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First record of *Coxiella* sp. in *Ornithodoros hasei* parasitizing *Rhogeessa tumida* in México

Primer registro de *Coxiella* sp. en *Ornithodoros hasei* parasitando a *Rhogeessa tumida* en México

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Soft ticks represent a neglected group of ectoparasites associated with a wide range of vertebrates. In México, 24 species have been reported, the majority parasitizing bats. Several species are competent vectors of a wide range of pathogenic microorganisms. For this reason, the aim of the present work was to identify ticks associated with bats from Tuxpan de Rodriguez Cano, Veracruz, México. Bats were captured using mist nets and were visually inspected for tick presence. The ectoparasites were identified morphologically and molecularly with the use of the mitochondrial marker 16SrDNA, and molecular detection of several bacterial and protozoan pathogens was also performed. Twenty-five bats of 9 species were inspected. We collected 7 tick larvae morphologically identified as *Ornithodoros hasei* from a female black-winged little yellow bat (*Rhogeessa tumida*). Sequencing of the 400-bp fragment of the 16S rDNA gene, demonstrated a similarity of 96 % (373/388 bp) with *O. hasei* from Argentina and Brazil. In addition, the presence of *Coxiella* sp. was confirmed. Our findings provide relevant information on the biology of *O. hasei* by identifying *R. tumida* as a new host, providing the most north-eastern record for the geographical distribution of this tick in the Gulf of México and detecting the presence of a new endosymbiont in this tick.

Key words: Bats; biodiversity; ectoparasites; endosymbiont; México; soft tick.

Las garrapatas blandas representan un grupo desatendido de ectoparásitos asociadas con una amplia gama de vertebrados. En México se han reportado 24 especies, la mayoría parasitando murciélagos. Varias especies son vectores competentes de una amplia gama de microorganismos patógenos. Por esta razón, el objetivo del presente trabajo fue identificar garrapatas asociadas con murciélagos de Tuxpan de Rodríguez Cano, Veracruz, México. Los murciélagos fueron capturados usando redes de niebla y fueron inspeccionados visualmente para detectar la presencia de garrapatas. Los ectoparásitos se identificaron morfológica y molecularmente con el uso del marcador mitocondrial 16SrDNA. Adicionalmente, se realizó la detección molecular de varios patógenos bacterianos y protozoarios. Se inspeccionaron 25 murciélagos de 9 especies. Se recolectaron 7 larvas de garrapatas identificadas morfológicamente como *Ornithodoros hasei* de una hembra de murciélago amarillo de alas negras (*Rhogeessa tumida*). La secuenciación del fragmento de 400 pb del gen 16S rDNA demostró una similitud del 96 % (373/388 pb) con *O. hasei* de Argentina y Brasil. Adicionalmente, se confirmó la presencia de *Coxiella* sp. Nuestros hallazgos proporcionan información relevante sobre la biología de *O. hasei* al identificar a *R. tumida* como un nuevo huésped, proporcionando el registro más nororiental para la distribución geográfica de esta garrapata en el Golfo de México y detectando la presencia de un nuevo huésped-endosimbionte en esta garrapata.

Palabras clave: Biodiversidad; ectoparásitos; endosimbionte; garrapatas blandas; México; murciélagos.

Ticks are hematophagous ectoparasites associated with a great variety of vertebrates, among which mammals stand out. The existence of 3 living families and a fossil one is recognized, among which the soft ticks of the Argasidae family are prominent members. Currently, this family is composed by near 220 known species, which exhibit nesting behavior, as they remain within the dens of the hosts and feed on multiple occasions throughout their life cycle (Mans *et al.* 2019). Soft ticks are vectors of a wide range of pathogenic microorganisms, among which members of the genera *Borrelia* and *Rickettsia* are recognized (Parola and Raoult 2001). In particular, many members of the genus *Ornithodoros* are parasites of bats (Sándor *et al.* 2021).

Twenty-four species of the genus *Ornithodoros* occur in México, more than half of them are associated with bats (Guzmán-Cornejo *et al.* 2019). However, in the country, information on microorganisms related to *Ornithodoros* that parasitize bats is scarce and scattered. A single record described *Rickettsia lusitaniae* in *Ornithodoros yumatensis* from the Yucatán Peninsula, and in an undetermined *Ornithodoros* sp. of unknown geographic origin (Sánchez-Montes *et al.* 2016; Hornok *et al.* 2019). Nevertheless, in other countries of the Neotropical region, a wide range of potentially zoonotic microorganisms (*e.g.*, *Borrelia* sp.) have been identified in ticks parasitizing bats of the Emballonuridae, Mormoopidae, Noctilionidae, Phyllostomidae and Vespertilionidae families (Muñoz-Leal *et al.* 2021).

Ornithodoros hasei, a member of the *Ornithodoros talaje* group, is one of the most common and abundant soft ticks associated with bats across the Neotropical region and exhibits a wide distribution that ranges from northern México to Argentina (Colombo *et al.* 2020). This species has been recorded in association with 42 species of 26 genera of bats of the Emballonuridae, Mormoopidae, Noctilionidae, Phyllostomidae and Vespertilionidae families and 1 rodent species in 11 countries of the Neotropical region (Figure 1; Appendix 1). In México, records of *O. hasei* are scarce, with a first report made in the states of Yucatán and Sinaloa in 1963, and again in 2000 for both states (Kohls *et al.* 1965; Guzmán-Cornejo *et al.* 2019).

This tick species has recently been studied in South America for the presence of microorganisms, among which the presence of *Candidatus* Rickettsia wissemanii stands out, a new species from the spotted fever group (whose pathogenicity is unknown), which was detected in Argentina, Brazil, and French Guiana (Tahir *et al.* 2016; Luz *et al.* 2019; Colombo *et al.* 2020). Additionally, an uncharacterized member of the *Bartonella* genus has been detected in French Guiana (Davoust *et al.* 2016). However, no studies have been performed to identify other potentially pathogenic bacterial or parasitic agents in this tick species.

The aim of this study was to perform a morphological and molecular identification of soft ticks collected from bats, and to provide new records of tick-bat associations in México. Moreover, we aimed to detect tick-borne bacteria (*Anaplasma*, *Bartonella*, *Borrelia*, *Coxiella*, *Ehrlichia*, and *Rickettsia*) and protozoa (*Babesia* and *Hepatozoon*) in the collected ticks.

