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The Big Naked-backed Bat, *Pteronotus gymnonotus*, Chiroptera, Mormoopidae, in its northernmost geographic distribution range

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The Big Naked-backed Bat, *Pteronotus gymnonotus*, is one of the 15 species currently recognized of this genus, with relatively few specimens in scientific collections, besides being poorly studied. It has a geographical distribution spanning from México through Central America and reaching Perú and Brazil, in which it occupies a variety of habitats from desert to tropical forests below 400 meters above sea level. Here, we report the records that demonstrate its presence, and data about its natural history in southeastern México, the northernmost part of its geographic distribution range. Between June 2002 and July 2018, we captured specimens in 44 bat roosts located in southeastern México, including the Parque Estatal Agua Blanca, Macuspana, Tabasco; Grutas de Martínez de la Torre, Matías Romero Avendaño, Oaxaca; and in Cueva de Villa Luz, Tapijulapa, Tabasco. In the three locations mentioned, we recorded the occurrence of *P. gymnonotus* individuals, whose taxonomic identification at species level was corroborated by both morphological data and genetic analyses. Previously, the only records of *P. gymnonotus* in México were from only four specimens scattered across time, so these new recorded locations confirm the presence of this species in the country. In addition to this, in Agua Blanca State Park and Villa Luz Cave we found a reproductive resident population. The record from Grutas de Martínez de la Torre is located in the middle of the Tehuantepec Isthmus, a well known biogeographical barrier for many taxa in the transitional area to the Pacific lowland's region. We suggest that the occurrence of *P. gymnonotus* in México is also associated with large remnants of evergreen and gallery forests, located in the lowland areas along the Gulf of México and in the north and east of the Tehuantepec Isthmus.

El gran murciélago de espalda desnuda, *Pteronotus gymnonotus*, es una de las 15 especies actualmente reconocidas del género, de la cual existen pocos registros en colecciones científicas, además de ser poco estudiada. Tiene una distribución geográfica que se expande desde México a lo largo de América Central hasta el Perú y el Brasil, ocupando una variedad de hábitats desde el desierto hasta las selvas tropicales por debajo de los 400 metros sobre el nivel del mar. Se reportan los registros que atestiguan su presencia y datos sobre su historia natural, en el sureste de México, la parte más septentrional de su intervalo de distribución geográfica. Entre junio de 2002 y julio de 2018 capturamos murciélagos en 44 refugios localizados en el sureste de México. Encontramos individuos de *P. gymnonotus* en tres localidades: el Parque Estatal Agua Blanca, Macuspana, Tabasco; Grutas de Martínez de la Torre, Matías Romero Avendaño, Oaxaca y en la Cueva de Villa Luz, Tapijulapa, Tabasco. La identificación a nivel de especie fue corroborada con datos morfológicos y análisis genéticos. Anteriormente, los registros de *P. gymnonotus* en México correspondían sólo a cuatro ejemplares dispersos en el tiempo, por lo que su registro para estas nuevas localidades confirma definitivamente la presencia de esta especie en el país. Además, en el Parque Estatal de Agua Blanca y en la Cueva de Villa Luz encontramos una población residente reproductivamente activa. El registro correspondiente a las Grutas de Martínez de la Torre se encuentra en el centro del Istmo de Tehuantepec, zona que es bien conocida por ser una barrera biogeográfica para muchos taxones y en la zona de transición a la región de las tierras bajas del Pacífico. Sugerimos que la presencia de *P. gymnonotus* en México también está asociada a grandes remanentes de bosques siempre verdes y de galería, situados en las zonas bajas a lo largo del Golfo de México y en el norte y el este del Istmo de Tehuantepec.

Keywords: Biogeography; geographic distribution; Isthmus of Tehuantepec; México; Mormoopid bats.

Introduction

The Big Naked-backed Bat, *Pteronotus gymnonotus*, is a rare and poorly studied species belonging to the Family Mormoopidae. It is one of the 15 currently recognized species of *Pteronotus* (Pavan and Marroig 2017; Pavan and Tavares 2020). *P. gymnonotus* is relatively large and heavy, with a forearm length usually measuring 50 to 56 mm. and a body mass between 9.8 to 17.2 gr. The rostrum is conspicuously short and broad. It is mainly characterized by its naked back, resulting from its wing membranes meeting on the dorsal midline. The naked-looking rump is covered with very short fur and appears velvety when examined closely. The overall coloration of the upper parts is dark brown, rarely orange, with generally paler underparts; membranes are blackish brown (Smith 1972; Smith 1977; Pavan and Tavares 2020).

Very little is known about its biology and natural history (Pavan and Tavares 2020). *P. gymnonotus* is an aerial insectivorous bat that roosts exclusively in caves. Generally, this bat occurs at altitudes below 400 m, inhabiting a variety of habitats from deserts, dry and semi-deciduous forests, to savannas and tropical wet forests (Handley 1966;

Emmons and Feer 1997; Eisenberg and Redford 1999; LaVal and Rodríguez-Herrera 2002; Reid 2009; Pavan and Tavares 2020). In México, it is associated with tropical evergreen high forest (Álvarez-Castañeda and Álvarez 1991a), tropical deciduous forests (Guzmán-Soriano *et al.* 2013), water bodies and riparian vegetation (Davis *et al.* 1964; Ibáñez *et al.* 2000).

