

Morphological and molecular characterisation of several known nematode species of the genera *Criconema*, *Criconemoides* and *Mesocriconema* (Tylenchida: Criconematidae) from the USA and South Africa

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Summary. During nematological surveys in several locations of the USA and South Africa, and using integrative approach combining morphological and molecular analyses the following species were identified: *Criconema annuliferum*, *Criconema mutabile*, *Criconemoides annulatus*, *C. informis*, *Criconemoides* sp. A, *Mesocriconema nebraskense*, *M. sphaerocephalum*, *M. xenoplax* and *Mesocriconema* sp. A. These species were morphologically and morphometrically described and the SEM images were also given for some species. Molecular characterisations of the species using the D2-D3 expansions segments of 28S rRNA and *COI* mtDNA gene sequences were also provided. Based on the results of molecular dataset analysis, *Discocriconemella sinensis* Munawar, Cai, Subbotin & Zheng, 2019 and *D. parasinensis* Li, Munawar, Castillo & Zheng, 2022 were transferred to the genus *Criconemoides*.

Key words: *Criconema annuliferum*, *Criconema mutabile*, *Criconemoides annulatus*, *Criconemoides informis*, *COI* gene, D2-D3 of 28S rRNA gene, *Mesocriconema nebraskense*, *Mesocriconema sphaerocephalum*, *Mesocriconema xenoplax*, phylogeny, SEM.

During nematological surveys, several species of the genera *Criconema* Hofmänner & Menzel, 1914, *Criconemoides* Taylor, 1936 and *Mesocriconema* Andrassy, 1965 were found in South Africa and several states of the USA. Some species of these genera have been reported as parasitic and important pests of crops, causing damage of roots (Geraert, 2010). The genus *Criconema* currently contains more than 100 valid species (Geraert, 2010; Azimi & Pedram, 2020; Clavero-Camacho *et al.*, 2022; Archidona-Yuste *et al.*, 2023), the genus *Criconemoides* consists of nearly 50 species (Geraert, 2010; Munawar *et al.*, 2020; Hosseinvand *et al.*, 2023), whereas the genus *Mesocriconema* contains more than 90 species. *Mesocriconema* species are morphologically similar to

Criconemoides species and differ from it by having an open vulva and submedian lobes arising from reduced pseudolips (Brzeski *et al.*, 2002a, b; Geraert, 2010; Karani *et al.*, 2020).

The objectives of this work were: *i*) to carry out a morphological and morphometric characterisation of several criconematids found from the USA and South Africa; *ii*) to provide molecular characterisation of these species using sequences of the D2-D3 expansion segments of the 28S nuclear ribosomal RNA and partial *COI* gene; and *iii*) to analyse phylogenetic relationships of several criconematids from the USA and South Africa within representatives of the genera *Criconema*, *Criconemoides* and *Mesocriconema* using these genes.

MATERIALS AND METHODS

Nematode samples, light and scanning electron microscopic study. Soil samples were collected from the rhizosphere of different plants and locations as indicated in Table 1. Nematode specimens were extracted from samples using the rapid centrifugal-flotation method (Jenkins, 1964), fixed in 4% formalin or FPG (Netscher & Seinhorst, 1969), transferred to anhydrous glycerin (De Grisse, 1969) and mounted on Cobb's slides. Voucher nematode slides were deposited at the Nematology collection, ARC-Plant Protection Research Institute, Queenswood, South Africa. Measurements were made with a research microscope (Nikon Labophot-2) equipped with a drawing tube. Light micrographs were taken with an automatic Infinity 2 camera attached to a compound Olympus BX51 microscope equipped with Nomarski differential interference contrast. For scanning electron microscopy specimens were transferred to TAF (7 ml 40% formalin, 2 ml triethanolamine, and 91 ml distilled water) then dehydrated in increasing concentrations of alcohol in distilled water and finally into pure alcohol. Following conventional critical point drying and gold/palladium coating (15 nm), specimens were viewed with a FEI

ESEM Quanta 200 scanning electron microscope at 10 kV (Van den Berg *et al.*, 2017).

DNA extraction, PCR, sequencing and phylogenetic analysis. DNA was extracted from several specimens of each species using the proteinase K protocol. Detailed protocols for DNA extraction, PCR, cloning and sequencing were as described by Subbotin (2021). The D2-D3 expansion segments of 28S rRNA gene and partial *COI* gene were amplified and sequenced. The following primers were used for amplification in the present study: D2-D3 of 28S rRNA gene – D2A (5'-ACA AGT ACC GTG AGG GAA AGT TG-3') and D3B (5'-TCG GA GGA ACC AGC TAC TA-3') (Subbotin *et al.*, 2005) and partial *COI* gene – COIF5 (5'-AAT WTW GGT GTT GGA ACT TCT TGA AC-3') and COIR9 (5'-CTT AAA ACA TAA T GR AAA TGW GCW ACW ACA TAA TAA GTA TC-3') (Powers *et al.*, 2014). The PCR products were purified using QIAquick (Qiagen) Gel or PCR extraction kits and submitted for direct sequencing or cloned using pGEM-T Vector System II kit (Promega). Sequencing was conducted at Quintara Biosciences. The obtained sequences were submitted to the GenBank database under the following accession numbers: OR157945-OR157956 (*COI* gene) and OR159851-OR159868 (28S rRNA gene) (Table 1).

Table 1. Criconematid species used in the present study.

Species	Locality	Sample code	GenBank accession numbers	
			D2-D3 of 28S rRNA gene	<i>COI</i> gene
<i>Criconema annuliferum</i>	USA, California, El Dorado County	CD878, CD879	OR159851	OR157946
<i>C. annuliferum</i>	USA, Washington	CD920	OR159852	OR157945
<i>C. mutabile</i>	South Africa, Gauteng Province, Pretoria, Roodeplaat Nature Reserve	Tv11982	–	–
<i>Criconemoides annulatus</i>	USA, California, El Dorado County	CD879	OR159853	OR157947
<i>C. informis</i>	USA, California, Sacramento County	CD836	–	OR157956
<i>Criconemoides</i> sp. A	South Africa, KwaZulu Natal Province, Nottingham Road	CD370, CD554; N775	OR159854-OR159857	OR157950, OR157951
<i>Mesocriconema nebraskense</i>	USA, Kansas, Manhattan, Washington Marlatt park	CD869	OR159862	OR157952
<i>M. sphaerocephalum</i>	USA, Florida, Gainesville	CD1183	OR159858, OR159859	OR157948, OR157949
<i>M. xenoplax</i>	USA, California, Marin County	CD859	OR159867, OR159868	–
<i>M. xenoplax</i>	South Africa, Gauteng Province, Tarlton	CD553; Tyl1976	OR159863, OR159864	OR157955
<i>M. xenoplax</i>	USA, Kansas, Manhattan, Washington Marlatt park	CD863, CD865	OR159865, OR159866	–
<i>M. xenoplax</i>	South Africa, Mpumalanga Province, Groblersdal	Tv11928	–	–
<i>Mesocriconema</i> sp. A	USA, Florida, Gainesville	CD1182	OR159860, OR159861	OR157953, OR157954

The newly obtained sequences for each gene were aligned using ClustalX 1.83 with default parameters with corresponding published gene sequences of selected species of the genera *Criconemoides*, *Criconema* and others (Subbotin *et al.*, 2005; Powers *et al.*, 2014, 2016, 2021; Van den Berg *et al.*, 2017; Munawar *et al.*, 2019; Clavero-Camacho *et al.*, 2022; Li *et al.*, 2022; Hosseinvand *et al.*, 2020, 2023 and others). Outgroup taxa for each dataset were chosen according to the results of previously published data (Subbotin *et al.*, 2005). Sequence datasets were analysed with Bayesian inference (BI) using MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003). BI analysis under the GTR + I + G model for each gene was initiated with a random starting tree and was run with four chains for 1.0×10^6 generations. The Markov chains were sampled at intervals of 100 generations. Two runs were performed for each analysis. After discarding burn-in samples and evaluating convergence, the remaining samples were retained for further analysis. The topologies were used to generate a 50% majority rule consensus tree. Posterior probabilities (PP) are given on appropriate clades. Pairwise divergences between taxa were computed as absolute distance values and as percentage mean distance values based on whole alignment, with adjustment for missing data using PAUP* (Swofford, 2003).

RESULTS AND DISCUSSION

Within studied samples using traditional morphological taxonomic characters integrated with molecular criteria, we distinguished seven valid criconematid species: *Criconema annuliferum*, *Criconema mutabile*, *Criconemoides annulatus*, *Criconemoides informis*, *Mesocriconema nebraskense*, *M. sphaerocephalum*, *M. xenoplax*, and two unidentified species: *Mesocriconema* sp. A and *Criconemoides* sp. A. Seven of these species were found in the USA and three species were reported from South Africa (Table 1). Short descriptions of some species are given below.

Criconema annuliferum (de Man, 1921) Micoletzky, 1925 (Figs 1 & 2)

Specimens of this species were found in several samples collected in Washington and California (Table 1). This species was originally obtained from soil covered with herbs and anemone in a forest near Breda, The Netherlands and from a municipal park

of Bergen op Zoom, The Netherlands and described as *Hoplolaimus annulifer* by de Man (1921). Micoletzky (1925) transferred it to the genus *Criconema*. *Criconema annuliferum* is widely distributed in several European countries, Africa, Asia, New Zealand and South America (Clavero-Camacho *et al.*, 2022). Several species had been synonymised with this species (Geraert, 2010). Using the integrative taxonomical analyses, Clavero-Camacho *et al.* (2022) and Archidona-Yuste *et al.* (2023) distinguished the *C. annuliferum* species complex, which includes four cryptic species: *C. annuliferum*, *C. paraannuliferum* Clavero-Camacho *et al.*, 2022, *C. plesioannuliferum* Clavero-Camacho *et al.*, 2022 and *C. pseudoannuliferum* Archidona-Yuste *et al.*, 2023.

Measurements. See Table 2.

Female. Female body almost smooth to slightly curved ventrad. Lip region with two annuli. First annulus with a smooth margin and projecting outward or slightly upward. Second lip annulus strong, pointed outward and with a slightly smaller diameter than first annulus. Labial plate rounded, protruding slightly above lip first lip annulus. Submedian lobes absent. All body annuli slightly retrorse with smooth margins. An occasional anastomosis posterior to vulva, otherwise no markings in the lateral field. Stylet long and slender with cupped basal knobs. Excretory pore situated from one to four annuli posterior to base of pharyngeal lobe. Hemizonid not seen except in one specimen, it is one annulus long and situated directly anterior to excretory pore. Hemizonion not seen. Spermatheca indistinct in all specimens. Anterior vulval lip slightly indented in middle, overlapping the posterior lip. Vagina sigmoid. Anus distinct four to five annuli from terminus. Tail tapering to a narrow rounded knob. Last annulus sometimes slightly irregular.

Males. Not found.

Juveniles. Not found.

Remarks. The present specimens are morphologically and morphometrically very similar to the specimens described by various authors from different locations (Raski & Golden, 1965; Gomez Barcina *et al.*, 1989, 1991; Brzeski, 1998; Peneva *et al.*, 2000; Etongwe *et al.*, 2020) (Table 2).

Molecular characterisation. The D2-D3 of 28S rRNA (Fig. 3) and *COI* (Fig. 4) gene sequences of the Washington and California populations clustered with those of *C. annuliferum* populations from Belgium and Ireland. Intraspecific variation for the D2-D3 of 28S rRNA gene was 0.1-0.7% and for *COI* gene – 0-2.1%.

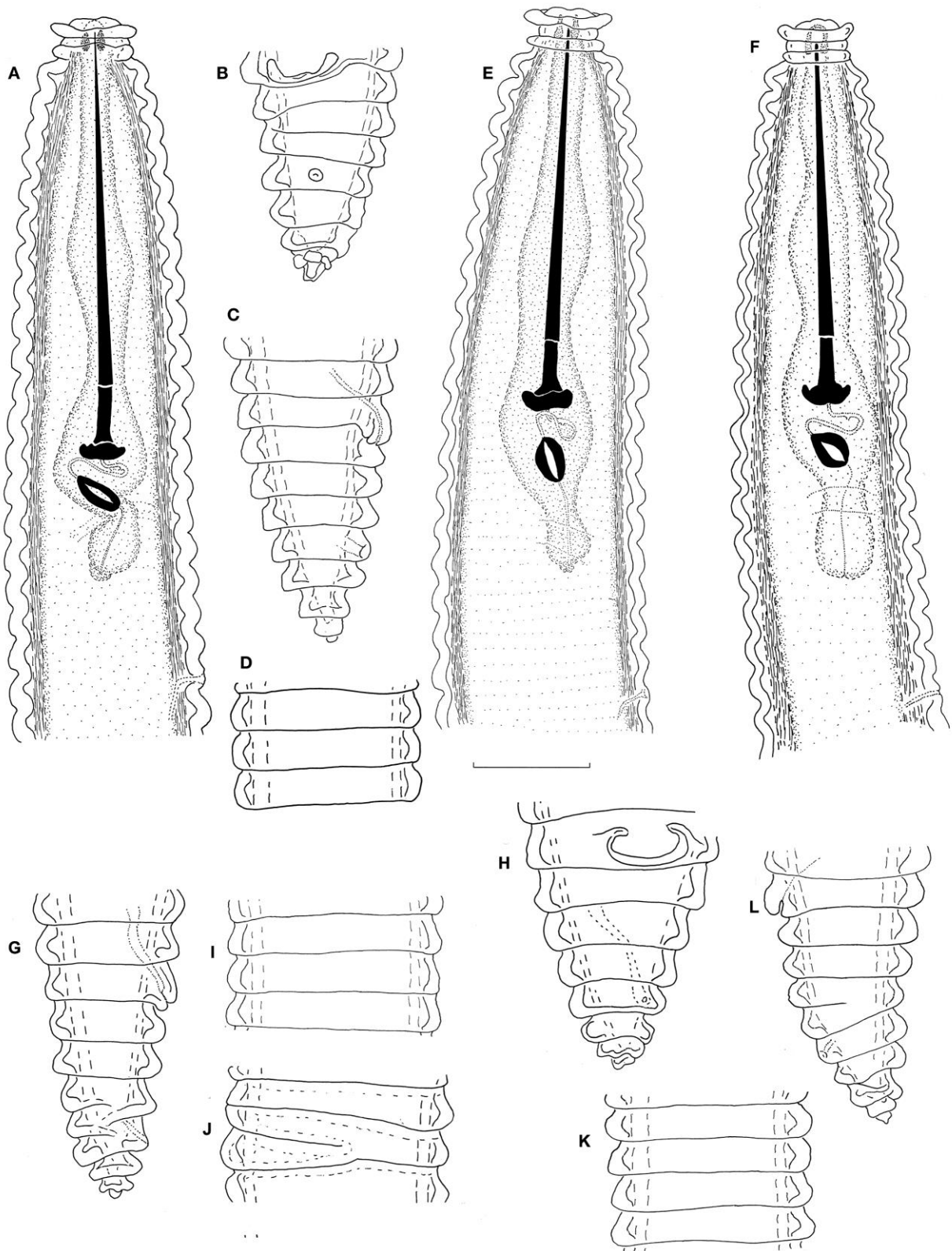


Fig. 1. *Criconema annuliferum*. CD920. Female. A: Anterior part of body; B: Ventral view of posterior region; C: Lateral view of posterior region; D: Annuli at midbody. CD879 Female. E: Anterior part of body; CD878. Female. F: Anterior part of body; G: Lateral view of posterior part of body; H: Ventral view of posterior part of body; I, J: Annuli at midbody. CD879 Female. K: Annuli at midbody; L: Lateral view of posterior part of body. Scale bar = 30 μ m.

