

# Description of a new tropical Heteroderidae, *Hylonema ivorense* n. gen., n. sp., and a new outlook on the family Heteroderidae (Nematoda : Tylenchida)

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## SUMMARY

*Hylonema*, a new genus in the Heteroderidae from Ivory Coast, is described and illustrated with *H. ivorense* n. sp. described and designated the type species. The authors suggest that the division of the Heteroderidae into the Heteroderinae, Meloidoderinae and Ataloderinae is highly artificial and serves no useful purpose ; it is proposed to abandon the use of these subfamilies. *Zelandodera* is considered a junior synonym of *Cryphodera* resulting in the following nomenclatorial changes : *C. podocarp*i (Wouts, 1973) n. comb. ; *C. nothophagi* (Wouts, 1973) n. comb. and *C. coxi* (Wouts, 1973) n. comb. *Sherodera* is considered a junior synonym of *Atalodera* and *S. lonicer*ae becomes *A. lonicer*ae (Wouts, 1973) n. comb. Thus, the family Heteroderidae is considered to consist of the following genera : *Heterodera* Schmidt, 1871 ; *Globodera* (Skarbilovich, 1959) Mulvey & Stone, 1976 ; *Punctodera* Mulvey & Stone, 1976 ; *Sarisodera* Wouts & Sher, 1971 ; *Meloidodera* Chitwood, Hannon & Esser, 1956 ; *Cryphodera* Colbran, 1956 ; *Atalodera* Wouts & Sher, 1971 and *Hylonema* n. gen.

## RÉSUMÉ

Description d'un nouvel Heteroderidae tropical, *Hylonema ivorense* n. gen., n. sp.,  
et considérations sur la famille des Heteroderidae (Nematoda : Tylenchida).

Les auteurs décrivent un nouveau genre d'Heteroderidae, *Hylonema* n. gen., ayant pour type et unique espèce *Hylonema ivorense* n. gen., n. sp. observé sur de jeune avodirés (*Turraeanthus africana*) en Côte d'Ivoire. Se fondant sur les caractéristiques de ce nouveau genre, les auteurs proposent d'abandonner l'usage des sous-familles généralement admises chez les Heteroderidae (Heteroderinae, Meloidoderinae et Ataloderinae). Le genre *Zelandodera* est considéré comme synonyme de *Cryphodera*, entraînant les changements de nomenclature suivants : *C. podocarp*i (Wouts, 1973) n. comb., *C. nothophagi* (Wouts, 1973) n. comb., *C. coxi* (Wouts, 1973) n. comb. De même, *Sherodera* est considéré comme synonyme d'*Atalodera* et *S. lonicer*ae devient *A. lonicer*ae (Wouts, 1973) n. comb. La famille des Heteroderidae comprend donc les genres suivants : *Heterodera* Schmidt, 1871 ; *Globodera* (Skarbilovich, 1959) Mulvey & Stone, 1976 ; *Punctodera* Mulvey & Stone, 1976 ; *Sarisodera* Wouts & Sher, 1971 ; *Meloidodera* Chitwood, Hannon & Esser, 1956 ; *Cryphodera* Colbran, 1956 ; *Atalodera* Wouts & Sher, 1971 et *Hylonema* n. gen.

Juveniles and males of a previously unknown member of the Heteroderidae were recovered by one of the authors (P.C.) from soil collected around the roots of "avodiré", *Turraeanthus africana* Pellegr., growing in a tropical rain-forest reserve at Banco, Ivory Coast. Examination and dissection of the roots of this tree revealed the presence of saccate females of an undescribed genus. The description of the unique host-parasite relationship observed is given in a subsequent article (Taylor, Cadet &

Luc, 1978). Detailed morphological and anatomical studies of the nematode were made resulting in the description of *Hylonema ivorense* n. gen., n. sp. given below.

Our inability to include this new genus in any of the existing subfamilies of the Heteroderidae indicated the importance of examining the validity of these subfamilies and some of the more recently described genera in order to develop a meaningful organization of this family.

## Materials and methods

Living males and juveniles were isolated from soil by standard extraction techniques. Specimens were killed and fixed with FP 4 : 1 (Netscher & Seinhorst, 1969) and mounted in glycerin on Cobb slides according to the rapid method of Seinhorst (1959).

Females were obtained by careful dissection of infected avodiré roots which had been fixed in F.A.A. for 48 hours or longer. Intact females were mounted in glycerin on Cobb slides as above. Vulval cones were prepared by dissecting the posterior portion of fixed females, removing the body contents in lactic acid (Taylor & Netscher, 1974) and mounting in glycerin jelly on Cobb slides.

Specimens were prepared for stereoscan electron microscope study (S.E.M.) as described by Sher and Bell (1975). Conventional optical photomicrographs were made with a Leitz "Orthomat" photomicroscope.

### *Hylonema ivorense* n.gen., n.sp.

#### MEASUREMENTS

*Females* : (n = 39) : L = 0.61 mm (0.34-1.01) ; width = 0.23 mm (0.16-0.34) ; L/w = 2.5 (1.9-4.6) ; stylet (n = 5) = 41  $\mu$ m (38-46).

*Males* : L (n = 50) = 1.02 mm (0.65-1.42) ; a (n = 26) = 39 (32-47) ; b (n = 25) = 6.9 (5.4-7.9) ; b' (n = 25) = 4.4 (3.3-6.2) ; stylet (n = 25) = 40.5  $\mu$ m (38-44) ; anterior portion of stylet = 22  $\mu$ m (19.5-24.5) ; m = 54 (51-56) ; stylet knobs (h  $\times$  w) = 3  $\times$  7  $\mu$ m (2.5-4.0  $\times$  6-10.5) ; o = 8 (5-11) ; spicules (n = 25) = 32  $\mu$ m (27-36.5) ; gubernaculum (n = 25) = 11  $\mu$ m (9-13) ; median bulb (l  $\times$  w) (n = 13) 13.5  $\times$  9  $\mu$ m (11.5-18  $\times$  8.5-10.5) ; distance from anterior end to center of median bulb (n = 13) = 94.5  $\mu$ m (80-110).

*Juveniles (2nd stage)* : L (n = 50) = 0.64 (0.60-0.73) ; a (n = 25) = 30 (25-36) ; b (n = 23) = 5.2 (4.1-5.8) ; b' (n = 25) = 2.5 (2.2-2.9) ; tail length (n = 25) = 83.5  $\mu$ m (70-96) ; c = 7.9 (7.1-8.9) ; c' = 6.1 (4.4-6.8) ; stylet (n = 25)

= 36  $\mu$ m (33-39.5) ; anterior portion of stylet = 18.5  $\mu$ m (16-21) ; m = 51 (47-55) ; stylet knobs (h  $\times$  w) = 3.0  $\times$  6.5  $\mu$ m (2.5-3.5  $\times$  5.5-8) ; o (n = 15) = 12.4 (8-16) ; median bulb (l  $\times$  w) (n = 11) = 11  $\times$  16.5  $\mu$ m (10-12  $\times$  15-19) ; distance from anterior end to center of median bulb = 88.5  $\mu$ m (85-93) ; hyaline terminal portion of tail ("h") = 70.5  $\mu$ m (55-88) ; h as % tail length = 84 (77-92).

