Adults and larvae of *Skrjabinocerca canutus* n. sp. (Nematoda: Acuariidae) from *Calidris canutus rufa* (Aves: Scolopacidae) on the southern Southwest Atlantic coast of South America

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Abstract

Adults and larvae of a new species of *Skrjabinocerca* Shikhobalova, 1930 (Nematoda: Acuarioidea) are described on the basis of light and scanning electron microscope studies. Specimens were recovered from *Calidris canutus rufa* Wilson (Aves: Scolopacidae) from the Southwest Atlantic coast of Uruguay. Data on the hosts, localities and main features of the four previously described species of the genus are provided. *S. canutus* n. sp. can be distinguished from its congeners by a combination of the following characters: non-recurrent cordons, shorter right spicule and possession of a delicate finger-like projection on the distal end of the left spicule. *S. prima* Shikhobalova, 1930 has a left spicule which is stilletto-shaped and sharply pointed, *S. europaea* Wong & Anderson, 1993 has recurrent cordons, *S. americana* Wong & Anderson, 1993 possesses two delicate digitiform projections on the distal end of its left spicule and *S. bennetti* Bartlett & Anderson, 1996 has subequal spicules.

Introduction

Skrjabinocerca Shikhobalova, 1930 comprises four species: S. prima Shikhobalova, 1930, S. americana Wong & Anderson, 1993, S. europaea Wong & Anderson, 1993 and S. bennetti Bartlett & Anderson, 1996 (Shikhobalova, 1930; Wong & Anderson, 1993; Bartlett & Anderson, 1996). The typespecies, S. prima, was described from the Pacific coast of Siberia and then reported from several families of birds in the Old World (Wong, Bush & Anderson, 1987; Wong & Anderson, 1993). Wong et al. (1987) redescribed S. prima based on specimens recovered from Recurvirostra americana in Canada. Later, Wong & Anderson (1993) named these specimens S. americana and described S. europaea for specimens recovered from birds in Iceland. Finally, Bartlett & Anderson (1996) erected S. bennetti for specimens from Numenius phaeopus hudsonicus in Canada.

The first record of Skrjabinocerca from South America was made by Castro et al. (2002). These authors recovered Skrjabinocerca specimens from one New World red knot Calidris canutus rufa, which was found dead on the Uruguayan coast. These specimens represent a new species, which is described in the present paper. Calidris canutus rufa makes one of the longest migratory flights known in the avian world. It breeds in the Canadian Arctic and occupies a wintering area in southern Argentina, migrating north in March and April (González et al., 1996). Considerable research has been focused on the red knot; however, there are gaps with respect to our knowledge of its parasites. Only two species of acuarioids have been reported from C. canutus, i.e. Viktorocara capillaris (Molin, 1860) from Siberia (Wong & Lankester, 1984) and *V. limosae* Daiya, 1966 from the USA (Wong & Anderson, 1991). Wong & Anderson (1990) failed to find any acuariids in three specimens of *C. canutus rufa* from Tierra del Fuego, Argentina.

The aim of this paper is to describe all of the developmental stages of *S. canutus* n. sp. found by Castro et al. (2002) parasitising *C. canutus* on the southern Southwest Atlantic coast of South America.

Materials and methods

Castro et al. (2002) found, during April, 2002, a dead New World red knot in the Laguna de Rocha (34°39′ S, 54°15′ W), Departamento Rocha, Uruguay. The rings present on the bird's legs indicated that the specimen had been ringed in New Jersey, USA, during May, 1999. These authors dissected the host and recovered the nematodes from the oesophagus, which were fixed in 10% formalin, stored in 70% alcohol and identified as Skrjabinocerca. These specimens were given to us for study, and were mounted in glycerine-alcohol and rolled under a coverslip in order to study various parts of the body from different angles. The drawings were made with the aid of a drawing apparatus. Measurements are given in micrometres, with the range in parentheses, except where otherwise indicated. Sixteen specimens of different development stages were dried using the critical point method for study using a scanning electron microscope (JEOL/SET 100[®]) and photographed.

