

Research Paper

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Pattern of anuran infection by acanthocephalans from the Cerrado, Northeastern Brazil with a summary for South America

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Abstract

In Brazil, acanthocephalans parasitise anurans in several biomes. In the present study, we performed an analysis of acanthocephalan infections across 175 anuran individuals from the Cerrado biome, belonging to ten species: *Boana raniceps*, *Pithecopus hypochondrialis*, *Scinax fuscomarginatus*, *Scinax x-signatus*, *Leptodactylus pustulatus*, *Leptodactylus macrosternum*, *Leptodactylus vastus*, *Physalaemus cuvieri*, *Adenomera hylaedactyla*, and *Elachistocleis piauiensis*. We also verified the specificity of the parasites using the S_{TD}^* index. Additionally, we conducted a survey of acanthocephalan infection in anurans in South America. The studied assemblage in the Brazilian Cerrado presented 57 parasitised hosts of 175 specimens (overall prevalence: 32.6%). In total, 437 acanthocephalans cystacanths were recorded, among which 286 presented the same morphotype but could not be identified, 148 belonged to the genus *Centrorhynchus*, and three belonged to *Oncicola*. Unidentified acanthocephalans had a higher prevalence in *L. vastus* (53.85%) and the highest intensity was in *L. pustulatus* (17 ± 16). The highest prevalence of *Centrorhynchus* sp. was in the species *S. fuscomarginatus* (28.57%), while the highest intensity was observed in *L. vastus* (111). The taxon *Oncicola* sp. it had a prevalence of 3.23% and an intensity of 3 only in *S. x-signatus*. The highest specificity was recorded for *Oncicola* sp. ($S_{TD}^* = 1$), whereas the lowest was found in *Centrorhynchus* sp. ($S_{TD}^* = 2.21$). Finally, according to the survey for South America, we found ten records of acanthocephalan taxa parasitizing 58 species of anurans distributed in seven countries (Brazil with the most records).

Introduction

Acanthocephala currently comprises about 1,298 described species (Amin 2013). These organisms make up one of the four subclasses of the phylum Rotifera (Nielsen 2012; Brusca *et al.* 2018) and are obligate intestinal vertebrate parasites with no free-living members (Kennedy 2006). In the adult stage, Acanthocephala bodies are cylindrical or slightly flattened, with retractable proboscises (cylindrical and with curved hooks) that are ideal for anchoring the parasite to the host's intestinal wall. Many species have rings of spines along their bodies (Nielsen 2012).

The life cycle and developmental stages of these parasites are remarkably similar across species, comprising the egg stage (containing a larva, the acanthor); the larval stages of acanthella and cystacanth in an intermediate arthropod host; and finally, the adult stage in a definitive vertebrate host (Kennedy 2006; Near 2002). At times, the acanthocephalan life cycle of some species may utilise paratenic or transport hosts (Near 2002). Proportionally, birds and fish are the most widely used definitive hosts, followed by mammals. In turn, amphibians and reptiles are less commonly used. As for habitat, acanthocephalans are predominantly aquatic parasites and are frequently found in freshwater vertebrates (Kennedy 2006). In the context of the life cycle, Perrot-Minnot *et al.* (2023) point out the need to expand and disseminate knowledge on the range of hosts used by each acanthocephalan species. In the case of acanthocephalans, the degree of specificity varies between intermediate, paratenic, and definitive hosts and constitutes a crucial factor for the distribution and abundance of the parasite (Kennedy 2006).

Acanthocephalans comprise part of a model parasite–host system that requires studies on their life cycles, their transmission strategies, and their host exploitation, as well as factors that contribute to host specialisation (Perrot-Minnot *et al.* 2023). Due to the small number of described acanthocephalan species, they have received less attention compared to other groups of endoparasitic metazoans. Nonetheless, it is still considered a successful group, as they infect all vertebrate taxa and are found in all biomes and ecosystems (Kennedy 2006). In a survey of anuran

endoparasites in South America by Campião *et al.* (2014a), acanthocephalans were found to be relatively rare, with 15 registered taxa, infecting 39 species of anurans. For comparison purposes, nematodes reached 150 registered taxa.

Amphibians are hosts to a rich diversity of associated parasites and can be infected at any time between the larval and adult stages (Bower *et al.* 2019; Duellman and Trueb 1994). Approximately 88 species of Brazilian amphibians (mostly anurans) had records of infection by helminths, including acanthocephalans (Campião *et al.* 2014a). In most anuran taxa studied, acanthocephalans are completely absent, or, when present, they are not the most prevalent or abundant parasites nor do they infect the widest range of host species (Aguiar *et al.* 2014; Bursey *et al.* 2001; Santos *et al.* 2013; Toledo *et al.* 2013; Toledo *et al.* 2017). In contrast, a study by Martins-Sobrinho (2017) was one of the few that recorded acanthocephalans as the most abundant and prevalent endoparasites in anurans of the families Hylidae and Phyllomedusidae. However, possible explanations for this finding are not discussed.

