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La Portada

Hembra lactante de juancito (*Ammospermophilus leucurus*) es la especie de mamífero diurna más común en la península de Baja California y varias partes de los desiertos de Noroeste de México. La imagen fue captada dentro del campamento de conservación de berrendos en Baja California cuando el individuo se acercó amigablemente a pedir ser alimentada. En muchas regiones de Baja California los junacitos interactúan mucho con la población humana (Fotografía de Sergio Ticul Álvarez-Castañeda)

Nuestro logo “Ozomatli”

El nombre de “Ozomatli” proviene del náhuatl se refiere al símbolo astrológico del mono en el calendario azteca, así como al dios de la danza y del fuego. Se relaciona con la alegría, la danza, el canto, las habilidades. Al signo decimoprimero en la cosmogonía mexica. “Ozomatli” es una representación pictórica de los mono arañas (*Ateles geoffroyi*). La especie de primate de más amplia distribución en México. “ Es habitante de los bosques, sobre todo de los que están por donde sale el sol en Anáhuac. Tiene el dorso pequeño, es barrigudo y su cola, que a veces se enrosca, es larga. Sus manos y sus pies parecen de hombre; también sus uñas. Los Ozomatin gritan y silban y hacen visajes a la gente. Arrojan piedras y palos. Su cara es casi como la de una persona, pero tienen mucho pelo.”

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DERECHOS DE AUTOR Y DERECHOS CONEXOS, año 11, No. 1, enero-abril del 2020, es una publicación cuatrimestral editada por la Asociación Mexicana de Mastozoología A. C., Hacienda Vista Hermosa 107, Colonia Villa Quietud, Coyoacan 04960. Distrito Federal, México**.** Telefono (612) 123-8486, www.mastozoologiamexicana.org, therya@mastozoologiamexicana.com. Editor responsable: Dr. Sergio Ticul Álvarez Castañeda. Reservas de Derechos al Uso Exclusivo No. 04-2009-112812171700-102, ISSN: 2007-3364 ambos otorgados por el Instituto Nacional de Derechos de Autor. Responsable de la última actualización de este número, Unidad de informática de la Asociación Mexicana de Mastozoología A. C. Dr. Sergio Ticul Álvarez Castañeda. Instituto Politécnico Nacional 195. La Paz, Baja California Sur, C. P. 23096. Tel 612 123 8486, fecha de la última modificación 25 enero 2020.

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El objetivo y la intención de *THERYA* es ser una revista científica para la publicación de artículos sobre los mamíferos. Estudios de investigación original, editoriales, artículos de revisión y notas científicas son bienvenidas.

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Epipubic bones of the Virginia Opossum (*Didelphis virginiana*) from México

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The epipubic bones of the marsupials have been little studied and the meaning of their linear dimensions is poorly known. We therefore evaluated epipubic bone size of Virginia Opossum (*Didelphis virginiana*) from Mexico, and estimated their proportions relative to skull size of individuals. Results showed that males have larger skull and acetabulum size than females, epipubic bones of females are almost half the size of a female's skull while that of the male is a little less than a third of the male cranial size. Therefore, epipubic bones are an important landmark of sexual dimorphism in *D. virginiana*, and our data may be useful to learn more about epipubic bones of other marsupials.

Los huesos epipúbicos de los marsupiales han sido poco estudiados y se sabe poco del significado de sus dimensiones lineales. Por tanto, evaluamos el tamaño del hueso epipúbico en tlacuaches mexicanos (*Didelphis virginiana*) y calculamos su proporción en relación al tamaño craneal de los individuos. Confirmamos que los machos tienen mayor tamaño de cráneo que las hembras y encontramos lo mismo para el acetábulo, y que los huesos epipúbicos de las hembras son casi la mitad del tamaño del cráneo de una hembra, mientras que en machos son menos de un tercio del tamaño del cráneo. Por lo tanto, los huesos epipúbicos son un punto de referencia importante del dimorfismo sexual en *D. virginiana*, y nuestros datos pueden ser útiles para aprender más sobre los huesos epipúbicos de otros marsupiales.

Key words: Didelphidae; Didelphimorphia; marsupium; morphometrics; pelvic girdle.

Introduction

Like platypus and echidnas (Subclass Prototheria) and some fossil placentals, marsupial mammals (Infraclass Marsupialia *sensu* Burgin *et al.* 2018) are characterized by the presence of epipubic bones (Reilly and White 2003), which are not found in current members of Infraclass Placentalia (*sensu* Burgin *et al.* 2018). These are paired bony structures that articulates with the pubis and extend forward into the ventral abdominal wall (Marshall 1979). In most species they are long bones, depressed and apically sharp, and have two faces, two edges and two ends (Ferrusquia-Villafranca 1964). Therefore, the pelvic girdle of the marsupials is composed of the bones ilium, ischium, pubis, and epipubics (Figura 1).

Function of epipubic bones of marsupials presumably reflects emphasis on different but non-mutually exclusive functions. It has been proposed, on one hand, that they serve as a support mechanism for the marsupium or pouch and the offspring that are found inside by helping the abdominal musculature in the support of the abdomen (Elftman 1929; White 1989). On the other, it has been stated that epipubic bones act as a lever to facilitate the rigidity of the body through the limbs during walking and jogging (Reilly and White 2003); both females and males have epipubic bones, but the latter lack a pouch in almost all species of marsupials. If these bony structures are linked to the presence of a marsupium to provide support, then males would be expected to show little developed epipubic bones. Accordingly, White (1989) reported that epipubic bones of species with marsupium, as Virginia Opossum (*Didelphis virginiana*) are longer, in general, in females than in males for a given mass (g); unfortunately, he did not report the dimensions of the epipubic bones he studied yet the size values of those bones he examined cannot be compared.

On the other hand, research data have shown that males adult Virginia Opossum are larger than females, condition that becomes apparent at the beginning of sexual maturity (Gardner 1982). Sexual dimorphism, therefore, may be a secondary consequence of reproductive activity; smaller size and lighter weight of females may be the result of spending more energy in rearing youngs (Gardner 1982; Tague 2003). Similarly, differences between sexes in cranial and mandibular dimensions were found in the Virginia Opossum from Georgia, USA (Patterson and Mead 2008). In addition, canine teeth of males, and pelvic and non-pelvic dimensions are larger as well (Tague 2003; Patterson and Mead 2009); unfortunately, none of these reports estimated epipubic bone size. In contrast, Ventura *et al.* (2002) informed that sexual dimorphism in size may not be a general pattern in *Didelphis* after examining South American opossums (*D. marsupialis, D. pernigra,* and *D. imperfecta*). Therefore, the relationship between length of this pelvic girdle structure and length of an individual remains unexplored.

Unfortunately, there are no data available on linear dimensions of both epipubic bones and specimens examined to evaluate these issues and to better understand the relationships between sexual dimorphism and epipubic bone size. However, Mexican species of opossum (Didelphidae) are a good data source to contribute further information about this topic, particularly *D. virginiana*. This is the most common opossum species in México, with a wide geographical distribution and with numerous specimens represented in biological collections (Gardner 1982; Astúa 2015).

The objective of this work is, then, to describe and measure the size of the epipubic bones for females and males of the Virginia Opossum from México and assess their size relative to a measurement of body length assessed as skull length. These results will also allow to estimate what percentage of the length of an individual, as revealed by skull length, represents the length of the epipubic bones and compare between sexes.

Materials and Methods

A total of 102 specimens of the Mexican Virginia Opossum (*D. virginiana*) deposited in the Mammal National Collection (CNMA) of Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM), were examined but a subsample of 45 (28 males and 17 females) adult specimens were included in the morphometric analysis due to their good preservation condition (Appendix 1). Adulthood was assessed according to the sequence of molar eruption and replacement of the last deciduous premolar (Gardner 1982), as well as fusion of the ilium, ischium, and pubis at the acetabulum (Tague 2003).

For each specimen, 16 pelvic and non-pelvic variables were taken with a digital vernier (Mitutoyo Co.) at a precision level of 0.01 mm. Pelvic variables recorded were six measurements of the right epipubic bone (Figure 1a): Epipubic greatest length (EGL), Epipubic length from the base (ELB), Epipubic length from the process (ELP), Epipubic base width (EBW), Epipubic medium height (EMH), and Epipubic medium depth (EMD); six measurements of the pelvic girdle (Figure 1b, 1c): Pelvis width (PW), Ischium width (IW), Pubic symphysis length (PSL), Pubis to ischium distance (PID), Pubis to acetabulum greatest distance (PAGD), and length of the Ilium, from it joins the acetabulum to its anterior most end (LI); and two of the acetabulum (Figure 1c): Acetabular width (AW), Acetabular height (AH). Non-pelvic variables were two conventional cranial measurements: Skull greatest length (SGL), and Zygomatic width (ZW), recorded according to Ryan (2011). Statistical significance of Student's t-test was set at $P \leq 0.05$; when data were not normally distributed a non-parametric Wilcoxon test was utilized. In addition, we also examined specimens of other Mexican opossum species for comparative purposes.

To illustrate how the skull, epipubic bones, the rest of the pelvic girdle and the vertebrae of the sinsacral look like, we prepared digital files and uploaded them into the IREKANI collection of images of CNMA at IBUNAM available at http://unibio.unam.mx/irekani/.

Results and Discussion

Our results produced 16 digital files (numbers: 12606-12621) containing photographs and curatorial data of juvenile, adult, female, and male specimens of the Mexican Virginia Opossum (*D. virginiana*), and the ring-tailed cat (*Bassariscus astutus*) just for visual comparative purposes with a placental mammal; for the first species resulted 14 files while just two for the latter species. One of the 14 files include the right epipubic bone of each species of Mexican opossums (Didelphidae). These are the first published data set that shows images of epipubic bones of Mexican species of opossums.

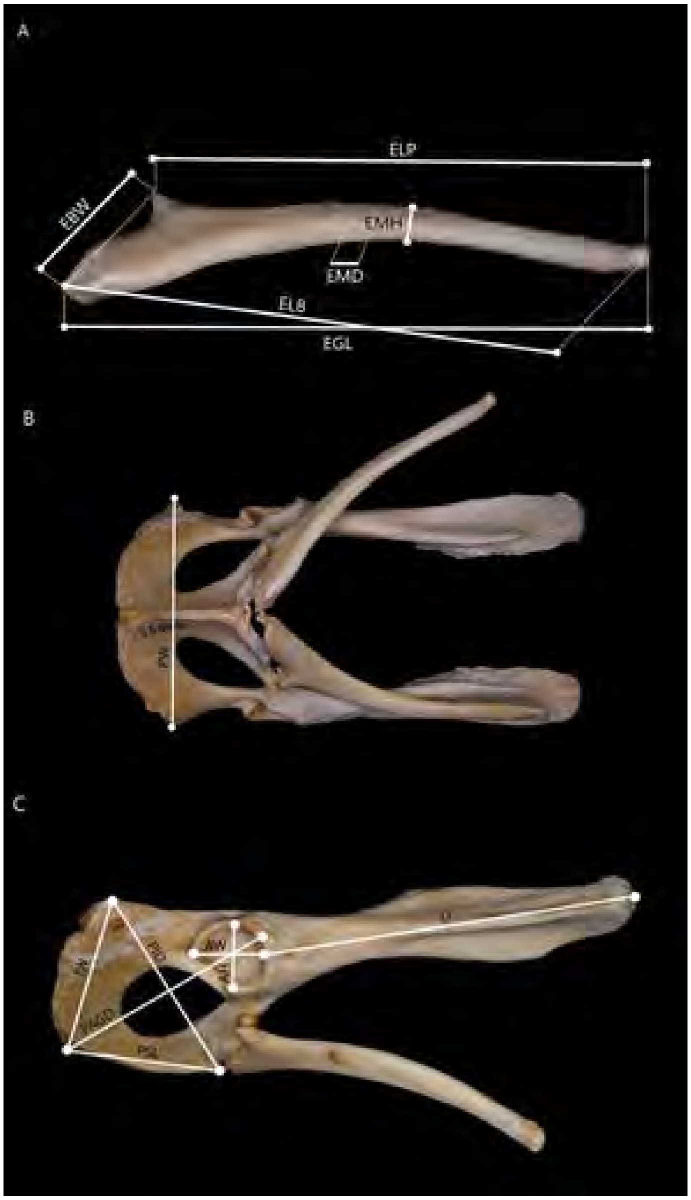

Figure 1. Pelvic measurements recorded in adult Mexican opossums (Didelphimorphia) from Mammal National Collection (CNMA) of Instituto de Biología, Universidad Nacional Autónoma de México (UNAM). A, lateral right view of the right epipubic bone. B, ventral view of the pelvic girdle. C, lateral right view of the pelvic girdle. Measurements names are indicated in text.

The epipubic bone of the Mexican Virginia Opossum is a long, thin bone with a shape almost right to a slightly curved and a thickening with a notch at its base; the shape of this bone in young individuals is practically the same as in adults. It is located in the ventral part of the pelvic girdle, where it articulates with the right pelvic bone and extends towards the front and a little downwards almost parallel to the ilium bone of the pelvic girdle, coinciding with that reported by Tague (2003) who additionally points out that epipubics extend from the superior border of the pubis to approximately the plane of the sacroiliac joint. Similarly, we found that the epipubic bone of other Mexican opossum species of the genera *Philander, Metachirus*, *Caluromys, Chironectes, Marmosa,* and *Tlacuatzin* is also elongated, thin and little curved, what makes it similar in shape to that of Mexican Virginia Opossum specimens. In addition, Flores (2009) reported that the distal portion of the epipubic bones of *Caluromys, Chironectes,* and *Marmosa* is clearly curved. Ferrusquía-Villafranca (1964)4 also mentioned that *Chironectes minimus* has an epipubic with an almost straight internal edge and the outer tubercle of the proximal end not very prominent, like *Caluromys derbianus*.

The two measurements of acetabulum size and those of length and width of skull of Mexican *D. virgininana* showed that males are larger than females. That is, the average values of the Acetabular width (AW), Acetabular height (AH), Skull greatest length (SGL), and Zygomatic width (ZW) had a significantly higher mean value in males than in females (Table 1); larger acetabulum may articulate with a larger femur head of a larger femur. Other research on the pelvic sexual dimorphism in the Virginia Opossum (Tague 2003) revealed that in general males have pelvis larger than females, since 14 of 16 absolute dimensions of the pelvis were significantly higher in males. Unfortunately, no data on acetabulum dimensions were provided therein. Provided that these variables may be estimators of size, our data then agree with previous reports for North American populations of this species (Gardner 1982; White 1989), that adult males of the Virginia Opossum are larger than females.

However, we did not find significant differences between sexes regarding the other six measurements we recorded for other pubic bones. This is, lengths, widths and distances involving ilium, ischium, and pubis (PW, IW, PSL, PID, PAGD, and LI; Table 1). This result is similar to that reported by Elftman (1929) and Ferrusquía-Villafranca (1964)4 who mention that pelvis of females and males are not different from edach other in *D. virginiana, P. opossum* and *C. minimus.*

Interestingly, we also found that although males display longer acetabulum, females have longer epipubic bones (mean EGL = 4.4 cm) than males (Table 1). This evidence of sexual dimporphism is supported by the variables Epipubic greatest length (EGL), Epipubic length from the base (ELB), and Epipubic length from the process (ELP) of females since are significantly larger than those that were recorded for males (Table 1). Our findings coincide with the results of White (1989), who states that females generally have longer epipubic bones than males for a given mass (not length). Our data therefore using a linear variable, length (mm), confirm what White (1989) reported using a variable of mass (g) regarding individual size between sexes. Ferrusquía-Villafranca (1964)4 also noted that females display relatively larger, more robust and curved epipubics than males.

In addition, our data showed then that the average greatest length of the epipubic bones (EGL) of adult males represents solely 29.13 % of the size of the average total length of their skull (SGL), while in females this proportion reaches 47.78 %; the epipubic bone of females is also relatively larger than that for males. For instance, in our sample examined (Table 1) SGL and EGL of an adult male (CNMA 45122) are, respectively: 110.70 and 37.44 mm, whereas for a female (CNMA 3523) these values are 97.36 and 47.22 mm (Figure 2). In contrast, the other three variables we recorded related with epipubic bones (Epipubic base width, EBW, Epipubic medium height, EMH, and Epipubic medium depth, EMD) did not show significant differences between sexes (Table 1).

Table 1. Descriptive statistics (mean, standard deviation, and range) and comparison of means of pelvic and non-pelvic variables (mm) between sexes of adult Virginia Opossum (*Didelphis virginiana*). * = significant difference at 0.05 level.

Variable	**Males** (*n* = 28)	**Females** (*n* = 17)	**Student´s t - test**	**Wilcoxon test**
Epipubic greatest length	38.45 ± 4.43 (31.00- 44.27)	43.97 ± 7.48 (27.78 -54.33)	0.003*	0.001*
Epipubic length from the base	31.98 ± 4.71 (22.80 - 39.45)	37.62 ± 6.92 (23.24 -48.61)	0.009*	0.008*
Epipubic length from the process	33.42 ± 4.09 (26.40 - 40.09)	39.51 ± 6.87 (24.78 -50.07)	0.004*	0.002*
Epipubic base width	11.60 ± 1.32 (8.03 - 13.35)	12.47 ± 1.86 (8.16 - 14.88)	0.117	0.105
Epipubic medium height	3.10 ± 0.50 (2.21 - 3.77)	3.28 ± 0.96 (1.43 - 5.29)	0.497	0.421
Epipubic medium depth	1.79 ± 0.36 (1.13 - 2.44)	1.98 ± 0.64 (0.56 - 2.82)	0.261	0.164
Pelvis width	40.94 ± 5.28 (34.25 -48.12)	37.20 ± 6.35 (24.27 - 43.8)	0.099	0.143
Ischium width	28.41 ± 5.90 (20.04 - 35.39)	28.48 ± 3.87 (19.53 - 33.26)	0.555	0.69
Pubic symphysis length	21.11 ± 3.16 (12.74 - 25.06)	20.42 ± 3.5 (12.57 - 24.63)	0.961	0.824
Pubis to ischium distance	32.04 ± 3.74 (23.92 - 37.84)	30.16 ± 3.65 (21.37 - 34.9)	0.109	0.076
Pubis to acetabulum greatest distance	35.76 ± 3.79 (27.12 - 42.56)	34.49 ± 3.95 (24.88 - 38.79)	0.297	0.361
Length of the Ilium	48.50 ± 4.09 (37.21 - 55.79)	48.42 ± 6.86 (32.96 - 56.45)	0.940	0.497
Acetabular width	9.87 ± 1.18 (7.37 - 12.39)	8.77 ± 1.09 (6.70 - 11.05)	0.003*	0.004*
Acetabular height	9.49 ± 1.12 (7.57 - 11.45)	8.18 ± 1 (6.17 - 10.07)	0.000*	0.001*
Skull greatest length	108.38 ± 11.81 (124.75 - 80.56)	99.08 ± 11.47 (72.23 - 115.76)	0.014*	0.017*
Zygomatic width	56.56 ± 7.16 (40.18 - 70.68)	50.35 ± 6.31 (36.44 - 58.98)	0.005*	0.007*

Figure 2. Skull length relative to epipubic bone length in adult Virginia Opossum (*Didelphis virginiana*) from México. Above: male (CNMA 45122); below: female (CNMA 3523). Body size of the first is larger but the latter has a larger epipubic bone.

Length of the epipubic bone for the two species of the genus *Didelphis* examined here, (*D. virginiana* and *D. marsupialis*) turned out to be the largest values in the sample for the opossum species of México. Accordingly, the smallest recorded epipubic bones corresponded to the smallest species of Mexican marsupials, the mouse opossums (*Marmosa mexicana* and *Tlacuatzin canescens*); females of these small marsupials do not have a marsupium; however, they display well developed epipubic bones. If proportionally small epipubic bones of mouse opossums is an evolutionary result of lack of marsupium remains to be tested. However, Flores (2009) reported larger development of epipubic bones in females of pouchless taxa.

Except *D virginiana*, the small sample size available for other species of Mexican opossums prevents comparisons between species. However, a tendency can be noted where the length of the epipubic bones of *D. virginiana, D. marsupialis, Philander opossum, Chironectes minimus* and *Metachirus nudicaudatus* represent almost half the size of the skull. Similarly, Flores (2009) found that the proximal size of the epipubic bones is long in *Didelphis*, *Caluromys, Philander* and *Marmosa* (except *M. rubra*). In contrast, length of the epipubic bones of *Caluromys derbianus, Marmosa mexicana,* and *T. canescens* are around a third of skull length.

In summary, epipubic bones is an important distinctive characteristic of marsupials, it has been little studied and there are still few available data on its morphology. However, our study makes available by first time summarized data based on length and images on epipubic bones of Mexican species of opossums, particularly the Mexican Virginia Opossum.

Our data confirm that males of Mexican opossums *Didelphis virginiana* are larger than females, and that epipubic bones are significantly larger in the latter; epipubic bone length of a female is almost half size her skull length. Therefore, epipubic bones are an important landmark of sexual dimorphism in *D. virginiana*, and our data may be useful to learn more about epipubic bones of other marsupial mammals. Undoubtedly, further research is needed to better understand the role of epipubic bones in the structure and function of pelvic girdle of marsupials.

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Appendix 1

Museum specimens of adult opossums collected in México and examined to assess size variation of epipubic bones. All are deposited at Mammal National Collection (CNMA) of Instituto de Biología, Universidad Nacional Autónoma de México (UNAM). * = day unknown; ** = day and month unknown.

Catalog number	Sex	Collection date	Type of preservation	Collecting locality
Didelphis virginiana				
43395	Male	14 June 2006	Skeleton only	Distrito Federal: Ciudad Universitaria, UNAM, Delegación Coyoacán, 2240 m.
43396	Female	11 April 2008	Skin and skeleton	Distrito Federal: Ciudad Universitaria, UNAM, Delegación Coyoacán, 2240 m.
11305	Female	10 August 1968	Skin and skeleton	Distrito Federal: Ciudad Universitaria, Delegación Coyoacán.
43393	Female	23 August 2007	Skin and skeleton	Distrito Federal: Jardín Botánico Exterior, Instituto de Biología, Ciudad Universitaria, UNAM. Delegación Coyoacán, 2260 m.
43392	Female	18 May 2004	Skin and skeleton	Distrito Federal: Jardín Botánico Exterior, Instituto de Biología, Ciudad Universitaria, UNAM. Delegación Coyoacán, 2260 m.
47207	Male	23 January 2011	Skeleton only	Distrito Federal: Reserva Ecológica del Pedregal, Jardín Botánico, Delegación Coyoacán, 2326 m.
34644	Male	December 1989*	Skin and skeleton	Distrito Federal: Reserva del Pedregal de San Ángel. UNAM. Coyoacán, 2250 m.
44100	Female	17 June 2011	Skin and skeleton	Distrito Federal: Jardín Botánico Exterior, Instituto de Biología, Ciudad Universitaria, UNAM. Delegación Coyoacán, 2260 m.
45114	Male	29 June 2008	Skin and skeleton	Distrito Federal: Espacio Escultórico, Reserva del Pedregal de San Ángel, Ciudad Universitaria, Coyoacán, 2215 m.
34858	Male	9 January 1992	Skin and skeleton	Distrito Federal: Cto. Exterior, Ciudad Universitaria, Delegación Coyoacán.
44101	Male	23 May 2011	Skin and skeleton	Distrito Federal: Calle Corregidora 536, Col. Ampliación Miguel Hidalgo, Delegación Tlalpan.
44051	Female	1 March 2007	Skin and skeleton	Distrito Federal: Reserva Ecológica del Pedregal de San Ángel de Ciudad Universitaria, Delegación Coyoacán, 2250 m.
44085	Male	30 March 2007	Skeleton only	Distrito Federal: Reserva Ecológica del Pedregal de San Ángel de Ciudad Universitaria, Delegación Coyoacán, 2250 m.
43375	Male	1 May 2006	Skeleton only	Distrito Federal: Reserva Ecológica del Pedregal de San Ángel de Ciudad Universitaria, Delegación Coyoacán, 2250 m.
43377	Male	2006**	Skin and skeleton	Distrito Federal: Reserva Ecológica del Pedregal de San Ángel de Ciudad Universitaria, Delegación Coyoacán, 2250 m.
43372	Male	31 August 2005	Skin and skeleton	Distrito Federal: Reserva Ecológica del Pedregal de San Ángel de Ciudad Universitaria, Delegación Coyoacán, 2250 m.
43373	Female	9 September 2005	Skin and skeleton	Distrito Federal: Reserva Ecológica del Pedregal de San Ángel de Ciudad Universitaria, Delegación Coyoacán, 2250 m.
3523	Female	11 September 1979	Skin and skeleton	Guerrero: Viveros El Huayacán, La Poza, Municipio Acapulco.
652	Male	25 April 1978	Skin and skeleton	Guerrero: Viveros El Huayacan, La Poza, Municipio Acapulco.
45117	Male	17 February 2009	Skin and skeleton	Guerrero: Hotel y Villas "Las Flores", 2.6 km SW Yetla, Municipio Coyuca de Benitez, 10 m.
45119	Female	3 February 2008	Skin and skeleton	México: Campamento Ecoturístico "El Vivero", 6.6 km SE Amecameca, Municipio Amecameca, 2849 m.
21866	Male	20 January 1985	Skin and skeleton	Guanajuato: Sta. Catarina, Municipio Catarina, 1700 m.
4158	Female	27 February 1980	Skin and skeleton	Guanajuato: 18 km WSW Dolores Hidalgo, Municipio Dolores Hidalgo, 2275 m.
4159	Female	26 February 1986	Skin and skeleton	Guanajuato: 8 km S San Miguel de Allende, Municipio San Miguel de Allende, 1920 m.
26464	Male	12 February 1983	Skin and skeleton	Morelos: Campo cañero, Tlaltizapán.
26459	Male	9 February 1985	Skin and skeleton	Morelos: 2 km SW Palpan, Municipio Miacatlan.
26461	Male	27 January 1985	Skin and skeleton	Morelos: 3 km SW Palpan, Municipio Miacatlan.
18790	Male	25 February 1981	Skin and skeleton	Guerrero: Puerto Marqués, Municipio Acapulco.
21989	Female	3 February 1985	Skin and skeleton	San Luis Potosí: Racho Estribo, 10 km S Naranjo, Municipio Cuidad de Maíz.
3790	Male	23 February 1984	Skin and skeleton	Puebla: Rancho La Carolina, Ayotoxco, Municipio Hueytamalco.
3792	Female	23 February 1984	Skin and skeleton	Puebla: Rancho La Carolina, Ayotoxco, Municipio Hueytamalco.
38906	Female	22 March 1996	Skin and skeleton	Oaxaca: 3 km W Sta. María del Mar, Municipio Juchitán.
44179	Female	23 November 2005	Skeleton only	Oaxaca: San Pedro Mixtepec, 18 km N Puerto Escondido, Municipio San Pedro Mixtepec, 222 m.
47914	Male	28 December 2005	Skin and skeleton	Oaxaca: Compañía Minera Cuzcatlán, 2.4 km SW San José del Progreso, Municipio San José del Progreso, 1590 m.
45141	Male	21 January 2007	Skin and skeleton	Oaxaca: Barranca Amarilla, 1.05 km S, 3.75 km W Cosoltepec, Municipio Cosoltepec, 1650 m.
47899	Male	8 November 2011	Skin and skeleton	Oaxaca: Compañía Minera Cuzcatlán, 2.13 km NW San José del Progreso, Municipio San José del Progreso, 1557 m.

Apendix 1 . Continuation

47900	Male	8 November 2011	Skin and skeleton	Oaxaca: Compañía Minera Cuzcatlán, 2.13 km NW San José del Progreso, Municipio San José del Progreso, 1557 m.
47902	Male	25 October 2011	Skin and skeleton	Oaxaca: Compañía Minera Cuzcatlán, 1.88 km NW San José del Progreso, Municipio San José del Progreso, 1559 m.
45122	Male	10 January 2008	Skin and skeleton	Sinaloa: Rancho "La Papalota" 3.1 km N Teacapan, Municipio Escuinapa de Hidalgo, 5 m.
45123	Male	28 October 2008	Skin and skeleton	Veracruz: Panteón Municipal de Tlacotalpan, Municipio Tlacotalpan, 3 m.
45124	Male	28 October 2008	Skin and skeleton	Veracruz: Panteón Municipal de Tlacotalpan, Municipio Tlacotalpan, 3 m.
45125	Female	28 October 2008	Skin and skeleton	Veracruz: Panteón Municipal de Tlacotalpan, Municipio Tlacotalpan, 3 m.
45126	Female	28 October 2008	Skin and skeleton	Veracruz: Panteón Municipal de Tlacotalpan, Municipio Tlacotalpan, 3 m.
45127	Male	28 October 2008	Skin and skeleton	Veracruz: Panteón Municipal de Tlacotalpan, Municipio Tlacotalpan, 3 m.
40769	Male	10 April 1999	Skin and skeleton	Tlaxcala: San Luis 6.1 km NNE Atlangatepec, Municipio Atlangatepec, 2520 m.
Didelphis marsupialis				
7562	Female	25 May 1963	Skin and skeleton	Tabasco: Teapa.
Philander opossum				
3797	Female	29 February 1981	Skin and skeleton	Veracruz: Las Cabañas, Municipio Zontecomapan.
Chironectes minimus				
6960	Female	17 December 1962	Skin and skeleton	Tabasco: Río Puyacatengo, 15 km E Municipio Teapa.
Metachirus nudicaudatus				
34759	Female	1990**	Skin and skeleton	Chiapas: Estación de Biología Chajul, Reserva Montes Azules, Municipio Ocosingo.
Caluromys derbianus				
46855	Female	28 August 2012	Skin and skeleton	Veracruz: Parque Ecológico Jaguaroundi, 1 km WSW La Cangrejera, Municipio Coatzacoalcos, 8 m.
Marmosa mexicana				
29410	Female	23 March 1990	Skin and skeleton	Oaxaca: 11 km SW La Esperanza, camino nuevo a San Isidro Municipio Santiago, 2000 m.
Tlacuatzin canescens				
46539	Female	9 April 2013	Skin and skeleton	Colima: La Encampanada, 6 km E Pueblo Juárez, Municipio Coquimatlán.

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Population estimate and identification of major conservation threats for the river dolphin (*Inia geoffrensis humboldtiana*) at the Colombian Orinoquia

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South American sub-continent, housed the largest diversity of river dolphins on the planet, here there are two species in the genus *Sotalia* and three species in the genus *Inia*. Tonina, present on the Orinoco basin, are exposed to many different anthropogenic threats, such as: the fragmentation and loss of aquatic ecosystems; acoustic contamination; risk of collision with boats; entanglement; deaths by retaliation, resulting from biological and operational interactions with artisanal and industrial fisheries; biomagnification of heavy metals such as mercury in the aquatic trophic web; capture of individuals for their usage as bait for the fishery of *Calophysus macropterus*, primarily on borderline localities between Colombia and Venezuela; and finally, the negative effects of climate change. We conducted a study to determine population sizes and anthropogenic threats affecting river dolphins populations during the beginning of high-water season, between November 2018 and February of 2019, along 1,402 km. We calculated the degradation index for streams of continental waters and density of the river dolphins. Water quality, habitat transformation, species exploitation, and the increment in number of human settlements were identified as the main conservation stressor in the analyzed area. We obtained density values by habitat type for different aquatic environments and population sizes for river dolphins and the value in the index of degradation, with a potential increment in value through time. River confluences were identified as priority areas for the conservation of the species. Water quality, habitat modification, and species exploitation were particularly intense. Our results highlight a potential transformation of the ideal conditions that allow for the establishment of the species, explaining its distribution with predicted values between 46.6 % and 70.1 % for the evaluated timeframe due to the effects of climate change on aquatic ecosystems. The Meta River, has the highest value for the index of freshwater ecosystems degradation followed by the Orinoco basin, water quality and species exploitation appear to be the major stressors for dolphins in these areas. Finally, river confluences were identified as conservation hot spots for dolphin populations. We point out on the importance of river dolphins as bioindicator, sentinel species, and one of the most susceptible to the negative effects of climate change.

El subcontinente Suramericano, contiene la mayor diversidad de delfines de río del planeta, registrándose dos especies para el género *Sotalia* y tres especies para el género *Inia*. La Tonina, presente en la cuenca del Orinoco, está expuesta a diferentes amenazas de origen antrópico, como: la fragmentación y pérdida de los ecosistemas acuáticos; contaminación acústica; riesgo de colisión con embarcaciones; enmallamientos; muerte por retaliación, producto de interacciones biológicas y operacionales con pesquerías artesanales e industriales; biomagnificación de metales pesados como el mercurio en la red trófica acuática; captura de individuos para su uso como atrayente en la pesquería de *Calophysus macropterus*; y finalmente, los efectos negativos del cambio climático. Esta investigación determinó los tamaños poblaciones y las amenazas de origen antrópico que están afectando las poblaciones de delfines de río durante el período de aguas en ascenso, entre los meses de noviembre 2018 y febrero de 2019, a largo de 1,402 km. Se calculó el índice de degradación de ecosistemas acuáticos continentales y la densidad de los delfines de río. La calidad del agua, la transformación del hábitat, la explotación de especies y el incremento en el número de asentamientos humanos se identificaron como los principales estresor para la conservación de la especie en el área analizada. Se obtuvieron los valores de densidad por ambientes acuáticos y los tamaños de poblacionales para los delfines de río y el valor en el índice de degradación, con un potencial incremento en el valor a través del tiempo. Las confluencias entre ríos fueron identificadas como áreas prioritarias para la conservación de la especie. La calidad del agua, la modificación del hábitat y la explotación de especies fueron particularmente intensas. Los resultados evidencian una transformación potencial de las condiciones ideales que permiten el establecimiento de la especie, explicando su distribución con valores predictivos entre 46.6 % y 70.1 % para el período de tiempo evaluado, influenciado por los efectos del cambio climático en los ecosistemas acuáticos. El Río Meta tiene el valor más alto para el índice de degradación de los ecosistemas acuáticos continentales seguido por la cuenca del Orinoco, la calidad del agua y la explotación de las especies parecen ser los principales estresor para los delfines en estas áreas. Finalmente, las confluencias de los ríos fueron identificados como puntos clave para la conservación para las poblaciones de delfines. Destacamos la importancia de los delfines de río como bioindicadores, especies centinela, y una de las más susceptibles a los efectos negativos del cambio climático.

Keywords: Aquatics mammals; climate change; Orinoco basin; pink dolphins; population density.

Introduction

The global decline in species richness and species diversity has been estimated to affect one to ten percent of worldwide biodiversity over a ten-year period (Sittig *et al.* 2018), but it has also been shown that human interaction accelerates extinction events (Wilcove *et al.* 1998; Chapin *et al.* 2000; Dawson 2011; IUCN 2013). To manage the effective conservation of a given animal species, an understanding of its habitat and life history is critical. Although many animal species have been described in detail, standardized population data are still lacking. These studies are necessary to monitor population development and for subsequently determining the level of threat to the species in question, in order to develop and prioritize conservation strategies (Sittig *et al.* 2018).

River dolphins are among the most threatened cetaceans on the planet (Reeves and Leatherwood 1994; Reeves *et al.* 2003; Davidson *et al.* 2009; Ávila et al. 2018); they have been only documented in South America and Asia, in geographic areas that in the last century have experienced some of the most intense transformations due to the impact of human activities (Reeves and Leatherwood 1994; IWC 2000; Reeves *et al.* 2000, 2003; Smith and Braulik 2008; Trujillo *et al.* 2010; Mosquera-Guerra *et al.* 2015). In 2005, it was reported the extinction of the Chinese river dolphin, or baiji, *Lipotes vexillifer* at the Yangtze River (Turvey *et al.* 2007; Ross *et al.* 2010), constituting one of the most recent extinctions of a large mammal (Trujillo *et al.* 2019). In addition, there are two other species of Asian dolphins under risk of extinction: *Platanista gangetica* (EN), distributed across the Ganges River complex (India and Nepal), and *P. minor* (EN), from the Indo (Pakistan) and Megna (Bangladesh) River systems (Smith *et al.* 2006; Smith and Braulik 2008). The South American sub-continent, housed the largest diversity of river dolphins on the planet with two species in the genus *Sotalia* and three species in the genus *Inia* (Mosquera-Guerra *et al.* 2015, 2018). The genus *Sotalia*, is represented by *S. fluviatilis* exclusive of continental environments of the Amazon basin (Da Silva 2002), and *S. guianensis*, documented from the mid-basin and the delta of the Orinoco river, the Maracaibo lake, and the Atlantic Coast in Central and South America from the south of Nicaragua to southern Brazil (Caballero *et al.* 2007). Molecular data point to a recent divergence of continental populations of *S. guianensis* (600,000 years), from their coastal counterparts (Carvajal-Castro *et al.* 2015; Caballero *et al.* 2017). Furthermore, vicariate events among basins, associated with the presence of rapids and waterfalls, and the influence of climatic fluctuations, gave origin to three species within the genus *Inia*: *I. geoffrensis* (Da Silva 2009), with the subspecies: *I. g. geoffrensis*, distributed on the Amazon basin (Da Silva 2002), and *I. g. humboldtiana*, occurring on the Orinoco basin (Herrera *et al.* 2017). *I. boliviensis*, from the Mamoré, Itenez, Grande, and upstreams from the Madeira River in Bolivia (Aliaga-Rossel 2002; Banguera-Hinestroza *et al.* 2002; Aliaga-Rossel *et al.* 2006; Ruiz-Garcia *et al.* 2008; Ruiz-Garcia 2010; Gravena *et al.* 2014). *I. araguaiaensis*, from the hydrologic complex of the Tocantins-Araguia rivers in Brazil (Hrbek *et al.* 2014).

Recently the international threatened category of *I. geoffrensis* was elevated from Data Deficient (DD), to Endangered (EN; da Silva *et al.* 2018), and in Colombia, this taxon is considered as vulnerable (VU; Trujillo *et al.* 2006; Minambiente 2017). In addition, the species is within in Appendix II of The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 2019). Populations of *I. g. humboldtiana*, present on the Orinoco basin (Trujillo 2000; Diazgranados and Trujillo 2004; Mosquera-Guerra *et al.* 2018a), are exposed to many different anthropogenic threats (Mosquera-Guerra *et al.* 2016), such as: the fragmentation and loss of aquatic ecosystems; acoustic contamination (Davidson *et al.* 2012); risk of collision with boats (Ávila et al. 2018). Entanglement; deaths by retaliation, resulting from biological and operational interactions with artisanal and industrial fisheries (Trujillo *et al.* 2006, 2010; Da Silva 2011; Mintzer *et al.* 2013). Biomagnification of heavy metals such as mercury in the aquatic trophic web (Mosquera-Guerra *et al.* 2015a, 2018c). Capture of individuals for their usage as bait for the fishery of the mota, simí, piracathinga or come muerto (*Calophysus macropterus*), primarily on borderline localities between Colombia and Venezuela on the Arauca, Meta, and Orinoco rivers (Mosquera-Guerra *et al.* 2015c). Finally, river dolphins are affected by the negative effects of climate change on their habitats and populations (Mosquera-Guerra *et al.* 2015b).

Because of the current scenario, urgent conservation actions are needed to guarantee the persistence of *I. g. humboldtiana* on the Colombian Orinoco basin; but their construction and implementation require appropriate data collection on the species habitat use (Gomez-Salazar *et al.* 2011), as well as, standardized and statistically supported population density estimations (Gomez-Salazar *et al.* 2012a). This information also provides elements for monitoring *I. g. humboldtiana* population trends in these rapidly changing landscapes of the Orinoco region (Reeves and Leatherwood 1994; IWC 2000; Reeves *et al.* 2000; Gomez-Salazar *et al.* 2012a). We determined the populations size and conservation threats of toninas in three regions of the Colombian Orinoquia (Meta, Casanare and Vichada), across the Meta, Ele, Cravo Norte, Casanare, Orinoco, Vichada and Inirida rivers, at the beginning of high-water season, between November 2018 and February of 2019, along a total of 1,402 km. Our information on *I. g. humboldtiana* occurrence, was used to feed predictive species distribution models for the next 20 years at the Colombian Orinoquia.

Material and Methods

Study area. Between November 2018 and February of 2019, three scientific expeditions were conducted: A) Meta (6.11027°, -67.28218° / 4.21653°, -72.04838°). B) Ele, Cravo Norte and Casanare Rivers (6.58977°, -70.7209°/ 6.04325°, -69.83514°). C) Orinoco, Vichada and Inirida Rivers (6.18417°, - 67.47140°/ 3.86514°, - 067.93397°); in order to evaluate the population status and Orinoquian pink dolphins (*I. g. humboldtiana*); as well as to identify the major threats for the subspecies in the region (Figure 1).

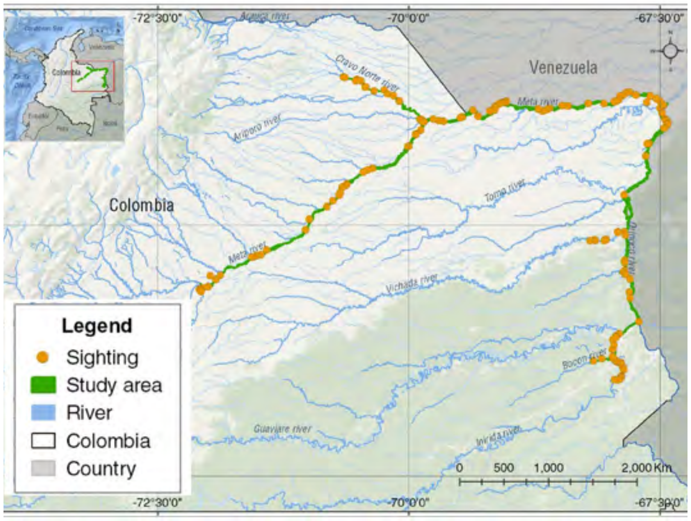


Figure 1. Study area: Meta river transect, from the municipality of Puerto Carreño (Vichada) up to Puerto Gaitán (Meta; 720 km). Ele, Cravo Norte and Casanare transect, from Arauca (Arauca) up to Paz de Ariporo (Casanare; 410 km), and Orinoco. Vichada and Inirida rivers transect, from Puerto Carreño (Vichada) up to Puerto Inirida (Guania; 210 km), and records of *I. g. humboldtiana* employed in the construction of different models of distribution for the species in the Colombian Orinoquia.

Transect design. Sampling was conducted with a combination of line and strip-transect methods (Gomez-Salazar *et al.* 2012a), performing four strip transects of 2.5 km altogether in length and every a width of 200 meters; then, switching into a line transect between 1.0 and 2.5 km, depending on river width. Boat speed ranged between eight and 12 km/hour and data gathering happened between 5:30 and 17:30 hours. The whole sampling occured within the high-water season, allowing for the evaluation of different types of habitats including main rivers, channels, confluences, tributaries, and river islands (Table 1). Boats ranged from 11 to 43 meters of length and were equipped with observation platforms on both bow and stern, varying from two to six meter in height and supporting six previously trained observers on each one. Observers were clockwise rotated in position each two hours. Each platform was considered independent and only one effort recorder knew about the differences in observations between the two platforms, registering them with assigning codes following Gomez-Salazar *et al.* (2012a).

Inia g. humboldtiana sighting locations were recorded in geographic coordinates with a GPS Garmin 64sc; sight angle was documented with a compass and distance from the dolphin was estimated with a laser range finder distance meter Bushnell Trophy 4X de 20 mm. For each observation the distance to the shore was estimated in ranges as follow: 0 to 50 m, 50 to 100 m, 100 to 150 m and 150 to 200 m; in the same way riversides were classified into: mainland; forest; bushes; beaches; cliffs; rocks; human settlement; floating grasses. In addition, information on the environmental conditions, including: glare strength; water type (backwaters, white waters, and mix waters, by limnological criteria); river state, was recorded *in situ*.

Habitat were stratified to generate a differential report on population density with ecological support following Gomez-Salazar *et al.* (2012a) and Trujillo *et al.* (2011): i) main river, ii) tributaries, iii) lake, iv) island, v) channels y vi) confluences. The sampling experimental design followed Gomez-Salazar *et al.* (2012a; 2012b), Williams *et al.* (2016), and involved a combination of two types of strip transects (parallel to the shore) and lineal (crossing diagonally the river width).

Human stressors and index of freshwater ecosystems degradation. We determined the degradation index of freshwater ecosystems by transect following Gomez-Salazar *et al.* (2012b), authors that consider 10 human stressors (Table 2 and 3), grouped into four categories i) water quality; ii) habitat modification; iii) species exploitation; and iv) human settlements and cities (Table 4). Each stressor was valued with a code, according to four categories of impact: 0) absence of disturbance; 1) low disturbance; 2) mid disturbance; and 3) high disturbance. Overall score index of freshwater habitat degradation was obtained by summing over these three major categories with overall value ranges from 0 to 8.5 (8.5 being the highest degradation). In addition, the information on human population size (Table 2) for each river area surveyed was obtained using the databases of the population census for each country surveyed (DANE 2018). The future trend in freshwater habitat degradation was estimated for each human stressor based on current knowledge of, for example, water development projects planned (Table 3). Information used to provide current and future degradation index scores consisted of observations in the field, published and unpublished reports, and personal communications with researchers from each location surveyed (see also Gomez-Salazar *et al.* 2012b).

Population estimation. Population estimate was calculated in DISTANCE version 5.0 y 6.0 (Buckland *et al.* 2001; Gomez-Salazar *et al.* 2011a) based on this formula: $D = n$

Table 1. Studied habitats by river: Main rivers, Channels, Confluences, Tributaries, and Islands for the transects: Meta; Ele, Cravo Norte and Casanare; and Orinoco, Vichada and Inirida rivers; Area; Transect length; *N* trans (number of transects by habitat type); *S* (stripe transects; and line transects).

Basin	**Rivers**	**Habitat type**	**Area Km²**		**Transect Length Km**		**No. trans**	
			S	**L**	**S**	**L**	**S**	L
Orinoco	Meta	Channel	65.7	-	131.4	-	53.0	-
		Tributary	3.7	-	7.3	-	3.0	-
		Main river	257.6	4.5	515.2	9.0	209.0	6.0
	Ele, Cravo Norte and Casanare	Channel	4.9	-	9.8	-	4.0	-
		Confluence	2.5	-	5.0	-	2.0	-
		Main river	100.3	-	200.6	-	82.0	-
	Orinoco, Vichada and Inirida	Channel	11.7	-	23.4	-	10.0	-
		Confluence	1.8	-	3.7	-	2.0	-
		Main river	189.1	25.5	378.2	50.9	127.0	25.0
		Island	6.8	-	13.6	-	6.0	-
		Tributary	27.0	-	54.0	-	7.0	-
Total		Subtotal by type of transect	671.1	30.0	1.342	60.0	537.0	31.0
		701.2		1.402		568.0		

Table 2. Principal human stressors responsible for freshwater degradation and their impact on the ecosystems proposed by Gomez-Salazar *et al.* (2012b).

Human stressors	Impact of stressors on freshwater ecosystems
Water quantity	Water withdrawals by domestic, industrial and agricultural needs, reservoir storage capacity (Alcamo *et al.* 2003, 2005).
Water quality	Source point and non-source point pollutants (*e. g.*, organic pollutants, increased nutrients, heavy metals, microbial contamination, toxic organic compounds), suspended particles, temperature (Hoekstra *et al.* 2011).
Habitat modification	Roads, dams, reservoirs, land transformation, land use intensity, agriculture, vegetation cover, fragmentation (Moyle and Randall 1998; Revenga *et al.* 2000; Vörösmarty *et al.* 2010; Alkemade *et al.* 2009).
Exploitation of species	Fishing pressure, destructive fishing practices (*e. g.*, blast fishing or fishing using poison or explosives), excessive by-catch and discards, aquaculture (GIWA 2002).
Climate change	Increasing water temperature, decreasing precipitation, increasing acidification, changes in primary production (Vörösmarty *et al.* 2000; Milà-Canals *et al.* 2009).
Introduced species	Increasing the rates of species introduced in freshwater systems and the success rate of those introduced (Falkenmark 1997; Karr and Chu 1999; Bennett *et al.* 2004).

$E(i)\ f(0)\ /\ 2L\ g(0)$. In which n is the number of observed groups of dolphins; $E(i)$ is the group mean observed in habitat (i); $f(0)$ is the probability of detection of a density from a perpendicular distance 0; L, refers to the length of the transect; and $g(0)$ is the probability of detection of a group on the line of the transect.

For $g(0)$ we follow the assumptions, as well as the indications in the calculation of the variance in Gomez-Salazar *et al.* (2011a). For the detection function, we analyze three different models in DISTANCE: uniform, half-normal and hazard rate, that were selected following the Akaike Information Criteria (AIC). Taking into account that we detected a gradient of dolphin density from the shore to the center of the river, the probability of detection $g(0)$ was calculated in a scaled manner using a range of distances (0 to 50 m, 50 to 100 m, 100 to 150 m and 150 to 200 m). The population size for river dolphins (Ni) was calculated for each habitat $Ni = Ai*Di$ (Gomez-Salazar *et al.* 2011a).

Data collection and distribution models for climate change scenarios. In order to construct models of potential distribution for *I. g. humboldtiana* in future climate change scenarios for 2018, 2023, 2028, and 2038. Occurrence data represented by 177 georeferenced records obtained from direct observations of dolphins across the Orinoco basin in 2018, were combined with climate datasets from ASCII files for 2020, 2030, 2040 and 2050 with the algorithm Maxent (Graham and Hijmans 2006, Phillips *et al.* 2006, Peterson et al. 2007). Occurrence data was filtered to avoid redundancy following protocols proposed in Phillips *et al.* (2009), and was visualized in ArcGIS 10.2.2 (ESRI 2014; Figure 1). Nineteen climatic variables, derived from Worldclim (Hijmans *et al.* 2005; Table 5), were used in combination with climate shapefiles obtained from the web portal Climate Change, Agriculture and Food Security (CCAFS), selecting the method Delta IPCC AR4 for the region B12. For the intermediate temporalities 2018, 2023, 2028 and 2038 a regression was performed in geostatistical software "R" (R Core Team 2013). We applied the cubic convolution interpolation method in order to downscale bioclimatic variables with a pixel resolution of 100 meters for the analyzed years (ESRI 2019). In addition, we also considered two hydrological variables: i) flux accumulation and ii) flux direction along with a digital elevation model.

In order to select the most informative climate variables for our *I. humboldtiana* presence data set, we implement the function *vifstep* from the *usdm* library in the software R (R Development Core Team 2011).

Results

Human stressors and estimation of freshwater ecosystems degradation. The index of freshwater ecosystems degradation, reported low to intermediate values ranging between 2.05 and 4.5, as follows by transect: a) Meta (4.5). b) Ele, Cravo Norte and Casanare (2.05). c) Orinoco, Vichada and Inirida Rivers (4.25; Table 6).

Table 3. Human stressors and definitions for each impact category proposed by Gomez-Salazar *et al.* (2012b). Codes for impact categories are (0) no disturbance reported, (1) low disturbance, (2) medium disturbance, (3) high disturbance. Some human stressors do not include high impact categories (–).

Human stressors		**Impact categories [range distance from the study area]**		
I. Water quality		Low (1)	Medium (2)	High (3)
1. Oil exploitation	Any size	100–200 km	50–100 km	Within 50 km
2. Tourism	Tourist resorts	50–100 km	Within 50 km	–
3. Ship traffic	Commercial, fishing, naval or transportation.	Sporadic routes.	Known shipping routes.	–
4. Mining	Any	100–200 km	50–100 km	Rango 50 km
II. Habitat modification				
5. Dams	Any size	500–1,000 km downstream or 100–200 km upstream.	200–500 km downstream or 50–100 km upstream.	Within 200 km downstream and/ or within 50 km upstream.
6. Waterways	Any size	500–1,000 km downstream or 100–200 km upstream.	500–1,000 km downstream or 100–200 km upstream.	Within 200 km downstream and/ or within 50 km upstream.
III. Exploitation of species				
7. Entanglements/ killing of dolphins to avoid competition for resources (fish).	Number of dead dolphins due to entanglements/ or direct killing.	Rare (recorded once or twice in the area).	Occasional (recorded once per year).	Frequent (recorded at least once per month).
8. Killing of river dolphins for bait	Number of dead dolphins killed for bait.	Rare (recorded once or twice in the area)	Occasional (recorded once per year).	Frequent (e.g., mota fishery established in the area).
9. Fisheries		Subsistence.	Commercial, main destination is cities within the river basin.	Commercial, main destination is cities within and outside the river basin.
IV. Human settlements and cities				
10. Human population size		Less than 100,000.	Between 100,000 and 200,000.	More than 200,000.

Table 4. Overall score index for each impact category (high, medium and low, see Table 3) and risk trend levels of freshwater ecosystem degradation. The overall score index is the sum of the means over the four main categories of human stressors (water quality, habitat modification, exploitation of species, cities and human settlements, Table 3).

	Overall score index	**Summing over the different types of human stressors**
🟥 High	Majority of human stressors are classified as high or medium, no stressors are classified as low.	≥ 4
🟨 Medium	Majority of human stressors are classified as medium.	≥ 3 and < 4
🟩 Low	Majority of human stressors are classified as low or no known, no stressors are classified as high.	< 3
Risk trend (within the next 10 years)		
↑	Risk is expected to increase (*e. g.*, construction of water development projects planned, increase number of oil stations, etc.).	
→	Risk is expected to remain similar, although some increase in human population size is expected.	
↓	Risk is expected to reduce given some conservation or management actions in the area.	
-	Risk not recorded in the area, and not expected to appear in the next year.	

Population status. For 1.402.2 km surveyed, at the beginning of the rainy season, a total of 654 individuals were recorded, discriminated by river as follows: Meta = 206; Ele, Cravo Norte and Casanare = 89; and Orinoco, Vichada and Inirida = 359 (Table 7).

The greatest values of density were registered for the type of habitat "confluences", with the confluence between the Meta-Orinoco yielding a density value D = 17.6 *Inia*/km^2, following by the confluence of the river system of Ele, Cravo Norte and Casanare, D = 1.2 *Inia*/km^2 (Table 8). Average group size was 2.9 (SD =1.5) for the Ele, Cravo Norte and Casanare rivers; 2.6 (SD = 1.9) Orinoco, Vichada and Inirida; and 2.0 (SD = 1.4) Meta.

Table 5. Bioclimatic variables used in the potential distribution models of *I. g. humboldtiana* in the Orinoco basins.

Variables	**Description**
Elevation	Height in meters above sea level
Bio 1	Annual average temperature
Bio 2	Average daytime range (Mean of the month (Max Temp - Min Temp))
Bio 3	Isothermality ((Bio 2/Bio 7) * 100)
Bio 4	Seasonality of temperature (Standard deviation * 100)
Bio 5	Maximum temperature of the hottest month
Bio 6	Minimum temperature of the coldest month
Bio 7	Annual temperature range (Bio 5 - Bio 6)
Bio 8	Average temperature of the wettest quarter
Bio 9	Average temperature of the driest quarter
Bio 10	Average temperature of the warmest quarter
Bio 11	Average temperature of the coldest quarter
Bio 12	Annual rainfall
Bio 13	Precipitation of the wettest month
Bio 14	Precipitation of the driest month
Bio 15	Seasonality of precipitation (Coefficient of variation)
Bio 16	Precipitation of the wettest quarter
Bio 17	Precipitation of the driest quarter
Bio 18	Precipitation of the warmest quarter
Bio 19	Precipitation of the coldest quarter
Rad	Solar radiation

Table 6. Score index and risk trends of freshwater ecosystem degradation, and human population size across the three areas surveyed. The direction of the arrows indicates whether the risk of degradation is expected to increase, decrease or remain the same. Overall score index is the sum of the means over the four main categories of human stressors (water quality, habitat modification, exploitation of species, cities and human settlements; Gomez-Salazar *et al.* 2012b).

Human stressors	**Rivers**		
	Meta river	**Ele, Cravo Norte and Casanare rivers**	**Vichada Orinoco and Inirida rivers**
Overall score risk	4.5	2.05	4.25
I. Water quality	2.5	0.75	2.25
1. Oil	3↑	1↑	-
2. Tourism	2↑	-	3↑
3. Ship traffic	2↑	1↑	3↑
4. Minning	3↑	1↑	3↑
II. Habitat modification	-	-	-
5. Dams	-	-	-
6. Waterways	-	-	-
III. Species exploitation	2→	1.3→	2→
7. Accidental entanglements / dolphin deaths due to competition for resources (Fishes)	2↑	2↑	2↑
8. Killing of river dolphins for bait	1↑	-	1↑
9. Fisheries	3↑	2↑	3↑
IV. Cities and human settlements	-	-	-
10. Human Population Size	181,276	3,331	34,274

The habitat type "main river" showed values ranging between D = 1.6 – 0.8 *Inia*/km^2 for Meta, Ele, Cravo Norte and Casanare; while, Vichada River had a value of D = 0.6 *Inia*/km^2. Channels had density values ranging from D = 0.3 to 0.5 *Inia*/km^2 only recorded for the Meta and Orinoco-Vichada. Finally, Island density was D = 0.6 *Inia*/km^2 for the Orinoco and Vichada (Figures 2a-b).

Niche modeling and climate change. We modeled the potential distribution of *I. g. humboldtiana* for predicted scenarios of climate change for the following temporal windows: 2018 yield an area of 1,467 km^2 (AUC: 0.97); 2023, 784.3 km^2 (AUC: 0.96), 2028, 575.6 km^2 (AUC: 0.96), and finally 2,038 440 km^2 (AUC: 0.94; Figures 3a-d).

Discussion

River dolphins are considered ideal biological models to understand the dynamics of the aquatic ecosystems at the basin scale; characteristics such as: i) low population size; ii) high habitat requirements; iii) differential use of their habitats; iv) location as top predators within the trophic web; v) long pregnancy (Martin and Da Silva 2018; Boede *et al.*

Table 7. Values of the density of *I. g. humboldtiana* in the different types of habitat sampled for each of the systems evaluated. *Di* is the densities for the habitat type, *Ai* is the survey area and *Ni* is the population size calculated for the river dolphins.

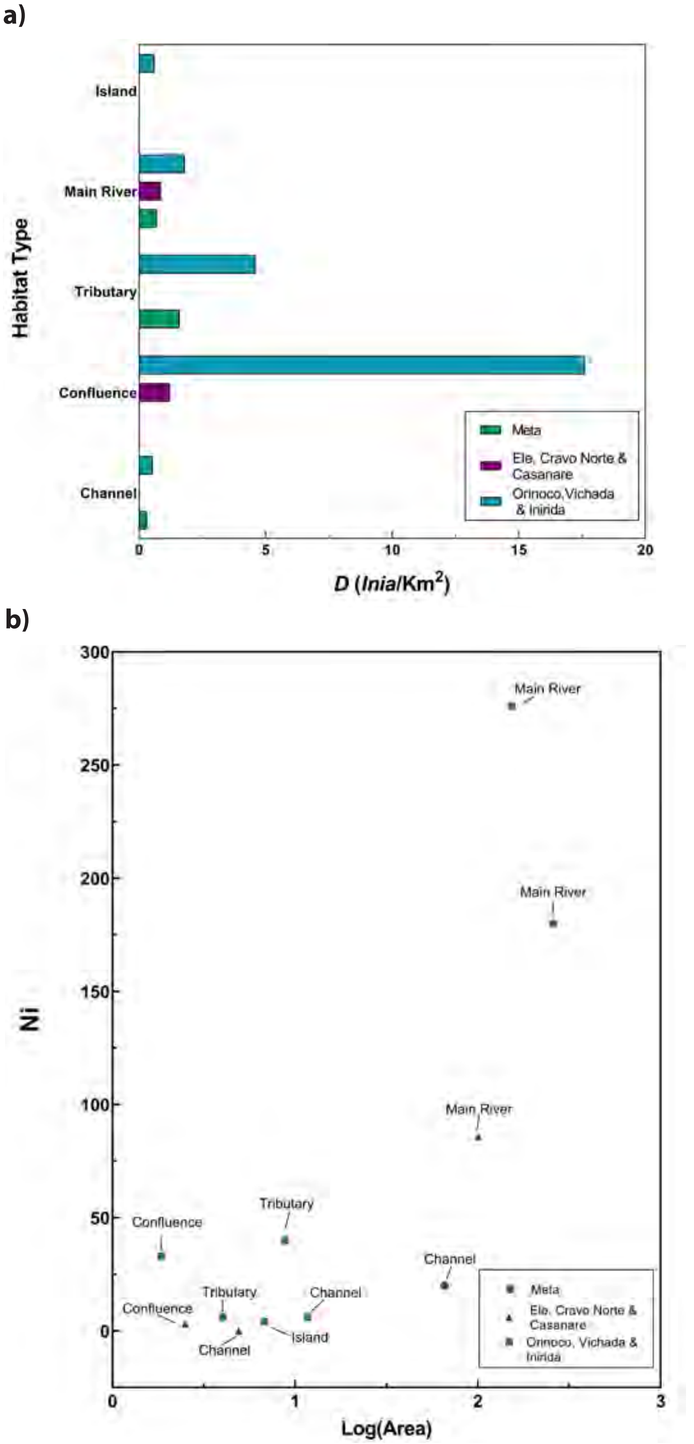
River	Habitat type	Area (km²)	*Di*	*Ni = Ai*Di*
Meta	Channel	65.7	0.3	20
	Tributary	4.0	1.6	6
	Main River	258	0.7	180
Ele, Cravo Norte and Casanare	Channel	4.9		0
	Confluence	2.5	1.2	3
	Main River	100.3	0.8	86
Orinoco, Vichada and Inirida	Channel	11.7	0.5	6
	Confluence	1.8	17.6	33
	Main River	153	1.8	276
	Island	6.8	0.6	4
	Tributary	8.8	4,6	40

2018); and vi) long term parental care (Boede *et al.* 2018). Make these cetaceans sensitive to the environmental changes, and by means sentinel and bioindicator species of the aquatic environments (Trujillo *et al.* 2010; Gomez-Salazar *et al.* 2012; Herrera *et al.* 2017; Mosquera-Guerra *et al.* 2018; Trujillo *et al.* 2019). The constant direct and indirect threats faced by river dolphins and their habitats across the Colombian Orinoquia, had made a priority the construction of conservation actions to guarantee their existence, as into account for the appropriate design of conservation strategies is the generation of well as the multiple structural functions these cetaceans offer to their environments. One of the most important aspects to take information on population size and its relationship with the health of the environment across species distribution (Trujillo *et al.* 2011; Mosquera-Guerra *et al.* 2018). After almost a decade of continues research, we have population estimates for *I. g. humboldtiana* across the Orinoco basin in the Arauca, Meta, Bita, Orinoco, Guaviare, Guayabero and Losada Rivers (Mosquera-Guerra *et al.* 2015, 2018; Trujillo *et al.* 2019).

Human stressors and estimation of freshwater ecosystems degradation. These values are in agreement with data reported in Gomez-Salazar *et al.* (2011) and Mosquera-Guerra *et al.* (2015, 2016) the mid Orinoco River. It is important to mention that human stressors have a differential intensity along the hydrologic systems evaluated, varying in parameters such as: water quality; the type of habitat modifications; fisheries exploitation; and boat traffic volume, among others.

Table 8. Average of the sighting rate (*n* / *l*), density estimate (*D*) and coefficient of variation to measure the rate of encounter CV (er) for the aquatic systems evaluated during the hydrological period of low water.

Habitat	Meta River			Ele, Cravo Norte and Casanare Rivers			Orinoco, Vichada and Inirida Rivers		
	N/L	D *Inia/* km²	Cv(er)	N/L	D *Inia/* km²	Cv(er)	N/L	D *Inia/* km²	Cv(er)
Channel	0.06	0.30	0.16				0.10	0.50	0.10
Confluence				0.20	1.20	0.10	3.10	17.60	0.08
Tributary	0.30	1.60	0.30	0	0	0	0.10	4.60	0.04
Main River	0.10	0.70	0.30	0.20	0.80	0.10	0.10	1.80	0.01
Island							0.10	0.60	0.03

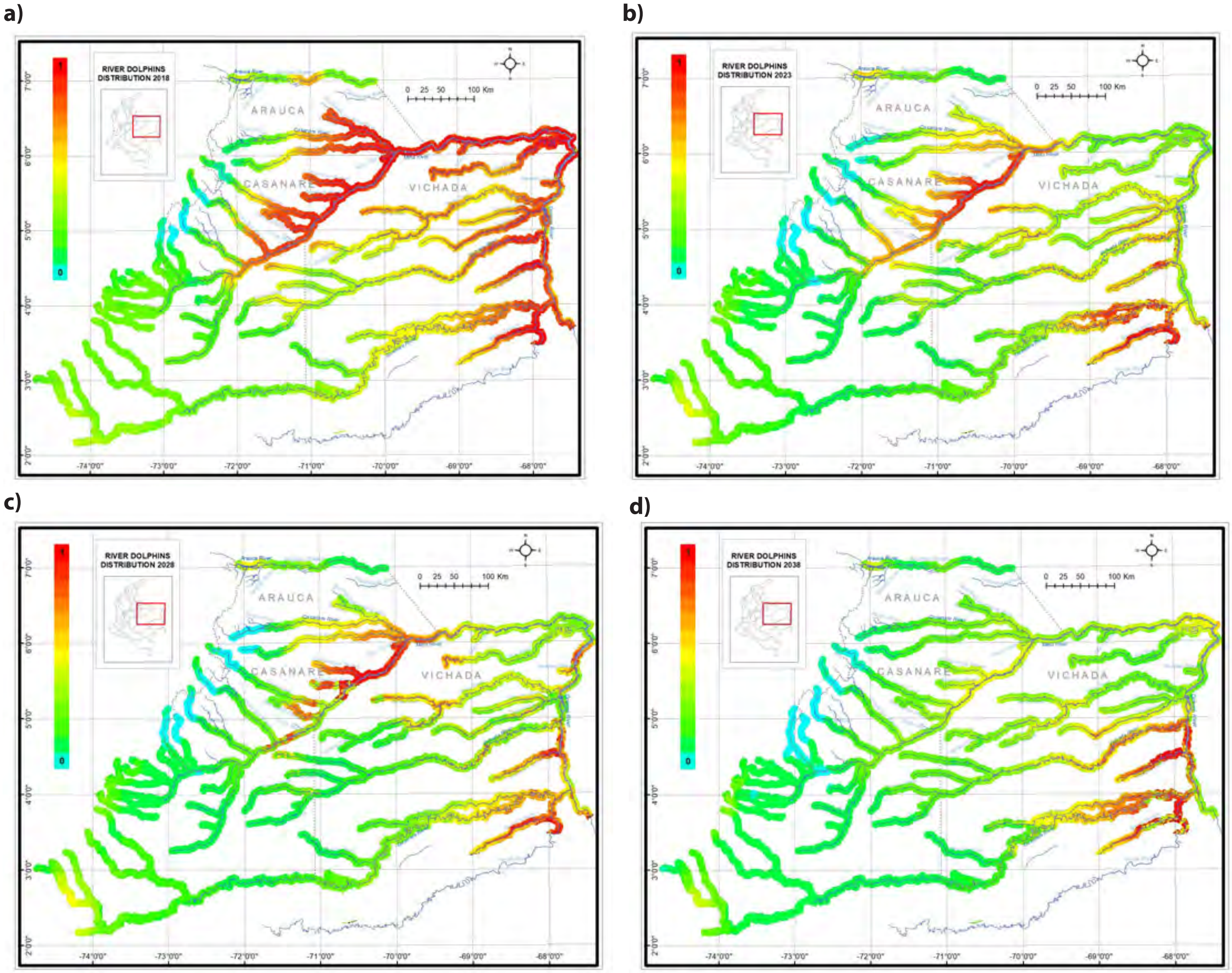


Figures 2. Values of density and population size of *I. g. humboldtiana*, in the different types of habitat sampled for each of the systems evaluated. a) values of density in km² and b) population size calculated for the river dolphins in Log (area).

Other aspect that contributes to the affectations complexity, is derived from the natural heterogeneity of the savannas of the Colombian *Llanos Orientales*, enclosing at least 156 different types of ecosystems, 49 correspond to areas with some degree of human transformation (Romero *et al.* 2004). The agroindustrial plantations establishment of African palms (*E. guineensis*), maize (*Z. mays*), and rice (*O. sativa*), and during the last twenty years, the increment in acacias (*Acacia sensu*) and eucaliptus (*Eucalyptus* sp.) plantations. In conjunction, monocultures are some of the transformation gears at the landscape scale in the Orinoquia (Andrade *et al.* 2009). Agro-industrial activities demand large volumes of water, situation that in combination with the natural hydrological stress, derived from the region seasonality, affecting, in particular, the tributaries contribution, compromising the ecological dynamics as a consequence of his dependence of structural changes in area and volume, importance variables for large aquatic vertebrates such dolphins. The situation aforementioned is particularly true for the Casanare, Cravo Sur, and Meta Rivers, tributaries of the Meta basin (Mosquera-Guerra *et al.* 2015). The increment in human settlements and cities, consequence of massive migration is an outgrowth of agroindustrial megaprojects in the Colombian Orinoquia (Mosquera-Guerra *et al.* 2016). Major human centers in the region are characterized by a poor infrastructure and coverage for water treatment. Sewage dumping in municipalities such as Puerto Carreño (Vichada), Cravo (Arauca) and Orocue (Casanare), as well as the disposal of solid residuals along the Meta, Ele, Cravo Norte, Casanare, Vichada, Orinoco, and Inirida rivers.

Deforestation and fires intentionally promote by human activities, along the river shores, compromised their structural stability, increasing the amount of sediments discharged into the river systems, and the total dissolved soils, affecting biogeochemical cycles, the turbidity, conductivity, acidity and amount of heavy metals. All these effects result in changes in the ecological dynamics of water systems (Mosquera-Guerra *et al.* 2015a, 2018c). Previous estimation showed that the region suffers an annual transformation of 1.3 % of its forest coverage.

In contradiction with these statistics, and despite the warnings they have raised among scientists, at the Consejo Nacional de Política Económica y Social (2014) implemented a new economic policy for the Altillanura (non-flooded savannah), in which the "Departamento de Planeación Nacional" (DNP) suggest that around 2.8 millions of hectares in the region are free to be transformed into productive systems (Mosquera-Guerra *et al.* 2015).



Figures 3. Models of potential distribution for *I. g. humboldtiana* in the Orinoco basin for a) 2018, b) 2023, c) 2028, and d) 2038.

We also evidence an expansion of oiling activities across the study area, in particular for the high and middle basin of the Meta River (Gomez-Salazar *et al.* 2011; Mosquera-Guerra *et al.* 2016). Since the 1980´s oil spills, due to subversive activities of the guerrillas, resulted in 1.5 million of barrels, contaminating primarily the aquatic systems of the Arauca and Casanare basins (Trujillo *et al.* 2010). Product of these perturbations, large amounts of heavy metals are released into the hydrological system, starting a process of biomagnification, with large vertebrate carnivores (river dolphins, giant otters, and cat fishes, among other animals) as final repositories of these metals in their tissues. Mosquera-Guerra *et al.* (2015a, 2018c), report the maximum amount of mercury (Hg) among South American river dolphins, in muscle tissue samples of *I. g. humboldtiana* from the Arauca River (3.5 mg/kg^{-1}).

We also identify that the inadequate closure of oil drills, are a potential threat of oil spills. The new economic policies that authorize the implementation of extractive techniques like the fracking emerge as new potential threat for the aquatic environments (Mosquera-Guerra *et al.* 2016). On the other hand, touristic activities, are generating an increment in the traffic of boats, raising the number of evidence of collisions (scars in the fins and even dead animals have been documented) in particular for the Orinoco and Vichada Rivers, also the considerable increment of acoustic contamination, associated with commercial activities, and human transportation, taking into consideration that these two rivers in a region that lacks of other ways to access affect the dolphin reproductive sites, such as the confluences of Meta-Orinoco and Vichada-Orinoco Rivers. The structural modification of the river courses to in order favor a greater volume of boat traffic (hydro-highways), will also carry many of the serious problems mentioned above. One of the major causes for the extinction of the Chinese baijii (*Lipotes vexillifer*) was the fragmentation of their population (Trujillo *et al.* 2010).

Population status. These results agree with information reported in Gomez-Salazar *et al.* (2011, 2012a, 2012b), Mosquera-Guerra *et al.* (2015, 2018) and Pavanato *et al.* (2016). The reported values of group size in the present work are within the averages documented by Gomez-Salazar *et al.* (2011) and Mosquera-Guerra *et al.* (2015), for Orinoco basin. Variation in density is strongly influenced by habitat type. The ecological heretogeity of aquatic habitats across the Orinoco basin, determines a differential spatial-temporal use of the river by these cetaceans. Species in *Inia* can differentially use, main rivers, their tributaries, and flooded forest environments at different spatial and temporal scales. Confluences, tributaries, lakes and flooded forest are commonly used for feeding; shallow waters are the environments where individuals of the species mate and socially interact; and lakes and channels are used for the birth and care of offspring (Trujillo 2000; Martin and da Silva 2004, 2006; Gomez *et al.* 2012, Mosquera-Guerra *et al.* 2018b). *Inia* is intrinsically dependent on the dynamics of flood pulses of the basins and their effect on the temporal and spatial distribution of their fish prey (Mosquera-Guerra *et al.* 2018b). Other studies have reported variations in density values for river dolphin density and group size associated with ecological factors such as flood pulses, highlighting that at low waters, river dolphins are concentrated on the channels, river confluences and tributaries. But, at high waters, individuals spread into other aquatic systems, associated with the flooded forest, in the foraging for fish preys (Trujillo *et al.* 2011, Gomez-Salazar *et al.* 2012a and Mosquera-Guerra *et al.* 2015a).

The present study corroborates, the ecological importance of river confluences for pink dolphins, in particular, Meta-Orinoco and Orinoco-Vichada; evidencing, its relevance as prioritized conservation areas for the subspecies (Figure 4a). River confluences are ecotones in which contrasting ecological conditions determine the selection of a differential fish communities. In the Orinoco basin, white water rivers such as the Meta, Arauca, and Casanare, encounter clear water rivers such as the Bita, Tomo, Tuparro and Vichada and are obligated passes for fish populations moving up and down-streams. The last generates: i) ideal conditions for dolphin fishing success and ii) it conditions the generation of social groups among dolphins.

The highest values among analyzed habitats, reported by confluences, agrees with Trujillo (2000), Trujillo and Diazgranados (2004), Gomez-Salazar *et al.* (2011), Trujillo *et al.* (2016) and Mosquera-Guerra *et al.* (2018b). These authors, also associated the greatest number of individuals with the confluence of the Meta-Orinoco Rivers. In part, the greatest density of dolphins reported for the confluences, is closely related with the presence of fish in these areas that offer connection among different aquatic environments. In summary the stressors of human origin that influence the population dynamic of river dolphins are: habitat degradation, loss of connectivity, contamination, conflict with fisheries, increment of the traffic, climate change, and construction of hydroelectric infrastructure (Sandin *et al.* 2008; Baum and Worm 2009; Gomez-Salazar *et al.* 2012b; Mosquera-Guerra *et al.* 2015a; Trujillo *et al.* 2010a). Population estimates for river dolphins in Colombia and South America, have produced concrete results during the last 12 years, resulting in the change in the category of threat for *I. geoffrensis* by the IUCN, from Data Deficient (DD) to Endangered species (EN) in 2018 along with the formulation and implementation of regional and national management plans.

We infer a strong annual population reduction of *I. g. humboldtiana* at the Orinoco basin (7.14 %). This inference is derived from the comparison of our population data (2017 to 2018; 654 individuals) with that in Gomez-Salazar *et al.* (2012), representing a decrease of 35.7 % in the number of individuals in six years. Our data is in agreement with Williams *et al.* (2016) for the Colombian Amazon; who reported a reduction of 10 % per year for the populations of *I. g. geoffrensis* between 1993 and 2007. This condition in both basins (Amazon and Orinoco) can be explained by the increasing in direct captures of dolphins to be used as bait for the fishery of the mota, simí, piracathinga or come muerto (*Calophysus macropterus*); augment in entanglements; and recently, strandings due to rapid changes in river flow.

Niche modeling and climate change. The Orinoquia is one of the most vulnerable ecoregions to climate change in Colombia. As suggested by the tools of climate action of the Ministry of Environment and Sustainable Development (MADS) of Colombia, and the Integral Regional Plan of Climate Change for the Orinoquia, it is thought that by 2100, temperature in the region will experience an increment between 2.61 °C and 2.7 °C above the average reference value (1976 to 2005), and precipitations will decrease in average a 10 % for the whole Orinoquian savannahs (CIAT *et al.* 2018). The region encloses strategic aquatic ecosystems highly vulnerable and with low resilience such as the humedales de sabana ecosystems that contribute with the hydrologic balance of many basins of Andean origin including the: Arauca, Casanare, y and Meta basins, as well as Orinoquian origin such as the: Bita, Tomo, Tuparro and Vichada basins, part of the Orinoco macrobasin. Within this context, it is necessary to identify those negative effects of climate change on the aquatic ecosystems associated with the ecoregion. River dolphins are natural bio-indicators, widely distributed across the basin, allowing for an exploration of the changes in the climate niche of a large aquatic mammals, responsible of the structure of the vertebrate community in this type of systems. Our results highlight a potential transformation of the ideal conditions that allow for the establishment of the species, explaining its distribution with predicted values between 46.6 % and 70.1 % for the evaluated timeframe. The areas that within our models are going to experience the most drastic changes are associated with the Inirida and Guaviare basins, area of transition between the bioregions of the Amazon and the Guayana.

This results are in agreement with Trujillo *et al.* (2010, 2011, 2016) and Mosquera-Guerra *et al.* (2015, 2018), these authors document the increment in habitat transformation important for river dolphin populations, due to the variability of the hydrologic courses across the Orinoco basin, phenomenon mostly associated with climate change. This situation is evidenced by the increment in the number of stranded of river dolphins between 2015 to 2019 in localities such as Caño Agua Limón, tributary the Arauca River, main channel of the Arauca River (Arauca) and Orinoco (Vichada), in the surroundings of Santa Helena island, in where more than 10 stranding events have been reported in recent years (Figure 4b).

Due to their high seasonality, the Colombian Orinoquia is one of the most vulnerable regions to the negative effects of climate change in the country. The whole region intrinsically depends on water pulses that determine the phenological cycles of plants and animals in particular fish production. Hydrometeorological data in the Orinoquia, have documented strong variations in temperature and hydrologic dynamics, with episodes of both drastic droughts and intense floods. As already mentioned, river dolphins are highly dependent on the stability of the river pulses, and their effect in the maintenance of the different aquatic habitats they use to complete their biological cycle.

a)

b)

Figures 4. **a)** Hunting behavior of two individuals of *I.g. humboldtiana* obtained at the confluences between the Meta-Orinoco and Bita-Orinoco rivers. b**)** Adult female's stranding events of *I. g. humboldtiana* in the Agua Limón spout (Arauca) in the Colombian Orinoquia.

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Richness and activity of arthropodophagous bats in an arid landscape of central México

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The insectivorous bats of arid and semi-arid ecosystems have been poorly studied in México. The aim of this work was to determine the richness and activity of insectivorous bats in arid landscapes of central México over an annual cycle and identify the landscape and environmental features related to relative abundance patterns of bats. We carried out captures with mist nets and active acoustic monitoring in 10 transects, semi-active monitoring in eight stations, and passive monitoring in two desert grassland and scrub sites in Aguascalientes and Jalisco, from January to December 2012. The activity index of each insectivorous species was calculated and related to the local features at the landscape level. An automated monitoring weather station was established in the study area to explore the potential effect of environmental conditions on activity through time. Two species of insectivorous bats were captured: *Myotis melanorhinus* and *M. occultus*; seven additional species belonging to three families were acoustically identified, with *Tadarida brasiliensis* as the most active species. Activity levels were concentrated during the spring (April-June) and from mid-summer to late fall (August-October). The null activity in winter (January-March) and the increased activity of *T. brasiliensis* in the spring suggest migratory movements of the species in the region. The highest values of the activity index were recorded in the proximity of water bodies and ravines. Overall activity was recorded at temperatures between 6.8 and 20.3 °C, and under wind speeds between 1.6 and 24.1 km/h.

Los murciélagos insectívoros de ecosistemas áridos y semiáridos han sido poco estudiados en México. El presente trabajo tuvo como objetivo el determinar la riqueza y actividad de murciélagos insectívoros en un paisaje desértico del centro de México a lo largo de un ciclo anual, así como identificar los elementos del paisaje y factores físicos que están relacionados con los patrones de abundancia relativa de los murciélagos. Se realizaron capturas con redes de niebla y monitoreo acústico activo en 10 transectos, semiactivo en ocho estaciones y pasivo en dos sitios de pastizal y matorral desértico de Aguascalientes y Jalisco, de enero a diciembre de 2012. Se estimó el índice de actividad de cada especie y se relacionó con las características locales del paisaje. Se estableció una estación de monitoreo automatizado en la zona de estudio para identificar si existían condiciones ambientales que afectaran la actividad de forma temporal. Se capturaron dos especies de murciélagos insectívoros, *Myotis melanorhinus* y *M. occultus*, y se identificaron acústicamente siete especies, pertenecientes a tres familias, siendo *Tadarida brasiliensis* la especie con mayor actividad. Los niveles de actividad se concentraron en dos temporadas, una en primavera y otra de mediados del verano hasta finales del otoño. La nula actividad en invierno e incremento de la actividad en primavera de *T. brasiliensis* podría indicar movimientos migratorios de la especie en la región. Los mayores valores del índice de actividad se registraron en los cuerpos de agua y cañadas. La actividad de murciélagos se registró en temperaturas entre los 6.8 °C y 20.3 °C y con velocidades de viento entre 1.6 y 24.1 km/h.

Keywords: activity index; aerial insectivores; landscape features; local features; migratory movements; ultrasonic detector.

Introduction

The arid and semi-arid ecosystems of México are composed primarily of desert shrubland and grasslands that make about 30 % of the remaining plant cover of the country (Comisión para el Conocimiento y Uso de la Biodiversidad 2019). These ecosystems are characterized by shrubs less than four meters high, with columnar cacti and agave as dominant species. These are also characterized by scarce rains that make them vulnerable to desertification, particularly facing the climate change scenario (Challenger and Soberón 2008). In these environments, the structure of plant communities changes significantly at small spatial scales, translating into highly heterogeneous landscapes that provide various resources for many species of mammals (Stapp 2010). As a result, the diversity of mammal assemblages in these ecosystems can be substantial (*i. e.* Elizalde-Arellano *et al.* 2014), including a high richness of insectivorous bats (*i. e.* Rojas-Martínez and Valiente-Banuet 1996).

Studies at the metacommunity level have found that the species within Vespertilionidae, Molossidae, and Phyllostomidae are dominant in arid environments of México (López-González *et al.* 2012). Despite the fact that insectivorous bats are the main guild in arid and semi-arid habitats in México, most studies on bats in these habitats have focused on documenting the interactions of nectarivores and frugivores with various species of agave and cactus plants (*e. g.* Silva-Montellano and Eguiarte 2003; Herrera and López 2017; Fleming and Holland 2018). In contrast, the patterns of diversity, behavior, and habitat use of insectivorous species are poorly known.

The use of ultrasonic detectors combined with net sampling has proved to be a valuable tool to determine the richness of insectivorous species, not only in tropical environments (MacSwiney *et al.* 2008) but also in arid and semi-arid ecosystems (López-González *et al.* 2015). In addition, these devices have made it possible to determine the elements of the landscape or local elements, such as bodies of water, that are key to promoting a higher diversity and as foraging sites in arid environments in northern México (López-González *et al.* 2016). In the present work, we used a combination of sampling techniques to describe the richness and activity patterns of insectivorous bats in a desert landscape of central México over an annual cycle, identifying those environmental factors and landscape elements that are related to the patterns observed.

Materials and Methods

Study area. The study area is located in the physiographic region known as Mesa del Centro, located between the Sierra Madre Occidental, the Sierra Madre Oriental, and the Trans-Mexican Volcanic Belt. The physiographic subprovince where the environmental system is located is called Llanuras de Ojuelos-Aguascalientes. The local climate temperate semi-arid (BS1kw), with a mean annual temperature between 12 and 18 °C and mean annual precipitation of 0.8 to 2.9 mm (García 2004). Two sampling sites were selected in the study area, located at opposite ends of an extensive plain. The first site belongs to the Ejido Palo Alto, in the municipality of Palo Alto, Aguascalientes (21° 56′ 4.4″ N, -101° 51′ 49.1″ W with a mean altitude of 2,397 masl, hereafter referred to as "ejido"). The second is a private ranch called "Las Chinampas", located in the municipality of Ojuelos de Jalisco, Jalisco (21° 53′ 6.9″ N, -101° 50′ 49.2″ W, 2,446 masl, hereafter referred to as "ranch"). The sites were separated by approximately 3.5 km (Figure 1). The study area is dominated by a mosaic of microphyll desert shrubland, rosetophilous desert shrubland, crasicaule shrubland, oak forest, eucalyptus forest, and natural grassland (Rzedowski 2006), with yucca trees (*Yucca* sp.) and cacti species of the genera *Coryphanta* and *Opuntia.* The vegetation cover tends to be more open in higher areas of the plain, while trees predominate in hillsides and ravines. The study sites include three artificial water reservoirs (*presones*) that were built by local ranchers to supply water for cattle, and a natural stream with small ponds.

