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A new species of big-eared climbing rat, genus *Ototylomys* (Cricetidae: Tylomyinae), from Chiapas, Mexico

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An allopatric population of big-eared climbing rats (*Ototylomys*) from the Northern Highlands of Chiapas, Mexico, is described as a new species. The new taxon is part of a unique montane rainforest community that includes several other endemic species in the limited geographic range between the Río Grijalva and the Central Depression of Chiapas. Several cranial, external, and molecular characters distinguish this new species of big-eared climbing rat from its more widely distributed congener, *Ototylomys phyllotis*. We performed principal component and discriminate function analyses of cranial measurements, and found that specimens of the new species consistently could be distinguished from other *Ototylomys* with strong statistical support. Compared with exemplars of *Ototylomys* from elsewhere in their range, the new species possesses a karyotype that differs by 3 additional biarmed chromosome pairs, is fixed or nearly fixed for distinct electromorphs at 12 allozyme loci, and the mean genetic distance exceeds 14%, based on comparisons of the mitochondrial cytochrome *b* gene between the new species of *Ototylomys* and representatives of *O. phyllotis*. The restricted distribution in montane karst rainforest suggests that the species and its habitat may be a matter of conservation concern.

Una población alopátrica de rata orejuda trepadora (*Ototylomys*) de las Tierras Altas del Norte de Chiapas, México se describe como una nueva especie. El nuevo taxón es parte de una comunidad única de bosque lluvioso montano que incluye varias especies endémicas en el área de distribución geográfica limitada entre el Río Grijalva y la Depresión Central de Chiapas. Varios caracteres craneales, externos, y moleculares distinguen la nueva rata orejuda trepadora de su congénere más ampliamente distribuido, *Ototylomys phyllotis*. Se realizaron análisis de componentes principales y de función discriminante de los caracteres craneales, y se encontró que los especímenes de La Pera fueron consistentemente distinguidos de otros *Ototylomys* con un fuerte soporte estadístico. En comparación con ejemplares de *Ototylomys* del rango, la nueva especie posee un cariotipo que difiere por 3 pares adicionales de cromosomas biarmados, está fijo o casi fijo por distintos electromorfos en 12 loci alozímicos. Adicionalmente, la media de la distancia genética comparada del gen mitochondrial citocromo b entre la nueva especie de *Ototylomys* y representantes de *O. phyllotis*, excede el 14%. La distribución restringida en el bosque lluvioso montano kárstico sugiere que la especie y su hábitat pueden ser de importancia para la conservación.

Key words: big-eared climbing rat, Chiapas, El Pozo, La Pera, Mexico, *Ototylomys*, Tylomyinae, Tylomyini

Northwest of the town of Berriozábal in the Mexican state of Chiapas is the Zona Sujeta a Conservación Ecológica "La Pera," a location of remarkable biodiversity and endemism (Fig. 1). La Pera is situated in montane rainforest in the southern foothills of Chiapas' Northern Highlands. The site abuts and overlooks the Central Depression of Chiapas, which is occupied in this area by the town of Berriozábal and the nearby capital city of Tuxtla Gutiérrez. The distinct hilltop located in La Pera is about 1,100 m in elevation (Fig. 1) and is part of the Sierra Madre Limestone, a shallow marine deposition of Cretaceous age (Steele 1985; Alvarado-Ortega and Than-Marchese 2012). Photographs of La Pera (also known as El Pozo) were published by Johnson (1989) and Lamoreux et al. (2015), and the locality was discussed and mapped by Lamoreux et al. (2015).

La Pera is the type locality of several species, including the lizard *Anolis parvicirculatus* Alvarez del Toro and Smith, 1956; the frog *Craugastor pozo* (Johnson and Savage, 1995); the salamander *Ixalotriton niger* Wake and Johnson, 1989; the crab *Sylvathelphusa kalebi* Villalobos and Álvarez, 2013; and the trees *Stenanona migueliana* Ortiz-Rodriguez and Schatz, 2014; *Amphitecna loreae* Ortiz-Rodriguez et al. 2016a; and *Tridimeris chiapensis* Ortiz-Rodriguez et al 2016b (in Ortiz-Rodriguez et al. 2014, 2016a, 2016b). All of these species are known only from the type locality, or from some additional nearby collecting sites. Several additional species, such as the lizard *Anolis alvarezdeltoroi*, the pit viper *Bothriechis rowleyi*, and a recently described tree *Mortoniodendron ocotense* have restricted distributions that include the La Pera locality (Ishiki and Wendt 2014; Johnson et al. 2015; Scarpetta et al. 2015). The diversity and endemism of the site may be related to the complex topography of a tropical karstic terrain (Clements et al. 2006; Villalobos and Álvarez 2013; Luna-Reyes et al. 2015). The crab genus *Sylvathelphusa* Villalobos and Álvarez, 2013 is represented by *S. kalebi* and by *S. cavernicola*, the former from a single locality in La Pera, and the latter from a few kilometers outside the conservation area. Both crab species inhabit karstic crevices. The 2 amphibians are listed as Critically Endangered on the IUCN Red List, and ongoing habitat change is a continuing concern for the unique biological community of La Pera.

In the early 1980s, field work at La Pera by Mark D. Engstrom revealed a population of *Ototylomys*, which he recognized as an undescribed species. In 1983, 2 of us (CAP and JWS, Jr.) began a collaboration with Engstrom to study allozyme variation in Mexican populations of *Ototylomys* including the undescribed species. This work revealed a number of fixed differences between *O. phyllotis* and the La Pera population that supported its recognition as a valid species. The population occasionally has been referenced in the literature (Lawlor 1982; Rogers et al. 2004; Dudley and Parish 2006), but the species remained undescribed. Habitat changes and human activity at the collecting locality make it increasingly urgent to document the biodiversity of this distinctive biological community.

Ototylomys has been regarded as a monotypic genus since Lawlor (1969) synonymized 2 previously recognized species as subspecies of *O. phyllotis*: *O. p. australis* from Costa Rica and *O. p. connectens* from the highlands of Chiapas and Guatemala, together with the nominate subspecies, ranging from the Yucatán peninsula through Nicaragua (Fig. 2). Beginning with the original description (Merriam 1901), the genus has been recognized

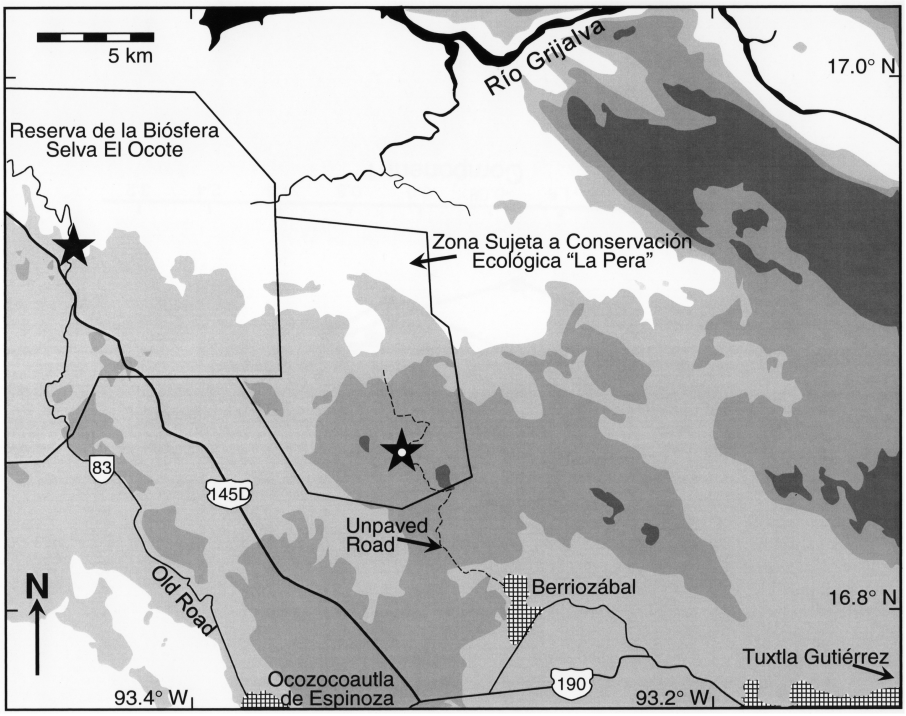

Fig. 1.—Collecting localities of *Ototylomys* nov. sp. in the vicinity of Berriozábal, Chiapas. The type locality of the new species 11 km northwest of Berriozábal at El Pozo is indicated by a dotted star in the La Pera Conservation Area. The black star indicates the collecting site 26 km north of Ocozocoautla. Gray shading represents elevation contours of 800, 1,000, and 1,200 m.

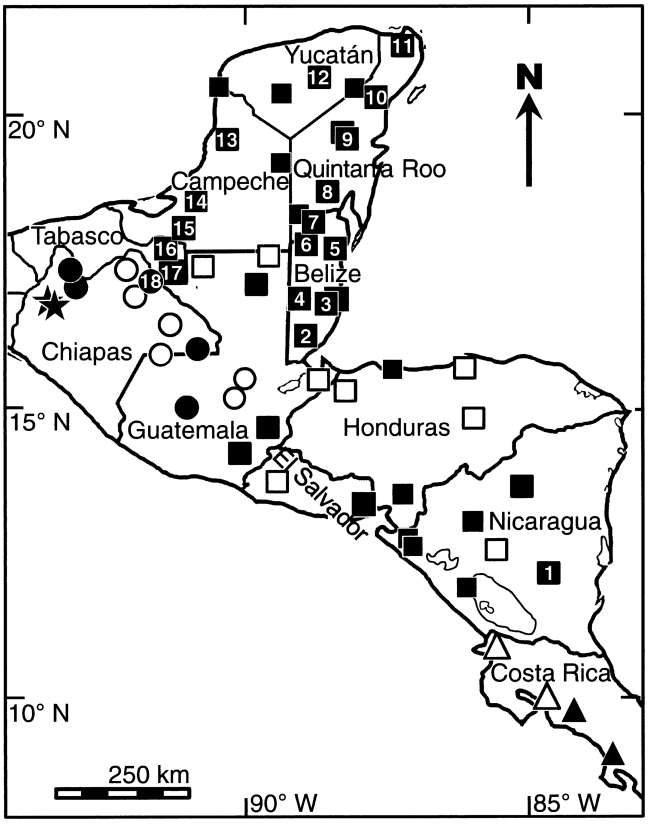

Fig. 2.—Locality records of *Ototylomys* in Central America, showing species distribution and specimens examined in this study. Stars represent collecting sites of the new species. Squares: *O. p. phyllotis*. Circles: *O. p. connectens*. Triangles: *O. p. australis*. Solid symbols are localities of specimens examined, with open symbols representing selected museum and literature records. In some cases, nearby localities are represented by a single symbol. Numbers represent localities included in the allozyme analysis (see Appendix I; Fig. 5).

as being closely allied with *Tylomys*, which shares such characters as a flattened skull with distinct supraorbital ridges (Lawlor 1969; Hall 1981). *Tylomys* and *Ototylomys* form the Tribe Tylomyini, which together with the vesper rats (Nyctomyini: *Nyctomys* and *Otonyctomys*) belong to the cricetid subfamily Tylomyinae (Reig 1984; Musser and Carleton 2005; Ramírez-Pulido et al. 2014), which is considered to have arisen from within a lineage of North American origin. These relationships have been supported by molecular studies (Bradley et al. 2004; Reeder and Bradley 2004; Corley et al. 2011).

