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Larval stages of trematodes from freshwater molluscs of the Yucatan Peninsula, Mexico

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Abstract. Examination of 4055 molluscs of 10 species from cenotes (= sinkholes) and other freshwater bodies in the Yucatan Peninsula, Mexico revealed the presence of larval stages of 13 trematodes. The following species were found: *Echinochasmus leopoldinae* Scholz, Ditrich et Vargas-Vázquez, 1996, *E. macrocaudatus* Ditrich, Scholz et Vargas-Vázquez, 1996 (Echinostomatidae), *Saccocoelioides* sp. (? *sogandaresi* Lumsden, 1963) (Haploporidae), *Crassicutis cichlasomae* Manter, 1936, pleurolophocercous ophthalmocercaria sp. (Homalometridae), *Ascocotyle* (*Ascocotyle*) sp., *Ascocotyle* (*Phagicola*) *nana* Ransom, 1920 (Heterophyidae), *Oligogonotylus manteri* Watson, 1976 (Cryptogonimidae), *Genarchella astyanactis* (Watson, 1976) (Derogenidae), xiphidiocercariae sp. 1, 2 and 3 (Lecithodendriidae?), and furcocercaria gen. sp. (Fellodistomidae). The life-cycle of the derogenid *Genarchella astyanactis* was studied for the first time. It was found that it differs from that of *G. genarchella*: the first intermediate host, *Pyrgophorus coronatus* (Pfeiffer, 1839), released cystophorous furcocercariae of *G. astyanactis* that developed, after ingestion by the second intermediate host, copepods (experimentally *Mesocyclops chaci* Fiers, Reid, Ilife et Suárez-Morales, 1996), into metacercariae resembling by their morphology juvenile trematodes found in the stomach of *Astyanax fasciatus*. No progenetic cercariae (metacercariae) found in *G. genarchella* were observed in the life-cycle of *G. astyanactis*. Rediae and cystophorous furcocercariae were recovered from naturally infected snails and snails experimentally kept in contact with eggs from the uterus of *G. astyanactis* adults.

The Yucatan Peninsula is characterized by the almost complete absence of superficial water bodies like rivers, lakes and streams. The most common freshwater bodies are cenotes (= sinkholes), connected with the subterranean water system (Hall 1977). The Peninsula is also interesting from the zoogeographical point of view because it lies near the transient area between the Nearctic and Neotropical regions. Despite this fact, current knowledge of the fauna of the Peninsula is still rather limited, which also concerns the helminth parasites of fishes. Since pioneer works by Pearse (1936), Manter (1936) and Stunkard (1938), only a few papers have been published by Mexican authors (Lamothe-Argumedo and Aguirre-Macedo 1991a,b, Salgado-Maldonado and Aguirre-Macedo 1991, Arizmendi 1992, Salgado-Maldonado 1993, Aguirre-Macedo and García-Magaña 1994). Investigations into the parasites of fishes from cenotes and other freshwater bodies of the Peninsula have been started quite recently (Moravec et al. 1995a,b, Scholz et al. 1995a,b, 1996a).

The above studies have demonstrated that trematodes, in particular their metacercariae, represent the dominant group of helminths parasitizing freshwater fishes in the Peninsula. In fishes from cenotes, digeneans were represented by 10 species parasitic as adults and 21 species as metacercariae (Scholz et al. 1995a,b). The identification of many metacercariae to species level was, however, difficult or even impossible in many cases without obtaining adults and without sufficient data on their life-cycles. Although some observations have been carried out (Scholz et al. 1994, 1995c, 1996b, Ditrich et al. 1996), the life-cycles of most trematodes parasitizing fish of the Yucatan Peninsula are still to be studied.

Studies of the biology of trematodes can also provide data on the mollusc fauna of the Peninsula, because no

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Table 1. Survey of larval stages recorded in fresh water molluscs from cenotes.

Locality	Host	No. of molluscs examined /dissected	*Echinomchasmus leopoldinae*	*Echinochasmus macrocaudatus*	*Saccocoelioides* sp. (*sogandaresi*?)	*Crassicutis cichlasomae*	*Oligogonotylus manteri*	*Ascocotyle* (*Ascocotyle*) sp.	*Ascocotyle* (*Phagicola*) *nana*	*Genarchella astyanactis*	xiphidiocercaria sp. 1	xiphidiocercaria sp. 2	xiphidiocercaria sp. 3 (Lecithodendriidae?)
cenote Chaamac	*Pyrgophorus coronatus*	441/157	6/0*	4/0	–	23/34	4/0	–	6/0	32/0	–	–	–
cenote Noc Chon-cunchey	*Pyrgophorus coronatus*	988/502	4/0	–	2/5	5/132	3/0	2	–	13/0	–	5/0	3/0
	Laevapex fuscus	2/2	–	–	–	–	–	–	–	–	–	–	–
cenote Chek–há	*Pyrgophorus coronatus*	2/2	–	–	–	–	–	–	–	–	–	–	–
cenote Chen-há	*Pyrgophorus coronatus*	1330/880	6/0	–	2/0	13/34	3/0	–	13/0	–	–	–	3/0
	Pisidium casertanum	6/6	–	–	–	0/2	–	–	–	–	–	–	–
cenote Ixin-há	*Pyrgophorus coronatus*	90/70	1/0	–	–	–	2/0	–	–	–	–	–	8/0
cenote San Pedro 2	*Pyrgophorus coronatus*	36/36	–	–	–	–	–	–	–	–	–	–	–
cenote Azul	*Pyrgophorus coronatus*	17/17	–	–	–	2/0	–	–	–	–	–	–	–
	Valvata humeralis	9/9	–	–	–	0/3	–	–	–	–	–	–	–
	Laevapex fuscus	4/4	–	–	–	–	–	–	–	–	–	–	–
	Mytilopsis sp.	8/8	–	–	–	0/2	–	–	–	–	–	–	–
cenote Dos Bocas	*Pyrgophorus coronatus*	169/70	–	–	–	–	4/0	–	–	–	0/3	–	–
	Helisoma anceps	69/12	–	–	–	–	–	–	–	–	2/4	–	–
Total		**3171/1775**	**17/0**	**4/0**	**4/5**	**43/207**	**16/0**	**2/0**	**19/0**	**45/0**	**2/7**	**5/0**	**14/0**

* number of molluscs with cercariae/number of snails with metacercariae

Table 2. Survey of trematode larval stages recorded in freshwater molluscs from rivers and inland lagoons

Locality	Host	No. of molluscs examined/dissected	*Crassicutis cichlasomae*	pleurolophocercous ophthalmocercaria sp. (Homalometridae)	furcocercaria sp. (Fellodistomidae)
swamp	*Pyrgophorus coronatus*	496/112	26/18*	–	–
Mitza	*Physella cubensis*	48/48	0/13	–	–
	Pyrgophorus coronatus	80/44	10/18	–	–
	Helisoma anceps	4/4		–	–
Laguna	*Valvata humeralis*	4/4	0/1	–	–
Bacalar	*Mytilopsis* sp.	40/27	0/8	–	1/0
	Pisidium casertanum	12/10	0/5	–	–
Laguna	*Helisoma anceps*	2/2	–	–	–
Paiyegua	*Laevapex fuscus*	2/2	–	–	–
	Pyrgophorus coronatus	120/95	8/36	1/0	–
Río Hondo	*Valvata humeralis*	54/49	0/9	–	–
La Unión	*Elimia clenchi*	1/1	–	–	–
	Pyrgophorus coronatus	6/6	–	–	–
Río Hondo	*Pomacea paludosa*	4/4	–	–	–
Ramonal	*Anodonta* sp.	1/1	–	–	–
	Mytilopsis sp.	10/10	0/4	–	–
Total		**884/419**	**44/112**	**1/0**	**1/0**

* No. of molluscs with cercariae/No. of snails with metacercariae

malacological survey has been performed in this region. During two short stays of two of the authors in Mexico, freshwater molluscs were collected and examined for presence of larval stages of trematodes. In order to identify larvae found, some experimental infections of fishes as potential intermediate hosts were carried out as well. The aims of the present paper are to provide the first account on the occurrence of larval stages of trematodes occurring in freshwater molluscs from the Yucatan Peninsula and to describe larval stages found.

MATERIALS AND METHODS

A total of 4055 molluscs of 10 species was collected in the following localities of the Yucatan Peninsula in January and February 1995 and in September 1996 (Tables 1 and 2):

a) cenotes (= sinkholes – see Scholz et al. 1995a for details): State of Yucatan: 1. Chaamac (20°52'N; 90°09'W); 2. Noc-choncunchey (20°49'N; 90°12'W); 3. Chek-há (ojo de agua) (20°52'N; 90°07'W); 4. Chen-há (20°54'N; 88°45'W); 5. Ixin-há (20°37'N; 89 °07'W). With the exception of cenote Chek-há visited in 1995, molluscs were sampled in all localities both in 1995 and 1996; State of Quintana Roo: 6. San Pedro 2 (20°27'N; 87 °50'W); 7. Cenote Azul (18°38'N; 88° 25'W); and 8. Dos Bocas (17°55'N; 88°51'W). All samples taken in 1995.

b) swamps and inland lagoons: State of Yucatan: 9. swamp Mitza (21°15'N, 89°40'W; 1995 and 1996); State of Quintana Roo: 10. Laguna Bacalar (18°38'N; 88°25'W); 11. Laguna Paiyegua (19°13'N; 88°30'W); c) rivers: 12. Río Hondo river at the village of La Unión (17°55'N; 88°51'W), 13. Río Hondo river at the village of Ramonal (18°16'N; 88°38'W) (all localities – 1995).

