Description of *Rhabditis (Pelodera) pseudoteres* n. sp. (Rhabditidae : Nematoda) with a redescription of its sibling *R. (P.) teres* (Schneider, 1866)

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SUMMARY

R. pseudoteres n. sp., a sibling species of *R. teres* (Schneider, 1866) is described. Although morphological differences are very minute, the status as distinct species was confirmed by cross-mating experiments in the laboratory. Differences are more obvious in the behaviour of dauer juveniles (J3); however, the possible role of " waving " behaviour in the life cycle of *R. pseudoteres* n. sp. remains unknown. *R. teres* and *R. pseudoteres* n. sp. have been treated as a single species in the past *(R. teres)*. Therefore the literature was reviewed in order to find out if former studies were done with *R. teres* or its sibling *R. pseudoteres* n. sp.

RÉSUMÉ

Description de Rhabditis (Pelodera) pseudoteres *n. sp. (Rhabditidae : Nematoda) et redescription de son espèce jumelle* R. (P.) teres *(Schneider, 1866)*

Rhabditis pseudoteres n. sp., espèce jumelle de *R. teres* (Schneider, 1866), est décrit. Bien que les différences morphologiques soient très faibles, les expériences de fécondation croisée ont démontré l'isolement sexuel des deux espèces. Les différences sont plus aisément reconnaissables dans le comportement des larves de troisième stade ou « dauer juveniles ».Toutefois le rôle possible de ce comportement d' « ondulation » dans le cycle biologique de *R. pseudoteres* n. sp. reste inconnu. *R. teres* et *R. pseudoteres* n. sp. ayant été considérés dans le passé comme une seule et même espèce, nous avons revisé les études faites sur *R. teres* s.l., de façon à connaître si elles s'appliquaient à *R. teres* ou à *R. pseudoteres* n. sp.

Sibling species are defined as pairs or groups of closely related species which are reproductively isolated but morphologically identical or nearly so (Mayr, 1975). A closer analysis of such complexes often shows that two, three, or even more well-defined species are involved. These differ from " ordinary " species only in that differences in morphological characters are very minute (see Bates, 1940, for *Anopheles " maculipennis "* or Grassle & Grassle, 1976, for *Capitella " capitata "*).

The fact that sibling species exist is not surprising. Since our taxonomic characters rely preferably on visual cues, it is quite reasonable to expect that the species divergence (particularly in non-optical animals) may have affected even other sensory fields. However, even in the most similar sibling species there are morphological differences which can only be discovered through examination. This has been shown recently for the *Rhabditis (Pelodera) " strongyloides "* - complex (Sudhaus, Schulte & Hominick, 1987).

Here I report on a further case where at least two distinct *Rhabditis* species have been included under only one name in the past. *Rhabditis (Pelodera) teres* was described by Schneider (1866). Several aspects of its live history have been more closely investigated since then (Dotterweich, 1938; Ludwig, 1938; Chuang, 1962; Jones, 1967).

Dauer juveniles of *R. teres* are known not to exhibit " waving behaviour " in order to make contact with a carrier insect (phoresis) (Sudhaus, 1976). However, I observed this characteristic behaviour in a laboratory culture grown from dung substrate of a cattle yard in Berlin (West). Detailed cross-mating experiments with the actual *R. teres* in the laboratory revealed that a sibling species exists, which is morphologically almost identical to *R. teres*. This new species will be described in the present paper as *Rhabditis (Pelodera) pseudoteres* n. sp. For detailed comparison it seems necessary to redescribe *R. teres* from the type locality.

Due to his limited knowledge about species diversity in *Rhabditis*, Schneider (1866) gave only a very brief description of his *R. teres*. This short description makes it difficult to decide, whether subsequent investigators worked with the original *R. teres* or its sibling *R. pseudoteres* n. sp. Critical reviewing of these papers revealed that in most cases a final decision cannot be made if the author does not mention special morphological features of the species he worked with.

