A MONOGRAPH OF THE GENUS *HELICOTYLENCHUS* STEINER, 1945 (NEMATA: HOPLOLAIMIDAE)

by

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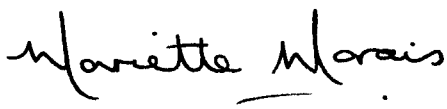
DECLARATION

I the undersigned hereby declare that the work contained in this dissertation is my own original work and has not previously in its entirety or in part been submitted at any university for a degree.



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ABSTRACT

The genus *Helicotylenchus* Steiner of the family Holplolaimidae is reviewed. The different morphometric and morphological characters used in species description are discussed. Thirty-five species occurring in South Africa, French Guiana and the French Caribbean Islands are redescribed, based on type and other material. A new species, viz. *H. marethae* n.sp. is described from South Africa. Apart from line drawings SEM micrographs are included for most species.

UITTREKSEL

In hierdie monograaf van die genus *Helicotylenchus* van die familie Hoplolaimidae, word die verskillende morfologiese en morfometriese eienskappe gebruik in spesie beskrywings, bespreek. Vyf-en-dertig van die spesies wat in Suid-Afrika, Frans Guiana en die Franse Karibiese Eilande voorkom word op grond van tipe of ander materiaal herbeskryf. 'n Nuwe spesie *H. marethae* afkomstig vanaf Suid-Afrika word beskryf. Behalwe vir lyntekeninge word SEM mikrograwe van meeste van die spesies ook gegee.

Aan my God, my Verlosser en Saligmaker vir U oneindige genade en liefde.

Aan my mense, wat die heeltyd saam gedroom het.

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1 INTRODUCTION

Historical review

Helicotylenchus dihystera, the type species of *Helicotylenchus* was described by Cobb in 1893 within the genus *Tylenchus* Bastian, 1865. In 1934 Filip'ev transferred this species and other related species to the genus *Tylenchorhynchus* Cobb, 1913. Steiner erected the genus *Helicotylenchus* in 1945 with *Helicotylenchus nannus* as the type species. Hoplolaiminae was re-defined as a subfamily by Thorne (1949) and he included the genera *Helicotylenchus, Hoplolaimus* von Daday, 1905 and *Rotylenchus* Filip'ev, 1936. The taxonomy of *Helicotylenchus* and *Rotylenchus* was clarified by Golden (1956) and the two genera were separated using two characters namely:

1. the position of the dorsal gland opening in relation to the stylet length (with the opening a third or more of the stylet length behind the stylet knobs for *Helicotylenchus* and with opening usually less than a third of that stylet length for *Rotylenchus*) and
2. the size and location of the phasmids. Golden (1956) recognized three *Helicotylenchus* and eight *Rotylenchus* species.

Whitehead (1958) created a new subfamily Rotylenchoidinae, to receive his new genus *Rotylenchoides* and other genera with characters intermediate between those of the subfamilies Hoplolaiminae Filip'ev, 1934 and Pratylenchinae Thorne, 1949. The only difference between *Rotylenchoides* and *Helicotylenchus* was the presence of a non-functional posterior ovary in *Rotylenchoides*. In addition, in 1958 Andrássy used the position of the dorsal gland opening to separate *Helicotylenchus* from *Gottholdsteineria* Andrássy, 1958. Perry *et al.* (1959) proposed that all species of spiral nematodes, except those with a large phasmid or scutellum, be placed in the

genus *Helicotylenchus* and that *Gottholdsteineria* be synonymized with *Helicotylenchus*.

Sher (1961) synonymized *Gottholdsteineria* with *Rotylenchus* and *H. nannus* with *H. dihystera* designating the latter species as the type of *Helicotylenchus*. He also emended the diagnosis for *Helicotylenchus*, that the oesophageal glands overlap the intestine on the ventral, lateral and dorsal sides and that the dorsal gland opening opens a quarter of the stylet length behind the stylet knobs. Eleven species were listed for *Helicotylenchus*.

Sher (1966) considered *Helicotylenchus* the least closely related to the other genera in the subfamily Hoplolaiminae because of the unique arrangement of the oesophageal glands. *Rotylenchoides* was considered most closely related to *Helicotylenchus* because of the similar arrangement and morphology of the oesophageal glands. The only difference seen between the two genera was the presence of a non-functional posterior ovary correlated with a more posterior position of the vulva in *Rotylenchoides*. *H. neoformis* and *H. intermedius* were excluded from *Helicotylenchus* because of the absence of a functional posterior ovary, and both species were transferred to *Rotylenchoides*.

Siddiqi (1970) assigned *Helicotylenchus* to the Rotylenchoidinae and in 1971 redefined this subfamily to contain genera with either one or two ovaries (Siddiqi, 1971). Siddiqi (1972a) transferred *Tylenchorhynchus africanus* var. *annobonensis* Gadea, 1960 to *Helicotylenchus* and elevated the variety name to the rank of a species, namely *H. annobonensis*. The number of species listed for *Helicotylenchus* has grown to 70 by 1972.

Shamsi (1973) proposed *Zimmermania* as a sub-genus of *Helicotylenchus,* with *H. (Zimmermania) erythrinae* as type and only species. The male tail, with a terminal process longer than the caudal alae characterized this new sub-genus. Siddiqi (1986) synonymized *Zimmermania* with *Helicotylenchus.*

Geraert (1976) transferred *Rotylenchus orientalis* Siddiqi & Husain, 1964 to *Helicotylenchus* because the posterior position of the dorsal gland opening, the weakly developed head framework and the structure of the oesophageal gland lobe corresponded with the arrangement found in *Helicotylenchus. H. orientalis* species formed the basis for the genus *Orientylis* as proposed by Jairajpuri & Siddiqi (1977) but Zancada & Lima (1986) considered the genus a junior synonym of *Rotylenchus.*

Andrássy (1976) placed *Helicotylenchus* in the subfamily Rotylenchinae Golden, 1971 and *Rotylenchoides* in the subfamily Radopholinae Allen & Sher, 1967. Khan *et al.* (1981) proposed that *H. intermedius* and *R. neoformis* might be intermediate forms between *Helicotylenchus* and *Rotylenchoides* for which a separate genus might be required eventually.

In the first of a series of papers on *Helicotylenchus,* Fortuner (1979) drew attention to the variable nature of the morphometrical and morphological characters used in the diagnosis of *Helicotylenchus* species (Fortuner & Quénéhervé, 1980; Fortuner *et al.,* 1981; Fortuner, 1984a, 1984b; Fortuner *et al.,* 1984). *Rotylenchoides* was synonymized with *Helicotylenchus* as it differed from *Helicotylenchus* only in the regression of a single organ, the posterior ovary, and because of the existence of intermediate forms in *Helicotylenchus* (Fortuner, 1984b). This action emphasises the close relationship between these two genera and indicates that the species with a

simple postvulval uterine sac are the products of an evolutionary trend already visible in *Helicotylenchus* sensu stricto.

The computer identification of nematodes started with two simultaneous projects in 1983-1984. Two teams worked independently but both selected the genus *Helicotylenchus* (Boag & Smith, 1983; Fortuner, 1983; Fortuner & Wong, 1983; 1985).

Siddiqi (1986) did not recognise the synonymization of *Rotylenchoides* with *Helicotylenchus*, and placed both genera in the subfamily Rotylenchoidinae. He also reinstated a number of species synonymized with *H. dihystera* by Fortuner *et al.* (1981).

Fortuner (1987) placed *Helicotylenchus* with *Pararotylenchus* Baldwin & Bell, 1981, *Rotylenchus*, *Scutellonema*, *Hoplolaimus* and *Antarctylus* Sher, 1973 in the subfamily Hoplolaiminae Filip'ev, 1934.

In 1995, Siddiqi described two new *Rotylenchoides* species, *R. subterminalis* and *R. attenuatus*. He proposed the new combinations of *Helicotylenchus (Rotylenchoides) subterminalis* and *H. (R.) attenuatus*.

Various authors published dichotomous keys even though it is difficult to compile such keys because of the lack of reliable identification characters (Perry *et al.*, 1959; Tarjan, 1964; Román, 1965; Sher, 1966; Thorne & Malek, 1968; Van den Berg & Heyns, 1975; Anderson, 1979; Van den Berg & Kirby, 1979; Orton Williams, 1983; Fotedar & Kaul, 1986; Wouts & Yeates, 1994). Boag & Jairajpuri (1985) attempted to overcome this problem and produced a workable compendium for 154 nominal *Helicotylenchus* species. Firoza & Maqbool (1995) published a diagnostic compendium

for the genus with a list of the 190 species they considered valid. Their compendium is unreliable, as intraspecific variability was not taken into consideration. The authors also used only the original descriptions of the species and did not take redescriptions into account. The number of recognized species has since grown to nearly 200 with the number of described species reaching 227. The fastest growth in the number of species was experienced was during the 1960s and 1970s (Fig. 1).

Molecular identification certainly holds promise but the definition of molecular markers for a particular species is a long, costly and difficult process. So far efforts have concentrated on the economically more important species, mostly in the family Heteroderidae (Diederich *et al.*, 2000). The first and only paper containing molecular information on *Helicotylenchus* was published in 1997. Polymerase chain reaction-restriction fragment length polymorphism (PCR-RFLP) of the Internal Transcribed Spacer Region (ITS) was advocated as a method of taxonomic analysis in genera such as *Helicotylenchus* which contain numerous species with few diagnostic morphological characters (Powers *et al.*, 1997).

Distribution

Helicotylenchus species occur on every continent. Their distribution (Fig. 2) is given throughout the manuscript according to the six biogeographical (zoogeographical) regions (Wallace, 1876; Crosskey & White, 1977). The most widely distributed and most common species is *H. dihystera. H. multicinctus* is the most common species in the Afro- and Neotropical Regions. *H. californicus, H. canadensis, H. digonicus, H. dihystera, H. erythrinae, H. exallus, H. multicinctus* and *H. pseudorobustus* have been reported from all six biogeographical regions (Tables 1-6).

2 BIOLOGY AND PATHOGENICITY

Helicotylenchus can survive in a variety of habitats. *H. stylocercus* was recovered from aerial soil found on the branches of trees in the Cloud Forest in Costa Rica, *H. dihystera* was found on boot leaves and sheaths of rice plants and *H. teres* (= *H. thornei*) on moss on tree trunks in Puerto Rico (Nandakumar & Rao, 1974; Norton, 1978; Vargas, 1989). The first tylenchid reported from continental Antarctica was a *Helicotylenchus* sp. (Yeates, 1979). *H. pseudorobustus* was reported from freshwater and *H. hydrophilus* has only been reported as occurring in or near wet environments (Thorne & Malek, 1968; Li, 1986; Bongers, 1988; Ye & Geraert, 1997; Marais & Swart, 1999). A number of *Helicotylenchus* spp., i.e. *H. cavenessi, H. crenacauda, H. dihystera, H. erythrinae, H. microcephalus, H. mucronatus* and *H. multicinctus* were reported from aquatic vascular plants (McSorley *et al.,* 1983; Esser *et al.,* 1985; Gerber & Smart, 1987). In contrast with these reports *Helicotylenchus* spp. have been found in areas with a mean annual rainfall of less than 100 mm (South African Plant-Parasitic Nematode Survey database). According to Wharton (1986) *Helicotylenchus* is capable of anhydrobiosis and can survive up to eight months in this state. No particular soil type is preferred and species have been found in soils with pH-values of 3.3 to 10.6 and with clay and sand percentages of up to 66 % and 100 % respectively (South African Plant-Parasitic Nematode Survey database).

Reproduction of *Helicotylenchus* is both amphimictic and by mitotic parthenogenesis (Hirschmann & Triantaphyllou, 1967; Triantaphyllou & Hirschmann, 1967; Orion & Bar-Eyal, 1995).

According to Jones (1978a; b) *H. dihystera* and *H. varicaudatus* feed as sedentary parasites and Yeates (1971) classified *Helicotylenchus* as browsing feeders,

migrating in the soil between feeds. Histological evidence indicates that some species are endoparasitic (Perry *et al.,* 1959; Ruehle, 1975; Padhi & Das, 1985), and egg clutches of *H. abunaami*, H. *dihystera*, *H. multicinctus* and *H. varicaudatus* were found along with adult nematodes in the roots (Zuckerman & Strich-Harari, 1963; Jones, 1978a; Padhi & Das, 1985; Orion *et al.*, 1999). According to Strich-Harari *et al.* (1966), *H. multicinctus* may migrate for distances of up to 120 cm from the pseudostem of bananas but this nematode can also survive and complete its life cycle as an ectoparasite (Orion & Bar-Eyal, 1995). Feeding activities of nematodes cause distortion and collapse of cells. The root development is affected such that the roots become blunt and malformed with fewer lateral roots (Fortuner, 1991). According to Orion *et al.* (1999) a cross section of the dark brown longitudinal lesions formed on banana roots reveal that the cells adjacent to the nematode-infected cell are significantly deformed as if they are collapsing compared to the isodiametric parenchyma cells in an uninfected root. These deformed cells are distributed for a distance of three to five cells (Orion *et al.,* 1999). *H. pseudorobustus* and *H. oleae* induced a single modified "food-cell" with high metabolic activity and their feeding affected only epidermal and cortical cells with no evidence of vascular damage (Vovlas & Larizza, 1994).

Several *Helicotylenchus* spp. are of economic importance. Plant-parasitic nematodes, particularly the genera *Helicotylenchus, Paratrichodorus* and probably also *Hemicycliophora* and *Xiphinema*, could be a problem in bentgrass [*Agrostis stolonifera* L. *palustris* Huds. (Farw.)] on putting greens in South Africa (Swart *et al.,* 2000). *Helicotylenchus* cause poor growth, yellowing and thinning of turf, poorly developed roots and premature sloughing of cortical tissues (Todd & Tisserat, 1985; Poinar & Georgis, 1994; Vargas, 1994; Dernoeden, 1995; Knight *et al.*, 1997).

Infestations of *H. dihystera* are linked with unhealthy bowling greens in Australia, 78 % reduction in top weight and greatly reduced root systems of olive seedlings in Egypt and reduction of leaf size and plant height of guava seedlings in South Africa (Diab & El-Eraki, 1968; Wallace, 1971; Willers & Grech, 1986). According to Firoza & Maqbool (1995) *H. dihystera* at 4 g^{-1} causes chlorosis, sparse root development and stunted shoots in brinjal, tomato and wheat. Interaction between the fungi *Fusarium oxysporum* f.sp. *psidii* and *H. dihystera* increases the incidence of leaf infections, defoliation, growth reductions and wilt incidence in guava seedlings (Hamiduzzaman *et al.,* 1997).

Mancini *et al.* (1983) found that *Pinus* seedlings acted as hosts to *H. digonicus* and that the nematodes reduced the overall development of the plants. *H. multicinctus* was found associated with declining *Pinus elliottii* Engelm. seedlings in the USA (Sharma *et al.*, 1989). According to Barham *et al.* (1974), *H. dihystera* may be of major importance in root disease of pines involving *Phytophthora cinnamomii.* Large populations of *Helicotylenchus* spp. were also often encountered in the rhizosphere of pine trees exhibiting poor growth in Nigeria (Gbadegesin *et al.*, 1992).

High population numbers of *H. indicus* cause stunting of sugar-cane under experimental conditions (Saeed *et al.,* 1989). The reduction in root - and shoot weight of maize plants might be due to inhibition of nutrient uptake of the plant. Several species of *Helicotylenchus* including *H. oleae* cause root necrosis and can affect the growth of olive trees (Inserra *et al.,* 1979; Cohn & Duncan, 1990).

H. multicinctus affects banana growth and yield because of damage to the root system and rhizome and this nematodes is a serious pest of banana world-wide (McSorley & Parrado, 1986; Bridge, 1988; Sarah, 1989). Secondary infection by fungi

enhances the process of root necrosis and aggravates root decay (Gowen & Quénéhervé, 1990).

3 MORPHOMETRIC AND MORPHOLOGICAL TAXONOMIC CHARACTERS

Material and methods

The South African specimens studied (Table 7) were extracted from the soil using the sugar centrifugal-flotation method (Jenkins, 1964), and specimens from the French West Indies and French Guiana (Table 7) were extracted from soil using the elutriation technique of Seinhorst (1962). Specimens were killed in water by gradual application of heat, fixed and preserved in TAF (distilled water, 40 % formalin and triethanolamine solution) and mounted in anhydrous glycerine (Southey, 1986; Hooper & Evans, 1993). For scanning electron microscopy, TAF-preserved specimens were used after dehydration in increasing concentrations of amyl acetate in pure alcohol and finally in pure amyl acetate. Following conventional critical-point drying and gold palladium-coating (21 or 25 nm), specimens were viewed with either a JEOL-35 stereoscan at 15 kV or with a Philips XL30 stereoscan at 10 kV (Marais & Buckley, 1992). Body and spicule length was measured along the median line and straight structures were measured along the median axis. Material examined has been deposited in the National Collection of Nematodes, Biosystematics Division, ARC-Plant Protection Research Institute, Pretoria, South Africa.

Taxonomic characters

Accurate measurements are essential for the identification and description of nematodes. To overcome differences in accuracy, two electronic systems for measuring nematodes were described (Boag, 1981; Fernández-Valdivia *et al.,* 1988). No important differences were noticed when Castillo *et al.* (1993) compared the measurements of a population of *Rotylenchus* sp. obtained by using classical methods and the electronic

method. The classical method and system introduced by De Man (1884) is used in this dissertation and the different symbols and abbreviations used are the following:

L = Total body length

$$a = \frac{\text{body length}}{\text{body width}}$$

$$b = \frac{\text{body length}}{\text{oesophageal length}}$$

$$b' = \frac{\text{body length}}{\text{anterior end to posterior end of oesophageal gland}}$$

$$c = \frac{\text{body length}}{\text{tail length}}$$

$$c' = \frac{\text{tail length}}{\text{body width at anus or cloaca}}$$

$$o = \frac{\text{distance of dorsal oesophageal gland opening from stylet knobs}}{\text{stylet length}} \times 100$$

$$m = \frac{\text{length of conus}}{\text{stylet length}} \times 100$$

$$V = \frac{\text{distance of vulva from anterior end}}{\text{body length}} \times 100$$

$$OV_1 = \frac{\text{length of anterior gonad}}{\text{body length}} \times 100$$

$$OV_2 \quad \frac{\text{length of posterior gonad}}{\text{body length}} \times 100$$

$$T = \frac{\text{length of gonad}}{\text{body length}} \times 100$$

Body

Habitus. Habitus or characteristic body posture of heat-killed specimens is variable within the genus and can be described as straight, C-shaped or spiral (Fig. 3 D, 3 F, 6 N). This character can be constant in a population as described by Fortuner *et al.* (1981) for *H. dihystera* and *H. pseudorobustus* or extremely variable as in *H. exallus* (Marais, 1998).

Body length. The average body length for *Helicotylenchus* is 650 µm, with the range for females from 350 µm (*H. minutus* in Van den Berg & Cadet, 1991) to 1350 µm (*H. coomansi* in Brzeski, 1998) and the range for males from 300 µm (*H. subterminalis* in Siddiqi, 1995) to 1260 µm (*H. coomansi* in Ali & Loof, 1975). According to Fortuner (1984b), the body length can be a relatively constant character. However, when the progeny of a single *H. dihystera* female was reared on ten different hosts, the means ranged from 610 to 748 µm (Fortuner & Quénéhervé, 1980).

Body width. The genus *Helicotylenchus* contains slender worms with a body-width range of 15 µm (*H. brevis* in Marais, 1998) to 50 µm (*H. macrostylus* in Marais & Quénéhervé, 1996) in females. The same character in males is slightly smaller, 12 µm (*H. brevis* in Marais, 1998) to 33 µm (*H. macrostylus* in Marais & Quénéhervé, 1996). In species descriptions the body-width is seldom given, and usually only ratio a is given. This ratio was found by Fortuner (1984b) to be a good taxonomic character with only a 4.5 point difference found in *H. dihystera* from different hosts (Fortuner *et al.*, 1981). The range for females in the genus is 17.2 (*H. brevis* in Marais, 1998) to 42 (*H.*

californicus in Van den Berg & Heyns, 1975) and for males 19.8 (*H. martini* in Van den Berg & Heyns, 1975) to 49 (*H. fericulus* in Siddiqi, 1995).

Body annuli. Annuli are the interstices between somatic transverse striae on the cuticle. According to Fortuner (1984b), the width of body annuli was unknown in more than half the described species, but since 1984, this character has usually been given more frequently. Within the genus, this character ranges from 0.6 µm (*H. retusus* in Prasad *et al.*, 1965) to 3 µm (*H. bradys* in Thorne & Malek, 1968).

Lip region (labial region)

The lip region is delimited by the anterior end of the body and the basal annulus. The lip region of the genus *Helicotylenchus* is either rounded (hemispherical) or flattened (truncate) and continuous with the body (Fig. 10 B, 20 C). This character is subject to high degree of variability and is highly subjective in interpretation.

Labial disc. The labial disc was defined by Caveness (1964) as "the more or less circular form of cuticle about the oral opening and delimited posteriorly by the first transverse striation". The form of this structure is usually seen only in *en face* view. Of the 25 *Helicotylenchus* species studied with a SEM, the labial disc shape varies from rounded (*H. californicus*) and oblong (*H. indicus*) to rectangular (*H. planquettei*) (Marais, 1998; Marais & Quénéhervé, 1999; Marais *et al.*, 2000).

Amphidial apertures. The amphidial apertures appear as a half ellipse between the labial disc and first lip annuli (Fig. 24A).

Lip annuli. The number of annuli varies from absent (H. *australis, H. belli, H. clarkei, H. conicephalus, H. girus, H. labiodiscinus, H. leioceophalus, H. longicaudatus,*

H. marethae n.sp., *H. martini, H. orthosomaticus, H. paraconcavus* and *H. silvaticus*) to species with two to three annuli (*H. delhiensis, H. sharafati* and *H. valdeclarus*) and species with up to eight annuli. Nine species have more than six annuli (*H. apiculus, H. cavenessi, H. cephalatus, H. digonicus, H. erythrinae, H. macrostylus, H. oscephalus, H. paracanalis, H. solani, H. verecundus* and *H. vulgaris*) and three of these species have eight labial annuli (*H. erythrinae, H. macrostylus* and *H. paracanalis*). The SEM has shown that anastomoses (Fig. 16 A) of annuli occur and this compounds the difficulty to determine the number of labial annuli as seen under the light microscope. The division of the first lip annulus into six sectors (four submedians and two smaller laterals) have been demonstrated in an Italian population of *H. multicinctus* and in *H. silvicola* (Vovlas, 1983; Van den Berg & Marais, 1995). No other *Helicotylenchus* species has been reported with a division of the first labial annulus (Sher & Bell, 1975; Abrantes *et al.*, 1987; Rahaman & Ahmad, 1996; Orion *et al.*, 1999).

Lateral field

The cuticle is marked laterally by four lines, sometimes interrupted by transverse striations at different sections of the body. The width of the lateral field was given in a number of descriptions, but the actual measurements are rarely given. The range for the genus is between 2.2 µm (*H. minutus* in Van den Berg & Cadet, 1991) and 12 µm (*H. macrostylus* in Marais & Quénéhervé, 1996) in females, and between 3 µm and 8 µm (*H. brevis* in Marais, 1998) in males. The presence of transverse striae in the lateral field (areolation) was used only in the species diagnosis of *H. areolatus* (Van den Berg & Heyns, 1975). Areolations except for those in the oesophageal region is uncommon. An exception is the presence of areolations in the region of the bursa; *H. exallus* is the only species where these areolations were not observed (Marais, 1998). The presence of crenations of outer lines of the lateral field is variable. The outer lines of *H. coomansi* is crenate except on the tail and in *H. intermedius* the lateral field is

slightly crenated (Fortuner, 1984b). The punctuations described by Tarjan (1964) in *H. egyptiensis* are, according Sher (1966), artefacts possibly due to impurities in the fixative or glycerine. This view has been confirmed as no punctuations were seen in the populations of *H. egyptiensis* from Martinique and Guadeloupe (Marais *et al.*, 2000).

With a few exceptions, e.g. *H. platyurus* (Brzeski, 1999), the outer two lines of the lateral field come together on the tail in a u-shaped pattern. The situation is more complex for the inner lines, but can according to Fortuner (1984b) be described as:

1. Y-shaped, the inner lines coming together posterior to the phasmids and continuing as a single central line for some distance (Fig. 4 F).
2. In some specimens, the common leg after the junction of the lines was so short that the junction could be better described as v-shaped (Fig. 21 I).
3. The two inner lines can also join in a u-shaped pattern (Fig. 8 G), with sometimes one of the lines continuing past the junction, which then appears more like the Greek letter μ (Fig. 9 C).
4. Sometimes the inner lines come in contact with the junction of the outer lines, and the whole end of the lateral field appears like the letter m (Fig. 20 E). In some species the junction of the lines is not complete and the "m" is open.

The tail

The tail is defined as that portion of the body between the body terminus and anus. The shape of the tail is the criterion most used in diagnoses, appearing in two-thirds of the diagnoses of new *Helicotylenchus* species. This extremely variable morphological character was described by Fortuner (1984b) with the following four states:

1. Straight with rounded end, e.g. *H. retusus* and *H. tumidicaudatus* (Fig. 34 E).

2. Bent and asymmetrical, i.e. more curved dorsally, with rounded end (e.g. *H. multicinctus*) (Fig. 30 Q). In *H. concavus, H. depressus* and *H. kermarreci*, the tail has a dorsal flattening (Fig 26 G).
3. More curved dorsally, dorsal side joining the ventral side at an angle (e.g. *H. digonicus*) (Fig 21 N).
4. More curved dorsally, with a rounded or pointed projection e.g. *H. crenacauda* and *H. pseudorobustus*. The projection may have a mucro (Fig. 17 K).

Tail length. The length of tail is given in only a very small percentage of the original descriptions, in only 17 descriptions up to 1984 according to Fortuner (1984b), and in a further 21 new descriptions and 33 redescriptions up to 2000. The range for the genus is 4 µm (*H. brevis* in Marais, 1998) to 38 µm (*H. rothangus* in Jairajpuri & Baqri, 1973) in females and 11 to 33 µm (*H. martini* in Van den Berg & Heyns, 1975) in males. In *H. dihystera,* host plants influenced the tail length (Fortuner & Quénéhervé, 1980).

Ratio c. Tail length appears in most species descriptions as a component of ratio c. The variability of the c-value is in general higher than the variability of the tail length. The range for ratio c is from 16.8 (*H. martini* in Marais, 1998) to 115.5 (*H. vulgaris* in Fortuner, 1991) in females and from 22 (*H. mundus* in Siddiqi, 1995) to 52.5 (*H. paracanalis* in Marais, 1998) in males.

Ratio c' and anal body width. Ratio c' conveys for the tail the same relationship as ratio a for body width. Thin, long tails will have high values and stubby, short tails will have small values. The range for the genus is 0.4 (*H. brevis* in Van den Berg, 1976) to 3.3 (*H. martini* in Van den Berg, 1978) in females and 1.2 (*H. attenuatus* on Siddiqi, 1995) to 2.4 (*H. arliani* Khan *et al.*, 1998) in males. The actual body width at anal level

is not given in species descriptions before 1990. The anal body width can not reflect the same relationship between tail length and anal body width as ratio c'. For example, the mean anal body width for the slender-tailed *H. martini* and for the stubby-tailed *H. brevis* are both 13 µm *vs* c' value of 3.3 and 0.4 respectively (Van den Berg, 1976; 1978).

Number of ventral tail annuli. The number of annuli on the ventral side of the tail to the centre of the tail terminus ranges from 3 (*H. crassatus* in Anderson, 1973) to 30 (*H. rohtangus* in Jairajpuri & Baqri, 1973). As a rule there is no difference in the shape of tail annuli of the different species. *H. areolatus, H. martini, H. coomansi* and *H. planquettei* described with a non-annulated part are the exception (Sher, 1966, Ali & Loof, 1975; Van den Berg & Heyns, 1975; Marais & Quénéhervé, 1999).

Sensory system

Some of the components of the nervous and sensory system are used as diagnostic characters.

Phasmids. The opening to the exterior of the lateral precaudal glands are termed phasmids. These structures are situated in the lateral field on the tail or anterior to the anus, their position varying between 16 annuli anterior to the anus (*H. incisus* in Darekar & Khan, 1979) to 14 annuli posterior to the anus (*H. martini* in Van den Berg, 1978).

Cephalids and hemizonid. Along the length of the nematode body several nerve commissures occur which connect the longitudinal nerves of the body to each other (Maggenti, 1981). Some of these commissures appear as refractive bodies just under the cuticle. The cephalids are situated in the cephalic region. The most commonly

recognised commissure is the hemizonid that extends across the ventral half of the body, opposite the oesophageal region. According to Smith (1974) it has been reported in many nematodes and may be present throughout the Nemata. In *H. dihystera* and *H. paragirus* the hemizonid was said to be absent (Steiner, 1945; Román, 1965; Saha *et al.*, 1974). The absence of the hemizonid in any *Helicotylenchus* species is doubtful and was most probably only not observed (Fortuner, 1984b). The hemizonion and caudalid are commissures situated posteriorly to the hemizonid and in region of the anus, respectively. The position of these commissures is difficult to observe, variable in position and were never used for identification (Anderson, 1973; Fortuner *et al.*, 1984b).

Excretory pore

The excretory pore is a ventral opening in the cuticle in the oesophageal region by which waste products of the excretory system are excreted. The position of the pore when, measured from the anterior end, can be used for identification because of a reasonably low coefficient of variation (CV) (Fortuner, 1984b). The range for the genus is 67 µm (*H. minutus* in Van den Berg & Cadet, 1991) to 211 µm (*H. macrostylus* in Marais & Quénéhervé, 1996) in females and 68 µm (*H. attenuatus* in Siddiqi, 1995) to 161 µm (*H. macrostylus* in Marais & Quénéhervé, 1996) in males. The relation of position of excretory pore to body length usually has a low CV and this character can be used for identification. The range for the genus is 9 % (*H. retusus*) to 24 % (*H. erythrinae*) in females and 11 % (*H. paracanalis*) to 24 % (*H. martini*) in males.

Alimentary tract

The alimentary canal is divided into three sections. The stomodeum begins at the oral opening and includes the mouth cavity and oesophagus. The mesenteron, formed from the embryonic endoderm, is the midgut or intestine proper. The

proctoderm or rectum follows the midgut and ends at the anal or cloacal opening (Maggenti, 1981; 1991).

Stoma. The stoma is constructed of two parts that originate from the esophastome and cheilostome. The cheilostome of *Helicotylenchus* includes the cephalic framework or labial framework, the stomatal cavity and stylet cone that was modified from fossoria. The stylet cone is hollow with a subterminal ventral opening. The esophastome is composed of a shaft with three knobs, disposed triradiately at its base. The knobs function as apodemes for stylet muscles (Maggenti, 1981; 1991).

The range for stylet length in females is from 16 µm (*H. babikeri* in Zeidan & Geraert, 1990) to 46 µm (*H. macrostylus* in Marais & Quénéhervé, 1996) and from 15 µm (*H. verecundus* in Zarina & Maqbool, 1991) to 36 µm (*H. coomansi* in Ali & Loof, 1975) in males. The stylet length has the smallest coefficient of variation among the quantitative characters, 1.7 % in the progeny of a single *H. dihystera* female and 1.6 to 4 % in field populations of the same species (Fortuner, 1979; Fortuner *et al.*, 1981). This study indicates there is a group of species in *Helicotylenchus* characterized by long bodies and stylets, the respective measurements ranging from 800 to 1300 µm and from 35 to 46 µm. Nine species are included in this group: *H. arliani, H. coomansi, H. dolichodoryphorus, H. macrostylus, H. orthosomaticus, H. paracanalis, H. rohtangus* and *H. tunisiensis* (Sher, 1966; Siddiqi, 1972a; Jairajpuri & Baqri, 1973; Ali & Loof, 1975; Van den Berg & Heyns, 1975; Kepenekci & Ökten, 1996; Marais & Quénéhervé, 1996; Khan *et al.*, 1998; Marais, 1998)

Andrássy (1962) named the stylet conus the metenchium and the shaft including the stylet knobs the telenchium. Ratio m evaluates the length of the conus compared to the length of the entire stylet. Although the variability of stylet and conus

length is not reduced by the use of ratio m, it is considered as valid by Fortuner (1984b). The value of this character ranges in females from 38.4 (*H. verecundus* in Zarina & Maqbool, 1991) to 63 (*H. labiatus* in Yeates & Wouts, 1992) and in males from 43 (*H. paracanalis* in Sauer & Winoto, 1975) to 56 (*H. macrostylus* in Marais & Quénéhervé, 1996).

The anterior faces of the stylet knobs can be indented, flattened, rounded or inclined backwards. In many species and even within populations, overlap occurs of these forms. The distinct backward slope of the knobs as found in *H. densibulatus* and *H. meloni* is rare. *H. kermarreci* is reported with slightly inclined knobs. The actual measurements of the width and height of the knobs are very seldom given in descriptions before 1975. The range for width of knobs in females is 2.6 µm (*H. pseudorobustus* in Van den Berg & Heyns, 1975) to 10 µm (*H. macrostylus* in Marais & Quénéhervé, 1996) and 3 µm to 9 µm (*H. macrostylus* in Marais & Quénéhervé, 1996) in males. The range for knob height is 2 µm (*H. fericulus*) to 5 µm (*H. macrostylus*) for females and 1 to 3 µm (*H. silvicola*) for males (Siddiqi, 1995; Van den Berg & Marais, 1995: Marais & Quénéhervé, 1996).

Oesophagus. The oesophagus is according to Maggenti (1991) the most complex organ in the nematode body as it is made up of four tissue types: nerve, muscle, gland and hypodermal. The oesophagus of *Helicotylenchus* can be subdivided into a corpus (procorpus and metacorpus), an isthmus and a glandular postcorpus.

The procorpus comprises the cylindrical anterior part of the oesophagus, which includes the dorsal gland opening (orifice) or DGO (Fortuner, 1984b). In *Helicotylenchus,* the DGO opens into the lumen often more posterior from the stylet base than in other hoplolaimids, especially *Rotylenchus.* According to Fortuner (1991),

the position of the DGO is extremely variable in the subfamily Hoplolaiminae. Its use, either for systematics or for identification, is very delicate. There is a tendency among hoplolaimids for a posterior migration of the DGO. The opening, which is only 1 or 2 µm from the stylet knobs in many tylenchs, is 3-10 µm behind the knobs in many hoplolaimids and up to 33 µm away in *Rotylenchulus*. The DGO position varies in *Helicotylenchus* from 3 µm (*H. labiatus* in Yeates & Wouts, 1992) to 23 µm (as measured in this study for *H. erythrinae*) for females and from 3 µm (*H. multicinctus* in Vovlas, 1983) to 20 µm (as measured in this study for *H. erythrinae*) for males. The current range for *Helicotylenchus* overlap with the range (1-10 µm) for *Rotylenchus* (Castillo *et al.*, 1993). Perry *et al.* (1959) proposed the ratio o (distance from stylet base to the DGO/ stylet length). This ratio was rejected by Fortuner (1984b), but it was used in most descriptions to the exclusion of DGO position, therefore for comparative purposes ratio o will be used in conjunction with DGO position in the present study.

The metacorpus is oval to rounded. The actual size of the median bulb is variable with the length ranging from 8.8 µm (*H. areolatus*) to 21 µm (*H. brevis* in Marais, 1998) in females and from 7 µm (*H. brevis* in Marais, 1998) to 14 µm (*H. paracanalis* in Marais, 1998) in males. The range for median bulb width is 6 µm (*H. aquili* Khan & Nanjappa, 1972) to 18 µm (*H. macrostylus* in Marais & Quénéhervé, 1996) for females and 5 µm (*H. exallus* in Marais, 1998) to 10 µm (*H. delanus* in Marais, 1998) for males. Fortuner (1990) proposed the index "bulb length/width" as a numerical character to enhance the ordinal character "shape of median bulb". This index enhances the view that the size of the median bulb is variable with a range of 0.8 (*H. cavenessi*) to 3.0 (*H. mucronatus*). The size of the median bulb valve can also be used as a taxonomic character. The range for valve length is 2 µm (*H. martini*) to 6 µm (*H. indicus*) and valve width 2 µm (*H. brevis*) to 5 µm (*H. indicus*).

The three oesophageal glands overlap the intestine ventrally, laterally and sometimes dorsally. According to Fortuner (1991) *Helicotylenchus* is distinctive among the hoplolaimids due to the arrangements of the glands overlapping the anterior end of the intestine on all sides, and by the position of the oesophageal lumen, asymmetrically between the dorsal gland and one of the subventral glands. Most other hoplolaimids have a symmetrical arrangement, with the lumen between the two subventral glands (Seinhorst, 1971). The view of Siddiqi (1986) that the glands are fused and form a single structure around the intestine is not supported by any formal study (Fortuner, 1991).

Before the mid 1980s the actual length of the oesophagus was seldom given in descriptions. The ratios b and b', which according to Fortuner (1984b) have very low taxonomic values, are usually given. The oesophagus length varies from 86 µm (*H. attenuatus* in Siddiqi, 1995) to 262 µm (*H. macrostylus* in Marais & Quénéhervé, 1996) in females and from 60 µm (*H. valdeclarus* in Orton Williams, 1983) to 166 µm (*H. macrostylus* in Marais & Quénéhervé, 1996) in males. The length to the end of the oesophageal glands varies from 107 µm (*H. brevis* in Marais, 1998) to 269 µm (*H. macrostylus* in Marais & Quénéhervé, 1996) in females and from 86 µm (*H. brevis* in Marais, 1998) to 188 µm (*H. macrostylus* in Marais & Quénéhervé, 1996) in males. The position of the oesophageal gland nuclei is given only once (in *H. crassatus*) even though the nuclei have been illustrated for a number of species (Anderson, 1973).

Intestine. The tubular intestine (mesenteron) is composed of a single layer of endodermal epithelium. The function of the intestinal fasciculi (or lateral canals) is not known but according to Byers & Anderson (1973), they form part of the normal endowment of the intestinal cells. These structures have been recorded in *H. canalis,*

H. marethae n.sp., *H. martini, H. paracanalis* and *H. silvicola* (Sher, 1966; Van den Berg & Marais, 1995; Marais, 1998).

Female reproductive system

The female reproductive system of *Helicotylenchus* is didelphic i.e. two uteri are present. Each reproductive branch can be separated into:

1. an ovary, the reproductive gland which produces the ova;
2. an oviduct, a tube which serves for the passage of ova from the ovary to uterus;
3. a median region which comprises the spermatheca, an enlarged region which functions as a reservoir for receiving and holding sperms from the male;
4. the crustaformeria, tall columnar secretory cells;
5. an uterus, a region functioning as a place of development of the egg;
6. a vagina, a canal lined with cuticle connecting the uterus to the vulva, the genital orifice (Maggenti, 1981; Castillo *et al.,* 1993).

Position of vulva and regression of the posterior genital branch. The position of the vulva varies between 47 % (*H. caroliniensis* in Fotedar & Kaul, 1985) and 92.1 % (*H. brevis* in Whitehead, 1958) of the body length. V is very constant, and its variability is less than that of its constituent characters. During the present study V value never had a CV of more than 4 % (*H digonicus, H martini, H mucronatus, H multicinctus* and *H pseudorobustus*). V varied only from 62.9 to 64.9, a CV of 13 % variation in a population of *H. dihystera* (Fortuner & Quénéhervé, 1980). Occasionally the posterior branch is reduced in size. Fortuner (1984b) proposed three states to illustrate the possible regression of the posterior branch. In this study I propose the following four states:

1. Two branches both functional, equally or almost equally developed (*H. dihystera*), vulva at 60 % of body length.

2. Two branches both functional, equally or almost equally developed, with the vulva in a more posterior position, vulva at 70 % (*H. limatus, H. multicinctus, H. pasohi, H. planquettei, H. pricei*).
3. Posterior branch non-functional, appearing as a row of degenerated cells (*H. delanus, H. intermedius, H. neoformis*).
4. Posterior branch non-functional, reduced to a postvulval uterine sac (*H. brevis, H. whiteheadi*).

Vulva flaps and epiptygma. Vulva flaps have been described in a number of species. Hui & Zhixin (1993) used this character to distinguish *H. membranatus* from *H. rotundicaudata.* Flaps were said to be absent from *H. bihari* and *H. indenticaudatus*, but according to Fortuner (1984b) it is not known if they are truly absent or particularly difficult to observe. These structures are extremely difficult to see and according to Perry *et al.* (1959), they were "best observed by pressing the specimen to remove the body contents and flatten the cuticle". Vulva flaps are not suitable for identification. The epiptygma are folds of cuticle folded into the vagina. They are probably present in all species of *Helicotylenchus* and this character has no systematic value (Geraert, 1976; Fortuner, 1984b).

Male reproductive system

The male reproductive system is single and outstretched, consisting of a testis, vas eferens, vesicula seminalis, vas deferens and ductus ejaculatorius. The cloaca is a chamber lined with cuticle, which receives the products of both the intestinal and reproductive tracts. The copulatory armature consists of the spicules, gubernaculum and capitulum, with corresponding muscles for the extrusion and retraction of the spicules. The spicules are paired cuticular organs functioning intermediately during copulation for the transfer of sperm. Two zones can be differentiated for each spiculus,

the shaft or main body, usually curved, and the manubrium, the enlarged cephalated proximal portion (Maggenti, 1981; 1991). The range for spicule length for the genus is from 14 µm (*H. attenuatus* in Siddiqi, 1995) to 36 µm (*H. coomansi* in Ali & Loof, 1975). The gubernaculum is a grooved cuticularized structure that guides the spicules during extrusion. Titillae, small projections on either side of the distal end were reported for *H. pricei* and *H. planquettei*. A recurved proximal end was also reported for *H. brevis* and *H. pricei* (Van den Berg, 1976; Marais & Quénéhervé, 1999). The gubernaculum length range for the genus is from 4 µm (*H. attenuatus* in Siddiqi, 1995) to 13 µm (*H. erythrinae* in Van den Berg & De Waele, 1989). The bursa is peloderan in all species and this character has no taxonomic value.

4 SYSTEMATICS

Classification of the genus

The classification of the genus *Helicotylenchus* followed here is based on Maggenti *et al.* (1988).

PHYLUM NEMATA COBB, 1919
CLASS NEMATODA RUDOLPHI, 1808
SUBCLASS SECERNENTEA (VON LINSTOW, 1905) DOUGHERTY, 1958
ORDER TYLENCHIDA THORNE, 1949
SUPERFAMILY TYLENCHOIDEA ÖRLEY, 1880
FAMILY HOPLOLAIMIDAE FILIP'EV, 1934
SUBFAMILY HOPLOLAIMINAE FILIP'EV, 1934
GENUS *HELICOTYLENCHUS* STEINER, 1945

Helicotylenchus Steiner, 1945

= *Rotylenchoides* Whitehead, 1958

= *Zimmermania* Shamsi, 1973

Diagnosis

Habitus straight to spiral. Lateral field with four lines, sparsely areolated except anteriorly. Head region in body contour, smooth or annulated but never longitudinally striated; lip sectors are rarely present. Phasmids punctiform, pre- or postanal; cephalids, hemizonion, hemizonid and caudalid present. Tail half to three-and-a-half anal body widths long; broadly rounded or asymmetrical, sometimes with digitate ventral projection or mucro. Stylet strong, cone about as long as shaft. Position of DGO from 3 µm to 23 µm from stylet base. Postcorpus overlaps intestine ventrally and laterally, rarely dorsally, all three glands of about the same length. *Female*: Vulva near

or well behind midbody; two genital tracts about equal or posterior tract reduced, sometimes to postvulval uterine sac. Epiptygma present, folded into vagina. Vulval flaps present, inconspicuous. *Male:* Slight secondary sexual dimorphism seen in smaller anterior end. Caudal alae peloderan.

Type species

Helicotylenchus dihystera (Cobb, 1893) Sher, 1961

= *Tylenchus dihystera* Cobb, 1893

= *Tylenchus olaae* Cobb, 1906

= *Tylenchorhynchus olaae* (Cobb, 1906) Micoletzky, 1922

= *Helicotylenchus olaae* (Cobb, 1906) Sher, 1961

= *Aphelenchus dubius* var. *peruensis* Steiner, 1920

= *Tylenchus spiralis* Cassidy, 1930

= *Helicotylenchus spiralis* (Cassidy, 1930) Sher, 1961

= *Helicotylenchus nannus* Steiner, 1945 (by Sher, 1961)

= *Helicotylenchus crenatus* Das, 1960 (by Sher, 1966)

= *Helicotylenchus dihysteroides* Siddiqi, 1972 (by Ali *et al*, 1973)

= *Helicotylenchus flatus* Román, 1965 (by Fortuner, *et al.*, 1981)

= *Helicotylenchus glissus* Thorne & Malek, 1968 (by Fortuner, *et al.*, 1981)

= *Helicotylenchus rotundicauda* Sher, 1966 (by Fortuner, *et al.*, 1981)

= *Helicotylenchus punicae* Swarup & Sethi, 1968 (by Fortuner, *et al.*, 1981)

= *Helicotylenchus teleductus* Anderson, 1974 (by Fortuner, *et al.*, 1981)

= *Helicotylenchus paraconcavus* Rashid & Khan, 1974 (by Siddiqi, 1986)

= *Helicotylenchus membranatus* Hui & Zhixin, 1993 (by GuoLiang, 1996)

Other valid species

Helicotylenchus abuharazi Zeidan & Geraert, 1990

Helicotylenchus abunaamai Siddiqi, 1972

(Synonym of *H. exallus* according to Ali *et al.*, 1973 re-instated by Sauer & Winoto, 1975)

Helicotylenchus acunae Fernandez, Razjivin, Ortega & Quincosa, 1980

Helicotylenchus acutucaudatus Fernandez, Razjivin, Ortega & Quincosa, 1980

Helicotylenchus acutus Teben'kova, 1983

Helicotylenchus affinis (Luc, 1960) Fortuner, 1984

= *Rotylenchoides affinis* Luc, 1960

Helicotylenchus africanus (Micoletzky, 1916) Andrássy, 1958

= *Tylenchus africanus* Micoletzky, 1916

= *Tylenchorhynchus africanus* (Micoletzky, 1916) Micoletzky, 1922

= *Tylenchorhynchus robustus* var. *africanus* (Micoletzky, 1916) Micoletzky 1922

= *Tylenchorhynchus africanus* (Micoletzky, 1916) Filip'ev, 1934

= *Rotylenchus africanus* (Micoletzky, 1916) Filip'ev, 1936

Helicotylenchus agricola Elmiligy, 1970

Helicotylenchus alinae Khan, Singh & Lal, 1998

Helicotylenchus amabilis Volkova, 1987

Helicotylenchus amplius Anderson & Eveleigh, 1982

Helicotylenchus angularis Mulk & Siddiqi, 1982

Helicotylenchus anhelicus Sher, 1966

Helicotylenchus annobonensis (Gadea, 1960) Siddiqi, 1972

= *Tylenchorhynchus africanus* var. *annobonensis* Gadea, 1960

Helicotylenchus apiculus Román, 1965

(synonym of *Helicotylenchus erythrinae* according to Siddiqi, 1972a)

Helicotylenchus aquili Khan & Nanjappa, 1972

= *Helicotylenchus arachisi* Mulk & Jairajpuri, 1975 (by Lal & Khan, 1997)

= *Helicotylenchus bihari* Mulk & Jairajpuri, 1975 (by Lal & Khan, 1997)

= *Helicotylenchus wajihi* Sultan, 1981 (by Lal & Khan, 1997)

Helicotylenchus areolatus Van den Berg & Heyns, 1975

Helicotylenchus arliani Khan, Singh & Lal, 1998

Helicotylenchus astriatus Khan & Nanjappa, 1972

Helicotylenchus atlanticus Fernandez, Razjivin, Ortega & Quincosa, 1980

Helicotylenchus attenuatus (Siddiqi, 1995) **n. comb.**

= *Rotylenchoides attenuatus* Siddiqi, 1995

Helicotylenchus australis Siddiqi, 1972

Helicotylenchus babikeri Zeidan & Geraert, 1990

Helicotylenchus bambesae Elmiligy, 1970

= *Helicotylenchus talonus* Siddiqi, 1972 (by Ali & Geraert, 1975)

Helicotylenchus belli Sher, 1966

Helicotylenchus bifurcatus Fernandez, Razjivin, Ortega & Quincosa, 1980

Helicotylenchus bradys Thorne & Malek, 1968

Helicotylenchus brevis (Whitehead, 1958) Fortuner, 1984

= *Rotylenchoides brevis* Whitehead, 1958

Helicotylenchus caipora Monteiro & de Mendonça, 1972

Helicotylenchus californicus Sher, 1966

Helicotylenchus canadensis Waseem 1961

= *Helicotylenchus cairnsi* Waseem, 1961 (by Sher, 1966)

= *Helicotylenchus pseudodigonicus* Szczygiel, 1970 (by Brzeski, 1985)

Helicotylenchus canalis Sher, 1966

Helicotylenchus caroliniensis Sher, 1966

Helicotylenchus caudatus Sultan 1985

Helicotylenchus cavenessi Sher, 1966

Helicotylenchus cedreus Volkova, 1987

Helicotylenchus cephalatus Brzeski, 1998

Helicotylenchus certus Eroshenko & Nguent Vu Tkhan, 1981

Helicotylenchus clarkei Sher, 1966

Helicotylenchus coffeae Eroshenko & Nguent Vu Tkhan, 1981

Helicotylenchus concavus Román, 1961

Helicotylenchus conicephalus Siddiqi, 1972

Helicotylenchus conicus Baĭdulova, 1981

Helicotylenchus coomansi Ali & Loof, 1975

Helicotylenchus cornurus Anderson, 1974

Helicotylenchus craigi Knobloch & Laughlin, 1973

Helicotylenchus crassatus Anderson, 1973

Helicotylenchus crenacauda Sher, 1966

= *Helicotylenchus pteracercus* Singh, 1971 (by Baqri & Ahmad, 1983)

= *Helicotylenchus indenticaudatus* Mulk & Jairajpuri, 1975 (by Lal & Khan, 1993)

= *Helicotylenchus indentatus* Chaturvedi & Khera, 1979 (by Baqri & Ahmad, 1983)

= *Helicotylenchus paracrenacauda* Phukan & Sanwal, 1981 (by Siddiqi, 1986)

= *Helicotylenchus parapteracercus* Sultan, 1981 (by Baqri & Ahmad, 1983)

= *Helicotylenchus pteracercusoides* Fotedar & Kaul, 1985 (by Siddiqi, 1986)

Helicotylenchus curvatus Román, 1965

Helicotylenchus curvicaudatus Fernandez, Razjivin, Ortega & Quincosa, 1980

Helicotylenchus delanus Marais, 1998

Helicotylenchus delhiensis Khan & Nanjappa, 1972

Helicotylenchus densibullatus Siddiqi, 1972

Helicotylenchus depressus Yeates, 1967

Helicotylenchus digitatus Siddiqi & Husain, 1964

Helicotylenchus digitiformis Ivanova, 1967

Helicotylenchus dignus Eroshenko & Nguen Vu Tkhan, 1981

Helicotylenchus digonicus Perry in Perry, Darling & Thorne, 1959

= *Helicotylenchus broadbalkiensis* Yuen, 1964 (by Sher, 1966)

Helicotylenchus discocephalus Firoza & Maqbool, 1993

Helicotylenchus distinctus Mohilal, Anandi & Dhanachand, 1998

Helicotylenchus dolichodoryphorus Sher, 1966

Helicotylenchus dumicola Siddiqi, 1995

Helicotylenchus egyptiensis Tarjan, 1964

Helicotylenchus elegans Román, 1965

Helicotylenchus eletropicus Darekar & Khan, 1980

Helicotylenchus erythrinae (Zimmermann, 1904) Golden, 1956

= *Tylenchus erythrinae* Zimmermann, 1904

= *Tylenchorhynchus erythrinae* (Zimmermann, 1904) Bally & Reydon, 1931

= *Anguillulina erythrinae* (Zimmermann, 1904) Goodey, 1932

= *Rotylenchus erythrinae* (Zimmermann, 1904) Goodey, 1951

= *Rotylenchus melancholicus* Lordello, 1955

= *Helicotylenchus melancholicus* (Lordello, 1955) Andrássy, 1958

= *Helicotylenchus spicaudatus* Tarjan, 1964 (by Sher, 1966)

Helicotylenchus exallus Sher, 1966

= *Helicotylenchus regularis* Phillips, 1971 (by Ali *et al.*, 1973)

(*Helicotylenchus abunaamai* Siddiqi, 1972 synonym of *H. exallus* by Ali *et al.*, 1973 reinstated by Sauer & Winoto, 1975)

Helicotylenchus falcatus Eroshenko & Nguen Vu Tkhan, 1981

Helicotylenchus fericulus Siddiqi, 1995

Helicotylenchus ferus Eroshenko & Nguen Vu Tkhan, 1981

Helicotylenchus girus Saha, Chawla & Khan, 1973

= *Helicotylenchus obtusicaudatus* Darekar & Khan, 1979 (by Lal & Khan, 1997)

= *Helicotylenchus incisus* Darekar & Khan, 1979 (by Lal & Khan, 1997)

Helicotylenchus goldeni Sultan & Jairajpuri, 1979

Helicotylenchus goodi Tikyani, Khera & Bhatnagar, 1969

= *Helicotylenchus gratus* Patil & Khan, 1983 (by Lal & Khan, 1997)

Helicotylenchus graminophilus Fotedar & Mahajan, 1974

Helicotylenchus haki Fotedar & Mahajan, 1974

Helicotylenchus hazratbalensis Fotedar & Handoo, 1974

(considered as synonym of *H. indicus* by Lal & Khan, 1993)

Helicotylenchus holguinensis Sagitov, Sampedro, Santos & Paneke, 1978

Helicotylenchus hydrophilus Sher, 1966

Helicotylenchus imperialis Rashid & Khan, 1972

Helicotylenchus incisus Darekar & Khan, 1979

Helicotylenchus indicus Siddiqi, 1963

= *Helicotylenchus microdorus* Prasad, Khan & Chawla, 1965 (by Nandakumar & Khera, 1970)

Helicotylenchus inifatus Fernandez, Razjivin, Ortega & Quincosa, 1980

Helicotylenchus insignus Khan & Basir, 1964

= *Helicotylenchus teres* (by Fotedar & Kaul, 1985)

(considered as a synonym of *Helicotylenchus indicus* by Lal & Khan, 1993)

Helicotylenchus intermedius (Luc, 1960) Fortuner 1984

= *Rotylenchoides intermedius* Luc, 1960

= *Helicotylenchus intermedius* (Luc, 1960) Siddiqi & Husain, 1964

= *Rotylenchoides intermedius* (Luc, 1960) Sher, 1966

Helicotylenchus interrogativus Eroshenko, 1981

Helicotylenchus issykkulensis Sultanalieva, 1983

Helicotylenchus jammuensis Fotedar & Mahajan, 1974

Helicotylenchus jojutlensis Zavaleta-Mejía & Sosa-Moss, 1979

Helicotylenchus kashmirensis Fotedar & Handoo, 1974

Helicotylenchus kermarreci Marais, Van den Berg, Quénéhervé & Tiedt, 2000

Helicotylenchus khani Fortuner, 1984

= *Rotylenchoides impar* Khan, Saha & Chawla, 1981

Helicotylenchus kherai Kumar, 1982

Helicotylenchus labiatus Román, 1965

Helicotylenchus labiodiscinus Sher, 1966

Helicotylenchus laevicaudatus Eroshenko & Nguent Vu Tkanh, 1981

Helicotylenchus leiocephalus Sher, 1966

Helicotylenchus lemoni Firoza & Maqbool, 1996

Helicotylenchus limarius Eroshenko, Nguen Ngok Tyau, Nguen Vu Tkhan & Doan Kan, 1985

Helicotylenchus limatus Siddiqi, 1995

Helicotylenchus lissocaudatus Fernandez, Razjivin, Ortega & Quincosa, 1980

Helicotylenchus lobus Sher, 1966

Helicotylenchus longicaudatus Sher, 1966

Helicotylenchus macronatus Mulk & Jairajpuri, 1975

(considered a synonym of *Helicotylenchus indicus* by Lal & Khan, 1993)

Helicotylenchus macrostylus Marais & Quénéhervé, 1996

Helicotylenchus magnicephalus Phukan & Sanwal, 1981

(considered a synonym of *Helicotylenchus microcephalus* according to Lal & Khan 1993)

Helicotylenchus marethae **n.sp.**

Helicotylenchus martini Sher, 1966

= *Helicotylenchus krugeri* Van den Berg & Heyns, 1998 (by Marais, 1998)

Helicotylenchus meloni Firoza & Maqbool, 1994

Helicotylenchus microcephalus Sher, 1966

= *Helicotylenchus mangiferensis* Elmiligy, 1970 (by Ali, 1976)

= *Helicotylenchus belurensis* Singh & Khera, 1980 (by Baqri & Ahmad, 1983; valid species according to Ebsary, 1991)

Helicotylenchus microtylus Firoza & Maqbool, 1993

Helicotylenchus minutus Van den Berg & Cadet, 1991

Helicotylenchus minzi Sher, 1966

Helicotylenchus monstruosus Eroshenko, 1984

Helicotylenchus montanus Teben'kova, 1983

Helicotylenchus morasii Darekar & Khan, 1980

Helicotylenchus mucrogaleatus Fernandez, Razjivin, Ortega & Quincosa, 1980

Helicotylenchus mucronatus Siddiqi, 1963

(syn of *Helicotylenchus erythrinae* according to Sher, 1966)

Helicotylenchus multicinctus (Cobb, 1893) Golden, 1956

= *Tylenchus multicinctus* Cobb, 1893

= *Tylenchorhynchus multicinctus* (Cobb, 1893) Micoletzky, 1922

= *Anguillulina multicincta* (Cobb, 1893) Goodey, 1932

= *Rotylenchus multicinctus* (Cobb, 1893) Filip'ev, 1936

= *Rotylenchus iperoiguensis* Carvalho, 1956

= *Helicotylenchus iperoiguensis* (Carvalho, 1956) Andrássy, 1958

Helicotylenchus mundus Siddiqi, 1995

Helicotylenchus neoformis Siddiqi & Husain, 1964

= *Rotylenchoides neoformis* (Siddiqi & Husain, 1964) Sher, 1966

Helicotylenchus neopaxili Inserra, Vovlas & Golden, 1979

Helicotylenchus nigeriensis Sher,1966

Helicotylenchus nitens Siddiqi, 1995

Helicotylenchus notabilis Eroshenko & Nguent Nu Tkhan, 1981

Helicotylenchus obliquus Maqbool & Shahina, 1986

Helicotylenchus oleae Inserra, Vovlas & Golden, 1979

Helicotylenchus orthosomaticus Siddiqi, 1972

Helicotylenchus oryzea Fernandez, Razjivin, Ortega & Quincosa, 1980

Helicotylenchus oscephalus Anderson, 1979

Helicotylenchus parabelli Volkova, 1987

Helicotylenchus paracanalis Sauer & Winoto, 1975

= *Helicotylenchus trivandranus* Mohandas, 1976 (by Fortuner *et al.*, 1981)

Helicotylenchus paradihysteroides Darekar & Khan, 1979

Helicotylenchus paraplatyurus Siddiqi, 1972

Helicotylenchus pasohi Sauer & Winoto, 1975

Helicotylenchus paxilli Yuen, 1964

Helicotylenchus persici Saxena, Chhabra & Joshi, 1972

Helicotylenchus pisi Swarup & Sethi, 1968

Helicotylenchus planquetti Marais & Quénéhervé, 1999

Helicotylenchus platyurus Perry in Perry, Darling & Thorne, 1959

Helicotylenchus plumariae Khan & Basir, 1964

Helicotylenchus pricei Siddiqi, 1995

Helicotylenchus pseudopaxilli Fernandez, Razjivin, Ortega & Quincosa, 1980

Helicotylenchus pseudorobustus (Steiner, 1914) Golden, 1956

= *Tylenchus pseudorobustus* Steiner, 1914

= *Helicotylenchus microlobus* Perry in Perry, Darling & Thorne, 1959 (by Sher, 1966)

= *Helicotylenchus phalerus* Anderson, 1974 (by Fortuner *et al.*, 1984)

Helicotylenchus rakii Narayanaswamy, 1987

Helicotylenchus retusus Siddiqi & Brown, 1964

= *Helicotylenchus impar* Prasad, Khan & Chawla, 1965 (by Nandakumar & Khera, 1970)

= *Helicotylenchus paragirus* Saha, Chawla & Khan, 1974 (by Orton Williams, 1980)

Helicotylenchus reversus Sultan, 1985

Helicotylenchus reynosus Razjivin, O'Relly & Pérez Milian, 1973

Helicotylenchus rohtangus Jairajpuri & Baqri, 1973

Helicotylenchus ryzhikovi Kulinich, 1985

Helicotylenchus sacchari Razjivin, O'Relly & Pérez Milian, 1973

Helicotylenchus saccharumi Jain, Upadhyay & Singh, 1986

Helicotylenchus sagitovi Fortuner, Merny & Roux, 1981

= *Helicotylenchus orientalis* Sagitov, Sampedro , Santos & Paneke, 1978

Helicotylenchus sandersae Ali & Loof, 1975

Helicotylenchus saxeus Siddiqi, 1995

Helicotylenchus scoticus Boag & Jairajpuri, 1985

Helicotylenchus serenus Siddiqi, 1963

Helicotylenchus seshadrii Singh & Khera, 1980

(considered a synonym of *H. paraplatyurus* according to Baqri & Ahmad, 1983, valid according to Ebsary, 1991)

Helicotylenchus shakili Sultan, 1981

Helicotylenchus sharafati Mulk & Jairajpuri, 1975

Helicotylenchus sheri Jain, Upadhyay & Singh, 1986

Helicotylenchus sieversii Razzhivin, 1971

Helicotylenchus silvaticus Lal & Khan, 1989

Helicotylenchus silvicola Van den Berg & Marais, 1995

Helicotylenchus similis Fernandez, Razjivin, Ortega & Quincosa, 1980

Helicotylenchus solani Rashid, 1972

Helicotylenchus sparsus Fernandez, Razjivin, Ortega & Quincosa, 1980

Helicotylenchus spitsbergensis Loof, 1971

Helicotylenchus steineri Fotedar & Mahajan, 1974

Helicotylenchus striatus Firoza & Maqbool, 1994

Helicotylenchus stylocercus Siddiqi & Pinochet, 1979

Helicotylenchus subterminalis (Siddiqi, 1995) **n. comb**

= *Rotylenchoides subterminalis* Siddiqi, 1995

Helicotylenchus subtropicalis Fernandez, Razjivin, Ortega & Quincosa, 1980

Helicotylenchus tangericus Sultan, 1981

Helicotylenchus teres Guar & & Prasad, 1972

= *Helicotylenchus thornei* Gupta & Chhabra, 1967

= *Helicotylenchus bakeri* Gupta & Chhabra, 1967

Helicotylenchus trapezoidicaudatus Fotedar & Kaul, 1985

Helicotylenchus tropicus Román, 1965

Helicotylenchus truncatus Román, 1965

Helicotylenchus tumidicaudatus Phillips, 1971

Helicotylenchus tunisiensis Siddiqi, 1963

Helicotylenchus unicum Fernandez, Razjivin, Ortega & Quincosa, 1980

Helicotylenchus urobeles Anderson, 1978

Helicotylenchus ussuriensis Eroshenko, 1981

Helicotylenchus valecus Sultan, 1981

Helicotylenchus valdeclarus (Orton Williams, 1983) Ebsary 1991

= *Rotylenchoides valdeclarus* Orton Williams, 1983

Helicotylenchus variabilis Phillips, 1971

Helicotylenchus varicaudatus Yuen, 1964

Helicotylenchus variocaudatus (Luc, 1960) Fortuner, 1984

= *Rotylenchoides variocaudatus* Luc, 1960

Helicotylenchus ventroprojectus Patil & Khan, 1983

Helicotylenchus verecundus Zarina & Maqbool, 1991

Helicotylenchus verrucosus Fernandez, Razjivin, Ortega & Quincosa, 1980

Helicotylenchus vietnamensis Eroshenko, Nguen Ngok Tyau, Nguen Vu Tkhan & Doan Kan, 1985

Helicotylenchus vindex Siddiqi, 1995

Helicotylenchus vulgaris Yuen, 1964

Helicotylenchus wajihi Sultan, 1981

Helicotylenchus whiteheadi (Ganguly & Khan, 1987) Firoza & Maqbool, 1994

= *Rotylenchus whiteheadi* (Ganguly & Khan, 1987) Castillo, Vovlas, Gomez-Barcina & Lamberti, 1993

= *Rotylenchoides whiteheadi* Ganguly & Khan, 1987

Helicotylenchus willmottae Siddiqi, 1972

(considered a synonym of *Helicotylenchus retusus* by Lal & Khan, 1993)

Reference to a new *Rotylenchoides* species, *R. cheni* was found in an abstract of a paper " Preliminary report of the survey on the occurrence of nematodes in citrus orchards in Sichuan Province" (Zhu *et al.*, 1991). No further information was found with regard to this species.