The ancestor of modern *O. phyllotis* populations occurred in the vicinity of Honduras and El Salvador (Gutiérrez-García and Vázquez-Domínguez 2012). From this area, those authors hypothesized that the species initially colonized the highlands of Guatemala and Chiapas, giving rise to *O. p. connectens*. Subsequent migrations moved north from Honduras into Belize and the Yucatán peninsula and south into Nicaragua and Costa Rica. Gutiérrez-García et al. (2014, 2015) date the initial dispersal and divergence of *O. phyllotis* populations in the Miocene at 14.5–7.4 Ma, and the colonization and divergence of Yucatán and Belizean populations approximately 5 Ma in the early Pliocene.

In this study, we describe the known biology of the La Pera population. Using morphological and molecular data sets, we also investigate the taxonomy of the population in relation to other tylomyine rodents.

Materials and Methods

Specimens examined.—Examined specimens of the new species and related taxa are listed in Appendix I and are deposited in research collections at the following institutions (specimen and voucher acronyms in parentheses): Angelo State University Natural History Collections (ASNHC; ASK); Carnegie Museum of Natural History (CM); Colección de Mamíferos, Centro de Investigación en Biodiversidad y Conservación, Universidad Autónoma del Estado de Morelos (CMC); Colección Nacional de Mamíferos, Universidad Nacional Autónoma de México (CNMA); Fort Hays University Sternberg Museum of Natural History (FHSM); Instituto de Ecología, Universidad Nacional Autónoma de México (IE); Institut des Sciences de l'Evolution de Montpellier (ISEM); University of Kansas Museum of Natural History (KU); Natural History Museum of Los Angeles County (LACM); Louisiana State University Museum of Zoology (LSUMZ); Michigan State University Museum (MSU); Museo de History Natural de la Universidad de San Carlos, Guatemala (MHNG); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); National Museum of Natural History, Smithsonian Institution (USNM); Oklahoma State University Collection of Vertebrates (OSU); Royal Ontario Museum (ROM); Biodiversity Research and Teaching Collections (BRTC), Texas A&M University (TCWC; AK); Museum of Texas Tech University (TTU); University of Florida Museum of Natural History (UF); University of Washington Burke Museum (UWBM).

These specimens were used for molecular and morphological analyses. Specimens were collected for the DNA portion of this study following the procedures described in the guidelines of the American Society of Mammalogists (Sikes et al. 2016).

Mensural data and statistical analyses.—Standard external measurements were recorded from the skin tags or from museum records. Sixteen cranial measurements were made with digital calipers and recorded to the nearest 0.01 millimeter (mm). Specimens from the Museum of Vertebrate Zoology (MVZ) and the Biodiversity Research and Teaching Collection (BRTC) were measured by NEB and again by CAP. If independent results were within 0.20 mm, the mean value was recorded; otherwise, a third measurement was made by CAP, and the 2 nearest measurements were averaged. Specimens from other collections were measured by CAP. Results were rounded to the nearest 0.1 mm for analysis. Only adult individuals (age groups IV–VI), identified as such based on patterns of molar tooth wear (Schmidly 1973), were included in the morphological analysis. Measurements are as follows: condylobasal length (CL), greatest length of skull (GLS), mastoidal breadth (MB), height of braincase (HBC), breadth of braincase (BB), breadth of rostrum (BR), least interorbital breadth (LIB), length of nasal suture (NS), zygomatic breadth (ZB), coronal length

of maxillary tooth row (MTR), palatal length (PL), postpalatal length (PPL), length of incisive foramen (IF), tympanic bullar length (TBL), tympanic bullar width (TBW), and mandibular length (ML). Capitalized color names in specimen descriptions are those of Ridgway (1912).

For the 16 cranial variables, measurements were included from specimens (Appendix I) collected at the following localities in Mexico: Chiapas ($n = 30$), Campeche ($n = 7$), and Tabasco ($n = 6$); in Belize ($n = 2$); and in Nicaragua ($n = 12$). These populations were compared to other populations delimited by morphologic characteristics to represent samples of *O. p. connectens* ($n = 11$), *O. p. phyllotis* ($n = 27$), and *Ototylomys* nov. sp. ($n = 19$). In the cranial variables, Lawlor (1969) reported no significant differences between sexes in *O. phyllotis*, and no sexual dimorphism was evident in the new species. Therefore, sexes were combined for all analyses.

For descriptive and comparative purposes, standard descriptive statistics (mean, range, variance, *SD*, and *SE*) were calculated for each variable and species (Table 1). For all morphometric analyses, variables were first transformed to natural logarithms. Specimens with missing measurements were excluded from analyses.

Levels of statistical significance among groups (localities) were estimated using multivariate analysis of variance (MANOVA) on the 16 cranial variables, followed by a Mann–Whitney (Ryan 1959) pairwise comparison and Bonferroni corrected *P*-values (Ury 1976). Canonical variates (CVs) derived from multigroup discriminant function classification and principal components (PCs) were computed using the 16 craniodental variables. To explain the variance in the data, a principal component analysis (PCA) was performed comparing all specimens included in the analysis. PCs were extracted from the variance–covariance matrix, and variable loadings are expressed as correlation coefficients of the extracted components or CVs with the original log-transformed cranial measurements. All analytical procedures were implemented using PAST version 3.15 (Hammer et al. 2001) and IBM SPSS version 22 (IBM Corp. 2013).

Chromosomes.—Somatic metaphase chromosomes were obtained from bone marrow cells using the method of Patton (1967) following a yeast pretreatment inoculation described in Lee and Elder (1980). Terminology of centromere position follows Patton (1967). The abbreviation FN refers to the number of autosomal arms (= fundamental number) and 2n refers to the diploid number. Due to the presence of short, second chromosome arms, precise characterization of the FN is somewhat subjective and interpretations may differ due to chromosomal contraction in metaphase.

Allozymes.—Allozyme methods followed Sites and Greenbaum (1983), Thompson and Sites (1986), and Murphy et al. (1996). Frozen tissue samples were homogenized in an equal volume of 0.01 M Tris, 0.001 M EDTA, 5×10^{-3} M NADP, pH 7.0. Horizontal starch gel electrophoresis was performed using wickless gel molds described by Murphy et al. (1996). A total of 25 putative protein loci were resolved (Table 2) for 176 samples. Enzyme stains were those described in Harris and Hopkinson (1976), Selander et al. (1971), or Murphy et al. (1996).

Five specimens of *Neotoma albigula* were included as an outgroup. Ingroup taxa included *Nyctomys sumichrasti* (2 specimens), *Tylomys nudicaudus* (2 specimens), *Ototylomys* nov. sp. (19 specimens), and *O. phyllotis* (148 specimens representing

Table 1.—Descriptive statistics comparing different samples of *Ototylomys* included in the morphometric analysis. Means and *SD*s were calculated for each variable and species-group taxon.

Variable	*O.* nov. sp.	*O. p. phyllotis*	*O. p. connectens*
	Mean ± *SD*	Mean ± *SD*	Mean ± *SD*
Breadth of braincase	16.04 ± 0.13	14.58 ± 0.13	14.86 ± 0.09
Breadth of rostrum	5.96 ± 0.12	5.38 ± 0.12	5.20 ± 0.10
Condylobasal length	38.71 ± 0.55	35.96 ± 0.55	36.23 ± 0.72
Greatest length of skull	41.61 ± 0.52	38.10 ± 0.52	39.02 ± 0.59
Height of braincase	8.87 ± 0.08	8.07 ± 0.08	8.00 ± 0.11
Least interorbital breadth	7.14 ± 0.10	5.92 ± 0.10	6.16 ± 0.12
Length of incisive foramen	6.94 ± 0.11	6.86 ± 0.11	6.85 ± 0.22
Length of maxillary tooth row	7.19 ± 0.08	6.37 ± 0.08	6.86 ± 0.13
Mandibular length	20.37 ± 0.28	19.12 ± 0.28	19.88 ± 0.25
Mastoidal breadth	14.74 ± 0.20	13.97 ± 0.20	13.92 ± 0.18
Nasal suture	14.44 ± 0.30	13.24 ± 0.30	13.71 ± 0.24
Palatal length	21.23 ± 0.34	19.46 ± 0.34	19.53 ± 0.30
Postpalatal length	14.56 ± 0.21	13.94 ± 0.21	14.38 ± 0.35
Tympanic bullar length	6.11 ± 0.14	6.56 ± 0.14	6.50 ± 0.21
Tympanic bullar width	5.14 ± 0.08	4.84 ± 0.08	4.66 ± 0.20
Zygomatic breadth	19.61 ± 0.26	18.54 ± 0.26	19.04 ± 0.29

Table 2.—Enzyme loci resolved in samples of *Ototylomys* and related tylomyine rodents by starch gel electrophoresis. E. C. = Enzyme Commission number. Buffer system 1 = Tris-citrate pH 8.0; 2 = Tris-citrate pH 6.7; 3 = Tris-HCl pH 8.5.

Enzyme	Locus	E. C.	Buffer system
Malate dehydrogenase	MDH1	1.1.1.37	1
Malate dehydrogenase	MDH2	1.1.1.37	1
Isocitrate dehydrogenase	IDH1	1.1.1.42	1
Isocitrate dehydrogenase	IDH2	1.1.1.42	1
Glucose-6-phosphate isomerase	GPI	5.3.1.9	1
Aspartate aminotransferase	AAT1	2.6.1.1	1, 2
Aspartate aminotransferase	AAT2	2.6.1.1	1
Phosphoglucomutase	PGM1	5.4.2.2	1
L-Lactate dehydrogenase	LDHA	1.1.1.27	1
L-Lactate dehydrogenase	LDHB	1.1.1.27	1
Purine-nucleoside phosphorylase	PNP-A	2.4.2.1	1
Mannose-6-phosphate isomerase	MPI	5.3.1.8	1
Aconitate hydratase	ACON-2	4.2.1.3	1
Phosphogluconate dehydrogenase	PGDHA	1.1.1.44	1
Superoxide disumutase	SOD1	1.15.1.1	1, 2
Glucose-6-phosphate dehydrogenase	G6PDH[a]	1.1.1.49	1
Glycerol-3-phosphate dehydrogenase	G3PDH[a]	1.1.1.8	1
Malate dehydrogenase ($NADPH^+$)	MDHP[a]	1.1.1.40	1
Fumarate hydratase	FUMH[a]	4.2.1.2	1
Peptidase	PEPA	3.4.13	3
Peptidase	PEPB1	3.4.13	3
Peptidase	PEPB2	3.4.13	3
Peptidase	PEPD	3.4.13	3
Catalase	CAT	1.11.1.6	3
Leucine aminopeptidase	LAP	3.4.11.1	3

[a]Enzyme resolved on a subset of specimens and not used in phylogenetic analysis.

18 localities; Fig. 2; Appendix I). In some cases, adjacent collecting sites of *O. phyllotis* were combined into a single locality (see Appendix I). The enzyme loci G6PDH, G3PDH, MDHP, and FUMH were scored for a subset of the specimens and were not included in the phylogenetic analysis.

Protein data for 21 loci were analyzed with PHYLIP, version 3.695 (Felsenstein 2005). Following Wiens (2000), we performed both a continuous maximum likelihood analysis (using the CONTML function of PHYLIP) and a neighbor-joining (NJ) tree based on the Cavalli-Sforza and Edwards (1967) chord measure (using the GENDIST and NEIGHBOR programs).