During a field journey on February 27, 2020, we trapped bats using mist nets at the ecotourism centre San Basilio (20º 58´03´´N, 97º 21´ 12´´W) located in the municipality of Tuxpan de Rodríguez Cano, Veracruz. Bats were collected from 20 to 22 hr. The specimens were carefully removed from the nets, identified with the help of specialized morphological keys of Medellín *et al.* (2007), and individualized in blanket bags. Each specimen was checked externally for the presence of ticks, which were collected with the help of forceps and fixed in 70 % ethanol. Once the procedure was finished, the mammals were released *in situ*.

For DNA extraction from ticks, a small incision was made behind the fourth pair of legs with a sterile needle for each specimen. Subsequently, the individuals were placed in a Cheelex-100 solution following the methodology of Aguilar-Domínguez *et al.* (2019). The exoskeletons were recovered and mounted on semi-permanent slides using Hoyer's medium to perform a morphological identification following Kohls *et al.* (1965). For molecular identification of the specimens, a 400-bp fragment of the mitochondrial 16S rRNA gene was amplified using the primers and thermal conditions according to Norris *et al.* (1996). Subsequently, conventional polymerase chain reactions (PCRs) were performed using specific primers to detect of several bacterial and protozoan pathogens, which are listed in Appendix 2. The reaction mixture was prepared in a final volume of 25

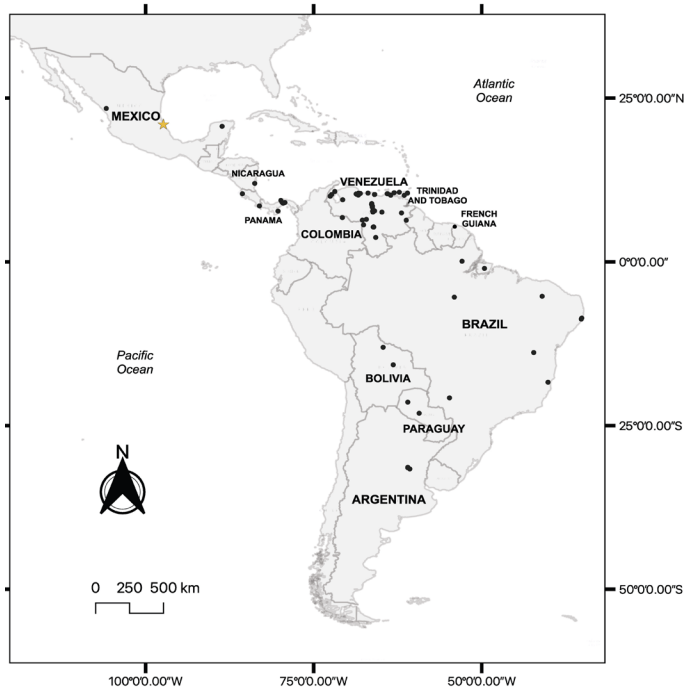

Figure 1. Geographic records of the soft tick, *Ornithodoros hasei* in the Neotropical region based on literature. We highlight in a yellow star the new geographic record found in Tuxpan, Veracruz on the eastern coast of México. Black points refer to previous records.

µL, using 12.5 µL of 2× GoTaq Green Master Mix (Promega Corporation, Madison, WI, USA), 2 µL of primers (2 µM, 1 µL each), 8.5 µL nuclease-free water and 500 ng DNA of each sample (2 µL).

Negative (nuclease free water) and positive (DNA of *Anaplasma ovis* [MG733099], *Bartonella vinsonii vinsonii* [KT326174], *Ehrlichia canis* [MH917714], *Hepatozoon* sp. from *Crotalus molossus* [MT385834], *Rickettsia amblyommatis* [KX363842], and *Theileria equi* [MT828308]) controls were included. Amplicons were sequenced at Macrogen, Korea. Finally, the sequences generated were compared to those deposited in GenBank using the BLAST-n tool. Additionally, for ticks and tick-borne pathogens, we made a phylogenetic reconstruction using the Maximum Likelihood method. We selected the best nucleotide substitution model using the Bayesian information criterion (BIC) and the maximum likelihood value (lnL) in MEGA v.10. Branch support was estimated using 10000 non-parametric bootstraps. Finally, to ascertain genetic diversity between the tick populations recovered in this study and those deposited in GenBank, we calculated the number of haplotypes and the number of unique haplotypes in DNAsp 5.10. To identify the relationship among haplotypes, minimal union networks were constructed using the program PopArt.

Bats collected correspond to 9 species of 2 families: Phyllostomidae (23 specimens: 15 *Artibeus jamaicensis*, 1 *Artibeus lituratus*, 3 *Chiroderma salvini*, 1 *Dermanura phaeotis*, 1 *Glossophaga soricina*, 1 *Platyrrhinus helleri*, and 1 *Sturnira ludovici*) and Vespertilionidae (2 specimens: 1 *Epistecus furinalis*, and 1 *Rhogeesa tumida*). A single *R. tumida* female was recorded to be infested by ticks. A total of 7 larvae were identified morphologically as *O. hasei*, because of the following traits: dorsal plate pyriform, 14 pairs of dorsolateral setae and 4 pairs of central setae; pointed hypostome with 3 rows of denticles (19 denticles in row I; 18 in row II, and 9 in row III); dentition formula 3/3 in the anterior two-thirds, then 2/2 towards the base (Figure 2a-c; Kohls *et al.* 1965). We recovered 400-bp sequences of the 16S-rRNA gene from all collected specimens. The sequences showed a similarity of 99 %–100 % (388/399 bp) among each other and 96 % (373/388 bp) with sequences of *O. hasei* from Brazil and Argentina (GenBank accession numbers MH600060 and MT077216). The phylogenetic analysis confirmed the identity of the species, grouping the reference sequences with those generated in the present work in a monophyletic clade with a support value of 99 % (Figure 2d).

We detected the presence of 9 haplotypes of *O. hasei* (Figure 2b). The most frequent haplotype detected was H5, with 3 sequences (27.3 %), followed by haplotype H2 with 2 (18.2 %). The remaining haplotypes were recorded once each one. None of the haplotypes was detected in more than one country. In México, only 2 haplotypes were detected that differ between 12 and 13 mutational steps with the other haplotypes detected in South America (Figure 2e).