The total of 209 anuran species are found in the Cerrado biome, with a high level of endemism (51.7%) (Valdujo *et al.* 2012). In the Cerrado in the state of Mato Grosso do Sul, two anuran species were reported as being infected by unidentified acanthocephalans (Queiroz *et al.* 2020). In the transition between the Cerrado and Atlantic Forest in the state of São Paulo, Aguiar (2021) found the infection of 13 anuran species by unidentified cystacanths and acanthocephalans of the Centrorhynchidae family. Thus, the present study aims to characterise the acanthocephalan fauna associated with ten anuran species from a Cerrado fragment in Northeastern Brazil, seeking to geographically expand the knowledge on anuran acanthocephalan fauna in the country. In addition, we present their levels of specificity. With the aim of contributing to knowledge about the geographic distribution of anuran acanthocephalans in South America, we also present the locality records for each species, considering that new publications with records of acanthocephalan infections in anurans from South America have been recorded after the last survey carried out by Campião *et al.* (2014a).

Materials and methods

Study area

Host collection was conducted in the Itamacaoca Protection Reserve – IPR (3°44'55"S 43°19'58"W; datum WGS84), a Cerrado area located in the Chapadinha municipality, Maranhão state, Northeastern Brazil (Figure 1). This reserve covers approximately 460ha and contains the Itamacaoca Dam, the main source of drinking water for the urban region of the municipality of Chapadinha (Silva *et al.* 2008). The Reserve is composed of a mosaic of vegetation, with riparian forests, gallery forests, cerrado fields, and relicts of Cerradão. However, due to the advance of the agricultural frontier in this municipality, the region has experienced habitat loss and fragmentation (Silva *et al.* 2008). The climate is tropical, with an average annual temperature of 27.6 °C and an average annual rainfall volume of 1452 mm. The rainy season runs from December to May and the dry season from June to November (Climate-Data 2021).

Data collection

Animal collections were carried out during the rainy season between January and March 2020, from 6:00 p.m to 10:00 p.m. Nine active searches were carried out, totaling 36 hours of

fieldwork. Searches were carried out by a minimum of two and a maximum of four people. Specimens were actively sought in the soil, at the edges of water bodies, and in the surrounding vegetation. After being manually collected, anurans were immediately stored in plastic bags filled with a small volume of water or in damp cloth bags. They were then transported to the herpetology laboratory at the Chapadinha Science Center of the Universidade Federal do Maranhão, where they were euthanised using a lethal dose (60 to 100 mg/kg) of Thiopental, administered intraperitoneally. Following euthanasia, the animals were tagged, identified, and weighed, and their snout-vent length was measured. Sex was determined by analysing the gonads during dissection. The taxonomic classification of hosts is in accordance with Frost (2021).

The anurans were dissected, and the lungs and gastrointestinal tract were analysed under a stereomicroscope. When present, acanthocephalans were counted and stored in vials with 70% alcohol. Subsequently, they were temporarily mounted on slides containing glycerol (McAllister and Bursey 2007), analysed under a light microscope, and identified to the lowest possible taxonomic level according to McDonald (1988), Van Cleave (1923), Smales (2007a), Santos & Amato (2010a), and Palmer *et al.* (2020). The hosts were fixed in a 10% formalin solution, stored in bottles with 70% alcohol, and deposited in the Claude d'Abbeville Herpetological Collection at the Chapadinha Science Center of the Universidade Federal do Maranhão, Brazil.

Ethical aspects

The collection and use of amphibians in the present study was authorised by the Instituto Chico Mendes de Biodiversidade (ICMBio/SISBIO - authorisation number: 71407-1, 71407-2) and the Commission for Ethics in the Use of Animals of the Universidade Federal do Maranhão (CEUA- UFMA - process no. 23115.031592/2019-38).

Quantitative descriptors

Prevalence and mean intensity of infection were calculated according to Bush (1997). Prevalence is the ratio between the number of hosts infected by a given species and the total number of hosts collected, multiplied by 100. Mean intensity is calculated by the total number of parasites of a species divided by the total number of hosts parasitised by that species. Both descriptors were calculated for each anuran species.

Host specificity

In order to determine the specificity of each acanthocephalans species to their hosts, the specificity index S_{TD}^* (Poulin and Mouillot 2005) was calculated using the following equation:

$$S_{TD}^* = \frac{\sum \sum_{i < j} \omega_{ij} (p_i p_j)}{\sum \sum_{i < j} (p_i p_j)}$$

where ω_{ij} is the taxonomic distinction between host species i and j , and p_i and p_j represent parasite prevalence in host species i and j . The index was calculated in the TaxoBiodiv2 program (Poulin and Mouillot 2005) only for acanthocephalans identified down to the genus level. The closer the index value converges to 1, the more specific the parasite. The maximum value is 5, when using five

