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The Introduction and Dispersal of Centrocestus formosanus (Nishigori, 1924) (Digenea: Heterophyidae) in Mexico: A Review

TOMÁŠ SCHOLZ[1]

Laboratorio de Parasitología, Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional (CINVESTAV-IPN) Unidad Mérida, Carretera Antigua a Progreso Km 6, A.P. 73 "Cordemex", C.P. 97310 Mérida, Yucatán, Mexico. e-mail: tomas@kin.cieamer.conacyt.mx

GUILLERMO SALGADO-MALDONADO

Instituto de Biología, Universidad Nacional Autónoma de México (UNAM), A.P. 53-173, C.P. 04510 México, D.F., Mexico. e-mail: gsalgado@ibiologia.unam.mx

ABSTRACT.—The taxonomy, distributional history, present occurrence, life cycle, morphology of developmental stages and epizootiology of the heterophyid trematode *Centrocestus formosanus* (Nishigori, 1924) in Mexico are reviewed. This parasite was most likely introduced to Mexico with the importation of the first intermediate host, the thiarid snail *Melanoides tuberculata*, from Asia in 1979. *Centrocestus formosanus* was first recorded in 1985 as metacercariae in fry of the first generation of black carp *Mylopharyngodon piceus* imported from China and subsequently in other fish from a farm in central Mexico. Since that time the trematode has spread rapidly over a wide area which includes central Mexico and both the Atlantic and Pacific coasts. This rapid spread has apparently been enabled by previous propagation of *M. tuberculata* in Mexico. Metacercariae of *C. formosanus* occur encysted on the gills of fish. They have been found in 39 species of fish of the families Atherinidae, Characidae, Cichlidae, Cyprinidae, Eleotridae, Gobiidae, Goodeidae, Ictaluridae, Mugilidae and Poeciliidae from 11 Mexican states (Colima, Guanajuato, Hidalgo, Jalisco, Michoacán, Morelos, San Luis Potosí, Sonora, Tabasco, Tamaulipas and Veracruz). The heron *Butorides striatus* is the only known natural definitive host in Mexico. Further research towards better understanding of all aspects of the life cycle, transmission, host-parasite relationships and the effective control of *C. formosanus* in Mexico is necessary. It should also include monitoring of the present distribution of *M. tuberculata* and its infection with larval stages of *C. formosanus*. Much more emphasis should be given to histopathological studies to assess actual impact of the parasite on fish of different species and age classes. The spectrum of natural definitive hosts and their epizootiological importance in the transmission and maintenance of the parasite in Mexico should also be better documented. Adequate preventive and control measures should be applied in aquaculture, with emphasis given to prevention of movement of infected fish stocks.

INTRODUCTION

The introduction of exotic species of fish to new areas has negative consequences which include introduction of fish parasites to new continents (Kennedy, 1994). There are numerous examples of dissemination of helminths of freshwater fish to new zoogeographical regions such as the cestode *Bothriocephalus acheilognathi*, monogeneans of the genera *Pseudodactylogyrus* and *Cichlidogyrus* and the nematode *Anguillicola crassus* (Hoffman, 1980; Buchmann *et al.*, 1987; Kennedy, 1994; Williams and Jones, 1994; Scholz, 1999). Some of

[1] Permanent address: Institute of Parasitology, Academy of Sciences of the Czech Republic, Branišovská 31, 370 05 České Budějovice, Czech Republic. e-mail: tscholz@paru.cas.cz

these helminth species may even endanger autochtonous fish populations (Font and Tate, 1994; Font, 1997).

Recently, several new fish parasites have been introduced to Mexico from other continents, including the heterophyid trematode *Centrocestus formosanus* (Nishigori, 1924). This species was originally described from Taiwan (then Formosa) and is widely distributed in Asia (Chen, 1942; Yamaguti, 1971; Premvati and Pande, 1974; Yanohara, 1985; Madhavi, 1986; Scholz *et al.*, 1990; Scholz, 1991). Martin (1958) reported *C. formosanus* from Hawaii, where it has been introduced probably from the Orient.

In Mexico metacercariae identified as *Centrocestus formosanus* were first reported by López-Jiménez (1987) from a fish farm at Tezontepec de Aldama (Hidalgo) from central Mexico. The identification of the metacercariae was confirmed by Arizmendi (1992) who described the life cycle of the parasite from cercariae to adults obtained from experimentally infected hosts.

Several studies (Arizmendi, 1992; Amaya-Huerta and Almeyda-Artigas, 1994; Salgado-Maldonado *et al.*, 1995) contain data on the occurrence and morphology of developmental stages of *Centrocestus formosanus* in Mexico. However, the existing information is scarce and fragmentary and does not reflect the veterinary importance of this parasite which may represent a potential danger for autochthonous fish in Mexico because of its suitability to heavily infect a wide spectrum of fishes of different families, including cichlids or cyprinids.