*Holotype* (female) : L = 0.42 mm ; width = 0.20 mm ; L/w = 2.1 ; stylet = 42  $\mu$ m ; dist. vulva to anus = 19  $\mu$ m.

#### DESCRIPTION

*Females* : Body size and shape variable, generally elongated and swollen one way or another ; anterior portion (« neck ») relatively long and distinct from rest of body. Body swelling usually progressive with the largest part of the body located either anteriorly or posteriorly (apparently depending on its ability to develop within host tissues). Posterior extremity generally rounded in profile, flattened between vulva and anus. Vulva subterminal ; vulval lips not observed in profile.

Cuticle thickened, 5  $\mu$ m anteriorly and 10-13  $\mu$ m at central and posterior portions ; apparently composed of two layers : an internal hyaline layer and an external irregularly cracked layer producing a very rugose surface (somewhat resembling a young *Heterodera* cyst). Cuticular surface with relatively deep, non-oriented striae ; no punctations as in *Heterodera* and *Sarisodera*.

"Head" conical but of unusual appearance with the cuticular structure contrasting with that of the rest of the body ; for the first 15-23  $\mu$ m from the anterior end the cuticle is thin (0.6-1.0  $\mu$ m) and marked by 15-20 regular transverse striae. In lateral view (optical microscope), the first 5 or 6 annules appear more distinct and separated, but no distinct labial annules could be discerned. If they correspond to the position of the cephalic framework, there are 2-3 labial annules. *En face* view (S.E.M.) shows a roughly quadrangular (rarely triangular) first annule (or labial disc) (Fig. 3, C-D), which is very distinct and narrower than the next annule.

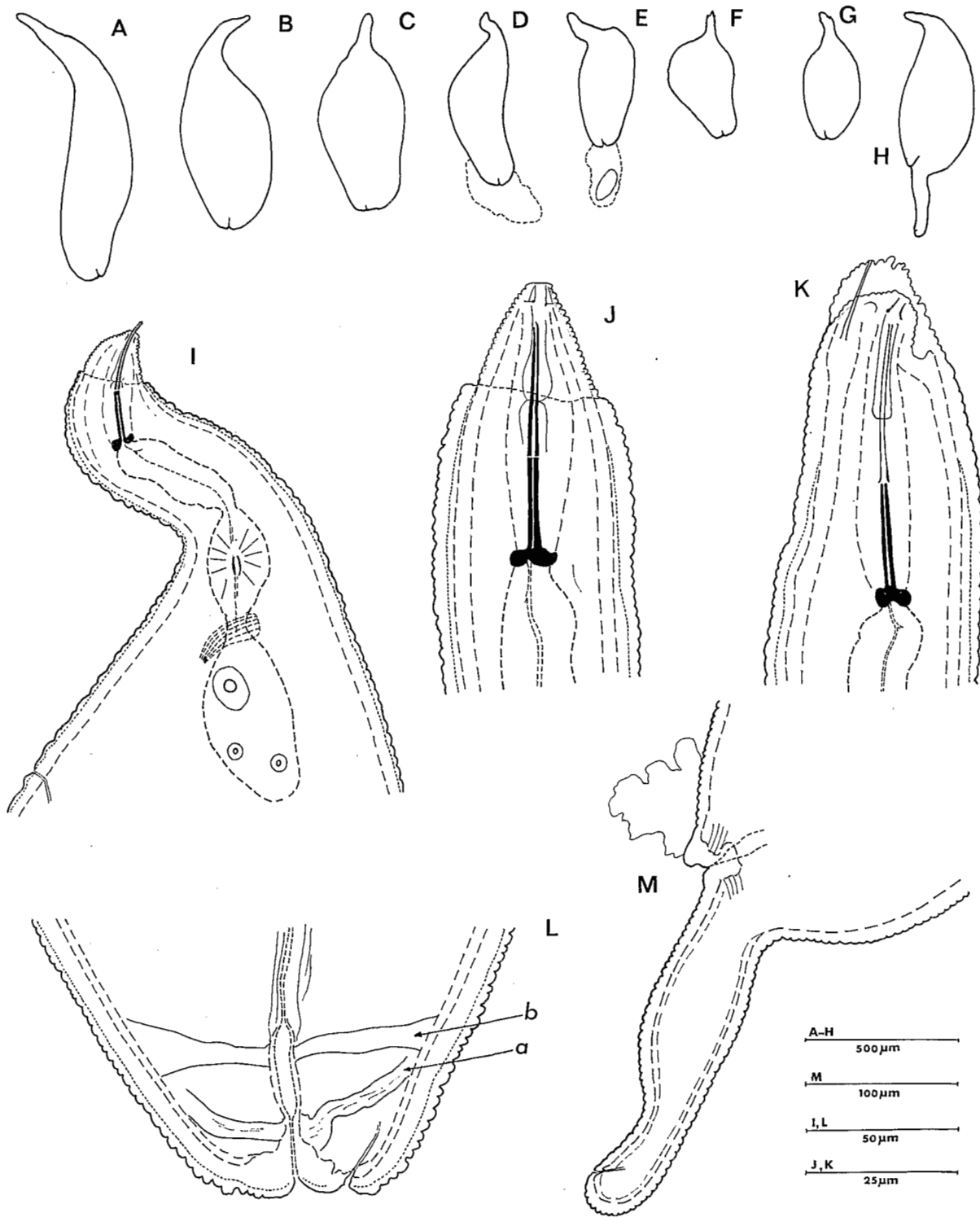


Fig. 1 : *Hylonema ivorense* n. gen., n. sp. : Female : A-G : outline of body ; I : œsophageal portion ; J, K : fore part ; L : posterior part (a : muscles ; b : underbridge). Abnormal female : H : outline of the body ; M : postvulval portion.

*Hylonema ivorense* n. gen., n. sp. Femelles : A-G : profils du corps ; I : région œsophagienne ; J, K : partie antérieure ; L : partie postérieure (a : muscles ; b : pont inférieur). Femelle aberrante : H : profil du corps ; M : partie post-vulvaire.

Buccal aperture roughly hexagonal; no amphidial apertures observed. The next (2nd) annule, rounded and larger, has irregularly scattered rounded protuberances. A hexaradiate basal plate is seen in *en face* view (optical microscope). Stylet long and slender; anterior portion slightly longer than posterior; stylet knobs generally rounded with flattened or slightly pointed anterior surfaces. Dorsal oesophageal gland duct opening approximately 5  $\mu\text{m}$  posterior to stylet base.

Procorpus massive, constricted at junction with metacarpus which is enlarged and nearly spherical (37  $\times$  34  $\mu\text{m}$ ) with well developed valve plates (7  $\times$  5  $\mu\text{m}$ ). Isthmus short; basal glandular portion containing a very large anterior nucleus and two smaller posterior nuclei.

Excretory pore small, difficult to locate. In two females it was located 136 and 184  $\mu\text{m}$  from the anterior end, at the level of the basal bulb of the oesophagus. Nerve ring thin, surrounding isthmus. Hemizonid, hemizonion, phasmids, cephalids not observed.

