



Helminth parasites of freshwater fish from Central America

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Abstract

This study is a compilation of current knowledge of the taxonomic composition and distribution of the helminth parasites of freshwater fish in Central America. A list of 111 adult helminth species up to day reported from 17 freshwater fish families from Central America was compiled. The data show a helminth parasite fauna in freshwater fish that is typical to the region. One hundred and two of the known helminth species are endemic to the area, 32 of which can be derived from South American genera. Nematodes were the most abundant group, followed by monogeneans and trematodes. None of the 29 helminth families recorded to date is exclusive to Central America, while 16 of the 65 recorded genera have been only recorded from this area. Twenty three of these genera are South American lineages. The data suggest that helminth parasites of freshwater fish from Central America constitute a recent fauna derived mainly from South America but not found there.

Key words: parasites; helminths; checklist; freshwater fishes; Central America; zoogeography; Platyhelminthes; Trematoda; Monogenea; Cestoda; Nematoda; Acanthocephala; Cichlidae; Poeciliidae; Characidae; Heptapteridae; cichlids; poeciliids endemism.

Introduction

Freshwater fish in Central America constitute a faunal assemblage distinct from those of North and South America, and the species within it are parasitized by their own helminth fauna. Between the Isthmus of Tehuantepec, in southern Mexico, and the Isthmus of Panama there are only two suckers and one catfish species, and no records of minnows, perches, darters or sunfishes, which jointly constitute the characteristic fauna of North America. With the exception of Lepisosteidae, no Nearctic fish families have been able to establish themselves farther south than Guatemala. Similarly, most South American fish families are not distributed further north than the Isthmus of Panama. Some of these families extend into Costa Rica, and only a few characids are found in Guatemala and southern Mexico; the siluriforms and characids are characteristic South American elements that are not widely distributed in Central America (Miller 1966; Myers 1966; Bussing 1985, 1998).

Many helminths parasitizing Central America fish are endemic to the region (Salgado-Maldonado 2006). But in general the parasites of freshwater fishes in Central America are poorly known (Choudhury *et al.* 2002; Scholz *et al.* 2004). In response to this, the present study is a compilation of current knowledge of the taxonomic composition and distribution of the helminth parasites of freshwater fish in Central America. Species lists are important because they are needed to successfully document and understand the causes and consequences of biotic diversity. Species lists form a vital element of distribution studies because they aid in generating hypotheses to guide the application of experimental or comparative methods. More research is needed especially in the tropical biodiversity hotspots, identification resources, including field guides, monographs

and species lists are required. Species lists improve the ease with which taxonomic information can be accessed. A list provides a portal to the information available about different species. They can be used to collate the literature and specimen information required to do taxonomy. Lists made available current nomenclature and specimens occurrence records. It is expected that this checklist will facilitate future research on taxonomy, biogeography, ecology, and biodiversity.

In this study I examine helminth parasite taxonomic characteristics and geographic distribution to describe this fauna's apparent geographic sources. The fundamental postulate underlying this research is that each host family has a typical set of helminth parasites and the distribution of these helminths reflects that of the fish families they parasitize (Salgado-Maldonado *et al.* 2005; Salgado-Maldonado 2006; Aguilar-Aguilar *et al.* 2008). This pattern has been empirically recognized by researchers studying the helminths of Central American fish (Scholz & Salgado-Maldonado 1994; Scholz *et al.* 1995b, 1996c; Mendoza-Franco *et al.* 2000; Vidal-Martínez *et al.* 2001b; Kritsky & Mendoza-Franco, 2003). Dogiel (1961), Chubb (1963), and Wootten (1973) all acknowledged the close relationship between parasites and their hosts, and between hosts and their environment, as determinants of the character of a regional helminth fauna. This pattern was empirically recognized also from several freshwater drainage basins in Mexico (Salgado-Maldonado *et al.* 2001, 2004a, b). Despite that these ideas have been established for a long time, Pérez & Choudhury (2005) mistakenly identified a large number of endemisms among the helminth parasites of freshwater fish in Mexico; political boundaries do not necessarily delimit biological distribution. In contrast Vidal-Martínez & Kennedy (2000) proposed that portions of Neotropical Mexico particularly the southeast, form part of a Mesoamerican region, which is supported by the data and analysis of Aguilar-Aguilar *et al.* (2003) and Salgado-Maldonado (2006), as well as the present study.



FIGURE 1. Map of Central America and neighbouring areas.

Study area

Central America (Fig. 1) constitutes the northern most portion of the Neotropics in general terms (Maldonado-Koerdell 1964; Stuart 1966). Bordered by the Pacific Ocean to the south, and the Caribbean Sea and Gulf of Mexico to the northeast, it extends approximately 3000 km from the Isthmus of Panama northwest to the Isthmus of Tehuantepec. The widest portion (~1000 km) is in northern Honduras and central Guatemala, and the narrowest is the Panama Canal Zone (60 km). Overall, it covers 10^6 km², most of which is mountainous: 25%

is below 600 m asl (Stuart 1966). Its intricate pattern of altitude and relief has produced a diverse ecological mosaic in which climate and ecosystem characteristic change abruptly over short distances (Hall & Pérez-Briñoli 2003). Its northern extent, delimited by the nature of its ichthyofauna, is the Río Papaloapan river, Veracruz, Mexico, on the Atlantic coast (Gulf of Mexico) and the Río Tehuantepec river, Oaxaca, Mexico, on the Pacific coast. The Panama region is a transitional zone between the South and Central American fauna (Miller 1966; Bănărescu 1995).

The region lacked primary freshwater fish until well into the Tertiary. During the Cenozoic, Central America existed as a peninsula, contiguous with what is today Mexico, and separated from South America by a marine boundary that covered what is currently Nicaragua, Costa Rica and Panama. Central America remained isolated from South America until the Pleistocene. The land bridge between the two continents emerged in the Paleocene and then again in the Pliocene, allowing the dispersion of terrestrial biota (Savage 1966; Rosen 1976, 1985; Bussing 1985; Smith 1985; Donnelly 1989; Coates & Obando 1996; Bermingham & Martin 1998). The freshwater systems of Central America, however, did not develop until the Pliocene, about 3 million years ago (Briggs 1995). Because of this physiography and geologic history, Central America has few freshwater fish species, despite being a tropical region (Nelson 2006).

During the Neogene, an ichthyofauna developed in the Central American area that was characterized by its extreme poverty in primary species, strictly freshwater, but dominated by secondary species, that is, fish that generally live in freshwater but can tolerate high salinities and are able to cross lower saline barriers (*sensu* Myers 1938, but see Rosen 1974 and Sparks & Smith 2005). The poecilids and cichlids (altogether 139 species), plus a diverse number of species derived from marine species (peripheral fish), are the most numerous fish component found in freshwater habitats in this geographic area (Miller 1966; Stuart 1966; Bussing 1985; Bănărescu 1995). The fresh- and brackish-water environments of Central America harbor 456 fish species, 104 primary freshwater fish, 165 secondary fish species and 187 peripheral (Miller 1966; Myers 1966). However recently Bussing (1998) states there are 350 freshwater fish species in Central America.

Materials and methods

A taxonomic species list of helminth parasites of freshwater fish from Central America was compiled. For the purposes of the present study, only adult helminth forms were included. The list is fundamentally based on current records for the distribution of the helminth parasites of freshwater fish for the part of Mexico corresponding to Central America (Salgado-Maldonado 2006, and references herein) and the remaining Central America countries (Price 1938; Caballero & Brenes 1957; Brenes 1961; Price & Bussing 1967, 1968; Kritsky & Fritts 1970; Kritsky & Leiby 1972; Watson 1976; de Chambrier & de Vaucher 1984; Lamothe-Argumedo & Ponciano-Rodríguez 1986a, b; Scholz *et al.* 1995a, b, 2004; Moravec 1998; Mendoza-Franco *et al.* 2000, 2003a, 2004, 2007; Aguirre-Macedo *et al.* 2001a, b; Aguirre-Macedo & Scholz 2005; Vidal-Martínez *et al.* 2001b; Choudhury *et al.* 2002; González-Solís & Moravec, 2004). The fauna of the Bahamas and the West Indies is closely related to that of the continent, although that of the Lesser Antilles is primarily South American (Bănărescu 1995). For this reason helminths that have been recorded in freshwater fish in the Bahamas, Bermuda, Cuba, Guadeloupe, and Trinidad, in addition to Central America, have been indicated in the list (Vigueras 1936; Mizelle & Kritsky 1969; Hanek *et al.* 1974; Kristsky & Thatcher 1974; Molnar *et al.* 1974; Petter 1977; Petter *et al.* 1977; Vinjoy *et al.* 1985; Moravec & Coy-Otero 1987; Harris & Lyles 1992; Moravec & Salgado-Maldonado 2002; Mendoza-Franco *et al.* 2006). It is quite possible that the monogenean species that have been reported only on islands to date, but whose host families are also distributed on the continent, may be present in Central America: *Curvianchoratus hexacleidus* Hanek, Molnar & Fernando, 1974; *Gussevia alii* (Molnar, Hanek & Fernando, 1974); *G. cichlasomatis* (Molnar, Hanek & Fernando, 1974); *G. dobosi* (Molnar, Hanek & Fernando, 1974); *Salsuginus bahamensis* (Hanek & Fernando, 1972); *S. bermudae*

