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Helminth parasites in freshwater fish from the Papaloapan river basin, Mexico

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Abstract A checklist based on previously published records and original data is presented for the helminth parasites reported in 35 fish species from nine families from the Río Papaloapan basin, east Mexico. The checklist contains 85 taxa from 39 helminth families. Trematodes and nematodes were the most abundant taxonomic groups. The helminth fauna in the fish of the Papaloapan River basin predominantly consists of Neotropical species that are largely autogenic. The introduced species *Centrocestus formosanus* was the most widely distributed helminth, infecting 16 host species. Ten of the recorded helminth species have only been found in fish from the Papaloapan. This inventory contributes 157 new host records, and reports the presence of 30 helminth species in the Papaloapan for the first time. This inventory shows the richness of helminth parasite species in the fish of the Papaloapan River basin in comparison with the other hydrological basins in Mexico. It also demonstrates that this fauna is typically Neotropical and quite similar to that from the neighboring basins of the Grijalva–Usumacinta system and the Yucatan Peninsula. The data also suggest highly effective transmission between environments within the same basin and that the regional parasite fauna is strongly influenced by fish community composition.

Introduction

Recent research on the helminth parasites of freshwater fish in Mexico's hydrological basins has increased knowledge of the helminth fauna in these areas. To date, helminth parasite inventories have been published for the freshwater bodies of the Yucatán Peninsula (Moravec et al. 1995a, b; Scholz et al. 1995a, b, 1996b; Salgado-Maldonado et al. 1997; Mendoza-Franco et al. 1999; Kritsky et al. 2000), the Balsas (Salgado-Maldonado et al. 2001a), Lerma and Santiago (Salgado-Maldonado et al. 2001b) and Pánuco river basins (Salgado-Maldonado et al. 2004a), the Ayuquila River in the Sierra de Manantlán, Jalisco (Salgado-Maldonado et al. 2004b), water bodies in the Sierra Madre Oriental (Aguilar-Aguilar et al. 2004), and the lowlands in the state of Tabasco drained by the Grijalva–Usumacinta system (Salgado-Maldonado et al. 2005). Helminth inventories have also been published for some fish families, particularly for the cichlids (Salgado-Maldonado et al. 1997; Vidal-Martínez et al. 2001a), poecilids and goodeids (Pineda-López et al. 2005). Information on the nematodes of freshwater fish in the Neotropics has been addressed by Moravec (1998). Two zoogeographic treatments aid in systematizing the knowledge generated on the distribution, richness and endemic areas of helminths in freshwater fish in Mexico (Vidal-Martínez and Kennedy 2000; Aguilar-Aguilar et al. 2003b). Notwithstanding, the helminth fauna data for fish from the Papaloapan River, one of the largest and most important watercourses in Mexico, are still scattered, mostly in taxonomic publications.

The Papaloapan River basin is the second largest hydrological basin in Mexico and is considered the northern limit of the Neotropical Region. It includes a 46,517 km² area in the states of Veracruz, Oaxaca and Puebla (17°N–19°N; 95°W–97°40'W) (Revel-Mouroz 1980). The rivers feeding the Papaloapan generally flow to the east. These tributaries include the Río Cajones,

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Río de la Lana, Río Grande–Santo Domingo, Río San Juan, Río Tesechoacán, Río Tonto, Río Valle Nacional and Río Jaltepec. The Papaloapan flows into the Gulf of Mexico at the Laguna de Alvarado in the state of Veracruz. The Papaloapan basin can be divided into two sections: the Upper Papaloapan, which includes waters above 1,000 m asl, and the Lower Papaloapan. Los Tuxtlas area in Veracruz, forms part of the Lower Papaloapan, even though it does have areas higher than 1,000 m asl.

A total of 44 fish species are known in the lotic and lentic waters of the Papaloapan River basin of which ten are endemic to it (Sevilla 1977; Miller 1986; Miller and Smith 1986; Espinosa-Pérez et al. 1998). It is an ichthyologic fauna characteristic of lowland tropical Mexico, and towards the east, it mixes with the ichthyologic fauna of the Usumacinta River.

Studies of the parasites of the fish in the Papaloapan basin began in 1954 and are largely taxonomic treatments concentrating mostly on fish in the Los Tuxtlas area and particularly Catemaco Lake, Veracruz (Caballero and Winter 1954; Lamothe-Argumedo 1974, 1977; Lamothe-Argumedo and Ponciano-Rodríguez 1986; Caballero-Deloya 1977; Salgado-Maldonado 1978; Salgado-Maldonado et al. 1992, 1998; García-Prieto 1990; García-Prieto et al. 1996; Pérez et al. 1992; Jiménez-García 1993; Moravec 1998; Moravec et al. 1998, 2000, 2002a, b; Caspeta-Mandujano et al. 1999, 2000a, b; Scholz and Salgado-Maldonado 2000, 2001; Scholz et al. 2001b; Páez-Rodríguez et al. 2002; Aguilar-Aguilar et al. 2003a; Mendoza-Franco et al. 2003b). More recent studies addressing the role of freshwater fishes as transmitters of the human gnathostomiasis have been done in the Temascal Reservoir, Oaxaca (Almeyda-Artigas 1991; Almeyda-Artigas et al. 1995; Lamothe-Argumedo 1977; Lamothe-Argumedo et al. 1989). No other water bodies in this basin have been studied. In response, the present study brings together previously published information and provides new data derived from our own research to update the knowledge of the helminth parasites of the fish of the Papaloapan River basin.

Materials and methods

A review of the literature dealing with freshwater fish helminth parasites in the Papaloapan River basin was made. In addition, a total of 1,088 fish was collected from 25 sites (Table 1, Fig. 1) in the Papaloapan River basin between March 1999 and July 2002. The following fish species were examined (family and sample size, *n*, follow each taxon parenthetically, taxa marked * are endemic to the Río Papaloapan basin as stated by Miller 1986; Miller and Smith 1986; Espinosa-Pérez et al. 1993): *Agonostomus monticola* (Mugilidae, 17); *Astyanax aeneus* (Characidae, 125); **Bramocharax caballeroi* (Characidae, 10); **Atherinella ammophila* (Atherinidae, 9); **Cichlasoma ellioti* (Cichlidae, 2); **C. fenestratum* (Cichlidae, 67); *C. octofasciatum* (Cichlidae, 4), *C. rob-*

ertsoni (Cichlidae, 3); *C. urophthalmus* (Cichlidae, 10); *Cichlasoma* sp. (Cichlidae, 27); *Oreochromis* sp. (Cichlidae, 3); *Petenia splendida* (Cichlidae, 1); *Eleotris* sp. (Eleotridae, 6); *Dormitator maculatus* (Eleotridae, 47); *Gobiomorus dormitor* (Eleotrididae, 50); *Dorosoma anale* (Clupeidae, 2), *D. petenense* (Clupeidae, 16); *Heterandria bimaculata* (Poeciliidae, 70); **Poecilia catemacoensis* (Poeciliidae, 25); *P. mexicana* (Poeciliidae, 319); *P. reticulata* (Poeciliidae, 34); **Poeciliopsis catemaco* (Poeciliidae, 24); *Poeciliopsis gracilis* (Poeciliidae, 35); *Poeciliopsis* sp. (Poeciliidae, 13); *Xiphophorus helleri* (Poeciliidae, 68); *Ophisternon aenigmaticum* (Synbranchidae, 42); *Rhamdia guatemalensis* (Pimelodidae, 48); *Sycidium gymnogaster* (Gobiidae, 11). Fish sample size per site are given in Table 2. We sampled localities in the Upper Papaloapan; including irrigation channels, streams and secondary rivers, and localities in the main Río Grande and Río Valle Nacional. Sampling localities of the Lower Papaloapan include streams and large rivers' tributaries to the main Papaloapan course. The principal trend of the Río Papaloapan was sampled near the Tlacotalpan village. Several streams and lakes at Los Tuxtlas region were also sampled (Table 1, Fig. 1).

