

CHAPTER 8

Identification of *Trichodorus/Paratrichodorus* Species (Diphtherophorina)

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I. INTRODUCTION

The Trichodoridae are a small family of four genera: *Trichodorus* Cobb, 1913, *Paratrichodorus* Siddiqi, 1974, *Monotrichodorus* Andrassy, 1976 and *Allotrichodorus* Rodriguez-Montessoro, Sher & Siddiqi, 1978 (Fig. 1). The subgenera *Nanidorus* and *Atlantadorus*, proposed by Siddiqi (1974) and used at generic level by Siddiqi (1980) but rejected by several subsequent reviewers of the Trichodoridae, were recently reinstated at the subgeneric level by Jairajpuri & Ahmad (1992). However, we do not follow this new point of view and consider the Trichodoridae as a family with four genera. The two largest genera, *Trichodorus* (47 species) and *Paratrichodorus* (28 species), are didelphic and occur world-wide. The two other genera, *Monotrichodorus* and *Allotrichodorus* with seven species each, are monodelphic and so far recorded only from South and Central America. The differentiation of the four genera of the family Trichodoridae and the identification of trichodorid species occurring in Europe, are presented in this contribution.

II. DISCUSSION AND APPRAISAL OF DIFFERENTIATING CHARACTERS AT THE GENUS LEVEL

A list of all the diagnostic characters which have been used for defining genera in the family Trichodoridae is presented here (Table I).

This also includes the differential features of *Atlantadorus* and *Nanidorus*, two genera erected by Siddiqi (1980) and considered as synonyms of *Paratrichodorus* (Decraemer, 1980; Decraemer & De Waele, 1981).

A. Primary Important Diagnostic Features (as^a in Table I)

The most important diagnostic characters at the genus level are:

FEMALE

1. Number of genital branches and related position of vulva.
Differentiation of didelphic and monodelphic genera.

TABLE I

LIST OF ALL DIAGNOSTIC CHARACTERS OF THE GENERA
OF THE TRICHODORIDAE WITH INDICATION^a
OF THE TAXONOMICALLY MOST IMPORTANT FEATURES

GENERAL MORPHOLOGY

- Habitus
- Body length
- Swelling of cuticle upon fixation^a
- Caudal pores
 - presence
 - number
 - position
 - development
- Presence of incisors in lateral field
- Tail
 - shape
 - length
- Excretory pore
 - position in relation to pharyngeal bulb
- Digestive system
 - length onchiostyle
 - ventral pharyngeal overlap
 - presence
 - length
 - dorsal intestinal overlap
 - presence
 - length
 - presence offset pharyngeal bulb
 - dorsal pharyngeal nucleus
 - position in relation to pharyngeal bulb
 - position in relation to subventral gland nuclei
 - size
 - subventral pharyngeal gland nuclei
 - position in relation to pharyngo-intestinal junction
 - position in relation to dorsal pharyngeal gland nucleus
 - size
 - presence of 2nd onchiostyle tip in dorsal slit of functional onchiostyle in adults

CHARACTERS OF FEMALE

- Number of genital branches^a
- Vulva
 - ratio V^a
 - shape in ventral view

(continued)

TABLE I (continued)

Vagina
length as a proportion of body diameter ^a
orientation
shape and dimension of vaginal sclerotizations ^a
development of vaginal constrictor muscles
Presence of spermatheca
Sperm cells
shape
position
Length of postvulvar uterine sac
Lateral advulvar body pores
presence ^a
number
Lateral body pores
presence
number
Position of anus
Position lateral cervical pores
CHARACTERS OF MALE
Males
presence / abundance
Spicules
shape
presence of capitular extension
length
ornamentation
development of capsule of suspensor muscles ^a
Gubernaculum: development
Precloacal supplementary papillae
total number
number in region retracted spicules
number in bursa region
position of precloacal supplements
distance between SP2-SP3
position of anteriormost supplement (SP3) in relation to the retracted spicules
distance of SP2 from cloacal opening
development of anteriormost supplement
Copulatory muscles ^a
extension/development
Ventromedian cervical papillae
presence
number
position in relation to excretory pore
position in relation to onchiostyle

(continued)

TABLE I (continued)

Lateral cervical pores
presence
position in relation to nerve ring
position in relation to excretory pore
Presence caudal alae (=bursa) ^a
Postcloacal papillae
presence
development
position in relation to cloacal opening

2. *Length of vagina as a proportion of corresponding body diameter.* Vagina shorter than half a body width in *Paratrichodoros*, longer in *Trichodoros*.
3. *Shape and dimensions of vaginal sclerotizations.* See further remark 3.
4. *Presence of lateral advulvar body pores.* Differentiation of the monodelphic genera: *Monotrichodoros* with 1 pore on each side at vulva level, *Allotrichodoros* without pores.

MALE

1. *Presence of caudal alae (=bursa).* Absent in *Trichodoros* (except for *T. cylindricus*) and in *Monotrichodoros*, always present in *Paratrichodoros* and *Allotrichodoros*.
2. *Degree of development of copulatory muscles and capsule of spicule suspensor muscles.* Both well developed and copulatory muscles extending far anteriorly in *Trichodoros* (Fig. 10B); both poorly developed and copulatory muscles restricted to bursa region in *Paratrichodoros*; copulatory muscles moderately developed in the monodelphic genera.

IN BOTH SEXES

1. *The reaction of the body cuticle upon fixation or heat killing.* From non-swollen to conspicuously swollen, mainly used to distinguish *Trichodoros*/*Monotrichodoros* from *Paratrichodoros*/*Allotrichodoros*.

REMARKS

1. *Swelling of the body cuticle.* So far, the degree of swelling of the body cuticle as a reaction to fixation or heat killing is included in the diagnoses of the genera of the

Trichodoridae. The genus *Paratrichodorus* (Fig. 1G,H,I) with the body cuticle usually much swollen (in various degrees), the genera *Trichodorus* (Fig. 1A,B,C) and *Monotrichodorus* (Fig. 1D,E,F) with the cuticle generally not swollen (except in very badly fixed specimens) and the genus *Allotrichodorus* (Fig. 1J,K) with the body cuticle varying from not swollen, to moderately swollen or distinctly swollen upon fixation.

2. *Caudal alae*. Caudal alae are present in all species of *Paratrichodorus* but are usually narrow and rather weak (Fig. 10D); in *P. porosus* they are inconspicuous. They are present in *Allotrichodorus* species in various degrees of development; in some species (e.g. *A. loofi*) they can hardly be considered as real caudal alae but at most as intermediate forms between species with caudal alae and those without. Similar observations were made for *Monotrichodorus sacchari* and some *Trichodorus* species such as *T. sparsus* (Loof, 1973; Decraemer, 1986) and *T. elefjohnsoni* (Bernard, 1992) with a thickened ventral cuticle in the cloacal region, considered as a rudimentary bursa.
3. *Vaginal sclerotizations*. The shape of the sclerotized ring at the junction between vulva and vagina in lateral optical section is a very important diagnostic feature at species level. The degree of development may, to some extent, show some taxonomic value at genus level. In *Trichodorus*, the vaginal sclerotizations are usually well developed and clearly differentiated in size and shape, although some species possess small to minute vaginal sclerotizations (Fig. 2). In *Paratrichodorus*, the vaginal sclerotizations are small to inconspicuous (Fig. 3). In *Monotrichodorus* and *Allotrichodorus*, the vaginal sclerotizations are well developed, varying from small to large, conspicuous (Fig. 4).
4. *Presence of lateral advulvar body pores*. This feature is one of the few differential characters between the monodelphic genera: *Monotrichodorus* females possess a pair of lateral advulvar body pores (Fig. 1F, arrow), in *Allotrichodorus* females they are absent. In all *Trichodorus* species, except *T. beirensis*, *T. eburneus* and *T. cedarus*, female specimens possess a pair of postadvulvar lateral body pores. In *Paratrichodorus* the lateral body pores are rarely located advulvar (i.e. within one body diameter from the vulva).

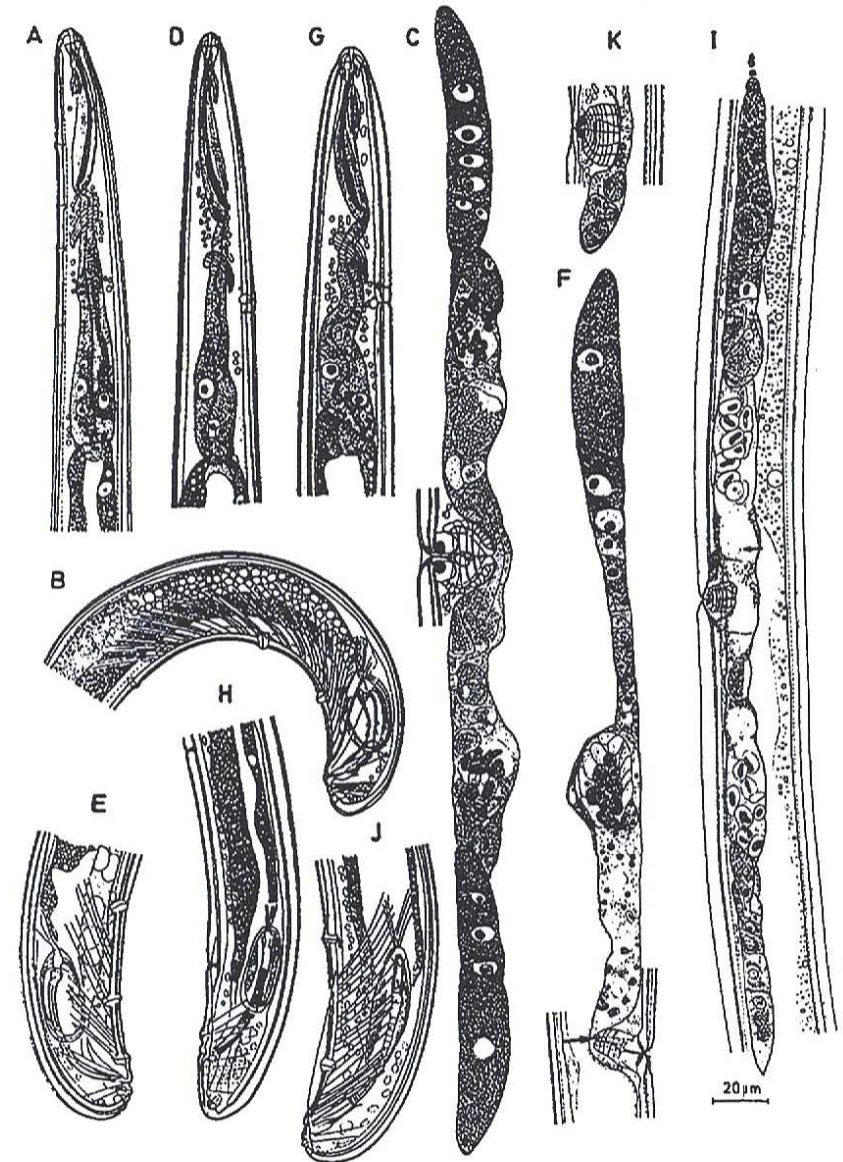


FIG. 1. The genera of the Trichodoridae: (A,B) *Trichodorus velatus*, ♂; (C) *T. taylori*, ♀; (D,F) *Monotrichodorus vangundyi*, ♂; ♀; (G,I) *Paratrichodorus weischeri*, ♀; (H) *P. pachydermus*, ♂; (J,K) *Allotrichodorus campanullatus*, ♂, ♀ (after Decraemer, 1991).

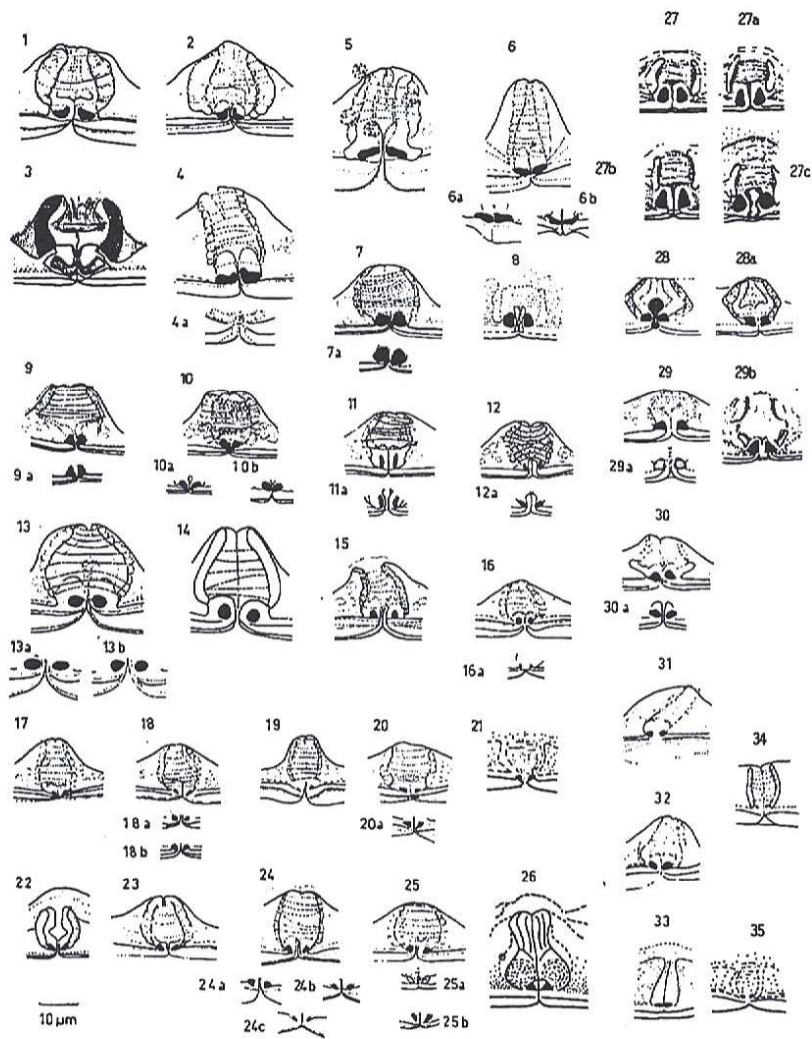


FIG. 2. Vaginal region and variability of vaginal sclerotizations in *Trichodorus* species (adapted from Decraemer, 1988b): (1) *T. californicus*; (2) *T. dilatatus*; (3) *T. intermedius*; (4) *T. elegans*; (5) *T. cottieri*; (6) *T. obscurus*; (7) *T. variopapillatus*; (8) *T. aquitanensis*; (9) *T. similis*; (10) *T. cylindricus*; (11) *T. primitivus*; (12) *T. viruliferus*; (13) *T. taylori*; (14) *T. persicus*; (15) *T. hooperi*; (16) *T. tricaulatus*; (17) *T. cedarus*; (18) *T. eburneus*; (19) *T. orientalis*; (20) *T. coomansi*; (21) *T. rinae*; (22) *T. borai*; (23) *T. aequalis*; (24) *T. sparsus*; (25) *T. proximus*; (26) *T. yokooi*; (27) *T. beirensis*; (28) *T. azorensis*; (29) *T. lusitanicus*; (30) *T. velatus*; (31) *T. pakistanensis*; (32) *T. borneoensis*; (33) *T. complexus*; (34) *T. petrusalberti*; (35) *T. sanniae* (27, 28, 29b after Almeida *et al.*, 1989).