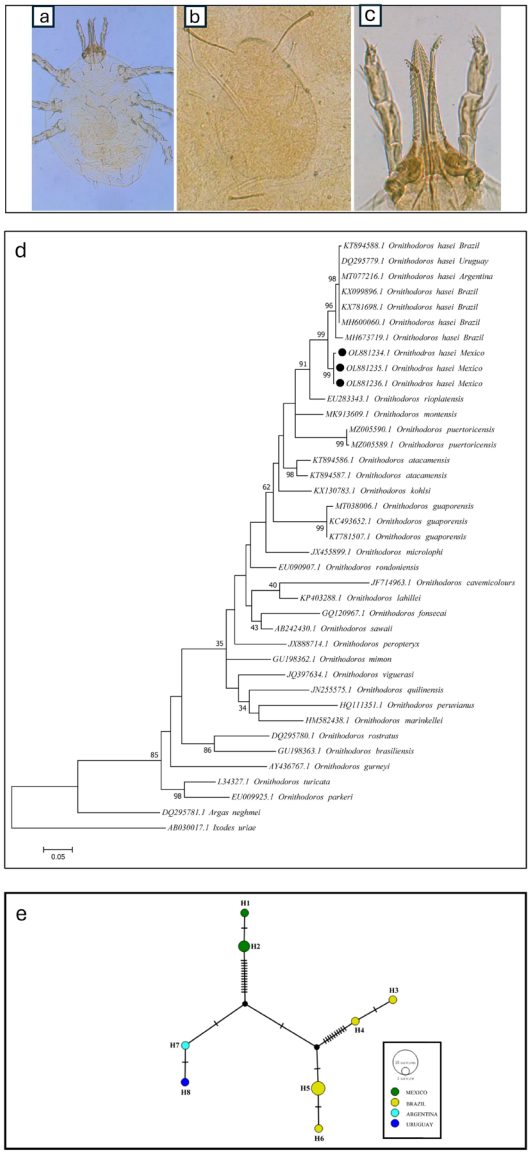

Figure 2. Morphological and molecular identification of *Ornithodoros hasei*. Optical micrographs of *O. hasei* larva collected in Tuxpan, Veracruz, México. a) Ventral view, b) dorsal plate, and c) hypostome; d) Phylogenetic reconstruction based on a partial fragment of the 16S-rDNA gene of several soft ticks inferred by Maximum Likelihood and based in the General Time Reversible Model (GTR). Sequences in the study are marked with solid figures. Bootstrap values are indicated at the nodes. Scale bar at the bottom represents the degree of divergence; e) haplotype network for the 16S-rDNA fragment of *O. hasei* from the Neotropical region. The colors correspond to each country. Black lines represent the mutational steps between each haplotype; black dots symbolize unrecovered haplotypes.

For tick-borne pathogen detection, all ticks were tested individually by PCR. Of these, 2 ticks (28.5 %) produced the expected PCR products for the 16S-rRNA gene of *Coxiella*. The sequences obtained were 100 % (615/615 bp) identical to each other; according to the BLAST analysis, our sequences were 99 % (610/615 bp) identical to that of the *C. burnetii* isolate of *Hyalomma asiaticum* from China (GenBank accession number MN880312). The phylogenetic analysis grouped our sequences in a monophyletic clade (support value of 95 %) with those of *Coxiella* endosymbionts isolated from other *Ornithodoros* species and several linages of *C. burnetii*, which belong to clade A (Figure 3).

The presence of DNA from other bacterial or parasitic agents was not detected. The obtained sequences were deposited in GenBank under the following accessions numbers: *Ornithodoros* 16S-rDNA (OL881234-36), and *Coxiella* 16S-rDNA (OL898409).

In México, records of ticks associated with bats of the Vespertilionidae family are scarce, with only 5 host species examined (*Corynorhinus mexicanus*, *Myotis nigricans extremus*, *M. velifer*, *M. vivesi* and, *Parastrellus hesperus*), which have been recorded in association with 5 soft tick species (*Ornithodoros yumatensis*, *O. brodyi*, *O. hasei*, *O. dyeri*, and *O. rossi*, respectively; Guzmán-Cornejo *et al.* 2019).

We identified for the first time the presence of a tick parasitizing *R. tumida*, particularly the soft tick *O. hasei*. Although Jones *et al.* (1972) mention the presence of *O. hasei* in *R. tumida* collected in Venezuela (Appendix 1), phylogenetic studies carried out identified the existence of the *tumida-parvula* species complex. Subsequent phylogenetic studies demonstrated the presence of 10 species of the genus *Rhogeesa* across the Neotropical region (Baird *et al.* 2009). In the case of *R. tumida*, this species has a restricted distribution ranging from northeastern México, through Central America, to the south of Brazil, Bolivia, and Ecuador, whereas the only species described for Venezuela is the tiny yellow bat (*Rhogeessa minutilla*), species in which the presence of *O. hasei* has been demonstrated in Colombia (Marinkelle and Grose 1981; Baird *et al.* 2009; Ceballos 2014). The present work increases the inventory of ectoparasites associated with *R. tumida*, since there are only historical records of the nycteribiid fly *Basilia anomala* from México (Guimaraes and D'Andretta 1956) and Guatemala (Theodor 1967) and the myobiid mite *Acanthophthirius longus* from Guatemala (Uchikawa and Baker 1993). To the best of our knowledge, there are only 3 previous historical records of *O. hasei* parasitizing members of the genus *Rhogeessa*: the tiny yellow bat (*R. minutilla*), one unidentified specimen from Venezuela, and the little yellow bat (*R. parvula*) from Colombia (Jones *et al.* 1972; Marinkelle and Grose 1981; Appendix 1). So, this work provides a new parasite–host association for this bat genus.

Our findings add a new location for *O. hasei* in México: this record represents the most northern finding of *O. hasei* on the Gulf of México, particularly in the transition zone with the Nearctic region (Guzmán-Cornejo *et al.* 2019). Furthermore, it is important to clarify that *O. hasei* is distributed from the north-west of México (Sinaloa) to Argentina and not from the southern part of México to Argentina, as mentioned by other authors (Davoust *et al.* 2016; Figure 1).

