# Studies on the development of *Anguillicola crassus* Kuwahara, Niimi et Itagaki, 1974 (Nematoda: Dracunculoidea) in the intermediate host

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Abstract. The development of the nematode Anguillicola crassus, a swimbladder parasite of eels, was experimentally studied in copepod intermediate hosts Cyclops strenuus and Acanthocyclops vernalis. The copepods, kept at a laboratory temperature of 20-22 °C, were infected with nematode second-stage larvae; the second moult of larvae (the only one in the intermediate host) was observed to start 10 days p.i., but third-stage larvae liberated from their cuticular sheath were first observed 20 days p.i. These proved to be infective for experimental eels. Free second-stage larvae as well as larvae from copepods were described. The morphology of A. crassus larvae and the mode of their development in the intermediate host were compared with those of other dracunculoid nematodes. From this point of view, Anguillicola members appear to represent an ancient group of dracunculoid nematodes.

The nematode Anguillicola crassus Kuwahara, Niimi et Itagaki, 1974, a pathogenic swimbladder parasite of eels, was originally known only from East-Asian countries (Japan, China), parasitizing there the Japanese eel, Anguilla japonica Temminck et Schlegel, and the introduced European eel, A. anguilla (L.). Only some ten years ago the parasite was introduced into Europe where it has quickly spread among eel populations in many countries (Moravec 1992), representing there, sometimes, a serious problem for cultures of European eel, A. anguilla (L.).

Although the development of A. crassus has been experimentally studied by Hirose et al. (1976) and Egusa (1979) in Japan and later on by many authors (De Charleroy et al. 1987, 1989, 1990; Haenen et al. 1989; Petter et al. 1989, 1990; Kennedy and Fitch 1990; Bonneau et al. 1991; Fioravanti and Restani 1992; and some others) in Europe, information on the development of this nematode remains still incomplete; this concerns also the larval development of A. crassus in the intermediate host. In the years 1991 and 1992 the present authors carried out some experimental observations on the development of A. crassus and the results are presented in this paper.

# MATERIALS AND METHODS

Gravid females of Anguillicola crassus with eggs containing motile second-stage larvae were recovered from the swimbladder of eels, Anguilla anguilla (L.), originating from the Elbe River near Hřensko, North Bohemia, caught in June 1991, and from Lake Burano near Rome, Italy, caught in March 1992. The nematodes were removed from the host's body and placed indi-

vidually in small vessels containing physiological saline where they readily laid their larvated eggs. Feeding experiments were made in petri dishes (diameter 9, 16 or 19 cm) filled with water. Each dish contained a few hundreds of copepods to which different quantities (usually about one thousand) of parasite's larvated eggs were added. Cyclops strenuus Fischer and Acanthocyclops vernalis (Fischer) originating from a few ponds near České Budějovice, South Bohemia, were used as experimental intermediate hosts. These were kept at the laboratory temperatures of 20-22 °C. They were fed with Paramecium and examined each day. Nematode larvae were fixed so that they were immobilized by heating them in a drop of water on a glass slide over a flame for several seconds. Ultimately, the killed larvae were examined with a light microscope. All measurements are based on at least 5 specimens examined. Drawings were made with the aid of a Zeiss microscope drawing attachment. The eels (body length 8-16 cm) used for experimental infection were originally obtained as elvers from Italy and then kept at a low temperature (10 °C) in the laboratory in České Budějovice for approximately one year, being fed with tubificids. Ten control eels were checked to ensure that they were not already infected naturally.

# **RESULTS**

# **Experimental infections of intermediate hosts**

Anguillicola crassus is ovoviviparous, which means that its mature eggs in uteri contain already fully formed motile larvae, in this case the second-stage larvae. The eggs are laid by females through the vulva into the host's swimbladder from which they get, via the pneumatic duct, into the fish digestive tract. After being passively transported with the faeces, they are eventually liberated into the water

In experiments in which the gravid females of A. crassus were placed in physiological saline and remained there

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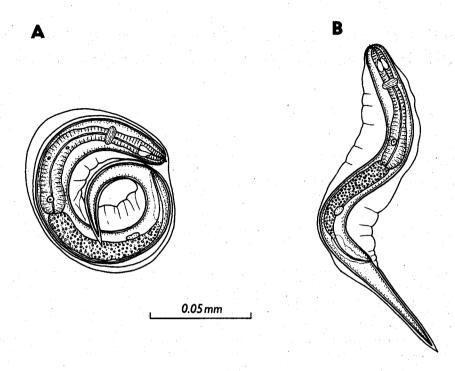


