FOLIA PARASITOLOGICA 42: 37–47, 1995

Cenotes (sinkholes) of the Yucatan Peninsula, Mexico, as a habitat of adult trematodes of fish

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Key words: Digenea, fish, cenotes, Yucatan, Mexico, zoogeography

Abstract. Examination of a total of 581 fish specimens of 15 species from 39 cenotes (sinkholes) in the Yucatan Peninsula, southeastern Mexico, revealed the presence of 10 species of adult trematodes. These were as follows: *Saccocoelioides sogandaresi* Lumsden, 1963, *Saccocoelioides* sp. (family Haploporidae), *Cichlasotrema ujati* Pineda et Andrade, 1989 (Angiodictyidae), *Crassicutis cichlasomae* Manter, 1936 (Homalometridae), *Magnivitellinum simplex* Kloss, 1966 (Macroderoididae), *Stunkardiella minima* (Stunkard, 1938) (Acanthostomidae), *Oligogonotylus manteri* Watson, 1976 (Cryptogonimidae), *Genarchella tropica* (Manter, 1936), *G. astyanactis* (Watson, 1976), and *G. isabellae* (Lamothe-Argumedo, 1977) (Derogenidae). *Saccocoelioides sogandaresi* is reported from Mexico for the first time. *Poecilia velifera* and *P. latipunctata* for *S. sogandaresi*, *Cichlasoma octofasciatum* for *C. cichlasomae*, *Cichlasoma friedrichstahli* and *C. meeki* for *O. manteri*, and *C. meeki*, *C. octofasciatum* and *Gobiomorus dormitor* for *G. isabellae* represent new host records. Most species found are described and figured and their host range and distribution are discussed.

The Peninsula of Yucatan is characterized by the almost complete absence of superficial waters like rivers or streams. There is only a very limited number of superficial water bodies, represented by shallow lakes ("lagunas") in the southern part of the Peninsula or small water bodies called "aguadas"; none of these water bodies have communication with subterranean waters. Due to the presence of limestone, rainfall is filtered through the soil surface and forms not only numerous caves, but also a complex subterranean water system. A typical feature of this system is the presence of "cenotes" (sinkholes).

On the basis of geomorphological characteristics, the "true" cenotes ("aguadas" supplied only by rainfalls without any communication with subterranean waters are not considered) can be divided into three types after Hall (1977): 1) "abierto" (open) with an opening of almost the same diameter as the diameter of the water surface; the walls are almost vertical; 2) "cántaro" with the opening considerably smaller than the diameter of the water body; 3) "caverna" (cave) with a lateral entrance. The most typical cenotes (types 1 and 2), which originate by dissolving the superficial layer of limestone and the opening of the subterranean water system to the surface, usually have the water surface about 10–20 metres below ground level.

Cenotes of the Yucatan Peninsula represent unique habitats with typical fauna, including several endemic species, above all of invertebrates (Pearse 1936). The fish fauna is composed both of common species occurring also in other types of waters and of "cave" fish such as *Typhliasina pearsei* (family Ophidiidae) and *Ophisternon infernale* (Synbranchidae) (Hubbs 1936). The importance of cenotes from the biogeographical point of view is also supported by the fact that the Peninsula of Yucatan represents a transient region, the fauna of which is formed and influenced by both Neotropical and Holarctic elements.

Despite many unique features of cenotes, the current knowledge of their distribution, hydrology and fauna is rather limited. The same can be said of the fish parasites, the occurrence, distribution, biology and ecology of which are still almost completely unknown. In the 1930's, a series of articles by American authors dealing with helminths, mainly trematodes, parasitizing fish in cenotes of the Yucatan Peninsula, was published (Manter 1936, Pearse 1936, Stunkard 1938). However, these authors reported only a limited number of fish helminths and only data on the occurrence were provided. Since then, only recently a few papers about the taxonomy and life cycles of several trematode species parasitizing cenote fish have been published (Scholz and Salgado-Maldonado 1994, Scholz et al. 1994, 1995 a, b).

In order to provide detailed data on the taxonomy, distribution, host specificity, life cycles, ecology and

pathogenicity of parasites of fish from cenotes, a long-term investigation was carried out in the Peninsula of Yucatan. This study revealed the presence of a large number of helminth species, some of which have not been reported from Mexico or are not well known or adequately described. The present paper, which represents the first part of a series of papers dealing with the parasite fauna of cenote fish of the Yucatan Peninsula, surveys the occurrence of adult trematodes. Although the findings of some adult trematodes reported here have already been reported in separate articles by the present authors (Scholz et al. 1995 a,b), these species are also included in the present account in order to provide a complete list of parasites found.

MATERIALS AND METHODS

The study was carried out in the Peninsula of Yucatan from September 1993 to January 1995. A total of 581 fish of the following 15 species was sampled and helminthologically 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 fish were taken from the following 39 cenotes of the Yucatan Peninsula (see Fig. 1 – numbers of cenotes correspond to those in the list given below; name of cenote, geographical position, sampling date, type of cenote and number of fishes sampled are given in descriptions):

Celestún zone (Ce; see Fig. 1.)

1. Noc-choncunchey: 20°48'53"N; 90°11'47"W; open cenote; 21 September 1993 – *Astyanax fasciatus* (5 specimens), *Cichlasoma meeki* (6 specimens), *Petenia splendida* (2); 2 February 1994 – *A. fasciatus* (8), *Poecilia petenensis* (1), *Poecilia velifera* (2), *Cichlasoma pearsei* (1), *Cichlasoma urophthalmus* (1); 13 September 1994 - *A. fasciatus* (5); 21 January 1995 – *A. fasciatus* (13).
2. Chaamac: 20°51'53"N; 90°09'18"W; open; 21 September 1993 – *A. fasciatus* (2), *P. velifera* (2), *Cichlasoma octofasciatum* (2); 21 January 1995 – *A. fasciatus* (3).
3. Dzaptún: 20°51'19"N; 90°14'09"W; open; 8 November 1993 – *A. fasciatus* (2); 2 February 1994 – *C. urophthalmus* (2).
4. Chek-há (ojo de agua): 20°51'39"N; 90°06'49"W; open; 8 November 1993 – *A. fasciatus* (2), *P. velifera* (1), *C. meeki* (1); 2 February 1994 – *A. fasciatus* (15).
5. Hunucmá: 21°00'03"N; 89°52'06"W; cave; 8 November 1993 – *Rhamdia guatemalensis* (2).

Chocholá zone (Ch)

6. Chen-há: 20° 41'24"N; 89° 52'36"W ; open; 18 October 1993 – *P. velifera* (10), *C. urophthalmus* (17); 27 June 1994 – *P. velifera* (5), *C. urophthalmus* (17); 27 August 94 – *P. velifera* (3), *C. urophthalmus* (7); 13 September 1994 – *R. guatemalensis* (8), *P. velifera* (1).