Rhabditis (Pelodera) teres (Schneider, 1866)
= *Anguillula mucronata* Grube, 1849 *(nomen oblitum)*
= *Pelodera teres* Schneider, 1866
= *Leptodera teres* (Schneider, 1866) Schneider, 1866
= *Rhabditis teres* (Schneider, 1866) Bütschli, 1873
= *Rhabditis donbass* Skrjabin, Shults & Serbinov, 1926

(Fig. 1)

MEASUREMENTS

See Table 1.

Table 1

Rhabditis (Pelodera) teres (Schneider, 1866)
Measurements (in µm) of specimens bred at 20° on 2 % agar plates with pieces of uncooked meat, heat relaxed in tap water.

	Females	*Males*	*Dauer juveniles*
n	10	10	10
L	1 165-1 688 (1 337)	810-1 085 (922)	365-464 (406)
Body diam.	68-108 (95)	49-69 (56)	18-29 (24)
Buccal cavity length	26-29 (28)	23-30 (25)	15-18 (17)
Tail length*	50-63 (59)	38-43 (40)	36-63 (52)
Gonad length**	675-1 125 (824)	450-756 (558)	32-45 (35)
V	54-64 (58)		
Spicules		40-45 (42)	
Gubernaculum		27	
a	13.5-17.8 (15.8)	15.5-18.2 (16.3)	16.0-20.7 (19.1)
b	5.4-8.0 (6.2)	4.3-5.5 (4.8)	2.9-3.4 (3.2)
c	18.7-28.8 (22.6)	20.2-26.7 (22.8)	6.9-10.7 (8.0)

* J3-tail in the dauer juvenile;
** anterior to posterior flexure (female); flexure to cloaca (male); genital primordium (dauer juvenile).

DESCRIPTION*

Adult : Cuticle about 1 µm thick, transparent with fine transversely and longitudinally arranged dots. Six lips surrounding mouth opening, moderately set off, bearing two minute papillae each, these are difficult to detect. Buccal cavity three edged prismatic. Three conspicuous little warts or teeth on each metarhabdion. Pharyngeal collar enveloping the posterior half of the stoma. Rhabditoid pharynx with a median bulb and a distinct isthmus. Lateral canals of " H "- (" excretory "-) system extending to the anal region in both sexes.

Female : Lips moderately offset, body width behind the lip region 84-96 (91) % of that of the expanded lip region. Pharyngeal collar enveloping 53-60 (56) % of total stoma length. Posterior bulb of pharynx 30-40 (36) µm in diameter. Corpus length corresponding to 52-55 (53) % of total pharynx length. Deirids at 162-196 (181) µm from anterior end, cervical pore at 162-216 (188) µm, i.e. 78-98 (87) % of length of pharynx. Two large glandular-like cells next to the cervical pore. Gonads amphidelphic with opposed reflexed ovaries. Length of anterior branch (vulva to flexure) 270-540 (415) µm, that of posterior one 310-585 (460) µm. Unflexed part of reproductive system 48-70 (60) % of total body length. Flexures reaching the vulva region. Ovoviviparous. Numbers of developing eggs in the reproductive tract 3-63 (35). Dimensions of eggs in early development 50-54 (51) µm × 29-32 (33) µm; eggs containing juveniles up to 73 × 44 µm. Pseudo-coelomocytes at the anterior gonad branch 14-18 µm. Tail end dome-shaped, 50-63 (59) µm long. Tail spine 15-28 (23) µm, i.e. 30-44 (38) % of total tail length. Rectum 18-30 µm. Phasmids conspicuous at 36-45 (42) µm from the tip of the tail.

