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Observations on the biology of *Rhabdochona kidderi texensis*, a parasite of North American cichlids

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Abstract

An examination of a sample of benthic invertebrates collected from the Upper San Marcos River in southwestern Texas, USA in September 1999 revealed that the nymph of the ephemeropteran *Tricorythodes curvatus* served as natural intermediate host of the nematode *Rhabdochona kidderi texensis* (Nematoda: Rhabdochonidae), an intestinal parasite mainly of the Rio Grande perch (*Cichlasoma cyanoguttatum*) in this locality; the prevalence of the parasite's third- and fourth-stage larvae in mayflies was 6.8% with the intensity of 1–2 larvae per nymph. Live *R. kidderi texensis* eggs collected from nematodes recovered from *C. cyanoguttatum* in Texas were transported to the Czech Republic, where they were used to experimentally infect nymphs of the palaearctic mayfly species *Paraleptophlebia submarginata*; the development of infective third- and fourth-stage larvae in this experimental intermediate host was completed after approximately 10 days at 19°C. Infected nymphs were fed to aquarium-reared fishes, four *Cichlasoma nigrofasciatum* and one *Oreochromis niloticus*, of which only three of the former became infected. The last (fourth) moult of a male nematode was observed in *C. nigrofasciatum* 23 days p.i. and adult males and gravid females with not fully mature (non-embryonated) eggs in uteri on days 40 and 51 p.i. The prepatent period of *R. kidderi texensis* is approximately two months.

Introduction

The nematode *Rhabdochona kidderi texensis* Moravec & Huffman, 1988 is an intestinal parasite of cichlid fishes (mainly *Cichlasoma* spp.). Originally it was described from the Rio Grande perch, *Cichlasoma cyanoguttatum* (Baird and Girard) (type host), and the African mouth-breeder, *Oreochromis mossambicus* (Peters), from the Upper San Marcos River in Texas by Moravec & Huffman (1988); conspecific juvenile forms were found in the mosquitofish, *Gambusia affinis* (Baird and Girard) (family Poeciliidae). Later, this nematode subspecies was reported from *Cichlasoma fenestratum* (Günther) and *C. urophthalmum* (Günther) from southern Mexico (Veracruz and Yucatán) (Pérez-Ponce de León *et al.*, 1996; Moravec, 1998; Moravec *et al.*, 1999). Neither the life cycle of this subspecies nor the nominotypical subspecies *R. kidderi kidderi* (Pearse, 1936), parasitic in the pimelodid catfish *Rhamdia guatemalensis* (Günther) and the blind cave fish *Ogilbia pearsei* (Hubbs) (Bythitidae, Ophidiformes) in Mexico, is known.

During a short visit of F.M. to Texas in September 1999, a sample of benthic invertebrates was collected from the Upper San Marcos River and examined for the presence of larvae of fish nematodes. The finding of the natural intermediate host of *R. kidderi texensis* and the results of subsequent experimental studies on the development of this parasite, carried out in the Czech Republic, are described below.

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Materials and methods

A sample of benthic macroinvertebrates was taken from the Upper San Marcos River in San Marcos, Hays County, southwestern Texas on 9 September 1999. This included the following organisms: Insecta: Ephemeroptera nymphs (*Tricorythodes curvatus*) (147 specimens), Odonata nymphs (36), Trichoptera larvae (15), Chironomidae larvae (2); Amphipoda: *Hyalella azteca* (49); Decapoda: small unidentified crayfish (2); Bivalvia: *Pisidium* spp. (12); Oligochaeta: large (3–7 cm long), unidentified specimens (5).

For examination, the invertebrates were pressed between two glass plates and inspected under the microscope using a low magnification (×36). Encapsulated larvae were removed from the intermediate host's tissue and teased from their capsules with very fine needles under the dissecting microscope. The liberated larvae were placed in a Petri dish containing physiological saline and were subsequently fixed by adding hot 4% formalin. The larvae were stored in 4% formalin.

