Redescription of *Pratylenchus teres* Khan & Singh, 1974 (Nemata: Pratylenchidae), with the description of a new subspecies from South Africa, and a phylogenetic analysis of related species

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A population of *Pratylenchus teres* from cotton and an unusual new subspecies, *Pratylenchus teres vandenbergae* from millet and tobacco at Rustenburg (RTB), South Africa, are described using light and scanning electron microscopy (SEM) and according to the D3 segment of the large-subunit (LSU) rDNA. The species is redescribed to include the variant RTB population having a shorter stylet range, absence of a sixth lateral line and four lip annules in about half of the population. In both populations the SEM lip patterns are similar to those of *P. bolivianus* Corbett, 1983. Their DNA sequences are identical and moderately distant from those of *P. crenatus* Loof, 1960, the originally diagnosed relative. A revised diagnosis and a phylogenetic analysis with biogeographical implications are presented.

Key words: *Gossypium hirsutum, Hirschmanniella* sp., lesion nematode, *Nicotiana tabacum, Pennisetum glaucum,* phylogeny, *Pratylenchus,* taxonomy.

Pratylenchus teres Khan & Singh, 1974, was described from two Indian populations as having three lip annules, a conoid, crenate tail, strong labial framework, slightly anchor-shaped stylet knobs, fine body annulation, and six lateral lines. The species lacked males, distinct spermathecae or sperm and was identified from soil around potato (*Solanum tuberosum* L.), mustard (*Brassica juncea* (L.)) Czerniak.) and safflower (*Carthamus tinctorius* L.). Other populations have been described from Guadeloupe in the Caribbean French West Indies (Van den Berg & Quénéhervé 2000) and recorded from Barbados (Cadet et al. 1994).

Recently, two populations of nematodes with features similar to those of *P. teres* were found in cotton (*Gossypium hirsutum* L.) soil from Jan Kempdorp (JK), and pearl millet (*Pennisetum glaucum* (L.) R.Br.) and tobacco (*Nicotiana tabacum* L.) soil at Rustenburg (RTB), South Africa. The RTB population from millet and tobacco was considered unusual by E van den Berg (ARC-Plant Protection Research Institute, Pretoria). In the present study, we characterise *P. teres* populations JK and RTB by morphological and molecular (D3 segment of the large-subunit (LSU) rDNA gene) means, and present a phylogenetic analysis including related species. While both populations appear to fall within the general original description of *P. teres,* they are designated here as morphologically distinct populations, with one being described as a new subspecies.

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Materials and methods

Culture, processing, measurement and phylogenetic analysis

Nematodes were tissue-cultured on Gamborg's B5 Medium on excised Iowa Chief maize (*Zea mays* L.) roots (Huettel & Rebois 1985) in a Precision Dual-Program incubator at 28 °C, and extracted with a Baermann funnel (Southey 1986). Nematodes were fixed in 4 % formalin for measurement. Some were measured without fixation for excretory pore location. They were then processed to glycerine by the formalin–glycerine method of Golden (1990). At least 20 specimens were examined for each population. Type material (slide T565V) with three specimens of *P. teres* from Amritsar, Punjab, India, was examined. Measurements were made with an ocular micrometer on a Leica WILD MPS48 Leitz DMRB compound microscope. Images and measurements were taken with Image Pro-Plus ver. 3.0 on a Zeiss Ultraphot microscope with differential interference contrast optics. All measurements were made in micrometres (µm) unless otherwise noted. Certain morphological characters were determined to be

either primitive or derived, based on the outgroup method for character polarity (Watrous & Wheeler 1981). The genus *Hirschmanniella* was selected as an immediate outgroup based on results from a recent molecular phylogeny (Carta et al. 2001) and its morphological characters determined (Sher 1968; Lopez & Salazar 1987; Loof 1991).

Scanning electron microscopy

Nematodes were either chemically fixed (Wergin & Stone 1981) and observed in a Hitachi S-570 SEM, or cryofixed from distilled water to liquid nitrogen and observed in a Hitachi S-4000 field emission SEM with an Oxford CT 1500 Cryotrans system (Wergin et al. 1993).

Molecular biology

Nematodes were prepared from two single adult females per population according to the procedure in Carta et al. (2001). The *P. teres* RTB sequence was submitted to GenBank, and aligned with other *Pratylenchus* sequences with the Clustal W program (European Bioinformatics Institute, http://www2.ebi.ac.uk/clustalw).

Taxonomic account

Pratylenchus teres Khan & Singh

Pratylenchus teres Khan & Singh, 1974: 209.

P. teres was originally described from specimens collected at Amritsar and Solan, India, from mustard, but the species was identified also in potato and safflower rhizospheres at Ludhiana, Punjab, India (Khan & Singh 1974). Later, another population from sugarcane on Sainte-Rose, Guadeloupe, was described (Van den Berg & Quénéhervé 2000). The specimens collected at JK and RTB, South Africa, generally conform to the descriptions of Khan & Singh (1974) and Van den Berg & Quénéhervé (2000). However, extended ranges for various measurements, new measurements and qualitative features for *P. teres,* and further comments on the comparative morphology of these nematodes are presented below.

Redescription

Original description amended to include characters of 3–4 lip annules (rather than 3), 4–6 lateral lines (rather than 6). Post-vulval sac (PVS) length extended to nearly three times mid-body width, upper limit of c′ extended from 2.5 to 3.0, and two or three lateral lines may exist at the middle of the tail apart from the single line originally described. When four lateral lines are present, the outer bands are gently aerolated, and superficial, interrupted longitudinal lines sometimes form within the inner and outer bands. The thickened cuticle at the tail apex frequently forms an asymmetrical projection. The regions around the vulva and excretory pore often protrude from the body. The post-vulval sac length relative to vulval body width ranges between 1 and 2.7 VD (Table 1).