Table 2. Measurements of *Criconema annuliferum* females compared with those from the literature. All measurements are in μm and in the form: mean \pm SD (range).

Character	Sample	USA, Washington (CD920)	USA, California (CD878)	USA, California (CD879)	Van den Berg & Heyns (1977)	Gomez Barcina <i>et al.</i> (1989)	References (a)
n		10	10	3	11	18	27
L		562 \pm 40 (507-616)	567 \pm 37.5 (510-626)	604-646	539 \pm 17.1 (503-558)	469 \pm 49 (348-541)	469-770
a		10.1 \pm 1 (8.1-11.3)	9.4 \pm 1.1 (8.1-11.5)	9.4-11.1	8 \pm 0.7 (7-10)	11 \pm 1.8 (9-14)	7.7-12
b		3.7 \pm 0.1 (3.5-3.9)	3.7 \pm 0.2 (3.5-4)	3.9-4.3	4 \pm 0.1 (3-4)	4 \pm 0.3 (3-4)	3-5
c		23 \pm 3 (17.8-28.7)	31.4 \pm 2 (20.7-44.8)	27.6-41.1	27 \pm 4.7 (22-38)	16 \pm 4.4 (11-23)	17-34.3
o		7.6 \pm 0.5 (7-8.3)	8.8 \pm 0.7 (7.8-9.8)	8	8 \pm 0.9 (6-8)	—	—
DGO		8 \pm 0.4 (7.5-9)	9 \pm 0.4 (8-9.5)	8	8 \pm 1 (6-9)	—	—
V		89 \pm 0.8 (88-90.5)	90 \pm 1 (88-91)	90-92	89 \pm 0.6 (89-90)	87 \pm 11 (85-89)	87-91
OVI		50 \pm 10 (41-67.5)	50.7 \pm 8.4 (40.5-65.4)	43-70	43 \pm 8.2 (36-45)	42 \pm 8.3 (32-60)	—
OV length		281 \pm 58.3 (227-380)	297 \pm 45.9 (250-307)	261-423	—	—	—
Stylet length		106.5 \pm 5.6 (98.5-116)	100 \pm 45.9 (93.5-109)	95-101	107 \pm 2.6 (102-111)	100 \pm 5.8 (88-107)	90-114
Metenichium length		88.5 \pm 4.8 (81.5-98.5)	82.5 \pm 3.9 (77-89)	76.5-84	87 \pm 2.1 (82-89)	86 \pm 1.4 (84-94)	—
Telenchium length		17.5 \pm 2.1 (12.5-20)	18 \pm 0.9 (17-19)	17.5-20	20 \pm 0.5 (20-21)	—	—
m		83 \pm 2.8 (76.3-87.3)	82 \pm 0.6 (81-83)	80.6-82.6	—	—	—
Stylet knob height		5 \pm 0.6 (4-6)	5.5 \pm 0.7 (4.5-6.5)	6	5 \pm 0.5 (4-6)	—	—
Stylet knob width		12 \pm 1 (10.5-13)	12 \pm 0.5 (11-12.5)	12.5-13	12 \pm 0.7 (11-13)	8-9	—
Exc. pore from anter. end		169.5 \pm 17.6 (144-195)	181 \pm 12 (165-201.5)	179-187	165 \pm 34.4 (159-197)	158 \pm 9 (141-170)	150-185
Width at midbody		56 \pm 7 (49-72)	61 \pm 6.2 (50-68)	58-62	67 \pm 4.8 (57-74)	41 \pm 4.2 (36-50)	—
Width at anus		27 \pm 2.4 (23.5-32.5)	24 \pm 3.2 (19-29)	23.5	—	—	—
Width at vulva		42 \pm 4.2 (33-48.5)	45 \pm 5.7 (34-50)	42.5-47	—	—	—
Annulus width		9.5 \pm 0.6 (9-11)	10 \pm 1.1 (8-11)	9-10	9 \pm 0.8 (7-10)	—	9-10
Tail length		24.5 \pm 2.1 (21.5-28.5)	19 \pm 3.8 (14-25.5)	15-22	21 \pm 3.2 (15-25)	32 \pm 7.9 (22-47)	16-26
Pharynx length		151.5 \pm 7.6 (137.5-162.5)	154 \pm 9.2 (143-171)	147-157	150 \pm 7.8 (135-160)	132 \pm 9.5 (117-146)	—
1st lip annulus diam.		22.5 \pm 1.9 (19-25)	22.5 \pm 1.4 (19-24)	22-24	24 \pm 1.3 (22-26)	21 \pm 3 (15-25)	—
2nd lip annulus diam.		21.5 \pm 2.1 (19-25.5)	20.5 \pm 1.3 (18.5-23)	20-21.5	22 \pm 1.8 (19-25)	—	—
1st body annulus diam.		30 \pm 2.3 (28-35.5)	31 \pm 2.6 (27-34)	31-32	34 \pm 2.6 (30-38)	—	—
2nd body annulus diam.		35.5 \pm 2.8 (31.5-41.5)	37 \pm 3.7 (31-41)	36.5-38	38 \pm 11.5 (38-46)	—	—
R		65 \pm 2.6 (62-70)	62 \pm 2.4 (60-68)	63-66	66 \pm 1.7 (62-68)	65 \pm 1.7 (62-68)	61-74
Rst		15 \pm 0.9 (13-16)	13 \pm 0.7 (12-14)	11-13	14 \pm 1.8 (12-18)	15 \pm 1.4 (13-18)	12-15
ROes		19 \pm 1.3 (18-21)	18 \pm 1.5 (17-21)	17-18	19 \pm 1.3 (17-21)	20 \pm 1.7 (16-24)	16-20
Rex		21 \pm 1.2 (19-23)	21 \pm 1.2 (20-24)	20-21	22 \pm 1 (20-23)	21 \pm 1.5 (19-24)	19-26
RV		8.5 \pm 0.5 (8-9)	8 \pm 0.7 (7-9)	7-8	9 \pm 0.4 (8-9)	10 \pm 0.8 (8-11)	6-11
RVan		3 \pm 0.4 (3-4)	3 \pm 0.8 (2-4)	3-4	3 \pm 0.3 (3-4)	4 \pm 1.2 (2-6)	3-4
Ran		4 \pm 0.4 (4-5)	3 \pm 0.6 (2-4)	3	5 \pm 0.5 (4-5)	7 \pm 1.1 (5-8)	3-7
VL/VB		1.4 \pm 0.08 (1.2-1.5)	1.3 \pm 0.1 (1.1-1.5)	1.2-1.4	1	1.8 \pm 0.1 (1.5-2)	1.1-1.7
St%L		19.1 \pm 1.1 (16.3-20.3)	17.8 \pm 1 (16.5-18.9)	15.7-17.8	20 \pm 0.7 (19-21)	—	15.8-20.2

Note: (a) Raski and Golden (1965), Szczygiel (1974) and Peneva *et al.* (2000).

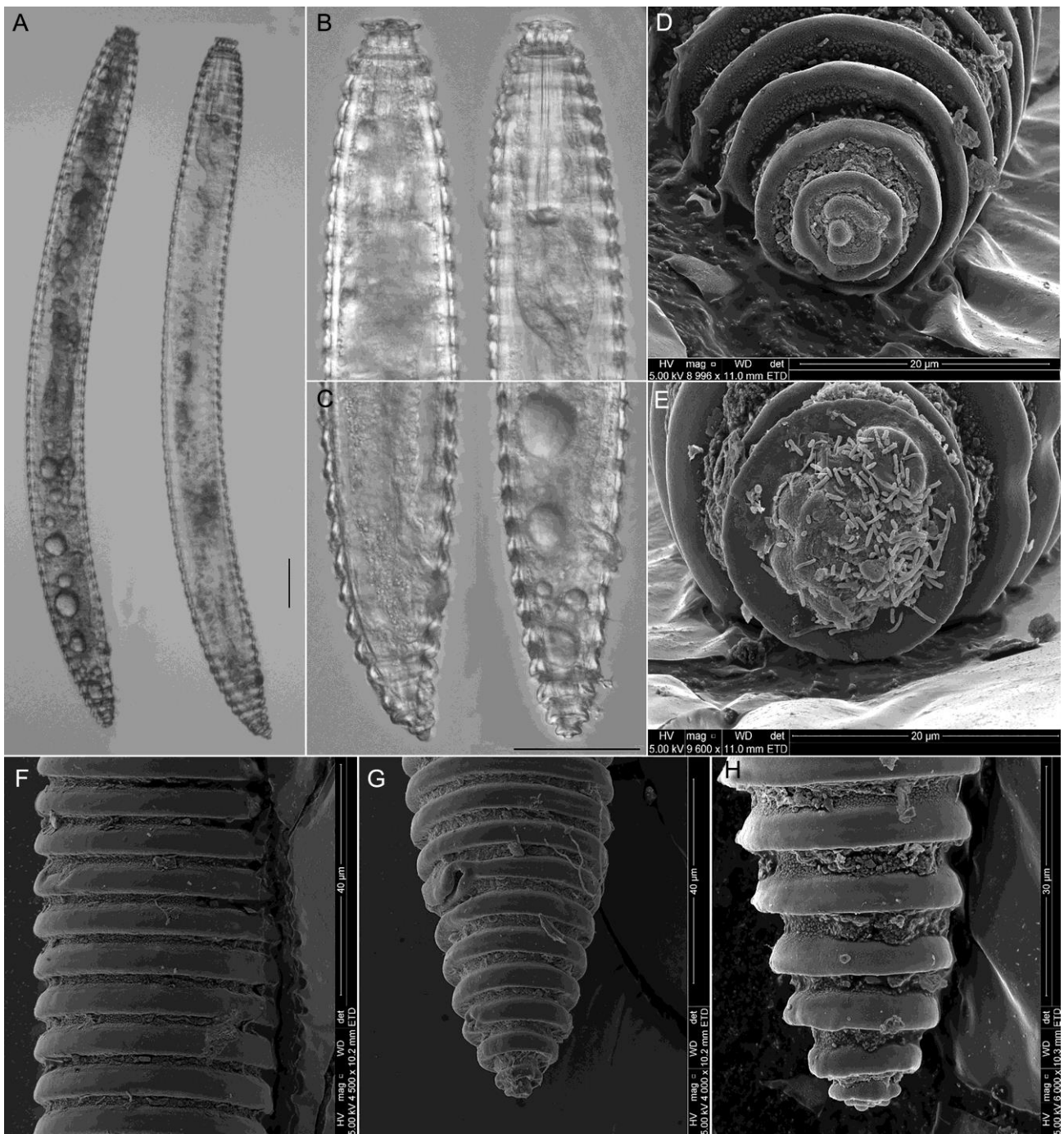


Fig. 2. *Criconema annuliferum*. CD878. Female. LM. A: Whole body; B: Anterior part of body; C: Posterior part of body. SEM. D, E: *En face* view of lip region; F: Annuli at midbody; G: Tail tip; H: Lateral view of posterior part of body. Scale bars: A-C = 60 μ m.

***Criconema mutabile* (Taylor, 1936) Raski & Luc, 1985
(Figs S1A-H & S2)**

Taylor (1936) described this species from African marigold (*Tagetes erecta* L.) from glasshouses of the Department of Agriculture in

Washington D.C., USA. Raski and Golden (1965) redescribed *C. mutabile* from the original materials used by Taylor (1936) and since then the species have been moved to a few other genera until 1985 when Raski and Luc (1985) in their reappraisal of the genus regarded *mutabile* as belonging to the genus *Criconema*. Several species have been consi-

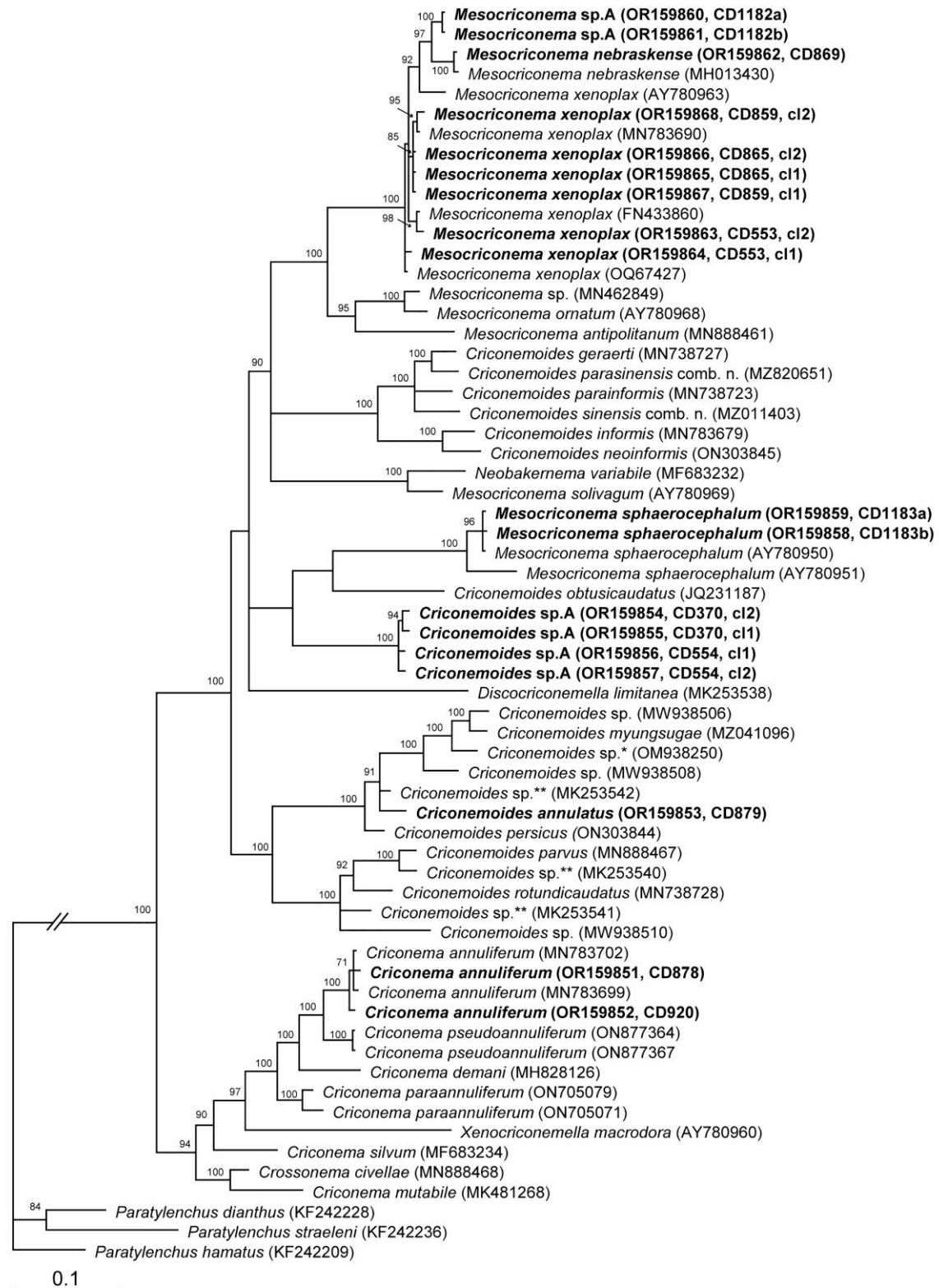


Fig. 3. Phylogenetic relationships within some representatives of the family Criconematidae. Bayesian 50% majority rule consensus tree from two runs as inferred from analysis of the D2-D3 of 28S rRNA gene sequence alignment under the GTR + I + G model. Posterior probabilities equal to, or more than, 70% are given for appropriate clades. New sequences are indicated in bold letters. * - identified as *Criconemoides annulatus* in the GenBank by Zhao (unpublished); ** - identified as *Mesocriconema* sp. by Munawar *et al.* (2019).