Male : Lips moderately offset (width at constriction 85-96 (92) % of that of lip region). Pharyngeal collar enveloping 43-57 (53) % of stoma length. Cervical pore at 140-189 (175) µm from anterior end, i.e. at 72-90 (81) % of pharynx length; deirids at 144-189 (157) µm. Diameter of posterior pharyngeal bulb 25-37 (30) µm. Single reflexed testis occupies 57-68 (60) % of total body length. Flexure usually ventral, sometimes (in three specimens) dorsal. Reflexed part 45-189 (106) µm long, i.e. 8-42 (20) % of length of the unflexed part. Two or three pseudo-coelomocytes next to the gonad flexure, 9-16 µm in diameter. Two large ejaculatory glands 171-220 µm long; the gland on left hand side constantly longer (up to 35 µm). Sperm cell diameter 7-11 µm. A patch of crystalline needles* or fibres always present in the tissue of the genital tract (Fig. 1, D, E) next to its fusion with the ejaculatory glands; length of a single needle 6-12 µm, several needles parallel, forming patches of about 30 × 40 µm. Bursa of peloderan type, ten pairs of papillae present, arranged 1 + 2/3 + 4. Papillae nos 1, 2, 3 in a precloacal position and reaching the edge of the bursa velum. Nos 7, 10 opening on the outer side, nos 5, 6, 8 and 9 pointing inwards. Papillae nos 5 and 6 only exceptionally (in three specimens) slightly thickened. Gap between papillae no. 3 and no. 4 18-24 (20) µm. Spicules brownish, joined together 13-14 µm or 28-34 (32) % of their total length (41-45 µm). Pair of spicules sometimes differing in length up to 5 µm; width at the capitula 16-22 (20) µm, corresponding to 39-53 (43) % of spicula length. Gubernaculum boat-shaped, 27 µm long and 5 µm broad. Gubernaculum length corresponding to 60-68 (64) % of total spicule length.

* Redescription based on a population from the type locality Berlin; specimens isolated from a compost heap and grown on agar plates.

* These typical needles are easy to detect and of great diagnostic value (see also Bütschli, 1873).