The following mollusc species were examined: *Pyrgophorus coronatus* (Pfeiffer, 1839) (Fig. 1), *Helisoma anceps* (Menke, 1839), *Laevapex fuscus* (C.B. Adams, 1841), *Physella cubensis* (Pfeiffer, 1839), *Valvata humeralis* (Pilsbry, 1890), *Elimia clenchi* (Goodrich, 1942), *Pomacea paludosa* (Say, 1829), *Mytilopsis* sp., *Pisidium casertanum* (Poli, 1791) and *Anodonta* sp.

Molluscs were collected using strainers, placed separately into glass tubes and kept in the light to stimulate the emerging of cercariae. After a few days, portions of the molluscs (see Tables 1 and 2) were removed from their shells by dissection needles and examined using the compression method. Any larval stages found were observed as temporary mounts stained with neutral red and urea solution to highlight the excretory system. For measurements, cercariae were fixed in hot

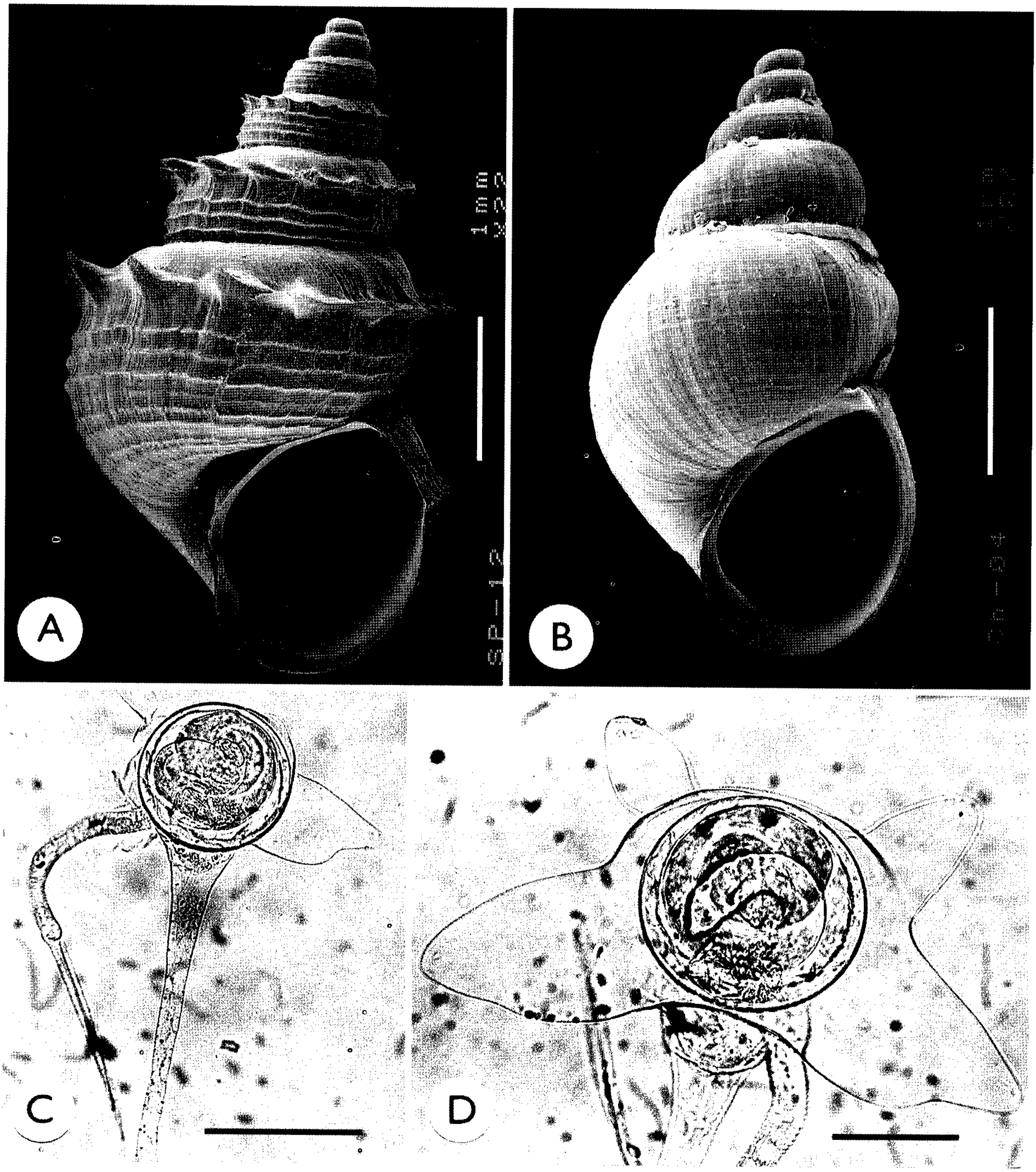

Fig. 1. A,B – *Pyrgophorus coronatus* – scanning electron micrographs of empty shells. This most common snail host abundant in all samples from cenotes forms typical populations with substantial morphological differences of the shell. **A** – cenote Chaamac, January 21, 1995, **B** – cenote Chek-há, January 30, 1995; **C, D** – cystophorous furcocercaria of *Genarchella astyanactis*. Scale bars 100 µm (**C**) and 50 µm (**D**).

4% formaldehyde. All measurements are given in mm as a range, with the mean in parentheses, if at least 10 specimens were measured.

Experimental infections were carried out in the Laboratory of Parasitology, CINVESTAV-IPN, Mérida. Experimental design and number of animals used in the experiments are given directly in comments to individual trematode species studied.

RESULTS

The present study revealed the presence of larval stages (sporocysts, rediae, cercariae, metacercariae) of 13 trematode species in freshwater molluscs from the Yucatan Peninsula. Data on numbers of molluscs and larval stages of trematodes recorded are given in Tables 1 and 2. The survey of larval stages found follows:

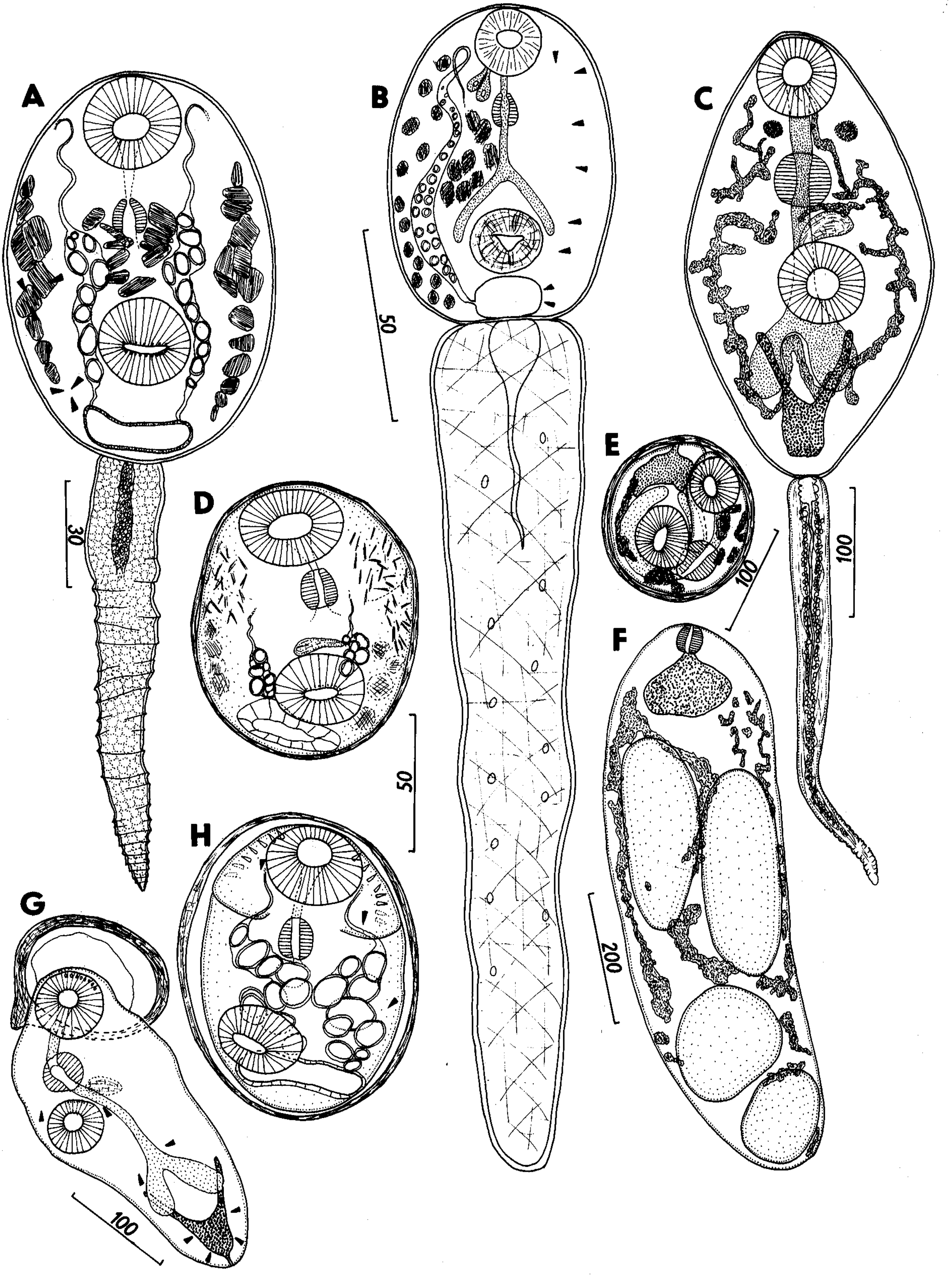

Fig. 2. *Echinochasmus leopoldinae* (**A** – cercaria; **D** – encysted metacercaria from gills of experimentally infected *Oreochromis niloticus*; 2 days post infection (DPI); **H** – encysted metacercaria from gills of experimentally infected *Cichlasoma meeki*; 7–8 DPI; *Echinochasmus macrocaudatus* (**B** – cercaria); *Saccocoelioides* sp. (? *sogandaresi*) (**C** – cercaria; **E** – encysted metacercaria; **F** – redia; **G** – metacercaria partly liberated from cyst). Scale bars in μm.

