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NEW SERIES, NO. 101

A Remarkable New Mouse (Muridae: Sigmodontinae) from Southeastern Peru: With Comments on the Affinities of *Rhagomys rufescens* (Thomas, 1886)

Lucía Luna

Bruce D. Patterson

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A Remarkable New Mouse (Muridae: Sigmodontinae) from Southeastern Peru: With Comments on the Affinities of *Rhagomys rufescens* (Thomas, 1886)

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A Remarkable New Mouse (Muridae: Sigmodontinae) from Southeastern Peru: With Comments on the Affinities of *Rhagomys rufescens* (Thomas, 1886)

Lucía Luna

Bruce D. Patterson

Abstract

Field surveys of the Manu Biosphere Reserve in southeastern Peru between 1999 and 2001 secured specimens of a remarkable new species of mouse (Rodentia: Sigmodontinae). Curiously, this mouse shares numerous traits with the enigmatic Brazilian mouse *Rhagomys rufescens* (Thomas, 1886), known only from a pair of fragmentary specimens collected in Atlantic forest habitats during the 19th century. The position of *Rhagomys* within the Sigmodontinae radiation has been *incertae sedis*, owing both to its unique features and the limited materials for phylogenetic analysis. Here we provide a diagnosis and description of the new mouse and assess its relationships to *Rhagomys rufescens* on the basis of morphology; ongoing studies will shed more light on its phylogenetic relationships using morphological and genetic data in a complete phylogenetic analysis. This newly identified species widens the distribution of the genus in a disjunct pattern of distribution in South America. As recently suggested by Smith and Patton (1999), the genus *Rhagomys* may represent an independent lineage of Neotropical sigmodontines, one perhaps deserving of tribal recognition.

Resumen

Evaluaciones de campo en la Reserva de Biosfera de Manu en el sureste de Perú durante 1999 y 2001 resultaron dentro en otros, en la colecta de tres especímenes de una remarcable nueva especie de ratón (Rodentia: Sigmodontinae). Curiosamente, este ratón comparte numerosas características con el enigmático ratón brasileiro *Rhagomys rufescens* (Thomas, 1886) conocido solamente de un par de especímenes incompletos colectados en la Mata Atlántica durante el siglo XIX. La clasificación de *Rhagomys* dentro de la radiación de los Sigmodontinae es *incertae sedis*, debido a sus características únicas y al limitado material para realizar análisis filogenéticos. Proveemos aquí una diagnosis y descripción de esta nueva especie de ratón y comentamos sus relaciones con *Rhagomys rufescens* basados en morfología; estudios en marcha darán luz a las relaciones filogenéticas usando datos morfológicos y moleculares.

La descripción de esta especie nueva amplía el rango de distribución del género *Rhagomys* en un patrón de distribución disjunta dentro de Sudamérica.

Como lo sugerido recientemente por Smith and Patton (1999), el género *Rhagomys* podría representar un linaje independiente dentro de los sigmodontinos neotropicales, uno que tal vez merezca reconocimiento tribal.

Introduction

Roughly a quarter of the world's mammal species live in the Neotropics (Wilson & Reeder,

1993), and new species are continually being uncovered there (Patterson, 2001). Of the 1,273 species currently recognized as living within the Neotropics, an overwhelming majority—1,037

species (81%)—live in South America (B. Patterson, unpubl.). That continent is divided into several faunal regions, reflecting internal homogeneity and external differentiation of its regional faunas (Hershkovitz, 1972; Koopman, 1982). The richest subregions in terms of both species richness and numbers of endemic species are the Amazon Basin, the tropical Andes, and the Atlantic Forest, respectively (Patterson, 2000). Over the past decade these three subregions have yielded most newly described species of mammals, although perhaps only proportionately to their diversity (cf. Mares et al., 2000).

In 1999, the Field Museum of Natural History (Chicago) and the Museo de Historia Natural, Universidad de San Marcos (Lima), initiated a new series of expeditions to inventory mammals, birds, and ectoparasites of the Manu National Park and Biosphere Reserve in southeastern Peru. This reserve spans habitats representing the Altiplano, Tropical Andes, and Amazon Basin faunal regions. Even at the start of our field program, it harbored the richest assemblages of mammals and birds yet recorded anywhere on the planet (Terborgh et al., 1984; Pacheco et al., 1993; Patterson et al., 1998). Nevertheless, each field season from 1999 to 2001 brought to light new species of mammals and recorded numerous other species not previously documented in the area.

Among the new species of mammals taken by Manu survey teams is a small sigmodontine rodent unlike any other. The suite of characters noted at the time of capture and during field preparation of the specimens—nail on big toe, elongated tongue, and spiny pelage—was unlike any described for a Neotropical sigmodontine. Although we attempted to secure additional examples at both localities where we encountered this mouse, only three specimens exist on which to base the following description and discussion. Despite superficial resemblances, this species is easily distinguished from other small, spiny sigmodontines (*Neacomys* and *Scolomys*) by its unique combination of external and cranial characters. Rather, numerous characters point to its phylogenetic relationship to *Rhagomys rufescens* (Thomas, 1886), an enigmatic mouse from coastal Brazil deemed *incertae sedis* in most appraisals of Sigmodontinae (Carleton & Musser, 1984; Reig, 1980, 1984, 1986; McKenna & Bell, 1997; Smith & Patton, 1999). The discovery of the new mouse and its inclusion in the genus *Rhagomys* raise important questions about the origin, biogeography, and systematics of South American mice and offer

new perspectives for assessing them. In this paper, we focus on the detailed diagnosis, description, and comparisons of the new mouse.

Material and Methods

Abbreviations and specimens examined and measured are listed in the Appendix.

The measurements we used were defined and illustrated by Myers et al. (1990), Voss (1991, fig. 3), and Musser et al. (1998, fig. 2). All external measurements except vibrissal length were taken in the field on fresh specimens using a ruler and were recorded on skin labels. Cranial measurements were taken with a Mitutoyo Digimatic caliper, which was accurate to the nearest 0.01 mm. Vibrissal lengths were measured on study skins (the longest one in the array of vibrissae was measured). Dorsal fur length was measured at the rump's midline on each specimen. Vibrissal and dorsal fur lengths were measured using a ruler.

Color nomenclature follows Ridgway (1912). Terminology of external anatomy follows Beddard (1902), Brown (1971), and Brown and Yalden (1971) for vibrissal nomenclature, whereas pes and manus nomenclature follows Voss (1988, 1991) and Musser et al. (1998). Cranial and molar terms follow usages in Hershkovitz (1962, 1967, 1977, 1994), Carleton (1980), Carleton and Musser (1989), Voss (1988, 1991), Voss and Carleton (1993), and Stepan (1995), whereas Howell (1926), Greene (1955), Carleton (1980), and Stepan (1995) defined and illustrated our terminology for postcranial skeletal morphology. For description of soft-part anatomy, Howell (1926) and Voss (1988) are followed for muscles, Tullberg (1899), Sonntag (1924), and Vorontzov (1979) for the tongue, Carleton (1973) for stomachs, Voss (1991) for gallbladder states, Vorontzov (1979) for intestinal tracts, and Voss and Linzey (1981) for male accessory glands. Our designation of mammary fields follows Voss and Carleton (1993). The age categories, based on toothwear stages, were described and illustrated by Voss (1991).

Abbreviation conventions for the maxillary or upper molars are M1, M2, and M3, while mandibular or lower molars are represented by m1–3, the first molar being M/m1.

Manual and pedal digits are represented by D1–5, the pollex and the hallux, respectively, being

D1. In either case, the locations of the digit will be specified in the text.

Results

Rhagomys longilingua, new species

HOLOTYPE—The holotype, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM 17013), is a male collected 20 September 1999 by Lucía Luna Wong (the senior author, field number LLW 661). Skin in good condition with right manus and pes intact; entire carcass (including skull) with unskinned left manus and pes preserved in fluid. Tissue samples preserved in liquid nitrogen are deposited at the Field Museum of Natural History, Chicago as (FMNH 170686).

External measurements of the holotype: head and body length (HBL), 103.0 mm; tail length (TL), 96.0 mm; hind foot length (HF), 17.0 mm; ear length (E), 13.6 mm; dorsal fur length (DFL), 8.0 mm; longest mystacial vibrissae length (MVL), 35.0 mm; longest superciliary vibrissae length (SVL), 26.0 mm; longest genal vibrissae length (GVL), 20.0 mm.

TYPE LOCALITY—Peru: Departamento de Cuzco, Provincia de Paucartambo, below “Suecia,” a roadside settlement in Manu Biosphere Reserve along the Río Cosñipata (Fig. 1); coordinates 13°06.032'S, 71°34.125'W; elevation approximately 1900 m. During our fieldwork, the restaurant “El Rocotal” stood near the places where the holotype and one paratype (FMNH 170687) were taken.

ETYMOLOGY—The species group name, *longilingua*, a noun in apposition, is formed from the Latin words *longus* (= long) and *lingua* (= tongue), in reference to one of the species's most distinctive features.

DIAGNOSIS—A small, spiny mouse with this unique combination of characters: digits of manus and pes with broad and square-shaped, blunt, callous tips with embedded claws. Tips are callous and have a crescent-shaped depression appearing heart-shaped in dorsal view. All digits with deep transverse grooves. Manual D3 and D4 are nearly equal in length, with D4 slightly longer. Claws of manus are very short and project little beyond the tip of the fingers. The hallux bears a nail. Plantar pads are structurally well-defined, fleshy, and flattened, with a heart-shaped callus on the interdig-



FIG. 1. Collecting localities of *Rhagomys longilingua*, new species: type locality (closed star), paratype locality (open star); base map from Pacheco et al. (1993).

ital pads. Thenar and hypothenar pads also have calluses covering their entire surface. Tongue is long, narrow, and thick, almost cylindrical in cross-section, and tapering toward the tip.

Ectotympanic small and flat. Parapterygoid fossae deep and narrow, with conspicuous, oval-shaped fontanelles about one-third the size of the pterygoid processes. On M1, an anteromedian crista protrudes from the anterolabial conule. M3 has only two well-defined cusps, the paracone and the protocone, and an undifferentiated heel. The m2 and m3 are nearly equal in size and shape, with very conspicuous metaconid, protoconid, posterolophid, and hypoconid elements. In all mandibular molars, an enamel ridge connects the hypoconid with the posterolophid, the postero-crista.

