

Article

Morphology of *Streptocara crassicauda* and *S. recta*, with a Review of the Genus *Streptocara* (Nematoda: Acuariidae) and an Identification Key to Its Species

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Abstract: The cosmopolitan genus *Streptocara* Railliet, Henry and Sisoff, 1912 (Nematoda: Acuariidae) comprises parasites of the upper alimentary tract of aquatic and, rarely, terrestrial birds. Two species of the genus *Streptocara* are redescribed from Bulgaria by means of light and scanning electron microscopy: *Streptocara crassicauda* (Creplin, 1829), based on specimens from *Larus genei*, *Larus minutus* (Laridae) and *Aythya ferina* (Anatidae), and *Streptocara recta* (von Linstow, 1879) from *Podiceps nigricollis* (Podicipedidae). This is the first record of *S. recta* from Bulgaria. The host and distribution records of the species of the genus *Streptocara* are reviewed. Six species are recognised as valid. *Streptocara crassicauda* (Creplin, 1829), *S. californica* (Gedoelst, 1919), *S. formosensis* Sugimoto, 1930 and *S. incognita* Gibson, 1968, seem to be parasites well-adapted to birds of the family Anatidae (Anseriformes) and occasionally found in other birds, whereas *S. recta* (von Linstow, 1879) and *S. longispiculata* Gibson, 1968, are specialists of Podicipediformes and Gaviiformes, respectively. *Streptocara indica* Fotedar and Chishti, 1974, is recognised as a junior synonym of *S. crassicauda*, and *Schistogendra oligopapillata* Zhang and An, 2002, is considered as a junior synonym of *Streptocara formosensis* Sugimoto, 1930. An identification key to the species of the genus *Streptocara* is proposed.

Keywords: avian parasites; Bulgaria; identification key; new synonymy; scanning electron microscopy; Spirurida; taxonomy



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1. Introduction

The family Acuariidae (Nematoda: Spiruridae) is a homogenous group of 45 genera and more than 300 species parasitizing almost exclusively birds; just a few taxa are known from mammals [1]. Traditionally, the family has been split into three subfamilies based on the anterior cuticular ornamentation in the form of cordons, collarette or ptilina [2,3]. A recent molecular study [1] demonstrated that the members of the subfamily Seuratiinae Chitwood and Wehr, 1934, do not form a monophyletic group and that the cuticular ornamentation in the form of collarette is a convergent character. As a result, it was suggested that the genera previously classified in Seuratiinae are placed in the subfamily Acuariinae, together with the acuariids characterized by cordons.

Acuariids of the genus *Streptocara* Railliet, Henry and Sisoff, 1912 (Acuariinae) are parasites in the upper alimentary tract of a diverse range of aquatic birds worldwide [3]. On some occasions, they may cause severe and even lethal infections in birds [4]. Amphipods are known as suitable intermediate hosts for *Streptocara crassicauda* (Creplin, 1829), while fish may serve as paratenic hosts [5]. Gibson [6] demonstrated the importance of the morphology of the cephalic region and the deirids for the taxonomy of the species of *Streptocara*, and recognised the following six taxa as valid within the genus: *S. crassicauda* (Creplin, 1829), *S. crassicauda longispiculata* Gibson, 1968, *S. recta* (von Linstow, 1879), *S. californica* (Gedoelst, 1919), *S. formosensis* Sugimoto, 1930 and *S. incognita* Gibson, 1968. Subsequently, *Streptocara indica* Fotedar and Chishti, 1974, was described [7] and

Streptocara longispiculata Gibson, 1968, was elevated to full species rank [8]. In this article, we provide detailed morphological descriptions of *S. crassicauda* and *S. recta* based on specimens from Bulgaria by means of light and scanning electron microscopy. We also review the host and distribution records of the members of the genus *Streptocara* and propose a key for their identification.

2. Materials and Methods

All materials belonging to the genus *Streptocara* deposited in the Helminthological Collection of the Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences (IBER) were studied. The following two species were identified:

Streptocara crassicauda ex *Larus genei* Breme (Charadriiformes: Laridae), a single bird collected at lake Pomorie, Bulgarian Black Sea coast, 13 October 1988, 3 male and 12 female nematodes collected from the stomach and oesophagus: IBER N000.486 (1 male and 10 females), N000.842 (1 male nematode), IBER N001.040 (SEM stub with 2 female nematodes) and IBER N001.041 (SEM stub with 1 male nematode); ex *Larus minutus* Pallas, one bird collected at lake Durankulak, Bulgarian Black Sea coast, 5 October 1988, with one female nematode, coll. number N000.492 (found in the caecum?); ex *Aythya ferina* (L.) (Anseriformes: Anatidae), 3 birds at lake Durankulak, Bulgarian Black Sea coast: one bird on 21 January 1993, 6 female nematodes from the stomach, coll. number IBER N000.862; on 24 January 1993, 4 male and 2 female nematodes from the stomach, coll. number N000.249; 24 January 1993, 1 male and 1 female nematodes from the proventriculus, coll. number IBER N000.865.

Streptocara recta ex *Podiceps nigricollis* Brehm (Podicipediformes: Podicipedidae): at lake Durankulak, Bulgarian Black Sea coast—from one bird, 8 October 1989—3 female nematodes, coll. number N000.659 (1 female) and N001.042 (SEM stub 2 females); from a single bird, 21 January 1991, 1 male and 1 female nematodes, coll. number N000.867; in the vicinity of the village of Elena, SW Bulgaria, one bird, 25 August 2005, 1 male and 1 female nematode, coll. number N000.895. All collected under the lining of the gizzard.

Nematodes were preserved in 70% ethanol. For light microscopy, specimens were cleared and examined as temporary mounts in glycerine. Specimens used for scanning electron microscopy (SEM) were transferred from 70% ethanol to 40% ethanol for 10 min, rinsed twice in 0.1 M cacodylate buffer (10 min each time), post-fixed in 1% OsO₄ for 2 h, dehydrated through a graded ethanol series and critical-point dried with CO₂ by BAL-TEC CPD 030. Specimens were coated with gold-palladium in a Polaron SC7640 sputter coater and examined using a LEO microscope at an accelerating voltage of 10 kV.

Metrical data are presented as the range, with the mean in parentheses.