It is widely distributed in the Neotropical region, with records from southern México (Veracruz) throughout Central America, and south to Perú, Colombia and Venezuela, northeast and central Brazil, Bolivia, and Guyana (Smith 1972; Simmons 2005; Reid 2009; Pavan and Tavares 2020). Although it can be locally abundant in the southern part of its continental distribution, it becomes less abundant and even rare northwards (Smith 1972; Simmons and Conway 2001; Solari 2019; Pavan and Tavares 2020).

Despite its wide geographical range, this species is relatively poorly represented in scientific collections, with only 618 voucher specimens from Central America (Costa Rica, El Salvador, Honduras, Nicaragua, and Panama) and 388 from South America (Brazil, Colombia, Peru, Suriname, and Venezuela) collected between 1901and 2016 (GBIF 2020). It is categorized as "subject to special protection" by SEMARNAT in México (NOM-059 SEMARNAT-2010) but overall considered as 'Least Concern' according to the IUCN (Solari 2019).

Most of the records for *P. gymnonotus* in México refer to only single specimens scattered across time. In fact, this species is considered rare not only in México, but also in most of its geographical distribution (Pavan and Tavares 2020). Davis *et al.* (1964) provided the first record of *P. gymnonotus* for México based on a single male collected in Cueva Laguna Encantada, Los Tuxtlas, Veracruz. This is its northernmost geographical record, but the species was not recorded again for more than 50 years in spite of subsequent searches made by other authors (Villa-R. 1966; Estrada *et al.* 1993), including three made by us in March 2005, April 2011 and July 2018. Likewise, Álvarez-Castañeda and Álvarez (1991a) reported one male from Yaxchilan, Chiapas; but its presence in this area could not be confirmed despite the collecting efforts made by Medellín *et al.* (1986), McCarthy (1987) and Medellín (1993). The species was reported in Tabasco by Ibañez *et al.* (2000), but prior to that was not found during the intensive field efforts made by Sánchez-Hernández and Romero (1995) and Castro-Luna (1999) in the area, nor later by Castro-Luna *et al.* (2007). Ibañez *et al.* (2000) reported the capture of two specimens, a female and a male, from Cueva de Villa Luz, Tapijulapa, Tabasco. Because the female was pregnant, these authors suggested the presence of an undetected reproductive population of *P. gymnonotus* in southeastern México. Finally, the most recent published record of *P. gymnonotus* in México is a single male from El Volcán de los Murciélagos, Calakmul, Campeche, captured in November 2010 (Guzmán-Soriano *et al.* 2013).

The main objectives for this study were: to report the records that demonstrate the presence of this species in southeastern México. To report two new localities in México, one from the state of Tabasco and the first from the state of Oaxaca, and to present data about the natural history of this species in the northernmost extent of its distribution.

Methods and Materials

Study area. We explored caves and some artificial roosts located in Southern México, a region including the states of Campeche, Chiapas, Oaxaca, Quintana Roo, Tabasco, Veracruz, and Yucatan, a low-lying and generally flat region except for the presence of the mountains and hills that make up the Sierra Atravesada, whose highest point "el paso de Chivela" rises to about 250 masl. The area is characterized by a variety of environments with tropical climates which can be humid, sub-humid or semi-dry determined by the presence and amount of rainfall varying from 500 to 4500 mm and with high temperature variation that oscillates between 15 to 34 °C (García 1988; Vidal *et al.* 2007; INEGI 2008). In general, the rains fall with a marked seasonality, clearly distinguishing a dry season from November to April, and a rainy season from May to October (Cavazos and Hastenrath 1990; Santos-Moreno and Ruiz-Velásquez 2007; Lorenzo *et al.* 2011). The heterogeneity of the landscape includes seven types of vegetation: the upper evergreen and sub-evergreen forest predominate, followed by medium forest (with two variants, sub-deciduous and sub-evergreen) with small areas of low deciduous forest, savannas, aquatic and underwater vegetations, forest gallery, thorny scrub, and xerophilous scrub (IGGUNAM 2007; INEGI 2008).

We prioritized sampling of bats inside and near the Tehuantepec Isthmus region, an area located between the -94° and -96° W meridians, which encompasses the states of Chiapas, Oaxaca, Tabasco and Veracruz (Figure 1). It consists of the narrowest land strip that separates the Pacific Ocean from the Gulf of México, spanning only 203 km (North to South), connecting the North American continent with Central America. This area is characterized by warm and humid climates, a rainy season in the summer, an annual average temperature of around 24 to 27 °C, and precipitation ranging from 1,100 to 2,600 mm (García-Romero 2003; Vidal and Matias 2003; Barragan *et al.* 2010).

