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Abstract

We provide a summary overview of the diversity of trematode parasites in freshwater fishes of the "New World," i.e. the Americas, with emphasis on adult forms. The trematode fauna of three regions, South America, Middle America, and USA and Canada (North America north of Mexico), are considered separately. In total, 462 trematode species have been reported as adults from the Americas. The proportion of host species examined for parasites varies widely across the Americas, from a high of 45% in the Mexican region of Middle America to less than 5% in South America. North and South America share no adult species, and one exclusively freshwater genus, *Creptotrema* Travassos, Artigas & Pereira, 1928 in the Allocreadiidae Looss, 1902 is the most widely distributed. Metacercariae of strigeiforms maturing in fish-eating birds (e.g., species of the Diplostomidae Poirier, 1886) are common and widely distributed. The review also highlights the paucity of known life-cycles. The foreseeable future of diversity studies belongs to integrative approaches and the application of molecular ecological methods. While opportunistic sampling will remain important in describing and cataloguing the trematode fauna, a better understanding of trematode diversity and biology will also depend on strategic sampling throughout the Americas.

Keywords: freshwater fish, fish fauna, fish family, South American species, trematode species

Introduction

The "New World" consists principally of two geologically old continents, collectively known as the "Americas," with divergent histories. Following the dismantling of Pangaea in the Late Jurassic, the two continents forged independent biogeographical ties as part of northern and southern landmasses, Laurasia and Gondwanaland. As these composite landmasses fragmented with sea-floor spreading in the early Cretaceous, South America broke away from Africa while North America separated from Europe and became contiguous with northeast Asia via the Asian-American peninsula (Rogers, 1993; Smith et al., 1994). After being separated for some 160 million years, South and North America were finally joined by a land bridge in the Miocene (Bacon et al., 2015; Montes et al., 2015). In the course of their tumultuous geological histories, both continents experienced phases of vast marine incursions, tectonic events that led to extensive orogeny and volcanism, and the effects of "ice-ages," most recently in the Pleistocene. The reconfiguration of drainages as a result of these geological and climatic processes facilitated both diversification and extinction of their aquatic fauna at various times (Mayden, 1992; Albert & Reis, 2011).

Old continental ties are manifested in the Holarctic relationships of several fish families of North America (Hocutt & Wiley, 1986; Burr & Mayden, 1992), whereas major components of the fish fauna of South America show clear Gondwanan influences (Lundberg, 1993). Intermixed with these components are fishes that have demonstrable marine origins. The fish fauna of Middle America (Miller et al., 2005; Matamoros et al., 2015) reveals the complexity of a transitional area and the impact of the Great American Biotic Interchange (GABI), a dynamic and ongoing process of colonization and radiation (Chakrabarty & Albert, 2011; Hulsey & López-Fernández, 2011).

The trematodes of freshwater fishes in this vast and complex region are equally diverse in composition and history, their biology shaped by their own evolutionary histories, those of their hosts, as well as the trophic webs in which they are embedded (Gibson, 1996; Marcogliese & Cone, 1997; Hoffman, 1999; Pérez-Ponce de León & Choudhury, 2005; Lafferty et al., 2006, 2008; Kohn et al., 2007). In this paper, we provide a summary overview of the diversity of trematodes in freshwater fishes of the Americas, with emphasis on adult forms, and with comments about their noteworthy biological characteristics. The names of contributors for particular regions appear near the headings of the respective sections.

South America (Margarita Ostrowski de Núñez & Cláudia Portes Santos)

The freshwater fishes of South America comprise c. 5,400 known species (Reis, 2013), with the major diversity being in the Amazon, Orinoco, and the Parano-Platense river systems.

The fauna falls broadly into three categories: (i) amphidromous species in marine families that can adapt to freshwater environments, such as mullets and sardines; (ii) families closely related to marine groups but entirely confined to continental habitats, such as Potamotrygonidae, Cichlidae, Rivulidae, Cyprinodontidae, Poecilidae, and Anablepidae; and (iii) groups that originated and diversified in freshwater habitats, such as Siluriformes, Characiformes, Gymnotiformes, Lepidosirenidae, Arapaimidae, Osteoglossidae, and Polycentridae (Reis, 2013).

