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Diversity of Acanthocephala parasites in Neotropical amphibians

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Review Article

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Abstract

Acanthocephalans constitute a small taxonomic group related to rotifers and specialized in a parasitic lifestyle. Anurans act as paratenic and definitive hosts and infections always occur trophically. Our objective is to describe and summarize the richness of acanthocephalans in Neotropical anurans. We conducted a literature review in the main research databases, compiling data published until August 2021. We identified 66 articles with records of acanthocephalan-anuran association, 53.03% were carried out in Brazil. We detected 108 species of anurans from 11 families parasitized by acanthocephalans. With the exception of Bufonidae, Hylidae and Leptodactylidae, which are relatively well-studied families, interaction with acanthocephalans remains largely unexplored for most anuran species. We found six families of acanthocephalans: Centrorhynchidae, Echinorhynchidae, Oligacanthorhynchidae, Cavisomidae, Neoechinorhynchidae and Plagiorhynchidae. Centrorhynchidae and Echinorhynchidae presented the largest number of taxa associated with anurans. The largest number of records corresponded to acanthocephalans in the larval stage (cystacanths), for which anurans act as paratenic hosts. We observed a lack of specific taxonomic resolution in the identifications of most reports, because a large part of the records in the larval stage make morphological identification difficult. Brazil, Mexico, Paraguay, Argentina, Ecuador and Peru are the countries with the most records, while Costa Rica, Venezuela, Colombia, Chile and Uruguay exhibited the lowest publication numbers, resulting in gaps in the distribution of acanthocephalans. We expanded the known number of anuran species parasitized by acanthocephalans, compared to the last published review. Overall, we aim to contribute to the understanding of diversity within this intriguing but understudied group.

Introduction

Acanthocephala is a monophyletic group exclusively comprising parasitic organisms. Phylogenetically, this group shares a relationship with rotifers, characterized by the presence of a syncytial epidermis (Storch and Welsch 1969; García-Varela and Nadler 2006; Perrot-Minnot *et al.* 2023). The name Acanthocephala (acantho = spines, cephala = head) derives from the group's main morphological feature: a spiny proboscis at the anterior end of their body, through which they attach to host tissues. The life cycle of acanthocephalans typically involves two or more hosts, with arthropods commonly serving as the first intermediate host, where the first larval stages develop (Nuñez and Drago 2017). In the adult stage, these animals are obligatory intestinal parasites of vertebrates. The fertilized eggs, eliminated with feces, contains an acanthor larva that develops into the infective acantela form in the intermediate host. Inside the arthropod, the acantela changes into a cystacanth, capable of infecting the vertebrate definitive or a paratenic host (Schmidt 1985; Monks 2021). In this context, amphibians emerge as a significant vertebrate group for the study of acanthocephalans, given their trophic role as predators of various arthropod species and, simultaneously, as prey for different groups of vertebrates, characterizing them as crucial trophic links in ecosystems. Thus, anurans can serve as definitive or paratenic hosts for acanthocephalans, influencing the successful completion of these parasite's life cycle (Goater *et al.* 2014).

Studies describing acanthocephalan species parasitizing amphibians from the Neotropical region have a longstanding history, dating back to the early 19th century when the first species was described (Rudolphi 1819). The first reviews assessing the knowledge on the group occurred in the beginning of the 20th century, when the pioneering parasitologist Lauro Travassos reviewed species of acanthocephalan parasites of anurans, but only for Brazilian hosts (Travassos 1919, 1926). A few years later, Yamaguti (1963) presented a comprehensive worldwide review that greatly contributed to the knowledge of Neotropical acanthocephalan species. Salgado-Maldonado (1982) produced a list of acanthocephalans from Central America and neighboring regions. At the beginning of the 21st century, reviews of parasitic acanthocephalans of anurans were published for South America (Campião *et al.* 2014), Mexico (García-Prieto *et al.* 2014), Argentina (Hernández-Orts *et al.* 2019), Brazil (Aguiar *et al.* 2021), and Venezuela (Cañizales 2020).