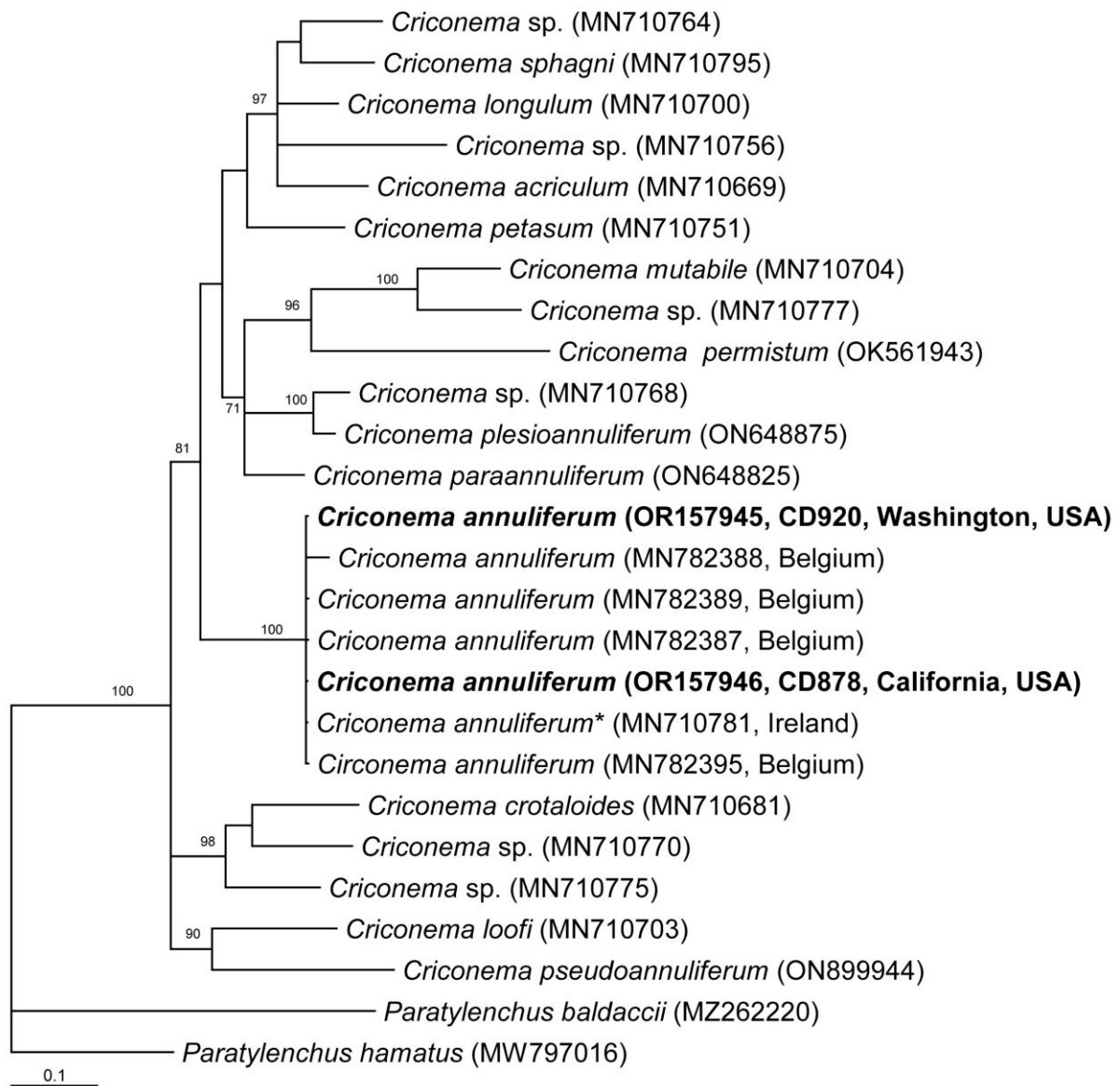


Fig. 4. Phylogenetic relationships within some representatives of the genus *Criconema*. Bayesian 50% majority rule consensus tree from two runs as inferred from analysis of the *COI* gene sequence alignment under the GTR + I + G model. Posterior probabilities equal to, or more than, 70% are given for appropriate clades. New sequences are indicated in bold letters. * - identified as *Criconemoides* sp. in the GenBank and Powers *et al.* (2021).

dered as synonyms of *C. mutabile* (Geraert, 2010). *Criconema mutabile* was found in many different countries and it was reported very often from agricultural soil and natural veldt in South Africa. Recently, this species was morphologically and molecularly characterised by Shokoohi *et al.* (2020) from South Africa and Iran. The present specimens were collected in 2009 in the Gauteng Province from Roodeplaat Nature Reserve, 2 m from the side of the Roodeplaat dam amongst grass and weeds (Tv11982) and used for morphological study only.

Measurements. See Table S1.

Female. Body form straight to slightly curved ventrad. Lip region with two annuli, first one pointing outward and second slightly retrorse. First with a smaller diameter than second. Lip annuli not set off from body annuli. SEM photographs show labial area with pseudolips projecting well above first lip annulus. All body annuli retrorse with smooth margins. Lateral field not demarcated except for rarely with a few irregularities at midbody or one or two anastomosis posterior to vulva and one with a few indents anterior to vulva. Stylet well developed with cupped basal knobs. Excretory pore

situated from four annuli anterior to three annuli posterior to posterior margin of pharyngeal lobe. Hemizonid one annulus long and situated from opposite to four annuli anterior to excretory pore. Hemizonion not seen. Spermatheca small, round to oblong and empty. Vulval lips not protruding and closed. Anterior lip not indented or overhanging the posterior lip. Vagina straight. Anus six to eight annuli from tail tip. Tail narrowing gradually to a rounded tip with a few small lobes.

Male. Not found.

Juvenile. Not found.

Remarks. The specimens are similar to those from all the previous descriptions of the species (Table S1). Molecular analysis of this sample is not given.

***Criconemoides annulatus* Cobb in Taylor,
1936
(Figs S3 & 5)**

Nine specimens of this species were collected in California. *Criconemoides annulatus* was originally collected from soil around Scrub Oak (*Quercus ilicifolia* Wangenh.) near Red Butte, Montana, USA, described by Taylor (1936) and re-described using the type specimens and collections from California and Idaho by Raski and Golden (1965). *Criconemoides annulatus* was recorded from various areas in North America, also Canada, Asia and Europe. Several species had been synonymised with *C. annulatus* (Choi *et al.*, 2000; Brzeski *et al.*, 2002a; Geraert, 2010; Powers *et al.*, 2021).

Measurements. See Table S2.

Female. Body slightly curved ventrad. Lip region with three annuli, first quite smaller than following two, all three slightly retrorse and not set off from body. Labial area low and not projecting above the first annulus. Lip region covered with bacteria and not much can be seen in the *en face* view. All body annuli slightly retrorse with smooth to slightly wavy margins. In a few cases the annuli appeared to have very fine longitudinal lines. Anastomosis rare, sometimes a few are visible on the first few annuli or a few may be present posterior to the vulva. Stylet long, sturdy with cupped basal knobs. Excretory pore situated from one annulus anterior to four annuli posterior to basal margin of basal pharyngeal lobe. Hemizonid rarely seen but where seen, it is one annulus long and situated opposite the excretory pore. Hemizonion not seen. Spermatheca indistinct and not containing sperm cells. Vulva an oval open slit. Vagina straight. Anus distinct two to five annuli from tail tip. Tail rounded with small irregular amalgamated lobes.

Male. Not found.

Juvenile. Very similar to female. Lateral field with a few irregularities and a few anastomosis. Posterior margins of annuli slightly crenate.

Remarks. These specimens compare well with those from the literature. Several authors reported a large variation in some of the morphological characters in this species such as stylet length, number of body annuli, Rex and RV values *etc.* (Raski & Golden, 1965; Popovici, 1988; Choi *et al.*, 2000). Table S2 gives measurements of the populations of this species provided by various authors as compared with original ones.

Molecular characterisation. The D2-D3 of 28S rRNA gene sequence of the California population of *C. annulatus* clustered with that of the Washington population (Fig. 3) and they were different in 2.7% (15 bp). The *COI* gene sequence of the California population of *C. annulatus* clustered with those of the Utah, Wyoming, Colorado, South Dakota and Quebec populations (Fig. 6). Intraspecific *COI* gene sequence variation reached 11.2% (81 bp).

***Criconemoides informis* (Micoletzky, 1922)
Taylor, 1936
(Figs S4 & 7A-D)**

Specimens of this species were collected in California, Sacramento County. Unfortunately, most specimens were covered with bacteria and not well preserved and mounted, and only two specimens could be measured. This species was described by Micoletzky (1922) from soil about the roots of aspen (*Populus tremuloides* Michx.) near Idaho Springs, Clear Creek, Colorado. Then this species was frequently reported from Europe, North America and Asia by various authors (Loof, 1965; Gomez Barcina *et al.*, 1989; Choi *et al.*, 2000; Eskandari *et al.*, 2010; Geraert, 2010). Hosseinvand *et al.* (2023) distinguished the *Criconemoides informis* group with several species: *C. informis*, *C. amorphous* De Grisse, 1967; *C. parainformis* Munawar *et al.*, 2020; *C. neoinformis* Hosseinvand *et al.*, 2023 and *C. geraerti* Munawar *et al.*, 2020.

Measurements. See Table S2.

Female. Body slightly curved ventrad. Lip region with two annuli, first pointing slightly upward and second pointing outward. First lip annulus with a smaller diameter than second. SEM shows labial disc protruding above first lip annulus, sub median lobes more broad and rounded, labial plates not very well developed. Diameter of first lip annulus markedly smaller than that of the second lip annulus. Lip annuli not set off from body annuli. All

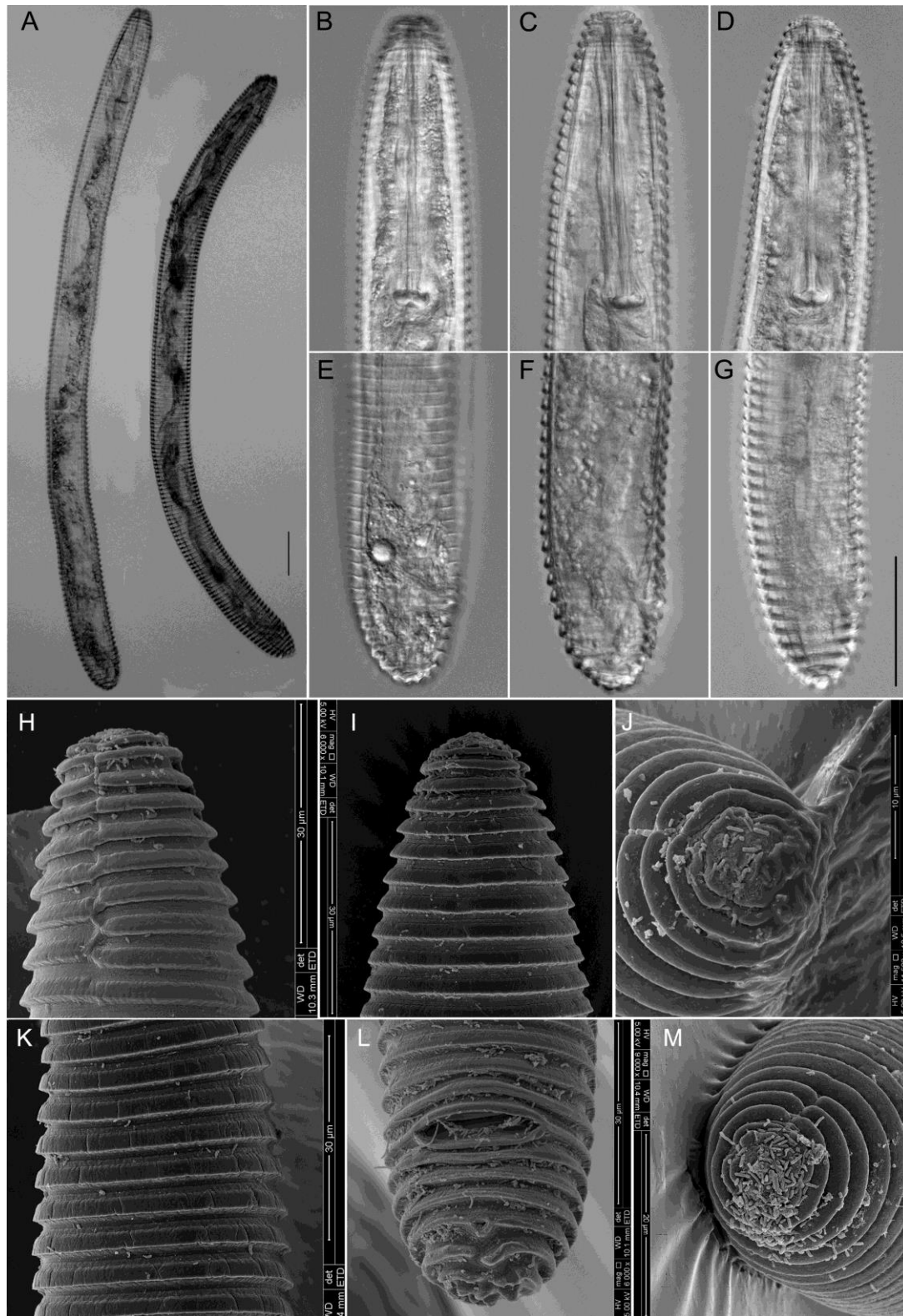


Fig. 5. *Criconemoides annulatus*. CD879. LM. Female. A. Whole body; B-D: Anterior part of body; E-G: Posterior part of body. SEM. H, I: Lateral view of anterior part of body; J, M: *En face* view of lip region; K: Annuli at midbody; L: Ventral view of tail region. Scale bars: A = 30 µm, B-G = 50 µm.



