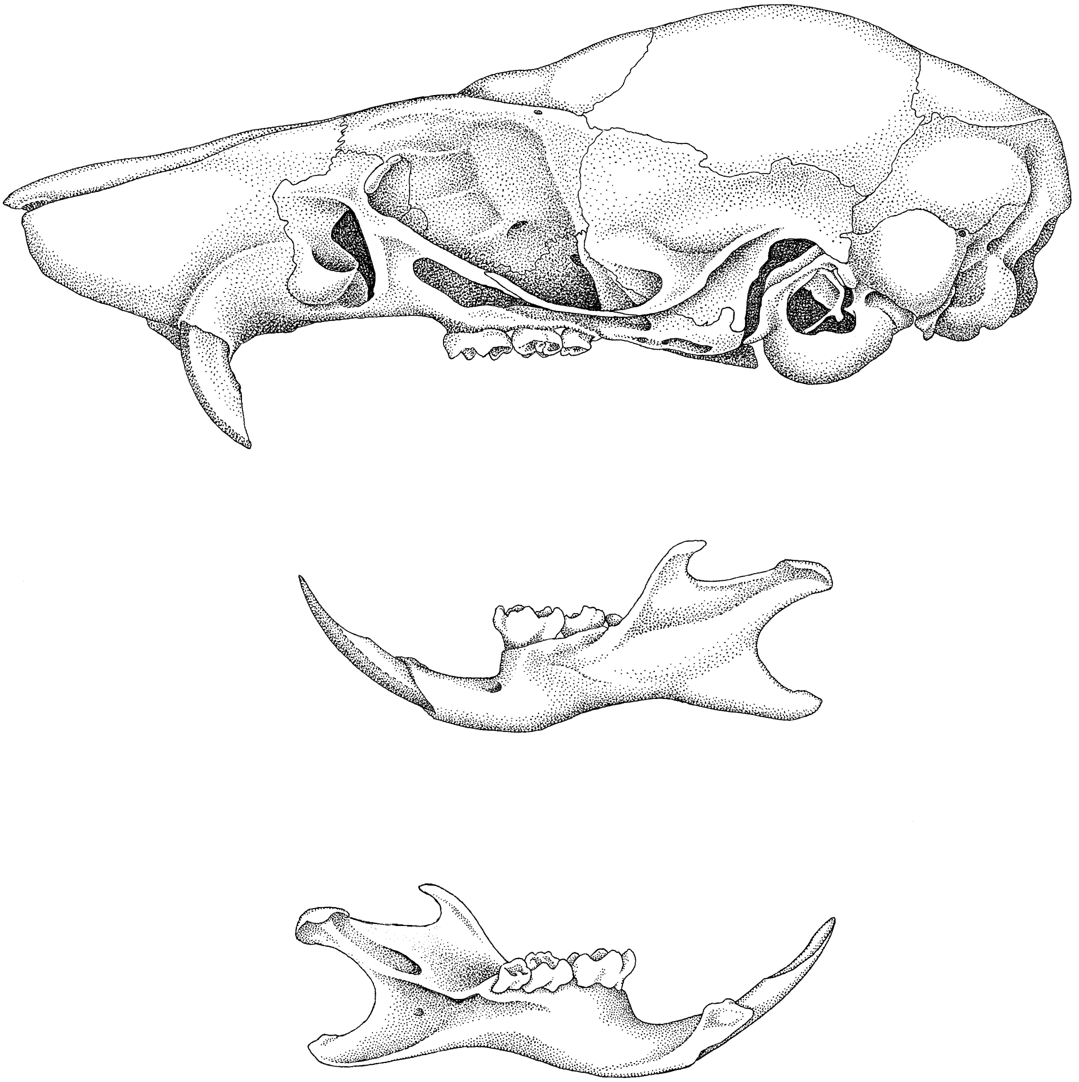

Fig. 10. Holotype of *Sommeromys macrorhinos*. **Top:** Lateral view of cranium. **Middle:** Lateral view of left dentary with incisor and molars. **Bottom:** Medial view of same dentary. Measurements are listed in table 1.

15–17), which has a skull that is about the same size as that of *Sommeromys*. In contrast with the shrew rats, the rostrum is so long because about 40% of its length projects beyond anterior faces of the incisors in the form of a tube in which the slightly convex dorsal surface is formed by the nasals and the sides are composed of the premaxillaries that have fused along their ventromedial margins and with the gnathic process. Greatest vertical height of the tube occurs just in front of the incisor faces. The rostrum above the incisor alveoli is also deep compared to the conformation in most other murines where the incisor roots are higher in the rostrum and closer to the nasals (see cranial illustrations in Musser, 1981b, 1982; Musser and Newcomb, 1983; Musser and Heaney, 1992). The rostrum of *Sommeromys* is essentially a long, deep, and narrow bony tube that extends over tops of the incisors and projects appreciably beyond their anterior margins.

We know of no other murine (or even any other species in the Muridae) with such a rostral configuration. In the Sulawesi and Philippine shrew rats, the nasals and premaxillaries do project slightly beyond anterior faces of the incisors, but the tube formed is very short compared with the rest of the very long rostrum (figs. 15–17).

In dorsal view (fig. 9), the long and narrow rostrum gives way to a moderately wide interorbit in which the frontal bones are slightly inflated, moderately large lacrimals, and a translucent braincase. Threadlike zygomatic arches define lateral outlines of the skull between rostrum and braincase. The braincase itself is oblong in dorsal perspective and globose. That latter conformation is best appreciated from lateral view where the braincase can be seen to swell above the straight outline defined by dorsal surfaces of the nasals. The oblong configuration is due to a deep occipital region that appreciably overhangs the occipital condyles (fig. 10). The globular image of the braincase is enhanced by its smooth surfaces without temporal ridging. Slight beads along dorsolateral margins behind the orbits are the only inconspicuous interuptions to the smooth surfaces not only of the braincase, but also of the interorbital region. It is the very delicate zygomatic arches and the smooth translucent braincase that gives the skull its gracile aspect.

In addition to the distinctive protruding rostrum and dorsal profile of the skull, several other features are notable when the cranium is viewed from lateral aspect (fig. 10). Each nasolacrimal capsule is located low on the rostrum near the base of each incisor alveolus; each is moderately inflated, not bulbous enough to be seen from dorsal aspect. The zygomatic plate is very narrow and its concave dorsal margin is without a projecting spine; therefore, no zygomatic notch is present in the dorsal maxillary root of the plate. The plate is erect but springs from the side of the cranium at an appreciable angle, so the infraorbital foramen is spacious and oblong in outline. The ventral root of the zygomatic plate originates anterior to the first upper molar, so the posterior margin of the plate lies in front of the toothrow. Each arch is slender and delicate and a substantial portion of it is contributed by the jugal. The squamosal root of each arch originates moderately low on the braincase; its posterior margin does not extend as a low ridge back to the occipitals; thus the braincase is smooth behind the zygomatic root. The side of the braincase is vertical above the zygomatic root. The squamosal posterior to the zygomatic root is complete, not perforated by a subsquamosal fenestra. Beyond the squamosal, the outer walls of the mastoid and exoccipital are also smooth as well as thin and slightly inflated, imparting a bulbous appearance to the occipital and mastoid regions. The deep occiput and the extent to which its posterior margin appreciably overhangs the occpital condyles can be appreciated in lateral view of the cranium.

In the orbital region, the ethmoid foramen is large and conspicuous in the postorbital wall (seen in fig. 10). An elongate sphenopalatine foramen penetrates the ventral medial wall of the orbit just above the second molar. Just anterior to it is the much smaller and separate dorsal palatine foramen (neither foramen is illustrated). The two openings are discrete in many murines (species of *Rattus*, for example), but coalesced into a single oblong opening in others (such as *Crunomys celebensis*, for example; see Musser, 1982: 23). The optic foramen is moderately large.

On each side of the braincase posterior to the orbit and above the pterygoid ridge, a wide alisphenoid strut forms the outer wall of the alisphenoid canal and separates the foramen ovale accessorius from the coalesced buccinator-masticatory foramina (fig. 11).

A spacious postglenoid foramen separates the dorsal and anterior margins of the auditory (ectotympanic) bulla from the adjacent squamosal, a conformation clearly seen in lateral view (figs. 10, 11). That portion of the periotic (also called petromastoid) exposed along the dorsal margin of the bullar capsule does not extend anteriorly in the form of a tegmen tympani to attach to the squamosal, and there is no posterior suspensory process on that latter bone. The tegmen tympani attachment between squamosal and bullar capsule is contrasted with the configuration lacking such a suspensory mechanism in Voss (1993: 19).

The rostral tube projecting beyond the incisors is dramatic when the cranium is stud-

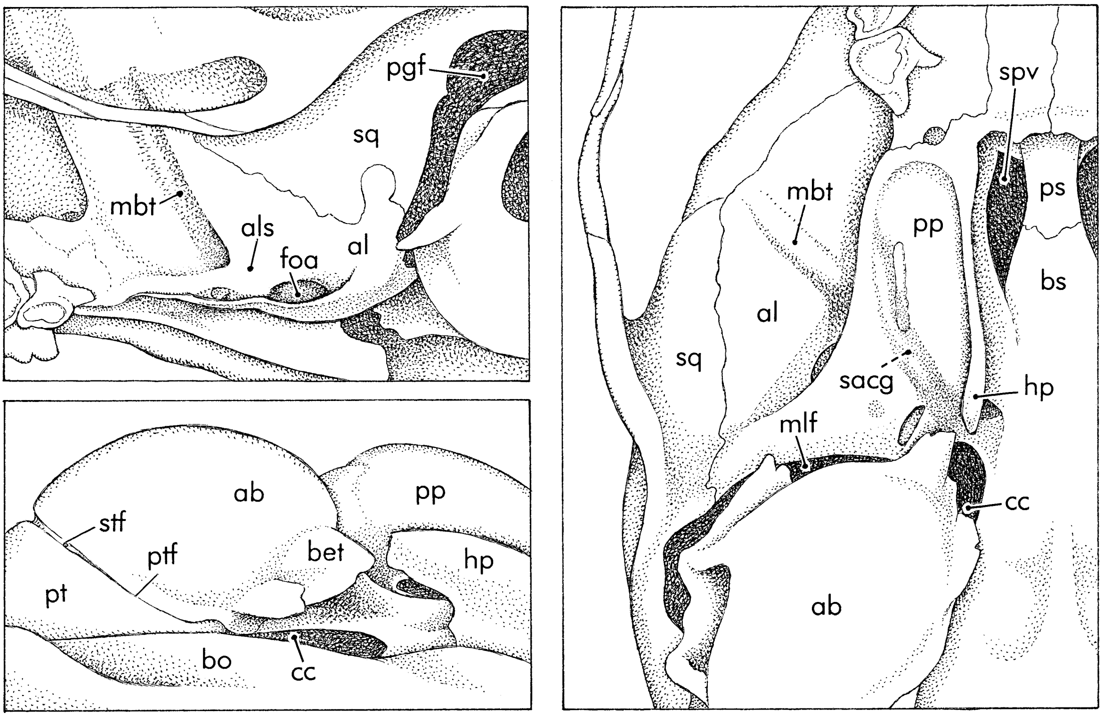

Fig. 11. Holotype of *Sommeromys macrorhinos* illustrating details in three cranial areas. **Upper left:** Left alisphenoid region. A robust and wide strut of the alisphenoid (**als**) separates the foramen ovale accessorius (**foa**) from the opening through which the masticatory and buccinator nerves emerge to course dorsad in a trough or groove (**mbt**) on the outer surface of the alisphenoid (**al**). **Lower left:** Right otic region. Exposed above the globose and small auditory bulla or ectotympanic (**ab**) with its bony eustachian tube (**bet**) is a wide posteromedial wedge of periotic (= petromastoid or petrosal, **pt**) that tapers to a thin flange between the bullar capsule and basioccipital (**bo**). The carotid canal (**cc**) is simply a gap between the basioccipital and anterolingual margin of the bullar capsule. Note the minute stapedial foramen (**stf**) in the periotic fissure (**ptf**). **Right:** Right pterygoid region. The pterygoid plate (**pp**) is hollow in its posterior third, and conceals the foramen ovale, opening to the transverse canal, and part of the oblique osseous channel for the secondary arterial connection (**sacg**) between the internal carotid artery and facial circulation. The posterior border of this hollow region is separated from the auditory bulla (**ab**) by a narrow middle lacerate foramen (**mlf**). Other abbreviations: **bs,** basisphenoid; **hp,** hamular process; **pgf,** postglenoid foramen (or fissure) between the auditory bulla and squamosal; **ps,** presphenoid; **spv,** sphenopalatine vacuity; **sq,** squamosal.

ied from ventral aspect (fig. 9). A small opening lies between the premaxillary bones (interpremaxillary foramen) just behind the incisors (not drawn because it is obscured by the incisor tips). Posterior to the incisors and well anterior to the molar rows are the heart-shaped incisive foramina interrupting the premaxillary-maxillary suture; about two-thirds of each foramen lies in the premaxillary. The bony palate is wide and long, the length due in part to the short incisive foramina, but also to its slight extension (0.5 mm) beyond the third molars. Ventral surface of the palate is generally smooth; even the palatine grooves, which lead to the posterior palatine foramina opposite the second molars, are shallow and barely evident. Behind the posterior rim of the palate is a wide mesopterygoid fossa in which the dorsolateral walls are breached by long and moderately wide sphenopalatine vacuities. Slim hamular processes of the pterygoids provide the boundary between the mesopterygoid fossa and adjacent pterygoid plates. Each plate is roughly rectangular in ventral view, and the anterior two-thirds, the region that is more typically referred to as the pterygoid fossa (or parapterygoid fossa), is thin, and its ventral surface is shallowly excavated and perforated by an irregularly shaped vacuity that was covered with tissue in life. The posterior third of each plate is remarkable. In other Sulawesian murines, such as *Crunomys celebensis*, for example (fig. 26), this posterior segment consists of a single plate. Its ventral surface lies above the opening of the transverse canal, is perforated by the large foramen ovale, sculptured by an oblique groove in which courses the secondary arterial connection between internal artery and facial arterial circulation, and defined posterolaterally by a wide and smooth moundlike margin to which a bullar process attaches. The irregular posterior border of the plate is separated from the auditory bulla by a large vacuity, the middle lacerate foramen. In *Sommeromys macrorhinos*, the posterior third of each plate is hollow, the ventral surface covered by a thin layer of bone concealing the foramen ovale, lateral opening to the transverse canal, and an arterial groove (figs. 11, 26). The overall conformation of the entire plate is of a slightly swollen and obviously hollow posterior third in which the ventral surface merges with the slightly concave pterygoid fossa. Two small foramina pierce this thin covering, a larger one in the posteromedial corner and a smaller one lateral to that. The smaller one is covered with tissue and the larger one was also probably similarly closed in life. The middle lacerate foramen, the gap between the posterior border of this inflated plate and the auditory bulla, is narrow and confined laterally by a bifid bony projection extending from the ectotympanic capsule to the margin of the pterygoid plate. In addition to the foramen ovale and transverse foramen, the hollow segment of each plate also partially conceals an oblique channel. In life, this trough contained a secondary connection to the facial circulation (ophthalmic and internal maxillary) that branched from the internal carotid artery (instead of the stapedial) after that vessel passed through the carotid canal (fig. 25). In this cephalic circulatory pattern, the stapedial artery is small, serving only the otic capsule, which is reflected in the basicranial region by a tiny stapedial foramen in the petrotympanic fissure (between petromastoid and bullar capsule); and a squamosoalisphenoid groove and sphenofrontal foramen are not present. The groove and sphenofrontal foramen are absent in the single specimen of *S. macrorhinos*, which is the usual condition in members of Murinae (Carleton and Musser, 1984; the lone exception is the Philippine *Batomys russatus*, Musser et al., 1998), and the stapedial foramen is a minute opening in the petrotympanic fissure. A similar pattern of vessels and their osteological landmarks is typical of *Crunomys celebensis* (figs. 25, 26), some Philippine (Musser and Heaney, 1992: 68) and Sundaic (Musser and Newcomb, 1983: 472) murines, as well as a host of Neotropical muroids (see the detailed descriptions and diagrams for this and alternative patterns in Carleton, 1980; Voss, 1988; Carleton and Musser, 1989; Voss and Carleton, 1993).