Individual diagnostic characters deserving special mention: tongue long; oval-shaped fontanelles about one-third the size of the pterygoid processes; M1 anteromedian crista protrudes from the anterolabial conule; M3 with only paracone and protocone; the m2 and m3 are nearly equal in size and shape, with very conspicuous metaconid, protoconid, posterolophid, and hypoconid

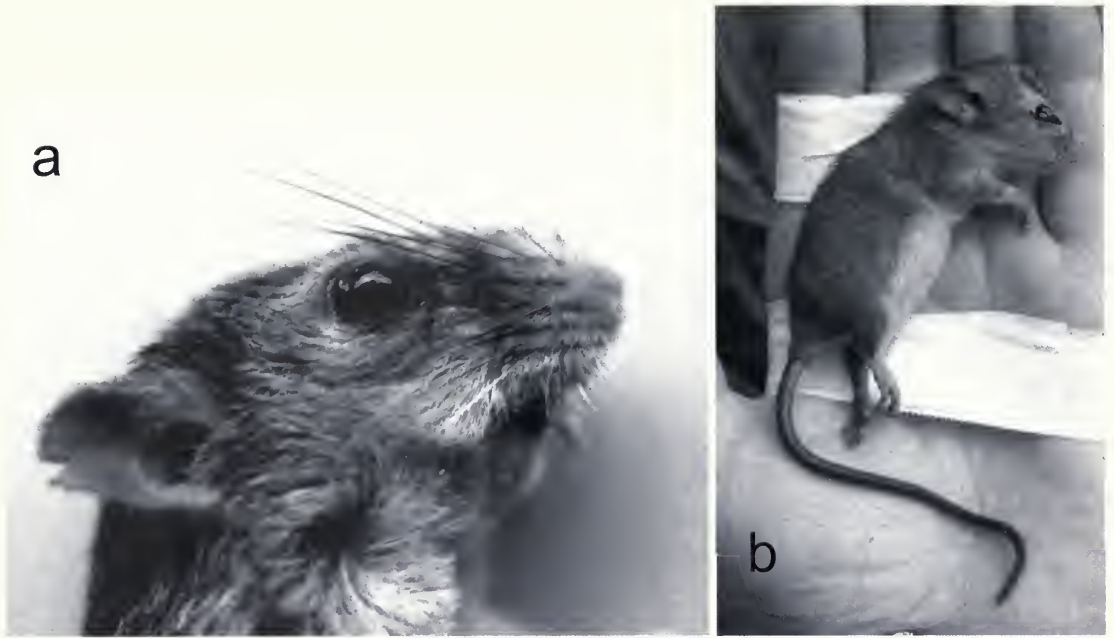


FIG. 2. *Rhagomys longilingua* specimens: **a**, female paratype, FMNH 170687; **b**, male paratype, FMNH 175218 (ant damage on face; photograph by C. Dick).

elements; all mandibular molars have a postero-crista.

PARATYPE—Because the holotype is a male prepared in the field as a skin with complete carcass in fluid, certain characters—skull morphology, mammary formula, and part of the alimentary system—could not be recorded. Description of these characters is of the female paratype catalogued by the Field Museum as FMNH 170687. The paratype was collected 19 September 1999 at the type locality by Sergio Solari (SS 1873); its skin is in good condition (save for a sewn tear in one of the flanks), with right fore- and hind feet; cranium, mandible, hyoid, and skeleton in good condition. The viscera were fixed in formalin and preserved in ethanol, and tissue samples were preserved in liquid nitrogen.

External measurements of the female paratype (measurements in mm): head and body length (HBL), 101.0; tail length (TL), 104.0; hind foot length (HF), 20.0; ear length (E), 14.0; dorsal fur length (DFL), 8.0; longest mystacial vibrissae length (MVL), 37.0; longest superciliary vibrissae length (SVL), 25.0; longest genal vibrissae length (GVL), 21.5. Cranial measurements (in mm): greatest length of skull (GLS), 28.3; condyloincisive length (CIL), 26.0; condylo-molar length (CML), 16.7; length of rostrum (LR), 7.7; rostral

breadth (RB), 5.1; orbital fossa length (OFL), 10.7; nasal length (NL), 8.5; nasal breadth (NB), 2.9; least interorbital breadth (LIB), 5.5; diastemal length (DL), 7.3; bony palate length (BPL), 6.9; bony palate breadth across first upper molars (BPB), 5.2; postpalatal length (PPL), 9.1; incisive foramina length (IFL), 3.5; incisive foramina breadth (IFB), 1.4; maxillary tooth-row length (MTL), 4.5; palatal bridge breadth (PBB), 2.5; first upper molar breadth (M1B), 1.3; zygomatic breadth (ZB), 15.9; braincase breadth (BB), 13.4; zygomatic plate breadth (ZPB), 3.3; incisor depth (ID), 1.9; braincase height (BH), 9.0; and mesopterygoid fossa breadth (MFB), 1.7. This specimen falls in toothwear class 2.

Description

Observations of pelage color and texture, external form, postcranial skeleton, and soft anatomy are based on the holotype and paratype; those of the cranium, dentition, postcranial skeleton, and part of the soft anatomy (tongue and intestines) are based on the paratype alone.

EXTERNAL MORPHOLOGY—*Rhagomys longilingua* is a small to medium-sized (25–35 g) Sig-

modontinae (*sensu* Carleton & Musser, 1984) mouse, with small ears and a tail that is subequal in length to head and body (Fig. 2).

The body pelage is short and close with a markedly spiny texture, the dorsal fur more spiny than the ventral fur. There are two types of dorsal and ventral hairs of approximately the same length (8 mm): spiny hairs and long, thin hairs. The former is slightly transparent, dorsally grooved, flat, rigid, and stout, broadest (0.25 mm) at its midpoint. The ventral spiny hair is slightly shorter (7.0 mm).

On the muzzle, over the eyes, on the cheeks, and between the forefeet and neck, the color corresponds to Ochraceous-Orange.

On the sides—the borders between the upper and underparts, the external sides of fore- and hind feet, the backside of the ears, and the chest—the color corresponds to Ochraceous-Buff. All the underpart pelage from the chin and the interior sides of the fore- and hind feet is Light Ochraceous-Salmon when moved under white light. In general, the body pelage is strongly countershaded.

The dorsal pelage is Olive-Brown in appearance, but it is difficult to characterize because it has a strongly hispid pattern produced by the combination of the two types of hair. Dorsal spines are transparent Light Olive-Gray at the base and throughout almost their entire length, becoming progressively brown and dark toward the tip. Fur is grayish at the base, with the last quarter of the length Ochraceous-Buff. Some hairs are slightly brownish at the tip. On the underparts, spines and fur are silvery-transparent at the base, becoming pinkish or rufescent toward the tips; hence the ventral surface coloration described above.

The dorsal pelage of the head is composed predominantly of spines. These are more cylindrical—less flat than the spines in the dorsum—and with tips more orange or brown. The postauricular field lacks spines; hairs here have a silvery base and Ochraceous-Buff tips. Ears are small (average 14 mm), covered internally by dense orange-brownish hair and externally by golden hairs. The eyes are well-defined due to a very conspicuous black ring of skin.

Facial vibrissae are arrayed in mystacial, submental, genal, superciliary, and interramal fields. The longest mystacial, superciliary, and genal vibrissae reach well beyond the posterior margins of the pinnae. Interramal vibrissae are composed of a single tuft of long hairs. Submental vibrissae are long and border the lower lip. Four of these

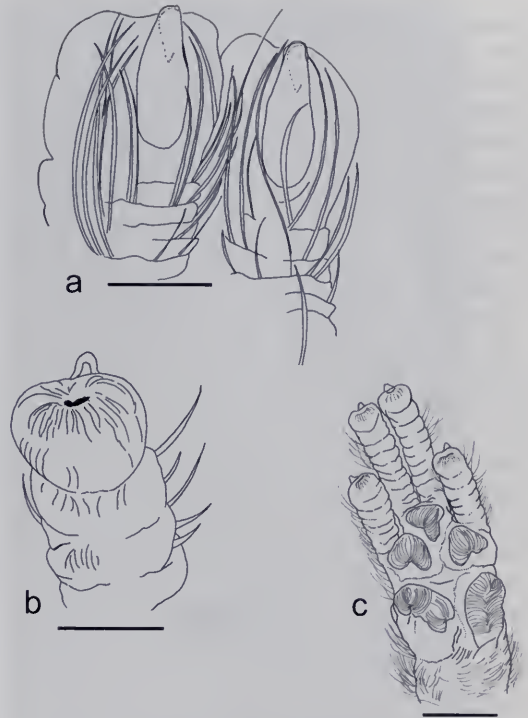


FIG. 3. Detail of the manus of *Rhagomys longiligua*, new species: **a**, dorsal view (FMNH 170687), scale bar = 1 mm; **b**, detail of digit 5 in ventral view (FMNH 170687), scale bar = 1 mm; **c**, ventral view (FMNH 170687), scale bar = 3 mm.

hairs were counted on the holotype specimen, while only two were counted in the female paratype. Two carpal vibrissae are present. Both are short, but the longer of the two reaches the proximal margin of the hypothenar pad.

There are six mammae in three pairs: one inguinal, one abdominal, and one postaxial.

The tail is slightly shorter than the head and body, weakly countershaded, and with a small tuft of hairs in the end. Ventrally, the tail is paler owing to absence of pigmentation in the skin and paler hairs (some middle hairs of the triplets are slightly pigmented in the middle region). Scales on the tail are arranged in an annular pattern. Hairs are arranged in triplets of the same size, which are shorter at the base of the tail and longer toward the tip. Each short hair is about two scale-rows long.

The five digits of the manus have a unique configuration for Sigmodontinae (Fig. 3). They are long with broad, squared, and blunt tips. A crescent-shaped depression in the middle of the apical pad, perpendicular to the claw axis, appears heart-

shaped in dorsal view (Figs. 3a and 3b). The surface surrounding the depression is callous. Digits have deep transverse grooves along their entire length. The three interdigital pads and single hypothenar and thenar pads are structurally well-defined, fleshy, and flat. A heart-shaped callus is noticeable on each of the three interdigital pads. Thenar and hypothenar pads also have calluses that nearly span the pads. The thenar callus reaches the margin of the pollical nail (Fig. 3c).

Manual D3 and D4 are nearly equal in length, with D4 slightly longer, and D2 and D5 are subequal, with D2 slightly longer. Pollex is vestigial with a small nail. Claws of manus are very short and project little beyond the tip of the fingers. Because they are very narrow and short (\approx three times longer than wide) and embedded in the fingertips, the claws are inconspicuous in ventral view, with only the tips visible. In lateral view, claws extend almost straight out and are therefore less concave proximally than in other sigmodontines. The surrounding tufts of hair reach the tip of the claws, some projecting slightly beyond the tip (Fig. 3a).

There are five nonopposable digits on the pes, similar to those described for the manus (Fig. 4). Each is long and has deep transverse grooves, with blunt tips bearing a central crescent-shaped depression surrounded by a callous surface. D2, D3, and D4 are increasingly elongated, and D5 reaches the middle of the second phalanx of D4. Hallux is short, level with the anterior margin of the second interdigital pad and the interphalangeal joint between phalanx 1 and 2 of D5 (Fig. 4a). There is a nail in the hallux instead of a claw (Fig. 4b).

The short, broad pes has six well-defined and fleshy plantar pads: four interdigitals, one hypothenar, and one thenar. Interdigital plantar pads are covered by heart-shaped calluses (Fig. 4c). The hypothenar pad is slightly smaller than the thenar pad and is contiguous with the fourth interdigital pad. The hypothenar pad lies intermediate at a level between the first interdigital and thenar pads. The distal margin of the thenar pad is level with the proximal margin of the hypothenar pad. Pedal claws are short, and the claw of D5 is so extremely short that it is nearly hidden from plantar view (length 1.25 mm, width 0.34 mm). Ungual tufts are level with the end of the digits, slightly beyond the claws. The soles of the feet are smooth except for the calluses on the plantar pads. The plantar surface, including the heel, is completely

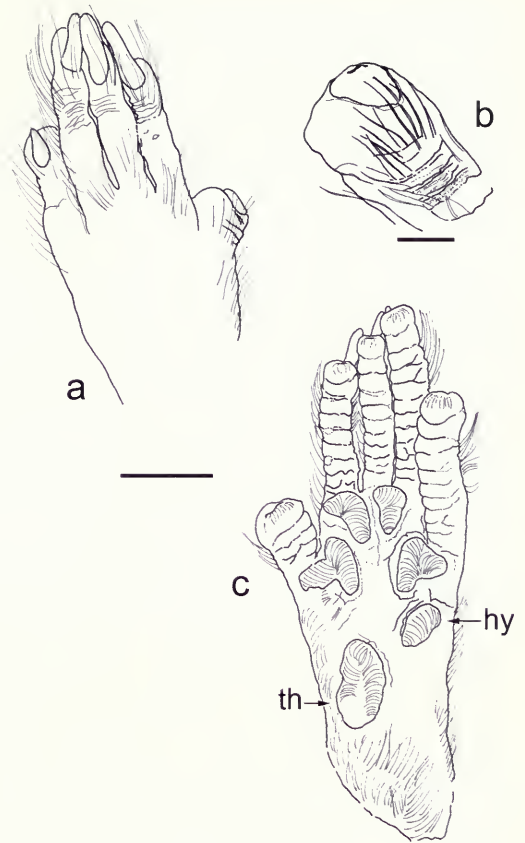


FIG. 4. Detail of the pes of *Rhagomys longilingua*, new species: **a**, dorsal view (FMNH 170687), scale bar = 3 mm; **b**, detail of the hallux-bearing nail (FMNH 170687); scale bar = 1 mm; **c**, ventral view (FMNH 170687), scale bar = 3 mm; th, thenar pad; hy, hypothenar pad.

naked; however, long hairs at the sides project over the calcaneum area.