For experimental work, about 30 gravid *R. kidderi texensis* females containing mature (larvated) eggs were collected from the intestines of *C. cyanoguttatum*. The fish were caught in the Upper San Marcos River in San Marcos, Texas, on 19 September 1999. The nematodes were placed in a vial with physiological saline, which was then placed in a thermoflask filled with ice, and transported by air to the laboratory of the Institute of Parasitology, ASCR, in České Budějovice, Czech Republic. The nematodes were distributed among three small Petri dishes (diameter 45 mm) filled with water (ten nematodes per dish) and the nematode bodies were torn by fine needles and the eggs teased out from the uteri. A small amount of detritus, pieces of dry leaves and some larval aquatic invertebrates, collected from the Malše River in České Budějovice, were added into each Petri dish; dish no. 1: seven *Paraleptophlebia submarginata* nymphs and ten *Ecdyonurus* spp. nymphs (both Ephemeroptera); dish no. 2: 20 Baetidae nymphs and one *Habroleptoides modesta* nymph (both Ephemeroptera); dish no. 3: ten unidentified Plecoptera nymphs and ten Trichoptera larvae (*Rhyacophila* sp.). The dishes were covered with a fine silon cloth fixed with a rubber ring and submerged in a larger plastic dish with aerated water kept at 19°C.

Experimental insect larvae were first examined 10 days after exposure to infection. By 33 days, all invertebrates were examined or had died, except for five *P. submarginata* nymphs (body length about 1 cm). As the latter were likely to be infected with infective larvae of the nematode, they were individually fed to four aquarium-reared *C. nigrofasciatum* (Günther) (body length 7.5–8.5 cm) and one *Oreochromis niloticus* (Linnaeus) (12 cm) kept at 20°C and fed with commercially supplied frozen chironomid larvae. Experimental fishes were examined on days 23, 40, 51 and 68 p.i.

All nematodes recovered were fixed in 4% formalin and examined microscopically either uncleared or cleared in glycerine. Drawings were made with the aid of a Zeiss microscope drawing attachment. All measurements are in micrometres unless otherwise stated.

Results

Natural R. kidderi texensis *infection in* C. cyanoguttatum

In September 1999, seven specimens of *C. cyanoguttatum* (body length 8–20 cm) from the Upper San Marcos River in San Marcos, Texas were examined and all (prevalence 100%) were infected with *R. kidderi texensis*; the intensity of infection was 5–237 (mean 60) nematodes per fish. The nematodes were always located in the middle part of the host's intestine.

Natural intermediate host of R. kidderi texensis

Of the aquatic invertebrates examined from the Upper San Marcos River in San Marcos in September, only the mayfly nymphs *Tricorythodes curvatus* Allen, 1977 (family Leptohyphidae) were found to harbour infective larvae of *Rhabdochona* Railliet, 1916. Since only one *Rhabdochona* species, *R. kidderi texensis*, is known to occur in fishes in this locality (see Underwood & Dronen, 1984; Moravec & Huffman, 1988; our own unpublished data), there is little doubt that these larvae belonged to this species. It is remarkable that *T. curvatus* was the only ephemeropteran species found in the sample; the mayfly nymphs were mostly advanced (female larvae containing numerous eggs), shortly before their emergence.

Of a total of 147 specimens of *T. curvatus* examined, ten were infected with *R. kidderi texensis* larvae (prevalence 6.8%), with eight mayflies harbouring one nematode larva each and two mayflies with two larvae each. Each larva was spirally coiled inside a thin-walled, lens-shaped, transparent capsule about 200 in diameter, located in the body cavity in the abdomen of the intermediate host. The larvae were at the third or the fourth larval stage.

The third-stage larva (fig. 1C,G) was 1618 long and 39 wide, with smooth cuticle. Its vestibule including prostom, the muscular oesophagus and the glandular oesophagus were 84, 96 and 453 long, respectively. The prostom was of a *Cystidicola*-type, 6 long and 6 wide, lined with two (dorsal and ventral) longitudinal thickenings, protruding anteriorly into the buccal cavity as small teeth. Deirids and the nerve ring were situated 54 and 111 from the anterior extremity; the excretory pore was not located. The tail was conical, sharply pointed, 90 long.

