FOLIA PARASITOLOGICA 42: 173–192, 1995

Metacercariae of trematodes of fishes from cenotes (= sinkholes) of the Yucatan Peninsula, Mexico

T. Scholz[*1,2], **J. Vargas-Vázquez**[1], **F. Moravec**[1,2], **C. Vivas-Rodríguez**[1], and **E. Mendoza-Franco**[1]

[1]Centre for Investigation and Advanced Studies of the National Polytechnic Institute (CINVESTAV-IPN), Unidad Mérida, Carretera Antigua a Progreso Km 6, A.P. 73 "Cordemex", C.P. 973 10 Mérida, Yucatán, México;

[2]Institute of Parasitology, Academy of Sciences of the Czech Republic, Branišovská 31, 370 05 České Budějovice, Czech Republic (address for correspondence)

Key words: Trematoda, metacercariae, fishes, cenotes, Yucatan, Mexico, zoogeography

Abstract. The paper presents a survey of the metacercariae of trematodes found in 581 fishes of 15 species from 39 cenotes (sinkholes) of the Yucatan Peninsula, southeastern Mexico. The following 21 species were found: *Echinochasmus* sp. 1, *Echinochasmus* sp. 2, Echinostomatinae gen. sp. (family Echinostomatidae), *Stunkardiella minima* (Stunkard, 1938), *Atrophecaecum* (?) *astorquii* (Watson, 1976), *Pelaezia loossi* (Pérez Vigueras, 1957) (Acanthostomidae); *Ascocotyle* (*Ascocotyle*) *tenuicollis* Price, 1935, *Ascocotyle* (*Ascototyle*) sp. 1, *Ascocotyle* (*Phagicola*) *diminuta* (Stunkard et Haviland, 1924), *Ascocotyle* (*Phagicola*) sp. 2 (= *Phagicola angrense* Travassos, 1916 of Salgado-Maldonado and Aguirre-Macedo, 1991), *Ascocotyle* (*Phagicola*) sp. 3 (Heterophyidae); *Cladocystis trifolium* (Braun, 1901) (Opisthorchiidae); *Oligogonotylus manteri* Watson, 1976 (Cryptogonimidae); *Clinostomum* cf. *complanatum* (Rudolphi, 1814) (Clinostomidae); *Diplostomum* (*Austrodiplostomum*) *compactum* (Lutz, 1928), *Posthodiplostomum minimum* (MacCallum, 1921), *Posthodiplostomum* sp. (Diplostomidae); Neodiplostomidae gen. sp. 1; Neodiplostomidae gen. sp. 2 (Neodiplostomidae); and *Apharyngostrigea* sp. (Strigeidae). All species found are described and figured, and their life cycles are briefly discussed.

In 1993–1995, a study on parasites of fishes from 39 cenotes (sinkholes), unique habitats typical of the Yucatan Peninsula (Pearse et al. 1936, Hall 1977), was carried out. The present paper, which is a continuation of a series of articles devoted to parasites of cenote fishes (Moravec et al. 1995a,b, Scholz et al. 1995), surveys the occurrence of the metacercariae of trematodes.

MATERIALS AND METHODS

The study was carried out in the Peninsula of Yucatan from September 1993 to January 1995. A total of 581 fishes of the following 15 species was examined: 1. *Astyanax fasciatus* (Cuvier) (a total of 124 specimens examined) (Characidae); 2. *Rhamdia guatemalensis* Günther (229) (Pimelodidae); 3. *Poecilia petenensis* Günther (10); 4. *P. latipunctata* Meek (4); 5. *P. velifera* (Regan) (51); 6. *Poecilia* sp. (23); 7. *Gambusia yucatana* Regan (20) (Poeciliidae); 8. *Cichlasoma friedrichstahli* (Heckel) (4); 9. *C. meeki* (Brind) (11); 10. *C. octofasciatum* (Regan) (5); 11. *C. pearsei* (1); 12. *C. synspilum* Hubbs (17); 13. *C. urophthalmus* (Günther) (77); 14. *Petenia splendida* Günther (2) (Cichlidae); 15. *Gobiomorus dormitor* (2) (Gobiidae).

Samples of fishes were taken from the following 39 cenotes (a list of cenotes with their description and number of fishes sampled from individual cenotes was provided by Scholz et al. 1995): State of Yucatan: 1. Noc-choncunchey (20°48'53"N; 90°11'47"W); 2. Chaamac (20°51'53"N; 90°09'18"W); 3. Dzaptún (20°51'19"N; 90°14'09"W); 4. Chek-há (ojo de agua) (20°51'39"N; 90°06'49"W); 5. Hunucmá (20°00'03"N; 89°52'06"W); 6. Chen-há (20°54'06"N; 88°44'50"W); 7. Homún (20°44'19"N; 89°17'49"W); 8. Chelentún (20°43'28"N; 89°20'44"W); 9. Xmucuy (20°33'36"N; 88°59'50"W); 10. Ixin-há (20°37'14"N; 89°06'40"W); 11. Xcangachén (20°36'43"N; 89°05'32"W); 12. Sacamucuy (20°33'33"N; 88°59'49"W); 13. Xtojil (20°41'07"N; 88°41'17"W); 14. Yokdzonot (20°42'24"N; 88°43'51"W); 15. Scan Yui (20°40'20"N; 88°32'51"W); 16. Kikil (21°11'37"N; 88°10'10"W); 17. San Gerardo (21°03'59"N; 89°41'30"W); 18. Dzibilchaltún (21°05'28"N; 89°38'55"W); 19. Tres Reyes (21°02'35"N; 89°34'18"W); 20. Noc-ac (21°04'22"N; 89°43'14"W); 21. Hodz-ob (20°55'15"N; 88°51'43"W); 22. Dzonot Cervera (21°22'36"N; 88°49'59"W); 23. Tixkanka (21°14'55"N; 88°58'45"W); 24. Zaci (20°41'29"N; 88°11'40"W); 25. Hubiku (20°49'79"N; 88°10'21"W); 26. Sahkaba (20°48'41"N; 88°07'27"W); 27. Xkeken (20°39'37"N; 88°14'33"W); State of Quintana Roo: 28. Cenote Azul (Puerto Aventuras) (not positioned); 29. San Pedro 1 (20°27'27"N; 87°50'04"W); 30. San Pedro 2 (20°27'27"N; 87°50'04"W); 31. Gran Cenote (20°14'44"N; 87°27'54"W); 32. Framboyán (20°08'16"N; 87°34'38"W); 33. Escondido (20°11'57"N; 87°29'57"W); 34. Cabañas (20°07'51"N; 87°27'57"W); 35. Box Toro (20°16'27"N; 87°29'09"W); 36. Kawash (20°14'44"N; 87°27'54"W); 37. Cenote Azul (Bacalar) (18°38'11"N; 88°24'46"W); 38. Dos Bocas (17°54'38"N; 88°51'20"W); 39. Los Cuates (17°55'00"N; 88°53'00"W). In addition, 16 *Astyanax fasciatus* from cenotes

* to whom correspondence should be addressed

Chaamac and Noc-choncunchey were incompletely examined for the presence of metacercariae on the gills in January and February 1995.

Fishes were routinely examined as outlined by Bykhovskaya-Pavlovskaya (1969), including the examination of the musculature and brain. Larvae were counted and some of them were isolated from hosts' tissues. Due to a high number of metacercariae in most fishes and time-consuming isolation of them, only a limited number of larvae could be evaluated. Isolated larvae were liberated from cysts using preparation needles and studied either as temporary (*in vivo*) or permanent mounts; the latter were fixed with ammonium-picrate after Ergens (1969). Measurements are given in micrometres (μm) unless indicated otherwise. Sucker ratio was counted as a mean of sucker length and sucker width ratios. Voucher specimens have been deposited in the helminthological collection of the Institute of Parasitology, Czech Academy of Sciences, České Budějovice, parasite collection of the Institute of Biology, Universidad Nacional Autónoma de México, México, and at the Laboratory of Parasitology, CINVESTAV-IPN Mérida.

Due to limited number of fish specimens examined in individual localities, prevalence and abundance data were not provided; mean intensity of infection, i.e. mean number of parasites per infected host (see Margolis et al. 1982), was counted.

SURVEY OF SPECIES

Family Echinostomatidae Poche, 1926

1. ***Echinochasmus*** sp. 1 Fig. 1A

Hosts and localities: *Cichlasoma urophthalmus* – Chen-há (18 October 1993, 27 June 1994) – 18 fish infected of 41 examined; mean intensity of infection 177 specimens per infected fish (minimum intensity 6 – maximum intensity 642 larvae); Hodz-ob (23 May 1994) – 8/11; 57 (1–230); Dzonot Cervera (23 May 1994) – 8/10; 33 (4–86); *Petenia splendida* – Noc-choncunchey (21 September 1993) – 1/2; 487.

Site of infection: gills.

Material studied: 9 specimens from *C. urophthalmus*.

Description: Cyst oval, very small, 85–94 × 41–62, surrounded by thin, hyaline membrane; cyst wall elastic, resistant to mechanical isolation. Metacercariae provided with collar armed with 20 spines, dorsally interrupted; length of spines 7–12. Oral sucker subterminal, 21–24 × 24–27; ventral sucker spherical, 18–21 × 23–27; sucker ratio about 1 : 1. Prepharynx and oesophagus short; pharynx oval; intestinal caeca wide and short, reaching only to acetabular level. Main collecting ducts widened, filled with discoid, transparent bodies (corpuscles). Other morphological features not visible due to small size of cysts and the impossibility of mechanically isolating the larvae.

Remarks: The metacercariae are characterised by their small size, the presence of a collar armed with 20 spines and the presence of numerous refractile corpuscles filling excretory system. The larvae are apparently conspecific with those designated as *Echinochasmus zubedakhaname* Násir et Díaz, 1968 by Lamothe-Argumedo and Aguirre-Macedo (1991). The authors obtained adult worms from chicks experimentally infected with larvae from *Cichlasoma urophthalmus* in Yucatan. However, there are distinct morphological differences between the larvae from Yucatan and those described by Násir et Díaz (1968) as *E. zubedakhaname* (cysts elongate and much smaller in the present larvae versus almost spherical and considerably larger in *E. zubedakhaname* – 253–291 in diameter), in the site of infection and in the spectrum of second intermediate hosts.

In addition, Lamothe-Argumedo and Aguirre-Macedo (1991) erroneously designated larvae (metacercariae) encysted in different internal organs of *Cichlasoma urophthalmus* as *E. zubedakhaname*. Field observations and experimental infections (unpublished data) revealed that *Echinochasmus* larvae occur exclusively on the gills of cichlid fishes; all larvae reported from other organs (mesentery, kidney, spleen, liver, stomach wall) of *C. urophthalmus* and identified by Lamothe-Argumedo and Aguirre-Macedo (1991) as *E. zubedakhaname*, are conspecific with *Oligogonotylus manteri* as documented by Scholz et al. (1994).

2. ***Echinochasmus*** sp. 2 Fig. 1B–C

Hosts and localities: *Astyanax fasciatus* – Noc-choncunchey (23 September 1994, 2 February 1994, 21 January 1995) – 18/31; 104 (5–574); Dzaptún (2 February 1994) – 1/2; 27; Dos Bocas (5 April 1994, 26 January 1995) – 1/17; 27; Gran Cenote (25 April 1994; 7 September 1994) – 7/18; 18 (1–34); Cabañas (9 May 1994) – 2/5; 7 (4–10); Escondido (9 May 1994) – 5/6; 150 (10–467); Framboyán (9 May 1994) – 1/1; 16.

Site of infection: gills.

Material studied: 12 specimens from *A. fasciatus*.

Description: Cyst widely oval, 123–156 × 85–141, covered by transparent, thin membrane; outer cyst thick, irregular in shape. Metacercariae elongate, 226–356 × 72–109, provided with weakly developed collar. Collar spines 22 in number, 6–8 long, arranged in one, dorsally interrupted row; spines visible only in encysted metacercariae, not observable after liberating larvae from cysts. Oral sucker subterminal, 30–59 × 42–73; with four orifices (probably opening of penetration glands present in cercaria – unpublished data). Ventral sucker spherical, 33–47 × 33–48; internal margin of sucker with small spines. Sucker ratio 1.04–1.20 : 1. Prepharynx short (up to 15); pharynx heart-shaped, 27–33 × 23–39; intestinal caeca wide and short, filled withiscoid,