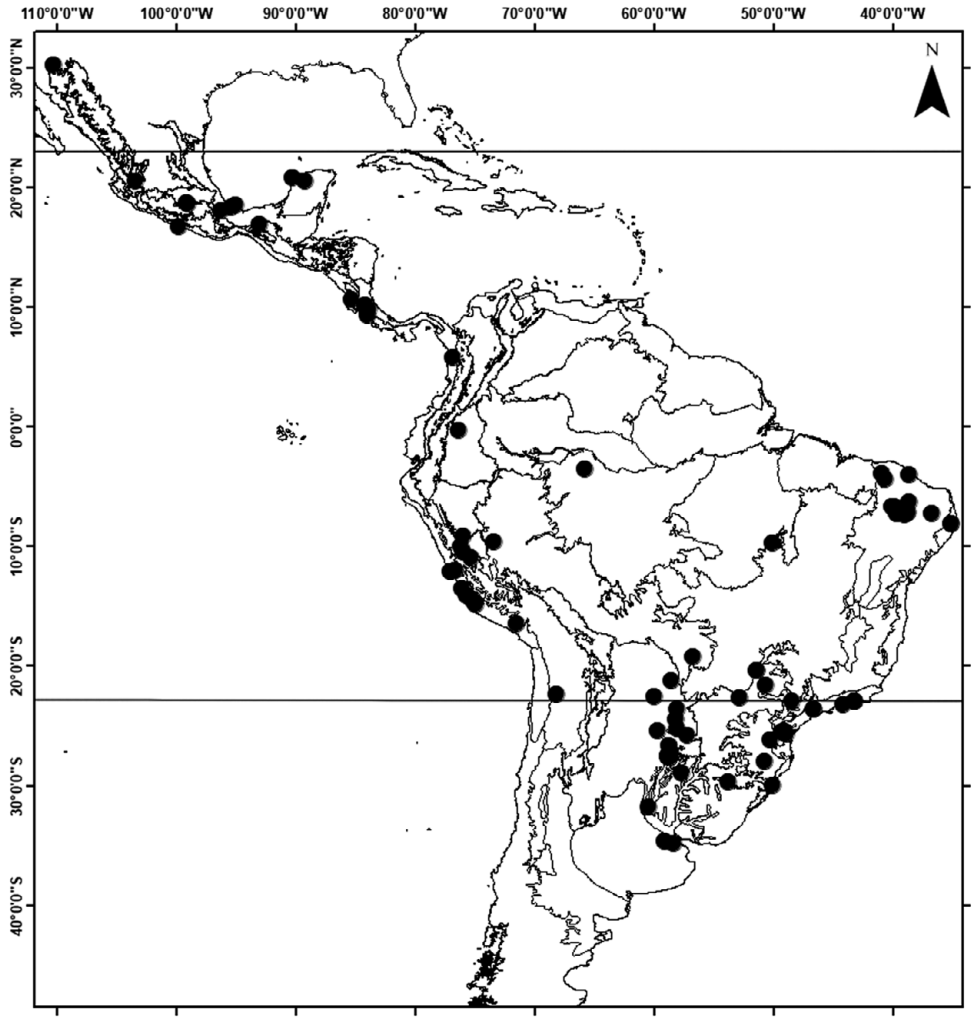

Figure 1. The reported associations of Acanthocephala parasites of anurans in countries within the Neotropical region. Each point is an association report; a general coordinate for the locality was included when not provided in published report.

These reviews hold substantial importance in advancing the taxonomic knowledge for the group. Nonetheless, such existing literature indicates the need for integrating and synthesizing all this information, since several species are distributed in various countries in the Neotropical region. Therefore, this study aims to (i) comprehensively synthetize the diversity of parasitic acanthocephalan species in Neotropical anurans, providing a consolidated compilation of the current knowledge; (ii) provide a list of parasitic acanthocephalans in anurans, including previously used synonyms, in order to promote a comprehensive and organized taxonomic spectrum; (iii) present an overview of research efforts in different locations, highlighting discrepancies and gaps in the understanding about the interactions between acanthocephalans and anurans throughout the Neotropical region; (iv) identify the anuran families that received most extensive research attention for their association with acanthocephalans, in order to uncover research trends and focal locations; (v) explore the role these anurans play in the acanthocephalan life cycle, providing a broad view of the interactions and ecological implications involved. By attaining these objectives, we aim to foster a more comprehensive and holistic understanding of the dynamics between acanthocephalans and anurans in the Neotropical region, thus contributing significantly to the advancement of knowledge in the fields of parasitology and ecology.

Material and methods

We conducted a literature review with searches in the following databases: Biological Abstracts; Helminthological Abstracts; Veterinary Records; PubMed; Scopus; Science Direct; Web of Science (ISI); Scielo; ResearchGate; BioOne; ISI; Jstor Academia; and Google Scholar, under the following selected keywords: 'Anura', 'Acanthocephala', 'Helminth', and 'Parasites'. Articles written in English, Spanish, and Portuguese, published up to August 2022, were considered in the selection. For each article, data were compiled about the geographical location of the association, parasite development stage, and parasite and host species and family. The original nomenclature for hosts has been updated according to the American Museum of Natural History (Frost 2023). Acanthocephala were classified based on Amin (1985, 2013) and Smales (2014).

Results

We identified a total of 66 publications, including reviews, that reported the association between amphibians and acanthocephalans across 11 countries in the Neotropical region (Figure 1). Brazil was the country with the greatest number of studies (53.03%), followed by Argentina (15.15%), Mexico (13.64%), Peru (9.09%),

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Table 1. Anuran hosts and their associated Acanthocephala parasites in the Neotropical region, with updated scientific names

