The genus *Discolaimus* in Southern Africa. I. Introduction and redescription of *D. krugeri* Furstenberg & Heyns, 1966 (Nematoda: Dorylaimida)

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A survey of the literature leads to the conclusion that males are rare or absent in about half of the known species of *Discolaimus* and probably seldom functional, except in two species where spermathecae are present in the female reproductive system, viz. *D. krugeri* and *D. levinae*. The structure of the female gonads and the location of the oesophageal gland nuclei are discussed. A redescription of *D. krugeri* is given, based on material from several localities in South Africa as well as a single male from Namibia.

Key words: Nematoda, *Discolaimus*, *D. krugeri*, morphology, taxonomy, southern Africa.

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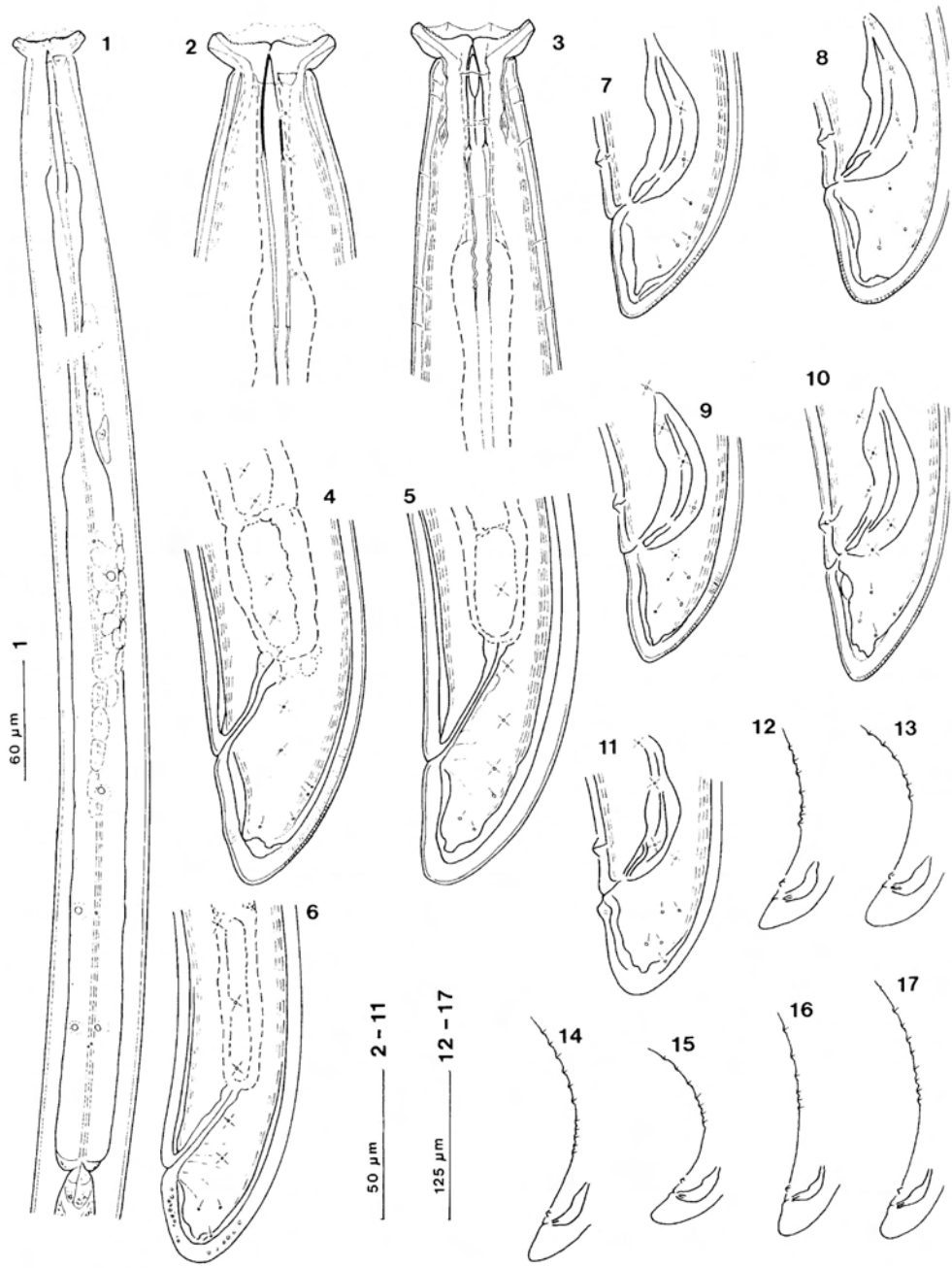
Introduction

