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Helminth parasites of South American fishes: current status and characterization as a model for studies of biodiversity

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Abstract

The South American subcontinent supports one of the world's most diverse and commercially very important ichthyofauna. In this context, the study of South American fish parasites is of increased relevance in understanding their key roles in ecosystems, regulating the abundance or density of host populations, stabilizing food webs and structuring host communities. It is hard to estimate the number of fish parasites in South America. The number of fish species studied for parasites is still low (less than 10%), although the total number of host–parasite associations (HPAs) found in the present study was 3971. Monogeneans, with 835 species (1123 HPAs, 28.5%), and trematodes, with 662 species (1127 HPAs, 30.9%), are the more diverse groups. Data gathered from the literature are useful to roughly estimate species richness of helminths from South American fish, even though there are some associated problems: the reliability of information depends on accurate species identification; the lack of knowledge about life cycles; the increasing number of discoveries of cryptic species and the geographically biased number of studies. Therefore, the closest true estimations of species diversity and distribution will rely on further studies combining both molecular and morphological approaches with ecological data such as host specificity, geographical distribution and life-cycle data. Research on biodiversity of fish parasites in South America is influenced by problems such as funding, taxonomic impediments and dispersion of research groups. Increasing collaboration, interchange and research networks in the context of globalization will enable a promising future for fish parasitology in South America.

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Introduction

There currently exists a consensus that parasite species represent a large fraction of the Earth's total biodiversity (Dobson *et al.*, 2008; Lafferty, 2012; Poulin, 2014), even though several questions remain about the magnitude of parasite diversity and their worldwide distribution. Luque & Poulin (2007) pointed out that studies on the biodiversity of fish parasites have intensified during past decades, but these organisms remain an underestimated component of the total biodiversity in many regions of the planet, suggesting that regional differences may reflect true biological patterns, which should be taken into account when selecting the target for local fish parasitology research. This situation is significantly increased when, in addition to taxonomic aspects, studies on the ecology of parasitic fauna are included.

South America is a region that includes six countries of megadiversity, with several regions of marine and freshwater environments. According to Miloslavich *et al.* (2011), marine areas of South America include almost 30,000 km of coastline and contain three different oceanic domains – the Caribbean, the Pacific and the Atlantic – including five marine subregions. The total number of marine fish species in South America has not been determined, but information about fish diversity by subregion is available (Miloslavich *et al.*, 2011), with three subregions having the highest number of species, namely the tropical east Pacific (1212), Humboldt Current System (1167) (Pacific Ocean) and the Brazilian Shelf (1294) (Atlantic Ocean). Concerning freshwater environments, larger river basins such as the Amazon, Orinoco, Paraguay and Paraná (among others) support a huge and complex network of tributaries that contains a high fish species biodiversity. According to Reis (2013), there are 6025 freshwater fish species in South America. This high regional fish biodiversity leads us to expect a high diversity of fish parasites as well. In this context, the study of South American fish parasites is of increased relevance in understanding their key roles in ecosystems, regulating the abundance or density of host populations, stabilizing food webs and structuring host communities. This knowledge could also be relevant to other topics of an applied nature, such as the impact of parasitism on regional pisciculture and fish-borne parasitic zoonoses. Thus, good knowledge of South American fish parasite diversity would be a useful tool for proper environmental management and conservation of global biodiversity.

Much of the research on this subject is dispersed, and several papers have been published in regional, local and unindexed journals; however, some checklists published during the past decade highlight the preliminary idea that fish helminth parasite biodiversity is clearly underestimated (Thatcher, 2006; Kohn *et al.*, 2007; Muñoz & Olmos, 2007, 2008; Santos *et al.*, 2008; Luque *et al.*, 2011; Cohen *et al.*, 2013; Paschoal *et al.*, 2015). This situation was reinforced by Luque & Poulin (2007) who stated that the number of host species with at least one parasite record was less than 10% of the total known fish species in the majority of countries of South America and the Caribbean, and pointed out that Brazil is a hotspot of parasite species biodiversity in South America, but they mentioned the possibility that these pattern differences may reflect regional discrepancies in study effort and local priorities for fish parasitology research.

This review provides an historical background and analysis of the current state of research on helminth parasites of fish in South America, and thence tries to point out some perspectives for future research in the region.

Historical background

The studies on helminth parasites from South America date back to the beginning of the 19th century, when the Portuguese court was transferred to Rio de Janeiro, together with the granting of permission for Austrian and Bavarian expeditions to collect specimens of invertebrates and vertebrates in the former Brazilian territory (Mason, 2015).

Sellow (1789–1831) and von Olfers (1798–1872) were important naturalists who collected helminths from vertebrates in South America, most of them described by Rudolphi (1771–1832) in his classical work *Entozoorum Synopsis* (Rudolphi, 1819). However, the most remarkable naturalist/collector was Natterer (1787–1843), who surveyed vertebrate hosts during a period of 18 years (from 1817 to 1835) in Brazil, crossing the whole country (Santos *et al.*, 2008). He sent to the collection currently known as the Naturhistorisches Museum, Vienna more than 1700 vessels containing parasitic helminths (Mason, 2012), a large number of them being collected from fish. Later, Diesing (1800–1867) described the majority of these species (unknown at the time) in the *Systema Helminthum* (Diesing, 1850, 1851, 1856), several of which are still recognized as valid. Rudolphi (1819) also worked on Natterer's material. During the same period, only a few putative species were described from fish in other countries, e.g. *Benedenia hendorffii* Linstow, 1889 and *Lophocotyle cyclophora* Braun, 1896, both from marine fish in Chile (Cohen *et al.*, 2013).

