Systematics of the Trichodoridae (Nematoda) with keys to their species

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SUMMARY

Keys are given for the identification of species in the Trichodoridae, partly based on the keys of Loof (1975) and Siddiqi (1974). Recent additions are included and for all species a drawing is given of the structure referred to in the key. The genus Paratrichodorus and the diagnostic value of the subgenera Paratrichodorus, Atlantadorus and Nanidorus are discussed.

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Keys are given for the identification of species in the Trichodoridae, partly based on the keys of Loof (1975) and Siddiqi (1974). Recent additions are included and for all species a drawing is given of the structure referred to in the key. The genus Paratrichodorus and the diagnostic value of the subgenera Paratrichodorus, Atlantadorus and Nanidorus are discussed.

RÉSUMÉ

Systématique des Trichodoridae (Nematoda) et clés de détermination des espèces


The Trichodoridae are economically, a very important group of nematodes as ectoparasites on the roots of many crop plants and as vectors of tobacco rattle virus and pea early browning virus. Despite the ease with which nematodes can acquire viruses from plants there are relatively few vectors. Of some 35 species of Trichodoridae, at least eleven transmit tobravirus (Hooper, 1973), so identification to species level may be very important.

During my study on Trichodoridae I came across several inadequacies in available descriptions and keys; these changes, together with recent additions made it necessary to modify the keys of Loof (1975) and Siddiqi (1974). For all the species I have included a drawing of the structure referred to in the key.

Suborder DIPHTHEROPHORINA
Coomans & Loof, 1970

Superfamily TRICHODOROIDEA
(Thorne, 1935) Siddiqi, 1961

The genera of the Trichodoridae (Thorne, 1935) Clark, 1961

Until recently the family Trichodoridae contained only the genus Trichodorus Cobb, 1913. Siddiqi (1974) split it into two genera; Trichodorus and Paratrichodorus; at the same time he divided Paratrichodorus into three subgenera: Paratrichodorus, Atlantadorus and Nanidorus.

Recently the monodelphic species (except P. westlindicus) were included in two new genera: Monotrichodorus Andrássy, 1976 for species closely related to Trichodorus. and Allotrichodorus Rodriguez-M., Sher & Siddiqi, 1978 for species closely related to Paratrichodorus (Atlantadorus).

Genus Trichodorus Cobb, 1913 s. str.

Definition

Trichodoridae. Cuticle not strongly swollen upon fixation. Posterior ventrosublateral oesophageal glands not overlapping the intestine, nor does the intestine anteriorly partly overlap the oesophagus. Dorsal oesophageal gland nucleus usually situated between both pairs of ventro-sublateral gland nuclei, near the posterior pair. Female reproductive system didelphic; spermathecae present; a pair of lateral body pores present within one body-width from the vulva. Vaginal sclerotization well developed. Males common; diagonal copulatory muscles well developed, extending far anteriorly to the spicular region, and responsible for ventral curvature of the male tail in death. Usually without caudal alae, exceptionally with small caudal alae. Spicules arcuate; suspensor muscles conspicuous. Preanal supplements three, exceptionally four, more or less evenly spaced, the two anterior ones nearly always located anterior to the spicules. Number of ventromedian cervical pores often 2 or 3, rarely 1 or 0.

Type species

Trichodorus primitius (De Man, 1880) Micolletzky, 1922.
Syn. Dorylaimus primitius De Man, 1880.