3. Results

3.1. *Streptocara crassicauda* (Creplin, 1829) Railliet, Henry and Sisoff, 1912

Redescription based on specimens from *L. genei*

General: Anterior end with 2 triangular pseudolabia, each bearing single amphid and one pair of papillae (Figures 1A,B and 2A–C). Sublabia absent. Collarette, delicate, reaching posteriorly to level about midlength of buccal cavity; collarette bearing about 80 small teeth on its posterior rim. Deirids 1.5–1.7 times as wide as long with five to eight cusps (Figures 1E and 2A), situated about two buccal lengths from anterior extremity. Postdeirids c. 2 µm in diameter (Figure 2F). Buccal cavity short. Nerve ring distinct; excretory pore situated posterior to it. Posterior part of muscular oesophagus similar in diameter to anterior part of glandular oesophagus. Cuticle distinctly thicker anteriorly of deirids (cuticular inflation) (Figure 1B) as well as in posterior part of body. Transverse cuticular striations interrupted along lateral sides of body (Figure 2E).

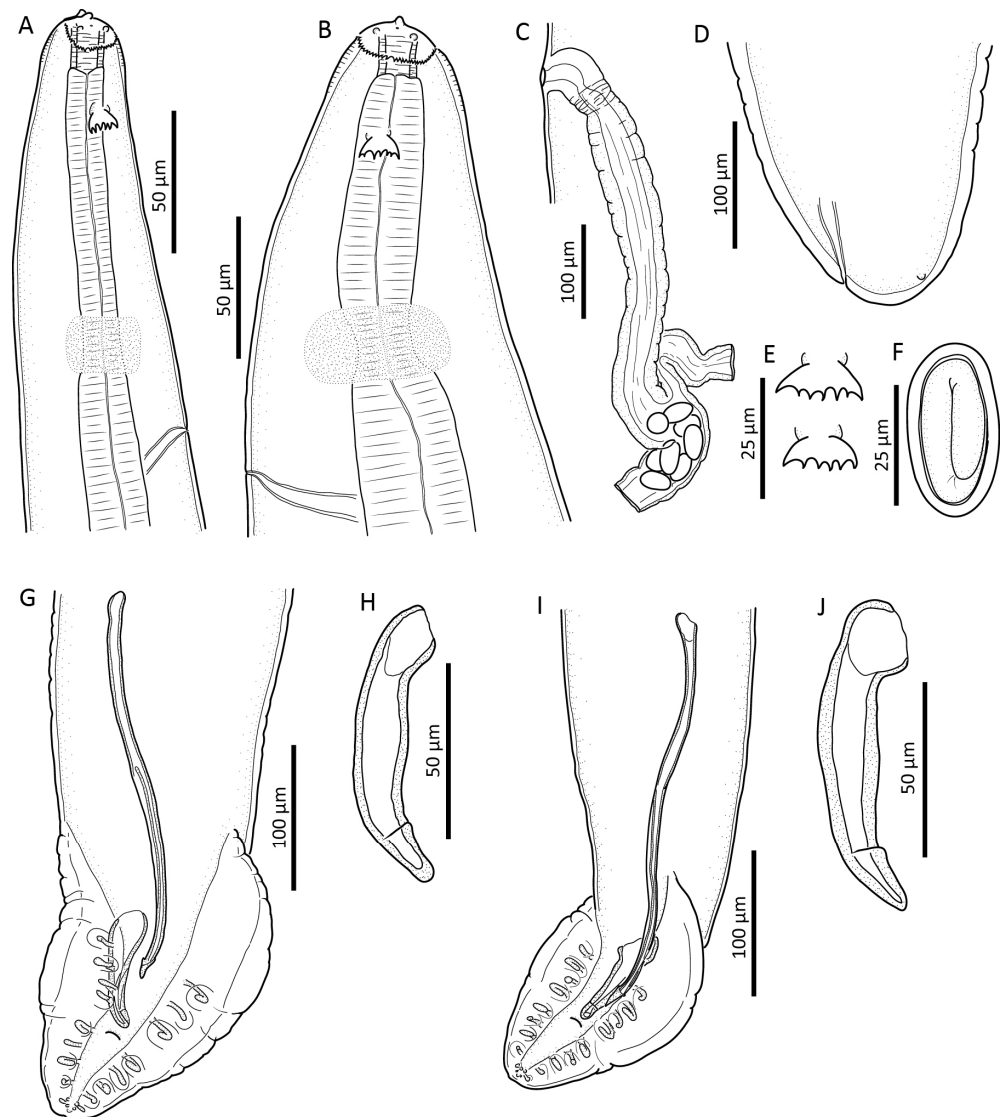


Figure 1. *Streptocara crassicauda* ex *Larus genei*, unless indicated otherwise. (A) Anterior end, male, lateral view; (B) anterior end, female, lateral view; (C) vagina; (D) posterior end, female, lateral view; (E) deirids; (F) egg; (G) posterior end, male, ventrolateral view; (H) right spicule, dextral view; (I) posterior end, male, ventrolateral view, ex *Aythya ferina*; and (J) right spicule, dextral view, ex *A. ferina*.

Male ($n = 2$, see Table 1 for other measurements): Small-sized acuariid nematodes with maximum width in posterior half of body. Body at level of cloaca 39 and 41 μm wide. Deirids 7–8 μm long, 11–12 μm wide. Buccal cavity 10 and 11 μm wide. Muscular oesophagus 26 and 32 μm wide. Glandular oesophagus 57 and 64 μm (60 μm) wide. Relative length between muscular and glandular oesophagus 1:2.9. Total length of oesophagus represented as portion of body length 1:2.4 and 1:2.6. Cuticle 3–4 μm thick; distance between striations 2 μm . Caudal region slightly ventrally and laterally curved. Caudal papillae: single median precloacal papillae and ten pairs, including four precloacal (one specimen with three precloacal papillae on left) and five postcloacal pedunculate papillae and one pair of postcloacal sessile papillae situated between bases of last pedunculate papillae (Figures 1G and 2D). Phasmids situated posterior to last pair of caudal papillae. Left spicule with projection near its distal end (Figure 1G). Right spicule robust, with retrograde projection near apex (Figure 1H). Relative length between right and left spicule 1:3.1.