CRANIUM—The skull of *R. longilingua* is strongly built, with a short, blunt, narrow (in relation to the interorbital region) rostrum (Fig. 5). The interorbital region is short and the braincase voluminous. The zygomatic arches are parallel-sided, enclosing a voluminous orbit, with a thin but conspicuous jugal. The upper incisors do not project beyond the anterior margin of the nasals, and the premaxillaries do not protrude beyond the anterior plane of the incisors. The nasolacrimal capsules are flat and inconspicuous in dorsal view, appearing like thin pockets opening toward the dorsum of the skull. Their posterior margins lie anterior to the anterior margin of the zygomatic plate. The nasals are broad distally, tapering posteriorly toward the frontals and forming a well-

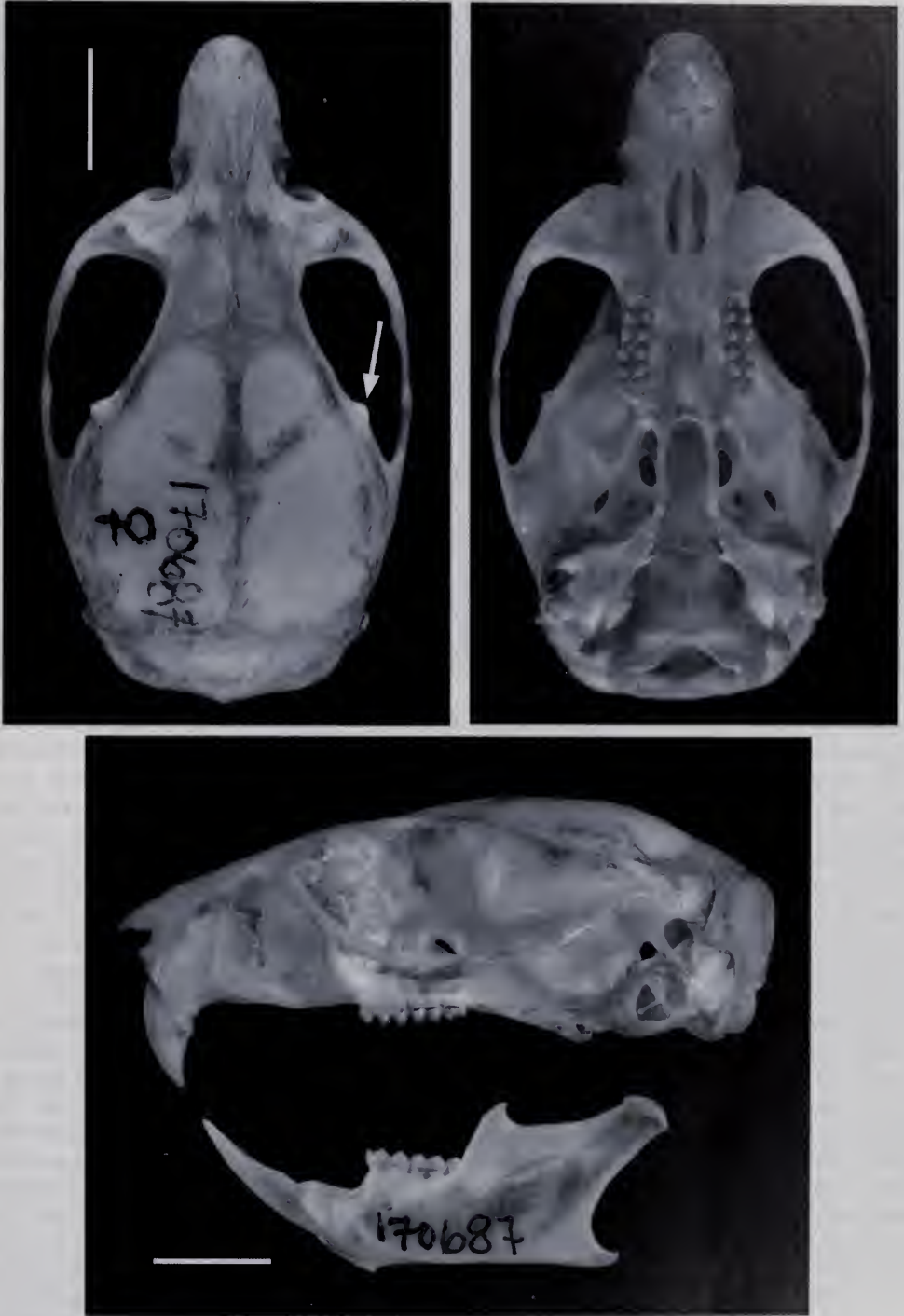


FIG. 5. Dorsal, ventral, and lateral views of cranium and lateral view of the mandible of the paratype of *Rhagomys longlingua*, new species (FMNH 170687); arrow points to the postorbital process. Scale bar = 6 mm.

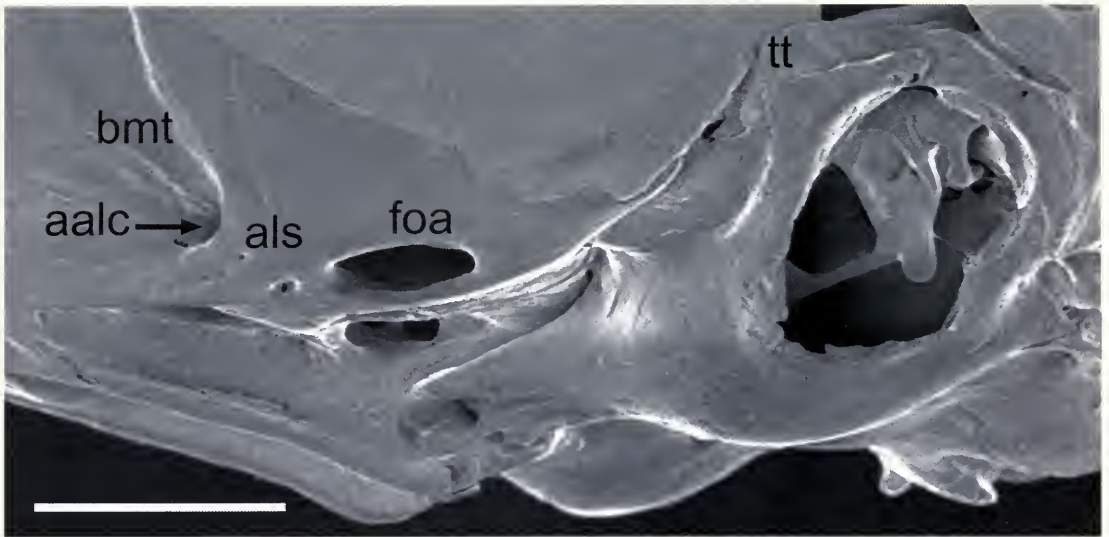


FIG. 6. Detail of the alisphenoid region of *Rhagomys longilingua*, new species (FMNH 170687): foa, foramen ovale accessorius; aalc, anterior opening of alisphenoid canal; bmt, buccinator-masticatory trough; als, alisphenoid strut; tt, tegmen tympani. Scale bar = 2 mm.

defined triangular suture anterior to the lacrimals. Posteriorly, the premaxillae extend slightly beyond the nasals. The zygomatic notch is shallow. The anterior border of the orbit is broad, thick, and perpendicular to the longitudinal axis of the skull. The zygomatic plate is of moderate width, straight, lacking a zygomatic spine, and closely pressed to the rostrum. Its anterior margin does not overlap the nasolacrimal capsule in lateral view. The antorbital bridge of the anterior root of zygomata is situated slightly below the rostrum. The first maxillary molar (M1) is located behind the posterior margin of the zygomatic plate.

The interorbital region is broad with posteriorly divergent, beaded margins. The interparietal is very broad but does not contact the squamosal. The lengths of the supraoccipital-parietal and the occipito-squamosal sutures are almost equal. The anterior face of the squamosal bone has a narrow postorbital process (arrow in Fig. 5) that is visible in dorsal view as a small knob inside the orbital fossa and serves as the origin for part of the anterior temporalis muscle.

The morphology associated with the orbitofacial circulation is unique in this mouse (Fig. 6). A very broad alisphenoid strut conceals the aperture of the anterior opening of the alisphenoid canal, which makes it visible only in frontal-lateral view. Instead, the only visible structure is a perfectly defined foramen ovale accessorius. The trough for the masticatory-buccinator nerve is

present, but the buccinator-masticatory foramen is fused with the anterior opening of the alisphenoid canal, hidden by the alisphenoid strut. The carotid arterial supply pattern is presumably derived (Bugge, 1970), corresponding to pattern three of Voss (1988). The stapedia artery does not divide into supra- and infraorbital arteries, and the squamosal-alisphenoid groove and sphenofrontal foramen are absent. In this pattern of carotid circulation, the stapedia foramen is absent and the pteriotic, usually visible ventrally, is hidden by the ectotympanic. The carotid canal is conspicuous, appearing under the eustachian tube.

The tegmen tympani overlaps a posterior suspensory process of the squamosal anterodorsal to the auditory bulla (see Fig. 6). The hamular process is broad, with its posterior end loosely fused to the mastoid tubercle of the periotic (Fig. 5). The mastoid tubercle and the dorsal anterior portion of the ectotympanic both form a contiguous ring in the middle ear. The mastoid fenestra of the periotic is a well-developed aperture in the suture between the periotic and the exoccipital. The malleus has a broad lamina completely exposed in lateral view of the skull and has a "parallel" orientation (*sensu* Carleton, 1980). A prominent orbicular apophysis is one-third as large as the lamina.