Fish at each site were captured using a DC Backpack Electrofishing device, using gill nets, or by angling. Captured fish were taken alive to the laboratory and were examined within 24 h using standard procedures. A complete examination for helminth parasites was done of each specimen. External surfaces including scales, skin, and fins were examined for ectoparasites using a stereomicroscope. Gills arches were examined individually. Examination for monogeneans was done immediately after the fish were taken out of water. The buccal cavity, opercula, and eyes were examined separately. The external surfaces of the internal organs (heart, liver, spleen, gall bladder, digestive tract, gonads, swim bladder and kidney, as well as the entire body cavity and mesentery) were inspected for free or encapsulated parasites, and then separated and examined individually. The intestine was opened longitudinally. The liver, spleen, kidney, and heart were compressed between glass plates and were examined for parasites. The body musculature was removed from the vertebral column, the skin removed from the fillets, and the fillets compressed between glass plates and inspected for helminths using a stereomicroscope. All collected helminths were sorted by taxon, cleaned and counted by organ. Trematodes (adult and metacercariae), monogeneans, cestodes (adults and metacestodes), and nematodes were fixed in hot 4% formalin. Acanthocephalans were placed in distilled water, refrigerated overnight (6–12 h) to evert the proboscis, and then fixed in hot 4% formalin. Trematodes, monogeneans, cestodes, and acanthocephalans were stained with Mayer's paracarmine or Ehrlich's haematoxylin, dehydrated using a graded alcohol series, cleared in methyl salicylate, and mounted whole. To study sclerotized parts, several specimens of each species of monogenean were fixed following Malmberg's semipermanent mount method (see Ergens 1969; Vidal-Martínez

Table 1 Codes and features of the localities sampled or reported in the literature from which hosts were collected (codes identify fish collections sites in Fig. 1)

Code (Fig. 1)	Locality name (habitat type)	State (coordinates)
	Upper Papaloapan	
(1)	Ajalpan (irrigation channel)	Puebla (18°24'22"N, 97°16'21"W)
(2)	Calipán (irrigation channel)	Puebla (18°17'31"N, 97°09'45"W)
(3)	Santa María Tecomavaca (stream)	Oaxaca (17°56'47"N, 97°01'42"W)
(4)	Santiago Dominguillo (stream)	Oaxaca (17°41'16"N, 96°56'02"W)
(5)	Río Grande at Guelatao	Oaxaca (17°18'26"N, 96°30'38"W)
(6)	Río Grande at San José del Chilar	Oaxaca (17°46'06"N, 96°57'16"W)
(7)	Puente Valle Nacional	Oaxaca (17°46'15"N, 96°18'33"W)
(8)	San Juan Valle Nacional	Oaxaca (17°46'15"N, 96°18'33"W)
	Lower Papaloapan	
	Arroyo San Juan Evangelista (stream)	Oaxaca (not positioned)
	Arroyo Agrio (stream)	Oaxaca (not positioned)
(9)	Arroyo San Juan Bautista (stream)	Oaxaca (17°43'13"N, 96°18'46"W)
(10)	Presa Temascal (reservoir)	Oaxaca (21°18'N, 96°04'W)
(11)	Mouth of the Río Papaloapan at lagoon Alvarado	Veracruz (18°45'N, 95°49'W)
(12)	Tlacotalpan village	Veracruz (18°36'N, 95°39'W)
(13)	Río Tesechoacán	Veracruz (18°36'N, 95°39'W)
(14)	Río San Juan	Veracruz (18°36'N, 95°39'W)
(15)	El Saltillo – Taller (stream)	Oaxaca (18°33'55"N, 95°25'44"W)
(16)	Cascada El Saltillo (water fall)	Oaxaca (18°31'N, 95°25'W)
	Río Frío	Veracruz (not positioned)
	Los Tuxtlas region	
(17)	Arroyo Balzapote	Veracruz (18°40'N, 95°10'W)
(18)	Río La Palma	Veracruz (18°33'21"N, 95°02'59"W)
(19)	Río Máquinas	Veracruz (18°36'41"N, 95°06'27"W)
(20)	Arroyo La Basura	Veracruz (18°31'27"N, 95°02'54"W)
(21)	Lake La Escondida	Veracruz (18°38'09"N, 95°07'28"W)
(22)	Río San Joaquín (river)	Veracruz (18°26'27"N, 95°09'44"W)
(23)	Lake Catemaco	Veracruz (18°25'N, 95°07'W)

et al. 2001a). Nematodes were cleared with glycerin for light microscopy and were stored in 70% ethanol. Voucher specimens of all taxa have been deposited in the National Helminth Collection (Colección Nacional de Helmintos CNHE), Institute of Biology, National Autonomous University of Mexico (UNAM), Mexico City. Infection parameters that have been utilized are those proposed by Bush et al. (1997), that is, prevalence (% infected) and mean intensity of infection (number of parasites per infected fish).

Results

A total of 85 taxa from 39 helminth families in 35 fish species from nine families was recorded. Table 2 presents the helminths, their hosts and collection locations as well as prevalence and mean intensity data for each helminth species. This inventory contributes 157 new host records and reports the presence of 30 helminth species in the Papaloapan for the first time.

In terms of the number of taxa recovered from the examined fish, trematodes were the most abundant group with 24 metacercariae and 9 adult species. The species *Stunkardiella minima* and *Oligogonotylus manteri* were recorded as both metacercariae and as adults (Table 2). Nematodes were also numerous and included 17 adults and 8 larvae. Monogenean fauna was well represented with data for 13 taxa. Cestodes and

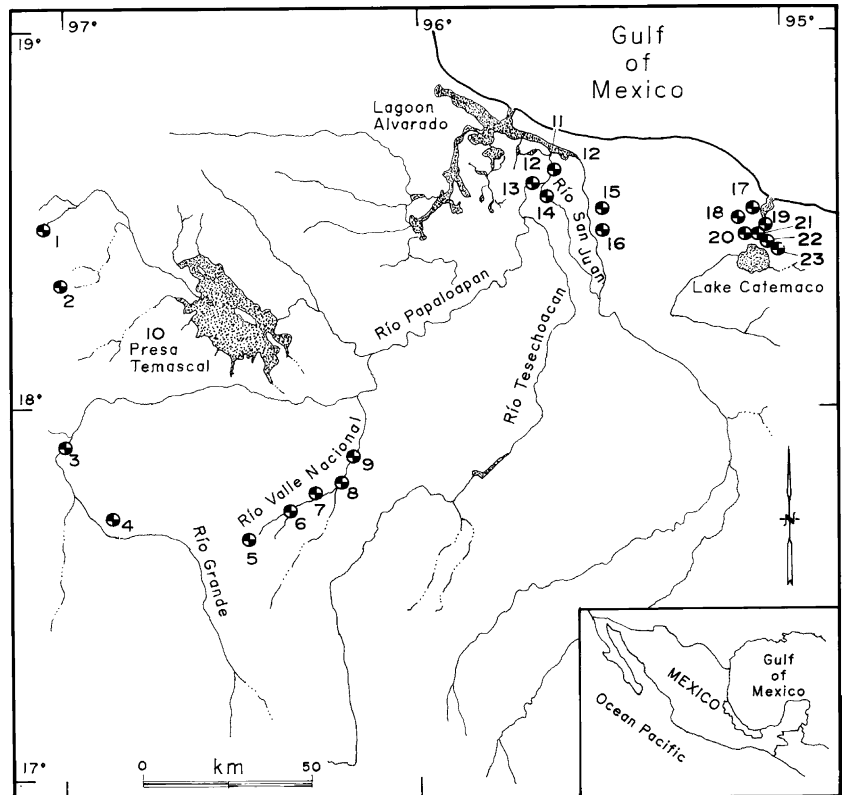
acanthocephalans had eight nominal taxa each, making them the least numerous of the recorded helminths.

