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Invited article

Diversity of helminth parasites of freshwater fish in the headwaters of the Coatzacoalcos River, in Oaxaca, Mexico

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ABSTRACT

We documented the diversity of helminth parasites of 25 fish species from 8 families occurring in the headwaters of the Coatzacoalcos river basin. This river flows along the border between the states of Oaxaca and Veracruz, in the region of the Isthmus of Tehuantepec, in south-eastern Mexico, and in northern Central America. We recorded 48 species, representing 44 genera and 29 helminth families. Six of the 25 fish species were examined for helminths for the first time; 60 new host records were reported. Nematodes and trematodes were the most abundant taxonomic groups. The helminth fauna from our study area consists of primarily central American species. Most species recorded from this area have also been captured from freshwater bodies between the Isthmus of Tehuantepec and the Isthmus of Panama. However, three species, including an acanthocephalan and two nematodes, are likely endemic to this area. We argue that, in contrast to the presence of larval helminths, which mostly depends on the geographical location of water bodies, adult helminths are an integral and consistent component of the regional community. Data on taxonomic composition and distribution of helminth fauna reported in this paper, contribute to a better understanding of this faunal component in northern Central America (CA). Furthermore, knowledge of helminth parasites of freshwater fish from Neotropical Mexico and CA facilitates prediction of which parasite species is likely to infect fish in a specific geographical area.

1. Introduction

Current inventory of helminth parasites of freshwater fish from Central America (CA) (Salgado-Maldonado, 2008) indicates differences from that, of both North America (Margolis and Arthur, 1979; Hoffman, 1999) and South America (Thatcher, 2006; Kohn et al., 2007; Eiras et al., 2010; Cohen et al., 2013); despite data still lacking for large zones within CA. Diversity analysis of fish parasites inhabiting several important rivers on the Isthmus of Tehuantepec, in Mexico, in the extreme north of CA, has not been conducted. Few papers that are available on fish parasites in the Coatzacoalcos River (Salgado-Maldonado et al., 2010; Pinacho-Pinacho et al., 2015; García-Varela et al., 2016; Andrade-Gómez et al., 2017; Barrios-Gutiérrez et al., 2018, 2019; Hernández-Mena et al., 2019) are all taxonomic reports. Therefore, to the best of our knowledge, data on species composition, distribution, and abundance of fish parasites in this river basin remain unavailable. This study reports data collected during two expeditions in March and April 2009, where we examined fresh water fish from the upper reaches of the Coatzacoalcos River. Our aim was to obtain information on the diversity of their helminth parasites.

2. Materials and methods

The Coatzacoalcos River (Fig. 1) is 325 km long, and flows along the south-eastern coast of Mexico. It originates in the Sierra Atravesada mountain range in the region of the Isthmus of Tehuantepec, in the state of Oaxaca, and opens into the southern Gulf of Mexico near the city of Puerto de Coatzacoalcos in the south-eastern State of Veracruz (Arriaga-Cabrera et al., 2000). The Isthmus of Tehuantepec is a narrow region where the distance between the coasts of the Gulf of Mexico and

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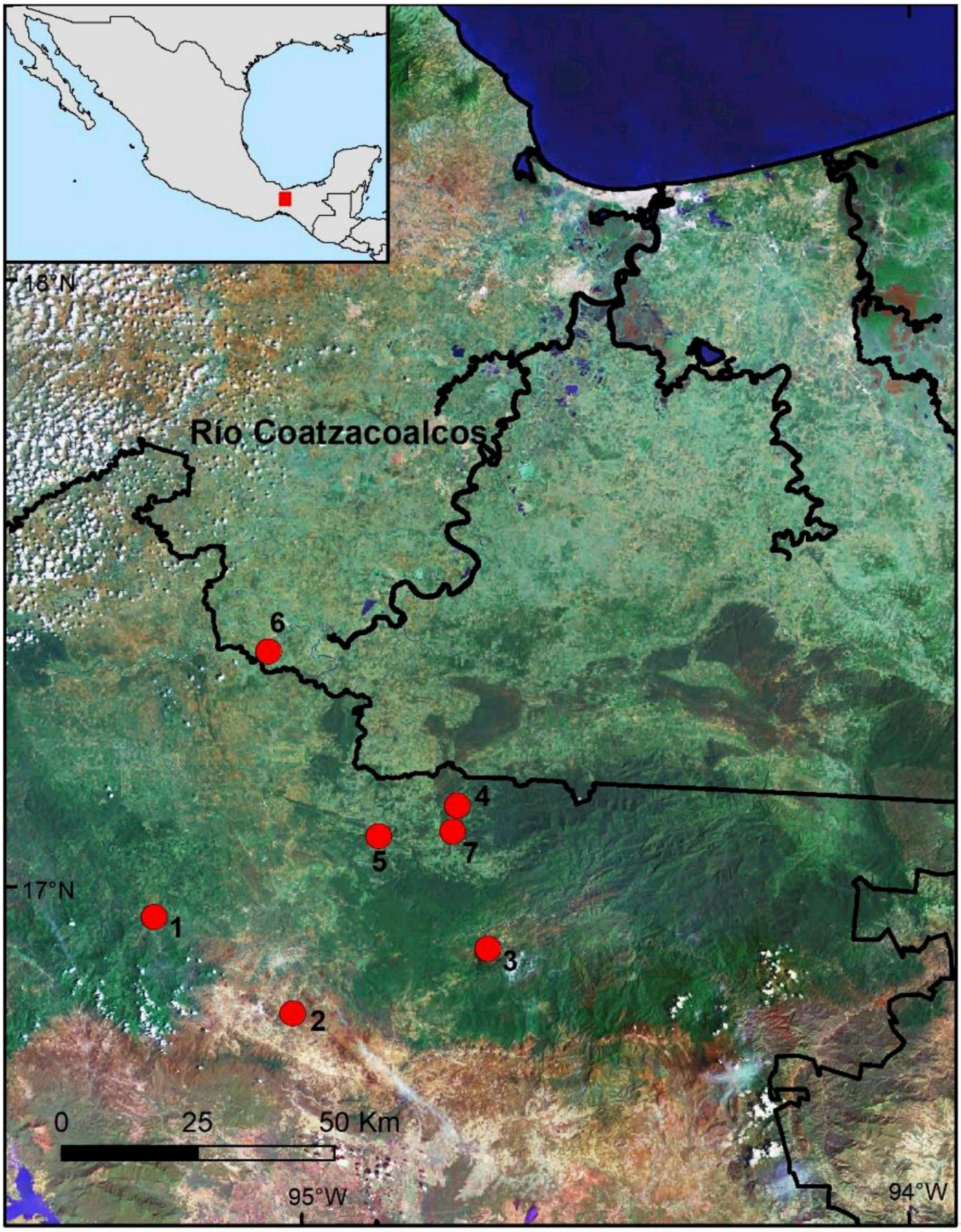

