



# Diversity of helminth parasites in amphibians from northeastern Brazil

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## Abstract

Historically, amphibian parasites have been poorly represented in ecological studies, hence, we know little about their diversity, distribution, and role in biological communities. The helminth fauna of four amphibian species (*Dermatonotus muelleri*, *Leptodactylus vastus*, *Rhinella diptycha*, and *Trachycephalus typhonius*) from three locations in the state of Piauí, northeastern Brazil was studied. In total, we found 2,024 parasite specimens of 13 helminth taxa (*Aplectana crucifer*, *Aplectana vellardi*, *Cosmocerca podicipinus*, *Cosmocercidae* gen. sp., nematode cysts, nematode larvae, *Ochoterenella digiticauda*, *Ochoterenella* sp., *Oswaldocruzia lopesi*, *Oswaldocruzia* sp., *Oxyascaris oxyascaris*, *Raillietnema spectans*, and *Rauschiella linguatula*), and ten new occurrences of parasitic helminths were recorded. The most abundant parasite species were *R. spectans* ( $n = 1,018$ ) and *A. vellardi* ( $n = 574$ ). All hosts presented high infection levels. The prevalence of infection of hosts ranged from 64.7 to 100%, the mean intensity of infection ranged from 6.1 to 69.3, and the mean abundance ranged from 5.5 to 69.3. The number of parasites per host ranged from 122 to 1,468. *Dermatonotus muelleri* was the host with the highest prevalence of infection ( $n = 93.9\%$ ) and *L. vastus* presented the highest richness ( $n = 10$  spp.). We also present an update of all helminth species associated with *D. muelleri*, *L. vastus*, *R. diptycha*, and *T. typhonius* in South America. This is the first study on the diversity of parasitic helminths associated with amphibians in the state of Piauí, northeastern Brazil.

**Keywords** Parasitism · Anurans · Richness · State of Piauí · Neotropical region

## Introduction

Although parasites represent an important component of nature parasitizing several groups of animals, including threatened vertebrates, e.g. Pisces, Amphibia, Reptilia, Aves, and Mammalia (Muniz-Pereira et al. 2009), the parasites have historically been underrepresented in ecological studies (Bower et al. 2019). The frequent description of new species (Araujo-Filho et al. 2015; Larrat et al. 2018; Felix-Nascimento et al. 2020; Matias et al. 2020; Morais et al. 2020), records of new hosts (Müller et al. 2018; Oliveira et al. 2019; Araujo-Filho et al. 2020; Silva-Neta et al. 2020) and the high prevalence of helminth infection in certain animal populations (Anjos et al. 2013; Lins et al. 2017; Amorim et al. 2019a; Souza et al. 2019; Dib et al. 2020; Madelaire et al. 2020) reinforce the need for greater effort in studies including parasites and it is essential to understand the diversity and distribution of these parasites in megadiverse regions such as the Neotropical region.

In Brazil, about 1,188 amphibian species are registered (Segalla et al. 2021). In the northeast region, about 226 species of amphibians are recorded (Freitas 2015) and at

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least 20 species are endemic (Garda et al. 2017). Despite this high species richness and the growing number of studies on amphibian helminth fauna in this region (Lins et al. 2017; Alcántara et al. 2018; Silva et al. 2018, 2019; Oliveira et al. 2019; Silva-Neta et al. 2020), there are still extensive knowledge gaps concerning their associated helminth fauna, including gaps for entire regions. For example, there are few studies on the diversity of parasites associated with amphibians in the state of Piauí. So far, only three helminth taxa (acanthocephalan cysthacanth, *Rhabdias breviensis* Nascimento et al., 2013, and *Rhabdias pseudosphaerocephala* Kuzmin et al., 2007) are reported parasitizing four species of amphibians: *Rhinella diptycha* (Cope, 1862), *Rhinella granulosa* (Spix, 1824), *Leptodactylus macrosternum* Miranda-Ribeiro, 1926, and *Proceratophrys cristiceps* (Müller, 1883) in the state of Piauí (Müller et al. 2018; Silva et al. 2019; Vieira et al. 2021) and only three other studies regarding helminths parasitizing reptile species in the state were published (Ávila and Silva 2010; Ávila et al. 2012; Matias et al. 2018).