Measurements. See Table 1 for measurements and Figs 1–3 for photographs of *P. teres* JK and *P. teres vandenbergae* n. subsp. (RTB).

Description of *Pratylenchus teres* JK population, Figs 1, 3C,E,F

Adult female. Body form straight to slightly curved. Fine body annulation. Three lip annules with gently rounded margins. Stylet knobs slightly cupped. Dorsal oesophageal gland opening 3 µm (live and fixed specimens) behind stylet. Strong labial framework, extending two annules backward. Oval to anteriorly wide, pear-shaped metacorpus, with oval valve often slightly asymmetrical. Elongate and narrow oesophageal glands. Oesophagus length 115–155 µm. Oesophageal gland overlap 35–47 µm. Excretory pore region often swollen in both live and fixed specimens, excretory pore situated 80–87 µm from anterior end. The four lateral lines are strongly crenate, with occasional perpendicular striations. The first lateral line begins at stylet level, increases to two and then to four near the posterior of the metacorpus. Four lines become three in the area between anus and phasmid after which one or two lines continue to just above tail tip. Body tapers symmetrically and gradually towards the vulva, but the vulval lips do not protrude. Post-vulval sac length (PVS) 28–35 µm, more than 1.5 times the vulval diameter (PVS/VD = 1.8–2.7). Tail distinctly narrowed from above anal region, length 30–37 µm, conical, with crenate tip, sometimes with a subventral or central projection.

Pratylenchus teres vandenbergae **n. subsp.**, Figs 2, 3A,B,D

Adult female. Body form slightly curved. Fine body annulation. Four lip annules in 53 % of specimens, three lip annules in others. Lip region continuous with the body; lip edges generally rounded, occasionally angular, with broad, flat

Table 1. Morphometrics of *Pratylenchus teres*. Range followed by mean ± standard deviation.

Character	Amritsar[a] (n = 17), India	Jan Kempdorp (n = 20), South Africa	Rustenburg (n = 32), South Africa	Rustenburg (holotype)	Sainte-Rose (n = 8), Guadeloupe	*P. teres* (all populations)
L (mm)	0.42–0.63, 0.55	0.47–0.63, 0.54 ± 0.4	0.50–0.64, 0.56 ± 0.3	0.56	0.47–0.53, 0.50 ± 0.2	0.4–0.6
a	22.1–39.9, 30.8	24.8–34.4, 30.5 ± 2.4	20–29.8, 24 ± 2.1	24.4	29–31, 30 ± 0.9	20–40
b	3.5–5.6, 4.6	3.2–5.5, 4.1 ± 0.5	3.7–4.9, 4.4 ± 0.3	4.7	4	3.2–5.6
c	11.5–27.0, 18.2	14.7–18.5, 16.1 ± 1.2	15.4–18.4, 6.8 ± 1.0	18	13–16, 14.5 ± 1	11.5–27
c′	1.5–2.5	2.5–3.2, 2.8 ± 0.2	1.9–2.6, 2.2 ± 0.2	1.9	3	1.5–3.2
V (%)	69–78, 70	69–75.5, 73 ± 1.4	70.8–76.7, 74.7 ± 1.4	76.6	69–74, 72 ± 2	69–78
Stylet (immature)	16–18, 16	15.5–16.5, 15.6 ± 0.42	14.5–15.5, 15 ± 0.22	15	17–18, 18 ± 0.4	14.5–18
Tail annules	24–30	27–35	23–29, 28–35	29	27–34	23–35
Spermatheca	Obscure, empty	Obscure, empty	Obscure, round (rare)	Obscure	Round, empty	Obscure to round
Lateral lines	6	4–6	4–5	4–5	6	4–6
PVS	1 VD	>1 VD (1.8–2.7)	>1 VD (1.3–1.9)	1.5 VD	>1 VD	1–2.7 VD

[a]Data for four females from Solan, India, are within the range of individuals from Amritsar (Khan & Singh 1974).
Lateral lines = number at mid-body, PVS = post-vulval sac, VD = vulval diameter.

anterior. Lip framework strong, extending at least two annules inward. Rounded stylet knobs slope backward gently from the shaft, slightly anteriorly flattened but not anchor-shaped. Dorsal oesophageal gland orifice between 2 µm (fixed specimens) and 3 µm (live specimens) behind stylet knobs. Oesophagus length 112–136 µm. Oesophageal gland overlap 31.3–42.3 µm. Metacorpus round to oval, with large, round, centred valve. Excretory pore located just above oesophago-intestinal junction, about a third of distance behind base of metacorpus to tip of oesophageal glands. Anterior end to excretory pore 80–90 µm. Excretory pore region often swollen in live and fixed specimens. Hemizonid two annules anterior to excretory pore, extending 3–4 annules. Vulva protruding. PVS length 20–35 µm. Of the 32 specimens measured, only one had a spermatheca; it was rounded with sperm. Lateral lines not strongly crenate but outer bands partially aerolated. Central fifth lines interrupted, not always visible. Tail conoid, crenate, 30–36 µm long, with thickened cuticle at tip for about four annules. A tail projection, especially prominent after fixation, is present in some specimens.

Specimens deposited in the USDANC, Beltsville, comprise *P. teres* JK slides G-12231–G-12234, *P. teres vandenbergae* RTB slides T-544t, T-5050p–T-5058p. Other paratypes were sent to the National Collection of Nematodes, Biosystematics Division, ARC-Plant Protection Research Institute Pretoria, South Africa; the Laboratoire des Vers, Muséum National d'Histoire Naturelle, Paris, France; and the Laboratorium voor Nematologie, Landbouwhogeschool, Wageningen, the Netherlands.