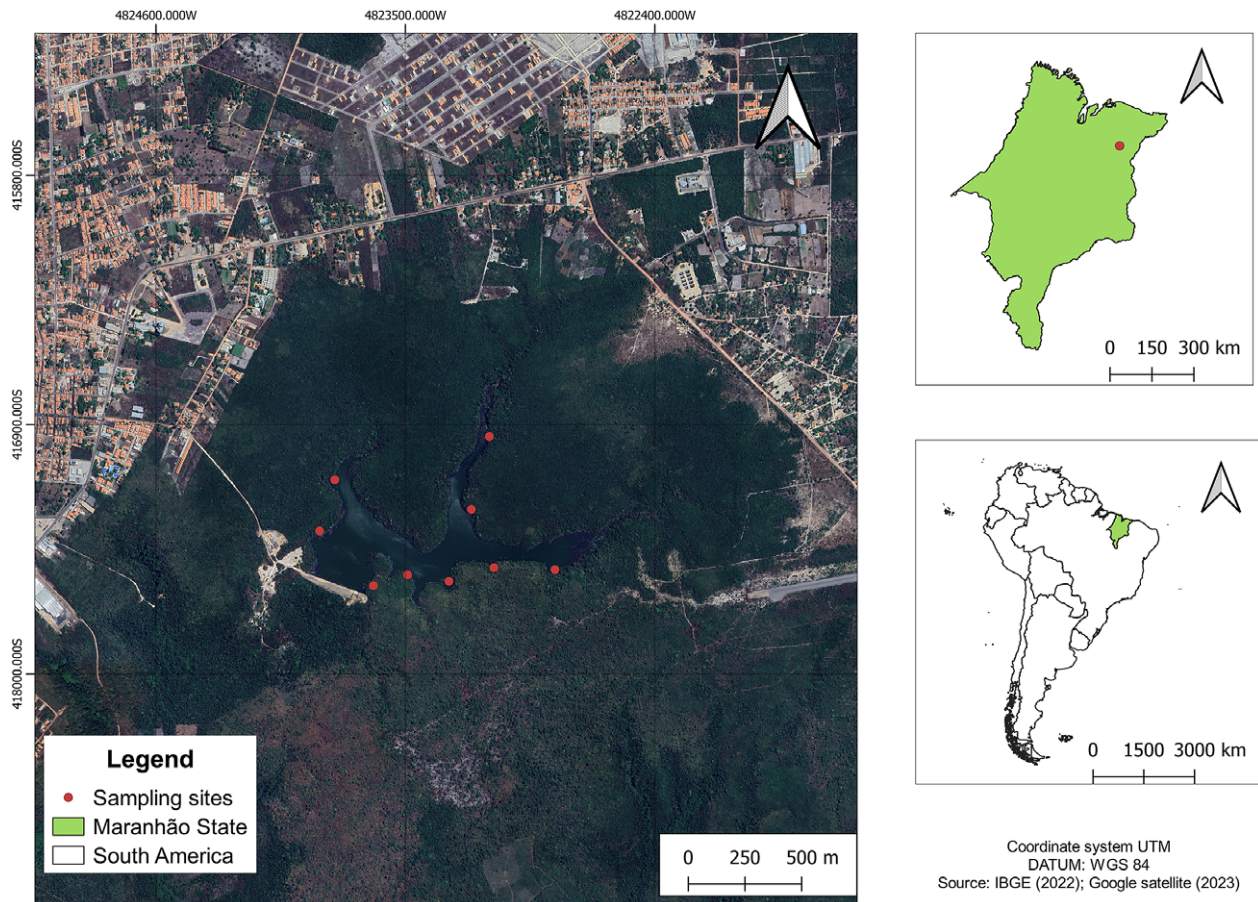


Figure 1. Itamaoca Protection Reserve – IPR located in the Chapadinha municipality, Maranhão state, Northeastern Brazil.

taxonomic levels and when all host species belong to different classes (Poulin and Mouillot 2005).

Bibliographic survey

Acanthocephalan records were verified in the following scientific bases: PubMed, Google Scholar, and Scielo. We only included studies where parasites were identified to at least the genus level and where the geographic coordinates or name of the host collection site were described in our analyses. The time range of publications was 1990–present. The following keywords were used in our research: “*anuran acanthocephalans in South America*”; “*anuran acanthocephalans followed by the name of each country in South America*”. Information on the species sampled in the present study was also included.

Results

Our anuran sampling in the IPR resulted in the capture of 175 anuran specimens, belonging to ten species and three families (Table 1). We recorded an overall prevalence of 32.6% (57 anurans infected by 437 specimens of acanthocephalans). Two taxa were identified in the cystacanth stage: *Centrorhynchus* sp., with 148 specimens being found to infect six species of anurans, and *Oncicola* sp., where three specimens were found in one species of anuran (Table 1). The former

presents a receptacle for the proboscis and is positioned in the middle part of the proboscis section located behind simple, spine-like thorns. In front of this insertion point, there are sturdy hooks that curve backward. The second is characterised by having cement glands that are nearly round in shape (Van Cleave 1923). The lemnisci are extremely elongated, resembling sub-cylinders, and they occupy over three-fourths of the body cavity’s length (Van Cleave 1923). Furthermore, 286 acanthocephalans cystacanth (that presented the same morphotype) found in nine species could not be identified due to a lack of clear visualisation of taxonomic characters.

Unidentified acanthocephalans had a higher prevalence in *L. vastus* (53.85%) and a lower prevalence in *L. pustulatus* (12.5%). The highest intensity was in *L. pustulatus* (17±16) and the lowest in *E. piauiensis* (1). The highest prevalence of *Centrorhynchus* sp. was in the species *S. fuscomarginatus* (28.57%) and the lowest in *L. macrosternum* (4%). The species *Oncicola* sp. had maximum specificity ($S_{TD}^* = 1$), whereas *Centrorhynchus* sp. was less specific ($S_{TD}^* = 2.21$).