Therefore, the present study was undertaken to study the diversity of parasitic helminths in amphibians in the state of Piauí, northeastern Brazil. We also present an update of all helminth species in South America associated with the four host species here studied. This is the first study on the diversity of parasitic helminths associated with amphibians in the state of Piauí, northeastern Brazil.

## Materials and methods

The hosts were examined from three locations in the state of Piauí: (i) Sete Cidades National Park (4°05'32" S, 41°40'48" W), municipalities of Brasileira and Piracuruca; (ii) Nazareth Eco Resort (4°48'1" S, 42°36'43" W), municipality of José de Freitas; and (iii) the campus of the Universidade Federal do Piauí (7°4'56.03" S, 41°26'11.25" W), municipality of Picos, northeastern Brazil. The hosts are deposited in the Scientific Collection of Herpetology of the Universidade Federal do Piauí, Picos campus.

For parasitological examination, the hosts were necropsied and the mouth, esophagus, stomach, small and large

intestines, lungs, heart, liver, gallbladder, kidneys, bladder, and celomic cavity were examined under a stereomicroscope. The helminths found were prepared on temporary slides, following the classic methodology for each taxonomic group. The nematodes were cleared with lactic acid (Andrade 2000) and for the species identification, the morphology and morphometry of the following characters were analyzed: body length and width, esophagus, tail length, the arrangement of the male caudal papillae, gubernaculum, the distance of vulva to anterior end, and egg size). For digeneans, the specimens were stained using the hydrochloric carmine technique (Amato et al. 1991) and for species identification, the body length and width, length and width of oral and ventral suckers, esophagus, pharynx, intestinal caeca, ovary, testes, and eggs were analyzed. All morphological analyses were performed in a digital image analysis system (Leica Application Suite, V3.8, Leica Microsystems, Wetzlar, Germany) coupled to a DM 5000B microscope with differential interference contrast (Leica Microsystems, Wetzlar, Germany). Helminths were identified based on Yamaguti (1961), Vicente et al. (1991), Anderson (2000), Gibbons (2010), and Fernandes and Kohn (2014). Then, the helminths were deposited in the Helminthological Collection of the Institute of Biosciences (CHIBB), Universidade Estadual Paulista, municipality of Botucatu, São Paulo state, Brazil. We analyzed the richness, prevalence, abundance, and mean intensity of infection according to Bush et al. (1997). We used descriptive analysis to correlate the parasite richness and abundance with the number of hosts examined. The effects of abundance and sampling effort (or more precisely, the number of hosts examined) were selected as good determinants of helminth diversity (e.g. Walther et al. 1995; Poulin et al. 2003; Campião et al. 2015a). Moreover, we present an update of all helminth species associated with *Dermatonotus muelleri* (Boettger, 1885), *Leptodactylus vastus* Lutz, 1930, *Rhinella diptycha* (Cope, 1862), and *Trachycephalus typhonius* (Linnaeus, 1758) in South America. For this, we analyzed all studies from the literature, and the references cited in these same articles, through the search on the topic in the main databases (e.g. Google Scholar, Scielo, Scopus, and Web of Science).

**Table 1** Parameters of infection of the amphibian species analyzed from northeastern Brazil

Hosts	NEH	NPH	NP	HR	P	MI ± SD	MA ± SD
<i>Dermatonotus muelleri</i>	33	31	1,468	6	93.9	47.3 ± 0.2	44.4 ± 0.2
<i>Leptodactylus vastus</i>	17	11	226	10	64.7	20.5 ± 0.4	13.2 ± 0.2
<i>Rhinella diptycha</i>	22	20	122	7	90.9	6.1 ± 0.1	5.5 ± 0.1
<i>Trachycephalus typhonius</i>	3	3	208	2	100	69.3 ± 2.7	69.3 ± 2.7
<b>Total / Mean</b>	<b>75</b>	<b>65</b>	<b>2,024</b>	<b>13</b>	<b>86.7</b>	<b>33.9</b>	<b>29.3</b>