Less than 5% of this immense fish fauna has been examined for parasites, which makes the total trematode diversity difficult to predict. Combining the records in Kohn et al. (2007) with some 14 species described since yields a count of 198 fully identified adult trematode species; this includes those of amphidromous fish, such as *Mugil* spp., *Rhamnogaster* sp., and *Centropomus* spp. These 198 species comprise two aspidogastrean and 28 digenean families from 104 genera, of which 82 genera are represented by one or two species, 20 by three to six species, and one (*Saccocoelioides* Szidat, 1954) by 15 species. Two species are of uncertain status. Collectively, the trematodes parasitize approximately 160 different freshwater fish species (excluding introduced fish species). Most trematode species (68%) parasitize only one species of fish, and 10% parasitize four or more hosts, whereas *Prosthenhystera obesa* (Diesing, 1850) Travassos, 1922 and *Genarchella parva* Travassos, Artigas & Pereira, 1928 are exceptional with 24 and 28 hosts, respectively.

The trematode assemblages from the Paraná and La Plata River systems in Brazil and Argentina, respectively, still remain our main source of information. Reports from the remaining South American countries include mostly marine species and a few in freshwater, except Suriname where no fish trematode appears to have been reported.

The following aspects of the fauna are noteworthy:

1. Composition of the fauna and remarks on selected families

The Haploporidae Nicoll, 1914 is the richest family with 37 species in 13 genera; eight genera are monotypic, four have two to five species and one (*Saccocoelioides*) contains 15. Four of the ten known life-cycles of freshwater fish trematodes belong to this family. Cladorchiidae Fischoeder, 1901, with 32 species in 22 genera, is also species-rich; 15 genera are monotypic and *Dadaytrema* Travassos, 1931 contains five species. The Allocreadiidae Looss, 1902 contains 18 species in five genera, one of them with five (*Auriculostoma* Scholz et al., 2004) and one with six (*Creptotrema* Travassos, Artigas & Pereira, 1928) species (Curran, 2008; Curran et al., 2011). The Cryptogonimidae Ward, 1917 contains 16 species in 11 genera. Ten genera are monotypic, and one (Parspina Pearse, 1920) has six species, four of them described in the last five years (Kohn & Fernandes, 2011; Ostrowski de Núñez et al., 2011; Arredondo & Ostrowski de Núñez, 2013). Four of the ten known South American fish-trematode life-cycles are of species in this family. The Apocreadiidae Skrjabin, 1942 contains nine species in four genera, one of them (*Crassicutis* Manter, 1936) with four species. The Derogenidae Nicoll, 1910 is represented by eight species in three genera; Genarchella Travassos, Artigas & Pereira, 1928 alone has four species, two of which, *G. genarchella* Travassos, Artigas & Pereira, 1928 and *G. parva*, parasitize 17 and 28 fish hosts, respectively. The five species of the Echinostomatidae Looss, 1899 belong to one genus, *Caballerotrema* Prudhoe, 1960, and parasitize hosts of the Arapaimidae, Osteoglossidae, and

Gymnotidae, fishes of freshwater origin. The Gorgoderidae Looss, 1899 is represented by nine species in three genera, of which one (*Phyllodistomum* Braun, 1899) has six species. The Zoogonidae Odhner, 1902 is interesting in that five of its six described species are restricted to the Patagonian region (*Steganoderma* Stafford, 1904 with four species, and *Limnoderetrema* Bray, 1987). The only freshwater species of the Didymozoidae Monticelli, 1888, *Brasicystis bennetti* Thatcher, 1979, is found in the River Amazon, in *Plagioscion squamosissimus*.