Intestine not observed; anus terminal, pore-like, 16-20  $\mu\text{m}$  from vulva.

Genital branches two, convoluted. Vulva a slit 43  $\mu\text{m}$  (40-46) long, located in a slight depression approximately 8  $\mu\text{m}$  below surface of posterior terminus. No bullae or fenestration observed. Underbridge conspicuous in certain specimens, located 43-54  $\mu\text{m}$  below level of vulva and parallel to it. Length of underbridge variable depending on size of female; average length 156  $\mu\text{m}$ . An expanded central area present, 54  $\mu\text{m}$  long and 36  $\mu\text{m}$  wide, with a central opening 9-10  $\mu\text{m}$  in diameter (Fig. 4, C). Underbridge in nonexpanded portion averages 8  $\mu\text{m}$  in width.

Note 1 : One very frequently observes one or even two anterior portions of stylets attached to the cuticle at the anterior end (Fig. 1, K) or included in a thin residual juvenile cuticle surrounding the anterior end of the female. At least, the last juvenile cuticle can be generally observed on females, even mature, exfoliating on different places of the body.

Note 2 : An abnormal female was observed in which the post vulval part of the body is

elongated and irregularly cylindrical (length = 240  $\mu\text{m}$ ; max. diameter = 60  $\mu\text{m}$ ). The tail is hemispherical (length = 19  $\mu\text{m}$ ;  $c' = 0.5$ ); no phasmids were observed (Fig. 1, H, M).

*Males* : Body straight or weakly curved, elongate, cylindrical, slightly more slender at the anterior end. A distinct narrowing of the body occurs at the level of the junction of the two parts of the stylet giving this part of the body a slightly conical appearance. Body generally twisted throughout its length; anterior and posterior extremes forming an angle of 90° with longitudinal axis.

Cuticle distinctly annulated, average width of annules 2.5  $\mu\text{m}$  at middle of body. Lateral field with four lines occupying one-fourth body diameter at middle of body. Lines of lateral field not fused in posterior portion of body.

Labial region rounded in relief, separated from rest of body by a distinct incisure; 5.5  $\mu\text{m}$  (4-6.5) high and 10  $\mu\text{m}$  (8-11.5) wide; with 4-5 annules. Anterior annule wider than others. Labial disc present, difficult to see with optical microscope. *En face* view with S.E.M. (Fig. 3, A) shows a generally rectangularly shaped buccal opening elongated dorso-ventrally and a labial disc also generally rectangular, rounded at the corners, and thinner at the center. The long axis of the disc is dorso-ventral. Amphidial openings are transverse slits located at the edge of the labial disc. Cephalic sclerotization strong. Basal plate convex, angular anteriorly and not extending below level of incisure separating lip region from rest of body. In lateral view the arches are distinct and clearly visible by their central thickenings. In *en face* view, basal plate can be seen as a wide central ring with six short branches slightly reflexed at their extremities and arranged regularly.

Stylet long, straight, rigid and moderately thick, with the posterior part very slightly longer than the anterior. Basal knobs wider than high, anteriorly concave with a short, blunt anteriorly directed point, and convex posteriorly.

Cephalids small, located at the levels of the third and tenth body annules.

Oesophagus with a thin procorpus but thicker at the anterior part than at the posterior.

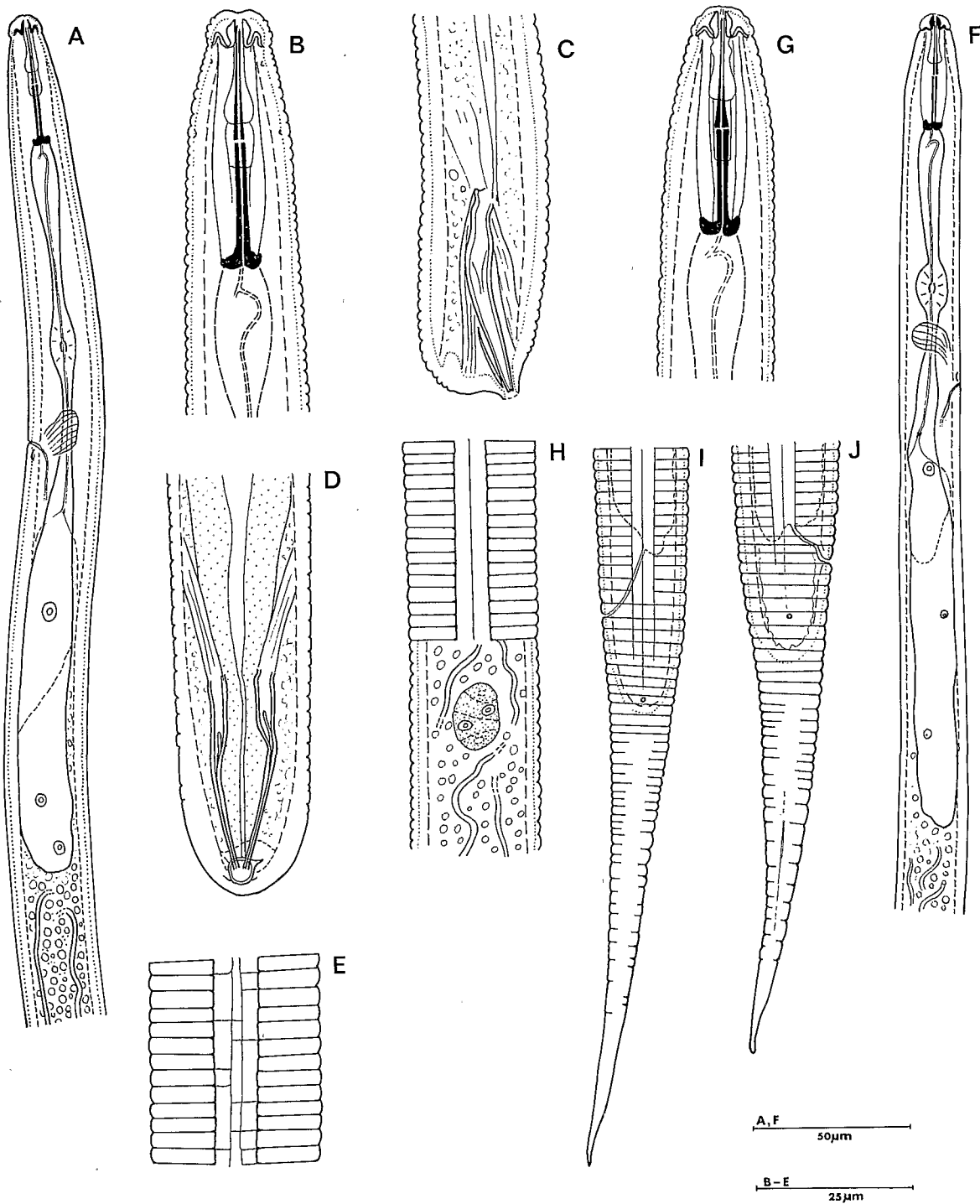


Fig. 2 : *Hylonema ivorense* n. gen., n. sp. Male A : œsophageal region ; B : fore part ; C : posterior part (lateral view) ; D : posterior part (ventral view) ; E : lateral field (at mid-body). 2nd stage juvenile : F : œsophageal region ; G : fore-part ; H : lateral field, intestine (« serpentine ») and genital primordium ; I, J : tails.