From the bibliographic survey, we found 31 eligible scientific articles according to our inclusion criteria, and after analysing this bibliography, we found ten records of acanthocephalan taxa parasitising 58 species of anurans in seven South American countries (Table 2; Figure 2). We observed that few locations on the continent have been sampled, and six countries still have no records of identified acanthocephalans in amphibians. Of the countries with records, Brazil was the most sampled, followed by Paraguay,

Table 1. Acanthocephalans and infected hosts from the Itamacaoca Protection Reserve, Maranhão state, Brazil. Specificity index (S_{TD}^*), prevalence (P %), mean intensity of infection (MII), and number of analysed hosts (N)

Host	N	Parasite	P %	MI I
Hylidae				
<i>Boana raniceps</i>	20	Unidentified Acanthocephala	30	2,17±1,86
		<i>Centrorhynchus</i> sp.	10	5,50±4,50
<i>Pithecopus hypochondrialis</i>	19	Unidentified Acanthocephala	15,79	9,67±7,59
<i>Scinax fuscomarginatus</i>	7	<i>Centrorhynchus</i> sp.	28,57	2
<i>Scinax x-signatus</i>	31	Unidentified Acanthocephala	25,81	2,13±0,93
		<i>Centrorhynchus</i> sp.	16,13	3,40±1,36
		<i>Oncicola</i> sp.*	3,23	3
Leptodactylidae				
<i>Leptodactylus pustulatus</i>	16	Unidentified Acanthocephala	12,5	17±16
<i>Leptodactylus macrosternum</i>	25	Unidentified Acanthocephala	44	8,27±13,41
		<i>Centrorhynchus</i> sp.	4	4
<i>Leptodactylus vastus</i>	13	Unidentified Acanthocephala	53,85	11,29±9,87
		<i>Centrorhynchus</i> sp.	7,69	111
<i>Physalaemus cuvieri</i>	22	Unidentified Acanthocephala	18,18	1,75±0,83
		<i>Centrorhynchus</i> sp.	4,55	1
<i>Adenomera hylaedactyla</i>	18	Unidentified Acanthocephala	27,78	3±1,90
Microhylidae				
<i>Elachistocleis piauiensis</i>	4	Unidentified Acanthocephala	25	1
Total =	175			

Note: means appear as ± 1 SD; * new registered host.

Ecuador, Colombia, Chile, Peru, and Argentina. *Centrorhynchus* sp. is the most widely distributed taxon, spanning across Brazil, Argentina, Chile, Paraguay, Colombia, and Peru.

Discussion

Our study provides the first record of acanthocephalans of the genus *Oncicola* in anurans of the genus *Scinax* and anurans of the family Hylidae. The genus *Oncicola* comprises 24 species and uses carnivorous mammals as definitive hosts (Amin 2013). It is rarely recorded in anurans, despite being highlighted as potential paratenic hosts (Goldberg *et al.* 2002). In amphibians, the genus *Oncicola* has already been recorded in Colombia in *Oophaga histrionica* (Dendrobatidae) (Goldberg and Bursey 2003) and Mexico in *Lithobates brownorum* (Ranidae) (Velazquez-Urrieta and León-Règagnon 2018), *L. vaillanti* (Ranidae) (Paredes-Calderón *et al.* 2004), and *L. forreri* (Ranidae) (Cabrera-Guzmán *et al.* 2010). Our record expands the knowledge of helminth infection to include amphibian fauna in Brazil and more specifically in the northeastern Cerrado.

Anurans are considered definitive hosts of acanthocephalans (Richardson 2013), but some species have been recorded as paratenic hosts (Santos and Amato 2010b; Schmidt 1985). The genus *Centrorhynchus* is an example of an acanthocephalan that uses amphibians to reach its definitive hosts (birds and terrestrial predators) (Hernandez-Orts *et al.* 2019; Kennedy 2006; Santos and Amato 2010b). The taxon comprises 100 species (Amin 2013)

and is one of the most frequently recorded acanthocephalan genera in South American anurans, distributed across Argentina, Brazil, Chile, Paraguay, Colombia, and Peru (Torres and Puga 1996; Goldberg and Bursey 2003; Campião *et al.* 2014a; Martins-Sobrinho *et al.* 2017; Oliveira *et al.* 2019; Oliveira *et al.* 2022). In Brazil, it has already been recorded in the Atlantic Forest (Graça *et al.* 2017; Martins-Sobrinho *et al.* 2017) and Caatinga (Oliveira *et al.* 2022). Santos (2010a) categorised the anuran *Rhinella fernandezae* as a paratenic host of *Centrorhynchus* sp., which suggests, in the present study, that the five species of anurans infected by this taxon are paratenic hosts. Although paratenic hosts are not obligatory for the physiological development of acanthocephalans, they may serve as a trophic level in these parasites' life cycles (Richardson 2013), providing protection during this period against the external environment in addition to more effectively directing the parasite to its definitive host (Parker *et al.* 2003).