Skrjabinocerca canutus n. sp.

Type-host: Calidris canutus rufa Wilson (New World red knot).

Type-locality: Laguna de Rocha (34°39′ S, 54°15′ W), Departamento Rocha, Uruguay.

Type-material: Holotype No. 5319, allotype No. 5320 and paratypes No 5321 deposited in the Helminthological Collection of the Museo de La Plata, La Plata, Argentina.

Site: Oesophagus.

Intensity: 22 males, 42 females, 8 third-stage larvae, 18 fourth-stage larvae, 13 juveniles (non-gravid females).

Etymology: The specific name refers to the host.

Description (Figures 1–31; Table 1)

General morphology. Acuarioidea, Acuariidae, Acuariinae, Skrjabinocerca Shikhobalova, 1930. Cuticle with fine transversal striations (Figure 13). Pseudolabia well developed, with apices continuous with anterolateral walls of buccal capsule. Amphids at base of pseudolabia. Two pairs of prominent cephalic papillae at short distance posterior to pseudolabia and disposed laterally in relation to cordons (Figures 1, 2, 10, 11). Cordons originating at dorsoventral sides of oral aperture and extend posteriorly as parallel cords as far as level of last quarter of muscular oesophagus, non-recurrent (Figures 1.2.10.11), with transverse markings (Figure 12). Buccal capsule lined with fine transverse striations. Deirids large, tricuspid and located posterior to nerve-ring (Figures 1, 2, 10, 11). Prominent lateral alae transversely striated, originate immediately posterior to deirids, diminish in size posteriorly and terminate in last quarter of body (Figures 2, 11). Oesophagus divided into shorter muscular portion and longer glandular portion. Postdeirids digitiform, located in third quarter of body, closely dorsal to lateral alae, asymmetrically disposed in relation to each other (Figures 13, 14).

Holotype (male). Total length 4.11 mm. Width 225. Buccal capsule 110 long. Nerve-ring 200 and deirids 208 from anterior end. Deirids 20 long. Cordons 325 long. Muscular oesophagus 335 and glandular oesophagus 1.66 mm long. Postdeirids 1.45 and 1.7 mm from posterior end. Postdeirids 15 long. Caudal region curved ventrally. Caudal alae narrow, with 4 pairs of precloacal papillae; fourth pair separated from others, and third pair more ventral than other pairs (both counting from cloaca) (Figures 5, 15, 16). Five pairs of pedunculate postcloacal papillae; first 3 larger; other 2 pairs separated from remainder and from each other (Figures 5, 16). One pair of sessile papillae located just ventral to last pair of pedunculate papillae (Figure 17). Phasmids near tip of tail (Figure 17). Area rugosa in form of single row of cuticular folds, 490 long, ending at level of third pair of precloacal papillae (counting from cloaca) (Figure 15). Left spicule 385 long, consisting of cylindrical proximal portion and



Figures 1–9. Adult of *Skrjabinocerca canutus* n. sp. from *Calidris canutus rufa.* 1. Anterior extremity of female showing non recurrent cordons, ventral view. 2. Anterior extremity of female showing tricuspid deirids and lateral ala, lateral view. 3. *Vagina vera, vagina uterina,* and eggs. 4. Posterior end of female showing single papilla just posterior to anus, phasmids and terminal rosette. 5. Caudal region of male showing spicules, papillae arrangement and end of area rugosa, ventral view. 6. Right spicule, dextro-lateral view. 7. Left spicule, dextro-lateral view. 8. Tip of left spicule, sinistro-lateral view. *Scale-bars*: 1-3, 100 μm; 4-7, 50 μm; 8,9, 20 μm.



Figures 10–15. Adult of *Skrjabinocerca canutus* n. sp. from *Calidris canutus rufa.* 10. Apical view showing pseudolabia, cephalic papillae and amphids (arrow). 11 Anterior extremity showing cordons, tricuspid deirid and lateral ala, lateral view. 12. Detail of cordon. 13. Asymmetrical postdeirids. 14. Detail of digitiform postdeirid and lateral ala. 15. Caudal region of male showing area rugosa, ventral view. *Scale-bars:* 10,15, 50 μ m; 11,13, 100 μ m; 12,14, 10 μ m.



