

Trematodes of the family Heterophyidae (Digenea) in Mexico: a review of species and new host and geographical records

T. SCHOLZ*†‡, M. L. AGUIRRE-MACEDO† and
G. SALGADO-MALDONADO§

† *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. 97310 Mérida, Yucatán, Mexico; e-mail: leo@kin.cieamer.conacyt.mx*

‡ *Institute of Parasitology, Academy of Sciences of the Czech Republic, Branišovská 31, 370 05 České Budějovice, Czech Republic; e-mail: tscholz@paru.cas.cz*

§ *Institute of Biology, National Autonomous University of Mexico (UNAM), A.P. 53-173, C.P. 04510 México, D.F., Mexico; e-mail: gsalgado@ibiologia.unam.mx*

(Accepted 26 May 2000)

A review of heterophyid trematodes found in Mexico, both as metacercariae encysted in fish and adults in fish-eating birds and mammals, is presented, including numerous new geographical and host records. Data on the morphology, spectrum of intermediate and definitive hosts, site of infection of metacercariae, distribution in Mexico and biology of the following species are provided (species first reported from Mexico marked with an asterisk): *Ascocotyle (Ascocotyle) gemina* Font, Overstreet and Heard, 1984; *A. (A.) leighi* Burton, 1956; *A. (A.) tenuicollis* Price, 1935; *A. (Leighia) chandleri* Lumsden, 1963; **A. (L.) mcintoshii* Price, 1936; *A. (L.) megalcephala* Price, 1932; *A. (L.) nunezae* Scholz, Vargas-Vázquez, Vidal-Martínez and Aguirre-Macedo, 1997; *Ascocotyle (Leighia) sp.*; **A. (Phagicola) ampullacea* Miller and Harkema, 1962; *A. (P.) diminuta* Stunkard and Haviland, 1924; *A. (P.) macrostoma* (Robinson, 1956); **A. (P.) longa* Ransom, 1920; *A. (P.) nana* Ransom, 1920; *Centrocestus formosanus* (Nishigori, 1924); **Euhaplorchis californiensis* Martin, 1950; *Galactosomum puffini* Yamaguti, 1941; **Haplorchis pumilio* (Looss, 1896); Heterophyidae gen. sp. (= *Haplorchoides* sp. of Scholz and Vargas-Vázquez, 1998); **Phocitreroides ovale* Martin, 1950; and **Pygidioopsis pindoramensis* (Travassos, 1929). Two of the above-listed species, *C. formosanus* and *H. pumilio*, have been introduced recently to Mexico, most probably from Asia with the imported thiarid snail *Melanooides tuberculata* (Müller). Metacercariae of heterophyid trematodes are among the most frequent and abundant parasites of fish in Mexico, in particular in its southeastern part.

KEYWORDS: Heterophyidae, fish, Mexico, taxonomy, biology, geographical distribution.

*To whom correspondence should be addressed.

Introduction

Trematodes of the family Heterophyidae are frequent intestinal parasites of fish-eating birds (Sepúlveda *et al.*, 1994, 1996, 1999) and their metacercariae encyst in different organs of fish (Yamaguti, 1971, 1975). In Mexico, metacercariae of heterophyids represent one of the dominant groups of trematodes parasitizing fish (Aguirre-Macedo and García-Magaña, 1994; Scholz *et al.*, 1995, 1997a; Salgado-Maldonado *et al.*, 1997; Scholz and Vargas-Vázquez, 1998; Scholz and Aguirre-Macedo, 2000). Despite this fact, little attention has been paid to these trematodes, most probably because of their small size and difficult taxonomy.

Scholz *et al.* (1997a) revised species of the *Ascocotyle*-complex and provided descriptions of metacercariae from fish and adults from naturally and experimentally infected hosts, and a key to identification of metacercariae from the Yucatán Peninsula. Data on the life cycles of heterophyids in Mexico are very scarce and cercariae of only a limited number of species are known (Ditrich *et al.*, 1997; Scholz *et al.*, 1997a, 2000).

Recent investigations into the helminth parasites in Mexico have revealed the presence of numerous trematodes of the family Heterophyidae, many of them previously not reported from this country. Considering the number of taxa recorded from Mexico for the first time, numerous new data on species previously reported and a shortage of the information about heterophyids in Latin America in general, the species of the family Heterophyidae found in Mexico are reviewed and data on their morphology, intermediate and definitive hosts, the site of infection in fish, geographical distribution and biology are provided.

Materials and methods

The present survey is based mainly on examination of numerous specimens of heterophyid trematodes collected recently by the present authors in different parts of Mexico (see Survey of species for individual localities), and on previously published data, in particular those of the present authors (Salgado-Maldonado and Aguirre-Macedo, 1991; Aguirre-Macedo and García-Magaña, 1994; Scholz *et al.*, 1995, 1997a, 1997b; Salgado-Maldonado *et al.*, 1997; Scholz and Vargas-Vázquez, 1998; Scholz, 1999). Localities from where cichlid fish were collected are described by Vidal-Martínez *et al.* (2000).

Most metacercariae from fish were observed *in vivo*; some were isolated from cysts using preparation needles and fixed with glycerin:picric acid (Ergens, 1969). Adult trematodes from naturally and experimentally infected hosts (the great blue egret—*Ardea herodias* Linnaeus, and chicks, ducks and mice, respectively) were fixed with hot 4% formaldehyde solution (see Scholz and Aguirre-Macedo, 2000) and stained with hydrochloric carmine (see Scholz and Hanzelová, 1998). Internal morphology, including the structure of the terminal genitalia and the number of circumoral spines, was observed using Nomarski interference contrast.

In addition to the types and vouchers studied previously by the present authors (see Scholz *et al.*, 1997a, 1997b), the paratypes of *Ascocotyle* (*A.*) *chandleri* and *A.* (*L.*) *ampullacea*, deposited in the US National Parasite Collection, Beltsville, MD, USA (USNPC 59584 and 59894, respectively), were examined. Reference specimens are deposited in the Natural History Museum, London, UK (BMNH); helminthological collection of the Laboratory of Parasitology, CINVESTAV-IPN Mérida (CHCM); National Helminthological Collection of Mexico, Institute of Biology, UNAM, Mexico City (CNHE); helminthological collection of the Institute of

Parasitology, Academy of Sciences of the Czech Republic, České Budějovice (IPCAS); and US National Parasite Collection, Beltsville, MD, USA (USNPC).

Species reported from Mexico for the first time are marked with an asterisk. All measurements given in descriptions are in micrometres (μm). Species of the *Ascocotyle*-complex are considered to belong to the genus *Ascocotyle* Looss, 1899 *sensu lato*, i.e. as defined by Sogandares-Bernal and Lumsden (1963). Subgeneric classification used in the present paper also follows that proposed by Sogandares-Bernal and Lumsden (1963), i.e. subgenera *Ascocotyle* Looss, 1899; *Phagicola* Faust, 1920; and *Leighia* Sogandares-Bernal and Lumsden, 1963, with some modifications. The systematics of the oviparous killifish (Cyprinodontidae) follows that presented in an unpublished annotated checklist by Dr Kenneth J. Lazara, American Museum of Natural History, New York (personal communication).

Survey of species

**Ascocotyle (Ascocotyle) gemina* Font, Overstreet and Heard, 1984
(figure 1A–D)

Metacercaria

Morphology. (Morphology based on seven flattened specimens from *Garmanella pulchra* Hubbs.) Cyst oval, with relatively thick external and thin, membraneous internal walls, 294 long and 250 wide. Body elongate, 470–680 long and 140–170 wide, slightly tapering anteriorly but with wide anterior end, covered with tegumental spines decreasing in size posteriorly. Tegumental spines simple-pointed, long and slender. Remnants of eye-spots scattered between pharynx and intestinal bifurcation. Preoral lobe feebly developed; oral sucker wide, 52–70 long and 65–95 wide, with massive, wide posterior appendage (solid prolongation), not reaching to pharynx. Oral sucker armed with 55–61 circumoral spines arranged in two complete rows each of 27–31 spines. Spine patterns 27+28 ($n=1$); 28+28 ($n=4$); 29+29 ($n=1$); 31+30 ($n=1$). Anterior spines longer (12–15 long and 3 wide) than posterior ones (10–13 long and 2–3 wide). Prepharynx 62–110 long; pharynx oval, 32–45 long and 35–40 wide; oesophagus relatively long, almost as long as prepharynx. Intestinal caeca short and wide, terminating at distance anterior to ventral sucker. Ventral sucker spherical, well-developed, postequatorial, 50–60 in diameter. Sucker ratio 1: 0.70–0.90. Testes symmetrical, near posterior extremity, 32–50 long and 30–40 wide. Ventrogenital sac feebly developed. Mouth of ventrogenital sac a slit-like opening, anterior to ventral sucker. Gonotyl present, without refractile bodies. Primordium of ovary postacetabular. Four pairs of flame cells observed: first pair anterior to pharynx, second between pharynx and intestinal caeca, third anterior to ventral sucker and fourth at level of excretory bladder. Excretory bladder X-shaped with short and wide arms.

Second intermediate host. *Garmanella pulchra* (Cyprinodontidae).

Site of infection. Mesenteries.

Distribution. Yucatán (Mitza near Progreso).

References from Mexico. Present study.

Specimens deposited. CHCM-353, CNHE 3935, IPCAS D-448, USNPC 90188.

Comments. Metacercariae found in *Garmanella pulchra* resemble those of *Ascocotyle (A.) sexidigita* Martin and Steele, 1970, and *A. (A.) gemina* Font, Heard and Overstreet, 1984, two taxa supposed to be sibling species (Font *et al.*,

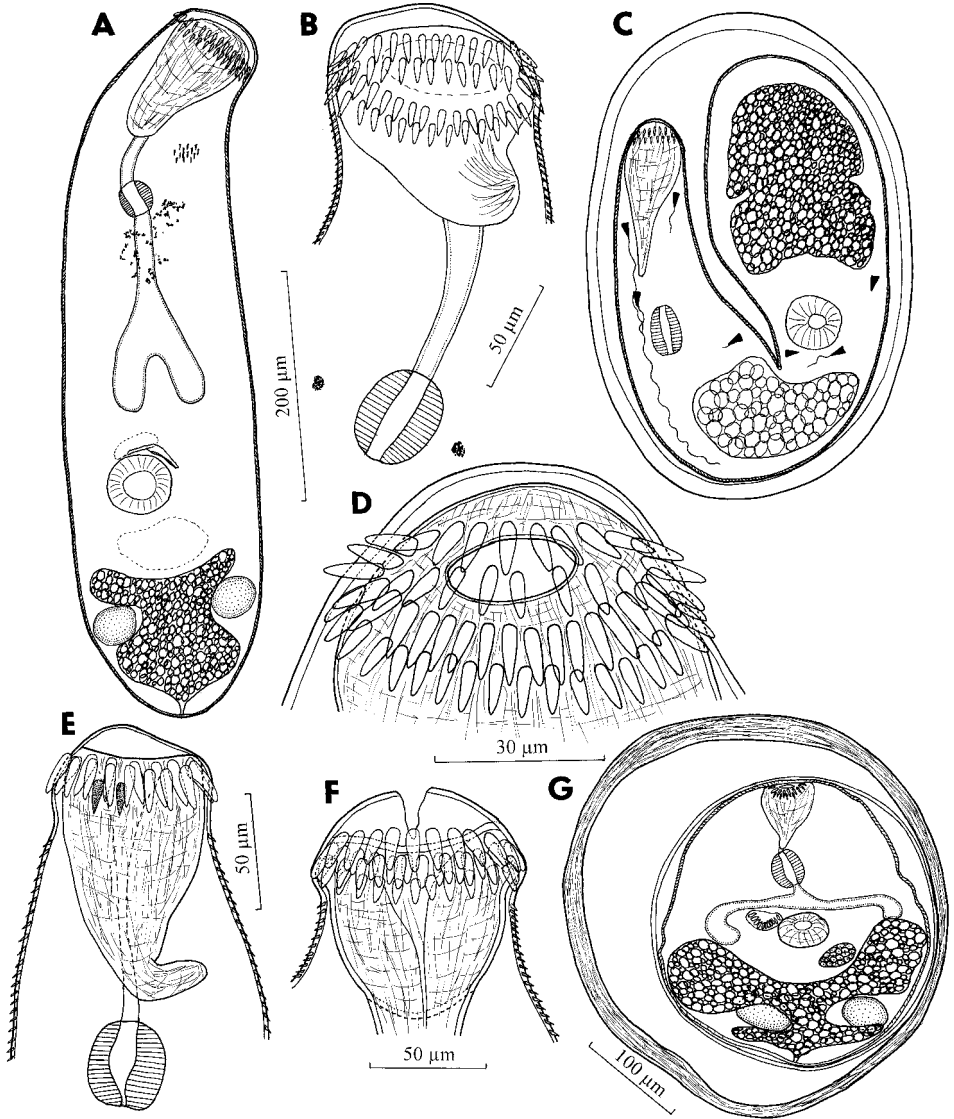


FIG. 1. (A–D) *Ascocotyle (Ascocotyle) gemina*. Metacercariae from the mesentery of *Garmanella pulchra*, Mitza, Yucatán. Spination patterns of circumoral spines 28+28 (A), 31+30 (B), and 29+29 (D). (E) *Ascocotyle (Phagicola) diminuta*. Adult from the intestine of *Ardea herodias*, Celestún, Yucatán. Note 16+2 circumoral spines (additional spines on the dorsal side dotted). (F) *Ascocotyle (Leighia) chandleri*. Metacercaria from the mesentery of *Cyprinodon variegatus*, Galveston Bay, Texas (paratype USNPC 54894); note 23+23 circumoral spines. (G) *Ascocotyle (Phagicola) nana*. Encysted metacercaria from the intestinal wall of *Cichlasoma fenestratum*, Catemaco Lake, Veracruz. (A) Excysted metacercaria, dorsal view; (B, E, F) anterior end, dorsal view; (C, G) encysted metacercaria; (D) detail of circumoral spines.

1984a). The species can be distinguished one from another by the number of refractile bodies within the gonotyl, the course of the uterus, average size of eggs, and infectivity of metacercariae of *A. gemina* for *Cyprinodon variegatus* Lacépède but

not for *Fundulus parvipinnis* Girard, the type host of *A. sexidigita*, described from California (Martin and Steele, 1970; Font *et al.*, 1984a).

All but one of the differential characters mentioned above are present only in adult worms and they cannot be applied to metacercariae that lack pockets within the gonotyl, their uterine loops are not completely formed and no eggs are present. The species of fish intermediate hosts of both trematode taxa (*Cyprinodon variegatus* or *Fundulus parvipinnis*, respectively) cannot be used for identification either because none of these fish occur in the locality under consideration. Nevertheless, the absence of the metacercariae in two species of *Fundulus* (*F. grandissimus* Hubbs, *F. persimilis* Miller) from Chelém lagoon connected with Mitza swamp suggests that they belong to *A. gemina* rather than to *A. sexidigita*. In addition, *Garmanella pulchra* is closely related to *Cyprinodon variegatus* whereas it is distantly related to, and ecologically different from *Fundulus parvipinnis*, a specific intermediate host of *A. (A.) sexidigita* (K. J. Lazara, personal communication). Further, the metacercariae of *A. (A.) gemina* also encyst in the mesenteries (Font *et al.*, 1984a), whereas those of *A. (A.) sexidigita* encyst within the wall of the intestine (Martin and Steele, 1970; Yoshino, 1972). For the reasons mentioned above, the metacercariae found in the mesentery of *G. pulchra* from Mexico are tentatively assigned to *A. gemina* until adult worms are available to confirm specific identification.

Font *et al.* (1984a) elucidated the life cycle of this trematode, reporting the hydrobiid snail, *Littoridinops monroensis* (Frauenfeld), as the first, the sheepshead minnow, *Cyprinodon variegatus*, as the second intermediate, and the clapper rail, *Rallus longirostris* Boddaert, as the definitive hosts of this parasite in Louisiana and Mississippi. Conti *et al.* (1986) and Sepúlveda *et al.* (1999) found adults of *A. gemina* in reddish and great egrets (*Egretta rufescens* (Gmelin) and *Casmerodius albus* (Linnaeus), respectively) from Texas and Florida.

***Ascocotyle (Ascocotyle) leighi* Burton, 1956**

Metacercaria

Morphology. Sogandares-Bernal and Lumsden (1964) did not describe metacercariae found in Mexico.

Second intermediate hosts. *Belonesox belizanus* Kner, *Poecilia sphenops* Valenciennes in Cuvier and Valenciennes (Poeciliidae).

Site of infection. Heart.

Distribution. Yucatán (Progreso).

References from Mexico. Sogandares-Bernal and Lumsden (1964).

Specimens deposited. None.

Comments. Sogandares-Bernal and Lumsden (1964) found metacercariae of *A. (A.) leighi* in two poeciliid fish from Progreso, Yucatán, most probably from Chelém lagoon. However, the authors did not provide any data on the morphology of metacercariae.

Metacercariae of *A. (A.) leighi* are encysted exclusively in the heart and they have been found in poeciliid and cyprinodontid fish in the USA and Mexico (Burton, 1956; Sogandares-Bernal and Bridgman, 1960; Sogandares-Bernal and Lumsden, 1964). They differ from those of *A. (A.) tenuicollis* encysted in the heart as well mainly in the number of circumoral spines (48–52 in total, i.e. 24–26 in each row, in the former taxon versus 32, i.e. 16+16 in *A. (A.) tenuicollis*) (Burton, 1956, 1958; Scholz *et al.*, 1997a).

Salgado-Maldonado and Kennedy (1997), and Salgado-Maldonado *et al.* (1997) reported metacercariae of *A. (A.) leighi* from the gills, mesenteries, heart and kidney of several species of cichlids from southeastern Mexico. Although few reference specimens were preserved and available to the present authors, it is possible to assume that most, if not all, metacercariae previously reported as *A. leighi* were misidentified and belonged to other species of the *Ascocotyle*-complex. Metacercariae from internal organs of cichlid, characid and poeciliid fish were conspecific with *A. (P.) nana* and those encysted in the gills of cichlids with *A. (A.) nunezae*. Metacercariae encysted in the heart of fish of different families might belong to *A. (A.) leighi* but all voucher specimens examined were conspecific with *A. (A.) tenuicollis*.

