

A review of the genus *Diplogasteritus* Paramonov, 1952 with description of a new species from Central Russia (Nematoda, Diplogasterida: Diplogasteridae)

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Gagarin, V.G. 2002. A review of the genus *Diplogasteritus* Paramonov, 1952 with description of a new species from Central Russia (Nematoda, Diplogasterida: Diplogasteridae). *Zoosystematica Rossica*, 11(1): 57-73.

The morphology and taxonomy of free-living nematodes of the genus *Diplogasteritus* Paramonov, 1952 are studied using the original material and literary data. The diagnosis of the genus *Diplogasteritus* is emended. Descriptions of species, synonymy and a key to species are given. The following new synonymies are established: *D. occidentalis* (Steiner, 1932) = *D. concolor* (Massey, 1962) = *D. austriacus* (Fuchs, 1938); *D. lineatus* (Fuchs, 1915) = *D. angustilaimus* (Sch. Stekhoven & Tenuissen, 1938) = *D. likoi* Kokordak, 1963 = *D. consobrinus* (de Man, 1920) = *D. stoeckherti* (Volk, 1950) = *D. taedus* (Massey, 1962); *D. nudicapitatus* (Steiner, 1914) = *D. aquaticus* Gagarin, 1977 = *D. ponderosus* (Massey, 1962). *Diplogasteritus arcuatus* (Massey, 1962), *D. brevicaudatus* (Sch. Stekhoven & Tenuissen, 1938), and *D. minutus* (Kreis, 1929) are considered *species inquirendae*. *Diplogasteritus paxi* (Paesler, 1962), *D. pterygatus* (Timm, 1961) and *D. subterraneus* (Hnatewytch, 1929) are considered *species incertae sedis*. *Diplogasteritus primitivus* sp. n. collected from rotten potato in Yaroslavl Prov. of Russia is described and illustrated.

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Introduction

The genus *Diplogasteritus* was established by Paramonov (1952). Paramonov considered the following main morphological characters as diagnostic for this genus: (a) presence of longitudinal ridges of cuticle, (b) stoma narrow and long, (c) cheilorhabdions distinctly separate from protorhabdions, (d) dorsal tooth of prostoma distinctly larger than subdorsal teeth, the latter small. The genus *Diplogasteritus* is very close to the genus *Diplogastrellus* Paramonov, 1952 and differs from this latter in the presence of two ovaries, while species of *Diplogastrellus* have a single, anterior ovary.

Paramonov included nine species in *Diplogasteritus*: *D. nudicapitatus* (Steiner, 1914) (type species), *D. filicaudatus* (Bütschli, 1874), *D. rhodani* (Steiner, 1914), *D. consobrinus* (de Man, 1920), *D. demani* (Schneider, 1914), *D. minutus* (Kreis, 1929), *D. austriacus* (Fuchs, 1938), *D. superbus* (Paesler, 1946), and *D. occidentalis* (Steiner, 1932). In his monograph, Paramonov (1961) included in the genus *Diplogasteritus* as many as 15 valid species.

Weingärtner (1955) considered the separate group of species, *nudicapitatus* – group, within the genus *Diplogaster* Schultze in Carus, 1857. This group included eight species: *Diplogaster* (*Diplogaster*) *dendrophilus* (Weingärtner in Körner, 1954), *D. (D.) consobrinus* (de Man, 1920), *D. (D.) austriacus* Fuchs, 1938, *D. (D.) nudicapitatus* Steiner, 1914, *D. (D.) superbus* Paesler, 1946, *D. (D.) stoeckherti* Völk, 1950, *D. (D.) lineatus* Fuchs, 1915, and *D. (D.) subterraneus* Hnatewytch, 1929.

Goodey (1963) included in the genus *Diplogasteritus* eight species, considered as *nudicapitatus* group sensu Weingärtner, and listed eight species that “may also belong to this genus”: *D. angustilaimus* (Sch. Stekhoven & Tenuissen, 1938), *D. brevicaudatus* (Sch. Stekhoven & Tenuissen, 1938), *D. eurycephalus* (Völk, 1950), *D. labiatus* (Cobb in Merrill & Ford, 1916), *D. liratus* (Schneider, 1860), *D. minutus* (Kreis, 1930), *D. occidentalis* (Steiner, 1932), and *D. zurstrasseni* (Sachs, 1950).

Massey (1962) synonymised the genus *Diplogasteritus* Paramonov, 1952 with the genus *Acrostichus* Rahm, 1928. He included in

Acrostichus the following 19 species: *A. toledus* Rahm, 1928 (type species), *A. angustilaimus* (Sch. Stekhoven & Tenuissen, 1938), *A. arcuatus* Massey, 1962, *A. austriacus* (Fuchs, 1938), *A. concolor* Massey, 1962, *A. consobrinus* (de Man, 1920), *A. demani* (Schneider, 1923), *A. dendrophilus* (Weingärtner in Körner, 1954), *A. lineatus* (Fuchs, 1915), *A. microstoma* (Goodey, 1929), *A. minutus* (Kreis, 1930), *A. nudicapitatus* (Steiner, 1914), *A. occidentalis* (Steiner, 1932), *A. ponderosus* Massey, 1962, *A. pterygatus* (Steiner, 1932), *A. rhodani* (Stefanski, 1914), *A. stoeckherti* (Völk, 1950), *A. superbus* (Paesler, 1946), and *A. taedus* Massey, 1962.

Lasarevskaja (1965) established a new genus, *Filipjevella*, with five species, placed previously in the genus *Acrostichus*: *F. minimus* (Lasarevskaja, 1964), *F. arcuata* (Massey, 1962), *F. concolor* (Massey, 1962), *F. ponderosa* (Massey, 1962), and *F. taeda* (Massey, 1962).

Andrássy (1984) reviewed the order Diplogasterida. He divided the genera *Diplogasteritus* and *Acrostichus*. The species with two ovaries and isolated vulval chamber were included in the first genus. The second genus comprised the species with one, anterior ovary and without isolated vulval chamber. *Filipjevella* was synonymised with *Diplogasteritus*. Andrássy included the following 23 species in *Diplogasteritus*: *D. nudicapitatus* (Steiner, 1914) (type species), *D. angustilaimus* (Sch. Stekhoven & Tenuissen, 1938), *D. aquaticus* Gagarin, 1977, *D. arcuatus* (Massey, 1962), *D. austriacus* (Fuchs, 1938), *D. brevicaudatus* (Sch. Stekhoven & Tenuissen, 1938), *D. concolor* (Massey, 1962), *D. consobrinus* (de Man, 1920), *D. dendrophilus* (Weingärtner in Körner, 1954), *D. filicaudatus* (Bütschli, 1874), *D. gubernatus* (Massey, 1974), *D. likoi* Kokordak, 1969, *D. lineatus* (Fuchs, 1915), *D. minimus* (Lasarevskaja, 1964), *D. minutus* (Kreis, 1930), *D. occidentalis* (Steiner, 1932), *D. paxi* (Paesler, 1962), *D. ponderosus* (Massey, 1962), *D. pterygatus* (Timm, 1961), *D. stoeckherti* (Völk, 1950), *D. subterraneus* (Hnatewytch, 1929), *D. superbus* (Paesler, 1946), and *D. taedus* (Massey, 1962). Andrássy demonstrated that most of the described species of *Diplogasteritus* are very similar in morphological characters and very difficult to distinguish. He suspected that the majority of nominal species are synonyms.

We considered the morphological characteristics of species of the genus *Diplogasteritus* using the published data (Paramonov, 1952; Weingärtner, 1955; Meyl, 1960; Massey, 1962; Andrássy, 1984; and others) and the extensive original material of *D. primitivus* sp. n., *D. dendrophilus* (Weingärtner in Körner, 1954), and *D. nudicapitatus* (Steiner, 1914). Measurements of

species whose names are synonymised (Tables 2, 3, 6) are taken from the original descriptions.