Despite being a small group that presents a low diversity of larval stages and life cycles, acanthocephalans are well distributed, both spatially and among hosts, even when compared to other larger and more diverse parasite groups, such as nematodes (Kennedy 2006). Contrary to the present study, in most surveys of anuran populations, these parasites are not usually representative (Aguir *et al.* 2014; Bursey *et al.* 2001; Santos *et al.* 2013; Toledo *et al.* 2013; Toledo *et al.* 2017). One exception to this is a study by Martins-Sobrinho *et al.* (2017), who found acanthocephalans in all nine anuran species analysed in the Atlantic Forest that were even more prevalent than nematodes. The species *Centrorhynchus* sp. in the species *S. x-signatus*, for example, had a prevalence of 45% and a

Table 2. Locations in South America and respective recorded acanthocephalan taxa in anurans

Country/locality	Parasite	Host	Source
Brazil			
Chapadilha, MA	<i>Centrorhynchus</i> sp.	<i>Boana raniceps</i>	Present study
		<i>Leptodactylus macrosternum</i>	
		<i>Leptodactylus vastus</i>	
		<i>Physalaemus cuvieri</i>	
		<i>Scinax fuscomarginatus</i>	
		<i>Scinax x-signatus</i>	
Chapadilha, MA	<i>Oncicola</i> sp.	<i>Scinax x-signatus</i>	Present study
Diamante do Norte, PR	<i>Centrorhynchus</i> sp.	<i>Boana albopunctata</i>	Graça et al. (2017)
Tapacurá, PE	<i>Centrorhynchus</i> sp.	<i>Dendropsophus branneri</i>	Martins-Sobrinho et al. (2017)
		<i>Dendropsophus decipiens</i>	
		<i>Dendropsophus elegans</i>	
		<i>Dendropsophus haddadi</i>	
		<i>Dendropsophus minutus</i>	
		<i>Boana albomarginata</i>	
		<i>Pithecopus nordestinus</i>	
		<i>Scinax auratus</i>	
		<i>Scinax x-signatus</i>	
		Maranguape, CE	
<i>Boana raniceps</i>			
<i>Dendropsophus minusculus</i>			
<i>Dendropsophus minutus</i>			
<i>Dendropsophus nanus</i>			
<i>Scinax x-signatus</i>			
<i>Leptodactylus fuscus</i>			
<i>Leptodactylus macrosternum</i>			
<i>Leptodactylus pustulatus</i>			
<i>Leptodactylus vastus</i>			
<i>Physalaemus cuvieri</i>			
<i>Proceratophrys renalis</i>			
<i>Pithecopus gonzagai</i>			
<i>Trachycephalus typhonius</i>			
Maranguape, CE	<i>Oligacanthorhynchus</i> sp.	<i>Rhinella diptycha</i>	Oliveira et al. (2022)
		<i>Scinax x-signatus</i>	
		<i>Leptodactylus vastus</i>	
Farias Brito, CE	<i>Pseudoacanthocephalus lutzi</i>	<i>Physalaemus cuvieri</i>	Oliveira et al. (2022)
Ipu, CE	<i>Oligacanthorhynchus</i> sp.	<i>Pleurodema diplolister</i>	Silva-Neta et al. (2020)
Serra do Mar Park, SP	<i>Pseudoacanthocephalus lutzi</i>	<i>Physalaemus cuvieri</i>	Toledo et al. (2013)
Imbé, RS	<i>Centrorhynchus</i> sp.	<i>Rhinella fernandezae</i>	Santos and Amato (2010b)
Angra dos Reis, RJ	<i>Anuracanthorhynchus tritaxisentis</i>	<i>Hylodes phyllodes</i>	Burseley et al. (2006)
Três Barras, SC	<i>Acanthocephalus</i> sp.	<i>Rhinella diptycha</i>	Hoppe et al. (2008)
		<i>Rhinella icterica</i>	

(Continued)

Table 2. (Continued)