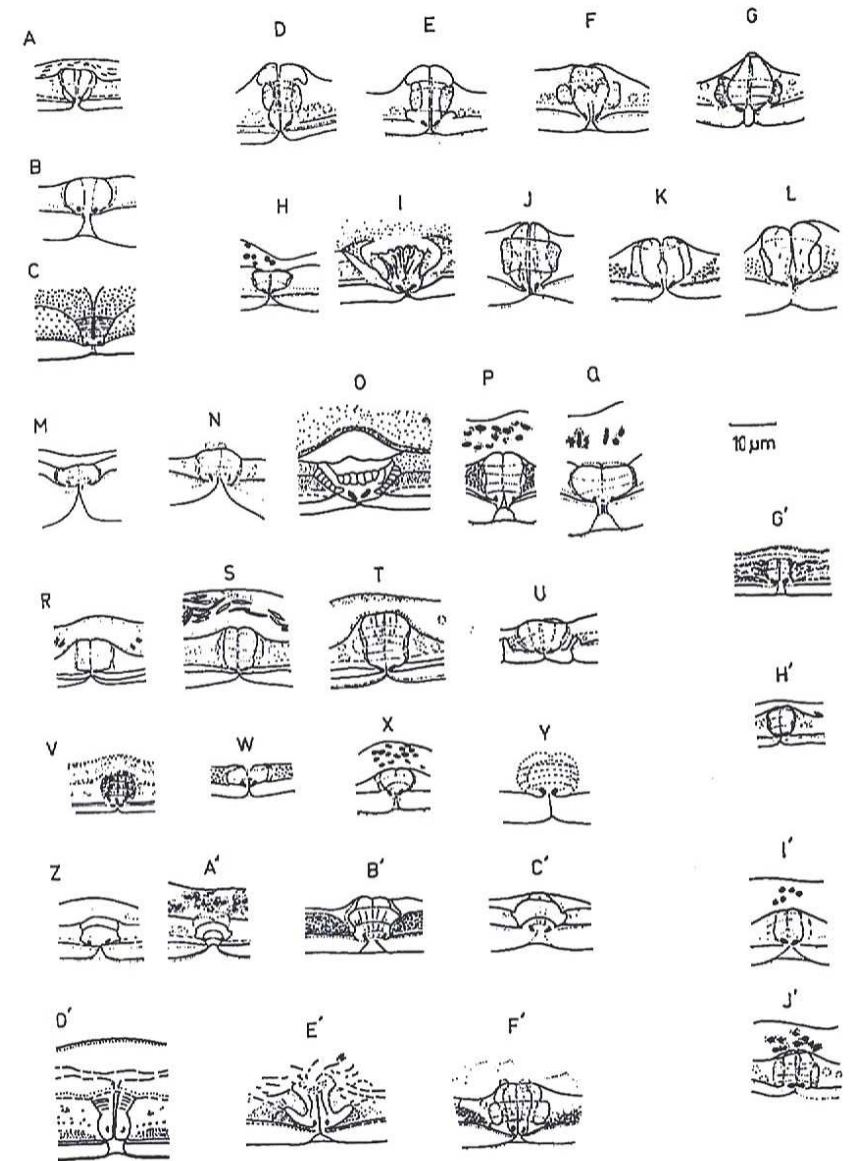


FIG. 3. Vaginal region and its variability in *Paratrichodorus* species (after Decraemer, 1988a): (A) *P. acutus*; (B) *P. catharinae*; (C) *P. mirzai*; (D,G) *P. anemones*; (H) *P. anthurii*; (I) *P. grandis*; (J,L) *P. pachydermus*; (M,N) *P. allius*; (O) *P. hispanus*; (P,Q) *P. lobatus*; (R,T) *P. minor*; (U) *P. porosus*; (V,Y) *P. rhodiensis*; (Z,A') *P. tansaniensis* (= *P. allius*); (B',C') *P. teres*; (D') *P. tunisiensis*; (E',F') *P. weischeri*; (G',H') *P. renifer*; (I',J') *P. nanus*.

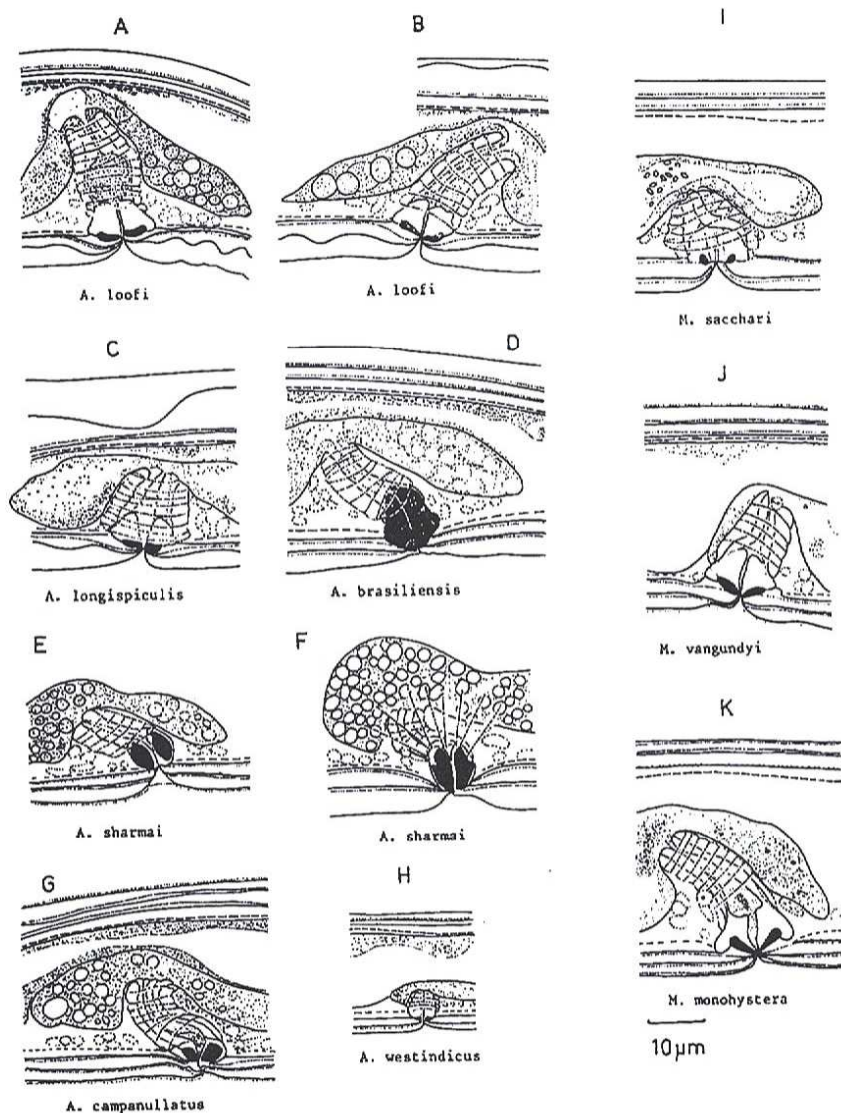


FIG. 4. Vaginal region in species of the monodelphic genera: (A,B) *Allotrichodoros loofi*, paratypes; (C) *A. longispicula*, holotype; (D) *A. brasiliensis*, holotype; (E,F) *A. sharmai*, paratypes; (G) *A. campanullatus*; (H) *A. westindicus*; (I) *Monotrichodoros sacchari*, paratype; (J) *M. vangundyi*, paratype; (K) *M. monohystera*.

B. Secondary Diagnostic Features

Some of the characters that have been used in the diagnoses of the genera are not suitable as diagnostic characters due to the large variability displayed (e.g. the position of the pharyngeal gland nuclei, body length, position of the excretory pore (Decraemer & De Waele, 1981; Decraemer, 1989). However, other variable features are useful but have a more limited taxonomic value at genus level:

1. *Habitus*. This feature can to some extent help to differentiate males of the genera *Trichodoros* (Fig. 10A)/ *Monotrichodoros* (posterior body region clearly curved ventrally) from those of *Paratrichodoros* (straight body, Fig. 10C)/ *Allotrichodoros* (usually straight body). However, the habitus is susceptible to fixation and typical straight females and straight males of *Paratrichodoros* and *Allotrichodoros* may also be observed as arcuate specimens or specimens with a slightly ventrally curved posterior body region especially in the latter genus.
2. *The presence or absence of antero-dorsal intestinal or postero-ventral/subventral pharyngeal gland overlap*. Although the pharynx-intestine junction in *Trichodoros* may vary inter- and intraspecifically (flat, with ventral pharyngeal overlap, with antero-dorsal intestinal overlap or with both pharyngeal and intestinal overlap together), the majority of the species have an offset (=flat) pharyngeal bulb. In *Paratrichodoros*, all types of overlapping may be observed but a ventral pharyngeal overlapping occurs most frequently and is also more pronounced. So far, in *Allotrichodoros* no clear pharyngeal overlap or an antero-dorsal intestinal overlap has been observed and in *Monotrichodoros* an offset bulb or at most a negligible ventral pharyngeal overlap has been observed.
3. *Presence of spermatheca*. In *Trichodoros*, except *T. nanjingensis* (Fig. 1C), *Monotrichodoros* (Fig. 1F) and *Allotrichodoros* all species possess a spermatheca; in *Paratrichodoros*, spermathecae have been observed in eight species, while in other species sperm is dispersed throughout the uterus, occasionally with some accumulation near the ovaries. Therefore, this character is of restricted value for differentiating the genus *Paratrichodoros* from the other trichodoridae genera.

4. *Shape of sperm cells.* *Trichodorus* (Fig. 8) and *Monotrichodorus* species have large sperm cells, the majority of them with a large sausage-shaped nucleus. In *Paratrichodorus* (Fig. 9), most species possess small sperm cells; however, some species have sperm as large as in the former genera. In *Allotrichodorus*, most species have well developed sperm cells with more or less globular nucleus.
5. *Spicule shape and ornamentation.* The spicule shape is an important diagnostic character for species differentiation. On genus level, its value is more restricted. It distinguishes males of *Paratrichodorus* with mainly straight spicules with transverse striae (Fig. 6) from *Trichodorus* males displaying a more pronounced differentiation in spicule shape together with a more diverse ornamentation (transverse striae, bristles, ventral flange, smooth) (Fig. 5), from *Monotrichodorus* males having long slender arcuate spicules with transverse striae and bristles and from *Allotrichodorus* males with long slender spicules less arcuate than in *Monotrichodorus* and with transverse striae (bristles only observed in *A. loofi*) (Fig. 7). The presence of a capitular extension of the spicules is restricted to two species of *Allotrichodorus*.
6. *Number of precloacal supplements (SP).* This character is not a useful taxonomic character on genus level. It can be used only to distinguish *Paratrichodorus* from the other genera, by those species with only 1 (2) precloacal supplements. *Trichodorus* species mainly have 3 SP (exceptionally 2, 4 or 5); *Paratrichodorus* have 1 to 4 SP but usually 3, (exceptionally 4); *Monotrichodorus* have 3 SP and *Allotrichodorus* usually have 3 'exceptionally 4'.
7. *Position of precloacal supplements in relation to the retracted spicules.* This feature is susceptible to fixation and of very restricted value at the genus level. *Trichodorus* males usually have 1 SP, *Paratrichodorus* and *Monotrichodorus* males have 2 SP and *Allotrichodorus* males have 3 SP within the spicular region.
8. *Vulva shape in ventral view.* This feature was used as a diagnostic feature for the characterization of the (sub)genera of *Paratrichodorus* (Siddiqi, 1974, 1980) and is, at present, of no taxonomic value at the genus level. Currently, only the genus *Allotrichodorus* is characterised by having one type of