Of the 85 recorded species, 58 (68%) are Neotropical, only three could be distinguished as Nearctic, four have broad geographic distribution and one is an introduced species. There was insufficient information to place the remaining taxa into one of these categories. A total of 28 (33%) of the 85 species are allogenic, which implies that they mature in birds and are dispersed by these definitive hosts; 57 (67%) are autogenic, which implies that they mature in fish and its entire life cycle is completed within an aquatic ecosystem (Esch et al. 1988) (Table 2).

The introduced species *Centrocestus formosanus* was the most widely distributed helminth among the examined hosts; metacercariae of this species were found infecting 16 host species. The other frequent helminth species were the metacercariae of *Uvulifer ambloplitis*, found infecting 13 fish species; metacercariae of *Asco-cotyle* (*Asco-cotyle*) *tenuicollis*, recovered from 12 host species; metacercariae of *Clinostomum complanatum* found in nine host species; and adults of the trematode *Crassicutis cichlasomae*, also found in nine host species. Larvae of the nematode *Spiroxys* sp. were recovered from 14 fish species and those of *Contra-caecum* sp. were found in 13 fish species (Table 2).

In some cases very few hosts were examined; however, the data still support the conclusion that the parasite transmission dynamic in this basin is generally

Fig. 1 The Río Papaloapan drainage basin of east Mexico, showing the fish collection sites (codes in Table 1)



intense and effective. This is shown by the high prevalence values for the different (adult and metacercariae) trematode species. For example, the prevalence of adult *Stunkardiella minima* in *Rhamdia guatemalensis* remained above 20%, and that of its metacercariae in different host species is even higher. Another instance is the prevalence of *Creptotrema agonostomi* in *Agonostomus monticola*, which was above 30%. The prevalence of the monogenean species also shows their high frequency in the Papaloapan basin. Though the metacestodes are less frequent, both *Monticellia ophisterni* and *Proteocephalus brooksi* had high prevalences (Table 2). Generally, the nematodes and acanthocephalans had more variable prevalences, though the capillariids and cystidicolids, as well as *Rhabdochona kidderi* and *Neoechinorhynchus golvani*, are very frequent in the fish of this basin.

The host species with the highest number of associated helminths was *Rhamdia guatemalensis* with 25 helminth taxa. It is followed by *Dormitator maculatus* with 22 taxa and *Cichlasoma fenestratum*, *Gobiomorus dormitor* and *Poecilia mexicana*, all with 21 taxa. The helminth communities in the remaining host species had lower richness. Of all the examined fish species, only the gobiid *Sycidium gymnogaster* ($n=11$) was parasite-free. Species richness per fish in the Upper Papaloapan (locations above 1,000 m) was lower than in the Lower Papaloapan. To date, only ten nominal helminth species in this inventory have been recorded in the fish of the Papaloapan basin: *Saccoceilioides chauhani* and *Anacanthocotyle anacanthocotyle* in *Astyanax fasciatus*;

Caballerorhynchus lamothei in *Ictalurus meridionalis*; *Spinitectus mexicanus* in *Heterandria bimaculata*; *Cucullanus mexicanus* and *Proteocephalus brooksi* in *Rhamdia guatemalensis*; and *Monticellia ophisterni*, *Pseudocapillaria (Ichthyocapillaria) ophisterni*, *Philometra ophisterni*, and *Gibsonnema ophisterni* all in *Ophisternon aenigmaticum*.

Discussion

Data for 35 fish species are included in this inventory, including four species of tilapia (*Oreochromis* spp.) and *Petenia splendida*, which are introduced into the Papaloapan River basin. A total of 31 of the 44 fish species recorded in the Papaloapan were examined, including 7 of its 15 endemic species. It is likely that the number of parasites reported in *Atherinella amnophila*, *Cichlasoma ellioti*, *C. octofasciatum*, *Petenia splendida*, *Eleotris* sp., and *Sycidium gymnogaster* is higher than that reported here, as very few individuals were examined for these host species. Host species from the main fish families in the Papaloapan were examined with the exception of Lepisosteidae, Cyprinidae, Catostomidae and Cyprinodontidae. The endemic species not examined in this study are *Atractosteus spatula*, *Hybopsis moralesi*, *Rivulus robustus*, *R. tenuis*, *Heterandria jonesi*, *Atherinella marvelae*, *A. sallei*, *Priapella bonita*, and *Rhamdia reddelli*. Ten of the 36 examined fish species had not been previously studied for parasites.

Table 2 Host association, number of hosts examined (N), prevalence (P), and mean intensity (MI) of helminth parasites collected from 35 fish species from Río Papaloapan basin, Mexico. ^aNew host record; ^bNew locality record (recorded first time in the Río Papaloapan basin). (Infection sites: *Bc* Body cavity; *Br* Brain; *Ey* eyes; *Fa* Fat; *Fi* Fins; *Ga* inside gill arches; *Gb* Gall bladder; *Gc* Gill cavity; *Gi* Gills; *Go* Gonads; *He* Heart; *In* Intestine (lumen); *Iw* Intestinal wall (serosa); *Ki* Kidney; *Li* Liver; *Me* Mesentery; *Mo* Mouth; *Mu* Muscles; *Sc* Scales of lateral line; *Sk* Skin; *Sp* Spleen; *St* Stomach; *Sw* Stomach wall; *Ub* Urinary bladder). Status: *Na* Nearctic; *Ne* Neotropical; *Al* Allogenic; *Au* Autogenic; *In* Introduced; *WW* world wide distributed

Helminth [Status]	Host	Infection sites	Locality	N	P(%)	MI	Reference
Adult Trematoda							
Acanthostomidae							
<i>Stunkardiella minima</i> (Stunkard 1938) [Ne, Au]	<i>Rhanchia guatemalensis</i>	In	Lago de Catemaco	1	100/9		Lamothe-Argumedo and Ponciano-Rodríguez 1986
		In	Lago de Catemaco	51	21.5/23.3		Pérez et al. 1992
		In	Lago de Catemaco	4	25/8		Present work
		In	San Juan Valle Nacional	3	100/1.3		Present work
		In	Puente Valle Nacional	11	27.3/8.7		Present work
		In	Tlacotalpan	8	25/3		Present work
		In	Río San Juan, Tlacotalpan	5	40/11		Present work
Allocreadidae							
<i>Creptotrema agonostomi</i> Salgado-Maldonado, Cabañas-Carranza and Caspeta-Mandujano 1998 [Ne, Au]	<i>Agonostomus monticola</i>	In	Río La Palma	9	77.8/48		Salgado-Maldonado et al. 1998
		In	Río La Palma	3	33.3/12		Present work
		In	Arroyo Balzapote	7	71.4/36.6		Present work
		In	Río Máquinas	15	33.3/1.8		Salgado-Maldonado et al. 1998
Apocreadidae							
<i>Crassicutis cichlasomae</i> Manter 1936 [Ne, Au]	<i>Cichlasoma elioti</i> ^a <i>Cichlasoma jenesstratum</i>	In	Arroyo San Juan Evangelista	2	50/2		Present work
		In	Lago de Catemaco	30	50/11.06		Jiménez-García 1993
		In	Lago de Catemaco	18	55.6/26.6		Present work
		In	Río Máquinas	14	78.6/7.9		Present work
		In	Arroyo Balzapote	3	100/19		Present work
		In	Lago La Escondida	12	66.7/4.9		Present work
		In	Río La Palma	2	50/11		Present work
	<i>Cichlasoma octofasciatum</i> ^a	In	Tlacotalpan	1	100/5		Present work
	<i>Cichlasoma roberisoni</i> ^a	In	Arroyo San Juan Evangelista	3	100/2		Present work
	<i>Cichlasoma urophthalmus</i>	In	Arroyo San Juan Evangelista	3	33.3/2		Present work
	<i>Cichlasoma</i> sp.	In	Tlacotalpan	10	20/6		Present work
	<i>Dorosoma petenense</i> ^a	In	San Juan Valle Nacional	8	12.5/1		Present work
	<i>Oreochromis</i> sp.	In	Lago de Catemaco	1	100/121		Present work
		In	Lago de Catemaco	1	50/17		Present work
Cryptogonimidae							
<i>Oligogonorylus manteri</i> Watson 1976 [Ne, Au]	<i>Cichlasoma octofasciatum</i> ^a <i>Cichlasoma urophthalmus</i>	In	Tlacotalpan	1	100/1		Present work
		In	Tlacotalpan	10	70/5.3		Present work
Derogenidae							
<i>Genarchella isabellae</i> (Lamothe-Argumedo 1977) [Ne, Au]	<i>Rhanchia guatemalensis</i> <i>Cichlasoma jenesstratum</i>	In	Lago de Catemaco	ND	ND		Lamothe-Argumedo 1977
		St	Lago de Catemaco	30	23/2		Jiménez-García 1993
		In		18	11.1/2		Present work
	<i>Gobionorus dormitor</i> ^a	In	Río La Palma	2	100/6.5		Present work
	<i>Ophisternon aenigmaticum</i> ^a	In	Tlacotalpan	24	4.2/2		Present work
		In	Río Tesechoacán	10	40/2.2		Present work