Figures 16–21. Adult of *Skrjabinocerca canutus* n. sp. from *Calidris canutus rufa.* 16. Posterior end of male showing papillae and spicules. 17. Tip of male tail, showing last pair of pedunculate papillae, sessile papillae and phasmids (arrow). 18. Tip of left spicule, sinistro-lateral view. 19. Tip of left spicule, dextro-lateral view. 20. Posterior extremity of female showing anus, single ventral papilla, phasmids and terminal rosette, ventral view. 21. Detail of terminal rosette, with surrounding small papillae (arrows) and knob at end of digitiform 'tubercles' (arrowhead), apical view. *Scale-bars:* 16, 100 μ m; 17,21, 10 μ m; 18,19, 5 μ m.

Species	S. prima	S. americana	S. europaea	S. bennetti	S. canutus n. sp.
	Shikhobalova, 1930	Wong & Anderson, 1993	Wong & Anderson, 1993	Barlett & Anderson, 1996	
Reference	Shikhobalova (1930)	Wong et al. (1987); Wong & Anderson (1993)	Wong & Anderson (1993)	Barlett & Anderson (1996)	Present study
Type host	Corvus frugileus pastinatus	Recurvirostra americana	Charadrius hiaticula hiaticula	Numenius phaeopus hudsonicus	Calidris canutus rufa
Other hosts	Charadriformes, Passeriformes, and Cuculliformes	Charadriformes	Calidris alpina schinzii, Tringa totanus	I	I
Localities	Northwest Pacific coast	Alberta (Canada) and Cuba*	Iceland and western Russia*	Nova Scotia (Canada)	Uruguay
Male (N)	3?	4	4	1	10 (paratypes)
Total length (mm)	6.22-6.58	5.0-6.2	5.3 (4.9-6.0)	5.1	4.94 (3.68-5.86)
Maximum width	219-230	140-200	183 (180-200)	168	185 (140-260)
Cordons (length)	427-441	250	I	320	342 (255-410)
Cordons	non recurrent	non recurrent	slightly recurrent	slightly recurrent	non-recurrent
Buccal capsule	114-130	112-145	104 (80-115)	104	109 (84-120)
Nerve-ring (dfae) [†]	I	170-223	169 (150-185)	230	170 (140-200)
Deirids (dfae)	235-277	233-285	209 (193-220)	233	220 (175-260)
Deirids (length)	19	I	1	1	19 (15-24)
Excretory pore (dfae)	I	1	261 (243-295)	1	not seen
Muscular oesophagus	350-390	255-370	326 (300-360)	458	323 (265-378)
Glandular oesophagus (mm)	1.65-2.47	1.5-1.8	1.8 (1.6-2.0)	1,85	1.57 (1.11-1.90)
Left spicule	390-395	400-445	411 (385-440)	365	370 (320-391)
Proximal part of left spicule	I	1	I		205 (137-245)
Right spicule	120-130	125-152	144 (130-160)	345	109 (100-115)