Fig. 1. The upper Coatzacoalcos river in Mexico showing the fish Collection sites; codes: **1**. El Platanillo river, tributary to Del Sol river (municipality Santo Domingo Petapa), coordinates 16.951111, −95.244167, altitude 416 m; **2**. Río Grande (El Barrio), 16.792167, −95.016083, 220 m; **3**. Río Negro (Santa María Chimalapa), 16.898528, −94.693694, 166 m; **4**. Río Modelo (Santa María Chimalapa), 17.134778, −94.745000, 115 m; **5**. Río Pánfilo (Matías Romero, Oaxaca), 17.083639, −94.873944, 60 m; **6**. Río Jaltepec (Jesús Carranza, Veracruz), 17.388444, −95.056111, 40 m; **7**. Río Escondido (Paraje San Francisco El Vado, Agencia Municipal Río Escondido, Santa María Chimalapa), 17.091083, −94.751694, 103 m. Note all sites in Oaxaca state, except # 6.

the Pacific Ocean is only ~190 km. A few places here reach an elevation of 300 m above sea level. The Coatzacoalcos River generally flows through the central area of the isthmus region (Kallman et al., 2004).

To provide a complete record of the host - helminth parasite systems in the headwaters of the Coatzacoalcos River basin, we aimed to sample as many fish species as possible. We sampled seven rivers (Fig. 1) during dry season, in March and April 2009. In this geographical region, two climatic seasons are recognized: wet (May to October) and dry (November to April) (Trejo, 2004). Due to very high precipitation (> 2500 mm), during the wet (rainy season) months, it is almost impossible to reach the headwaters of the Coatzacoalcos River basin. Therefore, we limited our sampling to the dry season.

We captured and examined fish for the presence of helminth parasites. Hosts were classified according to most recent nomenclature as described by Martínez-Ramírez et al. (2004), and Froese and Pauly (2019). At each sampling location, fish were captured using an electrofishing device. Live fish were transported to the laboratory and examined within 48 h. All external surfaces, viscera, and musculature of each fish host were examined under a stereomicroscope. All helminths observed in each fish were isolated and counted. Cestodes, digenean larvae, monogeneans, and nematodes were fixed in hot 4% neutral formalin. Some monogeneans were fixed with ammonium picrate (Ergens, 1969) and mounted unstained in Gray–Wess medium (Vidal-Martínez et al., 2001), for analysis of sclerotized structures. Acanthocephalans were placed in distilled water, refrigerated overnight (6–12 h) to evert the proboscis, and then fixed in hot 10% formalin. Digeneans, monogeneans, cestodes, and acanthocephalans used for morphological examination of whole mounts, were stained with Mayer's paracarmine, dehydrated using a graded alcohol series, cleared in methyl salicylate, and mounted in Canada balsam. Nematodes were cleared in glycerine for light microscopy and stored in 70% ethanol.

By focussing on parasite colonization strategies, we distinguished between autogenic and allogenic species according to Esch et al. (1988). Allogenic species mature in birds or vertebrates other than fish and therefore, have greater colonization potential and ability,

Table 1
List of helminths of 25 freshwater fish species recorded in the headwaters of Coatzacoalcos River basin, Isthmus of Tehuantepec zone, Mexico.
Localities and codes: EP, El Platanillo; RE, Río Escondido; RG, Río Grande; RJ, Río Jaltepec; RM, Río Modelo; RN Río Negro; RP, Río Pánfilo; (n = number of hosts examined in this locality; date Ma, March or Ap, April 2009); * host species not examined previously for helminths; ** new host record; IH, number of infected hosts by each species; IS, infection site of the helminth; P (%) prevalence; MI, mean intensity; A = Acanthocephala; C = Cestoda; D = Digenea; M = Monogenea; N = Nematoda; if = immature form; mc = metacercariae. Sites of infections are: Bc, body cavity; F, fins; G, gills; Gb, gall bladder; I, intestine; IC, intestinal caeca; L, liver; Me, mesentery; Mu, muscle; S, skin; St, stomach. Helminths are grouped as [Ca] Central American species; [Ec] Endemic to headwaters of Coatzacoalcos River basin; [Gw] Generalist, widely distributed in Mexico; [In] Introduced species; [?] Not enough data to situate the species.