Key to Trichodorus males

1. — No ventromedian cervical papillae in the onchiostyle region (Pl. I: Fig. 1) ........... 2
   — One or two ventromedian cervical papillae in the onchiostyle region (Pl. I: Fig. 2, cf. remark 1) ........... 13
2. — Ventromedian cervical papillae 0; (as in tail region + copulatory apparatus Pl. II: Fig. 15; remark 2)
   T. obscursus Allen, 1957 + T. obtusus Cobb, 1913
   — Ventromedian cervical papillae 1 (Pl. I: Fig. 3) ........... 8
   — Ventromedian cervical papillae 2 (cf. remark 3) ........... 3
   — Ventromedian cervical papillae 3 ........... 6
3. — Two supplements within reach of spicules; spicules striated (Pl. II: Figs., 1,2)
   T. borneensis Hooper, 1962
   — One supplement within reach of spicules; spicules not striated ........... 4
4. — Tail contour evenly rounded, terminal cuticle not conspicuously thickened; spicules not setose (Pl. II: Fig. 3)
   T. aequalis Allen, 1957
   — Tail contour not evenly rounded, terminal cuticle conspicuously thickened (Pl. II: Fig. 4) ........... 5
5. — Spicules not setose, almost straight (Pl. II: Figs. 6, 7)
   T. hooperi Loof, 1973
   — Spicules setose, curved proximally (Pl. II: Figs. 4, 5)
   T. sparsus Szczygiel, 1968
6. — Excretory pore situated between the 2nd and 3rd ventromedian cervical papillae
   (Pl. I: Fig. 8; Pl. II: Fig. 10; tail region + copulatory apparatus)
   T. pakistanensis Siddiqi, 1962
   — Three ventromedian cervical papillae located anterior to the excretory pore
   (Pl. I: Fig. 9) ........... 7
7. — Onchiostyle length 72-75 μm; body length 500-590 μm (Pl. II: Fig. 8; copulatory apparatus)
   T. longistylus Yokoo, 1964
   — Onchiostyle length 52-54 μm; body length 570-610 μm; (Pl. I: Fig. 9; oesophageal region; Pl. II: Fig. 9; tail region + copulatory apparatus)
   T. kurumeensis Yokoo, 1966
   — Onchiostyle length 58-60 μm; body length 510-850 μm; spicule length 42-45 μm; (Pl. III: Fig. 13; tail region + copulatory apparatus)
   T. cedars Yokoo, 1964
8. — Onchiostyle length over 130 μm; (Pl. II: Fig. 11; tail region + copulatory apparatus)
   T. elegans Allen, 1957
   — Onchiostyle length under 85 μm ........... 9
9. — Supplementary papillae situated anterior to spicules (Pl. II: Fig. 13)
   T. proximus Allen, 1957
   — Posterior supplementary papillae within reach of spicules ........... 10
10. — Spicules irregularly tapering, slightly expanded in distal third (Pl. II: Fig. 12)
   T. coltleri Clark, 1963
   — Spicules regularly tapering, not expanded in distal third (Pl. III: Figs. 2, 3) ........... 11
11. — First and second supplement close to the anus, opposite distal half of spicules when completely retracted (Pl. III: Fig. 3)
   T. intermedius Rodriguez-M. & Bell, 1978
   — Second supplement anterior to spicules when completely retracted ........... 12
12. — Two very similar species (synonymous? cf. remark 4). Third supplement 1.1 body width anterior to second supplement (Pl. III : Fig. 2).

T. dilatatus Rodríguez-M. & Bell, 1978

— Third supplement 0.8-1.0 body width anterior to second supplement (Pl. III : Fig. 1; Pl. I : Fig. 3 : oesophageal region).

T. californicus Allen, 1957

13. — One ventromedian cervical papilla located behind the excretory pore (Pl. I : Fig. 7; Pl. III : Fig. 5 : tail region + copulatory apparatus).

T. castellanensis Arias et al., 1965

— No ventromedian cervical papilla located posterior to the excretory pore (Pl. I : Fig. 2)

14. — Spicules distally very slender so that gubernaculum mainly appears ventral to spicules (Pl. III : Fig. 12; Pl. I : Fig. 2 : oesophageal region).

T. primitius (De Man, 1880) Micoletzky, 1922

— Gubernaculum never ventral to spicules

15. — Spicules transversely striated; tail with small caudal alae, narrow part of spicules with "bristles" (Pl. III : Fig. 4).

T. cylindricus Hooper, 1962

— Spicules not striated; caudal alae absent

16. — Spicules constricted near middle, with capitulum rather broad, only slightly offset (Pl. III : Fig. 8)

— Spicules not constricted near middle, with rounded offset capitulum (Pl. III : Fig. 6).

17. — Two ventromedian cervical papillae present (Pl. I : Fig. 4; Pl. III : Fig. 11 : tail region + copulatory apparatus).

T. lusitanicus Siddiqi, 1974

— Three ventromedian cervical papillae present (Pl. I : Fig. 9)

18. — Spicules stout, ventrally expanded in distal third (Pl. III : Fig. 10).

T. velatus Hooper, 1972

— Spicules more slender, not ventrally expanded in distal third (Pl. III : Fig. 8; Pl. I : Fig. 5 : oesophageal region).

T. virulferus Hooper, 1963

19. — Onchiostyle length 35-45 μm; spicule length 35-40 μm; three ventromedian cervical papillae (remark 5; Pl. I : Fig. 6 : Pl. III : Figs. 7, 9 : tail region + copulatory apparatus).

T. similis Seinhorst, 1963

— Onchiostyle length 41-58 μm; spicule length 40-45 μm; spicules slender; two or three ventromedian cervical papillae (remark 5; Pl. I : Fig. 10; Pl. III : Fig. 6 : copulatory apparatus).

T. variopapillatus Hooper, 1972

— Onchiostyle length 55-60 μm; spicule length 42-45 μm; spicules stout; three ventromedian cervical papillae; (Pl. III : Fig. 13 : tail region + copulatory apparatus).

T. cedarus Yokoo, 1964

Remarks to the key of Trichodorus males

1. In the original figure of T. cedarus Yokoo, 1964 two ventromedian cervical papillae are located within the onchiostyle region. However, since the type specimens are badly fixed we cannot be certain that in all fixed animals no cervical papillae would be found within the onchiostyle region. Consequently I mentioned both possibilities within the key. Mamiya (1967) observed no cervical papillae within the onchiostyle region in other specimens than the type specimens.

2. As Loof (1975) pointed out, the status of T. obtusus Cobb, 1913 has never been clear. As no redescription is available we can only rely on the original drawing and description of a male without ventromedian cervical papillae. The trichodorid collected by Thorne in 1931 from the type locality was described by Allen (1957) as T. obscurus. Both species were very similar, the only difference pointed out by Loof (1975) is that the spicules are much less strongly curved in T. obscurus.