Host family/species	Taxon	Country	Stage	Reference
Bufonidae				
Atelopus oxyrhynchus	*Acanthocephalus ula*	Venezuela	No reported	Cañizales 2020
Rhinella spinulosa	*Pseudoacanthocephalus lutzi*	Perú	No reported	Tantaleán *et al.* (2005)
Rhinella trifolium	*Pseudoacanthocephalus lutzi*	Perú	No reported	Tantaleán *et al.* (2005)
Rhinella limensis	*Pseudoacanthocephalus lutzi*	Perú	No reported	Amin and Heckmann (2014)
Rhinella arenarum	*Pseudoacanthocephalus* cf. *lutzi*	Argentina	No reported	Lajmanovich and Martínez de Ferrato (1995)
	Pseudoacanthocephalus lutzi	Argentina	Adult	Arredondo and Pertierra (2009)
	Pseudoacanthocephalus lutzi	Uruguay	No reported	Cordero (1933)
Rhinella beebei	*Oligacanthorhynchus* sp.	Venezuela	No reported	Cañizales 2020
Rhinella crucifer	*Centrorhynchus tumidulus*	Brazil	Cystacanth	Travassos (1926)
Rhinella diptycha	*Centrorhynchus* sp. *Oligacanthorhynchus* sp.	Brazil	Cystacanth	Oliveira *et al.* (2022)
Rhinella dorbignyi	*Centrorhynchus* sp.	Brazil	Cystacanth	Santos and Amato (2010)
	Pseudoacanthocephalus lutzi	Brazil	Adult	Santos and Amato (2010)
	Pseudoacanthocephalus cf. *lutzi*	Argentina	Adult	Draghi *et al.* (2020)
Rhinella granulosa	*Centrorhynchus* sp.	Paraguay	Cystacanth	Smales (2007b)
	Pseudoacanthocephalus caspanensis	Paraguay	Adult	Smales (2007b)
	Pseudoacanthocephalus lutzi	Paraguay	Adult	Smales (2007b)
Rhinella icterica	*Pseudoacanthocephalus lutzi*	Brazil	Adult	Smales (2007b)
	Pseudoacanthocephalus lutzi	Brazil	Adult	Pinhão *et al.* (2009)
	Pseudoacanthocephalus sp.	Brazil	Adult	Lux Hoppe *et al.* (2008)
Rhinella limensis	*Pseudoacanthocephalus lutzi*	Perú	No reported	Tantaleán *et al.* (2005)
Rhinella marina	*Centrorhynchus* sp.	Mexico	Cystacanth	Goldberg *et al.* (2002)
	Lueheia inscripta	Mexico	Adult	Salgado-Maldonado and Caspeta-Mandujano (2010)
	Oligacanthorhynchus sp.	Brazil	Cystacanth	Smales (2007b)
	Oncicola sp.	Mexico	Cystacanth	Espínola-Novelo and Guillén-Hernández (2008)
	Pseudoacanthocephalus correalimai	Brazil	Adult	Speare (1990)
	Pseudoacanthocephalus lutzi	Perú	No reported	Tantaleán *et al.* (2005)
	Pseudoacanthocephalus sp.	Venezuela	No reported	Cañizales 2020
	Pseudoacanthocephalus lutzi	Perú	Adult	Toledo *et al.* (2017)
Rhinella schneideri	*Pseudoacanthocephalus* sp.	Brazil	Adult	Lux Hoppe *et al.* (2008)
Rhinella spinulosa	*Pseudoacanthocephalus caspanensis*	Chile	No reported	Fernandez and Ibarra (1990)
	Pseudoacanthocephalus lutzi	Perú	Adult	Chero *et al.* (2016)
Rhinella trifolium	*Pseudoacanthocephalus lutzi*	Perú	No reported	Tantaleán 1976
Brachycephalidae				
Ischnocnema guentheri	*Pseudoacanthocephalus lutzi*	Brazil	Cystacanth and Adult	Sani *et al.* (2021)
Craugastoridae				
Craugastor melanostictus	*Pseudoacanthocephalus lutzi*	Costa Rica	Adult	Goldberg and Bursey (2008)
Craugastor rhodopis	*Centrorhynchus* sp.	Mexico	Cystacanth	Goldberg *et al.* (2002)
Haddadus binotatus	*Pseudoacanthocephalus lutzi*	Brazil	Cystacanth and Adult	Sani *et al.* (2021)
Dendrobatidae				
Oophaga histrionica	*Centrorhynchus* sp.	Colombia	Cystacanth	Goldberg and Bursey (2003)
	Oncicola sp.	Colombia	Cystacanth	Goldberg and Bursey (2003)

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Table 1. (*Continued*)

Host family/species	Taxon	Country	Stage	Reference
Hylodidae				
Hylodes lateristrigatus	*Pseudoacanthocephalus acutispinus*	Brazil	Adult	Bursey *et al.* (2006)
Hylodes fredi	*Anuracanthorhynchus tritaxisentis*	Brazil	Adult	Bursey *et al.* (2006)
Hylidae				
Boana albomarginata	*Centrorhynchus* sp.	Brazil	Cystacanth	Martins-Sobrinho *et al.* (2017)
Boana albopunctata	*Centrorhynchus* sp.	Brazil	Adult and Cystacanth	Graça *et al.* (2017)
Boana boans	*Oligacanthorhynchus* sp.	Ecuador	Cystacanth	Smales (2007a)
Boana fasciata	*Pandosentis napoensis*	Ecuador	Adult	Smales (2007a)
	Oligacanthorhynchus sp.	Ecuador	Adult	Smales (2007a)
Boana lanciformis	*Centrorhynchus tumidulus*	Brazil	No reported	Campião *et al.* 2014
	Oligacanthorhynchus sp.	Ecuador	Cystacanth	Smales (2007a)
Boana multifasciata	*Pseudoacanthocephalus lutzi*	Brazil	No reported	Machado *et al.* (2022)
Boana pulchella	*Pseudoacanthocephalus.* cf. *lutzi*	Brazil	Adult	Lajmanovich and Martínez de Ferrato (1995)
Boana pardalis	*Centrorhynchus tumidulus*	Brazil	No reported	Travassos (1926)
Boana raniceps	Centrorhynchidae gen. sp.	Brazil	Cystacanth	Oliveira *et al.* (2022)
	Pseudoacanthocephalus lutzi	Brazil	No reported	Machado *et al.* (2022)
Dendropsophus branneri	*Centrorhynchus* sp.	Brazil	Cystacanth	Martins-Sobrinho *et al.* (2017)
Dendropsophus decipiens	*Centrorhynchus* sp.	Brazil	Cystacanth	Martins-Sobrinho *et al.* (2017)
Dendropsophus elegans	*Centrorhynchus* sp.	Brazil	Cystacanth	Martins-Sobrinho *et al.* (2017)
Dendropsophus haddadi	*Centrorhynchus* sp.	Brazil	Cystacanth	Martins-Sobrinho *et al.* (2017)
Dendropsophus minusculus	*Centrorhynchus* sp.	Brazil	Cystacanth	Oliveira *et al.* (2022)
Dendropsophus minutus	Centrorhynchidae gen. sp.	Brazil	Cystacanth	Aguiar *et al.* (2021)
	Centrorhynchus sp.	Brazil	Cystacanth	Martins-Sobrinho *et al.* (2017)
	Centrorhynchus sp.	Brazil	Cystacanth	Oliveira *et al.* (2022)
Dendropsophus nanus	*Centrorhynchus* sp.	Paraguay	Cystacanth	Smales (2007b)
Dendropsophus sanborni	*Centrorhynchus* sp.	Paraguay	Cystacanth	Smales (2007b)
Dendropsophus triangulum	*Oligacanthorhynchus* sp.	Ecuador	Cystacanth	Smales (2007a)
Hypsiboas pulchellus	*Pseudoacanthocephalus* cf. *lutzi*	Argentina	Adult	Draghi *et al.* (2020)
Nyctimantis rugiceps	*Oligacanthorhynchus* sp.	Ecuador	Cystacanth	Smales (2007a)
Osteocephalus taurinus	*Oligacanthorhynchus* sp.	Ecuador	Cystacanth	Smales (2007a)
Phyllomedusa sp.	*Oligacanthorhynchus* sp.	Ecuador	Cystacanth	Smales (2007a)
Phyllomedusa tarsius	*Oligacanthorhynchus* sp.	Ecuador	Cystacanth	Smales (2007a)
Phyllomedusa sauvagii	*Centrorhynchus* sp.	Paraguay	Cystacanth	Smales (2007b)
Pithecopus gonzagai	*Centrorhynchus* sp.	Brazil	Cystacanth	Martins-Sobrinho *et al.* (2017)
Pithecopus nordestinus	*Centrorhynchus* sp.	Brazil	Cystacanth	Martins-Sobrinho *et al.* (2017)
	Centrorhynchus sp.	Brazil	Cystacanth	Sena *et al.* (2018)
Scinax acuminatus	*Pseudoacanthocephalus caspanensis*	Paraguay	Adult	Smales (2007b)
Scinax auratus	*Centrorhynchus* sp.	Brazil	Cystacanth	Martins-Sobrinho *et al.* (2017)
Scinax cf. *nasicus*	Centrorhynchidae gen. sp.	Brazil	Cystacanth	Aguiar *et al.* (2021)

