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Morphometric variability and value of the characters used for specific identification in *Trichodorus* Cobb, 1913

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Summary

The intraspecific variability and taxonomic value of the 39 characters used in the species diagnoses of *Trichodorus*, were studied. Only fourteen of them are retained as useful for identification purposes and will serve as base for the genus database for the NEMAID identification computer program.
Key-words : *Trichodorus*, taxonomy.

Résumé

La variabilité intraspécifique et la valeur taxonomique des 39 caractères utilisés dans les diagnoses des espèces de *Trichodorus* ont été étudiés. Seulement quatorze caractères sont retenus comme utilisable pour le procès d'identification. Ils formeront la base pour la gestion des data du genre dans le «NEMAID identification computer program».
Mots-clefs : *Trichodorus*, taxonomie.

Introduction

This paper deals with a study on the value of the characters used for species identification within the genus *Trichodorus*. It is part of a series of papers made additionally to the computer program NEMAID. This program was proposed by Fortuner & Wong (1984) to help in the identification of species in plantparasitic nematode genera.
Of the genus *Trichodorus*, 59 species have been described : 15 were referred to a new genus *Paratrichodorus* by Siddiqi (1974) and one species *T. monohystera* Allen, 1957 was classified by Andrassy (1976) within a third genus of the Trichodoridae, *Monotrichodorus* (Table 1).
At present the genus *Trichodorus* includes 38 species, of which 34 are valid. Twenty species are only known by their type population, often based on a limited number of specimens. Only of the following species three, or more populations were studied and measured : *T. aequalis, T. cedarus, T. eburneus, T. orientalis, T. primitivus, T. similis, T. sparsus* and *T. viruliferus*; however, often restricted to a small number of specimens.
The variability of quantitative and qualitative characters has rarely been examined. The standard deviation or variation coefficient of measurements was at first given by Hooper (1972); from 1978 on, it appeared in several species descriptions; in recent papers, it is generally included. In Loof's overall study of the taxonomy of Trichodoridae in 1975, diagnostic characters were discussed, including some data on intraspecific variation. The author concluded that we should more rely upon qualitative and meristic characters; the five demanian indexes were considered of little aid in the family Trichodoridae.
In this study, for those species where only the range of the observed values was given, the mid-range was calculated as an approximation of the mean value and used till the actual values of the means can be calculated from paratypes or other specimens (see Fortuner & Wong, 1984).

Material and Methods

A list of all diagnostic characters used for differentiating the 34 valid species in *Trichodorus* was established. The frequency of their appearance in the specific diagnoses is added.

GENERAL MORPHOLOGY

Body	
body length	26 %
body width	3 %
structure body cuticle	14.5 %
Anterior end	
head offset	3 %
Tail	
shape	9 %
thickness terminal cuticle	11.5 %
tail length	3 %
number caudal pores	9 %
Excretory pore	
position excretory pore	20.5 %

Digestive system	
length onchiostyle	41 %
ventral overlapping pharyngeal glands	6 %
dorsal overlapping by intestine	3 %
Characters of female	
Reproductive system	
ovaries : reflexed or not	6 %
vulva	
ratio V	3 %
shape in ventral view	11.5 %
vagina	
shape	29 %
shape sclerotization	64.5 %
spermatheca	3 %
lateral body pores	
number	53 %
position in relation to vulva	23.5 %
position ventrosubmedian body pores in relation to the vulva	3 %
Characters of male	
spicules	
length	26.5 %
shape	64.5 %
ornamentation	
setosity	6 %
striation	20.5 %
smooth	6 %
presence of velum	3 %
caudal alae	
presence	3 %
absence	9 %
precloacal ventromedian supplementary papillae	
number	35 %
position	73.5 %
position in relation to spicules	38 %
gubernaculum	
shape	26 %
position	6 %
length	6 %
ventromedian cervical papillae	
number	70.5 %
position in relation to onchiostyle base	17.5 %
position in relation to excretory pore	38 %
lateral cervical pores	
position	6 %

Discussion and appraisal of taxonomic characters

GENERAL MORPHOLOGY

Body length.

Differences in body length were used in the diagnoses of 26 % of the valid *Trichodorus* species; in half of them by the range of their values, in the other half indicated in terms of proportion. The range of mean values of the body length (µm) for *Trichodorus* species is : 554-1120 µm = 566 µm (♂), 571-1310 µm = 739 µm (♀). Intraspecific, the difference for the mean body length varied between 16 µm (*T. coomansi*, 2 populations with low number of specimens) and 385 µm (*T. sparsus*, 15 populations from different geographical origins) in males and between 7 µm (*T. coomansi*, 2 populations) and 345 µm (*T. sparsus*, 13 populations) in females.

In *Trichodorus*, relative little information is available on variability of body length. For thirteen species, the variation coefficient or standard deviation for body length was given, based upon a total of nineteen population, mostly relying upon a low number of specimens (1/3rd of the populations with 4-15 specimens); it was rather low (in ♂ : 9.8 - 11.7 %; in ♀ : 1.4 - 11.8 %). Evidently, variability increases with the number of populations studied, with different hosts (see BAUJARD, 1983 for African specimens of *T. eburneus*), and different geographical origins.

The influence of fixation, e.g. reflexed in a shrinkage of the body length was evidently in specimens used for the descriptions of *T. longistylus* (described with stout body) and *T. kurumeensis* (see MAMIYA, 1967); both species were synonymized with *T. cedarus* by SHISHIDA, 1979. LOOF (1973) remarked some variation in body length within the European populations of *T. sparsus*, and suggested that very small values of body length may be partly due to poor fixation. Similarly, SHISHIDA (1979) suspected that the differences in dimensions between Japanese specimens of *T. aequalis* and the type population may vary through fixation. Within a single population of *T. tricaulatus* SHISHIDA (1979) found the body length to be less variable than many other characters, but more variable than onchiostyle length and spicule length.

In agreement with LOOF (1975), and based upon variability studies of *P. minor* (BIRD & MAI, 1968), I consider the body length a non-suitable diagnostic character, not to include in the list for the NEMAID computer program (see DECRAEMER, 1989).

Body width.

This character was only used in the differential diagnosis of *T. pakistanensis*, a species distinguished in female from *T. borneoensis* by its slender body. In the genus *Trichodorus*, it is not useful taxonomically and will not be included in the NEMAID program.

Structure of the body cuticle.

A detailed description of the structure of the body cuticle is, except for *T. pakistanensis*, only given in recent papers. The multilayered structure of the body cuticle was described for 12 of the 34 valid species of the genus *Trichodorus*. A three-layered body cuticle consisting of : a thin outer layer, followed by a thicker middle and a slightly thinner inner layer, was observed in *T. coomansi*, *T. orientalis*, *T. persicus*, *T. petrusalberti*, *T. taylori*, *T. complexus*, *T. eburneus* and *T. hooperi*. Both inner layers may be well demarcated. Only in the first five species, all described by DE WAELE or in coorporation with him, this character was used in the respective species diagnoses. A two-layered body cuticle, i.e. without thin outer layer was described for *T.*

borai, T. pakistanensis, T. rinae and *T. sanniae*; but never used in the respective species diagnoses.
In all former twelve species, a fine striation of the subcuticle was observed; this was also the case for the following species : *T. dilatatus, T. hooperi, T. intermedius, T. pakistanensis, T. viruliferus.*
The ultrastructure of the body cuticle in trichodorids was studied in *P. allius* (= possessing an eight layered cuticle, see RASKI, JONES & ROGGEN, 1969) and in *T. christiei* = *P. minor* (with a two-layered cuticle consisting of an outer and inner cuticle, loosely connected and with several subdivisions; the outer cuticle being surrounded by a three-zone marginal layer, see HIRUMI, CHEN, LEE & MARAMOROSCH, 1968, and ROBERTSON & TAYLOR, 1977.
In general the body cuticle in *Trichodorus* species has not the same swelling reaction upon fixation as in species of the genus *Paratrichodorus*. So, rarely data were given on the swelling of the body cuticle upon fixation (except for e.g. *T. cottieri*).
I do not include the structure of the body cuticle in the list of diagnostic features used in the NEMAID program, since : 1) data on the structure of the body cuticle are available for only 35 % of the species of *Trichodorus*, and 2) at present, no proof of the specificity of the number of cuticular layers is available, as the 2-layered structure in five species could also be due to difficulties in observation of the thin outer layer, moreover in some specimens even more layers or sublayers can be observed.

ANTERIOR END

Head offset.
This character was only used in the species diagnosis of *T. pakistanensis*. The head was described as offset in *T. complexus* (slightly), *T. lusitanicus, T. primitivus, T. sparsus* and *T. viruliferus*, and as continuous with the rest of the body in *T. borai, T. dilatatus* (almost) and *T. similis*. It is not considered as a useful diagnostic character in the NEMAID program, since this feature may be influenced by fixation.

