

Morphometrical variability in *Helicotylenchus* Steiner, 1945. 3 : Observations on African populations of *Helicotylenchus dihystra* and considerations on related species

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SUMMARY

Multivariate analyses were used to compare ten African populations of *Helicotylenchus* to i) a typical *Helicotylenchus dihystra* from California, ii) two other African *Helicotylenchus* very different from *H. dihystra*. The analyses inferred that no difference could be found in morphometrical characteristics among the ten African populations and between those and the typical *H. dihystra*. It was concluded that, in spite of the high variability of several criteria commonly used in the taxonomy of *Helicotylenchus*, it was possible to identify the African populations as *H. dihystra*. Revised descriptions of *H. dihystra*, *H. morasii* and *H. paracanal* are presented. *H. punicae* Swarup & Sethi, 1968, *H. dihysteroides* Siddiqi, 1972, *H. flatus* Román, 1965, *H. rotundicauda* Sher, 1966, *H. glissus* Thorne & Malek, 1968, and *H. teleductus* Anderson, 1974, are proposed as new synonyms of *H. dihystra*; and *H. trivandranus* Mohandas, 1976, as a new synonym of *H. paracanal* Sauer & Winoto, 1975. *H. microlobus* Perry, 1959, and *H. teres* Gaur & Prasad, 1972, are reinstated as valid species. *H. caribensis* Román, 1965, *H. borinquensis* Román, 1965, and *H. leucernis* Khan & Ahmad, 1970, are considered *species inquirendae*. *H. sagitovi* is proposed as a new name for *H. orientalis* Sagitov *et al.*, 1978, homonym of *H. orientalis* (Siddiqi & Husain, 1964) Geraert, 1976.

RÉSUMÉ

Variabilité morphométrique chez *Helicotylenchus* Steiner, 1945. 3 : Observations sur des populations africaines d'*Helicotylenchus dihystra* et considérations sur les espèces proches

Des analyses multifactorielles furent utilisées pour comparer dix populations africaines du genre *Helicotylenchus* à 1) une population typique de *H. dihystra* provenant de Californie, 2) deux autres populations africaines d'*Helicotylenchus* très différentes de *H. dihystra*. Les analyses montrèrent qu'aucune différence ne pouvait être trouvée dans les caractéristiques morphométriques entre les dix populations et entre ces populations et la population typique de *H. dihystra*. Il est donc possible, en dépit de la forte variabilité de plusieurs critères souvent utilisés dans la taxonomie du genre *Helicotylenchus*, de conclure à l'identité des dix populations étudiées avec *H. dihystra*. Les descriptions de *H. dihystra*, *H. morasii* et *H. paracanal* sont complétées et corrigées. *H. punicae* Swarup & Sethi, 1968, *H. dihysteroides* Siddiqi, 1972, *H. flatus* Román, 1965, *H. rotundicauda* Sher, 1966, *H. glissus* Thorne & Malek, 1968 et *H. teleductus* Anderson, 1974, sont proposés comme nouveaux synonymes de *H. dihystra* et *H. trivandranus* Mohandas, 1976 comme nouveau synonyme de *H. paracanal* Sauer & Winoto, 1975. *H. microlobus* Perry, 1959 et *H. teres* Gaur & Prasad, 1972 sont réinstallés comme espèces valides. *H. caribensis* Román, 1965, *H. borinquensis* Román, 1965 et *H. leucernis* Khan & Ahmad, 1970 sont considérés comme *species inquirendae*. *H. sagitovi* nom. nov. est proposé pour *H. orientalis* Sagitov *et al.*, 1978, homonyme de *H. orientalis* (Siddiqi & Husain, 1964) Geraert, 1976.

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A study of specimens of *Helicotylenchus* from different hosts and countries in Africa demonstrated that many have the same general features, closely resembling the description of *H. dihystrera* (Cobb, 1893) Sher, 1961. However, identification of those specimens was difficult as every population contained individuals with the characteristics of several different species.

For example, tails were found identical to those illustrated for *H. digonicus* Perry, 1959, *H. cavenessi* Sher, 1966, *H. rotundicauda* Sher, 1966, *H. elegans* Román, 1965, *H. caribensis* Román, 1965, *H. flatus* Román, 1965, *H. borinquensis* Román, 1965, *H. glissus* Thorne & Malek, 1968, *H. punicae* Swarup & Sethi, 1968, *H. agricola* Elmiligy, 1970, *H. talonus* Siddiqi, 1972, and others. Fusion of inner incisures on the tail was sometimes as short as in *H. dihystrera*, sometimes as long as in *H. dihysteroides* Siddiqi, 1972. Other criteria were so variable that Sher's (1966) and Siddiqi's (1972 *a*) keys were impossible to use.

Variability of specimens within the same population could be explained in two ways : (i) The observed populations were composed of a mixture of several different species ; (ii) All specimens belong to *H. dihystrera* but individual variability within populations is greater than reported.

Two previous papers have attempted to assess the variability of the African *Helicotylenchus* of the "*dihystrera*" type (Fortuner, 1979 ; Fortuner & Quénehervé, 1980). The progeny, produced parthenogenetically from a single female parent, showed large variability of taxonomical criteria (Fortuner, 1979). Variations in host led to even greater variability (Fortuner & Quénehervé, 1980).

These two studies suggest that all African *Helicotylenchus* resembling *H. dihystrera* are in fact geographical or ecological isolates of *H. dihystrera*. To test this hypothesis, it was necessary to compare the intra- and inter-population variabilities of field populations of the "*dihystrera*" type by multivariate analysis.

The technique compared ten populations of the "*dihystrera*" type, chosen from the widest possible range of hosts and geographical origins, to specimens identified as *H. dihystrera* by S.A. Sher as well as two other populations belonging to two species : *H. morasii* Darekar & Khan,

1980, and *H. paracanalisis* Sauer & Winoto, 1975, which are strikingly different from *H. dihystrera*. After establishing the con-specificity of the African "*dihystrera*" type with *H. dihystrera*, it will be possible to comment on the variability of the commonly used taxonomic criteria and on the validity of the species of *Helicotylenchus*.

Materials and methods

Table 1 presents the number of specimens, the host, and the geographical origin of each of the thirteen populations studied. The slides are deposited in the ORSTOM collection.

For every female, seventeen quantitative characters were studied :

- LON : body length
- STY : stylet length
- STA : length of anterior part of stylet
- SGO : distance between dorsal gland opening and stylet base
- OVI : distance anterior end to oesophago-intestinal junction
- OGO : distance anterior end to end of oesophageal glands
- QUE : tail length
- DAN : anal body diameter
- DTV : distance anterior end to vulva
- DVU : vulval body diameter
- HAB : habitus (number of turns made by relaxed body)
- BLO : length of median bulb
- BLA : width of median bulb
- ANQ : number of tail annules
- ANP : number of annules from phasmid to anus
- AFI : number of annules from anus to fusion of inner incisures
- BFI : number of annules from fusion of inner incisures to tail

In addition, two morphological characters were considered :

- Shape of tail.
- Areolation of lateral fields.

Data analysis consisted of discriminant factor analysis (Romeder, 1973) and correspondence analysis (Benzecri, 1973). These methods have been briefly reviewed by Cuany and Rodolphe (1980).

Table 1
Description of the Populations Studied

Population	Sample Size	Host	Origin	Observations
A	20	Cocoa tree	Madagascar	
B	20	Banana tree	Canary Islands	
C	17	Forest	Senegal	
D	16	Millet	Senegal	
E	17	Upland rice	Senegal	Origin of Female Used in Fortuner, 1979
F	19	Groundnut	Gambia	
G	17	Maize	Gambia	
H	18	Tobacco	Senegal	
I	16	Groundnut	Senegal	
J	16	Papaya	Mauritania	
K	15	Potato	California	Identified as <i>H. dihystera</i> by S.A. Sher
L	17	Savanna	Ivory Coast	<i>Helicotylenchus morasii</i>
M	18	Forest	Ivory Coast	<i>Helicotylenchus paracanalisis</i>

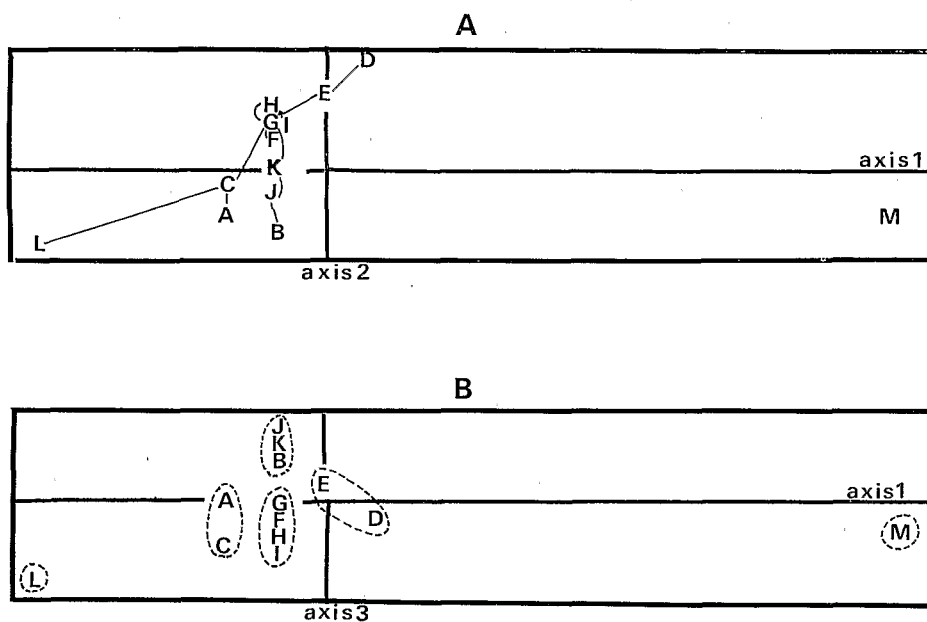


Fig. 1. Position of the thirteen populations (A to M) in relation to three axes (discriminant factor analysis). A : axes 1 and 2 with indication of the lowest distances. B : axes 1 and 3.

Results

ANALYSIS OF THE QUANTITATIVE CHARACTERS

Data for the thirteen populations, as defined by the seventeen quantitative characters, were subjected to a discriminant factor analysis.