Cuzamá zone (C)

7. Homún: 20°44'19"N; 89°17'49"W; cántaro; 3 November 1993 – *R. guatemalensis* (1), *Gambusia yucatana* (5).
8. Chelentún: 20°43'28"N; 89°20'4"W; cántaro; 3 November 1993 – *R. guatemalensis* (7).

Sotutá zone (S)

9. Xmucuy: 20°33'63"N; 88°59'50" W; open; 26 October 1993 – *R. guatemalensis* (6); 16 November 1993 – *R. guatemalensis* (2); 25 July 1994 – *R. guatemalensis* (14).
10. Ixin-há: 20°37'14"N; 89°06'40"W; open; 26 October 1993 – *R. guatemalensis* (8); 13 June 1994 – *R. guatemalensis* (20); 11 July 1994 – *R. guatemalensis* (17); 22 August 1994 – *R. guatemalensis* (14); 20 September 1994 – *R. guatemalensis* (14); 17 October 1994 – *R. guatemalensis* (15); 14 November 1994 – *R. guatemalensis* (2); 31 January 1995 – *R. guatemalensis* (16).
11. Xcangachén: 20°36'43"N; 89°05'32"W; cántaro; 16 November 1993 – *R. guatemalensis* (3).
12. Sacamucuy: 20°33'33"N; 88°59'49"W; cántaro; 10 October 1994 – *R. guatemalensis* (4); 31 January 1995 – *R. guatemalensis* (2).

Libre Unión zone (LU)

13. Xtojil: 20°41'07"N; 88°41'17"W; open; 13 October 1993 – *C. urophthalmus* (2).
14. Yokdzonot: 20°42'24"N; 88°43'51"W; open; 13 October 1993 – *R. guatemalensis* (1), *G. yucatana* (5).
15. Scan Yui: 20°40'20"N; 88°32'51"W; open; 25 January 1994 – *R. guatemalensis* (16).

Tizimin zone (Ti)

16. Kikil: 21°11'37"N; 88°10'10"W; open; 30 November 1993 – *P. velifera* (3).

Mérida Norte zone (NTM)

17. San Gerardo: 21°03'59"N; 89°41'30"W; open; 23 March 1994 – *A. fasciatus* (1).
18. Dzibilchaltún: 21°05'28"N; 89°38'55"W; open; 13 May 1994 – *A. fasciatus* (80), *P. velifera* (7), *G. yucatana* (2), *C. urophthalmus* (2).
19. Tres Reyes: 21°02'35"N; 89° 30'18"W; cántaro; 13 May 1994 – *R. guatemalensis* (1), *C. urophthalmus* (2).
20. Noc-ac: 21°04'22"N; 89°43'14"W; cántaro; 23 March 1994 – *R. guatemalensis* (1), *G. yucatana* (6).

Cenotillo zone (EM)

21. Hodz-ob: 20°55'15"N; 88°51'43"W; open; 23 May 1994 – *C. urophthalmus* (11).

Dzilam zone (NEM)

22. Dzonot Cervera: 21°22'36"N; 88°49'59"W; open 23 May 1994 – *A. fasciatus* (5), *R. guatemalensis* (1), *C. octofasciatum* (1), *C. urophthalmus* (10).
23. Tixkanka: 21°14'55"N; 88°58'45"W; cave; 23 May 1994 – *R. guatemalensis* (9).
24. Zaci: 20°41'29"N; 88°11'40"W; open; 18 April 1994 – *R. guatemalensis* (3), *C. urophthalmus* (1).

Valladolid zone (CV)

25. Hubiku: 20°49'79"N; 88 ° 01'21"W; cántaro; 18 April 1994 – *R. guatemalensis* (16).
26. Sahkaba: 20°48'41"N; 88°07'27"W; open; 18 April 1994 – *R. guatemalensis* (1), *P. velifera* (17).

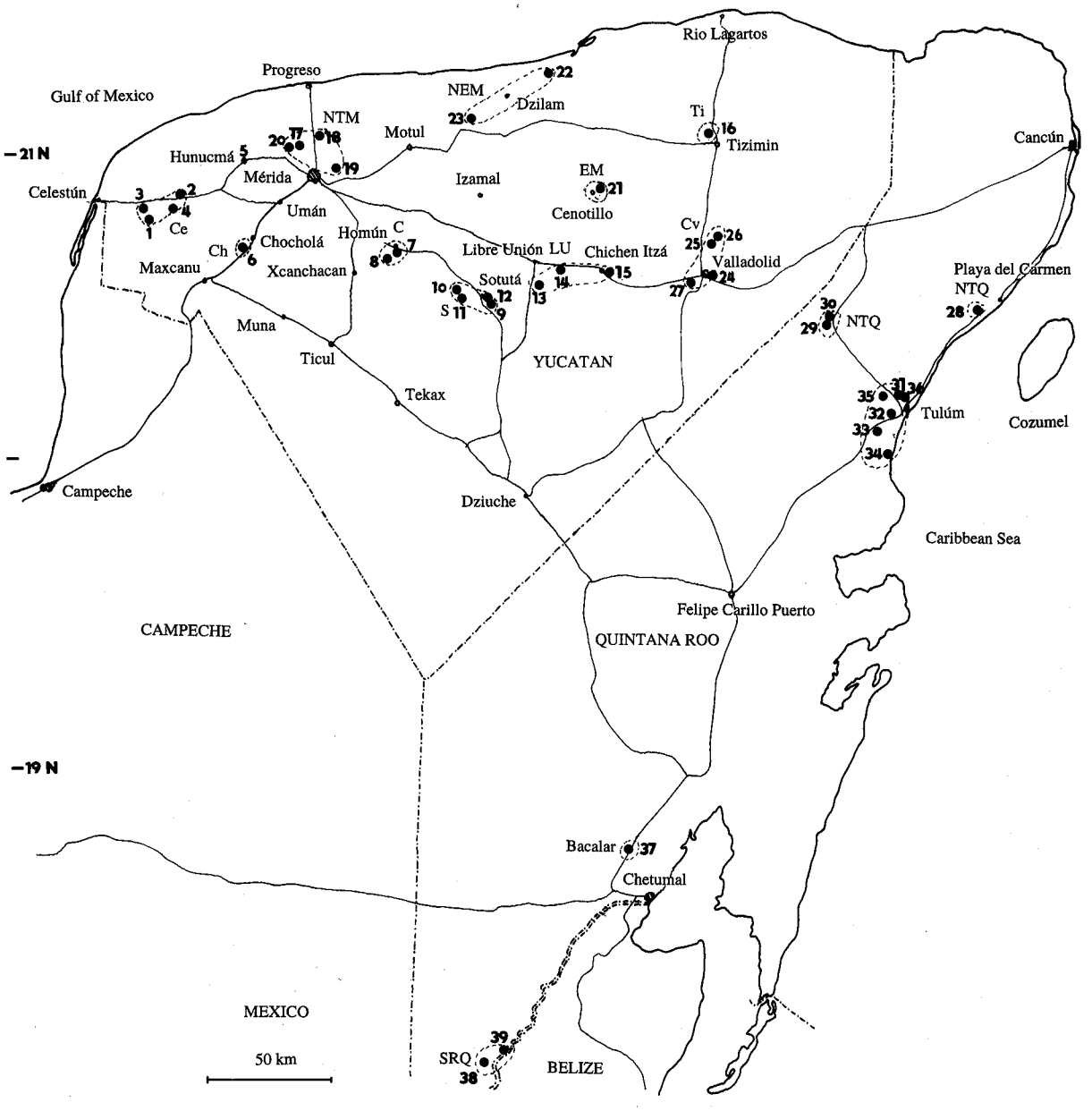

Fig. 1. The Peninsula of Yucatan, Mexico, with zones of cenotes and individual cenotes where fish were sampled (circles).

