A further sibling species of *Rhabditis (Pelodera) strongyloides* (Nematoda) : *Rhabditis (P.) cutanea* n. sp. from the skin of wood mice *(Apodemus sylvaticus)*

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SUMMARY

Rhabditis cutanea n. sp., a new larval-parasitic species from the skin of *Apodemus sylvaticus,* is described. Cross-mating experiments revealed isolation from *R. nidicolis* Sudhaus & Schulte, 1986, *R. orbitalis* Sudhaus & Schulte, 1986, and *R. strongyloides* (Schneider, 1860). There are two modifications of third stage larvae named " dauerlarva " and " infective larva ". It is hypothesized that the life-cycle will be completed in the nesting material of *Apodemus* spp. A diagnostic key is presented for the group of six nematode species resembling *R. strongyloides.*

RÉSUMÉ

Rhabditis (Pelodera) cutanea *n. sp., une nouvelle espèce jumelle de* Rhabditis (P.) strongyloides, *provenant de la peau du mulot gris* (Apodemus sylvaticus)

Une nouvelle espèce dont les larves parasitent la peau d'*Apodemus sylvaticus* est décrite sous le nom de *R. cutanea* n. sp. Des expériences de croisement ont démontré l'isolement génétique de *R. nidicolis* Sudhaus & Schulte, 1986, *R. orbitalis* Sudhaus & Schulte, 1986 et *R. strongyloides* (Schneider, 1860). Il existe deux types modifiés de larves du troisième stade, nommés « dauerlarva » et « larve infestante ». Il est supposé, que le cycle biologique est complété dans le matériau des nids d'*Apodemus* spp. Une clef de détermination est présentée pour le groupe des six espèces de nématodes voisines de *R. strongyloides.*

Nematodes described as *Rhabditis (Pelodera) " strongyloides "* have been isolated from decaying organic material, the dermis of mammals, and orbits of rodents. It now appears that several different species, all morphologically similar, have been included under this name. A recent revision (Sudhaus & Schulte, 1986) has described the following species, all isolated genetically (metagamely) from each other :

— *Rhabditis (Pelodera) strongyloides* (Schneider, 1860) (= *R. taurica* Mireckij & Skrjabin, 1965), living as a saprophage in the manure of stables, especially of chicken-houses. Third stage larvae of a separate strain of this species (Sudhaus & Schulte, in press) may invade the skin of various domestic mammals, causing dermatitis.

— *Rhabditis (Pelodera) orbitalis* Sudhaus & Schulte, 1986 living in the nests of mice. Its third stage larvae infect the orbits of rodents and live there parasitic in the lacrimal fluid. After about ten days they leave the rodent to complete the life cycle in the damp material of its nest. *R. orbitalis* has been reported from the Northern hemisphere from the orbits of fifteen different species of Muridae and Arvicolidae, and its life cycle was studied in detail by Schulte (1987).

— *Rhabditis (Pelodera) nidicolis* Sudhaus & Schulte, 1986 was found only once in the nesting material of a field vole *(Microtus agrestis)* in Berlin (Germany) together with *R. orbitalis.* The life cycle is still unclear, but presumably this species has a phoretic association, since the dauerlarvae show winking behaviour.

The present paper describes another cryptic species in this complex which has been confused with *R. strongyloides* in the literature (Stammer, 1956; Osche, 1956; Hominick & Aston 1980, 1981). It was isolated from the skin of *Apodemus sylvaticus* at Silwood Park, Ascot, UK (Hominick & Aston, 1981) and has been cultivated since then on nutrient agar plates. Cross-mating experiments between the three named species revealed metagamous isolation in both directions. Occasionally, the cross with *R. orbitalis* females gave L1-juveniles which lived for a while. Two grew to adults, but the male died soon after moulting while the female was sterile when mated with males of the new species (Sudhaus & Schulte, in press).

