

Distribution and morphology of two helminths recently introduced into European eel populations: *Anguillicola crassus* (Nematoda, Dracunculoidea) and *Paratenuisentis ambiguus* (Acanthocephala, Tenuisentidae)

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ABSTRACT: The occurrence of 2 helminths is reported in eel from 3 regions of the Federal Republic of Germany. Both species, *Anguillicola crassus* (Nematoda, Dracunculoidea) and *Paratenuisentis ambiguus* (Acanthocephala, Tenuisentidae) were recently introduced into Europe, probably from Japan and the USA, respectively. The morphology of *A. crassus* differs from the original description in a few features. Syntype specimens from Japan, however, showed that specimens from Japan and from Germany are conspecific. The morphology of *P. ambiguus* (first report from Europe) corresponds well with the original description from North America. In Germany it is shown to employ the same crustacean intermediate host as in North America, i.e. *Gammarus tigrinus*, an amphipod originally introduced purposely into Germany.

INTRODUCTION

In recent years several allochthonous helminths of eel have invaded Europe. Two species of the conspicuously large swim-bladder nematodes of the genus *Anguillicola* have been recently found in Italy (Paggi et al. 1982) and Central Europe, e.g. Germany (Neumann 1985, Peters & Hartmann 1986), the Netherlands (Van Banning et al. 1985) and Denmark (Køie 1988). The species occurring in Italy had been identified as *A. australiensis* (Paggi et al. 1982) but has now been described as *A. novaezelandiae* sp. nov., a species endemic to New Zealand (Moravec & Taraschewski 1988). Until now *Anguillicola* species from Australia (Johnston & Mawson 1940, Rid 1973) and New Zealand (Hine 1978) had not been distinguished as separate species. The species occurring in Central Europe has been suspected to be *A. crassus** (Van Banning et al. 1985), a species infecting eels in East Asia (Kuwahara et al. 1974), and earlier wrongly identified as *A. globiceps* by Egusa et al. (1969). Peters & Hartmann

(1986) emphasized, however, that its morphology did not correspond with any of the described *Anguillicola* species. Three other *Anguillicola* species, indigenous to East Asia, Australia and southern Africa, respectively (Moravec & Taraschewski 1988) have not to date been reported in Europe.

The intestinal acanthocephalan *Paratenuisentis ambiguus* is known as an endemic eel parasite of brackish waters along the east coast of the USA (Bullock & Samuel 1975). It has not previously been recorded from outside the USA. In the present communication, distribution and morphology of these 2 helminths (*Anguillicola crassus* and *P. ambiguus*), introduced into European eel populations is reported. Further, the first intermediate host of *P. ambiguus* in European waters is identified.

* The species had been described as *A. crassa* by Kuwahara et al. (1974) but is now named *A. crassus* by Moravec & Taraschewski (1988)

backs *Gasterosteus aculeatus* were used for the determination of infectivity of the acanthocephalan larvae within the amphipods.

RESULTS

Field data, laboratory cycle

For the results of the survey see Table 1 and Fig. 1. A correlation between eel length and infection by either of the 2 helminths was not apparent in the sampled size group.

Anguillicola crassus was highly abundant in the Ruhr lake. Prevalence and intensity of infection increased from 1986 to 1987. In the River Weser prevalence (only 1986 data available) was lower. In the Elbe estuary infection by *A. crassus* was lowest (only 1986 data available) and declined from sampling area 3A to 3C (Table 1).

Paratenuisentis ambiguus did not occur in the Ruhr lake. In the River Weser most eels were infected, with a mean of 98.2 worms per eel. One worm was found in a single eel of the Elbe estuary. In the River Weser 26.5 % of the sampled *Gammarus tigrinus* were infected by *P. ambiguus*. *G. tigrinus* did not occur in the other 2 waters. The experimentally infected *G. tigrinus* harboured 1 to 3 larvae per amphipod which were infectious for sticklebacks from the 34th day postinfection.