In the present paper available information about *Centrocestus formosanus* in Mexico, including data on the occurrence of the parasite in fish intermediate hosts, is summarized in order to identify existing gaps in the knowledge of the biology and epizootiology of this potentially important parasite and to stimulate further research in this area of fish parasitology.

MATERIALS AND METHODS

Cercariae found in *Melanoides tuberculata* from the Cuitzmala River near the village of Emiliano Zapata, Jalisco in Dec. 1998 were observed live. Illustrations and measurements were made from material fixed with hot 4% formaldehyde solution (*see* Scholz *et al.*, 2000). Data on the occurrence of *Centrocestus formosanus* metacercariae are based on investigations into the fish parasites carried out by the present authors in the states of Guanajuato, Jalisco, Morelos and Veracruz between 1991 and 1998 (G.S.M.) and the State of Tabasco in Nov. 1998 (T.S.). Metacercariae found on the gills of cichlid fish from Tabasco (*see* Table 2) were fixed with ammonium-picrate as described by Scholz and Aguirre-Macedo (2000). The gills of *Cichlasoma salvini* from the Puyacatengo River, Tabasco, heavily infected with *C. formosanus* were fed to two laboratory mice which were examined after 6 d. Adult trematodes recovered from mice were fixed with hot 4% formalin and stained with Schuberg's carmine (Scholz and Hanzelová, 1998).

Specimens studied are deposited at the National Helminthological Collection, Institute of Biology, UNAM, México (CNHE Nos. 3708 and 3709); U.S. National Parasite Collection, Beltsville, Maryland, USA (USNPC No. 88539); Natural History Museum, London, UK (NHBM 1999.2.2.5); Institute of Parasitology, České Budějovice, Czech Republic (IPCAS No. D-419); and Laboratory of Parasitology, CINVESTAV-IPN Mérida, Mexico (CHCM Nos. 315).

RESULTS AND DISCUSSION

TAXONOMY AND SPECIES IDENTIFICATION

Identification of Mexican material of *Centrocestus formosanus* was based on comparison with existing descriptions of life cycle stages of this parasite from South East Asia and Hawaii (*see* Arizmendi, 1992).

In this study metacercariae found in fish from Mexico were conspecific with those from Laos (Scholz *et al.*, 1990; Scholz, 1991) deposited in the helminthological collection of the Institute of Parasitology, České Budějovice (IPCAS No. D-271). Adult worms from Mexico also fully corresponded to those described from Asia (Chen, 1942; Premvati and Pande, 1974). It seems that this parasite has a low intraspecific variability because no marked morphological and biometrical differences among worms from the different zoogeographical regions were observed (Arizmendi, 1992; present study).

HISTORY OF INTRODUCTION

Centrocestus formosanus was first reported from Mexico by López-Jiménez (1987) as metacercariae encysted on the gills of the introduced cyprinid, the black carp *Mylopharyngodon piceus,* and other fish from a fish farm in central Mexico. López-Jiménez (1987) suggested that *C. formosanus* had been introduced to Mexico with the introduction of the black carp in 1979 and later infected other native fish in the Tezontepec de Aldama farm (López-Jiménez, 1987; Vélez-Fernández *et al.,* 1998).

Amaya-Huerta and Almeyda-Artigas (1994) and Salgado-Maldonado *et al.* (1995) questioned the introduction of the parasite directly with fish and doubted the possibility of reproducing black carp (around 1.5 m long) being eaten by birds or mammals, potential definitive hosts of the trematode. Amaya-Huerta and Almeyda-Artigas (1994) proposed that the parasite was imported as sporocyst or redial stages within the thiarid snail *Melanoides tuberculata* that was possibly introduced simultaneously with the black carp from China as a food for this malacophagous fish.

The following epizootiological data on *Centrocestus formosanus* support the contention about the parasite's introduction to Mexico in 1979 with snails (*Melanoides tuberculata*) from Asia: (1) Metacercariae of the trematode were not found on the gills of black carp brood stocks but on the gills of the first generation fry. This implies that these fish must have been infected at the farm with cercariae of *C. formosanus,* released from the first intermediate snail host. Furthermore, such small-sized fish would have easily been consumed by fish-eating birds or mammals and the life cycle would have been completed. Piscivorous birds are quite common around the Tezontepec de Aldama farm and they would have rapidly disseminated eggs of the parasite to new localities. (2) Metacercariae were found in a wide variety of fish cultured at Tezontepec de Aldama such as *Ctenopharyngodon idellus, Cyprinus carpio, Ictalurus punctatus, Hypophthalmichthys molitrix, Megalobrana amblycephala, Mylopharyngodon piceus, Oreochromis aureus,* hybrids of *O. mossambicus* and *O. urolepis hornorum* and *Poecilia reticulata* (López-Jiménez, 1987 and pers. comm.). As these fish were then moved to other fish farms in the states of Morelos and Puebla they could have disseminated the parasite to these regions. (3) The parasite has recently been recorded in fish from other regions of Mexico (Tabasco) where it was most likely absent before the 1990s, as indicated by previous intensive parasitological research carried out 10–15 y ago (Pineda-López, 1985; Pineda-López *et al.,* 1985a,b; Fucugauchi *et al.,* 1988; Aguirre-Macedo and García-Magaña, 1994). (4) *Centrocestus formosanus* has never been reported from countries where *Melanoides tuberculatus* lived for several decades, including regions with intensive parasitological research as the southern part of the United States, the Caribbean region or Brazil. As far the authors are aware, there had been no records of *C. formosanus* from the North American continent before it was reported by López-Jiménez (1987) from central Mexico.