27. Xkeken: 20°39'37"N; 88°14'33"W; cántaro; 23 February 1994 – *R. guatemalensis* (2).

North of Quintana Roo zone (NTQ)

28. Cenote Azul (Puerto Aventuras): not positioned; 23 February 1994 – *Poecilia latipunctata* (4), *Cichlasoma friedrichstahli* (3).

29. San Pedro 1: 20°27'27"N; 87°50'0"W; cántaro; 23 February 1994 – *R. guatemalensis* (11).

30. San Pedro 2: 20°27'27"N; 87°5'04"; open; 23 February 1994 – *R. guatemalensis* (8).

Centre of Quintana Roo (CQ)

31. Gran Cenote: 20°14'44"N; 87°27'54"W; cántaro; 25 April 1994 – *A. fasciatus* (13), *R. guatemalensis* (2), *C. urophthalmus* (1); 9 May 1994 – *A. fasciatus* (3); 6 September 1994 – *A. fasciatus* (2).

32. Framboyán: 20°08'16"N; 87°34'38"W; open; 9 May 1994 – *A. fasciatus* (1), *P. petenensis* (1), *C. synspilum* (1).

33. Escondido: 20°11'57"N; 87°29'57"W; open; 9 May 1994 – *A. fasciatus* (6).

34. Cabañas: 20°07'51"N; 87°27'57"W; open; 9 May 1994 – *A. fasciatus* (5); *C. meeki* (2); *C. octofasciatum* (1); *C. synspilum* (2); *C. urophthalmus* (4).

35. Box Toro: 20°16'27"N; 87°29'09"W; open; 9 May 1994 – *A. fasciatus* (4), *P. petenensis* (2), *Poecilia* sp. (1), *Gambusia yucatana* (2), *C. octofasciatum* (1).
36. Kawash: 20°14'44"N; 87°27'54"W; cántaro; 6 September 1994 – *A. fasciatus* (8); *R. guatemalensis* (1).

South of Quintana Roo (SRQ)

37. Cenote Azul (Bacalar): 18°38'11"N; 88°24'46"W; open; 5 April 1994 – *P. petenensis* (6), *C. friedrichstahli* (1), *C. meeki* (1), *C. synspilum* (10), *Gobiomorus dormitor* (2).
38. Dos Bocas: 17°54'38"N; 88°51'20"W; open; 5 April 1994 – *A. fasciatus* (3); 16 October 1994 – *A. fasciatus* (4); 26 January 1995 – *A. fasciatus* (10); *R. guatemalensis* (1); *Poecilia* sp. (1).
39. Los Cuates: 17°55'00"N; 88°53'00"W; open; 5 April 1994 – *C. meeki* (1).

The fish were caught using casting net or angling. They were transported live in 50 l containers to the Laboratory of Parasitology, CINVESTAV-IPN Merida, where they were examined by routine helminthological procedure, as outlined by Bykhovskaya-Pavlovskaya (1969). Worms were observed and measured either as temporary or permanent mounts, fixed either with Bouin's liquid or with 4 % formalin under a slight coverslip pressure, stained with Schuberg's (acid) carmine or Gomori's Trichrom, dehydrated in alcohol and mounted in Canada balsam. All measurements are in µm; sucker ratio is expressed as mean of ratios of length and width of suckers. Drawings were made using Olympus and Zeiss drawing attachments. Voucher specimens are deposited in the helminthological collection of the Institute of Parasitology, Czech Academy of Sciences, České Budějovice (IPCAS), parasite collection of the Institute of Biology, Universidad Nacional Autónoma de México, México (UNAM) and at the Laboratory of Parasitology, CINVESTAV-IPN Mérida; *Genarchella* specimens have also been deposited in the Natural History Museum, London, UK, and National Parasite Collection, U.S.N.M., Beltsville, Maryland, USA.

SURVEY OF SPECIES

Family Haploporidae Nicoll, 1914

1. ***Saccocoelioides sogandaresi*** Lumsden, 1963 Fig. 2A

Hosts and localities: *Poecilia velifera* (number of fish infected/intensity of infection [mean with range in parentheses]) – Chen-há (18 October 1993; 27 June 1994; 27 August 1994) – 5/2 (1–3); Chek-há (8 November 1993) – 1/2; *P. latipunctata* – Cenote Azul (Puerto Aventuras) (23 February 1994) – 2/2.
Site of location: intestine.
Material studied: 4 specimens (1 gravid) from *P. velifera*.

Description: Body pyriform, 237–516 × 170–304; maximum width near midbody. Surface covered by minute tegumental spines, becoming smaller posteriorly. Remnants of eyespots scattered in precaecal region. Oral sucker subterminal, 44–65 × 55–86; ventral sucker almost equatorial (gravid specimen) or distinctly preequatorial, 65–86 × 62–106. Sucker ratio 1 : 1.22–1.30. Prepharynx absent; pharynx strongly muscular, 39–55 × 40–62. Intestinal caeca wide and short, terminating at ovarian level. Genital pore posterior to pharynx; hermaphroditic sac oval, preacetabular. Testis single, located near posterior extremity, 72–103 × 56–85. Ovary almost spherical, intracaecal, 28–45 × 35–58. Vitellarium formed by several large follicles, scattered laterally along intestinal caeca, extending posteriorly to postovarian zone, confluent. Eggs large, operculate, 83–86 × 55–59.

Remarks: The specimens correspond well with those described as *S. sogandaresi* by Lumsden (1963). This species can easily be differentiated from congeners by the distribution of vitelline follicles which are confluent in the hindbody, the size of the eggs and the distinctly large pharynx (Lumsden 1963). *Saccocoelioides sogandaresi* was described from the poecilid *Molliensia* (= *Poecilia*) *latipinna* from brackish water ponds near Galveston Bay in Texas, USA (Lumsden 1963). As far the authors are aware, this trematode species has not previously been reported to occur in Mexican fish. *Poecilia velifera* and *P. latipunctata* represent new definitive hosts of *S. sogandaresi*.

***Saccocoelioides* sp.**

Host and locality: *Cichlasoma synspilum* - Cenote Azul (Bacalar) (5 April 1994) – 3/3 (2–4).
Site of location: intestine.
Material studied: 2 specimens from *C. synspilum*.