*Hylonema ivorense* n. gen., n. sp. Mâles : A : région œsophagienne ; B : partie antérieure ; C : partie postérieure (vue latérale) ; D : partie postérieure (vue ventrale) ; E : champ latéral (à mi-corps). Juvéniles du 2<sup>e</sup> stade : F : région œsophagienne ; G : partie antérieure ; H : champ latéral, intestin (« serpentin ») et primordium génital ; I, J : queues.

Median bulb reduced, fusiform, not well delimited, with weak musculature; valves poorly developed. Isthmus thin, short, encircled by a wide nerve ring. Basal bulb elongated, occupying most of the body cavity and overlapping the intestine ventrally or ventro-laterally. Three nuclei present, but difficult to observe; anterior (dorsal) nucleus larger than the others. Intestine with a single serpentine structure (= fasciculi), rarely anastomosing.

Excretory pore situated 140  $\mu\text{m}$  (113-165) from anterior end.

Hemizonid flat, not causing a bulging on the cuticle, from five annules in front of to one annule behind excretory pore, but in general one to three annules anterior to excretory pore and extending for two annules. Hemizonion not observed.

Testis single, long, outstretched, occupying more than one-third of the posterior portion of the body. Spermatozoa globular, highly refractive.

Spicules moderately thick, slightly curved ventrally, dilated at proximal end, thickened at the median part and bifid at the distal end. Gubernaculum thin, short, very slightly curved. Spicular sheath short, without process.

Tail absent to short, rounded, non-annulated at extremity or with one or two very wide annules. Cuticle with an internal thickening having the form of a band situated slightly dorsal in relation to the body axis and extending laterally. Bursa absent. No phasmids observed, even with S.E.M.

*Juveniles (2nd stage)*: Body straight or very slightly curved ventrally, elongated, cylindrical, tapering gradually posteriorly and slightly anteriorly, with a distinct constriction at the level of the juncture of the two parts of the stylet giving to anterior end a slightly conical appearance.

Cuticle marked by distinct transverse annulations, annules averaging 2  $\mu\text{m}$  in width at middle of body. Cuticle slightly thicker at the level of the narrow anterior part of body. Lateral field with three straight, parallel incisures not crossed by transverse striae, terminating posteriorly approximately at the level of the phasmids, and occupying one-fourth of body diameter at the middle of the body.

Labial region rounded, separated from rest of body by a distinct but not deep incisure; 5  $\mu\text{m}$  (4-5.5) high and 10.5  $\mu\text{m}$  (9.5-11.5) wide. Three annules present, the two posterior annules narrower than the anterior. Labial disc present, difficult to see with optical microscope. *En face* view with S.E.M. (Fig. 3, B) shows a short rectangular buccal opening, the longer axis being dorso-ventral; the labial disc itself longer dorso-ventrally with rounded contour; sometimes fusing dorsally and ventrally with the first labial annule for a short distance. Amphidial openings in the form of transverse slits located within the labial disc. Cephalic sclerotization pronounced. In lateral view basal plate appears slightly convex and rounded anteriorly, not extending posteriorly beyond the incisure separating labial region from rest of body. Arches clearly visible, principally by their central reinforcements. In *en face* view, dorsal plate consists of six branches, the sublaterals being closer together than the others.

Cephalids not observed.

Stylet straight, rigid, thin, posterior portion longer than anterior; basal knobs anchor-shaped with blunt anteriorly-directed points and convex posterior surface.

Oesophagus with an anteriorly enlarged procorpus, median bulb ovoid with conspicuous valve and musculature. Isthmus short, surrounded by a wide nerve ring. Basal portion massive, elongated; ventrally or ventro-laterally overlapping anterior portion of intestine for a considerable distance and occupying almost all of body cavity. Three nuclei present; the anterior (dorsal gland) largest and generally the only one visible. Dorsal gland transparent, subventral glands granular thus obscuring their nuclei.

Intestine with a single serpentine structure (= fasciculi), with no anastomoses.

Excretory pore situated 121  $\mu\text{m}$  (110-130) from anterior end. Hemizonid flat, extending one or two annules, and situated at the level of the excretory pore or one or two annules anterior or posterior to it. Hemizonion not observed.

Genital primordium oval, small; 13.5  $\mu\text{m}$  (11.5-19) long and 8  $\mu\text{m}$  (6.5-12) wide; situated 363  $\mu\text{m}$  (310-410) from anterior end; composed of four cells, only the two central (germinal) cells with large visible nuclei.