Genus *Diplogasteritus* Paramonov, 1952

= *Filipjevella* Lasarevskaja, 1965 (*nom. praeocc.*, non Allgen, 1935)

Type species: *Diplogaster nudicapitatus* Steiner, 1914.

Diagnosis (from Andrássy, 1984, emend.). Diplogasterinae. Body length 0.5–1.5 mm. Males shorter and slenderer than females. Cuticle thin, with fine transverse striae and 18–35 (usually 24–28) longitudinal ridges stretching from head to tail base. Anterior end of body tapered. Labio-tuberculus flattened, armed with six setiform labial papillae arranged around oral opening. In males, four additional cephalic setae situated behind labial papillae. Stoma in the shape of thin tube; its length usually 2–3 times its width. Cheilo- and promesostoma distinct, telostoma small, funnel-shaped. Cheilostoma with curved ribs. Dorsal tubercle of metastoma armed with large or small dorsal tooth. Two smaller subventral teeth situated behind dorsal tooth. Anterior section of oesophagus always longer than its posterior section. Amphid opening situated at the level of stoma. Female gonads paired; ovaries antidromous, their bends reaching vulva. Vulva in the shape of transverse ellipsoidal slit, pre- or equatorial. Uterus with characteristic isolated chamber situated opposite to vulva (vulval chamber). Testis simple, bent. Spicules free, sometimes with velum. Gubernaculum large, trough-shaped; its apex often armed with spines, branches or "cuff". Males with 8–10 pairs of genital setiform papillae and rudimental bursa. In both sexes, tail similar in shape and length, long and filiform. Free-living nematodes, usually inhabiting saprobic habitats.

Diplogasteritus primitivus sp. n.

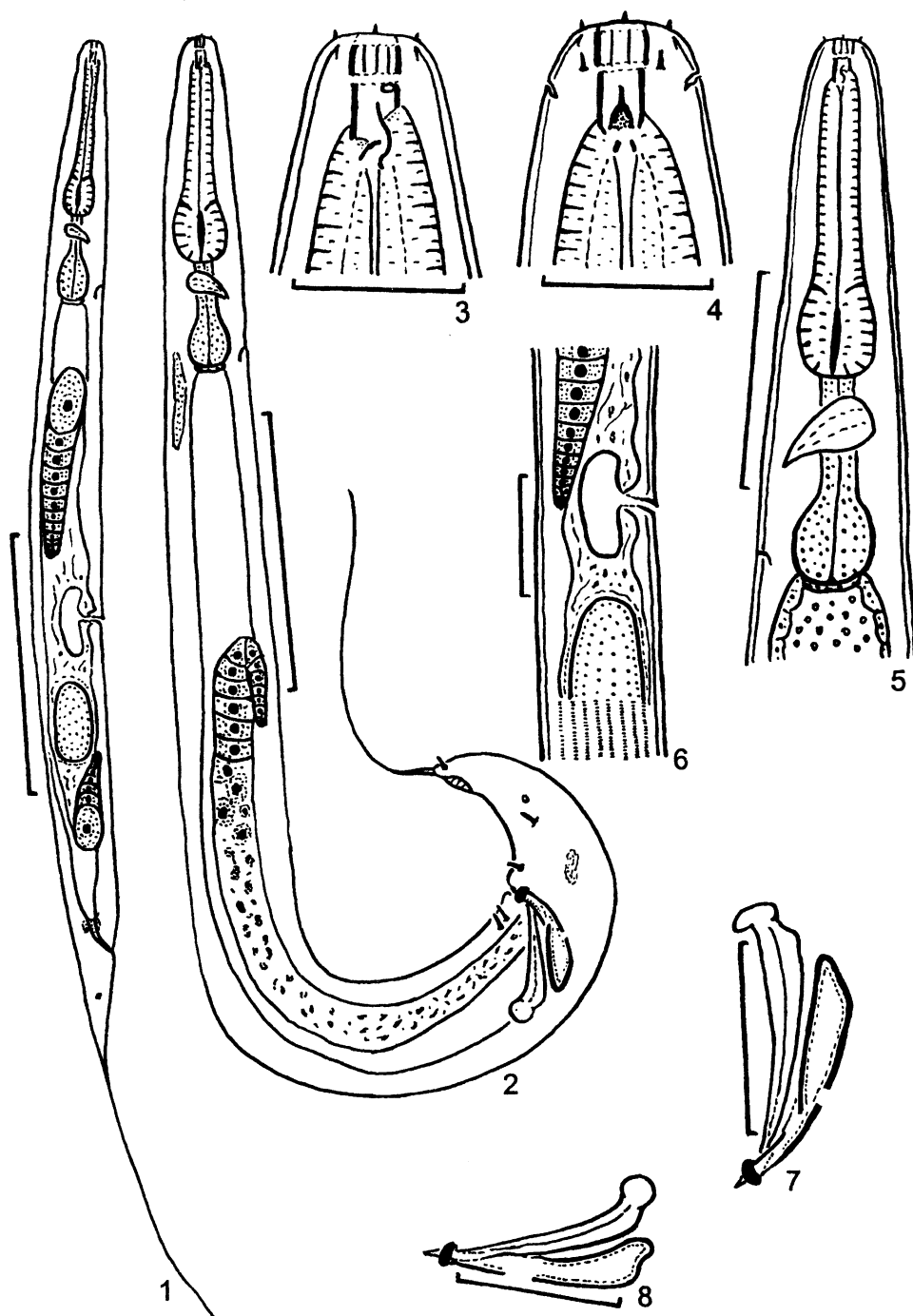
(Figs 1–8)

Holotype. ♂, **Russia**, Yaroslavl Prov., settlement Borok, rotten potato, 28.VI.1995, slide No. 3/1, Institute of Inland Waters Biology, Russian Academy of Sciences.

Paratypes. 10 ♀, 11 ♂, collected with the holotype, slide No. 4/1; 5 ♀, 8 ♂, collected from rotten potato, 9.V.1997.

Measurements. Holotype ♂: L = 715 µm, a = 21, b = 5.4, c = 4.8, c' = 4.8, spicules length 36 µm. Paratypes: see Table 1.

Description. **Female**. Body small; tail long. Cuticle thin, with fine transverse striation and 24–27 longitudinal ridges. Each ridge appearing as a pair of short lines. Anterior end of body tapered. Head flattened anteriorly. Lips absent. Six setiform labial papillae, about 6 µm long, arranged around



Figs 1-8. *Diplogasteritus primitivus* sp. n. 1, habitus of female; 2, habitus of male; 3, female head in ventral view; 4, male head in lateral view; 5, oesophagus of female; 6, vulva area; 7, 8, spicule and gubernaculum. Scales: 150 μ m (1), 100 μ m (2), 50 μ m (5, 6), 25 μ m (7, 8), 15 μ m (3, 4).

Table 1. Measurements of *Diplogasterius primitivus* sp. n.

Character	Decaying potatoes, 28.VI.1995				Decaying potatoes, 9.V.1997			
	females (n = 10)		males (n = 11)		females (n = 5)		males (n = 8)	
	range	mean	range	mean	range	mean	range	mean
L, μm	601-875	714	540-781	671	556-867	693	544-648	594
a	12-17	15	16-22	19	17-22	20	21-27	24
b	4.8-6.7	5.7	4.6-5.9	5.3	4.7-6.4	5.6	4.9-5.9	5.2
c	3.4-4.9	4.1	4.1-5.8	5.0	3.3-4.4	3.9	4.0-5.7	4.8
c'	6.3-10.2	8.0	4.0-5.8	5.0	9.7-11.8	10.4	4.8-6.5	5.6
V	44.2-50.0	46.6	—	—	45.0-49.8	46.5	—	—
Oesophagus length, μm	109-130	124	106-147	127	119-136	124	109-121	114
Posterior end of oesophagus – vulva, μm	171-280	208	—	—	158-259	197	—	—
Vulva – anus, μm	150-269	203	—	—	161-255	191	—	—
Posterior end of oesophagus – cloaca, μm	—	—	308-504	411	—	—	297-409	354
Tail length, μm	143-220	178	115-157	134	182-217	181	112-136	126
Head width, μm	8.0-9.0	8.5	7.5-8.5	8.0	9.0-10.0	10.0	8.0-10.0	9.0
Stoma length, μm	9.5-10.5	10.0	8.5-9.5	8.5	9.5-11.5	11.0	9.0-11.0	10.0
Stoma length : head width	1.1-1.3	1.2	1.0-1.2	1.1	1.1-1.2	1.1	1.1-1.2	1.1
Anterior section of oesophagus : posterior section of oesophagus	1.4-1.8	1.7	1.3-1.6	1.5	1.6-2.0	1.8	1.4-1.8	1.6
Tail : vulva – anus	0.7-1.1	0.9	—	—	0.8-1.2	0.9	—	—
Spicula length, μm	—	—	33-40	37	—	—	33-39	36
Gubernaculum length, μm	—	—	30-35	34	—	—	27-30	28
Spicula : gubernaculum	—	—	1.1-1.2	1.1	—	—	1.2-1.4	1.3

