

Three teratocephalid nematodes from Iran

Akbar KAREGAR ^{*,†}, Paul DE LEY ^{*,°} and Etienne GERAERT ^{*}

^{*} Instituut voor Dierkunde, Universiteit Gent, Ledeganckstraat 35, 9000 Gent, Belgium,

[†] Department of Plant Protection, Faculty of Agriculture, Bu-Ali Sina University, Hamadan, Iran, and [°] International Institute for Parasitology, 395a Hatfield road, St Albans AL4 0XU, UK.

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Summary - Three teratocephalid species, viz. *Teratocephalus lirellus*, *Euteratocephalus palustris*, and *Metateratocephalus crassidens*, were found in the rhizosphere of wild and cultivated plants in the Province of Hamadan in the West of Iran. Two Iranian populations of *T. lirellus* were compared with a Belgian population of the same species, kept in culture. Light and scanning electron microscopy of these species provided some interesting new information. SEM photos of ruptured cuticle of *E. palustris* revealed intra-cuticular structures which were somewhat flower-shaped and resembled those found in *Achromadora micoletzkyi* and *A. semiarmata*. *Euteratocephalus spiralooides* is synonymized with *E. palustris*. These species are recorded for the first time from Iran.

Résumé - *Trois nématodes tératocephalides originaire d'Iran* - Trois espèces de Tératocephalides, *Teratocephalus lirellus*, *Euteratocephalus palustris* et *Metateratocephalus crassidens* ont été récoltées dans la rhizosphère de plantes sauvages et cultivées dans la Province d'Hamadan dans l'ouest de l'Iran. Deux populations iraniennes de *T. lirellus* sont comparées avec une population belge en culture. L'étude de ces espèces en microscopie photonique et électronique a produit de nouvelles informations intéressantes. Des photos en microscopie électronique à balayage de zones fracturées de la cuticule d'*E. palustris* ont montré des structures intracuticulaires plus ou moins en forme de fleur, structures qui ressemblent à celles identifiées chez *Achromadora micoletzkyi* et *A. semiarmata*. *Euteratocephalus spiralooides* est synonymisé avec *E. palustris*. Ces espèces sont identifiées pour la première fois en Iran.

Key-words : *Euteratocephalus*, Iran, *Metateratocephalus*, morphology, nematode, SEM, taxonomy, *Teratocephalus*.

This article is part of a series on plant and soil nematodes in Iran, and it deals with three species of the suborder Teratocephalina Andrassy, 1974. *Euteratocephalus* and *Metateratocephalus* belong to the family Metateratocephalidae Eroshenko, 1973, and they share many characters with Chromadorida such as punctated cuticle, setae on lip region, large circle-spiral amphids posterior to stoma, numerous sublateral pores on body, and ventrosublateral to subventral pair of caudal setae (possibly homologous with phasmids of Secernentea). *Teratocephalus* is the type genus of the family Teratocephalidae Andrassy, 1958, which is characterized by moderately to strongly annulated cuticle, minute amphids, and four cephalic setae, but without deirids, phasmids or caudal setae, and sublateral pores on the body. Metateratocephalidae and Teratocephalidae combine secernentean and adenophorean features to different degrees and have been placed in different orders by different authors (see Boström, 1989). Further investigations are necessary to clarify their taxonomic position.

In this study, one species of each of these genera was studied with light microscope (LM) and scanning electron microscope (SEM) to evaluate previous information and find new data on the morphology of

these genera, with particular emphasis on cuticular structure in *Euteratocephalus*. New localities were added to their known distribution.

Materials and methods

Our specimens originate from three moist soil samples collected by the first author in July 1993 from natural grassland in "Ganjnameh" (Ha-1), from a mixed culture of wild cherry (*Prunus avium* L.) and alfalfa (*Medicago sativa* L.) in "Abbas Abad" (Ha-2), and from natural grassland along the banks of a brook in "Cheshmeh Farshe" (Ha-3). The three localities are near Alvand Mountain in Hamadan, Iran. Nematodes were extracted by centrifugal flotation, processed to dehydrated glycerine and mounted on aluminium slides with double cover slips.

Euteratocephalus palustris (de Man, 1880) Andrassy, 1958 was found in all three samples, *Metateratocephalus crassidens* (de Man, 1880) Eroshenko, 1973 in samples Ha-1 and Ha-2, and *Teratocephalus lirellus* Anderson, 1969 in samples Ha-2 and Ha-3. For comparison, we also studied a Belgian population of *Teratocephalus lirellus*. This population was originally collected by the second author in November 1994,

from very dark soil under leaf litter in a park forest (Mahy property) with mixed deciduous trees in Landegem (sample taken 2 m from an oak), and subsequently cultured on xenic medium: three-five drops of *E. coli* in 4 ml P-buffer (0.05M $\text{KH}_2\text{PO}_4/\text{K}_2\text{HPO}_4$ to pH 7.3) on 1% pure agar + 5 mg/ml cholesterol. The *Caenorhabditis* Genetics Centre strain code of the Belgian *T. lirellus* culture is PDL0011.

Four specimens of *T. lirellus* (two from Iran and two from Belgium), and four *E. palustris* were prepared by ultrasonic treatment for about 10 min followed by an ethanol concentration series of 25, 50, 75, 95, and 100% at 2-hourly intervals, ending with an overnight dehydration in 100% ethanol. They were then submitted to critical point drying and sputter-coated for observation with a JEOL LSM-840 scanning electron microscope (SEM). Also, the cuticles of two specimens of *E. palustris* were ruptured on purpose by scalpel and ultrasonic treatment in preparation for study with SEM.

Teratocephalus lirellus Anderson, 1969

(Figs 1, 2, 3A-C, 6A-J)

MEASUREMENTS

See Table 1.

DESCRIPTION

Female: Body almost straight to slightly arcuate ventrad from anterior end to anus, then strongly curved on the tail; almost cylindrical from base of stoma to vulva then narrowing gradually to posterior end (Fig. 6A). Cuticle coarsely annulated, annules with low rounded or somewhat angular margins, longitudinally striated by shallow incisures (Figs 1C, F, G; 2E-G). Cross sections show seventeen ridges (excluding lateral field) at midbody in two Iranian specimens and seventeen-twenty ridges at midbody in five Belgian females (Fig. 6E-F). Lateral fields with two distinct smooth incisures, demarcating a single wing (Figs 1G; 2G). First body annule broad, sloping anteriorly, second annule narrower than the others. Amphidial aperture small, an arcuate slit located in the first body stria (Figs 1C-E; 2B-D). Lip region well offset with six high and truncate lips, sloping downward; followed by well-developed "cervical expansions" divided into several sectors by transverse invaginations or "cephalic ribs" (Figs 1B-E; 2B-D). Each subdorsal and subventral lip with a cephalic seta (Figs 1A; 2A). Oral aperture hexagonal. Stoma consisting of two parts: an anterior wide part and a posterior narrow part enveloped by the pharyngeal collar. "Metarhabdions" small, oval, distinct in most Belgian and some Iranian specimens, at junction of stoma and pharyngeal collar. Pharynx without differentiation between isthmus and corpus. Excretory pore with a rim of raised cuticle, in Belgian specimens three to ten

annules posterior nerve ring and in Iranian specimens from three annules anterior to one annule posterior to nerve ring (Figs 2E; 6H). Deirids and phasmids apparently absent. Female reproductive system monodelphic, prodelphic; ovary compact; postvulval uterine sac (PUS) shorter than body diameter (Fig. 6G). Vulva a transverse slit, situated almost at middle of body (Figs 1F; 2F), protruding in some specimens; vagina with uniformly thick walls, occupying 29 body width in Belgian and Iranian specimens, respectively. Anus a transverse slit with protruding posterior lip (Figs 1H; 3A-B). Tail elongate, its posterior part thin and finely annulated, distally curved into half a circle or more, and terminating in a minute bifurcation (Figs 1I; 3C).

