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Nematodes parasitic in fishes of cenotes (= sinkholes) of the Peninsula of Yucatan, Mexico. Part 2. Larvae

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Abstract. This paper comprises a systematic survey of larval nematodes collected from fishes from cenotes (= sinkholes) of the Peninsula of Yucatan, southern Mexico, in 1993–1994. Larvae of the following nine species were recorded: *Physocephalus sexalatus*, Acuariidae gen. sp., *Spiroxys* sp., *Falcaustra* sp., *Hysterothylacium cenotae*, *Contracaecum* sp. Type 1, *Contracaecum* sp. Type 2, *Goezia* sp., and *Eustrongylides* sp. Larvae of *P. sexalatus* are recorded from fishes (*Rhamdia guatemalensis*) for the first time. The larvae are briefly described and illustrated and problems concerning their morphology, taxonomy, hosts and geographical distribution are discussed. Adults of these larvae are parasitic in piscivorous fishes, reptiles, birds and mammals (definitive hosts). Fishes harbouring the larvae of these parasites serve as paratenic hosts, being mostly an important source of infection for the definitive hosts.

This paper is a continuation of the senior authors' earlier work (Moravec et al. 1995a) on the results of the systematic study of fish nematodes collected from fishes in cenotes (= sinkholes) in the Peninsula of Yucatan, southeastern Mexico, in 1993–1994. The first paper treated nematodes parasitic in fishes as adults. Trematodes of the same material have been dealt with in the papers by Scholz et al. (1995a,b).

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 examined fresh, three fixed (preserved in 10% formaldehyde), museum specimens of the American eel, *Anguilla rostrata* (LeSueur), from the ichthyological collection of Centro de Investigaciones de Quintana Roo (Museo de Zoología) in Chetumal (Cat. Nos: MZ-CIQRO P 1212, 1213 and 1444), were also examined; these were collected from three cenotes in the State of Quintana Roo, Mexico, in the years 1983, 1986 and 1987. Larval nematodes were collected from the following localities:

State of Yucatan: Hubicu Cenote (20°49'79"N, 88°01'21" W) and Sahkaba Cenote (20°48'41"N, 88°07'27"W) (both Zona Valladolid); Ixin-há Cenote (20°37'14"N, 89°06'40"W) and Xmucuy Cenote (20°33'63"N, 88°59'50" W) (both Zona Sotuta); Chen-há Cenote (20°41'24"N, 89°52'27"W) (Zona Chochola); Noc-choncunchey Cenote (20°48'53"N, 90°11'47" W) (Zona Celestún); Dzonot Cervera Cenote (21°22'36"N, 88°49'59"W) (Zona Dzilam); and Hodz-ob Cenote (20°55'15" N, 88°51'43"W);

State of Quintana Roo: Box-toro Cenote (20°16'27"N, 87°29'09"W), Escondido Cenote (20°11'5"N, 87°29'57" W), Gran Cenote (20°14'44"N, 87°27'54"W), Cabañas Cenote (20°07'51"N, 87°27'57"W), Cenote Cristal I (not positioned), Cenote Salvaje, Rancho San Erick (not positioned) and Cenote Zacate, archeological zone of Xel-há (not positioned) (both Cozumel District) (all Zona centro); Dos Bocas Cenote (18°54'38"N, 88°51'20"W) and Cenote Azul (18°38'11"N, 88°24'46"W) (both Zona sur).

The nematodes were fixed in hot 4% formaldehyde. For optical microscopy examination they were cleared with glycerine. Drawings were made with the aid of an Olympus or a Zeiss microscope drawing attachments. For scanning electron microscopy the specimens were postfixed in 1% OsO_4, dehydrated through an ethanol series and aceton and then subjected to critical point drying. The specimens were coated with gold and examined with a JSM-6300 scanning electron microscope at an accelerating voltage of 15 kV. 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 (UNAM) in Mexico City, and in the Laboratory of Parasitology, CINVESTAV-IPN, in Mérida, Yucatan, Mexico. Measurements are given in millimetres.

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REVIEW OF SPECIES

Fam. Spirocercidae Chitwood et Wehr, 1932

1. ***Physocephalus sexalatus*** (Molin, 1860) larvae Fig. 1A–F

Description (9 specimens): Whitish nematodes with dense transverse striation of cuticle. Length of body 1.20–1.26, maximum width 0.065–0.075. Anterior end somewhat narrowed. Head end provided with two (dorsal and ventral) conical cephalic projections 0.003 high, four simple papillae and pair of lateral amphids. Vestibule well developed, 0.085–0.088 long, appearing to be broader in lateral than dorsoventral view. Deirids very small, situated approximately at border of first and second thirds of vestibule length. Nerve ring and excretory pore 0.103–0.115 and 0.113–0.125 from anterior extremity. Length of muscular oesophagus 0.100–0.148, of glandular oesophagus 0.408–0.450. Oesophagus opening into intestine through valve. Intestine straight, light-coloured. Rectum hyaline tube surrounded by three large unicellular rectal glands. Small oval genital primordium situated 0.355–0.388 from posterior end of body. Tail conical, 0.048–0.050 long, with small round terminal formation, 0.005 long, provided with about 15 minute papilla-like outgrowths.

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

Site of infection: mesentery (encysted).

Localities: State of Yucatan: Hubicu and Sahkaba (both 18 April 1994).

Prevalence and intensity: Hubicu – 5 fishes infected/16 fishes examined, intensity 1–8 larvae; Sahkaba – 1/1, 1.

Comments: The morphology and measurements of these larvae correspond, more or less, to the third-stage larvae of *Physocephalus sexalatus* (Molin, 1860), a common and widespread stomach parasite mainly of wild and domestic Suidae (less commonly of some other mammals as peccary, tapirs, equines, cattle, lagomorphs – see Anderson 1992), as described, for example, by Baruš et al. (1970), Sharpilo (1976) and others.

Numerous species of at least twenty genera of dung beetles (Coleoptera) have been shown to serve as intermediate hosts of *P. sexalatus* in the tissues of which infective larvae are found encapsulated. Various amphibians, reptiles, birds and mammals which have ingested infected beetles are known as paratenic hosts harbouring infective larvae of *P. sexalatus* encapsulated especially on the gut and mesentery (see Anderson 1992). The majority of these paratenic hosts are typical terrestrial animals (e.g., lizards, bats) with little or no contact with aquatic habitats, but Bartlett et al. (1987) reported *P. sexalatus*-like larvae for example from shorebirds, *Bartramia longicauda* and *Numenius americanus*, from Ontario, Canada.