This paper is the first in a series reporting on previously unstudied *Discolaimus* material in the collections of the Biosystematics Division of the ARC—Plant Protection Research Institute—and the Department of Zoology at the Rand Afrikaans University.

Nine *Discolaimus* species have thus far been described or reported from Southern Africa: *Discolaimus acuticapitus* Furstenberg & Heyns, 1966; *D. bicorticus* Furstenberg & Heyns, 1966; *D. brevis* Siddiqi, 1964 (reported by De Bruin & Heyns 1992); *D. intermedius** Heyns & Lagerwey, 1965; *D. krugeri** Furstenberg & Heyns, 1966; *D. levinae* Furstenberg & Heyns, 1966; *D. major** Thorne, 1939 (reported by Heyns 1963; Van der Vegte & Heyns 1963; Botha & Heyns 1990, 1991; De Bruin & Heyns 1992); *D. monoplanus** Heyns, 1963; *D. similis* Thorne, 1939 (reported by Furstenberg & Heyns 1996). Species marked with an asterisk have been recorded from the Kruger National Park.

Sauer & Annells (1985) described three new and two known *Discolaimus* species from Australia. They presented excellent SEM micrographs of the head regions of *D. major* and *D. silvicolus* Sauer & Annells, 1985, as well as a useful discussion not only of the head region morphology but also various other features of *Discolaimus*. They also remarked on the fact that males were either absent or rare in Australian populations of *Discolaimus*. A survey of the literature reveals that males are actually unknown in 15 of the approximately 29 nominal species. On the one hand one may be inclined to ascribe this absence of males purely to chance, since 17 of the original species descriptions were based on five or less adult specimens (*D. acuticapitus*: 3 females, 1 male; *D. affinis* Loof, 1964: 2 females; *D. albarossicus* Merzheevskaya, 1951: ? 1 female; *D. arenicolus* Yeates, 1967: 4 females; *D. auritus* Lordello, 1955: ? 1 female; *D. bicorticus*: 3 females 1 male; *D. elegans* Sauer & Annells, 1985: 5 females; *D. intermedius:* 1 female 1 male; *D. levinae*: 1 female 3 males; *D. monhystera* Thorne, 1939: 4 females 1 male; *D. monoplanus*: 1 female; *D. mucurubanus* Loof, 1964: 2 females; *D. papillatus* Khan *et al.*, 1994: 4 females 1 male; *D. perplexans* Siddiqi, 1964 (=*D. major apud* Andrássy, 1959): 2 females; *D. pizae* Monteiro, 1970: 3 females 2 males; *D. rotundicaudatus* Khan & Laha, 1987: 5 females; *D. tenax* Siddiqi, 1964: 4 females).



Figs 1 - 17. *Discolaimus krugeri*

1: oesophageal region, specimen from Hoedspruit; 2 head holotype; 3: dorso-ventral view of head, specimen from Umhloti; 4- 6: tail of holotype, and females from Hoedspruit and Umhloti respectively; 7-11: tail of allotype, and males from Mtshawu, Hoedspruit, Namibia and Umhloti respectively; 12-17: posterior region of allotype, and males from Mtshawu, Namibia, Hoedspruit, Umhloti and Umhloti respectively.