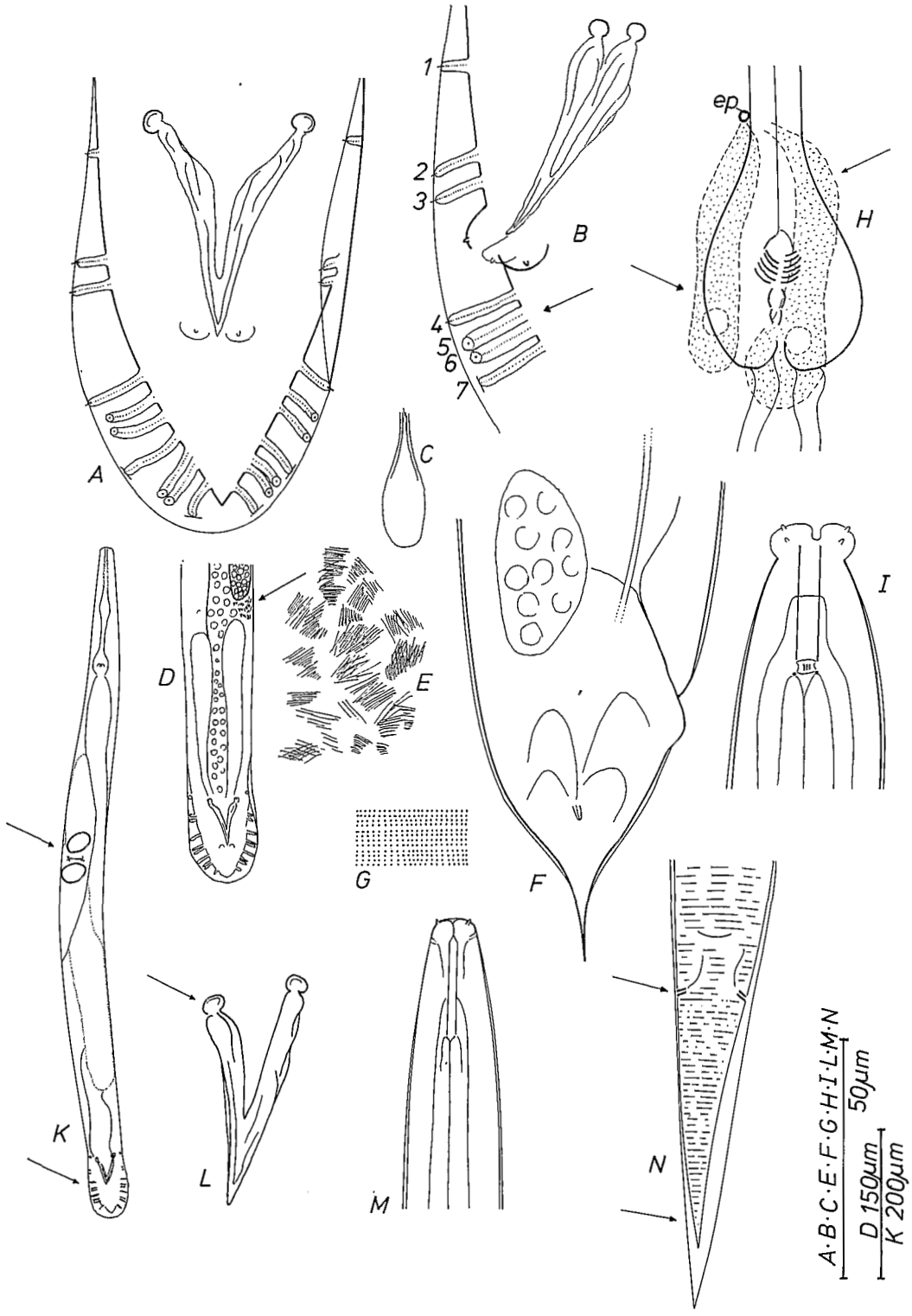

Fig. 1. *Rhabditis (Pelodera) teres* (Schneider, 1866). — Male. A : Bursa (ventral); B : Bursa (detail), demonstrating thickened papillae nos 5 and 6; C : Gubernaculum, ventral; D : Posterior body half (ventral) demonstrating the position of E : Crystalline needles enclosed in the tissue of the testis. Female; F : Caudal end, lateral; G : Cuticle structure; H : Posterior pharyngeal bulb, ventral (ep = cervical pore); I : Anterior region, ventral. — Intersex specimen. K : *In toto* (ventral); L : Aberrative spicules. — Dauer juvenile. M : Anterior region (lateral); N : Tail end (ventral).

Dauer juveniles : Lips not offset, J2-cuticle kept as a sheath (easy to differentiate by the tail end). Transverse striations on the J3-cuticle inconspicuous. Lateral field about 5 µm broad, running from two times stoma length from anterior end to 2/3 of tail length. Two central lines present. Tail of J3 ending elongate-conoid; phasmids opening at 5-29 (15) % of total tail length. Corpus occupies 54-61 (57) % of total length of pharynx. Cervical pore at 86-108 (101) µm from anterior end. Intestinal cells with stored granules.

Behaviour inert, never exhibiting " waving " movements. Tolerate desiccation (under room conditions) for at least 13 months.

Remarks : Occasionally, the tail spine was missing in the female (three cases). In two males papilla no. 1 was missing. One intersex specimen was found, combining male and female features : female amphidelphic genital tract harbouring two eggs (without segmentation); no testis but a well developed bursa with ten pairs of papillae present. Spicules aberrant (Fig. 1 K & I).

Diagnosis

Rhabditidae, subgenus *Pelodera;* bisexual, pharynx collar present. Tail end in the female dome-shaped. Vulva situated in the midbody region, ovaries amphidelphic. Male characterized by knob-shaped spicules, fused distally. Open bursa of peloderan type. Ten bursal papillae with three standing in a precloacal position. A patch of crystalline needles present in the tissue of the testis next to its fusion with the ejaculatory glands.

Table 2

Rhabditis (Pelodera) pseudoteres n. sp.
Measurements (in µm) of specimens bred at 20° on 2 % agar plates with pieces of uncooked meat, heat relaxed in tap water.

	Females	*Males*	*Dauer juveniles*
n	10	10	10
L	797-1 013 (1 005)	688-968 (778)	439-545 (499)
Body diam.	54-67 (61)	47-65 (54)	23-32 (27)
Buccal cavity length	27-31 (29)	23-29 (26)	16-19 (17)
Tail length*	36-48 (44)	27-36 (34)	40-50 (44)
Gonad length**	360-486 (421)	387-648 (445)	36-63 (48)
V	53-60 (58)		
Spicules		36-48 (42)	
Gubernaculum		22-27 (25)	
a	13.4-17.0 (14.8)	12.9-15.5 (14.5)	16.4-21.6 (18.6)
b	3.6-4.3 (4.2)	3.7-4.7 (4.0)	3.1-6.7 (5.2)
c	19.7-25.8 (22.3)	23.0-28.8 (25.4)	9.1-13.1 (11.3)

* J3-tail in the dauer juvenile.
** Anterior to posterior flexure (female); flexure to cloaca (male); genital primordium (dauer juvenile).

