Morphometrical variability in *Helicotylenchus* Steiner, 1945. 6 : Value of the characters used for specific identification

Renaud FORTUNER

*Nematology Lab, room 340, California Department of Food and Agriculture,
1220 N Street, Sacramento, California 95814, USA*

SUMMARY

The intraspecific variability and the taxonomic value of 43 characters used in diagnoses of new species of *Helicotylenchus* were studied. Only 23 of these characters were found to be useful for identification purposes : fourteen measurements, three nonvariable morphological characters, and seven variable morphological characters. The intraspecific variability was shown to make impossible the use of traditional dichotomous keys. Calculation by computer of coefficients of similarity is believed to be the only efficient and reliable method for identification of the species of *Helicotylenchus*. *Rotylenchoides* is proposed as a synonym of *Helicotylenchus*. *H. brevis, H. variocaudatus*, and *H. affinis* are proposed as new combinations. *R. impar* is renamed *H. khani* nom. nov. *H. intermedius* and *H. neoformis* are transferred back to *Helicotylenchus*. *Rotylenchoides desouzai* is transferred to *Rotylenchus* as *Rotylenchus desouzai* n. comb. *H. aerolatus* is corrected as *H. areolatus* without change in authority.

RÉSUMÉ

Variabilité morphométrique chez Helicotylenchus *Steiner, 1945. 6:
valeur des caractères utilisés pour l'identification des espèces*

La variabilité intraspécifique et la valeur taxonomique de 43 caractères utilisés dans les diagnoses des espèces nouvelles de *Helicotylenchus* ont été étudiées. Parmi ces caractères, seuls 23 sont considérés utiles pour les identifications : 14 caractères mesurables, 3 caractères morphologiques non-variables et 7 caractères morphologiques variables. Il est montré que la variabilité intraspécifique de la plupart de ces caractères rend impossible l'utilisation des clefs dichotomiques traditionnelles. Le calcul par ordinateur de coefficients de similarité est présenté comme la seule méthode efficace et sûre pour l'identification des espèces de *Helicotylenchus*. *Rotylenchoides* est proposé comme synonyme de *Helicotylenchus*. *H. brevis, H. variocaudatus* et *H. affinis* sont proposés comme nouvelles combinaisons. *R. impar* est renommé *H. khani* nom. nov. *H. intermedius* et *H. neoformis* sont retransférés dans *Helicotylenchus*. *Rotylenchoides desouzai* est transféré à *Rotylenchus* comme *Rotylenchus desouzai* n. comb. *H. aerolatus* est corrigé en *H. areolatus* sans changement d'autorité.

More than 150 names have been proposed for species in the genus *Helicotylenchus*, of which about 120 are still valid. When originally described, those species were differentiated from previously described ones on the basis of numerous characters. Some of these characters were used in various keys, the most complete ones being the keys of Sher (1966) and of Siddiqi (1972) as supplemented by Anderson (1979).

In spite of this intense taxonomic activity, identification of an unknown population of *Helicotylenchus* is still a difficult, if not impossible, process, because most characters used by the authors of the diagnoses and keys appear to vary within species.

Very few studies have been published on the variability of the characters used in the taxonomy of *Helicotylenchus*. Nandakumar and Khera (1970) and Azmi and Jairajpuri (1978) studied *H. indicus*. Some authors gave a description of new or already known species with a longer discussion on variability

than is generally the case, particularly van den Berg (van den Berg & Heyns, 1975 ; van den Berg, 1978 ; van den Berg & Kirby, 1979), Anderson (1973, 1974), and Geraert (1976). However, most of the conclusions of the present article stem from four studies (Fortuner, 1979 ; Fortuner & Quénéhervé, 1980 ; Fortuner, Merny & Roux, 1981 ; Fortuner, Maggenti & Whittaker, 1984) in which the variability within the progeny of a single larva, the variation induced by the host and the variability of field populations were successively evaluated. The first three papers dealt with *H. dihystera*, the fourth one with *H. pseudorobustus*.

These two species are good representatives of the genus *Helicotylenchus* because their measurements are in the medium range when compared with other species of the genus. *H. dihystera* is the type species of *Helicotylenchus*. Both *H. dihystera* and *H. pseudorobustus* have a worldwide distribution and have been reported from many different host plants.

What will be said of the variability within these species may be considered as valid for the whole genus.

Assessment of the variability of taxonomic characters in *Helicotylenchus* was attempted for the purpose of selecting good characters for a dichotomous or a tabular key. However, because no character exists which would separate well-defined groups of species within the genus, it was found impossible to devise a good working key. New identification schemes of a polytomous nature were needed and such a scheme, based on a coefficient of similarity, will be proposed in a future article.

Materials and methods

A list of all the characters used in the past 30 years for differentiating species in *Helicotylenchus* was established from the original descriptions of 120 species. These characters * are listed below with the frequency of their appearance in the published diagnoses :

GENERAL MORPHOLOGY

Body

length	26	%, see page	246
diameter ; ratio a	2.5	%, »	247
habitus	11	%, »	247
annules	4	%, »	249

Anterior end

offset or continuous	1	%, see page	249
shape	33	%, »	249
labial disc	6	%, »	249
annules	33	%, »	250

Lateral field

width	2.5	%, see page	250
transverse striation	2.5	%, »	250
punctation	1	%, »	251
crenation of outer lines	2.5	%, »	251
fusion of inner lines on tail	13	%, »	251

Tail

shape	63	%, see page	252
length ; ratio c	13	%, »	252
ratio c'	23	%, »	253
ventral tail annules	21	%, »	253
shape of tail annules	12	%, »	253

---

* The reliability of each character was assessed from the data from four previous studies by the author and collaborators as explained in the introduction, and from a few other studies. Except when otherwise stated, mentions of *H. dihystera* and *H. pseudorobustus* will refer to the observations made by the author in the course of the above-mentioned studies.

NERVOUS AND SENSORY SYSTEMS

Phasmids

position (from anus)	44	%, see page	253
position (in lateral field)	1.5	%, »	254
distinctness	1	%, »	254

Cephalids   3   %, see page 254

Hemizonid

position	1	%, see page	254
presence	3	%, »	254

EXCRETORY SYSTEM

Position of excretory pore	3	%, see page	254
Structure of excretory canal	1	%, »	255

DIGESTIVE SYSTEM

Stylet

length	57	%, see page	255
cone ; ratio m	2	%, »	255
shape of knobs	29	%, »	255

Labial framework   5   %, see page 256

Esophagus

dorsal gland opening ; ratio o	28	%, see page	256
median bulb	1	%, »	256
glandular bulb	1	%, »	256
length, ratio b, b'	1.5	%, »	257

Intestine

esophago-intestinal junction	1,5	%, see page	257
fasciculi (canals)	2.5	%, »	257

REPRODUCTIVE SYSTEM

Regression of posterior genital branch	2.5	%, see page	257

Vulva

position ; ratio V	12	%, see page	258
vulval flaps	1.5	%, »	258
other structures	1.5	%, »	258

Spermatheca   11   %, see page 258

CHARACTERS OF MALES

Presence of males	23	%, see page	259
Spicules	3	%, »	259
Other characters	1	%, »	259

Appraisal of taxonomic characters

GENERAL MORPHOLOGY

Body

Body length. Differences in body length are used in about a quarter of the diagoses of new species of *Helicotylenchus*. The differences are sometimes well

marked : *H. belli* (450-580 μm) is said to differ from *H. martini* (710-980 μm) in this character, *H. coomansi* (1 170-1 300 μm) from *H. anhelicus* (570-780 μm). In other cases, the ranges of measurements are closer (*H. imperialis* : 480-590 *vs. H. anhelicus* : 570-780 μm) or may even overlap (*H. goodi*, 640-840 *vs. H. belli* 710-980 μm).

Sher (1966) gave a range of body lengths of 590-790 [1] μm for *H. dihystera* (mid-range = 690 μm). Subsequent descriptions enlarged that range from 500 μm (Ali, Geraert & Coomans, 1973) to 900 μm (van den Berg & Heyns, 1975). Means, when indicated, varied from 600 μm (van den Berg & Heyns, 1975) to 674 μm (Anderson, 1974). Fields populations of *H. dihystera* were observed by the present author with mean lengths from 586 to 695 μm (unpublished data used in the analysis in Fortuner, Merny & Roux, 1981). The coefficients of variability were estimated at 4% (Fortuner, 1979), 5 to 9% (unpublished data for Fortuner, Merny & Roux, 1981). In *H. indicus* the C.V. of body length is 9% (Azmi & Jairajpuri, 1978).

From these observations, body length appears to be a reasonably constant character. However, when the progeny from a single female was reared on ten different hosts, the means ranged from 610 to 748 μm (Fortuner & Quénéhervé, 1980), which is a 138 μm host-induced difference.

The longest described *Helicotylenchus* is *H. coomansi* (L = 1 170-1 300 μm, mid-range = 1235 μm) and the smallest is *H. affinis* (mean body length = 408 μm). Body length can be used as a discriminating character but only when the difference in length between two species is more than 150 μm. A smaller difference may be accounted for by intraspecific variation.

Body diameter ; ratio a. The body diameter was not used in any diagnosis and, in fact, is seldom given in descriptions where only the ratio a (body length/diameter) appears.

---

[1] Too many recent descriptions follow the old custom of giving only the range of observed values but not the mean X, and even less the standard deviation s of the measurements. It is more informative to know that 95% of the individuals of the population (from which the sample was obtained) lies within the limits X — 2 s and X + 2 s, provided the character measured is normally distributed. In the present article, because more than half the species in *Helicotylenchus* were described with only the range, the mid-range was calculated as an approximation of the mean value of each measurement. This is statistically quite unjustified, and it is planned to calculate the actual values of the means from paratypes of all described species.

Ratio a gives a good idea of the general shape (stout or slim) of a species. Before it can be used, however, it must be shown to be taxonomically valid and useful. Does the diameter always vary proportionally to the length ? In other words, does a species described as "stout" remain so under varying conditions ? Does its shape change when the individuals age, or when the population changes its host plant ? Is the ratio less variable than its constituent characters, body length and diameter ? Ratio a was found by Fortuner (1984) to be a good taxonomic ratio. It relates characters often presenting a high correlation, but it is not very useful because it does not reduce the intraspecific variability of the diameter. It is recommended that future descriptions or redescriptions of species of *Helicotylenchus* should give the more reliable body diameter, but ratio a can be used in the meantime.

Ratio a gives the relationship between two characters which are highly correlated in living individuals. However, this high correlation may disappear when the characters are measured from specimens flattened by the cover slip. This makes the diameter increase without a corresponding increase of the body length.

Under different hosts, ratio a of *H. dihystera* varied from 25.3 to 29.7, four and a half points. In one population (B) from Fortuner, Merny & Roux (1981) with some flattened specimens, ratio a varied from 20.3 to 28.2, an eight point difference.