TAIL

Shape of the tail and structure of its terminal cuticle.
Within the genus *Trichodorus*, we can distinguish in male two large tail types : – 1) a tail with its terminal cuticle more or less of equal thickness, present in the majority of the species, resulting in a regularly rounded hemispherical tail (e.g. *T. similis* Fig. 3F), or a ventrally slightly concave tail (*T. complexus* Fig. 3D), and 2) a tail with a thickened terminal cuticle, resulting in a subhemispherical tail shape i.e. with a clearly protruding end in *T. cedarus, T. hooperi* and *T. sparsus*, or a shortly protruding end as in *T. borneoensis, T. cylindricus* (apparently not in type specimens cf Hooper, 1962) and *T. persicus*. In a few species the outer body cuticle is terminally thicker due to an indentation of the subcuticle (*T. orientalis*, and slightly in *T. intermedius* and *T. tricaulatus*) but without protruding end. The degree of thickness may be influenced by fixation.
The tail shape in general was used in the differential diagnoses of *T. aequalis* (see LOOF, 1973), *T. orientalis* and *T. sparsus*. No data were given by SHISHIDA (1979) on the thickness of the terminal cuticle in Japanese specimens of *T. aequalis*; from the figure of a male specimen we can deduce the presence of a slightly thickening of the cuticle. More specifically, the thickeness of the terminal cuticle was used as a diagnostic character in the differential diagnoses of *T. hooperi, T. orientalis, T. persicus* and *T. petrusalberti.*
In females the tail shape is always rounded, hemispherical to slightly conoid; the teminal cuticle is not thickened. The tail shape in male will be included in the NEMAID computer program.

Tail length.
This feature was only used in the species diagnosis of *T. primitivus* where females were distinguished from most other species by possessing a longer tail. This character is not included in the list for the NEMAID program.

Caudal pores.
The presence of caudal pores was only mentioned in one species diagnosis : i.e. of *T. pakistanensis* SIDDIQI, 1962. All *Trichodorus* species possess one pair of caudal pores, varying in position from subterminal to terminal. *T. coomansi, T. eburneus*, originally described with a single medioventral subterminal pore in female, and one caudal papilla in male (= diagnostic character), appeared to have a pair of pores close to each other (DE WAELE, 1983). So, this character will not be included in a general identification scheme used in the NEMAID computer program.

EXCRETORY SYSTEM

Position of excretory pore.
This character was used in the diagnoses of *T. aequalis, T. cedarus, T. coomansi, T. rinae, T. sparsus, T. variopapillatus* and *T. yokooi*. It's position was expressed in relation to the pharyngeal bulb and to the ventromedian cervical papillae; its distance from the anterior end (in µm) or the ratio = fore end to excretory pore/neck length (%) was never included in species diagnoses. The position of the excretory pore may show a great amount of variability (e.g. *T. rinae* VERMEULEN & HEYNS, 1984), so it will not be used in the NEMAID computer program.

DIGESTIVE SYSTEM

Length onchiostyle.
This character was used as a diagnostic criterion in 41 % of the species descriptions in *Trichodorus*, mainly by the range of values. The range of the mean value of the ochiostyle length within the genus was 40 µm (*T. cylindricus, T. similis*) - 147.5 µm (*T. elegans* ALLEN, 1957) = 107.5 µm for males; 40 µm (*T. cylindricus, T. similis*) - 145 µm (*T. elegans*) = 105 µm for females. Within a single species, the differences for the mean onchostyle length varied between 3 µm (*T. taylori*) and 21.4 µm (*T. aequalis*) in

males; and between 5 µm (*T. similis*) and 22 µm (*T. aequalis*) in females.
The onchiostyle length was considered as one of the most stable quantitative characters having the least variability (cf SHISHIDA, 1979 for *T. tricaulatus* and *T. aequalis*; BAUJARD, 1983 for the African specimens of *T. eburneus*). However, in a study of *T. cedarus*, SHISHIDA (1979) considered the variation in onchiostyle length (41 - 65 µm) between the Meiji Shrine populations (= from different hosts) large. Consequently, the author found the character of less value for species differentiation, although the small range of the mean values (51 - 57 µm in ♂ and 51 - 59 µm in ♀) and the low standard deviation/variation coefficient for a population of *T. cedarus* on *Cornus controversa*. The range for the onchiostyle length in *T. cedarus* lies within the range of other *Trichodorus*-species. So, the onchiostyle length appeared relatively constant between populations of a single species, although long-speared and short-speared populations are known for some species, (these populations are from different geographic origin : *T. primitivus* in HOOPER, 1962; *T. sparsus* in LOOF, 1973). The largest ranges for the absolute onchiostyle length (in µm) were given for *T. aequalus* : 29.5 (♂), 31.7 (♀); *T. californicus* : 28 (♂), 25 (♀); *T. eburneus* : 27.5 (♂), 21 ♀); *T. sparsus* : 27 (♂), 26 (♀); *T. yokooi* : 25 (♂), 15 (♀) and *T. rinae* : 23 (♂), 21 (♀).
The onchiostyle length can be used as a discriminating character but only when the difference in length between two species is more than 20 µm.

Pharynx.
Presence or absence of dorsal intestinal or ventral pharyngeal overlap. Within the genus *Trichodorus* the junction pharynx-intestine is characterized by 1) the presence of an offset pharyngeal bulb in the majority of the species (20), or 2) by a ventral overlap of the pharyngeal glands (8 species) or 3) by a dorsal overlap of the intestine (8 species). However, within a single species, one type can be found (e.g. in *T. aequalis*) of often two (*T. persicus*) or exceptionnaly three types (*T. eburneus*) can occur. They usually occur in different proportions, i.e. with one type being dominant, the other(s) rare. This character was rarely used in species diagnoses.
A slight ventral glandular overlap was observed in all specimens of *T. tricaulatus* and *T. viruliferus*; the character was used in their species diagnoses. A distinct ventral overlap was found in *T. rinae* (1/2 of the type specimens, cf DE WAELE, 1988) and in *T. eburneus* (in 75 % of the African specimens, cf BAUJARD, 1983); more rarely, a usually slight ventral overlap was observed in *T. variopapillatus, T. sparsus, T. cylindricus* and *T. cedarus*.
A distinct dorsal overlap occurs in *T. sanniae*; in most specimens of *T. taylori*, where it was used in the species diagnosis; in males and most females of *T. petrusalberti, T. persicus* and *T. orientalis*. It was also observed in about one half to one third of the specimens of *T. coomansi* and *T. proximus*, but occurred rarely in *T. eburneus, T. cylindricus* and *T. californicus*.
This character is of limited taxonomic use within this genus, partly because of its variability in some species and also by the absence of extensive studies on variability.

REPRODUCTIVE SYSTEM

Characters of female.
Presence of reflexed genital branches. Within the genus *Trichodorus* both genital branches are reflexed.
T. kurumeensis was described with the anterior branch outstretched, the posterior one reflexed. Together with *T. longistylus* (with both branches reflexed) it was synonymized with *T. cedarus*, having both branches reflexed (SHISHIDA, 1979) and thus explaining the anomaly in *T. kurumeensis*. EROSHENKO & TEPLAYAKOV, 1975 still included this character in the specific diagnosis of *T. yokooi*, closely related to *T. cedarus, T. longistylus* (= *T. cedarus*) and *T. kurumeensis* = *T. cedarus*).
So this character is of no use taxonomically in *Trichodorus*.

The vulva.
Position of the vulva; ratio V. According to LOOF (1975) the index V do not give any help at all in species differentiation in this genus. In *T. tricaulatus*, SHISHIDA (1979) concluded that the ratio V is by far the least variable of the ratios used, similarly for *T. aequalis* and *T. cedarus*. BAUJARD (1983) also found that the position of the vulva is, together with the onchiostyle length, the most stable biometric character in the African populations of *T. eburneus*. Ratio V was only used in the differential diagnosis of *T. sanniae* (V = 52-54 %) to distinguish it from *T. californicus* (V = 57-61 %) and *T. dilatatus* (V = 58 %; 54-61 %) by its more anterior position.
Since the ratio V is about the same in the great majority of species , varying between 49-64 % and with mean values between 52.5 % and 58.7 %, it will not be used in the NEMAID computer program.

Shape of vulva in ventral view. This criterion was used in the diagnoses of four species : *T. borai, T. hooperi, T. sparsus* and *T. velatus*. Generally, three main types were distinguished : a pore-like vulva (*T. aequalis, T. borai, T. borneoensis, T. complexus, T. proximus, T. sparsus, T. tricaulatus, T. viruliferus*); a transverse slit (*T. aquitanensis, T. californicus, T. cedarus, T. cottieri, T. cylindricus, T. dilatatus, T. hooperi, T intermedius, T. pakistanensis, T. similis, T. variopapillatus, T. velatus*) or a longitudinal slit (*T. rinae, T. sanniae*). In *T. orientalis*, the vulva opening was described as a large depression and in *T. taylori*, the vulva in ventral view was rounded, but not pore-like (see DE WAELE *et al.*, 1982).
Of 10 *Trichodorus* species, the shape of the vulva in ventral view is unknown, therefore this character will not be included in the list of diagnostic features used in the NEMAID computer program.