It is possible to outline the substantial and valuable contributions of some researchers to the development of South American helminthology throughout the 20th century, such as Travassos (1890–1970) and his students, who described several species of helminths, mainly of nematodes and trematodes from freshwater fish in Brazil (Dias *et al.*, 1990); Thatcher (1929–2011), who published more than 150 papers and several books on helminths and other metazoan parasites of fish from Amazonia (Boeger, 2011); Szidat (1892–1973), who was very important in Argentinian helminthology because, besides his description of more than 60 species, he introduced biogeographic concepts in his studies on fish parasites for the first time in South America (Ostrowski de Núñez, 1994; Choudhury & Pérez-Ponce de León, 2005); Tantaleán and Carvajal, who have increased our knowledge of helminth parasites from fish in Peru and Chile, respectively, and who are still publishing work focused on the taxonomy and ecology of these worms.

Taxonomy and systematics of the helminths parasitic in fish from South America

This section summarizes our knowledge on the parasitic flatworms (Platyhelminthes – Monogenea, Trematoda, Cestoda), roundworms (Nematoda) and spiny-headed

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worms (Acanthocephala) from South American fish, based on an extensive literary search gathered from different databases, i.e. Google Scholar, Web of Science and Biological Abstracts, and also supplemented from the Host–Parasite Database of the Natural History Museum, London, UK (Gibson *et al*., 2005). Furthermore, some checklists were considered: Cohen *et al*. (2013) for monogeneans; Kohn *et al*. (2007) for trematodes; Santos *et al*. (2008) for acanthocephalans; Moravec (1998), González-Solís & Mariaux (2011) and Luque *et al*. (2011) for nematodes; and Muñoz & Olmos (2007, 2008) for helminths from Chile.

Data on host–parasite associations (HPAs) from each country of South America (table 1) were considered, excluding hosts and parasites not identified at species level, as well as larval stages.

The following acronyms are used throughout the text: EMBRAPA, Empresa Brasileira de Pesquisa Agropecuária, Brazil; FIOCRUZ, Fundação Instituto Oswaldo Cruz, Brazil; INPA, Instituto Nacional de Pesquisas da Amazônia, Brazil; IPCAS, Institute of Parasitology, Biology Centre of the Academy of Sciences of the Czech Republic, České Budějovice; ISU, Idaho State University, USA; MHNG-PLAT, Muséum d'Histoire Naturelle, Geneva; MNHN, Muséum National d'Histoire Naturelle, Paris; SUNY, The State University of New York, USA; UA, Universidad de Antofagasta, Chile; UBA, Universidad de Buenos Aires, Argentina; UC, Pontificia Universidad Católica de Chile; UConn, University of Connecticut, USA; UEM, Universidade Estadual de Maringá, Brazil; UFPA, Universidade Federal do Pará, Brazil; UFPR, Universidade Federal do Paraná, Brazil; UFRA, Universidade Federal Rural da Amazônia, Brazil; UFRRJ, Universidade Federal Rural do Rio de Janeiro; UFRS, Universidade Federal do Rio Grande do Sul, Brazil; UFSC, Universidade Federal de Santa Catarina, Brazil; UNLP, Universidad Nacional de La Plata, Argentina; UNMdP, Universidad Nacional de Mar del Plata; UNMSM, Universidad Nacional Mayor de San Marcos, Peru; UofT, University of Toronto, Canada; USP, Universidade de São Paulo, Brazil; WBSR, Wellcome Bureau of Scientific Research, London, UK.

Monogenea

Monogeneans represent the most diverse group, with 835 species reported from the different countries and 1133 HPAs (tables 1 and 2). The first species to be described was *B. hendorffii* (Capsalidae) from the skin of *Coryphaena hippurus* Linnaeus, 1758 in Chile, followed by a long absence of studies (Cohen *et al*., 2013). With a few exceptions, not until 1965 did the number of publications steadily increase (fig. 1), starting with a series of papers entitled 'Studies on monogenetic trematodes' (Mizelle & Price, 1965; Mizelle *et al*., 1968; Mizelle & Kritsky, 1969a, b).

Freshwater monogeneans exhibited the major number of species, representing almost 64% of the HPAs. Of these, members of the family Dactylogyridae are by far the best known group, mostly parasitizing characiform fish in the Amazon River basin; even though gyrodactylids are also a species-rich group, being constantly the target of systematics and taxonomical studies (Boeger *et al*., 2006; Vianna *et al*., 2007, 2008; Kritsky *et al*., 2013). It is also worth mentioning the efforts to document the diversity of monocotylids of the genus *Potamotrygonocotyle* Mayes, Brooks & Thorson, 1981, specific parasites of potamotrygonid stingrays (Potamotrygonidae), which contains 12 species, 11 of which have been described only recently (Domingues & Marques, 2007, 2011).

Concerning the marine monogeneans, they also have representatives from both cartilaginous (4% of HPAs) and bony fish (32% of HPAs) hosts. The families with the highest number of reports are Diclidophoridae and Monocotylidae in osteichthyan and chondrichthyan hosts, respectively. The Atlantic Ocean exhibited the major number of HPAs (67%) compared to Pacific waters, these results are mainly due the numerous studies on marine teleost as hosts from the Brazilian coastal zone (Luque & Poulin, 2007; Justo & Kohn, 2015).

