LARVAE AND ADULTS OF *HYSTEROTHYLACIUM ADUNCUM* (RUDOLPHI, 1802) (NEMATODA: ANISAKIDAE) IN FISHES AND CRUSTACEANS IN THE SOUTH WEST ATLANTIC

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Summary :

Hysterothylacium aduncum (Rudolphi, 1802) is reported from five fishes and one invertebrate species. Third-stage larvae were found in the crustacean *Themisto gaudichaudii* and in mesenteries of the fishes *Engraulis anchoita* and *Merluccius hubbsi*; fourth-stage larvae were recovered from the digestive tract of *M. hubbsi* and *Scomber japonicus* and adult specimens were obtained from the stomach and intestine of *M. hubbsi, S. japonicus, Genypterus blacodes* and *Genypterus brasiliensis*. Nematodes are described, measured and illustrated. Parasitic prevalence, mean intensity and range were calculated in relation to different geographic zones, from the Argentinean-Uruguayan Common Fishing Zone to Patagonic areas. An increase of parasitism from the northern areas southwards was observed. The life-cycle of *H. aduncum*, involving the host species considered, is also postulated.

KEY WORDS : *Hysterothylacium aduncum*, nematodes, systematics, life cycle, Argentine.

MOTS CLÉS : Hysterothylacium aduncum, *nématodes, systématique, cycle biologique, Argentine.*

Résumé : LARVES ET ADULTES D'*HYSTEROTHYLACIUM ADUNCUM* (RUDOLPHI, 1802) (NEMATODA: ANISAKIDAE) PARASITES DE POISSONS ET DE CRUSTACÉS DE L'ATLANTIQUE SUD.

La présence de Hysterothylacium aduncum *(Rudolphi, 1802) chez cinq espèces de poissons et chez une espèce de crustacés est signalée dans ce travail. Les larves du troisième stade ont été trouvées chez le crustacé* Themisto gaudichaudii *et sur les mésentères des poissons* Engraulis anchoita *et* Merluccius hubbsi *; les larves du quatrième stade ont été prélevées dans l'appareil digestif de* M. hubbsi *et de* Scomber japonicus *et les nématodes adultes ont été récoltés dans l'estomac et dans l'intestin de* M. hubbsi, S. japonicus, Genypterus blacodes *et* Genypterus brasiliensis. *Les nématodes sont décrits, mesurés et figurés. La prévalence et l'intensité moyenne du parasitisme sont calculées chez les différents hôtes et dans les différentes zones géographiques s'étendant de la Zone de Pêche Commune Argentine-Uruguay aux côtes de la Patagonie. Une augmentation du parasitisme du nord au sud a été observée. Un schéma du cycle biologique de* H. aduncum *chez les espèces d'hôtes considérées dans cette étude, est proposé par les auteurs.*

INTRODUCTION

The nematode genus *Hysterothylacium* Ward & Magath, 1917 (Ascaridoidea, Anisakidae, Raphidascaridinae) comprises more than fifty species of nematodes parasites of teleosts (Deardorff & Overstreet, 1980). The adult worms mostly parasitize the digestive tract of fishes (Deardorff & Overstreet, 1980) whereas the larval stages live in different tissues of numerous fish species and in over 100 invertebrate species from seven phyla (Norris & Overstreet, 1976; Hurst, 1984; Marcogliese, 1996), which act as intermediate and/or paratenic hosts (Køie, 1993*a*).

Hysterothylacium aduncum (Rudolphi, 1802) Deardorff & Overstreet, 1981, has a circumpolar distribution in the Northern Hemisphere, and is found mainly in marine teleosts in temperate and cold waters (Berland, 1991) although Moravec *et al.* (1985) and Yoshinaga *et al.* (1987) also recorded it in freshwater hosts. *H. aduncum* has been reported in fishes collected in the North Eastern Atlantic and Seas of the North of Europe (Punt, 1941; Berland, 1961; Petter, 1969; Fagerholm, 1982; Petter & Cabaret, 1995) and Petter & Maillard (1987, 1988) confirmed its presence in a great number of fish species from the Mediterranean Sea and Petter & Radujkovic (1989) cited this species in the Adriatic Sea. This nematode is also common in the Pacific and Atlantic waters of North America (Margolis & Arthur, 1979; Love & Moser, 1983; Køie, 1993*b*, Marcogliese, 1996).

In the Southern Hemisphere, Beumer *et al.* (1982) summarized the presence of *H. aduncum* in fishes from Australia and its adjacent Antarctic territories, Hurst (1984) reported its third-stage larvae in different invertebrate species from New Zealand and Carvajal

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& Gonzalez (1995) confirmed its presence in coho salmon in the South of Chile.

In the South West Atlantic Ocean, unidentified nematodes of the genus *Hysterothylacium* have been cited by Rego *et al.* (1985) and Eiras & Rego (1987) in *Pagrus pagrus* from Brazil; by Nigmatullin & Shukhgálter (1990) in *Illex argentinus* from Argentina, by Reimer & Jessen (1981) (as *Thynnascaris* sp.), and Sardella & Timi (1996) in *Merluccius hubbsi* and by Cremonte & Sardella (1997) in *Scomber japonicus* from the Argentinean Uruguayan Common Fishing Zone (AUCFZ).