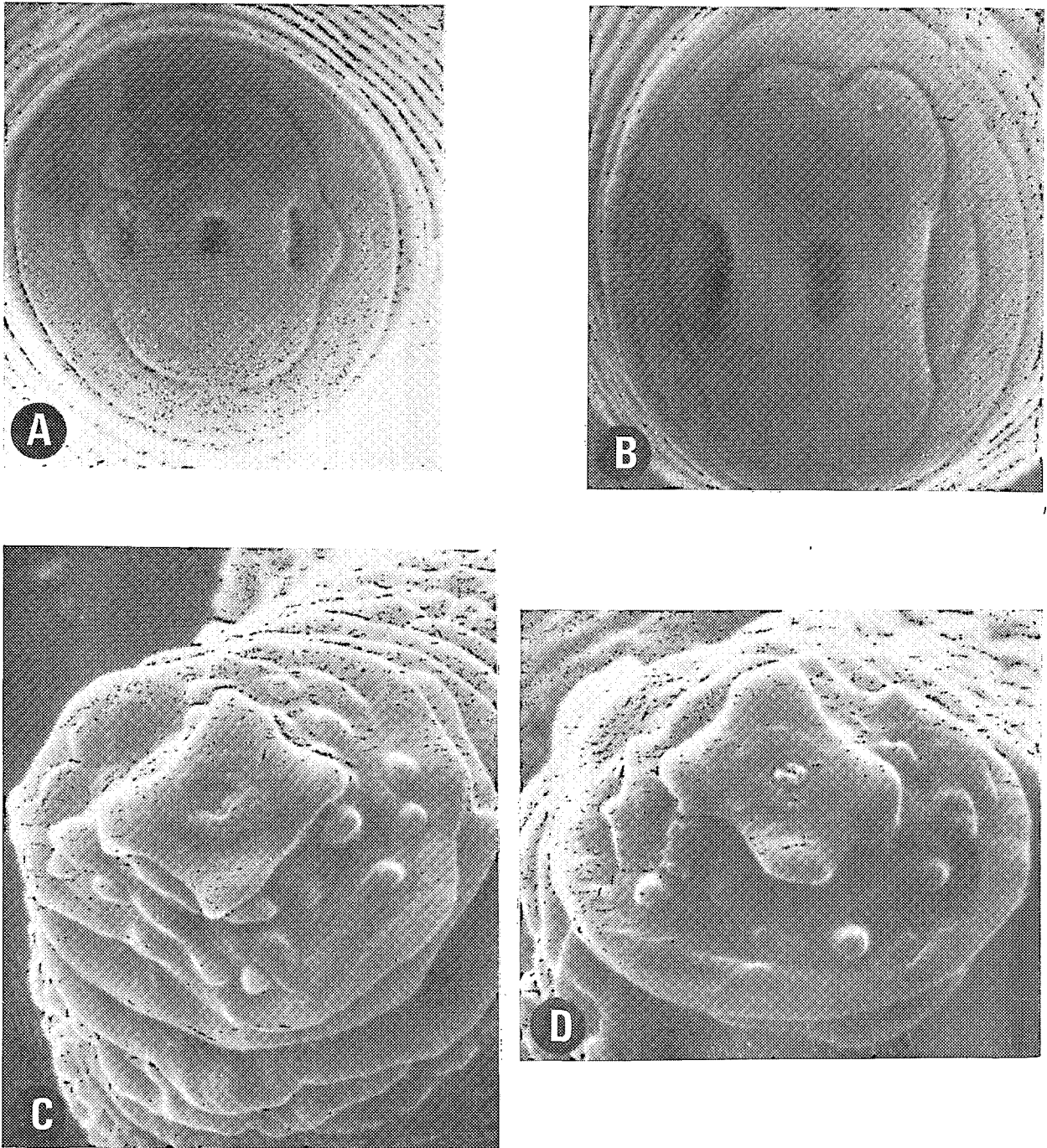


Fig. 3 : *Hylonema ivorense* n. gen., n. sp. SEM photographs (« en face » views) A : male ; B : 2nd stage juvenile ; C, D : female (approx.  $\times 10,000$ ).

*Hylonema ivorense* n. gen., n. sp. Photographies au microscope électronique à balayage. Régions labiales vues de face. A : mâle ; B : juvénile de 2<sup>e</sup> stade ; C, D : femelles (approx.  $\times 10\ 000$ ).

Tail elongate and tapering regularly to a pointed extremity; hyaline portion very long. Phasmids small, do-like, located 12  $\mu\text{m}$  (8.5-17) posterior to anus, without a lens-like structure.

*Type-host* : Roots of "avodiré", *Turraeanthus africana* Pellegr. (Meliaceae).

*Type-locality* : Forest reserve of the Banco, near Abidjan, Ivory Coast.

*Holotype* (female) : slide 94-WA-20148, deposited at the Laboratoire des Vers, Muséum national d'Histoire naturelle, 43 rue Cuvier, Paris, France.

*Paratypes* : 20 females, 30 males and 30 2nd stage juveniles, at the same place. One female, one male and two juveniles deposited in each of the following institutions : Laboratorium voor Nematologie, Landbouwhoogeschool, Wageningen, Netherlands ; Nematology Department, Rothamsted Experimental Station, Harpenden, England ; Instituut voor Zoologie, Rijksuniversiteit, Gent, Belgium ; Nematology Department, University of California, Riverside, U.S.A. ; Nematology Department, University of California, Davis, U.S.A. ; Plant Nematology Laboratory, U.S.D.A. Beltsville, U.S.A. ; Biosystematics Research Institute, Ottawa, Canada ; Entomology Division, D.S.I.R., Auckland, New Zealand ; Laboratoire de Nématologie, O.R.S.T.O.M., Dakar, Sénégal ; Laboratoire de Nématologie, O.R.S.T.O.M., Abidjan, Côte d'Ivoire.

#### CYTOLOGY

The relatively few eggs present in females dissected from infected roots and the infrequency of metaphase figures precluded a detailed cytological study of the species. However, on the basis of the few figures observed we believe that  $n = 7$  or 8.

#### **Taxonomic position of *Hylonema* n.gen. within the Heteroderidae and consideration of the validity of its subfamilies.**

*Hylonema* n. gen. can be accommodated easily within the family Heteroderidae since it pos-

sesses all the family characteristics (see below). However, it is impossible to classify *Hylonema* in any of the three recognized subfamilies, i.e. Heteroderinae, Meloidoderinae, and Ataloderinae. In fact *Hylonema ivorense* possesses characters present in genera belonging to each of these three subfamilies :

1. An underbridge is present in females of *H. ivorense*, a character previously described only from certain species of *Heterodera* and *Globodera*, both members of the Heteroderinae (Mulvey & Stone, 1976).

2. Males and juveniles of *H. ivorense* possess high arches in the basal plate of the cephalic framework, a character typical of the Meloidoderinae (Wouts, 1973 b).

3. In *H. ivorense* there is no cyst stage and only the anterior portion of the female cuticle is annulated, criteria characteristic of the Ataloderinae (Wouts, 1973 c). The latter character was verified by examination of paratypes of *Atalodera ucricola* Wouts, 1973 and *Sherodera loniceriae* Wouts, 1973, the only two described species in this subfamily.

The presence of the combination of these characters in *H. ivorense* prevented placing this genus in any of the existing subfamilies. Creation of a fourth subfamily to accommodate only this genus was considered ; however, the only apparent diagnostic character of such a subfamily would be the lack of egg retention by females. This did not appear to be of sufficient importance to create a new subfamily, especially since it is known that in the genus *Nacobbus*, *N. dorsalis* Thorne & Allen, 1944 retains eggs in the female whereas *N. aberrans* (Thorne, 1935) Thorne & Allen, 1944 does not (Sher, 1970).

Another possibility was to exclude *Hylonema* from the Heteroderinae by the absence of a cyst stage and from the Meloidoderinae by restriction of annulations on females to the anterior end. However, the diagnosis of the Ataloderinae would have to have been amended to accommodate *Hylonema*.

This approach was also unacceptable to us since many characters of *Hylonema* differ from the two species of this subfamily : absence of terminal cone bearing vulva and anus ;



