Description of three known and two new species of the genus *Tylocephalus* Crossman, 1933 with a revised taxonomy of the genus and key to species of the subfamily Wilsonematinae (Plectida)

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Summary. Descriptions of populations of *Tylocephalus auriculatus*, *T. cephalatus*, *T. nimius*, *T. longicornis* sp. n. and *T. primitivus* sp. n. are given on the basis of studies with light and scanning electron microscopy. *T. longicornis* sp. n. is characterised by a body length of 540-560 µm, cervical cuticular expansions bearing 20-25 annules and extending well posterior to the level of "subcephalic" setae, *cornua* 13 µm long with filiform terminus, tail 43-45 µm long, 49-57 somatic and 7 caudal setae. *T. primitivus* sp. n. is characterised by a body length of 300-450 µm, weakly developed cervical cuticular expansions bearing 7-11 annules and extending halfway to the level of "subcephalic" setae, *cornua* cylindrical and 3-5 µm long, tail 28-46 µm long, 10-16 somatic and 3-5 caudal setae. An emended diagnosis and a revised classification of the genus *Tylocephalus*, and a key for identification of species in the subfamily Wilsonematinae are given.

Key words: morphology, new species, SEM, taxonomy, *Tylocephalus*, Wilsonematinae.

The genus *Tylocephalus* Crossman, 1933 was established for the species *T. bacillivorus* Crossman, 1933, which was later synonymised with *Plectus auriculatus* Bütschli, 1873 by Anderson (1966). The latter became the type species of the genus *Tylocephalus*, which according to Anderson (1966) included two more species, viz. *T. cephalatus* (Cobb, 1893) Anderson, 1966 and *T. tentaculatus* (Fuchs, 1930) Anderson, 1966. No further species were added to the genus until Zell (1985) published the descriptions of *T. cornutus* Zell, 1985, *T. becki* Zell, 1985, *T. andinus* Zell, 1985, *T. annulatus* Zell, 1985 and *T. laticollis* Zell, 1985. He also transferred *T. tentaculatus* to *Wilsonema* Cobb, 1913 and considered it synonymous with *W. otophorum* (de Man, 1880) Cobb, 1913. Later two more species were added to the genus: *T. palmatus* Tahseen, Ahmad & Jairajpuri, 1995 and *T. nimius* De Ley & Coomans, 1997, both from studies by light and scanning electron microscopy. Currently this genus includes nine valid species. Among them *T. auriculatus* is the better known species, for which numerous descriptions are available including morphological data, description of a male, SEM-observations, and information on post-embryonic development and behaviour (Anderson, 1966; Gagarin, 1974; Eroshenko, 1977; Sauer & Annells, 1982; Sauer, 1985; De Ley & Coomans, 1997). Regarding the remaining eight species, only three of them have been reported after the original description: *T. annulatus* and *T. laticollis* by Bussau (1990) and *T. andinus* by Armendáriz & Hernández (1994). This paper continues our research on the morphology and systematics of the subfamily Wilsonematinae Chitwood, 1951 (De Ley *et al.*, 2002; Holovachov *et al.*, 2003; Holovachov & Háněl, 2004). It includes additional information on the morphology and distribution of three known species (*T. auriculatus, T. cephalatus* and *T. nimius*), descriptions of two new species (*T. primitivus* sp. n. from Europe and *T. longicornis* sp. n. from Central America), a revised classification of the genus

Tylocephalus, and a key for identification of species in the subfamily Wilsonematinae.

MATERIAL AND METHODS

The present study is based on specimens of five species of the genus *Tylocephalus*: *T. auriculatus* from Ukraine (Department of Zoology, Ivan Franko National University of L'viv, Ukraine) and Greece (Swedish Museum of Natural History, Stockholm, Sweden); *T. cephalatus* from Hawaii and Vietnam (courtesy Dr. G. Winiszewska, Museum i Instytut Zoologii, Warszawa, Poland); *T. nimius* from Costa Rica (courtesy Dr. A. Esquivel, Universidad Nacional de Heredia, Heredia, Costa Rica) and Korea (courtesy Dr. G. Winiszewska); *T. primitivus* sp. n. from Poland (courtesy Dr. G. Winiszewska) and Ukraine (Department of Zoology, Ivan Franko National University of L'viv, L'viv, Ukraine); *T. longicornis* sp. n. from Mexico (courtesy Dr. G. Winiszewska) and Costa Rica (courtesy Dr. A. Esquivel). All materials were mounted on permanent slides in glycerine with paraffin wax as support for the coverslip. For SEM studies, specimens of *T. primitivus* sp. n. from Poland were dismounted from permanent slides. In an attempt to restore the original morphology, specimens were rehydrated in two baths of distilled water for 24 h and fixed for a minimum of 24 h in a 5% aqueous formalin solution, followed by several rinses in 0.1 M phosphate buffer (pH 7.0). To avoid distortion and loss of rigidity to fragile structures, specimens were post-fixed for two hours in a 4% aqueous osmium tetroxide solution. Dehydration was through a series of 20% to absolute ethanol followed by critical point drying in a Tousimis Autosamdri®-810 (Rockville, MD, USA). Specimens were mounted on double-sided adhesive copper tape attached to aluminium stubs. Stubs were placed in a Hummer® V sputter coater (Alexandria, VA, USA) where a 25 nm layer of gold palladium was applied for three minutes. A Philips® EX30-FEG scanning electron microscope (Eindhoven, The Netherlands) was used to image the specimens at 10kV.

Coiled and curved structures were measured along the median line. Stoma length was measured from the mouth opening to the pharyngeal tubes. Amphid location was measured from the mouth opening to the anterior margin of the amphidial fovea. Measurements are given in the format: mean ± standard deviation and range where appropriate. Since the lip region of these nematodes is rather complex and includes several taxonomically important structures, we refer to Holovachov *et al.* (2003) regarding our usage of terminology.

DESCRIPTION

Tylocephalus auriculatus (Bütschli, 1873) Anderson, 1966 (Fig. 1)

(See also Gagarin, 1974; Sauer & Annells, 1982; De Ley & Coomans, 1997)

Measurements: Table 1.

Population from Ukraine.

Female. Body fusiform, weakly ventrally curved upon fixation. Cuticle thin, annulated. Lateral field 4.5-5.5 µm wide at midbody, consisting of two separate wings divided by striated cuticle, fading anteriorly at level of pharyngeal corpus and ending near tail terminus. Deirid setiform, at level of excretory pore, inside lateral field. Pharyngeal region with 11-14 somatic setae distributed as follows (n=3): a quartet of "subcephalic" setae (one pair subdorsal and one pair subventral) just posterior to cervical expansions, three pairs (one subdorsal, one subventral and one ventrosublateral) anterior to nerve ring, one to four setae between nerve ring and cardia. Body furthermore with 13-17 somatic setae (n=3): four to six setae between cardia and vulva, and nine to twelve setae between vulva and anus. Anterior end with pronounced bilateral and dorsoventral symmetry. Cervical cuticular expansions bearing a series of 9-13 annules, extending backward to the level of the quartet of "subcephalic" setae. Cornua flattened, leaf-shaped with finely rounded terminus, containing a distinct nerve. Subdorsal and subventral lip pairs modified into two median ridges, each with a pair of submedian flaps of cuticle, projecting forward and inward. Lateral lips modified, bearing two sublateral cuticular plates shaped like large quadrants. Lateral lips midlaterally extending in between quadrants, each forming a tapering tip, containing a nerve ending. Amphidial aperture 2 µm wide, circular, located at about half of stoma length. Stoma plectoid. Pharyngeal corpus cylindrical, plump, pharyngeal tubes present. Isthmus plump, surrounded by nerve ring at its anterior end and by renette cell at its posterior end. Basal pharyngeal bulb oval, with valves. Cardia embedded by intestinal tissue. Excretory gland duct weakly cuticularised, enveloped by renette cell. Excretory pore posterior to nerve ring. Coelomocytes present: one pair located in vicinity of renette cell and one pair halfway between cardia and anterior ovary,