Remarks: In cichlid fish in Mexico, *Saccocoelioides beauforti* (Hunter et Thomas, 1961) has been reported to occur in *Cichlasoma managuense*, *C. synspilum*, *C. urophthalmus* and *Petenia splendida* (Salgado-Maldonado, Pineda-López and Vidal-Martínez – unpubl. data). In addition, Guajardo-Martínez (1984) found *Saccocoelioides* sp. from *C. minckleyi* and García et al. (1993) reported *Saccocoelioides* sp. in *Oreochromis aureus*. Since the specimens studied by the present authors were in very poor conditions, it was not possible to identify them to species level and they are designated as *Saccocoelioides* sp.

Family Angiodictyidae Looss, 1902

3. ***Cichlasotrema ujati*** Pineda-López et Andrade-Salas, 1989

Host and locality: *Cichlasoma synspilum* - Cenote Azul (Bacalar) (5 April 1994) – 1/2.
Material studied: 2 specimens from *C. synspilum*.

Remarks: The trematodes found well correspond to those of *C. ujati* as described by Pineda-López and Andrade-Salas (1989) from the same host species. Since then, this species has been found in other cichlids, namely *C. helleri*, *C. fenestratum*, *C. pearsei*, *C. rectangulare*, *C. geddesi* and *Petenia splendida* (Salgado-Maldonado, Pineda-López and Vidal-Martínez – unpubl. data).

Family Homalometridae Cable et Hunninen, 1942

4. ***Crassicutis cichlasomae*** Manter, 1936 Fig. 2C

Hosts and localities: *Cichlasoma meeki* – Noc-choncunchey (21 September 1993) – 5/11 (1–34); Chekhá (8 November 1993) – 1/8; *C. octofasciatum* – Dzonot Cervera (23 May 1994) – 1/81; *C. pearsei* – Noc-choncunchey (2 February 1994) – 1/1; *C. synspilum* – Cenote Azul (Bacalar) (5 April 1994) – 6/4 (1–17); *C. urophthalmus* – Noc-choncunchey (2 February 1994) – 1/15; Chen-há (18 October 1993; 27 June 1994; 27 August 1994) – 19/10 (1–105); Dzaptún (2 February 1994) – 2/2; Zaci (16 April 1994) – 1/26; Gran Cenote (25 April 1994) – 1/3; Dzibilchaltún (13 May 1994) 2/3 (1–5); Dzonot Cervera (23 May 1994) –1/2.

Site of location: intestine.

Material studied: 31 specimens from *C. octofasciatum*.

Description (N = 10; mean ± SD; range in parentheses): Body widely oval, 783–270 × 502–127 (523–1850 × 391–816); maximum width slightly posterior to mid-body. Tegument very thick, without spination. Oral sucker subterminal, spherical, 109 ± 28 × 117 ± 19 (80–192 × 101–192); ventral sucker pre-equatorial, 119 ± 25 × 124 ± 25 (92–192 × 97–205); sucker ratio 1 : 1–1.12. Prepharynx short, up to 64 long; pharynx ovoid, 58 ± 15 × 68 ± 15 (38–103 × 50–107); oesophagus short, up to 70 long. Intestinal caeca narrow, surrounding genital organs and terminating at testicular level, slightly converging to each other. Testes large, slightly lobated, diagonal, close together. Anterior testis 106 ± 14 × 176 ± 26 (94–157 × 139–240); posterior testis 121 ± 23 × 193 ± 39 (94–182 × 157–294). Seminal vesicle sac-shaped, 74 ± 26 × 77 ± 47 (57–120 × 38–157); distal part of vesicle thin-walled, tubular, opening into short genital atrium. Cirrus lacking. Genital pore median, preacetabular. Ovary small, pretesticular, posterolateral to ventral sucker; 88 ± 22 × 103 ± 40 (57–113 × 55–170). Mehlis' glands posterior to ovary. Seminal receptacle large, close to ovary. Vitelline follicles overlapping caeca, reaching from level of intestinal

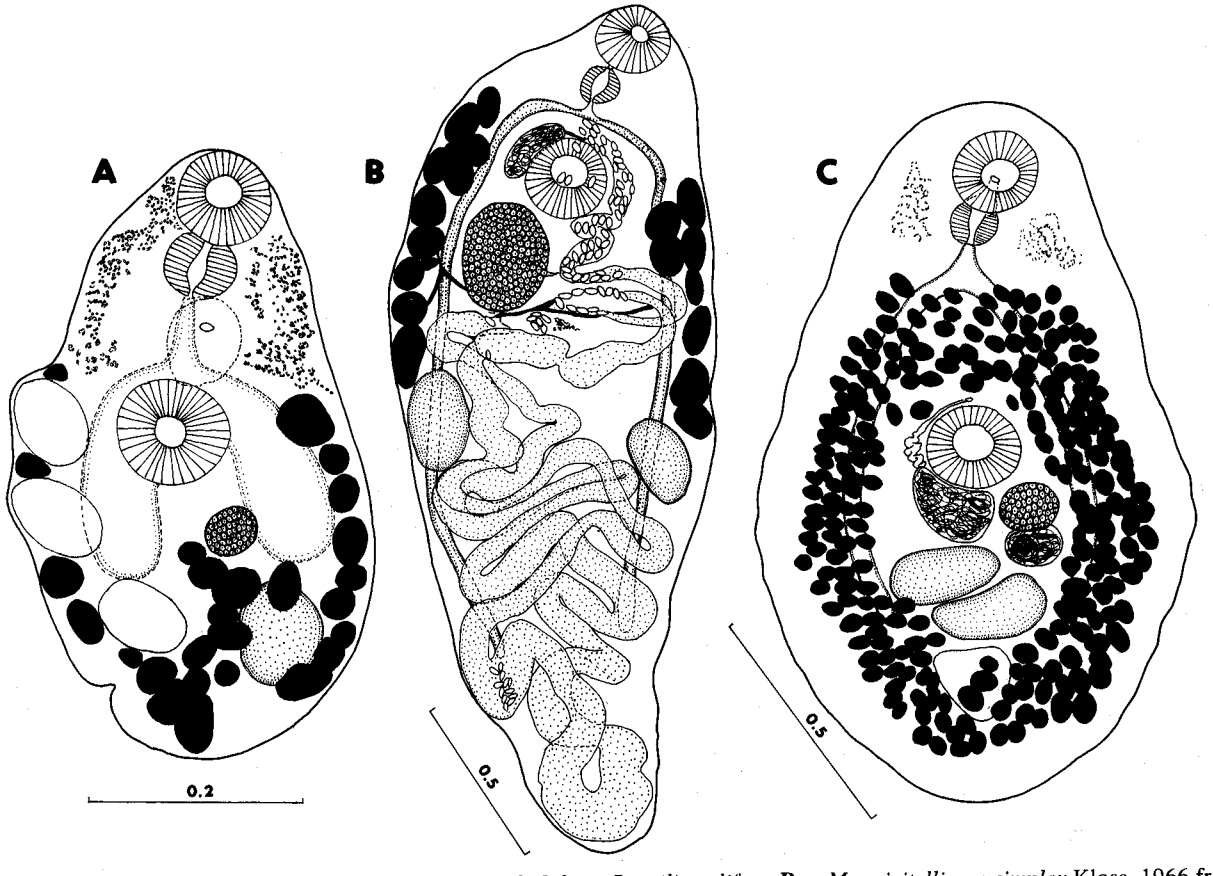

Fig. 2. A – *Saccocoelioides sogandaresi* Lumsden, 1963 from *Poecilia velifera*. **B** – *Magnivitellinum simplex* Kloss, 1966 from *Astyanax fasciatus*. **C** – *Crassicutis cichlasomae* Manter, 1936 from *Cichlasoma octofasciatum*. Scale bars in millimetres.

bifurcation almost to posterior extremity, confluent anterior to ventral sucker and posterior to testes. Eggs not observed in any worm studied. Excretory bladder short, 123 ± 46 × 145 ± 18 (82–170 × 132–164); excretory pore median, anterior to posterior extremity.