Figure 1 shows the position of the thirteen populations in relation to two pairs of axes : axes 1 and 2 (Fig. 1, A) and axes 1 and 3 (Fig. 1, B) which proved to be the more effective for discrimination. In the definition of axis 1, the variables STY, DTV, AFI, and BFI have the highest values, while variables STA, STY, SGO,

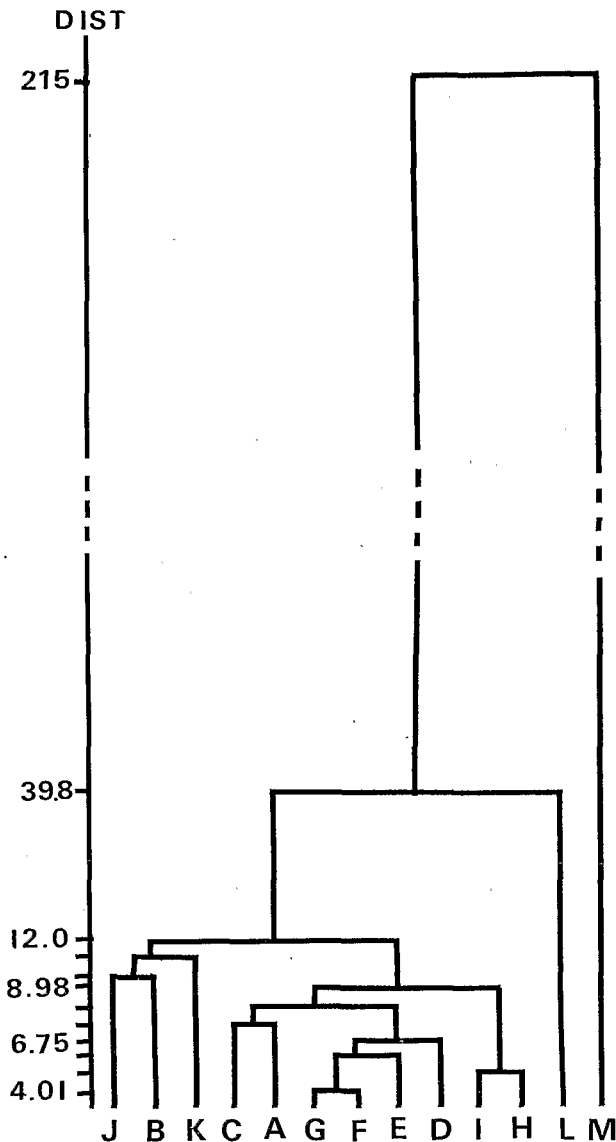


Fig. 2. Classification tree (dendrogram) of the thirteen populations. DIST = Distances between constellations.

and QUE are the most important in definition of axes 2 and 3.

For the thirteen populations, stylet length and length of anterior part of stylet appear to be the most discriminant characters among the seventeen.

Population L is characterized by low values of characters which define axes 2 and 3, and population M by high values of characters on axis 1. Populations of the central group are not differentiated on axis 1.

Mahalanobis' distances between the thirteen populations were computed and shown by a classification tree (dendrogram) (Figure 2). This shows that populations L and M are different from all others. On the contrary, the ten populations belonging to the "*dihystera*" type could not be distinguished from the *H. dihystera* population from California (A).

ANALYSIS OF THE POPULATIONS USING BOTH QUALITATIVE AND QUANTITATIVE CHARACTERS

The data were processed by means of correspondence analysis.

Populations L and M were not included in the correspondence analysis because their gross morphology is quite different from that of the populations of the "*dihystera*" type.

Five quantitative characters (SGO, BLO, BLA, AFI, BFI) were discarded because of their greater variability. For the remaining twelve quantitative characters, individual values were grouped into four classes for each character.

Five morphological characters are most commonly used by taxonomists to differentiate *Helicotylenchus* species and were considered in the analysis. Three of them could not be retained :

(1) *Shape and annulation of lip region.* In the populations studied all females had a grossly hemispherical lip region (Fig. 3, D, E, F) and the number of annules (about 4) was often difficult to observe. Some specimens presented a more flattened lip region (Fig. 3, G) or a clearly defined oral opening (Fig. 3, H) but not truly truncated lips were ever observed.

(2) *Shape of spermatheca and its position in the genital tract.* The spermathecae were always roundish, empty and offset (Fig. 3 I). In some specimens, one or both spermathecae seem to be in line with the genital tract (Fig. 3 J, K). However, in those cases, there are still four dorsal and two ventral cells in the walls of the spermatheca which is thus actually offset (Hirschmann & Triantaphyllou, 1968).

(3) *Shape of stylet knobs.* They can be flattened (Fig. 3, E), anteriorly indented (Fig. 3 D),

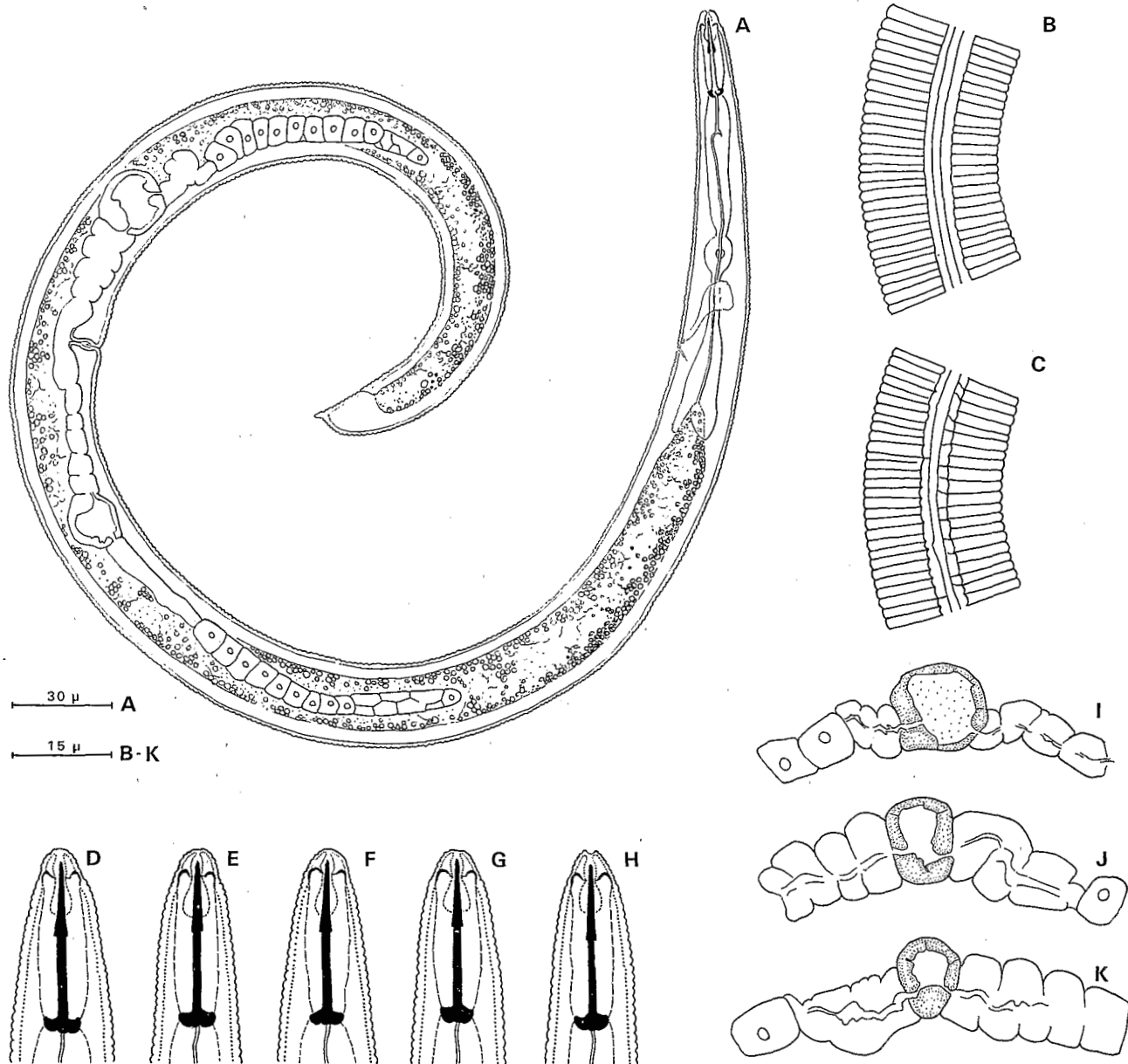


Fig. 3. *Helicotylenchus dihystra*. A : in toto view. B, C : lateral fields. D-H : shape and annulation of the lip region. I-K : position of spermatheca in genital tract.

or roundish (Fig. 3 F). Some specimens had knobs of a different shape on either side of the stylet (Fig. 3 G, H). All three shapes were observed from the progeny of a single female (Fortuner, 1979).

Two remaining qualitative characters were kept :

(4) *Tail shape*. The 181 specimens studied had various tail shapes : Figure 4 gives 46 examples. It is possible to group these forms in the following three states which were used for the analysis :

1. Tail rounded (Fig. 4, Shapes 1).

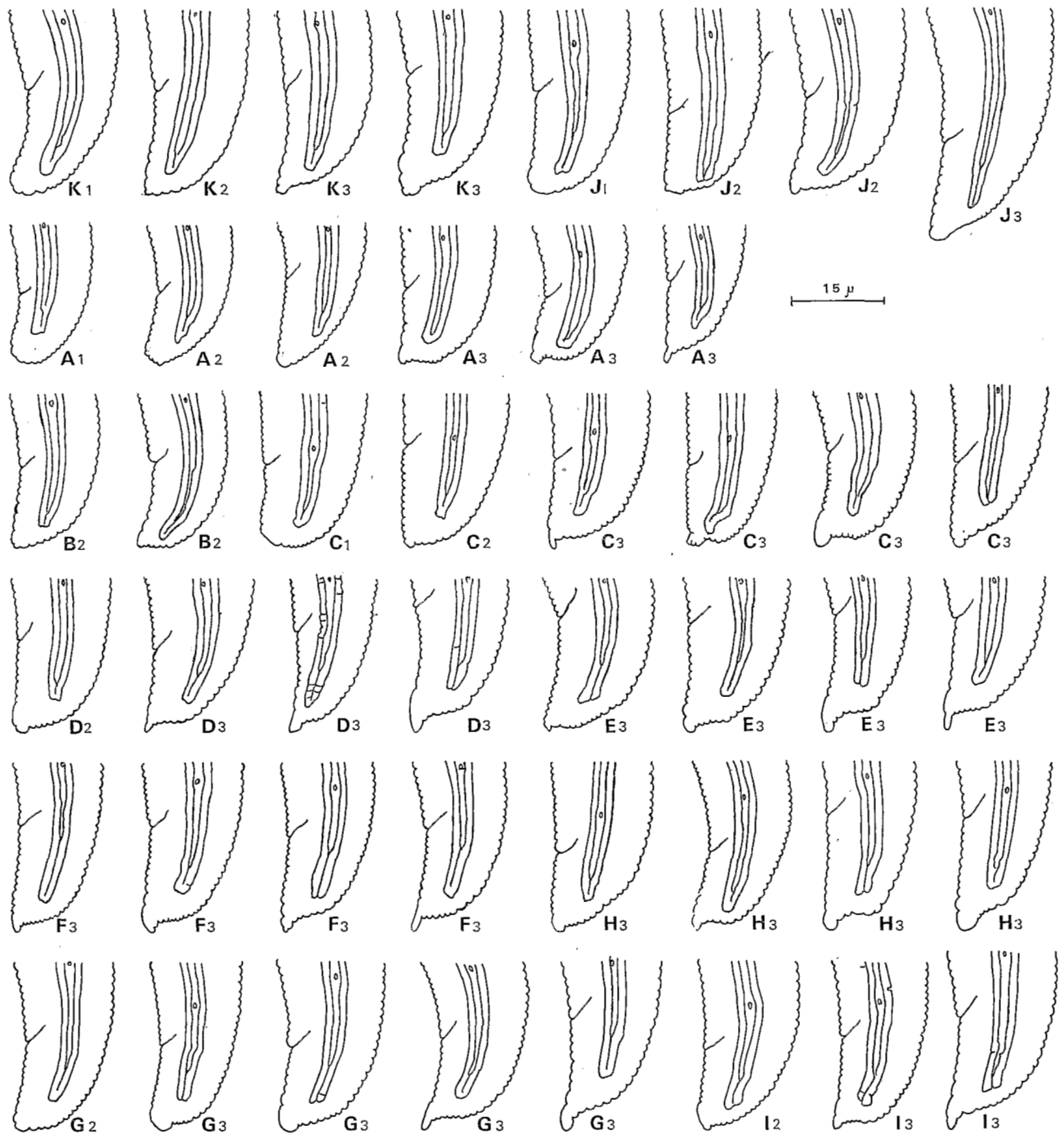


Fig. 4. *Helicotylenchus dihystra*. Shapes of tail. A-K : populations. 1-2-3 : category (see text).