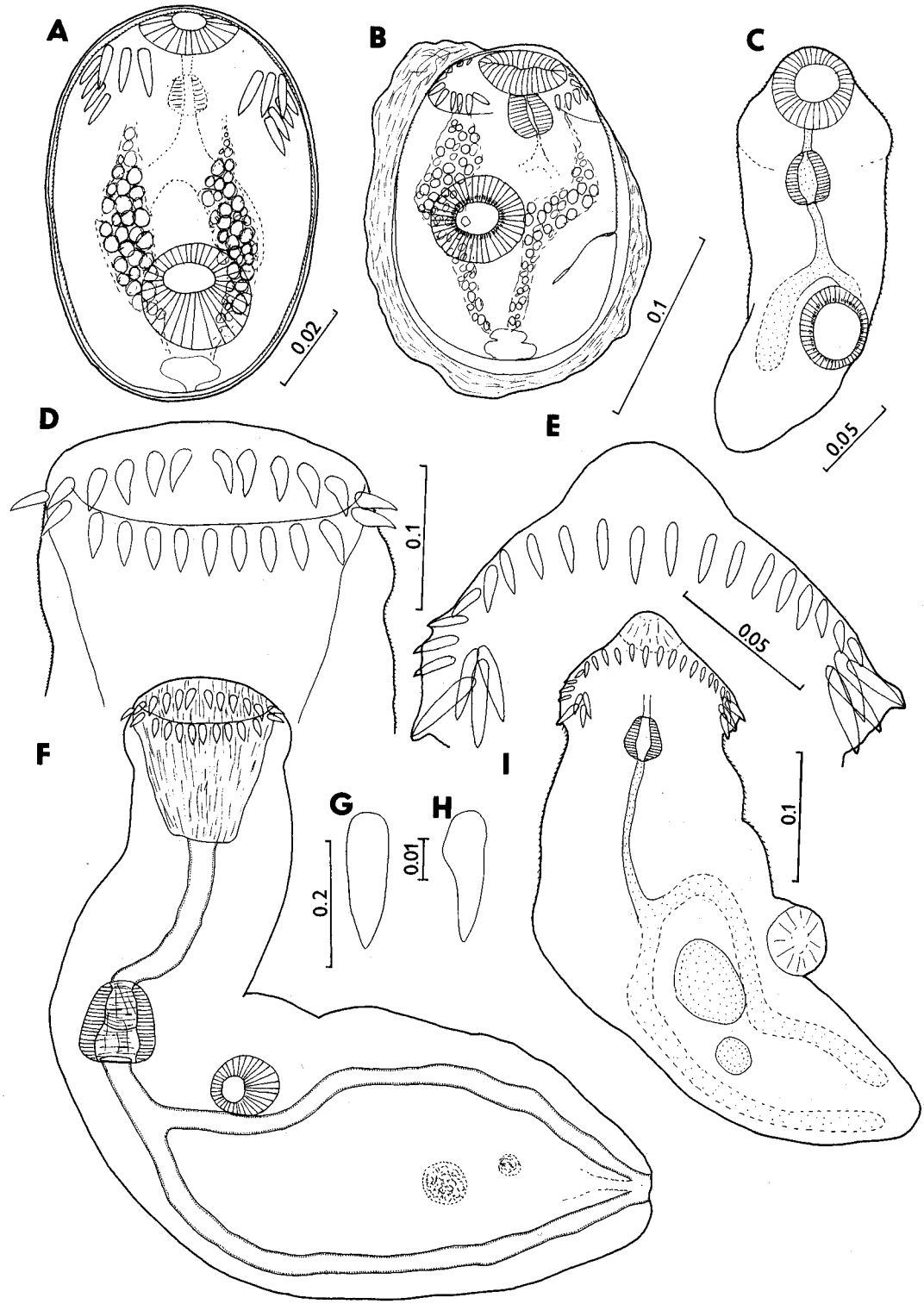

Fig. 1. A – *Echinochasmus* sp. 1 from *Cichlasoma urophthalmus*; **B–C** – *Echinochasmus* sp. 2 from *Astyanax fasciatus* (**B** – encysted larva; **C** – excysted metacercariae with disappeared collar spines); **D, F–H** – *Pelaezia loossi* (Pérez Vigueras, 1957) from *C. urophthalmus* (**D** – anterior end, **F** – total view, **G** – circumoral spine, frontal view, **H** – circumoral spine, lateral view); **E, I** – Echinostomatinae gen. sp. from *Astyanax fasciatus* (**E** – collar spines, **I** – total view). Scale bars in millimetres (mm).

transparent bodies (corpuscles). Excretory bladder two-chambered, main collecting vessels reaching anteriorly to ventral sucker, filled with refractile excretory granules. Flame cell formulla 2 × (2 + 2 + 2 + 2) = 16. First group of flame cells posterior to oral sucker, second at pharyngeal level, third anterolateral to ventral sucker and fourth anterolateral to excretory bladder.

Remarks: The larvae studied, which can easily be liberated from cyst walls, differ distinctly from those found in cichlid fishes by larger size and more oval shape of cyst, number of collar spines and by their smaller size.

3. **Echinostomatinae** gen. sp. Fig. 1E, I

Host and locality: *Astyanax fasciatus* – Box Toro (13 May 1994) – 1/4; 2.

Site of infection: eye.

Material studied: 1 excysted specimen from *A. fasciatus*.

Description: Cyst oval, thin–walled (not measured); body elongate, 517 × 188, with prominent collar, 136 wide, armed with one uninterrupted row of 27 spines. Collar spines consisting of 19 dorsal spines, becoming smaller laterally; length of unpaired, median spine 16.5; others measuring 9.5–16; angular (ventrolateral) spines considerably larger, 21.5–27, four on each side. Oral sucker terminal, weakly muscular, 50 wide; ventral sucker 58 × 50; sucker ratio 1 : 1.08. Prepharynx short; pharynx almost spherical, 33 × 30. Intestinal caeca narrow, reaching posteriorly to body extremity.

Remarks: The specimen from the eye of *A. fasciatus* is characterised by possessing 27 collar spines, consisting of 8 large angular spines and 19 smaller dorsal spines, arranged in one uninterrupted row. This indicates that the larva belongs to the subfamily Echinostomatinae. However, due to the fact that genital organs are not visible in the specimen preserved, a closer identification is not possible.

Family Acanthostomidae Poche, 1926

4. ***Pelaezia loossi*** (Pérez Vigueras, 1957) Fig. 1D, F–H

Hosts and localities: *Cichlasoma meeki* – Noc-choncunchey (21 September 1993) – 3/6; 6 (1–14); Chek-há (8 November 1993) – 1/1; 1; *C. octofasciatum* – Box Toro (12 May 1994) – 1/1; 2.

Site of infection: muscles, rarely scales, fins and eyes.

Material studied: 2 specimens from *C. meeki* and 1 from *C. octofasciatum*.

Description (N = 3): Cyst large, 912 × 504, oval, thin-walled; outer wall sometimes thickened. Excysted larva elongate, 1000–1480 × 244–480, with widened hindbody. Oral sucker funnel–shaped, 229–272 × 196–227, with one complete row of 23 circumoral spines; dorsal spines 34–38 long, ventral spines 34–36. Ventral sucker small, almost spherical; 74–103 × 76–98. Sucker ratio 2.48–2.83 : 1. Prepharynx long, up to 266; pharynx large, strongly muscular, 112–142 × 118–123. Intestinal caeca connected posteriorly, opening into excretory bladder. Primordia of genitalia spherical, located near posterior extremity. Excretory bladder Y-shaped, connected with intestinal caeca (hardly visible in permanent mounts).

Remarks: The metacercariae correspond in their morphology (funnel-shaped oral sucker equipped with 23 circumoral, large spines, intestinal caeca connected with the excretory system, strongly muscular pharynx, larger than the ventral sucker, etc.) to the larvae of *Pelaezia loossi* found by Ostrowski de Nuñez (1984), and Salgado-Maldonado and Aguirre-Macedo (1991) in the skin of head and the finrays of *Petenia kraussi* from Venezuela and from muscles of *Cichlasoma urophthalmus* from the coastal lagoon of Celestun, respectively.

Adults of *P. loossi* have been found in *Crocodylus acutus* in Cuba and *Alligator mississippiensis* in USA (Pérez-Vigueras 1957, Brooks and Overstreet 1977).

5. ***Stunkardiella minima*** (Stunkard, 1938) Fig.2C,E,G

Hosts and localities: *Rhamdia guatemalensis* – Yokdzonot (13 October 1993) – 1/1; 1; Xmucuy (26 October 1993) – 1/22; 6; Ixin-há (26 October 1993, 13 June 1994, 11 July 1994, 22 August 1994, 20 September 1994, 17 October 1994, 31 January 1995) – 26/106; 17 (1–120); Chelentún (3 November 1993) – 5/7; 3 (1–5); Homún (3 November 1993) – 1/1; 1; Hunucmá (8 November 1993) – 1/2; 7; Sahkaba (18 April 1994) – 1/1; 5; Sacamucuy (10 October 1994) – 1/6; 4; Dos Bocas (26 January 1995) – 1/1; 162; *Gambusia yucatana* – Yokdzonot (13 October 1994) – 1/5; 1.

Site of infection: fins, mostly pectoral, exceptionally eye lens and scales (*G. yucatana*).

Material studied: 17 specimens from *R. guatemalensis*.

Description (N = 9): Cyst almost spherical, hyaline, thin-walled, 203–215 × 186–202. Excysted larvae elongate, 432–620 × 118–147; body covered with small, rectangular spines, becoming smaller and less dense posteriorly. Oral sucker cup–like, terminal, 80–103 × 67–95, armed with one complete row of 20 spines; dorsal spines longer (length 19–23) and more slender than shorter (17–20) and broader ventral spines. Ventral sucker spherical, 43–52 × 35–54; sucker ratio 1.69–2.18 : 1 (mean 1.93 : 1). Prepharynx 65–130 long; pharynx strongly muscular, 39–63 × 28–63. Intestine single,

opening posteriorly near excretory pore. Excretory bladder Y-shaped, reaching anteriorly to ventral sucker.

Remarks: The morphology of the larvae from *R. guatemalensis*, especially the number of circumoral spines (20) and the presence of the single intestine opening near the posterior extremity, clearly indicates their conspecificity with *S. minima* adults found in the same fish host, the pimelodid *R. guatemalensis* (see Scholz et al. 1995). The fact that circumoral spines are somewhat more slender in the larvae than in adult worms apparently seems to represent only intraspecific variability.

Adults of *S. minima* have been found in *R. guatemalensis* by several authors (Stunkard 1938, Lamothe-Argumedo and Ponciano-Rodríguez 1986a); however, the occurrence of metacercariae of this trematode is reported for the first time. It is evident that definitive hosts, preferably larger catfishes, acquire infection after consuming small specimens harbouring *S. minima* metacercariae. The finding of *S. minima* larva in *G. yu- catana* indicates that other fishes may serve as second intermediate hosts of this parasite as well.

6. ***Atrophecaecum*** (?) ***astorquii*** (Watson, 1976) Fig. 2A–B,D,F

Hosts and localities: *Astyanax fasciatus* – Noc-choncunchey (21 September 1993, 13 September 1994) – 3/31; 2 (1–3); Dzaptún (8 November 1993) – 2/2; 78 (21–135); Chek-há (8 November 1993) – 1/17; 9; Cabañas (9 May 1994) – 1/5; 3; Escondido (9 May 1994) – 1/6; 10; Box Toro (12 May 1994) – 2/4; 15 (2–28); Dzonot Cervera (23 May 1994) – 1/5; 1; Chaamac (21 January 1995) – 3/5; 8 (5–10); Dos Bocas (26 January 1995) – 1/17; 1; *Poecilia petenensis* – Noc-choncunchey (2 February 1994) – 1/1; 32; Cenote Azul (Bacalar) (5 April 1994) – 1/6; 3; Framboyán (9 May 1994) – 1/1; 71; Box Toro (12 May 1994) – 2/2; 61 (35–87); *P. latipunctata* – Cenote Azul (Puerto Aventuras) (23 February 1994) – 1/4; 2; *P. velifera* – Noc-choncunchey (2 February 1994) – 1/2; 4; Chaamac (21 September 1993) – 2/2; 1437 (1130–1744); Chen-há (27 June 1994, 27 August 1994, 13 September 1994) – 4/9; 8 (2–12); *Gambusia yucatana* – Box Toro (12 May 1994) – 1/2; 43; Dzibilchaltún (13 May 1994) –1/2; 92; *Cichlasoma meeki* – Noc-choncunchey (21 September 1993, 2 February 1994) – 6/6; 41 (4–149); Chek-há (8 November 1993) – 1/1; 4; Hunucmá (8 November 1993) – 1/1; 539; *C. octofasciatum* – Box Toro (12 May 1994) – 1/1; 106; *C. pearsei* – Noc-choncunchey (2 February 1994) – 1/1; 8; *C. synspilum* – Cabañas (9 May 1994) – 1/2; 6; *C. urophthalmus* – Noc-choncunchey (2 February 1994) – 2/2; 85 (21–148); Dzaptún (8 November 1993) – 2/2; 2; Gran Cenote (25 April 1994) – 1/1; 4; Cabañas (9 May 1994) – 1/4; 5; Dzonot Cervera (23 May 1994) – 4/10; 33 (10–85); Chen-há (27 June 1994; 27 August 1994) – 18/41; 21 (1–71); *Petenia splendida* – Noc-choncunchey (21 September 1993) – 2/2; 200 (3–397).

Site of infection: fins (mainly pelvic), occasionally gills, scales, eyes, swimbladder.

Material studied: 5 specimens from *A. fasciatus*, 6 from *P. petenensis*, 5 from *C. meeki*, 1 from *C. octofasciatum*, 5 from *C. synspilum*, 5 from *C. urophthalmus* and 3 specimens from *P. splendida*.

Description (N = 10): Cyst transparent, thin-walled, oval or almost spherical, 192–211 × 150–193. Larvae elongate, 420–660 × 106–154. Forebody densely covered by minute tegumental spines. Oral sucker terminal, cup-like, 77–110 × 86–108, armed with one complete row of 20 fine, slender spines; dorsal spines longer (length 21–27) than ventral spines (19.5–23). Ventral sucker spherical, 35–50 × 32–45; sucker ratio 2.25–2.83 : 1 (mean 2.47 : 1). Prepharynx 50–135 long; pharynx strongly muscular, 40–53 × 30–55. Intestinal caeca weakly visible, with different width, opening posteriorly near opening of excretory bladder. Excretory bladder Y-shaped, with short stem and branches reaching anterior to ventral sucker.

Remarks: The metacercariae closely resemble those of *S. minima* described above, with the exception of the structure of the digestive system. Whereas *S. minima* larvae possess only one intestinal caecum, those found in cichlid, characid and poeciliid fishes have two intestinal caeca, opening near the posterior extremity. In addition, there are slight, but distinct differences in the shape and size of circumoral spines, which are more massive, shorter and wider, with distinct bases in *S. minima*, and in the sucker ratio, which is higher (2.25–2.83 : 1) in the present material than in the larvae of *S. minima* (1.69–2.18 : 1).

On the basis of the presence of two intestinal caeca, opening outside near the posterior extremity, and unequal in their size, with one caecum distinctly wider than the other, the larvae under consideration apparently belong to the genus *Atrophecaecum* Bhalerao, 1940 as defined by Lamothe-Argumedo and Ponciano-Rodríguez (1986b). There is only one species occurring in fishes from Latin America, *A. astorquii* (Watson, 1976), a parasite of *Rhamdia nicaraguensis* in Nicaragua (Watson 1976). Similar to the present material, this species has 20 circumoral spines. Although there are slight differences in the shape of spines, which are stouter (more massive) in *A. astorquii* adults (Watson 1976), the conspecificity of the larvae with this species seems to be very probable. The above differences in the shape of spines might represent intraspecific or interstadial variability as documented in *Stunkardiella minima* larvae and adults from *Rhamdia guatemalensis* (compare Scholz et al. 1995 and the present paper).

