Diversity of helminth parasites of eight siluriform fishes from the Aguapeí River, upper Paraná basin, São Paulo state, Brazil

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ABSTRACT

Fishes of the order Siluriformes, known as catfishes, have a global distribution with more than 3,600 valid species of which 2,087 occur in the Neotropical region. Despite being highly diverse, abundant, and of economic importance as food and ornamental fishes, knowledge about the diversity and distribution of their helminth parasites is fragmentary and scarce. Eight species of catfishes (Pterodoras granulosus, Trachydoras paraguayensis, Pimelodella avanhandavae, Loricariichthys platymetopon, Pterygoplichthys ambrosettii, Rhinelepis aspera, Hemisorubim platyrhynchos, and Sorubim lama) from the Aguapeí River, Upper Paraná River basin, municipality of Castilho, São Paulo State, Brazil, were surveyed for helminth parasites. Collected fishes were weighed, measured, and examined for helminth parasites following standard methodology. Fifty helminth parasite taxa (23 monogeneans, 13 digeneans, 11 nematodes, and three cestodes) were found from a total of 405 fishes screened. The helminth taxon that showed the highest mean intensity of infection and mean abundance was the nematode Rondonia rondoni from P. granulosus, followed by the nematode Parasynodontisia petterae from R. aspera. The ecological analyses were carried out at the component community level and at the infracommunity level. Trachydoras paraguayensis had the richest helminth component community. Pterygoplichthys ambrosettii had the most diverse helminth component community and R. aspera had the lowest. Both hosts are loricariids and have similar diet. However, the high parasite diversity of P. ambrosettii is due to the number of dactylogyrids species found (10), which are directly transmitted, whereas only three dactylogyrid species were found in R. aspera. At infracommunity level, the nematode species R. rondoni and P. petterae dominated the parasite communities. This study presents 38 new host records, contributing considerably to increase the diffuse knowledge of helminth parasites of Neotropical siluriforms.

1. Introduction

With the global increase in research on the biodiversity of freshwater environments, it is becoming more apparent that freshwater parasites are a fundamental part of this diversity. To date, parasites constitute one of the least studied groups in most biodiversity studies, even though they play a key role in the functioning of ecosystems as an integral component of trophic webs (Marcogliese and Cone, 1997; Lafferty et al., 2008; Adlard et al., 2015). Parasites are indicators of several biological aspects of their hosts and can be used in the assessment of environmental quality and richness (Sures et al., 2017). An adequate understanding of the dynamics of parasite communities in natural ecosystems, as well as the identification of spots of high parasite diversity, is important to fully understand how the biosphere works (Lafferty, 1997; Luque and Poulin, 2007). Consequently, knowledge of the diversity of parasites is crucial for any ecological and evolutionary studies as parasitism plays an important role in ecosystems by regulating the abundance or density of the host populations, establishing food chains, and structuring animal communities (Lafferty and Kuris, 2005; Thomas et al., 2005).

The Neotropical region contains the largest number of freshwater fish species, in which Characiformes, Siluriformes, and Gymnotiformes represent approximately 77% of the species (Albert and Reis, 2011). The order Siluriformes comprises more than 3,600 valid species of which 2,087 occur in the Neotropics distributed amongst 16 families. However, the real number of species and geographic distribution of
Neotropical siluriforms is unknown, with 35% of the species remaining to be described (Ota et al., 2015 and references therein). Siluriformes constitutes a monophyletic group whose species are keys to historical biogeography due to their global distribution and primarily freshwater habitat (Sullivan et al., 2006). Even though they are highly diverse, abundant, and of economic importance as food and ornamental fishes, there is a paucity of knowledge about their helminth parasites (Mendoza-Palmeiro et al., 2012; de Chambrier et al., 2015a).

Monogeneans represent the most diverse group of fish parasites in South America (Luque et al., 2016). From the vast global diversity of monogenean dactylogyrids from catfishes, 17 genera and more than 90 species are described originally from the Neotropical region with a recent increase in species described by means of integrative taxonomy (Cohen et al., 2013; Acosta et al., 2017a,b; Aguilar et al., 2017; Acosta et al., 2018, 2019; Franceschini et al., 2018; Yamada et al., 2018; Mendoza-Palmero et al., 2019; Franceschini et al., 2020). Moreover, Mendoza-Palmeiro et al. (2012) listed about 60 undescribed species from catfishes from the Peruvian Amazonia, which shows that the current number of known species of Neotropical dactylogyrids represents a small portion of the real diversity (Mendoza-Palmero et al., 2015). Trematoda is the second-richest group of fish helminth parasites in South America (Luque et al., 2016). However, it is estimated that less than 5% of the fish fauna in South America have been studied for digenean parasites (Choudhury et al., 2016). Kohn et al. (2007) presented the only exhaustive checklist of digenean parasites of fishes of South America, with 111 records of digeneans from 55 catfish species. However, the actual number of host-parasite associations for digeneans of siluriforms in South America has certainly increased over the last 12 years. Cestoda is the third species-rich group of helminths parasites of fishes in South America (Luque et al., 2016). Recently, Alves et al. (2017) published a checklist of fish cestodes from South America, presenting 238 records of cestodes from 77 siluriform species. Nematoda represents the fourth species-rich group of helminth fishes in South America (Luque et al., 2016). The most recent checklist of nematodes from Brazil listed 253 records in 77 siluriform fish species (Luque et al., 2011). Acanthocephalans are the least representative group of fish helminth parasites in South America (Luque et al., 2016). The latest checklist of acanthocephalans associated with fishes from Brazil presents only 21 records in 19 siluriform species (Sanctos et al., 2008). A list presenting previous records of helminths from the same catfish species sampled for this study is provided as Supplementary data.

