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A New Species of *Oryzomys* (Rodentia: Muridae) from Eastern Bolivia

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ABSTRACT

Specimens of *Oryzomys* referable to the *megacephalus* complex (Musser et al., 1998) collected in the Parque Nacional Noël Kempff Mercado (PNNKM), eastern Bolivia, are discriminated from three other currently recognized species of that group (*O. megacephalus*, *O. perenensis*, *O. laticeps*) by analysis of cranial morphometrics and molecular sequence of the cytochrome b gene. The Bolivian sample has the closest genetic relationship to *O. perenensis* (Kimura 2-parameter genetic distance × 100: 14.8) and *O. laticeps* (distance 12.0), but the genetic distance is large. The Bolivian sample is clearly separated from the others by both principal component and discriminant function analyses of cranial and body variables. We here describe it as a new species. Morphologically, it is intermediate in size, along with *O. perenensis*, between the smaller *O. megacephalus* and the larger-bodied *O. laticeps*. In pelage color and occlusal pattern it closely resembles *O. megacephalus*. The geographic range appears to be a relatively small area of the western basin of the Río Itenez that drains easternmost Santa Cruz and Beni Departments. Genetically verified populations of the four species are thus far allopatric, with the known range of the new species wedged between the geographic ranges of *O. perenensis* to the west and *O. megacephalus* to the east.

RESUMEN

Especímenes del complejo de especies *Oryzomys megacephalus* (Musser et al., 1998) colectados en el Parque Nacional Noël Kempff Mercado, al este de Bolivia, son discriminados de otras tres especies reconocidas para este grupo (*O. megacephalus*, *O. perenensis*, *O. lati-*

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ceps) usando análisis morfométrico del cráneo y secuencia molecular del gen mitocondrial citocromo b. La muestra boliviana muestra una relación genética con *O. perenensis* (distancia génetica Kimura 2-parameter × 100: 14.8) y *O. laticeps* (distancia 12.0) pero estas distancias géneticas son grande s. La muestra boliviana se separa claramente de los otros usando análisis de componentes principales y funciones discriminativas de medidas craneales y externas. Esta muestra es aquí descrita como una especie nueva. Morfológicamente es de tamaño intermedio junto con *O. perenensis*, entre un pequeño *O. megacephalus* y un *O. laticeps* grande. En color de pelaje y patrón oclusal la especie nueva se parece mucho a *O. megacephalus*. El rango geográfico al parecer es una pequeña área en la cuenca occidental del Río Guaporé/Itenez que desagua bien al este de los departamentos de Santa Cruz y Beni. Geneticamente, poblaciones confirmadas de las cuatro especies son alopátricas, con el rango de distribución para la especie nueva encajado entre los rango geográficos de *O. perenensis* al oeste y *O. megacephalus* al este.

INTRODUCTION

Rats of the *Oryzomys* ''*capito*'' complex (Muridae, Sigmodontinae) have received major revisionary study that has made them one of the better understood groups of South American rodents (Gardner and Patton, 1976; Musser et al., 1998; Patton et al., 2000; Weksler, 2003). Some species of this genus are the most common terrestrial murid rodents of lowland Neotropical forests, and large series of specimens from widespread localities have permitted extensive biogeographic analysis (Musser et al., 1998; Costa, 2003; Lessa et al., 2003). Nevertheless, many parts of the geographic range of the *Oryzomys* ''*capito*'' complex remain poorly sampled, and novelties might still be expected.

Three species complexes, including 11 species, have been defined within the formerly grouped ''*capito*'' complex (Musser et al., 1998; Patton et al., 2000). One of these, the *megacephalus* complex, includes at least four currently recognized species, *O. megacephalus* Fischer, 1814, *O. perenensis* Allen, 1901, *O. laticeps* Lund, 1840, and *O. yunganus* Thomas, 1902. Another named species, *O. seuanezi* Weksler, Geise, and Cerqueira, 1999, from the Atlantic forests of Brazil, includes the coastal populations designated as *O. laticeps* by Patton et al. (2000) and Costa (2003; M. Weksler, personal commun., 2004). There remains ambiguity concerning the relationships of true *laticeps*, which is known only from its lectotype (Musser et al., 1998; Weksler et al., 1999). As we do not resolve this issue, we follow Musser et al. (1998), Patton et al. (2000), and Costa (2003) and provisionally retain the name *O. laticeps* for the large, gray *Oryzomys* from coastal forests, although Weksler (personal commun.) argues on biogeographic grounds that *laticeps* is likely a synonym of *megacephalus*. Cytochrome b gene sequence analysis has indicated *O. yunganus* to be the sister group to a clade including *O. megacephalus*, *O. perenensis*, and *O. laticeps* (Patton et al., 2000), and we here follow Costa (2003) in using a restricted definition of the *megacephalus* complex that excludes *O. yunganus*. Species of this complex are morphologically similar and generally allopatric, making it difficult to distinguish small intraspecific geographic variation from species-level divergence. Integrated morphological, karyotypic, and molecular genetic analyses have proven key to untangling the relationships between taxa of this genus.

During mammal inventories of Parque Nacional Noël Kempff Mercado (PNNKM), in Santa Cruz Department, Bolivia, we found that the most commonly collected forest murid is a species of the *O. megacephalus* complex that differs from the described forms. Moreover, it occurs midway between the geographic ranges of *O. megacephalus* and *O. perenensis* that were mapped from specimens with molecularly supported identifications (Costa, 2003: fig. 7). Morphological and molecular analyses showed that this rat is distinct from other known members of the genus. We here describe and name it as a new species.

MATERIALS AND METHODS

MOLECULAR TECHNIQUES: Genomic DNA was extracted with the DNAeasy kit (Qiagen,

TABLE 1
Matrix of Kimura 2-Parameter Distances (×100) Within and Among Taxa of the *Oryzomys megacephalus* Complex of Species, Plus *O. yunganus*[a]

	New species $N = 5$	*laticeps* $N = 7$	*megacephalus* $N = 41$	*perenensis* $N = 19$	*yunganus* $N = 4$
New species	0.570 ± 0.280	11.992 ± 1.874	15.967 ± 2.154	14.795 ± 2.121	20.521 ± 2.683
laticeps		1.230 ± 0.400	14.101 ± 1.895	14.450 ± 2.064	18.386 ± 2.342
megacephalus			5.454 ± 0.791	16.437 ± 2.164	18.876 ± 2.221
perenensis				2.272 ± 0.393	18.695 ± 2.251
yunganus					5.558 ± 0.958

[a] Based on 801 base pairs of the mitochondrial cytochrome b gene. Mean ± 1 standard error; N = number of sequences.

Inc., Valencia, CA) from liver preserved in the field in 95% ethanol. The mitochondrial cytochrome b gene (cyt-b) in *Oryzomys* is 1143 base pairs (bp) long (Smith and Patton, 1999). We amplified the entire gene as two fragments of approximately equal length that overlapped by about 350 bp. Primer pair MVZ05-MVZ16 amplified the initial 800+ bases of the gene, and primer pair MVZ127-MVZ108 amplified the terminal 700+ bases of the gene (primer sequences in Smith and Patton, 1999; Patton et al., 2000; Leite, 2003). Double-stranded DNA was purified using the QIAquick PCR Purification kit (Qiagen, Inc., Valencia, CA) following protocols used in previous studies (Smith and Patton, 1999). The light strand of this template was then cycle-sequenced with primers MVZ05 and MVZ127 and run on an ABI 3730 capillary automated sequencer following manufacturer protocols using Big-Dye chain terminators. Sequences were aligned

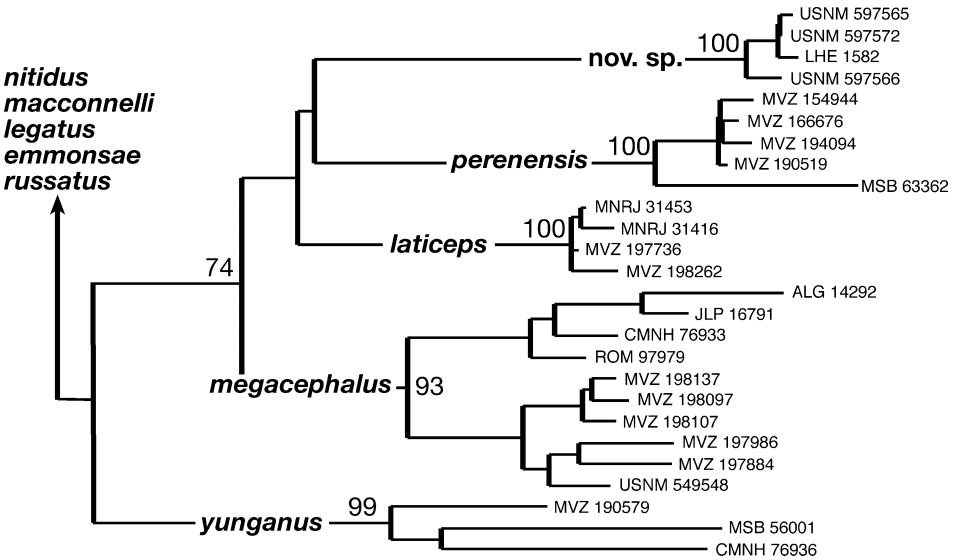

Fig. 1. Strict consensus of two equally most parsimonious trees based on a branch-and-bound analysis of 26 ingroup sequences, each 801 bp long, from the cytochrome b gene. Included are multiple sequences for each of four taxa of the *Oryzomys megacephalus* group and *O. yunganus*. The tree is rooted by comparison to single sequences from each of five species of the *O. nitidus* group. Voucher numbers are given for each specimen. Provenance and other data for all but the new Bolivian taxon can be found in Patton et al. (2000) and Costa (2003). Bootstrap values (based on 1,000 iterations) are given at each basal node. Tree length = 741 steps; consistency index = 0.520; homoplasy index = 0.480.

