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A re-examination of the molecular systematics and phylogeography of taxa of the *Peromyscus aztecus* species group, with comments on the distribution of *P. winkelmanni*

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The objectives of this study are to examine the available molecular data from the mitochondrial cytochrome-*b* gene (*Cytb*) and a concatenated dataset with this gene and two nuclear introns (*Adh*-1-I2 and *Fgb*-I7) to reexamine the systematic and phylogeographic conclusions reached by Sullivan *et al.* (1997) concerning the *Peromyscus aztecus* species group. The divergence of samples of *P. aztecus oaxacensis* across the Isthmus of Tehuantepec are further examined and taxonomic revisions are suggested. In addition, this study reviews the sources of data that lead to the conclusion that *P. winkelmanni* occurred in the Sierra Madre del Sur in Guerrero including a morphometric examination of a reported voucher. Bayesian and maximum likelihood analyses were conducted on a dataset of 31 *Cytb* sequences of all taxa in the *P. aztecus* group except for *P. a. cordillerae* and a concatenated dataset including five individuals of this group. Representative taxa of the *P. boylii*, *P. mexicanus*, and *P. truei* groups were included in both analyses. Body and cranial measurements of the voucher of the *P. winkelmanni* from Guerrero from which a *Cytb* sequence is reported to have been obtained was compared with measurements from specimens taken from the vicinity of Dos Aguas, Michoacán, including the type locality. We identified seven instances involving problematic identifications in GenBank. Once these issues were addressed, well-supported monophyletic sister clades of the *P. aztecus* and *P. boylii* species groups were recovered from phylogenetic analyses of *Cytb* sequences (Fig 1). Phylogenetic analyses of the *Cytb* and the concatenated datasets recover similar topologies that support the relationships of taxa of the *aztecus* group proposed by an earlier molecular study. Populations of *P. a. oaxacensis* southeast of the Isthmus of Tehuantepec represent a distinct species. Measurements of the voucher from Guerrero identified as the source of a *P. winkelmanni Cytb* sequence are smaller than *P. winkelmanni* for several characters. The divergent populations of *P. a. oaxacensis* from southeast of the Isthmus of Tehuantepec are recognized as two subspecies of *P. cordillerae*, *P. c. cordillerae* and *P. c. hondurensis*, whereas those northwest of the Isthmus are retained as *P. a. oaxacensis*. The lack of genetic divergence observed between *P. a. evides* and *P. a. oaxacensis* questions whether these two taxa should continue to be recognized as separate subspecies. Northern and southern populations of *P. spicilegus* demonstrate moderate divergence and additional examination of morphological and molecular differentiation within this taxon is warranted. The distribution of *P. winkelmanni* should be restricted to the vicinity of Dos Aguas, Michoacán, due to the lack of a voucher specimen that would confirm its reported occurrence in Guerrero.

Los objetivos de este estudio son examinar los datos moleculares disponibles del gen del mitocondrial citocromo-b (*Cytb*) y un conjunto de datos concatenados con este gen y dos intrones nucleares (*Adh*-1-I2 y *Fgb*-I7) para reexaminar las conclusiones sistemáticas y filogeográficas alcanzadas por Sullivan *et al.* (1997) sobre el grupo de especies de *Peromyscus aztecus*. Se examina más a fondo la divergencia de muestras de *P. aztecus oaxacensis* a lo largo del Istmo de Tehuantepec y se sugieren revisiones taxonómicas. Este estudio revisa las fuentes de datos que llevan a la conclusión de que *P. winkelmanni* se distribuye en la Sierra Madre del Sur de Guerrero, incluyendo un examen morfométrico de los ejemplares "voucher". Se realizaron análisis bayesianos y de máxima verosimilitud de 31 secuencias de *Cytb* de todos los taxa en el grupo de *P. aztecus,* excepto *P. a. cordillerae,* y un conjunto de datos concatenados que incluye cinco individuos de este grupo. En ambos análisis se incluyeron ejemplares representativos de los grupos *P. boylii, P. mexicanus* y *P. truei*. Las medidas somáticas y craneales de los ejemplares "voucher" de *P. winkelmanni* de Guerrero, de los que se obtuvo una secuencia de *Cytb,* se compararon con medidas de especímenes tomados en las cercanías de Dos Aguas, Michoacán, incluyendo la localidad tipo. Se detectaron siete casos que involucran identificaciones problemáticas en GenBank. Una vez que se abordaron estos problemas, se recuperaron los clados monofiléticos hermanos con buen soporte de los grupos de especies de *P. aztecus* y *P. boylii* a partir de análisis filogenéticos de secuencias de *Cytb*. Los análisis filogenéticos de *Cytb* y los conjuntos de datos concatenados recuperan topologías similares que apoyan las relaciones entre taxa del grupo *aztecus* propuesto por un estudio molecular anterior. La población de *P. a. oaxacensis* al sureste del Istmo de Tehuantepec representan una especie distinta. Las medidas de los "vouchers" de Guerrero identificado con secuencia *Cytb* como *P. winkelmanni* son más pequeñas que las de *P. winkelmanni* para varios caracteres. Las poblaciones divergentes de *P. a. oaxacensis* del sureste del Istmo de Tehuantepec se reconocen como dos subespecies de *P. cordillerae*, *P. c. cordillerae* y *P. c. hondurensis*, mientras que los del noroeste del istmo se conservan como *P. a. oaxacensis*. La falta de divergencia genética observada entre *P. a. evides* y *P. a. oaxacensis* cuestiona si estos dos taxones deberían seguir siendo reconocidos como subespecies independientes. Las poblaciones del norte y del sur de *P. spicilegus* demuestran una divergencia moderada y se justifica un examen adicional de la diferenciación morfológica y molecular dentro de este taxón. La distribución de *P. winkelmanni* debería estar restringida a las cercanías de Dos Aguas, Michoacán, debido a la falta de "vouches" que confirmara su distribución reportada en Guerrero.

Keywords: Isthmus of Tehuantepec*; Peromyscus cordillerae; P. aztecus oaxacensis; P. winkelmanni.*

Introduction

The *Peromyscus aztecus* group was first recognized by Carleton (1989) with a content of three distinct species: *P. aztecus* (Saussure, 1860); *P. spicilegus* Allen, 1897; and *P. winkelmanni* Carleton, 1977. Five montane subspecies have been recognized within *P. aztecus* by Carleton (1979, 1989): *P. a. aztecus* occurring in the Sierra Madre Oriental; *P. a. cordillerae* Dickey, 1928, occurring in the highlands of Mt Cacahuatique of El Salvador; *P. a. evides* Osgood, 1904 (including the synonym *yautepecus* Goodwin, 1955); occurring in the Sierra Madre del Sur; *P. a. hylocetes* Merriam, 1898, occurring in the Transmexican Volcanic Belt; and *P. a. oaxacensis* Merriam, 1898, occurring in the highlands of central Oaxaca in the Sierra Madre del Sur, across the Isthmus of Tehuantepec in the Tierras Altas de Chiapas, and south to Guatemala, Honduras, and El Salvador. The divergence and phylogenetic relationships among and within the taxa of the *P. aztecus* species group have been characterized and estimated by examination of cranial morphology (Carleton 1977, 1979; Bradley *et al.* 1996), glans and bacular morphology (Bradley and Schmidly 1987; Bradley *et al.* 1989, 1990), karyotypes (Carleton *et al.* 1982; Smith *et al.* 1989; Smith 1990), allozymes (Sullivan and Kilpatrick 1991) and cytochrome-*b* (*Cytb*) sequences (Sullivan *et al.* 1997).

Carleton (1977) reported that *P. winkelmanni* occurs in the oak-pine forest at elevations between 6,900 and 8,000 feet from three localities SE and WSW of Dos Aguas in Michoacán. In a karyotypic study, Smith *et al.* (1989) reported a specimen from the vicinity of Filo de Caballos in Guerrero which expanded the range of *P. winkelmanni* from the mountains of the Sierra Madre del Sur in southwestern Michoacán to the main portion of the Sierra Madre del Sur in Guerrero. The occurrence of *P. winkelmanni* in the Sierra de Coalcomán in Michoacán and the Sierra Madre del Sur in Guerrero areas separated by a deep canyon of the Rio Balsas was viewed as biogeographically implausible by Musser and Carleton (2005). They concluded that the identification of the vouchers of *P. winkelmanni* from Guerrero needed to be reconfirmed.

The gleaning mouse, *P. spicilegus*, occurs in western México along the flanks of Sierra Madre Occidental from Sinaloa and Durango to Jalisco and northern Michoacán in the western Transmexican Volcanic Belt (Carleton 1977, 1989; Bradley *et al.* 1996). Fixed differences were observed in allozyme data reported by Sullivan and Kilpatrick (1991) from *P. spicilegus* suggesting that samples from Michoacán and samples from Nayarit possibly represent different species. Although considerable morphological (Bradley *et al.* 1996) and chromosomal (Carleton *et al.* 1982; Smith *et al.* 1989; Smith 1990) variation has been reported for this taxon, no geographic pattern of that variation has been detected. Sequence analysis by Sullivan *et al.* (1997) only examined samples from the southern portion of the range of this species, leaving the question of the sequence differentiation between northern and southern populations unaddressed.

