

TYLENCHORHYNCHUS SPECIES FROM NAMIBIA (NEMATODA: BELONOLAIMIDAE)

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ABSTRACT

Key words: Belonolaimidae, Namibia, Nematoda, SEM, taxonomy, *Tylenchorhynchus*

One known and three new *Tylenchorhynchus* species are described and illustrated from Namibia. *Tylenchorhynchus kidwaii* n. sp. is characterised by a continuous lip region with 7-9 annuli, moderately sclerotized cephalic framework, strong stylet with well-developed basal knobs, absence of longitudinal striae, regularly areolated lateral field, and cylindrical tail with broadly rounded, annulated terminus. *Tylenchorhynchus namibiensis* n. sp. is distinguished by a set off, rounded head, moderately developed stylet, distinct basal knobs, areolated lateral field, and presence of a postanal intestinal sac. *Tylenchorhynchus spec.* is distinguished by small body size, set off head, interrupted longitudinal striae in neck region, weakly developed stylet with distinct basal knobs, non-areolated lateral fields, and conoid tail with smooth terminus. *Tylenchorhynchus brevilineatus* Williams, 1960 is reported and described for the first time from Namibia.

Uittreksel

TYLENCHORHYNCHUS-SPECIES VAN NAMIBIË (NEMATODA: BELONOLAIMIDAE)

Een bekende en drie nuwe Tylenchorhynchus spesies word uit Namibië beskryf. Tylenchorhynchus kidwaii n. sp. het 'n aaneenlopende lipgedeelte met 7-9 annules, redelik sterk gesklerotiseerde kopskelet, laterale veld met reëlmatige areolaries, geen lengteverlopende striasies nie en 'n stomperonde stertpunt met annulasies. Tylenchorhynchus namibiensis n. sp. het 'n geronde afgesnoerde lipgedeelte, laterale veld met areolaries en 'n postanale intestinale sak. 'n Ander nuwe Tylenchorhynchus-spesie word van 'n enkele eksemplaar beskryf maar voorlopig nie benaam nie. Tylenchorhynchus brevilineatus Williams, 1960 word vir die eerste keer uit suidelike Afrika aangemeld en beskryf.

INTRODUCTION

This is the second paper in the present series dealing with plant-parasitic nematodes from Namibia. For information on material and method of preparation see Rashid *et al.* (1990).

During the present study three new species of *Tylenchorhynchus* were found, of which two are described as *T. kidwaii* n. sp. and *T. namibiensis* n. sp. A third species is described from a single female but not named. *T. brevilineatus* Williams, 1960, recorded from Namibia for the first time, is also described and figured.

DESCRIPTIONS

***Tylenchorhynchus kidwaii* n. sp. (Fig. 1A-I and Fig. 2A-C)**

Measurements

Holotype female: L = 1,19 mm; a = 49,9; pharynx = 149 µm; b = 8,0; tail = 46,5 µm; c = 26,4; c' = 2,3; V = 55 %.

Paratype females (n = 6): L = 1,14 mm (1,08-1,24); a = 46,9 (41,6-52,0); pharynx = 145,7 µm (130,5-162); b = 7,9 (6,6-8,7); tail = 35,7 µm (34,5-39,0); c = 32,3 (29,2-38,0); c' = 1,6 (1,4-1,9); V = 53 % (51,4-57,0).

Paratype males (n = 6): L = 1,04 mm (1,01-1,08); a = 47,3 (39,7-51,8); pharynx = 139 µm (131,5-151,0); b = 7,55 (6,9-8,0); tail = 42,8 µm (39,0-48,0); c = 24,6 (22,6-27,4); c' = 2,7 (2,4-3,2); stylet = 20,3 µm (19,5-23,0).

Female: Body cylindrical, strongly ventrally curved to "C"-shaped when relaxed, tapering at both ends. Cuticle 1,5-2,0 µm thick, coarsely annu-

lated, annuli 1,0-1,5 µm wide. Lateral field with four incisures, originate as two lines just posterior to stylet knobs, a third line appears after a short distance, and dividing into two lines at the level of the median bulb (Fig. 1E); lateral fields regularly areolated (Fig. 3B); all four lateral lines extend beyond phasmid (Fig. 1H and I). Longitudinal cuticular striae absent. Lip region continuous with body, anteriorly flattened with rounded sides, about 4 µm high with 7-9 annuli; anterior cephalids dot-like in lateral view (Fig. 1D, F & Fig. 3A). Cephalic framework moderately sclerotized. Stylet 20,7 µm (19,5-23,0) long, strong, with tubular metenchium, basal knobs well-developed, rounded to slightly concave anteriorly. Dorsal pharyngeal gland orifice 1-2 µm from stylet base. Procorpus cylindrical or rarely swollen in posterior half; median bulb spherical to ovate, strongly muscular with well-developed valve; isthmus short; basal bulb elongate-pyriform; intestine slightly overlapped by basal bulb. Dorsal pharyngeal gland nucleus large, rather indistinct, anteriorly located; subventral gland nuclei smaller, located at middle or near base of basal bulb, difficult to discern. Pharyngo-intestinal valve indistinct. Intestine overlaps rectum, reaches to about middle of tail (Fig. 1H and I). Excretory pore 142,8 µm (128-155) from anterior end, varies in position from opposite to behind the basal bulb (Fig. 1B, C, D and F). Nerve ring 113,4 µm (102,5-120,0) from anterior end, encircling anterior or posterior end of isthmus. Hemizonid and deirid not seen. Intestinal fasciculi absent.

Reproductive system tylenchoid, ovaries paired, opposed, outstretched, oocytes in multiple rows in germinative zone. Spermatheca distinct, filled with small rounded sperm cells. Vulva a transverse slit with double epiptygma. Vagina length about half of vulval body width. Uterus with seven pairs of cells. Tail cylindrical with 23-29 annuli on ventral side, terminus broadly rounded, annulated (Fig. 1H, I and 3C). Phasmid at 55 % (35-64) of tail length.