— The two qualitative characters : shape of tail (States 1-2-3, as defined above, inside diamonds) and areolation (states 4-5-6, inside squares).

— The eleven populations : A to K, inside circles.

Axis 1 is defined by the highest value (4) of the quantitative characters underlined in the diagram (LON, STY, OVI, OGO, QUE, DAN, DTV, and DVU) compared to the lowest value (1) of the same characters.

It shows that populations A, I, C differ from D, E, J by their small size.

Axis 2 compares the high values (4) of characters STA and ANP to their low values (1) and the states 2 and 4 of the qualitative criteria to the states 3 and 6.

It shows that populations D, E, G, F, H, I are linked with states 3 and 6 and with the low values of STA and ANP, while populations A, J, B are linked with states 2 and 4 and with the higher values of STA and ANP.

Figure 5 shows that some states of the qualitative characters are linked : 5 and 6 with 3 on one hand and 4 with 1 and 2 on the other hand. This means that individuals with areolations in the lateral field (5-6) have also a ventral process on the tail (3) while specimens with lateral fields not areolated (4) have round (1) or dorsally curved (2) tails. The second combination is the one which is most frequently found in populations A, B and J, and the first one in all other populations.

However the segregation is not absolute and there exists in every population specimens of the various states of the qualitative characters. In order to estimate the value of the two groups of linked states of the qualitative characters defined above, a third analysis was performed in which the individuals were not grouped, as previously, according to their origin, but according to the states of the two qualitative characters.

ANALYSIS OF MORPHOLOGICAL GROUPS

Individuals with the same states of the qualitative characters have been distributed into

the seven groups presented in Table 2 which gives the number of specimens observed in each group.

The data were subjected to a discriminant factor analysis.

Figure 6 shows the distribution of points which represent the seven morphological groups on planes defined by axes 1 and 2 (Fig. 6 A) and axes 1 and 3 (Fig. 6 B).

Axis 1 is positively correlated with characters STA, HAB, and ANP and negatively correlated with characters QUE and ANQ.

There is a gradient along axis 1 from group 36 (where the values of anterior part of stylet, habitus and number of annules from phasmid to anus are low while values of tail length and number of tail annules are high) to groups 24 and 25 (where it is the reverse).

Axis 2 is negatively correlated with character STY. As group 15 is distinguished from the others by axis 2, it can be stated that the five individuals of group 15 are characterized by having a short stylet length.

Axis 3 is positively correlated with oesophageal length (characters OVI and OGO).

Groups 24 and 25, which appeared linked on the first two axes (Fig. 6 A) are distinguished by the third axis (Fig. 6 B).

Individuals with a ventral projection (groups 34, 35, 36) are loosely linked in the space defined by the three first axes.

With the exception of group 15 which appears well separated from all others, there is no clear separation between groups based on qualitative characters of tail and lateral fields. Groups based on qualitative characters linked in the preceding analysis (35 and 36 on one hand and 14 and 24 on the other hand) are not linked in the present one.

CONCLUSIONS

Data analysis based upon quantitative characters substantiated the difference existing between two populations of *Helicotylenchus* spp. and ten African populations which belong to the "*dihystera*" type. The same analysis failed to show that a population from California

Table 2
Morphological Groups Defined Among Individuals of the '*dihystera*'
Type and Number of Specimens Observed in Each Group

Tail Shape	Lateral Fields		
	4 = Not Areolated	5 = Lines on Oesophagus	6 = Lines on Tail or Body
1 = Rounded	14 (7 ♀)	15 (5 ♀)	—
2 = Dorsally Curved	24 (18 ♀)	25 (21 ♀)	—
3 = With Ventral Process	34 (24 ♀)	35 (81 ♀)	36 (23 ♀)

previously identified as *H. dihystera* was different from the ten African populations.

The use of two qualitative characters (tail shape and areolation of lateral fields) does not lead to a clear distinction between any of the populations studied. Individuals with different states for these qualitative characters were present in any of these populations. The qualitative characters did not differentiate species among the populations.

Some correlations exist between qualitative and quantitative characters, but they appear more as tendencies than as constant characteristics. They cannot be used to define different species.

The ten African populations which belong to the "*dihystera*" type and the population from California are conspecific and are *H. dihystera*.

The variations which were observed in the different African populations of *H. dihystera* appear to be individual variations. Also, the ten populations studied came from widely different origins and hosts (Tab. 1), and that could be an additional source of variation.

Description of species

The present study, together with the previous ones (Fortuner, 1979; Fortuner & Quénéhervé, 1980), enlarge the range of variation of several features in the description of *H. dihystera*. It was therefore necessary to present an emended description of this species and also of *H. morasii* (population L) and *H. paracanalii* (population M).

Helicotylenchus dihystera

(Cobb, 1893) Sher, 1961

Syn: *Tylenchus olaae* Cobb, 1906

Aphelenchus dubius var. *peruensis* Steiner, 1920

Tylenchus spiralis Cassidy, 1930

H. nannus Steiner, 1945

H. crenatus Das, 1960

H. flatus Román, 1965, n. syn.

H. rotundicauda Sher, 1966, n. syn.

H. glissus Thorne & Malek, 1968, n. syn.

H. punicae Swarup & Sethi, 1968

H. dihysteroideis Siddiqi, 1972

H. teleductus Anderson, 1974, n. syn.

FEMALES

Measurements (1). Mean body length from 590 μm (groundnut population from Senegal in present study) to 750 μm (pepper population in Fortuner & Quénéhervé, 1980), varies depending on the host (610 μm on maize, 750 μm on pepper in Fortuner & Quénéhervé, 1980). Range, smallest value : 500 μm (Ali *et al.*, 1973), highest value : 900 μm (Van den Berg & Heyns, 1975). Mean stylet length from 24 to 26.5 μm , varies under different hosts (24.3 μm on rice, 26.1 μm on pepper in Fortuner & Quénéhervé, 1980). Rarely, very small values measured in large populations : 20.9 μm in Van den Berg & Heyns (1975) (476 specimens), 22.5 μm in present study (181 specimens). Highest value : 28 μm (Sher, 1966).

(1) See Table 1 in Fortuner (1979) and Fig. 1 and Table 3 in Fortuner and Quénéhervé (1980).

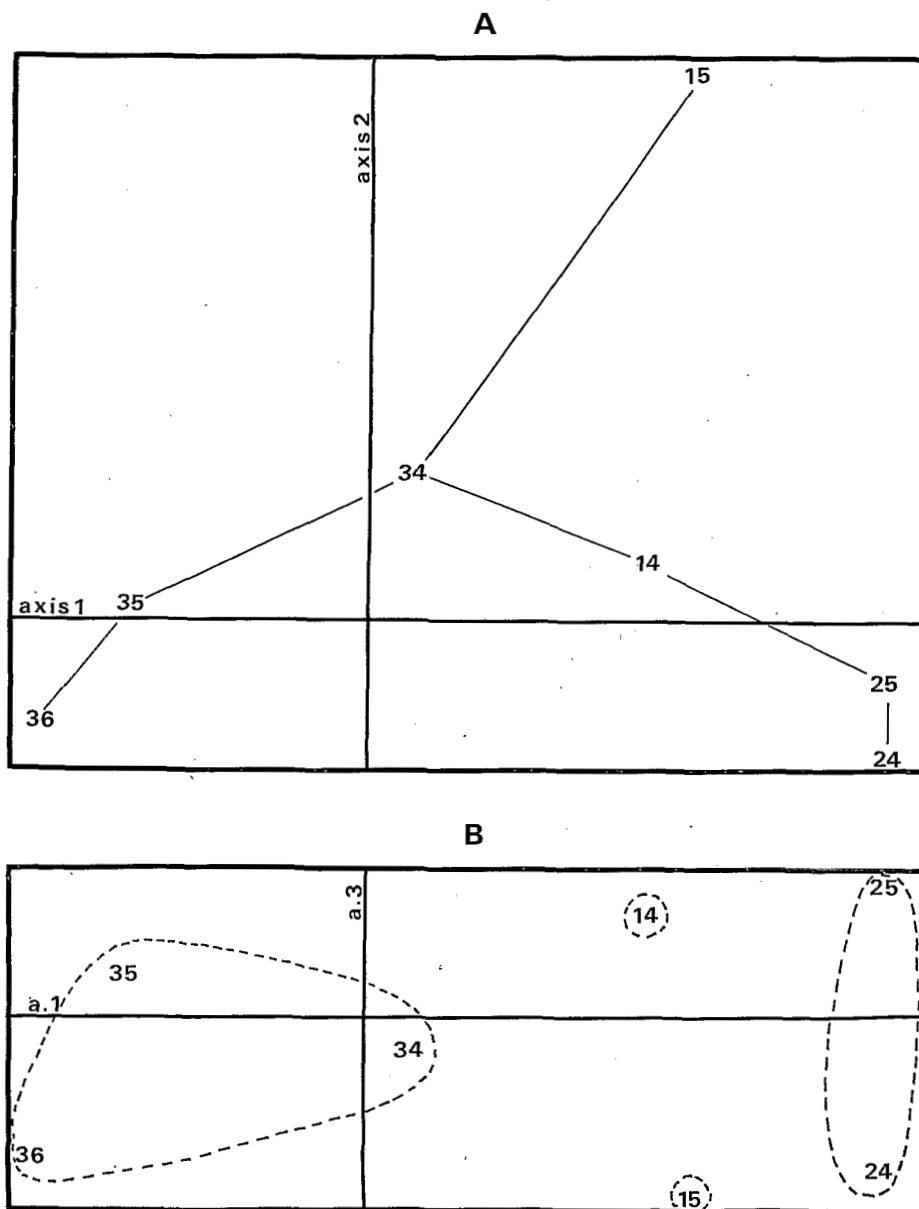


Fig. 6. *Helicotylenchus dihystra*. Points representing the seven morphological groups (discriminant factors analysis). A : on a plane defined by axes 1 and 2. B : on a plane defined by axes 1 and 3.

Ratios. Only V was justified in every population studied and its variability smaller than that of its constituent measurements. Mean V value from 62.5 to 65% varying slightly depending on the host : from 62.9 to 64.9% (Fortuner & Quénehervé, 1980). Smallest value : 57% in present study, 58% (Anderson, 1974). Highest value : 67% in several studies ; 71% was mentioned in

Van den Berg and Heyns (1975). Ratio "a" was justified in the populations studied, but its variability was not smaller than that of its constituent measurements and, therefore, it is not very useful in reducing the variability. Mean value from 23.2 to 29.5. Range from 18.6 (Van den Berg & Kirby, 1979) to 36 (Van den Berg & Heyns, 1975).