In the genus, ratio a varies from 17 *(H. persici)* to 41 *(H. unicus).* Because it is sometimes difficult to decide when a specimen is flattened, only differences of more than eigth points for ratio a will be accepted as significant for identification.

Habitus (Fig. 1, A). The thermal death position has been used to separate spiral-shaped species (= in shape of a 6) from those assuming a C-shape (= ventrally arcuate, ventrally curved, almost straigth, etc.). For some authors, as for example Tikyani, Khera & Bhatnagar, 1969 in the description of *H. goodi*, ventrally arcuate means spiral shaped. For the spiral shaped species, the tightness of the spiral was sometimes taken into consideration. *H. urobelus* is said to be "more openly spiral" than *H. californicus* (Anderson, 1978).

A spiral shape was observed in every specimen studied of *H. dihystera* and *H. pseudorobustus* and this character is very constant in these species. In other species, like *H. multicinctus* and *H. coomansi*, the body seems to be constantly C-shaped to almost straigth. The character habitus seems to be reliable for identification. However, it sometimes exhibits some variability. Killing and fixation of the specimens are very important. A spiral shaped species may be
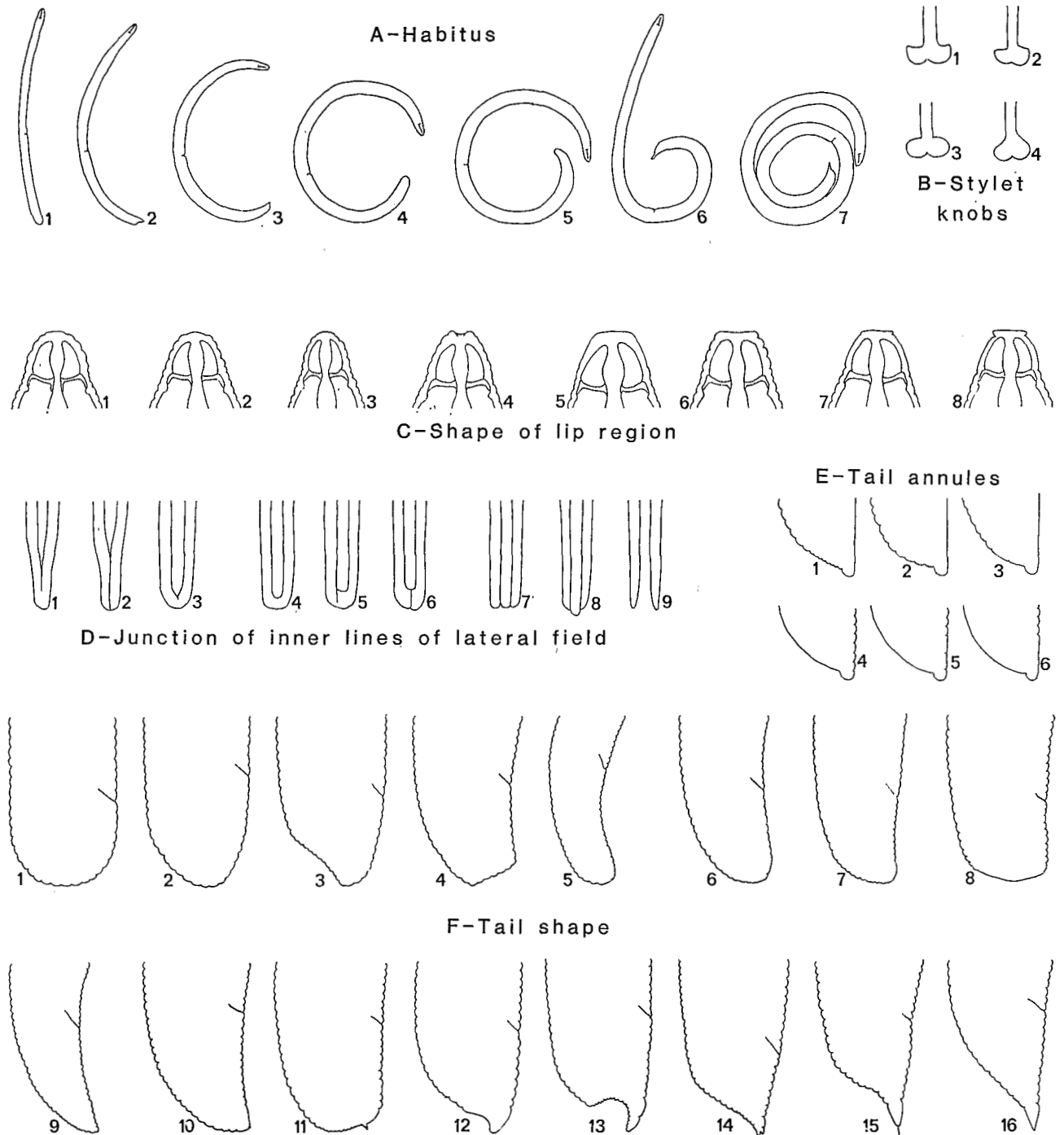
Fig. 1. Schematic representation of some morphological characteristics of *Helicotylenchus* spp. A. Body thermal death position. 1-4 : C-shaped ; 5-6 : spiral. B. Stylet knobs. 1 : indented ; 2 : flattened ; 3 : rounded ; 4 : sloping. C. Anterior end (lip region). 1-4 : hemispherical ; 4-6 : flattened ; 7-8 : labial disc visible in transverse view. D. Pattern of junction of inner lines in posterior lateral field. 1-2 : y ; 3 : v ; 4 : u ; 5-6 : mu ; 7-8 : m ; 9 : open m. E. Tail annulation. 1-3 : dorsal tail annules smaller, identical, or larger than the other tail annules ; 4-6 : ventral portion regularly annulated, coarsely annulated, or nonannulated. F. Tail shape. 1-3 : symmetrical, regularly rounded ; 4-8 : asymmetrical (more curved dorsally), with rounded end ; 9-10 : with dorsal and ventral sides joining at an angle. 11-16 : with terminal projection.

distorted by a bad killing until it presents a false C-shaped habitus. The habitus is variable in some species even when correctly fixed. A population of *H. paracanalis* (population M) and *H. cavenessi* vary from C-shaped to spiral (Fortuner, Merny & Roux, 1981). *H. paxilli* was described as "C-shaped, sometimes one and a half spirals." These species form a third group of species which possess both states of the character.

In spiral shaped species like *H. dihystera* and *H. pseudorobustus*, the tightness of the spiral is variable, from a tight spiral of almost two turns to a loose spiral of little more than one turn, and from a body regularly spiral to spiralled only in the posterior extremity. Azmi and Jairajpuri (1978) also observed in *H. indicus* a variable spiral shape. The tightness and disposition of the spiral cannot be used for identification ; species described as "in a loose spiral" or "in an open spiral" will not be distinguished from species spiral or tightly spiral.

Body annules. *H. talonus* described with annules 1.4-1.8 μm wide was differentiated from *H. bradys* by "finer body annules (3 μm wide at mid-body in *H. bradys*)..." In some instances, the difference is slight : *H. bihari* (with 1-2 μm wide annules) was said to differ from *H. australis* (annules 1.1 μm wide) by "...comparatively coarser body striae..." *H. arachisi* was said to differ from *H. concavus* by "...finer body striae..." (Mulk & Jairajpuri, 1975). *H. arachisi* has annules 1-2 μm wide ; this character was not described for *H. concavus*.

The width of body annules is unknown for more than half the described species of *Helicotylenchus*. In the genus, this character ranges from 0.6 μm *(H. impar)* to 3 μm *(H. bradys)*.

Only differences of 1 μm or more will be accepted for identification purposes.

Anterior end

Anterior end offset or continuous. This character was used only in the diagnosis of *H. elegans*, differentiated from *H. crenatus* by its lip region not being offset. *H. crenatus* was later synonymized by Sher (1966) with *H. dihystera* whose lip region is not, or only slightly, offset. This character was not used for other species and does not seem to be discriminating among species of *Helicotylenchus*. It will not be used for identification.

Shape of anterior end (Fig. 1 C). The anterior end (head, lips) of the species of *Helicotylenchus* is rounded (hemispherical, bulbous, hemispheroidal) or flattened (truncate, truncated, conical truncate, pyramidal truncate, trapezoidal, etc.).

In some cases, it is difficult to assign a meaning to some of the terms used, for example "broadly rounded". Siddiqi (1972) described *H. orthosomaticus* with "lip region elevated, broadly rounded...". His figures 4 C and D show heads with lips almost flattened. Anderson (1978) described *H. oscephalus* as "distinctive by its broadly rounded (hemispherical) head...". The head in his figure 1 B is rounded. Nandakumar and Khera (1970) noted that "many workers (...) have described the head to be conoid-rounded which falls in between hemispherical and truncate categories".

H. insignis is described with "head conoid" and illustrated with a flattened anterior end. *H. shakili* is described with "lip region conical" and illustrated with a rounded anterior end. *H. sharafati* is said to have "lip region truncate", but Fig. 2 C of Mulk and Jairajpuri (1975) presents a typically rounded lip region.

In *H. dihystera*, the anterior end was always rounded, but some variability was noted (Fortuner, Merny & Roux, 1981, Fig. 3 and Fig. 1 C in present article). *H. digonicus* differs from *H. dihystera* in having a flattened anterior end. *H. broadbalkensis* was described with anterior end flattened but not as much as *H. digonicus*. This species was synonymized with *H. digonicus* by Sher (1966).

Variability for this character exists in other species : Ali, Geraert & Coomans (1973) "found a variable head shape for most of the species. This shape may be slightly different according to the position of the head..." Siddiqi (1975) also notes that "in certain cases it is rather difficult to decide if the lip region is round or truncate...".

The character "shape of the lip region" can be used with two states : rounded or flattened, but it must be stressed that some species present both states of the character.

In addition to the character rounded/flattened, lip shape is also used to differentiate species supposedly with lips more or less elevated, more or less offset, broader or narrower, etc. than others. The variability of these characters is not known, and they will not be used for identification. Those who wish to use them must be aware that the precise form of the lip region cannot be inferred from published descriptions because of the high degree of subjectivity involved in its definition. The only way to evaluate such differences reliably would be to examine paratypes of the species under discussion.

Labial disc (Fig. 1 C). Caveness (1974) defined the labial disc as "the more or less circular form of cuticle about the oral opening and delimited posteriorly by the first transverse striation". In this sense, every *Helicotylenchus* possesses a labial disc. This structure is usually seen only in face view, and preferably with a S.E.M. Sher and Bell (1975)

and Hooper and Cham (*in* Stone, 1980) have discussed the S.E.M. aspect of the labial disc.