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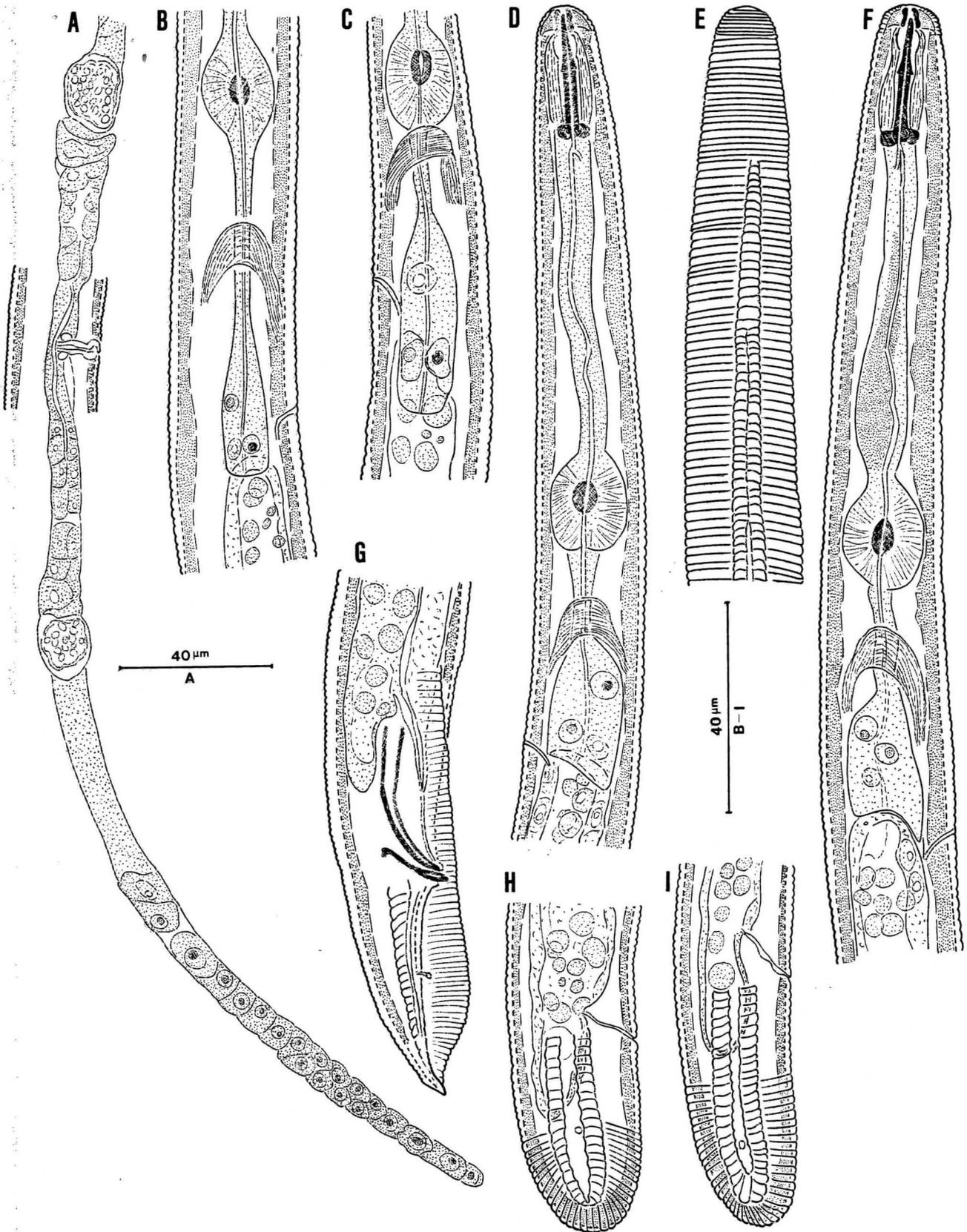


FIG. 1 *Tylenchorhynchus kidwii* n. sp. A. Female reproductive system (posterior branch); B. Male pharyngeal region, with long isthmus; C. Female pharyngeal region, excretory pore more anterior; D. Male anterior region; E. Female anterior region (surface view); F. Female anterior region; G. Male tail; H and I. Female tails

Male: Similar to female in general appearance. Monorchic, testis anteriorly outstretched. Spicules 27,0 µm (23,5–29,0) long, ventrally arcuate, cephalated. Gubernaculum 11,0 µm (9,5–12,5) long, knobbed at proximal end and curved distally. Caudal alae crenate, extend from slightly anterior to

the proximal end of the spicules to the tail terminus. Lateral field with four incisures, aerolated. Phasids distinct, at 42,2 % (36–47) of tail length, opening on caudal alae. Tail conoid, ventrally curved, terminus finely rounded, smooth.