Remarks: The species was originally described from *Cichlasoma mayorum* from Xtoloc cenote in Chichen Itza in Yucatan (Manter 1936). Subsequent studies have demonstrated that *C. cichlasomae* is a specific parasite of cichlid fishes (*Cichlasoma* spp. and *Petenia splendida*) occurring rather commonly also in water bodies other than cenotes. It has been found in southeastern Mexico (Veracruz, Tabasco, Chiapas, Campeche, Yucatan), Cuba, Nicaragua and Costa Rica (Manter 1936, Bravo-Hollis and Arroyo 1962, Moravec and Baruš 1971, Watson 1976, Osorio-Sarabia et al. 1987, Pineda-López and Andrade-Salas 1989, Lamothe-Argumedo and Pineda-López 1990). The life cycle of *C. cichlasomae* was studied by Scholz et al. (1995a). *Cichlasoma octofasciatum* represents a new definitive host of the parasite.

Family Macroderoididae McMullen, 1937

5. ***Magnivitellinum simplex*** Kloss, 1966 Fig. 2 B

Host and localities: *Astyanax fasciat* – Noc-chon-cunchey (2 February 1994) 4/1 (1–2); Dos Bocas (16 October 1994; 26 January 1995) – 7/18 (1–52).

Site of location: intestine.

Material studied: 35 specimens from *A. fasciatus*.

Description (N = 10; mean ± SD; range in parentheses): body elongate, 1121 ± 603 × 530 ± 238 (608–2520 × 272–954), maximum width near anterior third of body. Oral sucker spherical, subterminal, 125 ± 36 × 144 ± 43 (67–186 × 77–214). Ventral sucker situated near anterior quarter of body, 150 ± 49 × 156 ± 53 (90–243 × 101–246), sucker ratio 1 : 1.14 (1 : 1.01 - 1 : 1.27). Prepharynx 27 ± 2 (25 – 31); pharynx oval, 57 ± 20 × 60 ± 13 (31–90 × 42–83); oesophagus 28 ± 10 (15–52) long. Intestinal caeca narrow, terminating rather far from posterior extremity. Testes lateral, almost symmetrical, located near lateral body margins, overlapping caeca; size of testes 188 ± 63 × 142 ± 58 (125–320 × 65–278). Cirrus sac curved beside ventral sucker, 196 ± 76 × 80 ± 18 (50–275 × 47–102). Genital pore median, preacetabular. Ovary submedian, spherical, pretesticular and postacetabular, 177 ± 82 × 142 ± 75 (88–330 × 55–262). Vitellarium formed by two lateral groups of 8-11 large follicles situated between intestinal bifurcation and anterior testis; size of follicles 25 – 179 × 22 – 125. Uterus tubular, forming numerous loops filling most intracaecal space and posterior part of body. Eggs small, operculate, 39 ± 3 × 21 ± 3 (30–45 × 13–28; N = 44).

Remarks: The species *M. simplex* was originally described from *Astyanax fasciatus* in Brazil (Kloss 1966). Jiménez-Guzmán (1973) reported its occurrence from the same fish host in Nuevo León, northern Mexico. There are almost no substantial differences between the material described by the above authors and the specimens found in cenotes. Kloss (1966) reported slightly larger size of the body (up to 3.54 mm) and size of eggs 36–47 × 21–23 µm; Jiménez-Guzmán (1973) found smaller, more slender trematodes (average body size 1.883 mm), containing eggs measuring 42 × 20 µm in average.

Family Acanthostomidae Poche, 1926

6. ***Stunkardiella minima*** (Stunkard, 1938) Fig. 3

Host and localities: *Rhamdia guatemalensis* – Scan Yui (25 January 1994) 1/1; San Pedro 1 (23 February 1994) – 1/1; San Pedro 2 (23 February 1994) – 4/18 (1–65); Ixin-há (13 June 1994; 11 July 1994; 22 August 1994; 20 September 1994; 17 October 1994; 31 January 1995) – 22/9 (1–54); Xmucuy (25 August 1994) – 1/19; Sacamucuny (31 January 1995) – 2/3 (1–4); Chen-há (13 September 1994) – 2/1.

Site of location: intestine.

Material studied: 109 specimens from *R. guatemalensis*.

Description (N = 10; mean ± SD; range in parentheses): body elongate, 1389 ± 167 × 391 ± 64 (1056–1620 × 328–552), covered with scale-like, rectangular tegumental spines, up to 5 long, becoming smaller and less dense posteriorly. Oral sucker terminal, cup-like, 197 ± 16 × 179 ± 13 (170–218 × 157–201), provided with one complete row of 20 spines (N = 99); only exceptionally 19 (N = 2) or 21 (N = 8) spines present. Dorsal spines longer (length 35–52) and more slender than shorter (26–40) and massive ventral spines. Ventral sucker spherical or oval, 107 ± 11 × 117 ± 11 (90–128 × 102–144); sucker ratio 1.40–1.98 : 1 (mean 1.68 : 1). Prepharynx 118 ± 14 (97–134) long; pharynx large, strongly muscular, 101 ± 11 × 114 ± 14 (82–128 × 85–138); only one caecum developed, opening laterally to excretory pore. Testes diagonal, oval, anterior testis 137 ± 38 × 166 ± 38 (86–218 × 120–237), posterior testis 169 ± 45 × 166 ± 31 (102–262 × 126–220). Seminal vesicle posterolateral to ventral sucker, divided into two parts; proximal part sacculate, 276 ± 74 × 86 ± 12 (202–350 × 74–99), distal part tubular; genital pore near anterior margin of ventral sucker. Ovary pretesticular, spherical, 96 ± 21 × 101 ± 19 (63–126 × 77–131). Seminal receptacle large, 95 ± 17 × 125 ± 26 (70–125 × 83–154). Vitellarium formed by two groups of 7–11 follicles each, situated laterally, anterior to testes; size of follicles 22–93 × 25–77. Uterus tubular, forming several loops between ovary and ventral sucker; eggs

operculate, 27 ± 5 × 16 ± 2 (20–31× 12–21). Excretory bladder Y-shaped, long, ith anterior branches reaching anterior to ventral sucker.

