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New records of *Riggia cryptocularis* (Isopoda: Cymothoidae) parasitizing two *Odontostilbe* species (Characiformes: Characidae) in the Paraguay River Basin, Paraguay, with a review of *Riggia* host species

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Abstract. *Riggia* are freshwater cymothoids known to parasitize fish throughout South America. In Brazil, a male *R. cryptocularis* was previously found parasitizing the characid *Odontostilbe paraguayensis*, which was thought to be an accidental host given its small size and known *Riggia* reproductive requirements. Here, 759 *O. paraguayensis* and *O. pequira* specimens collected in Ñeembucú department, Paraguay were dissected to evaluate presence of *R. cryptocularis*. Two fish of each species were parasitized by male *R. cryptocularis*. An additional 810 individuals from 29 fish species from sites with *R. cryptocularis* were inspected, with no other host species identified. Our findings increase the known records of *R. cryptocularis* from two to six and expand their range by over 750 km, and our addition of four *Odontostilbe* hosts with no other recorded hosts suggests this isopod may actively select *Odontostilbe*. A comprehensive review of *Riggia* literature was also conducted to improve our understanding of host selection in *Riggia*, increasing previous estimates of hosts from 15 to 31 species. Further *Riggia* studies should include a wider range of fish species and report host characteristics to enable both parasitologists and fish ecologists to contribute to this research and greatly improve our understanding for host-parasite interactions.

Key words: Crustacea; freshwater; Ñeembucú, South America.

Resumen: **Nuevos registros de *Riggia cryptocularis* (Isopoda: Cymothoidae) parasitando dos especies de *Odontostilbe* (Characiformes: Characidae) en la Cuenca del Río Paraguay, Paraguay, con una revision de las especies huésped de *Riggia*.** *Riggia* son cimotoides de agua dulce conocidos por parasitar peces a través de América del Sur. En Brasil, se encontró un *R. cryptocularis* macho parasitando al characido *Odontostilbe paraguayensis*, que se pensaba que era un huésped accidental dado su pequeño tamaño y los requisitos reproductivos de *Riggia*. Aquí, 759 *O. paraguayensis* y *O. pequira* especímenes recolectados en el Departamento de Ñeembucú, Paraguay fueron disecados para evaluar la presencia de *R. cryptocularis*. Dos peces de cada especie fueron parasitados por un *R. cryptocularis* macho. Se inspeccionaron a 810 individuos adicionales de 29 especies de peces de sitios con *R. cryptocularis*, sin que se identificara ninguna otra especie de huésped. Nuestros hallazgos aumentan los registros conocidos de *R. cryptocularis* de dos a seis y expandan su hábitat en más de 750 km, y nuestra adición de cuatro huéspedes *Odontostilbe* sin encontrar hospedadores adicionales implica que este isópodo podría seleccionar deliberadamente *Odontostilbe*. También se realizó una revisión exhaustiva de la literatura de *Riggia* para mejorar nuestra comprensión de la selección de hospedadores en *Riggia*, aumentando las estimaciones previas de hospedadores de 15 a 31 especies. Otros estudios de *Riggia* deberían incluir una amplia variedad de especies de peces e informar las características del huésped para permitir que tanto los parasitólogos como los

ecologistas de peces contribuyan a esta investigación y mejoren nuestra comprensión de las interacciones huésped-parasito.

Palabras clave: Crustáceos; agua dulce; Ñeembucú, Sudamérica.

Introduction

Cymothoid isopods are relatively large parasites (typically 10–50 mm) that attach to the skin or gills, reside in the buccal cavity, or burrow into the peritoneal cavity of their fish hosts (Smit *et al.* 2014). These parasitic isopods can have detrimental effects on host fish including lesions and deformations at attachment sites, stunted growth and shortened lifespan, changes in host behavior, and even death (Reviewed in Rameshkumar & Ravichandran 2012; Smit *et al.* 2014). As one of the largest isopod families, Cymothoidae is comprised of nearly 400 species representing more than 40 genera (Ahyong *et al.* 2011). The majority of cymothoids are found in marine ecosystems (85% of known species; Hata *et al.* 2017), but some have been recorded in freshwater systems in Africa and Asia (at least four and six species, respectively; Brusca 1981), with relatively higher levels of freshwater diversity in South America (at least 27 species; Hata *et al.* 2017).

One genus of the freshwater cymothoids in South America, *Riggia* Szidat 1948, is identified by a fused pleon and pleotelson in adult females, and is separated from the genus *Artystone* by having five abdominal plates with an unciform and convex telson all fused together in contrast to individual freely moving plates in *Artystone* (Rodríguez-Haro *et al.* 2017). *Riggia* also has a boot-like mandible and interestingly, lacks an incisor (see generic redescription by Bastos & Thatcher (1997) for full details). *Riggia* contains six known species: *Riggia acuticaudata* Thatcher *et al.* 2002, *Riggia brasiliensis* Szidat & Schubart 1960, *Riggia cryptocularis* Thatcher *et al.* 2003, *Riggia nana* Szidat & Schubart 1960, *Riggia paranensis* Szidat 1948, and *Riggia puyensis* Rodríguez-Haro *et al.* 2017. All species have been recorded in Brazil, with only *R. paranensis* and *R. puyensis* also recorded in Argentina (Szidat 1948) and Ecuador (Rodríguez-Haro *et al.* 2017, respectively) (Table I). Undescribed *Riggia* sp. have also been recorded parasitizing fish in the Amazon of Brazil and Peru, although the exact locations are unclear from the available literature (Table I; Thatcher 2000; Scholz 2008; Anaguano-Yancha & Brito 2015). In addition to the Amazon, *Riggia* have been detected in smaller basins, such as the Rio Itabapoana (Bastos & Thatcher 1997) and Lago Guaíba (Albert 2008) of Brazil, as well as through the Río de la Plata Basin of Brazil and Argentina (Fig. 1A). However, despite its location at the confluence of major river systems in the Río de la Plata Basin and the presence of many of the host fish species within Paraguay, no studies have evaluated *Riggia* presence in this region.