3. The characters used until now to distinguish the four species: T. borneoensis, T. aequalis, T. sparsus and T. hooperi (cf. Loof, 1975) thickened terminal cuticle and tail contour are in my opinion not so apparent especially between T. borneoensis and the other species. Therefore I used other characteristics in the key to distinguish T. borneoensis from the other species.

4. In the males both species have to be distinguished by a very small difference in the location of supplementary papillae. In the holotype male of T. dilatatus the distance between the anterior supplementary papilla and the second supplementary papilla is 42 μm, i.e. 1.1 times the body width at this level. In four males from Allen’s collection of T. californicus the distance between both papillae (measured along the ventral line) varied between 35-41 μm i.e. 0.8-1.0 times the body width. Consequently the only difference mentioned between T. dilatatus and T. californicus (cf.
Rodriguez-M. & Bell, 1978) becomes negligible. T. californicus shows some variation in the position of the lateral cervical pore in relation to the single ventral cervical pore, the excretory pore and the nerve ring. I observed the lateral cervical pore varying between a position just behind the nerve ring, i.e. 12.5 μm anterior to the ventral cervical pore to a position slightly (3.5 μm) behind the excretory pore i.e. about 26 μm behind the nerve ring.

5. The measurements for T. similis and T. variopapillatus include personal measurements, that extend the range so far published.

Key to Trichodorus females

1. — Onchiostyle length 140-150 μm (Pl. IV : Fig. 1 : vulva region). T. elegans Allen, 1957
   — Onchiostyle length under 100 μm ........ 2

2. — Sclerotized pieces at vagina rather close to one another (i.e. aperture of the sclerotized ring rather small (Pl. IV : Fig. 2) .... 3
   — Sclerotized pieces at vagina more clearly separated (i.e. aperture of the sclerotized ring large) (Pl. IV : Fig. 21) ........... 10

3. — Sclerotization of vagina in lateral view appearing as very large quadrangular to rounded triangular pieces; two pairs of lateral pores (one pair just anterior to half way between base of oesophagus and vulva, one pair half to one body width behind the vulva); vaginal area rounded (elongated when contracted due to fixation) (Pl. IV : Figs. 2-4)
   T. variopapillatus Hooper, 1972
   — Sclerotization of vagina smaller 4

4. — Onchiostyle length under 50 μm ........ 5

5. — Onchiostyle length over 50 μm ....... 7

6. — Sclerotization of vagina oblique in lateral view; onchiostyle length 42-50 μm; vagina with large lobes distally (Pl. IV : Fig. 5)
   T. velatus Hooper, 1972
   — Sclerotization of vagina rounded triangular in lateral view (Pl. IV : Fig. 6); one pair of lateral pores .................. 6

7. — A pair of ventrosubmedian pores behind the vulva; sclerotization of vagina appearing parallel to the vaginal lumen in lateral view; onchiostyle length 58-62 μm (Pl. IV : Fig. 13)
   T.cedrus Yokoo, 1964
   — No ventrosubmedian pores behind the vulva but a pair of lateral pores ........ 8

8. — Sclerotization of vagina appearing as more or less triangular, prominent, pieces in lateral view ................... 9
   — Sclerotization of vagina differently structured and smaller (Pl. IV : Fig. 15); onchiostyle length 57-68 μm; body length 700-1,010 μm
   T. cotti Clark, 1963

9. — Onchiostyle length 62-75 μm; body length 680-1,130 μm; sclerotization of vagina large, vaginal region rounded (Pl. IV : Fig. 14)
   T. intermedius Rodriguez-M & Bell, 1978
   — Onchiostyle length 66 μm; body length 1,170 μm; sclerotization of vagina smaller, vaginal region cylindrical (Pl. IV : Fig. 39)
   T. obscurus Allen, 1957

10. — Sclerotized ring of vagina broad; in lateral view sclerotization of vagina appearing as two rods parallel to the vaginal lumen; three pairs of lateral pores; onchiostyle length 44-54 μm (Pl. IV : Figs. 18-22; vaginal region)
    T. primitinus (De Man, 1880) Micoletzky, 1922
   — Sclerotized ring narrower; sclerotization of vagina different in lateral view (Pl. IV : Fig. 30) .................. 11

11. — Sclerotization of vagina in lateral view appearing as two small triangular pieces (Pl. IV : Fig. 24) .................. 12
   — Sclerotization of vagina larger (Pl. IV : Figs. 37-40) .................. 18

12. — Vagina more or less rhomboid with typical internal differentiation; onchiostyle length 35-48 μm; body length 620-890 μm (Pl. IV : Figs. 31-33 : vaginal region)
    T. viriliferus Hooper, 1963
   — Shape of vagina different .................. 13

13. — Vagina barrel-shaped or elongated with parallel walls (Pl. IV : Figs 23, 24) ........ 14
   — Vagina tapering towards the uterus (Pl. IV : Figs. 35, 36) ........ 17