Species	<i>S. prima</i> Shikhobalova, 1930	<i>S. americana</i> Wong & Anderson, 1993	S. europaea Wong & Anderson, 1993	<i>S. bennetti</i> Bartlett & Anderson, 1996	S. canutus n. sp.
Distal postdeirid (dfpe) [‡] (mm) Proximal postdeirid (dfpe) (mm) Postdeirid (length) Area rugosa (length)	- - 490-593	1 1 1 1	- - 12 folds (from figure 20)		1.74 (1.10-2.05) 2.10 (1.81-2.57) 17 (13-23) 505 (435-600)
Female (N)	6?	4	4	3	10 (paratypes)
Total length (mm)	6-6.58	6.2-6.6	5.925 (5.1-6.7)	5.3 (5.6, 5.9)	4.93 (3.65-5.75)
Width at vulva level	219-270	195-260	225 (200-250)	244 (220, 225)	229 (165-260)
Cordons (length)	490-575 (1/11-1/13)	250		490 (426, 420)	410 (350-460)
Cordons	non-recurrent	Non-recurrent	slightly recurrent	slightly recurrent	Non-recurrent
Buccal capsule	98-132	100-145	107.5 (90-125)	108 (100, 100)	110 (95-130)
Nerve-ring (dfae) [†]	170-216	178-230	173 (150-185)	225 (-, 230)	157 (115-192)
Deirids (dfae)	230-270	255-320	207 (160-232)	290 (255, 210)	201 (145-253)
Deirids (length)	26	I	I	I	26 (22-30)
Excretory pore	230	I	268 (202-325)	I	283 (275-290) ⁺
Muscular oesophagus	376-500	350-450	356 (320-400)	360 (440, 390)	359 (255-450)
Glandular oesophagus (mm)	1.83-2.00	1.6-2.0	1.85 (1.4-2.2)	(1.5, 2.0)	1.64(1.16-1.85)
Vulva (dfpe) [‡] (mm)	1.26-1.46	1.4-1.8	1.3 (1-1.5)	1.9(1.3, 1.1)	1.05 (0.85-1.28)
Egg length	49-52	40-41	49-50	46 (46, 48)	46 (42-50)
Egg width	26-29	22-23	25-27	22 (21, 23)	27 (22-32)
Distal postdeirid (dfpe) (mm)		I	I	Ι	1.99 (1.65-2.45)
Proximal postdeirid (dfpe) (mm)		I	I	I	2.23 (1.72-2.50)
Postdeirid (length)		I	I	I	20 (15-24)
Tail	160-196	150-162	151 (145-155)	91 (150, 150)	137 (110-185)
Postanal papilla (dfpe)	91-124	1	1	1	107 (85-120)
Number of caudal tubercles	5-10	variable	variable	6-8	variable
*Wong & Anderson (1993) assun	ned that the specimens	recovered from Cuba and	Russia belonged to S. ame	ricana and S. europaea, resp	pectively.

Table I continued.

[†] dfae, distance from anterior end. [‡] dfpe, distance from posterior end. ⁺N = 2.

guttered distal region with small membranous triangular projection on ventro-dextral side of distal extremity (Figures 7–9, 18, 19). Right spicule 100 long, with tapered distal end and rounded tip (Figure 6). Tail 160 long.

Allotype (female). Total length 5.42 mm. Width 245 at level of vulva. Buccal capsule 100 long. Nervering 200 and deirids 225 from anterior end. Deirids 30 long. Cordons 485 long. Muscular oesophagus 590 and glandular oesophagus 1.31 mm long. Postdeirids 2.57 and 2.58 mm from posterior end. Postdeirids 22 long. Uterus didelphic, prodelphic. Vulva 1.18 mm from distal end. Vagina divided into vagina vera and uterina; vagina vera 85 long (Figure 3). Large papilla located ventrally, closely posterior to anus and 115 from tip of tail (Figures 4, 20). Tail 148 long, bearing rosette of short, terminal, digitiform, papilla-like structures ('tubercles') surrounded by small number of small papillae (Figures 4, 20, 21). Phasmids prominent, located anterior to terminal rosette (Figures 4, 20, 21). Eggs embryonated, with thick, membranous shell, $27-30 \times 43-49$ (N = 20) (Figure 3).

