

Chapter 3

Review of the *Oryzomys couesi* Complex (Rodentia: Cricetidae: Sigmodontinae) in Western Mexico

MICHAEL D. CARLETON¹ AND JOAQUIN ARROYO-CABRALES²

ABSTRACT

The status and distribution of eight species-group taxa of the *Oryzomys couesi* group (Rodentia: Cricetidae: Sigmodontinae) described from western Mexico are evaluated based on morphological and morphometric comparisons. Four of these are recognized as valid species within the region: *Oryzomys albiventer* Merriam, 1901 (including *molestus* Elliot, 1903), from inland plateau of the Mesa de Anáhuac; *O. couesi mexicanus* J.A. Allen, 1897 (including *bulleri* J.A. Allen, 1897; *lambi* Burt, 1934; *rufus* Merriam, 1901), from Pacific coastal plain, contiguous lower mountain slopes, and interior valleys along the Ríos Tepalcatepec–Balsas; *O. nelsoni* Merriam, 1898, from Isla María Madre; and *O. peninsulae* Thomas, 1897, from the southern tip of the Baja California Peninsula. Three other taxa named from uplands in interior Mexico—*aztecus* Merriam, 1901; *crinitus* Merriam, 1901; and *regillus* Goldman, 1915—are provisionally retained within *O. couesi*, but further study of their specific stature and relationships is required. The recommended taxonomic changes within western Mexico serve to discuss directions for future revisionary research that will refine the definition and distribution of *O. couesi* sensu stricto in Middle America.

INTRODUCTION

North and Middle American populations of the *Oryzomys palustris* group (sensu Merriam, 1901; Goldman, 1918) have been allocated to as many as 18 species (Merriam, 1901) or to as few as three (Hall, 1981). The systematic contributions of Goldman (1918) and Hall (1960) have played historically influential roles in reversing the early view of specific diversity within the *O. palustris* group. In his revision of the genus, Goldman (1918), perhaps emulating the revisionary model of *Peromyscus* as set forth by his colleague Osgood (1909), demoted many of Merriam's species to intergrading geographic races of the widely ranging, polytypic forms *O. couesi* and *O. palustris*. Within the *O. palustris* group, Goldman designated two sections, the *O. palustris* section, which contained the single North American species, and the *O. couesi* section, which contained

the nominotypical species and six geographically isolated specific allies within Middle America (i.e., *O. antillarum*, *O. cozumelae*, *O. fulgens*, *O. gatunensis*, *O. nelsoni*, and *O. peninsulae*). Goldman's specific classification was essentially maintained through the middle 1900s (Miller and Kellogg, 1955; Hall and Kelson, 1959). Subsequently, Hall (1960) considered *couesi* to be synonymous with *O. palustris* based on perceived intergradation of populations along coastal Texas in certain cranial and chromatic traits. Although argued within a very localized geographic context, Hall swept all of Goldman's (1918) subspecies of *couesi*, including those in western Mexico and Central America, under his expansive definition of *O. palustris*. His action set a broad-brushed precedent for assessing and taxonomically conveying morphological variation among populations of the *Oryzomys palustris* group. Soon

¹ Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0111 (carletonm@si.edu).

² Laboratorio de Arqueozoología “M. en C. Ticul Álvarez Solórzano,” Subdirección de Laboratorios y Apoyo Académico, INAH, Moneda # 16, Col. Centro, 06060 México, D. F., México (arromatu5@yahoo.com.mx).

afterward, other Middle American forms retained as species by Goldman (1918) or Hall and Kelson (1959) were pro forma brought into *O. palustris* as well (*cozumelae* by Jones and Lawlor 1965; *azuerensis* and *gatunensis* by Handley, 1966; *fulgens*, *nelsoni*, and *peninsulae* by Hershkovitz, 1971; *antillarum* by Hall, 1981).

Judged against today's standards of systematic documentation, presentation of data and analysis to support these sweeping taxonomic changes has been at best perfunctory, at worst nonexistent. Reexaminations of the purported zone of intergradation between *couesi* (*aquaticus*) and *O. palustris* (*texensis*) in Texas tellingly exposed the fragile underpinnings of such an inclusive definition of *O. palustris* (Benson and Gehlbach, 1979; Schmidt and Engstrom, 1994). As a result of these regional studies, *O. couesi* (Alston) was resurrected as a species distinct from North American *O. palustris* (Harlan), but most other Middle American taxa have remained as synonyms of a broadly ranging *O. couesi* (e.g., Honacki et al., 1982; Corbet and Hill, 1991; Musser and Carleton, 1993, 2005), an arrangement based on classificatory inertia rather than on actual documentation of consanguinity.

Herein, we review morphological and morphometric evidence for intergradation among forms of the *Oryzomys couesi* complex whose distribution lies in western Mexico. The region encloses striking topographic and biotic diversity and accordingly has proven to be strategic for unraveling specific diversity in other taxonomically problematic rodent genera, such as *Peromyscus* (Carleton, 1977; Carleton et al., 1982; Bradley et al., 1989, 1996) and *Sigmodon* (Zimmerman, 1970; Carleton et al., 1999; Peppers et al., 2002). Eight type specimens of species-group epithets currently allocated to Goldman's (1918) *O. couesi* section originate from this area (see fig. 1). In particular, we address the status and relationships of taxonomically recognized populations of *Oryzomys* that occur at the southernmost tip of Baja California (*O. couesi peninsulae*), on the Tres Marias Islands (*O. nelsoni*), along coastal lowlands in Sonora (*O. c. lambi*) and from Sinaloa through Oaxaca (*O. c. mexicanus*), and on the inland plateau region of Jalisco (*O. c. albiventer*). In

addition, we discuss possible systematic affinities of other taxa named from uplands in interior Mexico—*O. c. regillus* (Michoacán), *O. c. aztecus* (Morelos), and *O. c. crinitus* (Distríto Federal).

MATERIALS AND METHODS

Specimens that form the basis of this report principally consist of skins with their associated skulls and are contained in the following institutional and museum collections (abbreviation in parentheses): American Museum of Natural History, New York (AMNH); Carnegie Museum of Natural History, Pittsburgh (CM); Dickey Collection, University of California, Los Angeles (UCLA); Museum of Natural History, University of Kansas, Lawrence (KU); Field Museum of Natural History, Chicago (FMNH); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM, formerly the U.S. National Museum); the Natural History Museum, London (BMNH, formerly the British Museum of Natural History), and the University of Michigan Museum of Zoology, Ann Arbor (UMMZ). Type specimens and original series of most taxa described for populations of *Oryzomys* in western Mexico were examined firsthand, namely those of *albiventer* Merriam, 1901; *aztecus* Merriam, 1901; *bulleri* Allen, 1897; *crinitus* Merriam, 1901; *mexicanus* Allen, 1897; *nelsoni* Merriam, 1898; *peninsulae* Thomas, 1897; *regillus* Goldman, 1915; and *rufus* Merriam, 1901. Original topotypes of *lambi* Burt, 1934, were consulted, but we did not personally examine the holotype; William T. Stanley examined and measured the FMNH type of *molestus* Elliot, 1903, for us.

Approximately 600 specimens were examined (see registration numbers and full locality information under Taxonomic Summary) and measured, of which 284 adults were grouped into 11 geographically cohesive samples for univariate and multivariate analyses. According to current taxonomic understanding, these operational taxonomic units (OTUs), their abbreviations as employed in figures, specific localities, and sample sizes are recognized as follows:

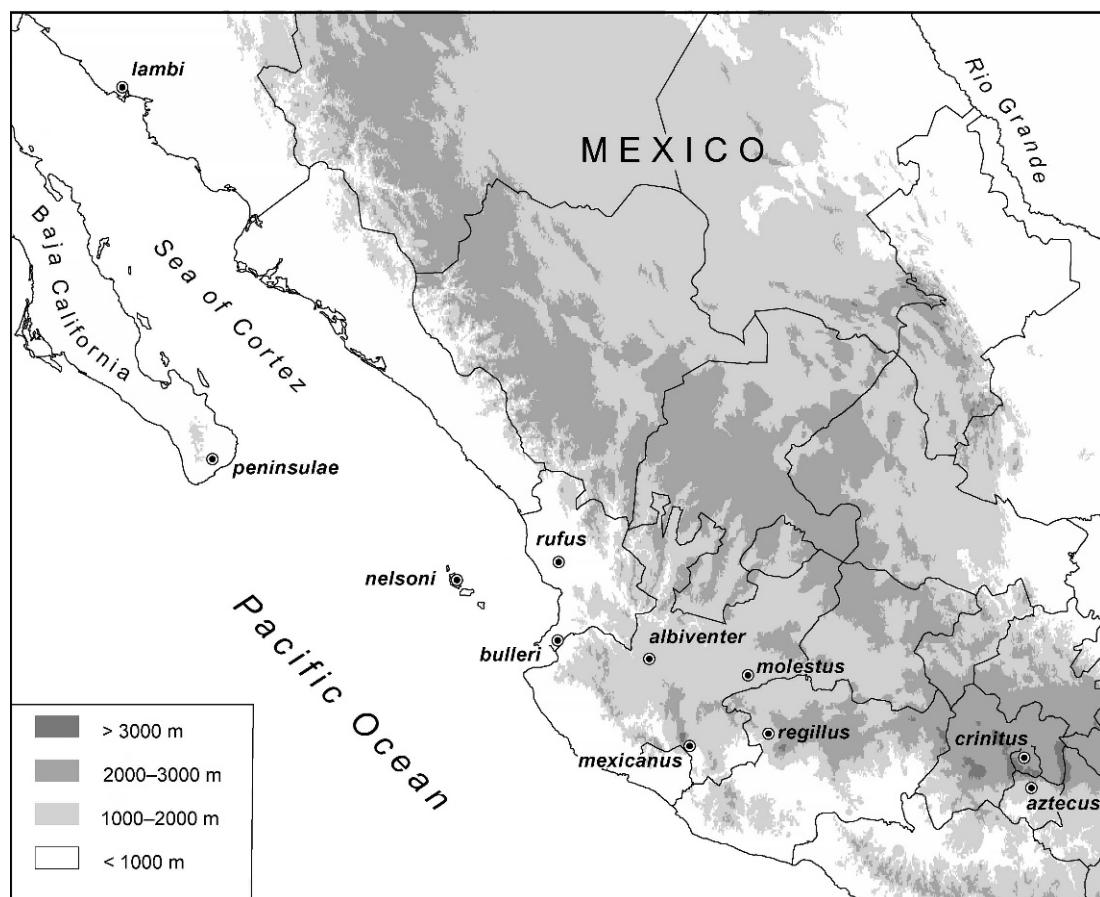


Fig. 1. Type localities of 11 taxa of the *Oryzomys couesi* species group described from western and central Mexico and discussed in the present study. Taxa and localities include: *albiventer* Merriam (1901) from Ameca, Jalisco; *aztecus* Merriam (1901) from Yautepec, Morelos; *bulleri* Allen (1897) from Valle de Banderas, Nayarit; *crinitus* Merriam (1901) from Tlalpan, Distrito Federal; *lambi* Burt (1934) from San José de Guaymas, Sonora; *mexicanus* Allen (1897) from Tonila, Jalisco; *molestus* Elliot (1903) from Ocotlán, Jalisco; *nelsoni* Merriam (1898) from Isla María Madre, Nayarit; *peninsulae* Thomas (1897) from Santa Anita, Baja California; *regillus* Goldman (1915) from Los Reyes, Michoacán; *rufus* Merriam (1901) from Santiago, Nayarit. Topography of Mexican sierras is indicated by 1000 m elevational bands.

Oryzomys couesi albiventer: (J3) Jalisco, Ameca, $N = 12$.

Oryzomys couesi mexicanus: (C1) Colima, vicinity of Santiago, $N = 33$; (C2) Colima, 5 mi NW Manzanillo, $N = 20$; (J1) Jalisco, localities to the N and E of Barra de Navidad, $N = 60$; (J2) Jalisco, Cuitzamala, $N = 20$; (N1) Nayarit, 1 mi S Cuautla, $N = 62$; (N2) Nayarit, San Blas and vicinity, $N = 23$; (N3) Nayarit, Chacala and Las Varas, $N = 16$; (N4) Nayarit, 2 mi E San Pedro Lagunillas, $N = 20$.

Oryzomys couesi peninsulae: (BC) Baja California Sur, San José del Cabo, $N = 14$.

Oryzomys nelsoni: (TM) Nayarit, Tres Marias Islands, Isla María Madre, $N = 4$.

Four external dimensions were transcribed from skin tags to the nearest whole millimeter (mm): total length (TOTL); tail length (TL); hindfoot length (HFL); and ear (pinna) length (EL). 17 cranial and three dental variables were measured to 0.01 mm (most are defined and illustrated in Carleton and Musser, 1995, and Musser et al., 1998), using

handheld digital calipers while viewing crania under a stereomicroscope. These measurements, and their abbreviations as used in text and tables, are: occipitonasal length (ONL); greatest zygomatic breadth (ZB); breadth of braincase (BBC); depth of braincase (DBC); breadth across occipital condyles (BOC); interorbital breadth (IOB); length of rostrum (LR); breadth of rostrum (BR); depth of rostrum (DR); length of incisive foramen (LIF); breadth across incisive foramina (BIF); length of diastema (LD); postpalatal length (PPL); length of bony palate (LBP); breadth of bony palate (BBP); breadth of zygomatic plate (BZP); length of auditory bulla (LAB); coronal length of maxillary tooth row (CLM); width of the upper first molar (WM1); depth of the upper incisor (DI).

Five age classes were defined according to stage of eruption of the upper third molar (M3) and relative wear of the upper molars (M1–3): (1) juvenile—M3 not erupted, or if erupted not reaching the occlusal plane; (2) immature—all molars fully erupted, little wear on M1–2 but no wear on M3; (3) young adult—upper molars, including M3, lightly worn, enamel pattern retaining well defined cusps and ridges, dentinal connections narrow; (4) full adult—M1–3 moderately to heavily worn with blunt cusps, wide dentinal connections, and enamel pattern variously obscured; (5) old adult—occlusal wear so advanced that the enamel pattern is largely obliterated, dentinal lakes of cusps are broadly continuous, and molars basinlike. We use the abbreviations M1–3 or m1–3 to individually reference the upper (maxillary) and lower (dentary) molars, respectively.

Standard descriptive statistics (mean, range, standard deviation) were derived for the 11 OTUs using only those specimens judged to be young, full, or old adult. External data are provided as general guidance to identification (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 20 craniodental variables, all of which were first transformed to natural logarithms. With only three specimens, the topotypes of *lambi* were entered as

unknowns in the discriminant-function analysis and their probabilities of group membership calculated a posteriori, as were the holotypes of *aztecus*, *bulleri*, *crinitus*, *molestus* (as measured by W.T. Stanley, FMNH), *regillus*, and *rufus*. 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).

RESULTS AND COMPARISONS

INTRASAMPLE AGE AND SEX VARIATION: Superficial perusal of skulls in series of western Mexican *Oryzomys* reveals substantial range in size, shape, and pronunciation of cranial ridges, an impression remarked on by others who have worked with examples of *Oryzomys* (Merriam, 1901; Goldman, 1918; Paradiso, 1960; Park et al., 1974; Humphrey and Setzer, 1989). Some of this variation plausibly corresponds to the age of individuals, as suggested by occlusal wear of molars, but consistent size differences between the sexes are also evident and seemingly vary independently of age. Such casual visual impressions are reinforced by statistical comparisons among age and sex cohorts within our largest OTU of *O. couesi mexicanus* (N1, N = 62).