Brazil is considered a hotspot for biodiversity and holds the highest number of freshwater fish species in the Neotropical region (Heywood, 1995; Luque and Poulin, 2007). The Upper Paraná river basin harbors approximately 211 fish species in ten orders, 41 families and 126 genera, of which 37% belong to Siluriformes (Ota et al., 2018). Ichthyofaunistic surveys of the Aguaipe River (Upper Paraná River basin, municipality of Castilho, São Paulo State, Brazil) in 2011 and 2012 revealed that Siluriformes constituted the largest portion (45.2%) of the fish orders present (Vilela et al., 2013). Prior to the present study, Yamada et al. (2017) was the first and only study on the ecology of helminth communities of siluriform hosts [Auchenipterus osteomystax (Miranda, 1918) and Trachelyopterus galeatus (Linnaeus, 1766)] from the same portion of the Aguaipe River. Therefore, the aim of this study was to characterize the helminth fauna of eight of the most abundant siluriform species from the Aguaipe River.

2. Material and methods

2.1. Sampling of hosts and helminth parasites

This study was conducted in one portion (approximately 3 km of sampling area) of the Aguaipe River [21°03′36″ S, 51°45′39″ W (Fig. 1)], a tributary of the Paraná River, municipality of Castilho, São Paulo State, Brazil. The sampling area is located inside the conservation unit “Reserva Particular do Patrimônio Nacional (RPPN) Foz do Rio Aguaipe”.

Catfishes belonging to eight species were collected from August 2013 to November 2014 by angling, gill nets, and multifilament cast nets (Table 1). The fishes were collected under the permit license number 577/2015 IBAMA (Brazilian Institute of Environment and Renewable Natural Resources). Hosts were euthanized using spinal cord severance and most of the fish specimens were placed individually in plastic bags, frozen, and transported to the Department of Parasitology, Institute of Bioscience, São Paulo State University (UNESP), municipality of Botucatu, São Paulo State, Brazil. Some hosts were examined on site. In the laboratory, they were defrosted, weighed, measured, and examined for helminth parasites. Classification and nomenclature of hosts followed Froese and Pauly (2018).

The body, fins, nasal cavity, gills, eyes, and inner face of the operculum of the fish hosts were examined for ectoparasites. Following external examination, a longitudinal incision in the ventral surface was made and all inner organs were removed and separated. The visceral cavity and all organs were examined using a stereomicroscope. The helminths collected were preserved in 70% ethanol and some were preserved in 96% ethanol for molecular analyses. For species identification, the monogeneans were mounted on slides with Hoyeer’s or Grey’s medium, and/or a mixture of glycerin-ammonium picrate (GAP) to study sclerotized structures (Humason, 1979; Kritsky et al., 1986a; Ergens, 1969), while some specimens were stained with Gomori’s trichrome to study internal organs. Digeneans and cestodes were stained with carmine and cleared with clove oil, while the nematodes were cleared with lactophenol (Eiras et al., 2006). The parasites were identified and analyzed using an Olympus BX51 microscope equipped with DIC and phase contrast optics and the Qwin Lite 3.1 (Leica) computerized system for image analysis with differential interference contrast (DIC). The methodology described in Días et al. (2004) was followed to estimate the number of specimens of the nematode Rodenia rondoni Travassos, 1920 from Pierororas granulosus (Valenciennes, 1821).

Voucher specimens are deposited in the Helminthological Collection of the Instituto de Bio-ciências de Botucatu (CHBB), São Paulo State, Brazil (deposit numbers provided in Table 2).

2.2. Statistical analyses

The prevalence, infection/infestation mean intensity, and mean abundance of the parasites were determined following Bush et al. (1997). Analyses were carried out at component community level (all helminths in all hosts) and at infracommunity level (all helminths in each individual) (Holmes and Price, 1986).