Table 1
Rhabditis (Pelodera) cutanea n. sp.
Dimensions (in µm) of living specimens bred at 20° on 2 % agar plates with pieces of uncooked meat, heat relaxed in physiological saline.
Figures in brackets are mean

	11 females	*11 males*	*10 infective larvae*	*11 dauerlarvae*
Body length	1003-1780 (1423)	888-1159 (1040)	602-689 (645)	481-639 (556)
Body width	60-115 (86)	50-68 (62)	23-40 (32)	25-40 (29)
Buccal cavity length	26-34 (30)	22-31 (27)	22-24 (23)	22-24 (23)
Pharynx length	192-255 (219)	184-205 (191)	148-157 (153)	135-148 (141)
Tail length (1)	39-61 (54)	30-46 (36)	30-45 (38)	36-49 (40)
Gonad length (2)	418-956 (706)	505-713 (630)	54-72 (66)	54-72 (61)
V	57-59 (58)	spic : 46-61 (54) gub : 29-40 (34)	G (3) : 54-60 (56)	57-64 (60)
a	14.8-18.4 (16.7)	12.7-18.4 (16.2)	16.3-24.6 (20.4)	16.0-22.0 (19.1)
b	5.2-7.3 (6.4)	4.5-5.8 (5.4)	4.0-4.5 (4.2)	3.5-4.4 (3.9)
c	22.7-31.0 (26.6)	24.0-32.7 (28.1)	14.8-21.2 (16.8)	12.8-15.6 (14.1)

(1) L_3-tail in the dauerlarva; (2) anterior to posterior flexure (female), flexure till cloaca (male), primordium (third stage larva); (3) middle of gonad primordium as % of body length.

Rhabditis (Pelodera) cutanea n. sp.

= *Rh. strongyloides apud* Stammer, 1955, 1956 *(partim);* Osche, 1956 *(partim),* 1958; *nec* (Schneider, 1860).

= *Pelodera strongyloides apud* Hominick & Aston, 1980 *(partim),* 1981 *(partim).*

The new species shows all the characteristics listed for the species complex by Sudhaus and Schulte (1986). Therefore only those features that help to differentiate it are mentioned in the following description.

Adult : Cuticle about 1.1 µm thick, fine transverse and longitudinal striae composed of tiny dots. Lips moderately offset, body width at the constriction behind the lips compared to that in the expanded lip region, about 87-97 (92.3) % in the female and 93-100 (96.4) % in the male. Cheilorhabdions inconspicuous. Buccal cylinder three-edged prismatic, about 5 (fem.) or 4 (male) µm wide, length about 6-7 (fem.) or 5-8 (male) times of the width and 12-14 (fem.) or 12-17 (male) % of pharyngeal length. Three distinct teeth on each metarhabdion. In specimens examined in tap water instead of physiological saline, the pharyngeal tissue is pushed forward to envelop the buccal cavity like a pharyngeal collar, which naturally is lacking. Median bulb in the female 24-33 (29) µm, in the male 20-29 (24) µm wide, corresponding to 69-89 % of the diameter of the posterior bulb, which measures 30-46 (37) µm in the female and 27-34 (30) µm in the male. Corpus from anterior end to beginning of the isthmus occupies 52-56 % of length of pharynx. Anterior part of pharynx with transverse markings. Cervical (" excretory ") pore at 82-104 % of pharyngeal length, 161-241 (208) µm (fem.) or 152-185 (167) µm (male) from anterior end followed by two large cervical cells, each 61-88 µm long. Lateral " excretory " canals inconspicuous, but reach the anal region in the female.

Female : Amphidelphic branches of reproductive system occupy 39-56 % of body length, flexures 68-117 % of the length of a branch. Length of the posterior branch corresponds to 80-128 % of that of the anterior one. Only a few (1-8) eggs, in first steps of segmentation in the reproductive tracts, with dimensions 49-67 (58) × 28-40 (33) µm. Diameter of pseudo-coelomocytes at the flexure of the ovaries 13-22 µm. Dome-shaped tail without thickening of the cuticle, with a very short terminus (spine), 6-11 (9.5) µm long, that means 15-21 % of tail length. Phasmids conspicuous at a distance of 27-36 (32) µm from the tip of the spine. Rectum 31-40 µm long.

Male : Testis occupies 54-67 % of body length, laterally reflexed part 117-262 (186) µm long, corresponding to 20-35 % of length of the testis. Diameter of pseudo-coelomocytes lying distally to flexure 9-12 µm. Length of the two ejaculatory glands differs by about 21-23 µm, their blind end 229-299 (255) µm anterior to the cloaca, about 68-75 % of body length (from anterior end).