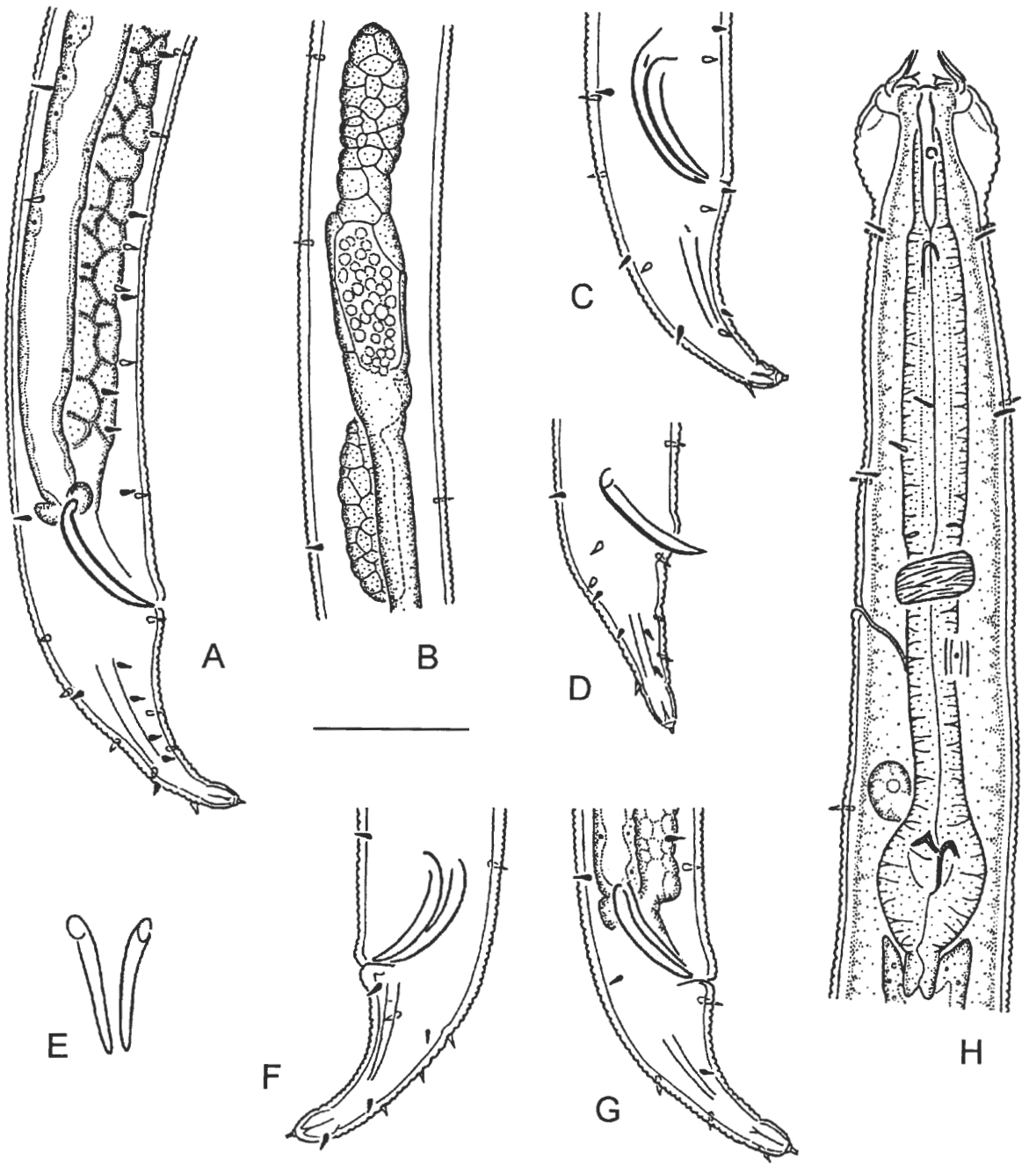

Fig. 1. *Tylocephalus auriculatus* (Bütschli, 1873) Anderson, 1966. Males from Ukraine (A-E) and Greece (F-H). A, C-D, F-G: Posterior region; B: Reproductive system, ventral to the right; E: Spicules, ventral view; H: Pharyngeal region. Scale bar: A-H – 20 µm.

ventral to intestine. Female reproductive system didelphic, amphidelphic, ovary branches reflexed. Vulva equatorial, transverse. Vagina short, encircled by a single sphincter muscle. Epiptygmata absent. Anterior genital branch located on right-hand side of intestine, posterior genital branch located on left-hand side of intestine. Intrauterine egg measuring 53x29 µm. Rectum short and stout. Tail gradually narrowing, arcuate ventral, with five caudal setae distributed as follows (n=3): a single subdorsal seta on left side at one-fifth of tail length, one subventral pair at middle of tail, and one subdorsal pair (including "spur" on left side) at four-fifths of tail length. Caudal glands and spinneret present.

Male. General morphology similar to female except sexual characters and the following features. Pharyngeal region with 14-15 somatic setae distributed as follows (n=2): a quartet of setae (one pair subdorsal and one pair subventral) just posterior to cervical expansions, five setae or three pairs (one subdorsal pair or a single seta, one subventral and one ventrosublateral pair) anterior to nerve ring, four to six setae between nerve ring and cardia. Body furthermore with 27-32 somatic setae (n=2) between cardia and cloaca: 7-13 subdorsal and 14-25 subventral setae. Cervical cuticular expansions bearing a series of 7-9 annules. Testes two, opposed, poorly developed. Spicules slightly asymmetrical, arcuate ventrad. Gubernaculum absent. Tubular supplements, precloacal and postcloacal sensilla absent. Tail with 9-14 caudal setae (n=3) distributed as shown in Figs 1A, C-D. The posteriormost seta (spur) is always located left subdorsal.

Specimens from Greece.

Female. Similar to population from Ukraine except for the following features. Lateral field 3 µm wide at midbody. Body (excluding the pharyngeal region) with 7 somatic setae (n=1): two setae between cardia and vulva, and five setae between vulva and anus. Cervical cuticular expansions bearing a series of 6-7 annules. Intrauterine egg measuring 43x30 µm.

Male. Similar to population from Ukraine except for the following features. Body (excluding the pharyngeal region) with 14 somatic setae (n=1) between cardia and cloaca: seven subdorsal and seven subventral setae. Testes two, opposed, normally developed, *vas deferens* carrying numerous oval spermatozoa. Tail with 5-8 caudal setae (n=2) distributed as shown in Figs 1F-G. The posteriormost seta (spur) is always located left subdorsal.

Material examined. Ukraine: (1848) the Crimea, Yalta district, Kishka mountain, moss (*Frullania dilatata*), July 1998, legit O. Holovachov; (1659) the Crimea, Alushta district, Au-Dag mountain, June 1996, legit O. Holovachov. Greece: (1) Samos, Kokari, soil with grasses near the shoreline, June 1988, legit B. Sohlenius; (15) Samos, Potami beach, dry sand with litter, grasses and juniper bushes (*Juniperus oxycedrus* L.), 3 October 1989, legit S. Boström.

Identification. The specimens generally agree in morphology and morphometric ranges with the original description of *T. auriculatus* by Bütschli (1873) and subsequent descriptions of the species by Anderson (1966), Gagarin (1974), Sauer & Annells (1982) and De Ley & Coomans (1997)

Tylocephalus cephalatus (Cobb, 1893) Anderson, 1966 (Fig. 2A-E)

Measurements. See Table 2.

Population from Hawaii.