Adult trematodes of *A. (A.) leighi* are not known from Mexico because specimens found in the intestine of *Casmerodius albus* from Pátzcuaro Lake (Michoacán), identified by G. Pérez Ponce de León as *A. leighi* (Lamothe-Argumedo *et al.*, 1997; CNHE 1532), belonged in fact to *A. (A.) tenuicollis* (figure 2).

***Ascocotyle (Ascocotyle) tenuicollis* Price, 1935**
(figure 2)

Metacercaria

Morphology. Aguirre-Macedo and García-Magaña (1994: 17; figure 7a, b), Scholz *et al.* (1995: 179; figure 3A, C–E) and Scholz *et al.* (1997a: 163; figure 1E–G,

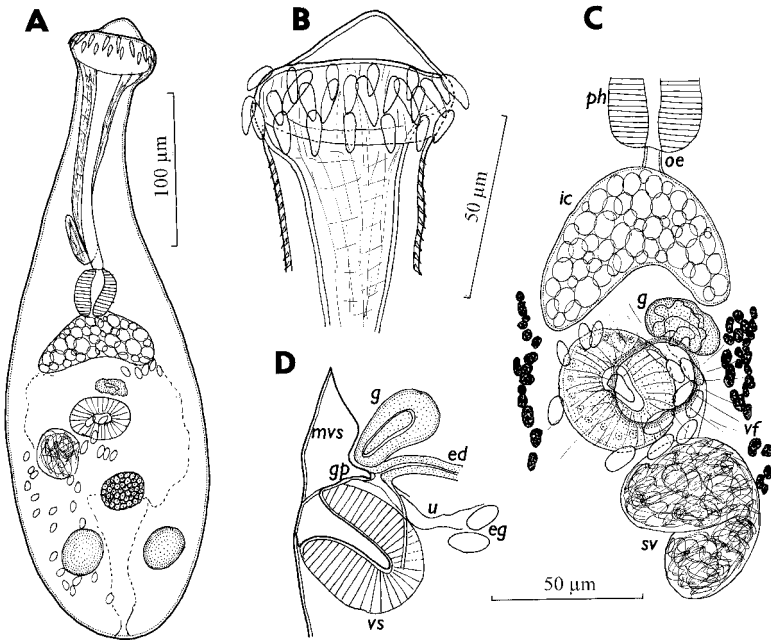


FIG. 2. *Ascocotyle (Ascocotyle) tenuicollis*. Adults from the intestine of *Casmerodius albus*, Pátzcuaro Lake, Michoacán, misidentified as *Ascocotyle leighi* (CNHE 1532). (A) Total view, ventrally; (B) anterior end (spines of the posterior row on the dorsal side not figured); (C, D) detail of the terminal genitalia, ventral and lateral views, respectively. Abbreviations: ed, ejaculatory duct; eg, eggs; g, nototyl; gp, genital pore; ic, intestinal caecum; mvs, mouth of ventrogenital sac; oe, oesophagus; ph, pharynx; sv, seminal vesicle; u, uterus; vf, vitelline follicles; vs, ventral sucker.

I) provided detailed descriptions of metacercariae that can easily be distinguished from those of other *Ascocotyle* species by combination of the following features: cyst spherical, thin-walled; body pyriform; preoral lobe prominent; posterior appendage long, curved to convoluted, reaching to pharynx or overlapping it; oral sucker with 32 circumoral spines forming two complete rows of 16 spines each; intestinal caeca short, very wide, sacciform, preacetabular, containing discoidal corpuscles; excretory bladder voluminous, filled with large lipid droplets.

Second intermediate hosts. *Astyanax fasciatus* (Cuvier), *Bramocharax caballeroi* Contreras-Balderas and Rivera-Teillery (Characidae); *Poecilia catemacensis* Miller, *P. latipunctata* Meek, *P. mexicana* Steindachner, *P. petenensis* (Günther), *P. velifera* (Regan), *Poeciliopsis catemaco* Miller (Poeciliidae); *Cichlasoma argentea* Allgayer, *C. aureum* (Günther), *C. fenestratum* (Günther), *C. friedrichstahli* (Heckel), *C. geddesi* (Regan), *C. helleri* (Steindachner), *C. intermedium* (Günther), *C. lentiginosum* (Steindachner), *C. managuense* (Günther), *C. nourissati* (Allgayer), *C. octofasciatum* (Regan), *C. pearsei* (Hubbs), *C. salvini* (Günther), *C. synspilum* Hubbs, *C. urophthalmus* (Günther), *Cichlasoma* sp., *Petenia splendida* (Günther) (Cichlidae); *Ophisternon aenigmaticum* Rosen and Greenwood (Synbranchidae).

Site of infection. Heart, exceptionally gill arches.

Distribution. Campeche (El Vapor, El Viento, La Pera, Palizada, Rancho II, Santa Gertrudis); Chiapas (Cedros, Lacanjá); Quintana Roo (Bacalar, Box Toro, Cabañas, Cenote Azul, Escondido, Framboyán, La Unión, Laguna Paiyegua, Mahahual, Ramonal, Raudales, Río Hondo); Tabasco (Camellones Chontales, El Espino, Puyacatengo, Santa Anita, Tucta, Yumká); Veracruz (Catemaco, Los Tuxtlas—Balzapote, La Palma, Las Máquinas); Yucatán (Celestún, Chaamac, Chen-há, Dzibilchaltún, Mitza, Noc-choncunchey, Sahkaba).

References from Mexico. Aguirre-Macedo and García-Magaña (1994); Scholz *et al.* (1995, 1997a); Salgado-Maldonado *et al.* (1997); Scholz and Vargas-Vázquez (1998); Vidal-Martínez *et al.* (2000); present study.

Specimens deposited. CHCM-137, IPCAS D-345.

Adult

Morphology. Scholz *et al.* (1997a: 163 and 165; figure 1A–D, H) described adults from naturally and experimentally infected definitive hosts. The adult of *A. (A.) tenuicollis* from the intestine of *Casmerodius albus* Linnaeus from Pátzcuaro Lake (Michoacán), previously misidentified as *A. leighi* (CNHE 1532—see Comments), is illustrated in figure 2.

Definitive hosts. *Ardea herodias*, *Casmerodius albus*, *Buteogallus anthracinus* (Deppe), *Phalacrocorax olivaceus* (Humboldt).

Site of infection. Intestine.

Distribution. Jalisco (Salinas de Careyes), Michoacán (Pátzcuaro), Yucatán (Celestún).

References from Mexico. Aguirre-Macedo and García-Magaña (1994); Scholz *et al.* (1997a); present study.

Specimens deposited. CHCM-361, IPCAS D-344.

Comments. Cichlids are the most suitable second intermediate hosts but fish of other families may also harbour metacercariae that are normally encysted within the bulbus of the heart (Scholz *et al.*, 1997a). Adults have been found in four species of fish-eating birds in Mexico, two of which (*A. herodias* and *P. olivaceus*) are new definitive hosts of this parasite. Sepúlveda *et al.* (1999) found *A. (A.) tenuicollis* to

belong to the most frequent (prevalence 54%) and numerous (mean intensity of infection 112 specimens; range 1–1260) helminth parasites of *Casmerodius albus* in Florida.

Ascocotyle (Leighia) chandleri Lumsden, 1963
(figure 1F)

Metacercaria

Morphology. Metacercaria of this species found in Mexico was described by Scholz *et al.* (1997a: 166; figure 2F–H). The authors identified this metacercaria as *A. (L.) chandleri* on the basis of the presence of 28+29 circumoral spines, a large, branched excretory bladder, the morphology of the terminal genitalia with a large, pad-like gonotyl with several refractile bodies, the anterior position of the testes and the site of infection in the second intermediate host belonging to the same family as the type host, *Cyprinodon variegatus*.

Second intermediate host. *Fundulus persimilis* (Cyprinodontidae).

Site of infection. Intestinal wall.

Distribution. Yucatán (Chelém lagoon).

References from Mexico. Scholz *et al.* (1997a).

Specimens deposited. IPCAS D-352.

Comments. Only one metacercaria was found during a study on the species of *Ascocotyle* parasitizing fish in southeastern Mexico (Scholz *et al.*, 1997a). Since it was partially damaged and studied within the cyst, new material is necessary to confirm the occurrence of *A. (L.) chandleri* in Mexico. *Ascocotyle (L.) chandleri* was described from metacercariae encysted in the liver of *Cyprinodon variegatus* (Cyprinodontidae) and *Mollienesis latipinna* (= *Poecilia latipinna* (Lesueur)) from Texas, USA (Lumsden, 1963). This author also found an immature worm, supposedly conspecific with *A. (L.) chandleri*, in the great egret (*Casmerodius albus*).

Lumsden (1963) reported 54 circumoral spines in *A. (L.) chandleri* forming two circlets of 27 spines each but examination of a paratype from *Cyprinodon variegatus* (USNPC 54894) revealed the presence of only 46 (23+23) spines (figure 1F), indicating variation in the number of spines in this species.

Adults of this trematode were first found in the roseate spoonbill (*Ajaia ajaja* (= *Platalea ajaja* Linnaeus)) from Texas (Dronen, 1985). Sepúlveda *et al.* (1996) reported *A. (L.) chandleri* from the little blue heron (*Egretta caerulea* (Linnaeus)) from Florida, with high values of prevalence (45%) and mean intensity of infection (385 specimens; range 1–3986).

Although Yamaguti (1971) placed this species within the nominotypical subgenus *Ascocotyle*, its morphology (vitelline follicles between the ventral sucker and testes, the uterus reaching anteriorly to the pharynx, long intestinal caeca reaching to the testes) corresponds to the diagnosis of the subgenus *Leighia* as proposed by Sogandares-Bernal and Lumsden (1963). Therefore, this species is considered here to be a member of the subgenus *Leighia*.

****Ascocotyle (Leighia) mcintoshi*** Price, 1936
(figures 3, 4)

Metacercaria

Morphology. (Morphology based on five flattened specimens from *Xiphophorus* sp.) Cyst large, oval to almost spherical, 420–432 in diameter, surrounded by thick

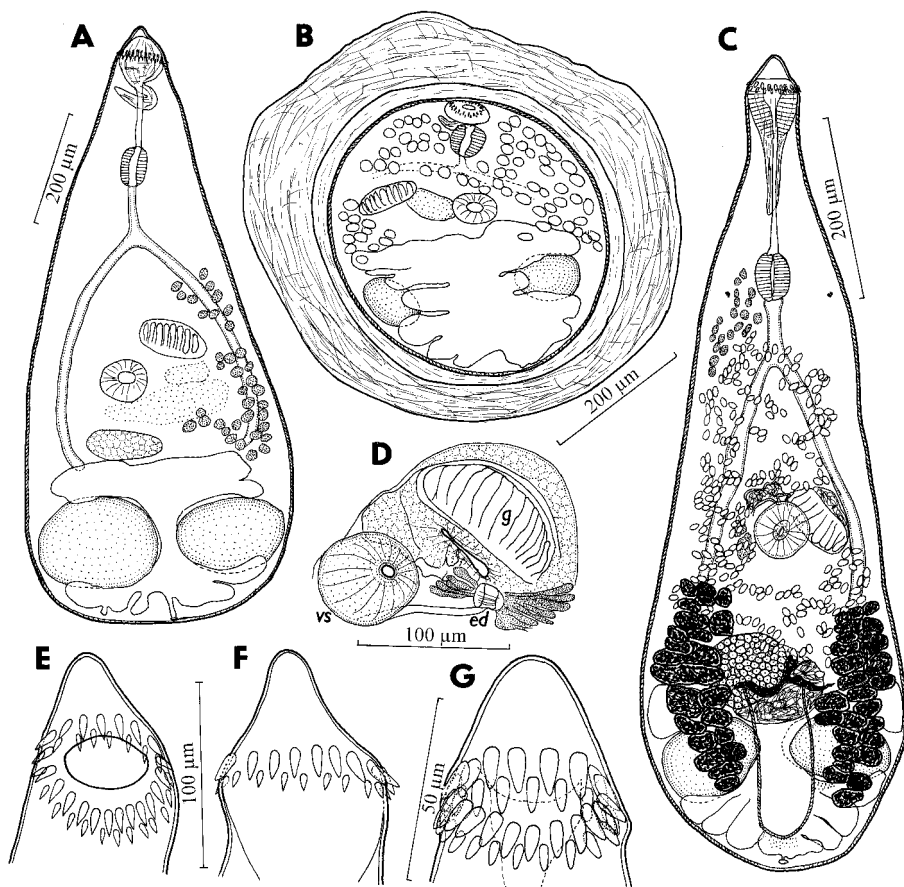


FIG. 3. *Ascocotyle (Leighia) mcintoshi*. (A, B, D–F) Metacercariae from the mesenteries of *Xiphophorus* sp. (A, D) and *Poecilia mexicana* (B, E, F), Río Las Máquinas, Veracruz. (C, G) Adults from chick experimentally infected with the mesenteries of *Xiphophorus* sp., 2 days post infection. (A) Total view of excysted metacercaria, ventrally; (B) encysted metacercaria; (C) total view of adult, ventrally; (D) terminal genitalia, ventrally (for abbreviations see figure 2); (E–G) circumoral spines (E, F—21+21 spines; in F only spines on the ventral side figured; G—20+20; dorsal view). In (A) and (B), cells with granular content figured only partly.

layer of host tissue and thick (thickness 17–20), mechanically resistant, hyaline internal layer. Body of metacercaria pyriform, 1036–1560 long and 416–556 wide, covered with tegumental spines. Most part of body filled with numerous small, transversely oval brownish droplets (lipoid?). Preoral lobe prominent; oral sucker subterminal, 35–70 long and 36–77 wide; posterior appendage conical, often curved or bent, not reaching to pharynx. Oral sucker surrounded with 38–42 circumoral spines forming two complete rows of 19–21 spines each; spination pattern 19+19 ($n=1$) and 21+21 ($n=3$). Anterior spines 12–18 long and 4–7 wide; posterior spines 9–12 long and 3–5 wide. Prepharynx 86–278 long; pharynx oval, 52–70 long and 45–80 wide; oesophagus slightly shorter than prepharynx. Caeca long and narrow, surrounding ventral sucker and reaching to ovary, slightly curved medially. Ventral sucker almost spherical, slightly postequatorial, 40–87 long and 55–80 wide. Sucker

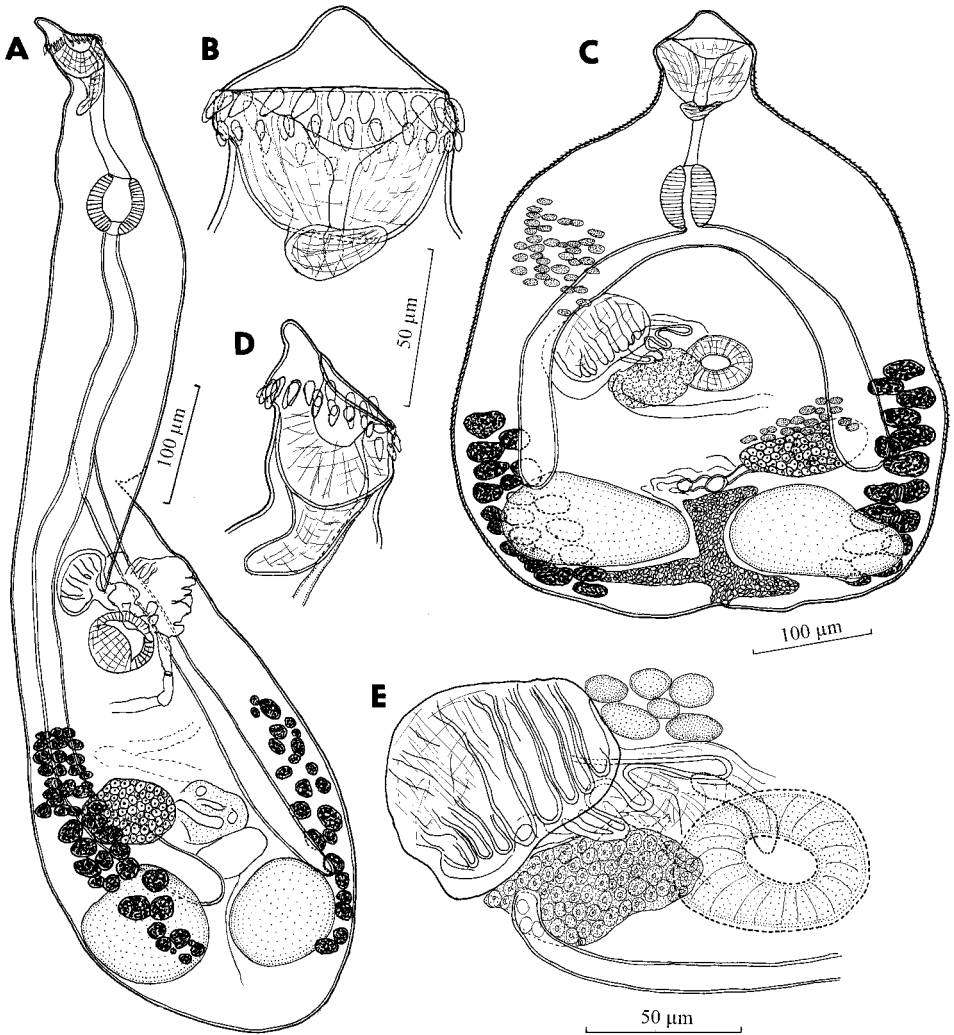


FIG. 4. *Ascocotyle (Leighia) mcintoshi*. Metacercariae from the gills (?) of *Xiphophorus* sp., Laguna Azul, Los Tuxtlas, Veracruz (A, D) and the heart (?) of *Poecilia mexicana*, Rio La Palma, Veracruz (B, C, E—contracted specimen). (A, C) Total view of excysted metacercaria, dorsally; (B, D) anterior end (spination pattern 20+20 in B; in D some spines lost); (E) terminal genitalia, dorsally. In (C), cells with granular content figured only on one side.

ratio 1: 0.95–1.62. Testes symmetrical, close to posterior extremity, 37–170 long and 92–232 wide. Genital sac well-developed, with numerous out-pocketings, anterosinistral to acetabulum, containing very large gonotyl with 8–11 prominent refractile bodies. Mouth of ventrogenital sac slit-like, transversely oval, anterolateral to ventral sucker. Primordium of ovary postacetabular, transversely oval, 50 long and 112 wide. Excretory bladder X-shaped, with short and wide arms, laterally branched in posterior part.

Second intermediate hosts. *Poecilia mexicana*, *Xiphophorus* sp. (Poeciliidae).

