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Tapeworms (Cestoda: Proteocephalidea) of teleost fishes from the Amazon River in Peru: additional records as an evidence of unexplored species diversity

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Abstract: This paper represents an update of the previous list of adult proteocephalidean tapeworms (Cestoda) parasitizing freshwater teleosts from the Peruvian Amazon, which was presented by de Chambrier *et al.* (2006a). Four new samplings made it possible to almost double the number of species found, all of them representing new geographical records from Peru. With 34 newly added species, a total of 63 proteocephalidean cestodes (46 named species of 27 genera) are now reported from Amazonia in Peru (compared to 54 named species of 28 genera from its Brazilian part). The genera previously unreported by de Chambrier *et al.* (2006a) are *Ageneiella*, *Brayela*, *Endorchis*, *Ephedrocephalus*, *Gibsoniela*, *Harriscolex*, *Jauella*, *Lenhataenia*, *Manaosia*, and *Megathylacus*. Four species, namely *Jauella glandicephalus*, *Monticellia belavistensis*, *M. santafesina*, and *Proteocephalus hobergi*, are reported from the Amazon River basin for the first time. *Harriscolex piramutab* (Woodland, 1934) n. comb. is proposed for specimens previously identified as *Proteocephalus piramutab* Woodland, 1934 from *Brachyplatystoma vaillantii*. The highest number of proteocephalidean cestodes is reported from *Pseudoplatystoma fasciatum* (a total of 10 cestode species), *Zungaro zungaro* (previously named *Paulicea luetkeni*; 9 species) and *Phractocephalus hemioliopterus* (6 species). A high number of unnamed species found in Peru (17), which most probably represent taxa new to science including at least two new genera, demonstrates that the species richness of proteocephalidean cestodes in Amazonia is still poorly known.

Keywords: Catfish - freshwater fish - Siluriformes - Peru - Pimelodidae - Amazonia - species diversity - faunal survey.

INTRODUCTION

The Amazon River basin is by far the largest river basin in the world and drains roughly 40 percent of the South American continent. This river basin hosts the most diverse fish fauna in planet, with about 2,500 species described and another 1,000 species estimated to be described (Junk *et al.*, 2007). However, recent large-scale environmental degradation due to anthropogenic pressure such as deforestation, water pollution, overfishing and intensive farming has had negative effect on water ecosystems, including considerable decrease of population density of big pimelodid catfishes (Siluriformes) in the Brazilian part of Amazonia (Angelini *et al.*, 2006; Pelicice & Agostinho, 2008; Boni *et al.*, 2011; Reis, 2013).

These fishes serve as definitive hosts of a unique rich fauna of proteocephalidean tapeworms (Cestoda) that probably underwent explosive radiation and represent an interesting model for co-evolutionary studies because of strict host specificity of most taxa (de Chambrier & Vaucher, 1997, 1999; Zehnder & Mariaux, 1999; de Chambrier *et al.*, 2004a; Hypša *et al.*, 2005). Unlike most parts of the Brazilian Amazonia, in which population density of big catfish has declined (Angelini *et al.*, 2006; Pelicice & Agostinho, 2008), numerous stocks of these fishes including pimelodids still inhabit the Peruvian part of the Amazon River basins.

Parasitological examination of 276 fishes of 73 species from the Amazon River and its tributaries around Iquitos, Loreto Region in Peru, carried out by the present authors and their co-workers in 2004 and 2005, revealed an extraordinary richness of proteocephalidean tapeworms, which were all reported from Peru for the first time (de Chambrier & Scholz, 2005; de Chambrier *et al.*, 2006a). De Chambrier *et al.* (2006a) listed as many as 29 species of 17 genera found in 10 species of siluriform fishes and cichlids. New sampling in this region in 2006, 2008, 2009 and 2011 made it possible to obtain additional material that includes many cestodes not having been previously reported from Peru or from the Amazon River basin; some may even be new to science. To provide a robust baseline for forthcoming analyses of zoogeographical patterns

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and phylogenetic relationships of proteocephalideans in the Neotropical Region, updated information is presented on the species composition, host-parasite associations and geographical distribution of these cestodes, which represent an important component of the parasite fauna of Neotropical fishes (Thatcher, 2006).

MATERIAL AND METHODS

A total of 611 fish from the Amazon River and its tributaries around Iquitos (72º50'-73º40'W; 3º34'-4º53'S), Loreto Region, Peru, were examined for parasites in September 2006 and 2008, and in October 2009 and 2011. Intestines of freshly captured hosts as well as those sold on the market of Belén in Iquitos were transported in coolers to the provisional laboratory (courtesy of Acuario Río Momón in Iquitos), where they were immediately examined. For morphological evaluation, only specimens in good condition were used, but quantitative parameters such as intensity or abundance could not be reliable assessed.

Cestodes were gently washed in saline, fixed with hot (almost boiling) 4% formaldehyde solution and then processed using standard procedure used for fish tapeworms as described by de Chambrier *et al.* (2014). Fragments of strobila were also fixed with 96% molecular-grade ethanol for molecular analyses (DNA sequencing), which forms part of a large-scale study on the phylogenetic relationships of cestodes supported by the National Science Foundation project (programme Planetary Biodiversity Inventory; see www.tapeworm.uconn.edu). In the present paper, scanning electron micrographs (SEM) of the scoleces of five species are provided (Figs 1-5); these species were not studied using SEM or their SEM pictures were based on contracted or deformed specimens.

Most specimens found are deposited in the Natural History Museum, Geneva, Switzerland (MHNG-PLAT), which hosts one of the most comprehensive collections of proteocephalidean cestodes (http://www.ville-ge.ch/mhng/dpt_inve_coll_e.php#platyhelminthes). See Table 1 for more details. Classification of cestodes, including original descriptions of taxa, follows the Global Cestode Database (Caira *et al.*, 2012). However, the recently erected order Onchoproteocephalidea, which groups the proteocephalideans and some 'hooked' tetraphyllidean cestodes (see Caira *et al.*, 2014), is not considered herein for the reasons presented by Arredondo *et al.* (2014), especially because no morphological synapomorphies of the new order were provided by Caira *et al.* (2014). Field numbers correspond to the numbers of fish examined in field protocols (PI = Peru, Iquitos, Loreto Region, Peru; letters after host number distinguish different worm samples). Since 2008, every fish dissected was photographed together with its field number (PI); in 2009 and 2011, tissue samples, usually a small piece of musculature, of every infected fish were taken and fixed with 96% molecular-grade ethanol for future DNA sequencing to confirm host identification. Photographs of fishes and their tissue samples are available upon request from the authors.

Names of teleosts follow those in FishBase (Froese & Pauly, 2014) and PlanetCatfish (http://www.planetcatfish.com) except for *Brachyplatystoma rousseauxii* (Castelnau), which was erroneously reported as *B. flavicans* (Castelnau) by de Chambrier *et al.* (2006a) following Fishbase (see Lundberg and Akama, 2005; http://www.planetcatfish.com/). In addition, *Zungaro zungaro* (Humboldt) was wrongly reported as *Paulicea luetkeni* (Steindachner) (for current nomenclature, see Froese & Pauly, 2014; John Lundberg, pers. comm.).

