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Chapter 5

A New Species of *Reithrodontomys*, Subgenus *Aporodon* (Cricetidae: Neotominae), from the Highlands of Costa Rica, with Comments on Costa Rican and Panamanian *Reithrodontomys*

ALFRED L. GARDNER¹ AND MICHAEL D. CARLETON²

ABSTRACT

A new species of the rodent genus *Reithrodontomys* (Cricetidae: Neotominae) is described from Cerro Asunción in the western Cordillera de Talamanca, Costa Rica. The long tail, elongate rostrum, bulbous braincase, and complex molars of the new species associate it with members of the subgenus *Aporodon*, *tenuirostris* species group. In its diminutive size and aspects of cranial shape, the new species (*Reithrodontomys musseri*, sp. nov.) most closely resembles *R. microdon*, a form known from highlands in Guatemala and Chiapas, Mexico. In the course of differentially diagnosing the new species, we necessarily reviewed the Costa Rican and Panamanian subspecies of *R. mexicanus* based on morphological comparisons, study of paratypes and vouchers used in recent molecular studies, and morphometric analyses. We recognize *Reithrodontomys cherrii* (Allen, 1891) and *R. garichensis* Enders and Pearson, 1940, as valid species, and allocate *R. mexicanus potrerograndei* Goodwin, 1945, as a subjective synonym of *R. brevirostris* Goodwin, 1943. Critical review of museum specimens collected subsequent to Hooper's (1952) revision is needed and would do much to improve understanding of *Reithrodontomys* taxonomy and distribution in Middle America.

INTRODUCTION

Among the mammals collected in Costa Rica during 1966 and 1967, when Gardner held an appointment with the Louisiana State University International Center for Medical Research and Training, is a specimen of a diminutive male *Reithrodontomys*. The specimen was trapped in a small marshy area along one side of an equally small elongated pool located at the base of Cerro Asunción on the Cerro Buenavista massif generally known as Cerro de la Muerte. These cerros lie within the western reaches of the Cordillera de Talamanca, an old and high mountain system that dominates the landscape of western Panama and southeastern Costa Rica (fig. 1). First assumed to be an immature *Reithrodontomys creper*, the mouse was promptly identified as an adult upon preparation, but of a species

unknown to the senior author at the time. Several days of trapping at the collecting site and elsewhere on the Cerro Buenavista massif over the next five months failed to produce additional specimens.

Gardner had long assumed that this harvest mouse was closely related to *R. rodriguezi* Goodwin (1943), a little known form described from Volcán Irazú, based on Hooper's (1952: 174) misleading statement that the skull of *R. rodriguezi* was "smaller than *microdon*" (an obvious lapsus contradicted by his own measurements). Indeed, McPherson (1985) later reported the specimen as *R. rodriguezi*. However, direct comparison with known specimens of *R. rodriguezi*, which is distinctly larger, and with those of other species of the subgenus *Aporodon* from Central America, makes clear

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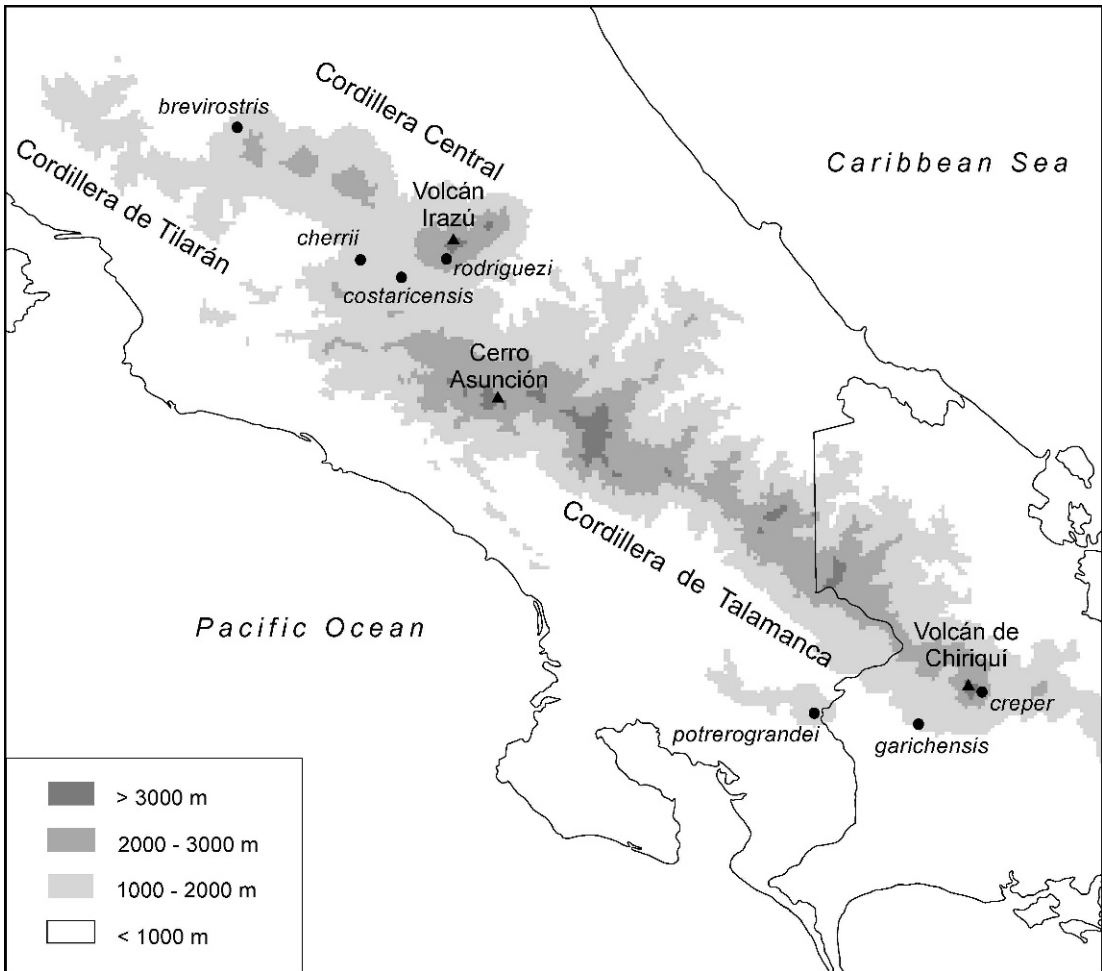


Fig. 1. Map of central and eastern Costa Rica and western Panama illustrating type localities of *Reithrodontomys* taxa and topographic features mentioned in the text. The small harvest mouse, *R. musseri* n. sp., of central interest to this paper was collected at 3,300 m near the base of Cerro la Asunción in the western Cordillera de Talamanca. Species-group epithets of the subgenus *Aporodon* and their type localities include: *brevirostris* Goodwin (1943) from Laja Villa Quesada, provincia de Alajuela, Costa Rica; *cherrii* Allen (1891) from San José, provincia de San José, Costa Rica; *costaricensis* Allen (1895) from Cerro La Carpintera, provincia de Cartago, Costa Rica; *creper* Bangs (1902), from Volcán de Chiriquí, provincia de Chiriquí, Panamá; *garichensis* Enders and Pearson (1940) from Río Gariché, provincia de Chiriquí, Panamá; *potrerograndei* Goodwin (1945) from Agua Buena, provincia de Puntarenas, Costa Rica; and *rodriguezi* Goodwin (1943) from Volcán de Irazú, provincia de Cartago, Costa Rica. The southern Mesoamerican highlands (collectively the Talamancan Highlands of Costa Rica and western Panama, sensu Savage, 1982) are delineated by 1000 m elevational bands.

that the Cerro Asunción animal represents a previously unknown species allied with the *tenuirostris* group (sensu Hooper, 1952) that we herein describe as new. Pursuant to evaluating the distinctiveness and probable

relationships of the new species, we necessarily studied certain other forms of *R. (Aporodon)* described from Costa Rica and Panama and report our taxonomic impressions derived from those examinations.

MATERIALS AND METHODS

Specimens examined consist of round skins and skulls that are deposited in the following institutions: Academy of Natural Sciences of Philadelphia (ANSP); American Museum of Natural History, New York (AMNH); Louisiana State University Museum of Natural Sciences, Baton Rouge (LSUMZ); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM).

Standard external measurements (TL, total length; T, tail; HF, hind foot; E, ear) are those recorded on the specimen labels. Twenty-one cranial and four dental measurements were taken with dial calipers accurate to 0.05 mm as follows (see Hooper, 1952, or Carleton and Musser, 1995, for definition and illustration of variables): ONL (distance from posterior surface of supraoccipital to tips of nasals); ZB, zygomatic breadth; BBC, breadth of braincase; DBC, depth of cranium (distance between basioccipital-basisphenoid plane and top of cranium); IOB, least interorbital breadth; LPS, length of suture between the parietals; LR, length of rostrum (distance from posterior margin of malar root of zygomatic arch to anteriormost point of nasal on same side); BR, breadth of rostrum across the nasolacrimal capsules; LN, length of nasals; BN, breadth of nasals (measured across both nasals near distal tips above the exposed incisors); LD, length of upper diastema (distance between posterior margins of upper incisors to a plane connecting anterior faces of first molars); LIF, length of incisive foramina; BIF, breadth across both incisive foramina at the premaxillary-maxillary suture; LBP, length of bony palate; PPL, postpalatal length (distance between posterior margin of palate, not including median spine, to the middle notch of the basioccipital); BBP, breadth of bony palate at the level of the first molars; PDB, postdental breadth (breadth across palate at the constriction behind the molar rows); BMF, breadth of mesopterygoid fossa; BZP, breadth of zygomatic plate; LAB,

length of auditory bulla; HIF, height of infraorbital foramen; DI, anterior-posterior depth of upper incisors; BI, breadth of upper incisors (measured across tips of both incisors above lateral wear taper); CLM, crown length of maxillary tooth row; WM1, coronal width of upper right first molar. Capitalized names of colors are based on Ridgway (1912).

Four age classes were roughly defined according to stage of eruption of the upper third molar (M3) and relative wear of the upper molars (M1–M3): (1) juvenile—M3 not erupted, or if erupted lacking any wear; (2) young adult—upper molars, including M3, lightly worn, enamel pattern retaining well defined cusps and ridges, dentinal connections narrow; (3) full adult—M1–M3 moderately to heavily worn with blunt cusps, wide dentinal connections, and enamel pattern variously obscured; (4) old adult—occlusal wear so advanced that the enamel pattern is largely obliterated, dentinal lakes of cusps are broadly continuous, and molars basinlike.

Standard descriptive statistics (mean, range, standard deviation) were derived for locality or species samples using only those specimens judged to be adult. External data are provided as general indication of size and bodily proportions (table 1) but were not subjected to morphometric comparisons. Canonical variates (CVs) derived from multigroup discriminant function classification and principal components (PCs) were computed using only the 25 craniodental variables, all of which were first transformed to natural logarithms. Principal components were extracted from the variance-covariance matrix, and variable loadings are expressed as Pearson product-moment correlation coefficients of the extracted components or canonical variates with the original cranial measurements. All analytical procedures were implemented using statistical routines contained in Systat for Windows, Version 10.2 (2002).

TAXONOMY

CHARACTERISTICS OF THE SUBGENUS
APORODON: Howell (1914) named *Aporodon* as a subgenus to contain those species with

TABLE 1
Measurements of Select Taxa of Central American *Reithrodontomys* (*Aporodon*)
(See Materials and Methods for variable abbreviations. Statistics include the mean, sample size in parentheses, and range.)

