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Life Cycle of *Oligogonotylus manteri* (Digenea: Cryptogonimidae), a Parasite of Cichlid Fishes in Southern Mexico

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ABSTRACT: The life cycle of the cryptogonimid, *Oligogonotylus manteri* Watson, 1976, was studied under natural and experimental conditions. Field study showed that aquatic snails, *Benthonella gaza* (Prosobranchiata: Rissoidae), were the first intermediate host and cichlid fish, *Cichlasoma urophthalmus*, either the second intermediate or definitive hosts. Laboratory-reared cichlids, *Cichlasoma synspilum*, were exposed to *O. manteri* cercariae from naturally infected snails by placing them into water or force-feeding with remnants of snails harboring *O. manteri* cercariae. The development of metacercariae in experimentally infected *C. synspilum* was completed 6 days postexposure (DPE) at 22–24°C. Metacercariae from the gills, fins, body surface, and intestinal walls of naturally infected *C. urophthalmus* and experimentally infected *C. synspilum* were used to expose *C. synspilum*, *Oreochromis niloticus* (Cichlidae), and *Poecilia reticulata* (Poecilidae). Adult worms were detected in *C. synspilum* 16 DPE at 22–24°C and juveniles only in *O. niloticus* and *P. reticulata*. Results of both feeding experiments and examination of naturally infected cichlid fish from the Yucatan Peninsula revealed that metacercariae previously reported as *Echinochasmus zubedakhaname* were *O. manteri*.

KEY WORDS: *Oligogonotylus manteri*, Digenea, experimental infection, life cycle, *Benthonella gaza*, *Cichlasoma* spp., Yucatan, Mexico, developmental stages.

The cryptogonimid *Oligogonotylus manteri* was originally described from cichlid fishes in Nicaragua (Watson, 1976). Since that time, it has been reported as a common intestinal parasite of cichlids in Mexico as well (Osorio-Sarabia et al., 1987). Despite the wide distribution and frequent occurrence of this digenean, little is documented about its biology. Consequently, the purpose of this study was to provide information on the life cycle of this parasite.

Another aim of this investigation was to test the assumption that metacercariae, frequently found encysted in the intestinal wall, gills, and fins of *Cichlasoma urophthalmus* (Günther) in southeastern Mexico and hitherto apparently misidentified as *Echinochasmus zubedakhaname* Nasir et Díaz, 1968 (Lamothe-Argumedo & Aguirre-Macedo, 1991a), represent a developmental stage of *O. manteri*.

Materials and Methods

Study areas

The first was the coastal lagoon of Celestun, situated NW of Merida (20°45′–20°58′N, 90°15′–90°25′W), Yucatan, Mexico. The lagoon ranges in depth from 0.4 to 3.5 m. It is 28 km long and from 0.4 to 2.3 km wide, with a total area of 31 km², and opens southward into the Gulf of Mexico (Valdés et al., 1988). Salinity values in the lagoon fluctuate from almost fresh water in its northern part, where numerous springs are present, to 22.0–36.8 ppt in the southern part where the lagoon opens into the sea.

The second study area was a flooded quarry in the Mitza limestone factory, 25 km north of Merida (21°15′N, 89°40′W). The total area of the quarry is 9.3 ha and average depth of the water is 5.2 m, with a maximum depth of 8.5 m (Flores-Nava, 1990).

Samples of *C. urophthalmus* were also collected from other localities in the Yucatan Peninsula: the coastal lagoon at Rio Lagartos, Yucatan (21°34′–21°36′N, 87°51′–88°13′W); permanent lakes at Noh-Bek (19°04′N, 88°49′W) and Guerrero (18°42′N, 88°15′W), both in the state of Quintana Roo; the Champoton River (19°21′N, 90°40′W), Laguna El Vapor and Estero Pargo, a tidal channel, both in the Laguna Terminos complex (18°20′–19°00′N, 91°10′–92°00′W), all in the state of Campeche.

Examination of naturally infected hosts

During April, May, and August 1993, 589 snails, *Benthonella gaza* Dall (Prosobranchiata: Rissoidae), were sampled from Celestun and 290 from Mitza. In the laboratory, they were placed individually in glass tubes containing 10 ml of pond water and exposed to the light for several hours. The water was then examined for the presence of released cercariae by visual inspection. Thereafter, all snails were dissected and their rediae and cercariae studied as temporary mounts.

A total of 88 fishes included 30 *C. urophthalmus*, 26

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Table 1. Records of fish with *Oligogonotylus manteri* metacercariae.

Fish species	Locality	No. fishes examined	No. fishes infected	Prevalence (%)	Total no. worms	Intensity of infection: Mean	Intensity of infection: Range
Cichlasoma urophthalmus	Celestun*	30	28	93	506,374	18,033	1–178,871
C. urophthalmus	Celestun†	30	30	100	11,734‡	391‡	3–1,615
Bairdiella ronchus	Celestun	11	11	100	513	47	6–132
Lutjanus griseus	Celestun	26	15	60	373	25	1–127
Strongylura timucu	Celestun	3	1	33	6	6	6
Sphoeroides testudineus	Celestun	8	6	75	647‡	108‡	2–570
C. urophthalmus	Rio Lagartos	27	24	89	130,017	5,417	1–23,363
C. urophthalmus	Noh-Bek	30	2	7	45	23	4–41
C. urophthalmus	Guerrero	4	2	50	157	79	58–99
C. urophthalmus	Champoton	30	15	50	9,266	618	1–4,993
C. urophthalmus	El Vapor	30	7	23	33	5	1–19

* May 1988.
† April, May, and August 1993.
‡ Metacercariae from the intestinal wall are not included.