The uneven diversity of monogeneans, biased toward species parasitizing freshwater fish, is largely due to the efforts of an international partnership between Thatcher (INPA), Kritsky (ISU) and Boeger (UFPR), among other researchers (Boeger *et al*., 2006). They started a series of studies entitled 'Neotropical Monogenoidea' (currently in its 59th publication), which may be considered the benchmark series for any study focused on the taxonomy and systematics of this group in the South American hydrological drainages. Likewise, the substantial achievements of this research team contributed heavily to the geographical distribution of parasite richness, corresponding to their prolific taxonomic activities in Brazil (table 2).

Molecular phylogenetic reconstructions have been performed recently in systematics studies of Neotropical monogeneans (Boeger *et al*., 2014a; Sepúlveda *et al*., 2014; Mendoza-Palmero *et al*., 2015) and the use of this tool could shed light on the evolutionary history of this extraordinarily diverse group, as yet far from being completely known.

Trematoda

The second-richest group of helminths is represented by trematodes, i.e. digeneans and aspidogastreans, species of which have been reported from all countries of South America (662), apart from Bolivia, Guyana and Suriname. *Physochoerus tubulatus* (Rudolphi, 1819) was the first species reported in South America from the large eel *Muraena* sp., although, due to an inadequate description, the genus is considered *inquirendum* (Madhavi, 2008). Later, the number of publications increased, with a peak between 1979 and 1998 (fig. 1) when numerous helminthologists worked intensively; for example, Amato (UFRS), Kohn (FIOCRUZ), Fernandes (FIOCRUZ) and Thatcher, who mostly surveyed Brazilian fish hosts; Lunaschi (UNLP) who published a series of papers focused on freshwater fish hosts in Argentina; and Oliva (UA) who worked on marine fish hosts off the Chilean coast (Kohn *et al*., 2007). The earlier achievements of Manter and Travassos, whose contributions include the description of several species from marine fish in Galapagos and the neighbouring Pacific, as well as freshwater fish in Brazilian river basins, respectively (Manter, 1940; Dias *et al*., 1990), are also notable.

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Table 1. Geographical distribution of host–parasite associations, according to the main helminth taxa parasitic in South American fish (parasites and hosts with no specific identification, and parasite larvae were not considered).

	Monogenea				Trematoda				Cestoda				Nematoda				Acanthocephala				
	FW		MAR		FW		MAR		FW		MAR		FW		MAR		FW		MAR		
	Con	Ost	Con	Ost	Con	Ost	Con	Ost	Con	Ost	Con	Ost	Con	Ost	Con	Ost	Con	Ost	Con	Ost	Total
Argentina*	2	42	12	32	–	154	4	87	10	39	30	6	–	26	1	19	–	21	–	3	488
Bolivia	–	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	12
Brazil	33	552	4	180	–	197	3	352	62	117	28	3	2	404	3	95	–	60	–	22	2117
Chile	–	1	4	44	–	6	3	66	–	–	43	11	–	25	5	15	–	6	–	17	246
Colombia	–	14	–	6	1	14	1	4	4	4	18	–	2	6	–	–	–	9	–	–	119
Ecuador**	–	–	–	11	–	–	–	71	–	–	9	–	–	6	–	–	–	–	–	–	97
French Guyana	–	3	–	3	–	3	–	–	–	–	–	–	–	8	–	5	–	–	–	–	22
Guyana	–	2	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	4
Paraguay	–	1	–	–	–	7	–	–	2	41	–	–	–	119	–	–	–	2	–	–	172
Patagonia	–	–	16	15	–	–	6	56	–	4	–	8	–	8	–	5	–	17	–	4	139
Peru	4	58	6	60	–	8	6	54	14	59	31	4	–	25	5	10	–	6	–	1	351
Suriname	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–	7
Uruguay	–	–	5	8	–	3	1	6	–	2	9	1	–	1	–	–	–	1	–	–	37
Venezuela	–	–	–	2	–	9	–	69	15	5	20	–	3	24	–	4	1	8	–	–	160
Total	39	684	47	363	1	401	24	801	107	271	188	33	7	654	14	153	1	136	–	47	3971

FW, freshwater; MAR, marine; Con, Chondrichthyes; Ost, Osteichthyes.
*Including the Argentine–Uruguayan Common Fishing Zone. **Including the Galapagos Archipelago.

Table 2. Geographical distribution of parasite richness according to the main helminth taxa parasitic in South American fish (parasites with no specific identification and larval stages were not considered).

	Monogenea	Trematoda	Cestoda	Nematoda	Acanthocephala	Total
Argentina*	78	112	85	26	11	312
Bolivia	4	–	–	–	1	5
Brazil	471	266	121	143	37	1038
Chile	43	49	40	22	10	164
Colombia	16	43	21	4	6	90
Ecuador**	13	52	9	4	–	78
French Guyana	6	3	–	5	–	14
Guyana	2	–	–	2	–	4
Paraguay	1	3	40	46	1	91
Patagonia	24	28	8	10	8	78
Peru	120	47	88	26	6	287
Suriname	2	–	–	0	1	3
Uruguay	12	10	12	1	1	36
Venezuela	43	49	36	14	1	143
Total	835	662	460	303	83	2343

*Including the Argentine–Uruguayan Common Fishing Zone. **Including the Galapagos Archipelago.