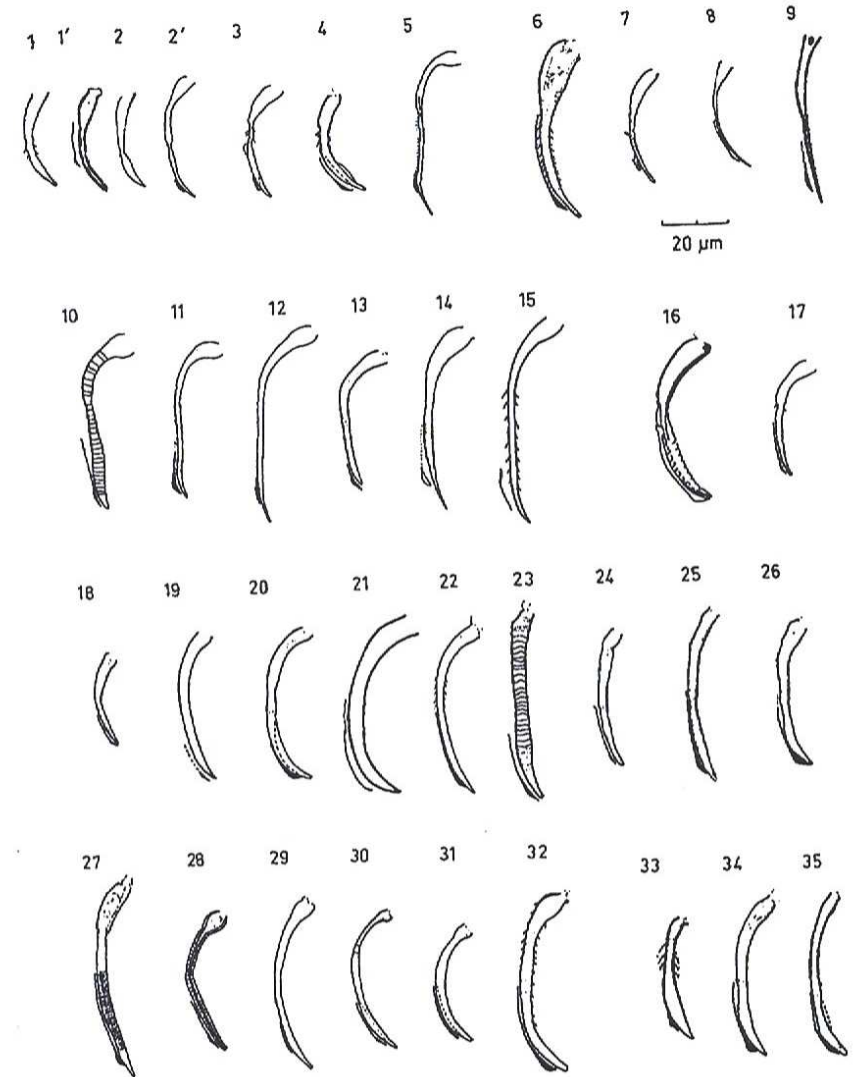


FIG. 5. Spicule shape in *Trichodorus* species (adapted from Decraemer, 1988a): (1) *T. beirensis*; (1') *T. lusitanicus*; (2) *T. azorensis*; (2') *T. orientalis*; (3) *T. viruliferus*; (4) *T. velatus*; (5) *T. sanniae*; (6) *T. dilatatus*; (7) *T. aquitanensis*; (8) *T. primitivus*; (9) *T. hooperi*; (10) *T. pakistanensis*; (11) *T. rinae*; (12) *T. petrusalberti*; (13) *T. eburneus*; (14) *T. persicus*; (15) *T. sparsus*; (16) *T. yokooi*; (17) *T. tricaulatus*; (18) *T. borai*; (19) *T. aequalis*; (20) *T. proximus*; (21) *T. obtusus*; (22) *T. sparsus*; (23) *T. elegans*; (24) *T. cedarus*; (25) *T. borneoensis*; (26) *T. intermedius*; (27) *T. taylori*; (28) *T. complexus*; (29) *T. coomansi*; (30) *T. variopapillatus*; (31) *T. similis*; (32) *T. californicus*; (33) *T. cylindricus*; (34) *T. cottieri*; (35) *T. obscurus* (1, 2 after Almeida *et al.*, 1989).

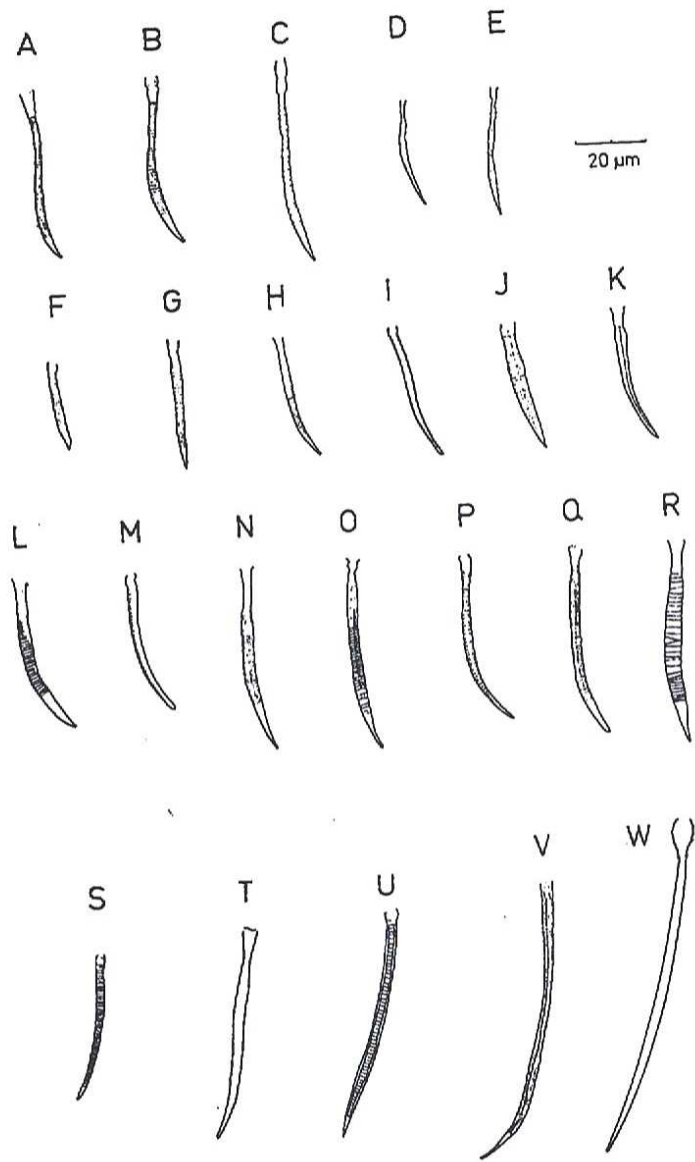


FIG. 6. Spicule shape in *Paratrichodorus* species (after Decraemer, 1988a): (A,B) *P. anemones*; (C) *P. hispanus*; (D,E) *P. weischeri*; (F) *P. allius*; (G,H) *P. porosus*; (I) *P. mirzai*; (J,K) *P. grandis*; (L) *P. pachydermus*; (M) *P. rhodesiensis*; (N) *P. teres*; (O) *P. sacchari*; (P) *P. tunisiensis*; (Q) *P. lobatus*; (R) *P. catharinae*; (S) *P. nanus*; (T) *P. alleni*; (U) *P. acaudatus*; (V) *P. minor*; (W) *P. atlanticus*.

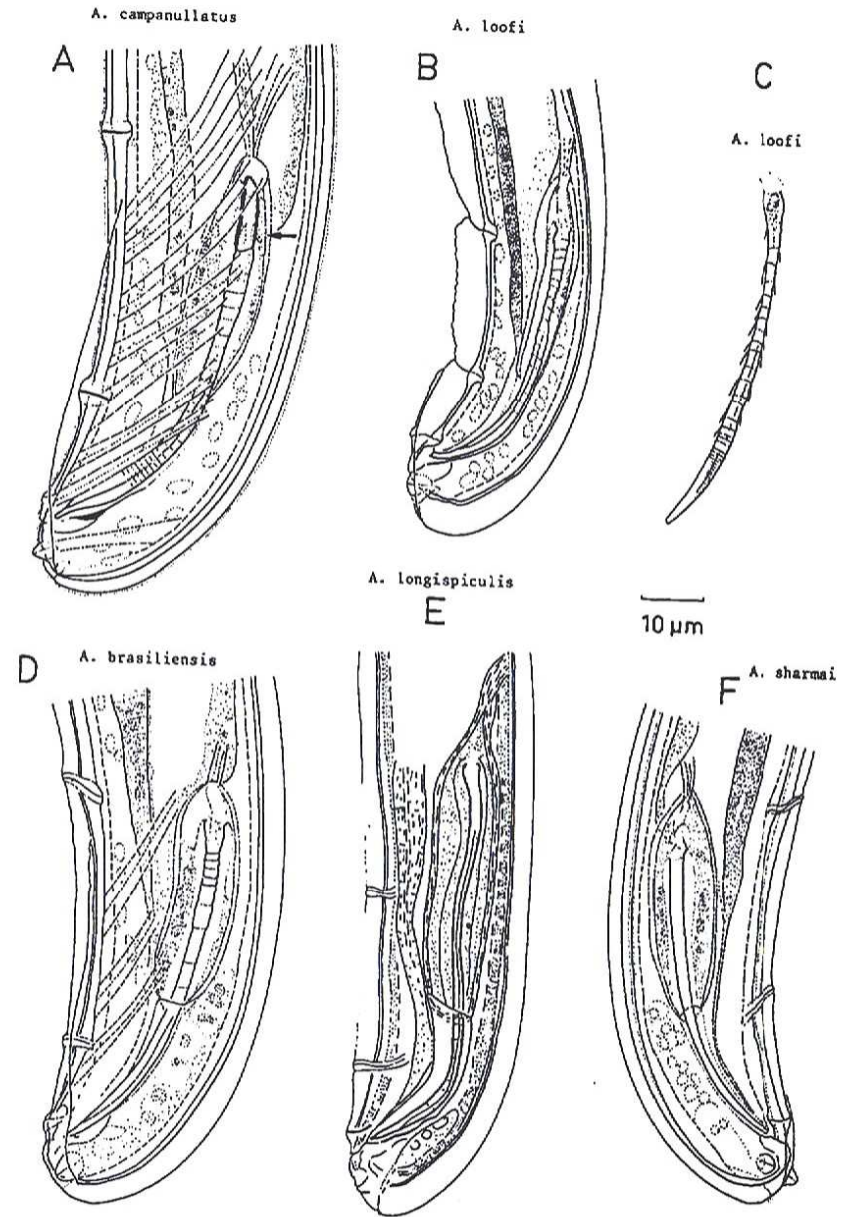


FIG. 7. Copulatory apparatus in *Allotrichodorus* species: (A) *A. campanullatus*; (B,C) *A. loofi*, paratypes; (D) *A. brasiliensis*, paratype; (E) *A. longispiculis* (after Rashid *et al.*, 1986); (F) *A. sharmai*, paratype.

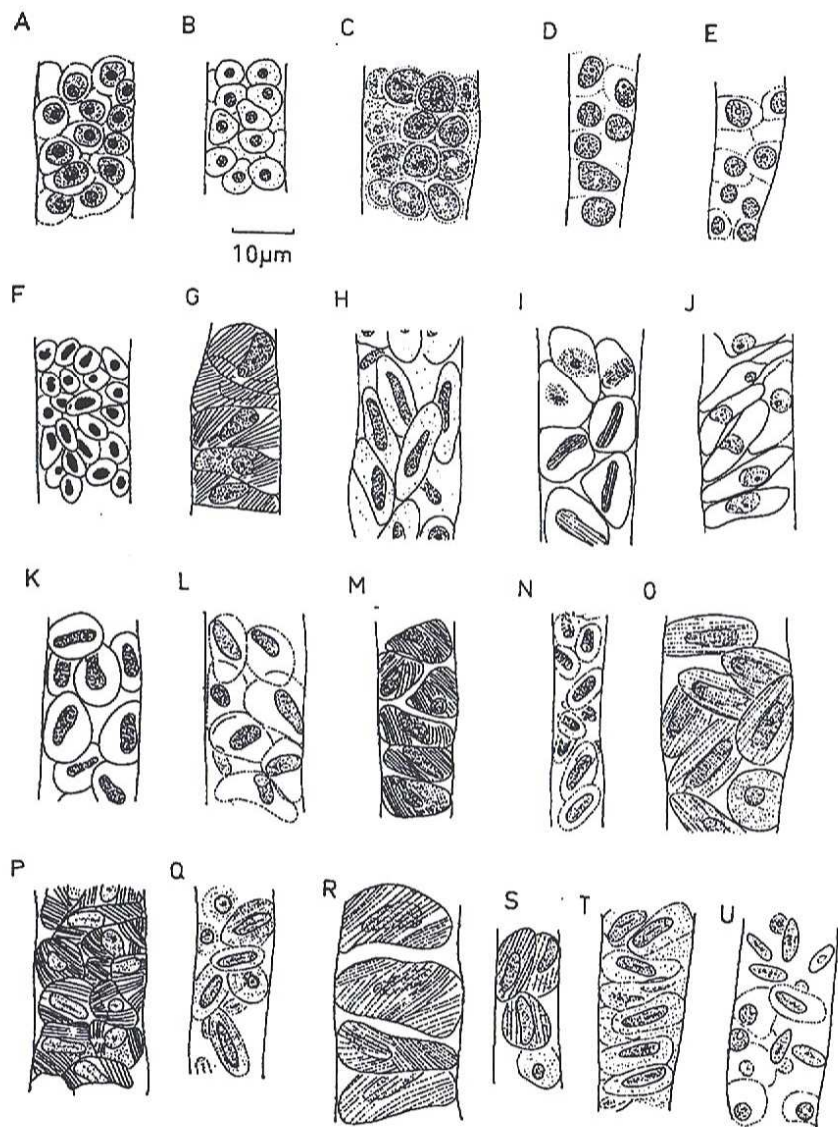


FIG. 8. Structure of sperm cells in *Trichodorus* species (adapted from Decraemer, 1988b): (A) *T. californicus*; (B) *T. dilatatus*; (C) *T. elegans*; (D) *T. intermedius*; (E) *T. lusitanicus*; (F) *T. proximus*; (G) *T. borneoensis*; (H) *T. coomansi*; (I) *T. cottieri*; (J) *T. cylindricus*; (K) *T. eburneus*; (L) *T. orientalis*; (M) *T. primitivus*; (N) *T. similis*; (O) *T. taylora*; (P) *T. cedarus*; (Q) *T. tricaulatus*; (R) *T. variopapillatus*; (S) *T. velatus*; (T) *T. viruliferus*; (U) *T. pakistanensis*.