The Ñeembucú Department in Paraguay is a highly biodiverse but understudied region surrounded by wetlands and bordered by the Paraguay and Parana rivers. Although much of the biodiversity in this region is poorly studied (but see De Egea *et al.* 2012 and Dickens *et al.* 2020), many of the genera and specific species known to host these cymothoid parasites have been recorded here (Colección Científica Para La Tierra, unpublished data). *Odontostilbe paraguayensis* Eigenmann & Kennedy 1903 (Characidae), is a relatively small benthopelagic fish (maximum standard length = 52 mm) that is found throughout the Paraguay and lower Parana river basins with a diet consisting of microcrustaceans, algae, and plants (Neiff *et al.* 2009). This species was found with a male *R. cryptocularis* (5 mm) in the Piraputanga River (Río de la Plata Basin), Mato Grosso do Sul state, Brazil (Thatcher *et al.* 2003). In contrast, the female isopod of this species is considerably larger (20 mm) and was recorded parasitizing an *Ancistrus* sp. (Loricariidae). Only one specimen of each sex was found (both in the peritoneal cavity of their respective host fish), and no other occurrences have been documented since the species was first described.

Thatcher *et al.* (2003) concluded that, because of the unique reproductive cycle of *Riggia* species, *O. paraguayensis* was likely an accidental host. *Riggia* cymothoids are thought to be protandrous hermaphrodites who enter hosts as small males and can rapidly grow into larger females if no others are present to reproduce with subsequent males entering the host (Thatcher 2000). The small size of *Odontostilbe* compared with the large female *R. cryptocularis* found in *Ancistrus* sp. suggests that this isopod would not be able to transform into the female without killing the host. However, no studies have evaluated host selection for this species, and the presence of *R. cryptocularis* has not been

Table I. Known locations and host fish of recorded *Riggia* species. 'ARG' is Argentina, 'BRA' is Brazil, 'ECU' is Ecuador, 'PER' is Peru, 'PRY' is Paraguay.

Parasite	Host	Parasite Location	Basin	Source
Riggia acuticaudata Thatcher *et al.* 2002	*Ancistrus* sp.	Mato Grosso do Sul state (BRA)	Río de la Plata	1, 2
Riggia brasiliensis Szidat & Schubart 1960	*Leporellus vittatus*	São Paulo state (BRA)	Río de la Plata	3, 4
	Leporinus copelandii			
	Leporinus octofasciatus			
	Schizodon nasutus			
	Pseudoplatystoma sp.	Amazonas state (BRA)	Amazon	5, 6
Riggia cryptocularis Thatcher *et al.* 2003	*Ancistrus* sp.	Mato Grosso do Sul state (BRA)	Río de la Plata	7
	Odontostilbe paraguayensis	Mato Grosso do Sul state (BRA), Ñeembucú department (PRY)	Río de la Plata	7, 8
	Odontostilbe pequira	Ñeembucú department (PRY)	Río de la Plata	8
Riggia nana Szidat & Schubart 1960	*Leporinus striatus*	São Paulo state (BRA)	Río de la Plata	3, 4
	Adontosternarchus clarkae	Rio Negro near Novo Airao, Amazonas state (BRA)	Amazon	9
	Eigenmannia macrops	Rio Negro, Amazonas state (BRA)		
	Eigenmannia virescens			
	Porotergus gimbeli	Rio Amazonas near Rio Tapajos (BRA)		
	Sternarchorhamphus muelleri			
	Sternarchorhamphus sp.	Rio Negro, Amazonas state (BRA)		
	Steatogenys elegans	Tarumã, Amazonas state (BRA)	Amazon	9, 10
Riggia paranensis Szidat 1948	*Cyphocharax platanus*	Rosario, Santa Fe province (ARG)	Río de la Plata	11
	Cyphocharax gilbert	Espirito Santo, Rio de Janeiro, Amazonas, Paraná states (BRA)	Amazon, Itabapoana, Río de la Plata	12-15
	Cyphocharax voga	Rio Grande do Sul state (BRA)	Lago Guaíba	16
	Characidium tenue			
	Hisonotus laevior			
	Hypostomus commersoni			
	Oligosarcus jenynsii			
Riggia puyensis Rodríguez-Haro *et al.* 2017	*Ancistrus* sp.	Para State (BRA)	Amazon	17
	Chaetostoma breve	Pastaza province (ECU)	Amazon	18, 19
	Chaetostoma microps			
Riggia sp.	*Chaetostoma* sp.	Pastaza province (ECU)	Amazon	20
	Rhamdia quelen			
Riggia sp.	*Monocirrhus polyacanthus*	Upper Amazon (PER*)	Amazon	21*
Riggia sp.	*Plagioscion squamosissimus*	Unclear - likely BRA	Unclear - likely Amazon	22, 23
Riggia sp.	*Sternarchorhamphus muelleri*	Unclear - likely BRA	Unclear - likely Amazon	22, 23