A cladistic analysis by Sullivan and Kilpatrick (1991) including allozyme data, chromosomal characters reported by Smith *et al.* (1989) and morphological characters from Bradley *et al.* (1990) demonstrated considerable differentiation between *hylocetes* and other subspecies (*aztecus*, *evides*, and *oaxacensis*) of *P. aztecus*. The level of genetic identity and the degree of allozymic, chromosomal and morphological divergence exhibited by *hylocetes* led Sullivan and Kilpatrick (1991) to conclude that this taxon should be reinstated as a species, *P. hylocetes*. Analyses of *Cytb* sequence data supported this conclusion and found substantial levels of genetic divergence between *P. hylocetes* and *P. aztecus* (Sullivan *et al.* 1997).

The molecular analysis of Sullivan *et al.* (1997) recovered *P. a. oaxacensis* as polyphyletic and they suggested that populations south and east of the Isthmus of Tehuantepec represented a distinct species that was strongly divergent from populations of *P. a. oaxacensis* in Oaxaca. Musser and Carleton (2005) noted that populations of *P. aztecus* occupying the highlands south of the Isthmus of Tehuantepec warrant further scrutiny but continued to recognize them as subspecies of *P. aztecus, P. a. oaxacensis*. Duplechin and Bradley (2014) recognized *oaxacensis* populations in México as a distinct species citing the genetic data and inferences of Sullivan *et al.* (1997) but stated that it was unclear whether populations in Oaxaca were referable to *P. a. aztecus*, *P. a. evides*, or *P. oaxacensis*. Bradley *et al.* (2017) recognized populations northwest and southeast of the Isthmus of Tehuantepec as *P. oaxacensis* without comment on the genetic differentiation of populations separated by this geographic feature.

Although considerable morphological variation has been observed among allopatric populations of *P. aztecus* that has warranted the recognition of subspecies (Carleton 1977, 1979, 1989), little genetic differentiation has been observed (Sullivan and Kilpatrick 1991; Sullivan *et al.* 1997) other than between populations northwest and southeast of the Isthmus of Tehuantepec. Qualitative data of glans and bacular morphology (Bradley and Schmidly 1987; Bradley *et al.* 1990) showed a close relationship of *aztecus* to *oaxacensis* and *evides* to *hylocetes*, whereas quantitative data depicted *aztecus* as being distinct from the other subspecies (Bradley *et al.* 1990). Phenetic analysis of allozymic data (Sullivan and Kilpatrick 1991) found that *evides* clustered with *oaxacensis* to the exclusion of *aztecus*. However, analyses of allozymic data (Sullivan and Kilpatrick 1991) and *Cytb* sequence data (Sullivan *et al.* 1997) recovered *evides* and *oaxacensis* in the same cluster or clade with *aztecus* in a separate cluster or a sister clade. The lack of congruence among datasets makes it difficult to resolve the relationships among the subspecies of *P. aztecus*.

Since the initial molecular systematic analyses of the *P. aztecus* group by Sullivan *et al.* (1997), mitochondrial and nuclear sequence data have been obtained from 15 additional specimens from this group. The objectives of this study are to analyze an expanded dataset of *Cytb* sequences and a concatenated dataset of mitochondrial (*Cytb*) and nuclear (*Adh*-1-I2 and *Fgb*-I7) markers to further resolve the phylogeography and phylogenetic relationships among the taxa of this group. Specifically, these analyses will address: 1) the differentiation between northern and southern populations of *P. spicilegus*; 2) The differentiation between *P. hylocetes* and subspecies of *P. aztecus*; 3) The differentiation and relationships of populations recognized as *P. a. oaxacensis* separated by the Isthmus of Tehuantepec; and 4) the relationships among subspecies of *P. aztecus*. Additionally, this paper examines the voucher of a specimen from which tissue and a karyotype were reported to have been obtained that led to the conclusion of Smith *et al.* (1989) and that was supported by Sullivan *et al.* (1997) that *P. winkelmanni* occurs in the vicinity of Filo de Caballos in Guerrero.

Materials and Methods

Collection and analyses of molecular data. All available cytochrome *b* (*Cytb*) sequences in GenBank (https://www.ncbi.nlm.nih.gov/genbank/) as of November 15, 2020, for taxa of the *P. aztecus* species group (*n* = 31); representative *Cytb* sequences from 9 taxa of its sister group, the *P. boylii* species group (*n* = 21); and two outgroup taxa from the *P. truei* species group (Table 1) were downloaded and aligned using ClustalW (Thompson *et al.* 1994) in MEGA7 (Kumar *et al.* 2016). After an initial Neighbor-Joining analysis (Saitou and Nei 1987) in MEGA7 and a Nucleotide Blast search of an outlying sequence, sequences from three taxa of the *P. mexicanus* species group were added to the *Cytb* dataset (Table 1). PartitionFinder 2.1.1 (Lanfear *et al.* 2016) was used to find the best partitioning scheme and the best model for each partition based on the AIC criterion under a likelihood framework using PhyML (Guindon *et al.* 2010) and the greedy algorithm (Lanfear *et al.* 2012). Maximum likelihood (ML) analysis with 1,000 bootstrap replicates and GTR+I+G model on all partitions was conducted with RAxML ver. 8.0 (Stamatakis 2014). The majority-rule consensus tree (MRC) with bootstrap support values was constructed in Mesquite ver. 3.5 (Maddison and Maddison 2011). A Bayesian analysis was conducted on the CIPRES portal (https://www.phylo.org; Miller *et al.* 2010) using the partitions and models identified with PartitionFinder for the *Cytb* dataset in MrBayes 3.2.3 (Ronquist and Huelsenbeck 2003). Default settings with two simultaneous MCMC runs of 10,000,000 generations with sampling every 1,000 generations were used and the log files for both runs were examined in Tracer 1.6 (Rambaut *et al.* 2014). A burn-in of 1,000,000 generations was set for each run and the runs were combined after discarding the burn-in to produce a MRC tree with posterior probabilities in Mesquite.

Kimura 2-parameter distances (=K2P; Kimura 1980) were estimated using MEGA7 based on *Cytb* alignments of individuals of the *P. aztecus* group in Table 1. Individuals were generally grouped by clades recovered in the phylogenetic analyses to determine mean K2P distances. However, subspecies of *P. aztecus* samples from México were grouped by biogeographic areas (mountain ranges). These mean K2P values were used to examine species boundaries based on levels of interspecific divergence observed among rodents and other mammals (Bradley and Baker 2001).

Sequences for two nuclear introns, alcohol dehydrogenase intron 2 (*Adh*-1-I2) and beta-fibrinogen intron 7 (*Fgb*-I7) were downloaded from GenBank for all available samples from the *P. aztecus* species group (*n* = 13), six taxa of the *P. boylii* species group, two taxa of the *P. mexicanus* species group and two taxa of the *P. truei* species group (Table 1). Sequences for these two nuclear introns were concatenated with a *Cytb* sequence obtained either from the same specimen or from a specimen from the proximity of the collecting locality of the nuclear sequence source (Table 1). A concatenated dataset of a *Cytb* and one or two nuclear genes was constructed for five samples reported to be from taxa of the *P. aztecus* group, nine samples from six taxa of the *P. boylii* group, and two samples from both the *P. mexicanus* and *P. truei* groups. Six additional samples represented by only *Cytb* sequences from *P. a. oaxacensis* from either side of the Isthmus of Tehuantepec were included in the analyses with concatenated sequences.

PartitionFinder 2.1.1 was used to find the best partitioning scheme and the best model for the concatenated dataset. A bootstrapped ML analysis was carried out for the concatenated dataset as with the *Cytb* dataset and the MRC tree with bootstrap support values was constructed in Mesquite. A Bayesian analysis was conducted on the CIPRES portal using the partitions and models identified with PartitionFinder for the concatenated dataset in MrBayes 3.2.3. The same parameters were used in this Bayesian analysis as used in the analysis of the *Cytb* dataset to produce a MRC tree with posterior probabilities in Mesquite.

Pairwise uncorrected p-values were estimated with MEGA7 for sequences of the two nuclear introns. These values were used to identify the species of the source of nuclear sequences from specimens determined as likely misidentified in the *Cytb* analysis, from different non-identical sequences reported from the same specimen, and sequences reported from species well outside of their known range.