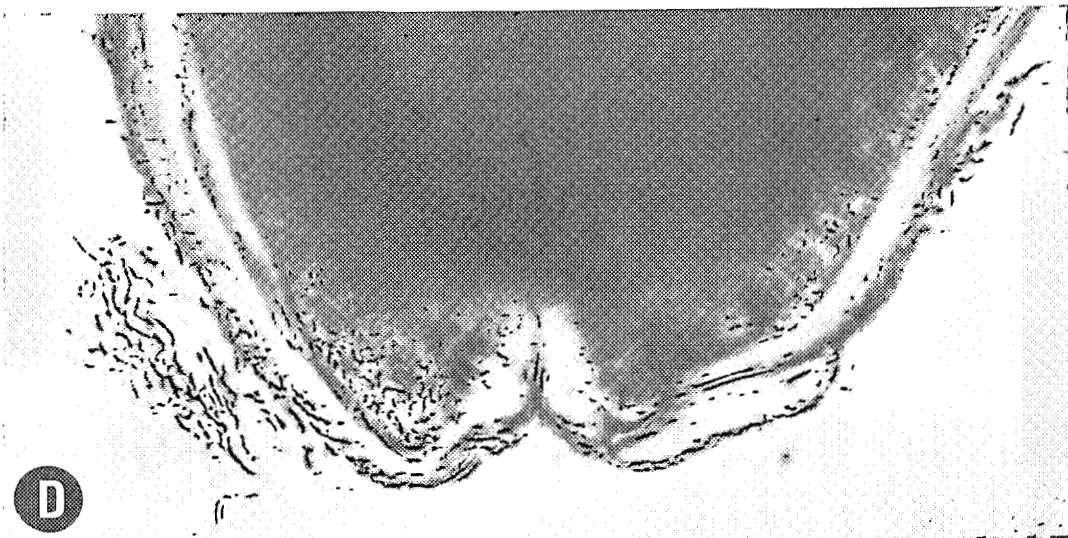
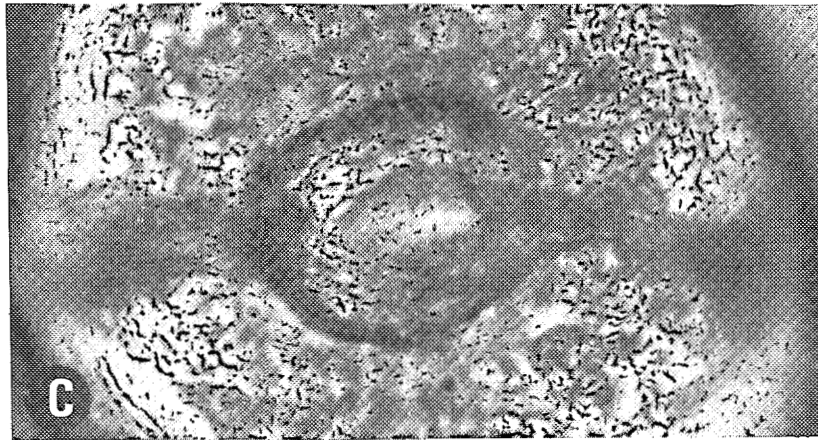
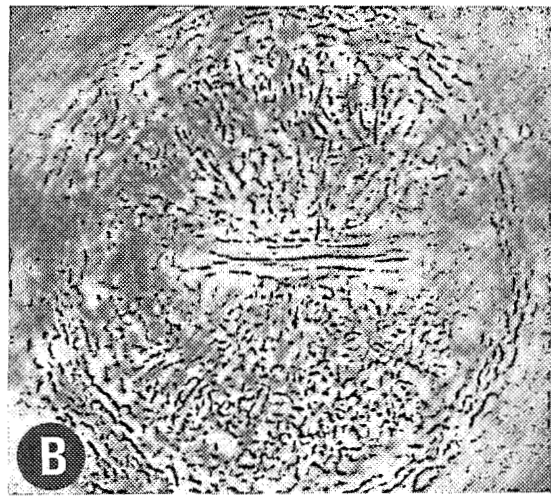
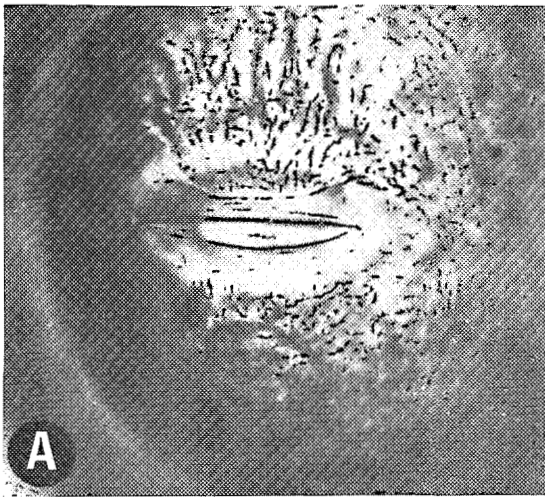


Fig. 4 : *Hylonema ivorense* n. gen., n. sp. Female A, B, C : end on view. A : surface view ; B : focus below showing the muscles ; C : underbridge ; D : lateral view of the vulval region.

*Hylonema ivorense* n. gen., n. sp. Femelle : A, B, C : région vulvaire, vue apicale ; A : vue en surface ; B : mise au point inférieure montrant les muscles dilateurs ; C : pont inférieur ; D : région vulvaire en vue latérale.

presence of an underbridge; high arch of the basal plate of juveniles and labial disc visible in males only by S.E.M. Such a heterogeneous subfamily would be too artificial.

This situation has raised the question as to whether the division of the Heteroderidae into subfamilies is accurate and if it serves any real purpose. We believe that this division into subfamilies is neither accurate nor useful; therefore, for the present time we prefer to abandon the use of subfamilies in the Heteroderidae. Our reasoning is detailed below.

The family Heteroderidae at present consists of ten genera classified as follows :

Subfamilies	Genera
Heteroderinae Filipjev & Sch. Stek., 1941	<i>Heterodera</i> Schmidt, 1871 <i>Globodera</i> (Skarbilovich, 1959) Mulvey & Stone, 1976 <i>Punctodera</i> Mulvey & Stone, 1976
Sarisoderinae Husain, 1976	<i>Sarisodera</i> Wouts & Sher, 1971
Meloidoderinae Golden, 1971	<i>Meloidodera</i> Chitwood, Hannon & Esser, 1956 <i>Cryphodera</i> Colbran, 1966 <i>Zelandodera</i> Wouts, 1973
Ataloderinae Wouts, 1973	<i>Atalodera</i> Wouts, 1973 <i>Sherodera</i> Wouts, 1973
?	<i>Hylonema</i> n. gen.

Within the subfamily Heteroderinae, the genera *Heterodera*, *Globodera* and *Punctodera* are closely related morphologically, whereas the fourth genus, *Sarisodera*, differs from this group in many important characters : in females there is a terminal cone formed by the protruding vulval lips and at the cone extremity the cuticle is thickened; whereas in the first three genera mentioned, the vulva and anus are situated in a shallow depression with a thin cuticle (vulval basin) and the terminal cone, when existing (*Heterodera*), constitutes a part of the body proper; in addition the vulva and sometimes the anus are surrounded by thinner cuticle (fenestræ). The cone structure of *Sarisodera*, in fact, is similar to that present in *Atalodera* and *Sherodera*. *Sarisodera* males are also quite different from males of the other three genera : their spicules are straight, thin and

pointed distally, and morphologically more similar to those of *Sherodera*, and the cloacal opening is nearly terminal. Thus, although these four genera share some common characters, e.g. presence of a cyst and a basic chromosome number of 9, *Sarisodera* differs from the other genera in important genital structures in both sexes making the subfamily Heteroderinae a heterogeneous group.

In fact, presence of a cyst is the major morphological character of the Heteroderinae; however, cysts have recently been described in genera belonging to groups outside the Heteroderidae. For example, cysts are found in *Meloidoderella* Khan, 1972, a member of the Meloidogynidae, and in *Meloidoderita* Poghossian, 1966, a member of the Criconematoidea. In the latter, the cyst is formed from the uterus and not from the entire body (Kirjanova & Poghossian, 1973). Since cyst-forming species occur in different taxonomic lines, relationships between the group *Heterodera-Globodera-Punctodera* and *Sarisodera* may be the result of convergence rather than similar ancestry, a statement in agreement with those of Wouts and Sher (1971), Wouts (1973 a) and Husain (1976), this later author creating the subfamily Sarisoderinae to make the separation more marked.