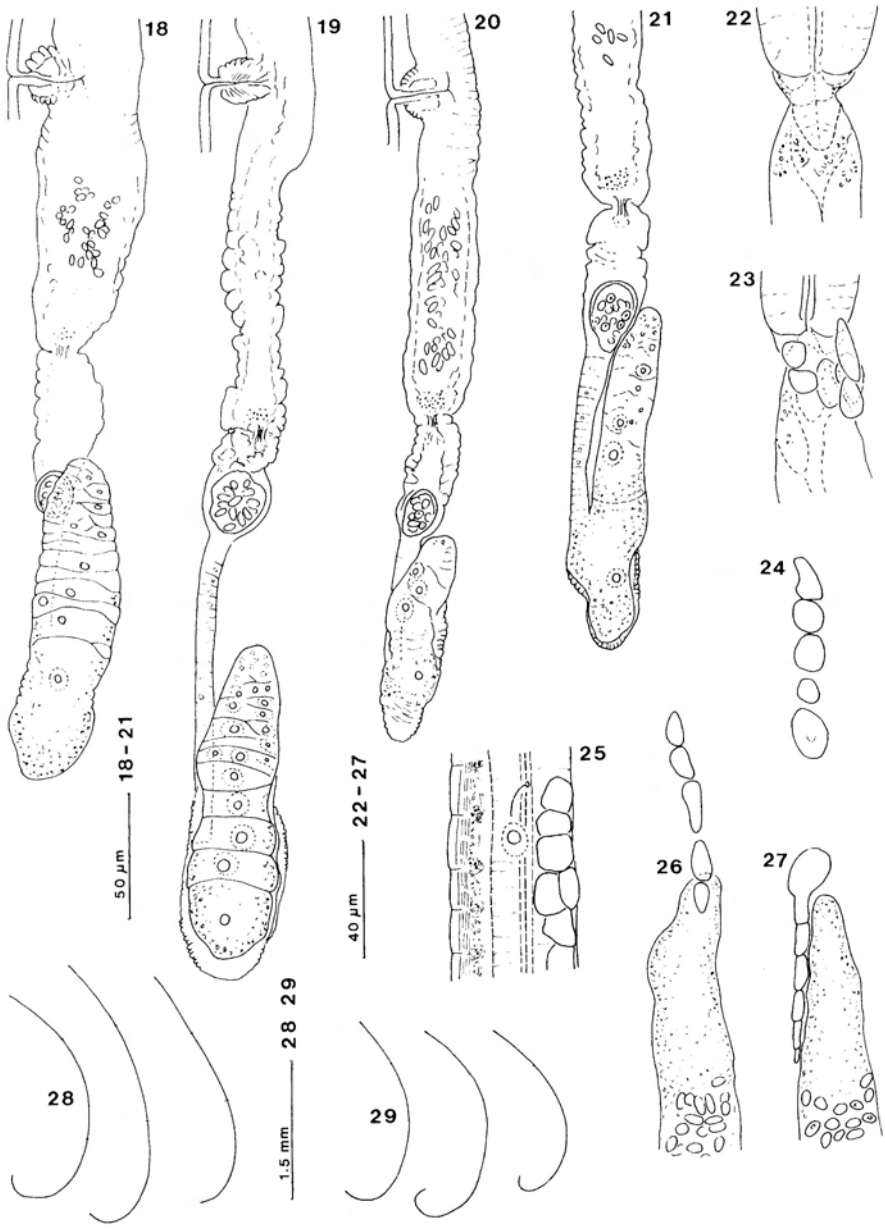
On the other hand, there are a number of species for which relatively large numbers of females have been found, either without or with very few males: *D. agricolus* Sauer & Annells, 1985: 15 females; *D. laksi* Khan & Laha, 1982: 15 females; *D. silvicolus:* 10 females; *D. paramajor* Coomans, 1966: 6 females 1 male; for *D. major* the only males recorded were the two reported together with 25 females from Australia by Sauer & Annells (1985), and for *D. similis* only one male was found among 21 females in South Africa by Furstenberg & Heyns (1966) while no males of this species were found by Thorne (1939, 1974) in the U.S.A., by Siddiqi (1964) in India or Loof (1964) in Venezuela; for *D. texanus* Cobb, 1913, Sauer & Annells (1985) found one male among 25 females in Australia—Thorne (1974), however, stated that males were "rather common" in "Intermountain and Western States" although absent in the "Northern Great Plains" of the U.S.A. *Discolaimus krugeri* seems to be the exception to the rule since the original description by Furstenberg & Heyns (1966) was based on equal numbers of males and females (six each) and the present paper reports a further five males and four females.