Family Opisthorchiidae Braun, 1901

7. ***Cladocystis trifolium*** (Braun, 1901) Fig. 8H

Host and locality: *Cichlasoma meeki* – Noc-choncunchey (2 February 1994) – 1/6; 2.

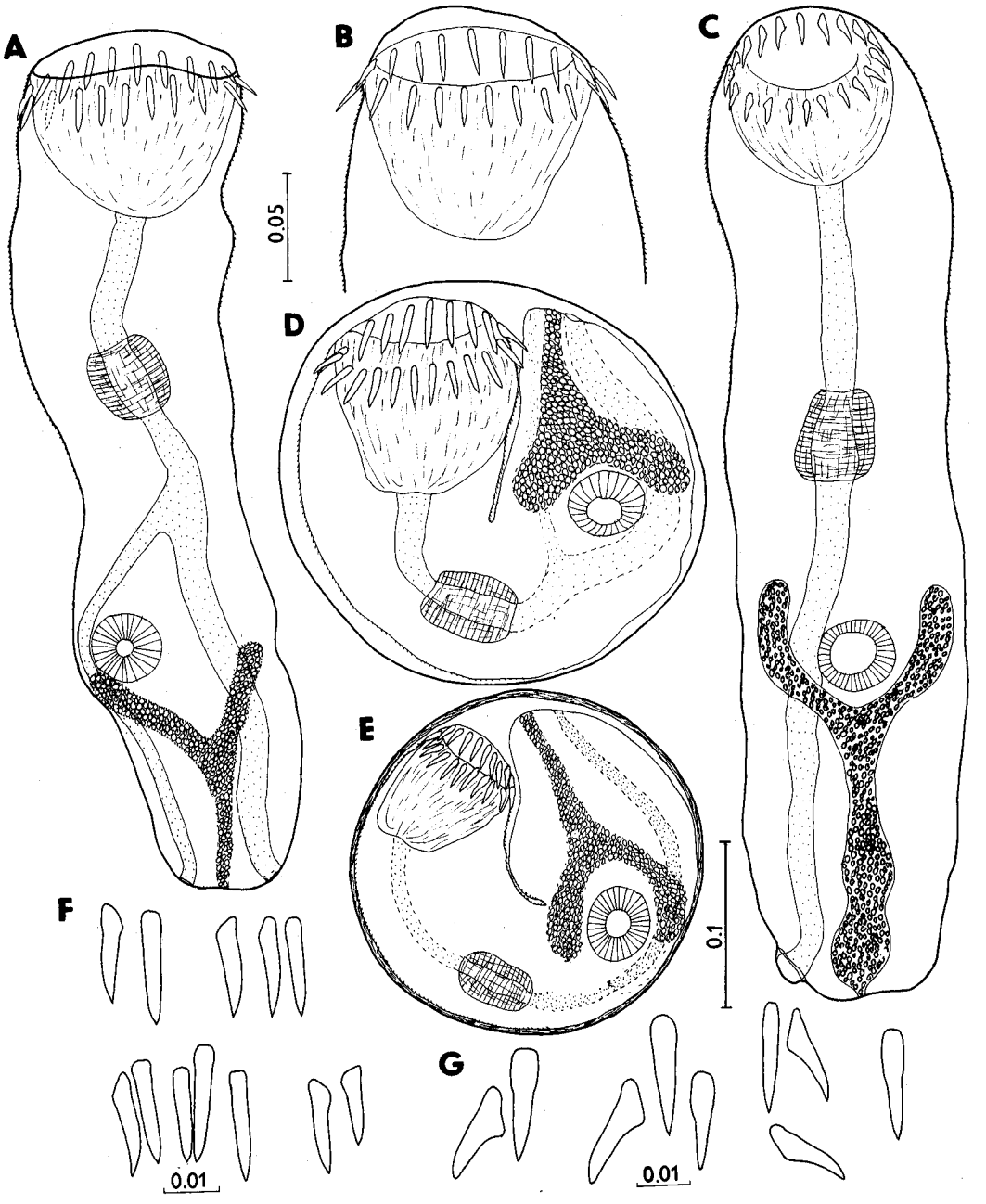

Fig. 2. A–B, D, F – *Atrophecaecum* (?) *astorquii* (Watson, 1976) from *Cichlasoma meeki* (**A** – total view, **B** – anterior end, **F** – circumoral spines) and *Petenia splendida* (**D** – encysted larva); **C, E, G** – *Stunkardiella minima* (Stunkard, 1938) from *Rhamdia guatemalensis* (**C** – total view, **E** – encysted larva, **G** – circumoral spines). Scale bars in millimetres (mm).

Site of infection: gills.

Material studied: 1 excysted specimen from *C. meeki.*

Description: Cyst oval, thin-walled. Excysted metacercaria elongate, 1,960 × 583. Oral sucker subterminal, 118 × 118; ventral sucker spherical 136 × 112, almost equatorial; sucker ratio 1 : 1.05. Prepharynx 122 long, pharynx weakly muscular, 99 × 52. Intestinal caeca long and slightly curved, reaching to posterior part of body. Genital primordia weakly developed, near posterior extremity. Excretory system forming longitudinal canal anteriorly reaching to oral sucker.

Remarks: The larva morphologically and metrically corresponds to metacercaria of the species *Cladocystis trifolium* as described by Pineda-López (1985) from the gills of cichlid fishes (*Cichlasoma synspilum* and *Cichlasoma* sp.) in Tabasco. Comparison of the present

material with the figure of *C. trifolium* (Fig. 7) in the paper by Pineda-López (1985) revealed that the pharynx was erroneously situated immediately behind the oral sucker and no prepharynx was present. However, the prepharynx is well developed and relatively long (122 in the larva from Yucatan and 58–156 in the metacercariae from Tabasco – see description of *C. trifolium* in Pineda-López 1985).

Cladocystis trifolium has been reported as a parasite of herons (*Egretta alba*, *Ardea cocoi*) in Tabasco (Mexico) and Brazil (Pineda-López 1985). However, Yamaguti (1971) stated that the finding of *C. trifolium* in the heron was evidently accidental, after swallowing infected fish by the bird; the same author reports the characid fish *Salminus maxillosus* as the definitive host of *C. trifolium*.

Family Heterophyidae Odhner, 1914

8. *Ascocotyle (Ascocotyle) tenuicollis* Price, 1935 Fig. 3A, C–E

Hosts and localities: *Astyanax fasciatus* – Cabañas (9 May 1994) – 1/5; 2; Escondido (9 May 1994) – 1/6; 230; *Poecilia petenensis* – Noc-choncunchey (2 February 1994) – 1/1; 150; Cenote Azul (Bacalar) (5 April 1994) – 1/6; 6; Framboyán (9 May 1994) – 1/1; 108; Box Toro (12 May 1994) – 2/2; 384 (217–550); *P. latipunctata* – Cenote Azul (Puerto Aventuras) (23 February 1994) – 2/4; 2 (1–3); *P. velifera* – Chen-há (18 October 1993) – 5/19; 11 (2–96); Sahkaba (18 April 1994) – 8/17; 75 (2–184); Dzibilchaltún (13 May 1994) – 5/7; 56 (25–172); *Cichlasoma octofasciatum* – Cabañas (9 May 1994) – 1/1; 10; *C. synspilum* – Cenote Azul (Bacalar) (5 April 1994) – 1/10; 4; Cabañas (9 May 1994) – 1/2; 52.

Site of infection: heart and mesentery (*A. fasciatus*).

Material studied: 9 specimens from *A. fasciatus*, 1 from *P. petenensis*, 12 from *P. velifera* and 4 from *C. octofasciatum*.

Description (N = 16; measurements of larvae from the mesentery of *A. fasciatus* in parentheses): Cyst widely oval, thin-walled, 183–336 × 174–310. Body pyriform, 267–614 × 91–221 (273–649 × 109–197); tegument finely spined, including posterior extremity. Eye-spot remnants scattered along oesophageal level. Preoral lobe well developed, 15–30 (13–24) long; oral sucker 36–65 (36–47) wide, with very long appendix, often curved, 62–135 (53) long. Two rows of 32 (32) circumoral spines present; anterior spines larger – length 12–19 (12), with dorsal spines longer than ventral ones; posterior spines finer and smaller – length 6–12 (6–8). Acetabulum sucker-like, 30–56 × 33–56 (33–36 × 31–39). Sucker ratio 1.13–1.31 : 1 (1.13–1.25 : 1). Prepharynx 79–95; pharynx 22–32 × 21–30 (22–28 × 21–22); oesophagus shorter than prepharynx. Caeca very short, wide, terminating anterior to ventral sucker. Testes symmetrical, near posterior extremity, 21–39 × 18–47 (21–24 × 18–27). Genital sac formed, anterolateral to acetabulum. Genital pore widely oval; gonotyl inconspicuous. Excretory bladder Y-shaped with short and wide arms.

Remarks: The presence of two complete rows of crown spines indicates that the metacercariae belong to the nomino typical subgenus of *Ascocotyle* Looss, 1899 (Yamaguti 1971). The morphology of the larvae, particularly number of circumoral spines, and their site of infection (heart) well correspond to characteristics of the species *Ascocotyle (A.) tenuicollis*. The larvae found in *A. fasciatus* were localised in the mesentery, which casts doubts about their conspecificity with *A. tenuicollis*, taking into account rather narrow site specificity of most *Ascocotyle* larvae (see, e.g., Font et al. 1984). However, no morphological differences between the larvae from *A. fasciatus* and those situated in the heart of poeciliid and cichlid fishes were found. Consequently, all the larvae are considered to be conspecific until more data on their life cycles are available.

Ascocotyle tenuicollis metacercariae have been found in the *conus arteriosus* of *Gambusia*, *Mollienesia* and *Chaenobryttus coronarius* in USA (Texas, Florida) – Yamaguti (1971). Life cycle of this species was studied by Ostrowski de Nuñez (1974), who reported freshwater fishes, *Cnesterodon decemmaculatus* and *Phalloceros caudimaculatus* (Cyprinodontiformes), as second intermediate hosts of *A. tenuicollis*. Definitive hosts are fish-eating birds (*Botaurus lentiginosus*, *Florida carulea caerulea*, *Hydranassa tricolor*) – Yamaguti (1971).

In Mexico, the metacercariae designated as *A. tenuicollis* have been found in the heart of the cichlids *Cichlasoma friedrichstahli*, *C. geddesi* and *C. pearsei* from Tabasco and Campeche (Aguirre-Macedo and García-Magaña 1995, Salgado-Maldonado, Pineda-López and Vidal-Martínez – unpubl. data).

9. *Ascocotyle (Ascocotyle)* sp. 1 Fig. 4

Host and locality: *Poecilia velifera* – Sahkaba (18 April 1994) – 1/17; 2.

Site of infection: gills.

Material studied: 1 excysted specimen from *P. velifera*.

Description: Cyst widely oval, thin-walled; body pear-shaped, 564 × 244, covered with tegumental spines; spines lacking in posterior quarter of body. Preoral lobe slightly developed, 15 long. Oral sucker 65 wide, with long appendage, 68 long. Circumoral spines (76 in number) arranged in two complete rows of 38 each;

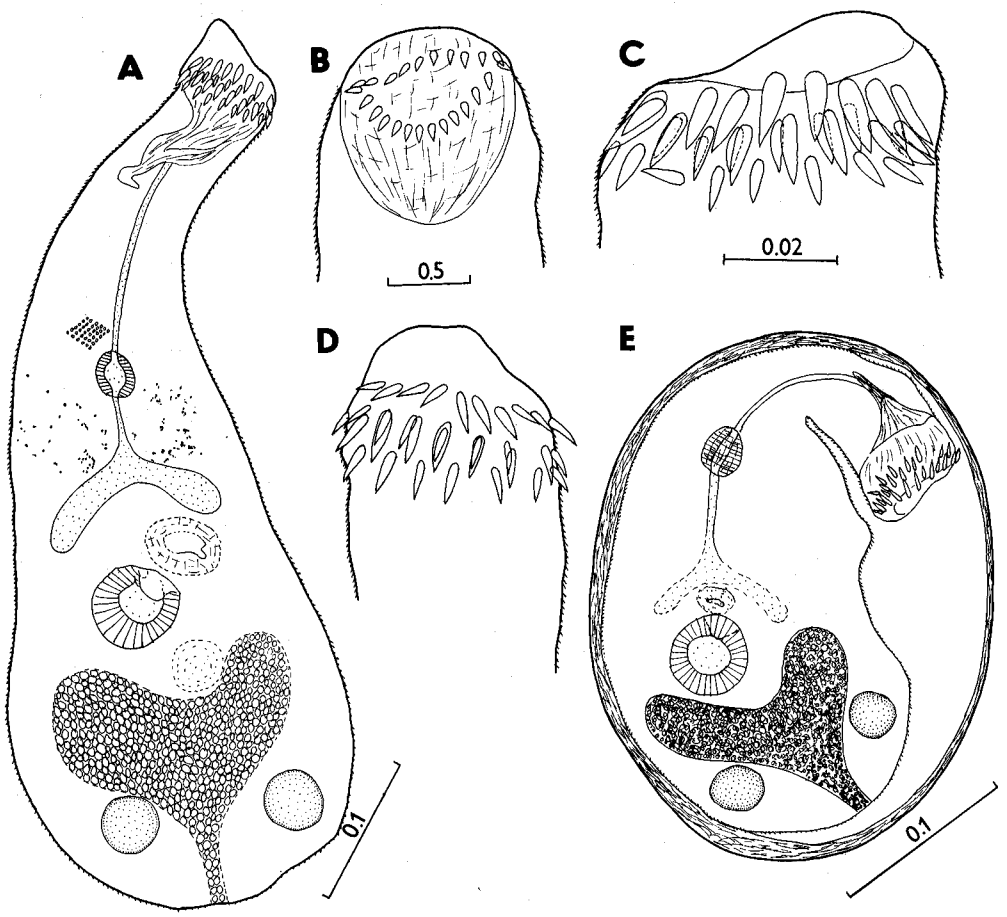

Fig. 3. A, C–E – *Ascocotyle (Ascocotyle) tenuicollis* Price, 1935 from *Cichlasoma octofasciatum* (**A** – total view) and *Poecilia velifera* (**C–D** – anterior end, **E** – encysted larva); **B** – Heterophyidae gen. sp. from *Cichlasoma meeki* (anterior end). Scale bars in millimetres (mm); scale given for Fig. 3C is valid also for Fig. 3D.

length of anterior spines 12–19, posterior spines 10–18 long. Acetabulum sucker-like, 56 × 65. Sucker ratio 1.07 : 1. Prepharynx present; pharynx oval, 36 × 34. Intestinal caeca wide and short, terminating at acetabular level. Gonads not observed; genital sac formed, anterolateral to acetabulum. Genital pore narrow, widely oval; gonotyl conspicuous, unarmed. Excretory bladder inflated, filling posterior third of body.