Species inquirenda

Helicotylenchus borinquensis Román, 1965

Helicotylenchus brassicae Rashid, 1972

Helicotylenchus caribensis Román, 1965

Helicotylenchus hoplocaudus Majrekar, 1972

Helicotylenchus leucernis Khan & Ahmad, 1970

Species described in *Helicotylenchus* and later transferred to other genera

Rotylenchulus parvus (Williams, 1960) Sher, 1961

Rotylenchus pumilis (Perry in Perry, Darling & Thorne, 1959) Sher, 1961

5 MORPHOLOGY AND DESCRIPTION OF SPECIES FROM THE FRENCH CARIBBEAN, FRENCH GUIANA AND SOUTH AFRICA

***Helicotylenchus dihystera* (Cobb, 1893) Sher, 1961** (Fig. 3, 4)

= *Tylenchus dihystera* Cobb, 1893

= *Tylenchus olaae* Cobb, 1906

= *Tylenchorhynchus olaae* (Cobb, 1906) Micoletzky, 1922

= *Helicotylenchus olaae* (Cobb, 1906) Sher, 1961

= *Aphelenchus dubius* var. *peruensis* Steiner, 1920

= *Tylenchus spiralis* Cassidy, 1930

= *Helicotylenchus spiralis* (Cassidy, 1930) Sher, 1961

= *Helicotylenchus nannus* Steiner, 1945

= *Helicotylenchus crenatus* Das, 1960

= *Helicotylenchus dihysteroides* Siddiqi, 1972

= *Helicotylenchus flatus* Román, 1965

= *Helicotylenchus glissus* Thorne & Malek, 1968

= *Helicotylenchus rotundicauda* Sher, 1966

= *Helicotylenchus punicae* Swarup & Sethi, 1968

= *Helicotylenchus teleductus* Anderson, 1974

= *Helicotylenchus paraconcavus* Rashid & Khan, 1974

= *Helicotylenchus membranatus* Hui & Zhixin, 1993

H. dihystera is the type species for the genus *Helicotylenchus* and was described from sugar-cane (*Saccharum officinarum* L.), Australia (Cobb, 1893b) and since reported from all six the biogeographical regions, viz.

Afrotropical Region

Angola (Siddiqi, 1972b), Burkina Faso (Cadet, 1985), Cameroon (Bridge *et al.,* 1995), Canary Islands (Fortuner *et al.,* 1981), Côte d'Ivoire (Coyne *et al.,* 1999), Democratic

Republic of the Congo (Elmiligy, 1970), Ghana (Coyne *et al.*, 1999), Kenya (Sher, 1966), Liberia (Sher, 1966), Madagascar (Luc, 1959), Malawi (Saka & Siddiqi, 1979), Mali (Baujard & Martiny, 1994), Mauritania (Fortuner *et al.*, 1981), Mauritius (Williams, 1960), Mozambique (Van den Oever *et al.*, 1998), Namibia (De Waele *et al.*, 1998), Niger (Baujard *et al.*, 1995), Nigeria (Sher, 1966), Reunion (Lamberti *et al.*, 1986), Senegal (Sher, 1966), South Africa (Kleynhans *et al.*, 1996), Sudan (Zeidan & Geraert, 1990), Swaziland (own record), Tanzania (own record), Uganda (own record), Zambia (Rajab *et al.*, 1999), Zanzibar (Rajab *et al.*, 1999) and Zimbabwe (Martin, 1955).

Australian Region

Easter Islands (Gallo, 1979), Fiji (Van den Berg & Kirby, 1979), New Zealand (Wouts & Yeates, 1984), Niue (Orton Williams, 1980), Samoa (Orton Williams, 1980) and Tonga (Orton Williams, 1980).

Nearctic Region

Canada (Sher, 1966) and USA (Sher, 1966).

Neotropical Region

Argentina (Doucet & Doucet, 1999), Belize (Bridge *et al.*, 1996), Brazil (Lordello & Zamith, 1956), Colombia (Stanton *et al.*, 1989), Costa Rica (Volkers & Gamboa, 1988), Cuba (Razjivin *et al.*, 1974), Dominica (Edmunds, 1969), Dominican Republic (Román & Grullón, 1975), French Guiana (Marais & Quénéhervé, 1996), Guadeloupe islands (Marais *et al.*, 2000), Guatemala (Sher, 1966), Jamaica (Sher, 1966), Martinique (Cadet *et al.*, 1994), Mexico (Zavaleta-Mejía & Sosa-Moss, 1979), Panama (Sher, 1966), Peru (Sher, 1966), Puerto Rico (Sher, 1966), San Salvador (Sher, 1966), Suriname (Maas, 1970), St Lucia (Edmunds, 1969), Trinidad and Tobago (Bala, 1984) and Venezuela (Loof, 1964).

Oriental Region

Bangladesh (Hamiduzzaman *et al.*, 1997), Brunei (Reddy, 1977), China (JingWu *et al.*, 1998), India (Baqri & Ahmad, 1983), Indonesia (Sher, 1966), Iran (Ali *et al.*, 1973), Israel (Sher, 1966), Korea (Kornobis & Dobosz, 1996), Malaysia (Sher, 1966), Oman (Mani *et al.*, 1998), Pakistan (Firoza & Maqbool, 1996), Philippines (Williams, 1969), Sri Lanka (Sher, 1966), Taiwan (own record), Thailand (Mizukubo *et al.*, 1992), Turkey (Geraert *et al.*, 1975) and Vietnam (Chau *et al.*, 1997).

Palaearctic Region

Armenia (Karapetyan, 1984), Belgium (Bongers, 1988), Bulgaria (Katalan-Gateva, 1980), Egypt (Elmiligy, 1970), Georgia (Tskitishvili, 1983), Germany (Braasch, 1987), Hungary (Braasch, 1987), Italy (Lamberti, 1981), Japan (Toida, 1984), Kazakstan (Baïdoluva, 1982), Kyrgyztan (Gritsenko, 1974), Madeira (Sher, 1966), Moldava (Koev, 1975), Morocco (Sher, 1966), Netherlands (Bongers, 1988), Poland (Brzeski, 1985), Portugal (Siddiqi, 1972b), Romania (Ivan, 1978), Russia (Kir'yanova & Krall', 1980), Slovakia (Stollárová, 1997), Spain (Castillo & Gómez-Barcina, 1993), Tunisia (Kleynhans *et al.*, 1996), Ukraine (Sigareva, 1985) and Uzbekistan (Tuarev & Khurramov, 1981).

Measurements

See Table 11.

Description

Female (n = 174): Habitus straight (1 %), C-shaped (2 %) to spiral (97 %). Lip 4 ± 0.5 (3-6) µm high and 7 ± 0.7 (6-9) µm wide; rounded (98 %) to slightly flattened (2 %) anteriorly, with four to seven annuli. Labial disc oval in *en face* view. Outer margins of labial framework extend 3 µm posterior from basal plate. Cephalids not seen. Stylet knobs 2 ± 0.4 (1-4) µm high and 5 ± 0.7 (2-8) µm wide, rounded posteriorly, anterior faces rounded (7 %), flattened (26 %) flattened and inclined backward (1 %) or

indented (66 %). Position of DGO 12 ± 1.9 (8-17) µm behind stylet knobs. Median bulb oval, 13 ± 1.5 (10-18) µm long and 9 ± 1.0 (7-12) µm wide; valve 4 µm long and 3 µm wide. Length of oesophagus 124 ± 14.8 (86-153) µm, with length to end of glands 142 ± 16.12 (68-184) µm. Oesophagus with 19 ± 16.1 (7-34) µm long ventral overlap. Excretory pore 109 ± 10.8 (90-143) µm from front, i.e. at 17 ± 1.4 (13-21) % of body length. Hemizonid one to three annuli long, located opposite to five annuli anterior to excretory pore *(n =50).* Hemizonion one annulus long, located three to twelve annuli posterior to excretory pore *(n = 9).* Fasciculi not seen. Width of annulus at midbody 1.3 ± 0.3 (0.7-2.2) µm. Body width at excretory pore 20 ± 6.7 (14-29) µm, at midbody 25 ± 4.3 (12-38) µm and at anus 14 ± 1.9 (10-21) µm. Two branches of reproductive system functional, length of posterior branch 91 ± 18.6 (58-158) % of corresponding anterior branch; anterior branch 148 ± 24.8 (104-228) µm and posterior branch 133 ± 24.5 (90-202) µm long. Epiptygma folded into vagina. Spermatheca off-set, thick-walled and empty. Lateral field 5 ± 0.8 (4-7) µm wide; crenated and areolated posterior to vulva and on tail; inner two lines end on tail in a v- (4 %), y- (93 %) or µ-shaped (3 %) pattern. Caudalid one annulus long located one annulus posterior to anus. Phasmid located from opposite to nineteen annuli anterior to anus; one specimen with phasmid four annuli posterior to anus. Tail 17 ± 3.5 (12-30) µm long, with eight to twenty-two ventral annuli; tail asymmetrically rounded, and dorsally curved, with or without ventral projection, if present with rounded end.

Male: Not found.

Remarks

The specimens were identified as *H. dihystera* because of mostly spiral habitus, stylet length (mean value: 26 µm), body length (mean value: 640 µm), position of vulva (mean V value: 64 %), phasmids anterior to anus, inner lines of lateral field end on tail mostly in y-shaped pattern, tail asymmetrically rounded, with or without terminal

projection, if present with rounded end, absence of males and empty spermatheca (Fortuner *et al.,* 1981). The present specimens agree with the amended description of Fortuner *et al.* (1981) and Fortuner (1991). The lower end of the range for body length (440 µm) is less than the previously reported 500 µm (Ali *et al.,* 1973). The range for stylet length exceeds the previous lowest and highest values (20 *vs* 20.9 µm in Van den Berg & Heyns, 1979) and (31 *vs* 28 µm in Sher, 1966) respectively. V value showed the least variation with a CV of 3 %; the lower range of 57 % equals that of Fortuner *et al.* (1981) and the upper range (72 %) exceeds the highest value (71 %) of Van den Berg & Heyns (1975).

***Helicotylenchus africanus* (Micoletzky, 1916) Andrássy, 1958** (Fig. 3, 5)

= *Helicotylenchus africanus* (Micoletzky, 1916) Andrássy, 1958

= *Tylenchus africanus* Micoletzky, 1916

= *Tylenchorhynchus africanus* (Micoletzky, 1916) Micoletzky, 1922

= *Tylenchorhynchus robustus* var. *africanus* (Micoletzky, 1916) Micoletzky 1922

= *Tylenchorhynchus africanus* (Micoletzky, 1916) Filip'ev, 1934

= *Rotylenchus africanus* (Micoletzky, 1916) Filip'ev, 1936

The species was described from "Algenwatten" upstream from the Victoria Falls, Zambia (Micoletzky, 1916) and since reported from the:

Afrotropical Region

Malawi (Saka & Siddiqi, 1979), Nigeria (Sher, 1966), Senegal (own record) and South Africa (Kleynhans *et al.*, 1996).

Neotropical Region

Brazil (Moreira & Huang, 1980).

Palaearctic Region

Algeria (Gadea, 1976).

Measurements

See Table 8.

Description

Female (n = 30): Habitus C-shaped (93 %) to spiral (7 %). Lip region 4 ± 0.9 (3-6) µm high and 7 ± 1.0 (6-11) µm wide; anteriorly rounded, with four to six annuli. Labial disc rectangular to slightly rounded in *en face* view. Outer margins of labial framework extend 3 µm backward from basal plate. Cephalids not seen. Stylet knobs 3 ± 0.4 (2-4) µm high and 6 ± 0.6 (5-8) µm wide; anterior faces flattened and inclined backwards (42 %), flattened (25 %) or indented (33 %). Position of DGO 10 ± 1.3 (8-12) µm behind stylet knobs. Median bulb oval, 13 ± 1.2 (11-16) µm long and 10 ± 1.1 (8-12) µm wide; valve 4 µm long and 3 µm wide. Length of oesophagus 139 ± 35.8 (119-212) µm, with length to end of glands 153 ± 22.2 (128-241) µm. Oesophagus with 25 ± 11.3 (12-43) µm long ventral overlap. Excretory pore 110 ± 11.2 (90-139) µm from front, i.e. at 14 ± 1.2 (12-17) % of body length. Hemizonid two to three annuli long, located from opposite to seven annuli anterior to excretory pore (*n = 21*). Hemizonion one annulus long, located thirteen annuli posterior to excretory pore (*n = 1*). Fasciculi not seen. Width of annulus at midbody 1.7 ± 0.3 (1.4-2.2) µm. Body width at excretory pore 19 ± 0.9 (16-22) µm, at midbody 24 ± 4.0 (18-35) µm and at anus 15 ± 1.7 (13-21) µm. Two branches of reproductive system both functional, equally developed, length of posterior branch 96 ± 12.5 (87-105) % of corresponding anterior branch; anterior branch 187 ± 53.5 (149-225) µm and posterior branch 183 ± 74.7 (130-236) µm long. Spermatheca off-set and filled with sperm. Epiptygma folded into vagina. Lateral field 5 ± 0.7 (4-7) µm wide, incompletely areolated posterior to vulva and on tail; inner two lines end on tail in a v- (57 %), y- (36 %) or m-shaped (7 %) pattern. Phasmid located from two to eight annuli anterior to anus. Rectum does not overlap anus. Tail 27 ± 3.6

(20-35) µm long, dorsally curved with an annulated rounded projection, rarely pointed, with eleven to eighteen ventral annuli.

Male (n = 4): Habitus straight (20 %) to C-shaped (80 %). Lip region 4 (3-4) µm high and 6 µm wide; anteriorly rounded with five to six annuli. Outer margins of labial framework extend 2 µm backwards from basal plate. Stylet knobs 2 µm high and 4 (3-5) µm wide, anterior faces slightly inclined backwards (40 %) or indented (60 %). Position of DGO 10 (7-11) µm behind stylet knobs. Length of oesophagus 131 µm, with length to end of glands 149 (128-163) µm. Oesophagus with 25 µm long ventral overlap. Excretory pore 115 (101-127) µm from front, i.e. at 16 (15-18) % of body length. Hemizonid and hemizonion not seen. Width of annulus at midbody 1.7 (1.5-1.9) µm. Body width at excretory pore 17 (16-19) µm, at midbody 19 (17-19) µm and at cloaca 12 (11-14) µm. Lateral field 4 (4-5) µm wide, areolated anterior to and opposite the bursa. Phasmids located half a body-width anterior to cloaca. Tail 22 (19-23) µm long, conical with a finger-like annulated tip.

Remarks

The specimens were identified as *H. africanus* because of mostly C-shaped habitus, long straight tail (20-35 µm) with lateral field areolated on tail and presence of males. Sher (1966) separated *H. africanus* from *H. erythrinae* and *H. pseudorobustus* because of the usually incomplete areolation of the lateral field on the female tail, longer length of the female tail and usually ventrad curved shape of the female body. The present specimens correspond to the description of Sher (1966) and Fortuner *et al.* (1984) and specimens previously reported from South Africa (Van den Berg & Heyns, 1975; Botha & Heyns, 1993). Characters of the female specimens that showed the least variation was ratio V, stylet length and ratio m with a CV of 3 %, 4 % and 4 % respectively. In contrast, with Fortuner (1984a) where a lower CV was shown in the measurements (length of oesophagus and length to end of glands), ratio b of the

present specimens showed a markedly lower CV than the measurement length of oesophagus (9 % *vs* 26 %).

***Helicotylenchus anhelicus* Sher, 1966** (Fig. 6, 7)

The species was described from willow (S*alix* sp.), California, USA (Sher, 1966) and subsequently reported from the:

Afrotropical Region

South Africa (own record).

Nearctic Region

Canada (Anderson & Eveleigh, 1982).

Palaearctic Region

Bulgaria (Katalan-Gateva, 1979) and Russia (Bolkova, 1989).

Measurements

See Table 8.

Description

Female (n = 14): Habitus C-shaped (29 %) to spiral (71 %). Lip region 4 ± 0.5 (3-5) µm high and 7 ± 0.6 (6-8) µm wide, anteriorly rounded, not set off, with five to six annuli. Labial disc round in *en face* view. Outer margins of labial framework extend 3 µm backward from basal plate. Cephalids not seen. Stylet knobs 3 ± 0.4 (2-3) µm high and 6 ± 0.4 (5-6) µm wide; anterior faces flattened (71 %) to indented (29 %). Position of DGO 13 ± 1.0 (11-15) µm behind stylet. Median bulb oval, 12 ± 0.5 (11-12) µm long and 9 ± 0.5 (8-10) µm wide; valve 3 µm long and 3 µm wide. Length of oesophagus 131 µm, with length to end of glands 139 ± 8.0 (130-147) µm. Oesophagus with 13 µm long ventral overlap. Excretory pore 93 ± 5.3 (82-99) µm from front i.e. 14 ± 1.1 (12-15) %

of body length. Hemizonid two annuli long, located two annuli anterior to excretory pore (*n = 2*). Hemizonion not seen. Fasciculi not seen. Width of annulus at midbody 1.6 ± 0.2 (1.4-2.1) µm. Body width at excretory pore 22 ± 3.0 (18-28) µm, at midbody 27 ± 3.5 (22-35) µm and at anus 13 ± 1.0 (12-16) µm. Two branches of reproductive system both functional, equally developed, length of posterior branch 82 ± 12.3 (62-98) % of corresponding anterior branch length; anterior branch 182 ± 24.8 (141-207) µm and posterior branch 144 ± 21.4 (111-176) µm long. Spermatheca rounded and filled with sperm. Epiptygma folded into vagina. Lateral field 6 ± 0.7 (4-7) µm wide; inner two lines end on tail in a v- (37 %), y- (21 %), u- (21 %), µ- (14 %) or m-shaped (7 %) pattern. Phasmids located three to eleven annuli anterior to anus; lateral field bulge out around phasmid in two specimens. Rectum does not overlap anus. Tail 14 ± 2.3 (10-17) µm long, bent and asymmetrical with rounded end, with seven to twelve ventral annuli.

Male (n = 14): Habitus C-shaped (36 %) to spiral (64 %). Lip region 4 ± 0.3 (3-4) µm high and 7 ± 0.4 (6-8) µm wide, anteriorly rounded to slightly flattened, with five to six annuli. Stylet knobs 2 ± 0.2 (2-3) µm high and 5 ± 0.3 (5-6) µm wide; anterior faces flattened (64 %) or indented (36 %). Position of DGO 13 ± 0.3 (11-5) µm behind stylet knobs. Length of oesophagus 123 µm, with length to end of glands 146 ± 9.2 (131-165) µm. Oesophagus with 8 µm long ventral overlap (*n = 1*). Excretory pore 92 ± 7.0 (85-107) µm from front, i.e. 14 ± 0.9 (12-15) % of body length. Hemizonion two annuli long, located from one annulus anterior to opposite excretory pore (*n=3*). Hemizonid not seen. Width of annulus at midbody 1.5 ± 0.4 (0.9-2.1) µm. Body width at excretory pore 20 ± 2.4 (17-24) µm, at midbody 23 ± 2.3 (20-28) µm and at cloaca 13 ± 1.0 (12-16) µm. Lateral field 5 ± 0.5 (4-6) µm wide; areolated opposite and anterior to bursa, as much as twenty-nine annuli anterior to anterior margin of bursa. Phasmids located one cloacal body width anterior to cloaca. The bursa does not reach to the tip of tail in half of the specimens.

Remarks

The present specimens were identified as *H. anhelicus* because of the presence of males, position of vulva (mean V value: 63 %), stylet length (mean value: 30 µm), rounded lip region and tail form. Sher (1966) used stylet length and position of vulva to separate *H. anhelicus* from *H. multicinctus*. The South African specimens correspond to the species description of Sher (1966) and were compared to paratype material. The female specimens differ from the paratype material in c-value (40.9-58.4 *vs* 33-46) and position of phasmid (three to eleven annuli anterior to anus *vs* two annuli posterior to five annuli anterior to anus). From a Russian population (Bolkova, 1989) the South African material differs in c-value (40.9-58.4 *vs* 35-41) and DGO (12-15 µm *vs* 9-10 µm) in females and in males in spicule length (24-27 µm *vs* 28-31 µm). Stylet length, ratio m and V showed the least variation in females with a CV of 3 %, 3 % and 2 % respectively. The same trend was found in males.

***Helicotylenchus areolatus* Van den Berg & Heyns, 1975** (Fig. 8, 9)

Helicotylenchus areolatus was described from soil on the bank of the Olifants River, Loskop Dam, Mpumalanga Province, South Africa (Van den Berg & Heyns, 1975) and since reported from *Eucalyptus* plantations in northern Kwazulu-Natal, South Africa (Kleynhans *et al.*, 1996).

Measurements

See Table 8.

Description

Female (n = 13): Habitus spiral. Lip region 3 ± 0.5 (2-4) µm high and 6 ± 0.5 (5-6) µm wide, anteriorly rounded, not set off, with four to five annuli. Labial disc rectangular in *en face* view. Outer margins of labial framework extend 3 µm backward from basal plate. Posterior cephalids nine to eleven annuli posterior from basal plate. Stylet knobs 2 ± 0.1 (2-3) µm high and 4 ± 0.6 (3-5) µm wide; anterior faces of stylet knobs flattened (58 %) or indented (42 %). Position of DGO 7 ± 0.5 (6-8) µm behind stylet knobs. Median bulb oval, 10 ± 1.4 (1.1-1.4) µm long and 7 ± 1.1 (5-9) µm wide, valve 4 µm long and 3 µm wide. Length of oesophagus 104 ± 9.1 (96-117) µm, with length to end of glands 122 ± 12.4 (109-136) µm. Excretory pore 82 ± 7.8 (70-91) µm from anterior end, i.e. at 18 ± 2.0 (15-21) % of body length. Hemizonid two to three annuli long, located from opposite to one annulus anterior to excretory pore (*n = 4*). Hemizonion one annulus long, 12 annuli posterior to excretory pore (*n=1*). Fasciculi not seen. Width of annulus at midbody 1.2 ± 0.2 (1.1-1.4) µm. Body width at excretory pore 17 ± 2.1 (14-19) µm, at midbody 20 ± 2.7 (15-24) µm and at anus 12 ± 1.1 (10-14) µm. Spermatheca set off, rounded and empty. Epiptygma folded into vagina. Lateral field 5 ± 0.5 (4-6) µm wide, incompletely areolated on posterior part of body; inner two lines end on tail in a v- (50 %) or y-shaped (50 %) pattern. Rectum does not overlap anus. Phasmids located from opposite to six annuli anterior to anus. Tail 11 ± 1.0 (9-13) µm long, bent and asymmetrical with rounded end and not annulated round tip, with six to thirteen ventral annuli.

Male (n = 1): Habitus C-shaped. Lip region slightly flattened, 4 µm high and 5 µm wide. Stylet knobs 3 µm high and 3 µm wide, anterior faces flattened. Excretory pore 96 µm from front, i.e. at 18 % of body length. Hemizonid three annuli long, located one annulus anterior to excretory pore. Hemizonion not seen. Width of annulus at midbody 1.4 µm. Body width at excretory pore 17 µm, at midbody 20 µm and at cloaca 11 µm. Lateral field incompletely areolated or crenate on posterior part of body. Tail 14 µm long with rounded projection.

Remarks

The present specimens were identified as *H. areolatus* because of the incompletely areolated field over the entire body, habitus, tail form and on the morphometric characters attributed to *H. areolatus* by Van den Berg & Heyns (1975). The present specimens agree with the original description and paratype material. Van den Berg & Heyns (1975) separated *H. areolatus* from *H. multicinctus* using habitus, the presence of areolations in the lateral field and lip and tail form. *H. areolatus* was also differentiated from *H. regularis* (= *H. exallus*) because of absence of an areolated lateral field in *H. regularis*. A character not mentioned by Van den Berg & Heyns (1975) but present in all the specimens is the presence of a non-annulated tail. Ratio V showed the least variation with CV of 4 %.

***Helicotylenchus brevis* (Whitehead, 1958) Fortuner, 1984** (Fig. 8, 10, 11)

= *Rotylenchoides brevis* Whitehead, 1958

Rotylenchoides brevis is the type species of the genus *Rotylenchoides* Whitehead, 1958, synonymized with *Helicotylenchus* by Fortuner (1984b). The species was described from *Musa* x *paradisiaca* L. in Tanzania (Whitehead, 1958) and has since only been reported from South Africa (Kleynhans *et al.,* 1996; Marais & Van den Berg, 1996; Van den Berg, 1996; Marais, 1998; Marais & Swart, 1999).

Measurements

See Table 9.

Description

Female (n = 50): Habitus straight (17 %) to C-shaped (83 %). Lip region 4 ± 0.5 (3-5) µm high and 9 ± 0.5 (8-10) µm wide, anteriorly flattened, not set off, continuous with body, with four to six annuli. Labial disc oval in *en face* view. Outer margins of labial framework extend 4 µm backward from basal plate. Cephalids not seen. Stylet knobs 3 ± 0.5 (2-4) µm high and 6 ± 0.9 (5-8) µm wide; anterior faces rounded (2 %), flattened (41 %) or indented (57 %). Position of DGO 8 ±1.4 (6-12) µm behind stylet knobs. Median bulb rounded or oval, 12 ± 2.4 (8-21) µm long and 10 ± 1.3 (8-14) µm wide; valve 4 µm long and 2 µm wide. Length of oesophagus 119 ± 10.5 (98-129) µm, with length to end of glands 125 ± 10.0 (107-156) µm. Oesophagus with 11 ± 5.7 (6-21) µm long dorsal or ventral overlap. Excretory pore 93 ± 11.5 (73-119) µm from front, i.e. at 20 ± 2.0 (15-23) % of body length. Hemizonid two annuli long, located two to six annuli anterior to excretory pore (*n = 21*). Hemizonion not seen. Fasciculi not seen. Width of annulus at midbody 1.3 ± 0.3 (0.7-1.8) µm. Body width at excretory pore 20 ± 3.1 (15-28) µm, at midbody 22 ± 2.8 (15-27) µm and at anus 13 ± 1.7 (9-19) µm. Posterior reproductive branch non-functional, reduced to a postvulval uterine sac; length of posterior branch 12 ± 4.1 (7-20) % of corresponding anterior branch length; anterior branch 143 ± 41.5 (95-219) µm and posterior branch 16 ± 4.1 (8-25) µm long. Spermatheca rounded, filled with sperm. Epiptygma folded into vagina. Lateral field 5 ± 0.8 (3-7) µm wide; outer two lines crenate posterior to vulva or incompletely areolated on tail in some specimens; inner two lines end on tail in an u- (47 %), µ- (31 %) or m-shaped (22 %) pattern on tail. Phasmids located three annuli anterior to three annuli posterior to anus. Tail short, 9 ± 1.5 (6-12) µm long, less than one anal body width, rounded with four to nine ventral annuli.

Male (n = 16): Habitus straight (36 %) to C-shaped (64 %). Lip region 3 ± 0.5 (3-4) µm high and 6 ± 1.0 (5-8) µm wide, anteriorly rounded with five to six annuli. Outer margins of labial framework extend 3 ± 0.4 (3-4) µm backward from basal plate. Stylet knobs 2 ± 0.5 (1.3) µm high and 4 ± 0.7 (3-5) µm wide; anterior faces flattened (18 %)

or indented (82 %). Position of DGO 7 ± 1.8 (6-9) µm behind stylet knobs. Median bulb oval, 9 ± 1.0 (7-12) µm long and 7 ± 0.6 (6-8) µm wide; valve 4 µm long and 2 µm wide. Length of oesophagus 94 ± 1.0 (93-94) µm long, with length to end of gland 103 ± 11.4 (86-120) µm. Excretory pore 73 ± 5.5 (68-83) µm from front, i.e. at 18 ± 1.2 (16-20) % of body length. Hemizonid and hemizonion not seen. Width of annulus at midbody 1.1 ± 0.3 (0.7-1.4) µm. Body width at excretory pore 13 ± 1.6 (11-15) µm, at midbody 15 ± 1.2 (12-17) µm and at cloaca 9 ± 0.4 (8-10) µm. Lateral field 3 ± 0.5 (3-4) µm wide; areolated in the region of the oesophagus and opposite bursa; inner two lines ending in a v-shaped pattern on tail in two specimens. Tail 14 ± 1.4 (11-17) µm long, conical. Bursa surround tail tip.

Remarks

The specimens were identified as *H. brevis* because of posterior position of vulva, presence of a postvulval uterine sac and tail shape. As the paratype material was not available, the present specimens were compared with previously identified South African material (Van den Berg, 1976). The present specimens correspond to the original description, but differ in stylet length (25-34 *vs* 26-29 µm) and greater variation in tail length, therefore also more variation in c-value (29.2-107.7 *vs* 36-55) in females. The ending of the inner two lines of the lateral field in a v-shaped pattern in two males from the Bergplaas Plantation was not seen in any other *Helicotylenchus* species. According to Van den Berg (1976) the proximal tip of the gubernaculum formed a small hook, this phenomenon was not seen in the *H. brevis* males studied here. Ratio V showed the least variation with a CV of 2 %.

***Helicotylenchus californicus* Sher, 1966** (Fig.12, 13)

Helicotylenchus californicus was described from *Tamarix ramosissima* Ledeb. California, USA and since reported from all the biogeographical regions, viz.

Afrotropical Region

South Africa (Kleynhans *et al.*, 1996).

Australian Region

Fiji (Van den Berg & Kirby, 1979).

Neotropical Region

Brazil (Costa Manso *et al.*, 1994) and Guadeloupe islands (Marais *et al.*, 2000).

Oriental Region

China (Yin, 1992), Pakistan (Khan *et al.*, 1989) and Turkey (Ertürk *et al.*, 1973).

Palaearctic Region

France (Scotto la Massése & Boulbria, 1980), Georgia (Bagatyriya, 1971), Hungary (Andrássy, 1973), Russia (Kankina & Milkus, 1983) and Tadjikistan (Kankina & Teben'kova, 1980).

Measurements

See Table 9.

Description

Female (n = 52): Habitus C-shaped (2 %) to spiral (98 %). Lip region 4 ± 0.5 (3-5) µm high and 8 ± 0.8 (5-8) µm wide, anteriorly flattened to rounded, not set off with four to seven annuli. Labial disc oval in *en face* view. Outer margins of labial framework extend 3 ± 0.3 (2-3) µm posterior from basal plate. Cephalids not seen. Stylet knobs 3 ± 0.4 (2-3) µm high and 5 ± 0.5 (4-6) µm wide, anterior faces rounded (15 %), flattened (25 %) or indented (60 %). Position of DGO 11 ± 1.4 (9-12) µm behind stylet knobs. Median bulb oval, 13 ± 1.6 (19-20) µm long and 10 ± 0.9 (8-12) µm wide, valve 4 µm long and 3 ± 0.3 (2-3) µm wide. Length of oesophagus 147 ± 13.2 (134-161)

µm, with length to end of glands 147 ± 11.1 (127-184) µm. Oesophagus with 11 ± 6.2 (3-19) µm long ventral overlap. Excretory pore 116 ± 11.3 (100-153) from front, i.e. at 16 ± 1.1 (13-19) % of body length. Hemizonid two annuli long, located from three annuli anterior to excretory pore to opposite excretory pore (*n = 12*). Hemizonion not seen. Fasciculi not seen. Width of annulus at midbody 1.7 ± 0.9 (1.1-2.5) µm. Body width at excretory pore 22 ± 2.6 (14-27) µm, at midbody 28 ± 4.0 (21-39) µm and at anus 15 ± 1.7 (11-18) µm. Two branches of reproductive system both functional, equally developed, length of posterior branch 78 ± 5.2 (69-88) % of corresponding anterior branch length; anterior branch 170 ± 31.8 (124-233) µm and posterior branch 141 ± 22.6 (113-174) µm long. Spermatheca axial, rounded and filled with sperm. Epiptygma folded into vagina. Lateral field 6 ± 0.8 (4-8) µm wide; inner two lines end on tail in a v- (5 %), y- (72 %), u- (10 %) or m-shaped pattern (13 %). Rectum does not overlap anus. Tail more curved dorsally with irregular ventral projection, 20 ± 3.7 (14-30) µm long, with five to seventeen ventral annuli, some specimens with a mucro.

Males (n = 28): Habitus C-shaped (97 %) to spiral (3 %). Lip region 4 ± 0.4 (4-6) µm high and 7 ± 0.8 (5-9) µm wide, broadly rounded, with five to six annuli. Stylet knobs 2 ± 0.3 (2-3) µm high and 5 ± 0.7 (3-6) µm wide, anterior faces of stylet knobs rounded (8 %), flattened (38 %) or indented (54 %). Position of DGO 12 ± 1.7 (9-14) µm behind stylet knobs. Excretory pore 113 ± 14.2 (101-166) µm from front, i.e. at 17 ± 2.1 (15-25) % of body length. Hemizonid two to three annuli long, located one to two annuli anterior to excretory pore (*n = 12*). Hemizonion not seen. Width of annulus at midbody 1.6 ± 0.3 (1.1-2.2) µm. Body width at excretory pore 19 ± 2.3 (14-22) µm, at midbody 22 ± 2.4 (16-25) µm, and at cloaca 14 ± 1.4 (10-16) µm. Lateral field 5 ± 1.9 (4-6) µm wide; areolated anteriorly and opposite bursa, as much as thirty-five annuli anterior to anterior margin of bursa. Tail 23 ± 2.6 (18-29) µm long, with ventrad-curved finger-like projection.

Remarks

The present specimens were identified as *H. californicus* because of spiral habitus, mostly anteriorly flattened lip region, stylet length (mean value: 27 µm), position of vulva (mean V value: 63 %), phasmids anterior to anus (mean value: five annuli anterior to anus), tail with irregular projection in females and spicule length (mean value: 25 µm). Sher (1966) distinguished *H. californicus* from *H. hydrophilus* by shorter stylet (24-27 *vs* 28-32 µm), more offset spermatheca and usually an irregular ventral tail projection. The present specimens correspond with the original description and were compared to paratype material and previously identified South African specimens (Van den Berg & Heyns, 1975; Van den Berg & Meyer, 1987). The males from Guadeloupe differ from a South African population (Van den Berg & Meyer, 1987) in spicule length (23-26 *vs* 28-30 µm), and from a Fijian population (Van den Berg and Kirby, 1979) in mean stylet length (25 *vs* 22 µm) and mean spicule length (25 *vs* 22.5 µm). The females from Guadeloupe differ in mean stylet length (27 *vs* 24.1 µm) and mean tail length (20 *vs* 17.9 µm) from a South African population. V value and stylet length showed the least variation with CV of 3 % and 5 % respectively.

***Helicotylenchus canalis* Sher, 1966** (Fig.12, 14)

The species was described from jungle soil in Opanaike, Sri Lanka (Sher, 1966) and since reported from the:

Afrotropical Region

South Africa (Kleynhans *et al.*, 1996).

Nearctic Region

USA (Esser, 1996).

Measurements

See Table 10.

Description

Female (n = 17): Habitus C-shaped (40 %) to spiral (60 %). Lip region 5 ± 0.5 (5-6) µm high and 10 ± 0.6 (9-11) µm wide, anteriorly slightly flattened to rounded, with five to eight annuli. Labial disc oval in *en face* view, not visible in lateral view. Outer margins of labial framework extend 5 ± 0.4 (4-5) µm backward from basal plate. Cephalids not seen. Stylet knobs 3 ± 0.4 (3-4) µm high and 7 ± 1.1 (4-9) µm wide; anterior faces of stylet knobs flattened (6 %) or indented (94 %). Position of DGO 11 ± 1.0 (9-12) µm behind stylet knobs. Median bulb oval, 14 ± 1.4 (11-16) µm long and 10 ± 1.3 (8-12) µm wide, valve 4 µm long and 2 µm wide. Length of oesophagus 160 ± 13.9 (132-171) µm, with length to end of glands 180 ± 8.8 (162-196) µm. Oesophagus with 13 ± 9.9 (3-30) µm long ventral overlap. Excretory pore 133 ± 7.8 (121-143) µm from anterior end, i.e. at 16 ± 1.2 (14-18) % of body length. Hemizonid and hemizonion not seen. Fasciculi present throughout whole body, seen in all specimens. Width of annulus at midbody 1.8 ± 0.2 (1.4-2.1) µm. Body width at excretory pore 23 ± 2.9 (17-29) µm, at midbody 37 ± 3.9 (31-44) µm and at anus 22 ± 1.8 (19-26) µm. Spermatheca empty, thick walled and offset. Two branches of reproductive system both functional, equally developed; length of posterior branch 94 ± 7.7 (89-100) % of corresponding anterior branch length; anterior branch 170 ± 42.7 (119-244) µm and posterior branch 158 ± 35.2 (119-203) µm long. Epiptygma folded into vagina. Lateral field 8 ± 1.0 (6-9) µm wide; inner two lines end on tail in a µ- (14 %) or m-shaped (86 %) pattern. Rectum does not overlap anus. Phasmids located from two to seven annuli anterior to anus. Tail 20 ± 2.6 (16-20) µm long, with seven to thirteen ventral annuli; more curved dorsally, with annulated rounded or pointed ventral projection.

Male: Not found.

Remarks

The present specimens were identified as *H. canalis* because of the presence of fasciculi, ventral tail projection and the absence of males. These specimens were compared to previously identified South African material (Van den Berg & Heyns, 1975). They differ from the original description and from the population of Van den Berg & Heyns (1975) in stylet length (38-43 *vs* 32-36 µm and 36-37.9 µm respectively). As reported by Fortuner (1984b) this study also showed that ratio m, stylet length and ratio V showed the least variation with CV of 3 %, 4 % and 4 % respectively.

***Helicotylenchus caroliniensis* Sher, 1966**

This species was described from swamp soil, South Carolina, USA and since reported from the:

Afrotropical Region

South Africa (Van den Berg & Heyns, 1975).

Oriental Region

India (Fotedar & Kaul, 1985).

Measurements

See Table 10.

Remarks

This species was identified by Van den Berg & Heyns (1975) from a specimen collected at Aliwal North, Eastern Cape Province. The single specimen deposited in the NCN has deteriorated and is no longer suitable for examination.

***Helicotylenchus cavenessi* Sher, 1966** (Fig. 15, 16)

Helicotylenchus cavenessi was described from cassava (*Manihot esculenta* Crantz) in the Ijebu Province, Nigeria (Sher, 1966). The species was since reported from five biogeographical regions, viz.:

Afrotropical Region

Cameroon (Bridge *et al.*, 1995), Malawi (own record) and South Africa (Kleynhans *et al.*, 1996).

Neotropical Region

Brazil (Costa Manso *et al.*, 1994), Cuba (Schliephake, 1985) and Venezuela (Crozzoli *et al.*, 1991).

Oriental Region

China (Hui & Zhixin, 1996), India (Fotedar & Kaul, 1985), Iran (Kheiri, 1972), Korea (Bae & Choi, 1997), Thailand (Ratanaprapa & Boonduang, 1975) and Vietnam (Eroshenko & Nguen Vu Thank, 1981).

Palaearctic Region

Egypt (Elmiligy, 1970), Hungary (Krall', 1978), Kazakstan (Baĭdulova, 1982), Portugal (Abrantes *et al.*, 1978) and Ukraine (Kir'yanova & Krall', 1980).

Measurements

See Table 10.

Description

Female (n = 18): Habitus C-shaped (25 %) to spiral (75 %). Lip region 4 ± 0.6 (3-5) µm high and 7 ± 0.7 (5-8) µm wide, slightly flattened to rounded anteriorly, with four to seven annuli. Anastomoses of lip annuli were present. Labial disc oval in *en face* view. Outer margins of labial framework extend 3 µm backward from basal plate. Stylet knobs 2 ± 0.4 (1-3) µm high and 5 ± 0.5 (4-6) µm wide; anterior faces of stylet

knobs indented (27 %) or flattened (73 %). Position of DGO 10 ± 0.5 (10-11) µm behind stylet. Median bulb oval, 12 ± 1.1 (9-14) µm long and 9 ± 1.1 (8-12) µm wide; valve 3 µm long and 3 µm wide. Length of oesophagus 118 ± 6.6 (109-128) µm, with length to end of glands 138 ± 11.5 (121-161) µm. Oesophagus with 12 ± 2.0 (9-15) µm long ventral overlap. Excretory pore 107 ± 14.6 (92-143) µm from front, i.e. at 17 ± 6.6 (14-20) % of body length. Hemizonid two to three annuli long, located directly anterior to excretory pore (n = 5). Hemizonion not seen. Fasciculi not seen. Width of annulus at midbody 1.4 ± 0.1 (1.1-1.6) µm. Body width at excretory pore 21 ± 2.1 (17-27) µm, midbody 27 ± 4.0 (21-36) µm and at anus 15 ± 1.4 (12-18) µm. Two branches of reproductive system functional, equally developed, length of posterior branch 80 ± 16.3 (49-113) % of corresponding anterior branch length; anterior branch 163 ± 41.3 (115-227) µm and posterior branch 126 ± 18.6 (93-165) µm long. Epiptygma folded into vagina. Lateral field 6 ± 0.8 (5-7) µm wide; areolated opposite to anterior ovarium in one specimen, incompletely areolated anterior and posterior to vulva, outer two lines crenate on tail in 50 % of specimens; inner two lines end on tail in a v- (36 %) or y-shaped (64 %) pattern. Phasmids located two annuli posterior to seven annuli anterior to anus. Rectum does not overlap anus. Tail 15 ± 2.5 (12-21) µm long, bent and asymmetrical with rounded end, with seven to fourteen ventral annuli.

Male: Not seen.

Remarks

The diagnostic characters given by Sher (1966) i.e. ending of lateral field and striations continuing around tail terminus is not reliable, because of variation of these characters as reported by Fortuner *et al.* (1981). *H. cavenessi* was separated from *H. dihystera* by position of the vulva, habitus sometimes C-shaped and lips sometimes appearing more flattened (Fortuner *et al.*, 1981). The South African specimens agree with all the criteria given by Fortuner *et al.* (1981) except for the position of the vulva

(62-66 *vs* 56-62 %) and phasmids (two annuli posterior to seven annuli anterior to anus *vs* three to seven annuli anterior to anus). The more posterior position of the vulva was also recorded in populations from China (V = 60-65 %) (Hui & Zhixin, 1996), India (V = 60-67 %) (Fotedar & Kaul, 1985) and South Africa (V = 60-68 %) (Van den Berg & Heyns, 1975). Contradictory to Fortuner (1984a) where a lower CV was shown in the measurement (length of oesophagus), ratio b of the present specimens showed a lower CV than the corresponding measurement (4 % *vs* 6 %). Ratio V showed the least variation of the morphometric characters with CV of 3 %.

***Helicotylenchus crenacauda* Sher, 1966** (Fig. 17, 18)

= *Helicotylenchus pteracercus* Singh, 1971

= *Helicotylenchus indenticaudatus* Mulk & Jairajpuri, 1975

= *Helicotylenchus indentatus* Chaturvedi & Khera, 1979

= *Helicotylenchus paracrenacauda* Phukan & Sanwal, 1981

= *Helicotylenchus parapteracercus* Sultan, 1981

= *Helicotylenchus pteracercusoides* Fotedar & Kaul, 1985

The species was described from the rhizosphere of rice (*Oryza sativa* L.) Java, Indonesia and since reported from all the biogeographical regions, viz.

Afrotropical Region

Cameroon (Bridge *et al.*, 1995), Côte d'Ivoire (Coyne *et al.*, 1999), Mozambique (Van den Oever *et al.*, 1998) and South Africa (Kleynhans *et al.*, 1996).

Australian Region

Fiji (Van den Berg & Kirby, 1979).

Nearctic Region

USA (Esser, 1997).

Neotropical Region

Brazil (Costa Manso *et al.*, 1994), Dominican Republic (Kermarrec & Belliard, 1977), Guadeloupe islands (Marais *et al.*, 2000), Suriname (Maas, 1970), Trinidad (Bala, 1984) and Venezuela (Crozzoli *et al.*, 1998).

Oriental Region

China (Guokun & Shaosheng, 1999), India (Lal & Khan, 1993), Malaysia (Sauer & Winoto, 1975), Pakistan (Sher, 1966), Sri Lanka (Ekanayake & Toida, 1997), Taiwan (Lin, 1970), Thailand (Pholcharoen & Boonduang, 1972) and Turkey (Kepenekci & Ökten, 1999).

Palaearctic Region

Spain (Arias & Romera, 1975).

Measurements

See Table 10.

Description

Female (n = 43): Habitus C-shaped (9 %) to spiral (91 %). Lip region 4 ± 0.7 (3-5) µm high and 6 ± 1.2 (3-8) µm wide, anteriorly rounded, not set off with four to six annuli. Labial disc round in *en face* view. Outer margins of labial framework extend 3 µm backward from basal plate. Stylet knobs 3 ± 0.5 (2-5) µm high and 5 ± 0.9 (3-6) µm wide; anterior faces rounded (4 %), flattened (33 %), indented (21 %) or slightly inclined backwards (42 %). Position of DGO 10 ± 1.6 (8-13) µm behind stylet knobs. Median bulb oval, 13 ± 1.3 (10-15) µm long and 9 ± 1.3 (6-11) µm wide; valve 3 ± 0.5 (3-4) µm long and 3 µm wide. Length of oesophagus 124 ± 11.1 (91-148) µm, with length to end of glands 122 ± 12.4 (19-136) µm. Oesophagus with 24 ± 9.7 (10-50) µm long ventral or dorsal overlap. Excretory pore 100 ± 13.2 (74-127) µm from front, i.e. at 16 ± 1.2 (13-18) % of body length. Hemizonid two to three annuli long, located from opposite to two annuli posterior to excretory pore (*n = 2*). Hemizonion not seen.

Fasciculi not seen. Width of annulus at midbody 1.4 ± 18.7 (1.1-2.2) µm. Body width at excretory pore 20 ± 3.8 (13-37) µm, at midbody 26 ± 5.5 (17-35) µm and at anus 14 ± 2.6 (10-20) µm. Two branches of reproductive system functional, equally developed, length of posterior branch 77 ± 18.4 (40-100) % of corresponding anterior branch length; anterior branch 177 ± 22.9 (148-217) µm and posterior branch 145 ± 16.2 (129-169) µm long. Epiptygma folded into vagina. Lateral field 6 ± 0.9 (4-7) µm wide; inner two lines end on tail in a v- (23 %), y- (74 %), m- (1 %) or µ-shaped (2 %) pattern. Rectum does not overlap anus. Phasmids located three to fourteen annuli anterior to anus. Tail 18 ± 4.4 (10-33) µm long, with seven to eighteen ventral annuli; indented tail terminus with a cuticular fold present in 35 % and a mucro in 2 % of the specimens.

Male (n = 5): Habitus C-shaped (60 %) to spiral (40 %). Lip region 4 ± 1.3 (4-6) µm high and 6 ± 0.8 (5-6) µm wide, anteriorly rounded, with five annuli. Stylet knobs 2 ± 0.2 (2-3) µm high and 4 ± 0.7 (3-4) µm wide; anterior faces indented. Position of DGO 8 ± 2.8 (6-10) µm behind stylet knobs. Length of oesophagus 89 µm, with length to end of glands 105 ± 5.0 (102-111) µm. Oesophagus with 24 ± 14.3 (13-24) µm ventral overlap. Excretory pore 83 ± 12.8 (75-105) µm from front, i.e. at 15 ± 0.8 (14-16) % of body length. Hemizonid and hemizonion not seen. Width of annulus at midbody 1.0 ± 0.3 (0.7-1.1) µm. Body width at excretory pore 16 ± 2.7 (15-21) µm, at midbody 18 ± 3.2 (16-24) µm and at cloaca 11 ± 1.6 (9-13) µm. Lateral field 4 ± .5 (4-5) µm wide; areolated anterior and opposite to bursa. Phasmids located one cloacal body width anterior to cloaca. Tail with finger-like ventrad-curved projection.

Remarks

The specimens are regarded as *H. crenacauda* because of the presence of the indented tail terminus. Sher (1966) separated *H. crenacauda* from *H. pseudorobustus* and *H. paxilli* by the indented tail terminus. The South African specimens were

compared with female paratype material of *H. crenacauda* from rice in Boga, Indonesia with which they correspond well. The material from both South Africa and the Guadeloupe islands agree with the original description (Sher, 1966) and the subsequent descriptions (Baqri & Ahmad, 1983; Crozzoli *et al.,* 1998; Marais, 1993). The variation in the morphometric and morphological characters supported the synonymy of H. *pteracercus, H. indentatus* and *H. parapteracercus* with *H. crenacauda* by Baqri & Ahmad (1983), the synonymy of *H. pteracercus, H. paracrenacauda* and *H. pteracercusoides* with *H. crenacauda* by Siddiqi (1986) and the synonymy of *H. indenticaudatus* with *H. crenacauda* by Lal & Khan (1993). Value V and m showed the least variation with CV of 4 %.

***Helicotylenchus delanus* Marais, 1998** (Fig. 19, 20)

The species was described from Elandshoogte Plantation, Mpumalanga Province, South Africa associated with patula pine (*Pinus patula* Schiede ex Schldl. & Cham.), and it is known only from the type locality (Marais, 1998).

Measurements

See Table 21.

Description

Female (n = 20): Habitus straight (42 %) to C-shaped (58 %). Lip region 4 ± 0.2 (3-5) µm high and 7 ± 0.5 (6-8) µm wide, anteriorly flattened, not offset, with five to six annuli. Labial disc rectangular in *en face* view. Outer margins of labial framework extend 3 µm backward from basal plate. Cephalids not seen. Stylet knobs 2 µm high and 5 µm wide, anterior faces flattened (28 %) or indented (72 %). Position of DGO 6 ± 0.9 (5-8) µm behind stylet knobs. Median bulb oval to nearly round, 12 ± 1.2 (10-14)

µm long and 9 ± 1.6 (8-14) µm wide; valve 3 µm long and 3 µm wide. Length of oesophagus 111 ± 9.4 (99-120) µm, with length to end of glands 128 ± 8.7 (114-145) µm. Oesophagus with 20 ± 6.4 (15-29) µm long ventral or dorsal overlap. Excretory pore 93 ±5.2 (82-103) µm from front, i.e. at 17 ± 1.4 (15-20) % of body length. Hemizonid two annuli long, located one to two annuli anterior to excretory pore (n = 5). Hemizonion not seen. Fasciculi not seen. Width of annulus at midbody 1.4 ± 0.2 (1.1-1.5) µm. Body width at excretory pore 16 ± 2.0 (10-14) µm, at midbody 21 ± 2.9 (15-26) µm and at anus 14 ± 2.6 (10-20) µm. Posterior branch of reproductive system reduced; length of posterior branch 25 ± 6.8 (17-30) % of corresponding anterior branch length; anterior branch 147 ± 27.5 (126-174) µm and posterior branch 33 ± 7.0 (25-44) µm long. Spermatheca round, offset, filled with sperm. Epiptygma folded into vagina. Lateral field 4 ± 0.8 (3-6) µm wide; inner two lines end on tail in a u- (12 %), µ- (50 %) and m-shaped (38 %) pattern. Phasmids located from five annuli posterior to opposite to anus. Caudalid not seen. Tail 13 ± 2.1 (9-17) µm long, more curved dorsally, with rounded end, with six to eleven ventral tail annuli.

Male (n = 8): Habitus C-shaped. Lip region 3 ± 0.3 (3-5) µm high and 6 ± 0.8 (5-8) µm wide, anteriorly flattened with five annuli. Outer margins of labial framework extend 2 µm backward from basal plate. Stylet knobs 2 µm high and 5 µm wide; anterior faces indented. Position of DGO 6 ± 0.6 (5-7) µm behind stylet knobs. Length of oesophagus 123 ± 11.0 (107-132) µm, with length to end of glands 132 ± 11.4 (118-148) µm. Oesophagus with 12 ± 2.5 (10-16) µm long ventral or dorsal overlap. Excretory pore located 90 ± 3.7 (85-94) µm from front, i.e. at 16 ± 0.8 (15-17) % of body length. Hemizonid and hemizonion not seen. Width of annulus at midbody 1.4 ± 0.3 (1.1-1.9) µm. Body width at excretory pore 17 ± 3.1 (14-23) µm, at midbody 19 ± 2.8 (15-24) µm and at cloaca 11 ± 0.9 (10-12) µm. Lateral field 5 ± 1.1 (5-8) µm wide; areolated opposite and anterior to bursa. Phasmids located less than one body width posterior to cloaca. Bursa extending to tip of tail. Tail with finger-like projection.

Remarks

H. delanus was characterized by the posterior position of the vulva (V = 73-78 %), reduced posterior reproductive branch (25-44 µm), mostly posterior position of phasmid, and tail shape in females and by body length (497-629 µm), position of excretory pore (85-94 µm), and lengths of stylet (22-26 µm), spicule (18-23 µm), and gubernaculum (6-8 µm) in males. Marais (1998) separated *H. delanus* from other species with a reduced posterior reproductive branch viz., *H. intermedius, H. neoformis* and *H. valdeclarus.*

***Helicotylenchus digonicus* Perry in Perry, Darling & Thorne, 1959** (Fig.21, 22)

= *Helicotylenchus broadbalkiensis* Yuen, 1964

Helicotylenchus digonicus was described from *Poa pratensis* L. in Wisconsin, USA and since reported from all six biogeographical regions, viz.

Afrotropical Region

Côte d'Ivoire (Seymour, 1978), Malawi (own record), Mozambique (own record), South Africa (Marais & Swart, 1998) and Tanzania (own record).

Australian Region

Australia (Mathur & McLeod, 1977) and New Zealand (Wouts & Yeates, 1994).

Nearctic Region

Canada (Sher, 1966) and USA (Perry *et al.,* 1959).

Neotropical Region

Argentina (Doucet & Doucet, 1997), Brazil (Sharma & Swarup, 1982), Guadeloupe islands (Marais *et al.,* 2000) and Mexico (Zavaleja-Mejía & Sosa-Moss, 1979).

Oriental Region

China (Hui & Zhixin, 1996), Jordan (Hashim, 1982), Korea (Bae & Choi, 1997), Pakistan (Maqbool & Hashmi, 1986), Taiwan (own record), Thailand (Ratanaprapa & Boonduang, 1975) and Turkey (Kepenekci & Ökten, 1996).

Palaearctic Region

Bulgaria (Katalan-Gateva, 1980), Croatia (Samota *et al.*, 1988), Czech Republic (Schöberlein *et al.*, 1998), Denmark (Anderson, 1972), Finland (Kurppa, 1988), Germany (Bongers, 1988), Hungary (Andrássy, 1973), Italy (Sher, 1966), Japan (Nakasono *et al.*, 1986), Jordan (Hashim, 1982), Kazakstan (Baïdulova, 1981), Libya (Saadabi, 1993), Netherlands (Bongers, 1988), Poland (Sher, 1966), Russia (Metlitskaya, 1984), Slovakia (Stollárová, 1998), Spain (Peña-Santiago, 1990), Tadjikistan (Sher, 1966), Turkmenia (Kir'yanova & Shagalina, 1976) and the United Kingdom (Yuen, 1964).

Measurements

See Table 11.

Description

Female (n = 158): Habitus C-shaped (4 %) to spiral (96 %). Lip region 4 ± 0.8 (5-9) µm high and 7 ± 0.8 (5-9) µm wide, anteriorly flattened not set off, with five to seven annuli. Labial disc rounded in en face view. Outer margins of labial framework extend 4 µm backward from basal plate. Anterior cephalids three to five annuli posterior to basal plate, posterior cephalids not seen. Stylet knobs 3 ± 0.4 (2-4) µm high and 5 ± 0.6 (4-7) µm wide; anterior faces of stylet knobs rounded (7 %), flattened (54 %), indented (32 %) or slightly inclined backwards (7 %). Position of DGO 11 ± 1.9 (8-16) µm behind stylet knobs. Median bulb oval, 13 ± 1.1 (10-16) µm long and 10 ± 1.2 (7-13) µm wide; valve 3 µm long and 2 µm wide. Length of oesophagus 129 ± 13.3 (101-12) µm, with length to end of glands 147 ± 24.6 (88-193) µm. Oesophagus with 20 ±

9.5 (6-50) µm long ventral or dorsal overlap. Excretory pore 109 ± 12.2 (86-149) µm from front, i.e. at 16 ± 1.6 (12-21) % of body length. Hemizonid two to three annuli long, located from two annuli anterior to one annulus posterior to excretory pore (n = 49). Hemizonion one annulus long, located 10 to 13 annuli posterior to excretory pore (n = 12). Fasciculi not seen. Width of annulus at midbody 1.3 ± 0.3 (0.7-2.2) µm. Body width at excretory pore 21 ± 2.5 (17-32) µm, at midbody 26 ± 3.2 (20-36) µm and at anus 15 ± 1.7 (10-20) µm. Two branches of reproductive system both functional; length of posterior branch 90 ± 21.2 (48-162) % of corresponding anterior branch length; anterior branch 164 ± 33.9 (109-249) µm and posterior branch 135 ± 24.6 (88-193) µm long. Spermatheca offset, empty and thick-walled. Epiptygma folded into vagina. Lateral field 6 ± 0.9 (4-9) µm wide; areolated anterior and posterior to vulva and crenate on tail; inner two lines end on tail in a v- (35 %), y- (39 %), u- (9 %), µ- (3 %) or m-shaped (14 %) pattern. Phasmids located six annuli posterior to fourteen annuli anterior to anus, usually not located in centre of middle field, touching inner ventral line. Rectum does not overlap anus. Tail 16 ± 2.9 (11-24) µm long, more curved dorsally, dorsal side joins the ventral side at an angle, with five to eighteen ventral annuli.

Male: Not found.

Remarks

The specimens are regarded as *H. digonicus* because of habitus mostly spiral, stylet length (mean value: 27 µm), body length (mean value: 675 µm) phasmids usually not located in centre of middle field, touching ventral inner line, tail more curved dorsally, dorsal side joins ventral side at an angle and no males. The position of the vulva in the present specimens differ from that of the type locality (57-70 *vs* 58-64 %), this wider range is also reflected in populations from China (Hui & Zhixin, 1996) and

Poland (Brzeski, 1998). Characters that showed the least variation was ratio's V, m and stylet length with CV of 4 %, 4 % and 7 % respectively.

***Helicotylenchus egyptiensis* Tarjan 1964** (Fig. 23)

The species was described from sugar-cane (*Saccharum officinarum* L.) Luxor, Egypt (Tarjan, 1964) and has since been reported from four of the biogeographical regions, viz.:

Afrotropical Region

Cameroon (Bridge *et al.*, 1995), Côte d'Ivoire (Coyne *et al.*, 1999), Malawi (Saka & Siddiqi, 1979), Senegal (own record) and Sudan (Zeidan & Geraert, 1990).

Australian Region

Fiji (Van den Berg & Kirby, 1979).

Neotropical Region

Brazil (Costa Manso *et al.*, 1994), Cuba (Fernández Díaz-Silviera & Ortega Herrera, 1998), Guadeloupe islands (Marais *et al.*, 2000) and Martinique (own record).

Oriental Region

India (Ali *et al.*, 1969), Pakistan (Firoza & Maqbool, 1996) and Thailand (Mizukubo *et al.*, 1992).

Palaearctic Region

Moldova (Kozhokaru & Korol'chuk, 1976).

Measurements

See Table 12.

Description

Female (n = 26): Habitus straight (4%), C-shaped (23 %) to spiral (73 %). Lip

region 4 ± 0.4 (3-5) µm high and 7 ± 0.5 (7-9) µm wide, anteriorly flattened, not set off with four to five annuli. Outer margins of labial framework extend 3 ± 0.5 (2-4) µm backward from basal plate. Cephalids not seen. Stylet knobs 3 ± 0.4 (2-4) µm high and 5 ± 0.5 (4-6) µm wide; anterior faces flattened (26 %) or indented (74 %). Position of DGO 10 ± 0.4 (9-11) µm behind stylet knobs. Median bulb oval, 13 ± 2.2 (11-22) µm long and 9 ± 1.2 (7-13) µm wide; valve 4 µm high and 3 µm wide. Length of oesophagus 121 µm (*n* = *1*), with length to end of glands 140 ± 7.1 (128-155) µm. Oesophagus with 15 µm long ventral overlap. Excretory pore 108 ± 5.4 (96-118) µm from front, i.e. at 17 ± 1.5 (14-19) % of body length. Hemizonid two annuli long, located opposite to two annuli anterior to excretory pore (*n* = *9*). Hemizonion one annulus long, located seven to ten annuli posterior to excretory pore (*n* = *5*). Fasciculi not seen. Width of annulus at midbody 1.5 ± 0.4 (1.1-2.2) µm. Body width at excretory pore 19 ± 3.0 (11-24) µm, at midbody 26 ± 3.4 (21-33) µm and at anus 16 ± 0.6 (15-17) µm. Two branches of reproductive system both functional, length of posterior branch 88 ± 17.6 (68-106) % of corresponding anterior branch length; anterior branch 165 ± 39.3 (109-204) µm and posterior branch 161 ± 24.9 (124-203) µm long. Epiptygma folded into vagina. Lateral field 5 ± 0.8 (4-7) µm wide; areolated opposite oesophageal region; inner two lines end on tail in a y- (95 %) or open m-shaped pattern (5 %). Phasmids located from one to six annuli anterior to anus. Tail 21 ± 3.5 (16-30) µm long, dorsally curved, with an annulated pointed or rounded ventral projection, with 16 to 30 ventral annuli.

Male: Not found.

Remarks

The specimens are regarded as *H. egyptiensis* because of mostly spiral habitus, lip region anteriorly flattened, stylet length (mean value: 25 µm), position of vulva (mean V value: 61 %), phasmid from one to six annuli anterior to anus, inner lines

ending mostly in y-shaped pattern, tail slightly longer than wide (mean c' value: 1.5), variable tail projection and absence of males. According to Tarjan (1964) *H. egyptiensis* is similar to *H. africanus*, *H. multicinctus* and *H. erythrinae* and he separated *H. egyptiensis* from these species because of absence of areolations on tail, presence of a ventral tail projection and higher c value and absence of males. The French Caribbean populations agree with the paratype material and description of the paratypes by Tarjan (1964) and Fortuner *et al.* (1984). The punctuations described by Tarjan (1964) were according to Sher (1966), artefacts possibly due to impurities in the fixative or glycerine. This is confirmed by the fact that no punctuations were seen in the populations from Guadeloupe and Martinique (Marais *et al.*, 2000).

***Helicotylenchus elegans* Román, 1965**

This species was described from roots of sugar-cane (*Saccharum officinarum* L.), Puerto Rico (Román, 1965) and since reported from the:

Afrotropical Region

South Africa (Van den Berg & Heyns, 1975).

Oriental Region

India (Saxena *et al.*, 1973).

Measurements

See Table 12.

Remarks

Van den Berg and Heyns (1975) identified this species from a specimen collected at Groblershoop, Northern Cape Province during 1967. It is the only record of this species in South Africa and the single specimen deposited in the NCN has deteriorated

and is no longer suitable for examination.

***Helicotylenchus erythrinae* (Zimmermann, 1904) Golden, 1956** (Fig. 21, 24)

= *Tylenchus erythrinae* Zimmermann, 1904

= *Tylenchorhynchus erythrinae* (Zimmermann, 1904) Bally & Reydon, 1931

= *Anguillulina erythrinae* (Zimmermann, 1904) Goodey, 1932

= *Rotylenchus erythrinae* (Zimmermann, 1904) Goodey, 1951

= *Rotylenchus melancholicus* Lordello, 1955

= *Helicotylenchus melancholicus* (Lordello, 1955) Andrássy, 1958

= *Helicotylenchus spicaudatus* Tarjan, 1964

The species was described from *Erythrina lithosperma* Miq. in Indonesia (Zimmermann, 1904) and since reported from all six the biogeographical regions, viz.

Afrotropical Region

Aldabra Islands (Van den Berg & Spaull, 1985), Cameroon (Bridge *et al.,* 1995), Canary Islands (Iglesias *et al.*, 1999), Côte d'Ivoire (Fortuner & Couturier, 1983), Madagascar (Luc, 1959), Malawi (Mughogho & Choo, 1969), Mauritius (Williams, 1960), Nigeria (Sher, 1966), Senegal (Netscher, 1970), South Africa (Van den Berg & Heyns, 1975) and Togo (De Guiran, 1965).

Australian Region

Easter Island (Gallo, 1979), New Zealand (Wouts & Yeates, 1994) and Solomon Islands (Ye & Geraert, 1997).

Nearctic Region

USA (Sher, 1966).

Neotropical Region

Belize (Bridge *et al.,* 1996), Brazil (Costa Manso *et al.,* 1994), Colombia (Grislaes López & Lescot, 1999), Costa Rica (Sher, 1966), Cuba (Fernández Díaz-Silviera & Ortega

Herrera, 1998), Dominica (Edmunds, 1969), French Guiana (Marais & Quénéhervé, 1996), Guadeloupe islands (Marais *et al.,* 2000), Jamaica (Coates-Beckford *et al.,* 1998), Martinique (Cadet *et al.,* 1994), Mexico (Zavaleta-Mejía & Sosa-Moss, 1979), Panama (Sher, 1966), Peru (Krusberg & Hirschmann, 1958), Puerto Rico (Williams, 1960), San Salvador (Sher, 1966), Suriname (Maas, 1970) and Venezuela (Crozzoli *et al.,* 1998).

Oriental Region

China (Lan, 1992), India (Baqri & Ahmad, 1983), Indonesia (Rashid *et al.,* 1988), Korea (Choo & Choi, 1979), Malaysia (Sauer & Winoto, 1975), Pakistan (Fotedar & Kaul, 1985), Philippines (Timm, 1965) and Sri Lanka (Anonymous, 1969).

Palaearctic Region

Czech Republic (Schöberlein *et al.*, 1998), Japan (Toida, 1984), Kazakhstan (Izatullaeva, 1969), Moldova (Kozhokaru & Korol'chuk, 1976), Poland (Brzeski, 1985), Russia (Anonymous, 2000), Slovakia (Stollárová, 1997) and Uzbekistan (Tuarev, 1981).

