FOLIA PARASITOLOGICA 42: 115–129,1995

Nematodes parasitic in fishes of cenotes (= sinkholes) of the Peninsula of Yucatan, Mexico. Part 1. Adults

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Key words: parasitic nematodes, fishes, cenotes, Mexico, Yucatan

Abstract. The present paper comprises a systematic survey of adult nematodes collected from fishes from cenotes (= sinkholes) of the Peninsula of Yucatan, southeastern Mexico, in 1993-1994. Examinations of a total of 533 fishes (17 species) originating from 39 cenotes from the Mexican states of Yucatan and Quintana Roo revealed the presence of the following nine nematode species: *Rhabdochona (Rhabdochona) kidderi*, *Procamallanus (Spirocamallanus) rebecae*, *P. (S.) neocaballeroi*, *Philometroides caudata*, *Hysterothylacium cenotae*, *Pseudocapillaria yucatanensis*, *Paracapillaria rhamdiae*, *P. teixerafreitasi* and *Capillostrongyloides* sp. (only females). Four species (*R. kidderi*, *P. rebecae*, *P. neocaballeroi* and *Capillostrongyloides* sp.) are briefly described and illustrated and some problems concerning their morphology, taxonomy, hosts and geographical distribution are discussed. Taxonomic changes include *Procamallanus (Spirocamallanus) neocaballeroi* (Caballero-Deloya, 1977) comb. n. and *Procamallanus (Spirocamallanus) rebecae* (Andrade-Salas, Pineda-López et García-Magaña, 1994) comb. n. The nematode fauna of fishes in cenotes of the Yucatan Peninsula shows its appurtenance to the Neotropical fauna with close affinities with that of fish nematodes from South America, but with a considerable degree of endemism.

In 1993 and 1994, extensive investigations into the parasite fauna of fishes in cenotes (= sinkholes) were carried out in the Yucatan Peninsula, southeastern Mexico, by the research team of the Centre for Investigations and Advanced Studies of the Polytechnic Institute (CINVESTAV-IPN) in Merida. The cenotes, representing the most frequent water bodies in this region with their often unique habitats, have already been characterized in the paper by Scholz et al. (1995a) where also data on the localities studied and the fish hosts examined during these investigations can be found. Of the material of helminth parasites collected, the results of the systematic evaluation of trematodes has already been published in the papers by Scholz et al. (1995a,b), whereas the survey of adult parasitic nematodes is presented in this paper; larval nematodes recorded will be dealt with in a separate contribution.

To date, the nematode fauna of fishes in cenotes in the Yucatan Peninsula has almost been unknown and the only paper dealing with these parasites is that of Pearse (1936); the author inadequately described two species of adult nematodes (*Rhabdochona kidderi* and "*Dujardinia*" *cenotae* (= *Hysterothylacium cenotae*) from the bagre, *Rhamdia guatemalensis*, and *Contracaecum* sp. larvae from the same fish species and from the cichlid *Cichlasoma mayorum* from a few localities; none of these parasites has been recorded from cenotes of this region since. Of the nine species of adult nematodes found during our research, three proved to be new to science and they have already been formally described in previous papers (Moravec et al. 1995a,b,c); a redescription of "*Dujardinia*" *cenotae* has already been published, too (Moravec et al. 1995d).

MATERIALS AND METHODS

The list of localities and the numbers of fishes examined from them have already been published in the paper by Scholz et al. (1995a). In addition to the above mentioned fishes that were completely examined, 25 specimens of *Cichlasoma urophthalmus* from Chen-há Cenote and 135 specimens of *Astyanax fasciatus* from cenotes Kawash, Box-toro and Gran Cenote were examined incompletely only for obtaining *Procamallanus* spp. for experiments; these fishes have been included in numbers given in this paper. Adult nematodes were collected from the following localities:

State of Yucatan: Chelentún Cenote (20°43'28" N, 89°20'04" W) and Homún Cenote (20°44'19" N, 89°17'49" W) (both Zona Cuzama); Cenote Chen-há (20°41'24" N, 89°52'36" W) (Zona Chochola); Ixin-há Cenote (20°37'14" N, 89°06'40" W), Xcangachén Cenote (20°36'43" N, 89°05'32" W), Xmucuy Cenote (20°33'63" N, 88°59'50" W) and Saca-

mucuy Cenote (20°33'33" N, 88°59'49" W) (all Zona Sotuta); Yokdzonot Cenote (20°42'24" N, 88°43'51" W) and Scan Yui Cenote (20°40'20" N, 88°32'20" W) (both Zona Libre Unión); Noc-ac Cenote (21°04'22" N, 80°43'14" W) (Zona Mérida); Tixkanka Cenote (21°14'55" N, 88°58'45" W) (Zona Dzilam); Xkeken Cenote (20°39'37" N, 88°14'33" W), Zaci Cenote (20°41'29" N, 88°11'49" W), Hubicu Cenote (20°49'79" N, 88°10'21" W) and Sahkaba Cenote (20°48'41" N, 88°07'27" W) (all Zona Valladolid);

State of Quintana Roo: Cenote San Pedro 1 (20°27'27" N, 87°50'00" W) and Cenote San Pedro 2 (20°27'27" N, 87°50'04" W) (both Zona norte); Gran Cenote (20°14'44" N, 87°27'54" W), Box-toro Cenote (20°16'27" N, 87°29'09" W), Kawash Cenote (20°14'44" N, 87°27'54" W) and Cenote Cabañas (20°07'51" N, 87°27'57" W) (all Zona centro); Cenote Azul (18°38'11" N, 88°24'46" W) and Cenote Dos Bocas (17°54'38" N, 88°51'20" W) (both Zona sur).

The nematodes were fixed in hot 4% formaldehyde (philometrids in 4% formaldehyde in physiological saline). For optical microscopy examination they were cleared with glycerine. Drawings were made with the aid of an Olympus or a Zeiss microscope drawing attachments. The specimens have been deposited in the helminthological collections of the Institute of Parasitology, Academy of Sciences of the Czech Republic in České Budějovice, of the Institute of Biology of the National University in Mexico City, and in the Laboratory of Parasitology, CINVESTAV-IPN, in Mérida, Yucatan, Mexico. All measurements are given in millimetres.

REVIEW OF SPECIES

Fam. Rhabdochonidae Travassos, Artigas et Pereira, 1928

1. ***Rhabdochona (Rhabdochona) kidderi*** Pearse, 1936
Fig. 1

Description: Small nematodes with smooth cuticle. Oval mouth opening surrounded by four minute cephalic papillae and two lateral amphids. Prostom funnel-shaped, wide, mostly without basal teeth, rarely minute basal teeth slightly outlined. Anterior margin of prostom internally armed with 14 small, forwardly directed teeth (3 dorsal, 3 ventral, and 4 on each lateral side, the latter forming pairs). Vestibule relatively long. Deirids very small, bifurcate, situated near mid-length of vestibule. Tail of males and young females ending in sharp cuticular spike, that of gravid females mostly with rounded tip.

Male (10 specimens): Length of body 5.64–8.70, maximum width 0.068–0.095. Prostom 0.015–0.021 long and 0.011–0.018 wide in lateral view. Length of vestibule including prostom 0.135–0.168, of muscular oesophagus 0.300–0.360, of glandular oesophagus 1.27–2.10. Nerve ring encircling muscular oesophagus 0.168–0.225 from antrerior extremity. Excretory pore and deirids at 0.249–0.294 and 0.066–0.078, respectively. Subventral preanal papillae occurring in following combinations: 5+5, 6+6, and 6+7. Additional lateral pair of preanal papillae present at level of second subventral pair (counted from cloacal opening). Of six postanal pairs of papillae, second pair lateral, remaining subventral. Longitudinal ventral cuticular ridges (area rugosa) absent. Left spicule very long, 0.651–1.167. Length of its shaft 0.306–0.540, representing 32–52% of whole spicule length; distal tip of protruded spicule bifurcate. Small (right) spicule 0.075–0.087 long, mostly without dorsal barb at distal tip (barb present only in one male). Length ratio of spicules 1 : 7.9–13.9. Tail conical, 0.159–0.252 long, with sharp terminal cuticular spike.

Female (10 specimens): Length of body of gravid females 6.42–9.26, width 0.082–0.095. Prostom 0.018 long and 0.015–0.018 wide in lateral view. Length of vestibule including prostom 0.144–0.162, of muscular oesophagus 0.300–0.369, of glandular oesophagus 1.14–1.66. Nerve ring, excretory pore and deirids at 0.171–0.201, 0.189–0.291 and 0.057–0.090, respectively. Tail conical, 0.111–0.177 long, in younger females terminating in sharp cuticular spike, in gravid females mostly with rounded tip. Vulva postequatorial, 2.52–3.63 from posterior end of body. Vagina muscular, long, directed anteriorly. Mature eggs oval, larvated, provided with fine, irregular flock-like superficial coating; size of mature eggs 0.045–0.051 × 0.021–0.024, thickness of egg wall 0.003.