Previous records of *H. aduncum* in the Argentine Sea comprise those of Szidat (1955) (as *Contracaecum aduncum*) in *Merluccius hubbsi;* Evdokimova (1973) (as *Contracaecum aduncum*) in *Paralichthys patagonicus* (Evdokimova's records of *C. aduncum* in *Scomber colias* and *Epinephelus alexandrinus* may be due to misidentifications of these hosts, which are not present in the area); by Gayevskaya *et al.* (1990) in *Dissostichus eleginoides* and by MacKenzie & Longshaw (1995) in M. *hubbsi* and M. *australis.*

The aim of this paper is to identify to the specific level nematodes of the genus *Hysterothylacium* found in different teleost species and in one species of crustacean collected in different zones of the Argentine Sea, to analyze its life cycle and to consider some biogeographic aspects in the studied area.

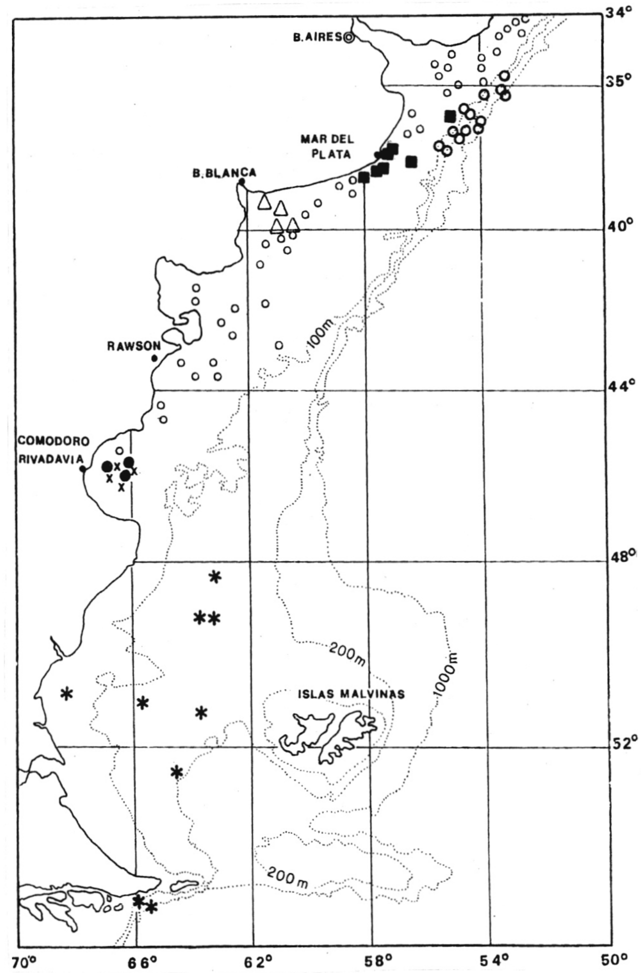


Fig. 1. — Geographic location of samples. Small open circles: *Engraulis anchoita* from AUCFZ; small filled circles: *E. anchoita* from Patagonian Zone; large open circles: *Merluccius hubbsi* from AUCFZ; filled squares: *Scomber japonicus* from AUCFZ; triangles: *S. japonicus* from El Rincón Zone; large filled circles: *Themisto gaudichaudii* from San Jorge Gulf; crosses: *Genypterus brasiliensis* from San Jorge Gulf; and asterisks: *G. blacodes* from Patagonian Zone.

MATERIALS AND METHODS

The present study was carried out in different areas of the Argentinean Shelf, between 34° and 56°S and 53° to 69°W from 1993 to 1995. Samples were collected during cruises of R.V. Cap. Oca Balda and Dr. E. Holmberg and from the commercial catches from Mar del Plata Port.

The following fish species were examined: 2,086 specimens of *Engraulis anchoita* Hubbs & Marini, 1935 from Argentinean-Uruguayan Common Fishing Zone (AUCFZ) and Patagonian Zone; 173 specimens of *Scomber japonicus* Hottuyn, 1782 from AUCFZ and El Rincón Zone; 159 specimens of *Merluccius hubbsi* Marini, 1933 from AUCFZ; 34 specimens of *Genypterus blacodes* Schneider, 1801 from Patagonian Zone and 31 of *G. brasiliensis* Reagan, 1903 from San Jorge Gulf. Thirty parasitized individuals of *Themisto gaudichaudii* Guérin-Méneville, 1836 (Crustacea: Amphipoda) obtained from zooplankton samples from San Jorge Gulf were also studied (Fig. 1; Table I).

Fish were measured for total length and sexed. As each fish was dissected, examinations of liver, stomach, caeca, intestine and its contents, swim bladder and gonads were made. Crustaceans were squashed between two glass plates and observed under a stereomicroscope. Nematodes were fixed in 4 % formalin and stored in 70 % ethanol. For light microscopy, specimens were cleared in lactophenol, in which they were kept during measuring and drawing. The illustrations were made with the aid of a drawing tube; measurements are given in millimeters (mm). The ratios of the main morphological features follow Petter & Maillard (1987, 1988) and the ratios between lateral alae at cervical level and oesophagus length were calculated according to Petter & Cabaret (1995). The material studied is deposited in the Invertebrate Collection (Helminths) of La Plata Natural Science Museum (LPNSM), La Plata, Argentina.

Prevalence and intensity of infection (Margolis *et al.*, 1982) were calculated in relation to the geographic location of the samples. No quantitative analysis was made for *T. gaudichaudii* because only parasitized specimens were examined.

Host species	Zone	Host length (cm)	No. hosts examined	Prevalence	Mean intensity	Range
E. anchoita	AUCFZ	4-19	544	26.33	9.13	1-266
	Patagonian	8-19	1,542	44.12	25.32	1-338
S. japonicus	AUCFZ	30-53	90	50.00	3.82	1-27
	El Rincón	29-44	83	77.11	4.63	1-23
M. hubbsi	AUCFZ	16-60	159	67.30	4.20	1-30
G. blacodes	Patagonian	39-127	34	41.18	55.14	1-253
G. brasiliensis	San Jorge Gulf	40-75	31	74.20	7.60	1-40

Table I. — Prevalence, Mean Intensity and Range of *Hysterothylacium aduncum* in different host species in relation to geographic zones.