Female. Body fusiform, weakly ventrally curved upon fixation. Cuticle thin, annulated. Lateral field 3 µm wide at midbody, consisting of two separate wings divided by striated cuticle, fading anteriorly at level of pharyngeal corpus and ending near tail terminus. Deirid setiform, at level of excretory pore, inside the lateral field. Pharyngeal region with eight to nine somatic setae distributed as follows (n=9): a quartet of "subcephalic" setae (one pair subdorsal and one pair subventral) at posterior end of cervical expansions, one ventrosublateral pair anterior to nerve ring, a subdorsal pair (or a single right subdorsal seta) and one subventral seta at level of excretory pore. Body with 12-16 additional somatic setae (n=4): three to four setae between cardia and vulva, and eight to twelve setae between vulva and anus. Anterior end with pronounced bilateral and dorsoventral symmetry. Cervical cuticular expansions bearing a series of 9-16 annules, extending backward to the level of the quartet of "subcephalic" setae. *Cornua* flattened, leaf-shaped, with finely rounded terminus, containing a distinct nerve. Subdorsal and subventral lip pairs modified into two smooth median ridges. Lateral lips modified, bearing two sublateral cuticular plates shaped like large quadrants. Lateral lips midlaterally extending in-between quadrants, each forming a tapering tip, containing a nerve

ending. Amphidial aperture 2 μm wide, circular, located at about half of stoma length. Stoma plectoid. Pharyngeal corpus cylindrical, plump, pharyngeal tubes present. Isthmus plump, surrounded by nerve ring at its anterior end and by renette cell at its posterior end. Basal pharyngeal bulb oval, with valves. Cardia embedded by intestinal tissue. Excretory gland duct weakly cuticularised, enveloped by renette cell. Excretory pore posterior to nerve ring. Coelomocytes present: one pair located in vicinity of renette cell and one pair halfway between cardia and anterior ovary, subventral to intestine. Female reproductive system didelphic, amphidelphic, ovary branches reflexed. Vulva equatorial, transverse. Vagina short, encircled by a single sphincter muscle. Epiptygmata absent. Anterior genital branch located on right-hand side of intestine in eight females and on left hand side in one female, posterior genital branch located on left-hand side of intestine. Intrauterine egg not seen. Rectum short and stout. Tail gradually narrowing, arcuate ventrad, with five caudal setae distributed as follows (n=10): a single subdorsal seta on left side of tail at one-fifth of tail length, one subventral pair at middle of tail, and one subdorsal pair (including "spur" on left side) at four-fifths of tail length. Caudal glands and spinneret present.

Male. Not found.

Specimen from Vietnam.

Female. Similar to population from Hawaii in all respects.

Male. Not found.

Material examined. USA, Hawaii: Oahu, rotting wood from a stub, 2 April 2000, legit R. Hołynski. Vietnam: Vinh Phu Province, Tam Dao National Park, soil, 14 April 1999, legit A. Stroinski and P. Węgnykowisz.

Identification. These specimens are identified solely by comparison with Cobb's (1893) original description of *T. cephalatus*, which is far from exhaustive. *T. cephalatus* is close to *T. auriculatus*. Separation of the two species is currently based mainly on the shape of median ridges (without paired flaps of cuticle on each median ridge *vs* with flaps in *T. auriculatus*), number of pharyngeal setae (8-9 *vs* 11-17 in *T. auriculatus*) and the relative length of the tail (c<10 *vs* c>10 in *T. auriculatus*).

Tylocephalus nimius De Ley & Coomans, 1997 (Fig. 3F-G)

Measurements: see Table 1.

Specimens from Korea.

Female. Body fusiform, weakly ventrally curved upon fixation. Cuticle thin, annulated. Lateral field 4.5 μm wide at midbody, consisting of two separate wings divided by striated cuticle, fading anteriorly at level of pharyngeal corpus and ending near tail terminus. Deirid setiform, at level of excretory pore, inside lateral field. Pharyngeal region with 15-16 somatic setae distributed as follows (n=2): a quartet of "subcephalic" setae (one pair subdorsal and one pair subventral) at level of posterior part of cervical expansions, five setae or three pairs (a single seta or one pair subdorsal, one subventral and one ventrosublateral pair) anterior to nerve ring, six setae between nerve ring and cardia. Body with 13-14 additional somatic setae (n=2): four to five setae between cardia and vulva, and nine setae between vulva and anus. Anterior end with pronounced bilateral and dorsoventral symmetry. Cervical cuticular expansions bearing a series of 16-22 annules, extending backward, well posterior to the level of the quartet of "subcephalic" setae. Cornua cylindrical, containing a distinct nerve. Subdorsal and subventral lip pairs modified into two median ridges. Lateral lips modified, bearing two sublateral cuticular plates shaped like large quadrants. Lateral lips midlaterally extending in-between quadrants, each forming a tapering tip, containing a nerve ending. Amphidial aperture 2 μm wide, circular, located at about half of stoma length. Stoma plectoid. Pharyngeal corpus cylindrical, plump, pharyngeal tubes present. Isthmus plump, surrounded by nerve ring at its anterior end and by renette cell at its posterior end. Basal pharyngeal bulb oval, with valves. Cardia embedded by intestinal tissue. Excretory gland duct weakly cuticularised, enveloped by renette cell. Excretory pore posterior to nerve ring. Coelomocytes present: one pair located in vicinity of renette cell and one pair halfway between cardia and anterior ovary, subventral to intestine. Female reproductive system didelphic, amphidelphic, ovary branches reflexed. Vulva equatorial, transverse. Vagina short, encircled by a single sphincter muscle. Epiptygmata absent. Anterior genital branch located on right-hand side of intestine, posterior genital branch located on left-hand side of intestine. Intrauterine egg not seen. Rectum short and stout. Tail gradually narrowing, arcuate ventrad, with five caudal setae distributed

Table 1. Measurements (in μm) of *Tylocephalus auriculatus* (Bütschli, 1873) Anderson, 1966 and *T. nimius* De Ley & Coomans, 1997.