The auditory (ectotympanic) bulla of *S. macrorhinos* is small relative to the size of the braincase, somewhat globular, and slightly inflated in dorsoventral plane. The ectotympanic capsule does not cover the entire ventral surface of the periotic (= petromastoid, petrosal) bone, but leaves exposed a wide posteromedial segment of the periotic as well as a tapered flange extending between capsule and basioccipital (fig. 11). The round and short bony eustachian tube does not touch the basioccipital. A vacuity between the basioccipital and anterolingual margin of the auditory bullae marks the penetration of the carotid artery into the braincase.

Dentary: Like the cranium, each dentary seems delicate in build and has generally smooth surfaces (fig. 10). As viewed from both labial and lingual aspects, from the long and narrow anterior portion in front of the molars to the elongate condyloid process, the dentary is basically a slim structure from which project large and discrete coronoid and angular processes. The degree of isolation of the angular process from the low body of the ramus is reflected in the deeply concave posterior and ventral margins of the dentary. The smooth labial surface is broken by a large mental foramen near the front of the molar row and roughened only by a low and inconspicuous ventral masseteric ridge; the dorsal component of that ridge is not evident. The alveolus for the lower incisor terminates below the anterior base of the coronoid process (determined by shining light in a fiber optic cable through the dentary and viewing it under a dissecting microscope), but there is no capsular process or other feature on either side of the dentary indicating this endpoint. The body of the dental ramus is smooth on the lingual surface, but the region posterior to the molar row is highlighted by a prominent lingual shelflike ridge extending from behind the molar row and below a large mandibular foramen to disappear near the base of the condyloid process.

Incisors: Upper incisors of *Sommeromys macrorhinos* are whitish, short, and emerge from the rostrum at less than a right angle to the occlusal plane of the molars, a configuration defined as opisthodont (see Thomas, 1919; Hershkovitz, 1962: 103; Voss, 1988: 281). Each is broad (1.7 mm near the tip) with a smooth and nearly flat enameled anterior surface that is bounded by low and inconspicuous ridges, one on the anterolateral margin, the other forming the anteromedial edge. The anterior faces incline toward the midsagittal plane, which produces a cutting edge in the form of an inverted V in frontal view with divergent sharp tips (fig. 12). The ivory-colored enamel is very thin.

Lower incisors are also broad (each is 1.7 mm wide) where they emerge from the dentaries and their enamel faces are smooth and rounded (convex in cross section). Elongate wear facets terminate in narrow awl-shaped tips (fig. 13). These teeth are the same color as the upper incisors and the enamel layer of each is very thin and smooth, marked only by inconspicuous ridges where enamel bands abut against the dentine.

Molars: Each upper molar is anchored by three roots, each lower by two, the primitive pattern for Asian murines (Musser and Heaney, 1992). The first upper molar has one robust lingual root, and large anterior and posterior anchors. Each second upper molar has an anterior and a posterior root, and a very large lingual root marked by a vertical furrow indicating that it may be divided distally in the alveolus. Each third upper molar has anterior, lingual, and posterior roots subequal in size. Large anterior and posterior roots anchor each lower molar.

Our observations are based on the number of roots exposed between the molar crown and bony palatal surface; we did not attempt to extract any of the teeth.

Occlusal surfaces of the molars are worn (fig. 14). Primary patterns formed by cusps and intercusp valleys can be traced, but details are either indistinct or obliterated by wear. The teeth are small, brachydont, cuspidate (rather than laminar, for example), and their enamel surfaces are gleaming white. In each cusp row, the molars abut against one another with little or no overlap. The anterior portion of the oval first upper molar is formed by three broadly coalesced cusps: a large lingual cusp t1 that is displaced well posteriorly relative to a large central cusp t2, and the remnant of a very small cusp t3 that is mostly coalesced with cusp t2 and represented by a slight bulge on the labial margin of the cusp row. Occlusal pattern of the second and third cusp rows has been transformed into a basin with a mound in the middle and bumpy outlines—the clear result of appreciable wear. However, three cusps can be detected behind the first row of cusps: a large lingual cusp t4 with a posterior extension, large central cusp t5, and smaller labial cusp t6. A posterior row of cusps is represented by a large mound in the basin, which is the central cusp t8, and by a posterolabial convexity that is the rim of the small cusp t9, which is confluent with cusp t6. The remnant of a posterior cingulum forms the posterior margin of the molar.

Cusp outlines on the elongate second molar are more distinct. A large cusp t1 and very small cusp t3 form the anterior portion of the tooth. The second row consists of a bulky and elongate cusp t4, a large central cusp t5, and a smaller labial cusp t6. A large mound-like cusp t8 forms much of the surface of the molar and is coalesced with a very small labial cusp t9 that is attached to the posterior margin of cusp t6. A small elongate posterior cingulum is plastered against the posterolabial corner of the molar.

We cannot detect a cusp t7 between cusps t4 and t8 on the posterolingual surface of each first and second molar. A cusp t7 is present in some murines such as the Sundaic *Lenothrix canus* and Indomalayan species of *Chiropodomys*, for example (Musser and Newcomb, 1983: 545 and 563, respectively).

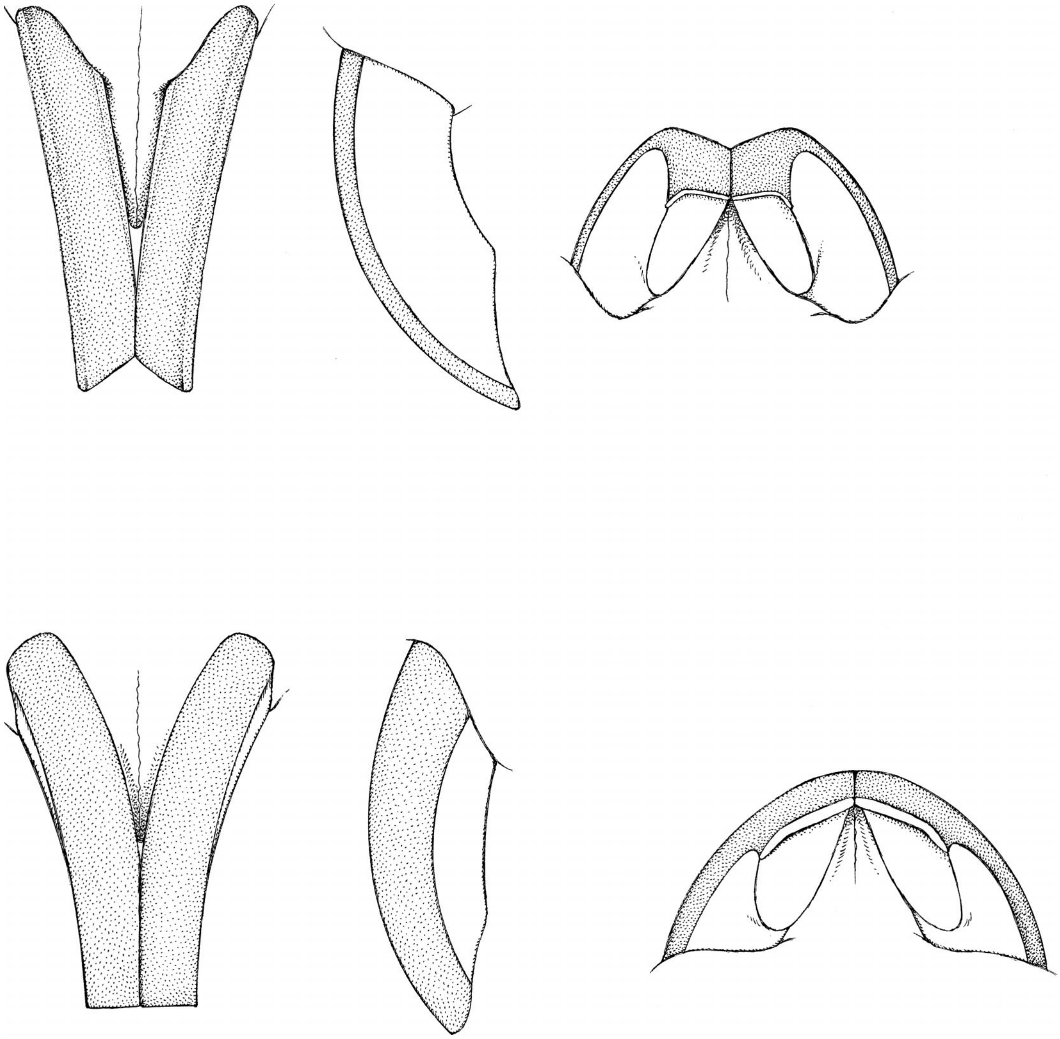

Fig. 12. Configuration of upper incisors. **Top:** *Sommeromys macrorhinos* (holotype). **Bottom:** *Tateomys macrorhinus* (AMNH 225076). Stippling on the incisors represents enamel. Note the contrast in the angle at which the anterior faces touch one another and the extent of enamel on the lateral surface of each tooth.

At certain stages of wear, especially in *Lenothrix*, cusps t4 and t7 coalesce to the degree that the posterolingual margin of the molar appears to be formed of only an elongate cusp t4. The configuration in the holotype of *S. macrorhinos* appears to represent only a large cusp t4; whether a cusp t7 might be present at a variable frequency in the species will have to be determined by study of more and younger specimens.

Each third upper molar is small relative to the size of each first and second molars. Cusp t1, which forms its anterolingual segment, is evident, as is the lingual margin of cusp t4, but the rest of the occlusal surface is worn to a featureless basin.

Each first lower molar is roughly rectangular and its occlusal surface is formed by three rows of cusps. The anterior two-thirds of the molar consists of the smaller anterolabial and anterolingual cusps joined with the much larger protoconid and metaconid to provide a wear surface in the shape of a large, slightly distorted X. As is usual in

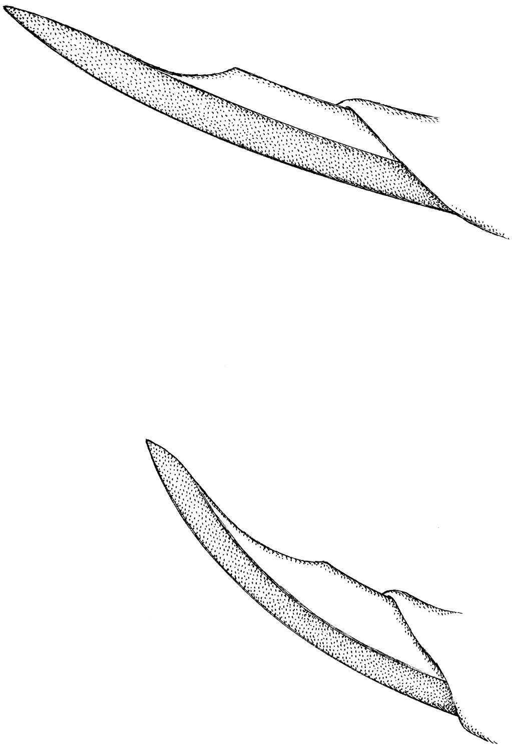

Fig. 13. Configuration of lower incisors drawn from the same specimens as shown in figure 12. **Top:** *Tateomys macrocercus*. **Bottom:** *Sommeromys macrorhinos*. The contrast is striking in degree of curvature and regression of dentine from the incisor tip.

most murines, the anterolingual cusp is larger than the anterolabial. Large entoconid and hypconid form most of the posterior one-third of the molar, and behind that row of cusps is a large and worn posterior cingulum. An anterior labial cusplet is not present (seen on the anterolabial margin of the protoconid in other Sulawesi murines, *Bunomys*, for example; Musser, 1991), but a posterior labial cusplet is evident, broadly coalesced with the hypoconid.

Occlusal pattern of the nearly square second lower molar consists of two rows of cusps and a large but worn posterior cingulum. Shape of the cusps and their position are similar to the two posterior rows of the first molar. The anterolabial margin of the molar does not support an anterolabial cusp, but a posterior labial cusplet is partially coalesced with the hypoconid.

The very small third molar has a roughly circular occlusal outline. Except for an enamel island and enclosed pit (representing the space between cusp rows), wear has transformed formerly cuspidate topography into a featureless basin.

COMPARISONS: Species in 8 of the 13 other genera native to Sulawesi are much larger in body size than *Sommeromys macrorhinos* and strikingly different in morphology. Each generic cluster is diagnosable by external, cranial, dental, and other traits, and all have a general ratlike external form without the peculiar physiogonomy of *S. macrorhinos* as reflected in that species by its fur texture, elongate muzzle, extremely long and dorsally prehensile tail, as well as configurations and proportions associated with front and hind appendages. Furthermore, none of the eight genera possess any of the cranial and dental traits that distinguish *Sommeromys*, especially its peculiar rostral elongation, gracile and smooth cranium, zygomatic plate configuration, derived cephalic arterial circulation, specialized incisors, and molar occlusal patterns.