The larva undergoing the third moult (fig. 1D) was 1918 long and 39 wide. Its vestibule including prostom, the muscular oesophagus and the glandular oesophagus were 75, 150 and 669 long, respectively. The old vestibule including the prostom of the third larval stage (6 long and 6 wide) was still inside the newly formed one; the newly formed prostom was 12 long and 9 wide. The nerve ring and the excretory pore were 108 and 144, respectively, from the anterior extremity; deirids were not observed. The tail was 114 long.

The female fourth-stage larva (fig. 1A,B,E,F) was 2244 long and 42 wide. Its vestibule including prostom, the muscular oesophagus and the glandular oesophagus were 99, 177 and 795 long, respectively. The prostom was of a *Rhabdochona*-type, 12 long and 9 wide, funnel-shaped, internally lined with six longitudinal thickenings protruding anteriorly into the buccal cavity as small

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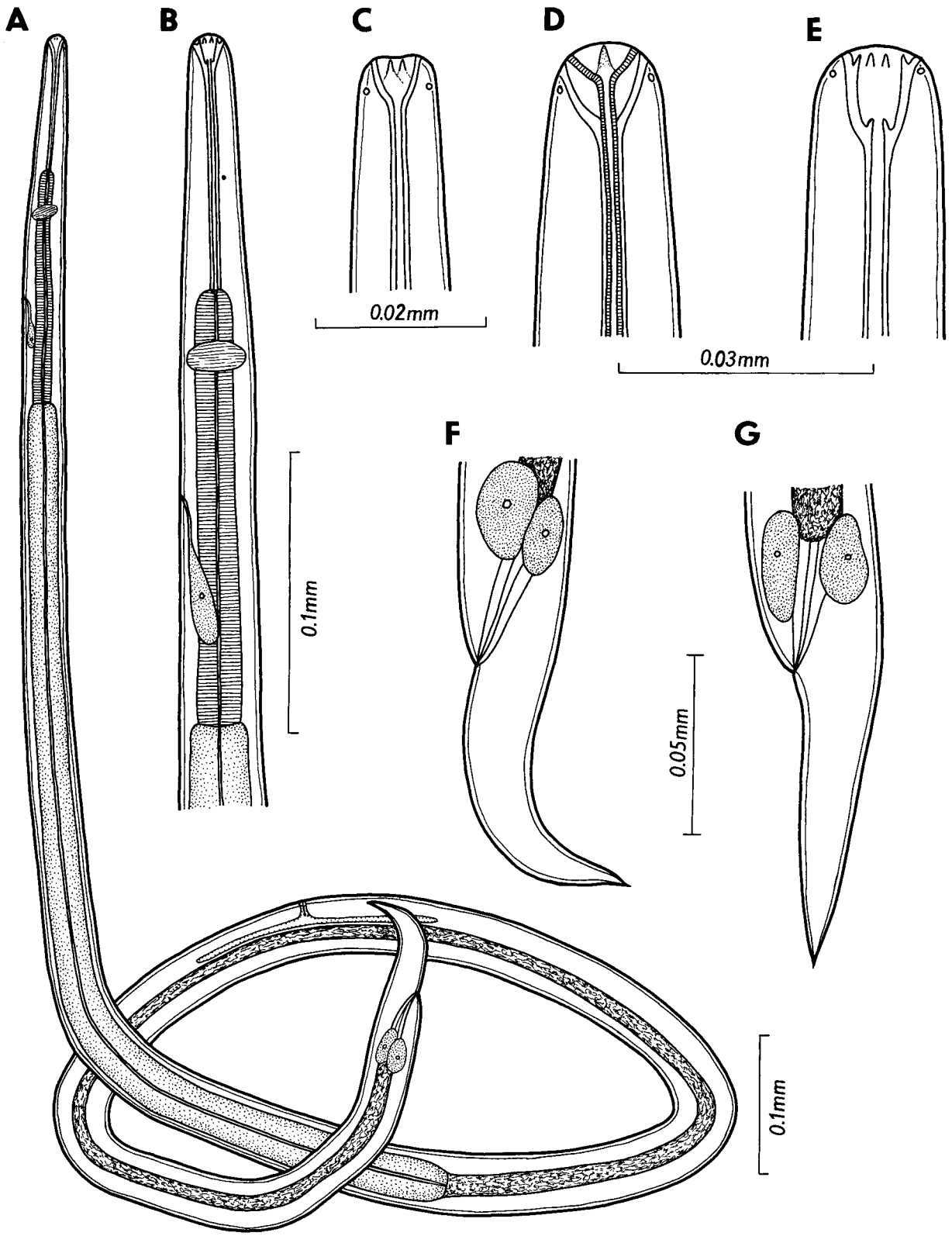

