

# A reappraisal of Tylenchina (Nemata). 9. The family Heteroderidae Filip'ev & Schuurmans Stekhoven, 1941 <sup>(1)</sup>

Michel LUC\*, Armand R. MAGGENTI and Renaud FORTUNER\*\*

Muséum national d'Histoire naturelle, Laboratoire des Vers, 61, Rue de Buffon, 75005 Paris, France; University of California, Department of Nematology, Davis, CA 95616, USA, and California Department of Food and Agriculture, Analysis and Identification (Nematology), 1220 N Street, Sacramento, CA 95814, USA.

## SUMMARY

Heteroderids and meloidogynids are considered as a single family, Heteroderidae, that is redefined to include three subfamilies; Heteroderinae with *Heterodera*, *Meloidodera*, *Globodera*, *Cryphodera*, *Atalodera*, *Sarisodera*, *Punctodera*, *Cactodera*, *Hylonema*, *Thecavermiculatus*, *Dolichodera*, *Verutus*, *Rhizonema*, *Afenestrata*, and *Bellodera*; Meloidogyninae with *Meloidogyne*; Nacobboderinae with *Nacobbodera*, *Meloinema* and *Bursadere*. This implies a drastic reduction of subfamilies in the group. *Hypsoperine*, with its two subgenera (*Hypsoperine*) and (*Spartonema*), is considered a junior synonym of *Meloidogyne*. *Nacobbodera* is revalidated as distinct from *Meloinema*.

## RÉSUMÉ

Réévaluation des Tylenchina (Nemata). 9. La famille des Heteroderidae Filip'ev & Schuurmanns Stekhoven, 1941

Les Heteroderides et les Meloidogynides sont considérés comme appartenant à une seule famille, les Heteroderidae, qui est redéfinie et comprend trois sous-familles : Heteroderinae (genres *Heterodera*, *Meloidodera*, *Globodera*, *Cryphodera*, *Atalodera*, *Sarisodera*, *Punctodera*, *Cactodera*, *Hylonema*, *Thecavermiculatus*, *Dolichodera*, *Verutus*, *Rhizonema*, *Afenestrata*, et *Bellodera*); Meloidogyninae (*Meloidogyne*) et Nacobboderinae (*Nacobbodera*, *Meloinema* et *Bursadere*). Ceci implique une importante diminution du nombre des sous-familles communément admises pour le groupe. *Hypsoperine*, et ses deux sous-genres (*Hypsoperine*) et (*Spartonema*), sont considérés des synonymes mineurs de *Meloidogyne*. *Nacobbodera* est considéré comme un genre valide, distinct de *Meloinema*.

The heteroderids, with *Heterodera* (including *H. marioni*, now *Meloidogyne* spp.), *Tylenchulus*, and *Paratylenchus*, were proposed as a new subfamily, Heteroderinae, by Filip'ev and Schuurmans Stekhoven (1941). The subfamily was raised to family rank, Heteroderidae, by Skarbilovich (1947), to superfamily rank, Heteroderodea, by Golden (1971) and Stone (1975), and even a suborder "Heteroderata" (= Heteroderina) was proposed by Skarbilovich (1959). These higher rankings have not been generally accepted, and Heteroderidae is here considered at family level (Maggenti *et al.*, 1987).

Within Heteroderidae, *Meloidogyne* was placed in a subfamily, Meloidogyninae, by Skarbilovich (1959), because of the absence of cysts, males with two genital branches, and the first moult occurring within egg. In fact, males have only one genital branch, and the last

characteristic proposed by Skarbilovich is not diagnostic within Tylenchina as it is characteristic of Secernentea. The subfamily was rejected by Goodey (1963), and by Siddiqi (1971), but it has been accepted by Golden (1971) and subsequent authors. Meloidogyninae was raised to family rank, Meloidogynidae, by Wouts (1973), and the two families have been accepted by several subsequent authors, namely Stone (1978) and Siddiqi (1986).

Several subfamilies have been split from "Heteroderidae" (Meloidoderinae Golden, 1971; Ataloderinae Wouts, 1973; Sarisoderinae Husain, 1976; Punctoderinae Krall' & Krall', 1978; Verutinae Esser, 1981), or from "Meloidogynidae" (Nacobboderinae Golden & Jensen, 1974; Meloinematinae Husain, 1976; Meloidoderellinae Husain, 1976). Some of those subfamilies

(1) This article is a part of a study on the classification of Tylenchina by the present authors and E. Geraert (Rijksuniversiteit, Gent, Belgium), and D. J. Raski (University of California, Davis).

\* Nematologist from ORSTOM.

\*\* Associate in the Department of Nematology, University of California, Davis.

have even been raised to family rank, for example, Ataloderidae and Meloidoderidae, both by Krall' and Krall' (1978). Also Coomans (1979) introduced the tribes Meloidoderini and Cryphoderini.

Luc, Taylor and Cadet (1978) accepted the family Heteroderidae but gave clear arguments to reject its division into the above subfamilies.

We accept heteroderids at family level, Heteroderidae, with three subfamilies : Heteroderinae, Meloidogyninae and Nacobboderinae.

There is no consensus of opinion concerning the classification of the " *Heterodera/Meloidogyne* group ". In keeping with our expressed philosophy (Luc *et al.*, 1987) of conservatism, i.e., to avoid whenever possible the temptation to inflate the classification either horizontally or vertically, we have treated the " group " in a fashion that reflects Thorne (1949), Paramonov (1967) and Wouts and Sher (1971). As such we reject Wouts (1973, 1985), Stone (1978) and Siddiqi (1986). Our disagreement with the latter proposals is the separation of *Heterodera* and *Meloidogyne* into separate families. Stone's super-family Heteroderoidea carries the same diagnosis that was used for the family Heteroderidae and therefore is merely a vertical inflation of the classification that supplies no new information.

Wouts (1973) proposed that Heteroderidae and Meloidogynidae be recognized as two families in Tylenchoidea, effectively destroying any reflection of a phylogenetic relationship between the families. Wouts justified the separation by stating there were no characters shared by the two and dismissing summarily those they might share. He further stated that if the initiation of body swelling by the second stage juvenile is accepted as derived then all other swollen forms in Tylenchina that do not have this character must be lumped into an artificial family! We do not accept this line of reasoning.

Siddiqi (1986) applies the concept of two families Heteroderidae and Meloidogynidae within the superfamily Hoplolaimoidea. This demands that acceptance be given to a superfamily that encompasses ecto-endoparasites, migratory endoparasites as well as sedentary endoparasites, with feeding habits that vary from grazers to sedentary nutritive cell feeders. It is our opinion that such application of the superfamily category destroys the very basis of a classification, i.e., predictability and the reflection of phylogeny.

In making our decision to maintain the " group " in a single family we have recognized that no single unique character is necessary to define a family. The family is an assemblage of related genera that have a shared evolution and related but differing characters, none of which can stand alone. One such character is the sedentary swollen female in and of itself it cannot designate the family (there being several examples of sedentary swollen females in Tylenchina); however, in combination with other characteristics such as male metamorphosis, lip region anatomy, oesophageal mor-

phology, etc.; these combinations take on a significance that does allow recognition of the family Heteroderidae with three subfamilies with representatives showing both ancestral and derived characters. Nacobboderinae is viewed as the most ancestral and Meloidogyninae as the most derived (see below).