Species of *Bunomys*, *Paruromys*, and *Taeromys* were once included within the morphological and geographic boundaries of *Rattus*, but are now recognized as separate genera (Musser and Newcomb, 1983) that, along with *Rattus* are members of a *Rattus*-like clade (Musser and Heaney, 1992: 126; Watts and Baverstock, 1994). They lack the diagnostic features of *Sommeromys* and also share the following derived cranial and dental traits distinguishing them as a group from *Sommeromys* and some other native Sulawesi murines (see the cranial and dental illustrations in Musser and Newcomb, 1983, and Musser, 1991): some combination of interorbital, postorbital, and temporal ridging (contrasted with a smooth and rounded braincase as well as smooth interorbital and postorbital dorsolateral margins unmarked by ridging or beading); posterior palatine foramina located posterior of palatine-maxillary suture and opposite anterolingual roots of third molars (at anterolateral margins of palatine-maxillary suture opposite the back third of each first molar or anterolingual root of the second molar in *Sommeromys*); large auditory bulla that is sufficiently inflated to

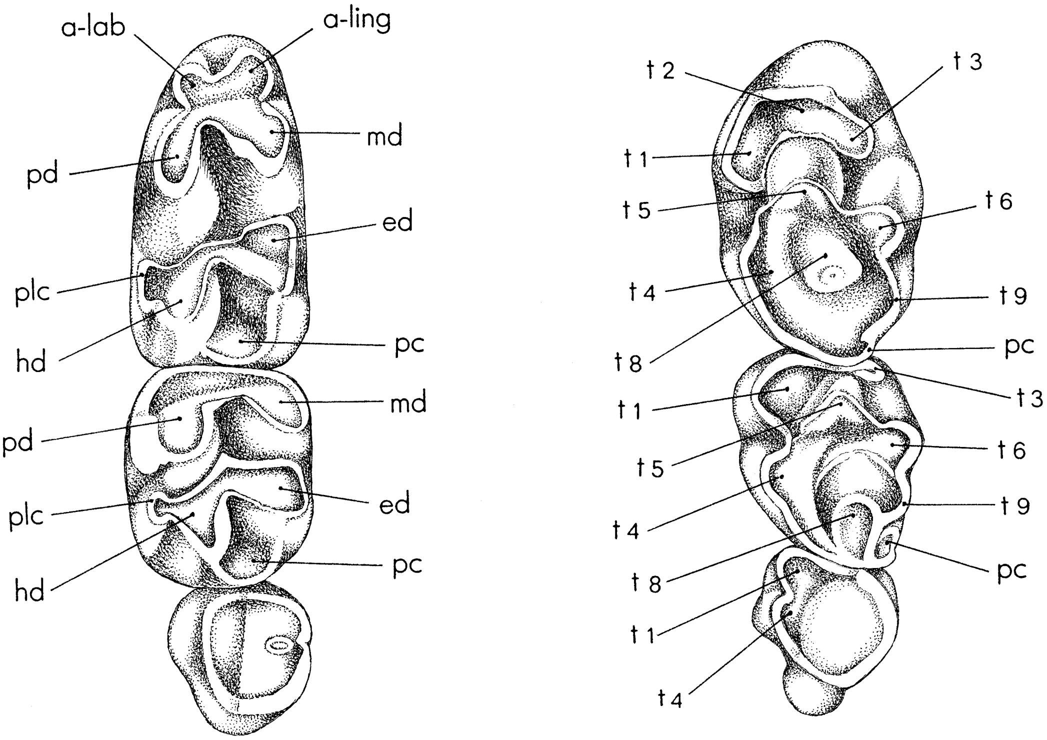

Fig. 14. Occlusal views of left mandibular (left side) and maxillary (right side) molar rows of the holotype of *Sommeromys macrorhinos*. **Maxillary molars:** Cusps are numbered according to Miller's (1912) notation and referred to in the text with the prefix "t". **Mandibular molars: a-lab,** anterolabial cusp; **a-ling,** anterolingual cusp; **ed,** entoconid; **hd,** hypoconid; **md,** metaconid; **pc,** posterior cingulum; **pd,** protoconid; **plc,** posterior labial cusplet.

shield the periotic so only a small posteromedial wedge is exposed between ectotympanic and basioccipital, the medial margin of the eustachian tube contacts the basioccipital and basisphenoid, and the passage for the internal carotid artery is a canal encircled by the ectotympanic and basioccipital margin (small bulla relative to the size of the cranium with the ectotympanic shielding less of the periotic, eustacian tube does not contact basioccipital, and the passageway for the internal carotid is a large gap between eustachian tube and basioccipital); first upper molar with five roots, second with four and third with three (each upper molar with three roots); first lower molar with four roots, second and third with three roots (each lower molar anchored by two roots). These character states are illustrated and explained in greater detail by Musser and Heaney (1992: 95–101), who discuss their distribution among the native Philippine *Rattus*-like genera (*Rattus*, *Bullimus*, *Tryphomys*, *Abditomys*, *Tarsomys*, and *Limnomys*).

Sulawesian species of *Maxomys* and *Haeromys* are endemic to the island, but representatives of each genus also occur to the west. The distribution of *Maxomys* includes islands on the Sunda Shelf and the Indochinese mainland; other species of *Haeromys* occur on Palawan and Borneo (Corbet and Hill, 1992).

The species of *Maxomys* were once included in *Rattus* (Musser et al., 1979, and Musser and Newcomb, 1983, discuss the taxonomic history of the group; Musser, 1991, provides cranial and dental illustrations), but whether defined by morphological (Musser et al., 1979; Musser and Newcomb, 1983) or molecular characteristics (Watts and Baverstock, 1994; Ruedas and Kirsch, 1997), the genus represents a monophyletic group of species either considered ‘‘. . . to be phylogenetically more closely related to *Chiromyscus*, *Niviventer*, *Dacnomys*, and *Leopoldamys* than to *Rattus*’’ (Musser, 1981b: 329), ‘‘. . . as a separate lineage within South-east Asian murines not particularly close to any other’’ (Watts and Baverstock, 1994: 717), or as having a ‘‘sister-group relationship’’ with two pairs of genera (*Sundamys* and a species of Australian *Rattus*, and *Niviventer-Leopoldamys*) (Ruedas and Kirsch, 1997: 385).

Mouselike in body size and physiognomy and arboreal in habitus, species of *Haeromys* are the smallest native murines on Sulawesi (see measurements and illustrations in Musser, 1990). They have a small body (62–78 mm), long and whiplike tail (up to 133 mm), and retain a suite of primitive cranial, dental, and chromosomal traits (Musser and Newcomb, 1983), and possibly spermatozoal characters (Breed and Musser, 1991). Phylogenetic affinities of the genus are unresolved, but speculations identify a tie to either Sundaic and Indochinese *Chiropodomys* or the Mindoran *Anonymomys* (Musser and Newcomb, 1983). There are certainly no morphological features indicating any close phylogenetic alliance with *Sommeromys*.

Lenomys meyeri and *Eropeplus canus* are among the largest of the native Sulawesi murines (length of head and body reaching 301 and 255 mm, respectively; Musser and Brothers, ms.), with stocky bodies covered in long and dense fur extending onto basal portion of the tail, and a bicolored tail equal to (*Lenomys*) or moderately longer than (*Eropeplus*) head and body. They share a stocky skull and mandible and other cranial traits, large molars, and a unique spermatozoal configuration (Musser, 1977 and 1981a, provides illustrations of skulls, dentitions, and the living *Lenomys*; Breed and Musser, 1991, describe and illustrate the spermatozoa). The two species are more closely related to each other than to any other Sulawesi murines, but any phylogenetic ties to species in faunas outside the island have not been established.

The three tufted-tailed and arboreal species of *Margaretamys* form another Sulawesi endemic cluster (Musser, 1981b). Body size ranges from small (96–114 mm in 14 adult *M. parvus*) to moderate (140–197 in 17 adult *M. elegans*). They share similar cranial and mandibular conformations, molar occlusal patterns, external physiognomy and limb proportions, and spermatozoal morphologies (Musser, 1981b; Breed and Musser, 1991). Their closest relatives have yet to be determined.

A ninth Sulawesian endemic genus, *Echiothrix*, contains two species (Musser and Brothers, ms.) of large-bodied shrew rats characterized by elongate muzzles and rostra (description, measurements, and photographs are provided by Musser, 1990) but otherwise unlike *Sommeromys*. *Echiothrix* matches genera such as *Lenomys* and *Eropeplus* in body size (with head and body up to 225 mm long), has a long bicolored tail (up to 258 mm), bristly fur, very large ears relative to body size, gracile front feet, and large and elongate hind feet with short outer and long central digits. The long rostrum is slender, not the chunky configuration of *Sommeromys*, and the rostral and and nasal bones barely project beyond the upper incisors. Except for the rostrum, other specializations associated with preying upon invertebrates (earthworms mostly), and a simplified pterygoid region, the skull resembles those of the other eight genera previously covered, especially *Maxomys*. It is large and robust, with a high, squarish and ridged braincase, and a wide zygomatic plate with an anterior margin similar in conformation to that present in other ratlike genera. In further contrast to *Sommeromys*, *Echiothrix* has the primitive cephalic arterial pattern (as do the other eight genera), and the pterygoid plate is rudimentary or missing (a derivation unique to *Echiothrix*). Incisors and molars of *Echiothrix* are small relative to size of skull and mandible. The upper incisors are orthodont in their relation to the rostum (opisthodont in *Sommeromys*), and their enamel faces do not incline medially toward the midsagittal plane to form an inverted V-shaped cutting edge, as is characteristic of *Sommeromys*. The small molars have simple, cuspidate coronal surfaces that quickly wear into basins, the uppers lack a posterior cingulum (present on first and second molars of *Sommeromys*), cusp t4 is a simple mound (large and elongate in *Sommeromys*), and cusps t6 and t9 are separate (united in *Sommeromys*). Lowers also have simple cuspidate occlusal surfaces and most specimens lack a posterior cingulum on the first and second molars (present in *Sommeromys*). Nothing in the morphology characterizing *Echiothrix* indicates a relationship closer to *Sommeromys* than being in the subfamily Murinae. In its external, cranial, dental, and chromosomal traits (Breed and Musser, 1991), *Echiothrix* also does not have close phylogenetic ties to species in the other genera of shrew rats indigenous to Sulawesi.

It is to the small-bodied species of shrew rats, *Melasmothrix* and *Tateomys* (fig. 2) as well as *Crunomys celebensis* (fig. 20) that *Sommeromys* bears the closest, but superficial, resemblance. The holotype of *Sommeromys* and a specimen of *Tateomys* were obtained on the same night and the collector thought he had trapped two kinds of shrew rats. The diurnal and terrestrial *Melasmothrix naso* has dark chestnut fur, short tail and legs, and long claws; *Tateomys rhinogradoides* is larger, with dark, brownish gray pelage, stout digging front claws, robust and elongate hind feet, a long tail, and is nocturnal and terrestrial; *Tateomys macrocercus*, nocturnal and scansorial, is smaller than the latter, similar to it in fur coloration, but has delicate front feet and long slender hind feet in which the digits bear small but long claws, and the tail is extremely long (see Musser, 1982, for additional descriptions measurements, and photographs).

These three shrew rats are closely related, united by their cranial, dental, and spermatozoal morphology (Corbet and Hill, 1992, submerged *Tateomys* within *Melasmothrix*), and seem to exhibit no close phylogenetic alliance with any other native Sulawesi murine (Musser, 1982; Breed and Musser, 1991). Of the three, *Tateomys macrocercus* is most like *Sommeromys* in external appearance and body size (table 2); specimens of each submerged in ethanol preservative appear to be the same species. The resemblance, however, is superficial and related to long muzzles, short front legs and small feet, long hind legs and feet, and a very long tail relative to the length of the head and body; these traits are probably associated with scansorial behavior and pursuit of invertebrates in a cool, wet, and mossy environment. In contrast to *Sommeromys*, *Tateomys macrocercus* has smaller eyes relative to the size of the head; does not have a free-standing pollex; claws on the front feet are longer and nearly straight (shorter and sickle-shaped in *Sommeromys*); front and hind legs are furred nearly to the wrist and ankle, respectively (over only proximal half of lower front leg and proximal two-thirds of lower hind leg in *Sommeromys*); hypothenar pad of hind foot is appreciably smaller than the larger

TABLE 2

Measurements (mm) of the Adult Examples of *Tateomys macrocercus, Sommeromys macrorhinos,* and *Crunomys celebensis* that are illustrated in Figures 15–17

	Tateomys macrocercus (AMNH 225072)	*Sommeromys macrorhinos* (holotype)	*Crunomys celebensis* (AMNH 224316)
Sex	♀	♂	♂
LHB	120	99	118
LT	173	186	82
LHF	30	31	25
LE	19	16	14
ONL	32.7	31.9	29.0
ZB	14.6	13.3	14.4
IB	6.0	5.5	5.6
LR	12.7	11.2	8.5
BR	5.5	5.3	5.9
BBC	14.5	12.7	11.6
HBC	9.0	8.9	8.7
BZP	1.2	1.4	2.2
LD	7.3	6.8	7.6
LBP	6.4	6.4	5.6
BBPM1	2.9	3.2	2.7
PPL	14.1	9.3	11.7
BMF	2.0	2.0	1.8
LIF	4.5	3.3	4.1
BIF	2.0	1.8	2.0
LB	4.7	4.5	4.2
CLM1–3	5.4	4.3	3.6
BM1	2.0	1.4	1.2
clm1–3	4.8	4.3	3.7

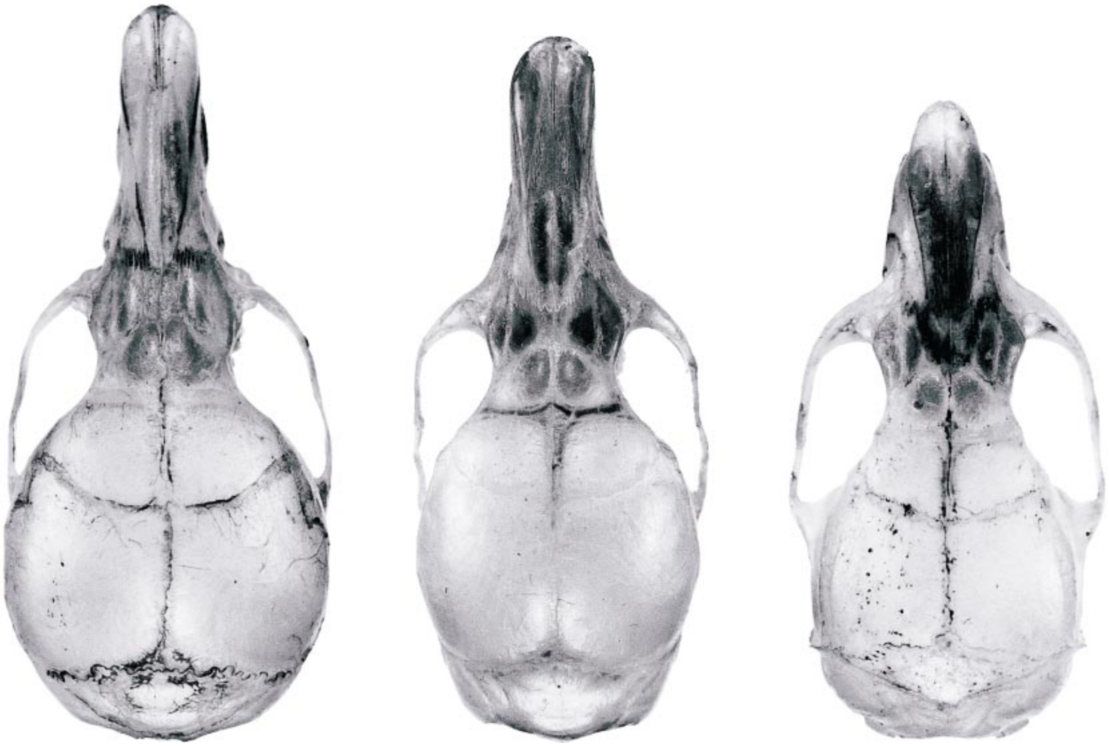

Fig. 15. Dorsal views of adult crania. **Left:** *Tateomys macrocercus* (AMNH 225072). **Middle:** *Sommeromys macrorhinos* (holotype). **Right:** *Crunomys celebensis* (AMNH 224316). ×2.

and elongate thenar (hypothenar and thenar small small and coequal in size in *Sommeromys*); although long, the tail is much shorter relative to the length of the head and body (the ratio, length of tail/length of head-and-body ×100 averages 145% for six examples of *T. macrocercus* versus 188% for the holotype of *Sommeromys*); the entire tail is haired in *T. macrocercus* and does not have a calloused dorsal grasping pad along the terminal portion; and the scrotum is larger relative to body size (about one-fourth) with the scrotal sac being densely covered with dark gray fur.

Although contrasting in external appearance with the other two species of shrew rats, *Tateomys macrocercus* represents them in cranial and dental traits. In dorsal view (fig. 15), skulls of *T. macrocercus* and *S. macrorhinos* appear similar—long nasals and rostrum, wide interorbit without dorsolateral ridging, gracile zygomatic arches, smooth and globose braincase, and posterior margin of the occipital region overhanging the occipital condyles—but again the resemblance is superficial. The shrew rat has a larger, round braincase (in dorsal perspective) with a wide interparietal covering most of the occipital region (smaller and oval braincase with a narrower interparietal in *Sommeromys*). When viewed from lateral and ventral perspectives, the skull of *T. macrocercus* is strikingly dissimilar to that of *S. macrorhinos* (figs. 16, 17). Only a small portion of the premaxillaries and nasals project beyond the upper incisors in the shrew rat, nasolacrimal capsules and incisive foramina are stretched (short in *Sommeromys*), each zygomatic plate is anchored above the first molar (well anterior to the first molar in *Sommeromys*) and has a convex or straight anterior margin (concave in *Sommeromys*), posterior palatine foramina are situated at the posteriolingual margins of second molars (more forward in *Sommeromys*, at the anterolingual margins), pterygoid plates are not covered by thin bone concealing opening to transverse canal and foramen ovale, alisphenoid struts are absent

Fig. 16. Ventral views of same specimens shown in figure 15. **Left:** *Tateomys macrocercus*. **Middle:** *Sommeromys macrorhinos*. **Right:** *Crunomys celebensis*. ×2.