14. — Two pairs of lateral pores ........ 16
   — One pair of lateral pores ........ 16

15. — Body length over 1,120 μm; onchiostyle length 49-70 μm; (Pl. IV : Fig. 23 : vaginal region)
    T. proximus Allen, 1957
   — Body length under 1,120 μm (Pl. IV : Figs. 24-28 + 29 : vaginal region)
    T. sparsus Szczygiel, 1968
    T. aequalis Allen, 1957
16. — Onchiostyle length 39-46 μm; vaginal sclerotization dot-like; body length 820-1,220 μm (Pl. IV : Fig. 30 : vaginal region)  

T. pakistanensis Siddiqi, 1962  

— Onchiostyle length 73-75 μm; vagina elongated (Pl. IV : Fig. 34); body length 570-840 μm  

T. longistylus Yokoo, 1964  

17. — Sclerotization of vagina in lateral view reniform to pyriform; onchiostyle length 53-57 μm; body length 650-920 μm (Pl. IV : Fig. 35 : vaginal region)  

T. borneensis Hooper, 1962  

— Sclerotization of vagina rounded; onchiostyle length 53-60 μm; body length 710-1,100 μm; (Pl. IV : Fig. 36 : vaginal region)  

T. hooperi Loof, 1973  

18. — Sclerotization of vagina in lateral view as rounded equilateral triangles; onchiostyle length 41-44 μm; (Pl. IV : Fig. 37)  

T. lusitanicus Siddiqi, 1974  

— Sclerotization of vagina different; onchiostyle length over 50 μm (cf. remarks 2, 3).  

19. — Sclerotization of vagina reniform with longest axis parallel to body wall in lateral view; onchiostyle length 55-80 μm; body length 720-1,250 μm; (Pl. IV : Fig. 38; vaginal region)  

T. californicus Allen, 1957  

— Sclerotization of vagina reniform with longest axis parallel to vaginal wall in lateral view; onchiostyle length 61-69 μm; body length 720-1,030 μm (Pl. IV : Fig. 40; vaginal region)  

T. dilatatus Rodriguez-M. & Bell, 1978  

Remarks to the key of Trichodorus females  


2. Females of T. dilatatus are morphologically very similar to T. californicus (cf. Rodriguez-M. & Bell, 1978). They have a comparable shape of the vagina but slightly differ in the shape of the triangular sclerotization of the vulva: in T. californicus the longest axis is parallel to the body wall and in T. dilatatus the longest axis is parallel to the vaginal wall.  

3. According to Allen (1957) females of T. obscurus cannot be distinguished from those of T. californicus. I have studied a few specimens of T. californicus from Allen's collection and a few specimens of T. obscurus from Beltsville collected by Schindler in 1957. I noticed a small difference in shape of the sclerotized vaginal ring (Pl. IV : Figs 38, 39) and in the distance between the sclerotized pieces in lateral view although I do not know if these differences will be found in a larger number of specimens and in the type material of T. obscurus (the difference in vaginal shape: rounded or elongated is probably due to fixation).  

Genus Paratrichodorus Siddiqi, 1974  

Validity of subgenera  

Siddiqi (1974) distinguished among the species of the genus Paratrichodorus three subgroups for which he proposed three subgenera: Paratrichodorus, Atlantadorus and Nanidorus.  

The basic diagnostic characters in the identification of Paratrichodorus and Atlantadorus are the posterior ventrosublateral oesophageal glands overlapping the intestine in Paratrichodorus and an anterior overlap of the intestine dorsally and dorsolaterally over the posterior part of the oesophagus in Atlantadorus (cf. Siddiqi, 1974; key on p. 270).  

Other diagnostic characters in the identification for the males of Paratrichodorus and Atlantadorus are:  

— the number of pairs of postcloacal ventrosubmedian papillae: one pair in Paratrichodorus and usually two pairs in Atlantadorus (Siddiqi, 1974; Loof, 1975).  

— the presence of lateral cervical pores located near the level of the excretory pore in Atlantadorus, and their usual absence in Paratrichodorus (Siddiqi, 1974).  

In females the subgenera are characterized on the base of the vulva-shape: a short longitudinal slit in Paratrichodorus and a pore-like opening in Atlantadorus.  

The subgenus Nanidorus is distinguished from the other subgenera mainly by the posterior position of the excretory pore near or posterior to the base of the oesophagus. The male specimens differ from the other subgenera by the very long spicules and the presence of only one ventromedian papilla; the females by the absence of lateral and caudal pores and by the shape of the vulva: a short transverse slit.
Discussion

In a population of Paratrichodorus (probably a new species, close to P. teres) specimens were found with posterior ventro-sublateral oesophageal glands overlapping the intestine either slightly or distinctly, together with an anterior overlapping by the intestine dorsally and dorso-laterally over the oesophageal bulb. Both characters were however used as important diagnostic characters for distinguishing Paratrichodorus from Allantadorus; as they have been found together in the same specimens they are no longer diagnostic. In Nanidorus the posterior ventro-sublateral oesophageal glands may overlap the intestine; the intestine does not overlap the oesophagus anteriorly.