Many variables display regular, incremental increases in mean size across the three adult age classes defined, producing age-correlated differences that contribute substantially to nongeographic variation within our locality samples (table 1). The magnitude of F values and their significance levels differ according to major anatomical regions of the skull: most measurements taken on the facial region (LR, BR, DR, LIF, BIF, LD), which experiences substantial postweaning growth, disclose clear mean differences with greater age and achieve moderate significance levels, whereas those dimensions measured on the neurocranium (BBC, BOC, DBC, IOB), whose maturation plateaus earlier in postnatal development, exhibit slight or no increases

TABLE 1
Arithmetic Means of External and Craniodental Variables and Results of One-way ANOVAs for Sex and Age Cohorts in Adult *Oryzomys couesi mexicanus* from Nayarit
 (OTU N1, $n = 62$; Y, A, and O = young, full, or old adult age class, respectively; see Materials and Methods for variable abbreviations.)

Variable	Sex			Age			$f(age)$
	M (N = 31)	F (N = 31)	$f(sex)$	Y (N = 45)	A (N = 13)	O (N = 4)	
TOTAL	254.3	235.3	19.2***	241.7	248.5	268.5	4.1*
TL	129.9	120.3	15.1***	123.2	128.5	136.0	3.7*
HFL	31.0	30.0	15.5***	30.5	30.4	31.0	0.4
ONL	30.1	28.8	12.5**	29.2	29.8	31.8	6.9**
ZB	16.0	15.2	17.7***	15.5	15.7	16.5	2.9
BBC	12.6	12.4	4.4*	12.5	12.4	12.6	0.4
BOC	6.8	6.7	3.8	6.7	6.7	6.8	0.5
DBC	9.5	9.3	7.7**	9.4	9.4	9.6	0.6
IOB	4.8	4.6	18.4***	4.7	4.7	4.8	0.7
LR	9.5	8.9	11.8**	9.1	9.3	10.3	7.2**
BR	5.8	5.5	11.6**	5.6	5.7	6.2	4.6*
DR	6.6	6.3	9.6**	6.4	6.5	7.1	6.5**
LIF	6.0	5.7	10.2**	5.8	6.0	6.2	3.7*
BIF	2.3	2.3	1.9	2.2	2.3	2.5	7.3**
LD	7.9	7.3	18.5***	7.5	7.8	8.3	5.6**
PPL	10.0	9.5	11.6**	9.6	9.8	10.7	5.0**
LBP	5.5	5.1	16.7***	5.3	5.2	5.8	4.5*
BBP	5.5	5.4	3.8	5.5	5.5	5.6	1.5
BZP	3.3	3.1	5.9*	3.1	3.3	3.5	6.8**
LAB	4.1	4.0	1.1	4.0	3.9	4.2	3.8*
CLM	4.56	4.54	0.2	4.55	4.50	4.67	1.6
WM1	1.29	1.30	0.3	1.30	1.29	1.32	0.2
DI	1.85	1.79	3.8	1.77	1.89	1.99	8.7***

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

with age and generally insignificant F values. Dimensions of the molars (CLM, WM1), which decrease in crown height with occlusal abrasion after eruption, do not grow in length and width, unlike osseous components of the skull; in contrast, the incisors substantially increase in girth with age (table 1). In nearly all of the age-sensitive variables, the significant differences reside between the young adult and full adult or old adult age classes, but not between the full adult and old adult age classes (according to Bonferroni post hoc multiple comparison tests). Such a pattern is predicated by sample sizes available for the three age groups and corresponding mean differences. We suspect that the underrepresentation of the old adult cohort in OTU N1 accounts for the fewer variables that exhibit significant age effects

and the generally smaller F values. The imbalance among age classes and predominance of young adults in OTU N1 typify age representation across all our analytical samples (young adults comprise ca. 70%, full adults 25%, and old adults only 5% of all measured crania, respectively).

Moderate to strong differences between the sexes were derived for most cranial measurements of *Oryzomys couesi*, males averaging 4%–8% larger than females depending upon the variable used as an index of size (table 1). Interestingly, molar dimensions (CLM, WM1) are among those few variables that yielded no significant differences, a finding that indicates that females possess more robust dentitions relative to the head skeleton. Humphrey and Setzer (1989), on the other hand, did obtain significant differ-

ences for molar measurements, but their variable definition was an alveolar length that would reflect changes in the bony palate (ANOVAs of LBP were significant for age and sex effects; table 1). Our next largest sample of *O. couesi* disclosed the same pattern of sexual and age variation, variable differences according to anatomical region, and attained significance levels (J1, $N = 60$ or 58; results not tabulated). The larger size of male *Oryzomys* was qualitatively noted by early researchers (Merriam, 1901; Goldman, 1918; Paradiso, 1960) and quantitatively verified by Humphrey and Setzer (1989) in subspecies of *Oryzomys palustris*. Furthermore, growth studies of laboratory *Oryzomys palustris* have demonstrated that well-marked differences in weight and head-and-body length of males and females become apparent by approximately 3–4 weeks in age (Park and Nowosielski-Slepowron, 1972), or shortly after weaning when dispersing subadults are entering the trappable population. The occurrence of strong sexual dimorphism in *Oryzomys* contrasts with the pattern of nongeographic variation reported for other oryzomyines, in which conspicuous age-related size differences are demonstrable, but size disparity between the sexes is statistically trivial (e.g., *Microryzomys*—Carleton and Musser, 1989; *Oligoryzomys*—Myers and Carleton, 1981, Carleton and Musser, 1995; *Zygodontomys*—Voss, 1991). On average, there is a slight female bias (56%) among all adult skulls suitable for measurement, but the proportion varies appreciably among individual OTUs (33%–85% females).

Humphrey and Setzer (1989) procedurally circumvented the problematic variation introduced by consistent sexual size dimorphism in *O. palustris* by confining their analyses to adult males, an approach achievable with the large museum series available for a common North American species. Such selectivity proved impractical for several taxa of interest here and would severely limit their sample sizes for morphometric comparisons. Only four specimens of *nelsoni* and 21 of *peninsulae* will ever be available for study; the 26 examples of *albiventer* that we managed to assemble exemplify the relative rarity of this taxon in North American collections of Mexican *Oryzomys*. To explore possible

biases in morphometric comparisons associated with imbalanced sex cohorts, we ran three iterations of discriminant-function analysis (using only females, only males, and both sexes) on three morphologically distinctive subspecies of *O. couesi* in western Mexico that vary in proportions of the sexes (*albiventer*, OTU J3 [4♀, 8♂]; *mexicanus*, OTUs C2 [17♀, 3♂], J2 [5♀, 15♂], N1 [31♀, 31♂]; *peninsulae*, OTU BC [10♀, 4♂]). Comparable and unambiguous phenetic structure among these five OTUs was disclosed in bivariate plots of the first two CVs extracted in each iteration (fig. 2), and the percent variation explained by the first two CVs is very similar in all three trials (81.1%–82.4%). Moreover, the hierarchy of craniodental phenetic resemblance among the five OTUs, based on Mahalanobis' distances between group centroids, is fully congruent. The exact clustering distances and relative disposition of OTUs on the first two CVs do differ according to the sexual subset analyzed, but such minor departures would be expected as a result of the different numbers of males and females available for each OTU and corresponding effects on covariance matrices.

In summary, we combined the sexes and three adult age classes in the following morphometric comparisons in order to amplify specimen numbers of the rarer taxa. Although the contributions of secondary sexual dimorphism and postweaning growth (age) to within-sample variation are statistically appreciable, those sources of variation are typically negligible relative to the extracted factors that emerged as taxonomically informative among samples. Indeed, the discriminant-function trials using one or the other or both sexes largely previewed the results we obtained with the full data set.

MORPHOMETRIC COMPARISONS: Pronounced disparity in size and pelage color was especially evident among populations in Jalisco, where key species-group taxa had been named (*albiventer* Merriam, 1901; *mexicanus* Allen, 1897), and initially sparked our suspicion about the possible existence of two species. Two well-defined morphologies were visually apparent in sorting locality samples: large-bodied, brightly colored specimens with broad skulls and robust molar rows versus

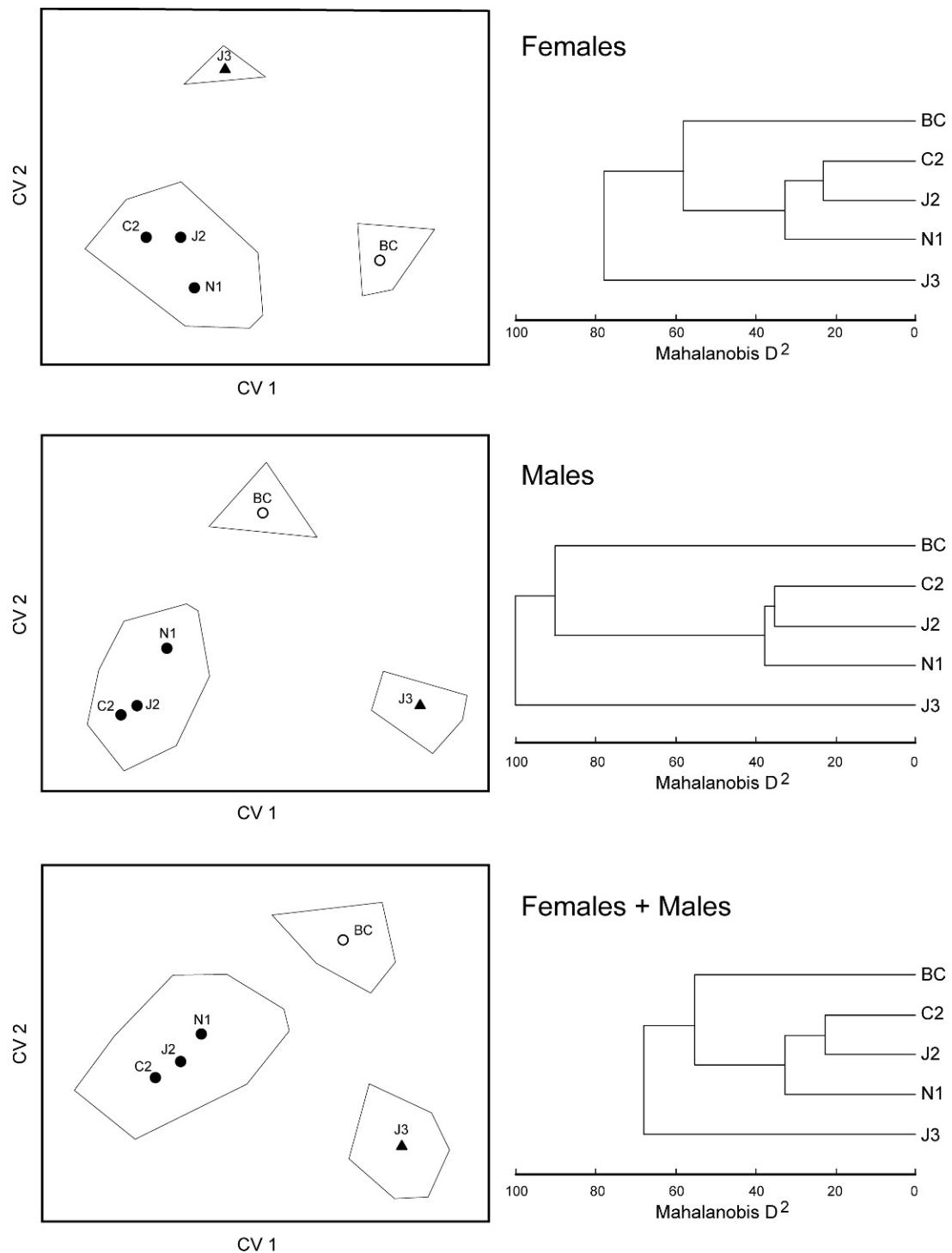


Fig. 2. Three iterations of discriminant-function analysis of select OTUs using only females, only males, and the sexes combined. Left column, projection of specimen scores onto the first two canonical variates extracted; right column, phenograms based on Mahalanobis distances among group centroids. See text for discussion.

smaller individuals with narrower skulls and more delicate molars (compare measurements for OTUs J1 and J3, table 2). Principal component ordination of all Jaliscan adults with intact skulls supplies additional evidence of substantial craniodental differentiation over small geographic distances. Projection of individual scores onto PCs I and II reveals two elliptical densities (fig. 3), one corresponding to specimens from the coastal plain and adjoining foothills in western Jalisco (= *mexicanus*, ca. sea level to 1000 m) and the other to those from uplands in central and eastern Jalisco (= *albiventer*, ca. 1200–1800 m). Although they marginally overlap, the major axes of these elliptical spreads are phenetically discrete (fig. 3), their Y-intercepts being significantly different between taxa (0.46 versus –1.68; $F = 25.2$, $P < 0.001$) while their slopes are comparable (0.65 versus 0.41; $F = 1.4$, $P = 0.245$). This covariation pattern among the specimens of *albiventer* and *mexicanus* is a familiar one that recalls multivariate contrasts recovered for other closely related, congeneric species of Muroidea (Voss et al., 1990; Voss and Marcus, 1992; Carleton and Musser, 1995; Carleton et al., 1999). Predictably, all variables load positively on the first component and most correlations are moderate to large ($r = 0.55$ – 0.98 ; table 3), indicating a general size factor. Although juveniles were omitted from our analyses, some postweaning growth still accounts for much of the elongate scatter observed within the species samples and for the oblique orientation of the group constellations on the first and second principal components. Those variables that load heavily on PC II, more or less orthogonal to the major axes of the taxon samples, emphasize the robust molars (CLM, WM1) of *albiventer* and, to a lesser extent, the relatively broader expanse of the incisive foramina (BIF) of *mexicanus* (tables 2, 3). The type specimen of *albiventer* (USNM 82236) nests comfortably among other large-bodied specimens from inland Jalisco (fig. 3). That of *mexicanus* (AMNH 2650/2128) was too damaged to include in the PCA, but its small molars (CLM = 4.63 mm, WM1 = 1.26 mm) conform to the smaller *Oryzomys* found commonly

throughout the coastal lowlands of western Jalisco.

We expanded our geographic perspective by including other samples of the broadly ranging *mexicanus* and two forms with localized distributions in western Mexico, *nelsoni* from the Tres Marías Islands and *peninsulae* from the Baja Peninsula. The only analytically suitable locality series of *albiventer* remains Merriam's (1901) original type series ($N = 12$) from Ameca, Jalisco. Discriminant-function analysis of the 11 OTUs representing these taxa disclosed three well-defined clusters in the first three canonical variates extracted (fig. 4), which collectively summarize about 75% of the between-sample variation. The largest cluster consists of the eight samples that represent *mexicanus*. Their centroids are closely approximate and they broadly overlap one another in canonical scores; a posteriori misclassifications among the eight is commonplace (24%–92% incorrect depending upon the OTU). The *mexicanus* aggregation is entirely separate from OTU J3 of *albiventer* along the first canonical variate, a hiatus mainly reflecting the uniformly larger size of the latter (tables 2, 4), a distinction also emphasized in the first component derived from PCA of all Jaliscan specimens.