Male: not found.

REMARKS

This species was originally described from Ellesmere Island and Quebec, Canada by Anderson (1969). It was subsequently reported from Spitzbergen (Loof, 1971; Boström, 1989), South Africa (Swart *et al.*, 1989), Austria (Andrássy, pers. comm.), and the Czech Republic (Hánel, 1996). The Iranian specimens are similar to the Belgian ones except for some small differences: the Iranian populations have wider ranges of tail length, a higher lip region, deeper longitudinal incisures, and a more posterior excretory pore. All our populations agree well with the original description of *T. lirellus* (Anderson, 1969), and with the populations described by Loof (1971) and Boström (1989) from Spitzbergen, except for the higher number of cuticular ridges in the original description (18-24), the longer tail in Loof's specimens ($c = 2.3-3.5$, $c' = 19-35$), and the cuticular ridges starting near the lip region in Boström (1989). A population was also described as *T. lirellus* by Swart *et al.* (1989) from South Africa, but the specimens had peculiar indentations of the cuticular ridge elevations (Fig. 4D, E in Swart *et al.*, 1989), a thicker tail terminus, and a male was found. This population possibly belongs to a different species, judging mostly from the cuticular ornamentation.

Euteratocephalus palustris (de Man, 1880)

Andrássy, 1958

(Figs 3D-I, 4, 5)

MEASUREMENTS

See Table 2.

DESCRIPTION

Female: Body slightly arcuate ventrad from anterior end to anus, then more curved on the tail; shape cylindrical from level of excretory pore to near anus, then narrowing gradually to posterior end (Fig. 5H).

Table 1. Morphometrics of females of *Teratocephalus lirellus* Anderson, 1969 from Iran and Belgium (all measurements in μm).

	Iran		Belgium		Iran		Belgium
	Ha-2	Ha-3	Landegem		Ha-2	Ha-3	Landegem
n	11	1	10	Excretory pore (e.p.)	85.2 \pm 6.1 (76.0-94.0)	94.0	69.1 \pm 1.8 (66.0-73.0)
L	496 \pm 46.8 (429-558)	498	473 \pm 12.7 (457-497)	n.r. (% neck)	61.8 \pm 1.4 (59.1-64.1)	62.4	61.8 \pm 1.5 (57.6-62.8)
Body width	16.1 \pm 0.8 (14.8-17.0)	16.1	15 \pm 1.0 (13.5-17.0)	e.p. (% neck)	73.5 \pm 4.1 (68.4-80.3)	80.3	60.4 \pm 1.1 (58.4-61.8)
Neck length	116 \pm 6.3 (108-126)	117	114 \pm 2.7 (110-119)	Rn.r. *	43 \pm 3.5 (39-50)	42	43 \pm 1.3 (41-45)
Tail length	119 \pm 21.2 (76-144)	128	112 \pm 5.9 (103-121)	Re.p. *	51 \pm 3.6 (45-57)	55	42 \pm 1.5 (39-44)
Anal body width	7.8 \pm 0.6 (6.3-8.5)	7.6	7.9 \pm 0.4 (7.0-8.5)	Rneck *	71 \pm 5.4 (63-77)	69	-
a	30.8 \pm 2.8 (27.3-37.0)	30.9	31.8 \pm 2.2 (28.2-35.5)	G1 (length)	77.6 \pm 14.9 (58.0-106.0)	99.0	70.5 \pm 6.0 (61.0-82.0)
b	4.3 \pm 0.3 (3.8-4.8)	4.3	4.1 \pm 0.1 (3.9-4.3)	G1 (%)	15.7 \pm 2.6 (12.0-19.9)	19.9	14.9 \pm 1.2 (13.4-17.1)
c	4.2 \pm 0.6 (3.6-5.7)	3.9	4.2 \pm 0.1 (4.1-4.4)	PUS	6.8 \pm 2.6 (2.7-11.0)	4.0	7.4 \pm 2.0 (5.0-10.0)
c'	15.4 \pm 2.7 (10.0-18.9)	16.8	14.4 \pm 1.0 (12.6-15.7)	PUS/body width (%)	42.7 \pm 16.6 (15.9-71.9)	24.8	49.5 \pm 13.1 (33.3-66.7)
Lip region height	4.4 \pm 0.46 (3.5-5.0)	4.5	3.7 \pm 0.26 (3.5-4.0)	V	51.3 \pm 2.2 (47.2-56.1)	50.4	50.7 \pm 0.8 (49.5-51.6)
Lip region width	7.3 \pm 0.39 (6.5-7.5)	7.2	7.1 \pm 0.39 (6.5-8.0)	V'	67.9 \pm 1.1 (66.5-70.1)	67.8	66.5 \pm 1.0 (65.2-68.2)
Stoma from anterior end	10.0 \pm 0.8 (9.0-11.0)	11.0	10.6 \pm 0.6 (10.0-11.5)	Vulva-anus/tail	1.0 \pm 0.2 (0.9-1.5)	0.9	1.1 \pm 0.06 (1.0-1.2)
Pharynx	109 \pm 6.5 101-119	110	109 \pm 2.5 104-112	Vagina	4.1 \pm 0.7 (3.1-5.4)	3.5	4.4 \pm 0.8 (3.5-6.0)
Bulbus	13.3 \pm 1.4 (10.3-14.8)	13.4	12.5 \pm 0.9 (11.0-14.0)	Rectum	12.4 \pm 4.2 (5.8-18.0)	7.2	11.5 \pm 1.1 (10.0-13.0)
Nerve ring (n.r.)	71.7 \pm 4.0 (65.0-79.0)	73.0	69.8 \pm 1.8 (68.0-74.0)	Annule at midbody	1.6 \pm 0.1 (1.4-1.9)	1.6	1.5 \pm 0.1 (1.4-1.7)