Diagnosis and relationships

Some information used in the diagnosis is given in Tables 1–3 and Fig. 4. *Pratylenchus teres* JK is similar to *P. teres* (Amritsar) in overall morphometrics, as well as in shape of stylet knobs, lip region, and tail tip. However, in *P. teres* JK, the PVS is distinctly longer than the body width rather than equal to it, which has also been noted in the population from Guadeloupe (Van den Berg & Quénéhervé 2000). In *P. teres* JK, the posterior body narrows gradually behind the vulva to a very narrow tail tip, unlike the occasional narrowing of the tail behind the anus in some specimens of *P. teres* (Amritsar). This difference in shape accounts for the higher c′-value in *P. teres* JK

Table 2. Lesion nematodes with three lip annules, four lateral lines and crenate tails: *Pratylenchus yassini, P. pratensis, P. convallariae, P. crenatus, P. sefaensis* and *P. pseudopratensis* (tail smooth). Range followed by mean ± standard deviation after original authors.

Character	*P. yassini*[a]	*P. teres*[b]	*P. crenatus*[c]	*P. pratensis*[d]	*P. convallariae*[e]	*P. sefaensis*[f]	*P. pseudopratensis*[g]
L (mm)	0.50–0.60, 0.55 ± 0.035	0.4–0.6	0.42–0.63	0.40–0.63	0.58–0.61	0.40–0.52, 0.45	0.41–0.50
a	28–34, 30 ± 2	20–40	22–40	22–30	23–27	25–31, 27	21–25
b	5–6.5, 5.6 ± 0.5	3.2–5.6	3.5–5.6	5.5–7.6	6–9	5–6.8, 5.8	5.8–7.4
c	14–19, 17 ± 1	11.5–18.4	11.5–27	14–27	17–28	19–24, 21	21–26
V (%)	71–75, 74 ± 1	69–78	78–86	76–80	78–81	77–80.5, 78.3	76–80
Stylet (immature)	16–18, 17 ± 0.5	14.5–18	14–18	12–16	16–17	13.5–16, 14.5	15
Tail annules	23–30, 28 ± 2	23–35	21–25	20–28	16–19	16–23	12–19
PVS	1.8–2.5 VD	1–2.7 VD	≥1 VD	≥1 VD	>1 VD (1.4–2)	>1 VD[h] (1.4)	>1 VD

[a]Zeidan & Geraert 1991 (Research Station population); [b]Khan & Singh 1974; [c]Loof 1960; [d](de Man 1880) Filipjev 1936; [e]Seinhorst 1959; [f]Fortuner, 1973); [g]Seinhorst 1968.
[h]Value derived from medians in Fortuner, 1973; *P. sefaensis* synonymised with *P. pseudopratensis* Seinhorst, 1968 (Frederick & Tarjan, 1989), but has crenate tail not in *P. pseudopratensis,* and found in Africa.
PVS = post-vulval sac, VD = vulval diameter.

Table 3. Morphometrics of lesion nematodes with (A), flat, undivided SEM faces, four lateral lines and acute tails: *Pratylenchus zeae, P. goodeyi, P. morettoi*; and (B) panduriform SEM faces: *P. bolivianus, P. neglectus, P. nizamabadensis, P. teres* and *P. wescolagricus;* all except *P. neglectus* may have four lip annules and crenate or indented tail termini. Range from original description followed by mean (Corbett, 1983), or mean and standard error (Roman & Hirschmann 1969).

Character	*P. zeae*[a]	*P. goodeyi*[b]	*P. morettoi*[c]	*P. nizamabadensis*[d]	*P. bolivianus*[e]	*P. wescolagricus*[f]	*P. neglectus*[g]	*P. teres*[h]
L (mm)	0.36–0.58, 0.54 ± 5.4	0.64–0.68	0.56–0.93	0.41–0.52	0.53–0.62, 0.59	0.50–0.68, 0.60	0.31–0.58	0.4–0.6
a	25–30, 27 ± 0.4	27–37	26–40	23.4–27	26–29, 27	25–32, 29	16.5–32.2	20–40
b	5.4–8, 6.5 ± 0.1	5.5–6.1	5.3–7.4	8.5–9.7	3.9–5.9, 5.2	5–6.6, 5.9	4.9–7.8	3.2–5.6
c	17–21, 15.2 ± 0.2	16–18	13–19	17–27	16–21, 19	17–25, 21	13.8–26.8	11.5–18.4
V (%)	68–76, 70.9 ± 0.2	73–75	73–80	67–78.7	80–82, 81	79–81, 80	75.5–86.6	69–78
Lip annules	3	4	3–4	4	3–4	4–3	2	3–4
Stylet (imm.)	15–17, 15.5 ± 0.1	17	14–19	17.5–18.7	17–20	17–19, 18	15–19	14.5–18
Tail annules	21–26	–	–	15–24	15–19	16–20	18–20	23–35
PVS	1 VD	1 VD	>1 VD	<1 VD	¼ VD	1 VD	Short	1–2.7 VD

[a](Graham 1951); Roman & Hirschmann 1969; [b]Sher & Allen 1953; [c]Luc, Baldwin & Bell 1986; [d]Maharaju & Das 1981; [e,f]Corbett 1983; [g](Rensch 1924) Filipjev & Schuurmans Stekhoven 1941; [h]Khan & Singh 1974.
Annules = annule number, PVS = post-vulval sac, VD = vulval diameter.