NEH – Number of examined hosts; NPH – Number of parasitized hosts; NP – Number of parasites recovered; HR – Helminth richness (number of parasites taxa); P (%) – Prevalence; MI ± SD – Mean intensity of infection ± standard deviation; MA ± SD – Mean abundance ± standard deviation

The research related to animals complied with all the relevant national regulations and institutional policies for the care and use of animals. The samples were collected with the following licenses: Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio (SISBIO, #22,508).

## Results

We examined 75 specimens of four amphibian species, 33 *D. muelleri*, 17 *L. vastus*, 22 *R. diptycha*, and three *T. typhonius*. The overall prevalence of infection with helminths observed in the 75 host specimens examined was 86.7%, i.e. 65 anurans were infected with at least one helminth taxon. All parasitized hosts presented high values for the analyzed parameters of infection. In total, we found 2,024 helminth parasite specimens. The prevalence of infection in hosts ranged from 64.7 to 100%; the mean intensity of infection ranged from 6.1 to 69.3; the mean abundance ranged from 5.5 to 69.3. The number of parasites per host ranged from 122 to 1,468 (Table 1).

We found 13 taxa of parasitic helminths: the nematodes *Aplectana crucifer* Travassos, 1925, *Aplectana*

*vellardi* Travassos, 1926, *Cosmocerca podicipinus* Baker and Vaucher, 1984, *Cosmocercidae* gen. sp., nematode cysts, nematode larvae, *Ochoterenella digiticauda* Caballero, 1944, *Ochoterenella* sp., *Oswaldocruzia lopesi* Freitas and Lent, 1938, *Oswaldocruzia* sp., *Oxyascaris oxyascaris* Travassos, 1920, *Raillietnema spectans* Gomes, 1964, and the digenean *Rauschiella linguatula* (Rudolphi, 1819). The most abundant parasite species were *Raillietnema spectans* ( $n=961$ ) and *Aplectana vellardi* ( $n=364$ ). Helminth parasites were found at eight infection sites and the small and large intestines were the most parasitized (Table 2).

In our compilation, we recorded 18 taxa of helminths associated with *D. muelleri*. *Aplectana crucifer* and *A. vellardi* represent new records of parasites associated with *D. muelleri*. For *Leptodactylus vastus*, 23 species of associated helminths were recorded and five taxa (*C. podicipinus*, *O. digiticauda*, *O. lopesi*, *O. oxyascaris*, and *R. linguatula*) represent new records of parasites. For *Rhinella diptycha*, we recorded 24 species of associated helminths and *A. vellardi* and *R. linguatula* represent new records of parasites associated with this bufonid. Finally, for *T. typhonius*, we recorded 23 species of associated helminths and *A. vellardi* is a new parasite record for *T. typhonius*. Overall, we found