The subsquamosal fenestra and the postglenoid foramen are present and well-developed (Fig. 5). The groove of the postglenoid vein appears shal-

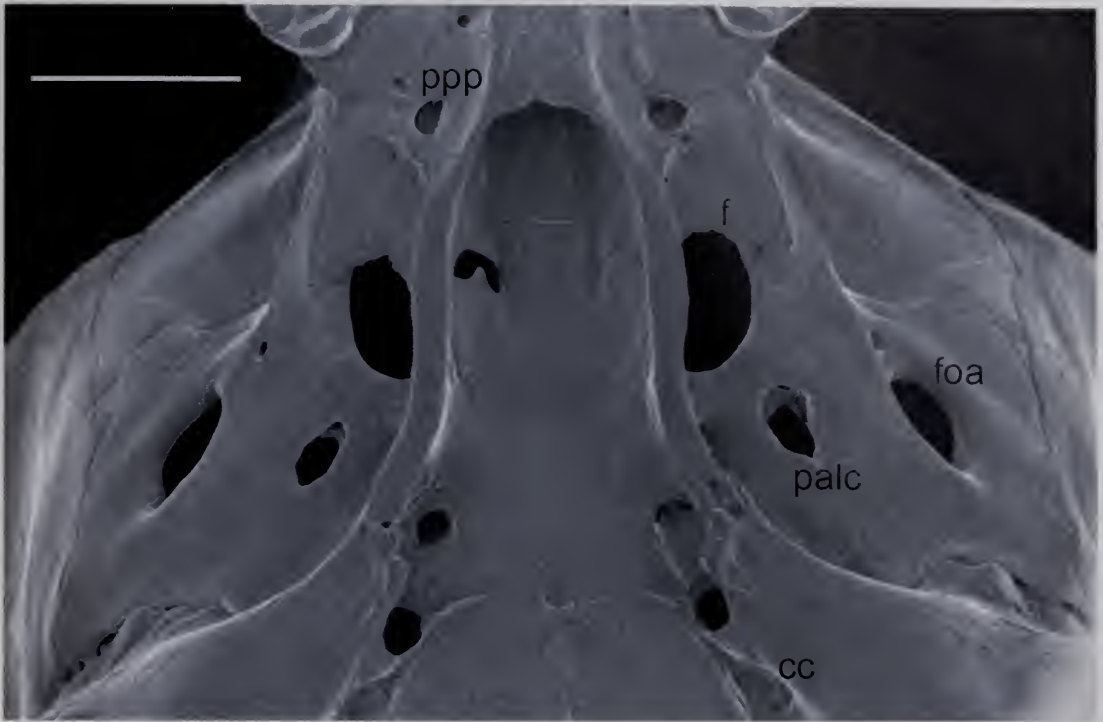


FIG. 7. Detail of mesopterygoid and parapterygoid fossae of *Rhagomys longilingua*, new species (FMNH 170687): ppp, posterolateral palatal pits; f, fontanelles; palc, posterior opening of the alisphenoid canal; foa, foramen ovale accessorius; cc, carotid canal. Scale bar = 2 mm.

low, owing to the shortness of the lamina of the petrotic that forms the tegmen tympani. The stapedial process of the bulla is inconspicuous, and the middle lacerate foramen is absent.

The incisive foramina are narrow and short (Fig. 5). The distance between the incisive alveoli and the anterior margin of the incisive foramina equals the length of M2–M3. The distance between the posterior margins of the incisive foramina and the anterior margins of M1 is equivalent to the length of M2. In shape, both foramina are parallel-sided and slightly narrower anteriorly than posteriorly. The most ventral suture of the premaxillaries and maxillaries is level with the last third of the incisive foramina. The maxillary septum of the incisive foramina is one-fourth the length of the incisive foramina. The masseteric tubercle appears as a conspicuous scar for the origin of the superficial masseter muscle.

There is a very long palate, with the posterior margin extending half the length of M3 past that tooth. The palate is also wide (*sensu* Hershkovitz, 1962); the distance between the inner borders of the first molars is greater than the length of either tooth. A medial process of the posterior palate is

absent. The palatal surface is smooth, without any traces of bony palate excrescences. The posterior palatine ridge (*sensu* Steppan, 1995) is absent or indistinct. Posterolateral palatal pits are well-defined depressions within which one or more small foramina are located, recalling Carleton's (1980) descriptive phrase, "multiple foramina recessed in fossa," and the midpoint of the posterolateral palatal pits is level with the anterior margin of the mesopterygoid fossa. The maxillary tooth rows are subparallel.

The anterior border of the mesopterygoid fossa is rounded. The bony roof of the mesopterygoid fossa is substantially complete, but constricted sphenopalatine vacuities are hardly visible between the presphenoid and basisphenoid suture (Fig. 7). The hamular processes of the pterygoids are subparallel but slightly divergent posteriorly, appearing lyre-shaped in ventral view. The suture between the palatines and the pterygoids is in the anterior third of the pterygoids.

Cranially, this species is distinguished by its particular basicranial configuration, especially the parapterygoid fossa and the carotid circulation (Figs. 6 and 7). The parapterygoid fossae are shal-

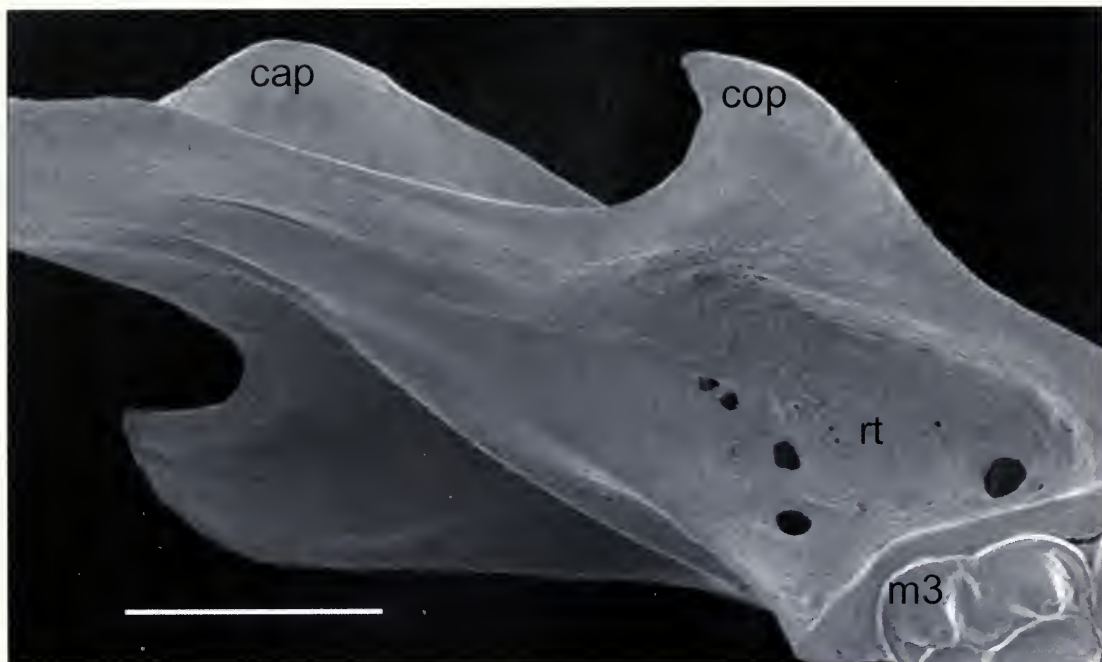


FIG. 8. Detail of the retromolar fossa in the inner part of the mandible of *Rhagomys longilingua*, new species (FMNH 170687): rt, retromolar fossa; cop, coronoid process; cap, capsular projection; m3, third lower molar. Scale bar = 2 mm.

low and narrow, extending to contact the anterior border of the ectotympanic, totally closing the middle lacerate foramen and giving the skull a solid appearance in ventral view. The fontanelles, formed by the posterior border of the palatine and the anterior ventral margin of the alisphenoid (named by Carleton & Musser, 1989), are extremely large, oval-shaped, and well-defined, with smooth borders. These occupy one-third of the length of the pterygoid in the mesopterygoid fossae. In addition, the posterior opening of the alisphenoid canal is small, well-defined, and oval-shaped, approximately one-fifth the size of the fontanelles. There is no groove for the infraorbital branch of the stapedia artery. This artery supplies only the middle ear, departing from the most primitive pattern.

The foramen ovale accessorius is visible in ventral view because of the narrow parapterygoid fossa. The bony ridge that forms the lateral edge of the parapterygoid fossa is pronounced only in the region anterior to the alisphenoid strut. In the alisphenoid strut region, the ridge disappears and the borders become smooth, rendering the foramen ovale accessorius.

The ectotympanics are almost flat. In lateral view, resting on a surface, the ectotympanics ap-

pear slightly above the pterygoid lobes. The ectotympanics have long, well-defined eustachian tubes that extend anteriorly under the pterygoid process. The carotid canal is well-defined (Fig. 7). The ectotympanic covers completely the pteriotic of the periotic. Lateral depressions of basioccipital are shallow, but there is a conspicuous ridge in the middle.

MANDIBLE AND HYOID—The mandible possesses a short angular process that extends only as far as the base of the condyloid process (Fig. 5). The coronoid process is short and level with the condyloid process. The angular notch is shallow, with its border parallel to the mandibular axis. A distinct capsular projection of the incisive alveolus lies underneath the angular notch and forms a conspicuous knob in dorsal view. A conspicuous inferior masseteric ridge extends slightly beyond the anterior margin of m1. A weak ventromedial process of the mandibular ramus (Steppan, 1995) is present. A deep and broad retromolar fossa is located between the base of the coronoid process and m3 (Fig. 8).

Although the thyrohyal bones of the hyoid apparatus were poorly preserved, the basihyal bone is entire and shows no entoglossal process. The

basihyal is arched rather than flat or perpendicular to the thyrohyal.

DENTITION—The upper incisors are orthodont, narrow, and without grooves in the enamel surface. The dentine fissure (*sensu* Steppan, 1995) corresponds to a long, straight slit. The cutting edge appears as an inverted V.

Molars are pentaloophodont, consisting of paracone, protocone metacone, hypocone, and mesoloph. The molars are bunodont and relatively low-crowned, with very conspicuous cusps (Fig. 5) and broad, well-defined flexi (Fig. 9, left). M1 is twice as long as M2; M3 slightly exceeds half the length of M2; M2 is squared; M3 is wider than long. The paraflexus and metaflexus in M1 and M2 nearly surround the interior margin of the paracone and metacone. The interpenetration of labial and lingual flexi extends slightly beyond the tooth-row midline.

In M1, the anteromedian flexus is deep, forming an anterolabial conule that is larger than the anterolingual one. A unique enamel element projects medially from the anterolabial conule. It seems that this structure, which we call the anteromedian crista, does not connect both conules in young adult specimens, such as the paratype specimen, which belongs to toothwear class 2. This structure may join both conules in old specimens until the teeth are worn. Thin ridges link the conules to the anterior mure of M1. In addition, a projection links the anterolabial conule to the anteroloph. Hershkovitz (1994, fig. 3) called this structure the anterolophule. But here, rather than emerging from the margin of the conule, it issues from the middle of the anterolabial conule and fuses with the anteroloph at its middle point. The paracone and protocone of M1 and M2 are connected to the medium mure by thin ridges.

A long and conspicuous anteroloph fuses with the parastyle in M1. A long anteroloph in M2 fuses with the paracone in its labial margin. This anteroloph projects back to the lingual side, forming a conspicuous protoflexus. There are small and shallow posteroflexus in M1 and M2. A long and conspicuous mesoloph fuses with the mesostyle in M1 and M2. All of these structures reach the labial side of the molar tooth row. The flexi of all molars (save the protoflexus of M1) terminate at an elevated cingulum; the cingulum completely encircling M2 and M3 gives the teeth distinctly sharp edges. M3 is small and shaped like a blunt, inverted triangle, with a sharp-edged cingula. It has a conspicuous paracone, protocone, antero-

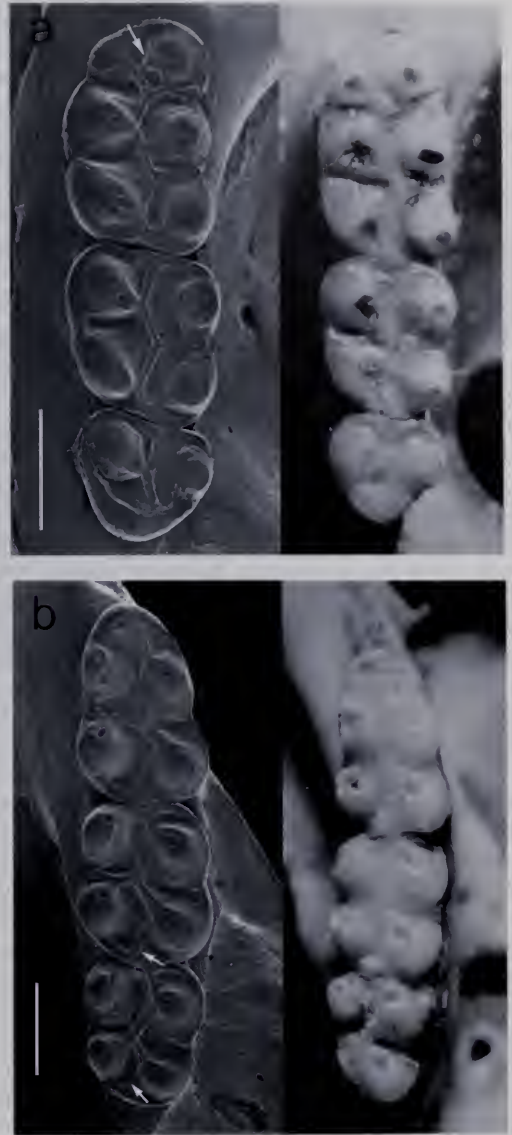


FIG. 9. Occlusal views of dentitions. **a**, Upper left molars: left, *Rhagomys longilingua* (FMNH 170687); right, *Rhagomys rufescens* (BMNH 86.2.8.5). Arrow points to the anteromedian crista. **b**, Lower right and left molars: left, *Rhagomys longilingua* (FMNH 170687); right, *Rhagomys rufescens* (BMNH 86.2.8.5); arrows point to the posterocrista. Scale bars = 1 mm.

loph, protoflexus, and median mure. The mesoloph and metacone are not evident.