oral opening. Stoma narrow and long. Ribs of cheilorhabdions distinctly visible. Length of dorsal promesorhabdion equal to that of cheilorhabdions; subventral promesorhabdions about twice as long as cheilorhabdions. Dorsal tubercle of metastoma comparatively large, with tooth on S-shaped curved plate. Two small subventral teeth situated considerably posterior to dorsal ones. Telostoma shallow. Amphid opening small, ellipsoidal, situated at the level of promesostoma. Width of body at proximal end of oesophagus 4-5 times the head diameter. Oesophagus slender. Anterior section of oesophagus 1.4-2.0 times as long as its posterior section. Excretory pore situated at the level of basal end of oesophagus. Cardia narrow, muscular. Female gonads paired; ovaries antidromous. Ovarial bends long, reaching vulva. Vulva preequatorial, in the shape of ellipsoidal slit. Vulval lips cuticularised, often protruded, with anterior lip being longer and covering genital pore. Vagina comparatively long, occupying about 1/3 of body diameter. Isolated chamber opposite to vulva, its length equal to or less than corresponding body diameter. In uterus, usually 1-2 eggs, 62-64 × 30-32 µm in size. Rectum about 1.5 times as long as anal diameter; rectal glands well developed. Tail long, strongly tapered at base, thereupon thin and filiform.

Male. General appearance similar to that of female, size smaller. Head armed with four supplementary setae 1.5 µm long situated a little caudal to six labial setiform papillae. Structure of stoma and oesophagus similar to those of female. Amphid opening in the shape of small transverse ellipse, situated at the level of anterior end of promesostoma. Testis simple, bent. Spicules slender, ventrally curved, with rounded heads; their apices pointed. Gubernaculum characteristic in shape and shorter than spicules. Basal part of gubernaculum with processes, its dorsal wall partially without sclerotisation. Processus narrowed to apex and with sclerotised ring ("cuff") at tip. Genital papillae setiform, a total of 8 pairs: 2 pairs precloacal, 6 pairs postcloacal, and 3 pairs as a part of rudimentary bursa. Tail similar to that of females, long and filiform.

Comparison. The new species differs from all species of the genus in two characters: S-like shape of dorsal metastomal tooth and presence of sclerotised ring, "cuff", at apical end of gubernaculum.

Etymology. The species name means "simply organised", "primitive".

***Diplogasteritus occidentalis* (Steiner, 1932)** (Figs 39-46)

occidentalis Steiner, 1932: 439, fig. 1-3 (*Diplogaster*);
Paramonov, 1952: 348 (*Diplogasteritus*).

austriacus Fuchs, 1938: 165, fig. 161-173 (*Diplogaster consobrinus* var.), **syn. n.**; Körner, 1954: 320 [*Diplogaster (Diplogaster)*]; Paramonov, 1952: 348 (*Diplogasteritus*).
concolor Massey, 1962: 70, fig. 2, D-F (*Acrostichus*), **syn. n.**; Lasarevskaja, 1965: 66 (*Filipjevella*);
Andrássy, 1984: 385 (*Diplogasteritus*).

Measurements. See Table 2.

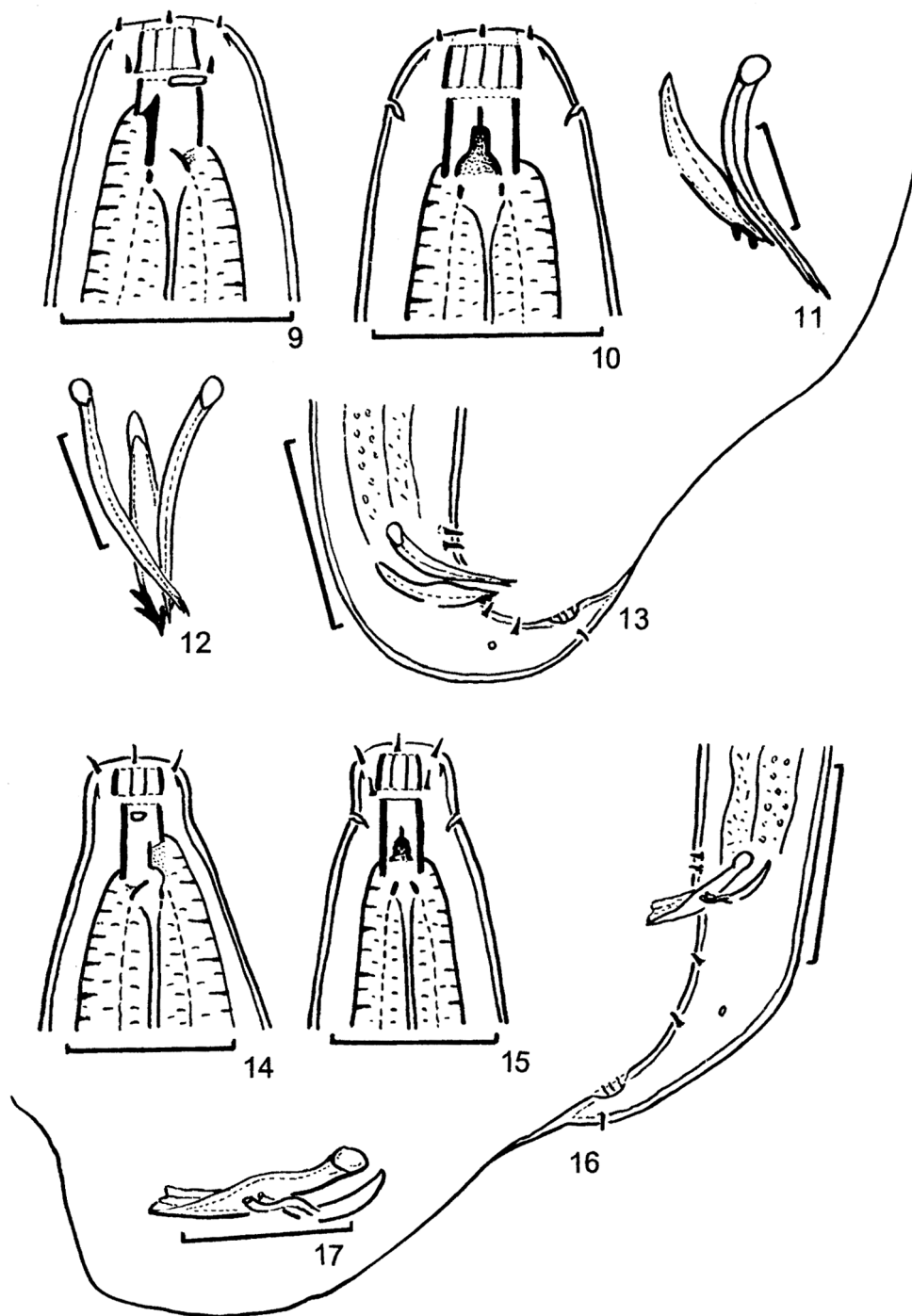
Description (generalised data). Cuticle with longitudinal ridges. Anterior end of body tapered; head 8-9 µm wide. Stoma in the shape of thin tube, 9-12 µm long. Cheilorhabdions as long as promesorhabdions or slightly shorter. Stoma armed with small dorsal tooth and two smaller subventral teeth. Anterior section of oesophagus 1.7-2.0 times as long as its posterior section. Female gonads paired; bends reaching vulva. Vulval isolated chamber present. Tail similar in both sexes, long and filiform, equal to or only slightly shorter than distance between vulva and anus, 5-15 times as long as anal diameter. Spicules slender, 25-35 µm long, with heads, with small velum at distal end. Gubernaculum large, trough-shaped, as long as spicules or slightly shorter; its apex armed with 1-2 pairs of spines.