Fig. 1. *Rhabdochona kidderi texensis* Moravec & Huffman, 1988, larvae from the natural intermediate host, the mayfly larva *Tricorythodes curvatus*. A, B, E, F, fourth-stage larva (A, general view; B, anterior end, lateral view; E, prostom, lateral view; F, tail); D, prostom of a moulting larva (third moult), lateral view; C, G, third-stage larva (C, cephalic end with prostom, sublateral view; G, tail).

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teeth; the base of prostom was provided with conspicuously large basal teeth. Deirids, the nerve ring and the excretory pore were 60, 129 and 165 from the anterior extremity, respectively. The anlage of the vulva was situated 690 from the posterior end of body. The tail was conical, sharply pointed, 87 long.

Experimental R. kidderi texensis *infection of palaearctic species of mayflies*

Of the Central European species of aquatic invertebrates used in the experiment with *R. kidderi texensis*, only the mayfly nymphs *Paraleptophlebia submarginata* (Stephens, 1835) (family Leptophlebiidae) were successfully infected with the eggs of this parasite.

Since only seven mayfly nymphs of this species were employed in the experiment and one of them soon died, only one mayfly nymph was examined for the presence of *Rhabdochona* larvae 10 days p.i. This nymph harboured a total of three *Rhabdochona* larvae in its abdomen: two unencapsulated third-stage larvae and one capsule, size 204 × 177, containing probably the young fourth-stage larva (this was not isolated from the capsule).

The body of these unencapsulated third-stage larvae was 885–1026 long and 33–36 wide. Their vestibule including prostom, the muscular oesophagus and the glandular oesophagus were 54–69, 117–135 and 273–294 long, respectively. The prostom was 6 long and 6 wide. Distance of the nerve ring from the anterior extremity was 69–87, that of the excretory pore in the larger specimen 123. The genital primordium was 264–312 from the posterior end of body. The tail was 57–72 long.

The remaining five surviving *P. submarginata* nymphs were considered as probably infected and, consequently, they were kept for additional 21 days and then fed to experimental fishes.

Experimental definitive host of R. kidderi texensis

Although four *C. nigrofasciatum* and one *O. niloticus* were fed with mayfly nymphs possibly harbouring infective larvae of *R. kidderi texensis*, only three *C. nigrofasciatum* were later found to be infected. The morphology of nematodes recovered in this experiment corresponds to the description of this subspecies given by Moravec & Huffman (1988).

The *C. nigrofasciatum* examined 23 days p.i. harboured a juvenile male just undergoing the last (fourth) moult (fig. 2). This was 4393 long and 63 wide. Its vestibule including prostom, the muscular oesophagus and the glandular oesophagus were 108, 201 and 1319 long, respectively. The old vestibule including the prostom of the fourth-stage larva (12 long and 12 wide) was still inside the newly formed one; the newly formed prostom was 21 long and 15 wide. The nerve ring and the excretory pore were 156 and 222 from the anterior extremity, respectively. The spicules were weakly sclerotized. The larger (left) spicule was 1722 long, its shaft was 519 long, forming 30% of the spicule length and 39% of the body length. The smaller (right) spicule was 84 long. The length ratio of spicules was 1: 20.5. The caudal end was provided with six pairs (five subventral and one lateral) of preanal papillae and six pairs (five subventral and one lateral) of postanal papillae. The tail was 180 long. The entire body was still inside the cuticle of the fourth-stage larva.