Field trips and sampling. Thirteen field trips were undertaken between June 2002 and July 2018 in search of mormoopid bats. Surveys were conducted during both the dry and rainy seasons, with a mean coverage of three to five nights in each locality. We used mist-nets (Avinet Nylon 30 mm mesh) and/or harp-traps (standard 4.2 m^2 model). The number of harp-traps and mist-nets varied according the characteristics of each site, but most times we used two of each one. The nets were set before sunset as determined by the expected bat flight routes, or trying to cover cave entrances (Kunz *et al.* 2009) and remained open for 5 to 7 hours. Every night, we took all captured bats regardless of the species, but when a single species had more of 25 individuals, only a representative portion was collected (approximately 10 to 20 specimens) and the rest were immediately released. Those animals were kept separately in soft cot-

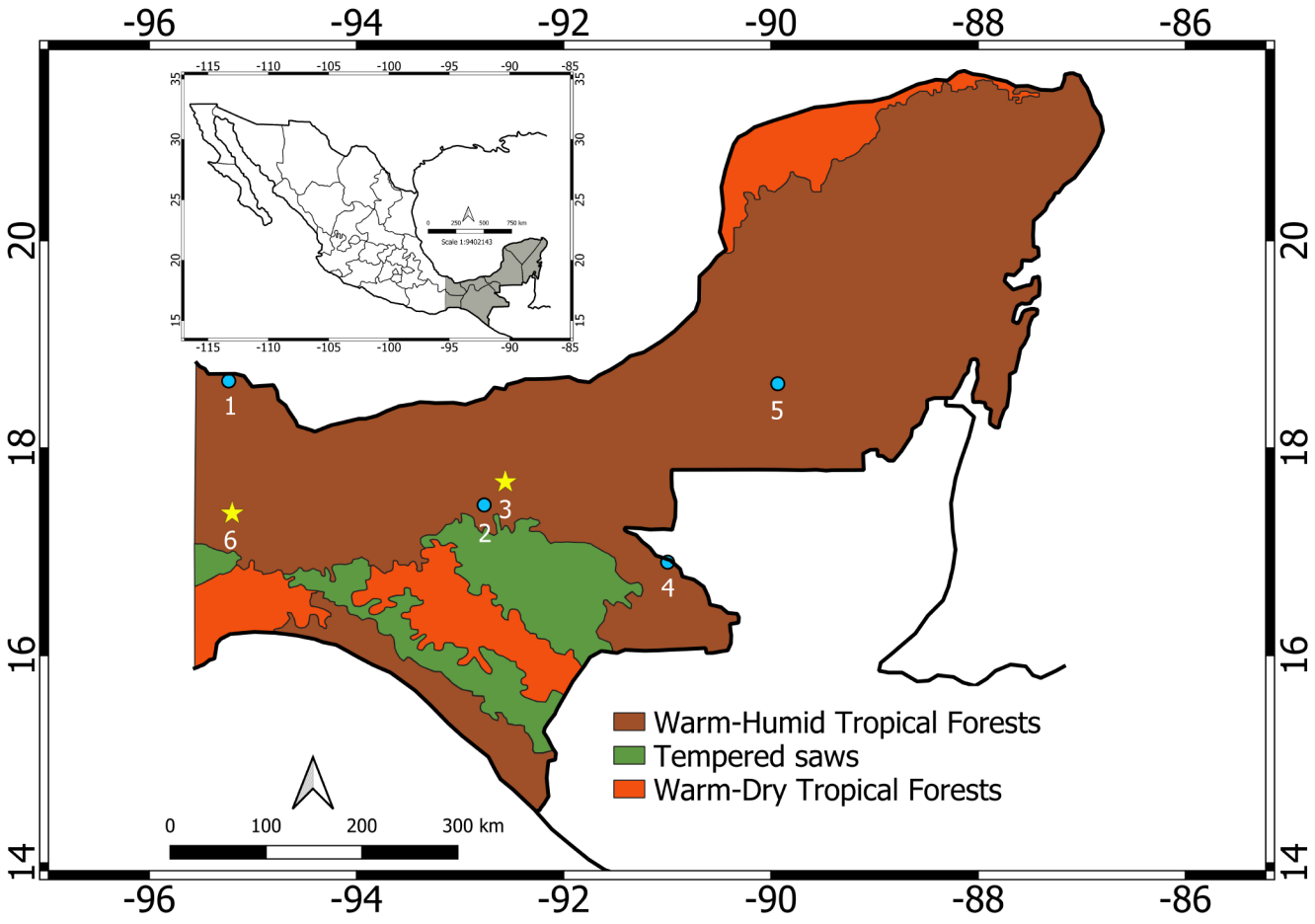

Figure 1. Map with all records known to date for *Pteronotus gymnonotus* in México 1) Cueva Laguna Encantada. 2) Cueva de Villa Luz. 3) Parque Estatal Agua Blanca. 4) Ruinas de Yaxchilan. 5) El Volcán de los murciélagos. 6) Grutas de Martínez de la Torre. Blue dots indicate previously reported localities, yellow stars the new ones described in this work. The depicted ecoregions were obtained from Atlas de Biodiversidad (CCA, CONABIO, INEGI, INE. 2010).

ton bags for a maximum of three hours and released after recording sex, weight, forearm measurements, and obtaining a biopsy from wing membranes using 3.0 mm biopsy punches (Fray Products Corp., Buffalo, NY). Tissue samples were stored at -20° C in 70 % ethanol and deposited in the tissue collection of the Laboratorio de Biología y Ecología de Mamíferos de la Universidad Autónoma Metropolitana-Iztapalapa (LBEM-UAMI).