Measurements

See Table 13.

Description

Female (n = 83): Habitus C-shaped (18 %) to spiral (82 %). Lip region 4 ± 0.3 (3-6) µm high and 7 ± 0.6 (4-8) µm wide, anteriorly rounded, not set off with five to seven annuli. Labial disc oval in *en face* view. Outer margins of labial framework extend 3 µm backward from basal plate. Cephalids not seen. Stylet knobs 2 ± 0.3 (1-3) µm high and 5 ± 0.5 (4-8) µm wide; anterior faces rounded (2 %), flattened (37 %), indented (60 %) or flattened and inclined backwards (1 %). Position of DGO 12 ± 4.4 (8-23) µm behind stylet knobs. Median bulb oval to round, 11 ± 1.3 (7-16) µm long and 8 ± 0.7 (7-11) µm wide; valve 4 µm long and 3 µm wide. Length of oesophagus 127 ± 11.0

(106-148) µm, with length to end of glands 140 ± 13.4 (109-167) µm. Oesophagus with 17 ± 5.7 (5-24) µm long ventral overlap. Excretory pore 103 ± 7.8 (88-128) µm from front of body, i.e. at 18 ± 1.6 (13-24) % of total body length. Hemizonid two to three annuli long, located one to two to annuli anterior to excretory pore (*n = 34*). Hemizonion one annulus long, located four to ten annuli posterior to excretory pore (*n = 7*). Fasciculi not seen. Width of annulus at midbody 1.5 ± 0.2 (1.1-2.5) µm. Body width at excretory pore 17 ± 2.0 (11-26) µm, at midbody 22 ± 3.0 (16-31) µm and at anus 15 ± 1.8 (12-20) µm. Two branches of the reproductive system both functional, length of posterior branch 93 ± 15.8 (50-136) % of corresponding anterior branch length; anterior branch 143 ± 29.6 (102-239) µm and posterior branch 135 ± 14.7 (86-247) µm long. Spermatheca set off, filled with sperm. Epiptygma folded into vagina. Lateral field 5 ± 0.7 (4-6) µm wide; crenate and incompletely areolated anterior and posterior to vulva; inner two lines end on tail in a v- (8 %), y- (24), u- (6 %), µ- (28 %), m- (33 %) or open m-shaped pattern (1 %). Caudalid one annulus long located three annuli anterior to two annuli posterior to anus. Phasmids located four annuli posterior to twelve annuli anterior to anus. Tail 21 ± 15.6 (13-29) µm long, with nine to seventeen ventral annuli; tail more curved dorsally with a rounded or pointed annulated ventral projection, mucro seen in 45 % of specimens.

Male (n = 48): Habitus straight (21 %), C-shaped (60 %) to spiral (19 %). Lip region 4 ± 0.4 (3-4) µm high and 7 ± 0.7 (6-10) µm wide, anteriorly rounded with five to six annuli. Outer margins of labial framework extend 2 µm backward from basal plate. Stylet knobs 2 ± 0.3 (1-3) µm high and 4 ± 0.5 (3-5) µm wide; anterior faces of stylet knobs flattened (54 %), indented (45 %) or flattened and inclined backwards (1 %). Position of DGO 13 ± 3.7 (8-20) µm behind stylet knobs. Length of oesophagus 113 ± 5.7 (102-120) µm, with length to end of glands 131 ± 11.7 (107-149) µm. Oesophagus with 19 ± 7.3 (5-27) µm long ventral overlap. Excretory pore 95 ± 8.3 (77-112) µm from front of body, i.e. at 17 ± 1.3 (14-22) % of total body length. Hemizonid two to three

annuli long, located from opposite to two annuli anterior to excretory pore (*n = 12*). Hemizonid one annulus long, located seven annuli posterior to excretory pore (*n = 1*). Width of annulus at midbody 1.4 ± 0.3 (0.7-1.8) µm. Body width at excretory pore 15 ± 1.6 (13-19) µm, at midbody 18 ± 2.4 (14-23) µm and at cloaca 12 ± 1.0 (10-14) µm. Lateral field 4 ± 0.5 (3-5) µm wide; incompletely areolated on posterior part of body and region of bursa, as much as four cloacal body widths anterior to bursa. Tail 19 ± 2.5 (13-26) µm long, with a ventrad curved, rounded or pointed ventral projection, mucro seen in 20 % of specimens.

Remarks

Sher (1966) distinguished *H. erythrinae* from *H. dihystera* and *H. multicinctus* by the pronounced ventral projection. The present specimens are regarded as *H. erythrinae* because of mostly spiral body, lip region anteriorly rounded, stylet length (mean value: 25 µm), body length (mean value: 620 µm), position of vulva (mean V value: 63 %), phasmids located one to six annuli anterior to anus, tail slightly longer than wide (mean c- value: 1.4) with mostly pointed ventral projection and presence of males. The specimens agree with the descriptions of the topotypes by Sher (1966). The upper range for body length (797 µm) and tail length (29 µm) differ from the 938 µm (body length) and 24 µm (tail length) reported by (Wouts & Yeates, 1994). The lower range for stylet length (20 µm) in males is higher than the 17.7 µm reported by Van den Berg & Spaull (1985) and the range of the spicule length exceeds the previous lowest value (15 *vs* 18 µm in Sher, 1966). V value showed the least variation with a CV of 4 %, the highest range (69 %) exceeds the highest value of 68 % as reported by Sauer & Winoto (1975). The females from a population from French Guiana (FG122 in Table 7) has a DGO located more posteriorly behind the stylet knobs (16-23 µm) and therefore also a higher o-value (63-90 %), exceeding that of the previous highest value for these characters in the genus (20 µm in *H. macrostylus* and 67 % in *H. retusus*)

(Saha *et al.*, 1974; Marais & Quénéhervé, 1996), the same trend was observed in the males of this population.

***Helicotylenchus exallus* Sher, 1966** (Fig. 23, 25)

= *Helicotylenchus regularis* Phillips, 1971

The species was described from wheat (*Triticum aestivum* L., nom. cons. subsp. *aestivum*) in South Dakota, USA (Sher, 1966) and subsequently reported from all the different biogeographical regions:

Afrotropical Region

Cameroon (Samsoen & Geraert, 1975), Democratic Republic of the Congo (Ali *et al.*, 1973), Kenya (Njuguna & Bridge, 1998) and South Africa (Marais & Swart, 1999).

Australian Region

Australia (Phillips, 1971) and New Zealand (Wouts & Yeates, 1994).

Nearctic Region

USA (Sher, 1966).

Neotropical Region

Columbia (Stanton *et al.*, 1989).

Oriental Region

China (Hui & Zhixin, 1996), India (Sher, 1966), Korea (Kornobis & Dobosz, 1996), Pakistan (Maqbool *et al.*, 1985), Thailand (Ratanaprapa & Boonduang, 1975) and Turkey (Ercan, 1976).

Palaearctic Region

Belgium (Bongers, 1988), Egypt (Youssef & Aboul-Eid, 1996), Poland (Brzeski, 1985), Russia (Romaniko, 1973) and Tadjikistan (Kankina & Teben'kova, 1980).

Measurements

See Table 12.

Description

Female (n = 88): Habitus straight (5 %), C-shaped (24 %) or spiral (71 %). Lip region 4 ± 0.5 (3-5) µm high and 7 ± 1.0 (5-9) µm wide, anteriorly rounded with five to seven annuli. Labial disc oval in *en face* view. Outer margins of labial framework extend 3 µm backward from basal plate. Anterior cephalids three to four annuli posterior from basal plate, posterior cephalids at four to seven annuli posterior to anterior cephalids. Stylet knobs 2 ± 0.4 (1-3) µm high and 5 ± 0.6 (4-7) µm wide; anterior faces rounded (1 %), flattened (35 %), indented (56 %) or flattened and inclined backwards (8 %). Position of DGO 11 ± 1.3 (8-13) µm behind stylet knobs. Median bulb oval, 12 ± 1.1 (10-16) µm long and 9 ± 1.1 (7-12) µm wide; valve 4 µm long and 3 µm wide. Length of oesophagus 129 ± 3.5 (16-29) µm, with length to end of glands 140 ± 13.4 (104-170) µm. Oesophagus with 18 ± 5.6 (9-28) µm long ventral or dorso-lateral overlap. Excretory pore at 106 ± 9.1 (90-136) µm from anterior end, i.e. at 17 ± 1.6 (12-22) % of body length. Hemizonid two annuli long, located one annulus posterior to 3 annuli anterior to excretory pore (*n = 11*). Hemizonid not seen. Fasciculi not seen. Width of annuli at midbody 1.3 ± 0.3 (0.7-2.2) µm. Body width at excretory pore 19 ± 2.3 (15-25) µm, midbody 26 ± 4.0 (18-30) µm and at anus 15 ± 2.2 (12-22) µm. Two branches of reproductive system both functional, length of posterior branch 88 ± 17.3 (61-138) % of corresponding anterior branch length; anterior branch 149 ± 23.8 (96-192) µm and posterior branch 125 ± 19.9 (88-165) µm long. Epiptygma folded into vagina. Lateral field 5 ± 0.8 (3-8) µm wide; crenate and incompletely areolated anterior and posterior to vulva, crenate on tail; inner two lines end on tail in an v- (16 %), y- (16 %), u- (7 %), µ- (11 %), m- (47 %) or open m-shaped (3 %) pattern. Phasmids located three annuli posterior to ten annuli anterior to anus. Rectum does not overlap anus. Caudalid one annulus long, located one annulus posterior to five annuli anterior

to anus. Tail 16 ± 2.8 (12-24) µm long, with six to fifteen ventral annuli, more curved dorsally, with or without pointed ventral projection; fine mucro seen in three specimens.

Male (n = 45): Habitus straight (23 %), C-shaped (66 %) to spiral (11 %). Lip region 4 ± 0.5 (3-5) µm high and 7 ± 0.7 (5-8) µm wide, anteriorly rounded with five to seven annuli. Outer margins of labial framework extend 3 µm backward from basal plate. Stylet knobs 2 ± 0.3 (2-3) µm high and 4 ± 0.3 (4-5) µm wide; anterior faces flattened (22 %) or indented (78 %). Position of DGO 10 ± 0.8 (9-11) µm behind stylet knobs. Medium bulb oval, 11 ± 1.0 (9-13) µm long and 7 ± 0.9 (5-9) µm wide; valve 3 ± 0.3 (2-3) µm long and 2 µm wide. Length of oesophagus 118 ± 13.4 (103-140) µm, with length to end of glands 131 ± 8.9 (110-148) µm. Oesophagus with 15 ± 6.0 (3-22) µm long ventral overlap. Excretory pore located 95 ± 8.4 (76-111) µm from anterior end, i.e. at 17 ± 1.0 (15-19) % of body length. Hemizonid two annuli long, located opposite to two annuli anterior to excretory pore (*n* = 6). Hemizonion not seen. Width of annulus at midbody 1.4 ± 0.2 (1.0-1.8) µm. Body width at excretory pore 16 ± 1.2 (14-19) µm, at midbody 20 ± 2.2 (15-25) µm and at cloaca 19 ± 3.0 (13-24) µm. Lateral field 4 ± 0.2 (3-6) µm wide, not areolated in the region of bursa. Phasmids located from half a body width anterior to opposite cloaca. Tail 19 ± 3.0 (13-24) µm long, with a finger-like projection, mucro seen in three specimens.

Remarks

The South African specimens were identified as *H. exallus* because of lip region anteriorly rounded, position of vulva (mean V value 64 %), stylet length (mean value 28 µm), body length (mean value 616 µm), phasmids posterior and anterior to anus, tail more curved dorsally, with or without projection and males present. The present specimens were compared with *H. exallus* material from New Zealand (Wouts & Yeates, 1994) and South Africa (Van den Berg & Heyns, 1975) and with the paratypes

of *H. regularis* Phillips, 1971 from a sclerophyll forest in Australia. The population from Dangerpoint showed variations in tail shape that encompasses both the shapes described by Phillips (1971) for *H. regularis* and Sher (1966) for *H. exallus* and therefore supports the synonimisation of *H. regularis* with *H. exallus* by Ali *et al.* (1973). The upper range for stylet length in females (32 µm) is higher than the 29.4 µm reported by (Van den Berg & Heyns, 1975) and the upper range for DGO (13 µm) is higher than the 11 µm of Wouts & Yeates (1994). The lowest range (18.3) for ratio a is lower than the (21) reported by Kornobis & Dobosz (1996). Although the range for c-value (28.2-66.9) is within the previous lowest (25 by Ali *et al.*, 1974) and highest (74.0 by Van den Berg & Heyns, 1975) values, the upper range for tail length (24 µm) is higher than the 19 µm of Wouts & Yeates (1994). Thorne & Malek (1968) described a gubernaculum with an elongated distal knob, this character was not seen in any of the South African or New Zealand material.

***Helicotylenchus hydrophilus* Sher, 1966** (Fig. 23)

Helicotylenchus hydrophilus was described from swamp soil, Florida, USA and since recorded from four biogeographical regions, viz.:

Afrotropical Region

South Africa (Marais & Swart, 1999).

Australian Region

Solomon Islands (Ye & Geraert, 1997).

Nearctic Region

Canada (Anderson & Eveleigh, 1982).

Oriental Region

China (Li, 1986).

Measurements

See Table 12.

Description

Female (n = 1): Habitus spiral. Lip region 5 µm high and 7 µm wide, anteriorly rounded, with four annuli. Outer margins of labial framework extend 4 µm backward from basal plate. Stylet knobs 3 µm high and 6 µm wide; anterior faces flattened. Position of DGO at 12 µm behind stylet knobs. Median bulb oval, 14 µm long and 10 µm wide. Length of oesophagus to end of glands 164 µm. Excretory pore 129 µm from front, i.e. at 15 % of body length. Hemizonid and hemizonion not seen. Fasciculi not seen. Width of annulus at midbody 1.4 µm. Body width at excretory pore 21 µm and at anus 17 µm. Spermatheca slightly offset and filled with rounded sperm. Lateral field 6 µm wide, areolated opposite oesophageal region; inner two lines end on tail in a y-shaped pattern. Phasmids located three annuli anterior to anus. Tail 22 µm long, with thirteen ventral annuli, tail rounded asymmetrically, with an annulated rounded ventral projection.

Male: Not found.

Remarks

H. hydrophilus can be separated from *H. erythrinae* by the longer female stylet, usually hemispherical digitate projection of the female tail and often shorter tail according to Sher (1966). The present specimen is regarded as *H. hydrophilus* because of longer body length (890 µm), stylet length (30 µm), tail length (22 µm) and rounded annulated ventral projection. The specimen corresponds well with description of the type specimens by Sher (1966).

***Helicotylenchus indicus* Siddiqi, 1963** (Fig. 16, 26)

= *Helicotylenchus microdorus* Prasad, Khan & Chawla, 1965

This species was described from *Cynodon dactylon* (L.) Pers. from Aligarh, India and was subsequently reported from the:

Afrotropical Region

Côte d'Ivoire (Plowright & Hunt, 1994) and South Africa (Kleynhans *et al.*, 1996).

Australian Region

Fiji (Van den Berg & Kirby, 1979), Samoa (Orton Williams, 1980) and Tonga (Orton Williams, 1980).

Oriental Region

Oman (Mani *et al.*, 1998), Pakistan (Fotedar & Kaul, 1985) and Thailand (Boonduang & Pliansinchai, 1980).

Measurements

See Table 14.

Description

Female (n = 51): Habitus straight (2 %), C-shaped (55 %) or spiral (43 %). Lip region 4 ± 0.6 (3-5) µm high and 7 ± 1.2 (6-10) µm wide, anteriorly flattened truncate with five to seven annuli. Labial disc oval in *en face* view. Outer margins of labial framework extend 3 ± 0.4 (2-4) µm backward from basal plate. Cephalids not seen. Stylet knobs 2 ± 0.5 (2-4) µm high and 5 ± 0.6 (3-6) µm wide; anterior faces flattened (53 %) or indented (47 %). Median bulb oval, 13 ± 1.2 (10-16) µm long and 9 ± 1.2 (7-12) µm wide; valve 5 ± 0.5 (5-6) µm long and 4 µm wide. Position of DGO 9 ± 1.3 (7-12) µm behind stylet knobs. Length of oesophagus 116 ± 21.0 (89-151) µm, with length to end of glands 128 ± 13.1 (102-157) µm. Oesophagus with 11 ± 4.1 (6-18) µm long

ventral overlap. Excretory pore 99 ± 9.1 (79-117) µm from front, i.e. at 18 ± 1.6 (14-22) % of body length. Hemizonid two to three annuli long, located one to seven annuli anterior to excretory pore (*n* = *6*). Hemizonion one annulus long, located nine annuli posterior to excretory pore (*n* = *1*). Fasciculi not seen. Width of annuli at midbody 1.2 ± 0.3 (0.7-1.8) µm. Body width at excretory pore 20 ± 2.7 (16-27) µm, midbody 23 ± 3.2 (18-32) µm and at anus 13 ± 1.2 (10-15) µm. Two branches of reproductive system both functional, length of posterior branch 57 ± 9.4 (49-67) % of corresponding anterior branch length; anterior branch 138 ± 16.8 (116-161) µm and posterior branch 81 ± 6.0 (74-85) µm long. Spermatheca rounded, thick-walled offset and empty in all specimens except for six specimens from Jessievale Plantation, Mpumalanga Province. Epiptygma folded into vagina. Lateral field 5 ± 0.8 (4-7) µm wide, crenate on tail; inner two lines end on tail in a v- (25 %), y- (15 %), u- (39 %) or m-shaped (21 %) pattern. Phasmids located two to eleven annuli posterior to anus. Tail 23 ± 3.0 (17-28) µm long, more curved dorsally, dorsal side joins the ventral side at an angle, with ten to twenty-one ventral annuli.

Male (n = 1): Habitus C-shaped. Lip region 5 µm high and 6 µm wide, flattened and truncate, with six annuli. Outer margins of labial framework extend 3 µm backward from basal plate. Stylet knobs 2 µm high and 3 µm wide, anterior face flattened. Length of oesophagus 104 µm, with length to end of oesophagus 134 µm. Oesophagus with 30 µm long ventral overlap. Excretory pore 87 µm from front, i.e. at 16 % of body length. Hemizonid and hemizonion not seen. Width of annulus at midbody 1.1 µm. Body width at excretory pore 15 µm, at midbody 19 µm and at cloaca 11 µm. Lateral field 5 µm wide, areolated in region of bursa. Phasmids located less than one body width posterior to cloaca. Bursa extending to tip of tail. Tail 21 µm long with a pointed finger-like, ventrad curved projection.

Remarks

The present specimens were identified as *H. indicus* because of the large median bulb valve (5 µm long and 4 µm wide), body length (mean value: 557 µm), truncate lip shape, position of vulva (mean V value: 65 %) and post-anal position of phasmids. The South African specimens were compared to specimens from India, Oman and Pakistan deposited in the USDA Nematode Collection. The same large median bulb valve was seen in these specimens. The present specimens agree with descriptions of *H. indicus* from India, Fiji, Pakistan and Thailand (Sher, 1966; Van den Berg & Kirby, 1979; Fotedar & Kaul, 1985; Mizukubo *et al.,* 1992). The lower range for c-value (21.2) is slightly less than the previously reported 22 (Chaturvedi & Khera, 1979). The upper range for stylet length (30 µm) exceeds the previous upper range of 29 µm (Marais, 1998). The mean stylet length (27 µm) also exceeds the 22.1 µm reported by Mizukubo *et al.* (1992). V value showed the least variance with a CV of 3 %; the highest range (70 %) exceeds the highest value (67 %) reported by Chaturvedi & Khera (1979).

In his revision of *Helicotylenchus* Sher (1966) synonymized *H. insignis* and *H. plumariae* with *H. indicus,* but the two species were reinstated by Shamsi (1979). *H. microdorus* and *H. thornei* were made synonyms of *H. indicus* by Nandakumar & Khera (1970). Boag & Jairajpuri (1985) accepted this synonymy. According to Siddiqi (1986) *H. microcodrus* is a probable synonym of *H. indicus,* but *H. thornei* is a valid species. Ebsary (1991) accepted this point of view. According to Marais (1993) no comment can be made on the synonymy of these species since none of the paratypes of these species were available for study. Lal & Khan (1993) proposed *H. insignis, H. plumariae, H. teres, H. hazratbalensis, H. macronatus* and *H. persici* as junior synonyms of *H. indicus* on the grounds of morphometric variations. Lal & Khan (1993) stated "all these species are considered as synonyms of *H. indicus* as these seem to be the geographical variants of *H. indicus*". The paratype material or previously identified material was not available for study for most of these species. A study of *H. macronatus* material

deposited in the USDA collection showed a median bulb valve 3 µm long and 2 µm wide, markedly smaller than the 5 µm and 4 µm of *H. indicus*. I therefore consider *H. macronatus* as a valid species. No confirmation can be made on the synonymy of the other species, as none of the paratype material was available for study.

***Helicotylenchus kermarreci* Marais, Van den Berg, Quénéhervé & Tiedt, 2000**

(Fig. 26, 27)

Helicotylenchus kermarreci was described from *Cocos nucifera* L., Ilet à Caret, the Guadeloupe islands, and is only known from this locality.

Measurements

See Table 14.

Description

Females (n = 11): Habitus straight (18 %) to C-shaped (82 %). Lip region 3 ± 0.3 (3-4) µm high and 8 ± 0.8 (7-8) µm wide, anteriorly rounded, not set off, with three to four annuli, the second annulus markedly wider than others. Labial disc oval in *en face* view. Outer margins of labial framework extend 3 µm backward from basal plate. Cephalids not seen. Stylet knobs 2 µm high and 4 ± 0.5 (4-5) µm wide; anterior faces flattened (27 %) or slightly inclined backwards (73 %). Position of DGO 8 ± 1.0 (6-9) µm behind stylet knobs. Median bulb oval, 12 ± 0.7 (11-13) µm long and 8 ± 0.8 (7-9) µm wide; valve 4 µm long and 3 µm wide. Length of oesophagus 132 ± 15.3 (109-153) µm, with length to end of glands 147 ± 7.8 (138-164) µm. Ventral overlap of oesophageal lobe 16 ± 9.6 (6-30) µm long. Excretory pore 99 ± 3.1 (95-105) µm from front, i.e. at 16 ± 1.5 (14-19) % of body length. Hemizonid two annuli long, located one to two annuli anterior to excretory pore (*n* = 9). Hemizonion not seen. Fasciculi not

seen. Width of annuli at midbody 1.8 ± 0.3 (1.4-2.1) µm. Body width at excretory pore 18 ± 1.3 (15-19) µm, at midbody 20 ± 2.6 (17-24) µm and at anus 14 ± 1.3 (11-16) µm. Two branches of reproductive system both functional, length of posterior branch 101 ± 11.9 (86-156) % of corresponding anterior branch length; anterior branch 106 ± 23.1 (85-159) µm and posterior branch 101 ± 26.2 (74-156) µm long. Spermatheca axial and filled with round sperm. Epiptygma folded into the vagina. Lateral field 4 ± 0.3 (4-5) µm wide; inner two lines end on tail in a v- (10 %), y- (50 %) or µ-shaped pattern (40 %). Rectum does not overlap anus. Phasmids located from two to seven annuli anterior to anus. Caudalid not seen. Tail 16 ± 2.9 (10-19) µm long, with seven to twelve annuli, dorsal side slightly flattened.

Males (n = 8): Habitus straight. Lip region 4 ± 0.2 (3-4) µm high and 6 ± 0.4 (6-7) µm wide, anteriorly rounded, with three to four annuli, second lip annulus markedly wider than others. Stylet knobs 2 ± 0.3 (1-2) µm high and 4 ± 0.6 (3-5) µm wide; anterior faces flattened (13 %) or indented (87 %). Length of oesophagus 129 ± 16.8 (111-144) µm, with length to end of glands 146 ± 5.2 (138-152) µm. Ventral overlap of oesophageal lobes 16 ± 10. (8-27) µm long. Excretory pore 95 ± 3.0 (90-99) µm from front, i.e. at 17 ± 1.1 (16-18) % of body length. Body width at excretory pore 16 ± 1.3 (14-17) µm at midbody 17 ± 1.4 (5-19) µm and at cloaca 12 ± 0.7 (11-13) µm. Hemizonid two annuli long, located one to three annuli anterior to excretory pore (*n = 3*). Hemizonion not seen. Lateral field 4 ± 0.3 (4-5) µm wide, areolated opposite oesophagus and bursa. Phasmids located one body-width anterior to cloaca. Tail 17 ± 1.9 (15-19) µm long.

Remarks

Marais *et al.* (2000) characterised *H. kermarreci* by stylet length (20-22 µm in females and 17-19 µm in males), second lip annulus markedly broader than other lip annulus in both sexes, female tail dorsally flattened and spicule length (18-20 µm). *H.*

kermarreci was separated from *H. concavus* and *H. depressus* the only other species with dorsally flattened female tails by stylet length, position of excretory pore, oesophagus length and position of phasmids in females. Although several species have stylets shorter than 23 µm, only four (*H. mundus, H. nitens, H. sandersae* and *H. vindex*) are similar in the position of the vulva, the shape of the lip region and the presence of males. *H. kermarreci* differs from *H. minutus, H. nitens, H. sandersae* and *H. vindex* in body length, c- and c'-value, oesophagus length, position of excretory pore from front or tail shape in females (Marais *et* al., 2000).

***Helicotylenchus macrostylus* Marais & Quénéhervé, 1996** (Fig. 15, 28)

Helicotylenchus macrostylus was described from the rhizosphere of *Dicorynia guianensis* Amshoff seedlings in a primary tropical rainforest near Paracou, French Guiana and also reported from *Eperua grandiflora* (Aubl.) Betham seedlings near Paracou, French Guiana (Marais & Quénéhervé, 1996).

Measurements

See Table 14.

Description

Female (n = 24): Habitus C-shaped (38 %) to spiral (62 %). Lip region 5 ± 0.5 (4-6) µm high and 9 ± 0.7 (8-10) µm, anteriorly flattened, with seven to eight annuli. Labial disc rounded in *en face* view. Outer margins of labial framework extend 4 µm backward from basal plate. Cephalids not seen. Stylet knobs 4 ± 0.6 (3-5) µm high and 8 ± 0.8 (7-10) µm wide; anterior face flattened (35 %) or indented (65 %). Position of DGO 18 ± 1.8 (14-20) µm behind stylet knobs. Medium bulb oval to rounded, 16 ± 1.3 (13-18) µm long and 11 ± 1.5 (7-13) µm wide; valve 4 µm long and 3 µm wide. Length

of oesophagus 213 ± 20.8 (189-262) µm, with length to end of glands 220 ± 15.4 (200-269) µm. Oesophagus with 11 ± 8.4 (5-24) µm long ventral overlap. Excretory pore 192 ± 7.0 (179-211) µm from front, i.e. at 19 ± 0.7 (17-20) % of body length. Hemizonid two to three annuli long, located seven to nineteen annuli anterior to excretory pore (*n* = *8*). Hemizonion not seen. Fasciculi not seen. Width of annulus at midbody 2.0 ± 0.4 (1.4-2.9) µm. Body width at excretory pore 26 ± 2.5 (21-32) µm, at midbody 42 ± 4.4 (35-50) µm and at anus 25 ± 2.2 (21-29) µm. Two branches of reproductive system both functional, length of posterior branch 92 ± 7.5 (80-99) % of corresponding anterior branch length; anterior branch 230 ± 86.2 (161-379) µm and posterior branch 206 ± 79.5 (145-365) µm long, posterior branch reflexed in two specimens. Spermatheca oval to round, filled sperm. Epiptygma folded into vagina. Lateral field 9 ± 1.1 (8-1) µm wide; outer two lines crenate on tail in one specimen; inner two lines end on tail in a u- (17 %), µ- (17 %) or m-shaped (66 %) pattern. Rectum does not overlap anus. Phasmids located five annuli posterior to four annuli anterior to anus; position of phasmid in lateral field variable. Tail 19 ± 3.2 (13-24) µm long, shape varying from asymmetrical with rounded end to often having a small ventral projection; with seven to eleven ventral tail annuli.

Male (n = 15): Habitus C-shaped (80 %) to spiral (20 %). Lip region 5 ± 0.4 (4-5) µm high and 8 ± 0.5 (7-9) µm wide, anteriorly flattened with six to seven annuli. Labial disc oval in *en face* view. Stylet knobs 3 ± 0.4 (2-3) µm high and 5 ± 0.4 (5-6) µm wide; anterior faces indented. Position of DGO 15 ± 1.4 (13-17) µm behind stylet knobs. Length of oesophagus 159 ± 10.0 (148-166) µm, with length to end of glands 178 ± 8.8 (163-198) µm. Oesophagus with 21 ± 10.0 (12-32) µm long ventral overlap. Excretory pore 150 ± 5.3 (140-161) µm from front, i.e. at 17 ± 0.7 (16-18) % of body length. Hemizonid two to three annuli long, located five to eleven annuli anterior to excretory pore (*n* = *7*). Hemizonion one annulus long, located from one annulus anterior to five annuli posterior to excretory pore (*n* = *2*). Width of annulus at midbody 1.8 ± 2.2 (1.4-

2.2) µm. Body width at excretory pore 21 ± 1.3 (18-23) µm, at midbody 28 ± 2.4 (23-33) µm and at cloaca 19 ± 1.2 (16-20) µm. Lateral field 6 ± 0.8 (5-8) µm wide, areolated opposite bursa. Phasmids located one cloacal body-width anterior to cloaca. Tail 23 ± 2.3 (20-27) µm long, with a finger-like tip observed in one specimen.

Remarks

H. macrostylus was characterized by body length (mean value: 1020 µm for females and 873 µm for males), stylet length (mean value: 43 and 34 µm for females and males respectively), tail length (mean value: 19 µm for females and 22 µm for males) and position of excretory pore (mean value: 192 and 150 µm for females and males respectively) and presence of males (Marais & Quénéhervé, 1996). *H. macrostylus* was separated from *H. coomansi* because *H. coomansi* had the longest stylet (36-42 µm) of all described *Helicotylenchus* species.

***Helicotylenchus marethae* n.sp.** (Fig. 29)

= *H. labiodiscinus* Sher, 1966 *apud* Marais, 1993

Measurements

See Table 15.

Description

Female (n = 9): Habitus spiral. Lip region 4 ± 0.4 (3-4) µm high and 6 ± 0.9 (4-7) µm wide, conically flattened, not set off, without annuli. Outer margins of labial framework extend 3 ± 0.6 (2-4) µm backward from basal plate. Cephalids not seen. Stylet knobs 2 ± 0.2 (2-3) µm high and 4 ± 0.5 (4-5) µm wide; anterior faces flattened (60 %) or indented (40 %). Position of DGO 9 ± 0.5 (8-9) µm behind stylet knobs. Median bulb shape varying from nearly round to oval, 11 ± 1.4 (9-13) µm long and 8 ±

1.0 (7-9) µm wide; valve 3 µm long and 2 ± 0.5 (2-3) µm wide. Length of oesophagus 107 µm long (*n* = *1*), with length to end of glands 118 ± 4.4 (110-125) µm. Oesophagus with 7 µm long ventral overlap. Excretory pore 100 ± 3.4 (96-106) µm from anterior end, i.e. at 18 ± 1.0 (16-19) % of body length. Hemizonid and hemizonion not seen. Fasciculi present in all specimens. Width of annuli at midbody 1.2 ± 0.1 (1.1-1.5) µm. Body width at excretory pore 18 ± 3.3 (12-20) µm, at midbody 24 ± 3.5 (18-28) µm and at anus 14 ± 1.6 (12-17) µm. Spermatheca rounded, thick walled and empty. Lateral field 5 ± 1.3 (4-7) µm wide; outer lines areolated opposite oesophageal region and also incompletely areolated on tail in some specimens; inner two lines end on tail in an u- (75 %) or m-shaped (25 %) pattern. Epiptygma folded into vagina. Rectum does not overlap anus. Phasmids large 2 µm in diameter, i.e. more than the width of the corresponding ventral tail annuli, located in middle of lateral field, three to ten annuli posterior to anus. Tail 19 ± 2.7 (15-22) µm long, with 13 to 19 ventral tail annuli, more curved dorsally, with rounded end.

Male: Not found.

Diagnosis

Helicotylenchus marethae n.sp. is characterised by the presence of a large phasmid (2 µm in diameter), presence of fasciculi and anteriorly flattened conical lip region without any annuli.

Relationship

Helicotylenchus marethae most closely resembles *H. canalis, H. martini, H. paracanalis* and *H. silvicola,* because of the presence of fasciculi. *H. marethae* can be separated from the type population of *H. canalis* by absence of lip annuli, body length (526-642 *vs* 670-900 µm), stylet length (24-27 *vs* 32-36 µm), shape of lip region (conically flattened *vs* hemispherical), tail shape (more curved dorsally, with rounded

end *vs* more curved dorsally, with annulated rounded or pointed ventral projection) and position of phasmid (three to ten annuli posterior to anus *vs* two to eight annuli anterior to anus). The new species further differs from a South African population of *H. canalis* (Van den Berg & Heyns, 1975) in oesophagus length (107 *vs* 132-171 µm), position of excretory pore from front (96-106 *vs* 121-143 µm), body width at midbody (18-28 *vs* 31-44 µm) and size of phasmid (2 µm, double the size of the corresponding ventral tail annuli *vs* 0.7-0.9 µm, smaller than the width of the corresponding ventral tail annuli). The new species can be distinguished from *H. martini* (according to Marais, 1998) in absence of males, mean c-value (30.2 *vs* 25.1), mean V-value (59 *vs* 57 %), mean tail length (19 *vs* 25 µm), tail shape (with annuli around tail tip *vs* not annulated around tail tip) and size of phasmid (2 µm, double the size of the corresponding ventral tail annulus *vs* 0.8-1.1 µm in diameter, i.e. the same size as the corresponding ventral tail annuli). It can be separated from the type material of *H. paracanalis* in absence of males and lip annuli, mean body length (569 *vs* 740 µm), mean c-value (30.2 *vs* 51), stylet length (24-27 *vs* 31-37 µm) and shape of lip region (conically flattened *vs* hemispherical) (Sauer & Winoto, 1975). It can also be separated from a South African population of *H. paracanalis* (Marais, 1998) in c'-value (1.1-1.6 *vs* 0.5-1.0), mean V-value (59 *vs* 63 %), position of excretory pore from front (96-106 *vs* 119-142 µm), position of phasmid (three to ten annuli posterior to anus *vs* one to six annuli anterior to anus), number of ventral tail annuli (13-19 *vs* 5-11) and size of phasmid (2 µm, double the size of the corresponding ventral tail annulus *vs* 0.6-1.1 µm, smaller than the width of the corresponding ventral tail annuli). From *H. silvicola* it can be separated by absence of males and lip annuli, and therefore the absence of a undivided first lip annulus *vs* first lip annulus divided into six sectors), mean body length (569 *vs* 675 µm), c-value (25.3-39.7 *vs* 42.1-79.6), mean V-value (59 *vs* 62 µm), stylet length (24-27 *vs* 29-32 µm), mean tail length (19 *vs* 12 µm) and size of phasmid (2 µm, double the size of the corresponding ventral tail annulus *vs* 0.7-1.1 µm, smaller

than the width of the corresponding ventral tail annuli, 1.1-1.4 µm).

Type host and locality

Collected among grasses in the Loteni Nature Reserve of the uKhahlamba-Drakensberg Park, Kwazulu-Natal, South Africa, on 28 December 1978 by E. van den Berg.

Type material

Holotype female (slide number 15650), nine female paratypes (slide number 15646-15647, 15650) deposited in the National Collection of Nematodes, ARC-Plant Protection Research Institute, Pretoria, South Africa.

Etymology

The species is named after Maretha Vermaak RD(SA) in recognition of her invaluable help and assistance.

***Helicotylenchus martini* Sher, 1966** (Fig. 14, 29)

= *Helicotylenchus krugeri* Van den Berg & Heyns, 1975

H. martini was described from soil around tea [*Camellia sinensis* (L.) Kuntze] Chipinge, Zimbabwe by Sher (1966) and since reported from two biogeographical regions, viz.:

Afrotropical Region

Democratic Republic of the Congo (Ali *et al.,* 1973) and South Africa (Marais, 1998).

Palaearctic Region

Georgia (Bagatyriya, 1971).

Measurements

See Table 15.

Description

Female (n = 138): Habitus C-shaped (7 %) to spiral (93 %). Lip region 4 ± 0.6 (3-6) µm high and 7 ± 0.9 (5-10) µm wide, truncate, not offset, without annuli. Labial disc oval to rectangular in *en face* view. Outer margins of labial framework extend 3 ± 0.4 (2-4) µm backward from basal plate. Anterior cephalids three to four annuli anterior to basal plate, posterior cephalids four to five annuli posterior to anterior cephalids. Stylet knobs 2 ± 0.4 (1-3) µm high and 5 ± 0.6 (3-6) µm wide; anterior faces rounded (5 %), flattened (58 %), indented (19 %) or flattened and slightly inclined backwards (18 %). Position of DGO 9 ± 1.6 (6-13) µm behind stylet knobs. Median bulb oval, 12 ± 1.1 (10-15) µm long and 8 ± 1.2 (6-11) µm wide, valve 3 ± 0.5 (2-4) µm long and 2 ± 0.4 (2-3) µm wide. Length of oesophagus 131 ± 24.6 (91-176) µm, with length to end of gland 152 ± 32.4 (105-259) µm. Oesophagus with 19 ± 11.0 (7-48) µm long ventral, dorsal or dorso-lateral overlap. Hemizonid two to three annuli long, located one to three annuli anterior to excretory pore (*n = 35*). Hemizonion one annulus long, located six to twelve annuli posterior to excretory pore (*n = 15*). Fasciculi present. Width of annulus at midbody 1.3 ± 0.3 (0.7-2.1) µm. Body width at excretory 18 ± 2.4 (13-23) µm, at midbody 23 ± 2.8 (16-30) µm and at anus 13 ± 1.3 (13-21) µm. Two branches of the reproductive system both functional, length of posterior branch 92 ± 21.3 (50-159) % of corresponding anterior branch length; anterior branch 133 ± 34.7 (71-203) µm and posterior branch 122 ± 26.9 (85-185) µm long. In a number of specimens from Tarkastad, Eastern Cape Province, more than one functional spermatheca was seen in a reproductive branch. Epiptygma folded into vagina. Lateral field 6 ± 0.9 (4-8) µm wide; outer two lines areolated posterior to vulva and on tail in some specimens; inner

two lines end on tail in a v- (5 %), y- (15 %), u- (72 %), m- (5 %) or open m-shaped (3 %) pattern. Phasmids located two to fourteen annuli posterior to anus. Caudalid not seen. Tail 24 ± 4.9 (14-40) µm long, rounded without ventral projection, tip annulation variable from absent to partially annulated, with seven to nineteen ventral annuli.

Male (n = 22): Habitus straight (22 %), C-shaped (55 %) to spiral (23 %). Lip region 5 ± 0.7 (4-6) µm high and 6 ± 0.6 (5-7) µm wide, truncate, not offset, without annuli. Outer limits of labial framework extend 2 µm backward from basal plate. Stylet knobs 2 ± 0.3 (1-2) µm high and 3 ± 0.7 (2-4) µm wide, anterior face flattened (57 %) or indented (43 %). Position of DGO 9 ± 0.9 (9-11) µm behind stylet knobs. Length of oesophagus 116 ± 20.3 (102-130) µm, with length to end of glands 126 ± 11.3 (109-142) µm. Oesophagus with 12 ± 4.6 (7-18) µm long ventral overlap. Excretory pore 102 ± 8.8 (85-115) µm from front, i.e. at 17 ± 2.1 (15-24) % of body length. Body width at excretory pore 15 ± 2.2 (11-18) µm, at midbody 18 ± 3.1 (13-25) µm and at cloaca 12 ± 1.8 (9-17) µm. Hemizonid two to three annuli long, located one to three annuli anterior to excretory pore (*n = 6*). Hemizonion not seen. Lateral field 5 ± 0.8 (4-6) µm wide, areolated opposite oesophagus and bursa. Phasmids located one to one and a half cloacal body width posterior to cloaca. Tail 21 ± 3.7 (16-30) µm long, with a pointed finger-like, ventrad curved projection.

Remarks

The present specimens were identified as *H. martini* because of truncate lip region, absence of lip annuli, long tail (mean value: 24 µm), and conspicuous phasmids near centre of tail. These specimens agree with the original and subsequent descriptions from South Africa (Van den Berg & Heyns, 1975; Van den Berg, 1976; Marais, 1993, 1998). *H. krugeri* was synonymized with *H. martini* by Marais (1998) after examination of previously identified *H. martini* and *H. krugeri* populations (Van den Berg & Heyns, 1975; Van den Berg, 1976; Marais, 1993; Marais & Buckley, 1992;

Kleynhans *et al.,* 1996; Marais & Swart, 1996; Marais & Van den Berg, 1996). It was concluded that the characteristics used to distinguish between these two species are highly variable. The morphometric characters of *H. martini* and *H. krugeri* agree and the species were also sympatric.

***Helicotylenchus microcephalus* Sher, 1966** (Fig. 6, 18)

= *Helicotylenchus mangiferensis* Elmiligy, 1970

= *Helicotylenchus belurensis* Singh & Khera, 1980

The species was described from oil palm (*Elaeis guineensis* Jacq.), Otubu Village, Benin Province, Nigeria (Sher, 1966) and since reported from a number of countries in five of the biogeographical regions, viz.:

Afrotropical Region

Cameroon (Bridge *et al.,* 1995), Côte d'Ivoire (Plowright & Hunt, 1994), Kenya (Sharma *et al.,* 1993), Madagascar (Luc, 1959), Malawi (Mughogho & Choo, 1969), Mozambique (Van den Oever *et al.,* 1998), South Africa (Kleynhans *et al.*, 1996) and Sudan (Zeidan & Geraert, 1990).

Australian Region

Fiji (Van den Berg & Kirby, 1979), Samoa (Orton Williams, 1980) and Tonga (Orton Williams, 1980).

Neotropical Region

Belize (Bridge *et al.,* 1996), Brazil (Costa Manso *et al.,* 1994), Cuba (Scliephake, 1985), Guadeloupe islands (Marais *et al.,* 2000) and Trinidad (Bala, 1984).

Oriental Region

India (Baqri & Ahmad, 1983), Jordan (Hashim, 1985) and Thailand (Ratanaprapa & Boonduang, 1975).

Palaearctic Region

Egypt (Elmiligy, 1970) and Spain (Romera & Arias, 1969).

Measurements

See Table 15.

Description

Female (n = 53): Habitus C-shaped (6 %) to spiral (94 %). Lip region 4 ± 0.4 (3-5) µm high and 6 ± 1.0 (5-9) µm wide; conical truncate not set off, with four to six annuli. Labial rounded in *en face* view. Outer margins of labial framework extend 2 ± 0.2 (2-3) µm backward from basal plate. Cephalids not seen. Stylet knobs 2 ± 0.4 (1-3) µm high and 5 ± 0.9 (3-8) µm wide; anterior faces rounded (14 %), flattened (50 %) or indented (36 %). Median bulb oval, 12 ± 1.1 (10-14) long and 9 ± 1.1 (7-12) µm wide; valve 3 µm long and 2 ± 0.3 (2-3) µm wide. Length of oesophagus 107 ± 7.7 (95-115) µm, with length to end of glands 127 ± 14.7 (99-161) µm. Oesophagus with 23 ± 7.1 (15-36) µm ventral or dorsal overlap. Excretory pore 96 ± 11.9 (69-120) µm from front, i.e. 17 ± 1.9 (12-23) % of body length. Hemizonid two to three annuli long, located from one to nine annuli anterior to excretory pore (*n = 23*). Hemizonion one annulus long, located nine to fourteen annuli posterior to anus (*n = 10*). Fasciculi not seen. Width of annulus at midbody 1.2 ± 0.3 (0.7-1.8) µm. Body width at excretory pore 18 ± 3.3 (13-29) µm, at midbody 22 ± 3.9 (12-29) µm and at anus 12 ± 1.7 (9-16) µm. Two branches of the reproductive system both functional, length of posterior branch 90 ± 15.0 (65-118) % of corresponding anterior branch length; anterior branch 127 ± 19.4 (84-157) µm and posterior branch 110 ± 16.0 (83-128) µm long. Spermatheca set off, empty. Epiptygma folded into vagina. Lateral field 5 ± 0.9 (3-7) µm wide; outer two lines crenated posterior to vulva; inner two lines end on tail in a v- (14 %), y- (71 %), u- (10 %) or m-shaped (5 %) pattern. Phasmids located one annulus posterior to nine annuli anterior to anus. Tail 16 ± 2.7 (13-23) µm long, with seven to seventeen ventral annuli;

tail with small ventral projection, mostly pointed, mucro seen in some specimens from Guadeloupe.

Male: Not found.

Remarks

The specimens are regarded as *H. microcephalus* because of mostly spiral habitus, conical, and anteriorly flattened lip region, stylet length (mean value: 24 µm), position of vulva (mean V value 62 %), tail with small ventral projection and absence of males. The specimens agree with the description of the paratype material (Sher, 1966) as well as with material from South Africa (Van den Berg & Heyns, 1975; Van den Berg, 1978; Marais & Buckley, 1992). The lower range for body length (429 µm) is less than the previously recorded 555 µm (Zeidan & Geraert, 1990). The lower range for DGO (8 µm) is also less than the 8.8 µm recorded by Van en Berg & Kirby (1979). A study of all the characters of the present specimens confirms the synonymization of *H. mangiferensis* and *H. belurensis* with *H. microcephalus* by Ali (1976) and Baqri & Ahmad (1983). Lal & Khan (1993) synonymized *H. magnicephalus* with *H. microcephalus* on the ground of similarities in height of lip region, lip annulation, fusion of the inner lines of the lateral field, stylet knobs and tail shape. According to the description of *H. magnicephalus* by Phukan & Sanwal (1981) the lip region is high, conoid, slightly truncate and without annulation. Lal & Khan (1993) however, did not recognise absence of lip annuli as a valid character. I have found the presence or absence of lip annuli a reliable and constant character in the genus *Helicotylenchus*. A study of *H. microcephalus* specimens from the French Caribbean and southern Africa (South Africa, Mozambique and Malawi) constantly showed lip annuli to be present. I therefore reinstate *H. magnicephalus* as a valid species.

***Helicotylenchus minutus* Van den Berg & Cadet, 1991** (Fig. 30)

The species was described from Mount Pelee, Martinique and is known only from its type locality (Van den Berg & Cadet, 1991).

Measurements

See Table 16.

Description

Female (n = 4): Habitus C-shaped (75 %) to spiral (25 %). Lip region 2 µm high and 6 µm wide, anteriorly rounded with four annuli. Outer margins of labial framework extend 2 (1-2) µm backward from basal plate. Anterior cephalids located three annuli posterior from basal plate, posterior cephalids located eight to twelve annuli posterior from basal plate. Stylet knobs 2 (1-2) µm high and 4 ± 0.4 (4-5) µm wide; anterior faces flattened (25 %) or indented (75 %). Medium bulb oval, 10 (9-11) µm long and 7 (6-7) µm wide; valve 3 (2-3) long and 2 µm wide. Oesophagus length 108 µm, with length to end glands 112 (92-125). Excretory pore 71 (65-76) µm from front, i.e. at 19 (18-20) % of body length. Hemizonid two annuli long, located from opposite to two annuli anterior to excretory pore. Hemizonion not seen. Fasciculi not seen. Width of annulus at midbody 1.4 µm. Body width at excretory pore 13 (11-13) µm, at midbody 14 µm ant at anus 10 (8-11) µm. Two branches of reproductive system both functional, length of posterior branch 56 (51-61) % of corresponding anterior branch length; anterior branch 96 (87-100) µm and posterior branch 54 (52-58) µm long. Spermatheca axial and filled with sperm. Epiptygma folded into vagina. Lateral field 3 (2-4) µm wide; ending of lateral field difficult to discern. Phasmids located two to six annuli anterior to anus. Tail 17 (16-18) µm long, with ten to thirteen ventral annuli, with a annulated, pointed ventral projection sometimes with mucro.

Males (n = 2): Habitus C-shaped. Lip region 2-3 µm high and 5-6 µm wide,

anteriorly rounded. Stylet knobs 1 µm high and 3-4 µm wide; anterior faces flattened. Length of oesophagus to end of glands 103 µm. Excretory pore 66-68 µm from front, i.e. at 19 % of body length. Hemizonid two annuli long, located one annulus anterior to excretory pore. Body width at excretory pore 11 µm and at cloaca 9 µm. Phasmids located less than one cloacal body width anterior to cloaca.

Remarks

Van den Berg & Cadet (1991) characterized *H. minutus* by a tail shape not commonly found in *Helicotylenchus*, the female having a long, irregular ventral tail projection with a finely rounded terminus with a single sharp pointed mucro and the male tail ending peg-like with a finely rounded terminus also with a mucro; small size of females and males; a slightly more posteriorly located vulva than which is normally found; a low broadly rounded lip region and a long oesophagus resulting in a low b value in both sexes.

***Helicotylenchus minzi* Sher, 1966** (Fig. 30, 31)

= *H. digonicus apud* Marais, 1993 populations KP1149, N249, N276, TVL779

H. minzi was described from citrus (*Citrus* sp.) at Kabri, Israel (Sher, 1966) and since reported from four of the biogeographical regions, viz:

Afrotropical Region

Mozambique (own record) and South Africa (Kleynhans *et al.*, 1996).

Australian Region

New Zealand (Wouts & Yeates, 1994).

Oriental Region

China (Zhang *et al.*, 1998) and India (Fotedar & Kaul, 1985).

Palaearctic Region

Bulgaria (Katalan-Gateva, 1980), Georgia (Bagatyriya, 1971) and Hungary (Andrássy, 1973).

Measurements

See Table 16.

Description

Female (n = 86): Habitus C-shaped (23 %) to spiral (77 %). Lip region 4 ± 0.4 (3-5) µm high and 7 ± 0.7 (5-8) µm wide, anteriorly flattened not set off, with four to seven annuli. Labial disc oval in *en face* view. Outer margins of labial framework extend 2 µm backward from basal plate. Cephalids not seen. Stylet knobs 2 ± 0.3 (2-4) µm high and 5 ± 0.6 (3-7) µm wide; anterior faces flattened (65 %), indented (26 %) or flattened and sloping backwards (9 %). Position of DGO 7 ± 1.4 (6-12) µm behind stylet knobs. Median bulb oval, 11 ± 1.3 (8-15) µm long and 8 ± 1.3 (6-13) µm wide; valve 3 ± 0.5 (2-3) µm long and 1 ± 0.5 (1-2) µm wide. Length of oesophagus 108 ± 5.7 (86-135) µm, with length to end of glands 113 ± 13.3 (90-142) µm. Oesophagus with 11 ± 5.7 (5-25) µm long ventral overlap. Excretory 88 ± 7.3 (7.3 (74-112) µm from front, i.e. at 18 ± 1.5 (14-22) % of body length. Hemizonid two to three annuli long, located two annuli posterior to three annuli anterior to excretory pore (*n = 18*). Hemizonion one annulus long, located three annuli posterior to nine annuli posterior to excretory pore (*n = 5*). Fasciculi not seen. Width of annulus at midbody 1.3 ± 0.2 (0.9-1.8) µm. Body width at excretory pore 18 ± 2.3 (15-27) µm, at midbody 22 ± 2.6 (17-28) µm and at anus 12 ± 1.8 (10-20) µm. Two branches of reproductive system both functional, length of posterior branch 70 ± 13.2 (50-91) % of corresponding anterior branch length; anterior branch 120 ± 21.2 (92-164) µm and posterior branch 77 ± 6.4 (72-89) µm long. Spermatheca off-set, filled with sperm. Epiptygma folded into vagina. Lateral field 4 ± 0.6 (3-6) µm wide, outer two lines crenate anterior and posterior to vulva,

areolated on tail in one specimen from Berlin Plantation, Mpumalanga Province; inner two lines end on tail in a v- (5 %), y- (14 %), u- (23 %), µ- (16 %) and m-shaped (42 %) pattern. Caudalid not seen. Phasmids located one annulus posterior to eleven annuli anterior to anus. Tail 14 ± 2.5 (10-19) µm long, tail mostly bent and asymmetrical or more curved dorsally, dorsal side joins the ventral side at an angle, with six to thirteen ventral annuli.

Male (n = 25): Habitus straight (36 %) to C-shaped (64 %). Lip region 4 ± 0.9 (3-6) µm high and 6 ± 0.6 (5-7) µm wide, anteriorly flattened with five to six annuli. Outer margins of labial framework extend 2 ± 0.2 (1-2) µm backward from basal plate. Stylet knobs 2 ± 0.4 (1-2) µm high and 3 ± 0.5 (2-5) µm wide; anterior faces flattened (50 %) or indented (50 %). Position of DGO 8 ± 2.0 (5-10) µm behind stylet knobs. Length of oesophagus 119 ± 16.2 (100-129) µm, with length to end of glands 119 ± 13.8 (107-149) µm. Oesophagus with 16 ± 9.1 (8-26) µm long ventral overlap. Excretory pore 90 ± 10.6 (72-108) µm from front, i.e. at 17 ± 1.3 (15-19) % of body length. Hemizonid two annuli long, located one annulus posterior to one annulus anterior to excretory pore (*n = 4*). Hemizonion not seen. Fasciculi not seen. Width of annulus at midbody 1.4 ± 0.2 (1.1-2.0) µm. Body width at excretory pore 15 ± 2.2 (10-18) µm, at midbody 19 ± 2.7 (15-25) µm and at cloaca 11 ± 1.3 (9-13) µm. Lateral field 4 ± 0.4 (4-5) µm wide, areolated opposite oesophagus and bursa. Phasmids located less than one body width posterior to cloaca. Bursa extending to tip of tail. Tail 18 ± 2.5 (13-24) µm long, with finger-like ventrad curved tip.

Remarks

H. minzi was characterized by the stylet length (26-29 µm), spermatheca with sperm, position of phasmids (three annuli posterior to six annuli anterior to anus level) and presence of males (Sher, 1966). The present specimens were identified as *H. minzi* because of the mostly spiral habitus, stylet length (mean value: 25 µm), body

length (mean value: 499 µm), position of vulva (mean V value: 64 %), phasmids mostly anterior to anus, tail mostly bent and asymmetrical. The South African specimens agree, with a few exceptions, with the descriptions by Sher (1966) and Wouts & Yeates (1994). The lower end of the range for body length (403 µm) in females is less than the 580 µm reported by Wouts & Yeates (1994). The upper range for female tail length (19 µm) is more than the 14 µm of the paratype material. V value showed the least variation with a CV of 3 %; the lower range of 59 % equals that of Sher (1966) and the highest range (69 %) exceeds the highest value (68 %) of Wouts & Yeates (1994).

***Helicotylenchus mucronatus* Siddiqi, 1964** (Fig. 17, 32)

H. mucronatus was described from the rhizosphere of grasses Simala, Punjab State, India (Siddiqi, 1964) and since reported from the:

Afrotropical Region

Cameroon (Ali & Geraert, 1975), Côte d'Ivoire (Coyne *et al.*, 1999), Ghana (Coyne *et al.*, 1999), Kenya (Waudo *et al.*, 1998) and Sudan (Ali *et al.*, 1973).

Australian Region

Niue (Orton Williams, 1980) and Tonga (Orton Williams, 1980).

Neotropical Region

Belize (Bridge *et al.*, 1996) and Guadeloupe islands (Marais *et al.*, 2000).

Measurements

See Table 16.

Description

Female (n = 18): Habitus C-shaped (79 %) to spiral (21 %). Lip region 4 ± 0.5 (3-4) µm high and 7 ± 0.8 (6-9) µm wide, anteriorly rounded with three to four annuli.

Labial disc round in *en face* view. Outer margins of labial framework extend 2 ± 0.4 (2-3) µm backward from basal plate. Cephalids not seen. Stylet knobs 2 ± 0.4 (2-3) µm high and 5 ± 0.8(4-6) µm wide; anterior faces flattened (36 %) or indented (64 %). Position of DGO 11 ± 1.4 (9-12) µm behind stylet knobs. Median bulb oval, 12 ± 0.8 (10-13) µm long and 8 ± 1.3 (7-11) µm wide; valve 3 µm long and 2 µm wide. Length of oesophagus 107 ± 2.2 (103-110) µm, with length to end of glands 124 ± 7.8 (112-142) µm. Oesophagus with 12 ± 6.8 (8-24) µm long ventral overlap. Excretory pore 91 ± 5.4 (80-100) µm from front, i.e. at 18 ± 1.1 (16-20) % of body length. Hemizonid two to three annuli long, located opposite to two annuli anterior to excretory pore (*n = 10*). Hemizonion not seen. Width of annulus at midbody 1.6 ± 0.4 (1.1-2.2) µm. Body width at excretory pore 18 ± 2.7 (15-23) µm, at midbody 21 ± 4.9 (15-32) µm and at anus 12 ± 1.7 (10-15) µm. Two branches of reproductive system both functional, length of posterior branch 78 ± 12.7 (52-87) % of corresponding anterior branch length; anterior branch 125 ± 30.0 (92-200) µm and posterior branch 99 ± 11.5 (79-119) µm long. Spermatheca off set and filled with sperm. Epiptygma folded into vagina. Lateral field 4 ± 0.4 (4-5) µm wide; outer two lines areolated or crenate on tail; inner two lines end on tail in a y- (27 %), u- (27 %) or m-shaped (46 %) pattern. Rectum does not overlap anus. Phasmids located one to six annuli anterior to anus. Tail 18 ± 3.2 (12-23) µm long, with seven to thirteen ventral annuli, dorsally curved with a non-annulated rounded or pointed ventral projection.

Male (n =3): Habitus C-shaped. Lip region 3 µm high and 6 µm wide, anteriorly rounded with four annuli. Outer margins of labial framework extend 2 µm backward from basal plate. Stylet knobs 2 µm high and 4 µm wide; anterior face flattened (34 %) or indented (66 %). Position of DGO 8 µm behind stylet knobs. Length of oesophagus 93 (96-96) µm, with length to end of glands 112 (105-123) µm. Oesophagus with 12 (9-15) µm long ventral overlap. Excretory pore 79 (71-85) µm from front, i.e. at 18 % of body length. Hemizonid and hemizonion not seen. Width of annulus at midbody 1.4

µm. Body width at excretory pore 15 (14-15) µm, at midbody 16 (15-16) µm and at cloaca 11 µm. Lateral field 3 (3-4) µm wide, areolated anterior to and in region of bursa. Phasmid located half a body width anterior to cloaca. Tail 17 (15-18) µm long, with a finger-like annulated projection, with mucro.

Remarks

H. mucronatus is characterized by mostly C-shaped habitus, anteriorly rounded lip region, stylet length (21-26 µm), body length (mean value: 494 µm), position of vulva (mean V value: 64 %), phasmids one to six annuli anterior to anus, tail slender with rounded or pointed non-annulated ventral projection and males present. The specimens were compared with the descriptions of Siddiqi (1964) and Ali & Geraert (1975). The lowest range for body length (437 µm) is lower than the 490 µm reported by Siddiqi (1964). The range for ratio a exceed the previous lowest and highest values (17.4 *vs* 20 in Ali & Geraert, 1975 and 35.0 *vs* 28 in Siddiqi, 1964). The lower range for c-ratio (23.4) is less than the previously reported value (26 in Siddiqi, 1964). The upper range for stylet length (26 µm) is higher than the 24.5 µm reported by Ali & Geraert (1975). V value showed the least variation with a CV of 4 %, the highest range (67 %) exceed the highest value (63 %) of Siddiqi (1964).

***Helicotylenchus multicinctus* (Cobb, 1893) Golden, 1956** (Fig. 30, 33)

= *Tylenchus multicinctus* Cobb, 1893

= *Tylenchorhynchus multicinctus* (Cobb, 1893) Micoletzky, 1922

= *Anguillulina multicincta* (Cobb, 1893) Goodey, 1932

= *Rotylenchus multicinctus* (Cobb, 1893) Filip'ev, 1936

= *Rotylenchus iperoiguensis* Carvalho, 1956

= *Helicotylenchus iperoiguensis* (Carvalho, 1956) Andrássy, 1958

H. multicinctus was described from banana (*Musa* sp.), Suva, Fiji (Cobb, 1893a) and since reported from all the biogeographical regions:

Afrotropical Region

Angola (Siddiqi, 1973), Botswana (own record), Burkina Faso (Cadet, 1986), Burundi (Gatsinzi, 1991), Cameroon (Bridge *et al.*, 1995), Canary Islands (Siddiqi, 1973), Côte d'Ivoire (Sher, 1966), Democratic Republic of the Congo (Elmiligy, 1970), Ethiopia (Siddiqi, 1973), Gambia (Merny *et al.*, 1974), Ghana (Afreh-Nuamah *et al.*, 1996), Kenya (Waudo *et al.*, 1998), Liberia (Sher, 1966), Madagascar (Luc, 1959), Mauritius (Lamberti *et al.*, 1987), Mozambique (Van den Oever & Mangane, 1992), Namibia (Van den Berg & Heyns, 1975), Nigeria (Sher, 1966), Reunion (Vilardebo & Guerot, 1976), Rwanda (Gatsinzi, 1991), Sao Tome & Principe (Vovlas *et al.*, 1994), Senegal (P. Cadet, personal communication), Seychelles (Siddiqi, 1973), South Africa (Kleynhans *et al.*, 1996), Sudan (Zeidan & Geraert, 1990), Swaziland (Keetch & Buckley, 1984), Tanzania (Speijer & Bosch, 1996), Uganda (Speijer & Ssango, 1999), Zambia (Anonymous, 1974), Zanzibar (Rajab *et al.* 1999) and Zimbabwe (Martin, 1969).

Australian Region

Australia (Sher, 1966), Fiji (Cobb, 1893a), Kiribati (Orton Williams, 1980), Niue (Orton Williams, 1980), Papua New Guinea (Troccoli & Geraert, 1995), Samoa (Siddiqi, 1973) and Tonga (Orton Williams, 1980).

Nearctic Region

USA (Sher, 1966).

Neotropical Region

Argentina (Costilla *et al.*, 1979), Belize (Bridge *et al.*, 1996), Brazil (Carvalho, 1956), Colombia (Sher, 1966), Costa Rica (Sher, 1966), Cuba (Sher, 1966), Dominica (Edmunds, 1969), Dominican Republic (Sher, 1966), French Guiana (Luc & Vilardebo, 1961), Grenada (Edmunds, 1969), Guadeloupe islands (Marais *et al.*, 2000), Guatemala (Sher, 1966), Jamaica (Siddiqi, 1973), Martinique (Cadet *et al.*, 1994),

Mexico (Wehunt & Edwards, 1968), Panama (Sher, 1966), San Salvador (Sher, 1966), Suriname (Maas, 1970), St Lucia (Edmunds, 1969), St Vincent (Edmunds, 1969), Trinidad and Tobago (Bala, 1984), Union Island (own record) and Venezuela (Crozzoli *et al.*, 1998).

Oriental Region

Bangladesh (Sher, 1966), Brunei (Siddiqi, 1973), China (Yin, 1992), India (Siddiqi, 1973), Iran (Maafi & Kheiri, 1993), Israel (Sher, 1966), Jordan (Bridge, 1978), Lebanon (Sikora & Schlosser, 1973), Malaysia (Sher, 1966), Oman (Mani *et al.*, 1998), Pakistan (Khan *et al.*, 1989), Philippines (Sher, 1966), Sri Lanka (Ekanayake & Toida, 1997), Thailand (Ratanaprapa & Boonduang, 1975), Turkey (Ökten *et al.*, 2000), United Arab Emirates (Siddiqi, 1973) and Vietnam (Chau *et al.*, 1997).

Palaearctic Region

Armenia (Pogosyan, 1969), Bulgaria (Katalan-Gateva, 1980), Crete (Vovlas *et al.*, 1994), Cyprus (Philis, 1995), Egypt (Elmiligy, 1970), Georgia (Sveshnikova, 1940), Italy (Vovlas, 1983), Kazakhstan (Izatullaeva, 1969), Lithuania (Rudzyavichene & Lugauskas, 1981), Moldova (Lisetskaya, 1973), Russia (Matveeva, 1974), Tunisia (Sher, 1966), Ukraine (Kir'yanova & Krall', 1980) and Uzbekistan (Azizova & Rizaeva, 1988).

Measurements

See Table 17 and 18.