The vagina.
Shape of the vagina. This character was used in 29 % of the species diagnoses in *Trichodorus* (*T. velatus, T. variopapillatus, T. yokooi, T. cylindricus, T. borneoensi, T.*

petrusalberti, T. tricaulatus, T. taylori, T. hooperi and *T. cottieri*. It is apparently influenced by fixation or the physiological condition of e.g. the vaginal constrictor muscles (see Pl. IV DECRAEMER, 1980). The variation of vaginal shape within a single population of *T. sparsus* was shown by LOOF (1973, p. 60, fig. 7). So because of its variability, this character is of minor diagnostic importance and only to be used for species with a clearly different shape of the vagina, and in connection with the type of arrangement of the vaginal constrictor muscles (as e.g. *T. velatus, T. viruliferus*).

Shape vaginal sclerotizations. The shape of the sclerotized ring at the junction between vulva and vagina, seen laterally in longitudinal optical section, is the most important diagnostic feature for species differentiation in females of *Trichodorus* (64.6 % of the species). It was also considered a good diagnostic character by ESSER (1971) and LOOF (1975).

In *Trichodorus*, the vaginal sclerotizations are usually well developed, and clearly differentiated in shape and dimensions (Fig. 1). About eleven groups of similar vaginal sclerotizations (in lateral view) can be distinguished :

1. usually large, roughly triangular structures with the tip bent towards inner vagina : *T. californicus, T. intermedius, T. dilatatus. T. elegans*;
2. large, more or less rectangular, parallel to the longitudinal body axis : *T. cottieri, T. obscurus*;
3. large triangular pieces with their tip directed towards the vulva : *T. variopapillatus, T. similis, T. cylindricus*:
4. large triangular, equalateral structures with one side parallel to the vaginal lumen : *T. lusitanicus*;
5. large quadrangular : *T. variopapillatus, T. aquitanensis*;
6. large rounded : *T. persicus, T. taylori*;
7. minute dot-like : *T. sanniae, T. petrusalberti*;
8. small rounded : *T. hooperi*; exceptionnaly in *T. tricaulatus, T. eburneus*;
9. small triangular, oblique structures : *T. cedarus, T. eburneus, T. orientalis, T. rinae, T. sparsus, T. tricaulatus*;
10. small rounded triangular to oval : *T. borneoensis, T. aequalis, T. borai, T. coomansi, T. eburneus, T. complexus, T. proximus, T. pakistanensis, T. velatus, T. yokooi*; rarely in *T. sparsus*;
11. elongated, oval pieces, mainly parallel to the vaginal lumen : *T. primitivus, T. viruliferus*.

In general, the shape of the vaginal sclerotizations is relatively stable within a species; but some variability in shape may occur as in : e.g. in *T. variopapillatus* : from rounded triangular to rectangular, and in *T. sparsus* and *T. eburneus* from usually small triangular to (rarely) oval or rounded. The orientation of the sclerotized pieces in lateral view may vary from mainly oblique to (rarely) almost parallel with the vaginal lumen or the body wall.

Additionally, the dimensions of the inner diamater of the sclerotized ring can be helpful in species identification (see DECRAEMER, 1980, key p. 88), but will not be included in the NEMAID computer program; hereby, about two groups can be distinguished :

1. aperture of sclerotized ring small, sclerotized pieces close to one another : *T. aequalis, T. borai, T. borneoensis, T. californicus, T. cedarus, T. complexus, T. coomansi, T. cottieri, T. cylindricus, T. dilatatus, T. eburneus, T. elegans, T. intermedius, T. obscurus, T. orientalis, T. pakistanensis, T. petrusalberti, T. rinae, T. sanniae, T. similis, T. tricaulatus, T. variopapillatus, T. velatus*;
2. aperture of sclerotized ring wide (2 µm), sclerotized pieces well separated : *T. aquitanensis, T. hooperi, T. lusitanicus, T. persicus, T. primitivus, T. sparsus, T. taylori, T. viruliferus*. In a few species of the first group, some variability was observed in *T. coomansi, T. proximus, T. californicus, T. eburneus, T. orientalis, T. tricaulatus, T. yokooi*; some specimens can possess a wider aperture probably due to fixation. The shape of the vaginal sclerotization is an important diagnostic feature but minor variabilities in shape should be take into account; it will be included in the list of characters for the NEMAID computer program.

Spermathecae.

All *Trichodorus* species are bisexual and possess a spermatheca between uterus and oviduct (HOOPER, 1975). Only in the diagnosis of *T. cedarus* YOKOO, 1964, the presence of a spindle-shaped spermatheca was mentioned. In the majority of the specimens, the spermatheca is usually filled with sperm. However, when sperm is absent, the spermatheca may be very poorly developed (recorded as absent in some paratype specimens of *T. dilatatus* and *T. intermedius*, RODRIGUEZ-M & BELL, 1978). So, this character is not a useful taxonomic character in this genus and will not be considered in the NEMAID computer program.

Lateral body pores / subventral body pores. In 19 out of 34 valid *Trichodorus* species (= 56 %) the number and/or position of lateral/subventral body pores is included in the diagnoses of the species. No information is available for *T. obtusus*, and in *T. borai* the lateral body pores were not visible (RAHMAN *et al.*, 1985).

In all *Trichodorus* species, except for *T. eburneus* and *T. cedarus*, female specimens possess a pair of lateral postadvulvar body pores i.e. within one body diameter from the vulva, rarely at its level (e.g. *T. obscurus, T. viruliferus*). In *T. eburneus* and *T. cedarus*, they are located subventrally or in a ventrosubmedian position. SHISHIDA (1979) mentioned "it is likely that the ventrosubmedian pore is homologous to the posterior lateral body pore". In the NEMAID computer program we will follow SHISHIDA (1979) and consider them as a single character.

Variability in the presence of the pair of postadvulvar body pores was only mentioned for *T. sparsus* by SZCZYGIEL (1968), who also found specimens without.

Prevulvar lateral body pores were found in eleven species; variability is relatively rare : – 1) two pairs in *T. aquitanensis* and *T. primitivus*, exceptionally in *T. eburneus* : 1 ♀ on 79 ♀ (BAUJARD, 1980) and *T. petrusalberti* : only 2 specimens (DE WAELE, 1988); – 2) one pair in *T. aequalis, T. coomansi, T. eburneus, T. persicus, T. petrusalberti, T.*

proximus, T. sparsus, T. tricaulatus and *T. variopapillatus*; – 3) absent in *T. persicus* : 1 ♀ out of 12, and *T. sparsus* : exceptionally.
SHISHIDA (1979) found for *T. tricaulatus,* the location of the postvulvar body pores in relation to the vulva very variable in comparison to the prevulvar one. In *T. coomansi* however, the position of the prevulvar body pore in relation to the vulva varies from 2.9 to 5.6 times the body diameter. The anteriormost pair of prevulvar body pores usually lies relatively far from the level of the vulva, and may have been overlooked by the authors of some species. The number and position of the lateral body pores is of very limited use and will not be included in the NEMAID computer program.

Characters of male.
Spicule length. The spicule length was used in about one fourth of the species diagnoses in *Trichodorus,* mainly expressed by their absolute value, sometimes in terms of proportions. The range of the mean value of the spicule length within the genus was 39 µm i.e. from 28 µm (*T. viruliferus*) to 67 µm (*T. petrusalberti*). Within a single species the differences for the mean spicule length varied between 1 µm (*T. taylori, T. yokooi*) and 13 µm (*T. aequalis*). The absolute spicule length varied from 26 µm (*T. viruliferus*) to 71 µm (*T. petrusalberti*); intraspecific, the maximum range for the absolute spicle length was 27 µm (*T. californicus*). According to LOOF (1973), the spicule length showed great variation (41-65 µm) among several populations of *T. sparsus,* with a difference of 12.5 µm between the mean value of the different populations. The author noted an overlap in spicule length between *T. aequalis* and *T. sparsus.* SHISHIDA (1979) found that the spicule length showed the least variability of all quantitative characters in *T. tricaulatus* with coefficient of variation 6.5 %, in *T. aequalis* (1.7 %), *T. cedarus* (4.1 %).
The spicule length is useful as differentiating character and is included in the NEMAID computer program, taking a variability range of 13 µm into account.