#### The family HETERODERIDAE

Filip'ev & Schuurmans Stekhoven, 1941

= Meloidogynidae Skarbilovich, 1959

= Meloidoderidae Golden, 1971

= Ataloderidae Wouts, 1973

#### Diagnosis

Tylenchoidea. Marked sexual dimorphism, body vermiform and slender in second-stage juveniles, robust in males and inflated in females. Cephalic framework well developed, secondarily reduced in females. Stylet robust; conus half the length of total stylet. Dorsal oesophageal gland opening close to base of stylet. Median oesophageal bulb usually large, with strong valves. Oesophageal glands overlapping intestine ventrally, and also laterally. *Female* : Sedentary in root tissues, globose (exception : *Verutus* with sausage-shaped females). Vulva most generally terminal or subterminal (exception : *Verutus* and *Meloidodera* where equatorial). Two genital branches, amphidelphic or prodelfic. Columned uterus with three rows of cells. Eggs laid in a gelatinous matrix (exception : *Verutus*) or totally or partially retained within female body of which the cuticle may be transformed (cysts). *Male*. Vermiform. Metamorphosis within juvenile cuticle (exception : *Meloidodera*). Body twisted in posterior part (exception : *Verutus*). No caudal alae (exception : *Bursadera*). Tail short or absent. *Second stage juveniles*. Tail conical, with long hyaline posterior part. Phasmids anterior to half tail length.

Sedentary obligate parasite of roots, forming galls in some cases.

#### Type subfamily

HETERODERINAE Filip'ev & Schuurmans Stekhoven, 1941

#### Other subfamilies

MELOIDOGYNINAE Skarbilovich, 1959

NACOBODERINAE Golden & Jensen, 1974

The subfamily HETERODERINAE

- Filip'ev & Schuurmans Stekhoven, 1941  
 = Meloidoderinae Golden, 1971  
 = Ataloderinae Wouts, 1973  
 = Sarisoderinae Husain, 1976  
 = Punctoderinae Krall' & Krall', 1978  
 = Verutinae Esser, 1981 (n. syn.)  
 = Cryphoderinae Wouts, 1985 (n. syn.)

**Diagnosis**

Heteroderidae. Cuticle strongly annulated. Annuli usually transformed in a lace-like pattern in swollen females. Cephalic framework strong, secondarily reduced in females; lateral sectors narrower or equal to submedian sectors. Stylet robust, usually over 20 µm.

*Female.* Sedentary, globose (exception : *Verutus*); neck short. No preadult vermiform female stage. Cuticle abnormally thick (exception : *Meloidodera*), variously patterned. Labial disc squarish well detached from completely fused subsequent labial sectors. Excretory pore situated at level of or posterior to median oesophageal bulb (exception : *Bellodera* where more anterior). Vulva terminal or subterminal (exception : *Verutus* and *Meloidodera* where equatorial). Perineum without finger-print like pattern. Eggs generally retained in female body of which the cuticle may be tanned and transformed into cyst; when totally or partially laid eggs embedded in a gelatinous matrix (exception : *Verutus*).

*Male.* Labial area regularly annulated, generally off-set. Cephalic sclerotization and stylet strong. Phasmids small or absent.

*Juveniles.* Second stage juveniles cephalic framework and stylet robust; stylet longer than 17 µm. Third and fourth stages swollen, with robust stylet.

*Biology :* Sedentary in roots; female inducing transfer cells (syncytium or giant cell with giant nucleus). Not causing galls on roots.

**Type genus**

*Heterodera* Schmidt, 1871

**Other genera**

- Meloidodera* Chitwood, Hannon & Esser, 1956  
*Globodera* Skarbilovich, 1959  
*Cryphodera* Colbran, 1966  
*Atalodera* Wouts & Sher, 1971  
*Sarisodera* Wouts & Sher, 1971  
*Punctodera* Mulvey & Stone, 1976  
*Cactodera* Krall' & Krall', 1978  
*Hylonema* Luc, Taylor & Cadet, 1978  
*Thecavermiculatus* Robbins, 1978  
*Dolichodera* Mulvey & Ebsary, 1980

*Verutus* Esser, 1981

*Rhizonema* Cid del Prado Vera, Lownsbery & Maggenti, 1983

*Afenestrata* Baldwin & Bell, 1985

*Bellodera* Wouts, 1985

**The genera in Heteroderinae**

*Verutus* Esser, 1981

**DIAGNOSIS**

Heteroderinae.

*Females.* No cyst stage. Body saccate, sausage-shaped or kidney-shaped. Cuticle thick, annulated over total body length; D-layer\* absent; multiple B-layer\* present; subcrystalline layer present. Vulva submedian, large, with protuberant vulva lips. No phasmids. Remnant of tail very short to absent. Eggs not retained in body, but deposited individually, without gelatinous matrix.

*Males.* Body not twisted. Stylet under 30 µm. Lateral field with four lines. Spicules strong, slightly curved. No phasmids. Tail short.

*Juveniles 2d stage.* Lateral field with four lines. Oesophageal glands filling body cavity. Tail pointed, with long hyaline, terminal part. Phasmids punctiform, small, devoid of lens-like structure.

*Nurse cells system :* a syncytium.

**TYPE SPECIES**

*V. volvingentis* Esser, 1981

**OTHER SPECIES**

*V. mesoangustus* Minagawa, 1986

**COMMENTS**

Esser (1981) proposed the subfamily Verutinae, under Heteroderidae, to contain that genus; he also discussed its affinities with *Rotylenchulus*. The only resemblance seems to be the female shape. Siddiqi (1986) placed Verutinae under Rotylenchulidae, together with Rotylenchulinae (*Rotylenchulus*, *Senegalonema*) and Acontylinae (*Acontylus*). *Verutus* belongs to Heteroderinae and represents an ancestral genus (see below).

\* Concerning ultrastructure of the cuticle and definition of its layers see Shepherd, Clark and Dart (1972) and Baldwin (1983).

*Meloidodera* Chitwood, Hannon & Esser, 1956

DIAGNOSIS

Heteroderinae

*Female*. No cyst stage. Body globose with short neck. Cuticle of medium thickness, whole body annulated, with modified pattern at anal-vulval region. D-layer absent. Subcrystalline layer present. Vulva median; vulval lips not protruding. Eggs either deposited or retained in body.

*Males*. Body twisted, short (under 0.6 mm). Lateral field with four lines. Spicules short (under 30 µm), slightly curved, obliquely directed. Tail short, hemispherical. No cloacal tubus. Phasmids punctiform, sub-terminal. No male metamorphosis within 2d stage cuticle.

*Juveniles, 2d stage*. Lateral field with four lines. Oesophageal glands filling body cavity. Tail conical, of medium length, with half length hyaline terminal part. Phasmids with or without lens-like structure.

*Nurse cell system* : a single giant cell with a single giant nucleus.

TYPE SPECIES

*M. floridensis* Chitwood, Hannon & Esser, 1956

OTHER SPECIES

*M. alni* Turkina & Chizkov, 1986

*M. belli* Wouts, 1973

*M. charis* Hopper, 1960

*M. eurytyla* Bernard, 1981

*M. tianshanica* Ivanova & Krall, 1985

SPECIES INQUIRENDAE

*M. armeniaca* Poghossian, 1960

*M. sikhotealinensis* Eroshenko, 1978

*M. tadzhikistanica* Kir'yanova & Ivanova, 1966

*Atalodera* Wouts & Sher, 1971

= *Sherodera* Wouts, 1974

DIAGNOSIS

Heteroderinae

*Females*. No cyst stage. Body globose, with projecting neck and terminal cone. Cuticle thick, annulated on fore part of body, with lace-like pattern on the posterior part. D-layer present. No subcrystalline layer. Vulva on prominent terminal cone, with thick cuticle, constituted by protruding and developed vulval lips. Anus situated on the side of posterior vulval lip. Eggs retained in body.

*Males*. Body twisted. Lateral field with four lines. Spicules > 30 µm, slightly curved, obliquely directed.

Tail short, hemispherical. Cloacal tubus short. No phasmids.

*Juveniles, 2d stage*. Lateral field with three lines. Oesophageal glands not filling body cavity. Tail conical, with hyaline part half of total length. Phasmids prominent, with lens-like structure.

*Nurse cell system* : a syncytium.