Ratios "b" (mean about 4.5-6), "b'" (mean about 4.5) and "m"⁽²⁾ (mean about 45-50) were justified in only half the populations studied. Ratios "c" (from 30 to 67) and "c'" (from 0.8 to 1.4) were mostly not justified, and ratio "o"⁽²⁾ was never justified and must not be calculated.

Description. Body spiral (from tight regular spiral of almost two turns to loose spiral with almost straight anterior end (Siddiqi, 1972 *b*, Fig. B) but never in a single circle or open to a C-shape). Lip region hemispherical (very rarely slightly flattened or with depressed oral opening producing a flattened appearance : Fig. 3 H in present paper) with three to six annules (annulation of variable distinctness, from no visible annules to clearly defined ones), labial disc nonvisible with transmitted light microscope. Stylet knobs generally indented to flattened (sometimes rounded). Dorsal oesophageal gland opening from 10 to 15 μm behind stylet base : very variable length, shorter in some populations : 9.3 μm (Fortuner, 1979) or, in the same population, depending on the host : 10.5 μm on groundnut, 14 μm on pepper (Fortuner & Quénéhervé, 1980); extremes of variation : 6 μm (Fortuner, 1979), 18 μm (Fortuner & Quénéhervé, 1980). Hemizonid and excretory pore anterior to oesophago-intestinal junction. Fasciculi ('canals') absent. Spermatheca offset (spermathecae appearing to be in-line were mentioned and explained in present paper, Fig. 3, J), roundish (from $7 \times 8 \mu\text{m}$ to $17 \times 21 \mu\text{m}$, sometimes may be more elongate : $14 \times 22 \mu\text{m}$) conspicuous (but may be inconspicuously hidden along genital tract, probably in young females before egg-laying), empty of sperm. Lateral field generally areolated on oesophageal region (some transverse lines were more rarely seen scattered on body and/or on tail). Inner incisures fusing on tail distally (length of fusion extremely variable, from distinct almost to end of lateral field to fused at the level of anus : Fig. 1, respectively i and k in Fortuner, 1979). Phasmid anterior to anal level generally five to nine annules before anus ;

may be as close as one annule or as far as fourteen annules from anus ; one specimen with phasmid two annules posterior to anus in Fortuner (1979), position in relation to incisures variable (in the center of lateral field or closer to one of the inner lines). Tail of variable length (11-26.5 μm ; mean : about 15-21) about one anal body width long, more curved dorsally with or without a ventral projection. Tail shape very variable (see Fig. 1 in Fortuner, 1979 ; Fig. 2 in Fortuner & Quénéhervé, 1980 ; Fig. 4 in present paper) ; the tail is always more curved dorsally but the terminus may be rounded as in *H. mullicinctus*, without any ventral projection as in typical *H. dihystera* or with projection of diverse length, shape and thickness. Number of tail annules variable : 6-12 (Sher, 1966) ; 5-14 (Van den Berg & Heyns, 1975) ; 5-17 (present study). Tail generally with a nonannulated ventral portion (sometimes annulated throughout its length) with dorsal-terminal annules of variable appearance (generally similar to body annules, sometimes finer or coarser).

MALES

Typically absent. *H. dihystera* is a parthenogenetic species. Very rarely, males are present : four were observed (Sher, 1966) in two large U.S.A. populations.

DIAGNOSIS

Helicotylenchus with spiral body, hemispherical lips, stylet of medium length (mean value : 24-26.5 μm), medium body length (mean value : 590-750 μm), vulva posterior (mean V value : 62.5-65%), phasmids anterior to anus, inner lines of the lateral field fused on tail, tail about as long as wide, with greater dorsal curvature, rarely asymmetrically rounded, with or without terminal projection, if present, projection with rounded end, no males and empty spermatheca.

SYNONYMS OF *Helicotylenchus dihystera*

Several species of *Helicotylenchus* share many of these characteristics (Tab. 3). Some of the populations described as new species are so closely related to *H. dihystera* that they have

⁽²⁾ m = anterior part of stylet/stylet length.
o = distance of dorsal gland opening/stylet length.

Table 3
Comparison of *Helicotylenchus* spp. close to *H. dihystrera*

	°Stylet Length (1) (μm)	°Tail Shape (1, 2, 3 : See Fig. 4)	°V % (1)	°Phasmids	°Body Length (1) (μm)	°Inner Lines of Lat. Field
<i>H. dihystrera</i>	24 to 26.5	Shapes 2 and 3 (Rarely 1)	°62.5 to 65	°Anterior to Anal level	°590-750	°Fused on Tail
<i>H. punicae</i>	= H.d. (27)	°= H.d. (2)	°= H.d. (63.5)	°= H.d.	°= H.d. (725)	°= H.d.
<i>H. dihystreroides</i>	= H.d. (25.5)	°= H.d. (2,3)	°= H.d. (63)	°= H.d.	°= H.d. (740)	°= H.d.
<i>H. flatus</i>	= H.d. (26.5)	°= H.d. (3)	°= H.d. (63.5)	°= H.d.	°= H.d. (620)	°= H.d.
<i>H. rotundicauda</i>	= H.d. (24.5)	°= H.d. (1,2,3)	°= H.d. (62)	°= H.d.	°= H.d. (730)	°= H.d.
<i>H. glissus</i>	= H.d. (25)	°= H.d. (3)	°= H.d. (63)	°= H.d.	°= H.d. (700)	°= H.d.
<i>H. teleductus</i>	= H.d. (26)	°= H.d. (1,2)	°= H.d. (63)	°= H.d.	°= H.d. (774)	°= H.d.
<i>H. pseudorobustus</i>	Longer (28)	°= H.d. (3)	°More Ant (61.5)	°= H.d.	°= H.d. (710)	°Not Fused
<i>H. microlobus</i>	Longer (29.5)	°= H.d. (3)	°More Ant (61)	°= H.d.	°= H.d. (685)	°= H.d.
<i>H. caribensis</i>	= H.d. (24)	°= H.d. (2)	°More Ant (61.5)	°= H.d.	°Smaller (445)	° ?
<i>H. borinquensis</i>	= H.d. (24)	°= H.d. (2,3)	°= H.d. (62)	°= H.d.	°Smaller (510)	° ?
<i>H. agricola</i>	= H.d. (24)	°= H.d. (2,3)	°= H.d. (63)	°= H.d.	°Smaller (515)	°Not Fused
<i>H. bambesae</i>	Shorter (23)	°= H.d. (3)	°= H.d. (62.5)	°= H.d.	°= H.d. (570)	°= H.d.
<i>H. crenacauda</i>	= H.d. (26)	°≠ H.d. (indent)	°More Ant (61.5)	°= H.d.	°= H.d. (670)	°= H.d.
<i>H. pteracercus</i>	= H.d. (24.5)	°≠ H.d. (indent)	°More Ant (61)	°= H.d./On Tail	°= H.d. (675)	°= H.d.
<i>H. caroliniensis</i>	= H.d. (26.5)	°Rounder (1,2)	°= H.d. (62.5)	°= H.d./On Tail	°= H.d. (750)	°= H.d.
<i>H. leiocephalus</i>	= H.d. (26.5)	°Rounder (1,2)	°More Ant (59)	°= H.d./On Tail	°= H.d. (770)	°= H.d.
<i>H. cavenessi</i>	= H.d. (25.5)	°= H.d. (1,2,3)	°More Ant (59)	°= H.d.	°= H.d. (630)	°= H.d.

(1) Mean values, either from the original description or, when the original description gave only a range of variation, estimated as the mean between the smallest and highest values.

been, or they should now be, considered as conspecific.

The synonymy of Sher's (1966) redescription of *H. dihystrera* listed: *Tylenchus olaae*, *Aphelenchus dubius* var. *peruensis*, *Tylenchus spiralis*, *Helicotylenchus nannus* and *H. crenatus*. Two other names have been since proposed.

H. punicae Swarup & Sethi, 1968, was considered by Siddiqi (1972 a) as probably conspecific with *H. dihystrera*. It had previously been considered as possibly conspecific with *H. retusus* Siddiqi & Brown, 1964, by Nandakumar and Khara (1970). Paratypes of *H. punicae* were kindly provided by Dr. E. Khan. They differ from *H. retusus* by the shape of the tail, which is regularly hemispherical in *H. retusus*, but dorsally bent with or without a rounded terminal projection in paratypes of *H. punicae* (Fig. 7). *H. retusus* is sometimes C-shaped whereas *H. punicae* always has a spiral body. The inner lines of the lateral field are fused for a varying distance in *H. punicae*. The spermatheca, which was not observed by the original descriptors, is rounded, offset from the genital tract and empty (Fig. 7).

The description and measurements in the original description of *H. punicae* and these observations are consistent with *H. dihystrera*. We, therefore, confirm the opinion of Siddiqi (1972 a) and propose *H. punicae* as a junior synonym of *H. dihystrera*.

H. dihystreroides Siddiqi, 1972, was separated from *H. dihystrera* because of a longer fusion of the inner lines of the lateral field (fused near mid-tail), greater distance between orifice of dorsal oesophageal gland and stylet (no measurement is given in the original description, but from the illustration (Fig. 1 H in Siddiqi, 1972 a) this distance can be estimated 14 µm) and a broader tail tip. After studying the variability in *H. dihystrera* from Nigeria, Ali *et al.* (1973) proposed *H. dihystreroides* as a junior synonym of *H. dihystrera*. Sauer and Winoto (1975) supported this proposition with their observations on the variability of *H. dihystrera* in Malaysia. We also support this proposal.

Four other species should also be considered as conspecific with *H. dihystrera*.

(i) *H. flatus* Román, 1965, not compared to *H. dihystrera* in the original description, is very similar to this species. The genital branches

were described with "obscure spherical bodies ... which probably were spermagonia". A structure called spermagonium was described by Perry (1959) as a sperm-producing organ in the genital branch of the hermaphroditic species *H. nannus* (= *H. dihystrera*) and other hermaphroditic *Helicotylenchus* spp. The spermagonium was identified by Yuen (1964), Triantaphyllou and Hirschmann (1964) and Hirschmann and Triantaphyllou (1965, 1968) as a nonfunctional spermatheca. The various "nonnucleated refractive bodies" or "irregularly shaped inclusions" which have been observed in the spermathecae of *Helicotylenchus* spp. are droplets of excretory material from the columella⁽³⁾ (Hirschmann & Triantaphyllou, 1968). If the "obscure spherical bodies" which Román (1965) saw were droplets of excretory material, then the reproductive system of *H. flatus* is not different from that of *H. dihystrera*.

Slides with paratypes of *H. flatus* dried and the type material was lost (Román, *in litt.*), but there is no doubt that it is conspecific with *H. dihystrera* and *H. flatus* is here proposed as a junior synonym to *H. dihystrera*.

(ii) *H. rotundicauda* Sher, 1966. In the original diagnosis this species was compared to *H. platyurus* Perry, 1959, but not to *H. dihystrera*. However these two species are very similar and in the key from the same article (Sher, 1966), both key out together at line 17 (striation absent or very coarse on distal ventral portion of tail terminus), and are separated at line 18 by shapes of stylet knobs and tail terminus.