HOSTS		HELMINTHS	LOCALITY (n)	IS	IH	P (%)	MI
CHARACIDAE							
Astyanax aeneus (Günther, 1860) [referred as *Astyanax finitimus* (Bocourt, 1868) by Schmitter-Soto (2017)]	M	[Ca]*Urocleidoides* cf. *strombicirrus* (Price and Bussing, 1967)	EP (19 Ma)	G	1	5.2%	11
			RN (24 Ma)	G	8	33.3%	3.7 ± 1.8
			RP (20 Ap)	G	1	5%	1
	D	[Ca]*Auriculostoma astyanace* Scholz, Aguirre-Macedo and Choudhury, 2004 CNHE 11311	RG (1 Ma)	I	1	100%	1
	D	[Ca]*Wallinia anindoi* Hernández-Mena et al., 2019 CNHE 11314–11,316	RN (24 Ma)	I, IC	9	37.5%	2.7 ± 3.3
			RJ (12 Ap)	I	1	8.3%	2
			RP (20 Ap)	I	1	5%	1
	D	[Ca]*Genarchella astyanactis* (Watson, 1976) CNHE 11318	RP (20 Ap)	I	1	5%	1
			RJ (12 Ap)	I	5	41.6%	1 ± 0
	D	[Ca]*Magnivitellinum* cf. *simplex* Kloss, 1966 CNHE 11317	RP (20 Ap)	I	2	10%	3.5 ± 0.7
	D	[In]*Centrocestus formosanus* (Nishigori, 1924) (mc)	RN (24 Ma)	G	1	4.1%	1
	D	[Gw]*Clinostomum* sp. (mc)	EP (19 Ma)	G, F, Me	5	26.3%	3.4 ± 2.8
	D	[Gw]*Uvulifer* cf. *ambloplitis* (Hughes, 1927) (mc)	EP (19 Ma)	S, F,Mu	6	31.6%	6.7 ± 12.9
	D	[Gw]*Apharyngostrigea* sp. (mc) CNHE 11332	RN (24 Ma)	Me	1	4.1%	1
			RJ (12 Ap)	Gb	1	8.3%	1
	N	[?]Capillaridae gen. sp.	RP (20 Ap)	St	1	5%	4
	N	[?]Acuariidae gen. sp. ** (if)	EP (19 Ma)	I	1	5%	1
	N	[Gw]*Contracaecum* sp. (if) CNHE 11344	RN (24 Ma)	L	2	8%	1.5 ± 0.7
			RP (20 Ap)	I	5	25%	2 ± 1
	N	[Gw]*Spiroxys* sp. (if) CNHE 11347	RN (24 Ma)	Me	2	8%	2.5 ± 0.7
			RJ (12 Ap)	Me	1	8%	2
CICHLIDAE							
Parachromis friedrichsthalii **(Heckel, 1840)**	D	[Ca]*Crassicutis cichlasomae* Manter, 1936	RJ (1 Ap)	I	1	100%	1
	D	[Gw]*Posthodiplostomum* sp. (mc) CNHE 11339	RJ (1 Ap)	Me	1	100%	1
	D	*Tylodelphys* sp. (mc)** CNHE 11328	RJ (1 Ap)	Me	1	100%	8
*****Paraneetroplus bulleri*** Regan, 1905	M	[Ca]*Sciadicleithrum* sp.**	RE (16 Ap)	G	3	18.7%	3.7 ± 2.3
	D	[Ca]*Crassicutis cichlasomae***	RE (16 Ap)	I	3	18.7%	8.3 ± 5.5
	D	[Gw]*Posthodiplostomum* sp. ** (mc) CNHE 11326	RE (16 Ap)	Me, Mu	2	12.5%	1