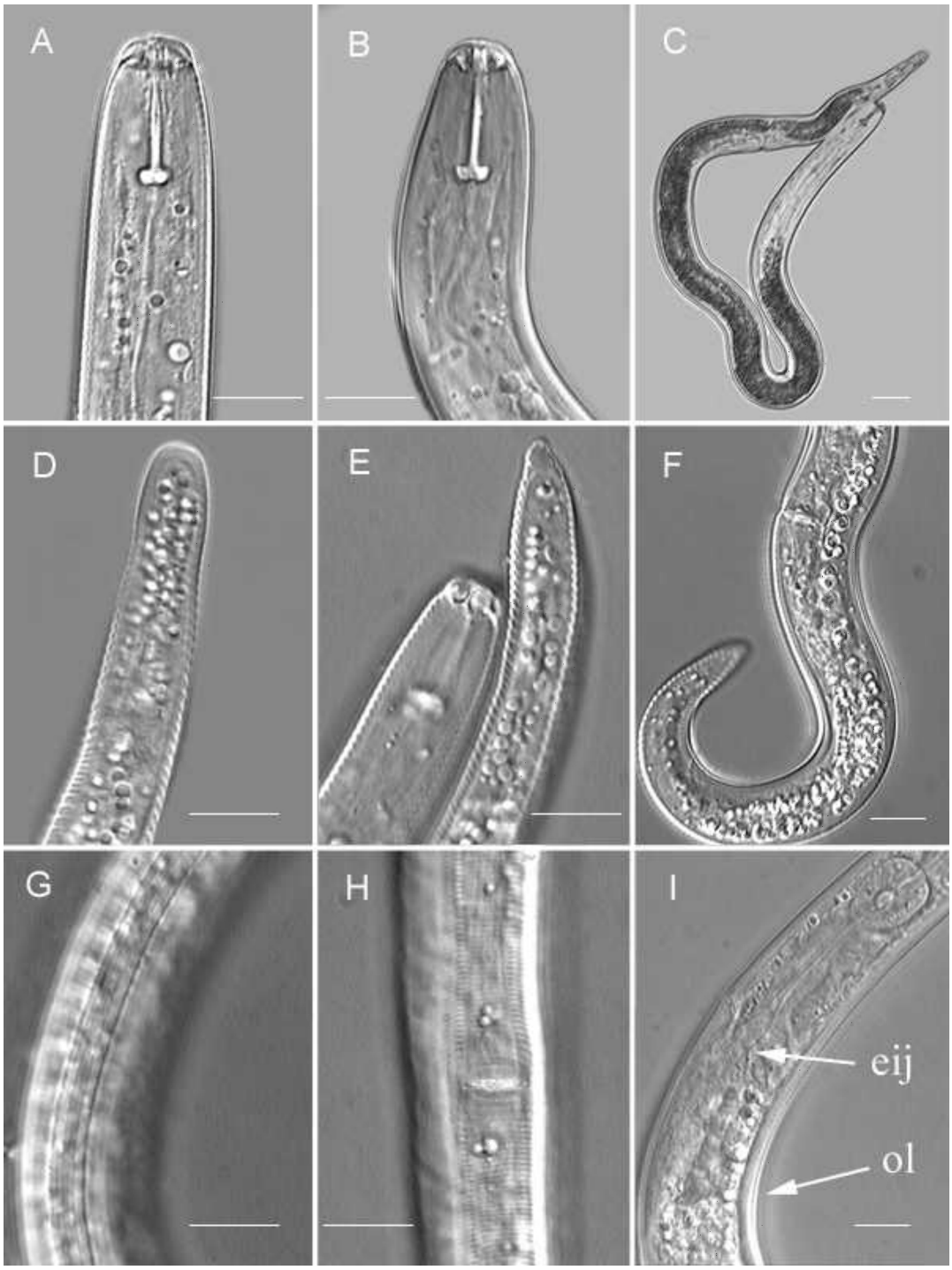

Fig. 1. *Pratylenchus teres* JK. **A**: anterior end, lips and stylet with anteriorly flattened knobs; **B**: anterior end, stylet with anchor-shaped stylet knobs, moderately high lip region; **C**: body; **D**: conoid tail; **E**: tail with projection, surface of labial framework; **F**: posterior body; **G**: lateral field, mid-body; **H**: vulva, ventral; **I**: oesophagus, including metacorpus–oesophago–intestinal junction (eij), and basal overlap (ol). Scale bars: C = 20 µm, others = 10 µm.