Subsequent spread of the parasite might have been by dissemination of the different developmental stages: eggs released by the definitive hosts (fish-eating birds), intramolluscan stages in infected *Melanoides tuberculata* snails, cercariae swimming freely in the water

or metacercariae encysted in fish. It is obvious, however, that further spread of *Centrocestus formosanus* and its successful colonization of new localities was only possible due to the presence of a suitable first intermediate host, *M. tuberculata* snails, throughout a wide area of Mexico (Contreras-Arquieta *et al.*, 1995a; Salgado-Maldonado *et al.*, 1995).

Although it cannot be ruled out that *Centrocestus formosanus* was introduced to Mexico more than once, all existing data listed above indicate only one introduction. In any case, it is evident that the trematode has established successfully in Mexico and it has become an integral part of the helminth fauna of fishes in this country.

PRESENT DISTRIBUTION IN MEXICO

Centrocestus formosanus was first reported in the State of Hidalgo in 1985 (López-Jiménez, 1987) but it was then found in other Mexican states in central Mexico (Michoacán, Morelos) and the Atlantic coast of Mexico (Veracruz, Tabasco) (Arizmendi, 1992; Amaya-Huerta and Almeyda-Artigas, 1994; Salgado-Maldonado *et al.*, 1995; Pérez-Ponce de León *et al.*, 1996; Table 1).

The present geographical distribution of *Centrocestus formosanus* metacercariae in Mexico now includes the states of Colima, Guanajuato, Hidalgo, Jalisco, Michoacán, Morelos, San Luis Potosí, Sonora, Tabasco, Tamaulipas and Veracruz (Tables 1, 2). However, the occurrence of the parasite in other states is highly probable and its absence is likely due to lack of investigations into the fish parasites in these states rather than actual absence of the parasite. Recently, *C. formosanus* (cercariae in *Melanoides tuberculata* and metacercariae in fish) was found in the State of Jalisco at the Pacific Coast of Mexico. This finding indicates a high potential of the parasite to colonize geographically very distant regions. Metacercariae of *C. formosanus* are now very frequent in numerous fish species in several localities throughout western, central and southeastern parts of Mexico and prevalence and infection intensity may reach extraordinarily high values.

LIFE CYCLE

The life cycle of *Centrocestus formosanus* was elucidated many years ago (*see* Yamaguti, 1975 for review). In Mexico, most developmental stages of the parasite were described in detail by Arizmendi (1992) from naturally infected first and second intermediate hosts and experimental definitive host.

First intermediate host.—The thiarid snail *Melanoides tuberculata* serves as the first intermediate host of *Centrocestus formosanus* in Mexico (Arizmendi, 1992; Amaya-Huerta and Almeyda-Artigas, 1994; Amaya-Huerta, 1995; Salgado-Maldonado *et al.*, 1995; present data).

This snail is native to India and was introduced to the southern United States during the 1940s and was later found in Venezuela and on several islands of the Lesser Antilles (Murray, 1971; Abbott, 1973; Perera *et al.*, 1987). In Martinique the snail was first found in 1979. It was also purposely introduced in 1985 to Désirade Island (Lesser Island) to eliminate populations of *Biomphalaria glabrata*, the intermediate host of human schistosomiasis (Pointier *et al.*, 1991, 1993). The snail appeared in Cuba as late as 1983 (Perera *et al.*, 1987), supposedly having been transported by migratory birds.

The snail was introduced to Mexico probably around the 1960s (Contreras-Arquieta *et al.*, 1995a). It was first reported by Abbott (1973) from Veracruz but then spread rapidly and, in 1995, was reported from more than 70 localities in 12 Mexican states (Chiapas, Chihuahua, Coahuila, Durango, Morelos, Nayarit, Nuevo León, Puebla, Quintana Roo, Tabasco, Tamaulipas, Veracruz) (Contreras-Arquieta *et al.*, 1995a; Contreras-Arquieta, 1998). The presence of *Melanoides tuberculata* in Mexico seems to have a negative impact on populations of native molluscs (Contreras-Arquieta *et al.*, 1995b).