Lower molars are very similar in structure, subequal in size, with conspicuous cusps, broad, well-defined flexids, and conspicuous cingula. The procingulum on m1 is without an anteromedian flexid; the procingulum extends from the an-

terolingual conulid labially into an anterolabial cingulum, which reaches the protoconid. There is no trace of a protostylid. The m1 has very conspicuous anterior and median murids. The anterolophid is absent. The mesolophid and mesostylid are fused, reaching the lingual side. The entolophid fuses with the last portion of the mesolophid, forming a mesolophid-mesostylid-entolophid junction. The posterolophid is long, reaching the entoconid.

Remarkably, m2 and m3 are almost identical in shape and size. Both have very conspicuous metaconid, protoconid, entoconid, hypoconid, anterior and median murids, and anterolabial cingula that fuse with the protoconids. They differ in that m2 has a mesolophid-mesostylid, whereas m3 has only an isolated mesostylid. All mandibular molars share what appears to be a continuation of the median murid but is in fact a projection of the hypoconid that connects to the posterolophid; this is called the posterocrista. In addition, the posterolophid of these molars reaches the entoconid, forming a posterocingulum. This cannot be confused with what Hershkovitz (1994) designated a distolophulid for *Oxymycterus*. The entolophid is absent on all lower molars.

POSTCRANIAL SKELETAL MORPHOLOGY—Axial skeletal counts include 13 ribs, 19 thoracicolumbar (dorsal) vertebrae, 4 sacral vertebrae, and 36 caudal vertebrae. The tuberculum of the first rib contacts transverse processes of both the seventh cervical and the first thoracic vertebrae. A conspicuous neural spine is present on the second thoracic vertebra. The hemal arches (Steppan, 1995) are absent from the caudal vertebrae; only hemal processes are present. These include, in order of conspicuousness, one located at the junction of the third and fourth caudal vertebrae, followed by the second and third and the fourth and fifth. The hemal processes located at the first and second junction and after the fifth vertebra are inconspicuous.

The humerus lacks an entepicondylar foramen, and the supratrochlear fossa is not perforated. The distal 60% of the tibia and fibula are fused (tibia-fibula fusion 11.02 mm, length of the tibia 17.42 mm). The trochlear process at the calcaneum is broad, and its position is intermediate (*sensu* Carleton, 1980), with a gap in lateral view between the proximal margin of the trochlear process and the posterior articular facet with the astragalus.

The metatarsals are short, which gives the pes a very broad shape. The metatarsals of D2, D3,

and D4 are approximately three times longer than wide.

The metatarsal of D5 is comparatively long, terminating level with the distal end of metatarsal of D4. This configuration contributes to a long D5 that reaches the middle point of the second phalanx of D4. The hallux is long, its second phalanx terminating about one-third the length of the first phalanx of D2.

VISCERA—The tongue is unusually long and narrow. The tongues of both specimens from the type locality were protruding well outside the mouth when collected dead. Because the specimens were fixed in formalin and then preserved in 70% ethanol prior to examination, measurements here do not connote natural dimensions.

The free portion of the tongue (apex linguae; Fig. 10) is long, narrow, thick, and tapered toward the tip. It is cylindrical and similar in shape to the tongue of some nectar-feeding bats. The apex linguae alone is approximately 18 mm long and 2 mm wide. The dorsal surface of the tongue is covered by papillae filiformes. There is a short median sulcus in the corpus that does not reach the tip. The torus linguae and the sulcus semilunaris are absent. Only one papillus circumvallatus was found in the corpus, seen as a small protuberance rising from between two lateral lips. In addition, small secondary papillae were detected over the papillus circumvallatus in close lateral view of the tongue. Six whitish papillae lenticulares were found behind the papillus circumvallatus.

The stomach morphology corresponds to the unilocular-hemiglandular pattern (Fig. 11), with an antrum and corpus that are subequal in area. The incisura angularis is shallow and broad, while the ascending antrum and the posterior end of the esophagus form an 80° angle. In cross-section, the bordering fold crosses the lesser curvature at the apex of the incisura angularis, and the glandular epithelium protrudes in a wide bulge into the corpus. In the liver, the gallbladder is absent.

This species has a relatively short intestine; the total length of the intestine is three times the length of the head and body. The small intestine is 2.7 times (204 mm) longer than the large intestine (76 mm). The large intestine has several bends and two big ampullae. The caecum is small (23 mm), representing 8% of the total intestine length. It is thin, with the external diameter equal to that of the adjacent portion of the large intestine. It has five bends and a small appendix scarcely differentiated from the rest of the caecum.

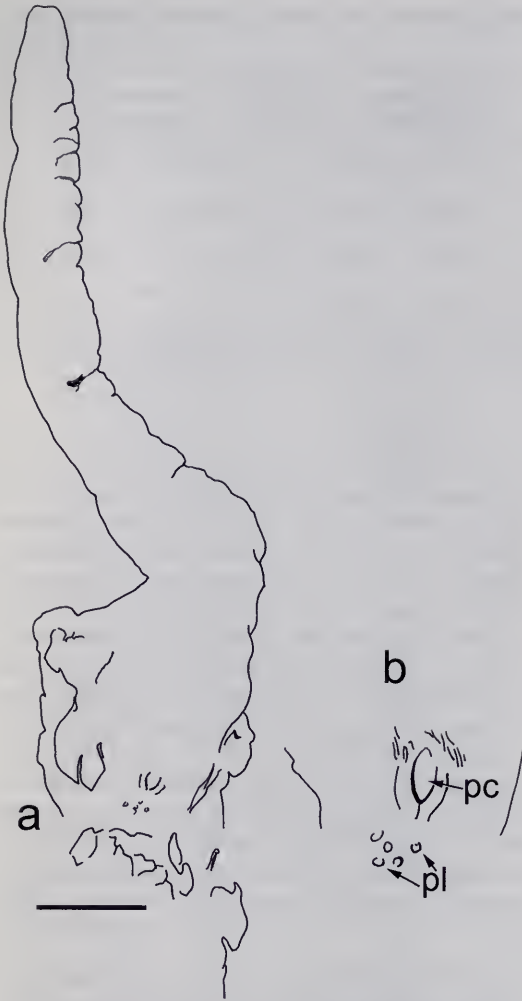


FIG. 10. Tongue of *Rhagomys longilingua*, new species: **a**, gross morphology of the tongue (FMNH 170687), scale bar = 3 mm; **b**, detail of papillae: pc, papillus circumvallatus; pl, papillae lenticulares.

The male accessory gland complement includes a pair of well-developed preputial glands that each extends well beyond the ventral flexure of the penis. The bulbourethral glands are thin projections, orange-brown in color, that run dorsally to the tract, almost reaching the vesicular gland in lateral view (see Voss & Linzey, 1981, fig. 1). The lateral ventral prostate is one-third the size of the medial ventral prostate, and the anterior prostate surrounds the vesicular glands. Vesicular glands are typical: J-shaped, robust, compact, and folded over so that they initially appear almost rounded. The dorsal prostates are present. The ampullary gland is small and shaped like a butterfly with its

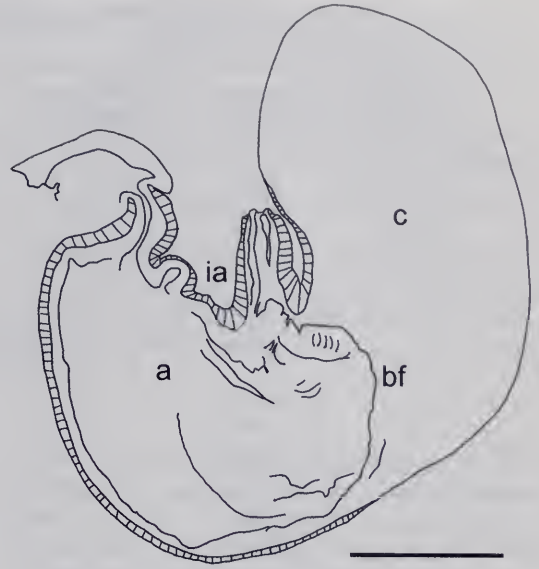


FIG. 11. Stomach morphology of *Rhagomys longilingua*, new species (MUSM 17013), scale bar = 5 mm: c, corpus; a, antrum; bf, bordering fold; ia, incisura angularis.

wings fully extended. The deferent ducts appear from the sides of the "butterfly."

Comparisons

Rhagomys longilingua can easily be distinguished in the field from other Sigmodontinae by its long tongue, the deep transverse grooves in the digits, the square shape of the tips of its digits and their crescent-shaped depressions, and the short, embedded claws. Despite these unique characters, *R. longilingua* bears a superficial resemblance to other small spiny mice such as *Scolomys* and *Neacomys*. From *Scolomys*, *R. longilingua* is distinguished by its larger size (Table 1), the well-defined countershading between the dorsal and ventral fur coloration, and more delicate dorsal spines. Externally, *R. longilingua* warrants more extended comparisons with *Neacomys*, which it resembles in color and pattern of coloration. Unlike *Neacomys*, however, *R. longilingua* has conspicuous Ochraceous-Orange cheeks. The ventral coloration of *R. longilingua* is completely uniform Light Ochraceous-Buff with tones of Light Ochraceous Salmon, while the venter of *Neacomys* varies from whitish (white with the base of the hair gray) to Cinnamon Buff on the flanks of

TABLE 1. External and cranial measurements of *Rhagomys longilingua*, new species. *Rhagomys rufescens*, *Scolomys juruaense*, and *Neacomys spinosus*.