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Table 1. (*Continued*)

Host family/species	Taxon	Country	Stage	Reference
Scinax cf. *similis*	Centrorhynchidae gen. sp.	Brazil	Cystacanth	Aguiar *et al*. (2021)
Scinax fuscomarginatus	Centrorhynchidae gen. sp.	Brazil	Cystacanth	Aguiar *et al*. (2021)
Scinax fuscovarius	Centrorhynchidae gen. sp.	Brazil	Cystacanth	Aguiar *et al*. (2021)
	Pseudoacanthocephalus sp.	Brazil	Adult	Santos *et al*. (2016)
Scinax nasicus	*Centrorhynchus* sp.	Brazil	Cystacanth	Azevedo-Ramos *et al*. (1998)
	Centrorhynchus sp.	Paraguay	No reported	Smales (2007b)
Scinax nebulosus	*Centrorhynchus* sp.	Brazil	Cystacanth	Azevedo-Ramos *et al*. (1998)
Scinax fuscomarginatus	*Centrorhynchus* sp.	Brazil	Cystacanth	Azevedo-Ramos *et al*. (1998)
Scinax x-signatus	*Centrorhynchus* sp.	Brazil	Cystacanth	Martins-Sobrinho *et al*. (2017); Oliveira *et al*. (2022)
	Oligacanthorhynchus sp.	Brazil	Cystacanth	Oliveira *et al*. (2022)
Smilisca cyanosticta	*Onicola luehi*	Mexico	Cystacanth	Goldberg *et al*. (2002)
Trachycephalus mesophaeus	*Centrorhynchus tumidulus*	Brazil	Cystacanth	Travassos (1926)
Trachycephalus typhonius	Centrorhynchidae gen. sp.	Brazil	Cystacanth	Aguiar *et al*. (2021)
Leptodactylidae				
Adenomera marmorata	*Centrorhynchus* sp.	Brazil	Cystacanth	Fabio (1982)
Atelopus bomolochus	*Centrorhynchus* sp.	Perú	Cystacanth	Iannacone (2003)
Adenomera diptyx	*Centrorhynchus* sp.	Argentina	Cystacanth	Zaracho and Lamas (2008); Zaracho *et al*. (2012)
Leptodactylus bufonius	*Pseudoacanthocephalus caspanensis*	Paraguay	Adult	Smales (2007b)
Leptodactylus elenae	*Centrorhynchus* sp.	Paraguay	Cystacanth	Smales (2007b)
Leptodactylus fragilis	*Lueheia inscripta*	Mexico	Adult	Salgado-Maldonado and Caspeta-Mandujano (2010)
Leptodactylus fuscus	*Centrorhynchus* sp.	Brazil	Cystacanth	Oliveira *et al*. (2022)
Leptodactylus chaquensis	*Centrorhynchus* sp.	Brazil	No reported	Sani *et al*. (2021)
	Centrorhynchus sp.	Argentina	Cystacanth	Schaefer *et al*. (2006)
Leptodactylus latinasus	*Centrorhynchus* sp.	Argentina	Cystacanth	Hamann *et al*. (2006)
Leptodactylus latrans	*Centrorhynchus giganteus*	Brazil	Cystacanth	Travassos (1919) and Travassos (1926)
	Centrorhynchus tumidulus	Brazil	Cystacanth	Travassos (1919) and Travassos (1926)
	Centrorhynchus sp.	Brazil	Cystacanth	Fabio (1982)
	Centrorhynchus sp.	Brazil	Cystacanth	Fabio (1982)
	Pseudoacanthocephalus cf. *lutzi*	Argentina	No reported	Draghi *et al*. (2020)
Leptodactylus leptodactyloides	Centrorhynchidae gen. sp.	Brazil	Cystacanth	Goldberg *et al*. (2009)
Leptodactylus macrosternum	*Centrorhynchus* sp.	Paraguay	No reported	Smales (2007b)
	Centrorhynchus sp.	Brazil	Cystacanth	Oliveira *et al*. (2022)
Leptodactylus vastus	*Centrorhynchus* sp.	Brazil	Cystacanth	Oliveira *et al*. (2022)
	Oligacanthorhynchus sp.	Brazil	Cystacanth	Oliveira *et al*. (2022)
Leptodactylus mystaceus	*Centrorhynchus* sp.	Brazil	Cystacanth	Fabio (1982)
Leptodactylus mystacinus	*Centrorhynchus* sp.	Brazil	Cystacanth	Fabio (1982)
	Centrorhynchidae gen. sp.	Brazil	Cystacanth	Queiroz *et al*. (2020)
Leptodactylus latrans	Centrorhynchidae gen. sp.	Brazil	Cystacanth	Goldberg *et al*. (2009)