Spicule shape. This character is the most important diagnostic feature for species differentiation in *Trichodorus* (Table 1). It reflects the presence of a high degree of interspecific differentiation. About seven groups of spicule shapes can be recognized :

A. Spicules with a constriction at mid-corpus (Fig. 2 : A-E) : *T. lusitanicus, T. orientalis, T. sanniae, T. velatus* and *T. viruliferus.* This constriction is usually located at the posterior border of the capsule of suspensor muscles. Some other species (e.g. *T. aequalis, T. hooperi, T. proximus* and *T. eburneus*) have at this level only a slightly marked narrowing of the spicule corpus;
B. Spicules proximally clearly curved ventrad, mid-corpus straight, distal tip straight of slightly ventrally bent (Fig. A, F-J; 3 I) : *T. eburneus, T. pakistanensis* (rarely), *T. rinae, T. persicus, T. petrusalberti, T. pakistanensis, T. sanniae, T. sparsus* (rarely); in the last three species some variability may be found in the corpus curvature;
C. Spicules with wide proximal part, tapering to a fine to very slender corpus (Fig. 2 K-N) : *T. dilatatus, T. aquitanensis, T. primitivus, T. hooperi* (less pronounced);
D. Spicules with capitulum clearly offset from calamus (Fig. 3 : A-F) : elongated : *T. taylori*; knob-like : *T. variopapillatus, T. similis, T. complexus, T. californicus, T. coomansi* (less pronounced);
E. Spicules with enlarged posterior corpus (Fig. 2 : Q-S) : *T. cylindricus, T. cottieri, T. obscurus*;
F. Spicules with long wide anterior end; cuticle of corpus deeply grooved (Fig. 2 : O-P) : *T. yokooi, T. tricaulatus*;
G. Spicules with corpus about equally wide, slightly tapered posteriorly (Fig. 3 : G, H, J-P) : *T. borai, T. aequalis, T. proximus, T. obtusus, T. elegans, T. sparsus, T. cedarus, T. borneoensis,* and *T. intermedius.*

The spicule shape is a good character for species differentiation. Variation is minor, only seen in slight differences in the degree of the curvature of the spicule corpus.

Ornamentation of spicules.
The ornamentation is rather diverse : – 1. smooth spicules (*T. sanniae, T. orientalis, T. primitivus, T. aquitanensis, T. hooperi, T. petrusalberti, T. borai, T. aequalis, T. proximus, T. obtusus, T. similis, T. variopapillatus*), – 2. transverse striae, except at both extremities (*T. pakistanensis, T. dilatatus, T. eburneus, T. persicus, T. yokooi, T. tricaulatus, T. elegans, T. cedarus, T. borneoensis, T. intermedius, T. taylori, T. complexus, T. coomansi, T. californicus, T. cylindricus, T. cottieri, T. obscurus*), – 3. the presence of a ventral flange (*T. velatus*), and – 4. the presence of bristles (*T. viruliferus, T. velatus, T. dilatatus, T. sparsus, T. variopapillatus, T. similis, T. californicus, T. cylindricus, T. tricaulatus*).
A study of trichodorid spicules under SEM by RODRIGUEZ-M & Bell (1979) revealed that the spicular ornamentation observed by LM are scales or derivations of scales (cf *T. tricaulatus* in SHISHIDA, 1979), forming an additional sheath covering the spicule body (= inner core of spongy material surrounded by a thick cuticle). The fine transverse striations appeared to be the origin or suture point of scales with the spicule body. Under the light microscopy, the distal ends of the scales sometimes looked separated from the spicule body (= bristles). These bristles are often difficult to observe, especially in retracted spicules; so setosity is considered of minor diagnostic importance and will not be included in the NEMAID computer program, although it was considered a good character by LOOF (1973). The other ornamentations are useful diagnostic features, present in the list of characters for the NEMAID program.

Caudal alae.
In contradiction to *Paratrichodorus,* caudal alae are not or poorly developed in the genus *Trichodorus.*
T. cylindricus is the only species were the presence of caudal alae, although inconspicuous, are considered as a diagnostic feature (HOOPER, 1962).
YOKOO (1964) described the presence of a small delicate bursa in *T. longistylus* as a diagnostic feature. *T. longisty-*

lus, based upon badly fixed specimens, was synonimized with *T. cedarus*, and further studies gave no evidence of the presence of caudal alae.

T. sparsus was described with "caudal alae absent" (Szczygiel, 1968). Loof (1973) redescribed the type population of *T. sparsus* and mentioned the presence of a thickened cuticle ventrolaterally in the male tail region as in *T. cylindricus* and also the male tail being ventrally concave suggesting the presence of lateral alae.

T. hooperi males were described by Loof (1973) as possessing a slightly thickened cuticle ventrolaterally in the precloacal region, but less strongly than in *T. sparsus*. However, no reference was made to caudal alae.

T. pakistanensis Siddiqi, 1962 was described with bursa absent in males, but the lateral cuticle of the tail sometimes gave a slight indication of a bursa.

The absence of caudal alae was included in the species diagnoses of *T. cedarus* by Mamiya (1967), *T. pakistanensis* and *T. viruliferus*.

Since caudal alae are only present in *T. cylindricus*, it is not included in the list of diagnostic characters used in the NEMAID computer program.

Precloacal ventromedian supplementary papillae (SP).

Number. This feature was mentioned in the diagnoses of 35 % of the species of the genus, although the number of precoacal ventromedian supplementary papillae is always three, rarely with a few exceptions (= "abnormal" specimens) : four SP in two out of 263 specimens of *T. cedarus* (Shishida, 1979), in two specimens of *T. hooperi* (Loof, 1973) and in one specimen of *T. eburneus* (= African specimens in Baujard, 1983); only two SP in one specimen of *T. sparsus* (Loof, 1973).

So this feature is not a useful diagnostic character in this genus.

Position. The position of the three precloacal ventromedian supplementary papillae was considered a diagnostic feature in 25 of the 34 valid *Trichodorus* species; in 13 of them it was expressed in relation to the spicular region by : – 1. the number of SP within spicular range, or – 2. the position of the posteriormost supplement (SP1) or – 3. in one species, by the position of the middle supplement (SP2) in relation to the retracted spicules.

In descriptions, their position was expressed by their respective distance from the cloacal opening (in µm, or in body widths, or as % of the body length or exceptionally, in length of spicules), or by the respective distance cloaca-SP1, SP1-SP2, SP2-SP3 (in µm, or in bodywidths); additionally, the proportions of the distances SP1-SP2 against SP2-SP3 were discussed.

Shishida (1979) found for *T. cedarus*, the distribution of precloacal supplements in relation to the spicules very stable. In *T. tricaulatus*, the distance of SP1-cloaca appeared the least variable, the distance SP2-SP3 the most, so the author concluded that the location of the posteriormost supplement (SP1) in relation to the spicules is another diagnostic character.

Baujard (1983) calculated that the position of the three precloacal supplements expressed by the proportion of their respective distances from the anterior body end in relation to the body length (variation coefficient (V.C.) 0.006-0.014) is far more stable than their position expressed by their absolute distance from the cloacal opening (V.C. 0.058-0.074).

Hooper (1963) found for *T. viruliferus* that the position of the three precloacal supplements was variable. As Shishida (1979), he stated that the position of SP1 was fairly constant, but the distance of SP1-SP2 and SP2-SP3 varied respectively between 1-1.5 and 2-3.5 body widths.

In more than 50 % of the *Trichodorus* species, the majority of the specimens have the posteriormost ventromedian papilla (SP1) located near the proximal end of the spicules. The position of precloacal papillae in relation to the spicules, can be used to define four groups of species in *Trichodorus*.

1. Species with one precloacal supplement clearly within spicule range, i.e. not at proximal end of spicule : *T. aquitanensis, T. cedarus, T. cottieri, T. cylindricus, T. elegans, T. petrusalberti, T. taylori.*
2. Species with the posteriormost supplement near the proximal end of retracted spicules (accepting a small range of variability from just anterior to just posterior to the spicule head) : *T. aequalis, T. borai, T. complexus, T. coomansi, T. eburneus, T. hooperi, T. obtusus, T. orientalis, T. pakistanensis, T. persicus, T. primitivus, T. proximus, T. rinae, T. sanniae, T. similis, T. sparsus, T. variopapillatus, T. velatus, T. viruliferus.*
3. Species with two supplements within spicular range (the location of the second supplement at about the spicule head, with a small range of variation) : *T. intermedius* and *T. borneoensis, T. californicus, T. dilatatus, T obscurus.*
4. Species without precloacal supplements in spicule range : *T. lusitanicus, T. tricaulatus, T. viruliferus, T. yokooi,* and mostly in *T. eburneus* (African specimens).

As the position of the precloacal supplements in relation to the spicules is a rather useful diagnostic character (taking a slight variability into account), it will be included in the NEMAID program.

Gubernaculum.

Length. This feature was mentioned only in two species diagnoses of *T. complexus* (by the absolute value) and *T. yokooi* (by the relative value). In general little attention has been payed to the gubernaculum. In several species descriptions its length is only given for the holotype; data on variability are poor. Shishida (1979) found that the length of the gubernaculum is one of the characters showing the least variability in *T. cedarus*. In *T. tricaulatus* however, the gubernaculum length appeared the most variable quantitative character.

Within the genus *Trichodorus*, the mean gubernaculum length varied between 4.5 µm (*T. orientalis*) and 26.0 µm (*T. petrusalberti*). The intraspecific variability between mean gubernaculum length was ranged between 0 µm (*T. taylori*) and 4 µm (*T. cedarus, T. viruliferus*). The absolute value of the gubernaculum lies between 4 µm (*T. orienta-*

lis) and 29 µm (*T. petrusalberti*) with a maximum intraspecific difference of 12 µm (*T californicus*).
Two thirds of the species have a mean gubernaculum length between 16-23 µm, only three species have a very short gubernaculum (10 µm) : *T. persicus, T. taylori, T. orientalis,* and two species have a long gubernaculum (mean length 25 µm) : *T. californicus, T. petrusalberti.* So the use of the gubernaculum length as diagnostic feature is rather restricted, and for use in the NEMAID program a variability from the mean value of 4 µm will be taken into account.