RESULTS

Survey of species found

Species not reported by de Chambrier *et al.* (2006a) are marked by an asterisk (*); species reported by de Chambrier *et al.* (2006a), but not found in 2006-2011, are also listed herein to provide a complete list of cestodes found. Collection numbers refer to the Natural History Museum, Geneva, Switzerland – MHNG-PLAT, unless otherwise stated. Cestode taxa are listed alphabetically.

Ageneiella sp.*

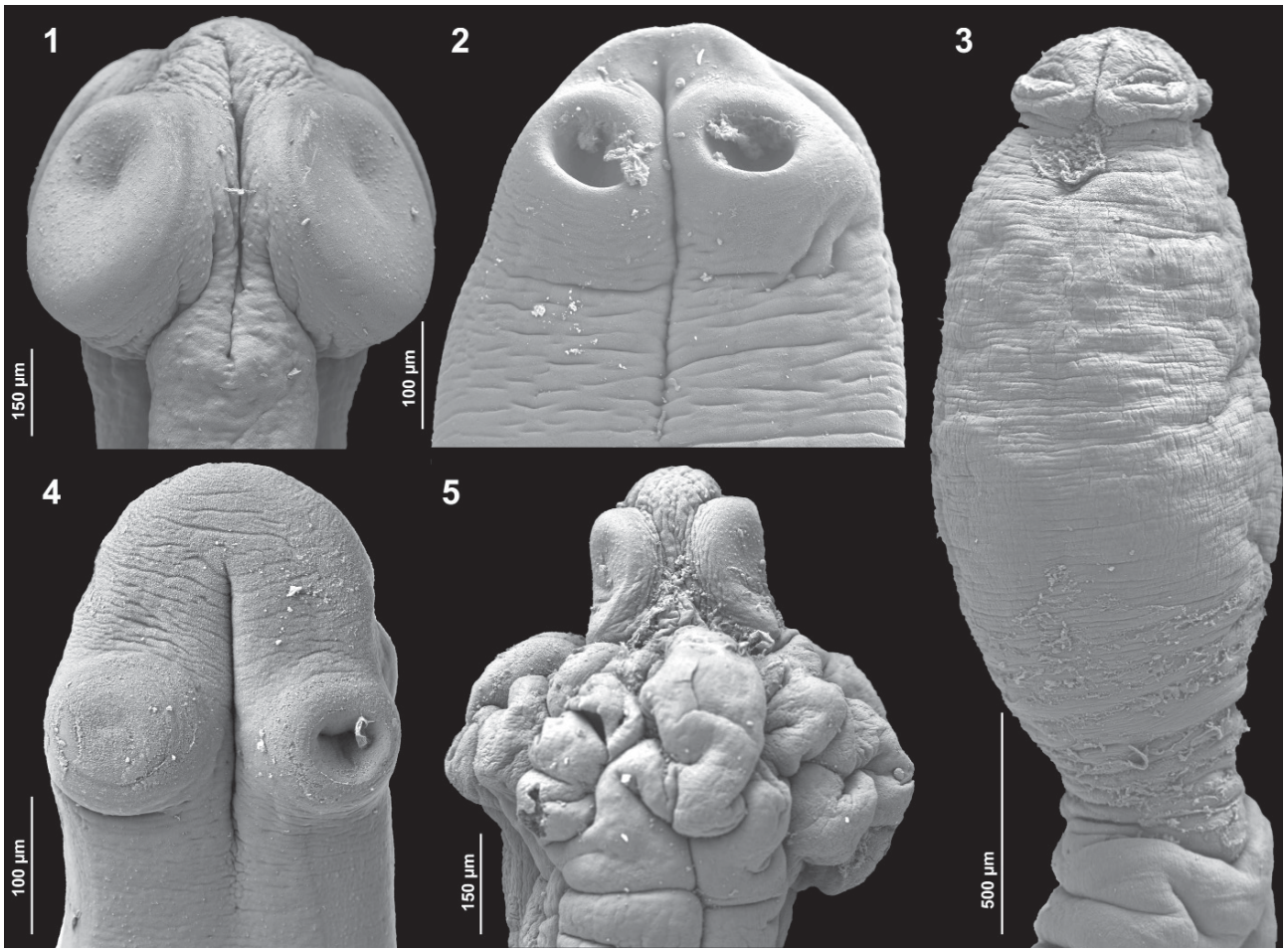
Host: *Ageneiosus inermis* (L.) (1 fish infected of 16 fish examined, i.e. prevalence of 6%).

Remarks: Specimens found in *A. inermis* are partly decomposed and contracted, which impedes their reliable identification to the species level. However, they apparently belong to an undescribed species of *Ageneiella* de Chambrier & Vaucher, 1999, a hitherto monotypic genus proposed to accommodate *A. brevifilis* de Chambrier & Vaucher, 1999 from *Ageneiosus brevifilis* (L.) (synonym of *A. inermis*) from Paraguay by de Chambrier & Vaucher (1999). They possess biloculate suckers with a sphincter and lateral lobes of the ovary penetrating into the cortex (see de Chambrier & Vaucher, 1999).

Immature cestodes were found in two additional *Ageneiosus* sp., but their identification is not possible.

Amphoteromorphus ovalis Carfora, de Chambrier & Vaucher, 2003*

Host: *Brachyplatystoma* cf. *filamentosum* (Lichtenstein); 1/3, 33%).



Figs 1-5. Scanning electron micrographs of representative scoleces of proteocephalidean cestodes found in the Peruvian Amazon. (1) *Nomimoscolex lopesi* from *Pseudoplatystoma fasciatum* (PI 708). (2) *Proteocephalus* sp. 2 from *Pterodoras granulosus* (PI 635). (3) *Jauella glandicephalus* from *Zungaro zungaro*. (4) *Proteocephalus kuyukuyu* from *Megalodoras uranoscopus* (PI 324). (5) *Spatulifer rugosa* from *P. fasciatum* (PI 708). 1, 3, 5 = lateral view; 2, 4 = dorsoventral view.

***Amphoteromorphus parkamoo* Woodland, 1935**

Host: *Zungaro zungaro* (3/30, 10%).

Remarks: Redescribed by Carfora *et al.* (2003), who confirmed the validity of the species.

Amphoteromorphus peniculus* Diesing, 1850

Host: *Brachyplatystoma rousseauxii* (1/3, 33%).

***Amphoteromorphus piriformis* Carfora, de Chambrier & Vaucher, 2003**

Host: *Brachyplatystoma rousseauxii* (1/3, 33%).

Remarks: *A. piriformis* was described from *B. rousseauxii* collected in Itacoatiara, Brazil in September 1992 and October 1995 (Carfora *et al.*, 2003).

Brayela karuatayi* (Woodland, 1934)

Host: *Platynematichthys notatus* (Jardine) (5/13, 38%).

Remarks: This species, which had never been found since its original description by Woodland (1934a), has recently been redescribed by de Chambrier *et al.* (2014) on the basis of new material collected in Peru. The authors also described correctly its scolex morphology and provided the evidence that the actual fish host of this cestode is *P. notatus*, not '*Glanidium* sp.' as reported in the original description (see de Chambrier *et al.*, 2014).

***Chambriella agostinhoi* (Pavanelli & Machado dos Santos, 1992)**

Host: *Zungaro zungaro* (11/30, i.e. 37%).

Chambriella paranaensis (Pavanelli & Rego, 1989)

Host: *Hemisorubim platyrhynchos* (1/12, 8%).