Morphometrics. External measurements (in mm) including total length (TL), length of tail (LT), length of hind foot (HF), and ear length (EL) were taken from the collectors' field tags. Head and body length (HB) was calculated by subtracting the tail length from the total length to provide comparable data for specimens with broken tails. Measurements were taken from specimens of *P. winkelmanni* collected from the following locations: Michoacán: 7.4 mi WSW Dos Aguas (*n* = 10); 6.3 mi WSW Dos Aguas (*n* = 3); 6.9 mi WSW Dos Aguas (*n* = 3) housed in the Texas Cooperative Wildlife Collection (TCWC). Seven dimensions of the skull, following those reported by Carleton (1977) were measured (±0.01 mm) with dial calipers including: skull greatest length (SGL), rostral length (RL), brain-case width (BCW), zygomatic breadth (ZB), interorbital width (IOW), molar row length

Table 1. Sequence data examined from specimens of the *Peromyscus aztecus*, *P. boylii* groups and out-group taxa (*P. attwateri*, *P. gratus*, and *P. mexicanus*). References: 1) Miller and Engstrom 2008; 2) Sullivan *et al*. 1997; 3) Bradley *et al*. 2014; 4) Platt *et al*. 2015; 5) Sullivan *et al*. 2017; 6) Saasa *et al*. 2012; 7) Amman *et al*. 2006; 8) Amman 2005; 9) Bradley *et al*. 2007; 10) Tiemann-Boege *et al*. 2000; 11) Bradley *et al*. 2000; 12) Bradley *et al*. 2017; 13) Bradley *et al*. 2004; 14) Cabrera *et al*. 2007; 15) López-González *et al*. 2014; 16) Reeder and Bradley 2007; 17) Durish *et al.* 2004; and 18) Bradley *et al.* 2016.

Taxon[1]	State	Location	GenBank Accession Number			Field or Catalog Number	Ref
			Cytb	*Adh*-1-I2	*Fgb*-I7		
***P. aztecus* Species Group**							
P. aztecus	Michoacán	5 km E Dos Aguas	FJ214683[2]			FN 22401	GenBank
	Michoacán	5 km E Dos Aguas		FJ214669[3]	FJ214695[3]	TK 45255[4]	GenBank
	El Salvador	Santa Ana, Parque Nacional Montecristo, Los Pines	EF989968			ROM 101489	1
	El Salvador	Santa Ana, Parque Nacional Montecristo, Los Pines	EF989969			ROM 101490	1
P. a. aztecus	Veracruz	Teocelo	U89966			2204	2
	Veracruz	Teocelo	U89967			235	2
	Veracruz	8.8 km N Huatusco	U89968			GK 4053	2
P. a. evides	Oaxaca	5.6 km S. Suchixtepec	U89970			GK 3439	2
	Oaxaca	9.7 km E Juquila	U89969			GK 3407	2
	Guerrero	6.4 km SSW Filo de Caballos	FJ214685*	FJ214670*	FJ214700*	TK 93391	3, 4, 4
	Guerrero	4 mi SSW Filo de Caballos	KY707306			TK 93385	5
	Guerrero	17.22 N x 99.28 W	AB703007			1950/171	6
P. a. oaxacensis	Honduras	Francisco, Morazan, La Tigra Parquae Nacional	FJ214688*[3]	FJ214675*[3]	FJ214714*[3]	TK 101037	GenBank
	Guatemala	Zacapa, 2 km N San Lorenzo	U89971			34194	2
	Guatemala	Alta Verapaz Yalijux Mountain, Chelemha Reserve	KF201657			TK 151047	3
	Oaxaca	1.4 km N Llano de las Flores	U89972			GK 3516	2
	Oaxaca	2.1 km S Llano de las Flores	U89973			CWK 2117	2
P. hylocetes	Michoacán	Estacion Cerro Burro, Microodas, 3,270 m	DQ000481*	AY994235*	FJ214705*	TK 45309	3, 7, GenBank
	Michoacán	Puerto Garnica	U89974			CWK 2040	2
	Morelos	2.43 km W Huitzilac	U89975			GK 2781	2
	Michoacán	Puerto Garnica	U89976			CWK 2035	2
	Michoacán	3.6 km W Mil Cumbres	U89977			GK 4229	2
	Michoacán	4.9 km S Los Azufres	U89978			GK 2853	2
P. spicilegus	Michoacán	Dos Aguas		AY994233	FJ214719	TK 45262	8, GenBank
	Michoacán	5 km E Dos Aguas		AY994234		TK 45255[4]	4
	Michoacán	Km 81 carr. Ario de Rosales and La Huacana	DQ000480*	AY994232*		TK 47888	3, 7
	Durango	San Juan de Camarones	AY322512			TK 70912	3
	Durango	San Juan de Camarones	DQ973107			TK 70919	9
	Michoacán	10.7 km E Uruapan	U89979			GK 4217	2
	Nayarit	8.1 km W Villa Carranza	U89980			GK 3253	2
P. winkelmanni	Michoacán	6.9 mi WSW Dos Aguas	AF131930*	FJ214678*	FJ214721*	GK 3311	3, GenBank
	Michoacán	19.3 km WSW Dos Aguas	U89981			GK 3287	2
	Michoacán	19.3 km WSW Dos Aguas	U89982			GK 3286	2
	Guerrero	Filo de Caballo	U89983			GK 3388	2
***P. boylii* Species Group**							
P. b. boylii	California	Monterey Co., Hastings Natural History Reservation	AF155386*			MVZ: K, Nutt 120	9
	California	San Diego Co., Heise County Park		AY994225*		TK 90233	7
P. b. rowleyi	Jalisco	30 km W Huejuquilla del Alto	AF155388*		AY274208*	TK 48636	10, 4
	Jalisco	2 km NW Mesconcitos		AY994227*		TK 93089	4
P. b. utahensis	Utah	Garfield Co., Henry Mts., Mt. Pennell, Sidehill Springs	AF155392*			MSB-NK 39457	9
	Utah	Washington Co., Beaver Dam Wash		AY994226*		TK 24389	8
P. beatae	Chiapas	Yalentay		AY994223		TK 93279	7

Table 1. Continuation...

Taxon[1]	State	Location	GenBank Accession Number			Field or Catalog Number	Ref
			Cytb	*Adh*-1-I2	*Fgb*-I7		
	Veracruz	Xometla	AF131921*	AY994222*		GK 3954	3, 8
	Veracruz	6.7 km NE, 81.6 km SE Perote			FJ214696*	TK 150106	GenBank
	Oaxaca	3 mi S Suchixtepec	AF131923			GK 3450	11
	Chiapas	12 km SE Ixtapa	AF131917			FN 33058	11
P. carletoni	Nayarit	Ocota de la Sierra	KF201663			TK 148445	3
	Nayarit	Ocota de la Sierra	KF201664			TK148432	3
	Nayarit	Ocota de la Sierra	KF201671			TK148428	3
P. kilpatricki	Michoacán	Km 81 between Ario de Rosales and La Huacana	KX523179			TK 47887	12
	Michoacán	Km 81 between Ario de Rosales and La Huacana	KX523180			TK 47890	12
	Michoacán	13.5 km SW Zitacuro	KX523183			Tk 150627	12
P. levipes	Michoacán	Las Minas, 3 km SW Tuxpan	DQ000477*	AY994224*		TK 47819	7, 7
	México	12 km S Acambay	AY322509*	KT361507*		TK 93400	13, GenBank
	México	14.1 km NW Villa del Carbon	KX523178*		FJ214707*	TK 112532	
						TK 113532*	12, 4
P. l. ambiguus	Nuevo Léon	Cola de Caballo	AF131928			GK 3840	3
P. l. levipes	Tlaxcala	2 km W Teacalco	AF131929			GK 4031	3
P. schmidlyi	Durango	6.2 km W Coyotes, Hacienda Coyotes	AY370610*	AY994228*	FJ214718*	TK 72443	9, 7, GenBank
	Durango	30 km SW Ojitos	AY322524*	AY994229*		TK 70812	13, 8
	Sonora	0.8 km N, 1.4 km E Yecora	EU234540			10889 CIB	14
	Chihuahua	3.2 km S, 0.8 km E Hueleyvo	KC403898			CRD 4001	15
Out-Group Taxa							
P. attwateri	Oklahoma	McIntosh Co., 4.9 km E Dustin	AY155384*	AY817626*	AY274207*	TK 23396	9, 7, 16
P. gratus	Michoacán	Aquililla, 4 km E Cuitzeo	AY376421*	AY994218*	FJ214703*	TK 46354	9, 7, 4
P. mexicanus	Chiapas	9 mi N Ocozocozulta	AY376425*		AY274210*	TK 93314	17, 16
P. nudipes	Nicaragua	Madriz, San Lucas, Los Mangos	FJ214687*	AY994238*	FJ214713*	TK 93600	4, 4, 4
P. nicaraguae	Nicaragua	Matagalpa, Selva Negra	KX998947			TK 93678	18

1. As designated in GenBank Accessions
2. Determined not from this location
3. Determined not from this taxon
4. Sequences from TK 45255 attributed to both *P. aztecus* (FJ214669 and FJ214695) and *P. spicilegus* (AY994234)

* Sequence concatenated

(MRL), and palatal breadth (PB) from specimens from 7.4 mi WSW Dos Aguas ($n = 7$). Measurements were also taken from a specimen from Guerrero that has the same field number (GK 3388) as the specimen from which a *Cytb* sequence was reported of *P. winkelmanni* by Sullivan *et al.* (1997).

Estimation of descriptive statistics (mean, range, and standard deviation) of all measurements was calculated for specimens of *P. winkelmanni*. Measurements from the Guerrero specimen (GK 3388, TCWC 045175) were compared to the descriptive statistics obtained from this sample of *P. winkelmanni* and those provided by Carleton (1977) including those of the holotype.