DNA sequence data.—Two primer pairs were used to amplify and sequence the cytochrome *b* (*Cytb*) gene in approximately 800-bp segments: L14724 (Irwin et al. 1991) with CB3H (Palumbi 1996) or MVZ-16 (Smith and Patton 1993) and F1 (Whiting et al. 2003) with H15915 (Irwin et al. 1991). Primers MVZ-16, WDRAT 400F (Edwards et al. 2001), H15149 (Irwin et al. 1991), and Neo700L (Peppers and Bradley 2000) were used as necessary to amplify and sequence smaller segments. Parameters for PCR reactions were as follows: 1 cycle of 94°C (3–5 min) was followed by 36 cycles of 94°C (1 min) denaturing, 46°C annealing (1 min), and 72°C (1 min) extension; the PCR was concluded by 1 cycle of 72°C (7 min). Negative (no DNA) controls were run with all amplifications to reveal instances of DNA contamination. PCR products were visualized on an agarose gel with ethidium bromide. Amplified products were purified using a Millipore Multiscreen PCR 96-Well Filtration System (Cat. No. MANU03050). The purified PCR products were cycle-sequenced using the primers described above, and sequenced products purified using Millipore Multiscreen Filter Plates for High Throughput Separations (Cat. No. MAHVN4510). Light- and heavy-strand sequences were collected on an ABI 377 automated sequencer (Applied Biosystems, Foster City, California), and were then edited and compiled using Sequencher versions 3.1.1 and 4.1.2 (Gene Codes Corp., Ann Arbor, Michigan). Alignments for *Cytb* were unambiguous (no indels) and were performed using the default parameters for the program MUSCLE ver. 3.8.31 (Edgar 2004; EMBL-EBI 2017). The open reading frame was verified using the program MEGA ver. 5.2.2 (Tamura et al. 2011). The Kimura 2-parameter model of evolution (Kimura 1980) was used to calculate genetic distances between selected taxa using PAUP* 4.0b10 (Swofford 2002). The best-fit model of DNA substitution was selected with the Akaike Information Criterion (Akaike 1974) as implemented in jModelTest 0.2 (Guindon and Gascuel 2003; Darriba et al. 2012).

Twelve sequences of the new species and 1 of *Tylomys watsoni* generated for this study were submitted to GenBank (accession numbers MF281975–MF281986 and MF317949). In addition to these, the ingroup also included 33 sequences of *O. phyllotis* and 1 each of *T. nudicaudus*, *N. sumichrasti*, and *Otonyctomys hatti* (Appendix I) from previous studies (Matocq et al. 2007; Corley et al. 2011; Gutiérrez-García and Vázquez-Domínguez 2012; Gutiérrez-García et al. 2014). In addition, 6 GenBank sequences were used as outgroups (Leite et al. 2014), including *Arvicola terrestris* (D'Elía 2003), *Eothenomys melanogaster* (Galewski et al. 2006), *Microtus oeconomus* (Brunhoff et al. 2006), *Myodes gapperi* (Cook et al. 2004), *N. albigula* (Matocq et al. 2007), and *Sigmodon hispidus* (Bradley et al. 2008). The ingroup sequences were chosen to maximize the geographic and phylogenetic variation.

Phylogenetic relationships among tylomyine rodents were estimated using both maximum likelihood (ML) and Bayesian inference (BI) optimality criteria using *A. terrestris*, *E. melanogaster*, *M. oeconomus*, *M. gapperi*, *N. albigula*, and *S. hispidus* to root the resulting trees. The ML analysis was performed in PhyML (Guindon and Gascuel 2003) using the following parameters: transition/transversion ratio estimated, model of evolution set to GTR, proportion of invariable sites estimated, number of substitution rate categories set to 4, gamma shape parameter estimated, the heuristic search techniques used to explore tree space included using 5 random starting trees, nearest neighbor interchange (NNI), subtree pruning and regrafting (SPR). Clade support was assessed using the nonparametric bootstrap procedure with 1,000 bootstrap replicates (Felsenstein 1985). Nodes having ML bootstrap support ≥ 70% were interpreted as evidence of significant support. The BI analysis coupled with Markov chain Monte Carlo (BMCMC) inference was performed in MrBayes v3.2. (Ronquist et al. 2012). Two independent BMCMC analyses were performed, each consisting of 4 chains, (1 cold and 3 hot) for 10×10^6 generations with sampling every 1,000 generations. Sequence evolution model parameters were treated as unknown variables with uniform default priors and were estimated as part of the analysis. Convergence was assessed based on examination of the *SD* of split frequencies < 0.01 after 10×10^6 generations and effective sample size (ESS) values (≥ 1,000 for ln *L* in Tracer—Rambaut et al. 2014). The first 25% of the generations were deleted as burn-in. We interpreted Bayesian posterior probabilities (PP) ≥ 0.95 as evidence of significant support for a clade (Wilcox et al. 2002).

Results

Morphometric analyses.—Examination of the La Pera specimens revealed a unique suite of morphological variables that consistently distinguished these individuals from related taxa. Another museum specimen (FHSM 9092), collected in 1970 from a locality 16 km northwest of La Pera, shares these diagnostic traits, and we regard that specimen as conspecific with the La Pera population. Morphological data are available as Supplementary Data SD1.

The multivariate analyses confirmed the close morphological similarity among the taxa. The first 2 canonical axes in the PCA accounted for 76.4% of the variation (I, 65.2%; II, 11.2%). The variables load positively (Table 3) were all positive for the first component with the 5 highest being GLS, PL, CL, ML, and ZB, respectively. For component II, all of the loadings were positive except for 6 negative ones (HBC, LIB, BR, BB, MTR, and TBW). PC supplies additional evidence of substantial craniodental differentiation over small geographic distances. Projection of individual scores onto PCs I and II reveals substantial overlap among specimens of the taxa *O. phyllotis*

Table 3.—Variable correlations (loadings) and variance explained of 16 log-transformed craniodental variables with derived principal components (PCs) extracted from ordination, and derived canonical variates (CVs) based on 16-group discriminant function analysis using specimens ($n = 56$) of *Ototylomys* from Chiapas, Campeche, and Tabasco, Mexico; Nicaragua; and Belize. *$P < 0.01$.

Variable	PC1	PC2	CV1	CV2
Breadth of braincase	0.814*	–0.505	0.782*	–0.106
Breadth of rostrum	0.815*	–0.093	0.370*	–0.004
Condylobasal length	0.964*	0.121	0.356*	–0.025
Greatest length of skull	0.978*	0.005	0.367*	0.011
Height of braincase	0.838*	–0.033	0.411*	–0.014
Least interorbital breadth	0.834*	–0.419	0.448*	–0.062
Length of incisive foramen	0.704*	0.382	0.346	–0.018
Length of maxillary tooth row	0.685*	–0.550	0.655*	0.676
Mandibular Length	0.941*	0.167	0.361*	0.360
Mastoidal breadth	0.847*	0.035	0.356*	0.169
Nasal suture	0.822*	0.197	0.111*	0.129
Palatal length	0.955*	0.036	0.390*	0.115
Postpalatal length	0.776*	0.436	0.170	–0.229
Tympanic bullar length	0.324*	0.694	–0.195	0.060
Tympanic bullar width	0.248	–0.134	–0.084	–0.146
Zygomatic breadth	0.927*	0.202	0.357*	–0.990
Eigenvalues	0.014	0.003	2.848	0.186
% Variance	65.180	11.230	93.900	6.100

phyllotis and *O. p. connectens*, but no overlap of the former with specimens of the new species (Fig. 3). See Table 3 for variable correlations and variance explained.

The discriminant function analysis (DFA) disclosed 3 well-defined clusters in the first CVs (populations of *Ototylomys*), and the differences among multivariate means were statistically significant (Wilks' lambda = 0.04, $F = 9.176$, $P < 0.001$). This analysis indicated that the new species possessed larger values on average, for all variables except TBL. The most discriminatory size-independent variable was TBL (Table 2). The classification analysis, associated with the DFA, revealed that among the 3 taxa (*Ototylomys* nov. sp., *O. phyllotis phyllotis*, and *O. p. connectens*) for which all individuals were correctly classified, 100% (19 of 19) of the *Ototylomys* nov. sp. specimens were correctly identified.

Chromosomes.—The karyotype of *Ototylomys* nov. sp. is 2n = 48 and FN = 84, with 19 pairs of biarmed chromosomes and 4 acrocentric pairs (Fig. 4). The biarmed elements are composed of 15 pairs of submetacentric to subtelocentric chromosomes and 4 metacentric pairs. The metacentric, submetacentric, and subtelocentric chromosome pairs ranged from large to small in size. The X and Y chromosomes are large subtelocentric and large submetacentric, respectively.

Allozymes.—Electromorphs were scored based on electrophoretic relative mobilities, and frequencies were estimated for each taxon and population (Supplementary Data SD2). MDH2 was monomorphic for all individuals examined, but *Ototylomys phyllotis* and the new species were fixed or nearly fixed for alternate electromorphs at 12 loci. Compared with *T. nudicaudus*, the new species was fixed for alternative electromorphs at 13 loci. The CONTML analysis supported monophyly of *Ototylomys*, with the La Pera population being sister to the

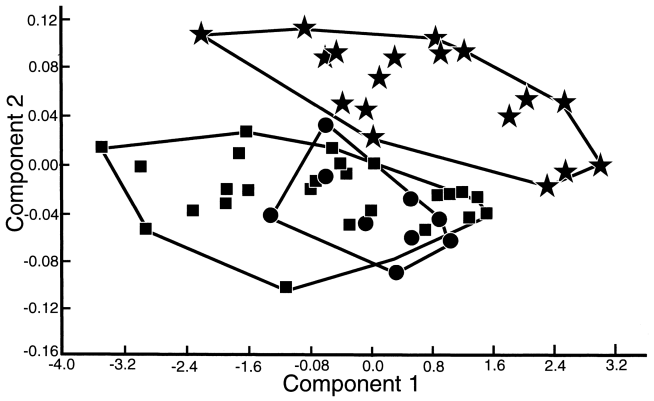

Fig. 3.—Results of principal component analysis performed on 16 log-transformed cranial variables measured on 60 specimens representing 3 operational taxonomic units of *Ototylomys*. *Ototylomys* nov. sp. is represented by stars, *O. p. phyllotis* by squares, and *O. p. connectens* by circles. The axes represent the projection of first 2 principal component analyses, including all information about size and shape within the 3 taxa examined. Polygons enclose individuals of each taxon.

Fig. 4.—Standard karyotype of a male *Ototylomys* nov. sp. (2n = 48, FN = 84) from Pozo de Petróleo, 11 km northwest (by road) Berriozábal, La Pera Conservation Area, Chiapas, México (MVZ 161245). Chromosomes are arranged by size into biarmed (top 3 rows) and uniarmed (bottom row) elements. The sex chromosomes are labeled.

remaining samples (Fig. 5). The topology of the NJ tree differed only in some short terminal branches of *O. p. phyllotis* populations (Supplementary Data SD3).