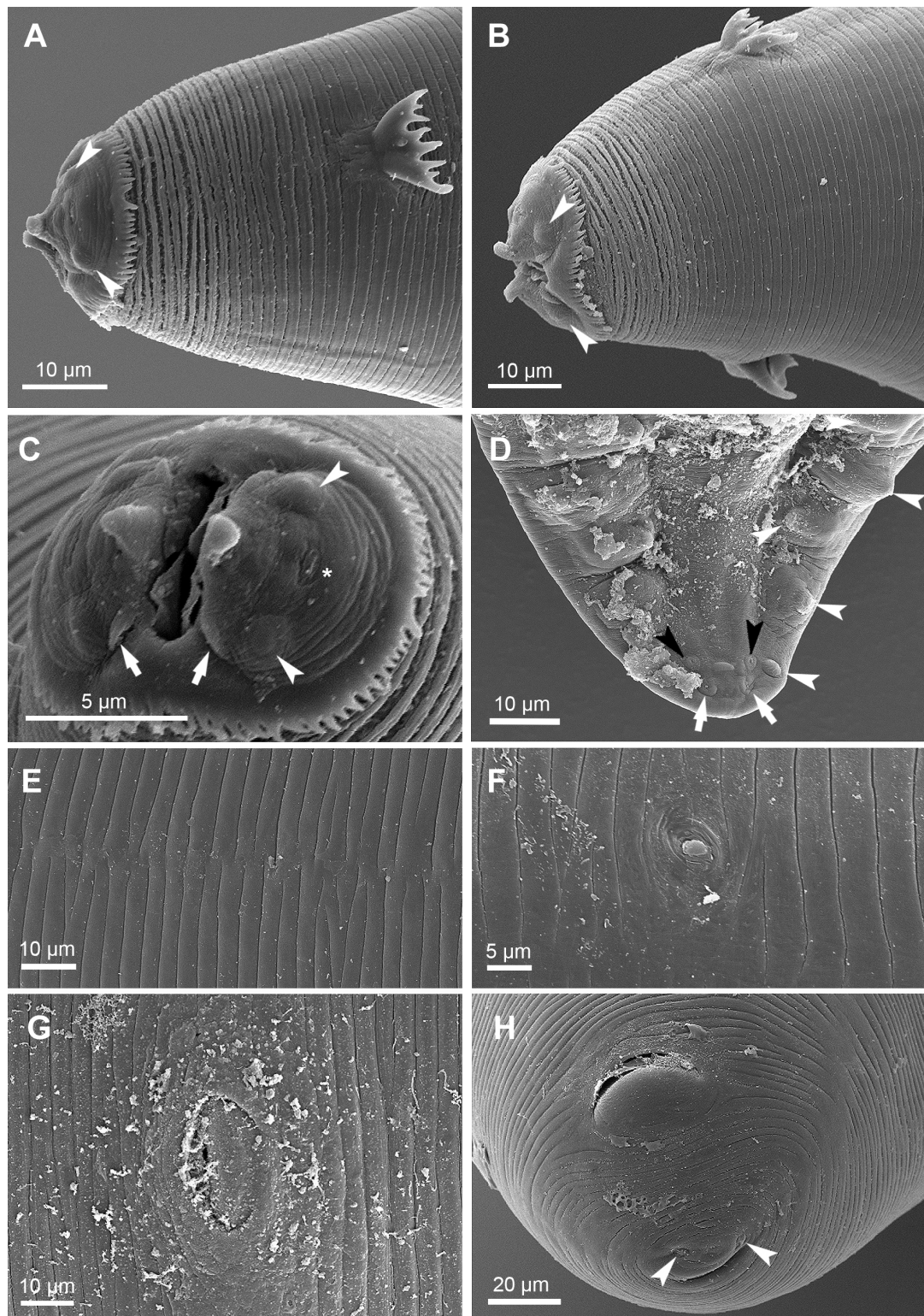


Figure 2. *Streptocara crassicauda*, female, unless indicated otherwise, SEM. (A) Anterior end, lateral view; note the cephalic papillae (arrowheads); (B) anterior end, ventral view; note the cephalic papillae (arrowheads); (C) anterior end, apical view note the cephalic papillae (arrowheads), the amphid (asterisk) and the lappet-like lobes (arrows); (D) posterior end, male, note the pedunculated papillae (white arrowheads), the sessile pair of papillae (black arrowheads) and the phasmids (arrows); (E) lateral field, note the cuticular striation; (F) postdeirid; (G) vulva; and (H) tail, note the phasmids (arrowheads).

Female ($n = 10$, except otherwise indicated; see Table 1 for other measurements): Small-sized nematode with maximum width at level of vulva; body width at level of anus 63–81 μm (73 μm). Tail short, blunt with subterminal phasmids (Figures 1D and 2H). Left postdeirid and right postdeirid at 5.3 and 4.9 mm, respectively from anterior body end (measured from specimen with body length 8.7 mm). Buccal cavity 11–14 μm (13 μm) wide. Muscular and glandular oesophagus 39–45 μm (41 μm) and 72–95 μm (87 μm) wide, respectively. Relative length between muscular and glandular oesophagus 1:2.6–3.6 (1:3.1). Total length of oesophagus represented as portion of body length 1:3.4–4.2 (1:3.9). Cuticle 6–11 μm thick; distance between transverse striations 3–4 μm . Vulva at 4.5–6.0 mm (5.0 mm) from anterior extremity (Figure 2G). Uterus didelphic (Figure 1C); *vagina vera* turn into posterior direction, with well-developed circular musculature in walls; *vagina uterina* longer. Eggs oval, 37–39 \times 19–21 μm (38 $\mu\text{m} \times 20 \mu\text{m}$, $n = 10$), containing first stage larva (Figure 1F).

Remarks. Nematodes from *L. genei* and *A. ferina* studied by us correspond morphologically to one another, although the latter have slightly smaller body dimensions (see Table 1 and Figure 1I,J). The material from Bulgaria falls within the known range of morphological variation of *S. crassicauda* (Table 1).

The morphology of *Streptocara crassicauda* from Bulgaria was studied by Vassilev [9]. In Bulgaria this nematode has been known to parasitize domestic and wild *Anas platyrhynchos* (L.), domestic chickens *Gallus gallus* (L.), and domestic turkey, *Meleagris gallopavo* L. summarised in [9] and *Alectoris chukar* (J. E. Gray) (Galliformes) [10].

Table 1. Metrical data of *Streptocara crassicauda* and *Streptocara recta* from various hosts and localities (in micrometres except otherwise indicated).