Rand & Wiles, 1987, *S. cubensis* Mendoza-Franco, Vidal-Martínez, Cruz-Quintana & Prats-León, 2006, *Trinidadactylus cichlasomatis* Hanek, Molnar & Fernando, 1974 (see Kritsky *et al.* 1986); *Trinigyrus hypostomatis* Hanek, Molnar & Fernando, 1974; *Unilatus unilatus* Mizelle & Kritsky, 1967; “*Urocleidoides*” *corydori* Molnar, Hanek & Fernando, 1974; *Urocleidoides curimatae* Molnar, Hanek & Fernando, 1974, “*Urocleidoides*” *kabatai* Molnar, Hanek & Fernando, 1974; “*Urocleidoides*” *margolisi* Molnar, Hanek & Fernando, 1974; “*Urocleidoides*” *trinidadensis* Molnar, Hanek & Fernando, 1974; *Gyrodactylus bullatarudis* Turnbull, 1956 (see Harris, 1986), *Gyrodactylus turnbulli* Harris, 1986; the same holds for the nematodes *Procamallanus* (*Spirocamallanus*) *desettae* (Petter, Golvan & Tcheprakoff, 1977); and *Rhabdochona cubensis* Moravec & Coy-Otero, 1987 (see Mizelle & Kritsky 1969; Hanek & Fernando 1972; Hanek *et al.* 1974; Molnar *et al.* 1974; Petter *et al.* 1977; Murith & Beverley-Burton 1985; Moravec & Coy-Otero 1987; Rand & Wiles 1987; Harris 1986; Kritsky *et al.* 1986, 2000; Kohn *et al.* 2006; Mendoza-Franco *et al.* 2006). However, inferred records of Central American species were not incorporated in the present analysis.

The criteria for include the species in the list was conservative, and it was not assumed that a species’ distribution is limited to Central America unless sufficient data supports this supposition. Taxa recorded in south-east Mexico, but whose position could be modified later with complete taxonomic treatments, were excluded from the list, even though some of these species could be Central American species (e.g. *Amphimerus* sp., *Amphoteromorphus* sp., *Ancyrocephalinae* gen. sp., *Dactylogyrus* sp., *Diplectanidae* gen. sp. *Gyrodactylus* sp., *Microcotylidae* gen. sp., *Proteocephalus* sp., among others). Also, three species recorded in freshwater fish, but distributed exclusively in coastal lagoons and brackish environments were not included: *Caballero-rhynchus lamothei* Salgado-Maldonado, 1977; *Psudoleptorhynchoides lamothei* Salgado-Maldonado, 1977 (*Acanthocephala*); *Vasorhabdochona cablei* Martin & Zam, 1967 (*Nematoda*) (see Salgado-Maldonado 2006). Also excluded was *Johnstonmawsonia* sp. from eels from Guadeloupe. The same was true for the helminth species of the tarpon *Megalops atlanticus* Valenciennes and of the bull shark *Carcharinus leucas* (Müller & Henle) because of their vagility and the primarily marine distribution of their hosts (see Watson & Thorson 1976; Mendoza-Franco *et al.* 2004). Helminth species recorded only in *Atherinopsidae*, *Goodeidae* and *Cyprinidae* were also not included due to their host families’ predominantly Nearctic distribution in the Mexican Highland Plateau (north of 19°). Two helminth species recorded from the state of Jalisco, Mexico (north of 19°) were not included, *Proteocephalus chamelensis* Pérez, Brooks & Berman, 1995 and *Procamallanus* (*Spirocamallanus*) *jaliscensis* Moravec, Salgado-Maldonado & Caspeta-Mandujano, 2000. Finally, larval forms and introduced helminth species were excluded. Total richness for the helminth species recorded to date in Central America can be determined by consulting Salgado-Maldonado (2006).

Results

The list presented here contains 111 adult helminth species reported for Central America to date (Tables 1 and 2). Some helminths have been recorded in fish from a number of families, but their frequency and abundance make it possible to link them unequivocally with a specific family. For example, the trematode *Genarchella isabellae* (Lamothe-Argumedo, 1977) has been reported in fish from five fish families, including its typical host *Rhamdia guatemalensis* (Günther) (*Heptapteridae*) (Lamothe-Argumedo 1977). Current data (Salgado-Maldonado 2006), however, allow it to be clearly associated with the cichlids: it has been recorded in 24 fish species, 19 of which are cichlids. Another example is *Neoechinorhynchus golvani* Salgado-Maldonado, 1977 reported in 31 fish species from 6 families, but 23 of these species are cichlids.

Data for fish species from 17 families are included in the list, with *Cichlidae* being the family with the highest number of adult helminth species in Central America ($S = 35$ helminth species). If grouped with the *Characidae* ($S = 17$) and *Heptapteridae* ($S = 11$), they account for 57% of the helminth species currently known in the area. A number of helminth species have also been reported in fish from the *Poeciliidae* ($S = 10$) and *Eleotridae* ($S = 5$).

Of the 111 adult helminth species of freshwater fish currently known in Central America, 102 (92%) are endemic to the area, 32 of which can be derived from South American genera. Eight of these species have been reported in South America (Table 2). The monogenean *Salsuginus seculus* (Mizelle & Arcadi, 1945) and the nematode *Rhabdochona kidderi* Pearse, 1936 are the only species already reported from North America (see Hanek & Fernando, 1972; Moravec, 1998; Moravec *et al.* 1999; Moravec & Huffman, 2001). Nematodes were the most abundant group, followed by monogeneans and trematodes (Table 1).

TABLE 1. Taxonomical diversity of helminth parasites of freshwater fishes from Central America.

	Families	Genera Total/Endemics	Species Total/Endemics
Trematoda	9	22/9	29/25
Monogenea	2	14/2	30/28
Cestoda	3	5/0	6/5
Acanthocephala	2	2/0	2/2
Nematoda	12	21/5	44/42
Totals	28	64/16	111/102

Of the 65 genera recorded in the area 43 are single species. Those with more than one species are *Sciadicleithrum* (8 species); *Rhabdochona* (6); *Procamallanus* (6); “*Urocleidoides*” (5); *Spinitectus* (4); *Cucullanus*, *Genarchella*, *Gyrodactylus*, *Saccocoelioides*, and *Paracapillaria* (all with 3); and *Campechetrema*, *Neochasmus*, *Phyllodistomum*, *Aphanoblastella*, *Gussevia*, *Salsuginus*, *Proteocephalus*, *Goezia*, *Hysterothylacium*, *Atractis*, *Orientattractis*, and *Pseudocapillaria* (all with 2 species).

Sixteen of the genera (24%) are endemic to Central America (nine trematodes, two monogeneans and five nematodes), and 23 (35%), 11 trematodes, 9 monogeneans, 2 cestodes and one genus of nematode, are South American lineages (Table 2). The genera *Salsuginus* (Monogenea) and *Cystoopsis* (Nematoda) are of Nearctic origin (Moravec 1998; Mendoza-Franco & Vidal-Martínez 2001; Mendoza-Franco *et al.* 2006). Twenty three genera (15 of nematodes) are broadly distributed. Given that the Ictaluridae and Lepisosteidae are of Nearctic ancestry (Miller 1966; Myers 1966; Bănărescu 1995; Miller *et al.* 2005), the five helminth species recorded in fish from these families were treated as being of Nearctic origin even though their distribution is restricted to Central America.

None of the helminth families recorded to date is exclusive to Central America (Table 2). Those families with the highest number of species are the Dactylogyridae ($S = 26$), Cryptogonimidae ($S = 8$), Capillariidae ($S = 8$) and Rhabdochonidae ($S = 7$). Fifteen of the remaining families are represented by two to six species, and ten families by only 1 species. The only suprageneric taxon endemic to Central America to date is the sub-family Neophilometrinae (Nematoda: Philometridae), proposed to include a single genus and species (Moravec *et al.* 2002).

A total of 11 nematode, two trematodes, and two monogeneans species are distributed exclusively on the Pacific slope of Central America, meaning they have not been collected on the Gulf of Mexico or Caribbean slopes; all of these are endemic to Central America (Table 2).