Sources: 1: Thatcher et al. 2002; 2: Oda et al. 2015; 3: Szidat & Schubart 1960; 4: Luque et al. 2013; 5: Thatcher 1995; 6: Thatcher 1997; 7: Thatcher et al. 2003; 8: This study; 9: Araújo 2002; 10: Baillie 2020; 11: Szidat 1948; 12: Bastos & Thatcher 1997; 13: Azevedo et al. 2002; 14: Lima et al. 2007; 15: Lins et al. 2008; 16: Alberto 2008; 17: Magalhães et al. 2018; 18: Rodríguez-Haro et al. 2017; 19: Plaul et al. 2019; 20: Anaguano-Yancha & Brito 2015; 21: Scholz 2008 *exact location is unclear; 22: Thatcher 2000; 23: Anaguano-Yancha & Brito 2015.

recorded since being described. Here, our primary aim was to evaluate the presence of *R. cryptocularis* infecting *O. paraguayensis* in the Ñeembucú department of southwest Paraguay. Because other *Riggia* species have been found parasitizing multiple hosts of the same and differing genera (Table I), *Odontostilbe pequira* Steindachner, 1882 was also examined alongside 29 additional species that share habitats with these *Odontostilbe* species.

Additionally, studies of *Riggia* cymothoids are often constrained to taxonomic descriptions of the parasite, with a paucity of knowledge regarding host characteristics, information which is essential to understanding host-parasite interactions. A shift from a solely parasitological perspective to one that is also relevant for fish ecologists can greatly increase the engagement of researchers in this understudied field and subsequently expand occurrence records for *Riggia* species As such, a secondary objective for this work was to review the body of available *Riggia* literature to summarize and improve our understanding of host-parasite relationships for this genus, with special consideration given to host characteristics.

Material and Methods

Study site: Situated in the southwest corner of Paraguay, the Ñeembucú department is bordered by the Paraguay and the Parana rivers along its western and southern edges, respectively, separating the department from Argentina on both sides. The regional climate is described as humid subtropical (Köppen-Geiger classification Cfa), and the capital city of Pilar (26.85726 °S, 58.30753 °W) has an average yearly temperature of 22.1 °C and rainfall of 1364 mm. Average monthly temperatures and rainfall are lowest in July (11.5 °C) and August (46 mm), respectively, and peak in January, averaging 27.6 °C and 151 mm of rain (climate-data.org; Accessed 16 May 2020). The city of Pilar has a population of around 30,000 and lies on the eastern bank of the Paraguay river at the confluence of the Arroyo Ñeembucú, into which the vast Ñeembucú Wetlands drain (Fig 1C). The region is relatively flat and lies at a low elevation (50–124 m), with over 85% of the region considered to be wetlands (De Egea *et al.* 2012).

Collection of hosts and parasites: Fish specimens were previously collected using a seine net (3 x 1 m) during general sampling trips as part of a regional fish biodiversity survey for Ñeembucú (Colección Científica Para La Tierra, unpublished data) in June–July 2017 and October–November 2018. Sampling was conducted at 24 riverine sites, including several locations along the Río Paraguay and Arroyo Ñeembucú in Pilar as well as throughout central Ñeembucú along the Río Tebicuary and the Arroyo Horco (Table II; Fig. 1B). Specimens were fixed in 10% formalin solution *in situ*, preserved in 70% ethanol, and housed in the Colección Científica Para La Tierra. All *O. paraguayensis* and *O. pequira* (Fig. 2) specimens in the collection were examined and dissected, and any isopods found were removed and persevered in 70% ethanol. At any site with a positive parasite presence in *Odontostilbe*, specimens of all fish species captured at that site were examined to determine if any other potential host species were present (Table III). Any host specimens found with *R. cryptocularis* were measured using a digital caliper, and parasites were identified and measured using Amscope software with an Amscope MU1003 camera. All *Riggia* specimens were identified as *R. cryptocularis* following the description of Thatcher *et al.* (2003), and two specimens were dissected to examine maxillary and individual pleopod morphology. The image plate of *Odontostilbe* species (Fig. 2) was made using a Nikon D3500 with Micro Nikkor 35mm lens by stacking 10–20 images using the program HeliconFocus 6.7 to increase the depth of focus and combining into a single image plate with GIMP (www.gimp.org).

Bibliographic search: A literature search on *Riggia* infections was carried out using Google Scholar by first searching the scientific name of every individual *Riggia* species (e.g. "*Riggia brasiliensis*"). Once a host species was identified for a given species, a secondary search was done as "parasite scientific name" + "host genus name" (e.g. "*Riggia brasiliensis*" + "*Leporellus*"). FishBase (www.fishbase.org/) was used to verify host scientific names and check for all synonyms for each species, which were subsequently added to the search. Any species name misspellings for either host or parasite that we found in the literature (e.g. "*R. acuticaudata*" is sometimes referred to as "*R. acuticauda*") were also included in the search. For example, the host species now known as *Cyphocharax platanus*, which was infected by *Riggia paranensis* (Szidat 1948), was originally identified as *Curimata platana* and is also sometimes referred to as *Cyphocarax platanus* in the literature. For this species, "*Cyphocharax*", "*Cyphocarax*", and "*Curimata*" were all (separately) searched with "*Riggia paranensis*". In some cases, a *Riggia* species was found parasitizing a fish but was