Morphology

Anguillicola crassus Kuwahara et al., 1974. The description of *A. crassus* presented here is restricted to

features seen by light microscope (LM) or SEM that were not described by Kuwahara et al. (1974) or are contradictory to the original description, which only included LM studies (Figs. 2 and 3; Table 2). The worms have a soft wrinkled outer cuticle (Fig. 3C, D, E) that covers the whole body. The circular mouth aperture is small so that only a few host's erythrocytes can pass into it at the same time (Fig. 3A); it is surrounded by 4 dorsolateral and ventrolateral cephalic papillae and 2 small lateral amphids (Fig. 3C). The anterior rim of the buccal capsule bears one row of 22, 24, 26 or 28 circumoral teeth (Fig. 3C). The oesophagus appears strongly muscular, consisting of 3 lobes, expanding at its posterior half (Fig. 2A, B, G and 3B); anteriorly, the oesophagus forms 6 slightly elevated, rounded lobes protruding into the buccal cavity (Fig. 3B). The valvular apparatus of the oesophagus is well developed (Fig. 2A, B, G). Male worms have 6 pairs of caudal papillae: 2 praeanales, 1 or 2 adanales and 2 or 3 postanales (Figs. 2C, D, E and 3D).

Paratenuisentis ambiguus (Van Cleave, 1921) Bullock & Samuel, 1975 belongs to the monospecific genus *Paratenuisentis* (Tenuisentidae, Eoacanthocephala). It has a prominent apical organ, often seen as a conspicuous elevation of the proboscis tip (Fig. 4E), posteriorly extending to the fourth circle of hooks. For all other features see Table 3, Fig. 4 and Bullock & Samuel (1975). The lengths of the lemnisci in males from Germany were almost equal, while a slight difference in length was measured in females. Bullock & Samuel (1975) considered the lemnisci as subequal and thus differentiated between a 'long' and a 'short' lemniscus (Table 3). In the present investigation both lemnisci often lay twisted at the worm's ventral side making their measurement difficult. Infective larvae

Table 1 Prevalences of *Anguillicola crassus* and *Paratenuisentis ambiguus* in eels, and *Gammarus tigrinus* in 3 waters of F. R. Germany

Worm species	Biotope (Stn)	Sampling season	Prevalence (%)	Mean intensity	Mean length of infected eels	Mean length of uninfected eels	n
<i>A. crassus</i> in eel	Ruhr lake (1)	Apr–Nov 86	78.6	3.4 (1–16)	39.9 (30–56)	39.1 (29–48)	103
	Ruhr lake (1)	Apr–Sep 87	97.5	13.6 (1–42)	41.6 (30–57)	41.5 (41.5)	40
	Weser (2)	Apr–Jun 86	43.3	4.2 (1–15)	44.7 (40–60)	45.3 (36–52)	23
	Weser (2)	Oct–Nov 86	51.1	8.3 (1–20)	41.6 (29–65)	44.9 (33–62)	49
	Elbe (3a)	Jun–Jul 86	13.2	1.4 (1–3)	28.5 (21–39)	29.3 (20–51)	154
	Elbe (3b)	Jun–Jul 86	8.1	1.4 (1–2)	25.2 (22–29)	23.7 (19–30)	123
	Elbe (3c)	Jun–Jul 86	1.8	2 (2)	29 (29)	21.8 (9–29)	57
<i>P. ambiguus</i> in eel	Ruhr lake (1)	Apr–Nov 86	0	–	–	39.7 (29–56)	103
	Weser (2)	Jun–Jul 86	87.2	98.2 (1–410)	45.7 (36–60)	46.5 (32–60)	47
	Elbe (3a–c)	Jun–Jul 86	0.3	7 (7)	25.0 (25)	26.1 (9–51)	334
<i>P. ambiguus</i> larvae in <i>Gammarus tigrinus</i>	Weser (2)	Jul 86	26.5	1.2 (1–2)	Not measured		200