Remarks: The larva studied is characterised mainly by the presence of two complete rows of circumoral spines, number of which is rather high (76 in total).

10. ***Ascocotyle (Phagicola) diminuta*** (Stunkard et Haviland, 1924) Figs. 5, 7B

Hosts and localities: *Poecilia petenensis* – Noc-choncunchey (2 February 1994) – 1/1; 72; Cenote Azul (Bacalar) (5 April 1994) – 4/6; 11 (7–18); Box Toro (12 May 1994) – 1/2; 10; *P. velifera* – Noc-choncunchey (2 February 1994) – 2/2; 86 (84–87); Chaamac (21 September 1993) – 2/2; 76 and hundreds of larvae; Chen-há (18 October 1993, 13 September 1994) – 7/19; 10 (1–23); Sahkaba (18 April 1994) – 3/17; 3 (1–7); Dzibilchaltún (13 May 1994) – 6/7; 7 (1–23); Chek-há (21 January 1995) – 1/1; 9.

Site of infection: gills.

Material studied: 3 specimens from *P. petenensis*, 2 from *P. latipunctata* and 14 specimens from *P. velifera*.

Description (N = 14): Cyst oval or elongate, 256–301 × 128–154, double-walled; outer wall granular, inner membrane transparent. Body elongate, tapering towards anterior end, 336–479 × 91–174, with spined tegument including posterior extremity. Remnants of eye-spots dispersed at oesophageal level. Dorsal preoral lip slightly developed, up to 23 long; oral appendage short. Oral sucker weakly muscular, 56–80 wide, armed with 18 circumoral spines forming one row of 16 spines and two additional dorsal spines; spines 15.5–21 (dorsal) and 16–18 (ventral) long (1 specimen with spines only 13.5 and 12 long); additional spines 8–14 long. Acetabulum

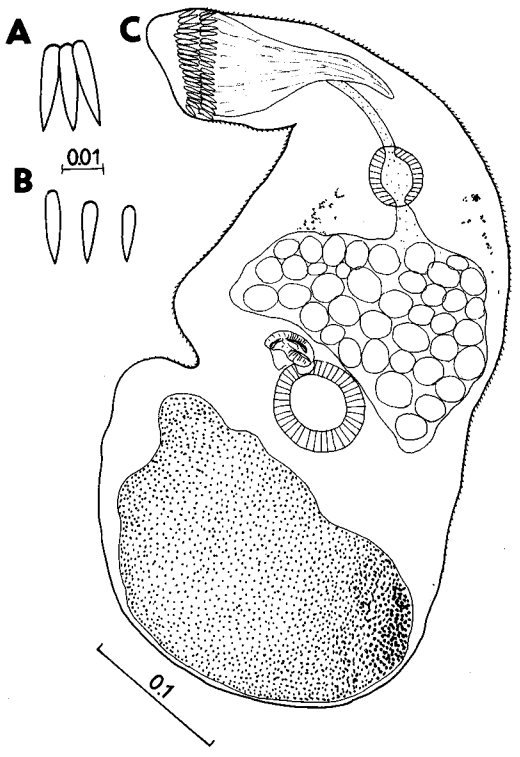

Fig. 4. *Ascocotyle* (*Ascocotyle*) sp. 1 from *Poecilia velifera* (**A** – dorsal circumoral spines; **B** – ventral circumoral spines; **C** – total view). Scale bars in millimetres (mm).

well-developed, sucker–like, 24–40 × 27–43 (Fig. 7B). Sucker ratio 1.80–2.83 : 1. Prepharynx 46–52 long; pharynx 25–37 × 21–32. Caeca short, terminating at acetabular level. Testes symmetrical, near posterior extremity, 21–32 × 20–43; ovary almost spherical, pretesticular, 19–23 × 24–25. Genital sac widely oval, anterolateral to ventral sucker; genital pore elongate, at distinct distance from acetabulum (Fig. 7B). Gonotyl inconspicuous. Excretory bladder Y-shaped.

Remarks: The metacercariae from *Poecilia* spp. differ from those of *Ascocotyle* (*Phagicola*) sp. 2 (*Phagicola angrense* of Salgado-Maldonado and Aguirre-Macedo 1991 – see below) by different number (always 16 + 2), size and shape of circumoral spines, smaller size of the body, which is distinctly more slender (maximum width of body 115–160 in *A. diminuta* versus 216–312 in *Ascocotyle* (*Phagicola*) sp. 2) and without widened hindbody, by the structure of the ventrogenital complex, which does not possess pockets present in *Ascocotyle* (*Phagicola*) sp. 2, and by the spination of the whole body surface (smooth posterior to the testes in *Ascocotyle* (*Phagicola*) sp. 2). There are also differences in fish host (poeciliids versus cichlid fishes) and the site of infection (exclusively gills in *A. diminuta*).

In all the above features, the metacercariae from *Poecilia* spp. fit into the description of *A. diminuta* metacercariae as provided by Ostrowski de Nuñez (1993). This author resurrected the species *A. diminuta* from synonyms of *A. angrense* (see Sogandares-Bernal and Lumsden 1963) on the basis of the differences in the number of crown spines (16 + 2 versus 18 + 2) and the body spination, which covers the whole surface of *A. diminuta* metacercariae.

Due to the fact that many authors have considered *A. diminuta* to be a synonym of *A. angrense* (see Sogandares-Bernal and Lumsden 1963), the spectrum of the second intermediate hosts (fishes) and actual distribution of both taxa are not well known. Sogandares-Bernal and Lumsden (1963) reported larvae designated as *A. angrense*, which may actually belong to *A. diminuta* as well, from fishes of the genera *Belonesox*, *Mollienesia* (Poeciliidae), *Cyprinodon*, *Lucania* and *Fundulus* (Cyprinodontidae); some of these fishes (*B. belizanus*, *M. sphaenops*, *C. variegatus*) were caught in the Lagoon of Chelem near Progreso, which is situated relatively close to cenote Noc-choncunchey.

11. ***Ascocotyle* (*Phagicola*)** sp. 2 Figs. 6, 7A

Syn.: *Phagicola angrense* Travassos, 1916 of Salgado-Maldonado and Aguirre-Macedo (1991)

Hosts and localities: *Astyanax fasciatus* – Escondido (9 May 1994) – 1/6; 23; *Poecilia petenensis* – Noc-choncunchey (2 February 1994) – 1/1; 32; Cenote Azul (Bacalar) (5 April 1994) – 4/6; 3 (1–5); Box Toro (12 May 1994) – 1/2; 74; *P. velifera* – Noc-choncunchey (2 February 1994) – 2/2; 3 (1–4); Chen-há (27 June 1994) – 1/19; 1; Chek-há (21 January 1995) – 1/1; 3; *Gambusia yucatana* – Box Toro (9 May 1994) – 1/2; 2; Dzibilchaltún (13 May 1994) – 1/2; 1; *Cichlasoma friedrichstahli* – Cenote Azul (Bacalar) (5 April 1994) – 1/1; 2; *C. meeki* – Noc-choncunchey (21 September 1993) – 2/6; 2 (1–3); Los Cuates (5 April 1994) – 1/1; 4; Cabañas (9 May 1994) – 2/2; 16 (7–25); *C. octofasciatum* – Cabañas (9 May 1994) – 1/1; 124; Box Toro (12 May 1994) – 1/1; 3; *C. synspilum* – Cenote Azul (Bacalar) (5 April 1994) – 2/10; 3 (1–4); Cabañas (9 May 1994) – 2/2; 83 (4–162); Framboyán (9 May 1994) – 1/1; 14; *C. urophthalmus* – Chen-há (18 October 1993; 27 June 1994; 27 August 1994) – 38/41; 145 (11–1735); Noc-choncunchey (2 February 1994) – 1/1; 4; Gran Cenote (25 April 1994) – 1/1; 2; Cabañas (9 May 1994) – 4/4; 101 (31–151); Dzibilchaltún (13 May 1994) – 1/2; 1; Hodz-ob (23 June 1994) – 11/11; 157 (54–313); Dzonot Cervera (23 May 1994) – 10/10; 377 (18–1266).

Site of infection: wall of intestine and stomach, mesentery, swimbladder, spleen, kidney, liver, gonads, muscles, eyes, brain.

Material studied: 1 specimen from *P. velifera*, 3 from *C. meeki*, 1 from *C. octofasciatum*, 4 from *C. synspilum* and 20 specimens from *C. urophthalmus*.

Description (N = 13): Cyst almost spherical, 328–408 × 296–400, double–walled; outer membrane thick, inner

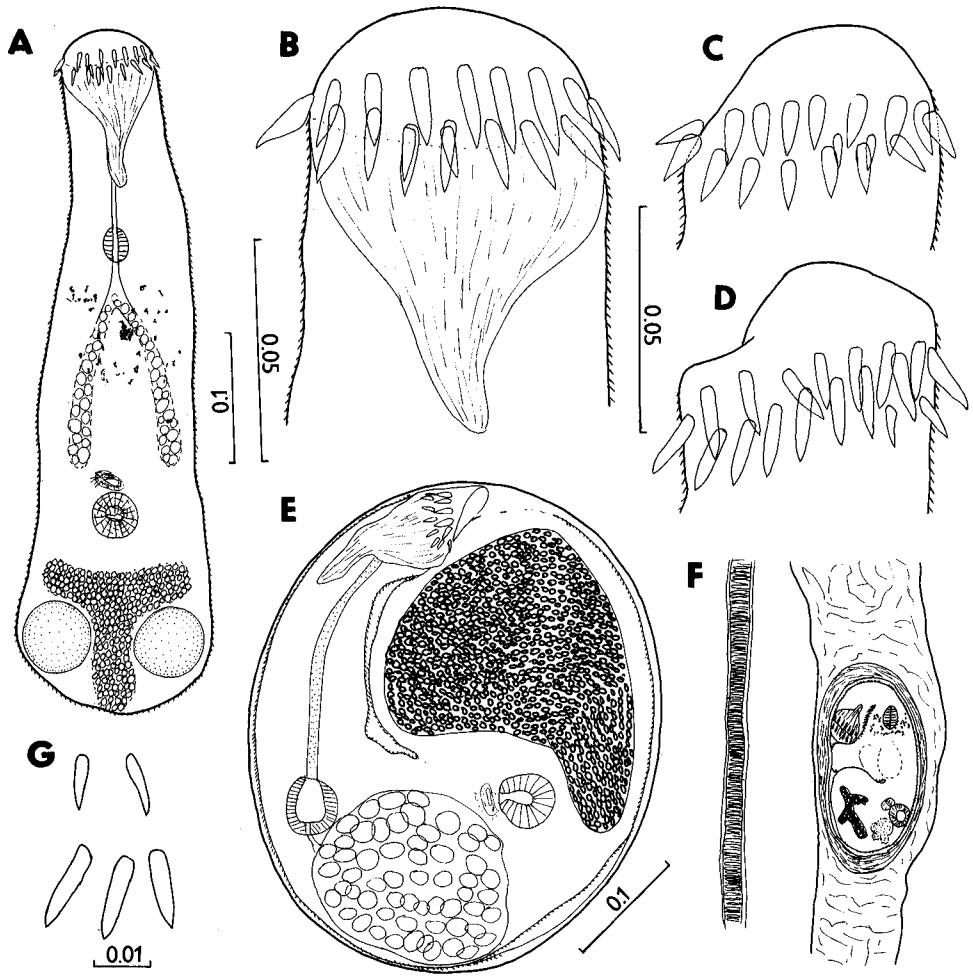

Fig. 5. *Ascocotyle (Phagicola) diminuta* (Stunkard et Haviland, 1924) from *Poecilia velifera* (**A** – total view, **B** – oral sucker, **C–D** – anterior end, **E** – encysted larva, **F** – gill filament with encysted larva, **G** – circumoral spines). Scale bars in millimetres (mm).

wall hyaline, thin. Body pyriform, 376–912 × 216–338; three quarters covered with tegumental spines reaching to ovarian level. Preoral lip weakly developed; mouth terminal. Oral sucker weakly muscular, 36–57 × 38–67, with 20 (N = 10) circumoral spines forming one complete row of 16 larger spines 11–16 long and 4 additional spines, 9–11 long; exceptionally 19 or 21 circumoral spines formed by 16 complete and 3 additional spines (N = 2) or 17 and 4 spines (N = 1). Oral appendage conical, short. Ventral sucker reduced, 40–65 × 40–61. Sucker ratio 1.03 : 1 – 1 : 1.25. Prepharynx 52–116 long; pharynx 35–43. Caeca wide, at acetabular level curved medially, almost reaching each other at ovarian level, filled with platelets. Testes symmetrical, displaced to lateral margins by expanded excretory bladder, 70–98 × 71–95. Genital sac anterolateral to acetabulum, with wide genital pore situated immediately anterolaterally to margin of acetabulum. Gonotyl weakly muscular, with 12–13 pockets (Fig. 7A). Excretory bladder Y- or X-shaped, with inflated stem and wide arms curved along intestinal caeca. Flame cell formula 2 × (2 + 2 + 2 + 2) = 16, with one pair of cells at pharyngeal level, other near intestinal bifurcation, third at acetabular level and posterior between ovary and testes (Fig. 6C).