Although the sample of *peninsulae* is intermediate to those of *mexicanus* and *albiventer* in external size (table 2), cranial size and shape differences contribute to its sharp isolation from the latter OTUs along canonical variates 1–3 (fig. 4). Larger size in nearly all variables sets apart *peninsulae* from the various OTUs of *mexicanus* along the first canonical variate (correlations positive, coefficients moderately large; table 4). A subset of dimensions conveys certain shape differences that affect separation of *peninsulae* along the next two latent variates, including a deeper braincase (DBC), broader rostrum (BR), and expansive bony palate (LBP, BBP). Noteworthy are the absolutely and relatively broad incisive foramina (BIF) that characterize specimens of *peninsulae*, features that also contribute to the morphometric isolation of the Baja sample, especially on the second canonical variate (table 4). The incisive foramina in *peninsulae* even average wider than the large-bodied taxa *albiventris*

TABLE 2
**External and Craniodental Measurements (in mm) of Samples of the *Oryzomys couesi*
Complex in Western Mexico**

(Sample statistics include the mean, $\pm 1 SD$, and the observed range; variable abbreviations are defined in Materials and Methods; column headings reflect our taxonomic recommendations.)

Variable	<i>O. couesi mexicanus</i>		<i>O. peninsulae</i>	<i>O. albiventer</i>	<i>O. nelsoni</i>
	Jalisco (J1, N = 58)	Nayarit (N1, N = 62)	Baja California (BC, N = 14)	Jalisco (J3, N = 12)	María Madre (TM, N = 4)
TOTL	245.7 \pm 25.1 195–301	244.8 \pm 19.5 210–288	265.6 \pm 22.3 227–305	285.4 \pm 22.2 245–314	322 \pm 28.8 282–344
TL	132.3 \pm 13.2 102–160	125.1 \pm 10.7 105–150	136.8 \pm 10.8 114–156	155.4 \pm 14.3 129–173	181.5 \pm 14.6 160–191
HBL	113.3 \pm 12.8 91–141	119.7 \pm 11.0 96–144	128.9 \pm 12.3 113–152	130.0 \pm 8.2 116–142	140.5 \pm 14.8 122–153
HFL	30.2 \pm 1.7 26–34	30.5 \pm 1.2 27–33	32.0 \pm 1.2 29–34	36.1 \pm 1.9 33–40	37.3 \pm 1.7 35–39
ONL	29.4 \pm 1.4 26.4–32.5	29.5 \pm 1.5 26.7–33.2	31.5 \pm 1.7 27.8–34.3	32.9 \pm 1.3 30.0–34.5	34.8 \pm 2.5 31.7–37.8
ZB	15.8 \pm 0.9 13.8–18.0	15.6 \pm 0.8 13.9–17.9	17.1 \pm 0.9 15.1–18.7	17.6 \pm 0.6 16.6–18.3	18.0 \pm 1.0 16.6–18.9
BBC	12.5 \pm 0.4 11.7–13.5	12.5 \pm 0.4 11.7–13.3	12.9 \pm 0.2 12.4–13.3	13.2 \pm 0.3 12.8–13.8	13.4 \pm 0.3 13.0–13.6
BOC	6.7 \pm 0.3 6.1–7.3	6.7 \pm 0.2 6.3–7.2	6.8 \pm 0.2 6.2–7.0	7.1 \pm 0.2 6.9–7.6	7.2 \pm 0.3 6.8–7.6
DBC	9.1 \pm 0.3 8.3–9.8	9.4 \pm 0.4 8.4–10.5	9.9 \pm 0.4 9.4–10.8	9.7 \pm 0.3 9.3–10.1	10.0 \pm 0.2 9.9–10.2
IOB	4.7 \pm 0.2 4.1–5.1	4.7 \pm 0.2 4.3–5.3	4.9 \pm 0.2 4.7–5.3	4.8 \pm 0.2 4.5–5.1	5.2 \pm 0.3 4.8–5.6
LR	9.2 \pm 0.6 8.3–10.7	9.3 \pm 0.7 8.2–11.1	10.0 \pm 0.7 8.4–11.1	10.3 \pm 0.7 9.0–11.4	11.3 \pm 0.9 9.9–11.9
BR	5.8 \pm 0.4 5.0–6.7	5.6 \pm 0.4 4.8–6.9	6.4 \pm 0.5 5.4–7.4	6.1 \pm 0.3 5.4–6.5	7.0 \pm 0.6 6.2–7.5
DR	6.6 \pm 0.4 5.8–7.5	6.5 \pm 0.4 5.7–7.4	6.8 \pm 0.5 5.7–7.7	7.1 \pm 0.5 6.2–7.7	8.1 \pm 0.7 7.0–8.7
LIF	5.8 \pm 0.3 5.0–6.5	5.9 \pm 0.4 5.0–6.7	6.4 \pm 0.5 5.5–7.3	6.5 \pm 0.4 5.7–6.9	6.4 \pm 0.3 6.1–6.9
BIF	2.2 \pm 0.2 1.9–2.7	2.3 \pm 0.1 2.0–2.7	2.6 \pm 0.2 2.3–3.2	2.4 \pm 0.2 1.9–2.6	2.5 \pm 0.1 2.4–2.6
LD	7.4 \pm 0.5 6.1–8.6	7.6 \pm 0.6 6.4–9.1	8.3 \pm 0.7 7.1–9.7	8.3 \pm 0.7 7.2–9.5	8.8 \pm 0.7 8.0–9.6
PPL	9.8 \pm 0.7 8.0–11.4	9.7 \pm 0.7 8.3–11.3	10.3 \pm 1.0 8.6–12.5	11.0 \pm 0.6 9.5–11.7	11.5 \pm 1.0 10.5–12.7
LBP	5.5 \pm 0.3 4.9–6.2	5.3 \pm 0.3 4.6–6.2	5.9 \pm 0.3 5.2–6.3	6.2 \pm 0.3 5.6–6.7	6.5 \pm 0.6 5.7–7.2
BBP	5.6 \pm 0.2 5.2–5.9	5.5 \pm 0.2 5.1–6.0	6.1 \pm 0.2 5.5–6.6	6.0 \pm 0.2 5.7–6.2	6.2 \pm 0.2 5.9–6.4
BZP	3.1 \pm 0.2 2.6–3.6	3.2 \pm 0.3 2.6–3.8	3.3 \pm 0.3 2.7–3.9	3.7 \pm 0.2 3.5–4.0	4.2 \pm 0.3 3.7–4.5
LAB	4.0 \pm 0.1 3.7–4.4	4.0 \pm 0.2 3.5–4.4	4.1 \pm 0.2 3.9–4.5	4.5 \pm 0.2 4.2–4.8	4.4 \pm 0.3 4.1–4.6
CLM	4.60 \pm 0.14 4.23–4.94	4.56 \pm 0.17 4.22–4.91	4.72 \pm 0.11 4.53–4.94	5.24 \pm 0.19 4.74–5.51	4.92 \pm 0.12 4.75–5.00
WM1	1.35 \pm 0.05 1.21–1.45	1.30 \pm 0.07 1.04–1.40	1.36 \pm 0.05 1.26–1.44	1.53 \pm 0.06 1.45–1.64	1.52 \pm 0.04 1.47–1.56
DI	1.75 \pm 0.12 1.53–1.98	1.81 \pm 0.14 1.54–2.19	2.18 \pm 0.21 1.83–2.59	2.06 \pm 0.13 1.83–2.26	2.31 \pm 0.18 2.06–2.47

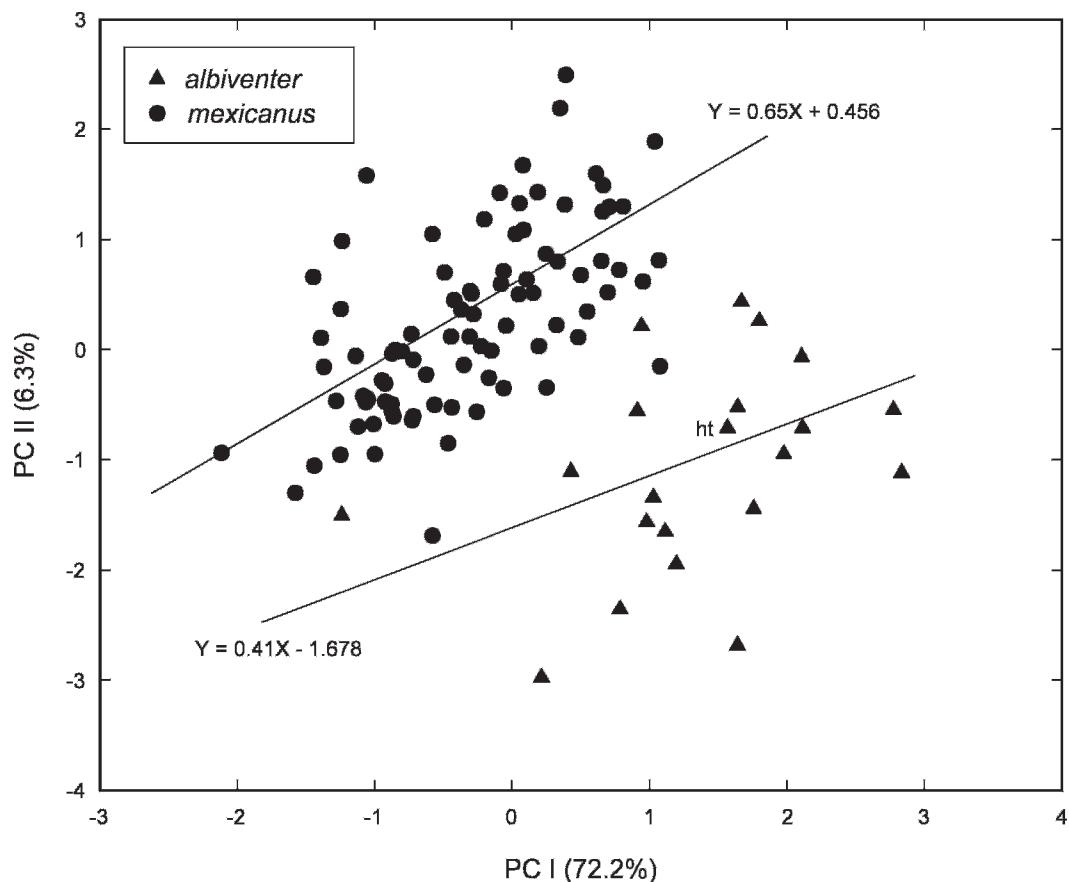


Fig. 3. Projection of specimen scores onto first two axes extracted from principal component (PC) ordination of 20 log-transformed variables as measured on intact skulls ($N = 108$) representing *Oryzomys couesi albiventer* and *O. c. mexicanus* from Jalisco, Mexico. The position of the type specimen (holotype) of *albiventer* Merriam (USNM 82236) is indicated by "ht." See table 3 for variable correlations and variance explained.

and *nelsoni* (table 2). Clustering (UPGMA) based on Mahalanobis' distances between centroids does indicate a closer phenetic affinity between *peninsulae* and OTUs of *mexicanus*, compared with *albiventris* and *nelsoni*, and simultaneously its strong differentiation from any one of them (fig. 5). In principal-component and discriminant-function analyses confined to samples of *peninsulae* and *mexicanus* (not illustrated), contrast in incisor girth (DI) emerges as an important variable for separation of the two taxa (table 4), in addition to those already mentioned. No specimen of *peninsulae* was mistakenly associated with another OTU according to post hoc probabilities of group membership.

Variable loadings that influence the isolation of *albiventris* similarly apply to the OTU of *nelsoni*, insofar as the first three variates extracted are concerned (fig. 4). Compared with examples of *mexicanus* and *peninsulae*, specimens of *nelsoni* and *albiventris* are large *Oryzomys* that possess more robust skulls and notably heavier molars (table 2), differences evidenced in the loadings on canonical variates one and two (table 4). Clear-cut circumscription of the four specimens of *nelsoni* from those of *albiventer*, however, is captured on the fourth and fifth variates (not plotted), which principally emphasize the massive development of the rostrum (LR, WR, DR, BZP) and upper incisors (DI) in *nelsoni* (tables 2, 4). Given the scope of taxa

TABLE 3
**Correlations (Loadings) of 20 Log-transformed
 Craniodental Variables with Derived Principal
 Components (PC) Extracted from Ordination
 Using Intact Specimens ($N = 108$) of
Oryzomys couesi albiventer and *O. c. mexicanus*
 in Jalisco, Mexico**
 (See fig. 3; variable abbreviations are defined
 in Materials and Methods.)

Variable	PC I	PC II
ONL	0.98***	0.03
ZB	0.94***	-0.02
BBC	0.75***	-0.09
BOC	0.71***	-0.05
DBC	0.84***	-0.03
IOB	0.59***	0.19
LR	0.93***	0.15
BR	0.87***	0.28
DR	0.92***	0.18
LIF	0.87***	0.12
BIF	0.65***	0.40**
LD	0.94***	0.15
PPL	0.93***	0.18
LBP	0.81***	-0.25
BBP	0.84***	-0.22
BZP	0.91***	-0.18
LAB	0.68***	-0.26
CLM	0.64***	-0.59***
WM1	0.55***	-0.65***
DI	0.87***	-0.11
Eigenvalues	0.069	0.006
% variance	72.2	6.3

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

under consideration, covariation among these variables emerged as minor compared with the overarching patterns of between-group variation summarized by the first three canonical variates. Nonetheless, their unique and consistent expression in *nelsoni* accounts for its strong differentiation in the phenogram generated from Mahalanobis' distances between OTU centroids (fig. 5). The weak clustering association obtained between *nelsoni* and *albiventer* approximates that derived for *peninsulae* and OTUs of *mexicanus*.

Those type specimens with intact skulls were entered as unknowns in a 10-group discriminant-function analysis for classification according to a posteriori probabilities of group membership. The OTU of *O. nelsoni* was excluded as a classificatory option; furthermore, DI was omitted in calculating discriminant coefficients because the incisors in the

type specimen of *aztecus* (USNM 51173) could not be measured. Type material of the three species-group taxa that originate within coastal plain were all definitely assigned to *mexicanus* (fig. 6), including the holotypes of *bulleri* Allen (AMNH 6663 to N3) and *rufus* Merriam (USNM 91404 to N2), as well as the three original topotypes of *O. couesi lambi* Burt (UCLA 51201 to N2, UCLA 51026 to C2, UCLA 51038 to J1); none demonstrated even a low level of affinity for the OTUs of *albiventer* or *peninsulae*. Those taxa described from upland localities in central Mexico were variously affiliated (fig. 6). The specimen of *molestus* Elliot (FMNH 8667), described from Ocotlán, Jalisco, was dispersed just peripheral to the type series of *albiventer* (Ameca, Jalisco) but definitely classified with that OTU ($P = 1.00$); the type of *albiventer* Merriam (USNM 82236) naturally clustered among the original type series. Type specimens of *aztecus* Merriam (USNM 51173, Yautepec, Morelos) and *regillus* Goldman (USNM 125945, Los Reyes, Michoacán) plotted at the margin of our large representation of *mexicanus*, but their canonical scores statistically aligned them with those OTUs (the greatest affinity of both with J2), not with *albiventer*. Finally, the holotype of *crinitus* Merriam (USNM 50182, Tlalpan, Distrito Federal) was associated with the series of *peninsulae*, at an unexpectedly strong level of probability ($P = 0.996$). The large values measured for the incisive foramen width (BIF), rostral breadth (BR), and braincase depth (DBC) of this specimen (table 5), variables that importantly contribute to the discrimination of *mexicanus* and *peninsulae* (see above), presumably influenced its multivariate disposition and a posteriori classification in *peninsulae*.

