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First Molecular Evidence of *Hepatozoon* spp. in the Mexican Black-Tailed Rattlesnake (*Crotalus molossus nigrescens*) from an Urban Ecological Reserve in Central Mexico

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Abstract

Species of the genus *Hepatozoon* are among the most widespread haemogregarine parasites infecting reptiles; however, information regarding their occurrence in native snakes from Mexico remains scarce. This study investigated the molecular occurrence of *Hepatozoon* spp. in free-ranging Mexican black-tailed rattlesnakes (*Crotalus molossus nigrescens*) rescued within the Reserva Ecológica del Pedregal de San Ángel (REPSA), an urban protected area in central Mexico. Opportunistically sampled squirrels were also included to explore the occurrence of these parasites in sympatric mammals. Blood samples from 26 rattlesnakes, six Mexican gray squirrels (*Sciurus aureogaster*), and three rock squirrels (*Otospermophilus variegatus*) were screened by PCR targeting a partial fragment of the 18S rRNA gene. *Hepatozoon* spp. DNA was detected in six rattlesnakes (23.1%) and two Mexican gray squirrels (33.3%), whereas all rock squirrels tested negative. Phylogenetic analyses suggested the presence of two distinct *Hepatozoon* lineages: one showing phylogenetic affinity with *Hepatozoon* cf. *ophiosauri*, detected in all positive rattlesnakes and one squirrel, and another closely related to *Hepatozoon griseisciuri*, identified in a second squirrel. These findings represent the first molecular detection of *Hepatozoon* in *C. molossus nigrescens*, the first record of infection in *S. aureogaster*, and the first report of a *H. griseisciuri*-like lineage in Mexico. Although parasite identification was based exclusively on partial 18S rRNA gene sequences, this study expands current knowledge of *Hepatozoon* diversity in Mexican wildlife and provides important baseline information for future studies integrating molecular, morphological, and ecological approaches to better understand parasite diversity and transmission in protected urban ecosystems.

Keywords: *Hepatozoon*; haemogregarines; rattlesnake; squirrel; wildlife disease; phylogeny; urban protected area; Mexico

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1. Introduction

Species of the genus *Hepatozoon* are among the most widespread haemogregarine parasites infecting terrestrial vertebrates and have been reported from a broad diversity of amphibians, reptiles, birds, and mammals worldwide. Their life cycle is heteroxenous, involving hematophagous arthropods as definitive hosts and vertebrates as intermediate hosts, where asexual development occurs. Unlike many other vector-borne protozoa, transmission of *Hepatozoon* generally occurs through the ingestion of infected arthropods, although predation and vertical transmission have also been documented in some vertebrate groups, particularly reptiles [1]. Snakes are considered one of the principal vertebrate hosts of *Hepatozoon* species and play an important role in the maintenance of these parasites in natural ecosystems. Infection has been reported in numerous snake species from different geographic regions, where transmission is thought to occur through the consumption of infected prey, including amphibians, lizards, and small mammals, or, less frequently, by ingestion of infected hematophagous arthropods [2–5]. Although most infections appear to be subclinical, some *Hepatozoon* species have been associated with hematological alterations and reduced fitness, highlighting their potential relevance for wildlife health and conservation. Mexico harbors one of the richest snake faunas in the world; however, the diversity and distribution of *Hepatozoon* species infecting native snakes remain poorly understood. To date, *Hepatozoon* infections in snakes from Mexico have been documented only sporadically. The parasite was originally described as *Hepatozoon fusifex* from free-ranging *Boa constrictor* in Sinaloa and was later reported microscopically in captive *B. constrictor* from Colima [6,7]. More recently, molecular evidence confirmed the presence of *Hepatozoon* spp. in the pine snake *Pituophis deppei* as part of a broader survey of Mexican squamate reptiles, highlighting the genetic diversity of these parasites in the country [6,8]. Squirrels (family *Sciuridae*) are among the most common small mammals inhabiting natural and urban ecosystems throughout Mexico and constitute an important prey resource for numerous predatory reptiles, including rattlesnakes. Through these trophic interactions, squirrels may participate in the transmission cycles of parasites exhibiting predator–prey life histories, such as species of the genus *Hepatozoon*. Although infections with *Hepatozoon* spp. have been documented in gray squirrels (*Sciurus carolinensis*) in North America and red squirrels (*Sciurus vulgaris*) in Europe, no molecular studies have investigated these parasites in native Mexican squirrels [9–11]. Therefore, evaluating sympatric squirrel populations may provide valuable information on potential mammalian hosts involved in the local ecology and circulation of *Hepatozoon* spp. within wildlife communities. The Mexican black-tailed rattlesnake (*Crotalus molossus nigrescens*) is a native pit viper widely distributed in central Mexico and represents one of the characteristic predators of the xerophytic ecosystems of the "Reserva Ecológica del Pedregal de San Ángel" (REPSA), an urban protected area located within Mexico City. This reserve preserves one of the last remnants of the original volcanic ecosystem of the Valley of Mexico and supports a high diversity of native vertebrates living under increasing anthropogenic pressure [12,13]. Understanding the diversity of parasites circulating within wildlife populations inhabiting this reserve contributes not only to the knowledge of host–parasite associations but also to conservation medicine and long-term wildlife health surveillance. Therefore, the aim of this study was to investigate the molecular occurrence and phylogenetic relationships of *Hepatozoon* spp. infecting free-ranging *C. molossus nigrescens* from the REPSA. In addition, sympatric squirrels were included because of their ecological relevance as potential prey species and their possible participation in the local transmission cycle of these haemogregarines.