<i>tenuirostris</i> species group				<i>mexicanus</i> species group			
<i>R. musseri</i>				<i>R. "mexicanus"</i>			
Variable	new species	<i>R. microdon</i>	<i>R. rodriguezi</i>	<i>R. brevirostris</i>	<i>cherrii</i>	<i>garichensis</i>	<i>potrerograndei</i>
TL	161	176.4 (18) 163–189	201.7 (3) 190–222	187.3 (4) 169–202	186.7 (10) 168–202	192.3 (4) 185–199	176.6 (8) 156–188
T	99	104.0 (18) 87–112	117.7 (3) 107–130	116.3 (4) 108–125	109.0 (10) 101–117	114.7 (4) 110–120	109.3 (8) 98–118
HF	19	19.4 (18) 16–21	21.0 (3) 20–22	19.3 (4) 19–20	18.7 (10) 17–20	20.7 (4) 20–21	17.8 (8) 16–19
E	14	16.6 (16) 14–19	16.0 (3) 15–18	13.3 (4) 13–14	15.9 (10) 14–18	14.5 (4) 13–16	12.9 (8) 12–13
ONL	21.1	22.5 (18) 20.7–23.5	24.3 (2) 23.8, 24.9	22.0 (10) 20.7–22.6	23.8 (14) 22.2–24.7	23.5 (16) 22.2–24.6	21.6 (2) 20.9, 22.3
ZB	10.3	10.6 (18) 10.1–11.3	12.1 (2) 11.8, 12.4	11.3 (10) 10.9–11.6	12.5 (14) 11.7–12.9	11.7 (16) 11.0–12.3	10.8 (2) 10.8, 10.8
BBC	10.7	11.0 (18) 10.1–11.8	11.9 (2) 11.4, 11.8	10.9 (10) 10.7–11.1	11.7 (14) 11.4–11.9	11.3 (16) 10.6–11.8	10.7 (5) 10.4–10.8
DBC	7.0	7.2 (18) 6.9–7.5	8.5 (2) 7.4, 9.7	7.2 (10) 6.9–7.6	7.3 (14) 7.1–7.8	7.3 (16) 6.7–7.8	7.2 (5) 7.0–7.5
IOB	3.6	3.8 (18) 3.5–4.1	3.9 (2) 3.8, 3.9	3.7 (10) 3.6–4.0	3.7 (14) 3.4–4.1	3.8 (16) 3.5–4.0	3.5 (8) 3.3–3.7
LPS	5.2	5.0 (18) 4.2–5.4	4.6 4.3–5.3	4.8 (10) 4.3–5.3	5.2 (14) 4.8–5.8	5.4 (16) 4.3–5.9	5.4 (7) 4.9–6.2
LR	7.6	8.3 (18) 7.7–8.8	8.5 (3) 8.0–9.1	7.6 (10) 6.9–8.0	8.1 (14) 7.5–8.7	8.5 (16) 7.5–9.0	7.2 (5) 7.0–7.8
BR	3.6	3.9 (17) 3.7–4.1	4.1 (3) 4.0–4.4	4.2 (10) 3.8–4.3	4.3 (14) 4.1–4.6	4.2 (16) 4.0–4.5	4.0 (5) 3.9–4.2
LN	7.6	8.4 (18) 7.5–9.2	8.9 7.0–8.0	7.5 (10) 7.0–8.0	8.3 (14) 7.5–8.9	8.7 (16) 8.0–9.8	7.5 (5) 7.3–7.6
BN	2.0	2.3 (18) 2.1–2.6	2.5 2.1–2.6	2.3 (10) 2.1–2.6	2.3 (14) 1.9–2.6	2.4 (16) 2.1–2.6	2.2 (5) 2.1–2.3
LD	5.4	5.8 (18) 5.5–6.1	6.4 5.4–6.1	5.8 (10) 5.4–6.1	5.9 (14) 5.3–6.2	6.2 (16) 5.7–6.8	5.5 (2) 5.3, 5.7
LIF	4.1	4.3 (18) 4.1–4.5	4.3 (3) 4.2–4.3	4.1 (10) 3.8–4.4	4.5 (14) 4.1–4.8	4.4 (16) 3.9–4.9	3.7 (8) 3.5–4.1
BIF	1.5	1.6 (18) 1.5–1.7	1.8 1.5–1.7	1.6 (10) 1.5–1.7	1.7 (14) 1.5–1.8	1.7 (16) 1.5–1.8	1.5 (2) 1.4, 1.6
LBP	3.3	3.5 (18) 3.1–3.8	4.0 (2) 3.9, 4.1	3.5 (10) 3.3–3.9	3.9 (14) 3.6–4.2	3.9 (16) 3.5–4.2	3.5 (8) 3.3–3.6
PPL	6.8	7.3 (18) 7.0–7.6	8.7 6.9–7.9	7.5 (10) 6.9–7.9	8.1 (14) 7.4–8.6	7.8 (16) 7.4–8.2	7.1 (2) 6.9, 7.4
BBP	4.3	4.5 (18) 4.1–4.7	5.1 4.3–4.7	4.5 (10) 4.3–4.7	4.8 (14) 4.7–5.1	4.8 (16) 4.7–5.0	4.3 (2) 4.3, 4.3
PDB	3.3	3.4 (18) 3.3–3.6	3.5 3.2–3.7	3.5 (10) 3.2–3.7	3.6 (14) 3.5–3.9	3.7 (16) 3.4–4.0	3.1 (4) 2.9–3.3
BMF	1.4	1.6 (18) 1.5–1.7	1.5 (2) 1.4, 1.5	1.5 (10) 1.3–1.7	1.6 (14) 1.4–1.9	1.6 (16) 1.4–1.8	1.5 (4) 1.5–1.6
BZP	1.3	1.4 (18) 1.3–1.6	1.5 (3) 1.5–1.6	1.5 (10) 1.3–1.6	1.7 (14) 1.4–1.9	1.5 (16) 1.3–1.6	1.3 (8) 1.2–1.4
LAB	3.4	4.0 (18) 3.7–4.1	4.1 3.4–3.6	3.5 (10) 3.4–3.6	3.9 (14) 3.7–4.2	3.8 (16) 3.5–4.2	3.5 (2) 3.4–3.5

TABLE 1
(Continued)

<i>tenuirostris</i> species group				<i>mexicanus</i> species group			
<i>R. musseri</i>				<i>R. "mexicanus"</i>			
Variable	new species	<i>R. microdon</i>	<i>R. rodriguezi</i>	<i>R. brevirostris</i>	<i>cherrii</i>	<i>garichensis</i>	<i>potrerograndei</i>
HIF	2.3	2.4 (18) 2.1–2.6	3.0	2.6 (10) 2.3–2.9	2.7 (14) 2.4–3.0	2.6 (16) 2.5–2.9	2.4 (8) 2.2–2.6
DI	1.01	1.04 (18) 0.92–1.11	1.13	1.10 (10) 0.95–1.23	1.28 (14) 1.10–1.41	1.11 (16) 1.02–1.20	1.09 (8) 1.00–1.20
BI	0.95	1.13 (18) 1.05–1.25	1.20	1.29 (10) 1.04–1.46	1.39 (14) 1.20–1.56	1.26 (16) 1.15–1.40	1.22 (8) 1.10–1.30
CLM	2.97	3.15 (18) 2.96–3.36	3.33	3.01 (10) 2.85–3.18	3.48 (14) 3.37–3.64	3.27 (16) 3.17–3.43	3.07 (6) 2.95–3.15
WM1	0.96	0.93 (18) 0.89–0.98	1.04	0.93 (10) 0.86–1.00	1.06 (14) 1.03–1.13	0.99 (16) 0.94–1.04	0.94 (6) 0.92–1.00

accessory enamel crests and tubercles in their upper molars. Hooper (1952) substantially amplified the unifying traits of the subgenus *Aporodon* and, in doing so, reapportioned certain species between the subgenera *Aporodon* and *Reithrodontomys*. Hooper’s view of the specific contents of *Aporodon* has been so far sustained as monophyletic in molecular analyses using cytochrome *b* sequences (Arellano et al., 2005). The essential subgeneric characteristics identified by Hooper (1952: 127–128) include: pelage long and lax, the upperparts dark in tone and reddish to tawny in hues; a tail longer than the head and body, usually monocolored and scantily covered with short hairs; toes of the hindfoot, especially digit 5, longer relative to the metatarsum, with larger cushiony plantar pads; braincase greatly inflated, extending to or beyond the lateralmost expanse of the zygomatic arches, and elongate relative to the rostral portion of the skull; zygomatic arches anteriorly squared, with a narrow zygomatic plate and indistinct dorsal notch; cusps of the upper molars opposite, their occlusal topography complex, including complete mesolophids and mesostyles/ids on the first and second molars; upper and lower third molars reduced in size but resembling a compact facsimile of the second molars in enamel configuration. Our examination of the specimen (LSUMZ 13227) from Cerro Asunción confirms these same morphological features in every detail.

Within the subgenus *Aporodon*, Hooper further defined two species associations, the

R. mexicanus species group (*R. brevirostris*, *R. gracilis*, *R. mexicanus*), and the *R. tenuirostris* group (*R. creper*, *R. microdon*, *R. rodriguezi*, *R. tenuirostris*). Unlike the several discrete character states that are useful for objectively segregating the subgenera, the features that distinguish the species groups are based on subtle shape contrasts of the cranium as perceived by Hooper (1952: 166): “Exceedingly long narrow rostrum, strongly constricted frontals, and bulbous braincase are features that set the *tenuirostris* group apart from the other species of *Aporodon*.” The cranium of LSUMZ 13227 is distinctive in its nearly tubelike anterior rostrum, which results from the comparatively longer nasals and the anteriorly extended contact between the nasals and premaxillae; its narrowly constricted, smoothly contoured interorbital region; and a globular braincase that exceeds the breadth of the weakly developed zygomatic arches (fig. 2). Such proportional traits are shared with members of the *R. tenuirostris* group but not with most members of the *R. mexicanus* group.

Among species of the *tenuirostris* group, the Cerro Asunción harvest mouse does not require critical comparison with examples of *R. creper* and *R. tenuirostris*, species that are easily discriminated solely in view of their size, by far the two largest within the genus (e.g., $T \geq 120$ mm, $HF \geq 22$ mm, $ONL \geq 24.5$ mm, $CLM \geq 3.9$ mm; as per Hooper, 1952: tables 6, 7). External proportions and cranial size also are sufficient to sort LSUMZ

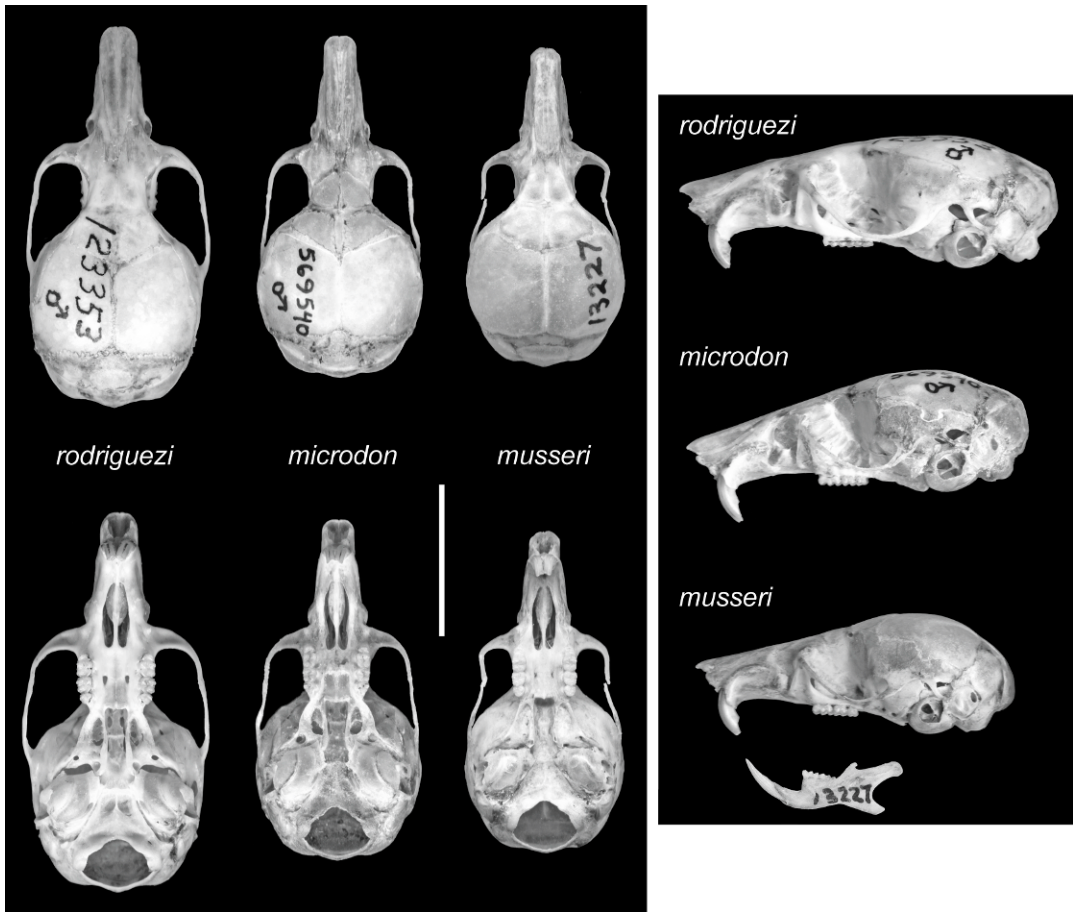


Fig. 2. Dorsal, ventral, and lateral views (ca. 2 \times ; bar = 10 mm) of adult skulls of Central American representatives of the *Reithrodontomys* (*Aporodon*) *tenuirostris* group: *R. rodriguezi* (UMMZ 123353, a male from Volcán Irazú, provincia de Cartago, Costa Rica); *R. microdon* (USNM 569540, a male from 5 km SW San Mateo Ixtatán, departamento de Huehuetenango, Guatemala); and *R. musseri*, n. sp. (LSUMZ 13227, holotype, a male from Cerro la Asunción, provincia de Cartago, Costa Rica).