RESULTS

Hysterothylacium aduncum (Rudolphi, 1802) Deardorff & Overstreet, 1981 (Figs. 2-3).

THIRD-STAGE LARVA (Fig. 2, *a-g*)

Hosts: *Themisto gaudichaudii*, *Engraulis anchoita* and *Merluccius hubbsi*.

Habitat: Hemocoel of *T. gaudichaudii* and visceral cavity and mesenteries of *E. anchoita* and *M. hubbsi*, rarely encapsulated.

Material deposited: one larva from *T. gaudichaudii* (LPNSM Coll. N° 3963) and one larva from *E. anchoita* (LPNSM Coll. N° 3964).

In *Scomber japonicus*, nematodes were found encapsulated in the visceral cavity and mesenteries. These capsules were melanized, and the worms inside the capsules had degenerated. Some of them were identified as *Hysterothylacium* sp.; the rest were considered unidentified.

Three third-stage larvae of *Hysterothylacium* sp. were found in mesenteries of two specimens of *Genypterus brasiliensis*, but their stage of conservation did not allow a specific identification.

Description

Body thinner anteriorly. Cuticle transversally striated, lateral alae with support v-shaped in cross-section, extending immediately behind the anterior extremity up to the caudal end (width at level of oesophagus: 15 μ). Oral opening usually with T- formed aspect; no distinct lips present, with a ventral boring tooth and two subventral and two subdorsal papillae. Oesophagus 9.94-14.05 of body length, ventriculus about as long as wide; ventricular appendage thin, ratio oesophagus length/ventricular appendage length 1.81-3.10; intestinal caecum longer than ventricular appendage, ratio oesophagus length/caecum length 1.35-2.79. Excretory pore situated immediatly behind the level of nerve ring. Filament-like gonads present, extending from the distal extremity of the ventricular appendage to the anus. Genital tubules of female double, situated laterally, vulva not visible; male with one ventral coiled tubule. Conical tail ending in a spike. Caudal process of the next stage with fine spines observed inside the tail.

Measurements of the third-stage larvae are given in Table II, larvae from *T. gaudichaudii* and *E. anchoita* are similar in length, whereas in larvae from *M. hubbsi* bigger sized specimens were observed. Relative values of parameters are given in Table IV.

FOURTH-STAGE LARVA (Fig. 2, *h-k*)

Hosts: *Merluccius hubbsi* and *Scomber japonicus*.

Habitat: Digestive tract.

Material deposited: one larva from M. *hubbsi* (LPNSM Coll. N° 3962).

Description

Body thinner anteriorly. Cuticle transversally striated, lateral alae with support v-shaped in cross-section, starting behind the base of the lips (width at level of oesophagus: 36 μ), extending all along the body, becoming narrower posteriorly. Three lips and interlabia present as in adults; lips about as long as wide, slightly constricted at anterior end; interlabia length about half of lip length; two lateral double papillae present on the dorsal lip. On each subventral lip, one double and one simple papilla, in addition to the amphids, are present. Oesophagus 8.72-11.48 of body length, ventriculus about as long as wide; ventricular appendage thin, ratio oesophagus length/ventricular appendage length 2.13-4.67; intestinal caecum longer than ventricular appendage, ratio oesophagus length/caecum length 1.28-2.19. Excretory pore situated immediately behind the level of nerve ring. Characteristic « cactus-tail » present. All the specimens examined showed an outline of the genitalia. Some individuals were found