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Table 1. (*Continued*)

Host family/species	Taxon	Country	Stage	Reference
Leptodactylus pentadactylus	*Oligacanthorhynchus* sp.	Ecuador	Cystacanth	Smales (2007a)
	Pseudoacanthocephalus sp.	Ecuador	Cystacanth	Smales (2007a)
Leptodactylus pustulatus	*Centrorhynchus* sp.	Brazil	Cystacanth	Oliveira *et al.* (2022)
Leptodactylus podicipinus	*Centrorhynchus* sp.	Paraguay	Cystacanth	Smales (2007b)
Leptodactylus melanonotus	*Centrorhynchus* sp.	Mexico	Cystacanth	Goldberg *et al.* (2002)
Physalaemus albonotatus	Centrorhynchidae gen. sp.	Brazil	Cystacanth	Aguiar *et al.* (2021)
Physalaemus biligonigerus	*Pseudoacanthocephalus lutzi*	Argentina	Adult	Gutiérrez *et al.* (2005)
Physalaemus centralis	Centrorhynchidae gen. sp.	Brazil	Cystacanth	Aguiar *et al.* (2021)
Pseudopaludicola boliviana	*Centrorhynchus* sp.	Argentina	Cystacanth	Duré *et al.* (2004)
Physalaemus cuvieri	*Centrorhynchus* sp.	Paraguay	Cystacanth	Smales (2007b)
	Centrorhynchus sp.	Brazil	Cystacanth	Oliveira *et al.* (2022)
	Pseudoacanthocephalus lutzi	Brazil	Cystacanth and Adult	Aguiar *et al.* (2015)
	Pseudoacanthocephalus lutzi	Brazil	Adult and Cystacanth	Leivas *et al.* (2018)
	Pseudoacanthocephalus lutzi	Brazil	Adult	Toledo *et al.* (2013)
Physalaemus nattereri	*Centrorhynchus* sp.	Paraguay	Cystacanth	Smales (2007b)
Physalaemus signifer	*Centrorhynchus* sp.	Brazil	Cystacanth	Fabio (1982)
Physalaemus soaresi	*Centrorhynchus* sp.	Brazil	Cystacanth	Fabio (1982)
Physalaemus olfersii	Centrorhynchidae gen. sp.	Brazil	Cystacanth	Toledo *et al.* (2013)
Pleurodema diplolister	*Oligacanthorhynchus* sp.	Brazil	No reported	Silva-Neta *et al.* (2020)
Microhylidae				
Elachistocleis bicolor	Centrorhynchidae gen. sp.	Brazil	Cystacanth	Aguiar *et al.* (2021)
Odontophrynidae				
Odontophrynus americanus	*Oligacanthorhynchus* sp.	Paraguay	Cystacanth	Smales (2007b)
Proceratophrys renalis	*Centrorhynchus* sp.	Brazil	Cystacanth	Oliveira *et al.* (2022)
Ranidae				
Lithobates brownorum	*Oncicola* sp.	Mexico	Cystacanth	Yáñez-Arenas and Guillén-Hernández (2010)
Lithobates cf. *forreri*	*Oncicola* sp.	Mexico	No reported	Velázquez-Urrieta and León-Règagnon (2018)
Lithobates psilonota	*Oncicola* sp.	Mexico	Cystacanth	Romero-Mayén *et al.* (2016)
Lithobates sp. *colima*	*Neoechinorhynchus golvani*	Mexico	Adult	Cabrera-Guzmán *et al.* (2007)
	Oncicola sp.	Mexico	Adult	Cabrera-Guzmán *et al.* (2007)
Lithobates vaillanti	*Centrorhynchus* sp.	Mexico	Cystacanth	Paredes-Calderón *et al.* (2004)
	Centrorhynchus sp.	Mexico	Cystacanth	Goldberg *et al.* (2002)
	Oncicola sp.	Mexico	Cystacanth	Paredes-Calderón *et al.* (2004)
	Plagiorhynchus sp.	Mexico	Cystacanth	Paredes-Calderón *et al.* (2004)
Lithobates warszewitschii	*Pseudoacanthocephalus lutzi*	Costa Rica	No reported	Bursey and Goldberg (2007)