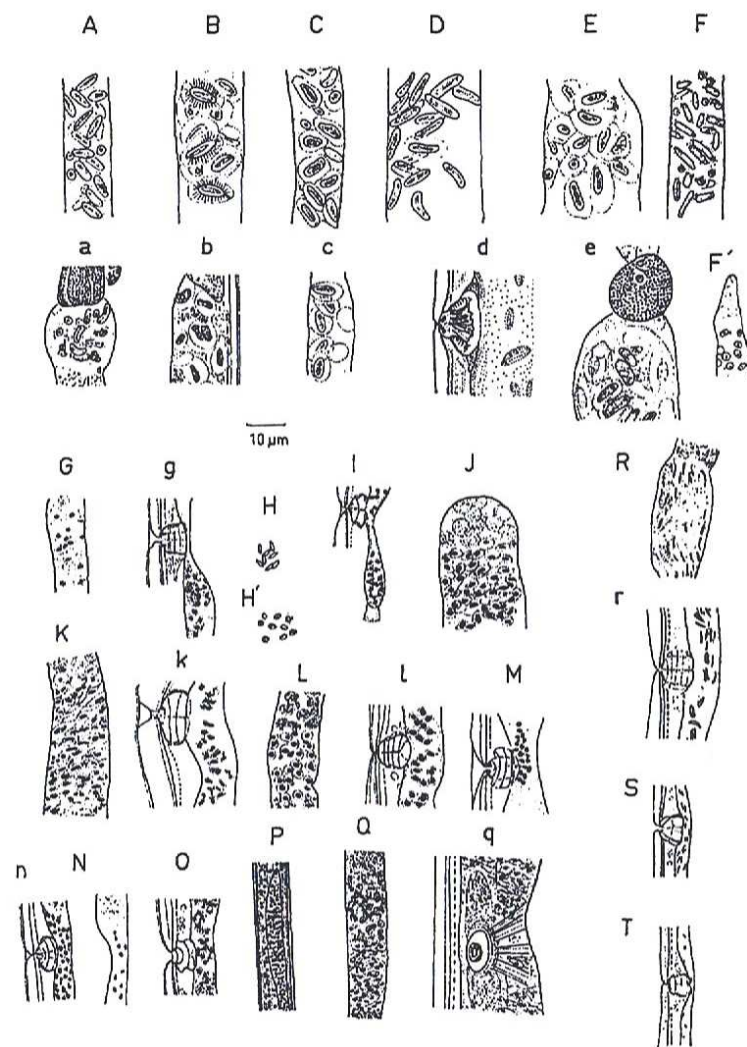


FIG. 9. Structure of sperm cells in *Paratrichodorus* species (adapted from Decraemer, 1989): (A,a) *P. anemones*, ♂, ♀; (B,b) *P. weischeri*, ♂, ♀; (C,c) *P. pachydermus*, ♂, ♀; (D,d) *P. grandis*, ♂, ♀; (E,e) *P. hispanus*, ♂, ♀; (F) *P. porosus*, ♂; (F') *P. mirzai*, ♂; (G,g) *P. allius*, ♂, ♀; (H) *P. alleni*, ♂; (H') *P. acaudatus*, ♂; (I) *P. anthurii*, ♀; (J) *P. catharinae*, ♂; (K,k) *P. lobatus*, ♂, ♀; (L,l) *P. minor*, ♂, ♀; (M) *P. nanus*, ♂; (N,n) *P. rhodesiensis*, ♂, ♀; (O) *P. tansaniensis* (= *P. allius*), ♀; (P) *P. tunisiensis*, ♂; (Q,q) *P. teres*, ♂, ♀; (R,r) *P. minor*, ♂, ♀; (S) *P. acutus*, ♀; (T) *P. renifer*, ♀.

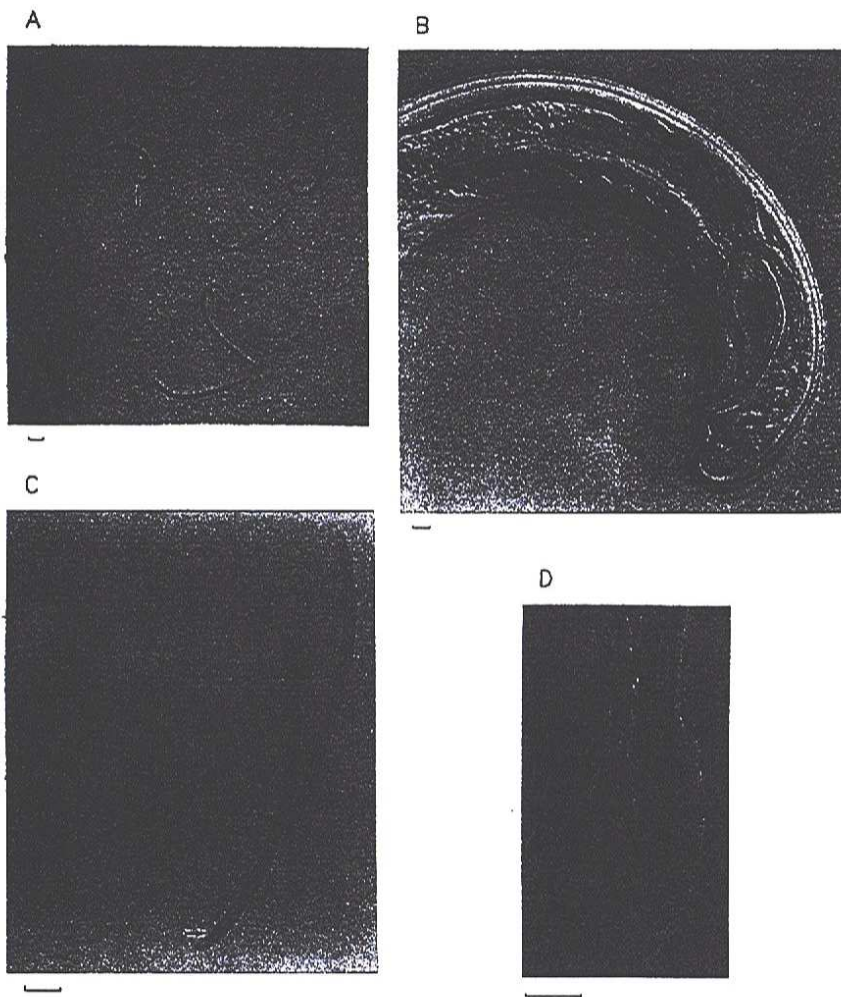


FIG. 10. (A,B) *Trichodorus variopapillatus*, habitus, 6 ♂♂ 1 ♀ (scale 100 μm); male tail and copulatory apparatus with indication of copulatory muscles (scale 10 μm); (C) habitus of *Paratrichodorus anemones* 2 ♂♂, 1 ♀ (arrow pointed to ♂, scale 100 μm); (D) *P. teres*, posterior body region of a male with indication of the bursa (scale 10 μm).

vulva shape in ventral view (a transverse slit-shape), whereas the other genera have 2 or 3 different types of vulva shape in ventral view (a pore, a transverse slit or a longitudinal slit).

9. *Number of ventromedian cervical papillae (CP)*. In *Trichodorus* species the number varies between 0 and 4, the majority of the species with 2CP and an about equal distribution among the species of 1CP and 3CP (CP absent in *T. obscurus*). The majority of the *Paratrichodorus* species have 1CP, *Monotrichodorus* species have 1CP and *Allotrichodorus* species have either 1 or 0 CP. The number of ventromedian cervical papillae is of restricted taxonomic importance on genus level, differentiating only the genus *Trichodorus* from the other genera when more than 1CP is present (except *P. mirzai* with 2CP).

Table II gives a review of the features differentiating *Trichodorus* and *Paratrichodorus*, the two trichodorid genera which occur in Europe.

TABLE II
DIFFERENTIATING CHARACTERS BETWEEN *Trichodorus*
AND *Paratrichodorus*.

<i>Trichodorus</i>	<i>Paratrichodorus</i>
IN BOTH SEXES	
Body cuticle non-swollen upon fixation	Body cuticle swollen upon fixation
Sperm cells large to medium sized	Sperm cells large to minute
Sperm nucleus globular or sausage-shaped	Sperm nucleus globular, sausage, small oval or thread-shaped
Generally with offset pharyngeal bulb	Usually with ventral pharyngeal overlap or dorsal intestinal overlap
IN FEMALE	
Vagina usually the corresponding body width long	Vagina shorter than half the corresponding body width
Vaginal sclerotization usually well developed (large to small)	Vaginal sclerotization little developed (small to minute)

(continued)

TABLE II (continued)

Spermathecae present (1 exception)	Spermathecae present or absent
Lateral advulvar body pores present (2 exc.)	Lateral advulvar body pores rare
IN MALE	
Caudal alae absent (1 exc.)	Caudal alae present
Copulatory muscles well developed	Copulatory muscles little developed
Capsule of spicular suspensor muscles well developed	Capsule of spicular suspensor muscles weakly developed
Spicules usually curved, diverse shape and with ornamentation diverse	Spicules usually straight, similar shape, shaft striated
1-3 ventromedian cervical papillae (0 or 4 exc.)	0 or 1 ventromedian cervical papillae (rarely 2CP)
Posterior body region curved ventrad	Posterior body region usually straight

C. Key to the Genera of the Trichodoridae

FEMALES

1. Genital system monodelphic2
 Genital system didelphic3
2. 1 pair of lateral advulvar body pores, cuticle non-swollen
 *Monotrichodoros*
 (Fig. 1F)
- No lateral advulvar body pores, cuticle non-swollen to strongly
 swollen *Allotrichodoros*
 (Fig. 1K)
3. Body cuticle non-swollen, vagina up to half a body width long,
 vaginal sclerotizations in lateral view well developed, small
 to large *Trichodoros*
 (Fig. 1C)
- Body cuticle swollen, vagina clearly less than half a body width
 long, vaginal sclerotizations very small *Paratrichodoros*
 (Fig. 1I)

MALES

1. Bursa present, body cuticle usually well swollen, copulatory
 muscles restricted to spicule region2

- Bursa absent (few exceptions), cuticle non-swollen, copulatory
 muscles extending shortly to far beyond region of retracted
 spicules3
2. Body cuticle strongly swollen, spicules mainly straight,
 copulatory muscles and capsule spicular suspensor muscles
 poorly developed, sperm small to large; pharynx mostly
 with ventral overlap of its glands or dorsal intestinal
 overlap *Paratrichodoros*
 (Fig. 1G,H)
- Swelling of body cuticle variable, spicules long slender, with
 or without capitular extension, copulatory muscles and capsule
 spicular suspensor muscles moderately developed, sperm
 large; pharynx mostly offset *Allotrichodoros*
 (Fig. 1J)
3. Spicules mostly curved, rarely elongated, diverse in shape;
 copulatory muscles extending far anteriorly beyond spicule
 region; 1-3 (0, 4 exc.) ventromedian cervical papillae
 (CP); usually 1 precloacal supplement (SP) in spicule region
 *Trichodoros*
 (Fig. 1A,B)
- Spicules slender, curved; copulatory muscles extending to just
 anterior to the retracted spicules; 1 CP; usually 2 SP in spicule
 region *Monotrichodoros*
 (Fig. 1D,E)

III. DISCUSSION OF DIFFERENTIAL CHARACTERS AT THE SPECIES LEVEL (DECRAEMER, 1988a,b, 1989)

For species diagnoses (=differential diagnoses/relationships: different headings indicating the characterisation of a new species) up to 48 characters were used for *Paratrichodoros* species, 42 characters for *Trichodoros* species, 21 characters for *Monotrichodoros* species and 10 characters for *Allotrichodoros* species. Half of the most important diagnostic characters (i.e. characters appearing in 20% or more species per genus) are shared by both *Trichodoros* and *Paratrichodoros*, several with a varying degree of taxonomic value. A quarter of these characters are also shared with the monodelphic genera (Table III).

TABLE III

LIST OF DIAGNOSTIC FEATURES USED IN AT LEAST 20% OF THE SPECIES OF THE GENERA OF THE TRICHODORIDAE WITH PERCENTAGE OF THEIR OCCURRENCE PER GENUS (ADAPTED FROM DECRAEMER, 1988a).

CHARACTERS SHARED BY *TRICHODORUS* AND *PARATRICHODORUS* (RESPECTIVELY *MONOTRICHODORUS* AND *ALLOTRICHODORUS*)

Body length: 29.5% / 39.5% (57% / 0%)
 Onchiostyle length: 50.5% / 65% (57% / 57%)
 Position of excretory pore: 25% / 29% (14% / 0%)
 Shape of vaginal sclerotizations: 71.5% / 47% (14% / 85.7%)
 Spicules
 length: 33.5% / 47% (42% / 57%)
 shape: 73.5% / 32.5% (14% / 57%)
 ornamentation: 21% / 18% (0% / 0%)
 Preclonal supplements
 number: 33.5% / 43% (0% / 0%)
 position: 73.5% / 47% (57% / 0%)
 Ventromedian cervical papillae
 number: 73.5% / 32.5% (14% / 85.7%)
 position: 46% / 11% (57% / 14%)

TRICHODORUS

Shape of vagina: 25%
 Number and position of lateral body pores in female: 61%
 Position of preclonal papillae in relation to spicules: 61%
 Ventromedian cervical papillae
 position in relation to onchiostyle: 25%
 position in relation to the excretory pore: 46%

PARATRICHODORUS

Ventral overlap pharyngeal glands: 43%
 Shape vulva in ventral view: 43%
 Number of postclonal papillae: 21.5%

MONOTRICHODORUS

Ratio V: 57%
 Shape of vulva in ventral view: 57%
 Length of postvulvar uterine sac: 42%
 Position of lateral cervical pores in female: 28%
 Position of preclonal papillae in relation to spicules: 57%
 Swelling of the body cuticle: 42%

ALLOTRICHODORUS

Number of ovaries: 28.5%
 Presence of capitular extension of spicules: 57%

A. Primary Diagnostic Features

The most important diagnostic features at species level are for all genera:

in female: the shape of the vaginal sclerotizations;
 in male: the shape of the spicules.