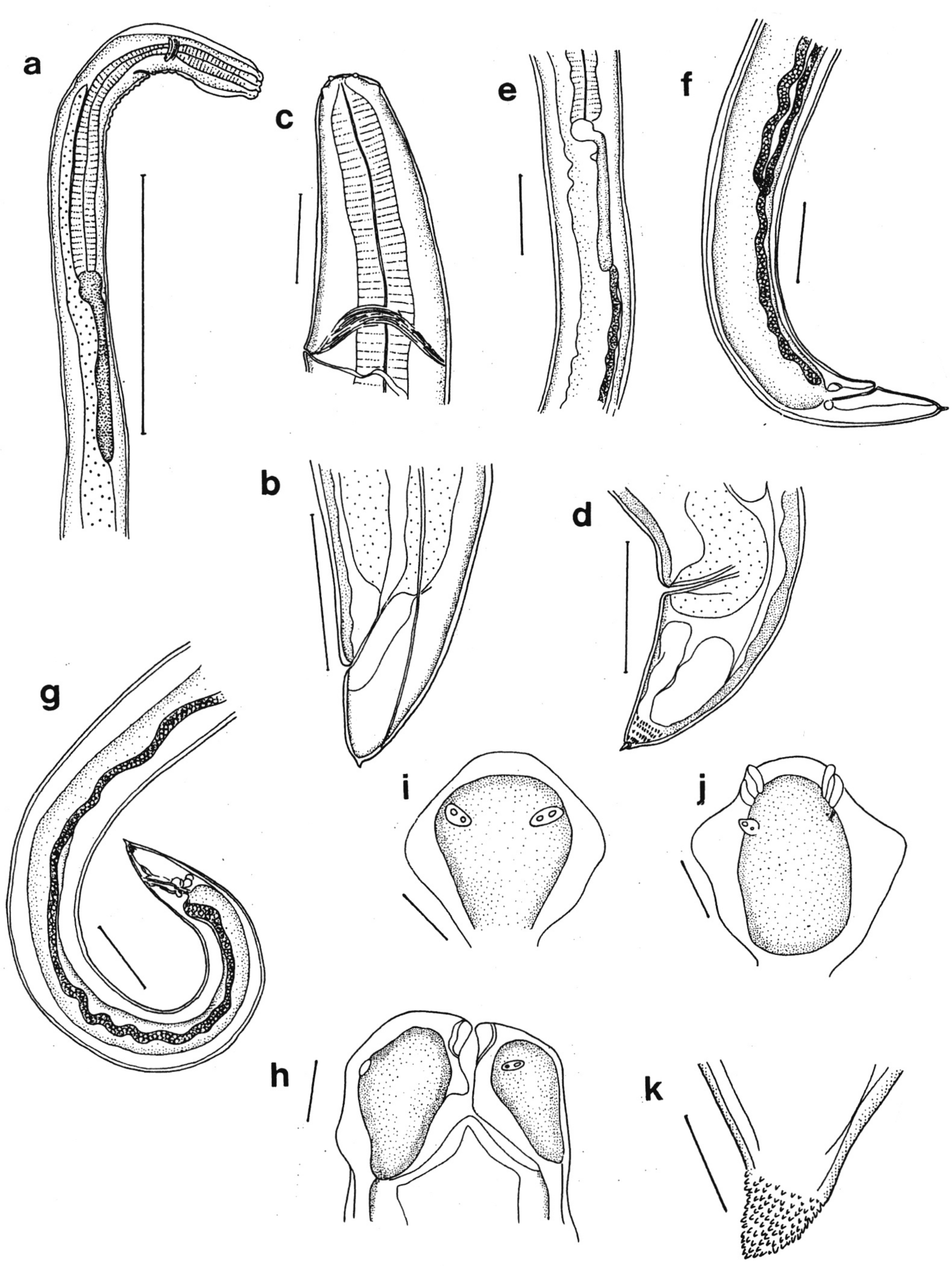


Fig. 2. — a-b: Third stage larvae of *H. aduncum* in *Themisto gaudichaudii*; a: anterior part, median view; b: posterior end and lateral alae; c-d: L3 in *Engraulis anchoita*; c: anterior end, nerve ring and excretory pore; d: posterior end, lateral view; e-g: L3 in *M. hubbsi*; e: male, ventricular appendage and proximal genital tubule; f: female, double filament-like gonad, lateral view; g: male, posterior end, simple filament-like gonad, lateroventral view; h-k: L4 in *M. hubbsi*; h: anterior end, lateral view; i: dorsal lip; j: lateroventral lip; k: « cactus-tail ». Scale lines (in micrometers): a: 500; b, h, i, j, k: 50; c, d: 100; e, f, g: 250.

in the process of shedding their cuticles, moulting to the adult stage.

Measurements of the fourth-stage larvae are given in Table II. Relative values of parameters are given in Table IV.

Adult stage (Fig. 3)

Hosts: *Merluccius hubbsi, Scomber japonicus, Genypterus blacodes* and G. *brasiliensis.*

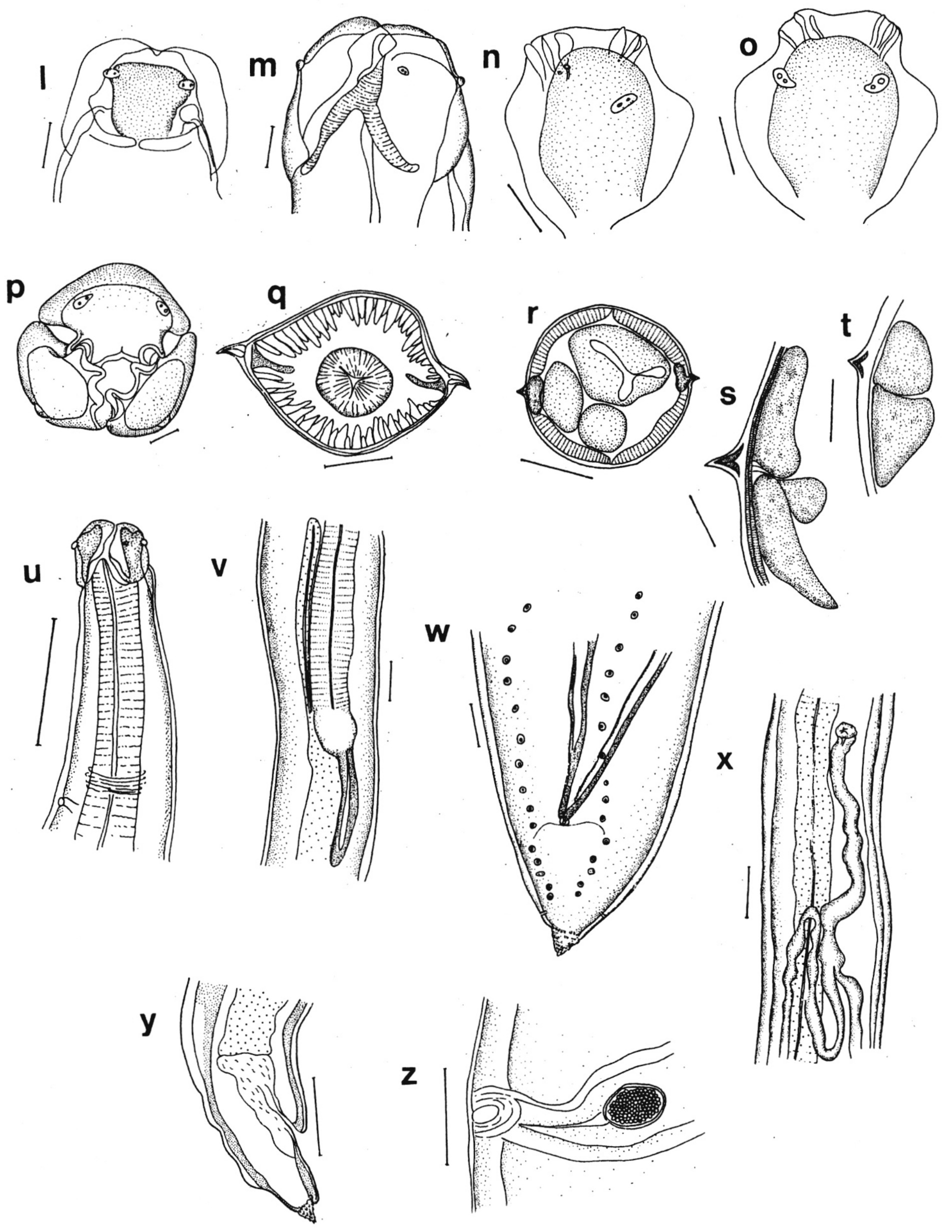
Habitat: Stomach and intestine.