Distinguishing characters of *D. austriacus*: dorsal tooth small, cheilorhabdions as long as promesorhabdions or slightly shorter; spicules slender, arcuate, with small velum; gubernaculum large, as long as spicules or slightly shorter, with 1-2 pairs of spines at apex.

Remarks. The species was collected from detritus of decomposing wood in USA, Germany and Austria (Andrássy, 1984) and from galleries of bark beetle in USA (Massey, 1962). In Russia, it was found in soil of warm-house for true mushrooms (Sumenkova, 1965) and detritus of decomposing wood (Gagarin, 1999).

Discussion. *D. austriacus* (Fuchs, 1938) was described from numerous females and males, collected from decaying wood in Germany (Fuchs, 1938). The species is described and illustrated quite well. Spicules are thin, arcuate; gubernaculum is massive, its apex armed with two pairs of spines. Afterwards this species was redescribed and reillustrated very well by Weingärtner (1955) from numerous females, males and larvae. This species is not distinguished morphologically from *D. occidentalis* (Steiner, 1932). We consider *D. austriacus* (Fuchs, 1938) as a synonym of *D. occidentalis* (Steiner, 1932).

D. concolor (Massey, 1962) was described from one mature female and one mature male, which were collected from galleries of bark beetle on *Abies concolor* (Gord. & Glend.) in New Mexico, USA. The species is described rather briefly. The structure of stoma (cheilorhabdions as long as promesorhabdions, small dorsal tooth)



Figs 9-17. 9-12, *Diplogasteritus dendrophilus* (original): 9, female head in ventral view; 10, male head in lateral view; 11, male tail; 12, spicule and gubernaculum. 13-17, *D. nudicapitatus* (original): 13, male head in ventral view; 14, female head in lateral view; 15, 16, spicules and gubernaculum; 17, male tail. Scales: 50 μ m (17), 30 μ m (11, 15, 16), 15 μ m (12-14), 10 μ m (9, 10).

Table 2. Measurements of *Diplogasteritus occidentalis* and its new synonyms.

Character	<i>D. occidentalis</i>		<i>D. austriacus</i>		<i>D. concolor</i>	
	females	males	females	males	females	males
L, μm	630-640	430-600	630-1120	660-840	530	500
a	24-25	20-27	23-34	27-35	14	16
b	5.5-5.9	5.2-6.3	6.0-8.1	5.2-7.0	5.0	4.0
c	4.0-4.2	5.0-5.3	2.3-5.1	4.3-6.5	3.7	5.7
c'	8.6-11.1	5.2-6.1	7-15	—	6.8	3.7
V	46-48	—	39-49	—	47	—
Head width, μm	8-9	8	8-9	8	9	—
Stoma length, μm	9	9	9-10	9	12	—
Anterior section of oesophagus : posterior section of oesophagus	1.7	—	1.7	—	2.0	—
Tail : vulva – anus	1.0	—	0.9-1.0	—	1.0	—
Spicula length, μm	—	25	—	27-35	—	25
Gubernaculum, μm	—	23	—	25-34	—	25

and structure of male genitalia (thin and almost straight spicules, apex of gubernaculum armed with one pair of spines) correspond to those of *D. occidentalis* (Steiner, 1932). We consider *D. concolor* (Massey, 1962) as a synonym of *D. occidentalis* (Steiner, 1932).

***Diplogasteritus lineatus* (Fuchs, 1915)** (Figs 32-38)

lineatus Fuchs, 1915: 199, fig. 74-78 (*Diplogaster*); Micoletzky, 1921: 410 [*Diplogaster (Fuchsia)*]; Körner, 1954: 320 [*Diplogaster (Diplogaster)*]; Paramonov, 1952: 348 (*Fuchsia*); Meyl, 1960: 27, fig. 116 a-e (*Diplogasteritus*).

consobrinus de Man, 1920: 47, fig. 1-10 (*Diplogaster*), **syn. n.**; Paramonov, 1952: 348 (*Diplogasteritus*); Körner, 1954: 320 [*Diplogaster (Diplogaster)*]; Meyl, 1960: 28, fig. 121 a-e (*Diplogastrellus*).

angustilaimus Sch. Stekhoven & Tenuissen, 1938: 34, fig. 15 (*Diplogaster*), **syn. n.**; Goodey, 1963: 173 (*Diplogasteritus*).

stoeckerti Völkl, 1950: 61, fig. 25 (*Diplogaster*), **syn. n.**; Paramonov & Sobolev in Skryabin et al., 1954: 210 (*Diplogasteritus*); Weingärtner, 1955: 287 [*Diplogaster (Diplogaster)*].

taedus Massey, 1962: 68, fig. 1 E-H (*Acrostichus*), **syn. n.**; Lasarevskaja, 1965: 65 (*Filipjevella*); Andrassy, 1984: 387 (*Diplogasteritus*).

likoi Kokordak, 1969: 126, fig. 7-12 (*Diplogasteritus*), **syn. n.**

Measurements. See Table 3.

Description (generalised data). Cuticle with longitudinal ridges. Head 8-11 μm wide. Stoma in the shape of thin tube, 9-13 μm long. Cheilostoma with thin ribs. Cheilorhabdions longer than promesorhabdions. Dorsal tooth comparatively small; subventral teeth small, hardly visible. Anterior section of oesophagus 1.4-2.0 times as long as its posterior section. Female gonads paired, bent. Vulval isolated chamber comparatively small. Tail similar in both sexes, long and filiform; in females, tail shorter than distance between vulva and anus, 7-8 times as long as anal diameter. Spicules 27-42 μm long, thin and arcuate, with heads. Gubernaculum large, trough-shaped, its apex pointed, smooth, without spines and "cuff".

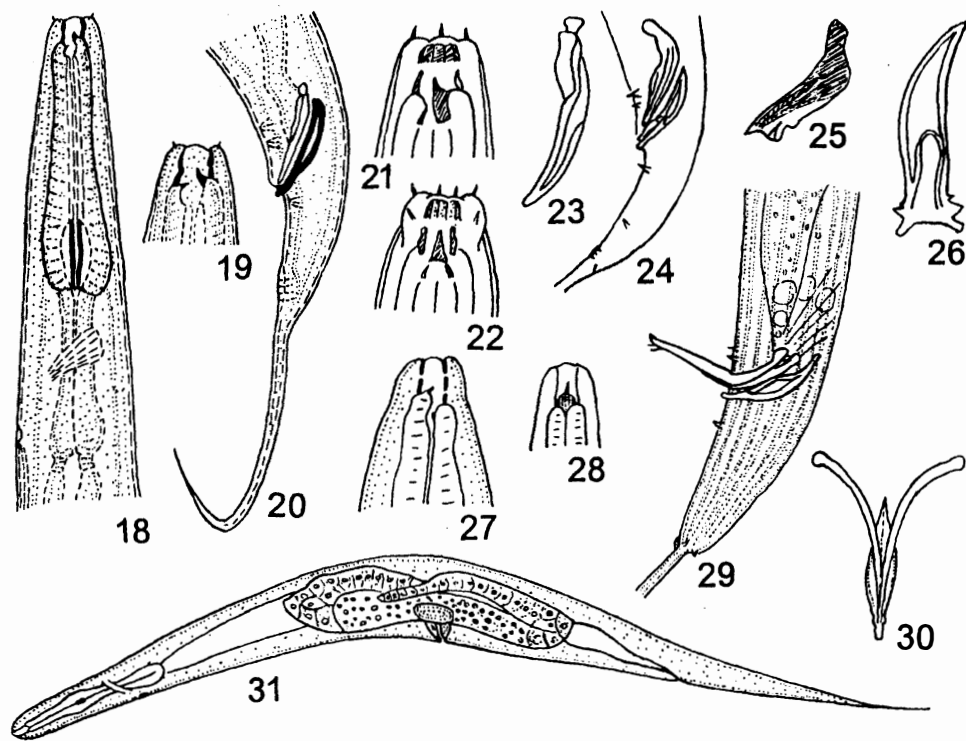
Distinguishing characters of *D. lineatus*: dorsal tooth comparatively small, cheilorhabdions longer than promesorhabdions; spicules thin and arcuate, without velum, their distal ends pointed; apex of gubernaculum smooth, without spines and "cuff".