DNA sequence data.—The best-fit model of evolution was the general time-reversible model with an estimated proportion of invariant sites and a gamma distribution of rates (GTR+I+G). Gene trees recovered by both ML and Bayesian optimality criteria resulted in identical tree topologies with the exception of some of the terminal branches within *O. phyllotis* and were combined (Fig. 6). Ingroup branches were all well supported with the exception of the sister group relationship between *Tylomys* and the La Pera specimens. Kimura's 2-parameter genetic distance between *T. watsoni* and *T. nudicaudus* was

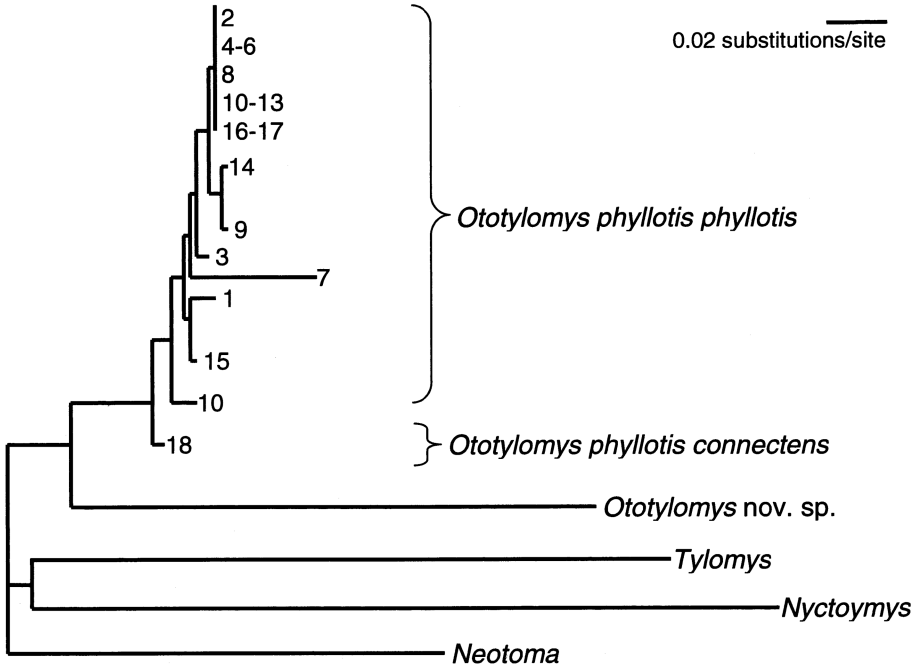

Fig. 5.—Continuous maximum likelihood analysis of allozyme data of representative specimens of 18 populations of *Ototylomys phyllotis*, as compared with an undescribed species of *Ototylomys* from Chiapas and 2 other genera of tylomyine rodents. *Neotoma albigula* is the outgroup. See Appendix I and Fig. 2 for *O. p. phyllotis* locality numbers.

9.79%, whereas the mean genetic distance between the new species and *T. nudicaudus* was 17.38% (15.63% between the new species and *T. watsoni*). The new species also was strongly differentiated from *O. phyllotis*; mean Kimura's genetic distance was 14.58%. Seven *Cytb* haplotypes were recovered among the 12 sequenced individuals from La Pera; intraspecific pairwise genetic distances ranged from 0% to 1.42%.

Discussion

Morphological comparison among 16 cranial variables within populations of *Ototylomys* revealed significant differences among the 3 taxa examined; however, these differences were limited to only a few variables, as supported by the MANOVA. The main variable that discriminates the new species from the other 2 taxa is the GLS (41.61 ± 0.52), compared with 38.10 ± 0.52 in *O. p. phyllotis*, and 39.02 ± 0.59 in *O. p. connectens*. Cranial measurements average larger in the new species compared to *O. p. phyllotis* and *O. p. connectens*. Specimens from La Pera are well characterized by BB and smaller auditory bullae compared with examples of *O. phyllotis*. Variable loadings are in Table 3.

The karyotype of *O. phyllotis* (2n = 48, FN = 78) has 32 biarmed and 14 acrocentric chromosomes (Hsu and Benirschke 1973). According to unpublished data from Mark D. Engstrom and Priscilla K. Tucker (reported in Lawlor 1982), *Ototylomys* from La Pera differs from Yucatán specimens of *O. phyllotis* by 3 pericentric inversions. Their observation is consistent with the karyotype of the new species described herein. In contrast, members of the genus *Tylomys* possess (2n = 36–52) karyotypes that consist mostly of uniarmed chromosomes and variation among species is due to Robertsonian (fusion–fission) changes (Pathak et al. 1973).

The 18 samples of *O. phyllotis* form a monophyletic cluster in both analyses of the allozyme data (Fig. 5; Supplementary Data SD3), although the arrangement of samples within *O. p. phyllotis* differs substantially between the 2 analyses. These data do not provide resolution of relationships among populations, although both analyses separate the widely distributed subspecies *O. p. phyllotis* from the subspecies *O. p. connectens*, which is restricted to parts of Chiapas and adjacent areas of Guatemala. Our samples of *O. phyllotis* (2–17) represent populations that would be included in the YP (Yucatán Peninsula) phylogenetic major group, which immigrated relatively recently into the region of Belize and the Yucatán peninsula according to Gutiérrez-García and Vázquez-Domínguez (2012). Neither our allozyme data nor the mtDNA *Cytb* sequence data of these authors (and see below) resolved much phylogeographic structure within this group.

The allozyme data provide strong evidence that the La Pera specimens genetically are well separated from both *O. phyllotis* and *T. nudicaudus*. Approximately half of the protein loci examined exhibited fixed differences between species. The phylogenetic analyses of the allozyme data (Fig. 5; Supplementary Data SD3) indicate that the new species is sister to *O. phyllotis*, supporting M. D. Engstrom's initial identification of the La Pera population as congeneric but not conspecific with *O. phyllotis*.

Our mtDNA sequence data also provide strong evidence that the series from La Pera, Chiapas, represents an undescribed species. The 12 individuals we sequenced comprise a highly differentiated monophyletic group compared to *Tylomys* or

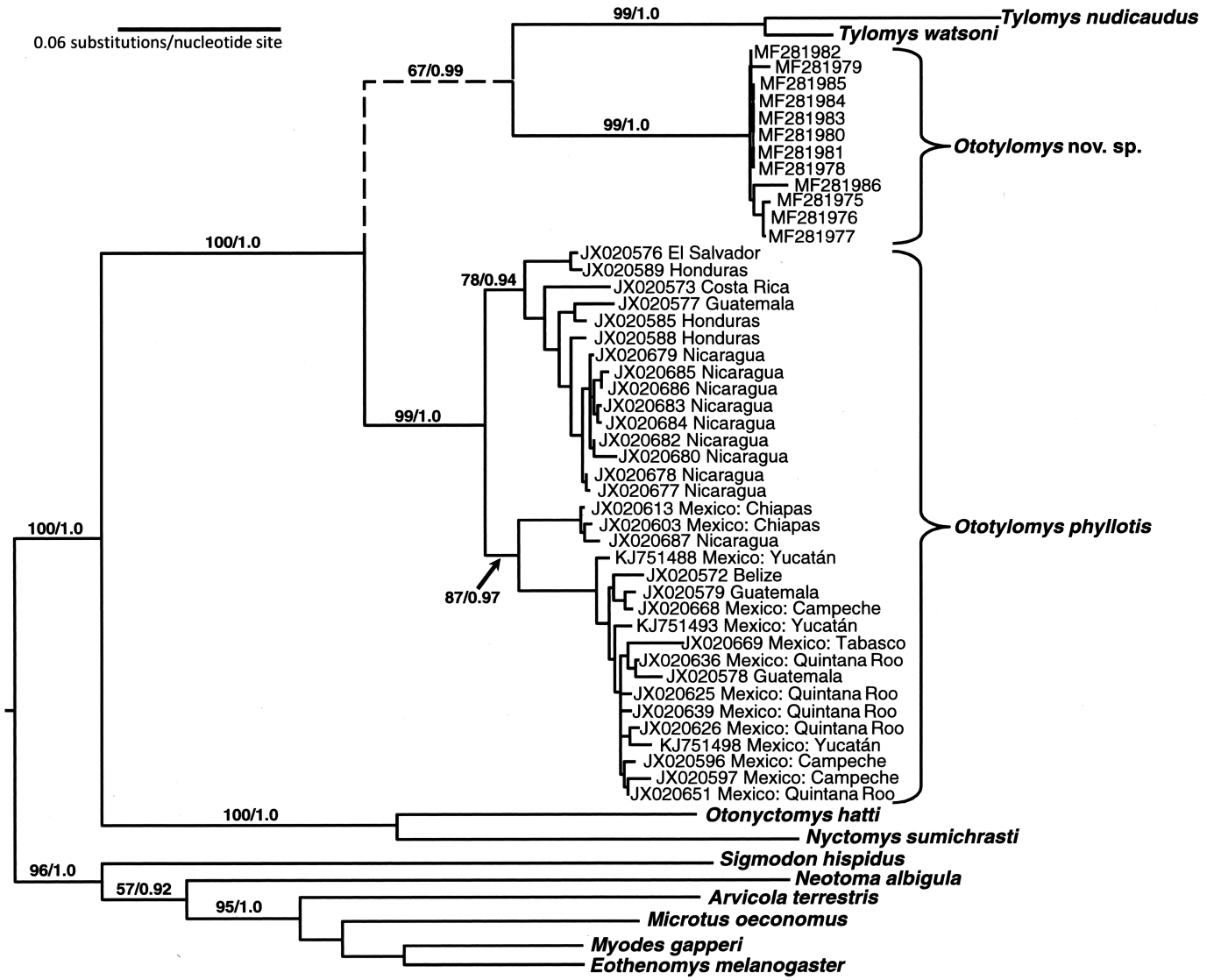

Fig. 6.—Maximum likelihood (ML) phylogram (−ln *L* = 8,735.26888) of the Tylomyinae (*Nyctomys sumichrasti*, *Otonyctomys hatti*, *Ototylomys phyllotis*, *O*. nov. sp., *Tylomys nuducadus*, and *T. watsoni*) based on *Cytb* sequence data, under the GTR+I+G model of evolution, with *Arvicola terrestris*, *Eothenomys melanogaster*, *Microtus oeconomus*, *Myodes gapperi*, *Neotoma albigula*, and *Sigmodon hispidus* as outgroups. ML bootstrap values are shown above nodes followed by Bayesian inference (BI) posterior probabilities. A dashed branch line indicates the only ingroup node that is not well supported by the ML optimality criterion. Terminal labels of *O. phyllotis* indicate GenBank accession numbers followed by the collecting locality. See Appendix I for specific locality information.

O. phyllotis. Although the *Cytb* phylogeny differs from our allozyme tree with regard to placement of the new species, support for the sister group relationship between the new species and *Tylomys* is weak. Moreover, we consider the allozyme results as more robust, given that those data represent multiple nuclear gene loci. The mean Kimura genetic distances we calculated between the new species and *O. phyllotis* (14.58%), *T. nudicaudus* (17.38%), or *T. watsoni* (15.63%) exceeded values often obtained between distinct rodent genera (Baker and Bradley 2006). The strong differentiation documented for the La Pera series, covering morphometric, chromosomal, and molecular data, supports its recognition as a new species, and the preponderance of evidence indicates that this new species is allied with *Ototylomys*.