TABLE 2

Descriptive Statistics (Mean, Standard Error, Sample Size, and Range) of Cranial Measurements of Four Species of the *Oryzomys megacephalus* Group

Character	Species			
	New species	*laticeps*	*megacephalus*	*perenensis*
Total length (TL)	264.57 ± 4.86 7 241–282	275.75 ± 2.60 4 271–281	236.08 ± 3.52 12 218–257	261.56 ± 3.36 25 227–303
Tail length (TaL)	119.57 ± 2.80 7 110–130	130.00 ± 2.55 4 123–135	112.00 ± 2.63 12 95–126	125.92 ± 2.07 25 107–151
Hind foot (HF)	29.43 ± 0.57 7 27–31	33.0 ± 0.41 4 32–34	28.08 ± 0.38 12 27–31	32.15 ± 0.29 27 29–35
Ear length (E)	21.43 ± 0.37 7 20–23	22.25 ± 0.48 4 21–23	21.92 ± 0.29 12 21–24	21.11 ± 0.19 27 19–24
Condylo-incisive length (CIL)	29.76 ± 0.35 10 27.67–31.25	31.26 ± 0.13 4 30.94–31.57	28.23 ± 0.23 21 26.58–30.33	30.45 ± 0.24 33 27.80–34.01
Occiptal condyle breadth (OCB)	7.14 ± 0.06 9 6.92–7.38	7.04 ± 0.05 4 6.96–7.16	6.58 ± 0.05 19 6.28–7.11	6.86 ± 0.05 33 6.13–7.43
Mastoid breadth (MB)	12.36 ± 0.10 8 11.95–12.89	12.69 ± 0.11 4 12.41–12.98	11.63 ± 0.11 21 10.87–12.80	12.49 ± 0.08 33 10.96–13.28
Basioccipital length (BOL)	4.86 ± 0.06 9 4.64–5.24	5.26 ± 0.10 4 5.03–5.50	4.48 ± 0.07 21 4.14–5.07	4.66 ± 0.05 33 4.05–5.25
Rostral length (RL)	10.26 ± 0.16 10 9.11–10.70	12.64 ± 0.18 4 12.31–13.13	11.02 ± 0.18 4 9.43–12.31	12.39 ± 0.17 33 9.96–14.22
Rostral width-1 (RW-1)	6.32 ± 0.15 10 5.69–7.03	6.70 ± 0.10 4 6.57–6.99	5.99 ± 0.06 20 5.50–6.44	6.53 ± 0.07 33 5.60–7.39
Rostral width-2 (RW-2)	5.21 ± 0.11 10 4.63–5.77	5.83 ± 0.05 4 5.72–5.93	5.16 ± 0.06 21 4.62–5.63	5.31 ± 0.05 33 4.51–5.81
Orbital fossa length (OL)	11.53 ± 0.09 10 11.09–11.98	11.37 ± 0.13 4 11.01–11.62	10.54 ± 0.11 21 9.80–11.93	11.34 ± 0.07 36 10.32–11.96
Nasal length (NL)	13.03 ± 0.20 10 11.64–13.71	13.12 ± 0.29 4 12.44–13.82	12.34 ± 0.19 20 10.58–14.20	12.44 ± 0.14 36 11.05–14.16
Least interorbital constriction (IOC)	4.87 ± 0.07 10 4.52–5.23	5.31 ± 0.09 4 5.04–5.43	4.97 ± 0.07 21 4.46–5.61	5.36 ± 0.03 36 5.04–5.65
Diastema length (D)	8.79 ± 0.17 10 7.71–9.28	8.70 ± 0.15 4 8.48–9.14	8.11 ± 0.11 21 7.05–9.05	9.03 ± 0.09 33 7.95–10.52

TABLE 2
(*Continued*)

Character	Species			
	New species	*laticeps*	*megacephalus*	*perenensis*
Palatal length (PL)	14.55 ± 0.20 10 13.19–15.47	14.41 ± 0.09 4 14.22–14.65	13.29 ± 0.12 21 12.10–14.32	14.71 ± 0.11 33 13.35–15.47
Alveolar width (AW)	6.13 ± 0.07 10 5.76–6.38	6.42 ± 0.20 4 6.03–6.84	5.87 ± 0.05 21 5.40–6.32	6.26 ± 0.05 33 5.66–6.73
Incisive foramen length (IFL)	4.74 ± 0.11 10 4.32–5.46	4.83 ± 0.14 4 4.41–5.04	4.40 ± 0.07 21 3.87–5.04	4.69 ± 0.05 33 4.14–5.26
Maxillary toothrow length (MTRL)	4.92 ± 0.05 10 4.74–5.18	5.20 ± 0.10 4 4.96–5.45	4.64 ± 0.04 21 4.33–5.01	4.99 ± 0.03 33 4.58–5.43
Zygomatic breadth (ZB)	16.77 ± 0.31 9 15.05–17.96	16.85 ± 0.17 4 16.44–17.25	15.80 ± 0.14 20 14.81–17.46	16.92 ± 0.11 33 15.32–17.87
Zygomatic plate length (ZPL)	3.81 ± 0.12 10 3.14–4.24	3.83 ± 0.08 4 3.74–4.05	3.44 ± 0.06 21 3.02–3.88	3.76 ± 0.07 33 3.20–4.87
Cranial depth (CD)	10.64 ± 0.14 10 9.83–11.32	11.41 ± 0.09 4 11.16–11.55	10.41 ± 0.13 19 9.46–11.40	10.14 ± 0.07 33 9.41–11.09
Mesopterygoid fossa length (MPFL)	5.29 ± 0.13 8 4.62–5.78	5.06 ± 0.17 4 4.81–5.53	4.79 ± 0.09 18 4.33–5.94	5.13 ± 0.06 33 4.45–6.21
Mesopterygoid fossa width (MPFW)	1.86 ± 0.05 10 1.48–2.15	1.98 ± 0.08 4 1.81–2.17	2.04 ± 0.04 21 1.72–2.32	2.18 ± 0.03 33 1.68–2.53

and edited using the Sequence Navigator software (Applied Biosystems, Inc.).

SAMPLES: We obtained the entire 1143-bp gene sequence for five individuals of the PNNKM *Oryzomys* series and added these to a truncated database of 801-bp sequences containing multiple individuals of each of the recognized species of the *O. megacephalus* group (Musser et al., 1998). Our complete dataset includes 19 sequences of *O. perenensis*, 41 of *O. megacephalus*, and 7 of *O. laticeps*, in addition to those of the new taxon, plus 4 sequences of *O. yunganus*. We used two sequences each of the five species of the *O. nitidus* complex (*O. emmonsae*, *O. legatus*, *O. macconnelli*, *O. nitidus*, and *O. russatus*; Musser et al., 1998) as the outgroup in phylogenetic analyses, a position supported by other molecular studies (e.g., Weksler, 2003). Sequences not generated for this study have been analyzed previously (Patton et al., 2000; Costa, 2003); provenance and other supporting data for each of these can be found in those publications. GenBank accession numbers for specimens of *Oryzomys* n. sp. USNM 597565–66 and 597572 are AY940623–5.

ANALYSES: We performed two levels of phylogenetic analysis, using the maximum parsimony inference in PAUP*4.0b10 (Swofford, 2002). The first included all 86 sequences of the combined *O. megacephalus* group and *O. nitidus* group samples, plus those of *O. yunganus*. Given the size of the dataset, we restricted this analysis to a single heuristic search using stepwise addition and

TABLE 3

Character Comparisons Based on ANOVA Between *Oryzomys*, New Species, and Three Other Species of the *Oryzomys megacephalus* Complex

Character	Comparison	Critical difference	*p*-value
Total length (ToL)	*laticeps*	20.586	0.3608 ns
	megacephalus	14.188	0.0002***
	perenensis	12.756	0.6364 ns
Tail length (TaL)	*laticeps*	13.220	0.1437 ns
	megacephalus	9.111	0.1010 ns
	perenensis	8.192	0.1254 ns
Hind foot length (HF)	*laticeps*	1.988	0.0007***
	megacephalus	1.370	0.0541
	perenensis	1.222	0.0001***
Ear height (E)	*laticeps*	1.347	0.0283*
	megacephalus	0.947	0.0137*
	perenensis	0.844	0.4528 ns
Condylo-basilar length (CIL)	*laticeps*	1.432	0.0385*
	megacephalus	0.945	0.0045**
	perenensis	0.868	0.1163 ns
Occipital condyle breadth (OCB)	*laticeps*	0.298	0.4761 ns
	megacephalus	0.202	0.0001***
	perenensis	0.186	0.0041**
Mastoid breadth (MB)	*laticeps*	0.564	0.2446 ns
	megacephalus	0.391	0.0007***
	perenensis	0.363	0.0030**
Basioccipital length (BOL)	*laticeps*	0.333	0.0197*
	megacephalus	0.227	0.0011**
	perenensis	0.209	0.0579 ns
Rostral length (RL)	*laticeps*	1.003	0.0001***
	megacephalus	0.669	0.0078**
	perenensis	0.612	0.0001***
Rostral width-1 (RW-1)	*laticeps*	0.463	0.0995 ns
	megacephalus	0.309	0.0524 ns
	perenensis	0.283	0.1378 ns
Rostral width-2 (RW-2)	*laticeps*	0.329	0.00031**
	megacephalus	0.219	0.9799 ns
	perenensis	0.201	0.3151 ns
Nasal length (NL)	*laticeps*	0.911	0.8501 ns
	megacephalus	0.607	0.0221*
	perenensis	0.556	0.0385*
Orbital fossa length (OL)	*laticeps*	0.458	0.4692 ns
	megacephalus	0.306	0.0001***
	perenensis	0.280	0.1677 ns
Least interorbital constriction (IOC)	*laticeps*	0.268	0.0018**
	megacephalus	0.179	0.2616 ns
	perenensis	0.163	0.0001***
Diastema length (D)	*laticeps*	0.613	0.7689 ns
	megacephalus	0.409	0.0037**
	perenensis	0.374	0.2107 ns

TABLE 3
(*Continued*)

Character	Comparison	Critical difference	*p*-value
Palatal length (PL)	*laticeps*	0.709	0.6901 ns
	megacephalus	0.473	0.0001***
	perenensis	0.432	0.4687 ns
Alveolar width (AW)	*laticeps*	0.310	0.0663 ns
	megacephalus	0.206	0.0137*
	perenensis	0.189	0.1598 ns
Incisive foramen length (IFL)	*laticeps*	0.353	0.6439 ns
	megacephalus	0.235	0.0114*
	perenensis	0.215	0.6224 ns
Maxillary toothrow length (MTRL)	*laticeps*	0.223	0.0143*
	megacephalus	149	0.0002***
	perenensis	0.136	0.2701 ns
Zygomatic breadth (ZB)	*laticeps*	0.803	0.8379 ns
	megacephalus	0.546	0.0013**
	perenensis	0.503	0.5425 ns
Zygomatic plate breadth (ZPL)	*laticeps*	0.362	0.9125 ns
	megacephalus	0.242	0.0053**
	perenensis	0.221	0.6616 ns
Cranial depth (CD)	*laticeps*	0.520	0.0045**
	megacephalus	0.347	0.3063 ns
	perenensis	0.317	0.0026**
Mesopterygoid fossa length (MPFL)	*laticeps*	0.446	0.3092 ns
	megacephalus	0.310	0.0022**
	perenensis	0.287	0.2786 ns
Mesopterygoid fossa width (MPFW)	*laticeps*	0.198	0.2587 ns
	megacephalus	0.132	0.0024**
	perenensis	0.121	0.0001***
PC-1	*laticeps*	0.774	0.3115 ns
	megacephalus	0.537	0.0001***
	perenensis	0.498	0.7324 ns
PC-2	*laticeps*	0.706	0.0032**
	megacephalus	0.490	0.0001***
	perenensis	0.454	0.0001***
PC-3	*laticeps*	1.057	0.0065**
	megacephalus	0.734	0.3148 ns
	perenensis	0.681	0.0552 ns

Fisher's PLSD posterior test used for comparisons between pairs of taxa; ns = nonsignificant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

tree-bisection-reconnection (TBR) branch swapping. This analysis (not presented below) confirmed the previous studies of Patton et al. (2000) and Costa (2003) regarding the monophyly of each of the species in the *O. megacephalus*-group, with bootstrap support of 96 to 100 at each basal node. We then performed a second analysis using a truncated dataset comprised of 1 sequence from each outgroup species and 3–6 of the most divergent sequences from each species clade identified in the initial analysis. For this

TABLE 4
Factor Loadings on the First Three Axes of a Principal Components Analysis Based on 20 Log-transformed Cranial Variables

Variable	PC-1	PC-2	PC-3
logCIL	0.948	0.054	−0.091
logOCB	0.573	−0.096	0.389
logMB	0.806	0.325	0.227
logBOL	0.610	−0.498	0.139
logRL	0.509	0.668	−0.057
logRW-1	0.868	−0.012	−0.113
logOL	0.892	−0.108	−0.084
logNL	0.584	−0.478	−0.214
logRW-2	0.696	−0.073	0.247
logIOC	0.506	0.541	0.249
logD	0.863	0.045	−0.379
logPL	0.910	0.030	−0.227
logAW	0.831	0.162	0.170
logIFL	0.628	−0.206	−0.053
logMTRL	0.593	0.220	0.382
logZB	0.922	0.035	−0.063
logZPL	0.751	−0.276	−0.028
logCD	0.221	−0.324	0.726
logMPFL	0.675	−0.339	−0.309
logMPFW	0.235	0.607	−0.209
Eigenvalue	10.122	2.136	1.466
% Variance explained	50.6	10.7	7.3

smaller dataset, we again used maximum parsimony but with the branch and bound search option, to provide an optimal recovery of minimum-length trees. In both analyses, we treated variable nucleotide characters as unordered and given equal weight, and assessed the robustness of nodes by bootstrapping (Felsenstein, 1985), with 1000 iterations.