So far, trematodes have been reported from marine (65% of HPAs) and freshwater teleosts (32% of HPAs). Only a few representatives have been found in chondrichthyans, i.e. two holocephalids harboured two species of aspidogastreans, and 12 elasmobranchs were parasitized mainly by members of the genus *Otodistomum* Stafford, 1904.

Regarding the HPAs, the trematodes showed the highest number (1227), even more than the most species-rich group (Monogenea), which seems to be greatly influenced by 'generalist' species that infect a wide spectrum of hosts, sometimes unrelated ones. For instance, *Aponurus laguncula* Looss, 1907 has been reported from 11 marine hosts belonging to nine families within four orders (Kohn *et al*., 2007). However, a re-assessment of the taxonomical status of this species from the western Mediterranean, combining morphological and molecular methods, suggested the presence of at least two morphologically distinct species of the '*A. laguncula* species complex' (Carreras-Aubets *et al*., 2011; Pérez-del-Olmo *et al*., 2016). In the same way, Oliva *et al.* (2015) demonstrated that the opecoelid *Helicometrina nimia*, a common digenean in marine fish from Chile, is in fact two different species. Thus, these 'generalist' species may correspond to more than a single taxon, and a higher diversity is expected rather than a euryxenic specificity (Miller *et al*., 2011).

In a special issue of the journal *Systematic Parasitology* (March 2016, Issue 3, pp. 219–306), distinguished trematodologists provided a comprehensive series of papers summarizing knowledge on the biodiversity of fish trematodes (Cribb, 2016). For marine species of Atlantic and eastern Pacific Oceans, Bray *et al*. (2016) compiled an extensive database of records, where they found a lower diversity of fauna in South America (through the ecoregions of Spalding *et al*., 2007) compared with the richest areas (Caribbean, Gulf of Mexico and Mediterranean sea). Nevertheless, part of the south-western Atlantic (somewhere from Cabo Frio, Brazil to the northern limit of the Patagonian coast, Argentina) presented the maximum number of records from the South America coastal zone, which is in accordance with our results (table 1). Freshwater trematodes from the Americas were reviewed by Choudhury *et al*. (2016), in particular by Núñez (UBA) and Santos (FIOCRUZ) for South American taxa. They outlined the lowest proportion of host species examined for parasites in this region (less than 5% of potential hosts) and stated that two hydrological systems in Brazil and Argentina are the main source of information, similar to the present results (87% of HPAs are derived from these two countries).

Experimental infections have been performed to elucidate trematode life cycles in South America (Choudhury *et al*., 2016), but molecular tools have shown a remarkable capacity for linking life-cycle stages, mainly when the larvae are morphologically distant from the adult forms (Jensen & Bullard, 2010; Locke *et al*., 2011; Womble *et al*., 2016). Despite several records of metacercariae from freshwater fish in South America (Ostrowski de Núñez & Gil de Pertierra, 2004), few data are available using an integrated morphological and molecular approach, e.g. *Austrodiplostomum compactum* (Lutz, 1928) (= *A. mordax*) has been isolated from more than 30 fish hosts (see references in Rosser *et al*., 2016); however, several of these larval diplostomids may corresponds to *A. ostrowskiae* Dronen, 2009. Sequences of mitochondrial genes from metacercarie in *Satanoperca* spp. from Brazil and Peru matched those from both larval and adult stages of *A. ostrowskiae* from eight fish (Cichlidae, Heptapteridae) and one species of fish-eating bird in Mexico, El Salvador and Venezuela (Locke *et al*., 2015; García-Varela *et al*., 2016). Most likely, these species are sympatric in South America (García-Varela *et al*., 2016).

Hence, as advocated by Choudhury *et al*. (2016), we agree that further robust taxonomic studies on fish trematodes should address an integrative approach rather than one based on a singular method of circumscription.

Cestoda

The tapeworms represents the third species-rich group, with 460 species found in all but four countries (table 2), even though they showed only 15% of HPAs (table 1).

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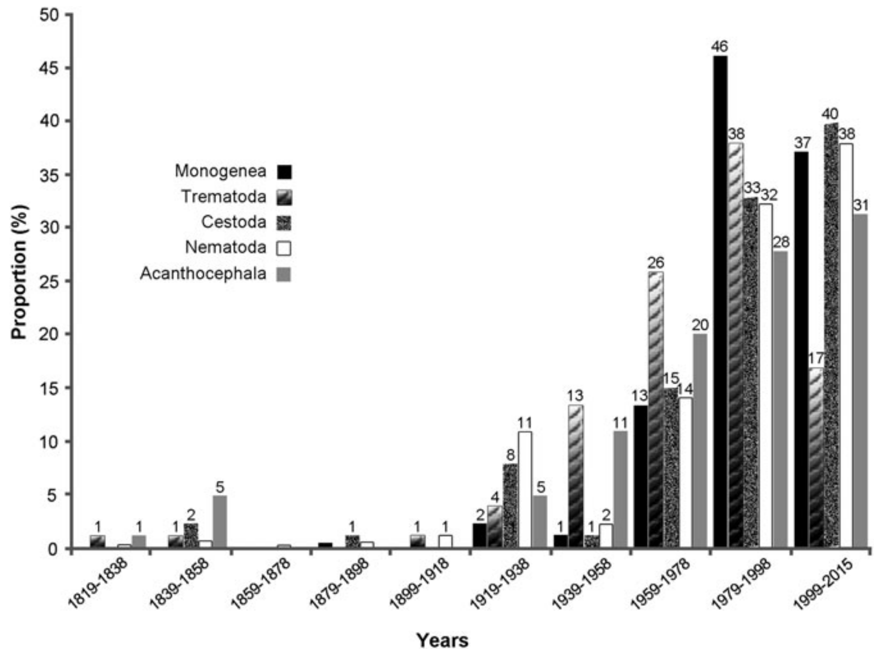

Fig. 1. Proportion of descriptions of new species and/or new geographic records (by countries) according to the main helminth taxa parasitic in fish from South America since 1819.