Material deposited: one male and one female from *M. hubbsi* (LPNSM Coll. N° 3961 1), one male and one female from *G. blacodes* (LPNSM Coll. N° 3959 1), one male and one female from *G. brasiliensis* (LPNSM Coll. N° 3960 1), one male and one female from *S. japonicus* (LPNSM Coll. N° 3965).

Description

Body thinner anteriorly. Cuticle transversally striated, lateral alae with support v-shaped in cross-section, starting behind the base of the lips and extending all along the body, becoming narrower posteriorly (width: 45 µ at base of lips; 36 µ at oesophagus level; 30 µ at middle of body; 15 µ at posterior part; 10 µ at tail

Fig. 3. — l-z: Adult *H. aduncum* in *Genypterus blacodes*: l: anterior end, dorsal view; m: anterior end, lateral view; n: dorsal lip; o: lateroventral lip; p: anterior end, apical view; q: cross section at level of oesophagus; r: female, cross section at level at the middle of the body; s: cross section of lateral alae at the middle of the body; t: cross section of lateral alae at posterior end; u: anterior extremity, lateral view, nerve ring and excretory pore; v: oesophagic region, ventriculus, intestinal caecum and ventricular appendage; w: adult *H. aduncum*, male, posterior end, ventral view; x-z: adult *H. aduncum*, female; x: vulvar region, ventral view; y: vulva and vagina, lateral view and egg; z: posterior end, lateral view. Scale lines (in micrometers): l, m, n, o, p, q, s, t, w: 50; r, u, v, x, y: 250; z: 100.



level). Lips longer than wide, formed by a pulp and membranous lateral flanges; constriction at anterior end more evident than in fourth-stage larva; two lateral double papillae present on the dorsal lip. On each subventral lip, one double and one simple papilla, in addition to the amphids, are present. Interlabia length about half of lip length. Oesophagus 6.5-11.5 of body length, ventriculus about as long as wide; ventricular appendage thin, ratio oesophagus length/ventricular appendage length 2.60-6.35; intestinal caecum longer than ventricular appendage, ratio oesophagus length/caecum length 1.18-3.94; ratio of oesophagus length/maximal width of lateral alae: 59; ratio of ventricular appendage/maximal width of cervical alae: 14.9. Excretory pore situated immediatly behind the level of nerve ring. Tail with the characteristic mucronate spined appearance.

Measurements of the adult specimens are given in Table III. Relative values of parameters are given in Table IV.

Male

The spicules are ventrally alate. The spicule length in relation to the body length varies in the specimens examined (Table III). About 21 to 33 pairs of precloacal papillae are arranged in two subventral rows, the ten posterior pairs being closer together. One large medioventral precloacal papilla, one adcloacal and five post-

Host	L3			L4	
	T. gaudichaudii	*E. anchoita*	*M. hubbsi*	*M. hubbsi*	*S. japonicus*
Number measured	8	21	4	4	2
Total length	4.95-12.37	4.91-15.84	9.49-18.86	8.10-24.55	14.96-15.95
Maximum width	0.12-0.30	0.09-0.33	0.25-0.34	0.12-0.40	0.19-0.27
Distance from anterior end to:					
– nerve ring	0.18-0.28	0.21-0.36	0.25-0.40	0.25-0.52	0.36-0.38
– excretory pore	0.20-0.39	0.25-0.46	0.28-0.45	0.27-0.42	0.39-0.42
Oesophagus length	0.67-1.23	0.69-1.69	1.15-2.02	0.93-2.14	1.43-1.69
Ventriculus length	0.02-0.09	0.04-0.09	0.08-0.10	0.06-0.14	0.08-0.12
Ventriculus width	0.04-0.10	0.04-0.09	0.08-0.08	0.05-0.08	0.08-0.11
Ventricular appendage length	0.30-0.57	0.31-0.61	0.48-0.71	0.35-0.76	0.44-0.49
Intestinal caecum length	0.39-0.68	0.38-0.91	0.66-1.50	0.41-1.04	0.77-0.77
Tail length	0.08-0.18	0.07-0.21	0.10-0.19	0.11-0.24	0.14-0.19

Table II. — Measurements of third and fourth-stage larvae of *Hysterothylacium aduncum* collected from different host species.