(sturdy struts in *Sommeromys*), a large stapedial foramen and other traits reflect the primitive murine carotid cephalic arterial pattern (derived in *Sommeromys*), and the dentary is longer and more slender.

The two species are unlike in details of incisor configuration. Upper incisors in both species have cream-colored enamel layers, but in the shrew rat, they are orthodont (emerge at a right angle) relative to the rostrum instead of opisthodont as in *Sommeromys*; the anterior faces meet in midline to form a smooth convex surface rather than inclining towards the midline and forming a V-shaped trough, and the enamel layer extends over the anterior lateral half of the tooth (fig. 12). *Tateomys macrocercus* has longer, straighter, and thinner lower incisors in which the dentine has retreated farther from the tips, transforming the distal portions into long enamel daggers (fig. 13).

Upper and lower molars of *Sommeromys macrorhinos* and *Tateomys macrocercus* are anchored by the same number of roots (three below each upper, two below each lower, a primitive configuration), occlusal surfaces of molars are cuspidate in both species, and the third molars are small relative to others in the toothrows (figs. 18, 19). The two species contrast in that *T. macrocercus* has wider, more robust upper molars; cusp t3 is large and set apart from cusp t2 on the first molar; cusp t4 lacks an elongate posterior projection; cusp t9 on first and second molars is discrete, much larger relative to cusp t8, and set apart from cusp t6; and posterior cingula are absent. Occlusal surfaces of lower molars are generally similar in *S. macrorhinos* and *T. macrocercus*, but in the latter, the coalesced first and second cusp rows on the first molar have a more tubercular (high, pointed cusp outline) configuration and the posterior cingulum at the back of each first and second molar is much smaller relative to each tooth.

Sommeromys macrorhinos is not a shrew rat in the sense that term is used for the large-

Fig. 17. Lateral views of crania and dentaries of the same specimens depicted in figures 15 and 16. **Top:** *Tateomys macrocercus*. **Middle:** *Sommeromys macrorhinos*. **Bottom:** *Crunomys celebensis*. ×2.

bodied species of *Echiothrix* or the smaller species of *Melasmothrix* and *Tateomys*. The majority of morphological specializations defining those taxa are not shared by *Sommeromys*.

Crunomys celebensis is the only other shrew rat indigenous to Sulawesi (see the descriptions, measurements, and photographs in Musser, 1982). Other species in the genus (*C. fallax*, *C. melanius*, and *C. suncoides*) are native to the islands of Luzon, Mindanao, Camiguin, and Leyte (Rickart et al., 1998). *Crunomys celebensis* is ‘‘a terrestrial forest rat with a short and broad head, a stocky body, small ears, short legs, narrow hind feet, and short tail; the impression is of a chunky, little short-tailed rat built close to the ground’’ (Musser, 1982: 19; also see measurements in table 2). It is the antithesis of *Sommeromys* in overall external appearance and does not possess any of the specializations seen in the head, tail, digits, claws, hind feet, and plantar pads of *S. macrorhinos*. (Compare the live pose of *S. macrorhinos* in figure 1 with that of *C. celebensis* in figure 20.) Furthermore, the scrotum is strikingly smaller relative to body size (about one-tenth of head and body length) with a brownish black scrotal sac sparsely covered by dark hairs.

The Sulawesi *Crunomys* has a small and stocky skull, which, like the external physignomy, contrasts starkly with the gracile, smooth, domed skull of *S. macrorhinos* (figs. 15–17). Unlike the latter, *C. celebensis* has a shorter and wide rostrum, stout zygomatic arches, low weakly ridged braincase in which the posterior margin of the occiput does not overhang the occipital condyles, much shorter (in anteroposterior plane) and wider interparietal located midway between parietals and occiput, oblong incisive foramina, smaller bullae, and a stout dentary with a prominent incisor capsule projecting from its lateral surface.

Other than sharing the primitive number of molar roots, nothing in morphology of the dentition points to a close relationship between *Crunomys celebensis* and *Sommeromys macrorhinos* (figs. 18, 19). The former

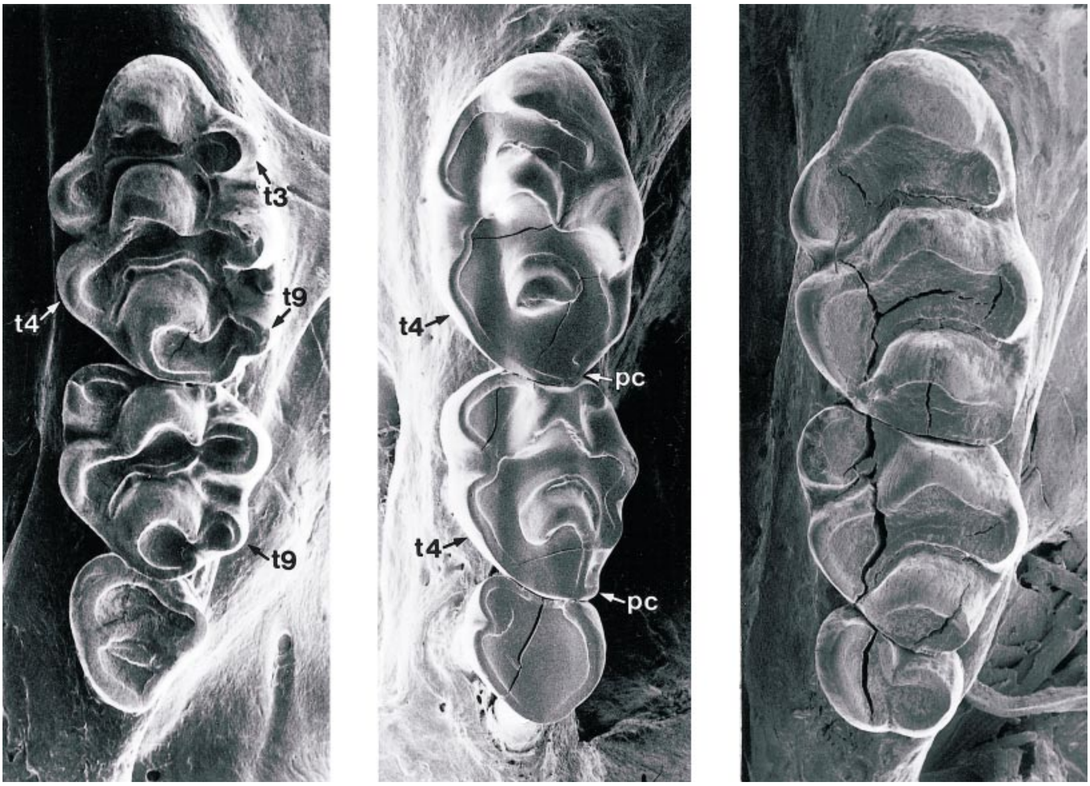

Fig. 18. Occlusal views of left maxillary molar rows. **Left:** *Tateomys macrocercus* (AMNH 225077; CLM1–3 = 5.0 mm). **Middle:** *Sommeromys macrorhinos* (holotype; CLM1–3 = 4.3 mm). **Right:** *Crunomys melanius* (AMNH 224316; CLM1–3 = 4.0 mm). This is a Philippine species and we illustrate its moderately worn molars instead of the Sulawesian *C. celebensis* because the molars of that species are too worn in all of the only three known examples (see fig. 15 in Musser, 1982: 25). Compared with *S. macrorhinos*, *T. macrocercus* has wide, robust molars with a large cusp t3 that has not coalesced with cusp t2 on the first molar; discrete cusp t9 that is set apart from cusp t6 on first and second molars, normal cusps t4 (without a posterior extension), and lacks posterior cingula (**pc**). Occlusal surface of *Crunomys* is simple compared with that of *S. macrorhinos*. See figure 14 for cusp terminology as exemplified by *S. macrorhinos*.

has stout upper and lower incisors with deep orange enamel faces; the basic configuration is similar to incisors of all the other Sulawesi murines except for those of the species of *Echiothrix*, *Melasmothrix*, and *Tateomys*. Compared with the molars of *Sommeromys*, molar rows are diminutive relative to the size of the cranium and mandible in *Crunomys*; third upper and lower molars are more reduced in size relative to others in each toothrow; occlusal surfaces of cusp rows are basined rather than cuspidate, even in young individuals; first and second upper molars lack posterior cingula (present in *Sommeromys*); cusp t4 is without a posterior projection (present in *Sommeromys*); cusp t9 is small and nearly completely united with cusp t8, well separated from cusp t6 on the first upper molar and absent from the second upper molar (present on both teeth and united with cusp t6 in *Sommeromys*); cusp rows are simple and laminar on lower molars (cuspidate in *Sommeromys*); the first two cusp rows on the first lower molar coalesce into a deeply basined structure (X-shaped wear surface in *Sommeromys*); and the posterior cingulum on first and second molars is smaller relative to molar size.

As unalike as they are in most characteristics, the two species do share a very few

Fig. 19. Occlusal views of left mandibular molar rows of same specimens shown in figure 18. **Left:** *Tateomys macrocercus* (clm1–3 = 4.7 mm). **Middle:** *Sommeromys macrorhinos* (clm1–3 = 4.3 mm). **Right:** *Crunomys melanius* (clm1–3 = 4.1 mm). Note the differences between *S. macrorhinos* and the other two species in conformation of the anterior half of each first molar, and the smaller posterior cingula (arrows) relative to molar size in *T. macrocercus* compared with the other two species

derived features; their significance to understanding phylogenetic relationships will be explored in the Discussion.

External body form of *Sommeromys macrorhinos* suggests an affinity with Sulawesi shrew rats, but detailed comparisons of cranial and dental morphology indicate otherwise. Still, we wondered if there were similarities in stomach morphology because *S. macrorhinos* eats insects, and, although shrew rats consume primarily earthworms, they also prey on insects (Musser, 1982, and observations recorded in field journals). We had already surveyed the stomach anatomy in shrew rats and other Sulawesian murines for a different project and discovered a wide range in anatomical design, from the generalized configuration found in *Rattus* to the specialized morphologies in small-bodied and large-bodied shrew rats. How does the stomach of *S. macrorhinos* compare?

Stomach morphologies of all the Sulawesian endemics exhibit one of two anatomical designs. The unilocular-hemiglandular stomach characterizes most species; Carleton (1973: 10) has described such a stomach as:

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

The fully distended stomach of *Rattus hoffmanni* (fig. 21) resembles the general

Fig. 20. *Crunomys celebensis*. Compare the external form of this small rat with that of *Sommeromys macrorhinos* in figure 1.

unilocular-hemiglandular conformation. It is slightly different in that the simple bordering fold, which marks the junction of glandular and cornified squamous epithelium, extends from the incisura angularis and recurves slightly to the left past the esophageal opening, and then posterior to a point opposite on the greater curvature, not quite bisecting the stomach. All of the antrum and a small area of the corpus to the left of the sagittal plane of the stomach is lined with glandular mucosa; cornified epithelium covers the rest of the corpus. This single-chambered hemiglandular morphology, in which the glandular zones are separated by a smooth bordering fold and the incisura angularis is shallow, forms the gastric conformation that Carleton (1980: 101) suggested represents the primitive evolutionary state among muroid rodents. The general unilocular-hemiglandular design is common to Sulawesian species in which the diets are composed of insects and fruit (*Margaretamys*); seeds (*Haeromys*); fruit, vegetative plant parts, and insects (*Lenomys* and *Eropeplus*); arthropods, snails, earthworms, fruit, and fungi (*Bunomys*); fruit, vegetative plant parts, and fungi (*Taeromys*); and fruit only (*Rattus*). In these species, the extent of glandular epithelium lining the antrum relative to the area of cornified epithelium of the corpus resembles the pattern in *Rattus hoffmanni* with a range of variation in which the the glandular portion does not extend beyond the level of the esophageal orifice to a configuration where the glandular lining penetrates the corpus well past the esophageal opening.

The gastric morphology of *Paruromys dominator* (fig. 21) is a variant of the unilocular-hemiglandular design and is unique among Sulawesian murines. The stomach is a U-shaped sac with the antrum forming the left segment and the corpus the right; the broad incisive angularis and base of the esophagus lie deep between these arms. A deep constriction on the dorsal and ventral surfaces divides the stomach so it appears bisaccular from the outside. In mid-frontal section, the apex of the incisura angularis is far to the right of the esophageal orifice. The bordering fold extends from the apex of the incisura angularis diagonally to a point on the greater curvature on the antral side. Compared with the gastric pattern seen in *R. hoffmanni*, cornified epithelium lines the entire corpus and penetrates a significant distal portion of the antrum; glandular mucosa is confined to the anterior half of the antral chamber. *Paruromys dominator* feeds only on fruit (Musser's field journal notes).

The other gastric design conforms to what Carleton (1973: 10) described as the bilocular-discoglandular morphology, in which the

> . . . stomach has a deep incisura angularis that projects well past the esophageal opening, thereby imparting a more strongly-defined bipartite condition. . . . The fornix ventricularis arches further beyond the esophageal orifice than in a unilocular stomach, and recurves slightly toward the esophagus. The size of the corpus, especially the fornix ventricularis section, varies greatly between individuals, the degree of distension corresponding to the amount of food contained. The walls of the antrum are conspicuously muscular, particularly near the pyloric orifice. The zone of glandular epithelium, surrounded by a distinct bordering fold, is restricted to a small disc-shaped area on the greater curvature. Cornified epithelium covers the remainder of the antrum and corpus.

The fully distended stomachs of adult *Maxomys hellwaldii* (fig. 21), as well as the other species of Sulawesian *Maxomys*, are similar to Carleton's description of the bilocular-discoglandular conformation. A spacious fornix ventricularis inclines towards the esophagus and projects craniad well beyond the esophageal opening, the incisura angularis is deep, and the antral walls are muscular. The entire corpus and most of the antrum is lined with muscular cornified squamous epithelium. Glandular epithelium is restricted to a small patch in the antrum on the ascending part of the greater curvature; the glandular zone is bounded by a low and simple bordering fold. *Maxomys hellwaldii* and its congeners are diet generalists, eating fruit, arthropods, snails, earthworms, and small vertebrates.

Stomach morphology of Sulawesian shrew rats, whose diet consists primarily of dipteran larvae and earthworms, is strikingly different from all other Sulawesian murines. The stomach of *Echiothrix centrosa* (fig. 22) is unilocular and discoglandular. Its external shape resembles the unilocular-hemiglandular plan in that the structure is single-chambered with a spacious corpus in which the broad fornix ventricularis projects only slightly anterior to the esophageal orifice, and the incisura angularis is shallow and either even with the esophageal orifice or barely extends beyond it. The walls of the antrum and corpus are thicker and in places more muscular than the unilocular-hemiglandular stomach of *Rattus hoffmanni*. The entire corpus and antrum is lined with cornified epithelium; glandular epithelium occurs only in a diverticulum situated on the greater curvature about opposite the esophageal orifice. This small pouch is lined with thick glandular mucosa and connects with the main chamber of the stomach through a tiny aperture.