TABLE 2. Helminth parasites of freshwater fishes of Central America. Families and genera of helminths listed alphabetically. Geographical distribution in Central America is referred only to the country where each parasite has been recorded. Precise collection locations can be found in the references given for each record from Central American countries, and for records from Mexico from Salgado-Maldonado (2006). ¹Genus and species endemic to Central America; ²Species recorded from South America; ³South American genus, Central American species; ⁴Wide distributed genus, Central American species; ⁵North American genus, Central American species; ^pspecies recorded only from Central American Pacific versant.

TREMATODA

Acanthostomidae Poche, 1926

¹*Atrophecaecum* (?) *astorquii* (Watson, 1976) Lamothe-Argumedo & Ponciano-Rodríguez, 1986

Site: adults from intestine; metacercariae from fins, occasionally gills, scales, eyes and swimbladder.

Hosts and records: Heptapteridae: *Rhamdia nicaraguensis* (Günther), Nicaragua (Watson 1976); only metacercariae have been recorded in Mexico from Characidae: *Astyanax fasciatus* (Cuvier); Cichlidae: *Cichlasoma salvini* (Günther), *C. urophthalmus* (Günther), *Herichthys pearsei* Hubbs, *Parachromis managuensis* (Günther), *Petenia splendida* Günther, *Rocio octofasciata* (Regan), *Thorichthys aureus* (Günther), *T. helleri* (Steindachner), *T. meeki* Brind, *T. passionis* (Rivas), *Vieja synspila* (Hubbs); Clupeidae: *Dorosoma* sp.; Poeciliidae: *Gambusia yucatanana* Regan, *Poecilia latipunctata* Meek, *P. petenensis* Günther, *P. velifera* (Regan) from Yucatán Peninsula and Tabasco, Mexico.

²*Pseudoacanthostomum panamense* Caballero, Bravo-Hollis & Grocott, 1953

Site: Intestine

Hosts and records: Ariidae: *Sciades seemanni* (Günther), Panamá (Caballero, Bravo-Hollis & Grocott 1953); *Ariopsis felis* (Linnaeus), *Hexanematichthys assimilis* (Günther), *H. guatemalensis* (Günther), Yucatán Peninsula and Tabasco, Mexico.

²*Stunkardiella minima* (Stunkard, 1938) Lamothe-Argumedo & Ponciano-Rodríguez, 1985

Site: Intestine

Hosts and records: Heptapteridae: *Rhamdia nicaraguensis*, *R. managuensis* Nicaragua (Watson 1976); *R. laticauda* (Kner) Costa Rica (Caballero & Brenes 1957); *Rhamdia guatemalensis* (Günther), Yucatán Peninsula, Tabasco and Río Papaloapan Basin, Mexico.

Allocreadiidae Looss, 1902

³*Auriculostoma astyanace* Scholz, Aguirre-Macedo & Choudhury, 2004

Site: Intestine

Hosts and records: Characidae: *Astyanax fasciatus* Nicaragua (Scholz *et al.* 2004)

³*Creptotrema agonostomi* Salgado-Maldonado, Cabañas-Carranza & Caspeta-Mandujano, 1998

Site: Intestine

Hosts and records: Mugilidae: *Agonostomus monticola* (Bancroft) Jalisco, and Río Papaloapan Basin, Mexico; Ictaluridae: *Ictalurus balsanus* (Jordan & Snyder) Río Balsas Basin, Mexico

Angiodictyidae Looss, 1902

¹*Cichlasotrema ujati* Pineda-López & Andrade-Salas, 1989

Site: Intestine

Hosts and records: Cichlidae: *Cichlasoma geddesi* (Regan), *C. rectangulare*, *Herichthys pearsei*, *Petenia splendida* Günther, *Thorichthys helleri*, *Vieja bifasciata* (Steindachner), *V. fenestrata* (Günther), *V. intermedia* (Günther), *V. synspila*, Tabasco, Chiapas and Yucatán Peninsula, Mexico

Apocreadiidae (Skrajabin, 1942)

³*Crassicutis cichlasomae* Manter, 1936

Site: Intestine

Hosts and records: Cichlidae: *Cichlasoma* sp. Costa Rica (Bravo-Hollis & Arroyo 1962); *Amphilophus rostratus* (Gill), *A. citrinellum* (Günther), *A. labiatus* (Günther), *Cryptoheros spilurum* (Günther), *Hypsophrys nicaraguensis* (Günther), *Parachromis managuensis* (Günther), Nicaragua (Watson 1976); *Cichlasoma tetracantha* Cuba (Vinjoy *et al.* 1985); *Vieja maculicauda* (Regan), Nicaragua (Aguirre-Macedo *et al.* 2001b); *A. robertsoni* (Regan), *C. geddesi* (Regan), *C. mayorum* Hubbs, *C. rectangulare*, *C. salvini* (Günther), *C. urophthalmus*, *Herichthys cyanoguttatus* Baird & Girard, *H. labridens* (Pellegrin), *H. minckleyi* (Kornfield & Taylor), *H. pearsei* Hubbs, *Oreochromis* sp., *Parachromis friedrichsthalii* (Heckel), *P. managuensis*, *P. motaguensis* (Günther), *P. splendida*, *Rocio octofasciata*, *Theraps lentiginosus* (Steindachner), *Thorichthys aureus* (Günther), *T. ellioti* Meek, *T. helleri*, *T. meeki*, *T. passionis*, *Vieja argentea* (Allgayer), *V. bifasciata*, *V. fenestrata* (Günther), *V. hartwegi* (Taylor & Miller), *V. synspila*; Clupeidae: *Dorosoma petenense* (Günther) from Chiapas, Tabasco, Yucatán Peninsula, Río Papaloapan Basin, Río Pánuco Basin, and Coahuila, Mexico.

Callodistomidae (Odhner, 1910)

²*Prosthenhystera obesa* (Diesing, 1850)

Site: Gall bladder

Hosts and records: Characidae: *Astyanax fasciatus* Nicaragua (Aguirre-Macedo *et al.* 2001b); Ariidae *Cathorops melanophus* (Günther), *Potamarius nelsoni* (Evermann & Goldsborough); Centropomidae: *Centropomus undecimalis* (Bloch), *C. parallelus* Poey, Characidae: *Astyanax fasciatus*, *Brycon guatemalensis* Regan, Cichlidae: *Petenia splendida*, *Thorichthys helleri*, Ictaluridae: *Ictalurus furcatus* (Valenciennes) from Tabasco, Río Papaloapan Basin, and Yucatán Peninsula, México.

Cryptogonimidae Ward, 1917

¹*Campechetrema herrerae* Lamothe-Argumedo, Salgado-Maldonado & Pineda-López, 1997

Site: Intestine

Hosts and records: Cichlidae: *Parachromis friedrichsthalii*, *Petenia splendida*, *Rocio octofasciata*, Chiapas and Yucatán Peninsula, Mexico.

¹*Campechetrema* sp.*

Site: Intestine

Host and record: Ictaluridae: *Ictalurus punctatus* (Rafinesque), Veracruz, Mexico.

⁴*Neochasmus ackerti* Watson, 1976

Site: Intestine

Host and record: Pomadasysidae: *Pomadasys crocro* (Cuvier), Nicaragua (Watson 1976)

⁴*Neochasmus olmecus* Lamothe-Argumedo, Pineda-López & Andrade-Salas, 1989

Site: Intestine

Hosts and records: Centropomidae: *Centropomus parallelus*, *C. undecimalis*, Eleotridae: *Gobiomorus dormitor* Lacepède, Tabasco, Mexico

¹*Oligogonotylus manteri* Watson, 1976

Site: Intestine

Hosts and records: Cichlidae: *Amphilophus labiatus* (Günther), *A. citrinellus* (Günther), *A. rostratus* (Gill), *Hypsophrys nicaraguensis* (Günther), *Parachromis managuensis* (Günther), *Vieja maculicauda* (Regan), Nicaragua (Watson 1976; Aguirre-Macedo *et al.* 2001b); Cichlidae: *Cichlasoma geddesi*, *C. urophthalmus*, *Parachromis friedrichsthalii*, *Petenia splendida*, *Rocio octofasciata*, *Thorichthys aureus* (Günther), *T. helleri*, *T. meeki*, *T. passionis*, *Vieja synspila*, Characidae: *Astyanax fasciatus*, Clupeidae: *Dorosoma petenense* (Günther), Megalopidae: *Megalops atlanticus* Valenciennes, Chiapas, Tabasco, Yucatán Peninsula and Río Papaloapan Basin, Mexico.

¹*Olmeca laurae* Lamothe-Argumedo & Pineda-López, 1990

Site: Intestine

Hosts and records: Centropomidae: *Centropomus parallelus*, Characidae: *Astyanax fasciatus*, Cichlidae: *Thorichthys helleri*, *T. meeki*, Tabasco, Mexico.