To determine the ecological attributes of the helminth communities, the following indices were calculated: (a) Shannon-Wiener diversity index that was calculated at the component community level. This index was used to measure the order or disorder in a system, by attributing greater weight to rare species, and was relatively independent of sample size (Krebs, 1989; Begon et al., 2007); (b) Simpson index to analyze the diversity of parasites, which was calculated at component community level ranging from 0 (low diversity) to 1 (high diversity); (c) Berger-Parker index was used to demonstrate the dominance of parasite species, which was calculated at the infracommunity level (Krebs, 1989); and (d) Discrepancy index (D), described by Poulin (1993) that was used to evaluate the spatial distribution of parasites based on their abundance. This index ranges from 0 to 1, interpreted as: D = 0, all hosts harboring a similar number of parasites; D = 1, all parasites found in a single host. This analysis was calculated using the Quantitative Parasitology 3.0 software (Rózsa et al., 2000). Shannon-Wiener, Simpson, and Berger-Parker indices were calculated using the software PAST (version 4.3) (Hammer et al., 2001).
3. Results

A total of 405 host specimens were screened for ecto- and endohelminth parasites. Data on the number of helminth specimens collected by species, prevalence, mean intensity of infection, mean abundance, and infection/infestation sites for all helminths found, and whether each helminth represents a new host record are presented in Table 2. Photomicrographs of the helminths collected are available as Supplementary data (Fig. S1–S8).

Four hundred host specimens (99%) were infected with at least one helminth taxon. A total of 517,775 helminth specimens were recovered in this study, with a mean of 1,278.45 parasites per individual fish. Fifty helminth parasite taxa were found: 23 monogeneans, 13 digeneans, 11 nematodes, and three cestodes. Of the 38 adult helminth taxa found in this study, only five occurred in more than one host: the monogeneans *Ameloblastella formatrium* Mendoza-Franco, Mendoza-Palmero et Scholz, 2016 and *Telethecium nasalis* Kristky, Van Every et Boeger, 1996; the digenean *Genarchella* sp.; and the nematodes *Procamallanus (Spirocamallanus) inopinatus* Travassos, Artigas et Pereira, 1928, and *R. rondoni*. Of the 12 metacercarial and/or larval stage found in this study, only 3 occurred in more than one host: *Austrodiplostomum* sp. metacercariae and Type 1 metacercariae of Diplostomidae, and the nematode *Contracaecum* sp. larvae (see Table 2 for host species).

Metacercariae of *Austrodiplostomum* sp. were the most widely distributed helminth, occurring in seven fish species (except in *P. granulosus*). Type 1 metacercariae of Diplostomidae also showed wide distribution, occurring in six host species (see Table 2 for host species).

The helminth taxon that showed the highest mean intensity of infection \[8,442.6 ± 1,340.7 (1–42,560)\] and mean abundance \[7,870.2 ± 1,279.7 (0–42,560)\] was the nematode *R. rondoni* from *P. granulosus*, followed by the nematode *Parasynodontisia petterae* Moravek, Kohn et Fernandes, 1992 (mean intensity of infection \[449 ± 88.6 (4–1,432)\]; mean abundance \[389.2 ± 81.6 (0–1,432)\]) from *Rhinelepis aspera* Spix et Agassiz, 1829. The helminth taxon with the greatest number of specimens recovered was *R. rondoni* from *P. granulosus* (n = 464,343) followed by *P. petterae* (n = 11,676) from *R. aspera*. Table 3 summarizes data on overall prevalence, number of taxa, number of specimens, mean per individual host, richness, and mean richness of the helminths from the eight siluriform species, along with Simpson, Shannon-Wiener, and Discrepancy indices of the helminth communities of each host species. It was not possible to calculate the discrepancy index for *P. granulosus* because the maximum intensity was...
Table 2
Number of specimens (N); Prevalence (P); mean intensity of infection (MII); mean abundance (MA); and infestation/infection site (IS) of the helminths found in the eight fish species from the Aguapeí River, Upper Paraná River basin, municipality of Castilho, São Paulo State, Brazil. MII and MA are showed as mean ± standard error (minimum–maximum). Number of voucher specimens deposited at the Helminthological Collection of the Instituto de Biociências de Botucatu (CHIBB), São Paulo State, Brazil, are provided below the helminth tax name.