Additionally, this new record adds novel and valuable taxonomic information about the species. Since the description of this taxon in 1972 by Jones *et al.*, there has been an intense debate regarding the taxonomy of this species. The variability in the total length of the specimens from different countries of South America and the Caribbean (Jones *et al.* 1972) has led to the proposal of

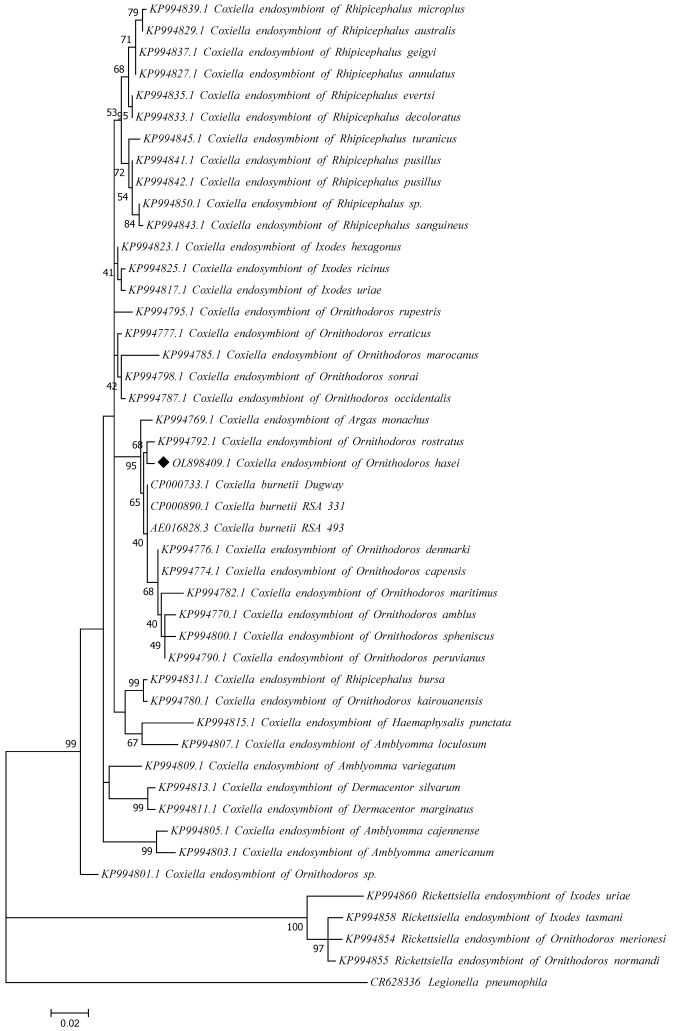

Figure 3. Phylogenetic reconstruction based on a partial fragment of the 16S-rDNA gene of several *Coxiella* linages inferred by Maximum Likelihood and based on Kimura two parameter Model (K2). Bootstrap values are indicated at the nodes. Scale bar at the bottom represents the degree of divergence. Sequences in the study are marked with solid figures.

the existence of possible cryptic species (Muñoz-Leal *et al.* 2018). The TCS network (statistical parsimony) revealed the presence of many unique and intermediate haplotypes (probably non-sampled haplotypes) from South American populations of *O. hasei* (Figure 3). This is consistent with the subsampling of this species throughout the Neotropical region, such as in the case of *Amblyomma aureolatum* from Brazil (Bitencourth *et al.* 2021). Our new data will help to elucidate the possible presence of a cryptic species complex or intraspecies variability. It is crucial to continue processing new morphological, molecular, and ecological data about *O. hasei* in order to clarify their taxonomic status.

Our current work also presents the first record of a *Coxiella* sp. in *O. hasei*, and the second one of this bacteria genus in a soft tick associated with bats, since the only previous record is from *Ornithodoros peruvianus* associated with *Desmodus rotundus* in Chile (Duron *et al.* 2015). In addition, our work represents the first molecular typifica-

tion of *Coxiella* sp. in México since this bacterial genus was previously detected using Next Generation Sequencing in the soft tick *Ornithodoros turicate* from the Bolson tortoise (*Ghopherus flavimarginatus*) in the northern Mapimi Biosphere Reserve (Barraza-Guerrero *et al.* 2020). However, this technique does not discriminate between C. *burnetii* and *Coxiella* endosymbionts. In previous studies, *C. burnetii* had been detected in solid organs and blood of bats from Brazil (Ferreira *et al.* 2018). To date, *C. burnetii* is the only species confirmed to be a vertebrate pathogen, capable of causing a systemic disease, that has been reported in bats from Brazil. The molecular phylogeny of *Coxiella* identified the presence of 4 clades (named as A-D). All *Coxiella* clades except one (D) include pathogenic and endosymbiont linages. Recently, Brenner *et al.* (2021) determined that both groups (*C. burnetii* and *Coxiella* endosymbionts) evolved from a common pathogenic ancestor. However, the zoonotic potential of other endosymbiont *Coxiella* in vertebrates, particularly bats, is unknown. Since no biological samples were taken from the vertebrate host in the present study, it is unknown whether the host is infected with the agent.

On the other hand, *Coxiella* endosymbionts seem to be very common in soft ticks, especially in the genus *Ornithodoros* (Duron *et al.* 2015). Previous studies for the detection of *Coxiella* failed to demonstrate the presence of this microorganism in *O. hasei* populations from South America (Tahir *et al.* 2016). For this reason, our record represents the first molecular identification of *Coxiella* in ticks associated with bats in the Neotropical region.

Recently, *Ca. R. wisemanni* was detected at a high prevalence in *O. hasei* from Argentina, Brazil and French Guinea (Tahir *et al.* 2016; Luz *et al.* 2019; Colombo *et al.* 2020). However, this microorganism was not identified in our study, possibly due to the low number of samples analysed. Yet, its presence was not ruled out, and more studies should be carried out to understand its potential distribution in the most north-eastern populations of *O. hasei*.

The findings of the present work highlight the need to continue with the systematic study of microorganisms associated with soft ticks from Mexican bats, since very little is known about the microbiome of these ectoparasites, which represent an important component of biodiversity.

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Appendix 1

List of known host species and localities of the soft tick *Ornithodoros hasei* across the Neotropical region. NR: Not recorded; F: Female; M: Male; N: Nymph; L: Larvae.