**Table 2** Hosts examined and their associated parasites in northeastern Brazil

Hosts	Helminths	NP	NPH	P	MI ± SD	MA ± SD	IS
<i>Dermatonotus muelleri</i>	<i>Aplectana crucifer</i> *	25	1	3.0	25.0 ± 0.0	0.7 ± 4.2	LI
	<i>Aplectana vellardi</i> *	364	9	27.2	40.4 ± 0.7	11.0 ± 62.3	SI/LI
	<i>Cosmocercidae</i>	67	6	18.1	11.1 ± 0.5	2.0 ± 11.4	S/SI/LI
	<i>Cosmocerca podicipinus</i>	40	4	12.1	10.0 ± 0.7	1.2 ± 6.8	SI/LI
	Nematode larvae	11	6	18.1	1.8 ± 0.2	0.3 ± 1.8	S/L
<i>Leptodactylus vastus</i>	<i>Raillietnema spectans</i>	961	5	15.1	192.2 ± 2.7	29.1 ± 164.7	SI/LI
	<i>Cosmocerca podicipinus</i> *	50	1	5.8	50.0 ± 0.0	2.9 ± 11.7	LI
	Nematode cyst	7	1	5.8	7.0 ± 0.0	0.4 ± 1.6	VM
	Nematode larvae	5	2	11.7	2.5 ± 0.7	0.2 ± 1.1	S/GC
	<i>Ochoterenella digiticauda</i> *	11	1	5.8	11.0 ± 0.0	0.6 ± 2.5	GC
	<i>Ochoterenella</i> sp.	1	1	5.8	1.0 ± 0.0	0.05 ± 0.2	GC
	<i>Oswaldocruzia lopesi</i> *	1	1	5.8	1.0 ± 0.0	0.05 ± 0.2	S
	<i>Oswaldocruzia</i> sp.	1	1	5.8	1.0 ± 0.0	0.05 ± 0.2	S
	<i>Oxyascaris oxyascaris</i> *	11	1	5.8	11 ± 0.0	0.6 ± 2.5	SI
	<i>Raillietnema spectans</i>	57	1	5.8	57.0 ± 0.0	3.3 ± 13.4	LI
<i>Rauschiella linguatula</i> *	82	1	5.8	82.0 ± 0.0	4.8 ± 19.2	SI	
<i>Rhinella diptycha</i>	<i>Aplectana vellardi</i> *	5	5	22.7	1.0 ± 0.2	0.2 ± 1.0	LI
	Nematode larvae	1	1	4.5	1.0 ± 0.0	0.04 ± 0.2	LI
	Nematode cyst	29	3	13.6	9.6 ± 1.0	1.3 ± 6.0	SI/UB/VM
	<i>Ochoterenella</i> sp.	41	2	9.0	20.5 ± 2.2	1.8 ± 8.5	GC
	<i>Oswaldocruzia lopesi</i>	3	3	13.6	1.0 ± 0.3	0.1 ± 0.6	SI
	<i>Oswaldocruzia</i> sp.	2	2	9.0	1.0 ± 0.5	0.09 ± 0.4	S/SI
<i>Trachycephalus typhonius</i>	<i>Rauschiella linguatula</i> *	41	4	18.1	10.2 ± 0.7	1.8 ± 8.5	SI
	<i>Aplectana vellardi</i> *	205	2	66.6	102.5 ± 5.0	68.3 ± 96.6	LI
	Nematode larvae	3	1	33.3	3.0 ± 0.0	1.0 ± 1.4	S

NP – Number of parasites recovered; NPH – Number of parasitized hosts; P (%) – Prevalence; MI ± SD – Mean intensity of infection ± standard deviation; MA ± SD – Mean abundance ± standard deviation; IS – Infection sites: LI – large intestine, SI – small intestine, S – stomach, L – liver, VM – visceral musculature, UB – urinary bladder, GC – general cavity. \* New parasite record

ten new records of parasitic helminths for the four amphibian species examined (Table 3).

The descriptive analysis showed a positive correlation between the number of parasites found and parasite species richness, and also between the number of hosts examined and the parasite species richness. Both correlations showed a strong trend in sampling effort (i.e. number of parasites found vs. parasite species richness,  $R^2=0.9502$ ; and the number of hosts examined vs. parasite species richness,  $R^2=0.9784$ ) (Fig. 1).

## Discussion

In this study, we recorded a high diversity of amphibian helminth parasites. All hosts presented high values for the analyzed parameters of infection (Table 1). Despite this high prevalence of infection and the growing number of studies on amphibian helminth fauna in Brazil (e.g. Campião et al. 2014, 2015a; Martins-Sobrinho et al. 2017), the number of studies still does not match the high richness of amphibian species occurring in the country. Here, we examine the helminth fauna of four amphibian species from northeastern Brazil and, from our literature compilation, report another ten taxa of helminth parasites associated with the examined