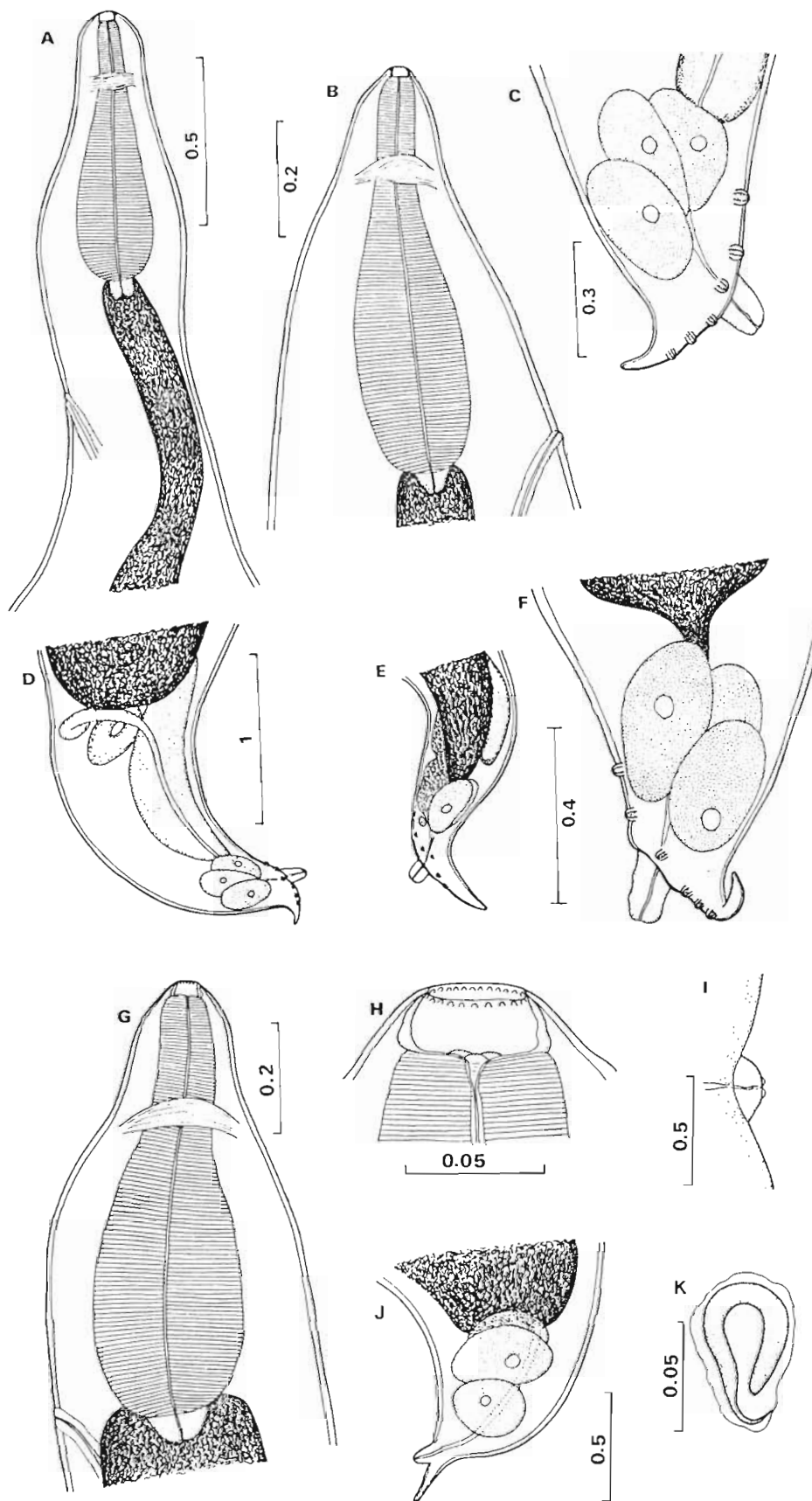


Fig. 2. *Anguillicola crassus*. Important features of male (A to F) and female (G to K) worms. Male: (A) anterior end of specimen with narrowed body in the oesophageal region; (B) head end, usual shape; (C, D) caudal end; (E, F) caudal ends of small and large males (same magnification). Female: (G) head end of largest specimen; (H) buccal capsule; (I) vulva; (J) caudal end; (K) sheathed larva from uterus. All scales in mm