Family Echinostomatidae Poche, 1926

1. *Echinochasmus leopoldinae* Scholz, Ditrich et Vargas-Vázquez, 1996 Fig. 2A,D,H

Description: Larval stages (sporocyst, rediae, cercaria) from snails were described by Scholz et al. (1996b).

First intermediate host: *Pyrgophorus coronatus*.
Localities: cenotes Chaamac, Noc-choncunchey, Chen-há and Ixin-há.

Comments: The life-cycle of this species has been studied by Scholz et al. (1996b); cenote Chaamac is the type locality of this recently described trematode. Field observations and experimental infections have demonstrated that cichlid fishes (preferably *Cichlasoma urophthalmus*) served as the second intermediate hosts of the parasite; chicks and mice were suitable definitive hosts under experimental conditions (Scholz et al. 1996b).

The present study supplements the description of *E. leopoldinae* cercaria regarding the morphology of the tail, which is covered by transversal tegumental ridges, the course of excretory canals, which are curved around the anterior part of the acetabulum, and the number of excretory corpuscles in cercariae (Fig. 2A). This number was relatively constant, ranging from 7 to 13 (mean 12; n = 6) on each side. Experimental infections of two laboratory-reared *Oreochromis niloticus* (L.) and *Cichlasoma meeki* Brind, kept separately with 50 cercariae from *P. coronatus* and examined 3 and 7 days post infection (DPI), demonstrated that these fish were suitable second intermediate hosts of the parasite (Fig. 2D,H).

Echinochasmus leopoldinae closely resembles another *Echinochasmus* species with 20 collar spines, *E. talanensis* Martorelli, 1985 from Argentina. Larval stages and adults of *E. leopoldinae* are very similar to those of this parasite, the life-cycle of which includes the snail *Littoridina parchappei,* the fish *Cnesterodon decemmaculatus* and passeriform bird *Pitangus sulphuratus bolivianus*. In addition to different host spectrum of both taxa, the main difference between them is the flame cell formula of cercariae: 2 [(1+1+3) + (2+2)] = 18 in *E. talanensis* versus 2 (1+3+3+3) = 24 in *E. leopoldinae* (Martorelli 1985, Scholz et al. 1996b).

2. *Echinochasmus macrocaudatus* Ditrich, Scholz et Vargas-Vázquez, 1996 Fig. 2B

Description: This species was described by Ditrich et al. (1996).

First intermediate host: *Pyrgophorus coronatus*.
Locality: cenote Chaamac.

Comments: Ditrich et al. (1996) studied the life-cycle of *E. macrocaudatus* under natural and experimental conditions. They found that the characid fish *Astyanax fasciatus* (Cuvier) served as the second intermediate hosts under natural conditions; the poeciliid *Xiphophorus variatus* (L.) was successfully infected in the experiments. Chicks and ducks were suitable experimental definitive hosts (Ditrich et al. 1996).

Nasir et Díaz (1973) described very similar cercaria to that of *E. macrocaudatus* from *Pyrgophorus* cf. *spiralis* sampled in Venezuela; it was named *Cercaria pyrgophspiralis* Nasir et Díaz, 1973. This cercaria resembles the cercaria of *E. macrocaudatus* in most morphological details, including the number of flame cells (16). Both cercariae resemble in some morphological features *Cercaria ameeli* Hedrick, 1943 and *C. limosae* Hedrick, 1943. The latter cercariae, however, have 20 flame cells (Nasir et Díaz 1973). The only substantial differences between *C. pyrgophspiralis* and *E. macrocaudatus* are the size (*E. macrocaudatus* is almost two times larger) and the relative length of intestinal caeca: while they reach to the posterior end of the body in *C. pyrgophspiralis,* they do not extend posterior to the acetabulum in *E. macrocaudatus* cercaria.

Family Haploporidae Nicoll, 1914

3. ***Saccocoeliodes*** sp. (? ***sogandaresi*** Lumsden, 1963) Fig. 2C,E–G

Description: Redia (Fig. 2F): Body elongate, 318–924 × 280–340 (715 × 317), without appendices and collar, containing 3–6 developing cercaria. Pharynx round, 42–49 (47) in diameter; gut flask-shaped or oval; birth pore anterior.

Cercaria (Fig. 2C): Distomatous ophthalmocercaria, swimming actively, strongly photopositive, encysting within 24 hours on surface of any object including host shell. Body 282–315 × 144–212 (296 × 185); tail 423–459 × 34–47 (442 × 41). Oral sucker circular, 54–56 (55) in diameter; acetabulum slightly larger, 55–58 (57). Distance between eyespots 55–68 (63). Prepharynx 40–48 (44) long; pharynx oval, 43–47 × 38–41 (45 × 40); oesophagus bifurcating at level of acetabulum; caeca asymmetrical in most cases, inflated. Excretory vesicle Y-shaped, overlapping posterior parts of caeca. Main collecting vessels bifurcating at pharyngeal level; flame cells not observed. Ellipsoid structure (hermaphroditic sac) overlapping acetabulum.

Metacercaria (Fig. 2E,G): Adolescaria ovoid, 176–181 × 171–175 (179 × 173), with distinct outer and inner cyst layers. Oral sucker 54–67; acetabulum 58–67. Prepharynx short, pharynx 44–49 × 40–44; oesophagus long; intestinal caeca short, terminating posterior to

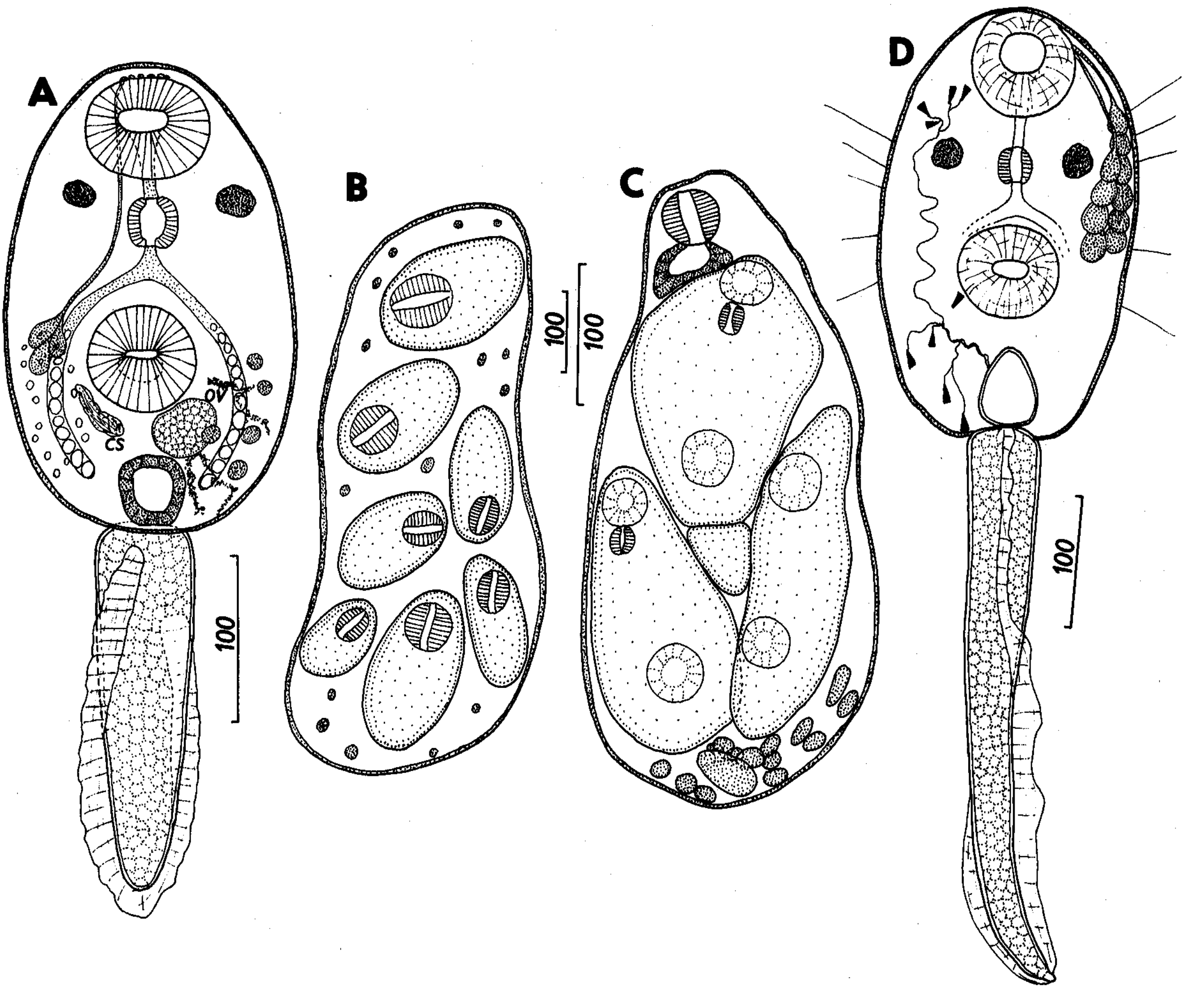

Fig. 3. *Crassicutis cichlasomae* (**A** – mature cercaria emerged from *Pyrgophorus coronatus;* cs – anlagen of cirrus-sac, ov – anlagen of ovary; **B** – sporocyst; **C** – redia); pleurolophocercous ophthalmocercaria of Homalometridae gen. sp. (**D**). Scale bars in μm.

acetabulum. Eyespots absent even in freshly encysted adolescariae.