It is interesting that *D. krugeri* and *D. levinae* (known from three males and one female only) are the only two species in which both spermathecae and spermatozoa have been recorded in the female reproductive system (Furstenberg & Heyns 1966). The only other species where the presence of spermatozoa was reported in the female are *D. acuticapitus*, *D. monoplanus* and *D. pizae*. It would be worthwhile to re-examine these three species for the presence of spermathecae.

Obviously, it is possible that spermatozoa may have been overlooked in other species, since few authors seem to have paid much attention to the reproductive system, most descriptions having sufficed with "gonads paired, opposed, reflexed". There-against, both Coomans (1965) in his detailed description of the female system of *D. paramajor*, and Sauer & Annells (1985) in their redescription of *D. major*, explicitly stated the absence of spermatozoa in the females, despite the presence of males in the populations. This strengthens the impression that in most *Discolaimus* species males are either totally absent, or rare and seldom functional.

Apart from Coomans' detailed description of the female reproductive system, and another such description by Khan *et al.* (1994) for *D. papillatus*, several other descriptions included less elaborate illustrations of the gonads. All of these showed the female reproductive system in *Discolaimus* to be of the typical, generalised dorylaim type without any special features. The only notable exception is *D. levinae*, where each reproductive branch contains two spermathecae, one in the uterus and another in the oviduct (Furstenberg & Heyns 1966). These authors also suspected spermathecae to be present in the oviducts of *D. krugeri*, confirmation of which is given in the present paper.

Thorne (1939) was the first to illustrate the five oesophageal gland nuclei in a *Discolaimus* species, viz. *D. major*. This showed the dorsal nucleus to be some distance behind the oesophageal expansion, the S_1N_1 and S_1N_2 some distance apart, and the S_2N_1 and S_2N_2 almost at the same level, near the base of the oesophagus. Between 1939 and 1970, when Loof & Coomans' comprehensive work on oesophageal gland nuclei in dorylaims was published, most authors describing *Discolaimus* species paid little attention to the nuclei, except for the dorsal nucleus which is normally the largest and most conspicuous. Exceptions were Lordello (1955) who referred to "five nuclei" in the oesophagus of *D. auritus*, even though his Fig. 1A seems to show six nuclei, albeit in rather unusual locations. Siddiqi (1964) showed only the dorsal and presumably one S_2N in *D. brevis*, and the dorsal plus the two S_1 nuclei in *D. tenax*. This does not imply that the other nuclei are absent in these two species, since in many specimens the nuclei are either difficult or even impossible to see, depending on how the specimens were killed, fixed and processed. Coomans (1966)



Figs 18-29. *Discolaimus krugeri*

18-21: posterior branch of female reproductive system of holotype, a female from Hoedspruit and two females from Umhloti respectively; 22: cardiac region without any associated cells, female from Hoedspruit; 23: cardiac region surrounded by numerous cells, male from Mtshawu; 24: group of cells in body cavity associated with apex of ovary, female from Hoedspruit; 25: dorsal view of part of basal bulb in region of dorsal nucleus, with associated flattened cells, also showing lateral body pores on left hand side, female from Umhloti; 26&27: strings of cells in body cavity, associated with anterior testes in males from Hoedspruit and Mtshawu; 28: female body posture, holotype and specimens from Hoedspruit and Umhloti. 29: male body posture, allotype and specimens from Mtshawu and Hoedspruit.

gave detailed data on the locations of the nuclei in *D. paramajor*, but no illustration.

The abovementioned work by Loof & Coomans (1970) supplied biometrical as well as graphic data on the locations of the nuclei in *D. texanus, D. mucurubanus, D. affinis, D. similis, D. major* and *D. major apud* Loof (1964) from Venezuela. In all of these, except the lastnamed, DN lies beyond the middle of the oesophagus (measured from front end to base of expanded part) and S_1N_1 and S_1N_2 lie some distance apart, with K more than 60 %. It is noteworthy that whereas in Thorne's (1939) original description of *D. major* K is approximately 69 %, it is 81–90 % in Loof & Coomans' 22 specimens from Western Europe and 86 % in Sauer & Annells' (1985) Australian specimens of *D. major*. This discrepancy will be looked at in a future paper in this series, where different populations of *D. major* and closely related species will be discussed.