MORPHOMETRIC ANALYSES: We obtained external variables (total length, tail length, length of the hind foot, and height of the ear) from specimen labels and recorded 20 cranial measurements with digital calipers to the nearest 0.01 mm. The variables are the same set used by Patton et al. (2000), who provide complete descriptions of each measurement: condyloincisive length [CIL], zygomatic breadth [ZB], mastoid breadth [MB], rostral length [RL], nasal length [NL], rostral width-1 [RW-1], rostral width-2 [RW-2], orbital length [OL], diastemal length [D], molar toothrow length [MTRL], incisive foramen length [IFL], palatal bridge length [PBL], alveolar width [AW], occipital condyle breadth [OCB], basioccipital length [BOL], mesopterygoid fossa length [MPFL], mesopterygoid fossa width [MPFW], zygomatic plate length [ZPL], and cranial depth [CD]. We assigned individuals to an age class based on tooth wear, using the pattern categories described by Myers and Carleton (1981), and included only adult specimens (age categories 3–5) in all statistical summaries and comparisons. For the latter, we used StatView, version 4.5 (SAS Institute, Inc., 1998) to calculate standard descriptive statistics (mean, standard error), compared samples of each species by ANOVA using Fisher's PLSD posterior test of significance for each pair of taxa, and visualized the relationship of each species sample in multivariate space using principal components following log-transformation. For canonical discriminant function analysis, also using log-transformed cranial variables for each a priori defined species, we used the software package Statistica, version 4.1 (StatSoft, Inc., 1994). Our selection of samples is not exhaustive, as prior studies (Musser et al., 1998; Patton et al., 2000) document relative character uniformity within each of the cis-Andean species of the *O. megacephalus* complex. The comparisons documented below are based on 18 specimens of the *Oryzomys*, n. sp., from eastern Bolivia, 4 of *O. laticeps* from coastal Brazil, 21 *O. megacephalus* from the southwestern Brazilian states of Mato Grosso and Mato Grosso do Sul, and 34 *O. perenensis* from western Amazonian Brazilian states of Amazonas and Acre, and the eastern Peru departments of Cusco and Madre de Dios. We measured all but the Brazilian samples of *O. perenensis* specifically for this study; for the latter we used a subsample of the 258 specimens analyzed in Patton et al. (2000). We measured width of the footpads with calipers on eight fluid-preserved specimens of *O. perenensis*, four of *O. laticeps*, four of *O. megacephalus*, and two of *O.* n.sp.

We compared pelage colors under natural spectrum light; colors when capitalized, are from Ridgeway (1912). We also give values from Smithe (1975) and descriptive names.

SPECIMENS EXAMINED AND GAZETTEER

Localities, in degrees, and number corresponding to the map (fig. 6) are given at the

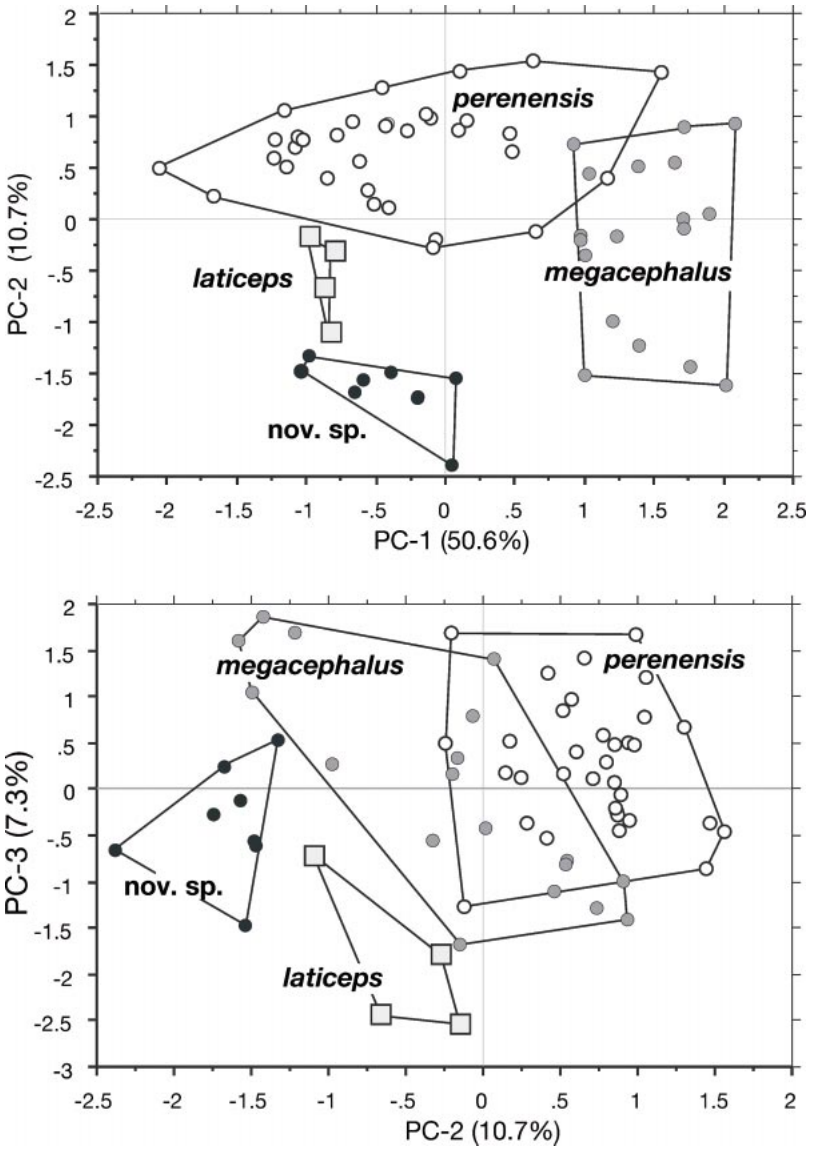

Fig. 2. Bivariate plots of individual scores of four taxa of the *O. megacephalus* complex along the first and second (top) and second and third principal components axes (bottom). Scores for each taxon are enclosed in a polygon and identified by name. The percent of the total variation explained by each axis is indicated.

beginning of each listing, for the Bolivian samples only. Specimens of species of the *O. megacephalus* complex that were compared are from populations for which molecular genetic data are available. Specimens measured for morphometric analysis are listed separately at the end of each taxon. See Materials and Methods for specimens sampled for molecular genetic analyses.

Museums are abbreviated as follows: MNK, Museo de Historia Natural Noël Kempff Mercado, Santa Cruz, Bolivia; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC,

TABLE 5
Standardized Discriminant Coefficients in Comparisons Among Four Species of the *Oryzomys megacephalus* Complex

Character	CV-1	CV-2	CV-3
logCIL	0.60137	1.599176	0.696075
logOCB	0.00422	−0.383512	−0.089688
logMB	−0.15465	−0.544803	−0.019106
logBOL	0.14234	0.313213	0.706709
logRL	0.36188	0.544815	0.333378
logRW-1	0.28271	−0.340953	−0.076575
logOL	−0.11181	−0.524758	0.038083
logNL	−0.87830	−0.075475	0.012545
logRW-2	−1.14483	0.103332	0.373810
logIOC	1.15849	0.524637	0.161669
logD	−1.20501	−0.391325	−0.406870
logPL	1.35186	−0.817506	−0.078400
logAW	−0.05335	−0.053106	−0.059271
logIFL	0.10496	−0.094369	−0.058589
logMTRL	0.07024	−0.382983	0.303447
logZB	0.20421	0.037359	−0.497290
logZPL	0.44796	−0.081082	−0.097800
logCD	−1.18676	−0.222314	0.252944
logMPFL	0.29101	−0.075321	−0.185278
logMPFW	0.19215	0.509802	−0.154018
Eigenvalue	9.86733	3.062892	1.272685
% Variance explained	69.474	21.565	8.961

Analyses are based on $\log_{10}$-transformed variables only.

USA; MVZ, Museum of Vertebrate Zoology, University of California at Berkeley, USA. All uncataloged specimens are in the collection of MNK.

Oryzomys, n.sp.: BOLIVIA, Departamento Santa Cruz: Provincia Velasco, Parque Nacional Noël Kempff Mercado: (1) El Refugio Huanchaca (14°42.553′S, 061°2.034′W, elev. 170 m), MNK 2010; USNM 597563–79, MNK uncataloged, IGP 45, IGP 47, IGP 55–6, LHE1582, NRS09, NRS 13, NRS 16, NRS 25, VCC 01–05, VCC08, VCC 11, VCC 15; (2) Huanchaca II (14°31.416′S, 060°44.364′W, elev. 700 m), USNM 588192; (3) Los Fierros (14° 33.338′S, 060° 55.717′W, elev. 200 m), MNK uncataloged LHE 1680; (4) Lago Caiman (13°35.98′S, 060°54.90′W), MNK 1949, 1952; (5) Dept. Santa Cruz, Provincia Velasco, Toledo (14°42.55′S, 061°9.534′W, a camp belonging to the El Refugio Huanchaca property, outside of the PNNKM, 14 km SW of El Refugio Huanchaca), MNK 2008, 2009, 2011, 2013, 2016; (6) San Martín (14°19.8′S, 062°25.2′W), MNK 1611. (7) Provincia Guarayos; Urubicha, Río Negro (14°58.33′S, 062°36.36′W), MNK uncataloged, field no. NR10, only skin seen; Departamento Beni; (8) San Joaquín (13°4.0′S, 064°49.0′W), USNM 460272, 460738; (9) Yutioles (13°15′S, 064°48′W), USNM 460429; (10) Curicha (12°37.02′S, 063°31.02′W), USNM 551653–4. Morphometric: adult (N = 7; ages 3–5) USNM 597563, USNM 597565, USNM 5975677, USNM 597569, USNM 597571–2, USNM 59776 (localities listed above).