Results

The initial Neighbor-Joining analysis of the *Cytb* dataset recovered sequence FJ214688, reported from a *P. aztecus oaxacensis*, as an outlier to both the *P. aztecus* and *P. boylii* clusters. A Nucleotide Blast of this sequence recovered 99 to 98 % identities with sequences of *P. nicaraguae* and *P. nudipes* of the *P. mexicanus* species group.

The expanded *Cytb* dataset, including representative taxa of the *P. mexicanus* species group, was partitioned by codon position. The Bayesian analysis using a GTR+I+G model for codons 1 and 3 and a GTR+I model for codon 2, recovered a well-supported phylogenetic tree (Fig. 1). The *Cytb* sequence (FJ214688) reported to be from a *P. a. oaxacensis* from Honduras (TK 101037) was recovered in a well-supported clade with sequences from taxa of the *P. mexicanus* species group sister to a sequence from a *P. nudipes*. The K2P distance between this sequence and sequences from the *P. aztecus* species group ranged between 13.4 to 17.5 % (Table 2) whereas the differentiation from a *P. nudipes* sequence was only 1.9 %. The Bayesian analysis of concatenated sequences using a GTR+I+G model for *Cytb* codons 1 and 3, HKY+I for *Cytb* codon 2, and HKY+G for *Adh*-1-I2 and *Fgb*-I7 recovered specimen TK 101037 from Honduras in the *mexicanus* species group clade as the sister taxon to *P. nudipes* (Figure 2). A p-distance of 0.3 % of the *Fgb*-I7 sequence FJ214714 was found with a *P. nudipes* sequence, but the *Adh*-1-I2 sequence FJ214675 from this specimen had a p-distance of 5.7 % from the *P. nudipes* sequence and values > 3.2 % from all taxa of the *P. aztecus* group for which *Adh*-1-I2 sequences were available.

The remaining 30 *Cytb* sequences reported to be from taxa of the *P. aztecus* species group were recovered in a well-supported clade (ML = 87; PP = 1.00) that was sister to a well-supported clade (ML = 99; PP = 1.00) of taxa of the *P. boylii* species group (Figure 1). Five subclades were recovered in the *aztecus* group clade representing *P. winkelmanni*, *P. spicilegus*, *P. a. oaxacensis* southeast of the Isthmus of Tehuantepec, *P. hylocetes*, and a clade containing *aztecus*, *evides*, and *oaxacensis* from northwest of the Isthmus of Tehuantepec. Although *P. winkelmanni* showed the greatest divergence from other taxa of the *P. aztecus* group (mean K2P = 8.79 %), its affinities were clearly with this group and not with the *boylii* group.

Sequences of *Cytb* from the gleaning mouse, *P. spicilegus*, were recovered in a well-supported (ML = 99; PP = 1.00) clade (Figure 1) that was divergent from other clades in the *aztecus* group with a mean K2P distance of 8.71 % (Table 2). Two subclades were recovered in the *spicilegus* clade, one containing northern samples from Durango and the other more southern samples from Michoacán and Jalisco. The mean K2P differentiation between these southern and northern groups was 3.33 %.

Although a *Fgb*-I7 sequence and three *Adh*-1-I2 sequences (Table1) are available from specimens of *P. spicilegus*, only one of the *Adh* sequences is from a specimen (TK 47888) for which a *Cytb* sequence is available. The analyses of the concatenated sequences from TK 47888 recover

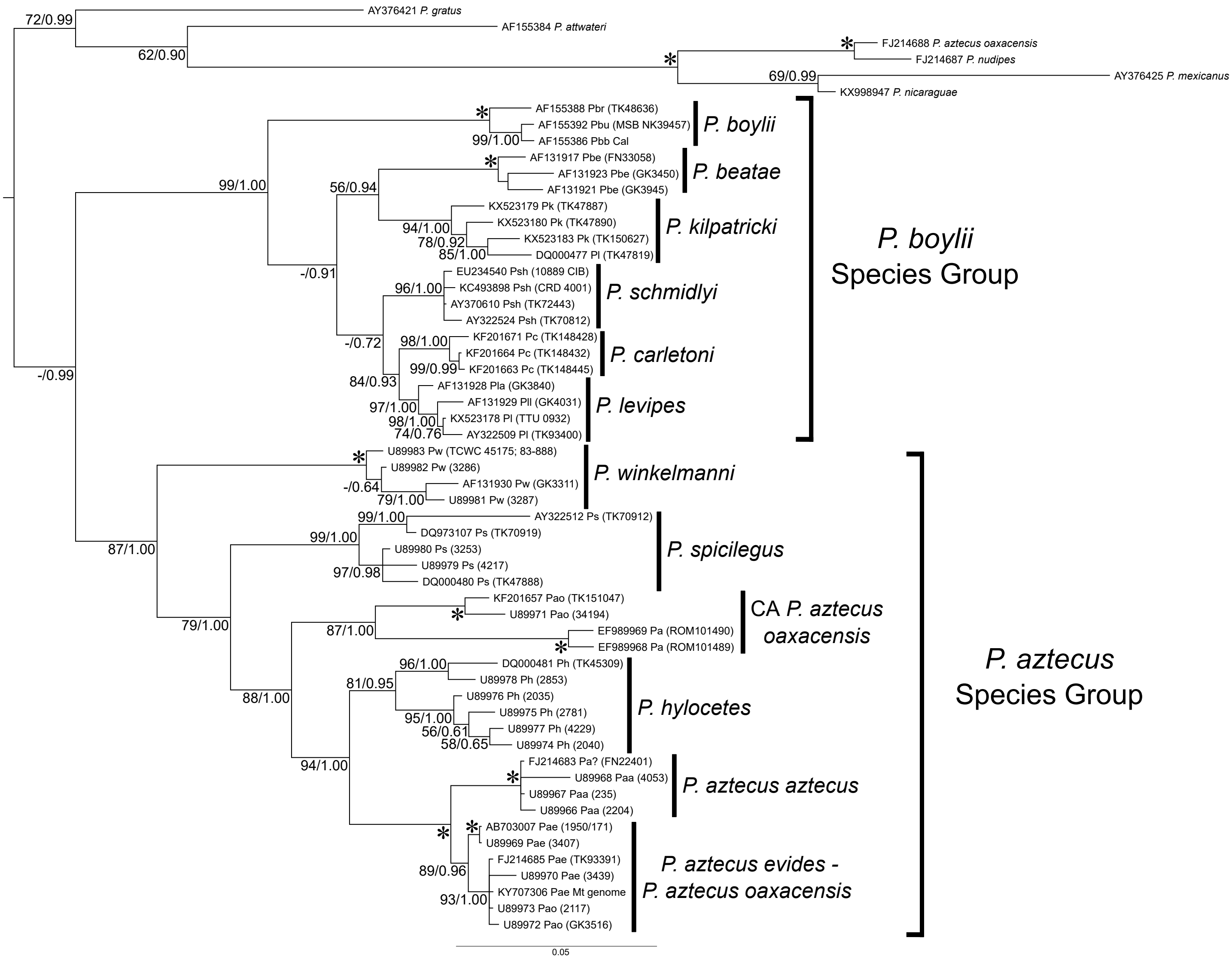

Figure 1. Bayesian tree of 31 *Cytb* sequences from samples reported to be from taxa of the *P. aztecus* species group and *Cytb* sequences from representative taxa of the *P. boylii*, *P. truei*, and *P. mexicanus* species groups. Nodal support is provided as Maximum Likelihood bootstraps and Bayesian posterior probability values (ML/PP: only if > 50 %). An asterisk (*) identifies nodes with fully realized support (ML = 100 and PP = 1.00).