TYPE SPECIES

*Atalodera ucru* Wouts & Sher, 1971

OTHER SPECIES

*A. loniceræ* (Wouts, 1974) Luc, Taylor & Cadet, 1978  
= *Sherodera loniceræ* Wouts, 1974

COMMENTS

Luc, Taylor and Cadet (1978) considered *Sherodera* a junior synonym of *Atalodera*, since the differential characters (shape of the hypertrophied vulval lips forming the cone and presence/absence of longitudinal labial striae in male) appeared insufficient to clearly separate these two monotypic genera. This proposal has been generally accepted. However Wouts (1985) restored *Sherodera*, considering it a "sister genus" of *Atalodera*. As Wouts did not afford new arguments for the validity of *Sherodera*, this genus is considered here, again, as a junior synonym of *Atalodera*.

*Cryphodera* Colbran, 1966

= *Zelandodera* Wouts, 1973

DIAGNOSIS

Heteroderinae

*Females*. No cyst stage. Body globose, with projecting neck; no terminal cone. Cuticle thick, annulated on whole body, except the vulval-anal area. Vulva terminal; vulval lips nearly flush with body contour to slightly protruded. Anus at some distance from vulva. Eggs retained in body.

*Males*. Body twisted. Stylet > 30 µm. Lateral field with three or four lines. Spicules < 30 µm, slightly curved, directed obliquely, with distal extremity pointed. No cloacal tubus. Tail hemispherical.

*Juveniles 2d stage*. Stylet length 25 to 40 µm. Lateral field with three (more rarely four) lines. Oesophageal glands filling body cavity. Tail conical, with hyaline terminal part half of total length. Phasmids with lens-like structure.

TYPE SPECIES

*Cryphodera eucalypti* Colbran, 1966

## OTHER SPECIES

- C. coxi* (Wouts, 1973) Luc, Taylor & Cadet, 1978  
= *Zelandodera coxi* Wouts, 1973
- C. nothophagi* (Wouts, 1973) Luc, Taylor & Cadet,  
1978  
= *Z. nothophagi* Wouts, 1973
- C. podocarpi* (Wouts, 1973) Luc, Taylor & Cadet,  
1978  
= *Z. podocarpi* Wouts, 1973

## COMMENTS

Luc, Taylor and Cadet (1978) discussed in detail the reasons why they considered *Zelandodera* a junior synonym of *Cryphodera*; characters used to separate these genera were dealing with slight variation in profile of the anal-vulval region, number of lip annuli in juveniles, and number of lines in male lateral field. The variation concerning the first cited character was not so pronounced that it could justify generic differences; the two other characters are considered only at specific level. That synonymization has been generally accepted. Nevertheless Wouts (1985) considered *Zelandodera* a valid genus, without producing any new arguments. Consequently the synonymization is maintained here. Baldwin, Mundo-Ocampo and Othman (1983) described *C. utahensis*, which differs notably from other species by the shape of the posterior part of the female. Wouts (1985) proposed a new genus, *Bellodera*, to contain that species which is accepted here (see below);

It is unfortunate that no data are known concerning the ultrastructure of the female cuticle and the nurse cell system in the genus *Cryphodera*. These two types of data would be very useful to clear the relationships of the genus.

*Bellodera* Wouts, 1985

## DIAGNOSIS

## Heteroderinae

*Females.* No cyst stage. Body globose with projecting neck; terminal cone well developed, but posterior extremity somewhat flattened. Cuticle thick, with superficial irregular transverse striae and minute pits between striae; D-layer absent; subcrystalline layer present. Excretory pore forwardly situated 27-56  $\mu\text{m}$  from anterior end. Vulva terminal; vulval slit large, not deeply sunken between hypertrophied vulval lips constituting the terminal cone; no fenestrae; no underbridge; no bullae. Anus situated at some distance from vulva, on posterior side of the cone. Eggs retained in body.

*Males.* Body twisted. Stylet > 30  $\mu\text{m}$ . Lateral field with four lines. Spicules at most 30  $\mu\text{m}$  long, nearly straight, directed obliquely, with distal extremity pointed. No cloacal tubus. Tail short, rounded.

*Juveniles 2d stage.* Stylet long (35-40  $\mu\text{m}$ ) lateral field with four lines. Oesophageal glands filling body cavity. Tail conical, of medium length, with hyaline terminal part half of total length. Phasmids with lens-like structure. Nurse cell system : a single giant cell with a single giant nucleus.

## TYPE AND ONLY SPECIES

- Bellodera utahensis* (Baldwin, Mundo-Ocampo & Othman, 1983) Wouts, 1985  
= *Cryphodera utahensis* Baldwin, Mundo-Ocampo & Othman, 1983

## COMMENTS

The only species of *Bellodera* shows some general resemblance with those species placed in *Cryphodera*. Wouts (1985) proposed a new genus, *Bellodera*, for *C. utahensis*, based on the two following characters : *i*) *Bellodera* is cystforming whereas *Cryphodera* is not; *ii*) the ornamentation of the female cuticle is a true " primitive " annulation in *Cryphodera* whereas in *Bellodera* it is constituted by ridges and pits which represent a more derived type. In fact, *Bellodera utahensis* does not possess a cyst, as defined by Luc *et al.* (1986); also it seems difficult to oppose annulation to " ridges ", and to consider such differences as sufficiently founded to constitute a good generic character. However two other characters are significant at generic level : *i*) in *Cryphodera* species, the posterior end of the female is roughly rounded, with vulval lips only slightly bulging from overall profile, whereas in *Bellodera* a strong terminal cone is present, rather peculiar because its top is flat and the vulval slit not, or only slightly, sunken; *ii*) in *Cryphodera* females, position of the excretory pore is typical of Heteroderinae i.e. at some distance from the anterior end, about at level of glandular part of the oesophagus (the values calculated on original figures are : *C. eucalypti* : 154  $\mu\text{m}$ ; *C. podocarpi* : 118  $\mu\text{m}$ ; *C. nothophagi* : 169  $\mu\text{m}$ ; *C. coxi* : 99  $\mu\text{m}$ ); whereas in *Bellodera* females the excretory pore is forwardly situated, i.e. at level of base of stylet, or 27-56  $\mu\text{m}$  from anterior end (stylet : 41.5-56  $\mu\text{m}$ ). This forward position of the excretory pore is exceptional in Heteroderinae, and is somewhat similar to the characteristic of Meloidogyninae.

*Thecavermiculatus* Robbins, 1978

## DIAGNOSIS

## Heteroderinae

*Females.* No cyst stage. Body globose, with prominent neck and no terminal cone. Cuticle thick, annulated in fore part or on the major part of body, with lace-like

pattern on posterior part; D-layer present. Subcrystalline layer present (very thick in *T. crassicrustatus*). Vulva sub-terminal, close to anus; vulval lips non-protruding; anal-vulval region flush with body contour. Eggs retained in female body, together with hatched second-stage juveniles.

*Males.* Body twisted. Lateral field with four lines. Spicules slightly curved, distally notched; no cloacal tubus. Tail very short. No phasmids.

*Juveniles, second stage.* Lateral field with four lines. Oesophageal glands not filling body cavity (except *T. crassicrustatus*). Tail pointed, of medium length, with long hyaline terminal part. Phasmids with lens-like structure.

*Nurse cell system* : a syncytium.

#### TYPE SPECIES

*T. gracililancea* Robbins, 1978

#### OTHER SPECIES

*T. andinus* Golden, Franco, Jatala & Astogaza, 1983  
= *Dolichodera andina* (Golden, Franco, Jatala & Astogaza, 1983) Wouts, 1985

*T. carolynae* Robbins, 1986

*T. crassicrustatus* Bernard, 1981

#### COMMENTS

Wouts (1985) considered *T. andinus* as a member of the genus *Dolichodera*; he underlined a series of characters that make *T. andinus* different from the two other species of the genus, among which : a short vulval slit (less than 10 µm) surrounded by an "initiation of circumfenestra" and the oesophageal glands filling the body cavity in the J2. Wouts (1985) estimated that such peculiar characters may justify a new genus for this species, but he chose to place it instead in *Dolichodera*. Actually this species fits better in *Thecavermiculatus* than in *Dolichodera*, a cyst forming genus. Consequently this species is returned to *Thecavermiculatus*.