Rhabditis (Pelodora) pseudoteres n. sp.
= *Rhabditis teres apud* Chitwood, 1933
= *Pelodera teres apud* Lukes, Prokopic & Hulinská, 1982

(Fig. 2)

Measurements

See Table 2.

Description

Adult : Cuticle transparent, bearing fine transverse and longitudinal rows of tiny dots. Cuticle layers about 1 µm apart. Cheilorhabdions inconspicuous, lip region set off by a pronounced constriction. Six subspherical lips bearing two minute papillae each. Buccal cavity three-edged prismatic, three little teeth on each metarhabdion. Pharyngeal collar enveloping more than half of stoma. Pharynx rhabditoid with a median bulb and a distinct isthmus. Lateral canals of the " H " (" excretory ") system inconspicuous.

Female : Lips offset, body width at the constriction behind the lips compared to the expanded lip region 77-86 (81) %. Pharyngeal collar enveloping 65-67 (65) % of buccal cavity. Median bulb of pharynx 26-36 (31) µm wide, the posterior one being 27-41 (36) µm wide. Corpus from anterior extremity to beginning to isthmus 55-59 (57) % of length of pharynx. Deirids at 144-207 (182) µm from anterior end; cervical (" excretory ") pore at 149-196 (182) µm, i.e. 70-87 (73) % of length of pharynx. Two large cells next to the cervical pore. Reproductive system amphidelphic, unflexed part occupying 43-55 (47.5) % of total body length. Flexures reaching the vulva region. Length of anterior branch 180-243 (215) µm, that of posterior one 180-243 (211) µm. Ovoviviparous, numbers of eggs or larvae found in the reproductive tract depending on the age of the female : only 1-4 in younger individuals compared to 18-33 (30) in older ones. Dimensions of eggs in early stages of development 54-81 (67) µm × 32-38 (37) µm; eggs containing hatching juveniles up to 90 × 50 µm. Pseudo-coelomocytes (usually two; Fig. 1, H) at the flexure of the anterior branch 14-16 µm in diameter. Tail end short-conical, becoming more dome-shaped in older females. Tail length 36-48 (44) µm; tail spine 16-23 (19) µm, i.e. 32-47 (42) % of total tail length. Rectum 22-32 µm long. Phasmids easy to detect at 27-41 (37) µm from tail tip.

Male : Lips offset (body diameter at the constriction 67-76 (71) % of that of the expanded lip region). Pharyngeal collar enveloping 60-66 (63) % of stoma length. Cervical pore at 144-180 µm from anterior end, or 71-86 (78) % of length of pharynx. Deirids at 144-158 (152) µm from anterior end. Diameter of posterior pharyngeal bulb 23-30 (27) µm. Testis from cloaca to