Remarks: de Chambrier *et al.* (2006a) designated this species erroneously as the type species of *Chambriella* Rego, Chubb & Pavanelli, 1999. Rego *et al.* (1999) actually did not explicitly mention the type species of the genus in its generic diagnosis on p. 314, but *C. agostinhoi* was mentioned as the type species of the genus in remarks to that species (Rego *et al.*, 1999: 317).

Chambriella sp. 1*

Host: *Brachyplatystoma vaillantii* (Valenciennes) (4/39, 10%).

Remarks: This cestode is a rare parasite of *B. vaillantii*.

Chambriella sp. 2 (= *Chambriella* sp. of de Chambrier *et al.*, 2006a)

Host: *Phractocephalus hemioliopterus* (Bloch & Schneider) (5/10, 50%).

Chambriella sp. 3*

Host: *Pseudoplatystoma fasciatum* (7/42, 17%).

Chambriella sp. 4*

Host: *Sorubimichthys planiceps* (Spix & Agassiz) (6/22, 27%).

Remarks: de Chambrier & Scholz (2008) reported but did not describe the morphology of this species, which may be new to science, similarly as the three species listed above (*Chambriella* spp. 1-3). Their taxonomic study is in preparation and will be presented in a separate account.

Choanoscolex abscisus (Riggenbach, 1896)

Host: *Pseudoplatystoma fasciatum* (14/42, 33%).

Remarks: Compared to de Chambrier *et al.* (2006a), new collections enabled us to obtain sufficient material of this cestode, which has been found in a wide spectrum of unrelated fish hosts (Rego, 1987, 1990; Rego & Pavanelli 1990; Rego *et al.*, 1999).
In its strobilar morphology, the species closely resembles *Spatulifer surubim* Woodland, 1934 from the same fish host, differing only in a much less developed metascolex. However, some intermediate forms with a more developed metascolex were found, which indicates that differences between these taxa of two different genera should be critically assessed. Molecular data also indicate close relatedness of *S. surubim* and *C. abscisus* from *P. fasciatum* (A. Waeschenbach, unpubl. data).

Choanoscolex sp.*

Host: *Sorubimichthys planiceps* (3/22, 14%).

Remarks: de Chambrier & Scholz (2008) reported cestodes of the genus *Choanoscolex* La Rue, 1911 that differ from those of *C. abscisus*, the only species of the genus (see above).

Endorchis piraeeba Woodland, 1934*

Host: *Brachyplatystoma* cf. *filamentosum* (1/3, 33%).

Remarks: At present, the genus includes *E. piraeeba* from *B. filamentosum* and *Endorchis auchenipteri* de Chambrier & Vaucher, 1999 from *Auchenipterus osteomystax* (Miranda Ribeiro) from the Paraná River in Paraguay (de Chambrier & Vaucher, 1999). In addition, de Chambrier & Vaucher (1999) reported unidentified cestodes of *Endorchis* from *Pimelodus* cf. *maculatus* Lacépède and *Trachelyopterus striatulus* (Steindachner) from Paraguay.
An immature specimen with a similar scolex was found in *Pseudoplatystoma fasciatum* (1/42, i.e. 2%).

Endorchis sp.*

Host: *Pimelodus altissimus* Eigenmann & Pearson (1/1).

Remarks: These specimens resemble those of *E. auchenipteri* but their large-sized Mehlis gland is unique among the Proteocephalidea.

Euzetiella tetraphylliformis de Chambrier, Rego & Vaucher, 1999

Host: *Zungaro zungaro* (5/30, 17%).

Remarks: Worms collected in 2009 were immature, but are supposed to belong to the only known species of the genus, which was described from the same host in Itacoatiara, Brazil (de Chambrier *et al.*, 1999). One immature specimen was also found in *Pseudoplatystoma fasciatum*.

Gibsoniela mandube (Woodland, 1935)*

Host: *Ageneiosus inermis* (2/16, 13%), *Ageneiosus* sp. (3/10, 30%).

Remarks: The species was described as *Anthobothrium mandube* Woodland, 1935, (Phyllobothriidae) and transferred to *Gibsoniela* Rego, 1984 by Rego (1984). From the same host (*A. inermis*) and same locality

(Amazon River in Brazil), Woodland (1935a) described *Endorchis mandube*, but Rego (1984) suggested that both species may be synonymous and de Chambrier (1990) confirmed this synonymy.
However, de Chambrier & Vaucher (1999) studied the type material and newly collected specimens of both taxa from the Amazon River and concluded that they represent two distinct species of the same genus. To avoid their homonymy, they proposed *Gibsoniela meursaulti* de Chambrier & Vaucher, 1999 to accommodate *Endorchis mandube*; tapeworms redescribed by Rego (1992) as *G. mandube* actually belonged to *G. meursaulti* (de Chambrier & Vaucher, 1999).

Harriscolex kaparari (Woodland, 1935)*

Host: *Pseudoplatystoma fasciatum* (3/42, 7%).

Remarks: Described as *Nomimoscolex kaparari* Woodland, 1935 by Woodland (1935a) from *Pseudoplatystoma tigrinum* (Valenciennes) in Brazil.

Harriscolex piramutab (Woodland, 1934) n. comb.

Host: *Brachyplatystoma vaillantii* (8/39, 20%).

Remarks: de Chambrier *et al.* (2006a) reported *Proteocephalus piramutab* Woodland, 1934 from *Brachyplatystoma vaillantii*. A detailed morphological study of newly collected specimens and material of *Proteocephalus piramutab* from museum collections, and their comparison with those of *H. kaparari,* revealed that the former species should be transferred to *Harriscolex* Rego, 1987, because it possesses a scolex with a dome-shaped anterior end and suckers with two triangular projections (see Rego, 1994). Therefore, a new combination, *Harriscolex piramutab*, is proposed for specimens previously identified as *P. piramutab*, including those reported from Peru by de Chambrier *et al.* (2006a).

Houssayela sudobim (Woodland, 1935)

Host: *Pseudoplatystoma fasciatum* (3/42, 7%).

Remarks: Described as *Myzophorus sudobim* Woodland, 1935 from *P. fasciatum* from the Amazon River in Brazil by Woodland (1935b) and found and redescribed by de Chambrier & Scholz (2005) for the first time since original description on the basis of a single specimen from *P. fasciatum* in Iquitos (PI 76a – 22. 4. 2004).

Jauella glandicephalus Rego & Pavanelli, 1985*
Fig. 3

Host: *Zungaro zungaro* (9/30, 30%).

Remarks: Described from *Zungaro jahu* (Ihering) (as *Paulicea luetkeni*) from the Paraná River in Brazil by Rego & Pavanelli (1985). This is the first record of the parasite in the Amazon River basin.

Lenhataenia megacephala (Woodland, 1934)*

Host: *Sorubimichthys planiceps* (11/22, 50%).

Remarks: The genus was erected by de Chambrier & Scholz (2008) to accommodate *Monticellia megacephala* Woodland, 1934, which is a common, host-specific parasite of *S. planiceps*.

Manaosia bracodemoca Woodland, 1935*

Host: *Sorubim lima* (Bloch & Schneider) (3/29, 10%).

Remarks: The species was described by Woodland (1935a) from '*Platysoma* sp.' (vernacular name 'braço de moça') in the Amazon River in Brazil. De Chambrier (2003) clarified the systematic position of this species, which is a rare parasite of *S. lima*. He considered *Paramonticellia* Pavanelli & Rego, 1991 to be a junior synonym of *Manaosia* Woodland, 1935.