Cuticle, when seen under LM, with transverse rows of fine punctations that are larger on lateral sides of body. SEM pictures of the ruptured cuticle show that the cuticle is composed of at least three distinct layers (Fig. 4A, B), and that the punctations are in fact intra-cuticular structures, visible with LM because the cuticle is transparent. Outermost layer thin, rough

and without distinct annulation. Middle layer thick, consisting of structures somewhat flower-like (Fig. 4E), arranged in transverse rows (Fig. 4D). Inner layer finely annulated. Lateral view of middle layer shows that the flower-like structures consist of oblique columnar structures slanted in different directions and connecting the inner layer to the outer layer

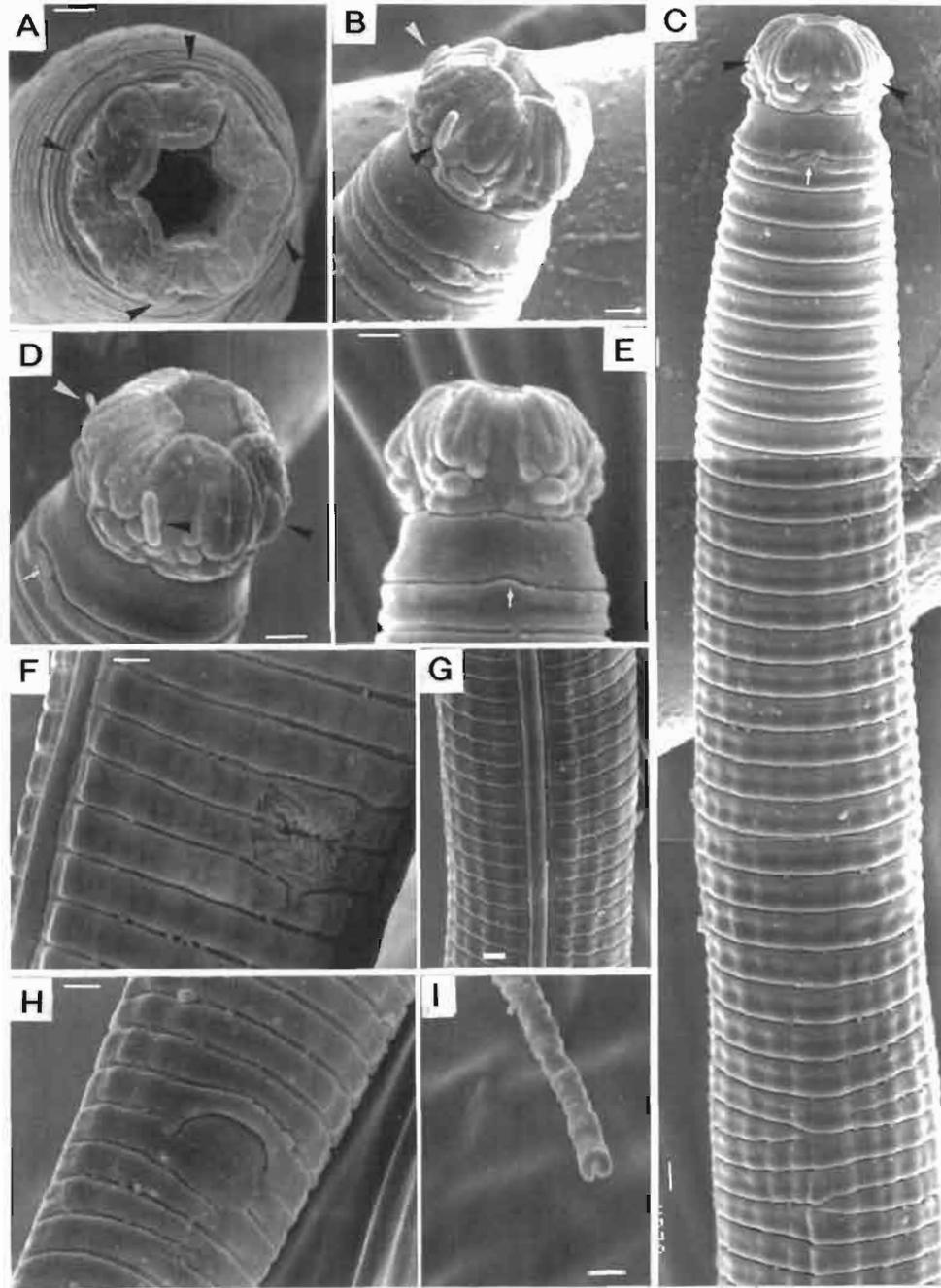


Fig. 1. *Teratocephalus lirellus* Anderson, 1969. Female (Belgian population). A: En face view of lip region; B, E: Lateral view of lip region; C: Lateral view of anterior end; D: Dorsal view of lip region; F: Vulva; G: Lateral field; H: Anus; I: Tail tip. (Arrowheads in A-D point at cephalic setae; small arrows in C-E show amphid; scale bars = 1 μ m).

(Fig. 4B). It seems that the punctations correspond to the points of attachment of the oblique columnar structures to the inner layer of the cuticle. In the ante-

rior and posterior regions of the body of most specimens, the larger lateral punctations are arranged in two rows separated by a smooth 1-2 μ m wide area.

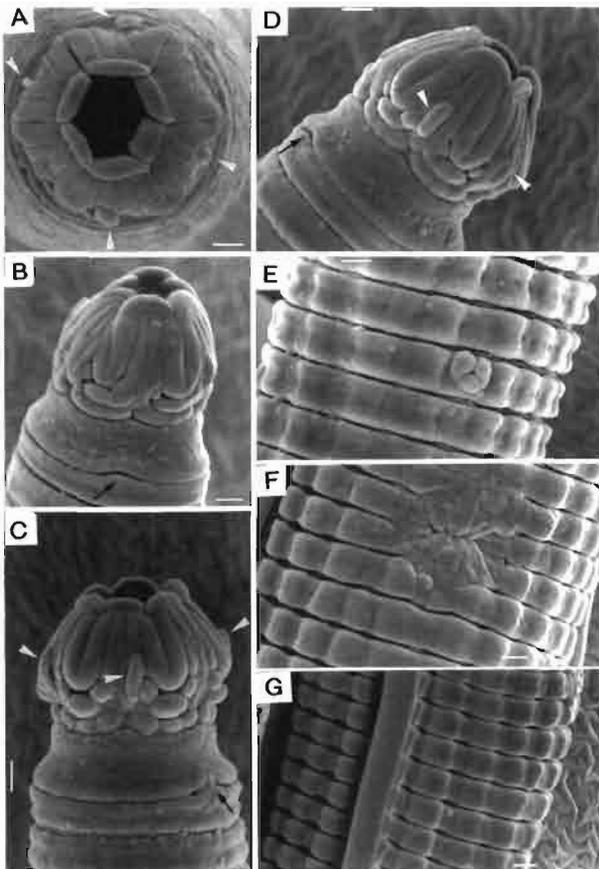


Fig. 2. *Teratocephalus lirellus* Anderson, 1969. Female (Iranian population). A-D: Views of lip region: en face (A), lateral (B), dorsal (C), and ventral (D); E: Excretory pore; F: Vulva; G: Lateral field. (Arrowheads in A, C, & D show cephalic setae; arrows in B, C & D point at amphid; scale bars = 1 μ m).