Taxonomy

Family Cricetidae Fischer, 1817
Subfamily Tylomyinae Reig, 1984
Tribe Tylomyini Reig, 1984
Genus *Ototylomys* Merriam, 1901
Ototylomys chiapensis, new species
La Pera Big-eared climbing rat;
Rata orejuda trepadora de La Pera

Ototylomys phyllotis connectens: Baker et al. 1971 [1973]:82 (part, faunal report based on a specimen collected in 1969, here reidentified as *O. chiapensis*).
Ototylomys phyllotis connectens: Hall 1981:629 (part, marginal locality record based on Baker et al. 1971 [1973]).

Ototylomys phyllotis: Lawlor 1982:3 (part, karyotypic report based on Engstrom and Tucker, cited as *in litt.*).

Ototylomys sp.: Rogers, Engstrom, and Arellano 2004:439 (allozyme data from 2 specimens included in the present study).

Ototylomys sp. nov.: Dudley and Parish 2006:4 (referenced as endemic to El Pozo [= La Pera]).

Holotype.—MVZ 159512, adult female. Skin and skull deposited in the Museum of Vertebrate Zoology at the University of California, Berkeley (Fig. 7; Supplementary Data SD4 and SD5). Collected 20 December 1980 and kept in captivity until 24 December 1980. Skull and study skin prepared by DSR (original catalogue number 1503). The uteri noted as slightly swollen. External and cranial measurements of the holotype are presented in Table 4. The supraorbital ridges extend to a slight point near the coronal suture. Upper and lower molars are well-worn (age group VI—Schmidly 1973). Dorsum is reddish-brown (Benzo Brown) overall, rust-colored (Chestnut-Brown) between the ears and in an irregular pattern in the vicinity of the midline. Dorsal hairs are Blackish Plumbeous at the base. Venter appears reddish-tan interspersed with light brown, individual hairs being Dark Plumbeous at the base and reddish-tan (Pale Ochraceous-Salmon) at the tips. A spot of uniformly white hair approximately 10 × 6 mm is present in the left axillary region. Some white-tipped hairs produce a white streak where the ventral pelage terminates around the genital region.

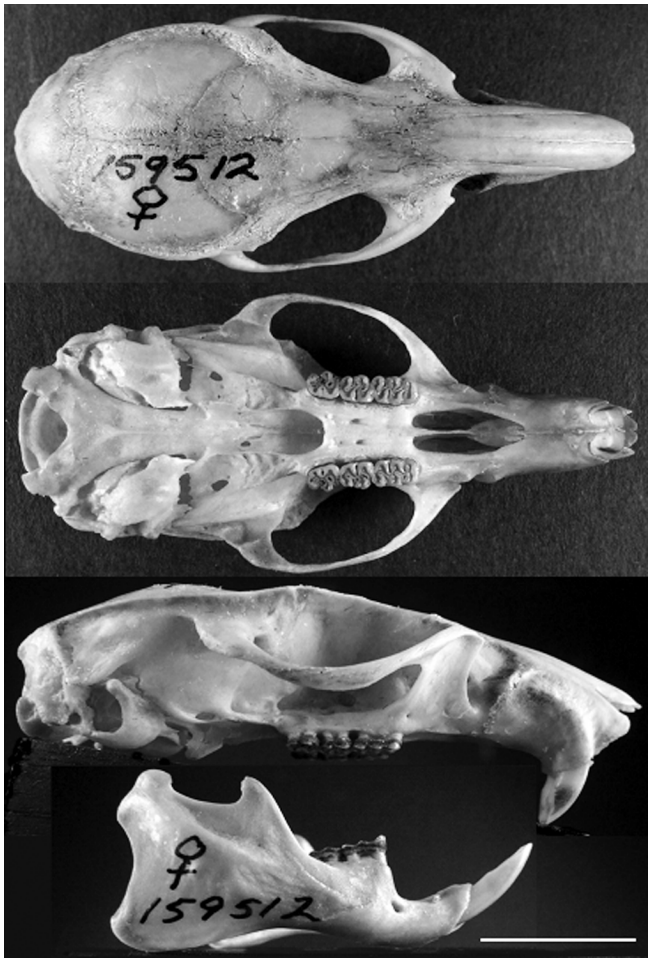

Fig. 7.—Skull of *Ototylomys chiapensis* holotype, MVZ 159512. Schmidly (1973) age class VI. Greatest length of skull = 43.8 mm. Bar represents 1 cm.

Type locality.—Pozo de Petróleo, 11 km northwest (by road) Berriozábal, La Pera Conservation Area, Chiapas, México. The type locality is in the Zona Sujeta a Conservación Ecológica "La Pera" in the Municipality of Berriozábal (Fig. 1). The specimen tag gives an elevation of 950 m, but topographic maps and published accounts of the site (e.g., Luna-Reyes et al. 2015) indicate an elevation in the range of 1,100–1,150 m.

The locality is variously known as El Pozo, Pozo de Petróleo, Pozo Turipache, Pozo La Pera, La Pera, El Suspiro, or Linda Vista (Wake and Johnson 1989; Johnson and Savage 1995; Dudley and Parish 2006; Johnson et al. 2010; Ochoa-Ochoa and Whittaker 2014; Lamoreux et al. 2015). The name "Pozo" (*well* in Spanish) is a reference to an abandoned exploratory oil well that was drilled at the location. "El Suspiro" is an abandoned coffee plantation approximately 3 km SE of the oil well (Wake and Johnson 1989).

Diagnosis.—Excluding the supraorbital ridges, the braincase of *O. chiapensis* is distinctly oval in the dorsal aspect, the entire lateral margins of the parietals forming a continuous arc. The curved parieto-squamosal suture is diagnostic. In comparison, *O. phyllotis* possesses a more angular braincase, with the posteriolateral margins of the parietals often nearly straight and diverging anteriorly. The tympanic bullae of *O. chiapensis* are less inflated and bulbous. The anterolateral margins of the incisive foramina are tapered medially in *O. chiapensis*, beginning near the maxilla-premaxilla suture, rather than broad and rounded anteriorly as in *O. phyllotis*. The edge of the zygomatic plate in *O. chiapensis* is concave ventral to the zygomatic spine, whereas it is straight and vertical in *O. phyllotis*. The postglenoid foramina are nearly closed in *O. chiapensis* and reduced to a narrow forward-facing slit, as compared with *O. phyllotis*, which has a distinctly open postglenoid foramen (diagnostic cranial characters illustrated in Fig. 8). Interorbital breadth is wider in *O. chiapensis* (6.6 mm or greater, often exceeding 7 mm) compared with *O. phyllotis* (less than 6.7 mm, and averaging 6.0 mm; Table 4; Supplementary Data SD1).

The mandible of the new species has a more distinct coronoid process than does *O. phyllotis*, and has a narrower and deeper mandibular notch (Fig. 8). In the new species, the mandibular notch undercuts the coronoid process, very deeply so in most specimens, and very slightly so in a few (Supplementary Data SD6).

In the field, *O. chiapensis* can be distinguished from *O. phyllotis* by the length of the hind foot, the absence of a distinct white spot of hair at the base of the ear (cf. Reid 2009), and the coloration of the ventral pelage. The hind foot of *O. chiapensis* is generally longer, ranging from 30 to 34 mm, whereas few specimens of *O. phyllotis* exceed 30 mm. Except in white patches, the ventral hairs of *O. chiapensis* are dark at the roots and tan or reddish-tan at the tips. In contrast, the ventral hair of *O. p. phyllotis* and *O. p. australis* is generally white- or cream-colored from base to tip. In *O. p. connectens*, the ventral hairs are slate-colored at the base and white at the tip.

Table 4.—Summary of external, cranial, and mandibular measurements of 2 species of *Ototylomys*. For each species, specimens examined in this study are shown, including the holotype (MVZ 159512) of *O. chiapensis*. In addition, literature reports for *O. phyllotis* are included for comparison. Body mass is in grams; all other measurements are in millimeters. Where more than 1 specimen is reported, the mean value, if available, is followed by the range in parentheses. Cranial data from literature citations are rounded to the nearest 0.1 mm. Summary data from this study include adult specimens, and exclude measurements on broken or damaged body parts (Supplementary Data SD1), with sample size shown for each variable.

Variable	*Ototylomys phyllotis*		*Ototylomys chiapensis*	
	Literature reports	This study	This study	Holotype
Head and body length	(95–190)[a] (124–164)[b]	152 (119–191) *n* = 40	172 (139–194) *n* = 18	187
Total length	309 (284–337)[c] (242–370)[d]	296 (236–352) *n* = 30	319 (275–361) *n* = 11	361
Tail	(100–190)[a,e] (109–174)[b] 156 (142–174)[c] (119–191)[d]	143 (115–176) *n* = 30	153 (135–174) *n* = 11	174
Hind foot	(23–30)[b] 27 (26–28)[c] (21–33)[d] (26–29)[e]	28 (24–35) *n* = 40	32 (30–34) *n* = 18	32
Ear	(21–26)[b] (24–25)[e]	23 (18–28) *n* = 40	25 (20–27) *n* = 18	26
Body mass	63[f] (34–84)[b] (80–120)[e]	72 (39–125.2) *n* = 16	103 (55–165) *n* = 16	110
Condylobasal length		36.7 (31.1–39.5) *n* = 34	38.7 (32.8–41.8) *n* = 19	41.5
Greatest length of skull	40.5 (39.0–41.8)[c,d]	38.6 (32.2–42.3) *n* = 39	41.5 (36.4–44.4) *n* = 17	43.8
Breadth of braincase		14.7 (13.2–16.1) *n* = 41	16.0 (15.2–16.8) *n* = 19	16.1
Least interorbital breadth	6.2 (5.9–6.8)[c]	6.0 (6 5–6.7) *n* = 41	7.1 (6.6–7.7) *n* = 19	7.2
Mastoidal breadth	14.8 (14.3–15.5)[c]	14 (11.4–15.4) *n* = 41	14.7 (13.3–15.9) *n* = 19	15.6
Breadth of rostrum	6.2 (5.8–6.8)[c]	5.3 (4.18–6.8) *n* = 41	6.0 (4.9–6.7) *n* = 19	6.5
Length of nasal suture		13.6 (9.6–15.6) *n* = 39	14.4 (12.2–16.4) *n* = 17	15.8
Zygomatic breadth	19.5 (18.5–20.4)[c,d]	18.8 (14.9–21.1) *n* = 41	19.6 (16.7–22) *n* = 19	20.6
Length of incisive foramen	7.5 (6.9–8.1)[c,d]	6.9 (5.8–8.1) *n* = 41	6.9 (5.8–7.9) *n* = 19	7.5
Height of braincase		8.1 (6.9–8.9) *n* = 41	8.9 (8.4–9.4) *n* = 19	8.7
Coronal length of maxillary tooth row	6.9 (6.4–7.3)[c,d]	6.6 (5.6–7.6) *n* = 41	7.2 (7.0–7.4) *n* = 19	7.2
Palatal length		19.8 (16.8–21.6) *n* = 33	21.2 (17.7–22.8) *n* = 19	22.5
Postpalatal length		14.1 (11.5–16.3) *n* = 40	14.6 (12.1–16.3) *n* = 19	16.0
Tympanic bullar length		6.5 (5.2–8.8) *n* = 41	6.1 (5.2–6.8) *n* = 19	6.5
Tympanic bullar width		4.8 (3.7–5.8) *n* = 41	5.1 (3.8–6.1) *n* = 19	4.8
Mandibular length		19.5 (16.2–21.4) *n* = 41	20.4 (17.5–22.7) *n* = 19	22.2

[a]Nowak 1999; [b]Reid 2009; [c]Lawlor 1969; [d]Hall 1981; [e]Arita 2014; [f]Helm 1975.