| Siluriform hosts and helminths | N | P (%) | MII | MA | IS |
|--------------------------------|---|-------|-----|----|----|
| **Doradoridae**                |   |       |     |    |    |
| Monogenea                      |   |       |     |    |    |
| **Cotylurus balliocirrus**     | 8,820 | 98 | 152 ± 21.5 (9–862) | 149.5 ± 21.3 (0–862) | G |
| **Vancleavesiananae**         | 10,659 | 98 | 180 ± 29.7 (2–1225) | 176.8 ± 29.4 (0–1225) | G |
| Digenese                       |   |       |     |    |    |
| **Dudayreura oxycephala**     | 638 | 66 | 16.3 ± 6.3 (1–246) | 10.8 ± 4.2 (0–246) | I |
| Type 1 metacercariae of Diplostomidae* (CHIBB 8731) | 1 | 1 | – | 0.01 ± 0.01 (0–1) | C |
| Cestoda                        |   |       |     |    |    |
| **Proctoecephaloidae gen. sp.** | 3 | 5 | 1 (1–1) | 0.05 ± 0.02 (0–1) | I |
| **Trachyderidae**              |   |       |     |    |    |
| Monogenea                      |   |       |     |    |    |
| **Ameloblastella magna**      | 67 | 48 | 2 ± 0.2 (1–5) | 0.9 ± 0.2 (0–5) | G |
| Type 1 metacercariae of Diplostomidae* (CHIBB 8736) | 22 | 7 | 4.4 ± 1.8 (1–11) | 0.3 ± 0.2 (0–11) | Go |
| Type 2 metacercariae of Diplostomidae* (CHIBB 8737) | 32 | 8 | 4.8 ± 2.6 (1–18) | 0.4 ± 0.3 (0–18) | G |
| Cestoda                        |   |       |     |    |    |
| **Proctoecephaloidae gen. sp.** | 1 | 1 | – | 0.01 ± 0.01 (0–1) | I |
| **Heptapteridae**              |   |       |     |    |    |
| Monogenea                      |   |       |     |    |    |
| **Aphanoblastella magna**     | 1 | 2 | – | 0.02 ± 0.02 (0–1) | G |
| **Vancleavesiananae**         | 339 | 87 | 9.7 ± 1.8 (1–48) | 8.5 ± 1.7 (0–48) | G |
| Cestoda                        |   |       |     |    |    |
| **Ameloblastella formianum**  | 18 | 20 | 2.2 ± 0.5 (1–5) | 0.4 ± 0.2 (0–5) | E |
| **Aphanoblastella magna**     | 10 | 7 | 3.3 ± 0.3 (3–4) | 0.2 ± 0.1 (0–4) | I |
| **Genachella sp.**            | 23 | 35 | 1.6 ± 0.2 (1–3) | 0.6 ± 0.1 (0–3) | S |
| **Phyllostomum sp.**          | 8 | 10 | 2.7 ± 0.2 (1–4) | 1.7 ± 0.2 (0–4) | I |
| Type 1 digenean (CHIBB 8745–55) | 35 | 5 | 17.5 ± 16.5 (1–34) | 0.8 ± 0.8 (0–34) | I |
| **Unidentified metacercariae** (CHIBB 8756) | 66 | 7 | 22 ± 16.1 (2–54) | 1.6 ± 1.3 (0–54) | G |
| Nematoda                       |   |       |     |    |    |
| **Brasilinema pimelodei**     | 313 | 57 | 13 ± 3.8 (1–75) | 7.8 ± 2.5 (0–75) | I |
| **Rondonia rondoni**           | 2,934 | 17 | 419 ± 280 (1–15) | 1.4 ± 0.7 (0–15) | I |
| **Procormus acrodon**         | 339 | 87 | 9.7 ± 1.8 (1–48) | 8.5 ± 1.7 (0–48) | G |
| Contraescucum sp. larvae* (CHIBB 8746–47) | 293 | 53 | 7.9 ± 1.7 (1–52) | 4.2 ± 1.0 (0–52) | SB |
| **Loricariidae**               |   |       |     |    |    |
| Monogenea                      |   |       |     |    |    |
| **Gyrodactylidae gen. sp. 1** | 8 | 5 | 2 ± 0.4 (1–3) | 0.1 ± 0.05 (0–3) | G |
| Digenese                       |   |       |     |    |    |
| **Heteropriapulus anchoragei** | 95 | 44 | 2.7 ± 0.7 (1–20) | 1.2 ± 0.3 (0–20) | G |
| **Heteropriapulus bittosus**  | 34 | 13 | 1 ± 0.1 (1–3) | 0.4 ± 0.08 (0–3) | G |
| **Heteropriapulus heterotorys** | 653 | 66 | 12.3 ± 2.4 (1–83) | 8.2 ± 1.7 (0–83) | G |
| **Heteropriapulus microcertras** | 171 | 60 | 3.5 ± 0.5 (1–20) | 2.1 ± 0.4 (0–20) | G |
| **Heteropriapulus pteroglychi** | 55 | 62 | 2.6 ± 0.6 (1–13) | 0.7 ± 0.2 (0–13) | G |
| **Heteropriapulus simplex**  | 113 | 62 | 11.3 ± 19 (1–69) | 7 ± 1.4 (0–69) | G |
| **Telebothria nasalis** (CHIBB 510-13L) | 144 | 44 | 4.1 ± 0.7 (1–17) | 1.8 ± 0.4 (0–17) | NC |
| **Trinigrus periginis**        | 294 | 12 | 29.4 ± 21 (1–246) | 14.7 ± 12.2 (0–246) | G |
| Unidentified (CHIBB 514–17L) | 14 | 12 | 1.4 ± 0.1 (1–2) | 0.2 ± 0.05 (0–2) | G |
| Unidentified (CHIBB 518–21L) | 24 | 10 | 1.4 ± 0.1 (1–9) | 0.3 ± 0.1 (0–9) | G |

(continued on next page)
The helminth component community of *P. gracilis* presented low diversity (Table 3). The only new host record in *P. gracilis* in this study is Type 1 metacercariae of Diplostomidae. The helmminth community of *Trachydoras paraguayensis* (Eigenmann et Ward, 1907) is the second most diverse, according to the diversity indices values (Table 3).