Species	*T. auriculatus*					*T. nimius*					
Country	Ukraine			Greece (Samos)		Korea		Costa Rica			
Population	1848		1659	1	15	A-20	A-23	539	374	474	547
Number and sex	3♀♀	2♂♂	1♂	2♀♀	2♂♂	2♀♀	1♀	4♀♀	2♀♀	1♀	1♀
Body length	484; 474; 504	463; 343	477	463; 424	360; 398	383; 411	390	441-498	416; 516	501	563
Body diameter	35.5; 31; 28	25.5; 19	25.5	30; 29	19; 24.5	22; 25.5	24.5	24.5-49.0	24.5; 34.5	29	31
Neck length	125; 126; 142	120; 95	123	123; 117	105; 113	120; 118	112	118-124	111; 120	127	135
Tail length	37; 32; 37	31; 27	33	37; 31	30; 29	31; 31	24.5	30.0-34.5	32; 33	38	35.5
ABD	14.5; 13; 13	18; 15.5	19	14.5; 12	15.5; 17	11; 13	12	12	12; 13	13	13
a	13.6; 15.3; 18.2	18.1; 18.2	18.7	15.4; 14.7	19.1; 16.3	17.3; 16.1	16.0	10.2-19.4	17.0; 15.0	17.3	18.1
b	3.9; 3.8; 3.5	3.9; 3.6	3.9	3.8; 3.6	3.4; 3.5	3.2; 3.5	3.5	3.7-4.1	3.7; 4.3	4.0	4.2
c	13.2; 14.7; 13.8	14.9; 12.9	14.3	12.6; 13.6	12.0; 13.8	12.3; 13.2	16.0	13.8-14.9	12.9; 15.5	13.3	15.8
c'	2.5; 2.4; 2.8	1.8; 1.7	1.8	2.5; 2.5	1.9; 1.7	2.8; 2.3	2.0	2.5-2.8	2.6; 2.5	2.8	2.7
Cornua length	7; 8; 8	8; 7	8	7; 5.5	7; 7	14.5; 13	13	12-13	13; 13	14.5	13
Expansion length	18; 15.5; 19	16; 12	18	13; 12	11; 12	21; 29	22	22-28	25.5; 21	25.5	28
Expansion width	20; 22; 22	20; 18	20	21; 19	17; 17	?; 22	21	20-22	20; ?	21	22
Amphid location	10; 9; 10	10; 9	11	8; 9	10; 10	13; 12	11	10-11	10; 11	10	13
Stoma length	20; 19; 20	18; 14.5	19	19; 20	17; 18	17; 19	14.5	17-20	18; 19	19	20
Corpus length	41; 44.5; 50	44; 37	44	41; 39	38; 41	41; 42	41	42-48	39; 42	?	53
Isthmus length	41; 42; 44.5	39; 36	38	39; 39	33; 36	40; 39	36	39-41	37; 39	?	44
Bulbus length	17; 14.5; 20	17; 15.5	19	18; 17	15.5; 17	18; 17	19	17-20	17; 19	?	19
Cardia length	7; 10; 5.5	5.5; ?	5.5	7; 7	5.5; 5.5	5.5; 9	5.5	5.5-8	5.5; 9	8	7
Nerve ring	72; 72; 81	72; 59	72	70; 68	62; 64	64; 66	?	62-68	60; 68	72	?
Excretory pore	81; 79; 91	84; 64	86	79; 77	66; 70	71; 73	66	70-79	69; 80	81	86
Deirid	83; 82; 93	86; 69	89	80; 77	67; 72	72; 76	67	77-82	70; 84	83	90
NR (%)	58.0; 57.5; 57.0	60.2; 62.4	58.6	56.8; 57.1	59.6; 56.9	53.7; 55.7	?	52.3-54.7	54.0; 56.5	57.0	?
EP (%)	65.2; 62.8; 64.1	70.4; 68.2	69.4	64.0; 65.7	62.8; 61.8	59.3; 62.3	58.4	58.9-64.8	62.0; 66.7	64.0	63.6
DEI (%)	67.0; 65.5; 65.6	71.3; 72.9	72.1	64.9; 65.7	63.8; 63.7	60.2; 64.2	59.4	63.9-66.1	63.0;79.4	65.8	66.9
Rectum or spicula	11; 13; 13	21; 20	24.5	12; 12	18; 18	13; 12	12	9-11	11; 12	11	14.5
Rectum/ABD	0.8; 1.0; 1.0	-	-	0.8; 1.0	-	1.2; 0.9	1.0	0.7-0.9	0.9; 0.9	0.8	1.1
Spur location	5.5; 5.5; 5.5	7; 9	7	?; 5.5	4.5; 5.5	5.5; 5.5	?	4.5-5.5	4.5; 4.5	5.5	5.5
V, % or T, %	50.9; 50.1; 52.4	57.8; 55.7	56.9	49.2; 51.3	53.4; 54.5	51.9; 49.7	50.7	47.4-49.5	48.7; 49.4	49.2	48.5
G1, %	12.6; 8.9; 11.0	-	-	10.1; 11.5	-	7.2; 9.5	9.1	9.1-14.0	11.8; 9.9	?	14.0
G2, %	13.1; 6.3; 9.7	-	-	12.7; 8.1	-	7.2; 7.3	10.0	7.4-14.7	10.2; 8.8	?	17.8
Vagina	5.5; 9; 9	-	-	7; 7	-	8; 9	7.0	7	8; ?	8	7
Body setae	31-35	61; ?	50	?; 25	33; ?	?; 33	42	33	43; ?	?	?

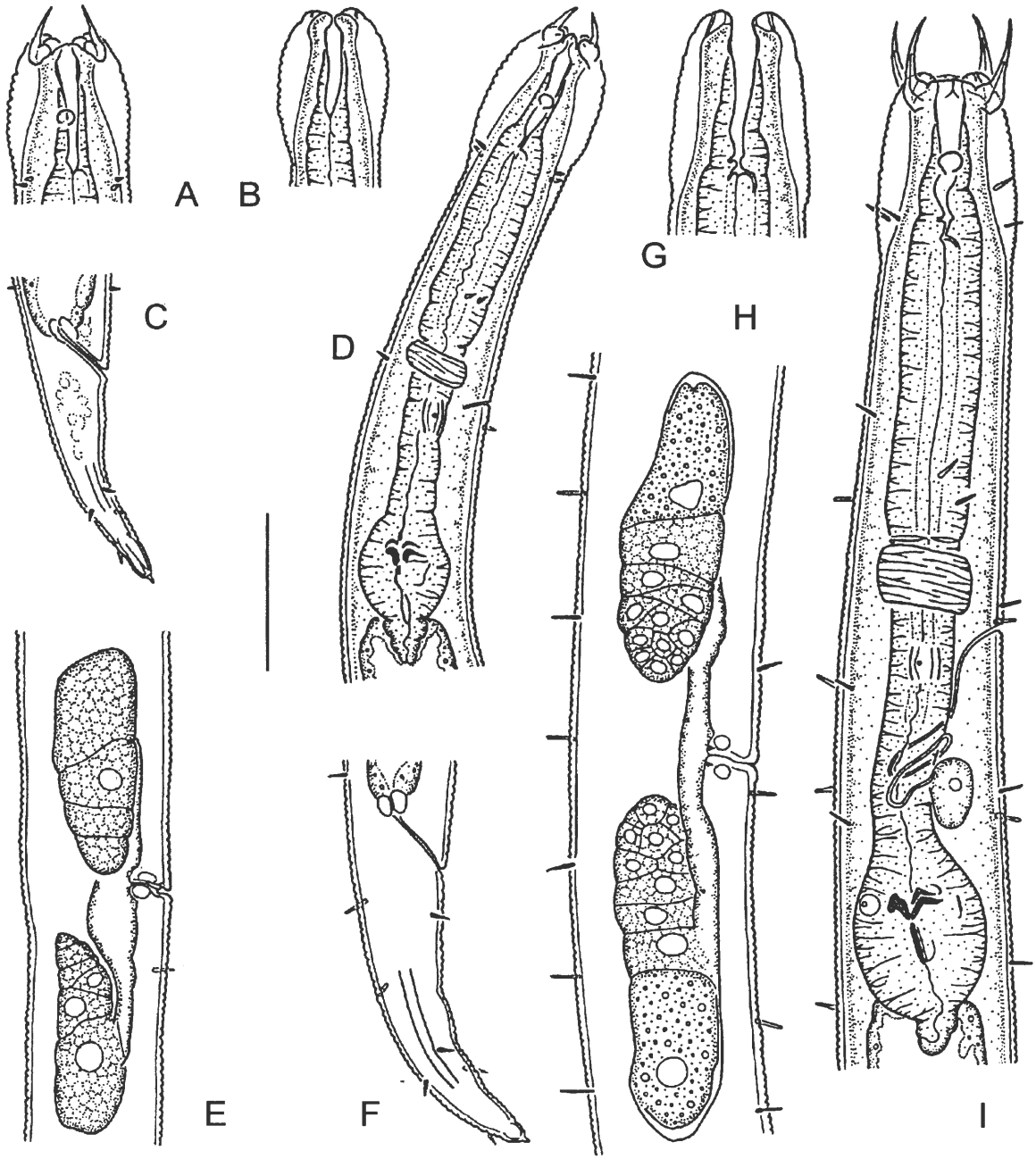

Fig. 2. *Tylocephalus cephalatus* (Cobb, 1893) Anderson, 1966 from Vietnam (A) and Hawaii (B-E) and *Tylocephalus longicornis* sp. n. from Costa Rica (F-I), females. A: Anterior end, combined view; B, G: Anterior end, optical median section; C, F: Tail; D, I: Pharyngeal region; E, H: Reproductive system. Scale bar: A-H – 20 μm.

as follows (n=3): a single subdorsal seta on left side of tail at one-fifth of tail length, one subventral pair at middle of tail, and one subdorsal pair (including "spur" on left side) located at four-fifths of tail length. Caudal glands and spinneret present.

Male. Not found.

Population from Costa Rica.

Female. Similar to specimens from Korea except for the following features. Lateral field 3.0 µm wide at midbody. Pharyngeal region with 14 somatic setae distributed as follows (n=3): a quartet of "subcephalic" setae (one pair subdorsal and one pair subventral) at level of posterior part of cervical expansions, four to six setae (of which the ventrosublateral pair is always present) anterior to nerve ring, four to six setae between nerve ring and cardia. Body with 13-24 additional somatic setae (n=3): five to nine setae between cardia and vulva, and nine to fifteen setae between vulva and anus. Cervical cuticular expansions bearing a series of 15-21 annules. Intrauterine egg (n=3) measuring 49-55x28-29 µm.