Diesing (1850) described several species collected by Natterer in Brazil and, seemingly, this is the first account on the group in fish from South America. The number of studies has increased regularly since 1919, reaching a peak between 1999 and 2015 (fig. 1). The National Science Foundation–Planetary Biodiversity Inventories (NSF–PBI) project 'A survey of the tapeworms (Cestoda: Platyhelminthes) from vertebrate bowels of the Earth' (2008–2014) has contributed largely for this growth, aiming to expand knowledge on the global diversity of tapeworms (see http://tapewormdb.uconn.edu). The project funded long-term studies on South American fish hosts from both freshwater and marine systems, which were carried out mainly by de Chambrier (MHNG) and Gil de Pertierra (UBA), both focusing on teleost hosts, as well as by Ivanov (UBA) and Marques (USP), both targeting elasmobranch hosts, together with other recognized cestodologists, e.g. Reyda (SUNY, Oneonta), Caira (UConn) and Scholz (IPCAS). Prior this period, the contributions of Woodland (WBSR) and Brooks (UofT) are also noteworthy; the former described 32 new species of proteocephalideans belonging to eight new genera from specimens collected in the early 1930s in the Amazon River, Brazilian streams (de Chambrier *et al.*, 2014), whereas the latter and partners have described more than 35 new species, 15 of which belong to the genus *Acanthobothrium* Blanchard, 1848 (Brooks *et al.*, 1981; Marques *et al.*, 1997). The studies of Rego (FIOCRUZ) and Pavanelli (UEM) in the 1980s and 1990s are worth mentioning, due to their contribution on the taxonomy of proteocephalideans in Brazil (Rego *et al.*, 1999). Recently, de Chambrier *et al.* (2015) updated a previous list of adult proteocephalidean tapeworms parasitizing freshwater teleosts from the Peruvian Amazon, and Alves *et al.* (2015) proposed a new genus and a new species parasitic of an endemic Amazonian siluriform fish.

Among the extant orders of tapeworms, assuming that Proteocephalidea is not included in the Onchoproteocephalidea (Arredondo *et al.*, 2014), 13 have been recorded in fish from South America, making the Proteocephalidea the most representative group so far, with over 100 species within 37 genera, primarily infecting freshwater siluriforms (81% of HPAs) in the Amazon and Paraná River basins. For instance, the second-richest order, Onchoproteocephalidea (*pro parte*), has only about 44 described/reported species, parasitizing marine and freshwater elasmobranchs (only *Acanthobothrium chilensis* Rego, Vicente & Herrera, 1968 is known from a teleost fish).

Despite the richest fauna of cestodes being in freshwater teleosts (45% of HPAs; table 1), the species infecting elasmobranchs from marine and freshwater systems are relatively well documented (295 HPAs) when compared with other helminth taxa (a total of 133 HPAs), exhibiting a large variety of forms and usually oioxenous (i.e. species-specific) associations with their hosts (Caira & Jensen, 2014). Marine teleosts, including two diadromous fish hosts (*Galaxias* spp.) showed the least number of records (6% of HPAs), being parasitized almost exclusively by botriocephalideans. The frequency of these cestodes varies between different depths of the ocean, and those infecting bathypelagic fish, living deeper than 1000 m, harbour a rather diverse fauna (Kuchta & Scholz, 2007). Since hosts at such depths are poorly studied for their parasites, together with several other obstacles involved in the study of botriocephalidean systematics (Kuchta *et al.*, 2008), a higher diversity is to be expected off the South American coast.

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Although marine teleosts are poorly known as definitive hosts of cestodes in South America, they are commonly reported as second intermediate or paratenic hosts for larval stages (metacestodes), mainly of diphyllobothriideans, 'tetraphyllideans' and trypanorhynchs (Palm, 1997; Luque & Poulin, 2004; Kuchta *et al.*, 2015). The accurate identification of these forms is generally problematic, because they lack key morphological traits that are present in their adult counterparts, and studies dealing with genetic characterization are scarce (Jensen & Bullard, 2010; Rozas *et al.*, 2012); the only exceptions are the larval trypanorhynchs that may be identified precisely based on their tentacular armature (Jensen & Bullard, 2010). Tetraphyllidean larvae tentatively termed *Scolex pleuronectis* Müller, 1788 and *S. polymorphus* Rudolphi, 1819 that have been reported widely in the south-western Atlantic Ocean (Luque & Poulin, 2004) are, in fact, a group of species that share morphological features (Jensen & Bullard, 2010). Maybe this collective group name even represents species from different taxa other than the artificial Tetraphyllidea (Jensen & Bullard, 2010).