### Table 3

| Host                  | P (%) | NT | N | MH | R   | MR | SI | SWI | DI  |
|-----------------------|-------|----|---|----|-----|----|----|-----|-----|
| **Doradidae**         |       |    |   |    |     |    |    |     |     |
| *Perodoras granulosus*| 100   | 6  | 484,466 | 8,211.28 | 1-4 | 3.67 | 0.08 | 0.21 | –   |
| *Trachyurus paraguayensis* | 100 | 14 | 2,293 | 32.75 | 1-8 | 4.4 | 0.73 | 1.68 | 0.54 |
| **Heptapteridae**     |       |    |   |    |     |    |    |     |     |
| *Pimelodella avanhandavae* | 100 | 12 | 3,856 | 96.4 | 1-5 | 3.2 | 0.41 | 0.93 | 0.78 |
| **Loricariidae**      |       |    |   |    |     |    |    |     |     |
| *Loricaria cichlids platyfish* | 100 | 8  | 8,753 | 109.4 | 1-4 | 2.8 | 0.52 | 0.93 | 0.41 |
| *Peyreguichthys ambrosettii* | 96  | 11 | 2,115 | 26.4 | 1-8 | 3.56 | 0.8 | 1.87 | 0.6  |
| *Rhinelepis aspera*   | 100   | 6  | 12,090 | 403  | 2-4 | 2.53 | 0.07 | 0.17 | 0.5  |
| **Pimelodidae**       |       |    |   |    |     |    |    |     |     |
| *Hemisarcomia platyhexa* | 95   | 7  | 1,253 | 59.7 | 1-4 | 2.34 | 0.31 | 0.69 | 0.6  |
| *Sorubim lima*        | 100   | 7  | 2,948 | 117.9 | 1-5 | 3.3 | 0.67 | 1.20 | 0.52 |

Infection/infestation sites: Su – surface; NC – nasal cavity; G – gills; E – eyes; Go – gonads; SB – swim bladder; L – liver; S – stomach; I - Intestine; F – flesh; C – cavity. 

* New host record.

* Data on P, MII, and MA have first been published in Acosta et al. (2018).

* Data on P, MII, and MA have first been published in Yamada et al. (2018).

* Data on P, MII, and MA have first been published in Acosta et al. (2017b).

* Data on P, MII, and MA and deposit number (CHIBB) have first been published in Franceschini et al., 2020.

* Deposit numbers (CHIBB) have first been published in Acosta et al. (2017b).
The monogenean *A. formatum*; the digeneans *Austrodiplostomum sp.* metacercariae, and the nematodes *Brasilinema pimelodellae* Moravec, Kohn et Fernandes, 1992, *R. rondoni*, and *Contraecuecum sp.* larvae are new host records for *P. avanhandavae*. The helminth component community of *Genarchella* is not very diverse, as *Hemisorubim platyrhynchos* host records for *Tomidae*, and Type 1 metacercariae are new host records for *D. platymetopon*. The helminth component community of *P. avanhandavae* also tends to show an aggregated pattern (Table 3). For dactylogyrids, the host species *P. avanhandavae* presented an unexpected diversity, harboring nine different species on the gills and one in the nasal cavity (see Table 2). The monogeneans *T. nasalis, Unilatus britannii* Mizelle, Kritsky et Crane, 1968, and *Unilatus unilatus* Mizelle et Kritsky, 1967; and the digeneans *Austrodiplostomum sp.* metacercariae are new host records for *P. avanhandavae*. The diversity of the helminth component community of *R. aspera* was the lowest among all host species analyzed in this study, which is shown by the diversity indices values. The monogenean *T. nasalis*; and the digeneans *Austrodiplostomum sp.* metacercariae, and Type 1 metacercariae of Diplostomidae represent new host records for *R. aspera*. The helminth component community of *Hemisorubim platyrhynchos* (Valenciennes, 1840) is not very diverse, as shown by the diversity indices values, and it tends to show an aggregated pattern. The monogenean *A. formatum*; and the digeneans *Austrodiplostomum sp.* metacercariae, and Type 1 metacercariae of Diplostomidae; and the nematode *Contraecuecum* sp. larvae represent new host records for *S. lima*.