Site of infection. Mesenteries, occasionally heart (?) and gills (?).

Distribution. Veracruz (Los Tuxtlas—La Palma, Laguna Azul, Las Máquinas).

References from Mexico. Present study.

Specimens deposited. CHCM-354, CNHE 3930, IPCAS D-399.

Adult

Morphology. (Morphology based on five hot-formalin fixed specimens from experimentally infected chick; 2 days post infection.) Body elongate, tapering towards anterior extremity, 820–980 long and 270–300 wide, entirely covered with scale-like tegumental spines. Preoral lobe prominent, conical, long; oral sucker subterminal, 50–55 long and 47–57 wide; posterior appendage long, often sinuous, not reaching to pharyngeal level. Sucker armed with 38–42 circumoral spines forming two complete rows of 19+ 19 ($n=1$); 20+ 20 ($n=2$); and 21+ 21 ($n=2$) spines each. Anterior spines 14–17 long and 4–6 wide; posterior spines 9–12 long and 3–4 wide. Prepharynx 40–125 long; pharynx muscular, oval to spherical, 55–72 long and 37–45 wide; oesophagus short. Intestinal caeca narrow, long, reaching posteriorly to excretory bladder, slightly curved medially at ovarian level. Ventral sucker spherical to transversely oval, slightly postequatorial, 55–67 long and 57–67 wide. Sucker ratio 1: 1.09–1.35. Testes symmetrical, close to posterior extremity, 60–102 long and 80–125 wide. Seminal vesicle posterolateral to ventral sucker, C-shaped, 28 long and 36 wide. Ventrogenital sac formed, containing very large, pad-like gonotyl with 10–12 refractile bodies. Mouth of ventrogenital sac large, slit-like. Genital pore anterosinistral to ventral sucker. Ovary dextral, nearly spherical, posterolateral to seminal vesicle, 60–70 long and 70–92 wide. Seminal receptacle voluminous, mediolateral to ovary, 62–87 long and 73–87 wide. Uterus sinuous; uterine loops anteriorly reaching to pharyngeal level, posteriorly crossing testes and reaching to posterior margin of ovary. Vitellarium forming two long lateral bands of vitelline follicles starting at acetabular level anteriorly and passing testes posteriorly. Eggs ($n=30$) operculate, 21 (19–22) long and 11 (9–13) wide. Excretory bladder voluminous, laterally branched; excretory pore terminal.

Definitive host. Chick (experimental).

Site of infection. Intestine.

Distribution. Not known.

References from Mexico. Present study.

Specimens deposited. CHCM-354, CNHE 3929, IPCAS D-447, USNPC 90190.

Comments. Metacercariae found in this study did not differ from those of *A. (L.) mcintoshi* as described by Leigh (1974) from *Gambusia affinis* Baird and Girard and *Poecilia latipinna*. Both fish species from Mexico represent new second intermediate hosts.

Dominant site of infection of metacercariae found in this study were the mesenteries but one specimen (figure 4A, D) was reported to occur in the gills (? musculature of gill arches) and another one (figure 4B, C) in the heart (?). Stein (1968) reported metacercariae of this trematode from the liver of *G. affinis* in Florida but Leigh (1974) found them in various organs such as mesenteries adjacent to the small intestine, attached to the visceral peritoneum, and in the liver, gall bladder and fat bodies.

Experimentally recovered adult trematodes were almost identical with those of *A. (L.) mcintoshi* as described by Price (1936), Yamaguti (1971) and Leigh (1974). Sepúlveda *et al.* (1996, 1999) found this trematode to be a relatively common parasite of the little blue heron (*Egretta caerulea*—prevalence 29%; mean intensity

84; range 1–963 specimens) but quite rare (prevalence 6%, mean intensity seven specimens) parasite of the great egret (*Casmerodius albus*) in Florida.

Ostrowski de Núñez (1992) described *Ascocotyle (Leighia) hadra*, a sibling species of *A. (L.) mcintoshi*, from Argentina. Both taxa differ one from another in only a few biological and morphological characteristics, most of them being related to cercariae (see Ostrowski de Núñez, 1992). Metacercariae can be distinguished by the absence of pigmentation in the former species (versus brownish colour of metacercariae of *A. (L.) mcintoshi*) and different spectrum of second intermediate hosts: *A. (L.) mcintoshi* infects *Gambusia affinis* whereas *A. (L.) hadra* only poeciliid fishes native to Argentina, *Cnesterodon decemmaculatus* (Jenyns) and *Jenynsia lineata* (Jenyns). Adults differ in body size (496–798 in *A. (L.) hadra* versus 680–1200 in *A. (L.) mcintoshi* and in the number of projections of the gonotyl (10–11 versus 13).

The specimens found in Mexico correspond to *A. (L.) mcintoshi* in brownish pigmentation of metacercariae, the larger size of adults and the spectrum of fish intermediate hosts. Geographical distribution also supports conspecificity of material from Yucatán with *A. (L.) mcintoshi*. The number of digital projections (pockets) of the gonotyl in the present material (8–11 in metacercariae and 10–12 in adults) was more similar to that reported for *A. (L.) hadra*. However, variability of this character and difficulties in counting precise number of projections cast doubts upon reliability of this feature to distinguish taxa that possess numbers of pockets that are not markedly different. Consequently, the specimens studied by the present authors are identified as *A. (L.) mcintoshi*.

Ascocotyle (L.) mcintoshi was described from white ibis, *Guara alba* (= *Eudocimus albus* (Linnaeus)), from Florida by Price (1936) and then reported by Stein (1968), Leigh (1974) and Sepúlveda *et al.* (1996, 1999) from the USA. The life cycle of this trematode was elucidated by Leigh (1974) who found the prosobranch snail *Littoridinops monroensis* to serve as the first intermediate host, in which ophthalmogymnocephalous cercariae developed. The present finding is the first record of *A. (L.) mcintoshi* from Mexico.

***Ascocotyle (Leighia) megalocéphala* Price, 1932**
(figure 5A–D)

Metacercaria

Morphology. Scholz *et al.* (1995: 179–180; figure 4) had described a metacercaria designated as *Ascocotyle (Ascocotyle)* sp. 1 that was later identified as *A. (L.) megalocéphala* by Scholz *et al.* (1997a). A description of six metacercariae from *Poecilia mexicana* is provided: cyst widely oval to almost spherical, 432–472 long and 288–368 wide, with thick outer wall, often brownish, and thinner internal wall. Metacercarial body flask-shaped, slightly tapering towards anterior end, 376–700 long and 220–330 wide, densely covered with simple tegumental spines. Spines almost completely covering ventral side of body except for small area around subterminal excretory pore; dorsally, spines reaching only to level of excretory bladder. Remnants of eye-spot granules scattered at pharyngeal level. Preoral lobe feebly developed (figure 5A) but in some living specimens may be protruded (figure 5C, D). Oral sucker spherical, 67–97 long and 80–140 wide, with conical posterior appendage, usually not reaching to pharynx, sometimes curved. Oral sucker armed with 74–80 fine but well-visible circumoral spines arranged in two complete rows of 36–40 spines each; anterior spines 12–17 long and 3–4 wide; posterior spines

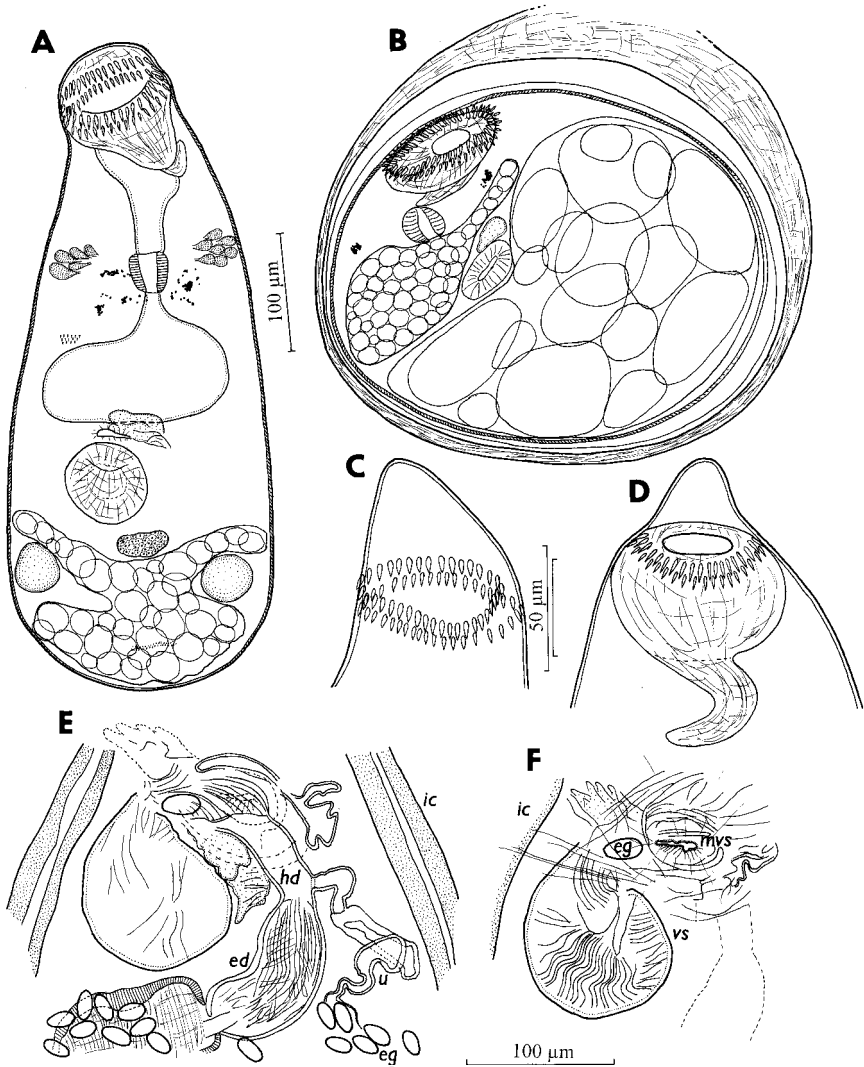


FIG. 5. (A–D) *Ascocotyle (Leighia) megaloccephala*. Metacercariae from the external surface of the intestine of *Poecilia velifera*, Chen-há cenote, Yucatán (A) and *P. mexicana*, Balzapote, Veracruz (B–D). (E, F) *Galactosomum puffini*. Adult from the intestine of *Larus occidentalis*, Isla Rasa, Baja California (CNHE 804). (A) Total view, ventrally; (B) encysted metacercaria; (C) circumoral spines (39+39); (D) anterior end (only spines on the ventral side figured); (E, F) terminal genitalia, more internal (E) and external (F) views, ventrally. Note presence of hermaphroditic duct (hd) in (E) and a slit-like opening (mouth) of the ventrogenital sac (mvs; for other abbreviations see figure 2) in (F).

10–16 long and 3–4 wide. Spination pattern 36+38 ($n=1$); 37+38 ($n=1$); 38+39 ($n=1$); 39+39 ($n=2$); 40+40 ($n=1$). Prepharynx 80–102 long; pharynx oval to almost pyriform, 40–72 long and 30–52 wide; oesophagus very short or indistinct. Intestinal caeca short and wide, often forming a sac, reaching only to anterior margin of ventral sucker. Ventral sucker spherical, postequatorial, 68–90 long and 62–80 wide. Sucker ratio 1: 0.55–0.80. Testes symmetrical, at distance from posterior

extremity, 37–80 long and 30–55 wide. Ventrogenital sac feebly developed, with simple, pad-like, transversely oval gonotyl. Primordium of ovary anteromedial to testes. Excretory bladder voluminous, X-shaped to sac-like, in encysted metacercariae occupying more than half of metacercarial body, filled with large droplets. Excretory pore subterminal, ventral.

Second intermediate hosts. *Poecilia mexicana*, *P. velifera* (Poeciliidae).

Site of infection. Wall of stomach and intestine, mesenteries.

Distribution. Veracruz (Los Tuxtlas—arroyo Balzapote); Yucatán (Mitza, Sahkaba).

References from Mexico. Scholz *et al.* (1995—as *Ascocotyle* (*A.*) sp. 1); Scholz *et al.* (1997a); present study.

Specimens deposited. CHCM-356a, CNHE 3925, IPCAS D-351, USNPC 90189.

Adult

Morphology. No substantial differences were observed between the specimen found in *Ardea herodias* from Celestún and that described by Scholz *et al.* (1997a: 176, 178; figure 7A, B, D) from the intestine of *Casmerodius albus* from the same locality. Therefore, only a brief description of newly collected specimen is provided here: body 800 long and 360 wide. Oral sucker 125 long and 197 wide. Sucker armed with simple spines forming two rows, with 38 spines in anterior complete row; posterior row with several spines apparently missing, most probably containing 38 spines as well. Anterior spines 25 long and 6 wide; posterior spines 21–22 long and 5–6 wide. Ventral sucker 56 long and 55 wide. Sucker ratio 1: 0.34. Testes 107–115 long and 137–160 wide. Ovary 100 long and 140 wide. Seminal receptacle 87 long and 97 wide. Eggs 19–21 long and 9–11 wide.

Definitive host. *Ardea herodias*, *Casmerodius albus*.

Site of infection. Intestine.

Distribution. Yucatán (Celestún).

References from Mexico. Scholz *et al.* (1997a); present study.

Specimens deposited. CHCM-356, CNHE 3925, IPCAS D-446.

Comments. Two species of *Poecilia* from Mexico represent new fish hosts of *A. (L.) megalcephala*. Stein (1968) reported the poeciliid *Mollienisia latipinna* (= *Poecilia latipinna*) as its natural intermediate host in Florida but he did not provide descriptions or figures of the metacercariae.

Ascocotyle (L.) megalcephala was described by Price (1932) from *Butorides* sp. from Puerto Rico. Up to date, adults have been found only in Puerto Rico (type locality) and Mexico (Price, 1932; Scholz *et al.*, 1997a). The heron *Ardea herodias* is a new definitive host of this trematode that seems to be a rare parasite of herons.

Ascocotyle (Leighia) nunezae

Scholz, Vargas-Vázquez, Vidal-Martínez and Aguirre-Macedo, 1997

Metacercaria

Morphology. Scholz *et al.* (1995: 184; figure 8A–G—as *Ascocotyle (Phagicola)* sp. 3) and Scholz *et al.* (1997b: 143; figures 9–15) provided detailed descriptions of metacercariae. The most typical characters enabling differentiation of *A. (L.) nunezae* from congeners are as follows: body elongate to conical, tapering anteriorly, entirely spined; preoral lobe feebly developed; posterior appendage conical, not reaching to pharynx; circumoral spines forming one complete row of 25–26 and seven to nine

accessory spines on dorsal side; intestinal caeca long, reaching to ovarian primordium, slightly curved medially around ventral sucker.

Second intermediate hosts. *Cichlasoma aureum*, *C. helleri*, *C. meeki* (Brind), *C. octofasciatum*, *C. passionis* Rivas, *C. pearsei*, *C. robertsoni* Regan, *C. salvini*, *C. synspilum*, *C. urophthalmus*, *Petenia splendida* (Cichlidae).

Site of infection. Gills.

Distribution. Campeche (El Viento, La Pera, Palizada, Rancho II, Santa Gertrudis, Zoh Laguna); Chiapas (Lacanjá); Quintana Roo (Box Toro, Cabañas, La Unión, Laguna Paiyegua, Los Cuates, Ramonal, Raudales, Río Hondo); Tabasco (Las Ilusiones, Puyacatengo, Yucateco, Yumká); Yucatán (Chaamac, Chek-há, Dzonot Cervera, Noc-choncunchey, Petentuche).

References from Mexico. Scholz *et al.* (1995—as *Ascocotyle (Phagicola)* sp. 3); Scholz *et al.* (1997a, 1997b); Scholz and Vargas-Vázquez (1998); Vidal-Martínez *et al.* (2000); present study.

Specimens deposited. CNHE 3729, 3731, IPCAS D-349.

Adult

Morphology. Adults from naturally and experimentally infected definitive hosts from Mexico were described and illustrated by Scholz *et al.* (1997b: 141, 143; figures 1–8).

Definitive hosts. *Casmerodius albus* (natural); chicks (experimental).

Site of infection. Intestine.

Distribution. Yucatán (Celestún).

References from Mexico. Scholz *et al.* (1997b).

Specimens deposited. CNHE 2849 (holotype); BMNH 1996.10.7.5; CHCM 185; IPCAS D-348; USNPC 86819 (paratypes).

Comments. Numerous recent findings of metacercariae from cichlid fish do not correspond with the fact that adults have been found only once in naturally infected hosts. In *Ardea herodias* from the type locality examined by the present authors, *A. (L.) nunezae* was not found, similarly during a large-scale survey of the parasites of the little blue heron (*Egretta caerulea*) and great egret (*Casmerodius albus*) carried out in Florida by Sepúlveda *et al.* (1996, 1999).

As pointed out by Scholz *et al.* (1997b), *A. (L.) nunezae* possesses features that place it in the intermediate position among *Ascocotyle* subgenera. Scholz *et al.* (1997b) placed this species to the nominotypical subgenus *Ascocotyle* following Yamaguti's (1971) concept of the subgenera of *Ascocotyle*. However, the authors overlooked that members of the subgenus *Ascocotyle* have the uterus confined mainly to the postacetabular area whereas those of *Leighia* in its original concept by Sogandares-Bernal and Lumsden (1963) possess uterine loops reaching anteriorly to the pharyngeal level. Therefore, *A. nunezae* is transferred to the subgenus *Leighia*.

