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CHARLES DE SOUSA SILVA

HELMINTOS ASSOCIADOS A ANFIBIOS DA CAATINGA: DIVERSIDADE, ECOLOGIA E FILOGENIA

FORTALEZA
2025

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Tese apresentada ao Programa de Pós-Graduação em Sistemática, Uso e Conservação da Biodiversidade, da Universidade Federal do Ceará, como parte dos requisitos para obtenção do título de Doutor. Área de concentração: taxonomia, sistemática e evolução biológica.

Orientador: Prof. Dr. Paulo Cascon
Coorientador: Prof. Dr. Drausio Honorio Morais

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Se toda a matéria do universo, com exceção dos nematódeos, fosse varrida fora, nosso mundo ainda seria reconhecível? [...] se pudéssemos então estudá-lo, descobriríamos que suas montanhas, colinas, vales, rios, lagos e oceanos estariam representados por uma película de nematódeos.

- Nathan Cobb

RESUMO

Na última década observou-se um crescente número de pesquisas com helmintos endoparasitos associados a anfíbios no Nordeste do Brasil. Esses trabalhos com abordagens diversas buscavam responder questões relacionadas a dinâmica entre a relação hospedeiro-parasito, além de perguntas taxonômicas, evolutivas e biogeográficas. Apesar desse avanço, ainda estamos distantes de compreendermos os fenômenos que influenciam essas dinâmicas ecológicas e resolver questões que envolvem o reconhecimento de espécies parasitas e a identificação de novas. Desse modo, este trabalho tem por objetivo contribuir ao preencher algumas dessas lacunas do conhecimento relacionadas as interações hospedeiro-parasito associados à anfíbios no Nordeste do Brasil. Questões específicas como (1) realizar um checklist de infecções parasitárias e avaliar a estrutura ecológica das interações em rede em anfíbios do Nordeste; (2) identificar e descrever uma nova espécie do gênero *Parapharyngodon* associado a um hospedeiro hilídeo na Caatinga; (3) registrar a ocorrência de infecção do gênero *Ozolaimus* em um hospedeiro hilídeo na Caatinga; e (4) avaliar a filogenia do gênero *Cosmocerca* e o status das espécies Neotropicais. Os métodos para a realização dessas diferentes abordagens são descritos individualmente em cada capítulo, sendo os dados disponibilizados para o desenvolvimento destas pesquisas provenientes de expedições em campo, coleções regionais e de literatura. Os resultados apresentados neste trabalho evidenciam a necessidade de fortalecer e incentivar o estudo nesse campo de conhecimento, em particular, para a região Nordeste que, no Brasil, encontra-se entre as regiões de menor conhecimento produzido acerca dessas relações de parasitismo associado à hospedeiros anfíbios.

Palavras-chaves: anfíbios; macroendoparasitos; região neotropical; parasitismo.

ABSTRACT

Over the past decade, a growing body of research has focused on endoparasitic helminths associated with amphibians in Northeastern Brazil. These studies, employing diverse methodologies, have sought to address questions pertaining to the dynamics of host-parasite relationships, as well as taxonomic, evolutionary, and biogeographical inquiries. Despite this progress, a comprehensive understanding of the factors that influence these ecological dynamics, and the resolution of issues related to parasite species recognition and the identification of novel species, remains elusive. Therefore, this study aims to contribute to filling these knowledge gaps concerning host-parasite interactions associated with amphibians in Northeast Brazil. Specific objectives include: (1) to compile a checklist of parasitic infections and evaluate the ecological structure of network interactions in Northeastern Brazilian amphibians; (2) to identify and describe a novel species of the genus *Parapharyngodon* associated with a hylid host in the Caatinga; (3) to document the occurrence of infection by the genus *Ozolaimus* in a hylid host within the Caatinga; and (4) to assess the phylogeny of the genus *Cosmocerca* and the status of Neotropical species. The methodologies employed for these diverse approaches are delineated individually within each chapter, with data derived from field expeditions, regional collections, and scholarly literature. The findings presented herein underscore the imperative to strengthen and promote research in this field of knowledge, particularly within the Northeastern region of Brazil, which, within the national context, exhibits one of the lowest levels of knowledge production regarding these parasitism relationships associated with amphibian hosts.

Keywords: amphibians; macroendoparasites; neotropical region; parasitism.

LISTA DE ILUSTRAÇÕES

SUMÁRIO

1. INTRODUÇÃO GERAL

O parasitismo está presente em 15 dos 35 filos de metazoários reconhecidos formalmente, sendo um dos modos de vida mais bem-sucedidos representando cerca de 41% da biodiversidade animal descrita na Terra, com aproximadamente 147.750 espécies reconhecidas (Weinstein; Kuris, 2016). Compreendemos o fenômeno do parasitismo como uma relação ecológica desarmônica interespecífica constituída por um organismo parasito, e um ou de alguns poucos indivíduos hospedeiros (Begon *et al*., 2007). Nessa relação existe uma unilateralidade de benefícios, sendo um dos associados prejudicado nessa relação (Neves, 2005).

Os parasitos desempenham um papel ecológico importante nas relações tróficas, por contribuírem para a manutenção da diversidade e evolução de seus hospedeiros (Poulin; Morand, 2000). A fauna de endoparasitos associados a anfíbios é rica e diversificada, abrangendo todos os grupos de helmintos (Acanthocephala, Nematoda e Platyhelminthys) em estágios larvais e adultos (Campião *et al*., 2014).

Certifica-se que, na América do Sul, o Brasil é o país com mais estudos sobre endoparasitos em anfíbios com cerca de 7% de sua anurofauna pesquisada para helmintos, no qual os representantes dos taxa Hylidae e Leptodactylidae são os hospedeiros mais amostrados (Campião *et al*., 2014; Martins-Sobrinho *et al*., 2017; Silva-Neta *et al*., 2020). Na última década, muitos estudos contribuíram para o conhecimento sobre a influência do parasitismo e espécies de helmintos associados a hospedeiros anuros no Nordeste brasileiro, com a maioria dos estudos conduzidos em ambientes de Caatinga.

Esses trabalhos colaboraram sob diferentes perspectivas: ecológicas (Silva *et al*., 2018; Oliveira *et al*., 2019; Madelaire *et al*., 2020), biogeográficas (Campião *et al*., 2014), novos registros (Nascimento *et al*., 2012; Lins *et al*., 2017; Martins-Sobrinho *et al*., 2017; Alcantara *et al*., 2018; Sena *et al*., 2018; Silva *et al*., 2019; Teles *et al*., 2014; 2015; 2017a; 2017b; 2018), fisiológicas (Madelaire *et al*., 2017), taxonômicas (Araújo-Filho *et al*., 2015; Felix-Nascimento *et al*., 2020) e filogenéticas (Muller *et al*., 2018; Morais *et al*., 2020).

Contudo, a dinâmica parasito-hospedeiro ainda apresenta lacunas significativas em nossa compreensão. No âmbito ecológico, estudos recentes têm buscado elucidar padrões de interações antagônicas e sua influência na estruturação de redes ecológicas (Vázquez et al. 2005; Chen et al. 2008; Dallas, Cornelius 2015). A análise de redes fornece dados fundamentais para identificar, entender e prever como os parasitos e hospedeiros interagem (Campião et al. 2015). Além disso, auxiliam compreender o papel da diversidade parasitária no funcionamento dos ecossitemas, na influência de atributos estruturais do hospedeiro e sua dinâmica em relação às teias alimentares, bem como nas respostas da comunidade a perturbações como migração, extinção ou invasão biológica (Bellay et al. 2018).

No Brasil, estudos sobre o padrão de interação em redes de hospedeiros anfíbios são escassos, com apenas um estudo realizado no Pantanal (Campião et al. 2015). Na Caatinga, o padrão de estrutura de rede e dinâmica parasito-hospedeiro é conhecido apenas para lagartos (Brito et al. 2014), sendo desconhecido para anfíbios. Além do eixo ecológico, questões taxonômicas e evolutivas permanecem desconhedidas para muitos taxa de helmintos, em particular, para os clados Cosmocercidae e Pharyngodonidae, frequentemente identificados em estudos ecológicos e de inventários (Santos et al. 2024; Silva-Neta et al. 2020; Martins-Sobrinho et al. 2017).

Cosmocercidea é um clado diverso e cosmopolita, com relações evolutivas complexas e pouco compreendidas (Anderson 2000; Sinsch et al. 2020; Chen, Zhang, et al. 2020; Alcantara et al. 2022). Portanto, faz-se necessário investigar as relações evolutivas

dentro dessa família, em particular, no gênero *Cosmocerca*, devido aos seus numerosos registros de infecção em anuros brasileiros e por ser o táxon, considerando a sua distribuição mundial, com a maior diversidade de espécies conhecidas presentes na região Neotropical (De Sousa-Silva et al. 2024a).

O mesmo se aplica ao táxon Pharyngodonidae, que possui grande diversidade e ampla distribuição, no entanto, são escassos registros de infecção em anuros e pouco se conhece sobre aspectos de sua ecologia (De Sousa et al. 2024b), evolução (Pereira et al. 2018) e sua dinâmica de interação parasito-hospedeiro (Mockett et al. 2017).

Diante do exposto, este trabalho soma esforços na construção da compreensão da dinâmica das relações parasito-hospedeiro. Com o objetivo de contribuir para o conhecimento acerca das relações existentes entre os hospedeiros anfíbios do Nordeste e seus parasitos, o presente estudo se propõe a explorar e desenvolver diferentes aspectos dessa dinâmica entre esses organismos.

2. APRESENTAÇÃO DOS CAPÍTULOS

Este trabalho explora a intricada relação entre parasitos e seus hospedeiros anfíbios no Nordeste brasileiro. Está subdividido em quatro capítulos referentes aos estudos desenvolvidos e alinhados aos objetivos da presente tese. Os capítulos um e dois têm início ainda nas expedições de campo do mestrado, onde durante as coletas, capturamos alguns indivíduos da espécie *Corythomantis greeningi* e ao realizarmos os procedimentos de necropsia, processamento e identificação dos parasitos em laboratório, encontramos duas espécies de faringodonideos (Pharyngodonidae). Um espécie, até então desconhecida, pertencia ao gênero *Parapharyngodon* e revelou-se uma nova espécie, cuja a descrição detalhada apresentamos adiante. Enquanto a outra, identificada como *Ozolaimus cirratus*, um parasito intestinal comumente relatado em lagartos iguanídeos (Lacertilia) nos intrigou por sua presença em um anfíbio, um hospedeiro incomum para este parasito. Esse relato de infecção apresenta questões de ecologia e distribuição dessa espécie de nematódeo, ampliando o conhecimento acerca de sua especificidade parasitária e fenômeno de transbordamento (*spillover*) a diferentes hospedeiros.

Em nosso terceiro capítulo, direcionamos nossa atenção para o gênero *Cosmocerca*, um nematódeo cosmopolita e parasito intestinal de répteis e anfíbios com inúmeros registros de infecção em hospedeiros anfíbios no Brasil. Essa investigação aprofunda o conhecimento das relações filogenéticas deste gênero, pois, a partir de nossos resultados fomos capazes de observar e relacionar aspectos evolutivos das espécies e seu padrão de distribuição zoogeográfico. Além disso, evidenciamos lacunas do conhecimento para as espécies com distribuição Neotropical que, atualmente, compreende a região com a maior diversidade do gênero no mundo. E, por consequência, abrimos caminhos para o desenvolvimento de novas pesquisas relecionadas a este gênero no Brasil. Acreditamos que essas lacunas de conhecimento, uma vez preenchidas, contribuirá significativamente para a compreensão da evolução e da diversificação desses parasitos.

No último capítulo, apresentamos uma análise integrada da estrutura de rede de interações parasito-hospedeiro utilizando dados coletados nos últimos 30 anos a partir dos registros de infecção em hospedeiros anfíbios com distribuição no Nordeste brasileiro. Essa abordagem pioneira realizada para a diversidade de parasito-hospedeiro com predominância presente no Domínio Caatinga nos permitiu traçar um panorama detalhado das relações entre parasitos e hospedeiros nessa região, revelando padrões de interação complexos e específicos. Essa análise integrada lança luz sobre a importância da abordagem de redes para a compreensão da dinâmica parasitária e da evolução das interações entre parasitos e hospedeiros. Além disso, disponibilizamos uma lista atualizada das espécies de hospedeiros e seus parasitos associados.

3. CAPÍTULO 1 - A NEW SPECIES OF *PARAPHARYNGODON* (OXYUROIDEA: PHARYNGODONIDAE) INFECTING *CORYTHOMANTIS GREENINGI* (ANURA: HYLIDAE) FROM NORTHEAST BRAZIL

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A NEW SPECIES OF *PARAPHARYNGODON* (OXYUROIDEA: PHARYNGODONIDAE) INFECTING *CORYTHOMANTIS GREENINGI* (ANURA: HYLIDAE) FROM NORTHEAST BRAZIL

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ABSTRACT

Currently, 66 species of *Parapharyngodon* are known, with only twelve reported from the Neotropical realm. *Parapharyngodon pereiramendoi* n. sp. is described herein from the host anuran *Corythomantis greeningi* in the Caatinga biome, a Brazilian semiarid region. *Parapharyngodon pereiramendoi* n. sp. presents a triangular oral opening with four bilobed lips, which one with a pair of distally located rounded papillae, gubernaculum absent, a short V-shaped support in postcloacal lips, and three pair of caudal papillae, while females have three simple lips divided into six parts, opening of the post-bulbar excretory pore, vulva in equatorial position, and conical tail. Lateral alae are absent in males and females. Here, we describe the 67th species of *Parapharyngodon* in the world, and the thirteenth from the Neotropical realm, contributing to the taxonomy of the genus *Parapharyngodon*, as well as increasing the knowledge of helminthfauna in neotropical hylids.

Keywords: Amphibians; Neotropical realm; Taxonomy.

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3.1 Introduction

The Hylidae is the largest and most diverse taxon of amphibians in Brazil, with about 374 species, corresponding to approximately 32.7% of the Brazilian anuran species (SEGALLA et al., 2021). Regarding parasitological studies with Hylidae host species in the Northeastern region of Brazil, studies have been published in recent years related to the following hosts: *Boana albomarginata* (Spix) (MARTINS-SOBRINHO et al., 2017), *Boana multifasciata* (Günther) (MACHADO et al., 2021), *Boana raniceps* (Cope) (NASCIMENTO et al., 2012; MACHADO et al., 2021), *Dendropsophus branneri* (Cochran), *D. elegans* (Wied-Neuwied), *D. haddadi* (Bastos and Pombal), *D. minutus* (Peters) (MARTINS-SOBRINHO et al., 2017), *Scinax auratus* (Wied-Neuwied), *S. x-signatus* (Spix) (MARTINS-SOBRINHO et al., 2017) and *Trachycephalus typhonius* (Linnaeus) (BENÍCIO et al., 2022).

The species *Corythomantis greeningi* Boulenger (Lophyohylinae) is a hylid widely distributed in the xeric and sub-humid regions of the Cerrado and Caatinga domains in Brazil (SILVA et al., 2014). The adult presents a length of around 8 cm and has a roughened body covered by mucous and granular glands that secrete toxic compounds that are effective against predators (JARED et al., 1999). *Corythomantis greeningi* presents life habits associated with vegetation, being found in bromeliads and tree trunks; it has a sit-and-wait foraging mode, reproduction during the rainy season, a strongly ossified skull, and a dorsoventrally flattened head covered by small spicules that contribute to minimizing water loss in arid environments (JARED et al., 1999, 2005; JUNCÁ et al., 2008).

Until now, there are only two studies on its helminth fauna (DE SOUSA-SILVA et al., in press; Pitombeira et al., in press), this being one of the several hylid hosts considered having their helminth composition undersampled. The nematode genus *Parapharyngodon* Chatterji is worldwide distributed with, currently, 66 valid species (GBIF, 2023). This genus of oxyurid nematodes is a gastrointestinal parasite with a life cycle including lizards as main hosts. However, some species are known to parasitize anurans (RAMALLO et al., 2002; MORSY et al., 2019).

Twelve *Parapharyngodon* species have been reported to infect anuran species: *Parapharyngodon alvarengai* Freitas infecting *Rhinella icterica* (Spix) (LUQUE et al., 2005); *P. chamelensis* Velarde-Aguilar, Mata-Lopez, Guillen-Hernandez, and Leon-Regagnon and *P. hylidae* elarde-Aguilar, Mata-Lopez, Guillen Hernandez, and Leon-Regagnon in *Diaglena spatulata* (Gunther), *Triprion petasatus* (Cope), and *Trachycephalus typhonius* (Linnaeus) (VELARDE-AGUILAR et al., 2015); *P. curupira* Santos, Jesus, Macedo, Santos and Melo in *Osteocephalus taurinus* Steindachner (SANTOS et al., 2022); *P. duniae* (BURSEY; BROOKS, 2004) and *P. hugoi* Pereira, Campião, Luque, Tavares in *T. typhonius* (BURSEY; BROOKS, 2010; PEREIRA et al., 2017); *P. garciae* (Schmidt & Whittaker) in *Eleutherodactylus coqui* (Thomas) and *Eleutherodactylus* spp. (SCHIMIDT; WHITTAKER, 1975; DYER et al., 1995); *P. grenadaensis* Bursey, Drake, Cole, Sterner, Pinckney and Zieger in *Rhinella marina* (Linnaeus) (BURSEY et al., 2013); *P. politoedi* Santos, Argolo, Santos & Rodrigues in *Osteocephalus taurinus* Steindachner (SANTOS et al., 2018); *P. osteopili* (Adamson) in *Osteopilus septentrionalis* (Duméril & Bibron) (ADAMSON, 1981); *P. verrucosus* (Freitas) and *P. silvoi* Araújo-Filho, Brito, Almeida, Morais & Ávila in *Dermatonotus muelleri* (Boettger) (MCALLISTER et al., 2010; ARAÚJO-FILHO et al., 2015; ALCANTARA et al., 2018). Here, we describe a new species of *Parapharyngodon* infected an anuran host from brazilian Northeast.

3.2 Materials and Methods

Eleven specimens of *C. greeningi* (adult males; mean snout-vent length [SVL] ± SD; 76 ± 7.48 mm, range: 64.62–89.97 mm) were collected in the Ecological Station of Aiuaba, Ceará State, Brazil (06°35'35" S, 40°08'31" W, 466 m a.s.l.) between February 2014 and September 2016. The host specimens were fixed in 10% formaldehyde, stored in 70% ethanol, and deposited in the Herpetological Collection of the Universidade Federal do Ceará (CHUFC 7368–7370, 7383, 7398, 7403, 7409, 7422, 7425, 7433, and 13302; collection license no. 29613-1 from Instituto Chico Mendes de Conservação da Biodiversidade and authorized by ethical Committee on Animal Experimentation and Use from Cariri Regional University CEUA/URCA under number 00026/2015.2).

Each specimen fixed was necropsied through a longitudinal ventral incision and examined for helminths in the following organs: gastrointestinal tract, liver, kidneys, lungs, and body cavity. The nematodes were collected and preserved in 70% ethanol and subsequently cleared in lactic acid for morphological studies (TRAVASSOS 1950). Measurements of the specimens are presented as the values of the holotype followed by the range in parentheses (reported in micrometres, except when indicated), using a computerized image analysis system (U). The drawings were made with the aid of a light camera mounted on a Leica DMLS microscope with phase contrast optics. For scanning electron microscopy, the nematodes fixed were washed in distilled water, post-fixed in 1% osmium tetroxide, dehydrated to the critical point of CO2, metallized with gold+palladium, and analysed using a TESCAN scanning electron microscope (VEGA 3) in the Scanning Electron Microscopy Laboratory, Rural Federal University of Amazônia.

The holotype and paratypes of the new species of *Parapharyngodon* were deposited in the Helminthological Collection of the Oswaldo Cruz Institute (CHIOC, vouchers CHIOC 39677a, 39677b, and 39677c), Rio de Janeiro State, Brazil. Voucher specimens were deposited in the Helminthological Collection of the Department of Biodiversity and Biostatistics of the Institute of Biosciences, São Paulo State University, UNESP (CHIBB), Botucatu, São Paulo State, Brazil.

3.3 Results

A total of 309 nematode specimens were found infecting the intestine of *C. greeningi*. Based on morphological characteristics, the nematodes were identified as a new species of *Parapharyngodon*.

OXYUROIDEA Cobbold, 1864
PHARYNGODONIDAE Travassos, 1919
***Parapharyngodon* Chatterji, 1933**
Parapharyngodon pereiramendoi De Sousa-Silva sp. n.