Monitoring with mist nets. In each site, five mist nets were placed during four nights per month to capture bats along streams, slopes, and bodies of water (Figure 1), consider-

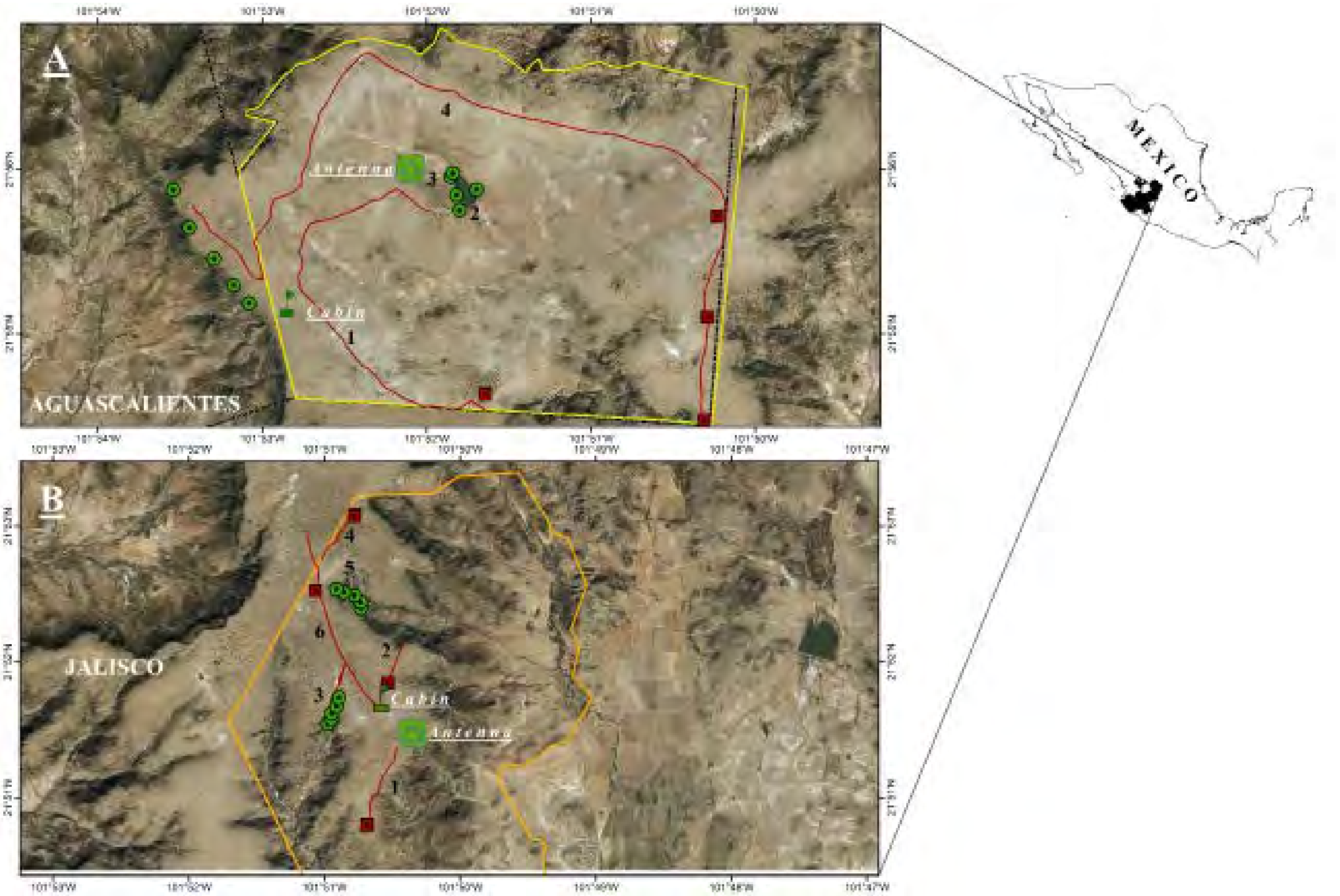

Figure 1. Location of the two study sites in the central region of México. Red lines show the recording routes; green circles mark the location of mist nets; red squares mark fixed recording stations. Numbers correspond to route numbers. The antenna where the fixed detector for passive monitoring was attached is indicated. Yellow polygons denote the limits of premises. A: Ejido Palo Alto; B: Las Chinampas ranch. Black lines: state limits; yellow line: Ejido Palo Alto property; orange line: Las Chinanpas ranch property; green circles: mist nets; red squares: ccoustic monitoring points; red line: routes

ing that these areas may be used as feeding sites or flight routes for many species on their way to or from the plain. Nylon nets were 12 m long, with 38 mm mesh size (Avinet Research Supplies, United States), and were placed considering a minimum separation of 50 m. These nets were kept open during five hours (starting at dusk) and were reviewed at 30-minute intervals. The individuals captured were photographed, weighed, measured, and identified to species according to the criteria described in Medellín *et al.* (2008). The sex and reproductive condition of each individual captured were determined. The individuals captured were released in an open space to record their vocalizations. These recordings were used to supplement our reference acoustic library and identify the pulses stored by ultrasonic detectors. Finally, we searched for bat shelters in crevices and cracks of slopes and ravines, as well as among the vegetation of plains (especially among dry yucca leaves), but did not spot any shelter near the study sites.

Acoustic monitoring. To maximize the spatial and temporal coverage of the sampling, we used hand-held detectors to conduct active and semi-active monitoring, as well as fixed detectors for passive monitoring. The routes of movements (active monitoring) for acoustic sampling were selected seeking to cover the maximum surface area sampled in each site; the only limitation was the use of the existing dirt roads only, aiming to include both plain and ravine areas that harbor oak forest, grasslands with oak trees and yuccas, as well as hillsides, ravines, and water bodies (Figure 1). A total of 10 routes of varying lengths were established across the study area, four in the ejido and six in the ranch (Table 1). Two routes in the ejido (1 and 4) and two in the ranch (4 and 6) were traveled in vehicle at 4 to 6 km/h, while routs 2 and 3 of the ejido, as well as routs 1, 2, 3, and 5 of the ranch, were walked at a similar speed. Each route was traveled once per night for two non-consecutive nights each month, reversing the order and direction of the monitoring every night. In addition, four fixed recording stations were set in each site (fixed points - semi-active monitoring). The use of fixed points as supplements of routes contributes to better determine the spatial and temporal variation in the activity of bats (Stahlschmidt and Brühl 2012). At each fixed point, we recorded five minutes per night for two non-consecutive nights per monitoring month. The monitoring along routs and at fixed points started at dusk with a duration of six to seven hours (from 19:00 to 20:00 to 2:00 to 3:00 h, approximately). We used an EchoMeter three ultrasonic detector (Wildlife Acoustics, Inc., United States) for recording files in real-time and with the full spectrum. We used a sampling rate of 256 kHz, a trigger of 7 kHz, and 24 dB; files had a maximum duration of one minute and were stored using a *.WAV format. The detector was equipped with a Garmin 18x GPS (Garmin, United States), making it possible to record the location where pulses of bat species were recorded.

Table 1. Description of the routes set for the monitoring of bats in the study area. The route length is indicated in parenthesis. Rout Number (RN).

Study premises	RN	Vegetation types	Observations
Ejido Palo Alto	1	Predominantly grassland with isolated shrubs; crosses a small eucalyptus forest	On the plain (4.7 Km)
	2	Dense and low shrubland, dominated by thorny bushes; some areas with bare soil	On the plain; borders part of the largest reservoir (0.33 Km)
	3	Dense and low shrubland, dominated by thorny bushes; some areas with bare soil	On the plain; borders part of the smallest reservoir (0.58 Km)
	4	Predominantly grassland with isolated shrubs; starts and ends in the grassland-oak forest ecotone, and crosses some patches of low thorny shrubland	On the plain; ends at the border of two ravines (11 Km)
Las Chinampas ranch	1	Predominantly open grassland; crosses a small oak forest area	On the plain; crosses a small ravine (1.2 Km)
	2	Predominantly open grassland; it ends in an area with shrubs and oak forest	On the plain; it ends in a ravine (0.6 Km)
	3	Grassland with scattered oaks, prickly-pear cacti, and yucca trees; riparian areas with shrubs, oak trees, and agaves	Along the ravine with two small bodies of water (0.73 Km)
	4	Caespitose grassland with scattered oak trees; ends in an area with shrubs and oak forest	On the plain; it ends in a ravine (1.1 Km)
	5	Shrubland with agaves, prickly-pear cacti, thorny bushes, and isolated oaks	Along a rocky ravine (0.57 Km)
	6	Grassland with isolated oak trees and yuccas	On the plain (2.8 Km)

This was supplemented by passive monitoring, placing a SongMeter Model SM2BAT automated ultrasonic detector equipped with an SMX-US microphone (Wildlife Acoustics, Inc., United States) attached to an antenna placed at each site (Figure 1). A sampling rate of 384 kHz was used, Mono-L channel, which was stored as *.WAC format. These automated detectors were set to record continuously for 10 minutes each hour, from dusk to dawn, during 20 to 25 days/month (depending on the life of batteries). This method was used to identify peaks of activity throughout the year that may indicate migration periods of the various species. All the sounds were recorded in sound cards of high memory capacity (Secure Digital High Capacity-SDHC cards).

Analysis of sounds. The files stored by ultrasonic detectors in *.WAC format (native format) were converted to *.WAV format using the program WAC2WAV 3.3.0. (Wildlife Acoustics, Inc., United States). WAV files were loaded in the program *BatSound* v.4.1 (Pettersson Elektronic AB, Uppsala, Sweden) to visualize and analyze the sounds contained in recordings. We used different parameters of pulses (maximum frequency [FMAX], minimum frequency [FMIN], frequency of maximum energy [FME], duration [DUR], and interval between pulses [IPI]). FMIN and FMAX were calculated by subtracting -10dB from FME (Fenton 2004), while IPI was calculated from the end of a pulse to the beginning of the next, based on the oscillogram.

We estimated the activity index (IA) for each species in each route by adding up the number of 1-min blocks in which a species was detected as "present" (Miller 2001). We defined that a species was "present" when three or more consecutive pulses were clearly visualized in a block. Subsequently, for each route (including the fixed points), each month, and each species, we divided the total number of 1min blocks with sound pulses recorded by the total number of minutes of recording. IA represents a gross estimate of the proportion of time that bats are active, and provides a standardized method to compare the relative abundance of a species through time in either multiple sampling sites or a single site (Miller 2001).

The shape and characteristics of ultrasonic pulses were analyzed with the program BatSound v.4.1, and then were compared with reference pulses obtained from fieldwork, the literature, and the acoustic libraries available. This comparison allowed us to identify the pulses to species level. For comparison purposes, these parameters were calculated in a similar way in the present study.

Environmental parameters. An automated monitoring station was set in the study area to determine the potential relationship of environmental conditions with the activity of the different species. The weather station (Vantage Pro2 Windows USB WeatherLink, Davis Instruments, United States) was set at approximately 3 m high on a ranch antenna. The weather station continuously recorded and stored the following data: wind speed and direction, ambient temperature and humidity, and precipitation. These variables were related only to the activity recorded in the passive monitoring station close to the weather station.

Results

Species richness through capture and acoustic monitoring. During the period between January and December 2012, only two bat individuals were captured in nets: one male of *Myotis melanorhinus* (Vespertilionidae) captured in March on the shore of the largest body of water (on the plain, rout 2 of the ejido), and one male of *M. occultus* (Vespertilionidae) captured in September on the shore of the body of water located in the ranch (near a small ravine, on rout 3). The acoustic analysis led to the identification of six species and a sound type assigned to *M. occultus/M. californicus*, belonging to three families: Mormoopidae, Molossidae, and Vespertilionidae (Table 2).

Activity related to landscape features and environmental parameters. The average (annual) activity index within the routes monitored for all species combined was 0.007, indicating that bat vocalizations were recorded in less than 1 % of the total recording time. The activity levels of the different species of insectivorous bats were concentrated in two seasons: the first, clearly defined in spring (April to May); the second, longer, from mid-summer to late fall (August-December; Figure 2). The fixed detectors used for passive monitoring recorded activity only in March, April, and May, where 85 % of the recorded sounds (*n* = 28 pulses) corresponded to *T. brasiliensis,* while 15 % were produced by *M. melanorhinus* and *M. velifer*.

Table 2. Average values of the characteristics of search phase pulses recorded during the annual period in the Palo Alto region, Aguascalientes and Jalisco. FME: Frequency of Maximum Energy. FMIN: Minimum Frequency. FMAX: Maximum Frequency. DUR: Duration. IP: Interval between pulses. FMIN and FMAX were calculated by subtracting -10dB from FME (Fenton 2004). Values are the mean ± standard deviation. NS: Number of sequences. Five pulses were measured in each sequence.

Identification	FME (kHz)	FMIN (kHz)	FMAX (kHz)	DUR (ms)	IP (ms)	NS
Mormoops megalophylla	52.7 ± 1.2	51.2 ± 2.0	53.6 ± 1.7	9.4 ± 1.6	151.2 ± 60.3	4
Nyctinomops macrotis	14.6 ± 2.1	13.6 ± 1.7	19.9 ± 1.3	13.0 ±0.9	332.1 ± 22.1	4
Tadarida brasiliensis	23.9 ± 3.2	23.1 ± 1.4	26.2 ± 1.5	9.4 ± 2.0	234.0 ± 23.1	48
Eptesicus fuscus	32.1 ± 4.9	29.0 ± 1.8	41.0 ± 1.9	6.4 ± 2.2	103.2 ± 7.8	10
Myotis melanorhinus	51.9 ± 4.3	50.7 ± 2.1	59.3 ± 2.5	6.0 ± 3.3	142.0 ± 12.4	26
Myotis occultus/ californicus	44.8 ± 0.3	41.7 ± 0.8	54.2 ± 1.3	5.5 ± 2.0	88.8 ± 9.5	22
Myotis velifer	39.5 ± 4.5	37.6 ± 3.3	42.1 ± 2.5	3.6 ± 1.3	141.0 ± 11.8	5

The results of the acoustic monitoring indicate that the highest activity of insectivorous bats concentrated in areas with bodies of water (rout 2 of the ejido and rout 3 from the ranch). In these routes, activity of bats was detected 16 % of the total recorded time for the large pond of the ejido (rout 2), and 13 % of the time for the ravine with water bodies in the ranch (rout 3; Figures 3A, 3B, 4A and 4B; Table 1). The concentration of activity in routes with water bodies was more evident for the vespertilionid species of the genus *Myotis,* while the activity of the molossid *Tadarida brasiliensis* was more homogeneous in all routes (Figures 3A, 3B, 4A and 4B).

The temperature in study sites ranged from 1.7 up to 26.1 °C during the recording periods (19:00 to 3:00 h) throughout the year; the activity of bats was never recorded either below 6.8 °C or above 20.3 °C. On the other hand, while wind speed in the area ranged between 0 and 38 km/h throughout the year, the activity of bats occurred between 1.6 and 24.1 km/h. The species of the genus *Myotis* recorded activity between 9.8 and 16.7 °C, when wind speed ranged between 11.2 and 15.3 km/h. *T. brasiliensis* was active in the region when the temperature ranged between 6.8 and 20.3 °C, at wind speeds ranging between 11.6 and 20.9 km/h.

Discussion

Species richness through capture and acoustic monitoring. The present study represents one of the first efforts to describe the activity patterns of insectivorous bats in arid landscapes dominated by open grassland and shrubland. The low capture rate of individuals in mist nets may reflect the low local abundance of bats, as reported in other temperate ecosystems dominated by pastures (*i. e.*, Holloway and Barclay 2000). On the other hand, it is well known that many insectivorous species tend to be successful at evading mist nets (MacSwiney *et al.* 2009), which might have reduced the probability of capture. In addition, the study area, particularly the plain, is constantly exposed to low temperatures and high wind speeds (up to 38 km/h or 10.5 m/s), which may inhibit the activity of both bats and their prey, which typically are more active in habitats with wind speeds below 6 m/s or 21.6 km/h (Arnett *et al.* 2011; Welig *et al.* 2018).

The present study recorded only seven species of insectivorous bats through acoustic detection techniques. However, other species of the genera *Myotis* (*e. g.*, *M. volans, M. auriculus*) *Lasiurus* (*L. blossevillii*) and *Aeorestes* (*A. cinereus*) probably occur in the study area as well, because Palo Alto is located within their distribution range and the characteristics of the habitat are consistent with those used by most of these species (Álvarez-Castañeda *et al.* 2008).

It is also feasible that species of other guilds use this area as a transit or foraging sites. The species potentially present include the nectarivorous bats *Choeronycteris mexicana*, *Leptonycteris nivalis,* and *L. yerbabuenae*, which probably use the low areas of the plain that host a greater amount of flower resources (Valiente-Banuet *et al.* 1996). These species are hardly recorded in an acoustic sampling, since their echolocation sounds are short, multi-harmonic, of modulated frequency (FM), and produced at a very short distance from their target (González-Terrazas *et al.* 2016).

Spatial variation of insectivorous species. The artificial water bodies located in study sites were built by local ranchers to supply water for livestock. In northern México and other arid areas of the world, these artificial water reservoirs are key landscape elements for insectivorous bats, particularly in the dry season (López-González *et al.* 2015, 2016; Razgour *et al.* 2018). A similar pattern was observed in this study, with higher activity indices in the three bodies of water of the plain. In addition to the bodies of water, the recordings at fixed points indicated that open areas near the border of a zone of ravines ranked second in terms of the activity of insectivorous bats. These results are consistent with those reported for other open landscapes of North America, where natural water bodies and ravines are the sites showing the greatest activity (*i. e.,* Holloway and Barclay 2000).

The species of the genus *Myotis* (family Vespertilionidae), characterized by its slow flight at a low height, are the species that showed the highest use of areas near water bodies in both the ejido and the ranch. The only two captures in the net (*M. melanorhinus* and *M. occultus*) occurred around water bodies. The preference of *Myotis* spp. for streams and water bodies can be due to several factors. In the first place, in arid areas, water bodies and the associated riparian vegetation display a greater abundance of insects (Hagen and Sabo 2012; Korine *et al.* 2016). In addition, the large amount of feces excreted by livestock visiting these sites for drinking water promotes a higher volume of organic matter that boosts the abundance of insects (López-González *et al.* 2015). Besides, these sites are attractive for bats to drink water (Adams and Thibault 2006). The species of *Myotis* were also active in ravines, areas that offer higher availability of shelters in trees and rocky walls (Holloway and Barclay 2000; Everette *et al.* 2001). The species of the genus *Myotis* usually have short and broad wings that confer limited maneuverability in open areas, thus avoiding to fly in these areas (for example, grasslands) and instead use mostly linear elements (roads, rocky walls, rows of trees or shrubs, etc.) and streams as flight routes (Limpens and

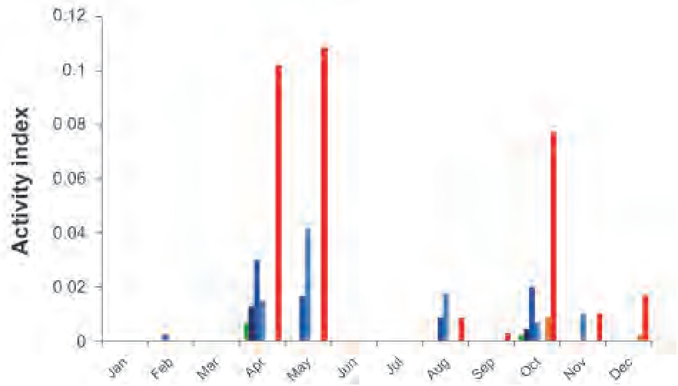

Figure 2. Levels of monthly activity of insectivorous bats recorded along routes in the study area. Green = *Mormoops megalophylla*, Dark blue = *Eptesicus fuscus*, Medium blue = *Myotis melanorhinus*, Light blue = *Myotis occultus/Myotis californicus*, Orange = *Nyctinomops macrotis*, and Red = *Tadarida brasiliensis*.

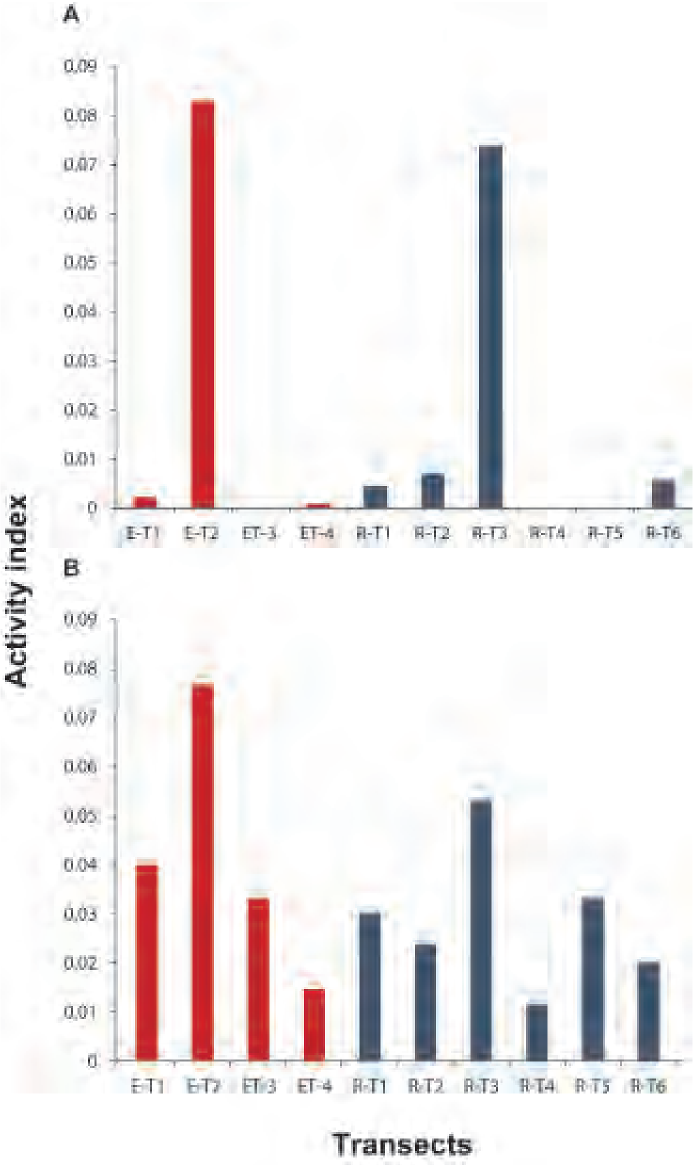

Figure 3. Activity levels of A: *Myotis* spp., and B: *Tadarida brasiliensis* in the routes of ejido (red) and ranch (blue), recorded during January-December 2012. E = Ejido, R = Ranch, T = route or transect; the number indicates route number, either in the ejido or in the ranch.

Kapteyn 1991). It has been speculated that these species may benefit from the linear elements because of the availability of topographic features for spatial orientation (they produce pulses of relatively high frequencies, resulting in a relatively low sonar range), and because these lower the risk of predation and provide protection against strong winds (Limpens and Kapteyn 1991).

The big free-tailed bat, *Nyctinomops macrotis* (family Molossidae), was active mainly in the largest body of water of the ejido and in ravine areas in both sites. It is highly likely that the low number of records of *N. macrotis* derives from its high flight (frequently close to 200 m; Griffin and Thompson 1982), which would suggest that this species does not perceive the different components of the landscape at ground level (Ávila-Flores and Fenton 2005). At various points located in the study area but outside routes, audible vocalizations were occasionally attributable to this species (R. Ávila, *pers. obs.*), suggesting that this species uses the landscape in a relatively homogeneous manner. *N. macrotis* could be identified based on the recordings typical of the species that at the same time were related to sounds that are audible to humans, as observed in other regions inhabited by this species (Mora and Torres 2008). An accurate record of its audible vocalizations was not conducted because not all the field team members were trained to identify this species.

The molossid bat *Tadarida brasiliensis*, another high-flight bat, was the most abundant species in the study area. Like *N. macrotis*, its high flight may make this species perceive the landscape in a more homogenous way (Ávila-Flores and Fenton 2005), but it nonetheless used areas near bodies of water more frequently (Figure 3). As is the case of *Myotis* spp., these areas may provide a higher abundance of food, as well as protection against strong winds, given these were located in small ravines and gullies. The detection of an abundant number of pulses in fixed detectors and fixed evidence that this species is capable of using open habitats nearly as often as ravines and areas of woody vegetation.

The limited information obtained for *Mormoops megalophylla, Eptesicus fuscus*, and *M.velifer* preclude an adequate description of its habitat-use patterns. *Mormoops megalophylla* was detected in a body of water (ejido), in ravines (ranch), and open areas near ravines (Figure 4B). Apparently, this species uses the various habitats in the study area in a relatively similar way. For its part, *E. fuscus,* considered a generalist species that occurs commonly in arid habitats of central México (Kurta and Baker 1990), was recorded

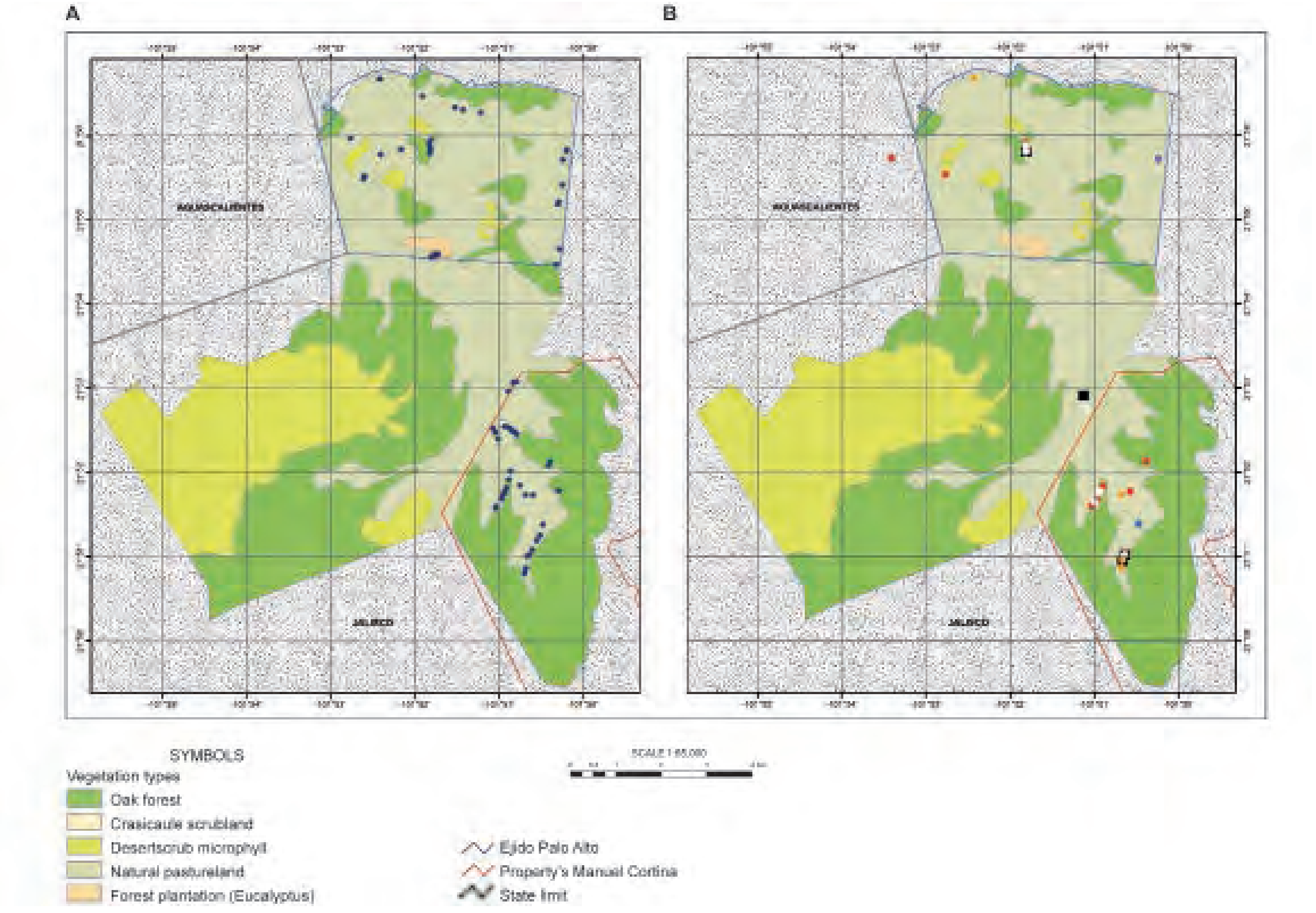

Figure 4. Recording sites by acoustic monitoring of species of insectivorous bats in the study area. A: records of molossid bats, where white squares = *Nyctinomops macrotis*; Blue points = *Tadarida brasiliensis*. B: records of mormopid and vespertilionid bats, where black squares = *Mormoops megalophylla*; orange points = *Eptesicus fuscus*; red points = *Myotis melanorhinus*; white points = *Myotis occults*; blue points = *Myotis velifer.*

mainly in ravines and adjacent open areas, while *M. velifer* was detected in a few occasions in the fixed detector placed in the ejido (*i. e.*, in open areas) in April. Specimens of this species have been observed found in the study area resting on beams of the ex-hacienda Palo Alto in August (Álvarez-Castañeda *et al.* 2008), but the colony apparently consisted of a few individuals. The low abundance previously observed in the area could explain the few records of activity of this species in our study sites.

Temporal variation of insectivorous species. The species of the family Molossidae (*N. macrotis* and *T. brasiliensis*) were recorded in the Palo Alto region most of the year. Although *N. macrotis* was recorded a few times in the recordings, its presence was identified in several months of monitoring without the assistance of ultrasonic detectors. *T. brasiliensis* was detected in seven of the 12 monthly sampling events, with noticeable absences during the winter (January-March) and part of the summer (June-July), and with two peaks of activity in spring and autumn (Figure 2). In April, May, and October, the activity of this species was significantly relative to the other months, making it possible to record sounds during 8 to10 % of the recording time. The absence of records of *T. brasiliensis* in June and July is worth mentioning, since this period of time coincides with the onset of rains, the reproduction of the species, and a high abundance of insects (López-Vidal *et al.* 2008). These observations suggest that the increased activity of *T. brasiliensis* detected in spring may reflect the migratory movements of the species; this is difficult to confirm because its migratory routes in México are not known in detail yet.

The members of the family Vespertilionidae (*E. fuscus*, *M. melanorhinus*, *M. occultus,* and *M. velifer*) are active during a large part of the year in the Palo Alto region but virtually disappear between November and March. In México, it has been reported that these species usually make short altitudinal migrations to reach their hibernation sites (Villa 1967). The virtual absence during the coldest months seems to support this hypothesis, although it is unlikely that these populations hibernate in the Palo Alto region, considering that they tend to move toward higher sites in search of shelters that are sufficiently cold. The search for shelters and the interviews with local inhabitants did not provide evidence about hibernation shelters in the region. The individuals of the genus *Myotis* found in Palo Alto likely hibernate in the closest mountainous area, located some 80 to 90 km to the northeast (limits between Aguascalientes and Jalisco), reaching altitudes close to 3,000 masl. Until now, the few known hibernation shelters for *M. velifer* in México are occupied from September-October to February-March (*e. g.* Ávila-Flores and Medellín 2004; Ayala-Berdon and Solís-Cárdenas 2017).

Nocturnal activity and environmental parameters. The characteristics of our sampling design and the scarcity of data preclude a robust analysis of daily activity patterns of the different species of bats. However, the combination of the data for all sampling events allows us to get an overall picture of the patterns of activity for the most common species in the area. In the case of the species of the genus *Myotis*, which tend to be more active shortly after dusk elsewhere (Hayes 1997), no peak of activity was detected between 20:00 and 3:00 h. In contrast, *T. brasiliensis*, a species that can travel across more than 50 km in a single night (Best *et al.* 2003), seems to display a peak of activity between 21:30 and 22:00 h. This pattern is similar to the one reported by Ávila-Flores *et al.* (2005) for *T. brasiliensis* in México City, with a peak of activity two hours after dusk.

The low activity of bats recorded in the Palo Alto region restrained the statistical analysis of the effect of the local climatic conditions. However, the available information documents that in the area no activity of bats occurs at temperatures either below 6.8 °C or above 20.3 °C. In addition, the activity of bats occurred at wind speeds of 1.6 and 24.1 km/h. The data obtained is insufficient to know whether *Myotis* spp. and *T. brasiliensis* are active at wind speeds above 24.1 km/h, but we can affirm that the peak activity of these species occurs when the wind flows below this speed. This is consistent with observations for North American insectivorous species that display peak activity when wind speed is below 6 m/s or 21.6 km/h (Arnett *et al.* 2011).

The present work represents one of the first efforts to determine the richness and activity of insectivorous bats in arid environments with desert shrubland. The low species richness and low activity levels recorded result from the environmental conditions that prevail in the plain, characterized by strong gusts of wind and low temperatures. In this area, similar to other arid areas, artificial water bodies ("presones") are an important element that promotes the activity and foraging of insectivorous bats (López-González *et al.* 2015). Maintaining these water elements is essential, particularly in the dry season, as our results show that it is in this season that insectivorous bats are most active, with the likely migratory movement of *T. brasiliensis*.

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The large jaguar that lived in the past of México: a forgotten fossil

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In the 1970's, Oswald Mooser delivered to the Instituto de Geología, Universidad Nacional Autónoma de México, a fossil jaw recovered from the Chapala region, Jalisco, that he identified as *Panthera onca*. The collection label indicates doubts about this taxonomic assignment; an issue that remains unsolved. The aim of this work is to study the taxonomy and biogeographic implications of this material. With this aim, morphological and morphometric comparisons were made using fossil and current feline specimens. Additionally, a review of the fossil record of *P. onca* in Mexico was carried out using the material deposited in collections and reported in the literature. Our results indicate that the jaw from Jalisco belongs to a large Pleistocene form of jaguar historically called *P. onca augusta*. With the present record, there is a total of 10 paleontological localities in México where fossil jaguar records have been reported. Curiously, only one of these locations matches with the current distribution of this feline in North America, the San Josecito Cave in Nuevo León. With this information, there is evidence to confirm that the range distribution of the jaguar has been reduced significantly since the Pleistocene to the present.

En los 70, Oswald Mooser entregó al Instituto de Geología, Universidad Nacional Autónoma de México, una mandíbula fósil recuperada de la región de Chapala, Jalisco, que identificó como *Panthera onca*. La ficha de colección señala dudas sobre esta asignación taxonómica, un tema que no se ha resuelto. El objetivo de este trabajo fue estudiar la taxonomía y las implicaciones biogeográficas de este material. Para esto, se realizaron comparaciones morfológicas y morfométricas utilizando especímenes de felinos fósiles y actuales. Adicionalmente, se realizó una revisión del registro fósil de *P. onca* en México utilizando el material depositado en colecciones y reportado en la literatura. Nuestros resultados indican que la mandíbula de Jalisco pertenece a una forma grande de jaguar del Pleistoceno que históricamente ha sido llamado *P. onca augusta*. Con este registro, hay un total de 10 localidades paleontológicas en México donde se han reportado jaguares fósiles. Curiosamente, solo uno de estos lugares coincide con la distribución actual de este felino en América del Norte, la Cueva de San Josecito en Nuevo León. Con esta información, hay evidencia para confirmar que el rango de distribución del jaguar se ha reducido significativamente desde el Pleistoceno hasta el presente.

Key words: distribution; felid; San Josecito Cave; Chapala; *Panthera onca augusta*.

Introduction

Jaguar is the common name of the big New-World felid *Panthera onca* (Linnaeus 1758). This species is the only American extant species of the pantherine lineage (Seymour 1989; Barnett *et al.* 2016). The jaguar is characterized by its similar appearance with the African leopard, *P. pardus*; both have spots and rosettes on their skin, but the jaguar is slender, and its teeth are smaller (Seymour 1989). phylogenetically, *P. onca* is more related to the leopard *P. pardus*, the lion *P. leo*, the extinct lion cave *P. spelaea*, and the American lion *P. atrox*, than to the snow leopard *P. uncia*, the tiger *P. tigris*, the extinct *P. palaeosinensis*, and *P. blytheae* (Johnson *et al.* 2006; Mazák *et al.* 2011; Tseng *et al.* 2014). Nevertheless, the origin of the jaguar is not yet clear. Some authors have indicated that there were forms that lived in Eurasia and part of Africa during most of the Pleistocene, under two subspecies: *P. onca gombaszoegensis* and *P. onca georgica* (Shultz *et al.* 1985; Hemmer and Kahle 2005; Hemmer *et al.* 2001; 2003; 2010); but other authors differed from this taxonomic scenario, and considered the Eurasian jaguar-like animal as a different species, *P. gombaszoegensis* (Arroyo-Cabrales 2002; O'Regan 2002; Marciszak 2014; Stimpson *et al.* 2015).

The oldest fossil record of *P. onca* in North America comes from the Middle Pleistocene of northern United States (Shultz *et al.* 1985; Seymour 1989), and the species became abundant during the Late Pleistocene (Kurtén 1973). Some authors argued that it was probably present in the continent since the Late Pliocene or Early Pleistocene times (Johnson *et al.* 2006).

The distribution of this species in the past ranged from Washington, United States, to Chilean Tierra del Fuego (Seymour 1989; Soibelzon and Prevosti 2013; Arias-Alzate *et al.* 2017; Prevosti and Forasiepi 2018). Nowadays, its distribution is restricted from northern México to northern Argentina, but it should be noted that this distribution is constituted mostly patchy (Seymour 1989; de la Torre *et al.* 2017; Quigley *et al.* 2017; Arias-Alzate *et al.* 2017; Jędrzejewski *et al.* 2018). Curiously, laying México in the northern part of the current species distribution, the fossil record in this country is poorly represented (Arroyo-Cabrales 2002), unlike in United States (Kurtén 1973).

In order to contribute to the knowledge of the evolutionary history of the jaguar in North America and specifically in México, this study focuses on a fossil right jaw of a this feline (Figure 1) from San Luis Soyatlán, a town sitting in the southern border of the Chapala Lake, in the State of Jalisco. This specimen was donated to the Museum of the Instituto de Geología, Universidad Nacional Autónoma de México, by Osvaldo Mooser (swiss dentist and amateur paleontologist) in 1977 (Figure 2), but was never studied thoroughly and officially entered the IGM Paleontological Collection. Despite its fragmentary nature, its study provides relevant evolutionary and taxonomic information. Additionally, to the study of this material, a review of the fossil record of *P. onca* for México is presented with the biogeographic and ecological implications.

Figure 1. Buccal (left) and lingual (right) views of the specimen of *Panthera onca* IGM 9518.

Materials and Methods

The fossil material (IGM 9518) is housed at the Colección Nacional de Paleontología, Museo Ma. Del Carmen Perrilliat (IGM), at the Instituto de Geología, Universidad Nacional Autónoma de México (UNAM) in México City, México.

Comparison. Specimen IGM 9518 was compared with material of *Leopardus* spp.: from the Museo Estación Biológica de Rancho Grande, Venezuela: EBRG 563, 589, 1183, 1374, 1493, 1617, 3017, 2214, 3159, 9609, 805, 1618, 1904, 3200, 17585; *Panthera leo*: from the Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Mastozoología, Argentina: MACN-Ma 23.1; Argentinean *P. onca*: frm the Museo de La Plata, Argentina: MLP 10-9, and from MACN 26.217; Venezuelan *P. onca*: EBRG 3196 (female), 20224 (female), 20238 (male), 21702 (female), 21703 (male), 22467; *Puma concolor*: EBRG 128, 275, 1418, 1705, 1902, 2304, 17059, 20787, 22400.

Also, some comparison data were obtained from bibliographic sources, as Carbot-Chanona and Gómez-Pérez (2014), Hemmer *et al.* (2001; 2010), Kurtén (1973), Merriam and Stock (1932), Montellano-Ballesteros and Carbot-Chanona (2009), Simpson (1941), and Rufolo (1998).

Size was evaluated by a scattered plot using the mesiodistal length and buccal-lingual width of the lower canine. Measurements were taken with an analog caliper (± 0.1 mm, max. 150 mm) and are given in millimeters (mm). Dental abbreviations are as follows: lower canine, c1; third lower premolars, p3; fourth lower premolar, p4; and first lower molar, m1.

Results

Order Carnivora Bowdich 1821

Family Felidae Fischer de Waldheim 1817

Subfamily Pantherinae Pocock 1917

Genus *Panthera* Oken 1816

Panthera onca (Linnaeus 1758)

Panthera onca augusta (Leidy 1872) (Figure 1)

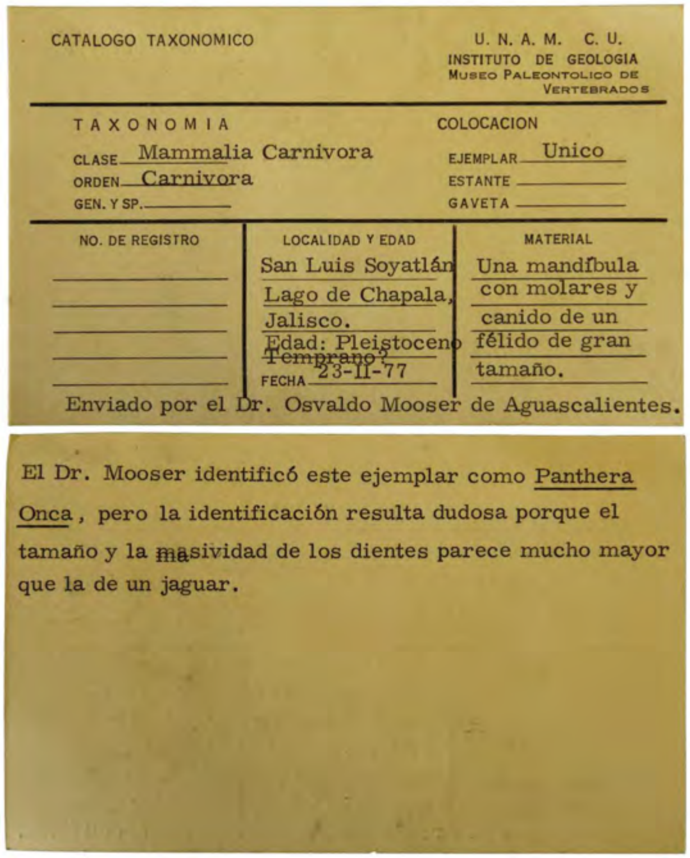
Referred material. IGM 9518 is an incomplete right jaw (Figure 1), with preserved c1, but with broken crown, p3, p4, and m1.

Measurements. c1 length and width: 19.2 mm, 16.8 mm; p3 length and width: 15.1 mm, 7.5 mm; p4 length and width: 20.0 mm, 10.2 mm; m1 length and width: 21.1 mm, 10.9 mm. Length dental system (p3-m1): 56.3 mm. Height of the mandibular ramus at the level of p3: 33.8 mm. Height of the mandibular ramus at the level of m1: 31.2 mm.

Locality. IGM 9518 comes from the vicinity of San Luis Soyatlán, Arandas Municipality, Jalisco State (IGMloc 1442). San Luis Soyatlán is located on the southwestern border of the Chapala Lake. Although the exact point of origin of IGM 9518 is unknown, Lucas (2008) mentions for San Luis

Soyatlán the presence of Quaternary deposits outcrops. The museum label (Figure 2) indicates that this fossil comes from the Early Pleistocene, however this has not been confirmed yet. If it were true, this would be one of the oldest known jaguars in the America continent.

Description and comparison. The specimen represents a large feline (Figure 3). Because c1 is conical and robust it belongs to the pantherine group, unlike the machairodontines where this tooth is more acute and slightly compressed. Also, c1 is larger than those of specimens of in *Puma* and living jaguars; its size matches with Pleistocene jaguars (*P. onca augusta* and *P. onca georgica*), but it is not as big as in *P. atrox* (Figure 3). Lateral sides of the crown are smooth, while in *P. atrox*, *P. spelaea*, and *P. leo* a crest running along the crown is usually appreciated (see "Discussion" for further explanation). The p3 and p4 have three cusps, where the central cusp (*i. e.*, protoconid) is the largest. A well differentiated posterior cingulum is also present in these teeth. This morphology is also observed in other species of the genus *Panthera* and *Puma*; although in *P. atrox* the p4 cingulum is more differentiated. The m1 is robust as in other species of *Panthera* and *Puma*, and less blade-lake than in machairodontines. The diastema between c1 and p3 is less broad than in *P. leo* and *P. atrox*.



CATALOGO TAXONOMICO

U. N. A. M. C. U.
INSTITUTO DE GEOLOGIA
MUSEO PALEONTOLICO DE
VERTEBRADOS

TAXONOMIA
CLASE Mammalia Carnivora
ORDEN Carnivora
GEN. Y SP.

COLOCACION
EJEMPLAR Unico
ESTANTE
GAVETA

NO. DE REGISTRO	LOCALIDAD Y EDAD	MATERIAL
	San Luis Soyatlán	Una mandíbula
	Lago de Chapala,	con molares y
	Jalisco.	canido de un
	Edad: Pleistoceno	félido de gran
	Temprano?	tamaño.
	FECHA 23-II-77	

Enviado por el Dr. Osvaldo Mooser de Aguascalientes.

El Dr. Mooser identificó este ejemplar como Panthera Onca, pero la identificación resulta dudosa porque el tamaño y la masividad de los dientes parece mucho mayor que la de un jaguar.

Figure 2. Museum label from 1977, with collecting information of the fossil jaguar (IGM 9518) from San Luis Soyatlán, Jalisco (México). This label shows the doubts of O. Mooser identification: "Dr. Mooser identified this specimen as "Panthera Onca", but the identification is doubtful because the size and massiveness of the teeth seems much greater than that of jaguar" (author's translation).

Discussion

Taxonomic notes. In the Figure 3 it can be noticed that IGM 9518 is a large felid. In the American continent big felids are represented by pantherines, cougars, and the extinct long-teeth machairodontines (Turner 1997). IGM 9518 differs from machairodontines by its rounded canine and premolars. Also, is larger than any *Puma concolor* analyzed. Although the Soyatlán jaw is not complete, it can be certain that it belongs to *Panthera* because its size and dental morphology.

In North America, three species of *Panthera* have been reported: the extinct cave lion *P. spelaea*, the American lion *P. atrox*, and the still present jaguar *P. onca* (Seymour 1989; Barnett *et al.* 2016). Recently, a new pantherine species, called *P. balamoides*, was reported for the Pleistocene of a Quintana Roo cenote in México (Stinnesbeck *et al.* 1918), but in our opinion its morphology remember that of ursids, not that of a pantherine; for this reason we do not consider it in our study.

The morphology of IGM 9518 is relatively similar to that of American pantherines species, except for the absence of a crest in the lower canine. Nelson and Goldman (1933) indicate that *P. onca* typically lacks a longitudinal ridge (or groove) in the canines. However, we observe that in the lower canines of some South American members this ridge is present (*e. g.* MLP 10-9 and MACN 26.217 from Argentina). But, this crest is always present in all the *P. atrox* and *P. spelaea* observed. So, the absence of this crest allows us to refer IGM 9518 to *P. onca* and not *P. atrox* neither *P. spelaea*.

In 1977, O. Mooser reached the same taxonomical conclusion, however, in the museum's label it can be read that there is a doubt about this assignation; "…the identification is doubtful because the size and massiveness of the teeth seems much greater than that of a jaguar" (Figure 2). Our morphometric analyses corroborate this observation; this specimen does not match in size with any living jaguar, male and female even (see Figure 3). Curiously, this condition was previously observed in other Pleistocene jaguars. Simpson (1941) considered that Pleistocene forms from North America were morphologically similar to the living ones but different in size. Simpson (1941) assigned the fossil specimens to the subspecies *P. onca augusta* (Leidy, 1872), which is 15 to 20 % larger than the living forms (Kurtén 1973; Seymour 1989). Although the subspecies concept is debatable (Wilson and Brown 1953), the usage of subspecific taxa is useful to describe the historical change in size of the *P. onca*. Seymour (1993) shown that in North America, the living and fossil members of *P. onca* differ in size cranially and postcranially. Also, the material from San Luis Soyatlán is not the only Mexican material that presents a large size. This condition is also present in specimens from San Josecito Cave in Nuevo León, as can be seen in Figure 3.

Past and present range distribution in México. México has few reports of fossil jaguar. Torres (1995), Arroyo-Cabrales (2002), Arroyo-Cabrales (2002), Morales-Mejía *et al.* (2009), and Ferrusquía-Villafranca *et al.* (2010), listed nine localities; the record here presented adds one additional locality, totaling 10 localities (Table 1; Figure 4). However, not all of these reports have been confirmed as corresponding to *Panthera onca*. The localities with confirmed material are five: 1) El Cedazo (Aguascalientes), 2) Loltún Grottoes (Yucatán), 3) Mina de San Antonio (San Luis Potosí), 4) San Josecito Cave (Nuevo León), and 5) Soyatlán/Chapala region (Jalisco).

Today, the Mexican jaguar is almost restricted to environments with closed vegetation in the Sierra Madre Occidental-Sierra Madre Sur, Sierra Madre Oriental, Sierra de Tamaulipas, and the Southern part of the country including the Yucatan Peninsula (Ceballos 2014; de la Torre *et al.* 2017; Quigley *et al.* 2017; Figure 4). It is important to highlight that only one fossil locality, San Josecito Cave, lies within the current range of the jaguar (see Figure 4). In other words, the only place known in North America where the jaguar has remained since the Pleistocene time is in the Sierra Madre Oriental of Nuevo León, México. Certainly, there are localities that do not match with the range distribution of the living jaguar reported by de la Torre *et al.* (2017) and Quigley *et al.* (2017), but they are in areas with a large probability of occurrence of this pantherine (*sensu* Jędrzejewski *et al.* 2018) like El Golfo and Rancho La Brisca (Sonora), Cuatro Ciénagas (Coahuila), Mina de San Antonio (San Luis Potosí), and Loltún Grottoes (Yucatán). Despite this, there are four fossil Mexican localities with low probability of occurrence of living jaguars: Brechas Coloradas (San Luis Potosí), Arroyo Cedazo (Aguascalientes), and Zacoalco and Soyatlán (Jalisco; Figure 4).

The reduction in the geographic distribution of jaguar has been previously mentioned. Seymour (1989) and Arias-Alzate *et al.* (2017) shown that during the Middle Pleistocene the range of *P. onca* extended to Canada. Then, during the Late Pleistocene this range was reduced to the United States, probably at the latitude of Virginia and Northern California. Historical data indicates that by the decade of 1950's the jaguar extended to California, Arizona, Nuevo México, and Southeastern Texas, with an already absence in the Mexican Central Plateau (Hall 1959). Quigley *et al.* (2017) showed that for 2008 the North American distribution was already restricted only to México, and that from 2008 to 2015 a 20 % of declination in the jaguar range. Jędrzejewski *et al.* (2018) mention that historically the jaguar had a range that covered *ca.* 1660 thousand km^2; currently, this range is of *ca.* 339 thousand km^2. Variation in the distribution and structure of populations have been attributed to climatic changes occurred during the Pleistocene-Holocene (Barnosky *et al.* 2003; Koch and Barnosky 2006; Arroyo-Cabrales *et al.* 2007; Barnosky 2008; Ceballos 2014; Arias-Alzate *et al.* 2017). Kurtén and Anderson (1980) and Arias-Alzate *et al.* (2017) pointed out that the reduction in the range distribution of the jaguar was the product of the influence of glacial and interglacial shifts. In addition, given that the range reduction continues nowadays, it is necessary to consider and discuss other variables, in particular anthropogenic pressure and emerging diseases.

In general, the diversity of the American Quaternary carnivores was deeply affected, where some became completely extinct (*e. g.* hyenas, long-teeth felines, American

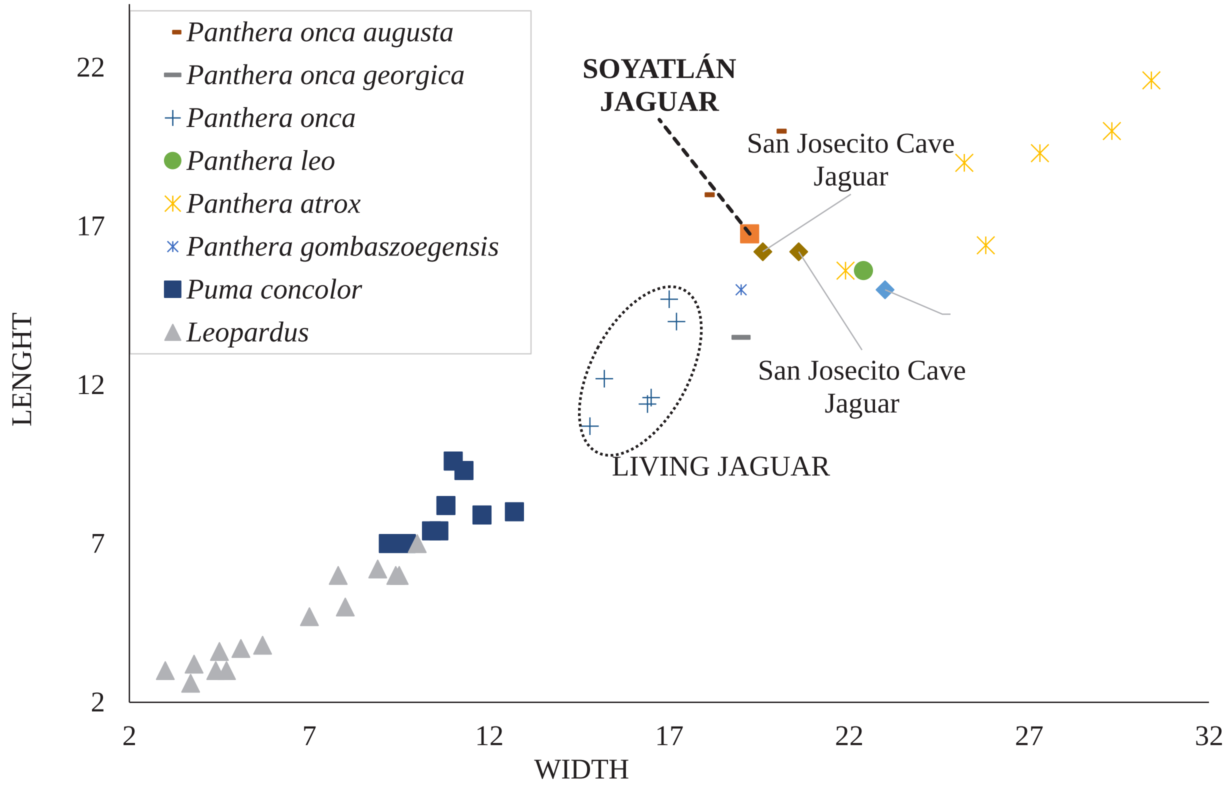


Figure 3. Size relationship (in mm) of the lower canine (c1) of specimen IGM 9518 with respect to other felids. Abbreviations: S. L., San Josecito cave.

lion, and Dire wolf), others modified their distribution (*i. e.,* local extinction), and few went through phenotypic changes (Koch and Barnosky 2006; Ceballos *et al.* 2010). In the case of the jaguar, there are evidences of the last two situations: 1) changes in its distribution (Figure 2; 4) changes in its phenotype (they became smaller).

The fossil record of jaguar in the central part of México is evidence that the conditions in the past were favorable for its presence there. The extant jaguar mainly lives in tropical rainforests, sub-deciduous and deciduous forests, and mangroves, and less frequently in conifer or oak forests, and xeric environments (Seymour 1989; Linares 1998; Ceballos 2014). Likely, the localities were fossil jaguars have been recorded during Pliocene-Pleistocene times were areas of close vegetation and environments that favored hunting opportunities (Stinnesbeck *et al.* 1982; Ceballos *et al.* 2010). For example, Arroyo El Cedazo, Aguascalientes, central México, currently has a vegetation associated with deserts and high human presence, but during the Rancholabrean time, it was an extensive grasslands or prairie capable of supporting herds of large grazing mammals, where gallery forests probably existed nearby (Mooser and Dalquest 1975). These habitat types are described as suitable hunting area for the jaguar (Crawshaw and Quigley 2002). Another possibility, compatible with the previous one, is that the potential jaguar prey migrated to the tropical areas where jaguar habits today in México, and that caused the current distribution of this feline, as happened with other carnivores (Ripple *et al.* 2014).

Curiously, many large mammals became extinct around the World during the Quaternary extinction (Koch and Barnosky 2006; Barnosky 2008; Arias-Alzate *et al.* 2017), and México was not an exception. Proboscidean (Gomphotheriidae and Mammutidae), xenathran (Glyptodontidae, Megatheriidae, and Mylodontidae), felids (machairodontines and American lion), and canids (Dire wolf), are completely extinct, while Pleistocene camels (Camelidae), and horses (Equidae) became locally extinct (Arroyo-Cabrales *et al.* 2007, 2010; Ceballos *et al.* 2010; Arias-Alzate *et al.* 2017). *P. onca augusta* is not present today in North America, so this large form of the jaguar became locally extinct too, probably due to the same phenomenon of megafauna extinction (Arias-Alzate *et al.* 2017).

It is important to mention that despite the reduction in the habitat of the jaguar, this species is extremely successful compared to other big extinct felids (*i. e.,* long-teeth felines and American lion). One hypothesis used to explain the extinction of other big felines, is focused on the degree

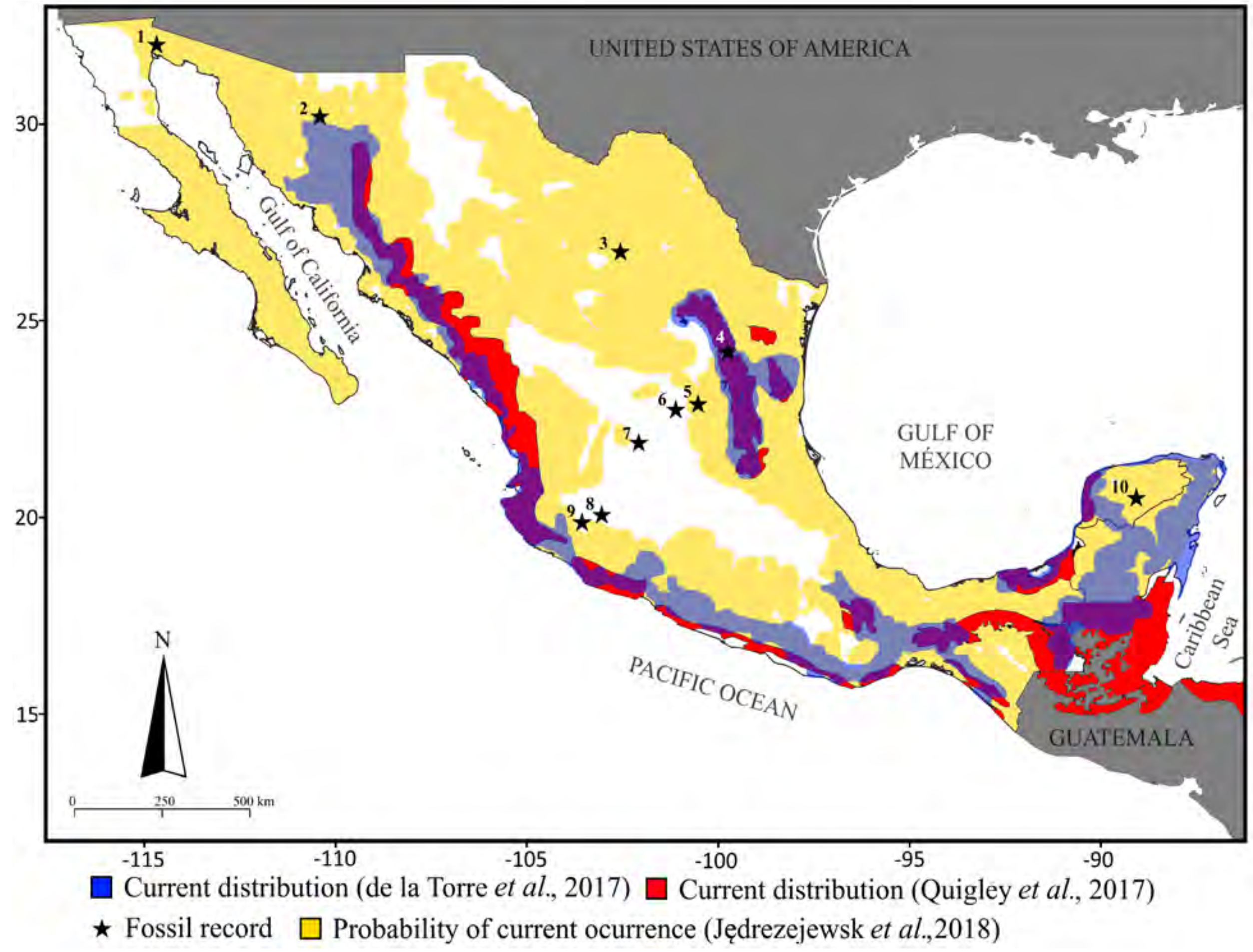


Figure 4. Past and present Mexican distribution of *Panthera onca*. Current distribution taken from de la de la Torre *et al.* 2017 and Quigley *et al.* (2017). Probability of current occurrence taken from Jędrzejewski *et al.* (2018). Fossil localities: 1) El Golfo; 2) Rancho La Brisca, Sonora; 3) Cuatro Ciénagas, Coahuila; 4) San Jocesito Cave, Nuevo León; 5)Mina de San Antonio; 6) Brechas Coloradas, San Luis Potosí; 7) El Cedazo, Aguascalientes; 8) Zacoalco; 9) Soyatlán, Chapala, Jalisco; 10)Loltún Grottoes, Yucatán. Fossil localities are those of Table 1.

Table 1. Mexican localities with fossil records of *Panthera onca*. Numbers in parentheses correspond to the localities depicted in Figure 4.

	Locality	Material	Age	References
Sonora	**El Golfo (1)**	Not reported material, but the specimen was conferred to jaguar specie (*Panthera* sp. cf. *P. onca*)	Pleistocene (Irvingtonian)	Arroyo-Cabrales (2002); Croxen III *et al.* (2007); Ferrusquía-Villafranca *et al.* (2010)
	Rancho La Brisca (2)	Not reported material	Pleistocene (Rancholabrean)	Arroyo-Cabrales (2002); Ferrusquía-Villafranca *et al.* (2010)
Coahuila	**Cuatro Ciénagas (3)**	Not reported material, and Contreras-Balderas *et al.* (2007) points that the report is doubtful because the material could also belong to *Puma*.	Pleistocene (Rancholabrean)	Contreras-Baldera *et al.* (2007); Ferrusquía-Villafranca *et al.* (2010)
Nuevo León	**San Josecito Cave (4)**	LACM* 192/264; 192/9008. Cranial and postcraneal material	27.000-45.000 YBP (Rancholabrean)	Kurtén (1973); Arroyo-Cabrales *et al.* (1995)
San Luis Potosí	**Mina de San Antonio (5)**	IGM 6705; 6706; 6707. Dental and postcraneal material	Pleistocene (Rancholabrean)	Torres (1995); Ferrusquía-Villafranca *et al.* (2010)
	Brechas Coloradas (6)	Not reported material	Late Pleistocene-Holocene (Wisconsinian)	Arroyo-Cabrales (2002); Ferrusquía-Villafranca *et al.* (2010)
Aguascalientes	**El Cedazo (7)**	IGM 56-102; 56-190; FC** 613. Cranial and postcraneal material	Pleistocene (Rancholabrean)	Mooser and Dalquest (1975); Arroyo-Cabrales (2002); Ferrusquía-Villafranca *et al.* (2010)
Jalisco **Chapala Lake**	**Zacoalco[a] (8)**	LACM 1757. Mandibular fragment conferred to jaguar specie (*Panthera* sp. cf. *P. onca*)	Pleistocene (Late Blancan)	Rufolo (1998); Lucas (2008); Arroyo-Cabrales (2002)
	Soyatlán (9)	IGM 9518. Mandibular fragment	Early? Pleistocene	New report in this work
Yucatán	**Lultún Grottoes (10)**	Under review material. Dental and postcraneal material	Pleistocene (Rancholabrean)	Arroyo-Cabrales and Álvarez (2003); Morales-Mejía *et al.* (2009); Personal review

[a] Rufolo (1998) described this specimen but the exact provenance of this fossil is unknown. Arroyo-Cabrales (2002) referred to the Zacoalco town to indicate the origin of Chapala jaguar. But, Lucas (2008) indicates that most of the material described by Rufolo (1998) comes from the villages of Chapala and Ajijic towns or near to San Luis Soyatlán.
*LACM: Natural History Museum of Los Angeles County, California, United States.
**FC: Fauna Cedazo, México.

of specificity of the diet. *P. onca* is a generalist hypercarnivore, this means that it has the capacity to consume a great diversity of prey, even preys with hard shells, such as turtles or armadillos (Emmons 1989; Seymour 1989). This probably conferred advantages to *P. onca* at the time when the availability of large prey was declining. The same selection process probably happened with the cougar *Puma concolor*. Both, cougar and jaguar are generalist predators although they have prey separation (Chinchilla 1997).

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First record of *Thomasomys cinereus* Thomas, 1882 (Rodentia, Cricetidae, Sigmodontinae) in Ecuador

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The Andean forests of southwestern Ecuador and northern Peru, hold a unique assemblage of species, given the existence of high habitat diversity. Our aim is to characterize the small mammal diversity at Yacuri National Park in southern Ecuador. We collected small non-volant mammals, using Sherman, Pitfall, and Tomahawk traps, in wet and dry habitats in the Yacuri National Park; and obtained some specimens of rodents and marsupials in the pluviseasonal forest in southern Ecuador. We registered several non-volant small mammal species, including the first Ecuadorian record of the olive-gray mouse (*Thomasomys cinereus*). This record expands the known species distribution, 10 km from the northernmost location in Peru within the same ecosystems.

Los bosques de los Andes del suroccidente de Ecuador y norte de Perú, comparten una diversidad única en especies de mamíferos, debido a la amplia diversidad de hábitats. Este estudio tuvo el objeto de conocer más acerca de los pequeños mamíferos del Parque Nacional Yacuri, para lo que se aplicaron métodos de captura de pequeños roedores y marsupiales en los bosques pluviestacionales del sur del Ecuador. Se registraron algunas especies de marsupiales, ratones marsupiales y roedores, entre los cuales una especie de roedor que resultó ser un nuevo registro del ratón gris oliváceo (*Thomasomys cinereus*) para Ecuador, el cual representa una extensión de 10 kilómetros de su distribución al norte de Perú, habitando los mismos ecosistemas peruanos en Ecuador.

Keywords: Andes; Sigmodontinae; Thomasomyini; Tumbes; Yacuri National Park.

Introduction

The genus *Thomasomys* currently includes 44 living species, and is one of the most diverse genera of sigmodontine rodents. This genus is distributed from northern Venezuela to southern Bolivia, occupying the subtropical forest, the cloud forest, upper montane forests, and moors "paramos". The Andes of Ecuador have been considered the center of diversification for this genus (Voss 2003).

Species of *Thomasomys* Coues 1884 are characterized by having elongated rostrums, relatively small zygomatic plates, a narrow interorbital region that appears to be hourglass shaped, round or square supraorbital margins and a rounded braincase (Pacheco 2015). Ecuador have 13 species of *Thomasomys*: *T. aureus*, *T. auricularis*, *T. baeops*, *T. caudivarius*, *T. cinnameus*, *T. erro*, *T. fumeus, T. hudsoni, T. paramorum, T. silvestris, T. taczanowskii, T. ucucha*, and *T. vulcani*. Five of which inhabit the western slopes and three of which inhabit the eastern slopes in the Ecuadorian Andes (Albuja 2011; Pacheco 2015; Tirira 2017). Ecuadorian species of *Thomasomys* distribute across the Andes from 1,220 to 4,500 masl (Pacheco 2015). Moreno and Albuja (2012) mention the species *Thomasomys onkiro* from the eastern foothills of the eastern Andes in the Ecuadorian province of Zamora Chinchipe. However, according to Pacheco (2015), the specimens that are the base of this mention would represent a new species more allied to *Thomasomys caudivarius*.

The composition of the non-volant mammal assemblage of the grasslands and montane forests of the southern Ecuadorian Andes has been the subject of few studies (but see Barnett 1999), while in the north and center Andes of Ecuador has been studied more extensively (Voss 2003; Lee *et al.* 2006; Lee *et al.* 2008; Boada 2008; Lee *et al.* 2010; MECN 2010; Lee *et al.* 2011; Ojala *et al.* 2013). Few studies have been carried out in the eastern Andes of the province of Zamora Chinchipe (Moreno and Albuja 2012), and most of them are focused along the Cordillera del Condor. This region has recently been the site of important discoveries of flora (Ulloa *et al.* 2012) and fauna (Albuja and Luna 1997; Boada 2011; Almendáriz *et al.* 2014). Here, we report results of small non-volant mammal survey conducted at Yacuri National Park including a species of *Thomasomys*, previously unknown from Ecuador.

Materials and methods

Yacuri National Park is located between the Ecuadorian provinces of Loja and Zamora Chinchipe, at the border with Peru. We sampled at an area located at 2,900 masl in the western foothills of the Eastern Cordillera in the province of Loja, which belongs to the evergreen high montane forest of the biogeographical section "Catamayo-Alamor." At this site, the canopy reaches up to 20 meters, and the ground is covered with forest litter (MAE 2013).

Data was collected between 2 and 13 July 2014. To capture small non-volant mammals, we used 100 Sherman traps, 50 Pitfall traps, and 50 Tomahawk traps. Sherman and Tomahawk traps were baited with a mixture of peanut butter, oatmeal and cod liver oil, sometimes alternating with tuna and salami. Traps were arranged in linear transects intercalating between two Sherman, one Pitfall trap (without fences) and one Tomahawk trap, covering different microhabitats such as ravines, freshwater streams and bush remnants in the grasslands. Sampling effort was 400 nights for Sherman trap, 200 for Pitfall traps and 200 for Thomahawk traps in the evergreen high montane forest of the biogeographical section "Catamayo-Alamor".

We captured only one specimen of *Thomasomys* in the montane forests of the western flank of the Andes, in the province of Loja. We preserved the specimen as skin, skull, skeleton, and samples of muscle and liver tissues stored in 98 % ethanol. It was deposited in the section of Mammalogy at the Departamento de Ciencias Biológicas de la Escuela Politécnica Nacional del Ecuador (MEPN).

The specimen of *Thomasomys* was identified at the species level using original descriptions of species of *Thomasomys* and other publications (Voss 1993; Pacheco 2003, 2015). Victor Pacheco of the Departamento de Mastozoología, Museo de Historia Natural, Universidad Mayor de San Marcos (Lima, Perú), a specialist on Thomasomyini, was also consulted about the identity of the collected specimen. The determination of the other species of small mammals was by revision of original descriptions and revision of specimens of the type localities or closer to it, of the Departamento de Ciencias Biológicas de la Escuela Politécnica Nacional (MEPN) and of the Museum of San Marcos (MUSM).

Four standard body measurements were obtained from this specimen in the field: head and body length (HBL), length of tail (LT), length of hind foot (LHF), and length of ear (LE). We also measured the length of the largest mystacial vibrissae (LMV) and the length of the largest superciliary vibrissae (LSV). Twenty tree craniodental measurements were recorded (Reig 1977; Luna and Pacheco 2002; Moreno and Albuja 2012): Greatest length of skull (GLS), condyloincisive length (CIL), condylomolar length (CML), length of rostrum (LR), breadth of rostrum (BR), length of orbital fossa (LOF), length of nasals (LN), breadth of nasals (BN), least interorbital breadth (IO), length of diastema (LD), length of bony palate (LBP), breadth of bony palate (BBP), length of incisive foramina (LIF), breadth of incisive foramina (BIF), length of maxillary toothrow (LM), breadth of palatal bridge across the first upper molars (BPB), breadth of first upper molar (BM1), zygomatic breadth (ZB), breadth of braincase (BB), breadth of zygomatic plate (ZP), depth of incisors (DI), height of braincase (HB), and width of mesopterygoid fossa (WMF). These measurements were taken with a digital calibrator of 0.01mm. The craniodental nomenclature was based on Musser *et al.* (1998), Luna and Pacheco (2002), Voss (2003), and Moreno and Albuja (2012). Values for these measurements are provided below.

Results

The phenotype of the specimen of *Thomasomys* (MEPN 12549) collected at Yacuri National Park (south of Loja province), did not coincide with the morphological characteristics of the species of *Thomasomys* already known from Ecuador. It was determined as a specimen of *Thomasomys cinereus*. This record is the first one of the species for Ecuador and extends the known species distribution by 10 km to the north (Figure 1A) from Huamba forest, in the town of Ayabaca, Department of Piura, in Peru (Pacheco 2015). The Ecuadorian individual is a typical member of *Thomasomys cinereus*, featuring hypsodont molars, the third lower molar mesolophid is adhered to entoconid, and genal vibrissae is absent (Pacheco 2015). External general coloration of this specimen is ashen gray (Figure 1B) with gray base and white tips, alternating with longer blackish hair, while the abdomen has a grayish-white color. The tail is thick, brown on top and whitish at the base, and lacks a white tip (Thomas 1882; Pacheco 2015). This specimen shows silver ungual tufts in the toes that exceed the length of the nail (Voss 1993), the hairs that cover the top of the metatarsus are white, but the skin is black. The picture in the description of Thomas (1882) shows a ring of blackish hair around the small eyes in relation to the head (Figure 1B).

Specimen MEPN 12549 corresponds to an adult female of age two according to molar enamel wear (Voss 1988). Its recorded measurements, in millimeters, are as follows: HBL = 113; LT = 147; LHF = 29; LE = 20; LMV = 41; LSV = 21; GLS = 31.86; CIL = 29.37; CML = 19.25; LR = 10.55; BR = 6.35; LOF = 10.75; LN = 12.83 BN = 4.11; IO = 5.08; LD = 8.34; LBP = 5.48; BBP = 3.35; LIF = 6.13; BIF = 2.23; LM = 5.26; BPB = 6.74; BM1 = 1.68; ZB = 17.40; BB = 14.23; ZP = 2.63; DI = 1.76; HB = 9.50; WMF = 2.27.

The skull of the Ecuadorian specimen of *Thomasomys cinereus* is slightly narrower than that of the holotype of the

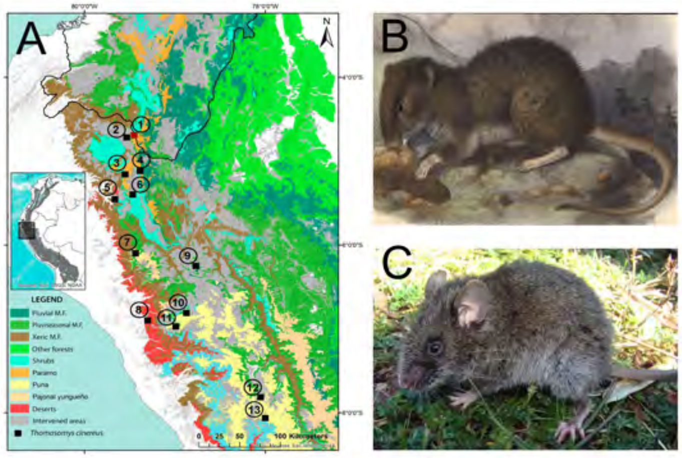

Figure 1. A) Map of recording localities of *Thomasomys cinereus* in northern Peru and southern Ecuador (see locality names in Appendix 1) in Andean montane forests (M.F.; Cuesta *et al.* 2009). The new Ecuadorian record from Yacuri National Park is shown with the red filled square. Records from Peru (in black squares) were taken from Pacheco (2015). *Thomasomys cinereus.* B) Plate IV in the original description by Thomas (1882). C) Specimen (MEPN 12549 female) from southern Loja, Ecuador.

species, from Cutervo, at 2,800 masl, in the Department of Cajamarca in Peru. Cranial and dental features match those indicated by Voss (1993), Pacheco (2003) and Pacheco (2015). These features include the absence of a rostral tube, for an incomplete premaxilla conjugation in the front of rostrum, same shape and arrangement of the zygomatic notch and zygomatic plate, and interorbital constriction hourglass shaped and flattened on its lateral view (Figure 2A). The palatal bone is short with a minute posterolateral palatal pits on each side, and with a palatal spine on the back, which is between the last molars. Basisphenoid-presphenoid suture without sphenopalatine vacuities (Figure 2B). Elongated and oval incisive foramina. The alisphenoid struts are not robust. The skull shows the circulation pattern 1, with a large stapedial foramen, a notorious squamosal-alisphenoid groove and a sphenofrontal foramen (Voss 1988). The tegmen tympani, of the periotic, overlaps the back suspensory process of the squamosal. Capsular process of the lower incisor alveolus not widely extended laterally below the coronoid process base.

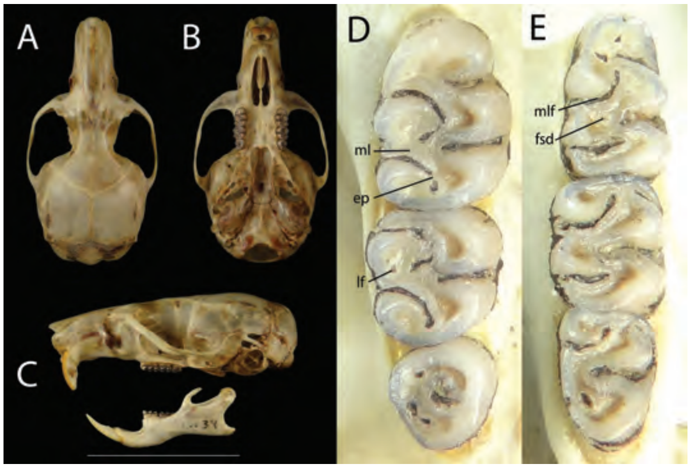

Figure 2. Skull and mandible of the specimen of *Thomasomys cinereus* from Loja (MEPN 12549 female): A) Dorsal, B) Ventral, C) Lateral view. Scale: 21 mm. Occlusal views of the molars (D: upper right; E: lower right) of specimen MEPN 12549 of *Thomasomys cinereus* from Loja, Ecuador. ep = enamel projection, fsd = fosetid, lf = labial fossetid, ml = mesoloph, mlf = mesolophid.

Long upper incisors, wide and almost orthodont; with orange color on the front. Molars have some degree of hypsodont, with paraflexus and metaflexus of first upper molar and second upper molar wrapping the paracone and metacone. The mesoloph of the specimen from Loja is more robust than indicated for *T. cinereus* by Voss (1993), because the mesoloph in Ecuadorian specimen is worn (Figure 2D), from the medial mure to the mesostyle, which is adhered to the paracone by a paralophule. In specimen MEPN 12549 this paralophule is almost in the rear half of the paracone and is connected at the middle in the mesoloph. Second upper molar also shows that behind the connection of the paralophule of the paracone and the mesostyle, there is a fossettid up to half the mesoloph (Figure 2D), which is also shown in specimen LSU 27056 (Voss 1993; Figure 9C). In the first upper molar there is an enamel projection from the metacone to the medium mure similar to a metalophule (Reig 1977), which divides the back metaflexus in two (Figure 2D). The procingulum of the first upper molar is divided by a worn anteromedian flexus equally in anterolabial and anterolingual conules. First lower molar and second lower molar do not present ectolophyd, as it is typical in this species of *Thomasomys*. Also, the mesolophid is adhered almost entirely to the front of the entoconid (Voss 1993; Figure 10C) where it is difficult to notice a median murid.

Discussion

With the report of *Thomasomys cinereus*, 14 species of *Thomasomys* are known from Ecuador, of a total of 431 mammal species cited for Ecuador (Tirira, 2017 with modifications).

In the area inhabited by *Thomasomys cinereus* we also collected the following sigmodontine rodents, *Microryzomys altissimus*, *Microryzomys* sp., *Nephelomys* cf. *nimbosus*, *Thomasomys taczanowskii*, and *Akodon orophilus*. These species differ from those mentioned by Lee *et al.* (2019).

The habitat of *Thomasomys cinereus* in Ecuador is composed mainly of three main tree genera *Aegiphila*, *Miconia*, and *Oreopanax*; these trees show stems up to 20 cm of DBH (Diameter Breast Height; MAE 2013).

The habitat of the Ecuadorian specimen of *Thomasomys cinereus* is similar to the habitats inhabited by the species in Peru, including pluviseasonal montane forests, shrubs, and Yungas from the Andes western side (Pacheco 2015). The species distributes south and north of "Huancabamba Depression" (Figure 1A), which has been regarded as a biogeographical barrier for small mammals (Jiménez *et al.* 2013; Carleton 2015). Further studies would assess the degree of differentiation of populations of *Thomasomys cinereus* south and north of the Huancabamba Depression.

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Appendix

Collection localities of *Thomasomys cinereus* in Ecuador and Peru (see also Figure 1); those from Peru were taken form Pacheco (2015).

Ecuador: Loja: 1) Guardianía, Yacuri National Park, 3,205 masl (-4.71247°, -79.44067°).

Peru: Piura: 2) Ayabaca, Bosque de Huamba, 44 Km E of Ayabaca, 2,950 masl (-4.71872°, -79.53085°). 3) Canchaque road, 15 km E, 2,137 masl (-5.40000°, -79.46466°). 4) Cerro Chinguela, ca. 5 km NE of Zapalache, 2,900 masl (-5.11667°, -79.38333°). 5) 33 road km SW of Huancabamba, 3,000 masl (-5.45545°, -79.66216°). 6) Pariamarca Alto, 2,900 masl (-5.15867°, -79.54901°). Lambayeque: 7) Bosque de Chimana, 2,550 masl (-6.10000°, -79.43333°). 8) Seques, 288 masl (-6.90000°, -79.30000°); Cajamarca: 9) Cutervo, San Andrés de Cutervo, Cutervo National Park, 100 m over El Tragadero, 3,000 masl (-6.24997°, -78.76653°). 10) Pisit, 3,399 masl (-6.81139°, -78.87052°). 11) 35 miles WNW of Cajamarca, 3,268 masl (-6.97180°, -78.98780°). La Libertad: 12) South of Huamachuco, 3,189 masl (-7.81483°, -78.05030°). 13) Cachicadan, 3,100 masl (-8.06463°, -78.00000°).

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Analysis of the application of ecological niche modeling in phylogeographic studies: contributions, challenges, and future

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The combined application of ecological niche modeling in phylogeographic studies has contributed to better understanding the relationship between the patterns of genetic variation of species and the abiotic conditions where their populations have evolved. This has allowed broadening and strengthening the spectrum of phylogeographic questions and hypotheses to be tested, based on the increasing availability of data, algorithms, and models. However, when these two approaches are combined, some of their limitations are also added, despite taking advantage of their strengths. This review explores some of the latest contributions of this application. We found that 44 % of the studies reviewed address the effect of the environment on the diversification and structure of lineages; 20 % of the models concern mammals and 27 %, reptiles; and 34 % of the articles addressed the biota of the Nearctic region. This review also explores the most important challenges and future perspectives resulting from this synergy.

La aplicación del modelado de nicho ecológico en estudios de filogeografía ha contribuido a entender la relación entre los patrones de variación genética de las especies y las condiciones abióticas en las que sus poblaciones se han diferenciado. Esta aplicación ha permitido ampliar y robustecer el espectro de preguntas e hipótesis filogeográficas a probar, apoyándose en la creciente disponibilidad de datos, algoritmos y modelos. Sin embargo, al combinar estos dos métodos, aún cuando se aprovechan sus fortalezas, es inevitable que también se sumen varias de sus limitantes. En esta revisión exploramos puntualmente algunas de las contribuciones más recientes de esta aplicación, encontrando que el 44 % de los estudios se enfocan en explorar el efecto del ambiente en la diversificación y estructura de los linajes, mientras que el 20 % de los modelos de estudio son mamíferos y 27 % reptiles, donde 34 % de los artículos se concentran en biota de la región Neártica. Asimismo, esta revisión explora los desafíos más importantes y las perspectivas a futuro que resultan de esta sinergia.

Key words: ecological niche; lineage divergence; niche conservatism; niche modeling; phylogeography; potential distribution.

Introduction

Understanding the relationship between geography, the distribution of species, and the patterns of species differentiation is a core element in the study of evolutionary biology (Avise 2000). Merging the knowledge about each of these aspects requires a unifying approach, where phylogeography is an integrating discipline that articulates information about the genetic structure, geographic distribution, and genealogy of natural populations (Avise 2000; Vázquez-Domínguez 2007). As such, phylogeography is a converging ground for various approaches to study biodiversity.

Taking into consideration the abiotic variables associated with geography is essential in phylogeography, given their influence in processes such as isolation, divergence and, eventually, speciation (Kozak *et al.* 2008). These scenopoetic variables are also the backbone of ecological niche modeling (Peterson *et al.* 2011), defined as the set of methods and techniques to assess the variables in the environment of living organisms, and how these variables are associated with the geographic distribution of organisms (Carstens and Richards 2007). Based on statistical or mechanistic approaches, ecological niche modeling (ENM) opens the possibility to explore the existing relationships between organisms and environmental conditions, by evaluating the drivers governing the occurrence of species in time and space (Svenning *et al.* 2011).

In parallel with the ongoing development of new ENM methods, there is a growing availability of large species distribution databases generated from geographic information systems, such as topological, climatic, oceanographic, and geological models (Varela *et al.* 2011). For this reason, ENM aims to identify and quantify the relationship between environmental factors and the distribution of populations at different scales, *i. e.*, to characterize and measure their ecological niche (Soberón 2007).

How do we define niche? The term "niche" is described in multiple ways in the literature. One of the earliest definitions is attributed to Grinnell (1917), who defined it as the climatic and environmental conditions required by a species in order to survive, along with the morpho-physiological and behavioral characteristics of the species that allow it to interact with the environment. For Elton (1927), the niche of an animal species is its place in the biotic environment, *i. e.*, its relationships with food and enemies, while Hutchinson

(1957) defines it as the 'n-dimensional' hyper-volume where the dimensions are environmental conditions and resources defining the requirements of an individual or a species in order to survive and maintain its populations. The contribution of the *n*-dimensional concept of Hutchinson is a cornerstone in the conceptual relationship of the ecological niche of a species and its geographic distribution. Thus, Grinnell's niche concept is based on climatic conditions operating at a large spatial scale; the Eltonian niche refers to fine-scale variables that can be either consumed or modified by a species, and the Hutchinsonian niche can include all sorts of relevant variables for the species, expressed at both fine and large spatial scales (Soberón 2007).