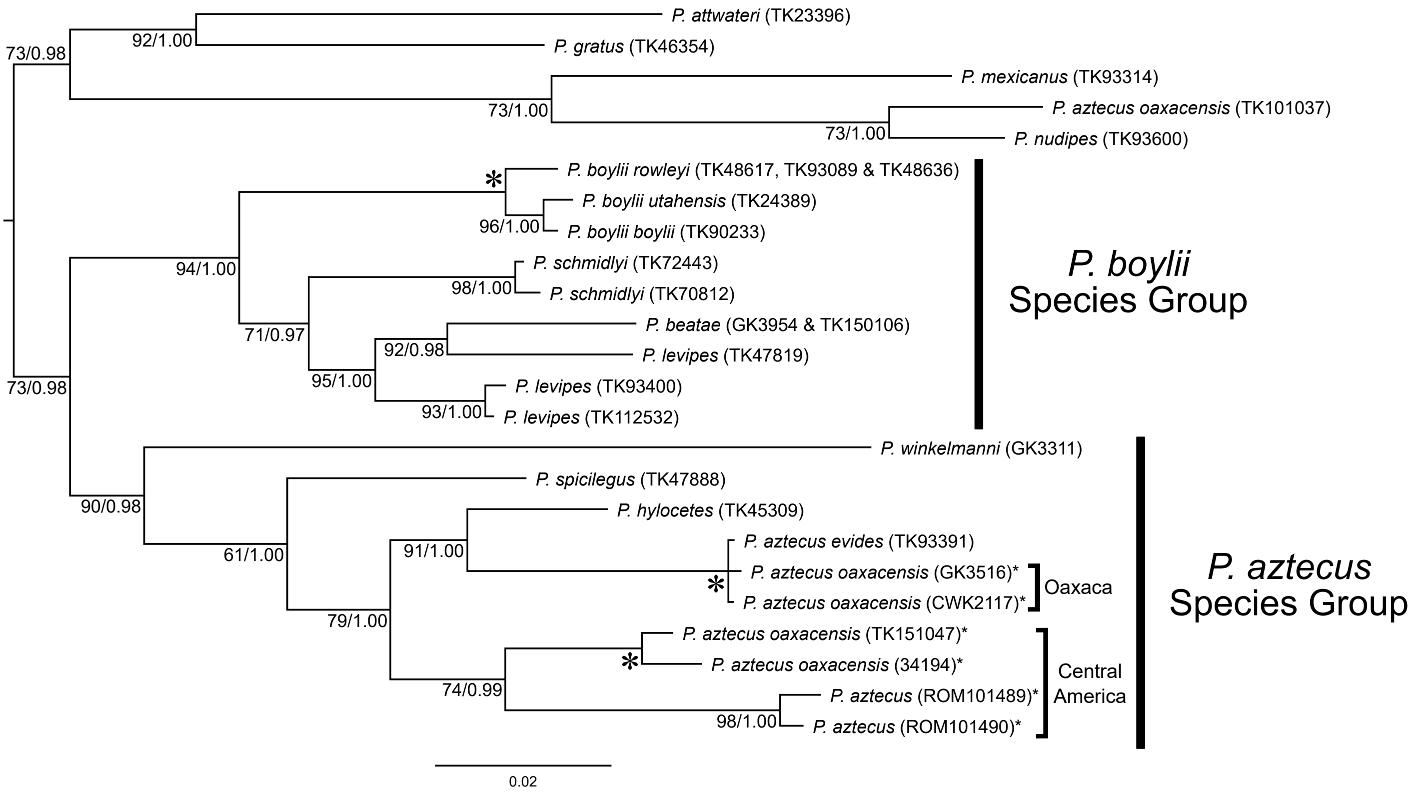

Figure 2. Bayesian tree of concatenated sequences (*Cytb*, *Adh*-1-I2, and *Fgb*-I7) from samples reported from five taxa of the *P. aztecus* species groups and representative samples from the *P. boylii, P. truei*, and *P. mexicanus* groups. Individuals represented only by a *Cytb* sequence are indicated with an asterisk (*) following the sample number. Nodal support is provided as Maximum Likelihood bootstraps and Bayesian posterior probability values (ML/PP: only if > 50 %). An asterisk (*) identifies nodes with fully realized support (ML = 100 and PP = 1.00).

this specimen of *P. spicilegus* as sister to a *hylocetes-aztecus*-Central American *oaxacensis* clade (Figure 2).

Populations of *P. a. oaxacensis* from Central America (southeast of the Isthmus of Tehuantepec) were recovered in a well-supported (ML = 87; PP = 1.00) clade (Figure 1) containing two well-supported subclades, one with samples from Guatemala and the other samples from El Salvador. The mean genetic differentiation (K2P) between these two subclades was 7.5 %. Samples of *P. a. oaxacensis* from northwest and southeast of the Isthmus of Tehuantepec had a mean K2P divergence of 7.9 % (Table 2). A similar topology for these samples was recovered in the analyses of the concatenated dataset (Figure 2), though only *Cytb* sequence data were available for samples of *P. a. oaxacensis*.

The remaining samples representing populations of *aztecus*, *evides*, *hylocetes*, and *oaxacensis* from north of the Isthmus of Tehuantepec were recovered in a well-supported (ML = 94; PP = 1.00) clade (Figure 1) sister to the *oaxacensis* clade from south of the Isthmus. Within the former clade, samples of *hylocetes* form a moderately well-supported (ML = 81; PP = 0.95) clade with a mean genetic differentiation (K2P) of 5.5 % from the *aztecus-evides*-northern *oaxacensis* clade (Fig. 1). Analyses of the concatenated dataset recovered *hylocetes* within a well-supported clade (ML = 91; PP = 1.00) as the sister taxon of *evides* and northern *oaxacensis* (Figure 2).

Two well-supported subclades were recovered in the *P. aztecus* clade from northwest of the Isthmus of Tehuantepec, one including samples of *P. a. evides* and northern samples of *P. a. oaxacensis* (Figure 1). Little genetic differentiation (mean K2P = 0.005) was observed between samples of *P. a. evides* from the Sierra Madre del Sur and the *P. a. oaxacensis* from the highlands of central Oaxaca. The other subclade contained samples of *P. a. aztecus* and a sequence (FJ214683) of a *P. aztecus* reported to be from 5 km E Dos Aguas in Michoacán (Figure1), a location from which *P. aztecus* has not previously been reported.

If the sequences for *P. a. aztecus* from two specimens (FN 22401 and TK 45255) both reported from 5 km E Dos Aguas, Michoacán, a locality well outside of the known range of this subspecies (Carleton 1989) are included in the concatenated dataset, this concatenated sequence of *P. aztecus* is recovered as sister to a *hylocetes-evides*-northern *oaxacensis* clade. The *Cytb* sequence from FN 22401 (FJ214683) was recovered in the *P. a. aztecus* clade with strong support (ML = 100; PP = 1.00) in the phylogenetic analyses of the *Cytb* dataset (Figure 1). The *Fgb*-I7 sequence from TK 45255 (FJ214695) was found to have p-distances of 1.0 % from *P. spicilegus*, 2.5 % from *P. nudipes*, and 3.2 % from *P. hylocetes* and *P. a. evides* sequences. The *Adh* sequence from TK 45255 (FJ214669) had a p-value > 3.2 % from all comparisons with *P. aztecus* species group taxa. A concatenation of these sequences was not included in our analyses.

Body and skull measurements from the voucher from Guerrero (GK 3388, TCWC 45175) for *Cytb* sequence U89983 from a *P. winkelmanni* was smaller for head and body length,

Table 2. Mean pairwise Kimura-2-parameter distances between clades recovered in the phylogenetic analysis of *Cytb* sequences below the diagonal and within the clades on the diagonal.

Taxa	*P. a. aztecus*	*P. a. evides*	*P. a. oaxacensis*	*P. hylocetes*	*P. spicilegus*	*P. winkelmanni*	*P. aztecus* El Salvador	*P. aztecus* Guatemala	*P. aztecus* Honduras
P. a. aztecus	0.0076								
P. a. evides	0.0295	0.0077							
P. a. oaxacensis	0.0302	0.0050	0.0015						
P. hylocetes	0.0642	0.0503	0.0494	0.0262					
P. spicilegus	0.0901	0.0876	0.0826	0.0805	0.0273				
P. winkelmanni	0.0881	0.0836	0.0824	0.0836	0.0833	0.0135			
P. aztecus El Salvador	0.0881	0.0912	0.0781	0.0770	0.1019	0.1049	0.0125		
P. aztecus Guatemala	0.0838	0.0708	0.0798	0.0777	0.0835	0.0892	0.0747	0.0175	
P. aztecus Honduras[1]	0.1597	0.1655	0.1589	0.1530	0.1534	0.1454	0.1749	0.1338	NA

[1] Sequence from a *P. nudipes*

the greatest length of skull and brain-case width, and at the minimal range for hind foot and molar row length compared with measurements from *P. winkelmanni* (Table 3). This specimen is cataloged as TCWC 45175 and identified as a *P. a. evides* collected on 30 July 1983 from Filo de Caballos, 7,900 ft, Guerrero, México. The sequence U89983 does, however, belong to the *P. winkelmanni* clade (Figure 1).

Discussion

Sequences associated with incorrect data. Several misplaced or problematic sequences were detected while downloading sequences or in our phylogenic analyses, including sequences FJ214688 (*Cytb*), FJ214675 (*Adh*), and FJ214714 (*Fgb*) from specimen TK 101037 (TTU 83698) from Francisco, Morazán, La Tigra Parque Nacional in Honduras identified in GenBank as from *P. a. oaxacensis* (Table 4). The specimen, TTU 83698 (TK 101037) is catalogued in Vertnet as a *P. mexicanus* and the results of the analysis of the *Cytb* sequence (FJ214688) and an analysis including a concatenation of these three sequences recovered this specimen within the *P. mexicanus* species group, sister to a specimen of *P. nudipes*. Based on our molecular analyses, sequences from TK 101037 from Honduras appear to be from a *P. nudipes* and not a *P. aztecus*, however, the *Adh* sequence FJ214675 from this specimen demonstrates a p-distance greater than 5.0 % from *P. nudipes*, suggesting contamination or concatenation of this sequence with some other taxon (Table 4).

Other problematic sequences include the collecting locality for FJ214683 (*Cytb*) and the taxon from which sequences FJ214669 (*Adh*), FJ214695 (*Fgb*) and AY994234 (*Adh*) were obtained (Table 4). These issues were resolved by examining the identification of the voucher specimen in Vertnet and/or calculating K2P (*Cytb*) or the p-distance (*Adh* and *Fgb*) to sequences of reference taxa. Cytochrome *b* sequence FJ214683 appears to be from a *P. a. aztecus* from Veracruz whereas AY994234 (*Adh*) and FJ214695 (*Fgb*) appear to be from a *P. spicilegus* from Michoacán (Table 4). Although the *Adh* sequence FJ214669 is reported to by from the same specimen (TK 45255) as *Adh* sequences AY994234, these two sequences have a p-distance of 3.9 %.