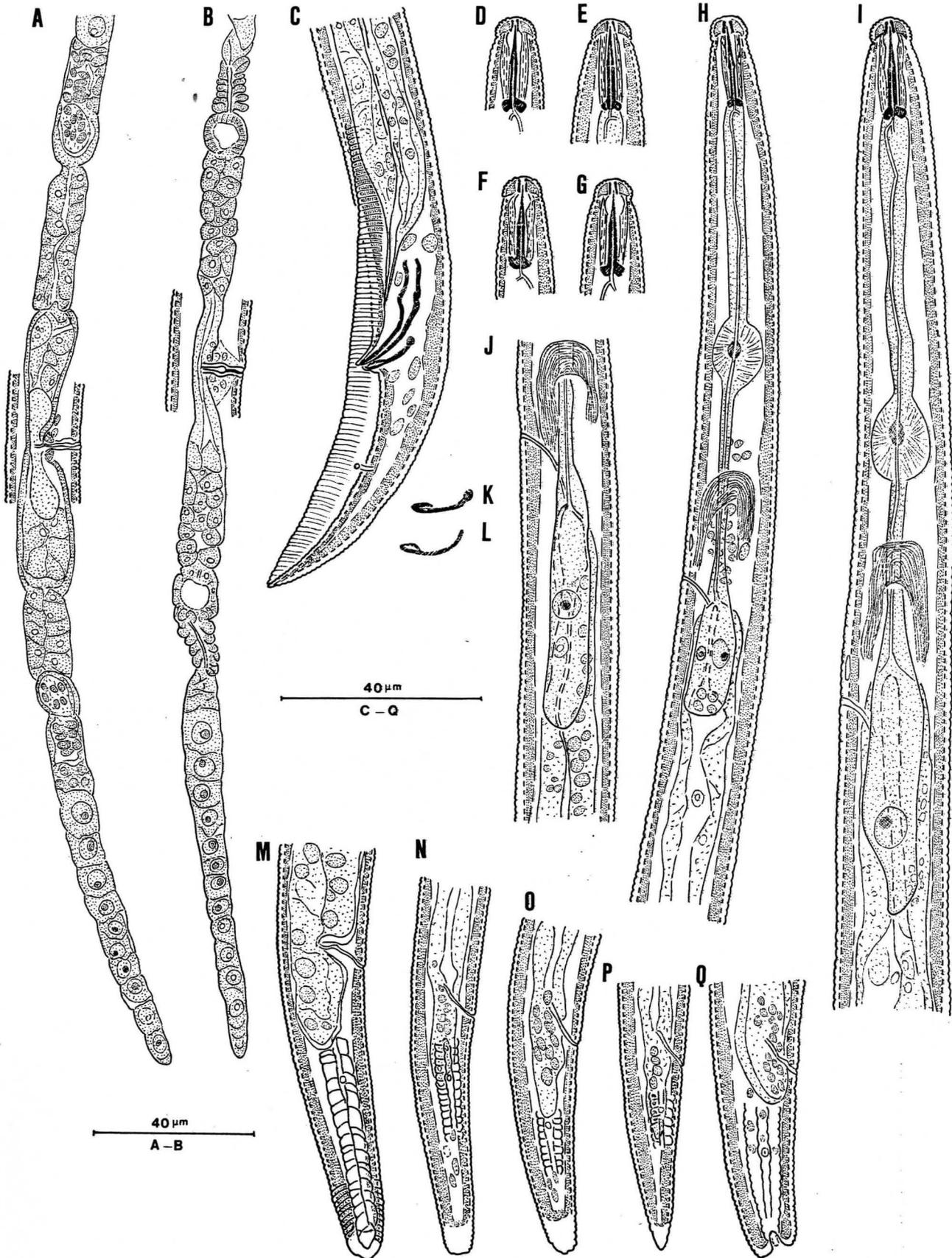
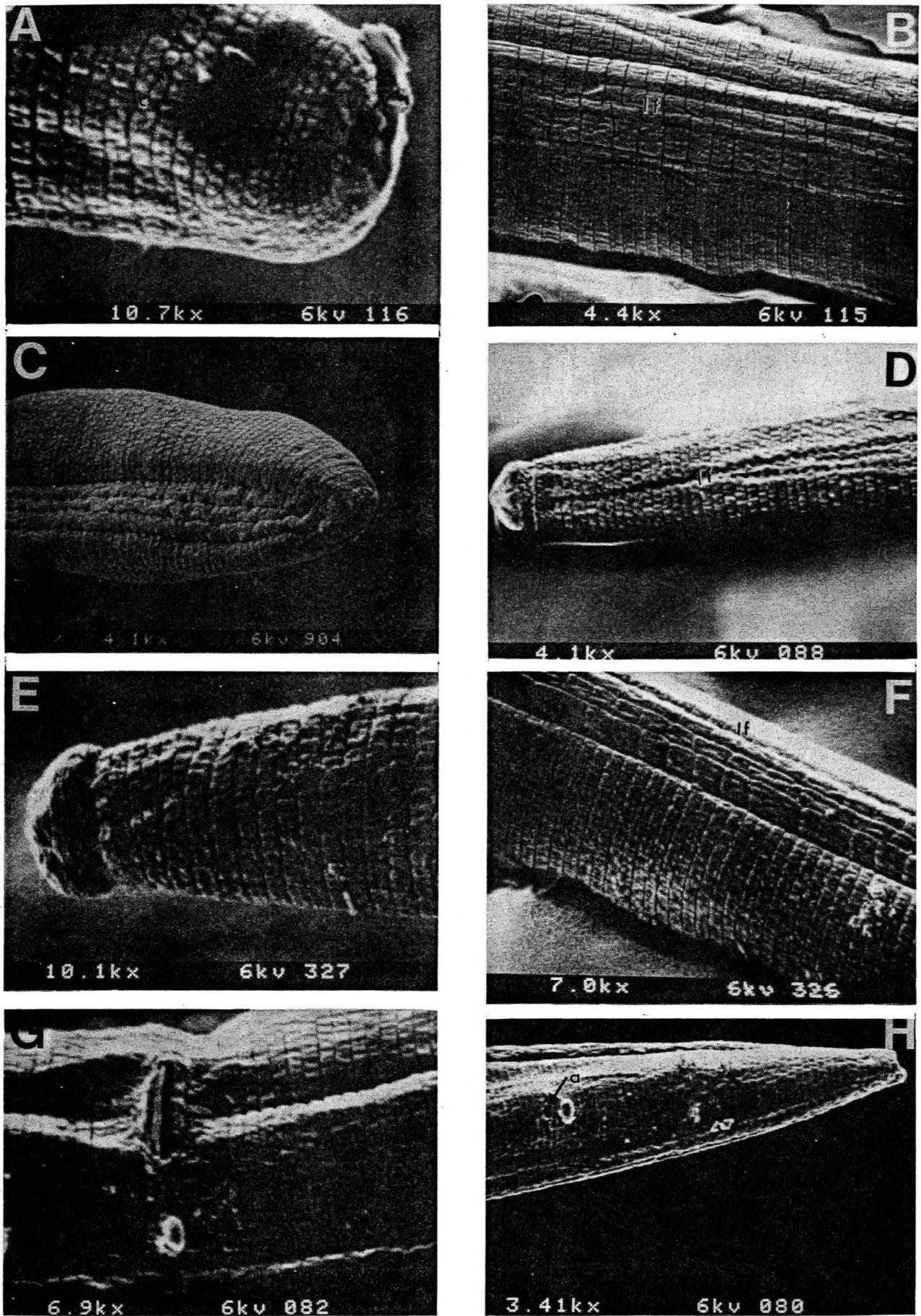