The great diversity of cestodes from the Amazon and Paraná River basins, corresponding to the territories of Argentina, Brazil, Paraguay and Peru (table 2), mirrors the extraordinary diversity of the freshwater fish fauna inhabiting these river systems (Reis, 2013; Poulin, 2014), but the true species richness is rather far from being well known.

Nematoda

Despite the high general diversity of the phylum Nematoda, those worms parasitic in fish from South America represent the fourth taxon in terms of species reported from different countries, after Monogenea, Trematoda and Cestoda (table 2). However, the HPAs for Nematoda (21%) outperform those of Cestoda (15%) and Acanthocephala (3%). The first record of a nematode parasitizing fish in South America dates from 1819, represented by the description of *Oncophora melanocephala* (Rudolphi, 1819) (= *Trichocephalus gibbosus*) (Camallanidae) from *Thunnus thynnus* (Linnaeus, 1758) off the Brazilian coast (Luque *et al.*, 2011). One century later (1819–1919) just a few species had been described (see fig. 1), mainly due to the efforts of Diesing, Molin and von Drasche, working on helminth fauna of fish from Brazil (Moravec, 1998; Luque *et al.*, 2011). The taxonomic studies rose again during 1920–1935, a period of extensive research by Travassos, working on nematodes from freshwater fish in Brazil.

From the early 1980s until the later 1990s, the number of new species proposals increased dramatically compared with the historical trend of Nematoda parasitic in fish until this period (fig. 1). This scenario was possible because of the collaborations between European and South American researchers (or institutions), e.g. Petter (MNHN) working mainly in the north of the subcontinent, but also in Paraguay, where she described seven species of nematodes in freshwater fish during the year of 1984 (Petter & Cassone, 1984; Petter, 1984). It is also worth mentioning the work of Moravec (IPCAS) during the 1990s, in partnership with some Brazilian researchers from the FIOCRUZ, as well as with Thatcher from the INPA, resulting in the description of several new taxa (about 16 new species and four new genera) (Moravec, 1998; Moravec & Thatcher, 1999); thereby contributing much to our knowledge on the biodiversity of nematodes from fish in the Neotropics.

In the past decade, the number of taxonomic papers has continued to increase, mainly as a result of the efforts from Argentinean and Brazilian research groups on fish parasites (Timi *et al.*, 2006, 2009; Pereira *et al.*, 2015a; Vieira *et al.*, 2015). Furthermore, during this same period, the checklist of González-Solís & Mariaux (2011) on nematodes parasitic in fish from Paraguay also contributed to the number of new locality records (27), according to our data compilation (fig. 1).

The numbers of HPAs for Nematoda in table 1 reflect the fact that the parasite fauna from freshwater systems (HPA = 661, representing 80% of the total) is better studied than that from marine zones (HPA = 167, representing 20% of the total), which is a trend noted in all South American countries (Luque & Poulin, 2007). The total number of HPAs is highly influenced by those from Brazil, a wide and diverse territory, retaining a highly diverse freshwater fish fauna. The obvious explanation is that sampling efforts (mainly taxonomic) have concentrated on the parasite fauna from freshwater fish throughout the continent (similar to that of the previous analysis by Poulin, 2004); however, why the researchers have concentrated their efforts on the freshwater ichthyofauna is hard to answer. Possibly, the high availability of fresh, or even alive, fish from freshwater environments could influence the choice of the taxonomists, since the freshness of a parasite when fixed is fundamental for the preservation of its real morphological traits. Nevertheless, the greater diversification of freshwater than marine parasites of fish (Poulin, 2016) cannot be discarded as an influencing factor.

Finally, regarding the phylum Nematoda, the primary problems concerning its general taxonomy are related mainly to the taxa richest in species, such as Anisakidae Railliet & Henry, 1912, Camallanidae, Railliet & Henry, 1915 and particularly Cucullanidae Cobbold, 1864. These families retain a high number of species with poor description, lacking important data on their characterization, and some of them parasitize a wide spectrum of hosts (e.g. *Procamallanus* (*Spirocamallanus*) *inopinatus* Travassos, Artigas & Pereira, 1928 and *Cucullanus pinnai* Travassos, Artigas & Pereira, 1928 and its subspecies) (Moravec, 1998; Luque *et al.*, 2011). The problem is even worse within cucullanids, due their rather uniform morphology (Vieira *et al.*, 2015). The lack of molecular data is also a barrier to the elucidation of these taxonomic issues, as recently observed by Pereira *et al.* (2015a, b), these problems including the detection of possible cryptic or sibling species, as in the case of those host-generalist parasites.

This situation would also be applicable to the taxonomy of larval stages common in marine teleost fishes, e.g. Anisakidae species, with zoonotic importance and widely distributed in South America (Tavares & Luque, 2006). Recent papers by Borges *et al.* (2012, 2015), Pantoja *et al.* (2015, 2016) and Mafra *et al.* (2015) have demonstrated the importance of molecular data for adequate diagnosis.

Acanthocephala

The fauna of acanthocephalans in fish from South America is the most depauperate compared with other

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helminth taxa, with only 83 species reported from the different countries, representing less than 5% of the total HPAs (tables 1 and 2). *Rhadinorhynchus pristis* (Rudolphi, 1802) was apparently the first species reported in the subcontinent, parasitizing marine fish off Rio de Janeiro, Brazil (Santos *et al.*, 2008). Later, some helminthologists contributed to our knowledge of acanthocephalans; for example, Travassos, Machado-Filho (among other researchers of the Laboratório de Helmintos Parasitos de Vertebrados, FIOCRUZ) and Thatcher. They described about 20 species, mainly from characiform fish in the Amazon and Paraná River basins (Santos *et al.*, 2008), which is reflected in the proportion of species reported during their respective periods of contribution (from 1923 to 2001; fig. 1) and in the geographical distribution of parasite richness (the majority of species being reported from Brazil; table 2). In a review of Acanthocephala in the Neotropical region, Amin (2000) suggested that this uneven distribution is due to the biased sampling efforts of research teams for some particular group of hosts or parasites, as we have already stated for the other groups of helminths.