First intermediate host: *Pyrgophorus coronatus.*

Locality: cenotes Noc-choncunchey and Chen-há.

Comments: Generic identification of the cercariae from *P. coronatus* was based on the similarity of their morphology to that of the haploporid trematodes of the genus *Saccocoelioides* (Yamaguti 1971, 1975, Ostrowski de Núñez 1975). In fishes from cenotes of the Yucatan Peninsula, the only *Saccocoelioides* species, *S. sogandaresi* Lumsden, 1963, was found in the intestine of *Poecilia velifera* and *P. latipunctata* (Scholz et al. 1995a). However, it remains uncertain, if it is indeed *S. sogandaresi*, because experimental infections of poeciliid fish, force-fed with adolescariae, were unsuccessful.

Cercaria of a *Saccocoelioides* sp., presumably *S. sogandaresi*, was described by Cable and Isseroff (1969) from *Amnicola comalensis*. However, the authors noted some morphological differences between their larval stages and original description of *S. sogandaresi* by Lumsden (1963). The cercariae from *P. coronatus* distinctly differ from those of Cable and Isseroff (1969) by their smaller size and by undifferentiated genital primordia. The redia and metacercaria belonging to the protandrous haploporid cercaria described by Cable and Isseroff (1969) differ from the same larval stages found in *P. coronatus* and they can be hardly conspecific.

Cercaria of *Saccocoelioides* sp. described from *Littoridina piscium* in Argentina (Ostrowski de Núñez 1975) is larger and its genital primordium is well differentiated into the testes and ovary.

Family Homalometridae Cable et Hunninen, 1942

4. ***Crassicutis cichlasomae*** Manter, 1936 Fig. 3A–C

Description: With the exception of the miracidium and sporocyst, developmental stages of this trematode were described by Scholz et al. (1995c),
Sporocyst (Fig. 3B): Body elongate, 658–745 × 218–236 (703 × 224), containing 10–24 rediae in various stages of development and tiny round granules.

First intermediate host: *Pyrgophorus coronatus.*

Second intermediate hosts: *P. coronatus, Physella cubensis, Valvata humeralis, Mytilopsis* sp., *Pisidium casertanum.*

Localities: cercariae: cenotes Chaamac, Noc-choncunchey, Chen-há, Cenote Azul, swamp Mitza, Laguna Bacalar and Río Hondo (La Unión); metacercariae: cenotes Chaamac, Noc-choncunchey, Chen-há, Azul, swamp Mitza, Laguna Bacalar and Río Hondo at the villages of La Unión and Ramonal (Tables 1 and 2).

Comments: The present study demonstrated that the prosobranch snail *P. coronatus* was erroneously identified as *Littorina angulifera* by Scholz et al. (1995c); this snail was reported to serve both as the first and the second intermediate host of *C. cichlasomae.*

Results of malacological examination of snails showed that other molluscs, including pulmonate snails and bivalves, served as the second intermediate hosts of this trematode. Numerous localities with positive findings as well as a high number of infected molluscs (Tables 1 and 2) correspond well with frequent occurrence of *C. cichlasomae* adults in cichlid fishes from the Yucatan Peninsula (Manter 1936, Salgado-Maldonado 1993, Scholz et al. 1995a,c).

The present study showed that no more than 6 cercariae emerged from one snail in a day, independant of the light intensity. Emerged cercariae were neither positively nor negatively phototactic, swimming tail first. Median group of penetrating glands was observed both in freely swimming cercariae and in cercariae not leaving host snails; the lateral groups of glands were found only in not emerging cercariae (compare fig. 9 in Scholz et al. 1995c with Fig. 3A in the present paper). Their absence in mature free swimming cercaria might indicate that these glands were emptied during the passage through the host tissues.

Additional details of the morphology of the cercaria were supplemented herein, i.e., the presence of genital anlagens of the ovary and cirrus-sac (Fig. 3A), situated posterior and posterolateral to the acetabulum, the presence of transparent round bodies within intestinal caeca and the presence of ventral finfold near the basis of the tail.

Although the present data did not enable us an assessment of the seasonal patterns in the occurrence of larval stages of *C. cichlasomae* in molluscs, different values of prevalence between two sampling dates (January – February 1995 versus September 1996) are remarkable. While 23 of 2304 *P. coronatus* collected in various localities in January and February shed mature cercariae and only in 5 cases cercariae could be found just in dissected snails, in September none of the 1804 snails examined was found to release cercariae of *C. cichlasomae*.

5. **Homalometridae** gen. sp. Fig. 3D

Description: Cercaria (Fig. 3D): Pleurolophocercous ophthalmocercaria, positively phototactic when dissected out of host tissue. Body 262–295 × 146–159 (285 × 156), provided with setae. Tail 187–298 × 33–37 (287 × 35), provided with narrow lateral finfold and papilliform tip. Oral sucker terminal, 49–51 × 54–61 (50 × 56); acetabulum slightly subequatorial, 51–53 × 58–61. Prepharynx longer than oesophagus; pharynx elliptical, 28–30 × 22–24 (29 × 23). Intestinal caeca short, ending at level of middle of acetabulum. Eye-spots relatively large, 17–20 (19) in diameter, distance between them 48–51 (50). Ten pairs of globular penetrating glands staining with neutral red grouped together between eyespots and acetabulum. Flame cell formula not completely determined; two doublets of flame cells between eyespot and oral sucker, one doublet and single cell at least two cells at level of excretory bladder on each side of body.

Host: *Pyrgophorus coronatus.*

Locality: Río Hondo (La Unión).

Comments: The morphology of the cercariae indicates they belong to the family Homalometridae (see Yamaguti 1975). Since only one infected snail was available and a limited number of cercariae was found, more precise identification was impossible.

Family **Heterophyidae** Odhner, 1914

6. ***Ascocotyle (Ascocotyle)*** sp. Fig. 4A,D

Description: Redia (Fig. 4D): Body sausage-shaped, 543–712 × 135–218 (616 × 201), containing germ balls and cercariae in different stages of development; some cercariae protruding (Fig. 4D). Pharynx 24–28 × 25–28 (26 × 27); gut short and stout. Birth pore not observed; developed cercariae in posterior part. Mature rediae brownish, with dark brown pigment in gut.
Cercaria (Fig. 4A): Parapleurolophocercous ophthalmocercaria, actively moving and strongly positively phototactic, S-shaped when not moving. Body pyriform,

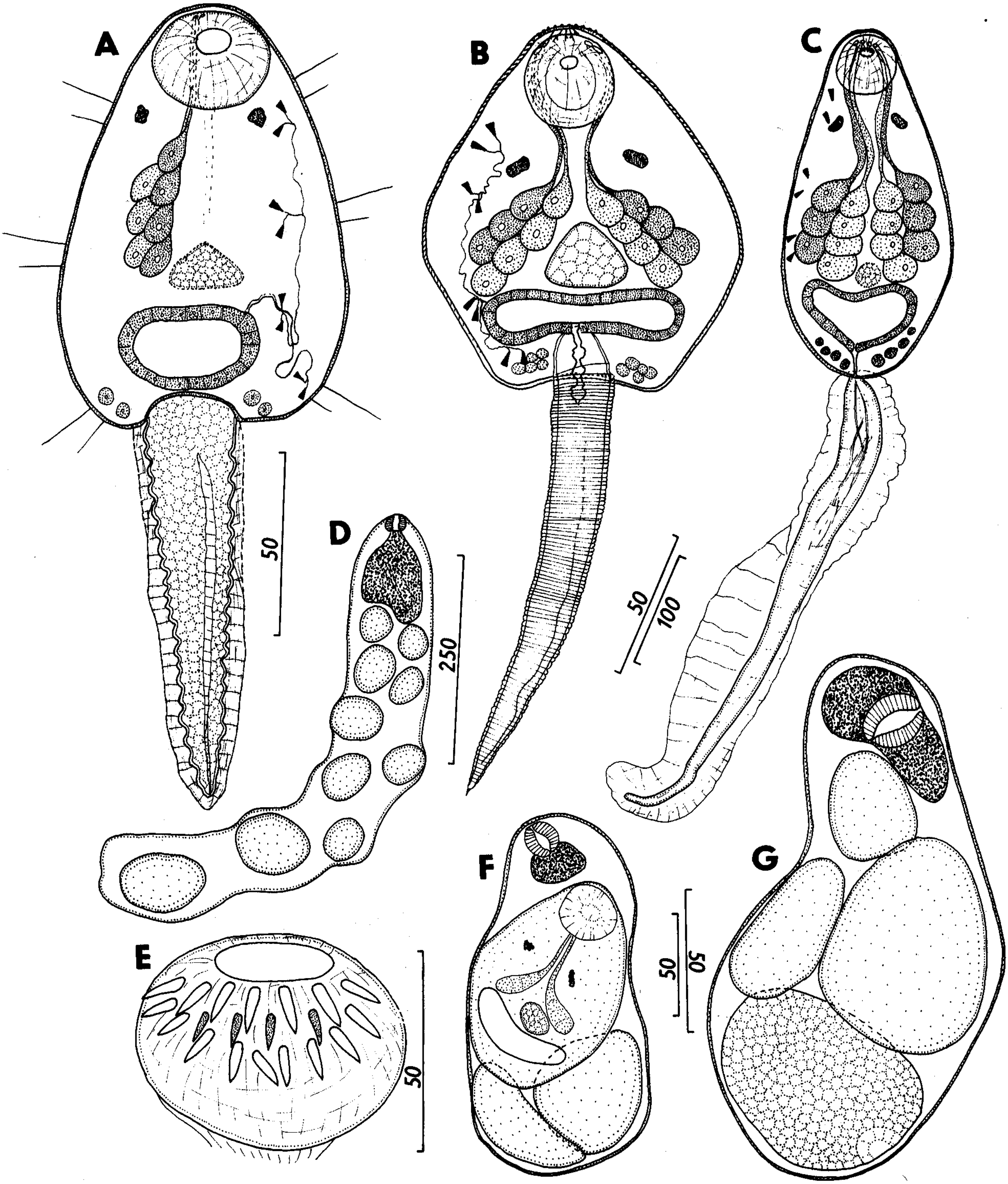

Fig. 4. *Ascocotyle* (*Ascocotyle*) sp. (**A** – cercaria; **D** – redia); *Ascocotyle* (*Phagicola*) *nana* (**B** – cercaria; **E** – circumoral spines of metacercaria from the intestinal wall of experimentally infected *Cichlasoma meeki* (37 DPI); **F** – mature redia; **G** – young redia); *Oligogonotylus manteri* (**C** – cercaria). Scale bars in µm.