Posteriorly, these smooth areas stretch from the tail to half the distance of anus-vulva, and anteriorly from excretory pore level to near the amphids, jointly comprising 10-55% of the total body length. Lateral field irregular without distinct incisures (Figs 3G; 4C). Body with numerous sublateral pores (Figs 3G; 4C, H). Seven to nine short setae are distributed along the body as follows: two ventro- or dorsosublateral setae anterior or posterior to the excretory pore, one or two setae between the beginning of intestine and anterior ovary, two or three setae between vulva and anus, and two caudal setae situated less than one anal body diameter posterior to the anus. Amphidial aperture small and pore-like, located posteriorly to base of stoma, its fovea large and circle-spiral (Figs 3D; 4A). Lip region continuous with the body contour, crown-shaped with refringent U-shaped lip rims under LM, but rounded with six closely touching separate lips

under SEM. Each lip has an internal ridge and a longitudinal incisure externally, starting at its base and extending up to the centre; a single, thick labial seta (broken off in some specimens) protrudes from the base of each lip. Each subdorsal and subventral lip also with a long cephalic seta, arising at its base and extending beyond its anterior rim (Fig. 3E, F, H, I). Oral aperture star-shaped in en face view (Fig. 3F). Stoma consisting of two parts, anterior part wide and posterior part narrow, enveloped by pharyngeal collar. Pharynx with a clear differentiation between the muscle cell texture of isthmus and that of corpus. Excretory pore posterior to nerve ring. A spiral-shaped organ present, located within dense gland-like tissue surrounding the isthmus. Deirids and true phasmids absent. Female reproductive system didelphic, amphidelphic; ovaries reflexed, their tips only exceptionally touching each other. Vagina 4.5-5.8 μ m long, extending over 17-28% of body width. Tail elongated-conoid, ventrally curved, ending in a bluntly rounded terminus.

Male: not found.

REMARKS

Swart *et al.* (1991) reviewed the genus *Euteratocephalus* Andr ssy, 1958 from a study of several populations from different countries, and provided SEM-pictures of a new species, *E. punctatus*. Our specimens agree fairly well with different populations of *E. palustris* and *E. spiraloides* (Micoletzky, 1913) Heyns, 1977 as described by Swart *et al.* (1991). These authors used the punctation on the subcuticle of the lateral field as the main species character, and they differentiated three species in the genus: *E. spiraloides* with lateral field demarcated by a few rows of large, modified punctations or not demarcated at all; *E. punctatus* with lateral field demarcated by a smooth area that is 3.5-4 μ m wide and extending over 67-92% of the total body length; and *E. palustris* with lateral field containing a smooth area 1-2.5 μ m wide and extending over about 10-40% of the total body length (the given figures for *E. punctatus* vary in the description by Swart *et al.*: 2.5-4 μ m, 67-92% in the diagnosis, and 2.5-4 μ m, 60-95% in the key).

However, Swart *et al.* (1991) did find one population from The Netherlands that was intermediate between *E. palustris* and *E. spiraloides* in body length and subcuticular ornamentation overlying the lateral field, and one population from Brazil that was intermediate between *E. palustris* and *E. punctatus*, especially in the width of the subcuticular ornamentation. In our populations, most specimens have a smooth area in the anterior and posterior parts of the body that is 1-2 μ m wide and extends over 10-55% of the total body length. However, in some specimens, the lateral field is demarcated by a few rows of large punc-