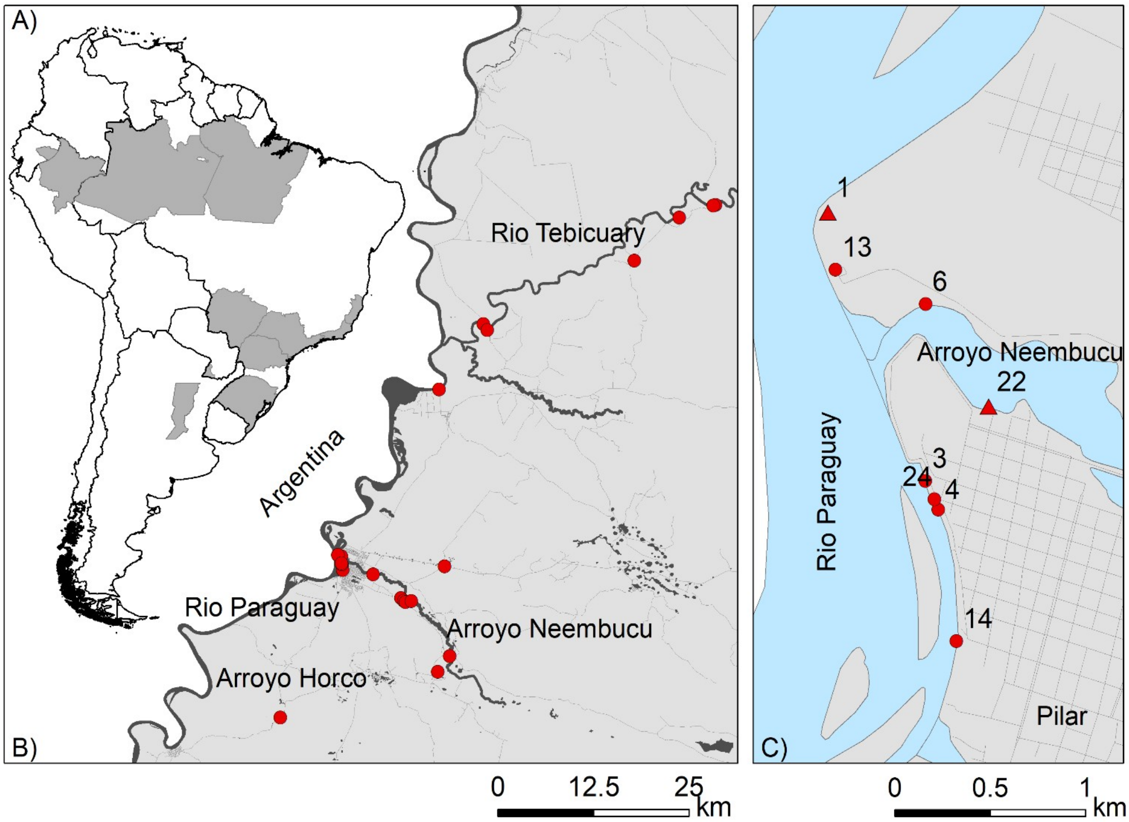

Figure 1. A) Gray areas represent states (Brazil), provinces (Argentina, Ecuador, Peru) or departments (Paraguay) with *Riggia* records. B) Sampling sites in Ñeembucú department, Paraguay on the Río Tebicuary, Río Paraguay, Arroyo Ñeembucú, and Arroyo Horco, and C) Sampling sites surrounding the city of Pilar with triangles representing sites with positive *Riggia cryptocularis* presence.

not identified or yet described to species. As such, we also searched for "*Riggia* sp." and added any additional host species found to our search process.

In addition, the 'Cited By' feature on Google Scholar was used for every article which originally or subsequently described a species. This included Thatcher *et al.* (2002) and Oda *et al.* (2015) for *R. acuticaudata*, Szidat & Schubart (1960) for *R. brasiliensis* and *R. nana*, Thatcher *et al.* (2003) for *R. cryptocularis*, Szidat (1948) and Bastos & Thatcher (1997) for *Riggia paranensis*, and Rodríguez-Haro *et al.* (2017) for *Riggia puyensis*. Citations for *Riggia* sp. were also searched, including Thatcher (2000), Scholz (2008), and Anaguano-Yancha & Brito (2015). Once all fish hosts were identified, FishBase was used to find relevant species information, including size and range distributions for each species. Because many of these fish species have incomplete or outdated information on FishBase, primary literature was used to fill gaps where needed.

Results

Riggia cryptocularis Thatcher *et al.* 2003 (Fig. 3)

Prevalence and intensity of infection: Two of 129 *O. paraguayensis* (1.6%) and two of 630 *O. pequira* (0.3%) specimens were infected across 24 sites in Ñeembucú (Table II), with one male isopod specimen in the peritoneal cavity per host fish. No female specimens were found. From the sites with isopod presence, an additional 810 specimens were examined representing 29 species from 11 families and four orders (Table III), but no other host species were found carrying *R. cryptocularis*.

The two *O. paraguayensis* hosts were from different sites on different rivers (site 1: Río Paraguay and site 22: Arroyo Ñeembucú; Table II), but in close proximity (<1 km) near the confluence of the two rivers in the city of Pilar (Fig. 1C). At infected sites, the number of *O. paraguayensis* specimens was relatively low (11 individuals at Site 1 and one specimen at Site 22), giving those sites the prevalence of infection 9.1% and 100%, respectively. No *O. pequira* specimens were found at site 22 but 43 specimens were caught at Site 1. Additionally, although nearly 400 *Odontostilbe* specimens were captured at sites in close proximity

Table II. 'N' indicates number of individuals caught and dissected at each site, and 'Hosts' indicates number of *Odontostilbe* host fish found with *Riggia cryptocularis* at each site.