Nine *Helicotylenchus* spp. were said to be distinct in having a labial disc. In lateral view with a conventional microscope, seven of these species *(H. australis, H. belli, H. clarkei, H. conicephalus, H. goodi, H. krugeri,* and *H. labiodiscinus)* have a non-annulated trapezoidal anterior end, with the labial disc and the first annule elevated above the rest of the lip region, and therefore visible. The elevation is more or less marked and the disc is more or less visible in some of these species.

The labial disc described for *H. phalerus* is more like a first annule, slightly distinct from the other four coarse ones. The lip region of this species is not different from *H. canadensis* redescribed as flattened by Sher (1966). *H. phalerus* has been synonymized with *H. pseudorobustus* by Fortuner, Maggenti and Whittaker (1984).

H. variabilis is "distinguished from *H. clarkei* by the less conspicuous labial disc..." (Phillips, 1971). In fact, *H. variabilis* is described and illustrated with anterior end flattened, and the labial disc is not visible in lateral view. It seems best to consider *H. variabilis* as having flattened lips and labial disc not visible in lateral view. The character "labial disc visible" can be used only to identify the seven species with non-annulated anterior end and labial disc elevated and visible in lateral view.

Lip annules. The annulation of the anterior end is used in about one-third of the diagnoses of species in *Helicotylenchus.* In some cases, the taxa are separated by presence/absence of striae, or coarser/finer striae or distinct/indistinct striae. In other cases, the number of annules is taken into account : *H. canadensis* is differentiated from *H. digonicus* in having four *vs.* three-four annules ; *H. flatus* differs from *H. tropicus* in having five *vs.* three-four annules, etc.

Some specimens of *H. dihystera* have no visible lip annules with transmitted light microscopy (but annules may become visible with interference contrast), other specimens have faintly marked striae, and others again have distinct annules. Adult females of *H. indicus* are said to have "indistinctly visible" annules, whatever that means, but the annules are invisible in the juveniles (Azmi & Jairajpuri, 1978). The distinctness of the annulation is variable in *H. pseudorobustus* and cannot be used to differentiate *H. microlobus, H. phalerus* and *H. bradys* which were synonymized to *H. pseudorobustus* by Fortuner, Maggenti and Whittaker (1984). The distinctness of the annulation of the lip region varies within some species and may depend on the fixation. This character has no diagnostic value.

Specimens of *H. dihystera* with visible annules generally have four annules, but three and five, and more rarely six, annules were also observed. When faintly marked, the annules are difficult to count. In *H. crassatus,* 50% of the specimens have four lip annules, 15% have three annules, 15% have three and four annules, 3% have five annules, and the rest of the specimens have indistinct annulations (Anderson, 1973). Most species share with *H. dihystera* a range of three to five/six annules. Only two species *(H. sharafati* and *H. delhiensis)* have two or three annules and only four *(H. apiculus, H. oscephalus, H. paracanalis,* and *H. solani)* have six or more annules. *H. densibullatus* has three, rarely two or four annules.

For identification purposes, specimens with no visible, or faintly visible, annules or specimens with three to five (six) visible annules cannot be differentiated. The character "number of lip annules" can only be used to identify the few species with either few (two to three) or many (six and more) lip annules.

The lateral field

Width of the lateral field. *H. abunaamai* was said to differ from *H. depressus* in not having an abnormally narrow inner band of the lateral fields (Siddiqi, 1972). This feature was not mentioned in the description of *H. depressus* and apparently Siddiqi inferred it from Fig. 2 D of Yeates (1967).

The width of the lateral field was not indicated in the original description of *H. californicus* (Sher, 1966) but Anderson (1973) said that "the lateral field is also wider (6-7 *vs.* 4.5 μ) in *H. cornurus* than in *H. californicus*". Anderson (1978) said that "Females of *H. urobelus* (...) have a wider lateral field (less *vs.* more than one-fifth of body diameter), ...[than those of *H. californicus*]". It is unfortunate that Siddiqi and Anderson did not plainly state if they were comparing their new species with paratypes of, respectively, *H. depressus* and *H. californicus.*

The width of the lateral field varied from 4.4 to 6.8 μm in different populations of *H. pseudorobustus.* Because of this great variability, this character will not be used for identification.

"Areolation" : presence of transverse striae in the lateral field. Areolated ([2]) lateral field is "a situation when the transverse striae enter the lateral fields"

([2]) And not « aerolated » as too often written. The misspelled specific name of *H. aerolatus* is here emended to *Helicotylenchus areolatus* van den Berg & Heyns, 1975, without change in authority (Code of Nomenclature, Art. 32, a, ii, and Art. 33, a, i).

(Caveness, 1974). Webster's Dictionary defines "areolated" as "divided into areolae"; and "areola" as "a small area, especially a surrounding area, like the colored ring around the nipple", or also "the interstice between the veins of leaves". In the second sense, areolated can be used for lateral fields completely and regularly divided into small areas by the successive transverse striae. In the species of *Helicotylenchus* described as "irregularly areolated" a few transverse striae enter the fields singly, at widely separated intervals. A single line does not create an area and, in this case, the use of the term "areolated" is improper.

Among 183 specimens from field populations of *H. dihystera* observed with direct light microscopy, 72 specimens had lateral field without any transverse striae at all, 75 had transverse striae only in the esophageal region and 36 had a few striae irregularly scattered on the tail and/or body (Fortuner, Merny & Roux, 1981). Every specimen of *H. pseudorobustus* observed with interference microscopy showed at least some transverse striations in the anterior part of the lateral field. In some samples of this species, scattered transverse lines were observed in a percentage of individuals. In other samples of the same species from different geographical origin, no striae were observed on body and/or tail, posteriorly to the esophageal region.

The observation of transverse lines in the lateral field probably depends on the type of microscopy used. The presence of lines seems to be a variable character. It will not be used for identification.

Punctation in the lateral field. H. egyptiensis was said by Tarjan (1964) to be "unique by the presence of subcuticular refractive dots or punctation most apparent beneath the inner lines of the lateral field". Sher (1966), redescribing *H. egyptiensis* from paratypes, said that "the subcuticular refractive dots or punctuations (sic) described and illustrated for this species are considered artifacts possibly due to impurities in the fixative or glycerine". This character does not need to be further considered.

Crenation of outer lines [3] *of the lateral field.* This character is most variable. Individuals can be observed with outer lines crenated only along part of the lateral field. It is probably that the position of the specimen influences the aspect of the lines : a

_____

[3] The term "incisure" carries the idea of a cut, a gash, or a notch, and is, therefore, improper for the lateral fields. "Involution" substituted for incisures by Caveness and Bosher (1959) is more correct, but has not caught on. "Lines" will be used, not in the mathematical sense of the term, but as "something that is distinct, elongated, and narrow" (Webster's New Collegiate Dictionary).

specimen in a perfectly dorso-ventral view will have straight lines whereas crenated lines will appear in specimens slightly tilted when the bulges of the transverse annules come into view. This character will not be used for identification.

Fusion of the inner lines at the posterior end (Fig. 1 D). With few exceptions, the two outer lines of the lateral field come together on the tail in a u-shaped junction ; more rarely they do not join and the field is open. In some specimens of *H. indentatus*, all four lines were described as "passing round the tail tip". The situation is more complex for the inner lines. In species like *H. dihystera*, the inner lines come together posterior to the phasmids and continue as single central line for a certain distance, appearing as a y-shaped junction (Fig. 1 D, 1-2). *H. dihysteroides* was differentiated from *H. dihystera* by the length of the common leg. The fusion of the lines occurred at mid-tail in *H. dihysteroides* whereas it was said to be more posterior in *H. dihystera*. Specimens from Nigeria (Ali, Geraert & Coomans, 1973), Malaysia (Sauer & Winoto, 1975) and several African populations (Fortuner, Merny & Roux, 1981) proved the level of the junction to be quite variable in *H. dihystera*. In some specimens of this species, the common leg after the junction of the lines was so short that the junction could be better described as "v-shaped" (Fig. 1 D, 3). In other specimens of the same origin the common leg was so long as to reach almost the anus level. The character "length of the common leg of the junction of the inner lines" must not be considered for identification.

The y or v patterns were also observed in some populations of *H. pseudorobustus*. In other populations, the two inner lines of the lateral field joined together in a u-shaped pattern (Fig. 1 D, 4), with sometimes one of the lines continuing past the junction which then looked more like the Greek letter mu (Fig. 1 D, 5-6). Rarely the u junction came in contact with the junction of the outer lines and the whole end of the lateral field looked like the letter m (Fig. 1 D, 6-7). In some species *(H. amplius)* the junction of the line is not complete and the "m" is open (Fig. 1 D, 9).

In a population of *H. paracanalis* studied by Fortuner, Merny and Roux (1981), the junction of the inner lines also was of the u and m patterns. An m pattern was described for *H. sharafati. H. coomansi* presents a u or mu junction (Fig. 1 E of Ali and Loof, 1975).

In conclusion, this character seems very variable, but at least for some species, it can be described as pertaining to one of the two categories below :
— y or v shaped junction ; or
— u, mu, or m shaped junction.

With many species this character has not been described ; in such cases it must not be inferred from the illustrations which may or may not be correctly drawn.

The tail

Shape of the tail (Fig. 1 F). The shape of the tail is the criterion used most, appearing in two-thirds of diagnoses of new *Helicotylenchus* species. It is also the most variable morphological character, widely different among individuals within the same species, the same population, and even within the progeny of the same female (Fortuner, 1979). The author observed various tail shapes in specimens of *H. dihystera* which were similar to shapes illustrated for over 70 other *Helicotylenchus* species.

Variability of tail shape been noted by several authors. Sher (1966) gave many examples of variability of this characters in the species he described or redescribed. Siddiqi (1972) said that "in certain cases it is rather difficult to decide (...) if the tail projection is less or more developed...".

On the other hand, some species appear to have more constant tail shapes. Szczygiel (1969) noted that "the shape of tail of *H. pseudodigonicus* sp. n. (...) was very constant in all examined specimens from many localities in Poland". Tail of *H. paracanalis* from Ivory Coast (population M in Fortuner, Merny & Roux, 1981) was also very constant. Both have hemispherical tails without ventral processes. Juveniles of some species with rounded tail show a ventral terminal process : *H. multicinctus*, (Zuckerman & Strich-Harari, 1963) ; *H. vulgaris*, (Yuen, 1965).