Fig. 6. Phylogenetic relationships within some representatives of the genus *Criconemoides* and *Mesocriconema*. Bayesian 50% majority rule consensus tree from two runs as inferred from analysis of the *COI* gene sequence alignment under the GTR + I + G model. Posterior probabilities equal to, or more than, 70% are given for appropriate clades. New sequences are indicated in bold letters.

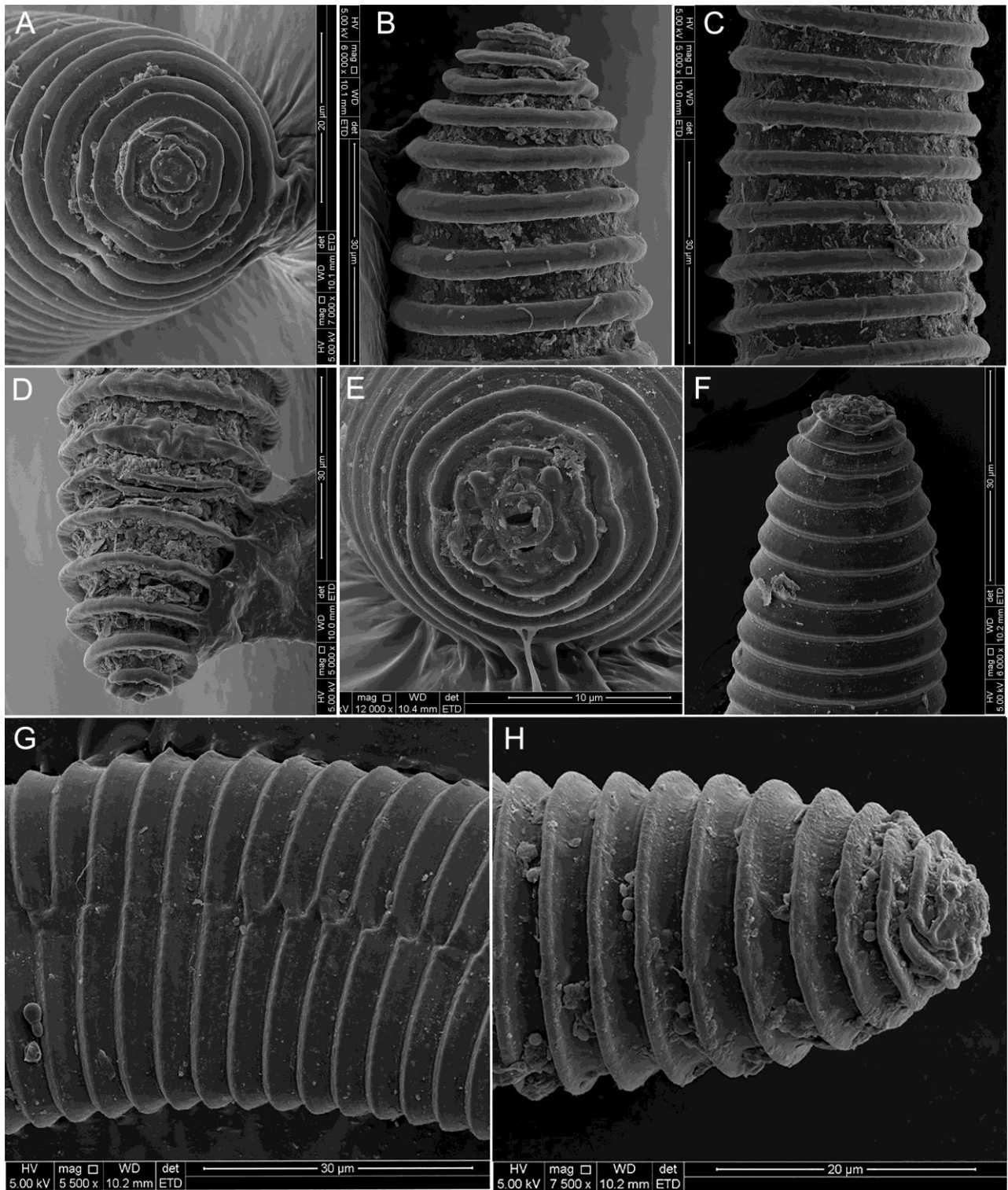


Fig. 7. *Criconemoides informis*. CD836. Female. SEM. A: *En face* view of lip region; B: Lateral view of lip region; C: Annuli at midbody; D: Ventral view of posterior part of body; *Mesocriconema sphaerocephalum*. CD1183. Female. SEM. E: *En face* view of lip region; F: Lateral view of anterior part of body; G: Annuli at midbody; H: Dorsal view of posterior part of body.

body annuli slightly retrorse and rounded with very slight irregular margins from about middle of body, becoming more irregular towards vulva and posterior to the vulva they can be very irregular. Anastomosis very rare. Stylet robust with cupped basal knobs. Excretory pore situated from two annuli anterior to opposite base of pharyngeal lobe. Hemizonid and hemizonion not seen. Spermatheca not seen in one specimen but in the other it was large, oblong and filled with sperm cells. Vulval lips closed. Anterior lip not indented and not overhanging the posterior lip. Vagina straight. Anus distinct, four annuli from tail tip. Tail tapering to a narrow tip with two or three irregular, indistinct lobes.

Male. Not found.

Juvenile. Two juveniles found but in very bad condition and not good for measuring. One specimen had 66 body annuli, rounded, retrorse with slight irregular margins from about midbody to tail terminus where they were slightly more irregular in the last four annuli.

Remarks. These two specimens compared well to the various descriptions of the species (Table S2).

Molecular characterisation. Only *COI* gene sequence was obtained for this sample. The sequence of Californian *C. informis* clustered with that of the Russian population of this species (Fig. 6) and they were different in 9.7% (62 bp).

Criconemoides sp. A from South Africa

This species was found in South Africa, KwaZulu Natal Province. Specimens of this sample were used for molecular analysis only. Phylogenetic position of this sample within the genus *Criconemoides* using D2-D3 of 28S rRNA and *COI* gene sequences is not well resolved and given in Figure 3 and 6.

Mesocriconema nebraskense Olson *et al.*, 2017 (Figs S5A-D & 9E-H)

Mesocriconema nebraskense was described in Spring Creek Prairie, Nebraska located in the Central Tall Grasslands ecoregion of North America. This species was found in several states of the USA (Powers *et al.*, 2014, 2021; Olson *et al.*, 2017) and recently from grasses in Korea (Mwamula & Lee, 2021).

Measurements. See Table 3.

Female. Body slightly curved ventrad. Lip region with two annuli. Stylet strong and well developed with cupped basal knobs. Vulva an open slit with anterior lip bearing two rounded

projections. Vagina always distinctly sigmoid. Anus distinct four to eight annuli from tail tip. Tail form varying form round to conoid.

Male. Not found.

Juvenile. Not found.

Remarks. Description of this population is similar to that provided by Olson *et al.* (2017). This species differs from *M. xenoplax* by shorter body and stylet lengths for females (Table 3).

Molecular characterisation. The D2-D3 of 28S rRNA gene sequence of *M. nebraskense* from Kansas differ only in 0.1% (1 bp) from that of North Dakota population (Yan *et al.*, 2018), whereas *COI* gene sequence was identical to that of population from Aurora Prairie, South Dakota published by Olson *et al.* (2017). Phylogenetic position of this species is given in Figures 3 and 6.

Mesocriconema sphaerocephalum Taylor, 1936 (Figs S1I-L & 7E-H)

Mesocriconema sphaerocephalum was described by Taylor (1936) from soil around roots of grass in Trinidad in the West Indies, redescribed by Raski and Golden (1965). This species was reported from North and South America, Europe, tropical Africa and Asia (Orton Williams, 1972; Geraert, 2010). The present specimens were collected from Florida, USA.

Measurements. See Table S3.

Female. Body slightly curved ventrad. SEM photos show a slightly elevated labial disc with a prominent mouth opening, distinct amphid openings, four small distinct, rounded submedian lobes. Labial plates not very prominent. Lip region with two annuli, first smaller than second, not set off from body annuli. All body annuli slightly retrorse with smooth margins. Lateral field area marked by numerous anastomosis and broken lines creating a zig zag effect. Stylet robust with cupped basal knobs. Excretory pore situated from opposite to two annuli posterior to base of pharyngeal lobe. Hemizonid and hemizonion not seen. Spermatheca indistinct and empty. Vulval lips closed. Vagina straight. Anus distinct, one to three annuli from tail tip. Tail tapering very slightly to a broadly rounded tip with one or two lobes on the terminus.

Male. Not found.

Juvenile. Not found.

Remarks. These specimens compare very well with the numerous descriptions of the species, although some of the characters vary quite a bit in different regions of the world, such as having longer stylets in Spain (Gomez Barcina *et al.*, 1991) compared to the shorter stylets of Venezuelan

specimens (Crozzoli & Lamberti, 2001) which were 44-53 vs 67-77 μm . Orton Williams (1972) give a stylet range of 30-69 μm . After analysing intraspecific morphological and morphometric variation, De Grisse and Loof (1970) found that populations of this species from the temperate zones had a slightly longer stylet than those from tropical countries. The number of annuli also varied quite a lot from 52 to 82, tail length from 4.5 to 19.5 μm with the c value ranging from 19 to 122. The South African specimens normally had much more anastomosis and breaks in the lateral field than the present specimens.

Molecular characterisation. After analysing the D2-D3 of the 28S rRNA gene sequences of *M. sphaerocephalum* from Italy and Venezuela, Subbotin *et al.* (2005) concluded that they were different and, perhaps, belonged to two sibling species. The D2-D3 of the 28S rRNA gene sequences of Florida population differed in 0-0.2% (0-1 bp) from that of Venezuela population and in 4.5-4.7% (25-26 bp) from that of Italian populations (Fig. 3). The *COI* gene sequences of Florida population were

identical or 0.3% (2 bp) to those from Puerto Rico (KU236638) and Florida (KY574841) published by Powers *et al.* (2016) and Olson *et al.* (2017) and differed in 14.0-17.5% (100-125 bp) from those from Missouri and Nebraska (Fig. 6).

***Mesocriconema xenoplax* Raski, 1952**
(Figs S6, 8 & 9A-D)

Mesocriconema xenoplax was originally described by Raski (1952) from the roots of grape (*Vitis vinifera* L. var. *sultanina*) grown on a *Vitis longii* rootstock, east of Fresno, Fresno County, California, USA and reported from many localities in the USA and worldwide (Geraert, 2010; Powers *et al.*, 2014). *Mesocriconema xenoplax* was found in two samples from South Africa and two samples from the USA (Table 1). The specimens from Tv11928 are some of the most recent specimens of this species found in South Africa and they are included in this morphological study only.

Measurements. See Table 3.

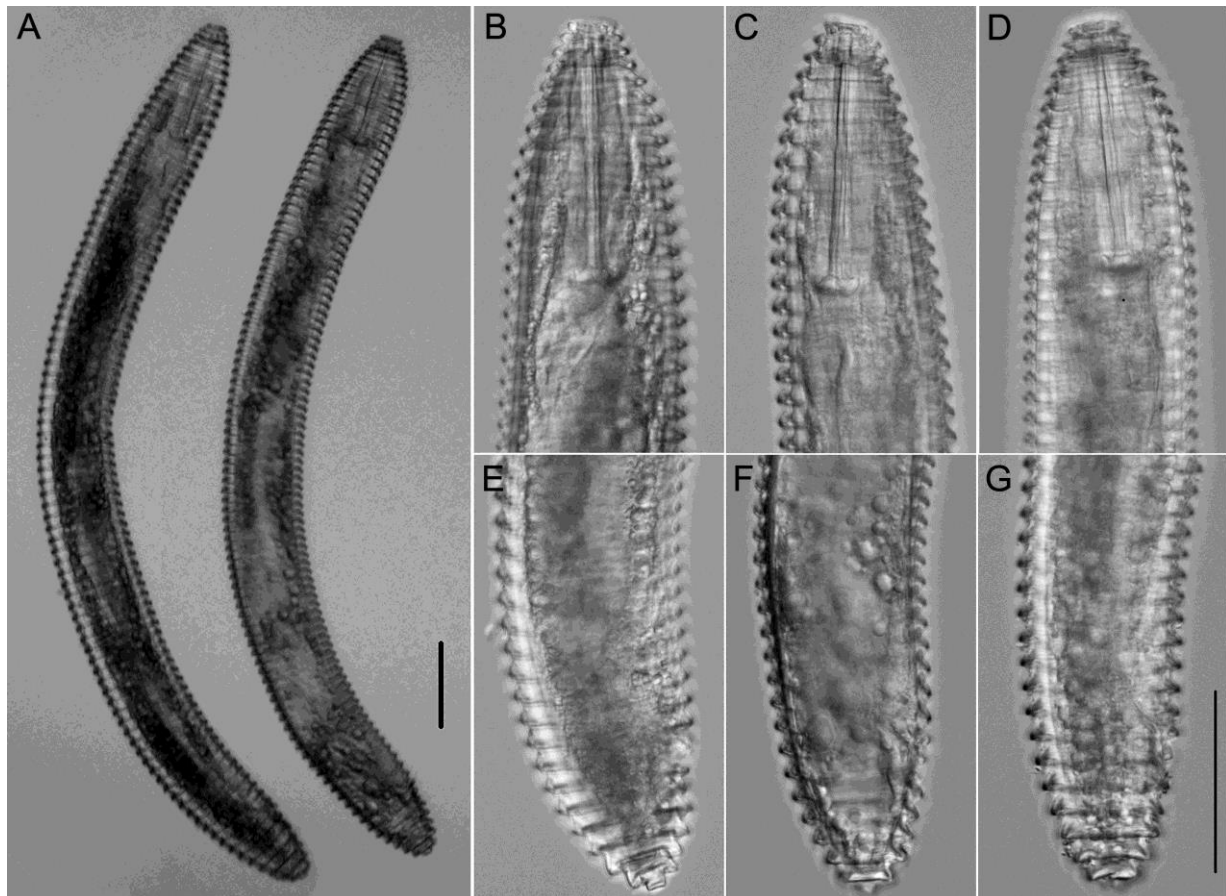


Fig. 8. *Mesocriconema xenoplax*. LM. CD865. Female. A. Whole body; B-D: Anterior part of body; E-G: Posterior part of body. Scale bars = 50 μm .

Table 3. Measurements of several females of *Mesocriconema* species. All measurements are in μm and in the form: mean \pm SD (range).