Despite the wide distribution of *Melanoides tuberculata* in Mexico and its role as an intermediate host of numerous trematodes (Yamaguti, 1975), there are scanty data on the occurrence of larval stages of *Centrocestus formosanus* in naturally infected snails in Mexico (Arizmendi, 1992; Salgado-Maldonado *et al.*, 1995). Amaya-Huerta and Almeyda-Artigas (1994) provided data on the chaetotaxy of *C. formosanus* cercaria.

In addition to larval stages of *Centrocestus formosanus*, rediae and cercariae of two other trematodes were found in *Melanoides tuberculata* in Mexico, namely those of *Haplorchis pumilio* (Looss, 1896) (Heterophyidae) and *Philophthalmus gralli* Mathis et Leger, 1910 (Philophthalmidae) (Scholz *et al.*, 2000). It is probable that at least the former species, previously not reported from Mexico, was introduced with infected *M. tuberculata* snails.

Second intermediate host.—Cercariae liberated from snails encyst on the gills of fish. In Mexico, a number of fresh- or brackishwater fish of the families Atherinidae, Cichlidae, Cyprinidae, Eleotridae, Goodeidae, Ictaluridae and Poeciliidae have been reported to harbour *Centrocestus formosanus* metacercariae (Table 1). It seems that there is a low host specificity of the trematode at the level of the second intermediate host but there are undoubtedly differences in susceptibility of respective fish species (Table 2). In addition to fish, Amaya-Huerta (1995) reported the frog *Spea multiplicata* (Pelobatidae) as an experimental second intermediate host of *C. formosanus*.

Definitive host.—The heron *Butorides striatus* is the only natural definitive host of *Centrocestus formosanus* reported from Mexico (Amaya-Huerta, 1995). However, it is probable that other fish-eating birds such as herons, cormorants or pelicans and mammals, like some rodents and carnivores, serve as definitive hosts of the parasite since chicks, ducklings and mice were also suitable experimental hosts (Arizmendi, 1992; Salgado-Maldonado *et al.*, 1995; present data).

MORPHOLOGY OF DEVELOPMENTAL STAGES

Most of the developmental stages of *Centrocestus formosanus* from Mexico were described and illustrated by Arizmendi (1992). In addition, Salgado-Maldonado *et al.* (1995) provided measurements of *C. formosanus* cercaria, metacercaria and adult. However, there are slight differences in the morphology of developmental stages as described by the above mentioned authors and those obtained in this study. In addition, published data contain some inaccuracies in measurements of their respective developmental stages as indicated by much larger dimensions of organs in metacercariae than in adults (*e.g.*, the oral sucker of the metacercaria was reported to be twice as long as that in the adult and the pharynx was also reported as being much larger in the metacercaria than in the adult) or incorrect length of the cercarial tail (Salgado-Maldonado *et al.*, 1995; Table 1).

Redia.—The redia of *Centrocestus formosanus* from *Melanoides tuberculata* from Mexico was described and illustrated by Arizmendi (1992; Fig. 1). It is elongate with a short gut and contains several cercariae in different developmental stages.

Cercaria.—The cercaria of *Centrocestus formosanus* is small, oculate, gymnocephalous (distome, leptocercous according to Amaya-Huerta and Almeyda-Artigas, 1994). It has a pyriform body and a narrow tail tapering posteriorly and provided with transverse tegumental annulations (Fig. 1). The cercaria was first reported from Mexico by Arizmendi (1992). The present study enabled us to describe some morphological details (Fig. 1), including the morphology of the gland cells. Each gland has a duct and these ducts from both sides do not connect together as described by Arizmendi (1992). Arizmendi described the cercaria of *Centrocestus formosanus* as possessing a well-developed acetabulum. However, only a cluster of cells representing a primordium of the acetabulum was observed in this study (Fig. 1) which agrees with the observations of Martin (1958).