Even though monogenean was the most diverse group, Berger-Parker index showed dominance by nematodes in six host species (Table 2). *A. formatum* larvae in *S. lima, P. petterae* in *R. aspera, R. rondoni* in *P. granulosus* and *P. avanhandavae*, *Ichtiohyus* *lateraliter* Moravec, Kohn et Fernandes, 1992 in *T. paraguayensis*, and *Raphidascaris* *Sprentascaris* *mahnerti* (Petter and Cassone, 1984) in *L. platymetopon*. The monogeneans *Nanayella ampolifacis* Acosta, Mendoza-Palmero, Silva et Scholz, 2019, and *Heteropriapulus heterotylus* (Sprent et León, 2004) were the dominant species in the hosts *H. platyrhynchos* and *A. avanhandavae*, respectively (Table 4).

### 4. Discussion

Monogenea was the most diverse parasite group collected in this study, representing 46% of the helminth taxa found. Monogenea represents a diverse group of parasites regarding numbers of species, as well as their morphology and ecology. Moreover, these parasites have a phylogeny that is well resolved at least to the family level (Poulin, 2002). Monogenea tends to be host-specific with most species infecting only one or few host species, which makes the parasites of this group suitable to investigate their diversification in the past and their diversity in the present (Poulin, 1992, 2002; Sasal et al., 1998). From the 23 monogenean species found in this study, only two species, *A. formatum* and *T. nasalis*, were found in more than one host species. The dactylogyrid *A. formatum* is recorded for the first time in a member of Heptapteridae (*P. avanhandavae*) since it is only known record in the literature is from the type-host *Hypophthalmus edentatus* Spix et Agassiz, 1829 (Mendoza-Franco et al., 2016) and now in the present study from *H. platyrhynchos*, but both belong to Pimelodidae. However, only a single specimen of *A. formatum* was found in *P. avanhandavae* in the present study, which could be an accidental infection. Both host species recorded in this study for *T. nasalis* belong to Loricariidae (*P. avanhandavae* and *R. aspera*). *Telesthecium nasalis* was described from the nasal cavity of *Osteoglossum bicirrhosum* (Cuvier, 1829) (Osteoglossiformes: Osteoglossidae) from the Amazon in Brazil (Kritis et al., 1996) and was reported only once more by Lemos et al. (2012) in the same host in the Brazilian Amazon. Every gall dactylogyrid species found in this study is a parasite of Neotropical siluroid hosts, presenting host specificity at family level (See host-parasite list of Supplementary data), with the exception of the occasional record of *A. formatum* aforementioned. Furthermore, 11 gall dactylogyrid species were recently described for some of the hosts from this study (Acosta et al., 2017a, 2018; 2019; Yamada et al., 2018), and such species have not yet been recorded in other siluroid host species or geographical locations. The host-parasite associations for dactylogyrids found in this study are similar to Braga et al. (2014), which revealed, by analyses of network interaction, that each freshwater fish order has a unique composition of genera of gall monogeneans in the Neotropics.

Digenaea was the second most diverse group in this study (26% of the helminth taxa found). Five adult digenean species were found: *Dadicryrema oxycephalum* (Diesing, 1836), *Dadatryrema sp.*, and Type 1 digenean from the intestine; *Genarchella sp.* from the stomach; and *Phyllodistomum sp.* from the gonads (Table 2). Species of *Dadatryrema* are generalist, being reported in several different host species in Brazil, Argentina, and Venezuela (Pantoja et al., 2019 and references therein). Species of *Genarchella* are widely distributed in characids and siluriforms in the Neotropical region, with several records in Mexico, Central America, Venezuela, Brazil, Argentina, and Uruguay (Scholz et al., 1995; Kohn et al., 2007). Species of *Phyllodistomum* usually inhabit the urinary bladder and/or ureters of marine and freshwater fishes globally (Stunzens et al., 2017; Cutmore and Gribb, 2018). Five species of *Phyllodistomum* are recorded in eight marine and freshwater fishes in South America (Kohn et al., 2007), and two species were recently described in the Neotropical region (Razo-Mendivil et al., 2013; Pérez-Ponce de León et al., 2015). The *Phyllodistomum* species from this study were found in the gonads of *P. avanhandavae*, however, the parasites might have moved from the urinary bladder. The findings of adult digeneans in fishes indicate that the studied environment is in suitable ecological conditions to enable these parasites to complete their life cycle, which is complex and requires the presence of invertebrates: mollusks as the first host, and some invertebrates (copepods and aquatic arthropods) as the second host.