Within the conceptual framework of the ecological niche, Soberón and Peterson (2005) point out four classes of factors that define the distribution of species: 1) abiotic conditions, such as climate and physical environment; 2) biotic factors, including the interactions with other organisms that modify the ability of a species to maintain its populations; 3) accessibility of the species to new areas, given its dispersal capability; 4) evolutionary capacity of populations to adapt to new conditions. These factors interact to various degrees over time and at different spatial scales to produce the complex geographic distribution of a species, whose understanding is essential for phylogeography.

The study of the ecological niche is based on two key elements; first, niche conservatism, defined as the evolutionary patterns within which species tend to share their ecological requirements with their ancestors (Wiens and Graham 2005). This results in two or more closely related species that are ecologically more similar than what would be expected according to their phylogenetic relationships (Losos 2008). Its counterpart is niche evolution (or niche divergence), which refers to the persistence and adaptation of populations to new environmental conditions (Holt 2014). It should be noted that although multiple studies integrating ENM to evolutionary aspects seek to discern between these two hypotheses, the drivers of niche evolution are still unknown (Holt 2014). For this reason, niche evolution assessment is currently an ongoing area of research.

What is phylogeography? Phylogeography works with the historical components of the spatial distribution of gene lineages, with time and space as core pillars. Avise (2000) defines it as "... the field of study concerned with the principles and processes governing the geographic distributions of genealogical lineages, especially those within and among closely related species". It involves the assessment of the genetic structure, distribution, and differentiation within and among natural populations throughout their distribution range, using molecular markers like DNA sequences. Another characteristic is the ability to estimate the lineages' age and the time of divergence between them, based on the diversification rate of the molecular marker used. The study of the geographic distribution of lineages has made it possible to describe historical events, including habitat fragmentation, expansion of the distribution range of species and populations, vicariance, migration and extinction events, as well as other spatial and temporal processes affecting population structure or promoting speciation. Indeed, Hardy *et al.* (2002) have documented consistent patterns in species, showing that these processes have been significant drivers in the diversification of lineages. Environmental factors like climate, and intrinsic factors including dispersal ability and ecological characteristics, have also played a key role (Vázquez-Domínguez 2007).

Material and methods

Literature assessment. This review considered articles that met three criteria: 1) inclusion of "Phylogeography" and "Niche modeling" as key words; 2) published between 2007 and July 2019; and 3) studies that specifically reflect the combined or integrating application of phylogeographic analyses and ecological niche modeling. We identified a total of 29 articles. The results showed that 44 % of these studies explore the effect of the environment on the differentiation and structuring of lineages, followed by 23 % that assess the effect of historical environmental changes on phylogeographic patterns in the groups studied; only 3 % addressed the integrative application of these methods for the assessment of species extinction risk (Figure 1a). On the other hand, 20 % of study models focus on mammals, 27 % on reptiles, 20 % on arthropods, and 10 % on amphibians (Figure 1b). Importantly, 34 % of the articles focused on components of the biota of the Nearctic region, 24 % on the Palearctic, and 18 % on the Neotropical (Figure 1c).

Results

The best of both worlds: the state of the art. The application of ENM to phylogeographic studies has contributed to assess the abiotic factors that govern the evolutionary history of the lineages structuring a species, jointly with the ecological-environmental factors structuring the genetic variation of species across their range and the landscape (Figure 2). It has also enabled exploring how these factors are associated with the lineages' divergence (Alvarado-Serrano and Knowles 2014; Suárez-Atilano *et al.* 2017). A relevant example of this application within a macroevolutionary framework is the theoretical study of Rangel *et al.* (2018), who used simulations of processes that shape the biota's geographic and evolutionary patterns (birds, mammals, and plants) of South America, and compared the climate simulations and models for the past 800,000 years with empirical speciation, biodiversity, and lineage extinction data. Their results suggest that climatic heterogeneity and topography have governed their evolutionary and diversification patterns. On the other hand, Mizerovska *et al.* (2019) evaluated the influence of changes in climate, topography, and rivers during the Plio-Pleistocene on the diversification of African rodents of the *Praomys jacksoni* complex. The results confirmed that the evolutionary history of the complex (five lineages) is associated with Pleistocene changes and diversification of the refugia represented by forested areas.

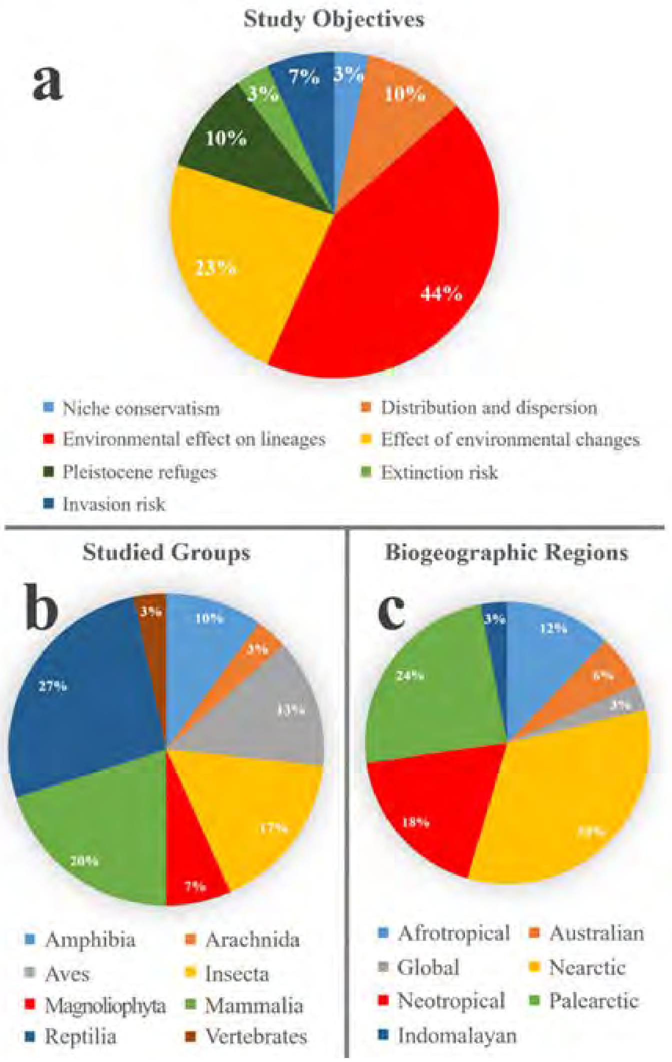

Figure 1. Graphs of the 29 studies reviewed in this study, broken down by percentages of **a)** objectives, **b)** biological groups studied, **c)** biogeographical regions where those studies were carried out.

Recently, the temporal focus of phylogeographic and niche studies has broadened, exploring both historical and current geographic patterns to produce ecological projections of past and future distributions. For instance, Martínez-Méndez *et al.* (2015) integrated analyses of evolutionary history, contemporary geographic distribution, and future distribution projections for the lizard *Sceloporus serrifer*, and concluded that populations inhabiting the lowest lands will become extinct before the year 2070. This approach has also been used to explore diversification patterns considering taxonomic categories (species, subspecies, etc.) as well as evolutionary lineages at the population level (de Queiroz 2007). For example, Smith *et al.* (2018) suggest that the building niche models to investigate lineages sheds light about the role of the environment in local adaptation and phylogeographic structuring patterns (*e. g*. Suárez-Atilano *et al.* 2017; these models also emphasize the importance of incorporating information regarding phylogeny and evolutionary models into ENM strategies. Therefore, a great variety of questions have been raised, as methods are continually emerging for the integrative use of ENM and phylogeography, which are summarized below. It should be noted that while *Therya* is a publication about mammals, the number of studies within the scope of interest in this review and on mammals is so limited that we also describe relevant examples related to other taxa.

Discussion

Applications of the combined use of ENM and phylogeography. One of the earliest studies where ENM was applied to phylogeography is the investigation of Hugall *et al.* (2002), involving an approach that compared paleodistribution models with phylogeographic information for a snail endemic to tropical forests in northern Australia. They established the location of historical refugia and contributed to the understanding of species expansion patterns from these refugia.

This approach gained popularity in the decade that followed and was used to address questions regarding the distribution and dispersal of species in relation to their genetic variation patterns. Some studies have focused on species with restricted ecological requirements (*e. g.* a specific habitat, a particular altitudinal range), as these can better illustrate the processes associated with the geographic patterns of genetic diversity. One example is the study by Igea *et al.* (2013) that evaluates the post-glacial expansion patterns of the Iberian desman *Galemys pyrenaicus*, a small semi-aquatic mammal inhabiting clean streams in the northern half of the Iberian Peninsula, which is endangered in most of its geographic range. The authors hypothesize that the strict ecological demands arising from its aquatic habitat, coupled with the effects of the Pleistocene glaciations, led to a marked phylogeographic structure and a genetic pattern associated with the distribution of glacial refugia.

Another topic frequently addressed is the influence of bioclimatic variables on the phylogeographic patterns of various species. Suárez-Atilano *et al.* (2017) characterized the ecological niches of two lineages of *Boa imperator*, in order to assess whether certain environmental factors are associated with the divergence and genetic variation between these lineages; interestingly, precipitation and temperature (mainly) were found to be closely related to the distribution and divergence of this reptile’s lineages. This work demonstrates that environmental variables may be appropriate predictors of the distribution and divergence of lineages, and that ENM contributes to validating evolutionary patterns from biogeographic and phylogeographic frameworks.

The establishment of some species on their original distribution areas during glacial cycles is known as glacial persistence. Some studies have aimed to measure and explain such persistence. Galbreath *et al.* (2009) analyze the response of the pika *Ochotona princeps* to climate changes in the Pleistocene, exploring the influence of changes in elevation on the genetic differentiation and historical demography of this alpine specialist. Based on the current phylogeographic structure and the ENM of this lagomorph lineages adapted to low temperatures, the authors have estimated its past and future distribution. Their results suggest that populations of this species increased during the last major glaciation, while the distribution range of some of their lineages declined during the Holocene, making them highly sensitive to climate warming.

The increasing availability of paleoclimatic information has supported phylogeographic and ENM studies for the identification and location of Pleistocene climate refugia, *i. e*., areas of favorable conditions where species survived during glaciations. For instance, Perktaş *et al.* (2015) reassessed the historical demography of the Eurasian green woodpecker *Picus viridis* by producing ENMs based on mitochondrial DNA lineages, which allowed the identification of potential glacial refugia. An excellent proposal on these topics is the one by Gavin *et al.* (2014) who emphasize the importance of adequately integrating the three major lines of evidence to infer the existence of past refugia: fossil records, ENM, and phylogeographic information.

An essential aspect of phylogeography to understand species divergence and evolutionary patterns (Kalkvik *et al.* 2012) is to determine the relationship between the diversification of lineages and variations of the ecological niche. Zink *et al.* (2014) explored the role of niche divergence in the configuration of the distribution ranges of sister species and their speciation process. Their results showed that sister lineages (also called phylogroups) with allopatric distribution share more characteristics of their ancestral niche than those expected by chance, but at the same time, they are distributed in different environments. Hence, they conclude, the latter supports the role of ecology in lineage diversification.

Niche conservatism and divergence. A key issue is to determine whether the ecological niches of species are preserved over time and the evolutionary implications of this trend. This aspect can be evaluated by testing niche conservatism and niche divergence models (Losos 2008; Warren *et al.* 2008), which allow understanding the relationship between ecological niche and its expression in phylogeographic patterns. However, constructing models to explore

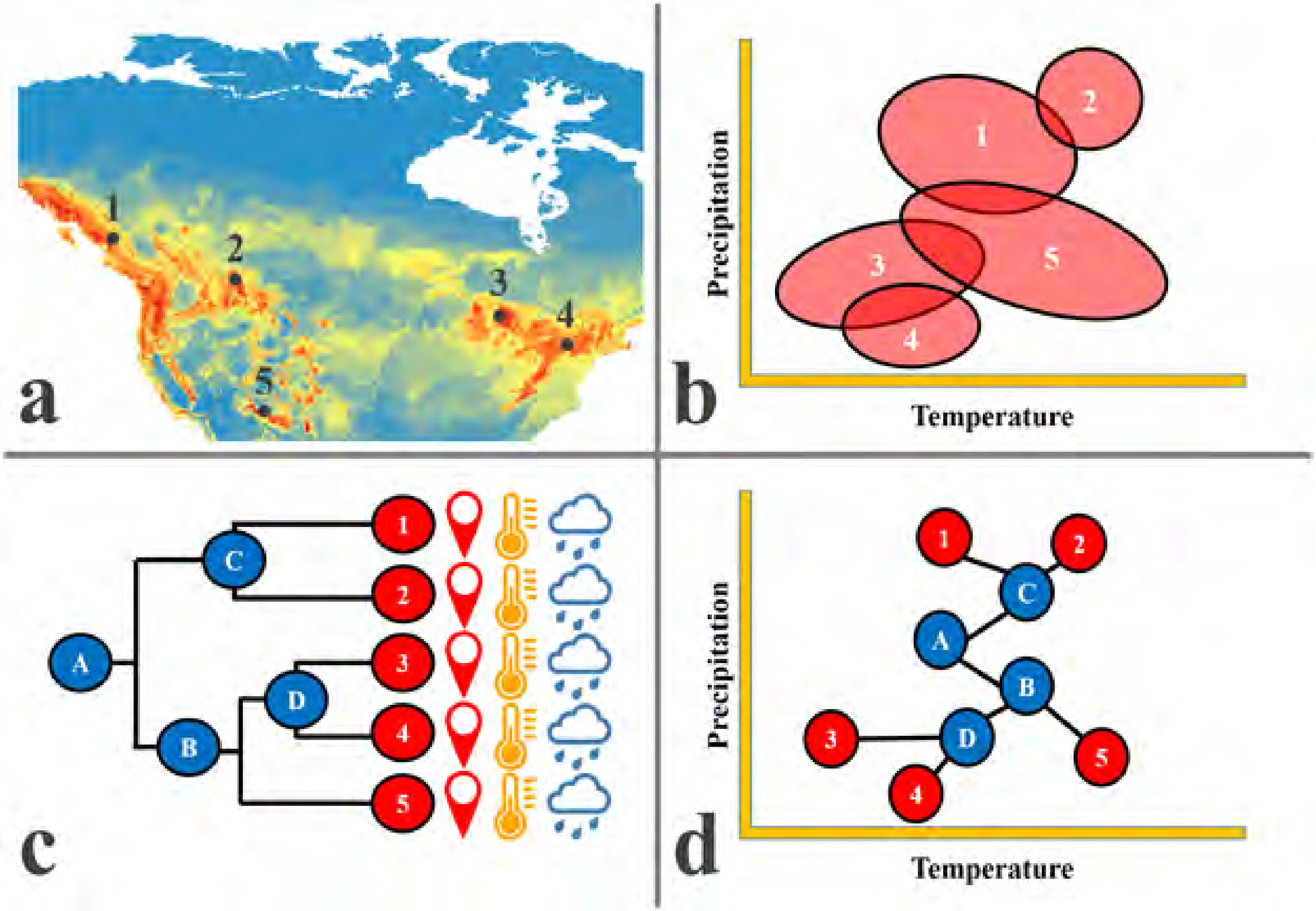

Figure 2. Outline of an integrative approach to ecological niche modeling (ENM) and phylogeography. **a)** ENM generated from presence/absence records in databases and with bioclimatic envelopes; the figure shows sites of capture and DNA collection (1-5) of different populations of the same species (American black bear, *Ursus americanus*, in this example). **b)** Ellipsoidal models of multivariate environmental conditions associated with the different populations sampled, from which ecological niches are characterized and measured. **c)** Phylogenetic relationships between the lineages obtained; the environmental values for each lineage can be derived from the respective coordinates. **d)** Example of phyloclimatic-spatial integration, where ancestral (environmental) states can be reconstructed from the relationships between lineages, assuming a Brownian evolutionary model, which facilitates summarizing the vast amount of evolutionary and climatic information.

these issues pose conceptual and methodological challenges, mostly because many of the variables involved in evolutionary processes, such as biotic interactions, cannot be included in ENM. There is, however, significant progress in the generation of models which currently serve as analytical baselines and which, in the future, could be supplemented by integrating phylogeographic methods. Rolland *et al.* (2018) integrated fossil and neontological data for 11,465 species of birds, mammals, reptiles, and amphibians to compare the evolution of climatic niches; these authors found that niches evolve at a significantly faster rate in endotherm *vs.* ectotherm organisms. Another example is the study of Velasco *et al.* (2018), who evaluated the effect of climate on species richness gradients of lizards of the genus *Anolis*, demonstrating a significant relationship at the regional level between climate and number of species, although with no evidence of niche conservatism.

On the other hand, a study that evaluates niche divergence and phylogeographic patterns is that of Ashrafzadeh *et al.* (2018), who tested the effect of isolation by distance and environment on the genetic structure of the Iranian brown bear (*Ursus arctos*), based on random regression methods of multiple matrices and niche models at the population level. They found a strong population structure (differentiation) and a low percent of overlap between population niches as a result of niche divergence.

From niche to fact: criticism, complexities, and progress. The adequate development of phylogeographic studies involves important considerations, such as the need to use multiple molecular markers; sufficient sampling coverage according to the scale of the study (local, regional, global); and analytical methods, especially given the analytical challenges that arise when determining divergence patterns and driving factors (*e. g.*, mutation rates, ancestral population sizes, generation times, migration). Also, the dating of divergence events demands considering that different sources of information (fossils, genes) can produce different dates for the same event, an outcome that warrants due consideration (Beaumont 2010; Gutiérrez-García and Vázquez-Domínguez 2011).

ENM and the set of techniques associated to it, even as an approach with vast potential for synergy with phylogeography and other fields of study, is not exempt from debate and criticism, mainly due to the need of more robust theoretical and methodological bases to improve its procedures and interpretation of results (Peterson 2011). According to Varela *et al.* (2011), some of the most debated methodological and conceptual issues are: 1) biases and scarcity of data for many of the current and fossil species; 2) higher certainty when determining the influence and biological relevance of environmental variables used; 3) ability to produce reliable representations of the biota's geographic distribution with methods based on presence-absence data. Also discussed is the current lack of robust and comparable evaluation and validation methods for the different algorithms used to estimate ENMs (Raxworthy *et al.* 2007; Lobo *et al.* 2008), the uncertainty associated with paleoclimate reconstructions commonly used in ENM (Varela *et al.* (2011)), and the effect of spatial and temporal autocorrelation (de Oliveira *et al.* 2014). Also debated are the impact of other aspects related to the functioning and statistical procedures of algorithms (Terrible *et al.* 2010; Peterson *et al.* 2015), the resolution and quality of bioclimatic envelopes (Varela *et al.* 2015), and the risks associated with spatial autocorrelation in the analysis of the geographic distribution of lineages (de Oliveira *et al.* 2014; Warren *et al.* 2014).

In particular, biases in presence records used to construct paleodistribution models limit the reliability of inferences derived without rigorous use of available fossil records and alternative sources of paleobiogeographic information (Davis *et al.* 2014). In paleoecology, a non-analogous climate is defined as the combination of past environmental conditions that no longer exist today (Williams and Jackson 2007), which has important implications when potential distribution models are projected to the past and future. Worth *et al.* (2014) suggest using different climate circulation models and sources of paleoclimatic information to establish biological criteria for a more rigorous selection of paleodistribution projections.

The criticism and debate are not limited to the technical implementation of ENM but also relate to fundamental theoretical aspects, particularly niche conservatism (Peterson 2011; Pyron *et al.* 2015). The debate focuses not only on the mechanisms required for niche conservatism and its relationship with the evolution of lineages but also on the evolution rate of ecological niches. Thus, some authors argue that ecological niches are characterized by a general high evolution rate, while others contend otherwise; however, no study has theoretically tested the comparability of the different case studies. Therefore, in line with other authors (Svenning *et al.* 2011; Alvarado-Serrano and Knowles 2014), we highlight the importance of considering the methodological limitations of ENM when applied to phylogeographic studies, particularly the difficulty of including the biotic and behavioral traits of the different species. Additionally, the results should be interpreted according to theoretical bases; spatial and temporal uncertainties associated with bioclimatic envelopes, and species presence records should be rigorously considered.

Fundamental niche and realized niche: shadows in the night. The integration of ENM to phylogeography has contributed to addressing key questions about the distribution and evolution of species, as well as regarding the methods and approaches used to conduct these assessments (Alvarado-Serrano and Knowles 2014). However, although significant progress has been made, theoretical and technical challenges still remain that should be overcome. The first is related to a central aspect within ecological niche theory: certainty about what is being measured. The fundamental niche is the multivariate range of physiological tolerances of a species (*e. g.*, temperature or humidity), within which positive population growth rates occur (Hutchinson 1957; Pulliam 2000; Peterson *et al.* 2011; Soberón and Peterson 2011); for its part, the realized niche is the existing and available subset of the fundamental niche that is actually accessible for a species, either naturally or as a result of anthropogenic factors (Pearman and Guisan 2008). However, both niche conservatism and niche evolution are related to changes in the fundamental rather than the realized niche. For this reason, changes in the realized niche do not necessarily reflect evolutionary changes or adjustment to new conditions within the fundamental niche (Soberón and Peterson 2011). Also, accurate estimates of the fundamental niche are hard to derive because explicit information on the physiological tolerance ranges is still missing for most species (Espindola *et al.* 2019); therefore, caution should be exercised when interpreting the results of ENM regarding phylogeographic patterns.

As regards of the complexities of integrating biological attributes into ENM, given that it uses only information on scenopoetic variables (Hutchinson 1957; Peterson *et al.* 2011), the inclusion of information about the mobility of species has been suggested, in order to establish the limits of the dispersal of individuals across the landscape, by using probabilistic density functions such as kernels (Worton 1989). Food preferences and other factors governing the distribution of species, including natural enemies and the landscape matrix (*i. e.*, continuous vegetation, mature trees, running water bodies, etc.), may also be used as biological criteria for model selection. On the other hand, the increasing availability of data on the biology of species (physiology, metabolism, behavior, etc.), will allow the future inclusion of this information in ENM to achieve an Eltonian approximation (Espindola *et al.* 2019).

Likewise, it is possible to integrate information related to biotic interactions such as predation, mutualism, or pollination, which could be incorporated as presence/absence of the different species when modeling the ecological niche of these species. Considering biological and ecological interactions is clearly a key element in the evolution of ENM despite the theoretical and technical challenges involved. Therefore, it is also essential to consider that some biotic interactions operate only at a very fine scale, as in the case of particular behavioral adaptations of individuals, which may be either unimportant or impossible to capture at a broader scale such as the one involved in ENM (Wiens 2011).

In conclusion, the construction of an ENM without considering the biological aspects of the species can lead to misleading interpretations about the environmental limits of its past and current distribution, thus compromising the certainty of predictions for the future. Also, the integration of biotic variables remains challenging due to the information gaps about the particular requirements of each species.

Recent advances and a promising future. Perhaps the most significant step forward in phylogeography is the development of theoretical and mathematical methods to determine divergence patterns and their association with demographic factors and historical changes in population sizes through comparative phylogeography (Gutiérrez-García and Vázquez-Domínguez 2011). The current possibility of having a large amount of nuclear genetic information, such as SNPs (Single Nucleotide Polymorphisms), compared with the traditional yet more limited cytoplasmic genome (mitochondrial DNA in animals and chloroplast DNA in plants) used in phylogeography, has allowed, among other advances, estimating historical demographic parameters of populations, including population size and gene flow, under a wide variety of evolutionary models (Avise *et al.* 2016). The integration of phylogeography not only to ENM, but to disciplines such as landscape genetics, which facilitate the direct evaluation of the relationship of environmental, ecological, behavioral, and life-history features of organisms with their respective distribution patterns, is highly promising for advancing the evaluation and interpretation of distribution and biodiversity diversification patterns (Diniz-Filho *et al.* 2015; Avise *et al.* 2016).

In addition, ENM is no longer a mere exploratory and visual confirmatory tool of genetic variation patterns in geography; it has gradually become a valuable tool for hypothesis setting and integrated approaches (Chan *et al.* 2011; Alvarado-Serrano and Knowles 2014). A number of methodological improvements have been proposed as a response to the limitations in the use of ENM in phylogeography (Svenning *et al.* 2011; Alvarado-Serrano and Knowles 2014; Luna-Aranguré *et al.* 2019). An excellent example is the contribution of Diniz-Filho *et al.* (2015), who developed a statistical method to calculate the uncertainty associated with ENM in the analysis of genetic divergence of the legume *Dipteryx alata*, which strengthen the procedures for selecting models in phylogeographic studies.

On the other hand, given that environmental conditions are variable and that the geographical distribution of species is not static, methods for the quantification of these changes are currently available in both cases, as well as for the resulting genetic variation patterns. A good example is the work of Brown and Knowles (2012), who generated spatial-temporal dynamic models, calibrated with demographic and carrying-capacity information for the American pika *Ochotona princeps*. In another example, McCormack *et al.* (2010) show a robust approach for studying allopatric lineages in early speciation stages. These authors compared the ecological niches of five lineages of the birds *Aphelocoma ultramarina* and *Aphelocoma californica* to determine whether allopatrically distributed taxa occupy similar niches. Their results point to the opposite, *i. e.*, some of the *Aphelocoma* species with a partially sympatric distribution show evidence of niche divergence.

Finally, He *et al.* (2013) used a spatially explicit demographic modeling of genetic differentiation, the results of which suggest that changes in environmental conditions and the distribution from the past to the present significantly contribute to structuring genetic variation. These authors underline the importance of broadening the scope of these studies by incorporating aspects of landscape genetics, to assess the landscape factors that govern genetic variation patterns within species.

The availability of data, algorithms, methods, and theory on both phylogeography and ecological niche modeling increases each day, providing more and better tools for integrated use (Alvarado-Serrano and Knowles 2014; Luna-Aranguré *et al.* 2019). However, understanding the relationship between the distribution of genetic variation of species and the environmental conditions around them remains challenging -- although fascinating --, especially given the errors and biases associated with the data, the relative uncertainty regarding the use of algorithms, the discrepancies in method application and interpretation, and the current gaps in the theory regarding the integration of different information sources. Thus, there are significant challenges that limit progress in the application of ENM to phylogeographic studies, as well as various approaches currently under development that seek to solve them. This demonstrates the huge potential that results from this synergy and the growing possibility that both disciplines become eventually unified. It is also important to note that, although the knowledge derived from ENM has been applied in phylogeography, the opposite has not occurred to integrate phylogeographic knowledge into the ENM field; the theoretical body of phylogeography could be the missing piece for optimum performance in the distribution patterns observed. Thus, a bilateral integration scenario offers the possibility of best practices in the ENM field, the broadening of the hypotheses to test, and a deeper understanding of the evolution of organisms in response to their environmental conditions.

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Ecological niche and potential distribution of the endangered *Bos javanicus* in south-western Java, Indonesia

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Understanding the ecological niche and spatial distribution of wildlife species is important for the conserving and enhancing of biodiversity in a landscape system. Banteng (*Bos javanicus*) is a vital and important source of germplasm and protected by Indonesia law and considered to be Endangered under the International Union for Conservation of Nature list. During 2015 to 2017, surveys were undertaken on the largest population of wild banteng occurring in Ujung Kulon National Park. Data were gathered from a long-term camera trapping to assess the ecological niche and distribution of banteng using Maximum Entropy Modelling (Maxent) algorithm. Over a period of 30,149 trap/nights there were high photo rates, indicating areas of high conservation importance for these species within the park. Distribution prediction indicated that habitat variables such as secondary forest, predation by *Cuon alpinus* and human impacts such as cultivated area and illegal activity, are critical to determining the habitat use of banteng. The results showed that banteng within the national park, mainly used the centre areas of the park with similar spatial use, both in wet and dry seasons. This study provides essential documentation of large Bovidae distribution in one of the four remaining habitats on Java, information for the development of management strategies within the park, and a basis upon which to develop future research on banteng.

Entender el nicho ecológico y la distribución espacial para el manejo de especies de fauna silvestre es importante para conservar y mejorar la biodiversidad en el sistema de paisaje. El banteng (*Bos javanicus*) es una fuente vital e importante de germoplasma y especies protegidas por la ley de Indonesia y se considera en peligro de extinción en la lista de la Unión Internacional para la Conservación de la Naturaleza. En 2015 a 2017 se realizarón investigaciones sobre la mayor población de bantengs silvestres en el Parque Nacional Ujung Kulon. Los datos se obtuvieron mediante cámaras trampa se usaron para evaluar el nicho ecológico y la distribución del banteng, utilizando el algoritmo de Modelado de Máxima Entropía (Maxent). Durante 30,149 trampas/noches, las tasas de captura fotográfica fueron altas, lo que indica áreas de gran importancia para la conservación de estas especies en el parque. La predicción de la distribución indicó que las variables de hábitat como el bosque secundario, la depredación por *Cuon alpinus* y los impactos humanos, como el área cultivada y la actividad ilegal, son fundamentales para determinar el uso del hábitat del banteng. Los resultados mostraron que dentro del parque nacional el banteng utilizaba principalmente las áreas centrales, con un uso espacial similar, en las estaciones húmedas y secas. Este estudio proporciona documentación esencial sobre la importante distribución de grandes bóvidos en uno de los cuatro hábitats que quedan en Java. También proporciona información para el desarrollo de estrategias de manejo en el parque y una base sobre la cual desarrollar futuras investigaciones del banteng.

Key words: Banteng; camera trap; distribution; habitat use; Maxent.

Introduction

Ujung Kulon is one of Indonesia's first national parks, and considered as biodiversity hotspot as well as a critical area for the preservation of medium-large mammals (Rahman *et al.* 2018). One of its most prominent mammals is the Endangered banteng (*Bos javanicus*). The species is protected by the Indonesian law (Attachment on Goverment Regulation No.7 of 1999 and Act No. 5 of 1990), listed on CITES Appendix I, and is one of the 25 species considered by the Indonesian government, in needs of special conservation attention (Ministry of Environment and Forestry Decree SK.180/IV-KKH/2015). The population of this species was believed to be limited to 905 individuals recorded in Ujung Kulon National Park in 1997, 15 individuals recorded in Baluran National Park in 2011, 100 individuals recorded in Alas Purwo National Park in 2011, and between 125 to 150 individuals in Meru Betiri National Park (Gardner *et al.* 2014). Regardless of its conservation status and its potential as an alternative future animal protein source, banteng has received little conservation attention and in Java, it locally compete with more charismatic species such as Javan rhinoceros (*Rhinoceros sondaicus*).

The natural history and conservation needs of many tropical forest ungulates such as banteng are poorly known despite the important functional roles of such species within the ecosystems, such as shaping vegetation structure through herbivory (Bowman and Panton 1991; Djufri and Wardiah 2017), dispersing seeds through their roles as mixed feeders (Matsubayashi *et al.* 2007; Gardner *et al.* 2014), preys for medium to large carnivores (Pudyatmoko *et al.* 2007; Rahman *et al.* 2018), and protecting habitats from invasive species (Pearse and Hipp 2014). Such knowledge are essential, given that tropical forest ungulates are strongly affected by various threats from natural disturbances as well as human activities (Di Marco *et al.* 2014). In addition, there is a tendency that the conservation status of large-bodied species like banteng, deteriorated significantly more than the small-bodied species (Di Marco *et al.*

2014) and lack of knowledge on the species' bio-ecological aspects will aggravate this situation. For this reason, understanding the ecological niche and factors that promote banteng's distribution is essential to develop proper conservation plans and determine the management strategies to ensure its persistence in this increasingly human-dominating landscape.

Spatial modelling is increasingly being used to study the ecological niches and distributions of various species (Wiens *et al.* 2009; Guisan *et al.* 2013; Lewis *et al.* 2017; Drouilly *et al.* 2018). One of the most popular species distribution modelling that uses presence-only data for inferring species distributions, habitat use, and environmental cues is the Maximum Entropy Modelling (Maxent; Phillips *et al.* 2006). This model allows users to fit models of arbitrary complexity (Warren and Seifert 2011; Rahman *et al.* 2017). Like many other tropical forest animals, banteng is difficult to monitor because of their elusive bahaviour. Using the presence records from camera traps, this study applied Maxent to model the habitat use and predict the potential distributions of banteng in Ujung Kulon National Park (UKNP). Use of camera traps to monitor terrestrial rare and cryptic animals in UKNP was initiated in 2011. This study was conducted to test the following hypotheses: i) banteng is highly dependent on primary and secondary forests compare to other forest types, and ii) undisturbed protected forest areas are essential for banteng conservation.

Materials and methods

Study areas. The study was conducted within the 323.24 km^2 Core Zone of UKNP. The National Park is located in the Java Sea of Banten Province in Indonesia (-6° 45′ S; 105° 20′ E, Figure 1) and represents a remnant of ancient lowland tropical rainforest that have survived the 1883 eruption of Krakatau supervolcano and tsunami (Hommel 1987; Fauzi and Stoops 2004). Even currently, the area still faces a significant threats of natural catastrophes by earthquakes and tsunamis (Giachetti *et al.* 2012), zoonotic diseases by livestock (Tiuria *et al.* 2008), and reduced forest diversity by the invasion of *Arenga obtusifolia* palm (Hariyadi *et al.* 2012). The study area was primarily comprised of low-to-mid elevation tropical forest, which has suffered some natural and anthropogenic modifications, ranged between 0 and 620 masl, and experienced a tropical maritime climate with a mean annual rainfall 3,250 mm. The heaviest rainfall occurred during the north-west monsoon from November to April, preceding a noticeably drier period with *ca*. 100 mm per month during the south-east monsoon from May to October. The mean monthly temperature varies between 25 ˚C and 30 ˚C with relative humidity ranged between 65 % and 100 % (Hommel 1987). According to the UKNP Vegetation Map, the area is covered by dense rainforest and composed of a mosaic of four main vegetation types: primary forest, secondary forest, mangrove-swamp, and beach forest (Appendix 1). At least eight large-medium sized mammal are known to co-exist, which include six ungulate species (*Rhinoceros sondaicus*, *Bos javanicus*, *Rusa timorensis*, *Muntiacus muntjak*, *Sus scrofa*, *Sus verrucosus*), felid (*Panthera pardus melas*), and canine (*Cuon alpinus*). However, in the past, these species faced varying degrees of threats from natural disasters and illegal human activities such as forest clearance, which have also led to the recent extirpation of some of these species (Hariyadi *et al.* 2012; Rahman *et al.* 2017). In UKNP, commercial poaching impacts might be minimal, resulted from the raised levels of active law enforcement patrols.

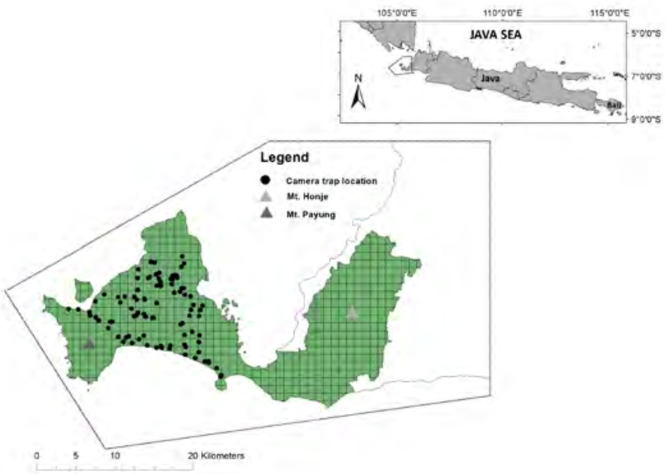

Figure 1. Camera trap locations in Ujung Kulon National Park (Indonesia).

Sampling design. A 329 km grid was superimposed over the study area and almost half of the park was sampled (134 km grid). Single cameras were placed as close as possible to each intersection between the horizontal and vertical lines which comprised the grid (Figure 1). A total of 108 Bushnell Trophy camera traps (Model #119405 and 119467) were operated between the months of December 2015 to January 2017 to detect animals over the 24 hours, followed by a 60 seconds video for each trigger. The time between successive triggers was set to 10 seconds. No cameras were baited and all videos were stamped with the date and time of recording. Cameras were set at 170 cm above the ground with a 10 to 20 degree angle leading to the ground (following the standard design of camera trapping by Rhino Monitoring Unit [RMU] team). All photographs were checked manually and encountered with mammals identified to species by the author. The camera traps were moved within the same grid when they did not capture any animal (zero presence) after two or three checking visits. Each photographed animal was identified to species. Sequential frames of the same species were counted as one photographic event, and unless individual identification was possible, any subsequent photograph of the same species taken within 30 minute interval would not be considered as a new photographic event or known as independent photographs. Location of each photograph was recorded using the latitude and longitude coordinate system and converted into digital data in GIS using ArcMap programme. Data were managed using camtrapR software (Niedballa *et al.* 2016).

Relative Abundance Indices. Relative Abundance Indices (RAIs) were used to report number of animal detections. To compute the RAI, all detections were summed for all camera traps over all days, multiplied by 100, and divided by the total number of camera trap nights (O'Brien *et al.* 2003). The RAI was calculated as the number of photo captures per 100 trap nights to allow comparisons of each grid cells within the same season and using Chi-square tests to test differences between seasons.

Species distribution modeling and validation. Presence data of banteng was used to model the ecological niche and potential distributions. As many as18 variables were considered as determinants of banteng's distributions in UKNP of which 14 accounted for environmental traits (vegetation, geomorphology, predation, and climate), and four accounting for human impacts (settlement, cultivated area, road, and illegal activity), the details are given in Appendix 2.

A distance raster was created using the Euclidean distance tool that measured the distance of each pixel to the nearest primary or secondary forest edge, river, presence of *C. alpinus* or *P. Pardus melas*, settlement, cultivated land, road, and illegal activity. Hereinafter, the distance value was extracted in ArcGIS 10.2.2 (ESRI; Phillips 2008). All distances were obtained from the Badan Kordinasi Survei dan Pemetaan Nasional (http://www.bakosurtanal.go.id/bakosurtanal/peta-rbi). Values for the other environmental variables were automatically extracted from the raster of each of camera trap' location. Environmental layers were created using Maxent software (Phillips *et al.* 2006). For any predicting Maxent model, all rasters were re-sampled to a 100 m grid cell size and a mask layer was created from the park's boundaries to restrict the analysis to the study area (Young *et al.* 2011).

For all combinations of the environmental variables, Pearson's correlation coefficient was used to check for multicollinearity that might have resulted in over-parameterization and reduced the predictive power and interpretability (Morueta-Holme *et al.* 2010). Such provided the variables used in the final dataset: distance to primary forest edge, distance to secondary forest edge, Normalized Difference Vegetation Index (NDVI), elevation, slope, distance to river, distance to presence of *C. alpinus* and *P. pardus melas*, annual rainfall, annual mean temperature, distance to settlement, distance to cultivated land, distance to road, distance to illegal activity (Appendix 3).

This study used the following Maxent v.3.3.3k settings: automatic feature selection, a regularization multiplier at unity, maximum of 500 iterations, 50 replicates, and a convergence threshold of 10^{-5}. This study also used a random test percentage of 10 %. In total, 100 pseudo-absences were randomized in the study area for the construction of the confusion matrix. A map of the potential distribution of the species was constructed using the logistic output, and the programme was run with "auto features" check (Phillips and Dudík 2008). The accuracy assessment of each model was measured using the Area Under The Curve (AUC) from the Receiver Operating Characteristic (ROC) curve (Woodward 1999; Thuiller 2003).

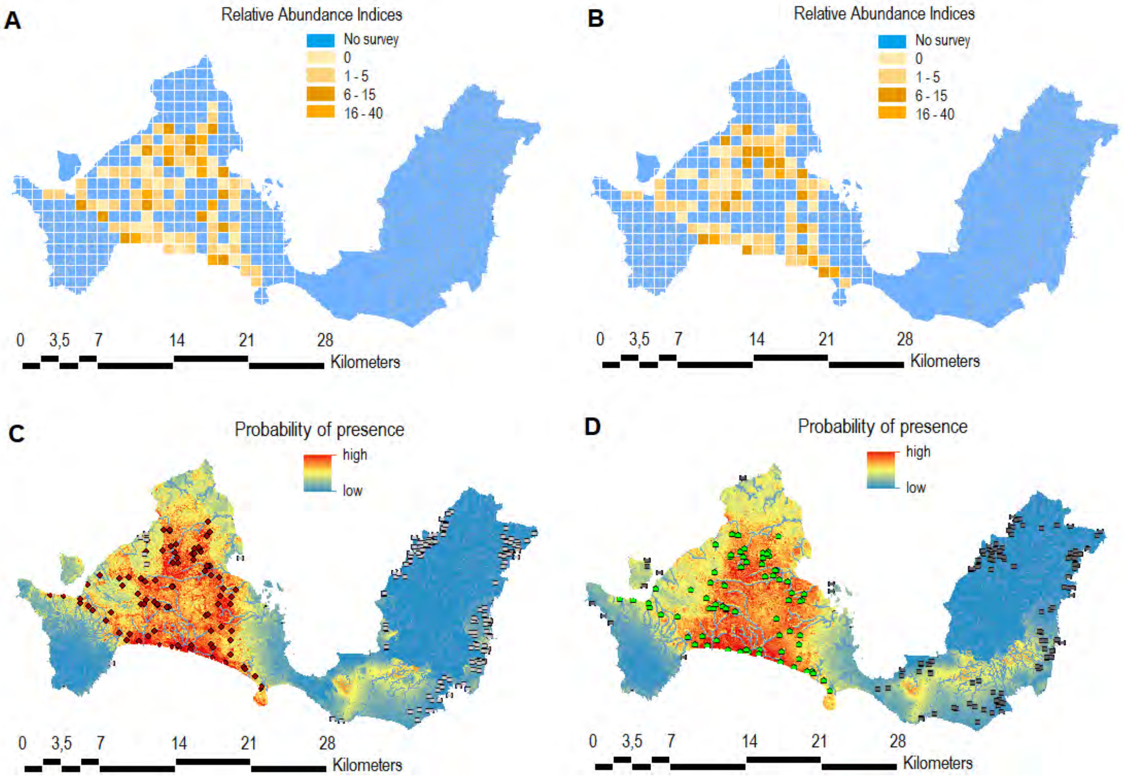

Figure 2. Relative abundance indices in each grid cells (A, B) and probability distribution map of banteng (C, D) in Ujung Kulon National Park (Indonesia) in the wet and dry seasons respectively. The presence of banteng recorded by camera trapping are indicated by red dots for wet season and green dots for dry season, while presence of illegal activity by human are indicated by light grey squares for wet season and by dark grey squares for dry season.

Table 1. The Area Under the Curve (AUC) and standard deviation for species model in two season at Ujung Kulon National Park. Number of independent photographs (NIP), Relative abundance index (RAI).

Season	NIP	RAI	AUC	Standard deviation
Wet	779	4.67	0.835	0.053
Dry	644	4.79	0.899	0.065

Variable contribution and response curve. This study used relative contribution and permutation importance as well as *Jackknife* test to assess the contributions of each environmental variable to the models (Phillips and Dudik 2008).

Results

Relative abundance indices (RAIs). This study recorded as many as 3,199 photographs of banteng with 779 independent photographs during the wet season (RAI = 4.67) and 645 during the dry season (RAI = 4.78). Differences between the seasons were insignificant ($\chi 2 = 0.1985$, d. f. = 1, $P > 0.05$). The highest RAI values both for the wet and dry seasons, were found within the core zone of UKNP (Figure 2A, B).

Species distribution modeling and validation. Areas predicted by the models as having high suitability conditions for banteng, were found almost on the entire park, except the high mountainous area at the southwest in both seasons (Figure 2C, D). All AUC values exceeded 0.835, indicating well-performed distribution models for banteng in each season (Table 1; Figure 3A, B).

Significant explanatory variables. Results of the habitat modelling, suggested that distance to the presence of *Cuon alpinus* was the most influential variable on the presence of banteng in a particular location, both in the wet and dry seasons (23.50 % and 21.70 %, respectively, Table 2) followed by distance to the nearest illegal activity (18.00 % and 19.70 %, respectively). Similarly, based on permutation importance, distance to the presence of *Cuon alpinus* was the most significant both in the wet and dry seasons (24.20 % and 24.90 %, respectively) followed by distance to the nearest illegal activity (9.80 % and 19.00 %, respectively). Distances to secondary forest edge and cultivated area were also shown to have positive influences on the banteng's occurrence contrary to distances to the presence of *Cuon alpinus* and illegal activity. The response curves were roughly unimodal for distance to secondary forest edge and bimodal for distance to the cultivated area during both seasons (Appendix 1, B2). Jackknife test suitability model showed the highest gain when "distance to the presence of *Cuon alpinus*" was used alone, while "distance to secondary forest edge" mostly increased the gain when it was omitted (Figure 3C, D).

Discussion

This study provided the first camera trap photographic analysis and presented an extensive dataset of banteng occurring in the UKNP, south-western Java. For more than two decades, the focus of the national park's management and various studies have been on the conservation of the Javan rhinoceros. The first unexpected result revealed by this study, was the quite large number of recorded ban-

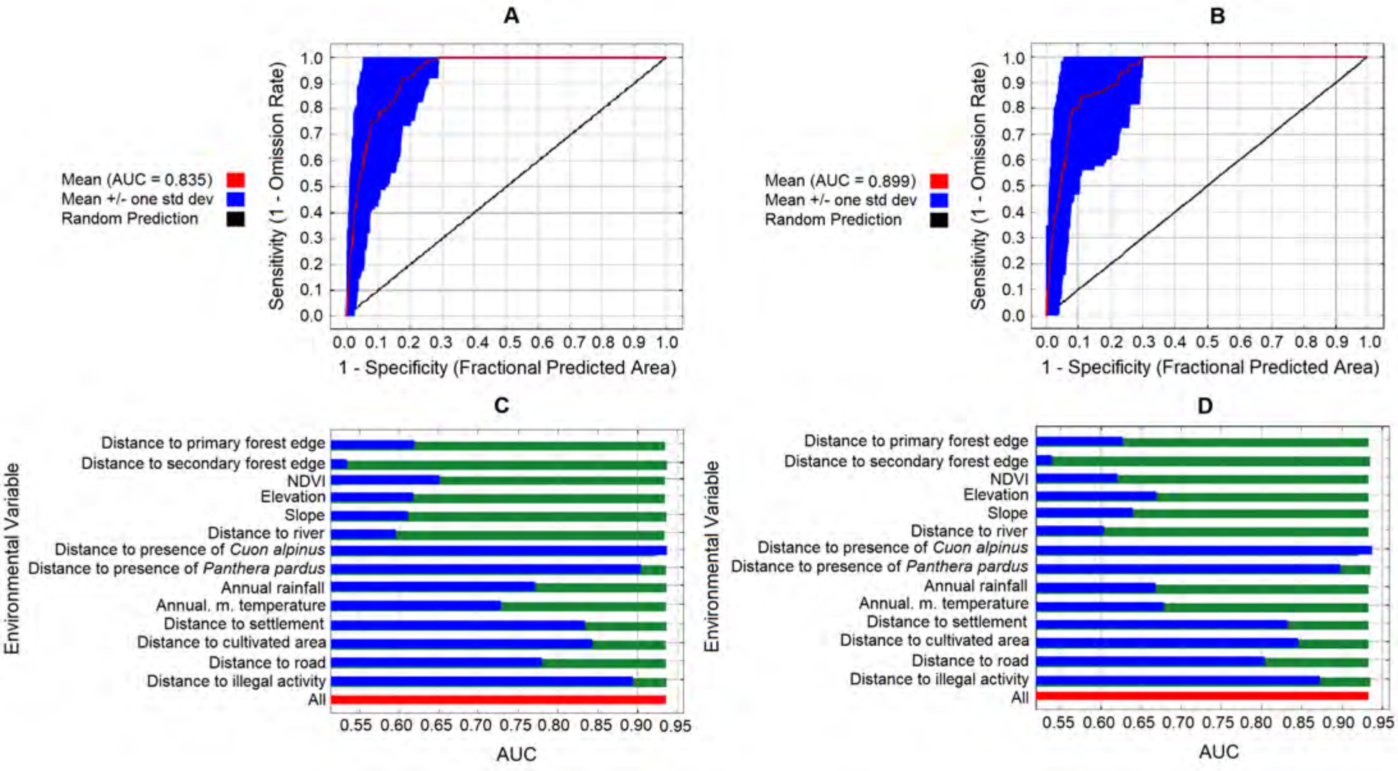

Figure 3. AUC values from distribution model (A, B), and Jackknife tests of AUC values of the Maxent models applied to banteng (C, D) in the wet and dry seasons respectively. For each variable, the blue bar corresponds to the model generated with this variable alone; the green bar corresponds to the model generated without this variable. The red bar corresponds to the model generated with all variables.

teng photographs, as this species is cryptic, *i. e.*, difficult to observe in the forest and considered to be rare in their natural habitat, particularly in the four remaining parks. Although data in this study were restricted to a single national park on the south-western tip of Java Island, the robust sampling design and the variety of surveyed habitats supported these results. Such provided essential basic knowledge for other areas of Java and the whole species' ranges. This measure is useful in a rapid assessment of the concentration sites occupied by the banteng.

The number of photographs per camera trap effort was much higher in the dry season, possibly related to a higher level of activity or more probably due to lower food availability. The abundance of food is inversely related to the proportion of time spent by animals to search and obtain food (Chappell 1980). Even if in most tropical forest, food is available throughout the year (Waide 2008), but in UKNP, it becomes less available during the dry season. This relative scarcity has lead to the broad movements of herbivores species and increases the probability of encounter (Rahman *et al.* 2017).

This study showed that banteng had strong preferences over forests located in lowland areas with high productivity of primary food source. Similar results were found among the banteng populations in Huai Kha Khaeng Wildlife Sanctuary of Western Thailand, where the species strictly uses lowland valleys of 160 to 600 masl (Prayurasithi 1987) and the population at Xe Plan Biodiversity Conservation Area in Laos (Steinmetz 2004). However, not all parts of the forest are occupied or preferred by banteng. Most of the population are concentrated away from the cultivation areas and settlements, which are far from human disturbances and have the least disturbed forest cover and fewest human presence (Pudyatmoko 2005). It seemed that abundance of food, low human pressure, and low level of predation by *Cuon alpinus*, offered the most optimum habitat for banteng. As regrowth of dominant fruit tree canopies is found to be abundant in secondary forest areas, their structures may be atractive to several species of herbivorous mammals (Brown and Lugo 1990; García-Marmolejo *et al.* 2015). Rahman *et al.* (2017) found that such structure supports the habitat needs of muntjac (*Muntiacus muntjak*), one of the main herbivorous mammals in UKNP. This study found that fruits, buds, soft leaves, flowers, bamboo and young grass were consumed by banteng as their daily dietary preferences. This result supported the previous findings by other researchers in Baluran National Park (Halder 1976; Pudyatmoko 2005), Alas Purwo (Pudyatmoko 2005) and Ujung Kulon (Hoogerwerf 1970; Pairah 2007) who concluded that the diets of banteng consists of grass, tree leaves, herbs, shrubs, twigs and fruits, and bark of certain tree species, as found in the faecal analysis and direct observations. Banteng can be classified as a mixed feeder that frequently forages in open grasslands, dry forest and on the edges of evergreen forests (Gardner *et al.* 2014). In Huai Kha Khaeng (Thailand), they utlilise up to 150 different plant species, such as bamboos, fruits, and leaves (Bhumpakphan and McShea 2011).

Table 2. The Relative Contribution (RC) and Permutation Importance (PI) of each environmental variable for each species as an average over the 50 replicates. Values are normalized to give percentages.

Environmental variable	Wet season		Dry season	
	RC	PI	RC	PI
Distance to primary forest edge	5.70	4.50	1.20	0.70
Distance to secondary forest edge	17.00	21.30	17.50	14.80
NDVI	0.10	0.30	0.80	1.50
Elevation	11.30	20.30	8.00	8.60
Slope	2.40	3.30	0.10	0.40
Distance to nearest river	1.20	2.60	1.90	6.00
Distance to presence of *Cuon alpinus*	23.50	24.20	21.70	24.90
Distance to presence of *Panthera pardus*	2.90	0.90	1.90	0.80
Annual rainfall	4.90	1.90	8.10	8.00
Annual mean temperature	2.80	2.80	3.50	0.00
Distance to nearest settlement	3.20	2.10	3.00	1.70
Distance to nearest cultivated area	6.80	5.60	8.40	13.40
Distance to nearest road	0.20	0.40	4.20	0.20
Distance to illegal activity	18.00	9.80	19.70	19.00

The primary and secondary forests that dominated in Ujung Kulon landscape, provided resources for cover and food for banteng. This research found that banteng occurrences were positively associated with forest cover. Furthermore, banteng benefitted directly from the secondary forest with regeneration of native plants. Banteng were likely to be more resilient and adaptable to life in recovered forests than previously suggested, as shown by their preferences for secondary forests in the Baluran National Park or Borneo areas (Gardner *et al.* 2014). Habitat protection from various threats especially human disturbance, would accelerate the recovery time of banteng populations than previously thought. They are known to be effective as seed dispersers (Matsubayashi *et al.* 2007) making them an essential parts of reforestation efforts. Along with the need of forest cover, in UKNP, palm (*Arenga obtusifolia*) tree density is also critical for banteng's habitat, as the fruits provided alternative source of food for the banteng especially during dry season. The central part of the national park has a high dominance of the invasive palm trees, yet it has the highest occupancy rate of banteng, which was estimated to be as much as a forest dominated areas.

The palm in the UKNP ecosystem was a part of the natural succession process that took place after the eruption of Mount Krakatau in 1883 (Putro 1997). Several studies have shown that invasion of this plant has reduced biodiversity in UKNP, both in flora and fauna (Putro 1997). Moreover, this plant has been identified as a potential limiting factor in the distribution of Javan rhinos because it prevented the growth of food plant species, thus created a nutrition-poor area in which rhinos roamed (Hariyadi *et al.* 2012). Although this invasive palm provides benefits for the banteng and other wild animals in UKNP, limiting the place where this invasive species grows is necessary. Controlling palm and other invasive plant species can potentially be used to improve the wild animals' accessibility to certain areas within the habitat, and this has been started since 1997 in UKNP.

However, a recent study indicated that red muntjac tends to come closer to cultivation areas close to the park, because agricultural crops are attractive especially in the dry season (Rahman *et al.* 2017). Banteng in this study seems to do the same and do not restrict their movements to the non-protected area. The immense potential of domestic animals associated with human settlements or the presence of livestock (domestic cattle and water buffalo) that were commonly seen grazing in adjacent areas or within the national park around the Honje mountains, have attracted the presence of banteng. Such interaction might lead to distrupted population health and transmission of diseases from domestic animals, humans and *vice versa* (Morand *et al.* 2014). Limiting grazing areas for livestock owned by local communities around protected area is needed, including do a joint routine patrols by park manager and local communities to minimize these threat.

The model suggested that the variable distance from the nearest settlement as human accessibility and human disturbance affecting banteng occurrences. Higher banteng's occurrences with greater distances from the settlement, might indicate the higher abundance and concentration of banteng's activities in these less disturbed areas. These results is in line with the study by Gardner *et al.* (2014), which shows that banteng in the tropical lowland dipterocarp forest of Sabah (Borneo) is more abundant in areas with limited human presence. High levels of human activities in the lowlands could indicate the lowest occupancy rate and detection of banteng. Also, banteng detection increased with distance to deforested areas, indicating that banteng avoided nearby sites with deforested areas. Banteng prefers habitats with forest cover, and they usually avoid areas with human activities (Pudyatmoko 2005; Gardner *et al*. 2014). All areas with no vegetation cover in the study area, were associated with human activities, including farmland, open grasslands for livestock, and near roads and settlements. In these areas, banteng were more susceptible to hunting. Other studies have shown that banteng and other hoofed species, avoid areas with higher hunting activity and in the long term, increased their nocturnality (Gardner *et al*. 2014; Lone *et al.* 2015; Gaynor *et al.* 2018). Although poaching were found to occur in several locations within the park, banteng were not the target, and based on the interviews with the local people, they were generally undisturbed. Bantengs were not hunted since they have caused little crop damage in the area. However, future agricultural expansion could increase potential human-banteng conflicts, as well as potential of transmitted diseases as described previously.

Dhole (*Cuon alpinus*) has a significant negative interaction and overlapping habitat with banteng. In some captures, it is possible to see the banteng predation activity by dhole. A group of dhole were targeting a calf by separating from its mother. On the other hand, dhole is almost entirely a diurnal hunter in UKNP as observed in another study by Nurvianto *et al.* (2015), probably due to the difficulties in coursing after fleet-footed prey in dense cover in darkness. Dholes have the advantage of large-sized prey hunts because they are living in groups (Rahman *et al.* 2019). The dhole's activity also overlaps with wild boar, but the level of consumption of wild boar by dholes is lower than with banteng (Kamler *et al.* 2012). This overlap is in agreement with the pattern of movement and distribution of herbivore animals, that are generally strongly associated with predators. Herbivores tend to adjust the movement through the avoidance strategy (Flaxman *et al.* 2011; Rosier and Langkilde 2011; Van Langevelde *et al.* 2013).

Other variables such as NDVI, elevation, slope, distance to river, annual temperature and annual precipitation were found to be insignificant, possibly because their variation were too small within the area studied or fell within the usual range for the banteng. The UKNP is an example of lowland tropical rainforest with low elevation and slope variation, which can reach to 800 masl (S. Hedges, press Comm. 2008). The increase showed a significant negative correlation with the presence of banteng (Namgyal and Thinley 2017). The positive effects of NDVI were found to be closely related to the herbivorous nature of the species because of their dependence on forests. From *ca.* 70 % of all forest habitat types in the UKNP, secondary forest were highly dominant and strongly associated with the presence of herbivore animals.

There were many camera trap studies focused on the Javan rhinoceros, and banteng photographs are consistently recorded as by-products. To date, there has been little support for ungulates research targeted in Indonesia, hence it is often difficult to execute a large scale, and long-term individual studies on ungulates. This study provides an outline of research and analysis that was easily customisable for use across species ranges and in standard formats. The modelling framework presented here, provided interesting results, with notably high and stable AUC values which are common for the species specialist like bantengs. Furthermore, concerning the map of banteng distribution to demonstrate the modelling strategy, this study has shown that banteng's occupation area has been restricted in the Ujung Kulon Peninsula. This study provided valuable baseline information on habitat use of banteng in UKNP that would assist the park management to detect changes to make effective conservation decisions and measures.

Moreover, one important thing to be noted is that habitat degradation and loss by natural catastrophes such as sea-level rise, cyclones, volcanic activity, and tsunami are still ongoing threats to banteng in UKNP (Yusuf and Francisco 2009). With the majority of the population concentrating in the centre and near the shoreline of the Ujung Kulon Peninsula, banteng and their preferred habitats are highly exposed to risks of tsunami lunge and inundation. Although annual probability predictions of an earthquake causing tsunami heights of greater than three metres at UKNP is relatively small, but over longer time-frames (> 100 years), tsunamis of 30 metres are probable (Horspool *et al.* 2014). Recently, on December 2018, a tsunami caused by a landslide in the Sunda Strait following a massive eruption of the Anak Krakatau volcano, struck the western tip of Java and southern end of Sumatra. The tsunami generated waves up to five metres, some of which crashed ashore Ujung Kulon, which would threaten the majority of areas with high banteng density, potentially leading to drowning or considerable alteration of primary habitat. To significantly reduce banteng extinction risk in UKNP, human intervention and long-term investment will be necessary. These would include both, an increase in UKNP's carrying capacity through habitat management or food supplementation and establishing additional independent populations that are less exposed to tsunamis and other threats present at UKNP.

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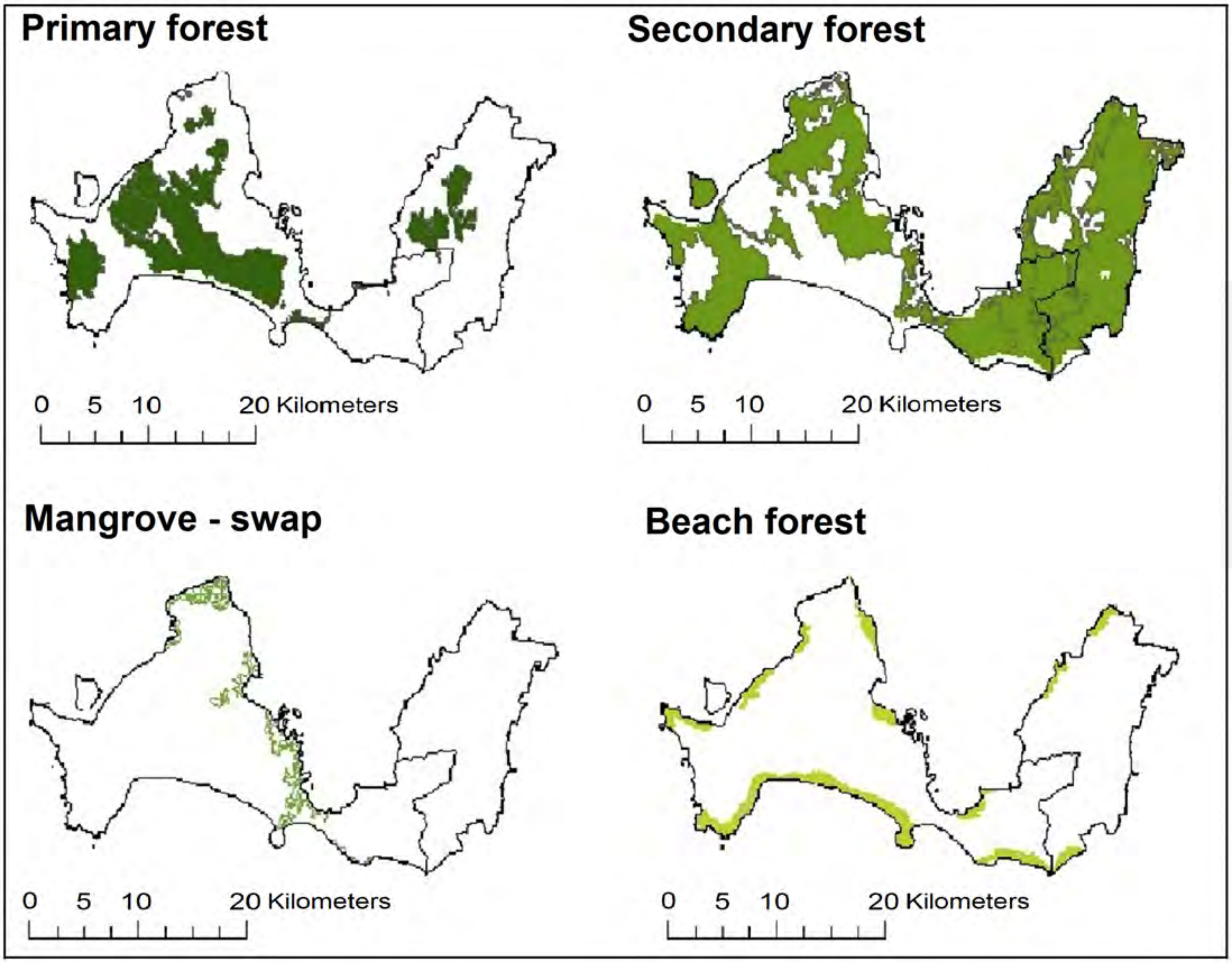
Appendix 1


Primary forest
Secondary forest
Mangrove - swap
Beach forest
0 5 10 20 Kilometers
0 5 10 20 Kilometers
0 5 10 20 Kilometers
0 5 10 20 Kilometers

Appendix 2

The environmental variables was considered to influence banteng distribution in Ujung Kulon National Park

Environmental variables classification	Variables	Measured analysis
Vegetation variables	Distance to primary and secondary forest edge, and vegetation productivity	Distance to the primary and secondary forest edge were extracted in ArcGIS 10.2.2, whilst vegetation productivity measured as the normalized difference vegetation index (NDVI, cf. Hansen et al. 2009)
Geomorphology variables	Elevation, slope and distance to nearest river	The first two variables were computed on a 1 km^2 grid resolution by averaging information extracted from a 90 x 90 m Digital Elevation Model (DEM; Landsat 8 (http://earthexplorer.usgs.gov; http://srtm.csi.cgiar.org). Slopes were generated using slope function in ArcGIS (Jarvis et al. 2008). Distance to the nearest river was extracted in ArcGIS 10.2.2
Predation	Distance to the nearest presence of *C. alpinus* and *P. pardus melas*	Distance to the nearest presence of *C. alpinus* and *P. pardus melas* were extracted in ArcGIS 10.2.2
Climate variables	Annual rainfall, rainfall of the wettest month, rainfall of the driest month, annual mean temperature, the maximum temperature of the warmest month, and minimum temperature of the coldest month	These variables, derived from monthly temperature and rainfall values recorded between 1950 and 2000 from a global network of climate stations, were downloaded from the WorldClim database (http://worldclim.org/bioclim). All layers were projected into WGS 1984 Zone 48 South
Human impact variables	Distance to the nearest settlement, cultivated area, road, and illegal activity by human	Distance to the nearest settlement, cultivated area, road, and illegal activity by human were extracted in ArcGIS 10.2.2

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Appendix 3

Pearson's correlations between the environmental variables used in the distribution modeling for banteng in Ujung Kulon National Park.

Variables	NDVI	Elevation	Slope	Distance to river	Distance to primary forest edge	Distance to secondary forest edge	Distance to settlement	Distance to cultivated area	Distance to road	Ann.m. temperature	Min.temp. of the coldest month	Max.temp.of the warmest month	Ann.rainfall	Rainfall during the wettest month	Rainfall during the driest month	Distance to illegal activity	Distance to presence of *C. alpinus*	Distance to presence of *P. pardus melas*
NDVI	1																	
Elevation	-.008	1																
Slope	-.032	.195**	1															
Distance to river	-.067	.242**	-.091	1														
Distance to primary forest edge	.094	-.499**	-.217**	.015	1													
Distance to secondary forest edge	-.040	.513**	-.059	.333**	-.329**	1												
Distance to settlement	.039	.508**	.155*	.024	-.560**	.240**	1											
Distance to cultivated area	.038	.514**	.122*	.039	-.553**	.217**	.388**	1										
Distance to road	.049	.517**	.116*	.044	-.514**	.243**	.503**	.070**	1									
Ann.mean temperature	-.013	-.512**	-.144*	-.180**	.580**	-.530**	-.561**	-.540**	-.542**	1								
Min.temp. of the coldest month	.033	**-.917****	-.150*	-.165**	.622**	-.513**	-.524**	-.478**	-.477**	**.976****	1							
Max.temp. of the warmest month	.010	.022**	-.156*	-.163**	.619**	-.528**	-.628**	-.575**	-.545**	**.989****	.677**	1						
Ann.rainfall	-.078	.050**	.166*	.144*	-.544**	.480**	.266**	.228**	.222**	-.680**	-.443**	-.468**	1					
Rainfall during the wettest month	-.186**	-.263**	.016	-.134*	.044	-.168*	-.667**	-.665**	-.686**	.258**	**-.822***	.292**	**.765****	1				
Rainfall during the driest month	.118	**-.952****	.057	.236**	-.354**	.500**	.529**	.486**	.520**	-.546**	-.553**	**-.751****	**.899****	-.609**	1			
Distance to illegal activity	-.013	-.512**	-.144*	.619**	-.528**	-.628**	-.575**	-.545**	.619**	.049	.517**	.116*	.044	.010	.022**	1		
Distance to presence of *C. alpinus*	-.065	.045**	.187*	.166*	-.522*	.450**	.270	.233**	.298**	-.540	-.333**	-.548**	.094	-.499**	-.217**	.015	1	
Distance to presence of *P. pardus melas*	-.088	.054**	.169*	.146*	-.577*	.490**	.266**	.256**	.233*	-.677**	-.413**	-.488**	.049	.517**	.116*	.044	-.514**	1

** Correlation is significant at the 0.01 level (2-tailed).
* Correlation is significant at the 0.05 level (2-tailed).

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Bat diversity of the Serranía de San Lucas (Bolívar and Antioquia), northern Colombia

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Serranía de San Lucas is an isolated mountain ridge in the Northern Andes, reaching above 2,500 masl, located between the Central and the Eastern Cordilleras in northeast Colombia, including parts of Bolívar and Antioquia departments. Due to its particular location and difficult access, there are few studies on its biological diversity. In order to clarify the geographical affinities of its bat fauna, we conducted a survey at four representative localities of this mountain range. Between 2015 and 2017, we conducted four assessments to characterize the bat species richness in San Lucas; these localities represent the dominant habitats in the area, including lowland, premontane forests, and swamps. We used three to six mist nets per night, between 17:30 and 23:00 h and identified species in the field, collecting specimens to corroborate and document the diversity in each location. Species accumulation curves and non-parametric estimators assessed efficiency of sampling; in addition, Jaccard's similarity index was used to assess beta diversity. Each species was assigned to a trophic guild for ecological analyses and comparisons of the assemblages. We recorded 47 species from six families, with Phyllostomidae being the most diverse (35 species). Although species richness at a local scale varied between 14 and 23 species, the heterogeneity among them shows a particular richness for San Lucas as a whole. A notable geographic record was *Mimon cozumelae*, which extends its known distribution in northern South America, while other four species are confirmed for the Magdalena Valley, reinforcing a trans-Andean influence. Our records reinforce a biogeographical connection with the region of Chocó-Nechí-Magdalena, thus contributing to validation of the perception that San Lucas shows greater affinity to the Central Cordillera than to the Eastern one. It is evident that several groups (*i. e.,* insectivorous) have not been fully sampled, and that new methods (diurnal roost searches and acoustical sampling) and longer survey efforts might reveal more additions to this list. Our study reveals some peculiarities in the diversity of bats of Serranía de San Lucas, including species typical of inter-Andean valleys and suggesting an influence of the trans-Andean zone, resulting in major similarities to assemblages from northwestern Colombia and South America, but with a specific composition that is indicative of the good state of conservation of the habitats in the study area and its relevance as a future, and necessary, protected area for the country.

La Serranía de San Lucas constituye un ramal montañoso aislado de los Andes del Norte, alcanzando más de 2,500 msnm, entre las cordilleras Central y Oriental, en el nororiente de Colombia, incluyendo parte de los departamentos Bolívar y Antioquia. Debido a su ubicación particular y difícil acceso, son pocos los estudios sobre su diversidad biológica. A fin de clarificar las afinidades geográficas de su quiropterofauna, se propuso un muestreo en localidades representativas de esta serranía. Entre 2015 y 2017, se realizaron cuatro evaluaciones a fin de caracterizar la riqueza de murciélagos de la serranía; estas localidades representan hábitats dominantes en la zona, incluyendo bosques de tierras bajas, bosques premontanos y ciénagas. Se utilizaron de tres a seis redes de niebla por noche, entre las 17:30 y 23:00 h. Se identificaron las especies en campo, recolectando ejemplares para corroborar y documentar la diversidad en cada localidad. Se realizaron curvas de acumulación de especies y estimadores no paramétricos para evaluar la eficiencia del muestreo, adicionalmente se calculó el índice de similitud de Jaccard para evaluar la diversidad beta. Cada especie fue asignada a un gremio trófico para los análisis ecológicos y comparaciones del ensamblaje. Registramos 47 especies pertenecientes a seis familias, siendo Phyllostomidae la más diversa (35 especies). Aunque la riqueza de especies a escala local varió entre 14 y 23 especies, la heterogeneidad entre ellas muestra una riqueza particular para la serranía de San Lucas. Registros geográficos notables incluyen a *Mimon cozumelae* que extiende su distribución en el norte de Sudamérica; mientras cuatro especies son confirmadas para el valle del Magdalena, reforzando una influencia transandina. Nuestros registros refuerzan una conexión biogeográfica con la región del Chocó-Nechí-Magdalena, lo cual contribuye a validar la percepción que San Lucas muestra mayor afinidad a la cordillera Central que a la Oriental. Se evidencia que muchos grupos (*i. e*., insectívoros) no han sido exhaustivamente muestreados y es posible que nuevas metodologías (búsqueda de refugios diurnos y muestreo acústico) y mayores esfuerzos en otras localidades revelen más adiciones a la lista. Nuestro estudio revela ciertas particularidades en la diversidad de murciélagos de esta serranía, incluyendo especies típicas de valles interandinos y sugiriendo una influencia de la zona Transandina, con mayores similitudes respecto a ensamblajes del noroccidente de Colombia y Sudamérica, aunque su composición específica también indica el buen estado de conservación de los hábitats situados en la zona de los muestreos y su relevancia como una futura, y necesaria, área protegida en el país.

Keywords: assemblages; Chiroptera; distribution; northern Andes; species richness.

Introducción

Durante los últimos años, se han encaminado esfuerzos notables para actualizar el conocimiento de los mamíferos en Colombia; una reciente actualización concluyó con el registro de 492 especies silvestres (Solari *et al.* 2013). A partir de revisiones taxonómicas o adiciones de nuevas localidades de distribución para varias especies neotropicales, este número se incrementó a 500 para el año 2014 (Ramírez-Chaves y Suárez-Castro 2014). Dos años después, se incrementó a 518 (Ramírez-Chaves *et al.* 2016), y el estimado más reciente incluye 528 especies (Ramírez-Chaves *et al.* 2018). Estos cambios reflejan la complejidad del estudio sistemático y taxonómico de los mamíferos en el país, incluyendo la constante revisión de colecciones y el estudio de nuevas áreas, a pesar de ser comparativamente mejor conocidos que otros vertebrados.

Un dato destacable en estos estudios ha sido la verificación que el grupo más diverso es el de los murciélagos (orden Chiroptera) con alrededor de 209 especies, seguido por los roedores (orden Rodentia) con alrededor de 132 especies. Al igual que la generalidad de los mamíferos, los murciélagos no se encuentran homogéneamente distribuidos en el país, debido a la gran variedad de hábitats y climas presentes, esperándose una mayor diversidad de especies en las zonas tropicales (Kattan *et al.* 2004; Mantilla-Meluk *et al.* 2009; Solari *et al.* 2013; Mantilla-Meluk *et al.* 2014). Los murciélagos son importantes elementos de los ecosistemas de bosque tropical; ellos influyen en la estructura, composición y dinámica de estos sistemas a través de procesos como la dispersión de semillas, polinización, e impactos sobre poblaciones de insectos (Kunz *et al.* 2011), y sirven como presas potenciales para diferentes depredadores como algunos mamíferos, búhos y serpientes (Gillette y Kimbourgh 1970). Por ello, se consideran indicadores de disturbios ambientales causados tanto por el hombre o por cambios climáticos drásticos (Jones *et al.* 2009), en adición a los importantes servicios ecosistémicos mencionados anteriormente.

Una de las zonas de alta montaña más interesantes de Colombia, virtualmente inexplorada, es la Serranía de San Lucas, cubierta en su mayor parte por selvas húmedas frecuentemente nubladas (Castaño-Uribe *et al.* 1999; Salaman *et al.* 2002). Se trata de una serranía topológicamente compleja y accidentada, lo cual ha permitido sugerir que presenta una biota bastante endémica, probablemente de afinidad andina (Hernández-Camacho *et al.* 1992), pero de la cual no se tienen datos empíricos que soporten dicha idea (Salaman *et al.* 2002). Este potencial endemismo también podría extenderse hacia los mamíferos, incluyendo los murciélagos.

La adecuada caracterización de la biodiversidad de una región como la Serranía de San Lucas, requiere la obtención de listados taxonómicos precisos y actualizados. Para esta región solamente existen estimados preliminares de la diversidad de mamíferos y murciélagos (Castaño-Uribe *et al.* 1999). Listas previas de murciélagos en zonas próximas a la Serranía San Lucas (pero no al interior), como Hershkovitz (1949) para dos localidades del departamento de Bolívar, incluye solo nueve especies, mientras que un estudio en la vereda La Cruz, municipio de Remedios (J. Campuzano, com. pers.) incluye resultados de varios muestreos realizados durante un año en un fragmento de bosque húmedo. Este último estudio resultó en una lista que incluye 19 especies.

Debido a estas imprecisiones en cuanto a datos sobre la diversidad, el propósito de nuestra investigación en la Serranía de San Lucas incluye la descripción y caracterización de la diversidad de murciélagos en esta región para mejorar nuestro entendimiento de sus afinidades faunísticas. Debido a su posición aislada respecto a la Cordillera Central, entender sus afinidades permitirá evaluar algunas interrogantes biogeográficas y ecológicas previamente planteadas respecto a los límites de la región denominada Chocó-Nechí-Magdalena (Hernández-Camacho *et al.* 1992).

Metodología

Área de estudio. La Serranía de San Lucas constituye el extremo norte de la Cordillera Central, ocupando la región sur del Departamento de Bolívar y el extremo oriental del Departamento de Antioquia, con una extensión aproximada de 200 km (norte-sur), alcanzando alturas de 2,700 m. Esta serranía está aislada de la Cordillera Central por el Río Nechí, que inunda una planicie en su extremo nordeste; así, sobre la isolínea de los 1,000 m, la serranía se encuentra separada por más de 75 km de la Cordillera Central, y por casi 65 km de la Cordillera Oriental, por el valle del Magdalena Medio colombiano (Figura 1). Desde el punto de vista biológico, se ha considerado como un enigma debido a que la inestabilidad política y social, acentuada por un prolongado conflicto armado, ha impedido el acceso a la zona, y cuando esto ha sido posible solo se ha logrado estudiar el límite inferior, por debajo de 1,500 m, y con esfuerzos limitados de muestreo, mayormente por avistamientos (Salaman *et al.* 2002). Las localidades visitadas se encuentran dentro del zonobioma del bosque húmedo tropical (*sensu* Hernández-Camacho *et al.* 1992), incluyendo mosaicos de paisaje con una matriz paisajística de bosques primarios, bosques secundarios en avanzado estado de regeneración, bosques riparios, pastizales, rastrojos, riveras de quebradas y ciénagas. Además, algunos de estos sitios están dedicados a la conservación a partir de iniciativas comunitarias como los encontrados en las localidades Ojos Claros y Cerro 1800.

Captura de animales. Entre abril de 2015 y febrero de 2017 se realizaron cuatro expediciones en diferentes localidades y épocas climáticas en las estribaciones de la Serranía de San Lucas (Tabla 1). Para la captura de murciélagos, se usaron de tres a seis redes por noche (6 o 12 m de largo), que estuvieron activas, en promedio, desde las 17:30 hasta las 23:00 horas. Las redes fueron revisadas cada 30 minutos o menos, según la actividad de los murciélagos en cada sitio y en cada noche. Se seleccionaron, primariamente, áreas naturales con poca intervención humana, pero también buscando incluir diferentes hábitats representativos.

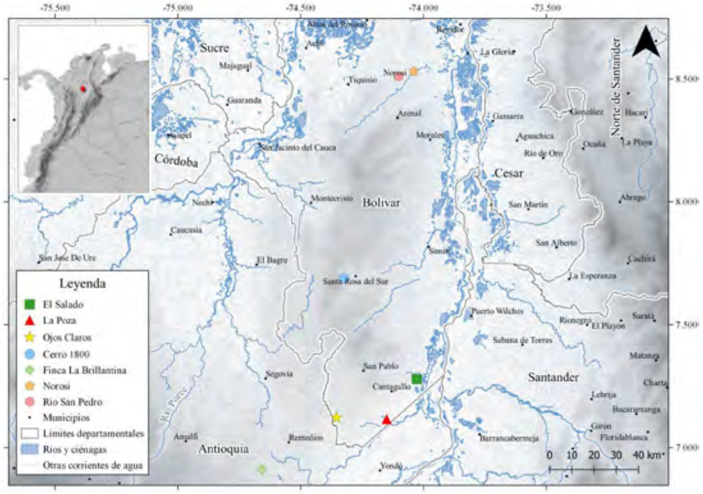

Figura 1. Ubicación de las cuatro localidades de muestreo en la Serranía de San Lucas en la región sur del Departamento de Bolívar y el extremo oriental del Departamento de Antioquia. Se incluye las localidades referenciadas en el texto: Norosí y Río San Pedro (norte de Bolívar; Hershkovitz 1949) y Hacienda La Brillantina, Remedios (oriente de Antioquia; J. Campuzano, no publ.).

Los murciélagos capturados fueron medidos y examinados (medidas externas, peso, estado reproductivo, condición general y presencia de ectoparásitos) para facilitar su determinación taxonómica. Esta determinación se realizó mediante el uso de las claves pertinentes (Gardner 2008; Díaz *et al.* 2016), hasta el nivel taxonómico que éstas lo permitieron (género o especie). A fin de documentar adecuadamente esta diversidad, algunos ejemplares se colectaron y prepararon según los procedimientos sugeridos por Sikes *et al.* (2016), siendo preservados como cuerpos completos y carcasas en alcohol, así como pieles disecadas, cráneos y esqueletos. De cada individuo colectado se tomó una muestra de tejido hepático para futuros estudios de identificación genética, también se colectaron ectoparásitos que se almacenaron en etanol al 96 %. Para las especies más comunes, los individuos ya identificados se liberaron en la misma cobertura donde fueron capturados. Todo el material colectado fue depositado en la Colección Teriológica de la Universidad de Antioquia (CTUA).

Tabla 1. Localidades incluidas en el muestreo, fechas y época de cada expedición, y esfuerzos de muestreo empleados en cada sitio. Las fechas de cada salida incluyen tanto las noches de muestreo efectivo como el acceso a cada localidad.

Localidad	Coordenadas	Elevación (msnm)	Fechas y época	Esfuerzo (m^2-hrs-noche)
		Departamento Antioquia		
Municipio de Remedios, Vereda Ojos Claros	74° 21′ 36.9″ W 7° 06′ 54.1″ N	290 - 509	14 abr - 09 may de 2015 (seca)	7,632
		Departamento Bolívar		
Municipio Santa Rosa del Sur, Vereda San Juan, Cerro 1800	74° 19′ 20.8″ W 7° 41′ 00.5″ N	1003 - 1225	22 - 29 jul de 2015 (seca)	1,290
Municipio Cantagallo, Vereda El Salado	74º 16′ 53.5″ W 07° 16′ 54.6″ N	91 - 134	16 - 31 oct de 2016 (lluvias)	1,266
Municipio Cantagallo, Vereda La Poza	74º 9′ 5.2″ W 7° 6′ 26.1″ N	85 - 159	10 - 27 feb de 2017 (seca)	1,836

Análisis de datos. Para evaluar la representatividad del muestreo construimos curvas de rarefacción de especies y calculamos los estimadores no paramétricos Chao1 (abundancia) y Chao2 (incidencia) empleando el programa EstimateS 9.1.0 (Colwell 2013). Generamos dichas curvas basadas en individuos con el fin de hacer comparaciones entre los sitios de muestreo (Colwell y Coddington 1994), debido a las diferencias en los esfuerzos de muestreo empleados. Adicionalmente, se realizó un análisis de diversidad beta calculando la similitud entre las cuatro localidades (Moreno 2001), para discutir las diferencias entre la composición de especies de estos sitios; un clúster jerárquico se realizó empleando un análisis calculado a partir del índice de similitud de Jaccard, en el programa PAST 3 (Hammer *et al.* 2001).

Como una primera aproximación al estudio del ensamblaje de murciélagos en la Serranía de San Lucas, se empleó la matriz de nichos tróficos y tallas desarrollada por McNab (1971) y empleada informativamente para caracterizar ensamblajes similares en Trinidad, Panamá, Costa Rica, Brasil, y la Guyana (Willig 1986; Lim y Engstrom 2001). Este sistema predice que solo una especie común ocupará cada celda de esta matriz de doble entrada, lo que abre la posibilidad de expandir la discusión a partir de las celdas donde más de una especie ocurre. Las categorías de nicho trófico siguen aquellas sugeridas por LaVal y Fitch (1977), y ampliadas por Patterson *et al.* (1996) y Lim y Engstrom (2001); las categorías de peso siguen la sugerencia por Lim y Engstrom (2001). A pesar de algunas limitaciones en este diseño (ver Discusión), consideramos que el aporte informativo es valioso para esta caracterización del ensamblaje.

Adicionalmente, se realizó un análisis del rol funcional que cumplen las especies de murciélagos, siguiendo a Soriano (2000). Esto se logra caracterizando los nichos y roles tróficos de cada especie, para obtener los equivalentes tróficos (ET) de cada gremio y estimar el porcentaje de aporte de cada gremio al ensamblaje total. Solo en el caso de *Trinycteris nicefori* se cambió la categorización sugerida por Soriano (2000) a una más acorde a lo que se conoce de su historia natural (Gardner 2008). Una ventaja de este análisis es que también permite la comparación de los resultados entre sitios de estudio, aumentando la perspectiva de uso de estos hallazgos.

Resultados

Luego de más de 50 noches efectivas de muestreo, se completó un esfuerzo de 12,024 m^2-horas-noche (Tabla 1), registrando un total de 590 individuos, e identificando 47 especies de murciélagos (Tabla 2) pertenecientes a seis familias y 33 géneros. En la localidad Ojos Claros registramos 23 especies (148 individuos), en el Cerro 1800 registramos 14 especies (79 individuos), en El Salado, 22 especies (283 individuos) y en La Poza, 21 especies (80 individuos). Algunos registros notables incluyen siete especies de insectívoros de follaje (*Gardnerycteris keenani*, *Lampronycteris brachyotis*, *Lophostoma silvicola*, *Micronycteris hirsuta, M. megalotis*, *Mimon cozumelae*, y *Tonatia saurophila*), y doce especies

Tabla 2. Especies de murciélagos y número de individuos capturados en cada una de las localidades (ver Figura 5).