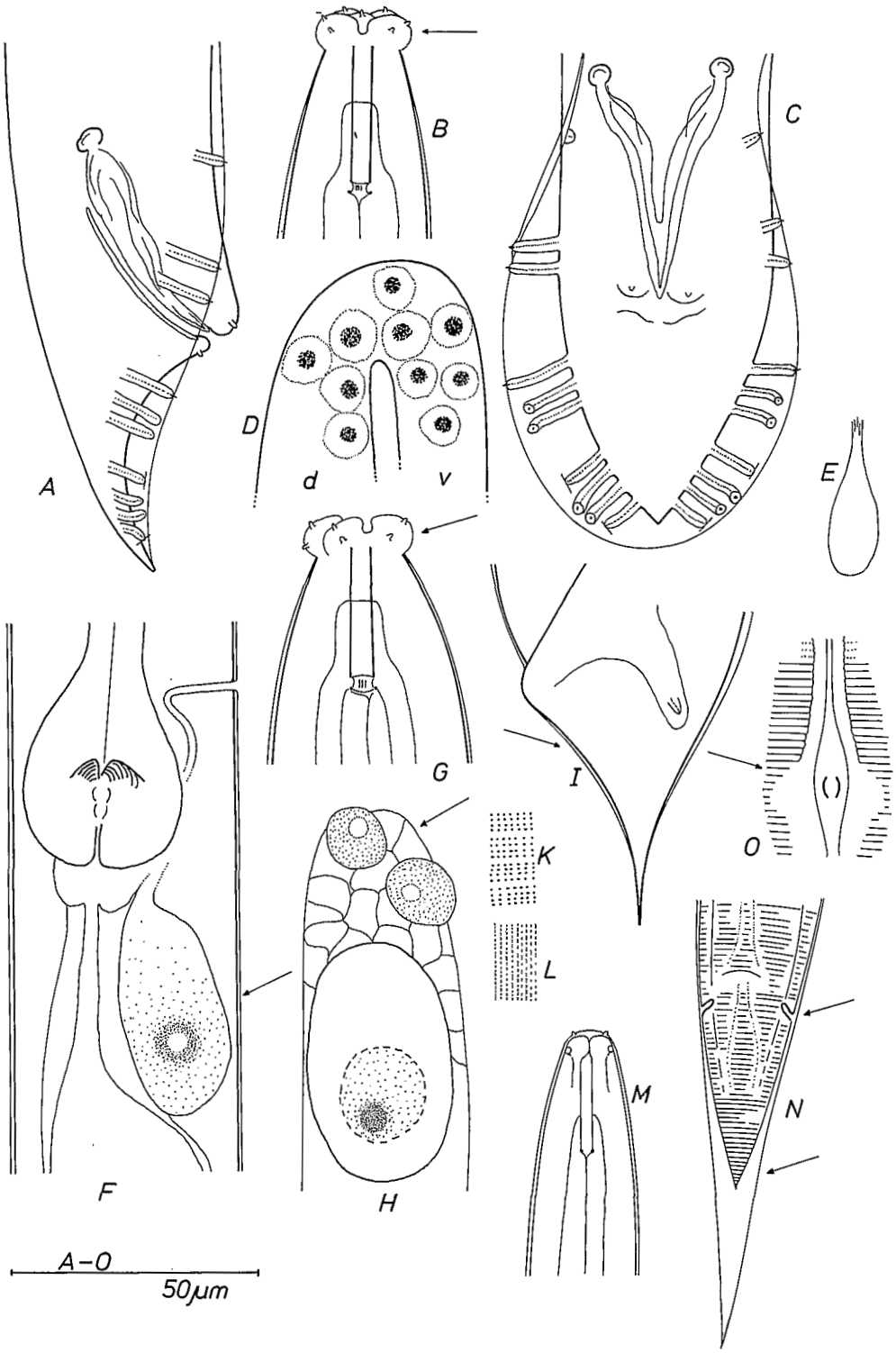

Fig. 2. *Rhabditis (Pelodera) pseudoteres* n. sp. — Male. A : Bursa (lateral); B : Anterior region (lateral); C : Bursa (ventral); D : Anterior flexure of testis (d = dorsal; v = ventral) with sperm cells; E : Gubernaculum (ventral). — Female. F : Foregut region (lateral); G : Anterior region (ventral); H : Anterior gonad flexure with an egg and the pseudo-coelomocytes; I : Tail end, (lateral); K : Cuticle structure, midbody region; L : Cuticle structure, caudal region. — Dauer juvenile. M : Anterior region (lateral); N : Tail end (ventral); O : Phasmid openings (lateral).

flexure occupies 48-67 (57) % of total body length. Reflexed part (usually ventral, sometimes lateral) 59-207 (163) µm long, i.e. 14-46 (33) % of length of unflexed part. Pseudo-coelomocytes (two) situated next to the gonad flexure measuring 9-14 µm in diameter. Two large ejaculatory glands 171-225 µm long, that on the left hand side being regularly longer [difference 13-36 (24) µm]. Sperm cells 8-12 µm in diameter. Bursa peloderan, ten pairs of papillae of equal size, formula 1 + 2/3 + 4. Papillae nos 1, 2, 3 reaching the edge of the bursa velum; nos 7 and 10 opening on the outer side, nos 5, 6, 8 and 9 pointing inwards. Gap between precloacal papillae (nos 1-3) and postcloacal group (nos 4-10) 16-18 (17) µm. Spicules brownish, joined together 14-15 µm or 31-37 (33) % of their total length (36-48 µm). Spicules occasionally different in length up to 3 µm; width at the capitula 20-23 (21) µm, corresponding to 44-55 (49) % of spicule length. Gubernaculum boat-shaped, 22-27 (25) µm long by 5 µm broad. Gubernaculum length corresponding to 49-60 (55) % of that of the spicules.