2. The marine character of the fauna

In addition to the aspidogastrean *Lobatostoma jungwirthi* Kritscher, 1974 and *Rohdella amazonica*, Giese, Silva, Videira, Furtado, Matos, Gonçalves, Melo & Santos, 2015, 17 digenean families (Acanthocolpidae Lühe, 1906, Apocreadiidae, Aporocotylidae Odhner, 1912, Bucephalidae Poche, 1907, Cryptogonimidae, Derogenidae, Didymozoidae, Faustulidae Poche, 1926, Haploporidae, Haplosplanchnidae Poche, 1926, Hemiuridae Looss, 1899, Lecithasteridae Odhner, 1905, Microscaphidiidae Looss, 1900, Monorchiidae Odhner, 1911, Opecoelidae Ozaki, 1925, Opisthorchiidae Looss, 1899, and Zoogonidae) have marine connections; their South American species are found principally in fishes of the first and second categories. Species of the remaining 11 families (Allocreadiidae, Cladorchiidae, Callodistomidae Odhner, 1910, Diplodiscidae Cohn, 1904, Echinostomatidae, Gorgoderidae, Macroderoididae McMullen, 1937, Plagiorchiidae Lühe, 1901, Proterodiplostomatidae Dubois, 1936, and Zonocotylidae Yamaguti, 1963) are mostly found in fishes of the third category and several of these may have freshwater origins. The marine affinities of the trematode fauna were first recognized by Szidat (1954) in his pioneering studies on fish parasites of the Rio de la Plata.

3. The relationship with species from Africa

Manter (1963) noted that South American species of Cladorchiidae, Cryptogonimidae, and Apocreadiidae seemed related to species in Africa, which reflected the former continuity of these southern continents. Gussev (1967) concluded, that "Brazilian fish parasites have higher similarity especially with Africa but also with India in the Paramphistomidae Fishchoeder, 1901, Gorgoderidae, Opisthorchiidae, Plagiorchiidae, and among parasites of siluriform fishes." Considering that Characidae and Osteoglossidae are the only exclusively freshwater fish families native to both Africa and South America (Nelson, 2006), trematodes parasitizing these host groups should be studied carefully. The Callodistomidae represents a good target because it (i) occurs in Africa and South America; (ii) has a small number of species (two monotypic genera in South America and two in Africa); and (iii) its species parasitize representative Gondwanan hosts such as Characiformes (Characidae, Ctenoluciidae, and Anastomidae in South America), Polypteridae in Africa, Perciformes (Sciaenidae in South America and Anabantidae in Africa), and Siluriformes (Pimelodidae in South America and Mochokidae in Africa).

4. The relationship with species from Australia and New Zealand

The Galaxiidae, a group of diadromous fishes found only in the Southern Hemisphere presents an interesting model system. Three (*Aplochiton*, *Brachygalaxias*, *Galaxias*) out of the seven existing galaxiid genera are present in the Patagonian Region, with *Galaxias maculatus* present also in Australia, Tasmania, and New Zealand. This fish species harbors two similar digeneans, *Steganoderma szidati* Viozzi, Flores & Ostrowski de Núñez, 2000 and *Limnoderetrema minutum* (Manter, 1954) Bray, 1985, in Argentina and New Zealand, respectively.

5. Life-cycles

Apart from the aspidogastrean *L. jungwirthi*, ten complete digenean life-cycles of species belonging to the Apocreadiidae, Cryptogonimidae, Derogenidae, and Haploporidae are known from experimental infections (Diaz et al., 2009; Diaz & Gonzalez, 1990; Martorelli, 1986a, b, 1989; Ostrowski de Núñez et al., 1999; Ostrowski de Núñez & Gil de Pertierra, 1991; Quintana & Ostrowski de Núñez, 2014; Simões et al., 2008; Szidat, 1970; Zylber & Ostrowski de Núñez, 1999). The marine character of the trematode fauna is reflected also by the origin of their mollusk intermediate hosts. Two species use *Pyrgophorus* sp., eight use *Heleobia* spp., and one uses *Aylacostoma chloroticum*, all "prosobranchian" mollusks of marine origin (Bouchet & Rocrois, 2005). Although lifecycles of digeneans of fish that originated and diversified in freshwater are not yet published, *Biomphalaria* sp. serves as the first intermediate host for at least one species of macroderoidid (unpublished data), and based on known life-cycles for species in the Cladorchiidae and Echinostomatidae, pulmonate snails can be expected to be suitable hosts. It is also well known that allocreadiids, bucephalids, and gorgoderids use bivalve mollusks as first intermediate hosts.