Authors of descriptions of new species have tried to convey the uniqueness of tail shape in their new taxa by using a great variety of descriptive terms for this character : tail hemispherical, dorsally bent, dorsally convex-conoid, more curved dorsally, indented, with concavity on dorsal side, etc. Any attempt to obtain a complete description of the complexity of tail shape ends up in gems like : "tail end tapers regularly up to distal third then becomes ventrally convex and dorsally concave appearing smooth and subdigitate with a narrow, hemispheroidal terminus...". In fact, if the details (which can probably be accounted for by intraspecific variability) are obliterated, it is possible to fit all shapes described to date into the following four categories :

1. Tail straight, with rounded end (example : *H. retusus*) Fig. 1 F, 1-3).

2. Tail bent and asymmetrical, (more curved dorsally) with rounded end (example : *H. multicinctus*) Fig. 1 F, 4-8).

3. Tail more curved dorsally, dorsal side joins the ventral side at a straight angle ; no projection (example : some specimens of *H. dihystera*) Fig. 1 F, 9-10).

4. Similar to number 3, with rounded or pointed projection (example : *H. pseudorobustus* or *H. erythrinae*) (Fig. 1 F, 11-16).

If the dorsal concavity on the tail of *H. concavus* is ignored the tail fits into category 1. The indentation in *H. crenacauda* can be seen as shape 4 with a ventral projection specially well marked. Any other shape can be fitted in one of the four basic categories.

The distinction between ventral projection short ("less than two tail annules long") and long ("two or more tail annules long"), introduced by Sher (1966) and used by every successive key-builder, will not be used because : (*i*) it is difficult to decide how long is "two tail annules long" in view of the variability of the width of the tail annules ; (*ii*) it is difficult to measure the length of the projection because it usually merges into the tail in a S curve ; and (*iii*) in *H. dihystera* the length of the projection is very variable from no projection at all to a small or long projection.

In some diagnoses, other features of the ventral projection were used such as "a wider tail projection" *(H. talonus)*, a characteristic terminus "long, digitate, dorsally bent" *(H. digitatus)*, a terminus "irregularly hemispherical" *(H. californicus)*, or an annulated terminus *(H. pseudorobustus)*. As far as can be determined from the variability in *H. dihystera* and *H. pseudorobustus*, little reliability can be placed on these features and they will not be used for identification.

Mucros were observed at the tip of otherwise rounded tail projections in some specimens of *H. pseudorobustus*, particularly in a sample from California. The presence of mucros was not considered diagnostic by Fortuner, Maggenti and Whittaker (1984).

Tail length ; Ratio c. The length of the tail is given in the original description of only seventeen species of *Helicotylenchus*. The lengths range from 8 μm (*H. brevis* in van den Berg, 1976), to 22-38 μm, mid-range 30 μm *(H. rohtangus)*.

In *H. dihystera* tail lengths of the various populations were variable with C.V. of about 10%. Different host plants caused the mean value of this character to vary from 14.5 to 17.6 μm, a 3 μm intraspecific variability. In different populations of *H. pseudorobustus*, the tail length varied from 16 to 19 μm, again a 3 μm variability.

Tail length was used in about one-fourth of the diagnoses as ratio c, body length/tail length. Ratio c expresses the relative length of tail compared to the body length. The hoplolaimids generally have

252

short tails with high ratio c. The length of the tail is significantly correlated to the length of the body in most populations of *H. dihystera*, but was not significantly correlated in the populations of *H. paracanalis* with a very short tail. The variability of ratio c is generally higher than the variability of tail length. It is best not to use ratio c, but to use the actual length of the tail, measured in micrometers. However, as the tail length is unknown for most species of the genus *Helicotylenchus*, ratio c can be used with caution for identification. It ranges from 19 *(H. persici)* to 90 *(H. vulgaris)*. Considering the variability of tail and body lengths, only differences of more than 15 points for ratio c will be considered for identification.

Ratio c'. The length of the tail has also been used in diagnoses as a constituent of ratio c' (tail length/ anal body width). Ratio c' conveys for the tail the same relationship as does ratio a for the body : long and thin (= filiform) tails will have high ratios c', short and stubby ones will have small values of c'. Hoplolaimids generally have short stubby tails, with small c'.

The two constituent characters of ratio c' were strongly correlated in a population of *H. paracanalis* with a very short tail (length about one-half of body diameter at anus), but were weakly correlated in populations of *H. dihystera* with relatively longer tails (about one to one and a half body diameters at anus). The variability of ratio c' is generally not lower than the variability of the tail length (Fortuner, 1984).

Three characters describing the tail length may be accepted for identification : actual tail length, ratio c, and ratio c'. If all three are used for the identification of an unknown population, an artificial weigth would be given to the character : "length of tail". It is best to use only one of the three characters. The actual length would be the best choice if it were known for more species. The second best choice is ratio c' which does not use the body length, and does not increase the weight of this character already used as the actual body length and ratio a.

Number of ventral tail annules. This is another favorite character, present in one-fifth of the diagnoses. In *H. dihystera*, the number of tail annules is quite variable, with C.V. 12 to 26%. Under different host plants, the average number varied from six to nine. The range of variation for this species was given as six-twelve annules by Sher (1966). It was enlarged later from four (Ali, Geraert & Coomans, 1973) to fourteen (van den Berg & Heyns, 1975). During the studies on *H. dihystera*, the author observed from four to seventeen tail annules, a thirteen annules intraspecific variability.

The number of annules ranges from five *(H. astriatus)* to 24 *(H. teleductus)*, a nineteen annules range. It is possible to use this character to discriminate some species, but its great variability much reduces its value for identification.

Shape of tail annules (Fig. 1 E). Some species were characterized by the appearance of tail annulation : "annules on tail terminus smaller than on body" *(H. bihari)*, "coarser terminal annulation" *(H. labiodiscinus)*, "a non-annulated section on the ventroposterior part of the tail" *(H krugeri)*, etc.

Specimens of *H. dihystera* were observed with annules on tail as large as, or smaller or coarser than on body, some with distinct annules, others with annules difficult to see. There was generally a non-annulated terminal section on the ventral side, but many individuals presented a completely annulated tail. A similar variability was seen in *H. pseudorobustus*.

The shape of annulation on the tail will not be used for identification.

NERVOUS AND SENSORY SYSTEM

Phasmids

Position in relation to anus

One of the most used characters (present in almost half the diagnoses), this character is also one of the most variable. The number of annules between the phasmid and the level of anus has a C.V. of 70% in the progeny of a single female (Fortuner, 1979) and from 15 to 57% in other populations of *H. dihystera*. Under different host plants, the phasmids varied from 6.75 to 8 annules above anus level, a suspiciously low variation(16%). Phasmids in field populations of *H. dihystera* varied from five to nine annules above anus (on average) a 60% variation which seems closer to the general rule. In *H. pseudorobustus*, the variation among field populations was from two to eight annules above anus.

Variability among other species of *Helicotylenchus* seems as great as that observed for *H. dihystera* and *H. pseudorobustus*. Anderson (1973) noted that in *H. crassatus*, "...right and left phasmids in a single specimen may be from zero to four body annules apart...". Nevertheless, slight differences in phasmid position have been used to differentiate species for example : *H. agricola* and *H. dihystera* with phasmids four-seven *vs.* five-eleven annules above anus, (values of Elmiligy, 1970 and Sher, 1966 respectively).

Considering the great range in position reported for phasmids in different species of *Helicotylenchus* (seven annules posterior to anus in *H. labiodiscinus*,

fifteen annules anterior to anus in *H. orthosomaticus)*, it is still possible to use this character for identification, but its great variability will have to be taken into account and only differences of more than six annules will be considered.

For identification and to avoid the use of negative values, the number of annules between phasmid and anus level will be counted after arbitrarily assigning a value of twenty to the position of the anus. Phasmids five annules anterior to anus will be noted 25, phasmids five annules posterior to anus will be noted fifteen. Thus, the extreme values reported for species of the genus are thirteen *(H. labiodiscinus)* to 35 *(H. orthosomaticus)*.

Position in the lateral field. H. coomansi Ali & Loof, 1975 was differentiated from *H. orthosomaticus* Siddiqi, 1972 by "... the phasmids being located (...) in the center of the lateral field" (phasmids were described as "close to inner dorsal incisure in *H. orthosomaticus*"). The same criterion was also used by Sher (1966) when differentiating *H. nigeriensis* from *H. californicus* and *H. hydrophilus* by "phasmids that are not in the center of the lateral field."

Sher (1966) stated that in *H. labiodiscinus* the phasmids "are usually not in the center of the lateral field". The use of the word "usually" seems to indicate some variability. Ali (1976) observed that phasmids of paratypes of *H. mangiferensis* Elmiligy, 1970 are either in the middle of the lateral field or on the inner ventral line. Phasmids of *H. dihystera* were generally in the center of the lateral field, but many specimens had phasmids shifted closer to one or the other inner lines. Phasmids of *H. pseudorobustus* are either in the center of the field or close to the ventral line.

In conclusion, this criterion (rarely used) seems to vary within populations of the same species and will not be used for identification.

Presence of distinct phasmids. H. crenatus was differentiated from *H. nannus* (= *H. dihystera)* by "... the presence of distinct phasmids which can be observed even under low magnification...". Sher (1966) studied topotypes of *H. crenatus* and could not distinguish this species from *H. dihystera*. It is probable that the greater distinctness of phasmids in the original specimens was an artifact due to fixation.

The presence of an "additional pore located thirteen annules above anus" observed in *H. thornei* (= *H. teres)* by Gupta and Chhabra (1967) is doubtful (Nandakumar & Khera, 1970).

Cephalids

The cephalids are possibly commissures connecting ventral and lateral nerves although their origin is unknown (Anderson, 1973). Their position was said to be a reliable taxonomic criterion : "the posterior cephalid may also vary between species in position, sometimes by several microns, and in size" (Anderson, 1973).

In most descriptions, this character is given, not in microns from the anterior end, but in annules behind the lip region. This is not recommended because : (*i*) it introduces an additional variability (the width of body annules may vary) ; (*ii*) there is no evidence that the position of the posterior cephalid is tied to a particular annule ; and (*iii*) the precise number of annules can be difficult to count because the annules just behind the lip region are usually smaller and less distinct. This character will not be used for identification.

The distinctness of the cephalids probably varies upon fixation and/or between individuals, and this character will not be used.

The number of annules between anterior and posterior cephalids was used in the diagnosis of *H. conicephalus*. The anterior cephalid is often smaller and more difficult to see or not visible at all.

Hemizonid

The hemizonid is a hypodermal commissure that connects ventral and lateral nerves. It has been reported in many nematodes and may be present throughout the Nematoda (Smith, 1974).

The position of this structure may vary, depending on the plane of focus, from one to four annules within an individual (Anderson, 1973). In a specimen of *H. pseudorobustus* the hemizonid was observed to shift its position depending on the plane of focus. It was observed so clearly in two different positions that the specimen could have been believed to possess two hemizonids. Because of this variability, and since this character has been rarely used in diagnoses, it will not be considered for identification.