Familia	Especie	Ojos Claros	Cerro 1800	El Salado	La Poza
Emballonuridae	*Centronycteris centralis*				1
	Rhynchonycteris naso			2	
	Saccopteryx bilineata	1		1	
	Saccopteryx canescens			1	
	Saccopteryx leptura				1
Mormoopidae	*Pteronotus parnellii*	1			2
Noctilionidae	*Noctilio albiventris*			8	2
	Noctilio leporinus			2	
Phyllostomidae	*Desmodus rotundus*	2		2	
	Chrotopterus auritus			1	
	Gardnerycteris keenani	1	1		1
	Lophostoma silvicola	1			3
	Micronycteris hirsuta	1			
	Micronycteris megalotis			2	
	Mimon cozumelae	1			
	Phyllostomus discolor			1	2
	Phyllostomus hastatus			1	1
	Tonatia saurophila		2		1
	Trachops cirrhosus	7			
	Trinycteris nicefori				1
	Lampronycteris brachyotis	1			
	Anoura cultrata		1		
	Glossophaga soricina			4	
	Hsunycteris thomasi	4			
	Lionycteris spurrelli	2			
	Lonchophylla robusta		2		
	Carollia brevicauda	51	30		
	Carollia castanea	9	5	48	16
	Carollia perspicillata	34	6	130	15
	Artibeus lituratus	4	15	19	
	Artibeus phaeotis	5	2	3	1
	Artibeus planirostris	4		15	8
	Artibeus ravus			10	
	Chiroderma salvini		1		
	Chiroderma trinitatum				1
	Chiroderma villosum	2		1	
	Platyrrhinus dorsalis		3		
	Platyrrhinus helleri	2		9	3
	Sturnira bakeri	1	8	3	4
	Uroderma convexum			18	6
	Vampyressa thyone	1	2		1
	Vampyriscus nymphaea	10			
	Vampyrodes major	2			
Molossidae	*Molossops temminckii*				1
	Molossus molossus			2	9
Vespertilionidae	*Myotis caucensis*	1			
	Myotis riparius		1		
Total de individuos		148	79	283	80
Total especies		23	14	22	21

representando las familias insectívoras Emballonuridae (5), Molossidae (2), Vespertilionidae (2), Noctilionidae (2) y Mormoopidae (1).

Al analizar la representatividad del muestreo por localidad, se observa un rápido incremento en la acumulación de especies a medida que aumentan los individuos capturados, pero ninguna de las curvas alcanza una asíntota (Apéndice 1). Con base en el esfuerzo realizado (Tabla 1), los estimadores de riqueza varían entre localidades (Apéndice 2) mostrando que la representatividad del muestreo puede estar por debajo del 70 % (Ojos Claros, 62.7 %, La Poza, 65.4 %) o por encima del 85 % (El Salado, 88 %, Cerro 1800, 92.2 %). En conjunto con las curvas de rarefacción, esto indica que, en localidades como Ojos Claros y la Poza, los ensamblajes estarían compuestos por muchas más especies de las registradas en el presente estudio.

El análisis de la composición de especies muestra una baja similitud entre los ensamblajes en cada localidad. Solo tres de las especies (*Sturnira bakeri*, *Artibeus phaeotis*, y *Carollia castanea*) fueron comunes a todas las localidades, mientras que se registraron entre cinco y nueve especies únicas por localidad (El Salado: 5 especies; La Poza: 6; Ojos Claros: 8; y Cerro 1800: 9; Tabla 2). Respecto a las especies compartidas entre localidades, se encuentra que las localidades de tierras bajas y hábitats asociados a ciénagas (La Poza y El Salado) presentan ensamblajes más similares entre sí, compartiendo el 34 % de las especies. Por otro lado, la localidad más disímil con respecto a las otras es Cerro 1800, compartiendo solo 16 % de las especies con El Salado, y 25 %, con La Poza. Po otro lado, Cerro 1800 y Ojos Claros comparten 23 % de sus especies, con ocho especies en común (Tabla 2). El clúster jerárquico (Figura 2) muestra estas similitudes.

Solamente 23 de las 48 celdas posibles en la matriz de nichos tróficos/pesos para el ensamblaje de la Serranía de San Lucas estuvieron ocupadas (48 %; Apéndice 3). Solo una especie de cada uno, carnívoros/piscívoros, omnívoros y frugívoros nómadas, ocuparon la clase de mayor peso; pero, mientras que los frugívoros nómadas muestran la mayor variación en tallas (cinco celdas, solo ausentes de la celda < 6 g), los dos grupos de insectívoros, aéreos y de follaje, y los nectarívoros ocupan las categorías de menor peso, aunque solo los insectívoros aéreos ocupan la celda de menor peso (< 6 g). En cuanto al análisis de roles funcionales, el gremio de frugívoros nómadas representó el mayor aportante, con el 26.8 %, seguido por los insectívoros aéreos con 21.3 %, y los insectívoros de follaje con 21.1 % (Apéndice 4).

Discusión

En este primer estudio de la quiropterofauna de la Serranía de San Lucas nuestro esfuerzo estuvo limitado al uso de redes de niebla, con sus correspondientes virtudes y defectos (Simmons y Voss 1998; Kunz y Parsons 2009); aun así, nuestros hallazgos muestran un ensamblaje característico de la complejidad de hábitats muestreados en el área de estudio. Por esta razón, los análisis y comparaciones a continuación se hacen con cautela y deben tomarse como preliminares (Fleming 1986; Willig 1986; Kalko *et al.* 1996). En este caso, y dada las condiciones particulares de este muestreo, se combinaron los datos de las cuatro localidades en la

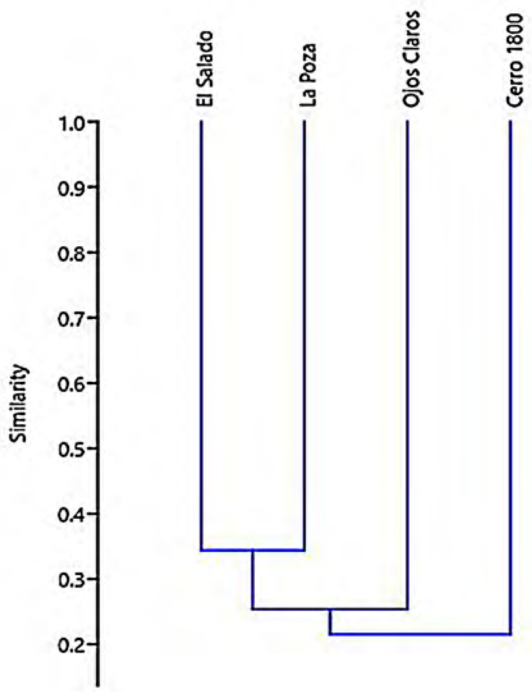

Figura 2. Clúster jerárquico de los cuatro ensamblajes en la Serranía de San Lucas, a partir del índice de Jaccard.

Serranía de San Lucas a fin de comparar cualitativamente la lista resultante (Tabla 2) con evaluaciones similares para el valle del Magdalena, Tolima (*i. e.*, Zona I en Bejarano-Bonilla *et al.* 2007) o Río Claro, en el oriente de Antioquia (Muñoz 1986).

Un primer aspecto a resaltar es que en San Lucas la fauna de murciélagos es más diversa (47 spp.) que la del valle del Magdalena (28 spp.) o Río Claro (27 spp.); sin embargo, esta diferencia no se debe a la presencia de especies endémicas a la serranía, ni a un muestreo más completo de la diversidad regional. Así, algunas especies, como *Molossops planirostris* o *Promops centralis* (valle del Magdalena) no fueron registradas por nosotros, ni tampoco *Anoura caudifer* (Río Claro). Otras especies "faltantes" incluirían a *Phylloderma stenops*, *Vampyrum spectrum* (en Remedios, E Antioquia; J. Campuzano, no publ.) y *Eumops auripendulus* (en Norosí, N Bolívar; Hershkovitz 1949); otras especies potenciales para esta región incluirían a *Thyroptera tricolor* (Thyropteridae), *Lonchorhina aurita* y algunos nectarívoros de las subfamilias Glossophaginae y Lonchophyllinae (Phyllostomidae). Esto puede ser resultado de las limitaciones propias de una primera evaluación, que no se evaluaron todos los hábitats de la zona, o que no se emplearon otras técnicas para el registro de especies, incluyendo la búsqueda de refugios diurnos o el muestreo del estrato arbóreo (Simmons y Voss 1998), y el registro de llamadas de ecolocación (Kalko *et al.* 1996; Zurc *et al.* 2017). Sin embargo, nuestra lista incluye especies como *Vampyrodes major*, *Vampyriscus nymphaea*, y *Mimon cozumelae*, que además de aportar al conocimiento sobre sus distribuciones geográficas, también sugieren una influencia de las regiones Chocó, Nechí y Magdalena, algo discutido previamente por otros autores (Hernández-Camacho *et al.* 1992; Martínez-Arias y Solari 2013). Es interesante que esta conexión en particular había sido indicada a partir de los estudios de la avifauna en el Cerro 1800 (Salaman *et al.* 2002).

En cuanto a la composición específica obtenida en el muestreo, llama la atención la captura de algunas especies que, aunque representadas por solamente de uno a dos individuos, dan idea de un ensamblaje particular y confirman el valor del gremio de especies insectívoras como un adecuado indicador del estado de conservación (Jones *et al.* 2009). La alta diversidad de este grupo se asocia a la existencia de ambientes con poca intervención humana (Fenton *et al.* 1992; Medellín *et al.* 2000), debido al rol ecológico ligado a sus dietas. El monitoreo de la diversidad y de las poblaciones de especies de insectívoros aéreos e insectívoros de follaje en asociación con los bosques que habitan puede ser útil para evaluar el efecto de perturbaciones ambientales (Solari *et al.* 2002; Díaz-Pulido *et al.* 2015).

Registros notables. Respecto a la distribución de especies, el hallazgo de *Mimon cozumelae* (Figura 3A) en Ojos Claros representaría el segundo registro de la especie para Colombia y para Sudamérica (Williams y Genoways 2008), siendo el registro previo un ejemplar de Chigorodó (Antioquia; Marinkelle y Cadena 1972; Solari *et al.* 2013). Es decir, el registro obtenido en la vereda Ojos Claros representa una extensión geográfica de más de 250 km al este de la distribución conocida. La distribución del género en Colombia (Solari *et al.* 2013; Hurtado y Pacheco 2014) es bastante restringida con registros correspondientes a *M. bennettii* para Socorré (Bolívar; Gregorin *et al.* 2008), Serranía de la Macarena (Meta; Cuervo-Díaz *et al.* 1986) y Serranía de Chiribiquete (Caquetá; Montenegro y Romero-Ruiz 1999).

El ejemplar CTUA 2406 es un individuo juvenil, macho, con osificación incompleta de las epífisis de las falanges y escaso o nulo gasto dental. Sin embargo, muestra todas las características que permiten asignarlo a este género. Aunque la taxonomía del género y la distinción entre especies es compleja (Hoppe y Ditchfield 2016), las medidas cráneo-dentales (Apéndice 5) y las características craneales y dentales (Figura 3B) permiten confirmar la identificación. Por ejemplo, la fosa mesopterigoidea (en forma de V) y la caja craneana poco inflada, y dentalmente, el tamaño relativo del talónido del tercer molar inferior son también característicos de *M. cozumelae*. Igualmente, la amplitud del tabique medio del proceso palatino en la premaxila, corresponde a la estructura ósea ubicada entre los forámenes incisivos, es ancha y muestra un foramen accesorio medio, que de acuerdo con Hurtado y Pacheco (2014) también ayudan a distinguir a esta especie de *M. bennettii*. La única discordancia presentada por este ejemplar fue la forma de los incisivos superiores, que se adelgaza para formar una punta (como en *M. bennettii*) en lugar de formar un borde amplio. Consideramos que esto podría deberse a la condición juvenil del ejemplar, con los dientes mostrando poco gasto, o a la variabilidad geográfica indicada por Hoppe y Ditchfield (2016). Además, coincidente con algunas descripciones, este ejemplar muestra la punta de

Figura 3. *Mimon cozumelae* (foto por J. Mosquera), registrado en la localidad Ojos Claros; a la derecha, detalles cráneo-dentales útiles para la identificación de la especie.

las alas de color blanquecino, así como manchas blancas en la base de las orejas (Dalquest 1957; Simmons y Voss 1998).

Otras especies poco comunes de este ensamblaje fueron *Pteronotus parnellii*, *Molossops temminckii*, *Lampronycteris brachyotis*, *Vampyriscus nymphaea*, y *Vampyrodes major*. Este hecho no significa que sean poco abundantes (o "raras") en la región, ya que más bien podría deberse a posibles sesgos metodológicos del muestreo. Inclusive, algunos de estos registros aportan al conocimiento de la distribución de las especies, como en el caso de *V. nymphaea* y *V. major* (Apéndice 6) que constituyen los primeros registros confirmados para el valle del Magdalena (Velazco y Simmons 2011; Rodríguez-Posada y Ramírez-Chaves 2012). También resultó llamativo el hecho que las cinco especies de embalonúridos fueran registradas en El Salado y La Poza, que constituyen ambientes con presencia de ciénagas y que son estacionalmente inundables (elevaciones por debajo de 200 m), y representativas del Magdalena Medio colombiano. Son igualmente importantes que dos especies nectarívoras, como *Lonchophylla robusta* y *Anoura cultrata* (Apéndice 6), solo fueran registradas, con solo un individuo en cada caso, en la localidad de Cerro 1800. Sin duda, esto muestra el escaso conocimiento que hay sobre estos ensamblajes y la necesidad de realizar más estudios sobre el reemplazo altitudinal en cadenas montañosas aisladas (Kattan *et al.* 2004).

Limitaciones metodológicas del muestreo. Debe resaltarse que estudios de mayor esfuerzo y duración, así como empleando una combinación de otras técnicas (Simmons y Voss 1998) resultan imprescindibles para lograr inventarios más completos. Los resultados indican que el muestreo no alcanzó una adecuada representatividad (> 85 %, Apéndice 2) en localidades como Ojos Claros y La Poza, indicando que aún faltan especies por registrar y que la composición regional del ensamblaje puede ser mayor a la esperada. Por otro lado, aunque el menor valor de riqueza específica se dio en Cerro 1800, el estimador de abundancia muestra una representatividad de 92 % (Apéndice 2), a pesar de ser la localidad donde se empleó el menor esfuerzo de muestreo (Tabla 1). Esto puede estar relacionado con los sesgos metodológicos antes señalados, pero también con las diferencias respecto al hábitat y estado de conservación de los sitios muestreados, las cuales aumentan la posibilidad de encontrar nuevas especies con un esfuerzo de muestreo más prolongado, en las mismas localidades o en otras con condiciones de hábitat similares.

Diversidad ecológica del ensamblaje. La descripción ecológica del ensamblaje se hizo mediante dos análisis que, aunque basan su premisa principal en una similar caracterización de los nichos tróficos, muestran diferencias en sus resultados, pero también coinciden en que hay una interesante diversidad de grupos ecológicos. Se ha sugerido que la incorporación de otros parámetros ecológicos (uso del dosel arbóreo, abundancia relativa, dieta) a estas matrices permitiría una evaluación más detallada de la segregación ecológica entre las especies, y un mejor entendimiento de la conformación de estos ensamblajes (Willig 1986).

Una característica particular del análisis de la matriz de nichos tróficos/pesos es que hubo solo una especie "común" (abundante) en las celdas en las categorías de pesos por sobre los 20 g, que corresponde a *Artibeus lituratus*, lo cual es una diferencia con los resultados mostrados por Lim y Engstrom (2001) para Iwokrama. La forma particular de esta matriz sugiere que hay una distribución "natural" de las especies, con especies pequeñas (< 20 g) caracterizando los gremios insectívoros aéreos y nectarívoros, mientras que las especies de mayor talla (> 37 g) caracterizan a los carnívoros/piscívoros y omnívoros. Otro dato de interés es que 12 celdas estuvieron ocupadas por solo una especie, lo que sugiere que aún hay "espacio" para otras especies en este ensamblaje, y que el muestreo no ha logrado completar una adecuada representatividad.

Conservación de la Serranía de San Lucas. Nuestros hallazgos resultan remarcables para la conservación de esta región desde el contexto geográfico, ecológico y social, porque comprenden los primeros muestreos dirigidos y sistemáticos de la quiropterofauna de la Serranía de San Lucas, además de incluir la colecta de ejemplares que permiten verificar estas identificaciones para documentar y/o verificar los patrones sugeridos de riqueza y endemismo de especies en esta región tan aislada (Castaño-Uribe *et al.* 1999; Salaman y Donegan 2001). Dada la escasez de estudios similares, esta información será útil para futuros análisis del estado de conservación, distribución y taxonomía de la fauna asociada a esta serranía. En esa misma línea, estos registros permitirán corroborar la relevancia de especies, ensamblajes y ambientes que merezcan ser parte de programas de conservación, así como estudios sistemáticos precisos y análisis biogeográficos más finos, que una vez se incorporen a los planes de manejo existentes contribuirán a la delimitación precisa de esta zona para su reconocimiento como área protegida en el corto plazo. Al mismo tiempo, nuevos diseños podrían proponerse para el estudio de ciertas especializaciones ecológicas, como en el caso de la dieta, actividad, y selección de refugios por especies de murciélagos. A largo plazo, aspectos puntuales de estos patrones podrían incorporarse a esquemas de monitoreo de las condiciones ambientales que las soportan.

Las particularidades de los registros obtenidos hasta este momento son alentadoras para futuros estudios, pero el estado de amenaza de estos bosques, debido a los avances de la minería informal, extracción maderera no regulada, y la situación de orden público, representan un riesgo cuya solución no puede ser postergada. El reconocimiento de estas características únicas de su biodiversidad, así como de los servicios ecosistémicos que ella presta, son un paso importante en ese sentido. Es de esperar que mayores estudios en esta región ayuden a completar algunos de los vacíos actuales para un mejor entendimiento del ensamblaje de murciélagos y sus roles ecológicos dentro de la Serranía de San Lucas.

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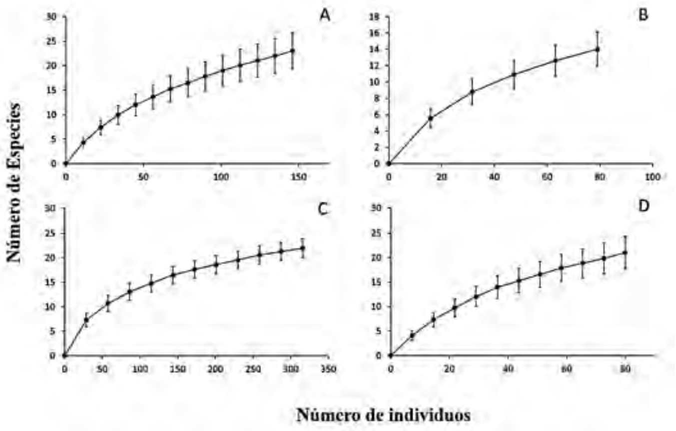
APÉNDICES

Apéndice 1. Curvas de rarefacción de especies de murciélagos en la Serranía de San Lucas por localidades de muestreo. A. Ojos Claros. B. Cerro 1800. C. El Salado. D. La Poza.



Apéndice 2. Estimadores de riqueza basados en abundancia e incidencia por localidad de muestreo en la Serranía de San Lucas.

Localidad		Ojos Claros	Cerro 1800	El Salado	La Poza
Riqueza de especies		23	14	22	21
Estimador de Riqueza					
Abundancia	Chao1	36.66 ± 11.11	15.18 ± 1.82	24.99 ± 3.41	32.11 ± 9.45
Incidencia	Chao2	43.31 ± 16.19	18.20 ± 4.40	25.18 ± 3.37	36.00 ± 11.8
Completitud		62.70%	92.20%	88.00%	65.40%

Apéndice 3. Matriz de nicho trófico y tallas para los murciélagos registrados en la Serranía de San Lucas durante el estudio. El número en paréntesis indica el número de especies comunes (o relativamente abundantes) en dicha celda.

Nicho trófico	< 6 g	6-10 g	11-19 g	20-36 g	37-69 g	> 69 g	Total
Insectívoros aéreos	6 (1)	2	1	2			11
Insectívoros de follaje		2	2	3			7
Nectarívoros		3 (1)	2				5
Frugívoros sedentarios			3 (2)	1			4
Frugívoros nómadas		2	6 (2)	3	1	1 (1)	13
Omnívoros			1	1		1	3
Carnívoros/ Piscívoros				1	1	1	3
Hematófagos				1			1
Total especies	6	9	15	12	2	3	**47**

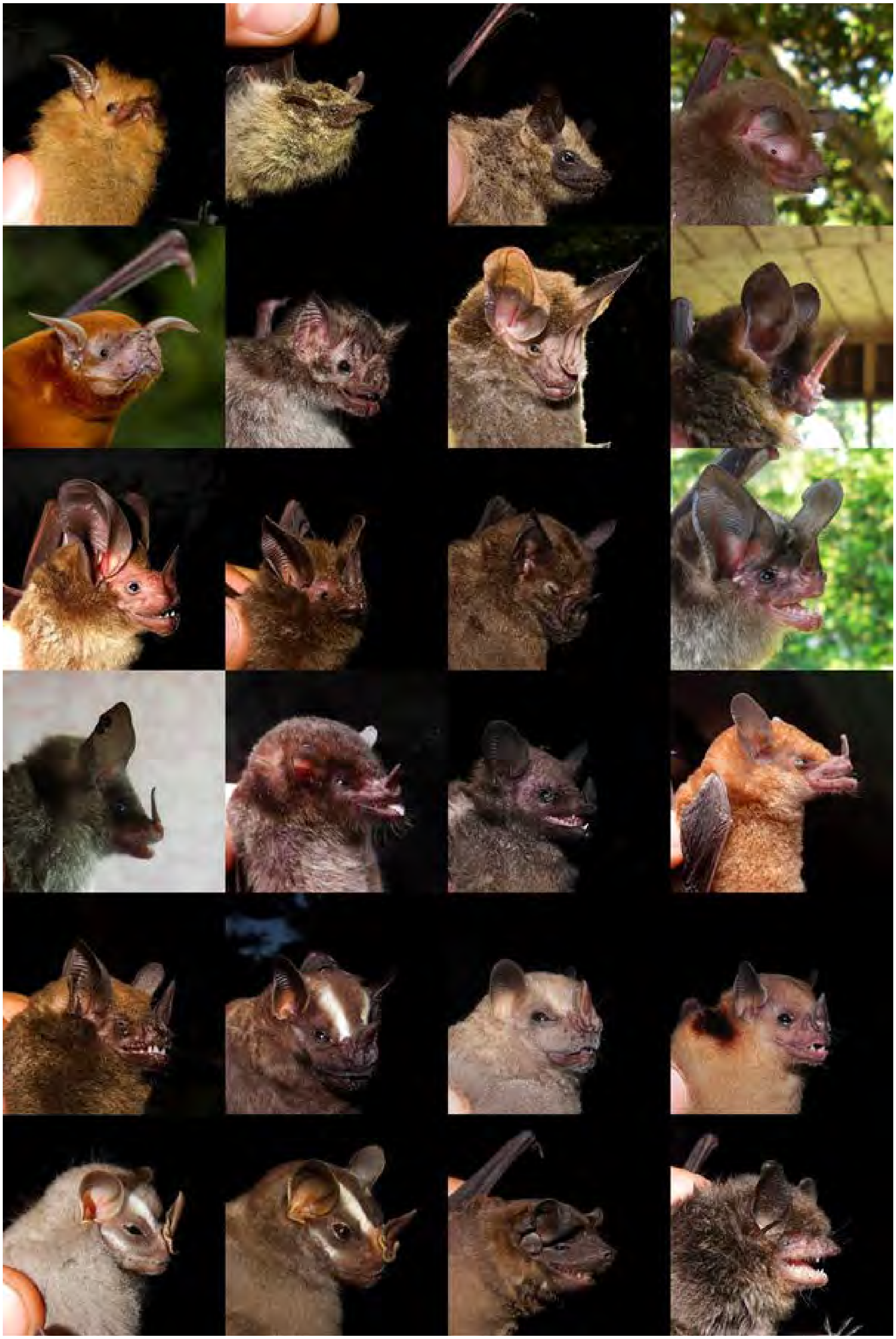
Apéndice 4. Equivalentes tróficos y categorías funcionales del ensamblaje de murciélagos (basado en Soriano, 2000). PIS: Piscívoros, CAR: Carnívoros, SAN: Sanguinívoros, GLE: Insectívoros de follaje, INS: Insectívoros aéreos, FRU_N: Frugívoros nómadas, FRU_S: Frugívoros sedentarios, NEC: Nectarívoros.

FAMILIA / ESPECIE	**Gremios**							
	PIS	**CAR**	**SAN**	**GLE**	**INS**	**FRU_N**	**FRU_S**	**NEC**
Emballonuridae								
Centronycteris centralis					1			
Rhynchonycteris naso					1			
Saccopteryx bilineata					1			
Saccopteryx canescens					1			
Saccopteryx leptura					1			
Mormoopidae								
Pteronotus parnellii					1			
Noctilionidae								
Noctilio albiventris	0.3				0.7			
Noctilio leporinus	0.6				0.4			
Phyllostomidae								
Desmodus rotundus			1					
Chrotopterus auritus		0.8		0.1			0.1	
Gardnerycteris keenani				0.8		0.2		
Lampronycteris brachyotis				0.8			0.2	
Lophostoma silvicola				0.8			0.2	
Micronycteris hirsuta				0.8			0.2	
Micronycteris megalotis				0.8			0.2	
Mimon cozumelae				0.8		0.2		
Phyllostomus discolor				0.4			0.3	0.3
Phyllostomus hastatus		0.2		0.3			0.3	0.2
Tonatia saurophila				0.8			0.2	
Trachops cirrhosus		0.7		0.2			0.1	
Trinycteris nicefori				0.6			0.2	0.2
Anoura cultrata				0.1			0.4	0.5
Glossophaga soricina				0.2			0.2	0.6
Lionycteris spurrelli				0.1			0.1	0.8
Hsunycteris thomasi				0.1			0.1	0.8
Lonchophylla robusta				0.1			0.1	0.8
Carollia brevicauda				0.2			0.8	
Carollia castanea				0.2			0.8	
Carollia perspicillata				0.2			0.8	
Artibeus lituratus				0.1		0.8	0.1	
Artibeus phaeotis				0.1		0.8	0.1	
Artibeus planirostris				0.1		0.8	0.1	
Artibeus ravus				0.1		0.8	0.1	
Chiroderma salvini						1		
Chiroderma trinitatum						1		
Chiroderma villosum						1		
Platyrrhinus dorsalis						1		
Platyrrhinus helleri						1		
Sturnira bakeri							1	
Uroderma convexum						1		
Vampyressa thyone						1		
Vampyriscus nymphaea						1		
Vampyrodes major						1		
Vespertilionidae								
Myotis caucensis					1			
Myotis riparius					1			
Molossidae								
Molossops temminckii					1			
Molossus molossus					1			
Equivalentes Tróficos (TE)	0.9	1.7	1	8.8	11.1	12.6	6.7	4.2
Porcentaje de Aporte	**1.91**	**3.62**	**2.13**	**18.72**	**23.62**	**26.81**	**14.25**	**8.94**
	PIS	**CAR**	**SAN**	**GLE**	**INS**	**FRU_N**	**FRU_S**	**NEC**

Apéndice 5. Medidas externas (longitud del antebrazo) y cráneo-dentales del ejemplar CTUA 2406 (*Mimon cozumelae*) comparadas con *M. cozumelae* y *M. bennettii*. Las medidas cráneo-dentales se tomaron siguiendo a Simmons y Voss (1998); aquellas de *M. cozumelae* corresponden a 12 individuos (machos) de México, y las de *M. bennettii* (1), a 6 individuos (machos) del norte de Brasil; los datos provienen de Gregorin *et al.* (2008). Las medidas de *M. bennettii* (2) corresponden a 6 individuos (machos) del sur de Brasil, los datos provienen de Hoppe y Ditchfield (2016).

Medida	**CTUA 2406**	***Mimon cozumelae***	***Mimon bennettii* (1)**	***Mimon bennettii* (2)**
Longitud antebrazo	54.7	56.5 ± 1.8	58.4 ± 0.8	52.7±2.0
GLS	24.9	25.6 ± 0.4	24.8 ± 0.4	25.2±0.3
CIL	22.79	23.2 ± 0.3	22.9 ± 0.5	
POB	4.77			
BB	9.58	10.0 ± 0.3	9.6 ± 0.1	9.7±0.1
MB	11.35			11.4±0.2
ZB	12.91	13.8 ± 0.3	13.0 ± 0.3	13.1±0.3
MTRL	9.57	9.4 ± 0.1	9.4 ± 0.2	9.1±0.0
M3M3	9.25			8.1±2.0

Apéndice 6. Registros correspondientes a especies características de la región. Primera fila (de izquierda a derecha): *Centronycteris centralis*, *Rhynchonycteris naso*, *Saccopteryx canescens*, *Pteronotus parnellii*; segunda fila: *Noctilio leporinus*, *Desmodus rotundus*, *Chrotopterus auritus*, *Gardnerycteris keenani*; tercera fila: *Lophostoma silvicola*, *Micronycteris megalotis*, *Phyllostomus hastatus*, *Tonatia saurophila*; cuarta fila: *Trinycteris nicefori*, *Anoura cultrata*, *Glossophaga soricina*, *Lonchophylla robusta*; quinta fila: *Carollia castanea*, *Artibeus lituratus*, *Chiroderma villosum*, *Sturnira bakeri*; sexta fila: *Vampyriscus nymphaea*, *Vampyrodes major*, *Molossus molossus*, *Myotis caucensis.*



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Checklist of ectoparasites of cricetid and heteromyid rodents in México

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We present an updated checklist of ectoparasite species (including mites, ticks, lice, and fleas) infesting cricetid and heteromyid rodents (Rodentia: Cricetidae and Heteromyidae) in México. For each parasite species, we include information on parasite taxonomy, host associations, collection localities, citations from the literature, and museum collections, when available. We recorded more than 172 mite, 114 flea, 22 tick, and 22 louse species from a minimum of 110 host species (82 cricetid and 28 heteromyid species) distributed across 31 states in México. This work represents the most up-to-date and comprehensive checklist of ectoparasite species parasitizing cricetid and heteromyid rodents in México.

Presentamos una lista actualizada de especies de ectoparásitos (ácaros, garrapatas, piojos y pulgas) que infestan roedores cricétidos y heterómidos (Rodentia: Cricetidae y Heteromyidae) en México. Para cada especie de parásito, incluimos información sobre la taxonomía de los parásitos, asociaciones con el hospedero, localidades de colecta, citas de la literatura y colecciones de museo, cuando están disponibles. Registramos más de 172 especies de ácaros, 114 pulgas, 22 garrapatas y 22 piojos de un mínimo de 110 especies de hospederos (82 especies de cricétidos y 28 heterómidos) distribuidas en 31 estados de México. Este trabajo representa la lista más actualizada y completa de las especies de ectoparásitos que parasitan a los roedores cricétidos y heterómidos en México

Key words: Cricetidae; fleas; Heteromyidae; Ixodida; lice; ticks; México; mites; Phthiraptera: Siphonaptera.

Introduction

Of the 2,552 described species of rodents (Rodentia) worldwide (Burgin *et al.* 2018), over 240 species are distributed in México and 110 of those are Mexican endemics (Ceballos and Arroyo-Cabrales 2012; Ramírez-Pulido *et al.* 2014). The families Cricetidae and Heteromyidae are particularly diverse in México, with approximately 150 and 40 species, respectively, representing the majority of the Mexican rodent fauna (Ceballos 2014; Burgin *et al.* 2018). Being so diverse, representatives of these rodent families are generally well-studied in México (*e. g.*, Rogers *et al.* 2011; Fernández *et al.* 2012; Fernández *et al.* 2014; Porter *et al.* 2017). Notably, there have been many attempts to characterize the parasite fauna of cricetid and heteromyid rodents. Surveys of the ectoparasites (mites, ticks, lice, fleas) of Cricetidae and Heteromyidae began early and have resulted in several checklists, some for all ectoparasites (*e. g.*, Whitaker and Morales-Malacara 2005) and others for each taxonomic group. For example, for lice Sánchez-Montes *et al.* (2013) and Sánchez-Montes *et al.* (2018) provide excellent reviews of sucking lice and chewing lice, respectively, from México (although we note that no cricetid or heteromyid rodents are known to have chewing lice). Ferris (1951), Kim *et al.* (1986), and Durden and Musser (1994a, 1994b) also are good references for general host-louse lists. Hoffmann (1990) is an excellent reference summarizing the chigger (Acari: Trombiculidae) fauna from México. For fleas, useful checklists and information are included in Hopkins and Rothschild (1966), Barnes *et al.* (1977), Muñiz *et al.* (1981), Morales-Muciño and Llorente-Bousquets (1985), Morales and Llorente (1986), Ayala-Barajas *et al.* (1988), Ponce-Ulloa and Llorente (1996), Acosta and Morrone (2003), Acosta *et al.* (2008), and Acosta (2014). Lastly, the parasite chapters in "Biology of the Heteromyidae" (Whitaker *et al.* 1993), "Biology of *Peromyscus* (Rodentia)" (Whitaker 1968) and "Biology of New World *Microtus*" (Timm 1985) are also good lists of all host-parasite associations (with references to original literature) for the Heteromyidae, *Peromyscus,* and *Microtus,* respectively. Preisser and Falcón-Ordaz (2019) also present a comprehensive list of all cricetid and heteromyid endoparasites known to date. All of these checklists are important for any parasitologist to have available when trying to identify ectoparaties of cricetid and heteromyid rodents. Given the diversity of these rodent families in México, a comprehensive list of all ectoparasties of Cricetidae and Heteormyidae is warranted, which we provide below.

To produce our checklist summarizing all major ectoparasite groups from cricetid and heteromyid species across México, we consolidated information from previously published checklists and searched for new host-parasite records. In our search of new records, we collected host-parasite records using Web of Science, using the following search terms: cricetid*/heteromyid* AND flea*/tick*/mite*/louse/lice AND Mexico. The ectoparasite records are grouped by phylum and arranged alphabetically at the order, family, genus, and species levels. For each parasite species, we included data on taxonomic authority, host associations, collection localities, citations from the literature, and museum collections, when available. Some parasite records are newly reported here after examination of specimens in the U. S. National Tick Collection, Georgia Southern University, Statesboro, Georgia, and The Acarology Laboratory, Museum of Biological Diversity, The Ohio State University. Parasite species listed as "sp." from different localities, host species, or publications may represent different species. The host genera *Chaetodipus*, *Dipodomys*, *Heteromys*, and *Perognathus* belong to the family Heteromyidae. All other host genera belong to Cricetidae. Note that we follow the mammal taxonomy of Burgin *et al.* (2018) where the heteromyid genus *Liomys* is now recognized as *Heteromys*. Thus, all previous "*Liomys*" host associations listed below are recorded under the genus *Heteromys*. Abbreviations for the museum records are as follows: AMNH = American Museum of Natural History, New York, New York, United States (U. S.). BYU = Brigham Young University Flea Collection, Monte L. Bean Life Science Museum, Provo, Utah, U. S. CAIM, ISET, Indre = Colección de Artrópodos con Importancia Médica of the Instituto de Diagnóstico y Referencia Epidémiologicos (formerly Instituto de Salubridad y Enfermedades Tropicales), Ciudad de México, México. CMNH = The Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U. S. CNAC = Colección Nacional de Ácaros, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, México CNC = Canadian National Collections of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada. CPFC, LAFC = Laboratorio de Acarología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad de México, México. ENCB = Escuela Nacional de Ciencias Biológicas, Ciudad de México, México. FMNH = Division of Insects, Field Museum of Natural History, Chicago, Illinois, U. S. GML = Gorgas Memorial Laboratory, Panama, Panama. IBUNAM = Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, México. KU, SEMC, SNOW = Snow Entomological Museum, University of Kansas, Kansas, U. S. (Emerson Collection. The K.C. Emerson collection is now at Oklahoma State University in Stillwater, Oklahoma). MNHN = Muséum National d'Histoire Naturelle, Paris, France. MHNCM = Museo de Historia Natural de la Ciudad de México, Ciudad de México, México. MWH = Personal Collection of Michael W. Hastriter, Monte L. Bean Life Science Museum, Provo, Utah, U. S. MZFC = Museo de Zoología Alfonso L. Herrera, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad de México, México. NMNH, USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C., U. S. NHM, BMNH = Department of Entomology, Natural History Museum, London, England OSAL = The Acarology Laboratory, Museum of Biological Diversity, The Ohio State University, Columbus, Ohio, U. S. PRICE INSTITUTE = Price Institute for Phthirapteran Research at the University of Utah, Salt Lake City, Utah, U. S. REL = Personal Collection of Robert E. Lewis, Now in the FMNH. RML = Rocky Mountain Laboratory, Hamilton, Montana, U. S. (the RML no longer has collections and all ectoparasites have been transferred to the USNM or USNTC) RPE = Personal Collection of Ralph Eckerlin, Northern Virginia Community College, Annandale, Virginia, U. S. USNTC = United States National Tick Collection, Institute of Coastal Plain Science, Georgia Southern University, Statesboro, U. S. ZISP = Zoological Institute, Russian Academy of Sciences, Saint-Petersburg, Russia.

Across nearly all (31) states in México, we document a minimum of 172 mite, 114 flea, 22 tick, and 22 louse species from at least 110 host species (82 cricetid and 28 heteromyid species). No ectoparasites were recorded from Aguascalientes. Across the 31 states with ectoparasites, mites, ticks, lice, and fleas are found in 27, 25, 23, and 29 of these states, respectiviely. Twenty Mexican states are documented here as having all four ectoparasite groups. Of the 82 cricetid species represented on our checklist, 53, 25, 31, and 59 species are parasitized by mites, ticks, lice, and fleas, respectively, and 5 host species are parasitized by all four ectoparasite groups. Of the 28 heteromyid species represented on our checklist, 28, 9, 12, and 10 species are parasitized by mites, ticks, lice, and fleas, respectively, and 5 host species are parasitized by all four ectoparasite groups.

Our numbers of ectoparasite species and host associations are likely underestimates for a variety of reasons. For one, not all hosts and parasites were identified to species; thus, several undetermined parasites may represent new species or immature stages (*e. g.*, for ticks) that were not, or could not, be identifed to species. Additionally, many cricetid and heteromyid species are not included in this checklist. With additional investigations, it is likely that more host associations will be uncovered, some of which may include new ectoparasite species. Despite these almost certain underestimates in our findings, there also is the possibility of incorrect, and thus inflated numbers of, associations due to ectoparasite contamination. During specimen processing, ectoparasites can easily become dislodged from their hosts becoming associated with the incorrect host by process of human error. Thus, we strongly encourage researchers to process each host specimen individually and carefully to avoid potential contamination (*e. g.*, Cook 1954).

Assembling checklists for parasites clearly reveals that more associations certainly exist; they simply are not documented and published. A potential way to document more host-parasite associations is to take all available data from host specimens in the field, including their parasites, resulting in a "holistic" or "extended" specimen (Cook *et al.* 2016; 2017; Webster 2017; Cook and Light 2019). Although there are exceptions (*e. g.*, Wenzel and Tipton 1966), field mammalogists collecting specimens, especially recently, have often ignored parasite collection despite their importance (Gardner 1996; Hoberg 2002; Cook and Light 2019). We strongly advocate for the collection of holistic specimens in the field, and then deposition of these materials in the appropriate repositories as these specimens will provide much needed data about parasite faunas and distribution of those faunas such that subsequent studies can be conducted (Bell *et al.* 2018; Preisser and Falcón-Ordaz 2019). Lastly, we note that our checklist is almost entirely the result of summarization of the literature. However, our search of the U.S. National Tick Collection at Georgia Southern University alone resulted in a minimum of 6 previously undescribed host-parasite associations and 9 new state records. Similary, examination of the Acarology Laboratory at The Ohio State University resulted in 6 new state records and 1 new mite species and host association. Natural history collections likely hold untold numbers of additional parasite records. Therefore, future checklists should examine natural history collections holdings, which will likely result in additional host-parasite associations and locality records.

Phylum: Arthropoda von Siebold, 1848

Class: Arachnida Lamarck, 1801

Subclass: Acari Leach, 1817

Superorder: Parasitiformes Reuter, 1909

Order: Ixodida Leach, 1815

Family: Argasidae Koch, 1844

Argas brevipes Kohls, Hoogstraal, and Clifford, 1961

BAJA CALIFORNIA SUR: 205 km N of La Paz: *Peromyscus* sp. nest (USNTC). Specimens in collections: USNTC.

Argas sp.

NUEVO LEÓN: Sierra de San Antonio Peña Nevada: *Peromyscus maniculatus* (Tijerina-Medina *et al.* 2006). No specimens in collections.

Ornithodoros nicollei Mooser, 1932

COLIMA: near Colima: *Hodomys alleni* (Brumpt *et al.* 1939,; Cooley and Kohls 1944; Hoffmann 1962). Unknown if specimens are in collections. SONORA: Tiburón Island, Sausal Valley: *Neotoma* sp. (Kohls *et al.* 1965). Specimens in collections: USNTC. UNKNOWN LOCALITY: *Hodomys alleni, Neotoma* sp. (Davis 1943; Hoffmann 1962; Kohls *et al.* 1965). Unknown if specimens are in collections.

Ornithodoros parkeri Cooley, 1936

BAJA CALIFORNIA: near Santiago: *Neotoma* sp. nest (Kohls *et al.* 1965). Specimens in collections: USNTC.

Ornithodoros talaje (Guérin-Méneville, 1849)

(synonym: *Ornithodoros dugesi* Mazzotti, 1943)

BAJA CALIFORNIA SUR: 30 km W of La Paz; 22 miles S of La Paz: *Neotoma bryanti*. 98 km NW of La Paz; 4 miles W of Puerto Viejo: *Neotoma* sp. nest. (USNTC). Specimens in collections: USNTC. COAHUILA: near Sabinas: *Neotoma micropus*, *Neotoma* sp. nest (Mazzotti 1943; Kohls *et al.* 1965). Unknown if specimens are in collections. Canyon de la Fragua; 94 miles N of Saltillo: *Neotoma* sp. (USNTC). Specimens in collections: USNTC. NUEVO LEÓN: 9 miles N of Santiago: *Neotoma* sp. nest. (USNTC). Specimens in collections: USNTC. SAN LUIS POTOSÍ: Bocas: *Neotoma leucodon* nest (Mazzotti 1949; Hoffmann 1962). 78 miles N of San Luis Potosí: *Neotoma* sp. (USNTC). Specimens in collections: USNTC. Note: *Neotoma albigula* was recognized as the original host. However, according to Bradley and Mauldin (2016), *N. albigula* from the eastern part of Mexico is now recognized as *N. leucodon*. SINALOA: 12 miles N of Los Mochis; 31 miles N of Los Mochis; 5 miles S of Culiacán: *Neotoma* sp. nest. (USNTC). Specimens in collections: USNTC. SONORA: 1 mile E of Kino: *Dipodomys deserti*. Cholla Valley: *Neotoma* sp. nest. S end of Tiburón Island; Kino Nuevo; 8 miles E of Kino: *Neotoma albigula*. 5 miles N of HERMOSILLO: 8 miles W of Hermosillo; 3 miles N of Guaymas; 13 miles N of Guaymas; 13 miles E of Esperanza; 11 miles N of Navajoa: *Neotoma* sp., *Neotoma* sp. nest. (USNTC). Specimens in collections: USNTC.

Ornithodoros turicata Dugès, 1876

BAJA CALIFORNIA SUR: 17 miles S of La Paz; 4 miles W of Puerto Viejo: *Neotoma* sp. nest. (USNTC). Specimens in collections: USNTC.

Ornithodoros (Alectorobius) sp. (near *tuttlei*)

BAJA CALIFORNIA SUR: Isla Espiritu Santo, Mpio. de La Paz: *Peromyscus eva* (Estébanes-González and Cervantes 2005). Specimens in collections: MZFC. Note: *Peromyscus eremicus* was recognized as the original host. However, *P. eremicus* from the southern parti of the Baja California peninsula is now recognized as *P. eva* (Álvarez-Castañeda *et al.* 2010).

Ornithodoros sp.

MORELOS: 5 miles N of El Pachon cave: *Neotoma* sp. (USNTC). Specimens in collections: USNTC. UNKNOWN LOCALITY: *Peromyscus difficilis* (Hoffmann *et al.* 1989; Whitaker and Morales-Malacara 2005). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Ixodidae Koch, 1844

Amblyomma inornatum Banks, 1909

DURANGO: *Sigmodon hispidus* (Eads and Borom 1975; Guzmán-Cornejo *et al.* 2011). Specimens in collections: USNTC. Note: *S. hispidus* is not distributed in Durango according to Ceballos (2014). Possible alternative hosts include *S. arizonae, S. fulviventer,* or *S. leucotis* Ceballos (2014). Note: Eads and Borom (1975) cite Hoffmann (1962) who indicates that adult *A. inornatum* have been taken in the Mexican states of Coahuila, Morelos, Sinaloa, and Veracruz. Eads and Borom (1975) referred to an unpublished record in the USNTC (RML50471) of a single nymph that has been identified as "probably" *Amblyomma inornatum*. GUERRERO: Agua de Obisop: *Sigmodon hispidus* (USNTC). Specimens in collections: USNTC. Note: *S. hispidus* is not distributed in Guerrero according to Ceballos (2014). Possible alternative hosts include *S. alleni*, *S. leucotis*, or *S. mascotensis* (Ceballos (2014). SINALOA: 28.5 miles N of Los Mochis: *Neotoma* sp. (USNTC). Specimens in collections: USNTC.

Amblyomma maculatum Koch, 1844

TABASCO: Jonuta: *Oryzomys* sp., *Sigmodon* sp. (USNTC). Specimens in collections: USNTC. Note: *Oryzomys* sp. was recorded in the original literature but may represent *Handleyomys* sp.

Amblyomma sp.

CHIAPAS: 9 km S of Las Margagitas: *Peromyscus boylii* (USNTC). Specimens in collections: USNTC. Note: *P. boylii* is not distributed in Chiapas according to Ceballos (2014). DURANGO: 2.9 km SE of Atotonilco: *Dipodomys ordii* (USNTC). Specimens in collections: USNTC. TABASCO: Frontera: *Hodomys alleni* (recorded as *Neotoma alleni*; USNTC). Specimens in collections: USNTC. Note: *H. alleni* is not distributed in Tabasco according to Ceballos (2014) YUCATÁN: *Heteromys gaumeri* (Quintero *et al.* 2001; Guzmán-Cornejo *et al.* 2011). Specimens in collections: CNAC. UNKNOWN LOCALITY: *Heteromys guameri, H. salvini* (Genoways 1973; Whitaker and Morales-Malacara 2005). No specimens in collections.

Amblyomma sp. 1 and *Amblyomma* sp. 2

JALISCO: Chamela Biological Station: *Heteromys pictus* (Gómez-Rodríguez *et al.* 2015). Specimens in collections: CNAC. Note: Other ticks and hosts are reported in Gómez-Rodríguez *et al.* (2015) from Chamela Biological Station; however, the paper is constructed in such a way that it is not possible to determine host-tick associations.

Dermacentor albipictus (Packard, 1869)

NUEVO LEÓN: Sierra de San Antonio Peña Nevada: *Peromyscus boylii, P. maniculatus, Heteromys irroratus* (Guzmán-Cornejo *et al.* 2016; Tijerina-Medina et al. 2006). No specimens in collections. Note: *P. boylii* is not distributed in Nuevo León according to Ceballos (2014).

Dermacentor parumapertus Neumann, 1901

DURANGO: 2.9 km SE of Atotonilco: *Dipodomys merriami* (USNTC). Specimens in collections: USNTC. SONORA: 5 miles N of Guamos: *Dipodomys merriami* (USNTC). Specimens in collections: USNTC.

Dermacentor sp.

BAJA CALIFORNIA SUR: San José del Cabo: *Dipodomys* sp. (USNTC). Specimens in collections: USNTC. DURANGO: 2.9 km SE of Atotonilco: *Dipodomys merriami, D. ordii, Perognathus flavus* (USNTC). Specimens in collections: USNTC. SAN LUIS POTOSÍ: El Salto Falls: *Oryzomys* sp., *Sigmodon hispidus* (USNTC). Specimens in collections: USNTC. Note: *S. hispidus* is not distributed in San Luis Potosi according to Ceballos (2014). A possible alternative host includes *S. leucotis* Ceballos (2014). Note: *Oryzomys* sp. was recorded in the original literature but may represent *Handleyomys* sp. SONORA: 89.5 miles S of Benjamin Hill: *Peromyscus boylii* (USNTC). Specimens in collections: USNTC.

Ixodes angustus Neumann, 1899

CHIAPAS: Cerro Tzontehuitz, 13 km NE of San Cristóbal de las Casas; San Juan Chamula: *Reithrodontomys microdon, Microtus guatemalensis* (Estébanes-González and Cervantes 2005; Guzmán-Cornejo *et al.* 2007). No specimens in collections. COAHUILA: Sabinas: *Neotoma* sp. nest (Hoffmann 1962; Guzmán-Cornejo *et al.* 2007). Specimens in collections: USNTC. OAXACA: 3 km SE of Totontepec, Totontepec: *Peromyscus melanocarpus*. 1 km N of Esperanza, Santiago Comaltepec, Distrito Ixtlán: *Handleyomys alfaroi* (recorded as *Oryzomys alfaroi*; Estébanes-González and Cervantes 2005; Guzmán-Cornejo *et al.* 2007). No specimens in collections. Note: Guzmán-Cornejo *et al.* (2007) call into question all tick identifications made by Estébanes-González and Cervantes (2005); the host-tick associations from these authors may be incorrect. UNKNOWN LOCALITY: *Neotoma* sp. (Hoffmann 1962; Whitaker and Morales-Malacara 2005). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Ixodes cookei Packard, 1869

NUEVO LEÓN: 10.9 km S, 10.8 km E of San Josecito: *Peromyscus* sp. (Montiel-Parra *et al.* 2007; Guzmán-Cornejo *et al.* 2007). Specimens in collections: CNAC.

Ixodes eadsi Kohls and Clifford, 1964.

PUEBLA: 6 km E of Totimehuacán: *Heteromys* sp. (Guzmán-Cornejo *et al.* 2007). Specimens in collections: CNAC. ZACATECAS: 1 mile N of Santa Rosa: *Heteromys irroratus* (USNTC). Specimens in collections: USNTC.

Ixodes granulatus Supino, 1897

OAXACA: 1 km S, 0.5 km W of Vista Hermosa, Santiago

Comaltepec: *Peromyscus mexicanus*. 11 km SW of La Esperanza to San Isidro, Santiago Comaltepec: *Handleyomys chapmani* (recorded as *Oryzomys chapmani*; Estébanes-González and Cervantes 2005; Guzmán-Cornejo *et al.* 2007). No specimens in collections. Note: Guzmán-Cornejo *et al.* (2007) call into question all tick identifications made by Estébanes-González and Cervantes (2005) and note that *I. granulatus* is an exclusively SE Asian species.

Ixodes minor Neumann, 1902

SAN LUIS POTOSÍ: 8 miles W of El Naranjo: *Sigmodon hispidus* (USNTC). Specimens in collections: USNTC. Note: *S. hispidus* is not distributed in San Luis Potosi according to Ceballos (2014). A possible alternative host includes *S. leucotis* Ceballos (2014). TAMAULIPAS: Acuña: *Sigmodon hispidus* (USNTC). Specimens in collections: USNTC.

Ixodes rubidus Neumann, 1901

SINALOA: 5 km NE of Santa Lucia: *Peromyscus boylii* (USNTC). Specimens in collections: USNTC. Note: *P. boylii* is not distributed in Sinaloa according to Ceballos (2014).

Ixodes sinaloa Kohls and Clifford, 1966

COLIMA: El Cobano; 25 miles SE of San Antonio: *Heteromys irroratus* (USNTC). Specimens in collections: USNTC. GUERRERO: 1.4 miles E of El Cobano: *Heteromys pictus* (USNTC). Specimens in collections: USNTC. JALISCO: Chamela Biological Station: *Heteromys pictus* (Keirans and Jones 1972; Gómez-Rodríguez *et al.* 2015). Specimens in collections: CNAC. 10 miles NW of San Patricio; 4 km W of Tuxpan: *H. pictus* (USNTC). Specimens in collections: USNTC. NAYARIT: 32 km SE of Tepic: *Oryzomys couesi* (Kohls and Clifford 1966; Guzmán-Cornejo *et al.* 2007). *O. palustris* (Keirans and Jones 1972; Whitaker and Morales-Malacara 2005). Specimens in collections: USNTC. Note: *O. palustris* is not distributed in Nayarit according to Ceballos (2014). SINALOA: 5 km SW of San Ignacio; 1 km SE of Sana Lucia; 1 km NE of Santa Lucia; 4.8 km NE of Copala; 6.4 km SW of Copala: *Heteromys pictus* (Kohls and Clifford 1966; Keirans and Jones 1972; Guzmán-Cornejo *et al.* 2007). Specimens in collections: USNTC.

Ixodes spinipalpis Hadwen and Nuttall, 1916

GUERRERO: Omiltemi; 1.6 km NW of Omiltemi: *Peromyscus* sp. (Guzmán-Cornejo *et al.* 2007). Specimens in collections: CNAC. MORELOS: Zempoala: *Peromyscus* sp. (Guzmán-Cornejo *et al.* 2007). Specimens in collections: CNAC. VERACRUZ: 0.8 km NE of Las Minas: *Peromyscus* sp. (Guzmán-Cornejo *et al.* 2007). Specimens in collections: CNAC.

Ixodes tancitarius Cooley and Kohls, 1942

MICHOACÁN: Cerro Tancítaro: *Reithrodontomys* sp. (Cooley and Kohls 1942; Hoffmann 1962; Whitaker and Morales-Malacara 2005; Guzmán-Cornejo *et al.* 2007). Specimens in collections: USNTC. VERACRUZ: 0.8 km NE of Las Minas: *Reithrodontomys* sp. (Guzmán-Cornejo *et al.* 2007). Specimens in collections: CNAC.

Ixodes woodi Bishopp, 1911

COAHUILA: Sabinas: *Neotoma micropus* (Robbins and Keirans 1987; 1992; Guzmán-Cornejo *et al.* 2007). Specimens in collections: USNTC. MORELOS: Zempoala: *Neotoma* sp. (Guzmán-Cornejo *et al.* 2007). Specimens in collections: CNAC.

Ixodes sp.

CAMPECHE: 7.5 km SW of Escárcega: *Sigmodon hispidus, Heteromys gaumeri* (USNTC). Specimens in collections: USNTC. Note: *S. hispidus* is not distributed in Campeche according to Ceballos (2014). A possible alternative host includes *S. toltecus* Ceballos (2014). CHIAPAS: Tzontehuitz, Volcán Tacana: *Reithrodontomys sumichrasti* (USNTC). Specimens in collections: USNTC. COLIMA: El Cobano: *Heteromys irroratus* (USNTC). Specimens in collections: USNTC. CIUDAD DE MÉXICO: Zacayuca: *Peromyscus gratus* (recorded as *P. truei*; USNTC). Specimens in collections: USNTC. GUERRERO: Omilteme: *Neotoma mexicana* (USNTC). Specimens in collections: USNTC. HIDALGO: 4 km E of San Felipe Orizatlan: *Baiomys taylori*. Pachuca: *Peromyscus difficilis* (USNTC). Specimens in collections: USNTC. JALISCO: Chamela Biological Station: *Heteromys pictus* (Gómez-Rodríguez *et al.* 2015). Specimens in collections: CNAC. MICHOACÁN: Tancitaro: *Peromyscus hylocetes* (USNTC). Specimens in collections: USNTC. NUEVO LEÓN: Sierra de San Antonio Peña Nevada: *Peromyscus boylii* (Tijerina-Medina et al. 2006). No specimens in collections. Note: *P. boylii* is not distributed in Nuevo León according to Ceballos (2014). PUEBLA: Matamoros: *Baiomys musculus*. Mata Maras: *Baiomys* sp. (USNTC). Specimens in collections: USNTC. TAMAULIPAS: Matamoros: *Perognathus merriami* (USNTC). Specimens in collections: USNTC. VERACRUZ: Texolo: *Peromyscus mexicanus*, *Sigmodon* sp. (USNTC). Specimens in collections: USNTC. YUCATÁN: 7.5 km W of Escárcega: *Ototylomys phyllotis*. 2 km N of Piste: *Peromyscus yucatanicus* (USNTC). Specimens in collections: USNTC. UNKNOWN LOCALITY: *Peromyscus difficilis* (Hoffmann *et al.* 1989; Whitaker and Morales-Malacara 2005). *Handleyomys alfaroi* (recorded as *Oryzomys alfaroi*), *Microtus guatemalensis*, *P. melanocarpus*, *Reithrodontomys microdon* (Guzmán-Cornejo *et al.* 2007). *Heteromys guameri, H. pictus*. (Genoways 1973; Whitaker and Morales-Malacara 2005). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Phylum: Arthropoda von Siebold, 1848
Class: Arachnida Lamarck, 1801
Subclass: Acari Leach, 1817
Superorder: Parasitiformes Reuter, 1909

Order: Mesostigmata Canestrini, 1891

Family: Ameroseiidae Evans, 1961

Ameroseius bassolsae (Vargas and Polaco, 2001)

UNKNOWN LOCALITY: *Dipodomys nelsoni* (Vargas and Polaco 2001). Unknown if specimens are in collections.

Sertitympanum contiguum Elsen and Whitaker, 1985

UNKNOWN LOCALITY: *Dipodomys nelsoni* (Vargas-Sandoval *et al.* 1991). Unknown if specimens are in collections.

Dermanyssidae Kolenati, 1851

Liponyssoides sanguineus (Hirst, 1914)

ESTADO DE MÉXICO: Tonatico: *Neotoma mexicana*. Barrientos: *Baiomys taylori* (Hoffmann *et al.* 1972). Tlapacoya: *Peromyscus difficilis* (Bassols 1981). Unknown if specimens are in collections. PUEBLA: San Pedro Atlixco: *Peromyscus* sp. (Hoffmann *et al.* 1972). Unknown if specimens are in collections.

Laelapidae Berlese, 1892

Subfamily: Laelapinae Berlese, 1892

Androlaelaps (Androlaelaps) grandiculatus Eads, 1951

BAJA CALIFORNIA SUR: Isla Espíritu Santo, Mpio. La Paz: *Chaetodipus spinatus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. San José del Cabo and Loreto: *C. spinatus* (Bassols 1981). Unknown if specimens are in collections. SAN LUIS POTOSÍ: 12 km S, 1.5 km E Sta. Ma. del Río: *Chaetodipus nelsoni*. 1 km E Huizache; 5 km SW Núñez: *C. penicillatus* (Bassols 1981). Unknown if specimens are in collections. Note: *C. penicillatus* is not distributed in San Luis Potosí according to Ceballos (2014).

Androlaelaps (Androlaelaps) leviculus Eads, 1951

CIUDAD DE MÉXICO: La Venta: *Peromyscus* sp. (Bassols 1981). Specimens in collections: MHNCM. OAXACA: Salina Cruz: *Heteromys pictus* (Bassols 1981). Specimens in collections: MHNCM. SAN LUIS POTOSÍ: Sta. Ma. del Río: *Onychomys torridus* (Bassols 1981). Specimens in collections: MHNCM. Note: *O. torridus* is not distributed in San Luis Potosí according to Ceballos (2014). SONORA: 12 km NE Puerto Peñasco: *Dipodomys sp.* (Bassols 1981). Specimens in collections: MHNCM.

Androlaelaps (Androlaelaps) setosus Fox, 1946

CIUDAD DE MÉXICO: Churubusco: *Microtus* sp. (Bassols 1981). Unknown if specimens are in collections. GUERRERO: Cocula: *Osgoodomys banderanus* nest (Bassols 1981). Unknown if specimens are in collections. SAN LUIS POTOSÍ: 31 km NE El Salto. *Reithrodontomys* sp. (Bassols 1981). Unknown if specimens are in collections.

Androlaelaps (Androlaelaps) sinuosa Furman, 1954

BAJA CALIFORNIA SUR: San Ignacio El Arco: *Chaetodipus rudinoris, Dipodomys* sp. Desierto de Magdalena: *Perognathus* sp. (Bassols 1981). Unknown if specimens are in collections. Note: *Chaetodipus baileyi* was recognized as the original host. However, according to Riddle *et al.* (2000), *C. baileyi* from the Baja California peninsula are now recognized as *C. rudinoris.*

Androlaelaps (Haemolaelaps) casalis (Berlese, 1887)

COLIMA: Playa de Oro: *Heteromys pictus, H. spectabilis* (Estébanes-González *et al.* 2011). Specimens in collections: IBUNAM. Note: *H. spectabilis* is not distributed in Colima according to Ceballos (2014). ESTADO DE MÉXICO: Carretera Tepic-San Blas, km 20: *Heteromys pictus* (Bassols 1981). Unknown if specimens are in collections. Jalisco: Chamela Biological Station: *Heteromys pictus* (Gómez-Rodríguez *et al.* 2015). Specimens in collections: CNAC. NAYARIT: Carretera Tepic-San Blas, km 20: *Heteromys pictus* (Bassols 1981). Unknown if specimens are in collections. SAN LUIS POTOSÍ: Rancho "El Estribo," 10 km SE of El Naranjo, Mpio. Ciudad del Maíz: *Sigmodon hispidus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. Note: *S. hispidus* is not distributed in San Luis Potosí according to Ceballos (2014). A possible alternative host includes *S. leucotis* Ceballos (2014).

Androlaelaps (Haemolaelaps) fahrenholzi (Berlese, 1911)

CHIAPAS: 16 km SW Tapachula: *Heteromys salvini*. Tzontchuitz: *Peromyscus zarhynchus* (Bassols 1981). Specimens in collections: MHNCM. COLIMA: Playa de Oro: *Baiomys musculus, Nyctomys sumichrasti* (Estébanes-González *et al.* 2011). Specimens in collections: IBUNAM. CIUDAD DE MÉXICO: El Zarco; Bosque de Chapultepec: *Microtus mexicanus*. 2.5 km W Parres: *Neotomodon alstoni*. 1.6 km E, 800m S Acopilco; 5 km Meyehualco: *Peromyscus difficilis*. Contreras: *P. melanotis*. La Venta: *Peromyscus* sp. El Guarda: *Reithrodontomys* sp. (Bassols 1981). Specimens in collections: MHNCM. ESTADO DE MÉXICO: 11 km N Barrientos: *Baiomys taylori*. Teotihuacán: *Heteromys irroratus*. Río Frío: *Microtus mexicanus* nest. Río Frío Llano Grande, cerca de Ojotongo; Lagunas de Zempoala: *Neotomodon alstoni*. Naucalpan de Juárez: *Microtus* sp. Lagunas de Zempoala: *Neotoma* sp. Popocatépetl, 200 m W Paso de Cortés: *Peromyscus maniculatus*. Iztaccíhuatl: *P. melanotis*. Río Frío Llano Grande: *P. melanotis*, *Peromyscus* sp. (Bassols 1981). Specimens in collections: MHNCM. GUERRERO: 6 km W Colotlipa: *Oryzomys palustris* (Bassols 1981). Specimens in collections: MHNCM. Note: *O. palustris* is not distributed in Guerrero according to Ceballos (2014). HIDALGO: Xoxali: *Peromyscus melanophrys, P. gratus* (recorded as *P. truei*), *Dipodomys ordii*. Parque Nacional El Chico: *Microtus mexicanus* (Bassols 1981). Specimens in collections: MHNCM. MORELOS: Tepoztlán: *Baiomys musculus* (Bassols 1981). Specimens in collections: MHNCM. JALISCO: 1 km S Acatlán: *Heteromys irroratus* (Bassols 1981). Specimens in collections:

MHNCM. OAXACA: 3 km SE of Totontepec, Mpio. Totontepec: *Peromyscus melanocarpus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. 12 km NW Tehuantepec: *Heteromys pictus*. Llano de las Flores: *Microtus mexicanus*. 7 km SW Suchixtepec; 16 km SW Suchixtepec: *P. boylii, Reithrodontomys sumichrasti*. Huajuapan de León: *P. gratus* (recorded as *P. truei*; Bassols 1981). Specimens in collections: MHNCM. Note: *P. boylii* is not distributed in Oaxaca according to Ceballos (2014). SONORA: Puerto Peñasco; Rancho Noche Buena; Guaymas: *Dipodomys* sp. 12 km NE Puerto Peñasco: *Onychomys* sp. (Bassols 1981). Specimens in collections: MHNCM. SAN LUIS POTOTSÍ: Rancho "El Estribo," 10 km SE of El Naranjo, Mpio. Ciudad del Maíz: *Sigmodon hispidus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. Note: *S. hispidus* is not distributed in San Luis Potosí according to Ceballos (2014). A possible alternative host includes *S. leucotis* (Ceballos 2014). VERACRUZ: 18 km NW of Teocelo, Mpio. Ixhuacán; 5 km W of Naolinco, Mpio. Naolinco: *Microtus quasiater* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. Cofre de Perote: *Neotomodon alstoni, Peromyscus* sp. 4 km N Jilotepec: *Peromyscus leucopus*. San Andrés Tuxtla: *Heteromys pictus* (Bassols 1981). Specimens in collections: MHNCM.

Eubrachylaelaps circularis (Ewing, 1933)

CHIAPAS: *Peromyscus levipes* (recorded as *P. boylii levipes*), *P. oaxacensis* (Furman 1955b). Unknown if specimens are in collections. Presa Raudales: *P. mexicanus*. Tzontehuitz: *P. zarhynchus, Reithrodontomys sumichrasti*. 16 km SW Tapachula: *Sigmodon hispidus* (Bassols 1981). Specimens in collections: MHNCM. Note: *S. hispidus* are not distributed in Chiapas according to Ceballos (2014). Possible alternative hosts include *S. hirsutus*, *S. mascotensis*, *S. toltecus*, or *S. zanjonensis* (Ceballos 2014). Similarly, *P. levipes* in not distributed in Chiapas according to Ceballos (2014). Possible alternative hosts include *P. aztecus*, P. *beatae*, *P. guatamalensis*, *P. gymnotis*, *P. leucopus*, P. *melanophrys*, P. *mexicanus*, *P. oaxacensis*, or *P. zarhynchus* (Ceballos 2014). CIUDAD DE MÉXICO: Ciudad de México: *Peromyscus* sp., *Neotomodon* sp. (Furman 1955b). Unknown if specimens are in collections. Note: *Neotomodon* sp. likely refers to *Neotomodon alstoni*, as this is the only species in the genus (*N. orizabae* and *N. perotensis* were synonymized with *N. alstoni*). 5 km Meyehualco; 1.6 km E Acopilco: *Peromyscus difficilis.* La Venta: *P. hylocetes*. Contreras: *P. melanotis.* Pedregal de San Ángel, Ciudad Universitaria: *P. gratus* (recorded as *P. truei*; Bassols 1981). Specimens in collections: MHNCM. ESTADO DE MÉXICO: 1 km N Barrientos: *Baiomys taylori.* Popocatépetl: *Microtus* sp., *Peromyscus melanotis*. Lagunas de Zempoala: *P. maniculatus* (Bassols 1981). Specimens in collections: MHNCM. GUERRERO: Omiltemi: *Peromyscus megalops* (Bassols 1981). Specimens in collections: MHNCM. JALISCO: Huascato: *Heteromys irroratus* (Bassols 1981). Specimens in collections: MHNCM. OAXACA: 6 km E of Esperanza, Mpio. Santiago Comaltepec, Distrito de Ixtlán; Cerro Zempoatepetl, 4 km E of Santa María Yacochi, Mpio. Tlahuitoltepec; 8 km S of Esperanza, Mpio. Santiago Comaltepec; 3 km E of Santa María Yacochi, Mpio. Tlahuitoltepec: *Peromyscus melanocarpus*. Cerro Zempoatépetl, 4.5 km N of Santa María Yacochi, Mpio. Tlahuitoltepec: *P. melanocarpus*, *Oryzomys couesi, Habromys lepturus*. 3 km SE of Totontepec, Mpio. Totontepec: *P. aztecus, P. melanocarpus, Reithrodontomys mexicanus.* 1 km S of Vista Hermosa, Mpio. Santiago Comaltepec: *P. melanocarpus, P. mexicanus*. 11 km SW of Esperanza, San Isidro, Mpio. Santiago Comaltepec: *Handleyomys alfaroi* (recorded as *O. alfaroi*; Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. Cerro Guiengola: *Peromyscus* sp. Llano de las Flores: *R. sumichrasti* (Bassols 1981). Specimens in collections: MHNCM. PUEBLA: 10 km San Martín Texmelucan, Mpio. San Martín Texmelucan: *Peromyscus maniculatus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. Atlixco: *P. difficilis.* (Bassols 1981). Specimens in collections: MHNCM.

Eubrachylaelaps debilis Jameson, 1950

CIUDAD DE MÉXICO: *Peromyscus* sp. (Furman 1955b). Unknown if specimens are in collections. ESTADO DE MÉXICO: 11 km N de Barrientos: *Baiomys taylori*. San Cayetano: *Peromyscus maniculatus*. Iztaccíhuatl: *P. melanotis*. Vertiente occidental del Popocatépetl: *Peromyscus* sp. (Bassols 1981). Unknown if specimens are in collections. MICHOACÁN: *Peromyscus* sp. (Furman 1955b). Unknown if specimens are in collections.

Eubrachylaelaps jamesoni Furman, 1955

CHIAPAS: Cerro del Cañón del Sumidero, 19 km from Tuxtla Gutiérrez: *Peromyscus mexicanus* (Furman 1955b). Specimens in collections: USNM.

Eubrachylaelaps martini Jameson, 1951

CIUDAD DE MÉXICO: Ajusco: *Neotomodon alstoni* (Jameson 1951). Specimens in collections: USNM. Km 42 between Ciudad de México and Cuernavaca; Parres: *N. alstoni*. La Venta, 2 km SW caseta de policía: *Peromyscus maniculatus* (Furman 1955b). Unknown if specimens are in collections. ESTADO DE MÉXICO: Llano Grande; Río Frío; Carretera a Cuernavaca km 41-43: *Neotomodon alstoni*. Zoquiapan: *Peromyscus sp.* (Furman 1955b). Unknown if specimens are in collections. MICHOACÁN: *Peromyscus hylocetes* (Jameson 1951). Specimens in collections: USNM. MORELOS: Tepoztlán: *Baiomys musculus* (Bassols 1981). Specimens in collections: MHNCM. VERACRUZ: Cofre de Perote: *Neotomodon alstoni* (Furman 1955b). Unknown if specimens are in collections.

Eubrachylaelaps rotundus Fonseca, 1937

GUERRERO: Omiltemi: *Peromyscus megalops* (Bassols 1981). Specimens in collections: MHNCM. OAXACA: 8 km S of Esperanza, Mpio. Santiago Comaltepec: *Peromyscus melanocarpus*. 11 km SW of Esperanza, San Isidro, Mpio. Santiago Comaltepec: *Handleyomys alfaroi* (recorded as *Oryzomys alfaroi*; Estébanes-González and Cervantes 2005).

Specimens in collections: IBUNAM. 7 km SW Suchixtepec: *P. boylii* (Bassols 1981). Specimens in collections: MHNCM. Note: *P. boylii* is not distributed in Oaxaca according to Ceballos (2014).

Eubrachylaelaps spinosus Furman, 1955

COLIMA: Playa de Oro: *Osgoodomys banderanus* (Estébanes-González *et al.* 2011). Specimens in collections: IBUNAM. GUERRERO: 4 km N Zacatula; Cocula; Gruta de Juxtlahuaca; Colotlipa: *Osgoodomys banderanus* (recorded as *Peromyscus banderanus*). Cacahuamilpa: *Peromyscus* sp. (Bassols 1981). Unknown if specimens are in collections. JALISCO: Chamela Biological Station: *Heteromys pictus* (Gómez-Rodríguez *et al.* 2015). Specimens in collections: CNAC, IBUNAM. MICHOACÁN: 4 mi E Apatzingán: *Peromyscus* sp. (Furman 1955b). Specimens in collections: FMNH, MNHM, NHM, USNM.

Gigantolaelaps boneti Bassols de Barrera, 1970

CHIAPAS: 10 km N, 15 km E de Raudales: *Handleyomys melanotis* (recorded as *Oryzomys melanotis*; Bassols 1981). Specimens in collections: MHNCM. Note: *H. melanotis* is not distributed in Chiapas according to Ceballos (2014). GUERRERO: Omiltemi: *Oligoryzomys fulvescens* (recorded as *Oryzomys fulvescens*; Bassols 1981). Specimens in collections: MHNCM. OAXACA: 1 km S Vista Hermosa, Mpio. Santiago Comaltepec: *Peromyscus mexicanus*. 11 km N Esperanza, San Isidro, Mpio. Santiago Comaltepec; 1 km N Esperanza, Mpio. Santiago Comaltepec, distrito de Ixtlán: *Handleyomys alfaroi* (recorded as *Orzyomys alfaroi*). 11 km SW Esperanza, San Isidro, Mpio. Santiago Comaltepec: *H. alfaroi* (recorded as *O. alfaroi*), *Megadontomys cryophilus*. Km 134 Tuxtepec-Oaxaca, 13 km W of Atepec, Mpio. Atepec: *P. melanocarpus*. Cerro Zempoaltepetl 4.5 N of Santa María Yacochi, Mpio. Tlahuitoltpec: *O. couesi* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. San Juan Lachao: *Handleyomys alfaroi* (recorded as *Oryzomys alfaroi*; Bassols de Barrera 1970; Bassols 1981). Specimens in collections: ENCB, MHNCM. VERACRUZ: El Cedeño, Jalapa: *Peromyscus* sp. (Bassols 1981). Specimens in collections: MHNCM.

Laelaps kochi Oudemans, 1936

CIUDAD DE MÉXICO: El Zarco; Bosque de Chapultepec: *Microtus mexicanus* (Bassols 1981). Specimens in collections: MHNCM. HIDALGO: Cerro las Ventanas; Parque Nacional El Chico: *Microtus mexicanus* (Bassols 1981). Specimens in collections: MHNCM. VERACRUZ: 18 km NW of Teocelo, Mpio. Ixhuacán; 5 km W of Naolinco, Mpio. Naolinco: *Microtus quasiater*. Baderillas 6 km NW of Xalapa, Mpio. Xalapa: *Peromyscus furvus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. Jilotepec: *P. leucopus* (Bassols 1981). Specimens in collections: MHNCM.

Laelaps nuttalli Hirst, 1915

OAXACA: 6 km E of Esperanza, Mpio. Santiago Comaltepec, distrito Ixtlán; 11 km SW of Esperanza to San Isidro, Mpio. Santiago Comaltepec: *Peromyscus melanocarpus, Handleyomys alfaroi* (recorded as *Oryzomys alfaroi*). 1 km S of Vista Hermosa, Mpio. Santiago Comaltepec: *P. mexicanus*. 1 km N of Esperanza, Mpio. Santiago Comaltepec, distrito Ixtlan: *H. alfaroi* (recorded as *O. alfaroi*; Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. VERACRUZ: 18 km NW of Teocelo, Mpio. Ixhuacán; 5 km W of Naolinco, Mpio. Naolinco: *Microtus quasiater* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. Note: *Laelaps nuttalli* is a specific parasite of *Rattus* sp. The host associations above may be accidental occurrences or misidentifications.

Laelaps oryzomydis Pratt and Lane, 1953

COLIMA: Playa de Oro: *Oryzomys couesi, Handleyomys melanotis* (recorded as *O. melanotis*; Estébanes-González *et al.* 2011). Specimens in collections: IBUNAM. *Laelaps pilifer* Tipton, Altman and Keegan, 1966. OAXACA: 11 km SW of Esperanza to San Isidro, Mpio. Santiago Comaltepec: *Handleyomys alfaroi* (recorded as *Oryzomys alfaroi*; Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Steptolaelaps heteromys Bassols, 1975

CHIAPAS: Tapachula: *Heteromys salvini* (Bassols 1981). Unknown if specimens are in collections. OAXACA: 1 km N of Esperanza, Mpio. Santiago Comaltepec, distrito Ixtlán: *Heteromys desmarestianus*. 11 km SW of Esperanza to San Isidro, Mpio. Santiago Comaltepec: *Handleyomys alfaroi* (recorded as *Oryzomys alfaroi*). (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Steptolaelaps liomydis (Grant, 1947)

BAJA CALIFORNIA SUR: San José del Cabo: *Chaetodipus spinatus* (Bassols 1981). Specimens in collections: MHNCM. CHIAPAS: Tuxtla; Río San Gregorio at Pan-American Highway: *Heteromys pictus* (Furman 1955a). Unknown if specimens are in collections. CHIHUAHUA: La Cieneguilla: *Heteromys irroratus* (Bassols 1981). Specimens in collections: MHNCM. COLIMA: Playa de Oro: *Heteromys pictus, H. spectabilis* (Estébanes-González *et al.* 2011). Specimens in collections: IBUNAM. Note: *H. spectabilis* is not distributed in Colima according to Ceballos (2014). CIUDAD DE MÉXICO: Cerro Zacatepec: *Peromyscus gratus* (recorded as *P. truei*; Bassols 1981). Specimens in collections: MHNCM. ESTADO DE MÉXICO: Teotihuacán, 7.6 km S de Jiménez: *Heteromys irroratus*. 2 km N Tlalnepantla: *Heteromys* sp. (Bassols 1981). Specimens in collections: MHNCM. GUERRERO: 4 km NE Colotlipa: *Heteromys pictus*. Cocula: *Heteromys* sp. (Bassols 1981). Specimens in collections: MHNCM. JALISCO: Rancho "Laurel," 1.5 km S of Contla, Mpio. Tamazula de Gordiano; Rancho "La Lagunita," 5 km SW of Epenche, Mpio. Mazamita: *Heteromys spectabilis* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. Chamela Biological Station: *H. pictus* (Gómez-Rodríguez *et al.* 2015). Specimens in collections: CNAC. Encarnación de Diaz: *H. irroratus* (Grant 1947). Unknown if specimens are in collections. Acatlán: *Heteromys* sp. (Bassols 1981). Specimens in collections: MHNCM. Note: Additional specimens reported in Furman (1955a), but specimens were lost. MICHOACÁN: Pátzcuaro: *Heteromys irroratus* (Furman 1955a). Unknown if specimens are in collections. NAYARIT: Km 20 Carretera Tepic-San Blas: *Heteromys pictus* (Bassols 1981). Specimens in collections: MHNCM. OAXACA: Cerro San Felipe; Monte Albán: *Heteromys irroratus* (Furman 1955a). Unknown if specimens are in collections. 7.6 km NE de Tehuantepec; 9 km NE de Tehuantepec; Cerro Guiengola; 8 km NE Salina Cruz: *H. pictus*. San Juan Lachao: *Oligoryzomys fulvescens* (Bassols 1981). Specimens in collections: MHNCM. PUEBLA: Totimihuacán: *Heteromys* sp. (Bassols 1981). Specimens in collections: MHNCM. SAN LUIS POTOSÍ: Rancho "El Estribo," 10 km SE of El Naranjo, Mpio. Cuidad del Maíz: *Sigmodon hispidus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. Note: *S. hispidus* is not distributed in San Luis Potosí according to Ceballos (2014). A possible alternative host includes *S. leucotis* Ceballos (2014). 12 km SE Santa María del Rio: *Heteromys irroratus*. 2 km NE El Salto: *Reithrodontomys* sp. (Bassols 1981). Specimens in collections: MHNCM. VERACRUZ: San Andrés Tuxtla: *Heteromys pictus* (Furman 1955a). Unknown if specimens are in collections. Catemaco; 14 km NE Catemaco: *H. pictus* (Bassols 1981). Specimens in collections: MHNCM.

Subfamily: Haemogamasinae

Brevisterna utahensis (Ewing, 1933)

HIDALGO: Xoxafí: *Peromyscus melanophrys* (Hoffmann *et al.* 1972). Unknown if specimens are in collections.

Eulaelaps stabularis (Koch, 1836)

OAXACA: 16 km SW de Suchixtepec: *Peromyscus boylii* (Hoffmann *et al.* 1972). Unknown if specimens are in collections. Note: *P. boylii* is not distributed in Oaxaca according to Ceballos (2014).

Haemogamasus ambulans (Thorrell, 1872)

CIUDAD DE MÉXICO: E. Zarco: *Microtus mexicanus* (Bassols 1981). Specimens in collections: MHNCM. ESTADO DE MÉXICO: Salazar: *Microtus* sp. Río Frío: *M. mexicanus* (Bassols 1981). Specimens in collections: MHNCM. VERACRUZ: 5 km W of Naolinco, Mpio. Naolinco: *Microtus quasiater* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Haemogamasus keegani (Jameson, 1952)

CIUDAD DE MÉXICO: 8.4 mi E Amecameca: *Peromyscus melanotis* (Jameson 1952). Unknown if specimens are in collections.

Haemogamasus liponyssoides Ewing, 1925

CHIAPAS: No data. Known hosts are mainly small rodents, likely cricetid and heteromyid rodents (Radovsky 1960). Unknown if specimens are in collections.

Ischyropoda armatus Keegan, 1951

BAJA CALIFORNIA SUR: Santo Domingo; Desierto de Magdalena: *Chaetodipus* sp. (Hoffmann *et al.* 1972). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. HIDALGO: Xoxafí: *Dipodomys ordii* (Hoffmann *et al.* 1972). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. SAN LUIS POTOSÍ: Santa María del Río: *Onychomys* sp. (Hoffmann *et al.* 1972). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Ischyropoda spiniger Keegan, 1951

BAJA CALIFORNIA SUR: San José del Cabo: *Chaetodipus spinatus*. Estero Salinas; Bahía Magdalena: *C. arenarius* (Hoffmann *et al.* 1972). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Hirstionyssinae

Echinonyssus alvarezi (Bassols-Batalla *et al.*, 1991; Quintero-Martinez, Moreno-Moreno and Vessi-Lobato, 1991)

CHIAPAS: Palenque: *Peromyscus mexicanus* (Bassols-Batalla *et al.* 1991). Specimens in collections: ENCB.

Echinonyssus galindoi (Strandtmann and Yunker, 1966)

CIUDAD DE MÉXICO: Contreras: *Peromyscus melanotis*. Bosque de Chapultepec: *Microtus mexicanus* (Bassols 1981). Specimens in collections: MHNCM. ESTADO DE MÉXICO: San Cayetano; Ajusco: *Peromyscus maniculatus*. Iztaccíhuatl: *P. melanotis*. Zoquiapan: *Peromyscus* sp. Naucalpan de Juárez: *Microtus* sp. (Bassols 1981). Specimens in collections: MHNCM. GUERRERO: Omiltemi: *Peromyscus megalops* (Bassols 1981). Specimens in collections: MHNCM. HIDALGO: Cerro las Ventanas; Parque Nacional El Chico: *Microtus mexicanus.* (Bassols 1981). Specimens in collections: MHNCM. MORELOS: Derrame del Chichinautzin: *Peromyscus difficilis* (Bassols 1981). Specimens in collections: MHNCM. OAXACA: 1 km N of Esperanza, Mpio. Santiago Comaltepec, distrito Ixtlán: *Reithrodontomys mexicanus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. Llano de las Flores: *Habromys lepturus* (recorded as *Peromyscus lepturus*; Bassols 1981). Specimens in collections: MHNCM. PUEBLA: Chiautzingo: *Peromyscus maniculatus, P. melanotis, Reithrodontomys chrysopsis, Heteromys irroratus* (Ramírez *et al.* 1980). Unknown if specimens are in collections. NE Chignahuapan: *P. boylii, P. leucopus, R. sumichrasti.* Ahuazotepec: *P. maniculatus, R. megalotis* (Bassols-Batalla *et al.* 1991). Specimens in collections: ENCB. Note: *P. boylii* is not distributed in Puebla according to Ceballos (2014).

Echinonyssus hilli (Jameson, 1950)

BAJA CALIFORNIA SUR: Loreto: *Chaetodipus spinatus* (Bassols *et al.* 1976). Unknown if specimens are in collections.

Echinonyssus incomptis (Strandtmann and Morlan, 1953).

PUEBLA: San Cristóbal el Seco: *Dipodomys phillipsi* (Hoffmann *et al.* 1972). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. SONORA: Caborca: *Dipodomys* sp. (Bassols 1981). Unknown if specimens are in collections.

Echinonyssus isabelae Estébanes and Smiley, 1977

VERACRUZ: 18 km NW of Teocelo, Mpio. Ixhuacán; 5 km W of Naolinco, Mpio. Naolinco: *Microtus quasiater* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Echinonyssus liomys (Herrin and Yunker, 1973)

MICHOACÁN: Caleta de Campos: *Heteromys pictus* (Bassols-Batalla *et al.* 1991). Unknown if specimens are in collections. NAYARIT: San Blas: *Heteromys pictus* (Bassols-Batalla *et al.* 1991). Unknown if specimens are in collections.

Echinonyssus microchelae (Strandtmann and Yunker, 1966)

COLIMA: Playa de Oro: *Heteromys pictus, H. spectabilis* (Estébanes-González *et al.* 2011). Specimens in collections: IBUNAM. Note: *H. spectabilis* is not distributed in Colima according to Ceballos (2014). PUEBLA: Pahuatlán: *Peromyscus leucopus* (Bassols-Batalla *et al.* 1991). Unknown if specimens are in collections.

Echinonyssus neotomae (Eads and Hightower, 1951)

MORELOS: Cerro del Chichinautzin: *Neotoma mexicana* (Bassols 1981). Unknown if specimens are in collections.