**Ascocotyle (Phagicola) ampullacea* Miller and Harkema, 1962
(figure 6)

Metacercaria

Morphology. (Morphology based on one specimen from *Gambusia yucatana* Regan, two from *Poecilia sphenops*, one from *Poecilia* sp. and two from *Belonesox belizanus*.) Cyst large, almost spherical, 342–365 long and 335–365 wide, with thick (13–20), mechanically resistant and elastic outer wall, and thin, transparent internal

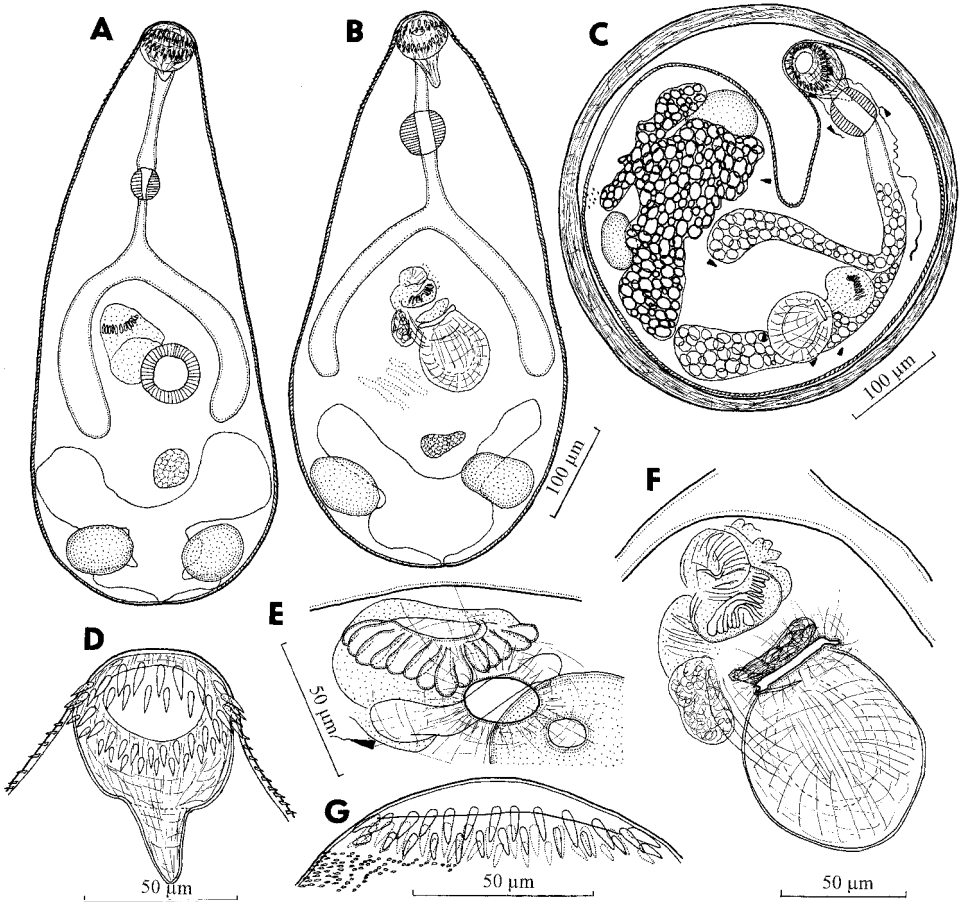


FIG. 6. *Ascocotyle (Phagicola) ampullacea*. Metacercariae from the muscles of *Gambusia yucatanana*, El Yucateco, Tabasco (A), gonads of *Belonex belizanus*, Chaamac cenote, Yucatán (B, D, F), mesentery of *Poecilia* sp., El Yucateco, Tabasco (C), and intestinal wall of *Poecilia sphenops*, Mitza, Yucatán (E, G). (A, B) Total view of excysted metacercaria, dorsally; (C) encysted metacercaria; (D) anterior end, dorsal view; (E, F) terminal genitalia, dorsal view; (G) circumoral spines; small tegumental, scale-like spines figured only on one side.

wall. Body flask-shaped, tapering anteriorly, 490–670 long and 230–279 wide, covered with small tegumental spines becoming smaller posteriorly. Preoral lobe indistinct; oral sucker spherical, subterminal, 45–47 long and 42–51 wide, with short, conical posterior appendage, not reaching to pharynx. Oral sucker armed with 44–54 circumoral spines forming two complete rows each of 22–27 spines each. Spination patterns 22+22 ($n=2$); 25+23 ($n=1$); 25+25 ($n=2$); 27+27 ($n=1$). Anterior spines 10–12 long and 2 wide; posterior spines 9–11 long and 2 wide. Prepharynx 35–120 long; pharynx oval, 42–47 long and 32–42 wide; oesophagus relatively short. Intestinal caeca long and narrow, surrounding ventral sucker, terminating anterior to excretory bladder, containing numerous spherical bodies. Ventral sucker spherical, slightly postequatorial, 58–62 long and 62–77 wide. Sucker ratio 1: 1.48–1.83. Testes symmetrical, near posterior extremity, 35–50 long and 47–60 wide. Ventrogenital sac anterosinistral to ventral sucker, containing gonotyl with 12–14 refractile bodies.

Primordium of ovary postacetabular. Flame cell pattern not determined but probably 16 flame cells present, arranged in four pairs. First pair situated between mouth and pharynx, second pair at acetabular level, third between acetabulum and excretory bladder and fourth pair at level of excretory bladder. Excretory bladder X-shaped, with prominent anterior arms and reduced posterior ones, filled with spherical droplets.

Second intermediate hosts. *Belonesox belizanus*, *Gambusia yucatanana*, *Poecilia sphenops*, *Poecilia* sp. (Poeciliidae).

Site of infection. Muscles (*G. yucatanana*), intestinal wall (*P. sphenops*), mesenteries (*Poecilia* sp.), gonads (*B. belizanus*).

Distribution. Tabasco (El Yucateco); Yucatán (Chaamac, Mitza).

References from Mexico. Present study.

Specimens deposited. CNHE 3923, IPCAS D-400.

Comments. Despite slight differences in the size of the prepharynx and oesophagus, and the site of infection, all metacercariae found in poeciliids from Tabasco and Yucatán are considered to be conspecific because of similar size and shape of cysts and their walls, a flask-shaped body, an indistinct preoral lobe, a conical posterior appendage not reaching to the pharynx, armament of the oral sucker, long and narrow intestinal caeca, and the presence of more than 10 refractile bodies within the gonotyl.

In all these features, the metacercariae fit best into the diagnosis of the species *A. (P.) ampullacea* as described by Miller and Harkema (1962) from *Procyon lotor* (Linnaeus) from North Carolina and as observed in its paratypes (USNPC 59584). It should be mentioned that refractile bodies within the gonotyl of adults of *A. (P.) ampullacea* were incorrectly described as spines by Miller and Harkema (1962). The only difference was in slightly higher number of circumoral spines in some metacercariae (22–27 spines but mostly 22–25 spines) than in adults (20–24). However, this may be due to intraspecific variation in the number of spines.

Stein (1968) first reported metacercariae of this trematode from the the intestinal mesenteries and body musculature of the poeciliid fish *Gambusia affinis* from Florida but the author did not provide any description or illustrations. Adults obtained from chicks fed with infected organs possessed 22 + 22 circumoral spines (Stein, 1968). The present findings represent a new geographical record of this fairly rare trematode known only from the USA and Mexico.

Ascocotyle (Phagicola) diminuta Stunkard and Haviland, 1924
(figure 1E)

Metacercaria

Morphology. Descriptions were provided by Scholz *et al.* (1995: 180–181; figures 5, 7B) and Scholz *et al.* (1997a: 172–173; figures 2A–E, 5A–D, F, 7E). Metacercariae can be distinguished from those of congeneric species by the elongate shape of cyst, the presence of 18 massive circumoral spines arranged in one complete row of 16 spines and two smaller additional spines on the dorsal side, narrow and long intestinal caeca reaching posterior to the ventral sucker, and a simple gonotyl lacking refractile bodies.

Second intermediate hosts. *Belonesox belizanus*, *Poecilia latipunctata*, *P. mexicana*, *P. petenensis*, *P. sphenops*, *P. velifera* (Poeciliidae); *Cyprinodon artifrons* Hubbs (reported as *C. variegatus* by Sogandares-Bernal and Lumsden, 1963), *Fundulus*

grandissimus, *F. persimilis*, *Floridichthys polyommus* Hubbs (reported as *F. carpio* Hubbs by Scholz *et al.*, 1997a) (Cyprinodontidae).

Site of infection. Gills.

Distribution. Quintana Roo (Box Toro, Cenote Azul, Ramonal); Veracruz (Los Tuxtlas—Balzapote); Yucatán (Chaamac, Chek-há, Chelém, Chen-há, Dzibilchaltún, Noc-choncunchey, Progreso, Sahkaba).

References from Mexico. Sogandares-Bernal and Lumsden (1963—as *Ascocotyle angrense*); Scholz *et al.* (1995, 1997a); Scholz and Vargas-Vázquez (1998); present study.

Specimens deposited. CHCM-358, IPCAS D-343.

Adult

Morphology. Scholz *et al.* (1997a: 173; figures 5E, G–I, 7F, G) described adults from naturally and experimentally infected hosts.

Definitive hosts. *Ardea herodias*, *Casmerodius albus* (natural), chicks (experimental).

Site of infection. Intestine.

Distribution. Yucatán (Celestún).

References from Mexico. Scholz *et al.* (1997a); present study.

Specimens deposited. CNHE 3924, IPCAS D-342, USNPC 88538, 90191.

Comments. Metacercariae from the gill filaments of poeciliid fishes (*Belonesox belizanus*, *Cyprinodon variegatus* (= *C. artifrons*) and *Mollienisia sphenops* (= *Poecilia sphenops*)) from Progreso, Yucatán, identified by Sogandares-Bernal and Lumsden (1963) as *Ascocotyle angrense*, were undoubtedly conspecific with *A. (P.) diminuta* because they possessed 16+2 circumoral spines (instead of 18+2 in *A. (P.) angrense*—see Ostrowski de Núñez, 1993 and Scholz *et al.*, 1997a).

In Mexico and the USA, only poeciliid and cyprinodontid fish serve as second intermediate hosts of *A. (P.) diminuta* (see Stunkard and Uzman, 1955; Sogandares-Bernal and Bridgman, 1960; Stein, 1968; Scholz *et al.*, 1997a). In Argentina, Ostrowski de Núñez (1993) found fish of the families Cichlidae and Jenynsiidae to be suitable second intermediate hosts.

Sepúlveda *et al.* (1999) found *A. (P.) diminuta* to be one of the most frequent parasites of the great egret (*Casmerodius albus*) from Florida, with prevalence of infection being 33% ($n=70$) and mean intensity 64 specimens (range 1–3580). Besides fish-eating birds, mammals such as raccoon, rats, mice and hamsters have been reported as definitive hosts of this trematode reported from a large area between northeastern USA (Connecticut, MD) and Argentina (Stunkard and Haviland, 1924; Stunkard and Uzman, 1955; Ostrowski de Núñez, 1993).

The life cycle of this trematode was first elucidated by Ostrowski de Núñez (1993) who found the hydrobiid snails *Littoridina castellanosae* Gaillard and *L. parchappi* d'Orbigny to serve as the first and cyprinodontid fish as the second intermediate hosts in Argentina. Scholz *et al.* (1997a) successfully infected fish with cercariae of *A. (P.) diminuta* released from the hydrobiid snail *Pyrgophorus coronatus* (Pfeiffer) in Yucatán.

***Ascocotyle (Phagicola) longa* Ransom, 1920**

(figure 7)

Metacercaria

Morphology. (Morphology based on 26 specimens from *Mugil cephalus* Linnaeus and *M. curema* Valenciennes in Cuvier and Valenciennes.) Cyst widely oval,

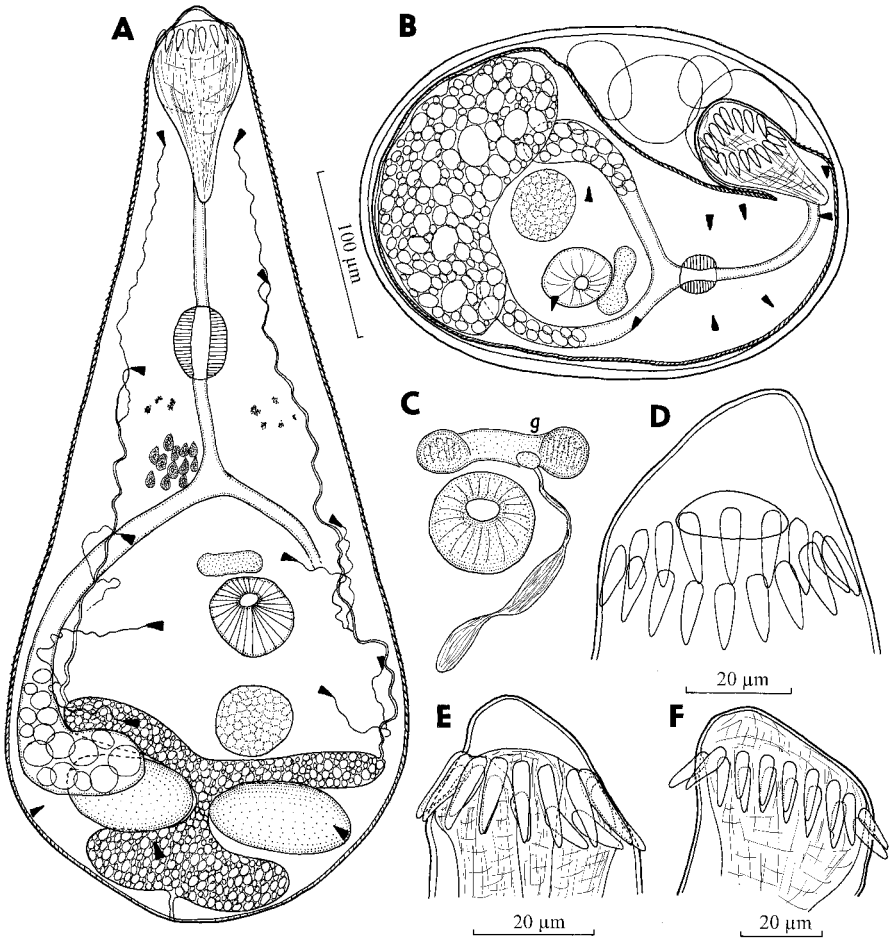


FIG. 7. *Ascocotyle (Phagicola) longa*. Metacercariae from the heart of *Mugil cephalus*, Río Cuitzmala, Jalisco (A–C) and the musculature of gill arches of *Dormitator latifrons*, Marismas de Chalacatepec, Jalisco (F), and adult from the intestine of *Ardea herodias*, Celestún lagoon, Yucatán (E). (A) Total view of excysted metacercaria, dorsally; (B) encysted metacercaria; (C) terminal genitalia, note bipartite gonotyl (g); (D–F) circumoral spines ($n=16$). (A, C) Free-hand schematic drawing; not in scale.

thin-walled, 154–286 long and 131–207 wide. Body pyriform, 323–554 long and 115–202 wide, covered with scale-like tegumental spines. Remnants of eye-spots posterior to pharynx. Region between pharynx and ventral sucker containing oval cells with granular contents (? gland cells). Preoral lobe moderately developed; oral sucker 36–54 long and 36–54 wide, with well-developed posterior appendage, often sinuous, only rarely reaching to pharynx. Oral sucker surrounded by one row of 16 massive circumoral spines ($n=19$), 9–15 long and 3–4 wide. Prepharynx 40–102 long; pharynx strongly muscular, 30–45 long and 23–34 wide; oesophagus relatively short. Intestinal caeca narrow and long, surrounding ventral sucker and primordium of ovary, curved medially at level of anterior branch of excretory bladder, filled with spherical corpuscles. Ventral sucker spherical, well-developed, postequatorial, 23–40 long and 23–37 wide. Sucker width ratio 1: 0.71–0.90. Testes symmetrical, near

posterior extremity, 27–50 long and 27–55 wide. Seminal vesicle two-chambered, postacetabular. Genital sac anterosinistral to acetabulum, containing bipartite gonotyl composed of two pad-like lobes (figure 7C). Primordium of ovary postacetabular, 18 long and 40 wide. Excretory bladder X-shaped, with short and wide arms, filled with numerous, dark granules. Flame cell formula most probably (posterior ducts not observed completely) $2 [(2+2)+(2+2)] = 16$. First flame cells posterolateral to oral sucker; second at pharyngeal level; third at level of caecal bifurcation; fourth anterolateral to acetabulum; fifth and sixth posterolateral to ventral sucker; seventh lateral to anterolateral to testes and eighth posteromedial to testes.

Second intermediate hosts. *Gobiesox fluviatilis* Briggs and Miller (Cyprinodontidae); *Dormitator latifrons* (Richardson) (Eleotridae); *Mugil cephalus*, *M. curema* (Mugilidae).

Site of infection. Heart, musculature of gill branches, body musculature, rarely intestinal wall, liver, gonads, mesenteries.

Distribution. Jalisco (El Jabalí, Marismas de Chalacatepec, Río Cuitzmala, Salinas de Careyes, San Nicolás).

References from Mexico. Scholz (1999); present study.

Specimens deposited. BMNH 2000.6.1.9, CHCM-352, CNHE 3928, IPCAS D-445, USNPC 88537, 90192, 90193.

Adult

Morphology. Scholz (1999) redescribed the species on the basis of examination of the type specimens and reference material from different hosts and geographical regions.

Definitive host. *Ardea herodias*.

Site of infection. Intestine.

Distribution. Yucatán (Celestún).

References from Mexico. Present study.

Specimens deposited. CNHE 3926, IPCAS D-295.

Comments. Metacercariae are frequent parasites of brackish-water fish, above all grey mullets (Hutton and Sogandares-Bernal, 1959, 1960; Manfredi and Oneto, 1997). In Mexico, they have been found only in fish from its western (Pacific) coast (Scholz, 1999; present study).

Adults of *A. (P.) longa* found in a number of birds, mainly herons, and mammals (see Scholz, 1999 for review) are reported from Mexico for the first time. Scholz (1999) synonymized *A. (P.) arnaldoi* Travassos, 1929, *A. (P.) byrdi* (Robinson, 1956) and *A. (P.) longicollis* (Kuntz and Chandler, 1956) with *A. (P.) longa* that is the most widely distributed species of *Ascocotyle* reported from North and South America, Europe, North Africa and Asia (Middle East) (see Scholz, 1999 for references).

Chieffi *et al.* (1992) reported human infections caused by a species of *Phagicola* (= *Ascocotyle (Phagicola)*), supposed to be *A. (P.) longa* by Manfredi and Oneto (1997). The latter authors discussed the capacity of this trematode to infect humans because of heavy infections of mullets with its metacercariae encysted in the muscles.

***Ascocotyle (Phagicola) macrostoma* (Robinson, 1956)**

Metacercaria

Morphology. To date, no data on metacercarial morphology exist.

Second intermediate host. *Poecilia velifera* (Poeciliidae).

Site of infection. ? Gill arches (see Comments).

Distribution. Yucatán (Chaamac).

References from Mexico. Scholz *et al.* (1997a).