DISCUSSION

TAXONOMIC RECOMMENDATIONS AND FUTURE STUDY: We recognize four species among our study samples from western Mexico: *Oryzomys albiventer* Merriam, *O. couesi mexicanus* J.A. Allen, *O. nelsoni* Merriam, and *O. peninsulae* Thomas (figs. 7–9). These forms can be objectively defined by a combination of qualitative morphological traits, demonstrate cohesive patterns of morphometric identity,

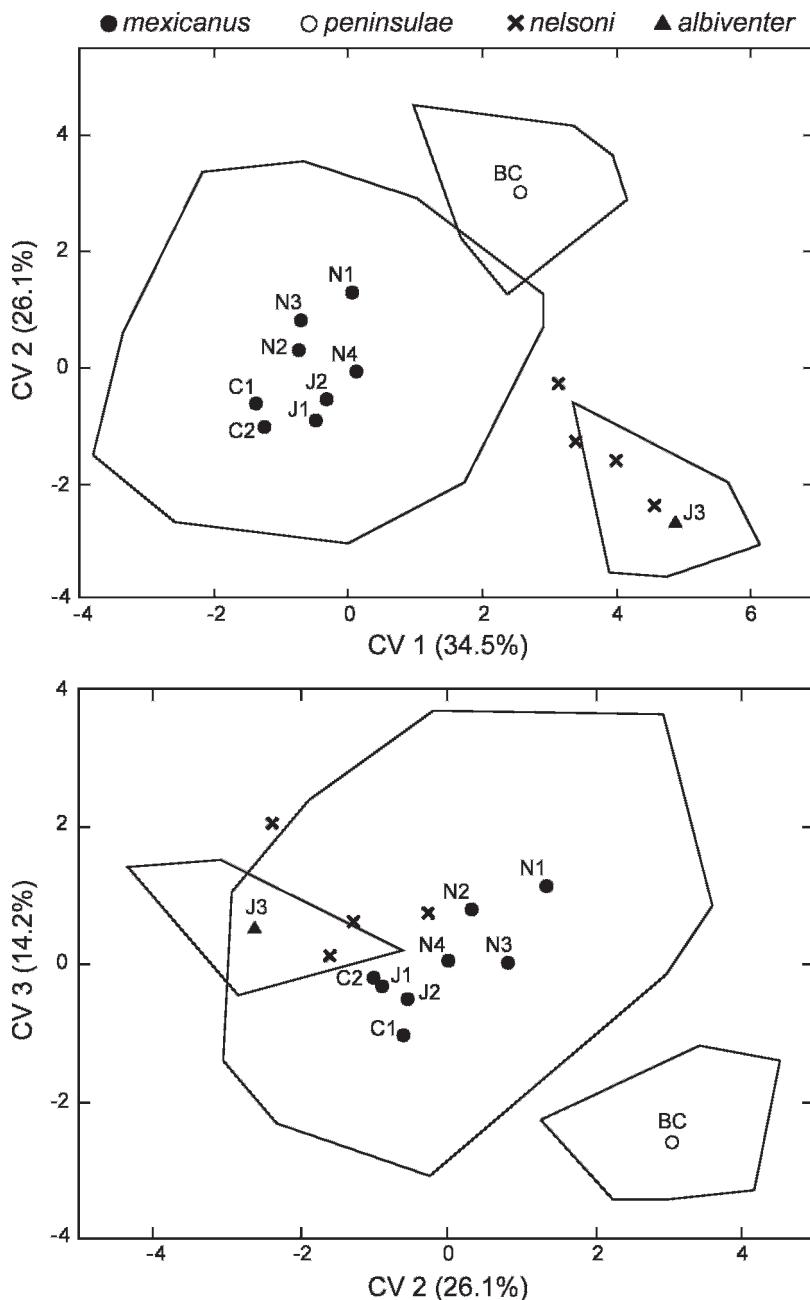


Fig. 4. Results of 11-group discriminant function analysis based on 20 log-transformed measurements of intact specimens ($N = 246$) representing the *Oryzomys couesi* group from western Mexico: top, projection of specimen scores on canonical variates (CV) 1 and 2; bottom, projection of specimen scores on canonical variates 2 and 3. Individual scores are plotted for the four known specimens of *O. nelsoni*; minimum convex polygons enclose individual scores around the centroid for OTUs of *albiventer* and *peninsulae*. To avoid visual clutter only centroids are indicated and a single bounding polygon encloses maximum dispersion for all specimens of *mexicanus*. See table 4 for variable correlations and variance explained.

TABLE 4
Correlations (Loadings) of 20 Log-transformed Craniodental Variables
with Derived Canonical Variates (CV)

(Based on 11-group discriminant function analysis of intact specimens, $N = 246$, representing *Oryzomys* in western Mexico; see fig. 4 for scatter plots of CVs 1–3. Variable abbreviations are defined in Materials and Methods.)

Variable	CV 1	CV 2	CV 3	CV 4	CV 5
ONL	0.69***	-0.07	-0.09	-0.22	0.27**
ZB	0.65***	-0.09	-0.22	-0.19	0.15
BBC	0.61***	-0.07	-0.05	0.09	0.25**
BOC	0.24*	-0.11	-0.01	0.13	0.20
DBC	0.65***	0.29***	0.04	0.05	0.13
IOB	0.46***	0.17	-0.03	-0.33***	0.27**
LR	0.59***	-0.11	-0.14	-0.16	0.28**
BR	0.46***	-0.05	-0.38***	-0.42***	0.29***
DR	0.55***	-0.16	-0.06	-0.33***	0.43***
LIF	0.62***	0.05	-0.15	-0.25**	0.01
BIF	0.56*	0.35***	-0.22*	-0.23*	0.16
LD	0.62***	0.05	-0.12	-0.23*	0.12
PPL	0.51***	-0.11	-0.04	-0.35***	0.15
LBP	0.65***	-0.29***	-0.31***	0.00	0.25**
BBP	0.70***	-0.05	-0.37***	-0.28**	0.16
BZP	0.62**	-0.08	0.12	-0.44***	0.13
LAB	0.62***	-0.21	0.03	-0.21	0.03
CLM	0.76***	-0.40***	-0.09	-0.11	-0.12
WM1	0.62***	-0.56***	-0.23*	-0.07	0.00
DI	0.75***	0.20	-0.15	-0.16	0.24**
Eigenvalues	2.19	1.66	0.91	0.73	0.41
Canonical Correlations	0.83	0.79	0.69	0.65	0.54
% variance	34.5	26.1	14.2	12.4	6.4

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

and occupy discrete geographic ranges (see emended diagnoses, distributions, and remarks under Taxonomic Summary). Such well-marked contrasts stand at odds with the conventional notion of intergrading subspecies as conveyed in past studies and influential classifications (Goldman, 1918; Hall, 1981). The genesis of the widely distributed, polytypic view of *O. palustris*, encompassing *couesi* and most other Middle American taxa, hinged on a geographically and taxonomically limited study (Hall, 1960) that was uncritically expanded in the latter 1900s (Handley, 1966; Hershkovitz, 1971; Hall, 1981), compelled more by the revisionary habit of the era than by fresh analyses of character data. Considered in this historical context, the sharp differentiation we encountered among western Mexican taxa, unexamined in any systematic detail since Goldman's (1918) revision, is unsurprising. These taxa have received mini-

mal study since their descriptions; they are not “cryptic” species.

As now understood (i.e., Weksler et al., 2006, plus species recognized herein), *Oryzomys* is a moderately speciose genus (8 species to date considered valid). The distribution of most species is confined to Neotropical environments of Middle America, but one inhabits temperate settings in southeastern North America (*O. palustris*) and another occupies the northernmost margin of South America (*O. gorgasi*). Even so reconstituted, *Oryzomys* still contains several species-level uncertainties. The widely ranging, polytypic definition of *Oryzomys palustris*, as classically formulated in Hall (1981), reminds us of other Middle American species whose composite nature has been emphatically documented by recent researches. For example, *Oryzomys rostratus* has been separated from *O. “melanotis”* (Engstrom, 1984);

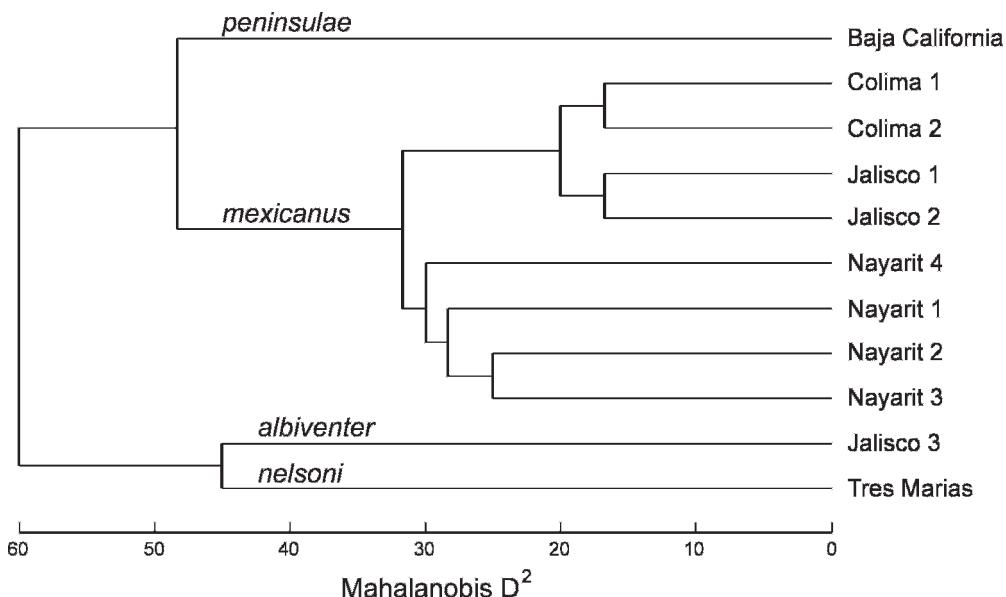


Fig. 5. Pattern of phenetic similarity among the 11 OTUs of *Oryzomys* from western Mexico based on UPGMA clustering of the squared Mahalanobis distances among group centroids as derived from discriminant-function analysis (see fig. 4). Currently recognized species-group taxa are shown above the appropriate stem subtending terminal OTUs.

Sigmodon arizonae, *S. hirsutus*, *S. mascotensis*, and *S. toltecus* have been recovered from *S. "hispidus"* (Zimmerman, 1970; Carleton et al., 1999; Peppers and Bradley, 2000; Peppers et al., 2002; Carroll et al., 2005); and *Peromyscus aztecus*, *P. beatiae*, *P. levipes*, *P. madrensis*, *P. sagax*, *P. simulis*, and *P. spicilegus* have been resurrected as valid species, all of them formerly masked under *P. "boylii"* (Carleton, 1977, 1979; Carleton et al., 1982; Rennert and Kilpatrick, 1987; Schmidly et al., 1988; Bradley et al., 1989, 1996; Castro-Campillo et al., 1999). In similar fashion, future taxonomic research upon *Oryzomys*, in particular the *O. couesi* section, will undoubtedly disclose greater systematic diversity, and some of those research avenues might explore or solidify the following points:

(1) The remoteness of the *Oryzomys* population that once existed at the tip of Baja California, far removed from the core generic distribution in mainland Mexico, prompted Nelson (1922: 124) to remark that it "may readily have been introduced in shipments of bananas or other farm products from Mazatlan or elsewhere along the main-

land coast, where a related species [i.e., *O. couesi mexicanus*] is plentiful." His conjecture on the nonnative status of the peninsular form may have influenced Hall (1981) to arrange it within a polytypic *O. palustris*. However, the morphological distinctiveness and morphometric separation of *peninsulae* that we observed are substantial and instead portray a species that evolved *in situ*, isolated appreciably longer from the mainland distribution of *Oryzomys* than a recent anthropogenic introduction would suggest.

The phenetic linkage of *O. couesi mexicanus* and *O. peninsulae* offers a preliminary kinship hypothesis to be tested with other data, and two biogeographic scenarios deserve consideration in reconstructing the latter's relict distribution. *Oryzomys peninsulae* may have differentiated from an ancestral stock whose distribution once covered the Baja Peninsula, extreme southwestern United States, and western Mexico. Several rodent species or species complexes today exhibit a similar distributional pattern (e.g., see ranges in Lawlor, 1983: appendix 10), suggesting that Pleistocene climatic changes and subsequent range contraction could have isolated

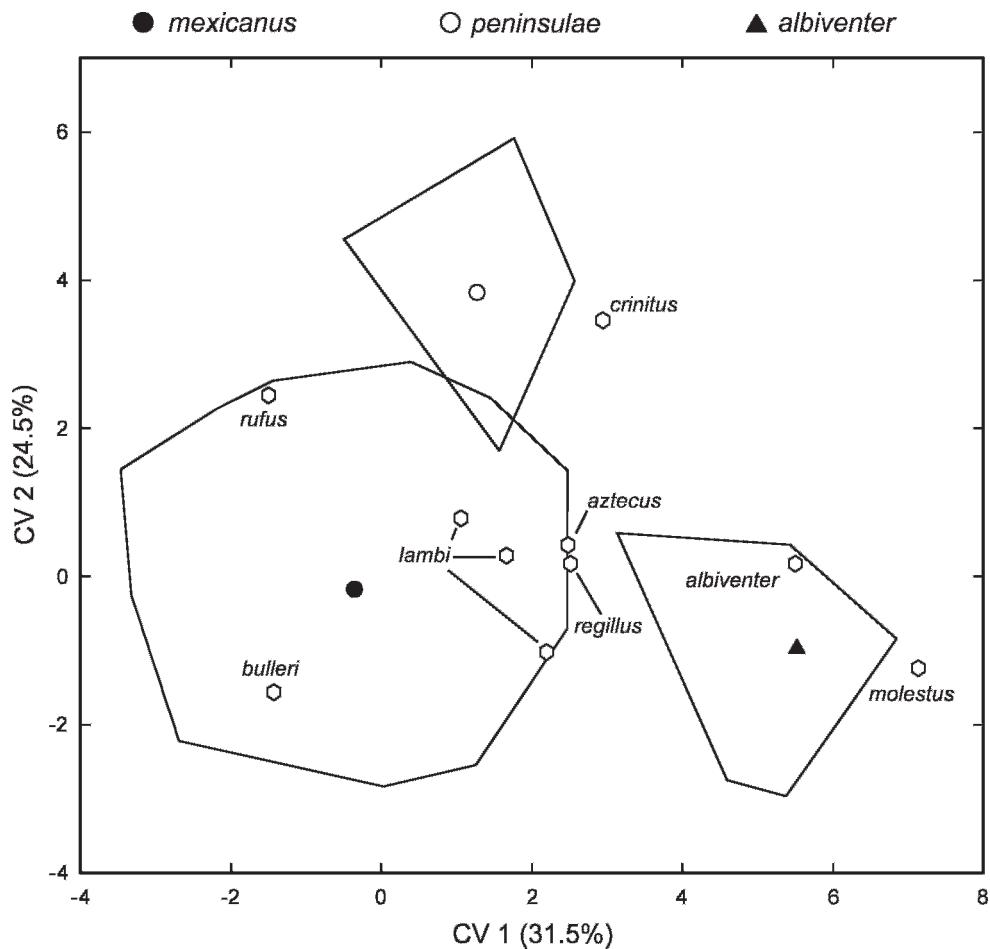


Fig. 6. Dispersion of type specimens of *Oryzomys* named from western Mexico based on a posteriori classification using discriminant coefficients extracted from 10-group discriminant function analysis of *albiventer*, *cousesi mexicanus*, and *peninsulae*. Minimum convex polygons enclose individual scores around the group centroid (or grand centroid in the case of *cousesi mexicanus*). See text for discussion.

an *Oryzomys* population at the tip of the peninsula. The extension of *O. couesi mexicanus* along the coastal plain in western Mexico, as far north as west-central Sonora (fig. 7), further intimates the former continuity of *Oryzomys* populations on the mainland surrounding the Sea of Cortez.