The present finding of *P. sexalatus* larvae in bagres, *Rhamdia guatemalensis*, is quite unusual, showing that fishes may also play a role of the paratenic host of this nematode. Apparently, fishes acquired *P. sexalatus* infection more or less accidentally while taking and ingesting infected beetles from the water surface. Although bagres are hardly available to the definitive hosts of *P. sexalatus* as food, they need not represent a blind alley in the development of this parasite; the nematode larvae might be transferable from bagres to some other, piscivorous paratenic hosts, for example fish-eating birds.

Fam. Acuariidae Railliet, Henry et Sisoff, 1912

2. **Acuariidae** gen. sp. larvae Fig. 1J–L

Description (2 specimens): Whitish nematodes with dense, fine transverse striation of cuticle. Length of body 2.40–3.78, maximum width 0.080–0.109. Pseudolabia triangular in lateral view, 0.008–0.009 long and 0.010–0.015 wide. Vestibule 0.073–0.096 in length. Deirids situated 0.078 from anterior extremity. Muscular oesophagus 0.313–0.501 long and 0.015–0.021 wide. Length of glandular oesophagus 0.940–1.100, width 0.040–0.054. Nerve ring and excretory pore 0.115–0.159 and 0.150–0.195, respectively, from anterior extremity. Intestine straight, light-coloured. Rectum short hyaline tube. Genital primordium not located. Tail conical, 0.060–0.093 long, with rounded tip.

Hosts: *Rhamdia guatemalensis* (Günther) (Pimelodidae, Siluriformes) and *Cichlasoma urophthalmus* (Günther) (Cichlidae, Perciformes).

Site of infection: mesentery.

Localities: State of Yucatan: Ixin-há (26 October 1993), Sahkaba (18 April 1994) and Chen-há (27 June 1994).

Prevalence and intensity: Ixin-há (*R. guatemalensis*) – 1 fish infected/90 fishes examined, intensity 1; Sahkaba (*R. guatemalensis*) – 1/1, 1; Chen-há (*C. urophthalmus*) – 1/34, 1.

Comments: These specimens represent undoubtedly the third-stage larvae of an acuariid nematode, probably a parasite of fish-eating birds. This identification is mainly based on the presence of large triangular pseudolabia, a very long vestibule and the general morphology. Determination of the species and genus is impossible. Fishes apparently serve as paratenic hosts of this species, whereas some aquatic arthropods are probably its intermediate hosts.

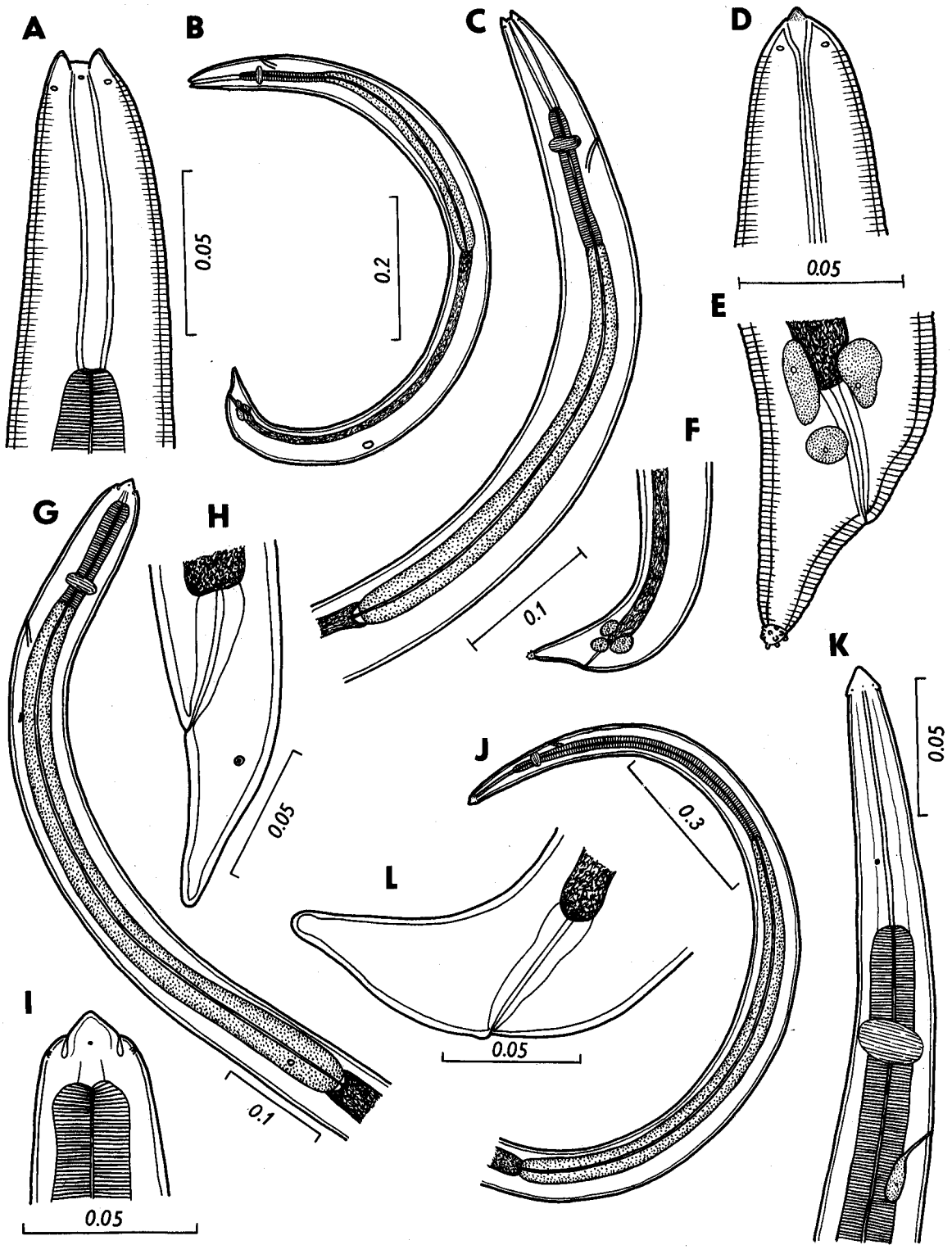

Fig. 1. Nematode larvae from fishes. **A–F** – *Physocephalus sexalatus* (Molin, 1860). (**A** – cephalic end, lateral view, **B** – total view, **C** – anterior end, **D** – cephalic end, dorsoventral view, **E** – tail, **F** – posterior end); **G–I** – *Spiroxys* sp. (**G** – anterior end, **H** – tail, **I** – cephalic end, lateral view); **J–L** – Acuariidae gen. sp. (**J** – anterior end, **K** – cephalic end, lateral view, **L** – tail).