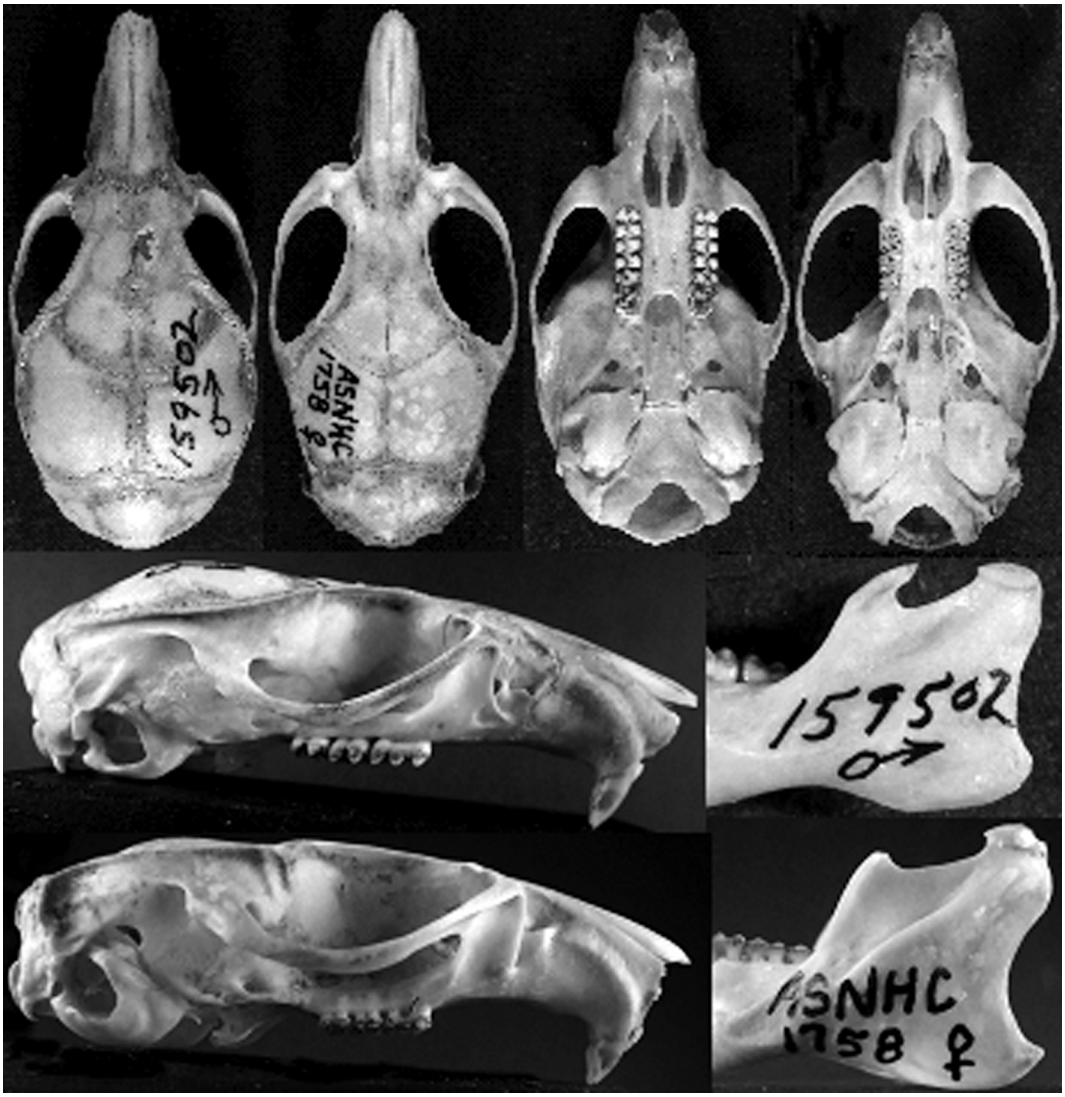

Fig. 8.—Comparison of mandible and skull of *Ototylomys chiapensis* paratype (MVZ 159502) from the type locality and *Ototylomys phyllotis* from Campeche (ASNHC 1758). For each pair of photographs, *O. chiapensis* is the skull or mandible on the left or the top, that of *O. phyllotis* on the right or the bottom. Specimen MVZ 159502 is Schmidly (1973) age class IV and the greatest length of skull = 38.0 mm. Specimen ASNHC 1758 is age class VI and greatest length of skull = 38.7 mm.

Paratypes.—From the type locality, adult specimen, skin and skull preparation unless otherwise indicated: MVZ 159501 male; MVZ 159502 male; MVZ 159503 male; MVZ 159504 male; MVZ 159505 male; MVZ 159506 male; MVZ 159507 male; MVZ 159508 male; MVZ 159509 male; MVZ 159510 female; MVZ 159511 female; MVZ 159513 female; MVZ 161245 male, skin, skull, and partial body skeleton; MVZ 161246 female, skull and partial body skeleton only; MSU 22405, male, skull and body skeleton only; ASNHC 3544 male, skull, disarticulated atlas, and alcoholic skin; ASNHC 3545 male, skull, disarticulated atlas, and alcoholic skin; TCWC 41455 (11-day-old offspring of TCWC 41454, born 18 August 1980) male, skull and articulated vertebrae C1–C5 only. Additional paratype collected 26 km N by road of Ocozocoautla, Chiapas, 28 December 1970: FHSM 9092, male, skin and skull.

The MVZ paratypes were collected 19–20 December 1980. The ASNHC specimen preparations are dated 6 August 1986, and may have been collected on or near 31 July 1986. The alcoholic skins catalogued with the ASNHC specimens are missing from the collection and were not examined. Specimens MVZ 159501–159504 also include catalogued glans penes cleared and stained, which could not be located in the collection and were not examined. Paratypes are illustrated in the Supplementary Data SD6–SD11.

We have ascertained that MSU 22405 is the *Ototylomys* specimen reported by Baker et al. 1971 [1973] from the oil well north of Berriozabál in La Pera. The specimen was catalogued in the MSU collection with an erroneous locality of Rayón, Chiapas, but with the elevation (3,500 feet, 1,065 m) of the La Pera locality, rather than the elevation (5,500 feet, 1,675 m) of Baker et al.'s 1971 [1973] Rayón locality. The other 2 *Ototylomys* specimens reported by Baker et al. 1971 [1973] (from near Solosuchiapa, and from near Rayón) were located in the MSU collection, and are correctly catalogued and identified

as *O. phyllotis* (see Appendix I). The Rayón specimen (MSU 15557) was collected and prepared on 18 July 1969, and the field crew left the locality the following day (Rollin H. Baker Field Itinerary, Michigan State University Museum, East Lansing, Michigan, 19 July 1969, in litt.). However, specimen MSU 22405 is dated 28 July, which is 4 days after they reported (Rollin H. Baker Field Itinerary, Michigan State University Museum, East Lansing, Michigan, 24 July 1969, in litt.; Baker et al. 1971 [1973]) collecting an *Ototylomys* at La Pera and retaining it alive. One of us (CAP) examined MSU 22405 and identified it as *O. chiapensis*. This identification confirms that the catalogued locality is in error, and that MSU 22405 is the big-eared climbing rat collected in 1969 by Baker et al. 1971 [1973] from the type locality of *O. chiapensis*. This specimen represents the earliest known record of *O. chiapensis*.

Other specimens examined.—TCWC 41454, adult female, skin and skull dated 29 August 1980, examined for allozyme data; TCWC 45914, male, alcoholic specimen and cleaned skull dated 6 January 1982, examined for allozyme data; and LACM 74223–74224 (adult female collected 31 July 1986, body skeleton and alcoholic skin prepared 6 August 1986 and a neonate male offspring of LACM 74223, alcoholic specimen), both examined for *Cytb* sequence data. ASNHC 3623 (alcoholic specimen, sex not recorded) examined for *Cytb* sequence data. These 5 topotypes were examined for molecular data, but we have not seen the vouchers, which are missing from their collections. The molecular data confirm that these specimens are conspecific with the type series.

In addition, 8 specimens collected from the type locality 14–17 December 2009 (CMC 2591 [adult male, skin, skull, and body skeleton], 2592 [subadult male, skin, skull, and body skeleton], 2593 [adult male, skin, skull, and body skeleton], 2594 [adult male, skin, skull, and body skeleton], 2637 [adult female, skin, skull, and body skeleton], 2660 [adult female, skin and skull], 2661 [adult female, skin, skull, and body skeleton], and 2683 [subadult female, skin, skull, and body skeleton]) were used in the *Cytb* molecular analysis and the vouchers were examined by 1 of us (DSR), but not included in the morphological analysis.

All of these specimens are excluded from the type series. However, the recorded external measurements, if available, are included in the species description (Supplementary Data SD1).

Etymology.—The specific name refers to the species distribution in the Mexican state of Chiapas.

Nomenclatural statement.—A life science identifier (LSID) number was obtained for the new species *O. chiapensis*: urn:lsid:zoobank.org:pub:0AE351C6-A448-4160-A7D0-E0EEDACE8F60.

Distribution.—Known only from the type locality and from 26 km N Ocozocoautla, both in the Mexican state of Chiapas (Figs. 1 and 2). The latter locality is in the municipality of Ocozocoautla de Espinoza at ca. 760 m elevation in the Reserva de la Biosféra Selva El Ocote, and is measured along the "old road" northwest of the city of Ocozocoautla de Espinoza (Johnson et al. 1976; Johnson and Savage 1995; Lamoreux et al. 2015).

Morphological description and comparisons.—Except in ventral white patches, hairs are bicolored, dark at the base and lighter at the tips. The dark roots range from Dark Neutral Gray to Blackish Plumbeous dorsally, and Deep Neutral Gray to Dark Plumbeous ventrally. The dark roots generally are not visible on the dorsum, though they may be exposed where the pelage is brushed against the grain. The roots of the ventral pelage do contribute to a mottled appearance on the venter, partly as a result of some hairs having a greater proportion of dark color. The dorsum is brown (Deep Mouse Gray to Deep Quaker Drab; or Benzo Brown in older, more reddish individuals, age groups V–VI), with irregular and indistinct rust-colored (Cinnamon-Drab—or Vandyke Brown to Chestnut-Brown in older, reddish rats) patches medially. Midlateral pelage trends toward the tan color found on the venter. The venter appears mottled tan-brown due to the bicolored hair, which is tan (Cartridge Buff or Ivory Yellow) or reddish-tan (Pale Ochraceous-Salmon, in older individuals) at the tips, and brown-gray at the roots. Distinct white spots are often present on the venter, particularly in the pectoral and inguinal regions. Hair in these spots is white from the roots to tip. The distribution and amount of white is variable and often asymmetrical, but does not appear to be correlated with age or sex. Rather than white patches, 4 paratypes have indistinct ventral white streaks resulting from some white-tipped hairs. See Supplementary Data SD4 and SD9 for color photographs of study skins.

The tail is long, scaly, and appearing hairless (though short sparse hairs are visible on close examination). In study skins, the tail is dark brown (Fuscous) dorsally and yellowish (Chamois) on the ventral surface. Tail scales may be rectangular, trapezoidal, pentagonal, rounded, or notched. Some portions of the tail may have fairly uniform rings of rectangular scales, but the heterogeneous scales result in at least some annulations that are uneven, incomplete, or oblique. The ears are hairless, broad, oval, thin, and translucent; Chaetura Drab to Chaetura Black in preserved specimens. Hind feet long.