Siddiqi (1986) considered *Rhizonema* a junior synonym of *Thecavermiculatus*. This is discussed below.

***Rhizonema*** Cid del Prado Vera, Lownsbery & Maggenti, 1983

#### DIAGNOSIS

Heteroderinae

*Females.* No cyst stage. Body globose with prominent neck and terminal cone. Cuticle thick, wavy; entire body annulated, except terminal cone. D-layer absent. No subcrystalline layer. Vulva and anus situated on terminal cone having a thickened cuticle. Phasmids not observed.

Eggs retained in female body together with hatched second stage juveniles.

*Males.* Body twisted. Lateral field with four lines. Spicules nearly straight, pointed, posteriorly directed. Cloacal tubus well developed. No phasmids.

*Juveniles 2d stage.* Lateral field with four lines. Oesophageal glands filling body cavity. Tail conical pointed with long hyaline terminal part. Phasmids with lens-like structure.

*Nurse cell system* : a single giant cell with a giant nucleus.

#### TYPE AND ONLY SPECIES

*R. sequoiae* Cid del Prado Vera, Lownsbery & Maggenti, 1983

= *Sarisodera sequoiae* (Cid del Prado Vera, Lownsbery & Maggenti, 1983) Wouts, 1985

= *Thecavermiculatus sequoiae* (Cid del Prado Vera, Lownsbery & Maggenti, 1983) Siddiqi, 1986

#### COMMENTS

Wouts (1985) proposed *Rhizonema* as a junior synonym of *Sarisodera*, as he considered the annulation of the female cuticle of the former genus a "secondary annulation" (?), with no taxonomic value. We agree that both genera share a great number of characters, namely the morphology of the posterior part of female, and male. But the annulation *vs* lace-like pattern of the cuticle in female is an important character we accept at the generic level. This is corroborated by the presence of D-layer in *Sarisodera* whereas it is absent in *Rhizonema*.

Siddiqi (1986) considered *Rhizonema* as a junior synonym of *Thecavermiculatus*, most probably because in both genera the hatched second stage juveniles are retained in the body of females (no arguments are presented justifying that synonymization). Matricidal hatching (see Luc, Taylor & Netscher, 1979), is observed in various groups of nematodes, and, although exceptional in Heteroderinae, its taxonomic significance is not apparent. On the other hand, several important characters differentiate the two genera, namely *i*) presence of a terminal cone and protuberant vulval lips in *Rhizonema*, which correspond (sexual coaptation) to the absence of male tail, the straight backward directed spicules and the well developed cloacal tubus (in *Thecavermiculatus* the vulva is flush with body contour and male presents spicules ventrally directed, no cloacal tubus and a short tail); *ii*) D-layer of cuticle absent in *Rhizonema* whereas present in *Thecavermiculatus* (Cliff & Baldwin, 1985); *iii*) *Rhizonema* incites the formation of a single giant nurse cell with a single giant nucleus (Cid del Prado Vera & Lownsbery, 1984) *vs* a syncytium for *Thecavermiculatus* (Baldwin, 1986).

**Hylonema** Luc, Taylor & Cadet, 1978

## DIAGNOSIS

## Heteroderinae

*Females.* No cyst stage. Body long ovoid to globose with prominent neck and no terminal cone. Cuticle thin and annulated only in anterior fore end; posteriorly thick, rugose with non oriented striae. No subcrystalline layer. Vulva subterminal, on flattened posterior body end; vulva lips not protruding. Underbridge present. No phasmids. No remnant of tail. Eggs not retained in female body, but deposited individually in a gelatinous matrix.

*Males.* Body twisted. Lateral field with four lines. Spicules strong, nearly straight, < 30 µm; cloacal tubus short, nearly terminal. No tail. No caudal alae. No phasmids.

*Juveniles.* Lateral field with three lines. Oesophageal glands filling body cavity. Tail long, elongate with a very long terminal hyaline portion. Phasmids punctiform, small.

*Nurse cell system* : a single giant cell with a single giant nucleus.

## TYPE AND ONLY SPECIES

*Hylonema ivorense* Luc, Taylor & Cadet, 1978

**Sarisodera** Wouts & Sher, 1971

## DIAGNOSIS

## Heteroderinae

*Females.* No cyst stage. Body globose, with neck of medium length; posterior end conical-truncated with deep vulval cleft, but with no defined terminal cone. Cuticle thick, with superficial lace-like pattern; D-layer present. Vulva terminal, with prominent hypertrophied lips, separated by a deep depression. Anus in the inner side of the posterior lip. Eggs retained in body.

*Males.* Body twisted. Stylet 40 µm. Lateral field with four lines. Spicules > 30 µm, straight, pointed at distal extremity, distally directed; cloacal tubus prominent. No tail; no phasmids.

*Juveniles 2d stage.* Stylet 40 µm. Lateral field with four lines. Oesophageal glands filling the body cavity. Tail conical, pointed, with terminal half hyaline. Phasmids with lens-like structure.

*Nurse cell system* : a single giant cell with a single giant nucleus.

## TYPE AND ONLY SPECIES :

*S. hydrophila* Wouts & Sher, 1971

**Heterodera** A. Schmidt, 1871

- = *Tylenchus (Heterodera)* A. Schmidt, 1871
- = *Heterodera (Heterodera)* A. Schmidt, 1871
- = *Heterobolbus* Railliet, 1896
- = *Bidera* Krall' & Krall', 1978
- = *Ephippiodera* Shagalina & Krall', 1981

## DIAGNOSIS

## Heteroderinae

*Females.* Cyst stage present. Body globose, lemon shaped, with short neck and terminal cone. Cuticle thick, with superficial lace-like pattern; D-layer absent; subcrystalline layer present or absent. Vulva terminal, vulval slit of variable length; vulval lips not protruding. Vulval area ambi- or bifenestrated. No anal fenestration. Underbridge generally present. Bullae present or absent. Eggs retained in body; in some cases egg mass also present.

*Males.* Body twisted. Lateral field with four (rarely three) lines. Spicules > 30 µm, slightly curved, directed obliquely, with distal extremity pointed or notched. No cloacal tubus. Tail very short, rounded.

*Juveniles 2d stage.* Stylet < 30 µm. Lateral field with four (rarely three) lines. Oesophageal glands filling body cavity. Tail conical, pointed; hyaline part variable, generally half tail length. Phasmids punctiform.

*Nurse cell system* : a syncytium.

## TYPE SPECIES

- Heterodera schachtii* A. Schmidt, 1871
- = *Tylenchus schachtii* (A. Schmidt, 1871) Örley, 1880
- = *Heterodera schachtii minor* O. Schmidt, 1930

## OTHER SPECIES

- H. amygdali* Kir'yanova & Ivanova, 1975
- H. arenaria* Cooper, 1955
- = *Bidera arenaria* (Cooper, 1955) Krall' & Krall', 1978
- H. avenae* Wollenweber, 1924
- = *H. schachtii* var. *avenae* Wollenweber, 1924
- = *Bidera avenae* (Wollenweber, 1924) Krall' & Krall', 1978
- = *H. schachtii major* O. Schmidt, 1930
- = *H. major* O. Schmidt, 1930
- = *H. ustynovi* Kir'yanova, 1969
- = *Bidera ustynovi* (Kir'yanova, 1969) Krall' & Krall', 1978