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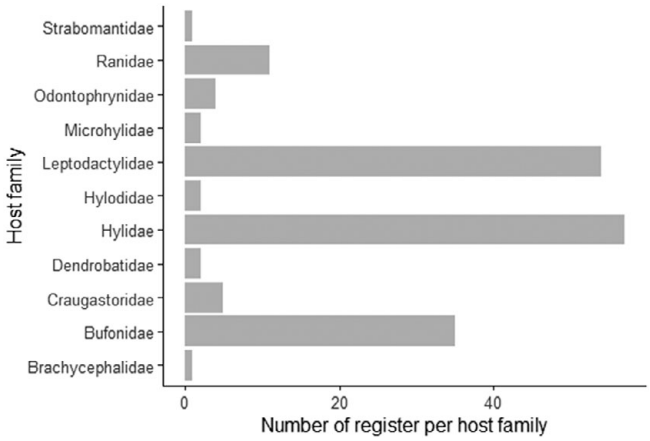

Figure 2. Records of acanthocephalan association in different families of anurans in Neotropical region. Each bar was constructed based on the number of associations, representing the number of anuran hosts and study effort for each anuran family.

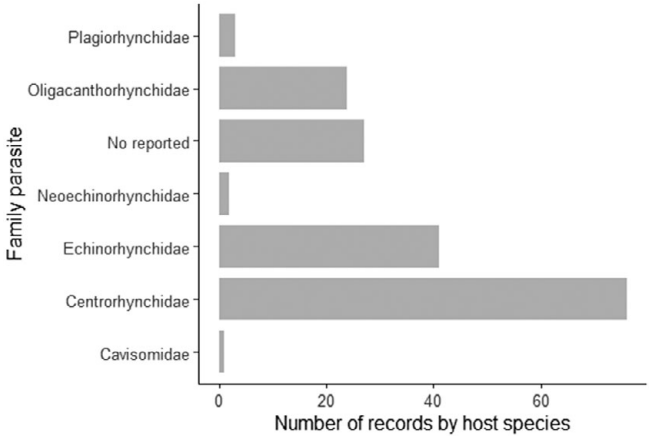

Figure 3. Number of records of Acanthocephala families reported as parasites of anurans in the Neotropical region.

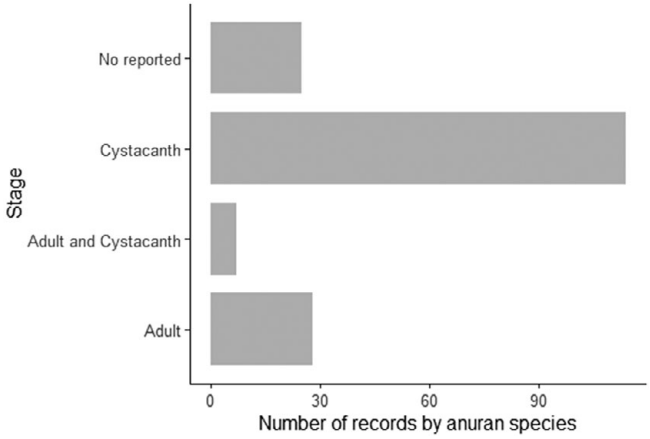

Figure 4. Number of records of development stages of Acanthocephala parasites of Neotropical anurans.

and Costa Rica (3.03%). Colombia, Venezuela, Paraguay, Chile, Uruguay, and Ecuador exhibited the lowest research representation each (1.52%). Brazil also had the greatest number of studied hosts (66 species), representing 61.11% of the studied species, while 13 studied anurans were from Paraguay, 11 from México, 10 from Argentina, 9 from Ecuador, 5 from Peru, 4 from Costa Rica, 3 from Venezuela, 1 from Uruguay, 1 from Chile, and 1 from Colombia; it is important to consider that some anuran species occur in more than one country (Table 1). Altogether, 108 anuran species distributed across 11 families have records of infection by acanthocephalans (Figure 2). Hylidae (37.96%), Leptodactylidae (28.7%), and Bufonidae (12.96%) are the families with the highest number of studied species, and Hylidae is the one with great study effort.

Nineteen acanthocephalan taxa were recorded, 12 of which were identified to the species level, representing 63.16% of the reports. Six families of acanthocephalans were detected in this review: Centrorhynchidae, Echinorhynchidae, Oligacanthorhynchidae, Cavisomidae, Neoechinorhynchidae, and Plagiorhynchidae. Centrorhynchidae and Echinorhynchidae presented the largest number of taxa associated with anurans (Figure 3). A total of 65.52% of acanthocephalans were found in the larval stage (cystacanths) and 16.09% in the adult stage. Cystacanths and adult together were also recorded in 4.02% of total records (Figure 4), and 14.37% of the records do not indicate the parasites stage of development (Table 2). The results indicate that anurans most frequently serve as paratenic hosts in the acanthocephalan life cycle. Hylidae, Leptodactylidae, and Bufonidae were the anuran families with the highest number of records as definitive hosts for acanthocephalans.

Discussion

This is the first effort to compile all records for 11 countries of the Neotropical region regarding the associations between acanthocephalans and anurans. The largest proportion of the analyzed reports (65.52%) corresponds to records on the parasite's larval stage. This indicates that anurans act as paratenic hosts in the life cycle of most acanthocephalan species. This result relates to the low number of records with specific identification – a recurring pattern observed. This is due to the impracticality of achieving specific identification based on morphological characters in larvae (i.e., cystacanths). Thus, non-specific reports were very common. This aspect, coupled with the scarcity of specialists in the field (Perrot-Minnot *et al.* 2023) and the inherent complexity of parasite identification (Selbach *et al.* 2019; Zhao *et al.* 2023), contributes to a taxonomic gap for acanthocephalans.