Species of *Melasmothrix* and *Tateomys* also have a unilocular-discoglandular stomach configuration as exemplified by *T. macrocercus* (fig. 22). The stomach is small relative to body size, resembling a muscular swelling of the duodenum rather than a spacious semicircular chamber at the end of the esophagus, which is the gastric conformation found in other Sulawesian murines. In *T. macrocercus*, the muscular walls of the antrum and corpus are lined with cornified squamous epithelium. Glandular epithelium, surrounded by a thick bordering fold that is confluent with the posterior margin of the greater curvature, is confined to an oblong zone in the central portion of the stomach chamber.

The insectivorous *Sommeromys macrorhinos* has a very different stomach morphology than that found in species of *Echiothrix*, *Melasmothrix*, and *Tateomys*, resembling the basic unilocular-hemiglandular design (fig. 22) except for two deviations. Glandular epithelium lining the thick-walled antrum also extends slightly past the esophageal opening

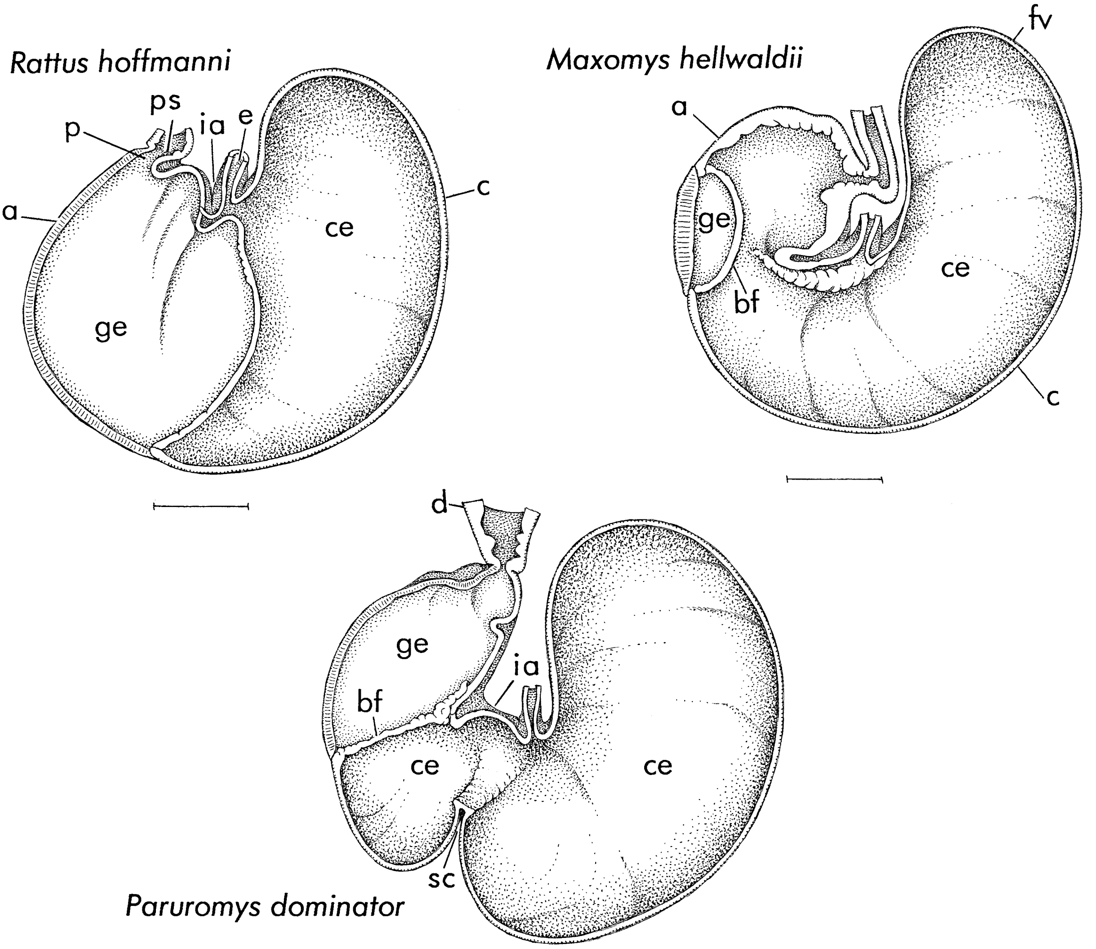

Fig. 21. Ventral view of stomachs (in midfrontal section) of *Rattus hoffmanni* (AMNH 226041), *Maxomys hellwaldii* (AMNH 224939), and *Paruromys dominator* (AMHH 224829). Abbreviations: **a,** antrum; **bf,** bordering fold; **c,** corpus; **ce,** cornified epithelium; **d,** duodenum; **e,** esophagus; **fv,** fornix ventricularis; **ge,** glandular epithelium; **ia,** incisura angularis; **p,** pylorus; **ps,** pyloric sphincter; **sc,** sagittal constriction. Gastric morphology of most species of endemic Sulawesian murines resembles one of these three conformations. Scale line equals 10 mm.

into the moderately thick-walled corpus. The fornix ventricularis of the corpus projects well anterior to the esophageal opening.

Gastric morphology characterizing *Sommeromys macrorhinos* is unlike that found in the species of small-bodied shrew rats and larger-bodied *Echiothrix*. With its long corpus relative to antral dimensions, the stomach is also dissimilar to any other species of Sulawesian murine except for *Crunomys celebensis*. The stomach of that animal consists of a balloonlike and thin-walled corpus with a much smaller thick-walled antrum (fig. 22).

Overall shape of the stomach is similar in *C. celebensis* and *S. macrorhinos*, but expansion of the corpus and extent of glandular and cornified epithelium differs. In the illustrated specimen of *C. celebensis* (AMNH 225042), the corpus (which is fully distended) is much larger relative to the antrum, its walls are much thinner, and cornified epithelium penetrates the antrum in a zone beneath the esophageal opening and below the bordering fold on the antral side of the greater curvature. The walls in these two areas consist of muscular folds and contrast with the smooth

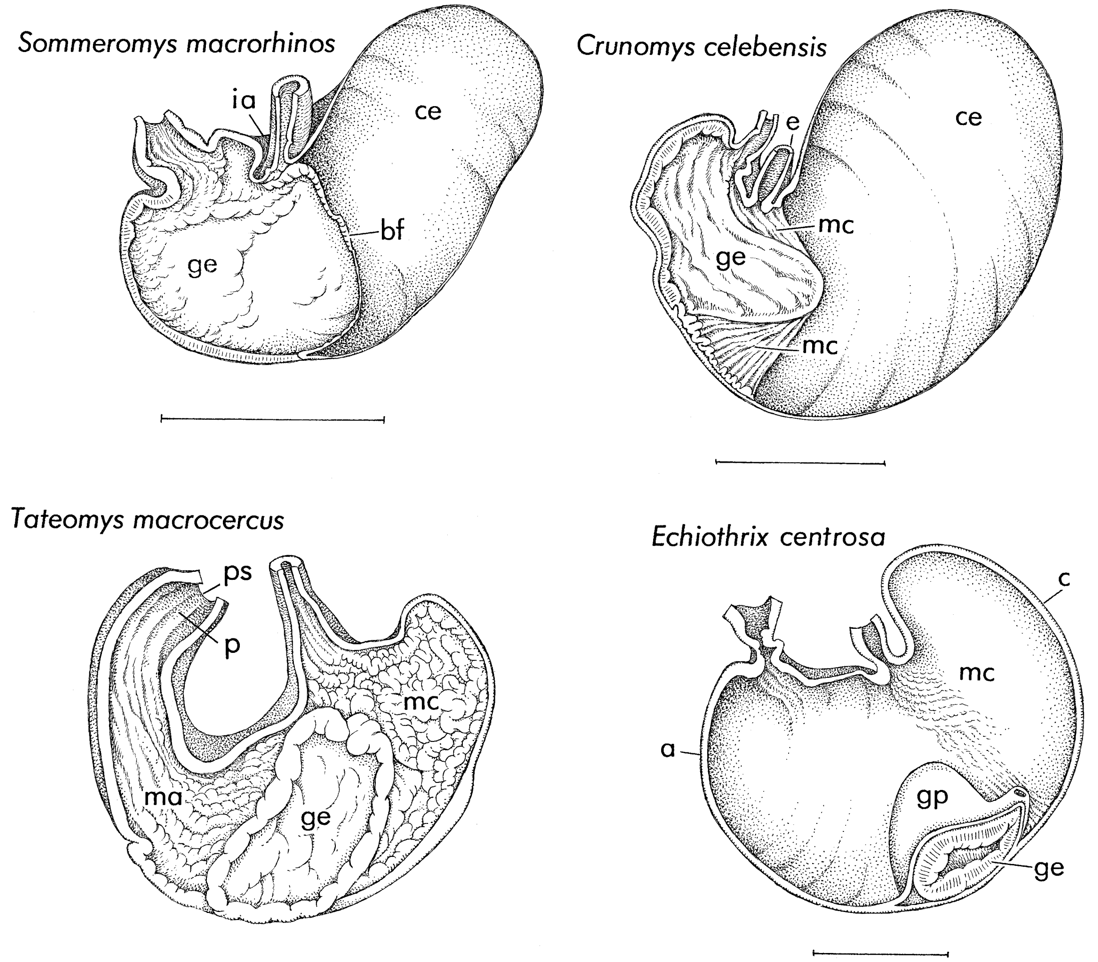

Fig. 22. Ventral view of stomachs (in midfrontal section) of *Sommeromys macrorhinos* (holotype), *Crunomys celebensis* (AMNH 225042), *Tateomys macrocercus* (AMNH 225075), and *Echiothrix centrosa* (AMNH 225043). Abbreviations: **gp,** glandular pouch; **ma,** muscular walls of the antrum; **mc,** muscular walls of the corpus; other abbreviations are as defined in figure 20. Scale line equals 10 mm.

walls of the corpus. Glandular epithelium is confined to the anterior two-thirds of the antrum, where it is bounded by the bordering fold sweeping from the pylorus into a bit of the corpus and back to the right side of the antrum. A second specimen (AMNH 224316) exhibits a morphology similar to AMNH 225042 except that the corpus is not distended and projects beyond the esophageal opening to about the degree seen in *Echiothrix* (fig. 22). However, convoluted folds of cornified epithelium in the crown of the corpus indicates it is capable of significant distension. The diet of *C. celebensis,* as documented by two of the three known specimens, consists entirely of insects.[4]

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[4] Stomachs are preserved from two out of the three known specimens of *Crunomys celebensis*. Musser (1982) thought, incorrectly as it turns out, the stomach contents of one of these individuals to resemble finely masticated white plant parts. The other specimen is the holotype, which he was reluctant to dissect at the time he described the species. We reexamined the white pulpy material from the first specimen, which under the microscope seemed to consist of tiny bits of animal tissue, and removed the stomach contents from the holotype, which clearly consisted of arthropod remains. David Grimaldi looked at the material and provided us with

ECOLOGY: Life history information for *Sommeromys macrorhinos* is scanty. Musser was told by members of the NAMRU survey team that they reached their campsite on Gunung Tokala by the evening of August 1, 1973. Despite a heavy, cold rain, one person managed to scatter a few Victor rat snap-traps on the ground near the camp before retiring to his tent. The next morning he found a shrew rat (*Tateomys rhinogradoides*; see Musser, 1982: 57) and the example of *S. macrorhinos* in the traps. The site was covered by primary mossy forest that was slightly disturbed by human activities.

At 2400 m in central Sulawesi, the vegetation on Gunung Tokala would be classified as tropical upper montane rain forest by botanists (Whitmore, 1984) and commonly referred to as moss forest. Its structure, composition, and the prevailing ambient temperatures and humidities are probably similar to the moss forest habitats farther north on the high slopes of Gunung Nokilalaki where Musser worked (he never visited the Tokala site). Descriptions and photographs of that forest formation are provided by Musser (1982: 71–79), Musser and Dagosto (1987: 39–46), and Musser and Holden (1991: 357–359). Judged by the trapping site of the holotype, *Sommeromys macrorhinos* is a member of that suite of murines restricted to montane rain forest habitats in central Sulawesi: *Melasmothrix naso*, *Tateomys rhinogradoides* and *T. macrocercus*, *Eropeplus canus*, *Margaretamys elegans* and *M. parvus*, *Haeromys* sp., *Bunomys penitus* and *B. prolatus*, and *Maxomys dollmani* and *M. wattsi* (see table 18 in Musser and Holden, 1991).

Sommeromys macrorhinos is apparently insectivorous. Contents of the stomach (saved and stored with the holotype) consist of nematodes, eggs of a muscoid fly, and insect fragments (cuticle, long and filamentous antennae, and a leg). According to D. A. Grimaldi (Department of Entomology, AMNH), who kindly identified the stomach contents for us, morphology of the leg and antennal fragments along with size and thickness of the cuticle pieces suggest they came from cockroaches. We have found nematodes in the stomachs of shrew rats and other species of rodents and suspect they are usual inhabitants of either the rodent gut or gastrointestinal tract of the prey items. We know that one *S. macrorhinos* ate a cockroach and ingested fly eggs but until more specimens of the rodent are obtained, we will not know the variety—if any—of insects taken or if soft-bodied invertebrates such as earthworms are also sometimes eaten.

Sommeromys macrorhinos likely forages on different forest substrates. It certainly seeks prey on the ground (it was caught in a trap set on wet, muddy, and slightly mossy ground) and probably above ground on tops of moss-covered rocks as well as moss-encrusted rotting tree trunks and limbs laying on the forest floor. Its very long and slender tail with its gripping capability, the long and narrow hind feet, long digits and bulbous interdigial pads, claw conformation, and over-

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the following report (samples are preserved with each respective specimen).

AMNH 224316 (holotype of *Crunomys celebensis*): Abundant tracheae and tracheoles, setiferous fragments of sclerites, which indicate one or more large insects (''definitely not spiders, or other kind of terrestrial arthropods''); large, sclerotized mandible with articulated palp and distal portion of short leg segment, which is ''most indicative of a large larval coleopteran (like a scarab grub)''; and a small midge (Sciaridae), which is likely a contaminant because it is ''too well preserved.''

AMNH 225042: The stomach contents appear to form an amorphous white mass, but is actually composed of ''very finely masticated, thoroughly digested, fine particles.'' The ''presence of characteristic tracheae (fine, tubular, whitish respiratory tubules) confirms insects. Size of tracheae suggests a fairly large insect, greater than 1 cm.'' The tracheae are ''not to be confused with nematodes, which are also in this sample.'' Grimaldi wrote how unusual it was that no insect sclerites are present, ''since these would persist in the gut at least as long (generally longer) than tracheae. Lack of such sclerites would suggest, again, a large larva whose head capsule was perhaps not ingested.''

In contrast to the Sulawesian *Crunomys*, at least one of the three known species of *Crunomys* endemic to the Philippines is vermiferous. Larry Heaney kindly loaned us an adult (FMNH 167889) and juvenile (FMNH 167888) *Crunomys melanius* collected on Camiguin Island. Stomach morphology of these specimens resembles that of *C. celebensis* with two exceptions: 1) a greater area of the antrum is covered by glandular epithelium; 2) cornified epithelium from the corpus extends into the antrum to a depth comparable to that seen in *C. celebensis* but it is smooth on either side of the glandular zone, without the muscular folds so characteristic of the Sulawesian species. Both specimens had partially digested segments of earthworms in their stomachs and nothing else. Diets of *C. fallax* from Luzon and *C. suncoides* from Mindanao are unknown.

all gracile body build also suggest scansorial and arboreal behaviors. The large fleshy interdigital palmar and plantar pads, along with the elongate digits and their curved and sharp claws would allow secure purchase on wet bark and mossy substrates at levels above the ground in woody shrubs and crowns of understory trees. At times the rat may leap from one branch to the other, a motility suggested by the long hind legs with their elongate feet (and small thenar and hypothenar tubercles occupying only a very small part of the otherwise smooth plantar surface). As it scampered, climbed, or leapt along and among twigs and branches, the animal would be stabilized by its projecting pollex and prehensile distal tail strip.