The fish examined 40 days p.i. harboured five female nematodes containing only a few eggs in their uteri, all of which were unembryonated. The nematodes were 6664–7956 long and 82–95 wide. The vestibule including prostom, the muscular oesophagus and the glandular oesophagus were 105–135, 216–300 and 1156–1768 long, respectively. The prostom, armed with 14 anterior teeth, was 18–24 long and 15–18 wide. The nerve ring and the excretory pore were 165–195 and 228–285 from the anterior extremity. The vulva was situated 1768–3060 from the posterior end (at 61–73% of the body length). The vagina was directed anteriorly. The size of unembryonated eggs was 36–39 × 21–24. The tail was 156–165 long.

The last infected fish was examined 51 days p.i. and it harboured two males and one female already with numerous thick-walled, but still unembryonated eggs. The males were 4814–4950 long and 54–66 wide. The vestibule including prostom, the muscular long oesophagus and the glandular oesophagus were 99–105, 225–249 and 1224–1251 long, respectively. The nerve ring, the excretory pore and bifurcated deirids were 156, 210–222 and 60 from the anterior extremity, respectively. The longer spicule was 1719–1844 long, its shaft 546–570 long, forming 31–32% of the spicule length. The length ratio of spicules was 1:19.1–22.8. Six pairs (five subventral and one lateral) of preanal papillae and six pairs (five preanal and one postanal) of postanal were present. The length of the tail was 213–228. The female was 7303 long and 90 wide. The vestibule including prostom, the muscular oesophagus and the glandular oesophagus were 132, 279 and 1618 long, respectively. The prostom was 21 long and 18 wide. The nerve ring, the excretory pore and deirids were 171, 255 and 72 from the anterior extremity, respectively. The vulva was 2883 from the posterior end (at 61% of the body length). The size of eggs was 33–39 × 21. The tail was 165 long.

The nematodes in all infected fishes were located in the middle part of the intestine.

The last experimental fishes (one *C. nigrofasciatum* and one *O. niloticus*) examined 68 days p.i. were not infected.

Discussion

The present study confirms that *Cichlasoma cyanoguttatum* is the principle definitive host of *Rhabdochona kidderi texensis* in the Upper San Marcos River, in which the parasite occurs with a high prevalence and intensity. It was also recorded rarely from *Oreochromis mossambicus* in this locality (Moravec & Huffman, 1988), but these might be accidental findings and it is not certain that this fish species served functionally as the definitive host. Juvenile forms of this nematode were found in *Gambusia affinis*, which probably served only as the paradefinitive host (Moravec & Huffman, 1988). Since *C. cyanoguttatum* represents a substantial part of biomass in the Upper San Marcos River, it is apparent that almost the whole population of this nematode passes through this fish species. The present experiments as well as some