		O. paraguayensis		***O. pequira***	
Site	**River**	**N**	**Hosts**	**N**	**Hosts**
1	Paraguay	11	1	43	0
2	Paraguay	54	0	-	-
3	Paraguay	1	0	26	0
4	Paraguay	-	-	1	0
5	Ñeembucú	-	-	5	0
6	Ñeembucú	-	-	4	0
7	Ñeembucú	-	-	2	0
8	Ñeembucú	-	-	4	2
9	Ñeembucú	-	-	48	0
10	Ñeembucú	-	-	4	0
11	Ñeembucú	-	-	25	0
12	Ñeembucú	-	-	2	0
13	Paraguay	46	0	251	0
14	Horco	-	-	48	0
15	Tebicuary	12	0	23	0
16	Tebicuary	-	-	15	0
17	Tebicuary	1	0	7	0
18	Tebicuary	-	-	89	0
19	Paraguay	1	0	4	0
20	Tebicuary	-	-	21	0
21	Tebicuary	-	-	4	0
22	Ñeembucú	1	1	-	-
23	Paraguay	1	0	4	0
24	Paraguay	1	0	-	-

to sites 1 and 22 (Sites 3, 4, 6, 9, 13, and 24; Fig. 1C), no parasites were found at any of those sites (Table II). Both *O. pequira* hosts were found at the same site on the Arroyo Ñeembucú (Site 8), several miles upstream from the sites of the infected *O. paraguayensis* hosts. No *O. paraguayensis* specimens and only four *O. pequira* specimens were captured at Site 8, giving it a prevalence of infection of 50%.

The parasites in *O. paraguayensis* measured 5.16 x 2.06 mm and 4.21 x 1.79 mm, taking up 19.4 and 17.1% of the standard length of their respective hosts (26.61 and 24.68 mm). The parasites in *O. pequira* measured 3.38 x 1.49 mm and 5.46 x 2.26 mm, taking up 11.8 and 18.5% of their hosts standard length (28.58 and 29.59 mm). Pleon and Pleotelson lengths and widths ranged from 1.28–2.28 mm (mean = 1.91 ± 0.44 mm) and 0.86–1.45 mm (mean = 1.20 ± 0.25 mm), respectively. With our addition of four male specimens to the previously recorded male specimen, the mean size of a *R. cryptocularis* male was re-evaluated as follows (n = 5 specimens incl. Thatcher *et al.* 2003): body length 4.63 mm, body width 1.98 mm, pleotelson length 1.96 mm, pleotelson width 1.26 mm. All other taxonomic characteristics of our *R. cryptocularis* agree with the findings of Thatcher *et al.* (2003).

Literature Search Results: At least 27 species from 20 genera, 12 families, and four orders have been known to host *Riggia* parasites (Table IV). This estimate could be as high as 31 species if the three occurrences of *Ancistrus* sp. are all different species, the one *Chaetostoma* sp. (Loricariidae) is a different species from *C. breve* and *C. microps*, and the one *Sternarchorhamphus* sp. (Apteronotidae) is different from *S. muelleri*. *Riggia* have been found in both large (Amazon and Río de la Plata) and relatively smaller basins, including Lago Guaíba and Rio Itabapoana basins of Brazil. Of the 31 possible infected species, 23 were infected in Brazil (Szidat & Schubart 1960; Araujo 2002; Thatcher *et al.* 2002, 2003; Alberto 2008; Bastos & Thatcher 1997; Thatcher 1995, 1997; Azevedo *et al.* 2002, Lima *et al.* 2007; Lins *et al.* 2008; Magalhães *et al.* 2018; Baillie 2020), followed by four in Ecuador (Anaguano-Yancha & Brito. 2015; Rodríguez-Haro *et al.* 2017; Plaul *et al.* 2019), two in Paraguay (Thatcher *et al.* 2003 and this study), and one in Argentina (Szidat 1948) (Fig 1A). The locations of three infections are unclear from the literature, but given the context of their respective sources, it is likely that *S. muelleri* and *Plagioscion squamosissimus* (Sciaenidae) (Thatcher 2000) were infected in Brazil and *Monocirrhus polyacanthus* (Scholz 2008) in Peru, although this is at odds with Anaguano-Yancha & Brito (2015) who asserts all three were infected in Colombia.

Although *Riggia* have only been detected in limited regions, many of the host species span considerably larger parts of South America. In particular, *Eigenmannia virescens* (Sternopygidae),

Figure 2. Voucher specimens of A) *Odontostilbe paraguayensis* and B) *Odontostilbe pequira*.

Leporinus striatus (Anostomidae), *Monocirrhus polyacanthus* (Polycentridae), *Plagioscion squamosissimus*, *Rhamdia quelen* (Pimelodidae), and *Steatogenys elegans* (Hypopomidae) span at least five countries in South America (Table IV). Host size information was included for only 16 species from studies reporting *Riggia* infection (not including this study), and there was considerable variation in how maximum length was reported across fish species on FishBase, with eight species listed as standard length (SL; omitting caudal fin) and 18 as total length (TL; including caudal fin). As a result, of these inconsistencies, drawing comparisons across species is difficult. The smallest infected fish was *Hypostomus commersoni*, which was around 2.5 cm (SL) with a young *R. paranensis* manca (Alberto 2008) but can grow to 60.5 cm (TL). In contrast, *Hisonotus laevior* specimens were 3.5–4 cm (SL) when infected with adult *R. paranensis* (Albert 2008) but have a maximum TL of only 7.5 cm.

Our search found several inconsistencies between the *Riggia* studies and reported information available on FishBase. Notably, the results of Rodríguez-Haro *et al.* (2017) and Plaul *et al.* (2019) were directly at odds with species information found on FishBase for *Chaetostoma microps*, with their average SL over 2 cm longer than the maximum listed TL and their study area not within the known distribution of the species. Finally, at least 13 species were found with only female *Riggia*, five with only males, four with both males and females, and two with sexless manca, while it was unclear which sex infected eight hosts. See Table IV for a complete summary of host and parasite information.