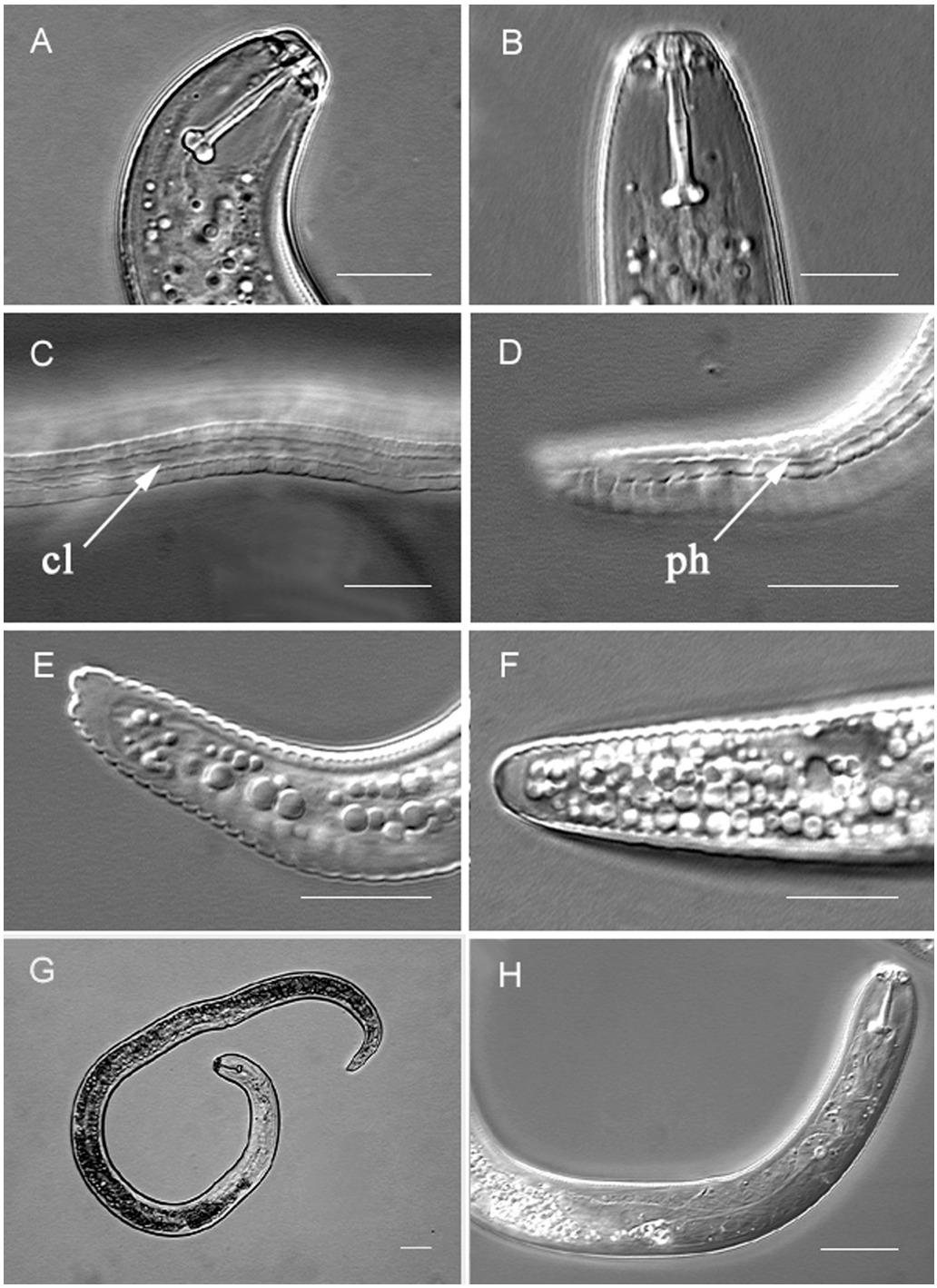

Fig. 2. *Pratylenchus teres vandenbergae*; **A**: anterior end, stylet with rounded knobs and high lip region; **B**, anterior end, stylet with broadly rounded knobs; **C**: midbody lateral field with partial aerolation in outer rows and interrupted central line (cl); **D**: tail, lateral field and phasmid (ph); **E**: tail tip with asymmetrical projection; **F**: conoid tail tip with thickened cuticle; **G**: body, **H**: head and oesophagus. Scale bars: A–F = 10 µm, G–H = 20 µm.

compared with *P. teres* (Amritsar) (Table 1). *P. teres* JK sometimes has fewer crenate lateral lines in the central part of the body than *P. teres* (Amritsar and Sainte-Rose). *P. teres* JK has a subventral or terminal tail projection in some specimens similar to that seen in *Pratylenchus convallariae* Seinhorst, 1959 (Loof 1991), *Pratylenchus pratensis* (de Man, 1880) Filipjev, 1936 (Loof 1974) and *Pratylenchus zeae* Graham, 1951 (Troccoli et al. 1996). *P. teres* JK also has a generally shorter stylet length than *P. teres* (Amritsar and Sainte-Rose).

P. teres JK differs from *P. teres vandenbergae* in the longer stylet, occasional extra lateral line, higher c′-value, gradually increasing vulval region width, the slightly anchor-shaped stylet knobs, the crenate lateral field, and the metacorpus shape. *P.* teres JK grows relatively poorly on maize roots compared to *P. teres vandenbergae*.

P. teres JK has crenate lateral lines, oval to pear-shaped metacorpus and a stylet knob shape in common with *Pratylenchus nizamabadensis* Maharaju & Das, 1981, but lower b- and c-values, as well as more tail annules and three rather than four lip annules.

P. teres vandenbergae can be distinguished from the *P. teres* (Amritsar) and JK populations by the shorter stylet, four lip annules in 53 % of the population, a higher, less rounded lip margin with a broader anterior end, and only four lateral lines with a central interrupted fifth line near the middle of the body. *P. teres vandenbergae* also has reduced crenation of the lateral lines, a less tapered tail region, and better growth on maize roots than the JK population (Table 1).

Both *P. teres* JK and *P. teres vandenbergae* differ from *Pratylenchus yassini* Zeidan & Geraert, 1991, by a panduriform SEM face view rather than one similar to that of *Pratylenchus crenatus* Loof, 1960 (Torres & Chaves 1999). Populations JK and Amritsar have a generally lower b-value and six lateral lines. *P. teres vandenbergae* has smaller stylet, a-, b-, and c-values.

P. teres vandenbergae differs from *P. nizamabadensis* in the slightly longer body and lower b-value, while it shares four lip annules and four lateral lines with this species. *P. teres vandenbergae* differs from *Pratylenchus goodeyi* Sher & Allen, 1953, in lower L, a- and b-values and stylet length, while they shares four lip annules and a similar tail shape. *P. teres vandenbergae* differs from *P. zeae* by the smaller b- and c-ratios, more symmetrical tail shape and smaller, backward-sloping stylet knobs (Table 3). *P. teres vandenbergae* can be distinguished from *P. pratensis* by a more anterior vulva, absence of males, the general absence of spermatheca or exceptional presence of a round rather than oval spermatheca, and the backward-sloping stylet knobs. *P. teres vandenbergae* is distinguished from *P. crenatus* by a more anterior vulva, finer body annulation, and shorter stylet; from *Pratylenchus sefaensis* Fortuner, 1973, in a more anterior vulva, longer body, lower c-value and greater number of tail annules; and from *Pratylenchus pseudopratensis* Seinhorst, 1968, by features similar to those of *P. sefaensis,* plus the presence of an annulated tail terminus, a lower b-value and the absence of males (Table 2).