Alternatively, *O. peninsulae* may have originated when the southernmost cape region of the Baja Peninsula was positioned as an island approximate to the Nayarit-Jalisco coast in the late Miocene (Carreño and Helenes, 2002). Geologic and tectonic evidence indicates that northwestward rifting (beginning approximately 5.5 million years

ago) and accelerated seafloor spreading (beginning approximately 3.5 million years ago) eventually brought the insular cape block to its present peninsular terminus, a geological nonconformity demarcated by the Isthmus of La Paz. The biotic legacy of the former juxtaposition of the southern cape block and west-central Mexico is suggested by the current distributions of certain plants and birds (Cody and Velarde, 2002; Cody et al., 2002). Phylogeographic analysis, using ancient DNA, may disclose sufficiently fine-scale genetic affinities to choose among these or other biographic scenarios.

TABLE 5
Measurements^a (mm), Sex, and Age of Type Specimens of the *Oryzomys couesi* Group in Western Mexico
(Y, A, and O = young, full, or old adult age class, respectively. Variable abbreviations are defined in Materials and Methods.)

	<i>O. albiventer</i>		<i>O. nelsoni</i>		<i>O. peninsulae</i>		<i>O. couesi mexicanus</i>		<i>O. couesi couesi</i>	
	albiventer	molestus ^b	nelsoni	peninsulae	mexicanus	bulleri	rufus	lambi ^c	crinitus	aztecus
		USNM 82236	FMNH 8667	USNM 89200	BMNH 98.3.1.107	AMNH 2650/2128	USNM 8359/6663	USNM 91404	UCLA topotypes	USNM 50182
Sex	M	M	M	M	M	M	F	—	M	M
Age	A	O	A	A	A	Y	O	—	Y	A
TOTL	288	325	342	298	249	242	250	226-229	307	290
TL	153	170	190	142	127	136	111-116	161	154	169
HFL	37.5	38	38	34	30	27	28	29-30	37	35
EL	—	15	—	18	13	11	—	17	—	36
ONL	32.7	36.1	37.7	33.8	—	28.0	28.1	30.2-30.4	32.6	33.5
ZB	17.9	19.4	18.6	18.3	—	14.9	15.9	15.9-16.5	17.0	16.9
BBC	13.7	14.1	13.3	13.2	—	12.7	12.2	12.1-12.4	13.4	13.0
BOC	7.2	7.7	7.2	—	—	6.4	6.4	6.7-6.8	6.9	7.2
DBC	10.2	10.6	9.9	—	—	8.7	9.3	8.8-8.9	10.6	9.9
IOB	5.0	5.5	5.2	—	4.7	4.5	4.8	4.6-4.7	5.0	5.0
LR	10.6	11.8	12.4	9.7	—	8.9	8.6	9.6-9.8	10.3	10.4
BR	6.4	7.2	7.2	7.1	—	5.1	5.7	5.8-6.1	6.5	6.3
DR	7.3	8.1	8.7	—	—	5.9	6.5	6.5-6.6	7.3	7.5
LIF	6.9	7.8	6.9	7.0	6.4	5.3	6.3	6.0-6.3	7.0	6.7
BIF	2.6	2.2	2.4	—	1.5	1.8	2.3	2.1-2.4	2.8	2.6
LD	8.8	10.1	9.6	8.8	8.2	6.8	7.5	8.1-8.5	9.0	8.5
PPL	11.1	12.9	12.7	12.1	—	9.3	8.9	10.1-10.3	11.3	11.2
LBP	5.9	6.6	7.2	6.0	5.7	4.8	4.9	5.1-5.4	5.6	6.0
BBP	6.2	—	6.0	5.6	5.4	5.3	5.6-5.8	5.9	5.9	6.2
BZP	3.5	3.9	4.3	3.6	3.5	2.7	3.2	3.2-3.3	3.1	3.2
LAB	4.5	4.9	4.4	4.4	4.2	3.9	4.3	4.2-4.6	4.8	4.3
CLM	5.17	5.60	4.96	5.22	4.63	4.46	4.24	4.32-4.77	4.87	4.97
WM1	1.58	1.63	1.56	1.53	1.26	1.28	1.26	1.40-1.46	1.44	1.44
DI	2.01	2.02	2.43	—	2.07	1.76	1.74	1.76-1.89	1.84	1.95

a External measurements as obtained from skin tags or given in original descriptions; craniodental measurements taken by the authors.

b Craniodental measurements supplied by W.T. Stanley, FMNH.

c Based on three original topotypes identified in Burt's (1934) subspecies description (UCLA 51021, M, YA; UCLA 51026, F, YA; UCLA 51038, F, A).

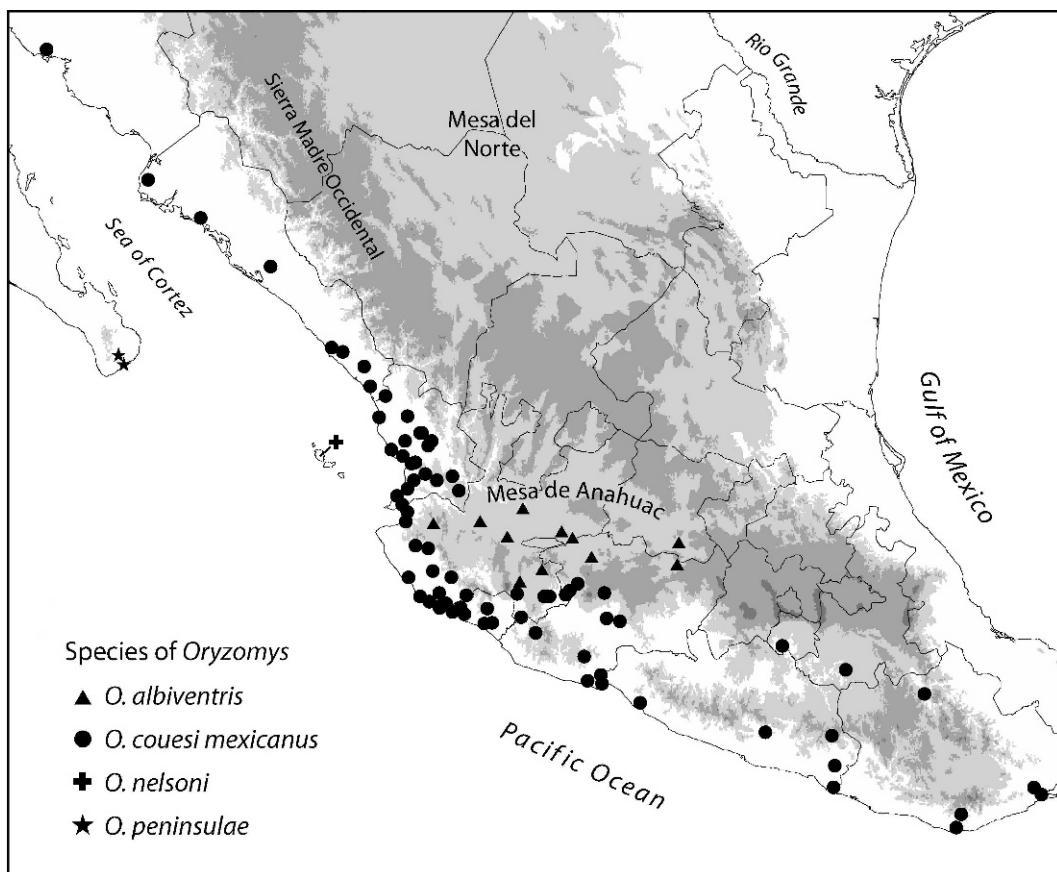


Fig. 7. Distribution of four species of *Oryzomys* here recognized in western Mexico, based on specimens examined by us. Gray shading represents the same elevation zones depicted in figure 1.

(2) The *Oryzomys* population that once inhabited Isla María Madre, the largest of the Tres Marias archipelago off Nayarit, has been accepted as a species by most authors since Merriam (1898) first described it as *O. nelsoni*. In spite of the small sample size (only four specimens known), the differentiation of *O. nelsoni* is sharply circumscribed from mainland forms and sustains its continued recognition as a species, following Merriam (1901) and Goldman (1918) and contra Hershkovitz (1971). In retaining *nelsoni* as a species, Goldman (1918) considered it to be closely allied to the nearest mainland form, *O. couesi mexicanus*. However, by its size, *O. nelsoni* invites careful comparison with *O. albiventer*, a species whose distribution is currently confined to the interior plateau region of west-central Mexico (fig. 7), re-

moved from the coastal lowlands where the progenitor of the island species must have once occurred. The two were paired as the phenetically most similar OTUs in all multivariate analyses of craniodental variables (figs. 4, 5), and this linkage provides a working hypothesis of relationship to be tested with other data. *Peromyscus madrensis*, another rodent endemic of the Tres Marias Islands, was apparently isolated early during the radiation of the *P. boylii* species group (Tiemann-Boege et al., 2000). In like manner, perhaps *O. nelsoni* represents an old lineage within the diversification of western Mexican *Oryzomys*, diverging from the common ancestor that also gave rise to *O. albiventer*.

(3) We elected a conservative course and retained *mexicanus* Allen as a subspecies of *O. couesi* in lieu of the detailed analyses and

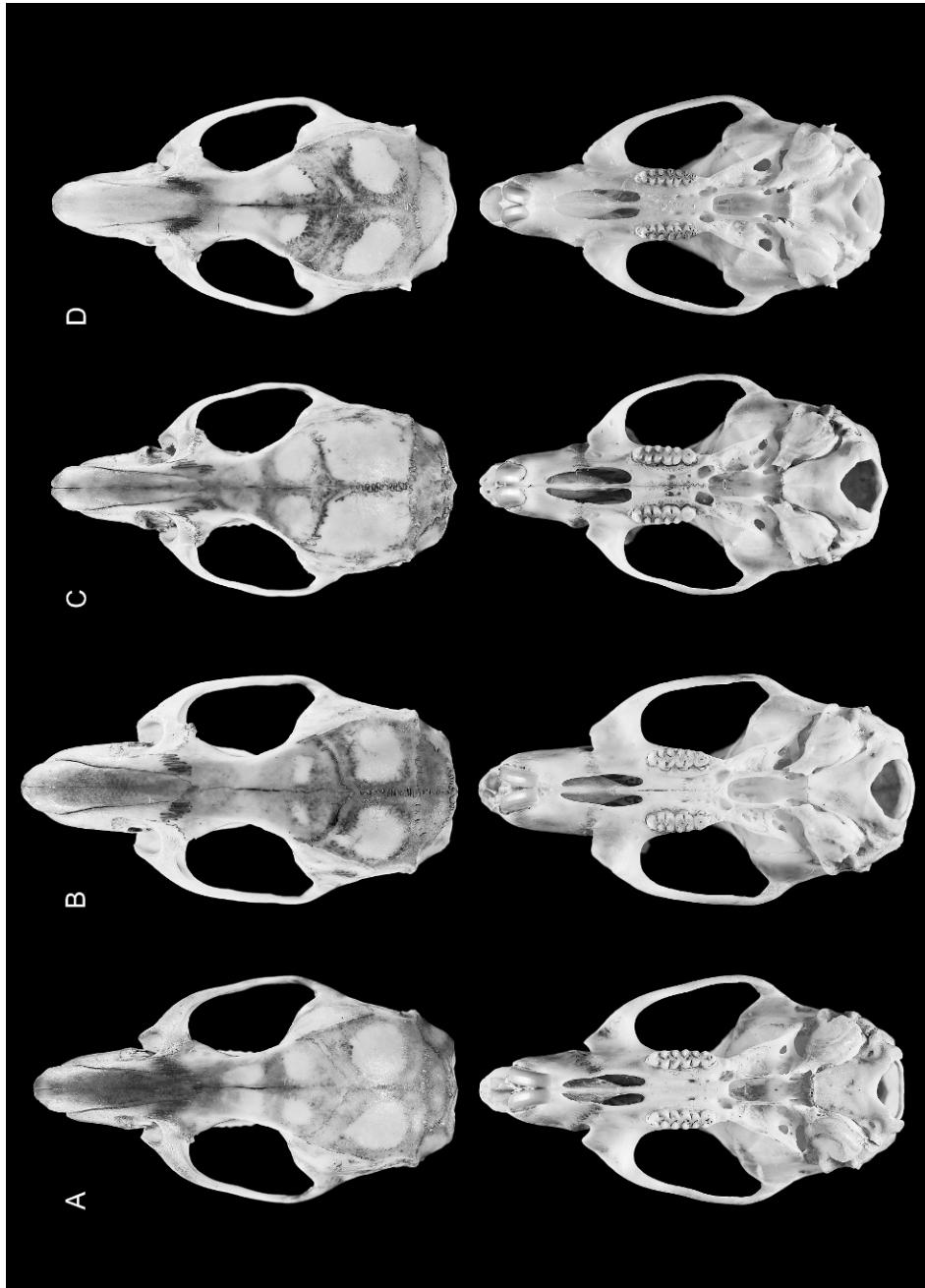


Fig. 8. Dorsal (upper row) and ventral (lower row) cranial views (ca. 2 \times) of adult *Oryzomys* representing species here recognized from western Mexico: **A**, *O. albibrevis* (USNM 82240, ONL = 33.8 mm), a young adult male from Jalisco, Ameca, 4000 ft; **B**, *O. nelsoni* (USNM 89201, ONL = 34.6 mm), an adult female from Nayarit, Isla María Madre, 800 ft; **C**, *O. peninsulae* (USNM 146610, ONL = 32.3 mm), a young adult male from Baja California Sur, San José del Cabo; **D**, *O. couesi mexicanus* (USNM 509418, ONL = 32.2 mm), a young adult male from Nayarit, 1 mi S Cuautla, near sea level.



Fig. 9. Lateral cranial views (ca. 2 \times) of the same specimens adult *Oryzomys* illustrated in figure 8: A, *O. albiventer*; B, *O. nelsoni*; C, *O. peninsulae*; D, *O. couesi mexicanus*.

broader geographic canvas required to clarify its status. Visual comparisons of skins and skulls suggested that, among the four species in western Mexico, examples of *mexicanus* most closely resemble those of *O. couesi* proper, whose type locality is Coban, Guatemala. Recent studies of *Sigmodon* "hispidus" and *Peromyscus* "boylei" cast suspicion on such a conclusion: subspecies distributed along the western versus eastern versants of Mexico in those so-called species have been demonstrated to be distinct from one another (see above references). In particular, the distribution of *O. couesi mexicanus* is extensively congruent with that of *Sigmodon mascotensis* (Carleton et al., 1999), its range penetrating the interior along the basin of the Río Balsas and following the coastal plain to the Isthmus of Tehuantepec. In this case, however, examples of the large-bodied *S. mascotensis* are readily distinguishable from the smaller *S. toltecus* where their ranges approach one another in the region of the

isthmus (Carleton et al., 1999; Peppers and Bradley, 2000). No such morphological dichotomy is apparent to us based on inspection of *O. couesi* specimens from the eastern lowlands of Mexico, the Isthmus of Tehuantepec, and Guatemala, including those that belong to the currently recognized subspecies *couesi* and *zygomaticus* (e.g., Hall, 1981). Other data sources and a broader geographic perspective are needed, one that stresses additional sampling in the Isthmus of Tehuantepec where *couesi mexicanus* and *O. c. couesi* are thought to intergrade (Goldman, 1918; Hall, 1981). Acquisition of topotypic material from the type localities of the several forms in eastern and southern Mexico placed in full synonymy under *O. c. couesi*—*jalapae* Allen and Chapman (1897), *jalapae rufinus* Merriam (1901), *jalapae apatelius* Elliot (1904), *goldmani* Merriam (1901), *teapensis* Merriam (1901)—may prove critical.