Lutjanus griseus (L.), 2 *Lutjanus synagris* (L.) (Lutjanidae), 7 *Lagodon rhomboides* (L.) (Sparidae), 11 *Bairdiella ronchus* (Cuvier), 1 *Cynoscion nebulosus* (Cuvier) (Sciaenidae), 3 *Strongylura timucu* (Walbaum) (Belonidae), and 8 *Sphoeroides testudineus* (L.) (Tetraodontidae) were collected by angling from the lagoon of Celestun. An additional 163 *C. urophthalmus* from the study localities mentioned above, including Celestun (see Table 1), were collected between May and July 1988.

All fish were examined externally and internally by routine helminthological procedure, as outlined by Bykhovskaya-Pavlovskaya (1969). Metacercariae were studied alive, either while encysted or after removal from cysts. Adult worms were observed and measured either as temporary or permanent mounts, fixed either with ammonium-picrate (Ergens, 1969) or with 4% formalin under slight coverslip pressure, stained with Schuberg's (acid) carmine, dehydrated in alcohol, and mounted in Canada balsam. All measurements are in μm, unless otherwise stated. The mean with standard deviation (SD) as well as minimum and maximum values (in parentheses) are included in the descriptions of developmental stages. Drawings were made using a Leitz drawing attachment.

Experimental animals

Five species of experimental animals were used: laboratory-reared, parasite-free cichlid fishes, *Cichlasoma synspilum* (Hubbs) and *Oreochromis niloticus* (L.); guppies, *Poecilia reticulata* (L.) (reared in an ornamental fish farm in Merida); laboratory mice (2 wk old, from laboratory stocks in the Laboratory of Parasitology, Faculty of Veterinary Sciences, University of Yucatan, Merida); and chicks (5 days old, from a chicken farm in Merida).

Experimental design

SECOND INTERMEDIATE HOST: Eleven hatchery-reared *C. synspilum* housed in individual small aquaria were exposed to 200–300 cercariae for 3–12 hr. Exposed fish were maintained in 10-liter aquaria on a diet of pelletized food and examined for metacercariae 1, 3, 4, 5, 6, 10, 15, and 20 days postexposure (DPE).

Tissues containing cercariae of *O. manteri* from naturally infected *B. gaza* snails were injected directly into the stomachs (i.e., force-fed) of 3 additional *C. synspilum*, using a Pasteur pipette. Regurgitated material was collected and readministered to the fish. Fish exposed in this manner were maintained as described above and examined 5, 7, and 16 DPE.

DEFINITIVE HOST: Pieces of intestine (approximately 1–3 mm long) and gills of naturally infected *C. urophthalmus* were force-fed to 19 *C. synspilum*, 9 *O. niloticus*, and 12 *P. reticulata*, which were dissected and examined 1, 2, 3, 4, 5, 7, 10, 13, 16, 19, 22, 25, and 28 DPE. An additional 7 *C. synspilum* were each force-fed between 8 and 50 metacercariae (6–7 days old) from the fins, body surface, and gills of experimentally infected *C. synspilum*. The exposed fish were held in 10-liter aquaria and examined 2, 3, 7, and 16 DPE.

Oral infections of *O. manteri* metacercariae from naturally infected *C. urophthalmus* were administered to 3 groups of chicks and laboratory mice (each group consisting of 5 chicks and 2 mice) as follows:

Group 1: Each host was fed pieces of the anterior third of the intestine of *C. urophthalmus* (from a swamp in Mitza) infected with several hundred *O. manteri* metacercariae.

Group 2: Each host was fed pieces of gills of *C. urophthalmus* (from Celestun) infected with 100–200 *O. manteri* metacercariae.

Group 3: Each host was fed pieces of the anterior third of the intestine of *C. urophthalmus* (from Celestun) infected with at least 1,000 *O. manteri* metacercariae.

Ten chicks and 4 mice served as controls. After infection, all animals, experimentals and controls, were fed pelletized food, and examined 1, 3, 8, 13, and 15 DPE (chicks) and 4 and 11 DPE (mice).

Reference specimens, including metacercariae from naturally infected *C. urophthalmus* and adults from experimentally infected *C. synspilum*, are deposited in

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the National Parasite Collection, U.S. National Museum, Beltsville, Maryland, Coll. No. 83754-55, and helminthological collection of the Laboratory of Parasitology, CINVESTAV-IPN, Merida.

Results

Natural infections

FIRST INTERMEDIATE HOST: A total of 136 *B. gaza* from Celestun (23.1%) and 32 from Mitza (11.0%) were found to be infected with larval stages (rediae, cercariae; Figs. 1–7) of *O. manteri* in their hepatopancreas.