Taxonomic summary
Type host.
Corythomantis greeningi (Hylidae: Lophyohylinae)
Type locality.
Ecological Station of Aiuaba, Aiuaba municipality, Ceará State, Northeastern Brazil (6.000°S, 39.999°W).
Site of infection. Large intestine
Numbers of parasite specimens/hosts. (309/11)
Prevalence. 100%
Mean intensity of infection. 28.1 ± 13.41
Range. 1–78
Other localities. Barro municipality (7°10'36"S, 38°46'54"W), Ceará state (Host: *C. greeningi*).
Etymology. The species is named after the indigenist Bruno Pereira and the conservationist Chico Mendes for their work in protection, preservation, and conservation of the Amazon Forest and the Indigenous peoples in Brazil.

Description

General: Robust and fusiform nematode, pale white (whitish), cuticle with well-defined transverse striations from the anterior portion of the body to the base of the caudal filament. Evident sexual dimorphism, with males approximately half the size of females. Lateral alae are absent in males and females. Male with triangular mouth opening, having four bilobed lips, one dorsal, two ventrolateral, and one ventral (Figs. 1b and 3a). Each lip has a pair of distally located rounded papillae. A pair of amphids located on the ventrolateral lips, close to the oral opening (Fig. 1b and 3a). Nerve ring in the first anterior third of the cephalic region (Fig. 1a, c). Esophagus with characteristics of Oxyuridae, bulb with developed muscular valve projected through the first portion of the intestine. Opening of the post-bulbar excretory pore. A pair of small, slightly sclerotized spicules (Fig. 1X). Gubernaculum absent. The cloacal region with a short V-shaped support (Fig. 2e and 3e). Three pairs of simple caudal papillae (one pair near the upper cloacal lip, one pair ad-cloacal, and the third pair fused located at the base of the caudal filament in males) (Figs. 1e, 2e, and 3b). The caudal alae is absent. Female with triangular oral opening with three simple lips divided into six; each lip possessing a pair of papillae (Figs. 1d and 3c), amphids opening in ventrolateral lips. Opening of the post-bulbar excretory pore. Vulva in equatorial position and conical tail. Eggs with a subterminal operculum, thick external coating, and not embryonated (Fig. 1g).
Male: [based on the holotype and 16 paratypes] total length 2.10 (1.36–2.65) mm. Body width at esophagus-intestine junction 166.7 (130–219). Nerve ring 134 (115–148) and excretory pore 596.7 (514–703) from anterior extremity. Esophagus total length 405 (370–448), representing 19% of total body length; corpus length 294 (264–328), corpus width 34.1 (24–

40), isthmus length 21.4 (14–31), isthmus width 24.8 (19–30), bulb length 90 (70–104), bulb width 96.6 (75–120) (Fig. 2f). Testicle extending anteriorly from mid- body region. Vas deferens not observed. Spicule poorly sclerotized, sharply pointed 51.6 (43–62). Anterior cloacal lip echinate, with smooth short projections irregular not well developed small finger-like outgrowths. Genital cone with short projection, present at the base of the posterior cloacal lip. Three pairs of mammilliform caudal papillae distributed: one pair just above the anterior cloacal lip, the second pair sublaterally ad-cloacal, and the third pair sharing a fused base near the base of the caudal filament (Figs. 1e, 2e, and 3b, e). Long tail inserted dorsally 100.9 (90–115).

Female: [based in one allotype and 20 paratypes] total length 3.13 (2.32–4.02) mm. Body width at esophagus-intestine junction 325.2 (196–401). Nerve ring 136.9 (116–158) and excretory pore 843.7 (666–1099) from anterior extremity. Esophagus total length 602.9 (545–643), representing 19% of total body length; corpus length 451.6 (406–481), corpus width 46.8 (41–51), isthmus length 26.5 (14–39), isthmus width 36.8 (32–45), bulb length 124.3 (101–139), bulb width 133.7 (120–158). Vulva with prominent lips situated at mid-region of the body, 1566.4 (1196–2000) from anterior end. Monodelphic, prodelphic, and post-bulbar ovary. Eggs thick-shelled, non-embryonated, with subterminal single operculum 116.6 (73–135) x 51.4 (35–66) (Fig. 1g). Tail conical, pointed 314.2 (229–387) (Figs 2b and 3d).

Remarks

Among the *Parapharyngodon* species that occur in the Neotropical region the male of *P. alvarengai*, *P. bainae*, *P. hispidus*, *P. largitor*, *P. riojensis*, *P. sanjuanensis*, *P. sceleratus*, *P. silvoi*, and *P. verrucosus* differs from males of *P. pereiramendoi* n. sp. by the absence of a genital cone, while in the new species it is present (Table 1), and the males of *P. curupira*, *P. hugoi*, and *P. politoedi* differs from males of *P. pereiramendoi* n. sp. by the presence of a lateral alae, while in the new species it is absent (Table 1). Regarding the females, *P. alverengai*, *P. bainae*, *P. curupira*, *P. hispidus*, *P. largitor*, *P. sceleratus*, and *P. verrucosus* differs from females of *P. pereiramendoi* n. sp. by having an ovary in a pre-bulbar position, while a new species have ovary in post-bulbar (Table 2), *P. hugoi*, *P. largitor*, *P. politoedi*, and *P. riojensis* differs from females of *P. pereiramendoi* n. sp. by having a vulva pre-equatorial or post-equatorial, while a new species have vulva equatorial (Table 2), *P. sanjuanensis* and *P. silvoi* differs from females of *P. pereiramendoi* n. sp. by having a spike stout in the caudal end, while a new species heve a cauda conical and pointed (Table 2). In addition to *P. pereiramendoi* n. sp., five other species have been described infecting hylid hosts: *P. chamelensis* (Neartic realm, BURSEY et al., 2015; VELARDE-AGUILAR et al., 2015), *P. curupira* (Neotropical realm, SANTOS et al., 2022), *P. hylidae* (Panamanian realm, BURSEY et al., 2015; VELARDE-AGUILAR et al., 2015), *P. osteopili* (Panamanian realm, BURSEY et al., 2015; ADAMSON, 1981), and *P. politoedi* (Neotropical realm, SANTOS et al., 2018). *Parapharyngodon pereiramendoi* n. sp. differs from *P. chamelensis* by the absence of a single papilla on the ventral lip of the oral region, lateral lobes of the V- shaped genital cone, and 1 single postcloacal papilla with 2 nerve endings located on the medium lobe of the posterior lip. It differs from *P. hylidae* by having a mouth with four lips and a non-pedunculated amphid. It differs from *P. politoedi* by the absence of a lateral alae and by having four bilobed lips. It differs from *P. osteopili* by the absence of the four large submedian papillae and an oral ring internal to the buccal cavity with six small papillae. *P. pereiramendoi* n. sp. differs from *P. curupira* by the presence of four bilobed lips and the absence of cephalic papillae and lateral alae.

3.4 Discussion

The diagnostic characteristics of the genus *Parapharyngodon* generated an extensive discussion for decades by several authors who sought to differentiate it from the genus *Thelandros*, which has very similar morphotype characteristics (ADAMSON, 1981, 1989; ADAMSON; NASHER, 1984; BURSEY et al., 2013; RAHIMIAN et al., 2014). In general, the diagnosis of *Parapharyngodon* includes, in males, genital cone frequently absent; six (3 pairs) to nine (4 pairs + 1) sessile caudal papillae; lateral alae often present in males and subterminal tail inserted dorsally. In females, spike or conical tail; vulva in the middle (equatorial) region of the body, with prebulbar ovary sometimes wrapped around the isthmus and esophageal body. Parasites of reptiles and amphibians (RAHIMIAN et al., 2014).

With the description of *Parapharyngodon pereiramendoi* n. sp., currently 67 valid species are recognized for this genus (VELARDE-AGUILAR et al., 2015, ARAÚJO-FILHO et al., 2015, RAMALLO et al., 2016, RIZVI et al., 2017, PEREIRA et al., 2017, SANTOS et al., 2018, FERREIRA et al., 2021; SANTOS et al., 2022), which can be differentiated based on, both, quantitative and qualitative characteristics. As the latter are zoogeographical region, the morphology of the cephalic region of both sexes, the presence or absence of the lateral alae on the body in males and females; characteristics of males such as the arrangement of caudal papillae, the morphology of the spicule and edge of the anterior cloacal lip (smooth or fringed), and female characteristics as the position of the ovary in concerning of the esophageal bulb, the morphology of the eggs, and the shape of the tail. The quantitative characteristics are the number of caudal papillae, size of the spicule, size of the esophageal bulb, distance from the nerve ring to the anterior region of the body, and maximum width of the lateral alae (RAHIMIAN et al., 2014; FERREIRA et al., 2021).

The diversity of pharyngodonids is still little known, but in recent years some research has aimed to elucidate issues related to evolution and phylogeny in host-parasite interaction (MOCKET et al., 2017) and the use of integrative taxonomy in Pharyngodonidae in Brazilian reptiles (PEREIRA et al., 2017, 2018). For the type locality of *P. pereiramendoi* n. sp. it was registered the occurrence of other pharyngodonid nematodes such as *Aleuris* sp. (BRITO et al., 2014), *P. alvarengai*, (ÁVILA et al., 2017; ALCANTARA et al., 2018a), *P. silvoi* (ALCANTARA et al., 2018b), *Pharyngodon* sp. (BRITO et al., 2014), *Ozolaimus cirratus* (Linstow) (DE SOUSA-SILVA et al., in press), *Skrjabinodon campiaoae* De Sousa et al., 2022 (BRITO et al., 2014; DE SOUSA et al., 2022), and *Spauligodon oxkutzcabiensis* (BRITO et al., 2014). Except for *P. silvoi*, which occurs in amphibians, the other species are all parasites of reptiles, these records are important because they show the diversity of this group and how little we know about the biology and ecology of these parasites and their dynamics of interactions with their hosts.

Another recent infection record by the genus *Parapharyngodon* was carried out in the anuran *Adelophryne maranguapensis* (Eleutherodactylidae), a host currently on thelist of endangered Brazilian amphibian species (OLIVEIRA et al., 2022) and endemic of a highland marsh (isolated fragment of humid forest) in Northeast Brazil. Although the species of this parasite has not been determined, we emphasize the need for a deeper investigation of this pharyngodonid in subsequent records on this or on other hosts in the study location, considering that environments such highland marsh in the Brazilian northeast are known to have high species diversity and endemism (GUEDES et al., 2000; BOTERO et al., 2014; ROBERTO; LOEBMANN, 2016; RODRIGUES-FILHO et al., 2016; CASTRO et al., 2019). For example, *Parapharyngodon garciai* was described in the anuran *Eleutherodactylus portoricensis* in Puerto Rico, therefore, we do not disregard the possibility of

Parapharyngodon sp. infecting *A. maranguapensis* turning out to be a new species.

Still, regarding the concern of the conservation status of *A. maranguapensis*, in general, species of oxyurid nematodes do not present important pathogens that threaten wild species (RAHIAMI et al., 2014). However, describing and advertising the diversity of these groups of endoparasites can provide valuable information about the biology and ecological traits of the parasite, as well as the habits of its hosts and their ecosystem interactions, information that may subsidize monitoring and conservation programs for endangered species (HORWITZ; WILCOX, 2005; VELARDI-AGUILAR et al., 2015).

The Ecological Station of Aiauba is an integral protection conservation unit that aims to maintain ecosystems free of alterations caused by human interference, admitting only the indirect use of its natural attributes, in addition to presenting as its goal objective the preservation of nature and the realization of scientific research (ÁVILA et al., 2017). As it comprises an extensive remaining area of arboreal Caatinga and a wide diversity of representative species of this biome, this environment is of great ecological value and is established among priority areas for biological conservation (TABARELLI; SILVA, 2003). *Parapharyngodon pereiramendoi* n. sp. together with other recently published work (BASSINI-SILVA et al., 2021; DE SOUSA et al., 2022), reinforce this information and highlight the importance of turning attention to these environments to consolidate care measures for their preservation and conservation, in addition to promoting public investments that can encourage, subsidize and maintain new studies and new approaches for taxonomic, ecological, biogeographical and phylogenetic research on these parasites.

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Conflict of interest

The authors declare that they have no conflicts of interest.

Ethical standards

All applicable institutional, national, and international guidelines for the ethical handling of animals and collection of zoological material were followed (SISBio # 29613 – 1 and 55467 – 1) including recommendations from the Ethics Committee for Animal Experimentation (CEUA #00026/2015.2).

Table 1. Selected characters in males of *Parapharyngodon* in Neotropical realm.

Species	Type Host	Locality (Country)	Male							
			Spicule	Spicule tip	Caudal papillae distribution (pre:ad:post clocal)	Unpaired post cloacal papilla	Cloacal lip	Genital cone	Lateral alae	References
P. alvarengai Freitas	*Trachylepis maculata* (Gray) (= *Mabuya maculata*) (Squamata: Scincidae)	Fernando de Noronha, State of Pernambuco (Brazil)	80 - 100	sharp	1:1:1	No	Smooth	Absent	Present	Freitas (1957)
P. bainae Pereira, Sousa e Souza Lima	*Tropidurus torquatus* (Wied-Neuwied) (Squamata: Tropiduridae)	Toledos, State of Minas Gerais (Brazil)	100 - 140	sharp	1:0:3	No	Echinate	Absent	Present	Pereira *et al*. (2011, 2018)
P. curupira Santos, Jesus, Macedo, Santos e Melo	*Osteocephalus taurinus* Steindachner (Anura: Hylidae)	Reserva de Desenvolvimento Sustentável Mamirauá, Tefé, Amazonas (Brazil)	64 - 97	sharp	1:1:1	No	Smooth	Present	Present	Santos *et al*. (2022)
P. hispidus Ferreira, Vieira, Silva, Ribeiro,	*Tropidurus hispidus* (Spix) (Squamata: Tropiduridae)	Petrolina, State of Pernambuco (Brazil)	110 - 123	sharp	1:0:3	No	Smooth	Absent	Present	Ferreira *et al*. (2021)

Ferreira e Muniz-Pereira										
P. hugoi Pereira, Campião, Luque e Tavares	*Trachycephalus typhonius* (Linnaeus) (Anura: Hylidae)	Miranda, State of Mato Grosso do Sul (Brazil)	40 -58	sharp	0:2:1	No	Echinate	Present	Present	Pereira *et al*. (2017)
P. largitor Alho e Rodrigues	*Hemidactylus mabouia* (Moreau de Jonès) (Squamata: Gekkonidae)	State of Rio de Janeiro (Brazil)	54 - 68	sharp	0:2:1	Yes	Smooth	Absent	Present	Alho & Rodrigues (1963)
P. pererira-mendoi n. sp.	*Corythomantis grenningi* Boulanger (Anura: Hylidae)	Aiuaba, State of Ceará (Brazil)	43 - 62	sharp	1:1:1	No	Echinate	Present	Absent	**This study**
P. politoedi Santos, Argolo, Santos, Rodrigues, Gonzaléz, Santos e Melo	*Osteocephalus taurinus* Steindachner (Anura: Hylidae)	Caxiuanã National Forest, State of Pará (Brazil)	53 - 75	sharp	1:1:1	No	Echinate	Present	Present	Santos *et al*. (2018)
P. riojensis Ramallo, Bursey e Goldberg	*Phymaturus punae* Cei, Etheridge and Videla (Squamata: Liolaemidae)	Province of La Rioja, (Argentina)	90 - 110	sharp	1:0:2	Yes	Echinate	Absent	Present	Ramallo *et al*. (2002)

P. sanjuanensis Ramallo, Bursey, Castillo, e Acosta	*Phymaturus williamsi* Lobo, Laspiur and Acosta (Squamata: Liolaemidae)	Province of San Juan (Argentina)	80 -180	sharp	2:0:2	No	Echinate	Absent	Present	Ramallo *et al.* (2016)
P. sceleratus (Travassos)	*T. torquatus* (Squamata: Tropiduridae)	Rio de Janeiro, State of Rio de Janeiro (Brazil)	82 - 100	sharp	2:1:1	Yes	Smooth	Absent	Present	Travassos (1923), Freitas (1957), Vicente *et al*. (1993), Velarde-Aguilar *et al*. (2015)
P. silvoi Araújo-Filho, Brito, Almeida, Morais e Ávila	*Dermatonotus muelleri* (Boetteger) (Anura: Microhylidae)	Exú, State of Pernambuco (Brazil)	57 - 71	blunt	1:1:2	Yes	Smooth	Absent	Present	Araújo-Filho *et al*. (2015)
P. verrucosus Freitas e Dobbin Jr.	*Diploglossus lessonae* Peracca (Squamata: Diploglossidae)	João Alfredo, State of Pernambuco (Brazil)	54 - 68	sharp	1:1:1	Yes	Smooth	Absent	Present	Freitas & Dobbin Jr. (1959)

Fonte: Elaborada pelos autores.

Table 2. Selected characters in females of *Parapharyngodon* in Neotropical realm.

Species	Type Host	Locality (Country)	Female				
			Ovary location	Vulva	Tail terminus	Eggs shell	References
P. alverengai Freitas	*Trachylepis maculata* (Gray) (= *Mabuya maculata*) (Squamata: Scincidae)	Fernando de Noronha, State of Pernambuco (Brazil)	Pre-bulbar	Equatorial	Spike stout	Thin, smooth	Freitas (1957)
P. bainae Pereira, Sousa e Souza Lima	*Tropidurus torquatus* (Wied-Neuwied) (Squamata: Tropiduridae)	Toledos, State of Minas Gerais (Brazil)	Pre-bulbar	Equatorial	Spike stout	Thick, punctated	Pereira *et al*. (2011, 2018)
P. curupira Santos, Jesus, Macedo, Santos e Melo	*Osteocephalus taurinus* Steindachner (Anura: Hylidae)	Reserva de Desenvolvimento Sustentável Mamirauá, Tefé, Amazonas (Brazil)	Pre-bulbar	Equatorial	Conical, pointed	Thick-shelled	Santos *et al*. (2022)
P. hispidus Ferreira, Vieira, Silva, Ribeiro, Ferreira e Muniz-Pereira	*Tropidurus hispidus* (Spix) (Squamata: Tropiduridae)	Petrolina, State of Pernambuco (Brazil)	Pre-bulbar	Equatorial	Spike stout	Thick, punctated	Ferreira *et al*. (2021)
P. hugoi Pereira, Campião, Luque e Tavares	*Trachycephalus typhonius* (Linnaeus) (Anura: Hylidae)	Miranda, State of Mato Grosso do Sul (Brazil)	Post bulbar	Pre equatorial	Conical	Thin	Pereira *et al*. (2017)
P. largitor Alho e Rodrigues	*Hemidactylus mabouia* (Moreau de Jonès) (Squamata: Gekkonidae)	State of Rio de Janeiro (Brazil)	Pre-bulbar	Pre equatorial	Spike stout	Thin, smooth	Alho & Rodrigues (1963)
P. pererira-mendoi n. sp.	*Corythomantis grenningi* Boulanger (Anura: Hylidae)	Aiuaba, State of Ceará (Brazil)	Post bulbar	Equatorial	Conical, pointed	Thick-shelled	**This study**

P. politoedi Santos, Argolo, Santos, Rodrigues, Gonzaléz, Santos e Melo	*Osteocephalus taurinus* Steindachner (Anura: Hylidae)	Caxiuanã National Forest, State of Pará (Brazil)	Post bulbar	Pre equatorial	Conical	Thick	Santos *et al*. (2018)
P. riojensis Ramallo, Bursey e Goldberg	*Phymaturus punae* Cei, Etheridge and Videla (Squamata: Liolaemidae)	Province of La Rioja, (Argentina)	Post bulbar	Post equatorial	Spike stout	Thin, punctated	Ramallo *et al*. (2002)
P. sanjuanensis Ramallo, Bursey, Castillo, e Acosta	*Phymaturus williamsi* Lobo, Laspiur and Acosta (Squamata: Liolaemidae)	Province of San Juan (Argentina)	Post bulbar	Equatorial	Spike stout	Thin, punctated	Ramallo *et al*. (2016)
P. sceleratus (Travassos)	*T. torquatus* (Squamata: Tropiduridae)	Rio de Janeiro, State of Rio de Janeiro (Brazil)	Pre-bulbar	Equatorial	Spike stout		Travassos (1923), Freitas (1957), Vicente *et al*. (1993), Velarde-Aguilar *et al*. (2015)
P. silvoi Araújo-Filho, Brito, Almeida, Morais e Ávila	*Dermatonotus muelleri* (Boetteger) (Anura: Microhylidae)	Exú, State of Pernambuco (Brazil)	Post bulbar	Equatorial	Spike stout	Thick, punctated	Araújo-Filho *et al*. (2015)
P. verrucosus Freitas e Dobbin Jr.	*Diploglossus lessonae* Peracca (Squamata: Diploglossidae)	João Alfredo, State of Pernambuco (Brazil)	Pre-bulbar	Equatorial	Spike stout		Freitas & Dobbin Jr. (1959)

Fonte: Elaborada pelos autores.