Molecular identification

The sequence for the *P. teres vandenbergae* D3 region of the LSU rDNA gene, submitted to GenBank as accession number AF196353 is:

CCAAGGAGTTTATCGTGTGCGCGAGTCATTGGGC
GTTGAAAACCCAAAGGCGCAATGAAAGTGAATGCT
CCGCAAGGAGCTTACGTGCGATCCTGGGCACCGC
GGTGTCCGGGCGCAGCATGGCCCCATCCTGACTG
CTTGCAGTGGGGTGCGGAAGAGCGTACGCGGTGA
GACCCGAAAGATGGTGAACTATTCCTGAGCAGGAT
GAAGCCAGAGGAAACTCTGGTGGAAGTCCGAAGC
GATTCTGACGTGCAAATCGATCGTCTGACTTGGTAT
AGGGGCGAAAGACTAATCGAAC

This sequence aligned identically with *P. teres* JK, GenBank Accession number AF303951.

Scanning electron microscopy

Scanning electron micrographs of the nematode face (Fig. 3) show a panduriform (broad hour-glass shape) fusion of lip sectors. The diagonal line at the top of the 'hour-glass' in Fig. 3B is a developmental artifact (Anderson & Townshend 1985). Of the 3–4 specimens observed from each population, nearly identical lip patterns were observed in *P. teres vandenbergae* (Fig. 3B) and *P. teres* JK (Fig. 3F).

Four relatively unwrinkled lip annules were visible in *P. teres vandenbergae* (Fig. 3D), while only three appeared in the JK population. There are four clearly defined lateral lines in the lateral field in *P. teres vandenbergae* (Fig. 3A), with a superficial fifth interrupted line in the centre. The outer bands have superficial aerolation, partly extending into

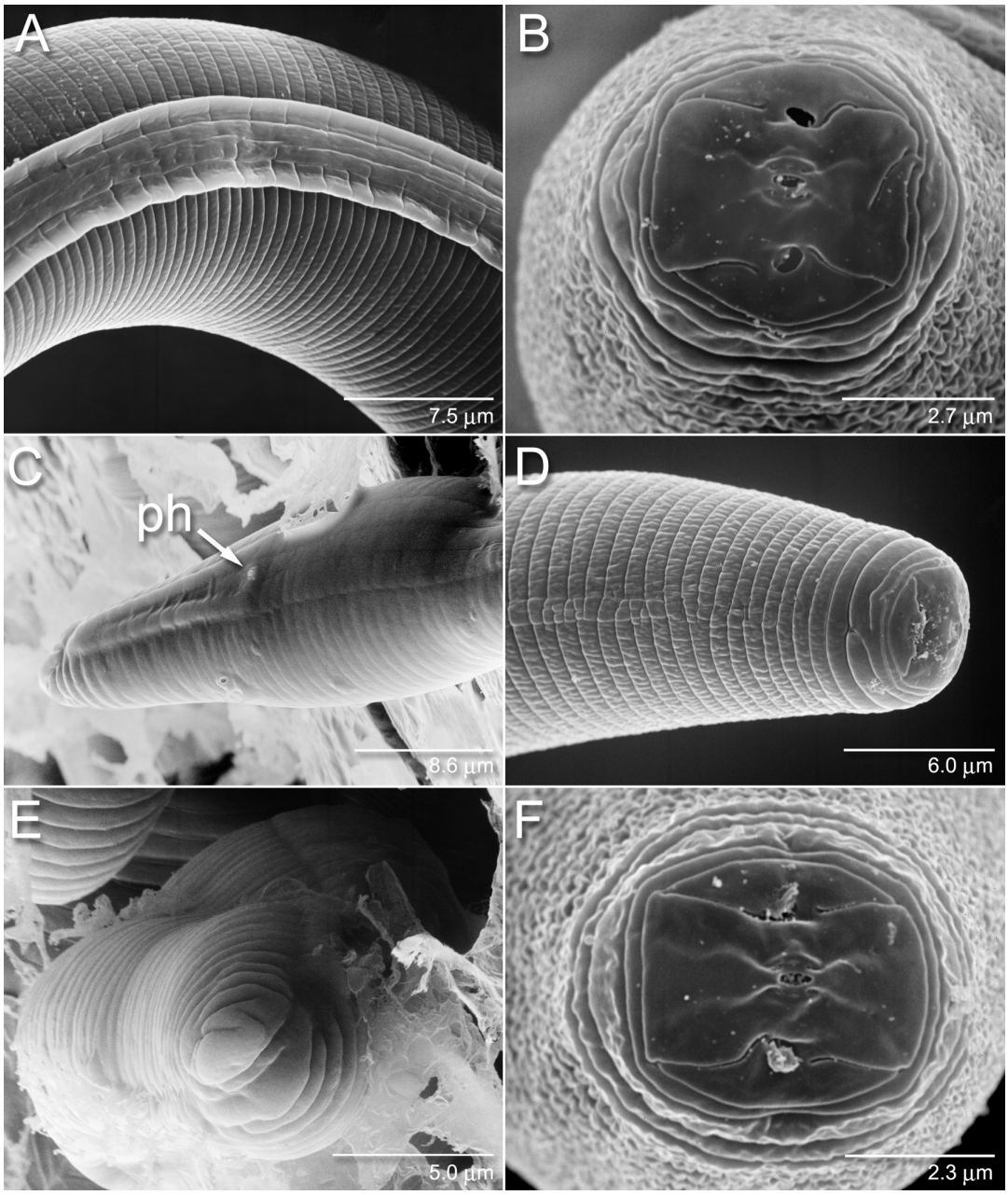

Fig. 3. Scanning electron micrographs. **A**: *Pratylenchus teres vandenbergae,* chemically-fixed lateral field; **B**: *P. teres vandenbergae,* chemically-fixed face view; **C**: *P. teres* JK, cryofixed tail with lateral field and phasmid (ph); **D**: *P. teres vandenbergae,* chemically-fixed anterior region with four lip annules; **E**: *P. teres* JK, cryofixed crenate tail tip; **F**: *P. teres* JK, chemically-fixed face view.