Fig. 1. Anguillicola crassus - second-stage larva. A - larva inside the egg shell; B - hatched larva still inside a loosened cuticular sheath from the second moult.

at laboratory temperatures, the nematodes laid the majority of their eggs (containing motile larvae) within 24 hours. Having been transferred to the water, most second-stage larvae hatched from the egg shell, remaining, however, inside the loosened cuticular sheath from the first moult. These larvae actively moved in the water, being attached by their tail tip to the bottom of the vessel, thus attracting the copepods which swallowed them readily.

When the larvae of A. crassus were ingested by a suitable copepod intermediate host (Cyclops strenuus or Acanthocyclops vernalis), these penetrated through the wall of the copepod's digestive tract to its haemocoel within a few hours to develop there further.

During this penetration, undoubtedly accomplished with the aid of the larval cephalic tooth, the second-stage larvae lost their cuticular sheath from the first moult. During their entire development in the intermediate host, the larvae moved in the haemocoel, being located most frequently around the intestine in the cephalothorax, less often in the abdomen or the furca.

The two copepod species, Cyclops strenuus and Acanthocyclops vernalis, experimentally infected with A. crassus larvae, showed obviously the same degree of infection; in addition to adult copepods, also specimens representing the last copepodite stage of the first species were frequently found to be infected. The percentage of infected copepods was about 80-90 % and the intensity of infection ranged within 1-8 nematode larvae per copepod. Heavily infected (harbouring about 5 larvae or more) copepods kept mostly to the bottom of the vessel and were less motile than uninfected ones or those infected with only 1-2 larvae. The highest rate of mortality of infected

copepods was observed during the first few days after infection when usually about 60-70 % of copepods died.

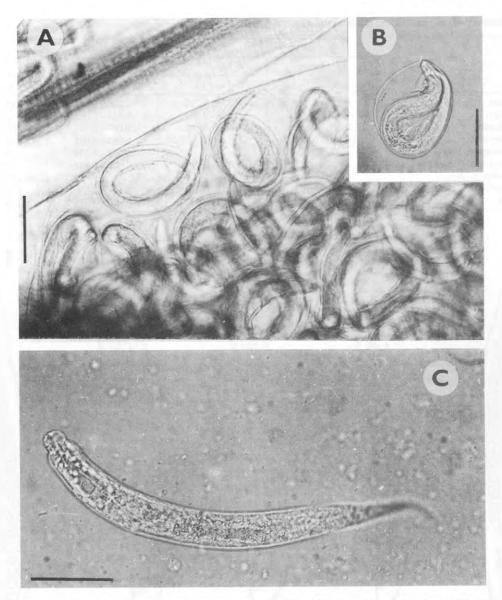
Before attaining the third larval stage at which they are infective to the fish host, larvae of A. crassus moulted once (the second moult) in the haemocoel of the copepod. At 20-22 °C, the larvae started to moult on the 10th day p.i., but fully formed third-stage larvae already liberated from their cuticular sheath from this moulting were found in copepods only on the 20th day p.i.; obviously, the rate of development was not the same for all larvae, because many larvae still inside the cuticular sheath were found, in addition to fully developed third-stage larvae, in infected copepods on the 20th day p.i. During their development in the copepod intermediate host, the larvae of A. crassus grew considerably in length, the body of thirdstage larvae being approximately three times longer than that of free second-stage larvae. The third-stage larvae remained unencapsulated in the haemocoel of the intermediate host, but they were less motile than second-stage larvae, with a tendency to stay spirally coiled.

The third-stage larvae from the intermediate host were already infective to the definitive host (eel) which was proved by our feeding experiments with small eels.

# Morphology and larval development

## a) **Eggs** Figs. 1 A, 2 A, B

The mature eggs are irregularly spherical or oval, with a thin, membraneous shell with almost smooth surface; their size is 0.090-0.099 x 0.081-0.090 mm. The eggs contain a fully formed, motile second-stage larva when laid; the larva retains the first-stage cuticle forming a loose



**Fig. 2.** Anguillicola crassus - second-stage larva. A - eggs containing fully formed second-stage larvae in the uterus of a gravid female; B - egg containing a larva; C - second-stage larva from copepod intermediate host 1 day p.i. (bar = 0.05 mm).

sheath around the body. In water the second-stage larvae hatch from the egg shell.

