

New morphological records of haemogregarines (Apicomplexa: Hepatozoidae) in caimans from the Atlantic Forest and the Amazon rainforest of Brazil

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South America is home to a remarkable diversity of reptiles, including six recognised species of caimans (family Alligatoridae), which are distributed into the genera *Caiman*, *Melanosuchus*, and *Paleosuchus* (King and Burke, 1989; Da Silveira, 2002; Marioni et al., 2021). However, recent taxonomic studies identified cryptic species within the genera *Caiman* and *Paleosuchus*, suggesting that the actual diversity of caimans may be underestimated (Bittencourt et al., 2019; Roberto et al., 2020). These crocodilians serve critical ecological functions as top predators, and act as long-lived hosts for a variety of parasites (Rueda-Almonacid et al., 2007; Tellez and Sung, 2018; Eugenia et al., 2025).

Parasitic taxa recorded from South American caimans include: digeneans (Catto and Amato, 1993, 1994); nematodes (Molin, 1858; Travassos, 1933; Cardoso et al., 2012); pentastomid (Junker and Boomker, 2006); leeches (Fermino et al., 2015) and blood protozoans such as trypanosomatids (Lainson, 1977; Fermino et al., 2015), haemosporidians (Lainson, 1995), and haemogregarines (Carini, 1909; Lainson et al., 2003). Haemogregarines of the genus *Hepatozoon*, particularly *Hepatozoon caimani* described by Carini (1909) and redescribed by Lainson et al. (2003), are the most

common blood parasites observed in Brazilian caimans (Viana and Marques, 2005; Viana et al., 2010a; Bouer et al., 2017; Soares et al., 2017; Clemente et al., 2023; Úngari et al., 2024).

Hepatozoon caimani is primarily transmitted by mosquitoes of the genus *Culex* (Pessôa et al., 1972; Lainson et al., 2003), with *Culex (Melanoconion) theobaldi* (Lutz, 1904) (Viana et al., 2010b) implicated in natural infections. Its life cycle includes fish, amphibians, and small caimans as paratenic hosts (Viana et al., 2012; Pereira et al., 2014; Cardoso et al., 2022). This species has been documented in four of the six Brazilian caiman species: *Caiman crocodilus* (Linnaeus, 1758), *Caiman latirostris* (Daudin, 1801), *Caiman yacare* (Daudin, 1801), and *Paleosuchus palpebrosus* (Cuvier, 1807) (Carini, 1909; Lainson et al., 2003; Soares et al., 2017; Clemente et al., 2023). Moreover, *Paleosuchus trigonatus* (Schneider, 1801) is the type host of *Hepatozoon serrei* (Physalix, 1914), and *Melanosuchus niger* (Spix, 1825) had records of unidentified haemogregarines (Smith, 1996; Lainson et al., 2003). Interestingly, Lainson et al. (2003) suggested that all caiman species may potentially harbour *H. caimani*.

Recent advancements in microscopy, histopathology, and molecular analyses have uncovered a complex of genotypes within *Hepatozoon* spp., indicating the presence of multiple cryptic species infecting Brazilian caimans (Úngari et al., 2024). These findings highlight the necessity for thorough studies on the distribution, diversity, and host associations of these haemogregarines across different biomes. Such research is essential for understanding their ecological roles, transmission dynamics, and potential impact on both the health of caimans and their conservation.

To address *Hepatozoon* infections in caimans, we conducted fieldwork in two Brazilian biomes from 2020 to 2023 (Fig. 1; Table 1). In the Atlantic Forest