Mariauxiella piscatorum de Chambrier & Vaucher, 1999

Host: *Hemisorubim platyrhynchos* (2/12, i.e. 17%).

Remarks: This species was found only in 2004 (de Chambrier *et al.*, 2006a).

Megathylacus jandia Woodland, 1934*

Host: *Zungaro zungaro* (2/30, 7%).

Remarks: This species was originally identified as *Megathylacus brooksi* Rego & Pavanelli, 1985, but a detailed study of type and new material of *Megathylacus* cestodes from the Amazon and Paraná River basins (de Chambrier *et al.*, 2014) has demonstrated conspecifity of this species with *M. jandia*, which was described by Woodland (1934a) from the Amazon River in Brazil.

Megathylacus sp.*

Host: *Pseudoplatystoma fasciatum* (4/42, 10%).

Remarks: These cestodes from *P. fasciatum* differ from *Megathylacus travassosi* by a few morphological characters and potentially belong to a new species. This species was collected also in 2004, but not reported by de Chambrier *et al.* (2006a).

***Monticellia amazonica* de Chambrier & Vaucher, 1997**

Host: *Calophysus macropterus* (Lichtenstein) (5/33, 15%).

Remarks: Scholz *et al.* (2008) redescribed the species on the basis of specimens found in Iquitos, Peru in 2005.

Monticellia belavistensis* Pavanelli, Machado dos Santos, Takemoto & dos Santos, 1994

Host: *Pterodoras granulosus* (Valenciennes) (1/24, 4%).

Remarks: This cestode, which was described by Pavanelli *et al.* (1994) from *P. granulosus* from the Paraná River basin in Brazil and then reported by de Chambrier & Vaucher (1999) from the Paraguay River in Paraguay, was found in Peru only once. It is the first record of this species from the Amazon River basin.

Monticellia lenha* Woodland, 1933

Host: *Sorubimichthys planiceps* (13/22, 59%).

Remarks: Originally described by Woodland (1933) from specimens found in *S. planiceps*, and redescribed by de Chambrier & Scholz (2008), who studied type specimens and new material from Iquitos collected in 2006 (see Table 2). It is a specific and the most frequent parasite of *S. planiceps*.

Monticellia santafesina* Arredondo & Gil de Pertierra, 2010

Host: *Megalonema platycephalum* Eigenmann (1/1).

Remarks: Described from *Megalonema platanum* (Günther) from the Paraná River basin in Argentina (Arredondo & Gil de Pertierra, 2010). This is the first geographical record of this cestode from the Amazon River basin. *M. platycephalum* represents a new definitive host of the parasite.

Monticellia ventrei* de Chambrier & Vaucher, 1999

Host: *Pinirampus pirinampu* (Spix & Agassiz) (4/30, 13%).

Remarks: *Monticellia ventrei* was described by de Chambrier & Vaucher (1999) from specimens found in *P. pirinampu* from the Paraguay River in Paraguay. Specimens found in Peru represent a new geographical record and expand the distribution area of the species to include the Amazon River basin.

Nomimoscolex admonticellia* (Woodland, 1934)

Host: *Pinirampus pirinampu* (11/30, 37%).

Remarks: This is a relatively common parasite specific of *P. pirinampu*, which was originally described by Woodland (1934b) from *Pinirampus* sp. from the Amazon River near Itacoatiara, Brazil.

Nomimoscolex lenha* (Woodland, 1933)

Host: *Sorubimichthys planiceps* (5/22, 23%).

Remarks: de Chambrier & Scholz (2008) redescribed the species based on 2 specimens they collected in Itacoatiara, Brazil in 1995 and 1 specimen from Iquitos, Peru in 2006. Interestingly, the prevalence of *N. lenha* in Brazil (22%, n = 9; see de Chambrier & Scholz, 2008) was almost identical to that in the same host from Peru.

***Nomimoscolex lopesi* Rego, 1989**
Fig. 1

Host: *Pseudoplatystoma fasciatum* (11/42, 26%).

Remarks: This species was studied using scanning electron microscopy for the first time (Fig. 1).

***Nomimoscolex sudobim* Woodland, 1935**

Host: *Pseudoplatystoma fasciatum* (10/42, 24%).

Remarks: Also found in *P. tigrinum* from Peru by de Chambrier *et al.* (2006a). The species was redescribed by de Chambrier *et al.* (2006b).

Nomimoscolex suspectus* Zehnder, de Chambrier, Vaucher & Mariaux, 2000

Host: *Brachyplatystoma* cf. *filamentosum* (1/3, 33%).

Remarks: Described from tapeworms found in *Brachyplatystoma filamentosum* (type host), *B. flavicans* (now *B. rousseauxii*) and *B. vaillantii* from the Amazon River in Brazil (Zehnder *et al.*, 2000); it was found in Peru only once.

Nomimoscolex* sp.

Host: *Pimelodus ornatus* Kner (2/13, 15%).

Remarks: These cestodes differ from *N. micro-acetabula* Gil de Pertierra, 1995 by a few morphological characters and potentially belong to a new species.

Nupelia sp.

Host: *Goeldiella eques* (Müller & Troschel) (3/28, 11%).

Remarks: Despite great efforts to collect more material allowing for its description, only one additional specimen from this species was found since 2005 (see de Chambrier *et al.*, 2006a). These tapeworms are mainly characterized by extraordinarily wide ventral osmoregulatory canals.

Peltidocotyle lenha (Woodland, 1933)

Hosts: *Sorubimichthys planiceps* (13/22, 59%); *Zungaro zungaro* (13/30, 43%).

Remarks: de Chambrier & Scholz (2008) reported the species from the type host, *S. planiceps*. *Zungaro zungaro* is another host of the tapeworm (Zehnder & de Chambrier, 2000).

Peltidocotyle rugosa Diesing, 1850*

Host: *Pseudoplatystoma fasciatum* (10/42, 24%).

Remarks: de Chambrier *et al.* (2006a) did not report this frequent parasite of *P. fasciatum*.

Proteocephalus gibsoni Rego & Pavanelli, 1991

Host: *Astronotus ocellatus* (1/4, 25%).

Proteocephalus hemioliopteri de Chambrier & Vaucher, 1997*

Host: *Phractocephalus hemioliopterus* (1/10, 10%).

Remarks: de Chambrier & Vaucher (1997) proposed a new name, *Proteocephalus hemioliopteri*, for *Myzophorus woodlandi* Rego, 1984 [syn. *Nomimoscolex woodlandi* (Rego, 1984) Rego & Pavanelli, 1992]; de Chambrier *et al.* (2005) redescribed this species, which was found only once in Peru.

Proteocephalus hobergi de Chambrier & Vaucher, 1999*

Host: *Oxydoras niger* (Valenciennes) (1/16, 6%).

Remarks: de Chambrier & Vaucher (1999) described the species from *Oxydoras kneri* Bleeker from the Paraná and Paraguay rivers in Paraguay. The specimens found in Peru represent new host and geographical records and the first report of the species from the Amazon River basin.

Proteocephalus kuyukuyu Woodland, 1935*

Fig. 4

Hosts: *Megalodoras uranoscopus* (Eigenmann & Eigenmann) (3/4, 75%); *Pterodoras granulosus* (2/24, 8%); *Pterodoras* sp. (1/1).