¹*Pseudocaecicola batallae* Lamothe-Argumedo, Salgado-Maldonado & Pineda-López, 1991

Site: Intestine

Host and record: Cichlidae: *Petenia splendida* Tabasco and Yucatán Peninsula, Mexico.

¹*Tabascotrema veri* Lamothe-Argumedo & Pineda-López, 1990

Site: Intestine

Hosts and records: Cichlidae: *Cichlasoma urophthalmus*, *Petenia splendida*, *Thorichthys pasionis*, *Vieja bifasciata*, Tabasco and Yucatán Peninsula, Mexico

Derogenidae Lühe, 1910

³*Genarchella astyanactis* (Watson, 1976) Scholz, Vargas-Vazquez & Salgado-Maldonado, 1995

Site: Stomach

Host and records: Characidae: *Astyanax fasciatus* Nicaragua (Watson 1976), from the same host species from Tamaulipas, Río Pánuco Basin and Yucatán Peninsula, Mexico.

³*Genarchella isabellae* (Lamothe-Argumedo, 1977) Kohn, Fernandes, Gibson & Fróes, 1990

Site: Stomach

Hosts and records: Cichlidae: *Cichlasoma geddesi*, *C. urophthalmus*, *Herichthys cyanoguttatus*, *H. minckleyi*, *H. pearsei*, *Parachromis friedrichsthalii*, *P. managuensis*, *Petenia splendida*, *Rocio octofasciata*, *Theraps coeruleus* Stawikowski & Werner, *T. lentiginosus*, *Thorichthys aureus*, *T. helleri*, *T. meeki*, *Vieja argentea*, *V. bifasciata*, *V. fenestrata*, *V. intermedia*, *V. synspila*, Eleotridae: *Dormitator maculatus* (Bloch), *Gobiomorus dormitor* Lacépède, Heptapteridae: *Rhamdia guatemalensis*, Poeciliidae: *Gambusia yucatanana* Regan, Synbranchidae: *Ophisternon aenigmaticus* Rosen & Greenwood, Chiapas, Tabasco, Río Papaloapan Basin, and Coahuila, Mexico.

³*Genarchella tropica* (Manter, 1936) Scholz, Vargas-Vazquez & Salgado-Maldonado, 1995

Site: Stomach

Hosts and records: Heptapteridae: *Rhamdia managuensis* (Günther), Nicaragua (Watson 1976); Heptapteridae: *Rhamdia guatemalensis*, Ictaluridae: *Ictalurus furcatus*, Poeciliidae *Gambusia yucatanana*, *Poecilia petenensis* (Günther), Veracruz, Tabasco and Yucatán Peninsula, Mexico.

Gorgoderidae Looss, 1901

^{3?}*Dendrorchis* sp.*

Site: Intestine, urinary bladder

Hosts and records: Clupeidae *Dorosoma petenense*, Goodeidae *Ilyodon furcidens* (Jordan & Gilbert), Eleotridae: *Eleotris* sp., *Gobiomorus dormitor* Río Papaloapan Basin and Jalisco, Mexico.

⁴*Phyllodistomum centropomi* Mendoza-Garfías & Pérez, 2005

Site: Intestine

Host and record: Centropomidae: *Centropomus parallelus* Río Papaloapan Basin, Mexico.

⁴*Phyllodistomum* sp.*

Site: Gall bladder

Hosts and records: Centropomidae: *Centropomus parallelus*, Cichlidae: *Cichlasoma geddesi*, *C. urophthalmus*, *Parachromis managuensis*, *Vieja synspila*, Eleotridae: *Guavina guavina* (Valenciennes), Poeciliidae: *Heterandria bimacu-*

lata (Heckel) Mexico
Haploporidae Nicoll, 1914

³*Culuwiya cichlidorum* Aguirre-Macedo & Scholz, 2005

Site: Intestine

Hosts and records: Cichlidae: *Vieja maculicauda* (Regan), *Tomocichla tuba* (Meek) Nicaragua; *Cichlasoma istlanum* (Jordan & Snyder), *C. urophthalmus*, *Herichthys minckleyi*, *Oreochromis aureus* (Steindachner), *O. niloticus*, *Parachromis managuensis*, *Petenia splendida*, *Theraps coeruleus* Stawikowski & Werner, *Tilapia* sp., *Vieja bifasciata*, *V. synspila*, Coahuila, Colima, Jalisco, Tabasco, Chiapas and Yucatán Peninsula, Mexico (Aguirre-Macedo & Scholz 2005).

³*Saccocoelioides chauhani* Lamothe-Argumedo, 1974

Site: Intestine

Host and record: Characidae: *Astyanax fasciatus* Río Papaloapan Basin, Mexico

³*Saccocoelioides cf. sogandaresi* Lumsden, 1963

Site: Intestine

Hosts and records: Poeciliidae: *Poecilia velifera* (Regan) Nicaragua (Aguirre-Macedo *et al.* 2001b); Poeciliidae: *Heterandria bimaculata*, *Poecilia latipunctata* Meek, *P. mexicana* Steindachner, *P. petenensis* Günther, *P. sphenops* Valenciennes, *P. velifera*, *Poeciliopsis catemaco* Miller, *P. gracilis* (Heckel), *Xiphophorus hellerii* Heckel, Characidae: *Astyanax aeneus*, Eleotridae: *Dormitator maculatus*, *Gobiomorus dormitor*, Gobiidae: *Sicydium multipunctatum* Regan, Goodeidae: *Allodontichthys zonistius* (Hubbs), *Ilyodon furcidens* (Jordan & Gilbert), *I. whitei* (Meek), Mugilidae: *Agonostomum monticola* from Jalisco, Veracruz, Tabasco, Yucatán Peninsula and the basins of the Rivers Papaloapan, Pánuco and Balsas, Mexico.

³*Saccocoelioides* sp.*

Site: Intestine

Host and record: Eleotridae: *Dormitator latifrons* Guerrero, Mexico
Macroderoididae McMullen, 1937

²*Magnivitellinum simplex* Kloss, 1966

Site: Intestine

Hosts and records: Characidae: *Astyanax fasciatus* Nicaragua (Aguirre-Macedo *et al.* 2001b), Characidae: *A. aeneus*, *A. mexicanus* (De Filippi), Ariidae: *Ariopsis felis* (Linnaeus), Goodeidae: *Ilyodon furcidens* Nuevo León, Jalisco, Río Pánuco Basin, Río Papaloapan Basin and Yucatán Peninsula, Mexico.

¹*Perezitrema bychowskyi* (Caballero y Caballero, 1975) Brooks, 1980

Site: Intestine

Hosts and records: Lepisosteidae: *Atractosteus tropicus* Gill, Nicaragua (Watson, 1976), recorded also from the same host species from Tabasco, Mexico. [The conspecificity of this species with *Perezitrema viguerasi* Baruš & Moravec recovered from *A. tristoechus* from Cuba can not be excluded, see Moravec & Salgado-Maldonado 2002]

¹*Wallinia chavarriae* Choudhury, Hartvigsen & Brooks, 2002

Site: Intestine

Hosts and records: Characidae: *Astyanax aeneus*, *Bryconamericus scleroparius* (Regan), Costa Rica (Choudhury, Hartvigsen & Brooks 2002)

MONOGENEA

Dactylogyridae Bychowsky, 1933

³*Ameloblastella chavarriai* (Price, 1938) Kritsky, Mendoza-Franco & Scholz, 2000

Site: Gills

Hosts and records: Heptapteridae: *Rhamdia laticauda* (Kner), Costa Rica, (Price 1938), *R. quelen* (Quoy & Gaimard) Trinidad (Molnar *et al.* 1974) (see Kritsky *et al.* 2000), *R. nicaraguensis* (Günther) Nicaragua (Mendoza-Franco *et al.* 2003a), *R. guatemalensis* Tabasco, Yucatán Peninsula and Río Papaloapan Basin, Mexico.

³*Aphanoblastella chagresii* Mendoza-Franco, Aguirre-Macedo & Vidal-Martínez, 2007

Site: Gills

Host and record: Heptapteridae: *Pimelodella chagresi* (Steindachner), Panama (Mendoza-Franco *et al.* 2007)

²*Aphanoblastella travassosi* (Price, 1938) Kritsky, Mendoza-Franco & Scholz, 2000

Site: Gills

Hosts and records: Heptapteridae: *Rhamdia laticauda*, Costa Rica, (Price 1938), *R. quelen* Trinidad (Molnar *et al.* 1974), *R. quelen* Panama (Kritsky *et al.* 2000; Mendoza-Franco *et al.* 2007), *R. nicaraguensis* Nicaragua (Mendoza-Franco *et al.* 2003a), *R. guatemalensis* Tabasco, Yucatán Peninsula and Río Papaloapan Basin, Mexico.