Following Loof & Coomans' paper, authors gave more attention to the nuclei. Khan & Laha (1982) illustrated the normal complement of five nuclei for *D. laksi* and *D. rotundicaudatus*. However, S_1N_1 and S_1N_2 are shown at about the same level in *D. laksi*, and nearly so in *D. rotundicaudatus*, which is rather unusual and needs confirmation. However, S_1N_1 and S_1N_2 are apparently also at about the same level in *D. papillatus* Khan *et al*., 1994, so this may be a common tendency in species from the Indian subcontinent. Sauer & Annells (1985) illustrated the nuclei in the five species described or redescribed from Australia, viz. *D. agricolus, D. elegans, D. silvicolus, D. major* and *D. texanus*. In all of these the locations of all five nuclei conform to the generalised pattern as found by Loof & Coomans (1970) for the genus *Discolaimus*.

More recently Andrássy (1998, 1999) proposed a modification to Loof & Coomans' system of expressing the spatial relationships of the nuclei, using as the fixed point of reference for S_1N_1; S_1N_2; S_2N_1; S_2N_2 (indicated as AS_1; AS_2; PS_1; PS_2 by Andrássy) the location of the dorsal nucleus (D) rather than the front end of the body or the level of the expansion in the oesophagus. There is some merit in this system, as well as in Andrássy's way of graphically presenting the data. The present paper thus uses both systems, in spite of possible criticism of repetition: the new system because of its merits, the old system for the sake of comparison with the existing literature on the species concerned. That part of the oesophagus lying posterior to the dorsal nucleus is termed the glandularium by Andrássy. The position of D is determined in the same way as in the Loof & Coomans system and K is also similarly calculated, viz. the position of S_1N_1 (=AS_1) expressed as a percentage of the distance between DN(=D) and S_1N_2 (=AS_2).

Discolaimus krugeri Furstenberg & Heyns, 1966

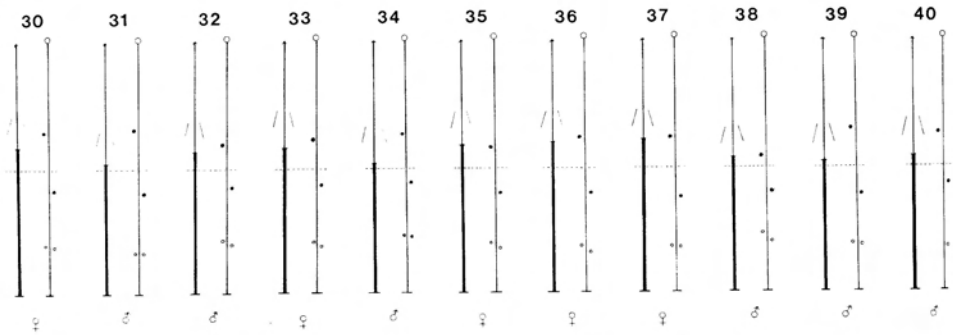
(Figs 1–40; Tables 1 & 2)

Material available

Of the type specimens only the holotype female and allotype male remained suitable for study, albeit much flattened. Also available were a male from near the bank of the Mtshawu River in the Kruger National Park, a female and male from Hoedspruit in the Northern Province, three females and two males from Umhloti in KwaZulu-Natal and a single male collected between Omaruru and Otjiwarongo in Namibia.

Description

Body assuming a wide-open C-shape when relaxed with most of the curvature in the posterior third, more so in the male than in the female. Cuticle consisting of several layers, with minute but distinct transverse striae in the thin outer layer, but also visible as oblique striae in the thicker middle layer around the tail. Cuticle 3–5 µm thick just behind the lip region, 3.5–4 µm around midbody, and 5–6 µm on dorsal side of tail. Lateral chord very narrow on anterior part of neck, gradually broadening to about



Figs 30-40. Position of oesophageal gland nuclei in specimens of *Discolaimus krugeri* from different populations, presented according to Andrassy's system. The left hand column in each figure represents the entire oesophagus measured from the anterior end of the body, with the glandularium encompassing the thickened section. (The position of the basal expansion is shown as in the conventional diagrams of Loof & Coomans, 1970). The right hand column represents the glandularium, showing the positions of the subventral gland nuclei. The horizontal stippled lines indicate the middle (50 %) of the oesophagus and glandularium respectively. 30&31: holotype and allotype from the Kruger National Park; 32: male from Mtshawu, 33&34: female and male from Hoedspruit; 35-39: three females and two males from Umhloti; 40: male from Namibia.