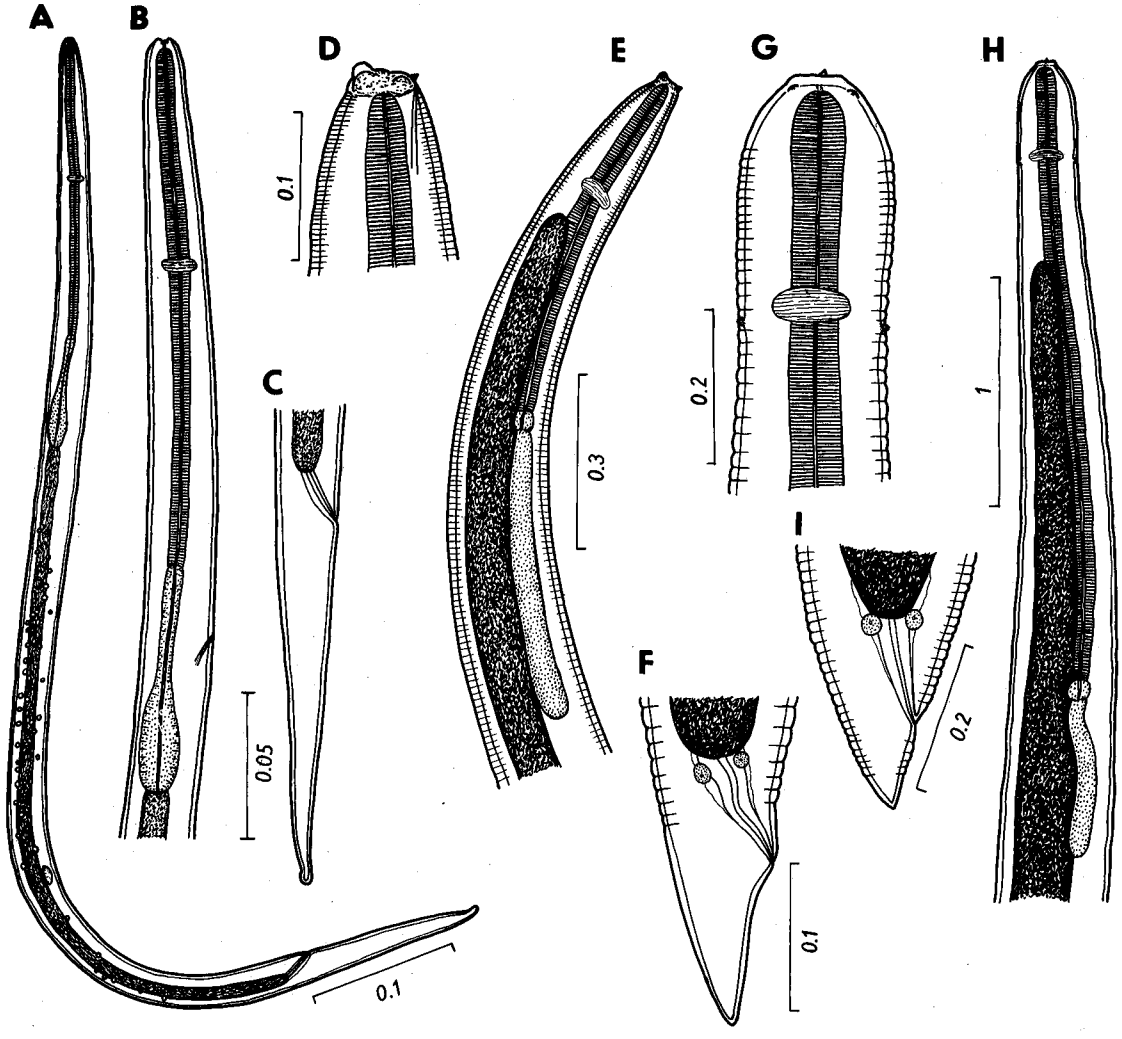

Fig. 2. Nematode larvae from fishes. **A–C** – *Falcaustra* sp. (**A** – total view, **B** – anterior end, **C** – tail); **D–F** – *Contracaecum* sp. Type 1. (**D** – cephalic end, lateral view, **E** – anterior end, **F** – tail); **G–I** – *Contracaecum* sp. Type 2. (**G** – cephalic end, ventral view, **H** – anterior end, **I** – tail).

Fam. Gnathostomatidae Railliet, 1895

3. ***Spiroxys*** sp. larvae Fig. 1G–I

Description (5 specimens from *C. meeki*): Small nematodes with finely transversally striated cuticle. Length of body 2.03–2.17, maximum width 0.060–0.078. Cephalic end provided with two large triangular lateral pseudolabia 0.012–0.015 long, each with two slit-like depressions at base; two cephalic papillae and one small amphid present on either side at level of base of pseudolabia. Stoma weakly developed, very short. Oesophagus divided into narrow, anterior muscular part and broader posterior glandular part. Length of muscular oesophagus 0.129–0.135, of glandular oesophagus 0.555 –0.675. Nerve ring and excretory pore 0.114–0.120 and 0.174–0.186, respectively, from anterior extremity. Deirids relatively large, situated posteriorly to excretory pore, at 0.246–0.264 from anterior end of body. Intestine brownish, straight; rectum a hyaline tube. Tail conical, 0.057–0.075 long, with rounded tip. Pair of relatively large lateral papilla-like phasmids present somewhat posterior to level of anal opening.

Hosts: *Cichlasoma meeki* (Brind), *C. urophthalmus* (Günther) (both Cichlidae, Perciformes), *Poecilia velifera* (Regan), *Poecilia* sp. (both Poeciliidae, Atheriniformes) and *Astyanax fasciatus* (Characidae, Cypriniformes).

Site of infection: abdominal cavity, mesenteries, intestinal wall.

Localities: State of Yucatan: Noc-choncunchey (21 September 1993), Chen-há (18 October 1993, 27 June, 29 August and 13 September 1994) and Dzonot Cervera (23 May 1994); State of Quintana Roo: Box-toro (13 May

1994), Escondido (11 May 1994) and Dos Bocas (5 April and 16 October 1994).

Prevalence and intensity: Noc-choncunchey (*C. meeki*) – 2 fishes infected/6 fishes examined, intensity 7–8 larvae; Chen-há: *C. urophthalmus* – 5/41, 1–7; *P. velifera* – 1/3, 1; *R. guatemalensis* – 2/8, 3–8; Dzonot Cervera (*A. fasciatus*) – 1/5, 1; Box-toro: *A. fasciatus* – 1/3, 4; *Poecilia* sp. – 1/1, 1; Escondido (*A. fasciatus*) – 2/6, 1–3; Dos Bocas (*A. fasciatus*) 2/7, 1–2.