<i>Gobiomorus dormito</i> ^a	He, In, Li, Me, St	Tlactotalpan	24	20.8/8	Present work
<i>Poecilia mexicana</i> ^a	Ey, Bc	Lago La Escondida	7	57.1/5.7	Present work
	Ey	Río La Palma	25	4/1	Present work
<i>Rhamdia guatemalensis</i>	Gc, Gi, Mu	Lago de Catemaco	51	27.4/24.3	Pérez et al. 1992
	Fi	Lago de Catemaco	4	25/1	Present work
	Fi, Gi, Me, Mo, Mu	Puente Valle Nacional	11	27.3/11	Present work
	Bc, Ey, Gi, Mu	Arroyo San Juan Bautista	6	16.7/25	Present work
	Bc, Me	Tlactotalpan	8	50/6.5	Present work
	Bc	Arroyo San Juan Evangelista	9	11.1/1	Present work
<i>Xiphophorus helleri</i> ^a	Bc	Arroyo Balzapote	8	12.5/1	Present work
Cryptogonimidae	In	Lago de Catemaco	ND	ND	Jiménez-García 1993
<i>Oligogonylus manteri</i>					
Watson 1976					
[Ne, Au]					
Remarks: Scholz et al. (1994, 1996) documented these metacercariae previously identified as <i>Echinochasmus zubeclakhaname</i> by Jiménez-García, 1993 to be <i>O. manteri</i>					
Diplostomidae					
<i>Diplostomum compactum</i>					
(Lutz 1928)					
[Ne, Al]					
<i>Diplostomum</i> sp.					
[?, Al]					
<i>Cichlasoma urophthalmus</i>	Ey	Tlactotalpan	10	10/1	Present work
<i>Rhamdia guatemalensis</i>	Ey	Tlactotalpan	8	37.5/2	Present work
	Ey	Lago de Catemaco	51	1.9/1	Pérez et al. 1992
<i>Cichlasoma aureum</i>	Ey	Laguna Pipi, Tlactotalpan	ND	ND	Caballero and Winter 1954
<i>Astyanax aeneus</i> ^a	Gc	Arroyo San Juan Bautista	18	5.6/2	Present work
	Ey	Puente Valle Nacional	18	5.6/1	Present work
	Ey	Lago de Catemaco	6	16.7/9	Present work
<i>Cichlasoma fenestratum</i> ^a	Ey	Lago La Escondida	7	14.3/1	Present work
<i>Poecilia mexicana</i> ^a	Me	Lago de Catemaco	25	8/4.5	Present work
<i>Poecilia catemacensis</i>	Me	Arroyo San Juan Evangelista	9	11.1/1	Present work
<i>Rhamdia guatemalensis</i>	Br, Ey, Fi, Gi, Mu	Lago de Catemaco	30	93/71.3	Jiménez-García 1993
<i>Cichlasoma fenestratum</i>	Gi, Me	Lago de Catemaco	18	22.2/1.2	Present work
<i>Cichlasoma fenestratum</i>	Bc, Gi, Li, Me, Mu	Lago La Escondida	12	58.3/2.9	Present work
	Gc	Río Teschoacán	10	10/1	Present work
<i>Cichlasoma urophthalmus</i>	Li, Me	Santiago Domingullo	63	1.6/3	Present work
<i>Poecilia mexicana</i>	Me	Puente Valle Nacional	18	11.1/26.5	Present work
	Li	Arroyo San Juan Bautista	14	7.1/2	Present work
	Li, Me	Arroyo San Juan Evangelista	7	42.9/2	Present work
	Ey, Li, Mu	Río La Palma	25	20/4.6	Present work
		Lago de Catemaco	25	32/2.1	Present work
<i>Poecilia catemacensis</i> ^a	Gi	Lago de Catemaco	24	4.2/2	Present work
<i>Poeciliopsis catemaco</i> ^a	Fi, Gc, Gi	Lago de Catemaco	18	33.3/22.7	Present work
<i>Cichlasoma fenestratum</i> ^a	Gi	Río Máquinas	14	42.9/12.2	Present work
	Bc, Fi, Me	Lago La Escondida	12	83.3/27.9	Present work
	Ey	Río Teschoacán	36	2.8/6	Present work
<i>Dormitator maculatus</i> ^a	Me	Tlactotalpan	36	5.6/3	Present work
		Río Teschoacán	10	20/2.5	Present work
<i>Ophistiernon aenigmaticum</i> ^a	Gi	Lago de Catemaco	25	4/1	Present work
<i>Poecilia catemacensis</i> ^a	Fi	Arroyo Balzapote	7	14.3/1	Present work
<i>Agonostomus monticola</i> ^a	Fi	Río La Palma	2	50/2	Present work
<i>Astyanax aeneus</i> ^a	Fi	Río Grande, Guelatao	9	11.1/3	Present work
<i>Cichlasoma fenestratum</i> ^a	Fi	Lago La Escondida	12	8.3/1	Present work
	Me	Río La Palma	2	50/2	Present work
		Río Máquinas	5	20/1	Present work

Table 2 (Contd.)