Echinonyssus teresae Estébanes and Smiley, 1997

OAXACA: Llano de las Flores, Km 132; Tuxtepec-Oaxaca, Mpio. Atepec; 11 km SW of Esperanza to San Isidro, Mpio. Santiago Comaltepec: *Microtus mexicanus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Echinonyssus triacanthus (Jameson, 1950)

SONORA: Caborca: *Dipodomys* sp. (Bassols 1981). Unknown if specimens are in collections.

Echinonyssus utahensis (Allred and Beck, 1966)

BAJA CALIFORNIA: San Quintín: *Peromyscus fraterculus* (Herrin 1970). Specimens in collections: Collection of F. J. Radovsky, whereabouts unknown. Note: *P. fraterculus* is not distributed in Baja California according to Ceballos (2014). ESTADO DE MÉXICO: El Zarco: *Microtus mexicanus* (Hoffmann *et al.* 1972). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Macrochelidae Vitzthum, 1930

Macrocheles hechti Machado, 1964

CIUDAD DE MÉXICO: El Zarco: *Reithrodontomys megalotis* (Hoffmann *et al.* 1972). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Macrocheles sp.

CIUDAD DE MÉXICO: El Zarco: *Microtus mexicanus, Reithrodontomys megalotis* (Bassols 1981). Unknown if specimens are in collections. HIDALGO: Cerro Las Ventanas, Parque Nacional El Chico: *Microtus mexicanus* (Bassols 1981). Unknown if specimens are in collections. SAN LUIS POTOSÍ: Rancho "El Estribo," 10 km SE of El Naranjo, Mpio. Ciudad del Maíz: *Sigmodon hispidus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. Note: *S. hispidus* is not distributed in San Luis Potosí according to Ceballos (2014). A possible alternative host includes *S. leucotis* (Ceballos 2014).

Macronyssidae Oudemans, 1936

Ornithonyssus bacoti (Hirst, 1913)

COLIMA: Playa de Oro: *Oryzomys couesi* (Estébanes-González *et al.* 2011). Specimens in collections: IBUNAM. SAN LUIS POTOSÍ: Rancho "El Estribo," 10 km SE of El Naranjo, Mpio. Ciudad del Maíz: *Sigmodon hispidus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. Note: *S. hispidus* is not distributed in San Luis Potosí according to Ceballos (2014). A possible alternative host includes *S. leucotis* (Ceballos 2014).

Ornithonysus sp.

JALISCO: Chamela Biological Station: *Heteromys pictus* (Gómez-Rodríguez *et al.* 2015). Specimens in collections: CNAC.

Acariformes Zachvatkin, 1952

Trombidiformes Reuter, 1909

Suborder Prostigmata Kramer, 1877

Myobiidae Mégnin, 1877

Radfordia megadontomys Bochkov and Guzmán-Cornejo, 2014

GUERRERO: Puerto del Gallo, Gral. Heliodoro Castillo: *Megadontomys thomasi* (Bochkov and Guzmán-Cornejo 2014). Specimens in collections: CNAC.

Radfordia peromyscus Bochkov and Guzmán-Cornejo, 2014

GUERRERO: Puerto del Gallo, General Heliodoro Castillo: *Peromyscus megalops* (Bochkov and Guzmán-Cornejo 2014). Specimens in collections: CNAC, ZISP.

Radfordia subuliger Ewing, 1938

GUERRERO: Puerto del Gallo, General Heliodoro Castillo: *Peromyscus beatae, Reithrodontomys sumichrasti* (Bochkov and Guzmán-Cornejo 2014). Unknown if specimens in collections: Unknown, possibly CNAC. JALISCO: San Gabriel, Puerto El Floripondio: *Reithrodontomys sumichrasti* (Bochkov and Guzmán-Cornejo 2014). Unknown if specimens in collections: Unknown, possibly CNAC.

Radfordia sp.

OAXACA: Cerro Zempoaltépetl, 5 km N of Santa María Yacochi, Mpio. Tlahuitoltepec: *Peromyscus* sp. (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Scutacaridae Oudemans, 1916

Imparipes cupes Delfinado and Baker, 1978

BAJA CALIFORNIA SUR: Isla Espíritu Santo, Zona Sur, Mpio. La Paz: *Chaetodipus spinatus.* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Tetranychidae Donnadieu, 1875

Pseudobryobia drummondi (Ewing, 1826)

VERACRUZ: 5 km W of Naolinco, Mpio. Naolinco: *Peromyscus levipes* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. Note: This is an accidental occurrence as *P. drummondi* is a plant feeding mite.

Superfamily: Trombiculoidea Ewing, 1944

Trombiculidae Ewing, 1944

Trombiculinae Ewing, 1944

Crypticula jacalae (Loomis and Webb, 1972)

HIDALGO: 13 km NE Jacala: *Peromyscus boylii* (Loomis and Webb 1972). Specimens in collections: FMNH, OSAL, USNM.

Euschoengastoides annectens Loomis, 1971

SONORA: 1 km NE Álamos: *Chaetodipus artus*. 13 km SSE Álamos: *Peromyscus fraterculus, C. artus, C. pernix*. 16 km SE Álamos; 22 km W Álamos: *C. pernix*. La Aduana: *C. goldmani*. 6 km N Navojoa: *P. fraterculus, C. goldmani* (Loomis 1971). Specimens in collections: FMNH, OSAL, USNM.

Euschoengastoides arizonae Loomis, 1971

BAJA CALIFORNIA: 48 km S San Felipe: *Chaetodipus penicillatus* (Loomis 1971). Specimens in collections: FMNH, USNM. BAJA CALIFORNIA SUR: 24 km S El Arco: *Chaetodipus rudinoris* (Loomis 1971). Specimens in collections: FMNH, USNM. Note: *Chaetodipus baileyi* was recognized as the original host. However, according to Riddle *et al.* (2000), *C. baileyi* from the Baja California peninsula are now recognized as *C. rudinoris*. CHIHUAHUA: 106 km S Hidalgo del Parral: *Dipodomys ordii* (Loomis 1971). Specimens in collections: FMNH, USNM. COAHUILA: 27 km E Cuatro Ciénegas: *Chaetodipus hispidus* (Loomis 1971). Specimens in collections: FMNH, USNM. SONORA: 15 km SW Agua Prieta: *Chaetodipus intermedius, C. penicillatus, Dipodomys merriami.* 18 km W Álamos: *D. merriami*. 13 km W Álamos: *Heteromys pictus*. 3 km SSE Álamos; 6 km SSE Álamos: *C. goldmani*. 13 km SSE Álamos: *Peromyscus fraterculus, C. artus, C. pernix*. Carbo; 8 km NW Guaymas; 8 km NW Guaymas: *C. penicillatus*. 21 km E Carbo; 8 km W El Novillo; 58 km N Quitovac: *C. baileyi*. El Novillo: *C. goldmani, C. pernix*. 15 km NW Guaymas: *Onychomys torridus*, *P. fraterculus*, *C. penicillatus.* 10 km S Hermosillo: *P. fraterculus*. Bahia Kino: *C. intermedius*. La Aduana; 3 km W Macuzari: *C. pernix*. 8 km S Naco: *O. leucogaster, D. merriami.* 81 km SE San Luis: *C. penicillatus, D. merriami*. 24 km W Sonoyta: *O. torridus.* Tajitos: *C. intermedius, C. penicillatus* (Loomis 1971). *Specimens in collections*: FMNH, USNM. Note: *O. leucogaster* is not distributed in Sonora according to Ceballos (2014).

Euschoengastoides expansellus Loomis, 1971

SINALOA: 22 km N Culiacán: *Chaetodipus artus, C. pernix, Heteromys pictus.* 18 km S Guamuchil: *C. pernix*. 13 km NW Guamuchil: *C. artus* (Loomis 1971). Specimens in collections: FMNH, OSAL, USNM. SONORA: 97 km S Navojoa: *Chaetodipus goldmani* (Loomis 1971). Specimens in collections: FMNH, USNM.

Euschoengastoides imperfectus (Brennan and Jones, 1954)

BAJA CALIFORNIA: 3 km N Puertecitos: *Chaetodipus formosus* (Loomis 1971). Specimens in collections: FMNH, USNM. SONORA: 25 km WSW Agua Prieta: *Chaetodipus intermedius, C. penicillatus* (Loomis 1971). Specimens in collections: FMNH, USNM.

Euschoengastoides loomisi (Crossley and Lipovsky, 1954)

COAHUILA: No data. Known hosts are mainly small rodents, likely cricetid and heteromyid rodents (Loomis 1956). Specimens in collections: SEMC.

Euschoengastoides neotomae Loomis, 1971

BAJA CALIFORNIA: Punta Banda: *Peromyscus fraterculus*. Isla de Salsipuedes: *P. interparietalis.* 13 km SE El Rosarito: *Neotoma bryanti* (Loomis 1971). Specimens in collections: FMNH, USNM. Note: *P. eremicus* was recognized as the original host. However, *P. eremicus* from the northern part of the Baja California peninsula is now recognized as *P. fraterculus* (Álvarez-Castañeda *et al.* 2010). *P. guardia* was recorded as the original host from Isla de Salsipuedes; however, *P. guardia* is not known to occur on this island and the most likely host is *P. interparietalis* (Ceballos 2014). *N. lepida* was recognized as the original host. However, all *Neotoma* from the Baja California peninsula are now recognized as *N. bryanti* (Patton *et al.* 2007). BAJA CALIFORNIA SUR: 11 km N Comandú; 5 km N San Antonio; 3 km S San Antonio: *Peromyscus eva*. 24 km S El Arco: *P. eva, Chaetodipus rudinoris.* 27 km W Santa Rosalía: *C. rudinoris* (Loomis 1971). Specimens in collections: FMNH, USNM. Note: *C. baileyi* was recognized as the original host. However, according to Riddle *et al.* (2000), *C. baileyi* from the Baja California peninsula are now recognized as *C. rudinoris. P. eremicus* from the northern part of the Baja California peninsula is now recognized as *P. eva* (Patton *et al.* 2007). SONORA: 13 km NW Cananea: *Peromyscus boylii*. El Novillo; 8 km N Guaymas: *P. fraterculus*. 15 km NW Guaymas: *Neotoma albigula.* 10 km S Hermosillo: *N. albigula, P. fraterculus, Chaetodipus penicillatus.* 18 km NE Imuris: *C. baileyi, C. penicillatus*. 11 km S, 3 km W Naco: *N. albigula, P. boylii* (Loomis 1971). Specimens in collections: FMNH, USNM.

Euschoengastoides opimus Loomis, 1971

BAJA CALIFORNIA: 10 km S Puertecitos: *Chaetodipus formosus* (Loomis 1971). Specimens in collections: USNM.

Euschongastoides ryckmani (Brennan, 1966)

SONORA: Isla Tiburón, Cholla Valley: *Chaetodipus* sp. (Brennan 1966). Unknown if specimens are in collections. 15 km NW Guaymas: *C. penicillatus* (Loomis 1971). Specimens in collections: USNM.

Euschoengastoides tanigoshii Loomis, 1971

SONORA: 21 km E Carbo: *Chaetodipus baileyi*. El Novillo: *Peromyscus fraterculus*. 18 km NE Imuris: *P. boylii, C. penicillatus.* 8 km S Naco: *P. boylii*. 11 km S, 3 km W Naco: *C. intermedius, C. penicillatus* (Loomis 1971). Specimens in collections: OSAL, USNM.

Euschoengastoides tumidus Loomis, 1971

CHIHUAHUA: 15 km WSW San Buenaventura: *Neotoma albigula* (Loomis 1971). Specimens in collections: USNM. DURANGO: 72-96 km N Casco: *Dipodomys ordii* (Loomis 1971). Specimens in collections: USNM. ESTADO DE MÉXICO: 6 km E, 3 km S Amecameca: *Peromyscus melanotis* (Loomis 1971). Specimens in collections: USNM. NAYARIT: 7-9 km E San Blas; 14 km E San Blas; 11 km E Ixtlán del Río: *Heteromys pictus* (Loomis 1971). Specimens in collections: USNM. SINALOA: 22 km N Culiacán: *Chaetodipus artus, C. pernix, Heteromys pictus.* 25 km E Culiacancito; 25 km N Mazatlán: *C. pernix*. Río Piaxtla, 88 km N Mazatlán: *Onychomys torridus, Peromyscus fraterculus, C. artus, C. pernix*. 27 km NW San Blas: *C. goldmani* (Loomis 1971). Specimens in collections: USNM. SONORA: 13 km NW Cananea: *Peromyscus boylii*. El Novillo: *P. fraterculus.* 18 km NE Imuris: *Chaetodipus penicillatus*. 11 km S, 3 km N Álamos; 13 km W Álamos: *Neotoma albigula*. 16 km E Álamos: *C. pernix*. 13 km SSE Álamos: *N. albigula, Peromyscus fraterculus, C. artus, C. pernix* (Loomis 1971). Specimens in collections: OSAL, USNM.

Euschoengastoides wadei Loomis, 1969

CAMPECHE: 7.5 km W Escárcega: *Ototylomys phyllotis* (Loomis 1969). Specimens in collections: OSAL, SEMC. YUCATÁN: 2 km N Pisté: *Ototylomys phyllotis* (Loomis 1969). Specimens in collections: SEMC.

Euschoengastoides webbi Loomis, 1971

BAJA CALIFORNIA: 1 km NW Arrastras: *Peromyscus fraterculus, Chaetodipus fallax, Dipodomys merriami.* 8 km N San Felípe: *C. spinatus* (Loomis 1971). Specimens in collections: OSAL, USNM. Note: *P. eremicus* was recognized as the original host. However, *P. eremicus* from the northern part of the Baja California peninsula is now recognized as *P. fraterculus* (Álvarez-Castañeda *et al.* 2010). BAJA CALIFORNIA SUR: 27 km W Santa Rosalía: *Chaetodipus rudinoris* (Loomis 1971). Specimens in collections: USNM. Note: *Chaetodipus baileyi was recognized as the original host.* However, according to Riddle *et al.* (2000), *C. baileyi* from the Baja California peninsula are now recognized as *C. rudinoris.*

Euschoengastoides sp.

JALISCO: Chamela Biological Station: *Heteromys pictus* (Gómez-Rodríguez *et al.* 2015). Specimens in collections: CNAC.

Eutrombicula alfreddugesi (Oudemans, 1910)

CAMPECHE: 7.5 km W Escárcega: *Handleyomys melanotis* (recorded as *Orzyomys melanotis*), *Ototylomys phyllotis, Sigmodon hispidus.* 103 km SE Escárcega: *S. hispidus* (Loomis 1969). Specimens in collections: FMNH. Note: *H. melanotis* and *S. hispidus* are not distributed in Campeche according to Ceballos (2014). A possible alternative host includes *S. toltecus* (Ceballos 2014). CHIAPAS: Carretera Panamericana; Río San Gregorio; *Neotoma mexicana* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. CHIHUAHUA: Barranca del Río Guachochic: *Peromyscus maniculatus* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. MICHOACÁN: 3 km N Pátzcuaro: *Sigmodon hispidus* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. Note: *S. hispidus* is not distributed in Michoacán according to Ceballos (2014). Possible alternative hosts include *S. alleni*, *S fulviventer*, or S. *mascotensis* (Ceballos 2014). OAXACA: 12 km NE Oaxaca: *Reithrodontomys fulvescens* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. QUINTANA ROO: 4 km NNE Felipe Carrillo Puerto: *Handleyomys melanotis* (recorded as *Oryzomys melanotis*), *Ototylomys phyllotis*. Pueblo Nuevo X-Can: *Ototylomys phyllotis* (Loomis 1969). Specimens in collections: FMNH. Note: *H. melanotis* is not distributed in Quintana Roo according to

Ceballos (2014). SAN LUIS POTOSÍ: Región de Bocas: *Neotoma micropus* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. VERACRUZ: 18 km NW Teocelo, Mpio. Ixhuacán: *Microtus quasiater* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. YUCATÁN: Chichén Itzá: *Otonyctomys hatti*. 2 km E Chichén Itzá: *Handleyomys melanotis* (recorded as *Oryzomys melanotis*). Pisté: *Peromyscus melanotis* (Loomis 1969). Specimens in collections: FMNH. Note: *H. melanotis* and *P. melanotis* are not distributed in Yucatán according to Ceballos (2014).

Eutrombicula batatas (Linnaeus, 1758)

GUERRERO: *Orzyomys couesi* (OSAL). Specimens in collections: OSAL. OAXACA: 12 km NE Oaxaca: *Oryzomys palustris* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. Note: *O. palustris* is not distributed in Oaxaca according to Ceballos (2014). TAMAULIPAS: *Orzyomys* sp. (OSAL). Specimens in collections: OSAL. VERACRUZ: Tres Valles: *Sigmodon* sp. (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. YUCATÁN: 3 km N Pisté: *Sigmodon hispidus* (Loomis 1969). Specimens in collections: FMNH. Note: *S. hispidus* is not distributed in Yucatán according to Ceballos (2014). A possible alternative host includes *S. toltecus* (Ceballos 2014).

Hexidionis (Hexidionis) allredi (Brennan and Beck, 1956)

BAJA CALIFORNIA: Las Arrastras: *Neotoma bryanti*. Isla Tiburón: *Dipodomys* sp. (Brennan 1966). Unknown if specimens are in collections. *Neotoma bryanti* (OSAL). Specimens in collections: OSAL. Note: *Neotoma lepida* was recognized as the original host. However, all *Neotoma* from the Baja California peninsula are now recognized as *N. bryanti* (Patton *et al.* 2007). SONORA: 6 km N Navojoa: *Neotoma albigula*. 13 km SSE Álamos: *N. albigula, Onychomys torridus, Peromyscus fraterculus, Chaetodipus artus, C. goldmani*. 10 km S Hermosillo: *N. albigula, P. fraterculus*. 3 km S El Novillo: *C. goldmani* (Lucas and Loomis 1968). Specimens in collections: FMNH.

Hexidionis (Hexidionis) jessiemae (Gould, 1956)

BAJA CALIFORNIA: Las Arrastras; Isla Tiburón: *Chaetodipus* sp. (Brennan 1966). Specimens in collection: Unknown, possibly USNM.

Hexidionis (Hexidionis) macropus Loomis and Lucas, 1970

BAJA CALIFORNIA SUR: La Burrera: *Peromyscus eva* (Loomis and Lucas 1970). Specimens in collections: OSAL. Note: *P. eremicus* was recognized as the original host. However, *P. eremicus* from the southern part of the Baja California peninsula is now recognized as *P. eva* (Álvarez-Castañeda *et al.* 2010).

Hexidionis (Hexidionis) navojoae Lucas and Loomis, 1968

SONORA: 6 km N Navojoa: *Neotoma albigula, Chaetodipus pernix*. 13 km SSE Álamos; 3 km S El Novillo: *Peromyscus fraterculus*. 8 km W La Estrella: *C. baileyi*. 10 km S Hermosillo: *P. fraterculus, C. penicillatus* (Lucas and Loomis 1968). Specimens in collections: FMNH, OSAL, USNM.

Hexidionis (Zosteridionis) breviseta (Loomis and Crossley, 1963)

NUEVO LEÓN: 8 km N, 5 km W La Gloria: *Perognathus merriami* (Loomis and Crossley 1963). Specimens in collections: SMEC.

Hexidionis (Zosteridionis) deserti Loomis and Lucas, 1970

BAJA CALIFORNIA: 18 km de San Felipe: *Dipodomys merriami* (Loomis and Lucas 1970). Unknown if specimens are in collections. SONORA: 34 km SE San Luis: *Dipodomys merriami*. 6 km N Puerto Peñasco; 2.5 km SE San Luis: *D. deserti* (Loomis and Lucas 1970). Unknown if specimens are in collections.

Hexidionis (Zosteridionis) doremi (Brennan and Beck, 1956)

SONORA: Known hosts are heteromyid rodents (Lucas and Loomis 1968). Specimens in collections: FMNH.

Hexidionis (Zosteridionis) harveyi Loomis and Lucas, 1970

SONORA: 15.3 km SW Agua Prieta: *Dipodomys merriami*. Specimens in collections: OSAL.

Hexidionis (Zosteridionis) polytechnica (Hoffmann, 1963)

ESTADO DE MÉXICO: Ojotongo; Lagunas de Zempoala: *Reithrodontomys* sp. (Hoffmann 1963). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Hoffmannina haramotoi Brennan and Goff, 1977

OAXACA: 1 km N of Esperanza, Mpio. Santiago Comaltepec, distrito Ixtlán; 8 km S of Esperanza, Mpio. Santiago Comaltepec: *Handleyomys alfaroi* (recorded as *Oryzomys alfaroi*). 11 km SW of Esperanza to San Isidro, Mpio. Santiago Comaltepec: *H. alfaroi* (recorded as *O. alfaroi*), *Microtus mexicanus, M. oaxacensis, Megadontomys cryophilus, Peromyscus melanocarpus, Reithrodontomys mexicanus, Heteromys desmarestianus*. Llano de las Flores, Km 132, Tuxtepec, Mpio. Atepec: *M. mexicanus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Hoffmannina suriana (Hoffmann, 1954)

CAMPECHE: 7.5 km W Escárcega: *Peromyscus leucopus, P. yucatanicus* (Loomis 1969). Specimens in collections: FMNH. CHIAPAS: Cerro del Cañón del Sumidero; 19 km NW Tuxtla Gutiérrez: *Peromyscus mexicanus* (Hoffmann 1954). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. MORELOS: Volcán Popocatépetl, 1 km SW San Pedro Atlixco: *Peromyscus difficilis* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. OAXACA: 3 km SW Totontepc, Mpio. Totontepec: *Peromyscus melanocarpus*. Cerro Zempoaltépetl, 5 km N Santa María Yacochi, Mpio. Tlahuitoltepec: *Microtus umbrosus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Hyponeocula arenicola (Loomis, 1954)

BAJA CALIFORNIA: 16 km S Paso de San Matías; 12 km S, 42 km E San Vicente; Valle Trinidad; 77 km SE Ensenada: *Dipodomys simulans* (Tanigoshi and Loomis 1974). Specimens in collections: FMNH, SMEC. Note: *Dipodomys agilis* was recognized as the original host. However, all *D. agilis* from the Baja California peninsula are now recognized as *D. simulans* (Sullivan and Best 1997; Patton and Álvarez-Castaneda 1999). COAHUILA: 18 km N Tanque Álvarez: *Dipodomys nelsoni* (Tanigoshi and Loomis 1974). Specimens in collections: FMNH, SMEC. DURANGO: 29 km SSW Tepehuanes: *Sigmodon leucotis* (Tanigoshi and Loomis 1974). Specimens in collections: FMNH, SMEC. SONORA: 15 km WSW Agua Prieta: *Chaetodipus intermedius, C. penicillatus, Dipodomys merriami.* 8 km S Naco: *D. merriami* (Tanigoshi and Loomis 1974). Specimens in collections: FMNH, SMEC.

Hyponeocula deserticola Tanigoshi and Loomis, 1974

SONORA: 3 km S El Novillo: *Chaetodipus goldmani.* A lo largo del Río Yaqui: Known rodent hosts are heteromyid rodents (Tanigoshi and Loomis 1974). Specimens in collections: FMNH.

Hyponeocula imitator Tanigoshi and Loomis, 1974

BAJA CALIFORNIA: 11 km N San Felipe: *Dipodomys merriami* (Tanigoshi and Loomis 1974). Specimens in collections: FMNH. SONORA: 8 km N Guaymas: *Chaetodipus penicillatus, Dipodomys merriami.* 14 km NW Guaymas (Bahía de San Carlos): *D. merriami* (Tanigoshi and Loomis 1974). Specimens in collections: FMNH.

Hyponeocula luciae Tanigoshi and Loomis, 1974

SINALOA: 2 km NE Santa Lucía: *Peromyscus boylii* (Tanigoshi and Loomis 1974). Specimens in collections: FMNH. Note: *P. boylii* is not distributed in Sinaloa according to Ceballos (2014).

Hyponeocula rugosa Tanigoshi and Loomis, 1974

SINALOA: 25 km N, 2 km E Culiacán: *Chaetodipus artus*. 18 km S Guamúchil: *C. pernix* (Tanigoshi and Loomis 1974). Specimens in collections: FMNH. SONORA: 2 km SSE Álamos: *Chaetodipus goldmani.* 8 km W Álamos (La Aduana): *C. pernix*. 13 km W Álamos en Agua Marín: *C. artus, C. goldmani*. 2 km W Tajitos: *C. penicillatus* (Tanigoshi and Loomis 1974). Specimens in collections: FMNH, OSAL.

Leptotrombidium panamensis (Ewing, 1925)

BAJA CALIFORNIA: Las Arrastras: *Neotoma bryanti* (Brennan 1966). Unknown if specimens are in collections. Note: *Neotoma lepida* was recognized as the original host. However, all *Neotoma* from the Baja California peninsula are now recognized as *N. bryanti* (Patton *et al.* 2007). CAMPECHE: 5 km S Champotón: *Ototylomys phyllotis, Heteromys gaumeri.* 7.5 km W Escárcega; 103 km SE Escárcega: *Sigmodon hispidus*. 65 km S, 128 km W Escárcega: *O. phyllotis* (Loomis 1969). Specimens in collections: FMNH. Note: *S. hispidus* is not distributed in Campeche according to Ceballos (2014). A possible alternative host includes *S. toltecus* (Ceballos 2014). CHIAPAS: 17 km NW Teopisca, camino a San Cristóbal Las Casas: *Peromyscus boylii*. Río San Gregorio at Carretera Panamericana: *Neotoma mexicana, P. mexicanus, Heteromys pictus* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. Note: *P. boylii* is not distributed in Chiapas according to Ceballos (2014). MICHOACÁN: Chorros del Varal: *Osgoodomys banderanus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. QUINTANA ROO: 4 km NNE Felípe Carrillo Puerto: *Ototylomys phyllotis, Heteromys gaumeri* (Loomis 1969). Specimens in collections: FMNH. OAXACA: Monte Albán: *Baiomys musculus*. Tehuantepec: *Peromyscus mexicanus* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. SONORA: 25 km SW Navojoa: *Chaetodipus pernix* (Ryckman and Roos 1955). Unknown if specimens are in collections. YUCATÁN: 2 km E Chichén Itzá: *Ototylomys phyllotis* (Loomis 1969). Specimens in collections: FMNH.

Leptotrombidium potosina (Hoffmann, 1950)

CIUDAD DE MÉXICO: Pedregal de San Angel: *Peromyscus gratus* (recording as *P. truei*; Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. MICHOACÁN: 9 km NW Zamora: *Reithrodontomys fulvescens*. 10 km E Zamora: *Heteromys irroratus* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. PUEBLA: Volcán Popocatépetl, 1 km SW San Pedro Atlixco: *Peromyscus difficilis* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. SAN LUIS POTOSÍ: Región de Bocas: *Neotoma micropus* (Hoffmann 1950). El Salto: *Oryzomys palustris* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. San Luis Potosí: *N. micropus* (OSAL). Specimens in collections: OSAL. Note: *O. palustris* is not distributed in San Luis Potosí according to Ceballos (2014).

Microtrombicula aequalis Webb Jr. and Loomis, 1971

SONORA: 8 km W of El Novillo: *Peromyscus boylii* (Webb and Loomis 1971). Specimens in collections: USNM.

Microtrombicula fisheri Webb Jr. and Loomis, 1971

BAJA CALIFORNIA SUR: La Laguna: *Peromyscus truei* (Webb and Loomis 1971). Specimens in collections: USNM.

Microtrombicula intermedia Webb Jr. and Loomis, 1971

SONORA: 13 km S-SE of Álamos: *Peromyscus fraterculus* (Webb and Loomis 1971). Specimens in collections: USNM.

Neotrombicula azteca (Hoffmann, 1952)

CIUDAD DE MÉXICO: La Venta: *Peromyscus hylocetes* (Hoffmann 1952). El Zarco: *Microtus mexicanus* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. ESTADO DE MÉXICO: La Cachucha, Lagunas de Zempoala: *Peromyscus maniculatus.* La Piedad, Lagunas de Zempoala: *Microtus* sp. Volcán Popocatépetl, 5 km E San Pedro Nexapa: *Reithrodontomys* sp. (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Neotrombicula bakeri (Ewing, 1946)

MICHOACÁN: 12 km NE Pátzcuaro; 10 km E Zamora: *Heteromys irroratus* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Neotrombicula caballeroi (Hoffmann, 1960)

CHIAPAS: Camino a San Cristóbal; 17 km NW Teopisca; San Cristóbal Las Casas: *Neotoma mexicana, Peromyscus boylii* (Hoffmann 1960a). Carretera Panamericana at Río San Gregorio: *P. mexicanus* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. Note: *P. boylii* is not distributed in Chiapas according to Ceballos (2014). DURANGO: La Michilía: *Peromyscus difficilis* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. ESTADO DE MÉXICO: Ojotongo, Lagunas de Zempoala: *Microtus* sp. Paraje Otlaltepec del volcán Popocatépetl: *Peromyscus melanotis.* Volcán Popocatépetl: *Reithrodontomys fulvescens* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Neotrombicula claudioi (Hoffmann, 1965)

ESTADO DE MÉXICO: Mirador del Poeta, Volcán Popocatépetl: *Neotomodon alstoni* (Hoffmann 1965). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. OAXACA: 1 km N Esperanza, Mpio. Santiago Comaltepec, Distrito Ixtlán: *Handleyomys alfaroi* (recorded as *Oryzomys alfaroi*). 8 km S Esperanza, Santiago Comaltepec; Cerro Zempoaltépetl, 4 km E Yacochi, Mpio. Tlahuitoltepec: *Peromyscus melanocarpus*. 11 km SW Esperanza to San Isidro, Mpio. Santiago Comaltepec: *Megadontomys cryophilus, Microtus oaxacensis, P. melanocarpus, Reithrodontomys mexicanus, Heteromys desmarestianus*. 3 km SE Totontepec, Mpio. Totontepec: *Megadontomys cryophilus, P. melanocarpus, R. mexicanus, H. desmarestianus*. Llano de las Flores, Km 132 Tuxtepec, Mpio. Atepec: *Microtus mexicanus*. Cerro Zempoaltépetl, 4.5 km N Santa María Yachochi, Mpio. Tlahuitoltepec: *Habromys lepturus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. VERACRUZ: 5 km W Naolinco, Mpio. Naolinco: *Microtus quasiater*, *Peromyscus levipes*. Banderilla, 6 km NW Xalapa: *M. quasiater* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Neotrombicula microti (Ewing, 1928)

ESTADO DE MÉXICO: La Piedra cerca de Ojotongo, Lagunas de Zempoala: *Microtus* sp. Volcán Popocatépetl, el Paraje Diego de Ordaz: *M. mexicanus* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Neotrombicula universitatis (Hoffmann, 1963)

SAN LUIS POTOSÍ: El Salto: *Heteromys* sp. (Hoffmann 1963). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Otorhinophila baccusi Loomis and Wrenn, 1973

COAHUILA: 27 km E Cuatro Ciénegas: *Chaetodipus hispidus* (Loomis and Wrenn 1973). Specimens in collections: FMNH, USNM. Note: Although *C. hispidus* to known to occur in Coahuila, it may not occur as far south as Cuatro Ciénegas. Other possible hosts include *C. eremicus* or *C. nelsoni*.

Otorhinophila desertorum Loomis and Wrenn, 1973

SONORA: 88 km SE San Luis: *Dipodomys merriami* (Loomis and Wrenn 1973). Specimens in collections: FMNH, USNM.

Otorhinophila intrasola Wrenn and Loomis, 1967

SINALOA: 3.5 km SW San Blas; 1.3 km NE El Fuerte: *Chaetodipus pernix.* 10.5 km NW San Blas: *C. artus* (Wrenn and Loomis 1967). Specimens in collections: FMNH, USNM. SONORA: 5 km SSE Álamos, Río Cuchujaqui: *Peromyscus fraterculus, Chaetodipus artus, C. pernix, Heteromys pictus.* 2 km SSE Álamos; 9 km W Álamos; 9 km E Navojoa; 6 km ENE Navojoa (Tierra Blanca): *C. goldmani.* La Aduana, 2.5 km N Navojoa; Cerca de la presa El Novillo a 50 km E, 4 km S Hermosillo: *C. goldmani, C. pernix.* 9 km W Minas Nuevas; 6 km E Navojoa: *C. pernix*. 6 km NW Guaymas (Bahía de San Carlos); 3.5 km S Hermosillo: *C. penicillatus.* 8 km E Carbo: *C. baileyi*. 300m W Tajitos: *C. intermedius* (Wrenn and Loomis 1967). Specimens in collections: FMNH, USNM.

Otorhinophila parvisola Wrenn and Loomis, 1967

BAJA CALIFORNIA: Las Arrastras: *Neotoma bryanti.* 3.5 km S Puertecitos: *Chaetodipus formosus*. Puertecitos: *N. bryanti, C. formosus, C. penicillatus.* 3 km N Puertecitos: *C. formosus, C. penicillatus* (Wrenn and Loomis 1967). Specimens in collections: FMNH, USNM. Note: *Neotoma lepida* was recognized as the original host. However, all *Neotoma* from the Baja California peninsula are now recognized as *N. bryanti* (Patton *et al.* 2007). SONORA: 6 km NW Guaymas (cerca de Bahía de San Carlos): *Neotoma albigula, Onychomys torridus, Chaetodipus penicillatus, Dipodomys merriami.* 2 km N Guaymas: *C. baileyi, C. intermedius*. 6.5 km NW Guaymas: *C. penicillatus*. Kino Nuevo en Bahía Kino; 5 km de Puerto Peñasco; Isla Tiburón: *N. albigula*. 600 m SE Puerto Peñasco: *N. lepida* (Wrenn and Loomis 1967). Specimens in collections: FMNH, USNM. Note: *N. albigula* is the incorrect host and/or that *N. devia* may also be a host from this particular locality.

Otorhinophila sinaloae Wrenn and Loomis, 1967

SINALOA: 34 km N Mazatlán (Río Piaxtla): *Chaetodipus pernix*. 8.5 km NW Culiacán: *Heteromys pictus*. 5 km NW, 300 m N Guamúchil: *C. artus* (Wrenn and Loomis 1967). Specimens in collections: FMNH, USNM.

Otorhinophila sola (Gould, 1956)

BAJA CALIFORNIA: 300 m N Puertecitos: *Neotoma bryanti, Chaetodipus penicillatus* (Wrenn and Loomis 1967). 10 km S Puertecitos: *C. formosus* (Loomis and Wrenn 1973). Specimens in collections: FMNH, USNM. Note: *Neotoma lepida* was recognized as the original host. However, all *Neotoma* from the Baja California peninsula are now recognized as *N. bryanti* (Patton *et al.* 2007).

Otorhinophila xerophila Loomis and Wrenn, 1973

BAJA CALIFORNIA: Misión de Calamajué: *Neotoma bryanti* (Loomis and Wrenn 1973). Specimens in collections: FMNH, USNM. Note: *Neotoma lepida* was recognized as the original host. However, all *Neotoma* from the Baja California peninsula are now recognized as *N. bryanti* (Patton *et al.* 2007).

Parasecia gurneyi (Ewing, 1937)

CAMPECHE: 5 km S Champotón: *Ototylomys phyllotis*. 7.5 km W Escárcega: *Peromyscus leucopus, Heteromys gaumeri* (Loomis 1969). Specimens in collections: FMNH. YUCATÁN: Chichén Itzá: *Peromyscus yucatanicus*. 3 km N Pisté: *P. leucopus* (Loomis 1969). Specimens in collections: FMNH.

Speleocola secunda Brennan and Jones, 1969

CAMPECHE: 7 km N, 51 km E Escárcega: *Peromyscus yucatanicus* (Loomis and Webb 1969). Specimens in collections: FMNH. YUCATÁN: 6 km S Mérida; 3 km N Pisté: *Peromyscus yucatanicus* (Loomis and Webb 1969). Specimens in collections: FMNH.

Schoengastiinae Vercammen-Grandjean, 1960

Cordiseta aberrans (Brennan and Jones, 1959)

CHIAPAS: 6 km NW Teopisca: *Peromyscus oaxacensis* (Brennan and Jones 1959). Specimens in collections: USNM. Carretera Panamericana at Río San Gregorio: *Neotoma mexicana, P. mexicanus.* Cerro del Cañón del Sumidero, 11 km NW Tuxtla Gutiérrez: *Heteromys pictus* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. MICHOACÁN: 12 km NE Pátzcuaro: *Heteromys irroratus* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Cordiseta hoffmanae (Brennan, 1960)

CHIAPAS: Tuxtla Gutiérrez: *Baiomys musculus* (Brennan 1960a). Specimens in collections: USNM. JALISCO: Chamela Biological Station: *Heteromys pictus* (Gómez-Rodríguez *et al.* 2015). Specimens in collections: CNAC. MICHOACÁN; *Heteromys* sp. (Brennan 1960a). Specimens in collections: USNM. OAXACA: Monte Albán: *Baiomys musculus* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Cordiseta mexicana (Hoffmann, 1954)

CAMPECHE: 5 km S Champotón; 7.6 km W Escárcega: *Heteromys gaumeri* (Loomis 1969). Specimens in collections: FMNH. CHIAPAS: Carretera Panamericana at Río San Gregorio: *Neotoma mexicana* (Hoffmann 1954). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. QUINTANA ROO: Pueblo Nuevo X-Cán: *Peromyscus yucatanicus* (Loomis 1969). Specimens in collections: FMNH.

Dermadelema furmani (Gould, 1956)

BAJA CALIFORNIA: 1 km N Puertecitos; 19 km NE Rancho Laguna Chapala: *Neotoma bryanti* (Pomeroy and Loomis 1984). Specimens in collections: FMNH. SONORA: 4 km NW El Desemboque: *Neotoma albigula, Peromyscus fraterculus*. 25 km N Guaymas: *P. fraterculus*. 30 km SW Pitiquito: *N. albigula*. 88 km SE San Luis: *Dipodomys merriami* (Pomeroy and Loomis 1984). Specimens in collections: FMNH. Note: *Neotoma lepida* was recognized as the original host. However, all *Neotoma* from the Baja California peninsula are now recognized as *N. bryanti* (Patton *et al.* 2007).

Dermadelema sleeperi Pomeroy and Loomis, 1984

BAJA CALIFORNIA: 3 km N Puertecitos: *Chaetodipus formosus*. 8 km N San Felipe: *Dipodomys merriami* (Pomeroy and Loomis 1984). Specimens in collections: FMNH. SINALOA: 1 km NE Santa Lucía: *Peromyscus boylii* (OSAL). *Specimens in collections*: OSAL. Note: *P. boylii* is not distributed in Sinaloa according to Ceballos (2014). SONORA: 88 km SE San Luis: *Dipodomys merriami* (Pomeroy and Loomis 1984). Specimens in collections: FMNH.

Ectonyx fusicornis Brennan, 1960

JALISCO: Chamela Biological Station: *Heteromys pictus*

(Gómez-Rodríguez *et al.* 2015). Specimens in collections: CNAC. PUEBLA: *Heteromys irroratus* (Brennan 1960b). Specimens in collections: OSAL, USNM. YUCATÁN: 3 km N Pisté: *Heteromys gaumeri* (Loomis 1969). Specimens in collections: FMNH.

Euschoengastia ambocalis Wrenn and Loomis, 1973

BAJA CALIFORNIA: 5 km S El Rayo: *Peromyscus truei*. 2.5 km S El Topo: *P. truei, Chaetodipus californicus, Dipodomys simulans.* La Rumorosa: *P. fraterculus.* (Loomis and Somerby 1966). Specimens in collections: FMNH. Note: *P. fraterculus* are not distributed in Baja California according to Ceballos (2014). *Peromyscus eremicus* was recognized as the original host. However, *P. eremicus* from the northern part of the Baja California peninsula is now recognized as *P. fraterculus* (Álvarez-Castañeda *et al.* 2010). *Dipodomys agilis* was recognized as the original host. However, all *D. agilis* from the Baja California peninsula are now recognized as *D. simulans* (Sullivan and Best 1997; Patton and Álvarez-Castaneda 1999).

Euschoengastia ampliseta Loomis and Somerby, 1966

DURANGO: 60 m W Buenos Aires (22 km W El Salto): *Peromyscus boylii*, *P. melanotis.* 600 m W El Salto: *P. melanotis* (Loomis and Somerby 1966). Specimens in collections: FMNH. JALISCO: No data. Known hosts are mainly small rodents, likely cricetid and heteromyid rodents. (Wrenn 1987). Unknown if specimens are in collections.

Euschoengastia barrerai Hoffmann, 1960

CHIHUAHUA: Barranca del Río Guachochic: *Peromyscus maniculatus* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. CIUDAD DE MÉXICO: La Venta: *Peromyscus hylocetes* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. DURANGO: 600 m W Buenos Aires; 20 km W El Salto: *Peromyscus melanotis.* (Loomis and Somerby 1966). Specimens in collections: FMNH. La Michilía: *P. difficilis* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. ESTADO DE MÉXICO: 250 m W Paso de Cortés; Popocatépetl: *Peromyscus maniculatus* (Hoffmann 1960b; Whitaker *et al.* 1991). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. Ojotongo, Lagunas de Zempoala: *Microtus* sp., *Neotoma* sp., *Peromyscus maniculatus*. La Piedra, Lagunas de Zempoala: *Microtus* sp., *Reithrodontomys* sp. La Cachucha, Lagunas de Zempoala: *P. maniculatus*. Nevado de Toluca: *Reithrodontomys* sp. Mirador del Poeta, Volcán Popocatépetl: *M. mexicanus, Neotomodon alstoni* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. NUEVO LÉON: Cerro Potosí 18 km N Galeana: *Peromyscus maniculatus* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. PUEBLA: 10 km W San Martín Texmelucan, Mpio. San Martín Texmelucan: *Peromyscus maniculatus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. 2 km W Atenco de Aljojuca: *Dipodomys phillipsi* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. Note: Wrenn (1987) also notes this species from Veracruz and Nuevo Léon. Additional hosts for this species include *Neotoma albigula, Neotomodon alstoni, Neotoma* sp., *P. melanotis,* and *Peromyscus* sp. (Whitaker *et al.* 1991). Although Whitaker *et al.* (1991) state than an additional host from Veracruz and Nuevo Léon may be *N. albigula*, this species does not occur in these states (Ceballos 2014). SONORA: 5 km SSE Álamos, Río Cuchujaqui: *Peromyscus fraterculus* (Loomis and Somerby 1966). Specimens in collections: FMNH.

Euschoengastia criceticola Brennan, 1948

BAJA CALIFORNIA: 5.5 km S El Rayo: *Peromyscus truei.* 2.5 km S El Topo: *Neotoma macrotis, N. bryanti, P. truei, Chaetodipus californicus, Dipodomys simulans.* La Rumorosa: *P. fraterculus, P. maniculatus, C. fallax.* 5 km SW La Rumorosa; Sierra San Pedro Mártir; El Socorro; 6 km E José del Castillo: *D. simulans,* 9 km W Santo Tomás, *P. californicus* (Loomis and Somerby 1966). Specimens in collections: FMNH. Note: *N. fusipes* from Baja California is now recognized as *N. macrotis* (Matocq 2002). *Neotoma lepida* was recognized as the original host. However, all *Neotoma* from the Baja California peninsula are now recognized as *N. bryanti* (Patton *et al.* 2007). *Dipodomys agilis* was recognized as the original host. However, all *D. agilis* from the Baja California peninsula are now recognized as *D. simulans* (Sullivan and Best 1997; Patton and Álvarez-Castaneda 1999). *Peromyscus eremicus* was recognized as the original host. However, *P. eremicus* from the northern part of the Baja California peninsula is now recognized as *P. fraterculus* (Álvarez-Castañeda *et al.* 2010). HIDALGO: *Peromyscus difficilis* (OSAL). Specimens in collections: OSAL.

Euschoengastia fronterizae Wrenn *et al.*, 1976

COAHUILA: Sierra Fronteriza; 40 km SE Boquillas del Carmen: *Peromyscus difficilis* (Wrenn *et al.* 1976). Specimens in collections: FMNH.

Euschoengastia gagarini Brennan, 1962

GUERRERO: *Heteromys irroratus* (Brennan 1962). Specimens in collections: USNM.

Euschoengastia heteromyicola Wrenn and Loomis, 1974

BAJA CALIFORNIA: La Rumorosa; 5 km W, 4.4 km S La Rumorosa: *Dipodomys simulans* (Wrenn and Loomis 1974). Specimens in collections: FMNH, USNM. Note: *Dipodomys agilis* was recognized as the original host. However, all *D. agilis* from the Baja California peninsula are now recognized as *D. simulans* (Sullivan and Best 1997; Patton and Álvarez-Castaneda 1999).

Euschoengastia marginalis Wrenn and Somerby, 1974

BAJA CALIFORNIA: 2.4 km S El Topo: *Neotoma macrotis, N. bryanti, Chaetodipus californicus* (Wrenn and Loomis 1974). Specimens in collections: FMNH, USNM. Note: *N. fusipes* from Baja California is now recognized as *N. macrotis* (Matocq 2002). *N. lepida* was recognized as the original host. However, all *Neotoma* from the Baja California peninsula are now recognized as *N. bryanti* (Patton *et al.* 2007).

Euschoengastia multisetosa Loomis and Somerby, 1966

BAJA CALIFORNIA: 5.5 km S El Rayo: *Peromyscus truei*. 2.5 km S El Topo: *P. truei*, *Chaetodipus californicus.* La Rumorosa: *P. fraterculus, P. maniculatus, Peromyscus* sp., *C. fallax* (Loomis and Somerby 1966). Specimens in collections: FMNH, OSAL, USNM. Note: *Peromyscus eremicus* was recognized as the original host. But *P. eremicus* from the northern part of the Baja California peninsula is now recognized as *P. fraterculus* (Álvarez-Castañeda *et al.* 2010).

Euschoengastia numerosa Wrenn and Loomis, 1974

SONORA: 84 km SE San Luis: *Dipodomys merriami* (Wrenn and Loomis 1974). Specimens in collections: FMNH, USNM.

Euschoengastia obscura Wrenn and Loomis, 1974

BAJA CALIFORNIA: 6 km SW Paso de San Matías; 5 km W, 4.4 km S La Rumorosa: *Dipodomys simulans* (Wrenn and Loomis 1974). Specimens in collections: FMNH, USNM. Note: *Dipodomys agilis* was recognized as the original host. However, all *D. agilis* from the Baja California peninsula are now recognized as *D. simulans* (Sullivan and Best 1997; Patton and Álvarez-Castaneda 1999).

Euschoengastia otophila Loomis and Bunnell, 1962

BAJA CALIFORNIA: 5.5 km de El Rayo: *Peromyscus truei* (Loomis and Bunnell 1962). Specimens in collections: FMNH, USNM. SINALOA: 700 m NE Santa Lucía: *Peromyscus boylii* (Loomis and Bunnell 1962). Specimens in collections: FMNH, USNM. Note: *P. boylii* is not distributed in Sinaloa according to Ceballos (2014). SONORA: 4 km S, 1.5 km W Naco: *Peromyscus boylii* (Loomis and Bunnell 1962). Specimens in collections: FMNH, USNM.

Euschoengastia radfordi Brennan and Jones, 1962

BAJA CALIFORNIA: La Rumorosa; 5 km W, 6 km S La Rumorosa: *Dipodomys simulans* (Loomis and Somerby 1966). Specimens in collections: FMNH, USNM. Note: *Dipodomys agilis* was recognized as the original host. However, all *D. agilis* from the Baja California peninsula are now recognized as *D. simulans* (Sullivan and Best 1997; Patton and Álvarez-Castaneda 1999). DURANGO: 600 m W Buenos Aires; 25 km W El Salto: *Peromyscus boylii* (Loomis and Somerby 1966). Specimens in collections: FMNH, USNM. SONORA: 32 km SE San Luis: *Dipodomys merriami* (Loomis and Somerby 1966). Specimens in collections: FMNH, USNM.

Euschoengastia simulans Wrenn and Loomis, 1974

DURANGO: 53 km W El Salto: *Peromyscus boylii* (Wrenn and Loomis 1974). Specimens in collections: FMNH, USNM.

Euschoengastia stephensi Loomis and Somerby, 1966

SONORA: 5.5 km NW Guaymas: *Onychomys torridus* (Loomis and Somerby 1966). Specimens in collections: FMNH, OSAL, USNM.

Euschoengastia zapoteca Hoffmann, 1965

OAXACA: Monte Albán: *Baiomys musculus* (Hoffmann 1965). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. 1 km Esperanza, Mpio. Santiago Comaltpec, distrito Ixtlán: *Reithrodontomys mexicanus*. Llano de las Flores, Km 132 Tuxtepec, Mpio. Atepec: *Peromyscus levipes*. Cerro Zempoaltepetl, 5 km N Santa María Yacochi, Mpio. Tlahuitoltepec: *Microtus umbrosus*. Cerro Zempoaltépetl, 4.5 km N Santa María Yacochi, Mpio. Tlahuitoltepec: *Microtus* sp. 11 km SW Esperanza to San Isidro, Mpio. Santiago Comaltepec: *M. mexicanus*. Cerro Zempoaltepetl, 4 km E Yacochi, Mpio. Tlahuitoltepec: *P. melanocarpus*. 3 km SE Totontepec, Mpio. Totontepec: *P. melanocarpus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. Note: *P. levipes* is not distributed in Oaxaca according to Ceballos (2014). VERACRUZ: Banderillas, 6 km NW Xalapa, Mpio. Xalapa: *Peromyscus furvus*. 18 km NW Teocelo, Mpio. Ixhuacán: *Microtus quasiater* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Euschoengastia sp.

VERACRUZ: 5 km W Noalinco, Mpio. Naolinco: *Microtus quasiater* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Kayella lacerta (Brennan, 1948)

BAJA CALIFORNIA: Isla Salsipuedes: *Peromyscus interparietalis*. Las Arrastras: *Neotoma bryanti* (Brennan 1966). Specimens in collections: Unknown, possibly USNM. Note: *P. guardia* was recorded as the original host from Isla de Salsipuedes. However, *P. guardia* is not known to occur on this island and the most likely host is *P. interparietalis* (Ceballos 2014). *Neotoma lepida* was recognized as the original host. However, all *Neotoma* from the Baja California peninsula are now recognized as *N. bryanti* (Patton *et al.* 2007).

Neoschoengastia dalmati Brennan, 1951

COAHUILA: *Reithrodontomys* sp. (Brennan and Dalmat 1960). Specimens in collections: Unknown, possibly USNM.

Parascoschoengastia nuniezi (Hoffmann, 1944)

CHIAPAS: Carretera Panamericana at Río San Gregorio: *Peromyscus mexicanus* (Hoffmann 1990). Specimens in collections: IBUNAM.

Pseudoschoengastia anomala (Hoffmann, 1951)

CHIAPAS: No data. Known hosts are mainly small rodents, likely cricetid and heteromyid rodents (Brennan 1960a). Specimens in collections: Unknown, possibly USNM. CIUDAD DE MÉXICO: Cerro de Zacayuca; Pedregal de San Ángel: *Peromyscus gratus* (recorded as *P. truei*; Hoffmann 1951a). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. ESTADO DE MÉXICO: Cerca de Ojotongo; Lagunas de Zempoala: *Neotoma* sp. (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Pseudoschoengastia audyi Brennan and Jones, 1959

GUERRERO: *Heteromys irroratus* (Brennan and Dalmat 1960). Specimens in collections: Unknown, possibly USNM. JALISCO: *Baiomys* sp. (Brennan and Dalmat 1960). Specimens in collections: Unknown, possibly USNM. MICHOACÁN: *Heteromys pictus* (Brennan and Dalmat 1960). Specimens in collections: Unknown, possibly USNM. 12 km NE Pátzcuaro: *Heteromys irroratus.* 3 km N Pátzcuaro: *Sigmodon hispidus* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. Note: *S. hispidus* is not distributed in Michoacán according to Ceballos (2014). Possible alternative hosts include *S. alleni*, *S fulviventer*, or *S. mascotensis* (Ceballos 2014). MORELOS: *Oryzomys couesi* (Brennan and Dalmat 1960). Specimens in collections: Unknown, possibly USNM. SAN LUIS POTOSÍ: El Salto: *Oryzomys palustris* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. Note: *O. palustris* is not distributed in San Luis Potosí according to Ceballos (2014). VERACRUZ: *Baiomys musculus, Reithrodontomys* sp. (Brennan and Dalmat 1960). Specimens in collections: Unknown, possibly USNM.

Pseudoschoengastia brennani Hoffmann, 1960

CAMPECHE: 7 km N, 51 km E Escárcega: *Peromyscus yucatanicus* (Loomis 1969). Specimens in collections: Unknown, possibly FMNH. CHIAPAS: 6 km NW Teopisca: *Peromyscus boylii, P. oaxacensis.* 7 km N, 51 km E Escárcega: *P. yucatanicus.* Cerro del Cañón del Sumidero, 19 km NW Tuxtla Gutiérrez; Carretera Panamericana at Río San Gregorio: *P. mexicanus.* (Hoffmann 1960b). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. Note: *P. boylii* and *P. yucatanicus* are not distributed in Chiapas according to Ceballos (2014). QUINTANA ROO: 4 km NNE Felípe Carrillo Puerto: *Handleyomys melanotis* (recorded as *Oryzomys melanotis*), *Ototylomys phyllotis*. Pueblo Nuevo X-Can*: Peromyscus yucatanicus* (Loomis 1969). Specimens in collections: FMNH, USNM. Note: *H. melanotis* is not distributed in Quintana Roo according to Ceballos (2014). YUCATÁN: 6 km S Mérida; 3 km N Pisté: *Peromyscus yucatanicus*. 66 km NE Mérida: *Ototylomys phyllotis* (Loomis 1969). Specimens in collections: FMNH, USNM.

Pseudoschoengastia extrinseca Brennan, 1960

CAMPECHE: 5 km S Champotón; 7 km W Escárcega: *Heteromys gaumeri.* 65 km S, 128 km E Escárcega: *Ototylomys phyllotis* (Loomis 1969). Specimens in collections: Unknown, possibly FMNH. QUINTANA ROO: 4 km NNE Felipe Carrillo Puerto: *Ototylomys phyllotis, Heteromys gaumeri* (Loomis 1969). Specimens in collections: Unknown, possibly FMNH. YUCATÁN: 2 km E Chichén Itzá: *Ototylomys phyllotis.* Pisté: *O. phyllotis*, *Heteromys gaumeri* (Loomis 1969). Specimens in collections: Unknown, possibly FMNH. VERACRUZ: *Peromyscus mexicanus* (OSAL). Specimens in collections: OSAL.

Pseudoschoengastia guatemalensis Brennan, 1952

CHIAPAS: Cerro Tzontehuitz, 13 km NE San Cristóbal de las Casas, Mpio. San Juan Chamula: *Reithrodontomys microdon* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. COAHUILA: *Neotoma* sp.*, Peromyscus* sp. (Brennan and Dalmat 1960). Specimens in collections: Unknown, possibly USNM. ESTADO DE MÉXICO: Ojotango, Lagunas de Zempoala: *Peromyscus maniculatus* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. MICHOACÁN: *Heteromys pictus* (Brennan and Dalmat 1960). Specimens in collections: Unknown, possibly USNM. MORELOS: *Oryzomys couesi* (Brennan and Dalmat 1960). Specimens in collections: Unknown, possibly USNM. SAN LUIS POTOSÍ: El Salto: *Handleyomys rostratus* (recorded as *Oryzomys rostratus*), *Reithrodontomys* sp. (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. VERACRUZ: *Baiomys musculus, Peromyscus boylii, Reithrodontomys fulvescens* (Brennan and Dalmat 1960). Specimens in collections: Unknown, possibly USNM. Note: *P. boylii* is not distributed in Veracruz according to Ceballos (2014).

Pseudoschoengastia hypopsia Brennan and Jones, 1959

CHIAPAS: 11 km NW Tuxtla Gutiérrez: *Baiomys musculus* (Brennan and Jones 1959). Specimens in collections: USNM. Carretera Panamericana at Río San Gregorio: *Neotoma mexicana, Peromyscus mexicanus.* 17 km NW Teopisca, camino a San Cristóbal Las Casas: *P. boylii* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. Note: *P. boylii* is not distributed in Chiapas according to Ceballos (2014).

Pseudoschoengastia pedregalensis (Hoffmann, 1951)

ESTADO DE MÉXICO: Cerro de Zucayuca, Pedregal de San Ángel, *Baiomys taylori, Peromyscus gratus* (recorded as *P. truei gratus*; Hoffmann 1951a, Whitaker *et al.* 1991). Cerca de Ojotango, Lagunas de Zempoala, *Reithrodontomys* sp. (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. HIDALGO: No data. Known hosts are mainly small rodents, likely cricetid and heteromyid rodents (Brennan 1960a). Specimens in collections: USNM. MICHOACÁN: No data. Known hosts are mainly small rodents, likely cricetid and heteromyid rodents (Brennan 1960a). Specimens in collections: USNM. MORELOS: Lagunas de Zempoala, 1 km NE Laguna No. 1, Mpio. de Huitzilac: *Neotoma mexicana* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. No data. Known hosts are mainly small rodents, likely cricetid and heteromyid rodents (Brennan 1960a). Specimens in collections: USNM. OAXACA: 1 km S and 5 km E to Vista Hermosa, Mpio. Santiago Comaltepec: *Peromyscus melanocarpus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. VERACRUZ: Banderillas, 6 km NW Xalapa, Mpio. Xalapa: *Peromyscus furvus*. 18 km NW Teocelo, Mpio. Ixhuacán; 5 km W Naolinco, Mpio. Naolinco: *Microtus quasiater* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. No Data. Known hosts are mainly small rodents, likely cricetid and heteromyid rodents (Brennan 1960a). Specimens in collections: USNM.

Pseudoschoengastia scitula Brennan and Jones, 1959

CAMPECHE: 5 km S Champotón; 65 km S, 128 km E Escárcega: *Ototylomys phyllotis*. 7.5 km W Escárcega: *Handleyomys melanotis* (recorded as *Oryzomys melanotis*), *Ototylomys phyllotis, Peromyscus leucopus, Sigmodon hispidus, Heteromys gaumeri*. 7 km N, 51 km E Escárcega: *H. gaumeri*. 103 km SE Escárcega: *Ototylomys phyllotis*, *H. gaumeri* (Loomis 1969). Specimens in collections: Unknown, possibly FMNH. Note: *H. melanotis* and *S. hispidus* are not distributed in Campeche according to Ceballos (2014). A possible host includes *S. toltecus* (Ceballos 2014). CHIAPAS: Carretera Panamericana at Río San Gregorio: *Heteromys pictus* (Brennan and Jones 1959). Specimens in collections: USNM. GUERRERO: No data. Known hosts are mainly small rodents, likely cricetid and heteromyid rodents (Brennan 1960a). Specimens in collections: USNM. QUINTANA ROO: 85 km W Chetumal: *Ototylomys phyllotis*, *Heteromys gaumeri*. 4 km NNE Felipe Carrillo Puerto: *Handleyomys melanotis* (recorded as *Oryzomys melanotis*), *Ototylomys phyllotis*, *H. gaumeri*. Pueblo Nuevo X-Can: *Ototylomys phyllotis* (Loomis 1969). Specimens in collections: Unknown, possibly FMNH. Note: *H. melanotis* is not distributed in Quintana Roo according to Ceballos (2014). YUCATÁN: Chichén Itzá: *Ototylomys phyllotis*. Peto: *Heteromys gaumeri*. 2-3 km N Pisté: *Peromyscus yucatanicus*. 66 km NE Mérida: *O. phyllotis*, *H. gaumeri* (Loomis 1969). Specimens in collections: Unknown, possibly FMNH.

Walchioides gouldi (Hoffman, 1954)

CHIAPAS: Carretera Panamericana at Río San Gregorio: *Peromyscus mexicanus* (Hoffmann 1954). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Walchioides inevicta (Brennan, 1960)

PUEBLA: *Baiomys musculus*. Popocatépetl: *Neotomodon alstoni* (Brennan 1960a). Specimens in collections: USNM. Izucar de Matamoros: *Baiomys musculus* (OSAL). Specimens in collections: OSAL.

Walchioides whartoni (Brennan, 1960)

COAHUILA: *Neotoma* sp., *Peromyscus* sp. (Brennan 1960a). Specimens in collections: OSAL, USNM.

Leeuwenhoekiidae Womersley, 1944

Morelacarus cognatus (Brennan, 1966)

BAJA CALIFORNIA: Las Arrastras: *Neotoma bryanti* nest (Brennan 1966). Specimens in collections: USNM. Note: N. *lepida* from the Baja California peninsula is now recognized as *N. bryanti* (Patton *et al.* 2007).

Morelacarus morelensis (Hoffmann, 1960)

ESTADO DE MÉXICO: Cerca de Ojotongo; La Piedra; Lagunas de Zempoala: *Microtus* sp. (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. GUERRERO: Omiltemi: *Neotoma mexicana* (Hoffmann 1990). Specimens in collections: Unknown; Hoffmann collection is in the CNAC. MORELOS: Lagunas de Zempoala, 1 km NE Laguna No.1, Mpio. de Huitzilac: *Neotoma mexicana*. Camino a Atzompa, vertiente sur del Cuautépetl, Mpio. de Huitzilac: *Microtus mexicanus* (Hoffmann 1960b). Specimens in collections: USNM, IBUNAM.

Odontacarus (Tarsalacarus) bakeri (Hoffmann, 1951)

CIUDAD DE MÉXICO: Pedregal de San Ángel: *Peromyscus gratus* (recorded as *P. truei*; Hoffmann 1951b). Specimens in collections: IBUNAM. Pedregal de San Ángel: *Baiomys taylori* (Brennan and Dalmat 1960). Specimens in collections: Unknown, possibly USNM or FMNH. 1 km SE Zacatepec: *P. gratus* (recorded as *P. truei*; Hoffmann 1990). Specimens in collections: IBUNAM. ESTADO DE MÉXICO: Gruta de la Estrella, Tonatico: *Neotoma mexicana*. Ojotongo, Lagunas de Zempoala: *Neotoma* sp. (Hoffmann 1990). Specimens in collections: IBUNAM. MICHOACÁN: 10 km E Zamora: *Heteromys irroratus* (Hoffmann 1990). Specimens in collections: IBUNAM. PUEBLA: Volcán Popocatépetl, 1 km SW San Pedro Atlixco: *Peromyscus difficilis* (Hoffmann 1990). Specimens in collections: IBUNAM.

Odontacarus (Tarsalacarus) chiapanensis (Hoffmann, 1948)

BAJA CALIFORNIA: Known hosts are small rodents, likely cricetid and heteromyid rodents (Goff and Loomis 1977). Unknown if specimens are in collections. QUINTANA ROO: 4 km NNE Felipe Carrillo Puerto: *Ototylomys phyllotis*. Pueblo Nuevo X-Cán: *Peromyscus yucatanicus* (Loomis 1969). Specimens in collections: FMNH. OAXACA: 11 km SW Esperanza to San Isidro, Mpio. Santago Comaltepec: *Nyctomys sumichrasti* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Odontacarus (Odontacarus) kromani Goff and Loomis, 1973

BAJA CALIFORNIA: 11 km N del Cañón del Cajón, Sierra de San Pedro Mártir: *Peromyscus crinitus* (Goff and Loomis 1973). Specimens in collections: Unknown, possibly FMNH.

Odontacarus (Odontacarus) linsdalei (Brennan and Jones, 1954)

BAJA CALIFORNIA: Known hosts are small rodents, likely cricetid and heteromyid rodents (Goff and Loomis 1977). Unknown if specimens are in collections.

Odontacarus (Tarsalacarus) micheneri (Greenberg, 1952)

BAJA CALIFORNIA: Known hosts are small rodents, likely cricetid and heteromyid rodents (Goff and Loomis 1977). Unknown if specimens are in collections.

Odontacarus (Odontacarus) tubercularis (Brennan, 1952)

CAMPECHE: 5 km S Champotón: *Heteromys gaumeri* (Loomis 1969). Specimens in collections: FMNH. YUCATÁN: Chichén Itzá: *Ototylomys phyllotis, Peromyscus yucatanicus, Sigmodon hispidus.* Pisté: *Heteromys gaumeri* (Loomis 1969). Specimens in collections: FMNH. Note: *S. hispidus* is not distributed in Yucatán according to Ceballos (2014). A possible host includes *S. toltecus* (Ceballos 2014).

Sasacarus furmani (Hoffmann, 1954)

OAXACA: Monte Albán: *Baiomys musculus* (Hoffmann 1954). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Sasacarus whartoni (Hoffmann, 1951)

BAJA CALIFORNIA: Arroyo de Calamajué: *Peromyscus* sp. (Brennan 1966). Specimens in collections: USNM. PUEBLA: Matamoros: *Baiomys musculus* (Hoffmann 1951b). Specimens in collections: Unknown; Hoffmann collection is in the CNAC.

Whartonia guerrerensis Hoffmann, 1960

OAXACA: 1 km S and 5 km E to Vista Hermosa, Mpio. Santiago Comaltepec: *Peromyscus mexicanus*. 11 km SW of Esperanza to San Isidro, Mpio. Santiago Comaltepec: *Nyctomys sumichrasti* (Hoffmann 1960c; Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Xenodontacarus folius Loomis and Goff, 1973

SINALOA: 2 km NE Santa Lucía: *Peromyscus boylii* (Loomis and Goff 1973). Specimens in collections: USNM. Note: *P. boylii* is not distributed in Sinaloa according to Ceballos (2014).

Xenodontacarus serratus Loomis and Goff, 1973

MICHOACÁN: Chorros del Varal: *Osgoodomys banderanus*. (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Sarcoptiformes Reuter, 1909

Infraorder: Astigmata Canestrini, 1891

Glycyphagidae Berlese, 1887

Glycyphagus hylandi (Fain, 1969)

COLIMA: Playa de Oro: *Baiomys musculus* (Estébanes-González *et al.* 2011). Specimens in collections: IBUNAM. Note: This is likely a misidentification; *G. hylandi* is normally associated with the eastern chipmunk in the United States.

Glycyphagus hypudaei hypudaei (Koch, 1841)

CHIAPAS: Cerro Tzontehuitz, 12 km NE of San Cristóbal de las Casas, Mpio. San Juan Chamula: *Reithrodontomys microdon* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. OAXACA: 1 km N of Esperanza, Mpio. Santiago Comaltepec, Distrito Ixtlán and 3 km SE of Totontepec, Mpio. Totontepec: *Peromyscus melanocarpus, Reithrodontomys mexicanus.* Cerro Zempoaltepetl, 4 km E of Yacochi, Mpio. Tlahuitoltepec: *Handleyomys alfaroi* (recorded as *Oryzomys alfaroi*; Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. VERACRUZ: 18 km NW of Teocelo, Mpio. Ixhuacán; 300 km NW Cascadas Teocelo, 1.5 km SE Xico, Mpio. Xico: *Microtus quasiater.* Banderillas, 6 km NW of Xalapa, Mpio. Xalapa: *Peromyscus furvus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Glycyphagus liomys (Fain and Ide, 1978)

JALISCO: 9.8 mi W of Atenquique: *Heteromys irroratus* (Fain and Ide 1978). Specimens in collections: USNM. Chamela Biological Station: *Heteromys pictus* (Gómez-Rodríguez *et al.* 2015). Specimens in collections: CNAC. NOTE: This species was originally described in the genus *Dermacarus*, but it has not yet been formally recombined.

Glycyphagus mexicanus (Fain, 1969)

OAXACA: Ilacolula: *Baiomys musculus* (Fain 1969). Specimens in collections: NHM. NOTE: This species was originally described in the genus *Dermacarus*, but it has not yet been formally recombined.

Glycyphagus ornatus (Fain, 1967)

YUCATÁN: 3 km N of Pisté; 2 km E of Chichén Itzá: *Heteromys gaumeri* (Pence and Genoways 1974). Specimens in collections: USNM. NOTE: This species was originally described in the genus *Dermacarus*, but it has not yet been formally recombined. Recombination into *Glycyphagus* renders the name a junior secondary homonym of *Glycyphagus ornatus* Kramer, 1881.

Neolabidophorus verrucosus Fain and Lukoschus, 1978

ESTADO DE MÉXICO: *Chaetodipus penicillatus* (Fain and Lukoschus 1978). Specimens in collections: MNHN. Note: *C. penicillatus* is not distributed in Estado de México according to Ceballos (2014).

Neolabidophorus yucatanensis Pence and Genoways, 1974

YUCATÁN: 3 km N of Pisté: *Heteromys gaumeri* (Pence and Genoways 1974). Specimens in collections: USNM.

Histiostomatidae Kramer, 1876

Histiostoma tienhoveni (Oudemans, 1926)

CHIAPAS: Cerro Tzontehuitz, 13 km NE of San Critobal de las Casas, Mpio. San Juan Chamula: *Peromyscus zarhynchus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. Note: This species has been synonymized with *Rhopalanoetus fimetarium* (Canestrini and Berlese, 1881). It is a common inhabitant of cattle dung wherever people have taken them. It is typically phoretic on dung beetles, so the mammal associations are problematic - in this case, the species is probably misidentified.

Listrophoridae Canestrini, 1892

Geomylichus bassolsi Servín *et al.*, 1992

BAJA CALIFORNIA SUR: Isla Cerralvo: *Chaetodipus siccus* (Servín *et al.* 1992). Specimens in collections: IBUNAM. Note: *Chaetodipus arenarius* was recognized as the original host. However, *C. arenarius* from the costal plains of the southern part of the tip of the Baja california peninsula is now recognized as *C. siccus* (Álvarez-Castañeda and Ríos 2011).

Geomylichus brevispinosus Fain *et al.*, 1978

ZACATECAS: 4.3 km N, 5.4 km E of San Juan Capistrano; 0.8 km N, 0.4 km W of San Juan Capistrano: *Chaetodipus nelsoni* (Vargas *et al.* 1999). Unknown if specimens are in collections.

Geomylichus comitanensis Hoffmann and Servín, 1990

BAJA CALIFORNIA SUR: Comitán: *Chaetodipus amophilus* (Hoffmann and Servín 1990). Specimens in collections: CIB and possibly CNAC (Hoffmann collection is in the CNAC).

Geomylichus dipodomius (Radford, 1953)

COAHUILA: 5.4 mi W of General Cepeda: *Dipodomys nelsoni* (Fain *et al.* 1991; Vargas-Sandoval *et al.* 1991). Unknown if specimens are in collections. DURANGO: 0.2 km S, 1.5 km W of Villa Hidalgo; 1.3 km S, 0.7 km W of Laboratorio del Desierto; 4.3 km N, 2.8 km W of Laboratorio del Desierto: *Dipodomys nelsoni* (Vargas *et al.* 1999). Mapimí: *D. nelsoni* (Vargas *et al.* 2005). Unknown if specimens are in collections. NUEVO LEÓN: 4.6 km N, 14.0 km E of Jesús de Berrones; 1.7 km N, 10 km W of San Josecito; 4.0 km S, 3.3 km W of Puerto Carretas: *Dipodomys nelsoni* (Vargas *et al.* 1999). Unknown if specimens are in collections. SAN LUIS POTOSÍ: 6.0 km NE of La Palma Pegada: *Dipodomys spectabilis*. 21.4 km S of Matehuala; 2.0 km N, 0.4 km W of El Cedral: *D. nelsoni* (Vargas *et al.* 1999). Catorce: *D. ornatus* (recorded as *D. phillipsii*; Fain *et al.* 1978; Fain and Whitaker 1987). Unknown if specimens are in collections. Note: *D. phillipsii* from San Luis Potosí is now recognized as *D. ornatus* (Fernández *et al.* 2012).

Geomylichus durangoensis (Vargas et al., 1999)

DURANGO: 2.6 km S, 0.4 km E of Laboratorio del Desierto: *Chaetodipus nelsoni* (Vargas *et al.* 1999). Mapimí: *C. nelsoni* (Vargas *et al.* 2005). Specimens in collections: CNAC, NHM.

Geomylichus guaycurensis Servín et al., 1994

BAJA CALIFORNIA SUR: 17 km NE of La Paz: *Chaetodipus ammophilus* (Servín *et al.* 1994). Specimens in collections: IBUNAM. Note: *Chaetodipus arenarius* was recognized as the original host. However, *C. arenarius* from the costal plains of the southern part of the tip of the Baja california peninsula is now recognized as *C. ammophillus* (Álvarez-Castañeda and Ríos 2011; Rios and Álvarez-Castañeda 2013).

Geomylichus hispidus Vargas et al., 1999

NUEVO LEÓN: Linares: *Chaetodipus hispidus* (Vargas *et al.* 2005). Unknown if specimens are in collections. ZACATECAS: 1.3 km N, 6.0 km W of Chalchihuites: *Chaetodipus hispidus* (Vargas *et al.* 1999). Unknown if specimens are in collections.

Geomylichus nelsoni Vargas et al., 1999

DURANGO: 0.2 km S, 1.5 km W of Villa Hidalgo: *Chaetodipus nelsoni* (Vargas *et al.* 1999). Unknown if specimens are in collections. NUEVO LEÓN: 3.4 km N, 9.2 km W of San Josecito; 8 km N, 4.1. km E of San Josecito: *Chaetodipus nelsoni* (Vargas *et al.* 1999). Unknown if specimens are in collections. SAN LUIS POTOSÍ: 2.0 km N, 0.4 km W of el Cedral; 4 km W of Villa de Arreaga, Real de Catorce: *Chaetodipus nelsoni* (Vargas *et al.* 1999; Vargas *et al.* 2005). Unknown if specimens are in collections. ZACATECAS: San Juan Capistrano: *Chaetodipus nelsoni* (Vargas *et al.* 2005). Unknown if specimens are in collections.

Geomylichus oaxacae Fain and Estébanes, 2000

OAXACA: Mpio. Santa María Chimalapas: *Heteromys desmarestianus* (Fain and Estébanes 2000; Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Geomylichus penicillatus Vargas et al., 1999

DURANGO: 4.3 km N, 2.8 km W of Laboratorio del Desierto: *Chaetodipus penicillatus* (Vargas *et al.* 1999). Mapimí: *C. penicillatus* (Vargas *et al.* 2005). Specimens in collections: CNAC, NHM. Note: *C. penicillatus* is not distributed in Durango according to Ceballos (2014).

Geomylichus perognathi Fain and Whitaker, 1980

CHIHUAHUA: Casas Grandes: *Perognathus flavus* (Vargas *et al.* 1999). Unknown if specimens are in collections. DURANGO: 0.2 km S, 1.5 km W of Villa Hidalgo, Vicente Guerero: *Perognathus flavus* (Vargas *et al.* 1999, Vargas *et al.* 2005). Unknown if specimens are in collections. NUEVO LEÓN: 11 km SW of China: *Perognathus merriami*. 0.8 km S, 0.9 km W of Jesús de Berrones: *P. flavus* (Vargas *et al.* 1999). Unknown if specimens are in collections.

Geomylichus postscutatus Fain, 1976

COLIMA: Cabano: *Heteromys irroratus* (Fain *et al.* 1978). Playa de Oro: *H. irroratus, H. pictus* (Estébanes-González *et al.* 2011). Specimens in collections: IBUNAM. DURANGO: Vicente Guerrero: *Heteromys irroratus* (Vargas *et al.* 2005). Unknown if specimens are in collections. JALISCO: Chamela Biological Station: *Heteromys pictus* (Gómez-Rodríguez *et al.* 2015). Specimens in collections: CNAC. 1.3 km S, 5.5 km W of Huejuquilla El Alto: *H. irroratus* (Vargas *et al.* 1999). Unknown if specimens are in collections. NUEVO LEÓN: 8.0 km N, 4.1 km E of San Josecito; 0.3 km S, 6.2 km W of Huejuquilla El Alto: *Heteromys irroratus* (Vargas *et al.* 1999). Unknown if specimens are in collections. OAXACA: Dainzú: *Heteromys irroratus* (Vargas *et al.* 2005). Unknown if specimens are in collections.

Geomylichus texanus Fain et al., 1978

DURANGO: 0.2 km S, 1.5 km W of Villa Hidalgo; 0.1 km N, 0.7 km W of Laboratorio del Desierto: *Dipodomys merriami*, *D. ordii* (Vargas *et al.* 1999). Vicente Guerrero: *D. ornatus* (recorded as *D. phillipsii*; Vargas *et al.* 2005). Unknown if specimens are in collections. Note: *D. phillipsii* from Durango is now recognized as *D. ornatus* (Fernández *et al.* 2012). NUEVO LEÓN: 3.4 km N, 9.2 km W of San Josecito; 0.8 km S, 0.9 km W of Jesús María de Berrones: *Dipodomys merriami*, *D. ordii* (Vargas *et al.* 1999). Unknown if specimens are in collections. SAN LUIS POTOSÍ: 4.0 km W of Villa de Arreaga: *Dipodomys ordii*. 2.0 km N, 0.4 km W of El Cedral: *D. merriami* (Vargas *et al.* 1999). Real de Catorce: *D. merriami, D. ordii* (Vargas *et al.* 2005). Unknown if specimens are in collections. ZACATECAS: 1.3 km N, 6.0 km W of Chalchihuites: *Dipodomys ornatus* (recorded as *D. phillipsii*; Vargas *et al.* 1999). Note: *D. phillipsii* from Zacatecas is now recognized as *D. ornatus* (Fernández *et al.* 2012). Unknown if specimens are in collections.

Listrophorus mexicanus Fain, 1970

DURANGO: *Microtus mexicanus* (Fain 1970, Fain and Hyland 1974). Specimens in collections: NHM.

Listrophorus pitymys Fain and Hyland, 1972

OAXACA: Cerro Zempoaltepetl, 5 km N of Yacochi, Mpio. Tlhuitoltepec: *Microtus umbrosus, Reithrodontomys* sp. (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. VERACRUZ: 18 km NW of Teocelo, Mpio. Ixhuacán: *Microtus quasiater* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Prolistrophorus bakeri (Radford, 1949)

COLIMA: Playa de Oro: *Oryzomys couesi, Reithrodontomys fulvescens, Sigmodon mascotensis* (Estébanes-González *et al.* 2011). Specimens in collections: IBUNAM.

Prolistrophorus frontalis (Hirst, 1921)

COLIMA: Playa de Oro: *Baiomys musculus, Handleyomys melanotis* (recorded as *O. melanotis*), *Nyctomys sumichrasti, Oryzomys couesi, Osgoodomys banderanus* (Estébanes-González *et al.* 2011). Specimens in collections: IBUNAM. VERACRUZ: 18 km NW of Teocelo, Mpio. Ixhuacán: *Oligoryzomys fulvescens* (recorded as *Oryzomys fulvescens*; Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Prolistrophorus pernamboucensis (Fain, 1973)

OAXACA: Cerro Zempoaltépetl, 5 km E of Santa María Yacochi, Mpio. Tlahuitoltepec: *Peromyscus* sp. (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Prolistrophorus sclerobursatus (Fain and Estébanes, 1996)

JALISCO: Chamela Biological Station: *Heteromys pictus* (Gómez-Rodríguez *et al.* 2015). Specimens in collections: CNAC. OAXACA: Cerro Zempoaltépetl, 5 km E of Santa María Yacochi, Mpio. Tlahuitoltepec: *Peromyscus* sp., *Reithrodontomys* sp. (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. VERACRUZ: 18 km NW of Teocelo, Mpio. Ixhuacán: *Microtus quasiater*. Banderillas, 6 km NW of Xalapa, Mpio. Xalapa: *Peromyscus furvus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Myocoptidae Gunther, 1942

Myocoptes glareoli Samsinak, 1957

VERACRUZ: 18 km NW of Teocelo, Mpio. Ixhuacán: *Microtus quasiater* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM.

Myocoptes musculinus (Koch, 1840)

COLIMA: Playa de Oro: *Reithrodontomys fulvescens* (Estébanes-González *et al.* 2011). Specimens in collections: IBUNAM. SAN LUIS POTOSÍ: Rancho "El Estribo," 10 km SE of El Naranjo, Mpio. Ciudad del Maíz: *Sigmodon hispidus* (Estébanes-González and Cervantes 2005). Specimens in collections: IBUNAM. Note: *S. hispidus* is not distributed in San Luis Potosí according to Ceballos (2014). A possible alternative host includes *S. leucotis* (Ceballos 2014).

Phylum: Arthropoda von Siebold, 1848

Class: Insecta Linnaeus, 1758

Order: Phthiraptera Haekel, 1896

Suborder: Anoplura Leach, 1815

Family: Hoplopleuridae Ewing, 1929

Hoplopleura acanthopus (Burmeister, 1839)

NUEVO LEÓN: El Potosí: *Microtus mexicanus* (Emerson 1971). Specimens in collections: SNOW, USNM.

Hoplopleura arizonensis Stojanovich and Pratt, 1961

COAHUILA: Parras; Paila-Parras: *Sigmodon toltectus* (Emerson 1971). Specimens in collections: SNOW, USNM. Note: *S. toltectus* is not distributed in Coahuila according to Ceballos (2014). YUCATÁN: Pisté: *Sigmodon toltecus* (Emerson 1971). Specimens in collections: SNOW, USNM.

Hoplopleura difficilis Kim, 1965

MORELOS: Lagunas de Zempoala: *Peromyscus difficilis* (L. A. Durden unpub. data, Sánchez-Montes *et al.* 2013). No specimens in collections.

Hoplopleura emphereia Kim, 1965

CHIAPAS: Union Juárez: *Peromyscus guatemalensis* (Emerson 1971). Specimens in collections: SNOW, USNM. GUERRERO: Omiltemi: *Peromyscus megalops* (Emerson 1971). Specimens in collections: SNOW, USNM. Parque Estatal Cerro del Huizteco: *Peromyscus megalops* (Sánchez-Montes *et al.* 2016a). Specimens in collections: LFAC. JALISCO: Ciudad Guzmán: *Peromyscus* sp. (Emerson 1971). Specimens in collections: SNOW, USNM. OAXACA: Cerro Pelón: *Megadontomys cryophilus* (Emerson 1971). Specimens in collections: SNOW, USNM. 3 km al Sur de El Punto Ixtepeji: *Peromyscus megalops*. Oaxaca-Tuxtepec, km 134.5 de la Carretera 175: *Peromyscus aztecus* (Sánchez-Montes *et al.* 2016a). Specimens in collections: LFAC.

Hoplopleura ferrisi Cook and Beer, 1959

DURANGO: El Salto: *Peromyscus spicilegus* (Emerson 1971). Specimens in collections: SNOW, USNM. JALISCO: Zapotlanejo, Nevado de Colima: *Peromyscus levipes* (Emerson 1971). Specimens in collections: SNOW, USNM. Note: *P. levipes* is not distributed in Jalisco according to Ceballos (2014). MORELOS: Lagunas de Zempoala: *Peromyscus* sp. (Emerson 1971). Specimens in collections: SNOW, USNM. NAYARIT: "Tepico": *Peromyscus spicilegus* (Emerson 1971). Specimens in collections: SNOW, USNM. OAXACA: La Yerba-Buena, Mpio. de Santa Catarina Juquila: *Peromyscus melanurus* (Sánchez-Montes *et al.* 2013). Specimens in collections: CPFC. La Yerba-Buena: *P. aztecus*, *P. melanurus* (Sánchez-Montes *et al.* 2016a). Specimens in collections: LFAC. SINALOA: *Peromyscus spicilegus* (Emerson 1971). Specimens in collections: SNOW, USNM.

Hoplopleura hesperomydis (Osborn, 1891)

CHIHUAHUA: El Paso-Chihuahua City highway, about 55 km S of Ciudad Juárez: *Onychomys leucogaster* (Morlan and Hoff 1957). No specimens in collections. Note: This is considered an unusual and unlikely host-louse association. Note: *O. leucogaster* is not distributed in Chihuahua according to Ceballos (2014). ESTADO DE MÉXICO: Nevado de Toluca: *Peromyscus melanotis* (Emerson 1971). Specimens in collections: SNOW, USNM. JALISCO: Nevado de Colima: *Peromyscus melanotis* (Emerson 1971). Specimens in collections: SNOW, USNM.

Hoplopleura hirsuta Ferris, 1916

CHIAPAS: San Clemente; Tapachula: *Sigmodon hirsutus* (Emerson 1971). Specimens in collections: SNOW, USNM. CHIHUAHUA: Parral: *Sigmodon ochrognathus* (Ferris 1921; Sánchez-Montes *et al.* 2013). Specimens in collections: USNM. COLIMA: Hacienda Magdalena: *Xenomys nelsoni* (Ferris 1921; Sánchez-Montes *et al.* 2013). No specimens in collections. Note: Considered an unusual host-louse association. Sánchez-Montes *et al.* (2013) also reported *H. hirsuta* from *Neotoma micropus,* which likely represents contamination or a host or louse misidentification. NUEVO LEÓN: Pesquería: *Sigmodon toltecus* (Ramos-Casillas 2003; Sánchez-Montes *et al.* 2013). No specimens in collections. Note: *S. toltecus* is not distributed in Nuevo León according to Ceballos (2014). SAN LUIS POTOSÍ: El Salto: *Sigmodon toltecus* (Emerson 1971). Obregón; Miguel del Naranjo: *S. hispidus* (Sánchez-Montes *et al.* 2016b). Specimens in collections: SNOW, USNM. Note: *S. hispidus* is not distributed in San Luis Potosí according to Ceballos (2014). A possible alternative host includes *S. leucotis* (Ceballos 2014). SINALOA: Los Mochis: *Sigmodon arizonae* (Emerson 1971). Specimens in collections: SNOW, USNM. TAMAULIPAS: Matamoros: *Neotoma micropus* (Ramos-Casillas 2003; Sánchez-Montes *et al.* 2013). No specimens in collections. Note: This is considered an unusual host-louse association.

Hoplopleura quadridentata (Neumann, 1909)

TAMAULIPAS: Altamira: *Handleyomys rostratus* (recorded as *Oryzomys rostratus*; Ferris 1921; Sánchez-Montes *et al.* 2013). Specimens in collections: USNM. VERACRUZ: Orizaba: *Oligoryzomys fulvescens* (recorded as *Oryzomys fulvescens*; Ferris 1921). Specimens in collections: USNM.