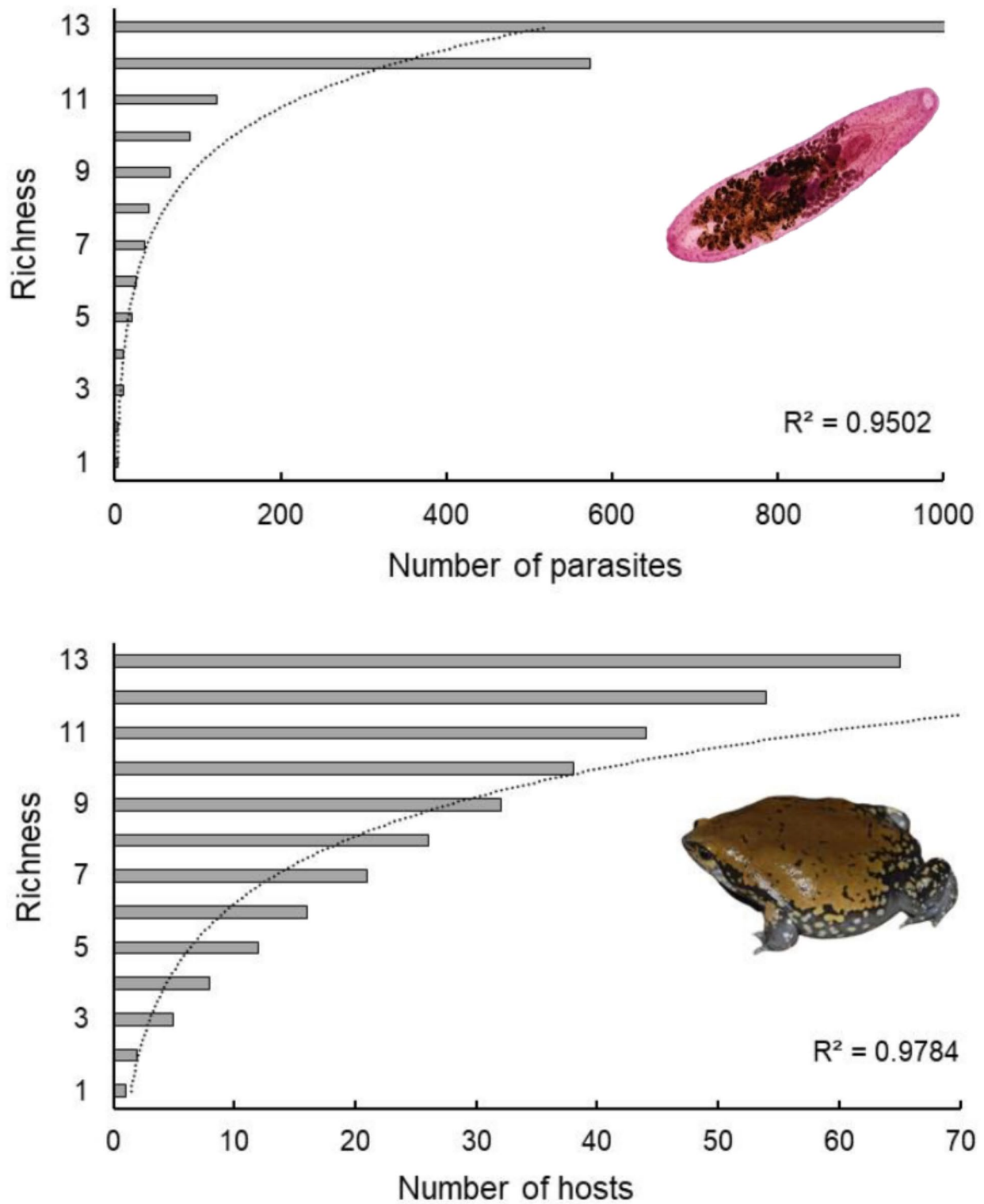
amphibian species in South America. These results confirm the strong influence of the study effort as a determinant of the richness of parasite species, as found in the study by Campião et al. (2015a), where the most studied hosts had, by far, the richest parasitic fauna. Therefore, it is clear that anurans that apparently have a low richness of helminths are, in fact, species that have been little studied (Campião et al. 2015a). Thus, further studies should increase the number of parasites associated with these host species.