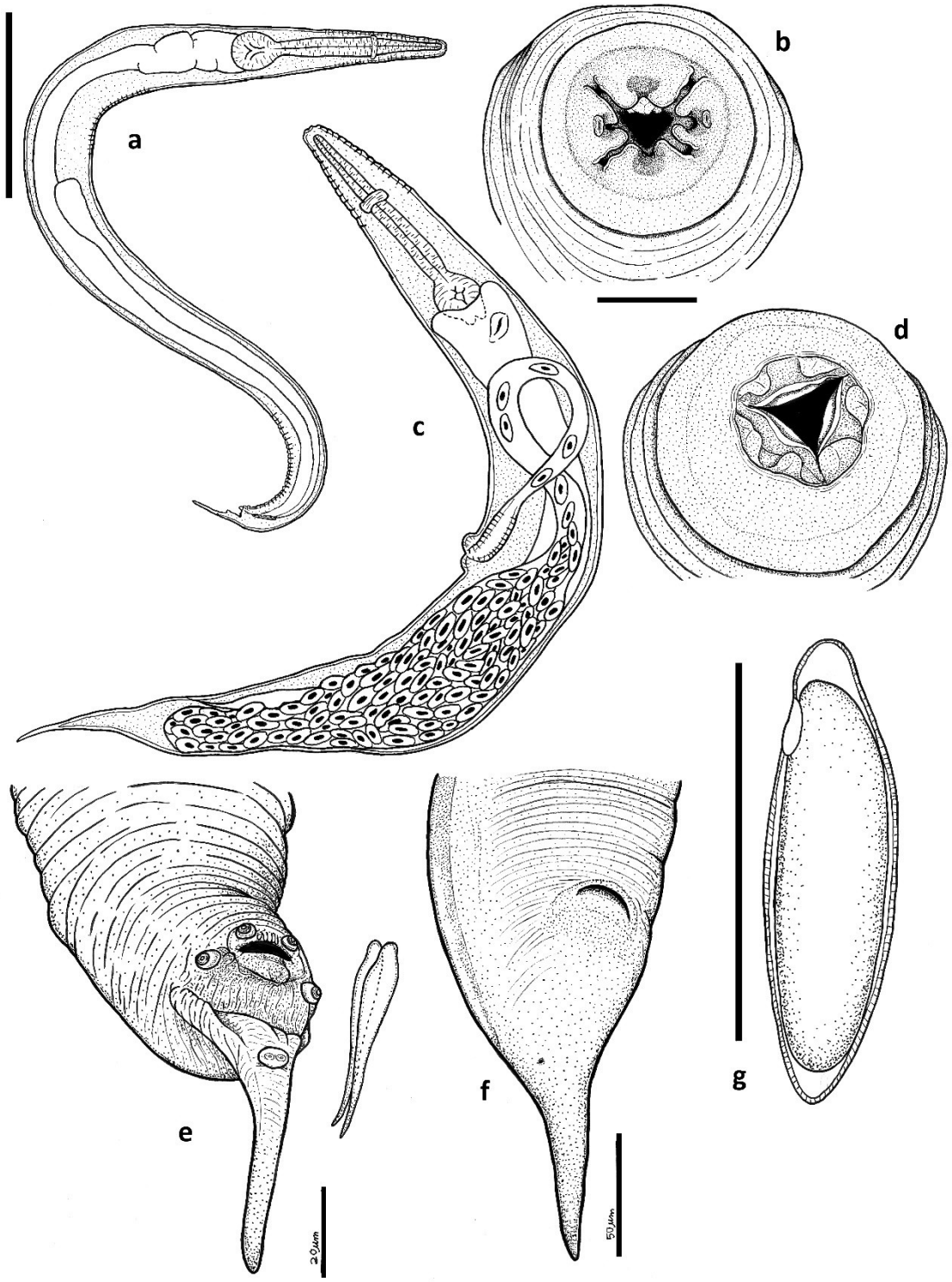

Figure 1. *Parapharyngodon pereiramendoi* n. sp.: (a) male in total length; (b) male en face view of anterior end; (c) general view of female; (d) female en face view of anterior end; (e) male, posterior end, ventre lateral view and a pair of spicules; (f) female, posterior end, ventral view; (g) egg.

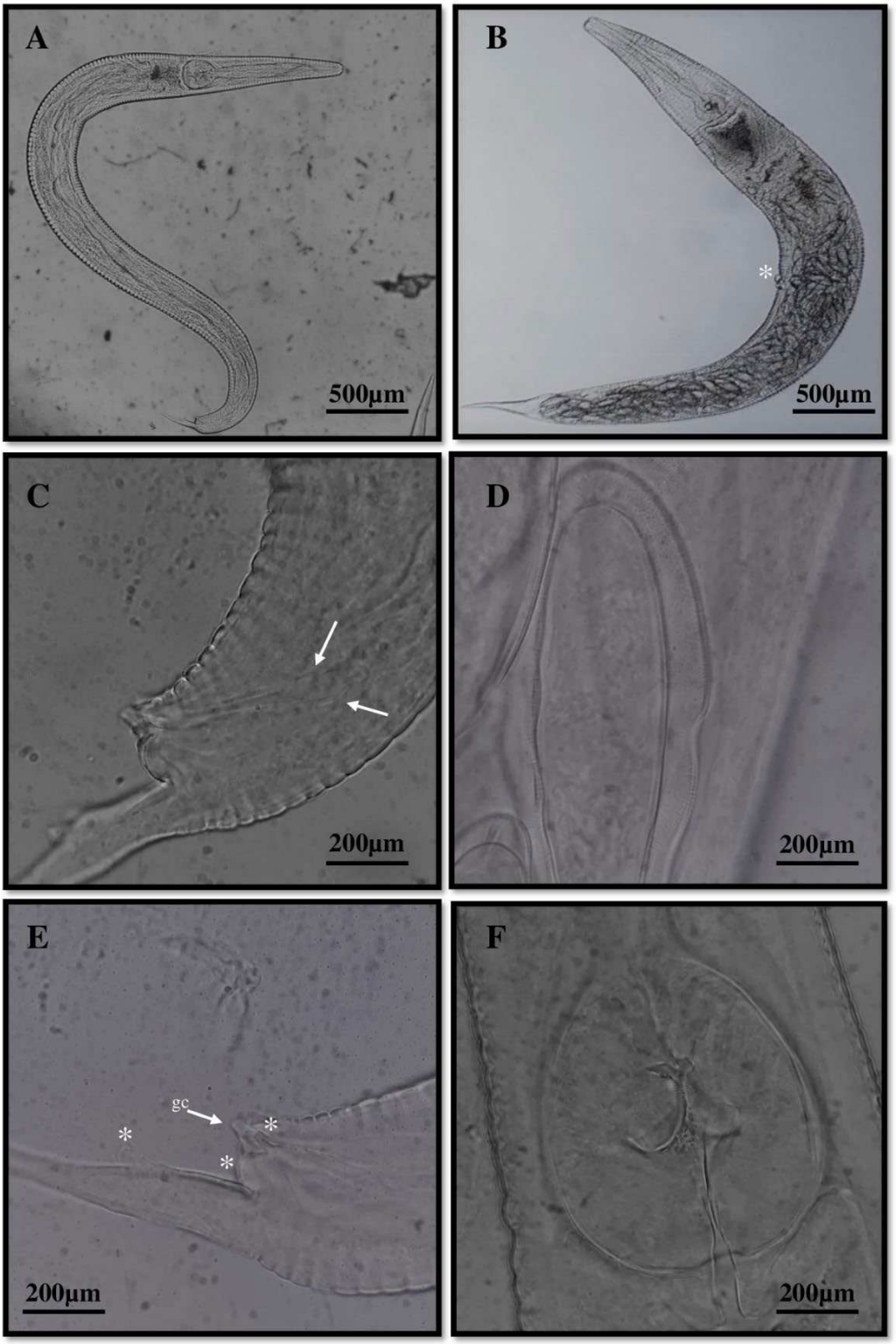

Figure 2. *Parapharyngodon pereiramendoi* n. sp.: (a) male in total length; (b) female in total length [*Vulva at midbody] (c) details of spicules (arrows); (d) details of eggs thick shell; (e) male, details of posterior end [* papillaes; gc – genital cone; arrow indicated support V-shaped]; (f) detail of eosophagel bulb.

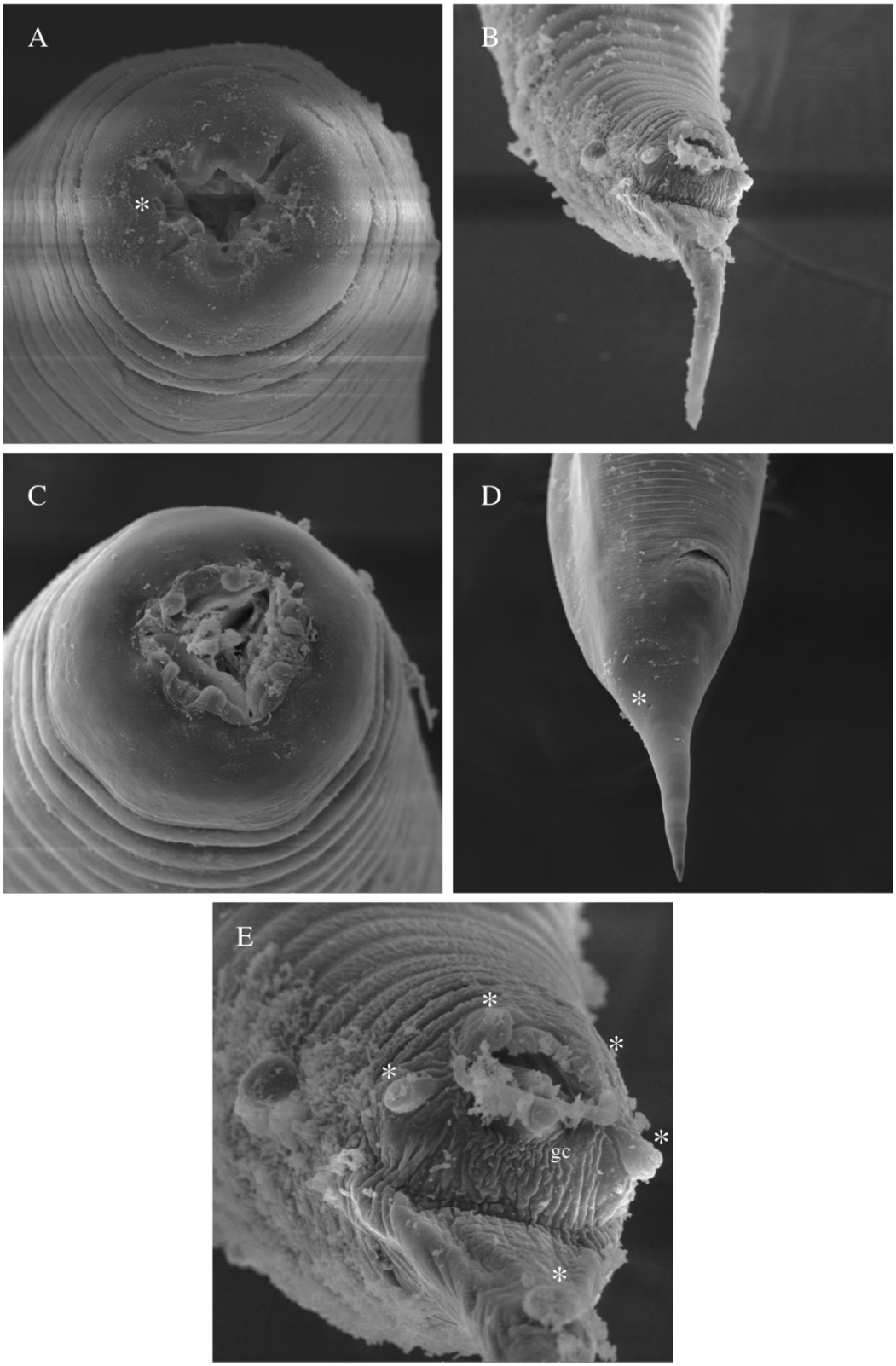

Figure 3. Scanning electron microscope images of *Parapharyngodon pereiramendoi* n. sp.: (a) male en face view of anterior end [*amphid]; (b) posterior end in male; (c) female en face view of anterior end; (d) conical tail in female [*phasmid]; (e) details of posterior end in male [* papillaes; gc – genital cone].

4. CAPÍTULO 2 - FIRST RECORD OF *OZOLAIMUS CIRRATUS* (OXYUROIDEA: PHARYNGODONIDAE) INFECTING CASQUE-HEADED TREE FROG *CORYTHOMANTIS GREENINGI* (ANURA: HYLIDAE) FROM NORTHEASTERN BRAZIL

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FIRST RECORD OF *OZOLAIMUS CIRRATUS* (OXYUROIDEA: PHARYNGODONIDAE) INFECTING THE CASQUE-HEADED TREE FROG *CORYTHOMANTIS GREENINGI* (ANURA: HYLIDAE) FROM NORTHEASTERN BRAZIL

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ABSTRACT

The *Ozolaimus* genus is characterized by presenting a dorsoventrally elongated mouth with two lateral lips, a long esophagus consisting of a strong anterior portion, a short with a fusiform fold, and a thin posterior portion ending in a distinct bulb, an anteriorly dilated intestine, and absent lateral wings. Between February 2014 and September 2016, eleven specimens of the anuran *Corythomantis greeningi* were collected manually at the Ecological Station of Aiuaba, Ceará State, Brazil. After analysis, nine specimens of *Ozolaimus cirratus* infecting the large intestine of the referred specimen were recorded. Knowledge is still scarce about the ecological dynamics of pharyngodonid parasites and their parasite-host relationships; thus, this work is the first to record the *Ozolaimus* genus infecting the casque-headed tree frog *Corythomantis greeningi* from the Caatinga biome. Priviously, the only registered hosts of *Ozalaimus* parasites were iguanid lizards.

Keys-words: Caatinga; Ecology; Host-parasite interation; Parasitism;

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4.1 Introduction

The nematodes of the superfamily Oxyuroidea have been classified into three taxa: Heteroxynematidae Skryabin & Shikhobalova, Oxyuridae Cobbold, and Pharyngodonidae Travassos (CHABAUD, 1974). Pharyngodonidae, by its turn, is composed of 24 genera (PEREIRA et al. 2018), of which seven have already been recorded in Brazil: *Alaeuris* Thapar, *Ozolaimus* Dujardin, *Parapharyngodon* (Chatterji,), *Pharyngodon* Diesing, *Skrjabinodon* Inglis*, Spauligodon* Skrjabin, Schikhobalova and Lagodovskaja, and *Thelandros* Wedl (BRITO et al. 2014; DE SOUSA et al. 2022; VICENTE et al. 1993).

Ozolaimus was originally described based on individuals parasitizing a young individual of *Iguana iguana* (Linnaeus) (MALYSHEVA 2016). This genus is characterized by presenting a dorsoventrally elongated mouth, in which can be found two lateral lips, a long esophagus consisting of a strong anterior portion (a short one with a fusiform fold), and a thin posterior portion ending in a distinct bulb with an anteriorly dilated intestine, in addition to absent lateral wings. Males have a short tail and a long spicule, while females have a gradually tapering tail. The reproductive system is located anteriorly with large eggs inside, and the anus is located near the posterior end of the body (VICENTE et al. 1993). Currently, there are five species of the genus distributed around the world: *O. cirratus* (Linstow), *O. ctenosauri* Caballero, *O. linstowi* Malysheva 2016, *O. megatyphlon* (Rudolphi), and *O. monhystera* Linstow (MALYSHEVA 2016).

Corythomantis greeningi Boulenger is an anuran of the Hylidae family, widely distributed in the xeric and sub-humid regions of the Cerrado and Caatinga domains in Brazil SILVA et al. 2014). The adult presents a length of around 8 cm and has a roughened body covered by mucous and granular glands that secrete toxic compounds that are effective against predators (JARED et al. 1999). *Corythomantis greeningi* presents life habits associated with the vegetation, being found in bromeliads and tree trunks; it has a sit-and-wait foraging mode, reproduction during the rainy season, a strongly ossified skull, and a dorsoventrally flattened head covered by small spicules that contribute to minimizing water loss in arid environments (JARED et al. 1999; 2005; JUNCÁ et al. 2008). Here, we report the nematode *Ozolaimus cirratus* infecting the digestive tract of *C. greeningi* in an area of Caatinga in the municipality of Aiuaba, Ceará State, Northeastern Brazil.

4.2 Materials and Methods

Eleven specimens of *C. greeningi* (adult males; mean snout-vent length [SVL] ± SD – 76 ± 7.48mm, range: 64.62 – 89.97 mm) were collected in the Ecological Station of Aiuaba, Ceará State, Brazil (06°35'35"S, 40°08'31"W) between February 2014 and September 2016 (Figure 1). The hosts specimens were euthanized with lidocaine 2%, dissected by a ventral longitudinal incision, and they had the following organs examined under stereomicroscopic for macroendoparasites: liver, lungs, heart, stomach, intestines, bladder and kidneys. The hosts specimens were fixed in 10% formaldehyde, stored in 70% ethanol, and deposited at the Regional Nucleus of Ophiology (NUROF) at the Federal University of Ceará under voucher 7368, 7369, 7370, 7383, 7398, 7403, 7409,
7422, 7425, 7433, and 13302.

Nematodes were fixed and preserved in 70% ethanol, then cleared in lactic acid (TRAVASSOS 1950) and mounted on temporary slides for identification. In morphological analysis and identification, we followed (VICENTE et al. 1993) and the specialized literature. The measurements were given in millimetres (mm) and were expressed as minimum and maximum values, followed by the mean in parentheses (Table 1). Morphological and morphometrical analyses of parasites were carried out using the Motic Images Plus™ software, version 2.0.

The parasitological descriptors as prevalence (P), mean intensity of infection (IMI), and mean abundance (AM) have been calculated following (BUSH et al. 1997). Some specimens were also analyzed using scanning electron microscopy and post-fixed in 1% osmium tetroxide, dehydrated in a graded alcohol series and dried at the critical point of CO2. The specimens were then mounted on an aluminum stub using conductive double-sided tape, coated with gold–palladium and examined using an Inspect S50 – FEI electron microscope at the Analytical Center from the Federal University of Ceará. All parasites were deposited at the Parasitological Collection of the Laboratory of Zoology from Universidade Regional do Cariri (LZ-URCA), under the numbers: vouchers URCA-P 801.

All applicable national guidelines for the care and use of animals were followed according to collection authorization issued by Chico Mendes' Institute (ICMBio/SISBio) Nº 29613 – 1 and 55467 – 1 for scientific activities aims and authorized by ethical Committee on Animal Experimentation and Use from Cariri Regional University CEUA/URCA under number 00026/2015.2. The study was reported in accordance with ARRIVE guidelines. All experiments were performed in accordance with relevant guidelines and regulations.

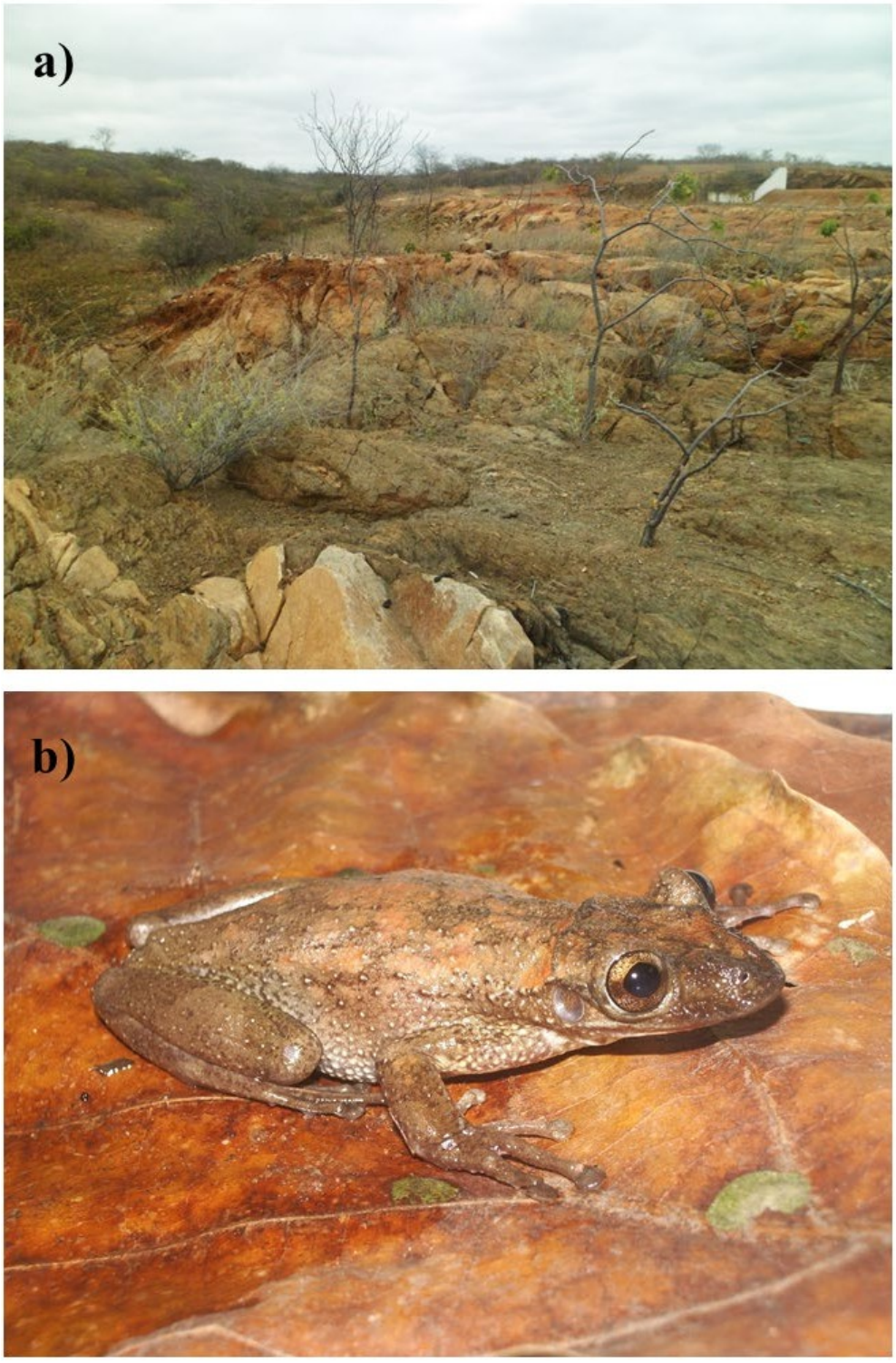

Figure 1. A) Benguê Reservoir in Ecological Station, Aiuaba, Ceará State. Semi-arid region with phytophysiognomy of the Caatinga environment. B) *Corythomantis greeningi* (Photo kindly provided by Professor Robson Waldemar Ávila).