Hosts: *Rhamdia guatemalensis* (Günther) (Pimelodidae, Siluriformes) and *Gambusia yucatana* Regan (Poeciliidae, Atheriniformes) (only juvenile specimens in latter).

Site of infection: intestine.

Localities: State of Yucatan: Chelentún (3 November 1993), Homún (3 November 1993), Ixin-há (29 October 1993, 16 June, 11 July, 22 August, 20 September, 17 October and 15 November 1994), Xcangachén (17 November 1993), Xmucuy (26 October and 16 November 1993 and 25 July 1994), Sacamucuy (10 October 1994), Yokdzonot (14 October 1993), Scan Yui (21 January 1994), Noc-ac (23 March 1994), Tixkanka (23 May 1994), Xkeken (23 February 1994), Zaci (18 April 1994), Hubicu (18 April 1994) and Sahkaba (18 April 1994); State of Quintana Roo: San Pedro 1, San Pedro 2 (both 23 February 1994) and Gran Cenote (6 September 1994).

Prevalence and intensity: *Rhamdia guatemalensis*: Chelentún – 2 fishes infected/7 fishes examined, intensity 1–3 nematodes; Homún – 1/1, 5; Ixin-há – 69/90, 1–38; Xcangachén – 2/2, 4–5; Xmucuy – 18/22, 1–72; Sacamucuy – 4/4, 6–125; Yokdzonot – 1/1, 2; Scan Yui – 12/16, 1–12; Noc-ac – 1/1, 11; Tixkanca – 5/9, 1–21; Xkeken – 2/2, 8–18; Zaci-ha – 3/4, 2–3; Hubicu – 3/16, 1–14; Sahkaba – 1/1, 2; San Pedro 1 – 8/11, 3–108; San Pedro 2 – 5/7, 5–39; Gran Cenote 1/2, 10; *Gambusia yucatana*: Homún – 1/6, 1.

Comments: Originally this species was inadequately described by Pearse (1936) from *Rhamdia*

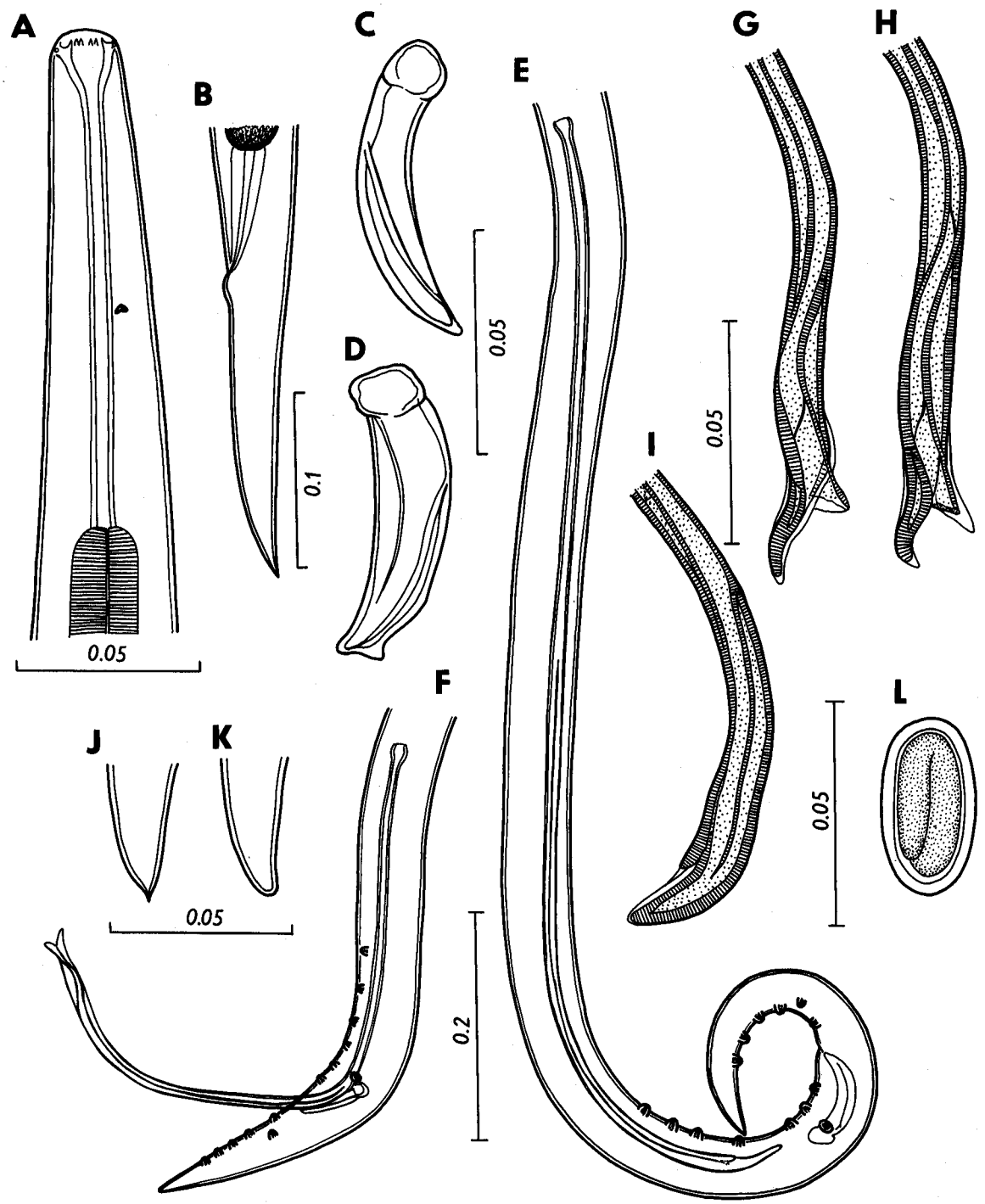

Fig. 1. *Rhabdochona kidderi* Pearse, 1936. **A** – anterior end; **B** – tail of female; **C, D** – small spicule; **E, F** – caudal ends of the largest and the smallest males; **G, H** – distal tip of large spicule (protruding out from body); **I** – same (inside body); **J, K** – tail tip of male and female; **L** – mature egg.

guatemalensis depressa, *R. g. decolor* and *R. g. stygeae* from five cenotes (= sinkholes) and from aquatic habitats of two caves in Yucatan. Subsequently it was reported by Chitwood (1938) from caves in Yucatan also from "*Typhlias*" (= apparently *Ogilbia pearsei* (Hubbs, 1938) (Bythitidae, Gadiformes)). It has not been recorded from Mexico since. The type specimens of *R. kidderi* were later re-examined by Gustafson (1949) and Moravec and Arai (1971).

The morphology and measurements of specimens of the present material correspond to the existing descriptions of *R. kidderi* from *Rhamdias guatemalensis* as given by Pearse (1936), Gustafson (1949) and Moravec and Arai (1971) and there is no doubt that they belong to this species. Moreover, one our locality (Scan Yui Cenote) is the same from where *R. kidderi* was found by Pearse (1936). Although Pearse (1936) reported only six anterior teeth in the prostom of this nematode, it was already pointed out by Chitwood (1938) that their actual number was fourteen. The present study based on numerous specimens has confirmed a considerable variability in the length of the left spicule in this species and made it possible to recognize a rather complicated structure of the distal end of this spicule. Characteristic features of *R. kidderi* are the very long left spicule with the bifurcate distal end, a small number of subventral preanal papillae in the male, and the anteriorly directed vagina in the female. By possessing 14 teeth in the prostom and by having no filaments or floats on the eggs, this species belongs to the subgenus *Rhabdochona* Railliet, 1916 according to the system by Moravec (1975).

In 1988, Moravec and Huffman described conspecific nematodes from *Cichlasoma cyanoguttatum* and *Tilapia mossambica* (both fam. Cichlidae) (juvenile forms also from *Gambusia affinis*, fam. Poeciliidae) from central Texas, U.S.A., for which they established an independent subspecies, *Rhabdochona kidderi texensis*. In contrast to the nominate subspecies, *R. k. texensis* has a markedly longer left spicule (1.67–1.98 mm) although the body size is approximately the same, different length ratio of spicules (1 : 18.7–22.5), somewhat smaller eggs and some other distinguishing features and it cannot be excluded that subsequent studies will prove it to be a separate species, different from *R. kidderi*.