- H. bifenestra* Cooper, 1955  
 = *Bidera bifenestra* (Cooper, 1955) Krall' & Krall', 1978  
 = *H. longicaudata* Seidel, 1972  
 = *Bidera longicaudata* (Seidel, 1972) Krall' & Krall', 1978
- H. cajani* Koshy, 1967  
 = *H. vigni* Edward & Misra, 1968
- H. canadensis* Mulvey, 1979
- H. cardiolata* Kir'yanova & Ivanova, 1969
- H. carotae* Jones, 1954
- H. ciceri* Vovlas, Greco & di Vito, 1985
- H. cruciferae* Franklin, 1945
- H. cyperi* Golden, Rau & Cobb, 1962
- H. daverti* Wouts & Sturhan, 1979
- H. delvii* Jairajpuri, Khan, Setty & Govindu, 1979
- H. elachista* Ohshima, 1974
- H. fici* Kir'yanova, 1954
- H. filipjevi* (Madzhidov, 1981) Stone, 1985  
 = *Bidera filipjevi* Madzhidov, 1981
- H. galeopsidis* Goffart, 1936  
 = *H. schachtii galeopsidis* Goffart, 1936
- H. gambiensis* Merny & Netscher, 1976
- H. glycines* Ichinohe, 1952
- H. goettingiana* Liebscher, 1892
- H. graduni* Kir'yanova in Kir'yanova & Krall', 1971
- H. graminis* Stynes, 1971
- H. graminophila* Golden & Birchfield, 1972
- H. hordecalis* Andersson, 1975  
 = *Bidera hordecalis* (Andersson, 1975) Krall' & Krall', 1978
- H. humuli* Filip'ev, 1934
- H. iri* Mathews, 1971  
 = *Bidera iri* (Mathews, 1971) Krall' & Krall', 1978
- H. latipons* Franklin, 1969  
 = *Bidera latipons* (Franklin, 1969) Krall' & Krall', 1978  
 = *Ephippiodera latipons* (Franklin, 1969) Shagalina & Krall', 1981
- H. lespedezae* Golden & Cobb, 1963
- H. leuceilyma* Di Edwardo & Perry, 1964
- H. limonii* Cooper, 1955
- H. longicolla* Golden & Dickerson, 1973
- H. mani* Mathews, 1971  
 = *Bidera mani* (Mathews, 1971) Krall' & Krall', 1978
- H. medicaginis* Kir'yanova in Kir'yanova & Krall', 1971
- H. mediterranea* Vovlas, Inserra & Stone, 1981
- H. menthae* Kir'yanova & Narbaev, 1977
- H. methwoldensis* Cooper, 1955
- H. mothi* Khan & Husain, 1965
- H. oryzae* Luc & Berdon Brizuela, 1961
- H. oryzicola* Rao & Jayaprakash, 1978
- H. oxiana* Kir'yanova, 1962
- H. pakistanensis* Maqbool & Shahina, 1986
- H. phragmitidis* Kazachenko, 1986
- H. plantaginis* Narbaev & Sidikov, 1987
- H. polygoni* Cooper, 1955
- H. raskii* Basnet & Jayaprakash, 1984
- H. rosii* Duggan & Brennan, 1966
- H. sacchari* Luc & Merny, 1963
- H. salixophila* Kir'yanova, 1969
- H. sonchophila* Kir'yanova, Krall' & Krall', 1976
- H. sorghi* Jain, Sethi, Swarup & Srivastava, 1982
- H. tadshikistanica* Kir'yanova & Ivanova, 1966
- H. trifolii* Goffart, 1932  
 = *H. schachtii* var. *trifolii* Goffart, 1932  
 = *H. paratrifolii* Kir'yanova, 1961  
 = *H. rumicis* Poghossian, 1961  
 = *H. scleranthii* Kaktina, 1957
- H. turcomanica* Kir'yanova & Shagalina, 1965  
 = *Bidera turcomanica* (Kir'yanova & Shagalina, 1965) Krall' & Krall', 1978  
 = *Ephippiodera turcomanica* (Kir'yanova & Shagalina, 1965) Shagalina & Krall', 1981
- H. urticae* Cooper, 1955
- H. uzbekistanica* Narbaev, 1980
- H. zeae* Koshy, Swarup & Sethi, 1971

#### COMMENTS

*Heterobolbus* in an objective junior synonym of *Heterodera*.

*Bidera* was proposed by Krall' and Krall' (1978) to contain *H. avenae* and related species (the "avenae group") characterized mainly by a very short vulval slit and the well individualized fenestrae, often situated at some distance from each other. However, it is difficult to establish clear differentiation between this group and other *Heterodera* species at generic level.

We agree with Mulvey and Golden (1983) who considered *Bidera* a junior synonym of *Heterodera*. Its species here are returned to the latter genus.

*Ephippiodera* was erected by Shagalina and Krall' (1981) for those species of *Bidera* in which the vulval bridge is very wide, this character being correlated with semifenestrae laterally directed and well separated from each other by a saddle-shaped, shallow depression. Although these species appear somewhat different from other *Heterodera* species, we consider such a variability of fenestrae as an intrageneric one. Consequently we concur with Wouts' (1985) conclusion that *Ephippiodera* is a junior synonym of *Heterodera*.

***Globodera* Skarbilovich, 1959**  
 = *Heterodera (Globodera)* Skarbilovich, 1959

#### DIAGNOSIS

##### Heteroderinae

*Females*. Cyst stage present. Body globose, spheroidal, with a short neck and no terminal cone. Cuticle thick,



with superficial lace-like pattern; D-layer present. Vulva terminal, of medium length. Vulval area circumfenestrated; superficial tubercles near vulva. No anal fenestration, but anus and vulva lying both in a "vulval basin". Underbridge and bullae rarely present. All eggs retained in body (no egg-mass).

*Males.* Body twisted. Lateral field with four lines. Spicules > 30 µm, distally pointed. No cloacal tubus. Tail short, hemispherical.

*Juveniles 2d stage.* Stylet < 30 µm. Lateral field with four lines. Oesophageal glands filling body cavity. Tail conical, pointed, with terminal half hyaline. Phasmids punctiform.

*Nurse cell system* : a syncytium.

#### TYPE-SPECIES

- Globodera rostochiensis* (Wollenweber, 1923) Behrens, 1975  
 = *Heterodera schachtii rostochiensis* Wollenweber, 1923  
 = *H. schachtii solani* Zimmermann, 1927

#### OTHER SPECIES

- G. achilleae* (Golden & Klindić, 1973) Behrens, 1975  
 = *Heterodera achilleae* Golden & Klindić, 1973  
*G. artemisiae* (Eroshenko & Kazachenko, 1972) Behrens, 1975  
 = *H. artemisiae* Eroshenko & Kazachenko, 1972  
*G. chaubattia* (Gupta & Edward, 1973) Wouts, 1984  
 = *H. chaubattia* Gupta & Edward, 1973  
 = *H. mali* Kir'yanova & Borisenko, 1975  
 = *G. mali* (Kir'yanova & Borisenko, 1975) Behrens, 1975  
*G. hypolyphi* Ogawa, Ohshima & Ichinohe, 1983  
*G. leptonepia* (Cobb & Taylor, 1953) Behrens, 1975  
 = *H. leptonepia* Cobb & Taylor, 1953  
*G. millefolii* (Kir'yanova & Krall', 1965) Behrens, 1975  
 = *H. millefolii* Kir'yanova & Krall', 1965  
*G. mirabilis* (Kir'yanova, 1971) Mulvey & Stone, 1976  
 = *H. mirabilis* Kir'yanova, 1971  
*G. pallida* (Stone, 1973) Behrens, 1975  
 = *H. pallida* Stone, 1973  
*G. pseudorostochiensis* (Kir'yanova, 1963) Mulvey & Stone, 1976  
 = *H. pseudorostochiensis* Kir'yanova, 1963  
*G. tabacum tabacum* (Lownsbery & Lownsbery, 1954) Behrens, 1975  
 = *H. tabacum* Lownsbery & Lownsbery, 1954  
*G. tabacum solanacearum* (Miller & Gray, 1972) Behrens, 1975  
 = *H. solanacearum* Miller & Gray, 1972  
 = *G. solanacearum* (Miller & Gray, 1972) Behrens, 1975

*G. tabacum virginiae* (Miller & Gray, 1968) Behrens, 1975

= *H. virginiae* Miller & Gray, 1968

= *G. virginiae* (Miller & Gray, 1968) Behrens, 1975

*G. zelandica* Wouts, 1984

#### *Cactodera* Krall' & Krall', 1978

#### DIAGNOSIS

##### Heteroderinae

*Females.* Cyst stage present. Body globose, with short neck and terminal cone. Cuticle thick, with superficial irregular transverse ridges interrupted by short markings, more or less longitudinal; D-layer present (absent in *C. betulae*). Vulva terminal surrounded by a circumfenestration; vulval slit < 20 µm; no underbridge; no bullae; annus without fenestration. All eggs retained in body (no egg-mass).