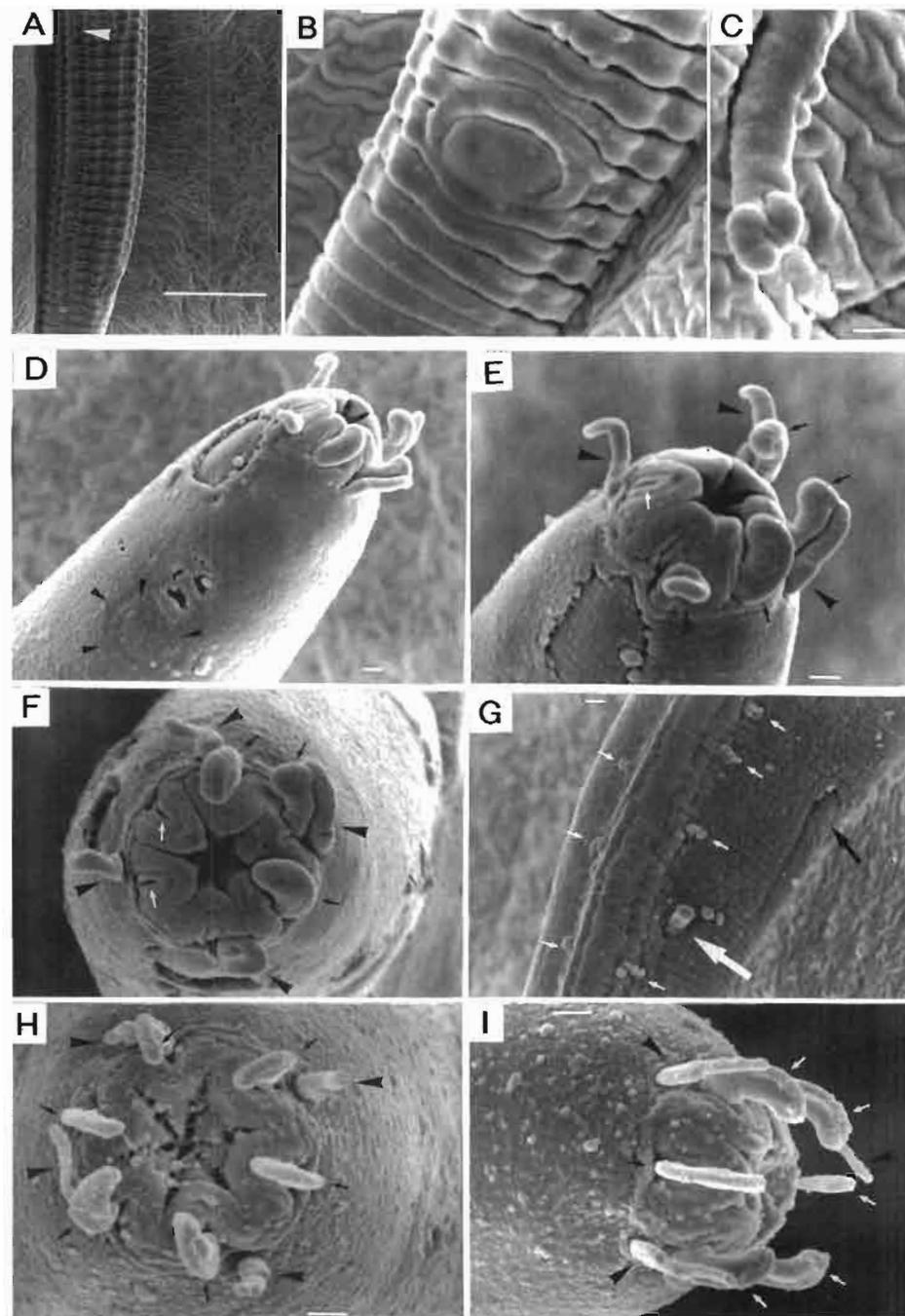


Fig. 3. *Teratocephalus lirellus* Anderson, 1969 (female, Iranian population, A-C) and *Euteratocephalus palustris* (de Man, 1880) Andrassy, 1958 female (D-I). A, B: Lateral and ventral views of anus; C: Tail tip; D: Lateral view of anterior end; E: Dorso-lateral view of lip region; F, H: En face views of lip region; G: Lateral view of caudal region showing sublateral pores (small arrows), caudal setae (white arrow) and anus (black arrow); I: Lateral view of head. (Arrowheads in A point at the end of lateral field, in D amphid, and in E, F, H & I cephalic setae; small white arrows in E, F point at the slit at the centre of lips; small black arrows in E, F & H show labial setae; small black and white arrows in I point at labial setae; H, I without ultrasonic treatment; scale bars = 10 μ m in A; 1 μ m in B-I).

Table 2. Morphometrics of *Euteratocephalus palustris* (de Man, 1880) Andrassy, 1958 and *Metateratocephalus crassidens* (de Man, 1880) Eroshenko, 1973 from Iran (all measurements in μm).

Origin	<i>E. palustris</i>			<i>M. crassidens</i>	
	Ha-2	Ha-1	Ha-3	Ha-2	Ha-1
n	9	8	3	4	1
L	828 \pm 35.6 (783-885)	787 \pm 61.6 (705-871)	737, 814, 832	458 \pm 37 (406-489)	397
Body width	29.1 \pm 2.8 (26-34)	24.7 \pm 3.2 (18.9-29.0)	26.0, 30.0, 31.4	21-23	15.7
Neck length	189 \pm 13.3 (164-202)	189 \pm 9.9 (179-204)	174, 176, 198	114 \pm 9.0 (106-122)	112
Tail length	85 \pm 6.0 (76-98)	81 \pm 7.1 (70-90)	75, 79	46 \pm 3.7 (41-50)	45
Anal body width	13.5 \pm 0.9 (12.1-14.8)	12.3 \pm 1.4 (10.3-14.8)	12.6, 13.5, 14.3	10.4 \pm 1.0 (9.6-11.8)	10.3
a	28.6 \pm 2.6 (25.7-31.8)	32.2 \pm 3.5 (28.2-38.9)	24.6, 25.9, 32.0	21 \pm 1.0 (19.7-21.9)	25.3
b	4.4 \pm 0.2 (4.2-4.8)	4.2 \pm 0.2 (3.9-4.5)	4.2, 4.6	4.0 \pm 0.2 (3.8-4.3)	3.5
c	9.8 \pm 0.7 (8.6-10.5)	9.8 \pm 0.9 (8.5-11.3)	9.3, 10.5, 10.9	9.8 \pm 0.1 (9.8-10.1)	8.8
c'	6.3 \pm 0.7 (5.7-7.8)	6.7 \pm 1.0 (5.6-8.3)	5.5, 5.6, 6.3	4.4 \pm 0.2 (4.2-4.7)	4.4
Stoma from anterior end	10.2 \pm 0.7 (9.4-11.0)	10.1 \pm 0.6 (9.0-10.8)	9.5, 10.0, 11.2	8-9	9.8
Pharynx	186 \pm 9.5 (166-197)	179 \pm 9.7 (167-194)	167, 171, 191	107 \pm 8.0 (100-116)	102
Bulbus	20 \pm 1.4 (17-22)	22 \pm 1.8 (19-24)	17, 18, 19	13.8 \pm 0.6 (13.4-14.4)	12.6
Nerve ring (n.r.)	96 \pm 5.7 (83-101)	92 \pm 4.5 (85-97)	90, 92, 103	62 \pm 3.8 (57-65)	62
Excretory pore (e.p.)	101 \pm 9.0 (85-111)	100 \pm 5.8 (93-108)	99, 107	71 \pm 5.5 (65-77)	68
n.r. (% neck)	51 \pm 3.9 (48.5-61.0)	48.6 \pm 1.3 (47.2-50.3)	51.7, 52.0, 52.3	54.6 \pm 2.0 (53-56)	55
e.p. (% neck)	54 \pm 5.3 (44-65)	53.0 \pm 0.9 (51.7-54.7)	54, 56, 57	62 \pm 1.4 (61-64)	61

End of Table 2 next page

Table 2. (cont.)

Origin	<i>E. palustris</i>			<i>M. crassidens</i>	
	Ha-2	Ha-1	Ha-3	Ha-2	Ha-1
G1 (%)	10.4 ± 1.7 (8.1-13.1)	9.0 ± 1.7 (6.7-11.5)	7.1, 9.3, 11.5	13.7 ± 2.1 (12-16)	9
G2 (%)	8.8 ± 2.7 (3.1-12.8)	8.7 ± 2.9 (6.1-14.5)	3.3, 6.4, 7.0	8.8 ± 1.5 (6.7-8.8)	7.8
V	53 ± 1.3 (51-55)	53 ± 1.3 (50-55)	51, 54	57 ± 1.5 (55-59)	57
V'	59.5 ± 1.3 (57-61)	59 ± 1.8 (56-61)	57, 59, 60	63 ± 1.8 (61-66)	64
Rectum	20 ± 2.3 (16-23)	17.5 ± 2.6 (15.0-22.5)	17, 19, 20	13 ± 2.3 (10-16)	10
Vulva-anus/tail	3.6 ± 0.3 (3.1-3.9)	3.6 ± 0.5 ± 0.2 (3.0-4.2)	3.3, 3.9, 4.3	3.3 (3.0-3.5)	2.8

tations without any smooth area. As we have no reason to suspect that our samples contain a mixture of species and as Swart *et al.* (1991) also encountered an intermediate population, we assume that the ornamentation at the level of the lateral field is variable within one species and therefore we consider *E. spiraloidea* to be a junior synonym of *E. palustris*. This synonymization was already proposed by Andr ssy (1958), but Heyns (1977) re-instated *E. spiraloidea* as a valid species.

The flower-shaped intra-cuticular structures appear very similar to those found in *Achromadora micoletzkyi* (Stefanski, 1915) Van der Linde, 1938 and in *A. semiarmata* Altherr, 1952 by Zeidan and Geraert (1990) and by Eyualem and Coomans (1995). Therefore, this character is yet another feature linking *Euteratocephalus* to the order Chromadorida (see discussion).