	D	[Gw]*Uvulifer* cf. *ambloplitis* **(mc)	EP (2 Ma)	Mu	1	50%	12
	N	[Ca]*Raillietnema kritscheri* Moravec, Salgado-Maldonado and Pineda-López, 1993**	RE (16 Ap)	I	7	43.7%	12 ± 8.5
	N	[?]*Cucullanus* sp.**	RE (16 Ap)	I	1	6.2%	1
	N	[Ec]Philometridae gen. sp.**	RE (16 Ap)	Bc	3	18.7%	3 ± 3.4
	N	[Ca]*Rhabdochona kidderi* Pearse, 1936**	RE (16 Ap)	I	6	37.5%	3 ± 3.1
	N	[?]Acuariidae gen. sp.** (if)	EP (2 Ma)	I	1	50%	2
	N	[Gw]*Contracaecum* sp. ** (if)	RE (16 Ap)	L, Me	2	12.5%	1
Theraps irregularis Günther, 1862	N	[Ec]Philometridae gen. sp.**	RN (6 Ma)	Mu	1	16.6%	1
	N	[Ec]*Rhabdochona* sp.**	RN (6 Ma)	Mu	3	50%	6.0 ± 2.6
Thorichthys callolepis **(Regan, 1904)**	M	[Ca]*Sciadicleithrum* sp.**	RN (30 Ma)	G	4	13.3%	1.7 ± 1.5
	M	[?]*Gyrodactylus* sp.**	RN (30 Ma)	F	2	6.6%	1.5 ± 0.7
	D	[In]*Centrocestus formosanus* **(mc)	RN (30 Ma)	G	4	13.3%	1.7 ± 0.5
	D	[Gw]*Clinostomum* sp. ** (mc)	RN (30 Ma)	F, Me, S	3	10%	2.3 ± 2.3
	D	[Gw]*Diplostomum* sp. ** (mc) CNHE 11324	RN (30 Ma)	E, G	7	23.3%	17.7 ± 27
			RJ (7 Ap)	E	5	71.4%	3.6 ± 1.9
	C	[?]*Ciclidocestus* sp.**	RN (30 Ma)	I	6	20%	2.1 ± 0.9
	N	[Gw]*Contracaecum* sp. ** (if)	RJ (7 Ap)	L	2	28.6%	1.5 ± 0.7
	N	[Gw]*Spiroxys* sp. ** (if)	RN (30 Ap)	Me	1	3.3%	1
Thorichthys helleri (Steindachner, 1864)	D	[Ca]*Crassicutis cichlasomae*	RM (8 Ma)	I	3	37.5%	1.3 ± 0.5
	D	[Ca]*Genarchella isabellae* (Lamothe-Argumedo, 1977) CNHE 11319	RM (8 Ma)	I	1	12.5%	5
	D	[?]*Cladocystis* cf. *trifolium* (Braun, 1901) (mc) CNHE 11330	RM (8 Ma)	I	2	25%	2.5 ± 0.7
	N	[Ca]*Procamallanus* (*Spirocamallanus*) *rebecae* (Andrade-Salas, Pineda-López and García-Magaña, 1994) CNHE 11341	RG (3 Ma)	I	2	66.6%	2.0 ± 1.4
			RM (8 Ma)	I	3	37.5%	2.6 ± 1.5
	N	[Ca]*Raillietnema kritscheri* **	RM (8 Ma)	I	2	25%	thousands
	N	[?]*Cucullanus* sp.**	RM (8 Ma)	I	1	12.5%	5
	N	[Gw]*Contracaecum* sp. ** (if) CNHE 11345	RM (8 Ma)	L	2	25%	1
	N	[Ca]*Rhabdochona* sp. (if)	RM (8 Ma)	L	2	25%	2 ± 1.4