SECOND INTERMEDIATE HOST: Metacercariae of *O. manteri* were found in 5 fish species from the lagoon of Celestun, with the highest infection level in *C. urophthalmus* (see Table 1); *L. synagris, L. rhomboides,* and *C. nebulosus* were negative. Whereas a majority of *O. manteri* larvae found in *C. urophthalmus* (Fig. 8) and *B. ronchus* were alive without signs of degeneration, larvae recorded in *S. testudineus, L. griseus,* and *S. timucu* were dead and partially decomposed.

Internal infections (metacercariae encysted in the wall of the anterior intestine) were found only in *C. urophthalmus* and 2 specimens of *S. testudineus*; other fishes were infected with *O. manteri* larvae located only superficially (in the gills, fins, or on the body surface).

Out of 11,734 metacercariae found in *C. urophthalmus* (those encysted in the intestinal wall not counted), 7,457 larvae were encysted in the gills and 4,262 in the fins; other encysting sites (body surface, heart, spleen) were quite exceptional. In other fish species, *O. manteri* larvae predominated in the fins, where from 53% of larvae in *L. griseus* to 100% in *S. timucu* were found.

DEFINITIVE HOST: Adult worms were found only in *C. urophthalmus* and they were recorded from all 7 sampling sites (Table 2). Worms were most common in the posterior third of the intestine.

Experimental infections

SECOND INTERMEDIATE HOST: All 11 *C. synspilum* subjected to free-swimming cercariae were found to harbor metacercariae, independent of the time of postexposure (1–20 days). A total of 353 *O. manteri* metacercariae were found in experimental fish. Encysting sites included the pectoral fins (56.7% of larvae found), caudal fin (18.4%), body surface (10.8%), gills (9.1%), pelvic fins (2.3%), dorsal fin (1.4%), anal fin (0.8%), and ventral fin (0.6%), respectively.

All 3 *C. synspilum,* force-fed with snails harboring *O. manteri* cercariae were found to be infected with a total of 171 *O. manteri* metacercariae, independent of the time postexposure. The sites of infection were the intestinal wall (62.0% of larvae), dorsal fin (16.4%), caudal fin (8.2%), body surface (5.3%), anal fin (2.9%), gills and pelvic fins (1.8%), ventral fin (1.2%), and pectoral fins (0.6%). External infections with metacercariae, i.e., those in gills, fins, and body surface, were apparently caused by penetration of free-swimming cercariae released from snail tissues vomited by fishes, because no migration of larvae from the intestine to these sites was observed.

Development of *O. manteri* metacercariae in experimentally infected *C. synspilum* at 22–24°C was as follows: 1 DPE: cercariae encysted, enclosed by a thin, hyaline membrane; pharynx faintly visible, ventral sucker partially formed; 2 DPE: ventral sucker still incomplete, anterior end still provided with spination typical of cercariae, including preoral spines; 3 DPE: preoral spines still present; pharynx clearly visible; 4 DPE: ventral sucker almost completely formed; preoral spines not observed; 5 DPE: metacercariae fully formed, with completely developed ventral sucker and digestive system; 6 and 7 DPE: metacercariae proved to be infective for the definitive host. In the following days (10–20 DPE), no changes were recorded in the morphology of metacercariae.

DEFINITIVE HOST: Since there were no differences between infections of fish challenged either with *O. manteri* metacercariae from the intestinal wall or those encysted in the gills of *C. urophthalmus,* results of experimental infections are summarized together (Table 3). Complete development of the trematode was only recorded in *C. synspilum* and it was as follows (Figs. 9–13; Table 4):

One and 2 DPE: worms show well-developed eyes and a large excretory bladder, filled with numerous dark granules; 3 and 4 DPE: remnants of eyes present in the form of diffused, dark granules; cephalic glands present; spherical, small anlagen of testes lying oblique to each other, near posterior extremity; 5 DPE: testes small but discernable; excretory bladder distinguishable; 7 DPE: remnants of eyes still present; excretory bladder difficult to distinguish; 10 DPE: testes large and seminal receptacle containing live spermatozooa; first gonotyls (2 in most specimens) present, situated anterior to ventral sucker; 13 DPE: eggs in uterus, but with not fully formed