Adult

Morphology. Scholz *et al.* (1997a: 175–176; figure 6A–F) redescribed this species on the basis of experimentally recovered adults. It is characterized mainly by the following features: a spindle-shaped body; a feebly developed anterior lobe; long, conical posterior appendage overlapping the pharynx; 18 massive, large (length 24–33) circumoral spines arranged in one complete row; the intestinal caeca reaching to the ovarian level.

Definitive host. Chick (experimental).

Site of infection. Intestine.

Distribution. Not known (? Yucatán).

References from Mexico. Scholz *et al.* (1997a).

Specimens deposited. IPCAS D-350.

Comments. Stein (1968) fed chicks upon viscera (liver and spleen) of the poeciliid *Mollienisia latipinna* (= *Poecilia latipinna*) from Florida and found adults of *A. (P.) macrostoma*. However, no description or illustrations were provided and the morphology of metacercariae is still unknown. Observations of Stein (1968) cast doubts upon the site of infection of metacercariae *A. (P.) macrostoma* from Yucatán, supposed to be encysted in the gills (Scholz *et al.*, 1997a). It seems that they may have been encysted in the internal organs rather than directly in the gill filaments.

Dronen (1985) reported adults of *A. (P.) macrostoma* from the intestine of the roseate spoonbill (*Platalea ajaja*) from Texas that may be the principal definitive host. Trematodes found in the same host from Florida and identified by Sepúlveda *et al.* (1994) as *Phagicola longa* (USNPC 83030) may also be conspecific with *A. (P.) macrostoma* (unpublished data) but they lack circumoral spines to confirm species identification.

Published data on the occurrence of *A. (P.) macrostoma* suggest its distribution being limited to southeastern USA and Mexico (Robinson, 1956; Stein, 1968; Dronen, 1985; Scholz *et al.*, 1997a).

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

(figure 1G)

Metacercaria

Morphology. Metacercariae were described by Salgado-Maldonado and Aguirre-Macedo (1991: 396–398, 400; figure 2), Aguirre-Macedo and García-Magaña (1994: 19–20; figure 8a, b; all as *Phagicola angrense*), Scholz *et al.* (1995—as *Ascocotyle (Phagicola)* sp. 2: 181–182; figure 6, 7A) and Scholz *et al.* (1997a: 168; figure 3D–J). The most typical characters are pyriform shape of body; indistinct preoral lobe; very short posterior appendage; fine circumoral spines forming one complete row of 16 (exceptionally 15 or 17) spines and four (rarely three to six) additional spines; long intestinal caeca curved medially around ventral sucker and reaching to excretory bladder; and well-developed gonotyl with numerous (about 15) refractile bodies (Scholz *et al.*, 1997a).

Second intermediate hosts. *Astyanax fasciatus* (Characidae); *Cichlasoma argentea*, *C. aureum*, *C. belone* (Allgayer) (= *C. coeruleus* (Stawikowski and

Werner)), *C. fenestratum*, *C. friedrichstahli*, *C. geddesi*, *C. helleri*, *C. intermedium*, *C. managuense*, *C. meeki*, *C. nourissati*, *C. octofasciatum*, *C. pasionis*, *C. pearsei*, *C. salvini*, *C. synspilum*, *C. urophthalmus*, *Petenia splendida* (Cichlidae); *Gambusia yucatana*, *Poecilia petenensis*, *P. velifera*, *Xiphophorus* sp. (Poeciliidae).

Site of infection. Intestinal wall, gonads, liver, kidney, spleen, mesenteries, muscles, swimbladder, rarely gills, heart and brain.

Distribution. Campeche (Champotón, El Vapor, El Viento, Estero Pargo, La Pera, Palizada, Santa Gertrudis); Chiapas (Cedros); Quintana Roo (Box Toro, Cabañas, Cenote Azul, Escondido, Gran Cenote, La Unión, Laguna Guerrero, Laguna Ocón, Los Cuates, Mahahual, Noh-Bek, Ramonal, Raudales, Río Hondo, Valle Hermoso); Tabasco (Balancán, Camellones Chontales, El Espino, El Guanál, El Yucateco, Jonuta, Las Ilusiones, Puyacatengo, Teapa, Tenosique, Yumká); Veracruz (Catemaco); Yucatán (Celestún, Chaamac, Chek-há, Chen-há, Dzibilchaltún, Dzonot Cervera, Framboyán, Hodz-ob, Mitza, Noc-choncunchey, Petentuche, Progreso, Río Lagartos).

References from Mexico. Salgado-Maldonado and Aguirre-Macedo (1991); Jimenez-García (1993); Aguirre-Macedo and García-Magaña (1994—all authors as *Phagicola angrense*); Scholz *et al.* (1995—as *Ascocotyle (Phagicola)* sp. 2); Salgado-Maldonado *et al.* (1997); Scholz *et al.* (1997a); Scholz and Vargas-Vázquez (1998); Vidal-Martínez *et al.* (1998, 2000); present study.

Specimens deposited. CHCM-123, CNHE 3728, IPCAS D-341, USNPC 90194.

Adult

Morphology. Adult worms from Mexico were described and illustrated by Salgado-Maldonado and Aguirre-Macedo (1991), Aguirre-Macedo and García-Magaña (1994: 20; figure 8c), and Scholz *et al.* (1997a: 168–170; figure 4). Scholz *et al.* (1997a) counted 16+4 circumoral spines in most (70%) of specimens studied; only a few trematodes possessed different spination patterns (14+4; 15+4; 16+5; 16+6; 17+4; 17+5).

Definitive hosts. *Ardea herodias*, *Buteogallus anthracinus*, *Casmerodius albus* (natural), chicks, laboratory mouse (experimental).

Site of infection. Intestine.

Distribution. Yucatán (Celestún).

References from Mexico. Salgado-Maldonado and Aguirre-Macedo (1991); Aguirre-Macedo and García-Magaña (1994)—all as *Phagicola angrense*; Scholz *et al.* (1997a); present study.

Specimens deposited. CHCM-359, IPCAS D-340, USNPC 86809, 90195.

Comments. Cichlids, in particular *Cichlasoma urophthalmus*, are the most suitable hosts of this trematode that belongs to the most widely distributed species of fish parasites in southeastern Mexico. Its metacercariae are also common in perciform fish in the northern part of the Gulf of Mexico (Mississippi, Florida) (Font *et al.*, 1984b).

Comments. The type host of *A. (P.) nana* is the arctic fox, *Alopex lagopus* (Linnaeus), and several mammals such as opossum, raccoon, Syrian hamster or mouse have been reported as experimental hosts (Ransom, 1920; Font *et al.*, 1984b). However, most adults obtained from natural definitive hosts were found in fish-eating birds such as *Ardea herodias*, *Buteogallus anthracinus*, *Casmerodius albus*, *Ixobrychus exilis* (Gmelin) and *Sula bassana* (Linnaeus) (Font *et al.*, 1984b; Salgado-Maldonado and Aguirre-Macedo, 1991; Scholz *et al.*, 1997a; Sepúlveda *et al.*, 1999).

Cercariae of *A. (P.) nana* were found in the snail *Pyrgophorus coronatus* from Yucatán (Ditrich *et al.*, 1997).

Ascocotyle (Phagicola) sp.
(figure 8)

Metacercaria

Morphology. (Morphology based on one specimen from *Cichlasoma urophthalmus*.) Body pyriform, markedly tapering anteriorly, 1240 long and 544 wide. Small unicellular glands situated laterally at acetabular level. Preoral lobe well-developed. Oral sucker subterminal, 78 long and 102 wide, armed with single row of 20 spines. Posterior appendage long, narrow and curved. Prepharynx 171 long. Pharynx strongly muscular, large, 71 long and 76 wide. Oesophagus very short. Intestinal caeca long, narrow, reaching to testes. Ventral sucker slightly postequatorial, 84 long and 92 wide. Sucker ratio 1:0.98. Testes large, symmetrical, near posterior extremity, 146–172 long and 182–198 wide. Ventrogenital sac

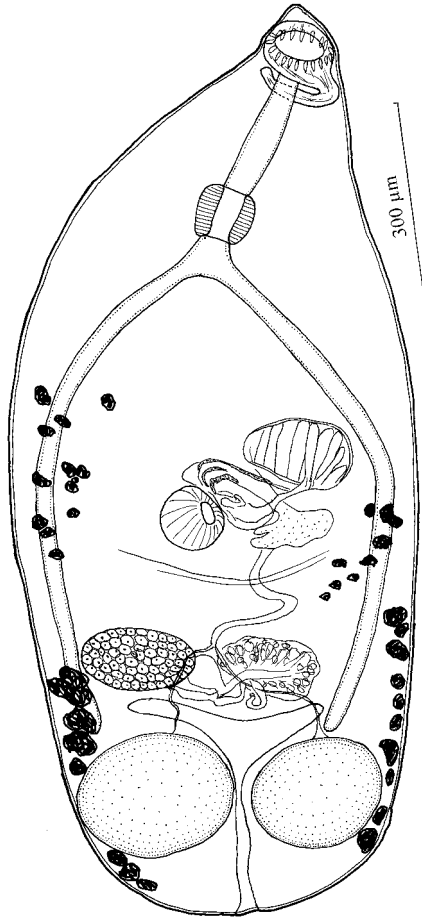


FIG. 8. *Ascocotyle (Phagicola) sp.* Excysted metacercaria from fins of *Cichlasoma urophthalmus*, El Vapor, Campeche.

well-developed, containing large gonotyl 81 long and 154 wide, with 10 large, finger-like retractile bodies. Ovary transversely oval, pretesticular. Vitelline follicles well-developed, lateral, between ovary and posterior extremity. Excretory bladder Y-shaped; excretory pore terminal.

Second intermediate host. *Cichlasoma urophthalmus* (Cichlidae).

Site of infection. Fins.

Distribution. Campeche (El Vapor).

References from Mexico. Vidal-Martínez *et al.* (2000); present data.

Specimens deposited. CHCM-30.

Remarks. The metacercaria found in fins (?) closely resembles those of *A. (L.) mcintoshi* as described above in all but one morphological features. The only difference is in spination of the oral sucker: *A. (L.) mcintoshi* possesses two complete rows of circumoral spines whereas the present metacercaria has only one circle, i.e. its oral sucker is armed with only 20 spines instead of 38–42 in *A. (L.) mcintoshi*. Both taxa also differ in the site of location (fins versus mesentery) and the second intermediate host (Cichlidae versus Poeciliidae). Therefore, the specimen studied is provisionally identified as *Ascocotyle (Phagicola)* sp. until new material is available.

Centrocestus formosanus (Nishigori, 1924)
(figure 9A—C)

Metacercaria

Morphology. The most detailed description of metacercariae from Mexico was provided by Arizmendi (1992: 5–6; figure 3).

Second intermediate hosts. Scholz and Salgado-Maldonado (2000) reported 39 fish species of the following families: Atherinidae, Characidae, Cichlidae, Cyprinidae, Eleotridae, Gobiidae, Goodeidae, Ictaluridae, Mugilidae and Poeciliidae. The eleotrids such as *Gobiomorus dormitor* Lacépède and *G. maculatus* (Günther) and mugilids such as *Agonostomus monticola* (Bancroft in Griffith and Smith) were the most susceptible hosts, harbouring up to 6000 metacercariae (Scholz and Salgado-Maldonado, 2000—table 2).

Site of infection. Gills.

Distribution. Scholz and Salgado-Maldonado (2000) listed localities in 10 Mexican states (Colima, Guanajuato, Hidalgo, Jalisco, Michoacán, Morelos, San Luis Potosí, Tabasco, Tamaulipas, Veracruz) where *C. formosanus* metacercariae were found. Recent findings from Río Grande—Guelatao (State of Oaxaca), Río Atoyac and Santa María Tecomavaca (Puebla), and Ciudad Obregón (Sonora) extend the distribution of *C. formosanus* to 13 Mexican states.

References from Mexico. Arizmendi (1992); Amaya-Huerta and Almeyda-Artigas (1994); Salgado-Maldonado *et al.* (1995); Vélez-Hernández *et al.* (1998); Scholz and Salgado-Maldonado (2000), present study.

Specimens deposited. CNHE 3708, IPCAS D-271.

Adult

Morphology. Experimentally recovered adults were described by Arizmendi (1992: 6–8; figure 4) and Salgado-Maldonado *et al.* (1995). Because of some discrepancies between biometrical data of these authors, basic measurements of six hot formalin-fixed specimens are provided: body flask-shaped, 370–460 long and 190–240 wide. Oral sucker 40–47 long and 47–57 wide, armed with a total of 32 circumoral

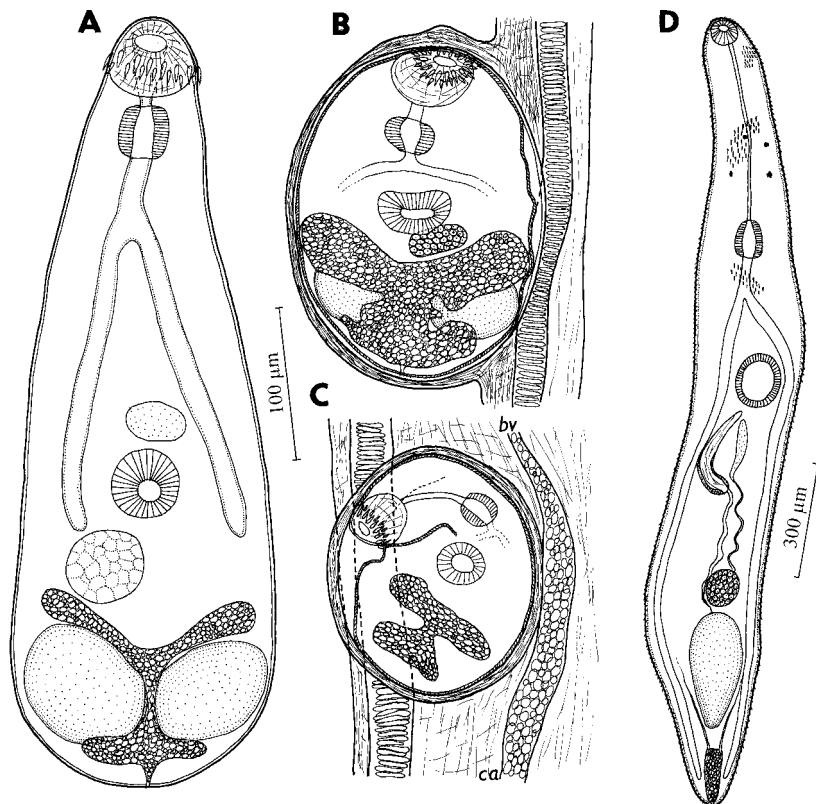


FIG. 9. (A–C) *Centrocestus formosanus*. Metacercariae from the gills of *Poecilia mexicana*, Río La Palma, Veracruz (A) and *Xiphophorus* sp., Río Las Máquinas, Veracruz (B, C). (D) Heterophyidae gen. sp. (= *Haplorchoides* sp. of Scholz and Vargas-Vázquez, 1998). Metacercaria from the gills of *Cichlasoma meeki*, Río Hondo, Quintana Roo. (A, D) excysted metacercaria, ventral view; (B, C) encysted metacercaria. Note position of metacercarial cyst close to the cartilage (ca; bv, blood vessel) of gill filaments.

spines arranged in two complete circles of 16 spines each. Anterior spines 10–14 long and 3–5 wide; posterior spines 10–12 long and 3 wide. Prepharynx 12–20 long; pharynx 37–42 long and 27–35 wide. Ventral sucker 42–55 long and 47–55 wide. Sucker ratio 1: 0.92–1.17. Testes 52–72 long and 60–120 wide. Ovary 45–67 long and 60–112 wide. Seminal receptacle 42–57 long and 45–67 wide. Eggs 32 ± 2 (27–35; $n=26$) long and 17 ± 2 (15–22) wide.

Definitive hosts. *Butorides striatus* (Linnaeus) (natural), chicks and mice (experimental).

Site of infection. Intestine.

Distribution. Hidalgo (Tezontepec de Aldama).

References from Mexico. Arizmendi (1992); Amaya-Huerta (1995—unpublished MSc thesis); Salgado-Maldonado *et al.* (1995); Scholz and Salgado-Maldonado (2000).

Specimens deposited. BMNH 2000.6.1.10, CHCM-245, CNHE 3709, IPCAS D-419, USNPC 88539.

Comments. *Centrocestus formosanus* was described from Taiwan (then Formosa)

and it was imported to Mexico most likely in 1979 (López-Jiménez, 1987). It has spread rapidly and is now one of the most abundant fish parasites in several regions (see Scholz and Salgado-Maldonado, 2000 for review). The thiarid snail of Asian origin, *Melanooides tuberculata* (Müller), serves as the first intermediate host in Mexico (Arizmendi, 1992; Salgado-Maldonado *et al.*, 1995; Scholz and Salgado-Maldonado, 2000).

****Euhaplorchis californiensis* Martin, 1950**

Metacercaria

Morphology. No data are available.

Second intermediate host. *Fundulus grandissimus* (Cyprinodontidae).

Site of infection. Brain.

Distribution. Yucatán (Chelém).

References from Mexico. Present study.

Specimens deposited. None.

Comments. During a study on the parasites of fish from the Chelém lagoon near Progreso, Yucatán, carried out in January 1994, heterophyid metacercariae were found in the brain of four of 15 *Fundulus grandissimus* (mean intensity 9 metacercariae; range 5–16 specimens). Metacercariae fitted in their morphology, in particular the presence of a conspicuous, pyriform gonotyl armed with anteriorly directed sclerites and the site of infection, into the diagnosis of the species *Euhaplorchis californiensis* described by Martin (1950a) from the brain of *Fundulus parvipinnis* in California.

In November and December 1999, 37 *F. grandissimus* from the same locality were examined but no metacercariae were found. Since no specimens found in January 1994 were preserved, no description, measurements or illustrations based on Mexican material are provided in this paper. *Fundulus grandissimus* represents a new second intermediate host of the trematode that is reported from Mexico for the first time.

Martin (1950a) described the life cycle of this trematode, reporting the prosobranch snail *Cerithidea californica*, harbouring rediae and oculate, parapleurolophocercous cercariae, to serve as the first intermediate, and chicks and Californian gull (*Larus californicus* Lawrence) as experimental definitive hosts, respectively.

***Galactosomum puffini* Yamaguti, 1941**

(figure 5E, F)

Adult

Morphology. Bravo-Hollis (1966: 125–127; figures 1–3) described adult specimens.

Definitive host. *Larus occidentalis* Audubon.