Table 2. *Anguillicola crassus*. Comparison of specimens from Japan and Europe. n = 10 (except types)

Measurement (mm)	Type specimens after Kuwahara et al. 1974 (Own measurements in brackets)		Non-type specimens from Japan (new data)		European specimens (present material)	
	♂	♀	♂	♀	♂	♀
Body length	20.5–55.9 (32.94)	47.1–71.5 (42.94)	12.92–21.76	30.87–44.74	5.77–23.12	16.23–36.72
Body width	0.9–2.8 (3.7)	3.0–5.6 (4.7)	0.816–1.02	1.63–3.50	0.340–1.77	1.36–5.00
Length of buccal capsule	0.015–0.025 (0.024)	0.018–0.028 (0.027)	0.021–0.027	0.027	0.021–0.027	0.024–0.027
Width of buccal capsule	0.045–0.060 (0.048)	0.045–0.060 (0.054)	0.048–0.060	0.060–0.063	0.048–0.057	0.054–0.063
Length of oesophagus	0.68–1.03 (0.76)	0.86–1.10 (0.98)	0.775–0.843	0.911–1.09	0.571–0.816	0.775–1.06
Max. width of oesophagus	0.24–0.41 (0.26)	0.30–0.49 (0.33)	0.207–0.218	0.231–0.272	0.135–0.258	0.258–0.381
Length ratio of oesophagus and body	1:27.0–69.0 (1:43.3)	1:39.0–65.9 (1:43.7)	1:16.7–25.8	1:33.9–41.1	1:10.1–29.2	1:20.9–34.6
No. of caudal papillae in male	5 (6)	–	5–6	–	6	–
Distance of vulva from posterior end	–	8.40–12.25 (?)	–	4.08–4.90	–	4.01–7.01
Length of tail	? (0.207)	? (0.231)	0.215–0.240	0.299	0.120–0.286	0.136–0.448
Hosts	<i>Anguilla anguilla</i> <i>Anguilla japonica</i>		<i>Anguilla anguilla</i>		<i>Anguilla anguilla</i>	
Occurrence	Japan		Japan		FR Germany	

(Fig. 4E) from the intermediate host were very similar to those described from North America by Samuel & Bullock (1981).

DISCUSSION

Morphology

Specimens of *Anguillicola crassus* from Germany differed from those from Japan described by Kuwahara et al. (1974) in their somewhat smaller body sizes, slight differences in the shape of the oesophageal region, the presence of 6 pairs of caudal papillae in the male, in contrast to 5, and the presence of a fourth (small) rectal gland (Fig. 2E) similar to that described by Yamaguti (1935) for *A. globiceps*. The different proportions seem to be due to different fixation (hot formalin versus cold formalin) and to allometric growth of the worms. The Japanese investigators did not use SEM and they probably missed the sixth pair of caudal papillae and the fourth rectal gland which is often overlapped by the 3 larger ones. A revision of the type specimens from Japan showed that they also carried 6 pairs of caudal

papillae and a fourth rectal gland, like the European specimens.

Concerning *Paratenuisentis ambiguus*, measurements obtained from European specimens fall within the range of sizes given for the American specimens. Mean values for the American specimens, however, were not presented by Bullock & Samuel (1975). Thus, it cannot be decided – even considering the American type specimens – whether the lemnisci of the American worms were more subequal than those of the European ones.

Taking all features into consideration, there are no doubts about the conspecificity of the European and the Japanese specimens of *Anguillicola crassus*, and the European and the American specimens of *P. ambiguus*.