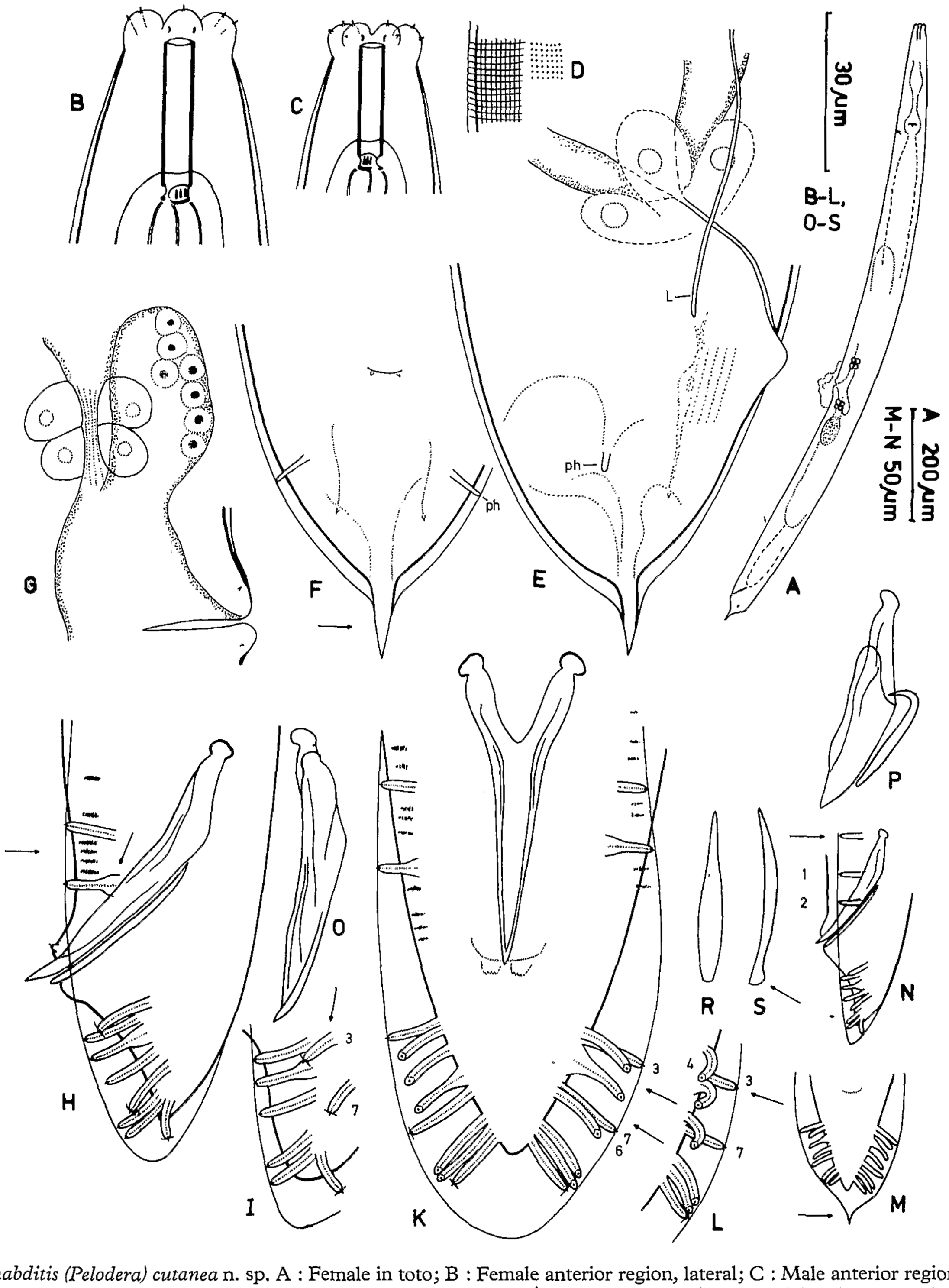

Fig. 1. *Rhabditis (Pelodera) cutanea* n. sp. A : Female in toto; B : Female anterior region, lateral; C : Male anterior region, ventral; D : cuticle structure. Female. E : caudal region, lateral (L = lateral canal, ph = phasmids); F : caudal region, ventral; G : region of the vulva, lateral (uterus, sphincter, *receptaculum seminis* with sperm cells). Male. H : tail, lateral; I : tail end, lateral; K : bursa, ventral; L : part of the bursa, ventral; M : aberrative bursa terminus, ventral; N : tail, lateral, with a supernumerary papilla; O, P : aberrations of spicules, lateral; R : gubernaculum, ventral; S : aberration of gubernaculum, lateral.

Sperm cells about 7.5 μm in diameter. Bursa velum proximally with fine transverse striae, and often several distinct rodlike cuticular structures in the region of precloacal papillae (Fig. 1, H, K). First and second bursal papillae typically spaced 6-18 μm apart. Bursa arranged slightly radially : papillae number 3, 7 and 10 (which open on the outer side of the bursa) shifted dorsad, so number 3 is located laterally to number 4, and number 7 is lateral to 6 (Fig. 1, I, K, L). Therefore, number 3 sometimes is hidden (Fig. 1, K) and easily overlooked. Occasionally it may be passed laterally by number 4 and then appears standing in the fourth position. Likewise number 7 may appear to be shifted slightly ahead, so that it seems to be in the sixth position (Fig. 1, L). However, they are always recognizable by having their terminals on the outer surface of the bursa velum, while papillae 4-6 open on the inner side. In contrast to the other three species, papillae 4-6 are spaced. Papillae 8-10 stand close together. The basis of papilla 2 and 5 conically swollen, the tenth papilla being shortened. Precloacal lip prominent, not enlarged owing to heat relaxation. Spicules sometimes different in length up to 4 μm, joined together 26-41 μm or 65-71 % of their total length (46-61 μm), the broadest with at the capitula about 18-25 μm. Gubernaculum length 57-68 % of that of the spicules.

Variability : In one specimen resp. the bursa was pointed distally (Fig. 1, M), papilla no. 1 was missing on the left hand side, and there was one additional papilla proximally to no. 1 on the left hand side (Fig. 1, N). Occasionally the spicules were somewhat stunted, especially one of them without a clear knob-head (Fig. 1, P). Once the gubernaculum was thickened distally on its back (Fig. 1, S).