***Metateratocephalus crassidens* (de Man, 1880)
Eroshenko, 1973
(Figs 6 K-O, 7)**

MEASUREMENTS

See Table 2

DESCRIPTION

Female: Body almost straight from anterior end to anus, then dorsally curved; cylindrical from the excretory pore to the flexure of posterior gonad, then narrowing gradually to the posterior end. Cuticle without distinct annulation but with transverse rows of fine punctations that are more prominent on lateral sides of body. SEM picture shows oblique columnar struc-

tures in the middle of the ruptured cuticle similar to those found in *E. palustris* (Fig. 7D). Lateral field without distinct incisures (Fig. 7E). Body pores present. Amphids large, circular with small and pore-like (or possibly tube-like) aperture, posterior to base of stoma. Lip region well offset, crown-shaped with U-shaped sclerotizations under LM, but with six leaf-like, closely touching, separate lips under SEM. Each subdorsal and subventral lip bearing two setae, while the lateral lips bearing only one seta. Four cephalic setae shorter and originating posteriorly to the labial setae; labial setae extending beyond the anterior lip margins (Fig. 7A-C). Anterior part of stoma wide and with well-sclerotized walls, posterior part narrow and enveloped by pharyngeal collar. Pharynx without any distinct differentiation between isthmus and corpus. Excretory pore posterior to nerve ring. A spiral-shaped organ located in dense gland-like tissue surrounding the isthmus. A pair of setae is located sublaterally halfway between the excretory pore and the basal bulb (possibly homologous to deirids). True deirids and phasmids absent. Female reproductive system didelphic, amphidelphic; ovaries reflexed, their tips usually touching each other. Vagina short, occupying about 1/3 of vulval body width. Tail elongated-conoid, dorsally curved, ending in a pointed terminus. Caudal setae situated ventro-sublaterally just posterior to the anus.

Male: not found.

REMARKS

Our material was compared with several populations described as *Metateratocephalus crassidens* (de

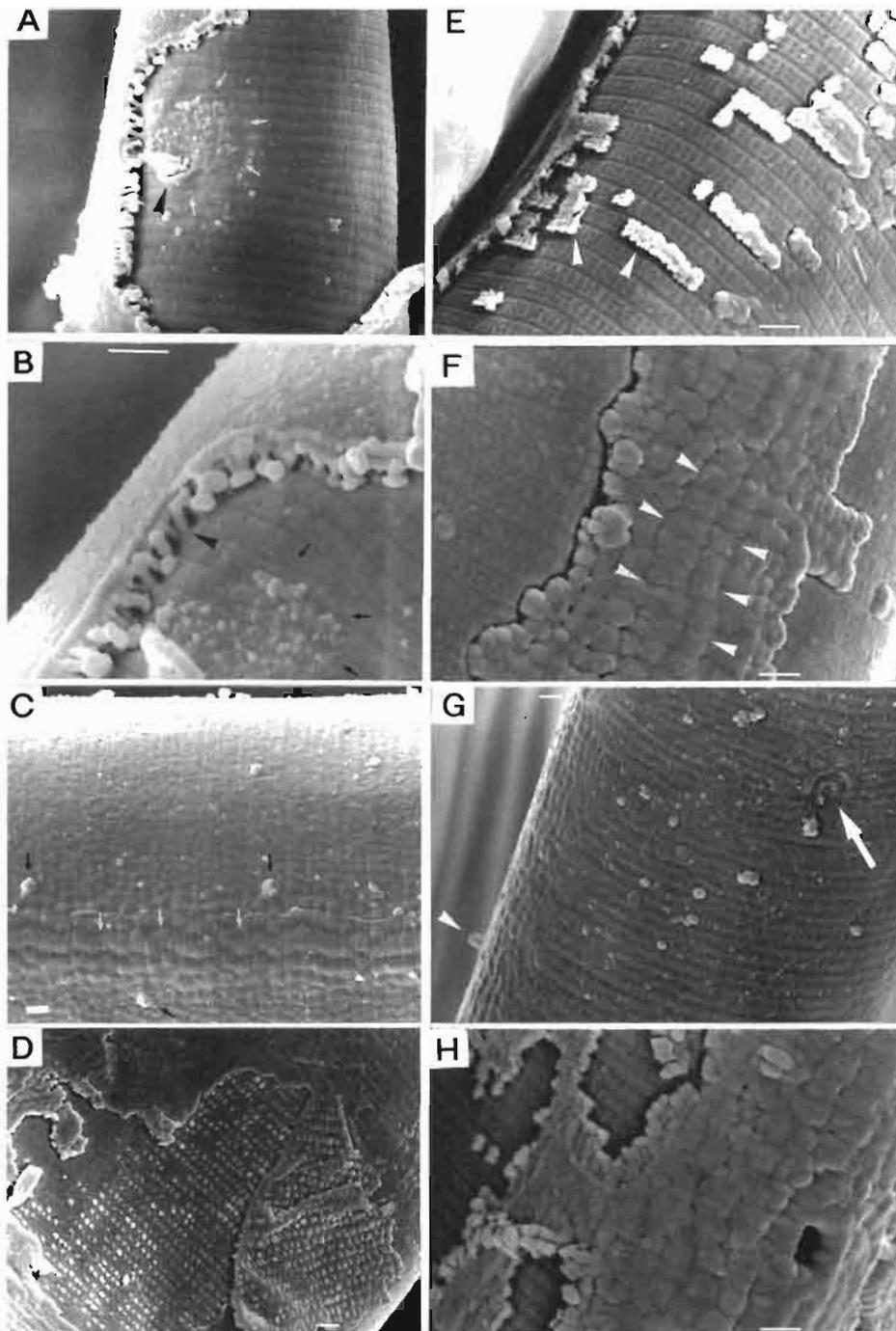


Fig. 4. Ruptured cuticle of *Euteratocephalus palustris* (de Man, 1880) Andrassy, 1958. A, B: Three layers of cuticle at level of amphid; C: Lateral field; D: Rows of punctations; E: Middle layer showing flower-like structures; F: Larger punctations on lateral field; G: Excretory pore and sublateral seta; H: Lateral pore. (Arrowhead in A points at amphidial aperture, in B shows oblique columnar structures that connect the inner layer to the outer layer, in E and F point at flower-like structures, and large punctations on lateral field, respectively; small black arrows in B point at amphid, in C at sublateral setae; large arrow in G point at excretory pore, arrowhead at sublateral seta). (Scale bars = 1 μ m).