6. Metacercariae

Most documented South American metacercariae from fish belong to species of Diplostomidae Poirier, 1886, Heterophyidae Leiper, 1909, and Echinostomatidae, that use mainly birds and mammals as definitive hosts (Ostrowski de Núñez & Gil de Pertierra, 2004; Machado et al., 1994). Metacercariae of species of Bucephalidae, Cryptogonimidae, and Allocreadiidae are also found (Ostrowski de Núñez, unpublished observations).

Middle America (Gerardo Pérez-Ponce de León & M. Leopoldina Aguirre-Macedo)

Eight countries (Panama, Costa Rica, Nicaragua, Honduras, El Salvador, Belize, Guatemala and Mexico) comprise Middle America (Winker, 2011), which includes the subregion of Central America (Matamoros et al., 2015) and sometimes the Caribbean islands. The region has also been called the Mexican Transition Zone (see Marshall & Liebherr, 2000; Miguez-Gutierrez et al., 2013), an area of "intense biotic interaction" facilitated by historical and ecological changes (Morrone, 2010). The freshwater fish fauna of Middle America comprises c. 800 species. Of these, freshwater fishes of Central America include 299 primary and secondary species (Matamoros et al., 2015). Mexico has around 500 species, 145 of which are primary and 350 secondary (Espinosa-Pérez, 2014). Members of the Neotropical fish families Characidae, Cichlidae, Heptapteridae, and Poeciliidae, with origins in South America, are distinctive components in lower and upper Central America. In Mexico, Neotropical elements, such as Cichlidae and Poeciliidae dominate the southern fauna, whereas Nearctic elements such as Cyprinidae, Percidae, Centrarchidae, Catostomidae, and Ictaluridae dominate the northern regions. The endemic fauna (e.g., Goodeidae and Atherinopsidae) is characteristic of central Mexico (Miller et al., 2005).

The trematode fauna, adults and larvae combined, comprises 114 species, of which 66 species occur as adults; this includes one species of aspidogastrean and 65 species of digenean. This count includes species commonly found in brackishwater fishes that have adapted to freshwater habitats, such as the Eleotridae, Mugilidae, Ariidae, and Centropomidae. Of the 114 species, 48 have been reported as metacercariae. *Pseudoacanthostomum panamense* Caballero, Bravo & Grocott, 1953 and *Oligogonotylus manteri* Watson, 1976 occur in freshwater fishes as both, adult and metacercariae. Overall, the trematodes belong to 24 families and have been reported from about 270 fish species in 25 fish families.

Trematodes exhibit the highest species richness among the freshwater fish helminth fauna of the region (Pérez-Ponce de León & Choudhury, 2010). However, in contrast to our knowledge of trematodes from Mexico, Central American freshwater fish helminths remain poorly known and under-surveyed (e.g., Watson, 1976; Bunkley-Williams & Williams, 1994; Aguirre-Macedo et al., 2001; Sandlund et al., 2010), or documented only in localized taxonomic reports (e.g., Sogandares-Bernal, 1955; Choudhury et al., 2002, 2006; Scholz et al., 2004; Aguirre-Macedo & Scholz, 2005).

Some notable aspects of the trematode fauna are as follows:

1. Twelve out of the 24 families contain only adult trematodes. Four families, Allocreadiidae (ten genera, 18 species), Cryptogonimidae (eight genera, 11 species), Apocreadiidae (two genera, seven species), and Gorgoderidae (one genus, seven species) account for most of the diversity. Lissorchiidae Magath, 1917, Microphallidae Ward, 1901, and Microscaphidiidae Looss, 1900 are represented by a single species each. Other families commonly reported in freshwater fish elsewhere in the Americas are also present here: Callodistomidae, Derogenidae, Haploporidae, and Macroderoididae.