External and skeletal measurements of *O. chiapensis* are presented in Table 4, with literature references and our measurements on *O. phyllotis* for comparison. *Ototylomys chiapensis* averages larger than *O. phyllotis* in most mensural features. Notably, *O. chiapensis* has a generally larger body mass and head and body length compared with *O. phyllotis* (Table 4).

The skull of *O. chiapensis* (Fig. 7) is dorsally flattened, barely domed in the center of the parietals and the interparietal. Braincase is heavy and robust, distinctly oval in the dorsal view, though angular points may be evident on the supraorbital ridge, and in some specimens, the posterior braincase may be angled, rather than smoothly curved (Supplementary Data SD7). The oval shape is consistently evident along the lateral margins of the parietals. The occiput is vertical and straight, roughly perpendicular to both the roof and base of the braincase. Supraorbital ridges well developed, formed by the frontal bone anteriorly, and posteriorly by the squamosal adjacent to its suture with the parietal. Posteriorly, the supraorbital ridge joins the occipital crest along the margin of the interparietal. Coronal suture is strongly curved, semicircular; lambdoid suture

broadly V-shaped. Interparietal large. Postglenoid foramina are reduced to a slit open to the anterior. Incisive foramina long and broad, but tapering anteriorly. The jugal bone is reduced. Anterior margin of zygomatic plate concave. Palate extends posteriorly to the middle of M3, and the posterior edge of the palate is U-shaped. Tympanic bullae relatively small, not appearing inflated. Dental formula I1/1, C0/0, P0/0, M3/3, molar morphology similar to *O. phyllotis*. The maxillary tooth row in *O. chiapensis* is 7.0 mm or longer, whereas the tooth row of *O. phyllotis* generally exceeds 7 mm only in specimens of *O. p. australis* from Costa Rica and in some specimens of *O. p. connectens*.

Mandibular notch and coronoid process are both well defined, with the coronoid process projected posteriorly. The scapulae are broad and fan-shaped with a well-developed spine and acromion process. The scapular spine (measured from the subscapular surface) averages 3.6 mm (range 3.5–3.7) in 3 specimens of *O. chiapensis*, compared with a mean of 2.7 mm (range 2.1–3.3) in 8 specimens we examined of *O. phyllotis* (Supplementary Data SD1).

The new species can be distinguished from *O. phyllotis* at the following 12 allozyme loci that are fixed or nearly fixed for alternative electromorphs: SOD1, IDH2, GPI, G3PDH, MDHP, AAT1, PGM1, FUMH, LDHB, ACON-2, PEP-B1, and PEP-B2. See Supplementary Data SD2 for the electromorphs fixed in each species. The karyotypes of the 2 species differ by 3 pericentric inversions (Fig. 4; cf. Hsu and Benirschke 1973).

Reproduction.—Four females collected 20 December 1980 included reproductive data. Two were noted as nulliparous, 1 as having no placental scars, and 1 (the holotype) with slightly swollen uteri. Of 4 females collected 15–17 December 2009, 1 was a nulliparous subadult, and the uteri of the other 3 were not swollen. Nine males collected 19–20 December 1980 included reproductive data (testes ranging in size from 3 × 2 to 15 × 8 mm), and 3 adult males collected 14 December 2009 had testes ranging from 8 to 15 mm in length. A subadult collected at the same time had testes measured at 5 mm.

One female (TCWC 41454) gave birth in captivity on 18 August 1980. Another female (LACM 74223) is recorded as having given birth on 31 July 1986. Both females were captured pregnant and produced a single young. Litters of 1 young also are observed in *O. phyllotis*, but the mean litter for that species varies from 1.75 to 2.75 depending on locality, and some females of *O. phyllotis* have litters as large as 4 (Helm 1975; Lawlor 1982; Itzá-Ortiz et al. 2011). The sample of 2 litters is too small to be certain that *O. chiapensis* typically is uniparous, but the evidence does suggest small litters in this species.

Development.—We examined the skull of an 11-day-old male neonate (TCWC 41455) of *O. chiapensis* (Supplementary Data SD11). The recorded external measurements of the specimen are 148-30-22-x, and the testes are noted as minute. The oval shape of the braincase is evident, particularly along the margins of the parietals. At this stage of development, the upper and lower 1st molars are barely beginning to erupt. M2 is partially visible, but not yet emergent. Lower incisors are emergent approximately 2 mm, and upper incisors approximately 3 mm; all incisors are white. Compared with adult specimens, the palate is disproportionately wide, and the cheek teeth diverge anteriorly. The rostrum is short relative to the skull. In the neonate, the zygomatic plate is nearly straight. The parietal bones do not touch, and the coronal and interfrontal sutures are partially open, forming a cross-shaped fontanel including the entire sagittal suture and portions of the coronal and interfrontal sutures. A large, open posteriolateral fontanel is present, bordered by the interparietal, exoccipital, mastoid, and squamosal bones. This fontanel continues forward forming a gap between the squamosal bone and the mastoid bone and tympanic bulla. The incisive foramina are short, commensurate with the shorter rostrum, and are broad and curved anteriorly, rather than abruptly tapering as in adults. At this stage, the supraorbital ridges are poorly developed along the frontal and parietal bones, and no ridges are present along the interparietal or supraoccipital. The braincase is noticeably domed compared with adult specimens, and the occiput is rounded, rather than square in the lateral view. The auditory meatus is large. Selected cranial measurements in millimeters of the neonate: GLS 28.6; MB 11.4; ZB 13.7; PL 13.0; LIB 5.8. Another 6-day-old male neonate (LACM 074224, the offspring of LACM 074223) was not examined by us, but is recorded as having external measurements of 158-67-23-12 and a body mass of 22 g.

Helm (1975) states that *O. phyllotis* reaches 50% of adult head and body length by 2 days old, as compared with *T. nudicaudus*, which does not reach that milestone until age 14 days. The 6-day-old specimen of *O. chiapensis* has a head and body length of 91 mm, or 53% of the mean adult head and body size, and a mass of 21% of the mean adult body mass. The 11-day-old rat had reached 68% of adult head and body length. *Ototylomys chiapensis* probably does not reach 50% of adult head and body length before 5–6 days of age, or 50% adult body mass until substantially later. *Ototylomys phyllotis* is known for having particularly precocial young (Helm 1975; Lawlor 1982; Reid 2009), but the new species appears not to share that characteristic to the same degree.

Diet.—Baker et al. 1971 [1973] reported that a captive *O. chiapensis* (species identification can be inferred from Rollin H. Baker Field Itinerary, Michigan State University Museum, East Lansing, Michigan, 24 July 1969, in litt.) preferred sunflower seeds, but rarely accepted fresh fruit. One of us (DSR) noted that captive *O. chiapensis* preferred cabbage over scratch grain. By comparison, *O. phyllotis* is said to readily eat seeds, leaves, and fruit (Lawlor 1969, 1982; Reid 2009), and *T. nudicaudus* likewise eats fruit as well as seeds (Baker et al. 1971 [1973]; Espinoza Medinilla 2014).

Ecology.—*Ototylomys chiapensis* is 1 of few rodents known to be restricted to karst habitats (Clements et al. 2006). The type locality is karst limestone topography with a rocky substrate, and with sinks and crevices (Baker et al. 1971 [1973]; Johnson et al. 1976; Wake and Johnson 1989). The site has minimal surface water, as is typical of karst landscapes, but precipitation often maintains moisture in the leaf litter. Although Wake and Johnson (1989) observed sufficient rainfall even in the dry season to maintain a damp substrate, Lamoreux et al. (2015)

found precipitation to be infrequent enough in the dry season to allow the leaf litter to dry. The site is described as montane rainforest (Breedlove 1981) with an estimated annual rainfall of 3,000 mm (Wake and Johnson 1989). According to Wake and Johnson (1989), nighttime lows are 14°C with daytime high temperatures of 32°C, and averages of 17°C at night and 23°C during the day. They describe the forest as consisting of "two canopies of straight-trunked, large to medium-sized trees" and with extensive populations of epiphytes in the canopy (Wake and Johnson 1989:7). Common tree species are listed by Ortiz-Rodriguez et al. (2014, 2016a). Baker et al. 1971 [1973] reported sparse ground vegetation at the site in 1969. However, the understory, consisting largely of mosses, as well as ferns and other small vascular plants, has become denser within the past several decades as light gaps have resulted from continued cutting of some canopy trees (Johnson et al. 1976; Wake and Johnson 1989). Coffee (*Coffea*) is cultivated in the area. Despite historic and ongoing human activity (Medina et al. 2006), several tracts of forest remain, particularly along ridges and in higher elevations.

The La Pera big-eared climbing rat is part of a diverse vertebrate community. Our survey (VertNet, accessed 26 June 2016—Constable et al. 2010) of vertebrate collection data for the La Pera locality found 15 species of anurans, 6 salamanders, 14 lizards, 8 snakes, 17 bats, 2 carnivorans, 16 rodents, and 1 shrew, in addition to 65 avian species representing some 9 orders and 29 families. *Peromyscus mexicanus* is by far the most abundant terrestrial mammal collected from La Pera, but *Oryzomys alfaroi*, *Heteromys desmarestianus*, and *Scotinomys teguina* are also common species in the mammalian community.

Our previously referenced survey of vertebrate collections found that 11 other cricetid rodent species including *T. nudicaudus* have been collected from the type locality of the new species. However, *O. phyllotis* is not known to be sympatric with *O. chiapensis*. Baker et al. 1971 [1973] reported having collected a specimen of *O. p. connectens* in 1969 from the oil well site in La Pera, but we identified their specimen (MSU 22405) as *O. chiapensis*. Contrary to published range maps (e.g., Hall 1981; Reid 2009; Arita 2014) which were based on Baker et al.'s 1971 [1973] Berriozábal record, the known geographic range of *O. phyllotis* in Chiapas does not extend west of the Río Grijalva or the Chiapenecan Volcanic Arc. Other recorded localities for *O. phyllotis connectens* in Chiapas are in the Eastern Highlands, at the edge of the Gulf Coastal Plain in the vicinity of Palenque, and in the Northern Highlands north of Río Grijalva (Fig. 2), all of which are considerably isolated from the *O. chiapensis* population. The nearest confirmed locality for *O. phyllotis* is near Rayón, Chiapas (Appendix I), roughly 50 km northeast of La Pera. *Ototylomys* is not recorded from the other physiographic regions of Chiapas (viz. Pacific Coastal Plain, Sierra Madre de Chiapas, Central Depression, or the Central Plateau).

Ototylomys chiapensis was collected in 1970 from an additional site 16 km northwest of the type locality at a few hundred meters lower elevation. Johnson et al. (1976) describe this location as a moist lower montane rainforest with karst limestone substrate. Although substantial agriculture was underway, they reported some stands of nearly virgin forest in areas not suitable for cultivation. Vertebrate biodiversity at this site is comparable to the type locality. Our survey of vertebrate natural history collections (27 July 2016) found 7 species of anurans, 3 salamanders, 11 lizards, 22 snakes, 18 bats, 7 rodents, and 110 bird species from this locality.