Table 1. Comparative measurements (in millimeters, with minimum and maximum values followed by mean in parentheses) of *Ozolaimus cirratus* between differents hosts in Brazil.

	O. cirratus (This study)		*O. cirratus* (Otávio et al. 2018)		*O. cirratus* (Vicente et al. 1993)	
Host	*C. greeningi*		*I. iguana*		*I. iguana*	
	Male	Female	Male	Female	Male	Female
Length	4.41 – 5.1 (4.9)	5.28 – 6.0 (5.62)	5.75 – 6.9	7.7 – 8.0	4.3 – 4.5	4.4 – 5.9
Width	0.37 – 0.46 (0.4)	0.47 – 0.57 (0.53)	0.6 – 0.67	0.8 – 1.0	0.49	0.7 – 0.76
1ª portion of the Oesophagus	0.8 – 0.89 (0.8)	1.13 – 1.15 (1.14)	0.81 – 0.91	1.1 – 1.15	0.7 – 0.76	0.92 – 0.98
2ª portion of the Oesophagus	0.91 – 1.0 (0.9)	1.13 – 1.41 (1.36)	0.77 – 1.02	1.05 – 1.17	0.52 – 0.6	0.6 – 0.7
Oesophagus total	1.75 – 1.84 (1.8)	2.43 – 2.56 (2.5)	1.7 – 1.92	2.2 – 2.3	1.5 – 2.0	
Bulb length	0.13 – 0.19 (0.16)	0.2 – 0.22 (0.21)	0.18 – 0.28	0.3 – 0.35	0.21	0.27
Bulb width	0.16 – 0.17 (0.17)	0.2 – 0.24 (0.22)	0.24 – 0.27	0.25 – 0.3	0.10 – 0.13	0.21
Anus		0.18 – 0.21 (0.2)				0.32 – 0.38
Espicule	0.98 – 1.78 (1.4)		1.8 – 2.5		1.6 – 1.9	

Fonte: Elaborada pelos autores.

4.3 Results

We found nine specimens of *Ozolaimus cirratus* (four males and five females) infecting the large intestine of *C. greeningi* individuals collected (Figure 2 and 3). Of the eleven hosts examined, only one individual (male, SVL – 74.77mm, 15.5g) was infected with *O. cirratus* (P = 9.1%; IMI = 9; AM =0.81). The other macroendoparsitic helminths associated with these hosts of *C. grenningi* are under analysis and will be published later (personal communication).

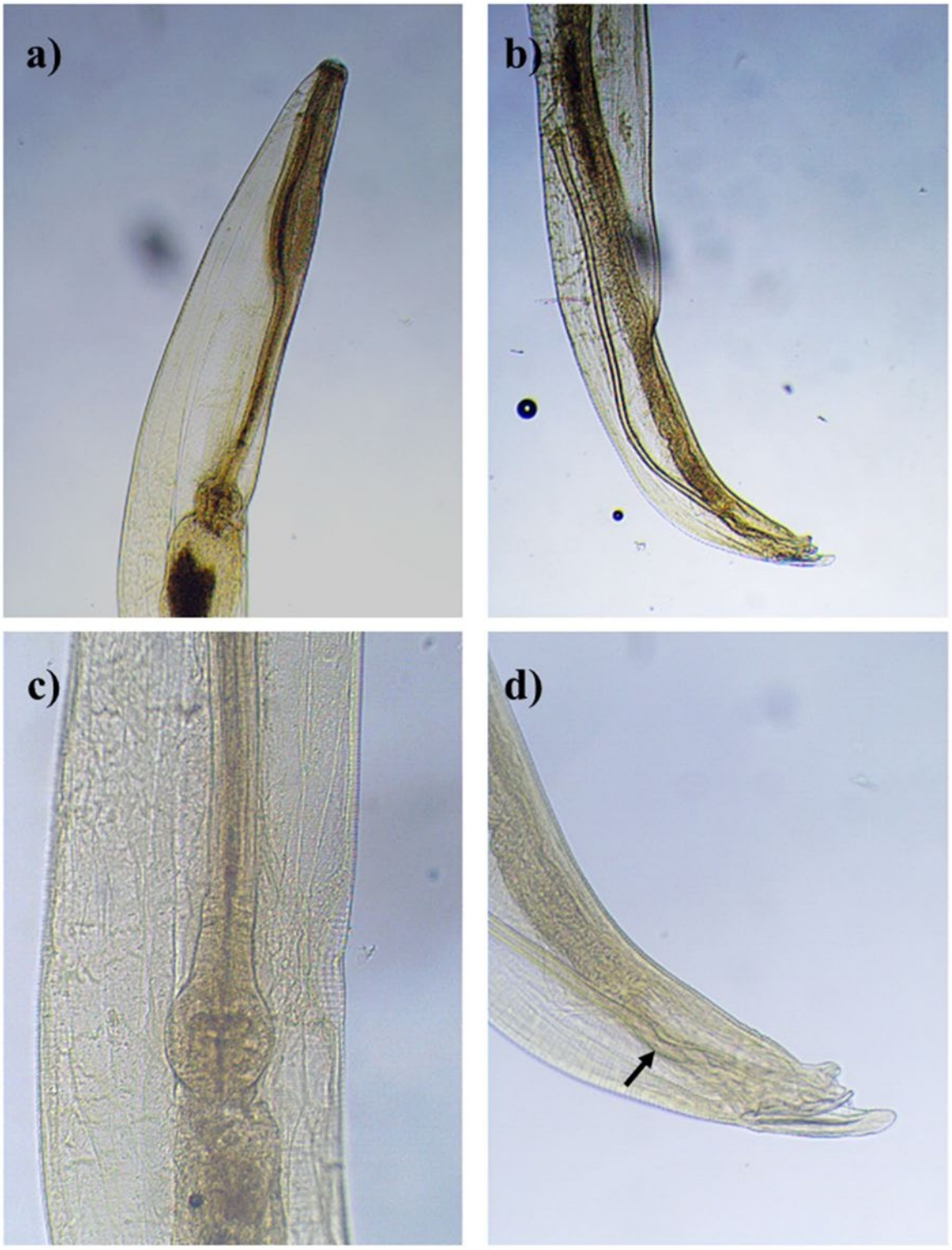

Figure 2. Light microscopy images of *Ozolaimus cirratus*. A) anterior end of the male; B) Posterior end of the male with visualization of the spicules; C) detail of the esophageal bulb; D) Detail of the dilatation at the end of the spicule.

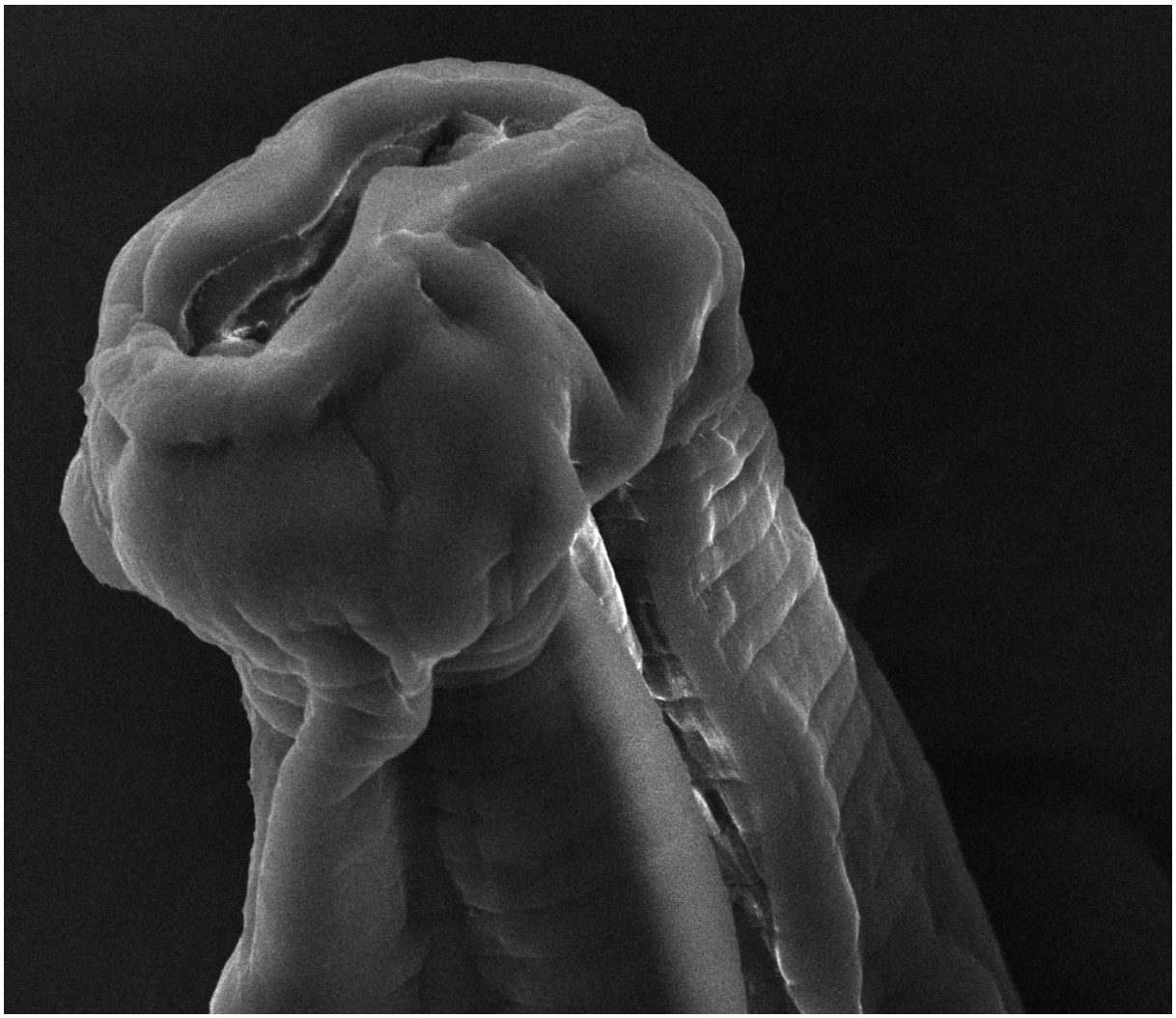

Figure 3. SEM micrograph of *Ozolaimus cirratus*, female anterior end, subventral view.

4.4 Discussion

Nematodes of the genus *Ozolaimus* are common intestinal parasites in iguanids (LOUKOPOULOS et al. 2007). Literature records indicate the occurrence of two species in Brazil: *O. cirratus* and *O. megatyphlon* (VICENTE et al. 1993). Although *O. cirratus* has shown low abundance in *C. greeningi*, in general, infections by the genus *Ozolaimus* as well as by other oxyurids are not usually considered pathogenic for their hosts (LOUKOPOULOS et al. 2007). However, we highlight that there have been reports of massive and lethal infections by *Ozolaimus* species in iguanid hosts (LOUKOPOULOS et al. 2007; MUNAKATA et al. 1999).

Ozolaimus cirratus has been identified based on its morphology, with its spicule structure being fundamental for its identification. This character differs *O. cirratus* from *O. megatyphlon* by possessing the terminal distal end dilatation from the spicule (VICENTE et al. 1993). This character was important, as it proved to be reliable and constant in other works that mention this species (BREVES et al. 2011; OTÁVIO et al. 2018). In addition, the morphometry of the specimens was verified and compared with those of other studies that recorded the species in other hosts (Table 1). We verified that the morphometry of the male individuals of *O. cirratus* in this work is similar to the measurements made by Vicente et al. (1993) concerning the following characters' body length, width, and spicule length. The morphometric values related to the excretory pore, nerve ring, and distance from the vulva to the anterior end were excluded because they were not visible in all individuals in the sample.

Currently, there is a discussion about which taxonomic criteria would be safer for the determination of *Ozolaimus* species. Several authors debate the importance of oesophageal morphology as a diagnostic criterion, nevertheless, there are still disagreements regarding the accuracy of studies that seek to elucidate such issues (BREVES et al. 2011; INGLIS et al. 1960; LEUSSINK 1958). While there are differences between different studies regarding the morphological variation of the oesophagus, this imprecision may be related to the fact that this structure presents itself in a plastic way within the species, causing confusion among the authors. On the other hand, we reinforce the need for more accurate studies aimed at collecting more diagnostic taxonomic information for the species of the genus and the verification of morphologically plastic traits between the species. Furthermore, Malysheva (2016) defends that there is a need for more studies that explore the structure and morphology of the animal's anterior extremity, with detailed studies on the composition and morphology of the mouth, as this is a safer taxonomic character. In addition, the use of molecular data can be an excellent tool to help elucidate such taxonomic problems within the genus.

Iguanidae lizards of the genera *Ctenosaura*, *Cyclura*, and *Iguana* were, until now, the only registered hosts of *Ozolaimus* (MALYSHEVA 2016). In the world, *Iguana iguana* has records of *O. linstowi* from Mexico (MALYSHEVA 2016), and *O. megatyphlon* from Greece (LOUKOPOULOS et al. 2007). In Brazil, *I. iguana* is infected by *O. cirratus* and *O. megatyphlon* (VICENTE et al. 1993; BREVES et al. 2011; ÁVILA; SILVA 2010). Oxyuridae has a strictly monoxenic life cycle, with transmission and development stages occurring in different ways within the group (ANDERSON 2000). We believe that the occurrence of *O. cirratus* in *C. greeningi* may be an occasional encounter of an accidental infection during the host's foraging behavior. Therefore, we believe that not implying that this species of anuran acts as a host for this parasite. This record may be related to the sympatric occurrence of two hosts *C. greeningi* and *I. iguana* in the same sampled locality (ÁVILA et al. 2017). On the other hand, all parasitic individuals observed were adults, and among females, the presence of eggs was visualized inside the uterus, which can suggest a spillover effect. Therefore, new samplings of *C. greening* in this and other locations are encouraged to verify the occurrence of this

phenomenon.

Knowledge is still scarce about the ecological dynamics of pharyngodonid parasites and their parasite-host relationships (BREVES et al. 2011). In other searches, it has been described and geographically expanded the occurrence record of another pharyngodonid *Parapharyngodon silvoi* Araújo-Filho et al. 2015 infecting the anuran *Dermatonotus muelleri* (Boettger) in the Caatinga domain (ARAÚJO-FILHO et al. 2015; ALCANTARA et al. 2018). Recently, another pharyngodonid was described, *Parapharyngodon curupira* Santos et al. 2022, for the hylid host *Osteocephalus taurinus* Steindachner from northern Brazilian Amazon region (SANTOS et al. 2022). To the best of our knowledge, up to now, this is the first record of *Ozolaimus* infecting hosts other than lizards of the *Iguana* genus.

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Author contributions
CSS and DHM conceived the research and led feldwork in Benguê reservoir in Aiuaba. CSS prepared the slides of specimens, imagens, tables and figures. PC and DHM actively participated in the discussion of the results, reviewed and approved the fnal manuscript.

Competing interests
The authors declare no competing interests.

Additional information
Supplementary Information The online version contains supplementary material available at: present within the article.

5. CAPÍTULO 3 - EXPLORING THE PHYLOGENETIC LANDSCAPE: UNRAVELING THE RELATIONSHIPS AND BIOGEOGRAPHY OF THE *COSMOCERCA* GENUS IN AMPHIBIANS

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EXPLORING THE PHYLOGENETIC LANDSCAPE: UNRAVELING THE RELATIONSHIPS AND BIOGEOGRAPHY OF THE *COSMOCERCA* GENUS IN AMPHIBIANS

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Paulo Cascon[1]

ABSTRACT

Cosmocerca genus is a cosmopolitan clade of endoparasitic nematodes of amphibians and reptiles currently comprising 37 species. With the growing number of molecular studies addressing different species of this genus throughout the world, we aim to investigate the phylogenetic relationships between the species of this group, to identify gaps and direct the development of new research for the genus and related species, mainly for that occurrence in the Neotropical region. We analyzed a total of 40 sequences of nuclear (internal transcript spacer (ITS)) and mitochondrial (cytochrome c oxidase subunit 1 (COI)) genetic markers from species that have the genetic material sequenced and available. Here, we found a strong association between the phylogeny of the parasites and their area of occurrence among the zoogeographical regions of the world. Still, we evidenced the scarcity of studies for the species from the Neotropical region. The analysis of these data can then support future research aimed at clarifying questions about the biology, phylogeography, and evolution of the species of the genus and allow advances in the understanding of the evolution of the Cosmocercidae clade.

Keys-words: Nematoda; Phylogeny; Phylogeography; Taxonomy.

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5.1 Introduction

Parasitism is one of the most successful modes of life exhibited by living organisms, measured by the frequency with which it has evolved, its diversity, the important role it plays in its biological relationships, as well as contributing to the maintenance of the diversity and evolution of its hosts (POULIN; MORAND, 2000). Among the various metazoan taxa existing on Earth that have some form of parasitic life (see DUNN et al. 2014), the Nematoda clade represents one of the most abundant and best studied.

Nematodes are cosmopolitan, megadiverse, and adapted to almost all habitats on the planet. They exploit a wide variety of niches and include free-living terrestrial and marine microbivores, meiofaunal predators, herbivores, and plant and animal parasites (PARKINSON et al. 2004). Presently, around 25,000 species are known (BLAXTER; KOUTSOVOULOS, 2015). However, estimates indicate a richness that ranges between 40.8 –

81.6 million species (LARSEN et al. 2017). Currently, nematodes are classified into three clades: Dorylaimia, Enoplia, and Chromadorea, based on small subunit ribosomal RNA phylogenetics (DE LEY; BLAXTER, 2002).

The Cosmocercidae (Chromadorea: Ascaridomorpha: Cosmocercoidea) is a cosmopolitan clade of endoparasitic nematodes of the digestive tract of vertebrates (ANDERSON, 2000) formed by three subfamilies Austraplectaninae Baker, 1981, Maxvachoniinae Chabaud and Brygoo, 1960 and Cosmocercinae Railliet, 1916 (BURSEY et al. 2011; HARNOSTER et al. 2022). The clade Cosmocercinae currently comprises 28 genera, of which seven - *Aplectana*, *Cosmocerca*, *Cosmocercella*, *Cosmocercoides*, *Neocosmocercella*, *Raillietnema*, and *Schrankiana* - are found in South America infecting amphibians (CAMPIÃO et al. 2014; PITOMBEIRA et al. In press).