This study confirms that *Rhabdochona kidderi* is the most distributed and the most frequent parasite of *Rhamdia guatemalensis* in cenotes and caves in the Peninsula of Yucatan in Mexico. Since this nominate subspecies has not so far been recorded outside Yucatan, it appears that it is endemic to this region where *Rhamdia guatemalensis* is its principal definitive host; *Gambusia yucatana* and some other fish may probably play a role of paratenic or paradefinitive hosts only.

Fam. Camallanidae Railliet et Henry, 1915

2. ***Procamallanus* (*Spirocamallanus*) *rebecae*** (Andrade-Salas, Pineda-López et García-Magaña, 1994) comb. n. Figs. 2–3

Description: Medium sized nematodes with almost smooth cuticle. Mouth opening circular, provided with eight papillae in two circlets and two lateral amphids. Orange-brown buccal capsule distinctly longer than wide, thick-walled, with simple, well developed basal ring. Inner surface of capsule provided with 14-18 spiral thickenings in lateral view. Muscular oesophagus shorter than glandular one. Deirids small, situated approximately at mid-way between nerve ring and anterior extremity; excretory pore approximately at mid-way between nerve ring and muscular oesophagus end. Tail of both sexes with three minute terminal cuticular spikes.

Male (5 specimens): Length of body 8.98–10.91, maximum width 0.245–0.313. Buccal capsule including basal ring 0.084–0.105 long, its width 0.060–0.069; basal ring 0.006–0.009 long and 0.042–0.057 wide. Spiral thickenings 14–18 in number. Length of muscular oesophagus 0.326–0.408, width 0.060-0.078; length of glandular oesophagus 0.517–0.707, width 0.054–0.090; length ratio of muscular and glandular oesophagus 1 : 1.5–2.1. Length of entire oesophagus and buccal capsule representing 10–12% of body length. Deirids, nerve ring and excretory pore 0.114–0.150, 0.258–0.272 and 0.313–0.438, respectively, from anterior extremity. Posterior end of body ventrally bent, provided with wide caudal alae supported by pedunculate papillae; caudal alae anteriorly interconnected by transverse mound, posteriorly they by far not reach to caudal end. Preanal papillae: 3 pairs of subventral pedunculate papillae; postanal papillae: 4 pairs of subventral and 2 pairs of lateral pedunculate papillae present; additional 2 pairs of small transversely elongate sessile ventral papillae surrounding cloacal opening. Spicules similar in shape, unequally long, well sclerotized, with pointed distal ends. Large (right) spicule 0.480–0.525 long; small (left) spicule less sclerotized, 0.261–0.315 long. Length ratio of spicules 1 : 1.7–1.9. Gubernaculum absent. Tail conical, 0.282–0.336 long; its tip rounded, bearing three minute, thin cuticular spikes 0.003 long.

Female (5 gravid specimens): Length of body 12.35–20.68 (body length of females containing larvae 12.34–14.67), maximum width 0.290–0.544. Buccal capsule including basal ring 0.099–0.110 long and 0.075–0.088 wide; basal ring 0.009–0.012 long and 0.048–0.055 wide. Spiral thickenings 14–18 in number. Length of muscular oesophagus 0.435–0.598, width 0.082–0.110; length of glandular oesophagus 0.700–1.120, width 0.082–0.122; length ratio of

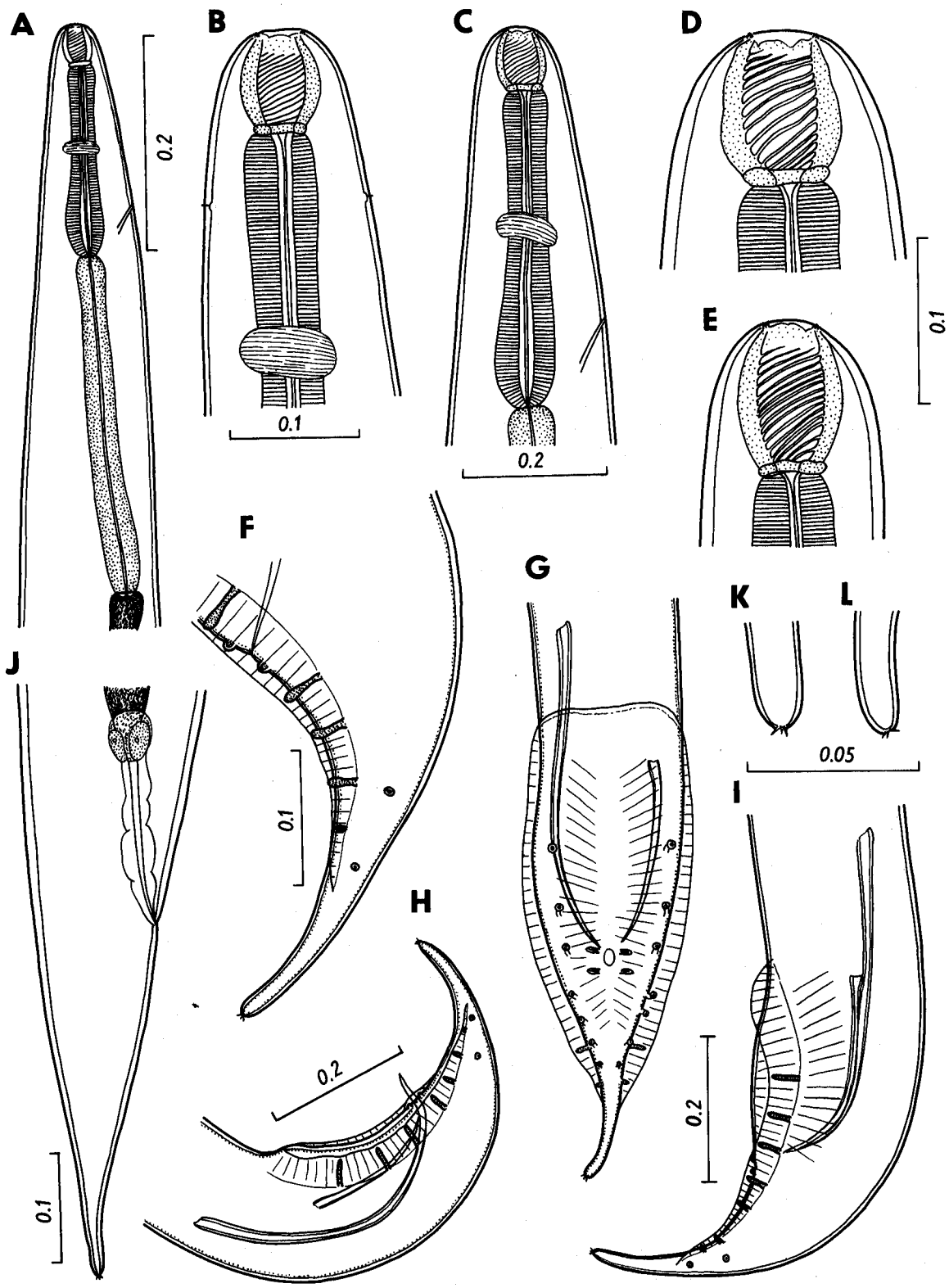

Fig. 2. *Procamallanus* (*Spirocamallanus*) *rebecae* (Andrade-Salas, Pineda-López et García-Magaña, 1994). **A** – anterior end of body; **B, C** – cephalic end, dorsal and lateral views; **D, E** – buccal capsule of female and male; **F** – tail of male, lateral view; **G** – caudal end of male, ventral view; **H, I** – same, lateral view; **J** – tail of female; **K, L** – tail tip of female and male.

muscular and glandular oesophagus 1 : 1.4–2.1. Length of entire oesophagus and buccal capsule representing 9–12% of body length. Deirids, nerve ring and excretory pore 0.165–0.170, 0.305–0.340 and 0.340–0.465, respectively, from anterior extremity. Intestine brown-coloured. Vulva slightly postequatorial, 6.77–10.65 from anterior extremity (at 51–55% of body length). Vagina muscular, directed posteriorly. Uterus with eggs or first-stage larvae 0.488–0.508 long and 0.023–0.025 wide (n = 5). Tail conical, 0.354–0.450 long; its posterior end narrow, rounded, bearing three minute terminal spikes 0.003–0.005 long.

Third-stage larva (1 specimen): Length of body 2.71, maximum width 0.069. Buccal capsule colourless, without distinctly separated basal ring, 0.039 long and 0.024 wide; its inner surface smooth, without spiral thickenings. Muscular oesophagus 0.189 long and 0.024 wide, length of glandular oesophagus 0.195, its width 0.021. Nerve ring and excretory pore 0.135 and 0.171, respectively, from anterior extremity; length ratio of muscular and glandular oesophagus 1 : 1.0. Entire oesophagus and buccal capsule representing 16% of body length. Oval genital primordium 1.56 from anterior end of body. Tail conical, 0.132 long, ending in three small cuticular spikes 0.003 long.