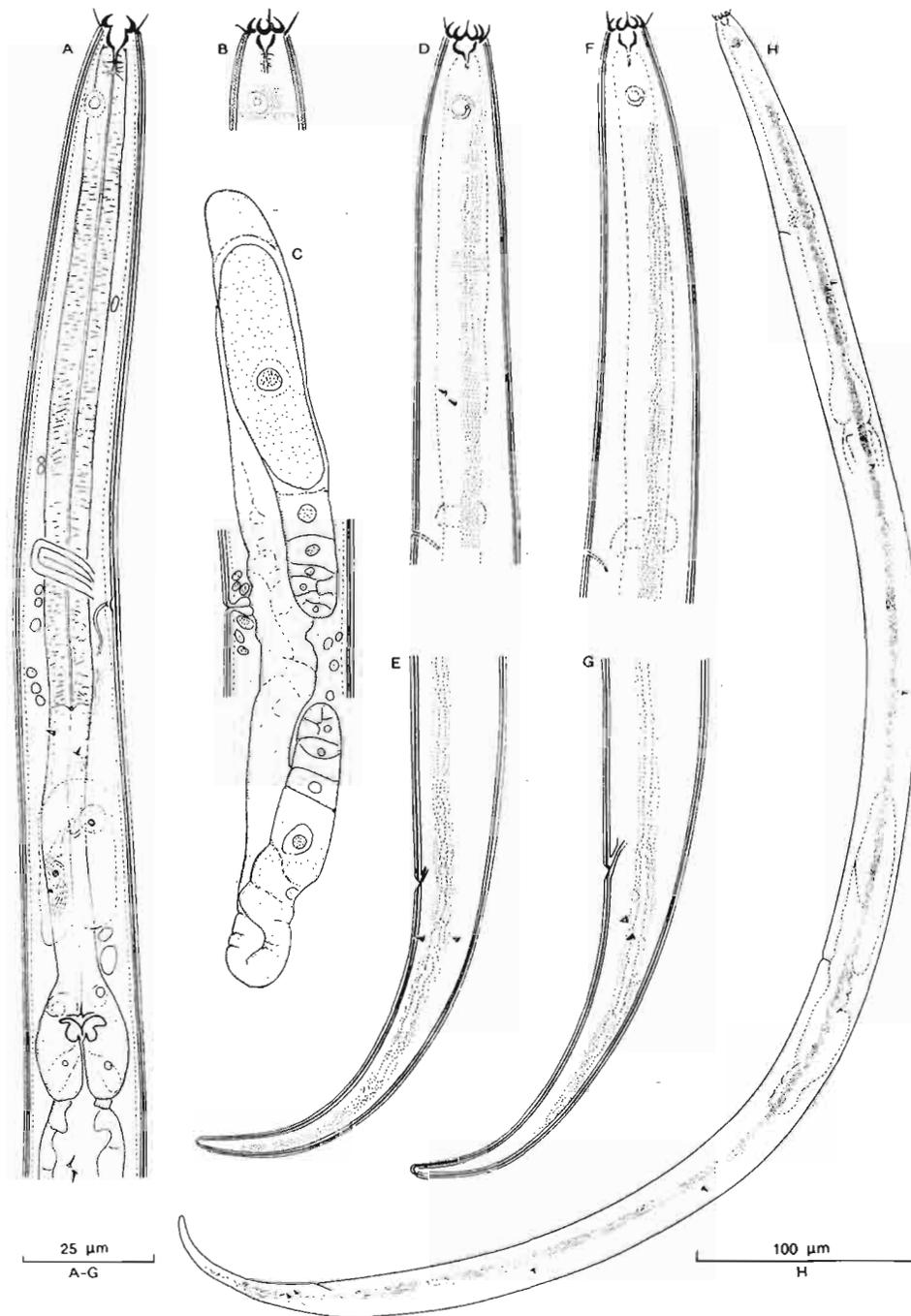


Fig. 5. *Euteratocephalus palustris* (de Man, 1880) Andrassy, 1958. Female. A: Pharynx; B: Anterior part; C: Reproductive system; D, F: Anterior parts showing punctations on lateral fields; E, G: Posterior parts with punctations on the lateral fields; H: General view showing the setae and punctation on the lateral field.