103–117 × 52–69 (111 × 64); tail 119–133 × 17–19 (128 × 18), provided with inconspicuous dorsoventral finfold and distinct, but narrow lateral finfold. Because of limited material, the finfolds on Fig. 4A are only drafted and more detailed study is necessary for the reliable description of their arrangement. Six pairs of sensory setae arranged in doublets: near eyespot, at midbody and at posterior extremity; anterior seta in each doublet always longer than posterior one. Distance between eyespots 27–29 (28). Oral sucker oval, 20–23 × 24–28 (21 × 25); anlage of ventral sucker triangular; pharynx and intestinal caeca not observed. Seven pairs of penetration glands, arranged in two groups of three and four cells differently stained in neutral red; their ducts running forward between eyespots and opening at anterior extremity. Two pairs of unicellular unopened glands intensively staining in neutral red in posterior extremity. Excretory bladder epithelial, large, 24–27 × 26–32 (26 × 29). Flame cell formula 2 [(2+2) + (2+2)] = 16.

First intermediate host: *Pyrgophorus coronatus.*

Locality: cenote Noc-choncunchey.

Comments: Morphology of the cercariae reveals characteristic features of the nominotypical subgenus *Ascocotyle* Looss, 1899: the presence of lateral finfold and absence of acicular spines and caudal spine (Ostrowski de Núñez 1993). However, species identification is not possible because experimental infections of fish have not been successful yet.

7. *Ascocotyle (Phagicola) nana* Ransom, 1920

Figs. 4B,E–G, 5

Description: Redia (Fig. 4F,G): Body sausage-shaped, 320–680 × 92–255 (574 × 138), containing cercariae in different stages of development and tiny granules of brownish pigment. Pharynx spherical, 22–25 (24) in diameter, gut flask-shaped, dark brown. Actively moving cercariae situated anteriorly.

Cercaria (Fig. 4B): Pleurolophocercous ophthalmocercaria, actively moving and positively phototactic. Body almost rectangular, 148–159 × 106–119 (154 × 110); tail 162–178 × 17–24 (171 × 22), provided with inconspicuous dorsoventral finfold and with caudal spine on its posterior end. Oral sucker almost circular, 27–33 × 25–32 (29 × 28); acetabulum poorly developed. Five acicular spines on anterior border of oral sucker. Eyespots in first third of body, distance between them 64–73 (67). Seven pairs of penetration glands arranged in two groups: lateral one containing 3, median one 4 cells; ducts of glands forming two pairs directed anteriorly between eyespots, opening at inner margin of oral sucker. Five pairs of unicellular unopened glands intensively stained with neutral red in posterior extremity. Excretory bladder epithelial, widely oval, 18–25 × 46–67 (23 × 61). Flame cell formula 2 [(2+2) + (2+2)]= 16.

Metacercaria (37 DPI; Figs. 4E,5): body pyriform, 600 × 290, anterior three quarters covered with small tegumental spines. Preoral lobe indistinct; oral sucker subterminal, 48 × 55, with short posterior solid prolongation. Sucker armed with 20 spines arranged in one complete of 16 circumoral spines and four accessory spines dorsally (Fig. 4E); spines in complete row 8–10 long and 2 wide; additional spines 8–9 long and 2 wide. Prepharynx short (40); pharynx muscular, 37 × 37; oesophagus 75 long; intestinal caeca very long, surrounding acetabulum and curved medially anterior to excretory bladder. Ventral sucker spherical, 47 × 50, situated slightly postequatorially (at 53% of body length). Genital sac formed, containing pad-like gonotyl armed with about 17 finger-like pockets. Testes symmetrical, near posterior extremity, measuring 37 × 42. Ovary postacetabular, 27 × 32. Excretory bladder Y-shaped.

First intermediate host: *Pyrgophorus coronatus.*

Second intermediate host (experimental): *Cichlasoma meeki.*

Localities: cenotes Chaamac and Chen-há.

Comments: Identification of cercariae is based on their morphology (see Ostrowski de Núñez 1993) and results of experimental infections of fish. Five laboratory-reared *Cichlasoma meeki* and 8 *Poecilia reticulata* were kept 24 hours in contact with cercariae from *P. coronatus*. Number of cercariae ranged from 30 (2 *C. meeki*) to 100 (6 *P. reticulata*); fish were dissected 8, 10, 12 and 37 DPI. In the intestinal wall of three fish (*P. reticulata* – 12 DPI; *C. meeki* – 8 and 37 DPI) were found three encysted metacercariae. The larvae found 8 and 12 DPI resembled in their morphology cercariae, including the presence of 5 acicular spines in the oral sucker and well preserved eyespots. Metacercaria found 37 DPI was fully formed. It corresponded completely in its morphology, including the shape of the body, its spination, number and arrangement of circumoral spines (Fig. 4E), length and shape of intestinal caeca and morphology of the gonotyl with numerous finger-like pockets (Fig. 5) to metacercariae of *A.* (*P.*) *nana* found in cichlid fishes from cenote fish in the Yucatan Peninsula (Scholz et al. 1995b, 1997).

In fishes from cenotes Chen-há and Chaamac, where cercariae were found in *P. coronatus*, metacercariae of *A.* (*P.*) *nana* occurred very common (Scholz et al. 1995b).

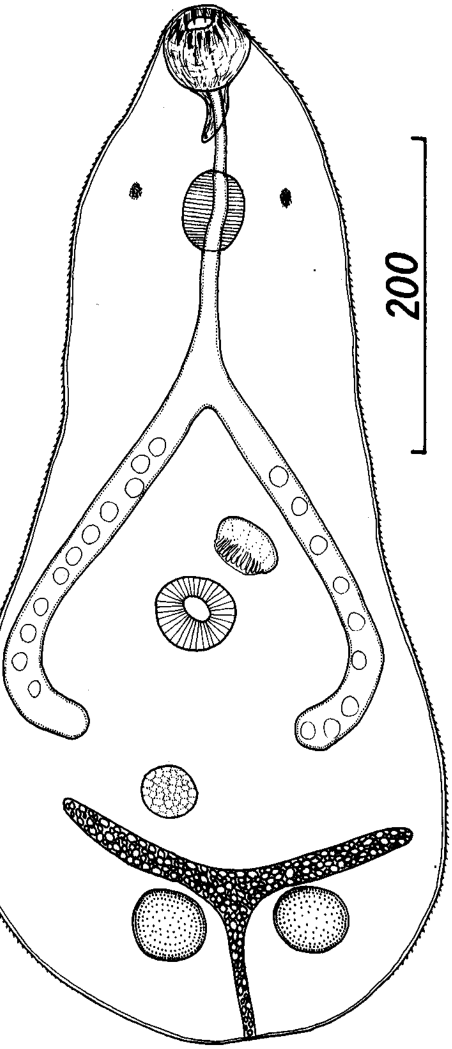

Fig. 5. *Ascocotyle* (*Phagicola*) *nana*. Metacercaria from the intestinal wall of experimentally infected *Cichlasoma meeki*, 37 DPI. Scale bar in µm.

Family **Cryptogonimidae** Ward, 1917

8. ***Oligogonotylus manteri*** Watson, 1976 Fig. 4C

Description: Larval stages from snails were described by Scholz et al. (1994).

First intermediate host: *Pyrgophorus coronatus*.

Localities: cenotes Chaamac, Ixin-há and Dos Bocas.

Comments: This species is a specific parasite of cichlids, which serve both as the second intermediate and definitive hosts (Scholz et al. 1994). The authors erroneously reported the prosobranch *Benthonella gaza* to serve as the first intermediate host of the parasite. It is evident that *P. coronatus* was misidentified. The present study demonstrated that *O. manteri* cercaria has not only dorsoventral, but also less developed lateral finfold on the tail (Fig. 4C); because of this feature, the cercaria is parapleurolophocercous. It was also observed that there are four pairs of unicellular unopened glands intensively stained by neutral red situated near the posterior extremity (Fig. 4C).

Family Derogenidae Lühe, 1910

9. ***Genarchella astyanactis*** (Watson, 1976) Figs. 1C,D, 6,7

Description: Sporocyst (Fig. 6A): Body sacciform, containing a few rediae (5–10).

Redia (Fig. 6B–D): Body elongate, 820–918 × 235–321 (876 × 296), containing 20–40 cercariae in various stages of development. Pharynx 50–57 × 32–36; gut containing dark brown pigment, reaching up to mid-body in young rediae (Fig. 6B,C), short and suppressed by developing cercariae in mature rediae (Fig. 6D).

Cercaria (Figs. 1C,D, 6E,F): Cystophorous furcocercaria (= furcocystocercous cercaria), slowly floating by pendulum-like movement of tail. Cyst shell transparent, created by two layers: thick internal membrane densely covering body with poorly differentiated organs, and external membrane, detached from internal membrane and creating four finlike wings and empty caudal appendage. Diameter of internal cyst layer 94–97 (95), maximum width of external membrane 293–311 (298). Tail forked, 445–512 × 17–24 (483 × 22); furci representing 2/5 of tail length. Cercaria, evaginated from cyst by light coverslip pressure, elongate, 123–138 × 25–28 (126 × 26). Oral sucker subterminal, 19–20 × 20–22 (20 × 21); acetabulum spherical, 20–22 × 21–25 (21–23). Prepharynx absent; pharynx spherical, 18–21 × 20–23 (20 × 22); gut not observed. Evaginated delivery tube elongate, with widened anterior (distal) end, containing spherical bodies.