Comments: The genus *Spiroxys* Schneider, 1866 is represented in North and Central America by seven species parasitizing mainly freshwater turtles (Baker 1987); of them, the following four species have been recorded from Mexico: *S. contortus* (Rudolphi, 1819), *S. corti* Caballero, 1935, *S. susanae* Caballero, 1941 and *S. triretrodens* Caballero et Zerecero, 1943. Because specific features are found in adults, the congeneric larvae from paratenic hosts (e.g., fishes) cannot be identified to species.

The intermediate hosts of *Spiroxys* spp. are various copepods, whereas fishes, amphibians (tadpoles, frogs, newts) and some invertebrates (dragonfly larvae, aquatic snails) serve as paratenic hosts (Hedrick 1935, Khromova 1971, Hasegawa and Otsuru 1978, Bartlett and Anderson 1985). *Spiroxys* larvae are frequently found in naturally infected fishes (e.g., Hedrick 1935, Hoffman 1967, Moravec and Baruš 1971, Moravec 1994); in Mexico, *Spiroxys* sp. larvae were reported from *Cichlasoma meeki* and *C. pasionis* from Tabasco by Osorio Sarabia et al. (1987). Our findings extend the list of fish host species.

The *Spiroxys* larvae from paratenic hosts are considered to be at the third larval stage.

Fam. Kathlaniidae Lane, 1914

4. *Falcaustra* sp. larvae Fig. 2A–C

Description (5 larvae from *C. urophthalmus*): Small, slender colourless nematodes with almost smooth cuticle. Length of body 0.909–0.948, maximum width 0.024–0.030. Cephalic end rounded, provided with six small lips; mouth papillae indistinguishable in lateral view. Deirids not observed. Body contains numerous distinct, almost regularly spaced hypodermal cell nuclei. Oesophagus 0.291–0.297 long, subdivided into anterior corpus (0.198–0.222 long and 0.007 wide) and posterior part (length 0.075–0.096), consisting of isthmus and bulb; bulb (0.042–0.045 long and 0.012–0.018 wide) lacks sclerotized valves. Mid region of oesophagus surrounded by numerous small pseudocoelomatic cells. Nerve ring encircling oesophageal corpus at its middle third, 0.063–0.099 from anterior extremity. Excretory pore at level of isthmus, 0.207–0.213 from anterior end of body. Oesophagus opens into intestine through small valve. Intestine light-coloured, straight, narrow. Small oval genital primordium situated ventrally in posterior part of body, at 0.303–0.348 from posterior extremity. Tail slender, conical, 0.114–0.147 long, with rounded tip.

Hosts: *Cichlasoma meeki* (Brind), *C. octofasciatum* (Regan), *C. urophthalmus* (Günther), *Petenia splendida* (Günther) (all Cichlidae, Perciformes), *Astyanax fasciatus* (Cuvier) (Characidae, Cypriniformes), and *Rhamdia guatemalensis* (Günther) (Pimelodidae, Siluriformes).

Site of infection: abdominal cavity (mainly surface of intestine), liver, gall-bladder, mesenteries, brain (free or encysted).

Localities: State of Yucatan: Noc-choncunchey (21 September 1993 and 21 September 1994), Chen-há (18 October 1993, 27 June, 4 and 11 July 1994), Dzonot Cervera (23 May 1994) and Hodz-ob (23 May 1994); State of Quintana Roo: Dos Bocas (5 April and 16 October 1994) and Box-toro (16 May 1994).

Prevalence and intensity: Noc-choncunchey: *C. meeki* – 1 fish infected/6 fishes examined, intensity 2 larvae; *P. splendida* – 1/1, 12; Chen-há: *C. urophthalmus* – 27/43, 1–400; *R. guatemalensis* 4/8, 1–5; Dzonot cervera (*C. urophthalmus*) – 6/1 0, 20–250; Hodz-ob (*C. urophthalmus*) – 3/11, 4–185 ; Dos Bocas (*A. fasciatus*) – 5/7, 17–100; Box-toro (*C. octofasciatus*) – 1/2, 2.

Comments: By their morphology and measurements these larvae correspond to those identified by Moravec et al. (1995c) as the third-stage larvae of *Falcaustra* sp. Type 2, originally described from freshwater fishes in Texas, U.S.A. The above authors reported these larvae as frequent parasites of the abdominal cavity, mesenteries and liver of the cichlid *Cichlasoma cyanoguttatum*, centrarchids *Lepomis auritus* and *Lepomis* sp. and the poeciliid *Gambusia affinis* from the San Marcos River and Spring Lake in central Texas. They supposed that these larvae belonged to one or more *Falcaustra* species parasitizing turtles and that fishes played a role of paratenic hosts of these nematodes.

The genus *Falcaustra* Lane, 1915 includes many species parasitic as adults mainly in turtles, less frequently in amphibians and fishes (but no species is known from fishes in North America) and one species was described even from a bird (Baker 1987). Their life cycles are unknown (Anderson 1992) and until recently there existed only two descriptions of *Falcaustra* third-stage larvae in the literature: third-stage larvae of probably *F. wardi* (Mackin, 1936), a parasite of North American turtles, were found in the snail *Lymnaea stagnalis* in Canada (Bartlett and Anderson 1985) and those of *F. babei* (Ha Ky, 1971), a fish parasite in Vietnam, were reported by Sey and Moravec (1986) as the hyperparasites of the fish trematode *Amurotrema dombrowskajae* Akhmerov, 1959. *Falcaustra*