Among endemic Sulawesian murines, narrow, sharp, and unpigmented incisors, like those seen in *S. macrorhinos*, are associated with diets consisting predominately of either arthropods or annelids, or a combination of the two groups. A long rostrum, especially the remarkably protractive structure of *S. macrorhinos*, may contain greater nasal epithelial area, compared with other murines of similar body size, and provide enhanced and acute olfactory ability, which is probably required to locate invertebrate prey during the night in odoriferous cool, wet, and densely mossy environments. Conformation of upper and lower incisors tips would allow the rat to impale cockroaches (especially the nymphs) and other soft-bodied invertebrates, and the cuspidate molars would help rend the prey into small bits, which characterized the residual parts found in the stomach of the holotype.

Sommeromys macrorhinos is probably also nocturnal. Among the small-bodied Sulawesi murines living in montane forest and subsisting on invertebrates, only *Melasmothrix naso*, which has dark chestnut fur, is diurnal. The small-bodied *Crunomys celebensis*, which also has dark chestnut pelage, but occurs in tropical lowland evergreen rain forest, is also diurnal (Musser, 1982). The other montane species of shrew rats, *Tateomys rhinogradoides* and *T. macrocercus*, are nocturnal and have grayish brown fur similar to the pelage color exhibited by *S. macrorhinos*. In our experience, small tropical muroid rodents that are active predominately during the day and prey on invertebrates have dark chestnut fur. Other examples in addition to *Melasmothrix naso* and *Crunomys celebensis* (Musser, 1982) are the Philippine murine species of *Crunomys* and *Archboldomys luzonensis* (Rickart et al., 1998), and the Neotropical sigmodontine species of *Scotinomys* (Hooper and Carleton, 1976).

THE NEW SPECIES OF LOUSE

Hoplopleura sommeri, new species

HOLOTYPE: Male collected by L. A. Durden from the pelt of the adult male *Sommeromys macrorhinos* (AMNH 226956) collected by members of NAMRU-2 survey at 2400 m on Gunung Tokala, Central Sulawesi, Indonesia on August 2, 1973. Deposited in the USNM.

REFERRED SPECIMENS: Four additional individuals, representing the allotype female and three female paratypes all recovered from the same host rat as the holotype. Allotype female deposited in USNM. Paratypes deposited in AMNH, NHM, and MZB.

DISTRIBUTION: Known from a single collection (five specimens) recovered from the holotype of *Sommeromys macrorhinos* from Gunung Tokala, Central Sulawesi.

ETYMOLOGY: The new species is named for Helmut G. Sommer in appreciation for his commitment to our projects on Sulawesian rodents and their ectoparasites.

DIAGNOSIS: Like its host, *Hoplopleura sommeri* is a distinctive taxon and unlikely to be confused with any other species of *Hoplopleura*. Especially distinctive morhological traits are the fluted appearance and the setal arrangements on the paratergal plates of both sexes, the shape and setation of the female subgenital plate, the morphology of the male genitalia, and the absence of anterior abdominal tergites, especially in the male.

DESCRIPTION: **Male** (fig. 23): Length of holotype, 0.768 mm. Head, thorax, and abdomen all lightly sclerotized.

Head. About as wide as long with relatively blunt anterior apex; 2 DAnHS, 3 DMHS, 1 SHS, 2 ApHS, 2 AnMHS, and 1 DAnHS present on each side; DPHS relatively short, extending slightly more than half distance to thoracic spiracle; 1 DAcHS medial to each DPHS; VPHS moderate in

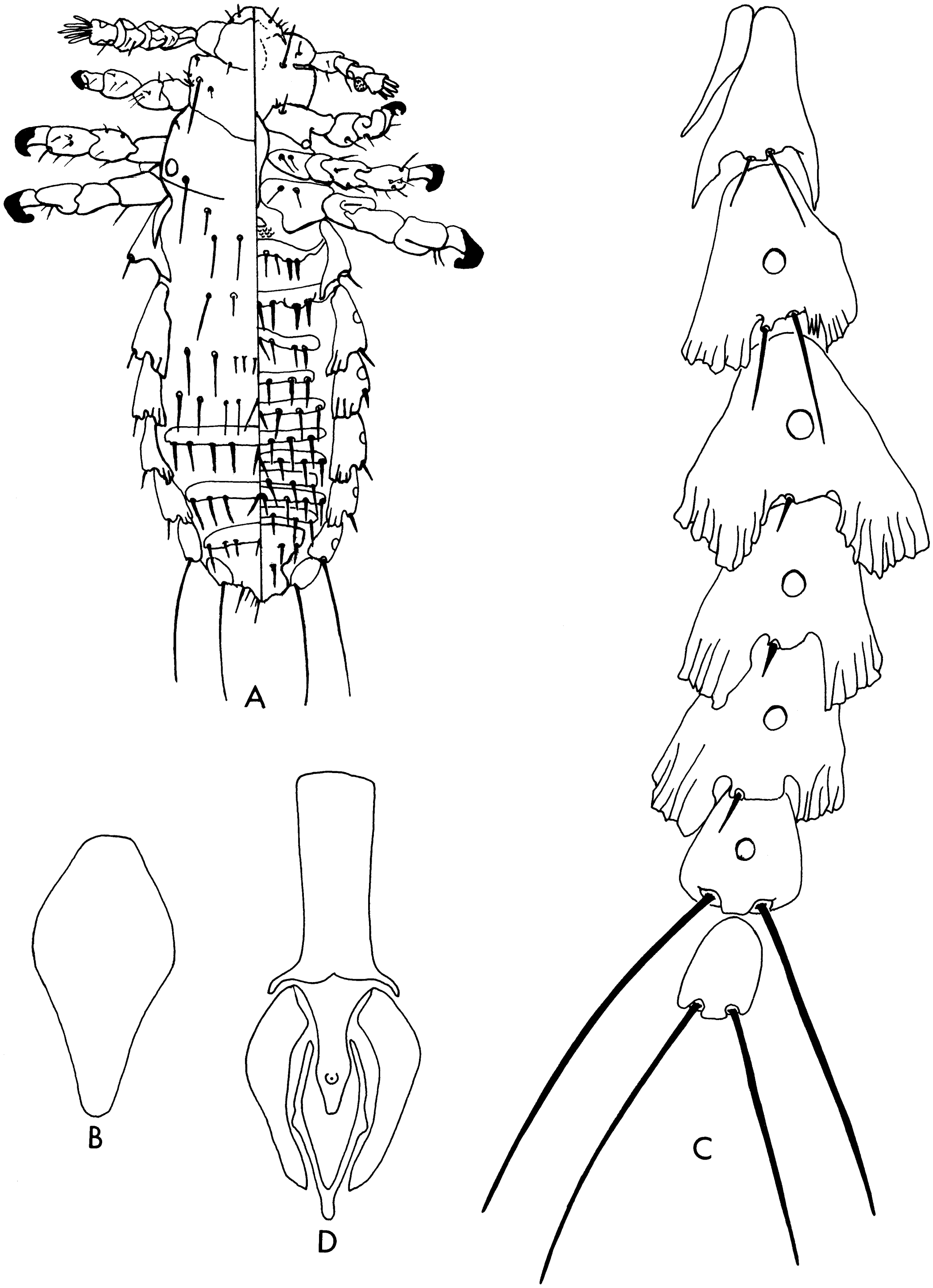

Fig. 23. *Hoplopleura sommeri*, male. **A,** dorsoventral view; **B,** thoracic sternal plate; **C,** paratergal plates; **D,** genitalia.

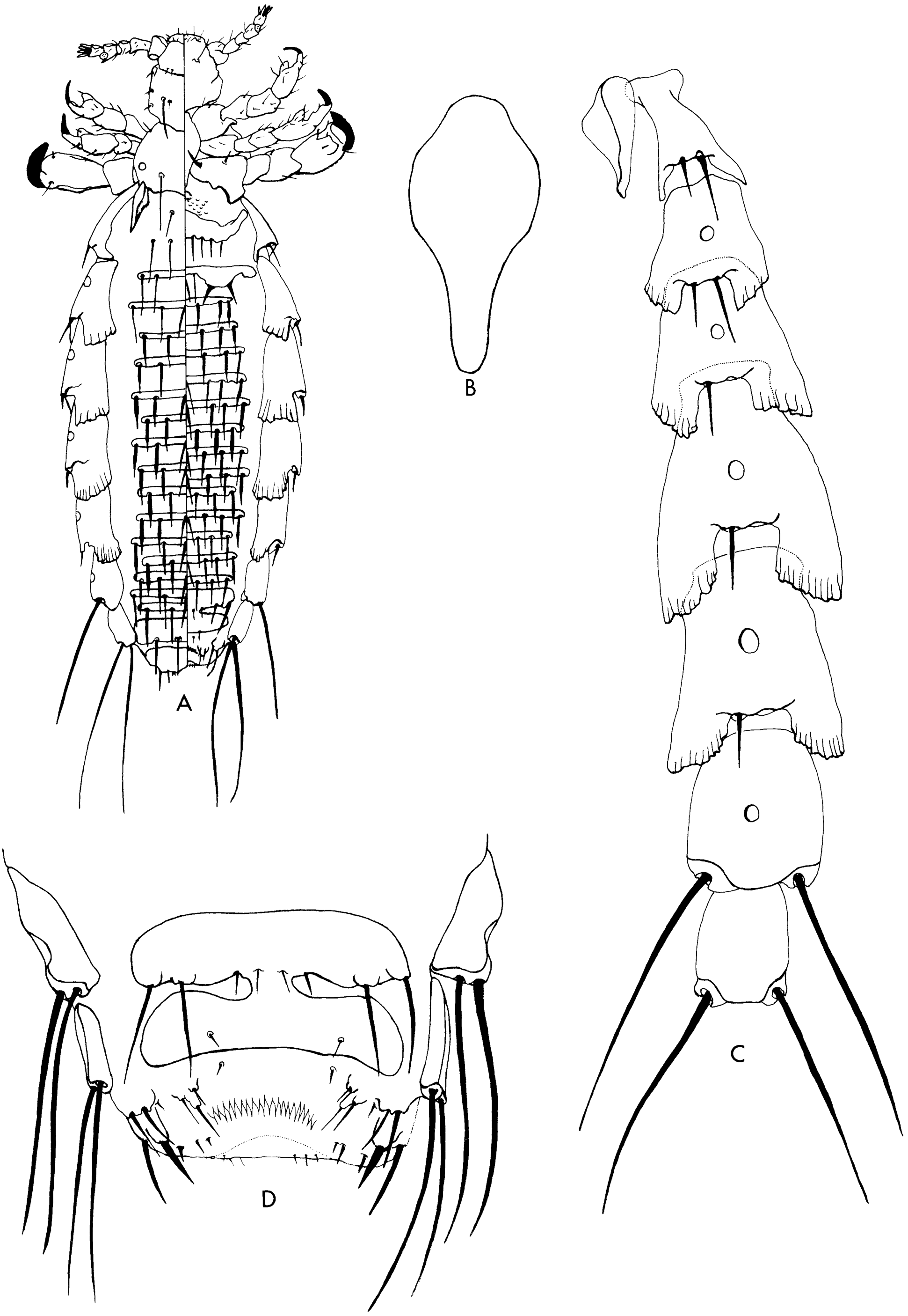

Fig. 24. *Hoplopleura sommeri*, female. **A,** dorsoventral view; **B,** thoracic sternal plate; **C,** paratergal plates; **D,** genitalia.

length. *Antennae*. 5-segmented with basal segment wider than second segment, about as wide as long.

Thorax. Broader than head with margins widening posteriorly; thoracic sternal plate (fig. 23B) tapering to broadly rounded posterior apex and to a squarish anterior apex, with convex lateral margins medially; mesothoracic spiracles displaced laterally, moderate in size (0.0210 mm in diameter); DPTS relatively short (0.0910 mm); 1 DPtS on each side. *Legs.* Fore and mid coxae subtriangular, forelegs small, each with narrow acuminate claw; mid and hind legs and associated claws progressively larger than fore legs but to a lesser extent than in most species of *Hoplopleura*.

Abdomen. Slightly wider than thorax. Tergites absent from abdominal segments 1–4; 1 narrow tergite on each of segments 6–8; 2 DLAS on segment 1, 4 DCAS on segment 2, 2 long DLAS and 2 short DCAS on segment 3, 4 long DLAS and 6 short DCAS on segment 4, 4 DLAS and 5 slender (but not shorter) DCAS on segment 5, 9 TeAS on segment 6, 7 TeAS on each of segments 7 and 8 with the medial 5 TeAS on segment 8 being distinctly smaller. One narrow sternite present on each of abdominal segments 1–4 and 8; 2 narrow sternites present on each of abdominal segments 5–7; 6–8 StAS present on each sternite; sternite 1 very small; sternites 2 and 3 each extending laterally to articulate with corresponding parartergal plates and both with 2 stout lateral StAS on each side; some posterior TeAS and StAS dagger-shaped. *Paratergal plates* (fig. 23C) present on abdominal segments 1–8; plates I–VII subtriangular; plates II and III each with 2 apical PrS, with 1 PrS distinctly longer than the other; plates IV–VI each with 1 relatively short PrS; plates VII and VIII each with 2 long apical PrS; plates III–VI with fluted sculpting apically; plates III–VII each with moderately sized spiracle.

Genitalia (fig. 23D). Basal apodeme short and weakly sclerotized with posterior medial indentation; parameres curved and broadening anteriorly; pseudopenis of moderate length, extending slightly beyond apices of parameres and with lateral flange on each side.

Female (fig. 24): Length of allotype, 0.985 mm (mean for series, 1.018; range, 0.800–1.185; *N* = 4).

Head, thorax, and legs. As in male unless indicated otherwise. 2 SHS on each side of head. Thorax distinctly broader than head. Thoracic sternal plate (fig. 24B) tapering more acutely than in male to broadly rounded posterior apex.

Abdomen. Lacking tergites dorsally on abdominal segments 1 and 2; 2 tergites on each of segments 3–10; tergites 1–15 narrow but tergite 16 broad; 2 DCAS on segment 1, 4 DCAS on segment 2, 4–5 TeAS on each tergite. 1 very small sternite on abdominal segment 1; 1 broad sternite on segment 2, 1 broad and 1 narrow sternite on segment 3, and 2 narrow sternites on each of segments 3–8; 6–8 StAS on each sternite; sternites 2 and 3 each extending laterally to articulate with corresponding paratergal plate; sternite 3 also expanded laterally with 2 stout StAS on each expanded section; some posterior TeAS and StAS dagger-shaped. *Paratergal plates* (fig. 24C) as in male but PrS on plates IV–VI slightly longer and exact shapes of plates slightly different (as in fig. 24C).

Genitalia (fig. 24D). Subgenital plate distinctly H-shaped with expanded anterior and posterior sections connected by narrow pedicel; 2 long lateral setae on posterior margin of anterior section on each side and 4 shorter central setae near pedicel of subgenital plate; gonopods VIII each with three distinct lobes with each lobe bearing 1 seta of moderate length; gonopods IX each bearing a stout seta; vulvar fimbriae distinct.

REMARKS AND DIAGNOSIS: *Hoplopleura sommeri* possesses some unusual morphological traits when it is compared to its congeners. Particularly notable is the reduction in anterior abdominal plates on the dorsal surface. This feature is well developed in the male, where abdominal segments 1–5 lack tergites, and partially developed in the female where segments 1 and 2 lack tergites. Reduced numbers of abdominal plates is a feature of several other species of *Hoplopleura* native to Sulawesi, especially species that parasitize the endemic squirrels on this island (Durden et al., ms.). Another morphological trait of *H. sommeri* that is shared with several of its congeners from Sulawesi is the lateral displacement of the mesothoracic spiracle. The H-shaped subgenital plate in the female and the lateral flanges on the pseudopenis of the male are other notable features of *H. sommeri*.