Shape. The shape of the gubernaculum was considered a diagnostic character in the diagnoses of *T. aquitanensis, T. cedarus, T. cylindricus, T. primitivus *, T. rinae, T. similis *, T. tricaulatus, T. viruliferus* and *T. yokooi **; in the * marked species correlated with their position in relation to the spicules.
The gubernaculum is a cuticular thickening of the dorsal wall of the cloaca, and consists merely of a thin linear platelike corpus with a keel-like thickening at its distal end and a thin ventro-medial extension (cuneus), projecting between the spicules; the cuneus, more difficult to observe, is rarely pictured.
In a few species the shape of the gubernaculum is slightly different : in *T. aquitanensis* and *T. primitivus,* the corpus of the gubernaculum is anteriorly convex for most of its length (only its distal part is flat), and so lying between the spicules, occasionally even ventral instead of dorsal to them (Seinhorst, 1963; Baujard, 1980). In *T. cylindricus* and *T. viruliferus,* gubernaculum with anterior two thirds spatulate (= cuneus), lying between the spicule shafts; corpus in distal part as typical for the genus, with distinct keel, ending on a finer process.
Since the shape of the gubernaculum is similar for most *Trichodorus* species, it is of limited diagnostic value in the genus and of little use in the NEMAID computer program.

Ventromedian cervical pores (CP).
Number. This feature appeared in 70.5 % of the species diagnoses of *Trichodorus.* No date were available for *T. obtusus.* Their number varied between zero and four; the majority of species have two or three pores : 0 CP (2 species), 1 CP (13 species), 2 CP (15 species), 3 CP (12 species) and 4 CP (1 species), variability was rare. Restricted variability was found in 5 species : *T. cedarus* : 3 CP in 253 out of 263 specimens, 4 CP in 1 specimen, 2 CP in 8 specimens, 1 CP in 2 specimens), *T. coomansi* (usually 2 CP except 1 ♂ with 3 CP), *T. eburneus* (usually 1 CP, 1 African ♂ without), *T. persicus* (usually 2 CP; out of 18 : 1 ♂ with 1 CP, 1 ♂ with 3 CP), *T. sparsus* (2 CP, 1 ♂ with 1 CP). Only in two species the variability was relatively high in the type population : in *T. tricaulatus* 23 % (20 ♂ out of 26 : 3 CP, 4 ♂ with 2 CP, 2 ♂ with 1 CP), and *T. variopapillatus* up to 50 % (half of population with 2 CP, the other half with 3 CP; Italian specimens : 3 CP).
The number of ventromedian cervical pores is a good diagnostic character taking some variability into account; it is used in the NEMAID computer program.
Position. This feature was included in 53 % of the species diagnoses. In the diagnoses of species, their position was expressed in relation to the excretory pore (13 species), or to the base of the onchostyle (6 species). The position of the CP was indicated by the distance (in µm) from the anterior body end (only in recent descriptions), or from the excretory pore (in µm, rarely in bodywidth), or by their interdistance, or from the base of the onchiostyle (in proportions of length onchiostyle).
From the few data available (5 species) appeared that the distance of the first ventromedian cervical pore to the anterior body end was rather constant (C.V. = 5.4-9.3 in *T. coomansi, T. eburneus, T. persicus*) but variable in *T. petrusalberti* and *T. rinae* (V.C. = 15.6-16.4).
The position of the CP in relation to the excretory pore (EP) appeared rather constant i.e. all pores were located anteriorly to the excretory pore in the majority of the species (26); exceptionally some variability was found in only five species : *T. coomansi, T hooperi, T. persicus, T. rinae* and *T. sparsus,* and restricted to a few "diverging" specimens.
The excretory pore was situated in between the ventromedian cervical pore (i.e. with 1 CP posterior to it) in *T. pakistanensis, T. coomansi, T. rinae* and some rare specimens of *T. hooperi* (1 ♂), *T. persicus* (1 ♂), *T. sparsus* (3 ♂). Rarely the ventromedian cervical papillae were all situated posteriorly to the excretory pore as in *T. sanniae and a few specimens of T. coomansi* (2 ♂) and *T. rinae* (1 ♂). In species with two or more ventromedian cervical pores, the distance between the anterior two pores was usually larger and less variable than the distance between the posteriormost pore and the excretory pore; however, in several populations some males were found with these distances being equal, and exceptionally reversed (Loof, 1973; Shishida, 1979, De Waele & Sturhan, 1987). The position of the ventromedian cervical pores in relation to the excretory pore will not be included in the NEMAID computer program.
In *T. aquitanensis* only, the presence of ventromedian cervical pores in the onchiostyle region was considered a diagnostic character. The occurrence of CP in the onchiostyle region is limited to 8 species : *T. aquitanensis* (1 or 2 CP), *T. cylindricus* (1 CP), *T. lusitanicus* (1 CP), *T. orientalis* (1 CP), *T. primitivus* (1 or 2 CP), *T. similis* (1 or 0 CP), *T. variopapillatus* (1 CP), *T. velatus* (1 CP). The presence of ventromedian cervical pores in the onchiostyle region of *T. cedarus* types (see Yokoo, 1964) was only a result of shrinkage of the body in the badly fixed specimens; in all other specimens studied, no evidence of CP in the onchiostyle region was ever found.
Wyss (1974) remarked for *T. similis* that the arrangement of CP in relation to the onchiostyle is variable : CP1 usually opposite the posterior third of the onchiostyle, may be opposite or even behind the onchiostyle base.
The presence of ventromedian cervical pores in the onchiostyle region may show some variability in a restricted number of specimens but can be used taxonomi-

cally; it will be considered as a differentiating character in the NEMAID computer programm, but taking some rare variability into account.

Lateral cervical pores. One pair of lateral cervical pores was usually observed in *Trichodorus* species; in *T. complexus* it was not found; in *T. borneoensis, T. hooperi, T. intermedius, T. obtusus, T. sparsus, T. yokooi* no data were available.
Its position is apparently rather constant; it was described in relation to the position of the ventromedian cervical pores, the base of the onchiostyle, the excretory pore, the nerve ring or exceptionally by its distance (in µm) from the anterior body end. In *T. cottieri* and *T. dilatatus* the position of the lateral cervical pores was included in their specific diagnoses. According to the position of the pair of lateral cervical pores we could distinguish the following species groups in *Trichodorus* :

1. lateral cervical pores in onchiostyle region (at 1/3 from onchiostyle base) : *T. aquitanensis, T. primitivus*;
2. lateral cervical pores near base onchiostyle (i.e. anterior to the nerve ring) : *T. borai, T. cylindricus, T. lusitanicus, T. similis, T. variopapillatus, T. velatus, T. viruliferus*;
3. lateral cervical pores situated between level nerve ring and anterior end pharyngeal bulb : *T. aequalis, T. californicus, T. cedarus, T. coomansi, T. cottieri, T dilatatus, T. eburneus, T. elegans, T. obscurus, T. orientalis, T. pakistanensis, T. persicus, T. proximus, T. taylori, T. tricaulatus*:
4. lateral cervical pores at level mid-pharyngeal bulb : *T. petrusalberti*;
5. lateral cervical pores near base of pharynx; *T. rinae, T. sanniae*.

This character will be included in the general NEMAID computer program as an additional character of minor importance since too few data on its variability were available.

Reflection on new or rarely used diagnostic characters

Sperm cells.
A useful diagnostic feature in *Paratrichodorus,* appears to be of minor importance in the genus *Trichodorus.* Most *Trichodorus* species have more or less oval cells with a sausage-shaped nucleus (e.g. *T. cottieri*); rarely globular cells with globular nucleus (e.g. *T. dilatatus*). Species differentiation is mainly found in the dimension of the sperm cells, exceptionally in structure. A fibrillar structure of the sperm cell is visible in most species (Decraemer, 1989). At present, data on the structure of the sperm cells are only available for 60 % of the *Trichodorus* species. This feature will not be included in the list of diagnostic characters as base for the NEMAID computer program.

Geographicalic distribution.
Since some species are likely to occur in some geographic locations and not or rarely in others, a first hint in species identification in *Trichodorus* can be based upon a classification of the species according to their main geographic distribution, as far as available :

1. Europe : *T. aquitanensis* (west), *T. cylindricus* (west, east), *T. hooperi* (west), *T. lusitanicus* (south), *T. primitivus* (west, east, north), *T. similis* (west, east, north, south), *T. sparsus* (west, east, north), *T. taylori* (south), *T. varipapillatus* (west, east, south), *T. velatus* (west, east), *T. viruliferus* (west, east, south);
2. U.S.A. : *T. aequalis, T. californicus, T. cedarus, T. dilatatus, T. elegans, T. intermedius, T. obscurus, T. obtusus, T. pakistanensis, T. primitivus, T. proximus, T. similis, T. viruliferus*;
3. Africa : *T. coomansi* (east), *T. eburneus* (west), *T. petrusalberti* (south), *T. rinae* (south), *T. sanniae* (south);
4. Asia : *T. aequalis* (Japan), *T. borneoensis, T. borai* (India), *T. cedarus* (Japan), *T. complexus* (India), *T. orientalis* (Iran), *T. persicus* (Iran), *T. pakistanensis, T. tricaulatus* (Japan), *T. yokooi* (east of U.S.S.R.);
5. Oceania : *T. cottieri* (New Zealand).