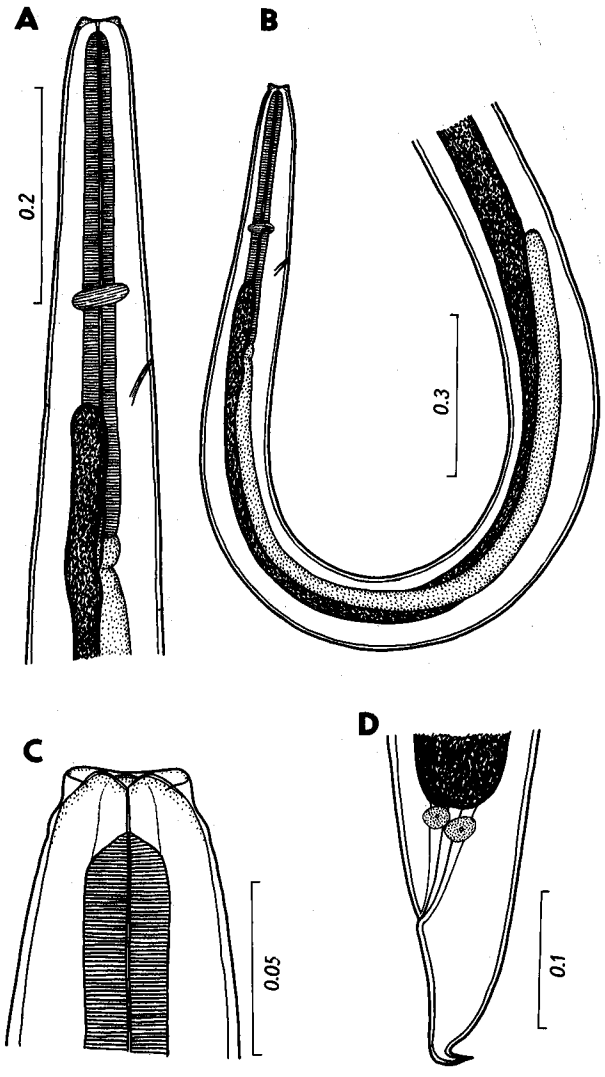

Fig. 3. *Hysterothylacium cenotae* (Pearse, 1936) larva from *Anguilla rostrata*. **A** – cephalic end; **B** – anterior end of body; **C** – cephalic end, lateral view; **D** – tail.

larvae were first reported from vertebrates by Moravec et al. (1995c), who found two types of congeneric larvae from fishes in Texas (in addition to the above mentioned Type 2 larvae they recorded also Type 1 larvae from the percids *Etheostoma fonticola* and *E. lepidotum*, characterized by the sharply pointed tail tip).

The transmission of *Falcaustra* species has not yet been determined. Bartlett and Anderson (1985) suppose that snails serve as paratenic hosts for *Falcaustra wardi* and Moravec et al. (1995c) speculate that fishes are the paratenic hosts of some *Falcaustra* species parasitizing turtles.

The findings of *Falcaustra* Type 2 larvae in fishes of Yucatan support the view of Moravec et al. (1995c) that they belong to one or more species parasitic in freshwater turtles. Large numbers of these larvae were recorded from fishes from the cenotes and lakes ("aguadas") with frequent occurrence of turtles (e.g., Chen-há Cenote, "aguada" Xpoc) where also larvae of other nematodes parasitic in turtles (*Spiroxys*, *Serpinema*) were commonly found in fishes.

Similar to observations by Moravec et al. (1995c) in Texas, the *Falcaustra* larvae occurred in fishes from some cenotes in Yucatan in large numbers, either unencapsulated or encapsulated in small round thin- or thick-walled capsules, each containing one to many larvae. Although these larvae were usually found in the abdominal cavity of fishes, mostly on the surface of the liver, intestine and mesenteries, they frequently penetrate into various organs (e.g., gall-bladder, swimbladder) and sometimes large numbers of unencapsulated larvae were found in the host's brain. It can be supposed that in such localisation they may be very harmful to its host fish. It appears that the highest degree of infection with *Falcaustra* larvae occurs in Yucatan in perciform fishes (cichlids) and the same was observed in Texas; this may be associated with the ecology of these fishes.

The nematode larvae from *Cichlasoma tetracantha* from Cuba, reported by Moravec and Baruš (1971) under the designation "Nematoda gen. sp. larvae", belonged evidently to the genus *Falcaustra,* too.

Fam. Anisakidae Railliet et Henry, 1912

5. ***Hysterothylacium cenotae*** (Pearse, 1936) larvae
Fig. 3

Description (5 specimens): Small, whitish nematodes. Length of body 4.16–6.53, maximum width 0.122–0.190. Cuticle with very fine transverse striation or almost smooth. Head end rounded, provided with cuticular mounds surrounding mouth opening. Anlagen of lips weakly developed. Oesophagus almost cylindrical, without any inflation at its anterior end, measuring 0.402–0.544 in length. Nerve ring and excretory pore 0.216–0.299 and 0.270–0.327, respectively, from anterior extremity. Ventriculus spherical, 0.030–0.039 in diameter. Posterior ventricular appendix long, measuring 1.23–1.69. Intestine straight, light-coloured. Intestinal caecum, extending anteriorly approximately to mid-distance between nerve ring and ventriculus, 0.090–0.141 long. Length ratio of intestinal caecum and ventricular appendix 1 : 12.0–13.7. Rectum hyaline tube. Three oval unicellurar rectal glands well developed. Tail conical, sharply pointed, 0.098–0.132 long.

Host: *Anguilla rostrata* (LeSueur) (Anguillidae, Anguilliformes).

Site of infection: encysted on surface of viscera and swimbladder.

Localities: State of Quintana Roo: Cenote Salvaje, Rancho San Erick (23 April 1983), and Cenote Zacate, archeological zone of Xel-há (24 April 1987) (both Cozumel District).

Prevalence and intensity: Salvaje – 2 larvae in 1 fish examined; Zacate – 12 larvae in 1 fish examined.

Comments: These nematodes represent the third-stage larvae of the genus *Hysterothylacium* Ward et Magath, 1917, including the forms parasitic as adults in various marine and freshwater fishes. Larvae of this genus differ from those of the related genus *Contracaecum* Railliet et Henry, 1912 (adults in birds and mammals) mainly in the position of the excretory pore near the nerve ring.

At present the genus *Hysterothylacium* comprises about 60 species parasitizing mainly marine fishes (Bruce et al. 1994). Of them, only four species are known from North American freshwater fishes: *H. cenotae* (Pearse, 1936) from the bagre *Rhamdia guatemalensis* from Mexico (Yucatan) (see Moravec et al. 1995a,b) and *H. brachyurum* Ward et Magath, 1917, *H. dollfusi* (Schmidt, Leiby et Kritsky, 1974) and *H. alanarum* Rye et Baker, 1984 from centrarchid and polyodontid fishes from the U.S.A. and Canada (Rye and Baker 1984). The identification of larvae of the present material as *H. cenotae* is based on their morphological similarity to the adults of this species (measurements and length ratio of ventricular appendix and intestinal caecum, shape of tail tip) and the fact that this is the only *Hysterothylacium* species occurring in cenotes in Yucatan (Moravec et al. 1995a,b).

The life cycle of this species is not known, but it is apparent that eels (*A. rostrata*) acquire infection in the environment of cenotes shared with bagres (*R. guatemalensis*), the definitive hosts of *H. cenotae*; eels probably play a role of paratenic hosts of this nematode species.