Oryzomys megacephalus: BRAZIL, Pará, Rio Xingu, 53 km SSW Altamira, USNM 549542–50, 549813–4; Mato Grosso, Barra do Garças, MVZ 197663; Mato Grosso do Sul, 54 km W. Dourados, MVZ 197675. Morphometric: (N = 18 adult); BRAZIL, Amazonas, 554848; Mato Grosso: Reserva Ecológica Cristalino, 40 km N Alta Floresta MVZ 197525; Fazenda Lagoa Bonita, 36 km N Barra do Garças, MVZ 197526; Fazenda São Luis, 30 km N Barra do Garças, MVZ 197528, 197530–1; Fazenda Noirumbá, 34 km NW Ribeirão Cascalheira, MVZ197535–6; Tocantins, Rio Santa Teresa, 20 km NW Piexe, MVZ 197533–4; Minas Gerais, Mata do Vasco, 12 km W Nova Ponte, MVZ197537–9. Localities listed above, USNM 549542–5, 549548.

Oryzomys perenensis: BRAZIL, Amazonas, Rio Juruá, Penedo, right bank, MVZ 190458–71; Rio Juruá, left bank, Igarapé Nova Empresa, MVZ 190481–84; Rio Juruá, right bank, Seringal Condor, MVZ 190485–94; PERU, Madre de Dios; Río Manu, USNM 530922–3, 559397–8, 559416; Río Tambopata, USNM390066–7, 399626, 53092–4; Junín, Vitoc, USNM 507246. Morphometric: (N = 34 adult) USNM 390066, USNM 530923–4, 559397; USNM 507246; MVZ 190458, MVZ 190460–71, MVZ 190481–4, MVZ 190485–94 (localities listed above).

Oryzomys laticeps: BRAZIL, Bahia, Jequié, USNM 545055–6; Ilheos (Ilhéus), USNM 304571; Fazenda Bolandeira, 10 km S Una, MVZ 197606, 197631. Morphometric: (N = 4 adult) USNM 545055–6, 304571; MVZ 197606 (localities listed above).

RESULTS

SEQUENCE DIVERGENCE: According to Kimura 2-parameter distances within and among each of the five taxa within the *megacephalus* complex sensu latu (table 1), the sample from eastern Bolivia is markedly different from all other species in the complex, being closest to *O. laticeps* from coastal Brazil (K2p mean of 11.99). The remaining comparisons were presented earlier by Patton

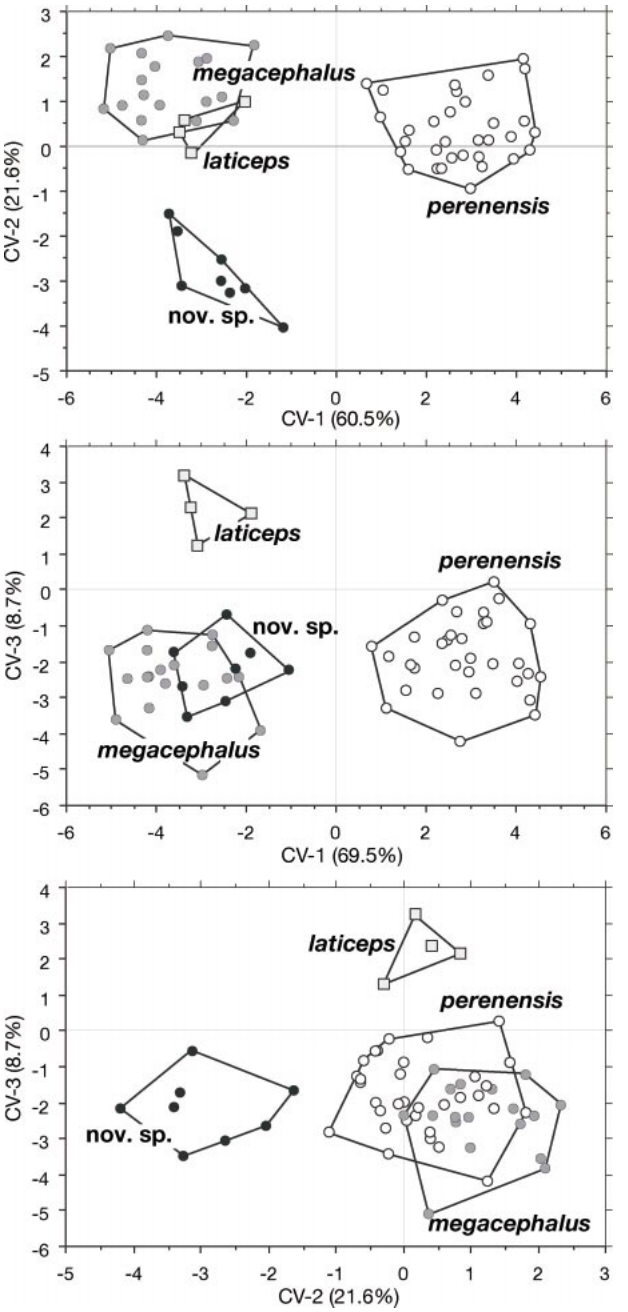

Fig. 3. Bivariate plots of group centroids on canonical variates derived from discriminant functional analysis. Individual scores of four taxa of the *Oryzomys megacephalus* complex along the first and second canonical variates. Scores for each taxon are enclosed in a polygon and identified by name. The percent of the total variation explained by each axis is indicated.

TABLE 6
Mean Width and Standard Deviation, in Millimeters, of Interdigital (ID) and Hypothenar Hind Foot Pads and Hind Foot Length of the Same Specimens

		HF		ID Pad 1		ID Pad 2		ID Pad 3		ID Pad 4		Hyp
Taxon	*N*	*x*	SD	*x*	SD	*x*	SD	*x*	SD	*x*	SD	*x*
O. perenensis	8	31.9	0.83	1.3	0.11	1.5	0.10	1.4	0.18	1.6	0.11	1.1
O. laticeps	4	32.0	1.82	1.3	0.08	1.4	0.07	1.4	0.08	1.5	0.12	1.1
O. megacephalus	4	29.5	1.73	1.1	0.14	1.4	0.13	1.3	0.16	1.2	0.21	0.8
O. acritus	2	29.5	0.71	1.6	0.35	1.5	0.21	1.5	0.11	1.6	0.07	1.7

et al. (2000: table 35). The numerical uniqueness of the Bolivian sample relative to other species is consistent with a species definition based on sequence divergence (e.g., Bradley and Baker, 2000), although we prefer not to base a species concept solely on a simple phenetic distance measure.

Members of the *O. megacephalus* group of taxa appear monophyletic with respect to other such groups in the genus, at least with the limited taxon and gene sequences available (Smith and Patton, 1999; Bonvicino and Moreira, 2001; Weksler, 2003). However, the level of bootstrap support uniting the four taxa of this complex, including the new Bolivian taxon, relative to *O. yunganus* and the outgroup members of the *O nitidus* complex, is only 71 (data from the large, 86-sequence analysis not shown). The branch-and-bound analysis of the truncated dataset of these taxa yielded two minimal-length trees of 740 steps (fig. 1). Of the 801 characters in the analysis, 515 are constant across all sequences, 65 are parsimony uninformative, and 221 are parsimony informative. The two trees differ only in the position of two sequences within the *O. laticeps* clade; all other nodes are shared in common. Bootstrap support for each species clade ranges from a minimum of 93 (the basal node of *O. megacephalus*) to 99 (basal node of *O. yunganus*) and 100 (basal nodes for the other three taxa). *Oryzomys yunganus* is consistently placed at the base of a clade containing the remaining four species, although again with only limited bootstrap support (74). The four taxa of the restricted *megacephalus* group (sensu Costa, 2003) exhibit a consistent hierarchical structure in both trees of (*O. megacephalus* (*O. laticeps* (*O. perenensis* + *O.* n.sp.))). However, none of the connecting nodes has bootstrap support greater than 50. As a consequence, we cannot offer a robust hypothesis of relationships among any of the four *megacephalus* group species with the limited amount of available sequence data. Thus, the apparent closer relationship between the new taxon and *O. laticeps* suggested by their more similar sequence divergence (table 1) cannot be supported by the hierarchical analysis. What is clear, however, is that both genetic distance and phylogenetic placement indicate equal uniqueness of the new Bolivian specimens in comparison to the other taxa in the group currently recognized as species (Musser et al., 1998; Patton et al., 2000; Costa, 2003).

MORPHOMETRIC DIVERGENCE: Summaries of external and cranial mensural variables (table 2) show the sample from Bolivia to be generally intermediate in most external and cranial dimensions between *O. megacephalus* and *O. perenensis*, with *O. laticeps* the largest of the four taxa. In pairwise comparisons, the new taxon is significantly different from one or more of these other three species in 3 of the 4 external and in 19 of 20 cranial variables, with the exception of tail length (Tal) and rostral width-1 (RW-1), different significantly from *O. laticeps* in 9 variables, from *O. megacephalus* in 18 variables, and from *O. perenensis* in 8 variables (table 3).

The first three axes of the Principal Components Analysis accounted for a total of 68.6% of the total variation present, and each of these axes had eigenvalues of 1.466 or greater. Not surprisingly, the unrotated factors on PC-1 were all positive and relatively high (table 4), suggesting a general size component. The position of individual specimens

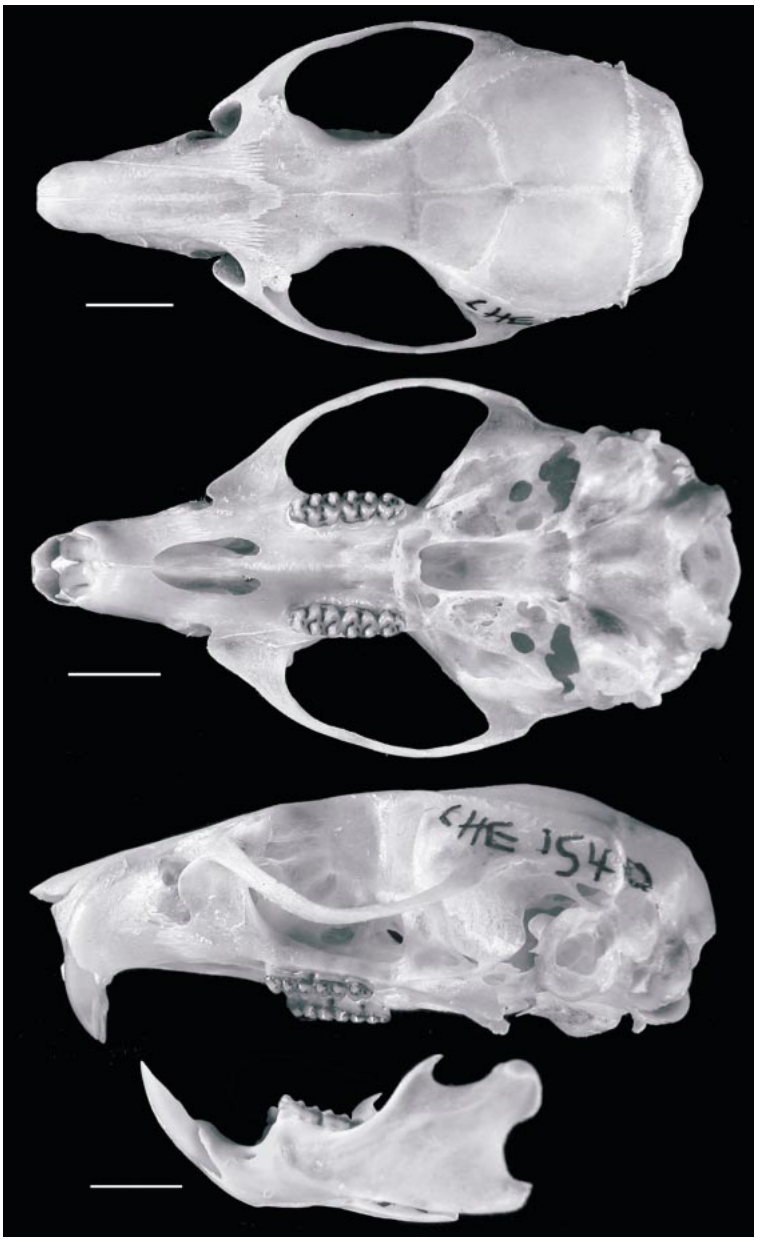

Fig. 4. Cranium and mandible of the holotype of *O. acritus* (MNK 3628).

along PC-2 generally is weighted most heavily by rostral length (logRL), mesopterygoid fossa width (logMPFW), and interorbital constriction (logIOC) opposing basioccipital length (logBOL) and nasal length (logNL), while position on PC-3 is weighted most heavily by cranial depth (logCD), occipitalcondyle breadth (logOCB), and maxillary toothrow length (logMTRL) versus diastema length (logD) and mesopterygoid fossa length (logMPFL).