Discussion

Riggia species have been found throughout South American river basins, but their life cycles, host preferences, and distributions remain poorly understood. Here, the number of known *R. cryptocularis* specimens is increased from two to six and their range is expanded by more than 750 km with the second recorded observation for this species and the first observation of any *Riggia* species in Paraguay. Despite widespread surveys throughout rural and urban Ñeembucú, all four occurrences were found in relatively close proximity to each other and concentrated around the city of Pilar.

All four isopods in this study were found in *Odontostilbe* species, relatively small fish that only grow to around 5 cm SL. In the description of *R. cryptocularis* Thatcher *et al.* (2003) suggested that *O. paraguayensis* was likely an accidental host for *R. cryptocularis*, owing to the small size of the host and the proposed reproductive cycle for *Riggia*

Table III. Names and numbers of specimens of fish species inspected from sites in Ñeembucú, Paraguay with positive *Riggia cryptocularis* presence in *Odontostilbe paraguayensis* and *O. pequira.* 'Max Length' is the maximum length as reported on FishBase (www.fishbase.org/; Accessed 16 May 2020), 'SL' is standard length, and 'TL' is total length.

Order	Family	Scientific Name	Maximum Length (cm)	Site 1	Site 8	Site 22
Beloniformes	Belonidae	*Potamorrhaphis eigenmanni*	22.8 SL	-	-	2
Characiformes	Anostomidae	*Leporinus striatus*	30.0 SL	1	-	-
		Schizodon nasutus	40.2 TL	1	-	-
	Characidae	*Aphyocharax anisitsi*	5.5 TL	27	20	-
		Aphyocharax dentatus	7.2 SL	2	3	-
		Aphyocharax nattereri	3.1 SL	-	10	-
		Aphyocharax rathbuni	2.7 SL	-	2	-
		Astyanax abramis	14.0 SL	-	2	-
		Astyanax asuncionensis	15.0 SL	-	2	-
		Astyanax erythropterus	-	1	-	-
		Astyanax lacustris	7.7 TL	24	-	1
		Bryconamericus exodon	5.7 SL	107	-	-
		Hemigrammus ulreyi	4.4 TL	-	3	-
		Hyphessobrycon eques	4.0 SL	1	36	-
	Crenuchidae	*Characidium aff. zebra*	7.4 SL	1	86	-
	Curimatidae	*Cyphocharax gillii*	10.0 SL	-	3	-
		Cyphocharax saladensis	9.8 TL	-	1	-
	Parodontidae	*Apareiodon affinis*	17.0 SL	-	-	14
	Serrasalmidae	*Mylossoma duriventre*	25.0 SL	-	-	2
		Serrasalmus maculatus	34.5 TL	-	-	6
	Triportheidae	*Triportheus nematurus*	18.3 SL	-	-	5
Perciformes	Cichlidae	*Bujurquina vittata*	9.0 SL	-	-	2
		Cichlasoma dimerus	11.7 SL	-	1	-
		Crenicichla vittata	26.0 SL	-	-	1
Siluriformes	Callichthyidae	*Corydoras hastatus*	2.4 SL	-	6	1
	Loricariidae	*Hisonotus maculipinnis*	4.0 SL	-	-	10
		Hypoptopoma inexpectatum	7.1 SL	-	1	7
		Hypostomus cochliodon	23.0 SL	-	2	-
		Otocinclus vittatus	3.3 TL	249	131	36
				414	**309**	**87**

(Thatcher 2000; Smit *et al.* 2014). However, our study examined a further 29 fish species, many of which attain much larger sizes (Table III) and some of which are known hosts of *Riggia* elsewhere (Table IV), with no other hosts identified, suggesting that *R. cryptocularis* actively select *Odontostilbe* hosts.

As free-swimming manca, some young cymothoids have been known to ambush small fish by attaching to the ventral surface and feeding on the pectoral fins and underside of the opercula until the fish dies (Thatcher 2000). Small fish that reside in or come to benthic regions to feed may be especially vulnerable to these attacks (Rodríguez-Haro *et al.* 2017), and some manca have been known to kill up to four small fish within a 24-hour period in a laboratory setting (Thatcher 2000). *Odontostilbe* species have been known to consume relatively large amounts of detritus (Melo *et al.* 2004), indicating they may spend time feeding in benthic areas and could be ideal temporary targets for feeding manca. However, even our smallest *Riggia* specimen displayed the characteristics of a juvenile male in the post-manca stage (seven segments and pair of pereopods; Smit *et al.* 2014), which could suggest that the isopods had selected these small fish as their permanent hosts.

Only two of the eight sites within close proximity around Pilar had positive parasite presence despite sampling over 400 *Odontostilbe* individuals at the remaining six sites. This could indicate the two sites with parasites are in small

Figure 3. Dorsal view of our smallest and largest *Riggia cryptocularis* specimens. The black line represents 1 mm.

coves where detritus can settle while the other sites have faster flowing water. As a result, a higher proportion of *Odontostilbe* diets could come from other food sources, causing them to spend less time on the river bottom and making them less vulnerable to manca attacks. Site 1 is particularly interesting because four times as many *O. pequira* were sampled but only one parasite was found, which was infecting *O. paraguayensis*. This could suggest niche partitioning between species at this site, with *O. paraguayensis* consuming more detritus or other bottom dwelling food items while *O. pequira* occupies higher areas in the water column.