FIG. 2 *Tylenchorhynchus namibiensis* n. sp.: A and B. Female preproductive system (posterior branch); C. Male tail region; D-G. Female heads, showing variation in stylet knobs; H. Male anterior region; I. Female anterior region; J. Female pharyngeal region with more anterior excretory pore; K and L. Gubernaculum; M-P. Female tails, showing variation; Q. Aberrant female tail

Differential diagnosis: *Tylenchorhynchus kidwail* n. sp. resembles *T. maximus* Allen, 1955, *T. annulatus* (Cassidy, 1930) golden, 1971, *T. wilskii* Kornobis, 1980, *T. sanwali* Kumar, 1982, *T. teeni* Hashim,

1984 and *T. eroshenkoi* Siddiqi, 1986. *T. kidwail* n. sp. differs from *T. maximus* by the stronger stylet, tubular metenchium, well-developed basal knobs, regularly areolated lateral field, presence of a sper-

TYLENCHORHYNCHUS SPECIES FROM NAMIBIA



SEM Photomicrographs of *Tylenchorhynchus kidwaii* n. sp. (A-C): A. Female head (lateral, 10 700 \times); B. Lateral field (4 400 \times); C. Female tail (4 100 \times); *Tylenchorhynchus namibiensis* n. sp. (D-H): D. Female anterior region, showing lateral field (4 100 \times); E. Female head region (lateral, 10 100 \times); F. Lateral field (7 000 \times); G. Vulval region (6 900 \times); H. Female tail (ventral 3 410 \times). (c = anterior cephalids, lf = lateral field, a = anus)

matheca filled with sperm cells and the straight tail. It differs from *T. annulatus* by larger body size (1,08–1,24 mm vs 0,57–0,85 mm), continuous lip region with 7–9 annuli, strong stylet, regularly areolated lateral field, and annulated tail terminus. The new species differs from *T. wilskii* by its continuous lip region, stronger but shorter stylet (19,5–23 µm vs 24–26 µm), longer tail and the phasmid being posterior to middle of tail. *T. kidwāii* n. sp. differs from *T. sanwali* by its greater body length (1,08–1,24 mm vs 0,45–0,71 mm), continuous lip region, stronger stylet, regularly areolated lateral field and posterior position of phasmid. The new species can be differentiated from *T. teeni* by its larger size (1,08–1,24 mm vs 0,63–0,73 mm), stronger stylet, tubular metenchium, continuous lip region, regularly areolated lateral field, absence of intestinal fasciculi, tail without hyaline cuticular portion and spicule shape. The new species differs from *T. eroshenkoi* by the longer body (1,08–1,24 mm vs 0,70–0,89 mm), shorter stylet (19,5–23 µm vs 24–26 µm), continuous lip region, areolated lateral field, annulated tail terminus and the presence of a postanal intestinal sac.

Type locality and habitat: Etosha Game Reserve: Under grass in Namutoni Rest Camp, collected July, 1986 by J. Heyns and A. Coomans.

Type specimens: Holotype female on slide 3067, three paratype females on slides 3090, 3091 and five paratype males on slides 3064, 3067, 3090, 3091 in the collection of the Rand Afrikaans University, South Africa. One paratype female and one male are deposited in the collection of the Instituut voor Dierkunde, Rijksuniversiteit Gent, Ledeganckstraat 35, 9000 Gent, Belgium.

***Tylenchorhynchus namibiensis* n. sp. (Fig. 2A–Q and Fig. 3D–H)**

Measurements

Holotype female: L = 0,83 mm; a = 36; pharynx = 181 µm; b = 4,8; tail = 48 µm; c = 17,3; c' = 2,8; V = 55 %.

Paratype females (n = 11): L = 0,81 mm (0,67–0,88); a = 43,3 (39,4–49,4); pharynx = 161,7 µm (137–178); b = 5,0 (4,1–6,4); tail = 46,5 µm (37–59); c = 19,6 (15,3–21,9); c' = 3,4 (3,0–4,1); V = 53,4 % (47,7–57).

Paratype males (n = 4): L = 0,74 mm (0,69–0,76); a = 40,7 (37,7–44,8); pharynx = 161 µm (135–170,5); b = 4,6 (4,1–5,6); tail = 47,3 µm (43,5–50,5); c = 15,7 (15–16,4); c' = 3,3 (2,9–3,6); stylet = 15,7 µm (14,5–17).

Aberrant female: L = 0,58 mm; a = 28,0; pharynx = 132 µm; b = 4,4; tail = 37,5 µm; c = 15,7; c' = 3,2; V = 55 %.

Female: Body slender, slightly to strongly ventrally curved after relaxation. Cuticle 1–1,5 µm thick, coarsely annulated, annuli about 1 µm wide. Lateral field marked by four incisures which originate just behind lip region as a single line, divide into two lines at about one spear length from basal knobs, a third line appears after a short distance and dividing into two lines at about the level of median bulb, extending as four lines to near the tail terminus, regularly areolated (Fig. 3D, F and H). Lip region low, rounded, distinctly set off from body by a deep constriction, with 6 to 9 annuli, six lobed, lateral sectors separated by longitudinal grooves, labial disc slightly elevated. Stylet 17 µm (15,5–19,5) long, slender, metenchium pointed, appearing non-

tubular, basal knobs rounded, concave or anchor-shaped, directed anteriorly or sloping posteriorly. Orifice of dorsal pharyngeal gland 1–2 µm from basal knobs. Procorpus cylindrical, median bulb spheroid to ovate with distinct valve, muscular; isthmus short to elongate; pharyngeal gland bulb elongate, overlaps intestine for two to three corresponding body widths. Dorsal pharyngeal gland nucleus distinct, located from middle to posterior half of pharyngeal bulb, subventral gland nuclei indistinct. Nerve ring 95,9 µm (86,5–103) from anterior end, encircling middle of isthmus. Excretory pore 116,5 µm (101–137,5) from anterior end, its position varying from opposite isthmus to anterior half of pharyngeal bulb. Hemizonid distinct, 2–4 annuli anterior to excretory pore. Deirid not seen. Intestine overlaps rectum, postanal intestinal sac variable in length (Fig. 2M–Q).