2. Materials and Methods

This study was conducted at the REPSA, a protected ecological reserve located within the campus of the Universidad Nacional Autónoma de México (UNAM) in southern Mexico City (19°18′31″–19°19′17″ N, 99°10′20″–99°11′52″ W). The reserve covers approximately 237 ha and preserves one of the last remnants of the original xerophytic volcanic ecosystem of the Valley of Mexico. Its heterogeneous landscape, characterized by lava fields, crevices, rocky outcrops, and native vegetation, provides suitable habitat for a diverse assemblage of reptiles, mammals, and other wildlife. As part of the wildlife rescue and relocation program coordinated by the Executive Secretariat of the REPSA, free-ranging Mexican black-tailed rattlesnakes (*C. molossus nigrescens*) reported within the university campus were rescued between August 2016 and September 2018. Snakes were captured using herpetological hooks and safely restrained with transparent acrylic tubes for blood collection. Sex was determined using a lubricated cloacal probe, and age class was estimated based on body size and field observations. A total of 26 rattlesnakes were sampled, including 16 males, eight females, and two individuals whose sex could not be determined. Opportunistically, six Mexican gray squirrels (*Sciurus aureogaster*) and three rock squirrels (*Otospermophilus variegatus*) admitted to the wildlife management program during the same period were also sampled because they represent potential prey species for rattlesnakes and could participate in the transmission cycle of *Hepatozoon*. Mammals were captured using Tomahawk live traps baited with oatmeal and chemically restrained using ketamine combined with xylazine or dexmedetomidine before blood collection. Approximately 0.4–0.8 mL of blood per 100 g of body weight was collected into EDTA tubes. After clinical examination, all animals were identified with microchips or natural markings and subsequently released at appropriate sites within the reserve. All procedures were carried out under permits issued by the Mexican Ministry of Environment and Natural Resources (SEMARNAT; SGPA/DGVS/03670/2015 and SGPA/DGVS/005615/18). Genomic DNA was extracted individually from 200 µL of whole blood using a 10% Chelex® 100 resin protocol (Bio-Rad Laboratories, Hercules, CA, USA) following the method described by García-González et al. [14]. DNA was recovered after centrifugation and stored at −20 °C until molecular analysis. Detection of *Hepatozoon* spp. DNA was performed by conventional PCR targeting an approximately 600 bp fragment of the 18S rRNA gene using primers HepF300 (5′-GTTTCTGACCTATCAGCTTTCGACG-3′) and HepR900 (5′-CAAATCTAAGAATTTCACCTCTGAC-3′) under previously described amplification conditions [15]. Each PCR reaction was carried out in a final volume of 25 µL containing 12.5 µL of GoTaq® Green Master Mix (2×; Promega Corporation, Madison, WI, USA), 0.5 µM of each primer, 2 µL of genomic DNA template, and nuclease-free water to the final reaction volume. A no-template control containing ultrapure water instead of DNA was included in every PCR assay. Amplification products were separated by electrophoresis on 2% agarose gels stained with SmartGlow® DNA stain (Accuris Instruments, Edison, NJ, USA) and visualized under ultraviolet illumination. Positive amplicons were purified using Agencourt AMPure XP magnetic beads (Beckman Coulter, Brea, CA, USA) and bidirectionally sequenced using the BigDye™ Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) on an ABI 3730XL Genetic Analyzer (Applied Biosystems, Foster City, CA, USA). Sequencing was performed by Macrogen Inc. (Seoul, Republic of Korea). Raw chromatograms were visually inspected, trimmed, and assembled into consensus sequences using Chromas version 2.6.6 (Technelysium Pty Ltd., South Brisbane, Australia). Consensus sequences were compared against the National Center for Biotechnology Information (NCBI) GenBank database using the BLASTn (https://blast.ncbi.nlm.nih.gov/Blast.cgi (accessed on 7 August 2026)) algorithm (National Center for Biotechnology Information, Bethesda, MD, USA) for preliminary taxonomic