The number of pairs of postcloacal ventro-submedian papillae is not useful in distinguishing the subgenera (especially Allantadorus) since of the five known species of Allantadorus (P. allanticus, P. anemones, P. grandis, P. pachydermus, P. porosus) only P. allanticus is described with two pairs of postcloacal ventro-submedian papillae. The other species of Allantadorus possess only one pair as in Paratrichodorus and Nanidorus.

The pair of lateral cervical pores in Allantadorus is not always located near the level of the excretory pore. I observed in P. pachydermus and P. anemones the pair of lateral cervical pores at some distance anterior to the ventromedian cervical pore. In P. grandis and P. porosus it lies at the level of the ventromedian cervical pore. In Nanidorus cervical pores are absent. In Paratrichodorus lateral cervical pores were not described. Siddiqi (1974) considered the pair of lateral cervical pores as very rarely present in the subgenus Paratrichodorus.

The difference in vulva-shape between the subgenera is very difficult to interpret. The vulva opening is always very small in trichodorids. In lateral view the vulva shape may be difficult to determine e.g. in P. anemones the funnelshaped vulva (Pl. VII : Fig. 13) may be considered as a large pore; it is however, difficult to distinguish it from a short longitudinal slit as is found in the subgenus Paratrichodorus.

In Nanidorus the excretory pore is not always near or posterior to the base of the oesophagus. In some specimens of P. (N.) minor it was seen opposite the middle of the posterior oesophageal bulb.

The absence of cervical pores is a character that is also found in the subgenus Paratrichodorus.

Conclusion

Since most differences between the three subgenera are very small and since even the main diagnostic character may be doubtful I prefer not to split up the genus Paratrichodorus into subgenera.

Definition

Trichodoridae. Cuticle strongly swollen when treated with acid fixative. Posterior subventral oesophageal glands overlap the intestine (except in P. nanus) or intestine anteriorly partly overlaps oesophageal bulb or both types of overlap occur. Females without lateral body pores within one body width from the vulva; vaginal sclerotization weakly developed; spermathecae present or absent. Males with caudal alae; copulatory muscles not extending anterior to bursa, male tail straight in death. Suspensor muscles inconspicuous. Two supplements within reach of caudal alae, well separated from the anterior third which is often reduced or only one supplement present. One or two pairs of large ventro-submedian postcloacal papillae. Usually one or no ventromedian cervical papillae, rarely three.

Type species

Paratrichodorus tunisiensis (Siddiqi, 1963)

Syn. Trichodorus tunisiensis Siddiqi, 1963

Siddiqi, 1974

Key to Paratrichodorus males (cf. remark 1)

1. — Males with a single ventromedian supplement (Pl. V : Fig. 1); no ventromedian cervical pores; posterior subventral oesophageal glands usually overlapping the intestine; intestine anteriorly not overlapping oesophageal bulb (Pl. V : Fig. 3) 2

— Males with two or three ventromedian supplements; ventromedian cervical pores present or absent ................. 3
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2. — Posterior subventral oesophageal glands not or only slightly hardly overlapping the intestine; oesophageal bulb small; onchoistyle length 21-23 μm; spicule length 42-44 μm (Pl. V : Fig. 1; Pl. V : Fig. 2 : oesophageal region)

*P. narus* (Allen, 1957) Siddiqi, 1974

— Posterior subventral oesophageal glands overlapping the intestine; oesophageal bulb large, elongated (Pl. V : Fig. 3); onchoistyle length 28-39 μm; spicule length 48-65 μm (Pl. V : Fig. 4)

*P. minor* (Colbran, 1956) Siddiqi, 1974

3. — Posterior subventral oesophageal glands overlapping the intestine; intestine anteriorly not overlapping the oesophagus (Pl. V : Fig. 5); males with one pair of large ventrosubmedian postcloacal papillae ................. 4

— Intestine anteriorly overlapping oesophageal bulb dorsally and dorsolaterally; posterior subventral oesophageal glands not overlapping the intestine (Pl. V : Fig. 6); males with two pairs of large ventrosubmedian postcloacal papillae .......... 11

— Intestine anteriorly overlapping oesophageal bulb and posterior subventral oesophageal glands overlapping the intestine (Pl. V : Fig. 7); onchoistyle length 53-57 μm; spicule length 44-48 μm; no cervical papillae

*Paratrichodus* sp. cf. *teres*

4. — Onchoistyle length 75-78 μm; no ventromedian cervical papillae; body length 750-845 μm (Pl. V : Fig. 8 : tail region + copulatory apparatus)

*P. acuatus* (Siddiqi, 1960) Siddiqi, 1974

— Onchoistyle length under 55 μm............ 5

5. — Three ventromedian cervical papillae; onchoistyle length 29-34 μm; length spicules 33 μm; (Pl. V : Fig. 9; tail region + copulatory apparatus)