TABLE 1.—Second intermediate hosts (fish) of *Centrocestus formosanus* in Mexico

Fish species	State	Locality	Reference
ATHERINIDAE			
Chirostoma humboldtianum	Michoacán	Laguna de Zacapu	Arévalo *et al.* (1994)
CICHLIDAE			
Oreochromis aureus	Hidalgo	Tezontepec de Aldama	López-Jiménez (pers. comm.)
O. mossambicus × *O. urolepis hornorum*	Hidalgo	Tezontepec de Aldama	López-Jiménez (pers. comm.)
CYPRINIDAE			
Carassius auratus	Morelos	Las Estacas	Amaya-Huerta and Almeyda-Artigas (1994) Salgado-Maldonado *et al.* (1995)
Ctenopharyngodon idella	Hidalgo	Tezontepec de Aldama	López-Jiménez (1987), Arizmendi (1992)
Cyprinus carpio	Colima	Laguna de Amela	Vélez-Hernández *et al.* (1998)
	Hidalgo	Tezontepec de Aldama	López-Jiménez (1987), Arizmendi (1992)
	San Luis Potosí	El Peaje	López-Jiménez (pers. comm.)
Hypophthalmichthys molitrix	Hidalgo	Tezontepec de Aldama	López-Jiménez (1987), Arizmendi (1992)
Megalobrema amblycephala	Hidalgo	Tezontepec de Aldama	López-Jiménez (1987), Arizmendi (1992)
Mylopharyngodon piceus	Hidalgo	Tezontepec de Aldama	López-Jiménez (1987), Arizmendi (1992)
ELEOTRIDAE			
Gobiomorus maculatus	Veracruz	Río Tecolutla	Campos (1992)
	Veracruz	Gutiérrez Zamora, El Salmoral, Tlacotalpan	Velázquez *et al.* (1994)
GOODEIDAE			
Ilyodon whitei	Morelos	Río Amacuzac	Caspeta-Mandujano (1994)
ICTALURIDAE			
Ictalurus punctatus	Hidalgo	Tezontepec de Aldama	López-Jiménez (1987—as "bagre"; pers. comm.)

TABLE 1.—Continued

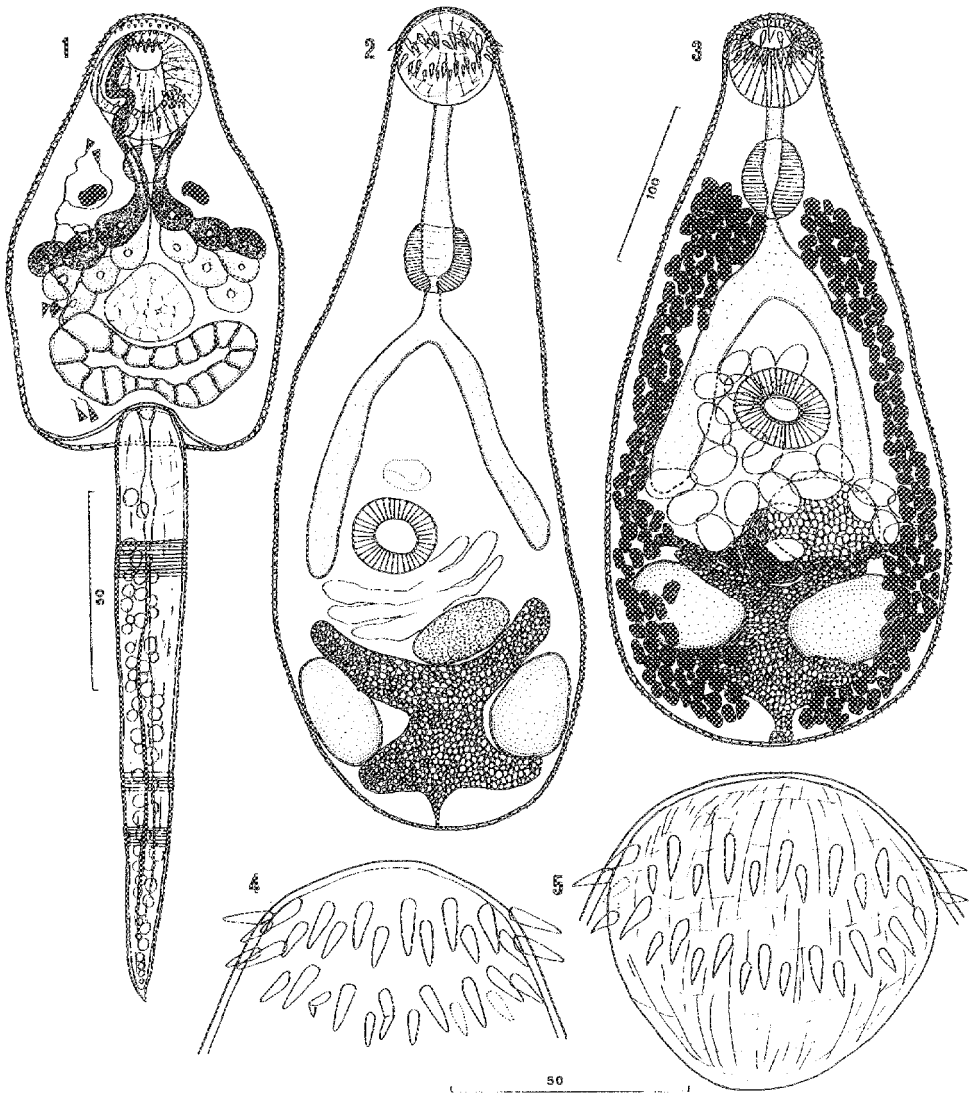
Fish species	State	Locality	Reference
POECILIIDAE			
Heterandria bimaculata	Morelos	Las Estacas	Amaya-Huerta and Almeyda-Artigas (1994) Salgado-Maldonado *et al.* (1995)
Poecilia latipinna	Morelos	Las Estacas	Amaya-Huerta and Almeyda-Artigas (1994) Salgado-Maldonado *et al.* (1995)
Poecilia reticulata	Hidalgo	Tezontepec de Aldama	López-Jiménez (unpubl. data)
Poecilia sphenops	Morelos	Las Estacas	Amaya-Huerta and Almeyda-Artigas (1994) Salgado-Maldonado *et al.* (1995)
Xiphophorus helleri	Morelos	Las Estacas	Amaya and Almeyda (1994) Salgado-Maldonado *et al.* (1995)
Xiphophorus maculatus	Morelos	Las Estacas	Amaya and Almeyda (1994) Salgado-Maldonado *et al.* (1995)