The hemizonid was reported to be absent in *H. nannus* (in Perry, 1959), *H. flatus* and *H. paragirus*. *H. nannus* and *H. flatus* were both later synonymized to *H. dihystera* with hemizonid present. The absence of the hemizonid in any *Helicotylenchus* species is doubtful and will not be accepted for identification. The hemizonion is another commissure, situated posteriorly to hemizonid. Its position was never used for identification and justly so, as it is very difficult to observe, variable in position and it may be confused with other commissure-like structures in its vicinity (Anderson, 1973).

EXCRETORY SYSTEM

Position of the excretory pore

A few species were differentiated by the position of the excretory pore, either measured from the

anterior end, or in relation to some structure in the esophagus : the anterior end of the glandular bulb or the esophago-intestinal junction.

It is possible to use the position of the excretory pore for identification when measured from the anterior end, because this character has a reasonably low C.V. in *H. dihystera* and the host plants produce only a limited variation (10 μm, from 100 to 110 μm). In *H. pseudorobustus*, the variability is also 10 μm, from 105 to 115 μm. The range in the genus is from 85 *(H. abunaamai* and *H. areolatus)* to 135 μm *(H. oscephalus).*

The position of the excretory pore in relation to esophageal structures will not be retained for identification because of the great additional variability introduced by the latter. Unfortunately this unreliable method has been used to indicate the position of the excretory pore in most specific descriptions.

Structure of the excretory canal

H. concavus was said to differ from all other species in the genus "by a collaret in the wall of the excretory canal close to its opening" (Román, 1961). This was not accepted as diagnostic by Sher (1966) because a similar structure was observed in other species of *Helicotylenchus.* The differences in sclerotization may well be fixation artifacts.

DIGESTIVE SYSTEM

Stylet

Length of stylet. Stylet length has the smallest coefficient of variability among quantitative characters : 1.7% in the progeny of a single female of *H. dihystera* (Fortuner, 1979), 1.6 to 4% in field population of the same species (Fortuner, Merny & Roux, 1981), 3% in *H. indicus* (Azmi & Jairajpuri, 1978). It varied slightly in *H. dihystera* under different hosts, with mean values differing to up to 2 μm (Fortuner & Quénéhervé, 1980). It varied from 25.5 to 28.5 μm in populations of *H. pseudorobustus.*

This character is readily used in diagnoses, and justly so, but some specific differences appear very small in view of a possible 3 μm host-induced or geographical variation. For example, *H. leiocephalus* is distinguished from *H. concavus* by its stylet of 24-29 μm ; the stylet of *H. concavus* was originally measured at 28-29 μm (Román, 1961), and remeasured by Sher (1966), from paratypes, at 29-32 μm. On the other hand, populations with different stylet lengths are sometimes considered as conspecific. Sher (1966) redescribed *H. vulgaris* with stylet 30-34 μm but said that two populations from southern France "exhibited a usually shorter spear, 25 to 30 μm".

Stylet lengths in *Helicotylenchus* range from 19 μm (18-20 μm) in *H. morasii* to 39-42 μm (mid-range =

40.5 μm) in *H. coomansi* and differences of more than 3 μm will be considered for identification.

Length of stylet cone ; ratio m. The length of the anterior part of the stylet (= cone, conus, apex, metenchium, etc.) was used in some diagnoses, not in its actual value, but as a constituent of ratio m defined by Andrássy (1962) as length of cone/length of stylet.

The cone usually has a slightly higher C.V. than the stylet itself, probably because the same error in measurement will be twice as important when the measured length is shorter by half. The variability of stylet and cone lengths is not reduced by the use of ratio m (Fortuner, 1984).

The ratio m evaluates the length of the cone compared to the length of the entire stylet. The two characters were stongly correlated in populations of *H. dihystera, H. paracanalis,* and *H. morasii* studied for Fortuner (1979) and Fortuner, Merny and Roux (1981). In the population of *H. dihystera* used for host plant studies (Fortuner & Quénéhervé, 1980), the correlation was good for two hosts (*Pueraria* and cotton), but the characters were not correlated at all in populations from the eight other hosts. This result is unexplained. In *H. pseudorobustus,* ratio m varied from 46 to 50 in different populations.

The value of this character ranges form 43 *(H. depressus)* to 55 *(H. goldeni).* Ratio m will be considered as valid and will be used for identification.

Shape of stylet knobs (Fig. 1 B). Many species of *Helicotylenchus* were described with spear knobs anteriorly indented (= cupped, hollow, anchor-shaped, concave anterior surface, anteriorly-directed, etc.). Others have knobs anteriorly flattened, rounded, or sloping backwards.

H. dihystera was redescribed by Sher (1966) with knobs indented anteriorly. In a population from Nigeria, indented knobs were observed in only half the specimens, the other half had flat knobs (Ali, Geraert & Coomans, 1973). The specimens of *H. dihystera* observed by the author had knobs of variable shape, from indented to flattened and more rarely rounded. Nandakumar and Khera (1970) studying variability in *H. indicus* noted that "shape of stylet knobs needs to be handled with caution, especially while studying fixed and mounted specimens". Azmi and Jairajpuri (1978) observed in the same species knobs "rounded to slightly anteriorly directed or with sloping to flattish anterior surface", which apparently covers the whole range of variation. The truly sloping shape of the knobs of *H. densibulatus* seems restricted to a few species only. Sloping knobs have been described for *H. solani* and *H. tangericus,* but the illustrations show rather flattened shapes.

For identification, only three shapes of the anterior surface of the knobs will be retained : concave, flat-to-rounded, and sloping backwards. Even then it will be found that many species and populations, when represented by large enough samples, overlap two of these three classes.

Labial framework

Some species have been distinguished by a labial framework (= cephalic framework, head skeleton, etc.) more developed *(H. conurus)*, not as conspicuous *(H. densibullatus)*, or more heavily sclerotized *(H. oscephalus)*. The conspicuousness and apparent development of sclerified structures such as the labial framework depends on fixation and the age of specimens. Appreciation of relative distinctness is largely a matter of personal opinion. This character will not be retained.

H. conurus was said to have a thicker and more depressed septum (= basal plate) than *H. californicus*. This is the only example of the use of this character and it will not be used for identification.

A few species were differentiated by the dimensions of the basal ring (= the outer margins of the basal plate, which extend posteriorly for a few microns). The variability of this structure is not known for the moment, but it will be used when it is known in microns. Depth of the basal rings given as number of annules, will not be retained for reasons discussed above in the paragraph on position of cephalids.

The esophagus

Dorsal gland opening (D.G.O.). In *Helicotylenchus*, the dorsal esophageal gland opens into the lumen of the esophagus more posteriorly behind the stylet base than is generally the case among Tylenchida and particularly *Rotylenchus*. Golden (1956) used this characteristic to separate *Helicotylenchus*, with the d.g.o. 1/3 or more of spear length behind spear knobs, from *Rotylenchus*, with d.g.o. usually less than 1/3 of that same length. Perry (1959) described two new species, *H. digonicus* and *H. platyurus* with intermediate values for this character. Sher (1961) consequently revised the separation between *Helicotylenchus* and *Rotylenchus* which he placed at 1/4 of the stylet length. Definite limits for this character are not given any more in the diagnosis of the genus *Helicotylenchus* : Corbett (1978) just said that "in many species the dorsal oesophageal gland duct is further from the spear base than in other Tylenchid genera".

While Perry (1959) found this character not very useful for generic differentiation, he noted that it could be used to identify species within *Helicotylenchus* and, because "the terminology for this character is lengthy and awkward", he proposed a

coefficient o = distance from the stylet base to the d.g.o./stylet length.

The use of ratio o was rejected by Fortuner (1984) who proposed to circumvent the awkwardness of the terminology by using an abbreviated formula such as "d.g.o. at × µm from stylet".

The position of the d.g.o. measured in microns behind the spear base was variable in *H. dihystera* with C.V. of 5 to 17% and varied under different hosts from 10.6 to 14.5 µm. Its mean value varied from 9 to 14 µm in populations of *H. pseudorobustus*. An additional variation is introduced when the esophageal lumen is bent between the stylet and the d.g.o., which artifically reduces the distance. In the species where the actual d.g.o. (and not ratio o) was given, it varied within the genus from 6 µm *(H. astriatus)* to 16 µm *(H. holguinensis)*, a 10 µm range which is small when compared to the 5 µm intraspecific variability. With these limitations, and considering that most specific descriptions give only the useless ratio o, this character has little value for identification.

The median bulb. A spherical median bulb filling the body cavity separated *H. caroliniensis* from all other *Helicotylenchus* spp. with a smaller, oval bulb. Because this particular shape is known in only one species it is not very valuable for identification.

The glandular bulb. The arrangement of the esophageal glands has played a great role in the definitions of *Helicotylenchus*, *Rotylenchus*, and the related genera (Sher, 1961 ; Seinhorst, 1971).

At specific level, the structure of the esophageal glands was used only once in *Helicotylenchus* : in *H. digonicus*, the glandular lobes are "generally separated and the nuclei of the subventral glands are smaller and more posterior than in *H. crassatus*" (Anderson, 1973). Because these characters are not described for most species in *Helicotylenchus*, they will not be used for identification. Anderson (1973) said that "the dorsal and subventral gland lobes [of *H. crassatus*] do not appear to be separated". His Fig. 2 C shows the glands in a lateral view. Apparently, the exact arrangement was not studied in cross-section. Jairajpuri and Siddiqi (1977, published 1979) described, in the diagnosis of the new genus *Orientylus*, glands overlapping the intestine, but "not forming a wrap-round over the anterior end of intestine". In fact, the esophageal glands of any *Helicotylenchus* sp. were never proved to be fused together into a single structure. Even when, as in *H. crassatus*, the glands cannot be distinguished as separate entities in lateral view, this is not a proof of structural fusion. Morphological studies, preferably from electron-microscope photographs of cross sections in the esophageal region, are needed to deter-

mine the structure of the esophageal glands in several *Helicotylenchus* spp. This character will not be accepted for the moment.

Length of the esophagus, ratios b and b'. The length of the esophagus has not been used in diagnoses, and is rarely given in descriptions of species of *Helicotylenchus*. This character was used in a few diagnoses as two ratios relating the body length to the distance from the anterior end to the esophago-intestinal junction (ratio b) and to the end of the esophageal glands (ratio b'). Fortuner (1984) showed the taxonomic value of ratios b and b' to be very limited. When only one ratio (b) is given, it is impossible to know whether the author used the distance anterior end to esophago-intestinal junction (true ratio b) or if he measured the distance to the end of the esophageal glands (ratio b').

The actual lengths of the esophageal structures are moderately variable, with C.V. of 4 to 7% in field populations of *H. dihystera* (Fortuner, Merny & Roux, 1981), and variation of about 10% under different hosts (Fortuner & Quénéhervé, 1980). The variability was low also for *H. indicus* (C.V. 5-6% in Azmi and Jairajpuri, 1978). In *H. pseudorobustus*, the length of esophagus varied from 110 to 130 μm and the length to the end of glands from 135 to 165 μm.