Field data, laboratory cycle

European eels have been helminthologically examined since the end of the eighteenth century and are still being investigated constantly. It can be concluded that any new helminth species is reported fairly

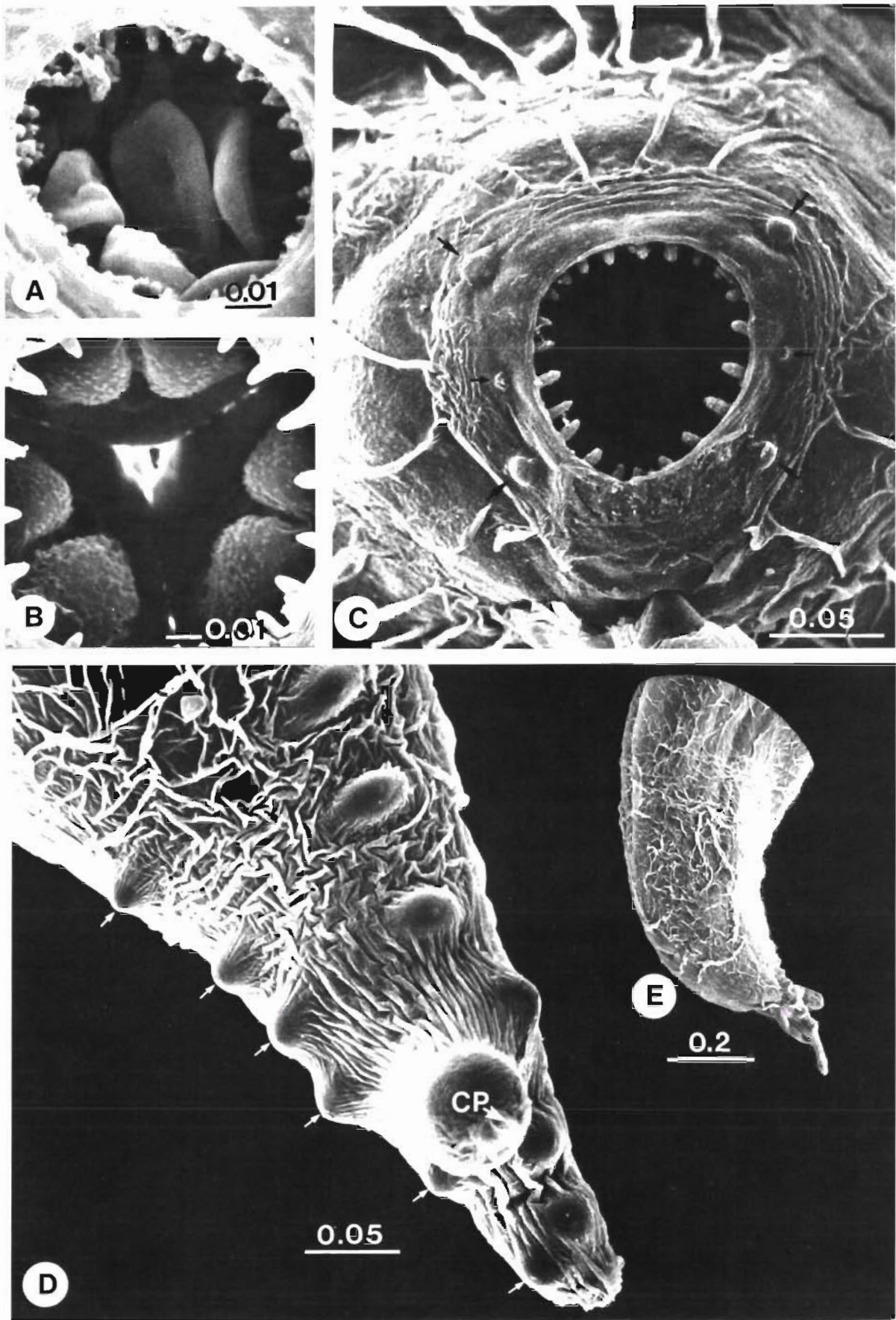


Table 3. *Paratenuisentis ambiguus*. Morphological data. Measurements in μm , except worm length which is in mm (mean in brackets); n = 10