# b) Free second-stage larvae Fig. 1 B

Free second-stage larvae are still inside the cuticular sheath from the first moult. Their body is slender, whitish to translucent, 0.270-0.300 mm long and 0.021-0.024 mm wide; the width of the cuticular sheath is about 0.045 mm. The cephalic end is armed with a dorsal conical cuticular tooth, apparently enabling the larva to emerge from the egg shell and to penetrate the gut wall of the intermediate host. The cuticle is very thin and smooth. The mouth opening is followed by a short, thin mouth tube. The anterior end of the larva is provided with two distinct, drop-like refractive formations (probably proteolytic glands). The internal organization of the body is not well

visible. The oesophagus is 0.096-0.102 mm long, its posterior part is somewhat expanded. The nerve ring encircles the oesophagus 0.030-0.036 mm from its anterior end. The excretory pore was not located. The intestine is relatively wide, sparsely granulated; the rectum is a thin-walled, colourless tube. The tail is conical, sharply pointed, 0.078-0.087 mm long. A small, little visible genital primordium is situated ventrally approximately at mid-length of the body.

# c) Development of second-stage larvae in the intermediate host

Having penetrated into the haemocoel of the copepod, the larvae loose their cuticular sheath from the first moult, but their morphology is still very similar to that of free second-stage larvae (Fig. 3 A). In the following three days

Table 1. Measurements of second- and third-stage larvae of A, crassus (in mm).

	Second - stage larvae						
	Free larvae	Larvae from copepods					
		1 day p.i.	3 days p.i.	6 days p.i.			
Length of body	0.270 - 0.300	0.270 - 0.297	0.258 - 0.303	0,336 - 0357			
Width of body	0.021 - 0.024	0.018 - 0.021	0.024 - 0.027	0.027			
Length of oesophagus	0.096 - 0.102	0.093 - 0.102	0.090 - 0.111	0.120 - 0.135			
Distance of nerve ring	0.030 - 0.036	0.060	0.054 - 0.075	0.069 - 0.072			
Distance of excretory pore		1 -	0.072 - 0.099	0.081 - 0.093			
Size of globular cephalic portion	•	0.003 x 0.006	0.006 x 0.012	0.009 - 0.012			
Genital primordium from		1 to 1 to 1		0.018 <sup>x</sup> 0.021			
anterior extremity	0.157 - 0.163	0.157 - 0.160	0.144 - 0.150	0.180 - 0.186			
Length of tail	0.078 - 0.087	0.060 - 0.072	0.060 - 0.075	0.084 - 0.087			

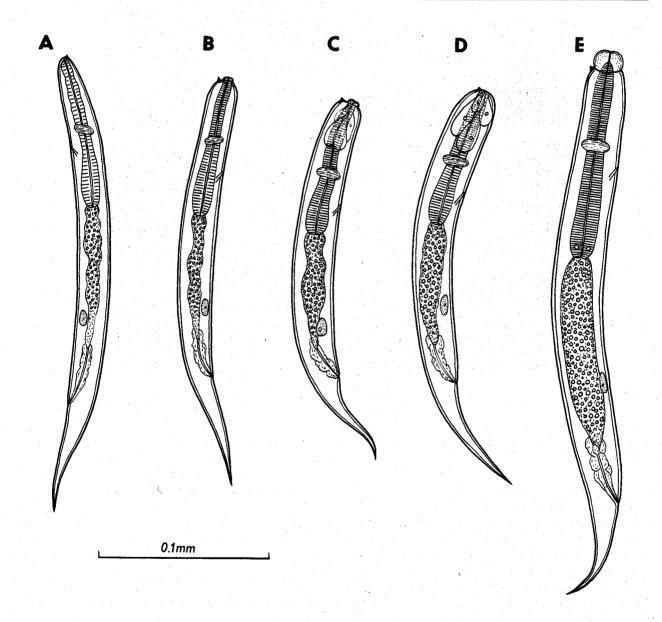


Fig. 3: Anguillicola crassus - development of second-stage larvae in copepods. A, B - larvae 1 day p.i.; C, D - larvae 3 days p.i.; E - larvae 6 days p.i.