Site of infection. Intestine.

Distribution. Baja California (Isla Rasa).

References from Mexico. Bravo-Hollis (1966).

Specimens deposited. CNHE 804.

Comments. *Galactosomum puffini* is a widely distributed parasite of fish-eating birds, above all of gulls (Laridae) and pelecans (Pelecanidae), reported from Japan, European part of the ex-USSR, USA, Puerto Rico, Panama and Colombia (Hutton, 1964; Yamaguti, 1971; Pearson, 1973; Rietschel and Werding, 1978). In Florida,

other species of *Galactosomum*, namely *G. cochleariforme* (Rudolphi, 1819), *G. spinetum* (Braun, 1901) and *Galactosomum* sp., were found in fish-eating birds and metacercariae of *G. spinetum* in the fish *Hyporhamphus unifasciatus* (Ranzani) (Hutton, 1964).

****Haplorchis pumilio*** (Looss, 1896)
(figure 10)

Metacercaria

Morphology. (Morphology based on five metacercariae from *Gobiomorus maculatus* and one metacercaria from *Dormitator latifrons*.) Cyst small, oval. Body elongate, 337–600 long and 113–184 wide, entirely covered with scale-like tegumental spines with rounded base and almost straight distal end. Remnants of eye-spots

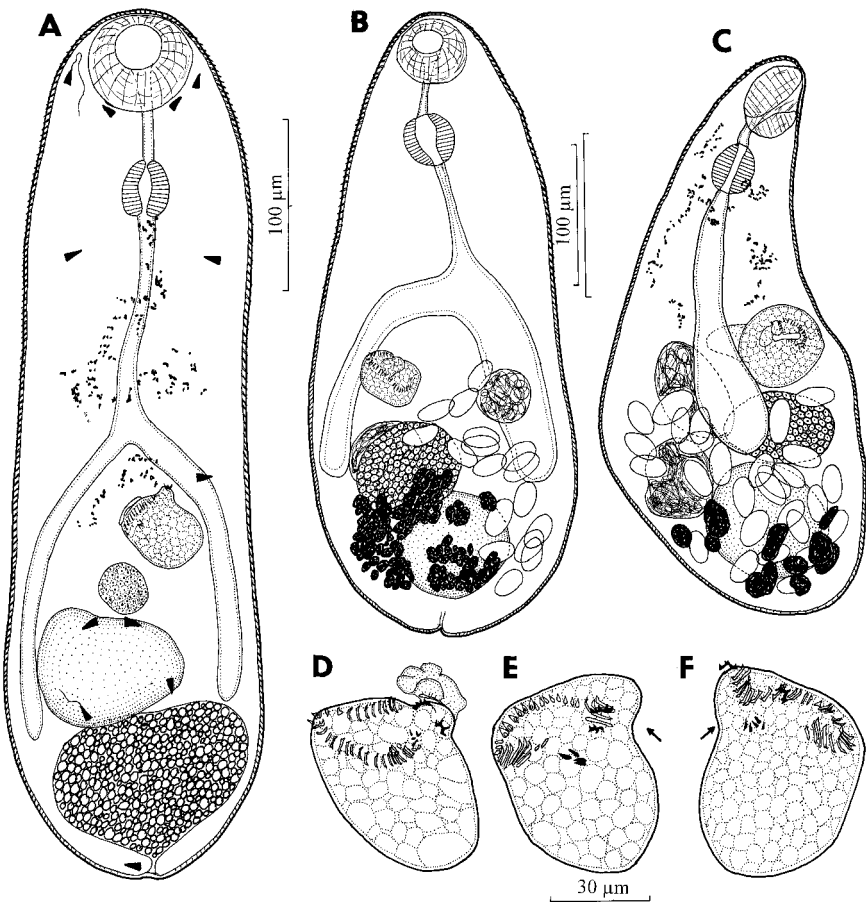


FIG. 10. *Haplorchis pumilio*. Metacercariae from the musculature of gill apparatus of *Dormitator latifrons* (A, E) and *Gobiomorus maculatus*, Marismas de Chalacatepec, Jalisco (D, F), and adults from mouse experimentally infected with fins of *Cichlasoma managuense*, El Espino, Tabasco (B) and gills of *Cichlasoma salvini*, Río Puyacatengo, Tabasco (C), 6 days post infection. (A) Total view of excysted metacercaria; (B, C) total views of adults, dorsally (B) and laterally (C); (D–F) ventral sucker, ventrally (D, E) and dorsally (F); longitudinal axis of the body indicated by arrow.

dispersed between pharynx and ventral sucker. Oral sucker large, spherical, subterminal, 50–62 long and 54–67 wide, without spines. Prepharynx 5–57 long; pharynx spherical, 32–42 long and 25–30 wide; oesophagus long. Intestinal caeca wide, reaching to testis, containing discoidal corpuscles (bodies). Ventral sucker reduced, feebly muscular, forming part of ventrogenital complex, slightly postequatorial, 39–40 long and 37–52 wide. Sucker ratio 1: 0.55–0.80. Ventral sucker armed with 28–31 concave bar-like sclerites with pointed ends, forming incomplete circle interrupted dorsally; anterolateral lobes with sclerites with fused bases; mid-dorsal lobe armed with seven to nine simple spines. Mouth of ventrogenital sac slit-like, perpendicular to body axis. Testis single, widely oval, postacetabular, 50–75 long and 62–92 wide. Ovary spherical, situated between ventral sucker and testis. Excretory bladder sacciform, voluminous, filled with small, dark granules. Excretory pore terminal.

Second intermediate hosts. *Cichlasoma helleri*, *C. managuense*, *C. salvini*, *Petenia splendida* (Cichlidae); *Dormitator latifrons*, *Gobiomorus maculatus* (Eleotridae).

Site of infection. Musculature of gill arches, head and fins.

Distribution. Jalisco (Marismas de Chalacatepec); Tabasco (El Espino, Río Puyacatengo, Yumká).

References from Mexico. Present study.

Specimens deposited. CNHE 3934, IPCAS D-279, USNPC 90186.

Adult

Morphology. (Morphology based on three hot formalin-fixed specimens from experimentally infected mouse; six DPI.) Body elongate, slightly tapering towards anterior extremity, 350–520 long and 180–210 wide, covered with serrate, scale-like tegumental spines. Oral sucker subterminal, 40–52 long and 35–57 wide; without circumoral spines. Prepharynx 7–22 long; pharynx oval to spherical, 32–40 long and 32–35 wide; oesophagus longer than prepharynx. Intestinal caeca long, reaching to testis. Ventral sucker feebly developed, recessed, slightly postequatorial, 37–52 long and 40–52 wide; sucker opening small, slightly anterolateral to sucker midline. Sucker ratio 1: 0.74–1.30. Anteroventral margin of ventral sucker armed with incomplete cirlet of 30–36 small bar-like sclerites with concave base and pointed lateral end; two groups of sclerites with fused bases on anterolateral lobes and a group of small simple spines on mid-dorsal lobe. Testis single, anterior to posterior extremity, 60–80 long and 67–105 wide. Seminal vesicle posterolateral to lateral to ventral sucker, 70 long and 40 wide. Ventrogenital sac formed; gonotyl absent. Mouth of ventrogenital sac large, slit-like. Ovary dextral, nearly spherical, anterodextral to testis, 30–50 long and 57–68 wide. Seminal receptacle voluminous, dorsal to ovary, 26–47 long and 32–42 wide. Uterus sinuous; uterine loops anteriorly reaching to ventral sucker, posteriorly near to posterior extremity. Vitelline follicles in post-ovarian region. Eggs operculate, 31 ± 1 (29–32; $n = 15$) long and 19 ± 1 (17–20) wide.

Definitive host. Chicks (experimental).

Site of infection. Intestine.

Distribution. Not known.

References from Mexico. Present study.

Deposition of specimens. CNHE 3730, IPCAS D-256, USNPC 90187.

Comments. Specimens from Mexico, both metacercariae and adults, correspond in all diagnostic features such as the armature of the ventrogenital complex, to *H. pumilio* (see Pearson, 1964). This trematode was originally described from Egypt

and it has been found in many fish-eating birds and mammals in North Africa, Asia and Australia (Pearson, 1964). In South-East Asia, *H. pumilio* belongs to the 'small intestinal flukes', i.e. trematodes causing human fish-borne trematodoses (Velasquez, 1982).

The present findings represent the first record of this parasite from America. It was probably introduced to Mexico with the thiarid snail *Melanooides tuberculata* similarly to *Centrocestus formosanus*. Scholz *et al.* (2000) found cercariae of *H. pumilio* in *M. tuberculata* collected in the Cuitzmala River situated very near from the locality where metacercariae of *H. pumilio* occurred.

Heterophyidae gen. sp. (*Haplorchoides* sp. of Scholz and Vargas-Vázquez, 1998)
(figure 9D)

Metacercaria

Morphology. (Morphology based on six flattened specimens from *Cichlasoma meeki*.) Cyst large, oval, thin-walled. Metacercaria elongate, tapering to both ends, 1273–1964 long and 280–343 wide, entirely covered with simple, long (length 9–13) and slender (width 2) tegumental spines. Two pairs of eye-spots at prepharyngeal level. Oral sucker small, subterminal, spherical, 48–77 long and 54–83 wide. Ventral sucker spherical, postequatorial, 84–122 long and 99–122 wide, with opening armed with fine simple spines, 2 long, arranged in two to three irregular circles. Sucker ratio 1: 1.50–2.06. Prepharynx variable in length, 176–462 long; pharynx large, heart-shaped, 80–98 long and 67–83 wide; oesophagus shorter than prepharynx. Intestinal caeca narrow and very long, reaching to posterior extremity. Single testis large, oval, intercaecal, anterior to excretory bladder, 186–212 long and 109–134 wide. Primordium of ovary oval, between ventral sucker and testis. Primordia of cirrus sac slightly curved, posterolateral to ventral sucker. Excretory bladder small, sacciform, filled with numerous dark granules. Excretory pore terminal.

Second intermediate hosts. *Strongylura timucu* (Walbaum) (Belonidae); *Centropomus undecimalis* (Bloch) (Centropomidae); *Cichlasoma aureum*, *C. meeki* (Cichlidae); *Sphaeroides testudineus* (Linnaeus) (Tetraodontidae).

Site of infection. Gills, fins, muscles.

Distribution. Campeche (La Caleta—Ciudad del Carmen); Quintana Roo (Ramonal, Río Hondo); Yucatán (Celestún).

References from Mexico. Scholz and Vargas-Vázquez (1998); Vidal-Martínez *et al.* (2000); present study.

Specimens deposited. CHCM-360, IPCAS D-385.

Comments. Metacercariae markedly differ from those of other trematodes in possessing an elongate body covered with very long, slender tegumental spines, a small oral sucker, much smaller than the acetabulum, a very long prepharynx, a heart-shaped pharynx and a single testis. In these features, the metacercariae best fit into the diagnosis of the genus *Haplorchoides* Chen, 1949 as defined by Yamaguti (1971). However, they differ from all species of *Haplorchoides* in having a well-developed (not reduced) ventral sucker lacking any sclerotized structures such as sclerites or spines, typical of *Haplorchoides* (see Yamaguti, 1971). Generic appurtenance of these metacercariae remains unclear and adult worms are necessary to assess their taxonomic position within the Heterophyidae.

**Phocitrema ovale* Martin, 1950
(figure 11)

Metacercaria

Morphology. (Morphology based on 16 live metacercariae from *Fundulus grandis-simus*.) Cyst almost spherical, thin-walled, 138–165 long and 128–163 wide. Excysted metacercaria elongate, 301–383 long and 138–163 wide, covered with conspicuous scale-like tegumental spines, pectinate in anterior third of body and decreasing in size posteriorly. Eye-spot remnants scattered between pharynx and acetabulum, sometimes present even in postacetabular region. Numerous cells with granular

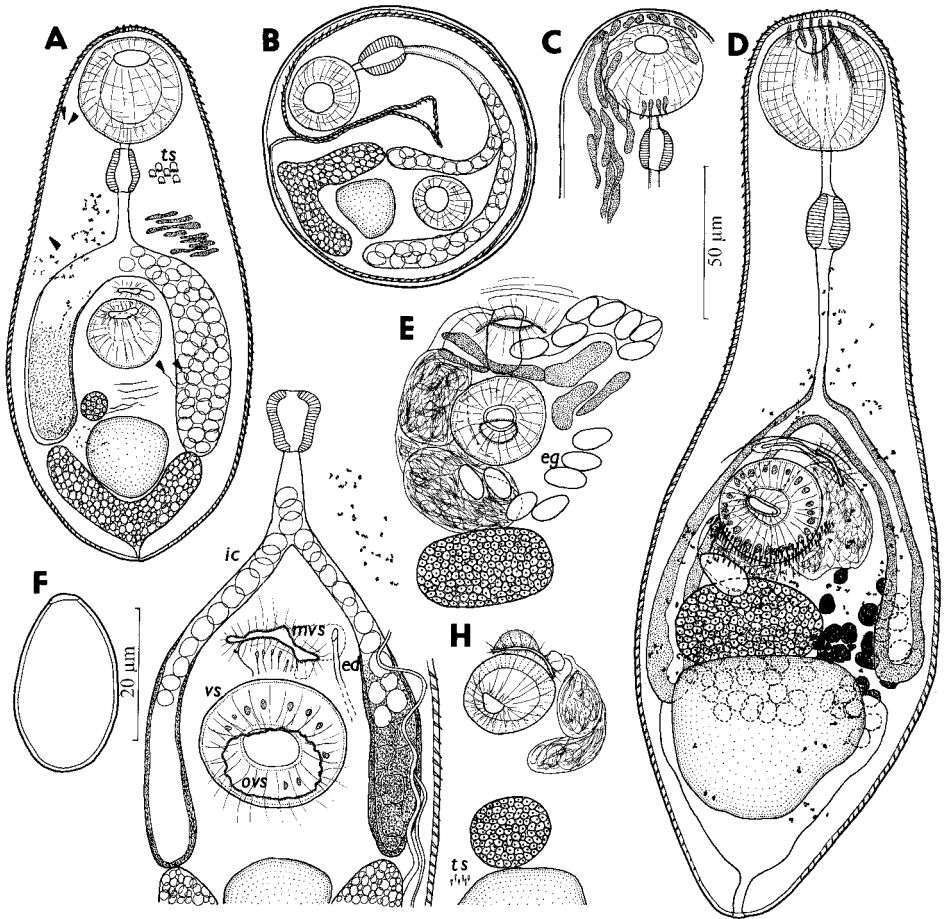


FIG. 11. *Phocitrema ovale*. Metacercariae from scales of *Fundulus grandis-simus*, Chelém lagoon, Yucatán (A, B, G) and adults from chicks experimentally infected with scales of *F. grandis-simus*, 2 and 4 days post infection (C–F, H). (A, D) Total view of excysted metacercaria and adult, respectively; ventrally; (B) encysted metacercaria; (C) detail of gland cells around oral sucker; (E, H) acetabular region with terminal genitalia, dorsal (E) and ventral (H) views; (F) egg; (G) intestinal caeca and acetabular region, ventrally; note granulation of cells of the intestinal wall. (A–C, E, G, H) Free-hand illustrations based on observations of live specimens; not to scale. Abbreviations: ovs, opening (mouth) of ventral sucker; ts, tegumental spines; for other abbreviations see figure 2.

content lateral to oesophagus and intestinal caeca. Oral sucker spherical to widely oval, 48–58 long and 48–68 wide. Prepharynx very short; pharynx strongly muscular, 25–32 long and 24–30 wide; oesophagus longer than prepharynx. Intestinal caeca long and wide, reaching to anterior arms of excretory bladder, filled with discoidal corpuscles; intestinal wall in posterior part with granular content (figure 11G). Ventral sucker spherical, slightly postequatorial, embedded in parenchyma, 46–50 long and 48–52 wide. Sucker ratio 1: 0.81–1.00. Testis single, large, near posterior extremity. Ventrogenital sac formed, thick-walled, anterior to ventral sucker. Ovary anterodextral to testis. Excretory bladder V-shaped, with short arms, reaching to anterior half of testis, containing numerous dark granules. Flame cell pattern not determined but cells apparently in pairs, with first pair posterolateral to oral sucker and one pair posterolateral to acetabulum.

Second intermediate hosts. *Floridichthys polyommus*, *Fundulus grandissimus*, *F. persimilis* (Cyprinodontidae).

Site of infection. Scales (internal side).

Distribution. Yucatán (Chelém Lagoon).

References from Mexico. Present study.

Specimens deposited. None.

Adult

Morphology. (Morphology based on eight hot formalin-fixed specimens from chicks infected with metacercariae from scales of *Fundulus grandissimus*, 4 days post infection; measurements of seven flattened specimens in parentheses.) Body small, pyriform, 320–370 (390–580) long and 170–250 (192–230) wide, covered with scale-like tegumental spines. Pectinate spines with four to six teeth covering ventral surface except for periacetabular zone, decreasing in size and less dense posteriorly. Dorsal side covered with spines up to anterior margin of testis. Remnants of eye-spots scattered throughout body between pharynx and posterior extremity. Oral sucker widely oval, 45–50 (52–70) long and 47–52 (49–75) wide. Sucker surrounded by numerous elongate cells with granular contents; four small gland cells present near base of oral sucker (figure 11C). Prepharynx 12–22 (7–60) long; pharynx strongly muscular, 17–22 (22–30) long and 17–22 (17–27) wide; oesophagus longer than prepharynx. Intestinal caeca thick-walled, narrow and long, reaching posteriorly to excretory bladder. Ventral sucker spherical, slightly postequatorial, 39–40 (44–59) long and 40–47 (42–52) wide, recessed in parenchyma, with small opening situated slightly dextral to median line of body, separated from mouth of ventrogenital sac. Tegument at level of posterior margin of ventral sucker covered with semilunar circle of narrow, simple spines arranged in two to three irregular rows. Sucker ratio 1: 0.81–0.95 (1: 0.64–0.84). Testis single, 47–63 (80–105) long and 52–72 (90–92) wide, in posterior third of body. Seminal vesicle postero- to laterodorsal to ventral sucker, voluminous, bipartite, with feebly separated chambers often overlapping one another. Ventrogenital sac well-developed, thick-walled, opening by slit-like mouth, anterosinistral to ventral sucker; gonotyl absent. Ovary just anterior to testis, slightly shifted dextral to median line of body, 32–42 (36–50) long and 45–65 (52–80) wide. Seminal receptacle spherical, anterolateral to testis (32–42 long and 32–42 wide). Vitelline follicles small, laterodorsal to ovary and testis, anteriorly reaching to posterior margin of acetabulum, posteriorly not overlapping testis. Uterus tubular; uterine loops filling most space between caecal bifurcation and posterior extremity. Eggs operculate, 25.0 ± 1.5 (range 23–28; $n = 36$) (20–28) long and 15.1 ± 1.3 (range

14–17.5) (10–16) wide. Excretory bladder V-shaped with short arms, not reaching to pretesticular level, containing numerous dark granules.