Morphological identifications. *Pteronotus gymnonotus* is easily distinguishable from other species of *Pteronotus* by its overall size (forearm length of 50 to 56 mm) and its naked back formed by its fused wing membranes in the dorsal midline, which are diagnostic characters (Medellín *et al.* 2008; Álvarez-Catañeda *et al.* 2017). Within its distribution range in México, *P. fulvus* is the only other bat species that could be confused with *P. gymnonotus*, but the former is smaller (forearm length between 41 to 49 mm) and much lighter (5 to 10 g; Figure 2).

Genetic identification. Species identification was confirmed using molecular techniques. We performed DNA extraction and amplification of a 607 bp fragment of the gene Cytochrome Oxidase Subunit I (COI) following Lopera-Barrero *et al.* (2008) and using primers VF1d and VR1d, according to Ivanova *et al.* (2006). The amplifications were sequenced 3'-5 'in an ABI PRISM 370xl sequencer. Sequences were edited and aligned in Geneious v. 5.6.4 using the Clustal W algorithm (Kearse *et al.* 2012) and deposited in GenBank (MK883711, MK883712, MT863621, MT863628). A Bayesian Inference analysis using Mr. Bayes v 3.2 program (Ronquist *et al.* 2012) was constructed including previously available sequences for *P. gymnonotus* from Guatemala and Panama, as well as sequences for the phylogenetically closest species *P. fulvus* and *P. davyi*. Sequences of *P. macleayii* and *P. quadridens* were used as the external group using the optimal evolutionary model estimated with jModeltest v 2.1.6 considering the Akaike information criterion (Posada 2008). In addition, using the program MEGA v. 5.0.5 (Tamura *et al.* 2011) and the Kimura 2 Parameters (K2P) model, genetic distances between the sequences of individuals of *P. gymnonotus*, *P. fulvus,* and *P. davyi* were estimated.

Statement of ethics. All bats were collected and handled following the procedures described by the American Society of Mammalogists (Sikes *et al.* 2016) and our institutional ethical guidelines (Anonymous 2010). Permits to capture and handle the bat species were provided by the Mexican government (SGPA/ DGVS Nos. 05853/13, 09131/14, 003061/18, 9377/19 and CC 08450/92).

Results

During the study period, we visited 44 bat roosts (caves, abandoned buildings and sewers, etc.; Table 1). *P. gymnonotus* was encountered only in three of the explored caves. We recorded *P. gymnonotus* in Parque Estatal Agua Blanca, Macuspana, Tabasco (17º 37.20´ N, -92º 28.34´ W, 100 masl; Figure 1). This area has a system of caves measuring 5,200m in length (Castro-Luna *et al.* 2007). The climate in this area is humid warm, with a mean annual temperature of 26.8 °C, with rains all year round, and average annual precipitation of 2,614 mm (Vargas 2012). We visited this locality in March 2005, April 2011, December 2014, and May 2016. During these visits, we captured a total of three males and twenty-eight females. Tissue samples (biopsy) were taken and stored at the LBEM-UAMI with the following registration numbers: 050305Pgy383, 050305Pgy384, 070411Pg1 to 070411Pg7, 20141201Pgym1 to 20141201Pgym16, 20160508PgyH1 to 20160508PgyH4, and 20160508Pgym1, 20160508Pgym2. The individuals of *P. gymnonotus* were captured late in the night, most of them between 21:00 to 0:30 hrs. Other bat species captured were *Balantiopteryx io*, *Carollia brevicauda*, *Lonchorhina aurita*, *Mormoops megalophylla*, *Natalus mexicanus*, *Pteronotus fulvus*, *P. mexicanus* and *P. psilotis*.

In July 2018, we captured two specimens of *P. gymnonotus* in Grutas de Martínez de la Torre, Matías Romero Avendaño, Oaxaca (17º 22.26´ N, -95º 11.98´ W; 50 masl; Figure 1). This site is located in northeastern Oaxaca state. It is a cave system surrounded by tropical evergreen forest with warm and humid climate, rainy season in summer and with annual precipitation ranging from <2,000 to 2,500 mm (INEGI 2008). The riparian vegetation is very abundant because a stream emerges from the cave, which joins the Jaltepec River 350 m away. Tissue samples (biopsy) were obtained and deposited in the (LBEM-UAMI), with the registration numbers Pgy23072018m1 and Pgy23072018m2. The bats were two adult males with scrotal testes, and both were collected in a mist net inside the cave at nearly 50 m from the entrance. They were captured late at night (22:00 and 23:30), with more than one hour difference between them. Other bat species captured were *Balantiopteryx plicata*, *M. megalophylla*, *P. fulvus*, *P. mexicanus*, *P. psilotis*, and *N. mexicanus*.