Dauer juveniles : Lips not offset, second stage cuticle kept as an enclosing sheath (easily seen by the end of its tail). Third stage cuticle exhibiting transverse striations, width of ten annules 14-16 µm; lateral field 4-5 µm broad, beginning at 40-50 µm from body end, running to middle of tail. Two central lines present. Tail of J3 ending short-conoid, phasmids at 12-36 (24) % of tail length. Phasmid apertures sclerotized, blind-ending shaped (Fig. 2, N). Corpus 56-61 (59) % of total length of pharynx. Cervical pore at 99-126 (123) µm from anterior end. Intestinal cells carrying stored substances.

If adequate conditions are offered (e.g. pieces of dried-up meat), these juveniles can be seen standing on their tails, moving forth and back or even sticking together forming a single waving « flame » consisting of numerous individuals. This behaviour was the key to the discovery of this species.

According to laboratory results, these dauer forms are able to tolerate desiccation (at room temperature and room humidity) up to 250 days.

Type specimens

Holotype male, allotype female, paratype females, males and immatures in the collection of Museum für Naturkunde der Humboldt Universität zu Berlin, Zoologisches Museum, Berlin, GDR. Other paratypes deposited in the following collections : Laboratoire des Vers, Muséum national d'Histoire naturelle, Paris, France; Laboratorium voor Nematologie. Landbouwhogeschool, Wageningen, Netherlands; Biologische Bundesanstalt für Land- und Forstwirtschaft, Institut für Nematologie, Münster, W-Germany; and in the collection of W. Sudhaus (Berlin).

Type locality

Soil mixed with straw and dung from a cattle yard at the dairy experimental station of the Technical University Berlin, Berlin (West). The sample was taken on April 18th, 1985.

Remarks

In one male papillae nos 1, 4, 5, 6 and 10 were missing on the left hand side of the body; in another male papillae nos 5, 9, 10 were missing on the right hand side. In one female the tail spine was missing.

Diagosis and relationships

Rhabditidae, subgenus *Pelodera;* bisexual, pharynx collar present. Tail end in the female domeshaped. Vulva situated in the mid-body region, ovaries amphidelphic. Male with knob-shaped spicules, fused distally. Open bursa of peloderan type. Ten bursal papillae with three standing in praecloacal position. Dauer juveniles exhibiting " waving " movements, their tail ending short-conical. The closest relatives of *R. pseudoteres* n. sp. are *R. teres* (Schneider, 1866) and *R. parateres* Cobb, 1924. Males of these species share the feature " three bursal papillae in praecloacal position ".

Since the female of *R. parateres* is well-characterized by its concave-conical tail, and the male by the thickened bursal papilla no. 5 (Cobb *in* Sudhaus, 1985), I can focus on differences from the sibling *R. teres.* The differentiating character most easily seen may be the absence of the crystalline needles or fibres in the males of *R. pseudoteres.* Further differences in the male are : Body and tail considerably shorter, resulting in different, although overlapping " a " and " c " values resp. Lips more set off, pharyngeal collar enveloping more than the posterior half of buccal cavity. Posterior pharyngeal bulb often narrower. Gubernaculum compared with total spiculum length relatively shorter. Differences in the female are : Lips are more offset, pharyngeal collar envelops more than (65 %) half of stoma. Cervical pore relatively nearer to the anterior body extremity if compared to stoma length; b-ratio different. Body considerably shorter by a smaller width. Tail end shorter, more conical. The reproductive tract relatively smaller, and harbours on the average a fewer number of eggs. Differences in the dauer juveniles are : Tail end of dauer juveniles short-conoid versus elongate-conoid. Phasmid openings formed different, annulation of cuticle more conspicuous. Total body considerably longer, although ranges are overlapping. Exhibiting " waving " behaviour.