Eight digenean taxa occurred as metacercariae in the hosts analyzed in this study (Table 2). Metacercariae of *Austrodiplostomum sp.* are widely distributed in the Neotropical Region in a broad variety of freshwater host families (Ramos et al., 2013). These metacercariae are usually found in the eyes (as in this study), which may lead to host’s blindness and even mortality (Locke et al., 2015). Five morphotypes of diplomodium metacercariae were found in this study. A considerable number of Type 1 metacercariae of Diplostomidae found in the body cavity of some host specimens was progenetic (Fig. S4G and Fig. S8E of Supplementary data). Metacercariae of *Clinostomum sp.* were found only in *L. platymetopon* (Table 2) in this study. However, metacercariae of *Clinostomum* have been reported in many different fish species in Brazil and all over the world, showing no host-specificity (Locke et al., 2014; Acosta et al., 2016a). The presence of metacercariae in fishes from the studied area indicates that this ecosystem possesses all the required hosts for digeneans with birds, reptiles, and even mammals as their final host, to complete their life cycle. Furthermore, it can be suggested that every host species from this study plays an important role as an intermediate host of these digeneans, being used as a food resource by their final host.

Nematoda was the third most diverse group in this study (22% of the helminth taxa found). Eight nematode species were found as adults, and three in the larval stage (Table 2). The hosts *T. paraguayensis* and *P.
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Table 4

Berg-Rarker index (B–P) for the helminth species of the eight siluriform species from the Aguapei River, Upper Parana River basin, municipality of Castilho, Sao Paulo State, Brazil. Abbreviations: met. – metacercariae; P. trachydrasorus – Paracotmetoelectricum trachydrasorus; Procamallanus (S.) inoinitus – Procamallanus (S.) inoinitus; P. (S.) inoinitus 4th stage larv. – Procamallanus (S.) inoinitus 4th stage larvae; Raphidascaris (S.) mahneri – Raphidascaris (S.) mahneri.

| Hemiascomin platyrhynchos | B–P | Sorubim lima | B–P | Rhinelepis aspera | B–P | Piranosorus granulosus | B–P |
|---------------------------|-----|-------------|-----|------------------|-----|-----------------------|-----|
| Nanayella amplusfacicul | 0.822 | Contracaecum sp. larvae | 0.378 | Paraynododiniasia petersae | 0.966 | Rondonia rondoni | 0.958 |
| Ameloblastella formalium | 0.079 | Nanayella fluctuностaria | 0.374 | Demoliodermis rhiapleisi | 0.027 | Vancleavesia juanacensae | 0.022 |
| Nanayella processualis | 0.068 | Spantulfer maringensis | 0.222 | Type 1 metacercariae | 0.004 | Costeolethrum holbroi | 0.018 |
| Type 1 metacercariae | 0.023 | Austrodiplostomum sp. met. | 0.009 | Heteropriapulus semitorituris | 0.002 | Dadaytrema oxycephalum | 0.011 |
| Austrodiplostomum sp. met. | 0.013 | Type 1 met. of Diplostomidae | 0.008 | Austrodiplostomum sp. met. | 0.001 |
| Type 1 met. of Diplostomidae | 0.002 | Manausia bracodema | 0.008 |
| Nemata larva | 0.001 | Genarchella sp. | 0.001 |

Pimelodethallia avanhandovea | B–P | Pterygoplychthys ambreti | B–P | Trachydrasorus paraguayensis | B–P | Loricarichthys platymeretobon | B–P |
|---------------------------|-----|------------------|-----|-------------------|-----|------------------|-----|
| Rondonia rondoni | 0.761 | Heteropriapulus heterocerus | 0.309 | Ichthyosarcis laterifilamenta | 0.458 | Raphidascaris (S.) mahneri | 0.642 |
| Aphysoblastella magnus | 0.088 | Heteropriapulus simplex | 0.268 | P. trachydrasorus | 0.180 | Diplostomidae met. Type 1 | 0.118 |
| Brazilhoma pinellidae | 0.081 | Tringyus peregins | 0.139 | Contracaecum sp. larvae | 0.128 | Clitmuncostom sp. metaceriaae | 0.003 |
| Spininctis uscrusentetis | 0.025 | Heteropriapulus broxolpletis | 0.081 | P. (S.) inoinitus 4th stage larv. | 0.063 | Diplostomidae met. Type 4 | 0.003 |
| Unidentified metacercariae | 0.017 | Telelethecium nasalis | 0.088 | Procamallanus (S.) inoinitus | 0.055 | Diplostomidae met. Type 5 | 0.002 |
| Type 1 digenean | 0.009 | Heteropriapulus anchordriatius | 0.045 | Neoparareuratum travassos | 0.053 | Gyrodactyli gen. sp. 1 | 0.001 |
| Genarchella sp. | 0.006 | Austrodiplostomum sp. met. | 0.032 | Ameloblastella sp. | 0.029 |
| Austrodiplostomum sp. met. | 0.005 | Heteropriapulus platyrhynchos | 0.026 | Type 3 met. of Diplostomidae | 0.014 |
| Contracaecum sp. larvae | 0.003 | Heteropriapulus bitomus | 0.016 | Type 2 met. of Diplostomidae | 0.010 |
| Dadaytrema sp. | 0.003 | Umlatlas umilatlas | 0.011 | Pavanelliella paranelli | 0.007 |
| Phygodistomum sp. | 0.002 | Umlatlas britani | 0.007 | Austrodiplostomum sp. met. | 0.001 |