Diphänism of the third stage larvae : We can find side by side two different types of third stage larvae, distinguishable on its morphological characteristics and behaviour patterns. They will be named herein as « dauerlarva » and « infective larva » resp. According to our observations both types arise from one common pre-stage. After metamorphosis has taken place, the dauerlarva cannot transform to the infective larva and vice versa. Dauerlarva as well as the infective larva wouldn't tolerate desiccation, but can be stored in tap water over a longer period of time. However, only dauerlarvae will resume development independent from mice on fresh medium (e. g. agar with decaying meat). The infective larva requires a living mouse host prior to completation of its life cycle. A similar diphänism of third stage larvae was discovered the first time in *R. orbitalis* and its genesis studied in detail by Schulte (1987).

Dauerlarva (Fig. 2, A-D) : Relatively clumsy, with inert behaviour, coiling up when disturbed, not winking, the second stage cuticle kept as an enclosing sheath (easily recognizable by the end of its tail). The epidermis provided with granules of stored material additional to that found in the intestinal cells. Therefore the structure of the cuticle as well as the inner organization are hardly visible. Cuticle finely transverse striated, width of 10 annules 15-17 μm, lateral field about 6 μm broad, running from two times the length of the stoma from the anterior end to the level of phasmid openings, obviously with only a single central line. Lips not offset, the anterior end of the second stage cuticle bearing a number of tiny sensillae, metastomal teeth hardly visible. Corpus occupies 48-55 % of the total length of pharynx, deirids at the region of the cervical pore. Distance between anterior end and cervical pore 103-153 (122) μm, the latter at 75-106 (86) % of total length of pharynx. Pulsations and transport of fluids visible at the beginning of the loop shaped « *sinus excretorius* ». Fore gut without viscous material, intestinal walls collapsed, its cells filled up with granules of stored material. Cell borders inconspicuous, nuclei appearing as brigthened zones. Tail of second stage cuticle ending conical pointing, tail end of L3 club shaped or finger like, its length occupies 2-2.4 fold the diameter of the body at the anal region. Phasmids inconspicuous, opening at 14-28 % of the length of L3-tail.