13227 from specimens of *R. rodriguezi*, notwithstanding its erroneous past assignment to that species (McPherson, 1985). Examination of Goodwin's (1943) type and topotype of *R. rodriguezi* (AMNH 141194, 141195), simple inspection of crania and their univariate measurements (fig. 2, table 1), and ordinations of craniodental variables verify that LSUMZ 13227 represents a very different species, far removed from our single intact skull of *R. rodriguezi* in morphometric space (fig. 3). In overall size and some aspects of cranial shape, the Cerro Asunción animal, collected in the Cordillera de Talamanca of Costa Rica, most closely resembles samples

of *R. microdon* (fig. 2), a species known only from the highlands of southern Mexico and adjacent central Guatemala. The biogeographic improbability of such a fragmented range casts doubt on the homogeneity of the Costa Rican specimen with the Guatemalan species, and careful examination underscores fundamental morphological differences between them (see detailed comparisons under the new species account below). Although *R. microdon* is the smallest species of the *tenuirostris* group known to date, the Cerro Asunción specimen is still more petite in most dimensions measured (table 1). In both principal component and discriminant function

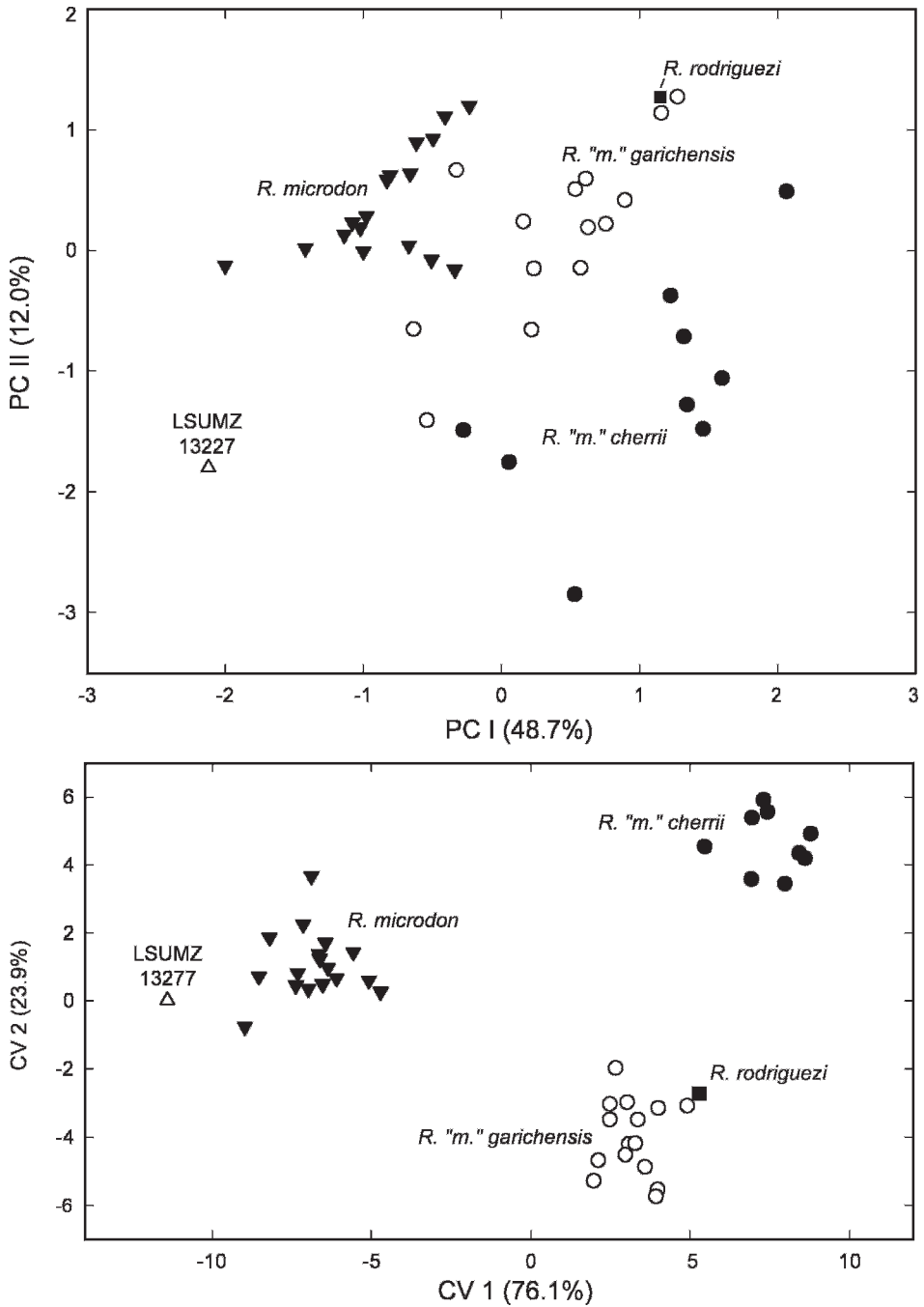


Fig. 3. Ordinations performed on 25 log-transformed craniodental variables, as measured on intact skulls ($N = 42$) representing selected taxa of Central American *Reithrodontomys* (*Aporodon*). **Top**, projection of individual scores onto the first two principal components (PC) extracted. **Bottom**, projection of individual scores onto the two canonical variates (CV) extracted from three-group discriminant function analysis; the Cerro Asunción specimen (LSUMZ 13227) and *R. rodriguezi* (UMMZ 123353) were entered as unknowns. See table 2 for variable correlations and percent variance explained.

TABLE 2
Results of Principal Component and Canonical Variate Analyses of Select Taxa of
Reithrodontomys (Aporodon) in Central America

(Correlations [loadings] of 25 log-transformed craniodental variables with derived factors are based on ordinations of 42 intact specimens; variable abbreviations are defined in Materials and Methods. See fig. 3.)

Variable	Correlations			
	PC I	PC II	CV 1	CV 2
ONL	0.91***	0.29	0.63***	−0.12
ZB	0.92***	−0.17	0.92***	0.00
BBC	0.74***	−0.16	0.63***	0.22
DBC	0.32*	0.02	0.27	−0.03
IOB	0.16	0.42**	−0.03	−0.19
LPS	0.23	−0.25	0.28	−0.27
LR	0.37*	0.82***	−0.06	−0.41**
BR	0.87***	0.07	0.73***	−0.16
LN	0.45**	0.69***	0.13	−0.41**
BN	0.30	0.81***	0.00	−0.31*
LD	0.60***	0.65***	0.29	−0.52***
LIF	0.39**	0.45**	0.12	0.07
BIF	0.47**	0.18	0.47**	−0.30
LBP	0.86***	0.08	0.72***	−0.15
PPL	0.90***	0.12	0.77***	−0.01
BBP	0.76***	0.07	0.77***	−0.36*
PDB	0.62***	0.10	0.60***	−0.28
BMF	0.08	0.42**	−0.03	0.00
BZP	0.78***	−0.11	0.58***	0.38*
LAB	0.21	0.13	0.00	0.37*
HIF	0.87***	0.01	0.71***	−0.06
DI	0.87***	−0.33*	0.76***	0.33*
BI	0.83***	−0.15	0.78***	0.01
CLM	0.81***	−0.24	0.77***	0.29
WM1	0.76***	−0.43**	0.85***	0.20
Eigenvalues	0.046	0.011	62.6	10.3
% Variance	48.7	12.0	85.8	14.2

*** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$ (attained probability levels are unadjusted).

analyses, LSUMZ 13227 falls at the extreme left margin of the first factor extracted (fig. 3), which generally grades specimens or samples in overall size (the loadings of many variables are large, positive, and highly significant on PC I and CV 1; table 2). In cranial shape, examples of *R. microdon* possess a notably longer rostrum (LR, LN, LD, LIF) and more inflated auditory bullae (LAB) compared with the Cerro Asunción specimen, and such variables largely account for the clear segregation of these two forms along the second principal component (fig. 3, top; table 2). Entered as an unknown in discriminant function analysis, including *R. microdon* and

two “subspecies” of *R. mexicanus* as prior defined groups, the a posteriori score of the Cerro Asunción specimen falls outside the variational sphere of *R. microdon*, although it is phenetically more closely associated with that species than with the examples of *R. mexicanus* (fig. 3, bottom).

Although LSUMZ 13227 cannot be assigned to any previously described species of the *tenuirostris* group, the possibility that it belongs with some taxon contained in the *mexicanus* group is considered next.

VARIATION IN COSTA RICAN AND PANAMANIAN *REITHRODONTOMYS (APORODON)*: After undertaking this study it quickly

became obvious that the specific diversity of *Reithrodontomys* in southern Central America is greater than one would assume from the literature (e.g., Hooper, 1952; Hall, 1981). As cautioned by Musser and Carleton (1993, 2005), all Middle American members of the genus deserve renewed systematic attention, and recent genetic studies have tellingly uncovered highly divergent clades that are inconsistent with current understanding of species limits (Sullivan et al., 2000; Arellano et al., 2003, 2005, 2006). Based on mitochondrial DNA evidence (cytochrome *b* sequences), Arellano et al. (2005) elevated *cherrii* Allen (1891), a Costa Rican form conventionally treated as a subspecies of *R. mexicanus*, to full species. In view of this emerging taxic complexity and in order to verify that no earlier name exists for the Cerro Asunción harvest mouse, we critically compared it with other montane taxa of the *mexicanus* species group in central Costa Rica and western Panama, namely *R. brevirostris* and the three subspecies of *R. mexicanus* as recognized by Hooper (1952)—*R. m. cherrii*, *R. m. garichensis*, and *R. m. potrerograndei*.

In short, the uniqueness of the Cerro Asunción animal evident from straightforward comparisons of skins and skulls is just as apparent in morphometric analyses that include examples of the *mexicanus* species group from Costa Rica and Panama. Among the four *mexicanus*-group taxa of concern, LSUMZ 13227 does overlap the smaller forms (*R. brevirostris*, *R. m. potrerograndei*) in certain univariate dimensions (table 1), but the multivariate perspective underscores its fundamental proportional differences from them (fig. 4). Along with its diminutive size, notable proportional contrasts involve the relative elongation of the rostrum (LR, LN, LD) and delicate structure of the incisors (DI, BI), variables that load heavily on the second principal component (table 3). Our taxonomic comparisons, supplemented by the various multivariate demonstrations of phenetic divergence, convince us that the Cerro Asunción specimen represents an unrecognized species of *Reithrodontomys*.