The other locality in which we captured *P. gymnotus* was the Cueva de Villa Luz, Tapijulapa, Tabasco (17º 27.58 ´N, -92º 46.75´ W; 80 masl; Figure 1). This cave is also known as Cueva del Azufre or Cueva de las Sardinas, it includes a main corridor of about 2 km long and more than 20 short side passages formed by the dissolving action of the stream current. The cave has at least 24 skylights, mostly vertical shafts with dissolution features. It has several chambers, some with vaults up to 15m high. However, the passages between the chambers are low. A cave map was published by Hose y Pisarowicz (1999). Its atmosphere contains dangerous concentrations of hydrogen sulfide, carbon monoxide, carbon dioxide, and other harmful gases, in addition to low levels of oxygen; the levels measured exceed the concentrations reported to be toxic for humans. The water, especially that which drips from organic masses known as snottites, is very acidic as well as some springs and streams that are inside the cave. It is a very active ecosystem, based on bacteria that synthesize sulfur and that, contrary to what is expected, allows the existence of a community of several thousand bats (Hose and Pisarowicz 1999; Plath *et al.* 2006; Guzman-Cornejo *et al.* 2012). Until now, no study has been carried out to understand how bats can fight against the high concentrations of toxic gases and acid fumes present in the atmosphere. The vegetation of the area corresponds to remnants of a high perennial forest, degraded by the clearings for crop and livestock areas. Riparian vegetation is abundant thanks to the large number of streams. Floristic lists of the cave surroundings area are in Gamboa and Ku (1998) and Moreno-Jiménez (2019).

Figure 2. Dorsal and ventral views of an adult female of *Pteronotus gymnonotus* (A, C) and an adult female of *P. fulvus* (B, D). Both specimens were captured in Parque Estatal Agua Blanca, Tabasco, México on December 01, 2014.

Table 1. Localities sampled in the southeast of México between 2002 and 2018 with their coordinates and arranged in alphabetical order according to the Mexican state, the name of the town and the dates they were visited.

Localities	Coordinates	Dates (dd,mm,year)
	Campeche	
Grutas de Xtacumbilxunaán, Bolonchén	19º 59.42´ N, -89º 45.83´ W	01/03/2005; 30/07/2013
Volcán de los Murciélagos, Calakmul	18º 31.37´ N, -89º 49.42´ W	21/02/2005; 19/07/2013
	Chiapas	
Cueva de Cerro Hueco, Tuxtla Gutiérrez	16º 73.33´ N, -93º 08.33´ W	07/06/2002; 10/05/2013
Cueva de El Aguacero, Ocozocouatla	16º 04.46´ N, -93º 31.52´ W	31/03/2014
Cueva de Galicia (El Fresnal), Chicomosuelo	15º 43.83´ N, -92º 22.71´ W	11/06/2002
Cueva de Nueva Alianza, Mapastepec	15º 25.29´ N, -92º 43.98´ W	07/04/2014
Cueva Lázaro Cárdenas, Tuxtla Gutiérrez	16º 53.91´ N, -93º 44.44´ W	10/06/2002
Cueva Los Laguitos, Tuxtla Gutiérrez	16º 49.32´ N, -93º 09.12´ W	07/06/2002; 11/11/2007; 11/05/2013
Finca la Esmeralda, Huixtla	15º 19.14´ N, -92º 30.84´ W	24/03/2009
Grutas de Arcoton, Ejido Artículo 27	16º 16.69´ N, -91º 49.96´ W	03/04/2014
Grutas de San Francisco, La Trinitaria	16º 05.89´ N, -92º 02.75´ W	08/06/2002; 04/04/2014
Grutas de Teopisca, Teopisca	16º 38.84´ N, -92º 29.63´ W	02/04/2014
Piedra de Huixtla, Huixtla	15º 11.90´ N, -92º 28.49´ W	06/04/2014
	Oaxaca	
Alcantarilla, Presa Benito Juárez, Tehuantepec	18º 15.49´ N, -89º 02.23´ W	29/07/2007
Cerro Huatulco, Santa María Huatulco	15º 50.59'N, -96º 21.07´ W	18/01/2018
Colonia Cuauhtemoc, Matías Romero	17º 05.04´ N, -94º 52.44´ W	26/03/2009
Cueva La Mata, Matías Romero	16º 36.82´ N, -94º 57.14´ W	23/07/2007
Grutas de Lázaro Cárdenas, Sto. Domingo Petapa	16º 55.40´ N, -95º 15.21´ W	10/06/2002; 27/07/2007
Grutas de Martínez de la Torre	17º 22.26´ N, -95º 11.98´ W	23/07/2018
Guiengola, Tehuantepec	16º 19.73´ N, -95º 15.28´ W	30/07/2007
Ojo de Agua, Tolistoque	16º 35.19´ N, -94º 52.42´ W	16/07/2013; 09/04/2014
San Sebastian de las Grutas, Ayoquezco de Aldama	16º 37.83´ N, -96º 58.40´ W	28/03/2009
2km al NW Tapanatepec, Tapanatepec	16º 22.16´ N, -94º 11.67´ W	24/07/2007
	Quintana roo	
Alcantarilla, Tres Garantías, Othón P. Blanco	18º 15.49´ N, -89º 02.23´ W	24/02/2005
Cueva de Kantemó, Dziuché	19º 55.84´ N, -88º 47.46´ W	26/02/2005; 21/07/2013
Cueva Ejido Pedro A. de los Santos	18º 57.55´ N, -88º 12.35´ W	25/02/2005
Grutas de Aktun Chen, Akumal	20º 21.64´ N, -87º 20.50´ W	25/07/2013
Pueblo Chiclero, Chacchoben	19º 10.49´ N, -88º 15.20´ W	25/02/2005
	Tabasco	
Campus Colegio de Posgraduados, Cárdenas	17º 57.27´ N, -93º 22.54´ W	02/03/2005; 19/07/2018
Cueva de Los Vientos, Tapijulapa	17º 27.50´ N, -92º 46.40´ W	03/03/2005
Cueva de Villa Luz, Tapijulapa	17º 27.58´ N, -92º 46.75´ W	05/06/2002; 05/05/2016; 20/07/2018
Grutas de Coconá, Teapa	17º 33.52´ N, -92º 56.07´ W	03/03/2005
Grutas de Cuesta Chica, Tapijulapa	17º 26.49´ N, -92º 45.54´ W	04/03/2005
Parque Estatal Agua Blanca, Macuspana	17º 37.20´ N, -92º 28.34´ W	05/03/2005; 06/04/2011; 01/12/2014; 08/05/2016
	Veracruz	
Cueva Arroyo del Bellaco, Pachuquilla	19º 13.32´ N, -96º 38.34´ W	01/06/2002
Cueva Boca del Cántaro, Pachuquilla	19º 13.78´ N, -96º 38.24´ W	12/04/2011
Cueva Cerro Colorado, Apazapan	19º 21.21´ N, -96º 41.77´ W	15/05/2014
Cueva del Vado de la Chachalaca, Apazapan	19° 20.25´ N, -96° 39.28´ W	07/03/2005; 08/12/2014
Cueva Huichapan, Apazapan	19º 21.35´ N, -96º 41.97´ W	16/05/2014
Cueva Laguna Encantada, San Andrés Tuxtla	18º 27.71´ N, -95º 11.18´ W	07/03/2005; 09/04/2011; 18/07/2018
Cueva Sala Seca, Cuitlahuac	18°50.00´ N, -96° 93.50´ W	02/06/2002
Roca del Zopilote, Juchique de Ferrer	19°47.88´ N, -96° 40.02´ W	06/06/2014
	Yucatan	
Cenote Hoctún, Hoctún	20º 51.37´ N, -89º 11.70´ W	27/07/2013
Grutas de Calcehtok, Calcehtok	20º 33.03´ N, -89º 54.73´ W	28/02/2005; 28/07/2013