Remarks: This species was first found in *R. guatemalensis* from cenotes in Yucatan and described as *Acanthostomum minimum* by Stunkard (1938). Lamothe-Argumedo and Ponciano-Rodríguez (1986a) established a new genus, *Stunkardiella*, with *A. minimum* as its type species. The same authors (Lamothe-Argumedo and Ponciano-Rodríguez 1986b) redescribed this species on the basis of specimens found in the same host, the pimelodid *R. guatemalensis*, from Catemaco Lake, Veracruz, Mexico. The present material corresponds well to that described by the above authors. Lamothe-Argumedo and Ponciano-Rodríguez (1986b) reported 19–20 circumoral spines in *S. minima*. In the present material, 99 specimens of 109 evaluated possessed 20 spines, whereas 19 and 21 spines were present only exceptionally (two and eight times, respectively). This clearly indicates that the number of spines in *S. minima* is rather stable and can serve as an important feature for identification.

Family Cryptogonimidae Ward, 1917

7. ***Oligogonotylus manteri*** Watson, 1976 Figs. 4 A–B

Hosts and localities: *Cichlasoma friedrichstahli* -- Cenote Azul (Puerto Aventuras) (23 February 1994) – 1/1; *C. meki* – Cenote Azul (Bacalar) (5 April 1994) – 1/3; Cabañas (9 May 1994) – 1/1; *C. synspilum* – Cenote Azul (Bacalar) (5 April 1994) – 2/2; Cabañas (9 May 1994) – 2/4 (2-5); *C. urophthalmus* – Gran Cenote (25 April 1994) – 1/9; Cabañas (9 May 1994) – 3/5 (4–7); Dzonot Cervera (23 May 1994) – 6/6 (1–11); *Astyanax fasciatus* – Box Toro (9 May 1994) – 1/2.

Site of location: intestine.

Material studied: 8 specimens from *C. urophthalmus* and *C. synspilum*; 2 specimens from *A. fasciatus*.

Description: (Since the specimens from cichlid fish correspond well to those described by Watson (1976) and Scholz et al. (1994), only description of two trematodes from *A. fasciatus* is presented): Body pyriform,

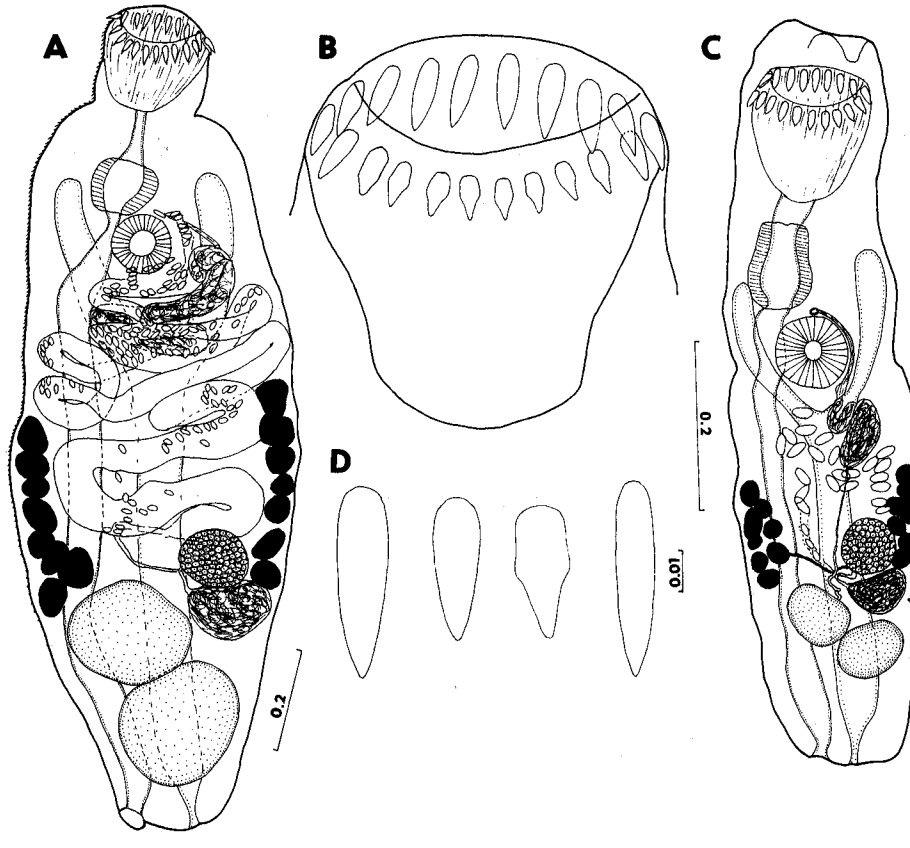

Fig. 3. *Stunkardiella minima* (Stunkard, 1938). **A, C** – total view; **B** – oral sucker; **D** – circumoral spines. Scale bars in millimetres (mm).

730–780 × 416–432; maximum width in midbody. Tegument covered with minute spines, becoming shorter and less dense posteriorly. Oral sucker almost terminal, with central part protruded; size of sucker 112–122 × 166–170. Ventral sucker spherical, slightly preequatorial, 96–99 × 109–112, enclosed in genital atrium with genital pore at centre; sucker ratio 1 : 1.35 –1.38. Prepharynx present, inflated, 26–35 long; pharynx large, strongly muscular, 67 × 96–99. Oesophagus short; intestinal caeca wide, reaching posteriorly near to body extremity, filled with large bodies. Genital pore close to anterior margin of ventral sucker. Gonotyls sucker-like, 5–6 in number, situated between prepharynx and genital pore. Testes oval, in tandem, overlapped by numerous eggs; anterior testis 67–90 × 71–83, posterior testis 65–106 × 61–69. Vesicula seminalis round, posterolateral to acetabulum. Ovary lobated, 66 × 63, anterolateral to testes. Uterus tubular, postacetabular, forming numerous loops filling entire hindbody. Eggs small, 21–23 × 9–11.

Remarks: The specimens from *A. fasciatus* are morphologically almost identical with those found in cichlid fish. There are only one small difference between them in the position of the oral sucker (terminal in the trematodes from *A. fasciatus* versus subterminal in those from cichlids). However, the presence of a few gonotyls as well as other morphological features, including egg size, clearly indicate conspecificity of the worms studied.

The finding of gravid trematodes of *O. manteri*, which has been considered to be a specific parasite of cichlids (Scholz et al. 1994), in the characid, *A. fasciatus*, indicates that the latter fish may serve as a suitable definitive hosts. However, only one of a total of 124 *A. fasciatus* examined was infected.

Scholz et al. (1994) gave evidence that cichlid fish are suitable second intermediate hosts of this parasite, becoming infected either after direct contact with freely swimming cercariae or after consuming snails containing *O. manteri* cercariae. Cichlids of the genus *Cichlasoma* serve as definitive host of the trematode (Watson 1976, Osorio-Sarabia et al. 1987, Scholz et al. 1994). The species *Cichlasoma friedrichstahli* and *C. meeki* are reported as definitive hosts of *O. manteri* for the first time.