What strikes us as more remarkable, however, is the pronounced separation that we encountered between the so-called sub-

species of *R. mexicanus* that Hooper (1952) recognized in Costa Rica and Panama. Their clear-cut distinction was immediately apparent based on our initial inspection of skins and skulls and is reflected in their strong differentiation in morphometric analyses. In the subsequent paragraphs, we review these taxa so long associated with *R. mexicanus* (*cherrii*, *garichensis*, *potrerograndei*), together with *R. brevirostris* and *R. rodriguezi*, and summarize our understanding of their morphological definition.

(1) *Hesperomys cherrii*³ Allen (1891) is the oldest form of *Reithrodontomys* named from Costa Rica (type locality: San José). Once the matter of its identification as a *Peromyscus* or *Reithrodontomys* was settled by lectotype designation (Osgood, 1907; see summary by Hooper, 1952: 153–154), the name was thereafter used to denote a well-marked subspecies of *R. mexicanus* (Howell, 1914; Hooper, 1952; Hall, 1981) until that taxon was resurrected as a species by Arellano et al. (2005).

³ Joel A. Allen (1891: 211) described a new species of mouse from Costa Rica as *Hesperomys* (*Vesperimus*) *cherrii*, which he named in honor of George K. Cherrie (1865–1948), an early naturalist and frequent collector for the American Museum of Natural History. Allen (1893: 238) afterward emended the spelling in the name combination *Sitomys cherriei* and cited *Hesperomys* (*Vesperimus*) *cherrii* as a synonym, but he (1895: 140) later repeated the original spelling in the name combination *Hesperomys* (*Vesperimus*) (= *Peromyscus*) *cherrii*. Both spellings are found in the subsequent literature into the 1950s, often with the alternative spelling cited in synonymy. In the two authoritative revisions of *Reithrodontomys*, Howell (1914: 73) employed *cherrii*, whereas Hooper (1952: 152) favored *cherriei*; neither author explained their orthographical choice. Beginning with Miller and Kellogg (1955), however, Allen's original spelling has been the common usage whether the taxon is recognized as a subspecies or species (Hall and Kelson, 1959; Hall, 1981; Musser and Carleton, 1993, 2005; Arellano et al., 2003, 2005).

Although Allen's (1893) deliberate subsequent use of *cherriei* is the prescribed formulation of a patronym according to today's ICZN (1999, Article 31.1.2), his (1891) original spelling as *cherrii* was correct insofar as personal surnames were variously latinized in the early descriptive literature (e.g., Nicolson, 1974). Allen's substitute epithet *cherriei* must be considered an unjustified emendation (Article 33.2.3), and its use by him and others constitutes an incorrect subsequent spelling (Article 33.3). We regard *cherrii* as the legitimate spelling in view of the Code's predisposition to preserve correct original spellings (Articles 31.1.3, 32.3; also see Brandon-Jones et al., 2007), its concern to avoid equivocation over the single "i" versus double "ii" termination (Article 33.4), and the clearly prevailing usage of *cherrii* over the past half century.

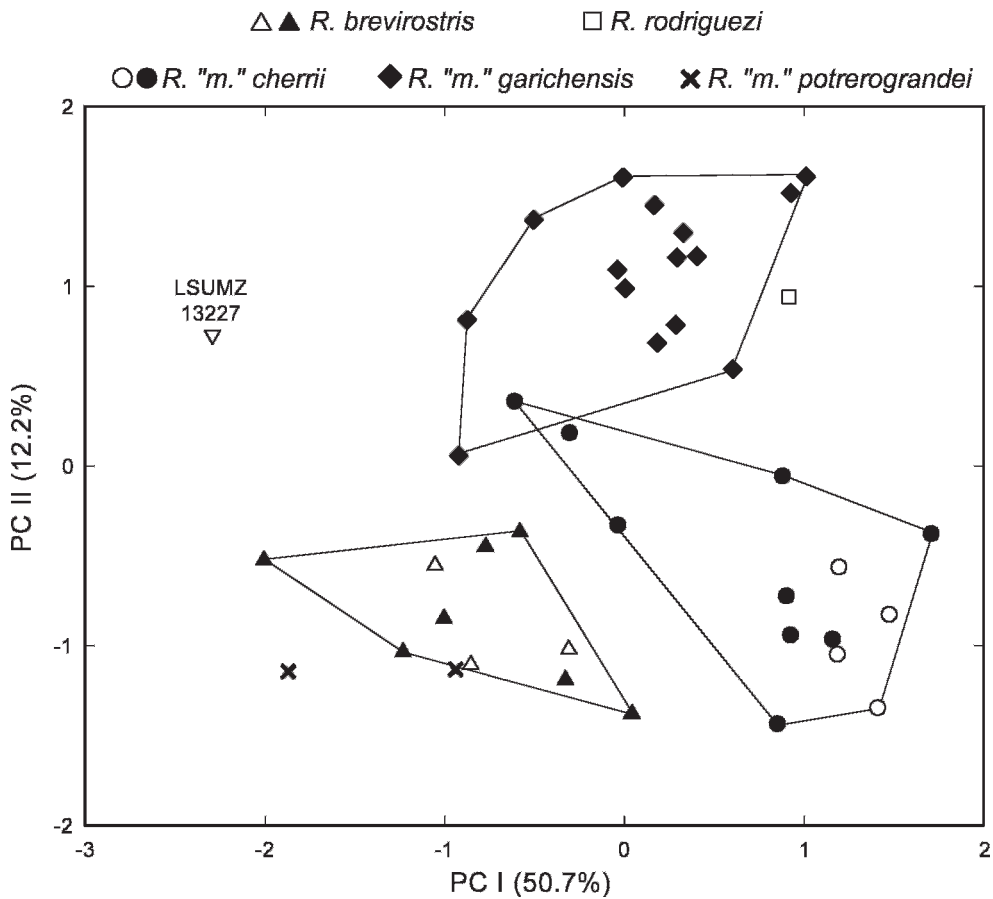


Fig. 4. Projection of specimen scores onto first two axes extracted from principal component (PC) analysis of 25 log-transformed variables, as measured on intact skulls ($N = 42$) representing selected taxa of *Reithrodontomys* (*Aporodon*) in Costa Rica and Panama. Maximally inclusive polygons are drawn for the three largest taxonomic samples (*brevirostris*, *cherrii*, *garichensis*) to visually emphasize their morphometric footprint. The open symbols for *cherrii* and *brevirostris* represent factor scores of vouchers used in the studies of Arellano et al. (2003, 2005); see text for discussion and table 3 for variable correlations and percent variance explained.

In their allozyme study of Mexican and Central American *Reithrodontomys*, Arellano et al. (2003) identified four specimens from 1 km SW Poás, provincia de San José, Costa Rica, as *Reithrodontomys* sp. B, which they believed to represent the taxon *R. mexicanus cherrii* and considered its possible recognition as a species. Arellano et al. (2005, 2006) later formalized this conclusion based on phylogenetic interpretations of cytochrome *b* sequences, using two of the four Costa Rican specimens that they had mentioned in their earlier report. We have examined all four

voucher specimens (LSUMZ 25164–5, 25375–6) and concur with their determination as *cherrii* Allen (1891). The small series displays the body size, pelage color, and cranial characteristics typical of the morphology that we understand as *cherrii*, as acquired from examination of some of the same specimens and localities that Hooper (1952) allocated to the taxon, including one topotype from San José (USNM 38525). In principal component analyses of craniodental data, the four molecular vouchers associated closely with other specimens of *cherrii* and

TABLE 3
Results of Principal Component Analysis of *Reithrodontomys (Aporodon)* from Costa Rica and Panama

(Correlations [loadings] of 25 log-transformed craniodental variables with derived principal components are based on ordination using 42 intact specimens; variable abbreviations are defined in Materials and Methods. See fig. 4.)

Variable	Correlations	
	PC I	PC II
ONL	0.96***	0.17
ZB	0.93***	−0.10
BBC	0.79***	0.03
DBC	0.29	0.04
IOB	0.41***	0.31*
LPS	0.21	0.43**
LR	0.78***	0.50***
BR	0.75***	−0.06
LN	0.74***	0.51***
BN	0.60***	0.15
LD	0.68***	0.35*
LIF	0.82***	0.17
BIF	0.46**	0.33*
LBP	0.79***	0.24
PPL	0.91***	−0.07
BBP	0.77***	0.41**
PDB	0.48**	0.40**
BMF	0.38*	0.22
BZP	0.84***	−0.36*
LAB	0.66***	0.34*
HIF	0.74***	−0.20
DI	0.78***	−0.51***
BI	0.70***	−0.53***
CLM	0.80***	0.08
WM1	0.74**	−0.01
Eigenvalues	0.055	0.013
% Variance	50.7	12.2

*** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$ (attained probability levels are unadjusted).

are phenetically removed from examples of *R. brevirostris* and the other Costa Rican subspecies of *R. mexicanus* (*garichensis* and *potrerograndei*; figs. 4, 5). The four specimens do plot toward the periphery of the elliptical constellation of scores that represent *cherrii*, but such a morphometric disposition is consistent with their advanced age (we graded three of the four as old adults based on tooth wear and the fourth as a full adult).

Examples of *cherrii* portray a relatively large and brightly colored harvest mouse, the

largest among the three former “subspecies” of Costa Rican *R. mexicanus* and approaching or overlapping *R. rodriguezi* in many craniodental measurements (table 1). The dorsal pelage is dominated by vibrant ochraceous-tawny hues, especially along the flanks, over the shoulders, and on the cheeks (Hooper, 1952, likened its pelage appearance to the golden mouse, *Ochrotomys nuttalli*). The color pattern of the dorsal metatarsum, as noted by Enders and Pearson (1940), is distinctive in *cherrii* and useful for segregating it from similarly sized *R. (Aporodon)* in Costa Rica. The white hairs that clothe the dorsal phalanges extend onto the metatarsum and accentuate a medial dark brown stripe, whereas the dorsal metatarsum in *brevirostris* and *garichensis* is generally dusky overall and lacks such distinctly white edges. The skull of *cherrii* is distinguished by its overall robust size and evenly arched dorsal profile, especially over the braincase and occiput; it is notably broad across the braincase and zygomata but has a proportionally shorter rostrum (figs. 6, 7A). The molar rows of *cherrii* are long ($CLM \approx 3.4\text{--}3.6\text{ mm}$) and its upper incisors are stoutly built and decidedly opisthodont in shape (fig. 7A). All such size and shape traits contributed prominently to the definition and cohesion of *cherrii* in the various multivariate analyses. Of particular significance are its broader braincase, shorter rostrum, and heavier dentition relative to *garichensis* (figs. 3, 4; tables 2, 3), and its uniformly larger size, exceedingly robust molars, and inflated auditory bullae compared with *brevirostris* and *potrerograndei* (fig. 5; table 4).