Helminth [Status]	Host	Infection sites	Locality	N	P(%) / MI	Reference
	<i>Cichlasoma urophthalmus</i> ^a	Fi	Río Tesechoacán	10	60/5	Present work
	<i>Cichlasoma</i> sp.	Fi	Puente Valle Nacional	13	30.7/4.0	Present work
	<i>Cichlasoma</i> sp.	Gi	San Juan Valle Nacional	8	25/1	Present work
	<i>Dormitator maculatus</i> ^a	Fi, Mu, Sk	Tlacotalpan	36	11.1/16.3	Present work
	<i>Gobiomorus dormitor</i> ^a	Fi, Me	Tlacotalpan	6	50/2.7	Present work
	<i>Petenia splendida</i> ^a	Fi	Arroyo Balzapote	3	33.3/2	Present work
	<i>Poecilia mexicana</i> ^a	Fi	Tlacotalpan	1	100/10	Present work
	<i>Poecilia mexicana</i> ^a	Fi	Río La Palma	25	4/1	Present work
	<i>Poecilia mexicana</i> ^a	Fa, Fi	Arroyo Balzapote	27	7.4/1.5	Present work
	<i>Poecilopsis gracilis</i> ^a	Fi	Río Grande, San José del Chilar	10	20/24	Present work
	<i>Rhamdia guatemalensis</i> ^a	Fi	Tlacotalpan	8	12.5/1	Present work
	<i>Xiphophorus helleri</i> ^a		Río Máquinas	25	4/1	Present work
Echinostomatidae						
<i>Drepanocephalus</i> sp.			Lago de Catemaco	30	7/ND	Jiménez-García 1993
[Ne, AI]						
<i>Echinochasmus leopoldinae</i> ^b			Tlacotalpan	11	9.1/2857	Present work
Scholz, Ditrich and			Lago de Catemaco	1	100/2091	Present work
Vargas-Vázquez 1996						
[Ne, AI]			Tlacotalpan	1	100/1	Present work
	<i>Petenia splendida</i> ^a	Gi	Arroyo Balzapote	27	14.8/5.7	Present work
	<i>Poecilia mexicana</i> ^a					
Heterophyidae						
<i>Ascocotyle (Ascocotyle)</i>			Lago La Escondida	5	20/6	Present work
<i>tenuicollis</i>		He				
Price 1935						
[Ne, AI]						
	<i>Bramocharax caballeri</i>	He	Lago de Catemaco	ND	ND	Scholz et al. 2001a
	<i>Cichlasoma fenestratum</i> ^a	He	Lago de Catemaco	18	11.1/33.5	Present work
	<i>Dormitator maculatus</i> ^a	He	Tlacotalpan	36	2.8/8	Present work
	<i>Dorosoma petenense</i> ^a	He	Lago de Catemaco	1	100/69	Present work
	<i>Gobiomorus dormitor</i> ^a	He	Tlacotalpan	24	4.2/113	Present work
	<i>Heterandria binaculata</i> ^a	Gi	Arroyo Balzapote	15	6.7/4	Present work
	<i>Ophisternon aenigmaticum</i>	He	Lago de Catemaco	27	7.4/44.5	Present work
				ND	ND	Scholz et al. 2001a
	<i>Poecilia mexicana</i> ^a	He	Tlacotalpan	10	20/19.5	Present work
		He	El Saltillo - Taller	1	100/6	Present work
		Gi, He	Río La Palma	25	4/3	Present work
		Ga, Gi, He, Me	Arroyo Balzapote	27	44/31.8	Present work
	<i>Poecilia catemacensis</i>		Lago de Catemaco	ND	ND	Scholz et al. 2001a
	<i>Poecilopsis catemaco</i>		Lago de Catemaco	ND	ND	Scholz et al. 2001a
	<i>Xiphophorus helleri</i> ^a	Fa	Arroyo Balzapote	8	12.5/1	Present work
	<i>Poecilia mexicana</i>	Gi	Río Máquinas	25	4/1	Present work
		Me	Río Máquinas	ND	ND	Scholz et al. 2001a
		He, Me	Río Máquinas	8	50/28	Present work
	<i>Xiphophorus helleri</i> ^a	Me	Río Máquinas	25	56/24.6	Present work
	<i>Xiphophorus</i> sp.	Me	Río Máquinas	ND	ND	Scholz et al. 2001a
	<i>Poecilia mexicana</i>	Iw, Sw	Arroyo Balzapote	ND	ND	Scholz et al. 2001a
				27	11.1/1.7	Present work
	<i>Poecilia mexicana</i>	Gi	Arroyo Balzapote	ND	ND	Scholz et al. 2001a
	<i>Ascocotyle (Leightia) mcintoshii</i>					
Price 1936						
[Ne?, AI]						
	<i>Ascocotyle (Leightia) megaloccephala</i>					
Price 1932						
[Ne?, AI]						
	<i>Ascocotyle (Phagicola) diminuta</i>					

Table 2 (Contd.)

Helminth [Status]	Host	Infection sites	Locality	N	P(%) / MI	Reference
	<i>Poecilium reticulata</i> ^a	Gi	Ajalpan	34	41.2/3.2	Present work
	<i>Poecilium sphenops</i>	Gi	Río La Palma	19	11/20	Scholz and Salgado-Maldonado 2000
	<i>Xiphophorus helleri</i>	Gi	El Saltillo - Taller	5	20/15	Present work
		Gi	Cascada El Saltillo	2	100/141	Present work
		Gi	Río La Palma	13	7.7/1	Present work
		Gi	Arroyo Balzapote	8	37.5/83.7	Present work
		Gi	Río Máquinas	11	36/30	Scholz and Salgado-Maldonado 2000
	<i>Rhamdia guatemalensis</i> ^a	Gi	Arroyo San Juan Evangelista	9	33.3/34	Present work
	<i>Poecilium mexicana</i> ^a	Gi	Arroyo Balzapote	27	3.7/1	Present work
<i>Haplorchis pumilio</i> ^b (Looss 1896) [WW, AI]						
<i>Pygidiospis pindoramensis</i> (Travassos 1929) [Ne?, AI]		Ga, He Fa	Arroyo Balzapote	ND	ND	Scholz et al. 2001a
	<i>Xiphophorus helleri</i>	Ga, He	Arroyo Balzapote	27	3.7/1	Present work
	<i>Poecilium catemaconis</i>	Ga, He	Lago de Catemaco	ND	ND	Scholz et al. 2001a
Opisthorehiidae		Ga, He		ND	ND	Scholz et al. 2001a
<i>Cladocystis trifolium</i> (Braun 1901) [Ne, AI]	<i>Cichlasoma fenestratum</i>		Lago de Catemaco	30	83/9.2	Jiménez-García 1993
Proterodiplostomidae						
<i>Crocodilicola pseudostoma</i> (Willemoes-Suhm 1870) [Ne?, Au]	<i>Rhamdia guatemalensis</i>	Me Bc	Arroyo San Juan Evangelista Lago de Catemaco	9 51	11.1/1 23/15.9	Present work Pérez et al. 1992
Strigeidae						
[?, AI]	<i>Poecilium mexicana</i> ^a	Me	Río La Palma	25	8/1.5	Present work
<i>Apharyngostrigea</i> sp. ^b	<i>Dormitator maculatus</i> ^a	Fi	Tlacotalpan	36	5.6/6	Present work
<i>Cotylurus</i> sp. ^b [?, AI]	<i>Dormitator maculatus</i> ^a	Fi, Gi	Tlacotalpan	11	9.1/1	Present work
Monogenea						
Dactylogyridae						
<i>Ameloblastella chavarrii</i> ^b (Price 1938) [Ne, Au]	<i>Rhamdia guatemalensis</i>	Gi Gi Gi Gi	Tlacotalpan Arroyo San Juan Evangelista Lago de Catemaco Tlacotalpan	8 9 4 8	62.5/76.4 33.3/3.7 25/8 62.5/93.2	Present work Present work Present work Present work
<i>Aphanoblastella travassosi</i> ^b (Price 1938) [Ne, Au]	<i>Rhamdia guatemalensis</i>	Fi, Gi	Lago de Catemaco Arroyo Balzapote	4 4	75/11.7 50/6	Present work Mendoza-Franco et al. 2003b
Mendoza-Franco, Scholz and Cabañas-Carranza 2003 [Ne, Au]	<i>Gobiomorus dormitor</i>		Río Máquinas	1	100/6	Present work
			Arroyo Balzapote	3	33.3/6	Present work
			Tlacotalpan	9	67/28	Mendoza-Franco et al. 2003b
			Arroyo San Juan Bautista	4	50/3	Mendoza-Franco et al. 2003b
		Gi	Tlacotalpan	24	12.5/2	Present work
		Gi	Río La Palma	2	50/11	Present work
		Gi	Río Frio	1	100/4	Present work

Table 2 (Contd.)