Country/locality	Parasite	Host	Source
Botucatu, SP	<i>Pseudoacanthocephalus lutzi</i>	<i>Rhinella icterica</i>	Pinhão <i>et al.</i> (2009)
Imbé, RS	<i>Pseudoacanthocephalus lutzi</i>	<i>Rhinella fernandezae</i>	Santos and Amato (2010a)
Campo Belo do Sul, SC	<i>Pseudoacanthocephalus</i> sp.	<i>Scinax fuscovarius</i>	Santos <i>et al.</i> (2016)
São Paulo, SP	<i>Pseudoacanthocephalus lutzi</i>	<i>Rhinella icterica</i>	Smales (2007a)
Campina Grande do Sul, PR	<i>Pseudoacanthocephalus lutzi</i>	<i>Physalaemus cuvieri</i>	Leivas <i>et al.</i> (2018)
Tapacurá, PE	<i>Centrorhynchus</i> sp.	<i>Pithecopus nordestinus</i>	Sena <i>et al.</i> (2018)
Capão do Leão and Rio Grande, RS	<i>Pseudoacanthocephalus</i> sp.	<i>Boana pulchella</i>	Silveira <i>et al.</i> (2022)
Capão do Leão and Rio Grande, RS	<i>Centrorhynchus</i> sp.	<i>Boana pulchella</i>	Silveira <i>et al.</i> (2022)
Núcleo Santa Virgínia, SP	<i>Pseudoacanthocephalus lutzi</i>	<i>Physalaemus cuvieri</i>	Aguiar <i>et al.</i> (2015)
Colombia			
Chocó Province	<i>Centrorhynchus</i> sp.	<i>Oophaga histrionica</i>	Goldberg and Bursey (2003)
Chocó Province	<i>Oncicola</i> sp.	<i>Oophaga histrionica</i>	Goldberg and Bursey (2003)
Chocó Province	<i>Polymorphus</i> sp.	<i>Oophaga histrionica</i>	Goldberg and Bursey (2003)
Paraguay			
Estancia Laguna General Diaz	<i>Pseudoacanthocephalus caspanensis</i>	<i>Rhinella fernandezae</i>	Smales (2007a)
		<i>Rhinella granulosa</i>	
		<i>Scinax acuminatus</i>	
Estancia Laguna General Diaz	<i>Centrorhynchus</i> sp.	<i>Leptodactylus chaquensis</i>	Smales (2007a)
		<i>Rhinella fernandezae</i>	
		<i>Rhinella granulosa</i>	
Estancia Laguna General Diaz	<i>Pseudoacanthocephalus lutzi</i>	<i>Rhinella granulosa</i>	Smales (2007a)
		<i>Leptodactylus podicipinus</i>	
Estancia Laguna General Diaz	<i>Acanthocephalus</i> sp.	<i>Leptodactylus chaquensis</i>	Smales (2007a)
Carapegua	<i>Centrorhynchus</i> sp.	<i>Dendropsophus nanus</i>	Smales (2007a)
Estancia Santa Maria	<i>Centrorhynchus</i> sp.	<i>Physalaemus cuvieri</i>	Smales (2007a)
		<i>Leptodactylus elenae</i>	
		<i>Dendropsophus sanborni</i>	
Estancia Santa Sophia	<i>Centrorhynchus</i> sp.	<i>Physalaemus nattereri</i>	Smales (2007a)
		<i>Phyllomedusa sauvagii</i>	
		<i>Physalaemus cuvieri</i>	
Rio Aguaray-Guazu	<i>Centrorhynchus</i> sp.	<i>Scinax nasicus</i>	Smales (2007a)
Pozo Hondo	<i>Oligacanthorhynchus</i> sp.	<i>Odontophrynus americanus</i>	Smales (2007a)
Argentina			
Corrientes	<i>Centrorhynchus</i> sp.	<i>Leptodactylus latinasus</i>	Hamann <i>et al.</i> (2006)
Corrientes	<i>Centrorhynchus</i> sp.	<i>Leptodactylus bufonius</i>	González and Hamann (2006)
Corrientes	<i>Centrorhynchus</i> sp.	<i>Scinax nasicus</i>	Hamann <i>et al.</i> (2009)
Corrientes	<i>Centrorhynchus</i> sp.	<i>Scinax nasicus</i>	Hamann <i>et al.</i> (2010)
Corrientes	<i>Centrorhynchus</i> sp.	<i>Leptodactylus chaquensis</i>	Schaefer <i>et al.</i> (2006)
Corrientes	<i>Centrorhynchus</i> sp.	<i>Leptodactylus bufonius</i>	Hamann <i>et al.</i> (2012)
Lujan	<i>Pseudoacanthocephalus lutzi</i>	<i>Rhinella arenarum</i>	Arredondo and de Pertierra (2009)
Buenos Aires	<i>Pseudoacanthocephalus lutzi</i>	<i>Rhinella arenarum</i>	Arredondo and de Pertierra (2009)

(Continued)

Table 2. (Continued)

Country/locality	Parasite	Host	Source
Chile			
Caspana	<i>Pseudoacanthocephalus caspanensis</i>	<i>Rhinella spinulosa</i>	Fernandez and Ibarra (1990)
Yaldad	<i>Centrorhynchus</i> sp.	<i>Eupsophus calcaratus</i>	Torres and Puga (1996)
Valdivia	<i>Centrorhynchus</i> sp.	<i>Eupsophus roseus</i>	Torres and Puga (1996)
Peru			
Lima	<i>Centrorhynchus</i> sp.	<i>Telmatobius jelskii</i>	Chero <i>et al.</i> (2014)
Lima	<i>Oncicola</i> sp.	<i>Telmatobius jelskii</i>	Chero <i>et al.</i> (2014)
Lima	<i>Pseudoacanthocephalus lutzi</i>	<i>Rhinella spinulosa</i>	Chero <i>et al.</i> (2016)
Huanuco	<i>Pseudoacanthocephalus lutzi</i>	<i>Rhinella marina</i>	Toledo <i>et al.</i> (2017)
Ecuador			
San Pablo de Kantesiya, Shushufundi and Tinalandia	<i>Oligacanthorhynchus</i> sp.	<i>Rhinella marina</i>	Smales (2007b)
		<i>Boana boans</i>	
		<i>Boana fasciata</i>	
		<i>Boana lanciformis</i>	
		<i>Dendropsophus triangulum</i>	
		<i>Nyctimantis rugiceps</i>	
		<i>Osteocephalus taurinus</i>	
		<i>Phyllomedusa</i> spp.	
		<i>Leptodactylus pentadactylus</i>	
San Pablo de Kantesiya, Shushufundi and Tinalandia	<i>Pandosentis napoensis</i>	<i>Boana fasciata</i>	Smales (2007b)
San Pablo de Kantesiya, Shushufundi and Tinalandia	<i>Acanthocephalus</i> sp.	<i>Leptodactylus pentadactylus</i>	Smales (2007b)

mean intensity of 5.4 ± 7.7 . However, in the present study, its prevalence was 16.13% and the mean intensity was 3.40 ± 1.36 in the same anuran species. Santos and Amato (2010b) found *Centrorhynchus* sp. in 84% of *Rhinella fernandezae* individuals in Rio Grande do Sul state. Silveira *et al.* (2022) found *Centrorhynchus* sp. in 59% of *Boana pulchella* hosts, also in Rio Grande do Sul State.