*Males.* Body twisted. Stylet < 30 µm. Lateral field with four lines. Spicules > 30 µm, slightly curved, pointed at distal extremity, obliquely directed. No cloacal tubus. Tail short, hemispherical.

*Juveniles 2d stage.* Stylet < 30 µm. Lateral field with four lines. Oesophageal glands filling body cavity. Tail conical pointed with terminal half hyaline. Phasmids punctiform.

*Nurse cell system* : a syncytium.

#### TYPE-SPECIES

- Cactodera cacti* (Filip'ev & Schuurmans Stekhoven, 1941) Krall' & Krall', 1978  
 = *Heterodera cacti* Filip'ev & Schuurmans Stekhoven, 1941

#### OTHER SPECIES

- C. acnidae* (Schuster & Brezina, 1979) Wouts, 1985  
 = *H. acnidae* Schuster & Brezina, 1979  
*Cactodera amaranthi* (Stoyanov, 1972) Krall' & Krall', 1978  
 = *H. amaranthi* Stoyanov, 1972  
*C. aquatica* (Kir'yanova, 1971) Krall' & Krall', 1978  
 = *H. aquatica* Kir'yanova, 1971  
*C. betulae* (Hirschmann & Riggs, 1969) Krall' & Krall', 1978  
 = *H. betulae* Hirschmann & Riggs, 1969  
*C. eremica* Baldwin & Bell, 1985  
*C. estonica* (Kir'yanova & Krall', 1963) Krall' & Krall', 1978  
 = *H. estonica* Kir'yanova & Krall', 1963  
*C. thornei* (Golden & Raski, 1977) Krall' & Krall', 1978  
 = *H. thornei* Golden & Raski, 1977

*C. weissii* (Steiner, 1949) Krall' & Krall', 1978  
= *H. weissii* Steiner, 1949

***Punctodera* Mulvey & Stone, 1976**

DIAGNOSIS

Heteroderinae

*Females.* Cyst stage present. Body globose, spherical to pear-shaped with short neck and no terminal cone. Cuticle thick, with superficial reticulate pattern; subcuticle provided with punctation; D-layer present; subcrystalline layer present, thick. Vulva terminal; vulval slit < 5 µm, surrounded by a circular circumfenestra; no perineal papillae; no underbridge; no bullae. Anus surrounded by circular (anal) fenestra. Eggs retained in body (no egg-mass).

*Males.* Body twisted. Lateral field with four lines. Spicules > 30 µm, slightly curved, distally pointed. No cloacal tubus. Tail very short, rounded.

*Juveniles 2d stage.* Stylet < 30 µm. Lateral field with four lines. Oesophageal glands filling body cavity. Tail conical, to conical-effilated with long hyaline terminal portion. Phasmids punctiform.

*Nurse cell system* : a syncytium.

TYPE SPECIES

*P. punctata* (Thorne, 1928) Mulvey & Stone, 1976  
= *Heterodera punctata* Thorne 1928

OTHER SPECIES

*P. chalcoensis* Stone, Sosa Moss & Mulvey, 1976  
*P. matadorensis* Mulvey & Stone, 1976

***Dolichodera* Mulvey & Ebsary, 1980**

DIAGNOSIS

Heteroderinae

*Females.* Cyst stage present. Body elongate-oval, with long neck and no terminal cone. Cuticle of medium thickness (3-4 µm), with fine irregular striae; subcrystalline layer present. Vulva subterminal circumfenestrate. Bullae present. No anal fenestration. Eggs retained in body.

*Males.* Not known.

*Juveniles 2d stage.* Stylet < 25 µm. Lateral field with four lines\*. Oesophageal gland filling body cavity. Tail conical, elongated; with hyaline terminal half. Phasmids punctiform.

TYPE AND ONLY SPECIES

*D. fluvialis* Mulvey & Ebsary, 1980

COMMENTS

*Dolichodera* is not well known. Males have not yet been found, and no data has been afforded on the ultrastructure of the cyst-wall (D-layer) or of the nurse cell system.

Note that Wouts (1985) placed *Thecavermiculatus andinus* in *Dolichodera*. This has been discussed above.

***Afenestrata* Baldwin & Bell, 1985**

= *Afrodera* Wouts, 1985

DIAGNOSIS

Heteroderinae

*Females.* Cyst stage present. Body globose, with very short and thin neck, and pronounced terminal cone with hypertrophied vulval lips. Cuticle thin and irregularly annulated on neck; thick, with superficial lace-like pattern on rest of body; D-layer absent. No subcrystalline layer. Vulva terminal; vulval slit deeply sunken between vulval lips; fenestration, bullae, underbridge absent. Anus subterminal, on posterior side of cone.

*Males.* Body twisted. Lateral field with four lines. Spicules terminal, posteriorly directed, straight, distal extremity pointed; cloacal tubus well developed. No phasmids. No tail.

*Juveniles.* Stylet 20 µm. Lateral field with four lines. Oesophageal glands filling body cavity. Tail conical, pointed, with hyaline terminal portion half its length. Phasmids punctiform.

*Nurse cell system* : a syncytium.

TYPE AND ONLY SPECIES

*Afenestrata africana* (Luc, Germani & Netscher, 1973) Baldwin & Bell, 1985  
= *Sarisodera africana* Luc, Germani & Netscher, 1973  
= *Afrodera africana* (Luc, Germani & Netscher, 1973) Wouts, 1985

COMMENTS

Observations by Baldwin and Bell (1985) (that contrary to the original description *Sarisodera hydrophila*, type species of the genus, does not possess cysts) justify the creation of the new genus *Afenestrata* for *S.*

\* Original description mentioned three lines. Reexamination of paratype juveniles revealed that four lines are present (Burrows & Stone in Stone, 1985).

*africana*, a species which does possess a cyst. Other major differences are: *i*) *S. hydrophila* incites the formation of single giant cell (Mundo-Ocampo & Baldwin, 1983 whereas *A. africana* incites a syncytium (Baldwin & Bell, 1985); *ii*) a D-layer is present in the female cuticle of *Sarisodera* (Baldwin, 1983), absent in *Afenestrata* (Cliff & Baldwin, 1985); *iii*) a "normal" neck in *Sarisodera* female *vs* very reduced in *Afenestrata*; *iv*) anus situated inside the posterior lip of the cone in *Sarisodera* *vs* outside in *Afenestrata*; *v*) juveniles of *Sarisodera* with a long stylet and phasmids with lens-like structure, whereas in *Afenestrata* the juvenile stylet is of medium length and phasmids are punctiform. *Afrodera* is an objective junior synonym of *Afenestrata*.

### Relationships between the genera of Heteroderinae; phylogeny within the subfamily

*Verutus* appears as the more ancestral genus in the subfamily as evidenced by several characters of the female: body elongated, sausage-shaped, vulva situated at mid-body, cuticle annulated over all the body and presenting a vestigial lateral field at the posterior part, remnants of a tail often discernible. Also considered as ancestral is the fact that the eggs not only are not retained in the female body, but are deposited individually, and there is no production of a gelatinous matrix.

These females show a rough resemblance to those of *Rotylenchulus* or *Senegalonema*; this may explain why Siddiqi (1986) excluded *Verutus* from Heteroderidae and placed it (and *Verutinae*) under *Rotylenchulidae*.