Remarks. The species was collected from slimy flux of trees and soil (Germany, Netherlands, Hungary, Zaire), from decaying wood and from galleries of bark beetle (Germany and USA) and sewage disposal plant (Czechoslovakia). In Russia, it was found in soil of Prioksko-Terrasnyi Nature Reserve (Solovjeva, 1986).

Discussion. *D. consobrinus* (de Man, 1920) was

Table 3. Measurements of *Diplogasteritus lineatus* and its new synonyms.

Character	<i>D. lineatus</i>		<i>D. consobrinus</i>		<i>D. angustilaimus</i>		<i>D. stoeckerti</i>		<i>D. taedus</i>		<i>D. likoi</i>	
	females	males	females	males	females	males	females	males	females	males	females	males
L, μm	800-1080	650-700	660-920	560-720	579	540-628	624-752	551-625	630	550	605-802	780-863
a	18-22	19-27	21-24	26-30	19	20	19-23	20-23	15	18	15-20	25-26
b	6-7	4.5-5.7	4.7-5.8	4.8-5.3	5.6	6.3	5.5-6.6	5.5-6.0	5.4	4.4	5-6	6.3-6.4
c	3.5-4.6	4.6-5.0	3.4-4.9	4.1-5.5	6.2	4.2	3.3-3.8	4.4-5.1	3.6	5.5	2.7-3.5	4.1-4.2
c'	7.8	4.7	7.8	—	4.4	5.9	8.2	—	—	—	—	7.7
V	44-49	—	43-49	—	49.7	—	45-48	—	4.3	—	42.4-50.7	—
Head width, μm	10-12	—	11	—	8	9	8-9	—	8	—	10	—
Stoma length, μm	10-12	—	13	—	10	—	9-10	—	10	—	10	—
Anterior section of oesophagus : posterior section of oesophagus	1.8-2.0	—	1.7	—	—	—	1.9	—	1.6	—	1.4	—
Tail : vulva – anus	0.9	—	0.7-0.9	—	0.5	—	0.9-1.1	—	0.8	—	1.2-1.7	—
Spicula length, μm	—	38	—	36-42	—	28	—	27-29	—	36	—	36-38
Gubernaculum, μm	—	29	—	32-40	—	25	—	19-22	—	23	—	21-28



Figs 18-31. 18-20. *Diplogasteritus gubernatus* (from Massey, 1974): 18, oesophagus of female; 19, female head in ventral view; 20, male tail. 21-26, *D. superbus* (from Weingärtner, 1955): 21, female head in ventral view; 22, male head in lateral view; 23, 26, gubernaculum; 24, male tail; 25, spicule. 27-31, *D. minimus* (from Lasarevskaja, 1964): 27, female head in ventral view; 28, female head in lateral view; 29, male tail; 30, spicules and gubernaculum; 31, general view of female.

described from numerous females and males collected from slime flux of trees in the Netherlands (de Man, 1920). Afterwards, this species was redescribed and reillustrated very well by Weingärtner (1955) from numerous females, males and larvae. Spicules are thin and arcuate, without velum; apex of gubernaculum is smooth, without spines and "cuff". Morphological characters, distinguishing this species from *D. lineatus* (Fuchs, 1920), are not found. We consider *D. consobrinus* (de Man, 1920) as a synonym of *D. lineatus* (Fuchs, 1915).

D. angustilaimus (Sch. Stekhoven & Tenuissen, 1938) was described from 4 males and 2 females collected from bottom sediments of a river and 14 males and 2 females from soil surface in Zaire. The species is described and illustrated poorly. The structure of stoma and male genitalia (slender spicules, gubernaculum without spines and "cuff") correspond to those of *D. lineatus* (Fuchs, 1915). We consider *D. angustilaimus* (Sch. Stekhoven & Tenuissen, 1938) as a synonym of *D. lineatus* (Fuchs, 1915).

D. stoeckherti (Völk, 1950) was described from 5 females and 2 males collected from garden soil in Germany. The description is rather detailed. Stoma is in the shape of thin tube. Dorsal teeth are comparatively large. Spicules are thin and arcuate; gubernaculum is almost straight, its apex is smooth, without spines and "cuff". We consider *D. stoeckherti* (Völk, 1950) as a synonym of *D. lineatus* (Fuchs, 1915).

D. taedus (Massey, 1962) was described from one mature female and one mature male collected from galleries of bark beetle *Dendroctonus terebrans* Oliv. on pine, *Pinus taeda* L. in New Mexico (USA). The species is described in detail and well illustrated. Dorsal teeth are comparatively large. Gubernaculum is massive, its apex is smooth, without spines and "cuff". The species is not distinguished morphologically from *D. lineatus* (Fuchs, 1915). We consider *D. taedus* (Massey, 1962) as a synonym of *D. lineatus* (Fuchs, 1920).

D. likoi Kokordak, 1969 was described from numerous females and males collected from sew-

age disposal plant in Czechoslovakia. The species is described and illustrated rather poorly, but the structure of the male genital apparatus (distal ends of spicules smooth, without velum; apex of gubernaculum without spines and "cuff") is similar to that of *D. lineatus* (Fuchs, 1915). We consider *D. likoi* Kokordak, 1969 as a synonym of *D. lineatus* (Fuchs, 1915).

***Diplogasteritus dendrophilus* (Weingärtner in Körner, 1954)**
(Figs 9-12)

dendrophilus Weingärtner in Körner, 1954: 320 (*Diplogaster*); Weingärtner, 1955: 281, fig. 13 [*Diplogaster* (*Diplogaster*)]; Meyl, 1960: 28, fig. 122 a-e (*Diplogastrellus*); Goodey, 1963: 173 (*Diplogasteritus*).

Material examined. Russia, Yaroslavl Prov.: 10 ♀, 10 ♂, settlement Borok, horse manure, 25.V.1998; 5 ♀, 4 ♂, same locality but cow manure, 23.VI.1997.

Measurements. See Table 4.

Description. Body small; tail long. Males shorter, females slenderer. Transverse striation of cuticle absent. Cuticle with 24 longitudinal ridges in vulva area. Anterior end of body strongly tapered. Body at proximal end of oesophagus 4-6 times as wide as head. Front edge of head flattened. Lips absent. Six setiform labial papillae 2 µm long situated around oral opening. Additionally, in males, four cephalic setae about 2 µm long situated behind labial papillae. Stoma thin and long, about twice as long as head diameter. Cheilostoma with six ribs. Dorsal promesothabdion equal to or longer than cheilothabdions. Both subventral promesothabdions about twice as long as cheilothabdions. Dorsal tubercle of metastoma narrow and small, armed with small flattened tooth. Two thin flattened teeth located adjacent to each tubercle on subventral sides of metastoma. Telostoma shallow, telothabdions visible from dorsal side only. Amphid opening in the shape of narrow ellipsoid slit, situated at the level of stoma. Anterior section of oesophagus about 1.5 times as long as its posterior section. Basal bulb of anterior oesophagus section well developed, with sclerotised striation. Cardia muscular. Excretory pore situated slightly anterior to basal oesophagus end. Female gonads paired; ovaries antidiromous. Vulva preequatorial, in the shape of transverse slit. Vulval lips not protruded. Vagina comparatively long, about 1/3 of body diameter at this level. Vagina striation sclerotised. Bean-like isolated chamber opposite to vulva; its length 1.3-1.5 times the body diameter. In uterus, usually 1-2 eggs, 50-56 × 26-31 µm in size. Ovarian bends long, reaching vulva. Rectum 1.0-1.5 times as long as anal diameter; rectal glands well developed. Testis simple, bent.