Once taxon source misidentifications or incorrect localities are recognized for sequences, the database (GenBank) needs to be corrected (see https://ncbi.nlm.nih.gov/genbank/update/ for instructions). Without correction of taxon misidentification and incorrectly reported source localities in the database the use of these sequences and their reported collecting localities will continue and may cause confusion in the literature. Sequence FJ214669 should be excluded from future analyses until its source can be verified.

Distribution of P. winkelmanni. *Peromyscus winkelmanni* was described by Carleton (1977) from a series of 12 specimens collected by John R. Winkelmann and Floyd Downs from 6.3 mi (by road) WSW Dos Aguas, Michoacán, México at an elevation of 8,000 feet. Additional specimens of this

Table 3. Quantitative morphometric data (mean, standard deviation and range) for selected characters from specimens of *P. winkelmanni* from the vicinity of Dos Aguas, Michoacán, and a voucher (TCWC 045175) associated with the development of a hypothesis of a population in the vicinity of Filo de Caballo, Guerrero.

		Body Measurements				Skull Measurements				
Source	n	TL	HB	LT	HF	GLS	BCW	ZB	IOW	MRL
Holotype		263	123	140	29	33.3	14.3	-----	5.3	5.2
Carleton (1977)	32	249.2±11.2	-----	129.1±7.9	27.6±0.67	32.5±0.88	-----	16.2±0.56	-----	5.3±0.14
Range		235–265	-----	120–140	27–29	31.2–33.9	-----	15.4–17.1	-----	5.1–5.6
Michoacán	16, 7	254.9±13.3	122.9±4.66	132±10.4	27.4±0.96	32.4±0.88	14.1±0.32	16.0±0.70	5.5±0.16	5.3±0.24
Range		230–273	113–133	117–149	26–28	30.7–33.6	13.4–14.3	14.8–16.8	5.3–5.7	5.1–5.5
Guerrero	1	190+	112	78+	26	29.8	13.3	15.5	5.4	5.1

taxon from the vicinity of Dos Aguas have been reported by Carleton (1977), Álvarez *et al.* (1987) and this study (Appendix 1). Although Carleton (1977) speculated that this taxon inhabited other areas of the coastal sierra in Michoacán, no additional populations have been discovered in Michoacán.

Smith *et al.* (1989) reported a specimen of *P. winkelmanni* based on the detection of a karyotype with a FN = 70 and only three large pairs of biarmed chromosomes from the vicinity of Filo de Caballos in Guerrero. Based on this karyotype, which was identical to karyotypes of *P. winkelmanni* from Dos Aguas, Smith *et al.* (1989) concluded that the geographic range of *P. winkelmanni* extended at least from southwestern Michoacán through the Sierra Madre del Sur in Guerrero. Although no voucher number was provided by Smith *et al.* (1989) for the Guerrero specimen, the field catalog (examined by CWK) records only one specimen (GK 3388) collected from "Guerrero, Filo de Caballo vicinity". This male specimen was initially identified as a "*P. evides*" and later noted to have a FN = 70 with comments later written in the margin including "*P. evides*? or in *P. mexicanus* group" and "*P. winkelmanni*".

Sullivan and Kilpatrick (1991) reported on the allozymes of *P. winkelmanni* from three locations WSW of Dos Aguas and two specimens from 4 mi S Filo de Caballos. Phenetic and cladistic analyses of these biochemical data supported the contention of Smith *et al.* (1989) as they placed these samples from Filo de Caballo in a *P. winkelmanni* cluster or clade. However, vouchers were not identified for the sources of tissues used by Sullivan and Kilpatrick (1991).

The molecular analysis of the *P. aztecus* species group by Sullivan *et al.* (1997) identifies the vouchers associated with the *P. winkelmanni* sequences in the appendix (page 439). Three sequences were obtained from two specimens (3286 and 3287) from 19.3 km WSW Dos Aguas, Michoacán, and a specimen (3388) from Filo de Caballo, Guerrero.

The specimen with the field number GK 3388 was cataloged as TCWC 045175 and is smaller in several measurements than a series of *P. winkelmanni*, including GK 3286 (TCWC 045614) and GK 3287 (TCWC 045615). The voucher for GK 3388 is cataloged as a *P. aztecus evides* and is not a *P. winkelmanni* based on our comparison of measurements. Thus, there are no vouchers available for specimens of *P. winkelmanni* from Guerrero. We suspect that the sequence obtained by Sullivan *et al.* (1997) was likely obtained from specimen GK 3288, a *P. winkelmanni* from 19.3 km WSW of Dos Aguas and cataloged as TCWC 045616. Mislabeling of Nunc tubes, slides, and other material associated with specimen GK 3288 led to reports of *P. winkelmanni* occurring in Guerrero. Given the absence of a voucher of a specimen of *P. winkelmanni* from Guerrero, the distribution of the forest mouse should be restricted to the vicinity of Dos Aguas, Michoacán.

Taxonomy of the P. aztecus *species group.* With the utilization of molecular data and the expansion of species concepts, the content of the genus *Peromyscus* has been expanded from 53 species recognized by Carleton (1989) and Musser and Carleton (1993), to 56 species recognized by Musser and Carleton (2005), to 66 species recognized by Pardiñas *et al.* (2017) and to 78 species currently recognized in the Mammal Diversity Database (Mammal Diversity Database 2020). Over 20 new species of *Peromyscus* have been recognized just in the past 10 years (Ávila-Valle *et al.* 2012; Bradley *et al.* 2014, 2015, 2017, 2019; Pérez-Consuegra and Vazquez-Domínguez 2015; Greenbaum *et al.* 2019; Lorenzo *et al.* 2016; Álvarez-Castañeda *et al.* 2019; López-González *et al.* 2019; Léon-Tapia *et al.* 2020).

Molecular data have been used to examine the phylogeography and phylogenetic relationships of several species groups including the *P. aztecus* (Sullivan *et al.* 1997), *P boylii* (Bradley *et al.* 2000; Tiemann-Boege *et al.* 2000), *P. maniculatus* (Bradley *et al.* 2019; Greenbaum *et al.* 2019), *P. mexicanus* (Pérez Consuegra and Vázquez-Domínguez 2015; Bradley *et al.* 2016) and *P. truei* (Durish *et al.* 2004) species groups. The molecular study of the *P. aztecus* species group by Sullivan *et al.* (1997) was conducted, however, before the development of several modern molecular phylogenetic approaches and their associated software and was based on short (<750 bp) fragments of the *Cytb* gene.

The content of the *P. aztecus* species group has increased from three species, *P. winkelmanni*, *P. spicilegus*, and *P. aztecus* proposed by Carleton (1979, 1989), to four with the reinstatement of *P. hylocetes* as a distinct species (Sullivan and Kilpatrick 1991; Sullivan *et al.* 1997; Musser and Carleton 2005), to five species with the reinstatement of *P. oaxacensis* as a distinct species (Duplechin and Bradley 2014; Bradley 2017). Although our molecular analyses are congruent with the recognition of five distinct species in the *P. aztecus* species group, we do not support recognition of *P. oaxacensis* as a distinct species.

Peromyscus oaxacensis was described as a distinct species by Merriam (1898) based on specimens from Cerro San Felipe, Oaxaca, México, 10,000 ft. This taxon was recognized as a species (Osgood 1909; Hall and Kelson 1959; Hooper and Musser 1964; Hooper 1968; Goodwin 1969; Hall 1981) with a distribution in the highlands of Oaxaca and Chiapas, México. Musser (1969) pointed out that the range of *P. oaxacensis* extended southward into Guatemala, El Salvador, and western Honduras. Hooper (1968) questioned whether *P. oaxacensis* and *P. hylocetes* might represent disjunct populations of a single species. Carleton (1977) concurred with Hooper's (1968) hypothesis and later formally placed *oaxacensis* and *hylocetes* together with *evides* as subspecies of *P. aztecus* (Carleton 1979).

The Isthmus of Tehuantepec has been hypothesized to be an effective barrier to gene flow acting as a vicariant event contributing to the isolation, diversification, and speciation of rodent populations. Isolation by the Isthmus resulting in speciation has been reported for *Habromys* (León-Paniaqua *et al.* 2007), *Microtus* (Conroy *et al.* 2001), and *Neotoma* (Ordóñez-Garza *et al.* 2014). Ordóñez-Garza and Bradley (2018) examined DNA sequence variation within populations of 11 species of cricetid rodents distributed across the Isthmus of Tehuantepec and found that the Isthmus only appeared to be an effective barrier to gene flow in the montane species *Reithrodontomys sumichrasti*. Sullivan *et al.* (2000) compared the phylogeography of this highland forest dwelling harvest mouse, *R. sumichrasti*, to the previously published (Sullivan *et al.* 1997) phylogeography of the co-distributed *P. aztecus*/*P. hylocetes* complex and concluded that these two species share a more common biogeographic history than can be accounted for by the independent response hypothesis.