Reexamination of museum material must be conducted to clarify the distributional limits of *cherrii*. Hooper (1952) supposed that *cherrii* would be found to intergrade with *garichensis* somewhere within the Cordillera de Talamanca, but specimens that we have examined from the western Talamancas in Costa Rica are either *garichensis* or *garichensis*-like in form (see next). We have not examined type material of *costaricensis* Allen (1895), but Allen’s description, the location of its type locality (Cerro La Carpintera, provincia de Cartago), and Hooper’s (1952) judgment solidify its classification as a junior synonym of *cherrii*. Based on Hooper’s

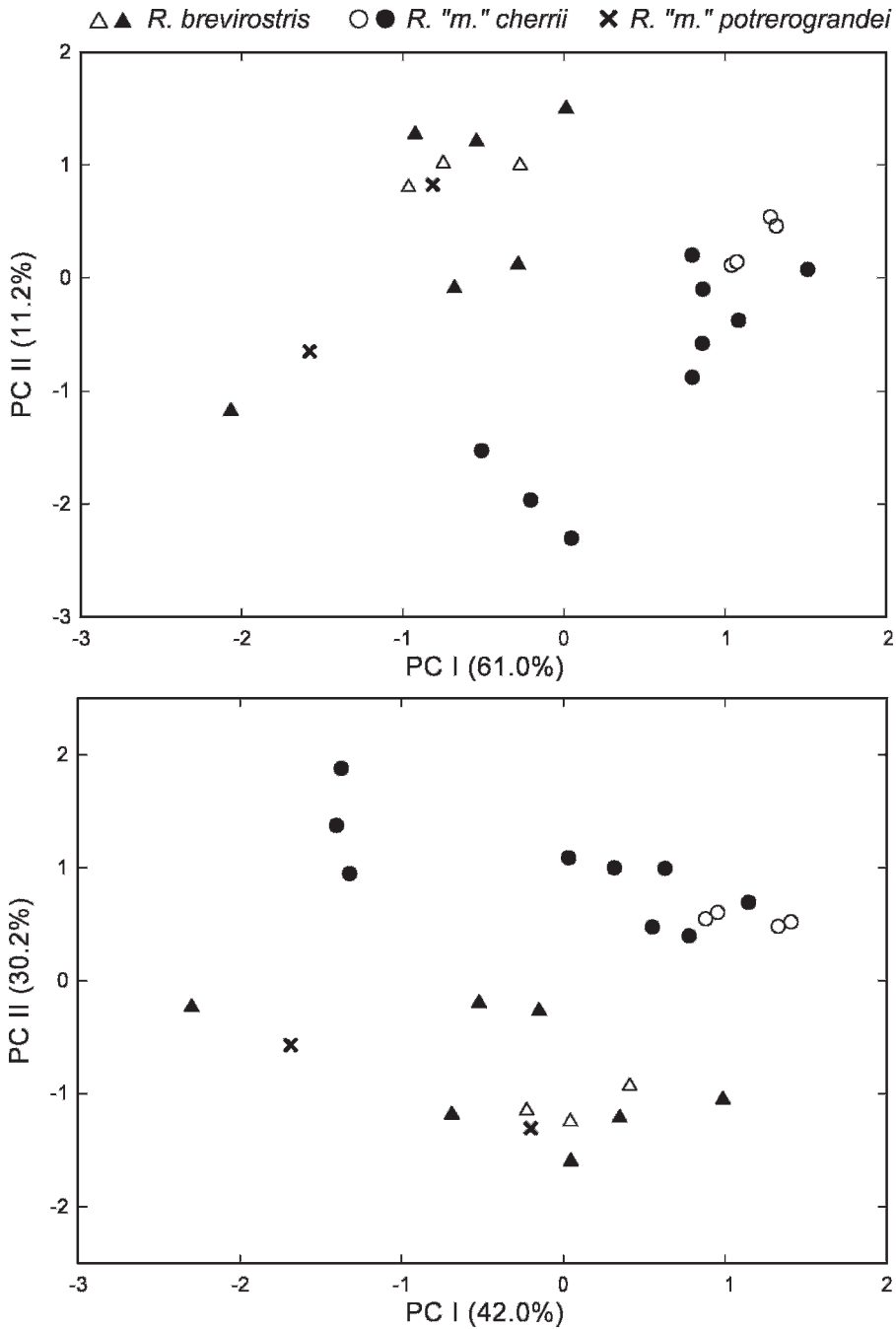


Fig. 5. Projection of specimen scores onto first two axes extracted from principal component (PC) analysis of 25 log-transformed variables, as measured on intact skulls ($N = 25$) representing selected taxa of *Reithrodontomys* (*Aporodon*) in Costa Rica. **Top**, dispersion of scores on the unrotated components. **Bottom**, dispersion of scores after varimax rotation procedure. The open symbols represent factor scores of vouchers used in the molecular studies of Arellano et al. (2003, 2005); see text for discussion and table 4 for variable correlations and percent variance explained.

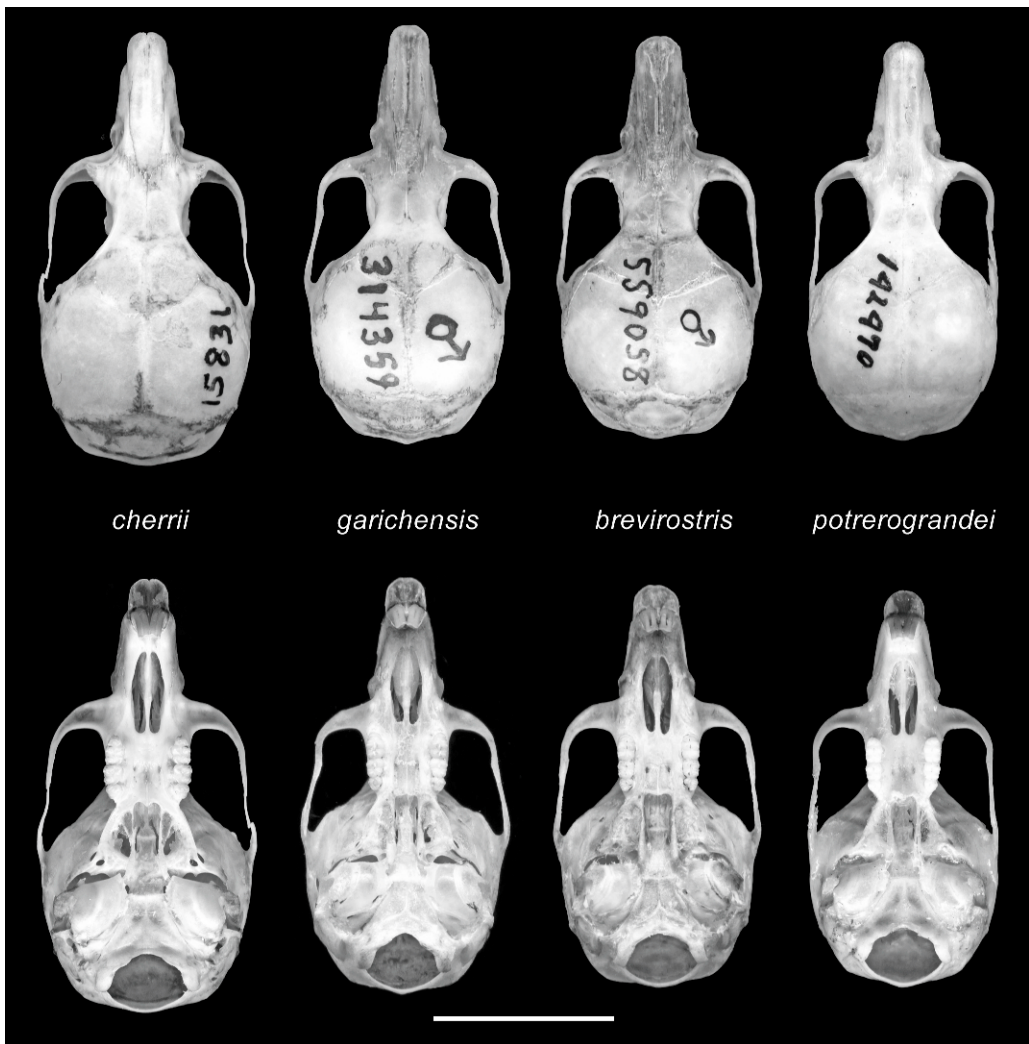


Fig. 6. Dorsal and ventral views (ca. 2 \times ; bar = 10 mm) of adult skulls of selected Central American representatives of the *Reithrodontomys* (*Aporodon*) *mexicanus* group: *R. cherrii* (LSUMZ 15831, a female from 2 km E San Ramón de Tres Ríos, provincia de Cartago, Costa Rica); *R. garichensis* (USNM 314359, a male from Cerro Punta, provincia de Chiriquí, Panama); *R. brevirostris* (USNM 559058, a male from Monteverde, provincia de Puntarenas, Costa Rica); and an original topotype of Goodwin's (1945) *R. mexicanus potrerograndei* (AMNH 142470, a male from Agua Buena, provincia de Puntarenas, Costa Rica), here allocated to *R. brevirostris*.

(1952) samples and specimens seen by us, the distribution of *cherrii* appears to be confined to the Valle Central of Costa Rica and contiguous middle-elevation slopes of the cordilleras Central and Talamanca.

(2) Enders and Pearson (1940) described *R. mexicanus garichensis* from western Panama (type locality: 5 mi SW El Volcán, Río

Gariché, provincia de Chiriquí), and the form has been thereafter retained as a diagnosable subspecies of a widely distributed *R. mexicanus* (Hooper, 1952; Handley, 1966; Hall, 1981). Enders and Pearson (1940) initially reported *garichensis* only from the type locality, but Hooper (1952) enlarged its known range within the Chiriquí region of

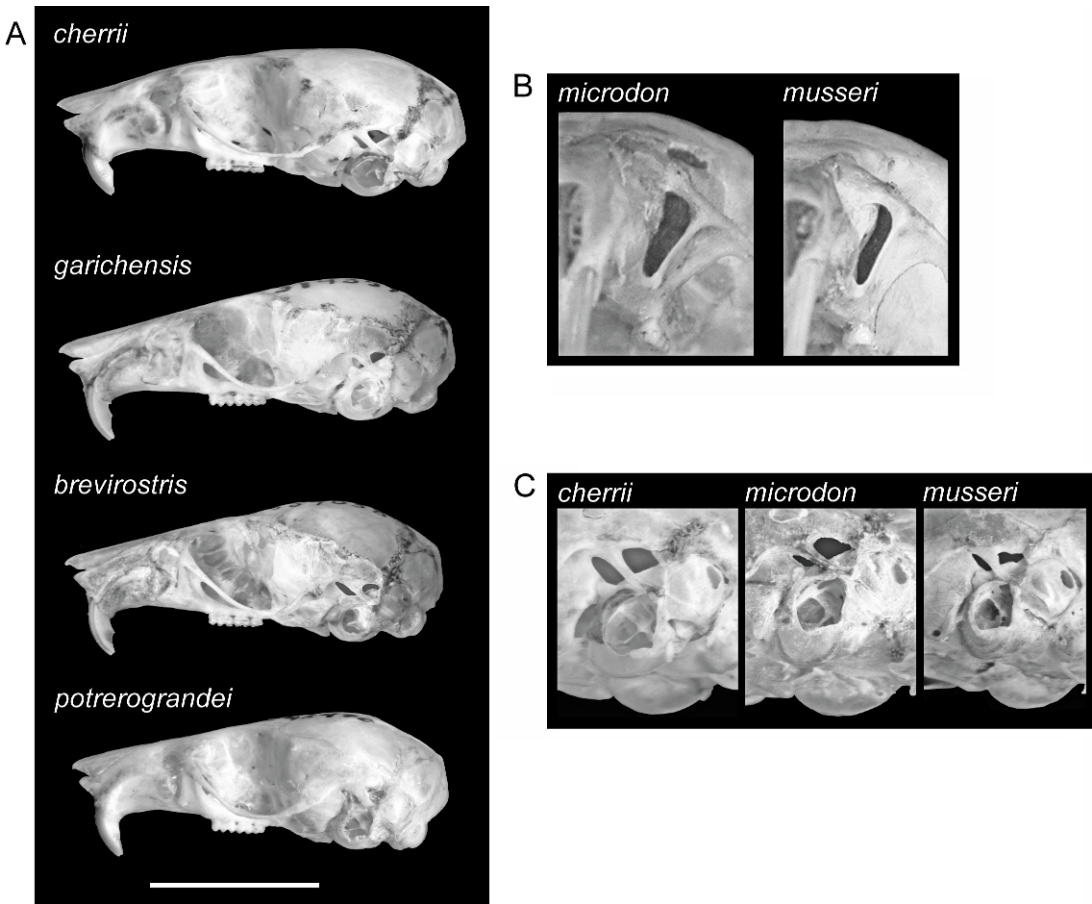


Fig. 7. Skulls of selected Central American representatives of *Reithrodontomys* (Aporodon): **A**, lateral views of the skulls of *R. cherrii*, *R. garichensis*, *R. brevirostris*, and an original topotype of *R. mexicanus potrerograndei* (see fig. 6 for catalog numbers and localities; bar = 10 mm); **B**, frontal view comparing the conformation of the infraorbital foramen in examples of *R. microdon* (USNM 569540 from 5 km SW San Mateo Ixtatán, departamento de Huehuetenango, Guatemala) and *R. musseri*, n. sp. (LSUMZ 13227, holotype from Cerro la Asunción, provincia de Cartago, Costa Rica); **C**, lateral view of bullar region in examples of *R. cherrii* (LSUMZ 15833 female, from 2 km E San Ramón de Tres Ríos, provincia de Cartago, Costa Rica), *R. microdon* (USNM 569540 from 5 km SW San Mateo Ixtatán, departamento de Huehuetenango, Guatemala), and *R. musseri*, n. sp. (LSUMZ 13227, holotype from Cerro la Asunción, provincia de Cartago, Costa Rica).

western Panama and expected that it would be found to occur in southeastern Costa Rica.