- Among South American countries, Peru, Argentina, and Brazil have the highest records of infection in amphibians by the genus *Cosmocerca* (SANTOS; AMATO, 2013). *Cosmocerca* species are widespread throughout all continents. Currently, there are 37 species assigned to *Cosmocerca* found in different biogeographic regions of the world: three from the Afrotropical region, four from the Australian region, one from the Nearctic region, 12 from the Neotropical region, four from the Oceanian region, five from the Oriental region, five from the Palaeractic, one from the Panamanian region, and two Sino- Japanese region. The Madagascan region and Sarahoarabian region do not have species reported. Regarding the Neotropical region, the following species have been recorded: *C. albopunctata* Alcantara et al. 2022, *C. brasiliensie* Travassos, 1925, *C. chilensis* Lent and Freitas, 1948, *C. cruzi* Rodrigues & Fabio, 1970, *C. gymnophthalmicola* Ávila e Da Silva, 2019, *C. paraguayensis* Moravec & Kaiser, 1994, *C. parva* Travassos 1925, *C. podicipinus* Baker & Vaucher, 1984, *C. rara* Freitas & Vicente, 1966, *C. travasssosi* Rodrigues & Fabio, 1970, *C. uruguayensis* Lent & Freitas, 1948, and *C. vrcibradici* Bursey & Goldberg, 2004. (ALCANTARA et al. 2022; ÁVILA & DA SILVA, 2019; BURSEY et al. 2015; FERREIRA-SILVA et al. 2022).

Cosmocerca genus has a monoxenic life cycle, infecting orally or directly penetrating the free-living larva through the skin of its host. After infection, the larva initially migrates to the lung, an organ necessary during development before definitively establishing itself in the host's digestive tract (ANDERSON, 2000). In Brazil, records of infection by these nematodes are concentrated mainly in the South and Southeast regions, parasitizing

species from the families Brachycephalidae, Bufonidae, Hylidae, Hylodidae, and Leptodactylidae (CAMPIÃO et al. 2014).

The Caatinga morpho-climate domain (CMD) is located in The Brazillian northeastern is characterized by possessing a distinct seasonality with high temperatures, irregular rainfall with precipitation levels of 300–1000mm annually, and prolonged drought periods, besides being the only natural region with limits restricted to the national territory (QUEIROZ et al. 2017). The CMD has a richness of 98 species of amphibians, 20 of which are endemic (GARDA et al. 2017). All this diversity present in this region represents potential hosts for a great hidden diversity of helminth parasites.

In the last decade, many studies contributed to the knowledge about helminth species associated with amphibians in northeastern Brazil, most of which were developed in Caatinga environments. With regard to the parasitological aspect, these works investigated from different perspectives ecological (SILVA et al. 2018; OLIVEIRA et al. 2019; MADELAIRE et al. 2020), biogeographic (CAMPIÃO et al. 2014), taxonomic (NASCIMENTO et al. 2012; ARAÚJO-FILHO et al. 2015; LINS et al. 2017; MARTINS-SOBRINHO et al. 2017; SENA et al. 2018; SILVA et al. 2019), physiological (MADELAIRE et al. 2017), and molecular (MULLER et al. 2018; MORAIS et al. 2020).

Considering studies related to the *Cosmocerca* genus, in recent past there has been a growing increase in those that use molecular techniques for the identification and characterization of new species (RIZVI et al. 2011; SATO et al. 2015; SINSCH et al. 2018; CHEN et al. 2020b). In the Neotropical region, the first study carried out sequenced genetic data contributed to the description of a new species of the genus, *Cosmocerca albopunctata* Alcantara et al. 2022 and also sequenced data from two other species, *C. parva* and *C. podicipinus* (ALCANTARA et al. 2022).

In this perspective, in order to better understand the systematics of the clade *Cosmocerca* we carried out a phylogenetic analysis of molecular data available in public databases about the *Cosmocerca* genus, where we aimed to (1) investigate the phylogenetic relationships inside of the genus, to contribute to the understanding of the molecular phylogeny of this group and its pattern of distribuition zoogeographic around the world and (2) highlight possible gaps in knowledge regarding taxonomy and species diversity directing the development of new research for the genus and related species.

5.2 Materials and Methods

5.2.1 Collection and process of molecular dates

We selected the molecular data from species of the genus *Cosmocerca* available in Genbank. A total of 40 sequences were selected (Table 1). Due to their availability, the cytochrome c oxidase I (COI) genes and the genomic DNA of the ITS gene were selected and used as molecular markers in this study. Seven species of *Cosmocerca* were selected for COI gene molecular marker and ten species were selected for ITS gene molecular marker. We sampled COI sequences for six described and named *Cosmocerca* species, one unidentified or unnamed *Cosmocerca* species, and *Cosmocercoides qingtianensis* as an outgroup. We sampled ITS sequences for three of the same species as COI, plus five additional named species and two unidentified or unnamed *Cosmocerca* species, and *Cosmocercoides pulcher* as an outgroup. The selected sequences aligned using ClustalW, and used to build phylogenetic trees using MEGA 11.0 software.

Phylogenetic analysis

A tree was constructed for each molecular marker. The reconstructions of the phylogenetic trees were performed using the Maximum Likelihood (ML) algorithm in the Mega 11.0 software (TAMURA et al. 2011). Branch support values were calculated based on 1000 bootstrap replicates. The "nearest-neighbor interchange" (NNI) criterion served as a heuristic method for the maximum likelihood of choice to determine the inferential tree when the initial tree was formed using the neighbor-joining algorithm (SINSCH et al. 2018). A substitution model test was performed for the sample universe of data, which according to the Bayesian information criterion, corrected by the Akaike information criterion (AIc) and maximum likelihood values for the ITS and COI gene sequences, the most suitable parameters were Kimura-2 (BIC – 6008.9and AIc – 5695.6) and Hasegawa- Kishino-Yano (BIC - 3459.7and AIc – 3205.5), respectively, using the gamma distribution with the five rate category. The Kimura 2-parameter method was used to estimate the inter- and intraspecific phylogenetic distance in the analyzed sequences. As for the substitution model, we use the nucleotide type, for substitutions include transitions + transversion, and the number of different bases per site was calculated by averaging all sequence pairs between the d (distance) ± SE groups and using the bootstrap produced by 1000 repetitions (SINSCH et al. 2018). For the rooting of the trees COI and ITS, the species *Cosmocercoides qinqtianensis* and *Cosmocercoides pulcher* was proposed as an outgroup, respectively. Subsequently, the trees were generated and visualized using Mega 11.0 software.

5.3 Results

Among 37 species occurring worldwide, 11 formally recognized species had their genetic material sequenced and available for molecular markers mitochondrial, nuclear, or both which are distributed across five major zoogeographic regions (Afrotropical: *C. daly*, *C. makhadoensis*, and *C. monicae*; Neotropical: *C. albopunctata*, *C. parva*, and *C. podicipinus*; Sino-Japanese: *C. japonica* and *C. simile*; Oriental: *C. kalesari*; Palaeractic: *C. longicauda* and *C. ornata*). Among these two are distributed throughout the Neotropics (*C. parva* and *C. podicipinus*), and currently, the species *C. albopunctata,* has records only for Brazil. In addition to the species above, three other species of the genus not yet formally described, however which have genetic data available for the selected molecular markers, were used in this study (see table 1).

The relationships of *C. japonica*, *C. simile*, and *C. ornata* are different between the COI and ITS trees. The phylogenetic results based on the COI mtDNA sequences clustered the species distributed in the Sino-Japanese realm with a high clade support value, with *C. simile* and *C. japonica* forming a monophyletic clade and sister group to *Cosmocerca* sp. X and *Cosmocerca ornata* (fig. 1). However, in the tree generated for the ITS gene sequences, the monophyletic clade formed by *C. simile* and *C. japonica* is the sister group of *Cosmocerca* sp. LL is most closely related to the clade formed by species occurring in the Afrotropical and Oriental realms (fig. 2).

The interespecific nucleotide divergence detected in COI mtDNA between *C. simile* and its congeners belonging to the same clustering are: *C. japonica* (13.1%) and *C. ornata* (13.8%).Between species with Neotropical distribution the distance from *C. parva* and its congeners are: *C. podicipinus* (10.1%) and *C. albopunctata* (17.8%), and between these two (18.4%). (Table 2). Regarding the ITS fragment, the genetic distance between the species of the Sino-Japanese clade *C. simile* and *C. japonica* is (2.1%). Concerning *C. ornata* and *C. simile* (15.7%), and *C. japonica* (16.9%). The genetic variation between *C. ornata* species and *Cosmocerca* sp. yL varied (0.03%) and was the lowest found in the study. The nucleotide distance between species of Afrotropical distribution *C. makhadoensis* and *C. monicae* is (1.9%). The *C. daly* was the species that diverged most from its congeners.

Phylogenetic analyses of COI and ITS gene sequences led to the formation of clades based mainly on their biogeographical occurrence patterns. The COI mtDNA tree originated monophyletic groupings with the formation of two main clades. The first includes species of Sino-Japanese distribution, including *C. japonica*, *C. simile*, and *C. ornata*. The *C. parva* and *C. podicipinus* formed the second clade with the Neotropical distribution species. *C. albopunctata* did not group with other species in the region of its distribution area (fig. 1). While the ITS gene tree reinforced the grouping of Sino- Japanese distribution species, *C. simile* and *C. japonica* as sister groups of *Cosmocerca* sp. LL. A second clade formed by Afrotropical and Oriental species. And a third, more distant clade representing the Palaeartic distribution species. The kinship of *C. daly* is unclear (fig. 2).

5.4 Discussion

Biogeographic regions are fundamental units for comparison in many studies with ecological and evolutionary approaches (HOLT et al. 2013). Phylogenetic information has been used to cluster species within these biogeographical units on a global scale and to quantify phylogenetic affinities between these regions (GRAHAM & FINE 2008; HOLT et al. 2013). The results provide evidence that identifies these zoogeographic realms containing distinct evolutionary histories for these groups of endoparasitic nematodes. In addition, in the future, may still be corroborated by phylogenetic studies of other parasitic taxa.

Phylogenetic trees contain essential information about the evolutionary relationships of species and have become increasingly available in recent decades, allowing the delineation of biogeographical regions (HOLT et al. 2013). Based on data on the geographic distribution and phylogenetic proximity of some groups of vertebrates, including amphibians, Holt et al. (2013) outlined 11 zoogeographical realms in the world. The phylogenetic pattern and zoogeographic distribution of these hosts, are reflected in the phylogenetic arrangement of the cosmocercid parasites addressed in this study.

The use of molecular markers has the advantage of being little influenced by the environment and having many informative characteristics available in each organism (TURCHETTO-ZOLET et al. 2013). These markers can provide fundamental information about phylogeny, phylogeography, estimation of genetic distances, and discrimination of subpopulations, as well as help to investigate the biogeographical history of species (ROSA; PAIVA 2009). Therefore, the use of the selected molecular markers was able to delimit and show in the generated tree groups of parasitic species based on their zoogeographic distribution pattern.

The COI molecular marker is often used to identify biogeographical groups, with the main advantage being that they do not present recombination events, thus being able to act as good genetic markers (TURCHETTO-ZOLET et al. 2013). In this study, the gene COI molecular marker grouped the genetic sequences of the *Cosmocerca* species into two zoogeographical realms of occurrence (fig. 1). For decades, the COI gene has been used to identify species, discriminate subspecies and study evolutionary events in several groups of metazoans (LUNT et al. 1996; HEINDLEDER et al. 2002; BRUFORD et al. 2003; GOVEIA, 2010; COLLIN et al. 2020; BARBOZA et al. 2023). Given the vast utility and success in the use of this marker, the use of the COI gene for population, taxonomic and phylogeographic studies have become more frequent among studies with this group of nematodes (SINSCH et al. 2018; CHEN et al. 2020b; ALCANTARA et al. 2022).

As the genetic sequencing data of *Cosmocerca* species increases and becomes available, the tendency is for the phylogenetic proposals initially made to be corrected and new relationships to appear. The tree generated from the analysis of the COI gene sequences presented a phylogeny different from that proposed by Chen et al. (2020a) for breaking down the kinship relationships between species occurring in the Sino-Japanese realm. Nevertheless, our results corroborate the phylogeny proposed by Chen et al. (2020b), which reinforces the monophyly between the species *C. japonica* and *C. simile* with low values of nucleotide divergence.

The genetic distances calculated for the molecular marker of the COI gene for specimens included in each clade are consistent with their zoogeographic distribution domain, except for *C. albopunctata*, which has origins in the Neotropical region and clustered with

species from the Sino-Japanese realm. We believe that this result may be related to the low volume of data about this species, and that further analysis may clarify aspects of its phylogeny with its Neotropical congeners.

Regarding the use of the ITS marker, the low genetic distance between the species of the clade formed by *C. ornata* and *Cosmocerca* sp., possibly indicates that *Cosmocerca* sp. represents an extension of the occurrence of *C. ornata* in the Sino-Japanese region. However, *C. ornata* is a nematode widely distributed throughout the Palearctic region (KIRILLOVA; KIRILOV 2021), which can enable future investigations to understand the evolutive origins, geographic distribution pattern, and taxonomy of this species. Even the tree generated from partial sequence data of the ITS gene, our study corroborated with Chen et al. (2020b) the proximity between the species of *C. simile* and *C. japonica*. In addition, we observed the ungrouped between the species of *C. longicauda* and *Cosmocercoides pulcher*, invalidating the concatenated tree proposal of Sinsch et al. (2018), where these species formed a sister group.Considering that the data used in this study are recent and the genetic information of other molecular markers for many of the species of *Cosmocerca* is still scarce, it was not possible to carry out a concatenated analysis of the genetic sequences of the species selected in this study. Species from the Neotropical group have only sequence data from the COI gene, while species from the Eastern Afrotropical and Palearctic groups have sequence data from the ITS gene. Although we have about 1/3 of the *Cosmocerca* species with their DNA data available in public banks and the use of these data based on COI and ITS gene sequences in this study proved to be great species delimiter. Perhaps it is still early to infer which molecular marker is more suitable for the identification of species of this genus, considering that recent works have been exploring other markers such as the genes of the 18S, 28S, 5.8S and 16S sequences (CHEN et al. 2020; SINSCH et al. 2020).

Given the taxonomic difficulties in identifying several groups of parasites, the use of molecular data associated with morphological traits for different groups of macroendoparasite helminths increases the chances of species being better characterized and new ones being described. Among the most recent works that cover this perspective of study, Sinsch et al. (2018), reinforce this idea by contributing by carrying out an integrative taxonomy study by relating morphological and genetic data of species of digenetic helminths and nematodes.

Traditionally, morphological studies have been used to identify nematodes (BURSEY et al. 2011; DE SOUSA et al. 2022; MATIAS et al. 2018; SILVA et al. 2018; SINSCH et al. 2020). The identification of *Cosmocerca* species is mainly done by observing the males and their structures in the posterior portion (HARNOSTER et al. 2022). However, recent efforts try to implement the use of integrative taxonomy for a better understanding in the identification of *Cosmocerca* species (ALCANTARA et al. 2022; CHEN et al. 2020b), as it already occurs in other genera such as *Rhabdias* (MORAIS et al. 2020; WILKENS et al. 2019; TKACH et al. 2014), *Cosmocercoides* (CHEN et al. 2018; TRAN et al. 2015) and *Oswaldocruzia* (WILKENS et al. 2021).

We reinforce that in taxonomic and phylogenetic studies with parasites, the traditional combination of morphological data and DNA sequences has contributed to the elucidation of new species, biogeographic delimitation, and resolution of phylogenies within this group (MORAIS et al. 2020; WILKENS et al. 2019; Muller et al. 2018). Furthermore, the increasing availability of parasite DNA sequences has also proved essential to discover the cryptic diversity of these organisms, elucidating patterns of connectivity and gene flow

between populations (CHEN et al. 2020b), and contributes to a better understanding of the life cycle and specificity of the parasite-host (SINSCH et al. 2018), all of which are key elements for comprehending coevolution and host-parasite dynamics (POULIN et al. 2019).

These results bring with them important ecological, biogeographic, and evolutionary implications for the elucidation of such issues as the zoogeographic distribution of species, speciation phenomena, and the occurrence of cryptic species complexes. Therefore, to resolve such issues, studies with integrative approaches that combine genetic, morphological, ecological, and behavioral data are necessary to develop knowledge and understanding of the *Cosmocerca* genus. Therefore, the application of these methods in taxonomic studies makes it possible to describe diversified patterns within the genus *Cosmocerca* (LEÓN; CHOUDHURY, 2010). As an implicit factor, the use of these methods may allow us to describe new taxa, or even discover new phylogenetic positions related to cryptic species complexes, as occurred with the species *Rhabdias pocoto* Morais & Muller, 2020 in the *Rhabdias pseudosphaerocephala* complex in northeastern Brazil (MULLER et al., 2018).

Contrary to what we observed about the amount of data on cosmocercid species sequenced for other zoogeographic regions, such as those of distribution in the Sino-Japanese realm, it is evident that works are scarce in South America. However, recently, a single investigation sequenced the genetic data of three of the twelve species of South American occurrence: *C. albopunctata*, *C. parva*, and *C. podicipinus*, standing out with a fundamental and pioneering work in this field of research and species recognition of the region (ALCANTARA et al. 2022). Because of this, we emphasize the need for investigations that seek to elucidate these taxonomic shadows, as occurs with the species *C. parva*. This species is cosmopolitan with wide occurrence in South American amphibians and different types of Brazilian biomes (AGUIAR et al. 2015; SANTOS; AMATO 2010; Sani et al. 2021; MARTINS-SOBRINHO et al. 2017; SENA et al. 2018). However, perhaps this is another example of cryptic diversity that can be elucidated using these molecular approaches. The sequenced data for *C. parva* (ALCANTARA et al. 2022) does not represent a population from the type locality of the species. Nevertheless, the the occurrence records of *C. parva* infecting the frog *Pseudopaludicola pocoto* in an area of Caatinga in northeastern Brazil could be a good object of investigation for a new description (SILVA et al. 2018).

Opposite these difficulties, the species richness of helminths is underestimated due to the lack of taxonomic precision associated with several groups that are identified only at the family or genus category (CAMPIÃO et al. 2014). The development of research carried out on the helminth fauna brings relevant data on studies with helminths because only a small part of the entire host diversity has been studied (SILVA-NETA et al. 2020).

In recent years, the number of studies involving the molecular characterization and consequent description of new species of Cosmocercidae has increased (CHEN et al. 2018; CHEN et al. 2020a; 2020b; ALCANTARA et al. 2021). However, understanding the phylogenetic relationships of this group is still a long way off, given that the number of species that had their genetic material sequenced is small and their biogeographical areas of occurrence are distinct. When we restrict ourselves only to the genus *Cosmocerca*, this becomes even more evident, since less than 30% of the officially recognized species have had their genetic material sequenced, and even fewer are those that occur in the Neotropical realm.

With the growing number of investigation on the issue in different regions of the

world, several works contribute significantly to the knowledge of the diversity of the helminth fauna, since they present fundamental data on the genetics, morphology, taxonomy, and systematics of these parasites in distinct biogeographical areas. The scarce knowledge about the Brazilian helminth fauna reinforces the need for further studies with deeper and longer-term ecological, evolutionary, phylogenetic, and phylogeographic analyses. The examination of these data then becomes fundamental so that the information conceived can subsidize new research, clarifying issues of biology, biogeography, and evolution of the species and the genus, allowing advances in the understanding of the evolution of the clade Cosmocercidae.

Disclosure statement

No potential conflict of interest was reported by the authors.

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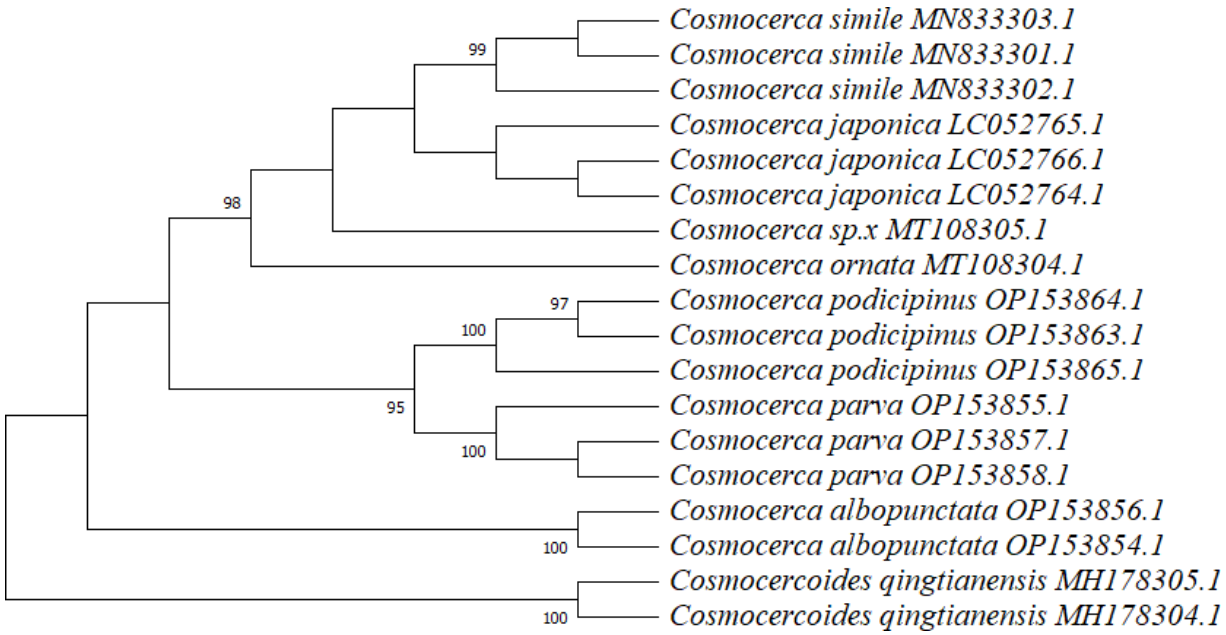

Figure 1. Phylogenetic tree carried out using the maximum likelihood method based on the molecular marker COI gene of eleven species of cosmocercid nematodes.