*P. mirzai* (Siddiqi, 1960) Siddiqi, 1974

— One or no ventromedian cervical papillae ..... 6

6. — One ventromedian cervical papilla (Pl. V : Fig. 5); onchoistyle length 48-49 μm; body length over 800 μm; (Pl. V : Fig. 12: tail region + copulatory apparatus)

*P. tunisiensis* (Siddiqi, 1963) Siddiqi, 1974

— No ventromedian cervical papilla...... 7


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7. — Testis degenerate, without sperm; onchiostyle length 47-52 μm; spicule length 45-52 μm (remark 2) (Pl. V: Fig. 10: tail region + copulatory apparatus)

P. teres (Hooper, 1962) Siddiqi, 1974
— Testis with well developed sperm
8. — Spicule length over 50 μm
P. lobatus (Colbran, 1965) Siddiqi, 1974
— Spicule length 50 μm or less
9. — Distance second supplement to anus about 45 % of spiculum length; spicule length 50 μm (Pl. V: Fig. 13)

P. allieni (Andrassy, 1968) Siddiqi, 1974
— Distance second supplement to anus about 90 % of spiculum length
10. — Spicule length 31 μm; onchiostyle length 45 μm (Pl. V: Fig. 14: tail region + copulatory apparatus)

P. allius (Jensen, 1963) Siddiqi, 1974
— Spicule length 42-44 μm; onchiostyle length 39-41 μm (Pl. VI: Fig. 1: tail region + copulatory apparatus)

P. rhodesiensis (Siddiqi & Brown, 1965) Siddiqi, 1974
11. — Two ventromedian preanal supplements, both within spicular range; spicule length 30-39 μm; onchiostyle length 43-48 μm (Pl. VI: Fig. 2: tail region + copulatory apparatus)

P. porosus (Allen, 1957) Siddiqi, 1974
— Three ventromedian preanal supplements, anterior supplement well anterior to head of retracted spicules
12. — Onchiostyle length more than 60 μm
13. — Onchiostyle length under 60 μm
14. — Spicule length 79-87 μm; spicules straight with rounded offset capitulum; onchiostyle length 68-82 μm (Pl. VI: Fig. 3: tail region + copulatory apparatus)

P. atlanticus (Allen, 1957) Siddiqi, 1974
— Spicule length 39-43 μm; spicules curved, capitulum not offset; onchiostyle length 64-72 μm (Pl. VI: Fig. 4: tail region + copulatory apparatus)

P. grandis Rodriguez-M. & Bell, 1978
15. — Tail short, round; spicules fine, 46-53 μm long (Pl. VI: Fig. 6); distance second preanal supplement to anus 38-64 % of spiculum length

P. anemones (Loof, 1965) Siddiqi, 1974
— Tail longer, narrower (trapezoid); spicules broader with different shape, 40-45 μm long (Pl. VI: Fig. 5); distance second preanal supplement to anus 75-94 % of spicule length

P. pachydermus (Seinhorst, 1954) Siddiqi, 1974

Remarks to the key of Paratrichodorus males


2. Males of P. teres (Syn. P. flevesnis Kuiper & Loof, 1962) can show a body length smaller than 800 μm, this being in contradiction with the key of Loof (1975).

KEY TO PARATRICHODORUS FEMALES

1. — Intestine anteriorly partly overlapping posterior oesophageal bulb dorsally and dorsolaterally, posterior subventral oesophageal glands not overlapping the intestine (Pl. VII: Fig. 1) .......... 2
— Intestine anteriorly not overlapping the oesophagus; posterior subventral oesophageal glands usually clearly, or rarely slightly, overlapping the intestine (Pl. VII: Fig. 3) .......... 6
— Intestine anteriorly overlapping posterior oesophageal bulb and posterior subventral oesophageal glands overlapping the intestine (Pl. VII: Fig. 8); onchiostyle length 50-60 μm; one pair of lateral pores (5.5-8.2 times the body width posterior to the vulva)

Paratrichodorus sp. (cf. teres)

2. — Spermatheca present .......... 3
— Spermatheca absent .......... 4
3. — One pair of subventral body pores behind the vulva (Pl. VII: Fig. 12); onchiostyle length 64-70 μm; body length 760-1130 μm

P. atlanticus (Allen, 1957) Siddiqi, 1974
— Lateral body pores anterior and posterior to vulva 0-2 on each body side; onchiostyle length 42-53 μm; body length 650-970 μm (Pl. VII: Fig. 13: vaginal region)

P. anemones (Loof, 1965) Siddiqi, 1974
4. — Onchiostyle length 65-72 μm; body length 900-1,040 μm (Pl. VII: Fig. 17: vaginal region)

P. grandis Rodriguez-M. & Bell, 1978
— Onchiostyle length under 65 μm .... 5
5. — Ventromedian pores near vulva present (2 pairs) (Pl. VII: Fig. 14); onchiostyle length 39-47 μm; body length 420-570 μm

P. porosus (Allen, 1957) Siddiqi, 1974
— No ventromedian body pores near vulva; lateral body pores posterior to vulva 2-5 on each body side; onchiostyle length 44-54 μm; body length 690-1,020 μm (Pl. VII: Fig. 2: part genital system; Fig. 1: posterior end of oesophagus)

P. pachydermus (Seinhorst, 1954) Siddiqi, 1974
6. — Caudal pores present (Pl. VII: Fig. 4) .... 7
— Caudal pores absent (Pl. VII: Fig. 5) .... 14
7. Onchiostyle length over 80 μm; body length 910-950 μm; sclerotized vaginal ring 2 μm thick (Pl. VII: Fig. 6).