Third-stage larva (5 specimens measured). Total length 3.15 (2.97-3.35) mm. Width 106 (80-125). Cephalic papillae located dorsally and ventrally to cordons (Figure 22). Buccal capsule 75 (60-85) long. Nerve-ring 130 (120-135) from anterior end. Prominent lateral alae transversely striated, originating at base of amphids (Figure 23). Deirids 148 (125-170) from anterior end, located on lateral alae, conical, 17 (15-20) long (Figures 23, 24). Cordons 141 (125-150) long. Muscular oesophagus 158 (130-180) and glandular oesophagus 1.33 (1.25-1.45) mm long. Postdeirids 1.26 (1.1-1.4) mm from posterior end, located slightly dorsally to lateral alae (Figure 25) and asymmetrically disposed in relation to each other. Postdeirids diamond-shaped, 14 (12-15) long. Single papilla present just posterior to anus (Figure 26), larger than in adult and fourth-stage larva. Tail 122 (115-130) long. Tip of tail with slight constriction and pointed protuberance (Figure 26). Genital primordium of male free within pseudocoelom at level of middle third of intestine. Genital primordium of female represented by vaginal primordium attached to hypodermis in posterior quarter of body and 2 branches, 1 directed anteriorly and 1 posteriorly.

Fourth-stage larva (5 specimens measured). Old and new cuticle present. Total length 3.99 (3.64-4.25) mm. Width 111 (85-155). Cephalic papillae laterally located in relation to cordons (Figure 27). Buccal capsule 79 (70-90) long. Lateral alae arise posterior to deirids (Figure 28). Nerve-ring 130 (120-140) from anterior end. Deirids 156 (130-175) from anterior end, bicuspid, 13 (12-15) long (Figure 29). Cordons 199 (160-230) long. Muscular oesophagus 256 (210-320) and glandular oesophagus 1.55 (1.35-1.99) mm long. Postdeirids 1.73 (1.62-1.85) mm from posterior end and asymmetrically disposed in relation to each other. Postdeirids linguiform, 15 long (Figure 30). Single prominent papilla present closely posterior to anus (Figure 31). Tail 138 (125-160) long. Tip of tail with fewer and smaller 'tubercles' than in adult (Figure 31). Reproductive tract clearly defined. Male with spicules incompletely differentiated. Female with vulva and vagina well differentiated.

Juvenile (5 non-gravid females measured). Old and new cuticle present. Total length 3.98 (3.55-4.49) mm. Width 169 (125-250). Cephalic papillae laterally located in relation to cordons. Buccal capsule 100 (70-150). Nerve-ring 146 (105-170) and deirids 176 (115-282) from anterior end. Deirids tricuspid, 15 (12-20) long. Cordons 220 (185-280) long. Muscular oesophagus 297 (200-360) and glandular oesophagus 1.7 (1.48-1.95) mm long. Postdeirids 1.6 (1.27-1.98) mm from posterior end. Postdeirids digitiform, 16 (15-18) long. Vulva 848 (750-1.05) from distal end. Vagina divided into vagina vera and uterina; vagina vera 80 (60-95) long. Single papilla located closely posterior to anus. Tail 129 (110-145) long, bearing smaller number of terminal 'tubercles' in rosette than mature adult. Phasmids prominent, located anterior to terminal rosette.

Remarks

Table 1 summarises the main diagnostic features and measurements of the previously and presently described species. *Skrjabinocerca bennetti* can be readily distinguished from *S. canutus* n. sp. in having sube-



Figures 22–26. Third- stage larva of *Skrjabinocerca canutus* n. sp. from *Calidris canutus rufa*. 22. Apical view showing cephalic papillae located dorsally and ventrally to cordons. 23. Anterior extremity showing lateral alae originating at base of amphid and, further posteirorly, deirid, lateral view. 24. Detail of conical deirid, located on lateral ala. 25. Detail of diamond-shaped postdeirid and lateral ala. 26. Posterior extremity showing prominent papilla and conical tip of tail. *Scale-bars*: 22,24,25, 10 μ m; 23,26, 50 μ m.