⁴*Dactylogyrus mizellei* Price, 1967

Site: Gills

Hosts and records: Poeciliidae: *Xiphophorus helleri* Guatemala (Price 1967; this species is a junior synonym of *D. intermedius* Kritsky, personal communication)

³*Diaphorocleidus petrosusi* Mendoza-Franco, Aguirre-Macedo & Vidal-Martínez, 2007

Site: Gills

Hosts and records: Characidae: *Brycon petrosus* Meek & Hildebrand, Panama (Mendoza-Franco *et al.* 2007)

¹*Guavinella tropica* Mendoza-Franco, Scholz & Cabañas-Carranza, 2003

Site: Gills

Hosts and records: Eleotridae *Gobiomorus dormitor* Jalisco, Tabasco and Río Papaloapan Basin, Mexico.

³*Gussevia asota* Kritsky, Thatcher & Boeger, 1989

Site: Gills

Hosts and records: Cichlidae: *Astronotus ocellatus* (Agassiz), Panama (Mendoza-Franco *et al.* 2007)

³*Gussevia heterotilapiae* Vidal-Martínez, Scholz & Aguirre-Macedo, 2001

Site: Gills

Hosts and records: Cichlidae: *Heterotilapia multispinosa* (Günther) Nicaragua (Vidal-Martínez *et al.* 2001b)

^{3?P}*Jainus hexops* Kritsky & Leiby, 1972

Site: Gills

Hosts and records: Characidae: *Astyanax fasciatus* Costa Rica (Kritsky & Leiby 1972)

²*Palombitrema heteroancistrum* Price & Busing, 1968

Site: Gills

Hosts and records: Characidae: *Astyanax fasciatus* Costa Rica (Price & Busing 1968), collected from the same host in Nicaragua (Mendoza-Franco *et al.* 2003a); Characidae: *Astyanax aeneus*, Cichlidae: *Cichlasoma urophthalmus* Tabasco and Yucatán Peninsula, Mexico.

³⁷*Pavanelliella scaphiocotylus* Kritsky & Mendoza-Franco, 2003

Site: Nasal cavity

Host and record: Heptapteridae: *Rhamdia guatemalensis* Yucatán Peninsula, Mexico

⁵*Salsuginus neotropicalis* Mendoza-Franco & Vidal-Martínez, 2001

Site: Gills

Host and records: Poeciliidae: *Belonesox belizanus* Kner, Nicaragua (Mendoza-Franco *et al.* 2003a), collected from the same host in Yucatán Peninsula, Mexico.

⁵*Salsuginus seculus* (Mizelle & Arcadi, 1945) Fleurish & Beverley-Burton, 1985

Site: Gills

Hosts and records: Poeciliidae: *Gambusia affinis* (Baird & Girard), Bahamas (Hanek & Fernando 1972), *G. yucatan* Tabasco, Mexico. This species has been previously recorded from North America (see Hanek & Fernando 1972).

³*Sciadicleithrum bicuense* Vidal-Martínez, Scholz & Aguirre-Macedo, 2001

Site: Gills

Hosts and records: Cichlidae: *Archocentrus nigrofasciatus* Günther, Nicaragua (Vidal-Martínez *et al.* 2001b)

Cichlidae (1); Nicaragua

³*Sciadicleithrum bravohollisae* Kritsky, Vidal-Martínez & Rodríguez-Canul, 1994

Site: Gills

Hosts and records: Cichlidae: *Vieja maculicauda* (Regan) Nicaragua (Mendoza-Franco *et al.* 2003a), *Amphilophus citrinellus*, *Cichlasoma geddesi*, *C. salvini*, *C. urophthalmus*, *Herichthys labridens*, *H. pearsei*, *Oreochromis aureus*, *Parachromis managuensis*, *Petenia splendida*, *Rocio octofasciata*, *Theraps lentiginosus*, *Thorichthys helleri*, *Vieja fenestrata*, *V. synspila* from Río Pánuco Basin, Tabasco, Chiapas, Río Papaloapan Basin and Yucatán Peninsula, Mexico.

³*Sciadicleithrum maculicaudae* Vidal-Martínez, Scholz & Aguirre-Macedo, 2001

Site: Gills

Hosts and records: Cichlidae: *Cichlasoma maculicauda* (Regan) Nicaragua (Vidal-Martínez *et al.* 2001b)

³*Sciadicleithrum meekii* Mendoza-Franco, Scholz & Vidal-Martínez, 1997

Site: Gills

Hosts and records: Cichlidae: *Archocentrus nigrofasciatus* Günther, Nicaragua (Vidal-Martínez *et al.* 2001b; Mendoza-Franco *et al.* 2003a), *Parachromis managuensis*, *Thorichthys helleri*, *T. meeki*, *T. callolepis* Tabasco, Chiapas and Yucatán Peninsula, Mexico.

³*Sciadicleithrum mexicanum* Kritsky, Vidal-Martínez, & Rodríguez-Canul, 1994

Site: Gills

Hosts and records: Cichlidae: *Cichlasoma trimaculatum* (Günther) Guatemala (Mendoza-Franco *et al.* 2000) *C. urophthalmus*, *Parachromis dovii* (Günther), *P. managuensis*, *Tomocichla tuba* (Meek), *Vieja maculicauda* Nicaragua (Vidal-Martínez *et al.* 2001b, Mendoza-Franco *et al.* 2003a), *C. urophthalmus*, *Parachromis friedrichsthalii*, *Petenia splendid*, *Rocio octofasciata*, *Thorynchthys aureus*, *Vieja synspila* Chiapas, Tabasco and Yucatán Peninsula, Mexico.

³*Sciadicleithrum nicaraguense* Vidal-Martínez, Scholz & Aguirre-Macedo, 2001

Site: Gills

Hosts and records: Cichlidae: *Amphilophus alfari* (Meek) Nicaragua (Vidal-Martínez *et al.* 2001b, Mendoza-Franco *et*

al. 2003a)

³*Sciadicleithrum panamensis* Mendoza-Franco, Aguirre-Macedo, & Vidal-Martínez, 2007

Site: Gills

Hosts and records: Cichlidae: *Aequidens coeruleopunctatus* (Kner) Panama (Mendoza-Fanco *et al.* 2007)

³*Sciadicleithrum splendidae* Kritsky, Vidal-Martínez, & Rodríguez-Canul, 1994

Site: Gills

Hosts and records: Cichlidae: *Parachromis friedrichsthalii*, *P. managuensis*, *Petenia splendida*, *Vieja synspila* Chiapas, Tabasco and Yucatán Peninsula, Mexico.

³“*Urocleidoides*” *costaricensis* (Price & Bussing, 1967) Kritsky & Leiby, 1972

Site: Gills

Hosts and records: Characidae: *Astyanax fasciatus* Costa Rica (Price & Bussing 1967; Kritsky & Leiby 1972), *A. fasciatus* and Curimatidae: *Steindachneria argentea* (Gill) Trinidad (Molnar *et al.* 1974), *A. fasciatus* Nicaragua (Mendoza-Franco *et al.* 2003a) from the same host from Río Balsas and Río Papaloapan Basins, Tabasco and Yucatán Peninsula, Mexico.

³*Urocleidoides flegomai* Mendoza-Franco, Aguirre-Macedo, & Vidal-Martínez, 2007

Site: Gills

Hosts and records: Lebiasinidae: *Piabucina panamensis* Gill Panama (Mendoza-Franco *et al.* 2007)

³*Urocleidoides reticulatus* Mizelle & Price, 1964

Site: Gills

Hosts and records: Poeciliidae: *Poecilia reticulata* Trinidad (Kritsky *et al.* 1986), *Belonesox belizanus*, *Poecilia mexicana*, *P. petenensis* Tabasco, Mexico.

³*Urocleidoides similuncus* Mendoza-Franco, Aguirre-Macedo, & Vidal-Martínez, 2007

Site: Gills

Hosts and records: Poeciliidae: *Poecilia gillii* (Kner) Panama (Mendoza-Franco *et al.* 2007)

³“*Urocleidoides*” *strombicirrus* (Price & Bussing, 1967) Kritsky & Thatcher, 1974

Site: Gills

Hosts and records: Characidae: *Astyanax fasciatus* Costa Rica (Price & Bussing, 1967), from the same host from Nicaragua (Mendoza-Franco *et al.* 2003a), *A. fasciatus*, *A. mexicanus* Tabasco and Río Pánuco Basin, Mexico.

Gyrodactylidae

¹*Anacanthocotyle anacanthocotyle* Kritsky & Fritts, 1970

Site: Gills

Hosts and records: Characidae: *Astyanax fasciatus* Costa Rica (Kritsky & Fritts 1970), *A. aeneus*, *A. fasciatus* Río Papaloapan Basin and Yucatán Peninsula, Mexico.