2. One hundred of the 114 species have been reported in Mexico, whereas Central America has 32 species, and the Antilles, eight. Most of the Central American trematode fauna is shared with that of Mexico (Sandlund et al., 2010). Only two species occur exclusively in the Antilles, the cryptogonimid *Pacacryptogonimus centropomi* Siddiqi & Cable, 1960 in Puerto Rico, and the macroderoidid *Perezitrema viguerasi* Baruš & Moravec, 1967 in Cuba.

3. The fauna represents a complex array of species from both Neotropical and Nearctic realms. Most fish families possess their own characteristic "core" helminth fauna, with limited host-sharing in transitional areas (Pérez-Ponce de León & Choudhury, 2005). The fauna of Central America and the Antilles is characteristically Neotropical, as indicated by species of *Acanthostomum* Looss, 1899, *Genarchella* Travassos, Artigas & Pereira, 1928, *Creptotrema*, and *Auriculostoma*.

4. The Allocreadiidae exemplifies the complex mixture of Nearctic and Neotropical elements within this region. *Allocreadium* Looss, 1900 and *Crepidostomum* Braun, 1900 are typical components of the Nearctic fauna (Hoffman, 1999), whereas *Auriculostoma* and *Creptotrema* show Neotropical connections (see Curran et al., 2011, 2012). At least five

genera of allocreadids are apparently endemic to Middle-America, where they diversified in close association with their hosts: *Margotrema* Lamothe-Argumedo, 1970 (two species), *Wallinia* Pearse, 1924 (two species), *Paracreptotrema* Choudhury, Pérez-Ponce de León, Brooks & Daverdin, 2006 (three species), *Paracreptotrematoides* Pérez-Ponce de León, Pinacho-Pinacho, Mendoza-Garfias, Choudhury & García-Varela, 2016 (one species), and *Pseudoparacreptotrema* Pérez-Ponce de León, Pinacho-Pinacho, Mendoza-Garfias, Choudhury & García-Varela, 2016 (two species) (Martínez-Aquino et al., 2014; Pérez-Ponce de León et al., 2016).

5. The Apocreadiidae, with seven species in two genera, is also well represented. *Crassicutis* currently contains four species parasitic in cichlids (Pérez-Ponce de León et al., 2008), but recent molecular analyses revealed that *C. cichlasomae* is a complex of seven cryptic species (Razo-Mendivil et al., 2010).

6. The Gorgoderidae is constituted by six nominal species of *Phyllodistomum* from Mexico, as well as two cryptic species in *Phyllodistomum lacustri* (Loewen, 1929) Lewis, 1935 (see Rosas-Valdez et al., 2011). Four species show close associations with cyprinodontiform fishes (see Pérez-Ponce de León et al., 2015 and references therein).

7. The Cryptogonimidae contains 11 species in eight genera. Five species from four genera (*Campechetrema* Lamothe-Argumedo, Salgado-Maldonado & Pineda-López, 1997, *Oligogonotylus* Watson, 1976, *Pseudocaecincola* and *Tabascotrema* Lamothe-Argumedo & Pineda-López, 1990) are found exclusively in cichlids and only in Middle America. A recent study (Razo-Mendivil et al., 2015) showed that *Tabascotrema verai* Lamothe-Argumedo & Pineda-López, 1990 is a complex of three cryptic species, which suggests that cryptic diversity will also be a challenge in the taxonomy of cryptogonimids. Given the large number of cryptogonimids that inhabit marine fishes along both Atlantic and Pacific coasts (see Pérez-Ponce de León et al., 2007), one may generate several testable hypotheses: (i) a marine origin for these Middle-American cryptogonimids of cichlids; (ii) a close relationship with freshwater cryptogonimids of North American centrarchids; and (iii) independent colonization events of/in Nearctic and Neotropical cryptogonimids. Centrarchids and cichlids are both members of the Percomorpha, and both families have demonstrable marine connections (Near et al., 2013). Clearly a phylogenetic analysis that includes both freshwater and marine cryptogonimids is needed to test these and other hypotheses of freshwater cryptogonimid monophyly and host associations.