Conclusions

The intraspecific variability of several diagnostic features, makes the use of traditional dichotomous keys difficult. Too many entries for a single species have to be included, which would make the dichotomous key unconvenient. So, new methods using a computer to identify species have been proposed (see the NEMAID computer program by Fortuner & Wong, 1984).
From this study a list of useful diagnostic characters can be deduced for species identification in *Trichodorus* Table 2).
This list will serve as base for the creation of a genus database for *Trichodorus* for the NEMAID program.

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Table 1 :
List of *Trichodorus* species.

T. acaudatus SIDDIQI, 1960 : see *P. acaudatus* (SIDDIQI, 1960) SIDDIQI, 1974.
T. acutus BIRD, 1967 : see *P. acutus* (BIRD, 1967) SIDDIQI, 1974.
T. aequalis ALLEN, 1957.
T. alleni ANDRASSY, 1968 : see *P. alleni* (ANDRASSY, 1968) SIDDIQI, 1974.
T. allius JENSEN, 1963 : see *P. allius* (JENSEN, 1963) SIDDIQI, 1974.
T. anemones LOOF, see *P. anemones* (LOOF, 1965) SIDDIQI, 1974.
T. aquitanensis BAUJARD, 1980.
T. atlanticus ALLEN, 1957 : see *P. atlanticus* (ALLEN, 1957) SIDDIQI, 1974.
T. borai RAHMAN, JAIRAJPURI & AHMAD, 1985.
T. borneoensis HOOPER, 1962.
T. bucrius LORDELLO & ZAMITH, 1958 : syn. of *P. porosus* (ALLEN, 1957).
T. californicus ALLEN, 1957.
T. castellanensis ARIAS, JIMINEZ & LOPEZ, 1965 : syn. of *T. primitivus* (DE MAN, 1880) MICOLETZKY, 1922.
T. cedarus YOKOO, 1964 : syn. *T. kurumeensis* YOKOO, 1966; syn. *T. longistylus* YOKOO, 1964.
T. christiei ALLEN, 1957 : see *P. christiei* (ALLEN, 1957) SIDDIQI, 1974 : syn of *P. minor* (COLBRAN, 1956) SIDDIQI, 1974.
T. clarki YEATES, 1967 : syn. of *P. lobatus* (COLBRAN, 1965) SIDDIQI, 1974.
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. elegans ALLEN, 1957.
T. flevensis KUIPER & LOOF, 1962 : syn of *P. teres* (HOOPER, 1962) SIDDIQI, 1974.
T. granulosus (COBB, 1920) MICOLETZKY, 1922 : see *Leptonchus granulosus* COBB, 1920.
T. hooperi LOOF, 1973.
T. intermedius RODRIGUEZ-M & BELL, 1978.
T. kurumeensis YOKOO, 1966 : syn. of *T. cedarus* YOKOO, 1964.
T. litchi EDWARD & MISRA, 1970 : syn. of *T. pakistanensis* SIDDIQI, 1962.
T. lobatus COLBRAN, 1965 : see *P. lobatus* (COLBRAN, 1965) SIDDIQI, 1974.
T. longistylus YOKOO, 1964 : syn. of *T. cedarus* YOKOO, 1964.
T. lusitanicus SIDDIQI, 1974.
T. minor COLBRAN, 1956 : see *P. minor* (COLBRAN, 1956) SIDDIQI, 1974.
T. mirzai SIDDIQI, 1960 : see *P. mirzai* (SIDDIQI, 1960) SIDDIQI, 1974.
T. monohystera ALLEN, 1957 : see *M. monohystera* (ALLEN, 1957) ANDRASSY, 1976.
T. musambi EDWARD & MISRA, 1970 : syn. of *P. mirzai* (SIDDIQI, 1960) SIDDIQI, 1974.
T. nanus ALLEN, 1957 : see *P. nanus* (ALLEN, 1957) SIDDIQI, 1974.
T. obscurus ALLEN, 1957 : syn. of *T. primitivus* apud THORNE, 1939 and GOODEY, 1951.
T. obtusus COBB, 1913.
T. orientalis DE WAELE & HASHIM, 1984.
T. pachydermus SEINHORST, 1954 : see *P. pachydermus* (SEINHORST, 1954) SIDDIQI, 1974.
T. pakistanensis SIDDIQI, 1962 : syn. of *T. litchi* Edward & Misra, 1970.
T. persicus DE WAELE & STURHAN, 1987.
T. petrusalberti DE WAELE, 1988.
T. primitivus (DE MAN, 1880) MICOLETZKY, 1922 : syn. of *Dorylaimus primitivus* DE MAN, 1880; syn. *T. castellanensis* ARIAS DELGADO, JIMINEZ MILLAN & LOPEZ PEDREGAL, 1965.
T. proximus ALLEN, 1957.
T. rhodesiensis SIDDIQI & BROWN, 1965 : see *P. rhodesiensis* (Siddiqi & Brown, 1965) SIDDIQI, 1974.
T. rinae VERMEULEN & HEYNS, 1984.
T. sanniae VERMEULEN & HEYNS, 1984.
T. similis SEINHORST, 1963.
T. sparsus SZCGYGIEL, 1968.
T. taylori DE WAELE, MANCINI, ROCA & LAMBERTI, 1982.
T. teres HOOPER, 1962 : see *P. teres* (HOOPER, 1962) SIDDIQI, 1974.
T. tricaulatus SHISHIDA, 1979.
T. tunisiensis SIDDIQI, 1963 : see *P. tunisiensis* (SIDDIQI, 1963(SIDDIQI, 1974.
T. variopapillatus HOOPER, 1972.
T. velatus HOOPER, 1972.
T. viruliferus HOOPER, 1963.
T. yokooi EROSHENKO & TEPLYAKOV, 1975.

Table 2 :
List of identification criteria retained for the species of the genus *Trichodorus*.

1. *List of quantitative characters :*

Characters	*Weights*	*Range mean values*	*Correction factors*
1. onchiostyle length	0.6	40-147.5 µm	22 µm
2. spicule length	0.8	28-67 µm	13 µm
3. gubernaculum length	0.4	4.5-26 µm	4 µm
4. number ventro-median cervical pores	0.8	0-4	2

2. *List of qualitative characters :*

TWO-STATE CHARACTERS (variable in some (species) : weights
5. tail shape : cuticle thickened and protruding or not 0.7
6. position ventromedian cervical pores in relation to onchiostyle : in onchiostyle region / outside 0.6

THREE-STATE NON VARIABLE CHARACTERS (present / absent) :
7. shape vulva in ventral view : pore-like / a transverse slit / a longitudinal slit 1.0

THREE-STATE CHARACTERS (variable in some species) :
8. pharyngo-intestinal junction : bulb offset / ventral overlapping pharyngeal glands / dorsal overlapping intestine 0.5
9. ornamentation spicules : smooth / with transverse striae with ventral flange 0.8
10. position precloacal supplements (SP) in relation to retracted spicules : 2 SP in spicular region / 1 SP clearly in spicular region (not near head spicules) / 1 SP near proximal end spicules 0 SP in spicule region 0.6