Examples of *garichensis* are similar in size to those of *cherrii*; however, the dorsal color is generally duller and darker in all pelages, the unicolored tail is relatively longer (table 1), and the hindfoot lacks the bright white edging observed in *cherrii* (Enders and Pearson, 1940). Although the cranium in specimens of *garichensis* is as long as that of

cherrii, its build is appreciably lighter (fig. 6)—the rostrum is narrower and comparatively elongate, the braincase and zygomatic arches are not so broad, and the tooth row is shorter (CLM \approx 3.2–3.4 mm) and narrower (table 1). Variables measured on the facial region of the cranium (LR, LN, LD) routinely correlated strongly with the second factor extracted and emphasized discrimination of specimens of *garichensis*

TABLE 4
Results of Principal Component Analyses of Select Taxa of the *Reithrodontomys*
mexicanus Species Group in Costa Rica

(Correlations [loadings] of 25 log-transformed craniodental variables with derived factors are based on ordinations of 25 intact specimens; variable abbreviations are defined in Materials and Methods. See fig. 5.)

Variable	Unrotated Correlations		Varimax Rotation Correlations	
	PC I	PC II	PC I	PC II
ONL	0.98***	0.05	0.79***	0.56**
ZB	0.96***	−0.12	0.68***	0.70***
BBC	0.85***	−0.47*	0.37	0.89***
DBC	0.11	−0.33	−0.13	0.32
IOB	0.30	−0.08	0.20	0.28
LPS	0.31	−0.62***	−0.13	0.71***
LR	0.91***	0.25	0.87***	0.37
BR	0.71***	0.29	0.73***	0.21
LN	0.92***	0.03	0.73***	0.53**
BN	0.53**	0.59**	0.79***	−0.12
LD	0.69***	0.62***	0.93***	−0.06
LIF	0.89***	0.13	0.78***	0.45*
BIF	0.31	0.05	0.28	0.17
LBP	0.83***	−0.27	0.47*	0.71***
PPL	0.92***	0.19	0.83***	0.42*
BBP	0.83***	−0.32	0.46*	0.79***
PDB	0.45*	−0.20	0.24	0.47*
BMF	0.36	−0.10	0.18	0.22
BZP	0.95***	−0.02	0.73***	0.58**
LAB	0.69***	−0.58**	0.18	0.88***
HIF	0.73***	0.40*	0.83***	0.16
DI	0.92***	0.00	0.72***	0.56**
BI	0.77**	0.46*	0.89***	0.13
CLM	0.83***	−0.47*	0.36	0.89***
WM1	0.85***	−0.39	0.43*	0.83***
Eigenvalues	0.070	0.013	0.048	0.034
% Variance	61.6	11.2	42.0	30.2

*** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$ (attained probability levels are unadjusted).

and *cherrii* along that axis (figs. 3, 4; tables 2, 3). Although the dorsal pelage of *garichensis* is not as vibrant as that of *cherrii*, it tends to be more brightly colored than the somber appearance of geographically contiguous *potrerograndei*. Furthermore, *garichensis* averages larger than that form (and *brevirostris*) in most craniodental measurements (table 1) and notably contrasts in the absolute and proportional length of its rostrum (figs. 6, 7A). Rostral variables (LR, LN, LD) contributed significantly to dispersion of the specimens along the second principal component, which highlights the segregation of *garichensis* (fig. 4; table 3). The heft and

shape of the upper incisors are especially helpful for identifying specimens of *garichensis*. Hooper (1952: 156) described the upper incisors of this taxon as “erect (strongly decumbent in *cherriei*).” Whether one characterizes the upper incisors of *garichensis* as nearly orthodont or as weakly opisthodont (fig. 7A), their absolutely or relatively smaller girth (DI, BI) emerged as a consistently significant influence in the morphometric separation of *garichensis* from *brevirostris*, *potrerograndei*, and especially *cherrii* (figs. 3, 4; tables 2, 3).

The distributional limits of *garichensis* are uncertain. One encounters much discrepancy

among Enders and Pearson (1940), Goodwin (1945), and Hooper (1952) in their allocation of locality series to *cherrii*, *garichensis*, or *potrerograndei*. For example, Enders and Pearson (1940: 2) tentatively assigned a specimen (ANSP 18321) collected at 11,000 feet (3,300 m) in the crater of El Volcán, provincia de Chiriquí, Panama, to *R. mexicanus cherrii*; Hooper (1952: 158) referred it to *R. mexicanus garichensis* in his generic revision; and some museum worker later reidentified the specimen as *R. m. potrerograndei*. Gardner suspected that ANSP 18321 might represent a Panamanian specimen of the new species described here because both were collected at comparable elevations, but our examination confirms that it is not the same as LSUMZ 13227. While superficially similar to specimens from Goodwin's (1945) type series of *R. m. potrerograndei* in color pattern, ANSP 18321 is not that taxon, nor an example of *cherrii*, based on tail length and cranial size and shape. Instead, the specimen compares closely with another (USNM 566463) obtained in the vicinity of Villa Mills, near 3000 m, provincia de Cartago, Costa Rica. Verifying whether such uncertainties represent an undescribed taxon or taxa related to the *mexicanus* group or involve new elevational and geographic records of *garichensis* will require critical review of museum material from southeastern Costa Rica and western Panama. The equivocation over taxonomic identity may partly issue from undetected sympatry of *garichensis* and *potrerograndei*. As a parallel example, Carleton and Musser (1995) documented several places of sympatry between the upland *Oligoryzomys vegetus* and lower-elevation *O. fulvescens* and complex interdigitation of their ranges in this same region, involving many of the same localities that Enders and Pearson, Goodwin, and Hooper reported for *garichensis* or *potrerograndei*. Like Hooper (1952), we suspect that *garichensis* ranges farther west into southeastern Costa Rica, adhering to the wet montane forests of the Cordillera de Talamanca, but, in contrast to Hooper's surmise, we do not believe that it there intergrades with *cherrii*. Our preliminary examinations have not uncovered the *garichensis* morphology in the Cordillera

Central or on mountains and volcanoes farther west in Costa Rica.

(3) We consider *brevirostris* and *potrerograndei* together because of their comparably small size and other morphological resemblances. Goodwin named both forms, *brevirostris* (1943) as a full species (type locality: Laja Villa Quesada, provincia de Alajuela, Costa Rica) and *potrerograndei* (1945) as a subspecies of *R. mexicanus* (type locality: Agua Buena, provincia de Puntarenas, Costa Rica). Hooper (1952) retained each at those same ranks, but, in the course of his taxonomic comparisons, he regularly noted similarities between the two, particularly as they jointly differ from *cherrii*. We examined Goodwin's (1943) three original topotypes of *R. brevirostris* and most of his (1945) type series of *R. mexicanus potrerograndei* (see appendix 1); many skulls of the latter taxon are badly damaged, however, and only two specimens were sufficiently intact to include in our multivariate analyses.

Arellano et al. (2005) utilized a second sample of the *mexicanus* complex from Costa Rica (Colima Tapanti, provincia de Cartago), which basally grouped with the large clade that they identified as *R. mexicanus* proper. This specimen (MVZ 174401) was apparently identified on the basis of its molecular affinity since it is a whole carcass preserved in fluid and is still called *R. sumichrasti* within the MVZ collection. The cleaned skulls of the molecular voucher and two others from the same locality (MVZ 174402–3) indicate that they are representatives of the Costa Rican species *R. brevirostris* and possess the truncate rostrum, flat cranial profile, and dainty molars that are definitive traits of the species. Accordingly, such dimensions, along with others reflective of small size, associate these specimens among known examples of *R. brevirostris* in the various principal component analyses (figs. 4, 5).

Diminutive appearance of the skin and skull serve to distinguish *brevirostris* and *potrerograndei* from specimens of *cherrii*, but size contrasts are generally less dramatic compared with those of *garichensis* (table 1). In general tone and expression of reddish-orange hues, specimens of *brevirostris* and *potrerograndei* are the most dully colored,

garichensis intermediate, and *cherrii* the brightest. As noted by Hooper (1952), the tail appears to be relatively longer in *brevirostris* compared with the larger *cherrii*. Our measurements (table 1) are consistent with such a proportional difference between the two (and *potrerograndei*), but sample sizes must be amplified to statistically substantiate the contrast. Compared with *cherrii*, the skulls of *brevirostris* and *potrerograndei* have a squat, boxy look, an impression conveyed by their flatter dorsal profile over the rostrum and orbit, less globose braincase, and more parallel sided and anteriorly squared zygomatic arches (figs. 6, 7A). In absolute size, the rostrum of *brevirostris* (and *potrerograndei*) is, true to its specific epithet, shorter than that of *cherrii*, but its proportion relative to cranial length is about the same (LR ca. 33%–34% of ONL). The rostrum in examples of *garichensis*, on the other hand, is longer, both absolutely and relatively (LR ca. 36% of ONL), than all three of those taxa. In ventral view, the smaller size of *brevirostris* and *potrerograndei* is notably evidenced by the tiny auditory bullae and short molar rows (CLM \approx 2.9–3.2 mm). The curvature of the upper incisors is basically opisthodont in *brevirostris* and *potrerograndei*, resembling *cherrii* but much less robust; as discussed above, the recurved incisor shape is useful for distinguishing all three taxa from samples of *garichensis*. In *brevirostris* and *potrerograndei*, the upper first molar is rectangular in outline. The squarish front end and consequent rectangular shape reflect configuration of the anterocone, which consists of distinct anterolabial and anterolingual conules divided by an anteromedian cleft; in specimens with lightly worn teeth, the anterolabial conule appears larger than its anterolingual companion. In examples of *cherrii*, the upper first molar is more oval shaped, its anterocone somewhat narrower and not conspicuously bilobate; the anterior rim of the anterocone is smooth, not creased with a median fold, although in some specimens there is an isolated anteromedian island. The shape of the upper first molar in *garichensis* resembles that of *cherrii*, but labial and lingual conules are more strongly indicated, including regular occurrence of an isolated median island. In principal component anal-

ysis, examples of *brevirostris* and *potrerograndei* overlap the younger and smaller specimens of *cherrii* on PC I but are jointly segregated from *garichensis* on PC II (fig. 4); as with *cherrii*, proportional rostral length (LR, LN, LD) and incisor development (DI, BI) contribute heavily to dispersion of scores along the second principal component (table 3). Confined to principal component analysis using only *cherrii*, *brevirostris*, and *potrerograndei*, samples of the latter two taxa are wholly isolated from those of *cherrii* (fig. 5); consistently smaller size, narrower zygoma and braincase, shorter rostrum and auditory bulla, and diminutive molar rows are among the many cranial features that account for the pronounced hiatus evident along PC II (table 4). These same ordinations supply no clear-cut separation of *brevirostris* and *potrerograndei*, although sample sizes are regrettably small.