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Table 1 (*continued*)

HOSTS		HELMINTHS	LOCALITY (n)	IS	IH	P (%)	MI
Thorichthys maculipinnis **(Steindachner, 1864)**	N	[Ca]*Procamallanus* (*Spirocamallanus*) *rebecae*	RE (1 Ap)	I	1	100%	3
Trichromis salvini **(Günther, 1862)**	D	[Ca]*Crassicutis cichlasomae*	RM (1 Ma)	I	1	100%	6
			RP (3 Ap)	I	1	33.3%	6
			RE (3 Ap)	I	1	33.3%	6
			RJ (9 Ap)	I	1	11.1%	3
	D	[Gw]*Diplostomum* sp. ** (mc)	RN (9 Ma)	E	1	11.1%	1
			RJ (9 Ap)	E	7	77.7%	20 ± 11.8
	D	[Gw]*Posthodiplostomum* sp. (mc)	RJ (9 Ap)	Me, Mu	2	22.2%	12.5 ± 14.8
	D	*Tylodelphys* sp. (mc) CNHE 11327	RJ (9 Ap)	Me	1	11.1%	5
	D	[?]*Cladocystis* cf. *trifolium* (mc) CNHE 11331	RG (1 Ma)	I	1	100%	80
	N	[Ca]*Raillietnema kritscheri* **	RJ (9 Ap)	I	1	11.1%	1
	N	[?]Acuariidae gen. sp.** (if)	RG (1 Ma)	I	1	100%	1
Vieja guttulata **(Günther, 1864)**	M	[Ca]*Sciadicleithrum* sp.**	EP (24 Ma)	G	4	16.6%	1.5 ± 1.0
			RJ (6 Ap)	G	1	16.6%	1
	M	[?]*Gyrodactylus* sp.**	RN (29 Ma)	F	1	3.4%	1
	D	[Ca]*Genarchella isabellae* **	EP (24 Ma)	St	1	24.1%	1
			RN (29 Ma)	I	2	6.9%	1
	D	[Gw]*Clinostomum* sp. ** (mc) CNHE 11323, 11336	RN (29 Ma)	G	2	6.9%	4 ± 4.2
	D	[Gw]*Diplostomum* sp. ** (mc) CNHE 11335	RN (29 Ma)	E, B	5	17.2%	2.8 ± 2.1
			RJ (6 Ap)	Me	1	16.6%	1
	D	[Gw]*Posthodiplostomum* sp. (mc) CNHE 11337, 11338	RN (29 Ma)	Me, Mu	3	10.3%	2 ± 1
			RJ (6 Ap)	Mu	1	16.6%	7
	C	[In]*Schyzocotyle acheilognathi* (Yamaguti, 1934)**	RJ (6 Ap)	Mu	1	16.6%	1
	C	[?]*Ciclidocestus* sp.**	RN (29 Ma)	I	1	3.4%	1
	N	[Ca]*Atractis vidali* González-Solís and Moravec, 2002	RN (29 Ma)	I	1	3.4%	37
	N	[Ca]*Raillietnema kritscheri* **	RN (29 Ma)	I	6	20.7%	9.1 ± 9.6
			RE (10 Ap)	I	1	10%	1.3
	N	[Ca]*Cucullanus angeli* Cabañas-Carranza and Caspeta-Mandujano, 2007**	EP (24 Ma)	I	8	33.3%	2.2 ± 3.1
			RN (29 Ma)	I	6	20.7%	2.0 ± 1.0
	N	[?]*Cucullanus* sp.	RE (10 Ap)	I	1	10%	1
	N	[Ca]*Rhabdochona kidderi* **	EP (24 Ma)	I	11	45.8%	9.1 ± 21.2
			RE (10 Ap)	I	2	20%	1
	N	[Gw]*Contracaecum* sp. ** (if)	RE (10 Ap)	Me	3	30%	1
			RJ (6 Ap)	Me, I	2	33.3%	1
	N	[Ca]*Hysterothylacium cenotae* (Pearse, 1936)	RN (29 Ma)	I	2	6.9%	1.5 ± 0.7
	N	[Ca]*Rhabdochona* sp. ** (if)	RN (29 Ma)	I	7	24.1%	5.3 ± 4.8
Vieja regani **(Miller, 1924)**	D	[Ca]*Crassicutis cichlasomae*** CNHE 11321	RM (5 Ma)	I	4	80%	2 ± 0.8
	D	[Ca]*Genarchella isabellae* ** CNHE 11320	RM (5 Ma)	St	3	60%	17.6 ± 13.6
	D	[Gw]*Posthodiplostomum* sp. ** (mc)	RG (5 Ma)	G	1	20%	1
	N	[Ca]*Raillietnema kritscheri* **	RG (5 Ma)	I	3	60%	thousands
	N	[Ca]*Rhabdochona kidderi* **	RM (5 Ma)	I	3	60%	6 ± 6.2
	N	[Gw]*Contracaecum* sp. ** (if)	RG (5 Ma)	Me	1	20%	1
ELEOTRIDAE							
Gobiomorus dormitor **Lacepède, 1800**	M	[Ca]*Guavinella tropica* Mendoza-Franco, Scholz and Cabañas-Carranza, 2003	RN (6 Ma)	G	3	50%	31.3 ± 31.2
			RM (4 Ma)	G	1	25%	12
			RE (1 Ap)	G	1	100%	9
	D	[Ca]*Genarchella isabellae*	RM (4 Ma)	I	1	25%	2
	D	[In]*Centrocestus formosanus* (mc)	RN (6 Ma)	G	3	50%	7.0 ± 5.3
	N	[Ca]*Paracapillaria teixeirafreitasi* (Caballero-Rodríguez, 1971)	RE (1 Ap)	St	1	100%	1
			RN (6 Ma)	St	1	16.6%	3
	N	[?]*Cucullanus* sp.	RE (1 Ap)	I	1	100%	1
	N	[Gw]*Contracaecum* sp. (if) CNHE 11342, 11343	RN (6 Ma)	L, Me; Mu	3	50%	3.6 ± 2.1
			RM (4 Ma)	I, Me	3	75%	9 ± 13.8
			RP (4 Ap)	Me	1	25%	1
			RE (1 Ap)	Me	1	100%	4
	N	[Gw]*Spiroxys* sp. (if)	RN (6 Ma)	Me	1	16.6%	1
	N	[Gw]*Falcaustra* sp. ** (if)	RN (6 Ma)	Me	1	16.6%	1
	N	[Ca]*Rhabdochona* sp. (if) CNHE 11346	RM (4 Ma)	I	2	50%	3 ± 2.8
			RP (4 ap)	I	1	25%	3
GOBIIDAE							
Awaous banana **(Valenciennes, 1837)**	A	[En]*Neoechinorhynchus chimalapasensis* Salgado-Maldonado et al. (2010)	RN (8 Ma)	I	7	87.5%	4.1 ± 2.5
	N	[Gw]*Contracaecum* sp.** (if)	RN (8 Ma)	Me	1	12.5%	1

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Table 1 (*continued*)