identification. Representative *Hepatozoon* sequences retrieved from GenBank were aligned with those generated in the present study using the ClustalW algorithm implemented in MEGA version 11.0.13. The final multiple sequence alignment consisted of 587 bp after trimming ambiguous positions. The best-fitting nucleotide substitution model was selected according to the corrected Akaike Information Criterion (AICc). Phylogenetic relationships were reconstructed using the Maximum Likelihood method implemented in IQ-TREE version 2.2.2 with 10,000 ultrafast bootstrap replicates. Alignment gaps were excluded from all analyses.

3. Results

The nucleotide sequences generated during this study were deposited in GenBank under accession numbers ON183251–ON183258 as *Hepatozoon* spp., reflecting the limited taxonomic resolution of partial 18S rRNA sequences for definitive species-level identification. Consequently, the taxonomic hypotheses presented in the phylogenetic analysis are based on sequence clustering with reference isolates and should be regarded as tentative rather than definitive species identifications. Conventional PCR targeting the 18S rRNA gene detected *Hepatozoon* spp. DNA in six of the 26 *C. molossus nigrescens* individuals, corresponding to a molecular prevalence of 23.1% (6/26). Two of the six *S. aureogaster* (33.3%; 2/6) were also positive, whereas none of the three *O. variegatus* yielded positive amplification products. BLASTn analysis assigned all sequences to the genus *Hepatozoon*. The six sequences obtained from *C. molossus* nigrescens and one sequence from *S. aureogaster* showed 100% nucleotide identity with a GenBank reference sequence currently annotated as *Hepatozoon* cf. *ophiosauri* (MN723845.1). The remaining sequence obtained from *S. aureogaster* exhibited 99.47% nucleotide identity with *Hepatozoon griseisciuri* (MK452253.1). Because partial 18S rRNA gene sequences provide limited taxonomic resolution within the genus *Hepatozoon*, these phylogenetic affinities are interpreted as tentative lineage assignments rather than definitive species identifications. Phylogenetic reconstruction using the Maximum Likelihood method recovered two distinct *Hepatozoon* lineages. The first clade included all sequences obtained from *C. molossus nigrescens*, one sequence from *S. aureogaster*, and the reference sequence of *H.* cf. *ophiosauri*, with a bootstrap support of 70%. The second clade comprised the remaining *S. aureogaster* sequence together with *H. griseisciuri* and additional *Hepatozoon* isolates previously reported from *Sciurus carolinensis*, with bootstrap support values of 90% and 97%, respectively (Figure 1).