Reproductive system tylenchoid. Ovaries paired, opposed, outstretched, oocytes in single file. Spermatheca small, rounded, empty or with few rounded sperm cells. Vulva a transverse slit (Fig. 3G). Vagina perpendicular to body axis, about half as long as vulval body diameter. Uterus with eight pairs of cells, arranged in groups of two or four pairs. Tail elongate, subcylindrical to conoid, variable in length, with 27–51 annuli on ventral side, terminus finely rounded to truncate, smooth or annulated, Phasmid at 37 % (25–45) of tail length. Anus a small, pore-like opening (Fig. 3H).

Male: Similar to female in general morphology. Monorchic, testis outstretched. Spicules arcuate ventrally, 22,3 µm (20,0–23,5) long. Gubernaculum also arcuate, proximal end knobbed or simple, distal end curved, 12,5 µm (10,5–14,5) long (Fig. 1 K and L). Bursa well-developed with finely crenated margin, enveloping tail. Lateral field with four incisures as in female but fading towards tail terminus. Cloacal opening with protruding lips. Phasmid at 31,8 % (24–37,6) of tail length.

Differential diagnosis: *Tylenchorhynchus namibiensis* n. sp. is distinguished by having a low, set off lip region, and a postanal intestinal sac. The new species closely resembles *Tylenchorhynchus aerolatus* (Baqri & Jairajpuri, 1969) Fortuner & Luc, 1987 and *T. avaricus* (Kleynhans, 1975) Fortuner & Luc, 1987 in most respects but differs from both species by the low lip region and the presence of a postanal intestinal sac. Other nearly similar species are *T. obtusus* (Siddiqi, 1978) Fortuner & Luc, 1987; *T. indicus* (Siddiqi, 1960) Fortuner & Luc, 1987 and *T. tonkiensis* (Mulk & Jairajpuri, 1975) Fortuner & Luc, 1987. From the first two species the new species differs by the areolated lateral fields and the presence of a postanal intestinal sac, it further differs from *T. obtusus* by vulval structure and smaller spicules (20,0–23,5 µm vs 22,0–28 µm). From *T. tonkiensis* the new species differs in having a smaller postanal intestinal sac, shorter spicules (20,0–23,5 µm vs 24–27 µm) and by the structure of the gubernaculum.

Type locality and habitat: Namib Desert: In moist sand in river-bed *en route* to water-hole in Kuiseb River, about 40 km east of Gobabeb, collected July, 1986 by J. Heyns and A. Coomans.

Type specimens: Holotype female on slide 4688, eight paratype females on slides 4695, 4701, 4702, 4714 and four paratype males on slides 4695 and 4699 in the collection of the Rand Afrikaans Univer-