HOSTS		HELMINTHS	LOCALITY (n)	IS	IH	P (%)	MI
HEPTAPTERIDAE							
Rhamdia guatemalensis **(Günther, 1864)**	M	[Ca]*Aphanoblatella travassosi* (Price, 1938)	RN (4 Ma)	G	1	25%	3
	D	[Gw]*Clinostomum* sp. (mc)	RN (4 Ma)	Me	1	25%	1
			RP (5 Ap)	F, G, Me	4	80%	26 ± 36
	D	*Crocrodilicola pseudostoma* (Willemoes-Suhm, 1870) CNHE 11333	RP (5 Ap)	I	1	20%	1
	N	[Ca]*Cucullanus mexicanus* Caspeta-Mandujano, Moravec and Aguilar-Aguilar, 2000	RP (5 Ap)	I	1	20%	1
	N	[Gw]*Contracaecum* sp.** (if)	RG (1 Ma)	Me	1	100%	1
			RP (5 Ap)	Me	2	40%	3.5 ± 3.5
Rhamdia laticauda **(Kner, 1858)**	M	[Ca]*Aphanoblatella travassosi* (Price, 1938)	RE (6 Ap)	G	1	16.7%	2
	D	[Gw]*Clinostomum* sp. (mc)	RE (6 Ap)	F	1	16.7%	2
	N	[Ca]*Rhabdochona kidderi*	RE (6 Ap)	I	2	33.3%	3 ± 1.4
MUGILIDAE							
Agonostomus montícola **(Bancroft, 1834)**	D	[Ca]*Creptotrema agonostomi* Salgado-Maldonado, Cabañas-Carranza and Caspeta-Mandujano, 1998	RN (1 Ma)	I	1	100%	5
		CNHE 11312	RP (2 Ap)	I	2	100%	3 ± 1.4
			RE (2 Ap)	I	2	100%	5 ± 1.4
	D	[Ca]*Saccocoelioides* cf. *sogandaresi* Lumsden, 1963	RP (2 Ap)	I	1	50%	1
	N	[Ca]*Dicheline mexicanus* Caspeta-Mandujando, Moravec and Salgado-Maldonado, 1999	RP (2 Ap)	I	1	50%	4
POECILIIDAE							
Poecilia mexicana **Steindachner, 1863**	M	[?]*Gyrodactylus* sp.	RE (13 Ap)	F	3	23%	1.3 ± 0.6
	N	[Gw]*Spiroxys* sp. (if)	RE (13 Ap)	Me	1	7.7%	1
	N	[Gw]*Falcaustra* sp. ** (if)	RE (13 Ap)	Me	1	7.7%	1
Poecilia sphenops **Valenciennes, 1846**	D	[Ca]*Saccocoelioides* cf. *sogandaresi*	RG (5 Ma)	I	3	60%	1
	D	[Gw]*Ascocotyle* (*Phagicola*) *diminuta* (Stunkard and Haviland, 1924) (mc)	RG (5 Ma)	G	1	20%	1
	D	[Gw]*Diplostomum* sp. (mc)	RJ (10 Ap)	E	7	70%	5.5 ± 3.4
	D	[Gw]*Posthodiplostomum* sp. (mc)	RG (5 Ma)	Me	1	20%	5
		CNHE 11325	RJ (10 Ap)	Me	1	10%	1
	C	[?]*Glossocercus* sp. (if)	RJ (10 Ap)	L	1	10%	1
Poeciliopsis gracilis **(Heckel, 1848)**	D	[Ca]*Saccocoelioides* cf. *sogandaresi* CNHE 11322	RG (4 Ma)	I	1	25%	1
Priapella intermedia **Álvarez and Carranza, 1952**	D	[Gw]*Uvulifer* cf. *ambloplitis* **(mc)	RG (1 Ma)	F	1	100%	3
Pseudoxiphophorus bimaculatus **(Heckel, 1848)**	D	[Ca]*Paracreptotrematoides* cf. *heterandriae* (Salgado-Maldonado, Caspeta-Mandujano and Vázquez, 2012) CNHE 11313	RP (8 Ap)	I	1	12.5%	14
	D	[In]*Centrocestus formosanus* (mc)	RP (8 Ap)	G	1	12.5%	3
	N	[Ca]*Spinitectus mexicanus* Caspeta-Mandujano, Moravec and Salgado-Maldonado, 2000	RP (8 Ap)	I	1	12.5%	2
****Xiphophorus clemenciae*** **Álvarez, 1952**	D	[Ca]*Saccocoelioides* cf. *sogandaresi* **	RG (3 Ma)	I	1	33.3%	1
	D	[In]*Centrocestus formosanus* **(mc)	RN (4 Ma)	G	2	50%	2
	D	[Gw]*Uvulifer* cf. *ambloplitis* **(mc)	RG (3 Ma)	F	1	33.3%	17
	N	[Gw]*Spiroxys* sp.** (if)	RG (3 Ma)	I	1	33.3%	28
Xiphophorus helleri **Heckel, 1848**	N	[?]*Contracaecum* sp. ** (if)	RJ (2 Ap)	Me	1	50%	1
****Xiphophorus mixei*** Kallman et al. (2004)	N	[?]Acuariidae gen. sp.** (if)	EP (5 Ma)	Mu	1	20%	1
****Xiphophorus monticolus*** Kallman et al. (2004)	M	[Ca]*Urocleidoides* sp. **	EP (9 Ma)	G	8	88.9%	9.0 ± 9.8
SYNBRABCHIDAE							
Ophisternon aenigmaticum **Rosen and Greenwood, 1976**	N	[Ca]*Pseudocapillaria* (*Ichthyocapillaria*) *ophisterni* Moravec, Salgado-Maldonado and Jimenez-García, 2000	RE (7 Ap)	I	1	14.3%	1
	N	[En]Philometridae gen. sp. **	EP (5 Ma)	S	2	40%	1.5 ± 0.7
			RN (3 Ma)	S	1	33%	3
	N	[?]*Contracaecum* sp. (if)	RG (1 Ma)	Me	1	100%	1
			RM (1 Ma)	Me	1	100%	2
			RN (3 Ma)	Me	1	33.3%	3
			RE (7 Ap)	Me	4	57.1%	2.5 ± 1.7
			RJ (3 Ap)	Me	2	66.6%	1.4 ± 2.8
	N	[Ca]*Rhabdochona* sp. **(if)	RE (7 Ap)	I	2	28.6%	1.5 ± 0.7

compared to autogenic species that mature in fish. Prevalence (number of infected fish out of total number of fish examined of that species, expressed as percentage) and mean intensity of infection (number of parasites per infected fish) were calculated according to Bush et al. (1997).

Voucher specimens of helminth taxa were deposited in the Colección Nacional de Helmintos (CNHE), Instituto de Biología, Universidad Nacional Autónoma de México, Mexico.