Only the actual values of these two lengths should be used for identification, however, these lengths are not known for most species of *Helicotylenchus* and for the moment these characters will not be used for identification.

Intestine

Esophago-intestinal junction. In many species, the esophago-intestinal junction is posterior to the level of the excretory pore. This arrangement was observed in every specimen of *H. dihystera* (Fortuner, 1979). This character was variable in populations of *H. pseudorobustus*, in which the junction was observed to be anterior, level, or posterior to the level of the excretory pore. This character will not be used for identification.

Presence of intestinal fasciculi. Intestinal fasciculi (= canals) were observed in "every", "most", or "some" specimens of five species *(H. canalis, H. krugeri, H. martini, H. paracanalis, and H. trivandranus)*. These structures were observed in seventeen out of twenty specimens from a population of *H. paracanalis* (Fortuner, Merny & Roux, 1981).

Canals were discussed under the name of "intestinal fasciculi" by Byers and Anderson (1973), and while their function is not yet known, it seems that they "form a part of the normal endowment of the

intestinal cells" of the species studied by these authors *(Tylenchorhynchus dubius)*. The presence of fasciculi can be used for identification of the few species in which they occur.

REPRODUCTIVE SYSTEM

Regression of the posterior genital branch

Most species in *Helicotylenchus* have two genital branches equally developed, or have a posterior branch slightly smaller than the anterior one *(H. multicinctus* for example). This smaller organ is functional.

Rotylenchoides intermedius Luc, 1960 has a posterior branch reduced to a post-uterine sac (P.U.S.) followed by a short row of small undifferentiated cells with no distinguishable nuclei. It is impossible to recognize ovary, spermatheca, or columella. Luc (1960) considered this species to be intermediate between *Helicotylenchus* and true *Rotylenchoides* where the posterior branch is reduced to a simple P.U.S. He noted that the two genera were identical except for the development of the posterior genital branch, to the extent that males of either genus cannot be differentiated.

Siddiqi and Husain (1964) accepted in *Rotylenchoides* only the species with a simple P.U.S. They placed in *Helicotylenchus* the species with a degenerate posterior branch such as *R. intermedius* and a taxon they described as new, *H. neoformis*. Sher (1966) did not agree and considered that *H. neoformis* and *R. intermedius* belonged to *Rotylenchoides*.

There are today more than 150 species of *Helicotylenchus* described with two genital branches equally, or almost equally, developed ; four species of *Rotylenchoides* with a simple P.U.S. *(R. brevis, R. variocaudatus, R. affinis,* and *R. impar)* and two intermediate species with degenerate posterior branch *(R. intermedius, H. neoformis)*.

Because *Rotylenchoides* differs from *Helicotylenchus* only in the regression of a single organ, and because of the existence of intermediate forms, *Rotylenchoides* Whitehead, 1958 is here proposed as a junior synonym of *Helicotylenchus* Steiner, 1945.

This action emphasizes the close relationship between the species assigned to these two genera and acknowledges the fact that the species with a simple P.U.S. are the end product of an evolutionary trend already visible in *Helicotylenchus sensu stricto*.

The following specific changes are now proposed :
Helicotylenchus brevis (Whitehead, 1958) n. comb.
    syn. : *Rotylenchoides brevis* Whitehead, 1958
H. variocaudatus (Luc, 1960) n. comb.
    syn. : *R. variocaudatus* Luc, 1960

H. affinis (Luc, 1960) n. comb.
   syn. : *R. affinis* Luc, 1960
H. khani nom. nov.
   syn. : *R impar* Khan, Saha & Chawla, 1981
   nec. H. impar Prasad, Khan & Chawla, 1965.

The following two species are transferred back
to *Helicotylenchus* :
H. intermedius (Luc, 1960) Siddiqi & Husain, 1964.
   syn. : *R. intermedius* Luc, 1960.
H. neoformis Siddiqi & Husain, 1964
   syn. : *R. neoformis* (Siddiqi & Husain, 1964)
   Sher, 1966

Rotylenchoides desouzai Kumar & Ananda Rao,
1976 because of the dorsal overlap of the esophageal
glands is considered closer to *Rotylenchus* (⁴) and is
transferred to this genus as :
Rotylenchus desouzai (Kumar & Ananda Rao, 1976)
n. comb.
   syn. : *Rotylenchoides desouzai* Kumar & Ananda
   Rao, 1976

With the grouping of most *Rotylenchoides* spp.
with *Helicotylenchus*, the regression of the posterior
genital branch becomes a valid specific character
with three states :
— two branches functional, equally or almost
equally developed.
— posterior branch nonfunctional, as a row of
degenerated cells.
— posterior branch reduced to a P.U.S.

The vulva

Position of the vulva; ratio V. The position of the
vulva along the body is determined genetically for
every species. It does not vary during the growth
of the individual. Ratio V is the distance from head
to vulva given as the percentage of the body length.
The two measurements constituting ratio V are
always very strongly correlated (coefficient of corre-
lation generally more than 0.95%). V is very con-
stant, and its variability is less than that of its
constituent characters. Thus, in a population of
H. dihystera under different hosts, the body length
varied from 610 to 748 μm, a 20% variation, but
V varied only from 62.9 to 64.9, a 3% variation
(Fortuner & Quénéhervé, 1980). V was also more
stable than the other allometric characters in *H.
indicus* (Azmi & Jairajpuri, 1978). In *H. pseudo-*

(⁴) Because of the far out D.G.O. "slightly more
than half stylet length from stylet base", this species
could have been proposed in the genus *Orientylus*
Jairajpuri & Siddiqi, 1977. However, I do not recog-
nise this genus as valid, and I will propose it elsewhere
as a synonym of *Rotylenchus*.

robustus, ratio V varied from 60 to 62% in mean
value.

In *Helicotylenchus*, ratio V varies from 51.5%
(H. haki) to 90.9% *(H. brevis)*. Ratio V will be used
for identification of species differing by more than
two points for this character.

Vulva flaps. Perry (1959) observed "small cuticular
lateral membranes to form crescent shaped guards
at the end of the vulva" in *H. nannus*. These struc-
tures were difficult to see as they were "best observed
by pressing the specimen to remove the body contents
and flatten the cuticule".

Vulva flaps have been described in a number of
species. In *H. pseudorobustus*, their appearance varied
from a fan-shaped conspicuous structure to a very
small straight-edged flap at the end of the vulva
(Fortuner, Maggenti & Whittaker, 1984).

Flaps were said to be absent in *H. bihari* and *H.
indenticaudatus*, but it is not known if they are
truly absent or particularly difficult to observe in
these species.

This structure will not be used for identification.

Other features of the vaginal region were discussed
for their possible taxonomic value by Anderson
(1973). The width of the vulval slit (= length of
vulva) could be diagnostic but is inconvenient to
measure. The epiptygma (or epiptygmata) are inward
folds of cuticle situated at the vulva opening. They
are present in *Helicotylenchus*, but are visible only
in a few specimens (Sher, 1966). They have not been
proved to be absent in any species of *Helicotylenchus*
and this character has no taxonomic value (Geraert,
1976). The thickness of the vaginal walls is variable.
A constriction of the vaginal wall near the vulva can
be seen only in some specimens but not in others of
a given species. The shape of the vaginal muscles
depends upon fixation.

These characters have no value for identification
(Geraert, 1976) and they will not be used here.

Position of spermatheca in genital tract

Spermathecae were described as either in line
or offset from genital tract, more rarely as present
or absent, visible or inconspicuous.

The spermatheca is a part of the genital tract and
it is not correct to note "spermatheca absent".

The development of the spermatheca during the
embryogenesis was described by Hirschmann and
Triantaphyllou (1967). The offset spermatheca in
H. dihystera is formed during the fourth molt, and
its dorsal bulge is already indicated at that stage.
It is composed of twelve cells, six in each side.
Fig. 5, E in Hirschmann and Triantaphyllou (1967)
shows the arrangement of the six nuclei, with four
dorsal and two ventral ones. Therefore, an offset

spermatheca is characterized by a typical arrangement of its cells. Alternatively, a spermatheca in line with the genital tract will have the same number (3) of cells on its dorsal and ventral sides. A spermatheca is either offset or in line with the genital tract depending on its embryogenesis. This character is not subject to variation and it is improper to describe "spermatheca in line or slightly offset".

In some specimens of *H. dihystera* we did observe a small, inconspicuous spermatheca which appeared to be in line with genital tract, but that was only due to its poor development and did not prevent this spermetheca from being cytologically offset, with the usual arrangement of nuclei (four dorsal, two ventral). The position of the spermatheca in the genital tract is of specific value, but cannot be used for the present because many authors have not understood its profound, cytological origin and have described a mere appearance due to the state of development of the specimen they studied.

Characters related to males

Presence of males

Perry (1959) described a "spermagonium" or sperm-producing organ in *H. nannus (= H. dihystera.* He thought this was an example of digonic hermaphroditism in phyto-parasitic nematodes. Similar structures were described later by a number of authors (see list in Hirschmann and Triantaphyllou, 1967) and even in more recent descriptions.

Yuen (1964), Triantaphyllou and Hirschmann (1964) and Hirschmann and Triantaphyllou (1965) questioned the existence of the so-called spermagonium, and Hirschmann and Triantaphyllou (1968) identified it as a nonfunctional empty spermatheca. The species of *Helicotylenchus* without males reproduce parthenogenetically.

H. dihystera is such a species : inoculation to rice of a single larva successfully produced a large population (Fortuner, 1979). However, Sher (1966) observed a few males in two large California populations. In some genera the sex ratio depends on external factors (see the review of published works on the subject in Northon, 1978). The question can be raised if a parthenogenetic "species" is really distinct from the bisexual species which engendered it. Yuen (1964) thought that the uniparental forms in *Helicotylenchus* were true species but she added that the possibility that they may be self-perpetuating pure lines cannot be eliminated.

In addition to this theoretical problem, the usefulness of the character presence/absence of males for identification is somewhat reduced by the difficulty of recognizing impregnated females. Sperma-

thecae were observed filled with a granular nucleated substance which was in fact the enlarged wall cells of the spermatheca (Geraert, 1976). In other cases non-nucleated inclusions (= refractive bodies) were reported in the spermathecae of *Helicotylenchus* spp. These inclusions are believed to be droplets of excretory material from the columella (Hirschmann & Triantaphyllou, 1968). Also, only a certain proportion of the female specimens will be impregnated at any time : Ali, Geraert & Coomans (1973) observed a population of *H. exallus* from Nigeria with spermathecae empty in about 40 % of the females. Sometimes sperm cells can be observed in spermathecae of females but no males are found.