Remarks: The metacercariae studied are apparently conspecific with the larvae identified as *Phagicola* (= *Ascocotyle*) *angrense* by Salgado-Maldonado and Aguirre-Macedo (1991). These larvae were found in the mesentery, liver, spleen, kidney and stomach wall of *Cichlasoma urophthalmus* from the coastal lagoon of Celestun, situated close to cenotes Noc-choncunchey

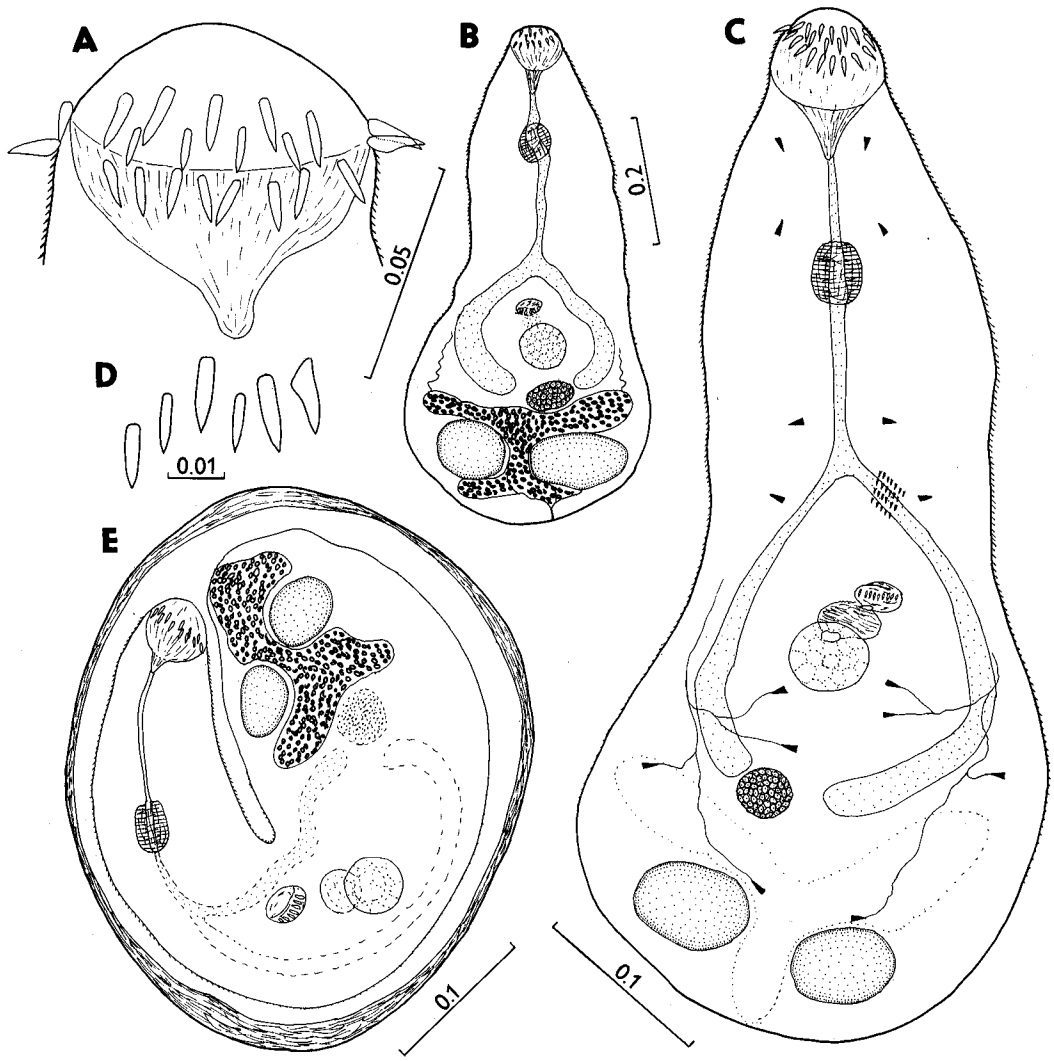

Fig. 6. *Ascocotyle* (*Phagicola*) sp. 2 from *Cichlasoma urophthalmus* (syn. *Phagicola angrense* of Salgado–Maldonado and Aguirre-Macedo 1991) (**A** – anterior end, **B–C** – total view, **D** – circumoral spines, **E** – encysted larva). Scale bars in millimetres (mm).

and Chen-há. Salgado-Maldonado and Aguirre-Macedo (1991) reported 20–22 circumoral spines forming one complete circle of 16–18 spines and 4 additional spines, while the larvae from cenotes possessed from 19 to 21 spines (16–17 plus 3–4).

Ostrowski de Nuñez (1993), who studied the life cycle of *Ascocotyle* (*Ph.*) *angrense* in Argentina, reported the number of circumoral spines of *A. angrense* adults being 20 (18 + 2), which is different from the present material. In addition, *A. angrense* differs from the present species by different structure of the gonotyl, which has no pockets present in the present material, by the site of infection (gills versus internal organs) and second intermediate hosts (*Phalloceros caudimaculatus* for *A. angrense* whereas preferably cichlid fishes for *Ascocotyle* (*Phagicola*) sp. 2). It seems evident that the present material is not conspecific with *A. angrense* and represents another species, probably not described until now. Ostrowski de Nuñez (personal communication) also suggested the species studied by Salgado-Maldonado and Aguirre-Macedo (1991) to represent a species other than *A. angrense*. However, precise species identification of the material from cenotes requires data on the life cycle of this parasite.

12. ***Ascocotyle* (*Phagicola*)** sp. 3 Fig. 8A–G

Hosts and localities: *Cichlasoma meeki* – Noc-choncunchey (21 September 1993, 21 January 1995)

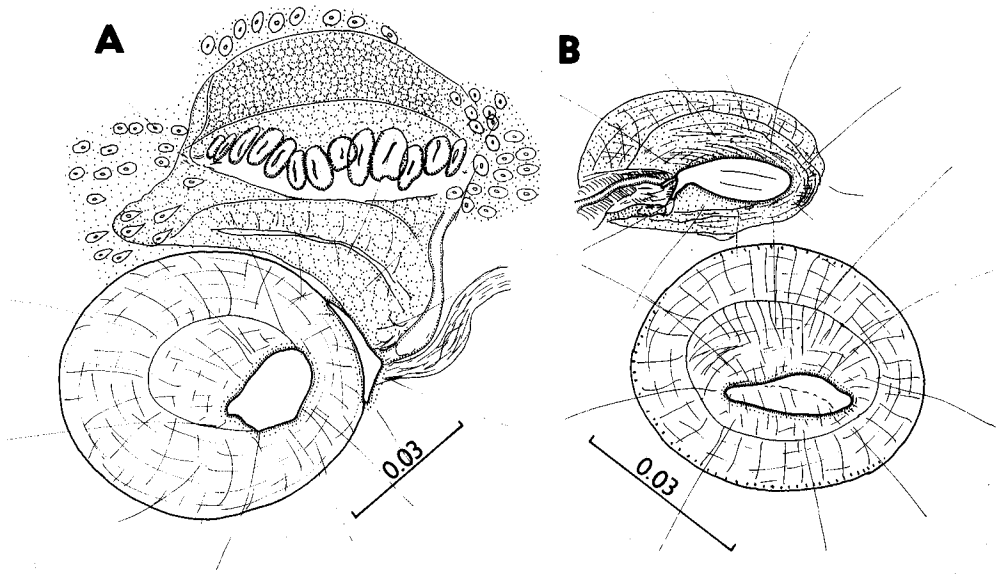

Fig. 7. **A** – *Ascocotyle (Phagicola)* sp. 2. Ventrogenital complex. **B** – *Ascocotyle (Phagicola) diminuta.* Scale bars in millimetres (mm).

– 6/6; 24 (5–87); Chek-há (8 November 1993) – 1/1; 6; Los Cuates (5 April 1994) – 1/1; 2; Cabañas (9 May 1994) – 1/2; 1; *C. octofasciatum* – Box Toro (12 May 1994) – 1/1; 3; *C. urophthalmus* – Noc-choncunchey (2 February 1994) – 1/1; 16.

Site of infection: gills.

Material studied: 7 specimens from *C. meeki*, 6 from *C. octofasciatum* and 2 from *C. urophthalmus*.

Description (N = 10; measurements of a specimen with small, wide spines from *C. urophthalmus* in parenthesis): Cyst oval, thick-walled, 256–392 × 144–288. Body elongate, tapering anteriorly, 476–833 × 103–190 (349 × 138); tegument finely spined including posterior extremity. Preoral lobe weakly developed; oral sucker terminal, 62–77 × 68–94 (74 × 65), with appendage up to 76 long. Acetabulum sucker-like, spherical, 50–76 × 56–72 (45 × 49); sucker ratio 1.04–1.46 : 1 (1.49 : 1). Circumoral spines (31–34 in number) arranged in one complete row of 24–26 (25) spines 12–16 (7) (dorsal) and 10–13.5 (ventral) long, and one additional dorsal row composed of 8–10 (8) small, 3.5–10 (5.5) long spines. Arrangement of spines as follows: 26 + 7 (5 specimens), 26 + 8 (N = 3), 24 + 7 (N = 1), 24 + 8 (N = 1), 25 + 8 (N = 2), 25 + 10 (N = 1), and 26 + 9 (N = 1). Prepharynx 110–126 long; pharynx 32–44 × 28–50; oesophagus shorter than prepharynx. Caeca long, crossing ventral sucker and reaching to excretory bladder. Eyespot pigment confined at prepharyngeal level. Testes symmetrical, displaced to lateral margins by expanded excretory bladder, up to 53 × 33 in diameter. Genital sac formed, anterolateral or almost anterior to acetabulum; genital pore widely oval; gonotyl inconspicuous. Excretory bladder Y-shaped.

Remarks: The metacercariae differ from other *Ascocotyle* metacercariae described above by different arrangement of crown spines, their number and shape. Due to the presence of additional spines, they apparently belong to the subgenus *Phagicola* Faust, 1920.

One larva found on the gills of *C. urophthalmus* differs from other metacercariae by shorter and wider circumoral spines. However, the arrangement of circumoral spines (25 + 8) and other morphological details indicate its conspecificity with *Ascocotyle* (*Phagicola*) sp. 3 larvae.

13. **Heterophyidae** gen. sp. Fig. 3B

Host and locality: *Cichlasoma meeki* – Chek-há (8 November 1993) – 1/1; 1.

Site of infection: muscles.

Material studied: 1 excysted specimen from *Cichlasoma meeki.*

Description: Cyst thin-walled, oval. Excysted larva elongate, 705 × 286; forebody densely covered with small, slender and sharp tegumental spines. Oral sucker rounded, 123 × 115, provided with one complete circle of 24 circumoral spines; dorsal spines 12 long, ventral spines 11. Ventral sucker small, 62 × 44; sucker ratio 2.25 : 1. Prepharynx 118 long; pharynx 62 × 59. Intestinal caeca long, reaching near posterior extremity, filled with discoid bodies.

Remarks: Due to the fact that the morphology of the larva was difficult to observe, its precise identification was impossible. Nevertheless, its morphology, above all the presence of circumoral spines, spination of the

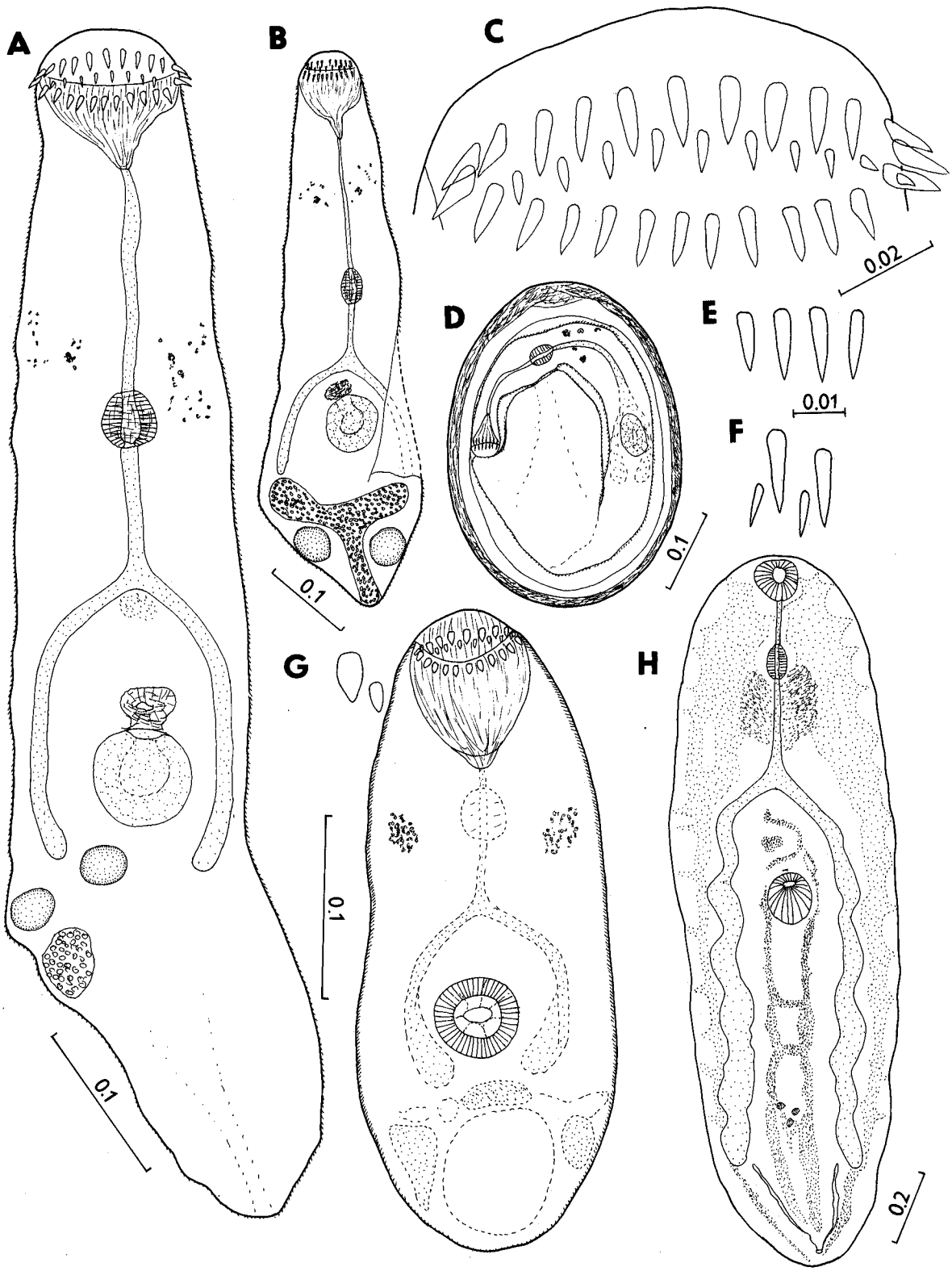

Fig. 8. *Ascocotyle (Phagicola)* sp. 3 from *Cichlasoma meeki* (**A–F**) and *C. urophthalmus* (**G**). (**A–B** – total view, **C** – anterior end, **D** – encysted larva, **E** – ventral circumoral spines, **F** – dorsal spines); **H** – *Cladocystis trifolium* (Braun, 1901) from *Cichlasoma meeki* (total view). Scale bars in millimetres (mm).