Host	Males				Females			
	M. hubbsi	*S. japonicus*	*G. blacodes*	*G. brasiliensis*	*M. hubbsi*	*S. japonicus*	*G. blacodes*	*G. brasiliensis*
Number measured	7	2	4	4	6	2	5	4
Total length	11.6-35.9	23.7-25.8	31.5-46.2	25.7-49.2	16.3-39.6	42.4-47.2	33.2-58.2	11.9-34.8
Maximum width	0.27-0.51	0.27-0.39	0.43-0.65	0.30-0.53	0.21-0.45	0.58-0.65	0.48-0.86	0.13-0.56
Distance from anterior end to:								
– nerve ring	0.28-0.55	0.35-0.39	0.58-0.82	0.35-0.68	0.31-0.55	0.64-0.72	0.52-0.84	0.26-0.64
– excretory pore	0.32-0.55	0.40-0.44	0.62-0.84	0.39-0.75	0.39-0.61	0.70-0.80	0.59-1.04	0.30-0.79
Oesophagus length	1.24-2.97	1.85-2.02	2.34-4.29	2.34-3.20	1.50-3.17	3.31-3.70	2.60-4.12	1.37-2.81
Ventriculus length	0.08-0.10	0.06-0.09	0.12-0.26	0.12-0.17	0.07-0.11	0.23-0.26	0.16-0.26	0.07-0.13
Ventriculus width	0.06-0.08	0.07-0.10	0.13-0.19	0.12-0.17	0.06-0.09	0.19-0.19	0.16-0.22	0.06-0.14
Ventricular appendage length	0.38-0.67	0.44-0.65	0.78-0.85	0.45-0.91	0.49-0.78	0.71-0.75	0.80-0.95	0.49-0.77
Intestinal caecum length	0.47-1.43	0.82-1.20	0.91-1.33	0.90-1.69	0.91-1.56	1.48-1.60	0.91-1.90	0.58-1.10
Tail length	0.10-0.17	0.13-0.17	0.13-0.17	0.14-0.18	0.12-0.32	0.30-0.35	0.36-0.48	0.16-0.33
Spicules	0.35-1.19	0.69-1.41	1.26-2.06	0.86-2.00	–	–	–	–
Vulva to anterior end	—	—	—	—	6.37-13.20	11.70-13.52	8.32-17.65	7.93-13.26
Eggs length	—	—	—	—	0.051-0.056	0.054-0.060	0.051-0.055	0.056-0.060
Eggs width	—	—	—	—	0.049-0.053	0.039-0.042	0.041-0.048	0.050-0.054

Table III. — Measurements of adults of *Hysterothylacium aduncum* collected from different host species.

	L/O	O/VA	O/IC	VA/IC	S/L %
Third-stage larvae from:					
T. gaudichaudii	7.81 (6.69-10.31)	2.24 (2.10-2.54)	1.71 (1.61-1.89)	0.75 (0.67-0.82)	—
E. anchoita	8.42 (6.42-10.67)	2.48 (1.81-3.06)	2.09 (1.58-2.79)	0.86 (0.66-1.35)	—
M. hubbsi	9.24 (8.21-9.75)	2.69 (2.33-3.10)	1.78 (1.35-2.39)	0.66 (0.35-0.77)	—
Fourth-stage larvae from:					
S. japonicus	10.06 (9.66-10.46)	3.38 (2.92-3.84)	2.02 (1.86-2.19)	0.61 (0.57-0.64)	—
M. hubbsi	10.81 (8.22-15.19)	3.03 (2.13-4.67)	1.80 (1.28-2.05)	0.63 (0.42-0.77)	—
Adult male from:					
S. japonicus	12.81 (12.79-12.84)	3.72 (2.85-4.59)	1.82 (1.18-2.46)	0.48 (0.41-0.54)	4.37 (2.82-5.93)
M. hubbsi	10.43 (9.34-12.11)	4.31 (2.60-5.71)	2.45 (2.08-3.14)	0.62 (0.36-0.96)	3.27 (1.99-6.24)
G. blacodes	12.48 (10.76-13.96)	3.79 (3.00-4.59)	2.78 (1.94-3.94)	0.76 (0.65-0.86)	4.54 (4.06-5.76)
G. brasiliensis	12.05 (10.27-15.76)	3.56 (3.43-6.35)	2.09 (1.83-2.60)	0.49 (0.29-0.66)	3.88 (2.77-5.00)
Adult female from:					
S. japonicus	13.23 (12.75-13.71)	4.79 (4.66-4.93)	2.27 (2.24-2.31)	0.48 (0.47-0.49)	—
M. hubbsi	11.14 (10.05-12.49)	3.35 (2.67-4.06)	1.93 (1.82-2.03)	0.55 (0.55-0.55)	—
G. blacodes	12.66 (11.07-14.13)	3.87 (2.86-4.58)	2.89 (2.11-4.03)	0.74 (0.60-0.88)	—
G. brasiliensis	12.24 (10.38-13.95)	3.88 (3.02-5.40)	2.73 (2.24-3.02)	0.75 (0.54-1.00)	—

L: total length; O: oesophagus length; VA: ventricular appendage length; IC: intestinal caecum length; S: spicules length.

Table IV. — Relative values of parameters of larvae and adults of *Hysterothylacium aduncum* from different host species.

cloacal pairs, including phasmids, are present, with the third pair from the cloaca doubled.

Female

Vulva without salient lips, opening in the posterior end of the first third of the body length. Uterine eggs with smooth thin shell.

Table IV shows the main morphometric ratios for third-stage and fourth-stage larvae and adults.

QUANTITATIVE DATA

The prevalence values of *H. aduncum* were high for all fish host species. The highest values of mean intensity were registered from *E. anchoita* and *G. blacodes* (Table I).