⁴*Gyrodactylus bullatarudis* Turnbull, 1956

Site: Gills

Hosts and records: Poeciliidae: *Poecilia sphenops* Costa Rica (Kritsky & Fritts 1970), *P. reticulata* Trinidad (Harris & Lyles 1992)

^{4P}*Gyrodactylus costaricensis* Kristky & Fritts, 1970

Site: Gills

Hosts and records: Poeciliidae: *Poecilia sphenops* Costa Rica (Kritsky & Fritts 1970)

⁴*Gyrodactylus neotropicalis* Kritsky & Fritts, 1970

Site: Gills

Host and records: Characidae: *Astyanax fasciatus* Costa Rica (Kritsky & Fritts 1970), from the same host species from Yucatán Peninsula, Mexico.

CESTODA

Bothriocephalidae

⁴*Bothriocephalus pearsei* Scholz, Vargas-Vázquez & Moravec, 1996

Site: Intestine

Hosts and records: Cichlidae: *Cichlasoma urophthalmus*, Heptapteridae: *Rhamdia guatemalensis* Yucatán Peninsula, Mexico.

Monticelliidae La Rue, 1911

²*Amphoteromorphus* sp.

Site: Intestine

Hosts and records: Centropomidae: *Centropomus parallelus*, *C. undecimalis* Tabasco, Mexico.

³*Monticellia ophisterni* Scholz, de Chambrier & Salgado-Maldonado, 2001

Site: Intestine

Hosts and records: Synbranchidae: *Ophisternon aenigmaticum* Rosen & Greenwood Río Papaloapan Basin, Mexico.

Proteocephalidae La Rue, 1911

⁵*Megathylacoides lamothei* (García-Prieto, 1990)

Site: Intestine

Hosts and records: Ictaluridae: *Ictalurus furcatus* Veracruz and Río Papaloapan Basin, Mexico; *I. balsanus*, *I. furcatus* Tabasco and Michoacán, Mexico (Rosas-Valdez *et al.* 2004).

⁴*Proteocephalus brooksi* García-Prieto, Rodríguez & Pérez, 1996

Site: Intestine

Hosts and records: Heptapteridae: *Rhamdia guatemalensis* Río Papaloapan Basin and Yucatán Peninsula, Mexico.

⁴*Proteocephalus gaspari* de Chambrier & Vaucher, 1984

Site: Intestine

Hosts and records: Lepisosteidae: *Atractosteus tropicus* Nicaragua (de Chambrier & Vaucher 1984)

ACANTHOCEPHALA

Echinorhynchidae Cobbold, 1876

⁴*Acanthocephalus* sp. 1*

Site: Intestine

Hosts and records: Cichlidae: *Cichlasoma urophthalmus* Yucatán Peninsula, Mexico.

Neoechinorhynchidae Ward, 1917

⁴*Neoechinorhynchus golvani* Salgado-Maldonado, 1978

Site: Intestine

Hosts and records: Cichlidae: *Amphilophus alfari* Nicaragua (Aguirre-Macedo *et al.* 2001b), Ariidae: *Ariopsis felis* (Linnaeus), *Cathorops aguadulce* (Meek), Belonidae: *Strongylura* sp., Cichlidae: *Amphilophus robertsoni*, *Archocentrus nigrofasciatus*, *Cichlasoma beani*, *C. geddesi*, *C. istlanum*, *C. rectangulare*, *C. salvini*, *C. urophthalmus*, *Herichthys cyanoguttatus*, *H. labridens*, *H. pearsei*, *Parachromis friedrichsthalii*, *P. managuensis*, *P. motaguensis*, *Petenia splendida*, *Rocio octofasciata*, *Thorichthys ellioti*, *T. helleri*, *T. meeki*, *T. pasionis*, *Vieja fenestrata*, *V. synspila*, Eleotridae: *Dormitator latifrons*, *D. maculatus*, *Gobiomorus dormitor*, Heptapteridae: *Hyporhamphus mexicanus*, Ictaluridae: *Ictalurus furcatus* Guerrero, Veracruz, Tabasco, Río Papaloapan and Río Pánuco Basins, and Yucatán Peninsula, Mexico.

NEMATODA

Anisakidae Railliet & Henry, 1912

^{4P}*Goezia nonipapillata* Osorio-Sarabia, 1982

Site: Intestine

Hosts and records: Cichlidae: *Cichlasoma istlanum* (Jordan & Snyder), *Oreochromis aureus*, *O. mossambicus*, *Tilapia zillii* Río Balsas Basin, Mexico.

^{4?}*Goezia* sp.*

Site: Intestine

Hosts and records: Cichlidae: *Vieja hartwegi*, Ictaluridae: *Ictalurus dugesii*, *I. balsanus* Chiapas and Río Balsas Basin, Mexico.

⁴*Hysterothylacium cenotae* (Pearse, 1936)

Site: Intestine

Hosts and records: Heptapteridae: *Rhamdia guatemlensis* Yucatán Peninsula, Mexico.

^{4P}*Hysterothylacium perezii* Gopar-Merino, Osorio-Sarabia & García-Prieto, 2005

Site: Intestine

Hosts and records: Ariidae: *Sciades guatemalensis* (Günther) Guerrero, Mexico.
Atractidae Railliet, 1917

^{4P}*Atractis bravoae* (Osorio-Sarabia, 1984) Moravec, 2000

Site: Intestine

Hosts and records: Atherinopsidae: *Atherinella balsana* (Meek), Cichlidae: *Cichlasoma istlanum* Río Balsas Basin, Mexico.

⁴*Atractis vidali* González-Solís & Moravec, 2002

Site: Intestine

Hosts and records: Cichlidae: *Herichthys pearsei*, *Vieja intermedia* Chiapas and Yucatán Peninsula, Mexico.

⁴*Orientattractis campechensis* González-Solís & Moravec, 2004

Site: Intestine

Hosts and records: Cichlidae: *Herichthys pearsei*, *Vieja bifasciata* Chiapas and Yucatán Peninsula, Mexico.

⁴*Orientattractis chiapasensis* González-Solís & Moravec, 2004

Site: Intestine

Hosts and records: Cichlidae: *Tomocichla tuba* (Meek) Nicaragua (González-Solís & Moravec 2004), *Vieja intermedia*, Chiapas, Mexico.

Camallanidae Railliet & Henry, 1915

⁴*Procamallanus (Spirocamallanus) chetumalensis* González-Solís, Moravec & Vidal-Martínez, 2002

Site: Intestine

Hosts and records: Ariidae: *Sciades assimilis* (Günther), Yucatán Peninsula, Mexico (González-Solís *et al.* 2002)

⁴*Procamallanus (Spirocamallanus) gobiomori* Moravec, Salgado-Maldonado & Caspeta-Mandujano, 2000

Site: Intestine

Hosts and records: Eleotridae: *Dormitator maculatus* (Bloch), *Eleotris picta* Kner, *Gobiomorus polylepis* Ginsburg, Jalisco, Mexico.

⁴*Procamallanus (Spirocamallanus) jaliscensis* Moravec, Salgado-Maldonado & Caspeta-Mandujano, 2000

Site: Intestine

Host and record: Mugilidae: *Agonostomus monticola* (Bancroft) Jalisco, Mexico

⁴*Procamallanus (Spirocamallanus) mexicanus* Moravec, Salgado-Maldonado & Caspeta-Mandujano, 2000

Site: Intestine

Hosts and records: Cichlidae: *Cichlasoma geddesi* (Regan), Veracruz, Mexico.

⁴*Procamallanus (Spirocamallanus) neocaballeroi* (Caballero-Deloya, 1977)

Site: Intestine

Hosts and records: Cichlidae: *Vieja maculicauda* (Regan), Nicaragua (Aguirre-Macedo *et al.* 2001b); Characidae: *Astyanax fasciatus*, *A. mexicanus*, *Bramocharax caballeroi*, Heptapteridae: *Rhamdia guatemalensis*, Tabasco, Yucatán Peninsula, and Río Pánuco and Río Papaloapan Basins, Mexico, Nicaragua

⁴*Procamallanus (Spirocamallanus) rebecae* (Andrade-Salas, Pineda-López & García-Magaña, 1994)

Site: Intestine

Hosts and records: Cichlidae: *Amphilophus alfari* (Meek), *Heterotilapia multispinosa*, *Vieja maculicauda*, Nicaragua (Aguirre-Macedo *et al.* 2001b); Cichlidae: *Amphilophus citrinellus* (Günther), *A. robertsoni* (Regan), *Cichlasoma geddesi*, *C. rectangulare*, *C. urophthalmus*, *Parachromis managuensis*, *P. motaguensis* (Günther), *Petenia splendida*, *Thorichthys callolepis* *T. helleri* (Steindachner), *T. meeki* Brind, *T. pasionis* (Rivas), *Vieja fenestrata* (Günther), *V. synspila* (Hubbs), Belonidae: *Strongylura* sp., Characidae: *Astyanax fasciatus*, Centropomidae: *Centropomus parallelus* Tabasco, Yucatán Peninsula and Río Papaloapan Basin, Mexico.