Females	Bullock & Samuel 1975*	Present study	Males	Bullock & Samuel 1975*	Present study
Length	4.4–13.7	6.8–11 (8.2)	As females	2.7–8.1	4.7–6.5 (5.6)
Maximal width	410–1520	504–990 (682)	As females	330–1010	522–792 (621)
Length of external praesoma	620–848	684–810 (752)	As females	440–680	594–699 (655)
Max. width of ext. praesoma	120–210	140–200 (166)	As females	100–170	144–180 (160)
No. proboscis hooks per row	13–17	14–17 (15.7)	As females	11–17	13–16 (14.1)
No. of hook rows	18–22	16–19 (17.9)	As females	14–18	14–17 (15.3)
Size of anterior hooks	40–55 $\times$ 8–11	40–50 $\times$ 7–11 (44.7 $\times$ 9.3)	As females	43–50 $\times$ 8–11	43–50 $\times$ 9–11 (46 $\times$ 9.8)
Size of posterior hooks	36–48 $\times$ 5–8	36–45 $\times$ 5–7 (38.6 $\times$ 6.8)	As females	38–47 $\times$ 5–7	34–40 $\times$ 5–7 (38 $\times$ 6.3)
Length of receptacle	390–1200	864–1080 (995)	As females	330–950	756–990 (869.6)
Length of long lemniscus	860–2490	1550–2340 (1780)	As females	630–2730	1422–1980 (1588)
Length of short lemniscus	750–2100	1260–1980 (1630)	As females	590–2640	1386–1944 (1559)
Length of vagina	130–210	144–198 (167)	Length of anterior testis	220–850	360–720 (482.4)
Length of uterus	140–390	207–324 (262)	Length of posterior testis	210–1040	468–900 (631.8)
Length of uterine bell & apparatus	130–520	198–324 (238)	No. of cement gland nuclei	26–48	30–43
Size of mature eggs (saline)	62–72 $\times$ 26–31	64–71 $\times$ 26–30 (67 $\times$ 29)	Length of cement reservoir	70–350	216–306 (256)
Hosts	<i>Anguilla rostrata</i>	<i>Anguilla anguilla</i>	As females	As females	As females
Occurrence	USA	FR Germany	As females	As females	As females

* Corresponding with the type specimens (US National Museum)

soon after its appearance. Thus, both new helminths must have invaded Europe within the last few years, probably with intercontinental live eel transports.

In this investigation *Anguillicola crassus* was found already widely distributed in diverse habitats in northern Germany: it was abundant in the eutrophic Ruhr lake (Stn 1) as well as in the low salinity (see Veh 1975) Weser river (Stn 2) and the mixohaline (see Möller 1984) Elbe estuary (Stns 3A to 3C). The wide distribution is probably assisted by a broad range of intermediate hosts or by being transmitted by ubiquitous intermediate hosts. The East Asiatic congeneric *A. globiceps* developed in various copepods and cladoceran intermediate hosts (Haung 1981). Only 2 copepods were tested as intermediate hosts of *A. crassus* in Japan: one was positive, one refractory (Hirose et al. 1976). Differences in prevalence in various localities may result from

many factors including a different abundance of infected intermediate hosts. Transmission appears to be restricted to freshwater or low-salinity environments as can be seen from the decrease in infection towards the open sea in the Elbe estuary (Table 1). The increase of infection, especially in intensity, in the Ruhr lake from 1986 to 1987 is conspicuous. During summer 1987 local fishermen complained about a striking decrease of the eel catch. Several dead eels were found. Prior to 1986 eels from Ruhr lake were investigated only for their intestinal parasites. Nevertheless, large worms inside the air-bladder would have been noticed. Thus, it can be concluded that the prevalence and intensity of infection in that habitat must have been much lower before 1986. Whether there is a connection between the decreasing catch and the increasing abundance of *A. crassus* remains uncertain.