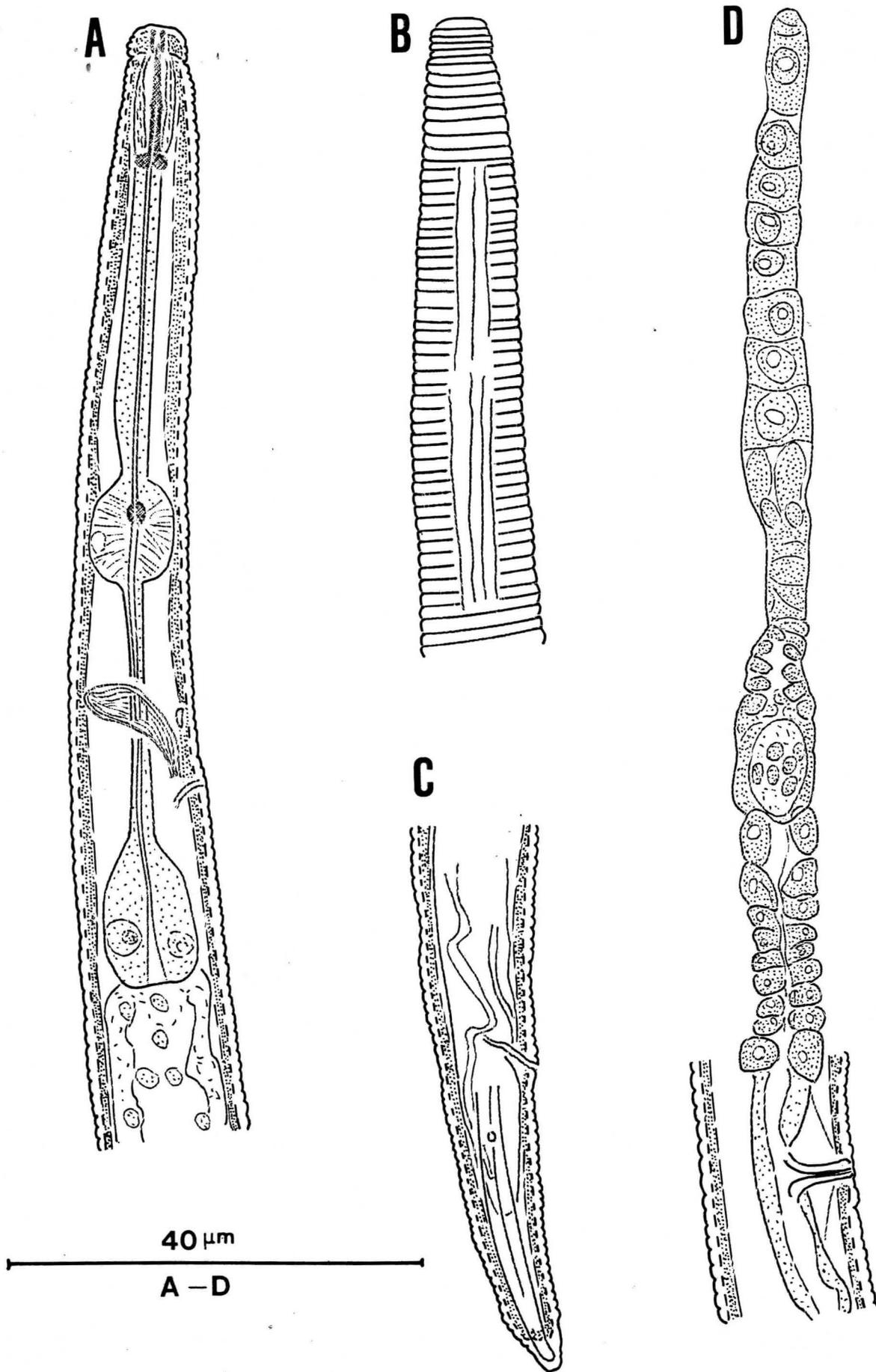


FIG. 4 *Tylenchorhynchus* spec. Female: A. Anterior region; B. Anterior region (surface view); C. Tail; D. Reproductive system (anterior branch).

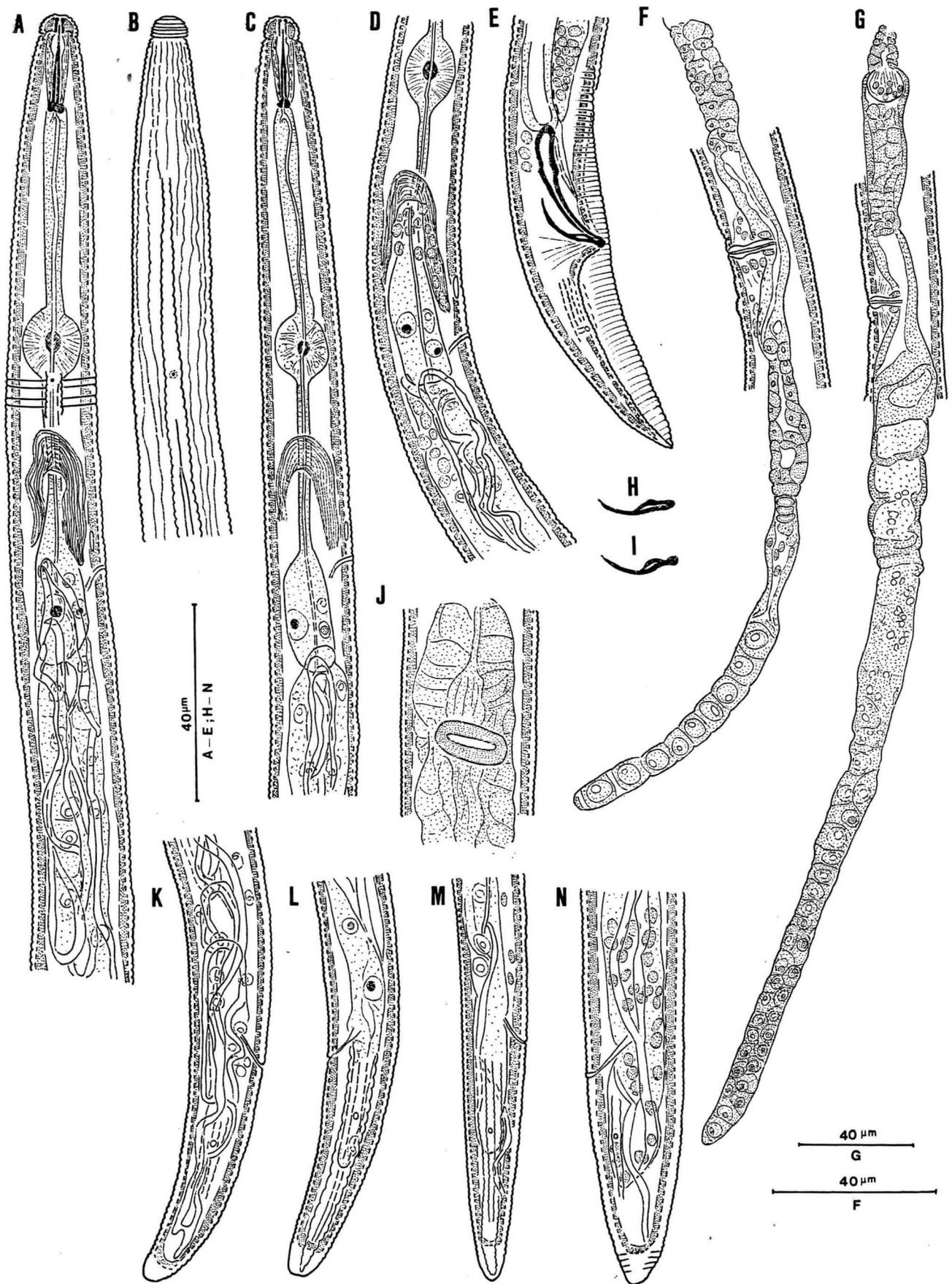


FIG. 5 *Tylenchorhynchus brevilineatus*: A. Female anterior region; B. Female anterior region (surface view); C. Male anterior region; D. Female pharyngeal region showing more posterior excretory pore; E. Male tail region; F and G. Female reproductive system (posterior branch); H and I. Gubernaculum; J. Vulval region (ventral view); K-N. Female tails, showing variation