Infective larva (Fig. 2, E-H) : Body generally longer (about 100 μm) than that of the dauerlarva, therefore appearing more slender (although with the same diameter of the body). Active, exposed with searching movements like « waving ». They always are unsheathed, granules of stored material in the epidermis nearly lacking, cuticle clearly annulated, width of 10 annules 18-22 μm, distinct lateral field 7-9 μm wide, bordered by the cordon-like ending annules of the cuticle. Fine transverse striations within the field, absent in the middle between two close longitudinal lines. Beginning of the lateral field 2.5 fold the length of stoma from the anterior end, extending posterior over the region of phasmid openings. Lips distinctly offset, mouth cavity closed distally, sensillae as well as metastomal teeth inconspicuous. Pharynx absolutely longer than that of the dauerlarva, corpus occupies 56-59 % of total length of pharynx. Deirids on the lateral field about the level of the cervical pore, distance between anterior end and cervical pore 124-153 (141) μm, its position corresponding to 81-103 (92) % of pharyngeal length. Pulsations on the « *sinus excretorius* » observed. Viscous material in the fore gut, separating its walls, is often pressed through the mouth by the pressure of the cover glass and forms concentric rings or streaks in the water (Fig. 2, L). Intestinal cells distinctly intermitted, with only a little amount of stored material. Tail end rounded, finger like or club shaped, tail length occupies 1.6-2.5 fold the anal body diameter. Phasmids strongly swollen, bubble like, their diameter 4.5-5.4 μm, opening about 15-30 (22) % of tail length, the wall of the pore strengthened.