However, other characters dictate maintaining *Verutus* within Heteroderidae. Particularly, the female of *Verutus*, as shown with SEM by Othman and Baldwin (1985), possesses the small, squarish, well detached labial disc we consider characteristic of the Heteroderinae. Moreover, the male of *Verutus*, even though not twisted posteriorly conforms to the type of the subfamily in lacking caudal alae and phasmids and having a very short, rounded tail. Also the second-stage juveniles are similar to those of other Heteroderinae, namely by the long conical tail provided with a long hyaline terminal part.

These juveniles have punctiform phasmids and the nurse cell system is syncytial two characters considered as derived by Baldwin (1986). Also Baldwin (1986) considers the lip pattern of males and second-stage juveniles as "highly derived", and the cuticle of the female as unique in Heteroderinae because of the presence of multiple B-layer.

So, one sees here the mixture of ancestral and derived characters in a taxon that is considered the most ancestral of the subfamily.

*Meloidodera* may also be considered an ancestral genus by the cuticle being annulated over the entire

body and having the vulva situated at mid-body. But the female is globose and there is no remnant of the lateral field or tail. Eggs are deposited in a gelatinous matrix and the posterior part of the male body is twisted. These last characters indicate a not so ancestral state as *Verutus*, but *Meloidodera* induces a single unilocular giant nurse cell and only in three species of five are the second-stage juveniles provided with lens-like phasmids. This variability in phasmids led Baldwin (1986) to suggest that *Meloidodera* could be polyphyletic, as underlined also by the lip pattern of males and second-stage juveniles, that varies from ancestral to derived types, with intermediate forms. Here also the mixture of ancestral and derived characters exists, but with a predominance of the former.

We may nevertheless consider *Verutus* and *Meloidodera* as representing an ancestral group within Heteroderinae, showing clearly through the first genus the affinities between Heteroderidae and Hoplolaimidae. Of course, when using the term group, we do not intend to give it any taxonomic value.

A second group is represented by the other non-cyst forming genera of Heteroderinae, i.e. *Atalodera*, *Cryphodera*, *Bellodera*, *Thecavermiculatus*, *Rhizonema*, *Hylonema* and *Sarisodera*, all these genera having globose females with a subterminal vulva.

Before examining this group of seven genera we must keep in mind some remarks:

- discovery of these genera is relatively recent (the oldest is *Cryphodera*, described in 1966, the other genera having been described from 1971 to 1984);
- all the species pertaining to these genera have been found on wild plants, in non-cultivated soils and on tree-roots, the exception are the *Thecavermiculatus* species which parasitize herbaceous plants. Such biotopes are rarely sampled, and heteroderids are often difficult to detect on tree-roots;
- consequently, it is very probable that many other species, and genera, could be discovered in the future by systematic sampling in wild areas.

Currently, we have only a meagre collection of samples of what could be a much larger group. Also it is not astonishing that the limited number of species (fourteen) in the group is distributed into seven genera, four of which are monotypic, one has two species and the last two four species.

This could explain the patchwork of characters used for differentiation (Tab. 1). If we retain as an ancestral character the annulation of the female body (as in *Verutus* and *Meloidodera*), then the most ancestral genera are *Cryphodera* and *Rhizonema*, but in both eggs are retained in the body (derived) and in *Rhizonema* a posterior cone exists (derived). *Hylonema* is the only genus of the group that does not retain eggs (ancestral) but the female possesses a underbridge and the juveniles have punctiform phasmids, characters considered as derived. We could continue this game: *Thecavermicula-*

*tus* is ancestral by the absence of cone in female and the lens-like phasmids in second-stage juvenile, but derived by inducing a syncytial nurse system, etc.

Instead of trying to produce a " phylogenetic " line among these genera, we prefer to give a list (Tab. 1) of the main characters used for their definitions, and their identification.

The remaining genera of Heteroderinae are those producing cysts. The cyst represents a more efficient protection of the eggs. Therefore we consider, as generally admitted, the cyst-forming genera as derived in comparison of the non cyst-forming ones among the Heteroderinae.

The cyst-forming genera of Heteroderinae may be divided into two groups. The first encompasses the genera formerly considered as *Heterodera s. lato*, i.e. *Heterodera s. str.*, *Punctodera*, *Cactodera* and *Globodera* to which *Dolichodera* must be added. *Afenestrata* is rather different and could constitute its own group. These six genera are characterized by the presence of cysts i.e., following the more recent definition (Luc *et al.*,

1986), " a persistent tanned sac which retains eggs and is derived from some or all components of the mature female body wall ". Note that all the cyst-forming Heteroderinae induce a nurse cell system composed of syncytium.

Among the " *Heterodera* group ", the cyst has similar characteristics; the anterior slender part, or " neck ", that remains attached to the globose part of the cyst when liberated in the soil (the " neck " cuticle, although thinner, is tanned and similar to the cuticle of the globose part); terminally around vulva the cuticle is thin and transparent and constitutes the vulval fenestration; such fenestrae break easily allowing the hatched J2 to escape from cyst.

Around this general scheme, these five genera differ from each other by a number of characters : the posterior part of the cyst may be rounded and plain (*Punctodera*, *Globodera* and *Dolichodera*) or the vulval area may be situated at the top of a cone, the cyst being lemon-shaped (*Heterodera* and *Cactodera*). The vulval fenestration is divided into two parts (bifenestration, ambi-

Table 1  
Main characters of the non cyst forming genera of Heteroderinae with sub-terminal vulva

	<i>Ataloder</i>	<i>Crypho-</i> <i>dera</i>	<i>Bellodera</i>	<i>Thecaver-</i> <i>miculatus</i>	<i>Rhizonema</i>	<i>Hylonema</i>	<i>Sariso-</i> <i>dera</i>
FEMALE							
cuticle annulated		+			+		
cuticle lace like patterned	+		+	+		+	+
D-layer	+	?	-	+	-	?	+
posterior cone	+	-	+	-	+	-	+
underbridge	-	-	-	-	-	+	-
eggs retained	+	+	+	+	+	-	+
matricidal hatching	-	-	-	+	+	-	-
MALES							
spicules > 30 µm	+	-	±	±	±	+	+
spicules bifids	-	-	-	+	-	-	-
tail hemispherical	+	+	+	+			
tail absent					+	+	+
2d STAGE JUVENILES							
lateral field lines	3	3/4	4	4	4	3	4
oesoph. gl. filling body cav.	-	+	+	±	+	+	+
phasmids " lens-like "	+	+	+	+	+	-	+
NURSE CELL SYST.							
syncytium	+	?		+			
single cell		?	+		+	+	+
HOSTS							
trees	+	+	+		+	+	+
herbac. plants				+			
NUMBER OF SPECIES	2	4	I	4	I	I	I

fenestration) separated by a more or less wide "vulval bridge" in *Heterodera*. A unique circle around the vulva (circumfenestration) exists in other genera; a circular fenestration is also present around the anus (anal fenestration) in *Punctodera* whose subcuticle is provided with numerous small punctations, *vs* plain in other genera. The presence of a tuberculate area in the vulval region is characteristic of the genus *Globodera*. *Dolichodera* differs by having more elongated cysts and a thinner cuticle. Males as well as J2's are very similar in all five genera.

Variations in the shape of vulval fenestration in the past have been used to divide *Heterodera* into three genera: *Heterodera s. str.*, *Bidera* and *Ephippiodera*. *Heterodera s. str.* has the two parts of the fenestration (amphifenestrae) roughly semi-circular and close each other, the vulval bridge being narrow. In *Bidera* and *Ephippiodera* the two fenestrae are rounded and more widely separated. *Ephippiodera* was distinguished from *Bidera* by the fact that the area separating the two fenestrae shows the profile of a saddle-like depression. Such variations are not considered here as generic and we agree with Mulvey and Golden (1983) and Wouts (1985) who placed *Bidera* and *Ephippiodera*, respectively, among junior synonyms of *Heterodera*.