The fossorial species *D. muelleri* presented the highest prevalence of infection (93.9%) and the highest abundance of parasites (1,468 individuals; 72.5% of the total). Besides, although the helminth fauna of *D. muelleri* has already been examined in other studies (e.g. Alcantara et al. 2018; González et al. 2020), two of the six parasite species found represent new host records, the total number of parasitic helminths associated with *D. muelleri* was increased to 18. In general, small anurans have low parasite diversity, despite their habit and taxonomy (Campião et al. 2015b). Apparently, fossorial species tend to have less richness of parasites. For example, *Pleurodema diplolister* (Peters, 1870) has hosted a more restricted helminth fauna, a result that might be associated with restricting the temporal window available to acquire parasites (Madelaire et al. 2020). On the other hand, other burrowing species (e.g. *Rhinella*

**Table 3** Update of helminth parasites associated with *Dermatonotus muelleri*, *Leptodactylus vastus*, *Rhinella diptycha*, and *Trachycephalus typhonius* in South America

Hosts	Helminths	HR	References
<i>Dermatonotus muelleri</i>	<i>Aplectana crucifer</i> , <i>A. hylambatis</i> , <i>A. membranosa</i> , <i>A. vellardi</i> , <i>Aplectana</i> sp., acanthocephalan cysthacanth, Cosmocercidae, <i>Cosmocerca podicipinus</i> , nematode larvae, <i>Ophiotaenia</i> sp., <i>O. cohospes</i> , <i>Parapharyngodon</i> sp., <i>P. silvoi</i> , <i>P. verrucosus</i> , <i>Physaloptera</i> sp., Pseudophyllidea, <i>Raillietnema spectans</i> , and unidentified larvae	18	Baker and Vaucher (1986); McAllister et al. (2010); Bezerra et al. (2012); Campião et al. (2014); Aguiar et al. (2015); Filho et al. (2015); Alcantara et al. (2018); González et al. (2019); González et al. (2020); Present study
<i>Leptodactylus vastus</i>	<i>Aplectana membranosa</i> , <i>Cosmocerca podicipinus</i> , <i>Falcaustra mascula</i> , <i>Rauschiella linguatula</i> , <i>Gorgoderina parvicava</i> , nematode cysts, nematode larvae, <i>Ochoterenella digiticauda</i> , <i>Ochoterenella</i> sp., <i>Oswaldocruzia lopesi</i> , <i>O. mazzai</i> , <i>O. subauricularis</i> , <i>Oswaldocruzia</i> sp., <i>Oxyascaris oxyascaris</i> , <i>Raillietnema spectans</i> , <i>Rhabdias fueleborni</i> , <i>R. cf. stenocephala</i> , <i>Schrankianella brasili</i> , <i>Schrankiana freitasi</i> , <i>S. inconspicata</i> , <i>S. larvata</i> , and <i>S. schranki</i>	23	Baker (1982); Vicente et al. (1991); Campião et al. (2014); Teles et al. (2014); Müller et al. (2018); Silva-Neta et al. (2020); Present study
<i>Rhinella diptycha</i>	<i>Aplectana membranosa</i> , <i>A. vellardi</i> , <i>Aplectana</i> sp., <i>Cylindrotaenia americana</i> , Cosmocercidae, acanthocephalan cysthacanth, encysted larvae (unidentified nematodes), <i>Rauschiella linguatula</i> , <i>Gorgoderina rochalimae</i> , nematode cysts, <i>Ochoterenella</i> sp., <i>Oswaldocruzia lopesi</i> , <i>O. mazzai</i> , <i>O. subauricularis</i> , <i>Oswaldocruzia</i> sp., <i>Plagiorchis rangeli</i> , <i>Physaloptera</i> sp., <i>Parapharyngodon</i> sp., <i>Rhabdias fueleborni</i> , <i>R. pseudosphaerocephala</i> , <i>R. sphaerocephala</i> , <i>Rhabdias</i> sp., <i>Raillietnema spectans</i> , and Tetrathyridium of <i>C. americana</i>	24	Campião et al. (2014); Graça et al. (2017); Müller et al. (2018); Amorim et al. (2019b); Madelaire et al. (2020); Present study
<i>Trachycephalus typhonius</i>	Acanthocephalan gen. sp., <i>Aplectana hylambatis</i> , <i>A. vellardi</i> , Ascarididae gen. sp., <i>Brevi-multicaecum</i> sp., Cosmocercidae gen. sp., <i>Falcaustra mascula</i> , nematode larvae, <i>Oxyascaris oxyascaris</i> , <i>Parapharyngodon</i> sp., <i>Physaloptera</i> sp., <i>Physalopteroides venancioi</i> , <i>Physocephalus</i> sp. 1, <i>Physocephalus</i> sp. 3, <i>Parapharyngodon hylidae</i> , <i>P. hugoi</i> , <i>Polystoma lopezromani</i> , <i>Porrocaecum</i> sp., Rhabdochoniidae gen. sp., <i>Rhabdias cf. elegans</i> , <i>Rhabdias</i> sp., undetermined helminth cyst, undetermined acanthocephalan cysthacanth	23	Campião et al. (2014, 2015b, 2016b); Draghi et al. (2015); Graça et al. (2017); Pereira et al. (2017); Present study