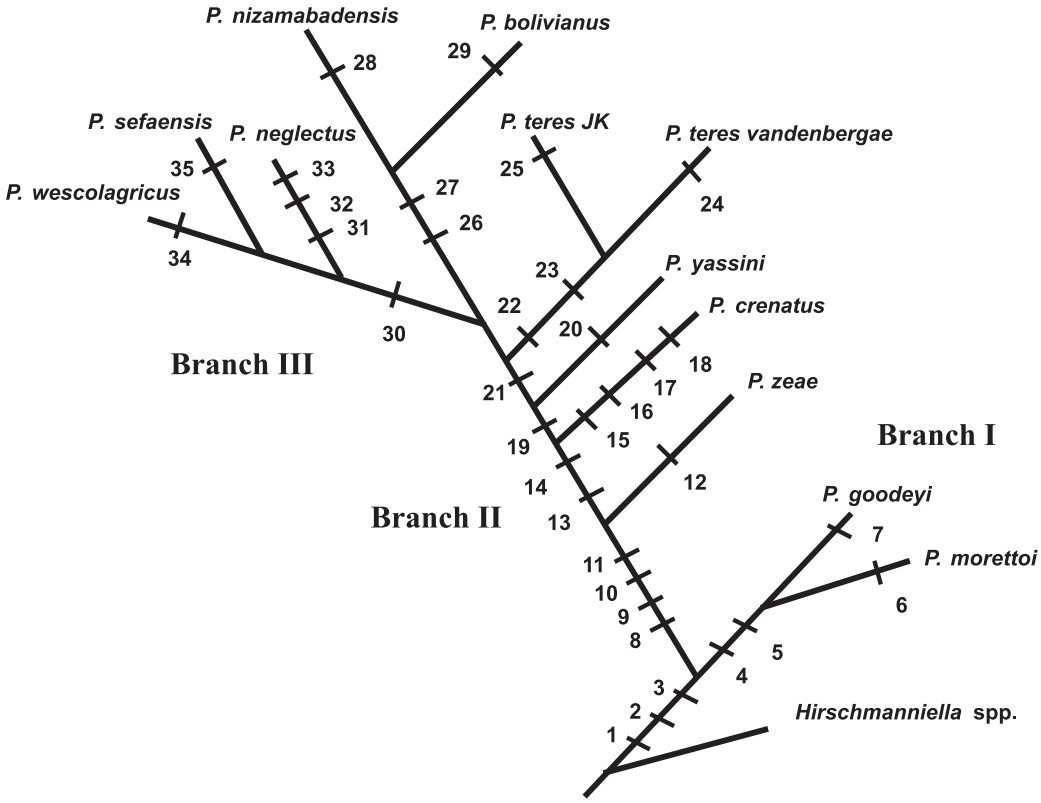

Fig. 4. Phylogenetic hypothesis of relationship among selected *Pratylenchus* spp. Branch I: *Hirschmanniella* spp., *Pratylenchus morettoi, P. goodeyi.* Branch II: *P. zeae, P. nizamabadensis, P. bolivianus, P. teres* JK, *P. teres vandenbergae, P. yassini, P. crenatus.* Branch III: *P. wescolagricus, P. sefaensis, P. neglectus.* Character designations: LA = Lip annule number, TA = tail annule number, LL = lateral line number, V = vulva % of body length, PVS/VD = post-vulval sac length divided by vulval body diameter, De Mann length ratio values: a = body (L)/ width, b = L/oesophagus, c = L/tail. Character states in *Hirschmanniella* considered ancestral to *Pratylenchus* spp. include: two female gonads, 4 LA, flat undivided face, acute tail projection, males present, 4 LL, L >1.0 mm, a >37, b >5, V <68, stylet >16 µm. Reversals from ancestral states noted as: (character state rev. character number). Derived character states on branches include: **1**, a <37; **2**, V >68; **3**, L <1 mm; **4**, L >0.6 mm; **5**, V = 73–80; **6**, PVS/VD >1; **7**, PVS/VD = 1; **8**, V = 68–78; **9**, L < 0.6 mm; **10**, no males; **11**, 3 LA; **12**, PVS/VD = 1; **13**, crenate tail; **14**, 5 LL; **15**, b< 5; **16**, 6 LL; **17**, PVS/VD ≥1; **18**, V >78; **19**, PVS/VD >1; **20**, TA >25; **21**, panduriform face; **22**, TA >25; **23**, b <5; **24**, stylet 14.4–15.5 µm (3–4 LA rev. 11); **25**, 6 LL; **26**, PVS/VD <1 (4 LL rev. 14); **27**, a <27 (3–4 LA rev. 11); **28**, c >21; **29**, V >80; **30**, V >75; **31**, non-crenate conical tail; **32**, 2 LA (4 LL rev. 14); **33**, PVS/VD <1; **34**, PVS/VD = 1 (L >0.6 mm rev. 9; 3–4 LA rev. 11); **35**, stylet 13.5–16 µm.

the inner row. The lateral field in population JK starts at four lines with outer aerolation. Just below the phasmid the four lines reduce to three and finally to two above the crenate tail-tip annules. The crenate tail tip of population JK (Fig. 3E) usually bears four annules per side above the very tip and an apical region with three folds.