Farther south, the status and relationships of several other epithets will bear on delimit-

iting the southern distributional occurrence of *O. couesi* proper. Jones and Engstrom (1986) considered *richmondi* Merriam (1901), whose type locality is in southeastern Nicaragua (Zelaya, 50 mi above Bluefields), to be another synonym that is inseparable from *O. couesi couesi*. Our examination of that type (USNM 36340/48705) indicates that it is an example of *O. couesi*, but evaluation based on denser geographic sampling is necessary before one might comment on subspecific divisions. Another *Oryzomys* described from southeastern Nicaragua (Zelaya, 7 mi below Rama) is the enigmatic *O. dimidiatus* Thomas (1905), known by only two specimens, but investigators who have examined the taxon have retained it as a valid species (Genoways and Jones, 1971; Jones and Engstrom, 1986; Musser and Carleton, 1993; Sánchez et al., 2001). In reporting the rediscovery of *O. gorgasi* Hershkovitz (1971), Sánchez et al. (2001) confirmed its distinction from other forms described from southern Central America, including *dimidiatus* Thomas (1905), *gatunensis* Goldman (1912), and *richmondi* Merriam (1901), the latter two taxa now placed under *O. couesi*. The distribution of *O. gorgasi* plausibly extends into southern Central America, and museum series from this region should be reexamined with the fresh perspective supplied by Sánchez et al. (2001).

(4) Within his arrangement of *O. couesi*, Goldman (1918: 37) identified a complex of related subspecies from central Mexico: "It [*O. c. crinitus*] is closely allied to the other forms inhabiting river valleys of the plateau region of Mexico—*O. c. aztecus*, *O. c. albiventer*, and *O. c. regillus*." As argued above, we acknowledge *O. albiventer* to be specifically distinct from *O. couesi mexicanus*, the form distributed along coastal plain and lower mountain slopes in western Mexico (fig. 7). Of the four taxa described from interior uplands, *O. albiventer* Merriam (1901: 279) is an older name than *regillus* Goldman (1915) and has page priority over *crinitus* Merriam (1901: 281) and *aztecus* Merriam (1901: 282). Evidence for the synonymy of these forms with *O. albiventer* is so far unconvincing, however.

Post hoc classification of the type specimens of the latter three taxa, based on 19

craniodental variables, associates them with *O. couesi mexicanus* (*aztecus* and *regillus*) or with *O. peninsulae* (*crinitus*), not with *O. albiventer*. The holotypes and type series of *aztecus* and *regillus* consist of large individuals whose dimensions measure at the upper limits of variation observed within typical *O. couesi mexicanus* (compare tables 2 and 5), and it is zoogeographically plausible that these names simply apply to more robust populations of the same species where they occupy higher elevations. Whether they represent yet another species within the *O. couesi* group must await improved sample sizes and additional data sources to discern broader patterns of variation and critically decide their status. We do not accept that populations represented by the type of *crinitus*, described from over 2000 m in the Valley of Mexico, and the series of *peninsulae*, described from near sea level at the tip of Baja California, form one and the same biological species. As in the case of *aztecus* and *regillus*, we view these discriminant-function results as indicative of taxonomic problems in need of resolution and the probable existence of greater species diversity than offered by our predefined OTUs. The recent photograph of a large, long-tailed *Oryzomys* from the Distrito Federal (Medellín and Medellín, 2006: 710), verifies that populations referable to *crinitus* Merriam still persist in the Valley of Mexico and invite elucidation of their systematic relationships.

(5) *Oryzomys fulgens* Thomas (1893) is a little-known and overlooked taxon, but clarification of its status will prove pivotal in deciding nomenclatural issues that concern *albiventer* and the other upland taxa, especially *crinitus*. Thomas described *fulgens* based on one of the three specimens originally used by Alston (1876) in his characterization of *Hesperomys couesi*. In doing so, Thomas selected a lectotype for *H. couesi* (specimen "a" = BMNH 75.2.26.15) and fixed its type locality (Coban, Guatemala). The type locality of the specimen that he designated as the type of *O. fulgens* ("b" = BMNH 70.6.20.3), collected by the French naturalist Adolphe Boucard (1839–1905), was given only as "Mexico, exact locality unknown." Thomas supposed that it originated from "southern Mexico, probably in or

near the Valley of Mexico," and his supposition about the source of Alston's specimen "b" has been repeated in the subsequent taxonomic literature on *Oryzomys* (Merriam, 1901; Goldman, 1918; Miller and Kellogg, 1955; Hall, 1981). No one has since offered a formal restriction of the type locality, however. In spite of the possible origin of *fulgens* from the Valley of Mexico, Merriam (1901) proceeded to name another species, *O. crinitus*, from the same region (Distrito Federal, Tlalpan) and suspected that it "will prove only a subspecies of *fulgens*." Merriam had not examined the type of *fulgens* but based his impression of their close similarity on Thomas' description, which he quoted in full. Apparently the indeterminate type locality of *fulgens* persuaded Merriam to name *crinitus* as a full species based on a well-prepared specimen newly collected by Nelson and Goldman, conveniently at hand, and with undoubted provenience.

When nearly all Middle American forms of *Oryzomys* were viewed as races of the older taxa *O. couesi* (Alston, 1876) or *O. palustris* (Harlan, 1837), the imprecise geographic source of the junior name *fulgens* Thomas (1893) was nomenclaturally inconsequential. Its possible senior status among *Oryzomys* taxa named from uplands in interior Mexico now invites careful archival research on Boucard's travels to see whether a definite type locality can be established and the name can be critically applied to *Oryzomys* populations. Having satisfied that crucial step, the relationship of *fulgens* to *albiventer*, *crinitus*, and *aztecus* can be addressed and synonymies allocated if appropriate.

(6) Individuals of *Oryzomys* commonly inhabit coastal wetlands (Sharp, 1967; Wolfe, 1982, 1985), are adept swimmers (Svhla, 1931; Hamilton, 1946; Esher et al., 1978), and are known to emigrate between near-shore islands (Forys and Dueser, 1993). Their semiaquatic habits and ecological preference readily explain the common presence of *Oryzomys* on continental-shelf islands and perhaps the one oceanic occurrence (*O. antillarum* on Jamaica). Several of these peripheral isolates acquired species-group epithets, all of which were hastily reallocated as subspecies of the all-inclusive *O. palustris* (Hershkovitz, 1971;

Hall, 1981). As demonstrated for *O. antillarum* by Morgan (1993) and documented herein for *O. nelsoni* and *O. peninsulae*, however, the differentiation of these insular and peninsular forms is appreciable and contradicts their continued maintenance under the one mainland species *O. couesi*. Other insular and peninsular forms (*azuerensis*, *cozumelae*, and *gatunensis*) now retained within *O. couesi* similarly deserve objective assessment of their status. The generic assignment of the subfossil form described from Curaçao (McFarlane and Debrot, 2001), a continental-shelf island in the Netherlands Antilles, and its possible synonymy with *O. gorgasi* also warrant attention (see comments in Musser and Carleton, 2005: 1148, and Weksler et al., 2006: 4).

CONSERVATION NOTES: *Oryzomys nelsoni* is known by only four specimens of the original type series (Merriam, 1898), obtained by Nelson and Goldman from María Madre Island in May 1897, and is considered extinct (Ceballos et al., 2002; Alvarez-Castañeda and Méndez, 2003; IUCN, 2006). The specimens were collected in moist herbaceous vegetation surrounding springs located on the upper slopes (~ 245 m) of María Madre (Nelson, 1899a, 1899b), the largest of the Tres Marias Islands. No other dedicated inventory of small mammals occurred until Don E. Wilson led a Biological Survey field team to the Tres Marias in March 1976. Wilson and colleagues located the area described by Nelson where *O. nelsoni* had been discovered but collected only *Rattus rattus*; Wilson (1991) inferred that the abundant presence of the commensal may have contributed to the extinction of *O. nelsoni*. Another Tres Marias endemic rodent, *Peromyscus madrensis*, was recovered in moderate numbers on Isla María Madre along with *Rattus rattus* (Carleton et al., 1982; Wilson, 1991).

Current evidence holds little promise that populations of *O. peninsulae* persist. The form is documented from only two localities, Santa Anita and San José del Cabo, in southernmost Baja California. The original series (6 specimens) from Santa Anita, the type locality (Thomas, 1897), was collected by Dane Coolidge (1873–1940), a freelance field collector and writer, in May 1896. The 15 USNM specimens from San José del Cabo

were obtained by Nelson and Goldman in January 1906; the companions afterward traveled to Santa Anita but failed to collect any topotypic examples of *O. peninsulae*. The localities are about 13 km apart and both were situated along the Río San José, a permanent river around the turn of the century that flowed through the predominantly arid landscapes in southern Baja California (Nelson, 1922; Goldman, 1951). Goldman (1918: 46) reported that “The range of the species seems to be centered in the marshes near the mouth of the San José River at San José del Cabo, extending a few miles inland along the course of the stream,” and that “The neighboring coast is extremely arid and unsuitable for habitation by an *Oryzomys*.” Subsequent habitat changes over the latter half of the 20th century in southern Baja California have been dramatic and would be inimical for a semiaquatic rodent tied to such a precarious ecological niche. The river no longer exists, having been sapped dry for irrigation projects, and the marshy lagoon at its mouth in San José del Cabo is polluted commensurate with development of the shoreline for tourism (Alvarez-Castañeda, 1994). Two deliberate attempts to rediscover *peninsulae* in the late 1900s proved unsuccessful: Michael A. Bogan and a Biological Survey field team visited San José del Cabo for one intensive night of collecting in 1979, and Ticul Alvarez-Castañeda (1994) surveyed habitats in and around both Santa Anita and San José del Cabo several times over 1991–1993. The vulnerability of *O. peninsulae* has been obscured by its confusion under *O. couesi*, a species viewed as broadly distributed and accordingly classified as Lower Risk—least concern (IUCN, 2006). The conservation status of *O. peninsulae* must be considered critically endangered, if not extinct, in view of its lack of documentation in over a century, its restricted geographic occurrence, and the environmental deterioration that has befallen its preferred habitat.

Of the two remaining species we identify within western Mexico, populations of *O. couesi mexicanus* appear to deserve the IUCN designation of “Lower Risk—least concern.” Large series of this species have been documented within the latter 1900s, e.g., from lowlands of Nayarit, Colima, and

Jalisco. On the other hand, we encountered few examples of *O. albiventer* in North American collections, only 26 specimens representing 11 localities. Most of these represent material collected by Nelson and Goldman in Jalisco over the years 1897–1903, supplemented by scattered specimens obtained by KU field crews over the years 1949–1969. The distribution of *O. albiventer* largely conforms to the sloping plateau, ca. 1200–1900 m, surrounding Lago de Chapala and its greater drainage basin. Given its hydrographic advantages and more mesic climate, the region has long attracted large-scale agricultural development, and Goldman (1951) described the dramatic environmental changes that had transpired between his early (1902–1903) and later visits (1926, 1935) to the area (see especially accounts for La Barca and Ocotlán). Although populations must be highly fragmented, we believe that the species survives in pockets of appropriate habitat. Efforts should be devoted to surveying the current status of *O. albiventer*, including refinement of its distribution based on vouchered specimens contained in Mexican collections. This refinement necessarily involves resolution of its relationship to the other forms described from central Mexico (see topics 4 and 5 above).

TAXONOMIC SUMMARY

Synonymies are presented below for the four species of *Oryzomys* recognized in western Mexico and trace their earliest identification and first subsequent usage in other name combinations. Emended diagnoses are presented for those two (*O. albiventer* and *O. peninsulae*) that have long been confused with *O. palustris* or *O. couesi* (e.g., fide Goldman, 1918, and Hall, 1981). We regard the status of *aztecus* Merriam, *crinitus* Merriam, and *regillus* Goldman from central Mexico as unresolved and provisionally retain them within *O. couesi* sensu lato (appendix 1). Specimens examined include all individuals personally seen and identified by us. An emended diagnosis is also given for the phylogenetically restricted construct of *Oryzomys*. See Weksler et al. (2006) for character traits and diagnoses of the new genera that have been removed from the

polyphyletic shell that so long characterized “*Oryzomys*” in its traditional usage (Merriam, 1901; Goldman, 1918; Hall, 1981).

Oryzomys Baird, 1857

Mus, Harlan, 1837: 385 (part, description of *palustris*).

Arvicola, Bachman, 1854 [in Audubon and Bachman, 1846–1854]: 214 (part, description of *oryzivora*).

Hesperomys (*Oryzomys*) Baird, 1857: 482.

Oryzomys, Allen, 1890: 187 (first usage as genus).

TYPE SPECIES: *Mus palustris* Harlan, 1837, by original designation.

EMENDED DIAGNOSIS: A clade of medium-sized oryzomyine species (Cricetidae: Sigmodontinae: Oryzomyini) characterized, in combination, by: supraorbital ridging well developed and interorbital shape cuneate; incisive foramina long, extending to or between the alveoli of the M1s; bony palate long, projecting behind the posterior margins of M3s, and posterolateral palatal pits conspicuous and internally perforated; ectotympanic bulla medium-sized, revealing ventral-medial wedge of the periotic; zygomatic plate broad, forming a moderately deep notch, and zygomatic arches sturdy, with small but consistently formed jugal; interparietal small and narrow, about half as wide as the caudal border of parietals; alisphenoid strut absent; carotid arterial circulatory pattern derived, lacking supraorbital and infraorbital branches (sphenofrontal foramen and squamosal-alisphenoid groove absent, stapedial foramen absent or minute, posterior opening to alisphenoid canal irregularly formed or occluded). Molars pentalophodont (mesolophids well developed) and cuspidate, cusps bunodont with lingual and labial series unevenly terraced; anterocone/id broad, anteromedian flexus/id absent, anteroloph discrete and well formed; satellite rootlets present on M1 (4-rooted) and m1 (3–4-rooted). Eight mammae present (pectoral, postaxial, abdominal, and inguinal pairs); pedal digits 1 and 5 notably shorter than central three; ungual tuft of hairs sparsely developed, covering less than half of the nail; plantar surface squamate and pads small, hypotenar pad minute or absent.

DISTRIBUTION: Palustrine, lacustrine, and riverine habitats in the southeastern United States, throughout much of Mexico and Central America, to northwestern South America (western Colombia and northwestern Venezuela), including many continental-shelf islands.