Fourth-stage larva (2 specimens): Length of body 4.83-7.44, maximum width 0.109–0.163. Buccal capsule almost colourless, basal ring not well distinguished; length of buccal capsule 0.048–0.072, width 0.045–0.048; inner surface of capsule with 13–14 spiral thickenings. Muscular oesophagus 0.272–0.340 long and 0.036–0.048 wide, length of glandular oesophagus 0.286–0.394, its width 0.039–0.042; length ratio of muscular and glandular oesophagus 1 : 1.1–1.2. Entire oesophagus and buccal capsule representing 11–13% of body length. Nerve ring and excretory pore 0.174–0.204 and 0.261–0.300, respectively, from anterior extremity. Vulva still covered by cuticle, 2.65–4.05 from anterior end of body (at 54–55% of body length). Genital primordium tubular. Tail conical, 0.213–0.261 long, ending in three small cuticular spikes measuring 0.003.

Hosts: *Cichlasoma meeki* (Brind), *C. synspilum* Hubbs and *C. urophthalmus* (Günther) (Cichlidae, Perciformes).

Site of infection: intestine.

Localities: State of Yucatan: Chen-há (18 October 1993, 27 June, 27 August and 13 September 1994); State of Quintana Roo: Cabañas (3 May 1994) and Cenote Azul (5 May).

Prevalence and intensity: *Cichlasoma meeki*: Azul – 1 fish infected/1 fish examined, intensity 5 nematodes; Cabañas – 1/2, 2; *C. syspilum*: Azul – 2/10, 1; *C. urophthalmus*: Chen-há – 41/66, 1–13; Cabañas – 1/4, 2.

Comments: This species has only recently been described under the name *Spirocamallanus rebecae* from three species of *Cichlasoma* (*C. helleri*, *C. pasionis* and *C. synspilum*) from Campeche and Tabasco, Mexico, by Andrade-Salas et al. (1994). It is apparent, however, that the same species was reported previously by Osorio Sarabia et al. (1987) from *Cichlasoma meeki*, *C. pasionis* and *Petenia splendida* from Tabasco as *Spirocamallanus pereirai* (Annereaux, 1946) (they reported 5 pairs of preanal papillae which is evidently erroneous); also the larvae reported by these authors (Osorio Sarabia et al. 1987) from *Cichlasoma meeki* and *C. pasionis* as *Procamallanus* sp. were undoubtedly the third-stage larvae of *P.* (*S.*) *rebecae*.

The specimens of the present material correspond, more or less, to the original description of this species; the only significant difference is the number of spiral thickenings (ribs) in the buccal capsule: we found 14–18 ribs in both males and females of the present material, whereas Andrade-Salas et al. (1994) reported 12–14 ribs. In our opinion, this difference is either within the intraspecific variability or can be ascribed to inaccuracies in observation of the previous authors. Characteristic features of this species is the shape and structure of the buccal capsule (number of ribs, simple basal ring), comparatively short glandular oesophagus, situation of deirids, unequal spicules, presence of well developed caudal alae in the male, not extending posteriorly to the end of the tail, number and arrangement of caudal papillae, and a long tail ending in both sexes in three small thin terminal spikes.

The gross morphology of *P.* (*S.*) *rebecae* suggests that this nematode belongs to the group of Neotropical freshwater species derived from the congeneric parasites of marine fishes (see Petter 1979, 1990). The third- and fourth-stage larvae of this parasite are described for the first time.

In contrast to species of the subgenus *Spirocamallanus* (e.g., *P.* (*S.*) *cricotus*, *P.* (*S.*) *hilarii*, *P.* (*S.*) *pimelodus*) the third-stage larvae of which already possess spiral thickenings (ribs) in the buccal capsule (Pereira et al. 1936, Fusco 1980, Moravec et al. 1993), the third-stage larvae of *P.* (*S.*) *rebecae* have a smooth buccal capsule without ribs and the ribs are present only in fourth-stage larvae; in this, *P.* (*S.*) *rebecae* resembles the species *P.* (*S.*) *fulvidraconis* and *P.* (*S.*) *intestinecolas* which do not form spiral thickenings in their buccal capsule during the third stage (Li 1935, Bashirullah and Ahmed 1976). A characteristic feature of both third- and fourth-stage larvae of *P.* (*S.*) *rebecae* is the presence of three minute terminal spines on the tail tip.

Procamallanus (*S.*) *rebecae* is reported from the territory of Mexican states of Yucatan and Quintana Roo for the first time and its findings in *Cichlasoma meeki* and *C. urophthalmus* represent new host records.

Since *Spirocamallanus* Olsen, 1952 is considered only a subgenus of the genus *Procamallanus* Baylis,

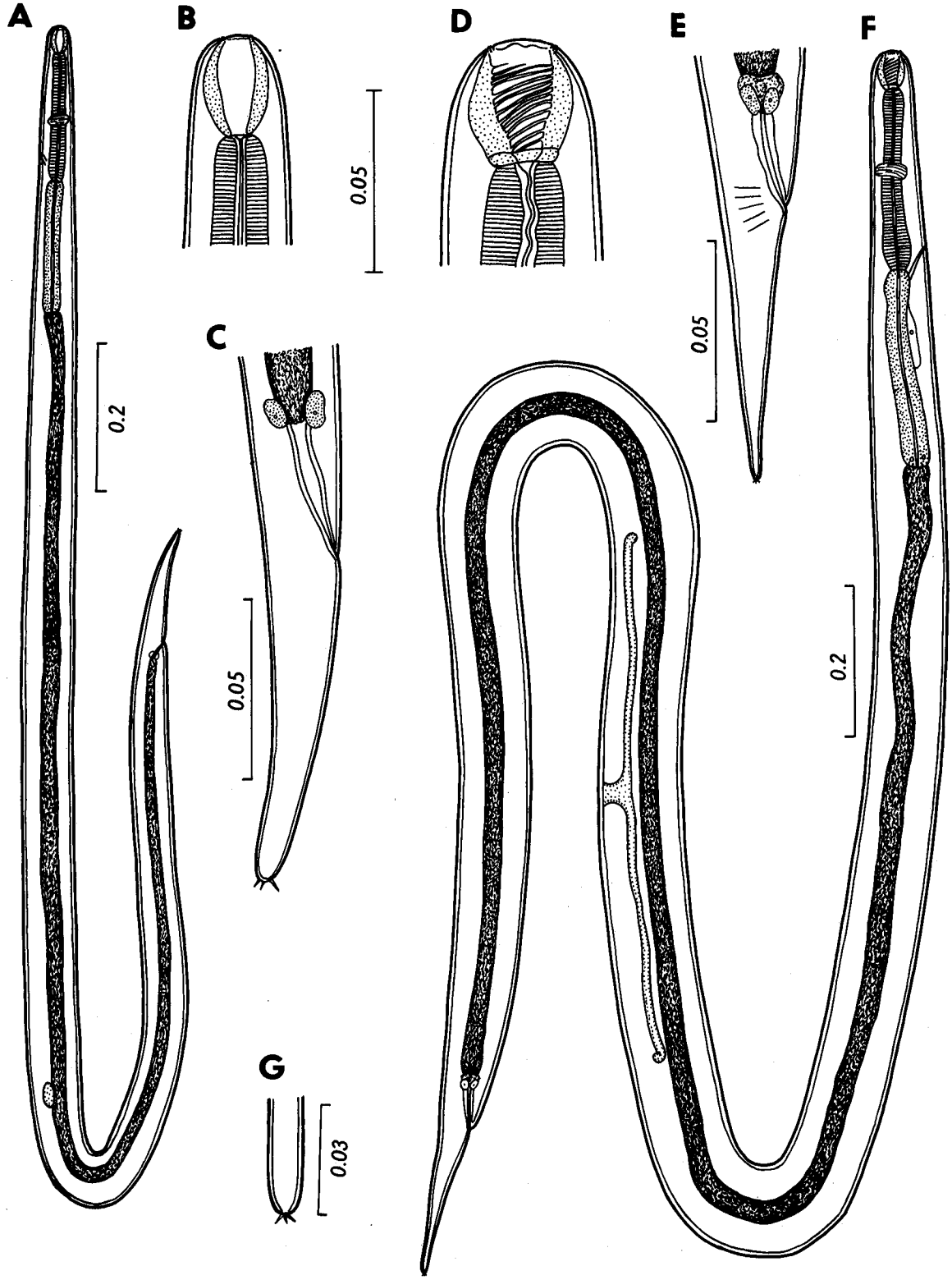

Fig. 3. *Procamallanus* (*Spirocamallanus*) *rebecae* (Andrade-Salas, Pineda-López et García-Magaña, 1994) – larvae. **A–C** – third-stage larva (**A** – general view, **B** – buccal capsule, **C** – tail); **D–G** – fourth-stage larva (**D** – buccal capsule, **E** – tail, **F** – general view, **G** – tail tip).