REMARKS

1. *Shape of the vaginal sclerotizations.* This feature is the most commonly used criterion for distinguishing females of *Trichodorus* and *Allotrichodorus*, and the second most important diagnostic feature in *Paratrachodorus* species. In *Trichodorus* (Fig. 2) the vaginal sclerotizations are usually well developed and about 11 groups of similar vaginal sclerotizations could be distinguished taking the following features into account: size, shape (round, rectangular, triangular, quadrangular, oval), orientation (oblique, parallel to longitudinal body axis or to vaginal lumen), dimension of the inner diameter of the sclerotized ring (small aperture: pieces close to one another; aperture about 2 μ m: pieces well separated) (Decraemer, 1988b). *Paratrachodorus* (Fig. 3) shows less differentiation in the shape and dimension of the vaginal sclerotizations than the other genera. About six groups of comparable vaginal sclerotizations were distinguished, mainly based upon shape (bold dots, narrow triangular, oval-shaped, reniform, broad rounded triangular or small quadrangular pieces) (Decraemer, 1989). In the monodelphic genera, vaginal sclerotizations also differ interspecifically by size and shape (Fig. 4). Some minor intraspecific variability has to be taken into account (e.g. in *Trichodorus* and *Allotrichodorus*).
2. *Spicule shape.* This feature is an important diagnostic character for species differentiation in *Trichodorus* and *Allotrichodorus*. In *Trichodorus* (Fig. 5) about seven groups of similar spicule shape can be recognized: spicules with constriction at mid-point; spicules proximally clearly curved ventrally, mid-shaft straight; spicules with a wide proximal part, tapering to a fine very slender distal portion; spicules with the capitulum clearly offset from the shaft; spicules with an enlarged posterior portion; spicules with a long wide anterior end; spicules about equally wide, slightly

tapering posteriorly (Decraemer, 1988b). In *Allotrichodoros* (Fig. 7) this character can be used to separate the species into two groups: species with males possessing spicules with a capitular extension (Fig. 7 A, arrow) and those without this feature. In both other genera, this feature is less important taxonomically since *Paratrichodoros* species (Fig. 6) have mainly straight spicules and show less differentiation in shape and *Monotrichodoros* species have spicules with more or less the same shape.

B. Secondary Important Taxonomic Features

The secondary important taxonomic characters (i.e. features with some variability to be taken into account) at species level are: length of onchiostyle, spicule length, position of precloacal supplements and number of ventromedian cervical papillae in males (of restricted use in *Paratrichodoros*).

REMARKS

1. *Onchiostyle length*. In *Trichodoros* and *Paratrichodoros*, this character appears relatively constant in populations of a single species (Decraemer, 1988b, 1989). The differences for the mean value of the onchiostyle length within a single *Trichodoros* species is maximally 21.5 μm and 13 μm for *Paratrichodoros* species. The range of the mean value of onchiostyle length within the genus *Trichodoros* is from 40 to 147.5 μm and from 22 to 82.5 μm for *Paratrichodoros*. In *Trichodoros*, however, long-speared and short-speared populations are known to occur in the same species e.g. in *T. sparsus*: onchiostyle length = 48-60 μm but 58-73 μm in two German populations (Loof, 1973) and *T. primitivus*: 40-50 (46) μm in Dutch specimens and 49-55 (52) μm in English specimens (Hooper, 1962). In *Allotrichodoros*, differences were observed between different populations (e.g. in *A. campanullatus*). Within a single species, the maximum difference for the mean onchiostyle length was 17.2 μm (*A. campanullatus*, females) and 12.0 μm (*A. campanullatus*, males). These values are less than for *Trichodoros* species. The range of the mean onchiostyle

length for the genus is from 32 μm (*A. westindicus*, females) to 70 μm (*A. guttatus*, males). *Monotrichodoros* species, except *M. monohystera*, are only known by their type population. The mean onchiostyle length within this genus varies from 44 μm (males) (*M. acuparvus*)/48.5 μm (females) (*M. monohystera*) to 58.5 μm (males)/59 μm (females) (*M. proporifer*).

2. *Spicule length*. In both didelphic genera, the spicule length shows little intraspecific variability: maximally 13 μm for *Trichodoros* and 25 μm for *Paratrichodoros*. In *Monotrichodoros*, the mean values of the spicule length vary between 42 μm (*M. acuparvus*) and 55 μm (*M. monohystera*). In *Allotrichodoros*, the range of the mean spicule length within the genus is from 49 μm (*A. campanullatus*) to 70 μm (*A. guttatus*). Within a single species, the difference of the mean spicule length is maximally 12 μm (*A. campanullatus*); these values are lower than for the didelphic genera.
3. *Position of precloacal supplementary papillae (SP)*. The position of SP is given in relation to the caudal alae (*Paratrichodoros*), or the region of the retracted spicules (all genera) and also by the absolute distance from the cloacal opening in μm , % of spicule length (monodelphic genera). In *Trichodoros*, four groups can be recognized: a) species with one precloacal supplement clearly within spicule range, b) species with the posteriormost supplement near the proximal end of the spicules (taking some variability into account from just anterior to just posterior to the spicule head), c) species with two supplements within spicule range and d) species without precloacal supplements in spicule range. *Paratrichodoros* species can be grouped in: a) species having the two posteriormost supplements opposite the distal half of the retracted spicules and b) species with the posterior two supplements more dispersed. As occurs in both didelphic genera, the position of the precloacal supplements in relation to the spicules shows some variability in *Allotrichodoros*, especially the position of SP3.
4. *Number of ventromedian cervical papillae (CP)*. This feature is of restricted importance in *Monotrichodoros* species (all with 1 CP in males) and in *Paratrichodoros*, the majority of the species also have 1 CP (only in *P. meyeri*, *P. weischeri*

and *P. rhodesiensis* has intraspecific variability been observed). In *Trichodorus* and in *Allotrichodorus*, the number of ventromedian cervical papillae is of higher taxonomic value. In *Trichodorus*, the number of CP varies between zero and four (intraspecific variability rare) and in *Allotrichodorus* this feature separates the species into two groups: species with 1 CP and species without CP, no intraspecific variability has been observed.

C. Additional Diagnostic Features for Species within the Respective Trichodorid Genera

In *Paratrichodorus*, structure of sperm cells, presence of spermathecae, shape of vulva in ventral view are all taxonomically helpful features. Tail shape, number of precloacal and postcloacal papillae and presence of male specimens are of minor and restricted diagnostic importance.

In *Trichodorus*, spicule ornamentation and shape of vagina together with the arrangement of the vaginal constrictor muscles are of additional help in species identification. Of minor importance are the number and position of lateral body pores in females, shape and position of gubernaculum and position of ventromedian cervical papillae in relation to the onchiostyle.

In *Monotrichodorus*, presence of lateral cervical pores in females, number of precloacal supplements in relation to the retracted spicules, shape of vulva in ventral view and presence of minute caudal alae are all of restricted taxonomic value (e.g. characterizing a single species).

In *Allotrichodorus*, tail shape, body length and presence of caudal pores are of restricted taxonomic value (i.e. differentiating one or a few species from the other species).

IV. COMPOSITION OF THE SUPERFAMILY TRICHODOROIDEA (THORNE, 1935) SIDDIQI, 1974

Family Trichodoridae (Thorne, 1935) Clark, 1961
Genus *Trichodorus* Cobb, 1913

Genus *Paratrichodorus* Siddiqi, 1974
syn. *Atlantadorus* Siddiqi, 1974
syn. *Nanidorus* Siddiqi, 1974
Genus *Monotrichodorus* Andrassy, 1976
Genus *Allotrichodorus* Rodriguez-M., Sher & Siddiqi, 1978

A. List of *Trichodorus* Species

T. aequalis Allen, 1957
T. aquitanensis Baujard, 1980
T. azorensis Almeida, De Waele, Santos & Sturhan, 1989
T. beirensis Almeida, De Waele, Santos & Sturhan, 1989
T. borai Rahman, Jairajpuri & Ahmad, 1985
T. borneoensis Hooper, 1962
T. californicus Allen, 1957
T. carlingi Bernard, 1992
T. cedarus Yokoo, 1964: syn. *T. kurumeensis* Yokoo, 1966; syn. *T. longistylus* Yokoo, 1964
T. complexus Rahman, Jairajpuri & Ahmad, 1985
T. coomansi De Waele & Carbonell, 1983
T. cottieri Clark, 1963
T. cylindricus Hooper, 1962
T. dilatatus Rodriguez-M. & Bell, 1978
T. eburneus De Waele & Carbonell, 1983
T. elefjohnsoni Bernard, 1992
T. elegans Allen, 1957
T. giennensis Decraemer, Roca, Castillo, Pena-Santiago & Gomez-Barcina, 1993
T. hooperi Loof, 1973
T. intermedius Rodriguez-M. & Bell, 1978
T. kilianae Decraemer & Marais, 1993
T. lusitanicus Siddiqi, 1974
T. magnus Decraemer & Marais, 1993
T. minzi De Waele & Cohn, 1992
T. nanjingensis Liu & Cheng, 1990
T. obscurus Allen, 1957: syn. *T. primitivus* apud Thorne, 1939 & Goodey, 1951
T. obtusus Cobb, 1913
T. orientalis De Waele & Hashim, 1984

- T. pakistanensis* Siddiqi, 1962: syn. *T. litchi* Edward & Misra, 1970
- T. parorientalis* Decraemer & Kilian, 1992
- T. paucisetosus* Bernard, 1992
- T. persicus* De Waele & Sturhan, 1987
- T. petrusalberti* De Waele, 1988
- T. philipi* De Waele, Meyer & Van Mieghem, 1990
- T. primitivus* (de Man, 1880) Micoletzky, 1922: syn. of *Dorylaimus primitivus* de Man, 1880; syn. *T. castellanensis* Arias Delgado, Jimenez Millan & Lopez Pedregal, 1965; syn. *T. mirabilis* Ivanova, 1977
- T. proximus* Allen, 1957
- T. rinae* Vermeulen & Heyns, 1984
- T. sanniae* Vermeulen & Heyns, 1984
- T. similis* Seinhorst, 1963
- T. sparsus* Szczygiel, 1968
- T. taylori* De Waele, Mancini, Roca & Lamberti, 1982
- T. tricaulatus* Shishida, 1979
- T. vandenbergae* De Waele & Kilian, 1992
- T. variopapillatus* Hooper, 1972
- T. velatus* Hooper, 1972
- T. viruliferus* Hooper, 1963
- T. yokooi* Eroshenko & Teplyakov, 1975

B. List of *Paratrichodorus* Species

- P. acaudatus* (Siddiqi, 1960) Siddiqi, 1974; syn. *T. acaudatus* Siddiqi, 1960
- P. acutus* (Bird, 1967) Siddiqi, 1974; syn. *T. acutus* Bird, 1967
- P. alleni* (Andrassy, 1968) Siddiqi, 1974; syn. *T. alleni* Andrassy, 1968
- P. allius* (Jensen, 1963) Siddiqi, 1974; syn. *T. allius* Jensen, 1963; syn. *P. tansaniensis* Siddiqi, 1974
- P. anemones* (Loof, 1965) Siddiqi, 1974; syn. *T. anemones* Loof, 1965
- P. anthurii* Baujard & Germani, 1985
- P. atlanticus* (Allen, 1957) Siddiqi, 1974; syn. *T. atlanticus* Allen, 1957
- P. catharinae* Vermeulen & Heyns, 1983
- P. grandis* Rodriguez-M. & Bell, 1978

- P. hispanus* Roca & Arias, 1986
- P. lobatus* (Colbran, 1965) Siddiqi, 1974; syn. *T. lobatus* Colbran, 1965; syn. *T. clarki* Yeates, 1967
- P. macrostylus* Popovici, 1989
- P. meyeri* De Waele & Kilian, 1992
- P. minor* (Colbran, 1956) Siddiqi, 1974; syn. *T. minor* Colbran, 1956; syn. *P. christiei* (Allen, 1957) Siddiqi, 1974; syn. *P. obesus* (Rasjivin & Penton, 1975)
- P. mirzai* (Siddiqi, 1960) Siddiqi, 1974; syn. *T. mirzai* Siddiqi, 1960; syn. *T. musambi* Edward & Misra, 1970
- P. nanus* (Allen, 1957) Siddiqi, 1974; syn. *T. nanus* Allen, 1957
- P. orrae* Decraemer & Reay, 1991
- P. pachydermus* (Seinhorst, 1954) Siddiqi, 1974; syn. *T. pachydermus* Seinhorst, 1954
- P. paramirzai* Siddiqi, 1991
- P. paraporosus* Khan, Jairajpuri & Ahmad, 1989
- P. porosus* (Allen, 1957) Siddiqi, 1974; syn. *T. porosus* Allen, 1957; syn. *T. bucrius* Lordello & Zamith, 1958
- P. queenslandensis* Decraemer & Reay, 1991
- P. renifer* Siddiqi, 1974
- P. rhodesiensis* (Siddiqi & Brown, 1965) Siddiqi, 1974; syn. *T. rhodesiensis* Siddiqi & Brown, 1965
- P. sacchari* Vermeulen & Heyns, 1983
- P. teres* (Hooper, 1962) Siddiqi, 1974; syn. *T. teres* Hooper, 1962; syn. *T. flevensis* Kuiper & Loof, 1962
- P. tunisiensis* (Siddiqi, 1963) Siddiqi, 1974; syn. *T. tunisiensis* Siddiqi, 1963
- P. weischeri* Sturhan, 1985

C. List of *Monotrichodorus* Species

- M. acuparvus* Siddiqi, 1991
- M. muliebris* Andrassy, 1989
- M. monohystera* (Allen, 1957) Andrassy, 1976; syn. *T. monohystera* Allen, 1957.
- M. parvus* Siddiqi, 1991
- M. proporifer* Siddiqi, 1991
- M. sacchari* Baujard & Germani, 1985
- M. vangundyi* Rodriguez-M., Sher & Siddiqi, 1978.