Remarks: This parasite of doradid catfishes was described by Woodland (1935c) from the kuyukuyu, vernacular name of *Oxydoras niger* (as *Pseudodoras niger*), from Codajaz, Brazil. Even though Woodland (1935c) found over 50 specimens, no one was mature. The same situation was observed in Peru and none of 347 cestodes found was fully mature. This may indicate hyperapolytic development, i.e. release of proglottids precociously before they contain any eggs, which then complete their development while free in the intestine of the host (see glossary in Khalil *et al.*, 1994), but no free proglottids were found in hosts infected with immature cestodes.

Proteocephalus macrophallus (Diesing, 1850)

Host: *Cichla monoculus* (2/15, 13%).

Proteocephalus microscopicus Woodland, 1935

Host: *Cichla monoculus* (6/15, 40%).

Remarks: Both species, similarly as *P. gibsoni* from another cichlid (see above), were not found since 2005 because no other hosts, *C. monoculus* and *A. ocellatus*, were examined.

Proteocephalus sophiae de Chambrier & Rego, 1994*

Host: *Zungaro zungaro* (6/30, 20%).

Remarks: This is a host-specific parasite of the *Z. zungaro*, described from the Amazon River in Brazil by de Chambrier & Rego (1994).

Proteocephalus sp. 1 of de Chambrier *et al.* (2006a)

Host: *Phractocephalus hemioliopterus* (2/10, 20%).

Remarks: Only immature specimens have been found.

Proteocephalus sp. 2 of de Chambrier *et al.,* (2006a)

Fig. 2

Host: *Pterodoras granulosus* (2/24, 8%).

Remarks: Additional immature specimens were found in 5 *P. granulosus* and possibly belong to the same taxon.

Proteocephalus* sp. 3

Host: *Pimelodus blochii* Valenciennes (2/8, 25%).

Remarks: All specimens are immature.

***Rudolphiella piracatinga* (Woodland, 1935)**

Host: *Calophysus macropterus* (10/33, 30%).

Rudolphiella* sp.

Host: *Pinirampus pirinampu* (5/30, 17%).

Remarks: These cestodes differ from both *R. myoides* Woodland, 1934 and *R. piranabu* Woodland, 1934 from the same host in Brazilian Amazon and potentially belong to a new species.

***Scholzia emarginata* (Diesing, 1850)**

Host: *Phractocephalus hemioliopterus* (10/10, 100%).

Remarks: This is the most frequent specific parasite of *P. hemioliopterus*.

***Sciadocephalus megalodiscus* Diesing, 1850**

Host: *Cichla monoculus* (1/15, 7%).

Remarks: Woodland (1933b) redescribed this taxa established by Diesing (1850), based on his material collected in the Amazon River in 1931. Rego *et al.* (1999) reported this species from the Paraná River basin and amended a generic diagnosis.

***Spasskyellina spinulifera* (Woodland, 1935)**

Hosts: *Pseudoplatystoma fasciatum* (12/42, 29%), *P. tigrinum* (Valenciennes) (2/13, 14%; no new material found since 2005).

Remarks: This species was originally described as *Monticellia spinulifera* by Woodland (1935b) from *P. fasciatum* from the Amazon River in Brazil. Freze (1965) proposed a new genus, *Spasskyellina*, to accommodate this species. De Chambrier & Vaucher (1999) synonymized the genus with *Monticellia*, but later de Chambrier *et al.* (2006a) listed *Spasskyellina* as a valid genus, ignoring the previous paper from 1999. Three species of *Pseudoplatystoma*, namely *P. corruscans*, *P. fasciatum* and *P. tigrinum*, from the Amazon and Paraná River basins in Peru, Brazil and Paraguay serve as definitive hosts of *S. spinulifera* (Woodland, 1935b; Rego, 1990; de Chambrier & Vaucher, 1999; de Chambrier *et al.*, 2006a; present study).

***Spatulifer maringaensis* Pavanelli & Rego, 1989**

Host: *Hemisorubim platyrhynchos* (Valenciennes) (2/12; 17%); *Sorubim lima* (3/29, 10%).

Remarks: Originally described from *H. platyrhynchos* and found by de Chambrier *et al.* (2006a) in the same host from Peru. Arredondo & Gil de Pertierra (2008) confirmed that tapeworms from this catfish and *S. lima* from the Paraná River basin are conspecific, which was supported by the present study.

***Spatulifer rugosa* (Woodland, 1935)**
Fig. 5

Host: *Pseudoplatystoma fasciatum* (14/42, 33%).

Remarks: Described as *Monticellia rugosa* from *P. fasciatum* from the Amazon River, Brazil by Woodland (1935a), who reported prevalence of 55%.

***Spatulifer* sp. (probably *S. surubim* Woodland, 1934)**

Host: *Pseudoplatystoma tigrinum* (1/13, 8%).

Remarks: Only immature specimens were found; see de Chambrier *et al.* (2006a).

***Travassiella jandia* (Woodland, 1934)**

Host: *Zungaro zungaro* (1/30, 3%).

Remarks: de Chambrier *et al.* (2014) synonymized *Travassiella avitellina* Rego & Pavanelli, 1987 described from *Zungaro zungaro* (in fact *Zungaro jahu,* see Lundberg & Littmann, 2003) with *Proteocephalus jandia* Woodland, 1934 described from *Z. zungaro* from the Amazon River in Brazil and proposed a new combination, *T. jandia* (Woodland, 1934). This is the rarest species found in *Z. zungaro* in Peru.
No new specimens were found since 2004 (see de Chambrier *et al.,* 2006a).

***Zygobothrium megacephalum* Diesing, 1850**

Host: *Phractocephalus hemioliopterus* (1/10, 10%).

Monticelliinae gen. sp.*

Host: *Phractocephalus hemioliopterus* (1/10, 10%).

Remarks: This material differs from all known species of the Monticelliinae and potentially belong to a new species and genus.

Proteocephalidea gen. sp.*

Host: *Cichlasoma amazonarum* Kullander (3/29, 10%).

Remarks: This material differs from all known species of the Proteocephalidae and potentially belong to a new species and genus.

DISCUSSION

Our four recent sampling trips in the Peruvian Amazon enable us to double the number of proteocephalidean cestodes reported in 25 species of fishes of the upper part of the Amazon River around Iquitos. Besides the 29 proteocephalidean species found in 8 species of pimelodid, 1 heptapterid and 1 doradid catfishes, and 2 species of cichlids, the present account adds another 34 species, thus providing evidence of the occurrence of as many as 63 species of these cestodes in Peru. Out of them, 46 species could be identified to the species level and represent already known taxa. This is only slightly less than the known fauna of the Brazilian part of Amazonia, from which 54 species have been reported (Table 1). However, more than a dozen species found only in Peru are probably new taxa awaiting formal description. In total, as many as 64 named species of proteocephalidean cestodes are now known from the Amazon River basin (Table 1).

Unlike Peru, with almost no history of studies on cestode parasites of freshwater teleosts, research on fish parasites in the Brazilian part of the Amazon River basin started as early as in the 19th century, when Diesing (1850) described several taxa based on material collected by an Austrian naturalist and explorer Johann Natterer, who spent 18 years in Brazil from 1817 to 1835. More systematic studies on proteocephalidean cestodes started in the early 1930's when W.N.F. Woodland published 9 papers with descriptions of 32 species and 8 genera of proteocephalidean cestodes from catfishes and other teleost fishes in the Amazon River in Brazil (de Chambrier *et al.*, 2014). After a couple of decades since Woodland's pioneer studies, Brazilian authors, especially A.A. Rego, studied the cestode fauna of fishes in Brazil (see Rego *et al.*, 1999 for references), even though many of the studies were carried out in the Paraná River basin (Rego & Pavanelli, 1992; Fig. 6). Since the mid 1990's, the senior author with co-authors have also contributed considerably, with a number of papers dealing with proteocephalideans from the Brazilian Amazon (see de Chambrier *et al.,* 2006a, 2014 and references therein).