*P. acuatus* (Siddiqi, 1960) Siddiqi, 1974

Onchiostyle length under 80 μm ...... 8

8. Spermatheca present (two very similar species; see remark 3) ................. 9

— No spermatheca ..................... 10

9. Oesophageal overlap one body width long (Pl. VII: Fig. 3); one lateral body pore postvulvar; onchiostyle length 47-52 μm; body length 630-1,035 μm (Pl. VII: Fig. 7; vaginal region)

*P. lobatus* (Colbran, 1965) Siddiqi, 1974

— Oesophageal overlap shorter than one body width; two lateral body pores; onchiostyle length 48-51 μm; body length 900-1,100 μm (Pl. VII: Fig. 10; vaginal region)

*P. tunisiensis* (Siddiqi, 1963) Siddiqi, 1974

10. Onchiostyle length under 35 μm; lateral body pores absent; body length 490-610 μm (Pl. VII: Fig. 11; vaginal region)

*P. mirzai* (Siddiqi, 1960) Siddiqi, 1974

— Onchiostyle length over 35 μm .......... 11

11. Lateral body pores present; onchiostyle length 41-52 μm; body length 770-1,320 μm; uteri without sperm (Pl. VII: Fig. 15; vaginal region)

*P. teres* (Hooper, 1962) Siddiqi, 1974

— Lateral body pores absent .............. 12

12. Vaginal sclerotization appearing as two hold dots in lateral view (Pl. VII: Fig. 18)

*P. rhodesiensis* (Siddiqi & Brown, 1965) Siddiqi, 1974

— Vaginal sclerotization smaller in lateral view .................................. 13

13. Body length 640-780 μm; onchiostyle length 37-42 μm (Pl. VII: Fig. 16; vaginal region)

*P. allius* (Jensen, 1963) Siddiqi, 1974

— Body length 470-650 μm; onchiostyle length 35-40 μm (Pl. VII: Fig. 19; vaginal region)

*P. tansaniensis* Siddiqi, 1974

14. Genital system mono-prodelphic (Pl. VIII: Fig. 1); vulva at 60-65 % (cf. remark 1)

*P. westindicus* Rodriguez-M., Sher & Siddiqi, 1978

— Genital system didelphic .................. 15

15. Tail acute (Pl. VIII: Fig. 2); onchiostyle length 22-26 μm; body length 375-610 μm

*P. acuatus* (Bird, 1967) Siddiqi, 1974

— Tail hemispherical .......................... 16

16. Posterior subventral oesophageal glands more or less overlapping the intestine (slightly or clearly) (Pl. VIII: Fig. 4) 17

— Non-overlapping base of oesophagus ...... 18

17. Excretory pore opposite oesophageal base (Pl. VII: Fig. 4); onchiostyle length 27-42 μm (mean 32 μm); body length 440-1,530 μm (mean 650 μm) (Pl. VIII: Fig. 3; vaginal region)

*P. minor* (Colbran, 1956) Siddiqi, 1974

— Excretory pore more anteriorly situated; onchiostyle length 30-34.5 μm; body length 475-500 μm


18. Excretory pore opposite anterior part of intestine (Pl. VIII: Fig. 5); onchiostyle length 21-23 μm; body length 490-600 μm; sclerotization of vagina in lateral view small, inconspicuous (Pl. VIII: Fig. 6)

*P. nanus* (Allen, 1957) Siddiqi, 1974

— Excretory pore opposite base of oesophagus; onchiostyle length 31-34 μm; body length 490-560 μm; sclerotization of vagina in lateral view kidney-shaped (Pl. VIII: Fig. 7)

*P. renifer* Siddiqi, 1974

Remarks to the key of Paratrichodorus females


3. *P. lobatus* (Colbran, 1965) Siddiqi, 1974 and *P. tunisiensis* (Siddiqi, 1963) Siddiqi, 1974 strongly resemble each other. *P. lobatus* only differs from *P. tunisiensis* by the length of the oesophageal overlap, i.e. one body width long in *P. lobatus* and shorter than one body width long in *P. tunisiensis*. 

width in all other species (including *P. tunisiensis*) of the genus *Paratrichodorus* and by the possession of only one lateral body pore (postvulvar) compared with two lateral body pores (one pre- and one postvulvar) in *P. tunisiensis*.

**Genus Monotrichodorus** Andrassy, 1976

Siddiqi (1974) presumed that *Trichodorus monohystera* Allen, 1957 with a posteriorly located vulva and a single anterior female gonad possibly belongs to a separate genus.

