Study of Teratocephalidae (Nematoda) from the Ukraine. II. Description of a population of *Teratocephalus tenuis* Andrássy, 1958 with a discussion of male sexual characters

Sven Boström* and Oleksandr Holovachov**

*Department of Invertebrate Zoology, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden, e-mail: sven.bostrom@nrm.se

**Department of Zoology, Biological Faculty, Ivan Franko National University of L'viv, Grushevsky str. 4, L'viv 79005, Ukraine.

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Summary. A population of *Teratocephalus tenuis* Andrássy, 1958 from the Ukraine is described from studies by light and scanning electron microscope. The specimens examined agree well with the original description of *T. tenuis* but have wider ranges of body length (490-587 vs 526-565 μ m), c'-ratio (5.3-8.4 vs 6.0-6.3) and annule width (1.4-1.9 vs 1.6 μ m), and differ by length of spicules (15-18 vs 12-13 μ m), structure of the cuticle (with vs without longitudinal striae), and the number of genital papillae in the male. The specimens at hand were also compared with populations of *T. lirellus* Anderson, 1969 from which they differ by a larger c-ratio (7.6-10.1 vs 2.6-5.8), and a smaller c'- ratio (5.3-8.4 vs 8-35). Male sexual characters of *T. bisexualis*, *T. rugosus* and *T. tilbrooki* were re-examined. The taxonomic value of male sexual characters for identification of bisexual species of *Teratocephalus* is discussed.

Key words: morphology, scanning electron microscopy, taxonomy, Teratocephalus, T. bisexualis, T. lirellus, T. rugosus, T. tenuis, T. tilbrooki.

Specimens of the genus Teratocephalus de Man, 1876 are commonly very slender with an a-ratio of more than 20 and exceeding 30 in several species. The comparatively low number of useful morphological characters and the often wide ranges of morphometric characters due to high intraspecific variability make species identification difficult, as for nematodes in general. Andrássy (1958, 1968) and Anderson (1969) considered the external structure of the cuticle a useful character to differentiate the species of this genus. The cuticle of many species is characterized by the presence of longitudinal ridges or incisures extending throughout most of the body length giving it a "tiled" appearance. These species were gathered within the Teratocephalus "lirellus-group" (except T. costatus Andrássy, 1958 = T. decarinus Anderson, 1969) and their systematics were discussed in a previous paper (Boström et al., 2000). Recent observations on a population of T. tenuis Andrássy, 1958 collected in Ukraine and described here from studies by light and scanning electron microscope, showed

that these specimens also have a cuticle interrupted by longitudinal incisures.

MATERIALS AND METHODS

Nematodes were extracted by a modified Baermann funnel method, relaxed by gentle heat, fixed in cold TAF, transferred to pure glycerine by a slow evaporation method and mounted on permanent slides in glycerine with paraffin wax as support for the coverslip. After measuring and observations, some females and a few males were washed with gradually added distilled water, resuspended in TAF and prepared for SEM. The specimens were postfixed in 1% osmium tetroxide (OsO₄), transferred to pure acetone through an acetone/distilled water series, critical point dried in liquid CO₂, mounted on stubs, gold-plated under vacuum to a thickness of 200 Å in a sputter, and examined in a Zeiss Novascan 30 SEM at an accelerating voltage of 15 kV. Regrettably males in useful positions could not be traced on the stub.

thus observations of male sexual characters by SEM were not possible. We were able to study type specimens (one female and one male each) of *Teratocephalus bisexualis* Meyer & Coomans, 1977 (WT 1926), *T. rugosus* Maslen, 1979 (WT 2005) and *T. tilbrooki* Maslen, 1979 (WT 2007), which are kept in the type collection of the Laboratory of Nematology, Wageningen University, the Netherlands.

DESCRIPTION

Teratocephalus tenuis Andrássy, 1958 (Figs. 1 & 2)

Measurements: See Tables 1 & 2.