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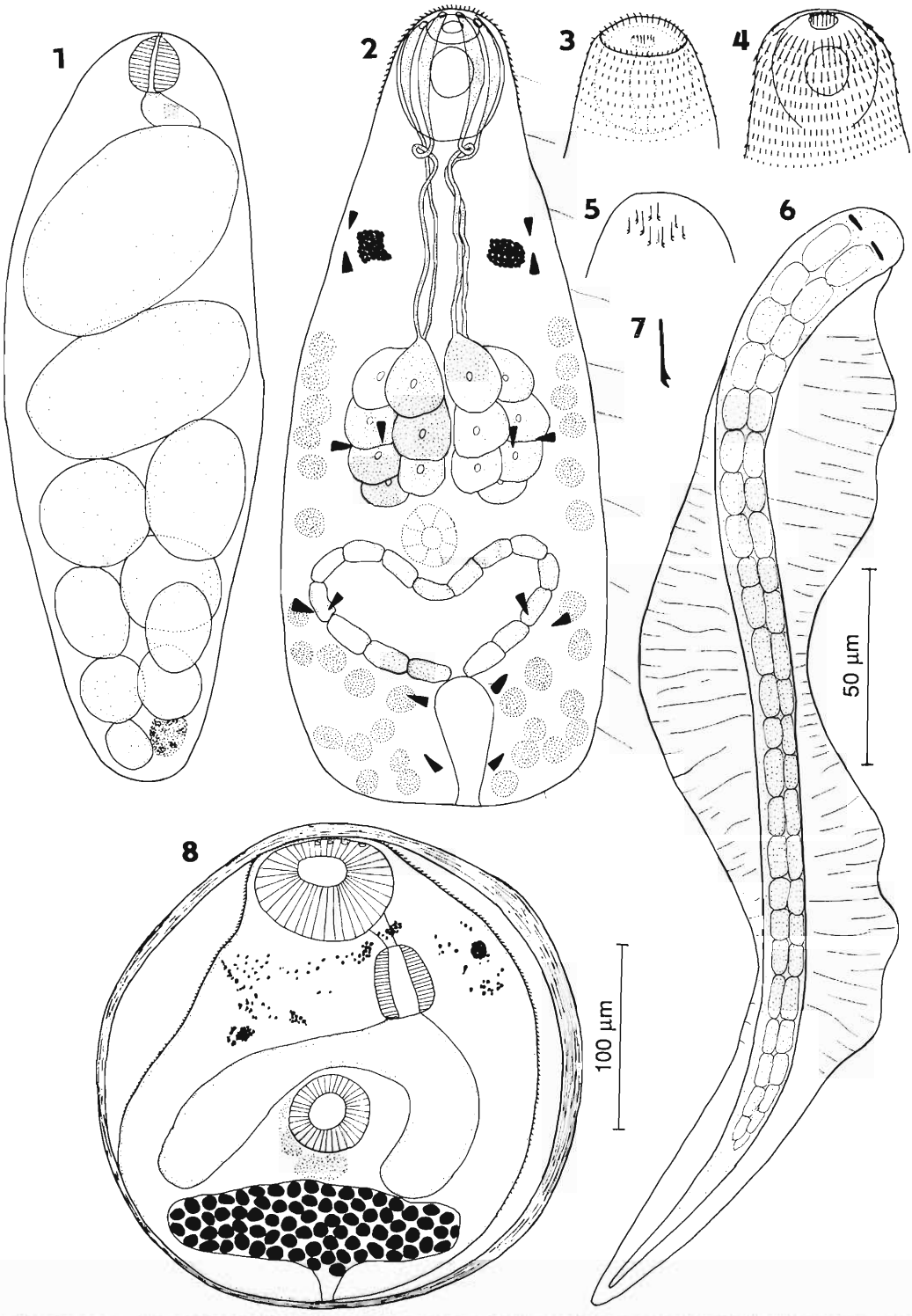

Figures 1–8. Larval stages of *Oligogonotylus manteri* from *Benthonella gaza* (1–7) and *Cichlasoma urophthalmus* (8). 1, Daughter redia with scale bar; 2–7, cercaria (2, body; 3, 4, anterior end with tegumental spines; 5, distribution of circumoral spines; 6, tail with scale bar; 7, circumoral spine, enlarged; length 5 µm); 8, metacercaria from the pectoral fins.

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Table 2. Occurrence of adult *Oligogonotylus manteri* in *Cichlasoma urophthalmus*.

Locality	Date	Number of fish		Prevalence (%)	Total no. worms	Infection intensity	
		Examined	Infected			Mean	Range
Celestun	V.88	30	30	100	1,252	37.0	2–115
Celestun	IV–VIII.93	24*	19	79	329	17.3	1–53
Rio Lagartos	VI.88	27	16	59	186	11.6	1–69
Noh-Bek	VI.88	30	17	56	215	2.6	1–47
Guerrero	VI.88	4	3	75	42	14.0	2–31
Champoton	VII.88	30	22	73	74	3.3	1–7
El Vapor	V.88	30	2	7	11	5.5	5–6
Estero Pargo	V.88	12	3	25	13	4.3	1–10

* Of 30 fish sampled, only 24 were examined for the presence of intestinal helminths.

contents and thin-walled capsules; 16 DPE: ripe, fully developed eggs in uterus.