Order	Family	Scientific name	Common name	Country	Locality	Tick stage	Collection date	Bacterial detected	Reference
Chiroptera	Emballonuridae	*Peropteryx* sp.	-	Venezuela	10 km S, 18 km W Machiques, Kasmera, Zulia	2L	15 April, 1968	NR	Jones *et al*. 1972
	Molossidae	*Eumops* sp.	-	Bolivia	San Joaquin, Beni and Magdalena	NR	March-September, 1963	NR	Kohls *et al*. 1965
		Molossus bondae	Bonda Mastiff Bat	Venezuela	About 10 km NW Urama, Yaracuy	1L	14 March, 1966	NR	Jones *et al*. 1972
		Molossus bondae	Bonda Mastiff Bat	Venezuela	Montalbán, Carabobo	2L	5 September, 1967	NR	Jones *et al*. 1972
		Molossus molossus	Pallas's mastiff bat	Colombia	Vereda El Socorro, Finca Los Trompillos, municipality of Arauca, Department of Arauca, Orinoquia region	11L	1 November 2021	NR	Ossa-López *et al*. 2023
		Molossus molossus	Pallas's mastiff bat	Colombia	NR	3	NR	NR	Marinkelle and Grose 1981
		Molossus nigricans	Ebon Mastiff Bat	Mexico	Piste, Yucatán	43L	July 20-21, 1962	NR	Kohls *et al*. 1965
		Molossus rufus	Black Mastiff Bat	Venezuela	1/4 km N San Juan, E side Río Manapiare, Harder	4L	5 July, 1967	NR	Jones *et al*. 1972
		Molossus rufus	Black Mastiff Bat	Venezuela	14 km E Cumaná, Hda. Guanital, Sucre	12L	9 December, 1966	NR	Jones *et al*. 1972
		Molossus rufus	Black Mastiff Bat	Venezuela	2 km N Tamanaco, near San Juan Río Manapiare, Harder	1L	19 July, 1967	NR	Jones *et al*. 1972
		Molossus rufus	Black Mastiff Bat	Venezuela	2 km N Tamanaco, near San Juan, Río Manapiare, Harder	2L	17 July, 1967	NR	Jones *et al*. 1972
		Molossus rufus	Black Mastiff Bat	Venezuela	2-3 km N, 4 km W Caripe, San Agustín, Monagas	36L	26 June-07 July 1967	NR	Jones *et al*. 1972
		Molossus rufus	Black Mastiff Bat	Venezuela	38 km NW Pto. Paez, Hato Cariben, Río Cinaruco, Apure	1M, 1N	17 January, 1966	NR	Jones *et al*. 1972
		Molossus rufus	Black Mastiff Bat	Venezuela	38 km NW Pto. Paez, Río Cinaruco, Apure	1F, 2N, 1L	17 January, 1966	NR	Jones *et al*. 1972
		Molossus rufus	Black Mastiff Bat	Venezuela	46 km NE Pto. Paez, Hato Cariben, Río Cinaruco, Apure	1M, 1N, 1L	13,17 January, 1965	NR	Jones *et al*. 1972
		Molossus rufus	Black Mastiff Bat	Venezuela	46 km NE Pto. Paez, Hato Cariben, Río Cinaruco, Apure	1L	28 July, 1965	NR	Jones *et al*. 1972
		Molossus rufus	Black Mastiff Bat	Venezuela	59 km SE , km 74, El Manaco, Bolivar	35L	8-17 June, 1966	NR	Jones *et al*. 1972
		Molossus rufus	Black Mastiff Bat	Venezuela	Ca. 2 km N Tamanaco, near San Juan, Río Manapiare, Harder	7L	24 July, 1967	NR	Jones *et al*. 1972
		Molossus rufus	Black Mastiff Bat	Venezuela	Near San Agustín, Monagas	25L	8 July 1967	NR	Jones *et al*. 1972
		Molossus rufus	Black Mastiff Bat	Venezuela	Near Tamanaco, ca. 4 km NE San Juan, Río Manapiare, Harder	14L	14,19 July, 1967	NR	Jones *et al*. 1972
		Molossus rufus	Black Mastiff Bat	Venezuela	Tamanaco, ca. 4 km NE San Juan, Río Manapiare, Harder	2L	14 July, 1967	NR	Jones *et al*. 1972
		Molossus rufus	Black Mastiff Bat	Venezuela	Tamanaco, ca. 4 km NE San Juan, Río Manapiare, T. F. Amazonas	6L	14 July, 1967	NR	Jones *et al*. 1972
		Molossus rufus	Black Mastiff Bat	Venezuela	Tamanaco, near San Juan, Río Manapiare, Harder	2L	25 July, 1967	NR	Jones *et al*. 1972
		Molossops temminckii	Dwarf Dog-faced Bat	Argentina	Sociedad Rural "Las Colonias", Esperanza city	5L	January 2018	NR	Colombo *et al*. 2020
		Mormoops megalophylla	Peters's Ghost-faced Bat	Venezuela	9 km N, 4 km E Guiria near Río Salado, Sucre	1L	7 July, 1967	NR	Jones *et al*. 1972
		Neoplatymops mattogrossensis	Mato Grosso Dog-faced Bat	Venezuela	33 km SSE Puerto Ayacucho, El Raudal, Harder	25L	4, 10 October, 1967	NR	Jones *et al*. 1972
		Tadarida sp.	-	Venezuela	38 km NW Pto. Paez, Río Cinaruco, Apure	1L	21 January, 1966	NR	Jones *et al*. 1972
		Tadarida sp.	-	Venezuela	Boca Mavaca, Río Orinoco, 84 km SSE Esperalda, Harder	5L	14 Frebruary, 1966	NR	Jones *et al*. 1972
		Tadarida sp.	-	Venezuela	Río Cunucunuma, near Belén, Harder	3L	13 January, 1967	NR	Jones *et al*. 1972
	Noctilionidae	*Noctilio albiventris*	Lesser Bulldog Bat	Brazil	Mato Grosso do Sul state	3L	2006-2008	NR	Muñoz-Leal *et al*. 2018
		Noctilio albiventris	Lesser Bulldog Bat	Colombia	Vereda El Socorro, Finca Los Trompillos, municipality of Arauca, Department of Arauca, Orinoquia region	86L	31 October 2021, 1 November 2021	NR	Ossa-López *et al*. 2023
		Noctilio albiventris	Lesser Bulldog Bat	Colombia	Vereda El Socorro, Finca Marsella, municipality of Arauca, Department of Arauca, Orinoquia region	43L	3 November 2021	NR	Ossa-López *et al*. 2023
		Noctilio albiventris	Lesser Bulldog Bat	Colombia	NR	4	NR	NR	Marinkelle and Grose 1981
		Noctilio albiventris	Lesser Bulldog Bat	French Guiana	Saint-Jean-du-Maroni	354L	January 2013	31L *Candidatus* Rickettsia wissemanii	Tahir *et al*. 2016
		Noctilio albiventris	Lesser Bulldog Bat	French Guiana	Saint-Laurent-du-Maroni	355L	January and February 2013	4L *Bartonella* sp.	Davoust *et al*. 2016
		Noctilio albiventris	Lesser Bulldog Bat	Trinidad	Santa Cruz,6 km by road W of Ascención	7L	13 August 1985	NR	Dick *et al*. 2007
		Noctilio leporinus	Greater Bulldog Bat	Bolivia	San Joaquin, Beni and Magdalena	Aprox 575L	March-September, 1963	NR	Kohls *et al*. 1965