From the Amazon River basin in Peru, de Chambrier *et al.* (2006a) reported 5 species of proteocephalideans from *Pseudoplatystoma fasciatum* and *Paulicea luetkeni* (= *Zungaro zungaro*) each, and 4 species in *Phractocephalus hemioliopterus* and *Pseudoplatystoma tigrinum*. In the present study, much higher numbers of cestodes were found in these hosts: 10 (and juveniles of 2 other species) in *P. fasciatum* (plus one unidentified species; 7 of these species were also reported from Brazilian Amazonia), 9 in *Z. zungaro* (1 unidentified species) and 6 in *P. hemioliopterus* (1 unidentified species). As typical for proteocephalidean cestodes in the Neotropical Region (e.g., de Chambrier & Vaucher, 1999), most species are specific to a single fish host, more rarely to congeneric host species. In the present study, 9 species were found in more than one fish host and only 2 species, namely *Proteocephalus kuyukuyu* and *Spatulifer maringaensis*, occur in fish of more than one genus (Table 2). However, there could be a sampling bias, considering that the number of dissected hosts per species varied considerably, from 1 to 42 specimens (Table 2). *Pseudoplatystoma fasciatum* was the most frequently examined host and also harboured the highest number of species of proteocephalideans.

Extensive material of proteocephalidean cestodes was collected in a wide spectrum of teleosts during six visits by the present authors and their co-workers to the Peruvian Amazonia. This material will make it possible to compare the species composition of the cestode fauna and host-parasite associations in the Amazon River basin with those in the Paraná River basin (Fig. 6). Some proteocephalideans occur in closely related hosts from different river basins, such as *Proteocephalus macrophallus* and *P. microscopicus* in species of *Cichla* Bloch & Schneider, 1801, or in recently separated 'couples' of fish hosts that occur only in one of the two principal river basins in South America, i.e. Amazon and Paraná, such as *Zungaro zungaro* in the former river basin and *Z. jahu* in the latter one.

Fig. 6. Map of South America with two principal river basins, Amazon and Paraná Rivers.

Table 1. List of species of proteocephalidean cestodes found in fishes from the Amazon River basin.

Species		Brazil	Peru
Amazotaenia yvettae de Chambrier, 2001		+	-
Amphoteromorphus ninoi Carfora, de Chambrier & Vaucher, 2003		+	-
Amphoteromorphus ovalis Carfora, de Chambrier & Vaucher, 2003		+	+
Amphoteromorphus parkamoo Woodland, 1935		+	+
Amphoteromorphus peniculus Diesing, 1850		+	+
Amphoteromorphus piraeeba Woodland, 1934		+	-
Amphoteromorphus piriformis Carfora, de Chambrier & Vaucher, 2003		+	+
Brayela karuatayi (Woodland, 1934)		+	+
Brooksiella praeputialis (Rego, dos Santos & Silva, 1974)		+	-
Chambriella agostinhoi (Pavanelli & Machado dos Santos, 1992)		-	+
Chambriella paranaensis (Pavanelli & Rego, 1989)		-	+
Choanoscolex abscisus (Riggenbach, 1896)		+	+
Endorchis piraeeba Woodland, 1934		+	+
Ephedrocephalus microcephalus Diesing, 1850		+	-
Euzetiella tetraphylliformis de Chambrier, Rego & Vaucher, 1999		+	+
Gibsoniela mandube (Woodland, 1935)		+	+
Gibsoniela meursaulti de Chambrier & Vaucher, 1999		+	-
Goezeella siluri Fuhrmann, 1915		+	-
Harriscolex kaparari (Woodland, 1935)		+	+
Harriscolex piramutab (Woodland, 1934) n. comb.		+	+
Houssayela sudobim (Woodland, 1935)		+	+
Jauella glandicephalus Rego & Pavanelli, 1985		-	+
Lenhataenia megacephala (Woodland, 1934)		+	+
Mariauxiella piscatorum de Chambrier & Vaucher, 1999		-	+
Manaosia bracodemoca Woodland, 1935		+	+
Megathylacus jandia Woodland, 1934		+	+
Monticellia amazonica de Chambrier & Vaucher, 1997		+	+
Monticellia belavistensis Pavanelli *et al*., 1994*		-	+
Monticellia lenha Woodland, 1933		+	+
Monticellia magna (Rego, Santos & Silva, 1974)		+	-
Monticellia santafesina Arredondo & Gil de Pertierra, 2010		-	+
Monticellia ventrei de Chambrier & Vaucher, 2009		-	+
Nomimoscolex admonticellia (Woodland, 1934)		+	+
Nomimoscolex dorad (Woodland, 1935)		+	-
Nomimoscolex lenha (Woodland, 1933)		+	+
Nomimoscolex lopesi Rego, 1989		-	+
Nomimoscolex microacetabula Gil de Pertierra, 1995		+	-
Nomimoscolex piraeeba Woodland, 1934		+	-
Nomimoscolex sudobim Woodland, 1935		+	+
Nomimoscolex suspectus Zehnder *et al.*, 2000**		+	+
Nupelia portoriquensis Pavanelli & Rego, 1991		+	-
Peltidocotyle lenha (Woodland, 1933)		+	+
Peltidocotyle rugosa Diesing, 1850		+	+
Proteocephalus gibsoni Rego & Pavanelli, 1991		+	+
Proteocephalus hemioliopteri de Chambrier & Vaucher, 1997		+	+
Proteocephalus hobergi de Chambrier & Vaucher, 1999		-	+
Proteocephalus kuyukuyu Woodland, 1935		+	+
Proteocephalus macrophallus Diesing, 1850		+	+
Proteocephalus microscopicus Woodland, 1935		+	+
Proteocephalus platystomi Lynsdale, 1959		+	-
Proteocephalus sophiae de Chambrier & Rego, 1994		+	+
Pseudocrepidobothrium eirasi (Rego & de Chambrier, 1995)		+	-
Pseudocrepidobothrium ludovici Ruedi & de Chambrier, 2012		+	-
Rudolphiella myoides (Woodland, 1934)		+	-
Rudolphiella piracatinga (Woodland, 1935)		+	+
Rudolphiella piranabu (Woodland, 1934)		+	-
Scholzia emarginata (Diesing, 1850)		+	+
Sciadocephalus megalodiscus Diesing, 1850		+	+
Spasskyellina spinulifera (Woodland, 1935)		+	+
Spatulifer maringaensis Pavanelli & Rego, 1989		+	+
Spatulifer rugosa (Woodland, 1935)		+	+
Spatulifer surubim Woodland, 1934		+	-
Travassiella jandia (Woodland, 1934)		+	+
Zygobothrium megacephalum Diesing, 1850		+	+
Total	**64**	**54**	**46**

* Pavanelli, Machado dos Santos, Takemoto & dos Santos, 1994
**Zehnder, de Chambrier, Vaucher & Mariaux, 2000

Table 2. List of fish hosts and their proteocephalidean cestodes found in the Peruvian Amazonia, with values of prevalence. Cestode species found in 2006-2011, but not reported by de Chambrier *et al.* (2006a), in bold.