Species	<i>S. crassicauda</i>			<i>S. recta</i>		
	Source	Gibson [6]	Present Study	Present Study	Gibson [6]	Smogorzhevskaya [11]
Host	Host range *	<i>Larus genei</i>	<i>Aythya ferina</i>	<i>Podiceps auritus</i>	<i>Podiceps cristatus</i>	<i>Podiceps nigricollis</i>
Locality	Canada	Bulgaria	Bulgaria	Canada	Ukraine	Bulgaria
Male	$n = 36$	$n = 2$	$n = 4$	$n = 4$	–	$n = 2$
Body length (mm)	3.4–5.1 (4.1)	4.3; 4.6	3.5–4.1 (3.8)	4.2–5.3 (4.7)	4.5–5.0	5.9; 6.0
Maximum body width	92–132 (106)	143; 161	93; 120 **	145–185 (168)	–	170; 183
Tail, length	59–73 (64)	63; 66	50; 63 **	74–86 (80)	90–113	72; 75
Collarette, length	12–15 (14)	10; 11	12–14 (13)	27–29 (28)	–	25; 26
Collarette, width	21–26 (23)	22; 23	20–23 (22)	45–46 (45)	–	37; 41
Deirids from anterior end, distance	28–46 (35)	34; 43	32–45 (36)	30–45 (39)	43–50	42; 47
Buccal cavity, length	17–21 (20)	20; 24	18–21 (20)	21–25 (23)	21–23	28; 29
Muscular oesophagus, length	336–468 (378)	420; 491	407–438 (425)	443–492 (476)	450–510	617; 635
Glandular oesophagus, length	940–1230 (1100)	1230; 1430	1180–1380 (1260)	1720–2070 (1900)	1800–2340	1970; 2350
Nerve ring from anterior end, distance	107–128 (177)	100; 113	106–108 (107)	129–132(130)	128–130	136; 143
Excretory pore from anterior end, distance	157–193 (177)	158; 182	149–175 (161)	174	150–170	188; 206
Caudal alae, length	129–234 (175)	161; 221	161; 217 **	197–276 (225)	220–260	295; 303
Left spicule, length	224–302 (257)	260; 269	271; 321 **	280–314 (293)	287–325	292; 313
Right spicule, length	67–84 (73)	83; 88	81–90 (86) ***	86–98 (92)	75–98	99; 103
Female	$n = 46$	$n = 10$	$n = 8$	$n = 4$	–	$n = 3$
Body length (mm)	5.5–12.9 (9.7)	8.1–10.4 (8.9)	7.5–8.6 (7.9)	10.3	6.2–11.4	11.3–14.5 (13.2)
Maximum body width	160–246 (200)	233–291 (263)	163–234 (182)	350	–	241–358 (314)
Tail, length	43–58 (53)	13–20 (17)	13–22 (19)	62	65	50–69 (67)
Collarette, length	13–17 (5)	11–14 (13)	13–15 (14)	36	23–38	30–36 (34)
Collarette, width	24–30 (27)	24–27 (25)	23–25 (24)	45	–	39–44 (41)
Deirids from anterior end, distance	28–43 (36)	36–50 (43)	32–41 (36)	62	25–60	38–51 (46)
Buccal cavity, length	17–20 (19)	22–26 (24)	18–21 (20)	22	23–28	29–36 (32)
Muscular oesophagus, length	330–603 (454)	505–631 (564)	425–568 (488)	600	460–581	469–814 (669)
Glandular oesophagus, length	1040–1760 (1420)	1720–2010 (1850)	1340–1970 (1540)	2610	2460–2490	2630–3130 (2920)
Nerve ring from anterior end, distance	95–142 (128)	90–132 (116)	90–115 (105)	154	60–105	141–188 (163)
Excretory pore from anterior end, distance	157–203 (192)	125–191 (171)	145–192 (167)	199	113–155	191–295 (247)
Vulva from anterior end, distance (%)	55–62 (59)	57–61 (59)	57–62 (59)	57	3.7–4.8	56–64 (0.59)

* *Anas platyrhynchos*, *A. clypeata* (= *Spatula clypeata*), *Aythya valisineria*, *A. marila*, *Bucephala clangula*, *B. islandica*, *Clangula hyemalis*, *Melanitta perspicillata*, *M. nigra* (= *Oidemia nigra*), *Oxyura jamaicensis*, *Lophodytes cucullatus* (L.), *Mergus merganser*, *M. serrator*, *Tympanuchus phasianellus* (L.) (= *Pedioecetes phasianellus*), *Actitis macularia* (L.) and *Cephus columba* Pallas; ** $n = 3$; *** $n = 2$.

3.2. *Streptocara recta* (von Linstow, 1879) Skrjabin, 1916

General: Anterior end with 2 triangular pseudolabia, each bearing single amphid and pair of papillae; anteriorly to amphids numerous small pores present (Figures 3A,B and 4A–D). Sublabia absent. Collarette, well-developed reaching posterior end of buccal cavity; collarette bearing about 60 small teeth on posterior rim. Deirids almost twice as wide as long with six or seven cusps (Figures 3D and 4A), situated behind buccal cavity. Postdeirids c. 2 μm in diameter, bifurcate (Figure 4F). Buccal cavity short. Nerve ring well-distinct; excretory pore situated posterior to it. Posterior part of muscular oesophagus similar in diameter to anterior part of glandular oesophagus. Cuticle thicker anteriorly of deirids as well as in posterior part of the body. Transverse cuticular striations interrupted along lateral sides of body (Figure 4E).