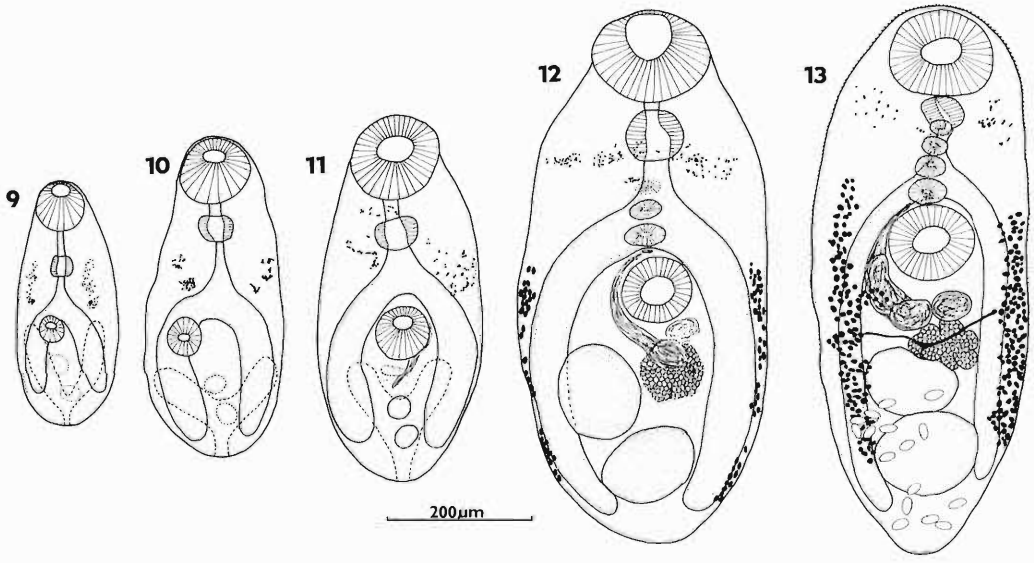
In the following days (19–28 DPE), measurements of worms (Table 4), as well as the proportion of gravid worms in the samples, gradually increased.

No mature or gravid worms were found in either *O. niloticus* or *P. reticulata*. Bodies of juvenile trematodes found in the intestinal lumen of *P. reticulata* 2 and 5 DPE were filled with numerous granules and vacuoles, which indicated that they were in the process of disintegration. All trematodes recorded in *C. synspilum* were located in the posterior (distal) third of the intestine.

Out of a total of 7 *C. synspilum* infected with *O. manteri* metacercariae from experimentally infected *C. synspilum*, serving as second intermediate hosts, only the 2 examined 3 and 7 DPE, harbored 2 and 8 trematodes, respectively. Trematodes were not found in either experimental or control chicks and mice.

DESCRIPTIONS OF DEVELOPMENTAL STAGES:

Redia from naturally infected *B. gaza* ($N = 20$; Fig. 1): Daughter rediae elongate, sacciform, without locomotory appendages; body 125 ± 41 (66–197) long, 43 ± 14 (20–75) wide. Oral opening terminal, pharynx strongly muscular, oval, 11 ± 3 (8–16) long, 11 ± 3 (8–16) wide. Cecum very short, sacculate. Birth pore located just posterior to pharynx. Several developing cercariae (up to 10) in rediae, with larger and more de-



Figures 9–13. Development of *Oligogonotylus manteri* adults in experimentally infected *Cichlasoma synspilum* at 22–24°C (9, 1 DPE; 10, 3 DPE; 11, 7 DPE; 12, 10 DPE; 13, 19 DPE).

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Table 3. Results of experimental infection of fish with *Oligogonotylus manteri* metacercariae from naturally infected *Cichlasoma urophthalmus*.

Fish	No. fish		Σ worms	Intensity mean (range)	Days post-exposure*	State of maturation
	Examined	Infected				
Cichlasoma synspilum	19	19	1,781	94 (4–620)	1, 3, 4, 7	Juvenile
					10, 13	Mature
					16, 19, 22, 25, 28	Gravid
Oreochromis niloticus	9	4	87	22 (17–41)	1, 2, 5	Juvenile
Poecilia reticulata	12	3	7	2 (1–4)	2, 4	Juvenile

* Only positive fish are mentioned; those examined 5, 10, 16 days postexposure (DPE) (*O. niloticus*), and 7 DPE (*P. reticulata*), respectively, were free of infection.

veloped cercariae in anterior part of redial body; measurements of largest cercariae up to 113 by 45. Mother rediae not observed.

Cercaria from naturally infected *B. gaza* (N = 16; Figs. 2–7): Oculate, pleurolophocercous cercaria. Body bell-shaped, 198 ± 28 (153–258) long by 108 ± 19 (68–130) wide; tail length 356 ± 56 (311–385), width 31 ± 3 (23–35); oral sucker 33 ± 6 (26–38) long by 31 ± 4 (20–35) wide.

Body spinous from anterior extremity to level of eye spots (Figs. 3, 4). Three or four anterior rows formed by hooklike spines, posterior spines (about 12–15 rows) simple and smaller. Hooklike preoral spines (Figs. 5, 7), usually 11 in number, located on dorsal lip of oral sucker; length of hooks 4–5. Body margins with long, hairlike sensory structures, distributed irregularly from anterior extremity to posterior end of body. Tail slightly curved dorsoventrally, provided with dorsoventral, hyaline fin-fold, beginning dorsally at first sixth and narrowing at last third of tail, beginning ventrally immediately behind proximal end of tail stem, with narrower part near middle of tail.