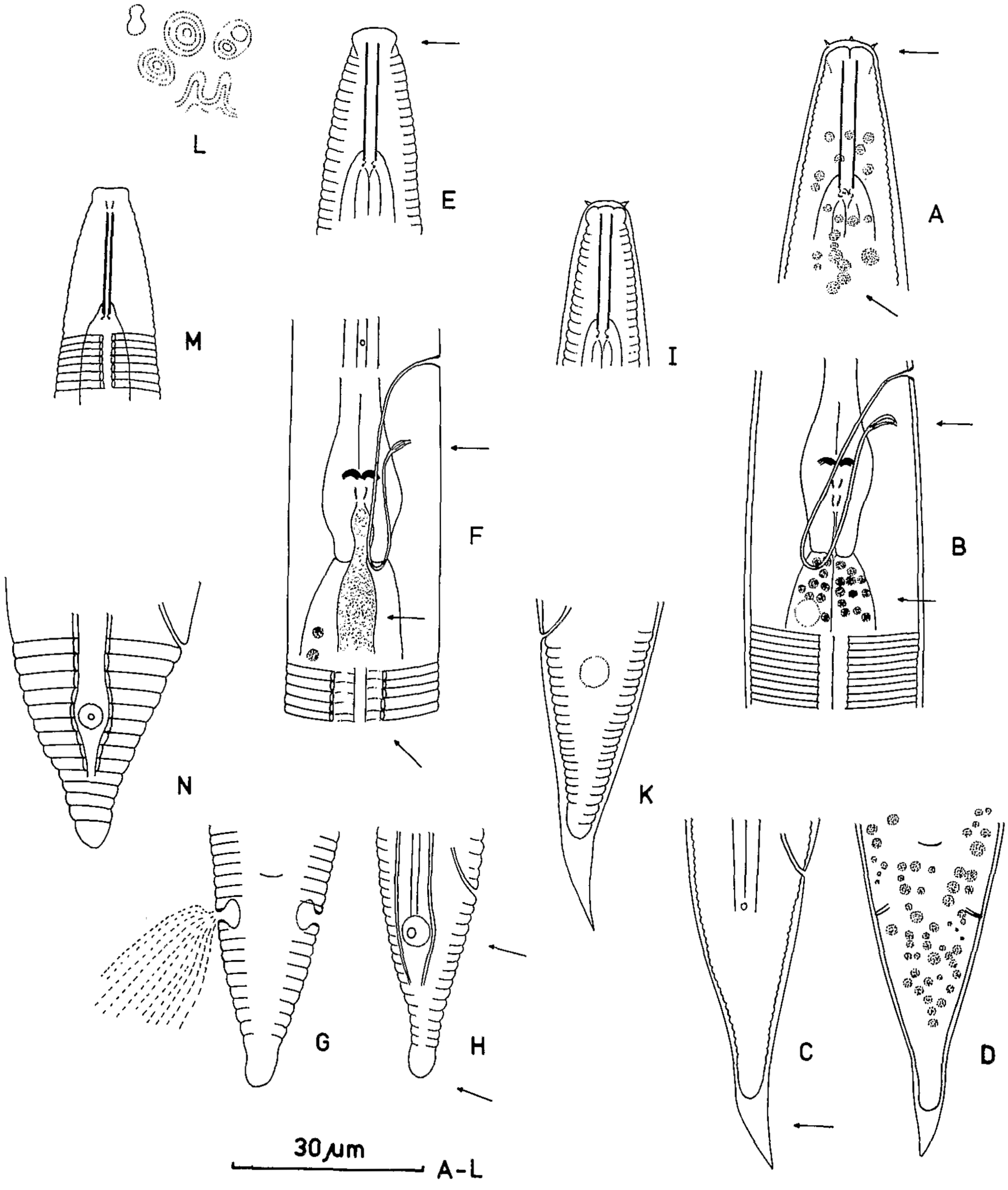

Fig. 2. *Rhabditis (Pelodera) cutanea* n. sp. Dauerlarva. A : anterior region, lateral; B : pharyngeal area, lateral; C : caudal region, lateral; D : caudal region, ventral. Infective larva. E : anterior region, lateral; F : pharyngeal area, lateral; G : caudal region, ventral (material squeezed out of phasmid on one side); H : caudal region, lateral. Prospective infective larva (just before moulting). I : anterior region, lateral; K : caudal region, lateral; L : Viscous material from foregut of infective larva or prospective infective larva in water; M, N : anterior and posterior region of third stage larva from the skin of *Apodemus sylvaticus* from Tennenlohe near Erlangen, Bavaria (after unpublished drawings by G. Osche, 1954).

TYPE SPECIMENS

Type material in the collection of W. Sudhaus : holotype female slide no. R94, allotype male R95, paratype females, males immat. R94-96. Other paratypes deposited in the following collections : Laboratoire des Vers, Muséum national d'Histoire naturelle, Paris, France; Laboratorium voor Nematologie, Landbouwhogeschool, Wageningen, Holland; Biologische Bundesanstalt für Land- und Forstwirtschaft, Institut für Nematologie, Münster, W.-Germany; and Museum für Naturkunde der Humboldt-Universität zu Berlin, Zoologisches Museum, Berlin, GDR.

DIAGNOSIS

R. cutanea n. sp. is easily distinguished from the other known species of the complex by its slight radial arrangement of the bursa caused by papillae 3 and 7 standing more laterally and the distinct gaps between papillae 4 to 6. Several rod-like structures of the cuticle precloacally, where the bursa arises, are usual, the flexure of the testis may be the longest, the spine of the female tail is often less than 9 µm, and the cervical cells are voluminous. Infective larvae are unsheathed, and their tails are rounded finger like or club shaped.

It further differs from *R. orbitalis* by its distinct metastomal teeth and transverse markings within the corpus, cervical pore usually farther back in relation to the pharynx, and the narrower terminal bulb. The female may be considerably longer, with its tail spine occupying less than 25 % of tail length. The male bursa is hardly striped proximally, with a greater distance between papillae nos. 1 and 2, and spicules in the proximal region are wider. Infective larvae have two central lines in the lateral field, phasmids formed otherwise, tip of tail without mucro.