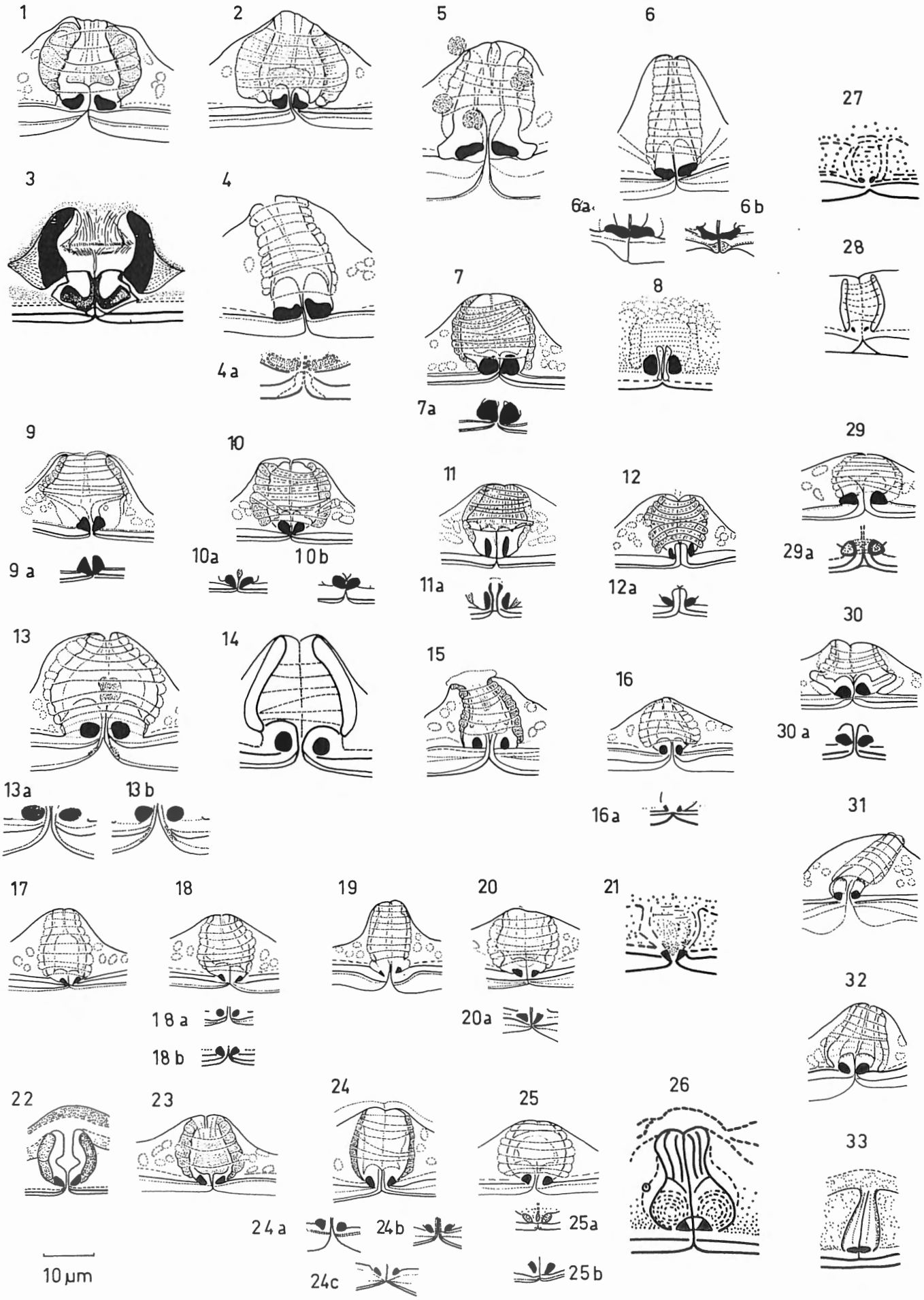
MULTISTATE CHARACTERS
11. shape vaginal sclerotizations 0.8
12. shape spicules 0.9
13. position lateral cervical pores 0.7
14. geographic distribution 0.5

Fig. 1. – Vaginal region and variability of vaginal sclerotizations in *Trichodorus* (after DECRAEMER, 1989). – *1 : T. californicus (redrawn after Decraemer, 1980), 2 : T. dilatatus, 3 : T. intermedius (redrawn after Rodriguez M. & Bell, 1978), 4-4a : T. elegans (4a redrawn after Allen, 1957), 5 : T. cottieri, 6, 6a-b : T. obscurus (6b redrawn from Decraemer, 1980), 7-7a : T. variopapillatus (redrawn from Decraemer, 1980), 8 : T. aquitanensis (redrawn from Baujard, 1980), 9-9a : T. similis (redrawn from Decraemer, 1980), 10, 10a-b : T. cylindricus (redrawn from Decraemer, 1980), 11-11a : T. primitivus (redrawn from Decraemer, 1980), 12-12a : T. viruliferus (redrawn from Decraemer, 1980), 13, 13a-b : T. taylori, 14 : T. persicus (redrawn from De Waele & Sturhan, 1987, 15 : T. hooperi (redrawn from Decraemer, 1980), 16-16a : T. tricaulatus (16a redrawn from Shishida, 1979), 17 : T. cedarus, 18, 18a-b : T. eburneus, 19 : T. orientalis, 20-20a : T. coomansi, 21 : T. rinae (redrawn from Vermeulen & Heyns, 1984), 22 : T. borai (redrawn from Rahman et al., 1985), 23 : T. aequalis (redrawn from Decraemer, 1980), 24, 24a-c : T. sparsus (redrawn from Decraemer, 1980), 25, 25a-b : T. proximus (25a redrawn from Allen, 1957), 26 : T. yokooi (redrawn from Eroshenko & Teplyakov, 1975), 27 : T. sanniae (redrawn from Vermeulen & Heyns, 1984), 27 : T. petrusalberti (redrawn from De Waele, 1988), 29 29a : T. lusitanicus (29a redrawn from Siddiqi, 1974); 30-30a : T. velatus (30a redrawn after Hooper, 1972), 31 : T. pakistanensis, 32 : T. borneoensis, 33 : T. complexus (redrawn after Rahman et al., 1985).* ▷

Fig. 2. – Tail and copulatory apparatus in *Trichodorus. – A : T. velatus. - B : T. sanniae (redrawn from De Waele, 1988). - C : T. viruliferus. - D : T. orientalis (redrawn De Waele & Haslim, 1984). - E : T. lusitanicus (paratype). - F : T. eburneus (holotype). - G : T. pakistanensis (paratype). - H : T. sparsus (redrawn from Loof, 1973). - I : T. rinae (redrawn from De Waele, 1988). - J : T. persicus (redrawn from De Waele & Sturhan, 1987). - K : T. dilatatus (paratype). - L : T. aquitanensis (redrawn from Baujard, 1980). - M : T. primitivus (redrawn from Decraemer, 1980). - N : T. hooperi (redrawn from Loof, 1973). - O : T. yokooi (redrawn from Eroshenko & Teplyakov, 1975). - P : T. tricaulatus (paratype). - Q : T. cottieri. - R : T. cylindricus (redrawn from Decraemer, 1980). - S : T. oscurus (redrawn from Decraemer, 1980).* ▷

Fig. 3. – Tail and copulatory apparatus in *Trichodorus. – A : T. taylori (paratype). - B : T. coomansi (paratype). - C : T. variopapillatus. - D : T. complexus (redrawn from Rahman et al., 1985). - E : T. californicus. - F : T. similis. - G : T. proximis. - H : T. sparsus. - I : T. petrusalberti (redrawn from De Waele, 1988). - J : T. borai (redrawn from Rahman et al., 1985). - K : T. aequalis (redrawn from Allen, 1957). - L : T. obtusus (redrawn from Cobb, 1913). - M : T. elegans. N : T. intermedius (paratype). - O : T. borneoensis (paratype). - P : T. cedarus. (figs. E-H redrawn from Decraemer, 1980).* ▷