	Noctilio leporinus	Greater Bulldog Bat	Brazil	Mato Grosso do Sul state	NR	2006-2008	NR	Muñoz-Leal *et al*. 2016
	Noctilio leporinus	Greater Bulldog Bat	Brazil	Serinhaém, Pernambuco	19L, 2N	nov, 2016	NR	Muñoz-Leal *et al*. 2018
	Noctilio leporinus	Greater Bulldog Bat	Colombia	NR	2	NR	NR	Marinkelle and Grose 1981
	Noctilio leporinus	Greater Bulldog Bat	Costa Rica	9 mi ENE of Puerto Golfito, Puntarenas Province	29L	March 15, 1963	NR	Kohls *et al*. 1965
	Noctilio leporinus	Greater Bulldog Bat	Nicaragua	Rama, Bluefiels	2L	April 29, 1963	NR	Kohls *et al*. 1965
	Noctilio leporinus	Greater Bulldog Bat	Panama	Yard of the Panama Hospital, Panama City	32L	March 17, 1931	NR	Matheson 1935
	Noctilio leporinus	Greater Bulldog Bat	Panama	Summit Canal Zone	NR	September 30, 1932	NR	Matheson 1935
	Noctilio leporinus	Greater Bulldog Bat	Panama	Pacora	1N, several larvae	June 21, 22, July 26, 1961	NR	Fairchild *et al*. 1965
	Noctilio leporinus	Greater Bulldog Bat	Panama	Navy firing point, Galeta Point, Canal Zone	2N	November 19, 1959	NR	Fairchild *et al*. 1965
	Noctilio leporinus	Greater Bulldog Bat	Paraguay	Fortín Juan de Zalazar	3L	25 September 1973	NR	Nava *et al*. 2007
	Noctilio leporinus	Greater Bulldog Bat	Paraguay	Fortín Juan de Zalazar	2L	27 September 1973	NR	Nava *et al*. 2007
	Noctilio leporinus	Greater Bulldog Bat	Trinidad	Avocat	10L**	September 21, 1961	NR	Kohls *et al*. 1965
	Noctilio leporinus	Greater Bulldog Bat	Trinidad	North Manzanilla	21L	February 28, 1957	NR	Kohls *et al*. 1965
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	19 km NW Urama, Yaracuy	50L	9 March, 1966	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	2 km N Tamanaco, near San Juan Río Manapiare, Harder	75L	18 July, 1967	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	2 km N Tamanaco, near San Juan, Río Manapiare, T. F. Amazonas	88L	17-19 August, 1967	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	20 km SSE Puerto Ayacucho Las Queseras, Harder	8L	24 September, 1967	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	23 km NW Valera, near Agua Santa, Trujillo	8L	24 August, 1965	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	35 km NW Pto. Cabello, Boca de Yaracuy, Yaracuy and Falcón	92L	22, 29 October, 1965; 2 October, 1965	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	38 km NW Pto. Paez, Río Cinaruco, Apure	255L	17 January 1966	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	42 km WNW ENcontrados, El Rosario, Zulia	4L	5 March, 1968	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	46 km NE Pto. Paez, Hato Caribean, Rio Cinaruco, Apure	2M, 4F, 3N, 863L	15 July 1965-17 January, 1966	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	5 km E Río Chico, nr. Puerto Tuy, Miranda	59L	5, 17 September, 1966	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	About 10 km NW Urama, Yaracuy	1L	11 March, 1966	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	About 10 km NW Urama, Yaracuy	3L	14 March, 1966	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	Moracoy, near San Juan, W side Río Manapiare, Harder	105L	24 July, 1967	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	Near Moracoy, ca. 15 km down Río Manapiare from San Juan, Harder	100L	14 July, 1967	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	Near San Juan, E side Rio Manapiare, Harder	1L	19 July, 1967	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	San Juan, Río Manapiare, Harder	57L	14 July, 1967	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	San Juan Río Manapiare, Harder	100L	20 July, 1967	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	W side Río Manapiare. near San Juan, Harder	200L	24 July, 1967	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	Yaracuy-Carabobo border, NW of Urama, Yaracuy and Carabobo	54L	17 March, 1966	NR	Jones *et al*. 1972
	Noctilio leporinus/Myotis albescens	Greater Bulldog Bat/Silver-tipped Myotis	Venezuela	Ca. 2 km N Tamanaco, nr. San Juan, Río Manapiare, Harder	11L	18, 26 July, 1967	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	10 km E Río Chico nr. Ticarigua La Laguna, Miranda	50L	9 November, 1966	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	21 km E Cumaná, Hda. Tunantal, Sucre	51L	10, 17 December, 1966	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	38 km NW Pto. Paez, Río Cinaruco, Apure	1L	13 January, 1966	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	42 km WNW ENcontrados, El Rosario, Zulia	2L	5, 28 March, 1968	NR	Jones *et al*. 1972
	Noctilio leporinus	Greater Bulldog Bat	Venezuela	5 km E Río Chico nr. Puerto Tuy, Miranda	5L	17 November, 1966	NR	Jones *et al*. 1972
	Noctilio sp.	NR	Panama	Gamboa (canal Zone), pipeline road	NR	May 14, 1962	NR	Fairchild *et al*. 1965
Phyllostomidae	*Artibeus jamaicensis*	Jamaican Fruit-eating Bat	Colombia	NR	54	NR	NR	Marinkelle and Grose 1981
	Artibeus jamaicensis s.l.	Jamaican Fruit-eating Bat	Venezuela	14 km S, 45 Km E Caicara, Hato La Florida, Bolivar	35L	NR	NR	Jones *et al*. 1972
	Artibeus jamaicensis s.l.	Jamaican Fruit-eating Bat	Venezuela	5 km NW Guasipati, Bolivar	6L	29 April, 1966	NR	Jones *et al*. 1972
	Artibeus jamaicensis s.l.	Jamaican Fruit-eating Bat	Venezuela	San Juan Río Manapiare, Harder	1L	24 July, 1967	NR	Jones *et al*. 1972