We visited this locality in Jun 2002, May 2016, and June 2018 and during this visits we captured six females and 14 males. Tissue samples were deposited in the LBEM-UAMI with the following registration numbers: 020605PGY1- 020605PGY3; 050516PGY1- 050516PGY10; 200718PGY1- 200718PGY7. Specimens were captured individually between 22:00 and 24:30 hrs. Eight species of bats representing four different families were identified in this cave: two Emballonuridae (*B. plicata*, *Saccopteryx bilineata*), five Mormoopidae (*M. megalophylla*, *P. davyi*, *P. gymnonotus*, *P. parnellii* and *P. personatus*), and one Vespertilionidae (*M. californicus*).

In the three localities, the momoopid species *P. fulvus* was particularly abundant, and although the characteristics of the caves did not allow us to determine the size of their populations, we observed that in each case there were thousands of individuals. In the study area *P. gymnonotus* and *P. fulvus* are quite similar to each other (Figure 2), but their differences in size, as well as the forearm values and weight allow their correct separation easily (Table 2). Our genetic analyses also confirmed the identifications made based on morphometric caracteristics, and genetic distances obtained (Table 3), as well as the phylogenetic reconstruction (Figure 3), clearly separate *P. fulvus* from *P. gymnonotus*. Due to the rarity of the *P. gymnonotus*, we highlight the presence of pregnant females in May 2016 in the Cueva de Villa Luz and in the Agua Blanca State Park.

Discussion

The presence of *P. gymnonotus* in México, the northernmost part of its geographical distribution, was supported only by scattered records in over fifty years (Davis *et al.* 1964; Álvarez-Castañeda and Álvarez 1991a; Ibañez *et al.* 2000; Guzmán-Soriano *et al.* 2013). The three locations reported here, in which we found *P. gymnonotus,* definitely reaffirm the presence of this species in the country.

Table 2. Weight and forearm values (mean, standard deviation, minimum and maximum) for females and males of *Pteronotus gymnonotus* and *P. fulvus* in four locations in the northernmost part of the distribution of *P. gymnonotus*.

	Pteronotus gymnonotus				***Pteronotus fulvus***			
	Mean	**D.S.**	**Min**	**Max**	**Mean**	**D.S.**	**Min**	**Max**
				Cueva de Villa Luz, Tapijulapa, Tabasco				
		Females (n = 6)*				Females (n = 14)*		
Weight	15.16	0.93	14.3	17.2	8.53	0.75	7	9.5
Forearm	52.61	1.26	50	53.8	44.48	0.72	43.4	46
		Males (n = 14)				Males (n = 20)		
Weight	14.02	1.25	12.2	15.9	7.46	0.59	5.8	8.7
Forearm	52.4	0.57	51.3	53.2	44.13	1.29	42.1	53.2
				Parque Estatal Agua Blanca, Macuspana, Tabasco				
		Females (n = 20)				Females (n = 20)		
Weight	13.39	1.13	9.8	14.8	7.16	0.68	6	8.1
Forearm	53.8	1.19	52.2	55.8	44.67	0.82.	43.7	46.3
		Males (n = 5)				Males (n = 20)		
Weight	14.18	1.3	12.8	15.6	7.46	1.2	6	10
Forearm	53.16	1.28	51.3	54.9	44.29	0.96	42.2	46.3
				Grutas de Martínez de la Torre, Matías Romero Avendaño, Oaxaca				
		Females (n = 0)				Females (n = 1)		
Weight					7.4		7.4	7.4
Forearm					42.6		42.6	42.6
		Males (n = 2)				Males (n = 2)		
Weight	15.3	0.07	15.3	15.4	7.55	0.35	7.3	7.8
Forearm	52.1	0.85	51.5	52.7	43.7	1.2	42.9	44.6
				El Volcán de los murciélagos, Calakmul, Campeche				
		Females (n = 0)				Females (n = 1)		
Weight					6.18	0.33	5.8	6.5
Forearm					44.5	0.6	43.2	45
		Males (n = 1)**				Males (n = 16)		
Weight	14.5		14.5	14.5	6.11	0.28	5.7	6.6
Forearm	54.1		54.1	54.1	44.2	1.06	43.2	46,7