8. Few life-cycles are fully or even partially known from natural hosts in Middle America. Most known life-cycles are of trematodes from cichlid fishes in southern Mexico, where snails such as *Pyrgophorus coronatus* or *Biomphalaria obstructa* are first intermediate hosts. The known life-cycles of the trematodes include four members of the family Cryptogonimidae, two of the Diplostomidae, two of the Echinostomatidae, two of the Heterophyidae, and one each of the Apocreadiidae, Cathaemasiidae Fuhrmann, 1928, Clinostomidae Lühe, 1901, Derogenidae, Macroderoididae, Opisthorchiidae Looss, 1899, and Proterodiplostomidae Dubois, 1936.

9. Metacercariae are very common in Middle American freshwater fishes. Forty-five of the 48 species reported as metacercariae complete their lifecycle in fish-eating birds and two families (Heterophyidae, with 19 species, and Diplostomidae with nine species) account for 67% of the diversity. Only three species, i.e., *Acanthostomum minimum* Stunkard, 1938, *Pseudoacanthostomum panamense* Caballero, Bravo & Grocott, 1953, and *Oligogonotylus manteri* Watson, 1976, occur in freshwater fishes as both, adult and metacercaria.

Canada and USA (Anindo Choudhury, Stephen S. Curran, and Robin M. Overstreet)

The freshwater fishes of North America (Mexico, Canada, and USA) comprise a little over 1,200 species in 214 genera from 53 families (Burkhead et al., 2012, citing Nelson et al., 2004). The fauna uniquely includes several evolutionarily old actinopterygian lineages (Acipenseridae, Polyodontidae, Lepisosteidae, and Amiidae) (see Burr & Mayden, 1992). The Cyprinidae makes up nearly a third of the primary freshwater fauna, but the Catostomidae, Centrarchidae, Ictaluridae, and Percidae are also diverse and widely distributed (Hocutt & Wiley, 1986; Burr & Mayden, 1992). The northern fauna consists of several families (Acipenseridae, Esocidae, Salmonidae, Percidae, and Cottidae) with Holarctic distributions. Several families (Acipenseridae, Salmonidae, Clupeidae) have anadromous members, and one (Cottidae) also contains numerous marine species. The fauna west of the Continental Divide is noticeably less diverse and is composed mainly of anadromous salmonids, catostomids, and the western cyprinids (Burr & Mayden, 1992). Cottids and several acanthomorph families (Percidae, Centrarchidae, Elassomatidae) have clear evolutionary ties with marine groups (Near et al., 2013). *Aplodinotus grunniens* is the only freshwater member of an otherwise marine family (Sciaenidae). The presence of *Herichthys cyanoguttatus* (Cichlidae) and *Astyanax mexicanus* (Characidae) in Texas marks a notable but limited northern incursion of deep Neotropical families. Poeciliids in the southern USA also provide a contrast with the northern fauna. The Mississippi River system has the richest fish fauna (> 375 species) as well as the highest endemicity (34%) (Burr & Mayden, 1992).

The trematode fauna of freshwater fishes in Canada and the USA consists of c. 198 species from 21 families (one aspidogastrean and 20 digenean). The fauna from the USA and Canada was last compiled by Hoffman (1999). Since then several new species have been described. The fauna is summarized as follows:

1. Nonaccidental and bona fide records of Aspidogastrea in North American fishes can be reduced to one species, *Cotylogasteroides occidentalis* (Nickerson, 1902) Yamaguti, 1963 in freshwater drum. Other records are either accidental (such as a species of *Cotylaspis* Leidy, 1857 in paddlefish) or a misconception (e.g., *Aspidogaster conchicola* Baer, 1827).
2. The Allocreadiidae (23 species) is widespread, diverse, and found in most major fish families except Catostomidae. *Allocreadium* (two species) is found in cyprinids, of the five species of *Bunodera*, three infect only sticklebacks, and *Crepidostomum* (c. 14 spp. if

one includes *Megalogonia ictaluri* Surber, 1928) has radiated into numerous host lineages, with the notable exception of cypriniforms (Caira, 1989). All three allocreadiid genera exhibit Holarctic distributions, but *Crepidostomum* and *Bunodera* Railliet, 1896 are considerably more species-rich in North America (Choudhury & Leon-Regagnon, 2005; Tkach et al., 2013). *Creptotrema* (one species, *C. funduli* Mueller, 1934) is closely related to *Megalogonia* Surber, 1928 and several Neotropical genera (Curran et al., 2012).

3. The Gorgoderidae, represented by 21 species of a single genus (*Phyllodistomum*) has also radiated in a diverse array of hosts in most major drainages, including the Arctic. Most species of *Phyllodistomum* have their own characteristic host associations, and the family is also common in the Holarctic region.

4. Several families have clear marine ties but are diverse in this region. Twenty species of Opecoelidae are known (Hoffman, 1999; Tracey et al., 2009); *Plagioporus* Stafford, 1904 (13 species) has radiated into diverse hosts in all major North American drainages, with the exception of the Arctic. The Cryptogonimidae (nine genera, 17 species) is mainly associated with hosts of the fish families Centrarchidae and Moronidae, both of which have marine ancestry (Near et al., 2013). Seven cryptogonimid genera have only one or two species. The Bucephalidae (8 species), also seems to have a predilection for the gastrointestinal tract of centrarchids, but *Paurorhynchus hiodontis* Dickerman 1954, which matures in the body cavity of hiodontid fishes, is a notable exception.

5. Among the regions being considered here, the Nearctic appears to be unique in the diversity of blood flukes of the family Aporocotylidae (11 species). Six species of *Sanguinicola* Plehn, 1905 are endemic to this region, and most species having been reported from the interior of the continent. Three freshwater species of the largely coastal/marine genus *Cardicola* Short, 1953 infect fishes of Pacific coastal streams in California and Oregon. Two species of *Asipensericola* Bullard, Snyder, Jensen & Overstreet, 2008 (one undescribed) occur in acipenseriform fishes (Bullard et al., 2008; Ash Bullard, pers. comm.).

6. Three families, the Lissorchiidae (19 species), Macroderoididae (14 species), and Azygiidae Lühe, 1909 have component genera with notable host-lineage specificity. All 17 species of *Lissorchis* Magath, 1917 are parasites of suckers (Catostomidae). Similarly, in the Macroderoididae, the five "nonprecocious" species of *Alloglossidium* are parasites of ictalurid catfishes (Hoffman, 1999; Kasl et al., 2014). Phylogenetic analyses indicate that catfishes are likely original hosts (Carney & Brooks, 1991; Smythe & Font, 2001). In contrast, the species of *Macroderoides* Pearse, 1924 infect a small group of divergent hosts (Tkach & Kinsella, 2011). In the Azygiidae, *Proterometra* Horsfall, 1933 has diversified in *Lepomis* (sunfishes) (LaBeau & Peters, 1995; Womble et al., 2016), and *Leuceruthrus* Marshall & Gilbert, 1905 is found in *Micropterus* spp. (black basses). *Azygia* Looss, 1899 (3 species) on the other hand, infects several distantly related fish hosts (of the families Amiidae, Centrarchidae, Ecocidae, Moronidae).

7. The Hemiuroidea Looss, 1899 (Hemiuridae, Lecithasteridae, Derogenidae) with 11 genera and 17 species is an assortment of disparate species; most appear to be either marine or secondarily adapted to freshwaters. Anadromous fishes, such as salmonids, smelts, sticklebacks, and clupeids are common hosts (e.g., *Derogenes varicus* (Mueller, 1784) Looss, 1901, *Deropegus aspina* (Ingles, 1936) McCauley & Pratt, 1961, *Brachyphallus* spp., etc.). Alternatively, *Thometrema lotzi* Curran, Overstreet & Font 2002, whose closest relatives are Middle American, is commonly found in the stomach of various centrarchids from northern Gulf of Mexico drainages.