Phylogenetic tree

The phylogenetic tree (Fig. 4) has three main branches based on face patterns, V-values, tail shape and other morphological characters. Ancestral character states present in the outgroup *Hirschmanniella* included four lip annules, four visible lateral lines, acute tail tip, undivided flat SEM face pattern, presence of males, two female gonads, L >1.0m, a >37, b >5, c >9, V <68, and stylet >16 µm. *P. teres* resides on the branch of tropical lesion nematodes with panduriform SEM faces (Table 3; Fig. 4, branch II) rather than the more temperate species also with crenate tails (Table 2, Fig. 4, branch III). The distinctly smaller

stylet size of *P. teres vandenbergae* compared to *P. teres* JK (Table 1) was considered a phylogenetically unique character sufficient to distinguish a monophyletic group.

Discussion

The new subspecies was erected primarily on the basis of the short stylet (14.5–15.5 µm), and different behaviour in culture. The occasional presence of a fourth lip annule and only 4–5 visible lateral lines are diagnostically useful ancestral character states. Other characters, the identical DNA sequences, and very similar SEM face patterns support the conspecificity of both South African populations.

Diagnoses were compared with species with relatively anterior vulvas of less than 76 %, including *P. teres, P. yassini, P. zeae* (3 LA) and *P. nizamabadensis* (4 LA). Vulval morphometrics are one of the most reliable characters in nematode taxonomy, especially within the genus *Pratylenchus* (Frederick & Tarjan 1989). Diagnoses were also made with species having relatively rare generic characters of crenate tails (Table 2) and/or four lip annules (Table 3). The first character is considered phylogenetically derived, and the second is ancestral relative to the outgroup of *Hirschmanniella.*

The number of lines in the lateral field are sometimes variable within *Pratylenchus* species (Loof 1978, 1991), but all species of *Pratylenchus* may have six lines, though some are obscured by the cuticle (Valette et al. 1997). In both described populations of *P. teres* there are four major lateral lines in the middle of the body, but *P. teres* populations other than *P. teres vandenbergae,* have two extra lines generally visible under the light microscope (Fig. 1G). The form and markings of the lateral field are very similar in *P. sefaensis* in which a central, fifth lateral line is sometimes present (Fortuner 1973) or *Pratylenchus wescolagricus* Corbett, 1983, where a fifth and sixth superficial line are sometimes visible (Corbett 1983). However, three lines of the lateral field do not extend so close to the tail tip in *P. teres.*

The qualitative features of the lateral field of *Hirschmanniella* spp., where there are four lines with outer bands aerolated (Lopez & Salazar 1987), are also remarkably similar to *P. teres.*

Among all these taxa for which SEM face patterns are known, *Hirschmanniella belli* Sher, 1968, and *P. zeae* have flat, undivided faces, while *Pratylenchus neglectus* (Rensch, 1924) Filipjev & Schuurmans Stekhoven, 1941 (Corbett & Clark, 1983; Sauer 1986), and *P. teres* have more derived panduriform faces. Other related flat-faced lesion nematodes are *Pratylenchus morettoi* Luc, Baldwin & Bell, 1986 (Luc et al., 1986) and *P. goodeyi.*

Related taxa with panduriform faces include *Pratylenchus bolivianus* Corbett, 1893, and *P. wescolagricus* (Corbett & Clark, 1983). The face patterns of both *P. teres* JK and *P. teres vandenbergae* are nearly identical to that of *P. bolivianus,* and very similar to *P. wescolagricus* followed by *P. neglectus* (Corbett & Clark 1983). One population of *P. neglectus* (described as *Pratylenchus minyus* Sher & Allen, 1953) from Australia (Sauer 1986) has a face pattern with greater similarity to that of *P. wescolagricus* than to another population of *P. neglectus* (Corbett & Clark 1983). The face of *P. crenatus* is distinctly different, having a very narrow, poorly defined 'hour-glass' face pattern (Torres & Chaves 1999).

The most similar molecular relatives of *P. teres* in insufficiently resolved tree branches of the D3 LSU rRNA gene were *H. belli* and *P. neglectus,* whereas *P. zeae* and *P. crenatus* are more distantly related (Carta et al. 2001). Although the morphological similarity of *P. teres* with *P. crenatus* reflected in Fig. 4 may not be a result of most recent common ancestry as evidenced by their different molecular sequences, the similarity in the molecule may also be homoplastic.

Branches I and II of the tree in Fig. 4 represent primarily tropical nematodes from Asia, Africa and South America. *P. goodeyi* is believed to be indigenous to Africa. *P. zeae* is common in Africa (Bridge 1996), but also found in tropical regions of the Middle and Far East, Australia and the USA (Loof 1991). *P. teres* occurs in Africa, India and the Caribbean (Khan & Singh 1974; Van den Berg & Quénéhervé 2000), *P. yassini* in Africa (Zeidan & Geraert 1991), *P. nizamabadensis* in India (Maharaju & Das 1981) and *P. bolivianus* in South America (Corbett 1983). Close morphological relatives to *P. teres* (Table 3), such as *P. nizamabadensis* and *P. bolivianus,* may have been in close proximity when Gondwanaland was in existence, spanning what is now India, Africa, the Caribbean and South America. If vicariant dispersal occurred as proposed for other nematodes (Ferris 1979), the Caribbean margin of the USA (Rosen 1975) might harbour a *P. teres*-like relative.

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