Male. Not found.

Material examined. Korea: (A-20) Kosong, Samji lake, pine forest, moss, 27 August 1987, legit Sowoñiewicz; (A-23) Phenian Park, pine litter, 6 August 1987, legit Sowoñiewicz. Costa Rica: (374) Tempisque Conservation Area, Cabo Blanco Absolute Reserve, secondary forest, fallen leaves gathered near *Bombacopsis quinata*, 15 December 1998, legit A. Esquivel; (474) La Amistad Caribe Conservation Area, Hitoy Cerere Biological Reserve, Espavel, primary forest, soil, roots and organic material, 6 Januray 1999, legit R. Gómez; (539) Osa Conservation Area, Golfo Dulce Forest Reserve, La Cascada, primary forest, moss growing over shrub leaves (*Osa pulchra*), 16 February 2000, legit A. Esquivel; (547) La Amistad Pacífico Conservation Area, National Park Tapantí-Macizo de la Muerte, El Pluviómetro, primary forest, fallen leaves gathered from the base of a tree trunk, 22 February 2000, legit H. Arias.

Identification. The specimens agree well in morphology and morphometric ranges with the original description of *T. nimius* by De Ley & Coomans (1997), particularly in the length of cornua (12-14.5 *vs* 12-14 µm in type population), length of cervical expansions (21-29 *vs* 17-26 µm in type population), number of annules on cervical expansions (15-22 *vs* 17-25 annules in type population), and extension of cervical expansions posterior to the level of the quartet of "subcephalic" setae.

Tylocephalus longicornis sp. n. (Fig. 2F-I)

Measurements: see Table 2.

Specimen from Costa Rica (holotype).

Female. Body fusiform, weakly ventrally curved upon fixation. Cuticle thin, annulated. Lateral field 3 µm wide at midbody, consisting of two separate wings divided by striated cuticle, fading anteriorly at level of pharyngeal corpus and ending near tail terminus. Deirid setiform, at level of excretory pore, inside lateral field. Pharyngeal region with 18 somatic setae distributed as follows: a quartet of "subcephalic" setae (one pair subdorsal and one pair subventral) at level of posterior part of cervical expansions, two pairs (one subdorsal and one ventrosublateral pair) anterior to nerve ring, one subventral pair at excretory pore, eight setae between excretory pore and cardia. Body with 31 additional somatic setae: 12 setae between cardia and vulva, and 19 setae between vulva and anus. Anterior end with pronounced bilateral and dorsoventral symmetry. Cervical cuticular expansions bearing a series of 25 annules, extending backward, well posterior to the level of the quartet of "subcephalic" setae. Cornua long, conoid, with filiform terminal part, arcuate inward, containing a distinct nerve. Subdorsal and subventral lip pairs modified into two median ridges, which are less prominent than in other species. Lateral lips modified, bearing two sublateral cuticular plates shaped like large quadrants. Lateral lips midlaterally extending in-between quadrants, each forming a tapering tip, containing a nerve ending. Amphidial aperture 3 µm wide, circular, located at about half of stoma length. Stoma plectoid. Pharyngeal corpus cylindrical, plump, pharyngeal tubes present. Isthmus plump, surrounded by nerve ring at its anterior end and by renette cell at its posterior end. Basal pharyngeal bulb oval, with valves. Cardia embedded by intestinal tissue. Excretory gland duct weakly cuticularised, enveloped by renette cell. Excretory pore posterior to nerve ring. Coelomocytes present: one pair located in vicinity of renette cell and one pair halfway between cardia and anterior ovary, subventral to intestine. Female reproductive system didelphic, amphidelphic, ovary branches reflexed. Vulva equatorial, transverse. Vagina short, encircled by single sphin-

cter muscle. Epiptygmata absent. Anterior genital branch located on right-hand side of intestine, posterior genital branch located on left-hand side of intestine. Intrauterine egg not seen. Rectum short and stout. Tail gradually narrowing, arcuate ventrad, with seven caudal setae distributed as follows: a single left subdorsal seta at anus level, a single right subventral setae just posterior to anus, a single left subdorsal setae at one-fifth of tail length, one subventral pair at middle of tail, and one subdorsal pair located along the posterior fifths of tail length, including the "spur" on left side near spinneret. Caudal glands and spinneret present.

Male. Not found.

Specimen from Mexico (paratype).

Female. Similar to specimen from Costa Rica except for the following features. Pharyngeal region with 17 somatic setae distributed as follows (n=1): a quartet of "subcephalic" setae (a pair of subdorsal and a pair of subventral) at level of posterior part of cervical expansions, two pairs (one subdorsal and one ventrosublateral pair) anterior to nerve ring, one subventral pair at excretory pore, seven setae between the excretory pore and cardia. Body with 40 additional somatic setae (n=1): 16 setae between cardia and vulva, and 24 setae between vulva and anus. Cervical cuticular expansions bearing a series of 20 annules. Amphidial aperture 4.5 μm wide.

Male. Not found.

Type locality and habitat. Costa Rica: (holotype) La Amistad Pacífico Conservation Area, National Park Tapantí-Macizo de La Muerte, Palmito, primary forest, water gathered from bromeliads, 4 May 1999, legit A. Esquivel.

Other locality. Mexico: (paratype) Tapachula, Chiapas, Union Juarez, alt. 1700 m a.s.l., near the Guatemala border, legit K. Jankiewicz.

Type specimens. Holotype female deposited in the nematode collection of Universidad Nacional de Heredia, Heredia, Costa Rica, and paratype female deposited in the nematode collection of the Museum i Instytut Zoologii, PAN, Warszawa, Poland.

Differential diagnosis. *Tylocephalus longicornis* sp. n. resembles *T. cornutus* in having conoid cornua and weakly developed median ridges, and *T. nimius* by having long cornua and cervical expansions extending well posterior to the level of the quartet of "subcephalic" setae. It differs from *T. cornutus* by the following features: longer cornua (13 μm vs nearly 8 μm in *T. cornutus* as calculated from Fig. 1b in Zell, 1985), cervical expansions extending posterior to the quartet of "subcephalic" setae (*vs* ending at level of the quartet of "subcephalic" setae), and larger number of annules on cervical expansions (20-25 *vs* 12). The new species differs from *T. nimius* by the structure of cornua (conoid and directed forward vs cylindrical and directed forward and inward) and median ridges (weak *vs* distinct), a longer tail (43-45 μm vs 25-38 μm), larger number of caudal setae (7 *vs* 5), and larger number of body setae (56-60 *vs* 33-51).

Tylocephalus primitivus sp. n. (Figs. 3A-E, 4)

Measurements: see Table 2.

Population from Poland (type population).