Description

(Female = 85): Habitus straight (28 %), C-shaped (37 %) or spiral (35 %). Lip region 4 ± 0.5 (3.5) µm high and 8 ± 1.0 (5-10) µm wide, anteriorly rounded, not set off with three to five annuli. Labial disc oval in *en face* view. Outer margins of labial framework extend 3 ± 0.4 (2-4) backward from basal plate. Anterior cephalids three to

four annuli posterior to basal plate, posterior cephalids six to ten annuli posterior to basal plate. Stylet knobs 2 ± 0.4 (2-4) µm high and 5 ± 0.8(3-7) µm wide; anterior faces of stylet knobs rounded (4 %), flattened (23 %) or indented (73 %). Position of DGO 9 ± 1.1 (7-12) µm behind stylet knobs. Median bulb oval, 12 ± 1.6 (9-19) µm long and 9 ± 1.0 (7-11) µm wide; valve 3 ± 0.4 (3-4) µm long and 3 µm wide. Length of oesophagus 112 ± 13.0 (92-138) µm, with length to end of glands 127 ± 11.6 (105-152) µm. Oesophagus with 13 ± 7.2 (5-27) µm long ventral overlap. Excretory pore 92 ± 10.4 (69-118) µm from front, i.e. at 17 ± 2.2 (13-24) % of body length. Hemizonid two to three annuli long, located from opposite to four annuli anterior to excretory pore (*n = 33*). Hemizonion one annulus long, located six to eight annuli posterior to excretory pore (*n = 5*). Fasciculi not seen. Width of annulus at midbody 1.4 ± 0.3 (0.7-2.2) µm. Body width at excretory pore 18 ± 2.4 (15-23) µm, at midbody 21 ± 3.8 (16-29) µm and at anus 13 ± 1.8 (10-17) µm. Two branches of reproductive system both functional, posterior branch reduced, length of posterior branch 65 ± 13.9 (31-90) % of corresponding anterior branch length; anterior branch 146 ± 35.0 (81-252) µm and posterior branch 94 ± 28.3 (58-152) µm long. Spermatheca axial, mostly filled with sperm. Epiptygma folded into vagina. Lateral field 4 ± 0.6 (4-6) µm wide; inner two lines end on tail in a v- (13 %), y- (17 %), u- (36 %), µ- (30 %) or m-shaped (8 %) pattern. Phasmids four annuli posterior to thirteen annuli anterior to anus. Tail 12 ± 2.2 (7-19) µm long, rounded to more curved dorsally, without a ventral projection, with five to fifteen ventral annuli.

Male (n = 38): Habitus straight (57 %) or C-shaped (43 %). Lip region 4 ± 0.5 (3-5) µm high and 6 ± 0.5 (5-7) µm wide, anteriorly rounded with three to five annuli. Outer margins of labial framework extend 3 ± 0.4 (2-4) µm backward from basal plate. Stylet knobs 2 ± 0.3 (1-3) µm high and 4 ± 0.4 (3-5) µm wide, anterior face of stylet knobs rounded (29 %), flattened (21 %) or indented (50 %). Position of DGO 9 ± 1.3 (4-10) µm behind stylet knobs. Length of oesophagus 117 ± 10.7 (104-133) µm, with length to

end of glands 124 ± 13.2 (100-146) µm. Oesophagus with 11 ± 2.9 (3-25) µm long ventral overlap. Excretory pore 91 ± 14.5 (65-127) µm from front, i.e. at 16 ± 1.7 (14-20) % of body length. Hemizonid one to two annuli long, located one to three annuli anterior to excretory pore (*n = 11*). Hemizonion not seen. Width of annulus at midbody 1.4 ± 0.2 (1.1-2.0) µm. Body width at excretory pore 16 ± 1.7 (13-20) µm, at midbody 18 ± 2.7 (14-25) µm and at cloaca 13 ± 2.3 (9-17) µm. Lateral field 4 ± 0.7 (3-5) µm wide; incompletely areolated anterior and opposite to bursa. Tail 18 ± 2.9 (12-24) µm long ventrad curved with rounded projection.

Remarks

The specimens were identified as *H. multicinctus* because of presence of males, C-shaped to straight habitus, stylet length (mean value: 25 µm), reduced posterior reproductive branch (31-90 % of anterior branch), position of vulva (mean V value: 68 %), phasmids located mostly anterior to anus, lip region rounded and tail rounded to more curved dorsally without a ventral projection in females. The present specimens agree with the amended descriptions of Sher (1966) and Fortuner (1991). The upper range of body length (826 µm) is more than the 710 µm reported by Vovlas (1983). The range for ratio a exceeds the previous lowest and highest values (17.7 *vs* 18.6 in Marais *et al.,* 2000 and 38.9 *vs* 35 in Fortuner, 1991). The upper range for tail length (19 µm) exceed the previous upper range of 17.3 µm (Van den Berg & Kirby, 1979). Vovlas (1983) reported a *H. multicinctus* population from Italy with a divided first lip annulus. This character was not reported in other *H. multicinctus* population (Marais & Buckley, 1992; Marais & Quénéhervé, 1999; Orion *et al.,* 1999; Marais *et al.*, 2000).

***Helicotylenchus paracanalis* Sauer &Winoto, 1975** (Fig. 34, 35)

= *Helicotylenchus trivandranus* Mohandas, 1976

H. paracanalis was described from a rainforest in Malaysia (Sauer & Winoto, 1975) and since reported from three biogeographical regions, viz.:

Afrotropical Region

Côte d'Ivoire (Fortuner *et al.*, 1981) and South Africa (Marais, 1998).

Australian Region

Fiji (Van den Berg & Kirby, 1979).

Oriental Region

India (Mohandas, 1976).

Measurements

See Table 18.

Description

Female (n = 23): Habitus C-shaped (15 %) to spiral (85 %). Lip region 5 ± 0.7 (4-6) µm high and 9 ± 0.7 (8-10) µm wide, anteriorly flattened with six to eight annuli. Labial disc round in *en face* view. Outer margins of labial framework extend 4 ± 0.6 (3-4) µm backward from basal plate. Stylet knobs 3 ± 0.5 (2-4) µm high and 7 ± 0.7 (6-8) µm wide; anterior faces flattened (48 %) or indented (52 %). Position of DGO 10 ± 0.9 (9-13) µm behind stylet knobs. Median bulb oval, 13 ± 1.3 (11-16) µm long and 10 ± 1.5 (8-13) µm wide; valve 3 ± 0.4 (3-4) µm long and 2 ± 0.3 (2-3) µm wide. Length of oesophagus 156 ± 13.6 (137-175) µm, with length to end of glands 179 ± 5.9 (162-199) µm. Oesophagus with 24 ± 14.0 (5-47) µm long ventral overlap. Excretory pore 128 ± 6.1 (119-142) µm from front, i.e. at 16 ± 1.1 (14-18) % of body length. Hemizonid two annuli long, located one to two annuli anterior to excretory pore (n = 3). Hemizonion not seen. Fasciculi seen in all the specimens. Width of annulus at midbody 1.3 ± 0.2 (1.0-1.7) µm. Body width at excretory pore 24 ± 2.3 (19-29) µm, at midbody 34 ± 5.0 (28-48) µm and at anus 21 ± 2.2 (17-25) µm. Two branches of reproductive system

both functional, length of posterior branch 98 ± 8.6 (92-108) % of corresponding anterior branch length; anterior branch 154 ± 54.0 (127-296) µm and posterior branch 139 ± 23.0 (125-166) µm long. Spermatheca axial, filled with sperm. Epiptygma folded into vagina. Lateral field 7 ± 0.8 (6-9) µm wide; outer two lines areolated posterior to vulva; inner two lines end on tail in an µ- (13 %) or m-shaped (87 %) pattern. Rectum does not overlap anus. Phasmids located one to six annuli anterior to anus. Tail 16 ± 2.1 (13-20) µm long, dorsally rounded without or with pointed projection, with five to eleven ventral tail annuli.

Male (n = 26): Habitus straight (18 %), C-shaped (61 %) to spiral (21 %). Lip region 5 ± 0.4 (4-5) µm high and 8 ± 0.5 (7-9) µm wide, anteriorly flattened with six to eight annuli. Outer margins of labial framework extend 2 ± 0.3 (1-2) µm backward from basal plate. Stylet knobs 2 ± 0.3 (2-3) µm high and 5 ± 0.5 (4-6) µm wide; anterior faces flattened (54 %) or indented (46 %). Position of DGO 9 ± 0.9 (8-11) µm behind stylet knobs. Length of oesophagus 123 ± 14.1 (103-137) µm, with length to end of glands 146 ± 10.5 (127-167) µm. Oesophagus with 23 ± 8.5 (6-34) µm long ventral overlap. Excretory pore 106 ± 8.8 (90-121) µm from front, i.e. at 14 ± 1.1 (11-16) % of body length. Hemizonid two annuli long, located three annuli anterior to excretory pore (*n = 2*). Hemizonion not seen. Width of annulus at midbody 1.4 ± 0.2 (1.0-2.1) µm. Body width at excretory pore 20 ± 2.4 (17-27) µm, at midbody 25 ± 2.4 (21-29) µm and at cloaca 15 ± 1.2 (13-17) µm. Lateral field 5 ± 0.8 (4-7) µm wide, areolated anterior to and in the region of the bursa. Phasmids located half a body-width anterior to cloaca. Tail 20 ± 2.7 (14-24) µm long, conical, with a mucro on the finger-like ventrad curved projection.

Remarks

The present specimens were identified as *H. paracanalis* because of presence of fasciculi and males, body length (668-998 µm in females and 668-840 µm in males),

stylet length (35-42 µm in females and 29-32 µm in males), position of vulva (V= 60-67 %), phasmids anterior to anus and tail dorsally rounded without or with pointed projection. Sauer & Winoto (1975) separated *H. paracanalis* from *H. canalis, H. nigeriensis* and *H. dolichodoryphorus*. The South African specimens were compared with and found similar to paratype material from Malaysia and also conforms to the original description (Sauer & Winoto, 1975) of *H. paracanalis* as well as to the subsequent descriptions by Van den Berg & Heyns (1979) and Fortuner *et al.* (1981).

***Helicotylenchus paraplatyurus* Siddiqi, 1972** (Fig. 34, 36)

This species was described from cultivated soil in Portugal (Siddiqi, 1972a) and since reported from three other biogeographical regions, viz.:

Afrotropical Region

Kenya (Sharma *et al.*, 1993), Senegal (own record) and South Africa (Kleynhans *et al.*, 1996).

Nearctic Region

USA (Wehunt *et al.*, 1991).

Oriental Region

India (Chaturvedi & Khera, 1979) and Korea (Bae & Choi, 1997).

Measurements

See Table 18.

Description

Female (n = 47). Habitus C-shaped (3 %) or spiral (97 %). Lip region 4 ± 0.5 (3-5) µm high and 7 ± 0.7 (6-9) µm wide, anteriorly rounded and not set off with four to six annuli. Labial disc oval in *en face* view. Outer margins of labial framework extend 3 ±

0.3 (2-3) µm backward from basal plate. Cephalids not seen. Stylet knobs 3 ± 0.4 (2-3) µm high and 5 ± 0.7 (4-6) µm wide; anterior faces flattened (22 %) or indented (78 %). Position of DGO 9 ± 1.5 (9-16) µm behind stylet knobs. Median bulb oval, 13 ± 1.2 (10-16) µm long and 10 ± 1.1 (7-13) µm wide; valve 3 µm long and 2 ± 0.4 (2-3) µm wide. Length of oesophagus 148 ± 19.4 (112-170) µm, with length to end of glands 153 ± 21.2 (107-192) µm. Oesophagus with 23 ± 8.8 (13-41) µm long dorsal or ventral overlap. Excretory pore 116 ± 13.2 (89-137) µm from front, i.e. at 16 ± 1.2 (14-19) % of body length. Hemizonid two to three annuli long, located one to two annuli anterior to excretory pore (*n = 11*). Hemizonion one annulus long, located eight to eleven annuli posterior to excretory pore (*n = 4*). Fasciculi not seen. Width of annulus at midbody 1.4 ± 0.2 (0.7-1.8) µm. Body width at excretory pore 21 ± 2.6 (16-30) µm, at midbody 27 ± 3.0 (22-35) µm and at anus 16 ± 1.7 (14-21) µm. Two branches of reproductive system both functional, length of posterior branch 83 ± 14.1 (58-112) % of corresponding anterior branch length; anterior branch 171 ± 34.8 (98-263) µm and posterior branch 148 ± 23.3 (114-197) µm long. Spermatheca off-set, thick walled and empty. Epiptygma folded into vagina. Lateral field 6 ± 0.8 (4-8) µm wide; outer two lines areolated posterior to vulva in some specimens; inner two lines end on tail in a v- (30 %), y- (52 %), u- (6 %) or m-shaped (12 %) pattern. Caudalid not seen. Phasmids one annulus posterior to sixteen annuli anterior to anus. Tail 16 ± 3.0 (11-23) µm long, more curved dorsally, dorsal side joining the ventral side at an angle, sometimes with a slight ventral projection, with eight to eighteen ventral annuli, posterior part of tail with a few narrow annuli.

Male: Not found.

Remarks

The present specimens were identified as *H. paraplatyurus* because of mostly spiral habitus, stylet length (25-31 µm), body length (541-959 µm), position of vulva

(mean V value: 64 %), phasmids located mostly anterior to anus, tail more curved dorsally, dorsal side joining the ventral side at an angle, sometimes with a slight ventral projection, posterior part of tail with a few narrow annuli. Siddiqi (1972) separated *H. paraplatyurus* from *H. platyurus, H. canadensis, H. caroliniensis, H. serenus, H. vulgaris* and *H. varicaudatus.* The present specimens differ from specimens previously reported from South Africa (Van den Berg & Heyns, 1975; Van den Berg, 1978) in body length (541-959 *vs* 600-800 µm), ratio a (19.2-47.7 *vs* 25.5-31.6), position of excretory pore (89-137 *vs* 94.9-137 µm), and a more anterior position of the phasmid (one annulus posterior to sixteen annuli anterior to anus *vs* one annulus posterior to four annuli anterior to anus). V value showed the least variation with a CV of 3 %.

***Helicotylenchus planquettei* Marais & Quénéhervé, 1999** (Fig. 37, 38)

H. planquettei was described from seedling *Dicorynia guianensis* Amshoff near Saül, French Guiana (Marais & Quénéhervé, 1999), it is only known from its type locality.

Measurements

See Table 19.

Description

Female (n = 17): Habitus C-shaped (13 %) to spiral (87 %). Lip region 4 ± 0.6 (3-5) µm high and 7 ± 0.5 (6-8) µm wide, anteriorly flattened not set off with four to five annuli. Labial disc rectangular in *en face* view. Outer margins of labial framework extend 2 ± 0.3 (2-3) µm backward from basal plate. Stylet knobs 3 ± 0.3 (2-3) µm high and 5 ± 0.6 (4-7) µm wide; anterior faces flattened (53 %) or indented (47 %). Position

of DGO 10 ± 1.1 (9-12) µm behind stylet knobs. Median bulb oval, 12 ± 0.7 (11-13) µm long and 9 ± 0.7 (7-10) µm wide; valve 3 µm long and 2 ± 0.2 (1-2) µm wide. Length of oesophagus 146 ± 25.9 (124-191) µm, with length to end of glands 147 ± 15.4 (128-192) µm. Oesophagus with 11 ± 1.3 (10-13) µm long dorsal and ventral overlap. Excretory pore located 106 ± 4.1 (99-113) µm from front, i.e. at 18 ± 1.0 (15-19) % of body length. Hemizonid and hemizonion not seen. Fasciculi not seen. Width of annulus at midbody 1.4 ± 0.2 (11-1.8) µm. Body width at excretory pore 20 ± 2.0 (16-23) µm, at midbody 27 ± 4.3 (21-37) µm and at anus 14 ± 1.1 (13-15) µm. Two branches of reproductive system both functional, length of posterior branch 73 ± 7.8 (61-85) % of corresponding anterior branch length; anterior branch 133 ± 33.5 (96-180) µm and posterior branch 95 ± 26.1 (74-153) µm long. Spermatheca rounded, filled with sperm. Epiptygma folded into vagina. Lateral field 5 ± 0.5 (4-5) µm wide; inner two lines end on tail in a µ- (6 %) or m-shaped pattern (94 %). Rectum does not overlap anus. Phasmids located three to six annuli anterior to anus. Tail 14 ± 2.1 (11-18) µm long, with four to eight annuli, with non-annulated 4 ± 0.5 (4-5) µm long ventral projection.

Male (n = 8): Habitus straight (17 %) to C-shaped (83 %). Lip region 3 ± 0.3 (3-4) µm high and 6 ± 0.3 (5-6) µm wide, anteriorly rounded with four to five annuli. Outer margins of labial framework extend 1 µm backward from basal plate. Stylet knobs 2 ± 0.3 (1-2) µm high and 4 µm wide; anterior faces flattened (17 %) or indented (83 %). Position of DGO 8 ± 1.7 (6-10) µm behind stylet knobs. Length of oesophagus 106 µm, with length to end of glands 117 ± 6.2 (111-127) µm. Oesophagus with 5 µm ventral overlap. Excretory pore 81 ± 3.1 (77-86) µm from front, i.e. at 17 ± 0.9 (16-18) % of body length. Hemizonid and hemizonion not seen. Width of annulus at midbody 1.4 ± 0.2 (1.1-1.54) µm. Body width at excretory pore 15 ± 1.1 (13-16) µm, at midbody 20 ± 1.3 (18-22) µm and at cloaca 11 ± 1.2 (10-12) µm. Lateral field 3 µm wide, areolated anterior and opposite to bursa. Phasmids located half a body-width anterior to cloaca.

Titillae are present. Tail 16 ± 0.5 (15-17) µm long, with finger-like ventral projection.

Remarks

H. planquettei was separated from *H. limatus, H. multicinctus, H. pasohi, H. pricei* and *H. valdeclarus*. All these species have a posterior genital branch reduced and more posteriorly located vulva. Marais & Quénéhervé (1999) characterised *H planquettei* by the posterior position of the vulva (V = 67-73 %), stylet length (28-31 µm in females and 22-24 µm in males), female tail with distinct non-annulated ventral projection and presence of titillae.

***Helicotylenchus pseudorobustus* (Steiner, 1914) Golden, 1956** (Fig. 36, 38)

= *Tylenchus pseudorobustus* Steiner, 1914

= *Helicotylenchus microlobus* Perry, Darling & Thorne, 1959

= *Helicotylenchus phalerus* Anderson, 1974

H. pseudorobustus was described from soil under moss near Altmott, Switzerland and subsequently reported from all the biogeographical regions:

Afrotropical Region

Cameroon (Bridge *et al.*, 1995), Côte d'Ivoire (Plowright & Hunt, 1994), Democratic Republic of the Congo (Ali *et al.*, 1973), Ghana (Coyne *et al.*, 1999), Kenya (Sharma *et al.*, 1993), Lesotho (Van den Berg & Heyns, 1975), Liberia (Lamberti *et al.*, 1992), Namibia (De Waele *et al.*, 1998), Nigeria (Gbadegesin *et al.*, 1992), South Africa (Kleynhans *et al.*, 1996), and Zambia (Lawn *et al.*, 1988).

Australian Region

Fiji (Van den Berg & Kirby, 1979) and New Zealand (Yeates & Wouts, 1992).

Nearctic Region

Canada (Anderson, 1974) and USA (Wehunt *et al.*, 1991).

Neotropical Region

Argentina (Doucet & Doucet, 1997), Belize (Bridge *et al.*, 1996), Brazil (Moreira & Huang, 1980), Colombia (Stanton *et al.*, 1989), Cuba (Razjivin *et al.*, 1974), Dominican Republic (Kermarrec & Belliard, 1977), Dominica (Edmunds, 1969), French Guiana (Marais & Quénéhervé, 1996), Guadeloupe islands (Marais *et al.*, 2000), Martinique (Quénéhervé *et al.*, 1997), Mexico (Mancini & Moretti, 1976), St Vincent & the Grenadines (Edmunds, 1969), Trinidad & Tobago (Bala, 1984) and Venezuela (Crozzoli *et al.*, 1991).

Oriental Region

China (Yin, 1992), India (Swarup & Sethi, 1968), Iran (Fortuner *et al.*, 1984), Iraq (Stephan *et al.*, 1985), Israel (Sher, 1966), Jordan (Hashim, 1985), Korea (Kornobis & Dobosz, 1997), Malaysia (Sauer & Winoto, 1975), Pakistan (Firoza & Maqbool, 1996), Sri Lanka (Ekanayake & Toida, 1997), Taiwan (Zhou, 1992), Thailand (Pholcharoen & Boonduang, 1972) and Turkey (Geraert *et al.*, 1975).

Palaearctic Region

Algeria (Ouanouki & Mitiche, 1991), Austria (Sher, 1966), Belgium (Geraert, 1976), Finland (Kurppa, 1988), Egypt (Salem *et al.*, 1994), France (Fortuner, 1985), Germany (Weischer, 1975), Greece (Koliopanos & Kalyviotis-Gazelas, 1979), Italy (Mancini & Moretti, 1976), Moldova (Lisetskaya, 1973), Netherlands (Sher, 1966), Poland (Brzeski, 1998), Portugal (Abrantes *et al.*, 1978), Russia (Metlitskaya, 1984), Spain (Castillo *et al.*, 1991), Switzerland (Steiner, 1914) and the United Kingdom (Jones, 1979).

Measurements

See Table 19.

Description

Female (n = 93): Habitus spiral. Lip region 4 ± 0.4 (2-4) µm high and 6 ± 0.9 (5-

10) µm wide, anteriorly rounded, not set off, with four to six annuli. Labial disc rounded in *en face* view. Outer margins of labial framework extend 2 ± 0.3 (2-3) µm backward from basal plate. Cephalids not seen. Stylet knobs 2 ± 0.4 (2-3) µm high and 5 ± 0.7 (4-6) µm wide; anterior faces rounded (13 %), flattened (45 %) or indented (42 %). Position of DGO 11 ± 2.6 (8-16) µm behind stylet knobs. Median bulb oval, 12 ± 1.4 (10-18) µm long and 9 ± 0.9 (7-12) µm wide; valve 3 ± 0.5 (3-4) µ long and 2 µm wide. Length of oesophagus 132 ± 16.8 (100-186) µm, with length to end of glands 130 ± 16.8 (100-186) µm. Oesophagus with 16 ± 4.8 (7-25) µm long ventral overlap. Excretory pore 100 ± 13.6 (81-148) µm from front, i.e. at 17 ± 1.3 (14-21) % of body length. Hemizonid two to three annuli long, located one to four annuli anterior to excretory pore (*n = 15*). Hemizonion one annulus long located eight to nine annuli posterior to excretory pore (*n = 4*). Width of annulus at midbody 1.2 ± 0.5 (0.7-2.2) µm. Body width at excretory pore 18 ± 2.2 (10-24) µm, at midbody 22 ± 3.1 (16-32) µm and at anus 13 ± 1.5 (10-17) µm. Two branches of reproductive system both functional, length of posterior branch 87 ± 22.3 (53-148) % of corresponding anterior branch length; anterior branch 143 ± 24.9 (98-198) µm and posterior branch 120 ± 18.7 (95-161) µm long. Epiptygma folded into vagina. Lateral field 5 ± 0.6 (3-8) µm wide; outer two lines crenate and areolated posterior to vulva and on tail; inner two lines end on tail in a v- (36 %), y- (34 %), u- (3 %), m- (7 %) or µ- (20 %) shaped pattern. Rectum does not overlap anus. Phasmids located from two annuli posterior to fourteen annuli anterior to anus. Caudalid one annulus long, located one annulus posterior to anus. Tail 17 ± 2.5 (11-23) µm long, with seven to fourteen ventral annuli, tail more curved dorsally with rounded or pointed ventral projection, mucro seen in some specimens.

Male: Not found.

Remarks

The specimens were identified as *H. pseudorobustus* because of spiral habitus,

rounded lip region, medium body length (439-740 µm), position of vulva (mean V value: 63 %), phasmids mostly anterior to anus, tail more curved dorsally with rounded or pointed projection and males absent. The present specimens agree with the amended description of Fortuner *et al.* (1984). The lower range for body length (439 µm) is less than the previously recorded 487 µm (Van den Berg & Kirby, 1979). The upper range for ratio c' (1.8) is marginally higher than the 1.7 recorded by Mancini & Moretti (1976). V value showed the least variation with a CV of 4 %. Stylet length and the position of excretory pore/L (%) also have a CV of less than 10 %, viz. 9 %.

***Helicotylenchus retusus* Siddiqi & Brown, 1964** (Fig. 34, 39)

= *Helicotylenchus impar* Prasad, Khan & Chawla, 1965

= *Helicotylenchus paragirus* Saha, Chawla & Khan, 1974

H. retusus was described from sugar-cane (*Saccharum officinarum* L.), Negros Oriental, Philippines (Siddiqi & Brown, 1964) and since reported from four biogeographical regions, viz.:

Australian Region

Fiji (Van den Berg & Kirby, 1979).

Neotropical Region

Brazil (Costa Manso *et al.*, 1994), Dominican Republic (Román & Grullón, 1975) and Martinique (Cadet *et al.*, 1994).

Oriental Region

India (Sher, 1966) and Thailand (Timm, 1965).

Palaearctic Region

Turkmenia (Kir'yanova & Shagalina, 1974).

Measurements

See Table 19.

Description

Female (n = 12): Habitus spiral. Lip region 4 ± 0.4 (4-5) µm high and 7 ± 0.7 (6-8) µm wide, anteriorly flattened not set off, with four extremely faint annuli. Labial disc rounded in *en face* view. Outer margins of labial framework extend 3 µm backwards from basal plate. Anterior cephalids not seen, posterior cephalids twenty-two annuli posterior from basal plate. Stylet knobs 2 ± 0.3 (1-3) µm high and 5 ± 0.5 (4-6) µm wide; anterior faces flattened (44 %) or indented (66 %). Position of DGO 12 ± 1.0 (10-13) µm behind stylet knobs. Median bulb oval, 12 ± 0.8 (11-13) µm long and 9 ± 0.9 (8-11) µm wide; valve 3 µm long and 2 ± 0.3 (2-3) µm wide. Length of oesophagus 119 µm long, with length to end of glands 127 ± 5.1 (121-135) µm. Oesophagus with 4 µm long ventral overlap. Excretory pore 100 ± 7.6 (90-115) µm from front, i.e. at 12 ± 1.3 (9-14) % of body length. Hemizonid two to three annuli long, located one to two annuli anterior to excretory pore (*n = 9*). Hemizonion one annulus long, located sixteen annuli posterior to excretory pore (*n = 3*). Fasciculi not seen. Width of annulus at midbody 1.3 ± 0.2 (1.1-1.8) µm. Body width at excretory pore 22 ± 2.0 (18-25) µm, at midbody 29 ± 1.9 (25-34) µm and at anus 17 ± 1.3 (15-18) µm. Two branches of reproductive system both functional, length of posterior branch 87 ± 22.3 (53-148) % of corresponding anterior branch length; anterior branch 124 ± 18.6 (100-152) µm and posterior branch 113 ± 6.5 (104-119) µm long. Spermatheca off-set, thick-walled and empty. Epiptygma folded into vagina. Lateral field 6 ± 0.6 (5-7) µm wide; inner two lines end on tail in a v- (11 %) or u-shaped (89 %) pattern. Caudalid one to two annuli long, located one annulus posterior to anus. Phasmids located ten to fourteen annuli anterior to anus. Rectum does not overlap anus. Tail 16 ± 1.4 (14-19) µm long, straight with rounded end, clavate, with fifteen to nineteen ventral annuli.

Male: Not found.

Remarks

The specimens were identified as *H. retusus* because of spiral habitus, stylet length (22-26 µm), body length (702-934 µm), position of vulva (mean V value: 62 %), phasmids anterior to anus, tail straight with rounded end and males not seen. The relation of position of excretory pore to body length is the smallest of all the *Helicotylenchus* species studied (mean value: 12 %). The present specimens agree with the type description of Siddiqi & Brown (1964) and the redescription of Sher (1966). There is a discrepancy between the illustration of the tail form in Siddiqi & Brown (1964) and that of Sher (1966). As the paratype material deposited in both the Rothamsted and CABI Bioscience collections are lost, the present specimens could not be compared to the type material and the correct version of the tail form verified. Lal & Khan (1997) removed *H. impar* from the synonymy with *H. retusus,* because of the shape of the tail form. These authors used previously identified material from India and the type description (Siddiqi & Brown, 1964) as their reference point, but ignored all the subsequent redescriptions of *H. retusus*. Sher (1966) used type material deposited in the nematode collection at Rothamsted and in the collections of K. F. Brown and M. R. Siddiqi for the redescription of the species. Siddiqi never questioned this description by Sher in his subsequent publications (Siddiqi, 1972a; 1986) and therefore I accept the description of Sher (1966) as the correct version. I reject the removal of *H. impar* as a junior synonym of *H. retusus* as stated by Lal & Khan (1997).

***Helicotylenchus serenus* Siddiqi, 1963** (Fig. 22, 40)

H. serenus was described from *Thuja* sp., Pakistan (Siddiqi, 1963) and since reported from the:

Afrotropical Region

South Africa (Kleynhans *et al.*, 1996).

Oriental Region

India (Sher, 1966).

Measurements

See Table 19.

Description

Female (n = 48): Habitus C-shaped (13 %) to spiral (87 %). Lip region 4 ± 0.3 (3-5) µm high and 7 ± 0.6 (6-9) µm wide, anteriorly rounded not set off with five to seven annuli. Labial disc rectangular in *en face* view. Outer margins of labial framework extend 3 ± 0.4 (2-3) µm backward from basal plate. Cephalids not seen. Stylet knobs 2 ± 0.4 (2-3) µm high and 5 ± 0.6 (4-7) µm wide, anterior faces rounded (7 %), flattened (33 %) or indented (60 %). Position of DGO 13 ± 1.8 (10-19) µm behind stylet knobs. Median bulb oval, 13 ± 1.3 (11-16) µm long and 10 ± 1.1 (7-13) µm wide; valve 3 ± 0.2 (2-3) µm long and 2 ± 0.2 (1-2) µm wide. Length of oesophagus 144 ± 9.8 (125-174) µm, with length to end of glands 124 ± 12.9 (102-152) µm. Oesophagus with 17 ± 7.1 (5-33) µm long ventral or dorsal overlap. Excretory pore 111 ± 12.7 (88-139) µm from front, i.e. at 16 ± 1.7 (14-19) % of body length. Hemizonid two annuli long, located one annulus anterior to excretory pore (*n= 3*). Hemizonion not seen. Fasciculi not seen. Width of annulus at midbody 1.4 ± 0.3 (0.7-2.0) µm. Body width at excretory pore 22 ± 2.1 (17-27) µm, at midbody 27 ± 3.4 (21-36) µm and at anus 15 ± 1.8 (11-19) µm. Two branches of reproductive system both functional, length of posterior branch 76 ± 20.9 (51-107) % of corresponding anterior branch length; anterior branch 169 ± 32.3 (103-260) µm and posterior branch 121 ± 20.5 (98-161) µm long; anterior and posterior branches reflexed in some specimens from the Baviaanskloof Wilderness Area, Eastern

Cape Province. Spermatheca off-set, thick-walled and empty. Epiptygma folded into vagina. Lateral field 6 ± 0.8 (4-8) µm wide; outer two lines areolated anterior and posterior to vulva and crenated on tail; inner two lines end on tail in a v- (32 %), y- (52 %), µ- (13 %) and m-shaped (3 %) pattern. Phasmids located five annuli posterior to seven annuli anterior to anus. Tail 20 ± 2.8 (15-26) µm long, bent and asymmetrical, i.e. more curved dorsally, with rounded tapering end, with fourteen to twenty ventral annuli.

Male: Not found.

Remarks

The specimens were identified as *H. serenus* because of absence of males, mostly spiral habitus, stylet length (mean value: 29 µm), phasmids located five annuli posterior to seven annuli anterior to anus, long tapering tail (mean value: 20 µm). Siddiqi (1963) differentiated *H. serenus* from *H. canadensis* by its conspicuous outer margins of labial framework, a more posteriorly located DGO and a longer and more conoid tail measuring more than one anal body width in length. The present specimens correspond to the description of Siddiqi (1963), Sher (1966) and Van den Berg (1978). The range for body length exceeds the previous lowest and highest values (571 *vs* 581 µm in Sher, 1966 and 821 *vs* 786 µm in Van den Berg, 1978). V value showed the least variation with a CV of 3 %; the higher end of the range (67 %) is higher than the previously reported 66 % (Van den Berg, 1978).

***Helicotylenchus stylocercus* Siddiqi & Pinochet, 1979** (Fig. 40, 41)

H. stylocercus was described from *Musa* AAA at Cato and *Musa balbisiana* Colba at Siquirres, Costa Rica (Siddiqi & Pinochet, 1979) and since reported from Brazil (Costa Manso *et al.*, 1994) and Colombia (Stanton *et al.*, 1989).

Measurements

See Table 20.

Description

Female (n = 24): Habitus straight (4 %), C-shaped (73 %) to spiral (23 %). Lip region 3 ± 0.3 (3-4) µm high and 6 ± 0.6 (4-7) µm wide, anteriorly rounded with five to six annuli. Labial disc round to oval in *en face* view. Outer margins of labial framework extend 3 µm backward from basal plate. Anterior cephalids located four to seven annuli posterior to basal plate; posterior cephalids located eight to ten annuli posterior to anterior cephalids. Stylet knobs 2 ± 0.3 (1-3) µm high and 4 ± 0.6 (2-5) µm wide; anterior faces flattened (50 %), inclined backwards (23 %) or indented (27 %). Position of DGO 12 ± 0.8 (11-14) µm behind stylet knobs. Median bulb oval, 12 ± 0.6 (11-13) µm long and 8 ± 0.7 (7-9) µm wide; valve 4 + 0.6 (3-4) µm long and 3 ± 0.5 (3-4) µm wide. Length of oesophagus 118 ± 6.6 (108-126) µm, with length to end of glands 132 ± 6.4 (119-148) µm. Oesophagus with 10 ± 3.4 (6-15) µm long ventral, dorsal or ventro-lateral overlap. Excretory pore 91 ± 4.9 (82-102) µm from front of body, i.e. at 16 ± 0.8 (15-18) % of body length. Hemizonid two to three annuli long, located one to two annuli anterior to excretory pore (*n = 11*). Hemizonion one annulus long, located three annuli posterior to excretory pore (*n = 1*). Fasciculi not seen. Width of annulus at midbody 1.3 ± 0.2 (1.0-2.0) µm. Body width at excretory pore 16 ± 1.0 (14-18) µm, at midbody 19 ± 1.8 (17-25) µm and at anus 11 ± 0.8 (10-13) µm. Two branches of reproductive system both functional, length of posterior branch 67 ± 14.1 (44-92) % of corresponding anterior branch length; anterior branch 140 ± 30.9 (87-182) µm and posterior branch 88 ± 9.7 (73-11) µm long. Spermatheca off-set and filled with sperm. Some specimens with more than one functional spermathecae in a reproductive branch. Epiptygma folded into vagina. Lateral field 5 ± 0.6 (4-6) µm wide;

outer two lines areolated and crenate anterior to and on tail; inner two lines end on tail in a y- (55 %) or µ-shaped (45 %) pattern. Caudalid one annulus long located one annulus anterior to one annulus posterior to anus. Phasmids located two to fourteen annuli anterior to anus. Tail 27 ± 3.0 (21-34) µm long, with fourteen to twenty-three ventral annuli; straight to ventrad curved, with sometimes indented terminus, pointed or rounded ventral projection, mucro seen in some specimens.

Male (n = 29): Habitus straight (16 %), C-shaped (68 %) to spiral (16 %). Lip region 3 ± 0.4 (3-4) µm high and 6 ± 0.4 (5-7) µm wide; with four to five annuli. Stylet knobs 2 ± 0.2 (1-2) µm high and 4 ± 0.3 (3-4) µm wide; anterior faces flattened (32 %), flattened and inclined backwards (46 %) or indented (22 %). Position of DGO 12 ± 1.2 (9-13) µm behind stylet knobs. Median bulb oval, 11 ± 0.7 (9-12) µm long and 7 ± 0.5 (6-8) µm wide; valve 3 ± 0.5 (3-4) µm long and 2 µm wide. Length of oesophagus to end of glands 120 ± 4.4 (112-127) µm. Excretory pore 86 ± 9.5 (66-99) µm from front, i.e. at 16 ± 1.4 (13-20) % of body length. Body width at excretory pore 14 ± 1.0 (12-16) µm, at midbody 17 ± 1.6 (14-20) µm and at cloaca 11 ± 0.9 (10-14) µm. Hemizonid two annuli long, located one annulus anterior to excretory pore (*n = 2*). Hemizonion not seen. Lateral field 4 ± 0.4 (3-5) µm wide, areolated opposite oesophageal region and bursa. Phasmids located half to one body-width anterior to cloaca. Tail 28 ± 2.2 (23-33) µm long, with a finger-like, pointed ventral projection. Two specimens with non-specific tail forms and no bursa.

Remarks

The present specimens were identified as *H. stylocercus* because of tail with pronounced ventral projection, mostly C-shaped habitus, stylet length (20-23 µm), position of vulva (mean V value: 66 %), phasmids two to fourteen annuli anterior to anus in females. Siddiqi & Pinochet (1979) differentiated *H. stylocercus* from *H. urobeles* and *H. crenacauda* in having a longer body size, longer tail with more annuli,

a longer, stouter ventral tail projection and a more posteriorly located DGO. The present specimens correspond to the species description (Siddiqi & Pinochet, 1979) and were compared to paratype material. The female specimens differ from Costa Rican material in body length (475-602 *vs* 650-940 µm), b-value (4.2-4.9 *vs* 5.6-8.2), stylet length (20-23 *vs* 24-27 µm), mean V-value (66 % *vs* 61 %). Stylet length, ratio m and V showed the least variation with CV of 4 %, 3 %, and 2 % respectively.

***Helicotylenchus tumidicaudatus* Phillips, 1971** (Fig. 42, 43)

H. tumidicaudatus was described from Retro Sliding, Queensland, Australia (Phillips, 1971) and since reported from the:

Afrotropical Region

South Africa (Kleynhans *et al.*, 1996).

Oriental Region

China (Zhang *et al.*, 1998).

Measurements

See Table 20.

Description

Female (n = 9): Habitus C-shaped (63 %) to spiral (37 %). Lip region 4 ± 0.6 (4-5) µm high and 8 ± 0.8 (6-8) µm wide, anteriorly flattened not set off, with three to five annuli. Labial disc round in *en face* view. Outer margins of labial framework extend 3 µm backward from basal plate. Anterior cephalids located three to four annuli posterior to basal plate, posterior cephalids five to eight annuli posterior to anterior cephalids. Stylet knobs 3 ± 0.2 (2-3) µm high and 6 ± 1.1 (5-7) µm wide; anterior faces indented. Position of DGO 10 µm behind stylet knobs. Median bulb oval, 14 µm long

and 11 µm wide; valve 4 µm long and 3 µm wide. Length to end of oesophageal glands 161 ± 3.0 (15-164) µm. Excretory pore 108 ± 8.8 (96-117) µm from front, i.e. at 13 ± 0.9 (12-14) % of body length. Hemizonid two annuli long, located one to three annuli anterior to excretory pore (*n = 3*). Hemizonion not seen. Fasciculi not seen. Width of annulus at midbody 1.8 ± 0.2 (1.1-2.0) µm. Body width at excretory pore 27 ± 3.2 (24-32) µm, at midbody 31 ± 4.3 (24-36) µm and at anus 21 ± 2.3 (17-24) µm. Two branches of reproductive system both functional, length of posterior branch 80 ± 5.6 (74-87) % of corresponding anterior branch length; anterior branch 199 ± 16.3 (187-222) µm and posterior branch 158 ± 10.6 (148-170) µm long. Spermatheca axial and filled with sperm. Epiptygma folded into vagina. Lateral field 8 ± 0.5 (7-8) µm wide; inner two lines end on tail in an u- (83 %) or v-shaped (17 %) pattern. Caudalid two annuli long, located one annulus posterior to anus. Phasmids located three to nine annuli anterior to anus. Tail 14 ± 2.6 (11-19) µm long, straight with rounded end, sometimes clavate with seven to ten ventral annuli.

Male (n = 5): Habitus C-shaped. Lip region 4 µm high and 6 µm wide, anteriorly flattened not set off with five annuli. Outer margins of labial framework extend 3 µm backward from basal plate. Stylet knobs 2 µm high and 4 µm wide; anterior faces indented. Position of DGO 12 ± 2.6 (10-14) µm behind stylet knobs. Length of oesophagus 131 µm (*n = 1*), with length to end of glands 143 ± 4.5 (140-146) µm. Oesophagus with 9 µm long ventral overlap. Excretory pore 118 ± 27.8 (140-146) µm from front, i.e. at 16 ± 1.7 (14-18) % of body length. Hemizonid and hemizonion not seen. Width of annulus at midbody 1.3 (0.8 (0.7-2.1) µm. Body width at excretory pore 22 ± 6.2 (16-29) µm, at midbody 28 ± 5.4 (22-33) µm and at cloaca 16 µm. Lateral field 6 ± 0.5 (5-6) µm wide, areolated anterior and opposite bursa. Phasmids located half a body width anterior to cloaca. Tail 23 ± 2.3 (22-26) µ long, with a finger-like annulated tip.

Remarks

The present specimens were identified as *H. tumidicaudatus* because of presence of males, mostly C-shaped habitus, stylet length (mean value: 30 µm), body length (mean value: 842 µm), phasmids anterior to anus, and tail straight with rounded end, sometimes clavate. According to Phillips (1971) *H. tumidicaudatus* resembles *H. retusus* from which it is distinguished by the presence of sperm in the spermathecae. The present specimens agree with the descriptions of Phillips (1971) and Van den Berg (1978) but differ in body length (743-1020 *vs* 715-944 µm), ratio a (22.9-35.4 *vs* 24-33.9), ratio c' (0.5-1.1 *vs* 0.5-1.0), value m (44-50 *vs* 43-47 %) and tail length (11-19 *vs* 9-15 µm) in females. The present male specimens differ in body length (604-890 *vs* 625-870 µm), ratio a (25.3-33.7 *vs* 28-38) and ratio c (27.8-32.6 *vs* 30-39). V value showed the least variation with a CV of 1 %. The relation of position of excretory pore to body length is the smallest of all the *Helicotylenchus* species studied (mean value: 13 %).

***Helicotylenchus variabilis* Phillips, 1971** (Fig. 42, 44)

H. variabilis was described from Retro Sliding, Queensland, Australia (Phillips, 1971) and since reported from the:

Afrotropical Region

South Africa (Marais, 1998).

Oriental Region

China (Zheng *et al.*, 1998).

Measurements

See Table 20.

Description

Female (n = 14): Habitus C-shaped (18 %) to spiral (82 %). Lip region 4 ± 0.3 (3-4) µm high and 7 ± 0.5 (6-7) µm wide, anteriorly flattened, not set off with five to six annuli. Labial disc oval in *en face* view. Outer margins of labial framework extend 2 ± 0.5 (2-3) µm backward from basal plate. Cephalids not seen. Stylet knobs 3 ± 0.4 (2-4) µm long and 5 ± 0.4 (4-5) µm wide; anterior faces flattened (46 %) or inclined backwards (54 %). Position of DGO 13 ± 1.3 (10-15) µm behind stylet knobs. Median bulb oval, 11 ± 0.8 (10-13) µm long and 8 ± 0.9 (7-10) µm wide; valve 2 µm high and 2 µm wide. Length of oesophagus 99 µm (*n = 1*), with length to end of glands 124 ± 9.6 (105-139) µm. Oesophagus with 20 µm long ventral overlap. Excretory pore 91 ± 10.4 (74-109) µm from front, i.e. at 16 ± 1.7 (13-19) % of body length. Hemizonid two annuli long, located one annulus anterior to excretory pore (*n = 4*). Hemizonion not seen. Fasciculi not seen. Width of annulus at midbody 1.3 ± 0.2 (1.0-1.7) µm. Body width at excretory pore 18 ± 1.5 (15-20) µm, at midbody 23 ± 3.1 (17-29) µm and at anus 14 ± 1.2 (12-16) µm. Epiptygma folded into vagina. Lateral field 5 ± 0.7 (4-7) µm wide, outer two lines areolated on tail; inner two lines end on tail in a v- (17 %), y- (75 %) or m-shaped (8 %) pattern. Rectum does not overlap anus. Phasmids located two to eight annuli anterior to anus. Tail 14 ± 2.3 (10-16) µm long, mostly bent and asymmetrical, more curved dorsally with seven to ten ventral annuli.

Male (n = 2): Habitus spiral. Lip region 4 µm high and 6 µm wide, anteriorly flattened with six annuli. Stylet knobs 1 µm high and 4 µm wide; anterior faces flattened and inclined backwards. Length of oesophagus to end of glands 123 µm. Excretory pore 96 µm from front, i.e. at 18 % of body length. Hemizonid and hemizonion not seen. Width of annulus at midbody 0.7-1.4 µm. Body width at excretory pore 13 µm, at midbody 16-17 µm and at cloaca 10-11 µm. Lateral field 4 µm wide, areolated opposite oesophageal region and bursa. Phasmids located half a body-width anterior to anus. Tail 17-19 µm long, with a finger-like annulated ventral

projection.

Remarks

The specimens were identified as *H. variabilis* because of mostly spiral habitus, anteriorly flattened lip region, stylet length (mean value: 27 µm), body length (mean value: 571 µm), phasmids anterior to anus and males present. Phillips (1971) differentiated *H. variabilis* from *H. clarkei* and *H. martini* by the position of phasmids, tail shape and c'-ratio. *H. variabilis* was described as having no lip annuli. Study of the paratype material showed that lip annuli are present. The present specimens conform to the original description (Phillips, 1971).

***Helicotylenchus vulgaris* Yuen, 1964** (Fig 38, 45)

H. vulgaris was described from grass, Rothamsted Experiment Station, England (Yuen, 1964) and since reported from four biogeographical regions, viz.:

Afrotropical Region

South Africa (Marais & Swart, 1999).

Australian Region

New Zealand (Wouts & Knight, 1993).

Oriental Region

Jordan (Hashim, 1985) and Turkey (Ertürk *et al.*, 1973).

Palaearctic Region

Bulgaria (Katalan-Gateva & Milkova, 1979), France (Fortuner, 1991), Germany (Fortuner, 1991), Italy (Mancini & Moretti, 1976), Moldova (Koev *et al.*, 1971), Netherlands (Bongers, 1988), Poland (Brzeski, 1998), Portugal (Abrantes *et al.*, 1987), Romania (Ivan, 1978) and the United Kingdom (Spaull, 1982).

Measurements

See Table 21.

Description

Female (n = 30): Habitus C-shaped (29 %) to spiral (71 %). Lip region 4 ± 0.5 (3-5) µm high and 9 ± 1.1 (7-11) µm wide; anteriorly flattened with five to nine annuli. Labial disc oval in *en face* view. Outer margins of labial framework extend 3 ± 0.5 (2-3) µm backward from basal plate. Cephalids not seen. Stylet knobs 5 ± 0.6 (4-7) µm high and 3 ± 0.3 (2-3) µm wide; anterior faces rounded (7 %), flattened (48 %) or indented (45 %). Position of DGO 13 ± 1.1 (11-15) µm behind stylet knobs. Medium bulb rounded to oval, 12 ± 0.9 (10-14) µm long and 9 ± 1.1 (7-11) µm wide; valve 3 ± 0.5 (2-3) µm long and 2 µm wide. Length of oesophagus 143 ± 11.2 (134-155) µm, with length to end of glands 153 ± 12.7 (127-174) µm. Oesophagus with 14 ± 4.3 (9-19) µm long ventral and dorsal overlap. Excretory pore 109 ± 9.7 (93-129) µm from front, i.e. at 15 ± 1.5 (12-18) % of body length. Hemizonid two annuli long, located from opposite excretory pore to one annulus anterior to excretory pore (*n = 12*). Hemizonion not seen. Width of annulus at midbody 1.0 ± 0.2 (1.1-1.8) µm. Body width at excretory pore 23 ± 3.1 (17-33) µm, at midbody 29 ± 3.6 (23-40) µm and at anus 16 ± 1.8 (13-20) µm. Two branches of reproductive system both functional, length of posterior branch 86 ± 18.4 (54-99) % of corresponding anterior branch length; anterior branch 202 ± 63.9 (135-293) µm and posterior branch 151 ± 44.2 (104-241) µm long. Epiptygma folded into vagina. Lateral field 6 ± 0.7 (5-7) µm wide; inner two lines end on tail in an u- (45 %), v- (32 %) or y-shaped (23 %) pattern. Rectum does not overlap anus. Phasmids located one annulus posterior to five annuli anterior to anus. Tail 12 ± 2.0 (9-16) µm long, bent and asymmetrical, i.e. more curved dorsally, with rounded end and five to thirteen ventral annuli. Annuli on tail end fine, subdivided and irregular around tip.

Male: Not found.

Remarks

These specimens were identified as *H. vulgaris* because of presence of fine subdivided annuli on tail tip. According to Yuen (1964), *H. vulgaris* is similar to *H. platyurus*, *H. tunisiensis*, *H. canadensis* and *H. cairnsi* but differ from these species in the truncate and broadly rounded tail end. The South African specimens were compared to paratype material from grass, Rothamsted from which they differ in b-value (4.5-5.9 *vs* 6.8-9.2) and position of phasmids (one annulus posterior to five annuli anterior to anus *vs* six to eighteen annuli anterior to anus). A shorter stylet length was also reported for populations from France and New Zealand (Sher, 1966; Wouts & Knight, 1993). The lower end of the range for body length (609 µm) is less than the previously reported 658 µm (Wouts & Knight, 1993). The upper range for position of DGO (15 µm) is higher than the 12 µm reported by Yuen (1964). V value showed the least variation with a CV of 2 %, the upper range of 68 % exceeds the highest value (65 %) reported by Fortuner (1991).

***Helicotylenchus willmottae* Siddiqi, 1972** (Fig. 42, 46)

Helicotylenchus willmottae was described from potato (*Solanum tuberosum* L. subsp. *tuberosum*), Ootacamund, India (Siddiqi, 1972) and since reported from three biogeographical regions, viz.:

Afrotropical Region

Lesotho (Kleynhans *et al.*, 1996) and South Africa (Kleynhans *et al.*, 1996).

Oriental Region

Pakistan (Firoza & Maqbool, 1992) and Sri Lanka (Kumarasinghe & Ekanayake, 1998).

Palaearctic Region

Georgia (Tskitishvili, 1983).

Measurements

See Table 21.

Description

Females (n = 17): Habitus spiral. Lip region 4 ± 0.4 (3-4) µm high and 7 ± 0.7 (6-9) µm wide, anteriorly flattened, not set off with five to seven annuli. Labial disc oval in *en face* view. Outer margins of labial framework extend 3 µm backward from basal plate. Stylet knobs 3 ± 0.5 (2-3) µm high and 5 ± 0.6 (4-6) µm wide; anterior faces rounded (7 %), flattened (50 %) or indented (43 %). Position of DGO 11 ± 1.2 (10-14) µm behind stylet knobs. Median bulb oval, 13 ± 1.0 (12-15) µm long and 9 ± 0.9 (8-11) µm wide; valve 3 µm long and 3 µm wide. Length of oesophagus 127 ± 9.2 (109-132) µm, with length to end of glands 147 ± 7.6 (138-166) µm. Oesophageal lobe with 20 ± 5.6 (14-29) µm ventral overlap. Excretory pore 113 ± 21.1 (94-160) µm from front, i.e. at 17 ± 2.4 (14-22) % of body length. Hemizonid and hemizonion not seen. Width of annulus at midbody 1.3 ± 0.3 (0.7-1.8) µm. Body width at excretory pore 17 ± 3.0 (12-20) µm, at midbody 23 ± 3.0 (19-29) µm and at anus 14 ± 2.4 (12-19) µm. Epiptygma folded into vagina. Lateral field 5 ± 0.8 (4-7) µm wide; outer two lines crenate anterior to vulva; inner two lines end on tail in a v- (38 %) or y-shaped (62 %) pattern. Rectum does not overlap anus. Phasmids located four annuli posterior to nine annuli anterior to anus. Caudalid not seen. Tail 16 ± 3.6 (11-21) µm long, rounded more curved dorsally with ten to eighteen ventral annuli.

Male: Not found.

Remarks

The specimens were identified as *H. willmottae* because of spiral habitus, body

length (mean value: 646 µm), stylet length (mean value: 27 µm), lip region anteriorly flattened, phasmids located anterior and posterior to anus and tail rounded more curved dorsally without a ventral projection. According to Siddiqi (1972) *H. willmottae* is close to *H. caroliniensis, H. canadensis, H. serenus, H. platyurus* and *H. paraplatyurus* but differs from them in having the DGO more than half the spear length behind the base of the spear. Lal & Khan (1997) synonymized *H. willmottae* with *H. retusus* because of similarity in tail shape, spear length and the absence of a labial disc. My study of specimens of *H. willmottae* and *H. retusus* showed that there is a definite difference in tail shape (rounded more curved dorsally *vs* straight with rounded end and clavate) and all *Helicotylenchus* species have a labial disc. I therefore reinstate *H. willmottae* as a valid species. The South African specimens agree with paratype material and the description by Siddiqi (1972) and Firoza & Maqbool (1992). The range for body length exceeds the previous range (554-814 *vs* 600-790 µm). The upper range for stylet length (31 µm) is higher than the previously reported 28 µm (Siddiqi, 1972). V value showed the least variation with a CV of 3 %.

6. CONCLUSION

The genus *Helicotylenchus* is a cosmopolitan genus and its members are important pathogens on a number of crop plants. This group of semi-endoparasitic nematodes is able to change the physiology of the host plant to suit their requirements (Vovlas & Larizza, 1994), inhibiting nutrient up-take and therefore the general growth of the plant. Feeding of these nematodes also facilitate the entry of other pathogens increasing the damaged caused to the plant (Barham *et al.*, 1974; Hamiduzzaman *et al.*, 1997).

Fortuner stated in 1984 that in spite of the intense taxonomic studies on the genus *Helicotylenchus*, it is still difficult to identify an unknown species, because of interspecific variation in the characters used by authors. The series of papers published by Fortuner in the 1980s highlighted this complex situation of interspecific variation (Fortuner, 1979; Fortuner & Quénéhervé, 1980; Fortuner *et al.*, 1981; Fortuner, 1984a, 1984b; Fortuner *et al.*, 1984).

In the present study, the morphometric characters, which showed the least variation, were the V and m values and stylet length. The most constant character was the V value. In none of the species studied, a CV greater than 4 % was obtained for this value. The two new characters introduced in this dissertation, regarding the position of the excretory pore, viz. excretory pore/body length x 100 and excretory pore/oesophagus length x 100, excretory pore/body length showed the least variation. In none of the species studied, this value had a CV greater than 11 %. This value showed also less interspecific variation than the corresponding measurement "excretory pore from front". In the search for a more reliable character with less interspecific variation than the OV_1 and OV_2 values and their corresponding

measurements. It was found that the "posterior reproductive branch length/anterior reproductive branch length x 100" value, although it still showed much variability, clearly illustrated the existence of intermediate stages in the regression of the posterior reproductive branch, and therefore supports the synonymization of *Rotylenchoides* with *Helicotylenchus* by Fortuner (1984b).

Other factors, which also hamper study of the genus, *Helicotylenchus* are:

1. Some very poor species descriptions with insufficient illustrations where the authors completely ignore variation within characters, compare the new species with only the original descriptions of closely related species and disregard all subsequent descriptions and information on the species.
2. Curators of nematode collections who are not willing to lend paratype material for study or charge exorbitant fees, for the loan of material.
3. Because of cut-backs in research funds, there is a general decline in the curation of research collections resulting in the subsequent deterioration of material making them of little use for study.

The rapidly expanding field of molecular study has potential to help and clarify the problem of interspecific variation in characters used in the description of species. The first and only paper containing molecular information on *Helicotylenchus* was published in 1997. Polymerase chain reaction-restriction fragment length polymorphism (PCR-RFLP) of the Internal Transcribed Spacer Region (ITS) was advocated as a method of taxonomic analysis in genera such as *Helicotylenchus* which contain numerous species with few diagnostic morphological characters (Powers *et al.*, 1997). According to Coomans (2000), molecular techniques have made systematics more exciting, but that it will be a mistake to replace the morphological approach with a molecular approach. Instead we have to combine morphological and molecular data

to arrive at a more satisfactory classification system.

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Table 1. Distribution of *Helicotylenchus* spp. in the Afrotropical Region

Helicotylenchus spp.	Countries and islands: Aldabra Islands	Angola	Botswana	Burkina Faso	Burundi	Cameroon	Canary Islands	Côte d'Ivoire	DRC	Ethiopia	Gambia	Ghana	Guinea	Kenya	Lesotho	Liberia	Madagascar	Malawi	Mali	Mauritania	Mauritius	Mozambique	Namibia	Nigeria	Niger	Reunion	Rwanda	Sao Tome' & Principe	Senegal	Seychelles	South Africa	Sudan	Swaziland	Tanzania	Togo	Uganda	Zambia	Zanzibar	Zimbabwe
abuharazi													x																											
abunaamai						x		x		x	x	x	x																											
affinis						x		x																													x			
africanus																		x						x					x		x								
agricola																																								
anhelicus																																								
areolatus																																								
attenuatus						x																																		
babikeri																																	x							
bambesae								x	x									x																					
brevis																																		x						
californicus																																x								
canadensis																																x								
canalis																																x								
carolinensis																																x								
cavenessi						x												x						x								x								
conicephalus																																	x							
crenacauda						x		x														x																		
delanus																																								
densibullatus									x									x																					
digitatus																																								
digonicus								x										x				x																		
dihystera				x		x	x	x	x			x		x		x	x	x	x	x	x	x	x	x					x		x								
dolichodoryphorus																									x															
dumicola						x																																		
egyptiensis						x		x										x											x										
elegans																																								
erythrinae	x					x	x	x									x	x										x											
exallus						x			x					x																										
hydrophilus																																								

Table 1 - continued

Countries and islands	*Helicotylenchus* spp.	*indicus*	*intermedius*	*labiodiscinus*	*limatus*	*longicaudatus*	*marethae* **n.sp.**	*martini*	*microcephalus*	*minzi*	*mucronatus*	*multicinctus*	*nigeriensis*	*nitens*	*orthosomaticus*	*paracanalis*	*paraplatyurus*	*pricei*	*pseudorobustus*	*saxeus*	*serenus*	*subterminalis*	*tropicus*	*tumidicaudatus*	*tunisiensis*	*variabilis*	*variocaudatus*	*vindex*	*vulgaris*	*willmottae*
Aldabra Islands																													
Angola												×																	
Botswana												×																	
Burkina Faso												×																	
Burundi												×																	
Cameroon		×		×					×		×	×		×				×	×	×		×					×	×	
Canary Islands												×																	
Côte d'Ivoire	×	×							×		×	×	×			×			×								×		
DRC								×				×							×										
Ethiopia												×																	
Gambia												×	×																
Ghana											×	×							×										
Guinea																													
Kenya									×		×	×			×		×		×										
Lesotho																			×										×
Liberia												×							×										
Madagascar									×			×																	
Malawi									×				×																
Mauritania																													
Mali																													
Mauritius												×																	
Mozambique									×	×		×																	
Namibia												×							×										
Nigeria		×		×					×			×	×						×			×							
Niger																													
Reunion												×																	
Rwanda												×																	
Sao Tome' & Principe												×															×		
Senegal												×					×												
Seychelles												×																	
South Africa	×		×			×		×	×	×		×				×	×		×		×		×		×			×	×
Sudan									×		×	×																	
Swaziland												×																	
Tanzania												×			×														
Togo																													
Uganda												×													×				
Zambia												×							×										
Zanzibar												×																	
Zimbabwe								×				×																	

Table 2. Distribution of *Helicotylenchus* spp. in the Australian Region

	Countries and islands									
Helicotylenchus spp.	Australia	Easter Islands	Fiji	Kiribati	New Zealand	Niue	Papua New Guinea	Samoa	Solomon Islands	Tonga
australis	x									
californicus			x							
canadensis					x					
crenacauda			x							
depressus					x					
digonicus	x				x					
dihystera	x	x	x		x	x		x		x
egyptiensis			x							
erythrinae		x			x				x	
exallus	x				x					
fericulus			x							
hydrophilus									x	
indicus			x					x		x
labiatus					x					
lissocaudatus					x					
microcephalus			x					x		x
minzi					x					
mucronatus						x				x
multicinctus	x		x	x		x	x	x		x
mundus			x							
paracanalis			x							
paxilli					x					
pseudorobustus			x		x					
retusus			x							
tumidicaudatus	x									
valdeclarus								x		
variabilis	x									
varicaudatus					x					
vulgaris					x					

Table 2. Distribution of *Helicotylenchus* spp. in the Australian Region

	Countries and islands									
Helicotylenchus spp.	Australia	Easter Islands	Fiji	Kiribati	New Zealand	Niue	Papua New Guinea	Samoa	Solomon Islands	Tonga
australis	x									
californicus			x							
canadensis					x					
crenacauda			x							
depressus					x					
digonicus	x				x					
dihystera	x	x	x		x	x		x		x
egyptiensis			x							
erythrinae		x			x				x	
exallus	x				x					
fericulus			x							
hydrophilus									x	
indicus			x					x		x
labiatus					x					
lissocaudatus					x					
microcephalus			x					x		x
minzi					x					
mucronatus						x				x
multicinctus	x		x	x		x	x	x		x
mundus			x							
paracanalis			x							
paxilli					x					
pseudorobustus			x		x					
retusus			x							
tumidicaudatus	x									
valdeclarus								x		
variabilis	x									
varicaudatus					x					
vulgaris					x					

Table 3. Distribution of *Helicotylenchus* spp. in the Nearctic Region

	Countries and islands		
Helicotylenchus spp.	Canada	Greenland	USA
amplius	x		x
anhelicus	x		x
belli			x
californicus			x
canadensis	x		
canalis			x
caroliniensis			x
clarkei			x
cornurus	x		
craigi			x
crassatus	x		
crenacauda			x
digonicus	x		x
dihystera	x		x
erythrinae			x
exallus			x
hydrophilus			x
labiodiscinus			x
leiocephalus			x
lobus			x
multicinctus			x
paraplatyurus			x
platyurus	x		x
pseudorobustus	x		x
spitsbergensis	x	x	x
truncatus			x
urobeles	x		
vulgaris			x

Table 4 - continued

	Countries and islands																												
Helicotylenchus spp.	Argentina	Barbados	Belize	Brazil	Colombia	Costa Rica	Cuba	Dominica	Dominican Republic	French Guiana	Grenada	Guadeloupe	Guatemala	Jamaica	Martinique	Mexico	Nicaragua	Panama	Peru	Puerto Rico	San Salvador	Surinam	St Lucia	St Vincent & the Grenadines	Trinidad & Tobago	Union Island	Venezuela
pseudopaxilli					x		x																					
pseudorobustus	x		x	x	x		x	x	x	x		x			x	x								x	x		x
retusus				x					x						x													
reynosus							x		x																			
sacchari							x																					
sagitovi				x																								
serenus				x																								
silvicola				x																								
similis							x																					
sparsus							x																					
stylocercus				x	x	x									x													
subtropicalis							x																					
tropicus									x			x																
truncatus									x											x								
unicum							x																					
verrucosus							x																					
vulgaris																x												

Table 5 – continued

	Countries and islands																					
Helicotylenchus spp.	Bangladesh	Brunei	China	India	Indonesia	Iran	Iraq	Israel	Jordan	Korea	Lebanon	Malaysia	Nepal	Oman	Pakistan	Philippines	Sri Lanka	Taiwan	Thailand	Turkey	United Arab Emirates	Vietnam
kherai				x																		
laevicaudatus																						x
labiodiscinus			x																			
leiocephalus			x																			
lemoni															x							
limarius																						x
macronatus				x											x							
magnicephalus				x																		
meloni															x							
microcephalus				x					x										x			
microtylus															x							
minzi			x	x				x							x							
morasii				x																		
mucronatus				x																		
multicinctus	x	x	x	x		x		x	x		x	x		x	x	x	x		x	x	x	x
neoformis				x																		
notabilis																						x
obliquus															x							
oleae			x																			
oscephalus															x							
paracanalis				x								x										
paradihysteroides			x	x											x							
paraplatyurus				x						x												
pasohi												x										
persici				x																		
pisi			x	x																		
platyurus			x												x							
plumariae				x																		
pseudorobustus			x			x		x	x	x		x	x		x		x	x	x	x		
retusus				x												x			x			
reversus				x																		
rothangus				x																		
sacchari			x																			
saccharumi				x																		
serenus															x							
seshadrii															x							
shakili				x																		
sharafati				x																		
sheri				x																		
silvaticus				x																		
solani				x																		
steineri				x																		
striatus															x					x		
tangericus				x																x		
trapezoidicaudatus				x																		
tumidicaudatus			x																			

Table 5 – continued

	Countries and islands																						
Helicotylenchus spp.	Bangladesh	Brunei	China	Cambodia	India	Indonesia	Iran	Iraq	Israel	Jordan	Korea	Lebanon	Malaysia	Nepal	Oman	Pakistan	Philippines	Sri Lanka	Taiwan	Thailand	Turkey	United Arab Emirates	Vietnam
tunisiensis			x																		x		
valecus					x																x		
varicaudatus			x		x																x		
variabilis			x																				
ventroprojectus					x																		
verecundus																x							
vietnamensis																							x
vulgaris										x											x		
whiteheadi					x																		
willmottae					x											x		x					

Table 6. Distribution of *Helicotylenchus* spp. in the Palaearctic Region

Countries and islands	*Helicotylenchus* spp.	*africanus*	*agricola*	*amabilis*	*anhelicus*	*acutus*	*bambesae*	*californicus*	*canadensis*	*cavenessi*	*cedreus*	*cephalatus*	*clarkei*	*coomansi*	*conicus*	*crenacauda*	*digitiformis*	*digonicus*	*dihystera*	*egyptiensis*	*erythrinae*	*exallus*	*interrogativus*	*leiocephalus*	*martini*
Uzbekistan																			x		x				
United Kingdom																		x							
Ukraine										x					x				x		x				
Turkmenia																		x							
Tunisia																			x						
Tadjikistan						x		x										x				x			
Switzerland																									
Spain																x		x	x		x				
Slovakia																		x	x		x				
Russia				x	x			x			x		x				x	x	x		x	x	x		
Romania																			x						
Portugal									x	x									x						
Poland									x			x		x				x	x		x	x			
Norway																									
Netherlands									x					x				x	x						
Morocco																			x						
Moldova																			x	x	x				
Madeira																			x						
Lithuania																									
Libya																		x							
Kyrgyztan																			x		x				
Kazakhstan										x								x	x						
Japan																		x	x		x				
Italy																		x	x						
Hungary								x		x								x	x						
Greece																									
Germany																		x	x						
Georgia								x					x						x						x
France								x																	
Finland									x									x							
Egypt		x					x		x	x									x			x			
Denmark																		x							
Czech Republic																		x			x				
Cyprus																									
Croatia																		x							
Crete																									
Bulgaria					x				x									x	x					x	
Belgium																			x			x			
Austria																									
Armenia																			x						
Algeria		x																							