Several recognized biogeographic regions make up the Neotropic, with diverse ecosystems, climates, and habitats found in Central and South America, as well as the Caribbean. The number and classification of these regions can vary between biologists and ecologists, but some of the main biogeographic regions within the Neotropic include Amazonia, Andean Region, Mesoamerica, Chaco, Atlantic Forest, Caribbean, and Gran Chaco (Morrone 2014; Morrone *et al.* 2022). In the Caribbean region, Mexico is the country with more records (9.77%), followed by Costa Rica (2.87%). For the subregion of the Antilles or Caribbean Antilles – made up of Cuba, Bahamas, Cayman Islands, Jamaica, Puerto Rico, and other islands – we found no records. Another area that harbors an important fraction of the world's biodiversity is the Amazon rainforest, which is one of the regions with the greatest biodiversity on earth and covers several countries in South America – mainly Brazil (first place in records and number of species), but also extends to Peru, Colombia, Venezuela, Ecuador, and smaller parts of other countries. The number of reports in the Amazon region is alarming in terms of comparison of species richness. For example, Venezuela,

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Table 2. Anuran species reported as hosts of unidentified Acanthocephalan in the Neotropical region

Anuran family and species	Reference	Stage	Country
Bufonidae			
Incilius marmoreus	Trejo-Meléndez *et al.* (2019)	No reported	Mexico
Rhinella granulosa	Madelaire *et al.* (2020)	Cystacanth	Brazil
Craugastoridae			
Craugastor melanostictus	Goldberg and Bursey (2008)	Cystacanth	Costa Rica
Eleutherodactylus caryophyllaceus	Goldberg and Bursey (2008)	Cystacanth	Costa Rica
Hylidae			
Boana raniceps	Aguiar *et al.* (2021); Campião *et al.* (2016)	Cystacanth	Brazil
Dendropsophus microcephalus	Azevedo-Ramos *et al.* (1998)	Cystacanth	Brazil
Dendropsophus nanus	Hamann and Kehr (1998)	Adult and Cystacanth	Argentina
	Parra *et al.* (2019)	No reported	Brazil
Phyllomedusa azurea	Campião *et al.* (2016)	Cystacanth	Brazil
Pseudis paradoxa	Campião *et al.* (2016)	Cystacanth	Brazil
Trachycephalus typhonius	Campião *et al.* (2016)	Cystacanth	Brazil
Leptodactylidae			
Leptodactylus fuscus	Campião *et al.* (2016)	Cystacanth	Brazil
	Lins *et al.* (2017)	Cystacanth	Brazil
Leptodactylus latrans	Stumpf (1982)	Adult and Cystacanth	Brazil
	Aguiar *et al.* (2021)	Cystacanth	Brazil
	Campião *et al.* (2016)	Cystacanth	Brazil
Leptodactylus podicipinus	Aguiar *et al.* (2021)	Cystacanth	Brazil
	Campião *et al.* (2016)	Cystacanth	Brazil
	Queiroz *et al.* (2020)	Cystacanth	Brazil
Leptodactylus syphax	Lins *et al.* (2017)	Cystacanth	Brazil
Pseudopaludicola pocoto	Silva *et al.* (2018)	Cystacanth	Brazil
Microhylidae			
Dermatonotus muelleri	Alcantara *et al.* (2018)	Cystacanth	Brazil
Odontophrynidae			
Proceratophrys aridus	Silva *et al.* (2019)	Cystacanth	Brazil
Proceratophrys cristiceps	Silva *et al.* (2019)	Cystacanth	Brazil
Ranidae			
Lithobates tarahumarae	Bursey and Goldberg (2001)	Cystacanth	Mexico
Strabomantidae			
Pristimantis cruentus	Goldberg and Bursey (2008)	Cystacanth	Costa Rica

with 1.72% of the records and 2.78% of the species (3 spp.) compared to Colombia. With 816 spp. anurans currently described (Batrachia 2023), only one (*Oophaga histrionica*) has records of parasitism by acanthocephalans, and for at least two decades no research has been carried out on the acanthocephalan associated with anuran species from Colombia. The highest concentration of data is found in South America, with 56.32% of the records for Brazil – records that are concentrated in the Atlantic Forest region and with a small percentage of the data in the northeastern area. The second southern country in South America with the highest registration is Paraguay, with 8.62%, followed by Argentina, with 6.9% of the reports, which make up what is known as El Chaco and an extensive plain mosaic of different habitats, including dry forests and savannas. Altogether, these data show that the diversity of Acanthocephala in the Neotropical region may be linked to the diversity of available hosts, and more importantly, it reflects the intensity of research efforts, as areas with the highest number of reports are those known to house institutions that traditionally have parasitologists.

Three families of acanthocephalans had greater representation among amphibians: Centrorhynchidae, Echinorhynchidae, and Oligacanthorhynchidae. Of these, Centrorhynchidae are the most reported, with *Centrorhynchus* sp. being the most recorded taxon.

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Given that these parasites primarily use birds and mammals as their definitive hosts, this finding suggests that anurans are frequently preyed upon by these vertebrates (Santos and Amato 2010). Although reports of infections by *Centrorhynchus* have been suggested as accidental cases in amphibians (McAlpine 1996), these parasites may use a wide range of species as probable paratenic hosts, thereby increasing the chances of completing their life cycle (Malcicka *et al.* 2015). However, members of the Echinorhynchidae family use anurans as their definitive hosts. *Pseudoacanthocephalus lutzi* Syns.: *Echinorhynchus lutzi* Hamann, 1891; *Acanthocephalus saopaulensis* Smales, 2007b, which was also one of the taxa with the highest number of records in this review, can be mentioned as an example. This species has been reported as a parasite of amphibians in Argentina (Lajmanovich and Martinez de Ferrato 1995; Gutiérrez *et al.* 2005; Arredondo and Gil de Pertierra 2009), Uruguay (Cordero 1933), Peru (Tantaleán 1976; Tantaleán *et al.* 2005), Paraguay, and Brazil (Smales 2007b).