Our analyses support the conclusion of Sullivan *et al.* (1997) that forms of *P. a. oaxacensis* southeast of the Isthmus of Tehuantepec represents a distinct species. Specimens from northwest of the Isthmus, including samples from near the type locality of *P. oaxacensis* in the highlands of Oaxaca, show little genetic differentiation from *P. a. evides* in the Sierra Madre del Sur. Our analyses do not support the inclusion of populations of *oaxacensis* from the Oaxacan highlands as a distinct species from *P. aztecus* as suggested by Bradley *et al.* (2017). Duplechin and Bradley (2014) questioned the taxonomic affinities of these Oaxacan highland populations, but we conclude they should be recognized as conspecific with *P. aztecus* (Figure 3) following Carleton (1979).

Samples of *oaxacensis* from southeast of the Isthmus form a well-supported clade, sister to a P. *hylocetes-P. aztecus* clade (Figures 1 and 2) but demonstrate considerable genetic differentiation from taxa of that sister clade. Two names appear to be available for this taxon. *Peromyscus hondurensis* Goodwin, 1941, was described from specimens from western Honduras (Muya, 5 mi N Chinacla, department La Paz, Honduras, 3,000 to 4,000 ft.), but was considered a southern representative of *P. oaxacensis* by Musser (1969). This taxon is represented in our sampling by two specimens from Guatemala (TK 151047 and 34194). Another potentially available name for this taxon is *cordillerae* described from specimens from northeastern El Salvador (Mt. Cacahuatique, Dept. San Miguel, 3,500 feet) as a subspecies of *P. boylii* by Dickey (1928) but considered a subspecies of *P. aztecus* by Carleton (1979). The samples from Parque Nacional Montecristo, El Salvador (ROM 101489 and ROM 101490), may or may not correspond to this taxon. Regardless, the available data advocate for the recognition of all populations of the *P. aztecus* species group located south of the Isthmus of Tehuantepec as a distinct species, and *Peromyscus cordillerae* Dickey, 1928, has priority (International Commission on Zoological Nomenclature 1999).

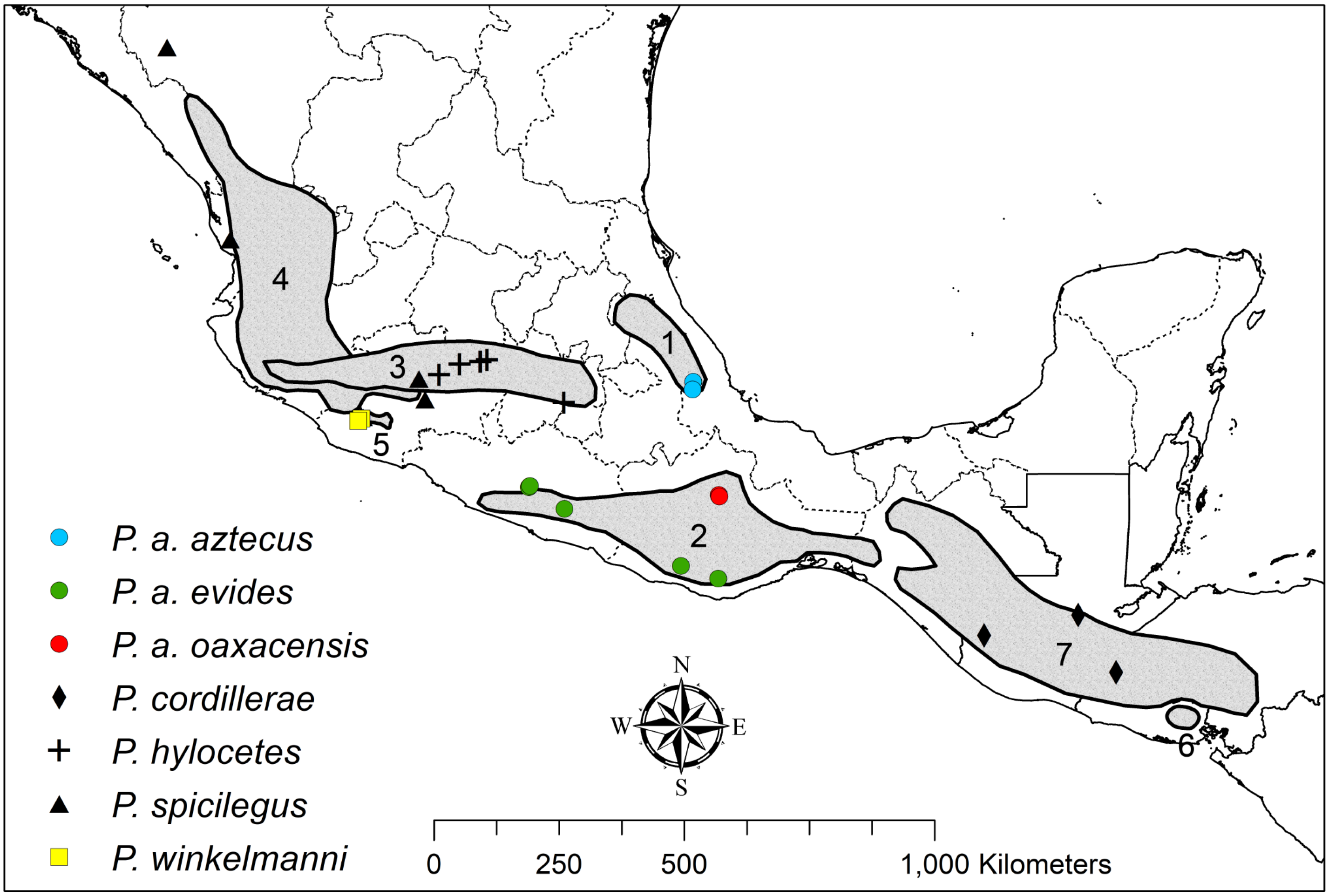

Figure 3. Distribution of taxa of the *P. aztecus* species group (map modified from Carleton 1989): 1) *P. aztecus aztecus*. 2) *P. a. evides* – *P. a. oaxacensis*. 3) *P. hylocetes*. 4) *P. spicilegus*. 5) *P. winkelmanni*. 6) *P. cordillerae cordillerae*, and 7) *P. cordillerae hondurensis*.

We suggest that *P. cordillerae* occurs in Guatemala, El Salvador, western Honduras, and the southern highlands of Chiapas, México (Figure 3). Further field and laboratory work are needed to resolve the geographic separation of *P. a. oaxacensis* and *P. cordillerae* in Chiapas. Two well-supported and highly differentiated subclades were recovered in the *P. cordillerae* clade, thus more than a single species may be present. Despite the high level of differentiation observed we refrain from further expansion of the number of Central American taxa of the *P. aztecus* group until samples are available from near the type localities on Mt. Cacahuatique (*cordillerae*) and in western Honduras (*hondurensis*). Instead, we tentatively consider *cordillerae* and *hondurensis* as distinct at only a subspecies level.

Levels of divergence and cladistic analyses of sequence data in this study support the earlier conclusion that *P. hylocetes* should be recognized as a distinct species (Sullivan and Kilpatrick 1991; Sullivan *et al.* 1997). Although morphological similarities are present between *hylocetes* and *P. a. oaxacensis*, Carleton (1979) pointed out that these morphological features appear to be subject to elevational effects and these two taxa both occur at higher elevations. In addition to biochemical and genetic divergence, Smith *et al.* (1989) reported differences in karyotypes with *P. hylocetes* having a FN = 72–74 and *P. aztecus* a FN = 68–70.

The data concerning the relationships of the allopatric subspecies of *P. aztecus* are difficult to interpret due to the inclusion of *hylocetes* as a subspecies but are generally incongruent (Bradley *et al.* 1990). However, phenetic analysis of both quantitative data for the glans and bacula (Bradley *et al.* 1990) and allozymic data (Sullivan and Kilpatrick 1991) identified *P. a. aztecus* as being distinct from the other subspecies. Phylogenetic analyses (Sullivan *et al.* 1997; this study) of sequence data recovered *P. a. evides* and *P. a. oaxacensis* in the same clade. In this study, less mean divergence was observed between *Cytb* sequences of *P. a. evides* and sequences of *P. a. oaxacensis* (K2P = 0.5 %) than among sequences of *P. evides* (K2P = 0.77 %). This lack of differentiation between these populations in the highlands of central Oaxaca and the Sierra Madre del Sur questions whether these two subspecies are allopat-

Table 4. Determination of collecting locality and likely source taxon for problematic GenBank data. Most likely source taxon is designated with an asterisk in the remarks.