Oral sucker subterminal, pharynx poorly developed, almost indiscernible, esophagus and ceca not developed. Eye spots located anterior to penetration (cephalic) glands. Penetration glands, occupying central part of body, each formed by 7 pairs of cells; diameter of gland cells 15–17. Ducts of glands forming 2 bundles of 2 tubules each, coursing over and opening around anterior margin of oral sucker as four large orifices. Cystogenous glands in 2 groups; anterior group lying lateral to penetration glands, formed usually by 6 glands; posterior group filling posterolateral part of body, consisting of approximately 13 glands (Fig. 2). Ventral sucker weakly developed, spherical, located between penetration glands and excretory bladder. Excretory vesicle thick-walled, Y-shaped. Flame cell formula 2 (2 + 2 + 2 + 2) = 16.

Metacercaria from naturally infected *C. urophthalmus* (N = 20; Fig. 8): Metacercariae found in experimentally infected *C. synspilum* were biometrically and morphologically identical to those found in naturally infected *C. urophthalmus*. The following description is based on larvae from the fins of *C. urophthalmus* from Celestun (the morphology, as well as measurements, of worms from the wall of the anterior intestine were identical to those of larvae from the gills, body surface, and fins).

Encysted metacercariae enclosed by thin, hyaline membrane of parasite origin and thick-layered cyst of variable thickness; size of cysts 178 ± 17 (149–207) by 164 ± 19 (132–201), thickness of outer wall 4 ± 1 (3–6). Body surface of metacercariae covered with numerous, simple, single-pointed tegumental spines, posteriorly smaller and less dense. Oral sucker large, subterminal, 48 ± 6 (35–59) long by 59 ± 7 (47–76) wide. Ventral sucker slightly postequatorial, its diameter 32 ± 4 (24–36) by 33 (33); sucker considerably smaller than oral sucker. Suckers' ratio (N = 7) 1.40:1 ± 0.34 (0.93–2.08) for sucker length and 1.64:1 ± 0.04 (1.60–1.69) for sucker width. Prepharynx short, 14 ± 4 (6–21) long; pharynx strongly muscular and large, 30 ± 4 (24–41) long by 33 ± 5 (27–50) wide. Esophagus relatively short, ceca wide, reaching far posterior to ventral sucker. Remnants of eye spots located lateral to oral sucker and pharynx. Two pairs of penetration glands, each consisting of 7 cells, located on lateral side of body between pharynx and ventral sucker. Gland openings clearly visible, as 4 orifices on anterior rim of oral sucker. Genital primordium poorly visible, located posterior to ventral sucker. Excretory bladder large, Y-shaped, with large lateral branches reaching

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Table 4. Measurements of *Oligogonotylus manteri* in experimentally infected *Cichlasoma synspilum*.

	Days postexposure									
	1	3	7	10	13	16	19	22	25	28
Number of worms	4	14	20	20	20	15	18	13	15	20
Body length*	258 ± 62	333 ± 81	362 ± 61	752 ± 155	764 ± 102	825 ± 233	844 ± 247	874 ± 51	891 ± 208	1,130 ± 204
	170–329	217–477	277–490	417–947	602–999	397–1,169	721–1,220	767–993	529–1,128	516–1,367
Body width	138 ± 19	146 ± 27	162 ± 23	342 ± 106	383 ± 61	431 ± 113	405 ± 100	474 ± 49	329 ± 41	585 ± 130
	106–161	103–199	126–206	153–520	300–488	220–593	198–573	370–553	273–418	388–861
Oral sucker										
Length	59 ± 9	72 ± 14	84 ± 141	131 ± 25	133 ± 19	136 ± 38	148 ± 20	156 ± 12	118 ± 12	174 ± 24
	44–68	50–103	38–108	94–153	106–173	103–179	94–173	143–91	100–141	141–244
Width	61 ± 64	79 ± 18	93 ± 13	140 ± 23	158 ± 59	158 ± 28	160 ± 22	163 ± 10	152 ± 22	196 ± 20
	47–66	53–108	70–126	73–167	120–409	123–176	133–176	92–103	132–176	162–235
Prepharynx	16 ± 4	21 ± 10	34 ± 12	28 ± 11	28 ± 11	27 ± 13	79 ± 84	22 ± 7	86 ± 18	36 ± 18
	47–66	9–53	14–59	11–62	11–53	9–49	68–138	12–41	9–58	47–74
Pharynx										
Length	45 ± 1	40 ± 6	42 ± 7	64 ± 10	68 ± 12	68 ± 11	46 ± 61	72 ± 5	64 ± 9	82 ± 19
	44–47	33–53	29–59	44–79	49–103	50–88	59–85	62–79	47–74	59–132
Width	42 ± 19	43 ± 11	48 ± 8	78 ± 11	84 ± 13	88 ± 26	79 ± 22	107 ± 7	80 ± 19	118 ± 19
	29–56	23–64	26–51	59–94	62–103	14–118	59–103	91–118	36–121	82–147
Acetabulum										
Length	34 ± 14	45 ± 9	54 ± 7	99 ± 21	107 ± 23	116 ± 31	112 ± 13	176 ± 30	104 ± 16	171 ± 20
	26–41	29–59	38–70	59–153	59–161	62–153	103–129	134–193	76–126	135–176
Width	30 ± 4	44 ± 9	52 ± 6	100 ± 19	104 ± 12	120 ± 35	99 ± 28	127 ± 16	147 ± 25	157 ± 20
	26–35	32–59	35–61	59–123	82–123	68–158	94–138	94–147	132–182	132–185
Position†	174 ± 77	191 ± 46	233 ± 92	375 ± 86	379 ± 64	361 ± 143	373 ± 146	423 ± 53	465 ± 156	522 ± 114
	153–196	123–279	161–300	106–493	291–488	64–599	59–92	332–526	252–861	356–873
Sucker's ratio										
Length	1.7 ± 0.2	1.6 ± 0.2	1.6 ± 0.2	1.4 ± 0.2	1.3 ± 0.1	1.2 ± 0.3	1.4 ± 0.1	1.3 ± 0.1	1.2 ± 0.1	1.2 ± 0.1
	1.6–2.0	1.4–2.0	1.3–1.8	0.9–1.7	1.1–1.6	0.7–1.8	1.1–1.7	1.1–1.7	1.0–1.4	1.0–1.6
Width	2.0 ± 0.5	1.7 ± 0.1	1.7 ± 0.1	1.4 ± 0.1	1.4 ± 0.3	1.3 ± 0.2	1.4 ± 0.1	1.3 ± 0.2	1.3 ± 0.1	1.3 ± 0.1
	1.3–2.5	1.4–1.9	1.3–1.7	1.2–1.8	1.2–1.6	1.0–1.7	1.2–1.6	1.1–1.5	1.0–1.4	1.1–1.5
Anterior testis										
Length	n.m.‡	n.m.	n.m.	n.m.	86 ± 25	69 ± 18	63 ± 32	112 ± 19	129 ± 12	122 ± 32
					50–133	44–81	33–118	79–141	118–15	65–168
Width	n.m.	n.m.	n.m.	n.m.	111 ± 28	61 ± 25	94 ± 83	123 ± 19	140 ± 14	143 ± 34
					53–153	44–91	53–156	85–144	123–171	65–190