	<i>Rhagomys longilingua</i> ¹	<i>Rhagomys rufescens</i> ²	<i>Scolomys juruaense</i> ³	<i>Neacomys spinosus</i> ⁴
HBL	98 (90–103) 3 7.00	94	80.2 (74–83) 4 4.272	90.5 (75–102) 8 8.036
TL	97.7 (93–104) 3 5.686	93	67.3 (60–72) 3 2	98.14 (74–113) 7 13.044
HF	19 (17–20) 3 1.732	20	20.5 (20–22) 4 1	23.12 (21–26) 8 1.959
E	13.9 (13.6–14) 3 0.231	[]	15 (14–16) 4 0.816	
DFL	8 (8–8) 2 0	7	9.3 (9–10) 3 0.577	9.4 (9–11) 10 0.699
MVL	36 (35–37) 2 1.414	34	36.33 (34–40) 3 3.214	32.3 (25–38) 10 3.592
SVL	25.5 (25–26) 2 0.707	[]	27.33 (24–29) 3 2.887	26.67 (20–32) 9 3.391
GVL	20.75 (20–21.5) 2 1.061	17	27.33 (26–29) 3 1.527	22.56 (19–30) 9 3.395
GLS	28.33	[]	22.52 (21.2–23.87) 5 1.101	23.23 (21.48–24.29) 10 0.948
CIL	25.52 (25.02–26.01) 2 0.7	[]	20.26 (18.82–21.25) 5 0.941	20.74 (19.21–22.35) 9 1.021
CML	16.3 (15.91–16.68) 2 0.544	[]	13.03 (12.2–13.53) 5 0.541	13.33 (12.42–14.45) 9 0.643
CIL-CML	9.22 (9.11–9.33) 2 0.156	[]	7.23 (6.62–7.72) 5 0.406	7.41 (7.11–8.05) 9 0.412
RL	7.7	8.61	5.69 (5.05–6.26) 5 0.489	6.43 (5.47–7.04) 10 0.418
RB	5.025 (4.99–5.06) 2 0.049	4.48	4.72 (4.35–5.25) 5 0.343	4.35 (3.92–4.24) 6 0.254
OFL	10.61 (10.5–10.72) 2 0.156	10.65	7.16 (6.56–7.68) 5 0.408	7.73 (7.25–8.39) 10 0.403
NL	8.55	8.69	8.43 (7.29–9.23) 5 0.9614	9.06 (8.25–9.98) 10 0.579
NB	2.95	3.09	2.62 (2.48–2.88) 5 0.162	2.64 (2.22–2.95) 10 0.208
IBL	5.64 (5.5–5.78) 2 0.198	5.48	5.61 (5.35–5.93) 5 0.222	4.47 (4.23–4.76) 10 0.204
DL	7.285 (7.24–7.33) 2 0.064	7.98	6.14 (5.72–6.57) 5 0.332	6.02 (5.4–6.67) 10 0.404
BPL	6.755 (6.65–6.86) 2 0.148	[]	3.96 (3.71–4.17) 5 0.218	4.05 (3.81–4.5) 10 0.203
BPB	5.095 (4.97–5.22) 2 0.177	5.29	4.62 (4.52–4.82) 5 0.123	4.64 (4.35–5.2) 10 0.241
PPL	8.79 (8.47–9.11) 2 0.453	[]	7.83 (7.06–8.19) 5 0.450	7.65 (6.75–8.53) 9 0.647
IFL	3.74 (3.5–3.98) 2 0.339	4.62	3.93 (3.54–4.31) 5 0.276	3.35 (3.14–3.69) 10 0.174
IFB	1.36 (1.28–1.44) 2 0.113	1.58	2.11 (2.04–2.23) 5 0.076	1.77 (1.48–2.08) 10 0.165
MTL	4.405 (4.29–4.52) 2 0.163	4.73	2.69 (2.63–2.73) 5 0.040	2.99 (2.84–3.16) 10 0.102
PBB	2.44 (2.36–2.52) 2 0.113	2.71	2.94 (2.84–3.1) 5 0.104	2.56 (2.34–3.04) 10 0.190
M1B	1.28 (1.26–1.3) 2 0.028	1.26	0.83 (0.79–0.89) 5 0.04	1.02 (0.91–1.12) 10 0.061
ZB	15.87 (15.86–15.88) 2 0.014	16.75	11.89 (10.99–12.65) 5 0.612	12.31 (11.58–13.19) 10 0.451
BB	13.63 (13.37–13.89) 2 0.368	[]	11.2 (11.01–11.42) 5 0.187	11.02 (10.71–11.26) 10 0.191
ZPB	3.13 (2.96–3.3) 2 0.24	3.65	1.69 (1.55–1.82) 5 0.106	2.13 (1.93–2.36) 10 0.162

TABLE 1. *Continued.*

	<i>Rhagomys longilingua</i> ¹	<i>Rhagomys rufescens</i> ²	<i>Scolomys juruaense</i> ³	<i>Neacomys spinosus</i> ⁴
ID	1.825 (1.74–1.91) 2 0.12	1.80	1.12 (0.97–1.24) 5 0.102	1.31 (1.16–1.46) 10 0.095
BH	9.155 (9–9.31) 2 0.219	[]	7.41 (7.29–7.51) 5 0.104	7.49 (7.23–7.65) 9 0.179
MFB	1.56 (1.4–1.72) 2 0.226	[]	1.88 (1.7–2.11) 4 0.170	1.56 (1.48–1.58) 4 0.699

Note: Measurements are in millimeters, values are the mean, range (in parentheses), sample size, and standard deviation. For abbreviations, see text. Brackets indicate measurements are not available.

^{1, 2, 3, 4} See Specimens Examined in Appendix for collection data.

some specimens. *Rhagomys longilingua* has broader feet and fleshy plantar pads with a callous surface and smooth sole, while *Neacomys* has small and smooth plantar pads and scaly soles. *Rhagomys longilingua* has a nail in the hallux, while *Neacomys* has a claw. In *R. longilingua*, D5 of the hind foot is longer in relation to D4 than in *Neacomys*. *Rhagomys longilingua* has three pairs of mammae instead of four, as in *Neacomys*.

While different from all other well-characterized sigmodontines, *R. longilingua* possesses a number of characters that were reported more than a century ago by Oldfield Thomas (1886) in his original description of *Hesperomys rufescens* (Fig. 12) from Rio de Janeiro. Thomas initially offered a brief, rudimentary description of external characters:

General colour rich-rufous all over, both above and below, the hairs everywhere slaty blue at their bases and rufous at their tips. Underside only slightly lighter than upper. Ears short, scarcely projecting beyond the fur, thickly covered with rufous-brown hairs. Feet yellow; toes whitish, fifth hind toe to end of second phalanx of fourth. Tail of medium length, unicolor, thinly covered with brown hairs, which forms an inconspicuous pencil at the tip.

On the basis of these characters, he proposed a superficial relationship between *Hesperomys rufescens* and *Hesperomys bicolor* (= *Oecomys bicolor*). “The two species together seem to belong to rather a synthetic type, combining the external characters of *Oryzomys* with the cranial ones of *Rhipidomys*. . . .” The cranial characters he mentioned were the general shape and proportions of the skull, including its short rostrum, similar interorbital shape, and inflated braincase, as in *Rhipidomys*. The long digit five of the hind foot that Thomas identified in *Hesperomys rufescens* is shared by *R. longilingua*.

Thomas subsequently distinguished the *Oryzomys-Oecomys* complex and *Rhipidomys-Thomasomys* complex, based mainly on palate length: the former group has a long palate and the latter a short one. In 1917, with a better-preserved specimen in hand, Thomas tried to specify the position of *Hesperomys rufescens*: “while belonging to the *Oryzomys-Oecomys* series, [it] certainly represents a genus distinct from any of its allies, its molar structure being indeed quite unique in the group. It may be called: *Rhagomys*, gen. nov.”

Thomas characterized the new genus using external, cranial, and dental characters:

General facies as in *Oecomys*. Feet modified for an arboreal life, with large plantar and digital pads. Mammae apparently 1–2 = 6 as in *Rhipidomys*.

Skull broad and low, with broad, smooth, rounded braincase; supraorbital edges square, not ridged. Zygomatic plate little projected forward. Palatal foramina short and little open. Posterior palate of the general structure of *Oryzomys* and *Oecomys*, not as in *Rhipidomys* and *Thomasomys*.

Upper incisors approaching the vertical angle with tooththrow about 80°, deep antero-posteriorly, their front surface flattened and inclined inwards. . . . Lower incisors of corresponding form, anteriorly, their roots extended backwards much beyond the normal, forming a prominent capsule outside the jaw, halfway between the coronoid and the condyle. Both the shape and the implantation of the incisors therefore indicate unusual gnawing powers.

Molars showing a remarkable modification of the structure found in *Oecomys* and *Oryzomys*, for while the number and positions of the cusps are the same, the various foldings and ridges between and connecting the cusps are almost entirely obsolete. The teeth are therefore almost as in certain Phyllostomid bats, with smooth glossy surface and simple conical cusps, which are evenly spaced, slightly slanted backwards, 6, 4, and 2 in number on the three teeth. Below the teeth are similarly modified, the cusp slanting forwards. (pp. 192–193).

Thomas believed that his new genus *Rhago-*

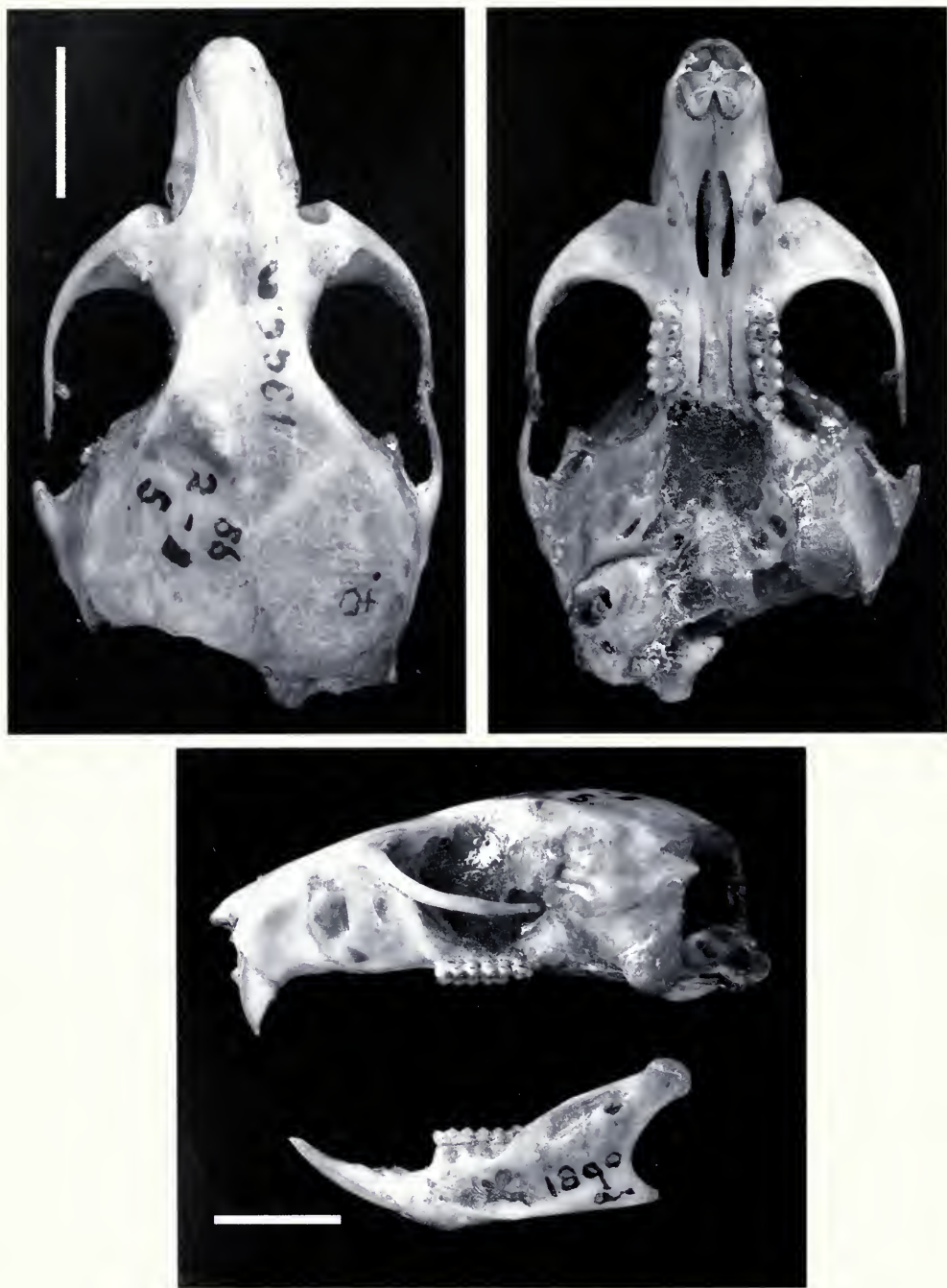


FIG. 12. Dorsal, ventral, and lateral views of cranium, lateral view of the mandible of the type of *Rhagomys rufescens* (Thomas, 1886), BMNH 86.2.8.5, adult female. Scale bar = 6 mm.

mys was closest to *Oecomys* in terms of external morphology and palatal structure but far from that genus in morphology of the incisors and molars. Although he compared *Rhagomys* with

the *Rhipidomys-Thomasomys* complex, he avoided making statements about their possible relationships, calling instead for a revision for the whole group.