Acanthocephalans are parasites of freshwater (74% of HPAs) and marine teleosts (25% of HPAs), except for *Megapriapus ungriai* (Gracia-Rodrigo, 1960) described exclusively from the freshwater stingray *Potamotrygon* sp. (reported as *P. hystrix*) in Venezuela (Weaver & Smales, 2014). Elasmobranchs are considered occasional/accidental or paratenic hosts rather than definitive ones, but there is no conclusive evidence on the host spectrum of the group (Weaver & Smales, 2014).

Members of Polymorphidae, largely reported from marine teleosts in South America, i.e. representatives of *Bolbosoma* Porta, 1908, *Corynosoma* Lühe, 1904 (*sensu* Van Cleave 1945), *Polymorphus* Lühe, 1911 and *Hexaglandula* Petrochenko, 1950 (see García-Varela *et al.*, 2013 for the controversial status of the latter genus), were not included in our dataset, because they are found only as larvae (cystacanths) from paratenic fish hosts (García-Varela *et al.*, 2013). Studies dealing with molecular characterization to link the larval forms and adults are limited in South America (Sardella *et al.*, 2005), not allowing an accurate species-level identification.

Since acanthocephalans do not (or rarely) cause significant human or veterinary disease, they are commonly neglected by helminthologists worldwide (Kennedy, 2006), which is corroborated by our dataset. Nevertheless, even though at a slow rate, recent efforts have been undertaken to depict the diversity of this group in South American fish (fig. 1; Vieira *et al.*, 2009; Arredondo & Gil de Pertierra, 2010, 2012; Lanfranchi & Timi, 2011; Braicovich *et al.*, 2014; Lisitsyna *et al.*, 2015; Mello *et al.*, 2015).

The data gathered from the literature proved to be useful to estimate roughly the species richness of helminths from South American fish, even though some problems are associated with the interpretation of this database: (1) the reliability of information is reliant on accurate species identifications; (2) the lack of knowledge on life cycles matching larvae and adults; (3) the discovery of increasing numbers of cryptic species, i.e. morphologically similar but genetically distinct; (4) the geographically biased number of studies. Therefore, the closest true estimation of species diversity and HPA patterns will rely on further studies combining both molecular and morphological approaches with ecological data, such as host specificity, geographical distribution and life cycles.

Searching for and detecting macroecological patterns

One of the foci of fish parasitology research that has received increasing attention in South America in recent years is macroecology – using fish as a model to test a set of ecological hypotheses aimed at detecting large-scale ecological patterns of diversity and distribution of the fish parasites as a result of evolutionary processes and biogeographical events.

Initially, fish parasitology research in South America was exclusively taxonomic. However, numerous papers on quantitative descriptions of fish parasite communities, especially marine species, have been published since the 1980s and 1990s, and many authors of these papers are researchers with significant taxonomic expertise from Argentina, Chile, Brazil and Peru. This characteristic of the former quantitative descriptive papers gave rise to extensive datasets suitable for testing macroecological hypotheses, in collaboration with overseas researchers. Later, a significant increase in the number of studies of macroecological patterns, using fish parasites as models, was observed in South America.

Therefore, numerous papers on a wide variety of fish parasite ecology topics, using various methodological approaches and large databases on host–parasite associations, have been published in recent years. We can highlight those on the biodiversity of parasite species distribution and its determinants (Luque *et al.*, 2004; Takemoto *et al.*, 2005; Luque & Poulin, 2007, 2008); on patterns of distribution of parasite populations, structure of parasite communities and nestedness (Poulin & Luque 2003; Timi & Poulin, 2003, 2008; Poulin *et al*. 2008; González & Oliva, 2009; Timi *et al.*, 2010; Amarante *et al.*, 2015), also including a quantitative approach to the structure and patterns of parasite specialization in host–parasite networks (Bellay *et al.*, 2013, 2015a, b). Special mention can be made of the research on the use of parasites as biological tags for discrimination of stocks of marine species of economic importance. Research groups from Chile, Argentina and Brazil have demonstrated how the South American Pacific Ocean (George-Nacimento & Oliva, 2015) and South American Atlantic Ocean (Cantatore & Timi, 2015) are areas where parasites can be used to consistently discriminate fish stocks.

The profusion of studies on parasitic macroecology by South American researchers, using fish as a model, demonstrates the great possibility of building more databases in order to test, with consistency, different assumptions on biodiversity and species distribution of the helminth parasites in the Neotropical fishes.

Current research groups and their geographic distribution

Interest in helminths from fish in South America has increased greatly during the past 20 years (fig. 1). In this section, the most active research groups from the

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subcontinent, who have published many papers on the taxonomy and ecology of helminth parasites of fish during the past 6 years, are introduced briefly. However, it is worth mentioning that there are many other researchers working on these subjects, who are not presented here.