Hoplopleura reithrodontomydis Ferris, 1951

CIUDAD DE MÉXICO: Ajusco, near México City: *Reithrodontomys chrysopsis* (Ferris 1951). No specimens in collections. GUERRERO: Parque Estatal Cerro del Huizteco: *Habromys schmidlyi, Reithrodontomys bakeri, R. sumichrasti* (Sánchez-Montes *et al.* 2016a). Specimens in collections: LFAC. OAXACA: La Yerba-Buena; Oaxaca-Tuxtepec, km 134.5 de la Carretera 175: *Reithrodontomys mexicanus* (Sánchez-Montes *et al.* 2016a). Specimens in collections: LFAC.

Hoplopleura similis Kim, 1965

VERACRUZ: Orizaba: *Oligoryzomys fulvescens* (Kim 1965). Specimens in collections: USNM.

Polyplacidae Fahrenholz, 1912

Fahrenholzia boleni McDaniel, 1968

COAHUILA: Plan de Guadalupe: *Perognathus merriami* (Light and Hafner 2007). Specimens in collections: Price Institute.

Fahrenholzia ehrlichi Johnson, 1962

HIDALGO: Ixmiquilpan: *Heteromys irroratus* (Emerson 1971). Specimens in collections: SNOW, USNM. JALISCO: 16 km N-NE of Ameca: *Heteromys irroratus* (Light and Hafner 2007). Specimens in collections: Price Institute. Etzatlán: *H. irroratus* (Emerson 1971). Specimens in collections: SNOW, USNM. Acotlán; Atamajec; Encarnación de Díaz: *H. irroratus* (Johnson 1962). Specimens in collections: USNM. Chamela Biological Station: *H. pictus* (Gómez-Rodríguez *et al.* 2015). Specimens in collections: CNAC. PUEBLA: 11 km (by road) SW of Alchichica; 3 km (by road) NE of Tilapa; 6 km N of Tilapa: *Heteromys irroratus* (Light and Hafner 2007). Specimens in collections: Price Institute. SAN LUIS POTOSÍ: El Salto: *Heteromys irroratus* (Emerson 1971). Specimens in collections: SNOW, USNM. TAMAULIPAS: Matamoros: *Heteromys irroratus* (Johnson 1962). No specimens in collections. ZACATECAS: 2 mi E of San Jerónimo: *Heteromys irroratus* (Light and Hafner 2007). Specimens in collections: Price Institute. Valparaíso: *H. irroratus* (Johnson 1962). Specimens in collections: USNM. Note: Sánchez-Montes *et al.* (2013) also list *Chaetodipus hispidus* and *C. penicillatus* (Heteromyidae) as hosts of *Fahrenholzia ehrlichi* in their host-louse list, but no such association could be found in their list by Mexican state. Johnson (1962) notes that paratypes are also in the collections of the British Museum (Natural History; now the Natural History Museum, London) and the Stanford University Natural History Museum.

Fahrenholzia ferrisi Werneck, 1952

VERACRUZ: Achotal: *Heteromys desmarestianus, H. desmarestianus* (recorded as *H. goldmani*; Werneck 1952; Johnson 1962). Specimens in collections: USNM. 8 km E-NE of Catemaco: *H. desmarestianus* (Light and Hafner 2007). Specimens in collections: Price Institute. YUCATÁN: Pisté: *Heteromys gaumeri* (Emerson 1971). Specimens in collections: SNOW, USNM.

Fahrenholzia hertigi, Johnson, 1962

VERACRUZ: 8 km E-NE of Catemaco: *Heteromys desmarestianus* (Light and Hafner 2007). Specimens in collections: Price Institute.

Fahrenholzia microcephala Ferris, 1922

GUERRERO: Parque Estatal Cerro del Huizteco, Mpio. de Taxco: *Heteromys pictus* (Sánchez-Montes *et al.* 2013; 2016a). Specimens in collections: CPFC, LAFC. JALISCO: Atamejac: *Heteromys irroratus* (Ferris 1922). Specimens in collections: USNM. 4.5 km SW of Jilotlán: *H. pictus* (Light and Hafner 2007). Specimens in collections: Price Institute. NAYARIT: Tepic: *Heteromys pictus* (Emerson 1971). Specimens in collections: SNOW, USNM. SINALOA: Matatán; San Ignacio; Santa Lucía: *Heteromys pictus* (Emerson 1971). Specimens in collections: SNOW, USNM. VERACRUZ: San Carlos: *Heteromys pictus*. Achotal: *H. desmarestianus* (recorded as *H. goldmani*). Valparaiso: *H. irroratus* (Ferris 1922). Specimens in collections: USNM, FMNH. Biological Station La Mancha: *H. pictus* (Light and Hafner 2007). Specimens in collections: Price Institute.

Fahrenholzia pinnata Kellogg and Ferris, 1915

CHIHUAHUA: about 55 km S of Ciudad Juárez along the El Paso-Chihuahua City highway: *Chaetodipus penicillatus, Dipodomys merriami* (Morlan and Hoff 1957). No specimens in collections. 6 mi NW of Ricardo Flores Magón: *D. merriami* (Light and Hafner 2007). Specimens in collections: Price Institute. Note: *C. penicillatus* is not distributed in Chihuahua according to Ceballos (2014). COAHUILA: Paila: *Dipodomys* sp. (Emerson 1971). Specimens in collections: SNOW, USNM. 2 mi E of Agua Nueva: *Dipodomys ordii*. 5 km S, 16 km W of General Cepeda: *D. nelsoni*. 2 km S of Santa Teresa: *D. merriami* (Light and Hafner 2007). Specimens in collections: Price Institute. ESTADO DE MÉXICO: Amecameca: *Dipodomys phillipsii* (Ferris 1922). Specimens in collections: USNM. PUEBLA: 11 km (by road) SW of Alchichica: *D. phillipsii*. 3.1 km SW of El Veladero: *Perognathus flavus* (Light and Hafner 2007). Specimens in collections: Price Institute. SONORA: Kino: *Dipodomys merriami, D. deserti* (Emerson 1971). Specimens in collections: SNOW, USNM. ZACETECAS: Valparaíso: *Dipodomys ornatus* (Ferris 1922). No specimens in collections. 1 mi SE of Bañon: *D. ordii*. 2 mi E of San Jerónimo: *D. phillipsii* (Light and Hafner 2007). Specimens in collections: Price Institute.

Fahrenholzia reducta Ferris, 1922

BAJA CALIFORNIA SUR: Miraflores: *Chaetodipus rudinoris*

(Emerson 1971). Specimens in collections: SNOW, USNM. Note: *Chaetodipus baileyi* was recognized as the original host. However, according to Riddle *et al.* (2000), *C. baileyi* from the Baja California peninsula are now recognized as *C. rudinoris.*

Fahrenholzia texana Stojanovich and Pratt, 1961

DURANGO: Hacienda Atotonilco: *Heteromys irroratus* (Light and Hafner 2007). Specimens in collections: Price Institute. JALISCO: Chamela Biological Station: *Heteromys pictus* (Gómez-Rodríguez *et al.* 2015). Specimens in collections: CNAC. OAXACA: *Heteromys irroratus* (Kim *et al.* 1986; Sánchez-Montes *et al.* 2013). No specimens in collections.

Fahrenholzia zacatecae Ferris, 1922

COAHUILA: 5 km S, 16 km W of General Cepeda: *Chaetodipus hispidus* (Light and Hafner 2007). Specimens in collections: Price Institute. ZACATECAS: Valparaiso: *Chaetodipus hispidus* (Ferris 1922). Specimens in collections: USNM. *C. hispidus* (Kim *et al.* 1986). No specimens in collections.

Neohaematopinus neotomae Ferris, 1942

COLIMA: Manzanillo: *Hodomys alleni* (Ferris 1942). Specimens in collections: USNM. GUERRERO: Parque Estatal Cerro del Huizteco: *Neotoma mexicana* (Sánchez-Montes *et al.* 2016a). Specimens in collections: LFAC. NUEVO LEÓN: Doctor Arroyo: *Neotoma leucodon*. Lampazos: *N. micropus* (Ramos-Casilla 2003). No specimens in collections. SINALOA: Concepción: *Hodomys alleni* (Emerson 1971). Specimens in collections: SNOW, USNM.

Neohaematopinus sp.

DURANGO: At border with Sinaloa: *Neotoma mexicana* (Emerson 1971). Specimens in collections: SNOW, USNM. SINALOA: Los Mochis: *Neotoma phenax* (Emerson 1971). Specimens in collections: SNOW, USNM. Note: Sánchez-Montes *et al.* (2013) recorded *Neohaematopinus sciurinus* ex *Hodomys alleni,* which must represent contamination or a louse or host misidentification.

Polyplax alaskensis Ewing, 1927

JALISCO: Nevado de Colima: *Microtus mexicanus* (Emerson 1971). Specimens in collections: SNOW, USNM. MORELOS: Lagunas de Zempoala: *Microtus mexicanus* (Emerson 1971). Specimens in collections: SNOW, USNM. NUEVO LEÓN: El Potosí: *Microtus mexicanus* (Emerson 1971). Specimens in collections: SNOW, USNM. OAXACA: Llano de las Flores: *Microtus mexicanus* (Emerson 1971). Specimens in collections: SNOW, USNM.

Polyplax auricularis Kellogg and Ferris, 1915

CHIAPAS: Tzontehuitz: *Peromyscus zarhynchus* (Emerson 1971). Specimens in collections: SNOW, USNM. CIUDAD DE MÉXICO: *Neotomodon alstoni* (Ferris 1923). Specimens in collections: USNM. DURANGO: Ojo Tongo: *Peromyscus* sp., *P. maniculatus*. Buenos Aires: *Peromyscus difficilis* (Emerson 1971). Specimens in collections: SNOW, USNM. ESTADO DE MÉXICO: Nevado de Toluca: *Peromyscus melanotis* (Emerson 1971). Specimens in collections: SNOW, USNM. GUERRERO: Parque Estatal Cerro del Huizteco: *Peromyscus beatae*, *P. megalops* (Sánchez-Montes *et al.* 2016a). Specimens in collections: LFAC. JALISCO: Nevado de Colima: *Peromyscus hylocetes*, *P. melanotis* (Emerson 1971). Specimens in collections: SNOW, USNM. NUEVO LEÓN: Cerro Potosí: *Peromyscus maniculatus* (Emerson 1971). Specimens in collections: SNOW, USNM. OAXACA: Totontepec: *Reithrodontomys mexicanus* (Ferris 1923). Specimens in collections: USNM. 21 km N of Guelatao: *Peromyscus beatae* (Sánchez-Montes *et al.* 2013). Specimens in collections: CPFC. 3 km S of Eñ Punto Ixtepeji; Oaxaca-Tuxtepec, km 134.5 de la Carretera 175: *P. beatae* (Sánchez-Montes *et al.* 2016a). Specimens in collections: LFAC.

Phylum: Arthropoda von Siebold, 1848
Class: Insecta Linnaeus, 1758
Order: Siphonaptera Latreille, 1825
Family: Ceratophyllidae Dampf, 1908
Subfamily: Ceratophyllinae Dampf, 1908

Amaradix euphorbi (Rothschild, 1905)

NUEVO LEÓN: Cerro Potosí: *Peromyscus melanotis, Peromyscus* sp. (Fox 1939; Tipton and Mendez 1968). Unknown if specimens are in collections. Note: This species is also in the literature as *Malaraeus euphorbi*.

Baculomeris schmidti (Traub, 1950)

CHIAPAS: Pueblo Nuevo: *Neotoma mexicana* (Hubbard 1958). Specimens in collections: Unknown, possibly BMNH. Tonala, El Triunfo: *Peromyscus* sp. (recorded as *Peromyscus chiapanensis*; Acosta *et al.* 2008). Specimens in collections: MZFC.

Ceratophyllus coahuilensis Eads, 1956

GUERRERO: San Miguel Totolapan, Puerto del Gallo: *Peromyscus megalops* (Acosta *et al.* 2008). Specimens in collections: MZFC.

Jellisonia (Jellisonia) breviloba barrerai Hastriter, 2004

CIUDAD DE MÉXICO: Meyehualco, 5 km E of Santa Cruz: *Peromyscus difficilis*. Cerro Zacayuca: *P. gratus* (recorded as *P. truei gratus*). 21 ? [*sic*] W of Zacatepec: *P. maniculatus* (Hastriter 2004). Specimens in collections: BMNH, MZFC, REL. GUERRERO: Chilpancingo de los Bravo, 0.5 km W of Omiltemi: *Peromyscus aztecus.* Chilpancingo de los Bravo, Omiltemi: *Megadontomys thomasi* (Acosta *et al.* 2008).

Specimens in collections: MZFC. MICHOACÁN: Coalcoman de Vázquez Pallares, Pallares 11.84 km SW of Dos Aguas: *Peromyscus winkelmanni*. Taxco de Alarcón, Parque Estatal El Huizteco: *P. levipes* (Acosta *et al.* 2008). Specimens in collections: MZFC. MORELOS: Lagunas de Zempoala, near Ojo de Agua: *Peromyscus difficilis*. Derrame Chichuinautzin: *Neotoma mexicana, P. difficilis* (Hastriter 2004). Specimens in collections: CMNH. OAXACA: Santiago Nacaltepec, San Lorenzo Pápalo: *Peromyscus aztecus* (Acosta *et al.* 2008). Specimens in collections: MZFC. PUEBLA: 1 km SW of San Pedro Atlixco: *Peromyscus difficilis* (Hastriter 2004). Specimens in collections: BMNH, CMNH, MZFC, REL. 2 km W Guadalupe Victoria, Mpio. de Guadalupe Victoria: *P. maniculatus* (Falcón-Ordaz *et al.* 2012). Specimens in collections: MZFC. QUERÉTARO: Pinal de Amoles, Chuvegé: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. TLAXCALA: Sanctorum de Lázaro Cárdenas, Camino Rural Benintо Juárez, La Joya: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. ORIENTAL BASIN: Multiple localities in Veracruz and Tlaxcala: *Peromyscus difficilis, P. maniculatus* (Acosta and Fernández 2015). Specimens in collections: MZFC.

Jellisonia (Jellisonia) breviloba breviloba Traub, 1950

COAHUILA: La Carbonara, 16 km SE of Arteaga: *Peromyscus* sp. (Hastriter 2004). Specimens in collections: CMNH. CIUDAD DE MÉXICO: "Country club": *Neotoma mexicana*. Pedregal de San Angel: *Peromyscus* sp. (Hastriter 2004). Specimens in collections: CMNH, FMNH, REL. San Andrés Tetepilco: *Microtus mexicanus* (Ayala-Barajas *et al.* 1988; Hastriter 2004). Specimens in collections: BMNH, CMNH, MZFC, USNM. Cerro Zacayuca: *Peromyscus gratus* (recorded as both *P. gratus* and *P. truei*; Barrera 1953, Hastriter 2004). Specimens in collections: BMNH, CMNH, MZFC. Calzada de Tlalpan: *M. mexicanus* (Muñiz *et al.* 1981). Calzada de Tlalpan, near the Country Club, 1m Topotipo: *M. mexicanus*. 400 m N, 21 W of Zacatepec: *P. maniculatus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. DURANGO: 16 km W of El Salto; 0.8 km SE of Buenos Aires, 6.5 km S of El Salto; 11 km S of El Salto; 1.6 km SW of Revolcaderos; 8 km E Revolcaderos; 8 km E of Revolcaderos near Sinaloa border; 9.7 km NE of Revolcaderos; 11 km NE of Revolcaderos; 3.2 km E of Revolcaderos, 11.3 km E of Sinaloa border; 8 km E of Revolcaderos; 3.2 km E of Revolcaderos, 14.5 km E of Sinaloa line; 4.8 km E of Revolcaderos, 12.9 km E Sinaloa line; 19.4 km E of Revolcaderos, 27.4 km E of Sinaloa line; 4.8 km E of Revolcaderos near highway, 14.5 km E of Sinaloa line; 8 km E of Revolcaderos near Highway, 14.5 km E of Sinaloa line; 48 km W of Durango: *Peromyscus* sp. 8 km W of Revolcaderos near Sinaloa border; 3.2 km E of Revolcaderos, 11.3 km E of Sinaloa border: *Neotoma* sp. (Hastriter 2004). Specimens in collections: CMNH, CNC, USNM. ESTADO DE MÉXICO: 1.8 km N of Barrientos; 3.2 km N of Tlalnepantla: *Peromyscus gratus* (recorded as *P. truei*; Hastriter 2004). Specimens in collections: CMNH, MZFC. Popocatépetl: *Microtus mexicanus, P. difficilis, Reithrodontomys chrysopsis* (Barrera 1968). Cerro Caldera: *P. difficilis*. 2 km N of Tlalnepantla; 2 km S of Coacalco: *P. gratus* (recorded as *P. truei*; Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. GUANAJUATO: 8 km SW of Ibarra: *Sigmodon fulviventer* (Hastriter 2004). Specimens in collections: CMNH. GUERRERO: 1.6 km NW of Omiltemi: *Peromsycus* sp. Puerto Chico, Camotla las Bravo: *Osgoodomys banderanus*. Playa Azul: *Peromyscus gratus* (recorded as *P. truei*; Hastriter 2004). Specimens in collections: CMNH, GML. San Miguel Totolapan, Estación Toro Muerto: *P. boylii*. Santiago Nacaltepec, San Lorenzo Pápalo: *P. aztecus* (Acosta *et al.* 2008). Specimens in collections: MZFC. Note: *P. boylii* is not distributed in Guerrero according to Ceballos (2014). HIDALGO: 12.9 km NE of Jacala: *Peromyscus hylocetes?* [= *P. aztecus*] (Hastriter 2004). Specimens in collections: CMNH. Note: Author is unsure of identification of *P. hylocetes*; neither *P. hylocetes* nor *P. aztecus* is distributed in Hidalgo near Jacala according to Ceballos (2014). Between San Juan Hueyapan and Presa San Carlos: *Microtus mexicanus, Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Sierra Madre Oriental: *Peromyscus* sp. (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC. JALISCO: Nevado de Colima, near La Joya: *Peromyscus hylocetes* (Hastriter 2004). Specimens in collections: CMNH. MICHOACÁN: Mt. San Miguel: *Microtus mexicanus* (Traub 1950). Specimens in collections: FMNH. Tlalpujahua: *Peromyscus maniculatus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. MORELOS: Derrame lávico del Chichinautzin: *Neotoma mexicana, Peromyscus* sp. (Pérez-Ortiz 1976). Derrame Chichinautzin: *N. mexicana, Peromyscus difficilis* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. NUEVO LEÓN: Cerro Potosí: *Peromsycus difficilis, P. melanotis* (Tipton and Mendez 1968; Hastriter 2004). Specimens in collections: BYU, CMNH, USNM. PUEBLA: Multiple localities: *Peromyscus difficilis, P. maniculatus* (Acosta and Fernández 2015). 2 km W of Aljojuca; 1 km SW of Sn. Pedro Atlixco (Ayala-Barajas *et al.* 1988). Las Esperanza, Las Esperanza: *Peromyscus* sp. (Acosta *et al.* 2008). 2 km W Guadalupe Victoria, Mpio. de Guadalupe Victoria: *P. maniculatus* (Falcón-Ordaz *et al.* 2012). Specimens in collections: MZFC. 1.6 km NE of Alchichica: *P. maniculatus* (Hastriter 2004). Specimens in collections: UNSM. QUERÉTARO: 2.5 km NW of Santa Inés and 2.8 km NW of Santa Inés: *Peromyscus furvus*. Maguey Verde: *P. difficilis* (Hastriter 2004). 6.56 km El Lobo, Xilitla-Jalpan Highway; Pinal de Amoles: *P. levipes*. 1 km S of Pinal de Amoles; 2 km W of Santa Inés: *P. difficilis*. 4 km SW of Tequisquiapan: *Perognathus flavus* (Acosta 2003; Acosta *et al.* 2008). Landa de Matamoros, 2 km W of Santa Inés: *P. difficilis* (Acosta *et al.* 2008). Specimens in collections: MZFC. SINALOA: 1 km NE of Santa Lucía; 19.2 km NE of Santa Lucía: *Peromyscus boylii* (Hastriter 2004). Specimens in collections: CMNH. 1.6 km E of Pánuco: *Neotoma mexicana* (Hastriter 2004). Unknown if specimens are in collections. Note: *P. boylii* is not distributed in Sinaloa according to Ceballos (2014). TLAXCALA: Tlaxco: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988; Hastriter 2004). Specimens in collections: CMNH, MZFC. 10 km E of Calpulalpan: *Peromyscus difficilis* (Barrera 1953). Parque Nacional Malinche: *Neotomodon alstoni, P. difficilis, P. gratus, P. leucopus, P. levipes, P. maniculatus, P. melanotis, Reithrodontomys fulvescens, R. megalotis* (Aguilar-Montiel *et al.* 2018). Parque Nacional Malinche: *Neotomodon alstoni* (Acosta and Fernández 2006; Acosta *et al.* 2008). El Carmen Tequexquitla, El Piñonal: *P. difficilis*. Huamantla, La Malinche (Caseta #4): *P. gratus*. Panotla, San Ambrosio Texantla, Barranca Huehuetitla; Sanctorum de Lázaro Cárdenas, Camino Rural Benito Juárez: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. VERACRUZ: Ixhuatlancillo, Rancho La Pala: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC.

Jellisonia (Jellisonia) breviloba Traub, 1950

ESTADO DE MÉXICO: Zacualpan, 8 km E of Zacualpan: *Peromyscus difficilis* (Acosta *et al.* 2008). Specimens in collections: MZFC. OAXACA: Santiago Nacaltepec, San Lorenzo Papálo: *P. melanophrys* (Acosta *et al.* 2008). Specimens in collections: MZFC. Note: these specimens were not identified to either of the two subspecies.

Jellisonia (Jellisonia) guerrerensis Morales, 1990

CHIAPAS: 17 km NW of Teopisca: *Peromyscus guatemalensis* (Hastriter 2004). Specimens in collections: MZFC. GUANAJUATO: Puerto del Gallo: *Oryzomys* sp. (Hastriter 2004). Specimens in collections: MZFC. Note: *Oryzomys* sp. was recorded in the original literature but may represent *Handleyomys* sp. GUERRERO: 1.6 km NW of Omiltemi: *Peromyscus* sp., *Reithrodonomys* sp. Agua Fria, 22 km SW of Yextla; Puerto Chico, Xochipala: *Peromyscus megalops*. Chilpancingo, 2.5 km E of Omiltemi; 4 km N of Omiltemi: *Megadontomys thomasi, P. megalops*. Omiltemi: *Peromyscus* sp., *Reithrodontomys* sp. Camotla, Leonardo Bravo: *Osgoodomys banderanus* (recorded as *P. banderanus*; Hastriter 2004). Specimens in collections: CMNH, MZFC. Chilpancingo de los Bravo, Omiltemi: *M. thomasi, Peromyscus* sp. Chilpancingo de los Bravo, 3.5 km SW of Omiltemi: *M. thomasi* (Acosta *et al.* 2008). Specimens in collections: MZFC. OAXACA: Tlahuitoltepec, near Santa María Yachochi: *Habromys lepturus, Handleyomys chapmani* (recorded as *Oryzomys chapmani*), *Peromyscus aztecus, P. melanocarpus*. 7 m SW of Suchixtepec: *Peromyscus* sp., *Reithrodontomys* sp. 16 km SW of Suchixtepec: *Peromyscus* sp. Llano las Flores, 87 km N of Oaxaca: *Microtus* sp. (Hastriter 2004). Specimens in collections: MWH, MZFC. Ixtlán de Juárez, 2.5 km SE of Santa María Yavesía; Santiago Comaltepec, Tuxtepec-Oaxaca Highway, km 77, Vista Hermosa: *P. mexicanus*. Santiago Comaltepec, Tuxtepec-Oaxaca Highway, km 79.5, La Esperanza: *P. melanocarpus* (Acosta *et al.* 2008). Specimens in collections: MZFC. VERACRUZ: La Joya: *Peromyscus* sp. (Hastriter 2004). Ixhuatlancillo, Rancho La Pala: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC.

Jellisonia (Jellisonia) hayesi Traub, 1950

CIUDAD DE MÉXICO: 5 km E of Sta. Cruz, Meyehualco: *Peromyscus difficilis* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. DURANGO: Hidalgo, 4 km S-SE of La Zarca: *Reithrodontomys zacatecae* (recorded as *Reithrodontomys megalotis zacatecae*; Acosta *et al.* 2008). Specimens in collections: MZFC. ESTADO DE MÉXICO: México City: *Microtus mexicanus* (Traub 1950). Specimens in collections: FMNH. Zacualpan, Zacualpan-Mamatla Highway, km 7: *Peromyscus difficilis* (Acosta *et al.* 2008). Specimens in collections: MZFC. GUERRERO: Omiltemi: *Peromyscus* sp. (Barrera 1958). Camotla, Mpio. de Chichihualco, Leonardo Bravo: *P. gratus* (recorded as *P. truei*; Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. 1.6 km SW of Omiltemi; 4.8 km E of Omiltemi; Omiltemi: *Peromyscus* sp. 1.6 km NW of Omiltemi: *Peromyscus megalops*. Camotla, Leonardo Bravo: *P. gratus, Heteromys* sp. Chilpancingo, Omiltemi: *Megadontomys thomasi, P. levipes*. Chilchihaulco, Camotla, Leonardo Bravo: *P. gratus* (Hastriter 2004). Specimens in collections: CMNH, MZFC. Note: Author is unsure of identification of *P. megalops*. JALISCO: 1 km S, 19 km W of Ciudad Guzmán: *Peromyscus* sp. Nevado de Colima: *Neotoma* sp., *Peromyscus hylocetes, Peromyscus* sp. (Hastriter 2004). Specimens in collections: CMNH. Taxco de Alarcón, Parque Estatal El Huizteco; Tetipac, Huizteco-Tetipac Highway, km 10, Los Llanos: *P. aztecus* (Acosta *et al.* 2008). Specimens in collections: MZFC. MICHOACÁN: Monte de San Miguel: *Peromyscus hylocetes* (Traub 1950; Hastriter 2004). Tancítaro, San Miguel: *P. aztecus*. 10 km S (by road) of Pátzcuaro: *Baiomys musculus, Peromyscus* sp. (Hastriter 2004). Specimens in collections: FMNH, MWH. Coalcoman de Vázquez Pallares, Pallares, 11.84 km SW of Dos Aguas: *P. winkelmanni* (Acosta *et al.* 2008). Specimens in collections: MZFC. Note: *P. aztecus* is not distributed in Michoacán according to Ceballos (2014). NUEVO LEÓN: Cerro Potosí: *Peromyscus difficilis* (Tipton and Mendez 1968). Unknown if specimens are in collections. Note: Tipton and Mendez (1968) state that the fleas species is morphologically close to *J. h. breviloba*. PUEBLA: 1 km SW of San Pedro Atlixco: *Peromyscus difficilis* (Ayala-Barajas *et al.* 1988). Atzitzintla, Santa Cruz Cuyachapa, Ejido Maguey Cenizo: *Microtus mexicanus*. La Esperanza: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. QUERÉTARO: 13.76 km SW of Amealco; 6.24 km W of Amealco; Amealco de Bonfil, 5 km NW of El Batán; 6.56 km El Lobo, Xilitla-Jalpan Highway; 1.2 Km S of Pinal de Amoles; Pinal de Amoles; Landa de Matamoros, 1 km NW of Santa Inés: *Peromyscus* sp. 1 km NW of Santa Inés; 1.5 km NW of Santa Inés; 5 km NW of El Batán; Landa de Matamoros, Xilitla-Jalpan Highway, 6.56 km El Lobo: *Peromyscus levipes*. Camargo; 11 km NW of Peña Bernal; Toliman, 11 km NW of Peña Bernal: *P. pectoralis*. Maguey Verde; Peña Bernal; 1 km S of Pinal de Amoles; Cadereyta de Montes, 1 km SE of Chavarría: *P. difficilis*. 2.8 km NW of Santa Inés: *P. furvus*. Rancho 99; 5 km SW of Tequisquiapan: *P. gratus*. 9 km SE of Tequisquiapan; 9 km SW of Tequisquiapan: *Baiomys taylori*. 1 km SW of Pinal de Amoles: *P. difficilis, P. levipes*. 1 km W of Santa

Inés: *P. levipes*, *Peromyscus* sp. Landa de Matamoros, 2 km W of Santa Inés: *P. difficilis, P. gratus*. 2.5 km NW of Santa Inés: *P. furvus, P. levipes, Peromyscus* sp. (Acosta 2003; Acosta *et al.* 2008). Specimens in collections: MZFC. TLAXCALA: El Carmen Tequexquitla, 2.5 km El Carmen: *Peromyscus maniculatus* (Acosta and Fernández 2015). La Malinche: *Neotomodon alstoni, P. difficilis, P. gratus, P. leucopus, P. levipes, P. maniculatus, P. melanotis, Reithrodontomys fulvescens* (Aguilar-Montiel *et al.* 2018). Sanctorum de Lázaro Cárdenas, Camino Rural Benito Juárez, La Joya: *Peromyscus* sp. El Carmen Tequexquitla, El Piñonal: *Heteromys irroratus* (Acosta *et al.* 2008). Specimens in collections: MZFC. SIERRA MADRE ORIENTAL: Multiple localities in Hidalgo and Querétaro: *Peromyscus difficilis, P. furvus, P. levipes* (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC.

Jellisonia (*Jellisonia*) *klotsi* Traub, 1944

CIUDAD DE MÉXICO: 42 km N of Cuernavaca: *Peromyscus aztecus.* 5 km SW of Parres: *Neotomodon alstoni, Reithrodontomys* sp. (Hastriter 2004). Specimens in collections: MZFC. Parres: *Reithrodontomys* sp. 5 km SW of Parres: *N. alstoni*. Km 42 Cuernavaca-México Highway: *P. hylocetes* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. El Zarco: *Microtus mexicanus* (Machado-A. 1960). Unknown if specimens are in collections. ESTADO DE MÉXICO: Lagunas de Zempoala, near Ojotongo: *Peromyscus maniculatus, Peromyscus* sp. Río Frío, Llano Grande; 4 km W of Río Frío: *Neotomodon alstoni* (Hastriter 2004). Specimens in collections: CMNH. Slopes of Volcán Popocatépetl: *Reithrodontomys megalotis* (Barrera 1953). Popocatépetl: *Reithrodontomys chrysopsis* (Barrera 1968). *N. alstoni, R. chrysopsis* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. GUERRERO: Omiltemi: *Peromyscus* sp. (Barrera 1958). San Miguel Totolapan, Puerto del Gallo; General Heliodoro Castillo, El Iris: *Peromyscus megalops*. Atoyac de Álvarez, Puerto del Gallo-Paraíso Highway, km 14: *Megadontomys thomasi* (Acosta *et al.* 2008). Specimens in collections: MZFC. JALISCO: Nevado de Colima: *Microtus mexicanus, Microtus* sp., *Peromyscus aztecus, P. melanotis, Peromyscus* sp., *Reithrodontomys* sp. (Hastriter 2004). Specimens in collections: CMNH, MZFC. Nevado de Colima: *P. melanotis* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Note: *P. aztecus* is not distributed in Jalisco according to Ceballos (2014). MICHOACÁN: Cerro Tancítaro, near Tancítaro: *Reithrodontomys chrysopsis* (Traub 1944; Barrera 1953; Hastriter 2004). Tancítaro, Mt. Tancítaro: *R. chrysopsis, Reithrodontomys* sp. (Hastriter 2004). Specimens in collections: BMNH, CMNH, FMNH, USNM. MORELOS: Lagunas de Zempoala, near Ojotongo: *Reithrodontomys* sp. Lagunas de Zempoala, near Ojo de Agua: *Neotomodon* sp., *Peromyscus difficilis* (Hastriter 2004). Specimens in collections: CMNH. Note: Author is unsure of the ID of *P. difficilis*. OAXACA: Ixtlán de Juárez, 4.5 km SE of Santa María Yavesía: *Peromyscus mexicanus*. Ixtlán de Juárez, 2.5 km SE of Santa María Yavesía: *Oligoryzomys fulvescens, P. aztecus* (Acosta *et al.* 2008). Specimens in collections: MZFC. PUEBLA: Popocatépetl: *Reithrodontomys* sp. (Hastriter 2004). Specimens in collections: CMNH, MZFC. QUERÉTARO: Jalpan de Serra, 4 km NE of Ahuacatlán de Guadalupe: *Peromyscus pectoralis* (Acosta *et al.* 2008). Specimens in collections: MZFC. TLAXCALA: 10 km NE of Calpulápan: *Reithrodontomys* sp. (Ayala-Barajas *et al.* 1988; Hastriter 2004). Specimens in collections: MZFC.

Jellisonia (*Jellisonia*) *maxwelli* Hastriter, 2004

NUEVO LEÓN: Chipinque: *Peromyscus* sp. (Hastriter 2004). Specimens in collections: CMNH.

Jellisonia (*Pleochaetoides*) *amadoi* Ponce-Ulloa, 1989

GUERRERO: El Faisanal, Sierra de Atoyac de Álvarez; La Golondrina, Atoyac: *Peromyscus megalops* (Hastriter 2004). Specimens in collections: MZFC. QUERÉTARO: 12 km NW of Peña Bernal: *Peromyscus pectoralis* (Acosta 2003). Specimens in collections: MZFC.

Jellisonia (*Pleochaetoides*) *bullisi* (Augustson, 1944)

HIDALGO: San Bartolo Tutotepec: *Peromyscus* sp. (Acosta *et al.* 2008). Sierra Madre Oriental: *Peromyscus* sp. (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC. NUEVO LEÓN: Cola de Caballo, Barrancas; 4 km SE of Monterrery; Chipinque: *Peromyscus* sp. (Hastriter 2004). Specimens in collections: MZFC. SAN LUIS POTOSÍ: San Bartolo, Mpio. Río Verde: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC.

Jellisonia (*Pleochaetoides*) *grayi* Hubbard, 1958

GUERRERO: Chilpancingo: *Megadontomys thomasi* (Hastriter 2004). Specimens in collections: MZFC. OAXACA: Miahuatlán de Porfirio Díaz, 2.3 km de Finca Infiernillo: *Heteromys* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. QUERÉTARO: 1 km S of Ahuacatlán de Guadalupe; 2 km S of Ahuacatlán de Guadalupe; 6.56 km El Lobo, Xilitla-Jalpan Highway; 8 km N of Jalpan; 1 km W of Santa Inés; 1.5 km NW of Santa Inés; 2 km W of Santa Inés; 4 km NW of Santa Inés; Landa de Matamoros, 2 km W of Santa Inés; Amealco de Bonfil, 5 km NW of El Batán: *Peromyscus levipes*. Landa de Matamoros, 1.5 km W of Santa Inés: *P. levipes* (recorded as *P. boylii levipes*). Jalpan de Serra, 8 km N of Jalpan; 4 km NE of Ahuacatlán de Guadalupe; 5.1 km SW of Ahuacatlán de Guadalupe: *P. pectoralis*. Landa de Matamoros, Peñamiller, Camargo; Ezequiel Montes, Peña Bernal; Peñamiller, Maguey Verde: *P. difficilis*. Landa de Matamoros, 2.8 km NW of Santa Inés: *P. furvus*. Landa de Matamoros, Xilita-Jalpan Highway, 6.56 km El Lobo: *P. boylii*. Camargo: *P. difficilis, P. pectoralis*. Maguey Verde: *P. difficilis, P. gratus*. Landa de Matamoros, Rancho 99: *P. gratus, P. pectoralis*. 1 km NW of Santa Inés: *P. levipes, P. beatae*. 1 km W of Santa Inés: *P. boylii, P. levipes, Peromyscus* sp. 2.5 km NW of Santa Inés: *P. beatae, P. furvus, P. levipes, P. boylii, Peromyscus* sp. 13 km NE of Tequisquiapan; 9 km SE of Tequisquiapan: *Baiomys taylori* (Acosta 2003; Acosta *et al.* 2008). NW Santa Inés:

P. boylii (Hastriter 2004). Specimens in collections: MZFC. Note: *P. beatae* is not distributed in Querétaro according to Ceballos (2014). SAN LUIS POTOSÍ: El Salto: *Peromyscus boylii*, *Sigmodon hispidus* (Hubbard 1958; Hastriter 2004). Specimens in collections: BMNH. 2 mi NE of El Salto; 8 mi N of Naranjo: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. 3 km NE of El Salto, 15 km N of Naranjo: *Peromyscus* sp. (Hastriter 2004). Specimens in collections: BMNH, CMNH, CNC, REL. Note: *S. hispidus* is not distributed in San Luis Potosí according to Ceballos (2014). A possible alternative host includes *S. leucotis* (Ceballos 2014). SIERRA MADRE ORIENTAL: Multiple localities in Hidalgo and Querétaro: *Peromyscus difficilis, P. furvus*, *P. levipes*, *P. gratus* (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC.

Jellisonia (*Pleochaetoides*) *ironsi* (Eads, 1947)

CHIAPAS: Comitán and Tninitaria: *Baiomys musculus* (Hubbard 1958; Hastriter 2004). Specimens in collections: BMNH, USNM. CIUDAD DE MÉXICO: La Venta and Cerro Zacayuca: *Baiomys taylori* (Barrera 1953; Hubbard 1958, Hastriter 2004). Specimens in collections: BMNH, CMNH, USNM. Pedregal de San Ángel: *B. taylori* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. DURANGO: Peña del Aguila: *Peromyscus* sp., *Reithrodontomys* sp. 4.4 km SE of Atotonilco: *Baiomys taylori* (Hastriter 2004). Specimens in collections: CMNH, REL, USNM. ESTADO DE MÉXICO: Chilpan; Tlalnepantla; 2 km N of Tlalnepantla: *Baiomys* sp. (Ayala-Barajas *et al.* 1988). Tlalnepantla: *Baiomys* sp. (Hatriter 2004). Specimens in collections: MZFC. GUERRERO: Atoyac de Álvarez, Puente de Lugardo: *Baiomys musculus*. Atoyac de Álvarez, El Faisanal: *Heteromys pictus* (Acosta *et al.* 2008). Specimens in collections: MZFC. JALISCO: Zapotlanejo: *Baiomys* sp., *Peromyscus* sp. (Hastriter 2004). Specimens in collections: REL, USNM. MORELOS: Tepoztlán: *Baoimys* sp. (Ayala-Barajas *et al.* 1988; Hastriter 2004). Specimens in collections: MZFC. NAYARIT: San Cayetano, 8 km W of Tepic: *Peromyscus* sp. 1.6 km W of Tepic: *Baiomys* sp. (Hastriter 2004). Specimens in collections: CMNH, CNC, USNM. OAXACA: 4.8 km E of Oaxaca, Benito Juárez National Park, Cerro San Felipe; Monte Albán: *Baiomys musculus* (Hastriter 2004). Specimens in collections: CMNH, USNM. 15 km NW of Miahuatlán: *Baiomys* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. PUEBLA: Matamoros: *Baiomys* sp. (Hastriter 2004). Specimens in collections: MWH. San Juan Atenco Cerro Caldera: *Baiomys taylori* (Acosta *et al.* 2008). Specimens in collections: MZFC. QUERÉTARO: Amealco de Bonfil, 5 km NW of Batán; Landa de Matamoros, 1 km NW of Santa Inés: *Peromyscus levipes*. Ezequiel Montes, Peña Bernal: *P. difficilis*. Colón, 4 km NW of Colón: *P. pectoralis*. Landa de Matamoros, Rancho 99: *P. gratus*. Tequisquiapan, 5 km SW of Tequisquiapan: *P. gratus, P. pectoralis*. Tequisquiapan, 9 km SE of Tequisquiapan: *Baiomys taylori* (Acosta *et al.* 2008). 4 km NW of Colón; 5 km SW of Tequisquiapan: *P. pectoralis*. 8 km N of Jalpan: *B. taylori, P. gratus*. 9 km SE of Tequisquiapan: *B. taylori* (Acosta 2003). Specimens in collections: MZFC. SAN LUIS POTOSÍ: El Salto, 11.2 km N of Naranjo; 3.2 km E of El Salto, 14.5 km N of Naranjo: *Baiomys taylori* (Hastriter 2004). Specimens in collections: CMNH, CNC. SONORA: Los Fresnos: *Baiomys taylori, Peromyscus fraterculus* (Zapata-Valdés *et al.* 2018). No specimens in collections.

Jellisonia (*Pleochaetoides*) *mexicana* Ponce-Ulloa, 1989

DURANGO: Revolcaderos, 1.6 km SW of Revolcaderos: *Peromyscus* sp. (Hastriter 2004). Specimens in collections: CMNH. GUERRERO: Nueva Delhi: *Neotoma mexicana.* 8 km E of Omiltemi: *Peromyscus* sp. (Hastriter 2004). Specimens in collections: CMNH, MZFC. Atoyac de Álvarez, Nueva Delhi: *Neotoma mexicana* (Acosta *et al.* 2008). Specimens in collections: MZFC. JALISCO: 9.7 km W of San Marcos: *Heteromys pictus* (Hastriter 2004). Specimens in collections: CMNH. NAYARIT: 5.5 km E of San Blas (Hotel Bucanaro): *Peromyscus fraterculus, Heteromys pictus* (Hastriter 2004). Specimens in collections: CMNH. SINALOA: 1 km NE of Santa Lucia: *Peromyscus spicilegus, Reithrodontomys fulvescens, Heteromys pictus.* 5 km NE of Santa Lucia: *P. spicilegus*. 1.9 km NE of Santa Lucía: *H. pictus*. 1.6 km E of Pánuco: *Neotoma mexicana* (Hastriter 2004). Specimens in collections: CMNH. SONORA: 12.9 km S-SE of Álamos on Río Cuchujaqui: *Heteromys pictus* (Hastriter 2004). Specimens in collections: CMNH.

Jellisonia (*Pleochaetoides*) *wisemani* Eads, 1951

CHIAPAS: Volcán Kagchiná, 3.5 km N of las Margaritas; Cueva Santa Rosa, 2 km N, 3 km W of Las Margaritas; Cueva Llano Redondo, 3 km N of las Margaritas: *Neotoma mexicana*. Pan American Highway over Río San Gregorio, 32 km from Guatemalan border: *Neotoma ferruginea* (Hastriter 2004). Specimens in collections: CMNH. CIUDAD DE MÉXICO: Pedregal de San Ángel: *Peromyscus gratus* (recorded as *P. truei*; Barrera 1953). Cuajimalpa de Morelos, 1 km del Potrillo, Parque Nacional Desierto de los Leones: *P. difficilis* (Acosta *et al.* 2008). Specimens in collections: MZFC. DURANGO: 4 km S-SE of la Zarca, Mpio: *Reithrodontomys megalotis* (Acosta *et al.* 2006). Specimens in collections: MZFC. Peña de Águila: *Peromyscus* sp. (Hastriter 2004). Specimens in collections: CMNH. ESTADO DE MÉXICO: Cueva de la Estrella Tonatico: *Neotoma mexicana* (recorded as *N. torquata*; Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. GUERRERO: La Joya Cacahuamilpa: *Peromyscus* sp. nest (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. 4.8 km E of Omiltemi; 8 km E of Omiltemi; 16 km S of Taxco (near Telcalpuco): *Peromyscus* sp. (Hastriter 2004). Specimens in collections: CMNH. HIDALGO: Tenango de Doria, El Potrero: *Megadontomys* sp., *Peromyscus furvus* (Acosta *et al.* 2008). Specimens in collections: MZFC. JALISCO: 4.8 km N of Guadalajara: *Peromyscus melanophrys* (Eads 1951; Hastriter 2004). Specimens in collections: KU, USNM. Huastaco: *P. levipes* (recorded as *P. boylii levipes*; Ayala-Barajas *et al.* 1988). Specimens in collections:

MZFC. Calderon Hacienda, 13 km E of Zapotlanejo, 39 km S of Guadalajara: *Baiomys* sp., *Peromyscus* sp. Zapotlanejo, 39 km S of Guadalajara: *Peromyscus* sp., *Reithrodontomys* sp. (Hastriter 2004). Specimens in collections: CMNH. Note: *P. levipes* is not distributed in Jalisco according to Ceballos (2014). MICHOACÁN: 3 km SW of Turundeo: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. 18 km W of Jiquilpan: *Peromyscus boylii*. Cerro Guyman: *Peromyscus* sp. 4.8 km NE of Pátzcuaro: *Sigmodon* sp. 4.8 km SW of Turundeo: *Peromyscus* sp. (Hastriter 2004). Specimens in collections: BMNH, CMNH, CNC, MZFC. 13 km SW of Jacona: *Reithrodontomys* sp. (Ayala-Barajas *et al.* 1988; Hastriter 2004). Specimens in collections: MZFC. Note: *P. boylii* is not distributed in Michoacán according to Ceballos (2014). MORELOS: Tepoztlán: *Peromyscus aztecus*, *Peromyscus* sp. (Hastriter 2004). Specimens in collections: MZFC. Derrame de Chichinautzin: *P. difficilis, Neotoma mexicana* (Pérez-Ortiz 1976; Ayala-Barajas *et al.* 1988; Hastriter 2004). Specimens in collections: MZFC. Tepoztlán: *P. hylocetes, Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Tepalcingo, Subestacion El Limón: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. Note: *P. aztecus* is not distributed in Morelos according to Ceballos (2014). OAXACA: Huajuapan de León: *Peromyscus* sp. 10 km SE of Miahuatlán: *Peromyscus melanophrys*. Monte Albán: *P. gratus, P. maniculatus* (Hastriter 2004). Specimens in collections: CMNH, MZFC. 10 km SE of Miahuatlán: *P. melanophrys, P. gratus* (recorded as *P. truei*; Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. PUEBLA: 6 km E of Totimihuacan: *Peromyscus boylii*. Villa Juárez: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Multiple localities: *P. furvus* (Acosta and Fernández 2015). Specimens in collections: MZFC. 5.6 km W-NW of Zapoltitic: *Heteromys pictus*. Villa Juárez, Xicotepec: *Peromyscus* sp. (Hastriter 2004). Specimens in collections: CMNH, MZFC. Note: *P. boylii* is not distributed in Puebla according to Ceballos (2014). QUERÉTARO: 3.7 km SW of Ahuacatlán de Guadalupe; Xilitla, 2 km NE of Jalpan-Xilitla Highway, km 192.3; 5 km NW of El Batán; 1 km NW of Santa Inés: *Peromyscus levipes*. Landa de Matamoros, 2.5 km NW of Santa Inés: *P. beatae*. 5 km SE of Tequisquiapan: *P. pectoralis*. Tequisquiapan, 9 km SE of Tequisquiapan; Pinal de Amoles, Ahuacatlán de Guadalupe: *Baiomys taylori*. Amealco de Bonfil, Galindo-Amealco Highway, km 11: *B. taylori, P. levipes*. Tolimán, 11 km NW of Peña Bernal: *P. melanophrys, P. pectoralis*. Peña Bernal: *Peromyscus difficilis, Peromyscus* sp. 14 km SW of Peña Bernal: *Heteromys irroratus*, *Sigmodon hispidus*. 11 km SW of Peña Bernal: *P. difficilis, P. melanophrys, P. pectoralis*. 5 km SW of Tequisquiapan: *P. gratus, P. pectoralis, Peromyscus* sp. Tolimán, 12 km NW of Peña Bernal: *P. difficilis, P. melanophrys, P. pectoralis* (Acosta 2003; Acosta *et al.* 2008). Specimens in collections: MZFC. Note: *P. beatae* and *S. hispidus* are not distributed in Querétaro according to Ceballos (2014). A possible alternative host includes *S. leucotis* (Ceballos 2014). VERACRUZ: Texolo: *Peromyscus* sp. (Traub and Johnson 1952b). Specimens in collection: AMNH. El Coderio, Jalapa; Texolo: *Peromyscus* sp. 4.8 mi NE of Las Minas: *Peromyscus mexicanus* (Hastriter 2004). Specimens in collections: AMNH, CMNH, MZFC. Xico, Texolo: *P. mexicanus*. Ixhuatlancillo, Rancho La Pala: *Peromyscus* sp. (Acosta *et al.* 2008). El Cedeño, Jalapa: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. SIERRA MADRE ORIENTAL: Multiple localities in Coahuila, Guanajuato, Hidalgo, Nuevo León, Puebla, Querétaro, Tamaulipas, and Veracruz: *Peromyscus maniculatus, Peromyscus* sp., *Dipodomys phillipsii* (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC. Note: *D. phillipsii* is not distributed in Coahuila, Nuevo León, or Tamaulipas according to Ceballos (2014). *Dipodomys phillipsii* in Guanajuato and Querétaro likely represent *D. ornatus* (Fernández *et al.* 2012).

Jellisonia sp.

CHIAPAS: Finca la Esperanza: *Peromyscus guatemalensis* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. CIUDAD DE MÉXICO: Cuajimalpa de Morelos, Cañada San Miguel, Presa, Parque Nacional Desierto de los Leones: *Reithrodontomys* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. GUERRERO: Agua Fría: *P. megalops*. Omiltemi: *Peromyscus* sp., *Reithrodontomys* sp. Puerto Chico, Xochipala: *Megadontomys thomasi, P. megalops* (Ayala-Barajas *et al.* 1988). Atoyac de Álvarez, El Faisanal: *Peromyscus megalops* (Acosta *et al.* 2008). Specimens in collections: MZFC. PUEBLA: 1 km SW of San Pedro Atlixco: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). La Esperanza: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. QUERÉTARO: *Jellisonia* sp. A: 2.8 km NW of Santa Inés: *Peromyscus furvus*. 1 km W of Santa Inés; 1 km NW of Santa Inés; 1.2 km S of Pinal de Amoles; 6.56 km El Lobo, Xilitla-Jalpan Highway: *P. levipes*. 1.2 km SW of Pinal de Amoles; 1 km S of Pinal de Amoles: *P. difficilis, P. levipes*. *Jellisonia* sp. B: 2 km S of Ahuacatlán de Guadalupe; 6.56 km El Lobo, Xilitla-Jalpan Highway; 1.2 km S of Pinal de Amoles; 1 km W of Santa Inés; 1.5 km W of Santa Inés: *P. levipes*. Maguey Verde: *P. difficilis*. 2.8 km W of Santa Inés: *P. furvus*. 1 km S of Ahuacatlán de Guadalupe: *P. levipes, P. pectoralis*. Camargo: *P. difficilis, P. pectoralis*. *Jellisonia* sp. C: Camargo; 9 km Amealco-La Estancia Highway; 1 km S of Pinal de Amoles; 1 km S of Pinal de Amoles: *P. difficilis*. 1.2 km S of Pinal de Amoles; 1 km W of Santa Inés: *P. levipes*. Maguey Verde: *P. gratus*. 1 km SW of Pinal de Amoles: *P. difficilis, P. levipes*. *Jellisonia* sp. D: Maguey Verde: *P. difficilis*. *Jellisonia* sp. E: 9 km Amealco-La Estancia Highway: *P. difficilis* (Acosta 2003). Specimens in collections: MZFC. 2 km S of Ahuacatlán de Guadalupe; 11 km Galindo-Amealco Highway: *Baiomys taylori* (Acosta 2003). Specimens in collections: MZFC. VERACRUZ: Zongolica: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC.

Kohlsia cora Traub, 1950

OAXACA: Ixtlán de Juáez, 6.5 km E-SE of Santa María Yavesía: *Peromyscus melanocarpus*. Miahuatlán de Porfirio Díaz, 1.2 km de Finca Brasil: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. QUERÉTARO: La Florida: *Peromyscus gratus* (Acosta 2003). Cadereyta de Montes, La Florida: *P. gratus* (Acosta *et al.* 2008). Specimens in collections: MZFC. Note from Traub *et al.* (1983): *Kohlsia cora* was previously only known from Puebla, Nuevo León, Chiapas and the mountains in southern Guatemala in a rodent nest.

Kohlsia fournieri Vargas, 1951

CHIAPAS: Comitán and La Esperanza: *Peromyscus guatemalensis* (Vargas 1951a; Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. OAXACA: Ixtlán de Juárez, 2.5 km SE of Santa María Yavesía: *Peromyscus aztecus* (Acosta *et al.* 2008). Specimens in collections: MZFC.

Kohlsia keenani Tipton and Méndez, 1961

CHIAPAS: Angel Albino Corzo, Reserva El Triunfo: *Handleyomys rhabdops* (recorded as *Orzyomys rhabdops angusticeps*; Acosta *et al.* 2008). Specimens in collections: MZFC. OAXACA: San Juan Atepec, Tuxtepec-Oaxaca Highway, km 91, Camino a San Isidro: *Peromyscus melanocarpus* (Acosta *et al.* 2008). Specimens in collections: MZFC.

Kohlsia linni Hubbard, 1958

CHIAPAS: Pueblo Nuevo: *Neotoma mexicana, Peromyscus boylii* (Hubbard 1958). Specimens in collections: BMNH. Note: *P. boylii* is not distributed in Chiapas according to Ceballos (2014).

Kohlsia martini Holland, 1971

CHIAPAS: km 145 Highway 175 de Oaxaca, approximately 90 mi N of Oaxaca: *Oryzomys* sp. (Holland 1971). Specimens in collections: CNC. Note: *Oryzomys* sp. was recorded in the original literature but may represent *Handleyomys* sp. OAXACA: Ixtlán de Juárez, 6.5 km E-SE of Santa María Yavesía; San Juan Atepec, Tuxtepec-Oaxaca Highway, km 91, on the road to San Isidro; Santiago Comaltepec, Tuxtepec-Oaxaca Highway, km 79.5, La Esperanza; Santiago Comaltepec, Tuxtepec-Oaxaca Highway, km 87, El Suspiro: *Peromyscus melanocarpus* (Acosta *et al.* 2008). Specimens in collections: MZFC. QUERÉTARO: Peñamiller, Camargo: *Peromyscus difficilis* (Acosta *et al.* 2008). Specimens in collections: MZFC.

Kohlsia ortizi (Vargas, 1951)

CHIAPAS: Comitán: *Peromyscus* sp. (Vargas 1951b; Hastriter 2004). 6 mi NW of Teopisca: *Peromyscus guatemalensis* (Hastriter 2004). Specimens in collections: BMNH, IBUNAM, INDRE. GUERRERO: Chilpancingo de los Bravo, 0.5 km W of Omiltemi: *Peromyscus aztecus*. Atoyac de Álvarez, El Molote: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. OAXACA: Ixtlán de Juárez, 4 km SE of Santa María Yavesía: *Peromyscus aztecus, P. mexicanus*. Miahuatlán de Porfirio Díaz, 2.3 km de Finca Infiernillo: *Heteromys* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC.

Kohlsia pelaezi Barrera, 1956

GUERRERO: Omiltemi: *Peromyscus* sp. (Barrera 1956; Barrera 1958; Ayala-Barajas *et al.* 1988). Agua Fría, Yextla: *Peromyscus megalops*. Camotla: *Osgoodomys banderanus* (recorded as *Peromyscus banderanus vicinior*). 1 mi SW of Omiltemi: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Atoyac de Álvarez, Nueva Delhi; Tlacotepec, 7 km Puerto del Gallo-El Paraíso Highway; Chilpancingo de los Bravo, Omiltemi; San Miguel Totolapan, Estación Toro Muerto; Atoyac de Álvarez, La Golondrina: *P. megalops*. General Heliodoro Castillo, El Iris: *Megadontomys thomasi*. Atoyac de Álvarez, El Molote: *Peromyscus* sp. San Luis Acatlán, Yerba-Santa: *Megadontomys* sp., *Peromyscus* sp. Atoyac de Álvarez, El Faisanal: *Handleyomys alfaroi* (recorded as *Oryzomys alfaroi*), *P. megalops*. Atoyac de Álvarez, 3 km S of Puerto del Gallo: *M. thomasi, H. alfaroi* (recorded as *O. alfaroi*). Atoyac de Álvarez, Los Retrocesos: *Neotoma mexicana, H. alfaroi* (recorded as *O. alfaroi*), *P. megalops, Heteromys pictus* (Acosta *et al.* 2008). Specimens in collections: MZFC. Note: Author was unsure of the identification of *Osgoodomys banderanus*. QUERÉTARO: La Florida: *Peromyscus gratus, P. pectoralis*. 4 km SW of Tequisquiapan: *Perognathus flavus* (Acosta 2003). Cadereyta de Montes, La Florida: *P. gratus*. Peñamiller, Camargo: *P. difficilis*. Pinal de Amoles, 1 km S of Ahuacatlán de Guadalupe; Pinal de Amoles, 1 km S of Pinal de Amoles: *P. levipes* (recorded as *P. boylii levipes*). Tequisquiapan, 4 km SW of Tequisquiapan: *Perognathus flavus*. Tolimán, 12 km NW of Peña Bernal: *P. pectoralis* (Acosta *et al.* 2008). Specimens in collections: MZFC. VERACRUZ: Xico, Texolo: *Peromyscus mexicanus* (Acosta *et al.* 2008). Sierra Madre Oriental: *Peromyscus* sp. (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC.

Kohlsia whartoni Traub and Johnson, 1952

CHIAPAS: Pueblo Nuevo: *Neotoma mexicana, Peromyscus boylii* (Hubbard 1958). Specimens are in collections: Unknown, possibly BMNH. Note: *P. boylii* is not distributed in Chiapas according to Ceballos (2014). GUERRERO: Atoyac de Álvarez, El Molote: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. HIDALGO: Tlanchinol: *Peromyscus aztecus* (Salceda-Sánchez and Hastriter 2006). Specimens in collections: CAIM, InDRE. OAXACA: Ixtlán de Juárez, 1.5 km SE of Santa María Yavesía: *Peromyscus aztecus*. Ixtlán de Juárez, 2.5 km SE of Santa María Yavesía: *P. aztecus, P. gratus* (recorded as *P. truei*), *Peromyscus* sp. Miahuatlán de Porfirio Díaz, 1.2 km de Finca Brasil; Miahuatlán de Porfirio Díaz, 2.3 km de Finca La Gloria: *Peromyscus* sp. Miahuatlán de Porfirio Díaz, 2.3 km de Finca Brasil: *Peromyscus* sp., *Heteromys* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. PUEBLA: Multiple localities: *Peromyscus levipes* (Acosta and Fernández 2015). Xicotepec, El Salto: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. VERACRUZ: Texolo: *Peromyscus* sp. (Traub and Johnson 1952a). Specimens in collections: FMNH. Catemaco: *Peromyscus mexicanus*. ½ mi NE of Las Minas (approximately 16 mi NE of Perote): *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Xico, Texolo: *P. mexicanus* (Acosta *et al.* 2008). Sierra Madre Oriental: *Peromyscus* sp. (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC.

Kohlsia zyanya Acosta *et al.*, 2009

OAXACA: Sierra de Juárez km 87 Tuxtepec-Oaxaca Highway: *Peromyscus melanocarpus*. Sierra de Juárez km 91 Tuxtepec-Oaxaca Highway; San Juan Atepec, km 91 Tuxtepec-Oaxaca Highway: *P. melanocarpus, P. mexicanus*. Sierra de Juárez, La Esperanza km 79: *P. melanocarpus, P. mexicanus, Peromyscus* sp. (Acosta *et al.* 2009). Specimens in collections: CAIM, Indre, MZFC.

Kohlsia sp.

CHIAPAS: Raundales: *Peromyscus mexicanus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. ESTADO DE MÉXICO: Slopes of Volcán Popocatépetl: *Peromyscus melanotis* (Barrera 1953). Specimens in collections: MZFC. OAXACA: 10 km S of San Juan Lachao: *Oryzomys* sp. (Ayala-Barajas *et al.* 1988). Miahuatlán de Porfirio Díaz, 1.2 km de Finca Brasil; Miahuatlán de Porfirio Díaz, 2.3 km de Finca Brasil: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. Note: *Oryzomys* sp. was recorded in the original literature but may represent *Handleyomys* sp.

Malaraeus eremicus (Baker, 1904)

SONORA: La Mesa: *Peromyscus maniculatus*. Los Fresnos: *P. fraterculus* (Zapata-Valdés *et al.* 2018). No specimens in collections.

Nosopsyllus fasciatus (Bosc, 1800)

CIUDAD DE MÉXICO: La Venta: *Peromyscus maniculatus* (Barrera 1953, Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC.

Opisodasys hollandi Traub, 1947

GUERRERO: 35 km SW of Xochipala: *Peromyscus boylii evides* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Note: *P. boylii* is not distributed in Guerrero according to Ceballos (2014).

Opisodasys robustus (Jordan, 1925)

DURANGO: Hidalgo, 4 km S-SE of la Zarca: *Peromyscus pectoralis, Perognathus flavus* (Acosta *et al.* 2006; 2008). Specimens in collections: MZFC. *Opisodasys* sp. QUERÉTARO: La Florida: *Peromyscus gratus* (Acosta 2003). Specimens in collections: MZFC.

Orchopeas fulleri Traub, 1950

HIDALGO: Tlanchinol: *Peromyscus furvus* (Salceda-Sánchez and Hastriter 2006). Specimens in collections: CAIM, InDRE.

Orchopeas leucopus (Baker, 1904)

BAJA CALIFORNIA: Rancho El Metate, S Juan de Dios, Matomi: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. CHIAPAS: Tuxtla Gutiérrez: *Peromyscus mexicanus* (Barrera 1955a; 1955b). Tuxtla Gutiérrez: *Peromyscus* sp. Sta. Inés: *Baiomys* sp., *Sigmodon hispidus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Note: *S. hispidus* is not distributed in Chiapas according to Ceballos (2014). Possible alternative hosts include *S. hirsutus*, *S. mascotensis*, *S. toltecus*, or *S. zanjonensis* (Ceballos 2014). CHIHUAHUA: Janos Biosphere Reserve: *Onychomys leucogaster, Peromyscus leucopus, P. maniculatus* (Fernández-González *et al.* 2016). No specimens in collections. GUANAJUATO: La Noria, 3 km E of S. Diego, La Unión: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. HIDALGO: Tlanchinol: *Peromyscus mexicanus* (Salceda-Sánchez and Hastriter 2006). Specimens in collections: CAIM, InDRE. NUEVO LEÓN: Rancho 14 de Marzo, de China, Monterrey: *Onychomys* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. QUERÉTARO: Cadereyta de Montes, La Florida: *Peromyscus gratus* (Acosta *et al.* 2008). Specimens in collections: MZFC. SAN LUIS POTOSÍ: 5 km SW of Núñez: *Neotoma* sp., *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. SONORA: Los Fresnos: *Peromyscus fraterculus, Sigmodon fulviventer* (Zapata-Valdés *et al.* 2018). No specimens in collections.

Orchopeas intermedius Hubbard, 1943

COAHUILA: Sabinas: *Neotoma micropus* (Salceda-Sánchez and Hastriter 2006). Specimens in collections: CAIM, InDRE.

Orchopeas neotomae Augustson, 1943

ESTADO DE MÉXICO: Popocatépetl: *Neotoma mexicana, Neotoma* sp. (Barrera 1968; Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. MORELOS: Lagunas de Zempoala: *Neotoma mexicana* (recorded as *N. torquata*; Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. NUEVO LEÓN: Cerro Potosí: *Neotoma leucodon* (recorded as *N. albigula*; Tipton and Mendez 1968). Unknown if specimens are in collections. Note: *Neotoma albigula* was recognized as the original host. However, according to Bradley and Mauldin (2016), *N. albigula* from the eastern part of Mexico is now recognized as *N. leucodon*. TLAXCALA: La Malinche: *Neotoma mexicana* (Aguilar-Montiel *et al.* 2018). Specimens in collections: MZFC.

Orchopeas schisintus (Jordan, 1929)

SONORA: Hermosillo: *Neotoma albigula, Peromyscus fraterculus, Dipodomys merriami* (Vargas 1960). Unknown if specimens are in collections. Rcho. Noche Buena, 30 km NNW Guaymas: *Neotoma* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC.

Orchopeas sexdentatus (Baker, 1904)

CHIHUAHUA: Janos Biosphere Reserve: *Neotoma albigula* (Fernández-González *et al.* 2016). No specimens in collections. MORELOS: Lagunas de Zempoala, 1 km NE de la Laguna: *Neotoma mexicana* (Barrera 1954a). Specimens in collections: MZFC.

Orchopeas sexdentatus ssp.

MORELOS: Lagunas de Zempoala: *Neotoma mexicana* (Barrera 1954a). Specimens in collections: MZFC.

Orchopeas sp.

CHIAPAS: Tuxtla Gtz.: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC.

Oropsylla (Opisocrotis) hirsuta (Baker, 1895)

SONORA: Los Fresnos: *Chaetodipus hispidus* (Zapata-Valdés *et al.* 2018). No specimens in collections.

Pleochaetis exilis (Jordan, 1937)

CHIHUAHUA: Janos Biosphere Reserve: *Onychomys arenicola, O. leucogaster, Peromyscus maniculatus* (Fernández-González *et al.* 2016). No specimens in collections. SONORA: La Mesa: *Onychomys torridus* (Zapata-Valdés *et al.* 2018). No specimens in collections.

Pleochaetis mundus (Jordan and Rothschild, 1922)

CIUDAD DE MÉXICO: Lomas de Chapultepec: *Peromyscus melanotis* (Dampf 1942). Specimens in collections: Collection of the author, NHM, NMNH. Km 3.5 México-Xochimilco Highway: *Microtus mexicanus, Peromyscus* sp. (Machado-A. 1960). Unknown if specimens are in collections. 5 km Sta. Cruz Meyehualco: *P. difficilis*. San Andrés Tetepilco: *P. maniculatus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. ESTADO DE MÉXICO: Popocatépetl: *Microtus mexicanus, Peromyscus difficilis, P. maniculatus* (Barrera 1968). Amecameca; Popo Park: *Peromyscus* sp. Cerro de la Caldera: *Peromyscus difficilis*. Popocatépetl, 5 km E Sn. Pedro Nexapa: *Peromyscus maniculatus*. Sn. Cayetano: *Reithrodontomys* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. HIDALGO: Arroyo Piedras Negras: *Reithrodontomys megalotis* (Barrera 1953; Ayala-Barajas *et al.* 1988). Xoxafi: *Peromyscus difficilis* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. JALISCO: La Barca: *Sigmodon hispidus* (Dampf 1942). Specimens in collections: Collection of the author, NHM, NMNH. Huastaco: *Peromyscus levipes* (recorded as *P. boylii levipes*). 7 km SE of Tonalá: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Note: *S. hispidus* is not distributed in Jalisco according to Ceballos (2014). Possible alternative hosts include *S. alleni*, *S. fulviventer*, and *S. mascotensis* (Ceballos 2014). MICHOACÁN: 3 km SW of Sn. Fco. Tlalpujahua: *Peromyscus maniculatus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Tancítaro: *Peromyscus hylocetes, Reithrodontomys chrysopsis* (Traub 1950). Unknown if specimens are in collections. MORELOS: Zempoala: *Peromyscus hylocetes* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. PUEBLA: Aljojuca; 2 km W of Atenco de Aljojuca, road to San Salavador el Seco; 1 km SW of San Pedro Atlixco: *Peromyscus* sp. 1 mi NE of Alchichica: *Peromyscus maniculatus* (Ayala-Barajas *et al.* 1988). 2 km W Guadalupe Victoria, Mpio. de Guadalupe Victoria: *P. maniculatus*. 1 km S Santa Cruz Coyotepec, Mpio. de San Salvador El Seco: *P. difficilis, P. maniculatus* (Falcón-Ordaz *et al.* 2012). Specimens in collections: MZFC. QUERÉTARO: 2 km NW of Peña Bernal; Landa de Matamoros, 1 km W of Santa Inés: *Peromyscus melanophrys*. Amealco de Bonfil, 4 km Amealco: *P. levipes*. 9 km N Amealco Highway; 9 km Amealco-La Estancia Highway; 8 km N Jalpan; Peñamiller, 0.5 km NW Camargo: *P. difficilis*. Amealco de Bonfil, 8.6 mi SW Amealco: *P. boylii*. 4 km NW Colón; Peñamiller; 5 km SE Tequisquiapan: *P. pectoralis*. Tequisquiapan, 9 km SE Tequisquiapan: *Baiomys taylori*. Ezequiel Montes, 5 km W Peña Bernal: *Sigmodon* sp. 14 km SW Peña Bernal: *Heteromys irroratus*. Colón, 14 km SW Peña Bernal: *Heteromys* sp. Amealco de Bonfil, 5 km NW El Batán; Cadereyta de Montes, 6 km S-SE San Joaquín: *P. difficilis, P. levipes*. 11 km Galindo-Amealco Highway: *B. taylori, P. levipes*. 5 km SW Tequisquiapan: *Peromyscus* sp., *P. gratus, P. pectoralis*. Peña Bernal: *Peromyscus* sp., *P. levipes, P. difficilis*. Camargo: *P. difficilis, P. gratus, P. pectoralis*. Tolimán, 11 km NW of Peña Bernal: *P. difficilis, P. melanophrys, P. pectoralis*. Peñamiller, Camargo: *P. difficilis*; *P. gratus* (recorded as *P. truei gratus*), *P. pectoralis*. 13.76 km SW of Amealco; 4 km NW Amealco; 4 km SW Amealco; 1 km W desviación, San Pedro Tenango: *N. leucodon* (recorded as *N. albigula*), *N. goldmani, P. levipes*. Maguey Verde: *N. leucodon* (recorded as *N. albigula leucodon*), *N. goldmani, P. gratus* (recorded as *P. truei gratus*), *P. difficilis, P. pectoralis* (Acosta 2003; Acosta *et al.* 2008). Specimens in collections: MZFC. TLAXCALA: Calpulalpan: *Peromyscus difficilis* (Barrera 1953). 10 km E Calpulalpan: *P. difficilis* (Ayala-Barajas *et al.* 1988). Tlaxco: *Peromyscus* sp. La Malinche: *Neotomodon alstoni, P. difficilis, P. gratus, P. leucopus, P. levipes, P. maniculatus, P. melanotis, Reithrodontomys fulvescens, Heteromys irroratus* (Ayala-Barajas *et al.* 1988; Aguilar-Montiel *et al.* 2018). Sanctorum de Lázaro Cárdenas, Camino Rural Benito Juárez, La Joya: *P. maniculatus* (Acosta *et al.* 2008). Specimens in collections: MZFC. Note: Several additional records from Traub (1950) with unclear localites and host associations. Note: *P. furvus* is not distributed in Tlaxcala according to Ceballos (2014). VERACRUZ: 3 km S El Frijol Colorado, Mpio. de Perote: *Peromyscus difficilis* (Falcón-

Ordaz *et al.* 2012). Specimens in collections: MZFC. ZACATECAS: Cerro el Panal: *Peromycus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. ORIENTAL BASIN: Multiple localities in Puebla, Tlaxcala, and Veracruz: *Peromyscus difficilis, P. furvus, P. maniculatus, Peromyscus* sp. (Acosta and Fernández 2015). Specimens in collections: MZFC.

Pleochaetis paramundus Traub, 1950

CIUDAD DE MÉXICO: El Zarco: *Peromyscus melanotis* (Barrera 1953; Ayala-Barajas *et al.* 1988). El Guadra: *P. hylocetes* (Barrera 1953). La Cima: *Peromyscus* sp. Parres: *Neotomodon alstoni, Neotomodon* sp. 2 km S Parres: *Neotomodon* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Note: *Neotomodon* sp. likely refers to *Neotomodon alstoni*, as this is the only species in the genus (*N. orizabae* and *N. perotensis* were synonymized with *N. alstoni*). DURANGO: Hidalgo, 4 km S-SE of la Zarca: *Onychomys torridus, Peromyscus maniculatus* (Acosta *et al.* 2006; 2008). Specimens in collections: MZFC. Note: *O. torridus* is not distributed in Durango according to Ceballos (2014). ESTADO DE MÉXICO: Slopes of Volcán Popocatépetl: *Peromyscus melanotis* (Barrera 1953). Popocatépetl, *P. hylocetes, P. melanotis*. Popocatépetl, Mirador del Poeta, *Neotomodon alstoni*. Popocatépetl, Diego de Ordaz, *N. alstoni* (Ayala-Barajas *et al.* 1988). Popocatépetl, *Microtus mexicanus, N. alstoni, P. maniculatus, P. melanotis, Reithrodontomys chrysopsis, R. megalotis* (Barrera 1968). Cerro Tlamacas: *M. mexicanus, N. alstoni, P. melanotis*. Monte Río Frío: *N. alstoni*, *Neotoma mexicana* (recorded as *N. torquata mexicana*), *Peromyscus* sp. 5 km SO Parres; Popocatépetl, Mirador del Poeta; Popocatépetl, Diego de Ordaz: *N. alstoni* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. GUERRERO: Chilpancingo de los Bravo, Omiltemi, Cañada de Agua Fría: *Megadontomys thomasi* (Acosta *et al.* 2008). Specimens in collections: MZFC. MICHOACÁN: Tancítaro: *Neotomodon alstoni* (Traub 1950). Specimens in collections: FMNH. MORELOS: 5.5 km N of Tres Cumbres: *Neotomodon alstoni* (Barrera 1953). Km 11 Tres Cumbres-Zempoala Highway: *Peromyscus hylocetes* (Barrera 1954a). 3 km S of Zempoala: *P. hylocetes*. 9 km N of Tres Marias: *N. alstoni* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. OAXACA: Ixtlán de Juárez, 8.75 km SE of Santa María Yavesía: *Peromyscus difficilis* (Acosta *et al.* 2008). Specimens in collections: MZFC. PUEBLA: La Esperanza: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. QUERÉTARO: Peñamiller, Maguey Verde: *Peromyscus difficilis* (Acosta *et al.* 2008). Specimens in collections: MZFC. TLAXCALA: 10 km NE of Calpulalpan: *Neotomodon* sp. La Malinche: *Neotomodon alstoni*, *Peromyscus difficilis, P. maniculatus, P. melanotis, Reithrodontomys chrysopsis, R. fulvescens* (Ayala-Barajas *et al.* 1988; Acosta and Fernández 2006; Aguilar-Montiel *et al.* 2018). Huamantla, La Malinche (Caseta #4): *N. alstoni*, *R. chrysopsis*. Tlaxco: *N. alstoni* (Acosta *et al.* 2008). Specimens in collections: MZFC. Note: *Neotomodon* sp. likely refers to *Neotomodon alstoni*, as this is the only species in the genus (*N. orizabae* and *N. perotensis* were synonymized with *N. alstoni*).

Pleochaetis sp.

GUERRERO: Puerto Chico, 38 km W of Xochipala: *Megadontomys thomasi*. 35 km SW of Xochipala: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. QUERÉTARO: 3.7 km SW of Ahuacatlán de Guadalupe; 13.76 km W of Amealco; 17 km N of Amealco: *Peromyscus levipes*. 6.24 km W of Amealco: *Reithrodonomys fulvescens*. Maguey Verde: *P. difficilis*. 1 km S of Pinal de Amoles: *Neotoma mexicana, P. difficilis, P. levipes, Peromyscus* sp., *R. fulvescens, R. sumichrasti*. Pinal de Amoles: *P. difficilis, P. levipes*. Camargo: *P. pectoralis, P. difficilis*. 1 km S of Ahuacatlán de Guadalupe: *P. levipes* (Acosta 2003). Tequisquiapan, 5 km SW of Tequisquiapan: *P. gratus* (Acosta *et al.* 2008). Specimens in collections: MZFC. SIERRA MADRE ORIENTAL: Multiple localities: *Peromyscus gratus* (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC.

Plusaetis apollinaris (Jordan and Rothschild, 1921)

CIUDAD DE MÉXICO: Cuajimalpa de Morelos, Cabeza del Toro, Parque Nacional Desierto de los Leones: *Peromyscus maniculatus* (Acosta *et al.* 2008). Specimens in collections: MZFC. GUERRERO: Atoyac de Álvarez, El Molote: *Megadontomys* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. HIDALGO: Cuatepec de Hinojosa, 4 km W of San Lorenzo Sayula: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. OAXACA: Ixtlán de Juárez, 2.5 km SE of Santa María Yavesía: *Peromyscus gratus* (recorded as *P. truei*). Ixtlán de Juárez, 6.5 km E-SE of Santa María Yavesía: *P. aztecus, P. difficilis, P. melanocarpus*. Ixtlán de Juárez, 8.75 km SE of Santa María Yavesía: *Microtus mexicanus, P. difficilis* (Acosta *et al.* 2008). Specimens in collections: MZFC. PUEBLA: Atzitzintla, Santa Cruz Cuyachapa, Ejido Maguey Cenizo: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. QUERÉTARO: 4 km NE of Ahuacatlán de Guadalupe: *Peromyscus pectoralis*. 11 km Galindo-Amealco Highway; 1 km NW of Santa Inés: *P. levipes*. Peña Bernal: *P. difficilis*. 9 km SE of Tequisquiapan: *Baiomys taylori* (Acosta 2003). Tequisquiapan, Tequisquiapan: *Heteromys irroratus* (Acosta *et al.* 2008). Specimens in collections: MZFC. TLAXCALA: Huamantla, La Malinche (Caseta #4): *Microtus mexicanus, Neotomodon alstoni, Peromyscus gratus, P. melanotis, Peromyscus* sp., *Reithrodontomys chrysopsis, R. megalotis*. Ixtenco La Malinche (Caseta #5): *N. alstoni, R. chrysopsis, R. megalotis*, *Peromyscus* sp. Tlaxco: *Neotomodon alstoni* (Acosta and Fernández 2006; Acosta *et al.* 2008). Specimens in collections: MZFC. ORIENTAL BASIN: Multiple localities in Puebla and Tlaxcala: *Peromyscus furvus, P. maniculatus* (Acosta and Fernández 2015). Specimens in collections: MZFC. Note: *P. furvus* is not distributed in Tlaxcala according to Ceballos (2014).

Plusaetis asetus (Traub, 1950)

ESTADO DE MÉXICO: Popocatépetl: *Microtus mexicanus, Peromyscus maniculatus, P. melanotis* (Ayala-Barajas *et al.* 1988). Slopes of Popocatépetl: *M. mexicanus, P. manicu-*

latus. Popocatépetl, Mirado del Poeta; Iztaccíhuatl, vert. Oriental: *Microtus mexicanus*. Popocatépetl, Paraje Providencial: *Peromyscus* sp. Popocatépetl, Mirador de Nexpayatla: *Microtus* sp. (Ayala-Barajas *et al.* 1988). Popocatépetl: *Microtus mexicanus, P. maniculatus, P. melanotis* (Barrera. 1968). Specimens in collections: MZFC. NUEVO LEÓN: Cerro Potosí: *Microtus mexicanus, P. difficilis, P. melanotis* (Tipton and Mendez 1968). Unknown if specimens are in collections. El Potosí: *Microtus* sp. (Ayala-Barajas *et al.* 1988). Sierra Madre Oriental: *Microtus* sp. (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC. PUEBLA: San Juan Tetla, Mpio. de Chiautzingo: *Microtus mexicanus* (Ramírez 1982). Unknown if specimens are in collections.

Plusaetis aztecus (Barrera, 1954)

CIUDAD DE MÉXICO: El Guarda: *Neotomodon alstoni*. La Venta: *P. gratus* (recorded as *P. truei gratus*), *Peromyscus maniculatus*. El Zarco: *P. gratus* (recorded as *P. truei gratus*; Barrera 1953b; Machado-A. 1960). La Cima: *Peromyscus* sp. El Zarco: *P. maniculatus*. Parres: *N. alstoni*, *Peromyscus* sp. 2 km SW of Parres; 2 km S of Parres: *Neotomodon* sp., *Reithrodontomys* sp. 5 km SW of Parres: *N. alstoni*. San NW Cayetano: *Reithrodontomys* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC or unknown. Note: *Neotomodon* sp. likely refers to *Neotomodon alstoni*, as this is the only species in the genus (*N. orizabae* and *N. perotensis* were synonymized with *N. alstoni*). Parque Nacional Insurgente Miguel Hidalgo y Costilla: *Microtus mexicanus, P. maniculatus, Reithrodontomys megalotis* (Méndez-L. 1974). Unknown if specimens are in collections. ESTADO DE MÉXICO: Slopes of Volcán Popocatépetl and La Venta: *Peromyscus maniculatus* (Barrera 1954b). Popocatépetl: *P. maniculatus, Peromyscus* sp., *Reithrodontomys chrysopsis*. Popocatépetl, 3.5 km E of San Pedro Nexapa: *Peromyscus* sp. Popocatépetl, Mirador de Nexpayantla: *P. melanotis*. Popocatépetl, Mirado del Poeta: *P. melanotis, Peromyscus* sp. Popocatépetl, Paso de Cortes; Popocatépetl, Paraje Diego de Ordaz: *N. alstoni*. Popocatépetl, Tlamacas: *P. melanotis, R. chrysopsis*. Popocatépetl, Paraje Providencial: *P. maniculatus*. 5 mi W of Río Frío: *N. alstoni*. 4 km W of Río Frío: *Reithrodontomys* sp. Zumpango: *Reithrodontomys* sp. (Ayala-Barajas *et al.* 1988). Popocatépetl: *Microtus mexicanus, Neotomodon alstoni, P. difficilis, P. maniculatus, P. melanotis, R. chrysopsis* (Barrera 1968). Specimens in collections: MZFC. San Cayetano: *M. mexicanus, Peromyscus* sp. (Machado-A. 1960). Unknown if specimens are in collections. JALISCO: Nevado de Colima: *Microtus mexicanus, Peromyscus melanotis* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. MORELOS: Tres Cumbres: *Neotomodon alstoni* (Barrera 1953). Specimens in collections: MZFC. NUEVO LEÓN: Cerro Potosí: *Microtus mexicanus, Neotoma leucodon* (recorded as *N. albigula*), *Peromyscus difficilis, P. melanotis, Peromyscus* sp. (Tipton and Mendez 1968). Unknown if specimens are in collections. PUEBLA: San Juan Tetla, Mpio. de Chiautzingo: *Reithrodontomys megalotis* (Ramírez 1982). Unknown if specimens are in collections. TLAXCALA: 10 km NE of Calpulalpan: *Reithrodontomys* sp. La Malinche: *Microtus mexicanus, Neotoma mexicana, Neotomodon alstoni, Peromyscus difficilis, P. gratus, P. levipes, P. maniculatus, P. melanotis, Reithrodontomys chrysopsis, R. fulvescens, R. megalotis, R. sumichrasti* (Ayala-Barajas *et al.* 1988; Acosta and Fernández 2006; Aguilar-Montiel *et al.* 2018). Specimens in collections: MZFC.

Plusaetis dolens dolens (Jordan and Rothschild, 1914)

CIUDAD DE MÉXICO: Pedregal de San Ángel: *Peromyscus gratus* (recorded as *P. truei gratus*). La Venta: *P. gratus* (recorded as *P. truei gratus*), *P. maniculatus*. Zacatepec: *P. gratus* (recorded at *P. truei gratus*; Barrera 1953). Specimens in collections: MZFC. Parque Nacional Insurgente Miguel Hidalgo y Costilla: *P. maniculatus* (Méndez-L. 1974). Unknown if specimens are in collections. ESTADO DE MÉXICO: Popocatépetl: *Microtus mexicanus, Peromyscus difficilis, P. maniculatus, Reithrodonomys chrysopsis*, *R. megalotis* (Barrera 1968). 4.5 km E of Chiconautla: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. GUERRERO: Atoyac de Álavarez, El Molote: *Megadontomys* sp. Chilpancingo de los Bravo, Omiltemi: *Megadontomys thomasi*. Omiltemi, Cueva de Borrega: *Peromyscus boylii*. San Miguel Totolapan, Estación Toro Muerto: *Peromyscus* sp., *Reithrodontomys* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. Note: *P. boylii* is not distributed in Guerrero according to Ceballos (2014). HIDALGO: Arroyo Piedras Negras: *Peromyscus difficilis, Reithrodontomys megalotis* (Barrera 1953). Specimens in collections: MZFC. MICHOACÁN: Monte San Miguel Tancítaro: *Peromyscus hylocetes* (Traub 1950). Unknown if specimens are in collections. Coalcoman de Vázquez Pallares, Pallares, 11.84 km SW of Dos Aguas: *P. winkelmanni* (Acosta *et al.* 2008). Specimens in collections: MZFC. MORELOS: Derrame del Chichinautzin: *Neotoma mexicana, Peromyscus difficilis* (Pérez-Ortiz 1976; Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. OAXACA: Ixtlán de Juárez, 8.75 km SE of Santa María Yavesía: *Peromyscus difficilis* (Acosta *et al.* 2008). Specimens in collections: MFZC. PUEBLA: La Esperanza: *Peromyscus melanophrys, Peromyscus* sp., *Reithrodontomys* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. QUERÉTARO: Amealco de Bonfil, 17 km N of Amealco: *Peromyscus levipes* (recorded as *P. boylii levipes*). 9 km N of Amealco Highway: *Baiomys taylori*. Cadereyta de Montes, 1 km SE of Chavarría: *P. difficilis*. El Pemoche: *Handleyomys chapmani* (recorded as *Oryzomys chapmani*), *Reithrodonomys mexicanus*. 1 km S of Pinal de Amoles: *R. sumichrasti* (Acosta 2003; Acosta *et al.* 2008). Specimens in collections: MZFC. SAN LUIS POTOSÍ: 11 km SE of Santa Maria del Río: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. TLAXCALA: Calpulalpan: *Peromyscus difficilis* (Barrera 1953). Specimens in collections: MZFC. La Malinche: *Neotoma mexicana, Neotomodon alstoni*, *P. difficilis, P. gratus, P. levipes, P. melanotis* (Aguilar-Montiel *et al.* 2018). Tlaxco, Predio Hermanos Cabrera; Hueyotlipan, 2 km E of San Andres Cuajimalpa: *Peromycus* sp. El Carmen Tequexquitla, El Piñonal; El Carmen Tequexquitla, El Piñonal: *P. difficilis*. Ixtenco, La

Malinche (Caseta #5): *N. alstoni*. Huamantla, La Malinche (Caseta #4): *N. alstoni* (recorded as *Peromyscus alstoni*), *P. gratus, Reithrodontomys chrysopsis, R. megalotis*. Españita, 3 km NW of Vicente Guerrero: *R. megalotis, Reithrodontomys* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. VERACRUZ: Xico, Texolo: *Peromyscus mexicanus* (Acosta *et al.* 2008). Specimens in collections: MZFC.