Definitive hosts. Chick, duck (experimental).

Site of infection. Intestine.

Distribution. Not known.

References from Mexico. Present study.

Specimens deposited. BMNH 2000.6.1.11, CHCM-351, CNHE 3936, IPCAS D-395, USNPC 90196.

Comments. Metacercariae were found exclusively in scales of three species of cyprinodontid fish that represent new second intermediate hosts. The parasite was infrequent in *Floridichthys polyommus* but very common in both species of *Fundulus*. The morphology of the metacercariae corresponds to that of metacercariae of *Phocitrema ovale* found in experimentally infected *Atherinopsis californiensis* Girard and *Fundulus parvipinnis* (Martin, 1950b).

Adults from experimental hosts were almost identical in their morphology and measurements, including the egg size, to those described by Martin (1950b) as *Phocitrema ovale*. There was only a slight difference in the shape of the body that was reported to be oval to pyriform by Martin (1950b: figure 1) whereas the trematodes from Mexico were elongate and pyriform, thus not corresponding to the specific name ‘*ovale*’. However, this difference may be related to different fixation of worms.

Martin (1950b: figure 1) illustrated the mouth of the ventral sucker to be common with that of the ventrogenital sac. In fact, both openings are distinctly separated one from another as observed both in living and fixed metacercariae and adults (figure 11D, G).

Natural definitive hosts of *P. ovale* are not known and adults were obtained only from experimentally infected hosts (Martin, 1950b; Yoshino, 1972) in California. Oculopleurolophocercous cercariae of *P. ovale* were found in *Cerithidea californica* (Prosobranchia). The present data expand the range of distribution of *P. ovale* to the Atlantic coast of Mexico, from which it is reported for the first time.

****Pygidiopsis pindoramensis*** (Travassos, 1929)
(figure 12)

Metacercaria

Morphology. (Morphology based on 12 metacercariae from *Poecilia catemaconis*, three from *Xiphophorus helleri* Heckel and one from *Poecilia mexicana*; measurements of flattened specimens fixed with GAP in parentheses.) Cyst widely oval to almost spherical, (230–340) long and (230–310) wide, with thick external wall and thin, hyaline internal wall. Body pyriform, 280–370 (500–650) long and 150–280 (250–310) wide, covered with scale-like tegumental spines, with convex base and serrate distal end, overlapping one another. Spines covering almost completely ventral side except for small area around subterminal excretory pore; dorsally spines reaching only to testicular level. Remnants of eye-spots at pharyngeal level. Oral sucker spherical, without posterior appendage, 30–38 (42–58) long and 30–40 (42–57) wide, with one complete row of 16 fine circumoral spines and four additional spines on dorsal side. Prepharynx 36–67 (32–97) long; pharynx oval, 26–32 (38–47) long and 20–28 (37–45) wide; oesophagus longer than prepharynx. Intestinal caeca long and narrow, surrounding ventral sucker, slightly curved medially in posterior part, reaching to ovarian level and containing discoidal corpuscles. Ventral sucker

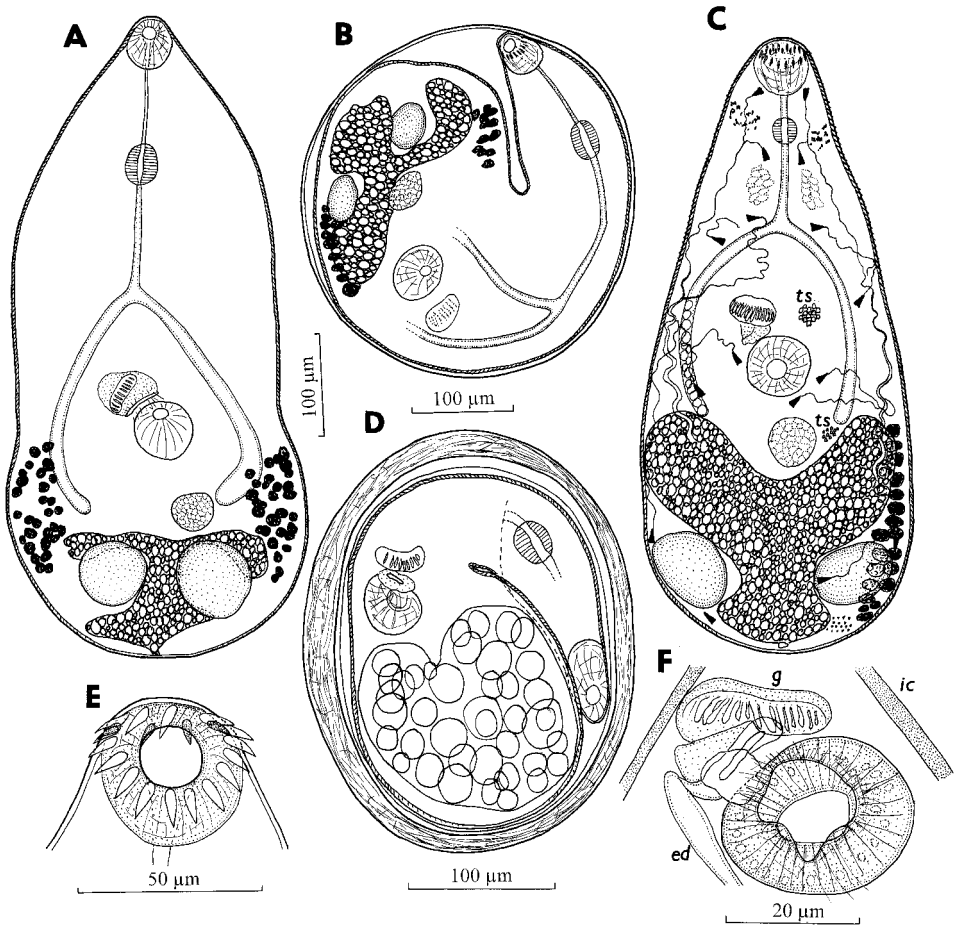


FIG. 12. *Pygidiopsis pindoramensis*. Metacercariae from the gill arches of *Poecilia catemacensis*, Catemaco Lake, Veracruz (A–C), fatty body of *Poecilia mexicana*, Balzapote stream, Los Tuxtlas, Veracruz (D, E), and mesentery of *Xiphophorus helleri.*, Catemaco Lake, Veracruz (F). (A, C) Total view of excysted metacercaria, dorsally (ts, tegumental spines); (B, D) encysted metacercaria (thick-walled external cyst wall not figured in B); (E) anterior end, ventral view; note 16 spines in one complete row and four additional spines on the dorsal side (dotted); (F) terminal genitalia, dorsally. (C) Free-hand schematic drawing.

spherical, slightly postequatorial, 32–37 (48–71) long and 37–43 (60–65) wide. Sucker ratio 1: 1.00–1.28 (1: 1.09–1.42). Testes symmetrical, close to posterior extremity, 23–35 (34–74) long and 24–45 (44–75) wide. Ventrogenital sac formed, anterosinistral to acetabulum, containing widely oval gonotyl with 13–17 narrow refractile bodies. Mouth of ventrogenital sac irregularly oval, opening anteroventral to cavity of ventral sucker. Ovary almost spherical, posterior to acetabulum, 18–25 (25–52) long and 26–31 (33–55) wide. Primordia of vitelline follicles forming two bands lateral to testes between ventral sucker and posterior extremity. Flame cell pattern 2 [(2+2)+(2+2)]=16. Excretory bladder Y-shaped with short and wide arms or X-shaped with feebly developed posterior lobes, filled with numerous small, dark granules. Excretory pore subterminal.

Second intermediate hosts. *Poecilia catemacensis*, *P. mexicana*, *Xiphophorus helleri*. (Poeciliidae).

Site of infection. Gill arches, heart, fatty body.

Distribution. Veracruz (Balzapote, Catemaco).

References from Mexico. Present study.

Specimens deposited. CHCM-355, CNHE 3933, IPCAS D-444.

Comments. Metacercariae of *P. pindoramensis* were previously found in the mesentery and ovary of cyprinodontid fish *Phalloceros caudimaculatus* (Hensel) and *Cnesterodon decemmaculatus* from Argentina (Ostrowski de Núñez, 1974).

Ostrowski de Núñez (1976) reported cercariae of *P. pindoramensis* from the prosobranch snail *Littoridina piscium* d'Orbigny from Argentina. The same author (Ostrowski de Núñez, 1996) described another species of *Pygidiopsis*, for which the name *P. australis* was proposed. This species cannot be distinguished in metacercarial or adult stage from *P. pindoramensis* and differs only in cercarial morphology (the arrangement of penetration glands and the absence of pigment granules).

Since the actual distribution of *P. australis* is not known and *P. pindoramensis* has been reported from North and South America (see Ostrowski de Núñez, 1996), the specimens from Mexico are tentatively considered to belong to the latter species.

Discussion

In the present review, 20 species of Heterophyidae are reported from Mexico, either as metacercariae encysted in fish or as adults in the intestine of fish-eating birds and mammals. Seven of these species, *Ascocotyle (Ascocotyle) gemina*, *A. (Leighia) mcintoshi*, *A. (Phagicola) ampullacea*, *Euhaplorchis californiensis*, *Haplorchis pumilio*, *Phocitrema ovale* and *Pygidiopsis pindoramensis*, are reported from this country for the first time. In the checklist of the helminth parasites of continental water fish of Mexico, Pérez-Ponce de León *et al.* (1996) listed metacercariae of only 10 species of heterophyid trematodes. In addition, most of them were not identified to species level or were misidentified.

Because of the number of incorrectly or not specifically identified species of the Heterophyidae from Mexico and confusions in the taxonomy of this group in the literature, a brief survey of these records is added with remarks on individual species reported.

Phagicola angrese of different authors (see below), *nec* Travassos, 1916

As demonstrated by Scholz *et al.* (1997a), metacercariae from the internal organs of cichlid fish from southeastern Mexico had been misidentified as *Phagicola angrese* (Travassos, 1916) (= *Ascocotyle (Phagicola) angrese* Travassos, 1916) by Salgado-Maldonado and Aguirre-Macedo (1991), Jiménez-García (1993), and Aguirre-Macedo and García-Magaña (1994). *Ascocotyle (P.) angrese* is characterized by the presence of 18+2 circumoral spines (versus 16+4 in *A. (P.) nana*) and its metacercariae encyst exclusively in the gills of the atheriniform fish *Phalloceros caudimaculatus* (Ostrowski de Núñez, 1993). To date, *A. (P.) angrese* has not been found in Mexico and its distribution may be limited to South America.

Ascocotyle (A.) sp. 1 of Scholz *et al.* (1995)

Scholz *et al.* (1997a) identified these metacercariae found in the intestinal wall of *Poecilia velifera* (Poeciliidae) from Sahkaba cenote, Yucatán as *A. (L.) megalocéphala*.

***Ascocotyle (Phagicola)* sp. 2 of Scholz *et al.* (1995)**

Metacercariae encysted in the internal organs of numerous cichlids and other freshwater fish were conspecific with *A. (P.) nana* (see Scholz *et al.*, 1997a).

***Ascocotyle (Phagicola)* sp. 3 of Scholz *et al.* (1995)**

Metacercariae from the gills of *Cichlasoma meeki* were described by Scholz *et al.* (1997b) as a new species for which the name *Ascocotyle (L.) nunezae* was proposed.

***Phagicola* sp. of Iruegas *et al.* (1983)**

In an unpublished contribution at a national congress, metacercariae were reported from the operculum and musculature of *Cichlasoma cyanoguttatum* (Baird and Girard) (Cichlidae) and *Poecilia mexicana* (Poeciliidae) from Río Pesquería in Nuevo León. Although no description or illustration of the metacercariae were provided, it can be assumed that the metacercariae belonged to the species *Ascocotyle (Phagicola) nana* that commonly occurs in Mexico as well as in southeastern USA (Font *et al.*, 1984b; Scholz *et al.*, 1997a).

Heterophyidae gen. sp. of Scholz *et al.* (1995)

This metacercaria apparently belonged to a species of the *Ascocotyle*-complex because of the presence of a complete row of circumoral spines, most probably to *A. (L.) nunezae*. However, this species possesses additional spines on the dorsal spines and its metacercariae encyst exclusively in the gills.

Despite a relatively high number of taxa reported from Mexico, further heterophyid trematodes may still be found in Mexico. There are several species such as *Ascocotyle (Ascocotyle) pachycystis* Schroeder and Leigh, 1965; *A. (A.) puertoricensis* Price, 1932; *A. (A.) sexidigita* Miller and Harkema, 1962; *A. (P.) mollieniscicola* Sogandares-Bernal and Bridgman, 1960; or species of *Galactosomum*, that occur in the neighbouring countries, especially in the southern part of the USA (Florida, Louisiana, Mississippi) (Price, 1932, 1935; Sogandares-Bernal and Bridgman, 1960; Miller and Harkema, 1962; Hutton, 1964; Schroeder and Leigh, 1965; Yoshino, 1972).

As demonstrated by Ostrowski de Núñez (1993), Scholz *et al.* (1997a), Scholz (1999) and in this study, the number of circumoral spines may be very constant and species-specific. However, this is valid mainly for those taxa that possess a relatively low number of spines such as *A. (P.) angrense* (18+2), *A. (P.) diminuta* (16+2), *A. (P.) longa* (16), *A. (P.) macrostoma* (18) or *A. (A.) tenuicollis* (16+16). In contrast, the number of spines may be subjected to some intraspecific variation in the species that have higher number of spines such as *A. (L.) megaloccephala* (36–40 in one row), *A. (L.) mcintoshii* (19–21 in one row) and *A. (L.) nunezae* (25–26+6–10).

Species of the *Ascocotyle*-complex represent the dominant group of heterophyids in Mexico but their subgeneric classification is unsatisfactorily resolved and a new arrangement should be proposed. However, such an arrangement requires a phylogenetic analysis of the group which will be possible only after more complete data on the morphology of individual species and their developmental stages, including cercariae, are available. Because of the existence of sibling species among heterophyids in North and South America (Font *et al.*, 1984a; Ostrowski de Núñez, 1992, 1996), life-cycle studies should be carried out and more thorough descriptions of

the morphology of metacercariae and adults of many taxa should be provided. Current classification, largely based on the topography of female genital organs (vitelline follicles, uterine loops) and the number of rows of circumoral spines, is apparently artificial and several species present intermediate characters which do not allow their placement within well-defined taxonomic entities.

Acknowledgements

The authors are indebted to Guillermina Cabañas-Caranza, Rafael Báez-Vález, Griselda Moreno-Navarette, Rogelio Aguilar-Aguilar, Petra Sánchez-Nava (Instituto de Biología, Universidad Nacional Autónoma de México, México); Juan Manuel Caspeta-Mandujano (Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Morelos); Dr Victor Manuel Vidal-Martínez, Isabel Jiménez-García, Clara Vivas-Rodríguez, David González-Solis, Edgar Mendoza-Franco and Gregory Arjona-Torres (CINVESTAV-IPN, Mérida, Mexico) for help in sampling and examining fish. Thanks are also due to Drs J. Ralph Lichtenfels and Patricia A. Pilit, US National Parasite Collection, Beltsville, MD, USA; and Rafael Lamothe-Argumedo and Luis García-Prieto, Institute of Biology, UNAM, Mexico City, Mexico, for lending types of species of *Ascocotyle* and vouchers of *Ascocotyle 'leighi'* and *Galactosomum puffini*, respectively.

This study was partly supported by scientific projects of the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Mexico, project No. M-135 (M. L. Aguirre-Macedo and V. M. Vidal-Martínez) and Consejo Nacional de Ciencia y Tecnología (CONACyT), Mexico, project No. 211085-5-3008N, and the Catherine McArthur Foundation. A stay of one of the authors (T. S.) in Mexico was supported by CONACyT México (catedra patrimonial) and CINVESTAV-IPN Mérida, and partly by the Institute of Parasitology, České Budějovice and the Grant Agency of the Czech Republic (project No. 206/98/0591). His short stays in the field stations Chamelá (Jalisco) and Los Tuxtlas (Veracruz) were supported by the Institute of Biology, UNAM, México. A stay of M. L. A.-M. in the Czech Republic in August 1999 was supported by the Ministry of Foreign Affairs of Mexico (Secretaría de Relaciones Exteriores).

References

- AGUIRRE-MACEDO, M. L. and GARCÍA-MAGAÑA, L., 1994, Metacercarias de cíclidos nativos del Sureste de México; taxonomía y claves para su reconocimiento, *Universidad y Ciencia*, **11**, 5–35.
- AMAYA-HUERTA, D., 1995, *Algunos aspectos de la transmisión y dispersión de Centrocestus formosanus (Trematoda: Centrocestinae) en el Estado de Morelos, México*. MSc thesis, Faculty of Biology, National Autonomous University of Mexico (UNAM), Mexico, 119 pp.
- AMAYA-HUERTA, D. and ALMEYDA-ARTIGAS, J., 1994, Confirmation of *Centrocestus formosanus* (Nishigori, 1924) Price, 1932 (Trematoda: Heterophyidae) in Mexico, *Research and Reviews in Parasitology*, **54**, 99–103.
- ARIZMENDI, M. A., 1992, Descripción de algunas etapas larvarias y de la fase adulta de *Centrocestus formosanus* de Tezontepec de Aldama, Hidalgo, *Anales del Instituto de Biología, Universidad Autónoma de México, Serie Zoología*, **63**, 1–11.
- BRAVO-HOLLIS, M., 1966, Reporte de *Galactosomum puffini* Yamaguti, 1941, trematodo con nueva localidad y nuevo hospedador, *Anales del Instituto de Biología, Universidad Autónoma de México, Serie Zoología*, **37**, 125–128.
- BURTON, P. R., 1956, Morphology of *Ascocotyle leighi*, n. sp. (Heterophyidae), an avian trematode with metacercaria restricted to the conus arteriosus of the fish, *Mollienesia latipinna* Le Sueur, *Journal of Parasitology*, **42**, 540–543.