Family Derogenidae Lühe, 1910

8. ***Genarchella tropica*** (Manter, 1936) Fig. 4E

Hosts and localities: *Rhamdia guatemalensis* – Xmucuy (26 October 1993; 25 July 1994) – 4/1 (1–2); 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) – 42/2 (1–5); Homún (3 November 1994) – 1/2; Xcangachén (16 November 1993) – 1/2; Scan Yui (25 January 1994) – 5/2 (1–4), San Pedro 2 (23 February 1994) – 3/27 (6–65); Tixkanka (23 May 1994) – 1/11; Chen-há (13 September 1994) – 2/1; Sacamucuy (10 October 1994) – 1/1; *Gambusia yucatana* – Noc-ac (23 March 1994) – 1/1.

Site of location: stomach.

Material studied: see Scholz et al. (1995b); in addition to this material, 59 specimens from *R. guatemalensis* from Ixin-há, Xmucuy and Sacamucuy cenotes were evaluated.

Remarks: The species has recently been redescribed from the material from cenotes in the Yucatan Peninsula (Scholz et al. 1995b). *Genarchella tropica* is a parasite of the pimelodid catfishes *Rhamdia guatemalensis* and *R. managuensis* in Mexico (Yucatan), Nicaragua and Panama (Scholz et al. 1995b).

The specimen found in *Gambusia yucatana* was a juvenile worm; consequently, this fish species may represent only an accidental host of *G. tropica*, adults of which have hitherto been reported only from the pimelodids (*Rhamdia* spp.) – Scholz et al. (1995b).

9. ***Genarchella astyanactis*** (Watson, 1976) Fig. 4F

Host and localities: *Astyanax fasciatus* – Noc-choncunchey (2 February 1994; 13 September 1994; 21 January 1995) – 8/4 (1–8); Chek-há (8 November 1993; 2 February 1994) – 7/1 (1–2); San Gerardo (23 March 1994) – 1/2; Gran Cenote (25 April 1994) – 2/1; Cabañas (9 May 1994) – 5/2 (1–3); Box Toro (9 May 1994) – 1/1; Escondido (9 May 1994) – 4/2 (1–5); Dos Bocas (16 October 1994; 26 January 1995) – 4/3 (1–5); Chaamac (21 January 1995) – 2/3 (2–3).

Site of location: stomach.

Material studied: see Scholz et al. (1995 b); besides this material, 10 specimens from *A. fasciatus* from cenotes San Gerardo, Cabañas, Dos Bocas, Box Toro and Gran Cenote were examined.

Remarks: the specimens found in *A. fasciatus* from cenotes are identical with those found in the same fish host species from Nicaragua by Watson (1976) and northern Mexico (Scholz et al. 1995b).

10. ***Genarchella isabellae*** (Lamothe-Argumedo, 1977) Figs. 4C–D

Hosts and localities: *Cichlasoma friedrichstahli* – Cenote Azul (Bacalar) (5 April 1994) - 1/11; *C. meeki* – Cenote Azul (Bacalar) (5 April 1994) – 1/8; Cabañas (9 May 1994) – 1/4; *C. octofasciatum* – Cabañas (9 May 1994) – 1/8; *C. pearsei* – Noc-choncunchey (2 February 1994) – 1/1; *C. synspilum* – Cabañas (9 May 1994) – 1/9; *C. urophthalmus* – Cabañas (9 May 1994) – 2/24 (20–28); Dzonot Cervera (23 May 1994) – 7/5 (2–8); *Gambusia yucatana* – Noc-ac (23 March 1994) – 1/1; *Gobiomorus dormitor* – Cenote Azul (Bacalar) (5 April 1994) – 1/6.

Site of location: stomach.