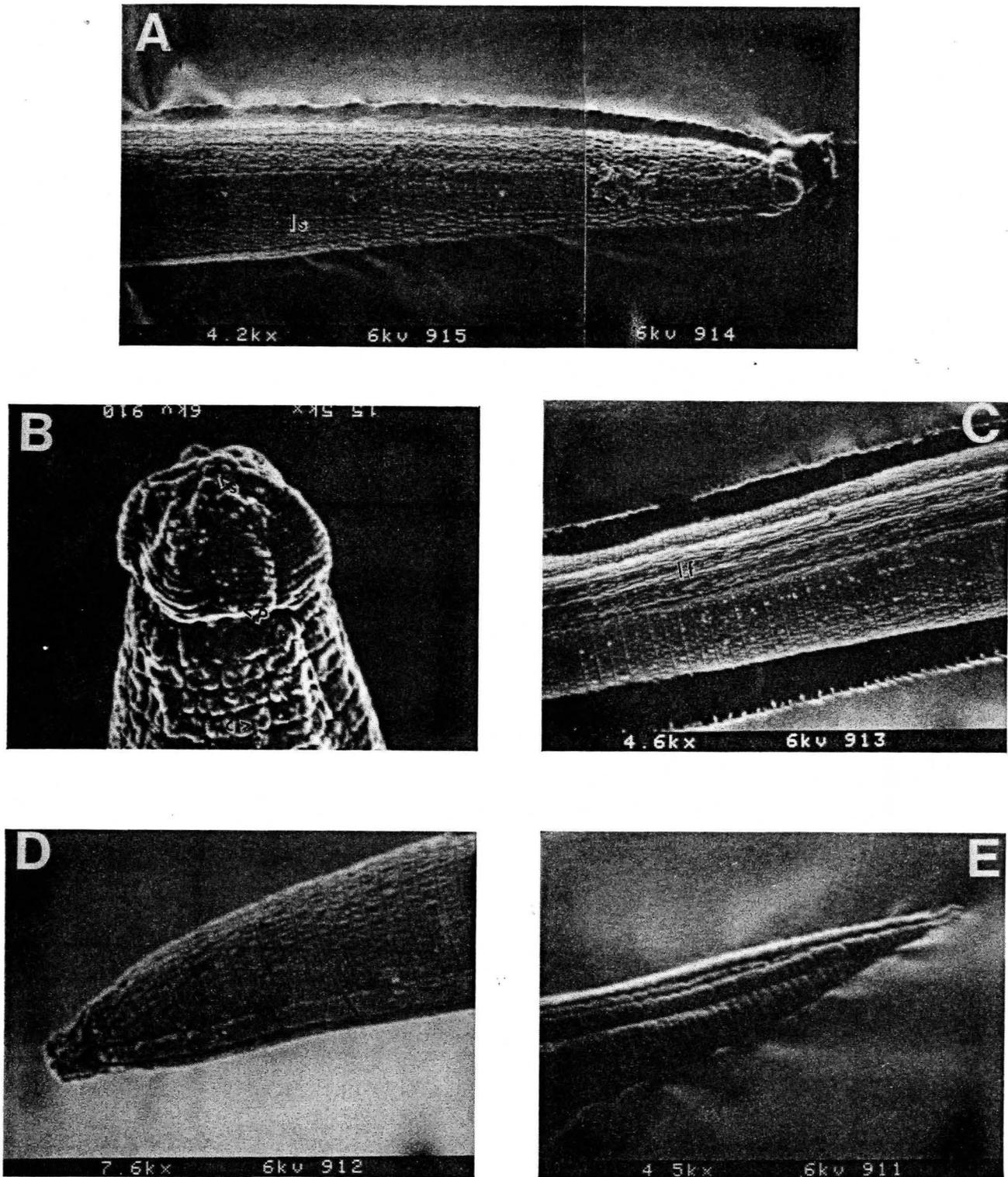


FIG. 6 SEM photomicrographs of *Tylenchorhynchus brevilineatus*. A. Female anterior region, showing longitudinal striae (4 200 \times); B. Female head (15 500 \times); C. Lateral field (4 600 \times); D and E. Female tails (7 600 \times and 4 500 \times). (ls = longitudinal striae, s = sensillae, p = papillae, c = anterior cephalids, lf = lateral field).

sity, South Africa. One paratype female and one paratype male deposited in Instituut voor Dierkunde, Rijksuniversiteit Gent, Ledeganckstraat 35, 9000 Gent, Belgium.

***Tylenchorhynchus* species (Fig. 4A–D)**

Measurements

Female: L = 0,37 mm; a = 24,8; pharynx = 93 μ m; b = 3,8; tail = 30 μ m; c = 12,5; c' = 2,4; V = 57,5 %.

Female: Small, body slightly ventrally curved when relaxed. Cuticle 1,5 μ m thick, finely annulated, annuli about 1 μ m wide. Lateral field rather indistinct in anterior region, three lines observed in posterior region, extending to tail terminus. A few interrupted longitudinal striae observed in anterior region. Lip region rounded, flattened at apex, distinctly set off, with 4 annuli. Stylet slender, 12 μ m long, metenchium pointed, appearing non-tubular,

basal knobs rounded. Orifice of dorsal pharyngeal gland 1,5 μm from spear base. Procorpus cylindrical; median bulb ovate, muscular, valve distinct, slightly anterior to middle of bulb; isthmus rather long; basal bulb pyriform. Dorsal pharyngeal gland nucleus large, distinct, located behind middle of basal bulb, subventral gland nuclei rather small, located near base of basal bulb. Nerve ring 66 μm from anterior end, at middle of isthmus. Excretory pore 73 μm from anterior end, posterior to nerve ring. Hemizonid distinct, opposite nerve ring, 5 annuli anterior to excretory pore. Pharyngo-intestinal junction indistinct. Intestine overlaps rectum up to middle of tail.

Reproductive system tylenchoid. Two genital branches, opposed, outstretched, oocytes in single file. Vulva a transverse slit. Vagina perpendicular to body axis, about half as long as vulval body diameter. Spermatheca ovate, with few sperm cells. Uterus with nine pairs of cells. Tail subcylindroid-conoid with 24 annuli on ventral side, terminus smooth, truncate. Phasmid at 22 % of tail length. Intestinal fasciculi more prominent in posterior region of body (Fig. 4C).

Differential diagnosis: *Tylenchorhynchus* spec. is distinguished by having a small body, set off head, and interrupted longitudinal striae in anterior region. This species resembles *T. contractus* Loof, 1964 and *Tylenchorhynchus* spec. Loof, 1964 but differs from both by smaller size (0,37 mm vs 0,42–0,63 mm and 0,42–0,47 mm respectively), smaller stylet (12 μm vs 16–18 μm and 15–16 μm respectively), and presence of longitudinal striae and a postanal intestinal sac. It further differs from *T. contractus* by the absence of a contraction of the cuticle behind the vulva.