HR – Helminth richness



**Fig. 1** Relationship between the number of parasites found and parasite species richness (upper panel), and the number of hosts examined and parasite species richness (lower panel) from northeastern Brazil. The dotted line represents the trend

*fernandezae* (Gallardo, 1957)) have already recorded high parasite richness ( $n=22$ , Hamann et al. 2013). Thus, our results ( $n=1,468$  of 6 taxa of parasitic helminths, Table 1) and literature review ( $n=18$  spp., Table 3) reinforce the need for further studies, in particular for species that perform estivation, as *D. muelleri* (Nomura et al. 2009). These results suggest that, for these species, other factors, in addition to the hosts' habitat, may influence the parasitism rates. Previous studies indicate that coevolutionary and biological restrictions on the host species may limit or allow infection of parasitic species regardless of the host's habitat (Campião et al. 2016a). Other host features, such as diet and behavior, might be equally important in determining parasite diversity and composition (Campião et al. 2015b).

The species richness and helminthological composition found in *R. diptycha* were similar to that found in the same species in other locations, e.g. states of Ceará and Rio Grande do Norte (Amorim et al. 2019b; Madelaire et al. 2020), and with other species of the genus (e.g. *R. granulosa*,  $n=7$  spp., Teles et al. 2018; *R. fernandezae*,  $n=5$  spp., Draghi et al. 2020). On the other hand, previous studies for other species of the genus found a more diverse richness and composition. For example, *R. fernandezae* ( $n=22$  spp., Hamann et al. 2013), *R. ictérica* ( $n=12$  spp., Santos et al. 2013) and *R. major* ( $n=15$  spp., Hamann and González 2015). Despite the large size and wide geographic distribution of *R. diptycha* in Brazil (Stevaux 2002; Pereyra et al. 2021), the number of studies related to its helminth fauna is still scarce (i.e. Amorim et al. 2019b; Madelaire et al. 2020). In this study, of the seven parasite taxa found in *R. diptycha*, two represent new records for this host. Overall, the number of parasitic helminths associated with *R. diptycha* increased to 24 spp.

Although we analyzed only three individuals of *T. typhonius*, all of them were infected with helminth parasites, with high values of mean intensity of infection and mean abundance (~70 parasites per host). The number of helminths found was also high ( $n=208$ ). In this host, we found only two helminth taxa: *A. vellardi* and non-identified nematode larvae. The first one represents a new host record. On the other hand, with the compilation of the literature, we found that among the hosts analyzed here, *T. typhonius* (together with *L. vastus*) was the second species with a greater richness of associated helminths ( $n=23$  spp., Table 3). Previous studies showed that, among tree frogs, *T. typhonius* hosted the richest helminth community and the highest taxonomic diversity value (Campião et al. 2015b).