Helminth [Status]	Host	Infection sites	Locality	N	P(%) / MI	Reference
[Ne, Au] <i>Proteocephalus brooksi</i>	<i>Rhamdia guatemalensis</i>	In	Lago de Catemaco	51	23/5.7	García-Prieto et al. 1996, Pérez et al. 1992 Present work
García-Prieto, Rodríguez and Pérez 1996 [Ne, Au]		In, Me	Tlacotalpan	8	87.5/16.7	
Metacestodes						
Dilepididae						
<i>Glossocercus auritus</i> (Rudolphi 1819) [Ne, Al]	<i>Poecilia catemacensis</i> <i>Poecilia mexicana</i>	Iw, Li, Me Li, Me Li, Me Me	Lago de Catemaco Lago La Escondida Lago La Escondida Puente Valle Nacional	23 2 7 18	4/1 100/1 28.6/1 5.6/4	Scholz and Salgado-Maldonado 2001 Scholz and Salgado-Maldonado 2001 Present work Present work
Dilepididae gen. sp. [?, Al]	<i>Dormitator maculatus</i> <i>Gobiomorus dormitor</i> <i>Rhamdia guatemalensis</i> <i>Astyanax aeneus</i>	Ki In, Mu	Tlacotalpan Tlacotalpan Arroyo San Juan Evangelista	36 24 9	5.6/1.5 12.5/1 11.1/2	Present work Present work Present work
Protocephalidea gen. sp. [?, ?]	<i>Ophisternon aenigmaticum</i>	Li, Me	Puente Valle Nacional	18	5.6/1	Present work
Tetraphyllidea gen. sp. [?, Au]	<i>Dormitator maculatus</i> <i>Gobiomorus dormitor</i>	In	Río Tesechoacán Tlacotalpan	10 36 6	90/17.9 2.8/1 16.7/1	Present work Present work Present work
Adult Nematoda						
Camallanidae						
<i>Procammallanus</i> (<i>Spirocammallanus</i>) sp. [Ne, Au]	<i>Dorosoma petenense</i>	In	Lago de Catemaco	15	6.7/1	Present work
<i>Procammallanus</i> (<i>Spirocammallanus</i>) <i>Neocaballeroi</i> (Caballero-Deloya 1977) [Ne, Au]	<i>Astyanax aeneus</i> <i>Rhamdia guatemalensis</i>	In Me In	Lago de Catemaco Lago de Catemaco Lago de Catemaco	ND 51 4 10 ND	ND 13.7/1.7 25/1 30/1.3 ND	Caballero-Deloya 1977 Pérez et al. 1992 Present work Present work Salgado-Maldonado et al. 1997
<i>Procammallanus</i> (<i>Spirocammallanus</i>) <i>rebecae</i> Andrade-Salas, Pineda-López and García-Magaña 1994 [Ne, Au]	<i>Cichlasoma fenestratum</i> <i>Cichlasoma</i> sp.	In In	Río de los Pescados Puente Valle Nacional	13	30.8/2.2	Present work
Capillariidae						
<i>Paracapillaria teixeiraifreitasi</i> (Caballero-Rodríguez 1971) [Ne, Au]	<i>Dormitator maculatus</i> <i>Gobiomorus dormitor</i>	In In In In In, St	Tlacotalpan Tlacotalpan Tlacotalpan Río Máquinas Lago de Catemaco	36 ND 24 10 10 27 10	2.8/6 ND 50/2.7 30/5.3 50/7 7.4/2.5 20/4	Present work Páez-Rodríguez et al. 2002 Present work Present work Moravec et al. 2000b Present work Present work
<i>Pseudocapillaria</i> (<i>Ichthyocapillaria</i>) <i>ophisterni</i> Moravec, Salgado-Maldonado and Jiménez-García 2000 [Ne, Au]	<i>Ophisternon aenigmaticum</i>	In	Lago de Catemaco	10	50/7	
Cucullanidae						
<i>Dichelyne mexicanus</i> Caspeta-Mandujano, Moravec and Salgado-Maldonado 1999 [Ne, Au]	<i>Agonostomus monticola</i>	In In	Río Tesechoacán Río Máquinas	9	11/3	Caspeta-Mandujano et al. 1999

<i>Cucullanus (Cucullanus) caballeri</i> Petter 1977 [Ne, Au]	<i>Gobiomorus dormitor</i> ^a	Tlacotalpan	6	16.7/11	Present work
	<i>Cichlasoma</i> sp. <i>Dormitator maculatus</i>	Río Máquinas Puente Valle Nacional Río La Palma	10 13 31	10/1 15.3/2.5 3.2/5	Present work Present work Caspeta-Mandujano et al. 1999
	<i>Rhamdia guatemalensis</i>	Río Máquinas Arroyo Balzapote Tlacotalpan	9 4 8	22/2 25/1 50/6.5	Caspeta-Mandujano et al. 1999 Caspeta-Mandujano et al. 1999 Present work
	<i>Rhamdia guatemalensis</i>	Arroyo San Juan Evangelista Valle Nacional Cascaida El Saltillo	9 14 1	11.1/1 14/2 100/1	Present work Caspeta-Mandujano et al. 2000a Caspeta-Mandujano et al. 2000a
<i>Cucullanus mexicanus</i> Caspeta-Mandujano, Moravec and Aguilar-Aguilar 2000a [Ne, Au]		Arroyo San Juan Bautista San Juan Valle Nacional Puente Valle Nacional	6 3 11	17/2 33/1 9/1	Caspeta-Mandujano et al. 2000a Present work Present work
	<i>Heterandria bimaculata</i>	Arroyo la Basura	11 16	73/3 77/5.5	Caspeta-Mandujano et al. 2000b Present work
	<i>Poecilia mexicana</i> ^a	Río Máquinas	10 10	70/1 10/1	Caspeta-Mandujano et al. 2000b Present work
	<i>Agonostomus monticola</i>	Río La Palma Río San Joaquín Río Frio Río San Joaquín	4 21 4 1	25/1 57.1/2 25/1 100/11	Caspeta-Mandujano et al. 2000b Present work Present work Present work
		Río Máquinas Arroyo Balzapote Río La Palma	18 7 2	16.7/1 100/8.6 100/6.5	Present work Present work Present work
<i>Spinitectus agonostomus</i> ^b Moravec and Barus 1971 [Ne, Au]		Río Máquinas Río Frio	3 1 4	66.7/1.5 100/5 100/11	Present work Present work Present work
	<i>Xiphophorus helleri</i>	Lago de Catemaco Arroyo Agrio	23 13	8.7/1.5 92.3/11	Montoya-Mendoza et al. 2004 Montoya-Mendoza et al. 2004
	<i>Ophisternon aenigmaticum</i>	Río Tesechoacán	9	55.5/2.6	Moravec et al. 2002a
	<i>Rhamdia guatemalensis</i>	Tlacotalpan Tlacotalpan	4 5	25/10 20/6	Moravec et al. 2002b Present work
	<i>Ophisternon aenigmaticum</i>	Río Tesechoacán	9	11/2	Moravec et al. 2002a
<i>Daniconematidae</i> <i>Mexiconema cichlasomae</i> Moravec, Vidal and Salgado-Maldonado 1992 [Ne, Au]					
<i>Philometridae</i> <i>Philometra ophisterni</i> Moravec, Salgado-Maldonado and Aguilar-Aguilar 2002 [Ne, Au]					
<i>Neophilometroides caudatus</i> (Moravec, Scholz and Vivas-Rodriguez 1995) [Ne, Au]					
<i>Quimperiidae</i> <i>Gibsonema ophisterni</i> (Moravec, Salgado-Maldonado and Aguilar-Aguilar 2002) [Ne, Au]					

Table 2 (Contd.)