Female. Body straight to slightly arcuate ventrad, more so in caudal region; almost cylindrical from base of stoma to vulva, than gradually narrowing to posterior end. Cuticle coarsely annulated, annules longitudinally striated by shallow incisures starting on 4-6th annule and forming 18-20 ridges (excluding lateral field) at midbody. In a few specimens cuticular ridges were not seen. Each annule also striated by very fine longitudinal incisures as seen by SEM. Cuticular blocks indistinct in LM. Lateral field with two distinct incisures demarcating a single wing. First body annule broad, twice as wide as the second one, sloping anteriorly; second annule only slightly narrower than the others. Amphid aperture small, an arcuate slit located in the first transverse body stria. Lip region well offset with six high and truncate lips, sloping downward. Each subventral and subdorsal lip with a single cephalic seta. Stoma consists of two parts: an anterior wide part and a posterior narrow part enveloped by the pharyngeal collar. Digestive system typical of the genus. Pharynx without differentiation between corpus and isthmus. Nerve ring 36-47 annules from anterior end. Excretory pore 4-8 annules posterior to nerve ring, 40-53 annules from anterior end. Pharynx terminus 72-85 annules from anterior end. Deirids and phasmids apparently absent. Female reproductive system monodelphic, prodelphic, situated on the right side of the body (dextral); ovary compact, reflexed dorsally. *Receptaculum seminis* present, appearing as a widened and more refractive part of the genital tube between the uterus and the oviduct. No sperm were seen. Postvulval uterine sac (PUS) slightly longer than vulval body width. However, in two specimens PUS was 52-53 µm long, or 3.4-3.9 VBW. These are considered aberrant and therefore not included in Table 1. Vulva pore-like in LM, situated posterior to midbody, vulval lips formed by cuticular ridges as seen in

SEM. Intra-uterine eggs $41-42 \times 11-12 \mu m$, each egg 3.6-3.7 times as long as its own diameter. Anus with raised anterior lip. Tail elongate conoid, posterior part finely annulated, terminus minutely bifurcate.

Male. General appearance similar to female, except for sexual characters. Body somewhat smaller and more slender, and more arcuate ventrad, almost C-shaped. Male reproductive system monorchic, on the right side of the body (dextral), testis reflexed ventrally anteriorly. One specimen with testis on left side of body (sinistral) and reflexed dorsally anteriorly. Spicules 1.4-1.9 times as long as anal body width, strongly curved ventrad with hemispherical dorsally curved manubrium. Gubernaculum absent. A single midventral precloacal papilla on 11-18th annule anterior to anus (16-24 µm from anus), one pair of subventral adcloacal papillae on either side of anus, and one pair of subventral postcloacal papillae on 15-19th annule posterior to anus (21-28 µm from anus). Tail elongate conoid, posterior part finely annulated, terminus minutely bifurcate.

Material examined. The specimens were collected from dust of rotting wood under the bark of a *Caprinus betulus* (L.) tree, "Roztochya Nature Reserve", L'viv Province, Ukraine, March 1999; *leg.* O. Holovachov.

Relationships. The specimens at hand agree rather well with the original description of T. lirellus Anderson, 1969 and other populations of this species described from different parts of the world showing wide ranges in intraspecific variability (Anderson, 1969; Loof, 1971; Boström, 1989; Swart et al., 1989; Karegar et al., 1997; Boström et al., 2000). The main differences between the present females and females from populations of T. lirellus are a higher c-ratio (8.1-10.1 vs 2.6-5.8), and a lower c'-ratio (6.4-8.4 vs 8-35). A single male of T. lirellus was described from a population in South Africa (Swart et al., 1989). The males of our population agree in morphology and sexual characters with the South African male but differ, as the females, by a higher c-ratio (7.6-9.5 vs 3.7) and a lower c'-ratio (5.3-7.2 vs 13). The specimens described here also agree well with the original description of T. tenuis in morphology and most morphometric characters, except for wider ranges of body length (490-587 µm vs 526-565 μ m), c'- ratio (5.3-8.4 vs 6.0-6.3) and annule width (1.4-1.9 vs 1.6 µm), and different length of spicules (15-18 vs 12-13 µm), structure of the cu-