According to Janovy *et al.* (1992), ecological factors are the main determinants of parasite population structure. For example, in a study carried out on a population of anurans of the species *Physalaemus cuvieri* in the Atlantic Forest, Leivas *et al.* (2018) found that acanthocephalans had higher infection rates than nematode species, mainly cystacanths from the Centrorhynchidae family, with a prevalence of 42.8% and an average intensity of 2.8 ± 1.7 . In this study, the host's diet was attributed to the high prevalence of acanthocephalans found by Leivas *et al.* (2018). In fact, host feeding habits are determinant for acanthocephalan infection (Kennedy 2006) since these parasites have a heteroxene life cycle, in which arthropods are the intermediate hosts (Kennedy 2006; Santos and Amato 2010b). As such, we can assume that the rarity of acanthocephalans frequently reported in studies is attributed to the absence or lower abundance of suitable intermediate hosts, preventing successful infection (Kennedy 2006; Campião *et al.* 2014b).

Although our small sample size did not allow for a detailed analysis of the environmental influence on the dynamics of

acanthocephalans and their hosts, it seems that each biome can impose an environmental dynamic of biotic and abiotic factors that interferes with the prevalence and intensity of different parasite taxa. The work of Thieltges *et al.* (2008) provides a broad review of several abiotic factors that affect metazoan infection rates such as temperature, salinity, PH, UV-radiation, hardness, and pollutants, as well biotic factors such as hyperparasites, physical disturbance by organisms, toxic exudates from organisms, decoy organisms, predation, and alternative hosts. For example, during the egg stage of acanthocephalans, transmission success is influenced by environmental factors that increase or decrease the pool of infectious stages and infection rates (Thieltges *et al.* 2008).

In natural environments, some organisms can ingest or filter certain species of parasites without serving as intermediate or definitive hosts and thus control parasite abundance in the environment. Therefore, it is expected that fluctuations in the population sizes of these filter-feeding/ingesting species will directly influence the increase or decrease in parasitism rates (Thieltges *et al.* 2008). Additionally, amphibian populations also experience fluctuations in terms of size due to their dependence on bodies of water for reproduction. In rainy years, survival and population growth are high, but in dry years, reproduction rates can drop, preventing population growth (Pough *et al.* 2023). Therefore, the patterns of acanthocephala infection recorded in our study may reflect some of

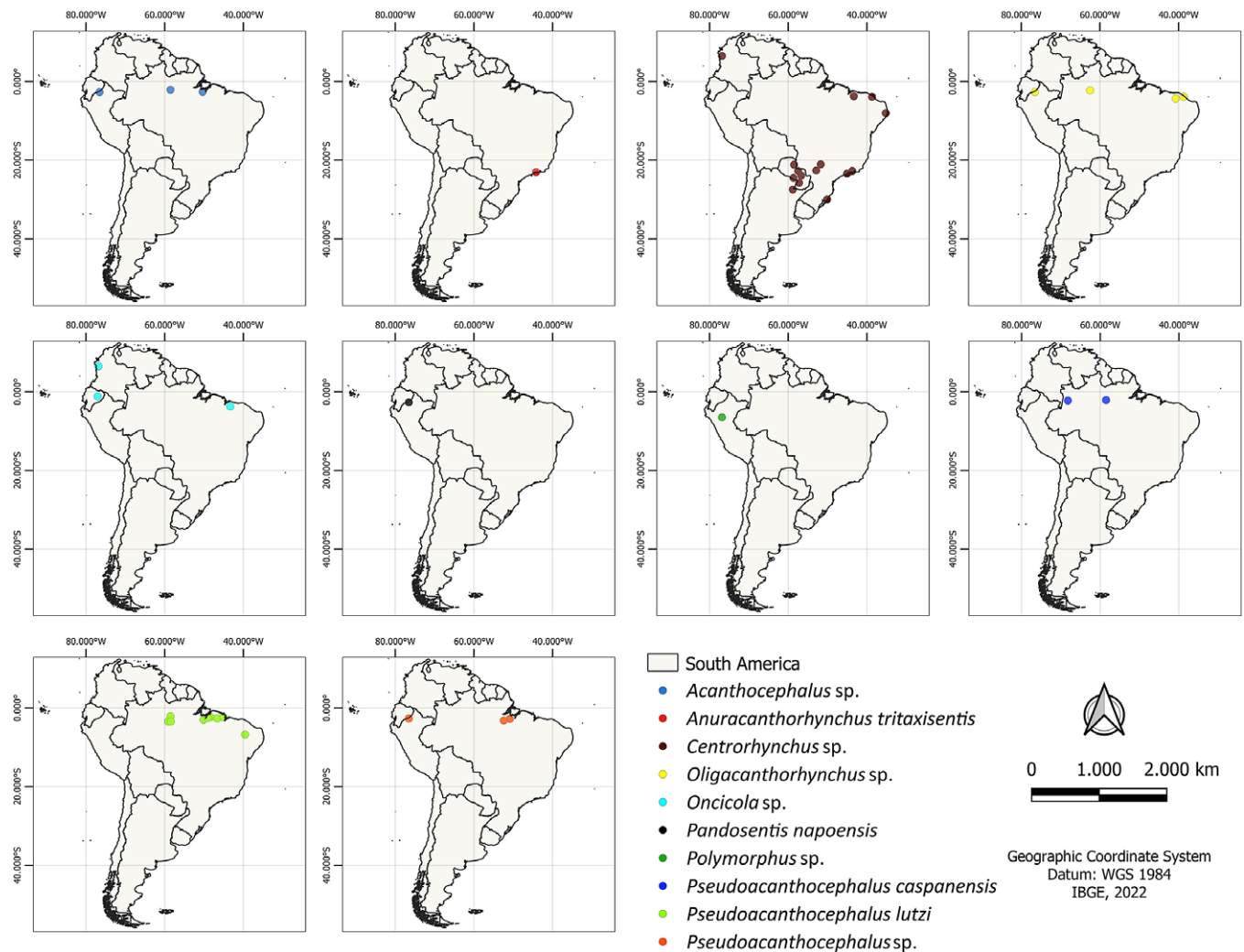


Figure 2. Records of anuran acanthocephalans identified at least to the genus level in South America.