avanhandovea had the most diverse nematode communities (3 adult species and 2 species in larval stage; and 3 adult species and 1 species in the larval stage, respectively (see Table 2)). Both host species are demersal (Froese and Pauly, 2019). T. paraguayensis is considered a bottom-feeder species, feeding on organisms from the substrate, with additional records of arthropods and debris (Agostinho et al., 1997; Peretti and Andrian, 2004), whereas P. avanhandovea feed mainly on insect larvae (Hahn et al., 2004). Host diet and habitat are important factors in helmint acquisition (Dociog, 1970; Guidelli et al., 2003). Nematodes have indirect life cycles, in which fish can act as both final and intermediate hosts (Morace, 1998). In life cycles with fish as final hosts, the eggs hatch in the water and are ingested by an invertebrate, which is then preyed upon by the final host (Eiras et al., 2010). Therefore, the feeding habits and the demersal habitat of T. paraguayensis and P. avanhandovea might expose them to a broader variety of nematode parasites than other potential hosts. The presence of nematode larvae in some fish species (T. paraguayensis, P. avanhandovea, H. platyrhynchos, and S. lima) in this study indicate that the environment is suitable for the completion of their life cycle, since fish-eating birds and mammals are abundant in the studied area (Matsunaka et al., 2014). Additionally, these fish species play an important role as inter- mediate hosts in the life cycle of these nematodes. The presence of anisakid larvae (Contracaecum sp.) in S. lima draws attention to the risk of human infection since this fish species is valued for consumption. Even though Contracaecum sp. larvae encyst in the viscera of fishes (Levshen et al., 2008), inappropriate evisceration and cooking of fish may result in human infection.

Cestoda was the least representative helminth parasite group in this study (6% of the taxa found). Only S. lima had a high infection with Spantulfer maringensis (Pavanelli and Rego (1989) (prevalence of 88%), and a moderate infection with Manausia bracodemora Woodland (1935) (prevalence of 24%). These two proteocephalids are known to para- sitize the sorubimine catfishes H. platyrhynchos and S. lima in South America (Alves et al., 2017). However, no infection with proteocephalids was recorded in this study for H. platyrhynchos.

Pterygoplychthys ambreti had the most diverse helminth community of this study, whereas R. aspera had the lowest (Table 2). Both hosts belong to Loricariidae, make use of a demersal habitat and have similar diet, feeding on fine particulate organic matter (mud), algae, and benthonic debris (Delariva and Agostinho, 2001; Orr and Fisher, 2009; Froese and Pauly, 2019). However, the high parasite diversity of P. ambreti is due to the number of dactylogyrids species (10) that is directly transmitted and not through the consumption of an inter- mediate host, whereas only three dactylogyrid species were found in R. aspera. Trachydrasorus paraguayensis had the second most diverse helminth component community, with a higher variety of parasite groups com- pared to P. ambreti (3 species of monogeneans, 4 digenens, 1 cest- ode, and 5 nematodes versus 10 species of monogeneans and 1 di- genean). The feeding habits of T. paraguayensis expose this host species to a broader variety of parasites, as discussed before, contributing to its helmint distribution.

To date, there have been only two other studies published on the helmint fauna (endoparasites) for two of the host species analyzed in this study. Guidelli et al. (2003) analyzed the endoparasite infra- communities of H. platyrhynchos from the Baia River, Upper Parana River floodplain, Brazil, and showed the digenean Crocodilocilicus pseu- destomata (Willemoes-Suim, 1870) as the most prevalent helmint taxon. However, this digenean species was not recorded in the present study. Ferrari-Hoeinghaus et al. (2007) presented a survey on digeneans from L. platymeretobon from the Upper Parana River floodplain, Brazil, and showed metacercariae Clitnusomus complanatum (Rudolph, 1819) as the most prevalent. Metacercariae of Clitnusomus were also found in L. platymeretobon from this study, but showed low prevalence (5%). As for the other hosts, the data available in the literature are related to hel- minth species descriptions or host records (see host-parasite list in Supplementary material).

The present study is the first complete survey on the diversity of helmints (ecto- and endoparasites) of the eight catfish hosts analyzed. With 38 new host records (see Table 2), this study contributes con- siderably to increasing the diffuse knowledge of helmint parasites of Neotropical siluriforms. Additionally, data on species diversity at component community and infracommunity levels of the parasites found will assist future comparative studies on the helmint fauna of the same host species in other areas of the Neotropical region. More studies on helminth diversity are still necessary for the Aguapei River since this study represents a small portion of the river (3 km of sampled area in a 420 km river). Therefore, the true diversity of parasites, in- cluding undiscovered species, is yet to be known.
Declaration of competing interest

The authors declare that there is no conflict of interest regarding the publication of this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijppaw.2020.01.003.

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