The Meloidoderinae is also a heterogeneous grouping. *Meloidodera* differs greatly from *Cryphodera* and *Zelandodera* by the equatorial position of the vulva, unique in the Heteroderidae. This character appears so important that Wouts (1973 b) stated that "it may be justified to raise *Meloidodera* to subfamily rank on the basis of this unique position of the vulva". *Cryphodera*, consisting of one species, and *Zelandodera*, possessing three, are so closely related that we consider them to be synonymous (see below).

The subfamily Ataloderinae consists of two monospecific genera, *Atalodera* and *Sherodera*, having so few distinguishing characters that we consider them as synonymous (see below).

Taking splitting to its extreme, we might have been justified in recognizing the subfamily Sarisoderinae Husain, 1976 and in creating another subfamily to accommodate *Sarisodera*, removing it from the Heteroderinae; another to accommodate *Cryphodera-Zelandodera*

while retaining *Meloidodera* in the Meloidoderinae; and a third to include only *Hylonema*. Thus the Heteroderidae would consist of six subfamilies, five of which would contain only a single genus! We believe that such a system is completely undesirable and unnecessary. At the present time we prefer to abandon the use of subfamilies in the Heteroderidae and consider it as a family containing the genera *Heterodera*, *Globodera*, *Punctodera*, *Sarisodera*, *Meloidodera*, *Cryphodera* (= *Zelandodera*), *Atalodera* (= *Sherodera*) and *Hylonema* n. gen.

In the future when new genera and species are described and when additional anatomical, morphological, cytological and physiological data are available, it may be possible to arrange the Heteroderidae into meaningful groupings. At the present we do not consider this possible.

### Family Heteroderidae

(Filipjev & Schuurmans Stekhowen, 1941)  
Skarbilovich, 1947.

DIAGNOSIS EMENDED (after Wouts, 1973 a) : Superfamily Tylenchoidea (Örley, 1880) Chitwood & Chitwood, 1937. *Female* : Swollen to subspherical, sedentary, didelphic. Cuticle annulated or non-annulated. Tail absent. Anus located terminally or dorsally subterminal. Excretory pore posterior to level of valve in median bulb. Basal plate subdivides head into six sectors, with the two lateral sectors narrower than the other four. Stylet longer than 17  $\mu\text{m}$ . Procorpus and median bulb not amalgamated. Median bulb ovate to spherical, with well developed musculature and crescentic valve plates. Oesophageal glands overlap intestine ventrally. *Juvenile (2nd stage)* : Vermiform; infective migratory stage. Basal plate subdivides head as in female. Stylet robust, longer than 16  $\mu\text{m}$ . *Male* : Vermiform, migratory. Body twisted as much as 180° from head to tail. Tail short or absent. Caudal alae absent. Stylet and cephalic framework well developed. Testis single.

TYPE GENUS : *Heterodera* Schmidt, 1871.

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### Genus *Heterodera* Schmidt, 1871

= *Heterobolbus* Railliet, 1896

= (*Heterodera*) Skarbilovich, 1959

DIAGNOSIS : Heteroderidae. *Female* : Cyst formed after death. Body with posterior protuberance (the vulval cone), more or less lemon-shaped. Cuticle with lacelike pattern of ridges. Vulval slit short to long (10-60  $\mu\text{m}$ ) sited at apex of vulval cone; underbridge and bullae present or absent. Perineal tubercles (Mulvey, 1973) absent. Vulval cone bi-, circum- or ambifenestrate. Anus dorsal, not on vulval lip. *Juvenile (2nd stage)* : Labial disc present but with low profile, seen clearly only under S.E.M. Cuticle of labial region of even thickness. Phasmids without lens-like structure in muscle layer. *Male* : Up to 1.5 mm in length. Labial disc present but with low profile. Tail present, length less than half body width.

TYPE SPECIES : *Heterodera schachtii* Schmidt, 1871  
= *H. (H.) schachtii* Schmidt, 1871 (Skarbilovich, 1959)

Genus *Globodera* (Skarbilovich, 1959)  
Mulvey & Stone, 1976

= *Heterodera (Globodera)* Schmidt, 1871 (Skarbilovich, 1959).

DIAGNOSIS : Heteroderidae. *Female* : Cyst formed after death. Body without posterior protuberance, spherical shape. Cuticle with lacelike pattern of ridges. Vulva terminal. Vulval slit short (< 15  $\mu\text{m}$ ). Underbridge and bullae rarely present. Perineal tubercles present. Vulval area circumfenestrate; no anal fenestra. Anus dorsal, not on vulval lip. *2nd stage juvenile* : Labial disc present but with low profile, seen clearly only under S.E.M. Cuticle of labial region of even thickness. Phasmids without lens-like structure in muscle layer. *Male* : Up to 1.5 mm long. Labial disc present but with low profile. Tail present, length less than half body width.

TYPE SPECIES : *Globodera rostochiensis* (Wollenweber, 1923) Mulvey & Stone, 1976.  
= *H. (G.) rostochiensis* Wollenweber, 1923 (Skarbilovich, 1959).

#### Genus *Punctodera* Mulvey & Stone, 1976

DIAGNOSIS : Heteroderidae. *Female* : Cyst formed after death. Body without posterior protuberance, spherical, ovoid or pear-shaped. Cuticle with lacelike pattern of ridges and subsurface pattern of punctations. Vulva terminal. Vulva slit very short, underbridge absent. Bullae present or absent. Perineal tubercles absent. Areas around vulva and anus each circumfenestrated and of similar size. Anus offset toward ventral margin of anal fenestra. *2nd stage juvenile* : Labial disc present but with low profile, seen clearly only under S.E.M. Cuticle of labial region of even thickness. Phasmids without lens-like structure in muscle layer. *Male* : Up to 1.5 mm long. Labial disc present but with low profile. Tail present, length less than half body width.

TYPE SPECIES : *Punctodera punctata* (Thorne, 1928) Mulvey & Stone, 1976.  
= *H. (Globodera) punctata* Thorne, 1928 (Skarbilovich, 1959).

#### Genus *Sarisodera* Wouts & Sher, 1971

DIAGNOSIS : Heteroderidae. *Female* : Cyst formed after death. Cuticle with lacelike pattern of ridges. Vulva sunken in a terminal cone. No fenestration around vulva or anus. *2nd stage juvenile* : Labial disc present but with low profile, seen clearly only under S.E.M. <sup>(1)</sup>. Cuticle of labial region of even thickness. Phasmids with or without lens-like structure in muscle layer. *Male* : Up to 1.5 mm long. Labial disc present but with low profile, only clearly seen under S.E.M. <sup>(1)</sup>. Tail absent.

<sup>(1)</sup> Observed on paratypes of *S. hydrophila* Wouts & Sher, 1971 and *S. africana* Luc, Germani & Netscher, 1973.