Metacercaria (Fig. 6G–I): Body elongate, measuring 320–416 × 90–162. Oral sucker subterminal, 46–62 in diameter; ventral sucker strongly muscular 67–72 × 54–84, with slit-like opening (Fig. 6G,H); prepharynx absent, pharynx muscular, almost spherical 29–32 × 29–31; oesophagus short; intestinal caeca long, reaching posteriorly near posterior extremity. Anlage of ovary (?) near posterior extremity, anterior to two vitelline follicles (Fig. 6D).

First intermediate host: *Pyrgophorus coronatus*.

Second intermediate host: *Mesocyclops chaci* Fiers, Reid, Ilife et Suárez-Morales, 1996 (Copepoda: Cyclopidae) (experimentally).

Locality: Chaamac.

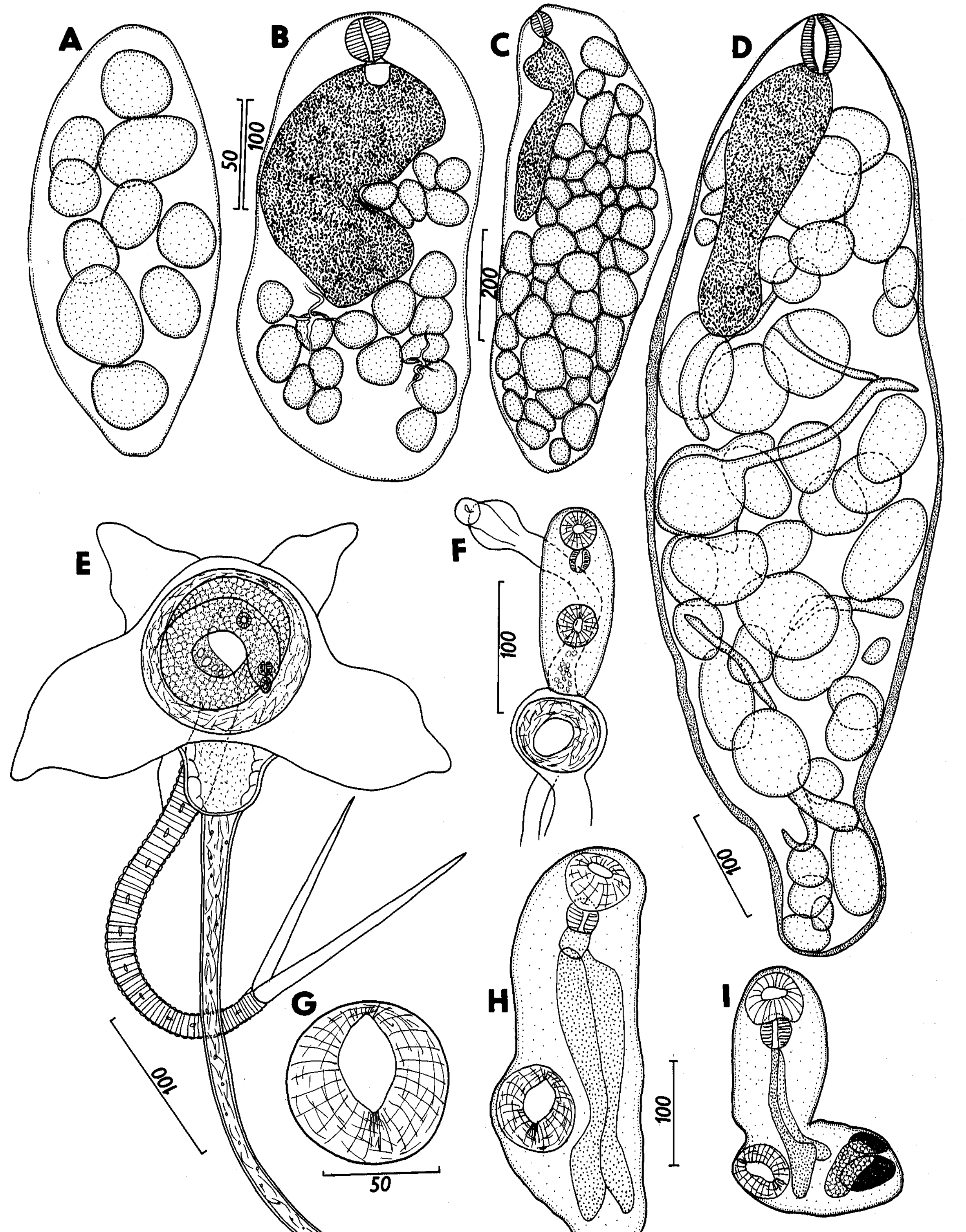

Fig. 6. *Genarchella astyanactis*. **A** – sporocyst; **B,C** – young rediae; **D** – mature redia with cercariae; **E** – cystophorous cercaria; **F** – body of cercaria with delivery tube; **G** – ventral sucker of metacercaria; **H,I** – metacercariae from experimentally infected *Mesocyclops chaci*, 19 DPI. Scale bars in μm.

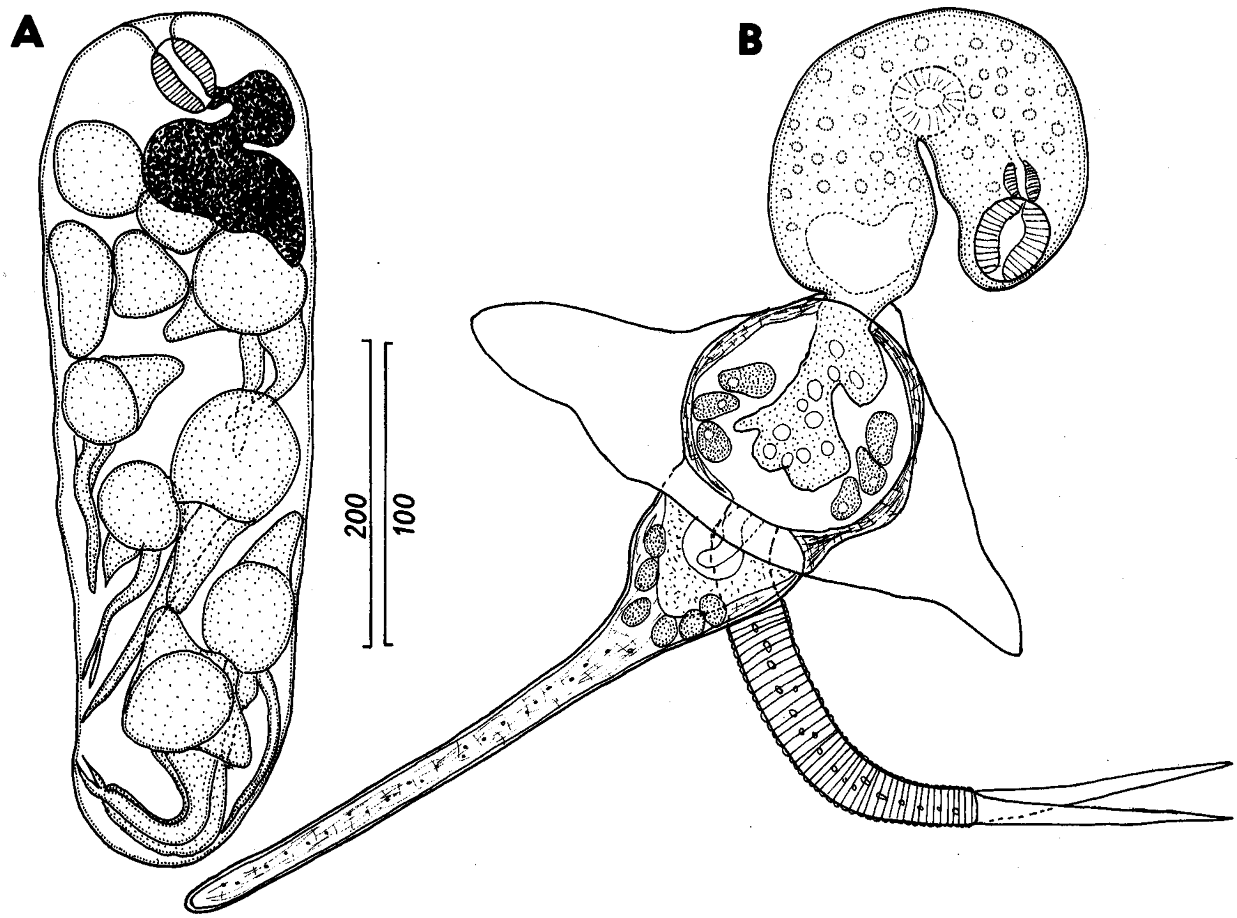

Fig. 7. *Genarchella astyanactis.* **A** – mature redia from experimentally infected *Pyrgophorus coronatus*, 95 DPI; **B** – cystophorous cercaria from the same host; cercarial body extruded by a coverslip pressure, 95 DPI. Scale bars in μm.

Comments: The morphology of the cercariae clearly showed that they belonged to the family Derogenidae (see Yamaguti 1975, Goater et al. 1990). The morphology of experimentally recovered metacercariae found in the body cavity of the copepod *Mesocyclops chaci*, above all the shape of the ventral sucker with incision-like aperture, corresponds to the morphology of juvenile trematodes of *G. astyanactis* found in the stomach of *Astyanax fasciatus* in the same cenote (data not shown; see also Scholz et al. 1995d).