Each of the four taxa of the *megacephalus* complex examined morphometrically is separable along combinations of PC-1 and PC-2 and, to a lesser extent, on PC2 and PC-3 axes (fig. 2). The new taxon from Bolivia

differs significantly from *O. laticeps* on PC-2 and PC-3 (table 3), from *O. megacephalus* on PC-1 and PC-2, and from *O. perenensis* on PC2. *Oryzomys laticeps* differs from the latter two on all three axes, but *O. megacephalus* and *O. perenensis* are broadly overlapping, particularly on the second and third axes.

Three canonical axes were extracted from the same set of morphological variables used in the PCA analysis, the first explaining 69.47%, the second 21.57%, and the third 8.96% of the total variance (table 5). The predefined species groups are each highly significantly different from one another, with the Mahalanobis D^2 for the comparisons between the Bolivian taxon and each of the other three species 42.56 (*O. laticeps*; $F_{(20,40)} = 3.029$, $p = 0.0014$), 51.14 (*O. perenensis*; $F_{(20,40)} = 9.957$, $p < 0.0001$), and 35.53 (*O. megacephalus*; $F_{(20,40)} = 5.971$, $p < 0.0001$). Not surprisingly, therefore, all individual specimens are correctly assigned to their respective species groups with posterior probabilities of group membership < 0.99989.

As is apparent from the bivariate plots of each pair of canonical axes, the new taxon from Bolivia is readily and completely separable from all other species along the second canonical axis (fig. 3, top and bottom panels), but overlaps with the scores of *O. megacephalus* on CV-1 and CV-3 (fig. 3, middle panel). *Oryzomys laticeps* is uniquely separable from the other three species on CV-3, and both *O. megacephalus* and *O. perenensis* are completely separable on CV-1 but overlap substantially on both CV-2 and CV-3. Based on the standardized discriminant coefficients, the combination of rostral width-2 and diastema length versus palatal length distinguish the Bolivian taxon from all others on the first axis (table 5). Clearly, in morphometric terms, the Bolivian taxon is markedly distinct from other members of the *megacephalus* complex of species distributed in the lowland tropical forests of cis-Andean South America.

Oryzomys acritus, new species
Figures 4–13; tables 2, 6

HOLOTYPE: MNK 3628, collected 6 November 1998 by Louise H. Emmons (field no. LHE1540). A young adult male with hindquarters terminating molt from juvenile to adult pelage, prepared as a skin and skull, liver tissue preserved in ethanol. External measurements recorded on label: TL = 261, T = 121, HF = 32, E = 20, weight = 57 g. Testes scrotal, 8 × 5 mm.

PARATYPES: USNM 588193, 597563–79; MNK (uncataloged) field nos. IGP 45, IGP 47, IGP 55–6, LHE 1582, NRS 09, NRS 13, NRS 16, NRS 25, VCC 01–5, VCC 08, VCC 11, VCC 15; all from the type locality; USNM 588192, from Huanchaca II; and MNK uncataloged LHE 1680, from Los Fierros. Only specimens from localities within PNNKM are designated as paratypes.

TYPE LOCALITY: Bolivia: Departamento de Santa Cruz, Provincia Velasco, Parque Nacional Noël Kempff Mercado, El Refugio Huanchaca, an outpost with a few buildings and an airstrip on private property, but within the park (14°42.553 ′S, 061°2.034 ′W [WGS 84]; elev. 170 m); on older published maps, the locality now known as El Refugio Huanchaca is shown as Huanchaca, an estancia. In 2004 the present owners added Huanchaca to their former designation of El Refugio, which appears on specimen labels and is the same locality. Captured in a deciduous forest 3.5 km north of the outpost.

DIAGNOSIS: A medium-sized terrestrial rat. Dorsal color near Olive Brown to Saccado's Umber (olive brown 28 of Smithe, 1975), cheeks and sides with orange tones, Buckthorn Brown to Ochraceous Tawny (clay color 26 to cinnamon 123A of Smithe); rostrum and top of head to behind eyes dusky, close to Deep Neutral Gray, lined with black-tipped hairs, contrasting with brown top of crown. Pelage long, tips of most hairs at mid-rump reaching 9 mm; ventral fur dense and long, 3–4 mm on chest between forelegs; hairs pale gray at base with long white tips, overall ventral appearance whitish, inner limbs white; white of inner hind legs continuous with whitish tops of feet. Hind foot pads large, interdigital and hypothenar pads wider than 1.3 mm. Cranium lacking squamosoalisphenoid groove and sphenofrontal foramen (Musser et al. 1998); bony palatal excrescences strongly developed (fig. 4). Upper second molar with a short paraflexus and a single fossette; lower second molar with a

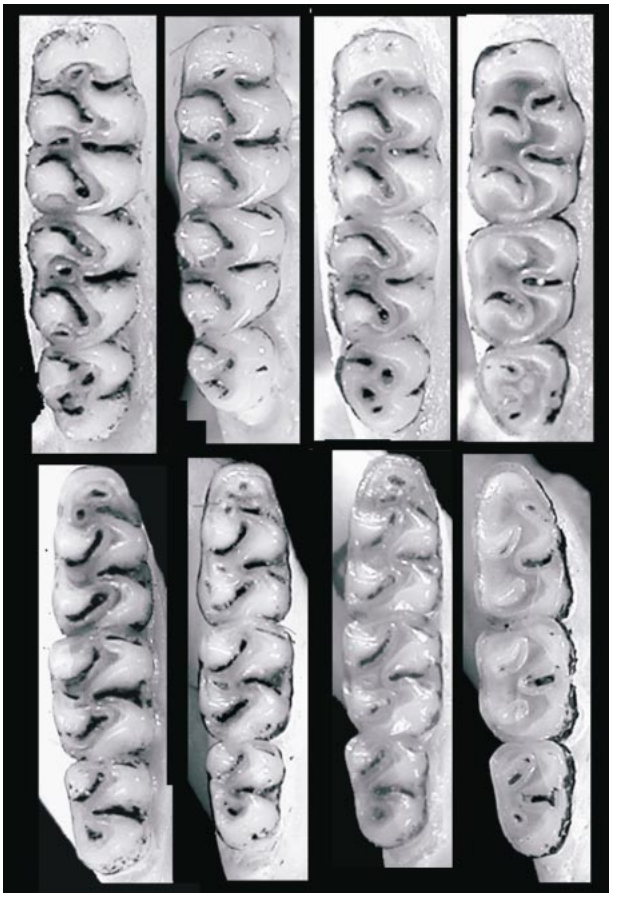

Fig. 5. Tooth wear series of *O. acritus*, age classes I to IV. Paratypes, from left to right (USNM 597564, 597577, 597576, 597563).

short hypoflexid opposite a lingual fossettid (fig. 5).

DISTRIBUTION AND HABITAT: *Oryzomys acritus* were captured by LHE at four localities in the PNNKM and one just outside its borders (fig. 4, localities 1–5). The park is on the Brazilian Shield; its vegetation is a mosaic of humid, semi deciduous and deciduous forests and liana forests, and wet and dry savanna and cerrado formations. The biota and geology are described in detail in Killeen and Schulenberg (1998) and the vegetation also in Panfil (2001). These rats were captured on the ground with Sherman, Tomahawk, and break-back traps and a standardized bait of oatmeal and raisins flavored with fish oil and essences of vanilla, banana, and coconut, in forests that ranged from evergreen riverine or gallery forest to deciduous and semideciduous terra firme and seasonally flooded forest bordering seasonally flooded pampa. One locality (Huanchaca II) is at 700 m on top of the Huanchaca meseta, but its forest is similar in species composition of both flora and fauna to that of the lower elevation sites where the species was found within the park (Killeen and Schulenberg, 1998). These forests either have a seasonally deciduous emergent canopy, sparse understory, and midstory varying in deciduousness depending both on the location and on the dryness of the particular year, or are liana forests, with low canopies and dense lianas at all levels. Additional specimens were identified in collections from near San Joaquín, Departmento Beni, and Guarayos, Departmento Santa Cruz. All localities identified thus far are in the area drained by western tributaries of the

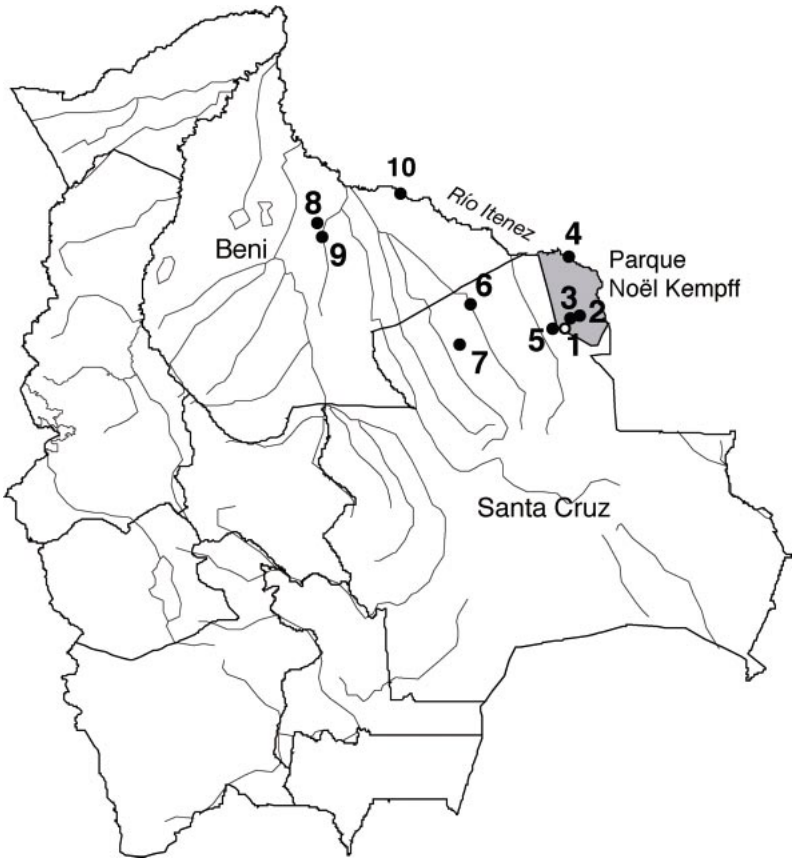

Fig. 6. Map of Bolivia showing known localities of *O. acritus*; see specimens examined for names and coordinates; open circle (locality 1) represents the type locality.

basin of the Río Itenez (named Rio Guaporé in Brazil: fig. 6).