Fig. 3. *Anguillicola crassus*. SEM-micrographs of important outer features. (A) Mouth opening with enclosed erythrocytes of eel host; (B) empty mouth showing the buccal cavity with 6 slightly elevated lobes that posteriorly transgrade into the 3 prominent oesophageal lobes; (C) mouth opening with circumoral teeth and surrounding 4 dorsolateral cephalic papillae (large arrows) and 2 lateral amphids (small arrows); (D) frontal view of caudal end of male showing 6 pairs of caudal papillae (arrows) and cloacal core (CP) on top of the cone-shaped ventral process; note the wrinkled upper layer of cuticle that surrounds the worm; (E) lateral view of male caudal end. All scales in mm

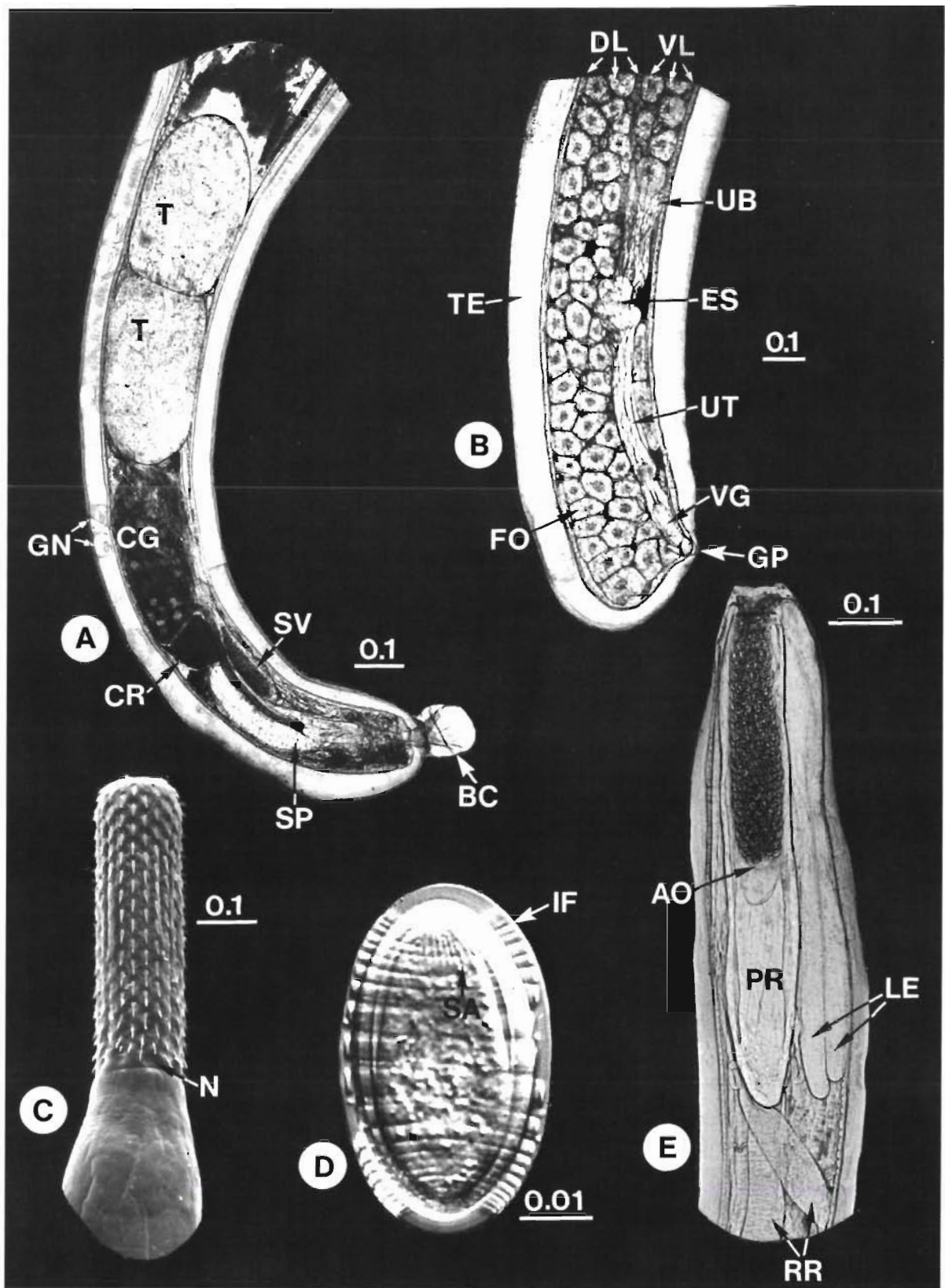


Fig. 4. *Paratenuisentis ambiguus*. (A, B, D, E) LM and (C) SEM micrographs of important features. (A) Posterior half of male, showing the sexual organs; the bursa copulatrix (BC) is evaginated; (B) posterior portion (posterior eighth) of female, with enclosed sexual organs; note that the ventral ligament sac (VL) terminates in the uterine bell (UB) while the dorsal sac (DL) encloses most of the uterus (UT) and vagina; (C) praesoma (proboscis and very narrow neck) showing the proboscis hooks arranged quincuncially; (D) embryonated egg with characteristic infoldings (IF) of the eggshell; (E) anterior half of infective larva; note the prominent apical organ at the tip of the invaginated proboscis. All scales in mm. AO: apical organ on top of invaginated proboscis; BC: bursa copulatrix (evaginated); CG: cement gland; CR: cement reservoir; DL: dorsal ligament sac; ES: egg-sorting apparatus; FO: floating ovary (ovarian ball); GN: giant nuclei (pair); GP: genital pore; IF: infoldings of eggshell; LE: lemnisci; N: neck; PR: proboscis receptacle; RR: receptacle retractors; SA: acanthor's apical spines; SP: Saeftigen's pouch; SV: seminal vesicle; T: testes; TE: tegument; UB: uterine bell; UT: uterus (the arrow points to an egg inside); VG: vagina enclosed by 2 sphincters; VL: ventral ligament sac