Capillariidae Railliet, 1915

⁴*Capillaria (Hepatocapillaria) cichlasomae* Moravec, Scholz & Mendoza-Franco, 1995

Site: Intestine

Host and record: Cichlidae: *Cichlasoma urophthalmus* Yucatán Peninsula, Mexico

⁴*Capillostrongyloides* sp.

Site: Intestine

Host and record: Characidae: *Astyanax fasciatus* Yucatán Peninsula, Mexico

⁴*Paracapillaria rhamdiae* Moravec, González-Solís & Vargas-Vázquez, 1995

Site: Intestine

Host and record: Heptapteridae: *Rhamdia guatemalensis* Yucatán Peninsula, Mexico.

⁴*Paracapillaria teixeirafreitasi teixeirafreitasi* (Caballero-Rodríguez, 1971)

Site: Intestine

Hosts and records: Eleotridae: *Dormitator maculatus*, *Gobiomorus dormitor*, Tabasco, Veracruz, Río Papaloapan Basin and Yucatán Peninsula, Mexico.

⁴*Paracapillaria teixeirafreitasi pacifica* Moravec, Salgado-Maldonado & Caspeta-Mandujano, 1999

Site: Intestine

Hosts and records: Eleotridae: *Dormitator maculatus*, *Gobiomorus polylepis*, Jalisco, Mexico.

¹*Paracapsaloides agonostomi* Moravec, Salgado-Maldonado & Caspeta-Mandujano, 1999

Site: Intestine

Host and record: Mugilidae: *Agonostomus monticola*, Jalisco, Mexico.

⁴*Pseudocapsalidia (Ichthyocapsalidia) ophisterni* Moravec, Salgado-Maldonado & Jiménez-García, 2000

Site: Intestine

Host and record: Synbranchidae: *Ophisternon aenigmaticum* Río Papaloapan Basin, Mexico.

⁴*Pseudocapsalidia yucatanensis* Moravec, Scholz & Vivas-Rodríguez, 1995

Site: Intestine

Host and record: Heptapteridae: *Rhamdia guatemalensis*, Yucatán Peninsula, Mexico.

Cosmocercidae Railliet, 1916

⁴*Raillietnema kritscheri* Moravec, Salgado-Maldonado & Pineda-López, 1993

Site: Intestine

Hosts and records: Cichlidae: *Cichlasoma urophthalmus*, *Herichthys pearsei*, *Vieja synspila*, Chiapas, Tabasco and Yucatán Peninsula, Mexico.

Cucullanidae Cobbold, 1864

⁴*Dichelyne mexicanus* Caspeta-Mandujano, Moravec & Salgado-Maldonado, 1999

Site: Intestine

Hosts and records: Cichlidae: *Cichlasoma beani* (Jordan), Ictaluridae: *Ictalurus balsanus*, *I. furcatus*, *I. punctatus*, Mugilidae: *Agonostomus monticola*, Tamaulipas, Veracruz, and basins of the rivers Balsas, Papaloapan and Santiago, Mexico.

⁴*Cucullanus angeli* Cabañas-Carranza & Caspeta-Mandujano, 2007

Site: Intestine

Host and record: Cichlidae: *Vieja intermedia* Chiapas, Mexico.

⁴*Cucullanus (Cucullanus) caballeroi* Petter, 1977

Site: Intestine

Hosts and records: Eleotridae: *Eleotris pisonis* (Gmelin), *Gobiomorus maculatus* Guadeloupe (Petter 1977), Cichlidae: *Cichlasoma* sp., Eleotridae: *Dormitator maculatus*, *Gobiomorus dormitor*, Heptapteridae: *Rhamdia guatemalensis*, Río Papaloapan Basin, Mexico.

⁴*Cucullanus mexicanus* Caspeta-Mandujano, Moravec & Aguilar-Aguilar, 2000

Site: Intestine

Host and records: Heptapteridae: *Rhamdia guatemalensis* Río Papaloapan Basin, Mexico.

²*Neocucullanus neocucullanus* Travassos, Artigas & Pereira, 1928

Site: Intestine

Host and record: Characidae: *Brycon guatemalensis* Chiapas, Mexico.

Cystidicolidae Skrjabin, 1946

⁴*Spinitectus agonostomi* Moravec & Barus, 1971

Site: Intestine

Host and records: Mugilidae: *Agonostomus monticola* Cuba and Guadeloupe (see Moravec 1998), and from the same host species from Jalisco and Río Papaloapan Basin, Mexico.

^{4P}*Spinitectus humbertoi* Caspeta-Mandujano & Moravec, 2000

Site: Intestine

Host and record: Profundulidae: *Profundulus labialis* (Günther), Guerrero, Mexico.

⁴*Spinitectus mexicanus* Caspeta-Mandujano, Moravec & Salgado-Maldonado, 2000

Site: Intestine

Host and record: Poeciliidae: *Heterandria bimaculata* (Heckel), *Poecilia mexicana* Steindachner, Río Papaloapan Basin, Mexico.

⁴*Spinitectus tabascoensis* Moravec, García-Magaña & Salgado-Maldonado, 2002

Site: Intestine

Host and record: Ictaluridae: *Ictalurus furcatus* Tabasco, Mexico.

Cystoosidae Maggenti 1981

⁵*Cystoopsis atractostei* Moravec & Salgado-Maldonado, 2003

Site: Intestine

Host and records: Lepisosteidae: *Atractosteus tropicus* Tabasco, Mexico.

Daniconematidae Moravec & Kjøie, 1987

¹*Mexiconema cichlasomae* Moravec, Vidal & Salgado-Maldonado, 1992

Site: Intestine

Hosts and records: Cichlidae: *Cichlasoma urophthalmus*, *Herichthys pearsei*, *Parachromis motaguensis*, *Thorichthys helleri*, *T. passionis*, *Vieja synspila*, Ariidae: *Cathorops melanopus* (Günther), Poeciliidae: *Xiphophorus hellerii* Heckel, Río Papaloapan Basin, Tabasco and Yucatán Peninsula, Mexico.

Philometridae Baylis & Daubney, 1926

¹*Neophilometroides caudatus* (Moravec, Scholz & Vivas-Rodríguez, 1995) Moravec, Salgado-Maldonado & Aguilar-Aguilar, 2002

Site: Intestine

Host and records: Heptapteridae: *Rhamdia guatemalensis* Río Papaloapan Basin and Yucatán Peninsula, Mexico.

⁴*Philometra ophisterni* Moravec, Salgado-Maldonado & Aguilar-Aguilar, 2002

Site: Intestine

Host and record: Synbranchidae: *Ophisternon aenigmaticum* Río Papaloapan Basin, Mexico.

Quimperiidae Gendre, 1928

¹*Gibsonnema ophisterni* (Moravec, Salgado-Maldonado & Aguilar-Aguilar, 2002) Moravec, Salgado-Maldonado & Aguilar-Aguilar, 2002

Site: Intestine

Host and record: Synbranchidae: *Ophisternon aenigmaticum* Río Papaloapan Basin, Mexico.
Rhabdochonidae Travassos, Artigas & Pereira, 1928

¹P *Beaninema nayaritense* Caspeta-Mandujano, Moravec & Salgado-Maldonado, 2001

Site: Intestine

Host and record: Cichlidae: *Cichlasoma beani*, Río Santiago Basin, Mexico.

²*Rhabdochona acuminata* (Molin, 1860)

Site: Intestine

Host and record: Characidae: *Brycon guatemalensis*, Chiapas, Mexico.

⁴P *Rhabdochona guerreroensis* Caspeta-Mandujano, Aguilar-Aguilar & Salgado-Maldonado, 2002

Site: Intestine

Host and record: Gobiidae: *Sicydium multipunctatum*, Guerrero and Jalisco, Mexico.

⁴*Rhabdochona kidderi* Pearse, 1936

Site: Intestine

Hosts and records: Cichlidae: *Vieja maculicauda*, Nicaragua (Aguirre-Macedo 2001b); Bythidae: *Typhliasina pearsei* (Hubbs), Cichlidae: *Amatitlania nigrofasciata* (Günther), *Cichlasoma istlanum*, *C. urophthalmus*, *Herichthys cyanoguttatus*, *H. labridens*, *Parachromis managuensis*, *Thorichthys helleri*, *Vieja bifasciata*, *V. fenestrata*, *V. synspila*, Clupeidae: *Dorosoma anale* Meek, Eleotridae: *Gobiomorus dormitor*, Heptapteridae: *Rhamdia guatemalensis*, Ictaluridae: *Ictalurus mexicanus* (Meek), Poeciliidae: *Gambusia yucatanana* Regan, *Poecilia mexicana*, basins of the rivers Balsas, Pánuco and Papaloapan, Jalisco, Tabasco and Yucatán Peninsula, Mexico.