Female. Body fusiform, weakly ventrally curved upon fixation. Cuticle thin, annulated. Lateral field 3 μm wide at midbody, consisting of two separate wings divided by striated cuticle, fading anteriorly at level of pharyngeal corpus and ending near tail terminus. Deirid setiform, at level of excretory pore, inside the lateral field. Pharyngeal region with six to seven somatic setae distributed as follows (n=5): one subdorsal pair of "subcephalic" setae posterior to cervical expansions, one ventrosublateral pair anterior to nerve ring, one subdorsal pair between nerve ring and cardia, plus one left subventral seta (in one specimen only) at excretory pore level. Body with four to five additional somatic setae (n=2): two to three setae between cardia and vulva, and one to two setae between vulva and anus. Anterior end with pronounced bilateral and dorsoventral symmetry. Cervical cuticular expansions bearing a series of 7-11 annules, weakly developed, extending about halfway to the "subcephalic" setae, apparently "collapsed" and not seen by SEM. Cornua with cylindrical distal part and bilobed tip, directed forward, containing a distinct nerve. Proximal part of cornua carries a basal flap, directed midlaterally. Subdorsal and subventral lips narrower than lateral ones, but not modified into distinct median ridges. Lateral lips modified, without sublateral cuticular plates (quadrants). Lateral lips midlaterally extending in-between cornua, each forming a rounded tip, containing a nerve ending. Amphidial

aperture 2 µm wide, circular, located at about half of stoma length. Stoma plectoid. Pharyngeal corpus cylindrical, plump, pharyngeal tubes present. Isthmus plump, surrounded by nerve ring at its anterior end and by renette cell at its posterior end. Basal pharyngeal bulb oval, with valves. Cardia embedded by intestinal tissue. Excretory gland duct weakly cuticularised, enveloped by renette cell. Excretory pore posterior to nerve ring. Coelomocytes present: one pair located in vicinity of renette cell and one pair halfway between cardia and anterior ovary, subventral to intestine. Female reproductive system didelphic, amphidelphic, ovary branches reflexed. Vulva equatorial, transverse. Vagina short, encircled by single sphincter muscle. Epiptygmata absent. Anterior genital branch located on right-hand side of intestine, posterior genital branch located on left-hand side of intestine. Intrauterine egg (n=4) measuring 47-55x20-29 µm. Rectum short and stout. Tail gradually narrowing, arcuate ventrad, with three to five caudal setae distributed as follows (n=5): one subventral pair at one-third of tail length (an additional left subdorsal seta at one-fifth of tail length present in one specimen), and one subdorsal pair (only a single left subdorsal seta present in one specimen) along the posterior fifths of tail length, including the "spur" on left side near spinneret. Caudal glands and spinneret present.

Male. Not found.

Specimens from Ukraine.

Female. Similar to population from Poland except for the following features. Lateral field 4.5-5.5 µm wide at midbody. Pharyngeal region with ten somatic setae distributed as follows (n=2): a quartet of "subcephalic" setae (one pair subdorsal and one pair subventral) just posterior to cervical expansions, one ventrosublateral pair anterior to nerve ring, one subventral pair at level of excretory pore, and one subdorsal pair posteriorly between the excretory pore and cardia. Body with four to six additional somatic setae (n=2): one to two setae between cardia and vulva and three to four setae between vulva and anus. Amphidial aperture 3 µm wide. Tail gradually narrowing, arcuate ventrad, with five caudal setae distributed as follows (n=2): a single subdorsal seta on left side of tail at one-fifth of tail length, one subventral pair at middle of tail, and one subdorsal pair at four-fifths of tail length.

Male. Not found.

Type locality and habitat. Poland: Puszcza Białowieska, department 485, wet meadow, August 1987, legit G. Winiszewska.

Other locality. Ukraine: Zakarpatska province, Peretchyn district, Zhornava village, beech forest, soil and litter, 25 April 1999, legit T. Lysachuk.

Type specimens. Holotype and three paratype females deposited in the nematode collection of the Museum i Instytut Zoologii, PAN, Warszawa, Poland. Two paratype females deposited in each of the nematode collections in Department of Invertebrate Zoology, Swedish Museum of Natural History, Stockholm, Sweden; Department of Zoology, Ivan Franko National University of L'viv, Ukraine.

Differential diagnosis. *Tylocephalus primitivus* sp. n. resembles *T. cephalatus* and *T. becki* by its small body size, median ridges without flaps and rather short cornua. It differs from *T. cephalatus* by having cylindrical cornua (*vs* flattened) and only one pair of "subcephalic" setae in type population (*vs* two pairs). The new species differs from *T. becki* by having cylindrical cornua (*vs* "thorn-shaped"), a smaller number of annules on cervical expansions (7-11 *vs* 20) and only one pair of "subcephalic" setae in type population (*vs* two pairs).

Remarks. *T. primitivus* sp. n. is interesting from a phylogenetic point of view as some characters in its anterior organisation appear to bridge the gap between the taxa *Ceratoplectus* Andrássy, 1984 in Plectinae and *Tylocephalus*, which represents the least derived taxon in Wilsonematinae (Holovachov *et al.,* 2003). The cornua in some species of *Tylocephalus* resemble the cephalic setae of *Ceratoplectus* (cf. De Ley & Coomans, 1994; Boström, 2003) and the former are clearly derived from the latter as evidenced by the homology in morphology of first- and second-stage juveniles of *T. auriculatus* (De Ley & Coomans, 1997). The short cylindrical cornua of the new species could constitute an intermediate stage between cephalic setae and the more developed cornua as they appear in most species of *Tylocephalus*. As seen under SEM, the lateral lips in *Ceratoplectus armatus* (Bütschli, 1873) Andrássy, 1984 are wider than the subdorsal and subventral lips and carry two radial incisures each (cf. De Ley & Coomans, 1994; Boström, 2003). In species of *Tylocephalus* the lateral lips are flattened and modified into a tapering midlateral projection containing a nerve ending and two adjacent sublateral small plates (qua-

Table 2. Measurements (in µm) of *Tylocephalus cephalatus* (Cobb, 1893) Anderson, 1966, *T. longicornis* sp. n. and *T. primitivus* sp. n. (HT = holotype).

Species	*T. cephalatus*		*T. longicornis* sp. n.		*T. primitivus* sp. n.		
Country	Hawaii	Vietnam	Costa Rica	Mexico	Poland		Ukraine
Number & sex	10♀♀	1 ♀	HT	1♀	HT	12 ♀♀	2♀♀
Body length	287±13 (267-310)	321	562	541	351	381±49 (313-447)	331; 336
Body diameter	18.0±1.4 (15.5-20.0)	20	31	27	25.5	27.4±7.0 (18-39)	22; 22
Neck length	89.9±2.8 (85.5-93.0)	102	146	141	101	109.6±11.2 (93-130)	94; 98
Tail length	30.1±1.1 (28-31)	33	43	44.5	30	36.2±7.4 (28.0-45.5)	34.5; 37
ABD	8.8±0.6 (8-10)	10	13	13	8	10.0±1.8 (8-13)	11; 10
a	16.0±0.9 (14.8-17.6)	16.1	18.1	20.3	13.7	14.3±2.0 (11.5-17.6)	14.9; 15.1
b	3.2±0.2 (3.0-3.5)	3.1	3.9	3.8	3.5	3.5±0.2 (3.1-3.7)	3.5; 3.4
c	9.5±0.3 (9.1-10.0)	9.6	13.0	12.2	11.7	10.7±1.0 (9.0-12.3)	9.6; 9.2
c'	3.5±0.3 (2.9-4.0)	3.3	3.3	3.4	3.9	3.6±0.4 (3.1-4.1)	3.1; 3.7
Cornua length	5.4±0.6 (4.5-7.0)	7	13	13	3	3.6±0.5 (3.0-4.5)	4.5; 4.5
Expansion length	14.0±2.2 (11-17)	15.5	25.5	28	10	9.6±1.1 (8-11)	12; 14.5
Expansion width	15.2±0.5 (14.5-15.5)	18	18	20	10	10.6±0.6 (10-11)	15.5; 14.5
Amphid location	8.3±0.8 (7-9)	10	9	10	9	9.0±0.9 (8-10)	7; 9
Stoma length	16.1±1.3 (13-18)	19	22	22	20	21.1±3.0 (17.0-25.5)	15.5; 17
Corpus length	29.7±1.2 (28-31)	30	47	44	35.5	40.3±4.9 (34.5-48.0)	33; 33
Isthmus length	26.1±1.7 (22-28)	33	46	44	30	33.6±3.6 (28-38)	29; 29
Bulbus length	14.7±1.2 (13-17)	17	22	24	13	14.8±1.9 (12-19)	12; 13
Cardia length	5.9±1.1 (4.5-8.0)	5.5	8	7	5.5	6.7±1.2 (4.5-8.0)	8; 9
Nerve ring	51.3±1.7 (48-53)	5.7	88	78	60	65.7±7.6 (55.5-74.5)	59; 58
Excretory pore	56.0±1.6 (53-58)	6.5	89	87	68	74.2±9.9 (63-93)	64; 66
Deirid	60.2±2.3 (57-63)	70	90	90	72	76.8±8.0 (69-89)	69; 70
NR (%)	57.1±1.1 (55.8-59.5)	55.4	56.5	55.1	59.3	59.9±1.8 (54.9-62.6)	62.4; 59.1
EP (%)	62.3±0.8 (60.7-63.3)	63.0	61.1	61.4	67.0	67.0±3.0 (62.6-72.4)	68.2; 67.0
DEI (%)	67.0±0.8 (66.2-68.7)	68.5	61.8	63.8	71.4	72.0±2.9 (68.1-76.2)	72.9; 71.6
Rectum	9.6±0.8 (9-11)	12	15.5	18	9	10.3±1.2 (9-12)	10; 10
Rectum/ABD	1.1±0.1 (1.0-1.3)	1.2	1.2	1.3	1.1	1.1±0.1 (0.8-1.3)	0.9; 1.0
Spur location	5.4±0.6 (4.5-7.0)	5.5	7	4.5	5.5	7.3±1.7 (5.5-11.0)	7; 7
V, %	52.0±1.1 (50.0-53.1)	52.6	49.2	48.7	53.8	53.2±1.4 (51.4-56.7)	53.7; 53.0
G1, %	7.6±1.9 (4.9-11.3)	?	11.5	10.1	13.3	12.5±1.7 (9.2-15.0)	12.1; 12.3
G2, %	8.5±3.0 (4.2-11.3)	?	12.1	9.9	13.6	12.5±1.5 (9.2-14.2)	12.8; 11.6
Vagina	6.0±0.6 (5.5-7.0)	7	7	8	4.5	5.0±0.6 (4.5-5.5)	7; 7
Body setae	26-30	?	56	64	13	14	21; 19