CONTENTS: *albiventer* Merriam, 1901 (including *molestus* Elliot, 1903); *antillarum* Thomas, 1898; *couesi* Alston, 1876 (including *apatelius* Elliot, 1904); *aquaticus* J.A. Allen, 1891; *aztecus* Merriam, 1901; *azuerensis* Bole, 1937; *bulleri* J.A. Allen, 1897; *cozumelae* Merriam, 1901; *crinitus* Merriam, 1901; *fulgens* Thomas, 1893; *gatunensis* Goldman, 1912; *goldmani* Merriam, 1901; *jalapae* J.A. Allen and Chapman, 1897; *lambi* Burt, 1934; *mexicanus* J.A. Allen, 1897; *peragrus* Merriam, 1901; *pinicola* A. Murie, 1932; *regillus* Goldman, 1915; *richardsoni* J.A. Allen, 1910; *richmondi* Merriam, 1901; *rufinus* Merriam, 1901; *rufus* Merriam, 1901; *teapensis* Merriam, 1901; *zygomaticus* Merriam 1901); *dimidiatus* Thomas, 1905; *gorgasi* Hershkovitz, 1971; *nelsoni* Merriam, 1898; *palustris* Harlan, 1837 (including *argentatus* Spitzer and Lazell, 1978; *coloratus* Bangs, 1898; *floridanus* Merriam, 1901; *natator* Chapman, 1893; *oryzivora* Bachman, 1854 [in Audubon and Bachman, 1854]; *planirostris* Hamilton, 1955; *sanibeli* Hamilton, 1955; *texensis* J.A. Allen, 1894); *peninsulae* Thomas, 1897.

REMARKS: In the early taxonomic literature on North American forms (Merriam, 1901; Goldman, 1918), Baird's *Oryzomys* was broadly conceived and included species groups and subgenera now removed to separate genera (Gardner and Patton, 1976; Carleton and Musser, 1989; Weksler, 2003, 2006; Weksler et al., 2006). The phylogenetically reified understanding of *Oryzomys* corresponds to the association of species placed in the *palustris-mexicanus* or *palustris* group, as designated, respectively, by Merriam (1901) and Goldman (1918). Thus, *O. albiventer*, *O. couesi mexicanus*, *O. nelsoni*, and *O. peninsulae* share with *O. palustris* those derived conditions that characterize the strict concept of *Oryzomys* (Carleton and Musser, 1989; Carleton and Olson, 1999; Sánchez et al., 2001) and that were amplified to infer the phylogenetic position of the genus within the oryzomyine radiation (Weksler, 2006).

The four western Mexican species further exhibit the trenchant characteristics of the *couesi* section within the *O. palustris* group, as denoted by Goldman (1918: 20) based on several pelage and cranial traits. In the *palustris* section, the pelage color is predominantly grayish brown, with long glistening guard hairs conspicuously overtopping the body fur; the pelage color is generally reddish brown, with the guard hairs only slightly longer than the body fur in the *couesi* section. Spacious, oval sphenopalatine vacuities perforate the walls of the mesopterygoid fossa, exposing much of the presphenoid bone in specimens of *O. palustris* (e.g., see character 36: state 0, as per Weksler, 2006); in forms of the *couesi* section, sphenopalatine vacuities are absent or weakly expressed as short, narrow slits near the basisphenoid-presphenoid suture (character 36: states 1 and 2, as per Weksler, 2006). Other differences reinforce Goldman's perception of a division. *Oryzomys couesi* and the western Mexican species all possess a small, circular sphenopalatine foramen in contrast to the larger, ovate shape of the foramen as observed in skulls of *O. palustris*. Schmidt and Engstrom (1994) drew attention to the utility of this contrast in separating crania of *O. palustris texensis* and *O. couesi aquaticus* where their populations overlap along coastal Texas, but the contrast holds between *O. palustris* and the four species in western Mexico as well. We noticed that the two sections also differ in the development of the anterolabial cingulum on the lower third molar: consistently present and forming a distinct ledge in the *couesi* section; absent or represented as a short spur in members of the *palustris* section (see Carleton and Musser, 1989: 44–45, for description and illustration of the condition in *O. palustris*). Plantar pads of the hindfoot are small in species of *Oryzomys* compared with many other oryzomyines, and the hypothenar pad is typically absent in *O. palustris* or tiny if present (Carleton and Musser, 1989; Weksler, 2006). A hypothenar pad is consistently present in all members of the *couesi* section for which we could ascertain its condition, its size slightly smaller than interdigital pads 1 and 4. Weksler (2006) scored incipient webbing as present between pedal digits 2–3

and 3–4 in his sample of *O. palustris* but absent in that of *O. couesi*, and Sánchez et al. (2001) indicated that such webbing also characterized *O. dimidiatus* and *O. gorgasi*. Based on examinations of the hind feet on dried skins and even fluid-preserved specimens of the taxa in western Mexico, we are uncertain about the condition of this trait. Certainly, webbing is not so obviously developed as in *O. palustris*, but slight webbing seemed to be present between digits 3–4 in some specimens. This character definition and variation should be critically reviewed within *Oryzomys* to better understand its taxonomic significance.

In summary, the *palustris* and *couesi* “sections” of Goldman's *palustris* group are sufficiently characterized morphologically to maintain them as the *palustris* and *couesi* species groups within the genus *Oryzomys* as now phylogenetically diagnosed. For the character variation summarized above, the *palustris* group displays more derived conditions and may possess more semiaquatic adaptations than the *couesi* group. Only *O. palustris* is currently recognized as a valid species within the *palustris* group; the principal alpha systematic uncertainty involves the status of *argentatus* Spitzer and Lazell (1978), a form described from the Florida Keys that has been treated as species or subspecies (see Musser and Carleton, 2005, for review). The other seven species fit with the *couesi* group, but as underscored by our findings in western Mexico, comprehension of species limits warrants additional research.

Oryzomys albiventer Merriam, 1901

Oryzomys albiventer Merriam, 1901: 279. *Type locality*: Mexico, Jalisco, Ameca, 4000 ft; *holotype*: USNM 82236 (skin and skull), a male collected 6 February 1897 by E.W. Nelson and E.A. Goldman.

Oryzomys couesi albiventer, Goldman, 1918: 38 (name combination, allocated as valid subspecies).

Oryzomys palustris albiventer, Hall, 1960: 173 (name combination, listed as valid subspecies).

Oryzomys molestus Elliot, 1903: 145. *Type locality*: Mexico, Jalisco, Ocotlán, 5000 ft; *holotype*: FMNH 8667 (skin and skull), a male collected June 1901 by F.E. Lutz (not examined).

Oryzomys couesi albiventer, Goldman, 1918: 38
(*molestus* allocated as full synonym, invalid as subspecies).

Oryzomys palustris albiventer, Hall, 1981: 609
(*molestus* listed as full synonym, invalid as subspecies).

EMENDED DIAGNOSIS: A species of the *O. couesi* group characterized by a combination of large size (HFL \approx 34–38 mm), tail relatively and absolutely long (TL \approx 140–170 mm), skull heavily constructed (ONL \approx 31–34 mm), and molars correspondingly robust (CLM \approx 5.0–5.4 mm).

DISTRIBUTION: Central and eastern Jalisco, southern Guanajuato, and northern Michoacán at intermediate elevations, 1200–1800 m (fig. 7).

REMARKS: *Oryzomys albiventer* is a large, brightly colored species with a long tail. Merriam's (1901) key diagnostic feature, "underparts white," and consequent choice of the specific name are somewhat misleading. The basal portion of ventral hairs is pale gray and the distal half a pure white in the type series from Ameca. The white tips do not obscure the basal gray and, to us, create a general effect of pale gray to grayish-white underparts. In the specimens from Ocotlán, the gray bases are more prominent and the underparts appear medium gray. Other aspects of Merriam's description are accurate, notably the large skull and long and wide molar rows which he emphasized in his comparisons with nearby species. Goldman (1918) repeated these salient contrasts in his rearrangement of *albiventer*, *mexicanus*, and *regillus* as subspecies of *O. couesi* in western Mexico.

Goldman (1918) reallocated *molestus* Elliot (1903) as a full synonym of Merriam's (1901) *albiventer* (then a subspecies of *O. couesi*), and we concur with their synonymy. Elliot based his new species on a single specimen, but four other individuals in USNM from Ocotlán, the type locality of *molestus*, conform to his description. The type specimen of *molestus* is a strikingly large individual (table 5), but it is, as noted by Goldman, an old adult and a male. Measurements of the type fit within the size range of *O. albiventer* as we understand the species, albeit at or toward the upper limits for most variables; still, discriminant-function analysis decidedly assigned the type to the *albiventer*

OTU. Two specimens from localities in northern Michoacán (Zamora and Queréndaro), which Goldman (1918) referred to *O. c. regillus*, are here considered examples of *O. albiventer* proper.

Although the distributional limits of *O. albiventer* require further documentation, the species so far appears to be endemic to the Mesa de Anáhuac, a small inland plateau (1200–1900 m) that is enclosed by southern ranges of the Sierra Madre Occidental and by the Transverse Volcanic Range. Characterized by a subhumid climate and subtropical vegetation, the region corresponds to one of the five zoogeographic zones that Guerrero Vázquez et al. (1995) identified within Jalisco.

SPECIMENS EXAMINED: Mexico, *Guanajuato*: Salvatierra, 5775 ft (KU 66597). *Jalisco*: Ameca, 4000 ft (USNM 82235–82246); 6 km NE Contla, 1310 m (KU 120611, 120612); 2 mi N and 0.5 mi W Guadalajara, 5200 ft (KU 31782, 31783); 27 mi S and 12 mi W Guadalajara (KU 31784); La Barca (USNM 129038); 2 mi SE Mascota, 5200 ft (KU 100509); Ocotlán, 5000 ft (USNM 120160–120163); 4 km W Tuxpan, 1380 m (KU 120613). *Michoacán*: Queréndaro (USNM 50180); Zamora, 4000 ft (USNM 120308).

Oryzomys couesi mexicanus J.A. Allen, 1897

Oryzomys mexicanus J.A. Allen, 1897: 52. *Type locality*: Mexico, Jalisco, Tonila, Hacienda San Marcos, 3500 ft; *holotype*: AMNH 2650/2128 (skin and skull), a male collected 30 December 1889 by Audley C. Buller.

Oryzomys couesi mexicanus, Goldman, 1918: 33 (name combination, allocated as valid subspecies).

Oryzomys palustris mexicanus, Hall, 1960: 173 (name combination, listed as valid subspecies).

Oryzomys bulleri J.A. Allen, 1897: 53. *Type locality*: Mexico, Tepic [Nayarit], Valle de Banderas; *holotype*: 8329/6663 (skin and skull), a male collected 2 February 1893 by Audley C. Buller.

Oryzomys couesi mexicanus, Goldman, 1918: 33 (*bulleri* allocated as full synonym, invalid as subspecies).

Oryzomys palustris mexicanus, Hall, 1981: 610 (*bulleri* listed as full synonym, invalid as subspecies).

Oryzomys rufus Merriam, 1901: 287. *Type locality*: Mexico, Tepic [Nayarit], Santiago, 200 ft;

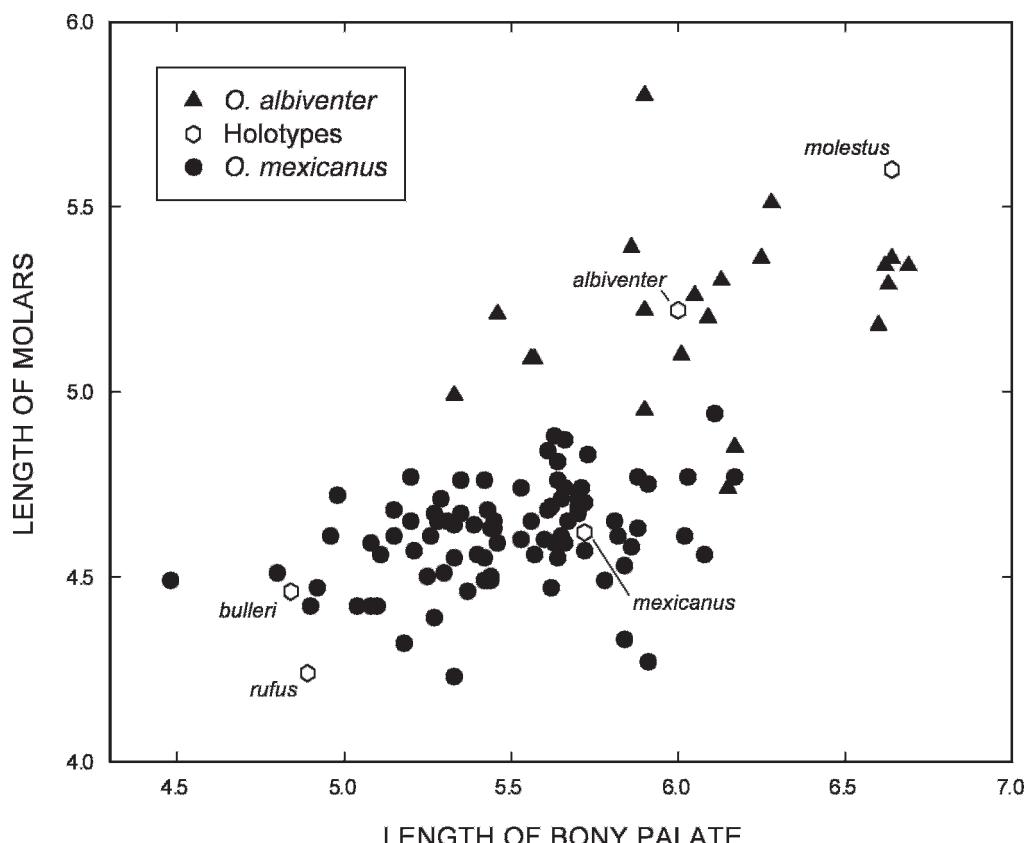


Fig. 10. Scatter plot of coronal length of molar rows versus length bony palate (in mm) for specimens of *O. albiventer* and *O. couesi mexicanus* from Jalisco. Values for type specimens of taxa described from Jalisco (*albiventer* Merriam, *mexicanus* Allen, *molestus* Elliot) and nearby Nayarit (*bulleri* Allen, *rufus* Merriam) are indicated.

holotype: USNM 91404 (skin and skull), a female collected 20 June 1897 by E.W. Nelson and E.A. Goldman.

Oryzomys couesi mexicanus, Goldman, 1918: 33 (rufus allocated as full synonym, invalid as subspecies).

Oryzomys palustris mexicanus, Hall, 1981: 610 (rufus listed as full synonym, invalid as subspecies).

Oryzomys couesi lambi Burt, 1934: 107. *Type locality*: Mexico, Sonora, San José de Guaymas; *holotype*: California Academy of Sciences 51024 (skin and skull), a female collected 20 January 1933 by C.C. Lamb (not examined).

Oryzomys palustris lambi, Hall, 1960: 173 (name combination, listed as valid subspecies).

DISTRIBUTION: Coastal plain and adjoining lower Pacific-facing slopes from central Sonora to southeastern Oaxaca; interior river valleys to central Michoacán, southern

Morelos, southern Puebla, and northwestern Oaxaca (fig. 7); most localities from sea level to 1000 m, exceptional occurrence at 1525 m in the Sierra de Autlán, Jalisco.

REMARKS: J.A. Allen (1897) named *mexicanus* and *bulleri* as new species based on one specimen of the former and two of the latter. Although their type localities are relatively near one another in western Mexico, he differentiated *mexicanus* with respect to *O. palustris* and *bulleri* to *O. couesi* rather than to one another. Working with larger series and better geographic representation, Goldman (1918) recognized the fundamental similarity of Allen's taxa and adopted *mexicanus* as the subspecific epithet, with *bulleri* as full synonym, for the populations of smaller *Oryzomys* widely distributed along Pacific coastal plain. Although the damaged

skull of the type of *mexicanus* prevented its use in our morphometric analyses, bivariate scatterplots of measurable variables depict both *mexicanus* and *bulleri* as falling within the range of samples drawn from coastal plain (fig. 10), in contrast to those originating from the inland plateau region (i.e., *albiventer* and *molestus*).