Many of the cranial characters in Thomas' description of *Rhagomys* are evident in *R. longilingua*: incisor capsule prominent, and the most striking feature, molar cusp arrangement. *Rhagomys longilingua* has molars with very conspicuous cusps and thin ridges connecting the conules with the median mure. The comparison Thomas made with phyllostomid bats almost perfectly describes the isolated pattern of the conules and conulids in the molars of both *R. rufescens* and *R. longilingua*.

Ellerman (1941) added further details to the description of the external morphology of *Rhagomys*:

The hallux in the type skin appears to lack a claw, but more specimens will be necessary before this character can be proved, as the skins examined are very old, and not in good condition. D.5 [digit V] hindfoot lengthened; tail long, not well haired. (p. 377)

The digital-length character he identified and the absence of a hallal claw are among the diagnostic characters for *R. longilingua*.

Moojen (1952) subsequently described *Rhagomys* as having a tail covered by hairs increasing in size toward the tip to form an inconspicuous apical tuft. He also noted that the manus and pes were naked, with calluses on their surface, stating:

... [cauda] finamente recoberta de pêlos que são mais longos na ponta formando um pincel pouco conspícuo ... Palmas e solas nuas con grandes callos.¹ (p. 51)

He used the term *calos* to designate the calluses in the plantar regions, no doubt to specify the presence of calluses rather than simply the plantar pads. Both of these traits also recall the condition of *R. longilingua*.

A more detailed, point-by-point comparison of *R. longilingua* with *R. rufescens* is warranted. Unfortunately, only two old specimens of *R. rufescens* exist for comparison, both at the Natural History Museum in London (BMNH). Each consists of a skin with damaged or lost skull, limiting the basis for comparison. During most of our analysis, the collections of the Natural History Museum in London were unavailable for study, owing to renovations in the mammal division. Our comparisons were accordingly based on digital and

analog images of the skull and skin of the type specimen (BMNH 86.2.8.5, female) by the museum's staff and colleague Guy Musser, as well as on information on *Rhagomys* published by Thomas (1886, 1917), Gyldenstolpe (1932), Ellerman (1941), and Moojen (1952). During the manuscript's review, we had the benefit of detailed observations of the holotype by curator Paula Jenkins and further inspection by the junior author.

COMPARISONS WITH *RHAGOMYS RUFESCENS*.—*Rhagomys longilingua* is readily distinguished externally from *Rhagomys rufescens* by its spiny fur; *Rhagomys rufescens* has soft, lax fur. This condition was confirmed by Paula Jenkins:

... *R. rufescens* has long, soft fur on the dorsum and flanks, slightly shorter on the venter and also slightly shorter and slightly harsher on the head. Individual hairs are long, thin and soft. The fur of this species is longer but as soft as that of *M. dryas*, *M. d. humilior* [both *Microrhagomys minutus*] and *Oligoryzomys stoltzmanni*, softer than *Oligoryzomys arenalis* and *O. n. messorius* [= *Oligoryzomys fulvescens*] and there is no trace of the spinous texture of *Nleacomys spinosus*. (in litt.; February 11, 2002).

Rhagomys longilingua has fingers and toes with conspicuous, deep, transverse grooves, with the claws embedded in the tips of the digits. These characteristics are faintly evident in the type material of *R. rufescens*. The two taxa share inconspicuous pelage countershading and tails that are roughly equal to HBL. Both have broad feet, with a nail (not a claw) on the hallux and an elongated D5 on the pes that reaches the middle of the second phalanx of D4. They also share calluses on the soles of manus and pes, as mentioned for *R. rufescens* by Moojen (1952).

Cranially, *R. longilingua* and *R. rufescens* are very similar (Figs. 5 and 12), but they also exhibit some differences. The interorbital region of *R. longilingua* is strongly beaded, with its narrowest point anteriorly, while in *R. rufescens*, the interorbital region is smooth and its narrowest point near the middle. The zygomatic notch in *R. longilingua* is slightly shallower than in *R. rufescens*. The postorbital process is conspicuous in *R. longilingua*, while in *R. rufescens*, no statement could be made; remnants of dry anterior temporalis muscle suggest the presence of a developed postorbital process; however, because of the fragile condition of the specimen, the skull has been coated with a layer of cement, which makes confirmation of this character unclear.

The basicranium of *R. rufescens* type is incom-

¹ "[Tail] finely covered with hairs which are longer at the tip forming an inconspicuous brush. Palms and soles naked with large calluses."

pletely known, limiting comparisons of the alisphenoid and basioccipital regions. Although the posterior palate is damaged in the type, Thomas (1917) assigned a long palate to *R. rufescens* after examining another BMNH specimen that apparently was subsequently lost (V. Pacheco, pers. comm.). Apparently, however, the posterior opening of the alisphenoid canal is smaller in *R. longilingua* than in *R. rufescens*.

The upper molar tooth row of *R. rufescens* is longer than in *R. longilingua* (4.73 mm for *R. rufescens*, versus 4.52 mm for *R. longilingua*; P. Jenkins, pers. comm.), while the width is the same (P. Jenkins, pers. comm.); consequently, the length-to-width ratio is noticeably smaller in *R. longilingua* than in *R. rufescens*. In both species, M3 only has two well-defined cusps (protocone and paracone; Thomas [1917] stated this for *R. rufescens*); however, *R. rufescens* has a bigger undifferentiated heel than *R. longilingua*, which makes M3 more of an inverted triangle. The mandibular molars are configured in a parallel manner: the length-to-width ratio is smaller in *R. longilingua* than in *R. rufescens*, and *R. rufescens* has longer teeth, with conspicuous posterolophids on m1 and m2.

Shared cranial characters include a strongly built skull, with short, narrow, and blunt rostrum; a strong alisphenoid strut that hides the aperture of the anterior opening of the alisphenoid canal; foramen ovale visible in ventral view, exposed by the narrow parapterygoid fossa and the absence of a ridge along the lateral edge of the alisphenoid; middle lacerate foramen completely closed; and highly cuspidate molar teeth. The mandible has a short angular process, extending only as far as the base of the condyloid process; a capsular projection of the incisor distinct as a conspicuous knob in dorsal view; a conspicuous inferior masseteric ridge; and deep and broad retromolar fossae in both species. Although the coronoid process is broken in the type of *R. rufescens*, it was apparently short and strong as in *R. longilingua*.

Descriptions of *R. rufescens* do not include many of the characters we have noted in *R. longilingua*, such as the long tongue, the crescent-shaped depression in the fingertips, cranial characters (such as the fontanelles in the parapterygoid fossae, the ectotympanic structure, and carotid circulation), postcranial characters, and soft characters. However, both taxa share a uniquely derived morphology that has never been seen before in other Sigmodontinae. The different fur texture—spiny fur in *R. longilingua* and the soft fur

in *R. rufescens*—seems a questionable basis for separating these two taxa into different genera. Other genera that show different degrees of pelage textures ranging from soft to spiny pelage are present in the Murinae subfamily as the genera *Margaretamys*, *Maxomys*, and *Niniventer* (M. Carleton, in litt., July 10, 2002). However, comparison of other characters may indicate it warrants a generic distinction.

COMMENTS ON THE MORPHOLOGY WITH RESPECT TO OTHER MURIDAE—The presence of a nail in the hallux of *R. longilingua* (Fig. 4b) differs from almost all Sigmodontinae except *R. rufescens*, in which this character was first scored by Thomas (1886) for South American mice. This condition is present in many arboreal mammals and is sometimes associated with opposability of the hallux, such as in some marsupials, extinct primates (Musser, 1979), and some arboreal rodents. As a result of convergence, this character is present in other members of the Muridae family, as in Dendromurinae and Murinae subfamilies. We examined this same character in the African climbing mouse *Dendromus mesomelas* (Muridae: Dendromurinae). This genus has similar toe morphology, with long digits, D5 elongate, and a very short hallux with a nail, all as in *R. longilingua*, but with substantially narrower feet. Surprisingly, the feet morphology of the Peruvian taxon is very similar to the one of the genus *Chiropodomys* (Muridae: Murinae). *Chiropodomys* has a short and broad manus and pes, with the hallux and pollex each bearing a nail; fingertips with thick pads; digits with deep transversal grooves; and similar large plantar pads sculptured with what Musser (1979) called semicircular striae (see Musser, 1979, figs. 13 and 14) that give *R. longilingua* its diagnostic callous pad surface. In spite of these similarities, *Chiropodomys* has longer, sharp-tipped, and more curved claws and thicker pads on the fingertips.

Similarities with members of the family Sigmodontinae include that, cranially, in dorsal view, the supraorbital ridges of *R. longilingua* are strongly beaded, as in members of the oryzomyine group of Hershkovitz (1962).

In ventral view, *R. longilingua* has a wide palate similar to oryzomyine, phyllotine, and ichthyomyine groups of Hershkovitz (1962).

Cranially, the most diagnostic characteristics of *R. longilingua* can be identified in ventral view. Therefore, the foramen ovale accessorius is conspicuously visible from this view due to the narrow parapterygoid fossa, and this may be associ-

ated with a small internal pterygoid muscle. Although the foramen ovale accessorius was also seen (in ventral view) in specimens of the akodontines *Necromys amoenus*, *N. lasiurus*, and some *Akodon*, in this case the foramen is associated with a much larger anterior opening of the alisphenoid canal, with which it fuses, forming a single foramen, which differentiates it from the one observed in *R. longilingua*.

The retromolar fossa of *R. longilingua* is deeper than in most Sigmodontinae, with the apparent exception of *R. rufescens*. This is the insertion point of one of the bodies of the temporalis muscle. The anterior part of the temporalis originates on the temporal ridge, almost reaching to the interparietal. Passing within the orbit, it inserts on the ventral surface of the coronoid process and its base. Perhaps this configuration explains the notably small size of the coronoid process. Dissection will be necessary to determine further details of this relationship.

Ecological Observations

HABITAT—The male holotype (MUSM 17013) and a female paratype (FMNH 170687) were found freshly dead in two different 50-m pitfall lines on consecutive days of sampling in dense cloud forest habitats at the type locality. The holotype was trapped at 1900 m elevation and the paratype was taken at about 2100 m elevation. While this description was in preparation, a third specimen was trapped in lowland *caña brava* habitat at 450 m, within a few meters of the banks of the Río Alto Madre de Dios near Maskoitania.² It was taken in a single-sprung Victor rat trap set 1 m above-ground along a horizontal cane. The trap was baited at sunset with a ball of oatmeal, peanut butter, vanilla extract, and fish oil wrapped in cheese-cloth, and the mouse was found at sunrise the following morning. The cane was approximately 5 cm in diameter. Assuming that this species is continuously distributed between both capture sites, its range encompasses lowland humid forest, montane forest, and lower cloud forest habitats.