⁴*Rhabdochona mexicana* Caspeta-Mandujano, Moravec & Salgado-Maldonado, 2000

Site: Intestine

Hosts and records: Characidae: *Astyanax aeneus*, *A. fasciatus*, *A. mexicanus* (De Filippi), basins of the rivers Balsas, Pánuco and Papaloapan, and Jalisco, Mexico.

⁴P *Rhabdochona salgadoi* Caspeta-Mandujano & Moravec, 2000

Site: Intestine

Host and record: Profundulidae: *Profundulus labialis*, Guerrero, Mexico.

⁴*Rhabdochona xiphophori* Caspeta-Mandujano, Moravec & Salgado-Maldonado, 2001

Site: Intestine

Host and record: Goodeidae: *Allotoca catarinae* (de Buen), *Xenotoca eiseni* (Rutter), Poeciliidae: *Xiphophorus helleri*, *Xiphophorus* sp. Colima and basins of the rivers Balsas, Pánuco and Santiago, Mexico.

* New species, see Salgado-Maldonado 2006

Discussion

According to the data the helminth parasite fauna in freshwater fish in Central America is typical to the region. Most of the known species are endemic to the area and can be derived from South American genera. As is the case with mollusks, aquatic insects, crustaceans and freshwater fish (Stehli & Webb 1985; Bănărescu 1995), the number of South American taxa far outnumbers those from North America.

Several authors suggested that the Central American helminth parasite fauna in freshwater fish developed

allopatrically in the area. They assumed that the ancestral fish stocks that colonized the area brought their ancestral parasites with them and then both hosts and parasites developed in isolation in Central America (Vidal-Martínez & Kennedy 2000; Vidal-Martínez *et al.* 2001b; Mendoza-Franco *et al.* 2007). The isolation of some bodies of water, such as the sinkholes (cenotes) of the Yucatan Peninsula, provided them with peculiar biotic and abiotic conditions that favored speciation processes, including differentiation of endemic forms (Moravec *et al.* 1995b; Scholz *et al.* 1996b). Apparently, the Central American helminth fauna developed primarily from radiation of migrants in a competition-free environment, diversifying opportunistically to occupy available niches.

The almost total absence of differentiation of endemic suprageneric taxa, as well as the relatively low number of endemic helminth genera (24%) suggest this fauna is young. In Central America, the Ichthyofauna is primarily composed of generalized fish genera which are broadly distributed in South America (Myers 1966; Bănărescu 1995). This is also the case with the area's helminth genera, of which a large proportion (35%) originated from genera that are broadly distributed and dominant in South America, where this fauna is rich and diverse. For example, the genera *Gussevia* and *Sciadicleithrum* (Monogenea), and *Procamallanus* and *Spinitectus* (Nematoda) are all South American and have the highest numbers of species in this region (Moravec 1998; Kritsky *et al.* 1994; Mendoza-Franco *et al.* 2000; Vidal-Martínez *et al.* 2001b).

There are very few North American freshwater fish in Central America and all are restricted to the extreme north (Myers 1966; Bănărescu 1995). Records exist, however, of helminth species in both the Lepistosteidae and Ictaluridae that are found in no other geographic area.

Dispersion and vicariance events that affected their hosts are what determined the current distribution of direct lifecycle parasites (Bentz *et al.* 2006). It is to be expected, therefore, that the direct lifecycle helminth groups are those that have experienced extensive diversification, resulting in a high number of species. The large number of dactylogyridae monogeneans, particularly *Sciadicleithrum*, supports this. Monogenean diversity in Central America is most likely higher than reported here, but the study of these parasites in this area is still incipient. The same phenomenon explains how some direct lifecycle nematode, such as the Atractidae, Cosmocercidae and some Capillaridae (Moravec 1998; Anderson 2000), have produced a large number of endemic species in Central America.

Indirect lifecycle helminths have had to confront the challenge of finding appropriate intermediate hosts in Central America. Camallanidae and Rhabdochonidae, the nematode families with the largest number of known species in the region, use broadly distributed and abundant copepods or aquatic insect larvae (Moravec *et al.* 1995b; Moravec 1998). Specificity in the nematode parasites of fish is much broader in their intermediary hosts than in their definitive hosts (Moravec 1994; Moravec *et al.* 1995a; Moravec & Vargas-Vazquez 1996).

Given the above, the current recorded trematode diversity in Central America is surprising. The data of Scholz *et al.* (1994, 1995a, 1996a) and Ditrich *et al.* (1996) suggest that a number of trematode lineages used intermediate hosts that were broadly distributed in the area and abundant in some locations. The prosobranchia *Pyrgophorus coronatus* (Pfeiffer) is thus used as intermediate host by 11 trematode species on the Yucatan Peninsula (Ditrich *et al.* 1997). The freshwater mollusk fauna here is depauperate, but this snail is a typical component in cenotes and predominates at almost all locations.

The virtual absence of acanthocephalans in Central America (Salgado-Maldonado *et al.* 1992) cannot be easily explained. Contrary to what Pérez & Choudhury (2005) erroneously stated the Characidae, Cichlidae and Heptapteridae (= Pimelodidae) as well as other Southamerican fish families do possess typical acanthocephalans in their ancestral area. As for example several species of *Echinorhynchus*, and *Palliolisentis* and *Neoechinorhynchus buttnerae* Golvan, 1956, and *Quadrigyryrus torquatus* Van Cleave, 1920 from Characidae; *N. paraguayensis* Machado-Filho, 1959, *Pandosentis iracundus* Van Cleave, 1920 and *Q. torquatus* from Cichlidae and *Deltacanthus scorzai* (Díaz-Ungría & Gracias-Rodrigo, 1957) (= *Acanthodelta scorzai*) from Pimelodidae (see Thatcher, 2006). Therefore the paucity of acanthocephalans in Mexican freshwaters can not

be explained as primary. It is most likely that the possible intermediate hosts for acanthocephalans in Central America are in fact highly diverse, but occur in very low abundance populations and are distributed microendemically. They therefore constitute a limiting factor for diversification of the acanthocephalan parasites of freshwater fish. In effect the peracarids and decapods are the most diverse groups of freshwater crustaceans in Mexico and consist mostly of microendemic species. Of the 184 known decapod species from Mexico and Central America, 153 are found in Mexico: 140 of these are endemic; 114 are distributed in a single location; and 22 of these genera are monotypical and endemic. In other words, the region's crustacean species are extremely rare, distributed in very few bodies of water and with populations containing few individuals (Álvarez, F. 2008, Curator, Colección Nacional de Crustáceos, Mexico, Instituto de Biología, Universidad Nacional Autónoma de México). For ancestral acanthocephalan stocks, this would have been the worst possible scenario to find upon arriving in Central America, no matter their origins. Due to the similarity of their lifecycles with acanthocephalan lifecycles, this explanation could also be assumed for cestodes.

A striking feature of this helminth fauna relates to the number of species of parasites associated to the most abundant fish families of Central America, the cichlids and the poeciliids. The Poeciliidae is the only fish family that has given rise to genera and suprageneric taxa endemic to Central America (Myers 1966; Rosen 1975; Bănărescu 1995); 56 species of Poeciliids are found in Central America (Myers 1966), however, there are records for only nine helminth species associated to this family. In contrast, only six to nine genera, but more than 100 species of Cichlidae are found in Central America (Miller 1966; Bănărescu 1995; Roe *et al.* 1997; Miller & Norris 2005), however, cichlids have a record of 33 helminth species.

As shown here, the helminth parasites of freshwater fish from Central America is a fauna that has been almost unable to invade Nearctic regions further north than the Transverse Volcanic Axis (approx. the 19° parallel) and is not found in South America.

The present data suggest that Central America is a center of diversification (*sensu* Minckley *et al.*, 2005) for the helminth parasites of freshwater fish. Central America has a typical helminth parasite fauna in freshwater fish with a high proportion of endemisms, that seems evolutionarily very recent. This said, the current state of knowledge of this fauna is incipient and further collections and basic research are needed to better understand it. For example, the differences between genera and species groups with similar distribution patterns (i.e. elements; *sensu* Bussing 1976) needs more research, as do the distribution patterns of helminths that also adapt to ichthyological provinces (Miller 1966; Bussing 1976). An understanding of the helminth fauna of freshwater fish in Central America will provide an adequate and robust reference framework for future research on the biogeography and ecology of these parasites.

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