1923 by the present authors (see Moravec and Amin 1978, Moravec and Sey 1988), the species is formally transferred to *Procamallanus* as *P.* (*S.*) *rebecae* (Andrade-Salas, Pineda-López et García-Magaña, 1994) comb. n.

3. ***Procamallanus*** ***(Spirocamallanus)*** ***neocaballeroi*** (Caballero-Deloya, 1977) comb. n. Fig. 4

Description: Medium sized nematodes with smooth cuticle. Oral opening circular, surrounded by four small sublateral sclerotized plates, eight papillae in two circlets and two lateral amphids. Orange-brown buccal capsule approximately as long as wide (usually slightly broader than long), thin-walled, its inner surface provided with 15–19 thin spiral thickenings (in lateral view) extending anteriorly to anterior end of capsule. Basal ring of capsule simple, well developed. Glandular oesophagus more than three times longer than muscular oesophagus; glandular oesophagus cylindrical, non-expanded near its posterior end. Excretory pore situated somewhat posterior to nerve ring, deirids at level of anterior border of nerve ring.

Male (5 specimens): Length of body 3.73–5.57, maximum width 0.100–0.150. Buccal capsule including basal ring 0.058–0.063 long and 0.058–0.060 wide; size of basal ring 0.008–0.013 × 0.033–0.038. Spiral thickenings 15–16 in number in lateral view. Length of muscular oesophagus 0.315-0.370, width 0.085-0.100, length of glandular oesophagus 0.950–1.170, width 0.080 –0.090; their length ratio being 1 : 3.0–3.3. Length of entire oesophagus and buccal capsule representing 27–35% of body length. Nerve ring and excretory pore 0.175–0.190 and 0.205–0.280, respectively, from anterior extremity; deirids in largest specimen 0.163 from anterior end. Narrow caudal alae present, by far not reaching to posterior end of tail. Caudal papillae: 4 pairs of preanal and 6 pairs of postanal papillae present. Postanals: subventral papillae of anterior four pairs large, of last pair very small, hardly visible; one pair of large lateral papillae situated at level of fourth subventral pair. Spicules well sclerotized, short, equally long, measuring 0.065–0.078. Gubernaculum absent. Tail conical, with rounded end, 0.120–0.135 long.

Female (5 gravid specimens with larvae): Body 16.60–20.47 long, their maximum width 0.310–0.400. Length of buccal capsule including basal ring 0.075–0.078, its width 0.080–0.083; size of basal ring 0.013–0.018 × 0.040–0.043. Spiral thickenings 18–19 in number in lateral view. Length of muscular oesophagus 0.440–0.565, width 0.130–0.135, length of glandular oesophagus 1.65–2.12, width 0.110–0.130; their length ratio being 1 : 3.8. Nerve ring and excretory pore 0.210-0.213 and 0.350-0.400, respectively, from anterior extremity. Vulva postequatorial, 9.05–11.40 from anterior end of body (at 55–56% of body length). Uterus containing numerous larvae 0.593–0.613 long and 0.033–0.035 wide (n = 5). Tail conical, relatively short (0.090–0.100); its posterior end forming terminal process 0.025 long. Phasmids situated approximately at mid-way between anus and posterior extremity, 0.050–0.053 from posterior end of body.

Host: *Astyanax fasciatus* (Cuvier) (Characidae, Cypriniformes).

Site of infection: intestine and pyloric caeca.

Localities: State of Quintana Roo: Box-toro (25 April, 12 May and 5 September 1994), Gran Cenote (12 May and 6 September 1994) and Kawash (5 September 1994).

Prevalence and intensity: Box-toro – 7 fishes infected/19 fishes examined, intensity 1–3 nematodes; Gran Cenote – 47/98, 1–8; Kawash – 36/56, 1–3.

Comments: The morphology and measurements of specimens of the present material correspond, more or less, to the description of *Procamallanus* (*Spirocamallanus*) *neocaballeroi* (Caballero-Deloya, 1977) and, consequently, they are considered to belong to this species. The above redescription extends the biometrical variability of this species and provides some new data on its morphology; deirids and phasmids as well as cephalic sclerotized plates and the last pair of minute caudal papillae in the male are described for the first time.

By its morphology, *P.* (*S.*) *neocaballeroi* belongs to the group of congeneric Neotropical species parasitizing freshwater fishes in South America, represented by *P.* (*S.*) *inopinatus* Travassos, Artigas et Pereira, 1928, *P.* (*S.*) *hilarii* Vaz et Pereira, 1934 and some others, characterized mainly by conspicuously small spicules of approximately the same length, reduced or completely lacking caudal alae in the male and by other features.

P. (*S.*) *neocaballeroi* was described from the intestine of *Astyanax fasciatus* from Lake Catemaco in Veracruz, Mexico (Caballero-Deloya 1977) and it has not been reported since. Our findings indicate that it is a frequent parasite of *A. fasciatus* in some cenotes of the central region of the State of Quintana Roo.

Fam. Philometridae Baylis et Daubney, 1926

4. ***Philometroides caudata*** Moravec, Scholz et Vivas-Rodríguez, 1995

Host: *Rhamdia guatemalensis* (Günther) (Pimelodidae) (Siluriformes).

Site of infection: swimbladder, abdominal cavity.

Localities: State of Yucatan: Ixin-há (28 October 1993, 13 June, 11 July, 22 August, 20 September, 17 October 1994) and Xmucuy Cenote (25 July 1994).