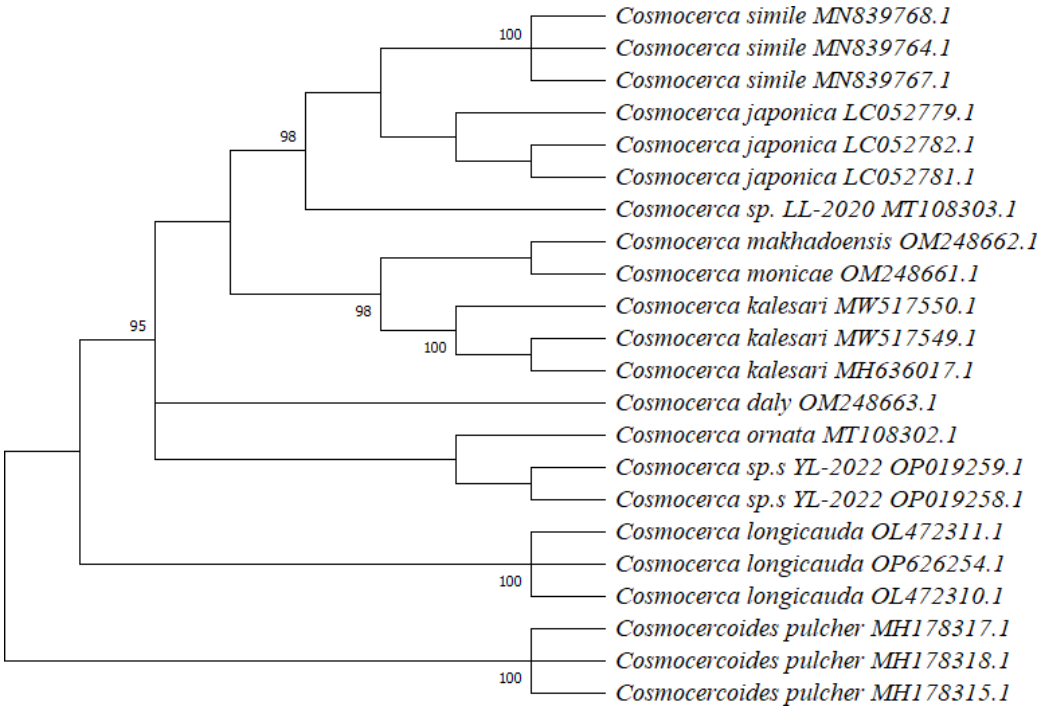

Figure 2. Phylogenetic tree carried out using the maximum likelihood method based on the ITS gene molecular marker of eleven species of cosmocercid nematodes.

Table 1. Species and sequences ITS and COI from *Cosmocerca* genus.

Species	ID Genbank	Distribution	Host	References
COI				
Cosmocerca simile	MN833303	Zhejiang, China	*Bufo gargarizans* Cantor, 1842	Chen et al. 2020b
	MN833302	Zhejiang, China	*B. gargarizans*	
	MN833301	Zhejiang, China	*B. gargarizans*	
Cosmocerca japonica	LC052764	Oita, Japan	*Rana ornativentris* Werner, 1903	Sato et al. 2015
	LC052765	Oita, Japan	*Zhangixalus viridis (*Hallowell, 1861)	
	LC052766	Oita, Japan	*Glandirana rugosa* (Temminck and Schlegel, 1838)	
Cosmocerca podicipinus	OP153865	Mato Grosso, Brazil	*Boana caiapo* Pinheiro et al. 2018	Alcantara et al. 2022
	OP153864	Mato Grosso, Brazil	*Boana caiapo* Pinheiro et al. 2018	
	OP153863	Mato Grosso, Brazil	*Leptodactylus latrans* (Steffen, 1815)	
Cosmocerca parva	OP153855	São Paulo, Brazil	*Dendropsophus nanus* (Boulenger, 1889)	Alcantara et al. 2022
	OP153858	São Paulo, Brazil	*Leptodactylus podicipinus* (Cope, 1862)	
	OP153857	São Paulo, Brazil	*L. podicipinus*	
Cosmocerca albopunctata	OP153856	São Paulo, Brazil	*Chiasmocleis albopunctata* (Boettger, 1885)	Alcantara et al. 2022
	OP153854	São Paulo, Brazil	*C. albopunctata*	
Cosmocerca ornata	MT108304	Guangxi, China	*Hylarana spinulosa* (Smith, 1923)	Chen et al. 2020b
Cosmocerca sp.x	MT108305	Yunnan, China	*D. melanostictus*	Chen et al. 2020b
Cosmocercoides qingtianensis	MH178305	Henan, China	*B. gargarizans*	Chen et al. 2018
	MH178304	Henan, China	*B. gargarizans*	
ITS				
Cosmocerca simile	MN839768	Zhejiang, China	*B. gargarizans*	Chen et al. 2020b
	MN839767	Zhejiang, China	*B. gargarizans*	
	MN839764	Zhejiang, China	*B. gargarizans*	
Cosmocerca japonica	LC052779	Oita, Japan	*Cynops pyrrhogaster* (Boie, 1826)	Sato et al. 2015
	LC052782	Oita, Japan	*R. ornativentris*	
	LC052781	Oita, Japan	*Z. viridis*	
Cosmocerca sp.	MT108303	Yunnan, China	*D. melanostictus*	Chen et al. 2020b

Cosmocerca ornata	MT108302	Guangxi, China	*Hylarana spinulosa* (Smith, 1923)	Chen et al. 2020b
Cosmocerca sp.s	OP019259	China	*O. schmackeri*	Liu et al. (unpublisehd)
	OP019258	China	*O. schmackeri*	
Cosmocerca daly	OM248663	South Africa	*Cacosternum boettgeri* (Boulenger, 1882)	Harnoster et al. 2022
Cosmocerca monicae	OM248661	South Africa	*Kassina senegalensis* (Duméril & Bibron, 1841)	Harnoster et al. 2022
Cosmocerca makhadoensis	OM248662	South Africa	*Phrynomantis bifasciatus* (Smith, 1847)	Harnoster et al. 2022
Cosmocerca kalesari	MH636017	India	*Duttaphrynus stomaticus* (Lütken, 1864)	Maity et al. 2021
	MW517550	India	*Euphlyctis cyanophlyctis* (Schneider, 1799)	
	MW517549	India	*E. cyanophlyctis* (Schneider, 1799)	
Cosmocerca longicauda	OL472311		slug and snails	Amoto et al. (Unpublished)
	OP626254	Inglaterra	Terrestrial gastropods	Andrus et al. 2022
	OL472310		slug and snails	Amoto et al. (Unpublished)
Cosmocercoides pulcher	MH178317	Tokyo, Japan	*Bufo japonicus* Temminck & Schlegel, 1838	Chen et al. 2018
	MH178318	Tokyo, Japan	*B. japonicus*	
	MH178315	Tokyo, Japan	*B. japonicus*	

Fonte: elaborada pelos autores.

Table 2. Nucleotide divergence among *Cosmocerca* species in the COI and ITS sequences.

COI

	C. simile	*C. japonica*	*C. podicipinus*	*C. ornata*	*C. parva*	*Cosmocerca* sp. XMT	*C. albopunctata*	*Cosmocercoides qingtianensis*
C. simile								
C. japonica	0,131							
C. podicipinus	0,203	0,202						
C. ornata	0,138	0,163	0,218					
C. parva	0,180	0,203	0,101	0,215				
Cosmocerca sp. XMT	0,145	0,154	0,210	0,153	0,186			
C. albopunctata	0,185	0,202	0,184	0,198	0,179	0,199		
Cosmocercoides qingtianensis	0,197	0,219	0,151	0,198	0,165	0,203	0,156	

ITS

	C. simile	*C. japonica*	*C. longicauda*	*C. kalesari*	*Cosmocerca* sp. yL	*C. ornata*	*Cosmocerca* sp. LL	*C. daly*	*C. makhadoensis*	*C. monicae*	*Cosmocercoides pulcher*
C. simile											
C. japonica	0,021										
C. longicauda	0,273	0,276									
C. kalesari	0,253	0,320	0,350								
Cosmocerca sp. yL	0,160	0,171	0,211	0,220							
C. ornata	0,157	0,169	0,207	0,225	0,003						
Cosmocerca sp. LL	0,074	0,056	0,279	0,284	0,202	0,198					
C. daly	1,078	1,034	1,248	1,113	1,002	1,007	1,088				
C. makhadoensis	0,176	0,182	0,259	0,046	0,173	0,172	0,193	1,076			
C. monicae	0,169	0,173	0,243	0,037	0,161	0,160	0,184	1,089	0,019		
Cosmocercoides pulcher	0,287	0,290	0,083	0,369	0,246	0,242	0,279	1,211	0,279	0,263	

Fonte: elaborada pelos autores.

6. CAPÍTULO 4 - WHAT IS THE DIVERSITY AND PATTERN OF NETWORK INTERACTIONS PARASITE-HOST IN AMPHIBIANS (ANURA) FROM CAATINGA DOMAIN? – A META-ANALYSIS

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WHAT IS THE DIVERSITY AND PATTERN OF NETWORK INTERACTIONS PARASITE-HOST IN AMPHIBIANS (ANURA) FROM CAATINGA DOMAIN? – A META-ANALYSIS

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ABSTRACT

The first records in the literature compiled on the parasitic fauna of amphibians in Northeastern Brazil date back to the 1990s. Since then, several new studies have been published on parasite-host relationships, parasite communities, and descriptions of new taxa. However, only in the last decade has there been a significant increase in these studies. Given this growth, we aim to provide a complete and updated compilation of helminth records associated with amphibians from the Brazilian Northeastern region and to analyse the dynamics and network structure formed between parasites and their hosts. Therefore, 33 studies were found in the specialized literature that addressed data from eight families, 15 genera, and 34 species of anuran amphibians, distributed mainly in areas of the morphoclimatic domain of the Caatinga and Atlantic Forest remnants in the Brazilian Northeastern. These data correspond to 35% of the total known species of the Caatinga, with Leptodactylidae being the most representative taxon. Regarding helminths, 51 species were recorded, belonging to 20 families and 32 genera. To evaluate the structure of the network, we used measures of connectivity, nesting, modularity, and centrality, that were considered to identify key species. The web presented 247 interactions with a highly connected structure formed by two parasite generalist species, non-nested and non-modular. We concluded that anuran amphibians from the Brazilian Northeastern possess a high parasitic diversity, being Bufonidae and Leptodactylidade taxa considered fundamental for the network structure. Herein, we provided the first analysis of the global framework of parasite communities in amphibians from Brazilian Northeastern, by using antagonistic network interactions.

Keys words: Anuran; Checklist; Ecological network; Hosts; Northeastern; Parasites.

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6.1 Introduction

The Caatinga morphoclimate domain (CMD) is located in the Brazilian northeast and holds an area of approximately 912,000 Km² representing about 10% of the national territory. This region is characterized by a distinct seasonality with high temperatures, irregular rainfall with precipitation levels of 300–1000mm annually and long drought periods (AB'SABER 2003; SILVANO; SEGALLA 2005; QUEIROZ et al. 2017). Despite being the only Brazilian natural region with limits restricted to the national territory, little attention has been given to the conservation of the Caatinga landscape and the diversity of its biota (SILVA et al. 2004; OLIVEIRA 2012). The CMD presents the fourth greatest biological richness of Brazil, with a high degree of endemism. The Brazilian Caatinga presents 98 amphibian species, from which 20 are endemic and the remaining occur also in transition areas between the biomes Cerrado, Amazon Forest, and Atlantic Forest (GARDA et al. 2017). The diversity of this group in the northeast region is distributed among 14 families, being Hylidae and Leptodatylidae the most representative taxa among anurans, with 39 and 28 species respectively (GARDA et al. 2017; SEGALLA et al. 2021).

Currently, Brazil has 1,188 amphibian species (SEGALLA et al. 2021), which represents 14.2% of the global diversity for this group (FROST, 2021). The vast majority of the species are anurans, including 1,144 species (two exotic and invasive species) distributed in 20 families and 107 genera (SEGALLA et al. 2021). Considering the taxonomical diversity of amphibians, several studies have been addressing aspects about their biology, ecology, taxonomy, behavior, and parasitism (DASZAK et al. 2003; CASSIANO-LIMA et al. 2011; ROBERTO et al. 2013; ANDRADE et al. 2016; SENA et al. 2018; MADELAIRE et al. 2020).

Even though Brazil is well known worldwide regarding parasitological researches on anurans, the hidden diversity that these parasites represent is far from being completely unraveled. Less than 10% of the described amphibian species in Brazil have data on their helminthfauna (CAMPIÃO et al. 2014). The first parasitological studies on Brazilian amphibians is from 1917 by Travassos (VICENTE et al. 1991), and since then, the number of publications have been increasing (NASCIMENTO et al. 2012; SILVA et al. 2018; OLIVEIRA et al. 2019; SILVA-NETA et al. 2020).

Due to the richness of species, amphibians act as hosts to a great diversity of parasites, being infected by the main helminth groups like Nematoda, Digenea, Cestoda and Acanthocephala in larval and adult stages (CAMPIÃO et al. 2014; TOLEDO et al. 2014). Furthermore, parasites are considered as bioindicators of environmental changes, providing information about the health and structure of ecosystems and trophic interaction networks (CAMPIÃO et al. 2009; KOPRIVNIKAR et al. 2012). Therefore, in view of the above and considering the importance and megadiversity of helminth endoparasites of amphibians, we aim 1) to provide a checklist of associations between parasites and their anuran hosts from the northeast region of Brazil based on compiled literature data from 1990 to 2022, and 2) to describe the network pattern of parasite-host interaction that exists within this set and verify which helminth and anuran species are most important in structuring the dynamics of infection in these communities.

6.2 Material and Methods

6.2.1 Collection of data

In order to carry out this checklist, literature was surveyed using the available databases: Scientific Electronic Library Online (Scielo), Google Scholar, Science Direct, Scopus, Medline (Pubmed), Web of Science, and CAPES Portal, using the following key-words combined: helminths, parasites, endoparasites, amphibians, anuran, infection, Brazil, and Northeastern. Data published in books, book chapters, and annals related to parasites were also included in the checklist. The criteria for inclusion of scientific production was the specific approach of infection of helminth endoparasites in amphibians in the Northeast of Brazil, published from 1990 to 2022.

6.2.2 Data analyses

To create the table of endoparasite species associated with amphibians, the following information was recorded and analyzed separately: host species, parasite, infection site and authors. The methods used for detection and identification of the hosts and parasites species in the literature cited were not taken into consideration. The data were also distributed and organized in graphics, presenting information on the anuran families.

6.2.3 Network analyses

We built a parasite-host interaction network from a binary matrix. The resulting matrix, with parasites as columns and hosts as rows, consisted of cells filled with 1 when interaction was recorded and 0 otherwise. To describe the structure of the web, we calculate the Connectivity, Nesting and Modularity (Q). Connectance is provided by the ratio between the number of existing interactions and the total number of possible interactions in the network, measuring how much species are linked in the community (Jordano et al. 2006). Nestedness measures how much the set of interactions of less connected vertices is a subset of interactions of more connected vertices.

Thus, a network is more nestedness the more specialist species interact with species that belong to a subset of the species with which generalists interact (Delmas et al. 2018). Modularity assesses the extent to which species form subgroups with a higher density of internal than external interaction. Modularity analysis can provide information on the level of specialization in communities concerning the affinities of interactions (Vázquez et al. 2009). The DIRTLPAb + binary modularity maximization algorithm was used (Beckett 2016), and estimated with the computeModules() function in the Bipartite package in the R program. As network metrics can be affected by intrinsic characteristics, such as the number of species that interact and sampling from different studies (Vizentin-Bugoni et al. 2016) the significance of the observed modularity was evaluated by comparing it with a null model. We used the Shuffles.web binary null model, similar to the one proposed by Vázquez et al. (2005), which limits the connectance and marginal totals of the matrices. The 95% confidence interval for the modularity metric (DIRTLPAb+) was estimated from 1000 simulated values, with a metric value considered significant if the confidence intervals do not overlap (0.025-0.975). To assess the role of species in the network following centrality metrics were used: Degree and mean degree, which analyzes how much a species is interacting with another in the network (number of interactions), contributing to examining the influence of the species on other species in the network, that is, the higher the degree of a species, the more potential influence it has on other species in the network; and Closeness which measures the proximity of a species to all other species in the network, indicating how quickly/efficiently a node is likely to influence the overall network (Delmas et al. 2018).

6.3 Results

Thirty-three studies published from 1990 to 2022 were selected, from which 16 are articles, 14 scientific notes, one dissertation and two monographs. Sixteen scientific journals were identified and listed in order of the largest number of publications related to helminth fauna of anurans in Brazilian Northeastern, with Herpetology Notes (n = 5) being the most representative journal, followed by Herpetological Review (n = 4), Zootaxa and Netropical Helminthology (n = 3), Acta Parasitologica, Brazilian Journal of Biology and Journal of Parasitology (n = 2) and Parasitoloy Research, Biota Neotropica, Journal of Natural History, Brazilian Journal of Veterinary Parasitology, Helminthologia, Comparative Parasitology, Cuadernos de Herpetología, Revista Brasileira de Zoologia e Biologia (n = 1), respectively. An interval of ten years was considered to observe the number of publications related to this topic. In the two first intervals, only one study was found, however, in the last decade, there was an increase of studies related to parasitology of anurans in the Brazilian Northeast, with the publication of thirty-one studies from 2010 to 2022 (Figure 1).

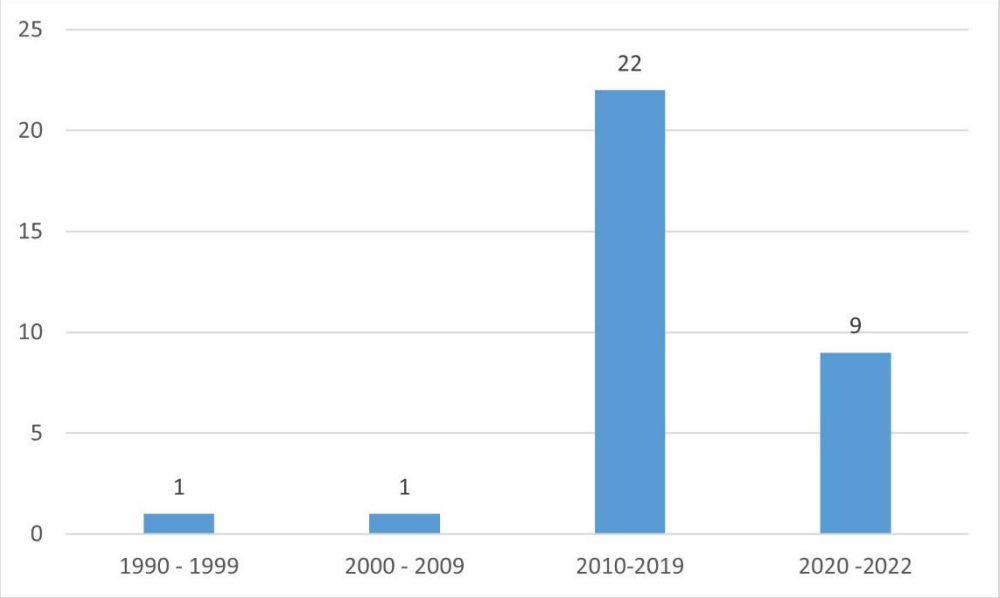

Figure 1. Number of publications related to endoparasite helminths infecting anurans in the Brazilian northeastern region between 1990 and 2022.