3. Results

We examined 410 freshwater fish representing 25 species and 8 families (Table 1). The distribution range of six species, including three cichlids and four poeciliids (Table 1), is mostly limited to the upper reaches of the Coatzacoalcos River basin. This study was therefore, the first time they had been examined for helminths.

We identified 48 helminth species, belonging to 44 genera and 29 families. Table 1 summarizes the parasites detected, their sampling locations, infection sites, prevalence, and intensity of infection. Our study contributes 60 new host records (Table 1). Most of the newly recorded hosts belong to the families Cichlidae (9 species examined; 45 new records), and Poeciliidae (9 species examined; 7 new records) (Table 1).

Nematodes 14 adult and 5 larval taxa were recorded, of which 12 were detected in new hosts. Nineteen trematodes; 9 adults and 10 larval taxa were recorded, of which 10 were detected in new hosts (Table 1). Six taxa of monogeneans were recorded. Cestodes 2 adults, 1 metacestode and Acanthocephalans, 1 species were the least rich groups in our study (Table 1).

Most helminth species that we detected have also been reported from Mexico and Central America. Among this helminth fauna (Table 1) four components were distinguished: 1) species that are endemic to the upper Coatzacoalcos River basin, 2) adults of Central American autogenic species that are local to this geographical region, 3) generalist (i.e. widely distributed) helminth larvae, and 4) alien (i.e. anthropogenically introduced) helminths. Two nominal species, *Magnivitellinum simplex* and *Crocodilicola pseudostoma* have been recorded from South America (Salgado-Maldonado, 2006). However, a comprehensive taxonomical analysis of either Mexican or South American species is lacking, such that it is not currently possible to describe their geographical distribution.

Three species are likely endemic to the upper reaches of the Coatzacoalcos River: the acanthocephalan *Neoechinorhynchus* (*Neoechinorhynchus*) *chimalapasensis* Salgado-Maldonado et al. (2010), a parasite of the gobiid *Awaous banana*; 2 new species (not yet described) of nematodes, namely *Rhabdochona* sp. a parasite of the cichlid *Theraps irregularis*, and a Philometridae gen. sp. nematode, from the skin of the synbranchid *Ophisternon aenigmaticum*.

Twenty-five Central American helminth species were recorded (Table 1); 23 of which mature in aquatic hosts, mostly fish; and two taxa, larvae of *Hysterothylacium cenotae* and few unidentified females and larvae of *Rhabdochona* sp. most likely mature in cichlids.

Ten larval taxa were identified as generalist (Table 1). Eight of them are allogenic, i. e. taxa that mature in and are transported by birds. And two larval nematodes *Spiroxys* sp. and *Falcaustra* sp. taxa that mature in and are transported by freshwater turtles (Moravec, 1998).

Two introduced species were identified, including the metacercariae of *Centrocestus formosanus* (Nishigori, 1924) and the Asian fish tapeworm *Schyzocotyle acheilognathi* (Yamaguti, 1934).

4. Discussion

The study results confirm that the parasitic helminths of freshwater fish identified from the upper basin of the Coatzacoalcos River are typical of Central American Neotropical fauna, as per earlier research (Salgado-Maldonado, 2008). Four helminth groups were identified: endemic species from the upper basin of the Coatzacoalcos River, autogenic Central American species with a regional distribution, generalist allogenic species with a wide distribution, and anthropogenic introduced species.

Two nematode species endemic to the Coatzacoalcos River were identified that are new to science and are undescribed: *Rhabdochona* sp. which parasitizes the cichlid *Theraps irregularis*, and Philometridae gen. sp. which infects the eel *Ophisternon aenigmaticum*. Helminths that parasitize the cichlids of Mexico and Central America have been studied extensively (Salgado-Maldonado et al., 1997; Vidal-Martínez et al., 2001; Salgado-Maldonado, 2006, 2008). We have also examined *O. aenigmaticum* specimens from the Papaloapan river basin (Salgado-Maldonado et al., 2005), and from freshwater bodies of Chiapas ((Salgado-Maldonado et al., 2011; Salgado-Maldonado et al., 2011). Therefore, the current findings regarding these two new nematodes suggest that these species are endemic. The acanthocephalan, *Neoechinorhynchus* (*Neoechinorhynchus*) *chimalapasensis*, which infects *Awaous banana*, a gobiid fish (Gobiidae), is a third endemic species found in the Coatzacoalcos River. However, helminths of gobiid fish from Mexico and Central America have not been studied extensively: only a small number of specimens of three gobiid species have been examined for helminths to date (Salgado-Maldonado, 2006). Therefore, the endemicity of *N.* (*N.*) *chimalapasensis* should be confirmed by examining more gobiid populations that inhabit different Central American water bodies.

The group of generalist helminth species comprises five larval forms that use fish as intermediate and/or paratenic hosts, and later complete their life cycle in ichthyophagous birds, meaning they are allogenic species. In contrast, the group of Central American helminths found in the upper basin of the Coatzacoalcos River comprises 23 species. These Neotropical species have been previously recovered from the Isthmus of Tehuantepec south of the southern Mexican border (Salgado-Maldonado, 2008). The parasitic helminths of freshwater fish from the upper basin of the Coatzacoalcos River are therefore considered an integral part of the diversified helminth fauna of Central American freshwater fishes. All these species are autogenic, complete their life cycle in aquatic environments, reach their sexual maturity in aquatic hosts, and are distributed alongside their host fish. This group of autogenic species are highly distinctive (see below) and can be clearly distinguished from the Nearctic North American and Neotropical South American faunas.