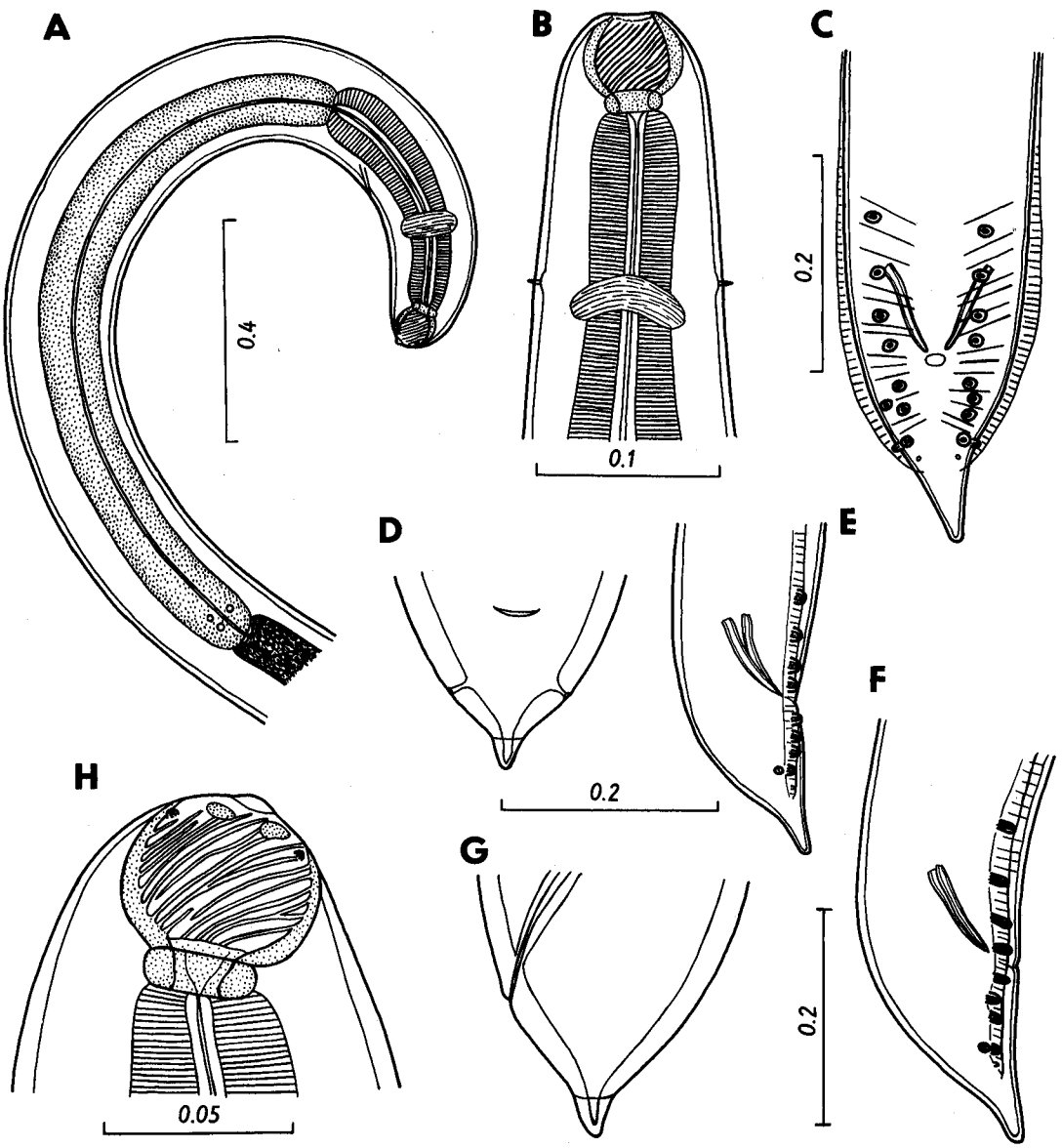

Fig. 4. *Procamallanus (Spirocamallanus) neocaballeroi* (Caballero-Deloya, 1977). **A** – anterior end of body, lateral view; **B** – cephalic end, dorsal view; **C** – caudal end of male, ventral view; **D** – tail of female, ventral view; **E, F** – caudal end of male, lateral view; **G** – tail of female, lateral view; **H** – buccal capsule.

Prevalence and intensity: Ixin-há – 8 fishes infected/90 fishes examined, intensity 1–2 nematodes; Xmucuy – 3/14, 1–2.

Comments: This species has already been discussed by Moravec et al. (1995c).

Fam. Aniasakidae Railliet et Henry, 1915

5. ***Hysterothylacium cenotae*** (Pearse, 1936)
Syn.: *Dujardinia cenotae* Pearse, 1936

Host: *Rhamdia guatemalensis* (Günther) (Pimelodidae, Siluriformes).

Site of infection: intestine.

Localities: State of Yucatan: Xmucuy Cenote (26 October and 16 November 1993; 25 July 1994); State of Quintana Roo: Kawash (6 September 1994).

Prevalence and intensity: Xmucuy – 6 fishes infected/21 fishes examined, intensity 1–4 nematodes; Kawash – 1/2, 2.

Comments: This species has already been discussed by Moravec et al. (1995d).

Fam. Capillariidae Neveu-Lemaire, 1936

6. ***Pseudocapillaria yucatanensis*** Moravec, Scholz et Vivas- Rodríguez, 1995

H o s t: *Rhamdia guatemalensis* (Günther) (Pimelodidae, Siluriformes).

S i t e o f i n f e c t i o n: intestine.

L o c a l i t i e s: State of Yucatan: Xmucuy (26 October 1993, 25 July 1994), Ixin-há (22 August, 20 September, 17 October and 14 November 1994), Tixkanka (30 May 1994) and Chen-há (13 September 1994).

P r e v a l e n c e a n d i n t e n s i t y: Xmucuy – 3 fishes infected/19 fishes examined, intensity 1–17 nematodes; Ixin-há – 5/90, 1–23; Tixkanka – 1/9, 1; Chen-há – 2/8, 2.

Comments: This species has already been discussed by Moravec et al. (1995b).

7. ***Paracapillaria rhamdiae*** Moravec, González Solís et Vargas-Vázquez, 1995

H o s t: *Rhamdia guatemalensis* (Günther) (Pimelodidae, Siluriformes)

S i t e o f i n f e c t i o n: stomach.

L o c a l i t i e s: State of Yucatan: Hubicu (25 April 1994), Ixin-há (20 September and 17 October 1994) and Chen-há (13 September 1994).

P r e v a l e n c e a n d i n t e n s i t y: Hubicu – 1 fish infected/16 fishes examined, intensity 1 nematode; Ixin-há – 4/90, 1–4; Chen-há – 1/8, 3.

Comments: This species has already been discussed by Moravec et al. (1995a).

8. ***Paracapillaria teixeirafreitasi*** (Caballero,1971) Fig. 5
Syn.: *Capillaria teixeirafreitasi* Caballero, 1971

Description: Small elongate nematodes. Anterior end narrow, rounded; mouth papillae indistinct. Two lateral bacillary bands extending along almost whole body length. Stichosome uniform in colour, consisting of single row of 37–45 stichocytes subdivided usually (mainly in posterior part of stichosome) into 5–10 transverse annuli; anterior stichocytes more elongated; nuclei of stichocytes large, well visible. Nerve ring encircling muscular oesophagus at its anterior third. Two small wing-like cells present at junction of oesophagus and intestine.

Male (3 specimens): Length of body 2.95–3.26, maximum width 0.030–0.040. Width of bacillary bands 0.018–0.022. Length of entire oesophagus 3.13–2.25 (69–72% of body length). Length of muscular oesophagus 0.163–0.180, of stichosome 1.95–2.09; number of stichocytes 43-45. Nerve ring situated 0.063–0.070 from anterior extremity. Spicule well sclerotized, with almost smooth surface, 0.145–0.188 long, 0.003–0.004 wide at its middle part; its proximal end somewhat expanded, distal end rounded. Spicular canal not developed. Surface of spicular sheath smooth, without spines. Tail rounded, 0.006-0.008 long (without membraneous bursa), provided with cuticular membrane (length 0.005) forming very short bursa. Bursa supported by two wide lateral digital projections (rays) curved to median line; their ends at level of posterior border of membraneous bursa in ventral view. One pair of large spherical subventral papillae present at base of lateral projections, being situated below level of cloacal opening. Another pair of minute ventral papillae present just anterior to cloacal opening.

Female (3 gravid specimens): Length of body 4.18–4.95, maximum width 0.050. Width of bacillary bands 0.020. Length of entire oesophagus 2.35–2.83 (56–57% of body length). Length of muscular oesophagus 0.175–0.205, of stichosome 2.18–2.62; stichocytes 37–39 in number. Nerve ring 0.058-0.068 from anterior end. Vulva situated 0.013–0.015 below level of oesophago-intestinal junction; vulvar lips not elevated or anterior lip somewhat elevated. Eggs arranged in single file in uterus. Eggs oval, polar plugs not protruding; egg wall markedly thin (0.001), appearing as one layered, with very fine superficial sculpture. Length of polar plugs 0.003, width 0.004. Contents of eggs uncleaved. Size of fully mature eggs 0.050 × 0.020–0.023. Ovary reaching posteriorly below level of intestine end. Anus subterminal, 0.008 long.

H o s t: *Gobiomorus dormitor* Lacépède (Eleotrie, Perciformes).

S i t e o f i n f e c t i o n: intestine.

L o c a l i t y: State of Quintana Roo: Cenote Azul (5 April 1994).

P r e v a l e n c e a n d i n t e n s i t y: in 1 out of 2 *G. dormitor* examined, 17 nematodes were found.

Comments: This species was described as *Capillaria teixeirafreitasi* from *Gobiomorus dormitor* from Laguna de Chairel, Tampico, Mexico (Caballero 1971) and it has not been recorded since. Although the caudal end of the male was inadequately described and the membraneous bursa on the male tail was not observed, Moravec (1987) tentatively transferred this species to the genus *Paracapillaria* Mendonça, 1963 on the basis of drawings in the original paper (Caballero 1971). The present study confirms this generic appurtenance.