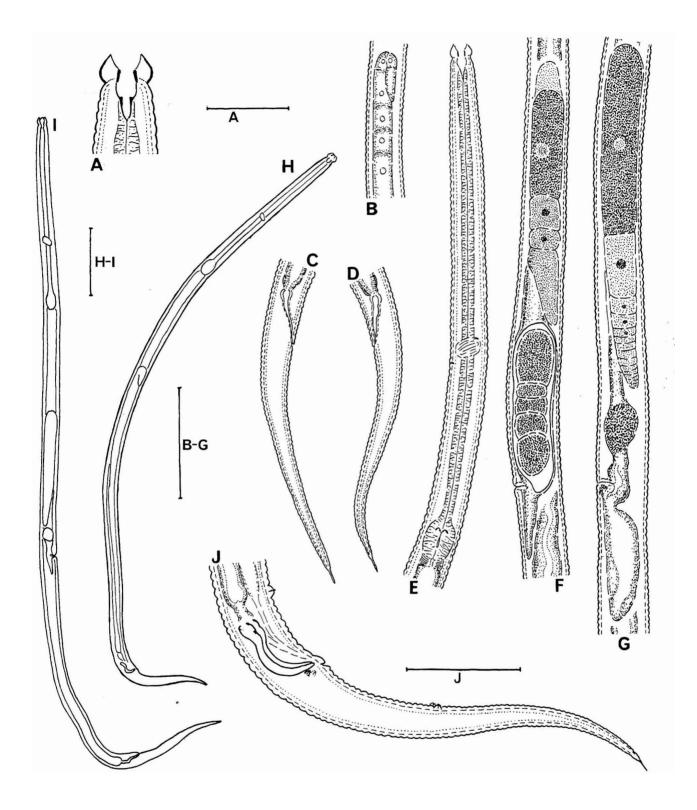


Fig. 1. *Teratocephalus tenuis* Andrássy, 1958. Female (A, C-G, I). A: Head end, optical median view; C & D: Tail; E: Pharyngeal region; F & G: Reproductive system; I: Entire body. Male (B, H, J). B: Recurved testis tip; H: Entire body; J: Tail region. Scale bars: A, 10 µm; B-G, 30 µm; H-I, 50 µm; J, 20 µm.

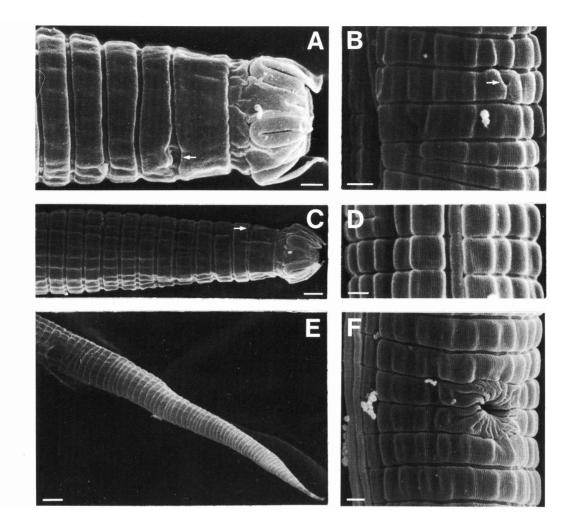


Fig. 2. Teratocephalus tenuis Andrássy, 1958. Female (A-F). A: Lip region, subdorsal view (arrows in A and C point at amphid aperture); B: Excretory pore (arrow); C: Anterior region, subventral view; D: Cuticle and lateral field; E: Tail region; F: Vulva. Scale bars: A, B, D, F, 1 µm; C, 2 µm; E, 4 µm.

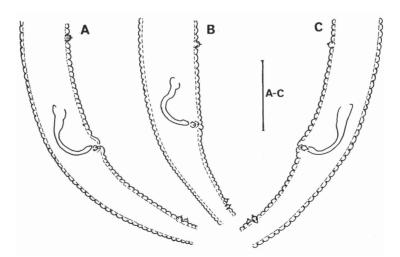


Fig. 3. Schematic tail region of paratype males of three species of *Teratocephalus*. A: *T. tilbrooki* Maslen, 1979; B: *T. bisexualis* Meyer & Coomans, 1977; C: *T. rugosus* Maslen, 1979. Scale bar: A to C - 20 µm.