TABLE 2.—New records of *Centrocestus formosanus* metacercariae in Mexico. Date = month and year; N = number of fish examined

Family Fish Species	State	Locality	Date	N	Prevalence [%]	Intensity Mean	Intensity Range
CHARACIDAE							
Bramocharax caballeroi	Veracruz	Río La Palma	2.97	7	43	3	1–5
CICHLIDAE							
Cichlasoma gadovii	Veracruz	Río La Palma	11.96	14	14	14	7–20
Cichlasoma geddesi	Tabasco	Yumka	11.98	3	67	21	3–38
Cichlasoma helleri	Tabasco	Yumka	11.98	10	10	4	4
Cichlasoma managuense	Tabasco	El Horizonte	11.98	2	100	1974	565–3383
Cichlasoma nigrofasciatum	Morelos	Río Amacuzac	12.95	22	5	1	1
Cichlasoma pasionis	Tabasco	Yumka	11.98	3	33	7	7
Cichlasoma salvini	Tabasco	Río Puyacatengo	11.98	13	31	57	5–164
CYPRINIDAE							
Algansea tincella	Guanajuato	Presa Ignacio Allende	4.95	22	14	58	2–168
Yuriria alta	Guanajuato	Presa Ignacio Allende	6.97	14	21	2	1–4
			9.97	3	33	5	5
ELEOTRIDAE							
Dormitator latifrons	Jalisco	Río Purificación	3.95	1	100	3	3
Gobiomorus dormitor	Veracruz	Río La Antigua	4.–10.91	30	100	133	10–670
	Veracruz	Río Tecolutla	8.91	60	98	123	2–660
	Veracruz	Río Papaloapan	5.–7.91	30	70	19	1–163
	Veracruz	Río La Palma	6.96	4	25	89	89
			11.96	7	57	67	29–181
			2.97	23	17	71	1–161
	Veracruz	Aroyo Balzapote	11.96	4	100	949	110–2580
	Veracruz	Río Máquinas	11.96	7	71	86	4–188
Gobiomorus maculatus	Jalisco	Río Purificación	3.95	5	100	1260	92–2400
	Jalisco	Río Cuitzmala	1.95	21	90	850	330–1542
			3.95	37	92	822	28–2187
			9.95	30	43	2824	1–5935
Gobiomorus polylepis	Jalisco	Río Cuitzmala	9.95	8	63	594	151–1167

TABLE 2.—Continued

Family Fish Species	State	Locality	Date	N	Prevalence [%]	Intensity Mean	Intensity Range
GOBIIDAE							
Gobionellus microdon	Jalisco	Río Cuitzmala	1.95	10	30	349	177–543
GOODEIDAE							
Goodea atripinnis	Guanajuato	Presa Ignacio Allende	6.97	11	27	5	2–11
Ilyodon whitei	Morelos	Río Amacuzac	11.94–11.95	520	49	73	1–690
			12.95	22	82	107	1–426
Goodeidae gen. sp.	Jalisco	La Manzanilla	11.94	1	100	1	1
MUGILIDAE							
Agonostomus monticola	Jalisco	Río Cuitzmala	1.95	7	86	415	235–740
			9.95	40	20	153	14–693
	Jalisco	Río Purificación	3.95	2	100	915	818–1012
	Veracruz	Río La Palma	11.96	6	50	6	1–17
	Veracruz	Río Máquinas	11.96	13	15	3	3
POECILIIDAE							
Heterandria sp.	Veracruz	Río La Palma	2.97	4	25	1	1
Poecilia sphenops	Jalisco	Río Purificación	3.95	22	5	1277	1277
	Morelos	Río Amacuzac	3.95	11	9	1	1
			12.95	43	14	5	1–13
	Veracruz	Río La Palma	11.96	19	11	20	2–38
Poecilia sp.	Guanajuato	Presa Ignacio Allende	6.97	1	100	1	1
Poeciliopsis gracilis	Morelos	Río Amacuzac	3.95	18	6	8	8
			12.95	15	20	1	1–2
Xiphophorus helleri	Veracruz	Río Máquinas	11.96	11	36	30	8–95



FIGS. 1–5.—*Centrocestus formosanus*. 1, cercaria from *Melanoides tuberculata*. 2, metacercaria from *Gobiomorus maculatus*. 3, adult from experimentally infected mouse, 6 d post infection. 4, 5, oral sucker of metacercaria with circumoral spines. (Scale is micrometers)

The flame cell pattern of *Centrocestus formosanus* from Mexico is 2 [(2 + 2) + (2 + 2)] (Arizmendi, 1992; present data; Fig. 1) and corresponds to that reported by Martin (1958) from Hawaii. Flame cells are arranged in pairs, most cells of each pair being close one to another.