Figures 27–31. Fourth- stage larva of *Skrjabinocerca canutus* n. sp. from *Calidris canutus rufa.* 27. Apical view showing cephalic papillae located laterally to cordons. 28. Anterior extremity showing lateral alae originating posterior to deirid, lateral view. 29. Detail of bicuspid deirid and origin of lateral ala. 30. Detail of linguiform postdeirid. 31. Posterior extremity showing single ventral papilla and terminal rosette. *Scale-bars*: 27,29, 10 μ m; 28,31, 50 μ m; 30, 5 μ m.

qual spicules and recurrent cordons (Bartlett & Anderson, 1996). The remainder of the Skrjabinocerca species are similar to the S. canutus in having dissimilar spicules; however, they differ in the possession of a longer right spicule (see Table 1 and references therein). S. prima can be differentiated from S. canutus in having a stilletto-shaped and sharply pointed left spicule, and a longer body and cordons (Shikhobalova, 1930). The main difference between S. americana and the species described here are the size and morphology of the left spicule, since the former has a longer spicule with two delicate, digitiform projections on its distal end (Wong et al., 1987; Wong & Anderson, 1993). In addition, S. americana possesses smaller eggs than the new species and the female has the single postanal papilla strongly developed, weakly developed or absent (Wong et al., 1987; Bartlett et al., 1989; Wong & Anderson, 1993), while in S. canutus it is always well developed. Finally, S. europaea can be differentiated from the present species because it has recurrent cordons and deirids located posterior to the nerve-ring (Wong & Anderson, 1993).

Discussion

The specimen of Calidris canutus rufa was infected with the third and fourth larval stages, juveniles and adults of Skrjabinocerca canutus n. sp. Gradual variations in several structures were observed between larval and adult stages. The cephalic papillae change their position between the third-stage and fourth-stage larva; the deirids are monocuspid in third-stage, bicuspid in the fourth and tricuspid in juvenile and adult stages; the lateral alae arise at the level of cephalic papillae in the third-stage larva and are just posterior to the deirids in the other stages; the postdeirids are diamond-shaped in the third-stage larva, linguiform in the fourth larval stage and digitiform in the adults; there is a large papilla present posterior to the anus in the third-stage larva which is little smaller in the fourth stage and is present in adult females but absent in males; and the third-stage larva has a pointed protuberance on the tip of its tail, whereas the fourthstage larva has a slightly developed terminal rosette of 'tubercles', which is fully developed in adult females and absent in males.

In general, the morphology and size of all Skrjabinocerca species is homogeneous (Table 1). The main characters used to distinguish between them are the size of the spicules, the shape of the distal extremity of the left spicule, and the recurrence or not of the cordons. The tip of the left spicule can be sharply pointed or have one or two delicate digitiform projections. We noted that this projection in S. canutus is often difficult to observe using the light microscope. This is because its membranous nature causes the projection to fold when the specimen is rolled under a coverslip. Moreover, this membranous, digitiform projection cannot be seen from the left side, because it arises ventro-dextrally (Figures 8,9). With regard to the cordons, we found one female specimen (among 50 adults observed) with one cordon which was slightly recurrent. A similar finding was made by Shikhobalova (1930) for S. prima. It is interesting to note that the cephalic papillae are located dorsally and ventrally to cordons in the third-stage larvae (Figure 22) but change their position after the moult to fourth stage (Figures 10, 27). This fact was figured by Bartlett et al. (1989) when describing the experimental development of S. americana.

The females of Skrjabinocerca species are characterised by the presence of some form of projections on the tip of tail. These structures were mentioned as 'sharply pointed papillae, gathered in the form of rosette' by Shikhobalova (1930), 'finger-like cuticular projections' by Bartlett et al. (1989), 'tubercles' by Wong & Anderson (1993) and 'blunt digitiform appendages' by Bartlett & Anderson (1996). We have observed, using the scanning electron microscope, that these structures have the same appearance as the usual caudal papillae in the males (see the knob on the tip of the projection indicated with an arrow head in Figure 21). It seems to indicate that they are not simple cuticular projections; therefore, we tend to agree with Shikhobalova (1930), who called them 'papillae'. Surrounding the main terminal rosette there are a variable number of small papillae, as observed by Wong & Anderson (1993) in S. europaea. The terminal rosette is also present in both sexes of the fourth-stage larva of S. canutus and also in S. americana (see Wong & Anderson, 1993), but it is lost in the adult male.

The presence of larval worms appear to indicate that these acuariids were acquired at some stopover

site in the south of Uruguay, while the bird was migrating north.

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