Locality and habitat: Etosha Game Reserve. Under dry grass and *Commiphora pyracanthoides* Engl trees on Tsumasa Hill in Halali Rest Camp. Collected July 1983 by J. Heyns.

Single female on slide 1660 in the collection of the Rand Afrikaans University, South Africa.

***Tylenchorhynchus brevilineatus* Williams, 1960 (Fig. 5A–N and Fig. 6)**

Synonym *Tylenchorhynchus indicus* Siddiqi, 1961.

Measurements

Females (n = 18): L = 0,74 mm (0,60–0,94); a = 36,6 (27,2–44,8); pharynx = 126,3 μm (109,5–143,5); b = 5,8 (4,9–7,2); tail = 46,5 μm (30,0–59,5); c = 16,2 (12,9–27,7); c' = 3,0 (1,7–4,3); V = 53,3 % (51–56,6).

Males (n = 9): L = 0,75 mm (0,58–0,91); a = 39,1 (30,3–43,5); pharynx = 131,3 μm (115–146); b = 5,6 (5,0–6,3); tail = 46,3 μm (40–53); c = 16,3 (13,5–19,6); c' = 2,7 (2,6–3,2); stylet = 16,2 μm (13–22).

Female: Body slightly to strongly ventrally curved after fixation, tapering at both extremities. Cuticle 1 μm thick, coarsely annulated, annuli 1 μm wide. Lateral field marked by four incisures originating as two lines slightly posterior to stylet base, a third line appearing at level of isthmus and immediately dividing into two, outer lines crenate, reaching up to tail terminus, inner lines smooth, fading away beyond phasmid, areolations observed only under SEM (Fig. 6).

Longitudinal, interrupted striae appearing just behind lip region, confined to pharyngeal region, cuticle appearing reticulated under SEM. Lip region distinctly set off from body by a deep constriction; with 6–9 annuli, six lobed, lateral sectors separated by longitudinal grooves, a papilla at the base of each lateral sector, labial disc slightly elevated, oral aperture surrounded by six small papilloid sensillae (observed under SEM) (Fig. 6B). Anterior cephalids 4 annuli behind head (Fig. 6B). Labial framework lightly sclerotized. Stylet slender, 16 μm (13,5–22) long, moderately developed, metenchium sharply pointed, appearing non-tubular, basal knobs rounded, closely appressed. Orifice of dorsal pharyngeal gland 1 μm from base of stylet. Procorpus cylindrical; median bulb spheroid with distinct valve at middle; isthmus short to elongate; pharyngeal bulb pyriform, overlapping pharyngo-intestinal valve slightly or completely. Dorsal pharyngeal gland nucleus distinct, large, varies in position from anterior to posterior part of pharyngeal bulb, subventral gland nuclei usually small, or as large as dorsal nucleus, located at same level or anterior to dorsal nucleus. Nerve ring 83,3 μm (70,5–98) from anterior end, varying in position from middle to base of isthmus. Excretory pore 104,8 μm (93–123) from anterior end, opposite anterior to posterior half of pharyngeal bulb. Hemizonid distinct, 2–5 annuli anterior to excretory pore. Deirid situated at about level of median bulb. Intestine overlaps rectum, extends behind phasmid. Intestinal fasciculi extend to tail terminus.

Reproductive system amphidelphic, ovaries outstretched, oocytes arranged in either single file or multiple rows. Vulva a transverse slit (Fig. 5J), vulval region with cuticle irregular on both sides. Vagina perpendicular to body axis, about half of vulval body diameter long, thick-walled. Spermatheca small, empty or with a few sperm cells. Uterus with seven pairs of cells. Two eggs observed in uterus of one specimen measuring 74,5 \times 20 μm . Tail subcylindroid-conoid, straight or dorsally or ventrally curved, with 29–35 annuli on ventral side, terminus smooth, finely to bluntly rounded, with thick hyaline cuticle (Fig. 5K–N). Phasmid at 27 % (20–37) of tail length.

Male: Similar to female in general morphology. Monorchic, testis outstretched anteriorly. Spicules 24,8 μm (22,5–27,5) long, ventrally arcuate. Gubernaculum 12,7 μm (11–16,5) long, curved, proximal end simple, distal end trough-like, knobbed or simple (Fig. 5 H and I). Bursa well-developed with crenate margins, enveloping tail terminus. Tail conoid, ventrally curved, terminus smooth, finely rounded. Phasmid at 28 % (23–37) of tail length. Lateral field with four lines which fade away on tail.

Discussion and relationships: These specimens are identified as *T. brevilineatus* Williams, 1960 mainly because of the presence of interrupted longitudinal lines, confined to the pharyngeal region. Our specimens are similar to the type population in most respects but differ by the presence of fasciculi and the irregular cuticle in the vulval region. *T. brevilineatus* is known from India (recorded as *T. indicus* by Siddiqi, 1961), Pakistan (Maqbool & Shahina, 1987) and South Africa (Kleynhans & Heyns, 1984). In most respects our specimens closely resemble the South African population described by Kleynhans & Heyns (1984), of which specimens were available for comparison. *T. brevilineatus* also resembles *T. gofarti* Sturhan, 1966 and *T. ventrosignatus* Tobar Jimenez, 1969 by the irregular cuticle in the vulval

region, but differs from both species in having longitudinal striae in the pharyngeal region. Other nearly similar species are *T. tobari* Sauer & Annells, 1981 and *T. gladiolatus* Fortuner, 1973. Our specimens differ from the former species in having a postanal intestinal sac and from the latter in having the longitudinal striae confined to the pharyngeal region.

Localities and habitats: Namib Desert: (1) Under grass next to the Kuiseb River, east of Gobabeb. (2) In moist sand, en route to water-hole in Kuiseb River, about 40 km east of Gobabeb. Etosha Game Reserve: (1) Under dry grass next to water-hole at Ondongab. (2) Okaukuejo, under reeds, near swimming pool. (3) Under grass in Namutoni Rest Camp. Ai-Ais: In moist soil under reeds. Collected July 1983 by J. Heyns and July 1986 by J. Heyns and A. Coomans.

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