Characters	Teratocephalus tenuis Andrássy, 1958				
n	10 QQ	10 ♂♂			
L	547±23.5 (511-587)	517±15.6 (490-538)			
L'	486±21.7 (452-521)	455±13.9 (426-470)			
Vulval/Maximal body width	12.8±1.6 (10.9-14.9)	10.8±0.6 (10.0-11.4)			
Neck length	134±6.4 (124-142)	131±2.7 (127-135)			
Tail length	61±4.5 (55-68)	62±5.1 (55-69)			
Anal body width	8.2±0.6 (7.4-9.2)	9.8±0.5 (9.0-10.4)			
a	43±4.5 (37-51)	48±3.1 (43-54)			
a'	39±3.9 (33-46)	42±2.7 (38-47)			
b	4.1±0.2 (3.8-4.3)	4.0±0.1 (3.8-4.1)			
b'	3.6±0.1 (3.4-3.8)	3.5±0.1 (3.3-3.6)			
c	9.0±0.6 (8.1-10.1)	8.4±0.7 (7.6-9.5)			
c'	7.5±0.8 (6.4-8.4)	6.4±0.6 (5.3-7.2)			
Nerve ring	75±2.4 (70-77)	71±0.9 (70-72)			
Excretory pore	85±2.3 (82-88)	79±2.4 (76-83)			
Nerve ring (% of neck)	56±1.6 (54-59)	55±1.2 (53-56)			
Excretory pore (% of neck)	62±1.0 (61-64)	61±1.6 (59-63)			
V/T (%)	56±1.3 (54-58)	50±2.6 (46-53)			
V'/T' (%)	64±1.3 (62-66)	57±2.9 (52-60)			
Vagina / Spicula	6.1±0.7 (5.0-7.4)	16.1±1.0 (14.9-17.8)			
PUS	15.1±2.3 (11.1-19.2)	. –			
PUS/VBW	1.2±0.2 (1.0-1.4)	-			
Rectum	13.8±0.6 (12.8-14.7)	-			
Rectum/ABW	1.7±0.2 (1.5-2.0)	-			
Annule width	1.7±0.2 (1.4-1.9)	1.6±0.2 (1.4-1.9)			
LRW	7.9±0.5 (7.1-8.8)	7.5±0.3 (6.9-7.8)			
LRH	4.2±0.5 (3.5-5.0)	4.2±0.3 (3.8-4.5)			
Buccal cavity	8.4±0.2 (8.1-8.8)	8.4±0.5 (7.6-9.0)			

Table 1. Measurements (in μ m) of *Teratocephalus tenuis* Andrássy, 1958 from Ukraine (dimensions are given as mean \pm standard deviation and range).

ticle (with vs without longitudinal striae), and the numbers of male genital papillae (see Table 2). The wider ranges may be due to intraspecific variability. The differences in the length of spicules are probably due to various ways of measuring (along arc vs along chord) and the structure of the cuticle may have been overlooked (I. Andrássy, in litt.). However, the differences in the numbers of male genital papillae are more difficult to explain (see also Discussion). Despite these differences we consider our population as belonging to *Teratocephalus tenuis*.

DISCUSSION

Among the *Teratocephalus* species originally described as lacking longitudinal striation of the cuticle (or structure of cuticle was not mentioned in the descriptions), only *T. terrestris* de Man, 1876 has been studied by SEM (Boström, 1989).

The rest of these species have not been studied by SEM and thus the fine structure of their cuticle cannot be stated with confidence. The longitudinal striation of the cuticle, typical for most specimens of the population of T. tenuis described here, could not be discerned by LM in a few females. This observation may indicate that the character is intraspecifically variable and must be considered when populations are identified to species level.

Studies of a bisexual population enabled us to make a detailed description of male genital papillae patterns. Our data agree well with the number and distribution of papillae given by Swart *et al.* (1989) for two other species of *Teratocephalus*, but disagree with all other observations including the original description of *T. tenuis* (Table 2). Whether the papillae patterns are similar in all species of the genus or differ between species could not be stated with confidence after analysis of the literature data. Even descriptions of presumed con-

Table 2. Comparison of some morphometric and morphological characters of males from different species and populations in the genus *Teratocephalus*.