Plusaetis equatoris (Jordan, 1933)

CIUDAD DE MÉXICO: El Guarda: *Neotomodon alstoni* (Barrera 1953). Specimens in collections: IBUNAM. La Venta: *Peromyscus maniculatus, P. truei* (recorded as *P. truei gratus*). El Zarco: *P. maniculatus* (Barrera 1953). Specimens in collections: MZFC. ESTADO DE MÉXICO: Slopes of Volcán Popocatépetl: *Peromyscus maniculatus* (Barrera 1953). Specimens in collections: MZFC.

Plusaetis mathesoni (Traub, 1950)

CHIAPAS: Puebla Nuevo: *Neotoma mexicana* (Hubbard 1958). Specimens in collections: Unknown, possibly BMNH. CIUDAD DE MÉXICO: Km 42 highway to Cuernavaca: *Peromyscus hylocetes*. La Venta: *P. gratus* (recorded as *P. truei gratus*), *P. hylocetes*, *P. maniculatus*. 5 km SW of Parres: *Neotomodon alstoni* (Ayala-Barajas *et al.* 1988). Cuajimalpa de Morelos, El Pantano, Parque Nacional Desierto de los Leones: *P. maniculatus*. Parte del Sendero Turístico, Parque Nacional Desierto de los Leones: *P. difficilis*. 1 km del Potrillo, Parque Nacional Desierto de los Leones: *N. alstoni* (recorded as *Peromyscus alstoni*), *P. difficilis, Peromyscus* sp. Sabandijas, Parque Nacional Desierto de los Leones: *R. chrysopsis* (Acosta *et al.* 2008). Specimens in collections: MZFC. El Zarco: *Microtus mexicanus, Peromyscus hylocetes, P. maniculatus, Peromyscus* sp., *Reithrodontomys* sp. (Machado-A. 1960; Ayala-Barajas *et al.* 1988). Parque Nacional Insurgente Miguel Hidalgo y Costilla: *M. mexicanus, P. maniculatus*, *R. megalotis* (Méndez-L. 1974). Unknown if specimens are in collections. ESTADO DE MÉXICO: Popocatépetl: *Microtus mexicanus, Neotomodon alstoni, Peromyscus difficilis, P. maniculatus, P. melanotis, Peromyscus* sp., *Reithrodontomys chrysopsis*, *R. megalotis* (Barrera 1968; Ayala-Barajas *et al.* 1988). Lagunas de Zempoala, Ojotongo; Nevado de Toluca, 4 mi S of Raíces; San Cayetano; 4 km W of Río Frío: *Reithrodontomys* sp. Popocatépetl, Paraje Diego de Ordaz: *N. alstoni, P. maniculatus, Reithrodontomys* sp. Popocatépetl, Paraje Providencial: *P. maniculatus, R. chrysopsis*. Popocatépetl, San Pedro Nexapa: *P. difficilis, Reithrodontomys* sp. Slopes of Popocatépetl: *P. hylocetes*. Monte Río Frío; 5 mi W of Río Frío: *N. alstoni* (Ayala-Barajas *et al.* 1988). Zacualpan, Zacualpan-Mamatla Highway, km 7: *P. difficilis* (Acosta *et al.* 2008). Specimens in collections: MZFC. GUERRERO: Omiltemi: *Megadontomys thomasi* (Barrera 1958). Chilpancingo de los Bravo, 3.5 km SW of Omiltemi; Chilpancingo de los Bravo, Omiltemi: *Peromyscus megalops*. Chilpancingo de los Bravo, 1 km W of Omiltemi: *Handleyomys chapmani* (recorded as *Oryzomys chapmani*), *M. thomasi*. Atoyac de Álvarez, El Molote: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. HIDALGO: El Chico: *Peromyscus maniculatus* (Barrera 1953; Ayala-Barajas *et al.* 1988). Sierra Madre Oriental: *P. maniculatus* (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC. JALISCO: Nevado de Colima: *Peromyscus melanotis* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. MICHOACÁN: Tancítaro: *Reithrodontomys chrysopsis, Peromyscus hylocetes* (Traub 1950). Specimens in collections: FMNH. MORELOS: Lagunas de Zempoala; Lagunas de Zempoala, 1 km NE of la Laguna; Km 11 of the Tres Cumbres-Zempoala Highway; Km 14 Tres Cumbres-Zempoala Highway: *Peromyscus hylocetes*. Ojo de Agua de Aclasingo: *Microtus mexicanus* (Barrera 1954a). Derrame del Chichinautzin: *P. hylocetes, Reithrodontomys chrysopsis* (Pérez-Ortiz 1976). Cuenca de "México" (sic), multiple localities above 2600 m in altitude: *R. megalotis, P. hylocetes, P. maniculatus* (Barrera 1954b). Atzompa; Zempoala: *P. hylocetes*. Derrame Chichinautzin: *P. difficilis*. 9 km N of Tres Marias: *Neotomodon alstoni* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. OAXACA: Ixtlán de Juárez, 1.5 km SE of Santa María Yavesía: *Peromyscus aztecus*. Ixtlán de Juárez, 2.5 km SE of Santa María Yavesía: *P. aztecus, P. gratus* (recorded as *P. truei*), *P. mexicanus*. Ixtlán de Juárez, 4 km SE of Santa María Yavesía: *P. aztecus, P. mexicanus*. Ixtlán de Juárez, 4.5 km SE of Santa María Yavesía: *P. mexicanus, Reithrodontomys mexicanus*. Ixtlán de Juárez, 6.5 km E-SE of Santa María Yavesía: *P. difficilis, P. gratus* (recorded as *P. truei*). Ixtlán de Juárez, 8.75 km SE of Santa María Yavesía: *P. difficilis* (Acosta *et al.* 2008). Specimens in collections: MZFC. PUEBLA: La Esperanza: *Peromyscus* sp. (Acosta *et al.* 2008). 1 km S Santa Cruz Coyotepec, Mpio. de San Salvador El Seco: *Peromyscus difficilis* (Falcón-Ordaz *et al.* 2012). Specimens in collections: MZFC. QUERÉTARO: 6.24 km W of Amealco: *Peromyscus levipes*. 9 km N of Amealco Highway; Peñamiller; Amealco de Bonfil, Amealco-La Estancia Highway, km 9: *P. difficilis, Peromyscus* sp. Peñamiller: *Sigmodon* sp. 1 km S of Pinal de Amoles: *P. difficilis, P. levipes* (recorded as *P. levipes* and *P. boylii levipes*). 1 km SW of Pinal de Amoles: *P. levipes, Reithrodontomys megalotis*. Pinal de Amoles, 1.2 km S of Pinal de Amoles: *Neotoma mexicana, P. boylii*. Pinal de Amoles, 1 km SW of Ahuacatlán de Guadalupe: *P. levipes* (recorded as *P. boylii levipes*; Acosta 2003; Acosta *et al.* 2008). Specimens in collections: MZFC. TLAXCALA: 10 km NE of Calpulalpan: *Neotomodon* sp., *Reithrodontomys* sp. La Malinche: *Neotomodon alstoni*, *Peromyscus difficilis, P. gratus, P. leucopus, P. maniculatus, P. melanotis, Reithrodontomys fulvescens* (Ayala-Barajas *et al.* 1988; Acosta and Fernández 2006; Aguilar-Montiel *et al.* 2018). Huamantla, La Maliche (Caseta #4): *P. gratus, Peromyscus* sp. Ixtenco, La Malinche (Caseta #5); Hueyotlipan, 2 km E of San Andrés Cuajimalpa: *Peromyscus* sp. Calpulalpan, San Felipe Hidalgo, Piedra Canteada: *Neotoma mexicana*. El Carmen Tequexquitla, El Piñonal: *P. difficilis*. Sanctorum de Lázaro Cárdenas, Camino Rural Benito Juárez, La Joya: *Reithrodontomys* sp. Panotla, San Ambrosio Texantla, Barranca Huehuetitla: *Heteromys irroratus* (Acosta *et al.* 2008). Specimens in collections: MZFC. Note: *Neotomodon* sp. likely refers to *Neotomodon alstoni*, as this is the only species in the genus (*N. orizabae* and *N. perotensis* were synonymized with *N. alstoni*). VERACRUZ: Ixhuatlancillo, Rancho La Pala: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. ORIENTAL BASIN: Multiple localities in Puebla, Tlaxcala, and Veracruz: *Peromyscus difficilis, P. maniculatus, Reithrodontomys megalotis, Heteromys irroratus* (Acosta and Fernández 2015). Specimens in collections: MZFC.

Plusaetis parus (Traub, 1950)

CIUDAD DE MÉXICO: Ciudad Universitaria; Cerro Zacatepec; 1.5 km E, 300 m S of Cerro Zacatepec; 400 m N of Cerro Zacatepec; Pedregal Zacatepec; Pedregal de San Ángel; Pedregal de San Ángel, Cd. Universitaria: *Peromyscus gratus* (recorded as *P. truei gratus*); La Venta: *P. gratus* (recorded as *P. truei gratus*), *P. maniculatus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. ESTADO DE MÉXICO: Chilpa: *Peromyscus* sp., *Reithrodontomys* sp. 4.5 km E of Chiconautla; Popopark: *Peromyscus* sp. Tlalnepantla: *Reithrodontomys* sp., *Sigmodon* sp. 2 km N of Tlalnepantla: *Baiomys* sp., *Peromyscus gratus* (recorded as *P. truei*), *Heteromys* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. GUERRERO: Camotla, Leonardo Bravo: *Peromyscus gratus* (recorded as *P. truei gratus*). Omiltemi: *Oryzomys* sp., *Peromyscus* sp., *Reithrodontomys* sp. 35 km SW of Xochipala: *P. boylii*. 22 km SW of Yextla: *P. megalops* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Note: *P. boylii* is not distributed in Guerrero according to Ceballos (2014). Note: *Oryzomys* sp. was recorded in the original literature but may represent *Handleyomys* sp. HIDALGO: Arroyo Piedras Negras: *Peromyscus difficilis*, *Reithrodontomys* sp. Road between Sn. Juan Huayapam and Presa San Carlos Huasca; 10 km S of "El Blanco", Zacualtipan: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. MICHOACÁN: Tlalpujahua: *Peromyscus maniculatus*, *Reithrodontomys* sp. 3 km SW of San Francisco Tlalpujahua: *P. maniculatus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. PUEBLA: 1 km SW of Sn. Pedro Atlixco: *Peromyscus difficilis*. 1 mi NE of Alchichica: *Reithrodontomys* sp. 12 km W of Ateuco de Aljojuca, San Salvador El Seco: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). 1.5 km S Oriental, Mpio. de Oriental; 2 km W Guadalupe Victoria, Mpio. de Guadalupe Victoria: *P. difficilis* (Falcón-Ordaz *et al.* 2012). Specimens in collections: MZFC. TLAXCALA: 10 km E of Calpulalpan: *Peromyscus difficilis*. La Malinche: *Neotomodon alstoni, P. difficilis, P. leucopus, P. levipes, P. maniculatus, P. melanotis, Reithrodontomys fulvescens* (Ayala-Barajas *et al.* 1988; Acosta and Fernández 2006; Aguilar-Montiel *et al.* 2018). 2.5 km NW El Carmen Tequexquitla, Mpio. de El Carmen Tequexquitla: *P. difficilis* (Falcón-Ordaz *et al.* 2012). Specimens in collections: MZFC. SIERRA MADRE ORIENTAL: Multiple localities in Coahuila, Guanajuato, Hidalgo, Nuevo León, Puebla, Querétaro, Tamaulipas, and Veracruz: *Peromyscus maniculatus, P. difficilis, Reithrodontomys* sp., *Reithrodontomys megalotis* (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC. ORIENTAL BASIN: Multiple localities in Puebla, Tlaxcala, and Veracruz: *P. difficilis, P. levipes, P. maniculatus, Peromyscus* sp., *Reithrodontomys fulvescens, R. megalotis, Dipodomys phillipsii, Heteromys irroratus* (Acosta and Fernández 2015). Specimens in collections: MZFC. VERACRUZ: 3 km S El Frijol Colorado, Mpio. de Perote: *Peromyscus difficilis, Reithrodontomys megalotis* (Falcón-Ordaz *et al.* 2012). Specimens in collections: MZFC.

Plusaetis ponsi (Barrera, 1955)

CIUDAD DE MÉXICO: Cuajimalpa de Morelos, Cabeza del Toro, Parque Nacional Desierto de los Leones: *Peromyscus maniculatus* (Acosta *et al.* 2008). Specimens in collections: MZFC. GUERRERO: Omiltemi: *Megadontomys thomasi* (Barrera 1955b, 1958). Specimens in collections: CAIM, InDRE, MZFC, USNM. Camotla, Chihihualco: *Osgoodomys banderanus* (recorded as *Peromyscus banderanus vicinior*). 1 mi NW of Omiltemi: *Peromyscus* sp. Puerto Chico, 38 km SW of Xochipala: *M. thomasi*, *P. boylii evidens*. Agua Fría, 22 km SW of Yextla: *P. megalops* (Ayala-Barajas *et al.* 1988). Atoyac de Álvarez, Puerto del Gallo-Paraíso Highway, km 14: *M. thomasi*, *Peromyscus* sp. La Golondrina; 3.5 km E of Omiltemi: *P. megalops*. Chilpancingo de los Bravo, Omiltemi: *M. thomasi, P. levipes, P. megalops*. Omiltemi, Cañada de Agua Fría: *Handleyomys guerrerensis* (recorded as *Orzyomys chapmani guerrerensis*), *M. thomasi, P. levipes*. 2.5 km E of Omiltemi: *M. thomasi*. San Miguel Totolapan, Estación Toro Muerto: *Peromyscus* sp., *Reithrodontomys* sp. Puerto del Gallo: *M. thomasi, P. megalops*. Tlacotepec, Cerro de Teotepec: *P. boylii*. Atoyac de Álvarez, El Molote; Leonardo Bravo, Carrizal del Bravo: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. Note: *P. boylii* and *H. guerrerensis* are not distributed in Guerrero according to Ceballos (2014).

Plusaetis sibynus jordani (Barrera, 1955)

CIUDAD DE MÉXICO: El Guarda: *Peromyscus hylocetes* (Barrera 1953). La Venta: *P. gratus* (recorded as *P. truei gratus*), *P. hylocetes, P. maniculatus* (Barrera 1953). Km 42 Free México-Cuernavaca Highway: *Peromyscus hylocetes.* El Zarco, Cerro de los Tepalcates, El Zarco: *P. maniculatus.* 1 km SE El Zarco: *Peromyscus maniculatus* (Barrera 1955a). La Cima: *Peromyscus* sp. El Zarco: *P. maniculatus*, *Peromyscus* sp. La Venta: *P. gratus* (recorded as *P. truei gratus*), *P. hylocetes, P. maniculatus*. Parres: *Neotomodon alstoni*, *Peromyscus* sp. 2 km S of Parres: *Neotomodon* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Note: *Neotomodon* sp. likely refers to *Neotomodon alstoni*, as this is the only species in the genus (*N. orizabae* and *N. perotensis* were synonymized with *N. alstoni*). Parque Nacional Insurgente Miguel Hidalgo y Costilla: *Microtus mexicanus, P. maniculatus* (Méndez-L. 1974). Unknown if specimens are in collections. ESTADO DE MÉXICO: Slopes of Volcán Popocatépetl: *Peromyscus hylocetes, P. maniculatus, P. melanotis* (Barrera 1953; 1955a). Slopes of Volcán Popocatépetl: *Microtus mexicanus, Neotomodon alstoni, P. difficilis, Peromyscus* sp., *Reithrodontomys chrysopsis* (Barrera 1955a; Barrera 1968; Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Mt. Popocatépetl; Slopes of Volcán Popocatépetl: *P. maniculatus*. Volcán Popocatépetl; Popocatépetl, Otlaltepec; Popocatépetl, Paso de Cortes; Monte Río Frío; Río Frío: *Peromyscus* sp. Popocatépetl, cerca Tlamacas: *N. alstoni, Neotomodon* sp., *P. melanotis*. Popocatépetl, 300 m SW of Tlamacas; Popocatépetl, Mirador del Poeta: *P. melanotis*. Popocatépetl, Mirador de Nexpayantla: *P. melanotis, Peromyscus* sp. Popocatépetl, Paraje Diego de Ordaz: *M. mexicanus, P. maniculatus, Peromyscus* sp. Popocatépetl, San Pedro Nexapa: *P. difficilis*. Popocatépetl, Paraje Providencial; Popocatépetl, 9 km W and 1.5 km N of Xalizintla: *P. maniculatus, Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Note: *Neotomodon* sp. likely refers to *Neotomodon alstoni*, as this is the only species in the genus (*N. orizabae* and *N. perotensis* were synonymized with *N. alstoni*). HIDALGO: Arroyo Piedras Negras: *Peormyscus difficilis* (Barrera 1953). Specimens in collections: MZFC. MICHOACÁN: Monte Tancítaro: *Microtus mexicanus, Peromyscus melanotis* (Traub 1950). Specimens in collections: FMNH. MORELOS: Km 42 highway to Cuernavaca: *Peromyscus hylocetes* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. VERACRUZ: Cofe de Perote: *Reithrodontomys* sp. (Ayala-Barajas *et al.* 1988). Sierra Madre Oriental: *Reithrodontomys* sp. (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC.

Plusaetis sibynus (Jordan, 1925)

CHIHUAHUA: Rancho La Cruz Guachochic-Batopilas: *Peromyscus maniculatus* (Barrera 1955a). Rancho La Cruz, 30 km SW of Guachochic: *Peromyscus maniculatus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. CIUDAD DE MÉXICO: La Cima: *Peromyscus* sp. La Venta: *P. gratus* (recorded as *P. truei gratus*), *P. hylocetes*, *P. maniculatus*. Parres: *Peromyscus* sp., *Neotomodon alstoni*. 2 km S of Parres: *Neotomodon* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Note: *Neotomodon* sp. likely refers to *Neotomodon alstoni*, as this is the only species in the genus (*N. orizabae* and *N. perotensis* were synonymized with *N. alstoni*). DURANGO: 8 km W of El Salto: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. GUERRERO: General Heliodoro Castillo, El Iris: *Megadontomys thomasi*. San Miguel Totolapan, Puerto del Gallo: *Peromyscus boylii* (Acosta *et al.* 2008). Specimens in collections: MZFC. Note: *P. boylii* is not distributed in Guerrero according to Ceballos (2014). JALISCO: Nevado de Colima: *Peromyscus melanotis* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. MICHOACÁN: Monte Tancítaro: *Peromyscus melanotis* (Jordan 1925). Unknown if specimens are in collections. MORELOS: km 42 highway to Cuernavaca: *Peromyscus hylocetes* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. NUEVO LEÓN: Ojo de Agua, Galena, and Cerro Potosí: *Microtus* sp., *Peromyscus* sp. (Fox 1939; Traub 1950). Cerro Potosí: *Microtus mexicanus, Microtus* sp., *Neotoma leucodon* (recorded as *N. albigula*), *Peromyscus difficilis, P. melanotis, Peromyscus* sp., *Reithrodontomys fulvescens* (Traub 1950; Tipton and Mendez 1968). Unknown if specimens are in collections. Notes: Additional records reported in Tipton and Mendez (1968). QUERÉTARO: 6.24 km W of Amealco; 1 km S of Pinal de Amoles: *Peromyscus levipes*. Camargo, Maguey Verde: *P. difficilis* (Acosta 2003). Landa de Matamoros, El Pemoche: *Handleyomys chapmani* (recorded as *Oryzomys chapmani huastecae*), *Reithrodontomys mexicanus*. Pinal de Amoles, 1.2 km S of Pinal de Amoles: *Netoma mexicana*, *P. boylii* (Acosta *et al.* 2008). Specimens in collections: MZFC. TLAXCALA: La Malinche: *Neotomodon alstoni*, *Peromyscus difficilis, P. gratus, P. leucopus, P. maniculatus, P. melanotis, Reithrodontomys fulvescens* (Aguilar-Montiel *et al.* 2018). Españita, 3 km NW of Vicente Guerrero: *P. gratus*. Huamantla, La Malinche (Caseta #4): *N. alstoni* (recorded as *Peromyscus alstoni*), *P. gratus, P. melanotis* (Acosta *et al.* 2008). Specimens in collections: MZFC. VERACRUZ: Cofre de Perote: *Reithrodontomys* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC.

Plusaetis soberoni (Barrera, 1958)

GUERRERO: Omiltemi: *Peromyscus* sp. (Barrera 1958). Atoyac de Ávarez, Puerto del Galo-Paraíso Highway, km 14: *Heteromys pictus*. General Heliodoro Castillo, El Iris: *Handleyomys alfaroi* (recorded as *Oryzomys alfaroi*), *Megadontomys thomasi, Oryzomys* sp. Chilpancingo de los Bravo, Omiltemi: *M. thomasi, Peromyscus levipes, P. maniculatus*, *Peromyscus* sp. 0.3 km N of Omiltemi: *P. maniculatus*. 2.5 km E of Omiltemi: *M. thomasi*. Cañada de Agua Fría: *P. boylii*. Omiltemi, Cañada Potrerillos: *P. megalops* (Acosta *et al.* 2008). Agua Fría, Yextla, 22 km SW: *P. megalops*. Camotla, Chichihualco: *Osgoodomys banderanus* (recorded as *Peromyscus banderanus vicinior*). 1 mi SW of Omiltemi, *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Note: *P. boylii* is not distributed in Guerrero according to Ceballos (2014). Note: *Oryzomys* sp. was recorded in the original literature but may represent *Handleyomys* sp. OAXACA: San Juan Lachao, 10 km S of San Juan Lachao: *Oryzomys* sp. (Ayala-Barajas *et al.* 1988). Ixtlán de Juárez, 1.5 km SE of Santa María Yavesía: *Oligoryzomys fulvescens*. Ixtlán de Juárez, 4.5 km SE of Santa María Yavesía, *Peromyscus mexicanus*. Ixtlán de Juárez, 8.76 km SE of Santa María Yavesía: *P. difficilis*. Ixtlán de Juárez, 6.5 km E-SE of Santa María Yavesía, *P. aztecus, P. difficilis, P. melanocarpus, P. mexicanus* (Acosta *et al.* 2008). Specimens in collections: MZFC. Note: *Oryzomys* sp. was recorded in the original literature but may represent *Handleyomys* sp.

Plusaetis sp.

CIUDAD DE MÉXICO: Cuajimalpa de Morelos, 1 km del Potrillo, Parque Nacional Desierto de los Leones: *Peromyscus difficilis*. El Pantano, Parque Nacional Desierto de los Leones: *P. maniculatus* (Acosta *et al.* 2008). Specimens in collections: MZFC. GUERRERO: San Miguel Totolopan, Puerto del Gallo: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. OAXACA: Ixtlán de Juárez, 4.5 km SE of Santa María Yavesía: *Peromyscus mexicanus*. Ixtlán de Juárez, 6.5 km E-SE of Santa María Yavesía; Ixtlán de Juárez, 8.75 km SE of Santa María Yavesía: *P. difficilis* (Acosta *et al.* 2008). Specimens in collections: MZFC. QUERÉTARO: Peñamiller, Camargo; Peñamiller, Maguey Verde: *Peromyscus difficilis*. Pinal de Amoles, 1.2 km S of Pinal de Amoles: *P. boylii* (Acosta *et al.* 2008). Specimens in collections: MZFC. VERACRUZ: Ixhuatlancillo, Rancho La Pala: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. TLAXCALA: Españita, 3 km NW of Vicente Guerrero: *Reithrodontomys megalotis, Reithrodontomys* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC.

Thrassis aridis Prince, 1944

CHIHUAHUA: Janos Biosphere Reserve: *Onychomys leucogaster, Dipodomys spectabilis* (Fernández-González *et al.* 2016). No specimens in collections. 35 mi S Ciudad Juárez: *Onychomys leucogaster* (Traub and Hoff 1951). Unknown if specimens are in collections. DURANGO: Hidalgo, 4 km S-SE of la Zarca: *Dipodomys nelsoni* (Fernández and Acosta 2005; Acosta *et al.* 2008). Specimens in collections: MZFC. Note: Acosta *et al.* (2008) lists this species as *Thrassis aridis campestris*.

Thrassis bacchi (Rothschild, 1905)

CHIHUAHUA: 35 mi S of Ciudad Juárez: *Onychomys leucogaster* (Traub and Hoff 1951). Unknown if specimens are in collections. Note: Stark (1970) reports additional records from Chihuahua and Guerrero.

Thrassis fotus (Jordan, 1925)

TLAXCALA: Calpulalpan: *Peromyscus difficilis* (Barrera 1953). 5 mi E of Calpulalpan: *P. difficilis* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Note: Stark (1970) reports additional records from Chihuahua, Tamaulipas, and Tlaxcala.

Dactylopsyllinae Jordan, 1929

Foxella ignota (Baker, 1895)

NUEVO LEÓN: Cerro Potosí: *Peromyscus melanotis* (Tipton and Mendez 1968). Unknown if specimens are in collections. SAN LUIS POTOSÍ: El Salto: *Sigmodon hispidus* (Hubbard 1958). Specimens in collections: BMNH. Note: *S. hispidus* is not distributed in San Luis Potosí according to Ceballos (2014). A possible alternative host includes *S. leucotis* (Ceballos 2014). Note: Hubbard (1958) also describes this association as likely accidental as *Foxella* normally parasitizes pocket gophers.

Ctenophthalmidae Rothschild, 1915

Anomiopsyllinae Baker, 1905

Anomiopsyllus durangoensis Holland, 1965

DURANGO: 8 km W Durango: *Peromyscus* sp. nest (Holland 1965). Specimens in collections: CNC. NUEVO LEÓN: Cerro Potosí: *Neotoma leucodon* (recorded as *N. albigula*; Holland 1965). Specimens in collections: CNC.

Anomiopsyllus nidiophilus Tipton and Méndez, 1968

DURANGO: 8 km W of Durango: *Peromyscus* sp. (Tipton and Mendez 1968). Specimens in collections: CNC. NUEVO LEÓN: Cerro Potosí: *Neotoma leucodon* (recorded as *N. albigula leucodon*; Tipton and Mendez 1968). Specimens in collections: BMNH, BYU, CNC, MZFC, USNM (with additional specimens at the Bishop Museum, GML, and RML).

Anomiopsyllus novomexicanensis Williams and Hoff, 1951

TLAXCALA: El Carmen Tequexquitla, El Piñonal: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC.

Anomiopsyllus nudatus hiemalis Eads and Menzies, 1948

COAHUILA: Sabinas: *Neotoma micropus, Neotoma* sp. nest (Vargas 1951e; Barnes *et al.* 1977; Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC.

Anomiopsyllus nudatus mexicanus Holland, 1965

CHIHUAHUA: Mesa del Huracán: *Neotoma* sp. nest (Holland 1965). Specimens in collections: CNC.

Anomiopsyllus oaxacae Barnes, 1965

OAXACA: 2 mi SE of Matatlán: *Baiomys musculus* (Barnes 1965). Specimens in collections: USNM.

Anomiopsyllus perotensis Acosta and Fernández, 2009

PUEBLA: Multiple localities: *Peromyscus difficilis, Dipodomys phillipsii* (Acosta and Fernández 2015). Specimens in collections: MZFC. VERACRUZ: near El Frijol Colorado, Mpio. of Perote: *Neotoma nelsoni* (Acosta and Fernández 2009). Specimens in collections: MZFC.

Anomiopsyllus sinuatus Holland, 1965

DURANGO: 48 km W of Durango: *Peromyscus* sp. nest (Holland 1965). Specimens in collections: CNC. 30 mi W of Durango: *Peromyscus* sp. nest (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. HIDALGO: Xoxafí: *Peromyscus difficilis* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. PUEBLA: Multiple localities: *Peromyscus difficilis* (Acosta and Fernández 2015). Specimens in collections: MZFC. VERACRUZ: Perote, 3 km S of El Frijol Colorado: *Peromyscus difficilis* (Acosta and Fernández 2015). Specimens in collections: MZFC.

Anomiopsyllus sp.

CHIHUAHUA: Vado de Fusiles: *Peromyscus manicula-*

tus (Traub and Hoff 1951). Specimens are in collections: Unknown, possibly AMNH. CIUDAD DE MÉXICO: San Ángel: *Neotoma* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. GUERRERO: Camotla, Mpio. de Chichihualco: *Osgoodomys banderanus* (recorded as *Peromyscus banderanus vicinior*; Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC.

Conorhinopsylla sp.

ESTADO DE MÉXICO: Popocatépetl: *Neotoma mexicana* (Barrera 1968). Popocatépetl, Mirador del Poeta: *N. mexicana* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC.

Stenistomera alpina (Baker, 1895)

VERACRUZ: Near El Frijol Colorado, Mpio. of Perote: *Neotoma nelsoni* (Acosta and Fernández 2009). Specimens in collections: MZFC.

Ctenophthalminae Rothschild, 1915

Ctenophthalmus (Alloctenus) caballeroi Barrera and Machado, 1960

CIUDAD DE MÉXICO: Cerro de la Marquesa; El Zarco: *Microtus mexicanus* (Barrera and Machado 1960). El Zarco: *Microtus* sp. nest (Morrone *et al.* 2000). Specimens in collections: IBUNAM. Popocatépetl: *M. mexicanus, Peromyscus difficilis, Reithrodontomys* sp. (Barrera 1968; Morrone *et al.* 2000). Specimens in collections: MZFC. ESTADO DE MÉXICO: Salazar: *Microtus mexicanus* (Machado-A. 1960). Specimens in collections: MZFC. Popocatépetl: *M. mexicanus, Peromyscus difficilis, Reithrodontomys chrysopsis, Reithrodontomys* sp. (Barrera 1968; Morrone *et al.* 2000). Specimens in collections: MZFC.

Ctenophthalmus (Alloctenus) expansus Traub, 1950

MICHOACÁN: Monte Tancítaro: *Reithrodonomys chrysopsis* (Traub 1950). Specimens in collections: FMNH.

Ctenophthalmus (Alloctenus) haagi Traub, 1950

COLIMA: *Microtus* sp. (Morrone *et al.* 2000). Specimens in collections: MZFC. CIUDAD DE MÉXICO: San Juan de Aragón: *Microtus mexicanus* (Barrera 1953). El Zarco: *Microtus* sp. nest, *M. mexicanus* (Barrera 1953; Hopkins and Rothschild 1966; Ayala-Barajas *et al.* 1988). Bosque de Chapultepec: *M. mexicanus* (Morrone *et al.* 2000). Churubusco: *M. mexicanus, Microtus* sp. Bosque de Chapultepec; San Andrés Tetepilco: *M. mexicanus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. DURANGO: 10 mi W of El Salto: *Microtus mexicanus* (Morrone *et al.* 2000). Specimens in collections: MZFC. ESTADO DE MÉXICO: Slopes of Volcano Popocatépetl: *Peromyscus melanotis, Microtus mexicanus* (Barrera 1953, Ayala-Barajas *et al.* 1988). Popocatépetl: *M. mexicanus*. (Ayala-Barajas *et al.* 1988). La Marquesa: *M. mexicanus* (Morrone *et al.* 2000). Specimens in collections: MZFC. Guerrero: Agua Fría, 22 km SW of Yextla; 1 mi SW of Omiltemi: *Peromyscus* sp. (Morrone *et al.* 2000). Specimens in collections: MZFC. Hidalgo: Singuilucan: *Microtus mexicanus* (Ayala-Barajas *et al.* 1988; Morrone *et al.* 2000). Sierra Madre Oriental: *M. mexicanus* (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC. JALISCO: Nevado de Colima: *Microtus mexicanus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. MICHOACÁN: Tancítaro, Mt. Tancítaro: *Microtus mexicanus, Microtus* sp., *Peromyscus* sp. (Traub 1950; Hopkins and Rothschild 1966; Morrone *et al.* 2000). Specimens in collections: BMNH (BMNH 1942.29), FMNH, NMNH. MORELOS: Atzompa: *Peromyscus hylocetes*. Cuautepetl-Huitzilac; Huitzilac; Lagunas de Zempoala: *Microtus mexicanus* (Ayala-Barajas *et al.* 1988). Mpio. de Huitzilac, Ojo de Agua de Oclatzingo: *Microtus mexicanus* (Barrera 1954a). Specimens in collections: MZFC. OAXACA: San Juan Atepec, Tuxtepec-Oaxaca Highway, km 91, road to San Isidro: *Megadontomys thomasi, Microtus oaxacensis, Handleyomys chapmani* (recorded as *Oryzomys chapmani*), *Oryzomys* sp., *Peromyscus melanocarpus, P. mexicanus, Peromyscus* sp. Santiago Comaltepec, El Suspiro, km 87, Tuxtepec-Oaxaca Highway: *M. thomasi, H. alfaroi* (recorded as *O. alfaroi*), *H. chapmani* (recorded as *O. chapmani*), *Oryzomys* sp. *P. melanocarpus, Peromyscus* sp. (Morrone *et al.* 2000). Ixtlán de Juárez, 4 km SE of Santa María Yavesía: *Microtus* sp. Ixtlán de Juárez, 6.5 km E-SE of Santa María Yavesía: *Microtus mexicanus, Orzomys* sp., *Peromyscus difficilis, P. melanocarpus, P. mexicanus.* Ixtlán de Juárez, 8.75 km SE of Santa María Yavesía: *P. difficilis.* Santiago Comaltepec, Tuxtepec-Oaxaca Highway, km 79.5, La Esperanza: *H. alfaroi* (recorded as *O. alfaroi*; Acosta *et al.* 2008). Specimens in collections: MZFC. Note: *M. thomasi* is not distributed in Oaxaca according to Ceballos (2014). These specimens are likely *M. cryophilus* or *M. nelsoni*. Note: *Oryzomys* sp. was recorded in the original literature but may represent *Handleyomys* sp.

Ctenophthalmus (Alloctenus) micropus Traub, 1950

COAHUILA: Sabinas: *Neotoma micropus* (Traub 1950). Specimens in collections: USNM. CIUDAD DE MÉXICO: El Zarco; Bosque de Chapultepec; Río de Churubusco; Las Cruces; Las Pilas; San Cayetano México: *Microtus mexicanus* (Machado-A. 1960; Sandoval *et al.* 1962). Specimens in collections: MZFC. Parque Nacional Insurgente Miguel Hidalgo y Costilla: *M. mexicanus, Peromyscus mexicanus, Reithrodontomys megalotis* (Méndez-L. 1974). Unknown if specimens are in collections. Churubusco: *M. mexicanus* (Ayala-Barajas *et al.* 1988; Morrone *et al.* 2000). Iztaccíhuatl: *M. mexicanus* (Morrone *et al.* 2000). Specimens in collections: MZFC. Note: *P. mexicanus* is not distributed in Ciudad de México according to Ceballos (2014). DURANGO: 10 mi W of El Salto: *Microtus* sp. nest (Morrone *et al.* 2000). Specimens in collections: MZFC. ESTADO DE MÉXICO: Popocatépetl: *Microtus mexicanus, Reithrodontomys chrysopsis* (Barrera 1968). Iztaccíhuatl: *M. mexicanus* (Morrone *et al.* 2000). Mt.

Iztaccíhuatl; Vert. Occidental: *M. mexicanus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. HIDALGO: Tlanchinol: *Peromyscus furvus* (Salceda-Sánchez and Hastriter 2006). Specimens in collections: CAIM, InDRE. Sierra Madre Oriental: *P. furvus* (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC. MICHOACÁN: 12 mi W of Hidalgo: *Microtus mexicanus* (Morrone *et al.* 2000). Specimens in collections: NMNH. MORELOS: Derrame del Chichinautzin: *Peromyscus difficilis* (Pérez-Ortiz 1976; Ayala-Barajas *et al.* 1988). Chichinautzin: *P. difficilis* (Morrone *et al.* 2000). Specimens in collections: MZFC. OAXACA: Ixtlán de Juárez, 6.5 km E-SE of Santa María Yavesía: *Microtus mexicanus* (Acosta *et al.* 2008). Specimens in collections: MZFC. PUEBLA: San Juan Tetla, Mpio. de Chiautzingo: *Microtus mexicanus, Neotomodon alstoni, Peromyscus melanotis* (Ramírez 1982). Unknown if specimens are in collections. QUERÉTARO: 2.5 km NW of Santa Inés; 1 km SW of Pinal de Amoles; Santa Inés; 2.8 km NW of Santa Inés: *Peromyscus furvus*. 1 km NW of Santa Inés: *P. levipes* (recorded as *P. boylii levipes*; Morrone *et al.* 2000; Acosta 2003). Specimens in collections: MZFC. ORIENTAL BASIN: Multiple localities in Puebla, Tlaxcala, and Veracruz: *Peromyscus furvus* (Acosta and Fernández 2015). Specimens in collections: MZFC. Note: *P. furvus* is not distributed in Tlaxcala according to Ceballos (2014).

Ctenophthalmus (Alloctenus) pseudagyrtes Baker, 1904

GUERRERO: General Heliodoro Castillo, El Iris: *Peromyscus megalops*. San Miguel Totolapan, Puerto del Gallo: *Megadontomys thomasi*, *P. megalops*. Leonardo Bravo, Carrizal del Bravo: *Peromyscus* sp. (Acosta *et al.* 2008). *Specimens in collections*: MZFC. NUEVO LEÓN: Cerro Potosí: *Microtus mexicanus, Peromyscus difficilis, P. melanotis, Peromyscus* sp. (Tipton and Mendez 1968; Morrone *et al.* 2000). Specimens in collections: NMNH. OAXACA: Ixtlán de Juárez, 4 km SE of Santa María Yavesía: *Mictrotus mexicanus, Microtus* sp. Ixtlán de Juárez, 6.5 km E-SE of Santa María Yavesía: *Peromyscus melanocarpus* (Acosta *et al.* 2008). Specimens in collections: MZFC. QUERÉTARO: El Pemoche; 2.8 km NW of Santa Inés: *Peromyscus furvus*. 1 km NW of Santa Inés: *P. levipes* (Acosta 2003). Landa de Matamoros, El Pemoche: *P. furvus* (Acosta *et al.* 2008). Specimens in collections: MZFC. Veracruz: El Cedeño, Xalapa; 1/2 mi NE of Las Minas, approximately 16 mi NE of Perote: *Peromyscus* sp. (Morrone *et al.* 2000). Specimens in collections: MZFC. SIERRA MADRE ORIENTAL: Multiple localities in Hidalgo, Querétaro, Tamaulipas: *Peromyscus furvus, P. levipes* (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC. Note: *P. furvus* is not distributed in Tamaulipas according to Ceballos (2014).

Ctenophthalmus (Alloctenus) tecpin Morrone, Acosta, and Gutiérrez, 2000

GUERRERO: Atoyac de Álvarez, 3 km S of Puerto del Gallo; Chilpancingo de los Bravo, Omiltemi, Cañada de Agua Fría: *Megadontomys thomasi*. Chilpancingo de los Bravo, 2.5 km E of Omiltemi: *Peromyscus megalops.* Chilpancingo de los Bravo, 4 km N of Omiltemi: *M. thomasi*, *P. levipes*. San Miguel Totolapan, Estación Toro Muerto: *Peromyscus* sp. San Miguel Totolapan, Puerto del Gallo: *M. thomasi, Oryzomys* sp., *P. boylii, P. megalops, Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. Note: *P. boylii is* not distributed in Guerrero according to Ceballos (2014). Note: *Oryzomys* sp. was recorded in the original literature but may represent *Handleyomys* sp. HIDALGO: Tlanchinol: *Peromyscus furvus, Handleyomys rostratus* (recorded as *Oryzomys melanotis rostratus*; Salceda-Sánchez and Hastriter 2006). Specimens in collections: CAIM, InDRE. Tenango de Doria, El Potrero: *P. furvus* (Acosta *et al.* 2008). Specimens in collections: MZFC. NUEVO LEÓN: El Potosí: *Microtus* sp., *Peromyscus difficilis* (Morrone *et al.* 2000; Salceda-Sánchez and Hastriter 2006). Specimens in collections: CAIM, InDRE, MZFC. OAXACA: Ixtlán de Juárez, 6.5 km E-SE of Santa María; Ixtlán de Juárez, 8.75 km SE of Santa María Yavesía: *Peromyscus difficilis* (Acosta *et al.* 2008). Specimens in collections: MZFC. QUERÉTARO: El Pemoche, Landa de Matamoros: *Handleyomys chapmani* (recorded as *Oryzomys chapmani*), *Peromyscus furvus* (Acosta 2003; Acosta *et al.* 2008). Specimens in collections: MZFC. TLAXCALA: Huamantla, La Malinche: *Microtus mexicanus, Neotomodon alstoni*, *Peromyscus difficilis, P. gratus*, *P. maniculatus, Reithrodontomys chrysopsis, R. megalotis, Heteromys irroratus* (Acosta and Fernández 2006; Acosta *et al.* 2008; Aguilar-Montiel *et al.* 2018). Specimens in collections: MZFC. VERACRUZ: Ixhuatlancillo, Rancho La Pala: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC.

Ctenophthalmus sp.

ESTADO DE MÉXICO: La Marquesa: *Microtus mexicanus*. Río Frío: *Peromyscus* sp. Popocatépetl, S. Pedro Tlanixco (Nexapa): *Reithrodontomys* sp. nest. Popocatépetl, San Pedro Nexapa: *Peromyscus difficilis, Reithrodontomys* sp. Popocatépetl, 5 km E of San Pedro Nexapa; Popocatépetl, Mirador del Poeta: *M. mexicanus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. DURANGO: 10 mi W of El Salto: *Microtus mexicanus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. GUERRERO: Agua Fría, 22 km SW of Yextla; Omiltemi; 1 m SW of Omiltemi: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. NUEVO LEÓN: El Potosí: *Microtus* sp. El Potosí, 18 km N of Galeana: *Peromyscus difficilis* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. OAXACA: Ixtlán de Juárez, 6.5 km E-SE of Santa María: *Peromyscus melanocarpus, P. gratus* (recorded as *P. truei*). Ixtlán de Juárez, 8.75 km SE of Santa María Yavesía: *P. difficilis* (Acosta *et al.* 2008). Specimens in collections: MZFC. VERACRUZ: El Cedeño, Jalapa; ½ mi NE of Las Minas; ½ mi NE of Las Minas, aprox. 16 mi NE Perote: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). *Specimens in collections*: MZFC. SIERRA MADRE ORIENTAL: Multiple localities in Hidalgo, Nuevo León, Puebla, Querétaro, and Veracruz: *Peromyscus difficilis, Peromyscus* sp. (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC.

Neopsyllinae Oudemans, 1909

Catallagia sp.

ESTADO DE MÉXICO: Popocatépetl: *Microtus mexicanus* (Barrera 1968). Specimens in collections: MZFC.

Epitedia wenmanni (Rothschild, 1904)

NUEVO LEÓN: Cerro Potosí: *Peromyscus melanotis, P. difficilis, Peromyscus* sp., *Microtus mexicanus* (Tipton and Mendez 1968). Unknown if specimens are in collections. El Potosí: *P. maniculatus*. El Potosí, 18 km N of Galeana: *P. difficilis, P. maniculatus* (Ayala-Barajas *et al.* 1988). Sierra Madre Oriental: *P. maniculatus* (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC.

Epitedia sp.

OAXACA: Ixtlán de Juárez, 4.5 km SE of Santa María Yavesía: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC.

Meringis altipecten Traub and Hoff, 1951

CHIHUAHUA: Janos Biosphere Reserve: *Onychomys arenicola, O. leucogaster, Peromyscus maniculatus, Dipodomys merriami*, *D. spectabilis* (Fernández-González *et al.* 2016). No specimens in collections. Vado de Fusiles: *D. merriami* (Traub and Hoff 1951). Specimens in collections: AMNH. DURANGO: Hidalgo, 4 km S-SE of la Zarca: *Onychomys torridus* (Acosta *et al.* 2006; 2008). Specimens in collections: MZFC. Note: *O. torridus* is not distributed in Durango according to Ceballos (2014). HIDALGO: Xaxafi: *Dipodomys* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. PUEBLA: 2 km W of Atenco de Aljojuca: *Peromyscus maniculatus, Dipodomys phillipsii* (Barrera 1954b). 2 km W of Aljojoca: *D. phillipsi* (Ayala-Barajas *et al.* 1988). 2 km W Guadalupe Victoria, Mpio. de Guadalupe Victoria: *P. maniculatus, Heteromys irroratus* (Falcón-Ordaz *et al.* 2012). Specimens in collections: MZFC. QUERÉTARO: Tolimán, Tolimán: *Heteromys irroratus, Heteromys* sp. (Acosta 2003; Acosta *et al.* 2008). Specimens in collections: MZFC. SAN LUIS POTOSÍ: 12 km SE of Sta. Ma del Río: *Dipdomys* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. ORIENTAL BASIN: Multiple localities in Puebla, Tlaxcala, and Veracruz: *Peromyscus maniculatus, Peromyscus* sp., *Dipodomys phillipsii* (Acosta and Fernández 2015). Specimens in collections: MZFC. VERACRUZ: 3 km S El Frijol Colorado, Mpio. de Perote: *Peromyscus maniculatus, Dipodomys phillipsii* (Falcón-Ordaz *et al.* 2012). Specimens in collections: MZFC.

Meringis arachis (Jordan, 1929)

CHIHUAHUA: Janos Biosphere Reserve: *Onychomys arenicola, O. leucogaster, Dipodomys merriami, D. spectabilis* (Fernández-González *et al.* 2016). No specimens in collections. Majalca Rd. Mex: *Dipodomys* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. 1.5 mi S. of México-USA border near Columbus, New México, USA: *Dipodomys spectabilis*. Near Columbus, New México: Kangaroo rat (*Dipodomys* sp.) or *Peromyscus* sp. (Hopkins and Rothschild 1962). Specimens in collections: BMNH. DURANGO: Hidalgo, 4 km S-SE of la Zarca: *Perognathus flavus* (Acosta *et al.* 2006; 2008). *Dipodomys nelsoni* (Fernández and Acosta 2005; Acosta *et al.* 2008). Specimens in collections: MZFC. OAXACA: Ixtlán de Juárez, 8.75 km SE of Santa María Yavesía: *Peromyscus difficilis* (Acosta *et al.* 2008). *Specimens in collections*: MZFC. QUERÉTARO: Tolimán, El Derramadero: *Peromyscus pectoralis* (Acosta *et al.* 2008). Specimens in collections: MZFC.

Meringis cummingi (C. Fox, 1926)

BAJA CALIFORNIA: Rancho El Metate, S. Juan de Dios Matomi: *Dipodomys* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC.

Meringis dipodomys Kohls, 1938

SONORA: 11 km NE of Puerto Peñasco; 60 km SW of Caborca (Km 2450): *Dipodomys* sp. 12 km NE of Puerto Peñasco: *Onychomys* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC.

Meringis parkeri Jordan, 1937

CHIHUAHUA: Janos Biosphere Reserve: *Onychomys arenicola, O. leucogaster, Dipodomys merriami* (Fernández-González *et al.* 2016). No specimens in collections.

Meringis sp.

BAJA CALIFORNIA: Rancho El Metate, S. Juan de Dios Matomi: *Dipodomys* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. SAN LUIS POTOSÍ: 1 km E of Huizache: *Onychomys* sp. 5 km SW of Nuñez: *Perognathus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC.

Phalacropsylla nivalis Barrera and Traub, 1967

ESTADO DE MÉXICO: Popocatépetl, 300 m SW of volcán Tlamaca: *Neotoma mexicana* (Acosta and Hastriter 2017). Mirador del Poeta, north slope of Popocatépetl: *N. mexicana, Peromyscus melanotis*; 9 km W Río Frío: *N. mexicana* (Barrera and Traub 1967). Río Frío: *N. mexicana*. Popocatépetl, Mirador del Poeta: *P. melanotis* (Ayala-Barajas *et al.* 1988; Acosta and Hastriter 2017). Specimens in collections: MZFC.

Strepsylla davisae Traub and Johnson, 1952

DURANGO: 5 mi W of El Salto: *Peromyscus* sp. (Traub and Johnson 1952c). Specimens in collections: AMNH. 11.2 km NE of Revolcaderos: *Peromyscus* sp. (Acosta 2011). Specimens in collections: CMNH, USNM. OAXACA: Ixtlán de

Juárez, 8.75 km SE of Santa María Yavesía: *Peromyscus difficilis* (Acosta *et al.* 2008). Specimens in collections: MZFC.

Strepsylla fautini Traub, 1950

MICHOACÁN: Tancítaro: *Peromyscus hylocetes* (Traub 1950). Mount Tancítaro: *P. hylocetes* (Acosta 2011). Specimens in collections: FMNH.

Strepsylla ixtlanensis Acosta, 2010

OAXACA: Ixtlán, 8.75 km SE of Santa María Yavesia: *Peromyscus difficilis* (Acosta 2011). Specimens in collections: MZFC.

Strepsylla longicauda Acosta, 2010

DURANGO: 804 m SE of Buenos Aires: *Peromyscus* sp. (Acosta 2011). Specimens in collections: CMNH.

Strepsylla machadoi Barrera and Traub, 1963

GUERRERO: Puerto Chico, Mpio. De Leonardo Bravo, Omiltemi: *Peromyscus* sp. (Barrera and Traub 1963). Ojo de Agua de Puerto Chico, Mpio. de Chichihualco: *Osgoodomys banderanus* (recorded as *Peromyscus banderanus*). Agua Fría, 22 km SW of Yextla; 5 mi SW of Omiltemi: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Chilpancingo de los Bravo, 4 km N of Omiltemi: *P. megalops, Peromyscus* sp. Chilpancingo de los Bravo, Omiltemi, Cañada de Agua Fría: *Megadontomys thomasi*. General Heliodoro Castillo, El Iris: *P. megalops.* San Miguel Totolapan, Estación Toro Muerto; Leonardo Bravo, Carrizal del Bravo: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. Chichihualco, Puerto Chico, Camotla: *Osgoodomys banderanus*. Los Retrocesos: *Handleyomys alfaroi* (recorded as *Orzyomys alfaroi*). Toro Muerto, San Miguel Totolapan; Leonardo Bravo, Carrizal de Bravo; km 18, Puerto del Gallo – El Paraíso Highway, La Golondrina; Nueva Delhi; 1.6 km SW of Omiltemi; Agua Fria, 22 km SW of Yextla: *Peromyscus* sp. Km 14 Puerto del Gallo – El Paraíso Highway; Chilpancingo, Omiltemi, Cañada de agua fría: *M. thomasi*. Tlacotepec, Puerto del Gallo: *M. thomasi, P. levipes, P. megalops, Peromyscus* sp. Tlacotepec, El Iris, 7 km W of Puerto del Gallo; Chilpancingo, 4 km N of Omiltemi: *P. megalops, Peromyscus* sp. Tlacotepec, El Iris: *M. thomasi, P. megalops, Peromyscus* sp. La Golondrina: *P. megalops* (Acosta 2011). Specimens in collections: BMNH, CMNH, MZFC, USNM.

Strepsylla mina Traub, 1950

CIUDAD DE MÉXICO: El Guarda: *Neotomodon alstoni, Peromyscus hylocetes.* Slopes of volcán Popocatépetl: *P. hylocetes, P. melanotis.* El Zarco: *P. maniculatus.* La Venta: *P. gratus* (recorded as *P. truei*), *P. hylocetes* (Barrera 1953). El Zarco: *P. hylocetes, P. maniculatus.* La Venta: *P. gratus* (recorded as *P. truei*), *P. hylocetes*. 2 km NE of Ajusco; Contreras: *Peromyscus* sp. Parres: *N. alstoni, Peromyscus* sp. Cuajimalpa de Morelos, Cabeza del Toro, Parque Nacional Desierto de los Leones: *P. maniculatus*. Cuajimalpa 1 km del Paraje Cruz Blanca, on firebreaks, Parque Nacional Desierto de los Leones: *P. difficilis* (Ayala-Barajas *et al.* 1988; Acosta *et al.* 2008; Acosta 2011). Specimens in collections: MZFC. Parque Nacional Insurgente Miguel Hidalgo y Costilla: *Microtus mexicanus, P. maniculatus* (Méndez-L. 1974). Unknown if specimens are in collections. ESTADO DE MÉXICO: Popocatépetl: *Neotomodon alsonti, Peromyscus melanotis, P. difficilis, P. maniculatus, P. hylocetes, Reithrodontomys chrysopsis, R. megalotis* (Barrera 1953; 1968; Ayala-Barajas *et al.* 1988; Acosta 2011). Specimens in collections: MZFC. 5 km E of San Pedro Nexapa: *Microtus mexicanus*, *P. difficilis*, *P. maniculatus*, *Peromyscus* sp., *Reithrodontomys* sp. Popocatépetl, San Pedro Nexapa: *P. difficilis, P. maniculatus, Reithrodontomys* sp., *Reithrodontomys* sp. nest (Ayala-Barajas *et al.* 1988; Acosta 2011). Lagunas de Zempoala, near Ojotongo: *P. maniculatus, Peromyscus* sp. Lagunas de Zempoala, near Morelos; Popocatépetl, 5.5 km S of San Pedro Nexapa: *Peromyscus* sp. Lagunas de Zempoala, La Cachucha: *P. maniculatus* (Acosta 2011). Specimens in collections: CMNH, MZFC. GUERRERO: Chilpancingo de los Bravo, Omiltemi: *Peromyscus megalops* (Acosta *et al.* 2008). Specimens in collections: MZFC. HIDALGO: El Chico: *Peromyscus maniculatus* (Ayala-Barajas *et al.* 1988; Acosta 2011). Specimens in collections: MZFC. JALISCO: Nevado de Colima: *Microtus mexicanus*, *Microtus* sp., *Peromyscus* sp. (Ayala-Barajas *et al.* 1988; Acosta 2011). Nevado de Colima near la Joya: *Microtus* sp., *Peromyscus hylocetes, P. melanotis, Peromyscus* sp. Nevado de Colima, 6.4 km W of La Joya: *Microtus* sp., *P. melanotis* (Acosta 2011). Specimens in collections: CMNH, MWH, MZFC, USNM. MICHOACÁN: Tancítaro: *Microtus mexicanus, Neotomodon alstoni, Peromyscus melanotis* (Traub 1950; Hopkins and Rothschild 1962). Tancítaro, Mt. Tancítaro: *M. mexicanus, P. melanotis* (Acosta 2011). Specimens in collections: BMNH, FMNH, USNM. MORELOS: Km 42, highwayCiudad de México to Cuernavaca: *Peromyscus hylocetes* (Ayala-Barajas *et al.* 1988). Km 14, highway Tres Cumbres-Zempoala: *Peromyscus maniculatus* (Barrera 1954a). Specimens in collections: MZFC. PUEBLA: San Juan Tetla, Mpio. de Chiautzingo: *Microtus mexicanus, Peromyscus maniculatus* (Ramírez 1982). Unknown if specimens are in collections. QUERÉTARO: 1 km S of Pinal de Amoles: *Peromyscus levipes* (Acosta 2003; Acosta 2011). Specimens in collections: CMNH, MZFC. TLAXCALA: Calpulalpan: *Peromyscus difficilis* (Barrera 1953). Specimens in collections: MZFC. SIERRA MADRE ORIENTAL: Multiple localities in Hidalgo, Querétaro, Veracruz: *Peromyscus* sp. (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC.

Strepsylla queretana Acosta, 2010

QUERÉTARO: Maguey Verde: *Peromyscus difficilis* Acosta 2011). Specimens in collections: MZFC.

Strepsylla schmidti Traub and Barrera, 1955

CHIAPAS: 17 km NW of Teopisca: *Peromyscus beatae, P. boylii* (Traub and Barrera 1955; Acosta 2011). Tzontehuitz: *P. beatae* (Acosta 2011). Specimens in collections: CMNH, USNM. Note: *P. boylii* is not distributed in Chiapas according to Ceballos (2014).

Strepsylla taluna Traub and Johnson, 1952

CIUDAD DE MÉXICO: El Zarco: *Peromyscus hylocetes.* La Venta: *P. maniculatus*, *Peromyscus* sp. Parres: *Neotomodon alstoni*, *Neotomodon* sp. (Ayala-Barajas *et al.* 1988; Acosta 2011). Specimens in collections: CMNH, MZFC. 2 km SW of Parres: *Neotomodon* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Note: *Neotomodon* sp. likely refers to *Neotomodon alstoni*, as this is the only species in the genus (*N. orizabae* and *N. perotensis* were synonymized with *N. alstoni*). ESTADO DE MÉXICO: Popocatépetl: *Neotomodon alstoni, Peromyscus melanotis, Reithrodontomys chrysopsis* (Barrera 1968). 5 mi W of Río Frío: *N. alstoni*. Laguna de Zempoala, N of Ojotongo: *Neotomodon* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. 8 km W of Río Frío: *N. alstoni.* Lagunas de Zempoala near Ojotongo: *Neotomodon* sp. (Acosta 2011). Specimens in collections: BMNH, MZFC. Note: *Neotomodon* sp. likely refers to *Neotomodon alstoni*, as this is the only species in the genus (*N. orizabae* and *N. perotensis* were synonymized with *N. alstoni*). MORELOS: 2 mi N of Tres Cumbres Marías; 3 mi N of Tres Marías: *Neotomodon alstoni*, *Reithrodontomys megalotis* (Traub and Johnson 1952c). Specimens in collections: AMNH. 11 km Tres Cumbres-Zempoala Highway: *Peromyscus hylocetes* (Barrera 1954a). 1 km NE of Lagunas de Zempoala: *P. maniculatus* (Ayala-Barajas *et al.* 1988; Acosta 2011). Specimens in collections: MZFC. Lagunas de Zempoala, near Ojo de Agua: *Neotomodon* sp. (Acosta 2011). Specimens in collections: USNM. Note: *Neotomodon* sp. likely refers to *Neotomodon alstoni*, as this is the only species in the genus (*N. orizabae* and *N. perotensis* were synonymized with *N. alstoni*). Tres Marías: *N. alsonti* (Hopkins and Rothschild 1962). Specimens in collections: BMNH. QUERÉTARO: El Derramadero: *Peromyscus difficilis, P. pectoralis* (Acosta 2003). Specimens in collections: CMNH. Tolimán, El Derramadero: *P. pectoralis* (Acosta *et al.* 2008). Sierra Madre Oriental: *Peromyscus difficilis* (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC. TLAXCALA: La Malinche: *Neotomodon alstoni*, *Peromyscus difficilis, Reithrodontomys fulvescens* (Aguilar-Montiel *et al.* 2018). La Malinche: *Peromyscus* sp. (Acosta and Fernández 2006). Ixtenco, La Malinche (Caseta #5): *Peromyscus* sp. (Acosta *et al.* 2008). Altamira, La Malinche (Caseta #5): *Peromyscus* sp. (Acosta 2011). Specimens in collections: MZFC.

Strepsylla tezontli Acosta, 2010

ESTADO DE MÉXICO: Iztaccíhuatl, Veriente oriental: *Microtus mexicanus, Peromyscus melanotis*. Popocatépetl, Cerro Tlamaca: *Neotomodon alstoni, P. melanotis.* Popocatépetl; Paso de Cortez: *N. alstoni.* Otlaltepec; Nexpayantla; 1 km NE of Mirador del Poeta; Paraje Providencial; Río Frío: *Peromyscus* sp. Paraje Zumpango: *P. melanotis* (Acosta 2011). Specimens in collections: MZFC. TLAXCALA: La Malinche: *Neotomodon alstoni*, *Peromyscus difficilis*, *P. melanotis* (Aguilar-Montiel *et al.* 2018). Specimens in collections: MZFC.

Strepsylla vargasi Acosta, 2010

ESTADO DE MÉXICO: *Peromyscus* sp., *Sigmodon* sp. (Acosta 2010). Specimens in collections: IBUNAM. NUEVO LEÓN: 7.4 km S, 0.2 km W of San Josecito: *Peromyscus* sp. 5.2 km N, 0.2 km W of San Josecito: *Peromyscus* sp. (Acosta 2010, 2011). NUEVO LEÓN: *Peromyscus* sp., *Sigmodon* sp. (Acosta 2011). Specimens in collections: IBUNAM. ZACATECAS: 4.3 km N, 5.4 km E of San Juan Capistrano: *Peromyscus* sp. (Acosta 2011). Specimens in collections: IBUNAM.

Strepsylla villai Traub and Barrera, 1955

CIUDAD DE MÉXICO: Pedregal de San Angel: *Peromyscus gratus* (recorded as *Peromyscus truei gratus*; Ayala-Barajas *et al.* 1988; Acosta 2011). Cuajimalpa de Morelos, Cabeza del Toro, Parque Nacional Desierto de los Leones: *Reithrodontomys* sp. (Acosta *et al.* 2008; Acosta 2011). 2 km SW of Parres: *Neotomodon* sp. Popocatépetl, Diego de Ordaz: *P. maniculatus.* Popocatépetl, Mirador del Poeta; Popocatépetl, Tlamacas: *P. melanotis*. Popocatépetl, Paraje Providencial: *P. maniculatus, P. melanotis*. Popocatépetl, Pie del Ventorrillo: *Peromyscus* sp. (Acosta 2011). Specimens in collections: MZFC. Note: *Neotomodon* sp. likely refers to *Neotomodon alstoni*, as this is the only species in the genus (*N. orizabae* and *N. perotensis* were synonymized with *N. alstoni*). ESTADO DE MÉXICO: Río Frío; 8 km W of Río Frío: *Neotomodon alstoni* (Acosta 2011). Specimens in collections: MZFC. GUERRERO: Taxco de Alarcón, Parque Estatal El Huizteco: *Peromyscus levipes* (Acosta *et al.* 2008). Specimens in collections: MZFC. OAXACA: Ixtlán de Juárez, 8.75 km SE of Santa María Yavesía: *Peromyscus difficilis* (Acosta *et al.* 2008). Specimens in collections: MZFC. PUEBLA: 1 km SW of San Pedro Atlixco: *Peromyscus difficilis*, *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Atzitzintla, Santa Cruz Cuyachapa, Ejido Maguey Cenizo: *Peromyscus* sp. (Acosta *et al.* 2008; Acosta 2011). Specimens in collections: MZFC. QUERÉTARO: Tolimán, El Derramadero: *Peromyscus pectoralis* (Acosta 2011). Specimens in collections: MZFC. TLAXCALA: 10 km E of Calpulalpan: *Peromyscus difficilis* (Traub and Barrera 1955, Acosta 2011). Specimens in collections: USNM. 10 km NE of Calpulalpan: *Neotomodon* sp. Humantla, La Malinche (Caseta #4): *Neotomodon alstoni, Reithrodontomys chrysopsis*. Sanctorum, on the rural road to Benito Juárez; Tlaxco: *Peromyscus* sp. (Acosta 2011). Tlaxco: *Peromyscus* sp. La Malinche: *N. alstoni*, *P. difficilis, P. gratus, P. maniculatus, P. melanotis, R. chrysopsis* (Ayala-

Barajas *et al.* 1988; Acosta and Fernández 2006; Aguilar-Montiel *et al.* 2018). Ixtenco, La Malinche (Caseta #5): *N. alstoni*. Huamantla, Las Malinche (Caseta #4): *Microtus mexicanus, P. melanotis, R. chrysopsis*. Sanctorum de Larzaro Cardenas, on the rural road to Benito Juárez, La Joya: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. Note: *Neotomodon* sp. likely refers to *Neotomodon alstoni*, as this is the only species in the genus (*N. orizabae* and *N. perotensis* were synonymized with *N. alstoni*). VERACRUZ: Perote, 3km S of El Frijol Colorado: *Peromyscus difficilis* (Acosta and Fernández 2015). Cofre de Perote: *Reithrodontomys* sp. (Acosta 2011). Specimens in collections: MZFC.

Strepsylla sp.

ESTADO DE MÉXICO: Popocatépetl: *Neotomodon alstoni, Peromyscus maniculatus, P. melanotis* (Barrera 1968). Popocatépetl, Diego de Ordaz: *P. maniculatus*. Popocatépetl, Mirador del Poeta; Popocatépetl Otlaltepec; Popocatépetl, Pie del Ventorrillo; Popocatépetl, 1 km NE Mirador del Poeta: *Peromyscus* sp. Popocatépetl, Praraje Providencial: *P. maniculatus, P. melanotis*. Popocatépetl, Paraje Zumpango; Popocatépetl, Tlamacas: *P. melanotis*. 5 mi W of Río Frío: *Neotomodon alstoni*. 2 km SW of Parres: *Neotomodon* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Note: *Neotomodon* sp. likely refers to *Neotomodon alstoni*, as this is the only species in the genus (*N. orizabae* and *N. perotensis* were synonymized with *N. alstoni*). GUERRERO: Omiltemi: *Peromyscus* sp. (Barrera 1958). Chilpancingo de los Bravo, Omiltemi: *Peromyscus megalops* (Acosta *et al.* 2008). Specimens in collections: MZFC. NUEVO LEÓN: Cerro Potosí: *Peromyscus difficilis, P. melanotis, Peromyscus* sp., *Microtus mexicanus* (Tipton and Mendez 1968). Unknown if specimens are in collections. Note: Tipton and Mendez (1968) reported this flea species as *Strepsylla* species and stated that it was to be described by Traub and Barrera. OAXACA: Santiago Comaltepec, Tuxtepec-Oaxaca Highway, km 87, El Suspiro: *Peromyscus melanocarpus* (Acosta *et al.* 2008). Specimens in collections: MZFC. TLAXCALA: La Malinche: *Microtus mexicanus, Neotomodon alstoni, Peromyscus difficilis, P. gratus, P. maniculatus, P. melanotis, Heteromys irroratus* (Aguilar-Montiel *et al.* 2018). 10 km NE of Calpulalpan: *Neotomodon* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Note: *Neotomodon* sp. likely refers to *Neotomodon alstoni*, as this is the only species in the genus (*N. orizabae* and *N. perotensis* were synonymized with *N. alstoni*). VERACRUZ: Cofre de Perote: *Reithrodontomys* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. SIERRA MADRE ORIENTAL: Multiple localities in Hidalgo and Querétaro: *Peromyscus levipes, Peromyscus* sp., *Reithrodontomys sumichrasti* (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC.

Wenzella obscura Traub, 1953

CHIAPAS: Tonala, El Triunfo: *Heteromys desmarestianus* (Acosta *et al.* 2008). Specimens in collecions: MZFC.

Rhadinopsyllinae Wagner, 1930

Rhadinopsylla fraterna (Baker, 1895)

ESTADO DE MÉXICO: Popocatépetl: *Neotoma mexicana, Peromyscus maniculatus* (Barrera 1968). Slope of Volcán Popocatépetl: *P. melanotis* (Barrera 1953). Popocatépetl, 300 m SW of Tlamacas: *Neotoma* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. NUEVO LEÓN: Cerro Potosí: *Peromyscus melanotis* (Tipton and Mendez 1968). Unknown if specimens are in collections.

Rhadinopsylla mexicana (Barrera, 1952)

CIUDAD DE MÉXICO: Parque Nacional Insurgente Miguel Hidalgo y Costilla: *Microtus mexicanus* (Méndez-L. 1974). Unknown if specimens are in collections. ESTADO DE MÉXICO: Slopes of Volcán Popocatépetl: *Peromyscus melanotis* (Barrera 1952a; Tipton and Mendez 1968). Popocatépetl: *Microtus mexicanus* (Barrera 1952a; 1968). Iztaccíhuatl, Vert. Occid.: *Neotomodon alstoni.* Iztaccíhuatl, Vert. Occid., 1 km E of Trancas: *M. mexicanus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. NUEVO LEÓN: Cerro Potosí: *Mictrotus mexicanus, N. leucodon* (recorded as *N. albigula*), *Peromyscus difficilis, P. melanotis, Peromyscus* sp. (Tipton and Mendez 1968). El Potosí, 18 km N of Galeana: *M. mexicanus, P. maniculatus* (Ayala-Barajas *et al.* 1988). Sierra Madre Oriental: *P. maniculatus* (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC.

Rhadinopsylla sp.

ESTADO DE MÉXICO: Lagunas de Zempoala, La Piedra; Nevado de Toluca, 16 mi SW of Toluca: *Microtus* sp. Monte Río Frío: *Neotoma mexicana* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. NUEVO LEÓN: Cerro Potosí: *Peromyscus maniculatus.* El Potosí, 18 km N of Galeana: *Microtus mexicanus, P. maniculatus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC.

Stenoponiinae Cunha, 1914

Stenoponia americana (Baker, 1899)

HIDALGO: Tenango de Doria, 21 km NE of Metepec (by road): *Megadontomys nelsoni* (Salceda-Sánchez and Hastriter 2006). Specimens in collections: CAIM, InDRE. Note: *Megadontomys* sp. are not distributed in Hidalgo according to Ceballos (2014). NUEVO LEÓN: Sierra San Antonio Peña Nevada: *Microtus mexicanus, Peromyscus maniculatus* (Tijerina-Medina *et al.* 2006). No specimens in collections. PUEBLA: Cerro Chingnautla, 3 km W (by road) of Chignautla: *Peromyscus levipes* (Salceda-Sánchez and Hastriter 2006). Specimens in collections: CAIM, InDRE.

Stenoponia ponera Traub and Johnson, 1952

CIUDAD DE MÉXICO: La Venta: *Peromyscus hylocetes, P. maniculatus* (Barrera 1953). Specimens in collections: MZFC. DURANGO: Laguna del Progresso: *Peromyscus* sp.

(Traub and Johnson 1952c). Specimens in collections: AMNH, USNM. ESTADO DE MÉXICO: San Cayetano: *Microtus mexicanus, Peromyscus* sp. (Machado-A. 1960; Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. La Venta: *Peromyscus hylocetes, P. maniculatus* (Barrera 1953). El Zarco: *M. mexicanus* sp. nest. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. NUEVO LEÓN: Cerro Potosí: *Peromyscus difficilis, P. melanotis, Peromyscus* sp., *Microtus mexicanus* (Tipton and Mendez 1968). Unknown if specimens are in collections. QUERÉTARO: 1 km SE of Chavarría, Cadereyta de Montes: *Peromyscus difficilis*. Pinal de Amoles, 1 km S of Pinal de Amoles: *Neotoma mexicana, P. difficilis, P. levipes, Peromyscus* sp. 1 km SW of Pinal de Amoles: *P. difficilis, P. levipes*. Pinal de Amoles, 3.5 km S of Pinal de Amoles; Pinal de Amoles, 5.6 km S of Tejamanil: *P. levipes* (recorded as *P. boylii levipes*; Acosta 2003, Acosta *et al.* 2008). Sierra Madre Oriental: *P. difficilis, P. levipes, Microtus mexicanus, Neotoma mexicana* (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC.

Stenoponia sp.

QUERÉTARO: 1 km S of Pinal de Amoles: *Peromyscus difficilis* (Acosta 2003). Specimens in collections: MZFC.

Hystrichopsyllidae Tiraboschi, 1904

Hystrichopsyllinae Tiraboschi, 1904

Atyphloceras echis Jordan and Rothschild, 1915

SONORA: La Mesa: *Peromyscus maniculatus* (Zapata-Valdés *et al.* 2018). No specimens in collections. QUERÉTARO: 1 km S of Pinal de Amoles: *Microtus mexicanus* (Acosta 2003). Specimens in collections: MZFC.

Atyphloceras multidentatus alvarezi Barrera, 1963

GUERRERO: Agua Fría, 32 km SW of Yextla: *Peromyscus megalops* (Barrera 1963). Camotla, Mpío. de Chichihualco: *Osgoodomys banderanus* (recorded as *Peromyscus banderanus*; Barrera 1963; Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC.

Atyphloceras tancitari Traub and Johnson, 1952

CIUDAD DE MÉXICO: La Venta: *Peromyscus maniculatus* (Barrera 1953; Hopkins and Rothschild 1962; Ayala-Barajas *et al.* 1988). Specimens in collections: BMNH, MZFC. Parque Nacional Insurgente Miguel Hidalgo y Costilla: *Microtus mexicanus* (Méndez-L 1974). Unknown if specimens are in collections. La Venta: *Peromyscus maniculatus* (Hopkins and Rothschild 1962). Specimens in collections: BMNH. ESTADO DE MÉXICO: Popocatépetl: *Neotomodon alstoni, Peromyscus difficilis, P. melanotis, Reithrodontomys* sp. (Barrera 1968; Ayala-Barajas *et al.* 1988). Nevado de Toluca, Ojo de Agua, 16 mi al SSO de Toluca: *Peromyscus* sp. Lagunas de Zempoala, Ojotongo: *Microtus* sp., *Reithrodontomys* sp. nest. Iztaccíhuatl, Vert. Occid: *P. melanotis*. Popocatépetl, Paraje Providencia: *N. alstoni, P. maniculatus*. Popocatépetl, 5 km E of San Pedro Nexapa; Popocatépetl, San Pedro Nexapa: *P. maniculatus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. GUERRERO: San Miguel Totolapan, Puerto del Gallo: *Megadontomys thomasi*. San Miguel Totolapan, Estación Toro Muerto: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. HIDALGO: Tlanchinol: *Reithrodontomys chrysopsis* (Salceda-Sánchez and Hastriter 2006). Specimens in collections: CAIM, InDRE. Note: *R. chrysopsis* is not distributed in this part of Hidalgo according to Ceballos (2014). MICHOACÁN: Tancítaro: *Reithrodontomys chrysopsis, Microtus mexicanus, Peromyscus hylocetes, P. melanotis* (Traub and Johnson 1952b; Barrera 1953; Hopkins and Rothschild 1962). Specimens in collections: BMNH, FMNH. MORELOS: Derrame del Chichinautzin: *Peromyscus difficilis* (Pérez-Ortiz 1976; Ayala-Barajas *et al.* 1988). Atzompa, Huitzilac: *P. hylocetes* (Ayala-Barajas *et al.* 1988). pecimens in collections: MZFC. OAXACA: Ixtlán de Juárez, 6.5 km E-SE of Santa María Yavesía: *Oryzomys* sp., *Peromyscus difficilis*, *P. melanocarpus*. Ixtlán de Juárez, 6.5 km SE of Santa María Yavesía: *P. mexicanus*. Ixtlán de Juárez, 8.75 km SE of Santa María Yavesía: *P. difficilis* (Acosta *et al.* 2008). Specimens in collections: MZFC. QUERÉTARO: Xilitla-Jalpan Highway: *Peromyscus levipes* (Acosta 2003). Specimens in collections: MZFC. TLAXCALA: La Malinche: *Neotomodon alstoni*, *Peromyscus difficilis, P. melanotis* (Aguilar-Montiel *et al.* 2018). Specimens in collections: MZFC.

Hystrichopsylla cryptotis Acosta and Morrone, 2005

HIDALGO: Tlanchinol: *Peromyscus furvus* (Salceda-Sánchez and Hastriter 2006). Specimens in collections: CAIM, InDRE. OAXACA: Ixtlán de Juárez, 6.5 km E-SE of Santa María Yavesía: *Peromyscus aztecus*. Ixtlán de Juárez, 4.5 km SE of Santa María Yavesía: *P. mexicanus* (Acosta *et al.* 2008). Specimens in collections: MZFC.

Hystrichopsylla dippiei Rothschild, 1902

NUEVO LEÓN: Cerro Potosí, 18 km N of Galeana: *Peromyscus maniculatus* (Ayala-Barajas *et al.* 1988). Sierra Madre Oriental: *P. maniculatus* (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC.

Hystrichopsylla llorentei Ayala and Morales, 1990

GUERRERO: Atoyac de Álvarez, Puerto del Gallo-Paraíso Highway, km 14; General Heliodoro Castillo, El Iris: *Peromyscus megalops* (Acosta *et al.* 2008). Specimens in collections: MZFC. OAXACA: Ixtlán de Juárez, 8.75 km SE of Santa María Yavesía: *Peromyscus difficilis* (Acosta *et al.* 2008). Specimens in collections: MZFC.

Hystrichopsylla occidentalis Holland, 1949

OAXACA: Ixtlán de Juárez, 6.5 km E-SE of Santa María Yavesía: *Microtus mexicanus, Peromyscus difficilis*. Ixtlán de Juárez, 8.75 km SE of Santa María Yavesía: *P. difficilis* (Acosta *et al.* 2008). Specimens in collections: MZFC.

Hystrichopyslla orophila Barrera, 1952

CIUDAD DE MÉXICO: Parque Nacional Insurgente Miguel Hidalgo y Costilla: *Microtus mexicanus* (Méndez-L. 1974). Unknown if specimens are in collections. Zarco: *M. mexicanus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. ESTADO DE MÉXICO: Slope of Volcán Popocatépetl: *Microtus mexicanus* (Barrera 1952b; 1953). Popocatépetl: *Microtus mexicanus, Peromyscus maniculatus, Reithrodontomys chrysopsis* (Hopkins and Rothschild 1962; Barrera 1968). Nevado de Toluca, 4 mi S of Raíces: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. MICHOACÁN: Tancítaro: *Neotomodon alstoni* (Traub and Johnson 1952c). Specimens in collections: FMNH. Note: See Morales and Llorente (1986) for additional information about this association. QUERÉTARO: 1 km S of Pinal de Amoles: *Peromyscus levipes* (Acosta 2003). Sierra Madre Oriental: *P. levipes* (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC.

Hystrichopyslla sp.

GUERRERO: Omiltemi: *Peromyscus megalops* (Barrera 1958). Omiltemi: *Peromyscus* sp. 22 km SW of Yextla: *Peromyscus megalops* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. NUEVO LEÓN: Cerro Potosí: *Neotoma leucodon* (recorded as *N. albigula*), *Peromyscus difficilis, P. melanotis* (Tipton and Mendez 1968). Unknown if specimens are in collections. Note: The specimens from Tipton and Mendez (1968) were reported as *Hystrichopsylla* species, to be described by Traub and Barrera. OAXACA: 7 km S of Suchitepec: *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. QUERÉTARO: 1 km S of Pinal de Amoles: *Peromyscus difficilis, P. levipes* (Acosta 2003). Specimens in collections: MZFC.

Ischnopsyllidae Wahlgren, 1907

Myodopsylla gentilis Jordan and Rothschild, 1921

OAXACA: Ixtlán de Juárez, 2.5 km SE of Santa María Yavesía: *Peromyscus mexicanus* (Acosta *et al.* 2008). Specimens in collections: MZFC.

Leptopsyllidae Rothschild, 1915

Leptopsyllinae Rothschild and Jordan, 1915

Peromyscopsylla draco Hopkins, 1951

CHIHUAHUA: Guachochic: *Peromyscus maniculatus* (Johnson and Traub 1954). Unknown if specimens are in collections. Guachochic a Batopilas, Sierra Tarahumara: *Peromyscus maniculatus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC.

Peromyscopsylla hesperomys adelpha (Rothschild, 1915)

DURANGO: Hidalgo, 4 km S-SE of la Zarca: *Peromyscus maniculatus* (Acosta *et al.* 2006; 2008). Specimens in collections: MZFC. ESTADO DE MÉXICO: Popocatépetl: *Peromyscus difficilis, P. maniculatus, P. melanotis* (Barrera 1968). Popocatépetl, 5.5 km E of San Pedro Nexapa: *P. maniculatus*. Popocatépetl, San Pedro Nexapa: *P. difficilis* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. GUERRERO: Tlacotepec, Cerro de Teotepec: *Peromyscus boylii* (Acosta *et al.* 2008). *Specimens in collections*: MZFC. Note: *P. boylii* is not distributed in Guerrero according to Ceballos (2014). MICHOACÁN: *Peromyscus* sp. (Johnson and Traub 1954). Unknown if specimens are in collections. Note: Tipton and Mendez (1968) also report that this flea species has been collected from Michoacán ex. *Peromyscus* sp. MORELOS: Laguna de Zempoala, 1 km NE de al Laguna: *Peromyscus hylocetes, P. maniculatus* (Barrera 1954a). Specimens in collections: BMNH, MZFC. Zempoala: *P. maniculatus* (Hopkins and Rothschild 1971). Specimens in collections: BMNH (BMNH 1958.328). NUEVO LEÓN: Cerro Potosí: *Peromyscus melanotis* (Tipton and Mendez 1968). Unknown if specimens are in collections. ZACATECAS: El Pinal: *Neotoma mexicana* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC.

Pulicidae Billberg, 1820

Ctenocephalides felis (Bouché, 1835)

CIUDAD DE MÉXICO: Chapultepec: *Microtus mexicanus* (Barrera 1953). Specimens in collections: MZFC. YUCATÁN: Mpio. of Oxkutzcab: *Peromyscus yucatanicus* (Peniche-Lara *et al.* 2015). No specimens in collections.

Echidnophaga gallinacea (Westwood, 1875)

CHIHUAHUA: Janos Biosphere Reserve: *Neotoma albigula, Onychomys arenicola, Peromyscus leucopus, Chaetodipus hispidus, Dipodomys merriami, D. spectabilis* (Fernández-González *et al.* 2016). No specimens in collections. MICHOACÁN: Zamora: *Heteromys* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. PUEBLA: Multiple localities: *Heteromys irroratus* (Acosta and Fernández 2015). 1.5 km S Oriental, Mpio. de Oriental: *H. irroratus* (Falcón-Ordaz *et al.* 2012). Specimens in collections: MZFC. QUERÉTARO: 8 km N of Jalpan: *Heteromys irroratus*. Maguey Verde: *Peromyscus difficilis* (Acosta 2003). Amealco de Bonfil, Galindo-Amealco Highway km 11: *Peromyscus levipes*. Jalpan de Serra, 8 km N of Jalpan: *H. irroratus* (Acosta *et al.* 2008). Specimens in collections: MZFC. SONORA: 60 km NW of Caborca (km 2450); Rancho Noche Buena, 30 km N-NW of Guaymas: *Neotoma* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. VERACRUZ: near El Frijol Colorado, Mpio. of Perote: *Neotoma nelsoni* (Acosta and Fernández 2009). Specimens in collections: MZFC.

Echidnophaga sp.

SIERRA MADRE ORIENTAL: Multiple locations in Nuevo León and Veracruz: *Peromyscus difficilis* (Gutiérrez-Velázquez and Acosta 2004). Specimens in collections: MZFC.

Euhoplopsyllus glacialis affinis (Baker, 1904)

NUEVO LEÓN: Sierra San Antonio Peña Nevada: *Neotoma goldmani, N. mexicana, Peromyscus boylii, P. maniculatus* (Tijerina-Medina et al. 2006). No specimens in collections. Note: *P. boylii* is not distributed in Nuevo León according to Ceballos (2014). QUERÉTARO: Peña Bernal: *Peromyscus difficilis* (Acosta 2003). Specimens in collections: MZFC.

Pulex irritans Linnaeus, 1758

QUERÉTARO: 8 km N of Jalpan: *Heteromys irroratus* (Acosta 2003; Acosta *et al.* 2008). Specimens in collections: MZFC.

Pulex simulans Baker, 1895

NUEVO LEÓN: Cerro Potosí: *Microtus mexicanus* (Tipton and Mendez 1968). Unknown if specimens are in collections. SONORA: 60 km NW of Caborca (km 2450): *Peromyscus* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. YUCATÁN: *Heteromys gaumeri* (Eckerlin 2005). Specimens in collections: CMNH B57315.

Pulex sp.

CIUDAD DE MÉXICO: San Ángel: *Neotoma* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC.

Tungidae Taschenberg, 1880

Tunga monositus Barnes and Radovsky, 1969

BAJA CALIFORNIA: San Martín Island: *Peromyscus maniculatus*. Mainland: *P. fraterculus, P. maniculatus* (Camargo *et al.* 2017). No specimens in collections. Bahía de San Quintín: *Neotoma bryanti, N. martinensis, Peromyscus fraterculus, P. maniculatus* (Barnes and Radowsky 1969). Specimens in collections: USNM. Note: *N. martinensis* is considered extinct. Note: Other hosts include *Peromyscus crinitus* and *Neotoma* sp. (Barnes and Radowsky 1969; Hastriter 1997; Linardi and Moreira de Avelar 2014). *P. maniculatus* is not known to occur on San Martin Island (Ceballos 2014). *P. eremicus* was recognized as the original host. However, *P. eremicus* from the northern part of the Baja California peninsula is now recognized as *P. fraterculus* (Álvarez-Castañeda *et al.* 2010). *N. lepida* was recognized as the original host. However, all Neotoma from the Baja California peninsula are now recognized as *N. bryanti* (Patton *et al.* 2007).

Rhopalopysllidae Oudemans, 1909

Rhopalopsyllinae Oudemans, 1909

Polygenis (Polygenis) adocetus Traub, 1950

QUERÉTARO: Peña Bernal, Ezequiel Montes: *Peromyscus* sp. 5 km SE of Tequisquiapan, Tequisquiapan: *Heteromys irroratus* (Acosta 2003; Acosta *et al.* 2008). Specimens in collections: MZFC.

Polygenis (Polygenis) gwyni (C. Fox, 1914)

CAMPECHE: 128 km E of Escarcega: *Sigmodon hispidus* (Eckerlin 2005). Specimens in collections: CMNH. Note: *S. hispidus* is not distributed in Campeche according to Ceballos (2014). A possible alternative host includes *S. toltecus* (Ceballos 2014). CHIHUAHUA: To the N of Rancho Santa Barbara: "Cotton rat" (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. MICHOACÁN: Mt. St. Miguel: "Rat" (Smit 1987). Specimens in collections: BMNH. Note: Host most likely to be a cricetid rodent. QUERÉTARO: San Miguel Palma, Peñamiller; 9 km SE of Tequisquiapan, Tequisquiapan: *Heteromys irroratus*. 5 km SE of Tequisquiapan, Tequisquiapan: *H. irroratus*, *Sigmodon hispidus* (Acosta 2003; Acosta *et al.* 2008). Specimens in collections: MZFC. Note: *S. hispidus* is not distributed in Querétaro according to Ceballos (2014). A possible alternative host includes *S. leucotis* (Ceballos 2014). QUINTANA ROO: *Sigmodon hispidus.* Isla Cozumel, 3.5 km N of San Miguel: *Reithrodontomys* sp. (Eckerlin 2005). Specimens in collections: CMNH. Note: *S. hispidus* is not distributed in Quintana Roo according to Ceballos (2014). A possible alternative host includes *S. leucotis* (Ceballos 2014). SAN LUIS POTOSÍ: San Bartolo Mpio De Río Verde: *Sigmodon* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC.