D. List of *Allotrichodoros* Species

- A. brasiliensis* Rashid, De Waele & Coomans, 1986
- A. campanullatus* Rodriguez-M., Sher & Siddiqi, 1978
- A. guttatus* Rodriguez-M., Sher & Siddiqi, 1978
- A. longispiculis* Rashid, De Waele & Coomans, 1986
- A. loofi* Rashid, De Waele & Coomans, 1986
- A. sharmae* Rashid, De Waele & Coomans, 1986
- A. westindicus* (Rodriguez-M., Sher & Siddiqi, 1978) Rashid, De Waele & Coomans, 1986; syn. *P. westindicus* Rodriguez-M., Sher & Siddiqi, 1978.

E. List of Trichodorid Species Recorded for Europe

- Trichodoros aquitanensis*
- T. azorensis*
- T. beirensis*
- T. cylindricus*
- T. giennensis*
- T. hooperi*
- T. lusitanicus*
- T. primitivus*
- T. similis*
- T. sparsus*
- T. taylori*
- T. variopapillatus*
- T. velatus*
- T. viruliferus*
- Paratrichodoros anemones*
- P. hispanus*
- P. macrostylus*
- P. minor*
- P. nanus*
- P. pachydermus*
- P. porosus*
- P. allius*
- P. teres*
- P. tunisiensis*
- P. weischeri*

Except for *T. hooperi*, *P. macrostylus* and *P. weischeri* all of the trichodorid species listed above have been recorded from Southern Europe (Alpey & Taylor, 1986; Roca & Lamberti, 1984), but some of them as for example *P. teres* are rare. *T. proximus* recorded from France in the European Atlas of Alpey & Taylor (1986) should be *P. pachydermus* (personal communication of Scotto La Massese, 1986).

V. KEY TO THE TRICHODORID SPECIES RECORDED FOR EUROPE

MALES (Scale of figures is 10 μ m)

1. Body cuticle well swollen (1); males abundant or rare; spicules usually straight; bursa present; copulatory muscles restricted to spicule or to bursa region (Fig. 11A,B)..... 2
- Body cuticle usually non-swollen; males abundant; spicules generally curved; bursa absent (exceptionally present); copulatory muscles well developed, extending beyond spicule region (Fig. 11C,D)..... 11

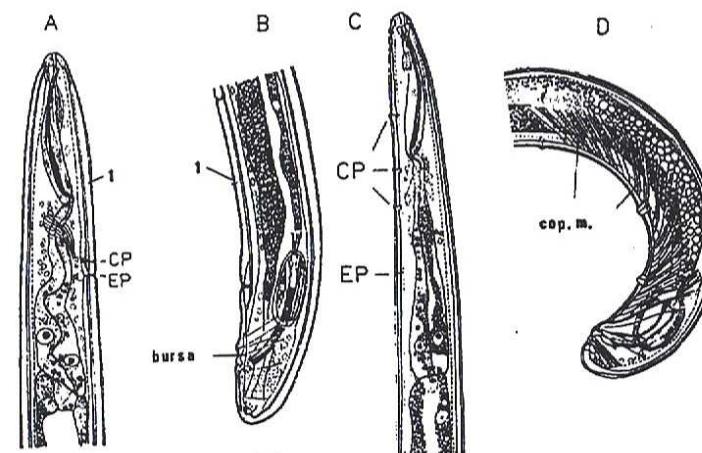


FIG. 11. Males: (A,B) *Paratrichodoros* with indication (1) of the swollen body cuticle; (C,D) *Trichodoros* with non-swollen cuticle and well developed copulatory muscles (cop.m.); CP, ventromedian cervical papillae, EP, excretory pore (from Decraemer, 1991).

2. 1 ventromedian cervical papilla (CP) present (Fig. 12A) 3
 CP absent (Fig. 12B) 8
3. Males with 2 SP; males usually rare; spicules (spic.) = 36-39 μm ;
 onchiostyle (onch.) = 45-48 μm *P. porosus*
 (Fig. 12D)
- Males with 3 SP; males abundant or rare (Fig. 12C) 4

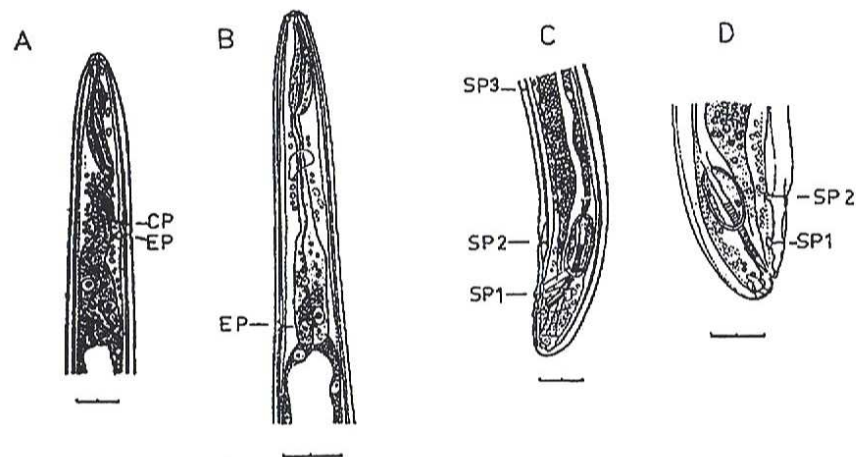


FIG. 12. *Paratrichodorus* males: (A,B) anterior body region with respectively 1 CP and without CP; (C,D) posterior region of a species with 3 precloacal supplements (SP) and one with two SP (A-C and D resp. from Decraemer, 1989 and 1991).

4. Spicule shaft proximally slightly narrower (except for extreme end) slightly less sclerotized and usually kinking (Fig. 13A) 5
- Spicules not narrowing and kinking proximally (Fig. 13B) 6
5. Spic.=34-37 (35) μm ; onch.= 43-48 μm ; recorded only from Germany *P. weischeri*
 (Fig. 6D,E)
- Spic. = 46-53 (49.5) μm ; onch. = 47-52 μm ; widely spread in Europe *P. anemones*
 (Fig. 13A,C)
- Spic. = 53-61.7 (56) μm ; onch. = 54.7-62.3 (59.4) μm ; so far only recorded from Spain *P. hispanus*
 (Fig. 13D)

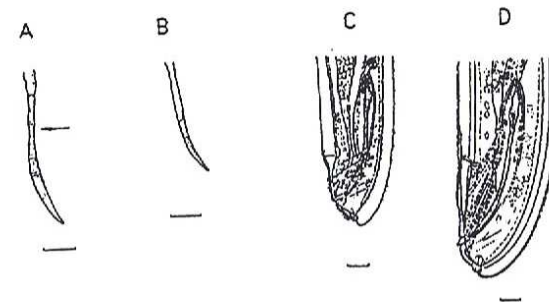


FIG. 13. Spicules: (A) spicule with a narrower, kinked proximal portion of the shaft (arrow); (B) spicule with shaft about equally wide, tapering distally. Tail and copulatory apparatus, (C) *P. anemones*; (D) *P. hispanus* (A,B and C,D resp. from Decraemer, 1988a and 1989).

6. Sperm cells large with large sausage-shaped nucleus (Fig. 14A) 7
- Sperm cells small with small oval nucleus; spic.=48-50 μm slendered; onch.= 48-49 μm ; tail short *P. tunisiensis*
 (Fig. 14B,C)

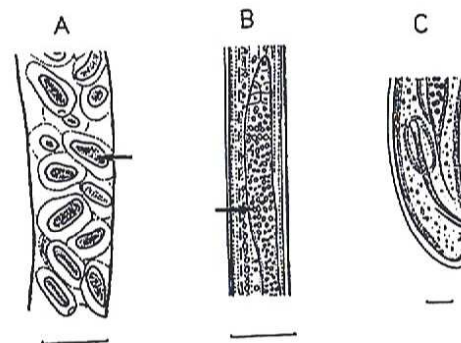


FIG. 14. Testis: (A) with large sperm cells with sausage-shaped nucleus; (B) with small sperm cells with oval nucleus (*P. tunisiensis*); (C) tail and copulatory apparatus (*P. tunisiensis*) (from Decraemer, 1989).

7. Onchiostyle very long (133-180 μm); CP and EP near base onchiostyle; spic.= 67.5-87.6 μm *P. macrostylus*
 (Fig. 15A,B)
- Onchiostyle shorter (45-60 μm); CP and EP more posteriorly; spic.=40-54 μm *P. pachydermus*
 (Figs. 12C; 15C,D)

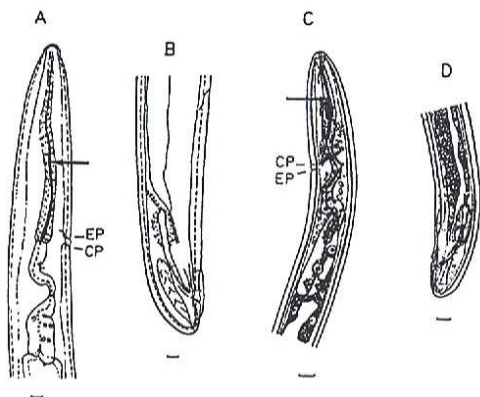


FIG. 15. *P. macrostylus* male: (A) pharyngeal region with very long onchiostyle; (B) posterior body region (A,B from Popovici, 1989); *P. pachydermus* male; (C) pharyngeal region with a rather short onchiostyle; (D) posterior body region (C,D from Decraemer, 1991).

8. Males with 1 SP; adult onchiostyle with small inner spear (Fig. 16A-E) 9
 Males with 2 or 3 SP; onchiostyle without inner spear (Fig. 17A,B) 10
9. Caudal pores lacking; no overlapping of pharyngeal glands (exceptionally minute); onch.=22-26 μm *P. nanus* (Fig. 16A-C)
- Caudal pores present; usually with overlapping of pharyngeal glands; onch.=32-39 μm *P. minor* (Fig. 16D,E)

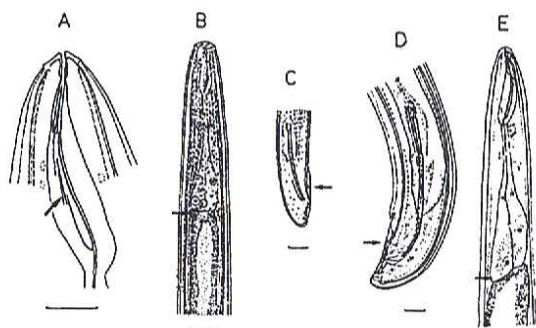


FIG. 16. (A) onchiostyle with indication of small inner spear (*P. minor*); *P. nanus*; (B) pharynx with offset bulb; (C) male tail region with one SP; *P. minor*; (D) posterior body region in male with one SP; (E) pharynx with indication of small overlap of subventral pharyngeal glands (B from Siddiqi, 1974; C,D and E resp. from Decraemer, 1989 and 1991).

10. Males with 3 SP; spic.=40-54 μm ; onch.=46-60 μm *P. teres* (Fig. 17A)
 Males with 2 SP; spic.=30.5 μm ; onch.=42 μm (Fig. 17B)
 *P. allius* syn. *P. tansaniensis*

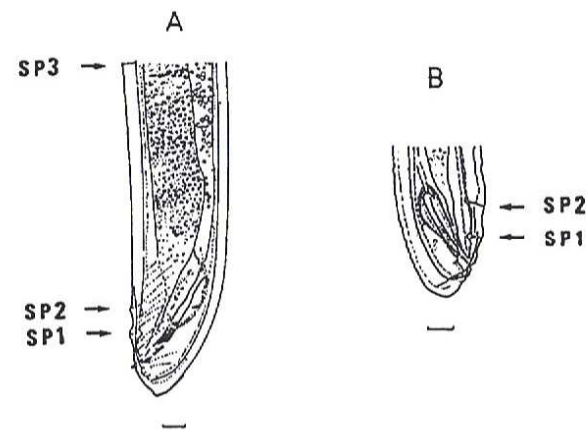


FIG. 17. Posterior body region in male with indication of precloacal supplements (SP1, SP2, SP3): (A) *P. teres*; (B) *P. allius* (A and B resp. from Decraemer, 1991 and 1989).

11. Body cuticle non-swollen but bursa present *T. cylindricus* (Fig. 18A)
 Body cuticle non-swollen, without bursa or at most with a slight ventral thickening in spicule region and tail; posterior body region curved ventrad upon fixation (Fig. 18B) 12

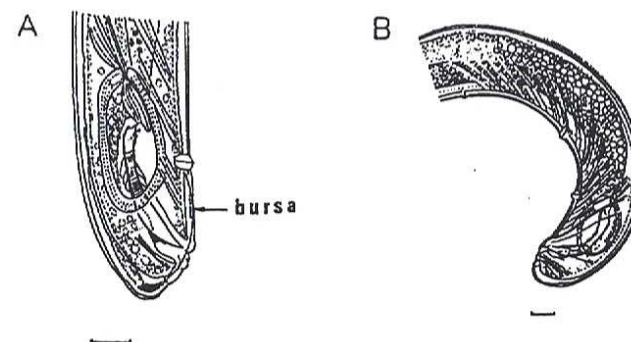


FIG. 18. Posterior body region: (A) *Trichodorus cylindricus*, a *Trichodorus* species with a clear bursa in male (from Decraemer, 1989); (B) *T. velatus* male, without bursa (from Decraemer, 1991).