Spicules massive, thick, about 1.2 times as long as cloacal diameter, with obliquely cut distal ends and with feebly marked heads. Gubernaculum small, about 1.4 times as long as spicule, consisting of two parts (basal part longer and more massive) and two S-like arcuate branches connected with inner side of basal part. Males with 8 pairs of genital papillae: 2 pairs precloacal, 6 pairs postcloacal, and 3 pairs as a part of rudimental bursa. In both sexes, tail similar in shape and length: strongly tapered at base, thereupon thin and filiform.

Remarks. The species was described from Germany, collected from slimy flux of trees (Weingärtner, 1955). It is recorded here from Russia for the first time.

***Diplogasteritus gubernatus* (Massey, 1974)**
(Figs 18-20)

gubernatus Massey, 1974: 79, fig. 49 (*Acrostichus*); Andrásy, 1984: 385 (*Diplogasteritus*).

Measurements (from Massey, 1974). ♀: L = 0.69-0.77 mm, a = 18.7-21.4, b = 6.0-6.2, c = 2.5-3.0, V = 39-43%. ♂: L = 0.57-0.59 mm, a = 18.3-24.2, b = 4.6-5.3, c = 3.9-4.3.

Description (from Massey, 1974). Cuticle with longitudinal ridges. Head 9 µm wide. Stoma comparatively wide, 10 µm long. Cheilostoma without ribs. Cheilothabdions equal to promesothabdions in length. Dorsal tooth robust, cuticularised; subventral teeth comparatively large. Anterior section of oesophagus 1.7 times as long as its posterior section. Female gonads paired, comparatively long; bends reaching vulva. Vulval isolated chamber comparatively small. Tail long, filiform, 1.5 times as long as distance between vulva and anus, 14 times as long as anal diameter. Spicules 25 µm long, slender, slightly arcuate, with heads. Gubernaculum large, slightly longer than spicules, their apices without spines and "cuff".

Distinguishing characters of *D. gubernatus*: dorsal tooth large, tail comparatively long, spicules only slightly arcuate, gubernaculum large and massive, without spines and "cuff".

Remarks. The species was found only in the USA (New Mexico) and associated with *Dendroctonus rufipennis*.

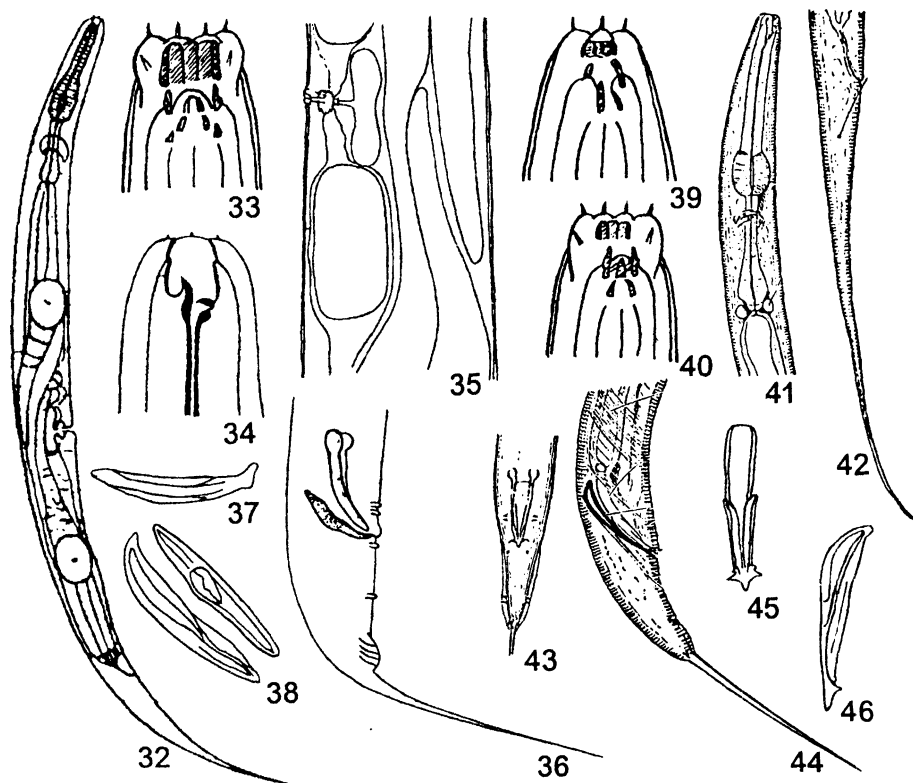
***Diplogasteritus minimus* (Lasarevskaja, 1964)**
(Figs 27-31)

minimus Lasarevskaja, 1964: 122, figs a-л (*Acrostichus*); Lasarevskaja, 1965: 63, figs a-b (*Filipjevella*); Andrásy, 1984: 386 (*Diplogasteritus*).

Measurements (from Lasarevskaja, 1964). ♀: L = 0.36-0.43 mm, a = 13-23, b = 5.1-6.2, c =

Table 4. Measurements of *Diplogasteritus dendrophilus*.

Character	Horse manure, 25.V.1998				Cow manure, 23.VI.1997			
	females (n = 10)		males (n = 10)		females (n = 5)		males (n = 4)	
	range	mean	range	mean	range	mean	range	mean
<i>L</i> , μm	551-676	625	496-657	556	711-829	760	561-616	582
a	20-26	24	21-27	24	22-28	26	23-32	27
b	5.5-6.7	6.0	5.5-6.7	6.0	7.0-8.2	7.6	5.7-6.5	6.2
c	2.3-3.0	2.4	2.4-3.2	2.8	1.9-2.2	2.1	2.4-2.7	2.5
c'	17.0-21.0	18.9	10.0-15.5	12.5	20.9-31.0	25.3	15.0-17.2	16.2
V	32.5-38.0	36.1	—	—	29.1-33.8	32.0	—	—
Oesophagus length, μm	92-112	104	91-98	93	97-102	100	91-99	95
Posterior end of oesophagus – vulva, μm	87-144	123	—	—	136-154	142	—	—
Vulva – anus, μm	116-154	136	—	—	137-168	151	—	—
Posterior end of oesophagus – cloaca, μm	—	—	213-353	261	—	—	238-269	253
Tail length, μm	238-294	262	178-238	202	322-434	367	210-252	234
Head width, μm	5.0-5.5	5.5	5.0-5.5	5.0	4.5-5.0	5.0	5.0	5.0
Stoma length, μm	10-11	11	10-11	11	11-12	12.0	10-11	11
Stoma length : head width	1.7-2.4	2.0	1.8-2.2	2.0	2.2-2.4	2.4	1.9-2.0	2.0
Anterior section of oesophagus : posterior section of oesophagus	1.4-1.6	1.5	1.5-1.6	1.6	1.5-1.7	1.6	1.4-1.6	1.5
Tail : vulva – anus	1.6-2.3	2.0	—	—	2.1-2.8	2.5	—	—
Spicula length, μm	—	—	20-22	21	—	—	21-22	22
Gubernaculum length, μm	—	—	14-17	15	—	—	16-17	17
Spicula : gubernaculum	—	—	1.2-1.5	1.4	—	—	1.2-1.3	1.3



Figs 32-46. 32-38, *Diplogasteritus lineatus* (32, 35, 36 from Fuchs, 1915; 33, 34, 37, 38 from Weingärtner, 1955): 32, habitus of female; 33, female head in lateral view; 34, female head in ventral view; 35, vulva area; 36, male tail; 37, spicule; 38, gubernaculi. 36-46, *Diplogasteritus occidentalis* (39, 40, 45, 46 from Weingärtner, 1955; 41-44 from Steiner, 1932): 39, female head in ventral view; 40, female head in lateral view; 41, oesophagus of female; 42, female tail; 43, cloaca area in lateral view; 44, male tail; 45, 46, gubernaculum.