Currently, Brazil includes the majority of the research groups in South America; they are distributed mainly in the north, south-east and south of the country. In the State of Pará, two groups have contributed mainly to helminth taxonomy, one resident in the UFPA, focusing on monogeneans (Branches & Domingues, 2014; Santos *et al*., 2015), and the other in the UFRA, working on some other taxa (Melo *et al*., 2013a, b) including the poorly known Aspidogastrea (Giese *et al*., 2014). In the south-east, some groups belonging to three different institutions have contributed to taxonomic knowledge, as follows. In the UFRRJ, research in the Laboratory of Fish Parasitology has focused on nematodes (Vieira *et al*., 2015), besides other taxa (Paschoal *et al*., 2016), including recent insights using an integrated taxonomic approach (Pereira *et al*., 2015a, b). Research by some groups from FIOCRUZ has dealt with the taxonomy of several helminth taxa (Justo & Kohn, 2012; Leão *et al*., 2015), including molecular characterization and diagnosis (Borges *et al*., 2015; Mafra *et al*., 2015). Finally, the Laboratory of Evolutionary Helminthology from USP includes a productive group focusing on the taxonomy of cestodes parasitic in Chondrichthyes (Marques *et al*., 2012; Marques & Reyda, 2015). It is also important to highlight the activity of researchers from UFRRJ in several studies on the ecology of parasites from fish (Amarante *et al*., 2015; Soares & Luque, 2015), which is a subject equally explored by the research group from the Laboratory of Ichthyoparasitology, UEM, State of Paraná (southern Brazil) (Bellay *et al*., 2015a, b). Also in Paraná, the group formed by researchers from the Department of Zoology of the UFPR, have produced one of the most impressive collections of literature on the morphological and molecular taxonomy of monogeneans (Boeger *et al*., 2014b, 2015).

Aspects concerning the pathology caused by helminths in fish are still poorly explored in South America, as well as their management and control. Just a few researchers are currently working on this subject. In Brazil two groups can be cited: one from the EMBRAPA, State of Amapá (Soares *et al*., 2016), and one from the Department of Aquiculture of the UFSC, State of Santa Catarina (Mello *et al*., 2015; Hashimoto *et al*., 2016).

The Argentinean research groups are mainly from the UNMdP as well as from the UBA. Some members of these groups are specialists on parasite ecology (Braicovich & Timi, 2015; Cantatore & Timi, 2015) who have published many papers on parasites as biological tags for stock discrimination (Alarcos *et al*., 2016; Cantatore *et al*., 2016). These researchers have also contributed to the taxonomic knowledge about some taxa, such as Monogenea (Irigoitia *et al*., 2014), Nematoda (Timi *et al*., 2014) and Acanthocephala (Braicovich *et al*., 2014). In Buenos Aires there are two groups working on helminths from fish, one that has been studying the taxonomy of cestodes (Gil de Pertierra *et al*., 2015; Menoret & Ivanov, 2015), and one that has been working on digeneans, including their taxonomy (Arredondo & Ostrowski de Núñez, 2013) and life-cycle surveys (Quintana & Ostrowski de Núñez, 2016).

The research group from the UA, Chile, has dealt with different subjects concerning helminths parasitic in fish, including ecological (Oliva *et al*., 2016) and taxonomic studies (molecular and morphological characterization) of some taxa (Oliva *et al*., 2014, 2015).

It is worth noting the network of interactions between the current research groups in South America. Researchers from Chile, Argentina and Brazil have been actively working in partnerships during recent years (Luque *et al*., 2010; Vieira *et al*., 2015; Alarcos *et al*., 2016), which represents an important step forward for knowledge of helminth biodiversity from this large and species-rich subcontinent.

Final comments

South America is undoubtedly a region where parasite biodiversity is clearly underestimated. The great ichthyological diversity of the region shows the huge dimension of the challenge for basic knowledge of helminth fauna from fish in this continent. This challenge is noticeably due to two major problems: lack of sufficient financial resources (funding) and the small number of research groups with excellence to address this task. It is important to mention at this point that, although most countries of South America do not have consolidated research groups on helminth parasites of fish, some early problems, such as the absence of interchangeable data, effort duplicity and the significant volume of unindexed publications, are clearly decreasing in the region.

Recently, Poulin (2014) mentioned the impossibility of making an inventory of all groups of parasites, for various reasons or limitations, but mainly due to taxonomic impediments and the presence of cryptic species. He suggested that it may be more advantageous in terms of knowledge of parasite biodiversity, to select consistent models, so as to take the opportunity to deepen some studies, e.g. taxonomy, host–parasite relationships and ecological aspects. South America has several promising and little-studied regions in this respect, with great fish-host diversity and peculiar ecological characteristics, e.g. the Amazon River basin, Pantanal wetlands and rivers of the Peruvian Andes, where there is a high degree of endemism and it is more likely to be possible to survey the entire parasite fauna of fish. From this perspective, significant advances in the study of parasite biodiversity could be achieved.

Interestingly, Scholz & Choudhury (2015) list some problems that prevented the further development of studies of freshwater fish parasites in North America, which are repeated in South America. Thus, international collaboration has been an essential feature of fish parasitology in the region. We would like to emphasize the strategic importance of increasing collaboration and expanding networks at the regional level and, fundamentally, with research groups with greater experience from other continents. The increase of exchanged information and research networks in the global context allows us to visualize a promising and productive future for fish parasitology in South America.

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Conflict of interest

None.

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