Table 6 -continued

Countries and islands	*microcephalus*	*minzi*	*monstruous*	*montanus*	*multicinctus*	*neopaxili*	*oleae*	*parabelli*	*paraplatyurus*	*paxilli*	*platyurus*	*pseudorobustus*	*retusus*	*ryzhikovi*	*sandersae*	*scoticus*	*sieversii*	*spitsbergiensis*	*tunisiensis*	*ussuriensis*	*varicaudatus*	*vulgaris*	*willmottae*
Uzbekistan					×																		
United Kingdom										×		×				×					×	×	
Ukraine																	×						
Turkmenia													×										
Tunisia					×																		
Tadjikistan				×	×																		
Switzerland					×							×											
Spain	×				×							×											
Slovakia																					×		
Russia			×		×			×		×		×		×				×		×	×		
Romania																						×	
Portugal									×			×										×	
Poland											×	×				×					×	×	
Norway																		×					
Netherlands										×		×									×	×	
Morocco																							
Moldova					×							×										×	
Madeira																							
Lithuania					×																		
Libya																							
Kyrgyztan																							
Kazakhstan					×																		
Japan																							
Italy					×	×	×					×			×				×		×	×	
Hungary		×																					
Greece												×											
Germany												×										×	
Georgia		×			×																		×
France												×									×	×	
Finland												×									×		
Egypt	×				×							×											
Denmark																							
Czech Republic																							
Cyprus					×																		
Croatia																							
Crete					×																		
Bulgaria		×			×																×	×	
Belgium												×											
Austria												×											
Armenia					×																		
Algeria												×											

Table7. Populations studied

Species	Number	Country	Province	Locality	Associated plant/plant type
H. africanus	KP1344	South Africa	Northern Cape	Kimberley, Riverton Holiday Resort	Reeds
H. africanus	TVL1222	South Africa	Mpumalanga	Mataffin	*Carya illoinensis* (Wangenh.) K. Koch
H. africanus	TVL1252	South Africa	Mpumalanga	Carolina, farm Blenheim	Grass
H. africanus	TVL1344	South Africa	Mpumalanga	Mataffin	Reeds
H. anhelicus	N676	South Africa	Kwazulu-Natal	Port Edward	Dune vegetation
H. anhelicus	N677	South Africa	Kwazulu-Natal	Port Edward	Dune vegetation
H. areolatus	N546	South Africa	Kwazulu-Natal	Kwambonambi, Adams Plantation	*Eucalyptus* plantation
H. brevis	KP0942	South Africa	Eastern Cape	Port Elizabeth, Kabega Park	*Watsonia* sp.
H. brevis	KP0952	South Africa	Eastern Cape	Seymour, Nico Malan Pass	Natural veld
H. brevis	KP0976	South Africa	Eastern Cape	Tsitsikamma National Park	Indigenous forest
H. brevis	KP1106	South Africa	Western Cape	Nature's Valley, Bloukrans River Pass	Indigenous forest
H. brevis	KP1166	South Africa	Western Cape	Wilderness National Park, Brownhooded Kingfisher Trail	Indigenous forest
H. brevis	KP1544	South Africa	Eastern Cape	Tsitsikamma National Park, Loerie Trail	Indigenous forest - *Dietes iridiodes* (L.) Sweet ex Klatt
H. brevis	KP1545	South Africa	Eastern Cape	Tsitsikamma National Park, Blue Duiker Trail	Indigenous forest - fern
H. brevis	KP1549	South Africa	Eastern Cape	Tsitsikamma National Park, Blue Duiker Trail	Indigenous forest
H. brevis	KP1553	South Africa	Eastern Cape	Tsitsikamma National Park, Blue Duiker Trail	Indigenous forest - *Argyrolobium colinum* Eckl. & Zeyh.
H. brevis	KP1563	South Africa	Eastern Cape	Tsitsikamma National Park, Mouth Trail	Indigenous forest - *Zantedeschia aethiopica* (L.) Spreng.
H. brevis	KP1565	South Africa	Eastern Cape	Tsitsikamma National Park, Mouth Trail	Indigenous forest - *Crassula* sp.
H. brevis	KP1567	South Africa	Eastern Cape	Tsitsikamma National Park, Dryfhoutbaai	Indigenous forest
H. brevis	KP1569	South Africa	Eastern Cape	Tsitsikamma National Park, Mooibaai	Indigenous forest - fern
H. brevis	KP1635	South Africa	Eastern Cape	Hogsback, Ter Doone	Indigenous forest
H. brevis	N474	South Africa	Kwazulu-Natal	Port Edward	Dune vegetation
H. brevis	N475	South Africa	Kwazulu-Natal	Umtentwini	Indigenous forest
H. brevis	N476	South Africa	Kwazulu-Natal	Umtentwini	Dune vegetation

Table 7 - continued

Species	Number	Country	Province	Locality	Associated plant/plant type
H. brevis	N480	South Africa	Kwazulu-Natal	Trafalgar	Dune vegetation
H. brevis	N533	South Africa	Kwazulu-Natal	Greater St. Lucia Wetland Park, Charters Creek	*Albizia adianthifolia* (Schmach.) W. F. Wight
H. brevis	N536	South Africa	Kwazulu-Natal	Umlalazi, Umlalazi Nature Reserve	Indigenous forest
H. brevis	TVL1420	South Africa	Mpumalanga	Ngodwana, Berlin Plantation	Indigenous forest
H. californicus	GUAD52	Guadeloupe		La Boucan	*Ananas comosus* (L.) Merr.
H. californicus	GUAD54	Guadeloupe		Goyave	*Avicennia germinans* L.
H. californicus	KP1058	South Africa	Western Cape	Langebaan	*Romulea tabularis* Eckl. ex Beg.
H. californicus	KP1167	South Africa	Western Cape	Wilderness National Park	Grass
H. californicus	KP1382	South Africa	Western Cape	Hermanus, Afdaks River	Grass
H. californicus	KP1505	South Africa	Western Cape	George, Bergplaas Plantation	Natural veld
H. canalis	KP1635	South Africa	Eastern Cape	Hogsback, Ter Doone	Indigenous forest
H. carolinensis	KP36	South Africa	Eastern Cape	Aliwal North	Grass
H. cavenessi	KP1524	South Africa	Eastern Cape	East London, Shelley Beach	Grass
H. cavenessi	OVS175	South Africa	Free State	Reddersburg, farm Mostertvlakte	Natural veld
H. crenacauda	GUAD80	Guadeloupe		Petit Canal	*Bocopa monnieri* (L.) Pennell
H. crenacauda	KP1135	South Africa	Western Cape	Prince Alfred's Hamlet, farm Lentelus	Natural veld
H. crenacauda	N563	South Africa	Kwazulu-Natal	Kwambonambi, Kwambonambi Plantation	Grass
H. crenacauda	OVS334	South Africa	Free State	Golden Gate National Park, Glen Reenen	Grass
H. crenacauda	TVL0882	South Africa	Mpumalanga	Bethal	Natural veld
H. crenacauda	TVL1316	South Africa	Mpumalanga	Carolina, Ndubazi Plantation	*Eucalyptus nitens* plantation
H. crenacauda	TVL1369	South Africa	Mpumalanga	Barberton, Nelshoogte Plantation	*Pinus* plantation
H. delanus	TVL1343	South Africa	Mpumalanga	Ngodwana, Elandshoogte Plantation	*Pinus patula* plantation
H. digonicus	GUAD50	Guadeloupe		Sainte Rose, Nolivier	*Saccharum officinarum* L.
H. digonicus	KP0714	South Africa	Eastern Cape	Graaff-Reinet, Van Rhyneveldspas Dam	Natural veld
H. digonicus	KP0724	South Africa	Eastern Cape	Barkly East	Natural veld

Table 7 - continued

Species	Number	Country	Province	Locality	Associated plant/plant type
H. digonicus	KP0751	South Africa	Eastern Cape	Barkly East	Natural veld
H. digonicus	KP0784	South Africa	Eastern Cape	Rhodes, Naudesnek Pass	Natural veld
H. digonicus	KP0798	South Africa	Eastern Cape	Dordrecht	Natural veld
H. digonicus	KP0963	South Africa	Eastern Cape	Addo Elephant National Park	*Euclea* sp.
H. digonicus	KP1165	South Africa	Western Cape	Wilderness National Park, Onder Langvlei	*Cyperus papyrus* L.
H. digonicus	KP1166	South Africa	Western Cape	Wilderness National Park, Brownhooded Kingfisher Trail	Indigenous forest
H. digonicus	KP1171	South Africa	Western Cape	Wilderness National Park, Ebb & Flow Camp	Indigenous forest
H. digonicus	KP1190	South Africa	Eastern Cape	Oviston	Natural veld
H. digonicus	KP1195	South Africa	Eastern Cape	Cradock, Halesowen Experiment Farm	Natural veld
H. digonicus	KP1197	South Africa	Eastern Cape	Aberdeen	Natural veld
H. digonicus	KP1211	South Africa	Eastern Cape	Steynsburg, farm Raaswater	Natural veld
H. digonicus	KP1341	South Africa	Eastern Cape	Tarkastad	Natural veld
H. digonicus	KP1571	South Africa	Western Cape	Nature's Valley, Keurboomsrivier Plantation	Indigenous forest
H. digonicus	KP1811	South Africa	Western Cape	Genadendal	*Cyclopia maculata* (Andrews) Kies
H. digonicus	OVS156	South Africa	Free State	Reddersburg, farm Mostertvlakte	Natural veld
H. digonicus	OVS160	South Africa	Free State	Reddersburg, farm Mostertvlakte	Natural veld
H. digonicus	TVL0670	South Africa	North West	Boekenhoutfontein	*Rhus* sp.
H. digonicus	TVL0724	South Africa	North West	Stoffberg, farm Skietpad	*Leonotis leonurus*R. Br.
H. digonicus	TVL0809	South Africa	Northern Province	Vaalwater, farm Middelboomfontein	Natural veld
H. digonicus	TVL0830	South Africa	Gauteng	Zoutpan	Natural veld
H. digonicus	TVL0849	South Africa	North West	Brits, Calder Nursery	*Ficus* sp.
H. digonicus	TVL0850	South Africa	Northern Province	Rooiberg	Natural veld
H. digonicus	TVL1220	South Africa	North West	Christiana	Natural veld
H. digonicus	TVL1265	South Africa	Mpumalanga	Carolina, farm Droogvallei	*Eragrostis curvula* (Schrad.) Nees

Table 7 - continued

Species	Number	Country	Province	Locality	Associated plant/plant type
H. digonicus	TVL1478	South Africa	Mpumalanga	Graskop, God's Window	Natural veld
H. digonicus	TVL1513	South Africa	Mpumalanga	Delmas, farm Rondevlei	*Digitaria eriantha*
H. digonicus	TVL1516	South Africa	Northern Province	Marken, farm Eastland	*Sclerocarya birrea* (A. Rich.) Hochst. subsp. *caffra* Hochst.
H. dihystera	FG025	French Guiana		Suzini	Grass
H. dihystera	FG033	French Guiana		Monjoly	*Spilanthes* sp.
H. dihystera	FG036	French Guiana		Cacao	*Piper nigrum* L.
H. dihystera	FG044	French Guiana		Cayenne	Grass
H. dihystera	GUAD19B	Guadeloupe		La Jaille, Baie Mahault	*Musa acuminata* Colla
H. dihystera	KP0667	South Africa	Eastern Cape	Middelburg, caravan park	*Asclepias fruticosa*L.
H. dihystera	KP1135	South Africa	Western Cape	Prince Alfred's Hamlet, farm Lentelus	Natural veld
H. dihystera	KP1165	South Africa	Western Cape	Wilderness National Park, Onder Langvlei	*Cyperus papyrus* L.
H. dihystera	KP1257	South Africa	Northern Cape	Neilersdrif	*Gossypium hirsutum* L.
H. dihystera	KP1263	South Africa	Northern Cape	Kanoneiland, Baklei eiland	*Vitis vinifera* L.
H. dihystera	KP1276	South Africa	Northern Cape	Keimoes, Currie's Camp	Grass
H. dihystera	KP1280	South Africa	Northern Cape	Keimoes, Currie's Camp	*Zea mays* L. subsp. *mays*
H. dihystera	KP1281	South Africa	Northern Cape	Keimoes, Currie's Camp	Reeds
H. dihystera	KP1400	South Africa	Western Cape	Hermanus, Maanschynbaai	Natural veld
H. dihystera	KP1421	South Africa	Western Cape	George, Karatara	Fynbos
H. dihystera	KP1447	South Africa	Western Cape	Hemel-en-Aarde Valley	*Citrus limon* (L.) Burm. F.
H. dihystera	KP1449	South Africa	Western Cape	Hemel-en-Aarde Valley	*Malus domestica* Borkh.
H. dihystera	KP1453	South Africa	Western Cape	Hemel-en-Aarde Valley	*Daucus carota* L. subsp. *sativus* (Hoffm.) Arcang. var. *sativus* Hoffm
H. dihystera	KP1462	South Africa	Western Cape	Hemel-en-Aarde Valley	*Allium cepa* L.
H. dihystera	MART060	Martinique		Gros Morne	*Alpinia* sp.
H. dihystera	N210	South Africa	Kwazulu-Natal	Sodwana Bay	Indigenous forest

Table 7 - continued

Species	Number	Country	Province	Locality	Associated plant/plant type
H. dihystera	N348	South Africa	Kwazulu-Natal	Verulam, Oakford	*Coffea arabica* L.
H. dihystera	N349	South Africa	Kwazulu-Natal	Shakaskraal	*Lycopersicon esculentum* Mill., nom. cons. var. *esculentum*
H. dihystera	N354	South Africa	Kwazulu-Natal	Vryheid, Stillwater Motel	Grass
H. dihystera	N554	South Africa	Kwazulu-Natal	Kwambonambi, Kwambonambi Plantation	*Pinus* plantation
H. dihystera	N564	South Africa	Kwazulu-Natal	Kwambonambi, Kwambonambi Plantation	*Pinus* plantation
H. dihystera	N644	South Africa	Kwazulu-Natal	Melmoth, Mooiplaas Plantation	*Pinus* plantation
H. dihystera	N652	South Africa	Kwazulu-Natal	Anerley	*Urtica dioica* L.
H. dihystera	TVL0805	South Africa	North West	Ottoshoop	Natural veld
H. dihystera	TVL1224	South Africa	Mpumalanga	Carolina, farm Goedehoop	*Eragrostis curvula* (Schrad.) Nees
H. dihystera	TVL1226	South Africa	Mpumalanga	Carolina, farm Goedehoop	*Acacia mearnsii* De Wild.
H. dihystera	TVL1258	South Africa	Mpumalanga	Carolina, farm Roodewal	*Lolium perenne* L.
H. dihystera	TVL1260	South Africa	Mpumalanga	Carolina	Natural veld
H. dihystera	TVL1268	South Africa	Mpumalanga	Carolina, farm Haarlem	Natural veld
H. dihystera	TVL1269	South Africa	Mpumalanga	Carolina, farm Witkop	*Zea mays* L. subsp. *mays*
H. dihystera	TVL1273	South Africa	Mpumalanga	Carolina, farm Haarlem	*Medicago sativa* L. subsp. *sativa*
H. dihystera	TVL1274	South Africa	Mpumalanga	Carolina, farm Appeldoorn	*Acacia mearnsii* De Wild.
H. dihystera	TVL1324	South Africa	Mpumalanga	Piet Retief, Hlelo Plantation	Indigenous forest
H. dihystera	TVL1368	South Africa	Mpumalanga	Barberton, farm Martinsdrif	*Psidium guajava* L.
H. dihystera	TVL1381	South Africa	Mpumalanga	Barberton, Nelshoogte Plantation	*Pinus* plantation
H. dihystera	TVL1401	South Africa	Mpumalanga	Nelspruit, Weltevreden	*Psidium guajava* L.
H. dihystera	TVL1409	South Africa	Mpumalanga	Nelspruit, Friedenheim Experiment Farm	Grass
H. dihystera	TVL1418	South Africa	Mpumalanga	Nelspruit, Maggiesdale	*Persea americanum* Mill.
H. dihystera	TVL1420	South Africa	Mpumalanga	Ngodwana, Berlin Plantation	Indigenous forest
H. egyptiensis	GUAD32	Guadeloupe		La Desirade, Terre de Bas	*Avicennia germinans* L.

Table 7 - continued

Species	Number	Country	Province	Locality	Associated plant/plant type
H. egyptiensis	MART085	Martinique		Fontaine Didier	Rainforest
H. elegans	KP360	South Africa	Northern Cape	Gariepwater	Grapevine
H. erythrinae	FG020	French Guiana		Montabo	Dune vegetation
H. erythrinae	FG033	French Guiana		Montjoly	*Spilanthes* sp.
H. erythrinae	FG044	French Guiana		Cayenne	Grass
H. erythrinae	FG115	French Guiana		Tampak, on bank of Oyapock river	*Manihot esculenta* Cranyz
H. erythrinae	FG122	French Guiana		Point 28, on bank of Oyapock river	*Musa* sp.
H. erythrinae	GUAD14	Guadeloupe		Morne à l'Eau, Goffrier	Mangrove
H. erythrinae	GUAD65	Guadeloupe		Roussel Bergnolles	*Artocarpus altilis* (Parkinson)
H. erythrinae	KP1165	South Africa	Western Cape	Wilderness National Park, Onder Langvlei	*Cyperus papyrus* L.
H. erythrinae	MART071	Martinique		Reculée	*Helionea caribea*
H. erythrinae	TVL1277	South Africa	Mpumalanga	Warburton, Jessievale Plantation	*Quercus* sp.
H. erythrinae	TVL1278	South Africa	Mpumalanga	Warburton, Jessievale Plantation	Natural veld
H. erythrinae	TVL1372	South Africa	Mpumalanga	Barberton, Nelshoogte Plantation	*Leonotis leonurus* (L.) R. Br.
H. erythrinae	TVL1381	South Africa	Mpumalanga	Barberton, Nelshoogte Plantation	*Pinus* plantation
H. erythrinae	TVL1420	South Africa	Mpumalanga	Ngodwana, Berlin Plantation	Indigenous forest
H. exallus	KP0978	South Africa	Eastern Cape	Tsitsikamma National Park	Indigenous forest, *Trichocladus crinitus* (Thunb.) Pers.
H. exallus	KP0981	South Africa	Eastern Cape	Tsitsikamma National Park	Indigenous forest, *Platylophus trifoliatus* (L.f.) D.Don.
H. exallus	KP0982	South Africa	Eastern Cape	Tsitsikamma National Park	Indigenous forest, *Chionanthus foveolatus* (E.Mey.) Stearn
H. exallus	KP0983	South Africa	Eastern Cape	Tsitsikamma National Park	Indigenous forest, *Canthium mundianum* Cham. & Schlechtd.
H. exallus	KP0985	South Africa	Eastern Cape	Tsitsikamma National Park	Indigenous forest
H. exallus	KP1171	South Africa	Western Cape	Wilderness National Park, Ebb & Flow Camp	Indigenous forest
H. exallus	KP1184	South Africa	Western Cape	Kraaifontein	*Psidium guajava* L.
H. exallus	KP1350	South Africa	Western Cape	Heroldsbaai	Natural veld

Table 7 - continued

Species	Number	Country	Province	Locality	Associated plant/plant type
H. exallus	KP1413	South Africa	Western Cape	Dangerpoint	Fynbos
H. exallus	KP1505	South Africa	Western Cape	George, Bergplaas Plantation	Natural veld
H. exallus	KP1520	South Africa	Western Cape	George, Bergplaas Plantation	Natural veld
H. exallus	KP1533	South Africa	Eastern Cape	Tsitsikamma National Park, Loerie Trail	Indigenous forest, ferns
H. exallus	KP1537	South Africa	Eastern Cape	Tsitsikamma National Park, Loerie Trail	Indigenous forest - *Agapanthus praecox* Willd.
H. exallus	KP1544	South Africa	Eastern Cape	Tsitsikamma National Park, Loerie Trail	Indigenous forest, *Dietes insolens* Goldbl.
H. exallus	KP1545	South Africa	Eastern Cape	Tsitsikamma National Park, Blue Duiker Trail	Indigenous forest, ferns
H. exallus	KP1546	South Africa	Eastern Cape	Tsitsikamma National Park, Blue Duiker Trail	Indigenous forest, moss
H. exallus	KP1549	South Africa	Eastern Cape	Tsitsikamma National Park, Blue Duiker Trail	Indigenous forest
H. exallus	KP1553	South Africa	Eastern Cape	Tsitsikamma National Park, Blue Duiker Trail	Indigenous forest - *Argyrolobium collinum* Eckl. & Zeyh.
H. exallus	KP1567	South Africa	Eastern Cape	Tsitsikamma National Park, Dryfhoutbaai	Indigenous forest
H. exallus	KP1659	South Africa	Eastern Cape	Coldstream, Lottering Plantation	*Eucalyptus* plantation
H. exallus	KP1824	South Africa	Eastern Cape	East London, Amalinda Fish Station Nature Reserve	Indigenous forest, grass
H. exallus	TVL0701	South Africa	North West	Boekenhoutfontein	Grass
H. exallus	TVL0702	South Africa	North West	Boekenhoutfontein	Grass
H. exallus	TVL1277	South Africa	Mpumalanga	Warburton, Jessievale Plantation	*Quercus* sp.
H. exallus	TVL1428	South Africa	Mpumalanga	Ngodwana, Berlin Plantation	Natural veld
H. hydrophilus	KP1655	South Africa	Eastern Cape	Coldstream, Lottering Plantation	Fynbos
H. indicus	N315	South Africa	Kwazulu-Natal	uKhahlamba-Drakensberg park, Loteni Nature Reserve	Natural veld
H. indicus	OVS323	South Africa	Mpumalanga	Harrismith, Retief's Pass	Grass
H. indicus	TVL1288	South Africa	Mpumalanga	Warburton, Jessievale Plantation	Natural veld
H. indicus	TVL1322	South Africa	Mpumalanga	Carolina, Ndubazi Plantation	*Eucalyptus nitens* plantation
H. indicus	TVL1346	South Africa	Mpumalanga	Ngodwana, Elandshoogte Plantation	*Pinus elliottii* plantation
H. indicus	TVL1374	South Africa	Mpumalanga	Barberton, Nelshoogte Plantation	Natural veld, Liliaceae

Table 7 - continued

Species	Number	Country	Province	Locality	Associated plant/plant type
H. indicus	TVL1378	South Africa	Mpumalanga	Barberton, Nelshoogte Plantation	Natural veld, Liliaceae
H. indicus	TVL1700	South Africa	Mpumalanga	Dullstroom, Millstream	Natural veld
H. kermarreci	GUAD	Guadeloupe		Ilet à Caret	*Cocos nucifera* L.
H. macrostylus	FG028	French Guiana		Paracou	Primary tropical rainforest, *Dicorynia guianensis* Amshoff
H. macrostylus	FG057	French Guiana		Paracou	Primary tropical rainforest, *Eperua grindiflora* (Aubl.) Betham
H. marethae **n.sp.**	N321	South Africa	Kwazulu-Natal	uKhahlamba-Drakensberg park, Loteni Nature Reserve	Grass
H. martini	KP0721	South Africa	Eastern Cape	Middelburg, air-field	Natural veld
H. martini	KP0726	South Africa	Eastern Cape	Jamestown	Natural veld
H. martini	KP0799	South Africa	Eastern Cape	Aliwal North	Natural veld
H. martini	KP1132	South Africa	Northern Cape	Petrusville	Natural veld
H. martini	KP1189	South Africa	Eastern Cape	Oviston	Natural veld
H. martini	KP1270	South Africa	Northern Cape	Kanoneiland, farm Vrede	*Juglans nigra* L.
H. martini	KP1343	South Africa	Eastern Cape	Sterkstroom	Natural veld
H. martini	KP1505	South Africa	Western Cape	George, Bergplaas Plantation	Fynbos
H. martini	KP1862	South Africa	Eastern Cape	Tarkastad	Natural veld
H. martini	N222	South Africa	Kwazulu-Natal	Newcastle, farm Pietsrust	Natural veld
H. martini	N225	South Africa	Kwazulu-Natal	Newcastle, farm Eikenhof	Natural veld
H. martini	N226	South Africa	Kwazulu-Natal	Newcastle, farm Eikenhof	Natural veld
H. martini	N229	South Africa	Kwazulu-Natal	uKhahlamba-Drakensberg park, Loteni Nature Reserve	Natural veld
H. martini	N301	South Africa	Kwazulu-Natal	uKhahlamba-Drakensberg park, Loteni Nature Reserve	Natural veld
H. martini	N624	South Africa	Kwazulu-Natal	Newcastle, farm Moorefield	Ferns
H. martini	N633	South Africa	Kwazulu-Natal	uKhahlamba-Drakensberg park, Giant's Castle	Natural veld
H. martini	TVL0772	South Africa	Mpumalanga	Pelgrimsrust	Natural veld
H. martini	TVL1152	South Africa	Mpumalanga	Graskop, Ceylon Plantation	Grass

Table 7 - continued

Species	Number	Country	Province	Locality	Associated plant/plant type
H. martini	TVL1255	South Africa	Mpumalanga	Carolina, farm Roodewal	*Populus* sp.
H. martini	TVL1284	South Africa	Mpumalanga	Warburton, Jessievale Plantation	*Zantedeschia aethiopica* (L.) Spreng.
H. martini	TVL1286	South Africa	Mpumalanga	Warburton, Jessievale Plantation	Natural veld
H. martini	TVL1287	South Africa	Mpumalanga	Warburton, Jessievale Plantation	Ferns
H. martini	TVL1314	South Africa	Mpumalanga	Badplaas, Ndubazi Plantation	Indigenous forest
H. martini	TVL1315	South Africa	Mpumalanga	Badplaas, Ndubazi Plantation	*Eucalyptus grandis* plantation
H. martini	TVL1349	South Africa	Mpumalanga	Nelspruit, Cromdale, farm Breda	Natural veld
H. martini	TVL1352	South Africa	Mpumalanga	Nelspruit, Cromdale, farm Breda	*Litchi chinensis* L.
H. martini	TVL1364	South Africa	Mpumalanga	Barberton, farm Grasslands	Natural veld
H. martini	TVL1368	South Africa	Mpumalanga	Barberton, farm Maritzdrif	*Psidium guajava* L.
H. martini	TVL1370	South Africa	Mpumalanga	Barberton, Nelshoogte Plantation	Ferns
H. martini	TVL1405	South Africa	Mpumalanga	Nelspruit, Maggiesdale	Natural veld
H. martini	TVL1700	South Africa	Mpumalanga	Dullstroom, Millstream	Natural veld
H. microcephalus	GUAD52	Guadeloupe		La Boucan	*Ananas comosus* (L.) Merr.
H. microcephalus	KP0808	South Africa	North West	Setlagole, farm Lynn Ranch	Natural veld
H. microcephalus	KP0811	South Africa	North West	Setlagole, farm Lynn Ranch	Natural veld
H. microcephalus	KP0814	South Africa	North West	Setlagole, farm Lynn Ranch	Natural veld
H. microcephalus	KP08158	South Africa	North West	Setlagole, farm Lynn Ranch	Natural veld, *Rhus* sp.
H. microcephalus	KP0816	South Africa	North West	Setlagole, farm Lynn Ranch	Natural veld
H. microcephalus	KP1280	South Africa	Northern Cape	Keimoes, Currie's Camp	*Zea mays* L. subsp. *mays*
H. microcephalus	N545	South Africa	Kwazulu-Natal	Kwambonambi, Longfields Plantation	*Eucalyptus* plantation
H. microcephalus	N553	South Africa	Kwazulu-Natal	Nyalazi Station	*Eucalyptus* plantation
H. microcephalus	N583	South Africa	Kwazulu-Natal	Nyalazi, Nyalazi Plantation	Natural veld
H. microcephalus	TVL0786	South Africa	Mpumalanga	Orighstad, Blyde River Nature Reserve	Natural veld

Table 7 - continued

Species	Number	Country	Province	Locality	Associated plant/plant type
H. microcephalus	TVL0796	South Africa	Mpumalanga	Lydenburg, Long Tom Pass	Grass
H. microcephalus	TVL1212	South Africa	Gauteng	Pretoria-North, Waterval	*Citrus sinensis* (L.) Osbeck
H. microcephalus	TVL1283	South Africa	Mpumalanga	Warburton, Jessievale Plantation	Natural veld
H. microcephalus	TVL1387	South Africa	Mpumalanga	Nelspruit, Weltevreden, farm Hilltop	*Mangifera indica* L.
H. minutus	MART	Martinique		Mount Pelee	Natural veld
H. minzi	KP1149	South Africa	Eastern Cape	Hofmeyer, farm Spitskop	Natural veld
H. minzi	N249	South Africa	Kwazulu-Natal	uKhahlamba-Drakensberg park, Loteni Nature Reserve	Natural veld
H. minzi	N276	South Africa	Kwazulu-Natal	uKhahlamba-Drakensberg park, Loteni Nature Reserve	Grass
H. minzi	TVL0579	South Africa	Northern Province	Steilloop	Natural veld, *Acacia* sp.
H. minzi	TVL0617	South Africa	Gauteng	Bronkhorstspruit, Tierpoort	Natural veld
H. minzi	TVL0779	South Africa	Mpumalanga	Orighstad, Blyde River Nature Reserve	Natural veld
H. minzi	TVL1354	South Africa	Mpumalanga	Nelspruit, farm Cromdale	Natural veld
H. minzi	TVL1403	South Africa	Mpumalanga	Nelspruit, Maggiesdale	Grass
H. minzi	TVL1464	South Africa	Mpumalanga	Ngodwana, Berlin Plantation	Natural veld
H. minzi	TVL1591	South Africa	Northern Province	Nylstroom, farm Olifantspoort	Natural veld, *Protea* sp.
H. minzi	TVL1676	South Africa	Northern Province	Nylstroom, Hoeksteen Boerdery	Natural veld
H. minzi	TVL1677	South Africa	Northern Province	Nylstroom, Hoeksteen Boerdery	Natural veld
H. minzi	TVL1700	South Africa	Mpumalanga	Dullstroom, Millstream	Natural veld
H. mucronatus	GUAD55	Guadeloupe		Goyave, Bonfilis	Rainforest
H. mucronatus	GUAD63	Guadeloupe		Sainte Rose, Grande riviere de Goyave	*Avicennia germinans* (L.) L.
H. multicinctus	FG098	French Guiana		Maripasoula	*Euterpe oleracea*Mart.
H. multicinctus	FG122	French Guiana		Ile Portal	*Astrocaryum vulgare* Mart.
H. multicinctus	GUAD19B	Guadeloupe		La Jaille	*Musa acuminata* Colla
H. multicinctus	KP1343	South Africa	Eastern Cape	Sterkstroom	Natural veld

Table 7 - continued

Species	Number	Country	Province	Locality	Associated plant/plant type
H. multicinctus	KP1823	South Africa	Eastern Cape	East London, Shelley Beach	Grass
H. multicinctus	N345	South Africa	Kwazulu-Natal	Port Edward, farm Downsouth	*Musa* x *paradisiaca* L.
H. multicinctus	N564	South Africa	Kwazulu-Natal	Kwambonambi, Kwambonambi Plantation	*Pinus* plantation
H. multicinctus	N650	South Africa	Kwazulu-Natal	Anerley	*Musa* x *paradisiaca* L.
H. multicinctus	TN0785	South Africa	Mpumalanga	Witrivier, Burgershall ARC-ITSC experiment farm	*Musa* x *paradisiaca* L.
H. multicinctus	TVL1408	South Africa	Mpumalanga	Nelspruit, Maggiesdale	*Musa* x *paradisiaca* L.
H. multicinctus	Union Island 03	Union Island		Richmond Bay	Natural veld
H. paracanalis	TVL1420	South Africa	Mpumalanga	Ngodwana, Berlin Plantation	Indigenous forest
H. paraplatyurus	KP0808	South Africa	North West	Setlagole, farm Lynn Ranch	Natural veld
H. paraplatyurus	KP1371	South Africa	Western Cape	George, Saasveld Forestry College	Indigenous forest
H. paraplatyurus	KP1505	South Africa	Western Cape	George, Bergplaas Plantation	Fynbos
H. paraplatyurus	KP1534	South Africa	Eastern Cape	Tsitsikamma National Park, Loerie Trail	Indigenous forest
H. paraplatyurus	N389	South Africa	Kwazulu-Natal	Heatonville	*Saccharum officinarum* L.
H. paraplatyurus	OVS171	South Africa	Free State	Reddersburg, farm Mostertvlakte	Natural veld
H. paraplatyurus	TVL0844	South Africa	Northern Province	Rooiberg	Natural veld
H. paraplatyurus	TVL1401	South Africa	Mpumalanga	Nelspruit, Weltevreden	*Psidium guajava* L.
H. paraplatyurus	TVL1476	South Africa	Northern Province	Warmbad, Mabalingwe	*Aloe transvaalensis* Kuntze
H. paraplatyurus	TVL1477	South Africa	Northern Province	Warmbad, Mabalingwe	*Crinum* sp.
H. planquettei	FG077	French Guiana		Saül	Primary tropical rainforest, *Dicorynia guianensis* Amshoff
H. pseudorobustus	FG033	French Guiana		Montjoly	*Spilanthes* sp.
H. pseudorobustus	FG044	French Guiana		Cayenne	Grass
H. pseudorobustus	FG066	French Guiana		Carbet Bertranc	Ferns
H. pseudorobustus	KP1154	South Africa	Northern Cape	Loxton	Natural veld
H. pseudorobustus	KP1183	South Africa	Eastern Cape	Graaff-Reinet	Grass

Table 7 - continued

Species	Number	Country	Province	Locality	Associated plant/plant type
H. pseudorobustus	KP1184	South Africa	Western Cape	Kraaifontein	*Psidium guajava* L.
H. pseudorobustus	KP1289	South Africa	Northern Cape	Dyasonsklip, McTaggert's Camp	*Vitis vinifera* L.
H. pseudorobustus	KP1592	South Africa	Western Cape	Swartberg Nature Reserve, Gamkaskloof	*Medicago sativa*L. subsp. *sativa*
H. pseudorobustus	KP1593	South Africa	Western Cape	Swartberg Nature Reserve, Gamkaskloof	*Chrysocoma ciliata* L.
H. pseudorobustus	KP1594	South Africa	Western Cape	Swartberg Nature Reserve, Gamkaskloof	*Zea mays* L. subsp. *mays*
H. pseudorobustus	KP1825	South Africa	Eastern Cape	East London, Amalinda Fish Station Nature Reserve	Indigenous forest, grass
H. pseudorobustus	MART093	Martinique		Reculée	Rainforest
H. pseudorobustus	N221	South Africa	Kwazulu-Natal	Babanango	Grass
H. pseudorobustus	N225	South Africa	Kwazulu-Natal	Newcastle, farm Eikenhof	Natural veld
H. pseudorobustus	N242	South Africa	Kwazulu-Natal	uKhahlamba-Drakensberg park, Loteni Nature Reserve	Natural veld
H. pseudorobustus	N245	South Africa	Kwazulu-Natal	uKhahlamba-Drakensberg park, Loteni Nature Reserve	Natural veld
H. pseudorobustus	N272	South Africa	Kwazulu-Natal	uKhahlamba-Drakensberg park, Loteni Nature Reserve	Natural veld - *Zanthedeschia* sp.
H. pseudorobustus	N289	South Africa	Kwazulu-Natal	uKhahlamba-Drakensberg park, Loteni Nature Reserve	Natural veld - *Eucomis* sp.
H. pseudorobustus	N301	South Africa	Kwazulu-Natal	uKhahlamba-Drakensberg park, Loteni Nature Reserve	Natural veld
H. pseudorobustus	OVS145	South Africa	Free State	Reddersburg	Grass
H. pseudorobustus	TVL0786	South Africa	Mpumalanga	Orighstad, Blyde River Nature Reserve	Natural veld
H. pseudorobustus	TVL1219	South Africa	Gauteng	Pretoria-North	*Cynara cardunculusi* L. subsp. *cardunculus*
H. pseudorobustus	TVL1266	South Africa	Mpumalanga	Carolina, farm Droogvallei	*Eucalyptus* sp.
H. pseudorobustus	TVL1329	South Africa	Mpumalanga	Piet Retief, Hlelo Plantation	*Acacia mearnsii* plantation
H. pseudorobustus	TVL1332	South Africa	Mpumalanga	Piet Retief, Hlelo Plantation	*Pinus taeda* plantation
H. pseudorobustus	TVL1370	South Africa	Mpumalanga	Barberton, Nelshoogte Plantation	Ferns
H. pseudorobustus	TVL1374	South Africa	Mpumalanga	Barberton, Nelshoogte Plantation	Natural veld, Liliaceae
H. pseudorobustus	TVL1436	South Africa	Mpumalanga	Ngodwana, Berlin Plantation	Indigenous forest
H. pseudorobustus	TVL1476	South Africa	Northern Province	Warmbad, Mabalingwe	*Aloe transvaalensis* Kuntze

Table 7 - continued

Species	Number	Country	Province	Locality	Associated plant/plant type
H. retusus	MART091	Martinique		St Anne	Natural veld
H. serenus	KP1200	South Africa	Western Cape	Prins Albert. farm Lammerkraal	Natural veld
H. serenus	KP1341	South Africa	Eastern Cape	Tarkastad	Natural veld
H. serenus	KP1343	South Africa	Eastern Cape	Sterkstroom	Natural veld
H. serenus	KP1421	South Africa	Western Cape	George, Karatara	Fynbos
H. serenus	KP1630	South Africa	Eastern Cape	Baviaanskloof Wilderness Area, Bergplaas	Grass
H. serenus	TVL0854	South Africa	North West	Northam	Natural veld
H. stylocercus	MART113	Martinique		Piton Dumauze	
H. tumidicaudatus	OVS114	South Africa	Free State	Winburg	Grass
H. tumidicaudatus	TVL1212	South Africa	Gauteng	Pretoria-North, Waterval	*Citrus sinensis* (L.) Osbeck
H. variabilis	TVL1404	South Africa	Mpumalanga	Nelspruit, Maggiesdale	*Rhoicissus* sp.
H. vulgaris	KP1240	South Africa	Northern Cape	Upington	*Tagetes minuta* L.
H. vulgaris	KP1243	South Africa	Northern Cape	Upington, Straussburg Estate	*Olea europaea* L. subsp. *europaea*
H. vulgaris	KP1255	South Africa	Northern Cape	Neilersdrif, Peace eiland	*Vitis vinifera* L.
H. vulgaris	KP1256	South Africa	Northern Cape	Keimoes, Smitseiland	*Vitis vinifera* L.
H. vulgaris	KP1289	South Africa	Northern Cape	Dyasonsklip, McTaggert's Camp	*Vitis vinifera* L.
H. vulgaris	KP1293	South Africa	Northern Cape	Upington, farm Klippunt	*Phoenix dactylifera* L.
H. vulgaris	KP1298	South Africa	Northern Cape	Keimoes, Tierberg Reserve	Natural veld
H. vulgaris	KP1773	South Africa	Northern Cape	Vaallus, farm Rooidam	*Vitis viniferaL.*
H. vulgaris	TVL1483	South Africa	Northern Province	Kruger National Park, Punda Maria	*Ficus sycomorus*
H. willmottae	KP1343	South Africa	Eastern Cape	Sterkstroom	Natural veld
H. willmottae	TVL1530	South Africa	North West	Hartbeespoort, Glenwood Farm	Natural veld

Table 8. Morphometric data of *H. africanus*, *H. anhelicus* and *H. areolatus*

	H. africanus		*H. anhelicus*		*H. areolatus*	
	South Africa		South Africa		South Africa	
Characters[a]	30 ♀♀	4♂♂	14 ♀♀	14 ♂♂	13 ♀♀	1 ♂
L	767 ± 70.6 (628-911)	719 (197-742)	677 ± 39.8 (630-770)	672± 42.9 (603-766)	468 ± 33.0 (410-541)	520
a	33.8 ± 5.5 (19.3-43.3)	39.4 (37.0-42.9)	25.0 ± 22.0 (22.1-28.7)	29.5 ± 2.4 (24.5-32.5)	23.8 ± 2.9 (20.7-29.6)	25.6
b	6.1 ± 0.5 (5.1-6.7)	5.7	5.3	5.7	4.5 ± 0.4 (4.0-5.1)	-
b'	5.1 ± 0.4 (4.2-6.0)	4.8 (4.4-5.4)	4.8 ± 0.3 (4.4-5.1)	4.6 ± 0.4 (4.2-5.3)	4.2 ± 0.7 (3.3-5.2)	4.5
c	28.4 ± 3.0 (21.2-33.4)	33.6 (32.1-37.2)	48.8 ± 0.3 (40.9-58.4)	31.8 ± 3.2 (27.5-38.0)	42.6 ± 4.1 (36.9-50.5)	31.7
c'	1.8 ±0.3 (1.2-2.3)	1.8 (1.4-1.9)	0.9 ±0.1 (0.8-1.1)	1.7 ± 0.2 (0.8-1.1)	0.9 ± 0.1 (0.9-1.1)	1.5
DGO	10 ± 1.3 (8-12)	10 (9-11)	13 ± 1.0 (11-15)	13 ± 1.6 (11-15)	7 ± 0.5 (6-8)	-
o	33 ± 5.1 (26-41)	44 (35-48)	43 ± 2.9 (39-49)	49 ± 5.4 (42-57)	33 ± 1.6 (30-35)	-
Stylet length	29 ± 1.2 (26-31)	24 (23-24)	30 ± 1.0 (28-32)	27 ± 0.9 (26-29)	23 ± 1.3 (21-25)	21
m	47± 1.9 (43-50)	44 (41-47)	48 ± 1.5 (46-51)	49 ± 1.3 (47-51)	44 ± 1.9 (41-47)	43
V	62 ± 1.9 (59-66)	-	63 ± 1.5 (60-66)	-	64 ± 2.4 (21-25)	-
OV_1	28 ± 7.8 (22-33)	-	27 ± 3.9 (20-31)	-	-	-
OV_2	27 ± 10.9 (19-35)	-	21 ± 2.6 (17-25)	-	-	-
T	-	-	-	39 ± 5.0 (29-44)	-	-
Spicule length	-	23 (19-25)	-	26 ± 1.5 (24-29)	-	22
Gubernaculum length	-	8 (7-9)	-	9 ± 0.9 (8-11)	-	-
Excretory pore/Oesophagus length[b] (%)	74 ± 5.7 (64-87)	77 (74-79)	70 ± 2.2 (68-73)	64 ± 3.6 (58-68)	77 ± 4.8 (69-83)	83

[a] All measurements in µm
[b] Length to end of glands

Table 9. Morphometric data of *H. brevis* and *H. californicus*

	H. brevis		*H. californicus*		*H. californicus*	
	South Africa		Guadeloupe islands		South Africa	
Characters[a]	50 EE	16 ♂♂	26 EE	16♂♂	26EE	12♂♂
L	480 ± 46.9 (376-594)	415 ± 27.5 (362-477)	669 ± 50.8 (565-747)	639 ± 62.8 (515-782)	769 ± 98.4 (599-936)	691 ± 52.9 (592-755)
a	22.0 ± 2.6 (16.9-27.9)	28.5 ± 2.2 (24.7-32.1)	25.7 ± 2.9 (20.1-30.9)	30.3 ± 4.1 (24.5-38.0)	27.8 ± 3.7 (22.1-35.3)	30.9 ± 2.5 (27.0-35.8)
b	4.6 ± 0.3 (4.4-5.0)	4.4-4.5 (n = 2)	4.8 ± .2 (4.6-5.0)	4.9	5.5 ± 0.5 (5.0-6.4)	5.4
b'	4.1 ± 0.6 (2.8-5.2)	4.0 ± 0.6 (2.8-5.2)	4.5 ± 0.2 (3.9-5.1)	4.4 ± 0.5 (3.4-5.1)	5.4 ± 0.5 (4.5-6.2)	5.1 ± 0.5 (4.2-5.7)
c	55.3 ± 9.8 (29.2-107.7)	30.6 ± 2.4 (26.3-35.6)	36.7 ± 6.0 (24.6-49.6)	28.8 ± 2.9 (23.1-33.3)	35.7 ± 4.4 (26.4-44.7)	29.0 ± 3.9 (24.7-39.4)
c'	0.7 ± 1.0 (0.3-0.9)	1.5 ± 0.2 (1.2-2.0)	1.3 ± 0.2 (0.9-1.8)	1.7 ± 0.2 (1.5-2.1)	1.2 ± 0.1 (1.0-1.5)	1.8 ± 0. (1.3-2.1)
DGO	8 ± 1.4 (6-12)	7 ± 1.8 (6-9)	12 ± 1.5 (9-14)	13 ± 1.2 (12-14)	11 ± 0.9 (9-12)	11 ± 1.1 (9-12)
o	26 ± 4.8 (19-40)	31 ± 6.9 (24-38)	44 ± 5.7 (35-52)	54 ± 4.5 (49-58)	41 ± 5.3 (35-52)	44 ± 5.8 (38-48)
Stylet length	31 ± 1.9 (25-34)	21 ± 1.8 (19-25)	27 ± 0.9 (26-29)	25 ± 1.0 (23-27)	26 ± 1.3 (26-28)	24 ± 1.0 (22-25)
m	50 ± 1.5 (46-53)	49 ± 2.2 (46-52)	49 ± 2.3 (45-53)	50 ± 3.0 (44-54)	47 ± 2.7 (43-51)	50 ± 2.4 (46-52)
V	88 ± 1.8 (83-91)	-	63 ± 1.9 (59-66)	-	63 ± 1.6 (60-67)	-
OV_1	30 ± 6.2 (20-39)	-	25 ± 3.7 (20-32)	-	6 ± 3.2 (21-31)	-
OV_2	3 ± 0.9 (2-6)	-	21 ± 2.6 (18-26)	-	22 ± 2.3 (19-25)	-
T	-	-	-	56 ± 4.1 (53-59)	-	-
Spicule length	-	17 ± 1.3 (15-17)	-	25 ± 1.2 (23-28)	-	26 ± 1.2 (24-28)
Gubernaculum length	-	7	-	9 ± 1.1 (6-10)	-	8 ± 1.3 (6-10)
Excretory pore/ Oesophagus length (%)[b]	74 ± 7.9 (57-89)	71 ± 4.4 (63-76)	75 ± 4.1 (69-84)	78 ± 5.2 (69-88)	83 ± 6.5 (69-95)	76 ± 2.8 (72-79)

[a] All measurements in µm
[b] Length to end of glands

Table 10. Morphometric data of *H. canalis, H. carolinensis, H. cavenessi* and *H. crenacauda*

	H. canalis	*H. caroliniensis*	*H. cavenessi*	*H. crenacauda*		
	South Africa	South Africa[a]	South Africa	Guadeloupe	South Africa	
Characters[b]	17 EE	1 E	18 EE	9 EE	34 EE	5 ГГ
L	859 ± 66.8 (703-958)	700	592 ± 67.0 (512-781)	703 ± 43.8 (636-760)	592 ± 89.3 (419-748)	538 ± 72.4 (463-658)
a	23.4 ± 2.0 (20.6-26.8)	25.0	22.7 ± 3.0 (17.3-30.7)	23.7 ± 1.8 (21.1-27.0)	24.7 ± 3.3 (18.1-30.2)	29.5 ± 2.0 (27.5-32.3)
b	5.2 ± 0.9 (4.1-6.7)	-	4.7 ± 0.2 (4.4-4.9)	5.6 ± 0.5 (5.0-6.0)	5.0 ± 1.1 (3.8-8.7)	5.4 ± 0.6 (5.0-5.8)
b'	4.8 ± 0.4 (4.0-5.5)	4.3	4.4 ± 0.4 (3.7-5.7)	4.7 ± 0.3 (4.3-5.1)	4.7 ± 0.6 (3.9-6.3)	4.6 ± 0.5 (4.0-5.2)
c	44.2 ± 6.5 (34.0-55.5)	38.8	39.4 ± 5.8 (31.3-58.0)	39.2 ± 3.7 (34.4-44.5)	32.7 ± 5.9 (21.1-50.6)	30.5 ± 4.9 (25.0-36.7)
c'	0.9 ± 3.1 (0.8-1.2)	1.2	1.0 ± 0.1 (0.8-1.3)	1.2 ± 0.1 (1.0-1.4)	1.3 ± 0.2 (1.0-2.0)	1.7 ± 0.3 (1.3-2.0)
DGO	11 ± 1.0 (9-12)	-	10 ± 0.5 (10-11)	9 ± 0.9 (8-10)	10 ± 1.6 (8-13)	8 ± 2.8 (6-10)
o	26 ± 3.1 (21-31)	39.4	41 ± 3.0 (37-45)	32 ± 3.1 (29-38)	43 ± 6.1 (33-56)	43 ± 3.8 (41-46)
Stylet length	40 ± 1.7 (38-43)	26.1	26 ± 1.5 (23-19)	27 ± 1.3 (25-28)	25 ± 2.5 (21-28)	23 ± 2.3 (21-26)
m	50 ± 1.5 (47-53)	45	48 ± 1.6 (44-50)	47 ± 1.3 (45-49)	45 ± 2.0 (42-51)	44 ± 3.0 (41-48)
V	60 ± 2.4 (55-63)	60	63 ± 2.7 (62-66)	63 ± 1.2 (62-65)	63 ± 2.0 (60-67)	-
OV_1	20 ± 3.8 (17-27)	-	28 ± 15.5 (20-41)	26 ± 2.9 (23-31)	26 ± 5.0 (21-37)	-
OV_2	19 ± 2.8 (17-23)	-	22 ± 3.1 (109-128)	22 ± 1.6 (19-23)	19 ± 3.6 (15-25)	-
T	-	-	-	-	-	-
Spicule length	-	-	-	-	-	21 ± 2.5 (19-25)
Gubernaculum length	-	-	-	-	-	9 ± 2.1 (7-11)
Excretory pore/Oesophagus length[c] (%)	75 ± 4.2 (69-82)	-	76 ± 4.8 (67-85)	72 ± 3.4 (69-78)	73 ± 6.4 (59-85)	74 ± 5.3 (68-77)

[a] According to Van den Berg & Heyns (1975)
[b] All measurements in µm.
[c] Length to end of glands

Table 11. Morphometric data on *H. digonicus* and *H. dihystera*

	H. digonicus		*H. dihystera*			
	Guadeloupe	South Africa	French Guiana	Guadeloupe	Martinique	South Africa
Characters[a]	12 EE	146 EE	29 EE	9 EE	4 EE	131 EE
L	579 ± 37.3 (525-632)	682 ± 72.1 (541-874)	604 ± 80.5 (440-754)	625 ± 55.6 (533-715)	570 (518-610)	653 ± 89.1 (457-894)
a	25.0 ± 1.9 (21.8-28.4)	26.2 ± 3.4 (19.1-35.4)	24.0 ± 3.4 (18.1-33.3)	26.2 ± 1.1 (24.9-27.9)	27.1 (25.4-281)	26.2 ± 3.7 (18.1-47.0)
b	4.9 ± 0.3 (4.5-5.3)	5.3 ± 0.6 (4.3-6.5)	4.9 ± 0.6 (4.2-6.0)	-	-	4.9 ± 0.6 (3.7-6.5)
b'	4.6 ± 0.4 (4.0-5.1)	4.6 ± 0.5 (3.5-6.3)	4.4 ± 0.4 (3.8-5.0)	4.4 ± 0.4 (4.0-5.2)	4.1 (3.7-4.6)	4.7 ± 0.7 (3.4-6.8)
c	44.4 ± 3.4 (38.7-48.2)	44.3 ± 8.6 (28.7-83.0)	36.9 ± 6.1 (23.5-46.9)	39.8 ± 5.1 (32.6-51.3)	46.6 (35.5-57.1)	39.1 ± 7.6 (15.3-59.9)
c'	1.0 ± 0.1 (0.7-1.2)	1.1 ± 0.2 (0.5-1.6)	1.1 ± 0.2 (0.9-1.5)	1.1 ± 0.1 (0.8-1.2)	1.0 (0.8-1.4)	1.2 ± 0.2 (0.7-1.2)
DGO	9 ± 1.0 (8-11)	10 ± 1.6 (9-16)	12 ± 2.0 (8-14)	11 ± 1.2 (9-12)	10 (10-11)	12 ± 1.8 (8-17)
o	36 ± 2.6 (33-41)	39 ± 5.7 (31-58)	46 ± 5.8 (36-56)	41 ± 3.9 (37-48)	41 (36-45)	44 ± 6.6 (30-66)
Stylet length	24 ± 1.3 (22-26)	27 ± 1.7 (23-31)	25 ± 2.1 (20-28)	25 ± 0.9 (24-27)	24 (23-26)	26 ± 1.8 (22-31)
m	49 ± 1.4 (49-54)	48 ± 2.1 (41-52)	48 ± 2.0 (42-52)	51 ± 1.4 (49-54)	47 (46-49)	48 ± 2.3 (42-58)
V	62 ± 1.2 (60-64)	64 ± 2.2 (57-70)	64 ± 2.3 (60-72)	65 ± 1.4 (63-68)	65 (63-66)	64 ± 1.9 (57-69)
OV_1	19 ± 0.6 (19-20)	25 ± 5.4 (13-39)	24 ± 1.9 (22-27)	25 ± 4.1 (22-29)	25 (23-26)	23 ± 4.5 (12-33)
OV_2	17 ± 0.7 (16-18)	21 ± 4.0 (14-33)	22 ± 2.6 (18-26)	24 ± 2.6 (22-26)	22	20 ± 3.8 (14-32)
T	-	-	-	-	-	-
Spicule length	-	-	-	-	-	-
Gubernaculum length	-	-	-	-	-	-
Excretory pore/Oesophagus Length[b] (%)	76 ± 5.0 (66-83)	74 ± 6.4 (54-92)	75 ± 7.4 (52-85)	78 ± 4.5 (74-84)	71 (67-75)	76 ± 6.5 (56-93)

[a] All measurements in µm
[b] Lengt to end of glands

Table 12. Morphometric data of *H. egyptiensis, H. elegans, H. exallus* and *H. hydrophilus*.

	H. egyptiensis		*H. elegans*	*H. exallus*		*H. hydrophilus*
	Guadeloupe	Martinique	South Africa [a]	South Africa		South Africa
Characters[b]	12 EE	14 EE	1 E	88 EE	45 ГГ	1 E
L	699 ± 57.3 (620-811)	611 ± 22.7 (588-649)	700	616 ± 59.4 (482-761)	561 ± 48.0 (438-658)	890
a	23.9 ± 2.2 (20.1-28.2)	25.5 ± 1.8 (22.2-28.1)	27.2	24.5 ± 3.0 (18.3-36.1)	28.3 ± 2.9 (22.7-34.9)	-
b	-	4.8± 0.2 (4.6-4.9)	5.2	4.8 ± 0.6 (3.8-6.2)	4.9 ± 0.4 (4.2-5.4)	-
b'	5.1 ± 0.4 (4.5-5.6)	4.3 ± 0.1 (4.0-4.4)	4.3	4.6 ± 0.5 (3.7-6.4)	4.4 ± 0.3 (3.5-5.1)	5.4
c	39.5 ± 4.6 (33.2-48.7)	26.5 ± 2.6 (20.1-30.4)	26.1	41.2 ± 7.9 (28.2-66.9)	30.6 ± 6.6 (21.7-40.9)	41.1
c'	1.1 ± 0.1 (1.0-1.3)	1.9 ± 0.2 (1.6-2.5)	1.6	1.0 ± 0.2 (0.5-1.4)	1.5 ± 0.2 (1.1-2.2)	1.3
DGO	10 ± 0.5 (9-10)	10 ± 0.3 (10-11)	-	11 ± 1.3 (8-13)	10 ± 0.8 (9-11)	12
o	38 ± 3.9 (36-41)	40 ± 2.1 (37-44)	40.0	39 ± 6.5 (25-52)	41 ± 3.8 (34-48)	41
Stylet length	25 ± 0.7 (24-26)	25 ± 0.8 (24-27)	27.5	28 ± 2.2 (25-32)	24 ± 1.4 (21-27)	30
m	49 ± 2.1 (46-53)	47 ± 1.5 (45-51)	48	48 ± 2.3 (42-52)	51 ± 4.5 (48-55)	49
V	60 ± 2.4 (54-63)	62 ± 1.0 (60-64)	60	64 ± 2.2 (59-69)	-	63
OV_1	26 ± 4.5 (20-31)	18 ± 2.3 (17-20)	28	24 ± 4.2 (16-34)	-	-
OV_2	22 ± 3.1 (17-27)	-	21	21 ± 3.5 (16-29)	-	-
T	-	-	-	-	-	-
Spicule length	-	-	-	-	23 ± 1.4 (21-27)	-
Gubernaculum length	-	-	-	-	8 ± 1.1 (6-10)	-
Excretory pore/Oesophagus length[c] (%)	76 ± 4.2 (68-81)	78 ± 3.7 (73-85)	-	73 ± 5.2 (62-87)	74 ± 6.7 (61-89)	-

[a] According to Van den Berg & Heyns (1975).
[b] All measurements in µm.
[c] Length to end of glands

Table 13. Morphometric data of *H. erythrinae*

Characters[a]	*H. erythrinae*					
	French Guiana		Guadeloupe		South Africa	
	38EE	11ΓΓ	18EE	13ΓΓ	23EE	14ΓΓ
L	649 ± 89.4 (463-797)	630 ± 56.5 (552-737)	649 ± 64.4 (547-760)	511 ± 29.1 (464-576)	596 ± 66.6 (489-706)	539 ± 51.7 (454-618)
a	25.6 ± 2.7 (19.5-29.5)	32.5 ± 4.0 (36.0-38.9)	26.4 ± 2.7 (22.3-30.8)	31.8 ± 2.3 (28.8-35.2)	27.5 ± 3.6 (21.0-33.5)	29.2 ± 3.1 (24.8-35.4)
b	5.3 ± 0.5 (4.4-5.8)	5.5 ± 0.3 (5.3-5.9)	5.3 ± 0.4 (4.8-6.4)	4.5 ± 0.3 (4.3-4.8)	4.6	5.2 ± 0.1 (5.0-5.3)
b'	4.6 ± 0.4 (3.8-5.0)	4.5 ± 0.4 (3.8-5.3)	4.8 ± 0.4 (3.8-5.4)	4.1 ± 0.2 (3.8-4.6)	4.3 ± 0.5 (3.4-5.0)	4.2 ± 0.3 (3.7-4.8)
c	33.4 ± 4.9 (24.0-46.8)	32.8 ± 2.7 (27.6-37.5)	29.2 ± 2.8 (23.3-33.5)	25.4 ± 2.6 (19.1-29.8)	30.3 ± 5.0 (22.7-41.8)	30.3 ± 3.8 (25.0-35.8)
c'	1.3 ± 0.2 (1.0-1.8)	1.7 ± 0.1 (1.5-1.9)	1.5 ± 0.2 (1.3-1.9)	1.8 ± 0.3 (1.4-2.4)	1.3 ± 0.2 (1.0-1.7)	1.6 ± 0.2 (1.2-2.1)
DGO	17 ± 4.2 (8-23)	15 ± 3.0 (10-20)	11 ± 1.1 (9-12)	10-11 (*n* = 2)	10 ± 0.8 (8-11)	9 ± 1.1 (8-12)
o	68 ± 15.3 (36-90)	67 ± 12.5 (46-87)	43 ± 4.4 (33-51)	47	36 ± 4.0 (32-47)	37 ± 4.7 (33-49)
Stylet length	24.1 ± 1.6 (21-28)	22 ± 1.0 (20-24)	25 ± 1.2 (23-28)	22 ± 0.9 (20-23)	28 ± 3.6 (26-30)	24 ± 0.6 (23-25)
m	47 ± 1.8 (44-53)	48 ± 1.8 (44-52)	50 ± 1.5 (47-53)	51 ± 1.6 (48-54)	50 ± 1.5 (47-52)	52 ± 1.6 (49-54)
V	62 ± 1.6 (59-65)	-	63 ± 1.8 (60-66)	-	64 ± 2.2 (60-69)	-
OV_1	21 ± 3.4 (15-29)	-	23 ± 6.3 (17-35)	-	27 ± 9.3 (20-41)	-
OV_2	9 ± 2.4 (17-24)	-	22 ± 7.7 (14-35)	-	21 ± 0.5 (20-21)	-
T	-	41 ± 4.4 (32-50)	-	44 ± 11.2 (29-64)	-	41 ± 4.4 (32-50)
Spicule length	-	23 ± 1.1 (21-25)	-	19 ± 1.5 (15-21)	-	21 ± 1.5 (18-23)
Gubernaculum length	-	8 ± 0.4 (8-9)	-	6 ± 0.3 (5-6)	-	7 ± 0.5 (6-8)
Excretory pore/Oesophagus length[b] (%)	73 ± 4.0 (63-84)	72 ± 4.3 (65-90)	73 ± 6.2 (55-82)	69 ± 7.9 (47-77)	73 ± 5.2 (65-82)	75 ± 5.7 (68-84)

[a] All measurements in µm
[b] Length to end of glands

Table 14. Morphometric data of *H. indicus*, *H. kermarreci* and *H. macrostylus*.