The tail shape of *H. rotundicauda* was described by Sher (1966) as "more curved dorsally, terminus irregularly hemispherical, without striations ventrally". His Fig. 6 B

⁽³⁾ Hirschmann and Triantaphyllou (1968) proposed the name tricolomella for the distal part of the uterus in *Helicotylenchus* because it has only three rows of cells instead of four in the typical quadricolumella described in *Ditylenchus* by Wu (1958). Both names do not apply to the related structure in *Anguina* which has several irregular rows of cells (Wu, 1967). The name crustaformeria was proposed by Wu (1967) because she thought this organ produces the egg shell, which is not proved. The name columella is here proposed because it fits all configurations of this organ, and does not prejudice its function.

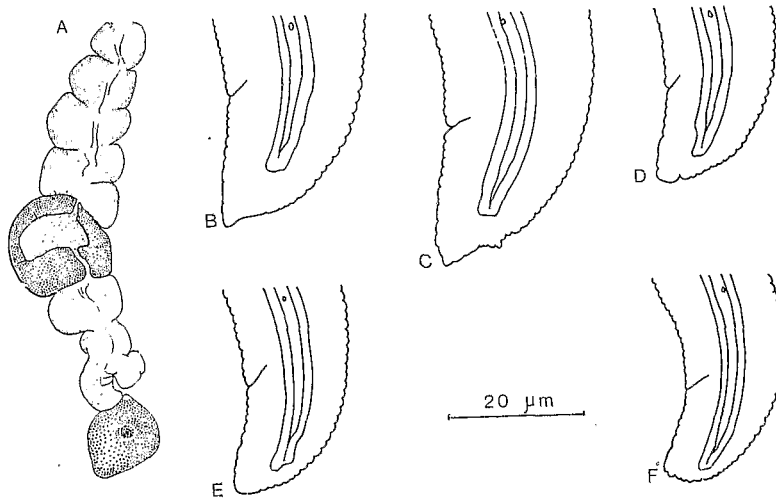


Fig.7

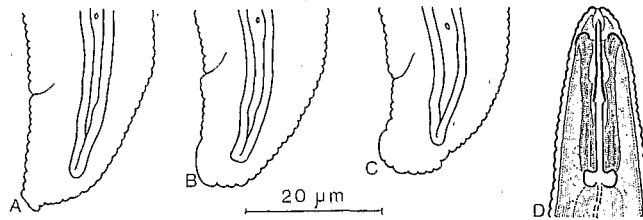


Fig.8

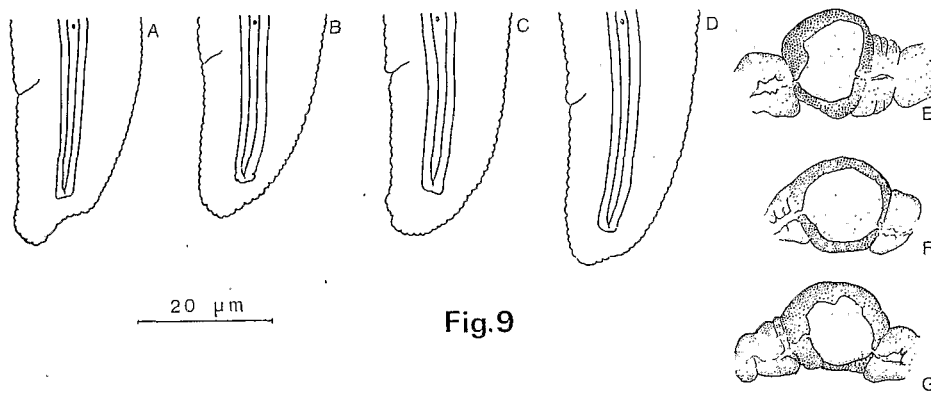


Fig.9

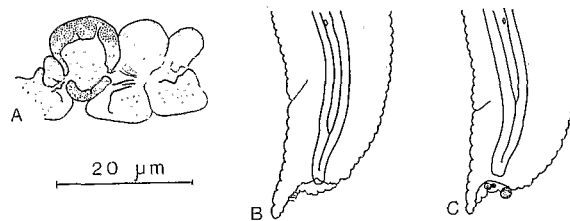


Fig.10

Fig. 7. *Helicotylenchus punicae*, paratypes, A : spermatheca, B-F : variations in tail shape. Fig. 8. *Helicotylenchus rotundicauda*, paratypes, A : variations in tail shape, -D : anterior end. Fig. 9. *Helicotylenchus teleductus*, paratypes, A-D : variations in tail shape, E-G : spermatheca. Fig. 10. *Helicotylenchus crenacauda*, paratypes, A : spermatheca, B-C : variations in tail shape.

presents a tail irregularly hemispherical not unlike tails of some *H. dihystrera* specimens in Fig. 4 of present paper (Shape 1 in populations A, C, J, K). Fig. 6 C of Sher is similar to that of many specimens of *H. dihystrera* (Shape 2 in populations A, C, D, G, J, K in Fig. 4). Paratypes of *H. rotundicauda*, kindly loaned by A. Bell, were examined. Most had tails similar to those described and illustrated by Sher (Fig. 8 B, C), but one paratype showed a ventral projection (Fig. 8 A) identical in shape to that presented in Fig. 1 m of Fortuner (1979). The same shapes of tails are observed in *H. dihystrera* and *H. rotundicauda*, but the proportions of individuals exhibiting the various shapes are different. Individuals of *H. rotundicauda* as described by Sher (1966) have mostly tails either irregularly rounded or more curved dorsally without projection, but some do have a ventral projection. In *H. dihystrera* as redescribed above, typical tail shapes are more curved dorsally with or without ventral projection, but some individuals can be observed with tails irregularly rounded.

Spear knobs are said to be rounded in *H. rotundicauda* and they do look rounded in most of the observed paratypes, but one specimen had knobs more flattened, almost cupped (Fig. 8 D). In *H. dihystrera* a wide variation exists in the shape of the knobs from indented to flattened or rounded.

The disposition of the inner lines of the lateral field was not described by Sher (1966) but fusion was described by Anderson (1974). Fusion of the lines was observed in all paratypes.

All other characteristics and measurements are similar in *H. rotundicauda* and *H. dihystrera*.

H. rotundicauda appears to be a geographical variant of *H. dihystrera* present only in California (4). It shares the same range of variation

as *H. dihystrera*, but differs as tail shape more hemispherical and shape of stylet knobs more rounded are emphasized. In our opinion, this is not sufficient to consider it as a distinct species and *H. rotundicauda* is proposed as a junior synonym of *H. dihystrera*.

(iii) *H. glissus* Thorne & Malek, 1968. Paratypes of this species are not available for loan, but specimens identified as *H. glissus* by R. B. Malek from a sorghum field near Forestburg in South Dakota were kindly loaned by J. D. Smolik. *H. glissus* was said to be distinctive "because of its almost unstriated lip region, variable digitate terminus, distance of esophageal gland outlet from spear base and monosexuality".

The lip region was described as "smooth or marked by excessively fine striae, apparently 5 in number". In the specimens studied, the lip annules were sometimes difficult to observe in bright field microscopy, but always easily seen with an interference contrast device of Nomarski fitted on a Leitz Ortholux, using a 1000 X magnification. The lip annulation should then be described as present, but difficult to observe. In *H. dihystrera* also, lip annules may be very difficult or impossible to resolve.

The shape of the tail, as illustrated in the original description and observed in the loaned specimens is identical with that of many *H. dihystrera* specimens. The distance of oesophageal gland opening to stylet (10 μ m) easily falls into the range of variation of *H. dihystrera* as indicated above. The specimens of *H. glissus* observed possess spermathecae roundish, empty of sperm and offset, similar to the corresponding structure in *H. dihystrera*. The excretory pore is either slightly posterior to the oesophago-intestinal junction, as originally described, or slightly anterior to it, as in *H. dihystrera*. The

(4) Sher indicates the distribution of *H. rotundicauda* as follows: Specimens of *H. rotundicauda* have been identified from the following habitats and localities in California, U.S.A.: ..., privet (*Ligustrum* sp.) Ontario, ..." It is clear that he meant Ontario, a city in San Bernardino County, California. Eight paratypes were deposited with the Canadian National Collection. Anderson (1974) studying the Canadian species of *Helicotylenchus* from the specimens in the Canadian National Collection, described *H. rotundicauda* "reported associated with privet in Ontario, by Dr. S. A.

Sher." It appears that Anderson confused Ontario, California and Ontario, one of the Canadian states. *H. rotundicauda* has not been observed from Canada, Anderson states that no specimens, other than the paratypes, are available in the Canadian National Collection of Nematodes."

H. rotundicauda was reported from Thailand by Ratanaprapa and Boonduang (1975). Nothing is said about the variability of the tail shape. It is impossible to decide if this population is really the "rotundicauda-like" variant of *H. dihystrera*.

coefficient V is 63 (61-64%) in the specimens observed. The inner lines of the lateral field, not described in the original description, are always fused on tail sometimes for a very short distance, but in one specimen from the level of anus.

Previous diagnostic characters of *H. glissus* resemble *H. dihystra* within the range of variation for this latter species as proposed above. *H. glissus* is proposed as a junior synonym of *H. dihystra*.

(iv) *H. teleductus* Anderson, 1974. This species was described from six females from Canada and has not been mentioned in the literature since. Anderson differentiated it from most species of *Helicotylenchus* by the posterior position of the dorsal gland opening and of the excretory pore, by the size and shape of the tail, and by the fine annulation that continues around the tail terminus.

The dorsal gland opening is 14 to 17 μm behind the spear base. This distance varies from 10 to 15, or even 18 μm , depending on the host in *H. dihystra*. The excretory pore is 129 μm (126-133) posterior to the anterior end in *H. teleductus*. In *H. dihystra*, the mean value is smaller, but the range of variation may reach high values, for example, 140.4 μm (Van den Berg & Heyns, 1975) or 130.3 μm (Zavaleta-Mejia & Sosa-Moss, 1979).

The tail of *H. teleductus* is 21-24 μm long which is within the range of *H. dihystra* (11-26.5 μm long). It is either dorsally concave as in *H. concavus* Román, 1961, or rounded. The rounded shape which was illustrated by Anderson (1974) is similar to many specimens of *H. dihystra*. The dorsally concave shape is rarer among *H. dihystra*, but was observed, for example, in populations C and J, (Shape 3, Fig. 4). The tail of *H. dihystra* has usually a nonannulated ventral section, but some specimens present a regularly annulated terminus: Fig. 1 w, h, i, and g in Fortuner (1979), or populations A and K (Shape 1), and populations B, C, G (Shape 2, Fig. 4).

The characters which were used in the diagnosis of *H. teleductus* can fit into the range of variation for *H. dihystra*. However, two other characters, disposition of the lines of the lateral field, and position of the spermatheca must be considered.

The spermatheca was said to be "axial or slightly offset dorsally" in *H. teleductus*. This is impossible because the position of the spermatheca in the genital tract is determined during the morphogenesis and can be either axial or offset, but not both.