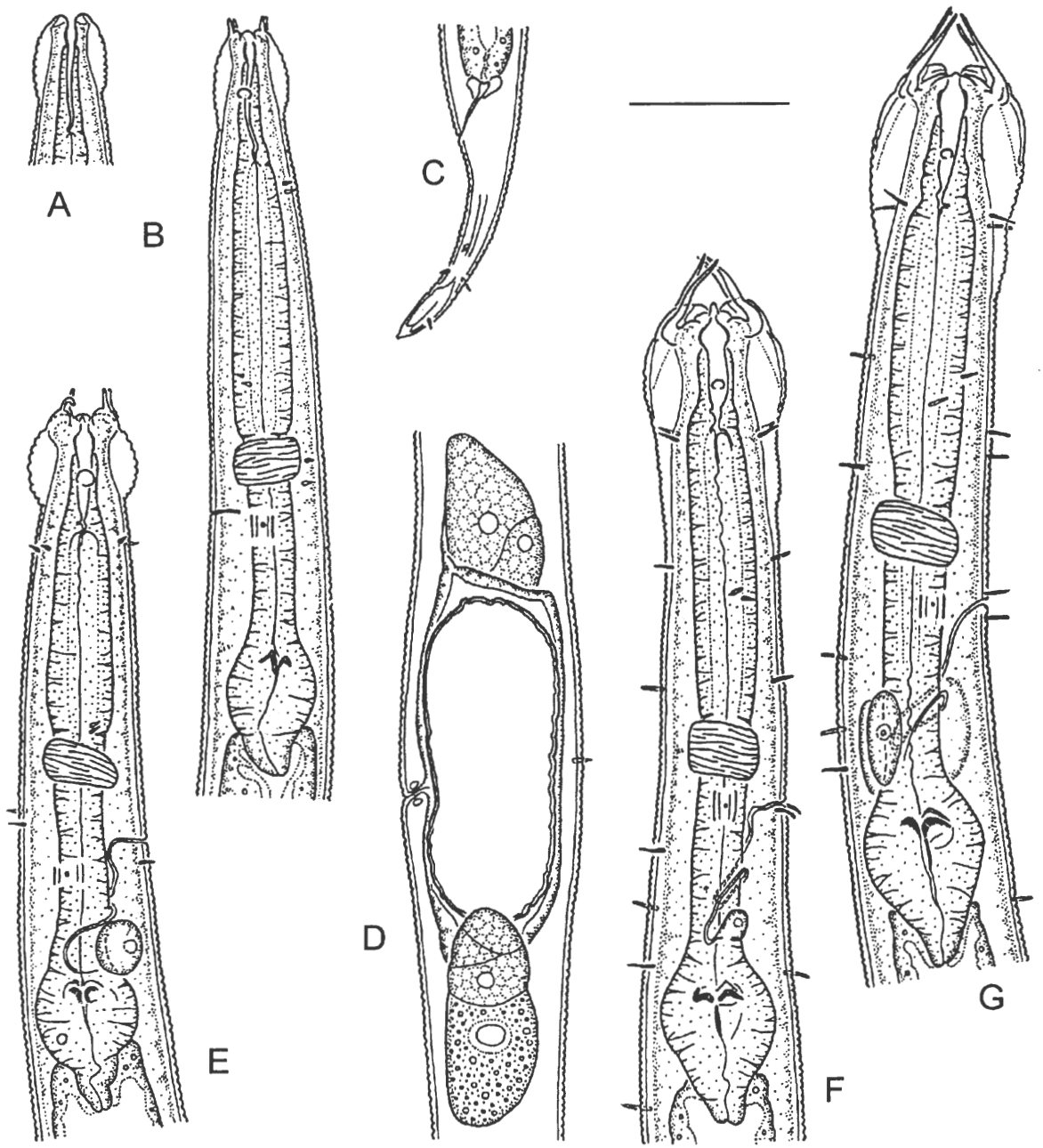

Fig. 3. *Tylocephalus primitivus* sp. n. from Poland (A-D) and Ukraine (E) and *Tylocephalus nimius* De Ley & Coomans, 1997 from Costa Rica (F) and Korea (G), females. A: Anterior end, optical median section; B, E, F-G: Pharyngeal region; C: Tail; D: Reproductive system with intrauterine egg. Scale bar: A-G – 20 μm.

drants) each (De Ley & Coomans, 1997). In *T. primitivus* sp. n. the midlateral projection appears more rounded (resembling the lateral lip of *Ceratoplectus*) and the sublateral plates are not developed. Since only one species of *Ceratoplectus* has been studied under SEM (*C. armatus*), descriptions of the labial region of at least *C. assimilis* (Bütschli, 1873) Andrássy, 1984 and *C. cornus* (Maggenti, 1961) Andrássy, 1984 are needed to confirm a possible close relationship between *T. primitivus* sp. n. and *Ceratoplectus*.

Tylocephalus Crossman, 1933

Diagnosis (emended). Wilsonematinae. Body length 0.3 to 0.6 mm. Anterior end with bilateral and dorsoventral symmetry. Cervical expansions bulbiform, annulated under LM and SEM, each extending anteriorly into a median ridge. Four cornua, setiform, cylindrical or flattened. Midlateral projection short oval. Lateral rims non-fimbriate. Amphid aperture circular, located at half of stoma length. Renette cell located ventrally, opposite to isthmus. Excretory gland duct weakly cuticularised, enveloped by renette cell. Excretory pore posterior to nerve ring. Stoma plectoid. Pharynx plectoid, divided into corpus and isthmus by a break in muscular tissue and subventral gland orifices, basal bulb with valves. Vulva equatorial. Female reproductive system didelphic, amphidelphic. Male reproductive system diorchic, testes opposed. Spicules paired, curved ventrad. Tubular supplements, precloacal, postcloacal sensilla and gobernaculum absent. Tail conoid at first, then cylindrical, ventrally curved. Caudal glands present, opening through a terminal spinneret.

Type species:

Tylocephalus auriculatus (Bütschli, 1873) Anderson, 1966
= *Plectus auriculatus* Bütschli, 1873
= *Wilsonema auriculatum* (Bütschli, 1873) Cobb, 1913
Syn.: *Tylocephalus bacillivorus* Crossman, 1933
= *Wilsonema bacillivorus* (Crossman, 1933) Chitwood et Chitwood, 1950.