Fish family	Fish host	No.	Cestode species	Preval.	PI No.*	Coll. No.**
Auchenipteridae	*Ageneiosus inermis*	16	***Ageneiella* sp.**	6%	827a,b	G 85110, 85111
			Gibsoniela mandube	13%	876a,b, 891a	G 85156, 85158, 85164
	Ageneiosus sp.	10	***Gibsoniela mandube***	30%	484, 504a,b, 561	G 63059, 63119, 63203, 63209–63211, 63229[1]
Cichlidae	*Astronotus ocellatus*	4	*Proteocephalus gibsoni*	25%	125	C 407; M 2222
	Cichla monoculus	15	*Proteocephalus macrophallus*	7%	116a, 130a	C 247; G 36523; M 2219; U 97156
			Proteocephalus microscopicus	21%	116b, 117a, 120a, 123a, 185b, 248a	C 247; G 36524, 36525, 37330, 37331; M 2220; U 97155
			Sciadocephalus megalodiscus	3%	185a	G 37332
	Cichlasoma amazonarum	29	**Proteocephalidea gen. sp.**	10%	470, 474d, 477a	G 63132, 63202, 63208
Doradidae	*Oxydoras niger*	16	***Proteocephalus hobergi***	6%	774a	G 85006
	Megalodoras uranoscopus	4	***Proteocephalus kuyukuyu***	75%	324a, 444a, 581a	G 60019, 60107, 60103, 66750, 69708
	Pterodoras granulosus	24	***Monticellia belavistensis***	4%	350b,c	G 60066, 60095
			Proteocephalus kuyukuyu	8%	636, 637	G 72081, 72971
			Proteocephalus sp. 2***	8%	350b,c, 634, 634b, 635a,b,x, 636, 638	G 60066, 60095, 69597, 69593, 69594, 69596[2]
	Pterodoras sp.	1	***Proteocephalus kuyukuyu***	(100%)	588a	G 66572, 69709
Heptapteridae	*Goeldiella eques*	28	*Nupelia* sp.	11%	438	G 63185
Pimelodidae	*Brachyplatystoma* cf. *filamentosum*	3	***Amphoteromorphus ovalis***	33%	516a	G 63125
			Endorchis piraeeba	33%	516	G 63126, 63206
			Nomimoscolex suspectus	33%	516a–c	G 63060, 63205, 63207
	Brachyplatystoma rousseauxii	3	***Amphoteromorphus peniculus***	33%	367a	G 60052, 63179
			Amphoteromorphus piriformis	33%	61d	G 36519
	Brachyplatystoma vaillantii	39	***Chambriella* sp. 1**	10%	396a, 398a, 399a, 838	G 60063, 60091, 63183, 85133
			Harriscolex piramutab	20%	236e, 308a,b, 362a, 398a, 399a, 400a, 437a	G 63216, 63152, 60024, 60054, 86402, 60053, 60058, 60088
	Calophysus macropterus	33	*Monticellia amazonica*	15%	573, 778a,b	G 79194, 85010, 85013
			Rudolphiella piracatinga	30%	408a, 409b, 755a, 778ad	G 60056, 60060, 85001, 85011, 85012, 85014[3]
	Hemisorubim platyrhynchos	12	*Chambriella paranaensis*	8%	95d	G 36430, 36431
			Mariauxiella piscatorum	17%	83b, 95a	C 404; G 36510, 36518
			Spatulifer maringaensis	17%	76a, 83b, 95d	C 410; G 36511; M 2224
	Megalonema platycephalum	1	***Monticellia santafesina***	(100%)	550a,b	G 69452, 69608
	Phractocephalus hemioliopterus	10	*Chambriella* sp. 2	50%	597, 613a,b, 727, 772	G 69618, 67060, 67065, 79199, 67054, 84851
			Proteocephalus hemioliopteri	10%	613	G 79200
			Proteocephalus sp. 1***	20%	270b, 273a	C 416; G 37335
			Scholzia emarginata	100%	355a, 465a, 597, 613, 707, 727, 772y, 823	G 63177, 60131, 69617, 69676, 69677, 69678, 84850, 85107
			Zygobothrium megacephalum	10%	270c	C 401; M 2227
			Monticelliinae gen. sp.	10%	772a	G 84860
	Pimelodus blochii	8	***Proteocephalus* sp. 3**	25%	658, 661b	G 69605, 69606, 79202, 79203
	Pimelodus latissimus	1	***Endorchis* sp.**	(100%)	571a,b	G 69536, 69537
	Pimelodus ornatus	13	***Nomimoscolex* sp.**	15%	517a, 519a	G 63127, 63212
	Pinirampus pirinampu	30	***Monticellia ventrei***	13%	776a–c, 809a,c,g, 835a,f, 880	G 85007–85009, 85020–85022, 79598, 85124, 85125, 79599
			Nomimoscolex admonticellia	37%	439, 672a, 674, 809b,d, 815b, 819b[4]	G 60087, 78984, 79173, 85023, 85026, 79596[5]
			***Rudolphiella* sp.**	17%	379a, 809e, 819a, 824, 850a	G 60070, 85025, 85161, 85108, 85152