Hoplopleura sommeri can be distinguished from its congeners by a combination of the following characters:

1. The absence of dorsal tergal plates (tergites) on the first 5 segments on the male abdomen and the absence of tergal plates on abdominal segments 1 and 2 in the female.
2. The unique arrangement of setae on the abdomen, particularly on the dorsal surface of the male where rows of 2, 4, 4, 10, and 9 DCAS, respectively, occur from anterior to posterior. Some of these setae are characteristic in size such as the 6 short central DCAS in row 4 in the male.
3. The number and length of setae inserted apically on the paratergal plates [notably, 1 long and 1 shorter seta on each of plates II and III, and 1 stout (in male) or 1 medium-sized (in female) seta on each of plates IV–VI], in addition to the fluted apical sculpting of plates III–VI.
4. The elongate subovoid shape of the thoracic sternal plate in both sexes.
5. The lateral displacement of the thoracic spiracles.
6. The genitalia of the male which have a short, weakly sclerotized basal apodeme about equal in length to the pseudopenis. The pseudopenis has a distinctive lateral flange on each side and is enclosed by anteriorly broadening parameres.
7. The genitalia of the female which consist of a broad, more or less H-shaped, subgenital plate with setae of characteristic lengths inserted at distinct sites (fig. 24D). The gonopods VIII also are distinctive in that each seta is borne on a distinct lobe.

Overall, no other species of sucking lice are likely to be confused with *H. sommeri*. Morphologically, it is most similar to some of the currently undescribed species of *Hoplopleura* that we have recovered from endemic Sulawesian squirrels (Durden et al., ms.) especially with respect to the reduction in the number of dorsal abdominal plates (tergites) in the males. However, *H. sommeri* may not be phylogenetically closely related to these squirrel lice. Males of some other species of *Hoplopleura*, such as *H. chysocomi*, *H. sembeli*, and *H. traubi*, that we have previously described as ectoparasites of Sulawesian murines (Durden, 1990; Durden and Musser, 1991), also have (to a lesser extent) reduced numbers of dorsal abdominal plates. Therefore, the exact phylogenetic relationships between *H. sommeri* and other species of *Hoplopleura*, especially those native to Sulawesi, must await more detailed character analyses and the description of additional species.

DISCUSSION

Of the more than 1300 Recent species among the 18 subfamilies within the family Muridae, not one of them has the unique rostral architecture of *Sommeromys macrorhinos*. Furthermore, no other murid exhibits the combination of specializations associated with external body form, pterygoid region, incisors, and the other traits that set the species apart. Among endemic species of Sulawesian murines, *S. macrorhinos* superficially resembles a long-tailed shrew rat in body form, but its diagnostic traits disassociate it from any close phylogenetic relationship with either the small-bodied species of *Tateomys* and *Melasmothrix* or the larger-bodied species of *Echiothrix*.

The shrew rat *Crunomys celebensis* is another matter. As different as it is from *Sommeromys macrorhinos* in external body form, the two species share three characters not seen in any other native Sulawesi murine. 1) A zygomatic notch is not present and the anterior margin of the zygomatic plate is either straight or concave. 2) The stapedial foramen is minute and the basicranial region exhibits the skeletal and foraminal configurations associated with a cephalic arterial circulation in which the arterial supply to the orbit and upper jaw (ophthalmic and internal maxillary arteries) is furnished by a secondary connection with the internal carotid with the reduced stapedial artery coursing only to the otic region. 3) The fornix ventricularis of the stomach extends appreciably anterior to the incisive angularis and esophageal orifice.

These shared traits are ambiguous in signaling any closer phylogenetic relationship to each other than to other Sulawesian murines. Absence of a zygomatic notch (indicating no anterior projection of the zygomatic plate beyond the anterodorsal margin of the dorsal

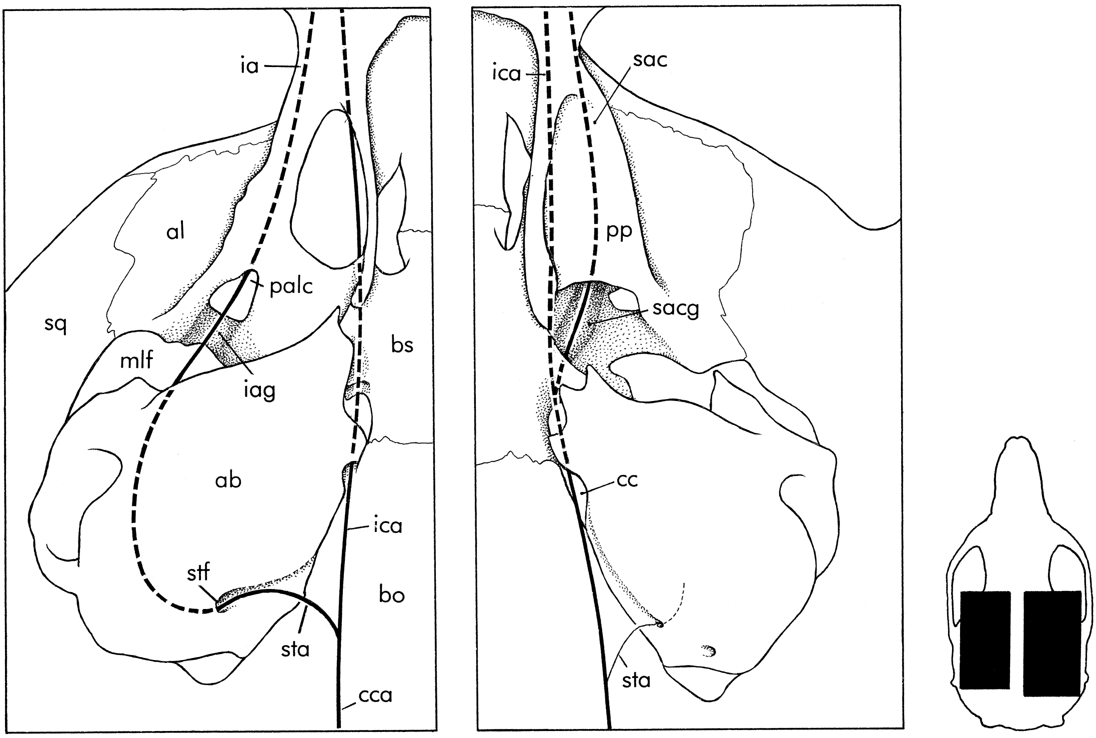

Fig. 25. Ventral views of two contrasting cephalic arterial circulations. **Left:** The primitive pattern that is widespread among murines (drawn from the holotype of *Archboldomys luzonensis*, FMNH 95122). After branching off the common carotid artery (**cca**) the stapedial artery (**sta**) enters the large stapedial foramen (**stf**) in the petromastoid fissure between periotic and auditory bulla and becomes the infraorbital artery (**ia**), which exits the periotic region through the middle lacerate foramen (**mlf**), coursing in a groove (**iag**) on the outside of the pterygoid plate and disappearing through the posterior opening of the alisphenoid canal (**palc**). After the stapedial branches off, the common carotid continues as the internal carotid artery (**ica**), entering the braincase through the carotid canal (**cc**). **Right:** The incomplete, derived, circulatory pattern found in *Crunomys celebensis* (drawn from the holotype, AMNH 224316). A small stapedial artrery serves only the periotic region through a minute stapedial foramen. Internal maxillary circulation (supplied by the infraorbital artery in the other pattern) is supplied by a secondary arterial connection (**sac**) that branches from the internal carotid artery and courses obliquely in a groove (**sacg**) across the dorsal surface of the pterygoid plate (**pp**). *Sommeromys macrorhinos* also has this pattern, but the secondary arterial connection and groove in which it courses are concealed by bone. See figure 26. Other abbreviations: **al,** alisphenoid; **bo,** basioccipital; **bs,** basisphenoid; **sq,** squamosal.

maxillary root of the zygomatic arch) and a straight or concave anterior margin has been regarded as a primitive configuration in muroids (Carleton, 1980; Voss and Carleton, 1993; Voss, 1993) and is unhelpful in assessing the strength of any phylogenetic link between *C. celebensis* and *S. macrorhinos*. The cephalic arterial pattern is a derived configuration (Carleton, 1980; Musser and Newcomb, 1983), but whether it indicates a real phylogenetic tie between the two species or independent derivation cannot be determined without cladistic analyses of all Sulawesi murines combined with samples from the Philippines, the Sundaic region, and Indochina. There is also a significant structural difference in the pterygoid region where the secondary arterial connection courses (figs. 25, 26). In *S. macrorhinos,* the posterior third of the pterygoid plate is covered by thin bone concealing openings to the transverse canal, foramen ovale, and a section of the trough for the secondary arterial connection between internal carotid artery and facial cir-

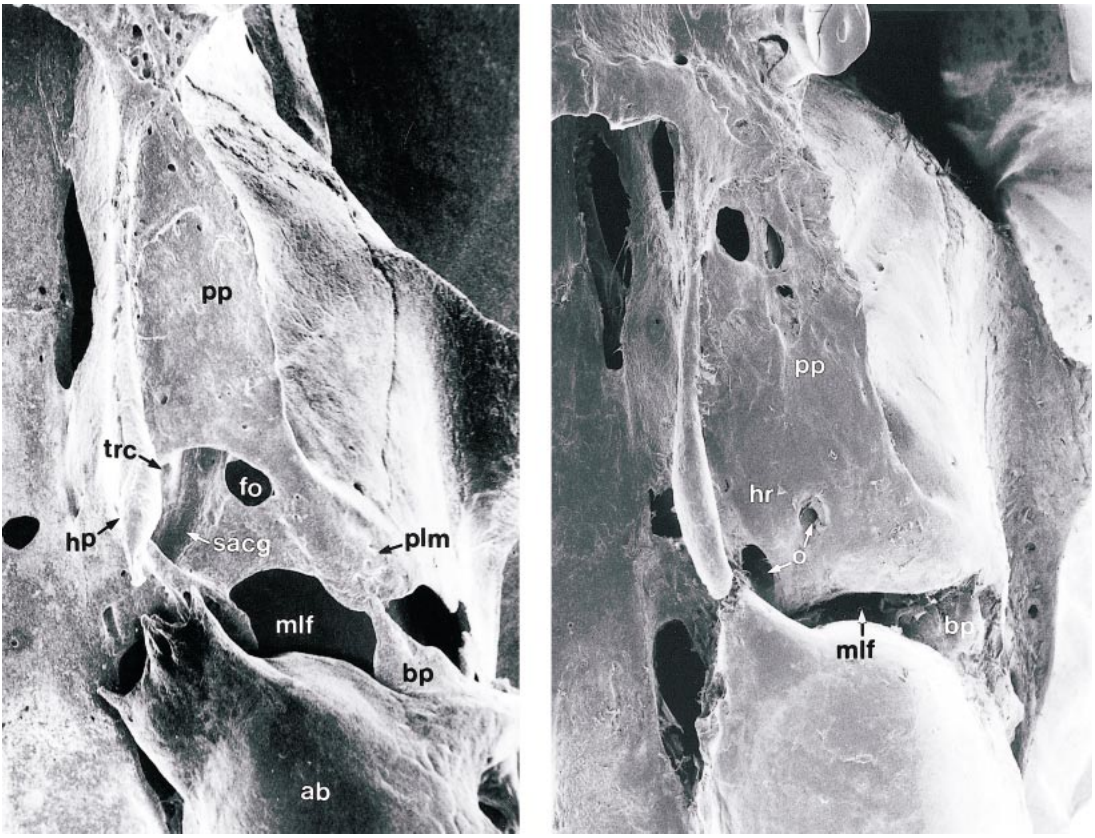

Fig. 26. Ventral views of left pterygoid plates (= pterygoid fossa, parapterygoid fossa; **pp**) obtained from scanning electron microscopy. **Left:** The configuration in *Crunomys celebensis* (the same specimen diagramed in figure 25), which represents the usual configuration in murines with the derived cephalic arterial pattern. In the posterior third of the pterygoid region can be seen the foramen ovale (**fo**), the left opening of the transverse canal (**trc**) slightly obscured by the hamular process of the pterygoid, (**hp**), an oblique groove in which the secondary arterial connection between internal carotid artery and facial circulation courses (**sacg**), and the mound-shaped posterolateral margin (**plm**) of the pterygoid plate to which is attached a bony process (**bp**) from the auditory bulla (**ab**). A spacious middle lacerate foramen (**mlf**) separates bullar capsule from posterior margin of the pterygoid plate. **Right:** The unique architecture in the holotype of *Sommeromys macrorhinos*. Within the hollow region (**hr**) of the pterygoid plate is concealed the foramen ovale, a portion of the oblique trough for the secondary arterial connection, and left opening of the transverse canal. The posterior margin of the plate is close to the auditory bulla, separated by a narrow middle lacerate foramen. The two openings (**o**) were originally covered by tissue; their function is unknown. See the diagrammatic portrayal of this region in figure 25.

culation; in *C. celebensis*, that posterior third is uncovered to reveal the openings of the tranverse canal and the foramen ovale as well as the groove for the secondary arterial connection. This is the usual conformation in murines; the architecture found in *S. macrorhinos* is unique. Both species have a unilocular-hamiglandular stomach and an expansive corpus. The general stomach design is primitive (Carleton, 1973), but the conformation of the corpus relative to the antrum is unusual; however, its phylogenetic significance is ambiguous, particularly in the context of the significant differences between the two stomachs. The corpus of *C. celebensis* is appreciably more expansive, with a smooth cornified epithelial lining except where it penetrates the antrum and transforms into muscular zones bounding the greatly reduced area of glandular epithelial. *Sommeromys* *macrorhinos* has a smaller corpus, and the relative distibution of glandular and cornified epithelium generally conforms to the basic unilocular-hemiglandular design, like that of *Rattus hoffmanni*, for example (figs. 21, 22).

There are no apparent morphological traits signaling a close relationship between *Sommeromys macrorhinos* and *Crunomys celebensis*. The two species, however, are united in their striking morphological, and presumably phylogenetic, isolation from all the other native Sulawesian murines. About half of the more than 40 native species are contained in four genera: *Bunomys*, *Paruromys*, *Taeromys*, and *Rattus*. In parallel with the clusters of indigenous Philippine murines, species in these four genera would correspond to the Philippine ''New endemics,'' a group of genera that ''have been closely associated with *Rattus*, to the degree that some checklists and revisionary studies have treated them as subgenera of that genus . . . , despite intentions of the original describers who did not perceive such an alliance'' (Musser and Heaney, 1992: 93). Other than being in the subfamily Murinae, neither *Sommeromys* nor the Sulawesian *Crunomys* bear any close phylogenetic relationship to this generic group of Sulawesian New Endemics.

Excluding *Sommeromys* and *Crunomys*, the rest of the native indigenous Sulawesian species cluster in eight genera that are also not closely related to the New Endemics. They can be sorted into six groups: 1) two species of *Echiothrix*, 2) one species of *Melasmothrix* and two species of *Tateomys*, 3) three species of *Margaretamys*, 4) one species of *Lenomys* and one of *Eropeplus*, 5) two species of *Haeromys*, and (6) six species of *Maxomys*. Each cluster constitutes a natural phylogenetic unit. The first four are endemic to Sulawesi; species of *Haeromys* and *Maxomys* have representatives on the Sunda Shelf and Indochina. Phylogenetic relationships between each group and faunas from outside of Sulawesi are unresolved. They may represent adaptive radiation from a single ancestral group reaching Sulawesi early in the geological history of the island, but a more tenable hypothesis is that each group represents evolution from an independent ancestral migration from regions outside of Sulawesi (probably continental Southeast Asia and islands on the Sunda Shelf).