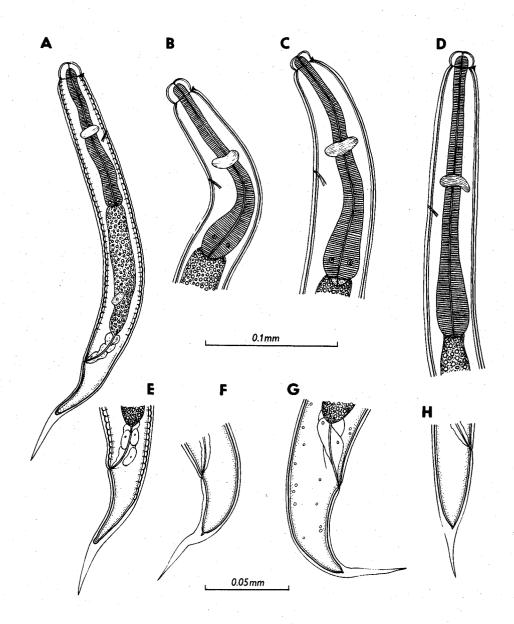


Fig. 4. Anguillicola crassus - development of transitory-stage larva during the second moult in copepods. A, E - general view and tail of larva 10 days p.i.; B, F - cephalic end and tail of larva 14 days p.i.; C, D, G, H - same of larvae 16 days p.i.

the larvae become somewhat shorter and thicker (Fig. 3 B-D). Their cephalic end becomes broad, its anteriormost portion being globular, separated from the body by a cuticular constriction; this part of the cephalic end can be retracted into the body. The larval tooth is situated dorsally at the base of the globular cephalic part. A few refractive unicellular cephalic glands are still visible. In the following days the larvae again continue to grow (see Table 1), but their morphology remains practically the same (Fig. 3 E); the cuticle of these larvae is hitherto smooth.

The first signs of the second moult (the first one in the intermediate host) are observed in larvae 10 days p.i. Their body is mostly somewhat shorter than that of younger larvae recorded on day 6 p.i. (see Table 1), but the oesophagus and the intestine are now much better visible; the latter is filled with numerous brownish granules (Fig. 4 A). A newly formed, densely transversely folded cuticle can be seen under the old one (Fig. 4 A, E). The new tail is distinctly shorter than before and there is hitherto no terminal spike on it.

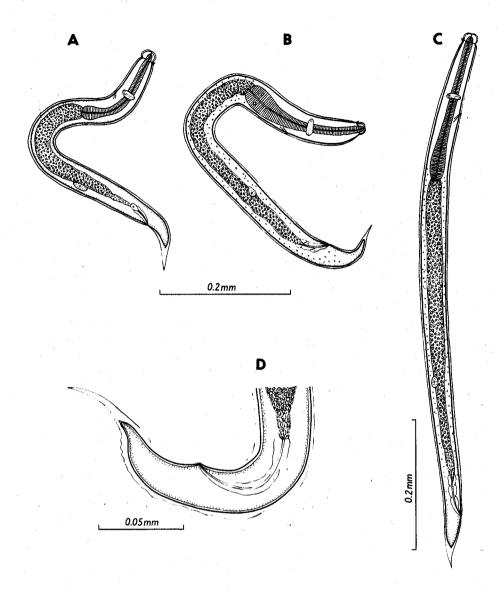


Fig. 5. Anguillicola crassus - larvae undergoing the second moult from copepods. A - larva 14 days p.i.; B, C - larva 16 days p.i.; D - tail of a moulting larva 17 days p.i.

During the following days the larvae remain inside the loosened old cuticle. They considerably grow in length (Table 1) and their internal organs become very distinct (Fig. 5). The tail tip is now provided with a small terminal spike. The first third-stage larvae liberated from the cuticular sheath from the second moult are recorded only 20 days p.i., but at this time, many other larvae have not yet finished their second moult.