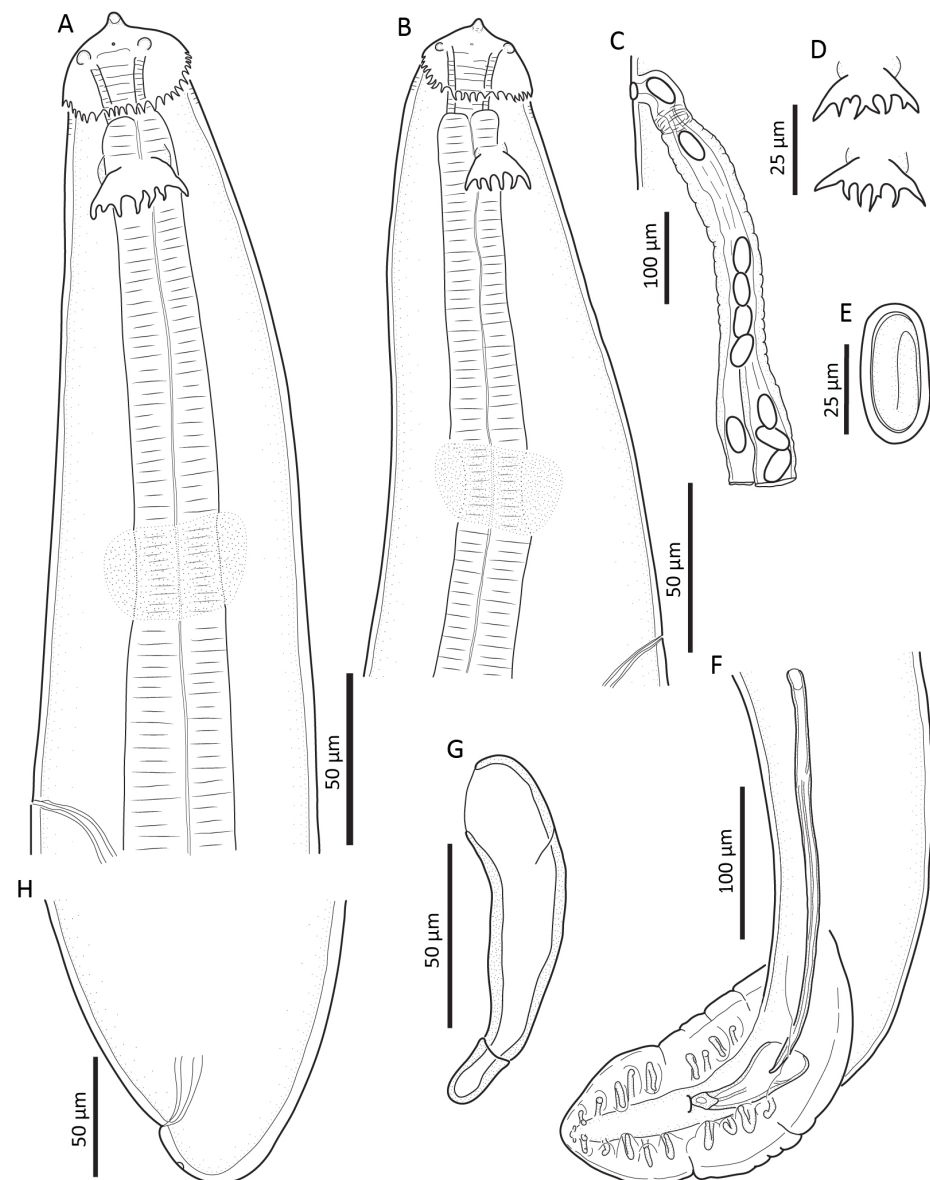


Figure 3. *Streptocara recta*. (A) Anterior end, female, lateral view; (B) anterior end, male, lateral view; (C) vulva; (D) deirids; (E) egg; (F) posterior end, male, ventrolateral view; (G) right spicule, sinistral view; and (H) posterior end, female, lateral view. Scale-bars a, b = 100 μm ; c = 50 μm .