Andrassy (1976) proposed a new genus *Monotrichodorus* based on *Trichodorus monohystera* Allen, 1957; the diagnosis of the new genus was shortly given under a footnote as: ‘very similar to *Trichodorus* but ovary one, straight.’

Rodriguez-M., Sher and Siddiqi (1978) reviewed the genus *Monotrichodorus* based on specimens of *M. monohystera* (Allen, 1957) Andrassy, 1976 and on a new species *M. vanguardyi*; the diagnosis of the genus was expanded.

Rodriguez-M., Sher and Siddiqi (1978) included the following character within the diagnosis of *Monotrichodorus*: ‘Dorsal oesophageal gland nucleus anterior to, and the same size as, the posterior subventral gland nuclei’; they differentiated *Monotrichodorus* from *Trichodorus* amongst other characters by the anterior position of the dorsal oesophageal gland nucleus. A study of the taxonomic value of the position of the oesophageal gland nuclei in Trichodoridae (paper in preparation), showed that the position of the oesophageal gland nuclei is not a useful diagnostic character within the Trichodoridae. There is a relatively large variability in the position of the oesophageal gland nuclei to one another, especially due to the variable position of the dorsal gland nucleus. The dorsal gland nucleus is as large as or usually somewhat larger than the nuclei of the posterior ventrolateral oesophageal glands; its position varies from the level of the anterior ventrolateral oesophageal gland nuclei to the level of the posterior ventrolateral oesophageal gland nuclei.

DEFINITION

Trichodoridae. Cuticle not swollen upon fixation. Posterior ventrosublateral oesophageal glands not overlapping the intestine. Female reproductive system monodelphic, prodelphic; with flexure at the oviduct; postvulvar uterine sac present. Vagina anteriorly directed, more than one-half body width, with strong musculature; vaginal sclerotization well developed. Lateral aduvlar body pores present. Vulva a transverse slit at about 80% of body length. Males with well developed diagonal copulatory muscles. Spicules long, slender, setose. Three ventromedian preanal supplements, at least one anterior to retracted spicule. Paired ventrolateral postcloacal papillae present. Single ventral cervical papilla anterior to excretory pore. In both sexes a single caudal pore present.

TYPE SPECIES


Syn. *Trichodorus monohyster* Allen, 1957

Other species

*Monotrichodorus vangundyi* Rodriguez-M., Sher & Siddiqi, 1978

Remark

Both species are very similar (synonymous?); the only difference lies in the position of the second preanal supplement, i.e. within the range of the retracted spicules or not. This difference is rather small to separate both species using males, since in the original description of *M. monohyster* Allen (1957) the second supplement is described at about the level of the proximal end of the spicules (see also Fig. 1C in Rodriguez-M., Sher & Siddiqi, 1978).

Key to Monotrichodorus females, based on Rodriguez-M., Sher & Siddiqi (1978)

— Paired lateral cervical pores present immediately behind the amphid opening

*M. vangundyi* Rodriguez-M., Sher & Siddiqi, 1978

— Paired lateral cervical pores absent


Genus Allotrichodorus Rodriguez-M., Sher & Siddiqi, 1978

DEFINITION

Trichodoridae. Cuticle swollen upon fixation. Intestine anteriorly overlapping oesophageal bulb dorsally and dorsolaterally. Female reproductive system monodelphic, prodelphic with flexure at oviduct; postvulvar uterine sac present. Spermatheca conspicuous. Vagina more than half body width in length with strong musculature; vaginal sclerotization conspicuous. Vulva a transverse slit at about 85%. In males caudal alae present. Ventral cervical papilla, if present, anterior to excretory pore. Spicules transversely striated, elongate, slender, setose; capitular extension having a dorsal groove or depression leading into proximal opening of spicule. Three ventromedian supplementary papillae within range of retracted spicules. Large paired lateroventral postcloacal papillae present. Caudal pores present.

TYPE SPECIES

*Allotrichodorus campanullatus* Rodriguez-M., Sher & Siddiqi, 1978

Other species *A. guttatus* Rodriguez-M., Sher & Siddiqi, 1978
KEY TO ALLOTRICHDORUS MALES

— One ventromedian cervical papilla; onchiostyle length 45-57 μm; spicule length 46-59 μm; body length 540-690 μm
A. campanullatus Rodriguez-M., Sher & Siddiqi, 1978

— No ventromedian cervical papilla; onchiostyle length 65-72 μm; spicule length 65-76 μm; body length 670-740 μm
A. guttatus Rodriguez-M., Sher & Siddiqi, 1978

KEY TO ALLOTRICHDORUS FEMALES, based on Rodriguez-M., Sher & Siddiqi (1978)

— Onchiostyle length 46-55 μm; body length 630-680 μm; vaginal sclerotization appears as two small bells in lateral view
A. campanullatus Rodriguez-M., Sher & Siddiqi, 1978

— Onchiostyle length 63-71 μm; body length 650-720 μm; vaginal sclerotization appears as two unequal drops in lateral view
A. guttatus Rodriguez-M., Sher & Siddiqi, 1978

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REFERENCES


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