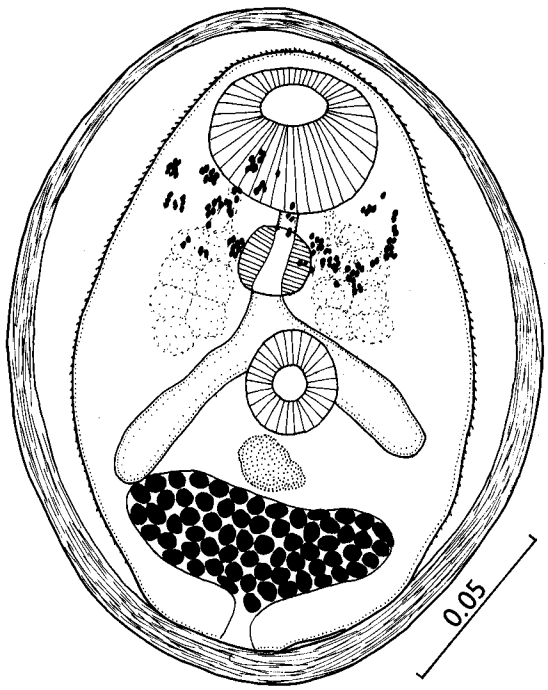

Fig. 9. *Oligogonotylus manteri* Watson, 1976 – encysted larvae. Scale bar in millimetres (mm).

tegument and the presence of long intestinal caeca filled with discoid corpuscles, indicates that it belongs to a heterophyid genus.

Family Cryptogonimidae Ward, 1917

14. ***Oligogonotylus manteri*** Watson, 1976 Fig. 9

Hosts and localities: *Poecilia petenensis* – Cenote Azul (Bacalar) (5 April 1994) – 6/6; 8 (3–18), *P. latipunctata* – Cenote Azul (Puerto Aventuras) (24 February 1994) – 1/4; 1; *Cichlasoma friedrichstahli* – Cenote Azul (Puerto Aventuras) (24 February 1994) – 1/3; 1; Cenote Azul (Bacalar) (5 April 1994) – 1/1; 1; *C. meeki* – Cenote Azul (Bacalar) (5 April 1994) – 2/2; 3 (1–4); Los Cuates (5 April 1994) – 1/1; 2; Cabañas (9 May 1994) – 2/2; 242 (140–344); *C. octofasciatum* – Cabañas (9 May 1994) – 1/1; 169; Box Toro (12 May 1994) – 1/1; 14; *C. synspilum* – Cenote Azul (Bacalar) (5 April 1994) – 2/10; 172 (1–343); Cabañas (9 May 1994) – 2/2; 412 (85–739); Framboyán (9 May 1994) – 2/2; 28 (18–37); *C. urophthalmus* – Dzaptún (8 November 1993) – 1/2; 251; Cabañas (9 May 1994) – 4/4; 1023 (733–1575); Hodz-ob (23 June 1994) – 2/11; 61 (31–90); Dzonot Cervera (23 May 1994) – 6/10; 377 (2–792) + 3 fishes with thousands of larvae; *Gobiomorus dormitor* – Cenote Azul (Bacalar) (5 April 1994) – 2/2; 129 (75–182).

Site of infection: gills, pectoral and pelvic fins, intestinal wall.

Material studied: 3 specimens from *P. petenensis*, 10 from *C. meeki*, 21 from *C. synspilum*, 10 from *C. urophthalmus* and 7 from *Gobiomorus dormitor*.

Remarks: Scholz et al. (1994) studied the life cycle of the trematode and provided descriptions of developmental stages, including metacercariae, based on the material from cichlid fishes from the Yucatan Peninsula. The present material well corresponds to that described by the above authors.

Family Clinostomidae Lühe, 1901

15. ***Clinostomum*** cf. ***complanatum*** (Rudolphi, 1814) Fig. 10A–B

Hosts and localities: *Astyanax fasciatus* – Dzonot Cervera (23 May 1994) – 1/5; 1; *Rhamdia guatemalensis* – Yokdzonot (13 October 1993) – 1/1; 23; Xmucuy (26 October 1993) – 13/22; 4 (1–23); Ixin-há (26 October 1993, 13 June 1994, 11 July 1994, 22 August 1994, 20 September 1994, 17 October 1994, 14 November 1994, 31 January 1995) – 64/106; 5 (1–43); Dzonot Cervera (23 May 1994) – 1/1; 27; Sacamucuy (10 October 1994) – 2/6; 3; *Poecilia petenensis* – Box Toro (12 May 1994) – 1/2; 2; *Cichlasoma urophthalmus* – Chen-há (18 October 1993, 27 June 1994) – 2/41; 2 (1–3).

Site of infection: gills, fins, operculum, muscles, mesentery, stomach and intestinal wall.

Material studied: 23 specimens from *R. guatemalensis*, 1 young specimen from *C. urophthalmus*.

Description (N = 6; measurements of the larva from *C. urophthalmus* in parentheses): Cysts large, widely oval or almost spherical, thick-walled; cyst diameter not measured. Body elongated, 6700–8730 (1450) × 1830–2090 (620), maximum width at middle or posterior thirds of body (at anterior body third). Oral sucker widely oval, lateral (almost terminal), 232–376 × 336–408 (118 × 128), situated in collar-like fold. Ventral sucker large, 954–1140 × 995–1120 (360 × 440); sucker ratio 1 : 2.89–3.21 (mean 1 : 2.97; 1 : 3.24). Pharynx small; oesophagus absent. Intestinal caeca long, forming numerous diverticles in hindbody (without diverticles). Primordia of two testes lobed, postequatorial, in tandem; anterior testis 528–640 × 464–690; posterior testis 448–730 × 568–700. Cirrus sac banana-shaped, anterolateral to anterior testis. Ovary small, intratesticular, lateral to mid-line of body. Uterine sac without evaginations, anterior to genitalia (female genital system weakly developed).

Remarks: The larvae correspond in their morphology and measurements to *C. complanatum* metacercariae, as figured, e.g., by Yamaguti (1975 – Fig. 1219). In Mexico, Pineda-López (1985), Osorio-Sarabia et al. (1987) and García et al. (1993) reported *C. complanatum* metacercariae from the mesentary, mouth, brain

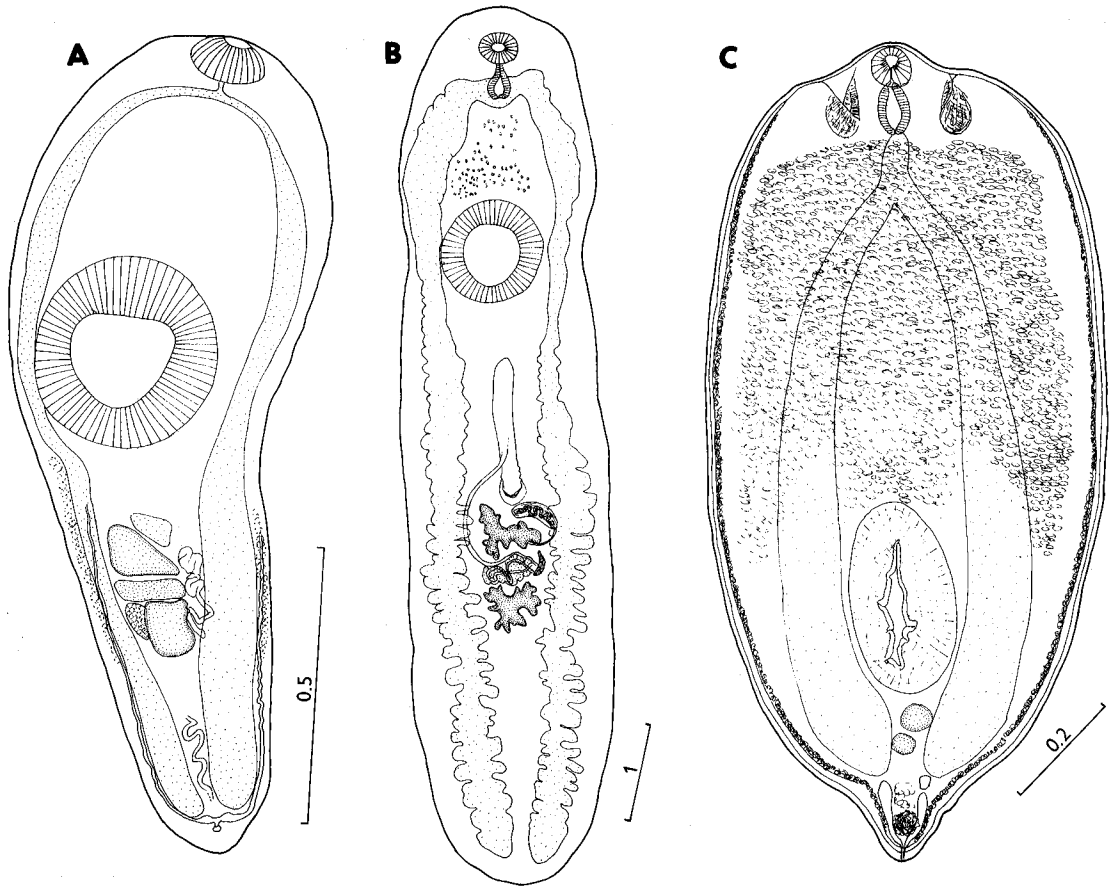

Fig. 10. A–B – *Clinostomum complanatum* (Rudolphi, 1814) from *Cichlasoma uropthalmus* (**A**) and *Rhamdia guatemalensis* **(B); C** – *Diplostomum (Austrodiplostomum) compactum* (Lutz, 1928) from *Cichlasoma meeki*. Scale bars in millimetres (mm).

and orbit of the cichlid fishes *Cichlasoma pasionis*, *C. pearsei*, *C. synspilum*, *C. urophthalmus*, *Petenia splendida*, *Oreochromis aureus* and *O. mossambicus* from Tabasco and Colima, Mexico. Salgado-Maldonado, Pineda-López and Vidal-Martínez (unpubl. data) reported *C. complanatum* metacercariae from 11 species of cichlids in Mexico.

Clinostomum complanatum is supposed to be a cosmopolitan parasite of fish-eating birds (members of the genera *Ardea*, *Ardeola*, *Cancroma*, *Egretta*, *Nycticorax*, *Butorides*, etc.) – Ukoli (1966), Yamaguti (1971). Metacercariae of this parasite have been found in many species of fishes of different families (Yamaguti 1971, 1975).

In *Rhamdia quelen* in Venezuela and *R. guatemalensis* in Yucatan, metacercariae of another *Clinostomum* species, *C. intermediale* Lamont, 1920, were found (Yamaguti 1971). Adults of *C. intermediale* are parasites of cormorants (*Phalacrocorax penicillatum*, *P. vigua*), hitherto recorded in Mexico (Nuevo León) and Venezuela (Bravo-Hollis 1948, Ukoli 1966, Yamaguti 1971). However, *C. intermediale* differs from *C. complanatum* by the position of the testes, which are both located by the posterior third of the body in the former species whereas the anterior testis is situated in the middle third of the body in *C. complanatum*. In addition, *C. intermediale* possesses trilobate testes, while those of *C. complanatum* have more lobes (Ukoli 1966) as the larvae studied. However, the taxonomy of *Clinostomum* is rather confused and a thorough revision is highly required; cosmopolitan distribution of *C. complanatum* also remains questionable (Ostrowski de Nuñez – pers. comm.). Consequently, the larvae found in fishes from cenotes are designated as *Clinostomum* cf. *complanatum*.

Family Diplostomidae Poirier, 1886

16. ***Diplostomum* (*Austrodiplostomum*) *compactum*** (Lutz, 1928) Fig. 10C

Hosts and localities: *Cichlasoma meeki* – Noc-choncunchey (21 September 1993) – 1/6; 2; Los

Cuates (5 April 1994) – 1/1; 4; Cenote Azul (Bacalar) (5 April 1994) – 1/1; 4; *C. synspilum* – Cenote Azul (Bacalar) (5 April 1994) – 2/10; 2; *C. urophthalmus* – Hodz-ob (23 June 1994) – 3/11; 1 (1–2); Chen-há (27 June 1994) – 1/41; 1.

Site of infection: eye (humour body).
Material studied: 5 specimens from *C. meeki*.