12. Spicules with a constriction (1) (+wavy cuticle) halfway their length, posteriorly shaft wider again (Fig. 19A,C)..... 13
 Spicules different (Fig. 19B)..... 18
13. Spicules with a ventral flange (2) *T. velatus* (Fig. 19C)
 Spicules without a ventral flange (Fig. 19A) 14

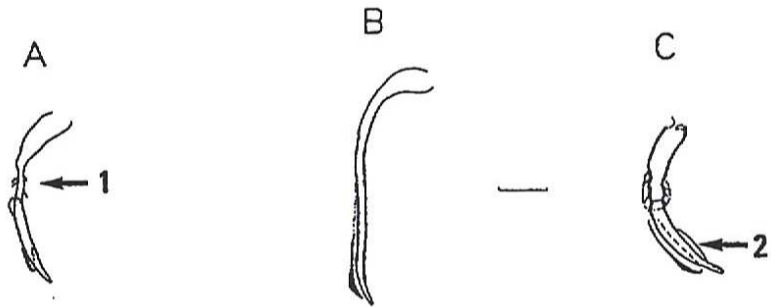


FIG. 19. *Trichodorus*: (A) spicule with a constriction (1) about halfway its length; (B) spicule without narrowing of shaft; (C) spicule with a ventral flange (2) (from Decraemer, 1988b).

14. Spicule shaft very slender (1) in distal half, (mid-shaft constriction may be obscure, bristles not always distinct); gubernaculum partly ventral to spicules *T. primitivus* (Fig. 20A,B)
 Spicules enlarged (2) distally, gubernaculum not ventral to spicules (Fig. 20C) 15

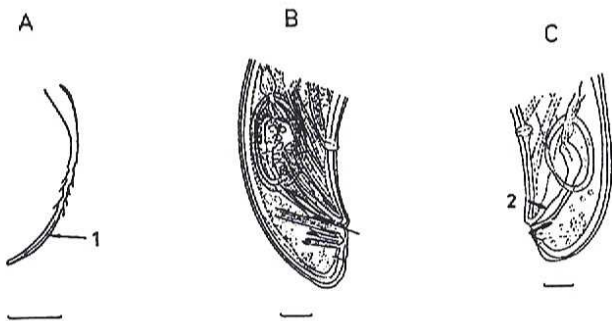


FIG. 20. (A) spicule with a very slender distal portion (arrow) (from Decraemer, 1988a); (B) *T. primitivus*, copulatory apparatus and tail; (C) spicule with enlarged distal part (arrow) (B,C from Decraemer, 1988b).

15. Portion anterior (1) to constriction (2) of spicule longer than distal portion (3) (Fig. 21A) 16
 Portion of spicule anterior to constriction shorter than or as long as distal portion (Fig. 21B)..... 17
16. Spicules with clearly indented shaft and distal end usually grooved; spic.=27-34 μm ; onch.=32-57 μm *T. beirensis* (Fig. 21A)
 Spicules with slightly indented shaft and distal end usually not grooved; spic.=29-34 μm ; onch.=55-66 μm *T. azorensis* (Fig. 21C)
17. Spicules rather stout, with long narrow zone at mid-spicule, usually with marked bristles; spic.=29-41 μm ; onch.=33-59 μm *T. lusitanicus* (Fig. 21B)
 Spicules slenderer with a usually shorter indented zone at mid-spicule, bristles less obvious; spic.= 26-37 μm ; onch.=37-53 μm *T. viruliferus* (Fig. 21D)

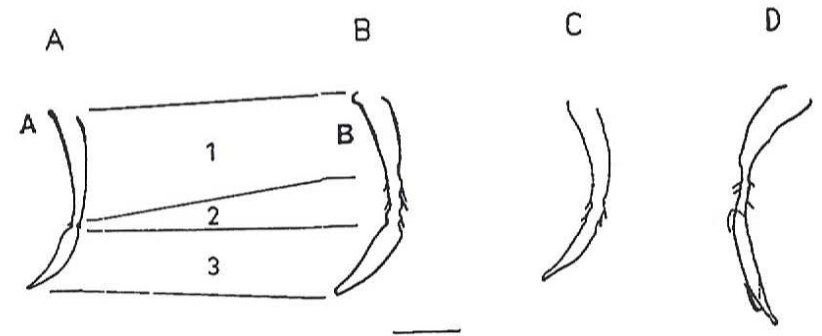


FIG. 21. Spicules: (A) *T. beirensis*; (B) *T. lusitanicus*; (C) *T. azorensis* (A-C, from Almeida *et al.*, 1989); (D) *T. viruliferus* (from Decraemer, 1988a).

18. Spicules with capitulum clearly offset from shaft (1); tail end with cuticle equally wide (Fig. 22A) 19
 Spicules gradually tapering, no offset capitulum; tail end with cuticle thickened or equally wide (Fig. 22B) 21
19. Capitulum of spicule knob-like; SP1 near end spicule (Figs. 22A; 23A,B) 20

Capitulum of spicule broad (about cylindrical) elongated;
 SP1 clearly in spicule range; spic.=57-65 μm onch.=61-
 70 μm *T. taylori*
 (Fig. 22C)

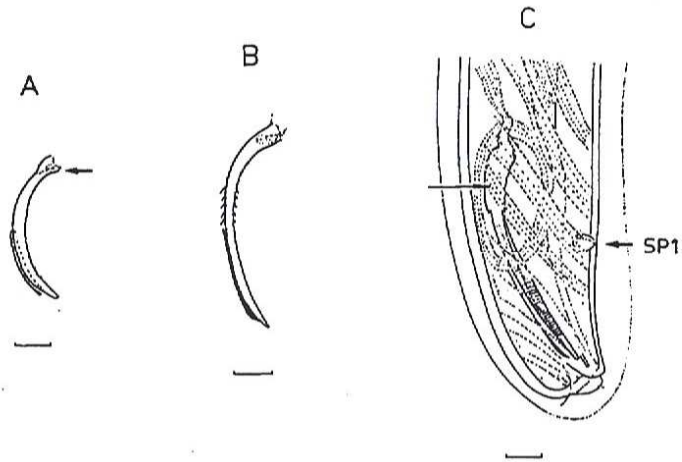


FIG. 22. (A, C) spicules with offset head; (B) spicule without differentiated head (A,B and C resp. from Decraemer, 1988a and 1988b).

20. Spicules slender, shaft narrowing towards capitulum; 2 or
 3 SP; spic.=40-49 μm ; onch.=50-56 μm *T. variopapillatus*
 (Fig. 23A)

Spicules stouter; 3 SP; spic.=33-44 μm ; onchiostyle shorter,
 onch.=38-50 μm *T. similis*
 (Fig. 23B)

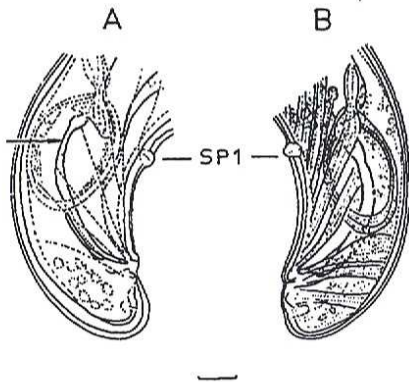


FIG. 23. Male tail and copulatory apparatus: (A) *T. variopapillatus* with indication of narrow manubrium; (B) *T. similis* (from Decraemer, 1988b).

21. Tail end cuticle thickened 22
 Tail end with cuticle equally wide *T. aquitanensis*
 (Fig. 24A)

22. Spicules shaft largely cylindrical, setose (not always distinct,
 indicated by irregular outline), proximally slightly curved;
 3 SP (exc. 2 SP) *T. sparsus*
 (Figs. 22B; 24B)

Spicules fine, tapering posteriorly, apparently not setose,
 almost straight; 3 SP (exc. 4) *T. hooperi*
 (Fig. 24C)

Spicules shaft with slightly larger manubrium posterior to a
 minute indentation at mid-calomus; slightly thickened
 terminal cuticle *T. giennensis*

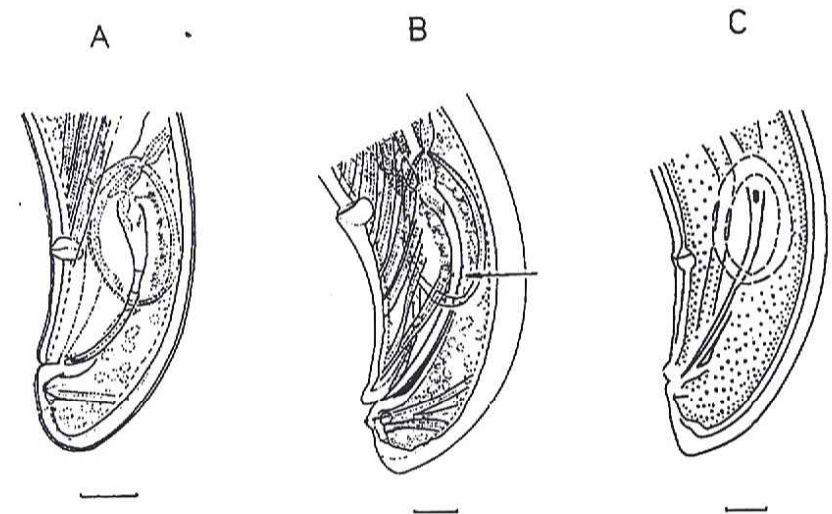


FIG. 24. Male tail and copulatory apparatus: (A) *T. aquitanensis*; (B) *T. sparsus* with indication of bristles (from Decraemer, 1988b); (C) *T. hooperi* (from Loof, 1973).

FEMALES (Scale of figures is 10 μm)

1. Body cuticle well swollen (1); vagina short, less than half a
 body width; vaginal sclerotizations small (Fig. 25A) 2
- Body cuticle non-swollen (2); vagina longer; vaginal
 sclerotizations well developed (Fig. 25B) 11

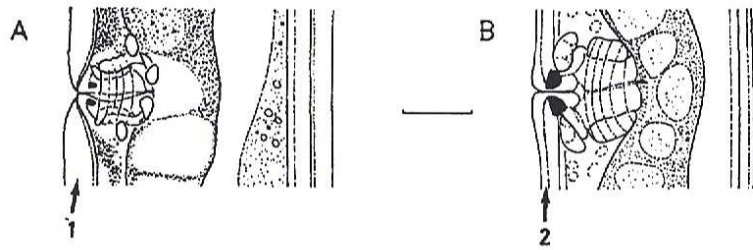


FIG. 25. Vaginal region: (A) *Paratrichodorus* with indication of swollen body cuticle; (B) *Trichodorus* with non-swollen body cuticle.

- 2. Sperm cells large with sausage-shaped nucleus (1) (Fig. 26A) 3
- Sperm cells minute (2) (Fig. 26B) 7

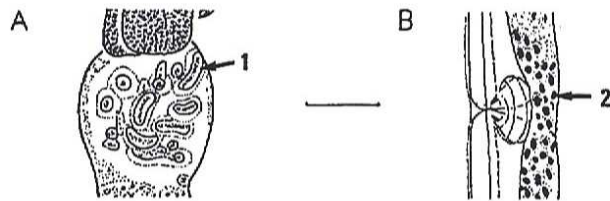


FIG. 26. Sperm cells: (A) with large sausage-shaped nucleus; (B) small sperm cells (from Decraemer, 1988a).

- 3. Body pores medioventral (advulvar) (1)(Fig. 27A) *P. porosus*
- No medioventral body pores (Fig. 27B) 4

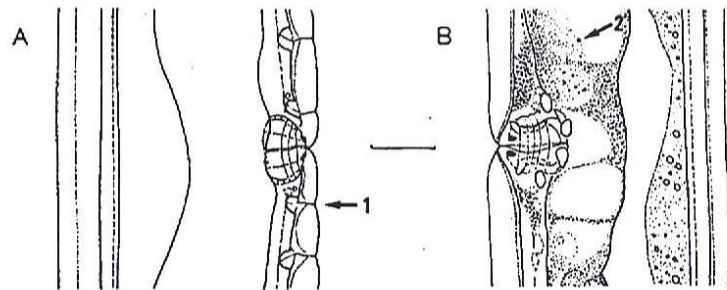


FIG. 27. Vaginal region: (A) with medioventral advulvar body pores (1) (*P. porosus*) (from Decraemer, 1991), (B) with lateral advulvar body pores (2) (*P. weischeri*) (from Decraemer, 1988a).

- 4. Spermathecae (1) present (Fig. 28A) 5
- Sperm (2) dispersed throughout uterus *P. pachydermus*
- (Fig. 28B)

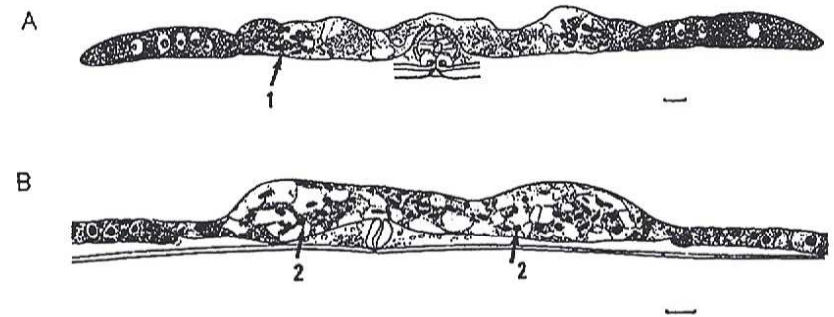


FIG. 28. Female reproductive system in *Paratrichodorus* species: (A) with spermathecae (1); (B) with sperm (2) dispersed through the uterus (A and B resp. from Decraemer, 1991 and 1980).