	Artibeus lituratus	Great Fruit-eating Bat	Brazil	Pinheiros, Espírito Santo	17L	2012	NR	Acosta *et al*. 2016
	Artibeus lituratus	Great Fruit-eating Bat	Costa Rica	Majica Ranch, Guanacaste Province	16L	August 10, 1960	NR	Kohls *et al*. 1965
	Artibeus planirostris	Flat-faced Fruit-eating Bat	Brazil	Mato Grosso do Sul state	289 L	2006-2008	NR	Muñoz-Leal *et al*. 2016
	Artibeus planirostris	Flat-faced Fruit-eating Bat	Brazil	Private Reserve of the Natural Patrimony Serra das Almas, Municipality of Crateús, state of Ceará	296L	July 2012, February 2013	NR	Luz *et al*. 2019
	Artibeus planirostris	Flat-faced Fruit-eating Bat	Brazil	southeastern region of the Amapá state	160L	October 2016 and November 2017	1 pool Candidatus R. wissemanii	Luz *et al*. 2019
	Carolia perspicillata	Seba's Short-tailed Bat	Brazil	Tamandaré, Pernambuco	34L, 17N	May-15	NR	Muñoz-Leal *et al*. 2018
	Carollia perspicillata	Seba's Short-tailed Bat	Venezuela	W side Río Manapiare, near San Juan, Harder	1L	24 July, 1967	NR	Jones *et al*. 1972
	Carollia sp.	-	Venezuela	Near Tamanaco, ca. 4 km NE San Juan, Río Manapiare, Harder	1L	19 July, 1967	NR	Jones *et al*. 1972
	Chiroderma salvini	Salvin's Big-eyed Bat	Venezuela	3 km N, 4 km W Caripe, San Agustin, Monagas	1L	27 July, 1967	NR	Jones *et al*. 1972
	Desmodus rotundus	Common Vampire Bat	Venezuela	35 km NW Pto. Cabello, Boca de Yaracuy, Yaracuy and Falcón	1L	30 October, 1965	NR	Jones *et al*. 1972
	Desmodus rotundus	Common Vampire Bat	Venezuela	38 km NW Pto. Paez, Río Cinaruco, Apure	1L	13 January, 1966	NR	Jones *et al*. 1972
	Glossophaga longirostris	Miller's Long-tongued Bat	Venezuela	46 km NE Pto. Paez, Hato Cariben, Rio Cinaruco, Apure	1L	July 14 1965	NR	Jones *et al*. 1972
	Glossophaga soricina	Pallas's Long-tongued Bat	Brazil	Serinhaém, Pernambuco	3L	November, 2008	NR	Muñoz-Leal *et al*. 2018
	Lonchorhina orinocensis	Orinocoan Sword-nosed Bat	Venezuela	46 km NE Pto. Paez, Hato Cariben, Rio Cinaruco, Apure	1L	24 July 1965	NR	Jones *et al*. 1972
	Lophostoma brasiliense	Pygmy Round-eared Bat	Brazil	Private Reserve of the Natural Patrimony Serra das Almas, Municipality of Crateús, state of Ceará	6L	July 2012, February 2013	NR	Luz *et al*. 2019
	Lophostoma silvicola	White-Throated Round-Eared Bat	Panama	Las Palmitas (Los Santos)	NR	January-February, 1962	NR	Fairchild *et al*. 1965
	Gardnerycteris crenulatum	Striped Hairy-nosed Bat	Brazil	Mato Grosso do Sul state	3L	2006-2008	NR	Muñoz-Leal *et al*. 2016
	Gardnerycteris crenulatum	Striped Hairy-nosed Bat	Venezuela	19 km NW Urama Km 40, Yaracuy and Carabobo	5L	26 October, 1965	NR	Jones *et al*. 1972
	Phyllostomus discolor	Pale spear-nosed bat	Colombia	NR	1	NR	NR	Marinkelle and Grose 1981
	Phyllostomus hastatus	Greater Spear-nosed Bat	Brazil	Mato Grosso do Sul state	55L	2006-2008	NR	Muñoz-Leal *et al*. 2016
	Phyllostomus hastatus	Greater Spear-nosed Bat	Venezuela	13 km NW Urama, Río Yaracuy, Yaracuy	4L	20 March, 1966	NR	Jones *et al*. 1972
	Phyllostomus hastatus	Greater Spear-nosed Bat	Venezuela	23 km NW Valera, near Agua Santa, Trujillo	2L	18 October, 1965	NR	Jones *et al*. 1972
	Phyllostomus hastatus	Greater Spear-nosed Bat	Venezuela	5 km S, 25 km E Carúpano, Manacal, Sucre	1L	3 August, 1966	NR	Jones *et al*. 1972
	Phyllostomus hastatus	Greater Spear-nosed Bat	Venezuela	6 km N Urama, Carabobo	9L	17 March, 1966	NR	Jones *et al*. 1972
	Phyllostomus hastatus	Greater Spear-nosed Bat	Venezuela	About 11 km NW Urama, near El Central, Yaracuy	2L	14 March, 1966	NR	Jones *et al*. 1972
	Phyllostomus hastatus	Greater Spear-nosed Bat	Venezuela	Moracoy, near Río Manapiare, Harder	25L	13 July, 1967	NR	Jones *et al*. 1972
	Phyllostomus hastatus	Greater Spear-nosed Bat	Venezuela	San Juan, Río Manapiare, Harder	1L	17 July, 1967	NR	Jones *et al*. 1972
	Phyllostomus hastatus	Greater Spear-nosed Bat	Venezuela	Near Moracoy, 15 km down Río Manapiare from San Juan, Harder	1L	NR	NR	Jones *et al*. 1972
	Phyllostomus hastatus	Greater Spear-nosed Bat	Venezuela	San Juan, Río Manapiare, Harder	1L	17 July, 1967	NR	Jones *et al*. 1972
	Phyllostomus hastatus	Greater Spear-nosed Bat	Venezuela	San Juan, Río Manapiare, Harder	50L	17 July, 1967	NR	Jones *et al*. 1972
	Platyrrhinus helleri	Heller's Broad-Nosed Bat	Panama	Las Palmitas (Los Santos)	NR	January-February, 1962	NR	Fairchild *et al*. 1965
	Platyrrhinus lineatus	White-lined Broad-nosed Bat	Brazil	Mato Grosso do Sul state	12 L	2006-2008	NR	Muñoz-Leal *et al*. 2016
	Sturnira giannae	Gianna's Yellow-shouldered Bat	Venezuela	4 km NNW Caracas, Distrito Federal	8L	23 July, 1965	NR	Jones *et al*. 1972
	Sturnira lilium	Little Yellow-shouldered Bat	Brazil	Caetité, Bahía	19L	December 2014	NR	Muñoz-Leal *et al*. 2018
	Sturnira lilium	Little Yellow-shouldered Bat	Venezuela	14 km E Cumaná, Hda. Guanital, Sucre	30L	8-9 December, 1966	NR	Jones *et al*. 1972
	Tonatia bidens	Greater Round-eared Bat	Brazil	Private Reserve of the Natural Patrimony Serra das Almas, Municipality of Crateús, state of Ceará	10L	July 2012, February 2013	NR	Luz *et al*. 2019
	Tonatia sp.	-	Brazil	Private Reserve of the Natural Patrimony Serra das Almas, Municipality of Crateús, state of Ceará	4L	July 2012, February 2013	NR	Luz *et al*. 2019
	Uroderma bilobatum	Tent-Making Bat	Panama	Las Palmitas (Los Santos)	NR	January-February, 1962	NR	Fairchild *et al*. 1965
	Uroderma magnirostrum	Brown Tent-making Bat	Venezuela	Near San Juan, Río Manapiare, Harder	20L	17 July, 1967	NR	Jones *et al*. 1972
Vespertilionidae	*Aeorestes cinereus*	Hoary bat	Colombia	NR	1	NR	NR	Marinkelle and Grose 1981