In contrast to the original description, the spicule in males of the present material is somewhat shorter (0.145–0.188 mm vs. 0.203 mm), stichocytes are more numerous (37–45 vs. 30–35) and the body of gravid females is smaller (4.18–4.95 vs. 6.95–7.45); however, we consider these differences to be within the limits of the intraspecific variability of this species. The present redescription of *P. teixeirafreitasi* confirms the validity

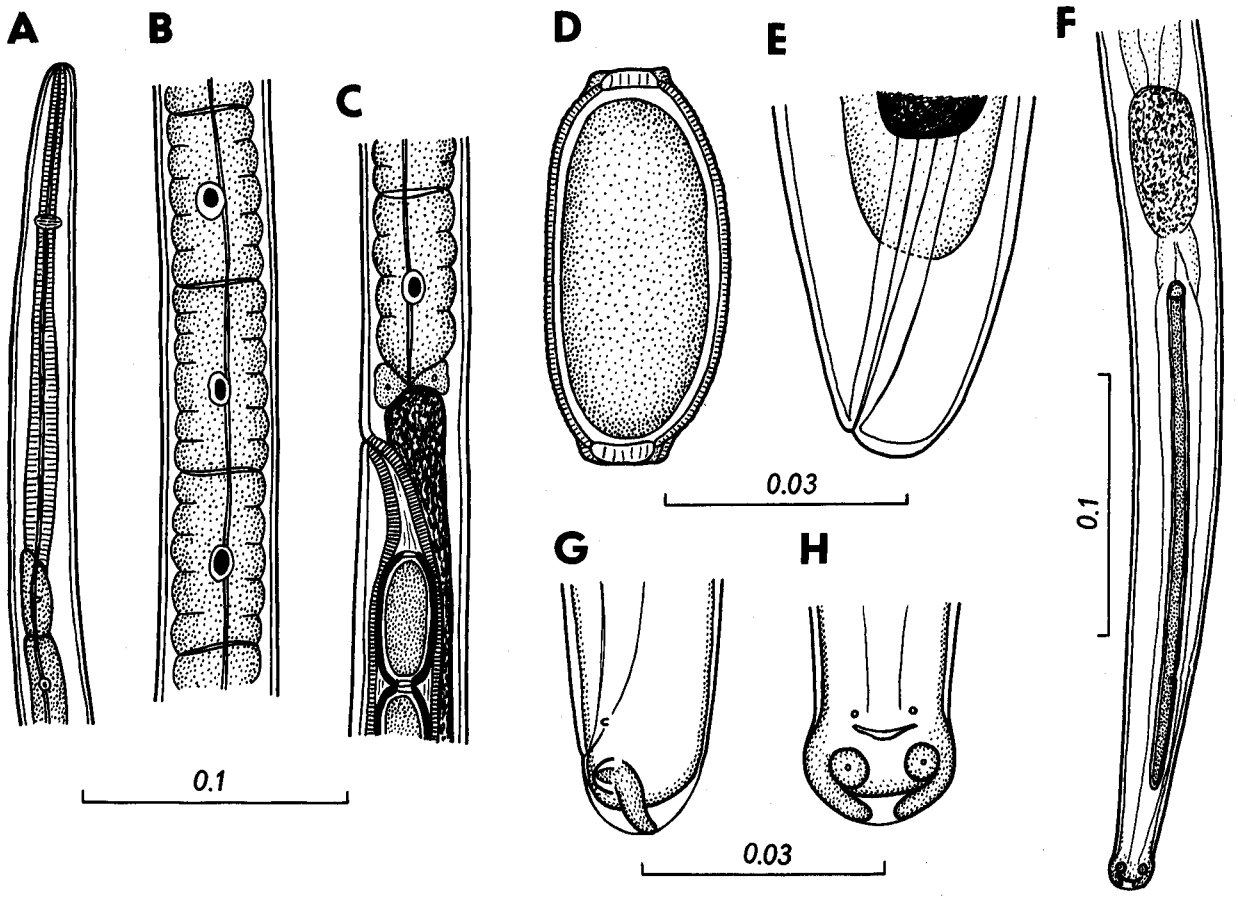

Fig. 5. *Paracapillaria teixeirafreitasi* (Caballero, 1971). **A** – anterior end of body; **B** – region of stichosome; **C** – region of vulva; **D** – egg; **E** – tail of female; **F** – caudal end of male; **G, H** – tail of male, lateral and ventral views.

of this species which differs from its congeners principally in the size and structure of eggs, length of the spicule, structure of the caudal bursa and in some other features.

9. ***Capillostrongyloides*** sp. Fig. 6

Description of female (5 specimens): Very small nematodes with comparatively wide posterior part of body. Body of gravid specimens 1.86–2.89 long and 0.050 to 0.080 wide. Cuticle smooth. Two lateral, not well visible bacillary bands present, extending along whole body length; their width 0.018–0.045. Oesophagus markedly short, 0.830–1.010 long, representing 33 to 54% of body length. Muscular oesophagus elongate, somewhat expanded at its posterior third, measuring 0.200–0.243. Stichosome consisting of single row of 28–34 stichocytes with large nuclei; stichocytes uniform in colour, conspicuously short, sometimes wider than long, some of them subdivided into 2–3 transverse annuli. Nerve ring encircling muscular oesophagus approximately at border of its first and second thirds, 0.070–0.078 from anterior extremity. Two distinct wing-like cells present at oesophago-intestinal junction. Vulva situated 0.030–0.038 behind level of oesophagus end, vulvar lips not elevated or, sometimes, anterior lip somewhat elevated. Eggs unembryonated (occasionally containing two blastomeres), barrel-shaped, polar plugs not protruding. Egg wall two-layered; inner layer hyaline, outer layer thin, with fine superficial sculpture. Size of eggs 0.050–0.060 × 0.025–0.035, wall 0.003 thick. Polar plugs 0.003–0.005 height and 0.010 wide. Eggs arranged in one file in anterior part of uterus and in two files at more distant part. Ovary reaching posteriorly to almost mid-length of rectum; length of rectum 0.070–0.079. Posterior end of body rounded, anus subterminal (almost terminal); cuticle of dorsal anal lip somewhat enflated; length of tail 0.003–0.005.

H o s t : *Astyanax fasciatus* (Cuvier) (Characidae, Cypriniformes).

S i t e o f i n f e c t i o n : intestine (?).

L o c a l i t y : State of Quintana Roo: Dos Bocas (12 April 1994).

Prevalence and intensity: in 1 out of 3 *A. fasciatus* examined, 5 nematodes were found.

Comments: The general morphology and measurements of females of the present material are almost identical with those of the species *Capillostrongyloides sentinosa* (Travassos, 1927) (syn.: *Capillaria minima* Travassos, Artigas et Pereira, 1928 and *Capillostrongyloides zederi* Freitas et Lent, 1935), as it was redescribed by Moravec (1987). *C. sentinosa* is a parasite of cypriniform fishes of the suborder Characoidei in Brazil and it was originally described from *Astyanax fasciatus* (type host) (in original paper reported as *Tetragonopterus* sp.) (see Travassos 1927, Travassos et al. 1928), the same fish species from which our Mexican specimens have originated. This fact as well as the morphological similarity of females of the present material to those of *C. sentinosa* make it possible, in our opinion, to assign tentatively our nematodes to the genus *Capillostrongyloides* Freitas et Lent, 1935, even though males have not been found. In the fact, it cannot be excluded that they belong to the same species, *C. sentinosa*. The specific identification of these capillariids from *Astyanax fasciatus* in Mexico will only be possible when also males are available.

By their morphology and markedly small measurements the females from *A. fasciatus* resemble also those of another capillariid species from Mexican fishes, *Paracapillaria rhamdiae* Moravec, González Solís et Vargas-Vázquez, 1995, a recently described stomach parasite of the bagre, *Rhamdia guatemalensis* (Moravec et al. 1995f). In the fact, the genera *Capillostrongyloides* and *Paracapillaria* Mendonça, 1963 are closely related and the latter may well represent only a subgenus of the first genus (see Moravec 1987). In contrast to *Capillostrongyloides* females of the present material, the females of *P. rhamdiae* have larvated eggs in the uterus.