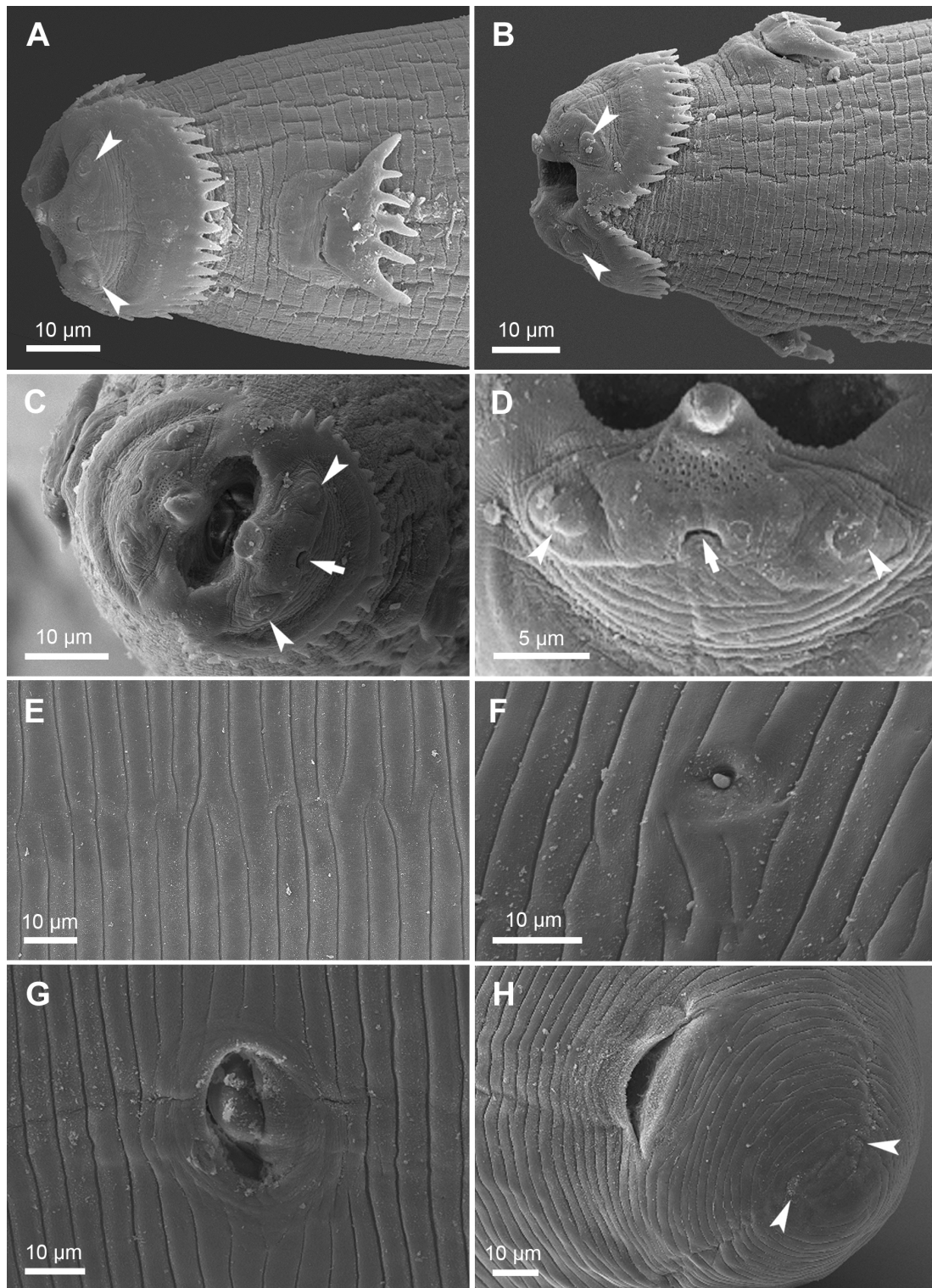


Figure 4. *Streptocara recta*, female, SEM. (A) Anterior end, lateral view; note the cephalic papillae (arrowheads); (B) anterior end, lateral view; note the cephalic papillae (arrowheads); (C) anterior end, apical view, note the cephalic papillae (arrowheads), the amphid (arrow); (D) pseudolabium, apical view, note the cephalic papillae (arrowheads), the amphid (arrow) and the field with pores anterior to the amphid; (E) lateral field, note the cuticular striation; (F) postdeirid; (G) vulva; and (H) posterior end, note the phasmids (arrowheads).

Male ($n = 2$, see Table 1 for other measurements): Small-sized nematode with maximum width in posterior half of body. Body width at level of cloaca 45 and 51 (48). Deirids 12–14 long, 20–21 wide. Buccal cavity 13–14 wide. Muscular and glandular oesophagus 21–29 (25) and 90–93 (92) wide, respectively. Relative length between muscular and glandular oesophagus 1:3.1 and 1:3.8. Total length of oesophagus represented as portion of body length 1:2 and 1:2.3. Cuticle 4–6 μm thick, distance between transverse striations 4–6 μm . Caudal region slightly ventrally and laterally curved. Caudal papillae: single median precloacal papillae and ten pairs, including 4 precloacal and 5 postcloacal pedunculated papillae and one pair of postcloacal sessile papillae situated between bases of last pedunculate papillae (Figure 3F). Phasmids situated posterior to last pair of caudal papillae. Left spicule with simple tip. Right spicule robust (Figure 3G). Relative length between right and left spicule 1:3.

Female ($n = 3$, see Table 1 for other measurements): Middle-sized nematode with maximum width in posterior part of body. Body width at vulva 240–300 μm (271 μm) and at level of anus 50–69 μm (57 μm). Tail short, blunt with subterminal phasmids (Figures 3H and 4H). Left postdeirid and right postdeirid at 9.3 mm and 8.7 mm, respectively from anterior body end (measured from specimen with body length 14.5 mm). Buccal cavity 15–20 μm (17 μm) wide. Muscular and glandular oesophagus 27–43 μm (38 μm) and 93–118 μm (106 μm) wide, respectively. Relative length between muscular and glandular oesophagus 1:3.8–5.6 (1:4.4). Total length of oesophagus represented as portion of body length 1:3.5–3.9 (1:3.7). Cuticle 9–13 μm thick, distance between striations 3–5 μm . Vulva at 7.2–8.3 mm (7.7 mm) from anterior extremity (Figure 3G). Uterus didelphic (Figure 3C); *vagina vera* turn into posterior direction, with well-developed circular musculature in walls; *vagina uterina* longer. Eggs oval, 34–39 \times 17–19 μm (37 $\mu\text{m} \times$ 18 μm , $n = 10$), containing first stage larva (Figure 3E).

Remarks. The material of *S. recta* from grebes in Bulgaria differs from the samples from Canada and Ukraine with its slightly longer body, longer muscular and glandular oesophagus and longer caudal alae (Table 1); however, it corresponds to those samples in the size and shape of the deirids and the size of spicules. This is the first record of *S. recta* from Bulgaria.

4. Discussion

4.1. Ultrastructural Details Revealed by the SEM

The scanning electron microscopy revealed a field of numerous small pores situated between the apex of each pseudolabium and the amphid of *S. recta*. A similar field of pores was documented by means of the SEM in *S. longispiculata* [8]: Figure 10. We could not distinguish such pores in *S. crassicauda*; however, the quality of the studied material did not allow us to obtain a high-resolution image. Chen and Yu [12] studied *S. crassicauda* by SEM; however, the quality of the images does not allow any detailed comparisons of the SEM images provided. We cannot distinguish pores anterior to amphids on the SEM images of *S. formosensis* Sugimoto, 1930 provided by Agüero and Diaz [13] and Zhang and An [14]; the material studied by the latter authors was described as *Schistogendra oligopapillata* Zhang and An, 2002 (recognised here as a junior synonym of *Streptocara formosensis* Sugimoto, 1930, see discussion below). Well-observed pores situated between the amphids and the apexes of the pseudolabia, have been documented also in *Decorataria decorata* (Cram, 1927) by Mutafchiev and Georgiev [15]: Figure 11. The function of the minute pores on the pseudolabia is currently unknown; further studies are also needed for understanding of their value for the taxonomy and systematics of the acuariid nematodes. The SEM study documented a pair of small lappet-like lobes at the lateral sides of each pseudolabium of *S. crassicauda* (Figure 2C), such structures are missing in the *S. recta* studied here or in *S. longispiculata* studied by Diaz and Kinsella [8]. The taxonomical value of this character needs further evaluation.

4.2. Review of the Genus *Streptocara*

The generic diagnosis of *Streptocara* as formulated by Gibson [6] is still valid. We considered that the most distinct characters for the genus, beside the specific collarette or the lack of cuticular ornamentation in form of cordons, collarette or ptilina, are: the lack of sublabia; the relatively short for acuariid nematodes buccal cavity; the relatively large deirids with usually three or more cusps; males with broad caudal alae bearing nine pairs of pedunculate caudal papillae, four precloacal and five postcloacal; as well as one pair of sessile papillae situated between the most posterior pair of pedunculated papillae, the vulva is situated slightly behind the mid-body and the female tail is short and rounded.

We recognise as valid the following six species in the genus *Streptocara*.

4.2.1. *S. crassicauda* (Creplin, 1829) Railliet, Henry and Sisoff, 1912

Synonyms: *Spiroptera crassicauda* Creplin, 1829; *Spiroptera pectinifera* Neumann, 1900; *Streptocara pectinifera* (Neumann, 1900) Railliet, Henry and Sisoff, 1912; *Streptocara indica* Fotedar and Chishti, 1980, new synonymy.