Polygenis (Polygenis) martinezbaezi Vargas, 1951

GUANAJUATO: Cortazar: *Sigmodon hispidus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Note: *S. hispidus* is not distributed in Guanajuato according to Ceballos (2014). Possible alternative hosts include *S. fulviventer* and *S. leucotis* (Ceballos 2014). GUERRERO: Atoyac de Álvarez, Puerto del Gallo-Paraíso Highway, Km 14: *Peromyscus* sp. Atoyac de Álvarez, El Faisanal: *Oryzomys palustris, Oryzomys* sp., *Heteromys pictus.* Chilpancingo de los Bravo, 4 km N of Omiltemi: *Peromyscus boylii.* Tetipac, Huizteco-Tetipac Highway, km 10, Los Llanos: *P. aztecus* (Acosta *et al.* 2008). Specimens in collections: MZFC. Note: *O. palustris* is not distributed in Guerrero and *P. boylii* is not distributed in Guerrero according to Ceballos (2014). Note: *Oryzomys* sp. was recorded in the original literature but may represent *Handleyomys* sp. JALISCO: 7 km S of Acatlán: *Heteromys* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. La Barca, Hacienda Briseñas: *Sigmodon* sp. (Smit 1987). Specimens in collections: BMNH. MICHOACÁN: La Barca, Jalisco, and Briseñas: *Sigmodon* sp. (Vargas 1951d). Specimens in collections: ISET. 10 km E of Zamora: *Heteromys irroratus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. OAXACA: Miahuatlán de Porfirio Díaz, 2.3 km de Finca Brasil: *Peromyscus* sp. (Acosta *et al.* 2008). Specimens in collections: MZFC. QUERÉTARO: Ezequiel Montes, 5 km W of Peña Bernal: *Sigmodon hispidus*. Peñamiller, San Miguel Palma: *Heteromys irroratus* (Acosta *et al.* 2008). Specimens in collections: MZFC. Note: *S. hispidus* is not distributed in Querétaro according to Ceballos (2014). Possible host includes *S. leucotis* (Ceballos 2014). TLAXCALA: El Carmen Tequexquitla, El Piñonal: *Heteromys irroratus*. Calpulalpan, San Felipe Hidalgo, Piedra Canteada: *Neotoma mexicana*. Huamantla, La Malinche (Caseta #4): *Reithrodontomys megalotis* (Acosta *et al.* 2008). Specimens in collections: MZFC.

Polygenis (Polygenis) odiosus Smit, 1958

CAMPECHE: 7.5 km W of Escárcega: *Ototylomys phyllotis* (Eckerlin 2005). Specimens in collections: CMNH. QUINTANA ROO: Isla Cozumel, 3.5 km N of San Miguel: *Oryzomys couesi*. Pueblo Nuevo X-Cán: *Peromyscus yucatanicus* (Eckerlin 2005). Specimens in collections: CMNH. YUCATÁN: 4 km N-NE of Felipe Carrillo Puerto; Uxmal; Mérida: *Peromyscus yucatanicus*. 3 km N of Piste; 66 km NE of Mérida; 5 km W of Merida: *Ototylomys phyllotis* (Eckerlin 2005). Specimens in collections: BMNH, CMNH, RPE. Mpio. of Oxkutzcab: *Ototylomys phyllotis* (Peniche-Lara 2015). No specimens in collections. 12 km N of Mérida: *Peromyscus yucatanicus* (Smit 1987). Specimens in collections: BMNH.

Polygenis (Polygenis) rozeboomi Vargas, 1952

COLIMA: Potrero Grande: *Sigmodon* sp. (Vargas 1952). Specimens in collections: BMNH, ISET.

Polygenis (Polygenis) vazquezi Vargas, 1951

CHIAPAS: Pan-American Highway over Río San Gregorio, 20 mi from Guatemalan border: *Neotoma ferruginea*, *Peromyscus guatemalensis* (recorded as *P. mexicanus guatemalensis*; Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Note: Flea specimens from Chiapas were originally reported as *Polygenis vulcanius* Smit, 1958, now a synonym of *P. vazquezi*. CIUDAD DE MÉXICO: kms 14 and 45 Free México-Cuernavaca Highway: *Neotomodon alstoni* (Vargas 1951c). Specimens in collections: IBUNAM. DURANGO: Hidalgo 4 km S-SE of la Zarca: *Perognathus flavus* (Acosta *et al.* 2006; Acosta *et al.* 2008). Specimens in collections: MZFC. GUERRERO: Atoyac de Álvarez, Nueva Dehli: *Handleyomys guerrerensis* (recorded as *Oryzomys chapmani guerrerensis*; Acosta *et al.* 2008). Specimens in collections: MZFC. HIDALGO: Huehuetla, Huehuetla: *Peromyscus mexicanus, Sigmodon hispidus* (Acosta *et al.* 2008). Specimens in collections: MZFC. Note: *S. hispidus* is not distributed in Hidalgo according to Ceballos (2014). A possible alternative host includes *S. leucotis* (Ceballos 2014). MORELOS: Comitán de Domínguez: *Sigmodon hispidus*. San Pedro Tapanatepec: *Heteromys pictus* (Smit 1987). Specimens in collections: BMNH. Note: *S. hispidus* is not distributed in Morelos according to Ceballos (2014). A possible alternative host includes *S. leucotis* (Ceballos 2014). OAXACA: Veracruz: *Peromyscus boylii*. Tepanatepec: *Heteromys pictus* (Hubbard 1958). Specimens in collections: BMNH. Note: *P. boylii* is not distributed in Oaxaca according to Ceballos (2014). PUEBLA: San Juan Tetla, Mpio. de Chautzingo: *Neotomodon alstoni* (Ramírez 1982). Unknown if specimens are in collections. 1.5 km S Oriental, Mpio. de Oriental: *Heteromys irroratus* (Falcón-Ordaz *et al.* 2012). Specimens in collections: MZFC. QUERÉTARO: Peñamiller, Peñamiller: *Sigmodon hispidus* (Acosta 2003; Acosta *et al.* 2008). 5 km SW of Tequisquiapan: *Heteromys irroratus* (Acosta 2003). Specimens in collections: MZFC. Note: *S. hispidus* is not distributed in Querétaro according to Ceballos (2014). A possible alternative host includes *S. leucotis* (Ceballos 2014). TLAXCALA: 2.5 km NW El Carmen Tequexquitla, Mpio. de El Carmen Tequexquitla: *Heteromys irroratus* (Falcón-Ordaz *et al.* 2012). Specimens in collections: MZFC. ORIENTAL BASIN: Multiple localities in Puebla, Tlaxcala, and Veracruz: *Peromyscus difficilis, Heteromys irroratus* (Acosta and Fernández 2015). Specimens in collections: MZFC. UNKNOWN LOCALITY: *Peromyscus boylii* (Smit 1987). Specimens in collections: BMNH.

Polygenis sp.

CAMPECHE: 128 km E of Escarcega: *Sigmodon toltecus* (listed as *S. hispidus microdon*; Ayala-Barajas *et al.* 1988; Eckerlin 2005). Specimens in collections: CMNH, MZFC. CHIAPAS: Ocosingo, Zona Arqueológica Monumento Natural, Ocosingo: *Ototylomys phyllotis, Heteromys desmarestianus* (Acosta *et al.* 2008). Specimens in collections: MZFC. JALISCO: 20 km de Guadalajara: *Baiomys* sp., *Heteromys* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. OAXACA: 13 km S of San Juan Lachao: *Oryzomys* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Note: *Oryzomys* sp. was recorded in the original literature but may represent *Handleyomys* sp. PUEBLA: 6 km E of Tutumihuacan: *Sigmodon* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. QUERÉTARO: 5 km W of Peña Bernal: *Sigmodon hispidus* (Acosta 2003). Specimens in collections: MZFC. Note: *S. hispidus* is not distributed in Querétaro according to Ceballos (2014). A possible alternative host includes *S. leucotis* (Ceballos 2014). QUINTANA ROO: Pueblo Nuevo Xcan: *Peromyscus yucatanicus, Peromyscus* sp. (Ayala-Barajas *et al.* 1988; Eckerlin 2005). Isla Cozumel, 3.5 km N of San Miguel: *Oryzomys couesi* (Eckerlin 2005). Specimens in collections: CMNH, MZFC. SAN LUIS POTOSÍ: 5 km SW of Nuñez: *Sigmodon* sp. (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. YUCATÁN: 3 km N of Pisté: *Oryzomys* sp., *Peromyscus yucatanicus* (Eckerlin 2005). Specimens in collections: CMNH. Península de Yucatán: *Oryzomys* sp. 2 km N of Pisté: *Peromyscus yucatanicus* (Ayala-Barajas *et al.* 1988). Specimens in collections: MZFC. Note: *Oryzomys* sp. was recorded in the original literature but may represent *Handleyomys* sp.

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Moon light and the activity patterns of Baird's tapir in the Calakmul region, Southern México

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The Baird's tapir (*Tapirella bairdii*) is an endangered species throughout its distribution area, however many aspects of its biology and ecology have been poorly studied, due to its evasive behavior and low densities. The goal of this study was to evaluate the activity patterns of *T. bairdii*, a large ungulate species from the Neotropics, in relation to moon phases in two sites with different degree of human perturbation: the Calakmul Biosphere Reserve (CBR) and the Nuevo Becal (NB) community. We monitored twenty waterbodies in each site for 18 months using camera traps. The photographic capture rate (CR) and the corresponding moon phases for both sites were recorded. The CR of *T. bairdii* was 0.054 in NB and 0.029 in CBR. *T. bairdii* was more active at night and dawn-twilight periods. In general, *T. bairdii* showed major activity during the dark moon phases but the differences with the light phases were not statistically significant. However, we found a trend of tapirs to be more active in dark nights and in the darkest hours in NB than CBR. The apparent preferences for dark nights in NB could be caused by the perturbation caused by human activities at site, which may have influenced the behavior of the tapir that avoid moving out in periods of abundant light in disturbed sites. More research is needed to confirm this finding.

El tapir de Baird (*Tapirella bairdii)* es una especie amenazada en toda su área de distribución, sin embargo, muchos aspectos de su biología y ecología han sido poco estudiados, debido a su comportamiento evasivo y a sus bajas densidades poblacionales. El objetivo de este estudio fue evaluar los patrones de actividad de *T. bairdii* en relación con las fases lunares en dos sitios con diferente grado de perturbación humana: la Reserva de la Biosfera de Calakmul (RBC) y el Ejido Nuevo Becal (NB). Se monitorearon 20 cuerpos de agua durante18 meses mediante el método de foto-trampeo. Se determinó la tasa de captura (TC) y se registraron las fases lunares correspondientes para ambos sitios. La TC de *T. bairdii* tapir fue de 0.054 en NB y de 0.029 en la RBC. *T. bairdii* fue más activo en el periodo nocturno-crepuscular. En general, *T.bairdii.* mostro una actividad importante durante las fases de oscuridad, pero estas diferencias no fueron significativas estadísticamente. Sin embargo, se encontró una tendencia de los tapires a moverse activamente en las noches y en las horas más obscuras en NB que en RBC. La preferencia aparente por las noches más obscuras en NB podría ser evidencia de la respuesta por parte de los tapires a la perturbación causada por actividades humanas en ese sitio, mostrando un cambio en su comportamiento evitando salir en periodos de abundante luz en sitios perturbados. Sin embargo, se requiere de mayor investigación para corroborar esta posibilidad.

Keys words: behavior; camera trap; human perturbation; luminosity; moon phases.

Introduction

The Baird's tapir (*Tapirella bairdii*, or usually known as *Tapirus bairdii,* see: Ruiz-Garcia *et al.* 2012, we use *Tapirella* in this study) is the largest terrestrial mammal of the Neotropics (Emmons and Feer 1997) and plays an important role in the forest dynamics through seed dispersal and predation (O´Farrill *et al.* 2013; Camargo-Sanabria and Mendoza 2016). Currently, the tapir is listed as endangered both globally (International Union for the Conservation of Nature) and in México (NOM-059-ECOL- 2010; SEMARNAT 2010) mainly due to uncontrolled hunting and habitat loss and fragmentation.

Tapirella bairdii is a solitary animal that can exhibit both diurnal and nocturnal behavior, even though several studies showed that they tend to be more active at night and crepuscular periods (Carbajal-Borges *et al.* 2014), probably because of the difficulty to dissipate the body heat, a situation that is common to all large animals (Randall *et al.* 1998; Foerster and Vaughan 2002). According to this, *Tapirella bairdii* would avoid the hottest hours of the day and restrict their movements to the cool hours of the day (Padilla and Dowler 1994; Foerster and Vaughan 2002). Moreover, several authors have observed differences in the activity patterns of this specie when other factors such as seasonality, sex, age of the individuals and moon light intensity were taken into account (Lizcano and Cavalier 2000, 2004; Foerster and Vaughan 2002; Tobler 2002; Holden *et al.* 2003; Noss *et al.* 2003; Norvarino *et al.* 2005; Medici 2010).

Although there is evidence showing that, some species with night habits reduce the intensity of their activity during nights with full moon in an effort to reduce the risk of predation by natural predators and/or humans (Prugh and Golden 2014); studies on the variation of activity patterns respect to moon light of tapir species have not lead to conclusive results yet. While Lizcano and Cavallier (2000) recorded a major nocturnal activity of the Mountain tapir (*Tapirus pinchaque*) during full moon phase, Medici (2010) found an opposite behavior pattern for the Lowland tapir (*Tapirus terrestris*) that tended to reduce its movements in full moon nights in the Brazilian Atlantic Forest. Besides, *Tapirus terrestris* did not seem to respond to the moon phases in the Brazilian Pantanal (Coelho *et al.* 2008).

In addition to the moon phase, tapirs activity can also be influenced by human activities; in areas where hunting, habitat encroachment and other non-timber extractive activities, and even ecotourism occur, tapirs can become completely nocturnal (Naranjo and Cruz 1998; Foerster and Vaughan 2002; Wallace *et al.* 2002). In this sense it has been confirmed that some species become nocturnal in areas where predators are abundant or where there is high hunting pressure (Griffiths and van Schaik, 1993, Ripple *et al.* 2001, Gaynor *et al.* 2018).

Despite several studies have investigated the effect of predation and hunting pressure independently, the relationship that may exist among daily activity patterns, moon phases and human perturbation is still unknown for most of the sites where tapir species inhabit. Therefore, the goal of this study was to evaluate the activity patters of *Tapirella bairdii* in relation to moon phases in two sites with contrasting degree of human perturbation: the Calakmul Biosphere Reserve (CB) and the Nuevo Becal community (NB). Our aim is to contribute to understand the species behavior under changes in luminosity due to different moon phases and if this interacts with different degrees of human perturbation in the forest. This information is relevant to advance in the knowledge of the behavior of wild *Tapirella bairdii*.

Material and Methods

Study site. This study took place in the Calakmul Biosphere Reserve (CBR) and the nearby forested community of Nuevo Becal (NB). Both sites are located in the Yucatán Peninsula in Southern México (Figure 1), that is principally covered by subhumid tropical forest that is marked by a dry season from January to May. During the wet season that usually occurs from June through December, precipitation ranges from 700 to 2,000 mm. The temperature average 25 °C all year long (García-Gil 2003). The vegetation types in the area are mainly humid tropical forest classified as 1) medium, semi-perennial forest; 2) low-flooded forest; 3) low-dry forest, and 4) secondary vegetation (Pennington and Sarukhán 1998). In the NB community there is a major coverage of medium, semi-perennial forest and larger ponds than in the CBR (Reyna-Hurtado and Tanner 2007).

Because of the geological structure of the Calakmul region of carbonate origin, there are not permanent water sources and most of the rainfall percolate to the underground, only in few specific places the water accumulated in the surface. These ponds, locally known as "aguadas" are source of water for wildlife and for many human communities of the region during the dry season (Reyna-Hurtado *et al.* 2010).

The CBR has an extent of 7,231 km^2 and was created in 1989. The area is protected by guards posted in two checkpoints at the entrance of the only road that leads toward the area and the only activities allowed inside are research and low-impact tourism, which are concentrated mostly around the Calakmul archeological city. The NB community is located at the eastern side of the CBR and comprises 520 km^2, was created in 1970. In this community, the most important activities are seasonal crops such as corn and beans, non-timber products extraction especially honey, charcoal and seeds, and subsistence hunting. This community still maintains forest in well stage of conservation in an approximately 80 % of its area (Reyna-Hurtado 2009). Also, there are two wildlife management and conservation units locally known as UMAS (Unidad de Manejo y Aprovechamiento de Fauna, in Spanish) where sport hunting take place usually once per year. These units aim to harvest mainly tropical deer (*Mazama sp.*) and wild turkey (*Agriocharis ocellata*).

Camera trapping. Twenty ponds (10 in each site) were monitored by setting up a single camera trap (Reconyx PC800 Hyperfire professional Reconyx, Inc) at 50 cm high in each pond from January 2014 to June 2015. The ponds were selected in a way that they would be at least 1.5 km away from each other. The cameras were programmed to take five consecutive photos (1 photo per second) each time the sensor detected movement and were checked every two months to change batteries and memory cards.

We used a 2-hour filter between tapir sequences to avoid having repetitive sequences of the same individual, unless individuals could clearly be distinguished, *e. g.* female vs male; adult vs juveniles, or individual with unique marks or scars. We determined the capture rate (CR) using classical method for each site (RBC and NB) with the following equation: CR = N/SE*1000 camera-trap days. With N = number of records and SE = sampling effort measured as the number of days multiplied by the number of cameras.

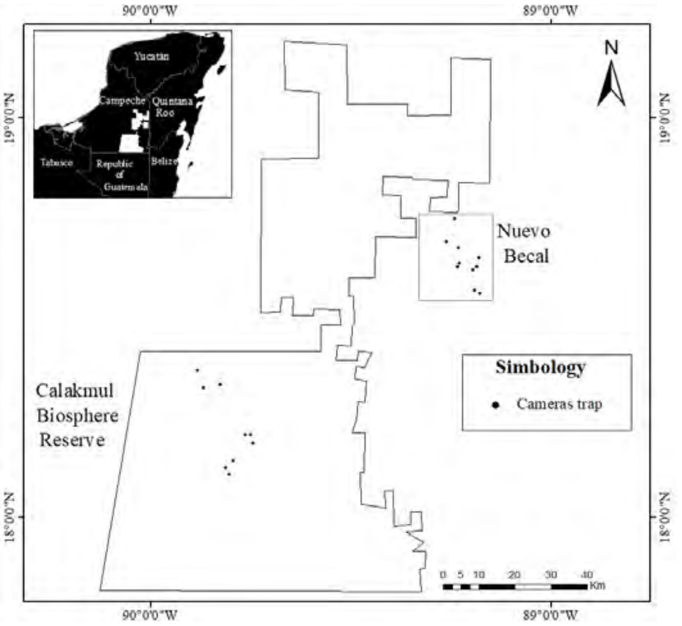

Figure 1. Study area with boundaries of the Calakmul Biosphere Reserve (CBR) and the community of Nuevo Becal (NB), with the location of the "aguadas" that were surveyed.

We examined tapir daily activity patterns in NB and RBC by using the capture events in each site. We represented the corresponding activity patterns in a graph that was generated with the software 'Overlap' (Meredith and Ridout 2014) using software R (R Core Team, 2018, R Studio ver. 1.1.463). After conversion of time to radians, the activity data from each site were subjected to a Rayleigh Test of Uniformity (Z), this analyses test if the data distribution differs from a uniform distribution (Zar 2010). Patterns of activity were described using non-parametric kernel density estimations. The proportion of overlap in activity (the coefficient of overlap, *Δ*), was estimated between sites. Because samples were greater of 75 records, the coefficient of overlap Δ4, was used to estimate activity overlap, as suggested by Meredith and Rideout (2014). The confidence interval (CI) between lower and upper 95 % limits in estimates of species activity overlap calculated as percentile intervals from 1000 bootstrap samples (Ridout and Linkie 2009).

Variations in the activity pattern in relation with the different moon phases were analyzed based on a moon calendar specific for the study area and the sampled period (obtained from the website www.tutiempo.net). Only the records between 18:30 and 6:00 hr were analyzed and classified according to the corresponding lunar phase. The moon phases were: dark phases, moon presents less than 50 % luminosity (new moon; waxing crescent; waning crescent), and light phases, moon presents more than 50 % luminosity (full moon; waxing gibbous; waning gibbous). To test for differences in the activity of *Tapirella bairdii* according to the different moon phases (dark phase *vs*. light phase) in all sampled ponds and in the different sites, we first tested for normality of the data with a Kolmogorov-Smirnov test, and then we conducted a paired t-test for each site to compare the frequency of records obtained in each phase. Finally, an ANOVA test was used to examine the differences between the frequencies of the records (number of photos obtained in one of the two moon phases) obtained in each phase between seasons for each site. The analyzes were conducted in SPSS Inc. (Statistical Package for Social Sciences), version 16.0. Chicago.

Results

Capture rate. The sampling effort was similar in both sites, with a total of 3,244 trapping nights in NB and 3,384 trapping nights in CBR, but the CR was almost twice higher in NB (CR = 54 records for 1,000 days/tramp) than in CBR (CR = 29 records for 1,000 days/tramp).

Activity patterns. Tapirs presented an unimodal activity patterns in both sites (CBR: Z = 33.03, *P* = 0.001 and NB: Z = 23.20, *P* = 0.001), with a large activity peak between 19:00 to 5:00 hr (Figure 2). The level of tapir's activity overlap was high: Δ = 0.86 (95 % confidence interval: 0.77 to 0.93) between sites (Figure 3a); Δ = 0.86 (95 % confidence interval: 0.78 to 0.93) in the dry season and Δ = 0.71 (95 % confidence interval: 0.55 to 0.85) in rainy season (Figure 3b). The overlap in the activity patterns in the different phases was: RBC Δ = 0.67 (95 % confidence interval: 0.46 to 0.73); with the large activity peak between 20:00 to 22:00 hr in the dark phases and between 0:00 to 1:00 hr in the light phases (Figure 3c); NB Δ = 0.77 (95 % confidence interval: 0.60 to 0.95); with the large activity peak between 20:00 to 0:00 hr in the dark phases and between 2:00 to 4:00 hr in the light phases (Figure 3d).

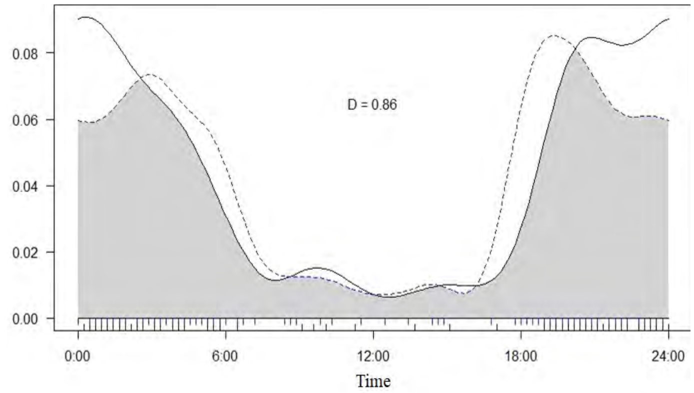

Figure 2. Proportion of overlap (D = level of overlap) in activity patterns of *Tapirella bairdii* in the Calakmul Biosphere Reserve (dashed line) and the community of Nuevo Becal (solid line).

Although a higher percentage of records of *Tapirella bairdii* were recorded during dark moon phases in both sites with 58.89 % (*n* = 53) in CBR and 61.88 % in NB (*n* = 86; Figure 4). The differences between dark and light moon phases within sites were not significant (CBR *t* = 0.84478, *g. l.* = 9, *P* = 0.210; NB *t* =1.5974, *g. l.* = 9, *P* = 0.0723). Similarly, when comparing the light and dark moon phases for all ponds, a tendency was found for the dark phases, but it was not significant (*t* = 1.809 *g. l.* = 19, *P* = 0.086). When comparing between season we did not find any evidence of preference for any moon phase in both sites (CBR: F^3_{86} = 0.773; *P* = 0.3851; NB: F^3_{135} = 0.0505; *P* = 0.480; Figure 5).

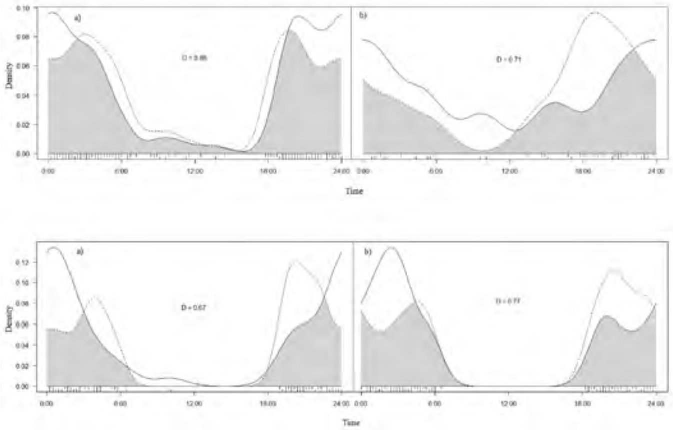

Figure 3. Proportion of overlap (D = level of overlap) in activity patterns of *Tapirella bairdii* in the Calakmul Biosphere Reserve (dashed line) and the community of Nuevo Becal (solid line) in dry season (a) and rainy season (b); and in activity patterns in the darks nights (dashed line) and ligth nigths (solid line) in the Calakmul Biosphere Reserve (c) and Nuevo Becal (d).

Discussion

Capture rate. Tapirs were more active in NB than in CBR or they are more abundant as have already been reported by Reyna-Hurtado and Tanner (2007) using track counts. Forest in NB is more humid with more water sources, a determining factor for tapirs. Moreover, the proportion of medium semi-perennial forest and low-flooded forest that

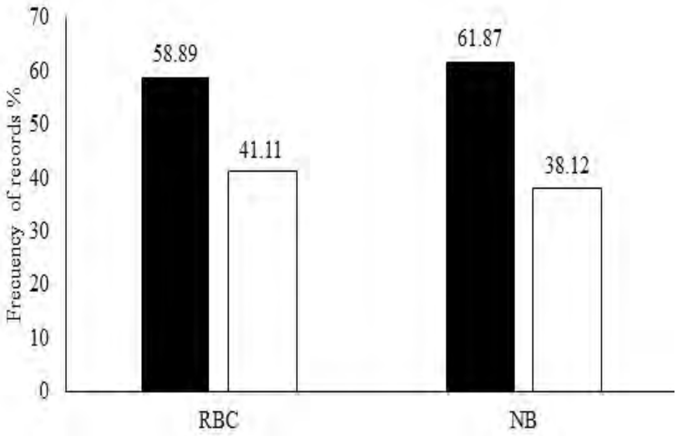

Figure 4. Records of *Tapirella bairdii* in the Calakmul Biosphere Reserve (CBR) and the community of Nuevo Becal (NB) in relation to moon phases: dark phases (in black) and light phases (in white).

tapirs tend to prefer, is higher in NB, in contrast with CBR that is more covered by medium and low-dry forest (Reyna-Hurtado and Tanner 2007). Even though hunting pressure exist in NB, tapirs do not constitute a favorite prey species and therefore do not suffer from this threat. In fact, this relatively high activity of tapirs in NB highlights the importance of communal forests outside of protected areas to preserve large endangered species.

Activity Patterns. Tapirella bairdii was more active during the night with crepuscular activity peaks at dawn and twilight hours, a pattern that has been commonly observed in other neotropical areas (van Schaik and Griffiths 1996; Foerster and Vaughan 2002). Despite more frequent captures of tapirs during the dark moon phases in both sites, the results in general for all sites were not significant. This result is similar to the study of *Tapirus terrestris* in the Pantanal, Brazil (Coelho *et al.* 2008). However, when comparing the data between seasons, a preference for light moon phase was found for the dry season of CBR and for dark moon phases in both seasons in NB. In NB there was a general tendency to prefer the dark nights, tendency that was observed also with the activity peaks. In both sites tapir activity peaks in sunrise and in the sunset. However, in the nights with moon light the activity peak for tapirs in CBR is between 0:00 and 1:00 hr while in NB is between 2:00 to 4:00 hr which coincide with the hours that the moon has settled down. These results suggest that tapirs prefer to move in dark nights and hours in NB than in CBR and that the human perturbation might have an effect on *Tapirella bairdii* behavior, as it is more active during dark moon phases in sites occupied by humans, probably in an effort to reduce predation risk or to minimize encounters with humans. As such, the intensity of the moon luminosity may modify the activity pattern of tapirs when they live in human perturbed forest.

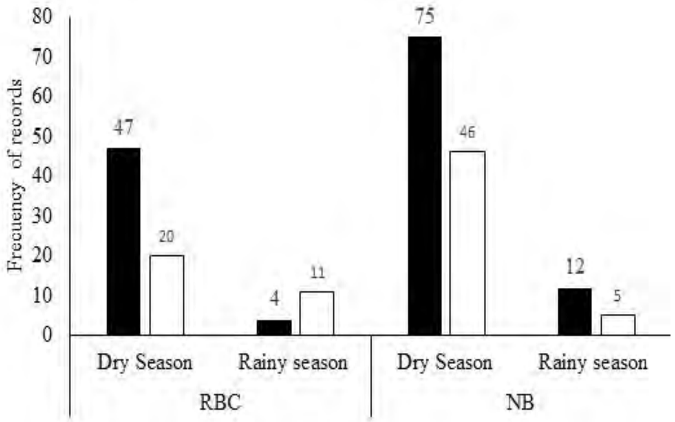

Figure 5. Records of *Tapirella bairdii* in the Calakmul Biosphere Reserve (CBR) and the community of Nuevo Becal (NB) in relation to moon phases: dark phases (in black) and light phases (in white), in the different seasons.

It is also possible that the forest cover around the water sources, *i. e.* ponds, facilitate the visits of tapirs as it may act as camouflage. For example, *Tapirus pinchaque* were more active during full moon nights in closed habitats in Colombia (Lizcano and Cavalier 2000) while *Tapirus terrestris* reduced its movements in open habitats during the full moon nights in the Atlantic forest, Brazil (Medici 2010). Therefore, forest cover is a factor that should be taken in consideration in future studies of the moon light effects in tapirs.

In order to improve the study of the relationship between moon light tapir activity, we recommend setting up cameras randomly in the forest and not only at pond; this will allow to monitor a larger area and to obtain more records of their long displacement that will complement the current work. We also recommend estimating the relative abundance of predators, especially the jaguar (*Panthera onca*) which is the main predator of the tapirs in the Neotropical forest, because its activity could influence the tapir patterns.

To conclude, we hope that this study serves as a baseline to compare the behavior of tapirs in other regions and to evaluate the impact of human activities in the behavior of an endangered species. In some cases, altering the behavior of a species may have consequences at the population and ecosystem level, as was shown by elks (*Cervus elaphus*) altered behavior in Yellowstone National Park in USA (Laundré *et al.* 2010). We do not know the consequences at the population level of *Tapirella bairdii* when preferring dark nights, but it is a topic that deserves future attention. Finally, this information may be helpful to evaluate, select or adapt other study methods, for example, when capture attempts are made for radio-telemetry purposes, or for well-designed eco-tourism activities. Thus, this study can contribute to gain a better understanding of *Tapirella bairdii* behavior in relationship with moon phases and human perturbation, information that can be useful for conservations purposes.

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Could a new record change the range of distribution of a little - known bat species (Vespertilionidae: *Eptesicus innoxius*)?

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We report the first record of *Eptesicus innoxius* in northwestern Ecuador, in the province of Esmeraldas, occurring in a disturbed area, at 134.3 km northwest from the nearest known locality in Ecuador, which represents an important latitudinal extension in the distribution of this species. A predictive distribution model is presented using a total of 43 records from localities of Ecuador and Perú, and its distribution area is determined by a minimum convex polygon (PMC). The sensitivity value obtained in the test data was 0.984 and the area under curve ROC (AUC) value obtained (0.979) indicates an acceptable confidence level. Based on new records and known records, we estimate its distribution area in 135,243 km^2. The environmental variables with the greatest influence in the distribution of *E. innoxius* were: Precipitation seasonality (37.4 %), minimum temperature of coldest month (20.1 %), precipitation of driest month (14.5 %), and mean temperature of wettest quarter (12.8 %). This data show that *E. innoxius* has been recorded mainly in tropical dry forest, but also has presence in humid areas. Within these new reports, we recommended an upgrade of its conservation status in Ecuador and Perú.

Se presenta el primer registro de *E. innoxius* al noroccidente de la costa ecuatoriana, en la provincia de Esmeraldas, dentro de una zona alterada, a 134.3 km noroeste del registro conocido más cercano en Ecuador, el cual representa una importante extensión en la distribución latitudinal conocida para esta especie. Se realizó un modelamiento predictivo de su distribución, utilizando un total de 43 registros de localidades presentes en Ecuador y Perú, y se determinó su área de distribución mediante el método del polígono mínimo convexo (PMC). El valor de sensibilidad obtenido en la prueba fue de 0.984 y el valor del área bajo la curva (AUC) fue de 0.979, lo cual indica un nivel de confianza aceptable. El área de distribución obtenida en base a los registros utilizados fue de 135,243 km^2. Las variables ambientales con mayor influencia en la distribución de *E. innoxius* fueron: estacionalidad de la precipitación (37.4 %), temperatura minima del mes más frío (20.1 %), precipitación del mes más seco (14.5 %), y temperatura media del cuatrimestre más lluvioso (12.8 %). De acuerdo con los registros, esta especie habita preferentemente en zonas de bosque seco, pero puede llegar a habitar en zonas de transición con mayor humedad. Basándonos en los nuevos registros obtenidos, se recomienda realizar una nueva evaluación de su estado de conservación en Ecuador y Perú.

Key words: Extension distribution; harmless serotine bat; northwestern Ecuador; predictive model.

Introduction

The bats of the genus *Eptesicus* Rafinesque (1820), are grouped into two subgenera and comprises approximately 18 species (Davis 1966; Corbet and Hill 1980; Hill and Harrison 1987; Simmons 2005; Davis and Gardner 2008). All New World species belong into the nominative subgenus. At a morphological level, species in the genus can be recognized by the absence of hairs in the uropatagium, proximal to the body; internal upper incisors larger than the external, usually with a secondary cusp, and lack of evident space between upper canines and premolars, among other features (Davis 1966; Albuja 1999; Davis and Gardner 2008; Díaz *et al.* 2016).

Eptesicus innoxius (Gervais 1841) is one of the smallest species within the genus, and is distributed on the western slope of the Andes, from southwestern Ecuador, in the provinces of Bolívar, Cotopaxi, Guayas, Los Ríos, Santo Domingo, El Oro and Loja, and northern Perú, between the departments of Tumbes, Piura and Lambayeque (Koopman 1978; Albuja 1999; Cadenillas *et al.* 2007; Pacheco *et al.* 2007; Pacheco *et al.* 2009; Davis and Gardner 2008; Carrera *et al.* 2010; Tirira 2017). It can be easily recognized by its size (forearm 34 to 39 mm), small skull (13.9 to 15.8 mm), and sagittal and lambdoidal crests poorly defined or absent (Davis 1966; Tirira 2017).

The type locality is located in the region of Amotape, Piura (Perú) in the ecological region known as Equatorial dry forest (Gervais 1841; Davis and Gardner 2008; Pacheco *et al.* 2009). Historical records of this species in Ecuador and Perú are located in Babahoyo (Los Ríos) and Puerto Etén (Lambayeque; Cabrera 1901; Davis 1966; Davis and Gardner 2008). Within Ecuador, its distribution includes dry tropical and subtropical forests (Bolívar, Guayas, Los Ríos, and El Oro) and some deciduous and semideciduous dry forest, while in Perú its distribution comprises the Pacific rainforest, Equatorial dry forest, and Coastal desert (Cabrera 1901; Davis 1966; Albuja 1999; Pacheco *et al.* 2009; Carrera *et al.* 2010; Burneo and Tirira 2014; Tirira 2017, Brito *et al.* 2018). Elevational range is 0 to 900 m (Tirira 2017), but there are some records in Loja and El Oro Provinces (Ecuador) and other localities in Perú above 1,000 m (Appendix 1).

Species distribution modeling have been developed to generate potential presence maps based on the concept of fundamental niche so that they can include areas with limited collection efforts (Stockwell and Peters 1999). The resulting predictive models have been widely used in studies of diversity, ecology and biogeography (Burneo *et al.* 2014; Burneo *et al.* 2015; Giménez *et al.* 2015; Loaiza and Pacheco 2017). Among the methods currently used to obtain the modeling of the species distribution is Maxent (Phillips *et al.* 2006), that estimates the probability of occurrence distribution of species, following the principle of maximum entropy, subject to the condition that the expected value of each environmental variable coincides with its empirical mean (Phillips *et al.* 2006; Merow *et al.* 2013). Among the various applications of Maxent are the prioritization of areas for initiatives of biological conservation end ecological restoration, modeling the effects of climate change on ecosystems, and the evaluation of patterns of propagation of invasive species (Phillips and Dudík 2008; Morales 2012).

The objective of this study is to propose a model for the geographical distribution of this species based on recently records obtained in the Ecuadorian provinces of Esmeraldas, Guayas and Los Ríos, as well as to review its threat status in Ecuador and propose conservation actions for this species.

Materials and methods

Field work. The collection locations (Figure 1A) were as follows: 1) Esmeraldas province: Recinto Pedro Carbo (-0° 22’ S, -79° 58’ W), sampled during January 2016, in rainy season, on a strongly fragmented area, with African oil palm plantations, the field work was carried out in a transition zone between mangrove and humid forest. 2) Guayas province: Bosque Protector La Prosperina (-2° 08’ S, -79° 58’ W), and Bosque Protector Cerro Blanco (-2° 08’ S, -80° 05’ W), both were sampled between January 2016 until March 2017 (rainy season); and Cerro del Muerto (-2° 38’ S, -80° 20’ W), sampled during May to August 2018 (dry season), all three privately owned, surrounded by intervened secondary tropical and dry forest areas; Area Nacional de Recreación Isla Santay (-2° 12’ S, -79° 50’ W), sampled during May to June 2018 (dry season), a protected area under the supervision of the Ministry on Environment of Ecuador, with mangroves, xerophilous scrub and wetlands ecosystems. 3) Los Ríos province: Cerro Cacharí (-1° 46’ S, -79° 27’ W), during February 2017 until February 2018, privately owned, approximately two kilometers from the city of Babahoyo, which has a cave and some cracks in its interior, and maintains relicts of dry forest. All the captures were made with mist nets located at ground and sub canopy level. We used four mist - nets each night in

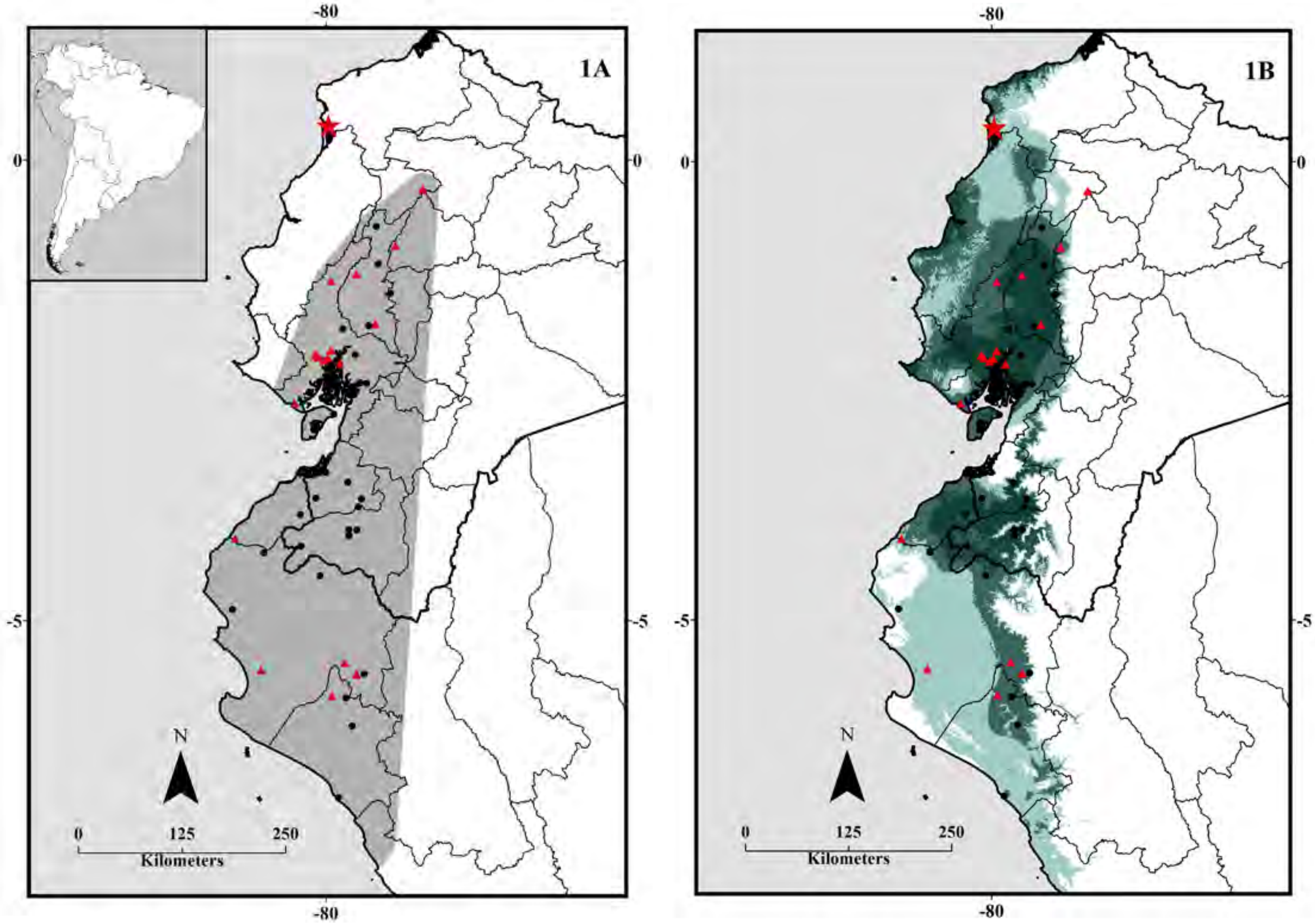

Figure 1. Study area, northern record and new localities in Ecuador. **1A:** Distribution area (PMC) of *E. innoxius*, and **1B:** Occurrence probability / predictive model of *E. innoxius* in Ecuador and Perú. Northern record (red star), new records (red triangles), and old records (black circles). Occurrence probability colors are: null (white), low (light blue), medium (light steel blue), high - medium (steel blue), and high (dark blue).

each locality, from 18 to 23 h, which were checked every fifteen minutes. Nets were placed at ground level and in subcanopy level, until reaching a height between 4 to 5 meters and were changed from location each time to prevent bats become familiar with them.

Additional locations. The study sites (Figure 1A) and other localities correspond to protected areas and forests of Guayas, Los Ríos and El Oro provinces. Climate is warm with a mean temperature of 25 °C and a high level of rainfall ranging from 2,500 to 3,000 m. Other localities in Loja and El Oro provinces correspond to dry interandean valleys and areas of deciduous dry forest.

Specimens collected and morphometric analysis. We reviewed seven specimens (three males and four females) deposited in the mammals' collection of the Museum of Zoology (MZUGM), at Universidad de Guayaquil, Facultad de Ciencias Naturales, and their identity was determined by an analysis from taxonomic characters described in the literature (Albuja 1999; Davis and Gardner 2008; Tirira 2017). The measurements were taken according to Carrera *et al.* (2010) and Díaz *et al.* (2016). External and cranial measurements were recorded for all specimens (Table 1). The nomenclature is as follows: total length (TL), body and head length (HB), tail length (T), ear length (E), forearm length (FA), hind foot length (HF), greatest length of skull (GLS), condylobasal length (CBL), braincase height (BBH), braincase breadth (BBC), zygomatic breadth (ZB), mastoid breadth (BM), postorbital constriction (POC), and palate length (PL).

Distributive modeling. We modeled the potential distribution of this species using the Maximum Entropy niche model (Maxent), which allows an estimate of the probability of occurrence of a species approximating the distribution of maximum entropy (Phillips *et al*. 2006; Phillips and Dudík 2008; Morales 2012; Merow *et al*. 2013).

To obtain the model, we proceeded to download the environmental variables of World Clim (www.worldclim.org), which comprise different types of bioclimatic factors in raster format. The 30s bioclimate file were downloaded in ESRI grid format (~ 1 km) and a cutout of the variables for Ecuador and Perú was carried out. The set of environmental variables obtained has eleven temperature variables and eight precipitation variables (19 bioclimatic variables) in order to generate variables with biological significance. The 19 variables represent annual trends, seasonality and extreme environmental factors detailed in Table 3. The digital environmental layers were used to obtain the potential distribution.

A total of 43 records were used to define the potential distribution, including: 7 records obtained during latest fieldwork, 18 obtained from the main museums of Ecuador and Perú, and 18 from databases belonging to natural history museums (Table 2). We applied the methodology described in Giménez *et al.* (2015), which consists in developing 10 replicas for the model, with 25 % of the records used as test data, 500 iterations and 10,000 background points in order to obtain a high precision in the modeling.

Table 1: External and descriptive measures of *E. innoxius*. The measurements are expressed in mm, the abbreviation is detailed in material and methods section. Observed range (above) mean and standard deviation (below).

Measures	**Davis (1966)**		**Tirira (2017)** Combined sexes	**Esmeraldas record** MZUGM 532 ♀	**This study** 3 ♂ 4 ♀
	4 ♂	13 ♀			
TL	-	-	-	75	68 - 77 75.1 ± 4.81
HB	-	-	53 - 54	43	40 - 55 46.5 ± 4.86
T	-	-	36 - 38	26	24 - 34 29.4 ± 3.82
E	-	-	10 - 14	12	7 - 12 10.3 ± 1.98
FA	35.3 - 38.5 36.7	34.0 - 38.7 37.0	34 - 40	37	35 - 39 37.1 ± 1.35
HF	-	-	8 - 10	5	4 - 8 6.1 ± 1.57
GLS	14.3 - 15.6 14.9	13.9 - 15.8 15.1	-	15.87	13.92 - 15.87 14.87 ± 0.69
CBL	-	-	-	13.62	12.53 - 13.62 12.95 ± 0.47
BBH	-	-	-	6.88	5.82 - 6.6 6.24 ± 0.26
BBC	6.5 - 7.3 6.85	6.5 - 7.1 6.9	-	6.88	6.88 - 7.65 7.20 ± 0.25
ZB	8.8 - 9.6 9.3	8.9 - 10.0 9.55	-	9.64	8.19 - 9.88 9.23 ± 0.60
BM	-	-	-	7.48	7.02 - 7.96 7.54 ± 0.34
POC	-	-	-	4.06	3.93 - 4.72 4.20 ± 0.27
PL	-	-	-	7.6	6.84 - 8.28 7.36 ± 0.50

This methodology was applied to make a jackknife and determine the environmental variables that best contributed to the model. After that, the model was replicated and a logistic model was selected as a grid file, in order to determine the areas with the highest probability of occurrence of this species. As a cut-off threshold, the minimum training presence option was selected, which is often recommended for species with a wide geographical distribution.

To estimate the habitat area of *E. innoxius*, we used an extension available for ArcGis called Xtools Pro, which allows to create polygons based on the records of a species, and to estimate its habitat in km^2 (https://xtools.pro/). The final maps were made with the ArcGis 10.3 program (ESRI 2014).

Table 2: Number of specimens used in the predictive niche modeling retrieved and verified in literature and Global Biodiversity Information Facility: GBIF (www.gbif.org)

Acronym	**Museum**	Specimens
AMNH	American Museum of Natural History	4
EBD	Estación Biológica de Doñana	1
FMNH	Field Museum of Natural History	1
LSUMZ	Lousiana State University Museum	3
MEPN	Museo de la Escuela Politécnica Nacional	1
MSU	Michigan State University Museum	1
MUSM	Museo de Historia Natural de San Marcos	6
MNHN	Museum National d'Histoire Naturelle	1
MZUGM	Museo de Zoología, Universidad de Guayaquil	7
QCAZ	Museo de Zoología, Quito (PUCE)	11
TCWC	Texas University Biodiversity Research	1
TTU	Museum of Texas Tech University	4
USNM	National Museum of Natural History, Smithsonian	2

Results

The morphological characteristics of the new specimens registered in the Ecuadorian coast, as well as the record obtained in the province of Esmeraldas (MZUGM 00532; Figure 2), fully agree with the diagnostic characteristic provided for the species by Davis (1966), Albuja (1999), and Díaz *et al*. (2016). Measurements provided by Tirira (2017), were inconsistent with the morphometry of *E. innoxius* (Table 1). The measures for males and females according to 18 specimens (4 M, 14 F) are:

Males: TL = 74 to 85, HB = 47 to 55, FA = 36 to 38, E = 7 to 15.3, T = 32 to 36.1, HF = 4 to 8, GLS = 13.92 to 15.20, CBL = 12.60 to 13.19, BBC = 7.19 to 7.65, ZB = 8.74 to 9.88, BM = 7.02 to 7.62, POC = 3.93 to 4.11, and PL = 6.84 to 8.28.

Females: TL = 68 to 94, HB = 40 to 53, FA = 33 to 39, E = 9 to 15, T = 24 to 39, HF = 7 to 10, GLS = 14.51 to 15.87, CBL = 12.31 to 13.62, BBC = 6.88 to 7.31, ZB = 8.19 to 9.65, BM = 7.48 to 7.96, POC = 4.06 to 4.72, and PL = 6.96 to 7.53.

Geographic distribution. The specimen of *Eptesicus innoxius* from Recinto Pedro Carbo (Muisne, Esmeraldas), is located at 134.3 km northwest from the northernmost known record, at Recinto Corriente Grande (Los Ríos), and constitutes the first report for the province of Esmeraldas (Davis and Gardner 2008; Tirira 2008; Burneo and Tirira 2014; Tirira 2017). The locality of Recinto Pedro Carbo is located near a mangrove area at an altitude of 13 m, within the floristic formation known as evergreen lowland forest of the coast (Ministerio de Ambiente del Ecuador 2013), between the northwestern and southwestern tropical zoogeographic regions (Albuja *et al.* 2012). Other localities reported for *E. innoxius* are located in the southwestern tropical and western subtropical regions (Albuja 1999; Tirira 2017).

In Perú, 11 localities were located in the Equatorial dry forest, another locality was in the Pacific rain forest, and only one was located in the Coastal desert, according to the classification system proposed by Brack - Egg (1986; Pacheco *et al.* 2009). The plant formations assigned to the different localities includes: dry low hill forest, dry mountain forest, and dry savanna forest (Ministerio de Ambiente del Ecuador 2015).

The potential distribution of *E. innoxius* extends throughout the Ecuadorian coastal and northern - central Perú (Figure 1B). Nevertheless, the areas of greatest importance for its distribution are located mainly in several Ecuadorian coastal provinces (Santa Elena, Guayas, El Oro and Los Ríos; Figure 1B). Although in Manabí province the occurrence probability ranges go from medium to high - medium, no records today confirm its presence here. This species is distributed in Loja province mainly toward areas of tropical dry forest, also occupying important areas within some dry interandean valleys where it reaches its highest altitudinal range.

Discussion

In Ecuador, *Eptesicus innoxius* appears to be rare in some localities, but it is usually quite common in others (Brito *et al.* 2018; Carrera *et al.* 2010). This species is present both in natural and protected areas and fragmented or secondary forests, mainly in dry forest and mangrove ecosystems, not in crops or urban environments. Although *E. innoxius* is considered a typical species of tropical dry forests, it has been recorded in several localities in tropical rain forest such as: Barraganete (Bolívar province, 237 m), and Recinto Corriente Grande (Los Ríos province, 88 m; Albuja 1999; Davis and Gardner 2008; Tirira 2017). There was a report from an area dominated by tropical humid forests, based on a specimen collected in the locality of Santa Rosa de Naranjal (Imbabura; QCAZ 10579; Lee *et al.* 2010). However, it was reidentified as *Myotis riparius* (Romero 2018).

Table 3: Percent contribution (% C) and permutation importance (PI) of each variable for the potential and logistic modeling.

Variables	**Description**	Modeling	
		% C	PI
bio_1	Annual mean temperature	0.7	0
bio_2	Mean diurnal range (max temp - min temp)	1.0	0.1
bio_3	Isothermality (* 100)	1.5	1.0
bio_4	Temperature seasonality (* 100)	0.2	0.1
bio_5	Maximum temperature of warmest month	0.1	0
bio_6	Minimum temperature of coldest month	20.1	35.8
bio_7	Temperature annual range	0.1	0.1
bio_8	Mean temperature of wettest quarter	12.8	0
bio_9	Mean temperature of driest quarter	0.7	2.3
bio_10	Mean temperature of warmest quarter	2.7	0
bio_11	Mean temperature of coldest quarter	0	0
bio_12	Annual precipitation	0	0.3
bio_13	Precipitation of wettest month	0	0
bio_14	Precipitation of driest month	14.5	54.2
bio_15	Precipitation seasonality	37.4	1.9
bio_16	Precipitation of wettest quarter	1.8	1.1
bio_17	Precipitation of driest quarter	4.5	0
bio_18	Precipitation of warmest quarter	0.6	0.4
bio_19	Precipitation of coldest quarter	1.3	2.8
Total		100	-

In Perú, geographic distribution of this species in relation to the probability of presence is not very broad; however, this seems to be associated with the distribution coming from Ecuador (Figure 1B). The most important areas are mainly located in the border of Tumbes and Piura Departments, highlighting an important distribution area within the Lambayeque region. Based on the modeling analysis obtained for this species, the probability of its presence in other regions is quite low. This could be explained due to the fact that *E. innoxius* seems to prefer areas with less extreme climatic conditions and a higher degree of humidity, and therefore has not been able to colonize other regions in Perú.

In Ecuador, *E. innoxius* is present in a greater variety of ecoregions, including areas of humid and montane forest, mangroves, flooded grasslands, with less presence in dry forest areas, while in Perú, this species has a greater presence in desert and dry forest areas, mainly in the regions of Piura and Lambayeque (Olson and Dinerstein 2002).

The estimated area of distribution was 135,243 km^2 (Figure 1A), which means that the new northwestern record represents a considerable increase with respect to the pre-


Figure 2. Specimen of *E. innoxius* (MZUGM 00532) captured in Recinto Pedro Carbo (Esmeraldas) / Photo by Jaime Salas.

viously reported distribution, in transition area between evergreen lowland forest of the coast and mangrove (Davis 1966; Koopman 1978; Albuja 1999; Davis and Gardner 2008; Tirira 2008; Carrera *et al*. 2010; Burneo and Tirira 2014; Tirira 2017). The results of our modeling coincide with the last distribution map indicated by Tirira (2017) for this species, in relation to the absence of *E. innoxius* in Manabí. A modeling similar to ours coincides with some zones of highest occurrence probability of *E. innoxius* in Ecuador (Romero 2018), including the occurrence probability of this species in northern Ecuador; however, that modeling is based on only 11 records and does not include other record localities in Perú.

Conservation status. Earlier evaluations about the conservation status of this species in Ecuador determined that deforestation has caused a considerable reduction of its natural habitat, limiting and restricting its distribution to protected areas, and is currently considered a Vulnerable species (VU) according to criterion B1 ab (*i, iii*; Tirira and Carrera 2011; Burneo *et al*. 2015). In IUCN red list, *E. innoxius* is categorized as Near Threatened (NT; Velazco and Aguirre 2016). Based on the modeling and distribution update carried out in this study (Figure 1) and the new records obtained, an upgrade of its conservation status in Ecuador is recommended, mainly due to the expansion of its distribution area to the northern, in highly fragmented areas.

The majority of records of *E. innoxius* in Ecuador have been obtained in several protected areas, such as the Bosque Protector Cerro Blanco and Reserva Ecológica Manglares - Churute (Guayas province), Reserva Ecológica Arenillas (El Oro province), and Bosque Petrificado de Puyango (El Oro / Loja provinces; Carrera *et al*. 2010), as well as in some non-protected areas in Bolívar, Guayas, and Los Ríos (Davis 1966; Koopman 1978; Albuja 1999; Davis and Gardner 2008; Burneo and Tirira 2014). New localities indicated in this study are: Bosque Protector Prosperina (Guayas province, 217 m), Cerro Cacharí (Los Rios province, 33 m), Cerro del Muerto (Guayas province, 46 m), and Area Nacional de Recreación "Isla Santay" (Guayas province, 7 m). In Perú, there is a record in the Coto de Caza "El Angolo", within the biome of Tumbes - Piura dry forest (Cadenillas *et al*. 2007). Other new localities reported in Perú are: El Abra (Lambayeque, 127 m), Laguna Ñapique (Piura, 9 m), Pampa de los Burros (Piura, 735 m), Quebrada metida del Zorro (Piura, 327 m), and Barrancos (Tumbes, 34 m; Appendix 1).

All these new records indicate the existence of localities that overlap with the zones of greater probability of presence for this species, being possible that *E. innoxius* could be registered in protected areas such as Parque Nacional Machalilla, and Refugio de Vida Silvestre Marino Costera Pacoche (Manabí province), Refugio de Vida Silvestre Manglares - El Morro, and Reserva de Producción Faunística Manglares - El Salado (Guayas province) (Figure 1B). It is necessary to continue monitoring in the area of distribution, and make sure its conservation through inclusion of this species as key species in the management plans of protected areas, or seeking refuges as Important Sites for the Conservation of Bats (SICOM) (Burneo *et al*. 2015).

In the southern region of Ecuador, some locations where this species has been recorded are currently greatly altered due to deforestation which has decreased much of the original vegetation cover, especially in some dry interandean valleys (Albuja 2011). However, the recent creation of protected areas and forests in Macara and Zapotillo localities (Reserva Natural Cazaderos, La Ceiba y Laipuna) in Loja Province, which are connected to the Reserva de Biosfera del Noroeste Amotapes - Manglares, might ensure protection and its long - term survival.

The distribution area indicated to the north of Perú, in spite of being considered in its majority as an area of low-medium probability of presence (Figure 1B), is a quite extensive area, with records until the southwest of Lambayeque, for which we consider that the conservation status of this species in Perú is going in the right direction, considering the recent creation of some binational protected areas. However, protected areas that harbor populations of this and other species are still reduced in Ecuador and Perú. A recently published work highlights the importance of the conservation of forests and natural refuges for the bat's conservation on Ecuadorian coast (Linares and Zavala 2018).

It is necessary to carry out studies focused on knowing and determining the population abundance both in Ecuador and in Perú, and other studies about its reproduction cycles, diet, migrations, roost preferences, as well as developing other conservation proposals that will ensure the survival of their populations and the conservation of the different ecosystems where this species lives (Tirira and Carrera 2011).

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Appendix 1

Locality records for *Eptesicus innoxius* in Ecuador and Perú used in potential distribution analyses: **ECUADOR, Bolívar:** Barraganete, 3 km al suroeste de Echeandía, 237 m (-1.45, -79.299; MEPN 1840) ♀; **Cotopaxi:** Hacienda Hnos. Cabrera, 195 m (-0.935, -79.246; QCAZ 18177 - 18178) ♀♀; **El Oro:** Cerro Chiche (Piñas), 547 m (-3.766, -79.647; TTU 102399) ♂; R. E. Arenillas (Palmales), 68 m (-3.674, -80.108; QCAZ 9063) ♀; R. E. Arenillas (Quebrada Seca), 709 m (-3.5, -79.766; QCAZ 9776) ♀; **Esmeraldas:** Recinto Pedro Carbo, 13 m (0.369, -79.970; MZUGM 00532) ♀; **Guayas:** Sector de San Ramón (Isla Puná), 8 m (-2.933, -80.133; AMNH 66822, 66825) ♂♀; Sector de Salitre, 8 m (-1.834, -79.815; USNM 534270) ♀; Sector de Yaguachi, 4 m (-2.116, -79.683; EBD 12631 - 12632, 12636 - 12649); B. P. Cerro Blanco (Sector Manantial), 34 m (-2.180, -80.031; TTU - 103325) ♀; La Pólvora (Isla Puná), 30 m (-2.764, -79.915; QCAZ 9067 - 9069, 9515 - 9518) ♀♂♀♂♀♀♂; R. E. Manglares Churute, 12 m (-2.509, -79.744; QCAZ 9073) ♂; R. E. Manglares Churute (Cerro Cimalón), 23 m (-2.426, -79.561; TTU 103514 - 103516, 103521 - 103522) ♀♂♂♀♀; R. E. Manglares Churute (Cerro Pancho Diablo), 11 m (-2.420, -79.631; TTU 103670) ♂; El Retiro (río Pucón), 39 m (-1.312, -79.943; QCAZ 12654) ♂; B. P. Prosperina, 217 m (-2.149, -79.978; MZUGM 00582) ♀; B. P. Cerro Blanco, 276 m (-2.142, -80.086; MZUGM 00443) ♂; B. P. Cerro Blanco, 64 m (-2.179, -80.021; MZUGM 00489) ♂; Cerro del Muerto, 41 m (-2.643, -80.340; MZUGM 00699) ♂; Área Nacional de Recreación "Isla Santay", 7 m (-2.211, -79.849; MZUGM 00727 - 00729) ♀♂♀; **Loja:** Río Pindo, 1021 m (-4.016, -79.667; AMNH 47226 - 47228, 47230 - 47232) ♀♂♀♀♂♂; Had. Casanga, 990 m (-4.017, -79.750; AMNH 47234) ♀; Valle del río Casanga, 1458 m (-4.083, -79.75; AMNH 257589) ♀; Las Cochas del Almendro, 550 m (-4.194, -80.270; QCAZ 11835) ♂; **Los Ríos:** 1.5 km al sur de San Carlos, en la vía Quevedo - Babahoyo, 76 m (-1.130, -79.433; MSU 31452, 31730) ♂♂; Recinto Corriente Grande, sobre el río Baba, 88 m (-0.722, -79.455; QCAZ 8897, 8904) ♂♀; Cerro Cacharí, 33 m (-1.779, -79.463; MZUGM 00491, 00496, 00606) ♂♀♀; **Santo Domingo:** La unión del Toachi, 815 m (-0.321, -78.952; QCAZ 17184) ♂. **PERÚ, Lambayeque:** Puerto Etén, sector costero cerca de Chiclayo, 5 m (-6.926, -79.864; USNM 103923 - 103927) ♀♀♀♀♀; Sector de Motupe, 132 m (-6.15, -79.716; FMNH 81033) ♀; 12 km al norte de Olmos, 150 m (-5.841, -79.783; LSUMZ 27258 - 27259) ♂♂; El Abra, entre el cerro Huacrupe y San Cristóbal, 127 m (-5.821, -79.936; MUSM 34642 - 34644) ♀♀♀; **Piura:** Amotape, 18 m (-4.883, -81.015; MNHN 6987) ♂; 4 millas al oeste de Suyo, 418 m (-4.516, -80.066; TCWC 12751 - 12753) ♀♀♀; Coto de Caza "El Angolo" (La Falda), 947 m (-4.265, -80.673; NCI, 2007) ♂; 44 km al norte de Olmos, 1517 m (-5.585, -79.586; LSUMZ 21309, 21310, 21816) ♀♂♀; Laguna Ñapique, 13.3 km al este de Séchura, 9 m (-5.538, -80.703; MUSM 20895) ♀; Pampa de los burros (El Zural), 735 m (-5.584, -79.668; MUSM 34645) ♀; Quebrada metida del zorro (El Garabo), 327 m (-5.463, -79.793; MUSM 34646 - 34650) ♀♂♀♀♀; **Tumbes:** Barrancos, 34 m (-4.114, -80.983; MUSM 20672); Quebrada Faical, 24 km al sureste de Pampas de Hospital, 727 m (-3.853, -80.280; LSUMZ 24504).

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Recent records of *Tapirella bairdii* and *Panthera onca* in a region highly transformed by human activities in southern Veracruz, México

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The tapir (*Tapirella bairdii*) and the jaguar (*Panthera onca*) are two of the largest Neotropical mammal species suffering population declines caused by habitat loss and degradation and hunting. Tapirs and jaguars are considered endangered and near threatened, respectively, by the IUCN, and in Mexico, both species are listed as endangered and considered species with priority for conservation. These species are usually associated with large and remote areas of preserved forest. To evaluate local diversity of medium and large sized mammals, we placed five camera traps, three in old forest and two in secondary forest (445 trap days) at Ejido Ramos Millán (municipality of Minatitlán), on the northernmost part of the Uxpanapa Valley, in the Gulf of Mexico coastal plain, state of Veracruz, Mexico. This region has been highly transformed by human activities, where agricultural and livestock activities have caused the loss of most of its natural forests, resulting in a highly fragmented landscape, dominated by livestock fields, crops and secondary forests. Here we document images of three adult individuals of jaguar and two adult individuals of tapir, one of which was a lactating female, and one adult male tapir. The new records were 23 Km north of the most recent reports located in well preserved primary forests in the Uxpanapa/Chimalapas border area. Our results suggest that the highly fragmented tropical landscapes composed of both old-growth and secondary forests remnants, are able to provide sufficient resources to maintain at least temporarily individuals of jaguars and tapirs.

El tapir (*Tapirella bairdii*) y el jaguar (*Panthera onca*) son dos de las especies de mamíferos neotropicales más grandes en México, Centro y Sudamérica. A lo largo de su distribución, sufren una disminución poblacional causada por la pérdida y degradación del hábitat y la caza. El tapir y jaguar son considerados en peligro y casi amenazados, respectivamente, por la UICN, y en México, ambas especies están consideradas en peligro de extinción y se consideran especies prioritarias para la conservación. Estas especies generalmente se asocian a grandes y remotas extensiones de bosque preservado. Para evaluar la diversidad local de mamíferos medianos y grandes, colocamos cinco fototrampas, tres en fragmentos de bosque viejo y dos en bosques secundarios (445 días trampa) en el Ejido Ramos Millán (municipio de Minatitlán), en la parte más al norte del valle de Uxpanapa, en la planicie costera del Golfo de México, estado de Veracruz, México. Esta región ha sido altamente modificado por las actividades humanas, en donde las actividades agrícolas y ganaderas han causado la pérdida de la mayoría de los bosques naturales, resultando en un paisaje fragmentado, dominado por pastizales ganaderos, cultivos y bosques secundarios. Aquí documentamos imágenes de tres individuos adultos de jaguar y dos individuos adultos de tapir, uno de los cuales era una hembra lactante y un tapir macho adulto. Los nuevos registros se localizaron 23 Km al norte de los registros más recientes ubicados en bosques primarios bien conservados en el área fronteriza de Uxpanapa/Chimalapas. Nuestros resultados sugieren que los paisajes tropicales altamente fragmentados, compuestos por fragmentos de bosque viejo y secundario, son capaces de proporcionar recursos suficientes para mantener al menos temporalmente individuos de jaguares y tapires.

Keywords: camera trap; jaguar; old forest fragments; secondary forests; tapir; tropical rain forest.

Introduction

Tapirs (*Tapirella bairdii*) and jaguars (*Panthera onca*) are two of the most threatened large terrestrial mammals in the Neotropics (Quigley *et al.* 2017; García *et al.* 2016). Both species are considered "endangered" and "near threatened", respectively, by the IUCN. In Mexico, they are listed as "endangered" (SEMARNAT 2010) due to habitat loss, habitat modification, and hunting (Chávez-Tovar *et al.* 2005; March and Naranjo 2005). Although historic distribution of both species extended over a broad distributional area (Chávez-Tovar *et al.* 2005; March and Naranjo 2005), local populations have been drastically reduced in most parts of the country (Chávez-Tovar *et al.* 2005; March and Naranjo 2005; Naranjo 2009; Chávez-Tovar *et al.* 2016). Because of their status as endangered species, the Mexican government has considered jaguars and tapirs as priority species for conservation (García *et al.* 2016; Quigley *et al.* 2017).

In southeastern Mexico, both jaguars and tapirs have been recently reported in tropical rainforests, tropical dry forests and cloud forests, along the states of Veracruz, Oaxaca, Chiapas, Tabasco, Campeche, Yucatán, and Quintana Roo (Chávez-Tovar *et al.* 2005; Naranjo 2009). However, the distribution of tapirs is more restricted, and no recent records have been reported in Tabasco and Yucatán (March and Naranjo 2005). Currently, both species still have relatively high population sizes in large forest fragments of difficult access, low human presence, and with some degree of protection (*e. g.,* Los Chimalapas and Sierra Norte in Oaxaca, Sierra Madre de Chiapas and Lacandona in Chiapas, Calakmul in Campeche and Sian Ka'an in Quintana Roo; Naranjo 2009; Chávez-Tovar *et al.* 2016; Botello *et al.* 2017). However, Chávez-Tovar *et al.* (2016) and Luja *et al.* (2017) indicated that jaguars may occur in unprotected or highly fragmented sites with human impact. Also, the two species play important roles in the ecosystem; tapirs are important herbivores and seed dispersers of various plant species (Naranjo 2009), and jaguars are the largest predators in the Neotropics (Chávez-Tovar *et al.* 2005).

Although jaguars and tapirs were historically distributed across the Coastal Plain of the state of Veracruz, in the northern portion of the Isthmus of Tehuantepec (Chávez-Tovar *et al.* 2005; March and Naranjo 2005), both species are thought to be nearly extirpated from the area (March and Naranjo 2005; SEMARNAT 2009), particularly, in the Uxpanapa valley, where livestock and agricultural activities have caused high deforestation rates since the 1970s (Ellis *et al.* 2011). For example, in Las Choapas and Minatitlán the forest cover decreased 17 % and 14 %, respectively, between 2001 and 2017 (Global Forest Watch 2018). In addition, this area has important petrochemical complexes, causing high pollution levels (Espinosa-Reyes *et al.* 2013). The most recent records for both species in Veracruz have been documented at most 10 km north from the Uxpanapa/Chimalapas border where the largest remnant of tropical rainforest in Mexico still exists, and it is believed that large viable populations of these two species still exist (Lira-Torres *et al.* 2014; Naranjo *et al.* 2015).

Local efforts by inhabitants in the Uxpanapa valley have promoted the regeneration and conservation of large extensions of secondary and old forest fragments. With these efforts, natural forest regeneration appears to provide suitable environmental conditions and resources that are already promoting the return of large mammals. Here we reported the presence of jaguar and tapir in sites previously unsampled with camera traps, in the northern portion of the Uxpanapa valley, being the most recent records of these two species in the municipality of Minatitlán.

Materials and methods

*Study site***.** Sampling was done in tropical rain forest remnants in the Ejido Gabriel Ramos Millán (17° 22′ 21.75″ N, -94° 10′ 33.68″ W), Municipality of Minatitlán, located on the upper northern limits of the Uxpanapa valley (southeastern Veracruz; Figure 1a, b). The original vegetation in the region was tropical rainforest extended along plains, soft hills and ravines (Hernández *et al.* 2013); but in the last 40 years, changes in land use derived from agricultural and livestock activities, and the large fire occurred in 1998, destroyed more than 70 % of the original vegetation cover (Hernández *et al.* 2013).

*Sampling***.** We conducted two sampling seasons, the first from July to October 2018 and the second from December 2018 to April 2019. We set five camera stations with one camera trap each (Cuddeback®, Bushnell® and Wildgame®). Three stations were placed in two old growth forest fragments as followed: Station 1 (17° 22′ 23.38″ N, -94° 13′ 48.25″ W, 117 masl), placed in a 380 ha fragment of old growth forest surrounded by a > 10,000 ha large fragment of secondary forest; Station 2 (17° 20′ 56.05″ N, -94° 10′ 1.90″W, 74 masl), placed in a 220 ha old-growth forest fragment surrounded by secondary forests and cattle pastures; and Station 3 (17° 21′ 06.37″ N, -94° 11′ 35.98″ W, 120 masl), placed in a 149 ha old-growth forest fragment surrounded by secondary forests and cattle pastures. Two more stations were placed in a 20-year secondary forests: Station 4 (17° 21′ 30.5" N, -94° 10′ 06.3″ W, 37 masl), placed in a forest fragment of 160 ha; and, Station 5 (17° 20′ 45.5″ N, -94° 09′ 07.7″ W, 68 masl), placed in a forest fragment of 166 ha (Figure 1c).

Camera traps were set at least 1.0 Km away from each other (1.6 Km on average) on natural paths, between 50 to 60 cm height on tree trunks (Lira-Torres *et al.* 2014; Briones-Salas *et al.* 2016). Every camera trap was georeferenced using a Garmin, Etrex® 20x global positioning system (GPS). The sampling effort was calculated in trap-days by multiplying the total number of camera traps set by the total number of days cameras were active (Briones-Salas *et al.* 2016), totaling 1,005 trap-days (445 trap-days between July and October, 2018, and 560 trap-days between December 2018 and April 2019). All images were deposited in the Phototrap Collection at the Institute of Biology, Universidad Nacional Autónoma de México, and are available for request.

Results

Of the five stations, four (stations 1, 2, 4 and 5) recorded individuals of jaguars (two stations) or tapirs (three stations) during the two sampling seasons: In station 1, in the first sampling season (between July 28 and August 31, 2018), we recorded 18 images and 10 independent events of two adult jaguars (Figure 2a, b). In the second sampling season (between December 24, 2018 and January 25, 2019), we recorded 10 images and 9 independent events of one adult jaguar. In station 2, in the first sampling season, we recorded one image of an adult jaguar on July 27, 2018, and an adult tapir in two independent events, the first on July 31, 2018 (Figure 2c), and the second in September 10, 2018. During the second sampling season (between December 26, 2018 and April 2nd, 2019), we recorded 11 images and eight independent records of an adult tapir. In station 4, in the first sampling season, we recorded one adult tapir in two independent events, the first on August 11th, 2018, and the second in October 6th, 2018 (Figure 2d). In the second sampling season (between December 25, 2018 and March 9th, 2019), we recorded 11 images and four independent events of an adult tapir. In station 5, during the first sampling season (between August 11 and September 3rd, 2018), we recorded 64 images in 12 independent events of

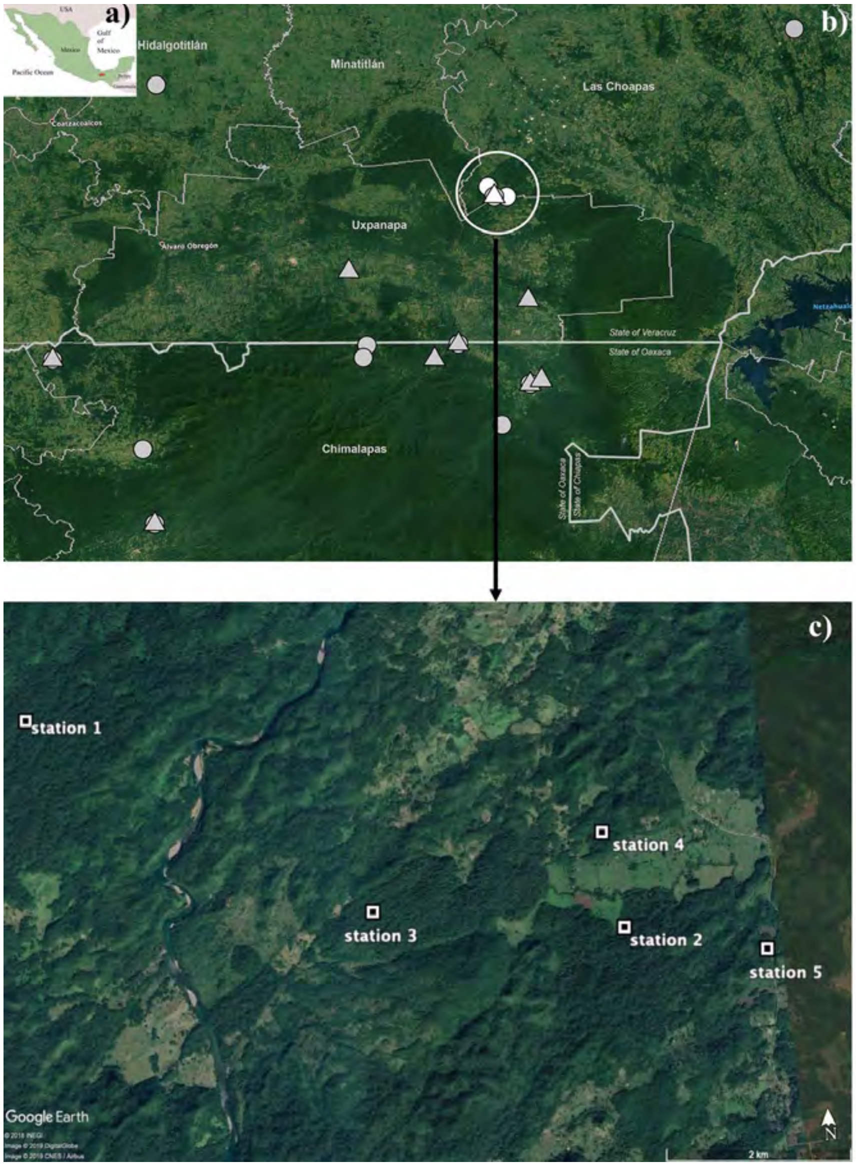

Figure 1. a) Location of the study area in southern Veracruz, Mexico. b) Historical (in gray) and recent (our study, in white), records for jaguar (circles) and tapir (triangles). c) location of the five camera stations within the "Ejido Ramos Millán", municipality of Minatitlán, Veracruz, Mexico.

adult tapirs. During the second sampling season (between December 23, 2018 and January 3rd, 2019), we recorded 27 images and three independent events of two adult tapirs (female and male). In many photographs it was possible to see that one tapir was a lactating female (Figure 2e), and in one video recorded in March 3rd, 2018, we documented an adult male (Figure 2f).

Discussion

Jaguars have been rarely recorded in the Uxpanapa valley. Only three records have been reported between 1990 to 2008 in three different sites, one located at approximately 50 km northeast, one 50 km northwest, and one 20 km south of our study site, between the Chimalapas/Uxpanapa border (Briones-Salas *et al.* 2016; Rodríguez-Soto *et al.* 2011). Our record represents the first record in the last 10 years in the Uxpanapa valley and the first historical record of the species in the municipality of Minatitlán, where the jaguar was considered already extirpated (SEMARNAT 2009). Jaguars are normally recorded in localities immersed in or connected to dense tropical forests (Chávez-Tovar *et al.* 2005). We believe that jaguars recorded here were not only in-transit dispersing individuals from nearby large preserved forests (*e. g.,* Chimalapas region), but animals residing in the site. In station 1, the same individual was photographed several days during the two sampling seasons along eight months, which suggests the old-growth forest fragment is part of its territory. Considering the size of the fragment where station 1 was set (> 10,000 ha, including secondary and old forest). We believe that this fragment can either work as a biological corridor or as a stepping-stone habitat (Luja *et al.* 2017), where jaguars can be established temporarily or even permanently. During our survey we abundantly recorded three main jaguar preys, the nine-banded armadillo (*Dasypus novemcinctus*), white-nosed coati (*Nasua narica*) and the collared peccary (*Pecari tajacu*; Chávez-Tovar *et al.* 2005). Additionally, the presence of karstic caves in the region may provide permanent refuge to jaguars (Chávez-Tovar *et al.* 2005).

Before our study, the last tapir records (2003-2015) were located not more than 10 km away from the border of the Chimalapas/Uxpanapa forest, which harbors one of the most important tapir populations in Mexico (Lira-Torres *et al.* 2014). However, our record extends as far as 22.5 km straight line to the north from "La Fortaleza" in Chimalapas, Oaxaca, into Minatitlán, Veracruz. Residents of Ejido Gabriel Ramos Millán indicated that tapir sightings began to occur approximately seven years ago (2011) in lowlands, floodplains and temporary streams. We believe that tapirs were already established within the forest remnants by the time camera-traps were placed. This is supported by the high frequency of independent photograps of individuals, the presence of adult tapirs of both sexes, and the record of a breeding female.

Secondary forests are the dominant component of lowland landscapes in the Neotropics (Melo *et al.* 2013). Much has been discussed about the importance of secondary forest for the conservation of biodiversity (Melo *et al.* 2013). Our records of jaguars and tapirs in human modified habitats suggest that local conservation efforts by the Ramos Millán people, preserving old growth and secondary forest in a fragmented landscape, have allowed the return of large mammals in sites where they were already extirpated. These species have been scarcely recorded in fragmented landscapes (*e. g.*, Marqués de Comillas region, Lacandona rainforest, Chiapas) as they prefer large fragments (at least 1,000 ha) of old-growth forest (Muench and Martínez-Ramos 2016). It has been documented

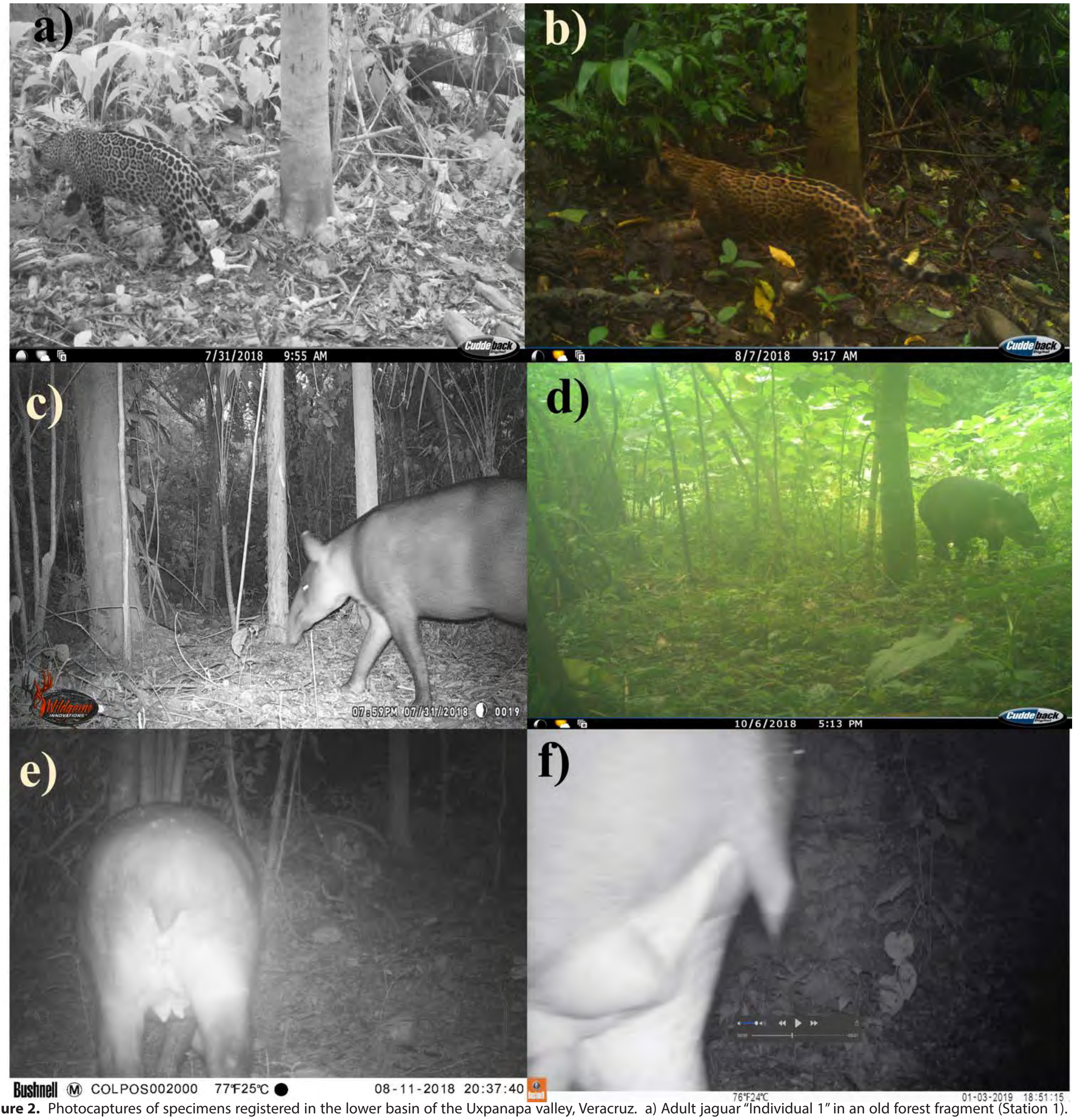

Figure 2. Photocaptures of specimens registered in the lower basin of the Uxpanapa valley, Veracruz. a) Adult jaguar "Individual 1" in an old forest fragment (Station 1). b) Adult jaguar "Individual 2" in an old forest fragment (Station 1). c) Adult tapir in an old forest fragment (Station 2). d) Adult tapir at day in a secondary forest fragment (Station 4). e) Adult tapir female (Station 4). f) Adult tapir male (Station 4).

that in natural protected areas with large forested fragments, tapirs prefer sites with abundant water (streams and swamps) and with secondary vegetation dominated by edible species (Naranjo 2009). It is likely that the collective decision of local people in Ejido Ramos Millán to preserve their forests and to prohibit hunting of both species, has promoted environmental conditions (such as abundant food and abundant water) that allow the establishment and reproduction of resident individuals within the northern part of Uxpanapa valley.

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