Species	Sample	<i>Mesocriconema xenoplax</i>			<i>M. nebraskense</i>			<i>Mesocriconema</i> sp.A.
		USA, California (CD859)	USA, Kansas (CD865)	South Africa (Tvi11928)	USA, Kansas (CD869)	USA, Florida (CD1182)		
Character								
n		7	6	9	4	12		
L		561 \pm 85.5 (495-746)	544 \pm 6 (489-669)	578 \pm 51.2 (515-685)	482 \pm 26 (458-519)	500 \pm 55.1 (435-626)		
a		9.6 \pm 0.7 (8.8-10.8)	12.2 \pm 0.8 (11.3-13.3)	9.4 \pm 0.9 (8.2-11.2)	9.7 \pm 0.7 (9.1-10.7)	11.2 \pm 1.2 (9.5-12.9)		
b		3.6 \pm 0.7 (3.5-3.8)	4.3 \pm 0.4 (3.7-4.5)	3.9 \pm 0.3 (3.4-4.4)	4.3 \pm 0.1 (4.2-4.5)	3.9 \pm 0.3 (3.5-4.5)		
c		21.9 \pm 2.6 (17.7-25.3)	23.8 \pm 4.6 (17.7-29.4)	21.2 \pm 2.4 (18.7-24)	19.5 \pm 1.6 (14.3-21.5)	18.8 \pm 2.3 (14.5-21.8)		
o		9.6 \pm 1.5 (7.8-11.3)	12.2 \pm 2.6 (10.1-16.2)	12.3 \pm 1.2 (11-14.4)	15.1 \pm 0.7 (14.3-16)	14.6 \pm 1.6 (11.3-17.4)		
DGO		7.5 \pm 1.6 (6-9)	7 \pm 0.8 (6-8)	10.3 \pm 0.8 (9.6-11.8)	8 \pm 0.6 (7.5-8.5)	7.5 \pm 0.7 (7-9)		
V		92 \pm 0.7 (91-94)	94 \pm 1 (93-96)	94 \pm 0.6 (93-95.5)	92 \pm 0.2 (92-92.5)	93 \pm 0.5 (92-94)		
OVI		–	47.3 \pm 8.7 (40.2-59.4)	65 \pm 13.2 (43.8-85.4)	48 \pm 1.1 (47.5-49)	44.2 \pm 4.1 (38.1-48.4)		
OV length		–	261 \pm 36.2 (213-301)	367 \pm 87.4 (300-574.5)	239 \pm 20.8 (225-254)	228 \pm 26.1 (180-252)		
Stylet length		75.5 \pm 2.9 (72-79.5)	60 \pm 9.9 (50-73)	84 \pm 3 (79.5-88)	50.5 \pm 2 (48.5-53)	52.5 \pm 2.2 (48-56)		
Metenichium length		57 \pm 1.8 (54.5-58)	43 \pm 7.8 (36-56)	64.5 \pm 2.6 (61-69)	36.5 \pm 1.5 (34.5-38)	38 \pm 1.3 (34.5-40)		
Telenchium length		18.5 \pm 1.3 (17-21)	17 \pm 2.3 (13-19)	19.5 \pm 0.9 (18.5-20.5)	13.2 \pm 1 (12.5-15)	15 \pm 1 (13-17)		
m		75.5 \pm 0.9 (74.1-76.5)	72.8 \pm 1.6 (72-73.8)	77 \pm 0.9 (75.6-78.3)	72 \pm 1.7 (70-74)	71.9 \pm 1 (69.8-74)		
Stylet knob height		5.5 \pm 0.4 (5-6)	5 \pm 0.8 (4-7)	5.5 \pm 0.5 (4.5-6)	5 \pm 1.2 (4-6.5)	5 \pm 0.7 (4-6.5)		
Stylet knob width		11.5 \pm 0.6 (10.5-12)	11 \pm 2 (9-14)	12 \pm 0.5 (11-12.5)	9 \pm 0.5 (8.5-9.5)	9.5 \pm 0.8 (7.5-10.5)		
Exc. pore from anter. end		157 \pm 22.9 (137.5-195.5)	143 \pm 18.5 (123.5-173.5)	163 \pm 15.4 (148-193.5)	128 \pm 6.8 (121.5-136)	135 \pm 17.4 (112.5-175)		
Width at midbody		59 \pm 6.8 (50.5-69)	46 \pm 6.3 (38-55)	64 \pm 5.2 (56-72)	50 \pm 4 (44-53)	45 \pm 3.7 (39-51.5)		
Width at anus		38 \pm 5 (31.5-45)	31 \pm 3.3 (28-36)	39 \pm 2.2 (36-42)	34.5 \pm 2.6 (31.5-37.5)	33 \pm 2.6 (28-37.5)		
Width at vulva		45 \pm 5.9 (37-54)	35 \pm 4.8 (31-43)	44.5 \pm 2.9 (40.5-48)	40 \pm 2.1 (37.5-42.5)	36.5 \pm 3.1 (32-41)		
Annulus width		6 \pm 1 (5-8)	6 \pm 0.7 (5.5-7)	6.5 \pm 0.5 (6-7.5)	5 \pm 0.3 (4.5-5)	5.9 \pm 0.7 (5-7.5)		
Tail length		26 \pm 5.4 (21-36)	23 \pm 3.5 (20-29)	28 \pm 4.3 (22-32)	25 \pm 3.2 (22-29.5)	27 \pm 5 (21-39)		
Pharynx length		144.5 \pm 9.6 (135-160)	129 \pm 17.6 (115-150)	152 \pm 5.5 (144-161)	112 \pm 8.2 (104.5-122)	127 \pm 13.2 (110-152)		
1st lip annulus diam.		14.5 \pm 1.7 (12.5-17)	15 \pm 0.5 (14-16)	19 \pm 2 (16-21.5)	14 \pm 1.2 (12.5-15.5)	17 \pm 1.4 (14.5-19.5)		
2nd lip annulus diam.		20 \pm 2 (18-23)	19 \pm 1.3 (18-21)	24 \pm 1.7 (22-26.5)	17.5 \pm 1 (17-19)	22 \pm 1.6 (18.5-25)		
1st body annulus diam.		23.5 \pm 1.9 (21.5-26)	23 \pm 2.5 (21-26.5)	28 \pm 1.8 (26-32)	21 \pm 1.2 (20-23)	25 \pm 1.8 (23-29)		
2nd body annulus diam.		26 \pm 1.8 (23.5-29.5)	26 \pm 3.4 (23-32)	32.5 \pm 2.4 (29-36)	24.5 \pm 1 (23.5-26)	28 \pm 1.9 (26-32)		
R		103 \pm 2.6 (100-107)	99 \pm 3.4 (94-104)	100 \pm 3.1 (95-105)	104 \pm 1.5 (103-106)	90 \pm 2.1 (87-94)		
RSt		17 \pm 1.4 (16-20)	14 \pm 1.3 (13-16)	17 \pm 1.1 (15-18)	13 \pm 1 (12-14)	11 \pm 0.7 (10-12)		
Roes		31 \pm 1.3 (29-32)	25 \pm 1.7 (24-28)	28 \pm 1.1 (26-29)	26 (n = 1)	23 \pm 2 (20-27)		
Rex		31 \pm 0.8 (30-32)	28 \pm 1.2 (27-30)	30 \pm 1.2 (28-32)	29 \pm 0.5 (29-30)	25 \pm 1.1 (24-27)		
RV		8 \pm 1.7 (7-11)	8 \pm 1.3 (6-10)	7 \pm 0.4 (6-7)	8.5 \pm 0.6 (8-9)	7 \pm 0.8 (6-9)		
RVan		1.5 \pm 0.8 (1-3)	2 \pm 1 (1-3)	0-1	1	0-1		
Ran		6 (5-7)	6 \pm 1.5 (4-7)	6 \pm 0.9 (5-7)	6.5 \pm 0.6 (6-7)	6 \pm 1.1 (4-8)		
VL/VB		1 \pm 0.2 (0.7-1.1)	0.9 \pm 0.2 (0.7-1.1)	0.8 \pm 0.1 (0.6-1)	0.9 \pm 0.05 (0.9-1)	1 \pm 0.08 (0.8-1.1)		
St%L		13.6 \pm 1.5 (10.4-14.6)	10 \pm 0.6 (10-11)	14.4 \pm 1.2 (12.4-16.1)	10.5 \pm 0.3 (10.2-10.8)	10.6 \pm 1 (8.5-12)		

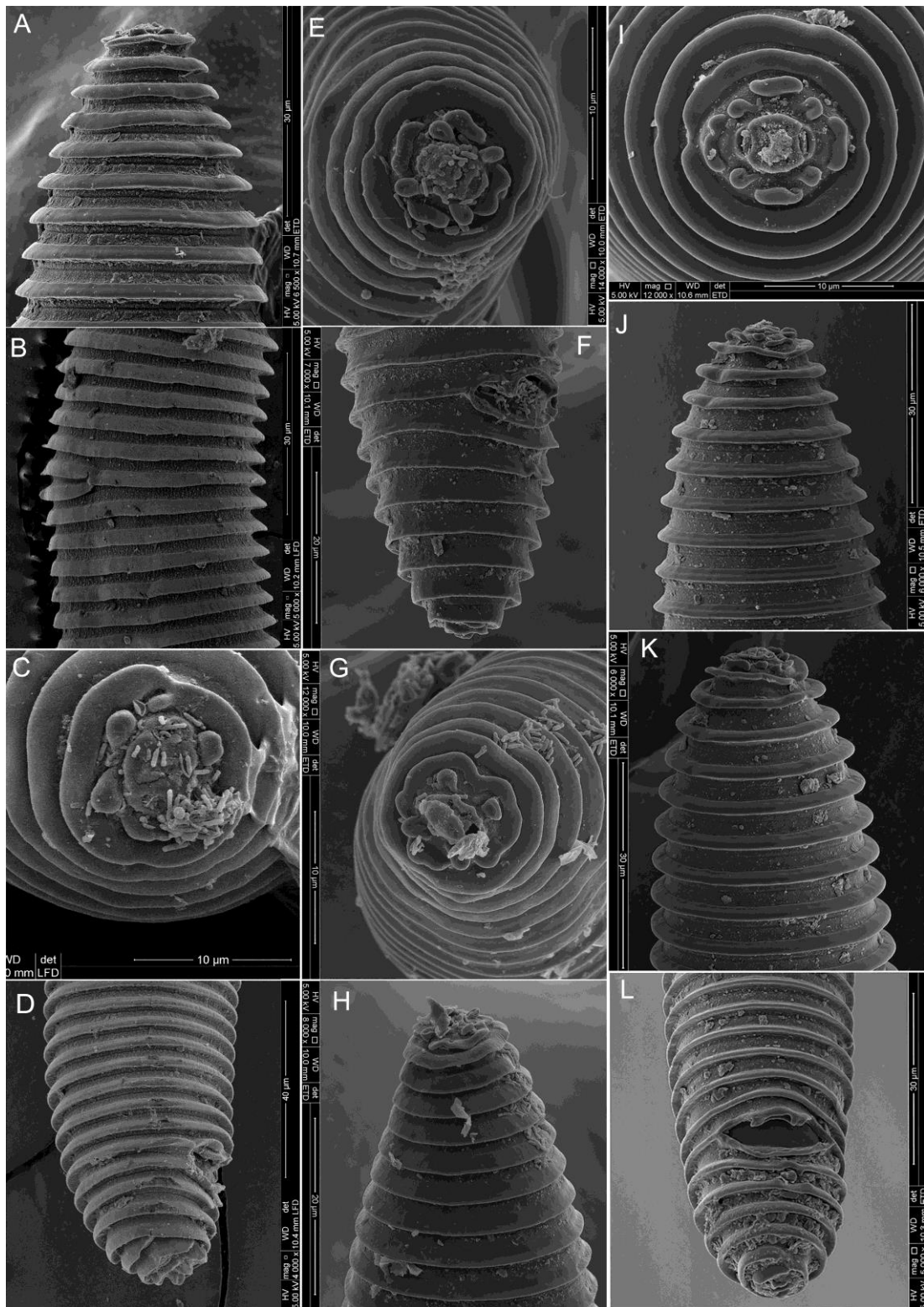


Fig. 9. *Mesocriconema xenoplax*. SEM. CD865. Female. A: Lateral view of anterior part of body; B: Annuli at midbody; C: *En face* view of lip region; D: Lateral view of posterior part of body. *Mesocriconema nebraskense*. SEM. CD869 Female. E, G: *En face* view of two lip regions; F: Ventral view of posterior part of body; H: Lateral view of anterior part of body. *Mesocriconema* sp. A. SEM. CD1182. Female. I: *En face* view of lip region. J, K: Lateral view of anterior part of body of two females; L: Ventral view of posterior part of body.

Female. Body slightly curved ventrad. Lip region with two annuli, first one pointing more outward and second one retrorse, not set off from body. First annulus usually divided into two parts by a deep lateral indentation but in some populations the indentation is not so distinct. Submedian lobes prominent, rounded and 2.5 to 3 µm in diameter. Labial plates normally large and prominent and in some cases appearing as an additional annulus. All body annuli retrorse with smooth margins, sometimes slightly irregular. Anastomosis rare. Stylet strong and well developed with cupped basal knobs. Excretory pore situated from one annulus anterior to six annuli posterior to base of basal pharyngeal lobe. Hemizonion not seen. Spermatheca mostly indistinct or small, round and empty. Vulva an open slit with anterior lip bearing two rounded projections. Vagina always distinctly sigmoid. Anus distinct four to eight annuli from tail tip. Tail form varying from round to conoid with one flat lobe or a few rounded lobes on the tip.

Male. Not found.

Juvenile. Not found.

Remarks. These specimens compared very well with those from the literature although some variation was observed. Orton Williams (1972) discussed the great variation in the arrangement of the submedian lobes and labial plates. Popovici and Ciobanu (2000) mentioned that all their females had sperm filled spermathecae. Some populations had fewer body annuli than others (Peneva *et al.*, 2000). Crozoli and Lamberti (2001) stated that anastomosis was common along the whole length of the body.

Molecular characterisation. The D2-D3 of the 28S rRNA gene sequences were obtained from three samples and they were different from that from Belgium in 0.2-1.3%. Phylogenetic relationships of this species with other criconematids are given in Figure 3. *COI* gene sequence analysis revealed that the South African sample belonged to the haplotype 10 as it has been defined by Powers *et al.* (2014) (Fig. 6).

***Mesocriconema* sp. A (Figs S5E-H & 9I-L)**

This sequence of the sample from Gainesville, Florida, USA is similar to those of *Mesocriconema ornata* (Raski, 1958) Loof & De Grisse, 1989 haplotype group 15 as identified by Powers *et al.* (2014). Powers *et al.* (2014) distinguished three haplotype groups 1, 15 and 16 within this species and stated that groups 1 and 15 both conformed to the morphospecies description and were only isolated from agricultural soils, yet the mean

pairwise *p*-distance of the *COI* haplotypes of the two groups was 21.6%. Because, the sequences of group 1 were significantly different from others, we could consider it as belonging to a true *Mesocriconema ornata*, because these samples were collected near the type locality, whereas others are considered to be representatives of an undescribed *Mesocriconema* sp. A.

Measurements. See Table 3.

Female. Body slightly curved ventrad. Lip region with two annuli. Body annuli retrorse with smooth margins, sometimes slightly irregular. Stylet strong and well developed with cupped basal knobs. Excretory pore situated from one annulus anterior to six annuli posterior to base of basal pharyngeal lobe. Spermatheca mostly indistinct or small, round and empty. Anus distinct four to eight annuli from tail tip. Tail form varying from round to conoid with one flat lobe or a few rounded lobes on the tip.

Male. Not found.

Juvenile. Not found.

Remarks. Measurements of this sample are similar to those of haplotype 15 provided by Powers *et al.* (2014).

Molecular characterisation. This species is related to *M. nebraskense* (Figs 3 & 6). The provided *COI* sequences are identical to that of a sample identified as *Mesocriconema ornata* from Alabama by Powers *et al.* (2014).