6. ***Contracaecum*** sp. larvae – Type 1 Fig. 2D–F

Description (5 specimens, 3 from *A. fasciatus*, 2 from *R. guatemalensis*; measurements of latter in parentheses): Body 4.88–5.49 (3.94–4.68) long and 0.218–0.231 (0.218–0.258) wide. Cuticle transversely striated, length of striae at middle of body 0.015–0.024 (0.018–0.024). Head end rounded, bearing small ventral tooth; anlagen of lips little developed; most larvae with small, round dorsal formation formed by inflated cuticle. Oesophagus narrow, 0.503-0.680 (0.625–0.775) long. Ventriculus small, size 0.030–0.036 × 0.030–0.036 (0.030–0.039 × 0.039–0.045); posterior ventricular appendix long and wide, measuring 0.449 –0.503 (0.449–0.666). Nerve ring 0.204–0.245 (0.190 –0.218) from anterior extremity. Intestinal caecum wide, extending anteriorly almost to nerve ring; its length 0.403–0.449 (0.435–0.598). Intestinal caecum to ventricular appendix length 1 : 1.00–1.18 (1 : 1.03 –1.11). Genital primordium indistinct. Tail conical, 0.122–0.136 (0.109–0.136) long.

Hosts: *Astyanax fasciatus* (Cuvier) (Characidae, Cypriniformes) and *Rhamdia guatemalensis* (Günther) (Pimelodidae, Siluriformes).

Site of infection: abdominal cavity, mesenteries, liver.

Localities: State of Yucatan: Noc-choncunchey (2 February and 21 September 1994) and Ixin-há (13 June and 11 July 1994); State of Quintana Roo: Escondido Cenote (9 May 1994) and Cabañas (2 May 1994).

Prevalence and intensity: Noc-choncunchey (*A. fasciatus*) – 7 fishes infected/15 fishes examined, intensity 1–11 larvae; Ixin-há (*R. guaemalensis*) – 2/90, 1; Escondido (*A. fasciatus*) – 1/6, 1; Cabañas (*A. fasciatus*) – 2/5, 1.

Comments: These larvae are characterized by the relatively small body measurements and by the presence of a very long ventricular appendix the length of which usually slightly exceeds that of the intestinal caecum. Similar *Contracaecum* larvae from fishes have been reported, for example, by Kloss (1966) and Moravec et al. (1993) from Brazil. The adult forms of these larvae are apparently parasitic in fish-eating birds; fishes serve either as the second intermediate hosts or as paratenic hosts.

7. ***Contracaecum*** sp. larvae – Type 2 Fig. 2G–I

Description (5 specimens from *C. urophthalmus* and *P. velifera*): Body brownish, 20.40–23.53 long and 0.680–0.775 wide. Transverse striation of cuticle more distinct on cephalic and caudal ends. Head end rounded, bearing small ventral cuticular tooth 0.003 long. Ventriculus small, rounded, size 0.082–0.095 × 0.082 –0.109; posterior ventricular appendix relatively short, measuring 0.476–0.666. Nerve ring 0.299–0.326 from posterior extremity. Deirids situated at level or slightly posterior to level of nerve ring, 0.299–0.340 from anterior end of body. Intestine brownish, dark. Intestinal caecum long, exteding anteriorly somewhat below nerve ring, measuring 1.72–1.93. Length ratio of intestinal caecum and ventricular appendix 1 : 0.3. Genital primordium indistinct. Rectum short hyaline tube; three small unicellular rectal glands present.

Hosts: *Astyanax fasciatus* (Cuvier) (Characidae, Cypriniformes), *Rhamdia guatemalensis* (Günther) (Pimelodidae, Siluriformes), *Poecilia velifera* (Regan), *P. petenensis* Günther (both Poeciliidae, Atheriniformes), *Anguilla rostrata* (LeSueur) (Anguillidae,

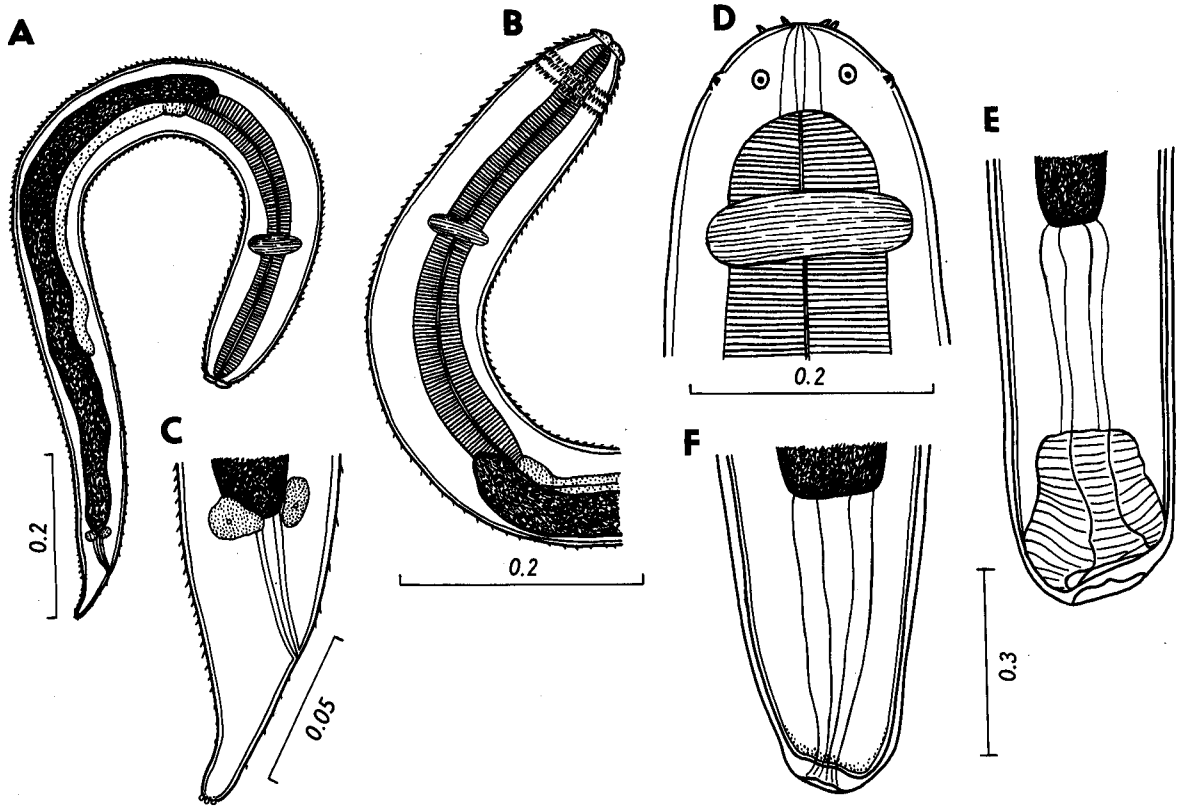

Fig. 4. Nematode larvae from fishes. **A–C** – *Goezia* sp. (**A** – total view, **B** – cephalic end, **C** – tail); **D–F** – *Eustrongylides* sp. (**D** – cephalic end, **E** – caudal end of male larva, **F** – caudal end of female larva).