	H. indicus		*H. kermarreci*		*H. macrostylus*	
	South Africa		Guadeloupe		French Guiana	
Characters[a]	51 ♀♀	1 ♂	11 ♀♀	8♂♂	24 ♀♀	15 ♂♂
L	557 ± 51.0 (436-657)	546	628 ± 57.9 (496-700)	555 ± 33.0 (527-625)	1020 ± 65.6 (853-1150)	873 ± 47.3 (811-964)
a	25.0 2.8 (19.4-31.7)	28.1	31.3 ± 3.4 (26.1-36.6)	32.8 ± 2.0 (30.6-35.7)	24.3 ± 2.5 (20.4-28.9)	31.5 ± 3.2 (26.9-38.3)
b	4.7 ± 0.5 (4.0-5.5)	4.7	4.9 ± 0.7 (3.9-5.7)	4.3 ± 0.5 (3.9-4.8)	4.7 ± 0.3 (4.1-5.0)	5.3 ± 0.2 (5.2-5.5)
b'	4.4 ± 0.5 (3.2-5.4)	4.1	4.3 ± 0.4 (3.5-4.9)	3.8 ± 0.2 (3.6-4.2)	4.6 ± 0.3 (4.0-5.0)	4.8 ± 0.2 (4.5-5.2)
c	26.4 ± 3.8 (21.1-36.2)	26.5	40.0 ± 7.2 (26.4-49.8)	33.6 ± 2.9 (27.8-36.9)	54.5 ± 10.9-(39.6-78.0)	40.1 ± 3.1 (34.3-45.5)
c'	1.7 ± 0.3 (1.2-2.4)	1.9	1.1 ± 0.1 (0.9-1.3)	1.3 ± 0.2 (0.8-1.6)	0.8 ± 0.1 (0.6-0.9)	1.2 ± 0.1 (1.0-1.5)
DGO	9 ± 1.3 (7-12)	-	8 ± 1.0 (6-9)	-	18 ± 1.8 (14-20)	15 ± 1.4 (13-17)
o	32 ± 4.5 (26-43)	-	38 ± 4.9 (29-44)	-	42 ± 4.2 (35-48)	46 ± 3.9 (41-51)
Stylet length	27 ± 1.6 (24-30)	23	21 ± 0.8 (20-22)	18 ± 0.7 (17-19)	43 ± 1.2 (42-45)	34 ± 1.4 (32-37)
m	51 ± 2.4 (47-57)	53	49 ± 1.9 (45-51)	52 ± 3.6 (48-55)	52 ± 1.6 (48-55)	52 ± 1.8 (50-56)
V	65 ± 2.0 (61-70)	-	63 ± 1.5 (59-65)	-	64 ± 0.9 (63-67)	-
OV_1	25 ± 3.3 (20-33)	-	16 ± 2.2 (12-19)	-	23 ± 7.9 (15-37)	-
OV_2	14 ± 2.8 (11-17)	-	16 ± 3.3 (13-23)	-	20 ± 6.9 (15-34)	-
T	-	-	-	38 ± 2.5 (35-42)	-	-
Tail length	23 ± 3.0 (17-28)	21	16 ± 2.9 (10-19)	16 ± 2.5 (15-19)	19 ± 3.2 (13-24)	22 ± 2.3 (20-27)
Spicule length	-	21	-	19 ± 0.7 (18-20)	-	32 ± 0.8 (31-33)
Gubernaculum length	-	6	-	6	-	11 ± 1.3 (9-13)
Excretory pore/ Oesophagus length[b] (%)	77 ± 6.7 (63-101)	65	67 ± 4.5 (60-76	65 ± 2.4 (61-68)	87 ± 5.5 (73-93)	84 ± 5.2 (79-99)

[a] All measurements in µm
[b] Length to end of glands

Table 15. Morphometric data of *H. marethae* n.sp., *H. martini* and *H. microcephalus*

	H. marethae n.sp.		*H. martini*		*H. microcephalus*	
	South Africa		South Africa		Guadeloupe	South Africa
Characters[a]	Holotype ♀	9 Paratype EE	138 EE	22 ГГ	8 EE	45 EE
L	569	569 ± 38.7(526-642)	590 ± 74.3 (451-787)	581 ± 65.6 (480-720)	664 ± 44.8 (565-711)	551 ± 60.4 (429-698)
a	20.0	23.1 ± 2.8 (20.0-28.6)	26.5 ± 3.8 (18.7-40.8)	33.2 ± 5.3 (24.4-43.5)	27.1 ± 1.6 (24.9-29.1)	26.1 ± 4.1 (19.7-37.8)
b	5.2	5.0 ± 0.5 (4.4-6.1)	5.7 ± 0.5 (4.7-7.1)	5.2 ± 0.4 (4.7-5.8)	4.8	4.6 ± 0.6 (3.8-5.8)
b'	5.6	5.2 ± 0.4 (4.8-5.6)	4.8 ± 0.4 (3.8-6.1)	4.8 ± 0.5 (4.4-6.5)	4.3 ± 0.2 (3.9-4.5)	4.7 ± 0.8 (3.8-6.7)
c	25.8	30.2 ± 5.1 (25.3-39.7)	25.0 ± 4.0 (17.0-42.1)	28.6 ± 4.6 (16.3-36.6)	38.2 ± 6.5 (26.6-49.6)	34.8 ± 5.5 (25.3-46.2)
c'	1.3	1.4 ± 0.1 (1.1-1.6)	1.9 ± 0.4 (1.1-3.0)	1.8 ± 0.4 (1.4-2.9)	1.3 ± 0.2 (1.1-1.4)	1.3 ± 0.2 (1.0-1.7)
DGO	8	9 ± 0.5 (8-9)	9 ± 1.6 (6-13)	9 ± 0.9 (9-11)	13 ± 1.0 (12-140	10 ± 1.2 (8-13)
o	31	33 ± 1.7 (31-35)	34 ± 6.4 (25-52)	52 ± 3.9 (48-57)	46 ± 3.5 (42-51)	43 ± 4.2 (34-54)
Stylet length	26	26 ± 1.1 (24-27)	24 ± 1.8 (20-29)	19 ± 1.7 (16-22)	27 ± 0.7 (26-28)	23 ± 1.3 (21-26)
m	51	49 ± 1.1 (47-51)	48 ± 2.5 (39-53)	50 ± 4.1 (43-55)	51 ± 1.7 (49-53)	46 ± 2.4 (42-53)
V	60	59 ± 1.0 (57-60)	57 ± 2.2 (50-68)	-	62 ± 2.2 (59-65)	63 ± 2.7 (57-69)
OV_1	-	-	22 ± 5.7 (10-32)	-	22	23 ± 3.5 (16-26)
OV_2	-	-	20 ± 4.0 (14-29)	-	-	20 ± 3.1 (15-25)
T	-	-	-	47 ± 5.9 (43-53)	-	-
Spicule length	-	-	-	23 ± 2.3 (20-28)	-	-
Gubernaculum length	-	-	-	7 ± 1.7 (5-9)	-	-
Excretory pore/Oesophagus length[b] (%)	87	85 ± 2.1 (82-87)	66 ± 14.2 (40-92)	81 ± 8.1 (70-95)	75 ± 2.9 (72-79)	76 ± 6.6 (66-87)

[a] All measurements in µm
[b] Length to end of glands

Table 16. Morphometric data of *H. minutus*, *H. minzi* and *H. mucronatus*

	H. minutus		*H. minzi*		*H. mucronatus*	
	Martinique		South Africa		Guadeloupe	
Characters[a]	4 ♀♀	2 ♂♂	86 EE	25 ГГ	18 EE	3 ГГ
L	370 (333-389)	349-359	499 ± 53.2 (403-629)	537 ± 46.8 (447-624)	494 ± 43.1 (437-560)	439 (396-484)
a	27.4	-	23.1 ± 2.9 (18.1-29.0)	28.6 ± 3.5 (21.6-34.1)	26.2 ± 5.2 (17.4-35.0)	28.4 (24.2-31.7)
b	3.5	-	4.9 ± 0.5 (4.3-5.9)	4.7 ± 0.2 (4.6-4.8)	4.5 ± 0.3 (4.1-4.9)	4.5 (4.4-4.5)
b'	3.3 (3.1-3.6)	3.4	4.5 ± 0.5 (3.8-7.9)	4.6 ± 0.5 (4.1-5.9)	4.0 ± 0.3 (3.7-4.5)	3.9 (3.7-4.1)
c	23.4 (21.3-27.5)	25.2-26.6	37.2 ± 6.8 (26.1-59.0)	31.0 ± 4.8 (20.7-38.3)	28.0 ± 4.2 (23.4-36.1)	26.3 (25.0-27.2)
c'	1.7 (1.2-2.0)	1.5	1.2 ± 0.2 (0.6-1.7)	1.5 ± 0.2 (1.1-2.0)	1.5 ± 0.3 (1.1-2.0)	1.5 (1.4-1.6)
DGO	-	-	7 ± 1.4 (6-12)	8 ± 2.0 (5-10)	11 ± 1.4 (9-12)	8
o (%)	-	-	30 ± 5.8 (23-51)	37 ± 9.8 (23-49)	47 ± 5.6 (38-54)	41
Stylet length	19 (18-20)	17-18	25 ± 0.9 (23-27)	22 ± 1.5 (20-24)	23 ± 1.1 (21-26)	20 (19-21)
m (%)	49 (47-50)	51-52	52 ± 2.6 (45-57)	53 ± 4.7 (43-58)	49 ± 2.1 (46-52)	48 (46-50)
V (%)	65 (65-66)	-	64± 1.9 (59-69)	-	64 ± 2.3 (60-67)	-
OV_1 (%)	25 (23-26)	-	24 ± 4.5 (18-35)	-	25 ± 2.3 (21-27)	-
OV_2 (%)	15 (14-17)	-	16 ± 1.2 (14-33)	-	20 ± 1.8 (17-22)	-
T (%)	-	-	-	-	-	59 (57-61)
Tail length	17 (16-18)	14	14 ± 2.5 (10-19)	18 ± 2.5 (13-24)	18 ± 3.2 (12-23)	17 (15-18)
Spicule length	-	16	-	22 ± 2.8 (19-28)	-	18 (17-19)
Gubernaculum length	-	4-5	-	5 ± 1.1 (4-7)	-	6
Excretory pore/Oesophagus length[b] (%)	64 (60-71)	64	78 ± 8.4 (61-92)	73 ± 8.3 (58-89)	73 ± 3.0 (69-80)	81 (78-84)

[a] All measurements in µm
[b] Length to end of glands

Table 17. Morphometric data of *H. multicinctus*

Characters[a]	*H. multicinctus*					
	Guadeloupe		French Guiana		South Africa	
	9 ♀♀	1 ♂♂	21 ♀♀	9 ♂♂	46 ♀♀	14 ♂♂
L	496 ± 46.8 (447-624)	518	483 ± 68.3 (388-678)	426 ± 55.1 (360-555)	547 ± 45.0 (476-654)	516 ± 60.4 (401-603)
a	25.3 ± 2.9 (18.6-28.7)	32.8	28.7 ± 2.4 (21.1-32.4)	26.4 ± 0.2 (27.0-27.5)	25.5 ± 3.4 (17.7-32.5)	30.3 ± 3.2 (24.1-37.5)
b	4.4 ± 0.2 (4.2-4.7)	4.4	4.3 ± 0.4 (3.6-5.1)	4.0 ± 0.2 (3.8-4.2)	5.0 ± 0.4 (4.3-5.3)	4.4 ± 0.5 (3.8-5.1)
b'	4.0 ± 0.2 (3.7-4.2)	4.1	3.9 ± 0.4 (3.3-4.7)	3.7 ± 0.2 (3.5-4.0)	4.3 ± 0.4 (3.5-5.4)	4.3 ± 0.4 (3.6-4.9)
c	44.2 ± 6.5 (33.1-52.0)	34.3	42.6 ± 6.8 (32.5-55.0)	28.2 ± 3.3 (24.6-35.3)	45.9 ± 6.6 (33.8-58.5)	31.1 ± 4.1 (24.0-39.3)
c'	1.0 ± 0.2 (0.8-1.3)	1.5	1.0 ± 0.1 (0.8-1.2)	1.5 ± 0.3 (1.0-1.8)	0.9 ± 0.2 (0.5-1.2)	1.5 ± 0.2 (1.2-2.2)
DGO	10	9	9 ± 0.9 (8-11)	9 ± 0.7 (8-10)	9 ± 1.5 (7-12)	7 ± 1.8 (4-9)
o	41 ± 0.9 (40-41)	41	38 ± 3.6 (34-45)	44 ± 6.5 (38-55)	36 ± 5.4 (28-47)	32 ± 10.0 (17-43)
Stylet length	24 ± 1.0 (22-26)	23	24 ± 1.2 (22-27)	21 ± 1.0 (19-23)	25 ± 1.9 (21-30)	22 ± 2.0 (18-25)
m	50 ± 2.4 (47-55)	49	50 ± 1.6 (47-53)	50 ± 2.5 (46-53)	49 ± 2.4 (44-54)	50 ± 2.5 (47-54)
V	69 ± 0.9 (67-70)	-	69 ± 1.5 (66-72)	-	68 ± 3.1 (63-75)	-
OV_1	29 ± 4.7 (18-33)	-	25 ± 5.3 (14-37)	-	29 ± 5.0 (23-41)	-
OV_2	17 ± 2.1 (14-20)	-	17 ± 3.9 (12-31)	-	17 ± 4.1 (11-24)	-
T	-	-	-	56 ± 4.9 (51-64)	-	-
Spicule length	-	18	-	16 ± 0.6 (16-17)	-	20 ± 2.2 (17-25)
Gubernaculum length	-	-	-	6	-	7 ± 1.5 (5-9)
Excretory pore/Oesophagus length[b] (%)	76 ± 3.9 (71-81)	70	72 ± 5.0 (64-82)	68 ± 4.2 (61-74)	70 ± 6.8 (56-85)	73 ± 7.2 (54-80)

[a] All measurements in µm
[b] Length to end of glands

Table 18. Morphometric data of *H. multicinctus*, *H. paracanalis* and *H. paraplatyurus*

Characters[a]	*H. multicinctus*		*H. paracanalis*		*H. paraplatyurus*
	Union Island		South Africa		South Africa
	9 ♀♀	10 ♂♂	23 ♀♀	23 ♂♂	48 ♀♀
L	754 ± 55.7 (666-826)	732 ± 54.2 (652-798)	830 ± 75.9 (668-998)	739 ± 43.6 (668-840)	727 ± 95.4 (541-959)
a	31.5 ± 3.8 (27.4-38.9)	35.1 ± 3.7 (28.6-40.7)	24.6 ± 2.5 (20.5-29.9)	29.7 ± 2.9 (25.0-35.3)	27.4 ± 4.6 (192-47.7)
b	-	6.9	5.3 ± 0.9 (4.6-7.3)	5.8 ± 0.6 (5.3-6.7)	5.1 ± 0.6 (4.1-6.4)
b'	5.3 ± 0.3 (4.7-5.6)	5.4 ± 0.4 (4.6-6.0)	4.6 ± 0.4 (3.8-5.4)	5.1 ± 0.4 (4.5-5.9)	4.8 ± 0.6 (3.7-6.3)
c	58.3 ± 5.7 (48.6-67.1)	35.4 ± 4.7 (28.8-42.6)	52.5 ± 6.1 (40.0-66.2)	37.0 ±4.9 (27.6-52.5)	51.6 ± 11.9 (31.8-80.9)
c'	0.8 ± 0.1 (0.8-0.9)	1.7 ± 0.3 (1.2-2.2)	0.8 ± 0.1 (0.6-1.0)	1.5 ± 0.2 (1.0-1.8)	1.0 ± 0.2 (0.6-1.9)
DGO	9 ± 0.7 (7-9)	9 ± 1.0 (7-10)	10 ± 0.9 (9-13)	9 ± 0.9 (8-11)	12 ± 1.5 (9-16)
o	34 ± 2.5 (39-36)	40 ± 3.9 (33-44)	28 ± 2.8 (22-33)	30 ± 3.2 (25-38)	43 ± 5.2 (34-55)
Stylet length	25 ± 0.6 (24-26)	22 ± 0.8 (21-23)	37 ± 1.3 (35-42)	30 ± 1.0 (29-32)	28 ± 1.8 (25-31)
m	47 ± 1.2 (46-49)	50 ± 1.6 (47-52)	48 ± 1.8 (44-51)	51 ± 1.7 (48-55)	48 ± 2.1 (41-54)
V	67 ± 1.7 (65-70)	-	62 ± 1.8 (60-67)	-	64 ± 2.2 (60-69)
OV_1	24 ± 3.8 (20-32)	-	18 ± 4.1 (15-270	-	25 ± 4.7 (14-34)
OV_2	20 ± 2.5 (17-24)	-	16 ± 1.6 (15-18)	-	23 ± 4.2 (18-34)
Spicule length	-	23 ± 1.1 (22-25)	-	24 ± 1.3 (22-27)	-
Gubernaculum length	-	7	-	9 ± 0.5 (8-10)	-
Excretory pore/Oesophagus length[b] (%)	77 ± 4.9 (68-83)	78 ± 5.9 (65-87)	73 ± (67-87)	73 ± 5.8 (61-80)	76 ± 7.1 (54-90)

[a] All measurements in µm
[b] Length to end of glands

Table 19. Morphometric data of *H. planquettei, H. pseudorobustus, H. retusus* and *H. serenus*

	H. planquettei		*H. pseudorobustus*		*H. retusus*	*H. serenus*
	French Guiana		French Guiana	South Africa	Martinique	South Africa
Characters[a]	18 EE	8 ГГ	25 EE	67 EE	12 EE	48EE
L	602 ± 18.4 (521-679)	480 ± 36.4 (426-513)	614 ± 29.1 (483-739)	578 ± 65.4 (439-740)	788 ± 94.2 (702-934)	702 ± 64.2 (571-821)
a	21.9 ± 2.1 (18.0-25.1)	26.6 ± 4.1 (20.4-33.1)	26.7 ± 13.5 (21.4-35.5)	26.7 ± 3.2 (19.2-35.3)	27.7 ± 2.0 (2.3-30.7)	25.8 ± 2.9 (20.3-31.2)
b	4.1 ± 0.3 (3.7-4.5)	4.8	4.7 ± 0.3 (4.3-5.0)	5.1 ± 0.6 (3.9-6.0)	5.9	5.4 ± 0.9 (4.2-6.8)
b'	4.1 ± 0.3 (3.6-4.8)	4.1 ± 0.3 (3.7-4.6)	4.2 ± 0.3 (3.4-4.7)	4.5 ± 0.5 (3.7-5.9)	6.1 ± 0.3 (5.7-6.5)	4.9 ± 0.6 (3.9-6.2)
c	42.9 ± 6.4 (27.2-50.6)	30.4 ± 2.6 (25.8-33.1)	33.4 ± 4.4 (25.0-41.5)	35.1 ± 5.5 (20.6-50.2)	50.4 ± 5.0 (43.1-58.7)	35.4 ± 4.6 (26.9-19.3)
c'	1.0 ± 0.2 (0.8-1.3)	1.4 ± 0.2 (1.1-1.6)	1.3 ± 0.1 (1.1-1.6)	1.4 ± 0.2 (1.0-1.8)	0.9 ± 0.1 (0.8-1.1)	1.3 ± 0.2 (1.0-1.7)
DGO	10 ± 1.1 (9-12)	8 ± 1.7 (6-10)	12 ± 1.5 (10-16)	10 ± 1.4 (8-13)	12 ± 1.0 (10-13)	13 ± 1.8 (10-19)
o	34 ± 3.5 (30-41)	37 ± 6.7 (27-44)	48 ± 6.8 (38-64)	42 ± 6.4 (30-53)	50 ± 3.8 (41-55)	44 ± 6.6 (35-66)
Stylet length	30 ± 0.7 (28-31)	23 ± 0.9 (22-24)	26 ± 1.3 (22-28)	23 ± 1.8 (20-27)	24 ± 1.3 (22-26)	29 ± 3.5 (26-32)
m	51 ± 1.3 (49-53)	53 ± 1.6 (51-55)	46 ± 1.9 (40-49)	47 ± 2.9 (42-54)	47 ± 1.9 (42-49)	48 ± 4.5 (44-54)
V	69 ± 1.3 (67-73)	-	65 ± 1.9 (62-71)	63 ± 2.1 (57-67)	62 ± 0.6 (61-63)	63 ± 2.1 (58-67)
OV_1	22 ± 4.0 (17-29)	-	22 ± 2.6 (17-24)	26 ± 4.4 (20-36)	16 ± 1.7 (14-18)	24 ± 3.8 (18-32)
OV_2	15 ± 1.9 (13-19)	-	20 ± 2.8 (16-23)	21 ± 1.7 (19-25)	15 ± 1.9 (13-17)	18 ± 2.5 (15-22)
Spicule length	-	20 ± 0.9 (19-22)	-	-	-	-
Gubernaculum length	-	6	-	-	-	-
Excretory pore/ Oesophagus length[b] (%)	72 ± 6.6 (55-84)	69 ± 3.1 (66-75)	75 ± 4.7 (66-83)	74 ± 6.0 (62-92)	78 ± 4.0 (73-84)	74 ± 9.2 (53-97)

[a] All meusurements in µm
[b] Length to end of glands

Table 20. Morphometric data of *H. stylocercus*, *H. tumidicaudatus* and *H. variabilis*

Characters[a]	*H. stylocercus*		*H. tumidicaudatus*		*H. variabilis*	
	Martinique		South Africa		South Africa	
	24 ♀♀	29♂♂	9 ♀♀	5 ♂♂	14 ♀♀	2 ♂♂
L	556 ± 28.0 (475-602)	548 ± 37.9 (482-614)	841 ± 91.6 (7431020)	772 ± 111.4 (604-890)	571 ± 34.3 (497-619)	527-530
a	29.1 ± 2.4 (23.8-33.0)	32.3 ± 3.6 (25.8-39.3)	27.8 ± 4.5 (22.9-35.4)	28.7 ± 3.6 (25.3-33.7)	24.2 ± 2.8 (20.4-29.6)	30-34
b	4.7 ± 0.3 (4.2-4.9)	5.0	-	4.2	5.3	-
b'	4.3 ± 0.3 (3.7-4.8)	4.7 ± 0.3 (3.8-5.2)	6.4 ± 1.3 (5.0-7.6)	4.8 ± 0.3 (4.5-5.0)	4.6 ± 0.5 (3.8-5.6)	4.3
c	21.9 ± 3.4 (17.1-32.9)	20.0 ± 1.8 (14.5-23.0)	58.9 ± 13.3 (42.2-79.9)	31.0 ± 2.7 (27.8-32.6)	43.2 ± 6.6 (35.5-56.6)	28.2-30.9
c'	2.4 ± 0.3 (1.8-2.9)	2.4 ± 0.3 (1.9-3.0)	0.7 ± 0.2 (0.5-1.1)	1.6 ± 0.03 (1.6-1.7)	0.9 ± 0.1 (0.6-1.1)	1.8
DGO	12 ± 0.8 (11-14)	12 ± 1.2 (9-13)	10	12 ± 2.6 (10-14)	13 ± 1.3 (10-15)	11
o	56 ± 3.9 (51-65)	59 ± 6.4 (41-66)	36	44 ± 8.7 (38-50)	48 ± 4.2 (42-54)	49
Stylet length	22 ± 3.7 (20-23)	20 ± 1.0 (17-23)	30 ± 1.9 (27-32)	28 ± 1.7 (25-30)	27 ± 1.1 (25-29)	22
m	49 ± 3.2 (47-54)	50 ± 2.0 (45-53)	46 ± 3.3 (44-50)	50	48 ± 2.1 (44-51)	50
V	66 ± 1.6 (63-68)	-	62 ± 0.9 (61-64)	-	64 ± 1.9 (60-66)	-
OV_1	24 ± 4.9 (15-33)	-	23 ± 0.8 (22-24)	-	-	-
OV_2	16 ± 1.4 (13-18)	-	18 ± 1.3 (17-20)	-	-	-
T	-	41 ± 5.2 (34-58)	-	-	-	-
Spicule length	-	20 ± 1.2 (19-22)	-	23 ± 1.7 (22-24)	-	20-24
Gubernaculum length	-	7 ± 0.7 (6-8)	-	6	-	6
Excretory pore/Oesophagus length[b] (%)	69 ± 2.9 (63-74)	74 ± 4.7 (62-82)	71 ± 1.8 (70-72)	71 ± 0.9 (71-72)	76 ± 9.1 (66-91)	77

[a] All measurements in µm
[b] Length to end of glands

Table 21. Morphometric data of *H. delanus*, *H. vulgaris* and *H. willmottae*

	H. delanus		*H. vulgaris*	*H. willmottae*
	South Africa		South Africa	South Africa
Characters[a]	20 EE	8ГГ	30 EE	17 EE
L	547 ± 44.6 (463-624)	571 ± 44.9 (497-629)	742 ± 65.4 (609-861)	646 ± 81.7 (554-814)
a	26.9 ± 3.4 (22.5-33.0)	30.1 ± 3.6 (24.8-36.2)	25.8 ± 2.9 (20.4-31.4)	27.4 ± 2.6 (24.3-32.0)
b	5.0 ± 0.5 (4.6-5.8)	5.1 ± 0.3 (4.8-5.3)	5.2 ± 0.5 (4.5-5.9)	5.0 ± 0.5 (4.3-5.6)
b'	4.3 ± 0.4 (3.5-5.0)	4.4 ± 0.4 (3.8-4.9)	4.8 ± 0.5 (4.0-5.9)	4.4 ± 0.4 (3.9-4.9)
c	44.2 ± 6.2 (35.8-56.5)	32.5 ± 1.6 (30.3-34.9)	64.1 ± 9.9 (47.6-89.4)	42.7 ± 7.6 (34.3-62.0)
c'	0.9 ± 0.1 (0.7-1.2)	1.5 ± 0.2 (1.4-1.9)	0.7 ± 0.1 (0.5-0.9)	1.1 ± 0.2 (0.8-1.4)
DGO	6 ± 1.0 (5-8)	6 ± 0.6 (5-7)	13 ± 1.1 (11-15)	11 ± 1.2 (10-14)
o	24 ± 4.4 (17-31)	26 ± 3.9 (23-33)	44 ± 3.3 (38-50)	42 ± 4.4 (37-51)
Stylet length	26 ± 0.9 (25-28)	25 ± 1.4 (22-26)	30 ± 1.2 (28-32)	27 ± 1.5 (26-31)
m	49 ± 2.5 (46-53)	54 ± 3.5 (50-57)	47 ± 1.7 (43-50)	47 ± 1.7 (45-51)
V	75 ± 1.4 (73-78)	-	65 ± 1.5 (62-68)	64 ± 1.7 (62-67)
OV_1	26 ± 4.9 (23-32)	-	28 ± 8.1 (20-39)	-
OV_2	6 ± 1.7 (4-8)	-	22 ± 6.0 (17-36)	-
T	-	-	-	-
Spicule length	-	21 ± 1.4 (18-23)	-	-
Gubernaculum length	-	7 ± 1.0 (6-8)	-	-
Excretory pore/Oesophagus length[b] (%)	73 ± 4.6 (67-81)	68 ± 6.1 (60-77)	71 ± 4.8 (62-83)	71 ± 4.6 (65-78)

[a] All measurements in µm
[b] Length to end of glands

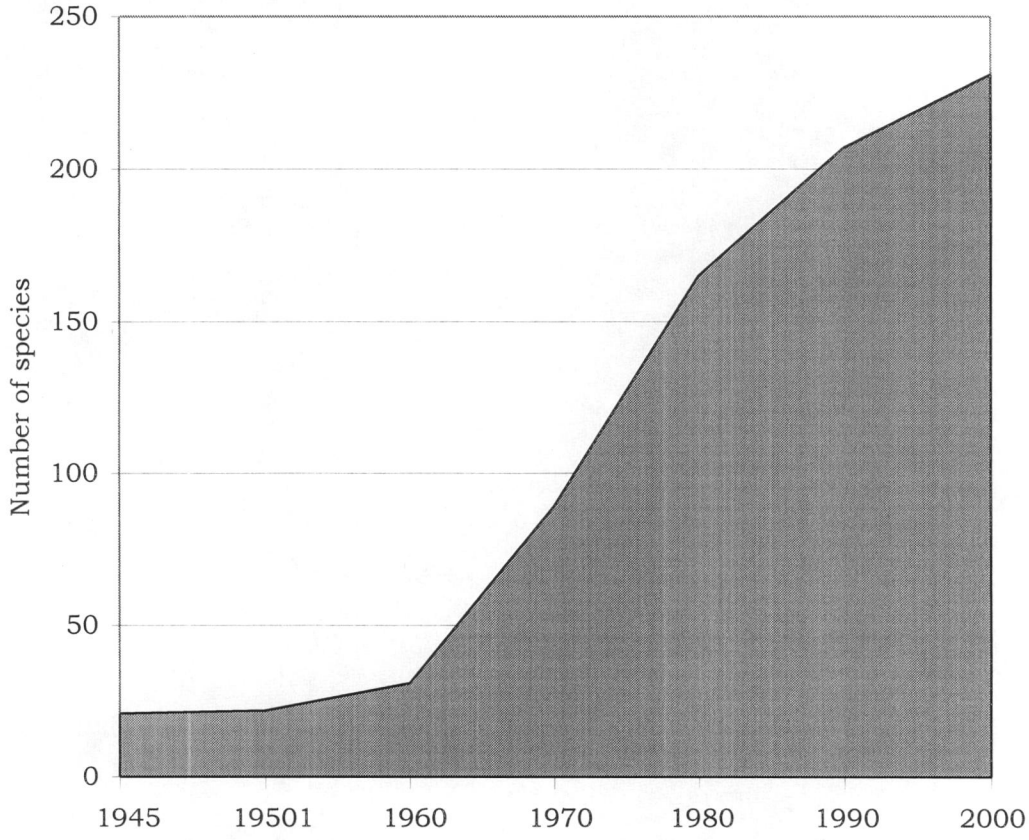
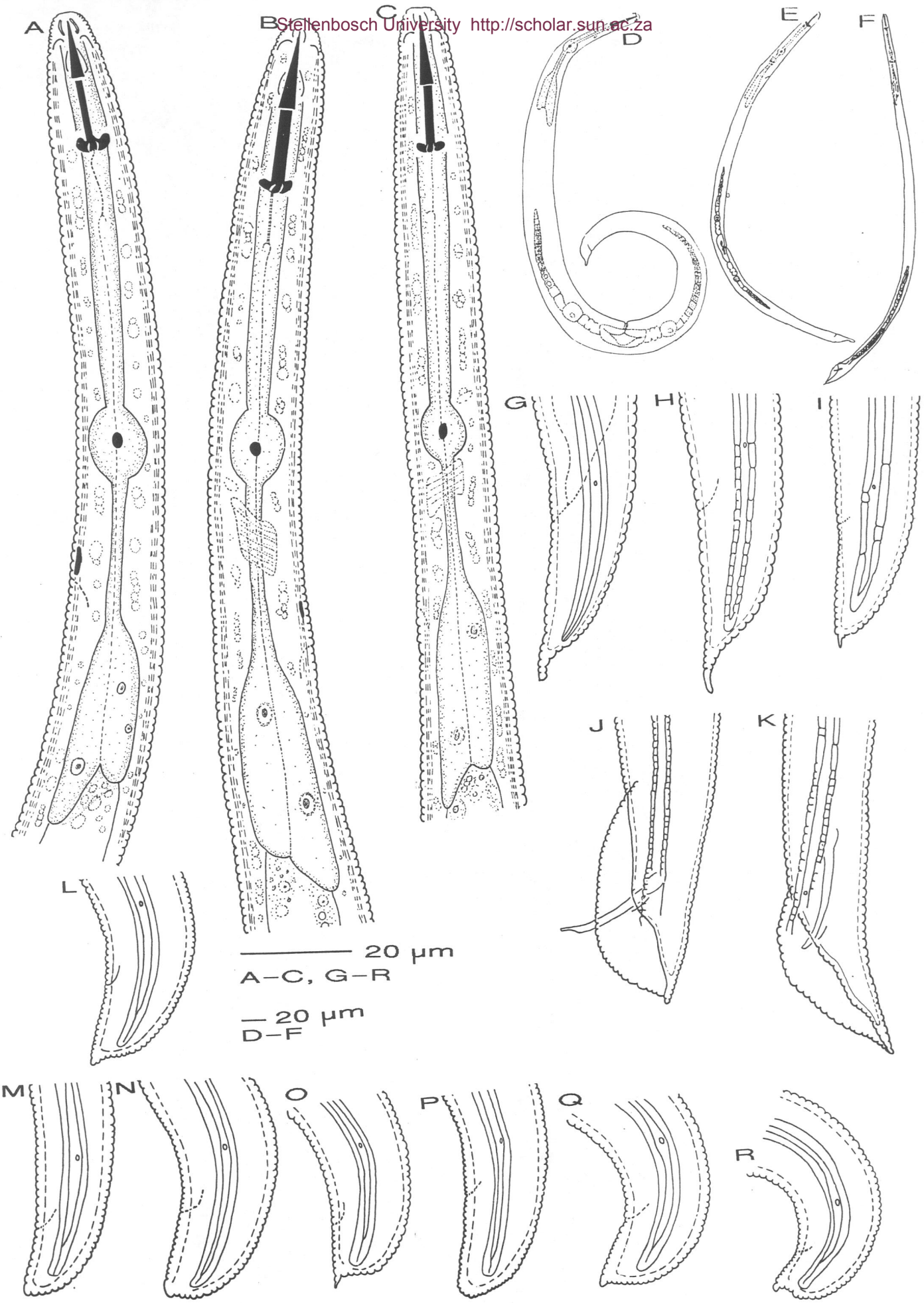


Fig. 1. Cumulative numbers of species described in *Helicotylenchus* from 1945 to 2000

Fig. 2. Distribution of the genus *Helicotylenchus*.

Fig. 3. ***Helicotylenchus dihystera***. Female: A: Oesophageal region; D: Habitus; L-R: Posterior part of body. ***Helicotylenchus africanus***. Female: B: Oesophageal region; E: Habitus; G-I: Posterior part of body; Male: C: Oesophageal region; F: Habitus; J-K: Posterior part of body.



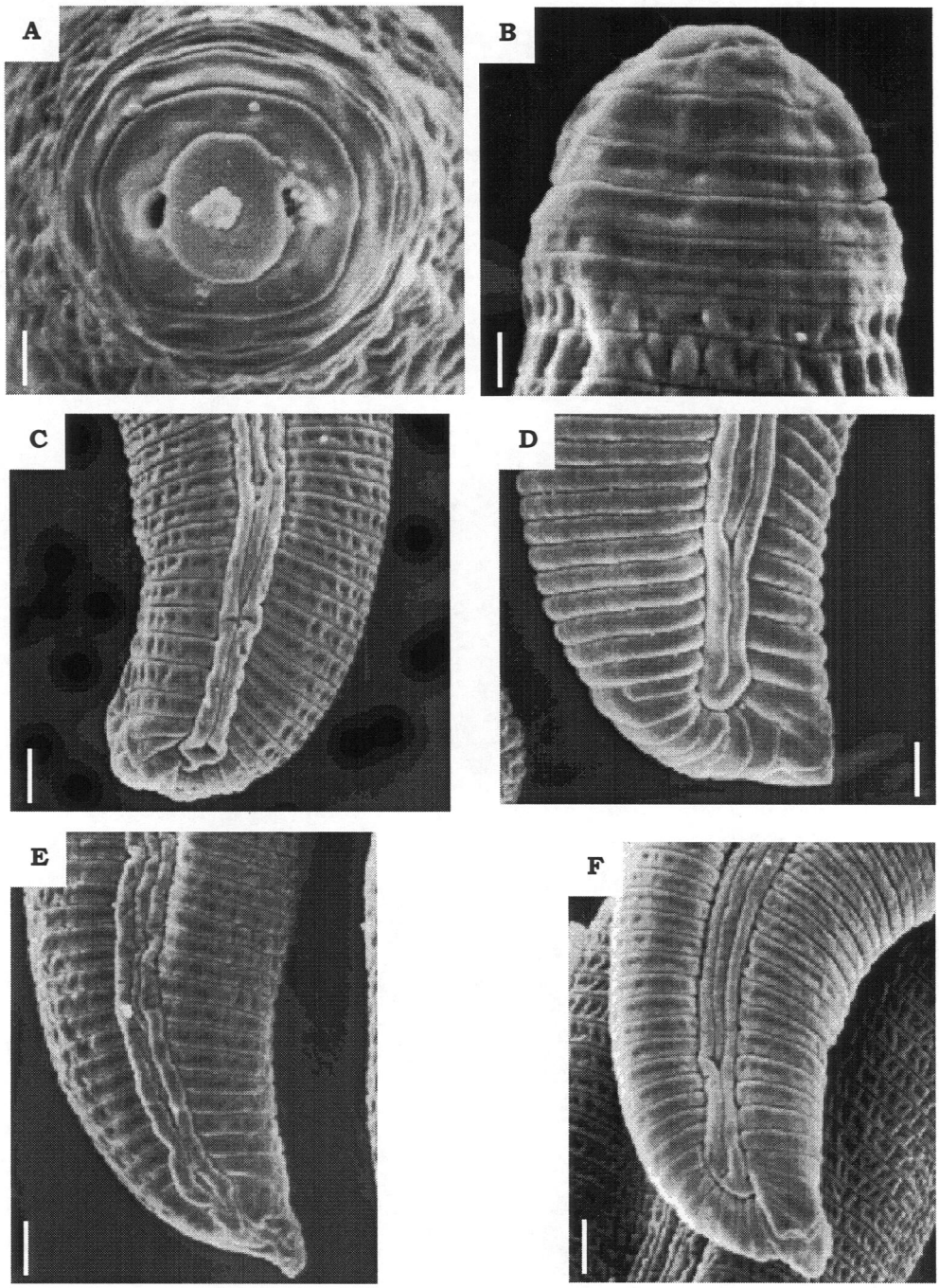


Fig. 4. *Helicotylenchus dihystera.* Female: A: *En face* view, lip region; B: Lateral view, lip region; C-F: Posterior of body. (Scale bar: A-B = 1 µm; C-F = 2 µm).

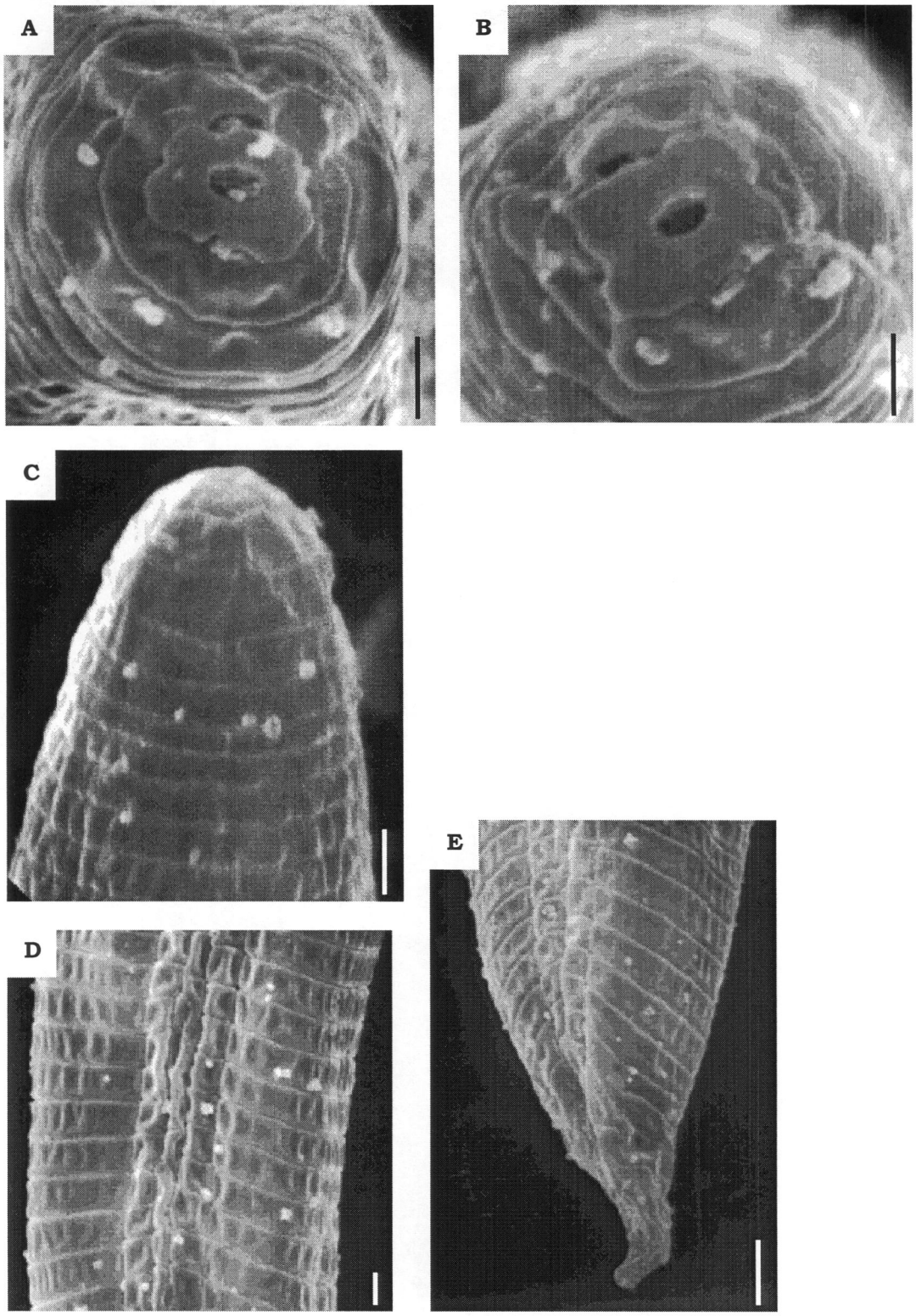
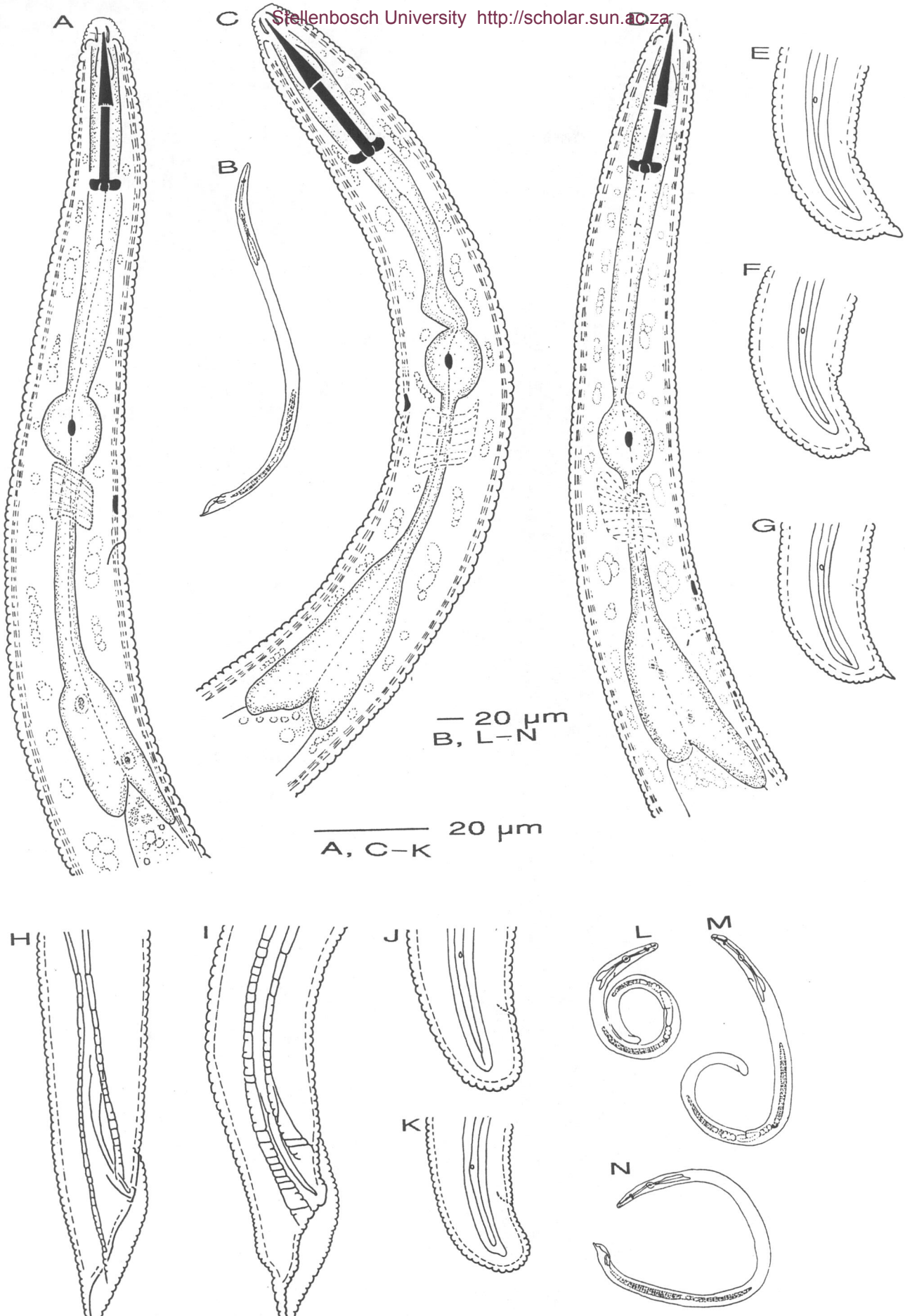


Fig. 5. *Helicotylenchus africanus.* Female: A-B: *En face* view, lip region; C: Lateral view, lip region; D: Lateral field, anterior to anus; E: Posterior part of body. (Scale bar: A-C = 1 µm; D-E = 2 µm).



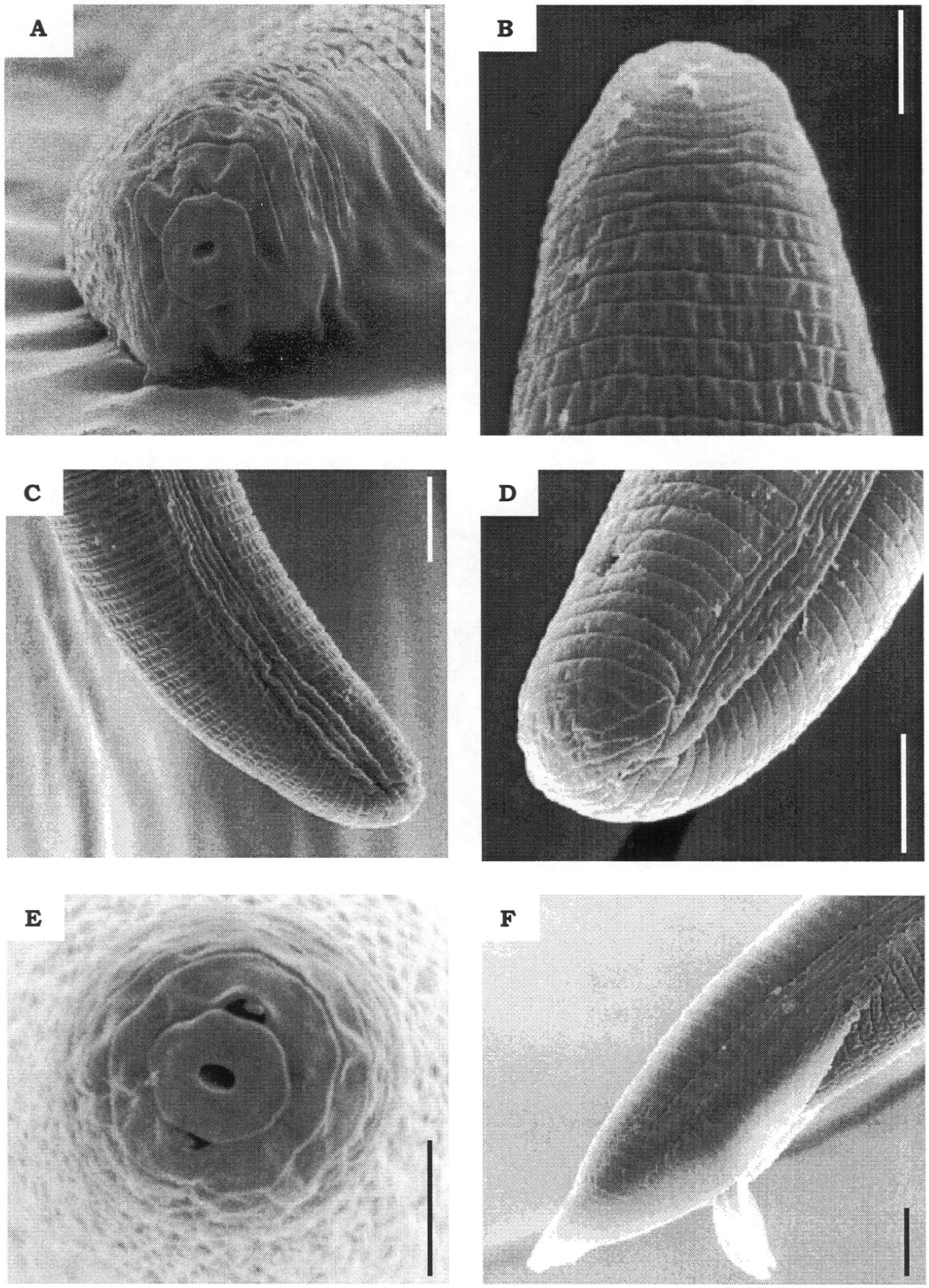
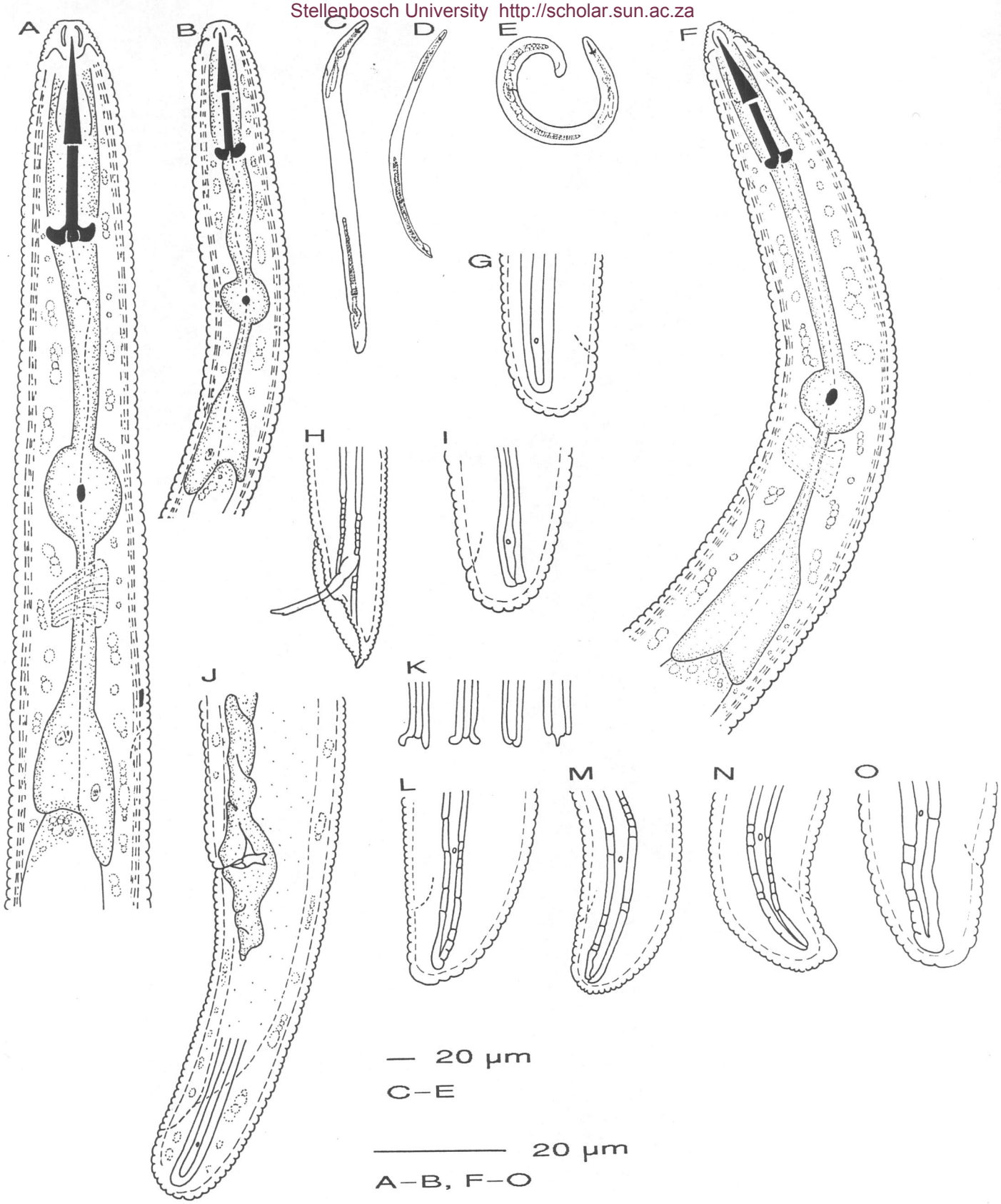


Fig. 7. *Helicotylenchus anhelicus*. Female: A: *En face* view, lip region; B: Lateral view, lip region; C-D: Posterior part of body; Male: E: *En face* view, lip region; F: Posterior part of body. (Scale bar: A-B, E = 2 µm; C-D, F = 5 µm).

Fig. 8. ***Helicotylenchus brevis.*** Female: A: Oesophageal region; C: Habitus; G, I: Posterior part of body; J: Posterior part of body with postvulval uterine sac; K: Variations in lateral field ending; Male: B: Oesophageal region; D: Habitus; H: Posterior part of body. ***Helicotylenchus areolatus.*** Female: E: Habitus; F: Oesophageal region; L-O: Posterior part of body.



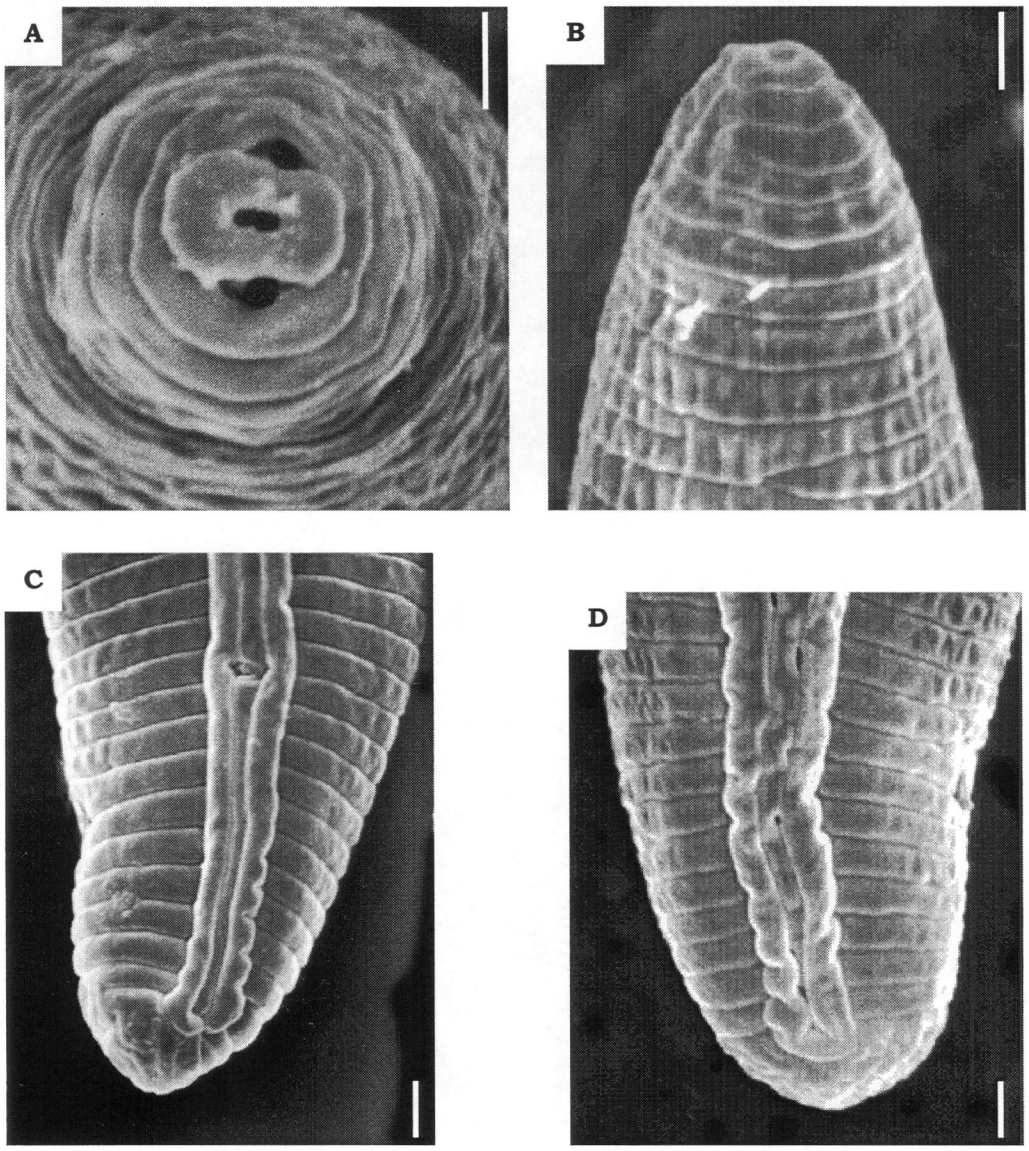


Fig. 9. *Helicotylenchus areolatus.* Female: A: *En face* view, lip region; B: Lateral view, lip region; C-D: Posterior part of body. (Scale bar: A-D = 1 µm).

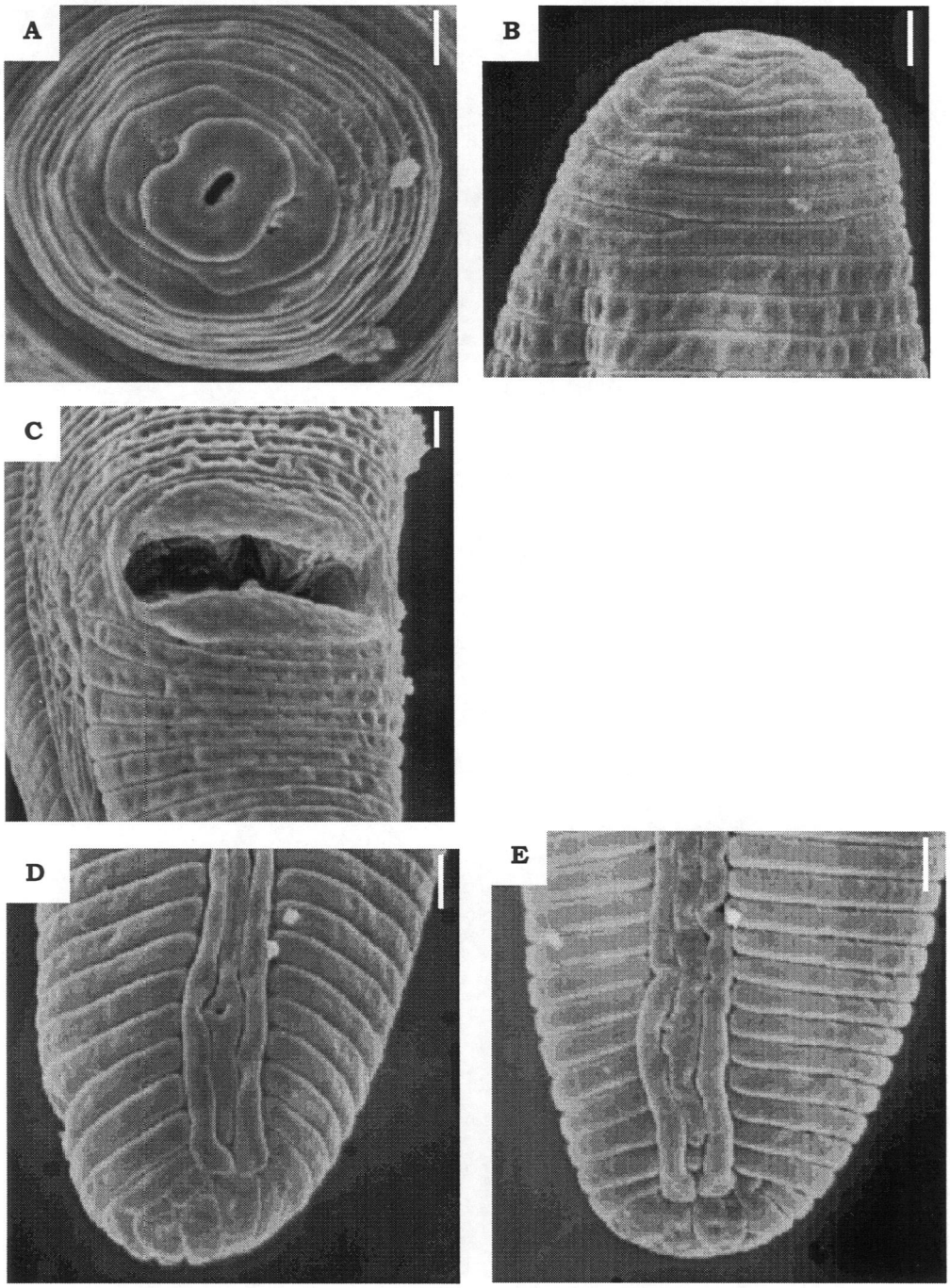


Fig. 10. ***Helicotylenchus brevis.*** Female: A: *En face* view, lip region; B: Lateral view, lip region; C: Ventral view, vulva; D-E: Posterior part of body. (Scale bar: A-E = 1 µm).

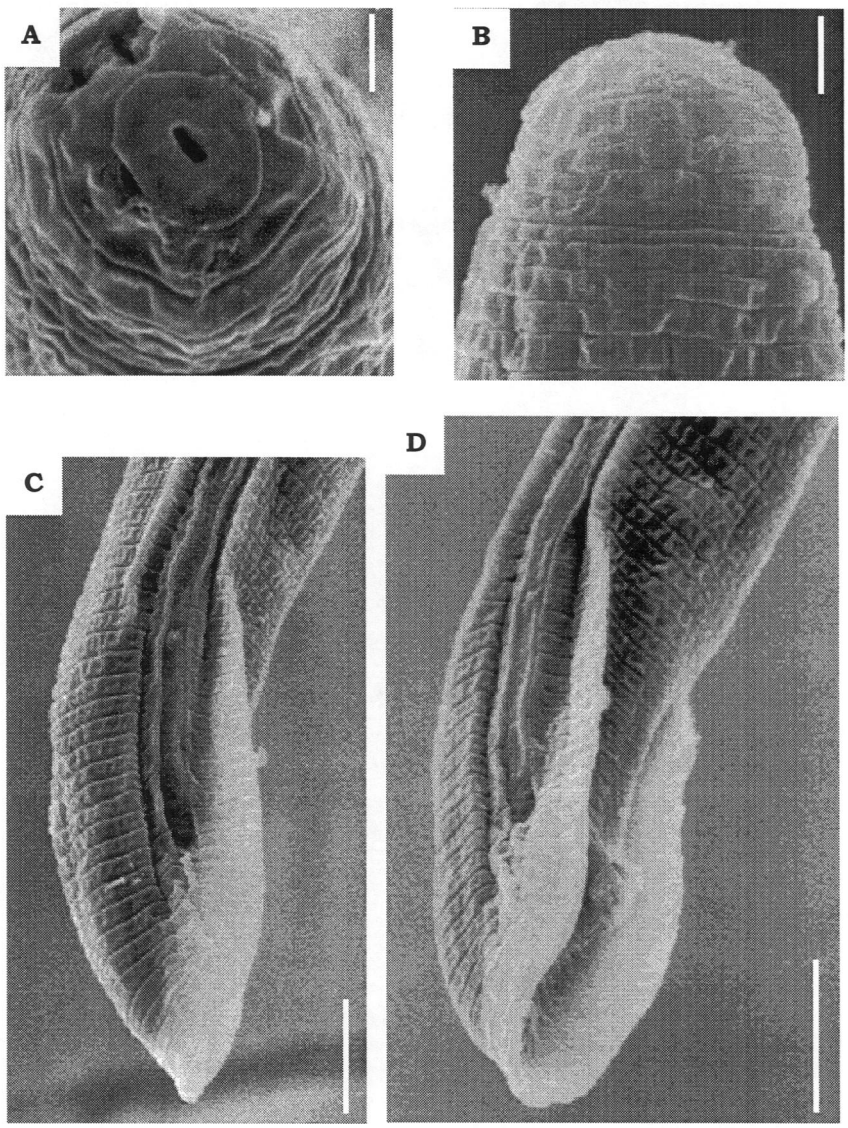
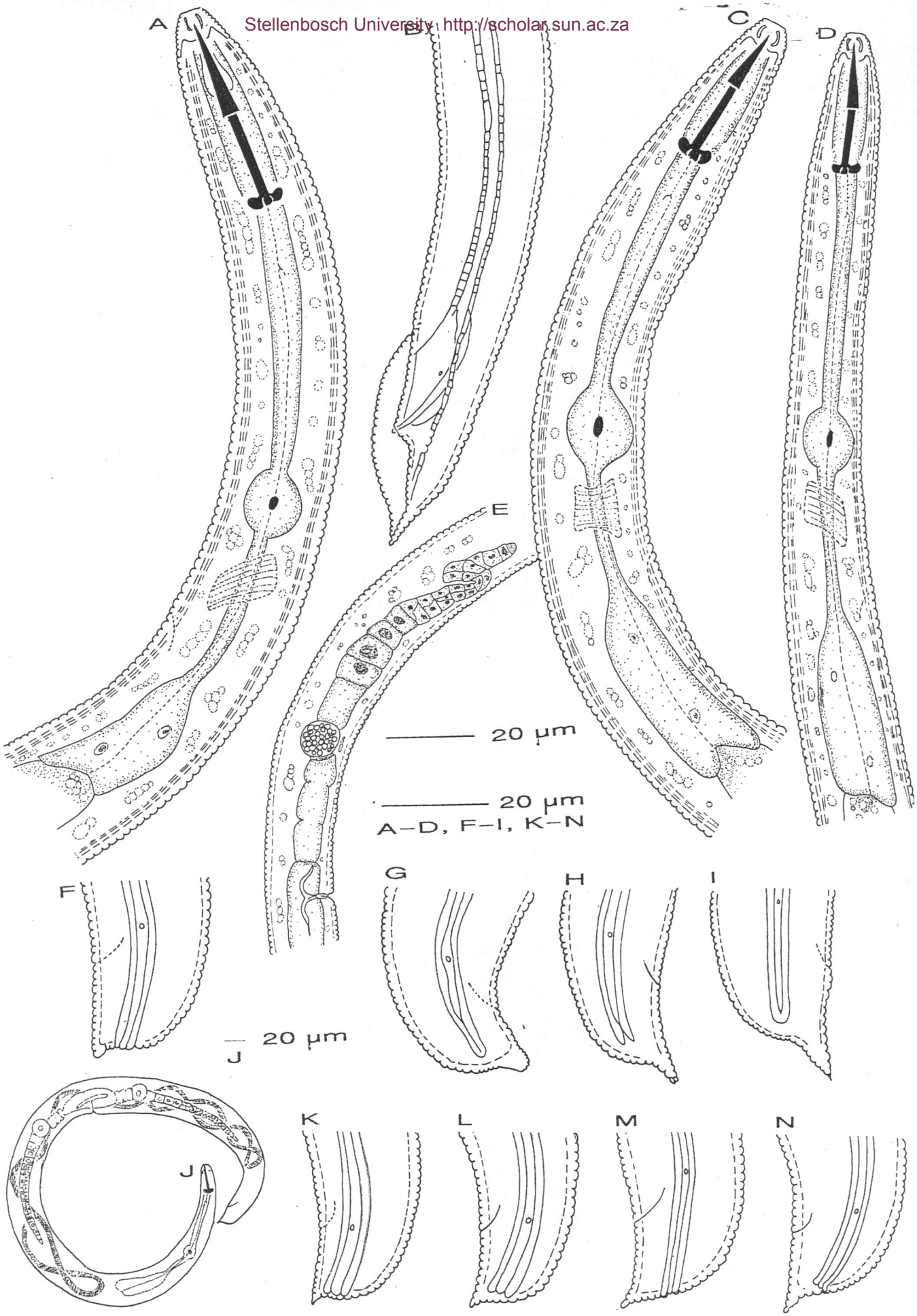


Fig. 11. *Helicotylenchus brevis.* Male: A: *En face* view, lip region; B: Lateral view, lip region; C-D: Posterior part of body. (Scale bar: A-B = 1 µm; C-D = 5 µm).