12–16 % of the body diameter from the base of the oesophagus onwards, and further increasing in width at the tail region. Lateral body pores more easily visible towards posterior end, where the lateral organs from which they originate become larger and more conspicuous. Lateral pores in a rather irregular single line, except posteriorly where they become slightly staggered; numbering 136–178 (152). Ventral pores mostly indistinct, present over entire length of body. Dorsal pores seen in some specimens only, indistinct, limited to anterior part of neck, numbering 9–17. Hemizonid distinct, situated opposite or anterior to nerve ring, at 136–178(15) µm from anterior end, the nerve ring at 144–184(160) µm. Lip region typical, expanded, angular. Amphid funnel to stirrup-shaped, 7–9 µm wide, or 27–36(31.3) % of the corresponding body diameter. Odontostyle 26–36(31.5) µm in length, 3.5–5.5 µm in diameter, the aperture 15–19.5(17.0) µm, always slightly more than half the odontostyle length at 51.4–57.1(54.3) %. (Due to a printing error the aperture was reported as 20–29 µm in the original description of *D. krugeri*). Odontophore 46–57(50) µm in length. Guiding ring broad, plicated, situated 3–7 m behind the lip region. Oesophagus with a moderate anterior swelling surrounding the base of the odontophore, followed by a second less conspicuous swelling before it narrows to 8–12 µm where it passes through the nerve ring, then rather abruptly expanding at 32–38 % to form the basal bulb, which is always roughly the same width throughout, but varies from 28 to 35 µm in diameter among specimens. Locations of oesophageal gland nuclei are given in Table 2 and graphically presented in Figs. 30–40. At the base of the oesophagus the surrounding sheath of connective tissue thickens to form a thick transparent ring around the base of the cardia. Cardia consisting of two sections, a proximal smaller apparently more muscular part and a distal longer conoid part projecting into the lumen of the intestine. Flattened cells of unknown origin or function partly envelope the anterior part of the basal bulb in some specimens of the Hoedspruit and Umhloti populations (Fig. 25). Varying numbers of ovoid-shaped cells may also occur in the cardiac region of some specimens in all populations (Fig. 23). Lastly, strings of glob-

Table 1
Biometrics of several populations of Discolaimus krugeri

	Holotype	Allotype	Mtshawu	Hoedspruit		Umhloti				Namibia	
	female	male	male	female	male	female	female	female	male	male	male
L (mm)	3.21	2.48	2.93	3.34	2.37	2.75	2.88	3.01	2.49	2.53	2.85
a	44[a]	31[a]	53	48	47	44	52	53	36	45	48
b	4.3	4.4	4.4	4.1	4.2	3.9	3.9	4.2	4.5	4.6	4.0
c	80	80	84	89	68	95	103	103	82	77	81
c'	0.95	0.91	0.88	0.96	1.0	0.81	0.80	0.83	0.74	0.89	0.97
V	57.9	-	-	55.3	-	54.2	53.5	56.1	-	-	-
Lip region width (µm)	45	38	39	40	38	41	40	41	34	34	41
Odontostyle (µm)	35	29	32	32	28	34	35	36	26	28	31
Odontophore (µm)	57	47	49	56	46	46	49	48	47	46	56
Oesophagus (µm)	728	569	653	804	567	702	722	720	554	544	687
Basal bulb (µm)	489	359	432	547	350	475	494	497	342	337	444
Basal bulb %	67	63	66	68	62	68	68	69	62	62	65
Tail length (µm)	40	31	38	38	35	29	28	29	31	33	35

[a] Specimen flattened

ular cells may be associated with the apices of ovaria and testes (Figs 24, 26 & 27). In some specimens cells of all three types were observed, in others none at all. Prerectum mostly longer than rectum, 38–55(47.5) µm and without posterior blind sac, rectum 33–47(39) µm long, equal to or slightly longer than the anal body diameter. Tail dorsally convex, the terminus bluntly rounded, shorter than or equal to anal body diameter; with three or four caudal papillae.