Helminth [Status]	Host	Infection sites	Locality	N	P(%) MI	Reference
Rhabdochomidae						
<i>Rhabdochona kidderi</i> Pearse 1936 [Ne, Au]	<i>Cichlasoma fenestratum</i>	In	Lago de Catemaco	30	13/6.5	Jiménez-García 1993
		In	Río Máquinas	14	57.1/9.9	Present work
		In	Lago La Escondida	12	33.3/1.5	Present work
		In	Río La Palma	2	50/30	Present work
		In	Río Máquinas	5	60/1.7	Present work
	<i>Cichlasoma</i> sp.	In	Puente Valle Nacional	13	69.2/5.2	Present work
	<i>Cichlasoma</i> sp.	In	San Juan Valle Nacional	8	87.5/24.6	Present work
	<i>Dorosoma anale</i> ^a	In	Río Máquinas	6	100/6.5	Present work
	<i>Gobionorus dormitor</i> ^a		Tlacotalpan	6	16.7/8	Present work
			Arroyo Balzapote	3	66.6/2	Present work
		In	Río Máquinas	10	80/6.9	Present work
		In	Río La Palma	2	50/1	Present work
	<i>Poecilia mexicana</i> ^a	In	Río Máquinas	18	5.6/2	Present work
		In	Río La Palma	13	15.4/1.5	Present work
	<i>Eleotris</i> sp. ^a	In	Río Máquinas	6	100/6.5	Present work
	<i>Asyanax aeneus</i>	In	Río Grande, Guelatao	9	11.1/1	Present work
		In	Santiago Domingullo	13	15.4/1	Present work
<i>Rhabdochona mexicana</i> ^b Caspeta-Mandujano, Moravec and Salgado-Maldonado 2000 [Ne, Au]		In, Me	Arroyo San Juan Bautista	18	72.2/4.4	Present work
		In, Me	Puente Valle Nacional	18	50/4.6	Present work
			Lago La Escondida	5	20/2	Present work
Larval Nematodes						
Anisakidae						
<i>Contracaecum</i> sp. [WW, AI]	<i>Asyanax aeneus</i> ^a	Me	Arroyo San Juan Bautista	18	5.6/1	Present work
		Bc	El Saitillo - Taller	1	100/2	Present work
		In	Puente Valle Nacional	18	11.1/1	Present work
		Me	Arroyo San Juan Evangelista	7	14.3/1	Present work
			Arroyo San Juan Bautista	18	5.6/1	Present work
	<i>Bramocharax caballeri</i> ^a	In	Lago de Catemaco	10	20/1	Present work
	<i>Cichlasoma fenestratum</i> ^a	Bc, Go, Me	Lago de Catemaco	18	5.6/3	Present work
		Me, St	Lago La Escondida	12	16.7/2	Present work
	<i>Cichlasoma urophthalmus</i>	In	Tlacotalpan	10	100/1.8	Present work
	<i>Cichlasoma</i> sp.	In	Puente Valle Nacional	13	7.7/3	Present work
	<i>Dormitator maculatus</i> ^a	Me	Tlacotalpan	11	18.2/1	Present work
	<i>Dorosoma anale</i> ^a	Me	Tlacotalpan	2	50/60	Present work
	<i>Gobionorus dormitor</i>	Me	Tlacotalpan	24	ND	Páez-Rodríguez et al. 2002
		Me	Tlacotalpan	24	29.2/4.1	Present work
	<i>Heterandria bimaculata</i> ^a	Me	Arroyo San Juan Evangelista	2	50/1	Present work
	<i>Ophisternon aenigmaticum</i> ^a	Me	Lago de Catemaco	27	11.1/1	Present work
		In, Me	Tlacotalpan	10	80/3.6	Present work
	<i>Poecilia mexicana</i> ^a	In	Río La Palma	25	12/1	Present work
		In		4	25/1	Present work
	<i>Rhamdia guatemalensis</i>	Bc	Lago de Catemaco	51	11.7/3.5	Pérez et al. 1992
		Me	San Juan-Valle Nacional	3	66.7/3	Present work
		Me	Puente Valle Nacional	11	81.8/11.8	Present work
		Me	Arroyo San Juan Bautista	6	33.3/2.5	Present work
		Me	Arroyo San Juan Evangelista	9	44.4/4.2	Present work
			Tlacotalpan	8	37.5/7	Present work

Table 2 (Contd.)

Helminth [Status]	Host	Infection sites	Locality	N	P(%) / MI	Reference
Adult Acanthocephala						
Acanthocephala gen. sp.	<i>Ophisternon aenigmaticum</i>	In	Río Tesechoacán	10	20/1	Present work
Cavosomidae						
<i>Caballerorhynchus lamotheti</i>	<i>Rhamdia guatemalensis</i> ^a	In	Arroyo San Juan Bautista	2	50/1	Present work
Salgado-Maldonado 1977						
[Ne, Au]						
Illiosentidae						
<i>Tegorhynchus brevis</i>	<i>Rhamdia guatemalensis</i> ^a		Tlacotalpan	5	20/1	Present work
Van Cleave 1921						
[Na?, Au]						
Neochimorhynchidae						
<i>Floridosentis</i> sp.	<i>Agonostomus monicola</i> ^a	In	Río La Palma	3	33.3/17	Present work
[Ne?, Au]						
<i>Neoechinorhynchus golvani</i>	<i>Cichlasoma fenestratum</i>	In	Lago de Catemaco	ND	ND	Salgado-Maldonado 1978
Salgado-Maldonado 1978				120	19.5/1.25	Salgado-Maldonado et al. 1992
[Ne, Au]				18	33.3/2.2	Present work
Remarks: originally the type host for <i>N. golvani</i> was reported as <i>C. aureum</i> ; however, this species do not inhabit in Lago de Catemaco (Miller and Smith 1998)						
	<i>Cichlasoma ellioti</i> ^a	In	Arroyo San Juan Evangelista	2	50/1	Present work
				30	27/14.5	Jiménez-García 1993
				18	33.3/2.2	Present work
	<i>Cichlasoma octofasciatum</i> ^a		Arroyo San Juan Evangelista	3	33.3/3	Present work
	<i>Cichlasoma urophthalmus</i>		Tlacotalpan	10	10/20	Present work
	<i>Dormitator maculatus</i>		Mouth of Papaloapan	184	76.1/18.7	Montoya-Mendoza et al. 2004
			Tlacotalpan	36	41.7/9.9	Present work
	<i>Gobiomorus dormitor</i>		Tlacotalpan	24	16.7/1.7	Present work
	<i>Rhamdia guatemalensis</i> ^a	In	Tlacotalpan	8	50/6.5	Present work
	<i>Heterandria bimaculata</i>		Lago de Catemaco	10	80/1.5	Salgado-Maldonado 1978
<i>Octospiniferoides chandleri</i>						
Bullock 1957						
[Na?, Au]						
Polymorphidae						
<i>Southwellina hispida</i>	<i>Gobiomorus dormitor</i>	Me	Tlacotalpan	ND	ND	Páez-Rodríguez et al. 2002
(Van Cleave 1925)						
[Wv, Al]						
Larval Acanthocephala						
Polymorphidae						
<i>Polymorphus</i> sp.	<i>Rhamdia guatemalensis</i>	In	Lago de Catemaco	4	25/1	Present work
[?, Al]						
<i>Polymorphus brevis</i>	<i>Cichlasoma fenestratum</i>	Bc, Ey, Me	Lago de Catemaco	ND	ND	Jiménez-García 1993
Van Cleave 1916	<i>Rhamdia guatemalensis</i>	Me	Lago de Catemaco	51	3.9/2	Páez-Rodríguez et al. 2002
[Na, Al]						

The number of specimens examined for four of the seven endemic species in this inventory was low, between two and ten individuals. However, enough specimens of the other endemic hosts were examined: 24 hosts were examined for *Poeciliopsis catemaco*, 25 for *Poecilia catemaconis* and 37 for *Cichlasoma fenestratum*. The atherinid *Atherinella ammnophila* and the clupeid *Dorosoma petenense* were the only hosts examined from these families, and the examination of a larger number of specimens from these families could provide additional helminth data that were not recorded in this inventory. The data collected to date shows that the helminths of endemic hosts are mostly generalist species with wide geographic distribution.

Data are provided for the Upper Papaloapan, a geographic area that has not been sampled previously. There are also new records for the Lower Papaloapan, including the previously sampled areas of Los Tuxtlas and Catemaco Lake, Veracruz. This new data helps in creating a more general panorama of the basin's helminth fauna.