Phylogenetic relationships reconstructed in this study using the D2-D3 of 28S rRNA gene sequences are congruent to those presented by other authors (Munawar *et al.*, 2020; Hosseinvand *et al.*, 2020, 2023; Li *et al.*, 2022; Nguyen *et al.*, 2022) and also revealed that genera *Criconemoides*, *Criconema*, *Discocriconemella* and *Mesocriconema* are not monophyletic. Nguyen *et al.* (2022) concluded that key morphological characters used in the classification of Criconematidae are the consequence of convergent evolution. Thus, the results of molecular dataset analysis show that the classification of Criconematidae needs to be revised.

The genus *Discocriconemella* was proposed by De Grisse and Loof (1965) when revising *Criconemoides* and up to now it included 31 species, which were characterised by the presence of a disc-shaped head (Geraert, 2010; Munawar *et al.*, 2019; Li *et al.*, 2022). Based on the results of molecular dataset analysis, Powers *et al.* (2014) transferred *Discocriconemella inarata* to the genus *Mesocriconema* and named as *M. inaratum*. The present analysis showed that the D2-D3 of 28S rRNA gene sequences of *D. sinensis* Munawar, Cai, Subbotin & Zheng, 2019 and *D. parasinensis* Li, Munawar, Castillo & Zheng, 2022 clustered with

those of *Criconemoides* species belonging to the *C. informis* group and based on this grouping, these species are considered here as representative of this genus: *Criconemoides sinensis* (Munawar *et al.*, 2019) comb. n. and *Criconemoides parasinensis* (Li *et al.*, 2022) comb. n., both described from China. The positions of these species within the genus *Criconemoides* were already noticed and discussed by Munawar *et al.* (2019) and Li *et al.* (2022).

The diagnosis for the genus *Criconemoides* provided by Siddiqi (2000) and Geraert (2010) is shorten and modified and given below.

Genus *Criconemoides*

Diagnosis. Criconematidae. Female: Small to moderately large (about 0.3-1 mm), sausage- or ring-like when relaxed. Annuli crenate, rough or smooth, with round to pointed edges. Cephalic annuli two to three, smaller than and not differentiated or separated by a collar from body annuli. Some species with cephalic annulus appearing as a large, anteriorly flattened disc. Submedian lobes absent or present. Stylet moderately long usually rigid. Vulva lips closed or open. Vagina straight. Tail short, conoid, convex-conoid or hemispheroidal. Male: Cephalic region rounded or conoid, lateral field with three to four incisures. Bursa distinct, subterminal.

Criconemoides sinensis (Munawar *et al.*, 2019) comb. n.

= *Discocriconemella sinensis* Munawar, Cai, Subbotin & Zheng, 2019

Criconemoides parasinensis (Li *et al.*, 2022) comb. n.

= *Discocriconemella sinensis* Li, Munawar, Castillo & Zheng, 2022

Among the species of the genus *Discocriconemella*, Orton Williams (1981) and Vovlas (1992) distinguished four groups based on configuration of the cephalic disc. Group 1 included species with round cephalic disc with an uninterrupted margin and *Criconemoides sinensis* comb. n., *C. parasinensis* comb. n. and *Mesocriconema inaratum* belonged to this group. *Discocriconemella limitanea* (Luc, 1959) De Grisse & Loof, 1965, the type species of this genus, belonged to group 2 having disc with ventral and dorsal deep indentations and this species formed a separate lineage within criconematids in phylogenetic trees. Munawar *et al.* (2019) showed that *D. hengsungica* Choi & Geraert, 1975 belonging to group 4 with round disc with paired

dorsal and ventral projections also formed a separate lineage, which was sister to *Xenocriconemella macrodora* (Taylor, 1936) De Grisse & Loof, 1965. Species belonging to group 3 with disc indented medially and laterally giving a four-lobed appearance are not still molecularly characterised. Thus, disc-shaped head appeared several times in criconematid evolution and can not be used as reliable taxonomic character for genus differentiation. We agree with the proposal made by Munawar *et al.* (2019) that it needs detailed molecular characterisation of other *Discocriconemella* species in order to facilitate their phylogenetic grouping and then use these results to revise this genus.

SUPPLEMENTAL MATERIALS

Figure S1. *Criconema mutabile* and *Mesocriconema sphaerocephalum*.

Figure S2. *Criconema mutabile*.

Figure S3. *Criconemoides annulatus*.

Figure S4. *Criconemoides informis*.

Figure S5. *Mesocriconema nebraskense* and *Mesocriconema* sp. A.

Figure S6. *Mesocriconema xenoplax*.

Table S1. Measurements of *Criconema mutabile*.

Table S2. Measurements of *Criconemoides annulatus* and *C. informis*.

Table S3. Measurements of *Mesocriconema sphaerocephalum*.

<http://www.russjnmematology.com/Articles/rjn312/Paper9VandenBerg-SUPPL.pdf>

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E. Van den Berg, L.R. Tiedt and S.A. Subbotin. Морфологическая и молекулярная характеристика нескольких известных видов нематод родов *Criconema*, *Criconemoides* и *Mesocriconema* (Tylenchida: Criconematidae) из США и Южной Африки.

Резюме. В ходе нематологических обследований в нескольких регионах США и Южной Африки и с использованием интегративного подхода, сочетающего морфологический и молекулярный анализы, были обнаружены следующие виды: *Criconema annuliferum*, *Criconema mutabile*, *Criconemoides annulatus*, *C. informis*, *Criconemoides* sp. A, *Mesocriconema nebraskense*, *M. sphaerocephalum*, *M. xenoplax* и *Mesocriconema* sp. A. Эти виды были описаны морфологически и морфометрически, а также для некоторых видов даются СЭМ фотографии. Также предоставлены молекулярные характеристики видов с использованием последовательностей генов сегмента D2-D3 28S рРНК и COI мтДНК. По результатам молекулярного анализа *Discocriconemella sinensis* Munawar, Cai, Subbotin & Zheng, 2019 и *D. parasinensis* Li, Munawar, Castillo & Zheng, 2022 переведены в род *Criconemoides*.

SUPPLEMENTAL MATERIALS: E. Van den Berg, L.R. Tiedt and S.A. Subbotin. Morphological and molecular characterisation of several known nematode species of the genera *Criconema*, *Criconemoides* and *Mesocriconema* (Tylenchida: Criconematidae) from the USA and South Africa. *Russian Journal of Nematology*, 2023, volume 31, issue 2, 139–159.

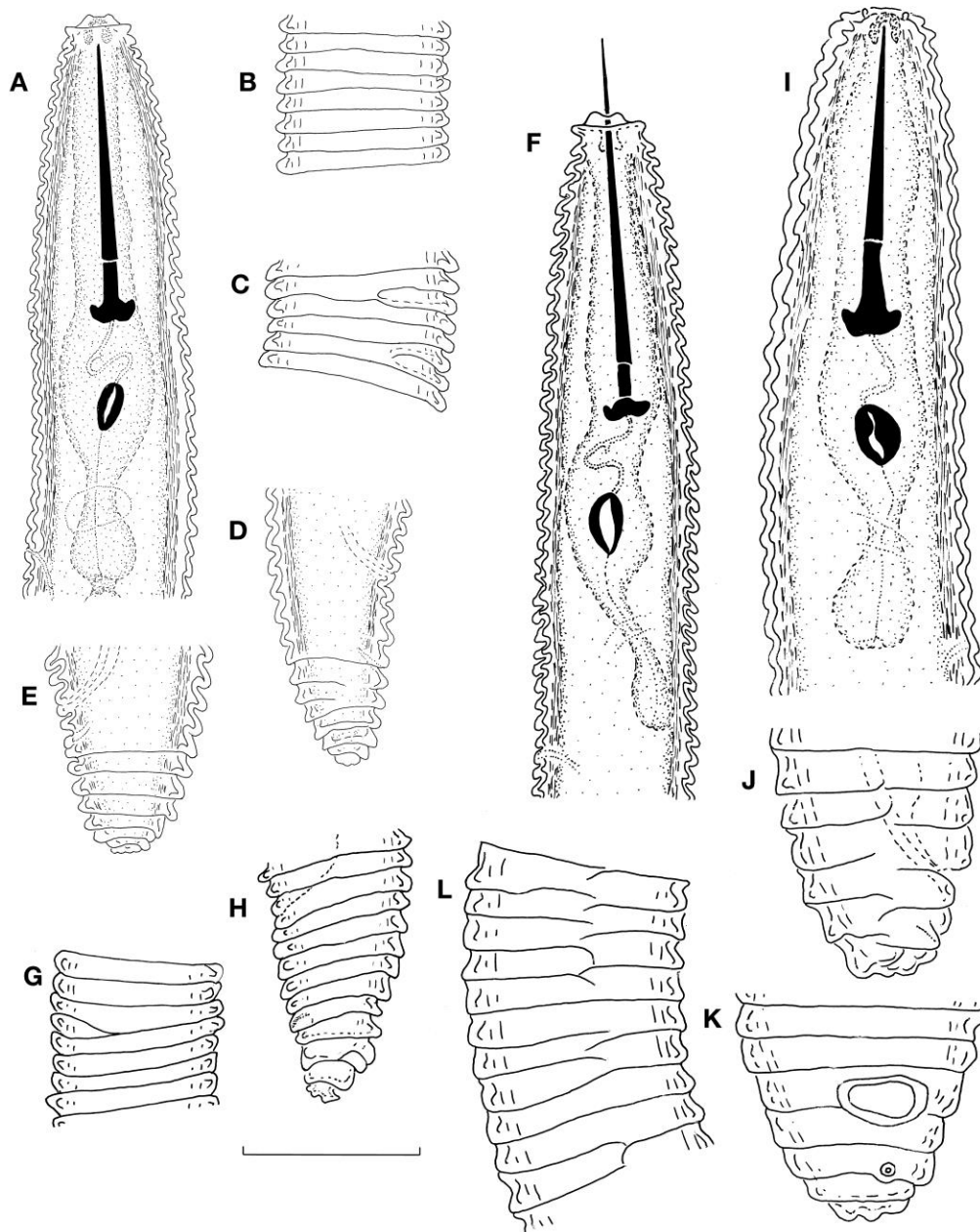


Fig. S1. *Criconema mutabile*. Tv11982. Female. A: Lateral view of anterior part of body; B, C: Annuli at midbody; D, E: Lateral view of two different tail areas. CD847 Female. F: Lateral view of anterior part of body; G: Annuli at midbody; H: Lateral view of posterior part of body. *Mesocriconema sphaerocephalum*. CD1183. I: Lateral view of anterior part of body; J: Lateral view of posterior part of body; K: Ventral view of posterior part of body; L: Annuli at midbody. Scale bar = 30 µm.

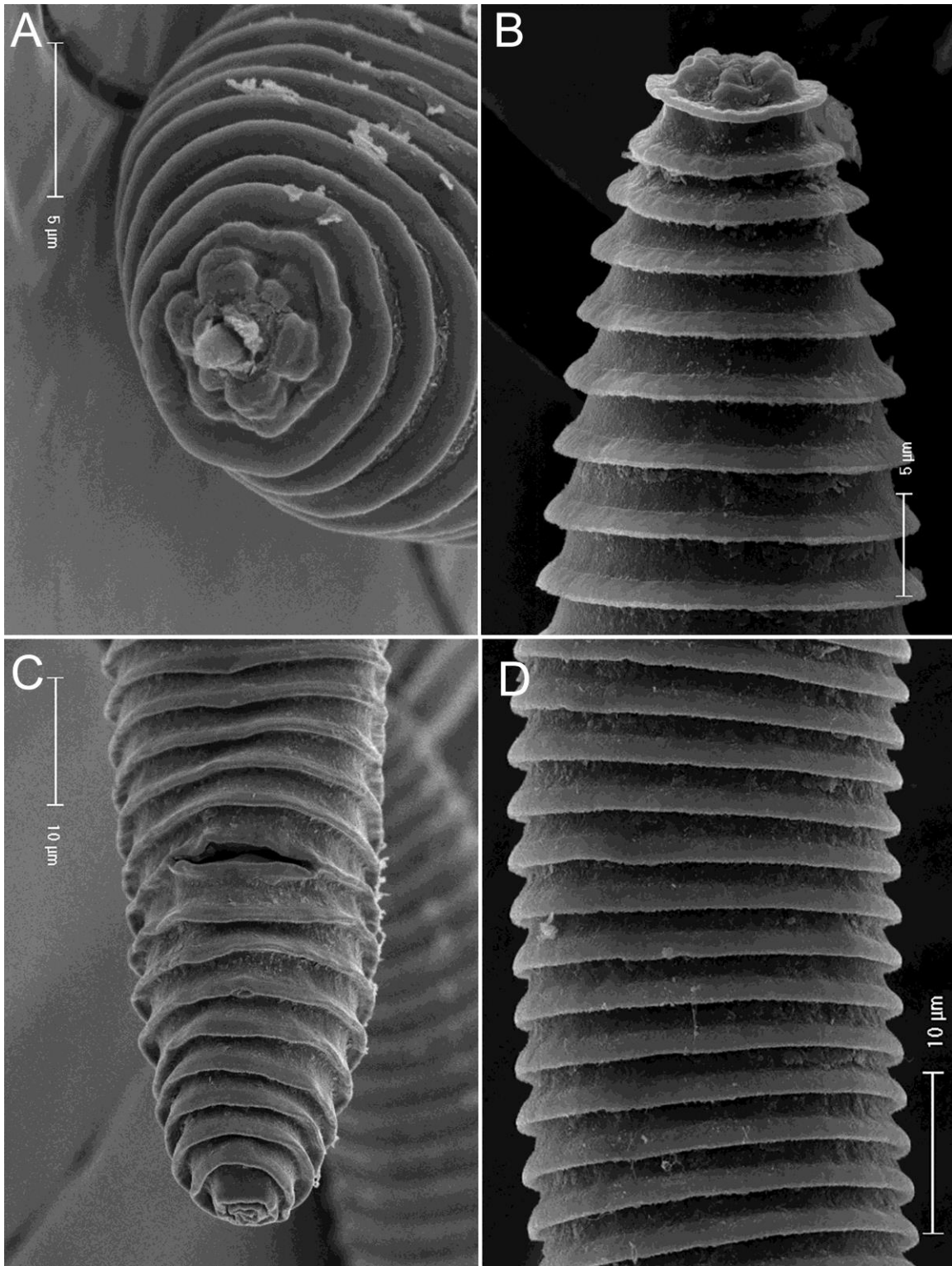


Fig. S2. *Criconema mutabile*. Tv11982. Female. A: *En face* view of lip region; B: Lateral view of lip region; C: Ventral view of posterior region; D: Annuli at midbody.