#### d) Third-stage larvae (infective larvae) Figs. 6, 7

Larvae of this stage were obtained from copepods 20 days p.i. These are slender, whitish, 0.876-0.972 mm long and 0.039-0.042 mm wide. Their cuticle appears to be almost smooth under the light microscope, but it is finely

transversely striated when examined with scanning electron microscopy. Two narrow (0.003 mm wide) cuticular alae extend along almost the whole body length. A pair of minute conical deirids is present, being situated somewhat behind the excretory pore level; it is distinctly visible under SEM. The cephalic end of the larva is rounded, the mouth is provided with two small lateral, anteriorly directed sclerotized teeth; each tooth is followed posteriorly by a sclerotized apparatus situated at level of the anterior end of oesophagus, which appears as bifurcate in lateral view; this apparatus is 0.009-0.012 mm long and 0.018 mm wide. Cephalic papillae are indistinct. The oesophagus is long, slender, distinctly broader at its posterior part; it is 0.252-0.300 mm long (26-34 % of the

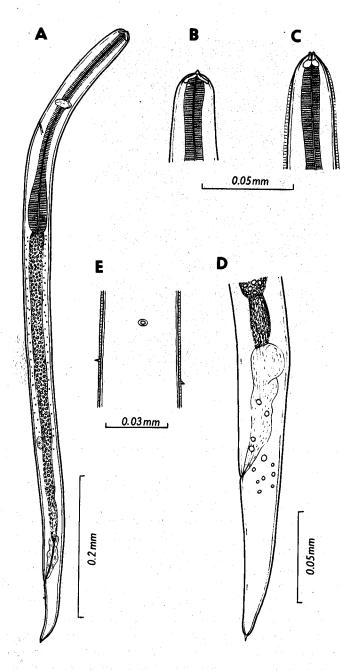


Fig. 6. Anguillicola crassus - third-stage (infective) larva from the copepod intermediate host (20 days p.i.). A - general view; B, C - cephalic end, lateral and dorsoventral views; D - posterior end of body; E - region of excretory pore and deirids, ventral view.

whole body length) and 0.009 mm and 0.024 mm wide at its anterior and posterior parts, respectively. The oesophagus opens into the intestine through a valve. The nerve ring encircles the narrow anterior part of oesophagus 0.117-0.132 mm from the anterior extremity; the excretory pore is located somewhat behind the nerve ring level, 0.168-0.171 mm from the cephalic end. The intestine is straight, narrow, containing numerous brownish granulae. The rectum is a hyaline tube; rectal glands are not well visible. The tail is conical, 0.075-0.081 mm long, bearing a distinct small cuticular spike at its tip; the length of the tail

represents 8-9 % of the whole body length. A small oval genital primordium is located ventrally, approximately at the border of the second and third thirds of the body length, i.e. 0.66-0.75 mm from the anterior extremity.

In order to verify that the third-stage larvae of A. crassus from intermediate hosts are already infective to the definitive host, a few tens of infected copepods containing the nematode larvae 21 days p.i. were fed to small, uninfected eels (A. anguilla) (body length 8-16 cm); most of the experimental eels were later found to be infected. Of the 11 experimental eels, 11 (61 %) became infected with the intensity 1-8 (mean 3) nematodes per fish.

## DISCUSSION

Although the life cycle of Anguillicola crassus was already studied by many authors, the early larval stages of this nematode and their morphological changes during their development in the intermediate host were described to some detail only by Petter et al. (1990) and Fioravanti and Restani (1992). The present data concerning the larval morphology are almost in accordance with their observations, but some morphological features (presence and location of the nerve ring, the genital primordium and cephalic glands in free second-stage larvae, the excretory pore and the genital primordium in developing second-stage larvae, presence of deirids in third-stage larvae, etc.) were not previously observed by these authors. The present study confirms that, during the development in the intermediate host, the nematode larvae undergo substantial morphological changes. The most striking changes concern, in addition to the structure of mouth and oesophagus, the tail which becomes much shorter in relation to the whole body length; while it forms 28-29 % of the overall length of body in free second-stage larvae, this is only 8-9 % in third-stage larvae. Characteristic features of infective third-stage larvae are the presence of a special sclerotized buccal apparatus, lateral alae, deirids, and a terminal spike on the tail. The gross morphology of the second- and third-stage larvae of A. crassus is similar to that of the same larval stages of the congeneric species A. globiceps, as described by Wang and Zhao (1980) in China.