Cross-mating experiments

The nature of reproductive isolation between *R. pseudoteres* n. sp. and *R. teres* (Schneider, 1866) could be demonstrated in a laboratory experiment : Virginal females were placed singly in a drop of bacterial suspension on the surface of an agar plate (ten replicates for each of the two species). Two males of the other species were added and the behaviour of males and females towards each other was observed under a dissecting microscope. If the females were still alive after three days without any offspring, the males were replaced by those of the same species (control).

R. teres-female × *R. pseudoteres*-males : Isolation praegamous; no copulation observed. Most of the females died probably from decaying material of eggs in the uteri. Fertility was confirmed in three cases as these females produced normal offspring after having copulated with *R. teres* males.

R. pseudoteres-female × *R. teres*-males : Isolation metagamous; copulation and sperm-transfer were observed in eight of the ten studied cases. However, eggs are never laid and obviously the female finally dies from decaying egg masses in the reproductive tract. Only two females survived for more than three days, and only one of them produced juveniles when fertilized by a male of the same species.

Distribution and ecology

Very little is known thus far about differences in ecological patterns of the two species. Both were found in decaying organic material or soil together with other microbiotrophic rhabditid species. In Berlin, sources of discovery were found to be only a few kms apart, so the two species must be treated as sympatric forms. Records concerning the distribution of "*R. teres*" were listed by Andrássy (1984). In these records, however, both species (*R. teres* and *R. pseudoteres* n. sp.) may have been confused. *R. teres* seems to be widespread. It was recorded from Lake Baikal (USSR) and several localities in Europe (Sudhaus, 1987). Besides the type locality, *R. pseudoteres* n. sp. was found in a sample from Lima (Peru), and in association with a carrion beetle (*Necrophorus* n. sp.) from Bielefeld, W. Germany (Sudhaus, pers. comm.). The specific character of both nematode species was further confirmed by successful crossings with the laboratory stems.

While dauer juveniles of *R. teres* are waiting in the soil until conditions are sufficient for growing and reproduction (Sudhaus 1976), those of *R. pseudoteres* n. sp. seem to be adapted to make contact with a carrier animal by means of their " waving " behaviour. However, it is difficult to decide at the moment, if *R. pseudoteres* n. sp. was involved in the cases, where "*R. teres*" was reported in association with arthropods, slugs and earthworms (Völk, 1950; Mengert, 1953; Ali, Wahab & El Kifel, 1974), since these authors did not pay attention to the presence or absence of crystalline needles in the genital tract of the males.

Table 3

Comparison of descriptions given for " *R. teres* " in the literature with data from the present study

Author(s)	*Suspected species on*	*Assumption based*
Allgén (1949)	?	—
Ali, Wahab & El-Kifel (1974)	?	—
Bütschli (1873)	*R. teres*	morphological characters
Chitwood (1933)	*R. pseudoteres*	body dimensions
Chuang (1962)	*R. teres*	indices after de Man
de Man (1927)	?	—
Goodey (1963)	*R. teres*	indices after de Man
Grube (1849)	*R. teres*	body dimensions
Ludwig (1938)	*R. teres*	indices after de Man
Lukes, Prokopic & Hulinska (1982)	*R. pseudoteres*	indices after de Man
Meyl (1960)	*R. teres*	indices after de Man
Micoletzky (1922)	?	—
Osche (1954)	?	—
Reiter (1928)	*R. teres*	morphological characters
W. Schneider (1939)	?	—
Schuurmans Stekhoven & Teunissen (1938)	?	—
Skrjabin, Shults & Serbinov (1926)	*R. teres*	body dimensions
Völk (1950)	?	—
Yokoo (1968)	*R. teres*	indices after de Man

(?) = no decision made

In Table 3 I tried to compare data from the literature with my own results. The comparison is based mainly on metric values (after de Man) given by the respective author. Unfortunately, these values are strongly influenced by different culturing conditions (Ludwig, 1938). Therefore, only in some cases a preliminary decision could be made whether the investigation was done with *R. teres* or *R. pseudoteres* n. sp.

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