Since *Anguillicola crassus* does not appear to show a preference for a specific habitat it may soon become widely spread in Europe.

The distribution of *Paratenuisentis ambiguus* was correlated with the distribution of its (single) intermediate host. It occurred in the River Weser, where *Gammarus tigrinus* is highly abundant (Fries & Tesch 1965) and highly infected. It did not occur in the Ruhr lake and almost not in the Elbe estuary, where *G. tigrinus* is absent. The role of *G. tigrinus* as the exclusive intermediate host of *P. ambiguus* has been proved in the field as well as in the laboratory.

Gammarus tigrinus is an indigenous species of mixohaline coastal waters between the St. Lawrence estuary and Florida (Steele & Steele 1972). Since 1939 it has been recorded from the west coast of England (Sexton 1939) in brackish and polluted waters. Hynes (1955) concluded that it had been introduced through the action of man. It was purposely introduced into the German River Weser (Werra) in 1957 to replace the indigenous gammarid fauna which had disappeared due to pollution (saline sewage; Schmitz 1960, Veh 1975). Since only laboratory offspring of English amphipods were brought into the river (Schmitz 1960) it is unlikely that the parasite was introduced with them.

The high intermediate host specificity of *Paratenuisentis ambiguus* should prevent a quick spread of this new helminth in Europe. However, *Gammarus tigrinus* is further expanding its distributional range: Pinkster et al. (1977) reported it from approximately one-third of the Netherlands.

Eoacanthocephalans have had a conspicuous speciation and radiation in North America (Amin 1986); in Europe *Paratenuisentis ambiguus* is now the second representative of its class.

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