We argue that this particular group of autogenic adult helminths identify a fauna typical of Central America, and illustrate its particular, distinctive character. We have excluded allogenic larval species from this characterisation as autogenic and allogenic species are biologically significantly different, and follow different ecological and evolutionary pathways (Kennedy, 1998; Criscione and Blouin, 2004; Fellis and Esch, 2005). The composition of the autogenic helminth species parasitizing the fishes in a particular region directly depends on the composition of the fish community of that region. This is because the dispersal capacity of the invertebrate intermediate hosts is usually lower than that of the definitive host fishes (Fellis and Esch, 2005; Karvonen et al., 2005). Therefore, these autogenic species might be an integral and consistent component of this region's ecological community (Karvonen and Valtonen, 2004). In contrast, the presence of allogenic species is likely to depend more on the geographical position of the water bodies, such as in relation to bird migration routes, potentially resulting in a less predictable distribution. Therefore, allogenic species may not be a consistent component of the parasite community (Karvonen and Valtonen, 2004). Allogenic species (with larvae that infect fishes) can reach distant, unconnected, and unrelated localities via migration of birds, their definitive hosts (Kennedy, 1998). Furthermore, allogenic species parasitize a number of host species in order to reach their definitive host through predation. They infect as many small fishes as possible, regardless of species, arguably because this increases their likelihood of reaching birds, which are the definitive and preferred hosts, regardless of bird size (Criscione and Blouin, 2004; Fellis and Esch, 2005). Therefore, given their high dispersal capacity and virtual absence of specificity to intermediate and paratenic host fish, allogenic helminths do not constitute a distinctive and consistent component of the parasitic helminth fauna of fish in a given locality.

The alien helminths identified in this study, the metacercariae of *Centrocestus formosanus* and the Asian fish tapeworm *Schyzocotyle acheilognathi*, are a major issue for conservation of native fish populations in the Coatzacoalcos river basin. The metacercariae of *C. formosanus* were first introduced in Mexico and are distributed together with the snail *Melanoides tuberculata* (Scholz and Salgado-Maldonado, 2000). *Schyzocotyle acheilognathi* is extensively distributed throughout Mexico due to the repeated introduction of Asian carp species (especially *Ctenopharyngodon idella*), which are widely used in aquaculture (Salgado-Maldonado and Pineda-López, 2003). Several studies have reported on the numerous host records, particularly in Mexico, and the pathology and damage caused to the host by *C. formosanus* (Scholz and

Salgado-Maldonado, 2000; Mitchell et al., 2005; Tolley-Jordan and Chadwick, 2012; McDermott et al., 2014) and *S. acheilognathi* (Salgado-Maldonado and Pineda-López, 2003; Kuchta et al., 2018).

The current knowledge regarding helminth parasites of freshwater fish from the Neotropical region of Mexico and Central America constitutes a solid basis for predicting which parasite species can be found parasitizing fishes in a given geographical area. This is because the local parasite fauna constitutes a subsample of the regional fauna (Holmes, 1990; Poulin and Morand, 2004), while the composition of the local and regional helminth fauna directly depends on fish fauna composition (Dogiel, 1961; Chubb, 1963; Wootten, 1973; Salgado-Maldonado et al., 2005; Salgado-Maldonado, 2006, 2008). As described in northern temperate environments (Dogiel, 1961; Chubb, 1963; Halvorsen, 1971; Choudhury and Dick, 1998), tropical freshwater fishes are parasitized by a suite of helminth species that are exclusive to particular fish families. These helminth species are distributed with and dispersed alongside the fish of these particular families (Salgado-Maldonado et al., 2005; Salgado-Maldonado, 2006, 2008; Choudhury et al., 2017). These characteristics allow a certain degree of predictability: the local fish fauna can help predict the most probable helminth species in an area. Moreover, new records of known helminth species or new species that are not yet taxonomically described, including endemic species, may be found when examining fish families that have previously been insufficiently studied or that are found in isolated water bodies.

The information in this study provides a snapshot of presence, abundance, and spatial distribution of the helminth fauna of fishes in the upper Coatzacolacos River basin. These data are essential for phylogenetic and ecological hypothesis planning and future biogeographical studies. Moreover, understanding a species' geographical distribution is the first step in undertaking effective conservation actions. Arguably, these kinds of investigation produce data that could be used to provide an assessment of human environmental impacts, or to generate data for public awareness of conservation objectives. For example, host parasite systems knowledge can be used to indicate changes in biodiversity status (Vidal-Martínez et al., 2009). Knowledge of fishes and other aquatic organisms in relation to parasite species can be used to control production of aquatic organisms or exploitation of natural resources. Likewise, environmental impact assessments could better assess the likelihood that an aquacultural development will affect natural populations, native species, or general biodiversity by accidently introducing exotic, undesirable alien parasite species to the natural fish population (see Salgado-Maldonado and Pineda-López, 2003; Salgado-Maldonado and Rubio-Godoy, 2014; Velázquez-Velázquez et al., 2015 for examples). Surveys and species lists are one of the few tools at the disposal of regulatory agencies and stakeholders who seek to protect the public and their goods or values by limiting the adverse environmental impacts of development. The presence of healthy ecosystems, including healthy host-parasite systems, should be taken into account when determining such impacts. Therefore, such surveys and data are considered important to fulfilling political, social, and scientific needs.

Declaration of competing interest

None.

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