Description: Larvae unencysted, body widely oval, 1300–1540 × 660–880, with maximum width near midline of body. Oral sucker subterminal, 55–74 × 64–80; two pseudosuckers situated lateral to oral sucker. Prepharynx absent, pharynx strongly muscular, 65–80 × 52–70; ventral sucker absent. Intestinal caeca wide, reaching posteriorly near body extremity. Brandes' organ large, 320–397 × 173–237, situated in posterior third of body; genital primordia present in form of two dark masses posterior to Brandes' organ. Anterior two thirds of body filled with numerous glandular cells.

Remarks: The larvae found in *C. meeki* are morphologically identical with those of *D. compactum* reported by Pineda-López (1985), Osorio-Sarabia et al. (1987) and García et al. (1993) from the eyes and brain of *Cichlasoma meeki*, *C. motaguense*, *C. synspilum*, *C. urophthalmus*, and *Petenia splendida* from Tabasco, and *Oreochromis aureus* from Colima, Mexico, respectively. *Diplostomum compactum* is a common parasite hitherto reported from as many as 14 cichlid species (*Cichlasoma* spp., *Petenia splendida*) in Mexico (Salgado-Maldonado, Pineda-López and Vidal-Martínez – unpubl. data). In addition, Pineda-López (1985) found *D. compactum* larvae in *Ictalurus meridionalis*. Dubois and Macko (1972) found adults in *Phalacrocorax olivaceus mexicanus* and *Ph. auritus floridanus* in Cuba, and Ostrowski de Nuñez (1982) in *Ph. brasiliensis brasiliensis* in Argentina and Venezuela.

17. ***Posthodiplostomum minimum*** (MacCallum, 1921) Fig. 11A

Hosts and localities: *Cichlasoma friedrichstahli* – Cenote Azul (Bacalar) (5 April 1994) – 1/1; 1; *C. meeki* – Chek-há (8 November 1993) – 1/1; 1; *C. octofasciatum* – Box Toro (12 May 1994) – 1/1; 2; *C. pearsei* – Noc-choncunchey (2 February 1994) – 1/1; 2; *C. urophthalmus* – Chen-há (18 October 1993) – 5/41; 12 (1–4); Zaci (18 April 1994) – 1/1; 2; Gran Cenote (25 April 1994) – 1/1; 2; Hodz-ob (23 June 1994) – 2/11; 4; Dzonot Cervera (23 May 1994) – 3/10; 3 (2–4).

Site of infection: muscles.
Material studied: 1 specimen from *C. meeki*, 1 from *C. octofasciatum* and 1 from *C. urophthalmus*.

Description (N = 3): Cyst thin-walled, transparent (diameter not measured). Body of excysted larva divided to forebody and hindbody, total length 663–1607; forebody widely oval, 451–952 × 390–560; hindbody heart-shaped, 212–655 × 230–536. Oral sucker subterminal, 36–57 × 44–47. Ventral sucker slightly postequatorial, almost spherical, 47–80 × 62–71; sucker ratio 1 : 1.38–1.61. Prepharynx absent; pharynx small, 30–38 × 18–26, almost completely ventral to oral sucker. Oesophagus short; intestinal caeca long, reaching near posterior extremity, becoming wider posteriorly. Brandes' organ spherical, 128 × 143. Sponge-biscuit-shaped proteolytic glands situated immediately posterior to Brandes' organ. Genital primordia situated in hindbody in form of groups of darkly stained cells. Anterior testis transversely oval; posterior testis V-shaped; ovary anterolateral to anterior testis. Posterior extremity with cone-shaped muscular papilla. Anterior third of body containing numerous cellular glands, grouped into four longitudinal bands.

Remarks: The morphology of the larva well corresponds to that of *Posthodiplostomum minimum* as described by Yamaguti (1975). This trematode is a common parasite of fish-eating birds in North America (Canada, USA, Cuba); metacercariae have been found from many freshwater or brackish fishes, including perciform genera *Lepomis*, *Perca*, *Stizostedion* (Yamaguti 1971). In Mexico, *P. minimum* metacercariae have been reported from the muscles, mesentery, fins and gills of *C. urophthalmus* from southeastern Mexico (Salgado-Maldonado 1993, Aguirre-Macedo and García-Magaña 1995). Pineda-López (1985) reported larvae, designated as *Posthodiplostomum* sp., from *Cichlasoma pearsei*, *C. synspilum*, *C. urophthalmus* and *Petenia splendida* in Tabasco, Mexico, which are apparently conspecific with the present material.

18. ***Posthodiplostomum*** sp. Fig. 11B

Hosts and localities: *Astyanax fasciatus* – Noc-choncunchey (2 February 1994) – 1/31; 1; *C. octofasciatum* – Box Toro (12 May 1994) – 1/1; 5; *C. pearsei* – Noc-choncunchey (2 February 1994) – 1/1; 2; *C. urophthalmus* – Hodz-ob (23 June 1994) – 2/11; 4 (1–7; Dzonot Cervera (23 May 1994) – 1/10; 1.

Site of infection: muscles.
Material studied: 5 specimens from *C. octofasciatum* and 3 from *C. urophthalmus*.

Description (N = 7): Cyst oval, hyaline (diameter not measured); body of excysted larva divided into elongate forebody, 306–472 × 207–254, and lanceolate hindbody, 333–443 × 197–226. Oral sucker almost terminal, considerably large, 59–82 × 91–118; ventral sucker spherical, 36–47 × 36–48; sucker ratio 1.81–2.33 : 1. Prepharynx absent; pharynx widely oval or almost spherical, 24–44 × 28–34. Brandes' organ weakly visible, 82 × 74. Secondary excretory system well developed.

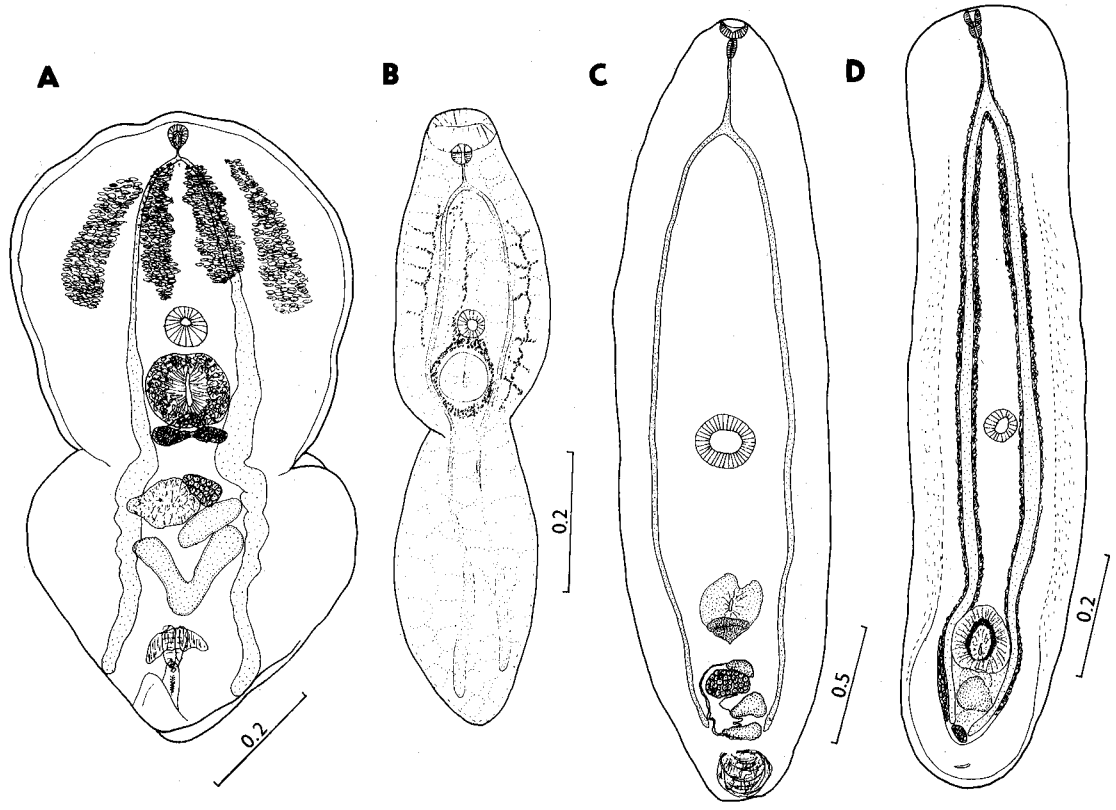

Fig. 11. A – *Posthodiplostomum minimum* (MacCallum, 1921) from *Cichlasoma urophthalmus*; **B** – *Posthodiplostmum* sp. from *Cichlasoma octofasciatum*; **C** – Proterodiplostomidae gen. sp. 1 from *Rhamdia guatemalensis*; **D** – Proterodiplostomidae gen. sp. 2 from *Astyanax fasciatus*. Scale bars in millimetres (mm).

Remarks: The most characteristic feature of the larvae is the size of the oral sucker, which is much larger than the ventral sucker. The morphology of the larvae from cenote fish indicates they belong to the genus *Posthodiplostomum* Dubois, 1936. However, species identification is not possible until more data, particularly those on the life cycle and morphology of adult worms, are available.

Family Proterodiplostomidae Dubois, 1936

19. **Proterodiplostomidae** gen. sp. 1 Fig. 11C

Host and locality: *Rhamdia guatemalensis* – Xmucuy (26 October 1993) – 1/22; 8.

Site of infection: stomach and oesophagus.

Material studied: 6 specimens from *R. guatemalensis*.

Description (N = 6): Larva unencysted, large, lanceolate, 2270–2620 × 660–790. Oral sucker subterminal, small, cup-like, 65–68 × 68–88. Ventral sucker spherical, equatorial, 157–195 × 198–224; sucker ratio 1 : 2.42–3.10. Prepharynx absent; pharynx posteroventral to oral sucker, 57–68 × 30–45. Oesophagus present, intestinal caeca long, passing Brandes' organs and terminating at level of genital primordia near posterior extremity. Brandes' organ in posterior fourth of body, oval, 160–230 × 186–262; darkly-stained proteolytic glands closely posterior to Brandes' organ. Genital primordia near posterior extremity, formed by hardly distinguishable masses of dark cells.

Remarks: The morphology of the larvae indicates that they belong to the family Proterodiplostomidae Dubois, 1936. Representatives of this family mature in reptiles (Szidat 1969, Yamaguti 1971) and there are some species reported to occur in Mexico (Pineda-López 1985).

20. **Proterodiplostomidae** gen. sp. 2 Fig. 11D

Hosts and localities: *Astyanax fasciatus* – Dzaptún (8 November 1993) – 1/2; 21; Box Toro (13 May 1994) – 1/4; 1; *Cichlasoma octofasciatum* – Box Toro (13 May 1994) – 1/1; 14.

Site of infection: swimmbladder and gills.

Material studied: 7 specimens from *A. fasciatus* and 6 from *C. octofasciatum*.

Description (N = 7): Cyst thin-walled, transpared (not measured); larva elongate, widened in anterior part, 816–1256 × 205–298. Oral sucker subterminal, small,

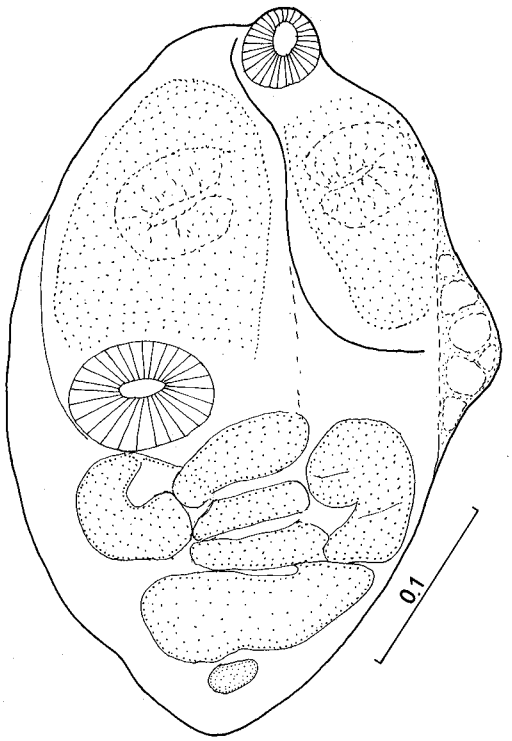

Fig. 12. *Apharyngostrigea* sp. from *Astyanax fasciatus*. Scale bar in millimetres (mm).

cup-like, 27–44 × 28–36. Ventral sucker spherical, equatorial, 37–57 × 40–55; sucker ratio 1 : 1.33–1.52. Prepharynx absent; pharynx posteroventral to oral sucker, 17–28 × 14–22. Oesophagus present, intestinal caeca long, passing Brandes' organs and terminating at level of genital primordia near posterior extremity; caeca lined with glandular cells. Brandes' organ in posterior fourth of body, oval, 67–160 × 65–109; genital primordia posterior to Brandes' organ, separated into testes and ovary.

Remarks: The morphology of the larvae indicate that they belong to the family Proterodiplostomidae Dubois, 1936. The metacercariae from *A. fasciatus* morphologically and metrically resemble those found in the gonads of *Ictalurus meridionalis* in Tabasco, Mexico, and designated as "*Diplostomulum* sp." (Pineda-López 1985). However, the larvae differ each other by shape of the body, which is tapering towards posterior end in the larvae from Tabasco while elongated, with wide anterior extremity in the metacercariae from *A. fasciatus*.

Family Strigeidae Railliet, 1919

21. ***Apharyngostrigea*** sp. Fig. 12

Host and locality: *Astyanax fasciatus* – Noc-choncunchey (10 February 1994) – 1/2; 2.

Site of infection: liver, mesentery.

Number of specimens studied: 2 specimens from *A. fasciatus*.

Description (N = 1): Cyst widely oval; body of excysted metacercaria with tapering posterior end, 410 × 275. Forebody with wide and deep depression (fold) and two pseudosuckers. Oral sucker terminal, 55 × 48. Ventral sucker widely oval, equatorial, 58 × 67; sucker ratio 1 : 1.22. Pharynx absent, caeca surrounding Brandes' organ. Brandes' organ large, formed by several lobes filling most part of hindbody. Genital primordia near posterior extremity. Two bands of dark cellular mass present between suckers.