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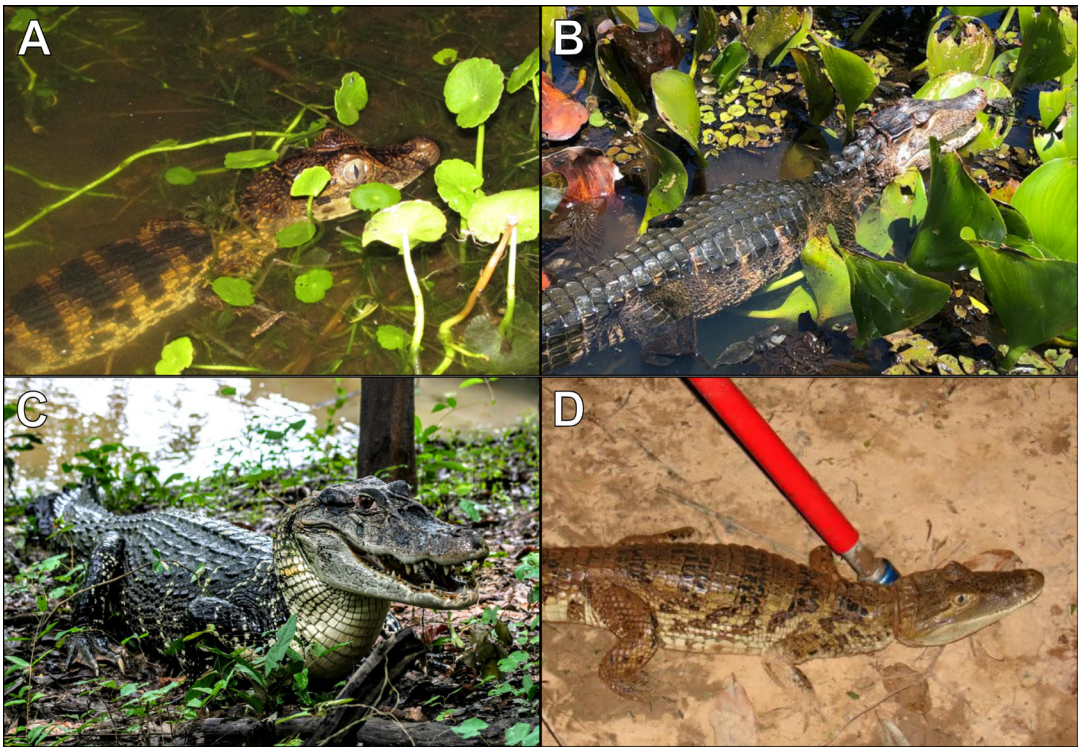


Figure 1. Caiman species sampled in this study from Brazil. Atlantic Forest areas: (A) *Caiman latirostris* and (B) *Paleosuchus palpebrosus*. Amazon region: (C) *Melanosuchus niger* and (D) *Caiman crocodilus*. Photos by Marcos E. Coutinho (A, B) and Joilson M. de Barros (C, D).

biome, three sites in the state of Alagoas were sampled: two conservation units, Reserva Extrativista Marinha Lagoa do Jequiá (10.0048°S; 36.0228°W, elevation 20 m) and Área de Proteção Ambiental Marituba do Peixe (10.3131°S; 36.3697°W, elevation 120 m); and one human altered area, Lagoa do Guaxuma (9.5897°S,

35.6661°W, elevation 10 m). In the Amazon biome, sampling was performed at Reserva Extrativista do Lago Cuniã (8.3187°S, 63.4968°W, elevation 90 m) in the state of Rondônia.

Caimans were captured during night surveys using a noose on a pole and were then immobilised with

Table 1. Occurrence of *Hepatozoon* parasites in caimans from Brazil, categorised by locality, host species, and biome. The total number of sampled individuals (n) and the number of positive hosts (n+) are presented for each age class. Age classes: < 26 cm for hatchlings (Class 1), 26–50 cm for juveniles (Class 2), 51–80 cm for young adults (Class 3), and > 80 cm for adults (Class 4).

Locality	Host sp.	Biome	Class 1 (n/n+)	Class 2 (n/n+)	Class 3 (n/n+)	Class 4 (n/n+)	Total (n/n+)
Apa Marituba do Peixe	<i>Caiman latirostris</i>	Atlantic Forest	-	6/2	6/1	-	12/3
	<i>Paleosuchus palpebrosus</i>	Atlantic Forest	-	2/1	-	-	2/1
Resex Jequiá	<i>Caiman latirostris</i>	Atlantic Forest	6/0	14/3	8/3	-	28/6
	<i>Paleosuchus palpebrosus</i>	Atlantic Forest	-	1/0	-	-	1/0
Lagoa do Guaxuma	<i>Caiman latirostris</i>	Atlantic Forest	2/0	16/5	7/3	-	25/8
Resex Lago Cuniã	<i>Caiman crocodilus</i>	Amazon Rainforest	-	2/1	6/5	-	8/6
	<i>Melanosuchus niger</i>	Amazon Rainforest	-	10/9	2/1	6/4	18/14