Species	L (µm)	с	c'	Spicula (µm)	Papillae arrangement*	Number of annuli from cloaca to		Longit.
						precloacal papilla	postcloacal papillae	striae
T. tenuis (current population)	490-538	7.6-9.5	5.3-7.2	14.9-17.8	1 mv precl 2 sv adcl 2 sv postcl	11-18	15-19	18-20
T. tenuis (Andrássy, 1958)	526-534	9.5-11	6.0-6.3	11.7-12.8	2x2 sv precl 2 sv adcl 2x2 sv postcl 2x2 sd postcl	?	?	?
T. tenuis apud Andrássy (1984)	500-530	8-11	?	. 12-15	2x2 precl 5x2 postcl	?	?	?
T. lirellus apud Swart et al. (1989)	533	3.7	13	15	1 mv precl 2 sv adcloac 2 sv postcl	12	14	16-18
<i>T. bisexualis</i> (Meyer & Coomans, 1977)***	406-429	6.1-7.4	?	?	1 mv precl	12	?	16-18
T. rugosus (Maslen, 1979)***	530-875	4.1-5.2	8.7-12.2	17-23.5	2 sv precl 2 sv adcl 2 sv postcl	13-17	13-19	13-17
T. dadayi apud Hernandez & Jordana (1988)	510-528	5.3-5.6	8-9	15-18	2 precl 2 adcl 2 postcl	10-12	15	12
T. sigillarius apud Kazachenko (1980)	430	3.7	?	16.9	?	?	?	?
T. diversiannulatus (Swart et al., 1989)	423-626	3.6-4.4	8.0-14.1	15-21	1 mv precl 2 sv adcl 2 sv postcl	10	13	12
T. costatus apud Novikova (1971)	370	6.7	?	12.6	2 sv precl 2 sv postcl	ca. 9**	ca. 14**.	?
T. costatus apud Hernandez & Jordana (1988)	413	5.3	7	15	2 precl 2 adcl 2 postcl	11	14	8
T. deconincki (De Coninck, 1935)	526	6.7	7	ca. 18**	1 mv precl 1 mv postcl	ca. 10**	ca. 22**	?
T. tilbrooki (Maslen, 1979)***	530-730	4.0-5.7	8.9-11.9	17-24	2 sv precl 2 sv adcl 2 sv postcl	18-23	20-26	?
T. tilbrooki apud Andrássy (1998)	600	4.6	12	18-19	2 sv precl 2 sv adcl 2 sv postcl	15	20	?
T. terrestris apud de Man (1876)	400	5-6	?	1.5 ABW	?	?	?	?
T. terrestris apud Mukhina (1981)	553	6.5	?	12	2 sv precl 2 sv adcl 2 sv postcl	ca. 8**	ca. 11**	?

Remarks:

*adcl - adcloacal; precl - precloacal; postcl - postcloacal; mv - midventral; sv - subventral; sd - subdorsal;

**measured or counted on illustration in paper;

***table gives data from the original description, while data from recent observations of type specimens are given in the discussion.

specific populations differ in this respect (e.g. T. costatus apud Novikova, 1971 and apud Hernandez & Jordana, 1988; T. tenuis apud Andrássy, 1958 and recent data), or information about papillae patterns are absent (e.g. T. sigillarius apud Kazachenko, 1980; T. terrestris apud de Man, 1876). Recent observations of type specimens of T. bisexualis, T. rugosus and T. tilbrooki (Fig. 3), showed that the papillae patterns are similar in all three males studied and identical with the patterns of the Ukrainian specimens of *T. tenuis* and the males described by Swart *et al.* (1989): a single midventral precloacal papilla, one pair of subventral adcloacal and one pair of subventral caudal (postcloacal) papillae. We may therefore assume that the numbers and distribution of male genital papillae are quite stable within the genus *Teratocephalus* and that some previous descriptions are probably erroneous. Similar specific patterns of male genital papillae in the Cephalobidae were re-

corded by De Ley (1997). The longitudinal striation of the cuticle in a large number of species, as well as the small body size could prevent accurate observations and cause misinterpretation. Further studies by LM and SEM are required to clarify the structure of the male copulatory apparatus, which may have a high value for elucidating the taxonomic position of the family Teratocephalidae in relation to other Cephalobina.

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