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Table 4. Continued.

	Days postexposure									
	1	3	7	10	13	16	19	22	25	28
Posterior testis										
Length	n.m.	n.m.	n.m.	n.m.	103 ± 21 59–144	58 ± 11 26–74	70 ± 35 50–129	98 ± 30 49–162	132 ± 11 118–147	127 ± 32 74–185
Width	n.m.	n.m.	n.m.	n.m.	113 ± 43 41–173	64 ± 10 47–74	93 ± 36 47–144	145 ± 29 129–162	137 ± 10 118–153	138 ± 30 82–179

* Mean ± SD and range.
† Distance of the middle of the acetabulum from anterior extremity.
‡ Not measured.

anteriorly to level of acetabulum, and with short posterior stem (Fig. 8).

Adult (Figs. 9–13): The morphology of adult worms recovered from naturally infected *C. urophthalmus* as well as their measurements (Table 4; Fig. 13) were identical to those of worms described by Watson (1976) and Osorio-Sarabia et al. (1987).

Discussion

The present study demonstrated that the developmental cycle of *O. manteri,* involving the aquatic snail *B. gaza* as the first intermediate, and cichlid fish, both as second intermediate or as definitive hosts, is similar to those of other trematodes of the family Cryptogonimidae, which have been studied (Yamaguti, 1971, 1975; Greer and Corkum, 1979, 1980; Font, 1987). A high level of infection in *B. gaza* snails from Celestun (prevalence 23.1%), together with the fact that they are abundant in this lagoon and that *C. urophthalmus* eats these snails in large quantities (Salgado-Maldonado, unpubl. obs.), may explain extremely high worm burdens in fish from this locality.

Morphology of larval stages from naturally infected snails was similar to that of rediae and cercariae of other cryptogonimid trematodes (Yamaguti, 1971, 1975; Greer and Corkum, 1979). Daughter rediae of *O. manteri* were typified by the absence of any locomotory appendages, presence of cercariae in different degrees of development and a very short, sacculate intestine. *Oligogonotylus manteri* cercariae were characterized by the presence of a tail with a hyaline fin-fold, 7 pairs of large penetration glands filling the middle region of the body, small cystogenous glands situated posterolaterally, and a Y-shaped, thick-walled excretory bladder, typical of the Cryptogonomidae (Yamaguti, 1971, 1975).

Experiments with *O. manteri* cercariae showed their high infectivity for *C. synspilum,* because all the fish were found to be infected with metacercariae. Free-swimming cercariae resulted in a high proportion (57%) of metacercariae encysted in pectoral fins, which tallies with data from natural conditions. On the other hand, cysts in gills of experimental hosts were remarkably few (9%); this contrasts to the findings in *C. urophthalmus* in nature.

Successful experimental infections of fish with *O. manteri* cercariae clearly demonstrated 2 modes of infection of the second intermediate

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host and explained 2, quite different types of encysting sites in their fish host—internal, i.e., in the wall of the intestine, and external, notably in the gills, fins, and on the body surface. In the former case, the fish acquired the infection by ingesting snails containing cercariae of the trematode, and in the latter case, they became infected after free-swimming cercariae penetrated their body surface, gills, and fins.