Hylidae, Leptodactylidae, and Bufonidae were the anuran families with the highest number of species associated with acanthocephalans, a similar pattern found for other helminths, making them the only three host families for all the main groups of parasitic helminths, including acanthocephalans (Campião *et al.* 2014; Cañizales 2020). These three anuran families encompass a remarkable diversity of species, varying greatly in size and life histories, and they are extensively distributed across South America (de Sá 2014). Size in particular is an important characteristic for helminth infection, as larger species live longer and thus have longer exposure to a variety of parasites (Campião *et al.* 2015; Gutiérrez *et al.* 2019). The great diversity within these families is another reason why they present the highest number of records and species parasitized by acanthocephalans in this review, a pattern observed in other helminth groups as well (Campião *et al.* 2014).

In contrast to findings in many studies that typically identify nematodes and other metazoans as the most prevalent parasites, certain hosts have already presented acanthocephalans as the most prevalent and abundant parasites (Martins-Sobrinho *et al.* 2017; Toledo *et al.* 2017; Leivas *et al.* 2018). The factors influencing acanthocephalan diversity, prevalence, and abundance remain not fully understood. However, it is well established that the host diet plays a significant role in the transmission and life cycle of acanthocephalans. In fact, the evolutionary history of acanthocephalans is mainly linked to the two most species-rich groups: the aquatic crustaceans and the fundamentally terrestrial insects (Amin 1985). Isopods have already been recorded as intermediate hosts of acanthocephalans (Amato *et al.* 2003) and have been considered significant constituents of several anuran diets (García-Padrón and Borrego Quevedo 2020). In this regard, the trophic niche can be an explanation on how frogs become infected with these helminths. One of the species with the highest number of records as host of acanthocephalans was *Rhinella marina*, which was reported with high prevalence (97%) (Toledo *et al.* 2017). *Rhinella marina* is distributed from Texas through Mexico and Central America and extends all the way to Brazil (Campbell 1998; Lee 1996; Espínola-Novelo *et al.* 2017). It has become an invasive species in several countries around the world, including islands, with reported occurrences in Australia, the southern United States, Hawaii, Fiji, the Philippines, Taiwan, and Europe. Drake *et al.* (2014) found a high prevalence of infection in 95% of *Rhinella marina* individuals collected on the Island of Granada. Similarly, Pinhão *et al.* (2009) noted a parasite prevalence of 100% and high abundance of acanthocephalans in a population of *Rhinella icterica* in Brazil. In addition to their large size (Solís *et al.* 2009; Frost 2023), both species have opportunistic feeding habits, have extensive foraging strategies (Strüssmann *et al.* 1984), and occupy terrestrial and aquatic habitats that increase the chances of parasite infections (Aho 1990). Even if body size is related to eating habits – since large species can feed on a greater variety of prey – generalist eating habits could contribute to the high prevalence of acanthocephalan infection even on smaller species (Leivas *et al.* 2018; Martins-Sobrinho *et al.* 2017).

The relatively low richness of acanthocephalans parasitizing anurans observed in this review corroborates the pattern reported by other authors (Barton et al. 1994; Campião *et al.* 2014; Goater *et al.* 2014) and can be explained by the low number of known species, approximately 1500 distributed around the world (Amin 1987; Poulin and Morand 2004; Kennedy 2006; Amin 2013; Monks 2021). Nevertheless, a crucial factor contributing to the observed low diversity of acanthocephalans is the limited number of studies conducted on this subject. Despite the obvious importance of understanding the associations between parasites and anurans, particularly in the Neotropical region — where the highest richness of these hosts is found — the main challenge lies in the scarcity of studies and in the limited fraction of hosts investigated. Therefore, we emphasize the importance of comprehensive parasite inventories. Moreover, the inclusion of molecular tools for identifying acanthocephalan species, already highlighted in other studies (Selbach *et al.* 2019; Zhao *et al.* 2023), can help fill one of the main gaps highlighted in this study, which is the lack of species level identification. At the same time, the inclusion of ecological information about hosts, such as diet and habitat, can contribute to a better understanding of the life strategies of acanthocephalans. Furthermore, studying the life cycle of acanthocephalans offers a very interesting and little-explored research theme for the Neotropical region. Such studies provide complementary information to taxonomy (and vice versa) (Blasco-Costa and Poulin 2017) and can also facilitate research into ecology and evolution. In this context, we expect that this scientific field will flourish in the Neotropical region, renowned for its exceptional biodiversity (IUCN 2020; Frost 2023).

Overall, our results highlight many information gaps if we take into account the exuberant and growing diversity of amphibians in the Neotropical region. The ongoing deforestation of ecosystems, the impacts of climate change, the rapid escalation of habitat destruction, alterations to ecosystems, and droughts are factors that have repercussions on the diversity, abundance, and survival of anurans and other vertebrates. The loss of species and populations also leads to the loss of their parasites, including parasites that have not yet been described (Greene and Lossos 1988; Dobson *et al.* 2008; Muniz-Pereira *et al.* 2009), depriving the access to crucial taxonomic and ecological information (Poulin and Morand 2004). Thus, parasitological inventories are essential as they provide the basis for investigations into evolutionary biology, systematics, taxonomy, conservation, and ecology of hosts and parasites. Throughout this article, we have broadened the understanding of the number of anuran species parasitized by acanthocephalans in comparison to the last existing review, with the intention of enhancing the available knowledge on the diversity within this captivating yet underexplored group of organisms.

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