Adult trematodes of *G. astyanactis* are very common in fish from this cenote (Scholz et al. 1995a), which tallies with extremely high proportion of snails infected with the cercariae.

Sixty juvenile infection-free snails *P. coronatus* were experimentally kept in contact with 200–300 eggs from the uterus of *G. astyanactis* adult, obtained from *A. fasciatus* (precise number of ripe eggs not determined). Only 24 snails survived 95 days, when they were dissected because no shedding cercariae were observed. In 2 snails dissected, larval stages were found. Three juvenile rediae without cercariae were found in the hepatopancreas of one specimen; 8 mature rediae (Fig. 7A) containing cystophorous furcocercariae (Fig. 7B) were observed in the other specimen.

The only *Genarchella* species, the life-cycle of which has already been elucidated, is *G. genarchella* Travassos, 1928. Szidat (1956) described progenetic cercaria of *G. genarchella* from the snail *Littoridina australis.* However, Martorelli (1989) found cystophorous cercaria and he described a monoxenous cycle of *G. genarchella* that comprises cystophorous cercariae and progenetic metacercariae; both stages were found in the same snail, *Littoridina parchappei.*

Cystophorous çercaria of *G. genarchella* differs from that of *G. astyanactis* above all in the absence of furca in the tail and different shape of the cyst, which lacks lateral wings. Martorelli (1989) never observed the

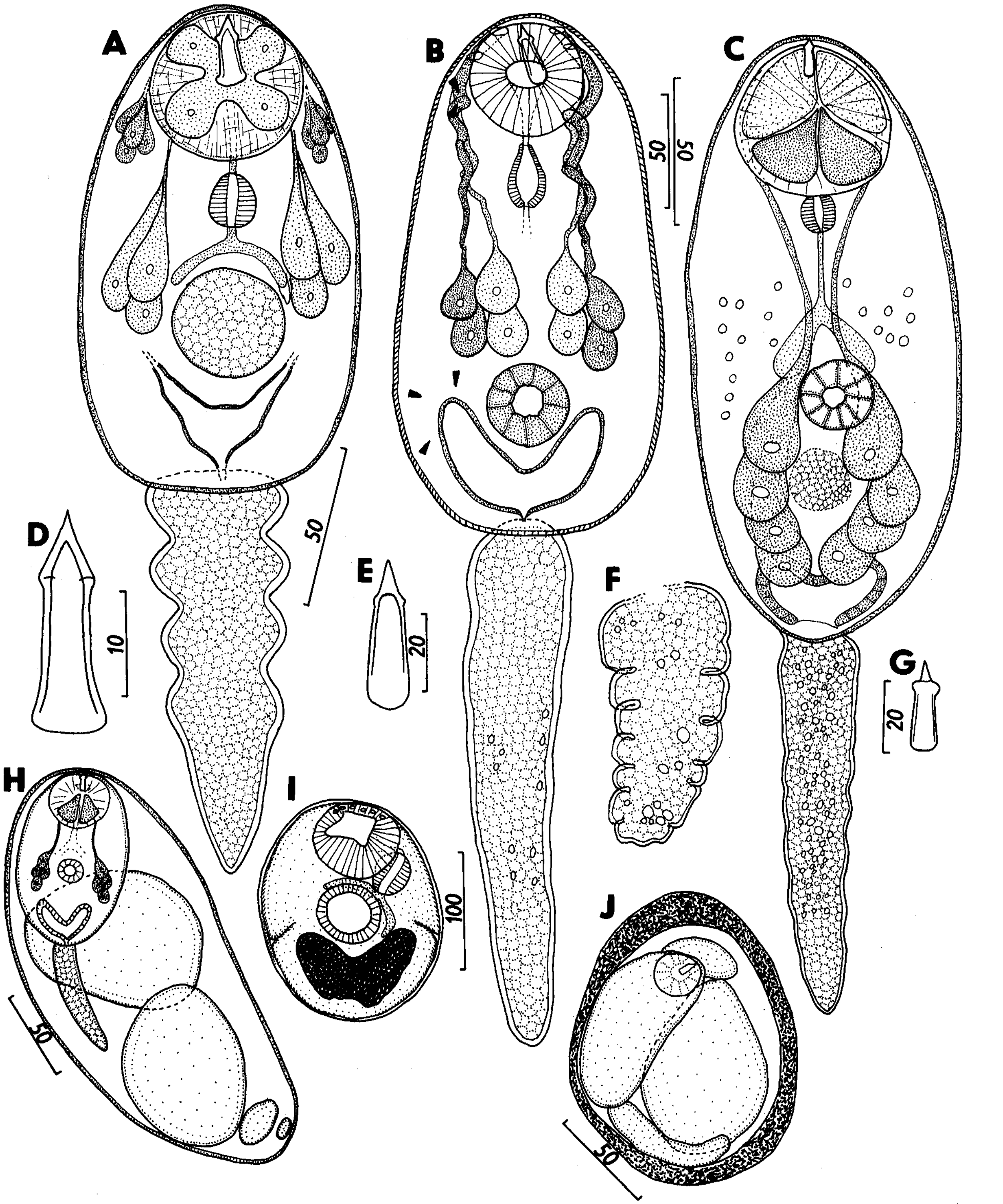

Fig. 8. Xiphidiocercaria sp. 1 (**A** – cercaria; **D** – stylet; **I** – encysted metacercaria); xiphidiocercaria sp. 2 (**B** – cercaria; **E** – stylet; **F** – contracted tail; **J** – sporocyst); xiphidiocercaria sp. 3 (Lecithodendriidae?) (**C** – cercaria; **G** – stylet; **H** – sporocyst). Scale bars in μm.

emergence of cystophorous cercariae from snails but he supposed that they were released as in other hemiurid trematodes (e.g., Køie 1979, Goater et al. 1990). Martorelli (1989) assumed that cystophorous cercariae of *G. genarchella* transform into progenetic metacercariae within rediae. The existence of such a cycle in *G. astyanactis* does not seem to be probable because progenetic cercariae (or metacercariae) were not found in any snails dissected.

Cercaria of *G. astyanactis* can be identical with *Cercaria propulsovelera* Nasir et Díaz, 1973 found in *Pyrgophorus* cf. *spiralis* from Venezuela (Nasir et Díaz 1973), since no difference between them were observed. Although *G. astyanactis* has hitherto been reported only from Mexico and Central America (Watson 1976, Scholz et al. 1995d), its occurrence in Venezuela cannot be excluded because its definitive host, *Astyanax fasciatus*, occurs also in South America.

10. **Xiphidiocercaria** sp. 1 — Fig. 8A,D,I

Description: Cercaria (Fig. 8A): Simple-tailed xiphidiocercaria, actively moving and positively phototactic. Body 196–211 × 125–139 (202 × 131); tail 192–223 × 23–28 (206 × 25). Oral sucker 46–52 × 51–59 (49 × 57) with virgule-like structure; acetabulum poorly developed, spherical, 34–39 (37) in diameter, slightly postequatorial. Stylet 19.5–20.3 × 3.6–3.8 (20.0 × 3.7) (Fig. 8D). Prepharynx developed; pharynx muscular, 19–24 × 12–18 (22 × 16); caeca short, terminating at acetabular level. Four pairs of cephalic glands lateral to oral sucker; three pairs of larger unicellular glands anterolateral to acetabulum. Excretory bladder V-shaped; flame cells not observed.

Metacercaria (Fig. 8I): Cyst widely oval, thin-walled, 174–208 × 152–177 (193 × 162). Metacercaria elongate; with stylet in middle or posterior part of body; oral sucker strongly muscular 71–81 × 79–88; ventral sucker smaller, postequatorial, 53–56 (55) in diameter. Prepharynx short; pharynx oval, muscular 31–37 × 31–34 (35 × 32); intestinal caeca reaching to acetabulum. Anlagen of genitalia posterior to acetabulum.

First intermediate host: *Helisoma anceps.*

Second intermediate host: *Pyrgophorus coronatus, H. anceps.*

Locality: cenote Dos Bocas.

Comments: Encystation of cercariae was observed within the same snail host, *H. anceps*. In *P. coronatus*, morphologically identical metacercariae were also found. The cercaria rather resembles *Cercaria abdulhameedi* Nasir, 1982 from other planorbid snail, *Biomphalaria straminea* from Venezuela, especially in its size, the shape of stylet, the ratio of sucker diameter, and Y-shaped excretory bladder. Nonetheless, there are some differences in the number and arrangement of penetration and cephalic glands (Nasir 1982).

11. **Xiphidiocercaria** sp. 2 — Fig. 8B,E,F,J

Description: Sporocyst (Fig. 8J): Body spherical to widely oval (111–138 × 103–109), with very thick wall, containing only one developed cercaria and few germ balls.

Cercaria (Fig. 8B,F): Simple-tailed xiphidiocercaria, actively moving and positively phototactic. Body 213–228 × 121–127 (225 × 124); tail 117–129 × 36–45 (122 × 40). Oral sucker spherical, 49–52 (50) in diameter; acetabulum postequatorial, spherical, 44–47 (46) in diameter. Stylet 39.1–40.5 × 5.9–6.2 (40.3 × 6.1) (Fig. 7E). Prepharynx very short; pharynx muscular, 9–13 × 6–9 (11 × 8); gut hardly observable. Four pairs of unicellular penetrating glands in midbody, with two pairs of prominent sinuous ducts forming loops at pharyngeal level and opening on anterior margin of oral sucker. Excretory bladder U-shaped; flame cell formula not completely determined; three flame cells near excretory bladder and two near oral sucker in both sides of body.

Host: *Pyrgophorus coronatus.*

Locality: cenote Noc-choncunchey.