TYPE SPECIES : *Sarisodera hydrophila* Wouts & Sher, 1971.

#### Genus *Meloidodera* Chitwood, Hannon & Esser, 1956

DIAGNOSIS : Heteroderidae. *Female* : No cyst stage. Cuticle annulated on entire body. Majority of eggs retained within body. Vulva subequatorial; anus ventrally subterminal, not protruding out of body contour. Phasmids terminal. *2nd stage juvenile* : Labial disc easily visible. Cuticle of labial region distinctly wider near basal plate than near labial disc. Dorsal and ventral parts of basal plate a high arch. Four lines in lateral field. *Male* : Labial disc prominent. Basal plate divides head into six sectors of approximately equal size. Not developing through saccate stage. No longitudinal striae on basal lip annule. Four lines in lateral field. Tail present.

TYPE SPECIES : *Meloidodera floridensis* Chitwood, Hannon & Esser, 1956

#### Genus *Cryphodera* Colbran, 1956

= *Zelandodera* Wouts, 1973; new synonymy.

DIAGNOSIS : Heteroderidae. *Female* : No cyst stage. Cuticle annulated on entire body. Majority of eggs retained within body. Vulva terminal; vulval lips protrude beyond body contour. No fenestration around vulva. Anus subterminal. *2nd stage juvenile* : Labial disc conspicuous to very flattened. Cuticle of labial region distinctly wider near basal plate than near labial disc. Dorsal and ventral parts of basal plate a high arch. *Male* : Labial disc prominent. Stylet as long or longer than that of 2nd stage juvenile. Longitudinal striae on basal lip annule.

TYPE SPECIES : *Cryphodera eucalypti* Colbran, 1956

OTHER SPECIES : *C. podocarpi* (Wouts, 1973) n. comb.

- = *Zelandodera podocarpi* Wouts, 1973  
*C. nothophagi* (Wouts, 1973) n. comb.  
 = *Zelandodera nothophagi* Wouts, 1973  
*C. coxi* (Wouts, 1973) n. comb.  
 = *Zelandodera coxi* Wouts, 1973.

## DISCUSSION :

Synonymisation of these genera was necessary for the reasons listed below. According to Wouts (1973 b) four characters may be used to separate *Cryphodera* from *Zelandodera*.

1. In *Cryphodera* the anus is separated from the vulva by a slight concave depression which is absent in *Zelandodera*. However, as seen in Figure 4 D-H (Wouts, 1973 b) there is a transition in the distinctness of this character from *C. eucalypti* to *Cryphodera* sp. to the three species of *Zelandodera*. In addition, the vulva-anus distance forms an overlapping series : *Z. coxi* = 38-70  $\mu\text{m}$  ; *C. eucalypti* = 40-51  $\mu\text{m}$  ; *Z. nothophagi* = 41-57  $\mu\text{m}$  and *Z. podocarpi* = 58-70  $\mu\text{m}$ . Greater differences than these exist between the two described species of *Sarisodera* ; therefore we consider such differences at the specific and not the generic level.

2. In *Cryphodera* the vulval lips are described as "pronounced, protruding terminally", whereas in *Zelandodera* the vulval lips are described as "protruding slightly out of body contour". Again Figure 4 D-H (Wouts, 1973 b) shows the transition of this character from *C. eucalypti* to *Cryphodera* sp. to *Z. podocarpi* to *Z. nothophagi* and *Z. coxi*. *Z. podocarpi* definitely has protruding vulval lips. Thus, we consider that these are specific differences but not generic.

3. It is stated that the "number of lip annules is usually higher in *Zelandodera* juveniles". That is, *C. eucalypti* = 3, *Z. coxi* and *Z. nothophagi* = 4, and *Z. podocarpi* = 5. Similar variation is found within the genus *Heterodera*, where it is useful only as a supplemental character in species separation. Thus, we consider such minor differences at the species and not the generic level.

4. Males of *Zelandodera* have four lines in the lateral field, whereas there are three in *Cryphodera*. Again, males of certain species of *Heterodera* have four lines, others have three.

Since these four characters appear to be specific in nature and since all other characters are identical, we consider *Zelandodera* as a junior synonym of *Cryphodera*.

Genus *Atalodera* Wouts & Sher, 1971

= *Sherodera* Wouts, 1973 ; new synonymy.

DIAGNOSIS : Heteroderidae. *Female* : No cyst stage. Cuticle annulated only in the anterior portion of the body. Eggs retained within the body. Anus and vulva terminal on protuberance. No fenestration around vulva or anus. *2nd stage juvenile* : Labial disc present but with low profile ; only clearly seen under S.E.M. <sup>(1)</sup>. Arches low. Stylet less than 30  $\mu\text{m}$  long. Oesophageal glands fill less than half the body width. Phasmids with distinct lens-like structure in muscle layer. *Male* : Up to 1.5 mm in length. Labial disc prominent <sup>(2)</sup>. Stylet longer than that of 2nd stage juvenile. Spicules more than 30  $\mu\text{m}$  long. Tail short or absent.

TYPE SPECIES : *Atalodera ucri* Wouts & Sher, 1971.

OTHER SPECIES : *A. loniceræ* (Wouts, 1973) n. comb.

= *Sherodera loniceræ* Wouts, 1973.

DISCUSSION : Wouts (1973 c) used only two characters to separate these genera : location of the anus in females and structure of the basal labial annule in males. In *Atalodera*, the anus is "located on transformed, flattened dorsal vulval lip" ; in *Sherodera* it is "located on rounded dorsal vulval lip". Study of specimens of *A. ucri* and *S. loniceræ* has convinced us that these differences are slight and are at the species level. More striking differences in this character exist between the two described species of *Sarisodera*. In fact, there appears to be a parallelism regarding this character between

<sup>(1)</sup> Observed on juvenile paratypes of *A. loniceræ*.

<sup>(2)</sup> S.E.M. observations on male paratypes of *A. loniceræ* showed that only the central part (about half the diameter) of the labial disc is elevated.

*Sherodera lonicerae* and *Sarisodera africana*. We have already noted the resemblance in vulval cone structure among these three genera. Similarly, we consider the presence or absence of longitudinal labial striae in the male as insufficient to separate genera. The striking similarity or identity of other characters convince us that *Sherodera* is a junior synonym of *Atalodera*.

### Genus *Hylonema* n.gen.

**DIAGNOSIS** : Heteroderidae. *Female* : No cyst stage. Cuticle annulated only in anterior portion of body. Eggs not retained within body. Anus and vulva subterminal, in a hollow depression. Vulval lips not protruding. No fenestration around vulva or anus. Underbridge present. *2nd stage juvenile* : Labial disc low, visible only on S.E.M. Arch medium. Tail long, filiform ; hyaline portion of tail very long. *Male* : Labial disc and arch as in 2nd stage juvenile. Tail short or absent. No phasmids observed, even on S.E.M.

**TYPE SPECIES** : *Hylonema ivorense* n. gen., n. sp. No other species.

*Diagnosis of H. ivorense* n. sp. : having characters of the genus.

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