Further differences to *R. nidicolis* are : female often longer, with uniform thickness of the cuticle on the tail in the region of the phasmids, the spine absolutely and relatively smaller; considerably greater distance between papillae nos. 1 and 2, proximal part of spicules usually wider; infective larvae with broader annules of cuticle, lips offset, genital primordium only half of the length, phasmids swollen.

Further differences compared with *R. strongyloides* are : the behaviour of coiling up to a spiral in water (when disturbed) is rare, the cuticle of the female tail (in the region of the phasmids) is not thickened; male ejaculatory glands are shorter, their blind end is far back (at 68-75 % of body length *versus* 61-66 %), and the joined part of the spicules (lamina) is shorter; infective larvae with lips offset, annules of the cuticle much broader, anterior part of the intestine filled with a viscous substance, and phasmids swollen.

EARLIER RECORDS, HOSTS, DISTRIBUTION, LIFE HISTORY

R. cutanea n. sp. was grown from larvae that emerged from hair follicles of several wood mice *(Apodemus sylvaticus)* captured in Observatory Copse (Ordnance Survey ref. SU 947 689), Silwood Park, Ascot, Berks., England. They were collected as they emerged from animals freshly killed prior to examination for parasites in September 1977, and have been cultured on 2.8 % Nigon's agar since then. Some aspects of their life history were described by Hominick and Aston (1981). There are earlier records from the same host in Germany from the region of Erlangen (Bavaria) (treated as " *R. strongyloides* " in Stammer, 1956; Osche, 1956) and Oldenburg (Low Saxonia). Unpublished drawings of Prof. G. Osche (Freiburg) from 1954 and 1958 show characteristics of the infective larvae (lips, cuticle structure, phasmids, terminus, Fig. 2 M, N), and the slightly radially arranged bursa of the male, with the third papilla apparently in the fourth position and exhibiting a gap between each of the three papillae postcloacally, whose tips open on the inner side of the bursa velum (see Osche, 1958, Fig. 2 a, " *Rhabditis strongyloides* "). We assume that larvae from the skin of *Apodemus flavicollis,* recorded by Stammer (1956), also belong to *R. cutanea.* It appears that *R. cutanea* is specific to *Apodemus,* since it was not found in the skin of *Clethrionomys glareolus* captured in the same place and at the same time (Hominick & Aston, 1981).

The life cycle of *R. cutanea* remains unknown.

A former hypothesis has discussed the possibility that hosts accumulate nematodes in the dermis during their life and the nematodes resume development when the host dies (Osche, 1962, 1966; Hominick & Aston, 1981). However, this remains the problem unsolved where and how the nematodes infect a new host.

Therefore we suppose that the larvae leave the host in its nest, propagate there as bacterial feeders, and forming new infective larvae which invade mice there while sleeping or providing the brood. This is most likely as the closely related *R. orbitalis* exhibits just such a life-cycle (Schulte, 1987), the only difference being their larvae invade the conjunctival sacs of the eyes instead of hair follicles of the skin.

Characteristics of the *Rhabditis (Pelodera) strongyloides*-group

Buccal cavity without pharyngeal collar, metarhabdions with distinct little teeth. Pharynx rhabditoid, haustrulum twofold behind the bulb flaps. Gonads of females amphidelphic, with a conspicuous sphincter of a double set of cells between oviduct and uterus (" dosator " after Belogurov, Muchina & Churikova, 1977). Males with large ejaculatory glands, bursa peloderan and open, bearing 10 pairs of papillae, arrangement (2/4 + 4) or (2/5 + 3). Papillae nos. 3, 7 and 10 ending with their tips on the outside of the velum, the rest pointing out inwards. Spicules yellow-brownish, relatively long, straight, and fused distally for two-thirds of their length. Gubernaculum as long as the intergrowth (lamina), proximally boat-shaped pointed.

DIAGNOSTIC KEY TO THE FEMALES

1 — Tail conical 2

— Tail ± domeshaped with a little spine 3

2 — Tail longish-conical, 80-168 µm long, about 3-4.5 times anal body diameter, often moderately bent backwards. Cervical pore opening at 77-89 % of pharynx length .... *punctata* Cobb, 1914

— Tail bluntly conical, only 50-90 µm long, about 1.5 times anal body diameter. Cervical pore at 58-78 % of pharynx length... *comandorica* (Belogurov *et al.*, 1977) n. comb.