ETYMOLOGY: From the Greek *akritos*, ''confused, mixed, doubtful'' (Brown, 1956), with reference to the mixed characters that can be confused with those of *O. megacephalus* or even *O. nitidus*.

DESCRIPTION: A medium-sized rat (table 2) of similar aspect and color to *Oryzomys megacephalus* sensu Patton et al. (2000). Above brown to yellow-brown with hairs gray-based, younger individuals darker and less yellowish than old animals; occasional individuals bleached slightly reddish overall. Sides paler than dorsum, yellowish to distinctly orange, brightest on cheeks and below ear; lateral color can extend from thigh forward to cheeks below eye and to whitish spot at base of mystacial vibrissae. Rostrum dusky above to behind eyes, with dusky-tipped cream or whitish hairs. Anteroventral base of ear with inconspicuous preauricular tuft of entirely whitish or pale gray hairs sometimes tipped with pale rufous, probably associated with a cutaneous gland. Pinnae brown, thinly clothed on the interior surface with whitish or, rarely, brown hairs. Skin surrounding eye blackish. Ventral pelage whitish; hairs quite long, pale gray at bases with long white tips; white of inner legs extending to join pure white of fore and hind feet; hair at wrists white-based; chin spot self-white. Pelage at mid-rump with majority of hairs measuring 8–10 mm (a few longer hairs may be present). Ventral pelage on chest between forelegs 3–4 mm. Tail dusky, paler below at base, but not prominently bicolored, clothed with inconspicuous short, fine, dusky hairs. Hind feet long and narrow (terrestrial type), with digits II–IV noticeably longer than I and

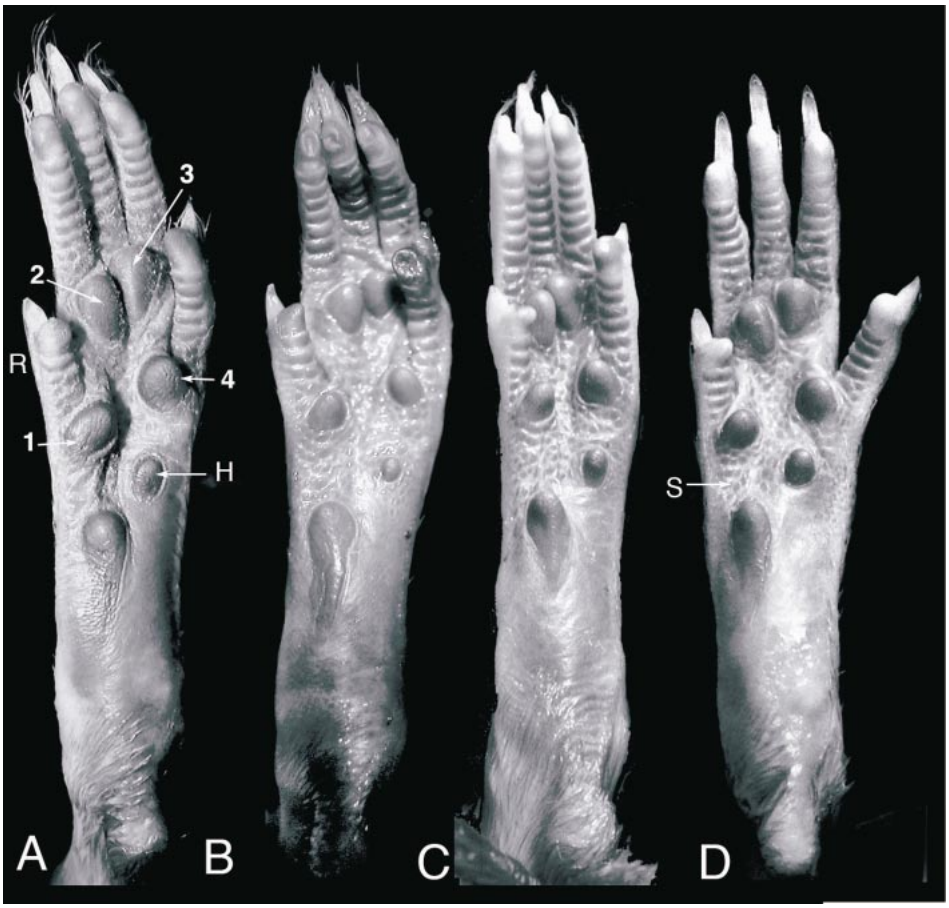

Fig. 7. Soles of left hind feet of (**A**) *Oryzomys acritus* (USNM 597574); (**B**) *O. megacephalus* (MVZ 197663), note tiny hypothenar pad; (**C**) *O. perenensis* (MVZ 191254); (**D**) *O. laticeps* (MVZ 197631). Interdigital pads are numbered; H indicates hypothenar pad; S indicates plantar squamae. R is adjacent to the single complete dermal ring on first digit of *O. acritus*; note presence of two rings in **B** and **C** and three in **D.**

V; soles brown but not strongly pigmented. Six footpads always present, hypothenar and fourth interdigital pads broad (fig. 7); thenar pad with strongly raised part of pad short and nearly round; squamae between and around pads inconspicuous.

Cranium similar to those of other members of the *megacephalus* group, with most diagnostic features as outlined by Musser et al. (1998), including no squamosoalisphenoid groove or sphenofrontal foramina; incisive foramen short and broad, teardrop-shaped (figs. 8, 9, 10); and bony palate long. Supraorbital ridge prolonged into strongly developed temporal ridge that extends across parietal to occipital suture. Parietal usually with a small but distinct contribution to lateral braincase wall exhibited by a ventrad extension of the posterolateral border of the parietal forward of the parieto-occipital suture (Musser et al., 1998: fig. 62); area of ventral contribution appears to decrease with age. Foramen ovale large and rounded, such that the opening is visible below the alisphenoid when the skull is viewed from the side (fig. 11). Anterior rim of auditory meatus usually notched, notch depth decreasing with age (fig. 11). Second upper molar with a long paraflexus, a short hypoflexus, and a labial fossette, but no medial fossette; second lower

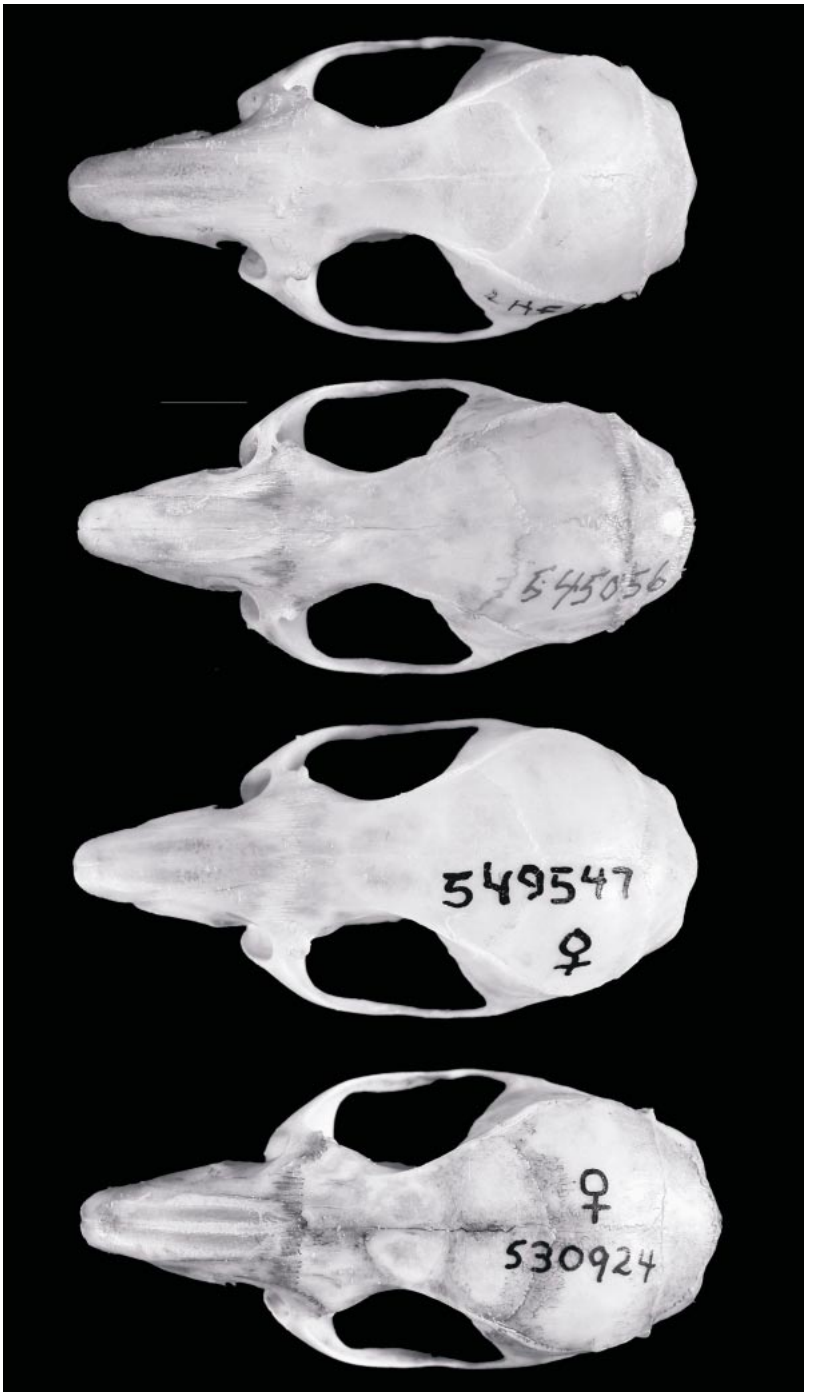

Fig. 8. Dorsal view of crania of four species of the *megacephalus* complex, from top down: *O. acritus* (USNM 597577), *O. laticeps* (USNM 545056), *O. megacephalus* (USNM 549547), *O. perenensis* (USNM 530924).