A definite life-cycle was observed in species of *Helicotylenchus* in the Great Plains. Reproduction occurred only during spring and early summer (Thorne & Malek, 1968). Specimens of bisexual species may be impossible to differentiate from parthenogenetic forms when collected outside the reproduction period.

On rare instances, males were reported for known parthenogenetic species. Sher (1966) described four males of *H. dihystera* from Riverside, California. Hashim (1982) described one male of *H. digonicus* from Jordan. The females associated with this male were not impregnated. The description of the male specimen given by Hashim (1982) fits the description of males of *H. minzi* known from Israel. The identification proposed by Hashim (1982) for the male he found needs to be confirmed.

It remains that males are absent, or at least extremely rare, in a number of species and the character "presence/absence of males" will be accepted for identification.

When males are present, a few male-related characters may be used.

Spicule length

A few species were differentiated by the length of the spicules. Because the studies on variability were conducted by the present author on parthenogenetic species *(H. dihystera, H. pseudorobustus)*, nothing is known about the variability of this character.

It will be accepted for the present with the same variability (3 μm) as the stylet, another sclerified structure. The range in the genus is from 15 μm *(H. intermedius)* to 35 μm *(H. coomansi).*

The length of the gubernaculum was used only in the diagnosis of *H. regularis.*

Other characters of males

The position of the phasmids in the male of *H. caipora* was used to differentiate this species from *H. multicinctus.*

Table 1

List of quantitative characters retained for the identification of species of *Helicotylenchus*

Characters	Range of average values in		Intraspecific variability
	Helicotylenchus *s. l.*	Helicotylenchus *s. str.*	
Body length (μm)	408-1 235	440-1 235	150
Ratio a	17-41	17-38	8
Body annule width (μm)	0.6-3.0	0.6-3.0	1
Tail length (μm)	8-30	12-30	3
Ratio c	19-90	19-90	15
Ratio c'	0.5-2.2	0.5-2	0.5
Number of tail annules	5-24	5-24	13
Position of phasmids in annules from anus level (anus = 20)	13-37	13-37	6
Excretory pore (μm from head)	85-135	85-135	10
Stylet length (μm)	19-40.5	19-40.5	3
Ratio m	43-55	43-55	4
D.G.O. (μm from knobs)	6-16	6-16	5
Ratio V	51.5-90.9	51.5-69.5	2
Spicule length (μm)	15-35	18-35	3

Table 2

List of qualitative characters retained for the identification of species of *Helicotylenchus*

TWO-STATE NON VARIABLE CHARACTERS (present or absent) :

Presence of males
Labial disc visible in lateral view
Presence of fasciculi (canals)

TWO-STATE CHARACTERS (variable in some species) :

Habitus :	*C-shape*	*Spiral*
Shape of lips :	*Rounded*	*Flattened*
Fusion of inner lines of lateral field :	*y/v*	*u/μ/m*

THREE-STATE CHARACTERS (variable in some species) :

Number of lip annules :	*2/3*	*4/5/6*	*6 and more*
Shape of knobs :	*Indented*	*Rounded-flat*	*sloping*
Female genital branches :	*2, functional*	*Post. branch degenerated*	*P.U.S.*

FOUR-STATE CHARACTERS (variable in some species) :

Shape of tail :	*hemispherical*	*rounded asymmetrical (ventrally bent)*	*dorsal and ventral sides joining at an angle*	*with rounded or pointed projection*

Males of *H. conurus* were said to be "heavier" than those of *H. californicus* (Anderson, 1974). If this refers to a difference in the ratio a, it is inconclusive (a = 32(28-35) *vs.* 30-36). Males of *H. conurus* also had a shorter spear than males of *H. hydrophilus* (Anderson, 1974), but the same character was already used by the author for the females of this species ans its use for males is redundant.

The males of *H. conurus* differed from males of *H. erythrinae* in the shape of the tail. This may be significant for identification.

The dichotomous key

The list of characters which can be used in diagnoses and for identification is given in Tables 1 and 2. Some other characters which can be used for differentiating only one or a few species have not been included in the table. An attempt was made to use the characters in these Tables in a dichotomous key but, as will be shown below, most of the characters retained were useless for such a purpose.

MEASUREMENTS

The most reliable measurements are stylet length and ratio V because their intraspecific variability is small and not enlarged by external factors.
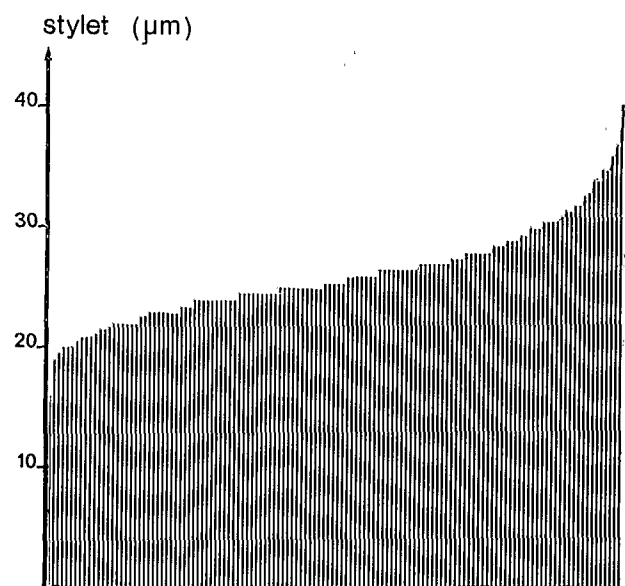
Fig. 2. Graphic representation of the lengths of the stylets of 126 species of *Helicotylenchus,* arranged by increasing values.

Figure 2 represents the stylet lengths in 126 species of *Helicotylenchus,* arranged in increasing values. It is evident from this figure that the stylet lengths increase by very small increments from the smallest stylet (19 μm) to the largest (40.5 μm). No gap in the successive lengths exists which could have been used to separate the species into two well defined groups. Any key statement such as "stylet longer than $\times$ μm *vs.* stylet smaller than $\times$ μm" will be inappropriate because of the many species with stylet lengths straddling the $\times$ μm limit. The other measurements (lengths of body, esophagus, spicule, etc., values of ratios V, a, c, etc.) present the same pattern of variation among the species of *Helicotylenchus.*

Measurements cannot be used in a dichotomous key except in the last few lines when other characters have reduced the number of species under consideration. For example we could use the stylet length if we had to differentiate only *H. morasii* (stylet of 19 μm) from *H. coomansi* (stylet of 40.5 μm). Other kind of characters must be used in the first part of the key to break the bulk of the species into manageable units.

NONVARIABLE TWO-STATE CHARACTERS

Nonvariable characters described as presence/absence (of males, of fasciculi) or visible/nonvisible (labial disc) can be used to differentiate groups of species.

However, only three such characters were accepted above as usable, and one of them (presence/absence of males) will not be accepted by all users in view of its ambiguities. The character "presence of fasciculi" can be used to differentiate five species, and the character "labial disc visible in transverse view" can differentiate seven species (but *H. krugeri* has both fasciculi and disc visible). After these eleven species have been set apart, the majority of the described species still have to be differentiated.

VARIABLE TWO-STATE AND MULTI-STATE CHARACTERS

Because of the intraspecific variability no mutually exclusive statement can be made using these characters. For example a line in a dichotomous key using the character "presence or absence of a ventral tail projection" is useless for the numerous species where this character is variable among individuals *(H. dihystera).* The published keys either overlook the intraspecific variability or resort to the expedient of inserting a few species twice in the key. Sher's key (1966) uses nineteen characters : four are measurements (stylet, phasmids, ratios o and c), five others were considered in this article as taxonomically

unreliable (lip annulation, shape of tail annules, position of spermatheca in genital tract, position of phasmids in lateral field, and areolation of lateral field). On the ten usable morphological characters, three are valid for a few species only (presence of fasciculi, labial disc visible in transverse view, median bulb filling body cavity). Finally the six characters most used in the key (size of tail projection, shape of head region, habitus, shape of knobs, shape of tail and fusion of inner lines of the lateral field) are variable. If the intra-specific variability of these characters were taken into account, most of the species would have to be inserted twice or several times in the key.

Even if such a key were proposed it would still be useless because of the variability of the samples it is supposed to help identify.

Conclusions

The traditional dichotomous key is unable to take into account the high intraspecific variability that has become apparent in recent years in the genus *Helicotylenchus*. Other methods of identification must be used. Tabular keys have been proposed in some genera, but are difficult to use in *Helicotylenchus* because of the great number of described species (more than 180). New methods using a computer to estimate the similarity between the sample to be identified and every successive species in the genus have been proposed by Boag and Smith (1983) and Fortuner (1983). An improved version of the latter method will be presented in the near future.

In the meantime it is hoped that the present comments on the intra-specific variability of the taxonomic characters will help authors of new species to present more realistic diagnoses. Too many descriptions are still published without any attempt to estimate this variability in the newly proposed taxa. It is also hoped that the present article will be a stimulus for additional studies on the variability of old species too scantily described.

REFERENCES

ALI, S.S. (1976). Some systematic problems in the Hoplolaiminae (Nematoda : Tylenchida). *Meded. Fac. LandbWetens. Gent.*, 41 : 1007-1012.

ALI, S.S., GERAERT, E. & COOMANS, A. (1973). Some spiral nematodes from Africa. *Biol. Jaarb. Dodonaea*, 41 : 53-70.

ALI, S.S. & LOOF, P.A.A. (1975). Two new species of *Helicotylenchus* Steiner, 1945 (Nematoda : Hoplolaiminae). *Nematologica*, 21 : 207-212.

ANDERSON, R.V. (1973). Morphology and description of *Helicotylenchus crassatus* n. sp. (Nematoda : Hoplolaimidae) from eastern Canada. *Can. J. Zool.*, 51 : 1195-1200.

ANDERSON, R.V. (1974). Canadian species of the genus *Helicotylenchus* Steiner, 1945 (Nematoda : Hoplolaimidae), their identifying characteristics and descriptions of three new species. *Can. J. Zool.*, 52 : 1365-1381.

ANDERSON, R.V. (1978). *Helicotylenchus urobelus* n. sp. (Nematoda : Hoplolaimidae) from New Brunswick, Canada. *Can. J. Zool.*, 56 : 1232-1234.

ANDERSON, R.V. (1979). A supplemental key to species of *Helicotylenchus* Steiner, 1945 (Nematoda : Hoplolaimidae) described since 1972 and a description of *H. oscephalus* n. sp. *Can. J. Zool.*, 57 : 337-342.

ANDRÁSSY, I. (1962). Über den Mundstachel der Tylenchiden (Nematologische Notizen, 9). *Acta zool. hung.* : 241-249.

AZMI, M.I. & JAIRAJPURI, M. S. (1978). Morphometric and allometric variations in the adults and juveniles of *Helicotylenchus indicus* Siddiqi, 1963. *Indian J. Nematol.*, 6 (1976) : 13-22.