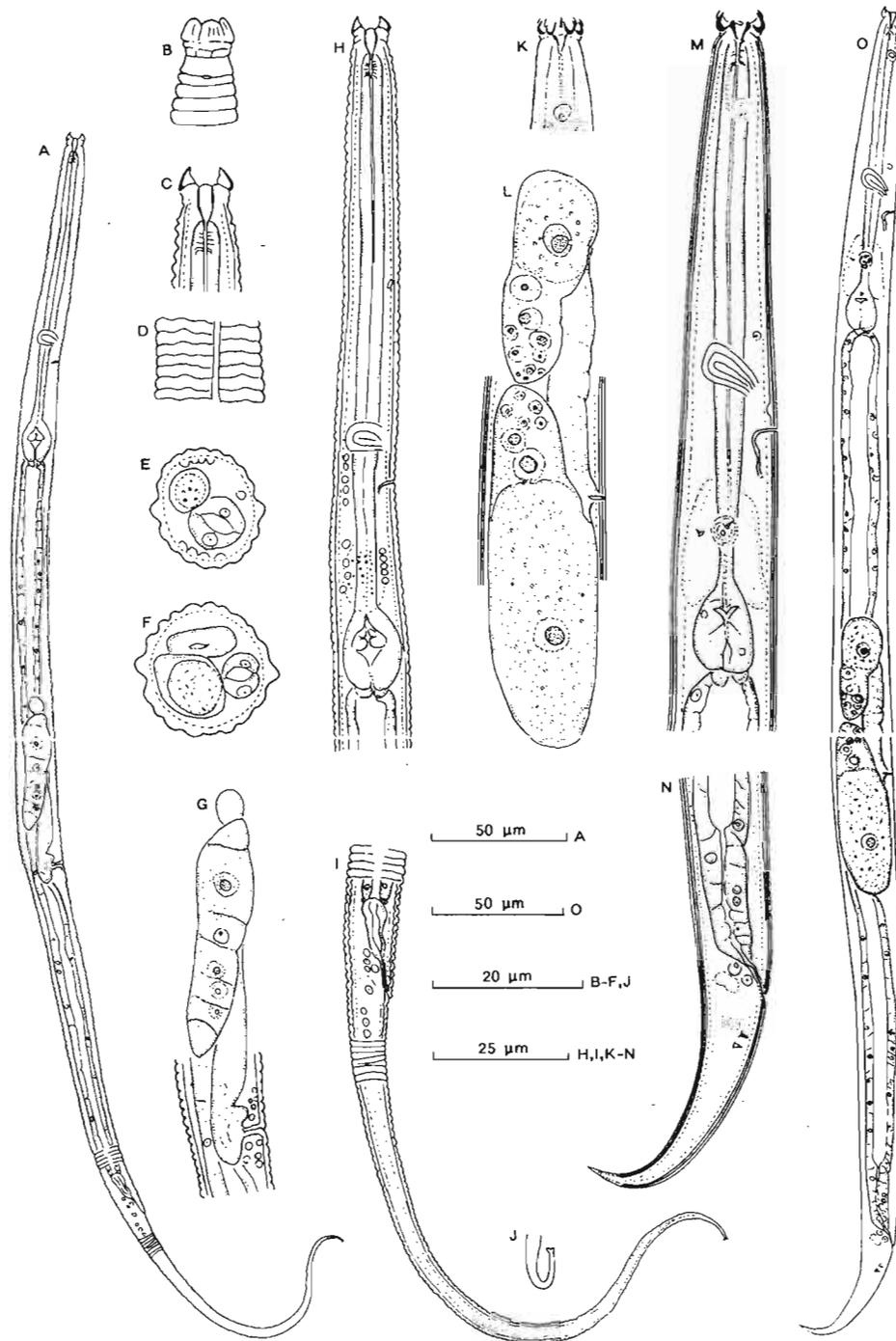


Fig. 6. *Teratocephalus lirellus* Anderson, 1969 (A-J) and *Metateratocephalus crassidens* (de Man, 1880) Eroshenko, 1973 (K-O). Females. A, O: General view; B, C, K: Anterior ends; D: Lateral field; E, F: Cross sections at midbody; G, L: Reproductive system; H, M: Pharynx; I: Tail; J: Tail terminus; N: Posterior end.

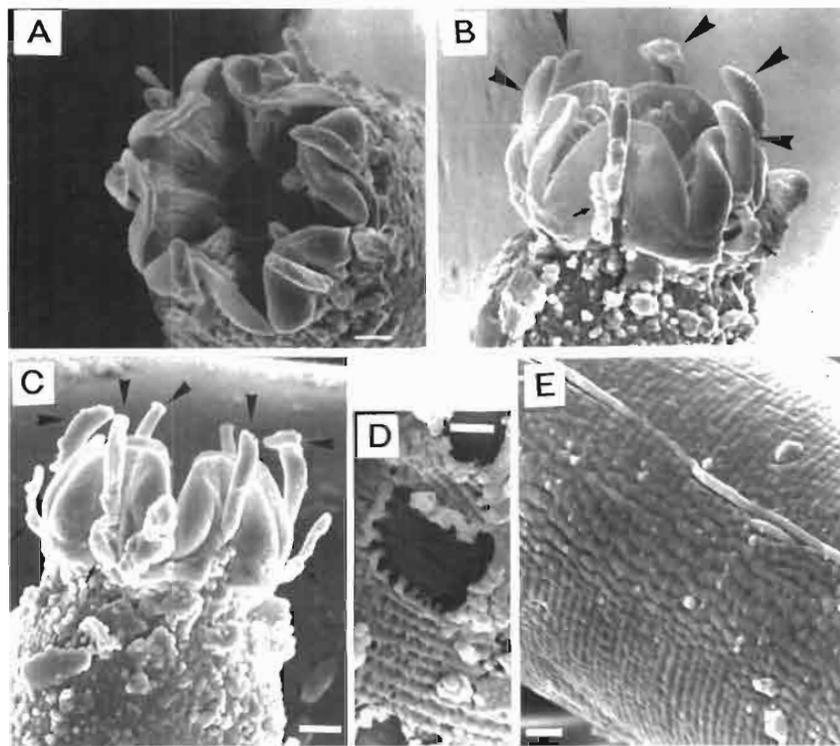


Fig. 7. *Metateratocephalus crassidens* (de Man, 1880) Eroshenko, 1973. Female. A: En face view of lip region; B: Ventral view of lip region; C: Lateral view of lip region; D: Ruptured cuticle; E: Punctuation on lateral field. (Scale bars = 1 μ m).

Man, 1880) Eroshenko, 1973 from Mount Kenya (Meyer & Coomans, 1977), from Spitzbergen (Loof, 1971; Boström, 1989), and from South Africa (Swart *et al.*, 1989). It agrees fairly well with the published descriptions of the species, but, in our populations, the position of the vulva is more posterior and the tail is slightly shorter, except in comparison to the population described by Boström (1989): V = 55-59 vs 50.5-53.0, 53-54, 50-55, 51-53, and c = 8.8-10.1 vs 6.6-8.3, 7.1-8.1, 7.8-10.5, 6.4-8.2, respectively. Nevertheless, our measurements are within the ranges (V = 53-60; c = 7-10) given in Andrassy (1984) and our populations are therefore regarded as belonging to *M. crassidens*. Boström (1989) and Swart *et al.* (1989) have published SEM views of *M. crassidens*. Comparison of their SEM photos with the photos presented here confirms similarities in the number of setae on the head, cuticular ornamentation, amphids, scattered body pores on the lateral sides of the body, a pair of ventrosublateral setae just posterior to anus, and a pair of ventrosublateral setae posterior to the excretory pore.

Discussion

The taxonomic position of the teratocephalids has been much discussed and they have been placed in

different orders by different authors. In a study of four teratocephalid species, Boström (1989) reviewed the many different proposed classifications. He compared SEM views of the genera *Metateratocephalus* Eroshenko, 1973 and *Teratocephalus* de Man, 1876, and he discussed the possible plesiomorphic vs apomorphic state of some external characters. His conclusion was that a further separation of the genera *Metateratocephalus* and *Teratocephalus* was necessary. Our findings entirely agree with those of Boström (1989). Moreover, it was shown that the cuticular ornamentation of *Euteratocephalus* resembles that of *Achromadora*. In view of the general agreement of *Teratocephalus* with most diagnostic characters of Cephalobina Andrassy, 1974, and considering the existence of several genera of Cephalobina with a "crown-shaped" lip region (*Brevistoma* Mukhina, 1981; *Panagrobelum* Andrassy, 1984; *Panagrobelus* Thorne, 1939; and the genera in the subfamily Acrolobinae De Ley, Siddiqi & Boström, 1993) we assume that *Teratocephalus* belongs in Rhabditida, Cephalobina, within its own superfamily, Teratocephaloidea Andrassy, 1958, while *Metateratocephalus* and *Euteratocephalus* belong in Chromadorida *sensu* Lorenzen (1994) in the family Metateratocephalidae Eroshenko, 1973. It is quite difficult to decide the exact position of this family within

the order, because it shows affinities in cuticular structure to Chromadoridae (Chromadorina) and similarities in stoma, pharynx and male supplement morphology to Plectidae (Leptolaimina). Unlike most Chromadorida, the forms in Metateratocephalidae admittedly lack caudal glands and spinneret, but this does not decisively exclude them from the order, since other exceptions are already known (e.g., *Chronogaster* Cobb, 1913 and *Prismatolaimus* de Man, 1880) and since the absence of true phasmids in Metateratocephalidae is an equally strong argument against their placement in Rhabditida (see also Boström, 1989 and Lorenzen, 1994). Our classification does not imply that we consider the Metateratocephalidae as totally unrelated to Rhabditida or Secernentea in general - such affinities cannot be excluded - but it is primarily intended to reflect the existence of a very significant discontinuity within "teratocephalids" as a group. In this, our proposal runs contrary to many previous classifications where all three genera studied here were united in a separate order, suborder or superfamily.

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