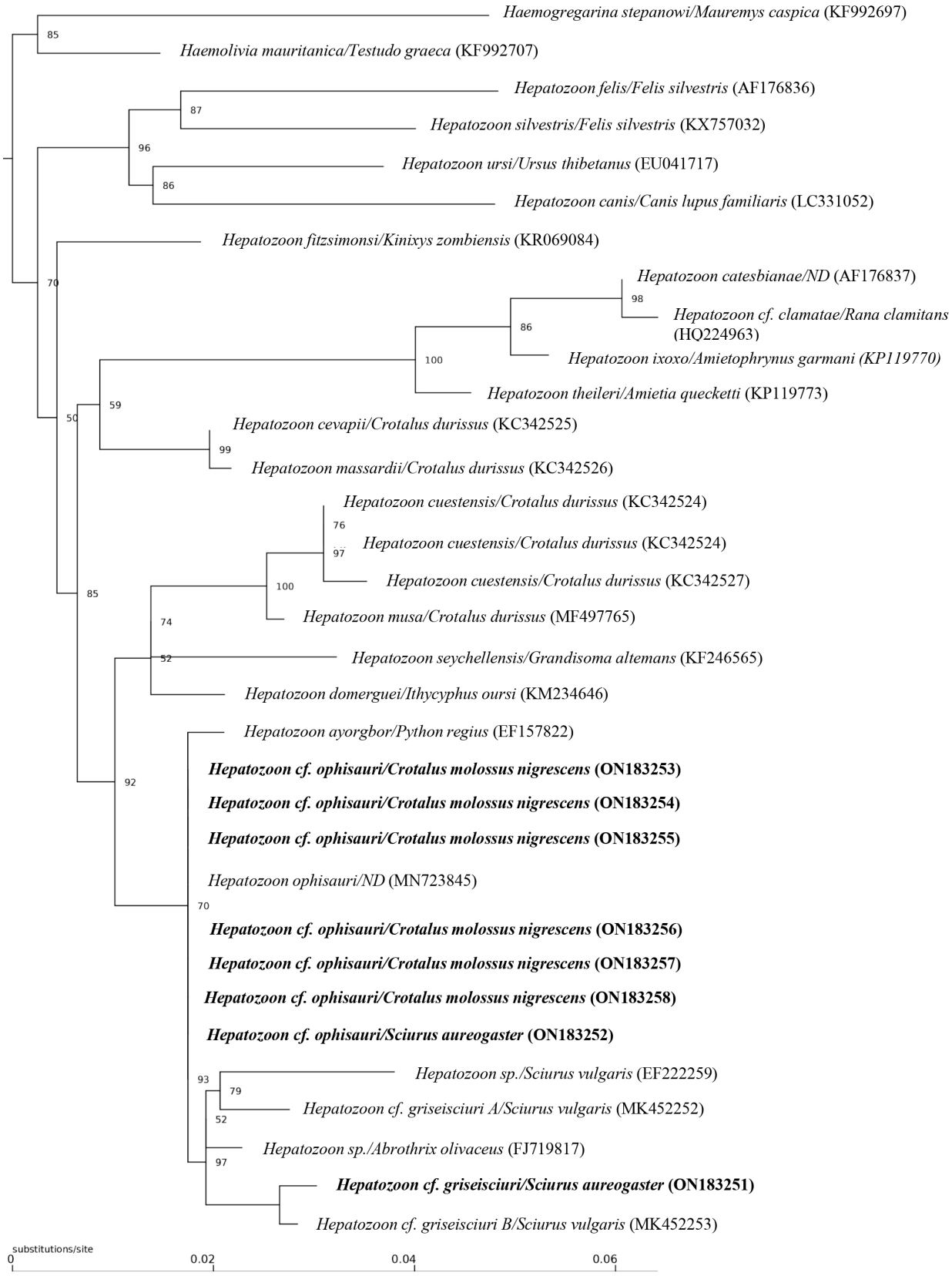


Figure 1. Phylogenetic tree based on a 587 bp alignment of the 18S rRNA gene of adeleorinid haemogregarines. Analysis was reconstructed using the Maximum Likelihood method under the GTR + G model. Sequences of the genera *Adelina* and *Klossia* were used as outgroups. Sequences obtained in the present study are shown in bold. The lineage detected in rattlesnakes and one *S. aureogaster* specimen is tentatively referred to as *H.* cf. *ophiosauri* following a conservative taxonomic approach based on partial 18S rRNA sequences.

4. Discussion

The molecular detection of two distinct *Hepatozoon* lineages in sympatric reptiles and mammals expands the currently recognized host range of these haemogregarines in Mexico and provides new insights into their circulation within the REPSA. Previous reports from Mexico have been limited to the description of *H. fusifex* in free-ranging *B. constrictor*, a microscopic report in captive *B. constrictor*, and the molecular detection of *Hepatozoon* spp. in *Pituophis deppei* and other squamate reptiles [6–8]. Our findings therefore extend both the known host range and the geographic occurrence of *Hepatozoon* spp. infecting native wildlife in Mexico.

Phylogenetic analyses showed that all rattlesnake isolates clustered with GenBank sequences currently annotated as *H.* cf. *ophiosauri*. Although *H. ophiosauri* has been morphologically redescribed, the reference sequences included in our phylogenetic analysis are not directly associated with comprehensive morphological characterization of the corresponding isolates. Furthermore, partial 18S rRNA gene sequences alone provide limited resolution for distinguishing closely related *Hepatozoon* species. Therefore, following current recommendations, we conservatively refer to the lineage detected in this study as *H.* cf. *ophiosauri*, pending confirmation using additional molecular markers and morphological evidence [16].