Increases in the prevalence and intensity of this nematode were observed for *E. anchoita* and *S. japonicus* from the AUCFZ southwards (Table I).

DISCUSSION

All the nematodes examined at larval and adult stages collected from the different hosts considered in the present study belong to the species *Hysterothylacium aduncum* (Rudolphi, 1802) Deardorff & Overstreet, 1981 *sensu lato*.

The *H. aduncum* third-stage larva is characterized, as the adult worm, by the arrangement of the digestive organs, the position of the excretory pore just behind the nerve ring and the typical « cactus tail » of the next stage visible (Punt, 1941; Berland, 1961; Petter, 1969).

The closed trophic relationships among fish and invertebrate intermediate hosts harboring the third-stage larvae and ichthyophagous fish harboring the fourth-stage larvae and the adult worms support its specific identity.

The morphometric ratios (L/O, O/VA and O/IC) of the third stage larva examined agree with those of *H. aduncum* third-stage larva from other regions of the world (Punt, 1941; Fagerholm, 1982; Hurst, 1984; Moravec *et al.*, 1985; Yoshinaga *et al.*, 1987; Petter & Maillard, 1988). The third-stage larvae of *Hysterothylacium* sp. found in the mesenteries of *S. japonicus* and *G. brasiliensis* could be assigned to *H. aduncum* because in these hosts the nematode was found as fourth-stage larvae and adults in the digestive tract.

In relation to fourth-stage larvae, the specimens examined showed identical morphologic features (shape of lips, outline of genitalia and « cactus tail ») than those cited by Punt (1941), Berland, 1961, Fagerholm (1982), Moravec *et al.* (1985) and Petter & Maillard (1988). Nevertheless, morphometric comparisons among Argentinean specimens and those described by these authors evidenced a great variability in both measurements and morphometric ratios, a similar situation was observed for the adult worms. These metrical differences are probably associated with the state of development of the parasites (Moravec *et al.*, 1985), and it could be a consequence of the state of development of the previous larval stages in intermediate hosts. Køie (1993*a*) stated that development of third-stage larvae of *H. aduncum* in crustaceans varies according to crustacean host and temperature and its growth is influenced by immunological responses of the host, being the development limited in encapsulated larvae as compared with free larvae in coelom.

The diagnostic characteristics of the nematodes examined in the present paper were in correspondence with those present in the previous descriptions of *H. aduncum* (Punt, 1941; Berland, 1961; Petter, 1969; Fagerholm, 1982; Moravec *et al.*, 1985; Petter & Maillard, 1987; Petter & Cabaret, 1995).

Furthermore, the specimens of *H. aduncum* from the Argentinean hosts described above can be identified as the subspecies *H. aduncum aduncum* by the following combination of characters: presence of cervical alae hardly wider than lateral alae; ratio of oesophagus/maximum width of cervical alae > 54 and ratio of ventricular appendage/maximum width of cervical alae > 15 (Petter & Cabaret, 1995).

The present study extends the list of intermediate and definitive hosts and the distribution area for *H. aduncum* in the South West Atlantic Ocean, including *T. gaudichaudii, S. japonicus, G. brasiliensis* and *E. anchoita* as new intermediate hosts and *G. blacodes, G. brasiliensis* and *S. japonicus* as definitive hosts. The presence of this nematode at larval and adult stage in M. *hubbsi* is also confirmed in a wider area.

All of the host species examined showed high levels of prevalence, *H. aduncum* being an ubiquitous species in the marine environment of Argentina. According to Berland (1961), no particular fish species can be regarded as the main definitive or intermediate host.

The high values of intensity recorded for third-stage larvae of *H. aduncum* in *E. anchoita* can be explained by its zooplanktivorous food habits during its entire life span (Angelescu, 1982; Angelescu & Anganuzzi, 1981). Norris & Overstreet (1976) pointed out that invertebrates act as an important source of larvae in the life cycle of this parasite.

Køie (1993*a*) showed that the development of the larvae in unhatched eggs accelerates with increasing temperature, but eggs kept at 5 °C were still infective after six months. A similar situation was reported by Möller (1978), who found that the survival of larvae from unhatched eggs increased linearly with decreasing temperature. The observed increase in the parasite burden for *E. anchoita* and *S. japonicus* from AUCFZ southwards may indicate a greater affinity of

H. aduncum for colder waters; Bakun & Parrish (1991) showed that the water temperature in the Argentine Sea decreases with increasing latitude. MacKenzie & Longshaw (1995) did not distinguish between the genera *Hysterothylacium* and *Contracaecum* parasitizing M. *hubbsi* around the Malvinas Islands and Patagonian waters, but these southern hake populations had higher prevalences of these nematodes than those of the AUCFZ. Future studies may consider this nematode species as a biological tag for fish stocks in the area.

In relation to the life cycle of *H. aduncum*, Køie (1993*a*) showed that the two first moults occur in the egg, reaching the third larval stage, that at least one intermediate crustacean host is obligatory in the transmission of this nematode, and that the third-stage larva is only infective to fishes after a certain growth in one (or more) intermediate host(s). The last two moults occur in the digestive tract of the definitive fish host species, generally gadoids.