8. The less diverse families are also instructive: The Apocreadiidae is represented by six species belonging in the widely distributed and typically marine genus *Homalometron* Stafford, 1904, (Fayton et al., 2016), one of which, *H. armatum* (MacCallum, 1895) Manter, 1947, occurs in *A. grunniens* from Manitoba to Mississippi. Deropristiidae Cable & Hunninen, 1942 (four species) is associated with sturgeons (three deropristiid species in three genera) and Atlantic eels (Anguillidae) (one species) (Choudhury, 2009). Callodistomidae, with its sole species, *Prosthenhystera oonastica* Tkach & Curran, 2015 in catfishes in southeast USA (see Tkach & Curran, 2015) may be a legacy of past host-switching events from Neotropical hosts. The Microphallidae (four species listed in Hoffman, 1999) presents a curious case; members of this large family mainly parasitize birds and mammals and some infections in fish may be incidental (Hoffman, 1999 records four species), but *Microphallus ovatus* Osborn, 1919 matures in fishes (Hoffman, 1999).

9. The remaining fauna is mostly a collection of single species from a mixture of families of southern or marine origin, e.g., Haploporidae (one species) in poeciliids, Didymozoidae (one species) in the ovary of catostomid fishes, Faustulidae Poche, 1926 (one species) in a variety of Pacific diadromous fishes (Gibson, 1996) and Cyathocotylidae Muhling, 1898 (one species) in catfishes.

10. Metacercariae of c. 81 species (45 genera, 12 families) have been listed from this region (Hoffman, 1999). The larvae of Diplostomoidea Poirier, 1886 (27 species) of (mainly) fish-eating birds are abundant and can reach high densities. The Cryptogonimidae (10 species) is widespread, while the Heterophyidae (25 species) is more common in coastal drainages. *Nanophyetes salmincola* Chapin, 1926 remains an important pathogen in Pacific coastal salmonids.

Conclusions

Integrative taxonomic approaches (Dayrat, 2005) are becoming more common in discovering diversity (Overstreet et al., 2002; Ferguson et al., 2012). It is also increasingly apparent that cryptic diversity will challenge our understanding of species-boundaries (Pérez-Ponce de León & Nadler, 2010; Nadler & Pérez-Ponce de León, 2011), and the way we understand and describe biodiversity (e.g., Rosas-Valdez et al., 2011). Life-cycle information for most taxa remains fragmentary and experimental life-cycle studies have become rare. However, molecular approaches provide a viable alternative in connecting larval and adult stages (e.g., Locke et al., 2011). Several trematode lineages with marine or freshwater continental connections provide excellent opportunities for multifaceted "parascript" studies (Brooks & McLennan, 1993).

Finally, more survey work is urgently needed throughout the Americas to better understand the diversity and biology of the fauna as a whole. The proportion of host species examined for parasites varies widely across the New World. In the USA and Canada, some 430 species of freshwater fishes (approximately 43% of the fish fauna) have been examined at least once for parasites (Hoffman, 1999). In Mexico, this proportion is about 45% (Pérez-Ponce de León & Choudhury, 2010). In the purely Neotropical regions, this proportion drops to c. 32% in Central America and even further to less than 5% in South America. With the exception of the systematic and often strategic sampling in Mexico over the past two decades, the sampling efforts in the Americas have been sporadic and uneven in coverage. This is as true for South America where little or nothing is known from entire countries, as it is for vast tracts of the USA and Canada (Kohn et al., 2007; Scholz & Choudhury, 2014). While exploratory and opportunistic surveys that describe new taxa remain important, hypothesis-driven sampling that is strategic and focused can yield data that address a range of issues in systematics, biogeography, and ecology, such as the phylogenetic relationships of widely distributed taxa, life-cycles, food-web dynamics in perturbed ecosystems, and patterns and processes of diversification across and within drainages and biogeographical regions.

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