3 — Lips not or hardly set off 4

— Lips ± offset from body 6

4 — Cuticle thickened at the level of phasmids 5

— Cuticle on the whole tail-dome with uniform thickness, spine short (6-11 µm) .... *cutanea* n. sp.

5 — Spine moderately bent ventrad, 14-31 µm long, valvular bulb narrow (31-39 µm), cheilorhabdions strengthened .... *nidicolis* Sudhaus & Schulte, 1986

— Spine straight, 9-20 µm long, valvular bulb broad (36-50 µm), cheilorhabdions not sclerotized .... *strongyloides* (Schneider, 1860)

6 — Cuticle thickened at the origin of the spine, spine often not clearly set off, 9-20 µm long, length of pharynx sometimes more than 257 µm .... *strongyloides* (Schneider, 1860)

— Cuticle on the dome of the tail with uniform thickness, spine set off, shorter than 16 µm, length of pharynx 257 µm at maximum 7

7 — Spine 6-11 µm long, that means 15-21 % of tail length, metarhabdions with distinct teeth, lips moderately offset, cervical pore at 84-104 % of pharynx length .... *cutanea* n. sp.

— Spine 9-16 µm long, that means 24-44 % of tail length, metarhabdion teeth not clearly visible, lips distinctly set off, cervical pore at 67-85 % of pharynx length .... *orbitalis* Sudhaus & Schulte, 1986

DIAGNOSTIC KEY TO THE MALES

1 — Lips not or hardly set off 2

— Lips ± set off from body 6

2 — Space between bursal papillae nos. 1 and 2 measuring more than 5 µm 3

— That space measuring 5 µm maximally 4

3 — Papillae of the copulatory bursa arranged somewhat radially (papillae nos. 3 and 7 in a more lateral position), velum bearing precloacally several cuticular markings, anterior ending of ejaculatory glands at 68-75 % of total body length, spicules measuring 46-61 µm, its intergrowth 26-41 µm .... *cutanea* n. sp.

— Bursal papillae not radially arranged, velum proximal without special markings, the beginning of ejaculatory glands at 61-66 % of total body length, spicules 55-82 µm long, its intergrowth measuring 40-58 µm .... *strongyloides* (Schneider, 1860)

4 — Cheilorhabdions sclerotized, length of stoma 23-31 µm .... *nidicolis* Sudhaus & Schulte, 1986

— Cheilorhabdions not sclerotized, stoma longer than 30 µm 5

5 — Lips separated by deep furrows, series of bursal papillae (2/4 + 4), distance between papillae nos. 1 and 2 only 1-3 µm ....*punctata* Cobb, 1914

— Lips not separated by deep furrows, bursal papillae spaced (2/5 + 3), distance between papillae nos. 1 and 2 about 4 µm .... *comandorica* (Belogurov *et al.*, 1977) n. comb.

6 — Metarhabdions with distinct teeth, cervical pore at more than 82 % of pharynx length, distance between bursal papillae nos. 1 and 2 measuring more than 6 µm, velum of bursa striped only slightly 3

— Teeth on metarhabdions hardly visible, cervical pore at 72-83 % of length of pharynx, space between bursal papillae nos. 1 and 2 measuring 4-6 µm, velum of bursa proximally with distinct stripes .... *orbitalis* Sudhaus & Schulte, 1986

HABITAT (SOURCE OF DISCOVERY)

1. Marine littoral zone .... *R. commandorica*

2. Edge of fresh water,, in decaying deposits, mud or on aquatic plants .... *R. punctata*

3. Manure of stables, third stage larvae of a separate strain even infecting the skin of warm-blooded animals .... *R. strongyloides*

4. Nesting material of a field vole *(Microtus agrestis)* .... *R. nidicolis*

5. Nesting material of different members of the families Muridae and Arvicolidae (rodents), third stage larvae infecting the conjunctival sacs of the orbits .... *R. orbitalis*

6. Most probably in the nesting material of *Apodemus* spp., third stage larvae invading hair follicles of the mice's skin .. .. *R. cutanea* n. sp.

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