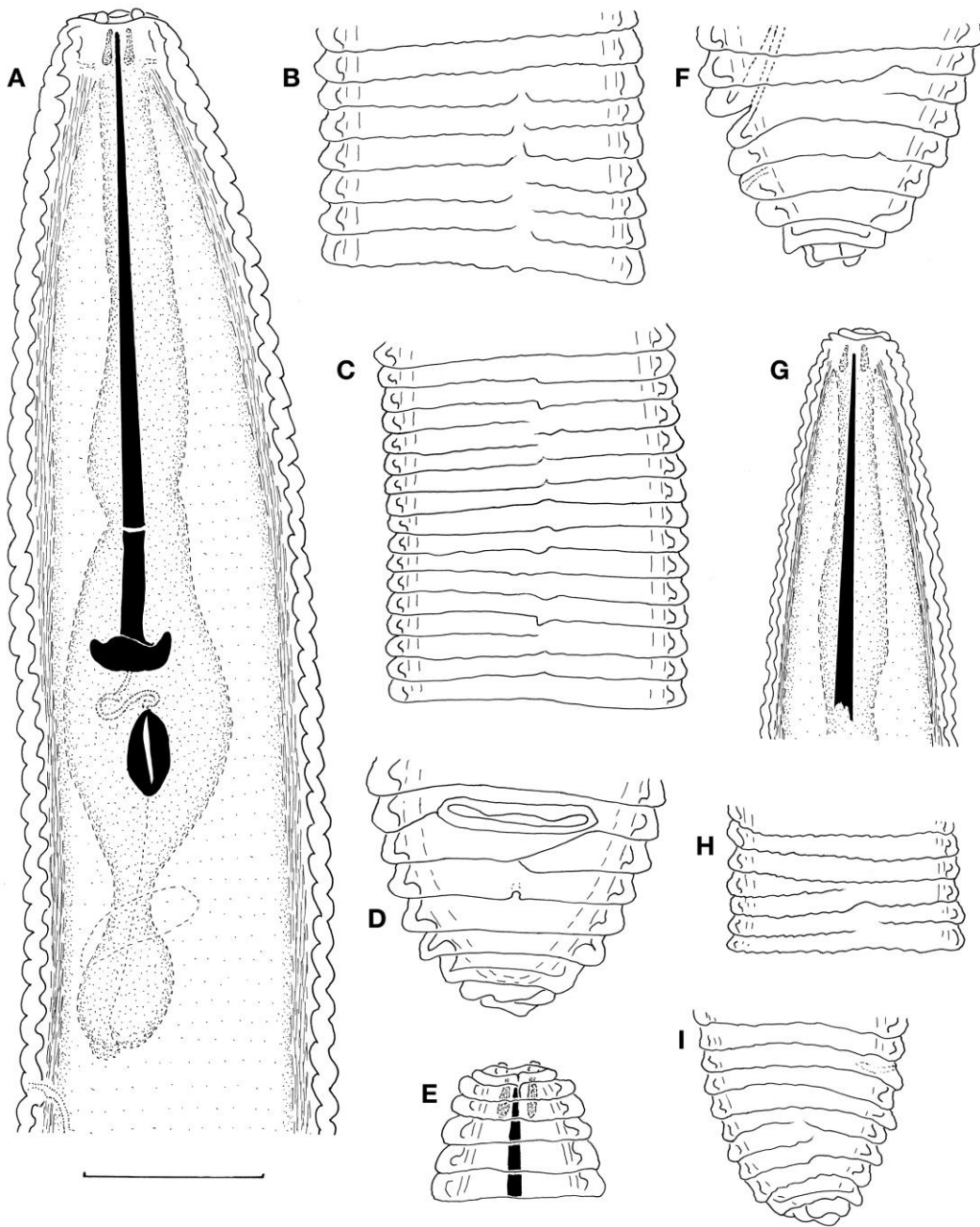


Fig. S3. *Criconemoides annulatus*. CD879. Female. A: Anterior part of body; B: Annuli on anterior part of body; C: Annuli at midbody; D: Ventral view of tail region; E: Lip region of another female; F: Lateral view of tail. Juvenile. G: Anterior part of body with broken stylet; H: Annuli at midbody; I: Lateral view of tail region. Scale bar = 30 μ m.

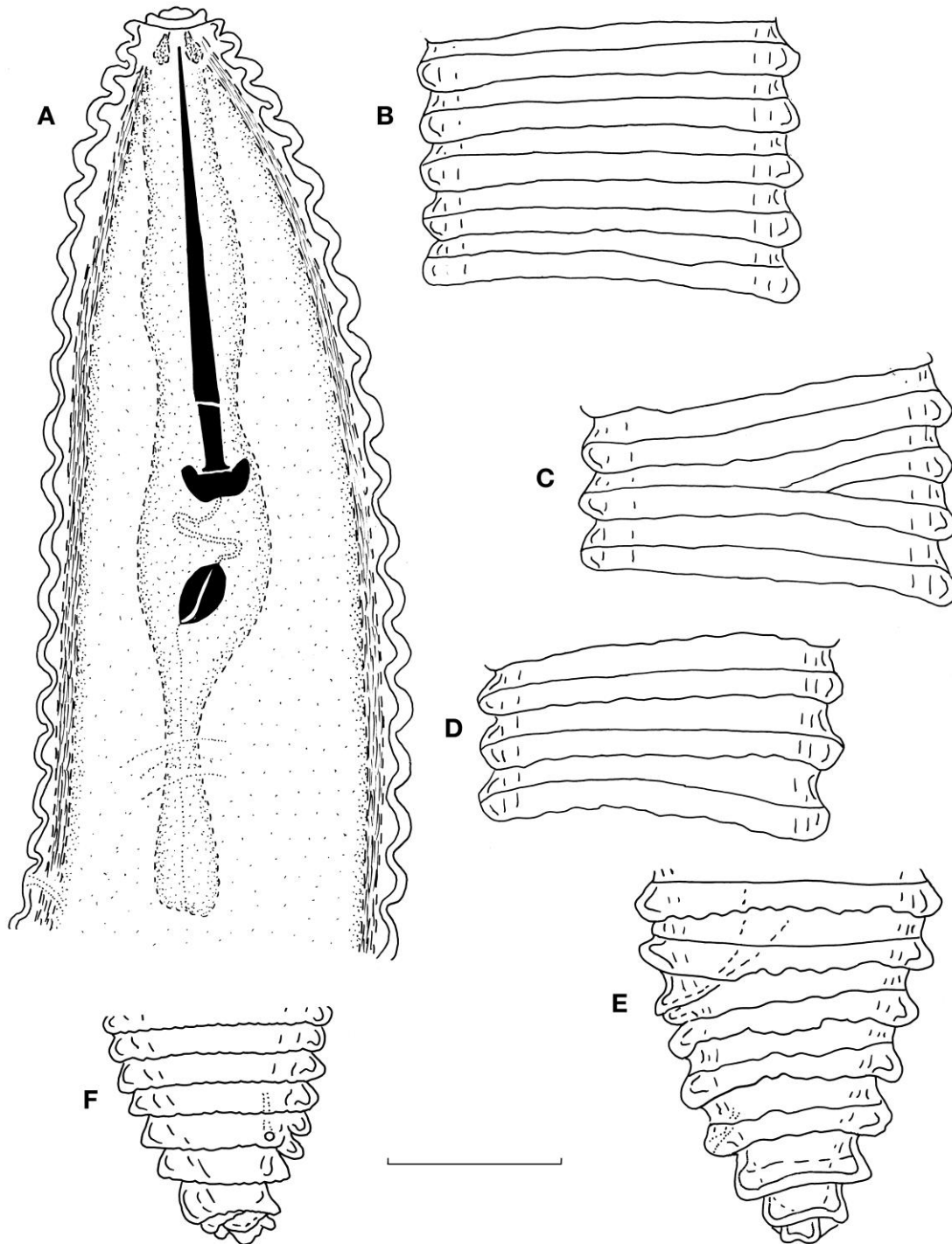


Fig. S4. *Criconemoides informis*. CD836. Female. A: Lateral view of anterior part of body; B, C: Annuli at midbody; D: Annuli anterior to vulva; E: Lateral view of posterior part of body; F: Ventral view of tail tip. Scale bar = 30 μ m.

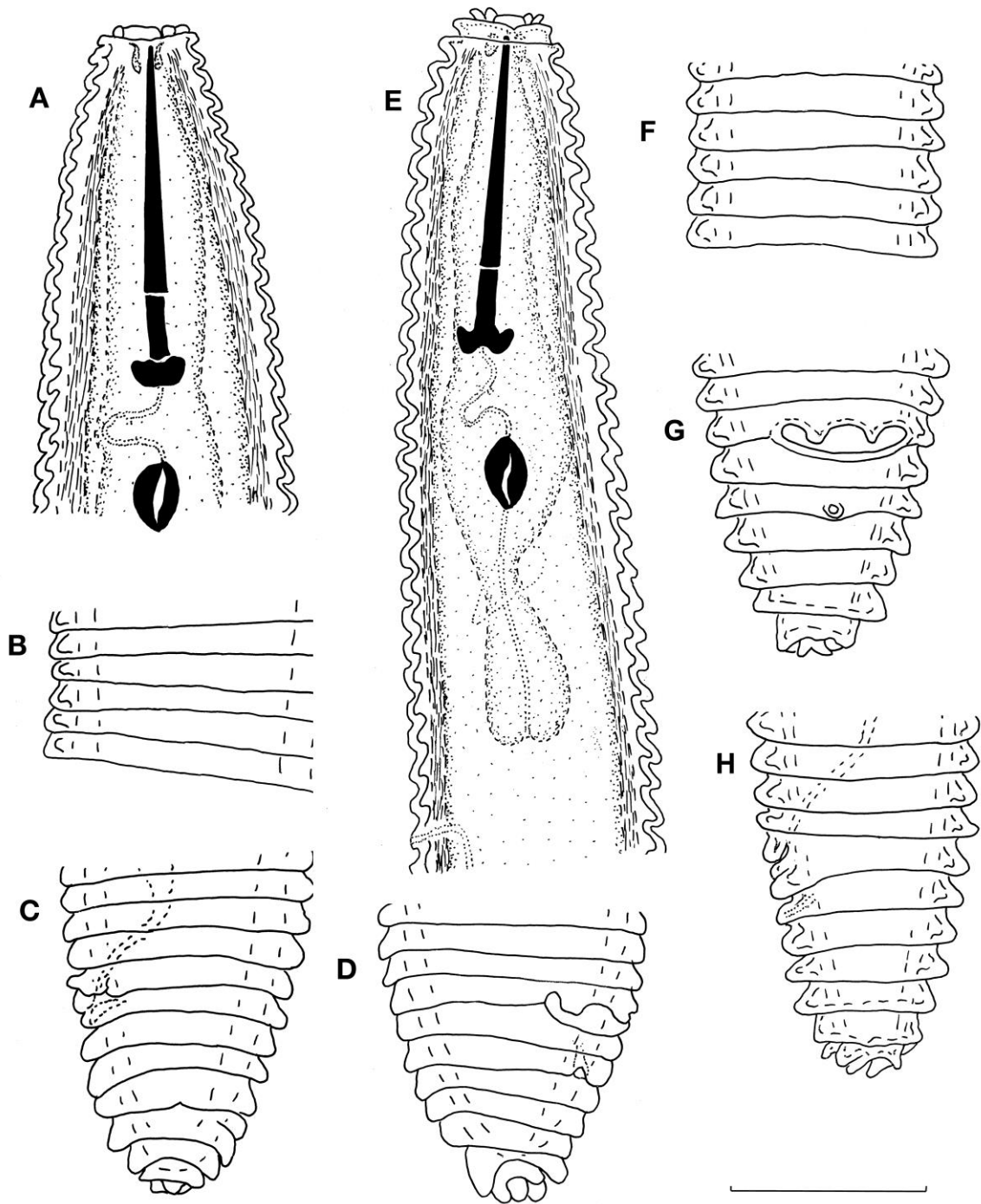


Fig. S5. *Mesocriconema nebraskense*. CD869. Female. A: Lateral view of anterior part of body; B: Annuli at midbody; C: Lateral view of posterior part of body; D: Ventral view of posterior part of body. *Mesocriconema* sp. A. CD1182. Female. E: Lateral view of anterior part of body; F: Annuli at midbody; G, H: Posterior part of body. Scale bar = 30 μ m.

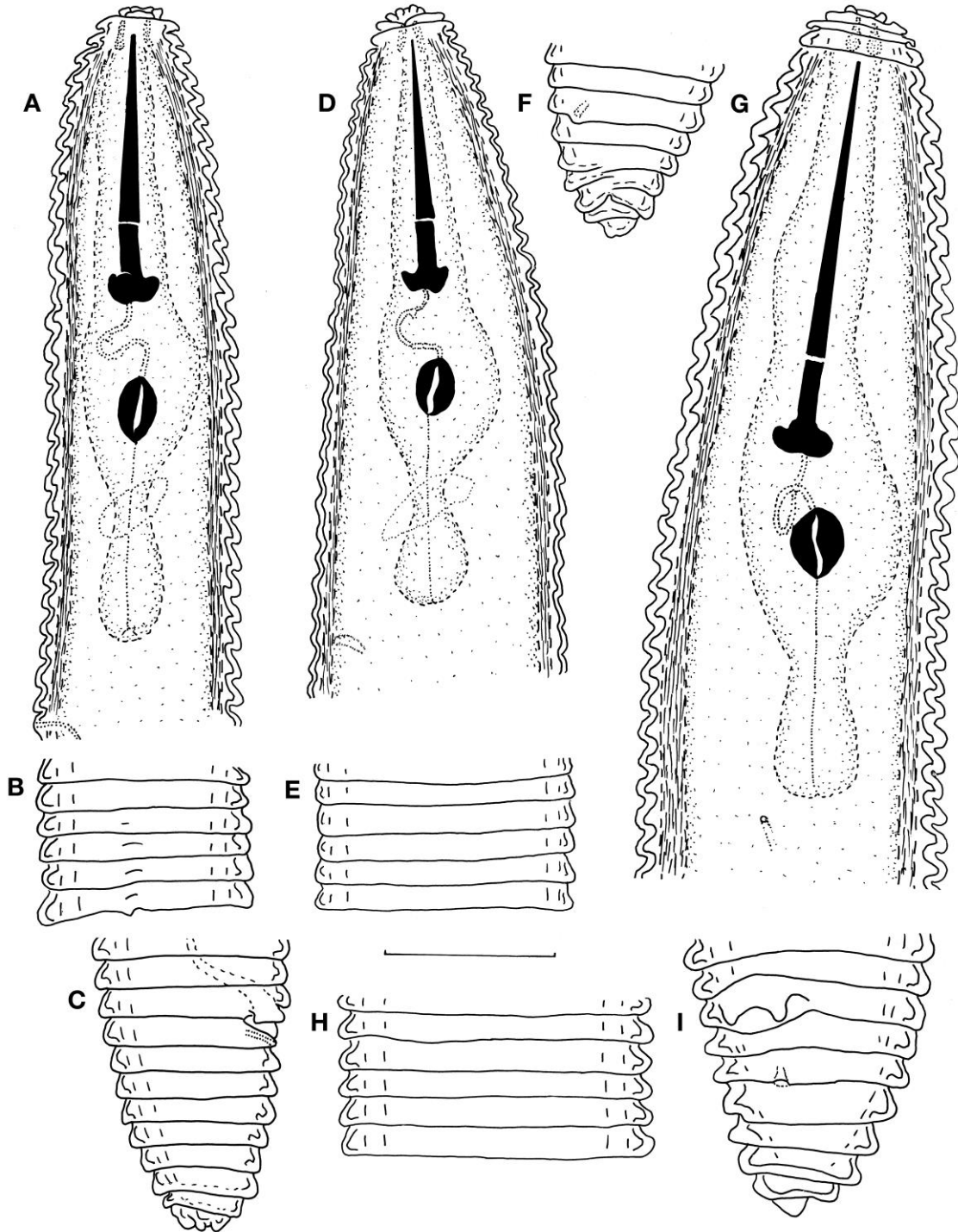


Fig. S6. *Mesocriconema xenoplax*. CD865. Female. A: Lateral view of anterior part of body; B: Annuli at midbody; C: Lateral view of posterior part of body. CD865 Juvenile. D: Lateral view of anterior part of body. E: Annuli at midbody; F: Ventral view of posterior part of body. CD 863. Female. G: Lateral view of anterior part of body; H: Annuli at midbody; I: Ventral view of posterior part of body. Scale bar = 30 μm .