Fig. 12. ***Helicotylenchus canalis.*** Female: A: Oesophageal region; J: Habitus; F, K-N: Posterior part of body. ***Helicotylenchus californicus.*** Female: C: Oesophageal region; E: Anterior reproductive branch; G-I: Posterior part of body; Male: B: Posterior part of body; D: Oesophageal region.



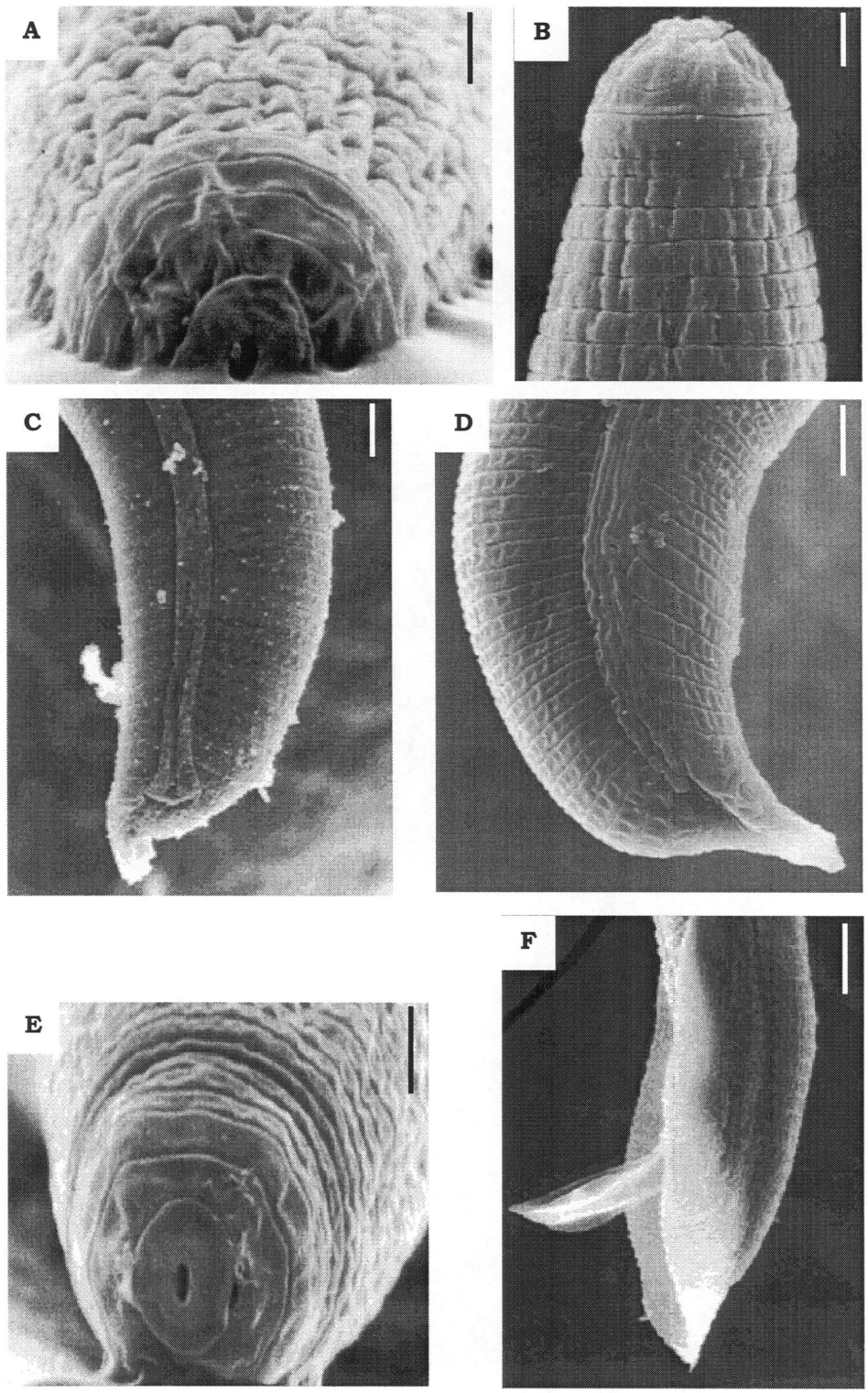


Fig. 13. ***Helicotylenchus californicus.*** Female: A: *En face* view, lip region; B: Lateral view, lip region; C-D: Posterior part of body; Male: E: *En face* view, lip region; F: Posterior part of body. (Scale bar: A, E = 1 µm; B = 2 µm; C-D = 3 µm; F = 5 µm).

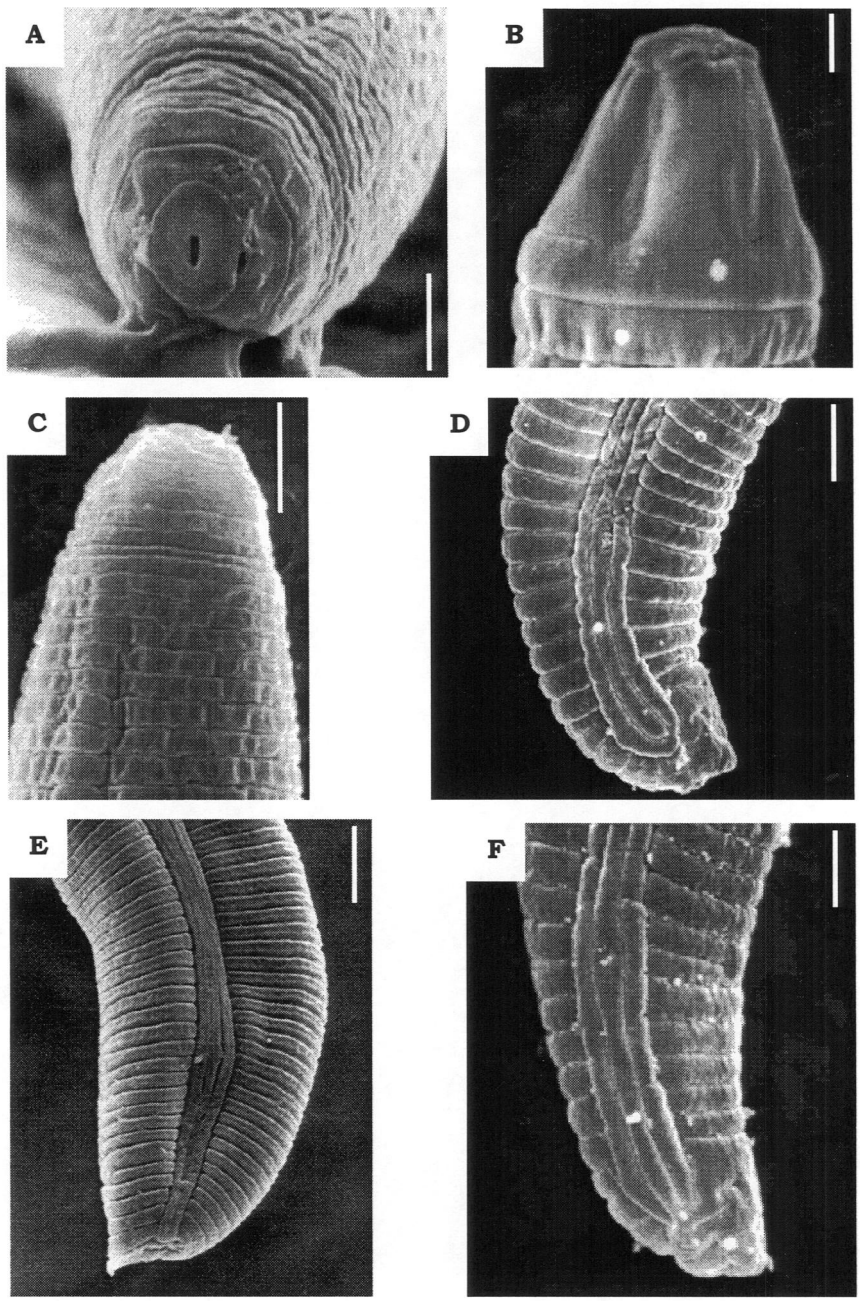
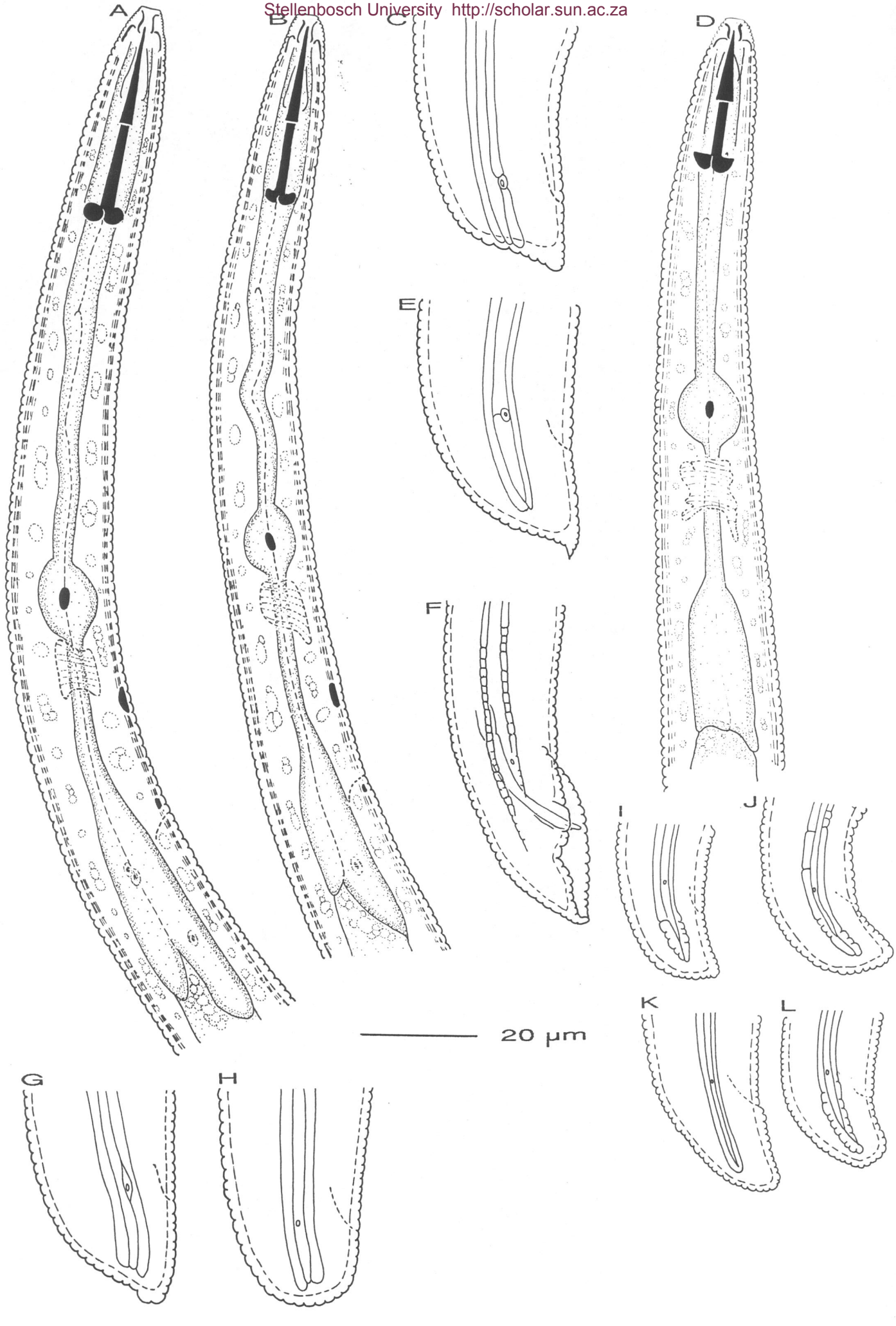


Fig 14. ***Helicotylenchus canalis.*** Female: A: *En face view,* lip region; C: Lateral view, lip region; E: Posterior part of body. ***Helicotylenchus martini.*** Female: B: Lateral view, lip region; D, F: Posterior part of body. (Scale bar: B = 1 µm; A, C-D, F = 2 µm; E = 5 µm).

Fig. 15. ***Helicotylenchus macrostylus.*** Female: A: Oesophageal region; C, E, G-H: Posterior part of body; Male: B: Oesophageal region; F: Posterior part of body. ***Helicotylenchus cavenessi.*** Female: D: Oesophageal region; I-L: Posterior part of body.



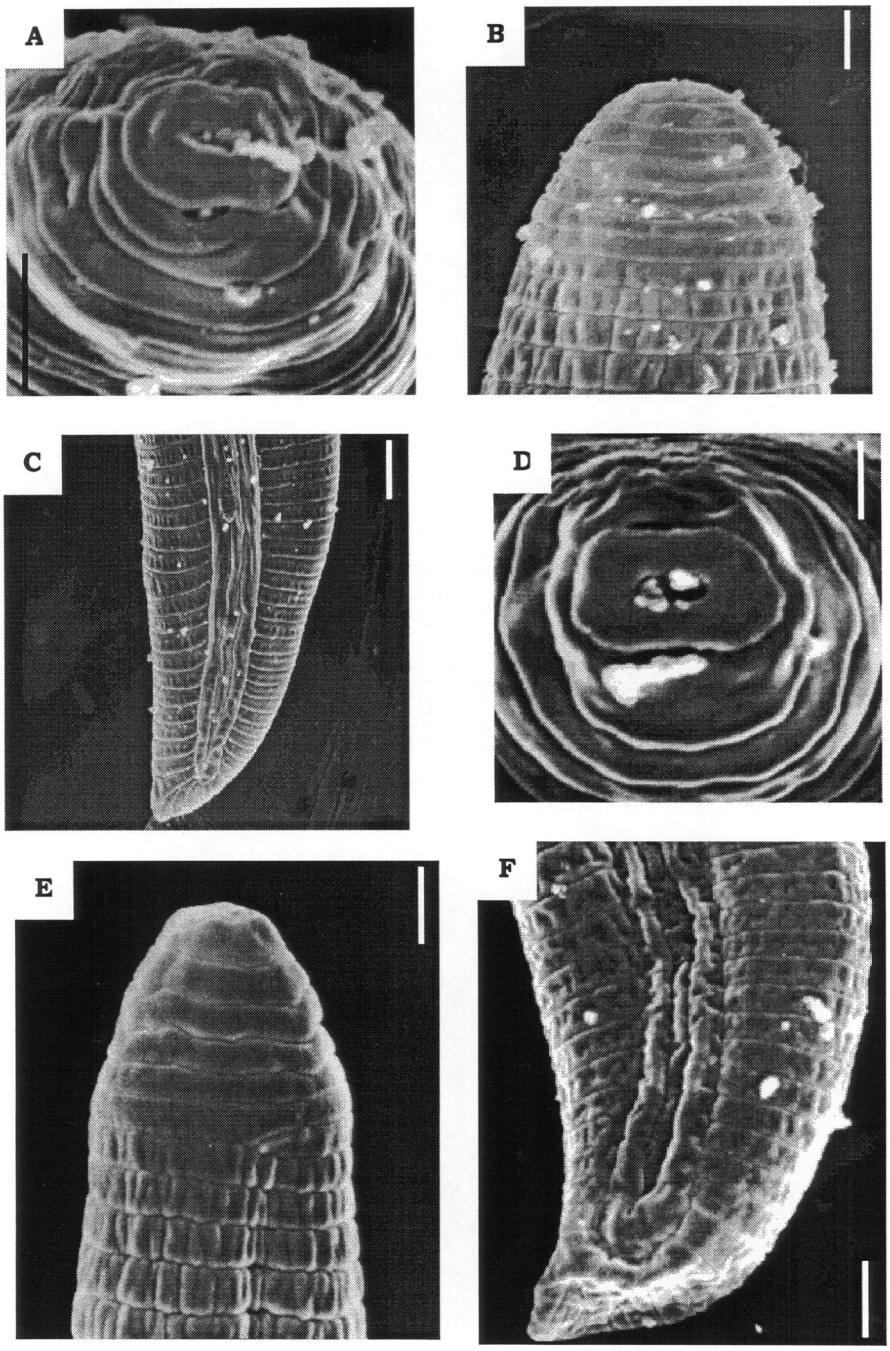
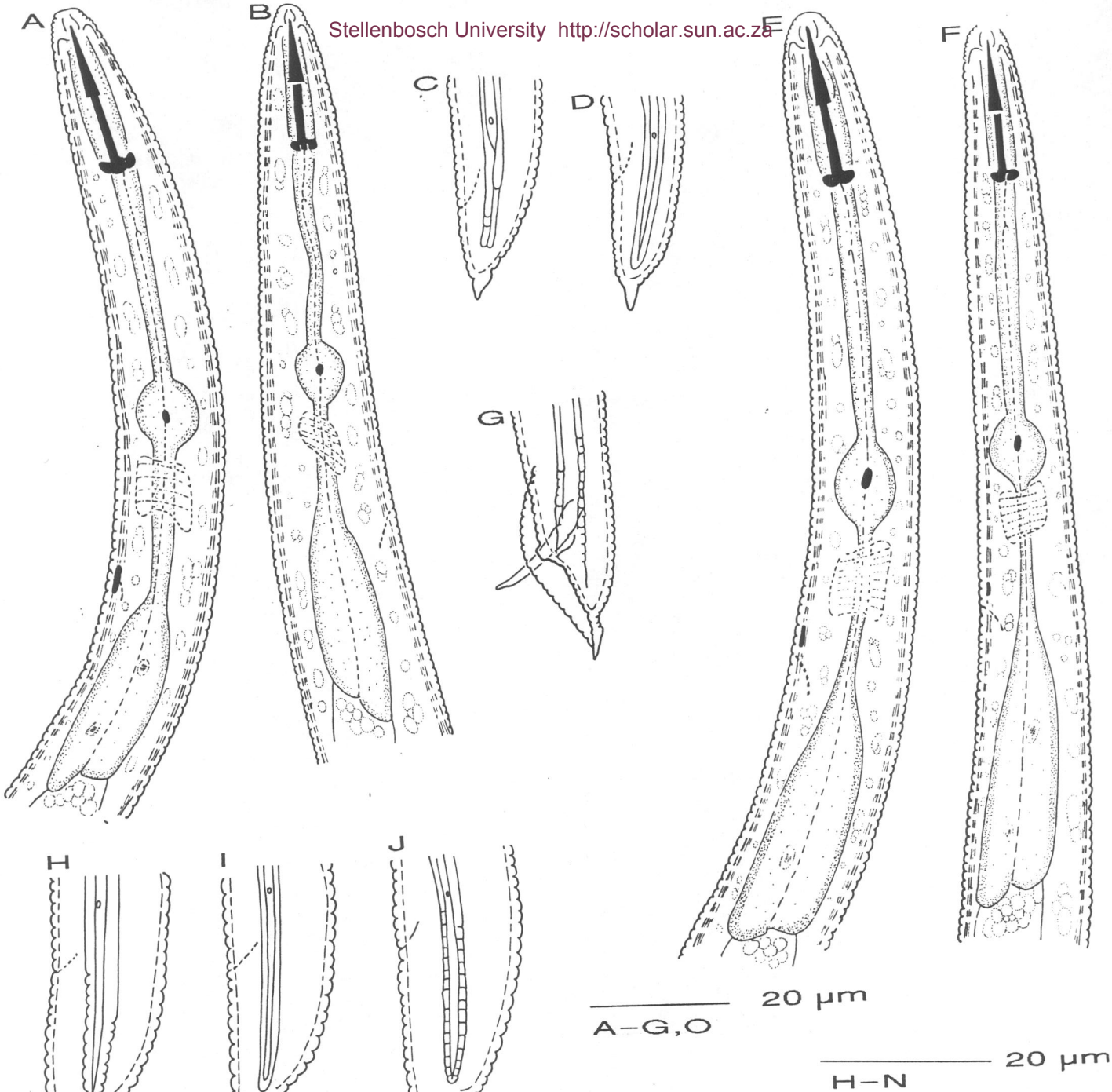


Fig. 16. ***Helicotylenchus cavenessi.*** Female: A: *En face* view, lip region; B: Lateral view, lip region; C: Posterior part of body. ***Helicotylenchus indicus.*** Female: D: *En face* view, lip region; E: Lateral view, lip region; F: Posterior part of body. (Scale bar: A-B, D-E = 1 µm; C, F = 2 µm).

Fig. 17. ***Helicotylenchus crenacauda.*** Female: A: Oesophageal region; H-N: Posterior part of body; Male: B: Oesophageal region; O: Posterior part of body. ***Helicotylenchus mucronatus.*** Female: C-D: Posterior part of body; E: Oesophageal region; Male: F: Oesophageal region; G: Posterior part of body.



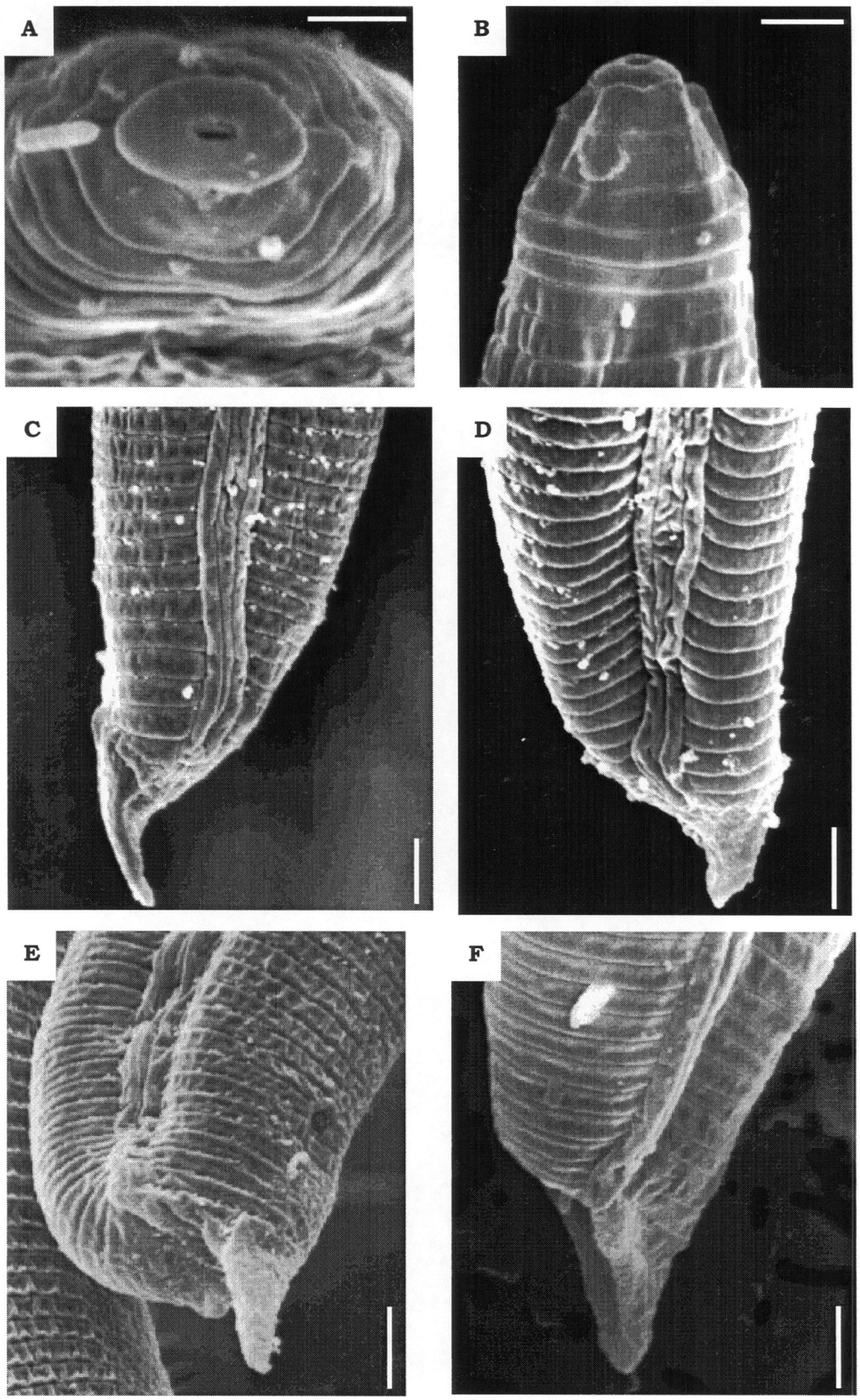
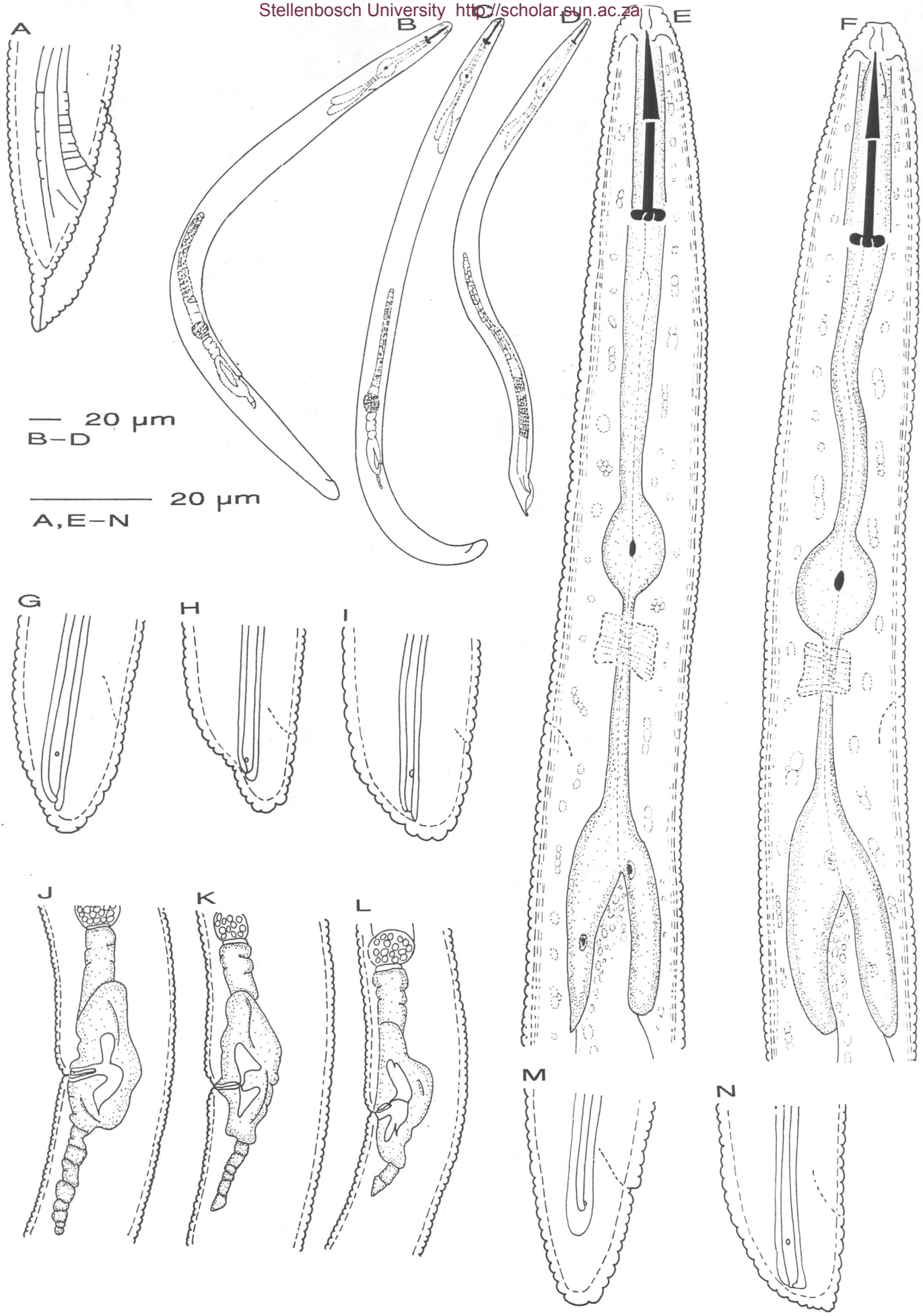


Fig. 18. ***Helicotylenchus microcephalus.*** Female: A: *En face* view, lip region; B: Lateral view, lip region; C-D: Posterior part of body. ***Helicotylenchus crenacauda.*** Female: E-F: Posterior part of body. (Scale bar: A-F = 1 µm).

Fig. 19. *Helicotylenchus delanus.* Female: B-C: Habitus; E: Oesophageal region; G-I, M-N: Posterior part of body; J-L: Posterior reproductive branch; Male: A: Posterior part of body; D: Habitus; F: Oesophageal region.



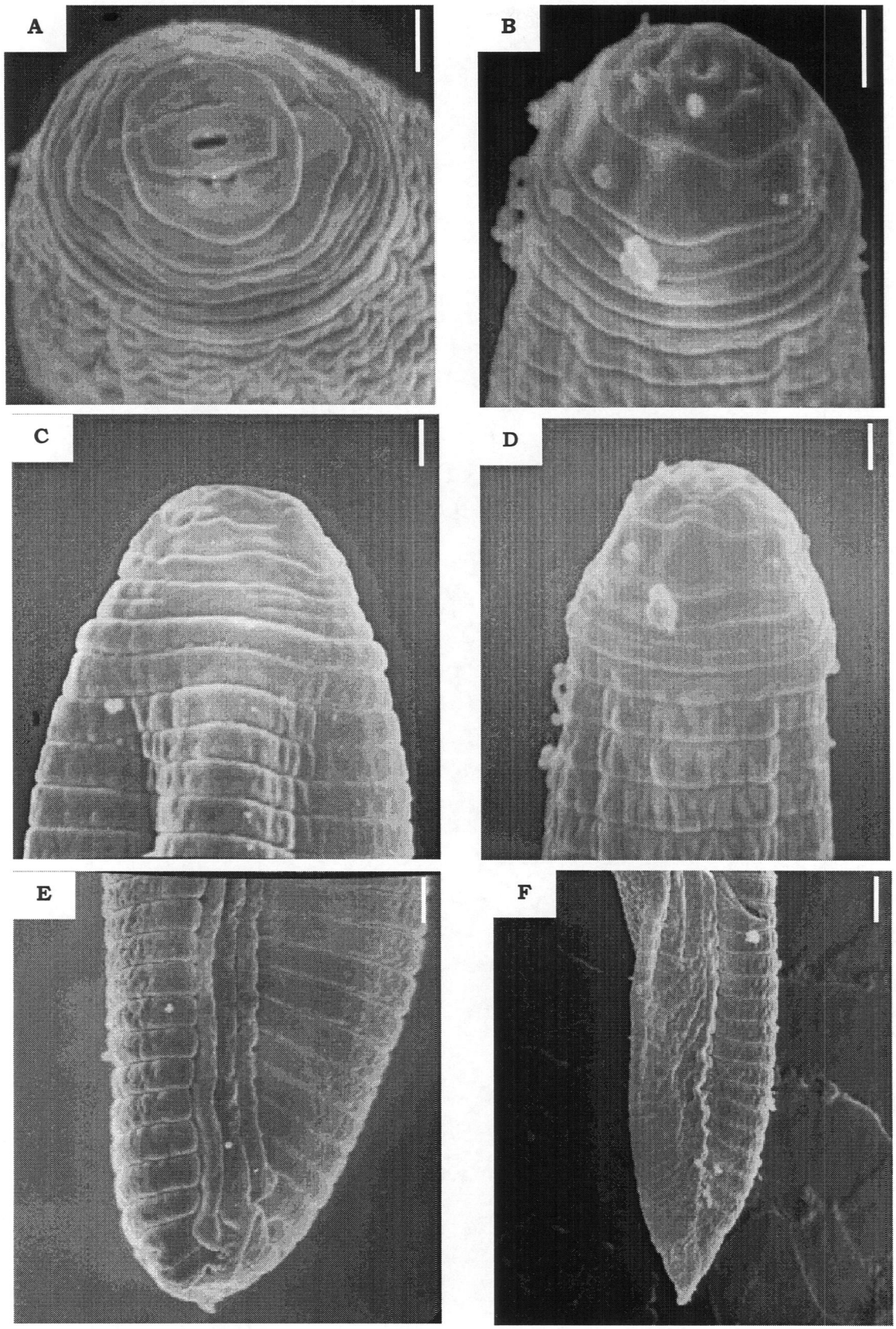
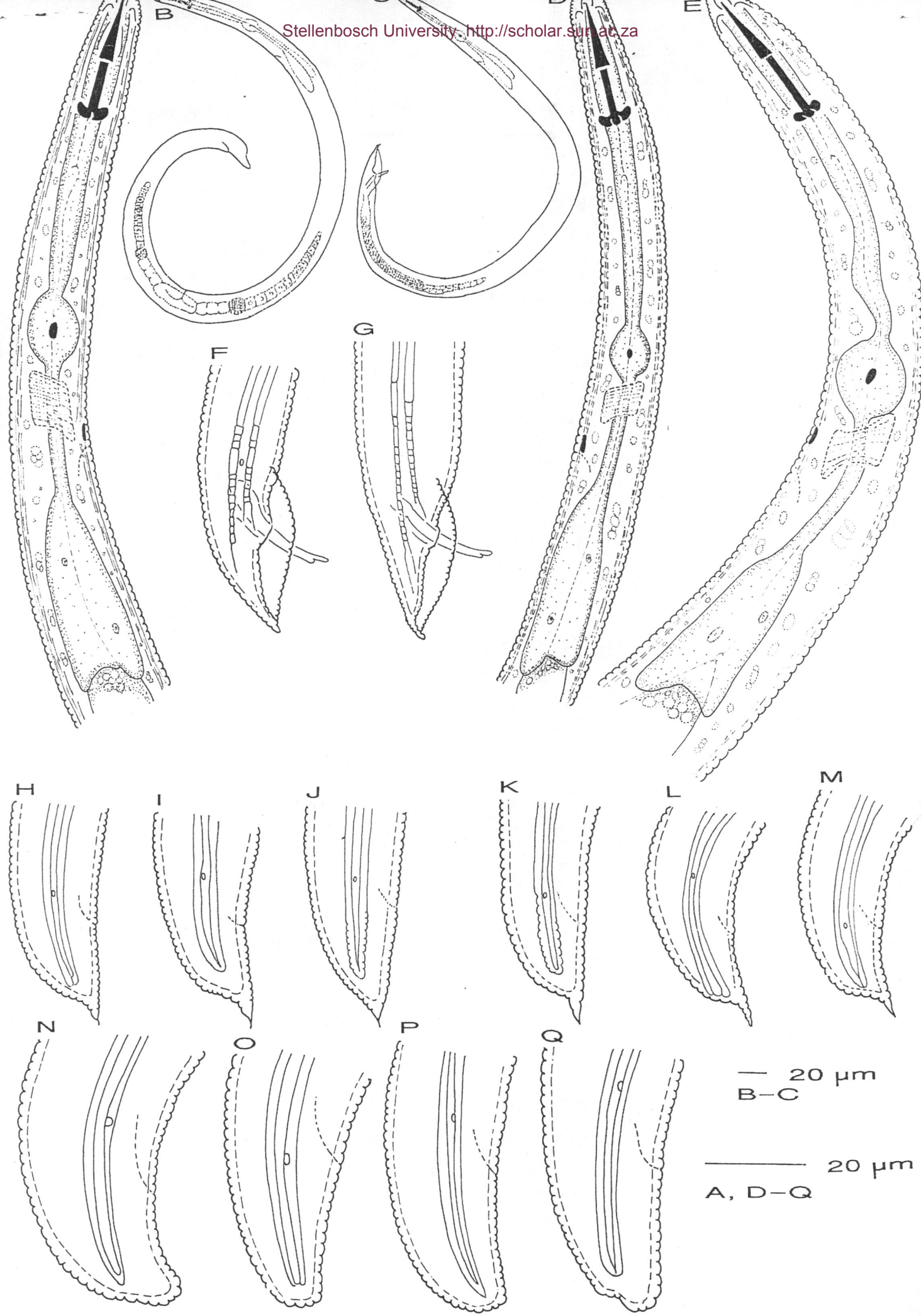


Fig. 20. ***Helicotylenchus delanus.*** Female: A: *En face* view, lip region; C: Lateral view, lip region; E: Posterior part of body; Male: B: *En face* view, lip region; D: Lateral view, lip region; F: Posterior part of body. (Scale bar: A-E = 1 µm; F = 2 µm)

Fig. 21. ***Helicotylenchus erythrinae.*** Female: A: Oesophageal region; B: Habitus; H-M: Posterior part of body; Male: C: Habitus; D: Oesophageal region; F-G: Posterior part of body. ***Helicotylenchus digonicus.*** Female: E: Oesophageal region; N-Q: Posterior part of body.



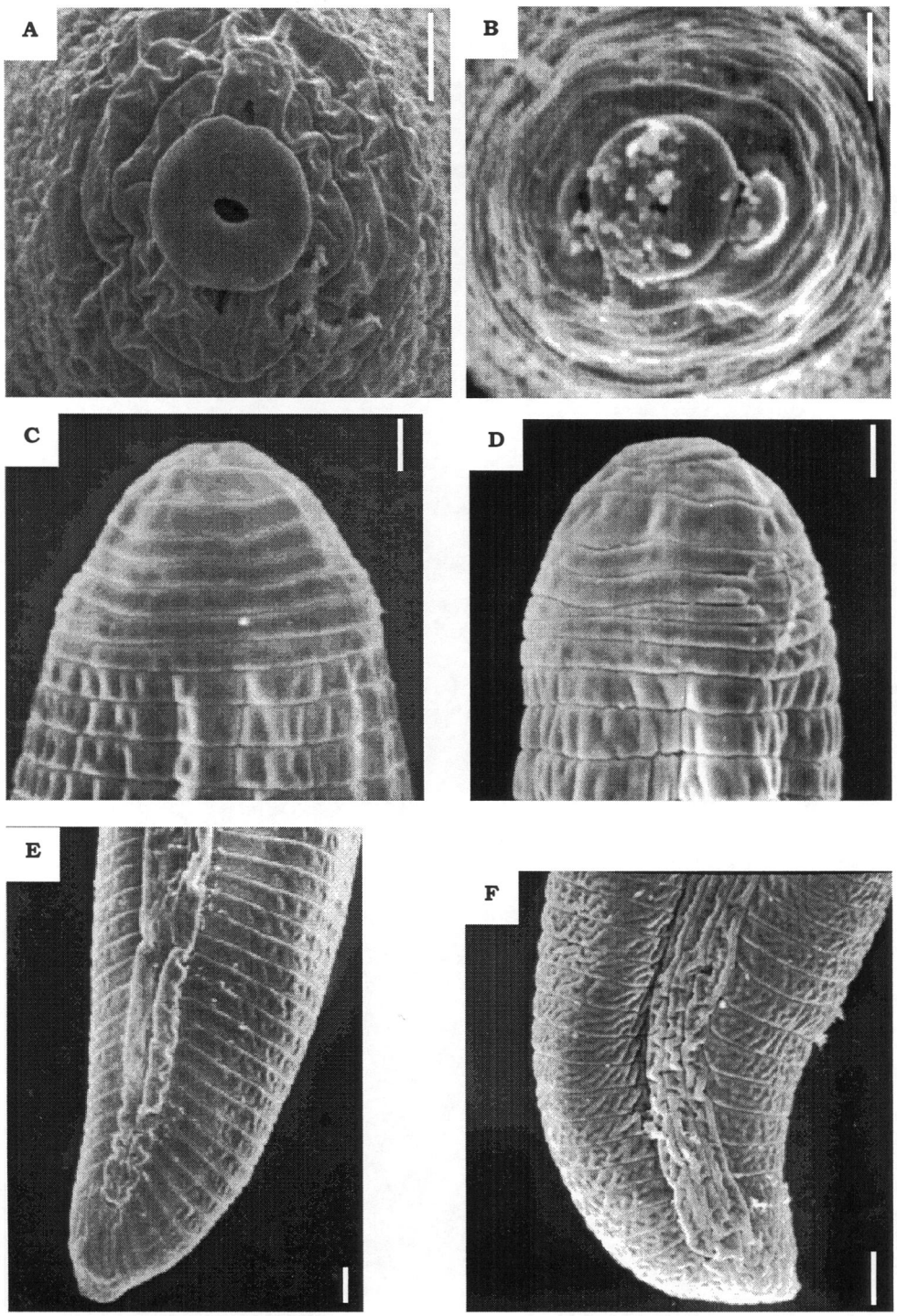
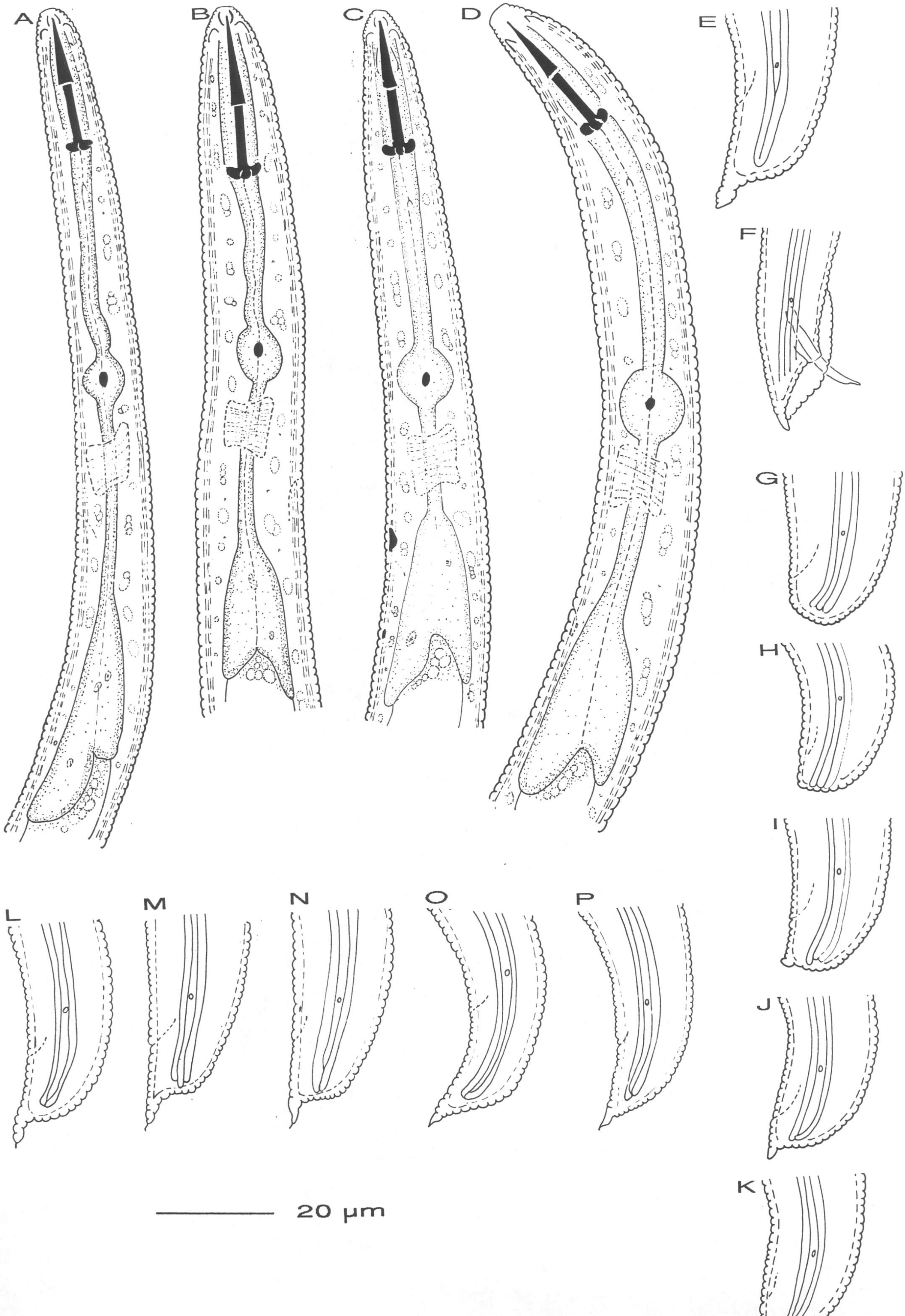


Fig. 22. *Helicotylenchus digonicus.* Female: A: *En face* view, lip region; C: Lateral view, lip region; E: Posterior part of body. ***Helicotylenchus serenus.*** Female: Female: B: *En face* view, lip region; D: Lateral view, lip region; F: Posterior part of body. (Scale bar: A-D = 1 µm; E-F = 2 µm).

Fig. 23. ***Helicotylenchus exallus.*** Female: A: Oesophageal region; G-K: Posterior part of body; Male: B: Oesophageal region; F: Posterior part of body. ***Helicotylenchus egyptiensis.*** Female: C: Oesophageal region; L-P: Posterior part of body. ***Helicotylenchus hydrophilus.*** Female: D: Oesophageal region; E: Posterior part of body.



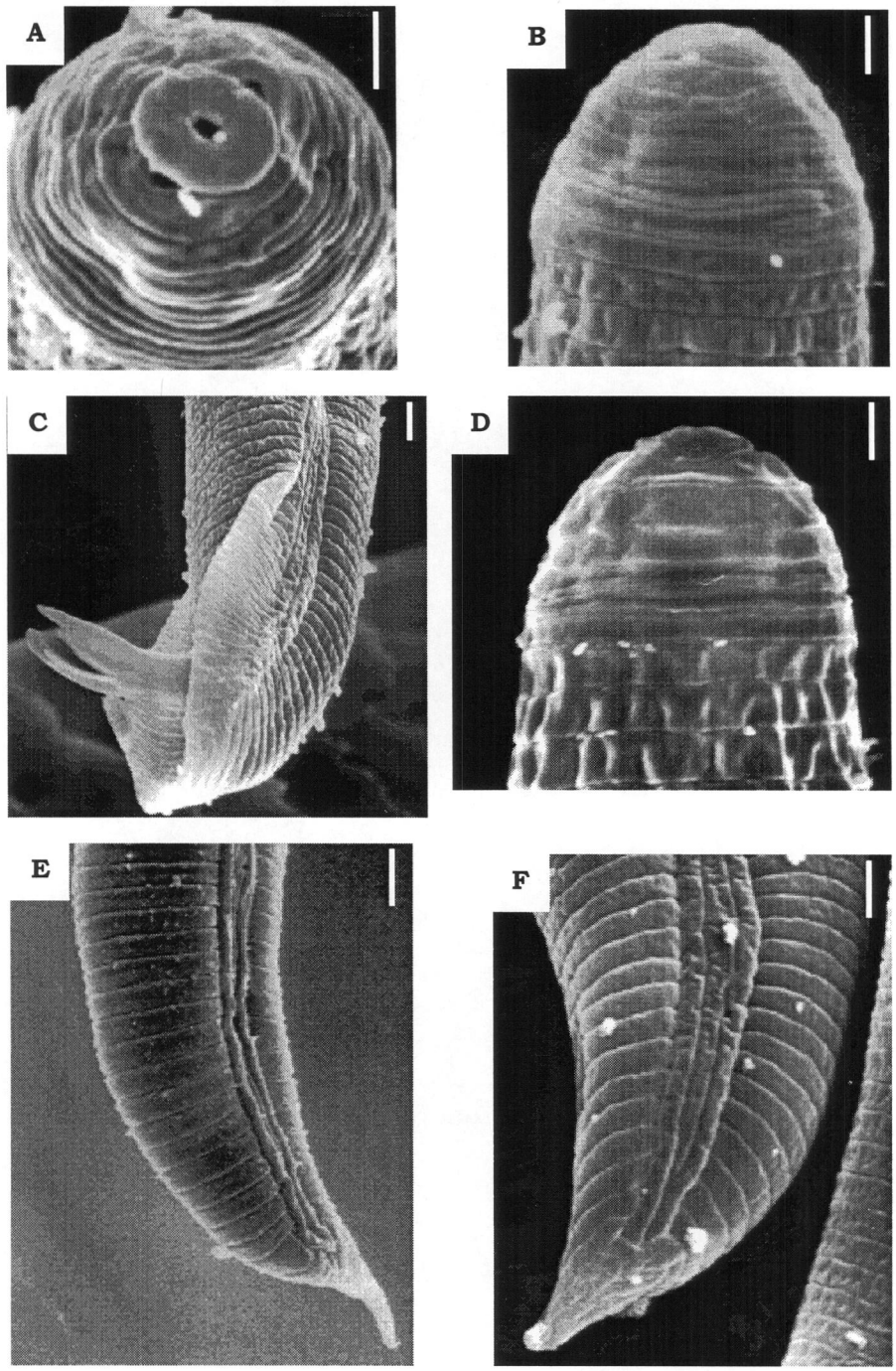


Fig. 24. ***Helicotylenchus erythrinae.*** Male: A: *En face* view, lip region; B: Lateral view, lip region; C: Posterior part of body; Female: D: Lateral view, lip region; E-F: Posterior part of body. (Scale bar: A-B, D = 1 µm; C, E-F = 2 µm).

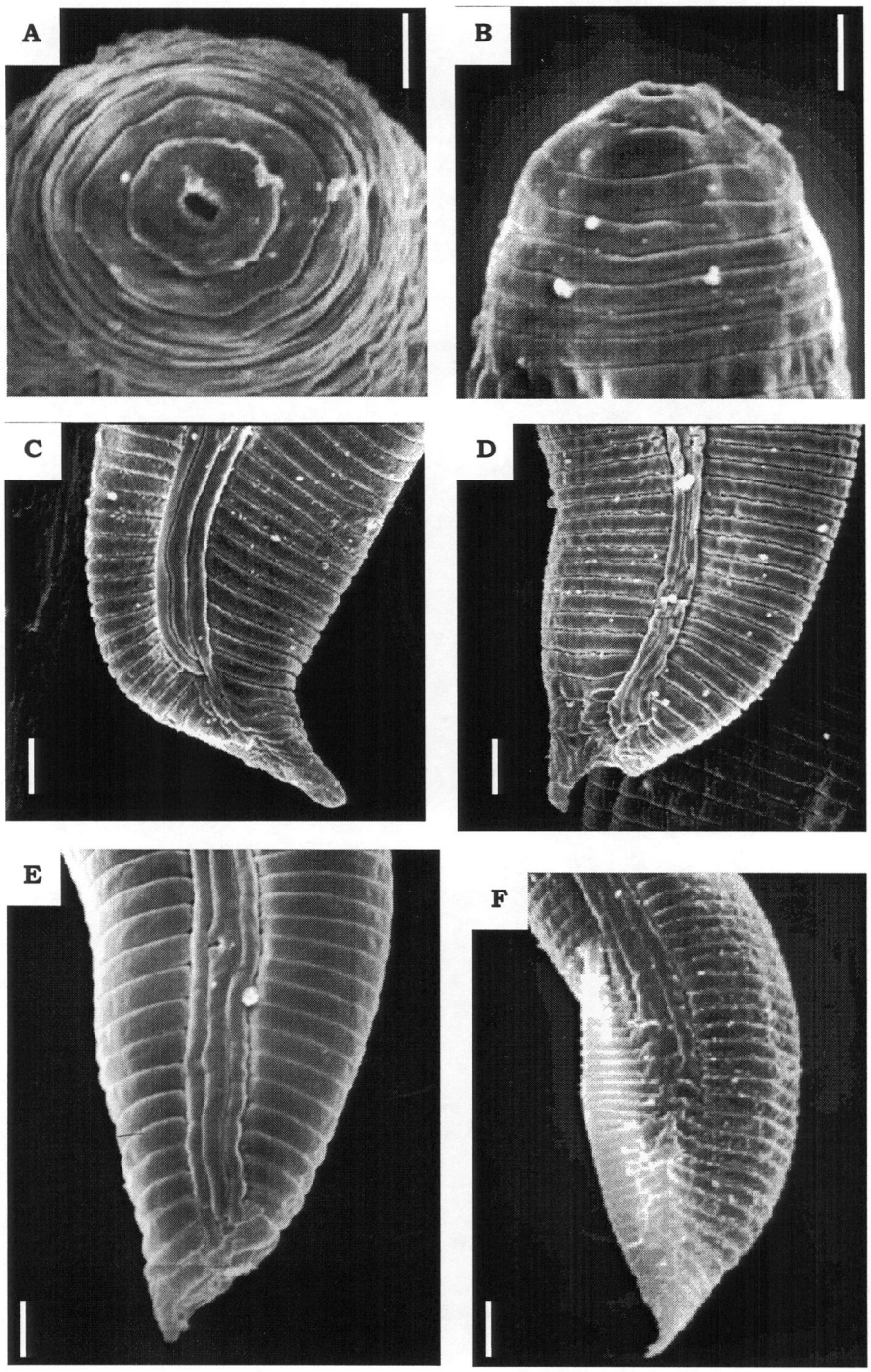


Fig. 25. *Helicotylenchus exallus.* Female: A: *En face* view, lip region; B: Lateral view, lip region; C-E: Posterior part of body; Male: F: Posterior part of body. (Scale bar: A-B = 1 µm; C-E = 2 µm; F = 3 µm).

Fig. 26. ***Helicotylenchus kermarreci.*** Female: A: Oesophageal region; E, G-J: Posterior part of body; Male: B: Oesophageal region; F: Posterior part of body. ***Helicotylenchus indicus***. Female: D: Oesophageal region; L-Q: Posterior part of body; Male: C: Oesophageal region; K: Posterior part of body.

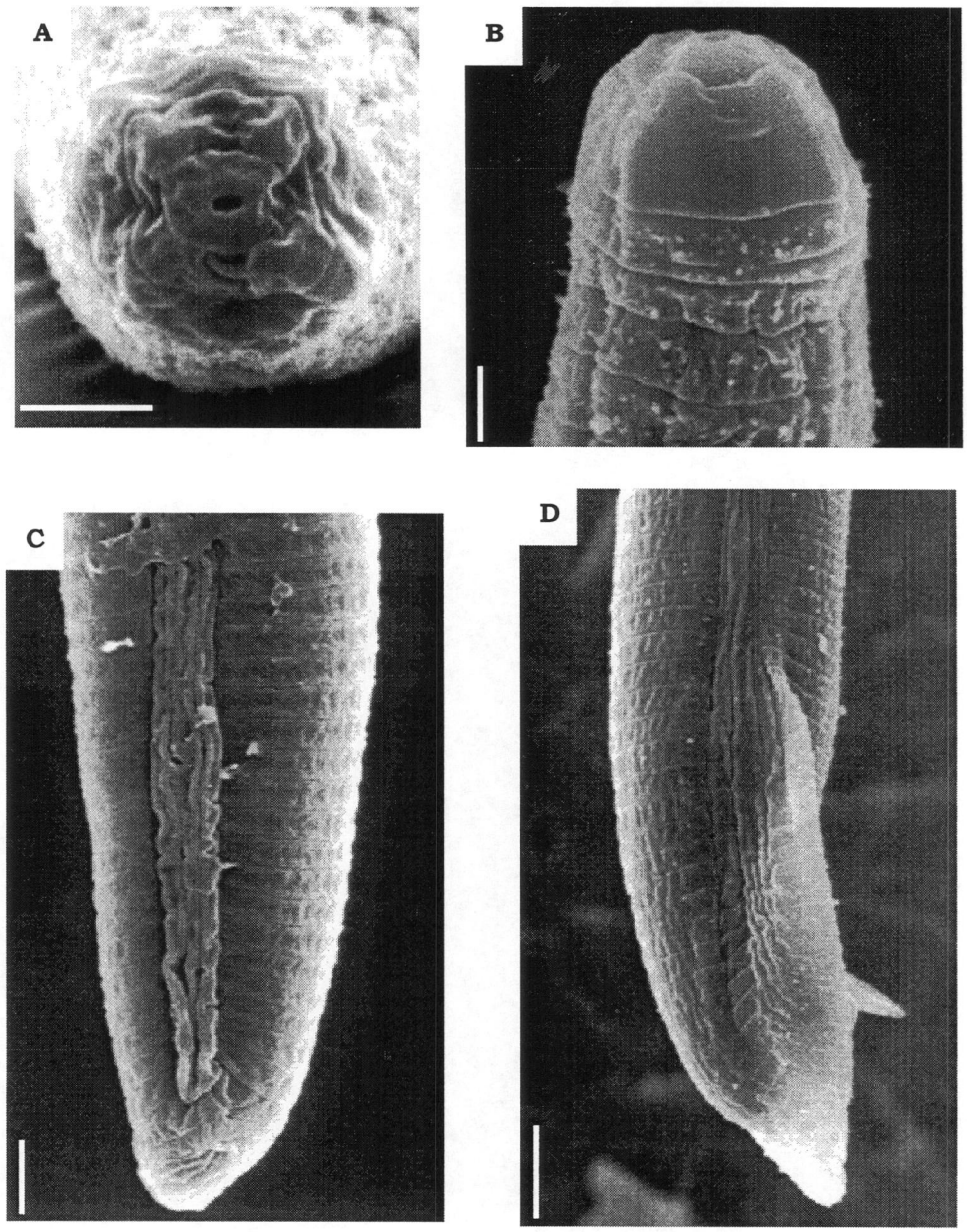
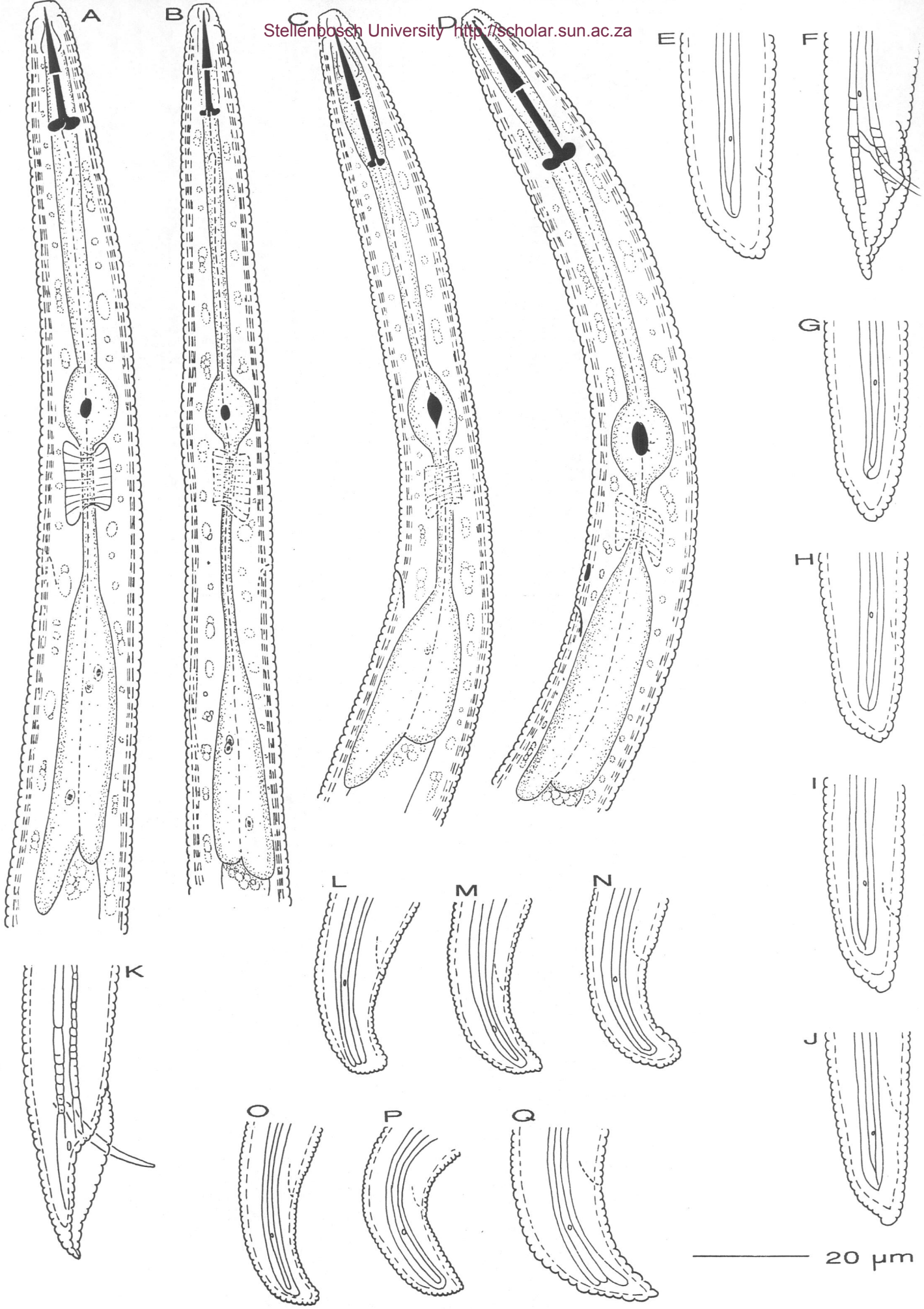


Fig. 27. *Helicotylenchus kermarreci.* Female: A: *En face* view, lip region; B: Lateral view, lip region; C: Posterior part of body; Male: D: Posterior part of body. (Scale bar: A-D = 2 µm).



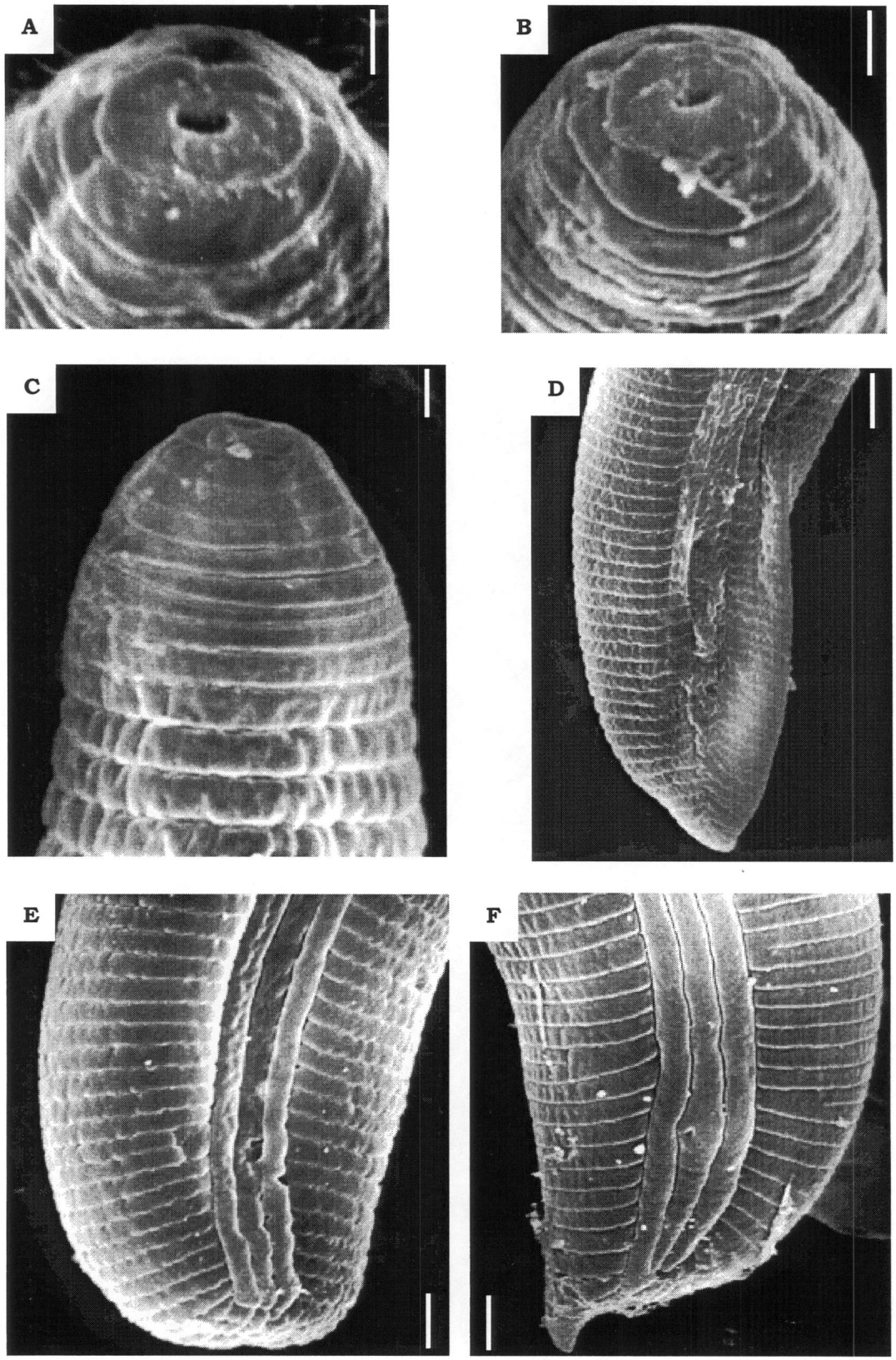


Fig. 28. *Helicotylenchus macrostylus.* Female: A: *En face* view, lip region; C: Lateral view, lip region; E-F: Posterior part of body; Male: B: *En face* view, lip region; D: Posterior part of body. (Scale bar: A-C = 1µm; D-F = 2 µm).

Fig. 29. *Helicotylenchus martini.* Male: A: Oesophageal region; Q-S: Posterior part of body; Female: B: Oesophageal region; C, I: Atypical reproductive system; J-P: Posterior part of body. ***Helicotylenchus marethae* n.sp.** Female: D: Oesophageal region; E-G: Posterior part of body; H: Habitus.