Comments: The cercaria from *P. coronatus* resembles in some morphological features *Cercaria paracumanensis* Nasir, 1971 from *Marisa cornuarietis* – Nasir (1971), *C. allomacarapanensis* Nasir et Díaz, 1968 from *M. cornuarietis* and *Pomacea glauca* (Nasir et Díaz 1968). However, there are distinct differences in the shape of the stylet (Fig. 8E) and in the number and position of penetrating glands.

12. **Xiphidiocercaria** sp. 3 (Lecithodendriidae?) — Fig. 8C,G,H

Description: Sporocyst (Fig. 8H): Body sac-like, thin-walled, 171–254 × 113–115, containing a few developing cercariae.

Cercaria (Fig. 8C): Virgulate, simple-tailed xiphidiocercaria, actively moving and positively phototactic. Body 154–168 × 88–98 (162 × 95); tail 95–122 × 27–37 (112 × 33). Oral sucker 49–53 × 58–63 (52 × 61), with prominent internal lobes; acetabulum equatorial to slightly postequatorial, spherical, 23–28 (26) in diameter. Stylet 22.4–24.7 × 4.6–6.0 (22.6 × 5.7) (Fig. 8G). Prepharynx absent; pharynx strongly muscular, 20–25 × 15–19 (22 × 18); gut bifurcating anterior to acetabulum, caeca terminating at acetabular level. Four pairs of large unicellular penetrating glands postacetabular, opening by single duct near anterior extremity. Genital primordium large, spherical, posterior to acetabulum. Excretory bladder epithelial, thick- walled,

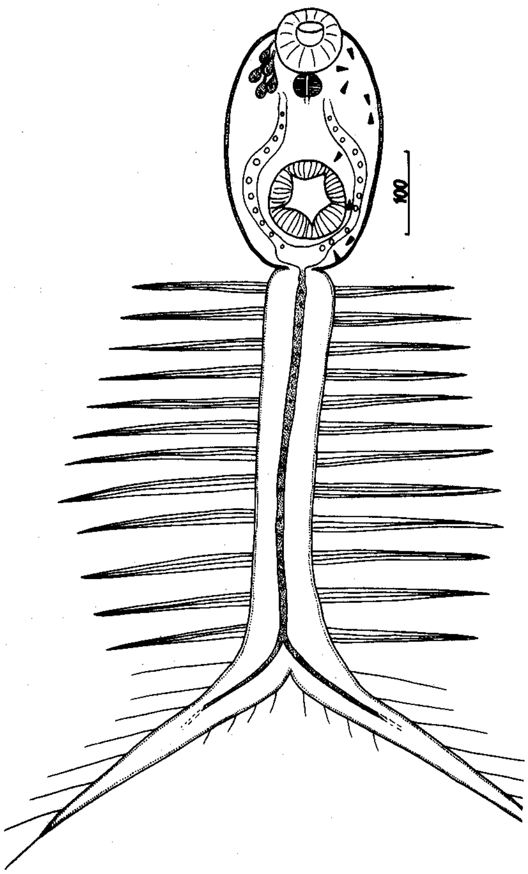

Fig. 9. Trichocercous furcocercaria of Fellodistomidae gen. sp. Scale bar in µm.

oval; flame cell formula not determined. Transparent spherical refractile bodies posterior to pharynx.

Host: *Pyrgophorus coronatus.*

Locality: cenotes Noc-choncunchey, Chen-há and Ixin-há.

Comments: The cercaria rather resembles *Cercaria cumanensis* Nasir, 1965 from *Marisa cornuarietis* from Venezuela that develops also in sporocysts. However, this microcotylous xiphidiocercaria has only two pairs of penetrating glands (Nasir 1965).

Cercaria from *P. coronatus* also resembles in its morphology members of the family Lecithodendriidae Lühe, 1901, mainly those of the genera *Loxogenes* Stafford, 1905 and *Pleurogenoides* Travassos, 1921, which are also virgulate, with four pairs of penetration glands and a small acetabulum (see Yamaguti 1975 – figs. 549, 558 and 569). Members of the above mentioned genera are common parasites of amphibians.

In cenote Ixin-há, metacercariae and adults of a lecithodendriid trematode, *Loxogenes* sp., were found in dragonfly naiads and frogs, respectively (F. Moravec – pers. comm.). It cannot be excluded that cercariae found in *P. coronatus* belong to this species. However, the confirmation of this assumption requires experimental evidence.

13. **Fellodistomidae** gen. sp. Fig. 9

Description: Sporocyst: Body filamentous, about 3 to 4 mm long, containing numerous cercariae.

Cercaria (Fig. 9): Trichocercous furcocercaria, slowly moving, without phototaxy. Body elongate, 309–336 × 134–150 (325 × 147); tail trunk 236–248 × 71–77 (245 × 73); one branch of furca 238–250 × 66–71 (244 × 68). Tail with 12 pairs of finlets, 76–173 long, furca with thick tegumental hairs 24–57 (55) long. Oral sucker prominent, 59–62 × 62–66 (60 × 64); acetabulum 55–59 × 55–59 (58 × 57). Prepharynx absent; pharynx 25–28 × 27–30 (27 × 29). Gut not observed. Five pairs of cephalic glands lateral to pharynx. Excretory bladder oval, filled with refractile concretions, tips of its arms reaching to pharyngeal level. Caudal tubule prominent, opening not observed. Flame cell formula 2 [(3+2) + (2 +2)] = 18.

Host: *Mytilopsis* sp.

Locality: Río Hondo (Ramonal).

Comments: Sporocysts were found in mantle tissues and gonads of only one specimen of *Mytilopsis* sp. Morphology of the cercaria resembles members of the family Fellodistomidae, which are mostly furcocercous and develop in various bivalves (Yamaguti 1975). The most similar cercaria, *Cercaria caribea LIII* Cable 1963, however, lacks a forked tail (Cable 1963). Other cercariae of fellodistomatid trematodes are furcocercarious in most cases and they develop in various species of Bivalvia (Yamaguti 1971).

Members of the Fellodistomatidae are parasites of marine, brackish water fish (Yamaguti 1971).

DISCUSSION

The examination of freshwater molluscs from the Yucatan Peninsula revealed the presence of 13 trematode species. Six of them could be identified to the species level on the basis of their morphology, results of experimental infections of potential intermediate and definitive hosts as well as data on the occurrence and morphology of metacercariae occurring in the same localities. Remaining larval stages could not be identified because sufficient data on their development and morphology of adult stages were not available.

In addition to the information about larval stages of trematodes, this study provided the first account on the occurrence of freshwater molluscs in the region.

Considering the geological structure of the Peninsula, the superficial layer of which is formed by limestone, rich malacofauna had been expected. However, the diversity of molluscs found was extremely poor: only 4 species of prosobranch snails, 3 species of pulmonates and 3 species of bivalve molluscs were recorded. The prosobranch snail *Pyrgophorus coronatus*, which served as the first intermediate host for as many as 11 of 13 trematode species, was a typical component of cenote fauna and predominated in almost all localities (Tables 1 and 2).

Since no malacological research has been carried out in the Yucatan Peninsula, the identification of molluscs was difficult despite their resemblance to some forms from southeastern USA (Florida) or South America. Consequently, some of the molluscs found were identified only to generic level. Their precise determination can be made only after a thorough study on the malacofauna of the region is performed. Although the mollusc fauna is predominately Nearctic, cercariae found apparently belong to the Neotropical fauna, similar to a majority of endohelminths recorded from freshwater fishes in Yucatan (Moravec et al. 1995a,b, Scholz et al. 1995a,b, 1996a). Some cercariae found in *P. coronatus* are undoubtedly related to those occurring in *Pyrgophorus* cf. *spiralis* from Venezuela (Nasir et Díaz 1973).

Despite poor diversity of malacofauna and a short period of mollusc sampling, a relatively high number of larval stages was found in some localities, e.g. in cenotes Noc-choncunchey, Chaamac and Chen-há. In these localities, metacercariae of trematodes were the commonest parasites of fish as well (Scholz et al. 1995b).

The life-cycle of *Genarchella astyanactis* was first elucidated in this study. It was almost completed from adult worms found in naturally infected definitive host, characid fish *Astyanax fasciatus*, to metacercariae recovered from experimental second intermediate host, the copepod *Mesocyclops chaci*. It was demonstrated that it distinctly differs from that found in congeneric species, *Genarchella genarchella*, as described by Szidat (1956) and Martorelli (1989). It is worth mentioning that the cycle of *G. astyanactis* includes two intermediate hosts, a prosobranchiate snail, *P. coronatus*, and a copepod. In this features as well as in the morphology of the cystophorous cercaria, the life-cycle of *G. astyanactis* is very similar to those of marine hemiuroid trematodes of the genera *Lecithocladium*, *Hemiurus*, *Brachyphallus*, and *Lecithochirium* (see Køie 1995) and fresh-water derogenid *Halipegus occidualis* Stafford, 1905 (Goater et al. 1990).

It is worth mentioning the results of the mollusc examination in Ixin-há cenote, where cercariae of three trematodes were found. Two of them are specific parasites of cichlid fishes. However, cichlids have never been observed in this cenote. The only fish captured in Ixin-há cenote was the pimelodid catfish *Rhamdia guatemalensis*, in which neither *Echinochasmus leopoldinae* nor *Oligogonotylus manteri* occur (Scholz et al. 1994, 1996b). It cannot, however, be excluded that some cichlids can migrate through subterranean water systems and could reach cenote Ixin-há. The cichlid *Cichlasoma urophthalmus*, serving as the definitive host of *O. manteri* and second intermediate host of *E. leopoldinae*, occurs in other cenotes of the central part of the Yucatan Peninsula.

The present study provided some new data on larval stages of trematodes. However, it is evident that further investigations into the larval stages of trematodes in freshwater molluscs of the Peninsula are necessary. Taking into account the richness of the fauna of adult trematodes and their metacercariae (Scholz et al. 1995a, b), larval stages of other species will undoubtedly be found.

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