The inner lines of the lateral field were described as "closed at their termination". From the illustration of Anderson (1974) this is what is called here "not fused". *H. dihystra* always has inner lines fused at their distal end.

Paratypes of *H. teleductus*, kindly loaned by Dr. Anderson, were examined. The spermatheca appears to be offset from the genital tract (Fig. 9), as in *H. dihystra*. The inner lines of the lateral field are separate almost to the end of the field, but there they fused for a very short distance (Fig. 9) as in some specimens of *H. dihystra* (Fig. 4: Population A, Shape 3). In *H. teleductus*, the inner lines never form an U-shaped junction as for example in *H. paracanalisis* (Fig. 15 E-G). The excretory pore was posterior to the oesophago-intestinal junction in one specimen, as reported in the original description, but anterior to the junction in another specimen. In two other specimens, the oesophagus was badly fixed and the exact location of the junction could not be ascertained.

In conclusion, *H. teleductus* differs from *H. dihystra* only in the range of some characters (more posterior excretory pore, more rounded tail, tail end more regularly annulated, inner lines of the lateral field fused only for a very short distance). Some populations of *H. dihystra* include specimens with similar values for these characters, which are also very variable in all populations studied. Those small differences are not considered to have diagnostic value. *H. teleductus* is here proposed as a junior synonym of *H. dihystra*.

SPECIES CLOSE TO *H. dihystra*

Other species must be considered valid, but are very close to *H. dihystra*. The list of such species can be a very lengthy one and the problem is to determine where to stop adding to it as a great number of *Helicotylenchus* differ from *H. dihystra* in only one or two characters. Among all these closely related species, we decided to discuss the following which may

prove the most difficult to differentiate from *H. dihystrera*.

H. pseudorobustus (Steiner, 1914) Golden, 1956, was redescribed by Sher (1966) from topotypes. It differs from *H. dihystrera* in having a longer stylet (26-30 μm), inner lines of the lateral field never fused on tail, and the vulva slightly more anteriorly situated. Sher (1966) gave only the range of variation for V : 59-64%, which is the same as *H. dihystrera*, but from the topotypes, kindly loaned by Dr. Mankau, we were able to calculate the mean value : 61.5%. This is smaller than the various reported means for *H. dihystrera*: 62.5-65%. Thorne and Malek (1968) reported a mean value of 61% and Ali *et al.* (1973) a range of 59.5-65%, estimated mean 62%, both smaller than 63%.

From Sher's (1966) key, *H. pseudorobustus* would also appear to differ from *H. dihystrera* in the longer ventral tail projection. The tail shapes illustrated for *H. pseudorobustus* by Sher (1966, Fig. 1 O, P) are similar to those of many specimens of *H. dihystrera* (shapes 3 in populations C, D, E, F, G and H, Fig. 4). Anderson (1974) stated that *H. pseudorobustus* "is readily recognized by the large, coarsely annulated tail projection". The projections in the topotypes vary from nonannulated to slightly or markedly annulated. Thorne and Malek (1968) described a projection which "usually is slightly annulated". Ali *et al.* (1973) described and illustrated some African specimens with nonannulated projections. The annulation of the tail projection in *H. pseudorobustus* is a variable feature. In *H. dihystrera* the projection is generally nonannulated, but some specimens present some annulation (Shape 3 in populations C, E, F, Fig. 4).

Siddiqi (1972 *a*) used other characteristics in the tail region to separate *H. pseudorobustus* from *H. microlobus* Perry in Perry, Darling & Thorne (1959) : areolation of the lateral field on tail (this is very variable in *H. dihystrera*), ventral and/or dorsal section of tail with finer annules in *H. pseudorobustus* (in *H. dihystrera* the width of tail annules appears to be variable). In view of the variability of these characters in *H. dihystrera* we think it unwise to use them to differentiate species. However, *H. microlobus* has inner lines of the lateral field fused on tail (Siddiqi, 1972 *a*) and, because of this character, should be accepted as a valid species contrarily to the

opinion of Sher (1966) and of Sauer and Winoto (1975). *H. microlobus* differs from *H. dihystrera* primarily in its longer stylet (29.5 μm).

The population of *H. pseudorobustus* described by Thorne and Malek (1968) (with stylet 30 μm , inner lines not fused and V = 61%) and by Ali, Geraert and Coomans (1973) from Zaire (with stylet 27-29.5 μm , inner lines not fused and V = 59.5-65%) can be accepted as *H. pseudorobustus*. Other populations with smaller stylets and fusion of inner lines not described were reported (Pholcharoen & Boonduang, 1972 ; Anderson, 1974 ; Sauer & Winoto, 1975 ; Van den Berg & Kirby, 1979) with phasmids on tail in some specimens. These populations may be variants of *H. pseudorobustus* or belong to some other species of *Helicotylenchus*.

H. caribensis Román, 1965, *H. borinquensis* Román, 1965, and *H. agricola* Elmiligy, 1970. These three species can be described as "small *H. dihystrera*" with mean body lengths from 445 to 515 μm .

H. agricola was said to differ from *H. dihystrera* also in stylet length (but the mean value, 24 μm , falls within the range of *H. dihystrera*), shape of the lip region (said to be broadly rounded to truncate, but Ali (1976) redescribed paratypes of *H. agricola* with hemispherical lips), rounded stylet knobs (but rounded knobs were observed in some specimens of *H. dihystrera* and Ali (1976) observed indented or flattened knobs), position of phasmids (four to seven annules anterior to anal level, but this is well within the observed range for *H. dihystrera*) and position of dorsal gland opening (7-8 μm behind stylet, also within the range of variation for *H. dihystrera*).

After studying type material of *H. agricola*, Ali (1976) concluded that "the differences with *H. dihystrera* are very small : in fact, only body length and spear length are different". As said above, the stylet length can be fitted within the range of variation of *H. dihystrera*, but not the body length. The difference may seem to be small (515 μm for *H. agricola* against 590-750 μm for *H. dihystrera*), but one must keep in mind that the mean value given for *H. dihystrera* has been compiled from ten previously published descriptions and from measurements of 24 populations by the present authors, representing a wide range of geographically and physiologically

different habitats. It would be difficult to include this measurement with the description of *H. dihystrera*.

H. agricola also differs from *H. dihystrera* in having the inner lines of the lateral field never fused on the tail. Consequently this species seems to be distinct from *H. dihystrera*.

H. caribensis and *H. borinquensis* were said to be very close to *H. agricola* by Ali (1976), but because specimens were not available for study, this author found it impossible to draw a conclusion about a possible synonymy. According to Dr. Román (*in litt.*) type specimens of these two species were lost. From the original descriptions, the only difference between *H. caribensis* and *H. borinquensis* is the tail shape without projection in the former and with a ventral projection in the latter. Both shapes as they appear in original figures (Fig. 2, D in Román, 1965 for *H. caribensis* and Fig. 7 F for *H. borinquensis*) resemble specimens of *H. agricola* as illustrated in Fig. 2 C of Elmiligy (1970). The arrangement of the inner lines of the lateral field is not described for either species. From the figures in the original descriptions, they appear to be not fused as in *H. agricola*. If we disregard the reported presence of a "spermatogonium" in *H. caribensis* and a "structure similar to a phasmid located at terminus of lateral field" in *H. borinquensis*, all other characteristics are remarkably similar for the three species. It is our opinion that all three are identical and should be synonymized (*H. caribensis* is the older name because of page priority over *H. borinquensis*). However, it is no longer possible to study type specimens for variability of tail shape, redescription of genital branches, assessment of the nature of the additional phasmid in *H. borinquensis* and structure of the lateral field on tail. It seems best to consider *H. caribensis* and *H. borinquensis* as *species inquirendae*, which leaves *H. agricola* as the valid species, at least for the moment.

H. bambesae Elmiligy, 1970 (synonym : *H. talonus* Siddiqi, 1972). This species was not (nor was *H. talonus*) compared to *H. dihystrera* in the original description. A study of the descriptions of both *H. bambesae* and *H. talonus* and of the remarks of Ali and Geraert (1975) when they synonymized these two species, discloses the following differences from *H. dihystrera*.

Styler is shorter, 23 (22-24 μm) long with a mean value outside the range of variation for *H. dihystrera*. Phasmids are closer to the anus : one to three annules anterior in *H. bambesae*, two to seven annules in the description of *H. talonus*. The corresponding number is generally five to nine annules anterior in *H. dihystrera*, but this character is very variable and phasmids were observed as close as one annule to anal level. Number of tail annules : four to five in *H. bambesae*, three to seven in *H. talonus*, usually higher, but very variable from five to seventeen in *H. dihystrera*.

The shape of the tail is not different from many specimens of *H. dihystrera* (Shape 3 in Fig. 4). The inner lines of the lateral field are fused on the tail. (They were said to be not fused by Elmiligy (1970) but redescribed as fused by Ali and Geraert (1975). The lines were said to be fused in *H. talonus*).

The shorter styler is the main difference between *H. bambesae* and *H. dihystrera*. The former species has a slightly smaller number of annules on the tail and between the phasmid and the anus than is generally accepted for *H. dihystrera*. Both species are close, but we prefer to accept *H. bambesae* as a distinct species. It comes also very close to *H. agricola*, but can be differentiated from this species by the inner lines of the lateral field which are fused on the tail in *H. bambesae*, but not in *H. agricola*.

H. crenacauda Sher, 1966, is easily differentiated from *H. dihystrera* by its indented tail terminus. Three other *Helicotylenchus* species also have indented tail ends : *H. pteracercus* Singh, 1971, *H. indenticaudatus* Mulk & Jairajpuri, 1974 and *H. orientalis* Sagitov *et al.*, 1978.

H. pteracercus was described as differing from *H. crenacauda* by the following characters :

— "Distinctive cuticular folds extending from the tip of the lateral fields to the end of the ventral tail projection". No such structure was mentioned for *H. crenacauda*, but Sher (1966) did note that "the terminal indentation of the female tail is usually filled with debris". Sauer and Winoto (1975) illustrated a population of *H. crenacauda* with a fold (Fig. 2 O and Q in Sauer & Winoto, 1975). Paratypes of *H. crenacauda*, kindly loaned by A. Bell were

examined and cuticular folds were observed usually filled with debris (Fig. 10 G, B and C).

— Phasmids more posteriorly situated : from three annules below to two annules above the level of anus instead of four to ten annules anterior in *H. crenacauda*. Van den Berg and Kirby (1979) identified a population from Fiji Islands as *H. pleracercus* because of the presence of cuticular folds. The position they give for the phasmids (six to sixteen annules anterior to anus) fits the description of *H. crenacauda* better. The presence of cuticular folds cannot be used as a differentiating character.

— Spermatheca was described as conspicuous and offset in *H. pleracercus*, but inconspicuous and not offset in *H. crenacauda*. Offset spermatheca seem to be in line with the genital tract when the dorsal bulge is dwarfed by an enlarged columella. In paratypes of *H. crenacauda*, the spermatheca is basically offset with four dorsal cells and two ventral ones (Fig. 10 A) and resembles *H. dihystra* (Fig. 3 I, J, and K).

— *H. pleracercus* was also said to differ from *H. crenacauda* by having a shorter tail with a greater number of annules, but in view of the great variability of these characters, this cannot be very conclusive. The only real difference between the two species remains the lower position of phasmids in *H. pleracercus*.