Conservation notes.—Ototylomys chiapensis is restricted to karst rainforest habitat in the mountains between the Río Grijalva and the Central Depression of Chiapas. Based on only 2 localities, the extent of its geographic range is unknown, but is likely restricted to forested areas of La Pera and El Ocote. Aside from a single specimen collected in 1970, all known individuals have been collected from the type locality. Lamoreux et al. (2015) noted human impact at the type locality including some logging activities and disruption of the substrate. The restricted geographic range and potential for habitat loss, combined with a possibly low reproductive output, make the La Pera big-eared climbing rat and its biological community a particular concern for conservation. Based on area of occupancy and the potential reduction in the extent and quality of the habitat, it is likely that the species qualifies as Critically Endangered under IUCN criteria. Further study is warranted to document the current range and habitat.

Supplementary Data

Supplementary Data SD1.—Morphological data used in morphometric analysis of *Ototylomys* and the species description of *Ototylomys chiapensis*.

Supplementary Data SD2.—Allozyme data used in phylogenetic analysis of *Ototylomys* and related genera.

Supplementary Data SD3.—Neighbor-joining analysis based on the Cavalli-Sforza and Edwards (1967) chord measure calculated from allozyme data *Ototylomys* and related genera.

Supplementary Data SD4.—Study skin of the holotype of *Ototylomys chiapensis*.

Supplementary Data SD5.—Skull of the holotype of *Ototylomys chiapensis*.

Supplementary Data SD6.—Lateral view of skulls and mandibles of adult *Ototylomys chiapensis* paratypes.

Supplementary Data SD7.—Dorsal view of skulls of adult *Ototylomys chiapensis* paratypes.

Supplementary Data SD8.—Ventral view of skulls of adult *Ototylomys chiapensis* paratypes.

Supplementary Data SD9.—Study skins of adult paratypes of *Ototylomys chiapensis*.

Supplementary Data SD10.—Skeleton of *Ototylomys chiapensis* paratype MVZ 161246.

Supplementary Data SD11.—Skull of neonate *Ototylomys chiapensis* paratype TCWC 41455.

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Appendix I

Specimens examined. Specimens included in the morphometric analysis are indicated in bold. Specimens examined for morphology, but not included in the morphometric analysis are enclosed in parentheses. Specimens examined for allozyme data are indicated in italics. Specimens examined for *Cytb* DNA sequence data are underlined, with GenBank accession numbers listed. The locality number indicates the localities of *Ototylomys phyllotis* in the allozyme analysis (Figs. 2 and 5; Supplementary Data SD2 and SD3). Museum acronyms are listed in the "Materials and Methods". Some outgroup sequences from GenBank lack vouchers or complete locality data. DNA sequences from specimens collected in Loltún Cave, Yucatán, were derived from destructive sampling of ancient material (Gutiérrez-García et al. 2014), and no museum vouchers are available. These specimens were not identified to subspecies, but we assign them to *O. p. phyllotis* based on locality and genetic similarity (Gutiérrez-García et al. 2015).

Taxon	Country or state	Locality	Specimens	GenBank accession number	Locality number
Arvicola terrestris	Switzerland		MVZ 155884	AY275106	
Eothenomys melanogaster			ISEM T-4338	AM392374	
Microtus oeconomus	Norway	Andøya Island		DQ452134	
Myodes gapperi	Minnesota			AY309431	
Sigmodon hispidus	Kansas	Ellis Co.: Hays	OSU 13231	AF425213	
Neotoma albigula	New Mexico	Hidalgo Co.	*ASNHC 4031–4035*		
		Otero Co.	TTU 76474	DQ179817	
Nyctomys sumichrasti	El Salvador	La Paz: ~3 mi NW San Luis Talpa	TTU 111529	JQ183064	
	Jalisco	6 km SE Chamela	*TTU 37740*		
	Honduras	El Hatillo, 6 mi NE Tegucigalpa on road to La Tigra	*TCWC 52264*		
Otonyctomys hatti	Campeche	44 km S Constitución	ROM 95790	JQ183060	
Tylomys watsoni	Costa Rica	Cartago: Moravia de Chirripo	(LSUMZ 8958)		
		Puntarenas: Monteverde	KU 142069	MF317949	
	Panama	Lab-reared from stock collected near Capria	(TTU 16526–16528)		
Tylomys bullaris	Chiapas	2 mi SE Tuxtla Gutiérrez	(TCWC 9407)		
Tylomys nudicaudus	Veracruz	Potero Ojo de Agua del Río Atoyac	(TTU 10005)		
		8 mi NW Potero Ojo de Agua del Río Atoyac	(TTU 16509–16510)		
	Chiapas	San Carlolampio, 23.9 mi SSE Zapaluta	(TCWC 9406)		
		Ruinas de Palenque	*ASNHC 2316*		
		9 km S Palenque, by road	*ASNHC 2317*		
		Izabal: Cerro San Gil	TTU 62082	DQ179812	
Ototylomys chiapensis	Chiapas	Pozo de Petróleo, 7 mi [11 km] NW (by road) Berriozábal	**ASNHC 3544, 3545,** 3623; CMC 2591–2594, 2637, 2660–2661, 2683; *TCWC 41454, (41455), 45914;* **MSU 22405**; ***MVZ 159501–159513,* 161245–161246;** LACM 74223–74224	MF281975-MF281986	
		26 km N Ocozocoautla	**FHSM 9092**		
Ototylomys phyllotis phyllotis	El Salvador	San Miguel: N side Laguna de Olomega, near border to La Union Dept.	TTU 64129	JX020576	
	Guatemala	El Peten: Tikal National Park, Flores, 60 km N, Flores Municipality	USNM 565152, 565482	JX020578–JX020579	
	Honduras	Atlantida: Lancetilla Botanical Garden	TTU 84372	JX020585	
		Colon: La Ceiba, S.A.G. Laboratorio	TTU 103970	JX020588	
		El Paraiso: 4–5 km NE Soledad	USNM 565166	JX020589	

Appendix I. *Continued*

Taxon	Country or state	Locality	Specimens	GenBank accession number	Locality number
	Nicaragua	Zelaya: Muelle de los Bueyes, on the Río Mico	*AK 251*		1
		Atlántico Norte: Rosa Grande	TTU 100337–**100338**	JX020685–JX020686	
		Atlántico Norte: El Balsámo	**TTU 100339–100340, 100341**	JX020683–JX020684	
		Chinandega: Bella Vista	**TTU 105095**	JX202682	
		Chinandega: San Cristóbal	**TTU 105104, 105105,** 105106, **105107**	JX020679–JX020680	
		León: Telica, San Jacinto	TTU 96968	JX020687	
		Matagalpa: Selva Negra	**TTU 88187, 96986, 105141, 105175**	JX020677–JX020678	
	Belize	Toledo District: Big Falls, Missouri Farm	*CM 92031*		2
		Toledo District: Bordering Jimmy Cut	*CM 92032*		2
		Toledo District: 0.7 km NNE Forestry Camp (Salmanaca), Columbia Forest Reserve	*CM 92035–92036*		2
		Stann Creek District: 6.8 km WNW Quam Bauk, Cockscomb Basin	*CM 92028*		3
		Stan Creek District: Cockscomb Basin Wildlife Sanctuary, at confluence of Cockscomb Branch and Mexican Branch	USNM 583075	JX020572	
		Cayo District: 1.6 km W. Augustine	*CM 91656, 92024–92025*		4
		Belize District: Altun Ha Ruins	*AK 7510–7513*		5
		Orange Walk District: Richmond Hill (Great Hill)	*CM 92026*		6
		Orange Walk District: Río Bravo Management Area	**UF 24797**		
		Orange Walk District: Hill Bank	**LSUMZ 7277**		
	Quintana Roo	Pucté	*ASNHC 1792–1795*		7
		2 km N, 8 km W Bacalar	*TCWC 37197–37198*		8
		2.5 mi NNE Felipe Carrillo Puerto	*TCWC 37201*		9
		3.5 mi N Felipe Carrillo Puerto	*TCWC 37205–37213*		9
		11 km NW Tulum, by road	*ASNHC 1796–1797*		10
		10 km W Cancún	*ASNHC 1790–1791; ASK 520, 523*		11
		17 km W Cancún	*ASNHC 1788–1789, ASK 570*		11
		Chemex Cobá, 20.551389°N, 87.805°W	IE Op12	JX020639	
		Ejido Señor, 19.768883°N, 88.103314°W	IE 14, 20	JX020625–JX020626	
		Mahahual, 18.908056°N, 87.864722°W	IE Op34	JX020651	
		Tres Garantías 18.266667°N, 89.043889°W	IE Op4	JX020636	
	Yucatán	Chichén Itzá	*ASNHC 1826–1831; TCWC 37225, 41484–41485*		12
		Loltún Cave, ~7 km SW Oxkutzcab, 20°15′N, 89°28′W	Vouchers unavailable	KJ751488, KJ751493, KJ751498	

APPENDIX I. *Continued*

Taxon	Country or state	Locality	Specimens	GenBank accession number	Locality number
	Campeche	Ruinas de Edzna	*ASNHC 1784*		13
		7.5 km W Escárcega	*ASNHC* **1758, *1759–1760,*** *1761–1762,* ***1763–1764,*** *1765–1771, 1775–1780,* ***1781***, 1782, ***5840***, 5842, 7242*; TCWC 37173, 37187–37192, 41459–41460, 41462–41468; ASK 280–283, 287, 317, 320, 363, 366, 371*	JX020596	14
		11 km S Candelaria	*ASNHC 1749–1752; ASK 205, 207*		15
		22 km S Candelaria	*ASNHC 1753–1755*		15
		Calkiní: El Remate, 14 km W Tancuche	ASNHC 7236	JX020597	
		Hopelchén: 18 km S X-Canhá	ASNHC 7244	JX020668	
	Tabasco	Balancán: 3.8 km SW Ruinas Acalán, by road	*ASNHC 1798–1799,* ***1800****, 1801–1803,* ***1804****, 1805,* ***1806****, 1807–1809,* ***1810****, 1811,* ***1812–1813****, 1814–1818; ASK 112, 115, 118–119, 121, 144, 165*; CNMA 33076	JX020669	16
		21 km SE Tenosique, Ejido Santo Marcos	*ASNHC1822; ASK 168, 304*		17
		28 km SE Tenosique, Ejido Santo Tomás	*ASNHC 1824–1825*		17
Ototylomys phyllotis connectens	Chiapas	6.6 mi (by road) S Palenque	***TCWC 37170–37171; ASNHC 1787***		18
		3.8 mi SW Palenque	***TCWC 41456–41457, 37172***		18
		Ruinas de Palenque	***ASNHC 1785***		18
		1.2 km E Ruinas de Palenque, by road	***ASNHC 1786***		18
		10 km S Solosuchiapa, 395 m	**MSU 15558**		
		6.5 km SE Rayón, 1,675 m	**MSU 15557**		
		Rayón	**MSU 24406**		
		Chajul Field Station, 16.12°N, 90.93°W	UWBM 80879, 80892	JX020603, JX020613	
	Guatemala	El Progresso: Planta San Miguel, 14.816972°N, 90.28694°W	MHNG 1341	JX020577	
Ototylomys phyllotis australis	Costa Rica	San José Province: 1 mi E Cangrejal	(LSUMZ 11523)		
		San José Province: San Ignacio de Acosta	(LSUMZ 9513)		
		Puntarenas Province: 5 mi NE Palmar Norte	(LSUMZ 15839)		
		Puntarenas Province	LSUMZ 1832	JX020573	