Oliveira et al. (2019) suggest that leptodactylids from northeastern Brazil (Caatinga biome) might harbor a lower richness of endoparasites compared to leptodactylids from other localities (e.g. 14 spp. in *Leptodactylus chaquensis* Cei, 1950 from the Brazilian Pantanal, Campião et al.

2016a). However, in the present study, *L. vastus* presented a high and similar richness of parasite species ( $n=10$  spp.) compared with several other leptodactylids of moderate-large size (*sensu* de Sá et al. 2014) from other localities, for example, 8 spp. in *Leptodactylus latrans* (Steffen, 1815) in the Atlantic Forest (Toledo et al. 2015; Graça et al. 2017); 7 spp. in *Leptodactylus ocellatus* (Linnaeus, 1758) in the Cerrado / Amazon ecotone (Goldberg et al. 2009); and 7 spp. in *L. chaquensis* in the Cerrado (Queiroz et al. 2020). Besides, in our extensive compilation, we recorded a high number of parasites associated with *L. vastus* ( $n=23$  species in total), including in regions of northeastern Brazil (Caatinga biome). Many of these parasite species, even those commonly found in amphibians, such as *O. lopesi* (Campião et al. 2014), were considered here as new records of helminths in the studied species.

We also found low parasite species richness for the same species analyzed by Oliveira et al. (2019) or congeneric species in other locations outside of northeastern Brazil (see Graça et al. 2017 and Queiroz et al. 2020). Thus, it is evident that it is not the parasite species richness in leptodactylids from northeastern Brazil or Caatinga biome that is smaller, but that there is a great lack of studies for most amphibian species and several regions with extensive knowledge gaps about parasitic helminths of amphibians. On the other hand, only one digenean species (*R. linguatula*) was found infecting one of the four species surveyed in the present study. A similar result was found by Alcantara et al. (2018) for *D. muelleri* from the Ceará state, e.g., hosts were infected only with nematodes. Digeneans have a complex life cycle involving a mollusk as a first intermediate host and also can use a second intermediate or paratenic host. Northeastern Brazil has long dry periods and little rainfall. Low local humidity can make it difficult to establish mollusk populations and thus justify the low diversity of these amphibian parasites in the region. Acanthocephalans and cestodes may be rare for a similar reason. How they depend on intermediate hosts to complete the biological cycle, the environmental variables could difficult the establishment of these parasites. Specifically, for the state of Piauí, this is the first study about the diversity of parasitic helminths associated with amphibians in this state. Our results reinforce the need for further studies in several areas of northeastern Brazil to a better knowledge of the amphibian parasite biodiversity in this region.

Recently, it has been demonstrated that the diversity of infected hosts is determined by biogeographical gradients in pools of species of the hosts. These findings emphasize the need to take into account the diversity of underlying species when assessing the host-parasite specificity (Wells et al. 2019). Studies on the diversity of amphibians in the sampled areas (e.g. Benício et al. 2015; Araújo et al. 2020) have

found a high species richness, including species endemic to certain biomes. These areas are inserted in a hotspot for the conservation of the world biodiversity – the Cerrado biome (Klink and Machado 2005) and an exclusively Brazilian biome – the Caatinga biome, considered one of the richest semi-arid regions in the world (Oliveira and Diniz-Filho 2010), with a high rate of endemism (Oliveira et al. 2012). Thus, we recommend future studies on the diversity and distribution of hosts and their associated helminth fauna in these highly diverse, threatened, and under-studied regions.

Our study is the first to address the diversity of amphibian parasites in the state of Piauí, northeastern Brazil. We also present ten new records of parasitic helminths with the four host species studied and an extensive compilation of parasites associated with them in South America. Our findings contribute to the knowledge of the parasite-host relationship, increasing our information on the diversity of parasitic helminths of amphibians in the state of Piauí. However, extensive knowledge gaps about amphibians and their associated helminth fauna are still evident in these semi-arid areas of the Neotropical region.

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## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

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