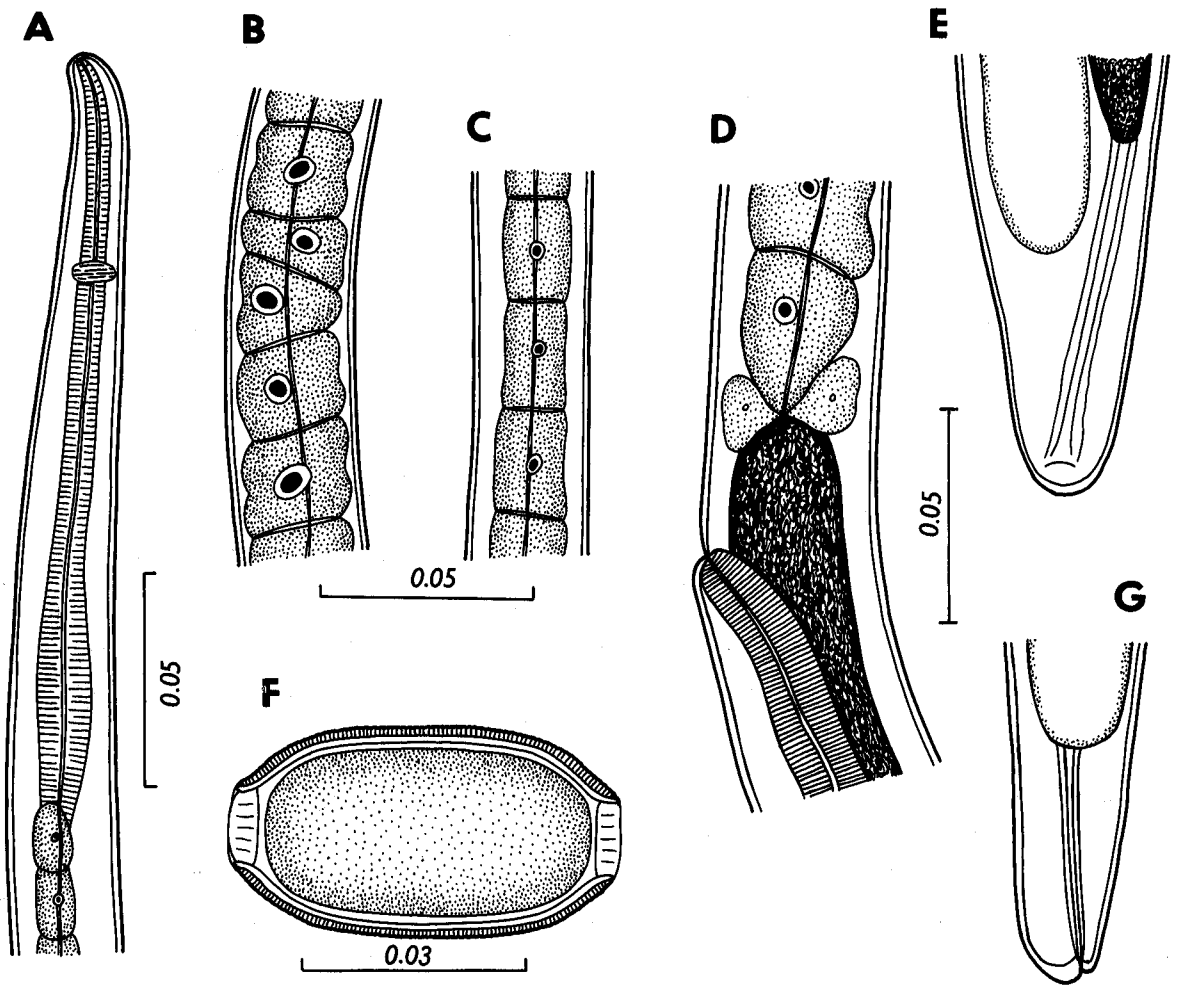

Fig. 6. *Capillostrongyloides* sp. female from *Astyanax fasciatus*. **A** – anterior end of body; **B** – region of posterior part of stichosome; **C** – region of anterior part of stichosome; **D** – region of vulva; **E** – caudal end, ventral view; **F** – egg; **G** – caudal end, lateral view.

DISCUSSION

Adult helminths are always much more important for the evaluation of a certain helminth fauna of fishes from the viewpoint of zoogeography, phylogeny and other aspects than larval stages which usually show only a low degree of host specificity and the occurrence of which depends, in addition to other factors, on the presence of other vertebrates (definitive hosts), frequently those migrating between distant geographical areas (e.g. some birds). Therefore, particularly the fauna of adult nematodes (as well as of other adult helminths) parasitizing freshwater fishes in cenotes of the Yucatan Peninsula is of special interest as it may provide significant information about the origin of these parasites and their hosts and shows its relations to other zoogeographical complexes.

The present study indicates that the fauna of adult nematodes parasitic in cenote fishes in the Peninsula of Yucatan includes nine species. Considering a relatively low number of fish species occurring in these habitats and a considerable uniformity of the ichthyofauna in most cenotes, the number of the adult nematode species recorded appears to be appropriate and comparable to that of the adult trematodes (Scholz et al. 1995a); but in contrast, the number of cestode and acanthocephalan species is markedly low.

It is noteworthy that all the species of adult nematodes exhibit a relatively high degree of host specificity, utilizing as definitive hosts either a single species of fish or fishes of the same genus (the finding of a juvenile *R. kidderi* in *Gambusia yucatana* suggests that this fish is a paratenic rather than a definitive host). It is interesting that more than one half (5) of these nematode species was recorded from the bagre, *Rhamdia guatemalensis*, the most characteristic and the most distributed fish in cenotes in this region (this is the only fish present in some cenotes, e.g. in the Cenote Ixin-há). However, due to different ecological conditions in different cenotes, there are also considerable differences in the species composition of the nematode fauna of *R. guatemalensis*. The highest number (4) of nematode species (*Rhabdochona kidderi*, *Philometroides caudata*, *Pseudocapillaria yucatanensis* and *Paracapillaria rhamdiae*) was found in the Cenote Ixin-há, three species (*Hysterothylacium cenotae*, *R. kidderi* and *P. caudata*) were recorded from the Cenote Xmucuy, and two species from the Cenote Chen-há, Tixkanka or Hubicu. In many localities, adult nematodes are represented in *R. guatemalensis* by a single species, *R. kidderi*, or are completely absent.

The occurrence of adult nematodes in other fish species seems to be restricted to a few localities. In cichlids (*Cichlasoma urophthalmus* and *C. meeki*), the nematode *Procamallanus* (*S.*) *rebecae* was found in three localities (Cenotes Chen-há, Cabañas and Azul). Both nematodes parasitizing *Astyanax fasciatus* were recorded only from cenotes in the State of Quintana Roo: *Procamallanus* (*S.*) *neocaballeroi* from three near-by Cenotes Kawash, Box-toro and Gran Cenote, while *Capillostrongyloides* sp. only from the Cenote Dos Bocas. The capillariid *Paracapillaria teixeirafreitasi* in *Gobiomorus dormitor* was recorded once in the Cenote Azul in Q. Roo.

Of the nine nematode species recorded in cenote fishes, only three species (*P.* (*S.*) *rebecae*, *P.* (*S.*) *neocaballeroi* and *P. teixeirafreitasi*) are known to occur as well in other types of water bodies in other regions in Mexico (Caballero 1971, Caballero-Deloya 1977, Osorio Sarabia et al. 1987, Andrade-Salas et al. 1994). All other species are hitherto known only from cenotes (*R. kidderi* also from caves) of the Yucatan Peninsula and it is probable that they are mostly endemic to this type of habitats in this region.

Regarding nematodes parasitizing fishes, one of the most important factors determining the presence or absence of a parasite species in a certain locality is the presence of a suitable intermediate host and a sufficient density of its population; species with direct development without an intermediate host are rare amongst fish nematodes (Moravec 1994). Unfortunately, the biology of most nematode species occurring in cenote fishes in the Yucatan Peninsula is not known. The life cycle was experimentally studied only in both *Procamallanus* species (*P. rebecae* and *P. neocaballeroi*) (see Moravec and Vargaz-Vázquez 1995e,f) utilizing copepods as intermediate hosts. Considering the life cycle patterns in other congeneric species, the intermediate hosts of *Rhabdochona kidderi* are probably some larvae of aquatic insects (mayflies or caddis-flies), those of *Hysterothylacium cenotae* are some benthic crustaceans (amphipods), and those of *Philometroides caudata* copepods. Fish capillariids may develop either with an obligate intermediate host (an oligochaete) or without it; however, in the latter case invertebrate paratenic hosts (oligochaetes) are mostly involved (Moravec 1994). It is apparent from our results that most nematode species parasitizing *Rhamdia guatemalensis* develop through benthic invertebrates, whereas nematodes utilizing planktonic copepods as intermediate hosts occur in *Cichlasoma* spp. and *Astyanax fasciatus*; this appears to be associated with differences in the ecology of these fishes, because *R. guatemalensis* is a typical benthic fish, whereas both *Cichlasoma* spp. and *A. fasciatus* are pelagic fishes.

This survey shows that most nematode species parasitic in cenote fishes in the Yucatan Peninsula belong to the morphological groups of species occurring in freshwater fishes in South and Central America (*Procamallanus* spp., *Philometroides caudata*, *Rhabdochona*

kidderi, *Paracapillaria* spp., *Capillostrongyloides* sp.). Species of *Pseudocapillaria* and *Hysterothylacium* occur both in the Nearctic and Neotropical Regions and it is difficult to establish any affinities of the representatives of these genera from Yucatan. Consequently, the results of this study indicate that the nematode fauna of cenote fishes in the Peninsula of Yucatan is typically Neotropical with a high degree of endemism.

Acknowledgements. Our thanks are due to E. Pérez-Díaz and M. Hernándes de Santillana, CINVESTAV-IPN Mérida, for the identification of fishes. We wish to thank also fellow-workers of the Laboratory of Parasitology and Histopathology of the same institution, namely R. Simá Alvarez, J. Güemez Ricalde and G. Arjona for their assistance in collecting fishes, and Mrs. I. Husáková from the Institute of Parasitology, Academy of Sciences of the Czech Republic in České Budějovice, for her technical help with preparation of figures. This study was supported by the grant no. PO99 from the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Mexico.

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Received 30 January 1995

Accepted 11 May 1995