Anguilliformes), *Cichlasoma synspilum* Hubbs, *C. urophthalmus* (Günther) (Cichlidae, Perciformes), and *Gobiomorus dormitor* Lacépede (Eleotridae, Perciformes).

Site of infection: abdominal cavity, mesenteries, liver.

Localities: State of Yucatan: Noc-choncunchey (2 February 1994), Chen-há (18 October 1993, 27 June and 13 September 1994), Xmucuy (25 October 1993, 25 July 1994), Dzonot Cervera (23 May 1994) and Hodz-ob Cenote (23 May 1994); State of Quintana Roo: Gran Cenote (25 April 1994), Cabañas (2 May 1994), Cenote Cristal I (not positioned) (4 March 1986) and Cenote Azul (5 April 1994).

Prevalence and intensity: Noc-choncunchey: *C. urophthalmus* – 1 fish infected/2 fishes examined, intensity 2 larvae; *P. latipinna* – 1/1, 1; Chen-há: *R. guatemalensis* – 2/8, 1–18; *P. velifera* – 2/13, 1; *C. urophthalmus* – 3/35, 1–3; Xmucuy (*R. guatemalensis*) – 4/21, 1–2; Dzonot Cervera: *A. fasciatus* – 1/3, 1; *C. urophthalmus* – 3/10, 1–2; Hodz-ob (*C. urophthalmus*) – 2/9, 1; Gran Cenote: *A. fasciatus* – 3/14, 2–3; *R. guatemalensis* – 1/2, 3; Cabañas: *A. fasciatus* – 1/5, 1; *C. synspilum* – 1/2, 1; *C. urophthalmus* – 1/4, 1; Cristal I (*A. rostrata*) – 1/1, 38; Cenote Azul (*G. dormitor*) – 1/2, 2.

Comments: This type of larvae differs from the foregoing type (Type 1) principally in very different length ratio of the intestinal caecum and the ventricular appendix, and in larger body. Adults of these larvae may belong to the morphological group of species represented by *C. microcephalum* (Rudolphi, 1819), *C. multipapillatum* (Drasche, 1882), *C. micropapillatum* (Stossich, 1890), *C. caballeroi* Bravo Hollis, 1939, *C. plagiaticum* Lent et Freitas, 1948 among others, parasitizing mainly fish-eating birds. Similar larvae were found, for example, in fishes in Cuba (Baruš and Moravec 1967, Moravec and Baruš 1971) and Brazil (Moravec et al. 1993). Fishes may apparently serve only as paratenic hosts.

8. ***Goezia*** sp. larva Fig. 4A–C

Description (1 specimen): Length of body 1.31, maximum width 0.093. Cuticle of whole body provided with numerous transverse rows of spines; altogether about 90 rows, each composed of some 72 spines, present. Spines distincly larger (length 0.003) on anterior

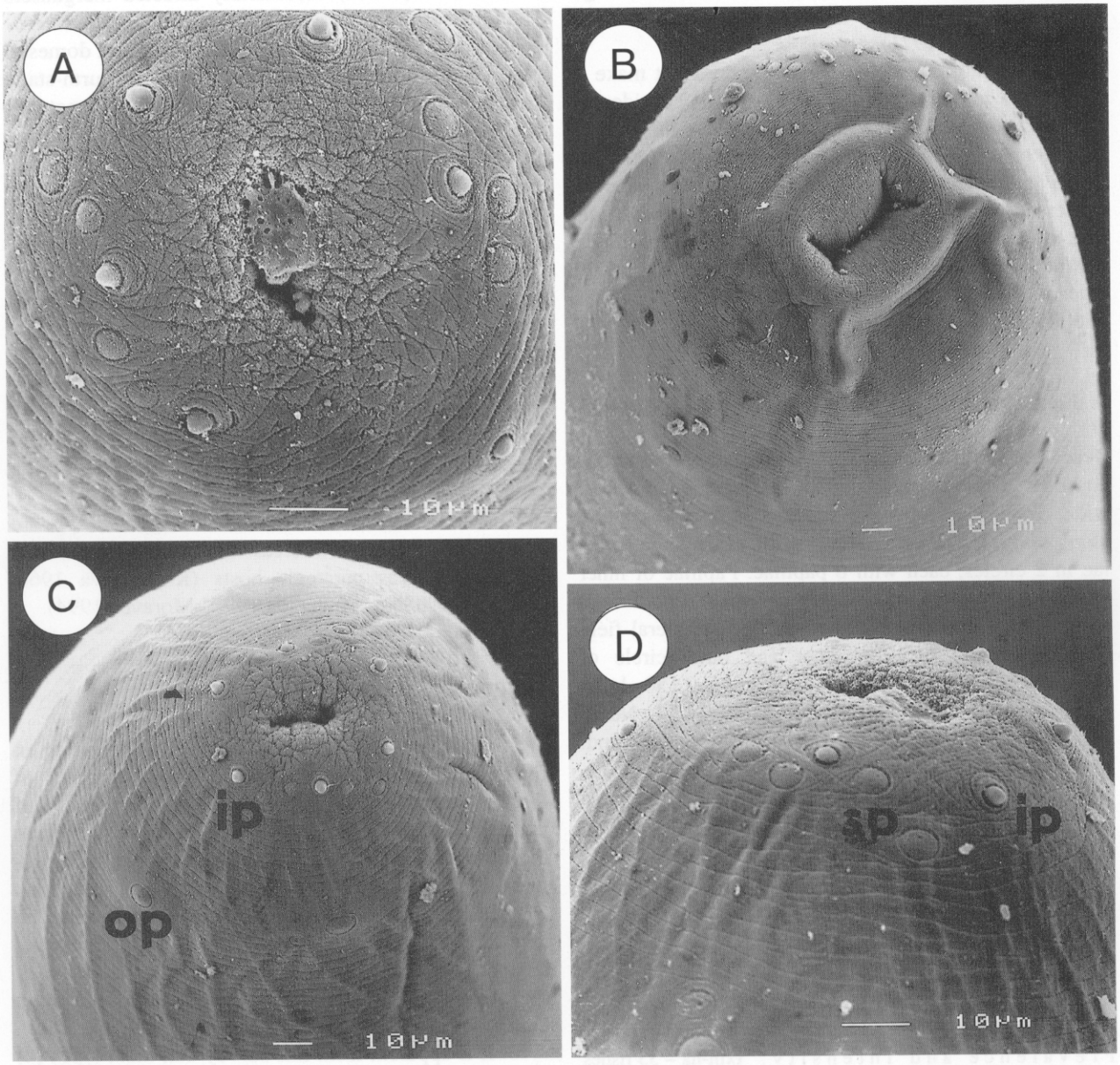

Fig. 5. *Eustrongylides* sp. larva form *Rhamdia guatemalensis*, SEM micrographs. **A** – cephalic end, apical view; **B** – caudal end; **C** – subapical view of cephalic end; **D** – cephalic end, lateral view. ip – inner cephalic papilla, op – outer cephalic papilla, sp – somatic papilla, a – anus.

part of body. Lips moderately developed. Oesophagus 0.228 long, provided with ventriculus 0.021 in diameter; ventricular appendix 0.780 long, length of anterior intestinal caecum 0.033. Tail conical, 0.066 long, with a few mucrons at tip.