Four male isopods were found but no females were identified in our fish specimens, which is likely due to the nature of our field sampling methodology. The Río Paraguay and Arroyo Ñeembucú, where the isopods were found, are both large rivers where seine-net sampling can only be conducted along shallow sections of the river's edge. Although some larger specimens were collected using this methodology, our survey results indicate a clear bias towards juvenile and/or relatively small fish (standard length <40 mm). The only recorded female specimen of *R. cryptocularis* (Thatcher *et al.* 2003) had a body size 4–6X longer than the four male parasites in this study and more than half the standard length of a majority of fish captured. Regardless of the influence of sampling method, male specimens are often less commonly found in studies for *Riggia* species (e.g. Bastos & Thatcher 1997; Oda *et al.* 2015). This trend is likely influenced by the suspected reproductive strategy for this genus in which males either transform into females or exit fish hosts after copulation and die. However, little is known of the male life cycle outside of this process, and although Thatcher (2000) indicates some young cymothoids have been observed rapidly parasitizing small fish not intended as permanent hosts, to our knowledge no published studies exist that evaluate *Riggia* manca temporary-

Table IV. For every fish species with a recorded *Riggia* infection, the maximum length and geographic distribution as recorded on FishBase (www.fishbase.org/), the length of infected individuals ('TL' for total length and 'SL' for standard length), the *Riggia* species and sex which infected it ('U' is unclear, 'F' is female, 'M' is male, and 'm' is manca), and source. 'ARG' is Argentina, 'BOL' is Bolivia, 'BRA' is Brazil, 'COL' is Colombia, 'ECU' is Ecuador, 'GUF' is French Guyana, 'GUY' is Guyana, 'PRY' is Paraguay, 'PER' is Peru, 'SUR' is Suriname, 'URY' is Uruguay, and 'VEN' is Venezuela.

Order	Family	Species	Max length (cm)	Length of infected	Distribution	Parasite - sex	Source
Characiformes	Anostomidae	*Leporellus vittatus*	30 SL	-	Amazon, Orinoco, and Paraná basins (BRA, PRY, PER)	*Riggia brasiliensis* - U	1, 2
		Leporinus copelandii	54 TL	-	Amazon, Paraná-Paraguay and São Francisco basins (BRA)	*Riggia brasiliensis* - U	1, 2
		Leporinus octofasciatus	31.2 SL	-	Northern Cubatão River in Santa Catarina; Paraná basin (ARG, BRA)	*Riggia brasiliensis* - U	1, 2
		Leporinus striatus	25 TL	-	Orissanga, Paraná, Paraguay, Uruguay basins (ARG, BOL, BRA, COL, ECU, PRY, PER, URY)	*Riggia nana* - F	1, 2
		Schizodon nasutus	40.2 TL	-	Paraná, Paraguay, Uruguay basins (ARG, BRA)	*Riggia brasiliensis* - U	1, 2
	Characidae	*Odontostilbe paraguayensis*	5.2 SL[22]	2.5-2.7 SL	Paraguay and lower Paraná basins (ARG, BRA, PRY)	*Riggia cryptocularis* - M	3, *
		Odontostilbe pequira	5.6 SL	2.9-3.0 SL	Paraguay and lower Paraná basins (ARG, BRA, PRY, URY)	*Riggia cryptocularis* - M	*
		Oligosarcus jenynsii	31 TL	18.2 SL	Iguazu, Paraná, and Uruguay basins; Laguna dos Patos (ARG, BRA, URY)	*Riggia paranensis* - F	4
	Crenuchidae	*Characidium tenue*	5.6 SL	~7.0 SL	Uruguay River and Laguna dos Patos (ARG, BRA)	*Riggia paranensis* - m	4
	Curimatidae	*Cyphocharax platanus*	13.4 SL	-	Río de la Plata basin below Sete Quedas Falls (ARG, BRA, PRY, URY)	*Riggia paranensis* - M/F	5
		Cyphocharax gilbert	24.2 TL	8.5-21.0 SL	Coastal drainages of Brazil from Bahia to eastern São Paulo state (BRA)	*Riggia paranensis* - M/F	6-10
		Cyphocharax voga	26.3 TL	17.8 SL	Paraguay and Paraná basins; Laguna dos Patos (ARG, RA, PRY, URY)	*Riggia paranensis* - F	4, 5, 9
Gymnotiformes	Apteronotidae	*Adontosternarchus clarkae*	18.6 TL	10.0 TL	Rio Negro of Amazon basin (BRA, VEN)	*Riggia nana* - F	11
		Porotergus gimbeli	24 TL	18.0 TL	Amazon basin (BRA)	*Riggia nana* - M	11
		Sternarchorhamphus muelleri	45.5 TL	25.0-28.0 TL	Amazon basin (BRA, PER, VEN)	*Riggia nana* - M/F	11
						Riggia sp. - F	7, 12
		Sternarchorhamphus sp.	-	-	Rio Negro of Amazon basin (BRA)	*Riggia nana* - F	11