Streptocara crassicauda is one of the most commonly reported acuariid species and has a cosmopolitan distribution. It is known as a parasite of domestic chickens and ducks as well as of a variety of wild birds belonging to the families Anatidae (Anseriformes), Alcidae, Charadriidae, Haematopodidae, Laridae, Recurvirostridae, Scolopacidae, Sternidae (Charadriiformes) but also from Gaviidae (Gaviiformes), Ardeidae (Ciconiiformes), Podicipedidae (Podicipediformes), Phalacrocoracidae (Pelecaniformes), Meleagrididae, Numididae, Phasianidae (Galliformes) and Sturnidae (Passeriformes) [6,11,16]. *Streptocara indica* Fotedar et Chishti, 1974, was described as a parasite of domestic chickens in Kashmir, India [7]. Although the description of *S. indica* was not very detailed and accurate, the provided measurements and drawings reveal that this species morphologically corresponds well to *S. crassicauda* and the two species can be distinguished only by the number of the caudal papillae of males. Unlike the other members of the genus *Streptocara* characterised by four pairs of precloacal papillae and six pairs of postcloacal papillae, *S. indica* was described as possessing five pairs of precloacal papillae and seven pairs of postcloacal papillae. We consider the genus *Streptocara* as a member of the subfamily Acuariinae (see Mutafchiev et al. [1]). The genera within Acuariinae possess four pairs of precloacal papillae whereas the members of the subfamily Schistorophinae Travassos, 1918, are characterised with a multiplication of the pairs of precloacal papillae [1,3]. Thus, it is more likely that the male described as *S. indica* was an abnormally developed specimen. The most posterior pair of postcloacal papillae in the description of *S. indica* is likely the pair of phasmids, which in appearance looks like a pair of small sessile papillae (see Figure 2D). Therefore, we consider *S. indica* conspecific with *S. crassicauda* and propose it as its junior synonym.

4.2.2. *S. recta* (von Linstow, 1879) Skrjabin, 1916

Synonyms: *Filaria recta* von Linstow, 1879; *Spiroptera recta* (von Linstow, 1879) Mueller, 1897.

Several authors considered *S. recta* as a grebe specialist [6,11,17]. This species has been reported from *Podiceps cristatus* (L.) (type-host), *Podiceps auritus* (L.), *P. nigricollis*, *Tachybaptus novaehollandie* (Stephens), *T. ruficollis* (Pallas), *Poliocephalus poliocephalus* (Jardine and Selby) and has European (probably Palaearctic), North American and Australian distribution [6,11,18]. Baruš et al. [16] recognised all records of *S. recta* from the former USSR and that from Japan by Yamaguti [19] as belonging to *S. crassicauda*. Considering the cosmopolitan distribution of the appropriate hosts of *S. recta*, it cannot be excluded that this species has a wider distribution than is currently known.

4.2.3. *S. californica* (Gedoelst, 1919) Gedoelst and Liégeois, 1922

Synonyms: *Yseria californica* Gedoelst, 1919; *Korjakinema gusi* Oshmarin, 1950; *Skrjabinobronema californicum* (Gedoelst, 1919) Yamaguti, 1961; *Streptocara dogieli* Belopol'skaya, 1952.

Streptocara californica has been reported mainly from anatid birds of the tribe Mergini (Anatinae): *Melanitta deglandi* (Bonaparte) (type-host), *Melanitta perspicillata* (L.), *Melanitta americana* (Swainson), *Melanitta nigra* (L.), *Melanitta fusca* (L.), *Bucephala islandica* (Gmelin), *Clangula hyemalis* (L.), *Mergus merganser* L., *Mergus serrator* L., *Somateria mollissima* (L.), *Somateria spectabilis* L. and, with a few exceptions, of hosts of other anatids, i.e., *Anas platyrhynchos* (Anatinae, Anatini), *Aythya valisineria* (Wilson) and *Aythya marila* (L.) (Aythyinae: Aythyini). The geographic range of this species is California, USA (type-locality) (Gedoelst 1919); British Columbia, Canada [6,20], Russian territories—Murmansk [17,20], Kamchatka [21,22], Chukotka [23], lower Ob River [24] and Yakutsk [25] as well as the Netherlands [26].

4.2.4. *S. formosensis* Sugimoto, 1930

Synonyms: *Streptocara somateriae* Rhyzhikov, 1960; *Paracuaria somateriae* (Rhyzhikov, 1960) Leonov, Tsimbaliuk and Belogurov, 1963; *Schistogendra oligopapillata* Zhang and An, 2002 new synonymy.

Streptocara formosensis is the only known species of *Streptocara* without a collarete. However, it resembles the other members of the genus by the structure of the pseudolabia, the large deirids bearing several cusps, the shape of the caudal alae and the arrangement of the caudal papillae in males as well as the rounded female tail and the position of the vulva.

Streptocara formosensis was described from domestic *A. platyrhynchos*. Subsequently, it has been reported from various anatid birds, mainly of the tribe Mergini: *Bucephala albeola* (L.), *Bucephala clangula* (L.), *B. islandica*, *C. hyemalis*, *M. deglandi*, *M. perspicillata*, *M. americana*, *M. fusca*, *M. merganser*, *M. serrator*, *S. mollissima*, *S. spectabilis*, and less often from the tribe Aythyini: *A. marila*, *Aythya nyroca* (Güldenstädt), *Aythya fuligula* (L.) in Japan (type locality), Canada, Russia (from Kaliningradskaya Oblast' to the Russian Far East), Estonia [6,16,27], and more recently it was reported from *Tachyeres leucocephalus* Humphrey and Thompson in Argentina [13] and *A. marila*, *B. clangula*, *C. hyemalis*, *M. nigra*, *M. fusca*, *M. merganser*, *Mergellus albellus* (L.) in Poland [28].