Development of *O. manteri* metacercariae (metamorphosis of cercariae) in experimental hosts was relatively quick, and as early as 5 DPE metacercariae were fully formed; experiments confirmed that 6-day-old worms were infective for the definitive host. Greer and Corkum (1979), however, reported at least 14 days as the minimum time for cercariae of other cryptogonimids to develop into infective metacercariae.

With the exception of *C. urophthalmus,* which is freshwater, with rather high salinity tolerance, all other fish species studied are euryhaline. The infection of 4 of these fishes, *L. griseus, B. ronchus, S. timucu,* and *S. testudineus,* showed that cercariae of *O. manteri* were able to penetrate through the surface of these fishes when they enter into this lagoon. However, almost all these larvae were dead, which indicated that these species did not represent suitable second intermediate hosts. Only *B. ronchus* harbored a larger proportion of live larvae. However, experimental infection of the cichlid *C. synspilum* with metacercariae encysted in the fins of *B. ronchus* was not successful (unpubl. data).

Experimental infections of laboratory-reared *C. synspilum* with metacercariae from naturally infected *C. urophthalmus* confirmed the assumption that these larvae, hitherto misidentified as those of the echinostomatid *E. zubedakhaname,* belong to the species *O. manteri* (compare Figs. 1 and 2 in Lamothe-Argumedo and Aguirre-Macedo [1991a] with Fig. 8 in the present study, as well as the descriptions of these larvae in the 2 papers). The identification of these metacercariae by Lamothe-Argumedo and Aguirre-Macedo (1991a) was based on experimental infections of chicks and laboratory mice fed the intestines and gills of *C. urophthalmus* containing metacercariae. These yielded mature echinostome trematodes, morphologically identical to those described by Nasir and Díaz (1968) as *E. zubedakhaname* (Lamothe-Argumedo and Aguirre-Macedo, 1991a, b). However, the morphology of these larvae, as described by Lamothe-Argumedo and Aguirre-Macedo (1991a), did not resemble that typical of an echinostomatid: a collar was absent, collar spines, well visible in echinostome metacercariae, were also lacking, the oral sucker was much larger than the relatively rather small acetabulum, being of the same size as the pharynx, and the excretory bladder was Y-shaped. Spines described by the above authors were most probably openings of cephalic glands, which are well developed both in the cercaria and metacercaria of *O. manteri* (Fig. 8 in the present paper). Lamothe-Argumedo and Aguirre-Macedo (1991a) evidently used at least 2 species of metacercariae for their experimental infections. Examination of *C. urophthalmus* from different localities in the Yucatan Peninsula (unpubl. data) revealed the presence of *Echinochasmus* metacercariae. These occurred exclusively in gills and can easily be differentiated from those of *O. manteri* by their internal morphology, size, and shape of cyst as well as their location in gill filaments. Our suspicion that Lamothe-Argumedo and Aguirre-Macedo (1991a) carried out mixed experimental infections was confirmed by our recovering *Echinochasmus* adults in mice and chicks experimentally infected with gills containing echinostome metacercariae from a swamp in Mitza.

The trematode *O. manteri* completed its development in experimentally infected *C. synspilum* within 16 DPE at 22–24°C, when the first embryonated eggs were recorded. In contrast to the relatively rapid developmental times for metacercariae of this species, maturation took about twice as long as in related trematodes (Greer and Corkum, 1979; Font, 1987).

The occurrence of *O. manteri* adults exclusively in *C. urophthalmus* showed limited host specificity at the level of the definitive host. Results of experimental infections of tilapias (*O. niloticus*) and guppies (*P. reticulata*) with *O. manteri* metacercariae, in which no adult worms were found, further indicate a narrow host specificity of this cryptogonimid. It seems that *O. manteri* is a specific parasite of cichlid fishes from the genus *Cichlasoma* and the related species *Petenia splendida* in southern Mexico and Central America (Watson, 1976; Osorio-Sarabia et al., 1987).

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Fourth Edition of the International Code of Zoological Nomenclature

The International Commission on Zoological Nomenclature proposes to publish a new edition of the code, taking into account the large number of possible amendments that have been received. It is planned that the Fourth Edition will be published during 1995 and that on 1 January 1996 its provisions will supersede those in the current (1985) edition.

The Commission's Editorial Committee met in Hamburg from 12–16 October 1993 to prepare a discussion draft for the new edition of the Code. Copies of this draft will be sent without charge to all subscribers to the *Bulletin of Zoological Nomenclature* and to members of the American and European Associations for Zoological Nomenclature. Any other institution or individual may order a copy from the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London, SW7 5BD, England. Bank charges on currency exchanges make it uneconomic to charge the cost of printing and postage (£3 or US$5) except for payment in sterling or US dollars. The draft will therefore be sent free of charge, but those able to pay in sterling or US dollars are asked to enclose a check for £3 or US$5 to cover the cost.

Before completing the definitive text of the Fourth Edition, the Commission will (in accordance with Article 16 of its Constitution) carefully consider all comments and suggestions on the draft. Zoologists and others are asked to send these to the Executive Secretary of the Commission at the above address as soon as convenient, and in any event not later than February 1995.

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