Sequence Accession Number	Gene or Intron	GenBank ID	Specimen Catalog Number	Collecting Locality	Vertnet ID	Bayesian Analyses A) *Cytb*; B) concatenated	Remarks
FJ214688	Cytb	*P. a. oaxacensis*	TK 101037 TTU 83698	Francisco, Morazán La Tigra Parque Nacional, Honduras	*P. mexicanus*	A: Sister to *P. nudipes*	K2P distance of 1.9% from *P. nudipes*[1]; >13 % from taxa of *P. aztecus* group *P. nudipes**
FJ214675	*Adh*-I2	*P. a. oaxacensis*	TK 101037 TTU 83698	Francisco, Morazán La Tigra Parque Nacional, Honduras	*P. mexicanus*	B: Sister to *P. nudipes*	p-distance of 5.7 % from *P. nudipes*[2]; *contamination or concatenation with sequence of some other taxon*
FJ214714	*Fgb*-I7	*P. a. oaxacensis*	TK 101037 TTU 83698	Francisco, Morazán La Tigra Parque Nacional, Honduras	*P. mexicanus*	B: Sister to *P. nudipes*	p-distance of 0.3 % from *P. nudipes*[3] *P. nudipes**
FJ214683	Cytb	*P. aztecus*	FN 2401 ROM 100795	5 km E Dos Aguas, Michoacán, México	*P. aztecus*	A. within *P. a. aztecus* clade	Vertnet locality given as Veracruz. *P. a. aztecus**
FJ214669	*Adh*-I2	*P. aztecus*	TK 45255	5 km E Dos Aguas, Michoacán, México	Not found		p-distance of 6.0 % from *P. a. evides*[4] and 3.2 % from *P. spicilegus*[5] Unknown taxon*
FJ214695	*Fgb*-I7	*P. aztecus*	TK 45255	5 km E Dos Aguas, Michoacán, México	Not found		p-distance of 5.1 % from *P. a. evides*[6] and 1.2 % from *P. spicilegus*[7] *P. spicilegus**
AY994234	*Adh*-I2	*P. spicilegus*	TK 45255	5 km E Dos Aguas, Michoacán, México	Not found		p-distance of 0.3 % from *P. spicilegus*[5] *P. spicilegus**

Reference sequences used for comparison 1) *P. nudipes* FJ214687. 2) *P. nudipes* AY994238. 3) *P. nudipes* FJ214713. 4) *P. a. evides* FJ214670. 5) *P. spicilegus* AY994232. 6) *P. a. evides* FJ214700. 7) *P. spicilegus* FJ214719 ric. More thorough sampling in the rugged mountains of Oaxaca is needed to understand the level of differentiation and distribution of these two subspecies. Unlike species, however, subspecies need not exhibit reciprocal monophyly (Patton and Conroy 2017).

Considerable local and individual variation was observed among samples of *P. a. evides* from Oaxaca (Goodwin 1969). In general *P. a. evides* is smaller in size, has less inflated bullae, sparsely haired tails, and exhibits subtle differences in pelage coloration when compared to *P. a. oaxacensis* (Carleton, 1989). Whether such differences are diagnostic and geographically discrete enough to warrant subspecies status remains to be seen. Goodwin (1969, map 67) found samples of these two taxa to overlap broadly. However, these reported morphological differences might function on a gradient (see Carleton 1979) from the lower elevation (*evides*) to the higher elevation (*oaxacensis*). Both a morphological and molecular evaluation of these taxa in the context of broader geographic sampling that includes type material is required. Until subject to more detailed study, we do not yet recommend that *evides* be synonymized with *P. a. oaxacensis*.

Considerable morphological (Bradley *et al.* 1996) and chromosomal variation (Carleton *et al.* 1982; Smith *et al.* 1989; Smith 1990) has been reported among populations of *P. spicilegus* but no apparent congruence was found (Bradley *et al.* 1996). A possible association of the morphological data with the allozymic data of Sullivan and Kilpatrick (1991) was discussed by Bradley *et al.* (1996). The fixed allelic difference reported by Sullivan and Kilpatrick (1991) between samples of *P. spicilegus* from Michoacán and Nayarit, occurred in populations that were quite distinct morphologically (Bradley *et al.* 1996). Although sequence data are not available for specimens of *P. spicilegus* from Nayarit, data are available from southern Durango. Considerable differentiation (K2P = 0.033) was detected between northern (Durango) and southern samples (Jalisco and Michoacán) in this study, like what was found in the morphometric study (Bradley *et al.* 1996). In addition, morphological divergence was reported along an elevational gradient in Jalisco, with individuals at higher elevations being larger (Sánchez-Cordero and Villa-Ramírez 1988). Further examination of molecular and morphological data is needed before subspecific recognition can be proposed.

Although additional research is needed to clarify the correct taxonomic position of several forms, we believe the following represents a concise summary of the most appropriate taxonomic designations in the *Peromyscus aztecus* species group based on available data. Nine taxa have been named in this species group and we here recognize five of these at the rank of species, three as additional subspecies, and one as a junior synonym (Figure 3). *Peromyscus winkelmanni* Carleton, 1977, is found in the vicinity of Dos Aguas, Michoacán, and is sister to all other members of the species group. *Peromyscus spicilegus* J. A. Allen, 1897, is found on the flanks of the Sierra Madre Occidental. *Peromyscus cordillerae* represents all members of the species group southeast of the Isthmus of Tehuantepec and is comprised of two subspecies, *P. c. cordillerae* Dickey, 1928, and *P. c. hondurensis* Goodwin, 1941, the boundaries of which remain poorly understood. *Peromyscus hylocetes* Merriam, 1898, is found at mid to high elevations in the Transmexican Volcanic Belt. The range of *P. aztecus* appears to be restricted to northwest of the Isthmus of Tehuantepec and the species contains three subspecies. *Peromyscus a. aztecus* (Saussure, 1860) is found in the Sierra Madre Oriental. The geographic delineation of the remaining two subspecies, *P. a. oaxacensis* Merriam, 1898, and *P. a. evides* Osgood, 1904 (including *yautepecus* Goodwin, 1955), remains poorly defined. Future research on the *P. aztecus* species group should focus on clarifying the status of *P. a. oaxacensis* versus *P. a. evides* and on *P. c. hondurensis* versus *P. c. cordillerae*. Such studies should also investigate the potential for unrecognized species or subspecies diversity in *P. cordillerae*, *P. spicilegus*, and *P. hylocetes*.

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This paper is dedicated to my friend and colleague David J. Schmidly. My (CWK) collaborations with Dave stem from when we were both graduate students in the early seventies and both examining the relationships among populations of the *Peromyscus boylii* species group. Our collaborations on this complex group of rodents led to a series of collecting trips in México between 1982 and 1985 supported by NSF. While those collecting trips provided specimens and other materials that have contributed to numerous publications, their greatest contributions were in the training of future mammalogists. On each of those trips, Dave invited students from Universities in México to join us in conducting this field work and many of those students have gone on to become very prominent mammalogists. Dave, we are indebted to you not only for your scholarly contributions, but also for the academic offspring that that you have fostered and nurtured that continue to contribute greatly to our knowledge of mammals of the southwestern United States, México, and Central America. Congratulation on having this issue of Therya published in your honor with contributions from your students, colleagues and friends.

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Appendix 1

Measurements from specimens of *P. winkelmanni* housed in the TCWC at Texas A&M University. Body measurements include total length (TL), length of tail (LT), hind foot (HF), ear height (EH) and cranial measurement of skull greatest length (SGL), rostral length (RL), brain case width (BCW), zygomatic breadth (ZB), interorbital width (IOW), molar row length (MRL), and palatal breadth (PB).

Field #	Sex	TL	LT	HF	EH	Catalog #
7.4 mi WSW Dos Aguas, 7900 ft., Michoacán, México						
GK 3281	M	263	134	28	22	TCWC 045610
GK 3283	M	272	149	28	24	TCWC 045611
GK 3284	F	258+	129+	28	23	TCWC 045612
GK 3285	M	242	122	27	23	TCWC 045613
GK 3286	F	250	128	26	22	TCWC 045614
GK 3287	F	261	140	28	21	TCWC 045615
GK 3288	M	230	117	27	23	TCWC 045616
GK 3568	F	240	119	26	22	TCWC 045618
GK 3570	F	261	139	27	25	TCWC 047665
GK 3565	F	256	133	27	24	TCWC 45617
6.3 mi WSW Dos Aguas, 7900 ft., Michoacán, México						
GK 3302	M	265	140	29	23	TCWC 045622
GK 3303	F	260	138	29	23	TCWC 045623
GK 3304	?	241	117	26	21	TCWC 045624
6.9 mi WSW Dos Aguas, 7900 ft., Michoacán, México						
GK 3309	F	230+	110+	27	23	TCWC 045619
GK 3310	M	273	140	28	24	TCWC 045620
GK 3311	M	233+	115+	27	23	TCWC 045621

Cranial Measurements

Field #	SGL	RL	BCW	ZB	IOW	MRL	PB
GK 3281	32.7	12.6	14.27	16.83	5.59	5.28	3.96
GK 3283	32.86	12.0	14.3	16.59	5.46	5.45	3.19
GK 3284	33.62	13.12	13.35	16.64	5.32	5.15	3.52
GK 3285	32.42	12.35	14.1	15.97	5.33	5.11	3.48
GK 3286	30.68	10.09	14.28	14.82	5.73	5.5	3.82
GK 3287	32.75	13.2	14.19	15.3	5.43	5.4	3.68
GK 3288	31.65	11.86	13.86	15.71	5.71	5.31	3.48