Fig. 4. – Sperm cells in *Trichodorus. – 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. taylori. - P : T. cedarus. - Q : T. tricaulatus. - R : T. variopapillatus. - S : T. velatus. - T : T. viruliferus.* ▷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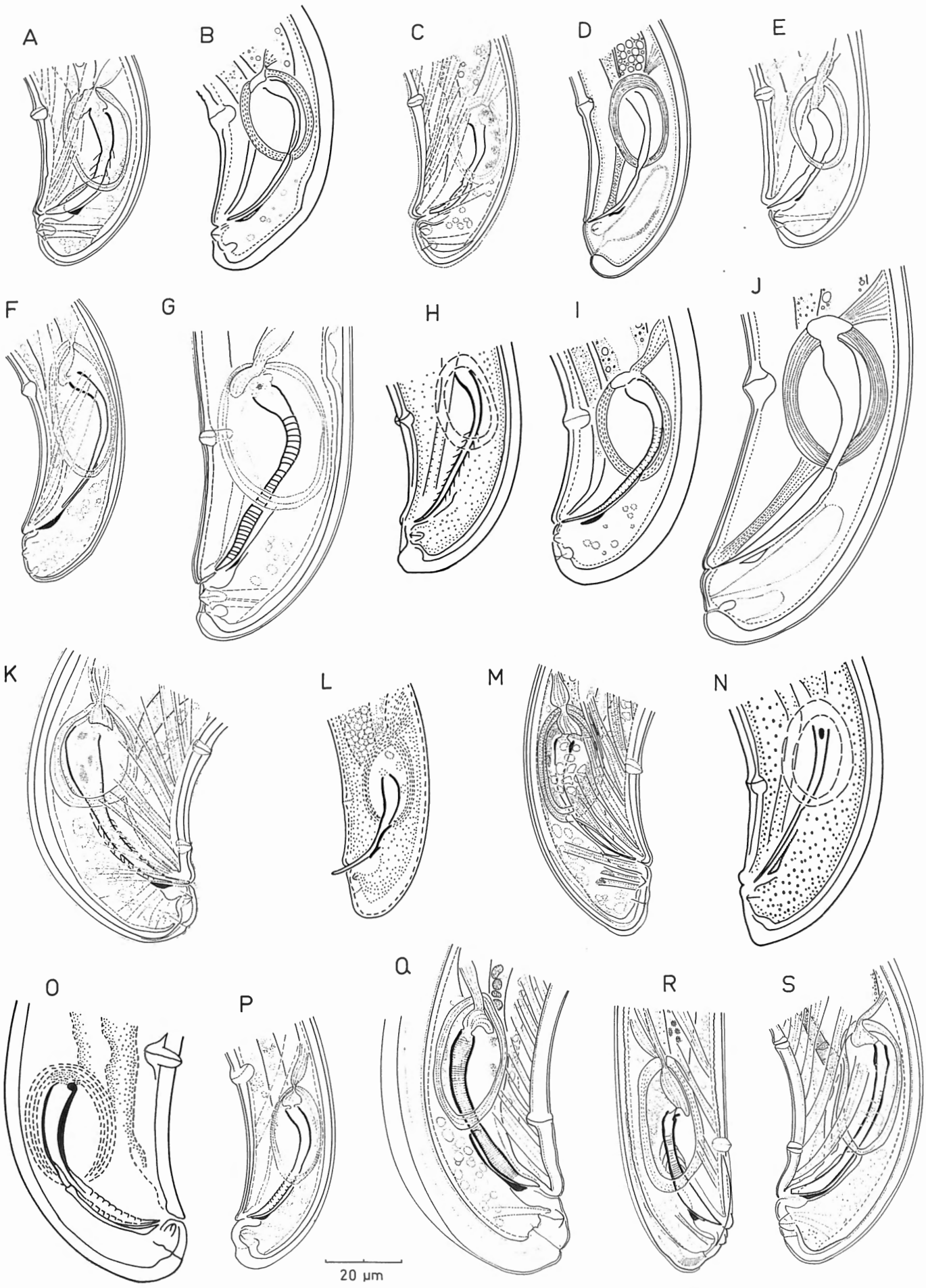
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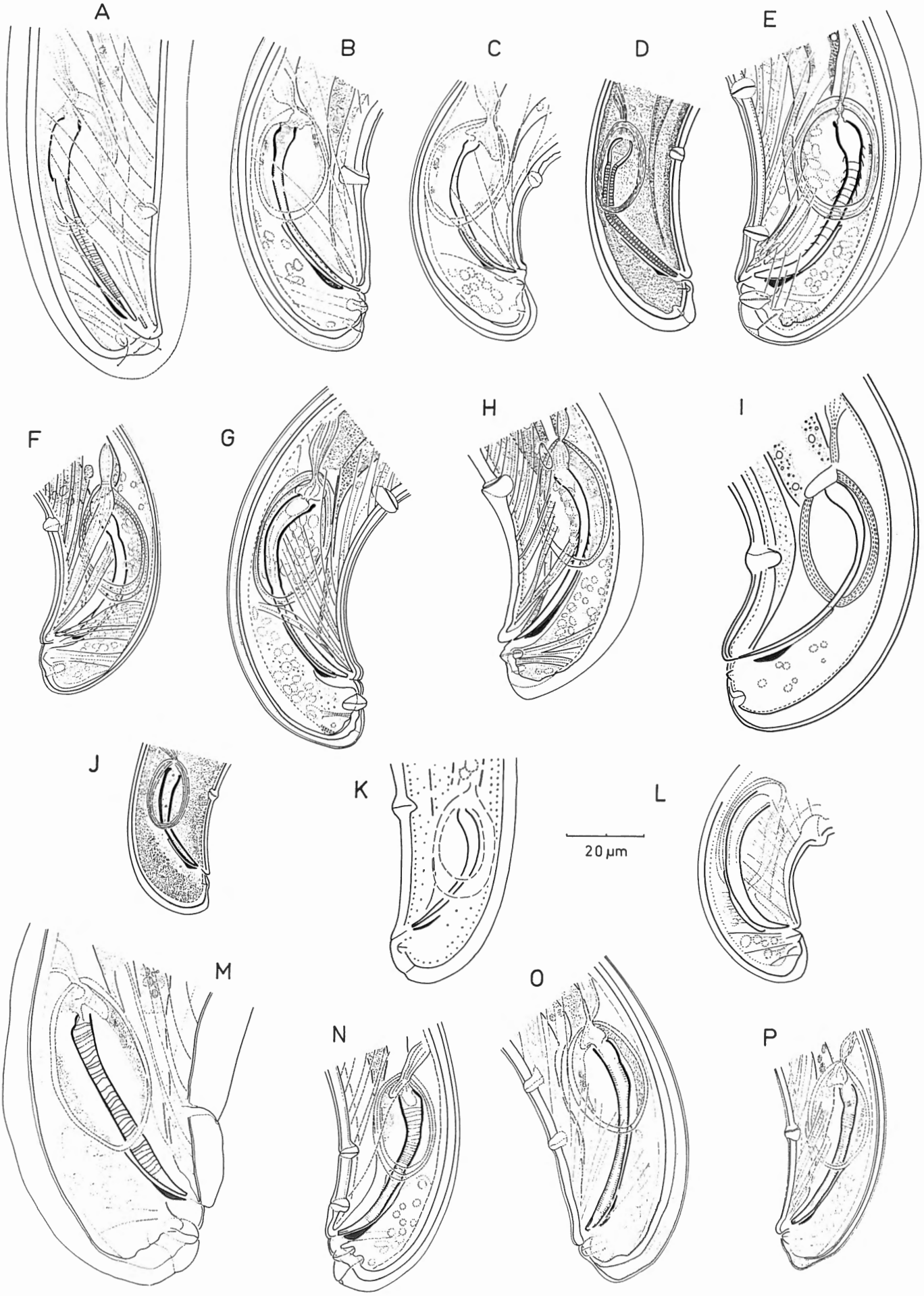
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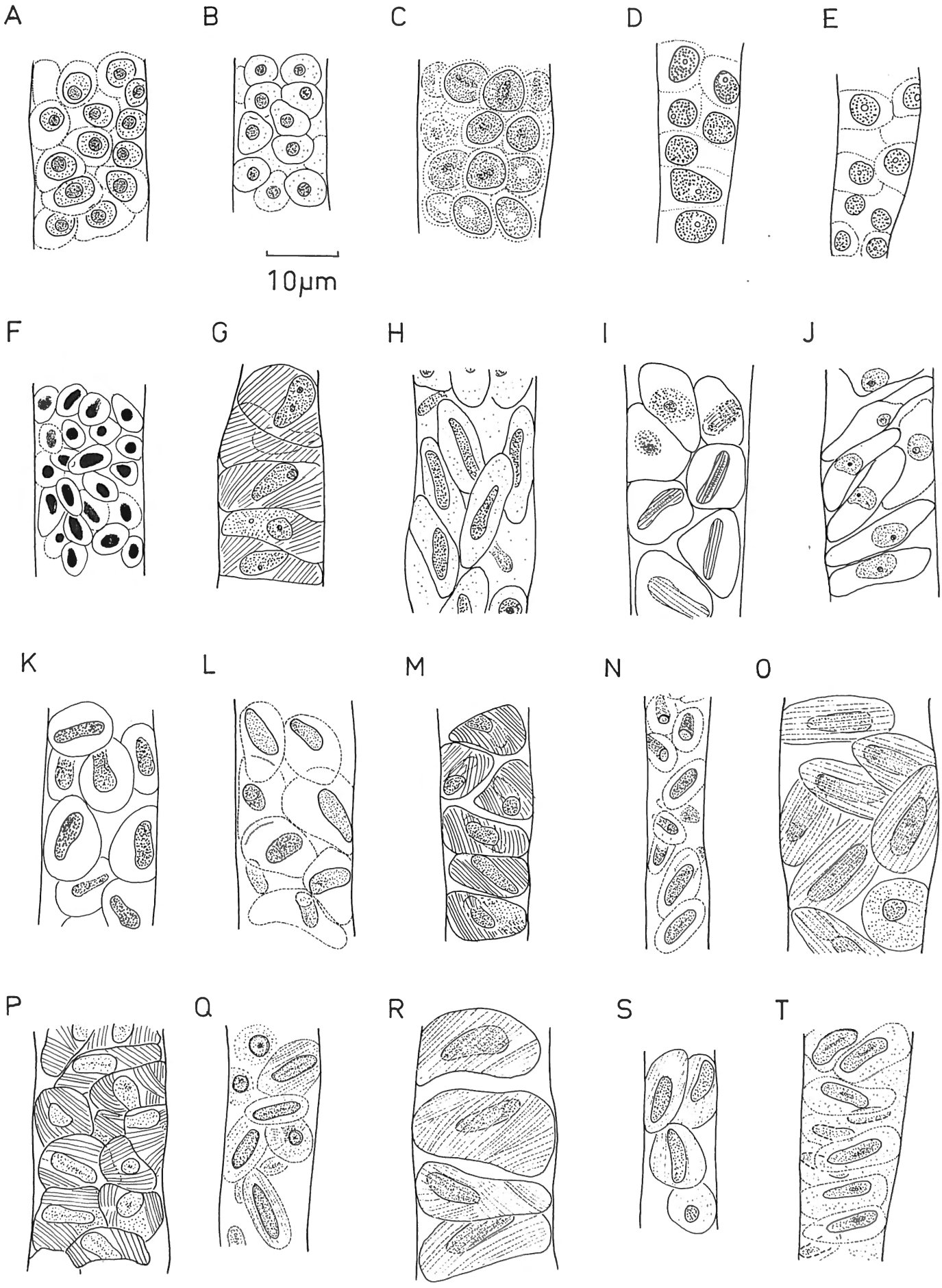
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