Compared to the species of Sulawesian New Endemics and the other six groups, *Crunomys celebensis* is, except for its derived cephalic arterial pattern, lack of alisphenoid strut, simple basined cusp patterns, and relatively small third molars ''. . . structurally a primitive small-bodied rat'' (Musser, 1982: 88). Many of its traits are pleisiomorphic: 1) external body form and body size, 2) moderately long rostrum relative to cranial length, 3) smooth dorsolateral margins of interorbital and postorbital regions and smooth braincase, 4) short incisive foramina, 5) zygomatic plates set anterior to molar rows, 6) bony palate ending anterior to backs of molar rows, 7) posterior palatine foramen situated opposite the back of each first molar or at junction of first and second molars, 8) sphenopalatine foramen coalesced with dorsal palatine foramen in the orbit, 9) slitlike sphenopalatine vacuities in mesopterygoid fossa, 10) pterygoid fossa complete and not breached by sphenopterygoid openings, 11) small auditory bullae with moderately long bony eustachian tubes, 12) size of bullar capsule relative to ventromedial wedge of exposed periotic, 13) intact squamosal dorsal to each bulla (subsquamosal fenestra absent), 14) no zygomatic notch, 15) unspecialized incisors, 16) upper molars anchored by three roots, lower molars by two, 17) no cusp t7 on upper molars, 18) posterior cingulum on first and second lower molars (see Musser, 1982, for more detailed description and illustrations of these traits), and 19) a unilocular-hemiglandular stomach (although the distribution of glandular relative to cornified epithelium is specialized). The only other species with a similar combination of primitive and derived external, cranial, and dental traits are those species of *Crunomys* native to the Philippines (Musser, 1982; Rickart et al., 1998). If the morphology of *C. celebensis* is a reliable indicator of phylogenetic ties to the Philippine species (molecular data would be useful for testing this hypothesis), then the Sulawesian *Crunomys* is a member of that part of the indigenous Philippine murine fauna; it is certainly unrelated, other than being a member of Murinae, to any other Sulawesian species.

In its own way, *Sommeromys macrorhinos* is similarly isolated, not only from the Sulawesian fauna, but from also any other murine occurring elsewhere. Some of its characters are primitive: 1) smooth interorbit and braincase, 2) shape of zygomatic plate, 3) location of maxillary molar row relative to posterior border of zygomatic plate, 4) alisphenoid struts, 5) relative position of posterior palatine foramina, 6) size of bullar capsule relative to ventromedial wedge of exposed periotic, 7) configuration of dentary where alvoelus for lower incisor ends, 8) number of maxillary and mandibular molar roots, 9) no cusp t7 on upper molars, 10) discrete posterior cingulum on first and second upper molars, 11) configuration of first two rows of cusps on each first lower molar, 12) a posterior cingulum on first and second lower molars, and 13) a unilocular-hemiglandular stomach.

Many of *Sommeromys's* diagnostic characters are derived: 1) long muzzle, absolute and relative length of tail; 2) dorsal calloused grasping strip along terminal one-sixth of tail; 3) free-standing digitlike pollex; 4) degree of body fur covering over lower front and hind legs; 5) long, slender, delicate hind feet; 6) widely separated hypothenar and thenar pads coequal in size and shape; 7) rostrum in the form of a cylinder projecting appreciably anterior to the incisors; 8) shape of incisive foramina; 9) translucent and globular braincase; 10) texture of bony palate and its length relative to molar rows; 11) peculiar conformation of the posterior third of the pterygoid plate; 12) cephalic arterial pattern, slightly inflated auditory bullae; 13) color of enamel and configuration of upper and lower incisors; 14) reduced cusp t3 on first upper molar; 15) elongate shape of cusp t4; 16) elongate conformation of cusp t4; 17) small size of cusp t9 and its union with cusp t6 and t9 on first and second upper molars; and 18) the small size of third upper and lower molars relative to first and second molars. Descriptions of the pollex, rostrum, incisive foramina, pterygoid plate, and incisors identify particularly striking specializations of *S. macrorhinos*.

Sommeromys macrorhinos and *Crunomys celebensis* are poorly known elements of the endemic Sulawesian murine fauna. The former is represented by a single specimen, the latter by three examples. It is extremely unlikely that the species are as rare in the wild as our samples suggest. Rather, because of their diet and behavior, they are not encountered, except accidentally, by conventional trapping techniques. Now that we know such distinctive species exist, efforts should be made to find and study them in their wilderness habitats and obtain additional specimens for study back at the laboratory. We need to know more about these special species, isolated as they are not only geographically on an oceanic island but also phylogenetically from each other and from any other group of species native to Sulawesi.

It is noteworthy that the species of sucking louse tied to *Sommeromys macrorhinos* belongs to the genus *Hoplopleura*, which has successfully radiated to parasitize several groups of rodents throughout most of the world. In fact, *Hoplopleura* is the most speciose genus of sucking lice and currently includes 146 recognized species (Durden and Musser, 1994; Castro et al., 1995, 1996, 1998; Castro and González, 1996; Chin, 1996; Pajot, 1996; Castro, 1997; Dubinina and Sosnina, 1997; Durden, 2001). Of these, 66 parasitize rodents in Murinae (table 3) and all but three of the remainder parasitize rodents in other subfamilies of Muridae and other families: murids (arvicolines, cricetines, dendromurines, gerbillines, and sigmodontines), echimyids, octodontids, and sciurids (Durden and Musser, 1994). Clearly, *Hoplopleura* has been very successful in adapting to parasitize representatives of different groups of rodents; also, three species of *Hoplopleura* exclusively parasitize pikas (Lagomorpha) in the Old World (Durden and Musser, 1994; Dubinina and Sosnina, 1997).

Although 47 recognized species of *Hoplopleura* parasitize New World sigmodontine rodents, this louse genus apparently has radiated most successfully to parasitize Old World murines (Durden and Musser, 1994). Because the generation time of these lice is at least three-fold shorter than that of their murine hosts, it seems surprising that the lice have not radiated into a greater number of genera to correspond with the radiation of their hosts. There are isolated cases of sucking lice restricted to certain rodent genera

TABLE 3

Principal Hosts and Known Geographical Distributions[a] of Species of *Hoplopleura* (Sucking Lice) Parasitic on Rodents in Murinae (Muridae)

Louse species	Host species	Distribution	Reference
H. aethomydis	*Aethomys namaquensis*	Southern Africa	Durden and Musser, 1994
H. affinis	*Apodemus* spp.	Eurasia	Durden and Musser, 1994
H. akanezumi	*Apodemus* spp.	Japan, People's Republic of China, Taiwan	Chin, 1996
H. apomydis	*Apomys insignis*	Philippines (Mindanao)	Durden and Musser, 1994
H. bidentata	*Hydromys chrysogaster*	Australia	Kuhn and Ludwig, 1967
H. blanfordi	*Cremnomys blanfordi*	India	Mishra, 1981
H. calabyi	*Pseudomys higginsi*	Australia (Tasmania)	Kuhn and Ludwig, 1967
H. captiosa	*Mus* spp.	cosmopolitan	Durden and Musser, 1994
H. chippauxi	*Arvicanthus niloticus*	West and Central Africa	Kim and Emerson, 1973
H. chrotomydis	*Chrotomys whiteheadi*	Philippines (Luzon)	Durden and Musser, 1994
H. chrysocomi	*Bunomys chrysocomus*	Indonesia (Sulawesi)	Durden, 1990
H. colomydis	*Colomys goslingi*	Zaire	Durden and Musser, 1994
H. confuciana	*Niviventer* spp.	People's Republic of China	Chin, 1996
H. cornata	*Rattus sordidus*	Australia (Queensland)	Kim, 1972
H. cutchicus	*Cremnomys cutchicus*	India	Mishra, 1981
H. delticola	*Mus musculus*[b]	Argentina	Castro, 1982
H. diaphora	*Berylmys bowersi*	Southeast Asia	Johnson, 1964
H. dissicula	*Sundamys muelleri*	Southeast Asia	Johnson, 1964
H. dissimilis	*Rattus turkestanicus*	People's Republic of China	Chin, 1996
H. enormis	*Lemniscomys rosalia*	Southern Africa	Johnson, 1960
H. gyomydis	*Pseudomys, fumeus*	Australia (Victoria)	Kuhn and Ludwig, 1967
H. himalayana	*Apodemus* spp.	India	Mishra, 1981
H. himenezumi	*Apodemus argenteus*	Japan	Durden and Musser, 1994
H. hybomyis	*Hybomys trivirgatus*	Nigeria	Kim and Emerson, 1973
H. hylomysci	*Hylomyscus* spp.	Ivory Coast	Pajot, 1996
H. inexpectans	*Myomys* spp. *Praomys* spp.	West, Central, and East Africa	Pajot, 1996
H. intermedia	*Mastomys* spp. *Praomys* spp.	Sub-Saharan Africa	Pajot, 1996

[a] Geographical distributions given are for the sucking lice only.

[b] Because *H. delticola* has not been recovered from *Mus musculus* outside of Argentina, we assume that this murine is not the true host of this louse.

TABLE 3 (*continued*)

Louse species	Host species	Distribution	Reference
H. irritans	*Rattus fuscipes* *Rattus lutreolus*	Australia	Kuhn and Ludwig, 1967
H. ismailiae	*Mastomys natalensis* *Myomys albipes*	East and Central Africa	Durden, 1991
H. johnsonae	*Mus.* spp.	Southeast Asia	Durden and Musser, 1994
H. khandala	*Golunda ellioti*	India	Mishra, 1981
H. kitti	*Berylmys* spp. *Leopoldamys edwardsi*	Southeast Asia	Durden and Musser, 1994
H. kondana	*Millardia kondana* *Millardia meltada*	India, Pakistan	Durden et al., 1990
H. laticeps	*Hybomys univittatus*	West and Central Africa	Durden, 1991
H. longula	*Micromys minutus*	Eurasia	Durden and Musser, 1994
H. malabarica	*Bandicota* spp.	Southern Asia	Durden and Musser, 1994
H. malaysiana	*Leopoldamys sabanus*	Malaysia	Johnson, 1964
H. mastacomydis	*Pseudomys fuscus*	Australia	Kuhn and Ludwig, 1967
H. musseri	*Maxomys musschenbroekii*	Indonesia (Sulawesi)	Durden, 1990
H. mylomydis	*Mylomys dybowskii*	Kenya	Johnson, 1960
H. myomyis	*Myomys daltoni*	West Africa	Kim and Emerson, 1973
H. nasvikae	*Malacomys longipes*	Zaire	Durden and Musser, 1994
H. oenomydis	*Oenomys* spp.	West, Central, and East Africa	Durden and Musser, 1994
H. pacifica	commensal *Rattus* spp.	worldwide in warmer climates	Johnson, 1964
H. pahari	*Mus pahari*	Southern Asia	Mishra, 1981
H. patersoni	*Aethomys* spp.	Central and southern Africa	Johnson, 1960
H. pavlovskyi	*Rattus turkestanicus*	Pakistan, Tajikistan	Durden at al., 1990
H. pectinata	*Maxomys* spp.	Southeast Asia	Durden, 1990
H. pelomydis	*Lemnisomys* spp. *Pelomys* spp.	Sub-Saharan Africa	Durden and Musser, 1994
H. rajah	*Maxomys surifer*	Laos	Durden and Musser, 1994
H. ramgarh	*Mus platythrix* *Mus saxicola*	India, Pakistan	Durden et al., 1990
H. rukenyae	*Mus* spp.	Sub-Saharan Africa	Durden, 1991
H. sahyadri	*Mus terricolor*	India	Mishra, 1981
H. sembeli	*Maxomys hellwaldii*	Indonesia (Sulawesi)	Durden, 1990
H. setzeri	*Grammomys* spp.	Central and East Africa	Johnson, 1960

TABLE 3 (*continued*)

Louse species	Host species	Distribution	Reference
H. sicata	*Niviventer* spp. *Rattus* spp.	Southern Asia	Mishra, 1981
H. silvula	*Vandeleuria oleracea*	India, Laos	Mishra, 1981
H. sinhgarh	*Mus platythrix*	India	Mishra, 1981
H. somereni	*Dasymys incomtus* *Dasymys rufulus*	East, Central, and West Africa	Pajot, 1996
H. sommeri	***Sommeromys macrorhinos***	**Indonesia (Sulawesi)**	**Present report**
H. spicula	*Rattus turkestanicus*	People's Republic of China	Durden and Musser, 1994
H. spiculifer	*Lemniscomys barbarus*	North, West, and East Africa	Johnson, 1960
H. traubi	*Maxomys wattsi*	Indonesia (Sulawesi)	Durden and Musser, 1994
H. uromydis	*Uromys caudimaculatus*	Australia (Queensland)	Kuhn and Ludwig, 1967
H. vietnamensis	*Leopoldamys sabanus*	Vietnam	Durden and Musser, 1994
H. zelotomydis	*Zelotomys hildegardeae*	Kenya, Zaire	Johnson, 1960

(including the enderleinellid louse genera *Atopophthirus* and *Phthirunculus* on the petauristine genus *Petaurista*, the enderleinellid genus *Microphthirus* on the petauristine genus *Glaucomys*, the mirophthirid louse genus *Mirophthirus* and the polyplacid louse genus *Typhlomyophthirus* on the platacanthomyine genus *Typhlomys*; Chin, 1980, 1998; Durden and Musser, 1994), but sucking louse–rodent associations at the generic level appear to be relatively rare. Closer host–parasite interrelationships have been documented between trichodectid chewing lice and their geomyid rodent hosts, but even here one louse genus (*Geomydoecus*) parasitizes several host genera (Hellenthal and Price, 1991; Hafner et al., 1994).

Although they have not yet all been described, we have now collected sucking lice from most of the rodents that are native to Sulawesi. Although a wide range of rodent genera, including many endemic taxa, are included, all of the sucking lice obtained so far belong to either the hoplopleurid genus *Hoplopleura* or to the polyplacid genus *Polyplax*. Host–parasite associations between native Sulawesi rodent genera and sucking louse genera include the following:

SCIURIDAE (SCIURINAE)
  Hyosciurus: *Hoplopleura*
  Prosciurillus: *Hoplopleura*
  Rubrisciurus: *Hoplopleura*
MURIDAE (MURINAE)
  Bunomys: *Hoplopleura* and *Polyplax*
  Echiothrix: *Polyplax*
  Eropeplus: *Polyplax*
  Haeromys: *Hoplopleura*
  Margaretamys: *Hoplopleura* and *Polyplax*
  Maxomys: *Hoplopleura* and *Polyplax*
  Melasmothrix: *Polyplax*
  Rattus: *Hoplopleura* and *Polyplax*
  Taeromys: *Hoplopleura*
  Tateomys: *Polyplax*
  Sommeromys: *Hoplopleura*

Representatives of these two sucking louse genera are widely distributed throughout much of the world and one or both of them have successfully radiated to parasitize all or most of the rodent species native to Sulawesi. In some cases, sucking lice presumably accompanied ancestral rodents as they colonized Sulawesi and then radiated in concert with their hosts. In other cases, however, some sucking lice may have ''switched'' by nonphyletic host tracking onto rodents that were not previously parasitized by lice (Hafner et al., 1994). Several of the Sulawesi louse taxa associated with native rodents have unusual morphlogical traits. Future taxonomic, phylogenetic and zoogeographical analyses of these lice may not only illuminate the evoloution and relationships among the lice but also among their rodent hosts.

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