These studies recorded data on parasitism in eight families, 15 genera and 35 species of amphibians, all of Anura, in terrestrial, arboreal, semi-aquatic and fossorial niches, distributed in the habitats from Caatinga and remains of Atlantic Forest in the Brazilian Northeastern, corresponding to approximately 35% of the known species from Caatinga domain. The anuran family with the highest number of records was Leptodactylidae with 13 host species infected, followed by Hylidae with 11, Bufonidae and Odontophrynidae with three, Microhylidae with two, and Phyllomedusidae, Eleutherodactylidae, and Ranidae with only one species recorded. Regarding helminths, a total of 82 endoparasites were reported, belonging to 20 families and 32 genera. These total, 59 are nematodes, nine digeneans, six cestodes, six acanthocephalans, one monogenean, and one pentastomid. Among those, 51 were identified at species level (42 nematodes, five digenetic, one cestode, two acanthocephalan, and one pentastomid) The remaining taxa were identified only at order, family or genus level. (See Table 1 and S1).

6.3.1 Network analysis

The parasite-host interaction network showed a low nestednnes pattern (NODF = 18.09), that is, a large number of species with a small number of interactions (specialists), while a small number of species with a greater number of interactions (generalists) interacted with each other (Figure 2). The network was represented by species of helminths and 35 species of anurans, resulting in a total of 247 quantitative interactions observed. The network connectance was high, presenting about 80% of the possible interactions, with the average degree of the species of 3.01 and 7.1, for helminths and anurans, respectively. The high connectance value indicates that the network forms a giant integrated component formed mainly by generalist helminth species and hosts, with many connections between them. The network was not modular (Q = 0.469), being all interactions connected except for a two pairs of species that were isolated from the other components of the network – *Chiasmocleis capixaba* Cruz, Caramaschi, and Izecksohn, 1997 (Microhylidae) and *Lithobates palmipes* (Spix, 1824) (Ranidae).

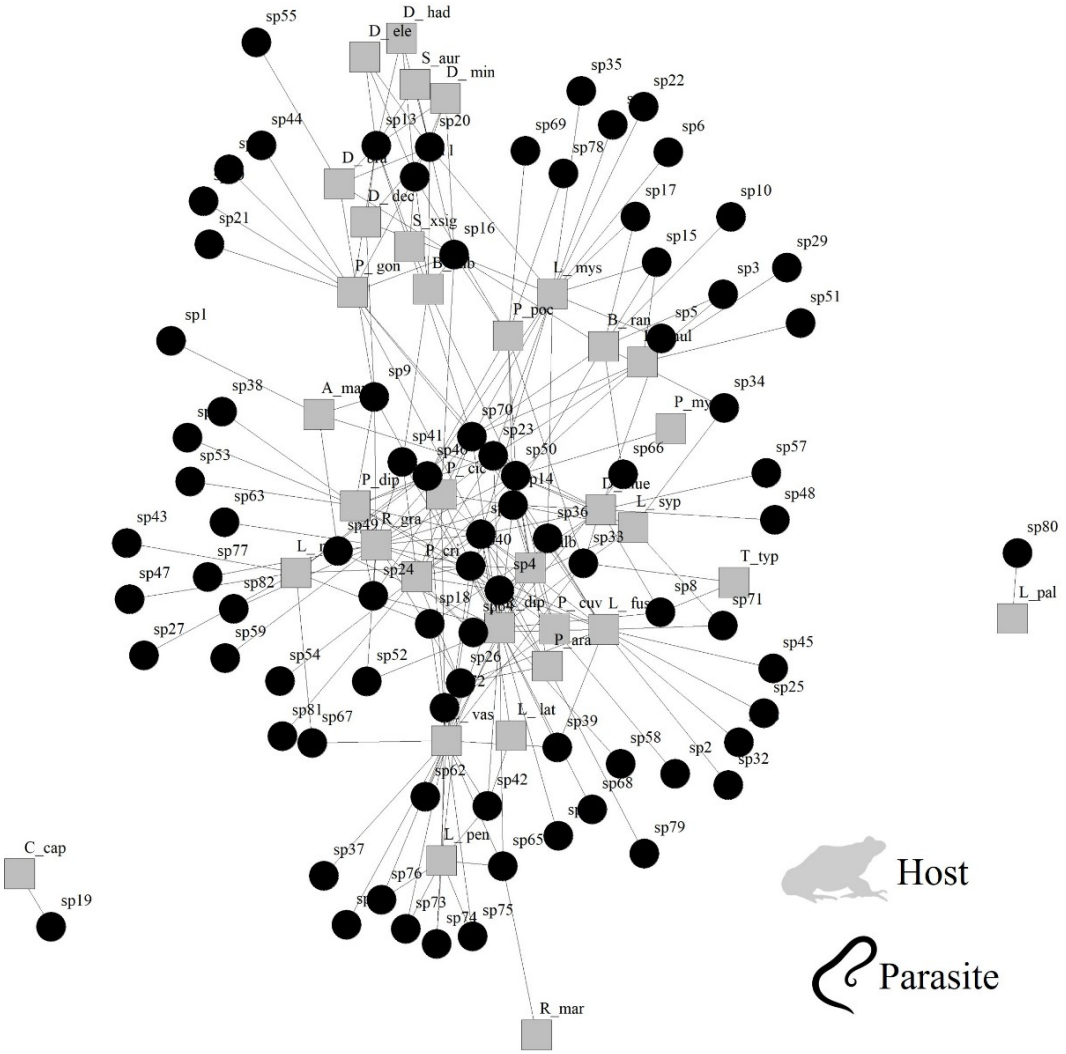

Figure 2. Representation of the network of interactions between anuran hosts and parasitic helminths in Northeastern Brazil.

The constructed network revealed two taxa and five species with a strong interaction within the network (Figure 2), the family Bufonidae being represented by the species *Rhinella diptycha* (Cope, 1862) (degree of connection: 22) and *R. granulosa* (Spix, 1824) (degree of connection: 17) and the family Leptodactylidae represented by three species *Leptodactylus vastus* Lutz, 1930 (degree of connection: 20), *L. mystaceus* (Spix, 1824) (degree of connection: 14) and *L. fuscus* (Schneider, 1799) (degree of connection: 14). Regarding the parasites, seven species stood out as the highest degree of interactions, being *Raillietnema spectans* Gomes, 1964 (degree of connection: 14), Physaloptera sp. (degree of connection: 13), *Oswaldocruzia mazzai* Travassos, 1935 (degree *of* connection: 12), *Rhabdias* sp. (degree of connection: 11) and *Aplectana membranosa* (Schneider, 1866), Cosmocerca *parva* Travassos, 1925 and the taxon Cosmocercidae each with ten interactions, respectively. Finally, the centrality evaluation, closeness degree and the betweeness degree, indicated that *R. diptycha* and *L. vastus* were the most important species in the network among the host set, follow by *R. granulosa*, *L. fuscus* and *L. mystaceus*, while *R. spectans* and *O. mazzai* were considered key-species for the parasite set.

6.4 Discussion

In the helminth communities analyzed, the most representative and diverse taxon was nematode, followed by Digenea, cestodes, acanthocephalans, and a single record for monogenean and pentastomid taxa. Nematoda is usually the predominant taxon in the structure and composition of the parasitic fauna in anurans (SILVA et al. 2018), where most of the nematodes found have a monoxenic life cycle with their larvae being found in the soil, which makes infection possible through penetration of their host's skin. About 60% of the hosts that had their helminth fauna inventoried have terrestrial or semi-aquatic habits and life history and ecological strategies that contribute to the encounter of these with their parasites.

Digeneans tends to be the second largest group in parasite diversity (CRIBB et al. 2002), often with infections in amphibians being more related to aquatic and semiaquatic frog clades (MACHADO et al. 2021). Diplostomidae, Glyptelmidae, Macroderoididae, and Plagiorchiidae were the digenetic taxa associated with anuran hosts in the Caatinga, divided into four genera (*Glypthelmins*, *Lophosicyadiplostomum*, *Plagiorchis* and *Rauschiella*) and three species (*G. linguatula* (Rudolphi, 1819), *P. rangeli* Artigas and Zerpa, 1961 and *R. linguatula* (Rudolphi, 1819)). The genus *Lophosicyadiplostomum* is a parasite of birds that uses anurans as intermediate hosts (HAMANN; GONZÁLEZ 2009). *Glypthelmins* is a cosmopolitan genus of amphibian parasites, which currently has eight species formally recognized based on molecular and morphological evidence and forms a sister group with the genus *Haematoloechus* (RAZO-MENDIVIL et al. 2006). Species of this genus have a heteroxenic life cycle with two hosts in their life cycle, an invertebrate as an intermediate host and a vertebrate as the definitive host (HAMANN, 2006). Regarding the Monogenea and Pentastomida taxa, both had only one record, which demonstrates that potentially these parasitic groups have difficulties establishing themselves or using the anuran species recorded here as hosts in their life cycles.

Of the total taxon surveyed in this study, 31 was unidentified at a specific level. Poulin (2018) reiterates the importance of identifying the species of parasites, therefore contributing to a better measurement of the existing diversity of parasites between different communities, and avoiding errors of underrated of parasite richness, imprecise estimates of diversity, or overestimation of parasites, parasitic similarities between different communities. Thus, we reinforce that the identification of parasitic species is not easy, requires time and taxonomic knowledge, and when possible, molecular techniques for species-specific identification are implemented (MULLER et al. 2018; MORAIS et al. 2020).

Regarding the remarkable growth of research in the last decade, we believe that it can be justified by both political and scientific issues. In the first half of the last decade, there were broad investments in public education through financial resources and research incentives in Brazil. Therefore, investing such resources in public universities boosted the development of basic and applied research in the most diverse fields of scientific knowledge (MARQUES 2019). Another factor that contributed to these results has been the consolidation of regionalized research groups in different universities in the Northeast that have concentrated their research and explored the diversity of different taxonomic groups of both parasites and hosts in environments of the Caatinga domain (TELES et al. 2015; 2018a; 2018b; SILVA et al. 2018; 2019; OLIVEIRA et al. 2019; FELIX-Nascimento et al. 2020) and Atlantic Forest domain (MARTINS-SOBRINHO et al. 2017; SENA et al. 2018; SILVA-NETA et al. 2020; MASCARENHAS et al. 2021; OLIVEIRA et al. 2022).

As for the parasitic diversity associated with the taxon Bufonidae, the reunion of data from Brazilian Northeastern began with the study of Vicente et al. (1991), that reported the nematodes *Oswaldocruzia subauricularis* (Rudolphi, 1819), *Rhabdias fuelleborni* Travassos, 1926, and *Rhabdias sphaerocephala* Goodey, 1924, parasitizing *Rhinella icterica*

(Spix, 1824) (= *Bufo marinus*). However, only from 2008 onwards that other helminthfauna studies for Rhinella granulosa and *Rhinella diptycha* (=*R. jimi*) were published (ANJOS et al. 2008; MÜLLER et al. 2018; TELES et al. 2018a; AMORIM et al. 2019; MADELAIRE et al. 2020; LIMA et al. 2021). Among the species of Bufonidae, *R. diptycha* is the only species with a record of infection by trematode (BENÍCIO et al. 2022).

Hylidae is the taxon with the greatest species occurrence in the Brazilian Northeastern, being largely represented in herpetofauna surveys and species description (ROBERTO et al. 2017; ORRICO et al. 2018), phylogeography (MENEZES et al. 2016), evolution, ecology, and physiology (JARED et al. 2015; LEITE-FILHO et al. 2017). However, there is only one study on the helminth fauna of hylid anurans for CMD with the host *Trachycephalus typhonius* (Linnaeus, 1758) (BENÍCIO et al. 2022). Most of the records for hylids anurans are from humid forest vegetation and Atlantic Forest (NASCIMENTO et al. 2012; MARTINS-SOBRINHO et al. 2017; MACHADO et al. 2021). The development of more research in the semi-arid region is necessary to better understand the host-parasite dynamics between hylid species, identify the parasite species associated with these hosts, and broaden the records of the geographic distribution of their helminths in the Northeastern. These studies contribute to the understanding of parasitic relationships and highlight the importance of the use of molecular tools for parasite identification since the findings of larvae and females hinder identification and limit discussions on parasite specificity.

Leptodactylidae was represented in the studies about endoparasites by 13 species, belonging to four genera: *Leptodactylus, Physalaemus, Pseudopaludicola*, and *Pleurodema* (VICENTE et al. 1991; CAMPIÃO, 2014; TELES et al. 2014; 2015; 2017a; 2018b; LINS 2016; LINS et al. 2017; MÜLLER et al. 2018; SILVA et al. 2018; OLIVEIRA et al. 2019; MADELAIRE et al. 2020; SILVA-NETA et al. 2020; SOARES et al. 2020). The literature presents a diverse parasitic fauna for hosts from *Leptodactylus* genus (CAMPIÃO et al. 2014; TELES et al. 2017a; MÜLLER et al. 2018; SILVA-NETA et al. 2020). While studies for the *Physalaemus* genus are scarce (OLIVEIRA et al. 2019; SILVA-NETA, et al. 2020).

6.4.1 Interaction networks

The network of parasite-host interactions between helminths and anurans from Brazilian Northeastern did not show a nestedness pattern, which makes it possibly less resistant to anthropic disturbances. Dehling (2018) explains that nestedness structure of a network increases its stability and makes well-connected generalist species more resistant against extinction. Fortuna and Bascompte (2006) studying the structure of real networks and simulated networks in response to habitat loss, observed that real networks lose species faster than simulated networks. However, due to their high degree of nesting and heterogeneity, they resist for longer time to disturbance.

In nestedness networks, specialist species are the first to be extinct because they have a smaller number of interactions, thus causing them to be replaced by generalist species that have a greater number of interactions and that, due to the robustness of the interaction between other high-level generalist species, degree of interaction are the last to be extinguished (RODRIGUES, 2016).

The low nesting and modular value can make the network more susceptible to anthropic disturbances (DEHLING, 2018). Modularity, like nesting, increases the robustness of the network against disturbances in the system, which makes it difficult to spread negative effects to other modules. Thus, non-nestedness or low-nesting networks may be characteristic of agonistic interactions in host-parasite networks. Furthermore, we can observe a large number of peripheric species of helminths with several isolated records of specific bindings with one to three hosts (Figure 2). This characteristic contributed the non-nestedness and not

modular structuring of the network agonistic.

Most interactions between helminths and their anuran hosts that occurred comprise very specifically and unique links, such as the sympatric occurrence of the species Aplectana crucifer, A. lopesi, A. meridionalis, A. travossosi, and Cosmocerca travassossi in L. mystaceus, P. silvoi in D. muelleri and, in particular, several taxa of digenetic trematodes and cestodes occurring singly in different anuran host species (See Table 1 and S1).

Another fundamental issue is how the data were used in this work. In this study, unequal factors such as collection methodologies, sampled location, the type of landscape (the Caatinga domain or Atlantic Forest domain), the collection effort employed, and especially the temporality in which these works passed and have been developed may have influenced the descriptive parameters of the network (PILOSOF et al. 2013; RUNGHEN et al. 2021). Therefore, future studies with a well-designed sample developed only in a morphoclimatic domain may come to corroborate or refute the network pattern presented in this work.

Network analyses enable to record interactions amongst the components of those system, the way that communities are organized, and the complexity of these interactions (BASCOMPTE; JORDANO 2007; METZ et al. 2007; SCHREIBER, 2008; BELLAY, 2013; MELLO et al. 2015). Recently, studies on ecological networks have been encompassing mutualistic plant-pollinator and plant-seed-disperser and antagonist relationships (LEWINSOHN et al. 2006; BASCOMPETE; JORDANO 2007; MELLO, 2010; FRANCISCO, 2017). Specifically, antagonistic interactions benefit only one of the involved species, such as herbivory and parasitism (SCHOWALTER, 2011; SOUZA, 2015; LOPES et al. 2020).

The network analysis identified the anuran and parasite core species that have higher interaction frequency aiming at verifying what are the most important species that structure and balance the host parasite interaction network in this study. *Raillietnema spectans* (Cosmocercidae) and *O. mazzai* (Molineidae) are core parasite species and could be considered generalists, given the number of host species parasitized. Besides, they configure as the most important parasite species for the structure of network. However, other species also had a relatively high frequency of interactions in the network, such as species from the taxa Cosmocercidae, Physalopteridae, and Rhabdiasidae.

Aplectana membranosa and *C. parva* are common, generalist species that occur widely in amphibians in the northeast as well as in other geographic locations (GONÇALVES et al. 2002; LUQUE et al. 2005; SILVA et al. 2018; OLIVEIRA et al. 2019; SILVA-NETA et al. 2020; GONZÁLEZ et al. 2021; MASCARENHAS et al. 2021). Both are monoxenic nematodes that infect their hosts through ingestion of larvae or penetration through the skin (ANDERSON, 2000) and that can also be considered important in structuring the parasite community of their hosts. Physaloptera is a diverse genus that infects all classes of terrestrial vertebrates, and rarely fishes (TELES et al. 2018a). Although, among amphibians, there are only two species described *Physaloptera amphibia* Linstow, 1889 and *Physaloptera tigrinae* Ali and Farooqui, 1969, using these as definitive hosts in the Palearctic and Oriental region, respectively (PEREIRA et al. 2012). For the Neotropical region, the taxon *Physaloptera* sp. is usually found in the larval stage in different anuran taxa, which makes it possible to infer that this parasite uses anuran hosts as paratenic hosts to reach its definitive hosts (MASCARENHAS et al. 2021).

The genus *Rhabdias* occurs throughout the world and are lung parasites of amphibians and reptiles (TKACH et al. 2014). Recent studies of the phylogeny of this genus with Neotropical species revealed the monophyly of Rhabdiasidae as well as the existence of an infection pattern of Rhabdias species associated with the phylogeny of their hosts (see MULLER et al. 2018). In our study, Rhabdias sp. treated here as a single taxon in our analysis may represent about five possible new species of the genus considering their occurrence

records by different hosts of the taxa Bufonidae, Hylidae, Leptodactylidae, Odontophrynidae, and Phyllomedusidae. The hidden diversity of *Rhabdias* in the Neotropics is evident and the presence of cryptic species occurring in different host taxa requires studies that use molecular techniques to identify these parasites as well as for a better understanding of these systematic and host-parasite relationships (MULLER et al. al. 2018).

The host species *Rhinella diptycha* and *R. granulosa* (Bufonidae) and Anuran leptodactylids like *L. fuscus, L. mystaceus and L. vastus* presented the highest degree of interaction, from which some are common to the host species of each genus. The data corroborate previous studies, reinforcing that phylogenetically close hosts tend to present similar parasitic faunas when compared with non-related hosts (BELLAY et al. 2011; 2013; KRASNOV et al. 2012; LIMA Jr. et al. 2012). We assume that these host species present more interactions due to the phylogenetic proximity, their sympatric occurrence, and their similar generalist habits, ingesting a great variety of prey. Thus, because they harbor greater helminth diversity shared, we can considered the species cited above key-species relative importance in structure network.

Chiasmocleis capixaba and Lithobates palmipes interacted with only one parasite each, which did not interact with any other amphibian. Parasite species with high specificity to stablish their interactions are selective regarding their host choice, which is reflected in the high modularity of the analyzed network (LOPES et al. 2020). Svensson-Coelho et al. (2014) stated that highly specialized associations are indicative of the existence of species groups that interact more among themselves, possessing functional traces that are compatible among the species. Thus, the antagonistic networks and high phylogenetic proximity among parasite lineages are highlighted, as well as their host specialization.

About half of the helminth species (n = 42, 51.2%) listed in this study maintain a single interaction with one host or with up to three anuran hosts (see Figure 2 and supplementary material), which makes it possible for parasite species that have higher specialization are more prone to be affected by the removal of a host species from the network if there are no records of other hosts. Such fact stresses the importance of host species that are considered generalists for the establishment of the network (BURGOS et al. 2007; LOPES et al. 2020). Moreover, according to Lopes et al. (2020), the establishment of the networks are key mechanisms for the maintenance of interactions and might be considered important in an evolutionary context of host-parasite relationships.

Studies analyzing the network structure of biological communities allow us to better understand the processes and complexity of ecosystems by being able to extract the properties of an ecological system according to the number and distribution of links between interacting organisms (RUNGHEN et al. 2021). We concluded that anuran amphibians from Brazilian Northeastern present a high parasitic diversity. Some hosts of generalist habits are infected by several helminths, being considered important for the network structure, as observed for some Bufonidae and Leptodactylidade. Even, more specialized species retain a smaller number of interactions, which is valid for both parasites and hosts, in a way that extremely specific interactions do not interact with the network itself and are presented as a weak point considering its specificity. On the other hand, although we have evidenced the existence of a great diversity of macroendoparasite helminths associated with these hosts, within this diversity there is a high percentage of taxa yet to be described and identified at a specific level, making it necessary to implement greater efforts in the field knowledge of this yet unidentified diversity.

The present study provided the first analysis of the global structure of parasite communities in amphibians from Brazilian Northeastern, by using antagonistic network interactions. Despite the increase in the number of studies in the last decade, the growing number of descriptions of new anuran species and the high diversity of endoparasitic

helminths for this vertebrate host group, the development of more research is imperative. Such studies must aim taxonomical and ecological approaches of parasites in amphibians, mostly nematodes that are the most common, as well as assess host-parasites interactions and life-cycle of these parasites. It is thus expected that with the increase of sampling efforts, new records of interactions will emerge and unravel the hidden diversity of amphibian parasites.