catchpoles. Following capture, we measured the snout-vent length (SVL) to estimate and classify their age as follows: < 26 cm for hatchlings (Class 1), 26–50 cm for juveniles (Class 2), 51–80 cm for young adults (Class 3), and > 80 cm for adults (Class 4) (Abercrombie and Verdade, 2002; Viana et al., 2010a). A maximum of 6 ml of blood was promptly drawn from the post-occipital vein with a 10 ml plastic syringe, without heparin. While still on the boat, three blood smears were prepared for each individual and fixed with methanol. After the smearing process, the animals were released at the site of capture.

The smears were stained with absolute methanol, coloured with 10% Giemsa for 50 minutes, and examined under an Olympus CX31 light microscope. Images were captured using an Olympus Qcolor 5 digital camera and processed with QCapture software to document parasite morphology (Olympus Corporation, Tokyo, Japan).

A total of 94 caimans were captured and sampled for *Hepatozoon*, of which 65 *C. latirostris* and three *P.*

palpebrosus were from Atlantic Forest regions, and 8 *C. crocodilus* and 18 *M. niger* from the Amazon rainforest areas (Fig. 1; Table 1). Of these, 38 (40%) caimans were positive for *Hepatozoon* parasites (Figs. 2, 3; Table 1). Additionally, the number of infected individuals by age class was: 0 out of 8 in Class 1; 21 out of 51 in Class 2; 13 out of 29 in Class 3; and 4 out of 6 in Class 4 (Table 1). Intraerythrocytic gamonts were elongated and sausage-shaped, with centrally positioned nuclei. In Amazonian caimans, some gamonts showed cytoplasmic vacuoles (Figs. 3C–F). Free gamonts, observed in all positive species, were elongated and slender (Figs. 2G–I and 3G–I). Two individuals of *M. niger* had free gamonts surrounded by a visible parasitophorous vacuole (Fig. 3I).

This study provides new records of *Hepatozoon* parasites in caimans from the Atlantic Forest and Amazon rainforest biomes, significantly expanding their known geographic distribution in Brazil. The detection of *Hepatozoon* parasitising *P. palpebrosus* inhabiting the Atlantic Forest represents the first record in this host