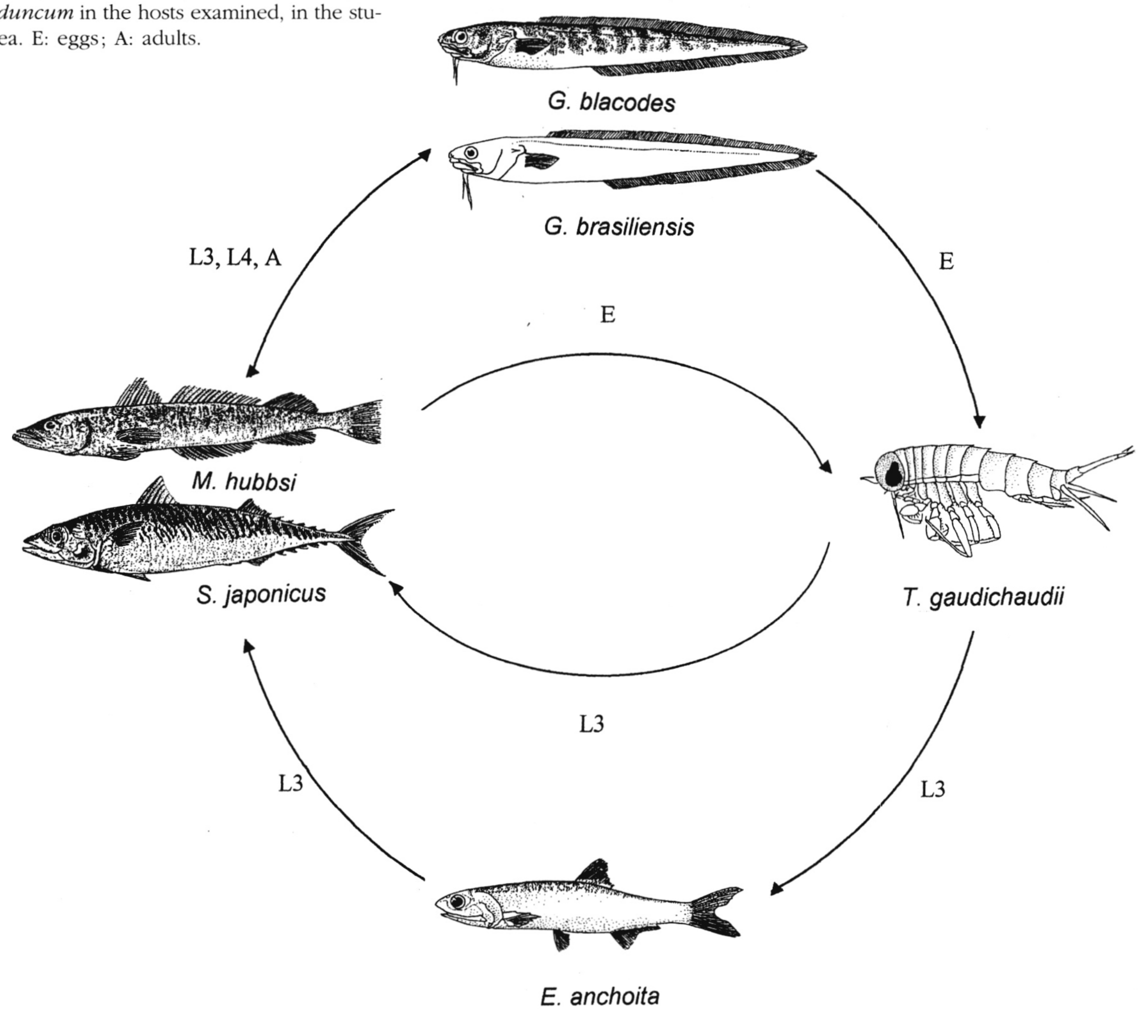
The planktonic amphipod *T. gaudichaudii* has a widespread distribution in the Argentinean Shelf (Ramírez & Viñas, 1985). Angelescu (1982) cited this crustacean as a frequent prey of *E. anchoita* and stated that this fish constitutes an important food item in the interspecific trophic webs in the South West Atlantic. Angelescu (1979, 1980) argued that the food spectrum of *S. japonicus* includes mainly *E. anchoita* and hyperiid amphipods.

Merluccius hubbsi feeds mainly on species of crustaceans, fish and squid. Also, cannibalistic behaviour is common both in juveniles and adult specimens. *E. anchoita* is its principal food item (Angelescu & Prenski, 1987; Prenski & Angelescu, 1993).

Genypterus blacodes feeds mainly on crustaceans and fishes, including mainly M. *hubbsi* & nototheniids (Renzi, 1986). There has been no study of the feeding habits of *G. brasiliensis*. Nevertheless, Sardella *et al.* (1997), based on quantitative differences between *G. blacodes* and *G. brasiliensis* in parasitism by the nematode *Cucullanus genypteri*, suggested that the two species have different feeding habits.

All the above information concerning the trophic webs among the host species investigated in the studied area, suggest the following life cycle of *H. aduncum* (Fig. 4): *T. gaudichaudii* harbour the third-stage larvae, acqui-

Fig. 4. — Postulated life cycle for *Hysterothylacium aduncum* in the hosts examined, in the studied area. E: eggs; A: adults.



ring them by feeding on plankton; *E. anchoita*, because of its planktivorous behaviour, also harbours the same larval stage. *S. japonicus* and *M. hubbsi* which feed on crustaceans and fishes are parasitized by third, fourth and adult stages of *H. aduncum*. Finally, *G. blacodes* and *G. brasiliensis*, situated at higher trophic levels, harbour mainly the fourth larval and adult stages.

Because of the known low specificity of this nematode species, other host species, such as *Paralichthys patagonicus* (Evdokimova, 1973), *D. eleginoides* (Gayevskaya *et al.*, 1990) and M. *australis* (MacKenzie & Longshaw, 1995) and a great number of unknown invertebrate and fish species, might be involved in the life cycle of *H. aduncum* in the South West Atlantic Ocean.

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