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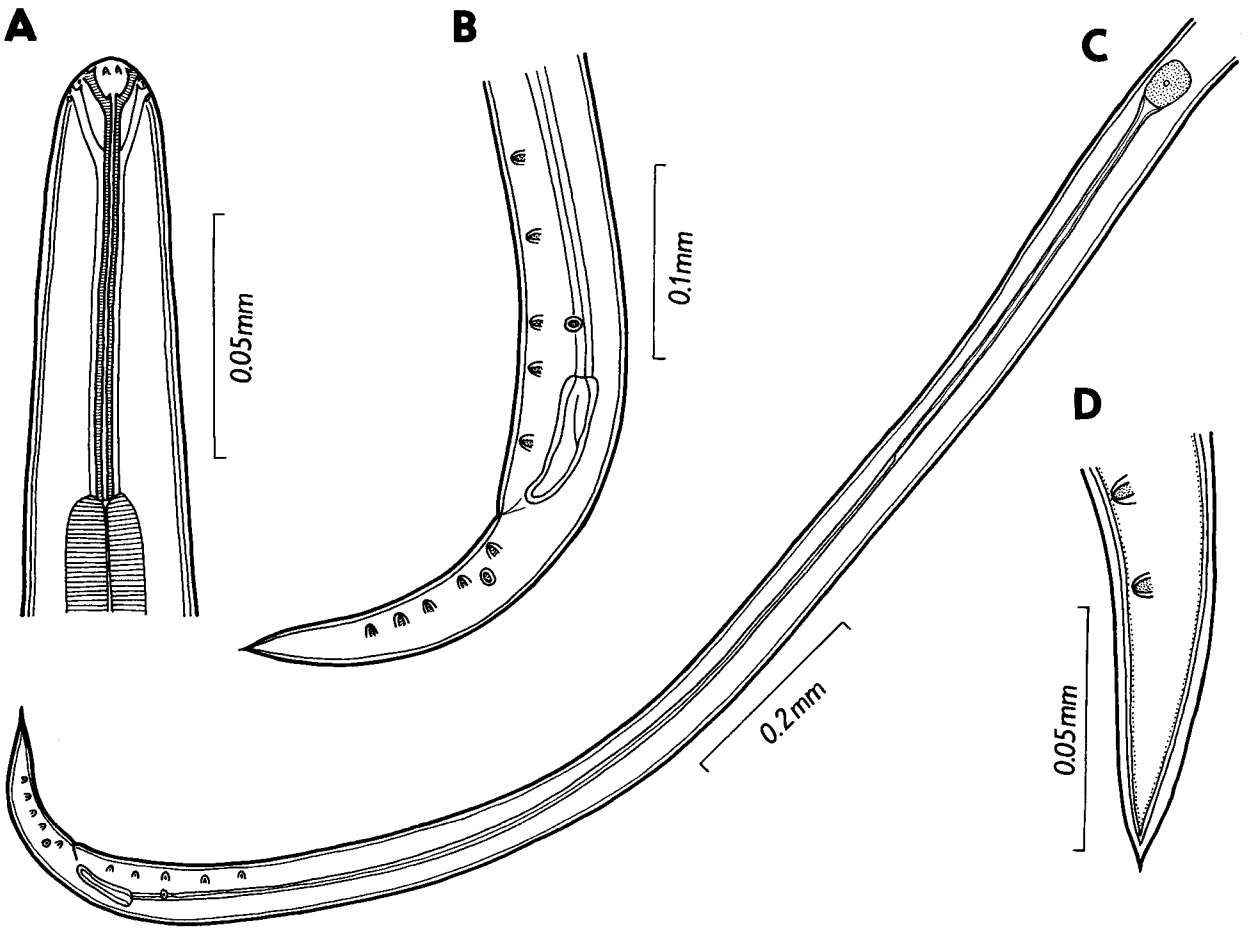

Fig. 2. *Rhabdochona kidderi texensis* Moravec & Huffman, 1988, a juvenile male undergoing the last moult from experimentally infected *Cichlasoma nigrofasciatum*, 23 days p.i. A, cephalic end (old vestibule of fourth-stage larva still inside that of new one); B, tail; C, posterior end of body; D, tip of tail (new tail inside cuticle of fourth-stage larva).

previously published data show that other *Cichlasoma* species can also serve as the definitive host for this parasite.