Declarations Ethical Approval
Not applicable.

Competing interests
Not applicable.

Authors' contributions
The manuscript in question was developed from the monograph of Ednalva da Silva Santos, with supervised by Charles de Sousa Silva and co-supervised by Drausio Honorio Morais. All people who meet criteria of article authorship are listed as authors, and all authors are sufficiently at work to assume responsibility for its content, including participation in the concept, analysis, writing or revision of the manuscript, as detailed below. Conception and study design: ESS and CSS; Methods used: Ednalva da Silva Santos Acquisition and compilation of data: Ednalva da Silva Santos; Analysis, interpretation of data: ESS, Isabela Hevily Silva Torquato and CSS; Construction of images: ESS and Isabela Hevily Silva Torquato; Writing the manuscript: Ednalva da Silva Santos, Isabela Hevily Silva Torquato, DH and CSS; Critical revision of paper: Paulo Cascon and Charles de Sousa Silva.

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Availability of data and materials
Data supporting the results of this study are available for free consultation and use as 'supplementary files' in the website of the journal Parasitology Research.

Table 1. Data on the literature of parasitism in anuran amphibians in the Brazilian Northeastern recorded from 1990 to 2022. Infection sites: B= bladder; Cav= body cavity; S= stomach; GT= gastrointestinal tract; I= intestine; SI= small intestine; LI= large intestine; L= lungs; K= kidneys; SAT= subcutaneous abdominal tissue. Phytophysiognomies: CA= Caatinga domain; AF= Atlantic Forest domain.

Host	Helminth	Species	Sites of infection	Phytophysiognomy	References
Bufonidae					
Rhinella granulosa (Spix, 1824)				CA	Madelaire et al. (2020); Müller et al. (2018); Silva-Neta et al. (2020); Teles et al. (2018)
	Acanthocephalan	Cystacanth			
	Cestode	*Cylindrotaenia americana*	SI		
		Unidentified cestode	LI		
	Digenetic	*Plagiorchis rangeli*			
	Nematoda	*Aplectana membranosa*	LI		
		Aplectana sp.	LI		
		Cosmocercidae	LI		
		Oswaldocruzia mazzai	SI		
		Oswaldocruzia sp.	SI		
		Physaloptera sp.	L		
		Parapharyngodon sp.			
		Raillietnema spectans	LI		
		Raillietnema sp.	LI		
		Rhabdias androgyna	L		
		Rhabdias breviensis	L		
		Rhabdias sp.	L		
		Schrankiana sp.			
Rhinella diptycha (Cope, 1862)				CA	Vicente et al. (1991); Anjos et al. (2008); Campião et al. (2014); Müller et al. (2018); Amorim et al. (2019); Madelaire et al. (2020); Lima et al. (2021); Benício et al. (2022)

	Cestode	*Cylindrotaenia americana*	SI		
	Digenetic	*Gorgoderina rochamilae*			
		Plagiorchis rangeli			
		Rauschiela linguatula			
	Nematoda	*Aplectana membranosa*			
		Aplectana sp.			
		Cosmocercidae	SI/LI		
		Nematode cyst	SI		
		Oswaldocruzia lopesi	SI/S		
		Oswaldocuzia mazzai	SI		
		Oswaldocruzia subauricularis	I		
		Parapharyngodon sp.	SI/LI/S		
		Physaloptera sp.	S		
		Raillietnema spectans	LI		
		Rhabdias fuelleborni	L		
		Rhabdias sphaerocephala	L		
		Rhabdias sp.	L		
		Aplectana vellardi			
		Nematode larvae			
		Ochoterenella sp.			
		Oswaldocruzia sp.			
		Rhabdias pseudosphaerocephala			
	Pentastomida	*Railiettiela mottae*			
Rhinella marina (Linnaeus, 1758)					Vicente et al. (1991)
	Nematoda	*Rhabdias fuelleborni*	L		
Eleutherodactylidae					
Adelophryne maranguapensis				AF	Oliveira et al. (2022)

Hoogmoed, Borges, and Cascon, 1994					
	Nematoda	Ascarididae gen. sp.			
		Aplectana sp.			
		Parapharyngodon sp.			
		Physaloptera sp.			
Hylidae					
Boana albomarginata (Spix, 1824)				AF	Martins-sobrinho et al. (2017)
	Acanthocephalan	*Centrorhyncus* sp.	GT		
	Nematoda	*Brevimulticaecum* sp.	GT		
		Cosmocerca parva	I		
		Cosmocerca sp.	I		
		Oswaldocruzia sp.	I		
		Physaloptera sp.	S		
Boana multifasciata (Günther, 1859)				AF	Machado et al. (2021)
	Acanthocephalan	*Pseudoacanthocephalus lutzi*	SI		
	Digenetic	*Glypthelmins* sp.	SI		
	Nematoda	*Cosmocerca brasiliense*	SI/LI		
		Physalopteroides venancioi	E		
		Physaloptera sp.	LI		
		Rhabdias sp.	L		
		Cosmocercidae	SI/LI		
Boana raniceps (Cope, 1862)				AF	Nascimento et al. (2012); Machado et al. (2021)
	Acanthocephalan	*Pseudoacanthocephalus lutzi*			
	Digenetic	*Lophosicyadiplostomum* sp.			
	Nematoda	*Rhabdias pseudosphaerocephala*	L		
		Aplectana travassosi			

		Cosmocerca brasiliense			
		Cosmocerca parva			
		Cosmocerca paraguayensis			
		Oswaldocruzia mazzai			
		Rhabdias sp.			
Dendropsophus branneri (Cochran, 1948)				AF	Martins-sobrinho et al. (2017)
	Acanthocephalan	*Centrorhyncus* sp.	GT		
	Nematoda	*Aplectana* sp.	I		
		Cosmocerca parva	I		
		Cosmocerca sp.	I		
		Porrocaecum sp.	GT		
Dendropsophus decipiens (Lutz, 1925)				AF	Martins-sobrinho et al. (2017)
	Acanthocephalan	*Centrorhyncus*sp.	GT		
	Nematoda	*Aplectana* sp.	I		
		Cosmocerca parva	I		
		Cosmocerca sp.	I		
Dendropsophus elegans (Wied-Neuwied, 1824)				AF	Martins-sobrinho et al. (2017)
	Acanthocephalan	*Centrorhyncus* sp.	GT		
	Nematoda	*Brevimulticaecum* sp.	GT		
		Cosmocerca sp.	I		
Dendropsophus haddadi (Bastos and Pombal, 1996)				AF	Martins-sobrinho et al. (2017)
	Acanthocephalan	*Centrorhyncus* sp.	GT		
	Nematoda	*Brevimulticaecum* sp.	GT		
		Cosmocerca sp.	I		

Dendropsophus minutus (Peters, 1872)				AF	Martins-sobrinho et al. (2017)
	Acanthocephalan	*Centrorhyncus* sp.	GT		
	Nematoda	*Brevimulticaecum* sp.	GT		
		Cosmocerca parva	I		
		Cosmocerca sp.	I		
Scinax auratus (Wied-Neuwied, 1821)				AF	Martins-sobrinho et al. (2017)
	Acanthocephalan	*Centrorhyncus* sp.	GT		
	Nematoda	*Cosmocerca parva*	I		
		Cosmocerca sp.	I		
Scinax x-signatus (Spix, 1824)				AF	Martins-sobrinho et al. (2017)
	Acanthocephalan	*Centrorhyncus* sp.	GT		
	Nematoda	*Brevimulticaecum* sp.	GT		
		Rhabdias sp.	Cav.		
Trachycephalus typhonius (Linnaeus, 1758)				CA	Benício et al. (2022)
	Nematoda	*Aplectana vellardi*	LI		
		Nematode larvae	S		
Leptodactylidae					
Leptodactylus fuscus (Schneider, 1799)				CA	Lins (2016); Müller et al. (2018); Silva-Neta et al. (2020)
	Cestode	Hexacante			
	Digenetic	*Glypthelmins linguatula*			
		Diplostomidae			
	Nematoda	*Aplectana membranosa*			
		Cosmocercidae			
		Falcaustra mascula			
		Ochoterenella sp.			

		Oswaldocruzia lopesi			
		Oswaldocruzia mazzai			
		Oxyscaris necopinus			
		Raillietnema spectans			
		Rhabdias sp.	L		
		Rhabdias breviensis	L		
		Schrankiana formusula			
Leptodactylus latrans (Steffen, 1815)				CA	Vicente et al. (1991)
	Nematoda	*Oswaldocruzia subauricularis*	LI; SI		
		Raillietnema spectans	SI		
Leptodactylus macrosternum Miranda-Ribeiro, 1926				CA	Campião et al. (2014); Félix-Nascimento et al. (2020); Müller et al. (2018); Silva-Neta et al. (2020); Teles et al. (2017a); (2018)
	Nematoda	*Cosmocerca podicipinus*			
		Oxyascaris oxyascaris			
		Foleyella convoluta			
		Rhabdias cf. *stenocephala*			
		Rhabdias sp.			
		Oswaldocruzia mazzai			
		Oxysomatium petrolinensis	LI		
		Oxyascaris caatingae	SI		
Leptodactylus mystaceus (Spix, 1824)				CA	Silva-Neta et al. (2020); Oliveira et al (in press)
	Nematoda	*Raillietnema spectans*			
		Aplectana crucifer			
		Aplectana meridionalis			
		Aplectana lopesi			
		Cosmocerca brasiliense			

		Cosmocerca paraguayensis			
		Cosmocerca parva			
		Cosmocerca sp.			
		Cosmocerca travassosi			
		Cosmocercidae			
		Multicaecum sp.			
		Ochoterenella sp.			
		Oxyascaris oxyascaris			
		Rhabdias sp.			
Leptodactylus pentadactylus (Laurenti, 1768)				CA	Vicente et al. (1991)
	Nematoda	*Falcaustra mascula*	LI		
		Oswaldocruzia subauricularis	I		
		Rhabdias fuelleborni	L		
		Schrankiana freitasi	LI		
		Schrankiana inconspicata	LI		
		Schrankiana larvata	LI		
		Schrankiana schranki	LI		
		Schrankiana brasili	LI		
Leptodactylus syphax Bokermann, 1969				CA	Lins et al. (2017)
	Acanthocephalan	Cystacanth	CAV		
	Digenetic	*Lophosicyadiplostomum* sp.	KID		
	Nematoda	*Aplectana membranosa*	SI;LI		
		Schrankiana formusula	LI		
		Physaloptera sp.	E		
		Unidentified larvae	CAV		
Leptodactylus vastus Lutz, 1930				CA	Vicente et al. (1991); Campião et al. (2014); Silva-Neta et al. (2020); Teles

					et al. (2014); (2016). Mueller et al. (2018); Benício et al. (2022)
	Digenetic	*Gorgoderina parvicava*	B		
	Nematoda	*Aplectana membranosa*	LI		
		Falcausta mascula	LI		
		Ochoterenella sp.	Cav		
		Oswaldocruzia mazzai	SI/LI		
		Oswaldocruzia subauricularis	I		
		Raillietnema spectans			
		Rhabdias fuelleborni	L		
		Rhabdias cf. *stenocephala*	L		
		Schrankiana freitasi	LI		
		Schrankiana inconspicata	LI		
		Schrankiana larvata	LI		
		Schrankiana schranki	LI		
		Schrankiana brasili	LI		
		Cosmocerca podicipinus	LI		
		Nematode cyst	VM		
		Nematode larvae	E/CAV		
		Ochoterenella digiticauda	CAV		
		Oswaldocruzia lopesi	S		
		Oxyascaris oxyascaris	SI		
		Rauschiella linguatula	SI		
Pleurodema diplolister (Peters, 1870)				CA	Vicente et al. (1991); Campião et al. (2014); Teles et al. (2015); Madelaire et al. (2020); Silva-Neta et al. (2020).
	Acanthocephalan	*Oligacanthorhynchus* sp.			
	Cestode	*Cylindrotaenia americana*			
		Plerocercoid			

	Nematoda	*Aplectana membranosa*			
		Aplectana sp.			
		Cosmocercidae			
		Falcaustra mascula			
		Oswaldocruzia mazzai			
		Oxyascaris oxyascaris			
		Raillietnema spectans			
Physalaemus albifrons (Spix, 1824)				CA	Oliveira et al. (2019); Silva-Neta et al. (2020)
	Acanthocephalan	Cystacanth	Cav/S		
	Nematoda	*Aplectana membranosa*			
		Oswaldocruzia mazzai	SI		
		Physaloptera sp.	S		
		Raillietnema spectans	LI/SI		
		Rhabdias cf. *brevienis*	L		
Physalaemus cicada Bokermann, 1966				CA	Oliveira et al. (2019); Silva-Neta et al. (2020)
	Acanthocephalan	Cystacanth	S		
	Cestode	*Cylindrotaenia americana*	SI		
	Nematoda	*Cosmocerca parva*	SI		
		Oswaldocruzia mazzai	I		
		Oxyscaris oxyscaris	SI		
		Raillietnema spectans	SI/LI		
		Rhabdias sp.	L		
		Schrankiana schranki	LI		
Physalaemus cuvieri Fitzinger, 1826				CA	Oliveira et al. (2019); Silva-Neta et al. (2020)
	Acanthocephalan	Cystacanth	Cav.		
		Acantocephalus cf. *saopaulensis*	LI		
	Nematoda	*Oswaldocruzia* cf. *mazzai*	SI		

		Physaloptera sp.	S		
		Raillietnema spectans	LI		
		Schrankiana schranki	SI		
Pseudopaludicola mystacalis (Cope, 1887)				CA	Silva-Neta et al. (2020)
	Nematoda	*Physaloptera* sp.			
Pseudopaludicola pocoto Magalhães, Loebmann, Kokubum, Haddad, and Garda, 2014				CA	Silva et al. (2018); Ávila et al. (2017); Morais et al. (2020)
	Acanthocephalan	Cystacanth			
	Nematoda	*Brevimulticaecum* sp.			
		Cosmocerca parva	S/I		
		Nematode unidentified			
		Oxyascaris oxyascaris			
		Physaloptera sp.			
		Rhabdias pocoto	L		
		Spiroxys sp.			
Microhylidae					
Chiasmocleis capixaba Cruz, Caramaschi, and Izecksohn, 1997				AF	Sluys et al. (2006)
	Nematoda	*Cosmocerca ornata*	I		
Dermatonotus muelleri (Boettger, 1885)				CA	Bezerra et al. (2012); Araújo-filho et al. (2015); Alcantara et al. (2018)
	Acanthocephalan	Cystacanth			
	Cestode	Plerocercoide	Cav/SAT		
	Nematoda	*Aplectana membranosa*	LI		

		Parapharyngodon silvoi	LI		
		Physaloptera sp.(larva)	SI		
		Raillietnema spectans	SI/LI		
		Nematoda unidentified	S/Cav		
		Aplectana crucifer			
		Aplectana vellardi			
		Cosmocercidae			
		Cosmocerca podicipinus			
Odontophrynidae					
Proceratophrys ararype Mângia, Koroiva, Nunes, Roberto, Ávila, Sant'Anna, Santana, and Garda, 2018				AF	Mascarenhas et al. (2021)
	Nematoda	*Aplectana membranosa*	LI		
		Falcaustra mascula	SI;LI		
		Oswaldocruzia mazzai	SI		
		Physaloptera sp.	E		
		Raillietnema spectans	LI		
		Strongyloides sp	SI		
Proceratophrys cristiceps (Müller, 1883)				CA	Sá e Fonseca (2014); Teles et al. (2017b); Silva et al. (2019); Silva-Neta et al. (2020); Sampaio et al. (2020)
	Acanthocephalan	Cystacanth	Cav		
	Digenetic	Trematode unidentified	K		
	Monogenetic	*Polystoma* sp.	I/B		
	Nematoda	*Aplectana membranosa*	LI/SI		
		Cosmocercidae (larva)	S/ SI/LI		
		Falcaustra mascula	LI		

		Oswaldocruzia mazzai	I		
		Oswaldocruzia sp.	SI		
		Physaloptera sp.	S		
		Raillietnema spectans	S		
		Rhabdias breviensis	L		
		Rhabdias sp.	L		
Phyllomedusidae					
Pithecopus gonzagai Andrade, Haga, Ferreira, Recco-Pimentel, Toledo, and Bruschi, 2020				CA	Martins-Sobrinho et al. (2017); Sena et al. (2018); Silva-Neta et al. (2020); Vicente et al. (1991)
	Acanthocephalan	*Centrorhyncus* sp.	S		
		Centrorhynchidae			
	Nematoda	*Brevimulticaecum* sp.	GT		
		Cosmocercidae gen. sp.	I		
		Cosmocerca parva	I		
		Cosmocercella phyllomedusae	I		
		Oxyascaris caudacutus	S/SI		
		Raillietnema minor	LI		
		Raillietnema spectans	I		
		Rhabdias sp.	Cav.		
Ranidae					
Lithobates palmipes (Spix, 1824)				CA	Vicente et al. (1991)
	Nematoda	*Subulascaris falcaustriformis*	LI		

Fonte: Elaborada pelos autores.

7. CONCLUSÃO GERAL

A partir desses estudos, evidenciou-se diferentes lacunas no conhecimento nas diferentes abordagens nos trabalhos com parasitos de anfíbios no Nordeste. Desse modo, concluimos que quanto aos estudos relacionados a familia Pharyngodonidae a descrição de *Parapharyngodon pereiramendoi* sp. n. reforça a importância de voltar a atenção para o desenvolvimentos de pesquisas na região semiárida do Nordeste e a necessidade de consolidar medidas de cuidado para sua preservação e conservação, além de promover investimentos públicos que possam incentivar, subsidiar e manter novos estudos e novas abordagens para pesquisas taxonômicas, ecológicas, biogeográficas e filogenéticas sobre esses parasitos.

Quanto ao registro de ocorrência de *O. cirratus* infectando *C. greeningi*, concluímos que o conhecimento ainda é escasso sobre a dinâmica ecológica dos parasitas faringodonídeos. Este registro é importante por destacar lacunas no conhecimento sobre esta espécie de parasita e suas relações com outros táxons de vertebrados, reforçando a necessidade de aprofundamento dos estudos dessas relações de parasitismo, abordando principalmente o ciclo de vida desses organismos.

No tocante a análise filogenética do gênero *Cosmocerca*, o crescente número de investigações sobre o tema em diferentes regiões do mundo tem contribuído significativamente para o conhecimento da diversidade da helmintofauna, pois apresentam dados fundamentais sobre a genética, morfologia, taxonomia e sistemática desses parasitas em distintas regiões biogeográficas. O escasso conhecimento sobre a helmintofauna brasileira reforça a necessidade de estudos mais aprofundados que incorporem análises ecológicas, evolutivas, filogenéticas e filogeográficas mais profundas e de longo prazo. O exame desses dados torna-se então fundamental para que as informações por eles produzidas possam subsidiar novas pesquisas, esclarecendo questões de biologia, biogeografia e evolução da espécie e do gênero, permitindo avanços na compreensão da evolução dos Cosmocercidae.

A análise de rede ecológica possibilitou identificar espécies chaves para a estabilidade da rede de interações parasito-hospedeiro, e ressaltou diversos tópicos necessários para um fortalecimento e melhoramento dos estudos com nematódeos e grupos de helmintos menos frequentes como os digenéticos, monogenéticos, cestódeos e pentastomídeos. Desse modo, reforça-se a necessidade de treinamento e capacitação de novos taxonomistas para esses grupos e a necessidade de implementação de estudos taxonômicos e técnincas moleculares para o estudo dessa diversidade.

Esperamos que a partir desses resultados, esses trabalhos possam servir de incentivo para novos estudos, escolhendo novas áreas geográficas para investigações com a utilização de novos hospedeiros que não possuem sua helminto fauna inventariada e dessa forma, as novas pesquisas venham a fazer uso de dados moleculares e da taxonomia integrativa para trazer novas perspectivas acerca da biologia, sistemática e evolução dos cosmocercídeos, e além desse, dos fisalopterídeos, molineídeos, rhabdiasídeos, e menos frequente, faringodonídeos, que representam as principais famílias presentes nos registros de infecção em hospedeiros anuros do Nordeste brasileiro.

Nossa pesquisa representa um avanço significativo no conhecimento da parasitofauna de anfíbios no Nordeste brasileiro. As descobertas de novas espécies, a ampliação do conhecimento sobre a distribuição e especificidade de parasitos já conhecidos, a elucidação de questões filogenéticas complexas e a análise integrada da rede de interações parasito-hospedeiro, tudo isso contribui para um entendimento mais profundo da biodiversidade parasitária e da dinâmica das interações entre parasitos e seus hospedeiros anuros.

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