	Hypopomidae	*Steatogenys elegans*	29.4 TL	15.0-18.0 TL	Guianas and Amazon basin (BOL, BRA, COL, ECU, GUY, PER, VEN)	*Riggia nana* - M/F	11, 13
	Sternopygidae	*Eigenmannia macrops*	25.2 TL	14.0 TL	Guianas and Amazon basin (BRA, GUY)	*Riggia nana* - M	11
		Eigenmannia virescens	44 SL	17.0 TL	Orinoco and Río de la Plata basins (ARG, BOL, BRA, COL, ECU, GUF, GUY, PRY, PER, SUR, URY, VEN)	*Riggia nana* - U	11
Perciformes	Polycentridae	*Monocirrhus polyacanthus*	8.0 SL	-	Amazon basin (BOL, BRA, COL, PER, VEN)	*Riggia* sp. - U	14
	Sciaenidae	*Plagioscion squamosissimus*	80.0 TL	-	Amazon, Orinoco, Paraná, Paraguay, and São Francisco basins and rivers of Guianas (ARG, BOL, BRA, COL, ECU, GUF, GUY, PER, SUR, VEN)	*Riggia* sp. - F	7, 12
Siluriformes	Heptapteridae	*Rhamdia quelen*	47.4 TL	11.2-11.6 SL	Widespread Mexico to Central Argentina (ARG, BOL, BRA, COL, ECU, GUF, GUY, PRY, PER, SUR, URY, VEN)	*Riggia* sp. - F	12
	Loricariidae	*Ancistrus* sp. 1	-	-	Mato Grosso do Sul state (BRA)	*Riggia acuticaudata* - F	15, 16
		Ancistrus sp. 2	-	-	Mato Grosso do Sul state (BRA)	*Riggia cryptocularis* - F	3
		Ancistrus sp. 3	-	-	Xingu River drainage above Altamira, Amazon basin (BRA)	*Riggia puyensis* - F	17
		Chaetostoma breve	30.0 TL	19.7 SL	Zamora River basin in the upper Marañon River drainage (Pastazas province, ECU).	*Riggia puyensis* - M/F	18, 19
		Chaetostoma microps	8.9 TL	11.3 avg SL	Andes of W ECU	*Riggia puyensis* - M/F	18, 19
		Chaetostoma sp.	-	6.8 SL	Upper Amazon of Alto Pastaza province (ECU)	*Riggia* sp. - F	12
		Hisonotus laevior	7.5 TL	3.5-4 SL	Laguna dos Patos (BRA)	*Riggia paranensis* - M	4
		Hypostomus commersoni	60.5 TL	~2.5 SL	Lower Paraná including the Iguazu, Paraguay basins, Río de la Plata and Dulce basins (ARG, BRA, PRY, URY)	*Riggia paranensis* - m	4
	Pimelodidae	*Pseudoplatystoma* sp.	-	-	Unclear	*Riggia brasiliensis* - F	20, 21

*This study

Sources: 1 - Szidat & Schubart 1960; 2 - Luque *et al.* 2013; 3 - Thatcher *et al.* 2003; 4 - Alberto 2008; 5 - Szidat 1948; 6 - Bastos & Thatcher 1997; 7 - Thatcher 2000; 8 - Azevedo *et al.* 2002; 9 - Lima *et al.* 2007; 10 - Lins *et al.* 2008; 11 - Araújo 2002; 12 - Anaguano-Yancha & Brito 2015; 13 - Baillie 2020; 14 - Scholz 2008; 15 - Thatcher *et al.* 2002; 16 - Oda *et al.* 2015; 17 - Magalhães *et al.* 2018; 18 - Rodríguez-Haro *et al.* 2017; Plaul *et al.* 2019; 20 - Thatcher 1995; 21 - Thatcher 1997; 22 - Neiff *et al.* 2009 host preference and how those hosts differ from permanent hosts.

Although it is possible that *Odontostilbe* is an accidental host for unlucky manca, our finding that this *Riggia* species is repeatedly parasitizing a host in which it cannot successfully reproduce highlights the necessity to more thoroughly investigate host-parasite interactions for freshwater cymothoids. Few studies report basic descriptions of host specimens or include detailed sampling methodology (but see Alberto 2008 and Araujo 2002), making it unclear whether they have investigated additional species with no positive results. Further studies should investigate a wider range of fish species at sites with parasites present to evaluate whether further host-parasite interactions may exist and include data for all fish considered when publishing new observations.

Our literature review revealed several inconsistencies and roadblocks in terms of reporting and accessing reliable and accurate fish host data. First, despite the reputation of FishBase as one of the best sources for taxa-specific information of both freshwater and marine species around the world, it fell short in providing appropriate information for many of our studied species. In particular, the maximum reported lengths and known geographic distributions for some fish species on FishBase were directly at odds with what was reported in studies recording *Riggia* infections. While FishBase was able to provide relatively accurate information for many of the species, these inconsistencies highlight not only the need for more fisheries research in region but also for research indirectly involving fisheries to provide more details of fish encounters (i.e. researchers studying parasites infesting fish should report more details on the location and characteristics of the fish). Second, one of the more surprising results of our literature review was the finding that up to 31 fish species have been infected with *Riggia* species. This estimate is more than twice of what has been previously reported (see Anaguano-Yancha & Brito 2015 and Rodríguez-Haro *et al.* 2017), an increase which is largely due to two sources that are not widely cited in the literature: 1) a study of cymothoids in Lago Guaíba, Brazil by Alberto (2008) and 2) a study of Amazonian cymothoids by Araujo (2002) which conducted surveys and used specimens from the Instituto Nacional de Pesquisas da Amazonia (INPA) ichthyological collections. Both of these studies are also unique in that they evaluated a large range of fish species (as opposed to most that only look at target species) and report appropriate measurements for specimens. Of particular note, the addition of seven host species by Araujo (2002) highlights the important contribution museum collections can make to our ecological knowledge and the necessity of making these records widely available. Finally, the difficulty in obtaining accurate records of *Riggia*-host interactions was greatly exacerbated by the lack of host-related information provided in the primary literature. Including more details of host characteristics and providing a list of additional species evaluated can enable both parasitologists and fish ecologists, especially those with access to museum collections, to greatly improve our records and knowledge of host-parasite interactions.

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