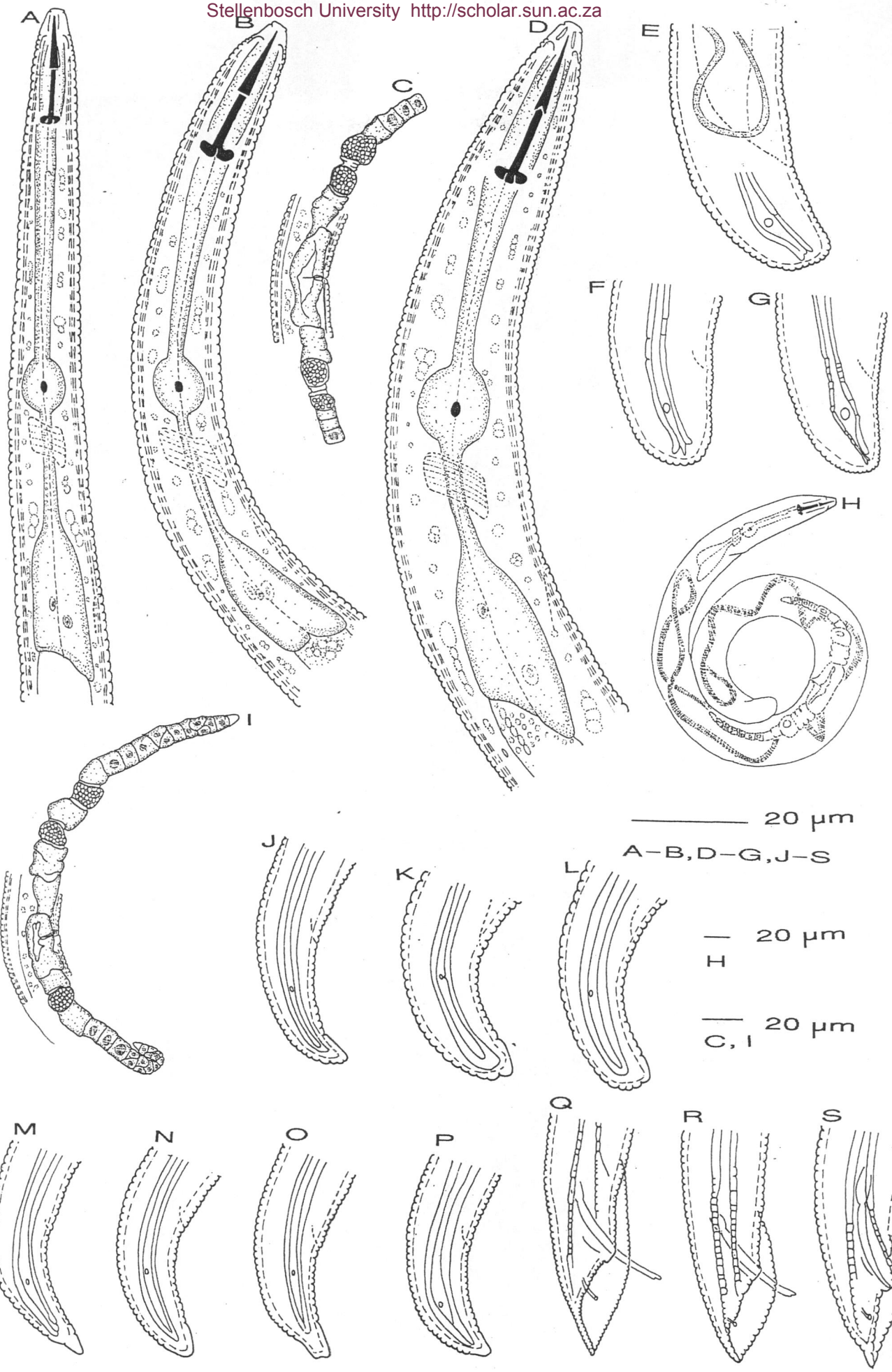
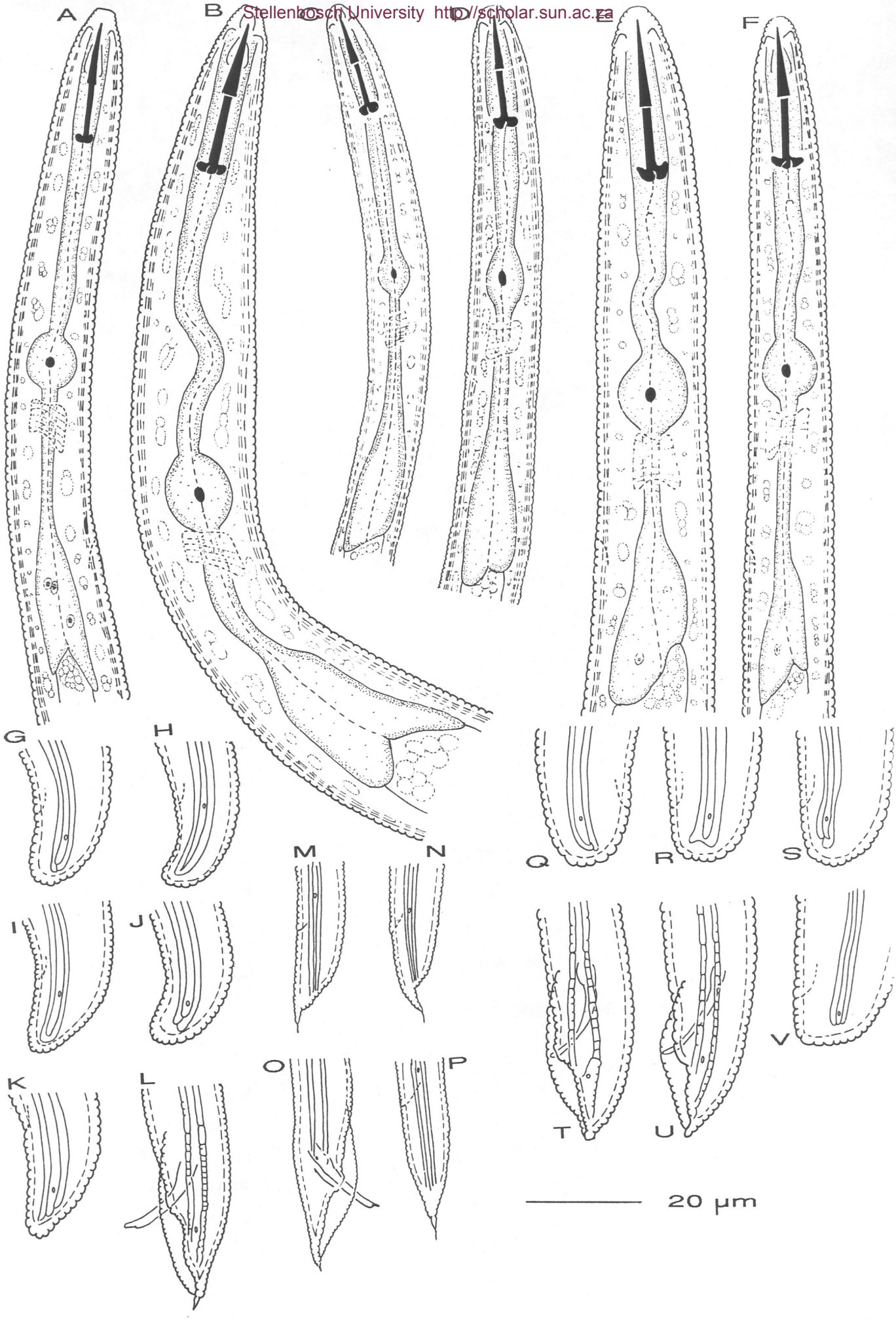


Fig. 30. ***Helicotylenchus minzi.*** Male: A: Oesophageal region; L: Posterior part of body; Female: B: Oesophageal region; G-K: Posterior part of body. ***Helicotylenchus minutus.*** Male: C: Oesophageal region; O: Posterior part of body; Female: D: Oesophageal region; M-N. P: Posterior part of body. ***Helicotylenchus multicinctus.*** Female: E: Oesophageal region; Q-S, V: Posterior part of body; Male: F: Oesophageal region; T-U: Posterior part of body.



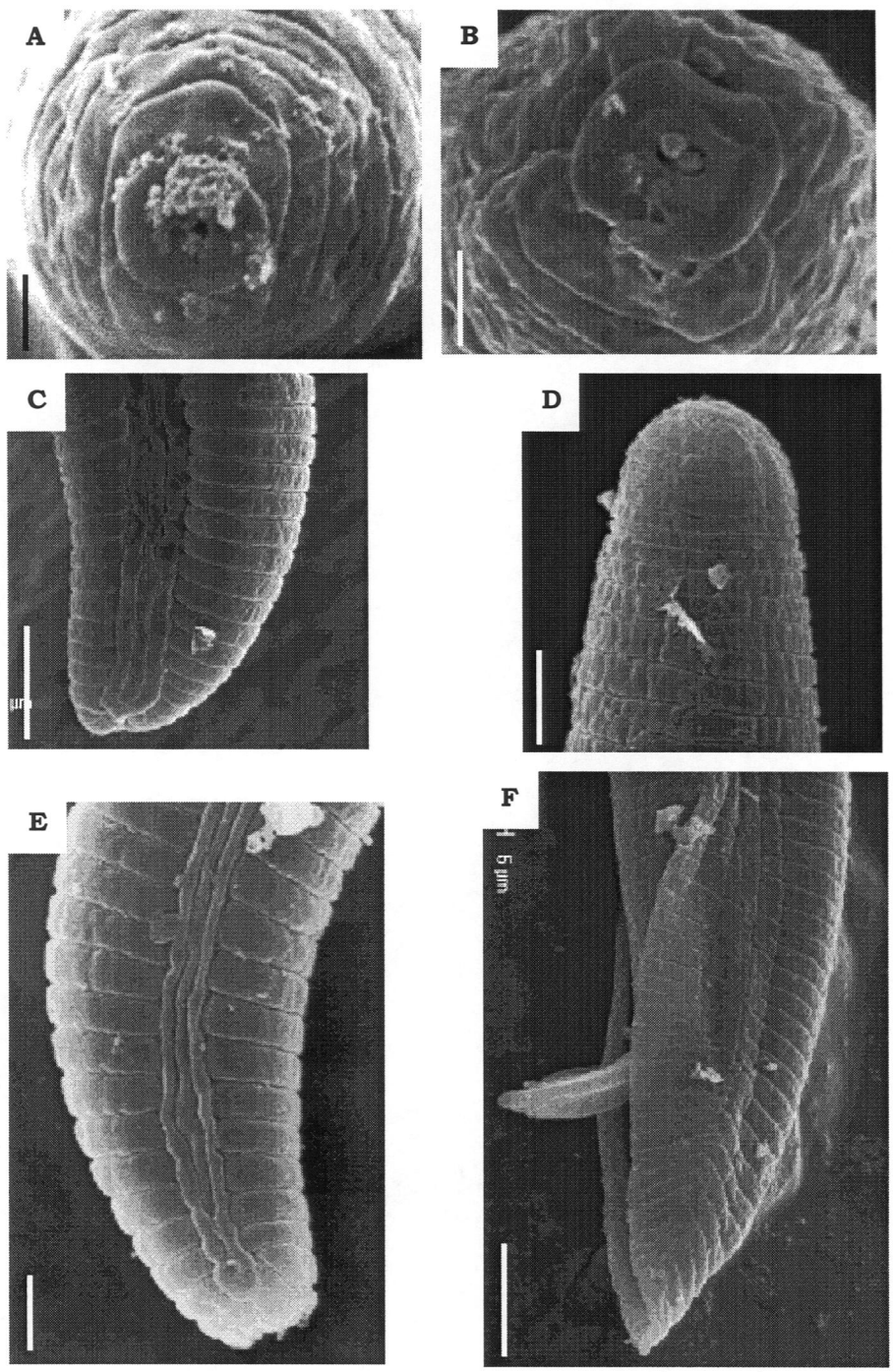


Fig. 31. ***Helicotylenchus minzi.*** Female: A: *En face* view, lip region; C, E: Posterior part of body; Male B: *En face* view, lip region; D: Lateral view, lip region; F: Posterior part of body. (Scale bar: A-B = 1 µm; D-E = 2 µm; C, F = 5 µm).

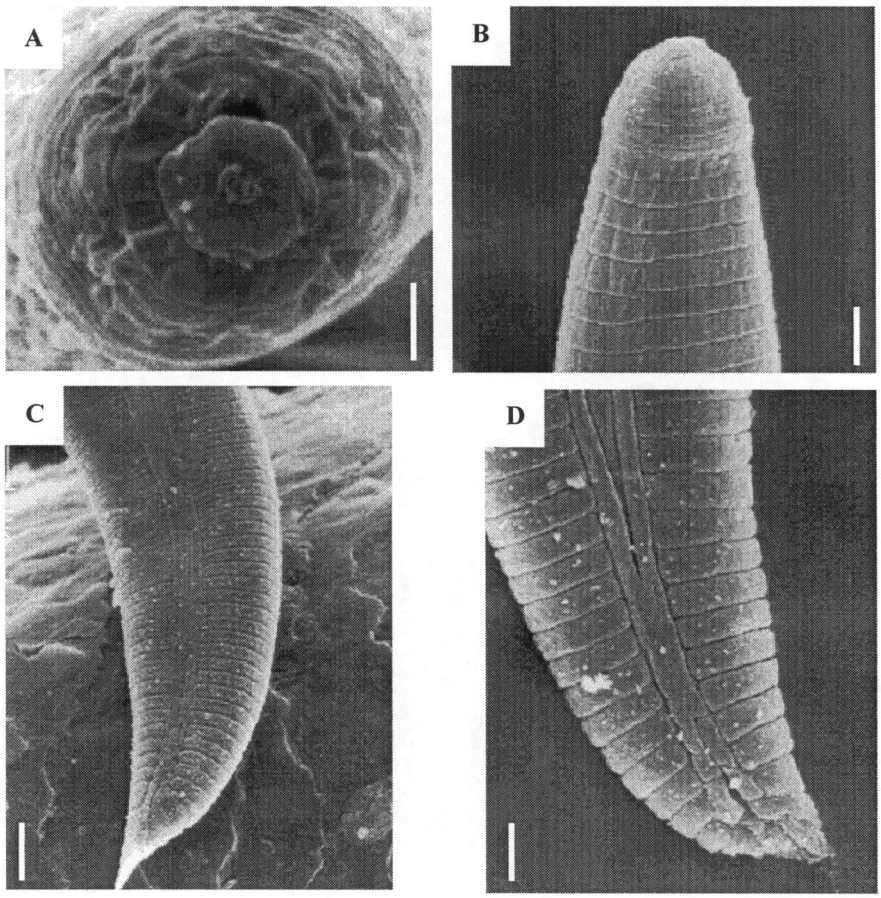


Fig. 32. *Helicotylenchus mucronatus.* Female: A: *En face* view, lip region; B: Lateral view, lip region; C-D: Posterior part of body. (Scale bar: A = 1 µm; B, D = 2 µm; C = 5 µm).

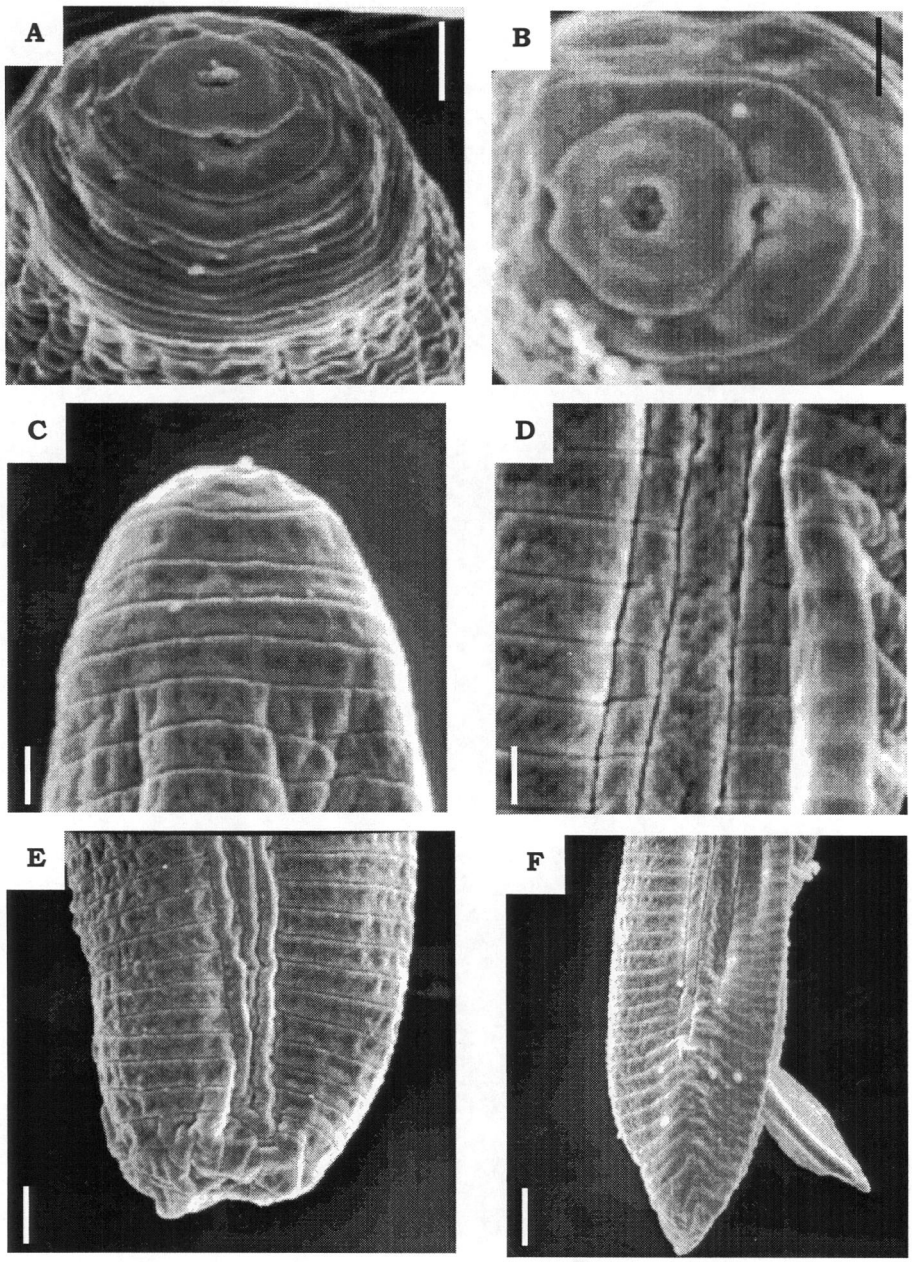
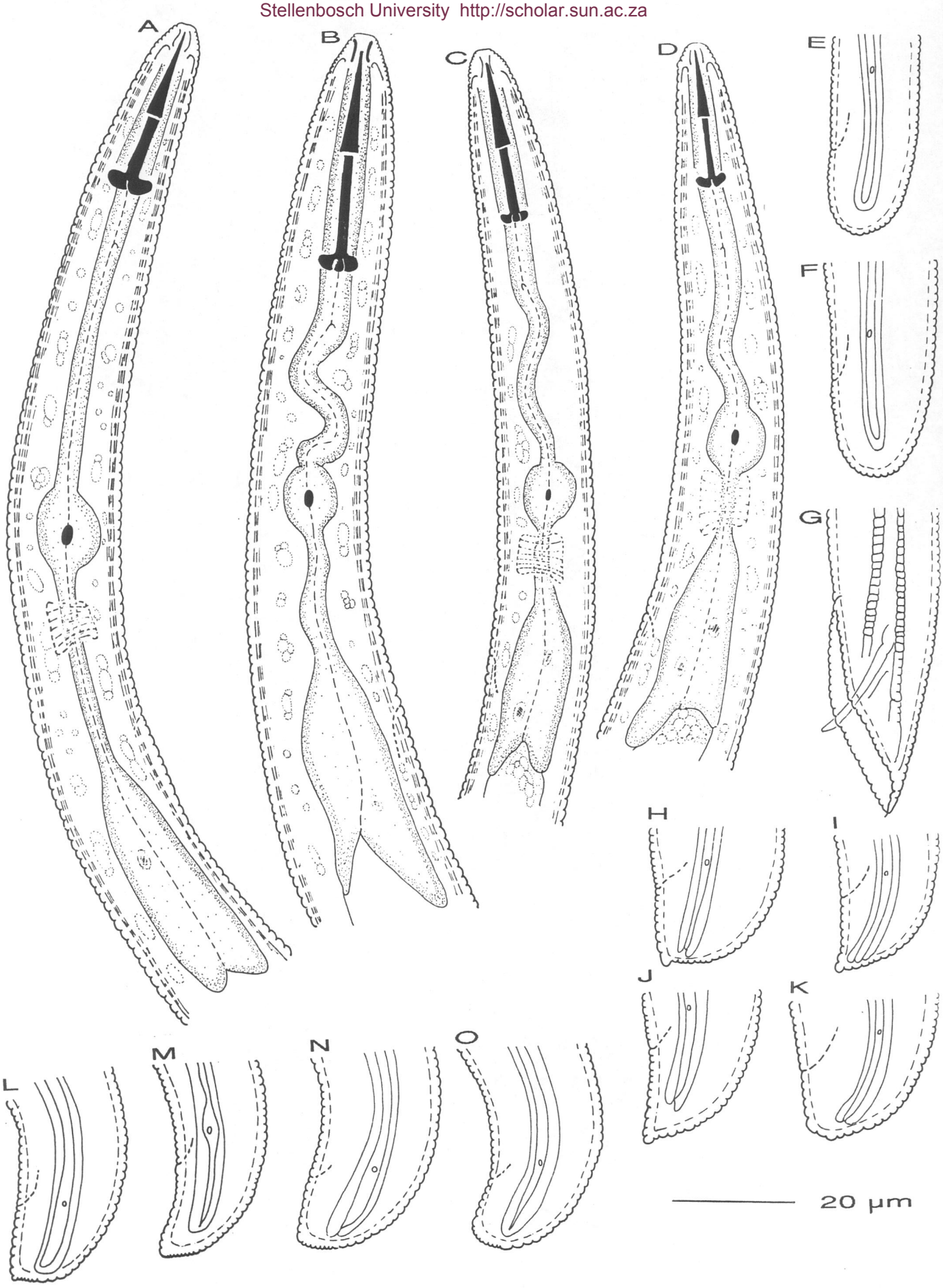


Fig. 33. ***Helicotylenchus multicinctus.*** Female: A: *En face* view, lip region; C: Lateral view, lip region; E: Posterior part of body; Male: B: *En face* view, lip region; D: Lateral field opposite to bursa; F: Posterior part of body. (Scale bar: A-F = 1 µm).

Fig. 34. ***Helicotylenchus paraplatyurus.*** Female: A: Oesophageal region; L-O: Posterior part of body. ***Helicotylenchus paracanalis.*** Female: B: Oesophageal region; H-K: Posterior part of body; Male: C: Oesophageal region; G: Posterior part of body. ***Helicotylenchus retusus.*** Female: D: Oesophageal region; E-F: Posterior part of body.



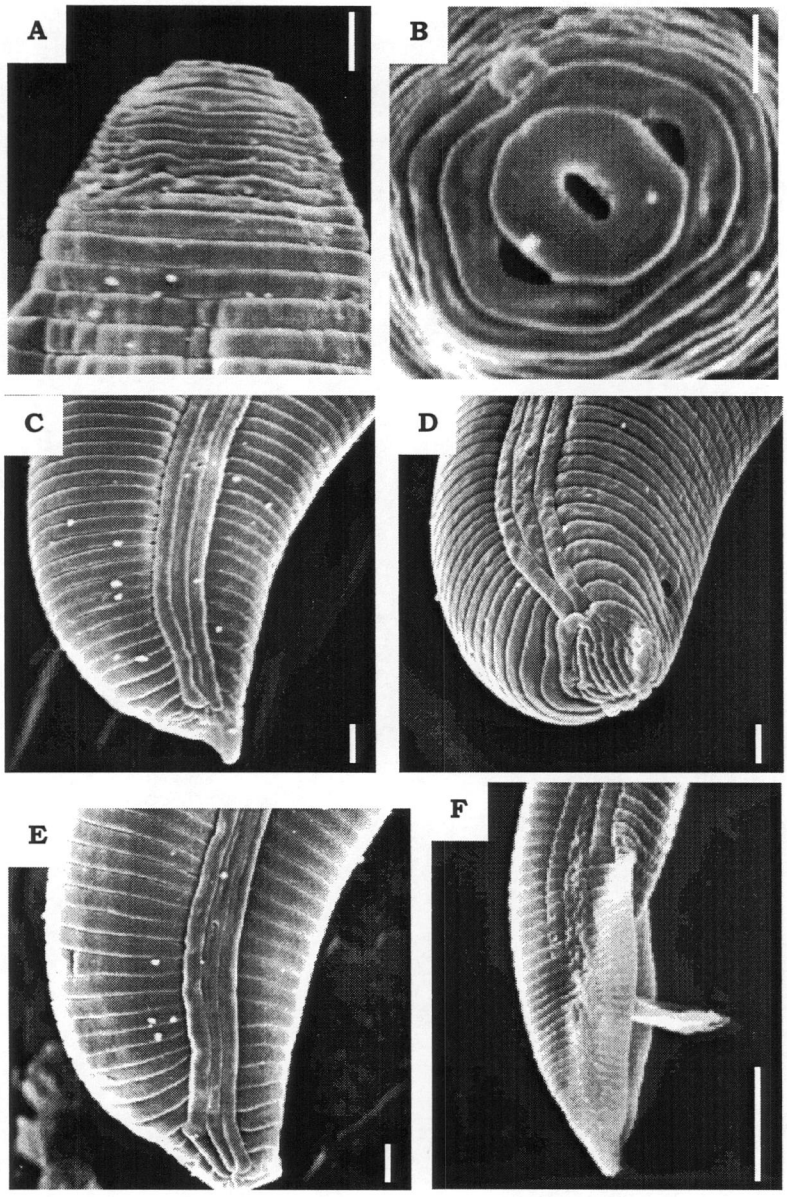


Fig. 35. ***Helicotylenchus paracanalis***. Female: A: Lateral view, lip region; B: *En face* view, lip region; C-E: Posterior part of body; Male: F: Posterior part of body. (Scale bar: A-B, F = 1 µm; C-E = 2 µm).

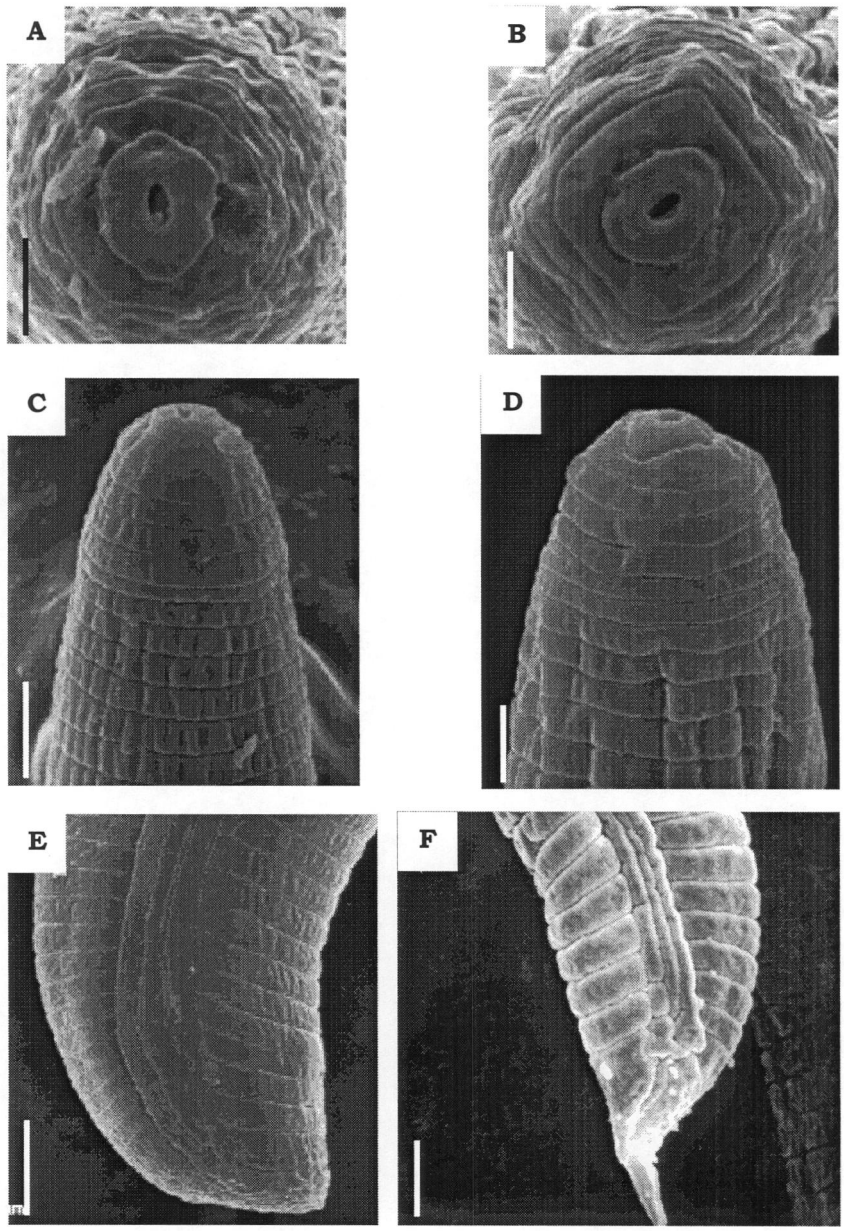


Fig. 36. ***Helicotylenchus paraplatyurus***. Female: A: *En face* view, lip region; C: Lateral view, lip region; E: Posterior part of body. ***Helicotylenchus pseudorobustus***. Female: B: *En face* view, lip region; D: Lateral view, lip region; F: Posterior part of body. (Scale bar: A-D, F = 2 µm; E = 5 µm).

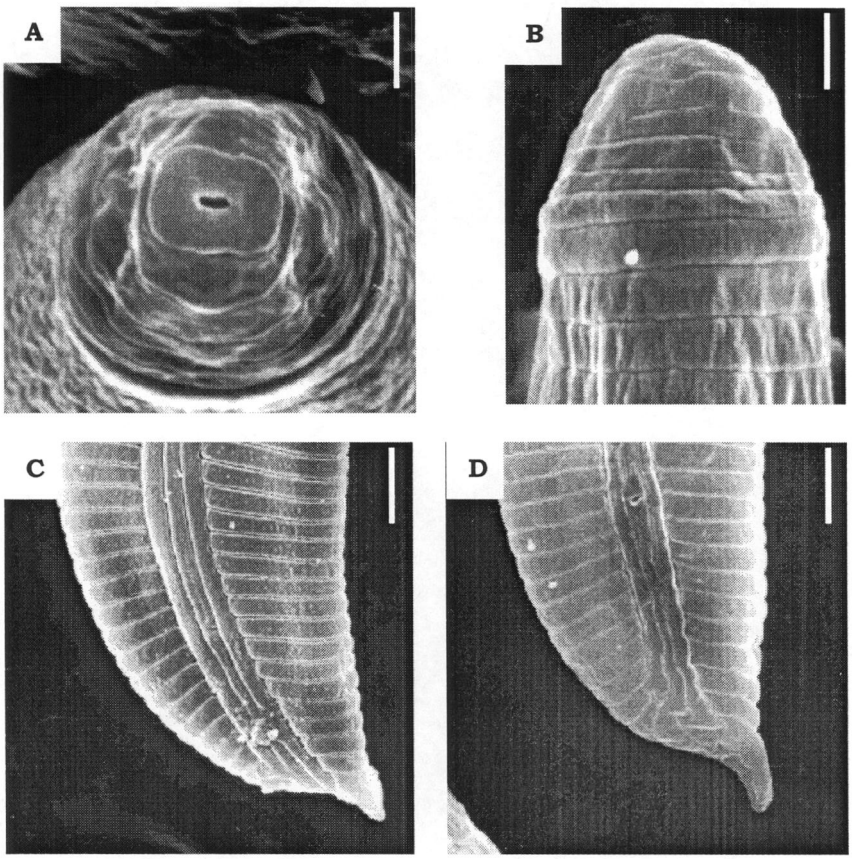
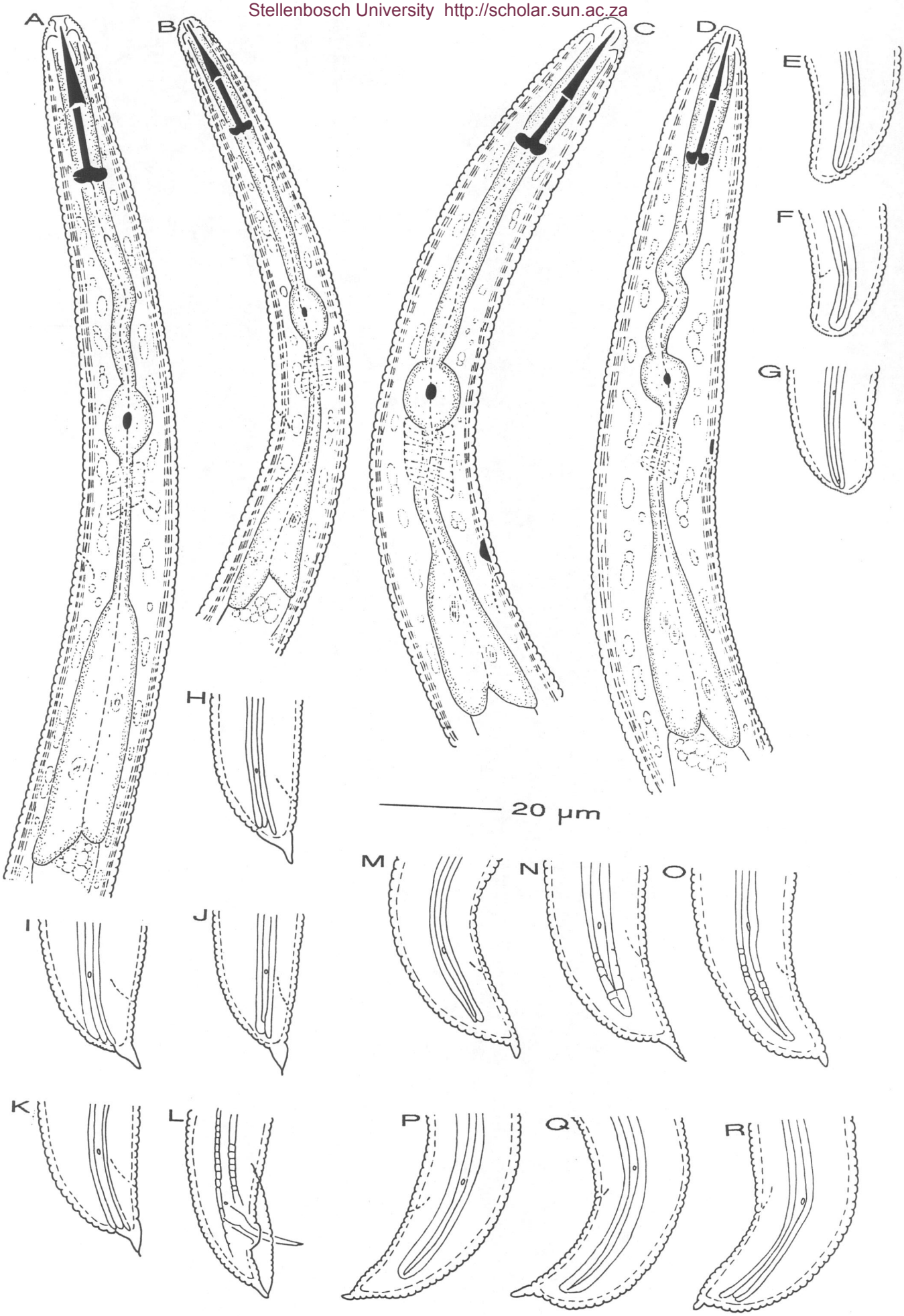


Fig. 37. *Helicotylenchus planquettei.* Female: A: *En face* view, lip region; B: Lateral view, lip region; C-D: Posterior part of body. (Scale bar: A-B = 1 µm; C-D = 2 µm).

Fig. 38. ***Helicotylenchus planquettei.*** Female: A: Oesophageal region; H-K: Posterior part of body; Male: B: Oesophageal region; L: Posterior part of body. ***Helicotylenchus pseudorobustus.*** Female: C: Oesophageal region; M-R: Posterior part of body. ***Helicotylenchus vulgaris.*** Female: D: Oesophageal region; E-G: Posterior part of body.



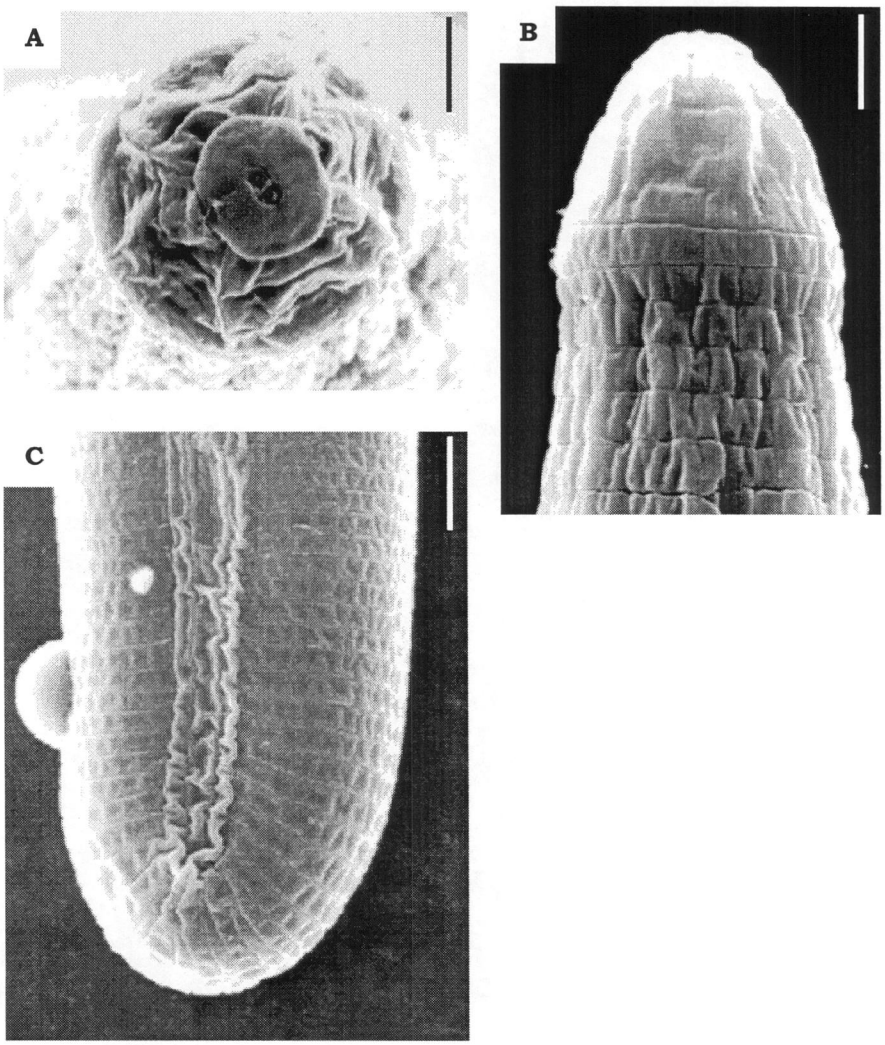
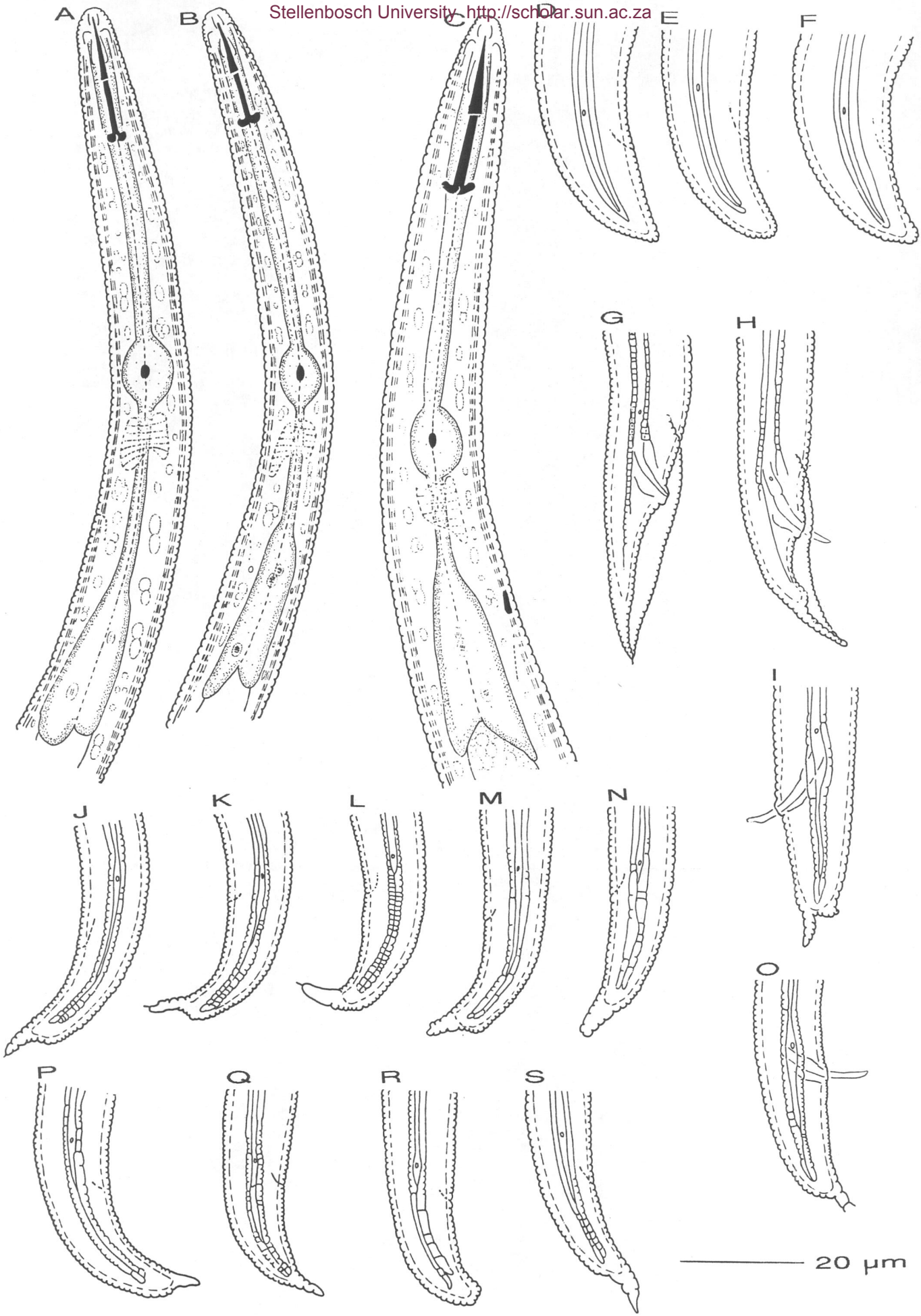


Fig. 39. *Helicotylenchus retusus.* Female: *En face* view, lip region; B: Lateral view, lip region; C: Posterior part of body. (Scale bar: A-B = 2 µm; C = 5 µm).

Fig. 40. ***Helicotylenchus stylocercus.*** Female: A: Oesophageal region; J-N, P-S: Posterior part of body; Male: B: Oesophageal region; G-H: Posterior part of body; I, O: Atypical posterior part of body. ***Helicotylenchus serenus.*** Female: C: Oesophageal region; D-F: Posterior part of body.



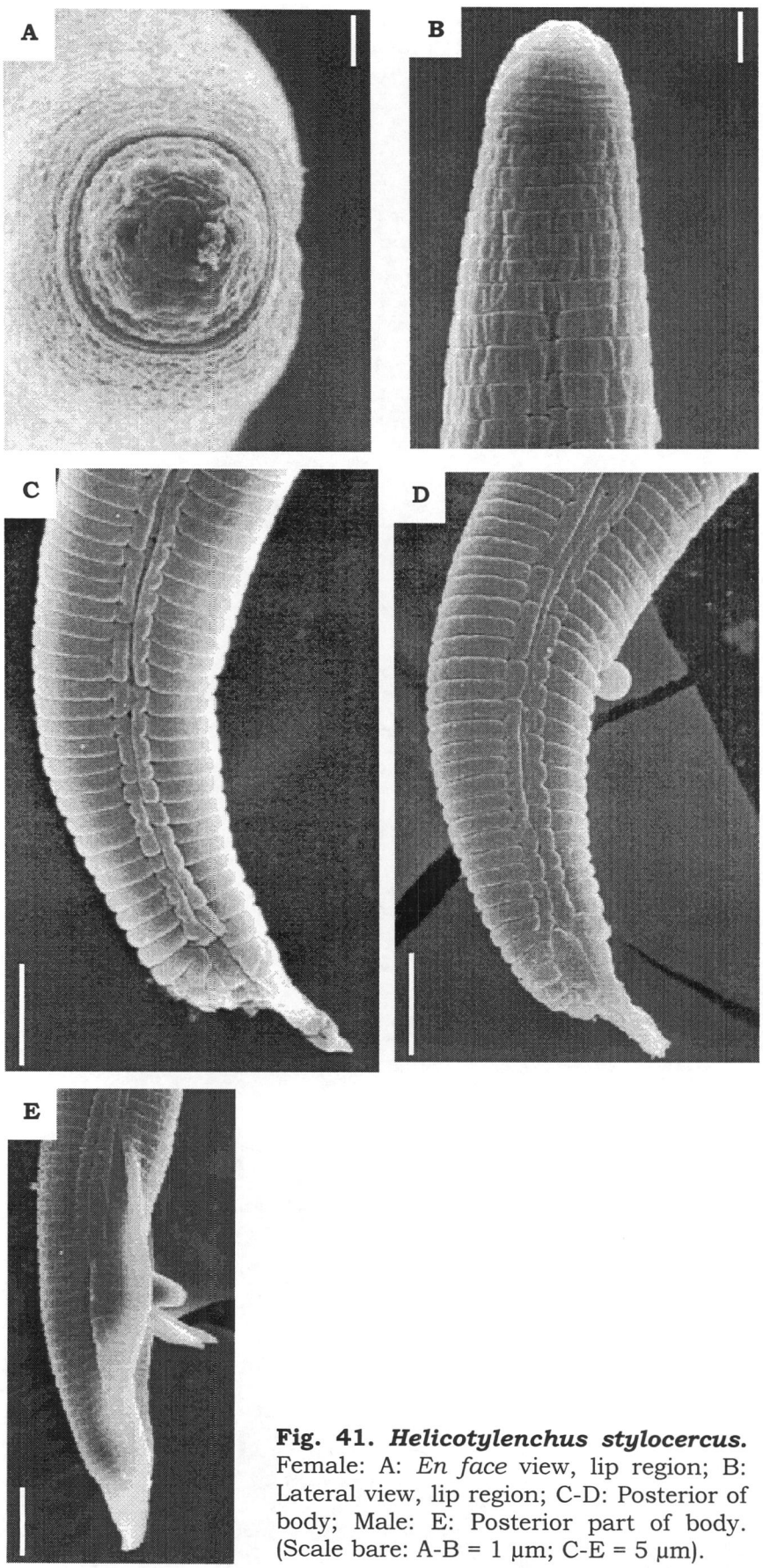
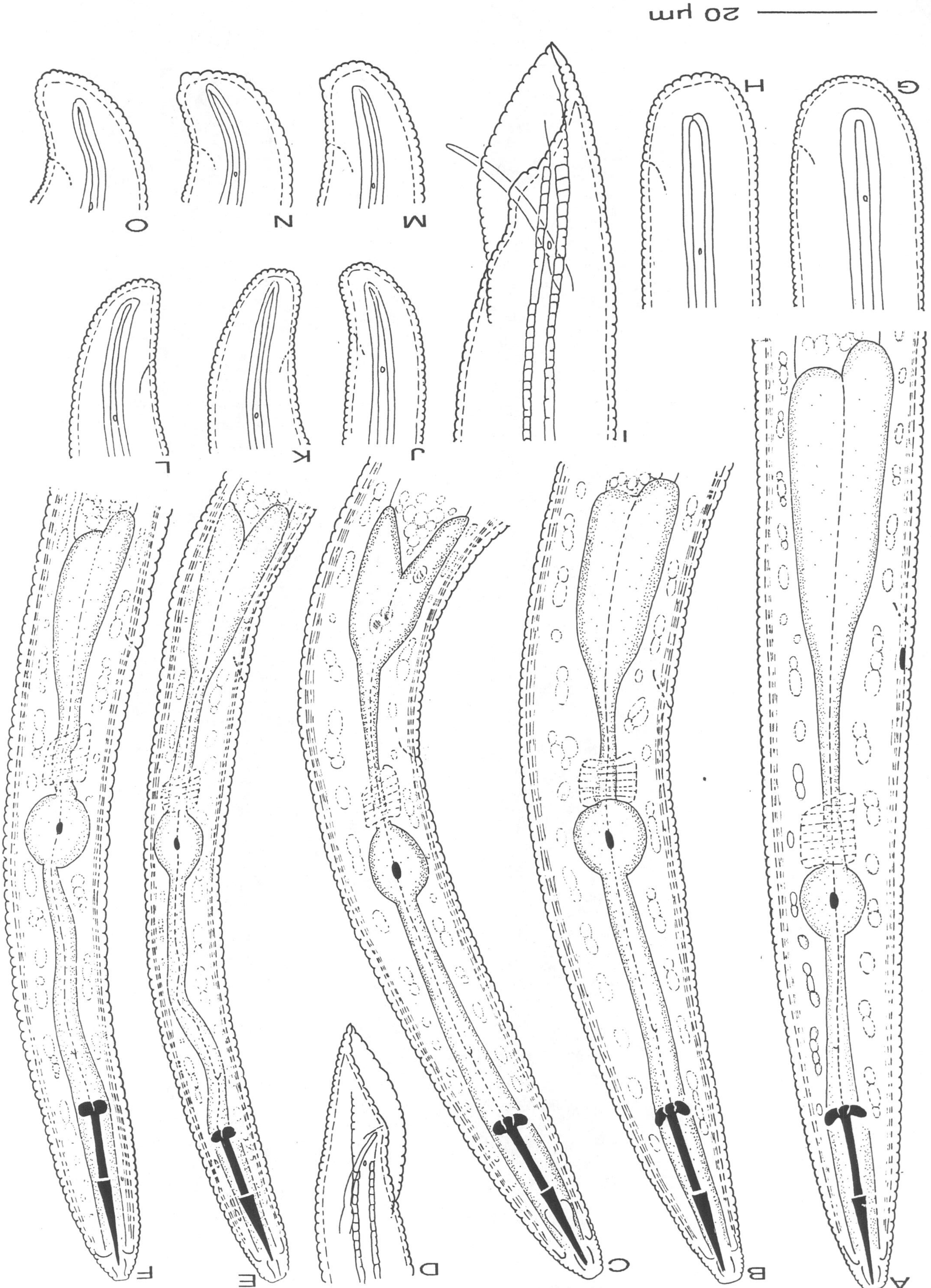


Fig. 41. ***Helicotylenchus stylocercus.*** Female: A: *En face* view, lip region; B: Lateral view, lip region; C-D: Posterior of body; Male: E: Posterior part of body. (Scale bare: A-B = 1 µm; C-E = 5 µm).

Fig. 42. ***Helicotylenchus tumidicaudatus.*** Female: A: Oesophageal region; G-H: Posterior part of body; Male: B: Oesophageal region; I: Posterior part of body. ***Helicotylenchus willmottae.*** Female: C: Oesophageal region; J-L: Posterior part of body. ***Helicotylenchus variabilis.*** Male: D: Posterior part of body; E: Oesophageal region; Female: Female: F: Oesophageal region; M-O: Posterior part of body.



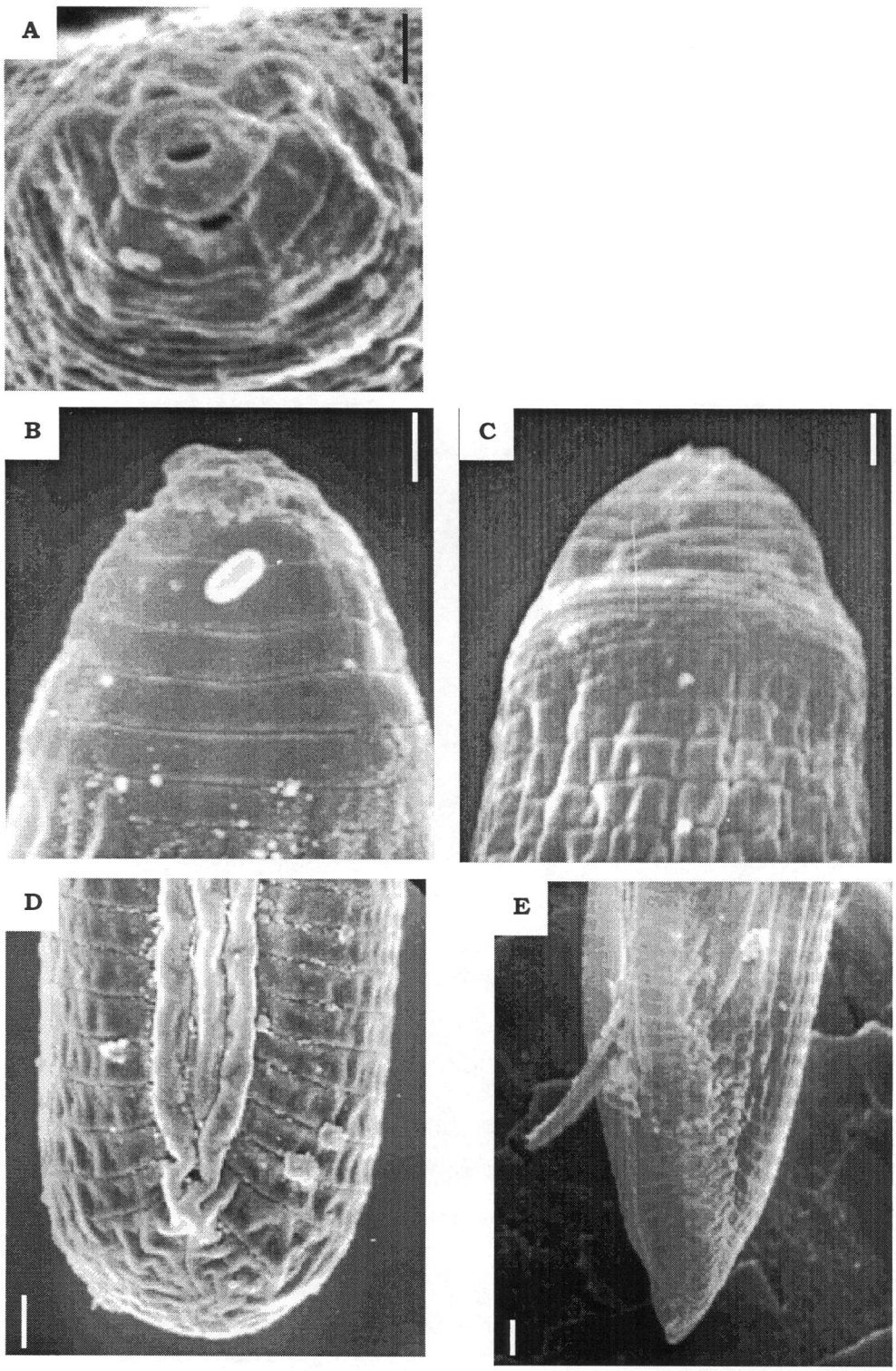


Fig. 43. *Helicotylenchus tumidicaudatus.* Female: A: *En face* view, lip region; B: Lateral view, lip region; D: Posterior part of body; Male: C: Lateral view, lip region; E: Posterior part of body. (Scale bar: A-E = 1 µm).

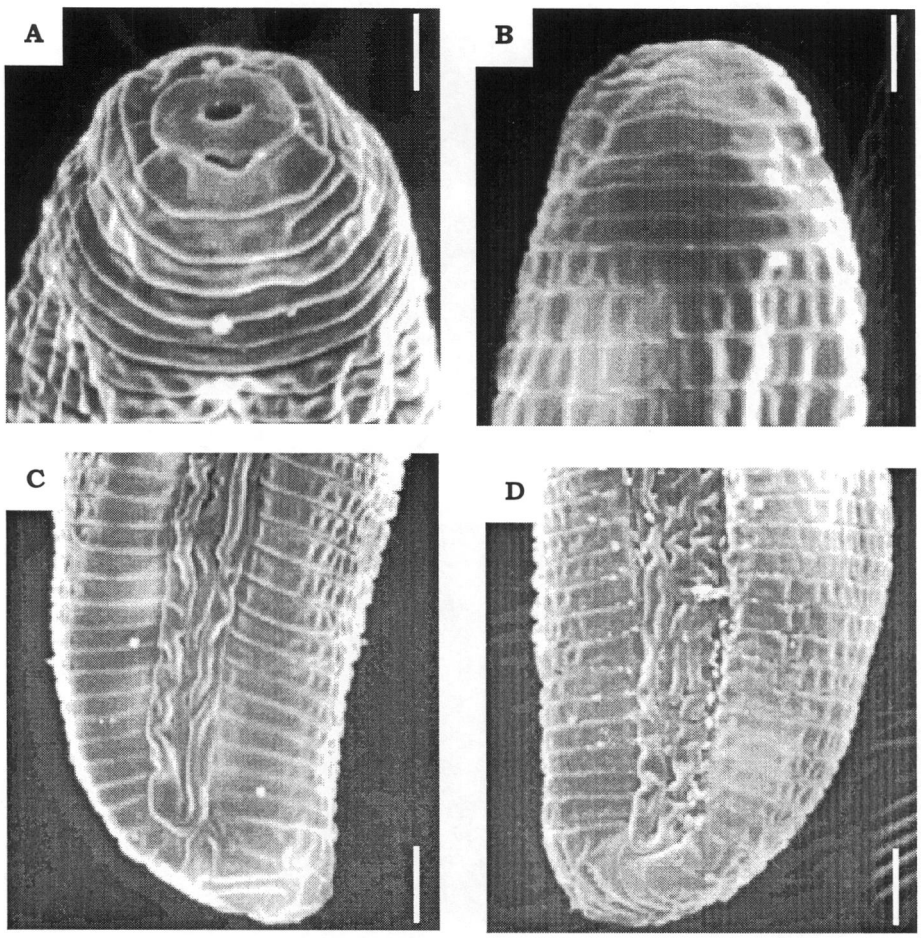


Fig.44. ***Helicotylenchus variabilis.*** Female: A: *En face* view, lip region; B: Lateral view, lip region; C-D: Posterior part of body. (Scale bar: A-B = 1 µm; C-D = 2 µm).

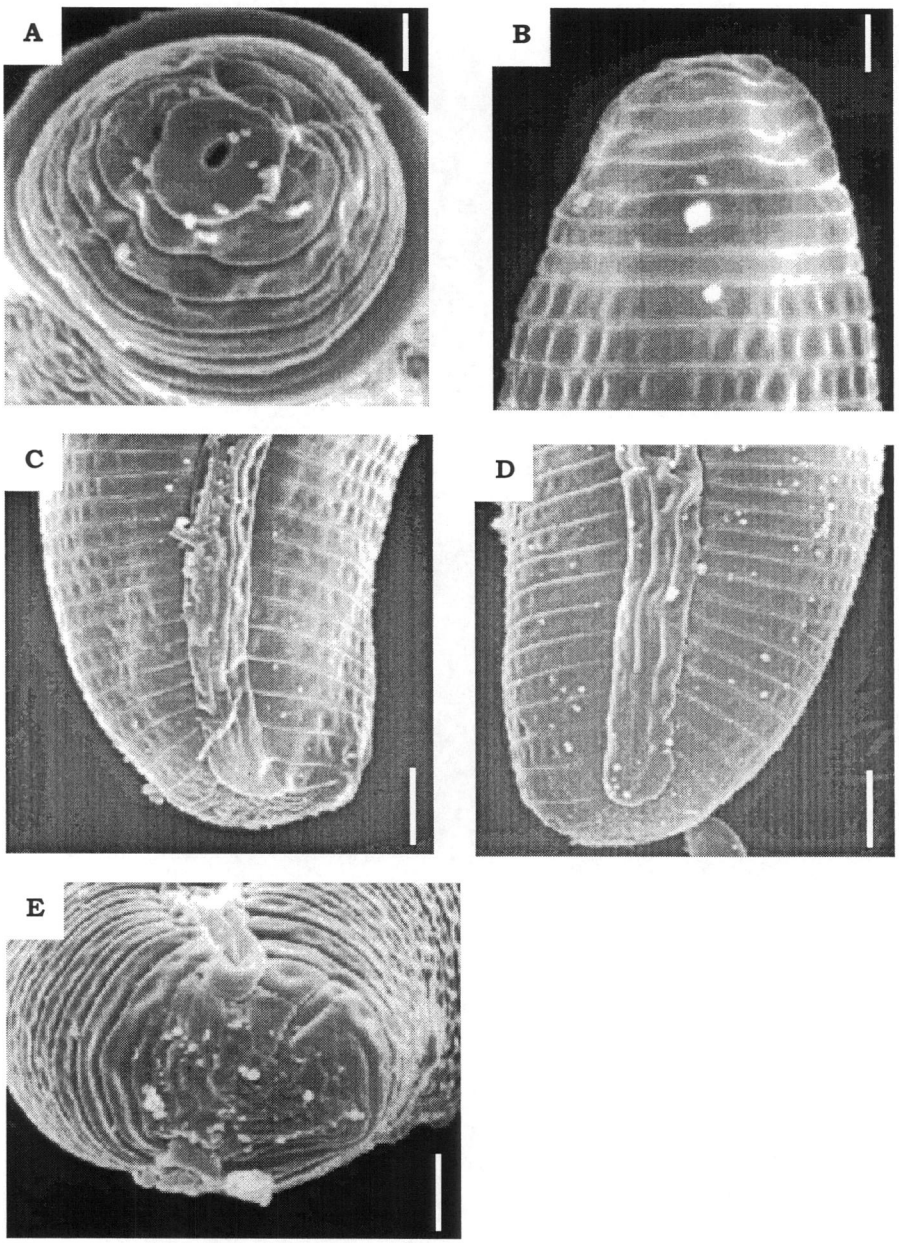


Fig. 45. ***Helicotylenchus vulgaris.*** Female: A: *En face* view, lip region; B: Lateral view, lip region; C-E: Posterior part of body. (Scale bar: A-B = 1 µm; C-E = 2 µm).

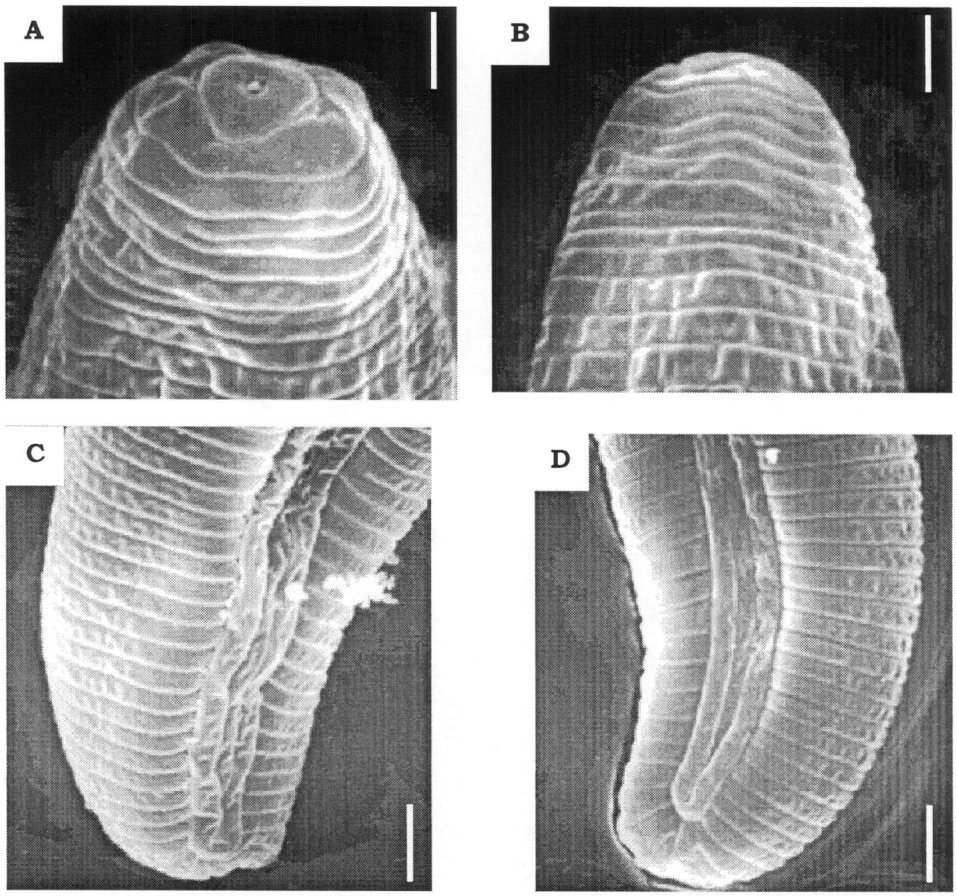


Fig. 46. ***Helicotylenchus willmottae.*** Female: A: *En face* view, lip region; B: Lateral view, lip region; C-D: Posterior part of body. (Scale bar: A-B = 1 µm; C-D = 2 µm).

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