		Eptesicus diminutus	Diminutive Serotine	Argentina	Sociedad Rural "Las Colonias", Esperanza city	3L	January 2018	3L Candidatus "R. wissemanii"	Colombo *et al*. 2020
		Eptesicus furinalis	Argentinian Brown Bat	Argentina	Cululú river banks, town of Cululú	4L	January 2018	NR	Colombo *et al*. 2020
		Eptesicus furinalis	Argentinian Brown Bat	Argentina	Santa Fe de la Veracruz city	3L	November 2017	NR	Colombo *et al*. 2020
		Eptesicus orinocensis	Orinoco brown bat	Colombia	Vereda El Socorro, Finca Los Trompillos, municipality of Arauca, Department of Arauca, Orinoquia region	33L	1 November 2021	NR	Ossa-López *et al*. 2023
		Eptesicus sp.	-	Argentina	Santa Fe de la Veracruz city	7L	November 2017	NR	Colombo *et al*. 2020
		Myotis nigricans	Black Myotis	Venezuela	Gueiira	NR	NR	NR	Schulze 1935
		Myotis velifer velifer	Cave Myotis	Mexico	Santa Lucía, Sinaloa	1L	July 28, 1963	NR	Kohls *et al*. 1965
		Rhogeessa minutilla	Tiny Yellow Bat	Venezuela	114 km N, 32 km W Maracaibo near Cojoro, Zulia	4L	24 June, 1968	NR	Jones *et al*. 1972
		Rhogeessa parvula	Little yellow bat	Colombia	NR	2	NR	NR	Marinkelle and Grose 1981
		Rhogeessa sp.	-	Venezuela	19 km NW Urama, Yaracuy	4L	9 March, 1966	NR	Jones *et al*. 1972
Rodentia	Cricetidae	*Necromys urichi*	Northern Grass Mouse	Venezuela	3 km N, 4 km W Caripe, San Agustín, Monagas	1L	24 June 1967	NR	Jones *et al*. 1972
Questing	NR	Tree hole	NR	Brazil	Marajó Island, Belém, Pará	1F	June 1941	NR	Cooley and Kohls 1944
	NR	Bat guano	NR	Panama	Pacora	Members of all life cycle	June 21, 22, July 26, 1961	NR	Fairchild *et al*. 1965

Appendix 2

Primers used for molecular detection of tickborne pathogens.

Parasite	Gene	Primers	Size (bp)	Positive control	Reference
Protozoa					
Babesia spp.	18S rDNA	**BAB01** CCGTGCTAATTGTAGGGCTAATACA **BAB02** GCTTGAAACACTCTARTTTTCTCAAAG	571	*Babesia bigemina* [MZ798903]	Almeida *et al*. 2012
Hepatozoon spp.	18S rDNA	**HepF300** GTTTCTGACCTATCAGCTTTCGACG **HepR900** CAAATCTAAGAATTTCACCTCTGAC	495	*Hepatozoon* spp. from *Crotalus molossus* [MT385834]	Ujvari *et al*. 2004
Bacteria					
Anaplasma/Ehrlichia spp.	16S rDNA	**EHR01F** GCCTAACACATGCAAGTCGAACG **EHR02R** GCCCAATAATTCCGAACAACG	495	*Anaplasma marginale* [MN453603]	Murphy *et al*. 2017
Bartonella spp.	gltA	**BhCS781.p** GGGGACCAGCTCATGGTGG **BhCS1137.n** AATGCAAAAAGAACAGTAAACA	379	*Bartonella quintana* [OM108475]	Norman *et al*. 1995
Borrelia spp.	flaB	**FlaoutF** AARGAATTGGCAGTTCAATC **FlaoutR** GCATTTTCWATTTTAGCAAGTGATG	470	*Borrelia burgdorferi* [MK370994]	Rudenko *et al*. 2009
Coxiella spp.	23S rDNA	**QR-FO** ATTGAAGAGTTTGATTCTGG **QR-RO** CGGCCTCCCGAAGGTTAG	1000	*Coxiella* endosymbiont of *Amblyomma mixtum* [OM307605]	Masuzawa *et al*. 1997
Rickettsia spp.	gltA	**RpCS.415** GCTATTATGCTTGCGGCTGT **RpCS.1220** TGCATTTCTTTCCATTGTGC	806	*Rickettsia amblyommatys* [MW539675]	de Sousa *et al*. 2006