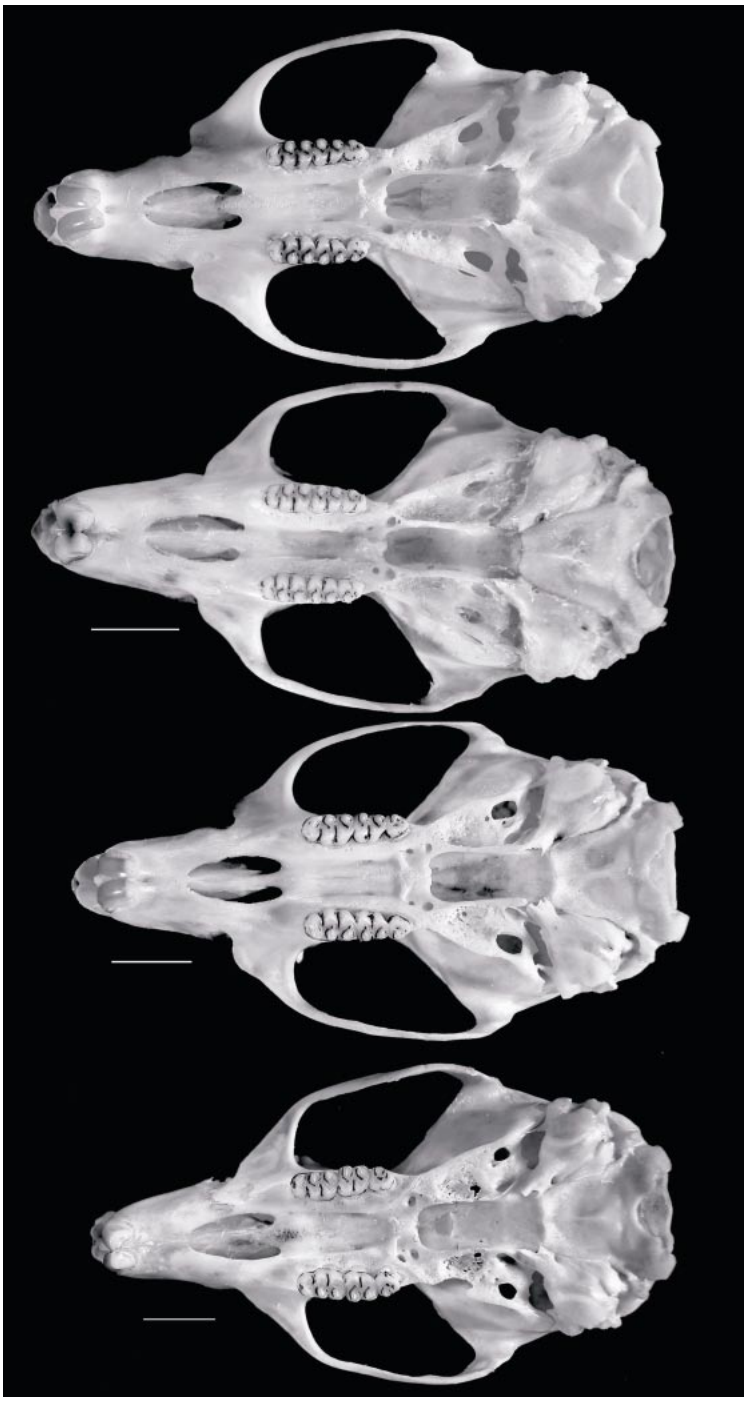

Fig. 9. Ventral view of crania, same specimens as in figure 8.

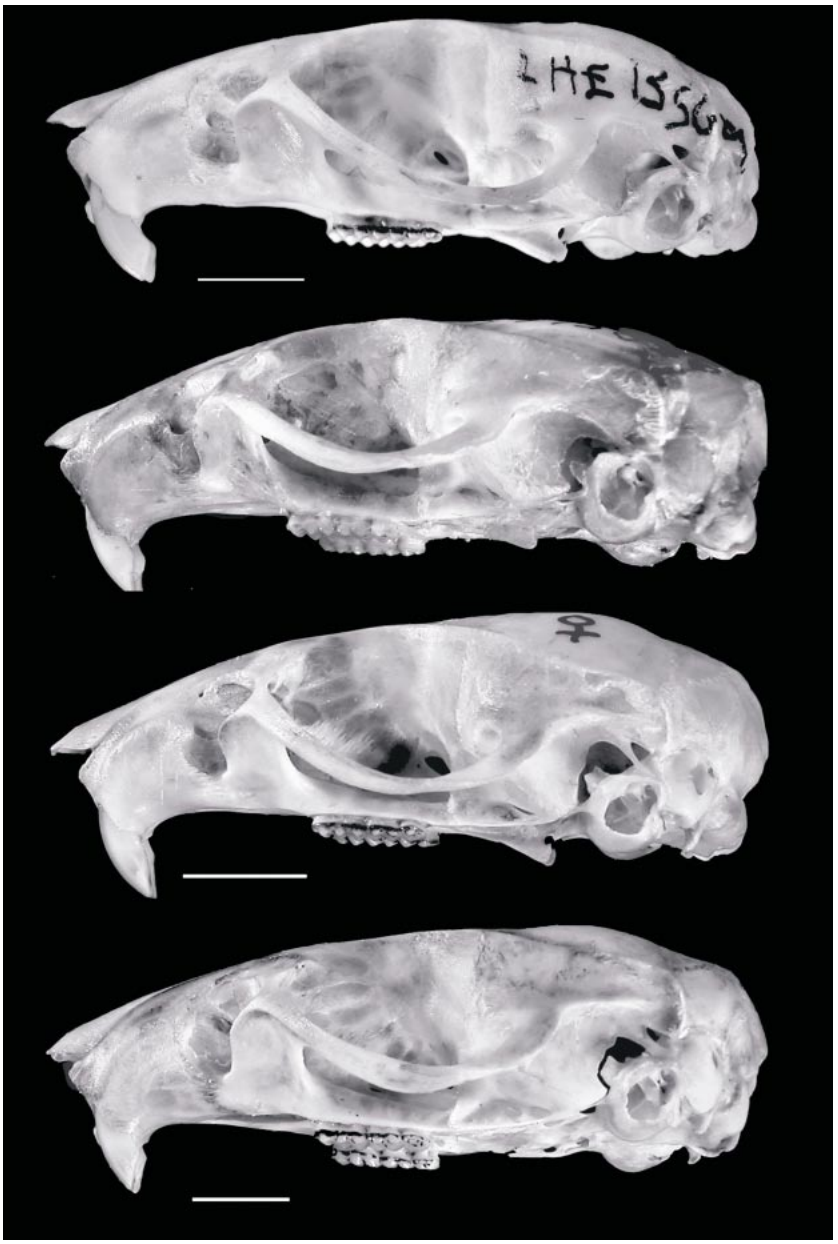

Fig. 10. Lateral view of crania, same specimens as in figure 8.

molar with hypoflexid reaching halfway or less across tooth, opposite a lingual fossettid (figs. 5, 12).

Comparison with Other Species

We compare *O. acritus* only with the geographically adjacent members of the *megacephalus* group, *O. perenensis* and *O. megacephalus*, and with the genetically most closely related *O. laticeps*. As comparisons between these and members of other *Oryzomys* species and species groups are detailed and illustrated in Musser et al. (1998), we mention only a few of them, and we did not

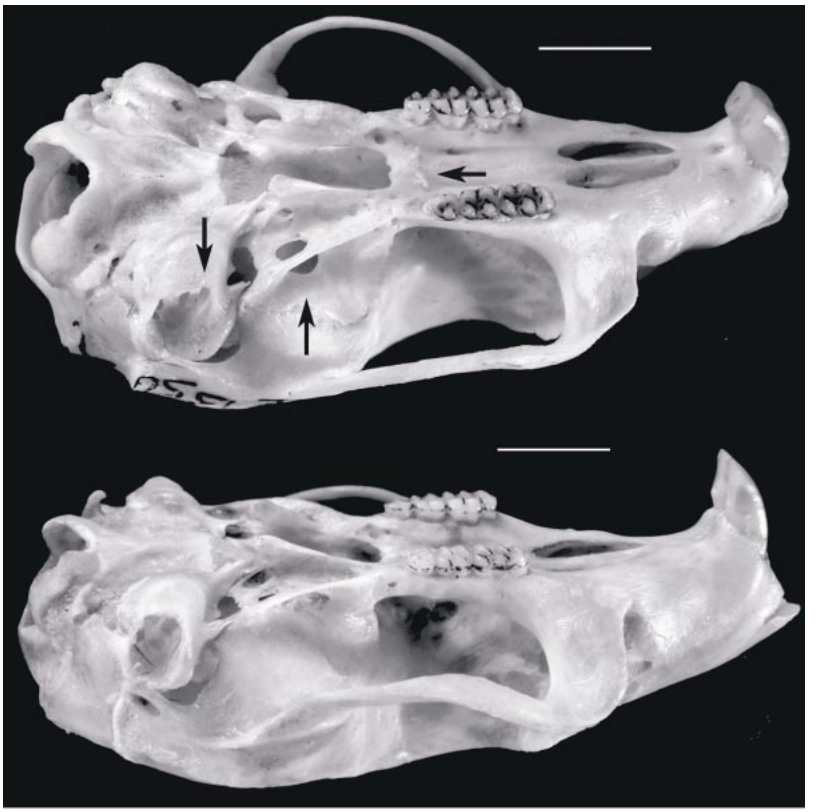

Fig. 11. Crania of young adult *O. acritus* (USNM 597577; above) and *O. megacephalus* (USNM 549548; below). Arrows point to notch in rim of meatus, large foramen ovale, and strongly developed bony palatal excrescences of *O. acritus*.

compare any *O. megacephalus* from north of the Amazon river. Externally, *O. acritus* is distinguishable from lowland populations of *O. megacephalus* and *O. perenensis* by its longer dorsal and ventral pelage (however, montane *O. perenensis* are similarly long furred). It is distinguishable from *O. perenensis* and *O. laticeps* by its orange-toned lateral color, and from lowland *O. perenensis* by its whiter venter (fig. 13) and white interior ankles. *Oryzomys laticeps* lacks the pale preauricular tuft that is present in the other three species, and its ventral pelage can have a yellowish tinge, unlike the generally pure white ventral hair tips of the others. The dorsal pelage of both *O. acritus* and *O. megacephalus* is slightly paler and more warm toned (yellow or reddish) than that of *O. perenensis* and *O. laticeps* (fig. 13), such that some older, redder individuals could be confused in the hand with *O. nitidus* (as can some *O. megacephalus*). Sympatric *O. nitidus* are larger, with a much clearer, brighter, and better defined orange lateral pelage and a bicolored tail. *Oryzomys acritus* has a dusky rostrum with blackish hair tips, contrasting with its brown crown, and differs from *O. megacephalus*, whose paler, Buffy Brown tipped rostral hairs do not contrast with the crown (fig. 13). *Oryzomys perenensis* and *O. laticeps* also have dusky rostra with dark-tipped hairs, but their crowns are darker and do not contrast with the rostral color.