In view of the extensive similarities between *brevirostris* and *potrerograndei*, many of them also remarked on by Hooper (1952), it is curious that he retained one as a species and arranged the other as a subspecies of the widely distributed *R. mexicanus*. His taxonomic decisions were undoubtedly guided by the geographic samples available at the time, by his predisposition to express interpopulation differences as geographic variation and intergrading races, as was the revisionary practice during the middle of the 20th century, and by his generous application of the biological species concept. To the north, along Caribbean-facing, middle-elevation slopes of the Cordillera de Talamanca, Hooper had vouchered evidence of the sympatric occurrence (Estrella de Cartago) of *brevirostris* and the very different *cherrii*. To the south, *potrerograndei* was separated from *cherrii* by an extensive unsurveyed gap in the western Cordillera de Talamanca (see Hooper, 1952: map 8). He therefore supposed that the smaller *potrerograndei* would be found to intergrade with the intermediate-sized, geographically contiguous *garichensis* and, through it, with the larger *cherrii*. The three localities available to Hooper (1952: 163) led him to interpret the geographic range of *R. brevirostris* as “confined to the Caribbean watershed.” Our preliminary inspection of museum material slightly broad-

ens the known distribution of *R. brevirostris*: a USNM series from Monteverde⁴, which lies in the Cordillera de Tilaran, extends its range about 45 km west of the type locality (Villa Quesada); the MVZ series from Colima Tapanti, which is situated on the northwestern slopes of the Cordillera de Talamanca, extends its eastern limits about 18 km east of Estrella de Cartago. The Monteverde locality sits astride the continental divide, and it seems plausible that further survey or examination of museum material collected after Hooper's (1952) study will disclose the occurrence of *R. brevirostris* along Pacific-facing slopes as well, closer to the known range of the morphologically similar *potrerograndei* in southeastern Costa Rica.

(4) The species *R. rodriguezi* Goodwin (1943) is rare in museum collections, and our examinations lead us to concur with past studies that have retained the taxon as a valid species (notably Hooper, 1952). Divorced of the specimen herein described as *R. musseri* (called *R. rodriguezi* by McPherson, 1985), the species distribution is documented only from the upper slopes of Volcán Irazú in the Cordillera Central. Goodwin (1943) thought that *R. rodriguezi* was closely related to *R. tenuirostris*, but Hooper (1952) tentatively considered it to be phyletically nearest to *R. creper*. Although we omitted both of those species in our morphometric comparisons, we are impressed by the regular affinity displayed by *R. rodriguezi* to specimens of *garichensis* (figs. 3, 4), the former slightly larger in size but comparable in shape to the latter (compare figs. 2 and 6).

SUMMARY AND TAXONOMIC RECOMMENDATIONS: We recognize *R. cherrii* (Allen, 1891) and *R. garichensis* Enders and Pearson

⁴ The specimens from Monteverde were originally reported as *Reithrodontomys gracilis harrisi* by Reid and Langtimm (1993) in their faunal report on certain Costa Rican small mammals. As one of three who supplied rodent identifications for their paper, the junior author wishes to apologize to those authors for the errant identification. At the time, my eye was insufficiently calibrated to discriminate the subtle features necessary to identify Middle American "reithros." Moreover, I failed to observe the cardinal rule in rendering any species determination: always first verify the accuracy of names used in the comparative collection consulted to supply an identification. As we have disturbingly discovered, curators have been lax in applying names subsequent to Hooper's (1952) revision and have failed to return to type material for substantiation of their use.

(1940) as valid species and provisionally associate *potrerograndei* Goodwin (1945) as a subjective synonym of *R. brevirostris* Goodwin (1943). The recognition of these additional species in Costa Rica and Panama is a defensible hypothesis based on morphology alone. To be sure, our sample sizes are small and age representation is uneven among them. Still, the exploratory multivariate results we obtained for the "subspecies" of *R. mexicanus* recall the morphometric signatures that have been recovered between closely related (congeneric) species of muroid rodents (Voss et al., 1990; Voss and Marcus, 1992; Carleton and Musser, 1995; Musser et al., 1998; Carleton et al., 1999, 2002; Patton et al., 2008). Noteworthy are the repeatedly oblique orientation of taxon constellations relative to the first two factors extracted, the parallel dispositions of their major axes, the sign and strength of correlations between the original variables and latent factors, and non- or barely overlapping dispersion of scores in principal component and especially canonical variate ordinations. The stability of the morphological differences and morphometric patterns consolidated above should be tested through expanded geographic examinations and analyses of larger samples.

Results of molecular studies, as they so far exist for these Costa Rican taxa—namely *R. brevirostris* and *R. cherrii* (Arellano et al., 2005, 2006)—underscore the genetic distinctiveness and distant phyletic affinity of these identifiable morphologies. In view of the morphological differentiation of *R. garichensis* relative to other *Aporodon* species that have been genetically analyzed, one anticipates that it too will exhibit comparably strong molecular divergence. Arellano et al. (2005, 2006) allocated their voucher (MVZ 174401) from Colima Tapanti to *R. mexicanus* proper, but we advise continued use of the regionally applicable name *R. brevirostris* in lieu of expanded geographic representation and denser taxon sampling in DNA studies. We suspect that the *R. mexicanus* crown clade (their clade I) revealed in the studies of Arellano et al. will prove to be a species complex.

After perusing *Reithrodontomys* specimens from Costa Rica and Panama, our impression is that, subsequent to Hooper's (1952)

classic revision, names such as *cherrii*, *garichensis*, and *potrerograndei* have been applied indiscriminately as newly collected specimens were accessioned into museums (including our own!). Such loosely considered identifications have obscured the morphological definition of these taxa and the cohesiveness of their distributions. We have initiated review of that material.

Although such a review should be undertaken to augment knowledge of *Reithrodontomys* taxonomy and distribution in Middle America, present evidence makes clear that the Cerro Asunción specimen represents a previously unknown taxon allied with the *tenuirostris* group (sensu Hooper, 1952) that we are pleased to name as:

***Reithrodontomys musseri*, sp. nov.**

Figures 2, 8; table 1

Musser's Harvest Mouse

Reithrodontomys rodriguezi, McPherson, 1985: 244; part.

HOLOTYPE: Adult male, LSUMZ 13227, caught and prepared by A.L. Gardner, field catalog number 9787, on 20 December 1966. The holotype is the only known specimen and consists of a skin and skull. The skull is intact except for broken zygomatic arches and damage to pterygoid processes; the skin is in good condition.

TYPE LOCALITY: Cerro Asunción, ca. 11,100 feet (3,300 m), provincia de Cartago, Costa Rica; ca. 09°34'05"N, 83°44'12"W (the coordinates define a place along the east side of the Panamerican Highway, just 0.4 km WNW of the peak of Cerro La Asunción—09°34'N, 83°44'W).

DISTRIBUTION: This species is known only from the type locality (see fig. 1).

DIAGNOSIS: *Reithrodontomys musseri* is a small, long-tailed harvest mouse belonging to the *tenuirostris* species group (sensu Hooper, 1952), subgenus *Aporodon*, and is most similar to *R. microdon* of the highlands of Chiapas, México, and the central highlands of Guatemala (figs. 2, 8). The color of the body is dark, especially dorsally from the top of the head to the base of the tail, but conspicuously paler and brighter along the sides. The venter is whitish pale buff with the gray basal color of the hair readily apparent

in the prepared skin. It is among the smallest of Neotropical *Reithrodontomys* (total length = 161 mm, tail = 99 mm) and has a small, delicate skull (ONL = 21.1 mm, CLM = 3.0 mm) with a relatively long, slender rostrum, weak zygomatic arches, and a conspicuously globose braincase (fig. 2). The rostrum is slightly concave in lateral profile and lacks a midventral keel behind the incisors. Nasals are depressed posteriorly along their contact and in the region of the nasal-frontal-premaxillary sutures. The interorbital region is short, hourglass shaped, and lacks supra-orbital ridges or beading. The root capsules of upper incisors terminate below the lower margin of the infraorbital canal. The braincase is rounded posteriorly in lateral profile (lacks a prominent boss at supraoccipital-interparietal contact) and is wider than the breadth across the zygomatic arches. The lateral margins of parapterygoid fossae are low and nearly straight. Auditory bullae are small, anteroposteriorly short, and the upper anterior rim of the auditory meatus is neither conspicuously inflated nor expanded laterally.

DESCRIPTION: *Reithrodontomys musseri* is a small (table 1), dark harvest mouse with dense, soft, and slightly woolly fur. The tail is relatively long ($T \approx 61.5\%$ of TL), notably longer than the head and body (fig. 8). Fur measures 7.7 mm on lower back with guard hair about 2 mm longer. There is a single superciliary vibrissa above each eye that reaches about half way to the ear tip on the dried specimen. A single postorbital vibrissa behind each eye is much shorter and reaches just behind the base of the ear. Mystacial vibrissae are long (up to 32 mm in length), numerous, and some extend at least 11 mm beyond tips of the pinnae on the dried skin. The pelage is darkest on the top of the head and along the back where it approaches Sepia or Fuscous. The color becomes paler laterally, grading through Buffy Brown to Ochraceous Tawny and Buckthorn Brown on the rostrum, cheeks, outer surfaces of legs, and along the lower sides of the body. Under artificial light the overall color of the back approaches Buffy Brown finely lined with darker hairs (near Clove Brown). The hairs on the upper and lower lips and the upper throat are self-colored white. Guard hairs are blackish throughout, except over the rump



Fig. 8. Dorsal views ($\times 1$) of museum study skins of *Reithrodontomys musseri* (LSUMZ 13227, holotype, a male from Cerro la Asunción, provincia de Cartago, Costa Rica) and *R. microdon* (USNM 275464 from Chemal, departamento de Huehuetenango, Guatemala).

above the tail where they are conspicuously longer and white tipped. The ventral pelage is whitish with the basal gray color of the hair readily apparent. The hairs on the dorsal surface of each wrist are dark, near the same color as the back. A wide, dark median stripe extends over the ankle to the base of the toes and is bordered with self-colored white hair. Ungual tufts on fore- and hind feet and hair covering the toes and upper surfaces of the forefeet and the toes of the hind feet are white. The hind feet are short (19 mm in the fresh specimen, 16 mm dry) and the otherwise naked plantar surface is sparsely haired for the proximal 2.5 mm; the palmar surface is naked. The weakly bicolored tail is dark above and paler below and, although appearing bare to the naked eye, is completely clothed in short hair. The centers of the tail scales are pigmented all along the tail and show through the white hair on the ventral surface. These white hairs are longer than the dark hairs on the upper surface of the tail (approximately three scales long versus one and a half scale lengths, respectively).

The skull is small, delicate, and has a relatively long, slender rostrum and a conspicuously inflated cranium (fig. 2). The rostrum is slightly concave in dorsal profile, and the nasals are depressed posteriorly along their contact and in the region of the nasal-frontal-premaxillary suture. The rostral processes of the premaxillae are narrow and terminate behind the nasals. The ventral suture between the premaxillae and maxillae lies anterior to a plane corresponding to the anterior inferior borders of the infraorbital foramina. The upper margin of each infraorbital foramen is evenly arched. The infraorbital canal lacks a ventral groove (lower medial wall incomplete); the root capsule of the upper incisors terminates below the lower margin of the infraorbital foramen. The posterior margin of the zygomatic plate lies approximately at the same plane as the anterior surface of the first upper molars and the posterior margins of the incisive foramina; the zygomatic notch is shallow. The incisive foramina are relatively long (LIF $\approx 75\%$ of LD), extending posteriorly to the anterior plane of the upper first molars. The braincase is large, globose, rounded posteriorly in lateral profile, wider than the breadth

across zygomatic arches, and conspicuously overhangs the squamosal roots of the zygoma. The zygomatic arches converge anteriorly and the malar region (jugal) is relatively narrow. Auditory bullae are small and short anteroposteriorly, and the upper anterior rim of the meatus is not conspicuously inflated. Postglenoid and subsquamosal foramina are small. Paroccipital processes are small and each tip is oriented anteromedially in line with the basioccipital and basisphenoid-auditory bulla contact. The upper margin of the foramen magnum is low, the area of the foramen above the condyles is much wider than high, and the foramen magnum appears to be more ventrally placed than in other *Reithrodontomys* examined. The capsular process of the root of the lower incisor protrudes laterally and upward from the ramus (a shallow groove separates it above from the ridge behind the coronoid process).

The dentition of *R. musseri* is delicately constructed, the incisors small pincers and the molar rows short and narrow. The anterior face of the upper incisors is pale yellow and their curvature is weakly opisthodont; the lowers are also a pale yellow. The main molar cusps (protocone-paracone, hypocone-metacone) are nearly opposite in occlusal position. The upper first molar is oval, with slight indication of a bilobate anterocone but no anteromedian fold; the upper first and second molars bear a mesoloph of very low relief that terminates in a small labial style; the upper first molar also possesses an anteroloph; no enteroloph or enterostyles are present. The lower first and second molars have mesolophids but no ectolophids. The upper third molar is appreciably smaller than the second molar, more or less circular in outline and about one-half its occlusal area. The lower third molar is nearly as long as the second molar, about three-quarters its occlusal area, and lacks a mesolophid but has an ectostylid; a reduced but discrete entoconid is evident, and a posterofossetid is isolated between the entoconid and hypoconid as an enamel island.