Merriam (1901: 287) considered his new species *rufus*, based on a single specimen, to be "similar in general to *bulleri* but smaller and redder." The type specimen is a small individual (table 5) but falls within the variational sphere of the larger series from Nayarit and Jalisco, whether viewed from a univariate or multivariate perspective (figs. 6, 10). The contrasts that impressed Merriam can be largely attributed to the age and gender differences of the types of *bulleri* (young adult male) and *rufus* (old adult female) and the tendency of the pelage of aged *Oryzomys* to become more reddish. Again, we agree with Goldman's (1918) synonymy of *rufus* under *O. couesi mexicanus*.

The three topotypes of *lambi* Burt (1934) at hand generally resemble other examples of the *Oryzomys* species that inhabits coastal lowlands in western Mexico (e.g., fig. 6, table 5), here called *O. couesi mexicanus*, and we include it among the synonyms of this "subspecies." Our maintenance of a trinomial is pro forma in this instance because we cannot here resolve the larger issue of the taxonomic and distributional limits of *O. couesi* sensu stricto. The subspecific range of *lambi* is depicted as restricted to its type locality in west-central Sonora, whether as a race of *O. couesi* (Hall and Kelson, 1959; Alvarez-Castañeda and Cortés-Calva, 1999) or *O. palustris* (Hall, 1981). We note that certain specimens from northern Sinaloa (e.g., 2 mi E Costa Rica, 3 mi N Higueras) are larger than those from southern Sinaloa and farther south along coastal plain in Nayarit, Jalisco, and Colima, and may belong with Burt's *lambi*. Denser sampling in central Sinaloa and refined analyses are needed to determine the relationships of these populations and whether *lambi* deserves formal subspecific retention.

Goldman (1918) viewed the distribution of the subspecies *mexicanus* to adhere to Pacific coastal plain and contiguous foothills, a range

conforming to his Arid Lower Tropical Zone (and Goldman, 1951) and essentially repeated in later taxonomic compendia of mammals (Hall and Kelson, 1959; Hall, 1981). However, specimens from certain localities that Goldman allocated to *aztecus* also represent *O. couesi mexicanus* proper in our judgment, and these reallocations extend its range into interior Mexico along the valleys of the Ríos Tepalcatepec and Balsas. A geographic range that covers coastal plain, Pacific-facing lower slopes of western sierras, and the Balsas Depression resembles other cricetid rodents found in western Mexico (e.g., *Sigmodon mascotensis*, *Hodomys allenii*, *Peromyscus perfulvus*, *Osgoodomys banderanus*) and presumably reflects a shared biogeographic history. The pattern is nearly exactly congruent to the biotic zone distilled from the distributions of the Mexican herpetofauna (Flores-Villela, 1993) but is not so precisely mirrored in those recognized in biogeographic syntheses of birds and mammals (Escalante Pliego et al., 1993; Fa and Morales, 1993).

SPECIMENS EXAMINED: Mexico, *Colima*: Armería, 200 ft (USNM 33284/45312–33285/45313, 33292/45320–33297/45325); 4 km S and 2 km W El Chavarín (CM 79555, 79556); Hacienda Magdalena, 1500 ft (USNM 33299/45327, 33300/45328); 5 mi N Manzanillo (KU 87515–87534); Paso del Río, 200 ft (UMMZ 100656–100669, 100689); 3 mi N Santiago (KU 87490–87492, 87653); 1 mi NE Santiago, 10 ft (KU 36867–36873); 2 km E Santiago (KU 87498); 3 km E Santiago (KU 87499–87514); 1 mi S and 4 mi W Santiago, 10 ft (KU 36874); 12 km W Santiago (KU 87493–87497). *Guerrero*: 5 km N Agua del Obispo, 3250 ft (KU 99899); 5.5 km N Agua del Obispo, 3400 ft (KU 99898); near Ometepec, 200 ft (USNM 71400–71405, 71419); Zihuatanejo Bay (UMMZ 80926, 80927, 80929, 80931); Petacalco, sea level (UMMZ 113850–113852); Tlalixtaquilla, 4200 ft (USNM 70277); 2 km SSE Zihuatanejo, Las Gatas (KU 35371–35379). *Jalisco*: 11 mi SW Autlán, 2000 ft (KU 105742); Sierra de Autlán, 5000 ft (UMMZ 95476, 95477); Cihuatlán, 15 ft (KU 109262–109265); 15 KM NW Cihuatlán (87454); Cuitzamala, 25 ft (KU 105743–105763); 2 km NW Emiliano Zapata, 20 m (KU 120615); Jilotlán de Los Dolores, 2400 ft (KU 111830, 111831); 8 mi E Jilotlán de Los

Dolores, 2000 ft (KU 111832–111837); 6 mi E Limón, 2700 ft (KU 103799); 2 mi S La Cuesta, 2400 ft (KU 111829); 2 mi N La Resolana, 1500 ft (UMMZ 95478, 95479); 2 mi SW La Resolana, 1100 ft (KU 40125, 40126–40129, 40138, 40139); 1 mi N Barra de Navidad (KU 97242–97244, 97246–97248); 3 mi NW Barra de Navidad, 30 ft (KU 97239–97241); 5 km NNW Barra de Navidad (KU 87455–87465, 87467–87472, 87474–87489); 0.5 mi N Navidad, 25 ft (UMMZ 100654, 100655, 101268–101270); 3 mi E Navidad, 50 ft (UMMZ 100641–100653); Navidad Bay (UMMZ 80912–80914, 80924); 14.5 mi S Pihuamo, 1100 ft (KU 111820–111827); 4 mi NNE Puerto Vallarta, 50 ft (KU 64494–64498); 4 mi SW Puerto Vallarta, 20 ft (KU 111828); 20 km WNW Purificación, 1400 ft (KU 93021, 93652); 30 km N and 10 km E Santiago (KU 87489); El Tabaco, 200 ft (KU 107669–107674); Tenacatita Bay (UMMZ 80897, 80906, 80911). Michoacán: 16 mi S Arteaga, 800 ft (KU 40132–40137, 40140); 0.5 mi SE Coalcomán, 3600 ft (UMMZ 100670–100672); near La Huacana (USNM 126497–126501); 1 mi E La Mira, 300 ft (KU 40141–40144); 9 mi S Lombardía, 1500 ft (KU 38652); 7 mi S Tumbiscatio, 2700 ft (KU 40130); Parque Nacional Uruapan (UMMZ 110560, 110561). Morelos: Puente de Ixtle (USNM 126943, 127496, 127497). Nayarit: Arroyo de Jiguite, Río Santiago, 100 m (USNM 523637, 523638); Aticama, 10 ft (KU 36860–36864); Chacala, 30 m (USNM 509467–509473, 523631–523636); 1 mi S Cuautla, near sea level (USNM 509389–509450, 510551–510560); 1.2 mi S (by road) El Casco, Río Chilte, 480 ft (USNM 511645–511652, 511751, 511752, 511884–511889); El Refilion, 850 m (USNM 509463–509466); 3.5 mi E (by road) El Venado, 100 m (USNM 509455, 510562); Estanzuela, 1380 m (USNM 509474); 1 mi E Ixtlan, 4000 ft (UMMZ 95475); 2 mi E Jalcocotan, 500 m (USNM 523624–523630, 524358, 524359); 1 mi NE Las Piedras, Río Tigrera (USNM 523639, 523640); 5 mi S Las Varas, 150 ft (KU 40124); 8 mi SSW Las Varas (KU 64480–64482); 4 mi NE San Blas, 100 ft (UMMZ 103184–103187); 8.8 mi E San Blas, Paso de Soquipá, 100 m (USNM 509456–509462, 510563); 10 mi E Ruiz, Platanares (KU 85830, 85831, 85837); 4 mi E Playa Los Corchos (USNM

553966, 554089); San Blas, 75 ft (USNM 89206–89208, 89240); 0.5 E San Blas, 10 ft (KU 36852–36859); 1 mi S San Francisco, 50 ft (KU 64490–64493); 2 mi SW San Juan de Abajo (USNM 512558–512561, 512759, 512760); 2 mi E San Pedro Lagunillas, E side lake, 1300 m (USNM 509474–509493, 510564–510567); 15 km S Santa Cruz, Playa Colorado (USNM 553963–553965, 554088); Santiago, 200 ft (USNM 91403, 91404); Teponahuaxtla (USNM 509451–509454, 510561); 2 mi WNW Valle de Banderas (KU 64483–64489). Oaxaca: Cuicatlán, 1800–1900 ft (USNM 69654, 69660); 1 km N Cuicatlán, 560 m (KU 29490–29492); 3 km NNE Cuicatlán, 600 m (KU 29487–29489); 1 km S Cuicatlán, 590 m (KU 29493); 2 km SSW Cuicatlán, 570 m (KU 29494); Huilotepec, 100 ft (USNM 73408, 73726); Llano Grande, 200 ft (USNM 71406, 71407, 71921, 73727, 73730); Plumas, 3000 ft (USNM 71415, 71417, 71418); Puerto Angel, 100–200 ft (USNM 71408–71414, 73745); Tehuantepec (USNM 73407). Puebla: Piaxtla, 3900 ft (USNM 70273–70276). Sinaloa: 2 mi E Costa Rica, 100 ft (KU 100502–100508); 24 km S Guasave, 20 ft (KU 90316); 3 mi N Higueras, 30 ft (KU 96669–96674); 6 mi NNW Teacpan, Isla Palmito del Verde (KU 98960, 98961); 6 mi W La Concha, 10 ft (KU 98962, 99156); 5 mi NW Mazatlán (KU 85825–85829); Rosario, 100 ft (USNM 91405); 8 km N Villa Unión, 450 ft (KU 96099, 96100); 1 mi N Zaragoza, 30 ft (KU 90314, 90315). Sonora: San José de Guaymas (UCLA 51021, 51026, 51038).

Oryzomys nelsoni Merriam, 1898

Oryzomys nelsoni Merriam, 1898: 15. *Type locality:* Mexico, Nayarit, Tres Marias Islands, María Madre Island, 800 ft; *holotype:* USNM 89200 (skin and skull), an adult male collected 13 May 1897 by E.W. Nelson and E.A. Goldman.

Oryzomys palustris nelsoni, Hershkovitz, 1971: 704 (name combination, listed as valid subspecies).

DISTRIBUTION: Known only from Isla María Madre, the largest of the Tres Marias, Nayarit.

REMARKS: Merriam (1898, 1901) aptly captured the distinguishing characteristics of his new form, in particular its large skull, massive and strongly decurved rostrum, and large, broad incisors (figs. 8, 9). Dimensions

that reflect Merriam's qualitative descriptions, particularly those measured on the rostrum, figure prominently among the several variables that account for isolation of the four specimens of *O. nelsoni* in discriminant-function analyses (table 4). Merriam also mentioned the island form's large body size, long tail, and big hind feet; in relative and absolute size, *nelsoni* possesses the longest tail among the species of the *O. couesi* group in western Mexico (table 2). Examples of *O. albiventer* lack such a robust rostrum and upper incisors as found in *O. nelsoni* but possess heavier molars (table 2). We must accept that the morphology evident in the small museum series of the Tres Marias Oryzomys is typical of the species. Sadly, *O. nelsoni* represents an instance where the investigator's sample statistics and population parameters are one and the same.

SPECIMENS EXAMINED: Mexico, *Nayarit*: Tres Marias Islands, Isla María Madre (USNM 89200–89203).

Oryzomys peninsulae Thomas, 1897

Oryzomys peninsulae Thomas, 1897: 548. Type locality: Mexico, Lower California [Baja California Sur], Santa Anita; holotype: BMNH 98.3.1.107 (skin and skull), a male collected on 23 May 1896 by Dane Coolidge.

Oryzomys palustris peninsulae, Hershkovitz, 1971: 704 (name combination, listed as valid subspecies).

Oryzomys couesi peninsularis, Alvarez-Castañeda, 1994: 99 (incorrect subsequent spelling, assessment of conservation status).

Oryzomys couesi peninsulae, Alvarez-Castañeda and Cortés-Calva, 1999: 448 (name combination, treated as valid subspecies).

EMENDED DIAGNOSIS: A species of the *O. couesi* group characterized by a combination of moderate size (larger than *O. couesi mexicanus*, smaller than *O. albiventer*) and dorsal pelage of head and forequarters predominantly gray toned. Cranium with deep braincase, zygomatic arches broadly spreading and squarely shaped, and incisive foramina long and exceptionally broad. Upper incisors relatively deep and curvature more nearly orthodont.

DISTRIBUTION: Known only from two localities in southernmost Baja California Sur, Nayarit.

REMARKS: Merriam (1901) and Goldman (1918) were clearly impressed by the differentiating traits of *O. peninsulae*, as emphasized by Thomas (1897), and many of their qualitative characterizations of its distinctly shaped skull contributed to its morphometric separation (e.g., "high braincase," "large and broadly open palatal slits," "rather large molars"). The pelage contrast between the grayish-brown forequarters and fulvous brown hindquarters is still appreciable in the century-old, now slightly faded skins that Nelson and Goldman collected at San José del Cabo and is unmatched for its constancy in other western Mexican Oryzomys. The orthodont shape of the upper incisors (fig. 9) impresses us as also diagnostic of the species, but the feature was not mentioned by the aforementioned authors.

The *Oryzomys* population isolated at the southernmost tip of the Baja Peninsula was maintained as a valid species until grandiosely synonymized under *O. palustris* by Hershkovitz (1971). Hall (1981: 610–611) later provided some post hoc rationale for its subspecific rank within *O. palustris* and considered "the degree of difference between *O. peninsulae* and *O. palustris mexicanus* of the eastern coast of the Gulf of California to be less than between some intergrading subspecies of *O. palustris* (e.g., *O. palustris texensis* and *O. p. aquaticus*). Hall's precept for the synonymy of *peninsulae*, the purported intergradation of *texensis* and *aquaticus*, has proven to be erroneous, the latter forms instead representing nonintrogressing races of the species *O. palustris* and *O. couesi*, respectively (Benson and Gehlbach, 1979; Schmidt and Engstrom, 1994). As we document above, the morphological identity of *O. peninsulae* is sharply and uniquely circumscribed relative to populations of *O. couesi mexicanus* and other *Oryzomys* in western Mexico. Such a "degree of difference" clearly advises specific recognition until controverted by other evidence.

SPECIMENS EXAMINED: Mexico, *Baja California Sur*: Santa Anita (BMNH 98.3.1.107, USNM 93398); San José del Cabo (USNM 146607–146620, 147340).

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APPENDIX 1

SUPPLEMENTARY SPECIMENS EXAMINED

The following specimens were additionally consulted apropos evaluation of taxa in western Mexico, but no decision about their status was reached. The pro forma listing as subspecies of *O. couesi* reflects their current classification (i.e., Hall, 1981), not a taxonomic recommendation.

Oryzomys couesi aztecus: Mexico, *Morelos*, Yautepec, 4100 ft (USNM 51171, 51172, 51173 [holotype], 51174, 51175); 10 mi S Cuernavaca (USNM 20907/36019).

Oryzomys couesi crinitus: Mexico, *Distrito Federal*, Tlalpan, 7600 ft (USNM 50181, 50182 [holotype], 50183).

Oryzomys couesi regillus: Mexico, *Michoacán*, Los Reyes (USNM 125936–125940, 125943, 125944, 125945 [holotype], 125946–125948); 1.5 N Los Reyes, 4400 ft (KU 96101–96103); 1.5 mi S Los Reyes, 4500 ft (KU 96104).