the scenarios that exist in this range of recruitment method, normally observed in anurans. However, only long-term sequence sampling will be able to clarify this trend.

In addition, anuran biology and transmission dynamics work in conjunction with abiotic factors in the parasite community at each location (McAlpine 1997). Therefore, the structure of the acanthocephalan community in the anurans of the present study probably results from the joint action of these factors, although it is not possible to separate the relative importance of each of them.

When considering biotic and abiotic factors, we must also consider anthropogenic impacts on parasite transmission dynamics (Thieltges *et al.* 2008), such as habitat fragmentation and degradation, to which gastrointestinal parasites are vulnerable (Kiene *et al.* 2021). The Itamaoca Reserve (i.e., the study collection site) suffers from fragmentation and loss of vegetation cover (Silva *et al.* 2008). This fragmentation can alter host density (due to the reduced size of the habitat), which can affect parasite diversity (Chakraborty *et al.* 2019), since infection rates can be mediated by the abundance of intermediate hosts in the environment and host accessibility to parasites (which is generally related to host abundance) (Kiene *et al.* 2021). Therefore, the chances of contact between intermediate and final hosts, and between hosts and

parasites, may be greater in fragmented areas, favoring transmission and possibly generating changes in the infection rates found in this study.

Janovy *et al.* (1992) state that the presence of a parasitic species in a host species is strongly influenced by evolutionary factors. However, the infection data obtained in the present study suggest an ecological influence on the observed infection pattern, corroborating the studies by Sampaio *et al.* (2022) and Oliveira *et al.* (2023). In the case of acanthocephalans, hosts from a given locality are probably more related ecologically due to similarities in diet and habitat than phylogenetically (McAlpine 1997; Kennedy 2006), which should explain the presence of *Centrorhynchus* sp. and *Oncicola* sp. in the anuran hosts of the present study.

The species *Oncicola* sp. was the only acanthocephalan associated with a single host species, with maximum specificity. A high degree of specialisation indicates a low chance of survival in a location if the host population becomes extinct (Kennedy 2006). However, Combes (2001) states that to ensure the continuity of the cycle, highly specific parasites must occur in stable environments and in continuous and abundant host populations. Furthermore, anurans likely serve as paratenic hosts for *Oncicola* sp. (Goldberg *et al.* 2002), which perhaps explains the fact that it was only found in one species. However, less

specific helminths, such as *Centrorhynchus* sp., probably cope better with local extinctions and fluctuations in the host population (Poulin *et al.* 2011).

In South America, there are records of acanthocephalans in Peru (Burseley *et al.* 2001; Chero *et al.* 2014), Chile (Fernandez and Ibarra 1990), Argentina (Arredondo and de Pertierra 2009; Gonzalez and Hamann 2006; Hamann *et al.* 2006), Colombia (Goldberg and Bursey 2003), Paraguay (Smales 2007a), Ecuador (Smales 2007b), and Brazil, with distributions in the Atlantic Forest (Aguiar *et al.* 2014; Graça *et al.* 2017; Martins-Sobrinho *et al.* 2017; Toledo *et al.* 2013), Cerrado (Aguiar *et al.* 2021; Queiroz *et al.* 2020), Caatinga (Oliveira *et al.* 2019; Oliveira *et al.* 2022; Silva-Neta *et al.* 2020), and Pantanal (Campião *et al.* 2016; Campiã *et al.* 2014b) biomes. Although Brazil's ecosystems remain insufficiently explored, they boast the highest diversity of acanthocephalans on the continent. Nonetheless, South America still remains undersampled, with five countries still lacking studies on this topic. Our survey highlights the need for further studies in this regard, seeking to understand patterns of infection by acanthocephalans.

We emphasise that new studies have been published following the checklist of parasitic helminths in anurans from South America, carried out by Campiã *et al.* (2014a) between 1925 and 2012. Thus, our study aims to contribute to the aforementioned survey, focusing on the geographic distribution of known acanthocephalans. However, there are still significant gaps in sampling, which shows that the true extent of the diversity and distribution of these organisms is far from being fully understood due to the limited data collection to date.

In summary, our study provides valuable information about the distribution of acanthocephalans in South American anurans, particularly in northeastern Brazil. Furthermore, our findings highlight the structural role of ecological and environmental factors, including host diet habits, on infection rates. Therefore, considering these factors, along with potential human impacts, a comprehensive investigation into infection patterns observed in this acanthocephalan population is essential.

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Competing interest. None.

Ethical standard. All authors gave their consent to participation in the study. The study was approved by the Instituto Chico Mendes de Conservação da Biodiversidade, with permission to collect the animals, and the ethics committee of the Universidade Federal do Maranhão.

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