Vulva transverse; vagina perpendicular to body axis, 28–33 µm long, 43–51 % of the corresponding body diameter. Some specimens with an indication of a weakly demarcated ovejector, 75–80 µm in length, distinguishable by oblique musculature, with at most a faint constriction separating it from the rest of the uterus. Uterus, measured from vagina to sphincter, 110–145(124) µm in length. Distal part of uterus, adjoining the sphincter, with some small darkish objects, reminiscent of the crystalloids found in some *Xiphinema* species. Between the broad *pars dilatata* and the long slender part of the oviduct consisting of flattened, discoid cells, there occur a globular, vacuolated or thick-walled part apparently serving as a spermatheca. Total length of oviduct 101–170 (131) µm, and of ovary 87–143(119) µm, the large variation probably resulting from specimens being in different stages of the reproductive cycle.

Male

Males on average somewhat smaller than females, 2.37–2.93(2.61) µm *vs* 2.75–3.34(3.04) µm, with accordingly narrower lip region, shorter odontostyle, etc. Furthermore, the basal bulb is also relatively shorter in the male than in the female, 62–66 (63.3) % *vs* 67–69(68.0) % in the female, with DO and DN accordingly further posterior: DN 44.1–48.2(47.0) % in the male *vs* 39.7–42.3(41.6) % in the female. Supplements consisting of an adanal pair and three to five more or less contiguous ones situated beyond the spicules, plus a series of three to six solitary ones further forward, the total number of ventromedian supplements varying from six to eleven (3+4 in allotype, 3+3 in the male from Mtshawu River, 4+3 in the male from Hoedspruit, 3+3 and 4+5 in the

Table 2

Locations of oesophageal gland nuclei in several populations of Dorylaimus krugeri *presented by two different methods*

	Holotype	Allotype	Mtshawu	Hoedspruit		Umhloti					Namibia
	f	m	m	f	m	f	f	f	m	m	m
System of Loof & Coomans (1970)											
DO	38.7	44.4	40.8	39.1	44.6	36.6	37.4	37.2	44.5	43.6	43.1
DN	41.6	48.1	44.1	42.3	48.1	41.5	40.2	39.7	48.2	47.2	46.4
DO-DN (µm)	21	21	23	26	20	20	20	19	23	20	23
S_1N_1	62.1	65.9	67.0	64.7	67.0	66.2	63.0	62.9	66.4	71.5	66.4
S_1N_2	75.7	79.1	76.6	75.3	77.6	76.9	72.2	77.2	80.0	79.0	77.7
S_2N_1	88.5	91.2	87.7	88.1	87.8	88.5	88.9	89.2	90.4	87.9	90.8
S_2N_2	88.9	91.4	88.5	89.2	88.0	89.5	90.4	89.4	90.8	89.3	90.8
K	60.1	57.7	70.2	68.4	64.1	69.8	63.5	61.9	57.4	76.8	63.9
System of Andrássy (1998, 1999)											
D	41.6	48.1	44.1	42.3	48.1	41.5	40.2	39.7	48.2	47.2	46.4
AS_1	35.3	34.5	40.7	38.8	36.4	42.3	38.2	38.5	35.2	46.0	37.2
AS_2	58.8	59.8	57.9	56.7	56.8	60.6	60.2	62.2	61.3	59.9	58.2
PS_1	80.2	83.1	78.6	79.1	76.5	80.5	81.5	82.0	80.8	76.7	-
PS_2	80.9	83.4	80.0	81.0	76.9	82.5	83.8	82.5	81.5	79.6	82.3

males from Umhloti and 5+6 in the male from Namibia. Spicules 53–64(57) µm along the curved median line. Lateral guiding pieces 12–15(13.5) µm long. Sperm cells in vas deferens oblong, measuring 7.5–8 x 4–4.5 µm.

Remark on Umhloti population

As can be seen in Fig. 6 there are granular inclusions (or small vacuoles?) in the cuticle on the tail of specimens from Umhloti. The tail is also shorter and more bluntly rounded than in other populations, resulting in greater c-ratio and smaller c'-ratio (Table 1). The spicules are somewhat differently shaped, narrower, and with the antecorpus equal to or slightly longer than the postcorpus (see Andrássy 1997 for spicule terminology), whereas decidedly shorter (41–45 % of spicule length) in other populations. Furthermore, in both the spicules and the lateral guiding pieces the proximal end is distinctly ventrally bent (Fig. 11). However, until more information about distribution and variation in this species become available, I shall refrain from designating this population as a distinct subspecies of *D. krugeri*, or possibly even a separate species.