The hind footpads of two taxa have distinguishing characters. We examined only three fluid specimens of *O. acritus*, one a juvenile, so a larger series could alter our perception of differences. *Oryzomys acritus* has broader first interdigital and hypothenar pads than

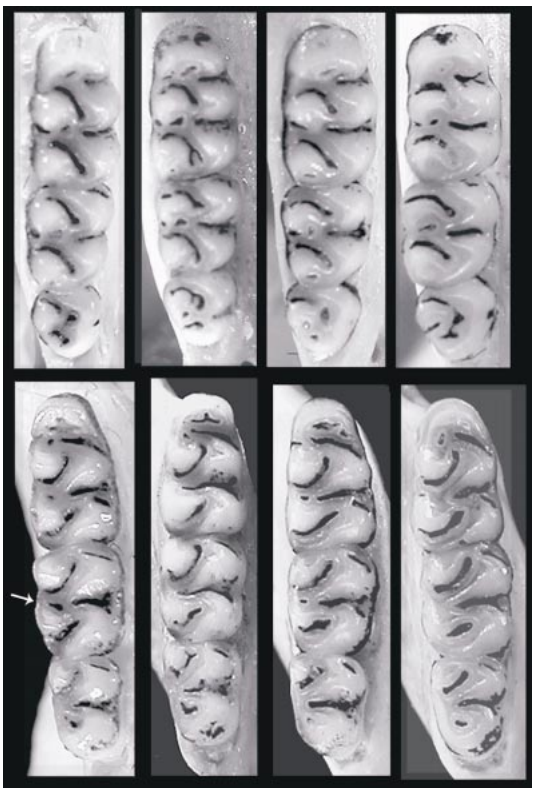

Fig. 12. Occlusal cheekteeth of four species of the *megacephalus* complex, maxillary teeth above, mandibular teeth below; left to right: *O. acritus* (USNM 597577), *O. laticeps* (USNM 304571), *O. megacephalus* (USNM 549547), *O. perenensis* (USNM 549524). Note presence of fossettid (arrow) in *O. acritus* and *O. megacephalus*, and absence of fossettid and longer hypoflexid (opposite fossettid) in the two others.

any of the other species (table 6). *Oryzomys megacephalus* is distinguished from all others by its small to tiny interdigital and hypothenar pads (fig. 7), a feature that is also illustrated in Voss et al. (2001: fig. 53). The plantar pads and squamae of *O. perenensis* are much more darkly pigmented than those of the other species. *Oryzomys laticeps* alone has large and prominent squamae, noticeable even on dried skins. The plantar skin of the first digit of all three *O. acritus* that we examined had a single complete dermal ''ring'', distal to several interrupted or broken rings (fig. 7), whereas *O. megacephalus* had two ($N = 3$) or three rings ($N = 1$) , *O. perenensis* had two2 rings ($N = 8$) , and *O. laticeps* had one ($N = 1$), two ($N = 2$), or three rings ($N = 1$). We examined this feature on fluid-preserved material only; larger samples are needed to confirm the constancy of these differences.

The lower second molars of both *O. acritus* and *O. megacephalus* have a short metaflexid opposite a lingual fossettid, whereas *O. perenensis* and *O. laticeps* have long hypoflexi and lack a fossettid in this tooth (fig. 12).[3] *Oryzomys acritus* shares with the other three species the long paraflexus of M2 that is linked to the absence of a medial fossette (Musser et al., 1998); this configuration thus remains a character that unites all members of the species complex (fig. 12).

The crania of the four *megacephalus* complex taxa are difficult to distinguish by qualitative characters, although the morphometric analysis shows that they are distinct in combination of size variables (figs. 2 and 3; table 2). Because for all measurements, the length ranges overlap among species, no simple size key can readily assign a cranium to species. *Oryzomys laticeps* is distinctly the largest taxon and *O. megacephalus* the smallest, with the other two taxa intermediate between them. Differences between the taxa are summarized in table 7, but we admit that specimens of *O. acritus* are not easy to distinguish from *O. megacephalus*, especially when the preparations are in poor condition.

DISCUSSION

The genus *Oryzomys* has been progressively dismantled by taxonomists (Gardner and Patton, 1976; Carleton and Musser, 1989; Musser et al., 1998; Voss and Carleton, 1993). Recent studies with nuclear DNA se-

[3] We note that in the photo of the teeth of the neotype (UMMZ 133811) of *Mus megacephalus* Fischer, 1814, from Paraguay, shown in Musser et al. (1998: fig. 119), a fossettid is not evident in m2. However, the hypoflexid is short, as in *O. megacephalus* from Brazil that we examined (fig. 12), and perhaps the fossettid was worn away on the neotype. The first lower molar of the neotype also does not show the prominent fossettid in the anteroloph of m1, visible in young specimens of all members of the *megacephalus* complex that we examined. Genetic evidence clearly associates some Paraguayan *O. megacephalus* with animals collected thousands of kilometers to the north (fig. 1; Patton et al., 2000: fig. 97), and we do not question the placement of samples from Pará in *O. megacephalus*.

Fig. 13. Anterior and lateral views of skins. Top, from left: *O. laticeps* (USNM 545056), *O. perenensis* (USNM 530924), *O. megacephalus* (USNM 549548), *O. acritus* (USNM 597565). Below, from top, *O. laticeps* (USNM 545056), *O. perenensis* (USNM 582890), *O. megacephalus* (USNM 549548), *O. acritus* (USNM 597563). Note the warmer dorsal color of *O. megacephalus* and *O. acritus*, the contrasting dusky rostrum of *O. acritus*, paler and more uniform head color of *O. megacephalus*, and the slightly whiter venter of *O. acritus* compared to more grayish underparts of the upper two specimens.

quencing (Weksler, 2003) support previous evidence (e.g., Voss and Carleton, 1993) that the genus *Oryzomys* is not monophyletic, and we anticipate that the *O. megacephalus* complex (including *O. yunganus*), the *O. subflavus* complex, the *O. nitidus* complex, and as many as six other taxa will in short order each be segregated into separate genera (Weksler, 2003). This question is only pertinent here in that our results clearly place *O. acritus* in a clade with *O. megacephalus*, *O. perenensis*, and *O. laticeps*.

To date, we have found sympatry of *O. acritus* with *O. nitidus* and *O. yunganus*,

TABLE 7
Summary of Distinguishing Characters Among Members of the *megacephalus* Group

Character[a]	*O. acritus*	*O. megacephalus*	*O. perenensis*	*O. laticeps*
Overall body size	medium	small	medium	large
Dorsal color	warm toned	warm toned	dark brown	dark brown
Ventral color	whitish	whitish	gray	whitish or cream
Length dorsal hair, mm	9–10	5–6	5–7	8–10
Length chest hair, mm	3–4	2–3	2–3	4
Lateral color	orange tones	orange–tones	yellow-brown	brown
Dorsal rostrum color	dusky	beige	dusky	dusky
Inner ankle color	whitish	whitish	gray	gray
Hypothenar pad	large	tiny dot	medium	medium
1st interdigital pad	large	small	medium	medium
Interdigital tubercles	inconspicuous	inconspicuous	inconspicuous	prominent
Rings on 1st digit pes	1	2–3	2	1–3
Preauricular tuft	present	present	present	absent
Lower m2 fossettid	present	present	absent	absent

[a] Pelage characters can vary with regional temperature (length) and age (color), as well as geographically.

each one a member of divergent species groups of the former ''*O. capito*'' complex, but thus far no sympatry has been detected with *O. perenensis* or *O. megacephalus*. Moreover, based on Emmons' data, *O. acritus* is sympatric with two species of the *O. subflavus* complex. In six of seven consecutive years of trapping in the PNNKM, Emmons found *O. acritus* to be the numerically dominant species of forest *Oryzomys*, with up to 2.7% capture rate. In the seventh trapping year (2004) *O. nitidus* was the numerically dominant murid, as is the case in Bolivian dry forests to the northwest, west, and southwest of the PNNKM. *Oryzomys nitidus* were caught in the same trap lines as *O. acritus*, but unlike *O. acritus*, *O. nitidus* were occasionally trapped in grasslands, along with species of the *O. subflavus* group.

The small known geographic range of *O. acritus* is sandwiched between the much larger ranges of *O. megacephalus* to the east, and *O. perenensis* to the west (fig. 14; Patton et al., 2000; Costa, 2003), and it could be a relictual species. Recent palynological evidence from the PNNKM suggests that humid forests have been expanding for the past 3,000 years, and currently occupy the most southerly position attained during at least the past 50,000 years (Mayle et al., 2000). The gallery forests of the Rio Itenez and humid forests associated with the Huanchaca meseta (a storm generator that captures moisture) may have maintained pockets of humid forest surrounded by pampa inhospitable to forest rodents, during periods of forest contraction, thus allowing the persistence of isolated populations of forest fauna and flora. *Oryzomys perenensis* shows strong genetic evidence consistent with recent rapid expansion (Lessa et al., 2003). Expanding populations of *O. perenensis* and perhaps *O. megacephalus* may have reached the edges of the range of *O. acritus* and confined its populations, since unlike *O. nitidus* complex rats, which show geographical overlap (Musser et al., 1998; Costa, 2003) , all *O. megacephalus* complex rats appear to be allopatric. This hypothesis should be testable by genetic techniques.

The mammal fauna of the PNNKM has several mammalian taxa in common with faunas of central Brazilian Cerrado and/or forest localities to the east, but not found much to the west of the Park or north of the Beni. These include the rodent genus *Kunsia* and the marsupial species *Monodelphis domestica*, *M. kunsi*, and *Caluromys philander*. Two recently described species of *Juscelinomys* (Emmons, 1999), currently known only from the PNNKM, have a single known congener (perhaps now extinct) that has been found only in the Distrito Federal of Brasilia, another possible example of relictual species surviving from an old, Central Brazilian Murid fauna.

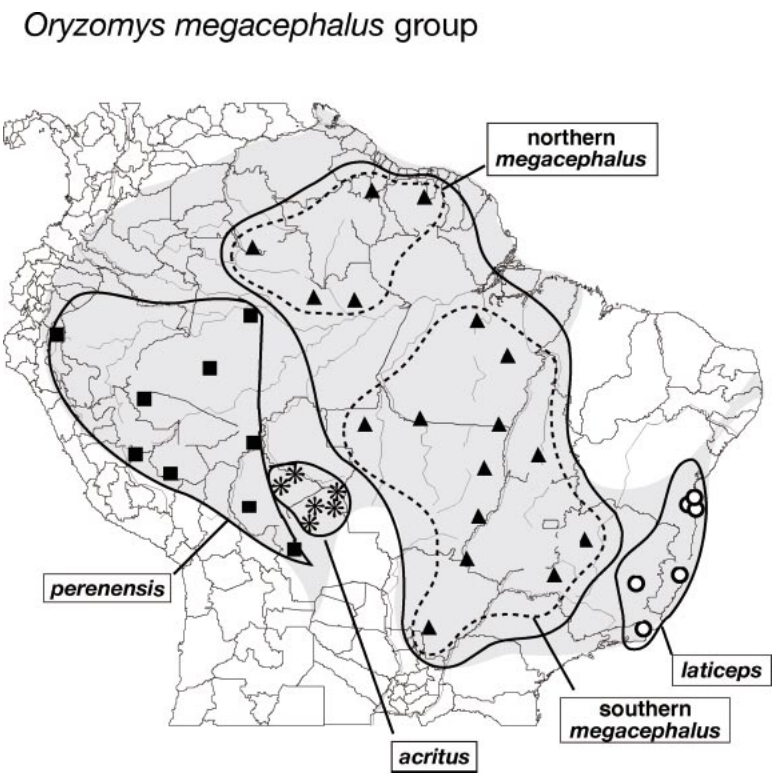

Fig. 14. Geographic ranges of *megacephalus* complex *Oryzomys*. Points indicate localities of specimens for which the cyt-b gene has been sequenced (many other localities are known); shading shows approximate geographic region occupied by the *O. megacephalus* complex. Modified from Costa (2003).

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