- BURTON, P. R., 1958, A review of the taxonomy of the trematode genera *Ascocotyle* (Looss) and *Phagicola* (Faust) of the family Heterophyidae, *Proceedings of the Helminthological Society of Washington*, **25**, 117–122.
- CHIEFFI, P. P., GORLA, M. C. O., TORRES, D. M. A. G. V., DIAS, R. M. D. S., MANGINI, A. C. S., MONTEIRO, A. V., WOJCIECHOWSKI, E., VIERIA TORRES, M. A. G. and SOUZA DIAS, R. M. D., 1992, Human infection by *Phagicola* sp. (Trematoda, Heterophyidae) in the municipality of Registro, Sao Paulo State, Brazil, *Journal of Tropical Medicine and Hygiene*, **95**, 346–348.
- CONTI, J. A., FORRESTER, D. J. and PAUL, R. T., 1986, Parasites and diseases of reddish egrets (*Egretta rufescens*) from Texas and Florida, *Transactions of the American Microscopical Society*, **105**, 79–82.
- DITRICH, O., SCHOLZ, T., AGUIRRE-MACEDO, L. and VARGAS-VÁZQUEZ, J. 1997, Larval stages of trematodes from freshwater molluscs of the Yucatán Peninsula, Mexico, *Folia Parasitologica*, **44**, 109–127.
- DRONEN, N. O., 1985, Digenetic trematodes from the roseate spoonbill, *Ajaia ajaja*, from the Texas Gulf Coast, *Transactions of the American Microscopical Society*, **104**, 261–265.
- ERGENS, R., 1969, The suitability of ammonium picrate-glycerin in preparing slides of lower Monogonoidea, *Folia Parasitologica*, **16**, 320.
- FONT, W. F., HEARD, R. W. and OVERSTREET, R. M., 1984a, Life cycle of *Ascocotyle gemina* n. sp., a sibling species of *A. sexidigita* (Digenea: Heterophyidae), *Transactions of the American Microscopical Society*, **103**, 392–407.
- FONT, W. F., OVERSTREET, R. M. and HEARD, R. W., 1984b, Taxonomy and biology of *Phagicola nana* (Digenea: Heterophyidae), *Transactions of the American Microscopical Society*, **103**, 408–422.
- HUTTON, R. F., 1964, A second list of parasites from marine and coastal animals of Florida, *Transactions of the American Microscopical Society*, **83**, 439–447.
- HUTTON, R. F. and SOGANDARES-BERNAL, F., 1959, Further notes on Trematoda encysted in Florida mullets, *Quarterly Journal of the Florida Academy of Sciences*, **21**, 329–334.
- HUTTON, R. F. and SOGANDARES-BERNAL, F., 1960, Studies on helminth parasites from the coast of Florida. II. Digenetic trematodes from shore birds of the west coast of Florida, *Bulletin of Marine Science of the Gulf and Caribbean*, **10**, 40–54.
- IRUEGAS, B. F., JIMENEZ, G. F. and GUAJARDO, M. G., 1983, Monitoreo de helmintos parásitos de peces de río Pesquería en el estado de Nuevo León, México. Resúmenes del VII Congreso Nacional de Zoología. Sociedad Mexicana de Zoología, Jalapa, Veracruz. (Cited after Pérez-Ponce de León *et al.*, 1996).
- JIMÉNEZ-GARCÍA, I., 1993, Fauna helmintológica de *Cichlasoma fenestratum* (Pisces: Cichlidae) del lago de Catemaco, Veracruz, México, *Anales del Instituto de Biología, Universidad Autónoma de México, Serie Zoología*, **64**, 75–78.
- LAMOTHE-ARGUMEDO, R., GARCÍA-PRIETO, L., OSORIO-SARABIA, D. and PÉREZ-PONCE DE LEÓN, G., 1997, *Catálogo de la colección nacional de helmintos*. Universidad Nacional Autónoma de México, México, D.F., 211 pp.
- LEIGH, W. H., 1974, Life history of *Ascocotyle mcintoshi* Price, 1936 (Trematoda: Heterophyidae), *Journal of Parasitology*, **60**, 768–772.
- LOOSS, A., 1896, Recherche sur la faune parasitaire de l'Égypte. Première partie, *Memoires de l'Institut Égyptien*, **3**, 1–252.
- LÓPEZ-JIMÉNEZ, S., 1987, Enfermedades más frecuentes de las carpas cultivadas en México, *Acuavisión, Revista Mexicana de Acuicultura*, **2**(9), 11–13.
- LUMSDEN, R. D., 1963, A new heterophyid trematode of the *Ascocotyle* complex of species encysted in poeciliid and cyprinodont fishes of southeast Texas, *Proceedings of the Helminthological Society of Washington*, **30**, 293–296.
- MANFREDI, M. T. and ONETO, M., 1997, *Phagicola longa* (Heterophyidae) in dogs from Chile: morphological findings and taxonomical problems. *Parasitologia*, **39**, 9–11.
- MARTIN, W. E., 1950a, *Euhaplorchis californiensis* n. g., n. sp., Heterophyidae, Trematoda, with notes on its life-cycle, *Transactions of the American Microscopical Society*, **69**, 194–209.
- MARTIN, W. E., 1950b, *Phocitreum ovale* n. g., n. sp. (Opisthorchiidae), with observations on its life cycle, *Journal of Parasitology*, **36**, 552–558.

- MARTIN, W. E. and STEELE, D. F., 1970, *Ascocotyle sexidigita* sp. n. (Trematoda: Heterophyidae) with notes on its life cycle, *Proceedings of the Helminthological Society of Washington*, **37**, 101–104.
- MILLER, G. C. and HARKEMA, R., 1962, Studies on helminths of North Carolina vertebrates. II. *Ascocotyle ampullacea* sp. n. (Trematoda: Heterophyidae) from the raccoon, *Journal of Parasitology*, **48**, 426–428.
- OSTROWSKI DE NÚÑEZ, M., 1974, Estudio sobre estados larvales de trematodes digéneos de peces Cyprinodontiformes *Physis*, *Sección B, Buenos Aires*, **33**, 45–61.
- OSTROWSKI DE NÚÑEZ, M., 1976, Fauna de agua dulce en la República Argentina. IV. Las cercarias de *Ascocotyle* (*A.*) *tenuicollis* Price 1935 y de *Pygidiopsis pindoramensis* Travassos 1929 (Trematoda, Heterophyidae). *Physis*, *Sección B, Buenos Aires*, **35**, 51–57.
- OSTROWSKI DE NÚÑEZ, M., 1992, Life history studies of heterophyid trematodes in the Neotropical region: *Ascocotyle* (*Leighia*) *hadra* sp. n. *Memorias do Instituto Oswaldo Cruz, Rio de Janeiro*, **87**, 539–543.
- OSTROWSKI DE NÚÑEZ, M., 1993, Life-history studies of heterophyid trematodes in the Neotropical Region: *Ascocotyle* (*Phagicola*) *diminuta* (Stunkard and Haviland, 1924) and *A.* (*P.*) *angrense* Travassos, 1916, *Systematic Parasitology*, **24**, 191–199.
- OSTROWSKI DE NÚÑEZ, M., 1996, Life history studies of heterophyid trematodes in the Neotropical region: *Pygidiopsis australis* sp. n., a sibling species of *P. pindoramensis* Travassos, 1929, *Acta Parasitologica*, **41**, 13–19.
- PEARSON, J. C., 1964, A revision of the subfamily Haplorchinae Looss, 1899 (Trematoda: Heterophyidae). I. The *Haplorchis* group, *Parasitology*, **54**, 601–676.
- PEARSON, J. C., 1973, A revision of the subfamily Haplorchinae Looss, 1899 (Trematoda: Heterophyidae). II. Genus *Galactosomum*, *Philosophical Transactions of the Royal Society of London, Serie B*, **266**, 341–446.
- PÉREZ-PONCE DE LEÓN, G., GARCÍA-PRIETO, L., OSORIO-SARABIA, D. and LEÓN-REGAGNON, V., 1996, *Listados faunísticos de México. VI. Helmintos parásitos de peces de aguas continentales de México* (México: Instituto de Biología, Universidad Nacional Autónoma de México), 100 pp.
- PRICE, E. W., 1932, Some new trematodes of the family Heterophyidae, *Journal of Parasitology*, **19**, 166–167.
- PRICE, E. W., 1935, Descriptions of some heterophyid trematodes of the subfamily Centrocestinae, *Proceedings of the Helminthological Society of Washington*, **2**, 70–73.
- PRICE, E. W., 1936, A new heterophyid trematode of the genus *Ascocotyle* (Centrocestinae), *Proceedings of the Helminthological Society of Washington*, **3**, 31–32.
- RANSOM, B. H., 1920, Synopsis of the trematode family Heterophyidae with descriptions of a new genus and five new species, *Proceedings of the U.S. National Museum*, **57**, 527–573.
- RIETSCHEL, G. and WERDING, B., 1978, Trematodes of birds from northern Colombia, *Zeitschrift für Parasitenkunde*, **57**, 57–82.
- ROBINSON, E. J. Jr., 1956, Two flukes, *Phagicola macrostomus* n. sp. and *Phagicola byrdi* n. sp. from the turkey vulture (Heterophyidae), *Journal of Parasitology*, **42**, 326–329.
- SALGADO-MALDONADO, G. and AGUIRRE-MACEDO, M. L., 1991, Metacercarias parásitas de *Cichlasoma urophthalmus* (Cichlidae [sic!]) *Pelaezia loossi* n. comb. y *Phagicola angrense* con descripción de adultos recuperados experimentalmente, *Anales del Instituto de Biología, Universidad Autónoma de México, Serie Zoología*, **62**, 391–407.
- SALGADO-MALDONADO, G. and KENNEDY, C. R., 1997, Richness and similarity of helminth communities in the tropical cichlid fish *Cichlasoma urophthalmus* from the Yucatán Peninsula, Mexico, *Parasitology*, **114**, 581–590.
- SALGADO-MALDONADO, G., PINEDA-LÓPEZ, R., VIDAL-MARTÍNEZ, V. M. and KENNEDY, C. R., 1997, A checklist of metazoan parasites of cichlid fish from Mexico, *Journal of the Helminthological Society of Washington*, **64**, 195–207.
- SALGADO-MALDONADO, G., VARGAS-RODRÍGUEZ, M. I. and CAMPOS-PÉREZ, J. J., 1995, Metacercariae of *Centrocestus formosanus* (Nishigori, 1924) (Trematoda) in freshwater fishes in Mexico and its transmission by the thiarid snail *Melanooides tuberculata*, *Studies of Neotropical Fauna and Environment*, **30**, 245–250.
- SCHOLZ, T., 1999, Taxonomic study of *Phagicola longa* (Ransom, 1920) (Digenea: Heterophyidae) and related taxa, *Systematic Parasitology*, **43**, 148–157.

- SCHOLZ, T. and AGUIRRE-MACEDO, M. L., 2000, Metacercariae of trematodes parasitizing freshwater fish in Mexico: a reappraisal and methods of study, in A. N. García-Aldrete, G. Salgado-Maldonado and V. M. Vidal-Martínez (eds) *Metazoan Parasites in the Neotropic: Ecological, Taxonomic and Evolutionary Perspectives. Commemorative Volume of the 70th Anniversary of the Instituto de Biología, Universidad Nacional Autónoma de México* (México: Instituto de Biología, Universidad Nacional Autónoma de México), 85–99.
- SCHOLZ, T., AGUIRRE-MACEDO, M. L., SABAS FLORES DÍAZ DE LEÓN, A. T. and DITRICH, O., 2000, Larval stages of trematodes in freshwater molluscs of Mexico: a review of present state and methodology for future research, in A. N. García-Aldrete, G. Salgado-Maldonado and V. M. Vidal-Martínez (eds) *Metazoan Parasites in the Neotropic: Ecological, Taxonomic and Evolutionary Perspectives. Commemorative Volume of the 70th Anniversary of the Instituto de Biología, Universidad Nacional Autónoma de México* (México: Instituto de Biología, Universidad Nacional Autónoma de México), 61–84.
- SCHOLZ, T. and HANZELOVÁ, V., 1998, *Tapeworms of the Genus Proteocephalus Weinland, 1858 (Cestoda: Proteocephalidae), Parasites of Fishes in Europe*. Studies of the Academy of Sciences of the Czech Republic, Academia Praha, 2/98, 119 pp.
- SCHOLZ, T. and SALGADO-MALDONADO, V., 2000, The dispersion and distribution of *Centrocestus formosanus* (Nishigori, 1924) (Digenea: Heterophyidae) in Mexico: a review, *American Midland Naturalist*, **143**, 185–200.
- SCHOLZ, T. and VARGAS-VÁZQUEZ, J., 1998, Trematodes parasitizing fishes of the Rio Hondo river and freshwater lakes of Quintana Roo, Mexico, *Journal of the Helminthological Society of Washington*, **65**, 91–95.
- SCHOLZ, T., VARGAS-VÁZQUEZ, J., AGUIRRE-MACEDO, L. and VIDAL-MARTÍNEZ, V. M., 1997a, Species of *Ascocotyle* Looss, 1899 (Digenea: Heterophyidae) from the Yucatán Peninsula, Mexico, *Systematic Parasitology*, **36**, 161–181.
- SCHOLZ, T., VARGAS-VÁZQUEZ, J., MORAVEC, F., VIVAS-RODRÍGUEZ, C. and MENDOZA-FRANCO, E., 1995, Metacercariae of trematodes of fishes from cenotes (sinkholes) of the Yucatán Peninsula, Mexico, *Folia Parasitologica*, **42**, 173–192.
- SCHOLZ, T., VARGAS-VÁZQUEZ, J., VIDAL-MARTÍNEZ, V. M. and AGUIRRE-MACEDO, M. L., 1997b, *Ascocotyle nunezae* n. sp. (Digenea: Heterophyidae), and notes on its life-cycle, *Journal of Parasitology*, **83**, 141–147.
- SCHROEDER, R. E. and LEIGH, W. H., 1965, The life history of *Ascocotyle pachycystis* sp. n., a trematode (Digenea: Heterophyidae) from the raccoon in south Florida, *Journal of Parasitology*, **51**, 594–599.
- SEPÚLVEDA, M. S., SPALDING, M. G., KINSELLA, J. M., BJORK, R. D. and MCLAUGHLIN, G. S., 1994, Helminths of the roseate spoonbill, *Ajaia ajaja*, in southern Florida, *Journal of the Helminthological Society of Washington*, **61**, 179–189.
- SEPÚLVEDA, M. S., SPALDING, M. G., KINSELLA, J. M. and FORRESTER, D. J., 1996, Parasitic helminths of the little blue heron, *Egretta caerulea*, in southern Florida, *Journal of the Helminthological Society of Washington*, **63**, 136–140.
- SEPÚLVEDA, M. S., SPALDING, M. G., KINSELLA, J. M. and FORRESTER, D. J., 1999, Parasites of the great egret (*Ardea albus*) and a review of the helminths reported for the species, *Journal of the Helminthological Society of Washington*, **66**, 7–13.
- SOGANDARES-BERNAL, F. and BRIDGMAN, J. F., 1960, Three *Ascocotyle* complex trematodes (Heterophyidae) encysted in fishes from Louisiana including the description of a new genus, *Tulane Studies in Zoology*, **8**, 31–39.
- SOGANDARES-BERNAL, F. and 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, *Journal of Parasitology*, **49**, 264–274.
- SOGANDARES-BERNAL, F. and LUMSDEN, R. D., 1964, The heterophyid trematode *Ascocotyle (A.) leighi* Burton, 1956, from the hearts of certain poeciliid and cyprinodont fishes, *Zeitschrift für Parasitenkunde*, **24**, 3–12.
- STEIN, P. C., 1968, New intermediate fish hosts for the heterophyid trematodes *Ascocotyle pachycystis*, *Ascocotyle ampullacea*, and *Phagicola macrostomus*, *Journal of Parasitology*, **54**, 631.
- STUNKARD, H. W. and HAVILAND, C. B., 1924, Trematodes from the rat, *American Museum Novitates*, **126**, 1–10.

- STUNKARD, H. W. and UZMANN, J. R., 1955, The killifish, *Fundulus heteroclitus*, second intermediate host of the trematode *Ascocotyle (Phagicola) diminuta*, *Biological Bulletin*, **109**, 475–483.
- TRAVASSOS, L., 1929, Revisao do genero *Ascocotyle* Looss, 1899, *Memorias do Instituto Oswaldo Cruz, Rio de Janeiro*, **23**, 61–97.
- VELASQUEZ, C. C., 1982, Heterophyidiasis, in G. V. Hillyer and C. E. Hopla (eds) *CRC Handbook Series in Zoonoses. Section C. Volume III* (Boca Raton, FL: CRC Press), pp. 99–107.
- VÉLEZ-HERNÁNDEZ, E. M., CONSTANTINO-CASAS, F., GARCÍA-MARQUEZ, L. J. and OSORIO-SARABIA, D., 1998, Gill lesions in common carp, *Cyprinus carpio* L., in Mexico due to the metacercariae of *Centrocestus formosanus*, *Journal of Fish Diseases*, **21**, 229–232.
- VIDAL-MARTÍNEZ, V. M., AGUIRRE-MACEDO, M. L., SCHOLZ, T., GONZÁLEZ-SOLÍS, D. and MENDOZA-FRANCO, E., 2000, *Atlas of Helminth Parasites of Cichlid Fishes of Mexico*. Studies of the Academy of Sciences of the Czech Republic, Academia Praha, in press.
- VIDAL-MARTÍNEZ, V. M., KENNEDY, C. R. and AGUIRRE-MACEDO, M. L., 1998, The structuring process of the macroparasite community of an experimental population of *Cichlasoma urophthalmus* through time, *Journal of Helminthology*, **72**, 199–207.
- YAMAGUTI, S., 1971, *Synopsis of Digenetic Trematodes of Vertebrates*. Parts I, II (Tokyo: Keigaku Publishing Co.), 1074 pp. + 347 pls.
- YAMAGUTI, S., 1975, *A Synoptical Review of Life Histories of Digenetic Trematodes of Vertebrates* (Tokyo: Keigaku Publishing Co.), 590 pp. + 219 pls.
- YOSHINO, T. P., 1972, Helminth parasitism in the Pacific killifish, *Fundulus parvipinnis*, from southern California, *Journal of Parasitology*, **58**, 635–636.