Schistogendra oligopapillata Zhang and An, 2002 was described from a domestic duck, *A. platyrhynchos*, from Nanjing, China [14]. This species differs from the other members of the genus *Schistogendra* Chabaud and Rousselot, 1956, recognised as a junior synonym of *Quasithelazia* Maplestone, 1932 [29,30] and was treated a species *incertae sedis* by Mutafchiev et al. [30]. *Schistogendra oligopapillata* resembles *S. formosensis* in the morphology of the anterior end and the deirids, the morphology of the posterior end of males and the tail of females, as well as, in most morphometrics (Table 2), except the position of the vulva, which was described as positioned at level of the second and third fifth of the body length by Zhang and An [14]. All acuariid genera are characterised by an equatorial or post-equatorial position of the vulva [3] and it is likely that the position of the vulva was incorrectly provided. Based on the above discussion we recognise *Schistogendra oligopapillata* as a junior synonym of *S. formosensis*.

Table 2. Metrical data of *Streptocara formosensis* from various hosts and localities (in micrometres except otherwise indicated).

Source	Gibson [6]	Kurochkin and Ryzhikov [27]	Zhang and An [14]
Host	Host range *		<i>Anas platyrhynchos</i>
Locality	Canada	Russia	China
Male	n = 8	n = 10	n = 8
Body length (mm)	5.1–7.8	5.7–7.2	5.9–7.0
Maximum body width	117–160	140–200	161–200
Tail, length	73–80	–	52–81
Deirids from anterior end, distance	143–231	110–240	109–169
Buccal cavity, length	41–49	30–60	26–31
Muscular oesophagus, length	584–1010	310–900	693–872

Table 2. Cont.

Source	Gibson [6]	Kurochkin and Ryzhikov [27]	Zhang and An [14]
Glandular oesophagus, length	1560–2550	2000–3700	1890–2730
Nerve ring from anterior end, distance	135–172	–	135–169
Excretory pore from anterior end, distance	188–224	–	185–234
Caudal alae, length	331–424	–	–
Left spicule, length	314–364	280–460	234–273
Right spicule, length	86–120	62–96	62–86
Female	n = 10	n = 20	n = 13
Body length (mm)	8.2–15.7	9.4–18.0	11.3–15.9
Maximum body width	172–240	170–520	210–336
Tail, length	49–60	–	39–52
Deirids from anterior end, distance	166–222	109–200	153–195
Buccal cavity, length	41–50	–	23–31
Muscular oesophagus, length	756–1144	660–1200	735–882
Glandular oesophagus, length	1840–3460	2160–3100	2100–3570
Nerve ring from anterior end, distance	98–185	–	156–208
Excretory pore from anterior end, distance	224–270	–	203–289
Vulva from anterior end, distance (%)	52–64 (61)	–	40
Eggs	35 × 19	30–40 × 18–32	34–38 × 20–23

* *Anas platyrhynchos*, *Bucephala clangula*, *B. islandica*, *B. albeola*, *Clangula hyemalis*, *Melanitta deglandi*, *M. perspicillata*, *Mergus merganser* and *M. serrator*.

4.2.5. *S. incognita* Gibson, 1968

This species was described from *Oxyura jamaicensis* (Gmelin) (Anatidae) in Canada and further reported as a parasite of *A. platyrhynchos* in the USA and Canada, *B. islandica* in Canada, and *Anser cygnoides* (L.) in former Yugoslavia [6]. *Streptocara incognita* was also reported as a highly pathogenic parasite causing death in captive *Phoenicopterus chilensis* (Phoenicopteriformes: Phoenicopteridae) in the San Francisco Zoological Gardens, USA [31] and the anatids *A. platyrhynchos* in Montana, USA [32], domestic Muscovy duck *Carina moschata* (L.) in Italy [33] and *Cygnus olor* (Gmelin) in Bosnia and Herzegovina [34]. A 28S rDNA sequence of *Streptocara incognita* Gibson, 1968 from *Tadorna tadorna* (L.) in France was published [1].

4.2.6. *S. longispiculata* Gibson, 1968

This species was initially described as a subspecies of *S. crassicauda* from *Gavia immer* (Brunnich) (Gaviiformes) from Chesapeake Bay, USA [6], and subsequently elevated to a full species rank by Diaz and Kinsella [8]. *Streptocara longispiculata* is known from a few records from loons in North America: *G. immer* in Florida, USA [35] and *Gavia stellata* (Pontoppidan) in the Northwest Territories, Canada [8].

4.3. Identification Key to the Species of the Genus *Streptocara*

We propose the following identification key to the species of *Streptocara* which takes into account the morphological characters for species of the genus provided above:

- 1a. Without cuticular collarette surrounding the cephalic region . . . *S. formosensis*
- 1b. Cuticular collarette surrounding the cephalic region present . . . 2
- 2a. Buccal cavity longer than 90 µm; deirids with three approximately equal in size cusps; . . . *S. californica*
- 2b. Buccal cavity shorter than 30 µm. Deirids with more than three cusps . . . 3
- 3a. Cuticular collarette reaches the posterior third of the buccal cavity; deirids about twice as wide as long, with 6–7 cusps. Left spicule with simple bluntly pointed distal end . . . *S. recta*
- 3b. Cuticular collarette does not exceed the midlength of the buccal cavity. Left spicule with distal tip that is not simple and bluntly pointed . . . 4

- 4a. Deirids as long as wide, deeply cleft medially, with well-developed most outer cusps and one, two or three smaller cusps in-between . . . *S. incognita*
 4b. Deirids wider than long with 5–8 similar in size cusps . . . 5
 5a. Cuticular inflation at the anteriorly extremity present. Left spicule shorter than 320 μm . . . *S. crassicauda*
 5b. Without prominent cuticular inflation at the anterior extremity. Left spicule longer than 380 μm . . . *S. longispiculata*

5. Conclusions

The species of the genus *Streptocara* are well-known parasites of aquatic birds. We recognise six species as valid within the genus. Out of these, *S. crassicauda*, *S. californica*, *S. formosensis* and *S. incognita* are common parasites of birds of the family Anatidae (Anseriformes), although some of these species have also been recorded from other aquatic birds and occasionally terrestrial birds of the orders Galliformes and Passeriformes. *Streptocara californica* and *S. formosensis* are more often reported from hosts of the tribe Mergini; however, the reasons for this affinity are not yet understood but could be due to some particular features of the life cycles of the nematodes, which are still unknown. *Streptocara recta* is a parasite of Podicipediformes, while *S. longispiculata* is a parasite of Gaviiformes. Our review of the genus *Streptocara* revealed that there have not been new species described within the genus for more than 50 years, suggesting that the species diversity is well-studied. This is likely due to the extensive helminthological studies carried out on waterfowls.

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