DIET AND TROPHIC ADAPTATIONS—The stomach

of the holotype of *R. longilingua* contained nothing but insects. Analyzing the finely triturated remains, we detected fly larvae (Diptera), a caterpillar (Lepidoptera), and ants (Hymenoptera: Formicidae) of the genus *Solenopsis*.

The various insect remains in the stomach suggest that this species is insectivorous, at least to a degree (given that many rodents are granivorous or herbivorous, it might generally be opportunistic). An insectivorous diet suits the morphology of the molar teeth, which are pentalophodont, with conspicuous cusps that may be classified as either crested or terraced (*sensu* Hershkovitz, 1967), and by a relatively short, small intestine and caecum (Vorontzov, 1979). The relative proportions of the small intestine and caecum are commonly associated with an insectivorous diet. Moreover, *Rhagomys* seems to have powerful mastication muscles, as judged from the conspicuous postorbital process and broad retromolar region (for the temporalis muscle) and the conspicuous inferior masseteric ridge (associated with a strong anterior deep masseter muscle).

Where and how this species forages are still unknown. The first two specimens were collected in a pitfall bucket-line fence, which is generally more effective for terrestrial, ground-foraging species. However, pitfalls also take arboreal mammals such as *Gracilinanus*, *Oecomys*, and *Rhipidomys*. The arboreal nature of this species is suggested by its highly specialized feet (broad feet with fleshy and conspicuously callous surface, digits with deep transverse grooves, and long D5 in relation to D4), and the palmar and plantar textures reported in *Chiropodomys* similar to the ones of *R. longilingua* suggest adaptations for movement on supports above the ground, where adhesion to surfaces may be more important than grasping supports (Musser, 1979). In addition, the short muzzle and enlarged eyes afford *R. longilingua* a wide field of frontal vision, as suggested by Hershkovitz (1972) for arboreal oryzomyines.

The capture of the third specimen in a distinctively arboreal setting and on smooth cane confirms its ability to exploit aboveground niches.

Rhagomys longilingua may use its long tongue as a probe to extract ants and other insects from cavities and crevices. Judging from the strongly built skull, this species may open holes in cane or other plants using its short and broad incisors and powerful mastication configuration (deep retromolar fossa, high and short hemimandibles, and conspicuous masseteric ridges) in order to expose the resources they contain.

² This male specimen (FMNH 175218) was prepared as an alcoholic specimen, with cleaned skull, larger ectoparasites in alcohol (CWD P-145), and heart, lung, and liver tissues in liquid nitrogen. Measurements are tallied in Table 1.

Discussion

Although there have been significant advances in the understanding of Sigmodontinae phylogenetics, we are still far from a complete picture (D'Elía, 2000). One of the problems is allocating forms treated as *incertae sedis* (Reig, 1986; McKenna & Bell, 1997; Smith & Patton, 1999) or as "plesiomorphic Neotropical muroids" (Voss, 1993). Each author has a distinct list of genera with uncertain relationships, but problematic forms include *Abrawayaomys*, *Aepeomys*, *Chilomys*, *Phaenomys*, *Rhagomys*, *Thomasomys*, *Wilfredomys*, *Delomys*, *Microakodontomys*, *Puno-mys*, *Scolomys*, *Reithrodon*, *Irenomys*, *Zygodontomys*, and *Pseudoryzomys*. Insufficient material and inadequate descriptions or analyses are certainly responsible for some of this confusion, and this is certainly the case with the two fragmentary samples of *R. rufescens*.

The possession of extraordinary unique characters for *R. rufescens* and *R. longilingua* suggest a relationship, one exclusive of other sigmodontines. To substantiate this will require a comprehensive phylogenetic analysis of Sigmodontinae. With incomplete material and uncertain generic affinities (Reig, 1980; Musser & Carleton, 1993), the tribal relationships of *Rhagomys* have invariably been treated as *incertae sedis* (Carleton & Musser, 1984; Reig, 1986; McKenna & Bell, 1997; Smith & Patton, 1999). However, the discovery of another species of *Rhagomys*, together with the detailed character sets now available for analysis of *R. longilingua*, open the door to comprehensive revisions of the tribes of sigmodontines. Given the enormous size of this assemblage (currently, more than 400 species in nearly 100 genera), a comprehensive treatment will be time-consuming. At present, comprehensive analyses of morphology and gene-sequence divergence are in progress. However, preliminary results of phylogenetic analyses based on 86 morphological characters (external and cranial characters) confirm *Rhagomys* as a monophyletic genus (90% of bootstrap support) without a clear tribal association (Luna, 2001).

Thomas (1917) had already noted interesting relationships based on the external and cranial morphology of *Rhagomys*, finding that this species was somewhat related to *Oecomys* (Oryzomyini) and to what he called the *Rhipidomys-Thomasomys* complex ("thomasomyines"). *Rhagomys longilingua* and perhaps also *R. rufescens* present characters that fall outside of the current diagnosis for Ory-

zomyini (Voss & Carleton, 1993). Both species lack the pectoral pair of mammae (Thomas, 1917), having only three pairs of mammae. (The oryzomyine *Scolomys juruaense* also has the same mammary formula [Patton & da Silva, 1995].) *Rhagomys longilingua* has a broad alisphenoid strut, which does not separate the buccinator-masticatory from the ovale accessorius foramina; rather, they are fused, and the former cannot be seen in lateral view. Character states suggesting a close phylogenetic relationship with the Oryzomyini include the presence of a long palate, the lack of a posterior suspensory process of the squamosal attached to the tegmen tympani, and the absence of a gallbladder. Character states that may suggest phylogenetic relationship with the "Thomasomyine" group are long ungual tufts, 3 pairs of mammae, 13 pairs of ribs, and the mesopterygoid fossae not fenestrated (Voss, 1993, table 3). However, the latter group is being revised by V. Pacheco, and new definitions of its components should soon be available. In addition, molecular and more detailed morphological studies are now under way that should offer a more thorough investigation of these two grand assemblages of mice and their relationships to *Rhagomys*.

This preliminary report of *Rhagomys* already identifies the following presumptive synapomorphies as supporting their sisterhood: nail in the hallux, cuspidate molars and the very short angular process of the mandible, bony ridge in the lateral edge of the parapterygoid fossa absent, then the foramen ovale accessorius visible from the ventral view related to a very small posterior opening of the alisphenoid canal.

COMMENTS ON THE BIOGEOGRAPHY OF THE GENUS—Although *R. longilingua* and *R. rufescens* share unique cranial and external characters, they are widely separated geographically—*R. rufescens* is only known from the Atlantic forest of Rio de Janeiro, while *R. longilingua* is only known from Manu Biosphere Reserve—and in external phenotype, without a succession of intermediates linking them. Either *R. longilingua* and *R. rufescens* are relicts of a nearly extinct, formerly widespread clade or else scientists have failed to sample them in intervening areas. An interesting example of this is the genus *Juscelinomys*, which was known for decades solely from two Brazilian species—in Lagoa Santa and the Distrito Federal. Recently, Louise Emmons (1999) described two more species from Bolivia. Regardless, *Rhagomys* must have been (or still is) continuously distributed across South America. The report of *R. longilingua* widens the geographical range of the in-

certae sedis genus *Rhagomys*, previously considered endemic to southeastern Brazil, and, as may be the case with other endemic genera (*Phaenomys*, *Abrawayaomys*, and *Microakodontomys*), it might also represent an independent lineage (Smith & Patton, 1999).

So far as presently known, *Rhagomys* has a distribution limited to the Brazilian Atlantic highlands (*R. rufescens*) and the eastern slope of the Andes (*R. longilingua*). It is the first mammalian group to show this unusual disjunct distribution pattern, but similar patterns of distribution have been reported for hylid frogs of the *Hyla parviceps* group (Duellman & Crump, 1974). Some authors have attributed distributional disjunctions to climate changes during the Pleistocene that caused fragmentation and reexpansion of forest corridors and refugia (Vuilleumier, 1971). However, the timing of disjunctions in *Rhagomys* remains unspecified, and many Neotropical disjunctions greatly antedate the Pleistocene (e.g., Lundberg et al., 1986). Calibration of the molecular clock of *Rhagomys* may be expected to shed light on this question.

Smith and Patton (1999) concluded that southeastern Brazil has been an important geographic center in the diversification of the sigmodontines; some of these have subsequently extended their ranges across South America. We expect to determine the timing of these events in *Rhagomys* after the analysis of its phylogenetic relationships with other Neotropical sigmodontines is completed. Our preliminary results suggest that *Rhagomys* represents a well-differentiated lineage of Sigmodontinae that warrants taxonomic recognition. Therefore, in order to understand the sigmodontine radiation as a whole, we hope to resolve the phylogenetic relationships of this genus in relation to the other Sigmodontinae.

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Appendix

Abbreviations

Abbreviations for institutions are as follows: Field Museum of Natural History, Chicago (FMNH); Natural History Museum, London (BMNH); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Museo de Historia Natural, Universidad Mayor de San Marcos, Lima, Peru (MUSM); University of Michigan Museum of Zoology, Ann Arbor (UMMZ).

Specimens Examined

This report is based on examinations of 36 specimens, as follows.

Dendromus mesomelas (2)—TANZANIA, 2. Putwa Region, Sumbawanga District, Mbizi Mountains, Mbizi Forest Reserve, ½ km S, 3 km E Wipanga, 07°52'30"S, 31°40'00", 2300 m (FMNH 171306, 171307).

Chiropodomys gliroides (2)—MALAYSIA, 2. Kuala Lumpur, Selangor, Kepong, Bukit Lagong Forest Reserve (UMMZ 117158, 117159).

Akodon aerosus (4)—PERU, 4. Cusco, Paucar-

tambo, Suecia, km 138.5 Carretera Shintuya, 1900 m (FMNH 170420, 170423, 170427, 170428).

Necomys lasiurus (3)—BRAZIL, 3. Pernambuco, São Lourenço da Mata, Estação Ecológica de Tapacurá (FMNH 123065, 123067, 123068).

Necomys amoenus (3)—PERU, 3. Arequipa, Chivay, 5 km NNE, 12000 ft (\approx 3600 m) (FMNH 107665, 107666, 107680).

Rhagomys longilingua (3)—PERU, 2. Cusco, Paucartambo, km 138.5 Shintuya Road, 1900 m (FMNH 170687, MUSM 17013). PERU, 1. Madre de Dios, Manu, along the Río Alto Madre de Dios near Maskoitania, 450 m (BDP 4000).

Rhagomys rufescens (1)—BRAZIL, 1. Rio Janeiro [sic] (BMNH 86.2.8.5*).

Neacomys spinosus (11)—PERU, 2. Inca Mines (FMNH 20088*, 20089*). PERU, 2. Puno, Santo Domingo (FMNH 52711*, 525712*). PERU, 1. San Martín, Moyobamba (FMNH 19360*). PERU, 2. Río Cayumba (FMNH 24762*, 24763*). PERU, 1. Pasco, Pozuzo, Río Pachitea (FMNH 24765*). PERU, 1. Puno, Segrario (FMNH 52710*). PERU, 1. Poco Tambo (FMNH 19691*). PERU, 1. Puerto Victoria (FMNH 51358).

Scolomys juruaense (7)—BRAZIL, 2. Amazonas, Penedo, right bank Río Juruá (MVZ 183165*, 183166*). BRAZIL, 2. Amazonas, Condor, right bank Río Juruá (MVZ 183167*, 183168*). BRAZIL, 3. Amazonas, Barro Vermelho, left bank Río Juruá (MVZ 183169*, 183170, 183171). BRAZIL, 1. Amazonas, Sobral, left bank Río Juruá, Amazonas (MVZ 183172).

* Specimens measured; see Table 1.

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