The cercaria of *Centrocestus formosanus* resembles that of *Ascocotyle* (*Phagicola*) *diminuta* and *A.* (*P.*) *nana* in the shape of the body and tail, the presence of acicular spines on the dorsal side of the mouth opening and a spine on the tip of the tail (Fig. 1; Ostrowski de

Núñez, 1993; Ditrich *et al.*, 1997). Amaya-Huerta and Almeyda-Artigas (1994) studied the chaetotaxy of cercariae from *Melanoides tuberculata* from Mexico (Morelos) and confirmed their identity with *C. formosanus*.

Metacercaria.—The metacercaria of *Centrocestus formosanus* from Mexico was described in detail by Arizmendi (1992). The metacercariae encyst on the gills and are surrounded by a semispherical, mechanically fairly resistant cyst. The metacercarial cysts invade the cartilage of the gill filaments and are usually located near the base of the gill cartilage (Vélez-Hernández *et al.*, 1998; present study). Due to their location, the cysts are difficult to isolate. Beside the typical site of location, the shape and size of cysts, the most characteristic feature of *C. formosanus* metacercariae is the presence of X-shaped excretory bladder containing dark excretory granules (Fig. 2). The metacercariae are pyriform or conical in shape when liberated from a cyst and entirely covered with tegumental spines (Fig. 2). The mouth is surrounded by two complete rows of 16 spines each; the number of circumoral spines appears to be quite constant (Figs. 4, 5). The genitalia are well developed, including the primordium of the uterus. Within the definitive host, trematodes mature rapidly becoming gravid within a few days (6 d postinfection; present data).

Adult.—Adult trematodes are small, pyriform, with a spinous tegument (Fig. 3). The oral sucker is armed with 32 spines forming two circlets of circumoral spines but it lacks the posterior appendage (solid prolongation) typical of other heterophyids of the subfamily Phagicolinae which occur simultaneously in fish in Mexico (Scholz *et al.*, 1997). The acetabulum of *Centrocestus formosanus* is well developed and is not transformed into a ventrogenital sac as in members of other heterophyid genera such as *Ascocotyle* or *Haplorchis* (Pearson, 1964; Scholz *et al.*, 1997).

Adults of *Centrocestus formosanus* have been reported in Mexico only from experimental hosts such as chicks, ducks and mice (Arizmendi, 1992; Salgado-Maldonado *et al.*, 1995), except for the finding of adults in the heron *Butorides striatus* from Morelos (Amaya-Huerta, 1995).

The paucity of records of adult trematodes from Mexico is undoubtedly related to scarcity of studies on the helminth fauna of fish-eating birds and mammals in this country. Moreover, adult trematodes are very small and they may easily be overlooked in the intestine of the host or may be misidentified if definitive hosts are examined a long time after their capture and only dead trematodes lacking circumoral spines are found. Although there are almost no field observations, it can be assumed that the present wide distribution of *Centrocestus formosanus* in Mexico has been facilitated by high vagility of its definitive hosts which might have disseminated parasite eggs into other areas.

PATHOLOGY IN FISH

Despite the fact that infections with *Centrocestus formosanus* metacercariae are often heavy and that this trematode has been reported as a causative agent of diseases of cultured fish in Asia, there are very few data on pathogenicity of metacercariae in fish hosts in Mexico. López-Jiménez (1987) claimed that metacercariae may cause severe problems, *e.g.*, decreasing respiratory capacity of fish and, in heavy infections, may lead to the death of fry, but it is not clear whether these data were based on the author's own observations.

Vélez-Hernández *et al.* (1998) did not observe pathological changes due to metacercarial cysts on gross examination of the gills of common carp (*Centrocestus carpio*) but microscopical examination by these authors revealed moderate to severe hyperplasia of cartilage of the primary lamellae. Other histological findings included mild hyperplasia of the lymphoid tissue in the gills, epithelial hyperplasia of lamellae, gill hyperaemia and congestion (Vélez-Hernández *et al.*, 1998). It should, however, be pointed out that Vélez-Hernández *et*

al. (1998) studied fish infected with quite low parasite burden (a total of 377 metacercariae in 28 carp) whereas infection of some fish may reach almost 6000 metacercarial cysts per fish (Table 2). It was observed that cichlid fish from the Puyacatengo River in Tabasco infected with several hundreds of *C. formosanus* metacercariae maintained in the laboratory died much more quickly after capture that uninfected congeners.