COMPARISONS: Of the other known Costa Rican taxa of the *mexicanus* group (sensu Hooper, 1952), *R. musseri* is superficially most similar to paratypes of *R. mexicanus potrerograndei* (a junior subjective synonym

of *R. brevirostris*) in size and color pattern. Both are smaller and darker than Costa Rican *R. cherrii* and *R. garichensis* and the two southern Central American representatives of the *tenuirostris* group (*R. creper* and *R. rodriguezi*). The fur of *R. musseri* is long and soft, dense, and slightly woolly, whereas that of *R. brevirostris* is shorter, smoother, and lies flat. *Reithrodontomys musseri* also has a grayish face, duller dorsal pelage, sparsely haired heels, a weakly bicolored tail, and the basal gray band of the ventral fur is conspicuous. In *R. brevirostris*, the face is more rufous, dorsal pelage is brighter and more rufous (in adults), the proximal plantar surface is more conspicuously haired, the tail appears unicolored, and the venter is clearer white with little of the basal gray showing through. Cranially, *R. musseri* is easily distinguished from *R. brevirostris* by the shape of the rostrum (relatively longer and, in lateral view, slightly concave above and more tapering anteriorly). The rostrum of *R. brevirostris* is relatively shorter, has a convex dorsal profile, and does not taper as conspicuously (figs. 2, 6). The braincase of *R. musseri* is lower, but conspicuously more globose and is wider than the breadth of the zygomatic arches. In *R. brevirostris*, the braincase is longer, tapers anteriorly, is not conspicuously globose, and is narrower than the breadth across zygomatic arches. The jugal region is narrower in *R. musseri* and the anterior margin of the zygomatic plate is inclined posteriorly (78° to the occlusal plane of the molars). The malar region in *R. brevirostris* is wider and the anterior margin of the zygomatic plate is nearly vertical (approximates 90°) to the occlusal plane of the molars. The root capsule of each upper incisor terminates just below the base of the infraorbital canal in *R. musseri*, but above the base in *R. brevirostris*. The auditory bullae are smaller in both species than in other Central American *Reithrodontomys*, but the anterior upper rim of the meatus is more inflated and protrudes laterally in *R. brevirostris*.

Musser's harvest mouse is smaller than other Central American *Reithrodontomys* and differs from them in many of the same features that distinguish it from *R. brevirostris* (e.g., globose braincase, tapering slender

rostrum lacking a keel, narrower jugal region), with the exception of *R. microdon*, which is not known south of the highlands of Guatemala. Features of the skin of *R. musseri* are comparable to a series of 17 skins of *R. microdon* from Guatemala in most details of color pattern and size (fig. 8). The primary differences are in the dorsal color (darker in *R. musseri*), texture of the dorsal fur (slightly woolly in *R. musseri*), amount and length of hair on proximal plantar surface (short and sparse on proximal quarter versus longer, denser, and extending as far as thenar pad in *R. microdon*). The two species have similar dentitions and are similar in many cranial features including size, a broad braincase, long slender rostrum, relatively weak zygomatic arches, and long premaxillae that extend anteriorly nearly to the tips of the nasals. Comparisons between the single specimen of *R. musseri* and 19 Guatemalan *R. microdon* reveal several cranial differences that distinguish the two species (fig. 2). The rostrum of *R. musseri* is dorsoventrally narrower behind the incisors and lacks a ventral keel; the nasals are conspicuously depressed along their midline contact for the posterior half of their length; the lateral margins of the nasal are relatively straighter and less convergent posteriorly; and the nasals are narrower above the nasal capsules (1.5 mm versus an average of 1.8 mm [1.7–2.1 mm; $N = 19$]; measured across both nasals). In *R. microdon*, the rostrum is deeper behind the incisors and has a small keel; the nasals are broader, taper posteriorly, and are not conspicuously depressed along their medial contact. The upper margin of the infraorbital foramen (frontal view) is a smoothly curved arc in *R. musseri*, but in *R. microdon* the dorsolateral portion of the upper margin is flat (straight) and the inner margin is not an evenly curved arc (fig. 7B). The infraorbital canal lacks a continuous floor in *R. musseri*, although a floor is clearly present in 17 of 19 *R. microdon* and is incomplete in 2. The braincase is relatively broader and more globose in *R. musseri* and lacks the interparietal-supraoccipital boss evident in *R. microdon* of comparable and older age (based on tooth wear). The auditory bullae are conspicuously shorter and slightly flattened ventrally in *R. musseri*,

and the auditory meatus also is shorter anteroposteriorly than high (fig. 7C).

REMARKS: *Reithrodontomys musseri* joins a suite of small terrestrial mammals that are indigenous to the southern highlands of Middle America (McPherson, 1985, 1986; Carleton and Musser, 1995; Carleton et al., 2002). Situated in central Costa Rica and western Panama, these middle- to high-elevation mountains vary in geological age from the late Oligocene–Miocene to Plio–Pleistocene depending upon the range (Castillo-Munõz, 1983), harbor cool and perennially moist forests, and are widely isolated from similar upland environments in northern Nicaragua and northwestern Colombia. Collectively termed the Talamancan Province or Talamancan Highlands in biogeographic studies (Savage, 1982; Carleton et al., 2002), the generative contribution of this mountainous complex to the taxic diversity of small mammals in lower Middle America is certainly underappreciated as reflected in current classifications (e.g., see discussion in Carleton and Musser, 1995: 357–358). Some species are widely distributed across the Talamancan Highlands (e.g., *Oligoryzomys vegetus*, Carleton and Musser, 1995; *Reithrodontomys creper*, Hooper, 1952), whereas others are apparently confined to certain cordilleras within it (e.g., *Cryptotis endersi*, Choate, 1970; *Reithrodontomys rodriguezi*, this study). *Reithrodontomys musseri* may be an example of a narrowly distributed species, but appreciation of its geographic range will require renewed and dedicated faunal survey. Once their morphological identities, relationships, and distributions are refined, *R. cherrii*, *R. garichensis*, possibly another as yet undescribed *Reithrodontomys*, and certain forms now classified under *R. sumichrasti* will emerge as other harvest mice endemic to the Talamancan Highlands.

Although the single specimen of *R. musseri* exhibits key features of the *tenuirostris* species group, as classically defined by Hooper (1952), we regard this allocation as provisional. The larger issues involve the morphological definability and monophyly of the species group. We find it noteworthy that Arellano et al. (2005) did not recover a *tenuirostris* group sensu Hooper in their molecular study of Middle American *Rei-*

throdontomys; in particular, *R. creper* formed a basal clade (their lineage IV) to two others composed respectively of representatives of the *mexicanus* (*R. gracilis*, *R. mexicanus*, *R. spectabilis*) and *tenuirostris* (*R. bakeri*, *R. cherrii*, *R. microdon*, *R. tenuirostris*) species groups. Denser taxon sampling may reveal a pattern of regionally localized cladogenesis, with multiple foci of radiation coincident with the major highland blocks of Middle America, and independent evolution of the *tenuirostris* morphotype. *Reithrodontomys musseri*, *R. rodriguezi*, and perhaps other forms considered to be members of the *R. mexicanus* group (notably *R. garichensis*) would be appropriate candidates to explore such a possibility within the southern Central American highlands.

ETYMOLOGY: *Reithrodontomys musseri* is named in honor of Guy G. Musser in recognition of his many outstanding contributions to our understanding of the systematics of rodents. Although his work with Old World Murinae of the Indo-Malayan region will be remembered foremost, his involvement with New World groups has been nonetheless significant and steady over several decades.

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APPENDIX 1

SPECIMENS EXAMINED OF *REITHRODONTOMYS*

Listed below are specimens that formed the basis for the study's morphological comparisons, sample statistics, and morphometric analyses. Other taxa and many more specimens in USNM were generally consulted but were not measured and critically compared. Specimens are given according to the taxa herein recognized.

Reithrodontomys brevirostris ($N = 20$): COSTA RICA: *Alajuela*, Laja Villa Quesada, 5000 ft (AMNH 139728–139730 [paratopotypes]); *Cartago*, Colima Tapanti, 1 km S Tapanti bridge over Río Grande de Orosi, on road to Refugio Nacional Tapanti, 1290 m (MVZ 174400–174403); *Limón*, “Talamanca” (USNM 37556); *Puntarenas*, Monteverde (USNM 559056–559058, 566462); *Puntarenas*, Agua Buena (Cañas Gordas), Savanna de Potrero Grande (AMNH 142461, 142462, 142466, 142467, 142470–142473; paratopotypes of *R. mexicanus potrerograndei* Goodwin, 1945).

Reithrodontomys cherrii ($N = 14$): COSTA RICA: *Cartago*, 2 km E San Ramón de Tres Ríos (LSUMZ 15829, 15831–15835); *Alajuela*, 1 km SW Poás, 1500 m (LSUMZ 25164, 25165, 25375, 25376); *San José*, Pozos, ca. 1 km N Santa Ana (LSUMZ 13226); *San José*, Escazú (USNM 250270); *Cartago*, Faldas Irazú (USNM 250271); *San José*, San José (USNM 38525).

Reithrodontomys creper ($N = 12$): COSTA RICA: *Cartago*, Cerro de la Muerte (USNM 284685–284688); *Limón*, Río Teribé, Valle el Silencio, Río Cotón (USNM 539908–539913); *San José*, San Gerardo de Dota (USNM 559043); *Puntarenas*, Monteverde, Reserva Bosque Nubosa (USNM 559060).

Reithrodontomys garichensis ($N = 16$): COSTA RICA: *Limón*, Río Teribé, Valle el Silencio, Río Cotón, 8000 ft (USNM 539915–539918). PANAMA: *Chiriquí*, Cerro Punta (USNM 314358–314363, 314365–314368, 314779); *Chiriquí*, El Hato, Volcán Barú crater (USNM 314780).

Reithrodontomys gracilis ($N = 2$): COSTA RICA: *San José*, Santa Ana (LSUMZ 15837, 15838).

Reithrodontomys microdon ($N = 19$): GUATEMALA: *Huehuetenango*, Todos Santos (USNM 76922); *Huehuetenango*, Chermal (USNM 275464); *Huehuetenango*, 5 km SE of San Mateo Ixtatán (USNM 569487, 569389, 569509–569511, 569523, 569524, 569538–569543); *Huehuetenango*, Finca la Chingada, 4 km SE of Zunil (USNM 569648, 569649); *Quetzaltenango*, Volcán Santa María (USNM 76965); *Quetzaltenango*, Ojo de Agua, 5 km ENE of Cabricán (USNM 569714).

Reithrodontomys musseri ($N = 1$): COSTA RICA: *Cartago*, Cerro Asunción (LSUMZ 13227 [holotype]).

Reithrodontomys rodriguezi ($N = 3$): COSTA RICA: *Cartago*, Volcán Irazú, 9400 ft (AMNH 141194, 141195 [holotype]; UMMZ 123353).

Reithrodontomys tenuirostris ($N = 13$): GUATEMALA: *Huehuetenango*, Yaiquich, 6 km NW of Santa Eulalia (USNM 569367, 569372–569374, 569421); *Huehuetenango*, 5 km SW of San Mateo Ixtatán (USNM 569444, 569519–569522, 569544, 569629, 569861).

Reithrodontomys sp. undetermined A ($N = 2$): COSTA RICA: *Cartago*, Villa Mills (USNM 566463); PANAMA: *Chiriquí*, Crater of El Volcán (ANSP 18321).

Reithrodontomys sp. undetermined B ($N = 2$): COSTA RICA: *Puntarenas*, Tres Colinas, Potrero Grande, 1915 m (LSUMZ 15836); *San José*, Fila la Máquina, ca. 7.5 km E Canaan, 8700 ft (LSUMZ 13225).