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

Site of infection: stomach.

Locality: State of Yucatan: Chen-há (13 September 1994).

Prevalence and intensity: in 1 out of 8 *R. guatemalensis* examined, 1 larva was found.

Comments: The genus *Goezia* Zeder, 1800 includes many species that are the parasites of freshwater and marine fishes and, less frequently, of aquatic reptiles. In addition to adult *Goezia*, congeneric juveniles (third- and fourth-stage larvae) occur frequently in various fish species serving only as paratenic hosts (Moravec 1994, Moravec et al. 1994). Intermediate hosts of *Goezia*

species are copepods in which the infective third-stage larvae may develop up to the length of 1.7 mm (Mozgovoy et al. 1971).

The morphology of *Goezia* larvae does not make it possible to identify the species. However, considering the ecological situation in the locality (Chen-há Cenote) where the larva of the present material was found in *Rhamdia guatemalensis*, especially the presence of a numerous local population of *Cichlasoma urophthalmus*, it may well be that this larva is conspecific with *G. nonipapillata* Osorio Sarabia, 1982; the latter is the only *Goezia* species described from freshwater fishes (cichlids) in Mexico.

9. ***Eustrongylides*** sp. larvae Figs. 4D–F, 5

Description (3 specimens): Larval body thread-like, white or brownish, 49.78–60.38 long and 0.571–0.680 wide. Two lateral rows of somatic papillae extending along body. Head end rounded, with 12 cephalic papillae in 2 circles, each with 6 papillae. Papillae of inner circle with narrow bases, finger-shaped. Papillae of outer circle low, with broad bases. A few lateral field papillae present between inner and outer circle of cephalic papillae. Buccal cavity 0.095–0.150 long, length of cylindrical oesophagus 11.49–14.24. Nerve ring encircling oesophagus 0.163–0.245 from head end. Anal opening terminal. Length of rectum 0.544–0.612. Male larvae with developing muscular copulatory bursa (Fig. 4E). Larvae undergoing their moult (outer cuticle loosen).

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

Sites of infection: encysted in musculature.

Localities: State of Yucatan: Ixin-há (28 October 1993, 13 June, 11 July, 22 August, 20 September and 17 October 1994) and Dzonot Cervera Cenote (23 May 1994).

Prevalence and intensity: Ixin-há – 35 fishes infected/90 fishes examined, intensity 1–11 larvae; Dzonot Cervera – 1/1, 1.

Comments: According to Measures (1988a), only two valid species of the genus *Eustrongylides* Jägerskiöld, 1909, *E. ignotus* Jägerskiöld, 1909 and *E. tubifex* (Nitzsch in Rudolphi, 1819) are known to occur in the New World; while the definitive hosts of the first species are piscivorous birds of the orders Ciconiiformes and Pelecaniformes, the host range of the latter includes Gaviiformes, Anseriformes, Ciconiiformes and Podicipediformes.

By the character of their cephalic papillae, the larvae of the present material (Fig. 5) resemble *E. ignotus*, but their possible appurtenance to this species should be confirmed experimentally.

Measures (1988d) successfully infected mergansers (*Mergus serrator*, *M. cucullatus*), herons (*Ardea herodias*), cormorants (*Phalacrocorax auritus*) and domestic ducks (*Anas platyrhynchos*) with *E. tubifex* fourth-stage larvae from fish in Ontario, Canada; the nematodes quickly matured in them and the females produced eggs 10–17 days postinfection. Our attempts to infect small domestic ducks (*A. platyrhynchos*) with *Eustrongylides* larvae from *Rhamdia guatemalensis* from Ixin-há Cenote were unsuccessful. The nematode fourth-stage larvae (5 per duck) were fed to 5 ducklings which were subsequently examined 10 days p.i.; only one non-developing but still living larva was found attached to the stomach wall of one experimental duck; other ducks were either free of nematodes or had only dead nematode larvae in their digestive tract. This supports the view that ducks are not suitable definitive hosts for this species and, consequently, that they are not conspecific with *E. tubifex*.

The intermediate hosts of *Eustrongylides* spp. are aquatic oligochaetes, whereas fishes, amphibians and reptiles serve as paratenic hosts (Karmanova 1968, Measures 1988b,c, Anderson 1992, Moravec 1994).

DISCUSSION

This survey shows that nematodes occurring in fishes only as larvae are rather frequent parasites of these hosts in cenotes in Yucatan. The number (9) of these forms represents one half of species found to form the nematode fauna of fishes in these ecologically remarkable habitats in Yucatan (see Moravec et al. 1995a). However, since many of these larvae cannot be identified to species without previous feeding experiments to definitive hosts, it may well be that some of the congeneric larvae recorded in fishes include more than a single species.

It is apparent from this survey that most types (4) of larval nematodes recorded from cenote fishes belong to species maturing in fish-eating birds (*Eustrongylides*, *Contracaecum*, Acuariidae gen. sp.), two types (*Falcaustra*, *Spiroxys*) represent larval forms of the parasites of reptiles (apparently of turtles), two types (*Hysterothylacium*, *Goezia*) are maturing in piscivorous fishes, and larvae of one species (*Physocephalus*) belong to the parasite of mammals. The most frequently found nematode larvae in cenote fishes were those maturing in fish-eating birds and reptiles, whereas the larvae of the parasites of mammals and piscivorous fishes were rather rare and restricted to a few localities.

It is apparent that in all these cases fishes play a role of paratenic hosts of these nematodes. Although the participance of fish is not obligate for completing their life-cycles, these hosts are very important from the

ecological point of view, representing usually the most significant source of infection for the definitive host.

The degree of host specificity of nematode larvae to their fish hosts is evidently lower than that of adult nematodes and they frequently occur in fishes belonging to phylogenetically distant fish orders (Moravec 1994); the same is indicated by the results of the present study, although a preference to certain host fishes is visible in some species (e.g., *Falcaustra* larvae occur mainly in perciform fishes). The presence of numerous nematode larvae may be rather harmful to their fish hosts and, of the larvae recorded in this study, larvae of the genera *Contracaecum*, *Falcaustra* and *Eustrongylides* seem to be the most pathogenic parasites.

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