Table S1. Measurements of *Criconea mutabile* females compared with those from the literature. All measurements are in μm and in the form: mean \pm SD (range).

Character	Sample South Africa (Tvl1982)	Reference (a)	Van den Berg (1984)	Crozzoli & Lamberti (2002)	Van den Berg <i>et al.</i> (2004)	Shokoohi <i>et al.</i> (2020)
n	15	83	29	20	6	3
L	376.5 \pm 35.5 (339-465)	270-580	298-532	330-377	360-430	302.7 \pm 69.9 (240-378)
a	11.7 \pm 1.1 (10-13.1)	8.5-17	9.3-15.1	10-12	10.2-14.6	11.9 \pm 2.4 (9.6-14.3)
b	3.9 \pm 0.2 (3.5-4.3)	3-5.1	3.3-5.3	3.6-4	4.1-4.4	2.8 \pm 0.9 (2.1-3.8)
c	19 \pm 2.7 (15.7-24)	17-34	16.5-41.4	16-19	14.5-23.3	20.9 \pm 7.2 (15.2-29.1)
o	8.9 \pm 1.5 (6.5-11.4)	–	6.2-10.3	–	8.2-8.9	–
DGO	4.5 \pm 0.7 (3.7-5.9)	–	4.4-6.6	–	4.5	–
V	92 \pm 0.6 (91-93)	89-94	91-95	90-92	91-93	90 \pm 0.0 (90-93)
OVI	43 \pm 5.3 (36.5-53)	–	26-76	–	36-40	–
OV length	161 \pm 32.8 (128.5-245.5)	–	–	–	–	–
Stylet length	52 \pm 3.2 (47.5-60)	45-65	46.7-71	56-60	45-55	67.7 \pm 7.4 (62-76)
Metenchium length	41.5 \pm 2.2 (37.5-45)	39-49	37.5-58.9	46-53	34.5-44	–
Telenchium length	10.5 \pm 0.8 (8.5-12)	–	8.8-13.2	–	9.5-12	–
m	79.5 \pm 2.8 (71.1-82.1)	–	–	84-86	–	–
Stylet knob height	3 \pm 0.5 (2-3.5)	–	2.2-4	–	3-4	2.2 \pm 0.7 (1.8-3.0)
Stylet knob width	7.5 \pm 0.7 (6.5-9)	–	6.6-10.7	–	7-8	6.4 \pm 0.5 (6-7)
Exc. pore from anter. end	97.5 \pm 8.7 (83.5-113)	79-107	73-145	90-104	94-115	–
Width at midbody	31.5 \pm 3.9 (20.5-38)	28-41	23.5-39.7	27-33	29-39	–
Annulus width	3.5 \pm 0.3 (3-4.5)	3.3-4.2	2.6-5.2	–	3-4	–
Tail length	20 \pm 3.5 (15.5-25)	10-24	12.9-26.1	18-24	17-27	15 \pm 3.5 (13-19)
Pharynx length	95 \pm 3.5 (88.5-102)	86-106	–	83-95	87-98	–
1st lip annulus diam.	11 \pm 0.5 (10.5-12)	10.5-14	9.9-15.4	–	10-12	–
2nd lip annulus diam.	13 \pm 0.6 (12-14)	–	11.8-15.8	–	12-14	–
1st body annulus diam.	15.5 \pm 1 (14-17.5)	–	14-18.8	–	14-17	–
2nd body annulus diam.	17.5 \pm 0.9 (16-18)	–	16.2-22.8	–	16-19	–
R	109 \pm 3.9 (103-119)	85-121	99-116	115-120	106-111	113 \pm 7.8 (104-118)
RSt	17 \pm 1.1 (15-18)	16-19	15-21	19-20	16-17	–
ROes	29 \pm 2 (26-33)	24-33	21-32	29-31	25-28	–
Rex	29 \pm 1.4 (26-31)	23-34	26-32	–	28-31	33 \pm 1.0 (32-34)
Rhem	29 \pm 1.4 (26-30)	27	27-30	–	27-29	–
RV	10 \pm 1 (9-12)	6-13	8-11	12-13	10-12	10 \pm 1.7 (8-12)
RVan	2 \pm 0.7 (1-3)	1-3	1-3	1-2	0-3	–
Ran	7 \pm 1.1 (6-10)	6-12	5-9	9-11	7-8	6 \pm 1.0 (5-8)
VL/VB	1.2 \pm 0.1 (1.1-1.5)	1-1.5	1-1.4	–	1.1-1.2	1.1 \pm 0.1 (1.0-1.1)
St%L	13.8 \pm 1.4 (11.7-16.2)	14-20	10.4-19.7	–	12.4-14.5	–

Note:(a) Raski and Golden (1965), Heyns (1970a, b), Sakwe and Geraert (1993).

Table S2. Measurements of *Criconemoides annulatus* and *C. informis* compared with those from the literature. All measurements are in μm and in the form: mean \pm SD (range).

Species	<i>Criconemoides annulatus</i>			<i>C. informis</i>		
	USA, California (CD879)		Choi <i>et al.</i> (2000)	USA, California (CD836)	References (a)	Tabolin <i>et al.</i> (2020)
Character	Females	Juvenile	Females	Females	Females	Females
n	9	1	138	2	68	12
L	712 \pm 59.9 (608-771)	588	320-1000	518, 558	320-630	454.6 \pm 53.9 (390-540)
a	13 \pm 0.9 (11.3-14.3)	14.9	8-18	7.7, 8.3	6.9-13	8.7 \pm 0.8 (8.0-10.4)
b	4.1 \pm 0.3 (3.5-4.4)	3.5	3-4.6	3, 3.5	2.9-4.7	3.5 \pm 0.3 (3.1-3.8)
c	47.6 \pm 14.1 (29.1-70.6)	40	21-47	26 (n = 1)	13.3-34	18.4 \pm 2.1 (15.6-21.4)
o	7.7 \pm 1 (6.5-8.6)	–	–	–	6.6-10.9	–
DGO	8.5 \pm 0.7 (7.5-9)	–	–	–	5-8	–
V	95 \pm 0.9 (94-96)	–	89-97	92, 93	87-93	–
OV1	57.2 \pm 18 (37.5-89.7)	170.5	–	44.1 (n = 1)	–	–
OV length	417.5 \pm 156 (228-691)	–	–	246.5 (n = 1)	–	–
Stylet length	105 \pm 4 (99.5-112.5)	–	65-108	79, 81	57-87	77.3 \pm 3.5 (69-87.5)
Metenichium length	82.5 \pm 4.3 (77-90.5)	64	–	62, 64	52-69	–
Telenchium length	22 \pm 2 (17.5-24.5)	–	–	17	–	–
m	78.9 \pm 2 (77.7-83.7)	–	76-88	78.5, 79.1	73-82	–
Stylet knob height	5.5 \pm 0.6 (5-6)	–	–	4.5, 5	4-4.5	–
Stylet knob width	13 \pm 0.7 (12-14)	–	–	11	9-14	–
Exc. pore from anter. end	182.5 \pm 13.3 (160-198.5)	156	–	145.5, 165	119-174	–
Width at midbody	54 \pm 5.2 (44-61.5)	39	–	67	40-63	–
Width at anus	44 \pm 4.2 (39.5-51.5)	29	–	33, 38	–	–
Width at vulva	33.5 \pm 4 (25.5-37.5)	–	–	46.5, 51	–	–
Annulus width	5.5 \pm 0.8 (4.5-6.5)	5	–	9, 10.5	–	–
Tail length	16.5 \pm 5.3 (9-25)	14.5	–	20, 21.5	16-38	25 \pm 2.1 (20-27.5)
Pharynx length	174 \pm 6.5 (158-179)	167	–	149.5, 185.5	119-174	–
1st lip annulus diameter	15 \pm 2 (11-17.5)	10	–	12, 12.5	14-23	–
2nd lip annulus diameter	19.5 \pm 2.2 (17.5-21.5)	14.5	–	17, 22	19-26	–
1st body annulus diameter	25.5 \pm 1.9 (21.5-27)	17.5	–	22, 26	23-33	–
2nd body annulus diameter	28 \pm 1.5 (25.5-30)	19.5	–	27, 33	26-38	–
R	145 \pm 5.9 (133-151)	154	113-157	60, 65	48-83	63.6 \pm 0.9 (62-65)
RSt	24 \pm 2 (21-26)	–	–	11, 12	8-14	11.3 \pm 0.8 (10-13)
ROes	38 \pm 2.5 (35-42)	47	33-52	20, 23	13-22	19.2 \pm 0.9 (17-20)
Rex	40 \pm 2 (36-42)	46	31-50	20, 21	14-25	20.9 \pm 0.6 (20-21)
Rhem	36, 40 (n = 2)	46	–	–	–	–
RV	6.5 \pm 0.9 (6-8)	7	6-13	6, 7	5-13	6.5 \pm 0.7 (6-8)
RVan	2.5 \pm 0.7 (1-3)	–	1-5	1, 2	1-5	–
Ran	3 \pm 1.3 (2-5)	5	2-9	4	3-5	3.5 \pm 0.5 (3-4)
VL/VB	0.8 \pm 0.2 (0.6-1)	–	–	0.8, 0.9	0.9-1.4	1.2 \pm 0.1 (1.1-1.3)
St%L	14.6 \pm 0.8 (13.5-15.9)	–	–	14.5, 15	11.7-19.7	–

Note: (a) Loof (1965), Gomez Barcina *et al.* (1989), Choi *et al.* (2000), Eskandari *et al.* (2010).

Table S3. Measurements of females of *Mesocriconema sphaerocephalum* compared with those from the literature. All measurements are in μm and in the form: mean \pm SD (range).

Character	Sample	USA, Florida (CD1183)	Van den Berg (1980)	Gomez Barcina <i>et al.</i> (1991)	References (a)
n		6	121	10	190
L		346 \pm 18 (326-374)	356 (281-429)	381.4 \pm 44.36 (322-459)	220-478
a		8.6 \pm 1 (7.2-9.8)	8.7 (7-12)	9 \pm 1.17 (7.7-11.5)	5.4-13
b		3.4 \pm 0.2 (3.2-3.7)	3.3 (2.9-3.9)	3.2 \pm 0.3 (2.7-3.7)	2.3-4.3
c		45.8 \pm 15.9 (31.8-76)	39.1 (19.2-61.4)	51.9 \pm 5.57 (38.2-57.6)	19-122
o		9.7 \pm 1.5 (7.2-11.8)	–	–	–
DGO		5 \pm 0.7(4-6)	5.3 (2.2-7.7)	–	–
V		94 \pm 0.9 (93-95.5)	94 (91-96)	95.2 \pm 1.03 (93-96)	85-97
OV1		50.2 \pm 5.1 (46.1-57.2)	54 (40-79)	59 \pm 13.6 (45-75)	–
OV length		178 \pm 25.5 (160-214)	–	–	–
Stylet length		51.5 \pm 2 (49-54.5)	55.2 (46.7-61.8)	71.2 \pm 3.64 (67-77)	30-69
Metenchium length		36 \pm 1.6 (34-38)	38.8 (33.1-44.1)	57.1 \pm 2.13 (54-61)	31-54
Telenchium length		15.5 \pm 0.6 (14.5-16)	16.4 (12.9-18.8)	–	–
m		69.8 \pm 0.8(68.7-70.6)	–	80.2 \pm 1.7 (77-83)	69-74
Stylet knob height		4.5 \pm 0.6 (3.5-5)	4.9 (4-6.6)	–	–
Stylet knob width		9.5 \pm 1 (8.5-11)	10.1 (7.7-14.0)	–	–
Exc. pore from anter. end		114.5 \pm 9.3 (109-133)	–	121.2 \pm 13.1 (94-131)	98-108
Width at midbody		40.5 \pm 3.2 (37-45.5)	–	42.2 \pm 2.66 (39-46)	31-54
Width at anus		20 \pm 3.5 (14.5-25)	–	21.4 \pm 1.26 (20-24)	12-25
Width at vulva		30 \pm 3.1(28-35.5)	–	–	–
Annulus width		5.5 \pm 0.8 (4.5-6.5)	5.5 (4.2-6.6)	–	–
Tail length		8.5 \pm 2.5 (4.5-12)	9.9 (5.9-19.5)	7.5 \pm 1.78 (6-12)	4-14
Pharynx length		105 \pm 2.8 (101.5-109)	–	118.4 \pm 6.97 (107-128)	85-126
1st lip annulus diam.		14.5 \pm 0.4 (14-15.5)	13.4 (9.2-14.7)	–	–
2nd lip annulus diam.		18 \pm 1(16-18.5)	17.4 (11.8-19.9)	–	–
1st body annulus diam.		20.5 \pm 0.6 (20-21.5)	20.9 (14.7-25.4)	–	–
2nd body annulus diam.		23 \pm 0.7 (22.5-23.5)	–	–	–
R		69 \pm 3.4 (62-72)	59-77	67-82	52-79
RSt		11.5 \pm 0.5 (11-12)	10-15	15 \pm 1.08 (14-17)	10-20
ROes		21 \pm 1 (20-22)	12-26	21 \pm 1.27 (19-23)	16-31
Rex		23 \pm 1.6 (22-26)	18-24	21 \pm 1.06 (19-22)	16-28
Rhem		–	18-23	–	16-24
RV		4	4-7	4.4 \pm 0.7 (4-6)	3-7
RVan		1 \pm 0.6 (0-2)	1-3.5	2.1 \pm 0.32 (2-3)	0-3
Ran		2 \pm 0.8 (1-3)	1-4	2.3 \pm 0.48 (2-3)	1-5
VL/VB		0.65 \pm 0.05 (0.6-0.7)	0.7 (0.5-0.9)	0.56 \pm 0.06 (0.49-0.62)	0.5-0.9
St%L		15 \pm 0.8 (14-16)	15.4 (13.7-18.3)	19.1 \pm 2.28 (17.1-22.2)	14-22
St%Oes		49.7 \pm 2.3 (47.9-52.9)	–	60.4 \pm 3.78 (55.5-65.4)	44-62.5

Note: (a) Orton Williams (1973), Chaves (1983), Sakwe and Geraert (1993), Crozzoli and Lamberti (2001).