BOAG, B. & SMITH, P. (1983). Computer assisted identification of nematodes. *Syst. Parasitol.*, 5 : 235-239.

BYERS, J.R. & ANDERSON, R.V. (1973). Morphology and ultrastructure of the intestine in a plant-parasitic nematode, *Tylenchorhynchus dubius*. *J. Nematol.*, 5 : 28-37.

CAVENESS, F.E. (1974). *A glossary of nematological terms*. Intern. Inst. Trop. Agric., Nigeria, 2nd Edition, revised, 68 p.

CAVENESS, F.E. & BOSHER, J. E. (1959). On the misuse of the term « incisure ». *Proc. helminth. Soc. Wash.*, 26 : 124.

CORBETT, D.C.M. (1978). Migratory soil Tylenchida. In Southey, J.F. (Ed.). : *Plant Nematology*. London, H.M. Stationery Office : 188-206.

ELMILIGY, I.A. (1970). Three new species of the genus *Helicotylenchus* Steiner, 1945 (Hoplolaiminae : Nematoda). *Meded. Fac. landbWetens. Gent*, 35 : 1099-1106.

FORTUNER, R. (1979). Morphometrical variability in *Helicotylenchus* Steiner, 1945. 1. The progeny of a single female. *Revue Nématol.*, 2 : 197-202.

FORTUNER, R. (1983). Computer assisted semi-automatic identification of *Helicotylenchus* species. The program NEMAID. *Calif. Pl. Pest Dis. Rep.*, 2 : 45-48.

FORTUNER, R. (1984). Morphometrical variability in *Helicotylenchus* Steiner, 1945. 5 : On the validity of ratios. *Revue Nématol.*, 7 : 137-146.

FORTUNER, R. & QUÉNÉHERVÉ, P. (1980). Morphometrical variability in *Helicotylenchus* Steiner, 1945. 2 : Influence of the host on *H. dihystera* (Cobb, 1893) Sher, 1961. *Revue Nématol.*, 3 : 291-296.

FORTUNER, R., MAGGENTI, A.R. & WHITTAKER, L. M. (1984). Morphometrical variability in *Helicotylenchus* Steiner, 1945. 4 : Study of field populations of *H. pseudorobustus* and related species. *Revue Nématol.*, 7 : 121-135.

FORTUNER, R., MERNY, G. & ROUX, C (1981). Morphometrical variability in *Helicotylenchus* Steiner, 1945. 3 : Observations on African populations of *Helicotylenchus dihystera* and considerations on related species. *Revue Nématol.*, 4 : 235-260.

GERAERT, E. (1976). Problems concerning the genera *Helicotylenchus* Steiner, 1945 and *Rotylenchus* Filipjev, 1936. *Nematologica*, 22 : 284-288.

GOLDEN, A. M. (1956). Taxonomy of the spiral nematodes *(Rotylenchus* and *Helicotylenchus)* and the development stages and host-parasite relationships of *R. buxophilus*, n. sp., attacking boxwood. *Univ. Maryland Agric. Exp. Stn. Bull.* A-85, 28 p.

GUPTA, N. K. & CHHABRA, H.K. (1967). *Helicotylenchus thornei n. sp.* (Nematoda : Hoplolaiminae) from a tomato plant field in Ludhiana, Panjab. *Res. Bull. Panjab Univ.*, 17 (1966) : 323-325.

HASHIM, Z. (1983). Description of the male and notes on the female of *Helicotylenchus digonicus* Perry in Perry, Darling & Thorne, 1959 (Nematoda : Tylenchida) from Jordan. *Nematologica*, 28 (1982) : 206-209.

HIRSCHMANN, H. & TRIANTAPHYLLOU, A.C. (1965). The question of digonic hermaphroditism in some spiral nematodes (*Helicotylenchus* spp.). (Abstr.). *Nematologica*, 11 : 39-40.

HIRSCHMANN, H. & TRIANTAPHYLLOU, A.C. (1968). Mode of reproduction and development of the reproductive system of *Helicotylenchus dihystera*. *Nematologica*, 13 (1967) : 558-574.

JAIRAJPURI, M.S. & SIDDIQI, M.R. (1979). Observations on the nematode genera *Orientylus* and *Calvatylus* (Rotylenchoidinae : Hoplolaimidae) with descriptions of three new species. *Indian J. Nematol.*, 7 (1977) : 101-111.

KAHN, E., SAHA, M. & CHAWLA, M.L. (1981). Two new species of Hoplolaimoidea (Tylenchida : Nematoda) from India. *Indian J. Nematol.*, 10 (1980) : 118-123.

KUMAR, A. C. & ANANDA RAO, L.V. (1976). *Rotylenchoides desouzai* n. sp. (Nematoda : Tylenchida). *J. Coffee Res.*, 6 : 64-68.

LUC, M. (1960). Trois nouvelles espèces du genre *Rotylenchoides* Whitehead, 1958 (Nematoda-Tylenchida). *Nematologica*, 5 : 7-17.

MULK, M. M. & JAIRAJPURI, M.S. (1975). Nematodes of leguminous crops in India. II. Five new species of *Helicotylenchus* Steiner, 1945 (Hoplolaimidae). *Indian J. Nematol.*, 4 (1974) : 212-221.

NANDAKUMAR, C. & KHERA, S. (1970). *Helicotylenchus indicus* Siddiqi, 1963 with certain remarks on the genus *Helicotylenchus* Steiner, 1945 and some of its species. *Indian J. Helminth.*, 22 : 46-52.

NORTON, D.C. (1978). *Ecology of plant-parasitic nematodes*, New York, John Wiley & Sons, xiii + 268 p.

PERRY, V.G., DARLING, H.M. & THORNE, G. (1959). Anatomy, taxonomy and control of certain spiral nematodes attacking blue grass in Wisconsin. *Bull. Wisc. Agric. Exp. Stn*, 207 : 1-24.

PHILLIPS, S.P. (1971). Studies of plant and soil nematodes. 16. Eight new species of spiral nematodes (Nematoda : Tylenchoidea) from Queensland. *Qd. J. agric. anim. Sci.*, 28 : 227-242.

ROMÁN, J. (1961). A new species of the genus *Helicotylenchus* (Nematoda : Hoplolaimidae) attacking sugarcane. *J. agric. Univ. Puerto Rico*, 45 : 300-303.

SAUER, M. R. & WINOTO, R. (1975). The genus *Helicotylenchus* Steiner, 1945 in West Malaysia. *Nematologica*, 21 : 341-350.

SEINHORST, J. W. (1971). The structure of the glandular part of the esophagus of Tylenchidae. *Nematologica*, 17 : 431-443.

SHER, S.A. (1966). Revision of the Hoplolaiminae (Nematoda) VI. *Helicotylenchus* Steiner, 1945. *Nematologica*, 12 : 1-56.

SHER, S. A. & BELL, A. H. (1975). Scanning electron micrographs of the anterior region of some species of Tylenchoidea (Tylenchida : Nematoda). *J. Nematol.*, 7 : 69-83.

SIDDIQI, M.R. (1963). Two new species of the genus *Helicotylenchus* Steiner, 1945 (Nematoda : Hoplolaiminae). *Z. Parasitkde*, 23 : 239-244.

SIDDIQI, M.R. (1972). On the genus *Helicotylenchus* Steiner, 1945 (Nematoda : Tylenchida), with descriptions of nine new species. *Nematologica*, 18 : 74-91.

SIDDIQI, M.R. & HUSAIN, Z. (1964). Three new species of nematodes in the family Hoplolaimidae found attacking citrus trees in India. *Proc. helminth. Soc. Wash.*, 31 : 211-215.

SMITH, J.M. (1974). Ultrastructure of the hemizonid. *J. Nematol.*, 6 : 53-55.

STONE, A.R. (1980). *Nematology Department*. Rothamsted Report for 1979, Part 1 : 141-142.

SZCZYGIEL, A. (1970). *Tylenchorhynchus polonicus* n. sp. and *Helicotylenchus pseudodigonicus* n. sp.

(Nematoda : Tylenchoidea) from Poland. *Bull. Acad. pol. Sci., Cl.* V, 17 (11-12) : 685-690.

TARJAN, A.C. (1964). Two new mucronate-tailed spiral nematodes (*Helicotylenchus :* Hoplolaiminae). *Nematologica,* 10 : 185-191.

THORNE, G. & MALEK, R.B. (1968). Nematodes of the Northern Great Plains. Part I. Tylenchida (Nemata : Secernentea). *S. Dakota agric. Exp. Stn Tech. Bull.,* 31 : 1-111.

TIKYANI, M.G., KHERA, S. & BHATNAGAR, G.C. (1969). *Helicotylenchus goodi* n. sp. from rhizosphere of great millet. *Zool. Anz.,* 182 : 420-423.

TRIANTAPHYLLOU, A.C. & HIRSCHMANN, H. (1964). Reproduction in plant and soil nematodes. *A. Rev. Phytopath.,* 2 : 57-80.

VAN DEN BERG, E. (1976). Some species of Tylenchoidea (Nematoda) from South Africa, with descriptions of two new species. *Phytophylactica,* 8 : 55-64.

VAN DEN BERG, E. (1978). On some *Helicotylenchus* and *Rotylenchus* species from South Africa (Nematoda). *Phytophylactica,* 10 : 7-12.

VAN DEN BERG, E. & HEYNS, J. (1975). South African Hoplolaiminae. 4. The genus *Helicotylenchus* Steiner, 1945. *Phytophylactica,* 7 : 35-52.

VAN DEN BERG, E. & KIRBY, M.F. (1979). Some spiral nematodes from the Fiji Islands (Hoplolaimidae : Nematoda). *Phytophylactica,* 11 : 99-109.

WHITEHEAD, A.G. (1958). *Rotylenchoides brevis* n. g., n. sp. (Rotylenchoidinae n. subfam. : Tylenchida). *Nematologica,* 3 : 327-331.

YEATES, G. W. (1967). Studies on nematodes from dune sands. I. Tylenchida. *N.Z.Jl Sci.,* 10 : 280-286.

YUEN, P.H. (1964). Four new species of *Helicotylenchus* Steiner (Hoplolaiminae : Tylenchida) and a redescription of *H. canadensis* Waseem, 1961. *Nematologica,* 10 : 373-387.

YUEN, P.H. (1964). The female gonad in the subfamily Hoplolaiminae with a note on the spermatheca of *Tylenchorhynchus. Nematologica,* 10 : 570-580.

YUEN, P.H. (1966). Further observations on *Helicotylenchus vulgaris* Yuen. *Nematologica,* 11 (1965) : 623-637.

ZUCKERMAN, B.M. & STRICH-HARARI, D. (1963). The life stages of *Helicotylenchus multicinctus* (Cobb) in banana roots. *Nematologica,* 9 : 347-353.