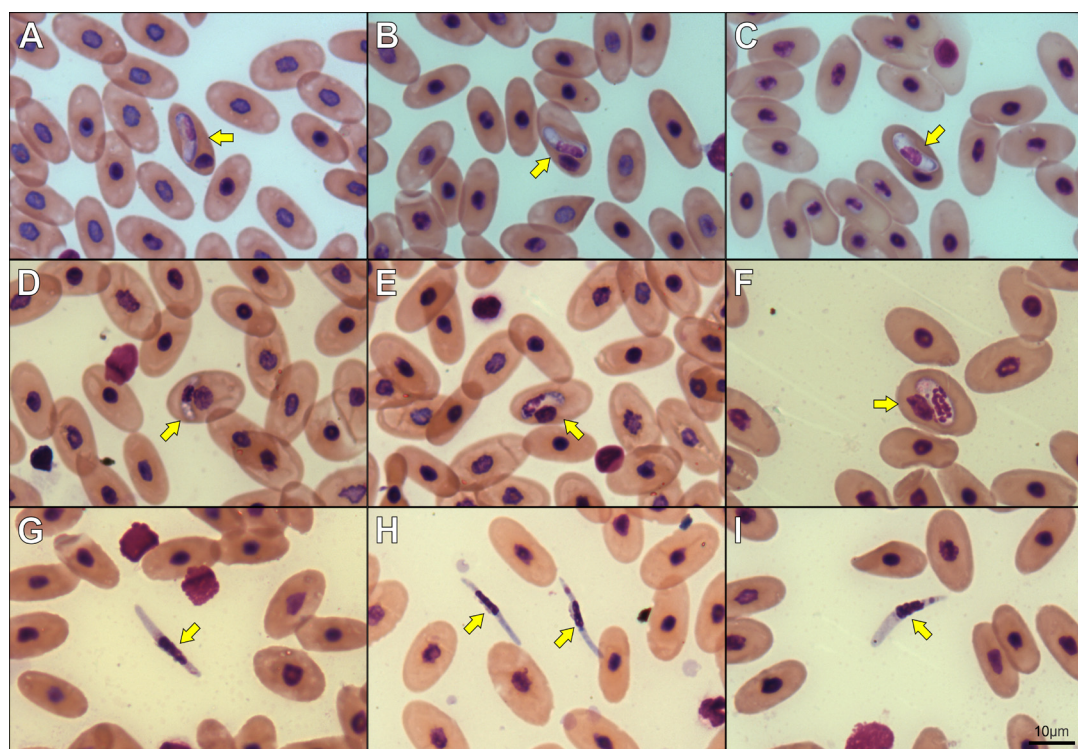


Figure 2. *Hepatozoon* parasites (yellow arrows) observed in caimans from the Atlantic Forest, northeast region in Brazil. Intraerythrocytic gamonts infecting: (A–C) *Caiman latirostris* and (D–F) *Paleosuchus palpebrosus*. Free gamonts in: (G) *C. latirostris* and (H, I) *P. palpebrosus*. Photos by Pedro H. Oliveira-Pereira.

species from that biome, underscoring its potential role as a host in various ecological contexts. Additionally, our findings extend the known distribution of *Hepatozoon* in *C. latirostris* to the northeastern regions of the Atlantic Forest, which have been underrepresented in the existing literature.

Although the morphological features of the parasites were consistent with those of *H. caimani*, such as elongated gamonts with centrally located nuclei and free gamonts tapering at the posterior end with an apical ring (Soares et al., 2017; Clemente et al., 2023), we noted some differences with the forms detected here. In caimans from the Amazon biome, gamonts exhibited denser cytoplasm, vacuoles, and encapsulated free forms, characteristics that are not typically associated with *H. caimani*. These differences suggest the possibility of undescribed diversity within the genus *Hepatozoon*, aligning with recent findings regarding cryptic diversity among caiman parasites (Úngari et al., 2024).

However, the absence of molecular data precludes definitive species identification. Given the limitations

of differentiating between *Hepatozoon* species using only morphology and the growing evidence of cryptic speciation, future studies should incorporate integrative taxonomic approaches combining morphology, histopathology, and molecular phylogenetics (Smith, 1996; Telford, 2009; Úngari et al., 2024).

Differences in *Hepatozoon* prevalence were noticed between age classes: no hatchling and smaller individuals (Class 1) were positive, whereas older and larger caimans (Classes 2, 3, and 4) harboured infections. This pattern suggests that parasite infection does not occur or may be incomplete during the host’s early life stages (Lainson et al., 2003). Furthermore, this finding is consistent with the survey by Viana et al. (2010a) in the Brazilian Pantanal, which highlights the caimans’ shift in feeding habits as a key factor for *Hepatozoon* infection. While hatchlings and early juveniles feed primarily on invertebrates, the consumption of vertebrates paratenic hosts, such as anurans and fishes (Viana et al., 2012; Pereira et al., 2014; Cardoso et al., 2022), increases with age, raising the risk of parasite exposure (Viana et al.,