2.6-4.8, V = 40-52%. ♂: L = 0.29-0.44 mm, a = 15-19, b = 4.4-5.6, c = 3.4-6.2.

Description (from Lasarevskaja, 1964). Cuticle with distinct longitudinal ridges. Anterior end of body tapered. Head about 9 µm wide. Stoma in the shape of thin tube, 7-19 µm long; cheilostoma without ribs. Cheilorhabdions as long as promesorhabdions or slightly shorter. Dorsal tooth comparatively small; subventral teeth hardly visible. Anterior section of oesophagus 1.4 times as long as its posterior section. Female gonads paired; bends reaching vulva. Vulval isolated chamber small. Tail similar in both sexes, long and filiform, as long as distance between vulva and anus or slightly shorter. Spicules 23-25 µm long, slender and arcuate, with heads and without velum. Gubernaculum large, trough-shaped, slightly longer than spicules; its apex with two pairs of spines.

Distinguishing characters of *D. minimus*: body comparatively small; cheilostoma without ribs,

dorsal tooth small; spicules thin and arcuate; gubernaculum comparatively large, its apex armed with two pairs of spines.

Remarks. This species was found in galleries of long-horned beetle, *Acanthocinus aedilis*, in Orenburg Prov. (Russia) (Lasarevskaja, 1964).

***Diplogasteritus nudicapitatus* (Steiner, 1914)** (Figs 14-17)

?*parvus* Cobb, 1893: 273, fig. 3 (*Diplogaster*).

?*intermedius* Cobb, 1906: 186, fig. 5 (*Diplogaster*).

nudicapitatus Steiner, 1914: 424, fig. 8-9 (*Diplogaster*);

Hirschmann, 1952: 325 [*Diplogaster* (*Diplogaster*)];

Paramonov, 1952: 348 (*Diplogasteritus*).

rhodani Stefanski, 1914: 62, fig. 14 (*Diplogaster*);

Paramonov, 1952: 348 (*Diplogasteritus*).

ponderosus Massey, 1962: 68, fig. 1 A-D (*Acrostichus*),

syn. n.; Lasarevskaja, 1965: 65, figs ♀, 3 (*Filipjevella*);

Andrássy, 1984: 386 (*Diplogasteritus*).

aquaticus Gagarin, 1977: 1247, fig. 3 (*Diplogasteritus*), **syn. n.**

Material examined. Russia, Yaroslavl Prov.: 10 ♀, 8 ♂, settlement Borok, sewage disposal sites, 27.VIII.1994; 10 ♀, 10 ♂, horse manure and goat manure, 12.VI.1995.

Measurements. See Tables 5 and 6.

Description. Size small; tail long. Males shorter, females slenderer. Cuticle thin, transversely striate, with longitudinal ridges, 24-26 such ridges in the vulva area. Front edge of head flattened. Six small and thin setiform labial papillae 0.5-0.7 µm long arranged around oral opening. In males, four additional setae about 1.0-1.3 µm long situated behind labial papillae. Head 7-9 µm wide. Body at the level of proximal end of oesophagus 4-5 times as wide as head. Length of stoma only slightly exceeding head diameter. Cheilostoma with six cuticularised curved ribs. Dorsal promesorhabdion equal in length to cheilorhabdions; subventral promesorhabdions about twice as long as dorsal promesorhabdion. Dorsal tubercle of metastoma large; its inner edge armed with comparatively large, sclerotised, stick-like tooth. Two smaller subventral teeth situated behind dorsal tooth. Telostoma shallow, feebly marked. Amphid opening in the shape of narrow ellipsoidal slit, situated at the level of dorsal tubercle of metastoma. Oesophagus slender; anterior muscular section of oesophagus 1.5-2.0 times as long as its posterior glandular section. Cardia thin, muscular. Female gonads paired; ovaries antidromous. Vulva in the shape of transverse slit. Vulval lips cuticularised, often protruded. Vagina long, about 1/3 of corresponding body diameter. Bean-like isolated chamber opposite to vulva; its length equal to or slightly less than body diameter at midbody. Ovaries long, bends often reaching vulva. In uterus, usually 1-2 eggs, 50-63 × 25-36 µm in size. Rectal glands well developed. Testis simple, bent. Spicules slender, sickle-like, with large heads and thin dorsal appendix. Gubernaculum about 0.9 times as long as spicules, semilunar in shape, its dorsal wall partially without sclerotisation, apex armed with two pairs of spines. In males, 8 pairs of long genital papillae: 2 pairs precloacal and 6 pairs postcloacal. In both sexes, tail similar in shape and length, strongly tapered at base, thereupon thin and filiform.

Remarks. The species is widely spread, occurs in saprobic conditions (Andrássy, 1984). In Russia, it was found in soils of South Karelia and Prioksko-Terrasnyi Nature Reserve, Moscow Prov. (Solovjeva et al., 1976; Solovjeva, 1986), polysaprobic water bodies (Gagarin, 1977, 1995), manure, compost (Gagarin, 2000), and rotten potatoes (Gagarin, unpublished).

Discussion. *D. ponderosus* (Massey, 1962) was described from one female and one male collected from galleries of bark beetle *Ips ponderosae* Sw. on western yellow pine, *Pinus pondero-*

sa, in New Mexico (USA). The species is described briefly. The stoma is in the shape of thin and long tube. Spicules are thin and strongly arcuate. Gubernaculum is shorter than spicules, its apex armed with two pairs of spines. This species is not distinguished morphologically from *D. nudicapitatus*. We consider *D. ponderosus* (Massey, 1962) as a synonym of *D. nudicapitatus* (Steiner, 1914).

D. aquaticus Gagarin, 1977 was described from 1 ♂ and 5 ♀ collected in sewage canal in Podolsk (Moscow Prov., Russia) and in plant stands of sewage canal in Zhigulevsk (Samara Prov., Russia). Morphological characters of this species lie in the range of morphological variability of *D. nudicapitatus* (Steiner, 1932). We consider *D. aquaticus* Gagarin, 1977 as a synonym of *D. nudicapitatus* (Steiner, 1932).

***Diplogasteritus superbus* (Paesler, 1946) (Figs 21-26)**

superbus Paesler, 1946: 118, fig. 10 (*Diplogaster*); Hirschmann, 1952: 397 [*Diplogaster* (*Diplogaster*)]; Paramonov, 1952: 348 (*Diplogasteritus*).

Measurements (from Weingartner, 1955). ♀: L = 0.59-1.06 mm, a = 20.0-24.4, b = 4.8-7.2, c = 3.4-6.4, V = 38-51%. ♂: L = 0.61-0.97 mm, a = 25.5-30.2, b = 5.2-6.9, c = 4.0-5.3.

Description (from Weingartner, 1955). Cuticle with longitudinal ridges. Head 32-35 µm wide. Labial papillae setiform, comparatively long. Cheilostoma with ribs. Cheilorhabdions only slightly shorter than promesorhabdions. Dorsal tooth large, subventral teeth small. Stoma 35 µm long. Anterior section of oesophagus 1.4 times as long as its posterior section. Female gonads paired, bent. Vulval isolated chamber small. Tail long and filiform; in females, tail shorter than distance between vulva and anus, 7-8 times as long as anal diameter. Spicules massive, strongly arcuate, 34-37 µm long, armed with wide velum at distal end. Gubernaculum shorter than spicules, its apex with two pairs of strong spines.

Distinguishing characters of *D. superbus*: dorsal tooth large, promesorhabdions only slightly longer than cheilorhabdions; spicules massive and strongly arcuate, with wide velum; gubernaculum shorter than spicules, its apex armed with two strong spines.