The helminth species richness reported here for the fish of the Papaloapan (85 species in 36 host species) is greater than that reported for the Balsas River basin (25 species in 13 host species, Salgado-Maldonado et al. 2001a), the Ayuquila River (28 species in 14 host species, Salgado-Maldonado et al. 2004b), and the Lerma and Santiago Rivers (43 species in 33 host species, Salgado-Maldonado et al. 2001b). In contrast, it is comparable to the species richness recorded in the Grijalva–Usumacinta system in the state of Tabasco (107 species in 49 host species, Salgado-Maldonado et al. 2005) and that for the Yucatán Península (93 species in 31 host species, Moravec et al. 1995a, b, c, 2002c; Scholz et al. 1995a, b, 1996a, b, 1997a, b, 2001; Scholz and Salgado-Maldonado 2001; Scholz and Vargas-Vázquez 1998; Mendoza-Franco et al. 1997, 1999, 2000, 2003a, b; Mendoza-Franco and Vidal-Martínez 2001; Kritsky et al. 2000).

The helminth diversity of the Papaloapan basin in terms of taxonomic groups coincides with a well-known pattern for helminth communities in freshwater fish in Mexico, with nematodes and trematodes being more abundant (Salgado-Maldonado and Kennedy 1997; Salgado-Maldonado et al. 2001a, b, 2004a, b, 2005; Aguilar-Aguilar et al. 2003c; Sánchez-Nava et al. 2004). Remarkably, the Papaloapan basin also has an abundant monogenean component compared to the reported abundances in other Mexican hydrological basins. However, previous examinations of freshwater fish for inventories of Mexican freshwater basins (Salgado-Maldonado and Kennedy 1997; Salgado-Maldonado et al. 2001a, b) did not adequately evaluate monogenean presence and diversity because the gills were not examined immediately after the killing of the host. The small size and fragility of the dactylogyrids that predominate in Mexican freshwater fish require that they be collected immediately and that proper fixing and handling procedures be used to avoid their destruction (see Mendoza-Franco et al.

1999, 2000, 2003a; Vidal-Martínez et al. 2001a). The low cestode and acanthocephalan diversity in this inventory also fit previously described patterns for Mexican freshwater fish.

Aguilar-Aguilar et al. (2003b) report a close biogeographic relationship between freshwater helminth faunas from the Papaloapan and those from Tabasco, the Yucatán Península and Nicaragua. The present data support the above and show that the helminth fauna composition in Papaloapan fish is related to that of the freshwater fish from the Grijalva–Usumacinta hydrological system in Tabasco (56% of species shared) (see Salgado-Maldonado et al. 2005) and from the Yucatán Península (42% of species shared) (see Moravec et al. 1995a, b; Scholz et al. 1995a, b, 1996a; Mendoza-Franco et al. 1999, 2000; Kritsky et al. 2000). The Grijalva–Usumacinta system is adjacent the Papaloapan, and, like the Yucatán Península, is located in southeast Mexico. Though knowledge on the helminth fauna of freshwater fish in Nicaragua is still incipient, current records show them sharing 28 helminth species (33%) with the fish of the Papaloapan (see Aguirre-Macedo et al. 2001a, b; Vidal-Martínez et al. 2001b; Mendoza-Franco et al. 2003a). In contrast, only 19% of the helminth species in the Balsas River basin are shared with the fish of the Papaloapan (see Salgado-Maldonado et al. 2001a). The Balsas River basin is adjacent the Papaloapan basin, but drains the western side of the Continental Divide, towards the Pacific Ocean.

The helminth fauna in the fish of the Papaloapan river basin predominantly consists of Neotropical species that are largely autogenic. The latter differs from the other basins in Mexico in which allogenic species are generally more numerous.

Ten of the recorded helminth species (12%) have only been found in fish from the Papaloapan. This means that they can be considered exclusive to this basin, and it provides a distinct character to the basin's helminth fauna. It would be premature, however, to say that these helminths are endemic to the Papaloapan as they were not found associated with endemic fish species. Four of these ten exclusive helminth species parasitize the swamp eel *O. aenigmaticum* and two more in the neotropical catfish *R. guatemalensis*. Both host species are also distributed outside the Papaloapan basin, in Central America. The remaining four exclusive helminth species also parasitize the fish that are distributed outside the Papaloapan. Further examination of these species could show the presence of these helminth species beyond the limits of the Papaloapan River basin.

Host specificity in each parasite species varied from those with strict specificity, such as the monogeneans, to the more frequent generalists found in several host species, like *A. (A.) tenuicollis*, *C. formosanus*, *P. minimum* and *Contracaecum* sp. It is noteworthy, however, that each host family has a closely associated suite of parasite species. For example, the helminth fauna of *Ophisternon aenigmaticum* is distinguished by the presence of the cestode *Monticellia ophisterni* and the nem-

atodes *Pseudocapillaria ophisterni*, *Philometra ophisterni* and *Gibsonema ophisterni*. Another is the mugilid *Agonostomus monticola*, which has a close relationship with the trematode *Creptotrema agonostomi*, the nematode *Spinitectus agonostomi* and even the acanthocephalan *Floridosentis mugilis*, which is only recorded from estuarine and marine mugilids. Helminth communities in characid fish are different from those of cichlid fish, which are distinguished by their association with the trematodes *Crassicutis cichlasomae*, *Oligogonotylus manteri* and *Genarchella isabellae*, the nematodes *Procamallanus (Spirocamallanus) rebecae*, and *Rhabdochona kidderi*, and the acanthocephalan *Neoechinorhynchus golvani*. There are cases of parasites, normally considered exclusive to a particular host group, transferring to fish outside this group. For instance, *C. cichlasomae* was found in the clupeid *Dorosoma petenense*, and *R. kidderi* was found in *Poecilia mexicana* and *Dorosoma petenense*. Nonetheless, there are significant quantitative differences in the infection levels between the common hosts and these atypical hosts. This is because, in the latter, these parasites are not as frequent and many do not mature.

This host specificity pattern is a determinant for the helminth fauna composition of the basin. As mentioned previously, there is a complex of helminth species in the Papaloapan that have not been recorded in other hydrological basins in Mexico, including *Saccocoelioides chauhani*, *Caballerorhynchus lamothei*, *Monticellia ophisterni*, *Philometra ophisterni*, *Gibsonema ophisterni*, *Spinitectus mexicanus* and *Cucullanus mexicanus*. The parasite fauna of the host *Ophisternon aenigmaticus* contributes 43% of these seven species and it is likely that these species may be found in other hydrological basins where this host lives.

If a host species is typical of a certain environment, then its parasites are also typical (Chubb 1963). Hence parasite host specificity is so important in determining the characteristics of the parasite fauna of a certain environment. Using this concept, if a group of hosts is abundant in an environment, their specific parasites might disseminate to other hosts, parasitizing hosts where they are not found normally (Dogiel 1961; Wootten 1973). Thus as Wootten (1973) stated, the helminth fauna composition of the Papaloapan basin is more influenced by its ichthyological composition than by limnological factors.

To delimitate host specificity at the host family level can be questionable. However, Vidal-Martínez et al. (2001b) suggest that in Central America and Mexico, these patterns can be related to certain hosts' very dynamic speciation processes. Cichlid speciation, for example, has been so rapid that no morphological or functional differences exist between different species from the same family for their parasite species. This in turn favors host switching between hosts of the same family.

This inventory shows the richness of helminth parasite species in the fish of the Papaloapan River basin in

comparison with other hydrological basins in Mexico. It also demonstrates that this fauna is typically Neotropical and quite similar to that from the neighboring basins of the Grijalva–Usumacinta system and the Yucatán Peninsula. The data also suggest highly effective transmission between environments within the same basin and that the regional parasite fauna is strongly influenced by fish community composition.

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