In view of the fact that that this trematode has a fairly low specificity to its second intermediate host, which enables it to infect a wide spectrum of fish species, evaluation of the pathogenicity of metacercariae is important for feral fish populations as well as aquaculture operations.

EPIZOOTIOLOGY

The history of the spread of *Centrocestus formosanus* after its introduction to this country clearly demonstrates that very little, if any, attention has been paid to the potential problem for aquaculture. The occurrence of *C. formosanus* in numerous species of native fish from a large part of Mexico also shows that efforts to eliminate this parasite or at least to prevent its rapid spreading throughout the Mexican territory have been negligible.

All available data suggest that *Centrocestus formosanus* has had favourable conditions for its rapid and wide range-expansion in Mexico: (1) a wide distribution of its first intermediate host that now encompasses 13 Mexican states (Contreras-Arquieta *et al.*, 1995a, b; Contreras-Arquieta, 1998; present data); (2) a low specificity at the level of the second intermediate host (Tables 1, 2) and, therefore, availability of potential fish hosts almost everywhere; (3) a wide spectrum of potential definitive hosts that may serve as reservoirs of the parasite; (4) the high mobility of definitive hosts enabling them to cross natural barriers that prevent spreading of parasite stages in aquatic animals (snails, fish) and to disseminate eggs to new regions; (5) lack of effective methods of prevention and control in fish farms which makes it possible to move infected fish stocks throughout the country.

Extraordinarily rapid distribution of the trematode to an extremely large area of Mexico since its first appearance in 1979 seems to have been realized mainly in two principal ways: (1) disseminaton of eggs with definitive hosts, in particular fish-eating birds; (2) movement of infected fish stocks from one fish farm to others throughout Mexico. Dissemination of the parasite into natural waters by infected feral fish may also have taken place in addition to accidental transfer of infected *Melanoides tuberculata* snails either by humans or birds.

PROSPECTS

Centrocestus formosanus is now a widely distributed parasite that infects a wide range of fish of different families. Recent records of *C. formosanus* in new hosts and regions, including the Pacific coast (Table 2), suggests that it continues its range-expansion. The parasite is already established in natural water bodies and its elimination is now practically impossible. It also seems unlikely that further spread of *C. formosanus* to new areas can be prevented because of favorable conditions that might allow the parasite to successfully colonize other parts of Mexico.

Despite this pesimistic scenario, the negative impact of this recently imported parasite on cultured fish might be decreased by the application of adequate preventive and control measures based on better knowledge of its biology and epizootiology. Some of these measures are briefly mentioned below: (1) cultured fish, in particular those intended for introduction to other farms, should be examined regularly for the presence of parasites and movement of parasite-free stocks of fish only should be allowed; (2) populations of snails (*Melanoides tuberculata*) in fish farms should be eliminated in order to prevent contact of

emerged cercariae with fish and their infection; (3) fish-eating birds and mammals should be prevented from feeding on fish or their carcasses in fish farms.

Numerous aspects of *Centrocestus formosanus* biology and epizootiology remain to be clarified. Despite extensive data on secondary intermediate hosts of the parasite in Mexico, actual susceptibility of these fish to *C. formosanus* infection needs to be better known. Moreover, the role of individual fish species in the maintainance and transmission of the trematode also needs study. Little is also known about the occurrence of *Melanoides tuberculata* in some parts of Mexico (Contreras-Arquieta *et al.*, 1995a). It is evident that the parasite cannot complete its life cycle in localities where a suitable intermediate host is absent. Therefore, monitoring of the present distribution of *M. tuberculata* and its infection with larval stages of *C. formosanus* is essential to predict the occurrence of the trematode in new areas and to prevent its introduction to fish farms in these regions. Much more emphasis should also be given to histopathological studies to assess the actual impact of the parasite on fish of different species and age classes. Spectrum of natural definitive hosts and their epizootiological importance in transmission and maintaining the parasite in Mexico should also be known better.

Vélez-Hernández *et al.* (1998) questioned the possible impact of *Centrocestus formosanus* on human health in Mexico. Taking into account the site of infection of metacercariae (gills of fish), it seems unlikely that this parasite might have any zoonotic importance in this country. Nevertheless, lightly fried fish are eaten whole, including gills, in some localities in Mexico as Pátzcuaro Lake. In any case, thorough cooking of fish is necessary to prevent potential human diseases caused by *C. formosanus*.

Centrocestus formosanus is undoubtedly an important parasite which should attract more attention of fish parasitologists, veterinarians, aquaculturist and fishery managers in Mexico. It is hoped that this review will stimulate further research for a better understanding of all aspects of the life cycle, transmission, host-parasite relationships and effective control of *C. formosanus*.

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