Other species:

Tylocephalus andinus Zell, 1985
Tylocephalus annulatus Zell, 1985
Syn.: *Plectus (Wilsonema) convexus* Zell, 1993
= *Plectus (Wilsonema) annulatus* (Zell, 1985) Zell, 1993 nec *Plectus annulatus* Maggenti, 1961
Tylocephalus becki Zell, 1985
Tylocephalus cephalatus (Cobb, 1893) Anderson, 1966
= *Plectus cephalatus* Cobb, 1893 nec *Wilsonema cephalatum* Cobb, 1913 (p. 443)
Tylocephalus cornutus Zell, 1985
Tylocephalus laticollis Zell, 1985
Tylocephalus longicornis sp. n.
Tylocephalus nimius De Ley et Coomans, 1997
Tylocephalus palmatus Tahseen, Ahmad et Jairajpuri, 1995
Tylocephalus primitivus sp. n.

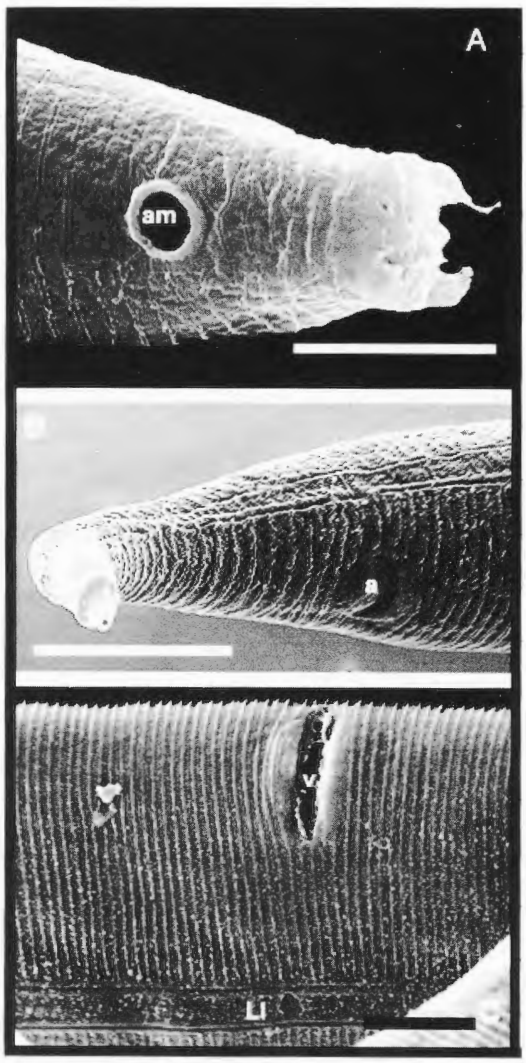

Fig. 4. Scanning electron micrographs of *Tylocephalus primitivus* sp. n. from Poland, females. A: Lateral view of anterior region showing amphid opening (am) and cephalic structures; B: Ventrosublateral view of tail region showing anus (a) and lateral field; C: Ventrosublateral view of vulva (v) and lateral field with two lateral lines (Ll). Scale bar: A-C – 5 µm.

Key to species of the subfamily Wilsonematinae*

1. Cornua with 2-5 tines each; flabella present and carry fimbriae; median ridge absent 2
- Cornua without tines, cylindrical or flat; flabella absent; median ridge present ..... *Tylocephalus* - 10
2 Cervical expansions distinctly annulated .... *Ereptonema* - 3
- Cervical expansions visually smooth 5
3 Cervical expansions with 10-12 striae; lateral rims smooth; tail with three setae ..... *E. andersoni*
- Cervical expansions with 4-6 striae; lateral rims fimbriate; tail with four setae 4
4 Cornua with two tines each, "claw-like" ..... *E. cheliferum*
- Cornua with three tines each; four flabella .... *E. arcticum*
5 Midlateral projection short; four flabella ..... *Neotylocephalus* - 6
- Midlateral projection long, digitate; two flabella ..... *Wilsonema* - 8
6 Pharyngeal region without setae; three caudal setae ..... *N. haryanensis*
- Pharyngeal region with four setae; four to six caudal setae 7
7 Flabella shorter than cornua; middle tine of cornua longer than the other two ..... *N. annonae*
- Flabella longer than cornua; outermost tine of cornua longer than the other two ..... *N. inflatus*
8 Tail long (c=5-6), vulva pre-equatorial (V=44-46%) ..... *W. longicaudatum*
- Tail shorter (c=7-18), vulva equatorial (V=47-57%) 9
9 Pharyngeal region with ten setae; tail with four setae ..... *W. bangaloreiensis*
- Pharyngeal region with six setae; five caudal setae, rectum short (7-14 μm, R/ABD=0.8-1.4)..... *W. otophorum*
- Pharyngeal region with four setae; four caudal setae, rectum long (18-28 μm, R/ABD=2.2-4.6) ..... *W. schuurmansstekhoveni*
10 Median ridge undeveloped, absent 11
- Median ridge present 13
11 Cervical expansions extending posterior to the level of "subcephalic" setae..... ..... *T. longicornis sp. n.*
- Cervical expansions extending to near the level of "subcephalic" setae 12
12 Body length >400 μm ..... *T. cornutus*
- Body length <400 μm ..... *T. primitivus*
13 Median ridge without flaps and without taps ("Zapfen") 14
- Median ridge with lateral flaps, without taps ("Zapfen") 16
- Median ridge without flaps, with taps ("Zapfen") 17
14 Cornua long (12-14.5 μm); cervical expansions long (17-29 μm), extending posterior to the level of "subcephalic" setae ..... *T. nimius*
- Cornua short (4.5-7 μm); cervical expansions short (11-17 μm), extending to near the level of "subcephalic" setae 15
15 Cornua conoid, convexly arcuate, without basal flap ..... *T. becki*
- Cornua flattened, with basal flap ..... *T. cephalatus*
16 Six caudal setae; "spur" at 13-15 μm from tail terminus ..... *T. palmatus*
- Five caudal setae; "spur" at 4-7 μm from tail terminus ..... *T. auriculatus*
17 Cervical expansions narrow; body length 500 μm ..... *T. annulatus*
- Cervical expansions oval; body length 400-500 μm ..... *T. andinus*
- Cervical expansions wide, rounded; body length 350-450 μm ..... *T. laticollis*

* - for the nomenclatorial data (authority of each species and synonymy) see Holovachov *et al.* (2003) and Holovachov & Hanél (2004); for the terminology of the labial region consult Holovachov *et al.* (2003); numerical data are given for females only.

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Holovachov O., Boström S., Mundo-Ocampo M. Описание трех известных и двух новых видов рода *Tylocephalus* Crossman, 1933, ревизия таксономии рода и ключ для определения видов подсемейства Wilsonematinae (Plectida)

Резюме. Даны описания популяций видов *Tylocephalus auriculatus, T. cephalatus, T. nimius, T. longicornis* sp. n. и *T. primitivus* sp. n. на основе данных световой и электронной микроскопии. Новый вид *T. longicornis* sp. n. характеризуется следующими признаками: длина тела 540-560 мкм, цервикальные расширения несут 20-25 колец кутикулы и продолжаются ниже уровня "субголовных" щетинок, видоизмененные головные сенсиллы 13 мкм длиной с нитчатой вершиной, длина хвоста 43-45 мкм, 49-57 соматических и 7 хвостовых щетинок. Новый вид *T. primitivus* sp. n. характеризуется следующими признаками: длина тела равна 300-450 мкм, слаборазвитые цервикальные расширения несут 7-11 колец кутикулы и продолжаются на половину расстояния до уровня "субголовных" щетинок, видоизмененные головные сенсиллы цилиндрические, 3-5 мкм длиной, хвост 28-46 мкм длиной, 10-16 соматических и 3-5 хвостовых щетинок. Предложен дополненный диагноз и классификация рода *Tylocephalus*, а также - ключ для определения видов подсемейства Wilsonematinae.