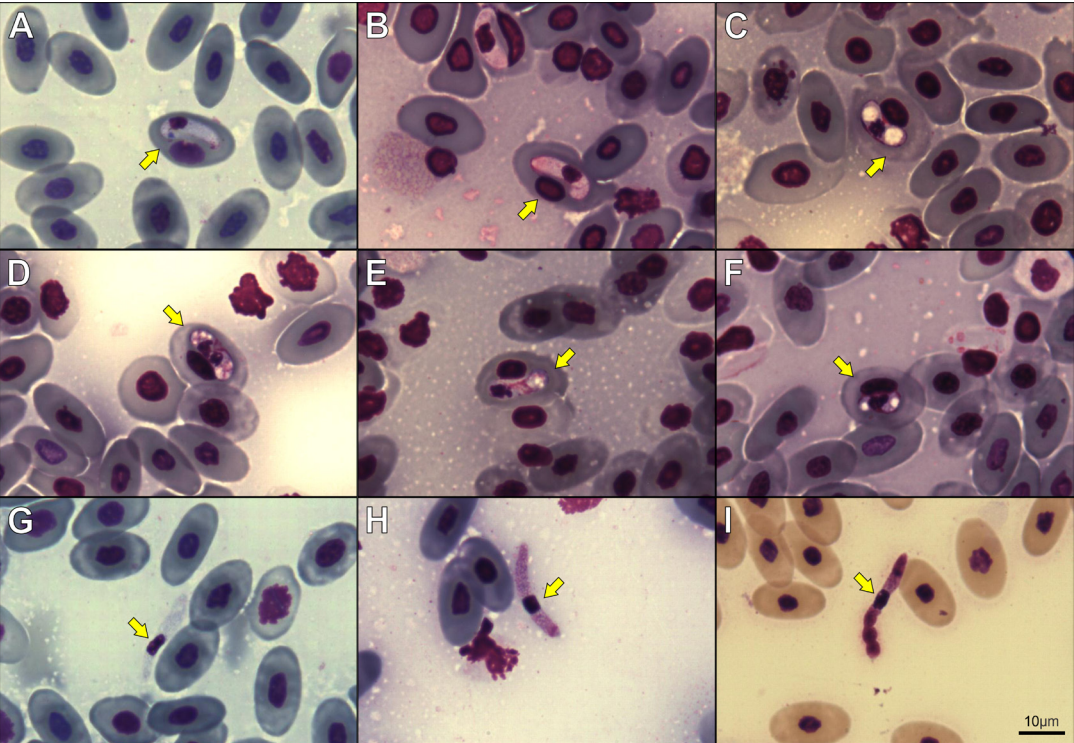


Figure 3. *Hepatozoon* parasites (yellow arrows) observed in caimans from the Brazilian Amazon. Intraerythrocytic gamonts infecting: (A, B) *Melanosuchus niger* and (C–F) *Caiman crocodilus*. Free gamonts in: (G) *C. crocodilus* and (H, I) *M. niger*. Photos by Pedro H. Oliveira-Pereira.

2010a). Therefore, young caimans (Class 1) likely do not have circulating gamonts in their blood.

Interestingly, the parasites found in sympatrically occurring *P. palpebrosus* and *C. latirostris* in the Área de Proteção Ambiental Marituba do Peixe, showed nearly identical morphology. This suggests that a single species of *Hepatozoon* may infect multiple sympatric host species, indicating low host specificity. This is a common feature of *Hepatozoon* species that was also observed in other reptilian hosts (O'Dwyer et al., 2013; De Paula et al., 2021), including records of *H. caimani* in different crocodilians (Lainson et al., 2003; Clemente et al., 2023). This finding highlights the importance of exploring cross-species transmission and host specificity of haemogregarines.

Overall, our study provides the first confirmed record of *Hepatozoon* spp. infection in *P. palpebrosus* from the Atlantic Forest biome, and expands the known distribution of these parasites in *C. latirostris* northeastern populations in this biome. We also provide new data on *Hepatozoon* infections in *C. crocodilus* and *M. niger* from the Amazon rainforest, and the observed parasite morphological variation suggests the presence of an unknown diversity within the genus. These findings highlight the need for further parasitological studies, including molecular characterisations to clarify cryptic species complexes and host-parasite dynamics in South American crocodilians.

Acknowledgments. We thank all who assisted with sampling and collections, especially Joilson Medeiros de Barros for sharing capture and handling techniques, and the residents of the Reserva Extrativista do Lago do Cuniã and Sistema Lacustre Sul de Alagoas for their hospitality, boats, piloting skills, and field guidance. We acknowledge the Companhia de Desenvolvimento dos Vales do São Francisco e do Parnaíba (CODEVASF) for field transport and the Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre at the Universidade Federal de Minas Gerais (UFMG) for institutional support. We are grateful to the Chico Mendes Institute for Biodiversity Conservation (ICMBio) for the research permits (no. 72113/1 and no. 74257). Funding was provided by the Fundo Brasileiro para a Biodiversidade in collaboration with Instituto Humanize (Grant 046/2021), the IUCN-SSC Crocodilian Specialist Group, and the Rufford Foundation (Grant 31840-1). We also thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Programa de Capacitação em Taxonomia (PROTAX) (CNPq, PROTAX 433909/2024-5) for financial support and a postdoctoral fellowship to AMP (PDJ 150357/2025-7), and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES/Brazil) for a doctoral scholarship to GMG. This project was conducted under the UFMG/ICMBio Technical Cooperation Program.

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