The rate of development of larval Anguillicola crassus in copepods was found somewhat different (slower) in our experiments when compared with data by other authors. According to De Charleroy et al. (1990), the larvae moult in the copepods and reach the third, infective stage after 10-12 days at 21°C and Petter et al. (1989) observed that the second moult took place on day 12 p.i. at 20-22°C; later Petter et al. (1990) reported that third-stage larvae first appeared on day 6 at a temperature varying from 18 to 29°C. According to Fioravanti and Restani (1992), the third-stage larvae develop in copepods within 7-8 days at 22-26°C. In contrast to these observations, fully formed third-stage larvae already liberated from the cuticular sheath were first found in our experi-

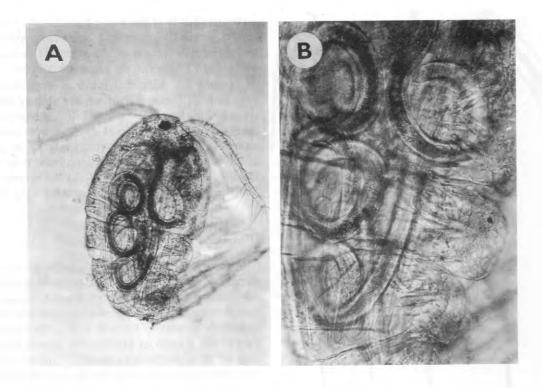


Fig. 7. Anguillicola crassus - third-stage larvae in the haemocoel of the intermediate host. A - heavily infected copepod; B - detail of A.

ments, held at 20-22 °C, only on day 20 p.i. The speed of this larval development is considerably influenced by water temperature. Petter et al. (1990) observed that it was very slow at 12 °C when larvae only started their second moult on day 62.

The present study confirms that copepods are easily infected with A. crassus larvae, serving apparently as its principal intermediate hosts. Hirose et al. (1976) were the first to find the copepod Eucyclops serrulatus as the intermediate host of A. crassus in Japan. In Europe, the experimental intermediate hosts of this parasite were mostly found to be various cyclopoid copepods (Paracyclops fimbriatus, Macrocyclops albidus, M. fuscus, Eucyclops serrulatus, E. macruroides, Cyclops strenuus, C. vicinus, Acanthocyclops robustus, A. vernalis, Diacyclops bicuspidatus), but also Diaptomus gracilis (Diaptomidae) (De Charleroy et al. 1987, 1990, Haenen et al. 1989, Petter et al. 1989, 1990, Kennedy and Fitch 1990, Bonneau et al. 1991, Boon et al. 1991, Fioravanti and Restani 1992). Moreover, Petter et al. (1990) found as an experimental intermediate host of A. crassus the ostracod Cypria ophthalmica in which the larvae developed to the third stage. Kennedy and Fitch (1990) mention that they successfully infected also juvenile Gammarus (Amphipoda) and even a single specimen of the brackish-water Eurytemora affinis, but it was not confirmed whether the parasite larvae can attain an infective stage in these hosts.

It has been demonstrated experimentally that eels eating copepods containing third-stage larvae of A. crassus can become infected from glass-eel stage onwards (Boon et al. 1990, De Charleroy et al. 1990, Kennedy and Fitch 1990, present study). But in addition to intermediate hosts (e.g. copepods), the source of infection for eels may be some fish serving as paratenic hosts, in which the infective larvae of the parasite survive in the body cavity or in the swimbladder. Such paratenic hosts of A. crassus were found both under experimental conditions (Lebistes reticulatus, Cyprinus carpio, Leuciscus idus - see Petter et al. 1989, De Charleroy et al. 1990) and in the natural environment of Belgium and Holland (Cyprinus carpio, Perca fluviatilis, Stizostedion lucioperca, Gymnocephalus cernuus, Lepomis gibbosus, Gasterosteus aculeatus - see Belpaire et al. 1989, Haenen and van Banning 1990, De Charleroy et al. 1990). The small paratenic hosts can be eaten by larger eels which thus become infected.