Remarks. The species is known from many localities with saprobic conditions in Germany, Italy and Poland (Andrássy, 1984). In Russia, it was found only in soil of Prioksko-Terrasnyi Nature Reserve (Solovjeva, 1986).

Table 5. Measurements of *Diplogasteritus nudicapitatus*.

Character	Sewage, 27.VIII.1994				Cow manure, 2.VI.1995			
	females (n = 10)		males (n = 8)		females (n = 10)		males (n = 10)	
	range	mean	range	mean	range	mean	range	mean
L, μm	741-938	810	650-780	707	610-736	674	487-575	536
a	19-22	21	18-25	22	16-20	18	16-22	19
b	5.4-6.4	5.9	5.1-5.7	5.4	5.7-6.8	6.2	5.2-6.3	5.6
c	2.9-3.4	3.2	3.4-4.2	3.8	2.4-2.9	2.6	2.6-3.2	3.0
c'	11.5-15.4	13.5	7.1-9.4	8.2	10.9-13.8	12.5	7.6-11.0	8.9
V	39.2-44.3	41.4	—	—	36.2-38.8	37.4	—	—
Oesophagus length, μm	126-147	138	122-137	130	102-118	109	90-109	97
Posterior end of oesophagus – vulva, μm	150-248	194	—	—	119-168	143	—	—
Vulva – anus, μm	170-270	221	—	—	134-182	160	—	—
Posterior end of oesophagus – cloaca, μm	—	—	336-448	394	—	—	234-287	258
Tail length, μm	238-287	257	168-210	183	240-281	262	161-217	181
Head width, μm	8.5-10.0	9.0	8.0-10.0	8.5	8.5-9.5	8.5	7.0-8.5	7.0
Stoma length, μm	8.5-11.0	10.0	8.5-10.0	9.0	8.5-10.0	9.0	8.0-9.0	8.5
Stoma length : head width	1.0-1.3	1.1	1.0-1.3	1.1	1.0-1.3	1.1	1.0-1.2	1.1
Anterior section of oesophagus : posterior section of oesophagus	1.6-2.0	1.8	1.7-2.0	1.9	1.7-2.0	1.9	1.6-2.0	1.8
Tail : vulva – anus	0.9-1.4	1.2	—	—	1.3-1.9	1.7	—	—
Spicula length, μm	—	—	35-39	38	—	—	32-36	34
Gubernaculum length, μm	—	—	28-31	29	—	—	22-28	25
Spicula : gubernaculum	—	—	1.2-1.4	1.3	—	—	1.3-1.5	1.4

Table 6. Measurements of *Diplogasteritus nudicapitatus* and its new synonyms.

Character	<i>D. nudicapitatus</i>		<i>D. ponderosus</i>		<i>D. aquaticus</i>	
	females	males	females	males	females	males
L, μm	540-1260	470-920	600	400	630-908	635-771
a	21-27	22-31	16	15	17-23	20-26
b	5.4-8.8	5.9-7.6	7	5	5.2-7.0	5.2-6.4
c	2.9-4.3	3.3-5.6	3	5	3.5-4.3	4.3-6.0
c'	—	—	—	—	10	5-7
V	39-41	—	48	—	43-48	—
Head width, μm	8-9	—	10	10	6	6
Stoma length, μm	9-10	—	10	10	5-6	5-6
Anterior section of oesophagus : posterior section of oesophagus	1.7	—	1.6	—	1.8-1.9	1.9
Tail : vulva – anus	0.9	—	1.8	—	0.9	—
Spicula length, μm	—	34-35	—	31	—	27-32
Gubernaculum length, μm	—	30	—	22	—	26-28

Species inquirendae

Diplogasteritus arcuatus (Massey, 1962). The species was described from one mature female collected from galleries of the black turpentine beetle, *Dendroctonus terebrans* Oliv., on loblolly pine, *Pinus taeda* L., near Lake City, Florida (USA). The species is described rather briefly; many important morphological characters are not given; male is not described. We consider *D. arcuatus* (Massey, 1962) to be a *species inquirenda*.

Diplogasteritus brevicaudatus (Sch. Stekhoven & Tenuissen, 1938). The species was described from 17 males, 2 females and 3 juveniles collected at soil in Zair. The morphological description of female is absent, that of male is rather detailed. Cheilorhabdions are not separated from promesorhabdions at the presented illustrations; vulval isolated chamber is not mentioned; structure of gubernaculum is characteristic: its proximal end claw-like; tail very short. We consider *D. brevicaudatus* (Sch. Stekhoven & Tenuissen, 1938) to be a *species inquirenda*.

Diplogasteritus filicaudatus (Bütschli, 1874). The species was described from numerous females collected from decaying wood in Germany (Bütschli, 1874). Males were not found. The species is described and illustrated poorly and is considered here to be a *species inquirenda*.

Diplogasteritus minutus (Kreis, 1930). The species was described from a single male collected from a pond in China. The description is brief and poorly illustrated. The genital appara-

tus of male is described insufficiently. We consider *D. minutus* (Kreis, 1930) to be a *species inquirenda*.

Species incertae sedis

Diplogasteritus paxi (Paesler, 1962). The species was described from five mature females and five mature males collected from decaying wood in Germany. The species has a distinctive construction of stoma, which is deep and wide, separated into three sections, and with one large dorsal and two subventral teeth. Gubernaculum is almost equal to spicules in length and characteristic in shape, which differs from those of all other species of *Diplogasteritus*. We consider *D. paxi* (Paesler, 1962) to be a *species incertae sedis*.

Diplogasteritus pterygatus (Timm, 1961). The species was described from numerous females and males collected from decaying banana inflorescence in Bangladesh. The description is detailed and well illustrated. However, some morphological features of this species (presence of cuticle ornamentation, structure of stoma, arrangement of stomal teeth, and absence of vulval isolated chamber) do not correspond to the diagnosis of the genus *Diplogasteritus*. We consider *D. pterygatus* (Timm, 1961) to be a *species incertae sedis*.

Diplogasteritus subterraneus (Hnatewytch, 1929). The species was described from 11 mature females collected from different insects in Germany (Hnatewytch, 1929). Males were not

found. The species is described in detail. Some morphological features (large and wide stoma, presence of two large dorsal teeth, absence of vulval isolated chamber) do not correspond to the diagnosis of the genus *Diplogasteritus*. We consider *D. subterraneus* (Hnatewytch, 1929) to be a *species incertae sedis*.

Key to species of *Diplogasteritus*

- 1(2). Body length less than 0.5 mm. ***D. minimus***
- 2(1). Body length 0.5 mm or more.
- 3(6). Apical end of gubernaculum smooth.
- 4(5). Tail 13-14 times as long as anal diameter; gubernaculum as long as or longer than spicule ***D. gubernatus***
- 5(4). Tail 7-8 times as long as anal diameter; gubernaculum always shorter than spicule ***D. lineatus***
- 6(3). Apical end of gubernaculum armed with different structures.
- 7(8). Apical end of gubernaculum with two S-like branches; dorsal stomal tooth small, hardly visible ***D. dendrophilus***
- 8(7). Apical end of gubernaculum armed with spines or "cuff"; dorsal stomal tooth larger.
- 9(10). Apical end of gubernaculum with characteristic sclerotised ring, "cuff" ***D. primitivus***
- 10(9). Apical end of gubernaculum with spines.
- 11(12). Spicules with broad velum; apical end of gubernaculum armed with 2 pairs of strong spines ***D. superbus***
- 12(11). Spicules without velum; apical end of gubernaculum armed with 1-2 pairs of small spines.
- 13(14). Apical end of gubernaculum always with two pairs of spines; dorsal stomal tooth larger ***D. nudicapitatus***
- 14(13). Apical end of gubernaculum often with one pair of spines only; dorsal stomal tooth smaller ***D. occidentalis***

Acknowledgements

The author thanks the Russian Foundation for Basic Research for financial support (grant no. 98-04-48029).

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Received after revision 17 June 2002