Remarks: The morphology of the larvae studied was barely observable. Nevertheless, shape of the body, which is provided with a wide depression (fold) in its anterior part, the presence of pseudosuckers, the absence of a pharynx, the structure of Brandes' organ and shape of genital primordia suggest that the larvae belong to the genus *Apharyngostrigea* Ciurea, 1927.

In addition to the above described larva, other strigeid metacercariae were found in muscles of *Cichlasoma friedrichstahli* from Cenote Azul (Bacalar) (5 April 1994) – 1/2; muscles and intestinal wall of *C. urophthalmus* from Chen-há (18 October 1993) – 5/3 (1–4); in pelvic and pectoral fins of *C. meeki* from Cenote Azul (Bacalar) (5 April 1994) – 1/3; and *C. synspilum* – Cenote Azul (Bacalar) (5 April 1994) – 3/4 (2–6). However, voucher specimens of these larvae were not available and possible conspecifity of some metacercariae with *Apharyngostrigea* sp. remains unclear.

In Mexico, strigeid larvae, designated as *Tetracotyle* sp. (collective name for metacercariae of several strigeid genera such as *Apharyngostrigea*, *Ichthyocotylurus* Szidat, 1935, *Apatemon* Szidat, 1928) larvae were also reported from the mesentery of several cichlid species, e.g. *Cichlasoma meeki*, *C. geddesi*, *C. helleri*, *C. pearsei*, *C. synspilum*, *C. urophthalmus* and *Petenia splendida* from Tabasco (Osorio-Sarabia et al. 1987, Salgado-Maldonado 1993).

DISCUSSION

The total number of metacercariae recorded, 21 species, is much higher than that of adult trematodes found in cenote fishes (10 species – see Scholz et al. 1995). In addition, the prevalence and mean intensity of infection with some larvae, e.g. those of *Echinochasmus* spp., *Ascocotyle* (*Phagicola*) sp. 2 and *Oligogonotylus manteri*, was very high. As demonstrated by Salgado-Maldonado (1993) in helminth parasites of the cichlid *Cichlasoma urophthalmus*, trematodes and, in particular, their larval stages form a dominant component of helminth communities of fishes in southeastern Mexico.

Of the larval species recorded, adults of only two trematodes, *Stunkardiella minima* and *Oligogonotylus manteri*, were found in fishes from cenotes (Scholz et al. 1995). Adults of other species likely parasitize vertebrates other than fishes, with the exception of *Atrophecaecum* (?) *astorquii*, which matures in the bagre, *Rhamdia nicaraguensis*. It can be assumed that definitive hosts of most of the species found at the stage of metacercaria are fish-eating birds, which are rather abundant in most cenotes, particularly in those situated in coastal region of the Yucatan Penisula (Celestun zones, cenotes near the coast of the Caribbean Sea in the State of Quintana Roo). This is the case of heterophyid larvae (*Ascocotyle* spp.). Definitive hosts of acanthostomid larvae (*Pelaezia loossi*) are supposedly reptiles, e.g. crocodiles or snakes.

With regards to species richness, dominant groups of metacercariae in cenote fishes were strigeoid larvae (7 species) and heterophyids (6).

From a geographical point of view, it is evident that the fauna of metacercariae is diversified and it consists of cosmopolitan species (*Clinostomum* cf. *complanatum*), species widely distributed in North and South America (heterophyids, strigeoid metacercariae) as well as of trematodes limited in their distribution to southeastern Mexico and Central America (*Stunkardiella minima*, *Oligogonotylus manteri*).

Acknowledgements. The authors are indebted to Dra. Margarita Ostrowski de Nuñez, Facultad de Ciencias Exactas y Naturales, Buenos Aires, Argentina, and Dr. William F. Font, SE Louisiana University, USA, for critical remarks and valuable advice, and to Drs. Guillermo Salgado–Maldonado, Institute of Zoology, UNAM, Mexico City, Raúl Pineda-López, UJAT, Tabasco, and Victor M. Vidal-Martínez, University of Exeter, England, for kind providing unpublished data about parasites of cichlid fishes. Thanks are also due to Esperanza Pérez-Díaz and Mirella Hernández de Santillana, CINVESTAV-IPN Merida, for the identification of fishes. The excellent assistance of Raúl Simá-Alvarez, Jorge Güemez-Ricalde, Gregory Torres-Arjona, Victor Ceja-Moreno and Miguel Herrera-Rodríguez, all CINVESTAV-IPN, Mérida, and Dr. Oleg Ditrich, Institute of Parasitology, České Budějovice, in sampling fishes is also greatly appreciated. This study was financially supported by the Comision Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Mexico, research project PO99.

REFERENCES

AGUIRRE-MACEDO M. L., GARCÍA–MAGAÑA L. 1995: Metacercarias de ciclidos autóctonos y claves para su reconocimiento. Universidad y Ciencia (in press).

BRAVO-HOLLIS M. 1948: Dos especies de *Clinostomum* (Trematoda) de aves procedentes de estado de Nuevo León, México. An. Inst. Biol., Univ. Nat. Auton. Mex., Ser. Zool. 18: 489–498.

BROOKS D. R., OVERSTREET R. M. 1977: Acanthostome digeneans from the American alligator in the southeastern United States. Proc. Biol. Soc. Wash. 90: 1016–1029.

BYKHOVSKAYA-PAVLOVSKAYA I. E. 1969: Parasitological Investigations into Fishes. Publishing House Nauka, Leningrad, 108 pp. (In Russian.)

DUBOIS G., MACKO J. K. 1972: Contribution a l'étude des Strigeata La Rue, 1926 (Trematoda: Strigeida) de Cuba. Annal. Parasitol. (Paris) 47: 51–75.

ERGENS R. 1969: The suitability of ammonium picrate – glycerin in preparing slides of lower Monogenoidea. Folia Parasitol. 16: 320.

FONT W. F., HEARD R. W., OVERSTREET R. M. 1984: Life cycle of *Ascocotyle gemina* n. sp., a sibling species of *A. sexidigitata* (Digenea: Heterophyidae). Trans. Am. Microsc. Soc. 103: 392–407.

GARCÍA M. L. J., OSORIO SARABIA D., CONSTANTINO F. 1993: Prevalencia de los parásitos y las alteraciones histológicas que producen a las tilapias de la laguna de Amela, Tecomán, Colima. Vet. Méx. 24: 199–205.

HALL F. G.. 1977: Cenotes y aguadas. In: Enciclopedía yucatanense. Tomo I. Gobierno del Estado de Yucatán, pp. 67–80.

LAMOTHE-ARGUMEDO R., AGUIRRE-MACEDO M. L. 1991: Metacercaria de *Echinochasmus zubedakhaname* parásito de *Cichlasoma urophthalmus* en Celestún, Yucatán, México. An. Inst. Biol. Univ. Nal. Auton. Mex., Ser. Zool., 62: 139–140.

LAMOTHE-ARGUMEDO R., PONCIANO–RODRIGUEZ G. 1986a: Estudio helmintológico de los animales silvestres de la estación de biología tropical "Los Tuxtlas" Veracruz. Trematoda III. Redescripción de *Stunkardiella minima* (Stunkard, 1938) Lamothe y Ponciano, 1985. An. Inst. Biol. Univ. Nal. Auton. Mex., Ser. Zool., 56: 323–336.

LAMOTHE-ARGUMEDO R., PONCIANO-RODRIGUEZ G. 1986b: Revisión de la subfamilia Acanthostominae Nicoll, 1914 y establecimiento de dos nuevos géneros. An. Inst. Biol. Univ. Nal. Auton. Mex., Ser. Zool., 56: 301–322.

MARGOLIS L., ESCH G. D., HOLMES J. C., KURRIS A. M., SCHAD G. A. 1992: The use of ecological terms in parasitology (report of an *ad hoc* committee of the American Society of Parasitologists). J. Parasitol. 68: 131–133.

MORAVEC F., VARGAS-VÁZQUEZ, SCHOLZ T., VIVAS-RODRÍGUEZ C., MENDOZA-FRANCO E. 1995a: Nematodes parasitic in fishes of cenotes (= sinkholes) of the Peninsula of Yucatan, Mexico. Part 1. Adults. Folia Parasitol. 42: 115–129.

MORAVEC F., VARGAS-VÁZQUEZ, SCHOLZ T., VIVAS-RODRÍGUEZ C., MENDOZA-FRANCO E. 1995b: Nematodes parasitic in fishes of cenotes (= sinkholes) of the Peninsula of Yucatan, Mexico. Part 2. Larvae. Folia Parasitol. 42: 199–210.

NASIR P., DÍAZ M. 1968: Studies of the freshwater larval trematodes XVII. The life cycle of *Echinochasmus zubedakhaname* n. sp. Z. Parasitenkd. 30: 126–133.

OSORIO-SARABIA V., PINEDA-LÓPEZ R., SALGADO-MALDONADO G.. 1987: Fauna helmintológica de peces dulceacuicolas de Tabasco. Estudio preliminar. Universidad y Ciencia 4 (7): 5–31.

OSTROWSKI de NUÑEZ M. 1974: Estudio sobre estados larvales de trematodos digeneos de peces Cyprinodontiformes. Physis, Buenos Aires, Seccion b 33 (84): 45–61.

OSTROWSKI de NUÑEZ M. 1977: El ciclo biológico de "*Diplostomum (Austrodiplostomum) compactum*" (Lutz, 1928) Dubois 1970 (= *Austrodiplostomum mordax* Szidat y Nani 1951) ("Trematoda, Diplostomatidae"). Rev. Mus. Arg. Cien. Nat. 2: 7–75.

OSTROWSKI de NUÑEZ M. 1982: Die Entwicklungszyklen von *Diplostomum (Austrodiplostomum) compactum* (Lutz, 1928) Dubois, 1970 und *D. (A.) mordax* (Szidat und Nani, 1951) n. comb. in Sudamerika. Zool. Anz. 208: 393–404.

OSTROWSKI de NUÑEZ M. 1984: Beitrage zur Gattung *Acanthostomum* (Trematoda, Acanthostomatidae) und zu den Entwicklungszyklen von *A. marajoarum* (Freitas & Lent, 1938) und *A. loossi* (Perez Vigueras, 1957) in Venezuela. Mitt. zool. Mus. Berl. 60: 179–201.

OSTROWSKI de NUÑEZ M. 1993: Life-history studies of heterophyid trematodes in the Neotropical Region: *Ascocotyle (Phagicola) diminuta* (Stunkard & Haviland, 1924) and *A. (P.) angrense* Travassos, 1916. Syst. Parasitol. 24: 191–199.

PEARSE A. P., CREASER E. P., HALL F. G. (Eds.) 1936: The Cenotes of Yucatan: A Zoological and Hydrographic Survey. Carnegie Institution of Washington, Publ. No. 457.

PÉREZ-VIGUERAS J. 1957: Contribución al conocimiento de la fauna helmintologica cubana. Memorias sobre la historia natural de la Isla de Cuba 23: 1–36.

PINEDA-LÓPEZ R. 1985: Infección por metacercarias (Platyhelminthes: Trematoda) en peces de agua dulce de Tabasco. Universidad y Ciencia 2: 47–60.

SALGADO-MALDONADO G. 1993: Ecología de los helmintos parásitos de *Cichlasoma urophthalmus* en Yucatán, México. PhD thesis, CINVESTAV–IPN, Mérida, Mexico.

SALGADO-MALDONADO G., AGUIRRE-MACEDO L. 1991: Metacercarias parasitas de *Cichlasoma urophthalmus* (Cichilidae [sic!]) *Pelaezia loossi* n. comb. y *Phagicola angrense* con descripcion de adultos recuperados experimentalmente. An. Inst. Biol. Univ. Nac. Auton. Mex., Ser. Zool., 62: 391–407.

SCHOLZ T., LAVADORES J. I. P., VARGAS V . J., MENDOZA F. E. F., RODRIGUEZ C. R., VIVAS R. C. 1994: Life cycle of *Oligogonotylus manteri* (Digenea: Cryptogonimidae), a parasite of cichlid fishes in southern Mexico. J. Helminthol. Soc. Wash. 61: 190–199.

SCHOLZ T., VARGAS-VÁZQUEZ J., MORAVEC F., VIVAS-RODRÍGUEZ C., MENDOZA-FRANCO E. 1995: Cenotes (sinkholes) of the Yucatan Penisula, Mexico, as a habitat of adult trematodes of fish. Folia Parasitol. 42: 27–35.

SOGANDARES-BERNAL F., LUMSDEN R. D. 1963: The generic status of the heterophyid trematodes of the *Ascocotyle* complex, including notes on the systematics and biology of *Ascocotyle angrense* Travassos, 1916. J. Parasitol. 49: 264–274.

STUNKARD H. 1938: Parasitic flatworms from Yucatán. Carnegie Institution of Washington. Publ. No. 491: 33–50.

SZIDAT L. 1969: Structure, development, and behaviour of new strigeatoid metacercariae from subtropical fishes of South America. J. Fish. Res. Bd. Canada 26: 753–786.

WATSON D. E. 1976: Digenea of fishes from Lake Nicaragua. In: T. B. Thorson (Ed.), Investigations of the Ichthyofauna of Nicaraguan Lakes. School of Life Sciences, University of Nebraska, Lincoln, pp. 251–260.

YAMAGUTI S. 1971: Synopsis of Digenetic Trematodes of Vertebrates. Parts I, II. Keigaku Publishing Co., Tokyo. 1074 pp. + 347 Plts.

YAMAGUTI S. 1975: A Synoptical Review of Life Histories of Digenetic Trematodes of Vertebrates. Keigaku Publishing Co., Tokyo, 590 pp. + 219 Plts.

UKOLI F. M. A. 1966: On *Clinostomum tilapiae* n. sp., and *C. phalacrocoracis* Dubois, 1931 from Ghana, and a discussion of the systematies of the genus *Clinostomum* Leidy, 1856. J. Helminthol. 40: 187–214.

Received 17 February 1995

Accepted 30 June 1995