- 5. Onchiostyle longer than 100 μm *P. macrostylus*
- (Fig. 29A)
- Onchiostyle shorter than 100 μm 6
- 6. Vaginal sclerotizations narrow triangular, 1.5-2 μm apart, oblique; usually 2 lateral body pores on each side (varying from 0-6 in total); pharyngeal and/or intestinal overlap; onch.= 42-53 μm *P. anemones*
- (Fig. 29B)
- Vaginal sclerotizations as slightly larger oval pieces, close, oblique; 1 lateral body pore on each side; dorsal intestinal overlap; onch.=56.4-63.5 μm *P. hispanus*
- (Fig. 29C)
- Vaginal sclerotizations small oval, 1.5-2 μm apart, parallel to vaginal lumen; 1 lateral body pore on each side; dorsal intestinal overlap; onch.= 43-48 μm *P. weischeri*
- (Figs. 3E',F'; 27B)

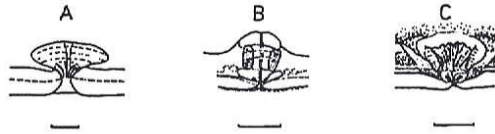


FIG. 29. Vaginal region: (A) *P. macrostylus* (from Popovici, 1989); (B) *P. anemones*; (C) *P. hispanus* (from Decraemer, 1988a).

7. Sperm cells minute thread-like, rarely globular; no lateral body pores; vaginal sclerotizations oval, slightly oblique or parallel to longitudinal body axis *P. minor* (Fig. 30A,E)

Sperm cells small globular, oval; vaginal sclerotization different, lateral body pores present or absent (Fig. 30B) 8

8. Onchiostyle small, 22-26.5 μm with small inner spear; pharyngeal bulb mainly offset (1); no lateral body pores; vaginal sclerotization small broad rounded triangular; vulva a transverse slit in ventral view; excretory pore (EP) generally near or posterior to pharyngo-intestinal junction *P. nanus* (Fig. 30B,C)

Onchiostyle longer; pharyngeal gland overlap (2), intestinal overlap or offset bulb; 0-2 lateral body pores; vaginal sclerotizations small oval; vulva a longitudinal slit in ventral view (Fig. 30A,D,F); EP more anteriorly 9

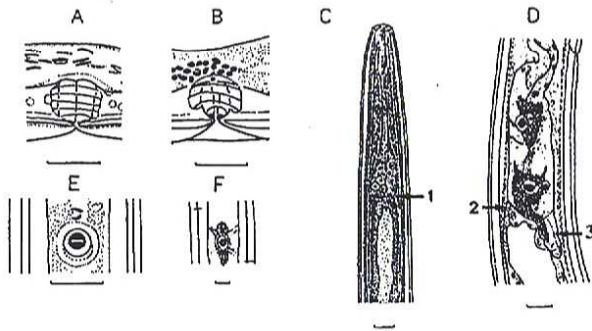


FIG. 30. (A) sperm cells minute thread-like (*P. minor*); (B) small globular sperm (*P. nanus*) (from Decraemer, 1988a); (C) pharynx with offset bulb (1) (*P. nanus*) (from Siddiqi, 1974); (D) pharynx with obvious overlapping of subventral pharyngeal glands (2) and small dorsal intestinal overlap (3) (*P. teres*) (from Decraemer & De Waele, 1980); (E) a transverse slit of the vulva in ventral view (*P. minor*), (F) a longitudinal slit of the vulva in ventral view (*P. teres*) (E,F from Decraemer, 1991).

9. Lateral body pores absent; onch.=37-48 μm ; small sperm in uterus or at reflexed end of genital branch *P. allius* (Fig. 31A)
- Lateral body pores present; onchiostyle generally longer; small sperm in uterus (Fig. 31B) 10

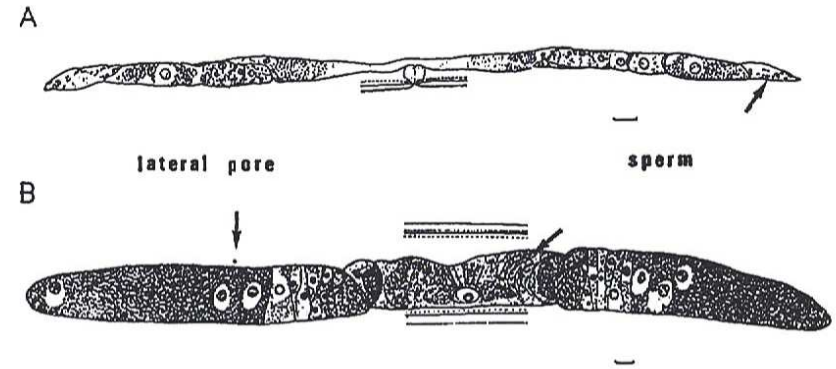


FIG. 31. Female reproductive system: (A) *P. allius* with sperm at level of the flexure of the genital branches (from Decraemer, 1988a); (B) sperm dispersed through uterus (*P. teres*) (from Decraemer, 1991).

10. Males usually rare in European populations; usually 1 lateral body pore on each side (varying from 1-4 in total); onch.=41-61 μm ; pharyngeal gland overlap and/or intestinal overlap (may be pronounced) or offset bulb; sperm may be observed as generated *P. teres* (Figs. 30D; 31B; 32A)

Sex ratio 1/1; 2 lateral body pores on each side; onch.=48-51 μm ; overlap of pharyngeal glands *P. tunisiensis* (Fig. 32B)

11. Vaginal sclerotizations as elongated oval pieces, well separated, parallel or almost parallel to vaginal lumen (Fig. 32C,D) 12

Vaginal sclerotizations different 13

12. Two prevulvar (= not advulvar) and 1 postadvulvar lateral body pore on each side; vagina elongated to rhomboid, constrictor muscles not differentiated; onch.=40-57 μm ; vaginal sclerotizations long more or less oval *T. primitivus* (Fig. 32C)

One advulvar lateral body pore only (prevulvar or at level V) on each side; vagina more or less rhomboid; vaginal constrictor muscles arranged in 2 groups; onch.=38-56 μm ; vaginal sclerotizations short oval *T. viruliferus* (Fig. 32D)

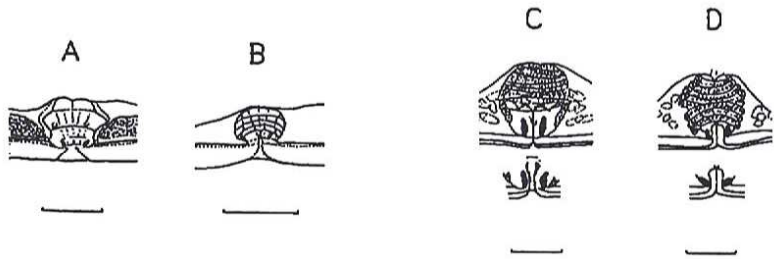


FIG. 32. Vaginal region: (A) *P. teres*; (B) *P. tunisiensis* (from Decraemer, 1988a). Vaginal sclerotizations as elongated oval pieces; (C) *T. primitivus*; (D) *T. viruliferus* (from Decraemer, 1988b).

13. Vaginal sclerotizations as large rounded quadrangular to trapezoid pieces close to one another or slightly separated (Fig. 33A-C) 14
 Vaginal sclerotizations (rounded) triangular or rounded small and relatively large 15
14. Vaginal sclerotizations close to one another; vagina barrel-shaped; 1 advulvar (prevulvar or at level V) and 2 postvulvar lateral body pores on each side; onch.=47-58 μm *T. aquitanensis* (Fig. 33B,C)
- Vaginal sclerotizations close to one another; vagina barrel-shaped (Fig. 34B); 1 prevulvar and 1 postadvulvar lateral body pore on each side; onch.=50-56 μm *T. variopapillatus* (Fig. 33A)
- Vaginal sclerotizations slightly separated; vagina rhomboid (Fig. 34A); 1 postadvulvar lateral body pore usually on each side; onch.=55-63 μm *T. azorensis* (Fig. 35A)

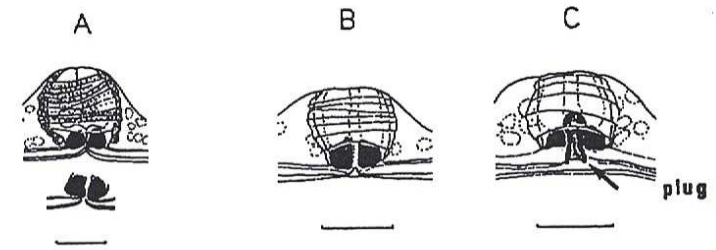


FIG. 33. Vaginal sclerotizations as large quadrangular to trapezoidal pieces in longitudinal optical section: (A) *T. variopapillatus* (from Decraemer, 1988b); (B,C) *T. aquitanensis*.

15. Vagina rhomboid-shaped (= mushroom-shaped) (Fig. 34A) 16
 Vagina barrel-shaped or pear-shaped (Fig. 34B,C) 18

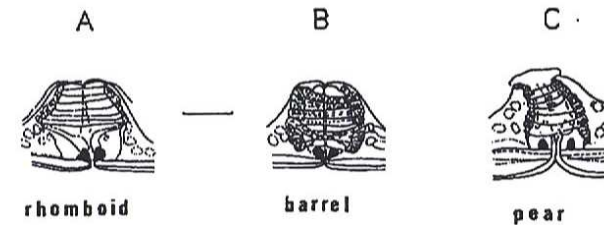


FIG. 34. Shape of vagina: (A) rhomboid-shaped (*T. similis*); (B) barrel-shaped (*T. cylindricus*); (C) pear-shaped (*T. hooperi*) (from Decraemer, 1988b).

16. Vaginal sclerotizations (rounded) triangular but well separated *T. lusitanicus* (Fig. 35B,C)
- Vaginal sclerotizations less separated in lateral view 17
17. Vaginal sclerotizations clearly triangular (exc. quadrangular), pieces very close; onch.=39-47 μm *T. similis* (Fig. 35D)
- Vaginal sclerotizations rounded triangular to quadrangular, pieces slightly more separated; onch.=42-52 μm *T. velatus* (Fig. 35E)

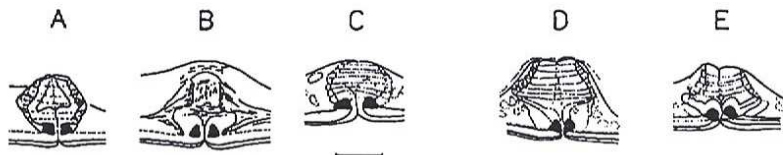


FIG. 35. Vaginal region: (A) vaginal sclerotizations square-shaped (*T. azorensis*); Vaginal sclerotizations (rounded) triangular: (B,C) *T. lusitanicus*; (D) *T. similis*; (E) *T. velatus* (A,B from Almeida *et al.*, 1989; C-E from Decraemer, 1988b).

18. Vagina pear-shaped (Fig. 36A,B) 19
 Vagina pear-shaped (Fig. 37A,B) 20
 19. Vaginal sclerotizations large, rounded, well separated;
 onch.=60-72 μ m; Vulva pore-like in ventral view *T. taylora*
 (Fig. 36A)
 Vaginal sclerotizations small, rounded, well separated;
 onch.=53-60 μ m; Vulva a transverse slit in ventral view
 *T. hooperi*
 (Fig. 36B)



FIG. 36. Vaginal region: (A) *T. taylora*; (B) *T. hooperi* (from Decraemer, 1988b).

20. No lateral body pores; vaginal sclerotizations large rounded
 triangular to almost oval pieces, slightly separated .. *T. beirensis*
 (Fig. 37A,B)
 Vaginal sclerotizations different, smaller 21
 21. Only 1 postadvulvar lateral body pore on each side;
 vaginal sclerotizations small triangular with tip directed
 towards vulva, pieces close to one another; V a transverse
 slit in ventral view *T. cylindricus*
 (Fig. 37C)

- 1 postadvulvar lateral body pore (rarely a prevulvar lateral
 pore present) on each side; vaginal sclerotizations small,
 oblique triangular and well separated *T. giennensis*
 1 postadvulvar and 1 prevulvar lateral body pore on each side;
 vaginal sclerotizations very small triangular, well separated;
 V pore-like in ventral view *T. sparsus*
 (Fig. 37D)

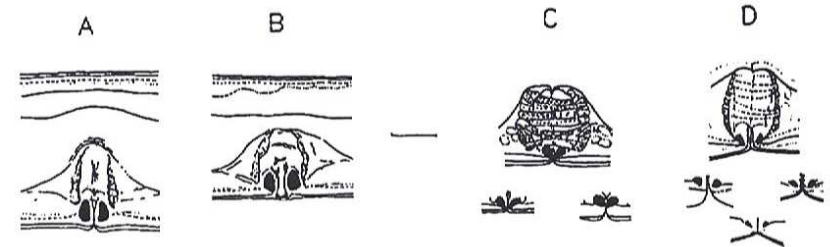


FIG. 37. Vaginal region: (A,B) *T. beirensis* (from Almeida *et al.*, 1989); (C) *T. cylindricus* with variability of shape of vaginal sclerotizations; (D) *T. sparsus* with variability of shape of the vaginal sclerotizations (C,D from Decraemer, 1988b).

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AN INTRODUCTION
TO VIRUS VECTOR NEMATODES
AND THEIR ASSOCIATED VIRUSES

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