The inner lines of the lateral field are fused on the tail in paratypes of *H. crenacauda* (Fig. 10 B and C).

H. indenticaudatus, with phasmids on the tail, is close to *H. pleracercus* and might prove to be difficult to differentiate from this species.

H. orientalis also has phasmids on the tail. This name was preoccupied by *H. orientalis* (Siddiqi & Husain, 1964) Geraert, 1976 (syn. : *Rotylenchus orientalis* Siddiqi & Husain, 1964). We propose the following change :

Helicotylenchus sagitovi nom. nov.

= *H. orientalis* Sagitov *et al.*, 1978

nec *H. orientalis* (Siddiqi & Husain, 1964) Geraert, 1976

H. caroliniensis Sher, 1966. Examination of paratypes showed the inner lines of the lateral field to be fused on the tail for varying lengths, from fused only at the very end of the field, as shown in Fig. 6 G-H of Sher (1966) to fused almost from the level of anus (Fig. 11). Tail shape was mainly similar to Shape 1 of Fig. 4,

but some Shapes 2 also occurred (Fig. 11 A). The ventral bulge mentioned by Sher, 1966, at anal level is no more pronounced than that in many *H. dihystra* specimens. The body describes a spiral of more than one turn. The spermatheca is offset.

H. caroliniensis is differentiated from *H. dihystra* by the lower position of the phasmids (on tail or slightly anterior to anus), the tail regularly striated around terminus, usually rounder than in *H. dihystra* and the large spherical median bulb.

H. leiocephalus Sher, 1966. The main difference from *H. dihystra* is the unstriated lip region. A careful study of paratypes using an interference contrast device of Nomarski failed to show any lines on the lips. In *H. dihystra*, the lip striation is visible, sometimes difficult to observe. The tail terminus has a dorsal unstriated portion. In some paratypes a faint annulation can be seen around the tail terminus with the Nomarski device. In *H. dihystra* the unstriated portion is ventral, but in some specimens the striation continues around terminus. Phasmids are close to the anus in *H. leiocephalus*, anterior to it or more often on the tail. The vulva is more anteriorly situated (V = 55-63%).

Sher (1966) showed the inner lines of the lateral field not fused. Anderson (1974) showed a very long fusion and stated that this was confirmed by correspondance with Dr. S. A. Sher. In the paratypes observed with the Nomarski device, the inner lines are fused for a varying distance. Posteriorly, one or both outer lines become faint and may disappear. This produces the illusion of a very long fusion of the inner lines if one of these inner lines is mistaken for the disappeared outer one (Fig. 12 B-E). The phasmids are variably positioned in the field : in the center, closer to the ventral inner line, or in the outer band of the field (Fig. 12 B and G).

H. cavenessi Sher, 1966. In the original description, this species was separated from *H. rotundicauda* by the longer fusion of the inner lines of the lateral field and the striations continuing around the tail terminus.

Paratypes of *H. cavenessi*, from the type collection at the California Department of Food and Agriculture, Sacramento, were examined by the present authors. The fusion of the inner

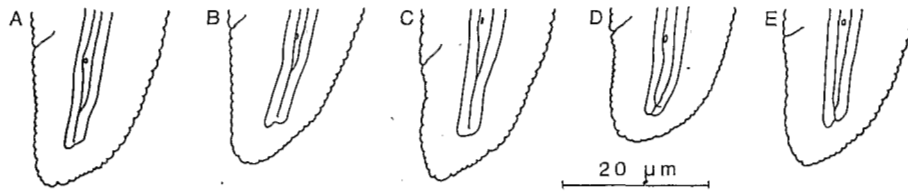


Fig.11

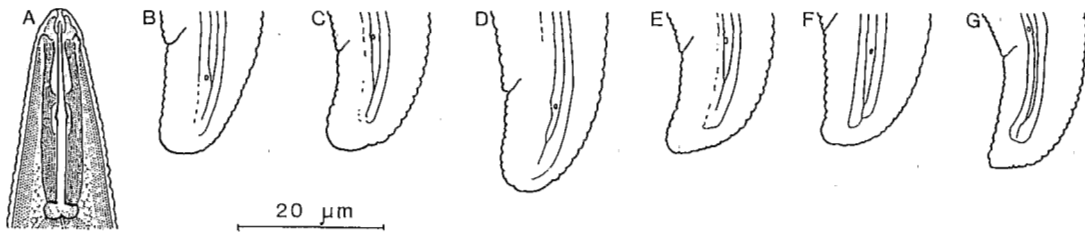


Fig.12

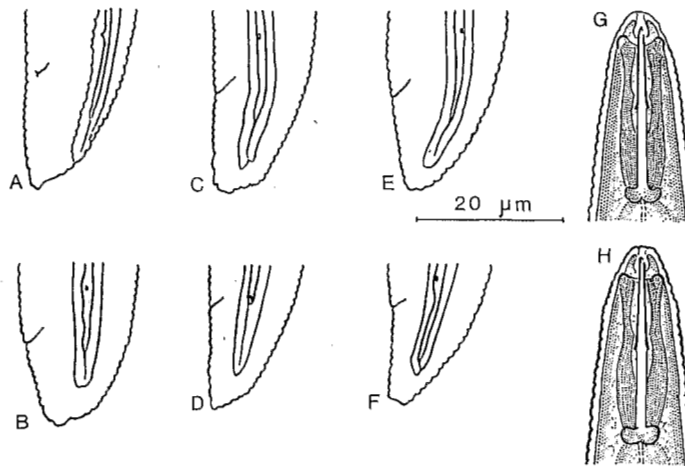


Fig.13

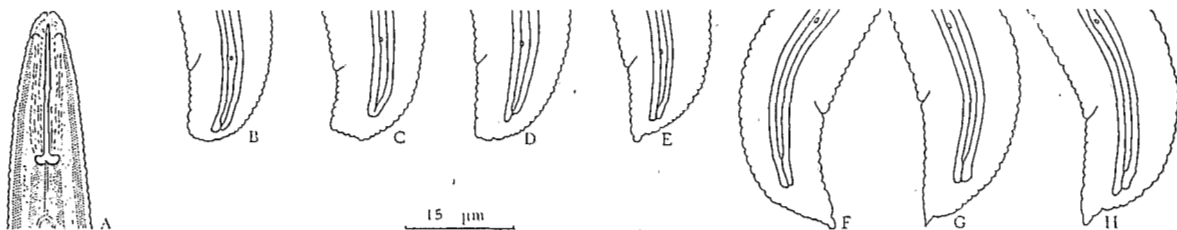


Fig.14

Fig. 11. *Helicotylenchus caroliniensis*, A-E : variations in tail shape. Fig. 12. *Helicotylenchus leiocephalus*, A : anterior end, B-G : variations in tail shape. Fig. 13. *Helicotylenchus cavenessi*, A-F : variations in tail shape, G-H : anterior end. Fig. 14: *Helicotylenchus morasii*, population-L, females, A : anterior-end, B-H : variations in tail shape.

lines of the lateral field is very long, but was very short in one specimen (Fig. 13). Striations were present around the tail terminus but, sometimes were very coarse giving tails an appearance sometimes observed in *H. dihystrera* (Fig. 13). Tail shape is similar to that of some *H. dihystrera* specimens. Two tails with small terminal projections were also observed (Fig. 13, A and B).

The habitus of *H. cavenessi* appears to be variable. Sher (1966) described "body in spiral shape ... curved ventrally to irregularly spiral". Among the eight paratypes examined by the present authors, five were distorted during fixation and three were C-shaped. The holotype, in the Davis nematode collection, is spiral shaped.

Lips are hemispherical, but Sher (1966) observed that "the lip region sometimes appears almost flattened anteriorly". This was also observed in the paratypes.

The vulva is more anteriorly situated in *H. cavenessi* than in *H. dihystrera*. The observed paratypes have $V = 59\%$ (56%-62%). This range is identical to that given by Sher (1966) and the mean value is outside the range for *H. dihystrera*.

The diagnostic characters given by Sher (1966) cannot be used, but *H. cavenessi* differs from *H. dihystrera* in the more anterior position of the vulva, an habitus sometimes in C-shape, and lips sometimes appearing more flattened.

H. leucernis Khan & Ahmad, 1970. This species is said to be close to *H. dihystra* (*sic*). Some characteristics in its description are bizarre. There are only five body annules: "Transverse striations are four in number and broken by lateral lines"; the buccal aperture is above the labial disc: "mounth [*sic*] opening located above oral disc which is surround by *viz.* [?] lips"; the dorsal oesophageal glands are ventrally situated: "dorsol [*sic*] oesophageal gland opens into the oesophagean lumen. These glands are situated ventrally to the intestine". The vulva possesses hitherto unrecorded structures, alas not described in the article: "Vulva is ... provided with two membranouslaps"; there are several hemizonids, but their position is not clear: "Hemizonids are very well marked and located at about two body annules"; *H. leucernis* is qualified as "Hermaphorodite", whatever that means; in the key accompanying the

description it is also said to possess a "bisexual spermatogonium". If this structure is equivalent of the spermatogonium described by Perry (1959) its position is different from that in any other known species: "spermatogonium are at the distal end". There are apparently several ovaries radiating all over the place: "Ovaries outstretched in various directions"; and the disposition of the oocytes is unheard-of: "oocytes forming a row of single files"; a structure called prerectum is present, but not described in more details; the tail bears a very long extension: "Tail ... forming beak like structure, which is about 52 u [*sic*]". Habitus, shape of the lip region, stylet length and position of phasmids are not described. The figure illustrating this description is much less monstrous than could be inferred from the description, but the total length (given as 0.77 mm) is only about 0.20 mm in the figure; the stylet length can be estimated as 17.5 μm , so far the shortest in this genus.

H. leucernis is differentiated from *H. dignostus* (= *H. digonicus*?) and *H. dihystra* (= *H. dihystrera*?) by "comparatively anterior location of the spear; in oesophageal of gland [*sic*] being not much posteriorly situated, and in having narrow lateral field". (The width of the lateral field is not given in the description.)

It is also said to differ from *H. insignis* (= *H. insignis*), *H. Plumelari* or *plumariae* (= *H. plumariae*?) and *H. canadiensis* by the size of tail as indicated by coefficient *c*, and from *H. crenatus* "in having big comparatively located phasmid" and a posteriorly located gland opening.

It is inconvenient that the authors did not provide clear illustrations or more complete descriptions of the many new and interesting features which they mentioned. While an examination of paratypes could provide new information on the taxonomic status of this species, it seems best because some important diagnostic characters are not described to consider it as *species inquirendae*.

H. morasii

Darekar & Khan, 1980
Population L (Fig. 14)

FEMALES

Measurements and ratios. Body length : 512 \pm 26 (407-596 μm); stylet length : 19.3 \pm

0.3 (18-20.5 μm); $a = 25.7$ (23.9-26.9); $b' = 4.5$ (3.8-5.5); $V = 63.4 \pm 0.8$ (60.8-66.9%).

Ratios b (about 6), c (about 43), c' (about 1), m (about 46) and 0 (about 40) were not statistically justified and cannot be calculated.