References

ANDRÁSSY, I. 1997. Nematodes in the Hévizi Lake (In Hungarian, with extensive English summary). *Allattani Közlemények* 82: 13–27.

ANDRÁSSY, I. 1998. The genus *Boreolaimus* gen.n. and its six species (Dorylaimida: Qudsianematidae), nematodes from the European Arctic. *Fundamental and Applied Nematology* 21: 553–567.

ANDRÁSSY, I. 1999. Once more: the oesophageal gland nuclei in the dorylaimoid nematodes. *Opuscula Zoologica Universitatis Budapestinensis* 31: 165–170.

BOTHA, A. & J. HEYNS. 1990. Dorylaimoidea (Nematoda) from the Kruger National Park. *Koedoe* 33: 47–59.

BOTHA, A. & J. HEYNS. 1991. Dorylaimoidea (Nematoda) from rivers in the Kruger National Park. *Koedoe* 34: 1–24.

COOMANS, A. 1965. Structure of the female gonads in members of the Dorylaimina. *Nematologica* 10 (Year 1964): 601–622.

COOMANS, A. 1966. Some nematodes from Congo. *Revue de zoologie et de botanique africaines* 74: 287–312.

DE BRUIN, S. & J. HEYNS. 1992. Dorylaimida (Nematoda) from Botswana. *South African Journal of Zoology* 27: 156–172.

FURSTENBERG, J.P. & J. HEYNS. 1966. Four new species of the genus *Discolaimus* Cobb, 1913 (Nematoda: Dorylaimoidea) from South Africa, with a description of the male of *D. similis* Thorne, 1939. *Nematologica* 11 (Year 1965): 467–479.

HEYNS, J. 1963. A report on South African nematodes of the genera *Labronema* Thorne, *Discolaimus* Cobb, *Discolaimoides* n.gen., and *Discolaimium* Thorne (Nemata: Dorylaimoidea). *Proceedings of the Helminthological Society of Washington* 30: 1–6.

KHAN, E. & S.K. LAHA. 1982. Seven new dorylaimid nematodes from Indian Agricultural Research Institute Farm, Dehli, India. *Indian Journal of Nematology* 12: 232–249.

KHAN, Z., W. AHMAD & M.S. JAIRAJPURI. 1994. Description of two new species of Dorylaimoidea from India. *Fundamental and applied Nematology* 17: 147–151.

LOOF, P.A.A. 1964. Free-living and plantparasitic nematodes from Venezuela. *Nematologica* 10: 201–300.

LOOF, P.A.A. & A. COOMANS. 1970. On the development and location of the oesophageal gland nuclei in the Dorylaimina. *Proceedings of the IX International Nematology Symposium*. Warsaw, 1967: 79–161.

LORDELLO, L.G.E. 1955. *Discolaimus auritus* n.sp. found inhabiting forest soil in Brazil (Nematoda: Dorylaimidae). *Proceedings of the Helminthological Society of Washington* 22: 29–31.

SAUER, M.R. & C.M. ANNELLS. 1985. Species of *Discolaimus* (Nematoda: Dorylaimoidea) from Australia. *Nematologica* 31: 121– 133.

SIDDIQI, M.R. 1964. Studies on *Discolaimus* spp. (Nematoda: Dorylaimidae) from India. *Zeitschift fuer Zoologische Systematik und Evolutionsforschung.* 2: 174–178.

THORNE, G. 1939. A monograph of the nematodes of the superfamily Dorylaimoidea. *Capita Zoologica* 8: 1–261.

THORNE , G. 1974. Nematodes of the Northern Great Plains. Part II. Dorylaimoidea in part (Nemata: Adenophorea). *Technical Bulletin Agricultural Experiment Station South Dakota State University. Brookings* 41: 1–120.

VAN DER VEGTE, F.A. & J. HEYNS. 1963. A report on nematodes found in soil and root samples from the Kruger National Park. *Koedoe* 6: 134–136.