* = Hembras preñadas.

** Datos obtenidos de Guzmán-Soriano *et al.* (2013).

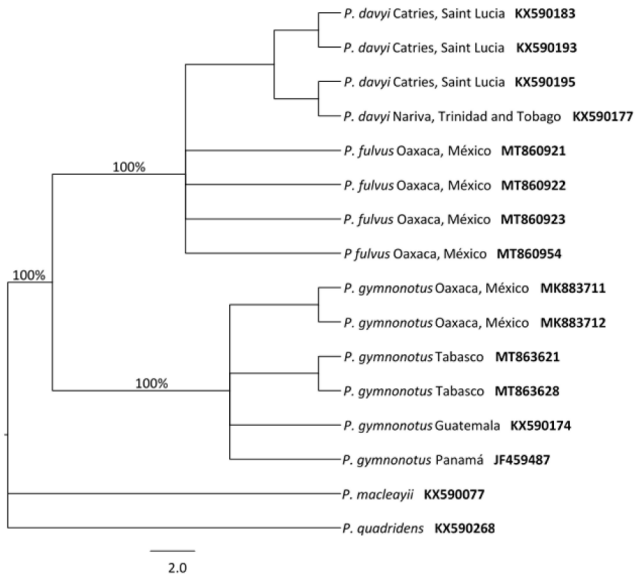

Figure 3. Phylogenetic reconstruction of mitochondrial data (COI) to confirm the identification of bats from Martínez de La Torre, Oaxaca (Genbank: MK883711 and MK883712) and Agua Blanca, Tabasco (Genbank: MT863621 and MT863628) as *Pteronotus gymnonotus*. Sequences of *P. gymnonotus* from Guatemala and Panama (Genbank: KX590174 and JF459487), *P. fulvus* from Oaxaca (Genbank: MT860921, MT860922, MT860923 and MT860954) and *P. davyi* from Saint Lucia and Trinidad and Tobago (Genbank : KX590183, KX590193, KX590197) were included for comparison. Sequences of *P. macleayii* and *P. quadridens* (Genbank: KX590077 and KX590268) were used as an external group. Values in branches indicate Bayesian posterior probabilities.

Parque Estatal Agua Blanca has been until now the locality with the largest number of specimens collected in México and most of Central America; only Deleva and Chaverri (2018) report a bigger roost for this species in Costa Rica. This locality is a protected natural area of 2,025 ha with tropical evergreen forest as the dominant vegetation type (Castro-Luna *et al.* 2007; Vargas 2012). According our observations *P. gymnonotus* seems to prefer to move and forage inside the gallery forest, a vegetation type that is also abundant in the area.

Our capture records at Grutas de Martínez de la Torre are important because this cave complex is located near the center of the Isthmus of Tehuantepec, 105 km South from the Gulf of México Coast and 134 km North from the Mexican Pacific Coast. This is an area that is well known for being a biogeographic barrier for many taxa (Mulcahy *et al.* 2006). In it, medium and low deciduous forests predominate, the kind of habitat in which Reid (1999) mentions the presence of *P. gymnonotus* in South America. The closest previous record corresponds to the Laguna Encantada, Veracruz, located 110 km to the North and we suggest that the Isthmus of Tehuantepec may have played an important role in allowing the expansion of *P. gymnonotus* northward until reaching the area of Los Tuxtlas, Veracruz. The absence of recent records in this area is probably related to the almost total loss of tall evergreen forests that the region has experienced in recent times (García-Romero *et al.* 2004; Taubert *et al.* 2018), and to the intensive use of the cave by the local population for ritual ceremonies (Münch 2012). This location is in the transitional area to the Pacific lowlands, a region in which individuals considerably larger than typical specimens of *P. fulvus*, and whose measures are very near to those of *P. gymnonotus*, have been occasionally recorded (Goodwin 1958, 1969; Smith 1972; Álvarez and Álvarez-Castañeda 1991b) suggesting suggesting possible hybridization between those species.

At Cueva de Villa Luz, Gordon and Rosen (1962) reported the presence of at least three large bat colonies, consisting mainly of bats from the Family Mormoopidae. The largest of these colonies is located approximately 150 m from the main entrance, a site with 32.3 °C and a relative humidity of 85 %. In 2018, using a hand net, we captured two specimens of *P. gymnonotus* among thousands of *P. fulvus* individuals in this site.