Although species of *Rhabdochona* Railliet, 1916 belong to the most frequent and most widely distributed parasites of freshwater fishes, very little is so far known about their development and life cycles. Weller's (1938) and Janiszewska's (1960) data on the experimental infection of amphipods with the eggs of *R. ovifilamenta* Weller, 1938 and on the finding of the larvae of *Rhabdochonoides barbi* (=*R. hellichi* (Šrámek, 1901)) in tubificids, respectively, are evidently erroneous (Moravec, 1972). Gustafson (1939, 1942) was the first to mention in his short notes that mayfly nymphs (*Hexagenia*) can be experimentally infected with the eggs of *R. cascadilla* Wigdor, 1918 and that the larvae in the intermediate host may exhibit a precocious development. In his later taxonomic paper, Gustafson (1949) mentions as intermediate hosts of three North American *Rhabdochona* spp. various mayfly nymphs (Ephemeroptera), and for *R. cotti* Gustafson, 1949 also mentions stone fly nymphs (Plecoptera). Infective larvae from ephemeropteran intermediate hosts have so far been recorded in *R. denudata* (Dujardin, 1845) and *R. phoxini* Moravec, 1968 in Europe (Shtein, 1959; Moravec, 1977, 1989), *R. oncorhynchi* (Fujita, 1921) and *R. coronacaudata* Belouss, 1965 in Japan (Shimazu, 1996; R. Hirasawa, Nara Women's University, personal communication) and *R. rotundicaudatum* Byrne, 1992 in Canada (Byrne, 1992). Larvae of the European species *R. hellichi* were recorded from the naturally infected trichopteran larvae (*Hydropsyche*) by Vojtková (1971) (erroneously reported as *R. denudata*), Moravec (1995) and Moravec *et al.* (1997).

Complete or incomplete life cycles have been experimentally studied in the European species *R. denudata*, *R. ergensi* Moravec, 1968 and *R. phoxini* Moravec, 1968 (Moravec, 1972, 1976, 1991) and in the North American species *R. canadensis* Moravec and Arai, 1971 (Barger & Janovy, 1994). Experimental intermediate hosts for all these species were ephemeropterans.

The finding of naturally infected intermediate hosts, the mayfly nymphs *Tricorythodes curvatus*, shows that, as with the majority of *Rhabdochona* species, this nematode utilizes ephemeropterans as intermediate hosts. Congeneric mayfly nymphs (*Tricorythodes* sp.) were successfully used also as intermediate hosts for another North

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American species, *R. canadensis* (Barger & Janovy, 1994). However, it is apparent from our experiments that the degree of host specificity at the level of the intermediate host is rather low in this nematode and that mayflies belonging to different families may serve as intermediate hosts, including those occurring in different continents. This finding is consistent with other *Rhabdochona* species as well (Moravec, 1976, 1989; Barger & Janovy, 1994).

The morphology of *Rhabdochona* larvae from insect intermediate hosts have been studied in detail only in *R. ergensi*, *R. hellichi*, *R. oncorhynchi* and *R. phoxini* (Moravec, 1972, 1976, 1995; Shimazu, 1996). In all these species, both third- and fourth-stage larvae were found in aquatic insect larvae, confirming the fact that larvae do not arrest their development in the intermediate host at the infective third stage, but develop further to at least the fourth stage, which becomes encapsulated; a long-term survival of larvae in an invertebrate may result in attaining practically the maturity of these nematodes (Gustafson, 1942; Shtein, 1959; Vojtková, 1971; Moravec, 1976; Byrne, 1992). The present data show that also in *R. kidderi texensis* there occur third- and fourth-stage larvae in mayflies, which differ morphologically mainly in the structure of the prostom. As in other *Rhabdochona* species, the third-stage larva possesses only two anterior prostomal teeth, whereas six anterior teeth are found in the prostom of the fourth-stage larva (the number of teeth in conspecific adults is 14 – see Moravec & Huffman, 1988). As in *R. hellichi*, the fourth-stage larva of *R. kidderi texensis* is characterized by conspicuously large basal teeth in the prostom, by which it differs from fourth-stage larvae of *R. ergensi*, *R. oncorhynchi* and *R. phoxini*; in adults of these species prostomal basal teeth are absent or highly reduced.

The speed of the development of *R. kidderi texensis* in the intermediate host at 19°C seems to be similar to that of *R. canadensis* as found by Barger & Janovy (1994) (development of third-stage larvae in approximately 10 days); the same development of *R. ergensi* and *R. phoxini* was much slower (approximately 20–30 days), but the water temperature was lower (13–15°C). The prepatent period of *R. ergensi* in the fish definitive host was 43 days at a laboratory temperature (Moravec, 1972). The results of our experiments show that this may be approximately two months in *R. kidderi texensis*.

The development of the nominotypical species *R. kidderi kidderi* has not yet been studied, but it may be similar to that of *R. kidderi texensis*.

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