The apparent discrepancy between the GenBank annotations and the phylogenetic interpretation presented here reflects different objectives rather than conflicting taxonomic conclusions. The nucleotide sequences generated in this study were deposited in GenBank under accession numbers ON183251–ON183258 as *Hepatozoon* spp., because species-level assignment based solely on partial 18S rRNA sequences was considered insufficiently robust. Consequently, the taxonomic hypotheses presented in the phylogenetic analysis are based on sequence clustering with reference isolates and should be regarded as tentative rather than definitive species identifications.

One squirrel isolate clustered within the same lineage detected in rattlesnakes, whereas the second grouped with *H. griseisciuri*. This finding represents the first molecular detection of *Hepatozoon* spp. in *S. aureogaster* and the first report of a *H. griseisciuri*-like lineage in Mexico. Genetically related *Hepatozoon* lineages have previously been reported in the eastern gray squirrel (*Sciurus carolinensis*) in the United States and the Eurasian red squirrel (*Sciurus vulgaris*) in the United Kingdom [9–11]. The occurrence of closely related *Hepatozoon* lineages in sympatric squirrels and rattlesnakes is particularly noteworthy because both host species coexist within the REPSA and may participate in the same ecological transmission network [13]. The detection of a *H.* cf. *ophiosauri*-like lineage in both sympatric rattlesnakes and one Mexican gray squirrel suggests that predator–prey interactions may contribute to the maintenance of this parasite within the REPSA ecosystem. Similar ecological scenarios have been proposed for reptile-associated *Hepatozoon* species, in which vertebrate prey become infected after ingesting infected arthropod vectors and may subsequently act as intermediate or paratenic hosts, facilitating parasite transmission to predatory reptiles through trophic interactions [1,17]. Although the present study was not designed to identify the definitive arthropod vector or experimentally demonstrate transmission, the phylogenetic clustering of parasites detected in both host groups is consistent with the hypothesis of a shared ecological transmission network. Future studies integrating vertebrate hosts, hematophagous arthropod vectors, blood smear examination, histopathology, and multilocus molecular analyses will be essential to clarify the transmission dynamics and life cycle of these parasites in this urban protected ecosystem.

The detection of *Hepatozoon* spp. in apparently healthy free-ranging animals agrees with previous studies indicating that these haemogregarines frequently establish subclinical infections in wildlife [1,16,17]. Although their pathogenic significance remains poorly

understood in most wild vertebrates, documenting parasite diversity contributes to understanding host–parasite interactions and provides valuable baseline information for wildlife health surveillance and conservation programs in protected areas such as the REPSA.

This study has some limitations. Sampling was opportunistic and restricted to animals admitted to the wildlife rescue and relocation program, resulting in a relatively small sample size. Parasite identification was based exclusively on partial 18S rRNA gene sequences, which provide limited taxonomic resolution for species-level identification within the genus *Hepatozoon*. In addition, blood smears were not prepared during field sampling; therefore, microscopic examination of circulating gamonts and morphological characterization of the parasites were not possible. Because haemogregarine taxonomy ideally relies on the integration of molecular and morphological evidence, the absence of visual confirmation represents an important limitation of the present study. Likewise, histopathological examinations and ectoparasite collections were not available, preventing the integration of molecular, morphological, pathological, and vector-related data.

5. Conclusions

This study documents the occurrence of two *Hepatozoon* lineages infecting free-ranging wildlife from the REPSA, including the first molecular detection of *Hepatozoon* spp. in *C. molossus nigrescens* and the first molecular record of *Hepatozoon* spp. in *S. aureogaster*. Although parasite identification was based exclusively on molecular evidence, these findings provide an important baseline for future studies integrating morphological, molecular, and ecological approaches to clarify the diversity, transmission dynamics, and host associations of *Hepatozoon* spp. in Mexican wildlife.

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Informed Consent Statement: Not applicable.

Data Availability Statement: The nucleotide sequences generated in this study have been deposited in the GenBank database under accession numbers ON183251–ON183258. All other data supporting the findings of this study are available from the corresponding author upon reasonable request.

Conflicts of Interest: The authors declare no conflicts of interest.

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