Mormoopid bats are commonly found living syntopically with other members of the same family, as well as with species from other families (Smith 1972; Emmons and Feer 1997). *P. gymnonotus,* living in the northernmost part of its geographic range, is not the exception. Five families and thirteen species of bats have been recorded associated with this species: three emballonurids (*B. io*, *B. plicata*, and *S. bilineata*), three phyllostomids (*C. brevicauda*, *D. rotundus,* and *L. aurita*), five mormoopids (*M. megalophylla*, *P. fulvus*, *P. mexicanus*, *P. personatus*, and *P. psilotis*), one natalid (*N. mexicanus*) and one vespertilionid (*M. californicus*; Gordon and Rosen 1962; Palacios Vargas 2009; Guzman-Cornejo *et al.* 2012; this paper).

In the caves visited by us, we always found *P. gymnonotus* associated with *P. davyi*. Pavan and Tavares (2020) observed that *P. gymnonotus* is rarely found syntopically with other species of naked-backed bats, with only a few sparse records of this situation. However, in the northernmost part of its geographic range, this species usually has been reported to co-occur with *P. fulvus* (Davis *et al.* 1964; Ibáñez *et al.* 2000; this paper).

Our data are indicative of the presence of a reproductive population of *P. gymnonotus* in the southeast of México. We found pregnant females in May 2016 in the Cueva de Villa Luz and in the Agua Blanca State Park. These females may belong to the same reproductive population, since both places are only 38 km apart. This population seems to be a resident one, because regardless of the year, our samples have covered the months of March to July, plus one in December, and we have always registered the presence of *P. gymnonotus* in the area.

Table 3. Genetic distance data between COI sequences of individuals of *P. gymnonotus* (Pgy), *P. fulvus* (Pfu) and *P. davyi* (Pda). Oaxaca (O), Tabasco (T), Guatemala (G), Antillas Menores (A). Data was obtained using the Kimura 2 Parameters (K2P) model.

	Pgy-O	Pgy-T	Pgy-G	Pfu-O	Pda-A
Pgy-O	-				
Pgy-T	1.1	-			
Pgy-G	0.7	0.3	-		
Pfu-O	8.6	8.1	7.8	-	
Pda-A	9.0	8.6	8.2	0.05	-

Beside this, all other *P. gymnonotus* specimens captured in our field trips were adults, without an evident reproductive status and only one juvenile male was registered in July for Cueva de Villa Luz. This suggests that *P. gymnonotus* in its northernmost geographic distribution has a monestral reproductive cycle, probably with births between late June - early July, data that are in agreement with the report of pregnant females in the same month in Nicaragua, El Salvador and México (Jones *et al.* 1971; Hayssen *et al.* 1993; Ibañez *et al.* 2000).

Pteronotus gymnonotus is an obligate cave-dweller bat. In Costa Rica colonies have been reported with more than 500 individuals in several karstic caves (Deleva and Chaverri 2018); also large assemblages of many thousands of individuals have been observed in karstic localities in northeastern Brazil (Rocha *et al.* 2011; Feijó and Rocha 2017; Vargas-Mena *et al.* 2018). In México, this species is not abundant, with only very few specimens collected in karstic caves in the Parque Estatal Agua Blanca, El Volcán de los Murciélagos and in the Grutas de Martínez de la Torre (Guzmán-Soriano *et al.* 2013; this paper). It is noteworthy that in México some records are from two non-karstic caves, Laguna Encantada and Villa Luz, both of volcanic origin.

There are studies mentioning that *P. gymnonotus* is more abundant in dry and semi-open environments (Pavan and Tavares 2020), but in México this species has been recorded in the ecoregion called warm-humid tropical forest located in the low areas along the Gulf of México and in the North and East of the Isthmus of Tehuantepec. Two earlier reports (Álvarez-Castañeda and Álvarez 1991a; Guzmán-Soriano *et al.* 2013) recorded this species in moist tropical deciduous forests and we found it associated with large remnants of tropical evergreen forest and especially in gallery forests. Finding *P. gymnonotus* in this type of environment is probably due to the fact that insectivorous bats often use riparian forests as feeding refuges due to the high availability of insects and the facilities they offer for flight and echolocation (Grindal *et al.* 1999; Robinson *et al.* 2002; Hagen and Sabo 2011).

During the last fifty years the processes of deforestation and habitat fragmentation have been very important in southeastern México, the northernmost geographic distribution range for *P. gymnonotus*. In México, the warm-humid tropical forests include the high and medium evergreen and sub-evergreen forests, which are found almost exclusively in the plains of the Gulf of México, the South and East of the Yucatán Peninsula and the East of Chiapas. It is estimated that these forests have been reduced by more than 80 % in recent years (Challenger and Soberón 2008) at an annual rate of deforestation between 1993 and 2007 of 0.83 %, although this deforestation rate tends to decrease in the area (Kolb and Galicia 2012). Currently these types of forests are only found in the most rugged terrain, but they also continue to be affected by factors such as selective timber extraction, firewood collection, grazing or man-induced fires. Bats have a high tolerance to landscape modification due to their ability to fly and the ease with which they can cross open areas (Medellín *et al.* 2000; Castro-Luna *et al.* 2007). In this context, we highlight the need for more precise information about the distribution, conservation status, and ecology of this species.

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