Description. Body spiral. Lip region hemispherical with 4-5 annules. Labial disc nonvisible. Stylet with indented, flattened or rounded knobs. Dorsal oesophageal gland opening 7.7 (7-9 μm) behind stylet base. Hemizonid and excretory pore anterior to oesophago-intestinal junction. Fasciculi absent. Spermatheca offset, roundish and empty of sperms. Inner lateral field incisures fusing on tail (rarely not fusing). Phasmids from anal level to 8 annules anterior, their position variable in the field. Tail of variable length 12.2 (8-18 μm); with 10 (7-13) annules. Tail shape variable, more curved dorsally with terminus rounded or more often with ventral projection.

MALES

Not seen.

IDENTITY OF POPULATION L

Population L fits the description of *H. morasii* well with some differences which are too slight to be considered of diagnostic value. The tail is slightly shorter in population L, but some specimens (Fig. 14 F and G) exhibit tails as long as those of *H. morasii*. There are four to five lip annules instead of five to six in *H. morasii*. The phasmids are slightly more anterior in *H. morasii* (five to ten annules anterior to anal level).

H. morasii and population L have the shortest stylet among *Helicotylenchus* with a mean of 19 μm and a range of 18 to 20 μm . Four other *Helicotylenchus* spp. have stylet length ranging from 18 to 21 μm :

H. bihari Mulk & Jairajpuri, 1975 has truncate lips.

H. digitatus Siddiqi & Husain, 1964 has phasmids post-anal, a very long tail (over two anal body width long) and a very long ventral process, longer than those in our specimens. The "bristle-like processes" which were seen on the tail tips of some paratypes are probably fixation artefacts.

H. microdorus Prasad, Khan & Chawla, 1965 has a body in C-shape, 650-740 μm long and its tail shape is rather different from that of specimens in population L.

H. teres Gaur & Prasad, 1972 *nom. nov.* (= *H. thornei* Gupta & Chhabra, 1967, *nec H. thornei* Román, 1965) has the phasmids more posterior ("just in level to anus") and the tail more rounded. The shape of the lip region was not given in the original description, but Gupta and Chhabra (1967) compared their new species to *H. digonicus* Perry, 1959, and *H. insignis* Khan & Basir, 1964, (both with truncate lips). Also, Gaur and Prasad (1972) state that *H. teres* differs from *H. thornei* Román in head shape, and this latter species has a rounded lip region. Consequently, lips of *H. teres* are most probably truncate and different from those of *H. morasii* and population L.

H. teres was proposed as a synonym of *H. indicus* Siddiqi, 1963 by Nandakumar and Khera (1970), but *H. indicus* has a longer stylet (21-23 μm against 19-21 μm for *H. teres*) and the phasmids are on the tail. These two species are therefore best considered as distinct taxa.

Population L differs from *H. dihystra* in the lower values of stylet length (STA and STY), shorter distance from dorsal oesophageal gland opening to stylet base (SGO) and tail length (QUE), as seen above. It also has a shorter body. Other characteristics are common to both species : spiral body with hemispherical lips, spermatheca offset and empty of sperm, inner incisures fusing on tail, phasmids anterior to anal level, and dorsally curved tail with or without projection.

H. paracanalisis

Sauer & Winoto, 1975

= *H. trivandranus* Mohandas, 1976 (n. syn.)

Population M (Fig. 15)

FEMALES

Measurements and ratios. Body length : 738 \pm 32 (622-834 μm); stylet length : 34.7 \pm 0.6 (32.5-37 μm); $a = 26.3$ (23.2-29.3); $m = 46$ (44.3-50.7); $V = 60.4 \pm 0.7$ (57.9-62.7%).

Ratios b (about 6), b' (about 4.5), c (about 80) and c' (about 0.5) not statistically justified.

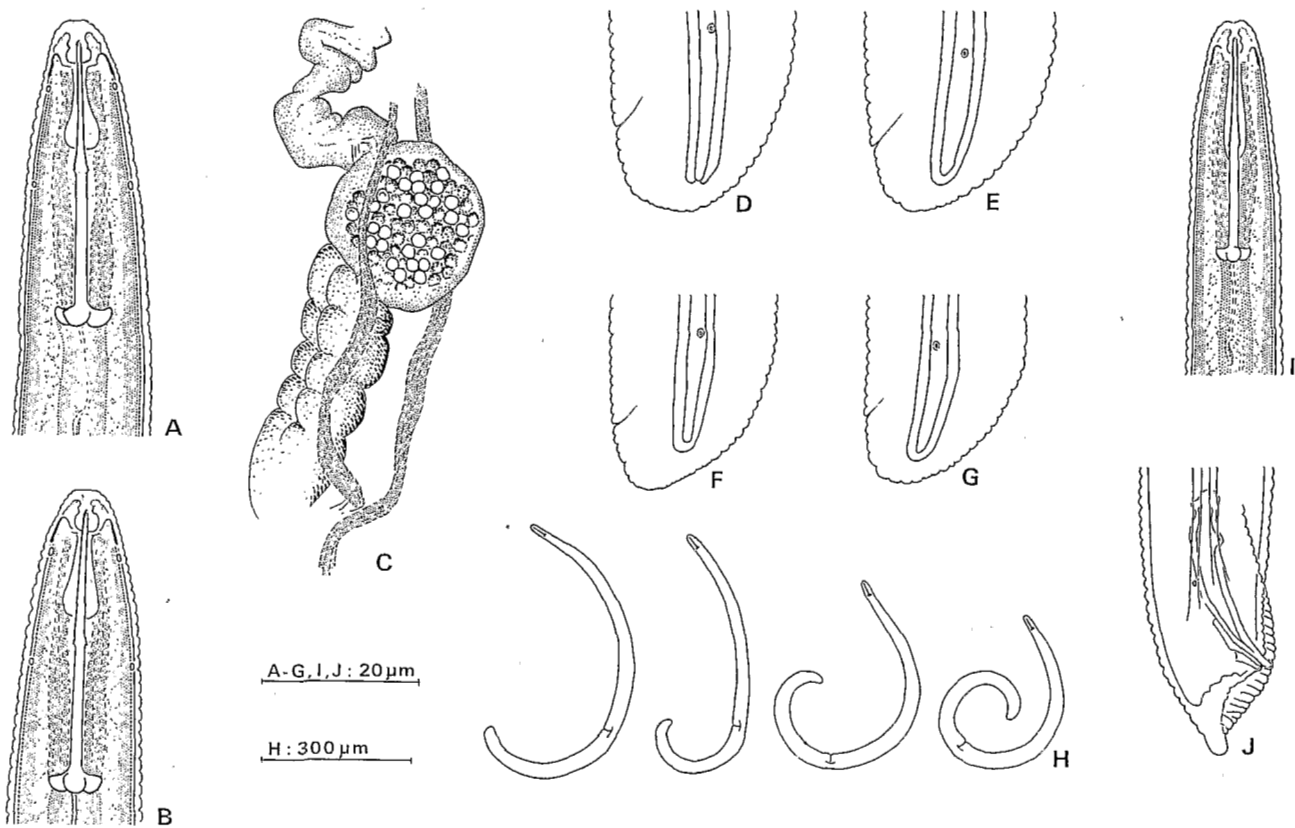


Fig. 15. *Helicotylenchus paracanalis*, population M. A-H : Females. A, B : anterior end. C : spermatheca and fasciculi ('canals'). D-G : variations in tail shape. H : variations in habitus. I-J : Males. I : anterior end. J : tail.

Description. Body generally in C-shape, sometimes closed into a complete circle or even a loose spiral (Fig. 15 H). Lips hemispherical (Fig. 15 A) sometimes slightly flattened (Fig. 15 B) with 5-6 annules. Labial disc nonvisible. Stylet knobs indented to flattened. Dorsal oesophageal gland opening 10 (9-11.5 μm) behind stylet base. Hemizonid and excretory pore anterior to oesophago-intestinal junction, rarely at level of junction. Fasciculi ('canals') present in eighteen out of twenty specimens. Spermatheca offset, roundish and full of sperms (Fig. 15 C); rarely empty and then difficult to see. Lateral field areolated in oesophageal region. Inner incisures not fusing on the tail, sometimes seem to coalesce with outer incisures, but this is visual artefact due to curvature of tail (Fig. 15 D). Phasmids anterior to anal level (from three to ten annules anterior), their position variable in the field. Tail very short, about

half anal body width long, with about seven (five to nine) annules ventrally, 9.3 (7.5-11.5 μm) long, annules on tail sometimes less distinct and/or smaller than body annules. Tail more curved dorsally, terminus hemispherical without projection.

MALES

Measurements and ratios. Body length : 608 (546-690 μm); $a = 26.8$ (24.4-31.6); $m = 49$ (46-51); stylet length : 29.4 (28-30 μm); spicules length : 24.7 (22-26 μm); gubernaculum length : 9-10 μm .

Description. Similar to female except for sexual differences. Fasciculi observed in three specimens, phasmids anterior to anus, situated in outer dorsal band of the lateral field (Fig. 15 J).

Table 4
Comparison of Four Populations of *H. paracanal*s

Population	Position of Phasmids	Number of Lip Annules	Spicule Length (μm)	Habitus	Ventral Tail Projection
Original description Sauer & Winoto (1975)	Close to anus (anal level to two annules anterior to anus in Fig. 4, N-O)	6-7	24 (20-25)	C-shape or ventrally arcuate	Ventral projection usually pointed, absent in one specimen
Specimens from Fiji Islands Van Den Berg & Kirby (1979)	Anal level to four annules anterior to anus	5-6	26.3 (20-28.3)	Form an open 6	Small ventral projection, absent in some specimens (as seen in Fig. 30)
Specimens described as <i>H. trivandranus</i> n. sp. Mohandas (1976)	1-8 annules anterior to anus	5-6	(27-28)	Spirally coiled about 1-1/2 times	Conspicuous, rounded or pointed
Present population M	3-10 annules anterior to anus	5-6	24.7 (22-26)	Variable from c-shape to spiral	Absent

IDENTITY OF POPULATION M

Specimens from population M fit well with the description of *H. paracanal*s (long stylet, presence of fasciculi, presence of males, short tails more curved dorsally, phasmids anterior to or at level of anus, inner incisures not fused on tail, etc.) except for a few characteristics (Tab. 4).

Another species, *H. trivandranus* Mohandas, 1976 is also similar to *H. paracanal*s except for a few characters (Tab. 4).

A population identified as *H. paracanal*s was described from Fiji Islands by Van den Berg and Kirby (1979). This population has intermediate values for the characters which differentiate *H. paracanal*s from *H. trivandranus* (Tab. 4). These intermediate values fall within a gap which separates those two species.

Table 4 shows that the slight differences exhibited by the four populations under discussion for five characteristics (while all other taxonomic criteria are remarkably similar) are best considered as intra-specific variations, and not relevant for specific discrimination.

Consequently population M is identified as *H. paracanal*s and *H. trivandranus* is proposed as a junior synonym of this species.

*H. paracanal*s was described from jungle in Malaysia. The population described by Van den

berg and Kirby (1979) was found from a "large tree" in Fiji Islands. *H. trivandranus* was described from *Piper nigrum* in Kerala (India), and population M (recorded as *Scutellonema* sp. by Alexandre, 1977) from a tree (Avodire) in a forest in the Ivory Coast. All four populations have a similar origin : forests in warm tropical countries.

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