The morphology of early larval stages of *Anguillicola* (as demonstrated in *A. crassus*) and the mode of their development in the intermediate host show clear affinities of this genus to other dracunculoids but, on the other hand, also some distinct differences. While the presence of the dorsal cephalic tooth is typical of the first-stage larvae in

some dracunculoid genera (e.g. Dracunculus, Philonema, Philometra), it is present only in second-stage larvae in Anguillicola. This is undoubtedly due to the fact that, in contrast to other dracunculoids, the first moult of larvae occurs already inside the egg and, consequently, only second-stage larvae are infective to the intermediate host. The presence of a special sclerotized mouth apparatus in Anguillicola third-stage larvae is also unique among dracunculoids; in our opinion, this apparatus is analogous with the buccal capsule of third-stage larvae in camallanids, thus indicating certain affinities of Anguillicola to the superfamily Camallanoidea.

It has been mentioned above that the larvae of A. crassus increase considerably in size during their development in the intermediate host, the body of third-stage larvae being approximately three times longer than that of second-stage larvae. On the other hand, larvae of most dracunculoids increase slightly in size or do not increase

at all during their development from the first to the third stage (e.g. Dracunculus, Philometra, Philometroides) or they even decrease in size (Avioserpens, Micropleura). According to Moravec (1978), a distinct increase in body sizes of larvae during their development in the intermediate host, as well as the absence of mucrones on the tail tip of infective larvae can be regarded as primitive characters among dracunculoid nematodes. Therefore, the early larval development of Anguillicola species provides further evidence for the ancientness of this group of parasites.

Paratenic parasitism in Anguillicola crassus is not exceptional among dracunculoids. This phenomenon has been known to occur with several other representatives of this nematode group (Dracunculus, Avioserpens, some Philometra species) (see Brackett 1938, Supryaga 1968, Molnár 1976, Moravec and Dyková 1978, Moravec 1984).

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## **ERRATUM**

F. MORAVEC, D. DI CAVE, P. ORECCHIA, L. PAGGI: Studies on the development of *Anguillicola crassus* Kuwahara, Niimi et Itagaki, 1974 (Nematoda: Dracunculoidea) in the intermediate host. Folia Parasitol. 40: 39-48, 1993.

Table 1 of the above mentioned paper, which appeared in the previous issue (No. 1) of this journal, was erroneously published incomplete. The complete Table 1 reads as follows:

Table 1. Measurements of second- and third-stage larvae of A. crassus.

	Second-stage larvae							
	•	Free larvae		Larvae from copepods				
en e				1 day p.i.	3 days p.i.	6 days p.i.		
Length of body Width of body Length of oesophagus Distance of nerve ring Distance of excretory pore Size of globular cephalic portion  Genital primordium from anterior extremit Length of tail	y	0.270 - 0.30 0.021 - 0.02 0.096 - 0.10 0.030 - 0.03 - 0.157 - 0.16 0.078 - 0.08	4 2 6 3	0.270 - 0.297 0.018 - 0.021 0.093 - 0.102 0.060 0.003 x 0.006 0.157 - 0.160 0.060 - 0.072	0.258 - 0.303 0.024 - 0.027 0.090 - 0.111 0.054 - 0.057 0.072 - 0.099 0.006 x 0.012 0.144 - 0.150 0.060 - 0.075	0.336 - 0.357 0.027 0.120 - 0.135 0.069 - 0.072 0.081 - 0.093 0.009 - 0.012 x 0.018 - 0.021 0.180 - 0.186 0.084 - 0.087		
	Transitory-stage larvae (second moult) Third-stage larvae							
	Larvae from copepods							
the state of the same of the s	10 days p.	i. 14 da	ys p.i.	16 days p.i.	17 days p.i.	20 days p.i.		
Length of body Width of body Length of oesophagus Distance of nerve ring Distance of excretory pore Size of globular cephalic portion  Genital primordium from anterior extremity	0,300 - 0.3 0,030 - 0.0 0,096 - 0.1 0,057 - 0.0 0,060 - 0.0 0,012 x 0.0 0,180 - 0.2	33 0.039 32 0.156 75 0.090 84 0.102 18 0.006	- 0.570 - 0.048 - 0.216 - 0.099 - 0.120 x 0.018	0.630 - 0.933 0.039 - 0.054 0.168 - 0.252 0.087 - 0.117 0.123 - 0.150 0.012 - 0.015 x 0.018 - 0.021 0.396 - 0.615		0.876 - 0.972 0.039 - 0.042 0.252 - 0.300 0.117 - 0.132 0.168 - 0.171		
Length of tail	0.042	0.0	)39	0.054 - 0.081	0.036 - 0.060	0.075 - 0.081		