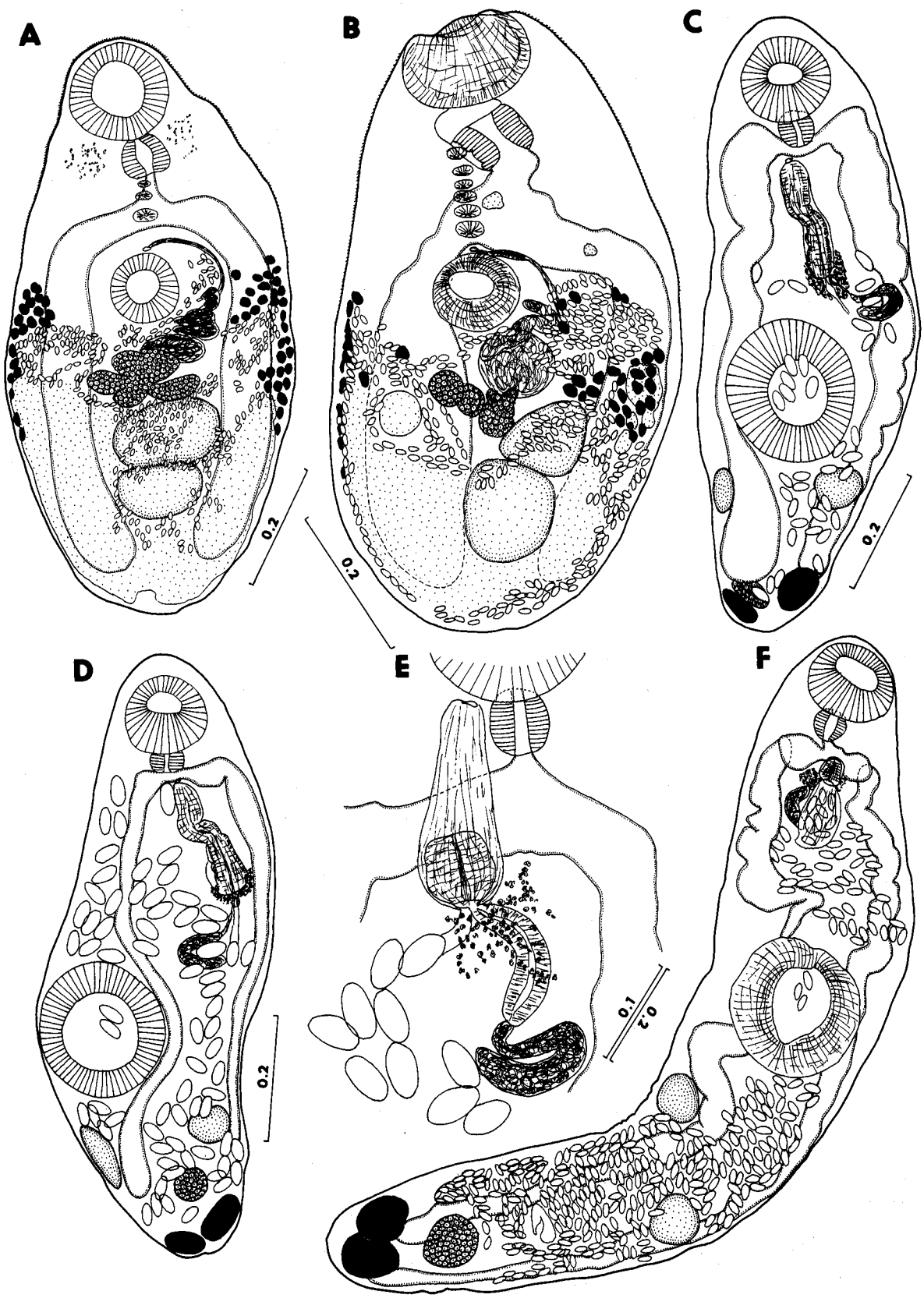

Fig. 4. **A** – *Oligogonotylus manteri* Watson, 1976 from *Cichlasoma urophthalmus*. **B** – *O. manteri* from *Astyanax fasciatus*. **C** – *Genarchella isabellae* (Lamothe-Argumedo, 1977) from *C. urophthalmus*. **D** – *Gobiomorus dormitor*. **E** – *G. tropica* (Manter, 1936) from *Rhamdia guatemalensis*. **F** – *G. astyanactis* (Watson, 1976) from *A. fasciatus*. Scale bars in millimetres (mm).

Material studied: 16 specimens from *C. urophthalmus*, *C. synspilum*, *C. meeki* and *G. dormitor* from cenotes Cabañas, Dzonot Cervera and Cenote Azul (Bacalar).

Remarks: The species *G. isabellae* was redescribed recently by Scholz and Salgado-Maldonado (1994) and Scholz et al. (1995b). Although originally described from the pimelodid *Rhamdia guatemalensis* (Lamothe-Argumedo 1977), the species *G. isabellae* seems to be a typical parasite of cichlid fishes (*Cichlasoma* spp., *Petenia splendida*) in southeastern Mexico and Central America (Scholz and Salgado-Maldonado 1994). The cichlids *Cichlasoma meeki* and *C. octofasciatum*, and the gobiid *G. dormitor* represent new definitive hosts of *G. isabellae*.

DISCUSSION

A total of 10 species of adult trematodes was found in fish from cenotes of the Yucatan Peninsula by the present authors. Manter (1936) and Stunkard (1938) described as new species three taxa from cenote fish, namely *Derogenes tropicus* (= *Genarchella tropica*), *Crassicutis cichlasomae* and *Acanthostomum minimum* (= *Stunkardiella minima*). The first species has not been found in Mexico since Manter's original description and different derogenids have erroneously been reported under this name from South American freshwater fish (see Kohn and Fernandes 1988, Kohn et al. 1990, Scholz et al. 1995b). Two last named species have been found in Mexico quite recently (Lamothe-Argumedo and Ponciano-Rodríguez 1986b, Osorio-Sarabia et al. 1987, Salgado-Maldonado 1993). Although described from cenote fish, these three species do not seem to be limited in their occurrence exclusively to cenotes and they can occur in fish from other water habitats such as lagoons and rivers (Watson 1976, Osorio-Sarabia et al. 1987, Scholz et al. 1995 a, b). However, at least *G. tropica* and *S. minima*, specific parasites of *Rhamdia guatemalensis*, can be considered as typical parasites of cenote fish.

In addition to the above mentioned trematodes, seven other species were found. Six species, namely *Saccocoelioides sogandaresi*, *Cichlasotrema ujati*, *Magnivitellinum simplex*, *Oligogonotylus manteri*, *Genarchella isabellae* and *G. astyanactis*, have already been found in fish from water bodies other than cenotes and they do not represent exclusively cenote parasites. Since these species seem to be specific parasites of *Astyanax fasciatus* (*M. simplex*, *G. astyanactis*), poeciliid (*Poecilia* spp. – *S. sogandaresi*) and cichlid fish (*Cichlasoma* spp., *Petenia splendida* – *C. ujati*, *O. manteri*, *G. isabellae*), which occur rather commonly in inland waters (aguadas, lagoons), they cannot be considered as typical components of cenote fauna.

As concerns zoogeographical affinities, three *Genarchella* species (see Kohn et al. 1990, Scholz et al. 1995 b), *Oligogonotylus manteri* and *Magnivitellinum simplex* apparently represent components of the Neotropical fauna.

The present results indicate that there is a rather narrow specificity to fish definitive hosts in most species found. Out of ten trematode species recorded, 3 taxa (*S. minima*, *M. simplex* and *G. astyanactis*) seem to be species-specific, 6 species are genus-specific (see also Kloss 1966, Yamaguti 1971, Jímenez-Guzmán 1973, Watson 1976, Lamothe-Argumedo and Ponciano-Rodríguez 1986b, Osorio-Sarabia et al. 1987, Salgado-Maldonado 1993, Scholz et al. 1995b). Distribution of *Saccocoelioides* sp. and its host spectrum cannot be considered until its species identification is possible.

Out of ten species found in cenote fish during the present study, only *Saccocoelioides sogandaresi* is reported from Mexico for the first time; other trematodes have already been reported from Mexican fish (Manter 1936, Stunkard 1938, Lamothe-Argumedo 1977, Jímenez-Guzmán 1973, Lamothe-Argumedo and Ponciano-Rodríguez 1986b, Osorio-Sarabia et al. 1987, Scholz and Salgado-Maldonado 1994, Scholz et al. 1994, 1995a, b). However, several species are reported from new definitive hosts: *S. sogandaresi* from *Poecilia velifera* and *P. latipunctata*, *C. cichlasomae* from *Cichlasoma octofasciatum*, *O. manteri* from *Cichlasoma friedrichstahli* and *C. meeki*, and *G. isabellae* from *C. meeki*, *C. octofasciatum* and *Gobiomorus dormitor*.

Acknowledgements. The authors are indebted to Dr. Guillermo Salgado-Maldonado, Institute of Zoology, UNAM, Mexico City, Dr. Raúl Pineda-López, Parasitology Laboratory, UJAT, Villahermosa, Tabasco, and Dr. Victor Manuel Vidal-Martínez, Hatherly Laboratories, University of Exeter, UK, for valuable advice and providing unpublished data on parasites of cichlid fish. Thanks are also due to B.Sc. Esperanza Pérez-Díaz and M.Sc. Mirella Hernández de Santillana, CINVESTAV-IPN Merida, for the identification of fishes. The excellent assistance of M.Sc. Raúl Simá-Alvarez, B.Sc. Jorge Güemez-Ricalde and Mr. Gregory Arjona-Torres, CINVESTAV-IPN, Mérida, in sampling fish is also greatly appreciated. The authors also thank Dr. Dagmar Peterová, Mrs. Marcela Holinková and Mrs. Irena Husáková, Institute of Parasitology, České Budějovice, for their help in staining and mounting voucher specimens. This study was supported by the grant No. PO99 of the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Mexico.

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Received 8 December 1994 Accepted 23 February 1995