Fish family	Fish host	No.	Cestode species	Preval.	PI No.*	Coll. No.**
	Platynematichthys notatus	13	***Brayela karuatayi***	38%	532a, 533a,b, 798a, 802	G 62587, 63128, 63213, 79595, 85018
	Pseudoplatystoma fasciatum	42	***Chambriella* sp. 3**	17%	318a, 319a, 359b, 361d, 457a, 708, 730	G 54741, 63149, 60090, 63172, 60025, 66566, 69695
			Choanoscolex abscisus	33%	319a, 320a, 347a,b, 359b, 361b,c[6]	G 60074, 63153, 60042, 63165, 63173, 63174[7]
			Endorchis* cf. *piraeeba (juv.)	2%	318a	G 63150
			***Euzetiella* sp.** (juv.)	2%	618	-
			Harriscolex kaparari	7%	705, 706, 708	G 66561, 69701, 69702
			Houssayela sudobim	7%	509b, 708a	G 62586, 66553, 66554
			***Megathylacus* sp.**	10%	78a, 629a, 708f, 730	G 22321, 36517, 74089, 74090, 66559, 69616
			Nomimoscolex lopesi	26%	322a, 332a, 347a, 359a, 361c, 456b[8]	G 60100, 63155, 60050, 63176, 79176, 60064[9]
			Nomimoscolex sudobim	24%	304c, 332a, 347a,b, 359c, 360b, 361c[10]	G 60067, 63156, 60022, 60049, 60093, 60102[11]
			Peltidocotyle rugosa	24%	76a, 304b,d, 358a, 361a, 451a, 457b[12]	G 36515, 60092, 63144, 60089, 60105, 60023[13]
			Spasskyellina spinulifera	29%	304d, 305a, 306a, 343a, 347a,b[14]	G 63143, 63146, 63147, 63162, 63166, 79193[15]
			Spatulifer rugosa	33%	303a, 318a, 320a, 332a, 347a,b, 360a[16]	G 60082, 60051, 63151, 63154, 60061, 60068[17]
	Pseudoplatystoma tigrinum	13	*Choanoscolex abscisus*	8%	225a	G 37317
			Nomimoscolex sudobim	15%	225a, 226a	G 37322, 37323
			Spasskyellina spinulifera	14%	225a, 226a	G 37339, 37340
			Spatulifer sp.***	8%	226a	G 37324; M 2225
	Sorubim lima	29	***Manaosia bracodemoca***	10%	490a, 586, 670	G 63123, 66570, 79210
			Spatulifer maringaensis	10%	586b,c, 662, 670a	G 66569, 66571, 69599, 69607, 79209
	Sorubimichthys planiceps	22	***Chambriella* sp. 4**	27%	440c, 485a, 585, 592, 594, 595	C 478; G 60048, 63120, 70835, 79198, 69592, 69697
			***Choanoscolex* sp.**	14%	356, 440c, 593	C479; G 4610, 69564
			Lenhataenia megacephala	50%	356a, 370c, 412b, 485a, 582a,b, 585[18]	G 86458, 54608, 60036, 63121, 66549, 68969[19]
			Monticellia lenha	59%	356a,d, 370b, 440a, 449a, 450b[20]	G 54628, 54740, 60038, 63220, 54606, 60045[21]
			Nomimoscolex lenha	33%	356a, 585, 592, 616, 728	G 54629, 63218, 63219, 79196, 69583, 69685, 67055, 69686
			Peltidocotyle lenha	59%	356a,b, 370a, 412a, 450a, 582, 585[22]	G 60039, 63167, 54605, 60037, 60035, 69539[23]
	Zungaro zungaro	30	*Amphoteromorphus parkamoo*	10%	231b, 358a,b, 364a	G 37309, 60069, 60071
			Chambriella agostinhoi	37%	302b, 357a, 363a, 364b, 387b , 445a[24]	C 402; G 60065, 60084, 60099, 63169, 60021[25]
			Euzetiella tetraphylliformis	17%	115, 583, 663, 664, 665	C 403; G 79195, 69610, 79207, 79208
			Jauella glandicephalus	30%	301a, 413b, 447a, 583, 663a,c, 664[26]	G 60062, 60079, 60076, 69682, 66573, 66574[27]
			Megathylacus jandia	7%	357a, 413a	G 63168, 60085
			Peltidocotyle lenha	43%	302a, 357a, 368a, 387a, 467a, 468a[28]	G 60027, 60020, 60072, 63180, 60101, 60134[29]
			Proteocephalus sophiae	20%	583, 663, 664, 665b, 845b,c,e,f, 892b	G 68968, 67663, 69679, 69680, 79169, 79206[30]
			Travassiella jandia	3%	115a	G 36520

Abbreviations: * Field number of the hosts, PI 1–136 April 2004, 137–276 April 2005, 300–469 September 2006, 470–545 October 2008, 546–752 October 2009, 753–910 October 2011; **G – Natural History Museum, Geneva, Switzerland (MHNG-PLAT); C – Institute of Parasitology, AS CR, České Budějovice, Czech Republic (IPCAS); M – Helminthological Collection of the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM); U – U.S. National Parasite Collection, Beltsville, Maryland, U.S.A. (USNPC). ***immature. Additional collection/host numbers: [1]G 63209–63211, 63229; [2]G 69597, 69598, 69603, 69604, 72972, 79201; [3]G 85015, 85137; [4]PI 825a, 835g, 880, 887, 890b; [5]G 79845, 85126, 79600, 79876, 85163; [6]PI 466b, 562, 563, 708, 725, 729, 730, 777a; [7]G 63201, 69462, 69704, 66567, 69690, 69693, 72970, 79174, 79175, 84853; [8]G 466b, 708b,c,g, 730; [9]G 63200, 66550, 66555, 66556, 66560, 66565, 69692; [10]PI 535a. 618, 708e,h, 730; [11]G 63163, 63175, 63131, 69699, 66551, 66558, 66564, 69694; [12]PI 466a, 563, 708h, 777a; [13]G 60129, 60132, 69535, 66552, 84854; [14]PI 536a,b, 708h, 730, 818a; [15]G 66553, 66568, 69691, 85027; [16]PI 378a, 466b, 509c, 534a, 536a,b, 708d, 726; [17]G 60080, 60097, 63164, 60083, 63199, 63124, 63129, 63130, 63215, 66557, 66562, 69696; [18]PI 592, 594, 595a,b, 611a,b, 728; [19]G 69538, 69580, 72946, 72947, 79577, 69568, 69591, 72973, 72974, 69600, 69602, 79877; [20]PI 485b, 582, 585, 592, 594, 595, 616, 728; [21]G 54607, 60043, 54742, 54743, 60041, 63122, 69581, 69703, 79197, 69567, 69700, 69683, 69684; [22]PI 592, 594, 595, 616, 665a, 666a, 728a; [23]G 69582, 69920, 69385, 69477, 69689, 69688, 69609, 69611, 69687; [24]PI 469a, 583; [25]G 60096, 60136, 69698; [26]PI 663a,c, 664, 665, 845a, 892a; [27]G 69681, 74081, 79204, 79205, 85139, 79808; [28]PI 663b, 664e, 845b,f; [29]G 60135, 79167, 79168, 85147, 85148; [30]G 85140, 85141, 85144, 85146, 79847.

In the present study, we focused on adult cestodes and thus only very few proteocephalidean larvae (merocercoids, see Chervy, 2002) were found. The identification of the latter based on morphological characteristics is impossible, but their molecular analysis will enable us to match their DNA sequences with those of adults, which were obtained in the framework of a NSF-PBI project "A Survey of the Tapeworms (Cestoda: Platyhelminthes) from the Vertebrate Bowels of the Earth" (www.tapeworms.uconn.edu). This approach (see also Jensen & Bullard, 2010) is the most feasible way to elucidate life cycles of Neotropical proteocephalideans, which are almost completely unknown. Based on the fact that large catfishes are predatory (piscivorous) and do not consume plankton, it is reasonable to assume that life cycles of many, if not most, proteocephalidean cestodes that mature in large catfishes in South America include two intermediate (or one intermediate and one paratenic) hosts, the second host being small planktonophagous fish similarly to the developmental cycles of *Proteocephalus ambloplitis* in North America (Hunter, 1928; Freze, 1965; Scholz, 1999; Scholz & de Chambrier, 2003).

To summarize, the present study enriched considerably the current knowledge of the species composition and distribution areas of members of one of the dominant groups of metazoan parasites of freshwater teleosts in the Neotropical Region. However, there are still many fish hosts that have never been examined for parasites and thus a number of new taxa probably remain to be discovered. This will depend on sampling effort and time dedicated to future collecting trips and taxonomic evaluation of newly collected cestodes, using combined morphological and molecular approaches. A recent discovery of a new genus from the little known auchenopterid catfish *Tocantinsia piresi* from the Xingú River in Brazil (Alves *et al.*, 2015) as well as the number of unidentified species found in Peru, which may represent new species, supports the argument that we are just at the very beginning of a long path towards representative mapping the species diversity, host-parasite relationships and zoogeography of the parasites of teleost fishes in one of the hottest spots of fish parasite diversity on the Earth. Since the existence of cryptic species among proteocephalidean cestodes cannot be excluded, it is impossible to provide a reliable estimate of the species richness of these parasites. However, it is reasonable to assume that the actual number of extant species would be at least twice as high as the number of the species currently considered to be valid.

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