Genera of the "*Heterodera* group" appear very close to each other and it is difficult to recognize ancestral *vs* derived genera in the group.

The genus *Afenestrata* possesses a cyst of a different type. The neck is very short and narrow compared to the body of the cyst and the cuticle is different in being thin (1.5-2 µm), translucent and annulated in contrast to the thick (16-24 µm), brownish and superficially lace-like patterned cuticle on the rest of the cyst (Taylor & Luc, 1979). The change in thickness of the cuticle at the base of the neck is abrupt and when mature the cyst ruptures at this level; the cysts found in the soil lack the neck portion; it is through this aperture that the hatched juveniles escape from the cyst. The posterior part of the cyst ends in a cone which consists of the hypertrophied vulval lips with very thick cuticle guarding a deeply sunken vulval slit; there are no fenestration, under-bridge, or bullae. Due to the rigidity of the surrounding cuticle, it is difficult to understand how such a vulva can open, even if *dilatatores vulvae* muscles are present. Perhaps these muscles are used to open the vulva when the young white female is mated.

The cyst in *Heterodera* group and in *Afenestrata*, shows however a resemblance on some points such as the superficial lace-like pattern and the lack of the D-layer (Cliff & Baldwin, 1985). Also the basic number of chromosomes ( $n = 9$ ) is the same ( $n = 9$ ) in both « *Heterodera* group » and *Afenestrata*.

*Heteroderinae s. auct.* is one group of plant-parasitic nematodes for which studies on phylogeny using the cladistic approach to taxonomy have been particularly developed.

The cladistic approach was initiated by Coomans (1979), followed by Ferris (1979, 1985) and Wouts (1985). Ferris (1979) took into consideration eight characters: vulva subequatorial or subterminal; female cuticle annulated or not; spicules shorter or longer than 30 µm; anus and vulva close together or widely separated; cyst present or not; J2 phasmids « lens-like » or punctiform; fenestration absent or present; female body irregular/lemonshaped or round/pear-shaped; the first cited type for each character was the "primitive" state and the second the "derived" state. So Ferris produced a cladogram where *Meloidodera* was considered the most primitive genus and *Punctodera* the most derived. However Baldwin (1986) concluded that supplementary characters (presence or absence of D-layer; type of nurse cell system) lead to a revision of the cladogram in its central portion i.e. for the majority of genera. Wouts (1985) produced a cladogram taking into consideration also the characters "D-layer present or not" and "J2 face primitive or derived"; he constructed a cladogram with six branches, each of them corresponding to a sub-family (Verutinae, Meloidoderinae, Cryphoderinae, Heteroderinae, Ataloderinae, Punctoderinae). *Heteroderinae s. auct.* was maintained at the family level. Doing this, he excluded the character "cyst present or absent", replacing it by a loose definition of the cyst forming species as "those species that show a change in colour of the female cuticle upon death of female, regardless of the extent of this colour change". Such a definition was rejected (Luc *et al.*, 1986) mainly because there is no biological basis for it. The artificial nature of Wout's classification is evident by the reassembling in the same subfamily, "Heteroderinae" of *Heterodera*, *Afenestrata* and *Hylonema*. The remaining cyst-forming genera (*Dolichodera*, *Globodera*, *Cactodera* and *Punctodera*) are grouped in the subfamily Punctoderinae. Wouts (1985) did not consider the nurse cell system. If this character is superimposed onto Wout's cladogram then discrepancies are evident in at least two subfamilies (Heteroderinae and Ataloderinae).

At the moment the data produced does not permit the defining of well founded taxonomic divisions in the group, therefore, we accept only the subfamily, Heteroderinae.

It is interesting that in his more recent review of the phylogeny of this group (Baldwin, 1986), no cladogram was given, or taxonomic divisions proposed.

#### The subfamily MELOIDOGYNINAE Skarbilovich, 1959

#### Diagnosis

Heteroderidae. Cuticle not abnormally thick, annulated in all stages of the male and female. Cephalic framework of medium sclerotization; lateral sectors

equal to wider than submedian sectors. *Female*. Sedentary, globose with projecting neck. No preadult vermiform female stage. Cuticle moderately thick; annulation forming finger-print like pattern around vulva and anus. Labial disc dumb-bell shaped, not detached from labial sectors. Cephalic framework and spear delicate. Excretory pore anterior to median oesophageal bulb, often only slightly posterior to stylet base. Vulva and anus terminal; perineal region flush or slightly raised. No cyst stage. Eggs not retained in female body but deposited in a gelatinous matrix (exception : *Meloidogyne spartinae* where eggs are deposited individually without gelatinous matrix). *Male*. Labial area low, not set-off, irregularly annulated. Lateral field with four lines. *Juveniles*. Second-stage juveniles migratory, vermiform. Cephalic framework and spear delicate. Labial area not set-off. Late second-stage sedentary, swollen (spike-tailed). Third and fourth stages occurring within the second stage cuticle, devoid of stylet.

*Biology* : Sedentary, causing galls on roots. Female inciting multinucleate nurse cells resulting from karyokinesis in the absence of cytokinesis.

#### Type and only genus

*Meloidogyne* Goeldi, 1892

#### Genus *dubium*

*Meloidoderella* Khan & Husain, 1972\*

#### The genera in Meloidogyninae

##### *Meloidogyne* Goeldi, 1892

- = *Caconema* Cobb, 1924
- = *Hypsoperine* Sledge & Golden, 1964
- = *Hypsoperine* (*Hypsoperine*) Sledge & Golden, 1964 (n. syn.)
- = *Hypsoperine* (*Spartonema*) Siddiqi, 1986 (n. syn.)

#### DIAGNOSIS

Meloidogyninae. Having the characters of the subfamily.

\* The correct authorities for *Meloidoderella*, and its only species *M. indica*, is "Khan & Husain, 1972" as corresponding to the first description given in the minutes of a congress, regularly published. The authority "Khan, 1972", posterior, has no validity and can not even be considered a synonym of the former, contrary to Siddiqi (1986).

#### TYPE SPECIES

- Meloidogyne exigua* Goeldi, 1892
- = *Heterodera exigua* (Goeldi, 1892) Marcinowski, 1909

#### OTHER SPECIES

- Meloidogyne acrita* Chitwood, 1949
- = *M. incognita acrita* Chitwood, 1949
- Meloidogyne acronea* Coetzee, 1956
- = *Hypsoperine acronea* (Coetzee, 1956) Sledge & Golden, 1964
- = *Hypsoperine* (*Hypsoperine*) *acronea* (Coetzee, 1956) Sledge & Golden, 1964
- M. africana* Whitehead, 1960
- M. aquatilis* Ebsary & Eveleigh, 1983
- M. ardenensis* Santos, 1968
- M. arenaria* (Neal, 1889) Chitwood, 1949
- = *Anguillula arenaria* Neal, 1889
- = *Tylenchus arenarius* (Neal, 1889) Cobb, 1890
- = *Heterodera arenaria* (Neal, 1889) Marcinowski, 1909
- = *M. arenaria arenaria* (Neal, 1889) Chitwood, 1949
- M. artiellia* Franklin, 1961
- M. bauruensis* Lordello, 1956
- = *M. javanica bauruensis* Lordello, 1956
- M. brevicauda* Loos, 1953
- M. californiensis* Abdel-Rahman & Maggenti, 1987
- M. camelliae* Golden, 1979
- M. caraganae* Shagalina, Ivanova & Krall', 1985
- M. carolinensis* Eisenback, 1982
- M. chitwoodi* Golden, O'Bannon, Santo & Finley, 1980
- M. christiei* Golden & Kaplan, 1986
- M. coffeicola* Lordello & Zamith, 1960
- = *Meloidodera coffeicola* (Lordello & Zamith, 1960) Kir'yanova, 1963
- M. cruciani* Garcia-Martinez, Taylor & Smart, 1982
- M. decalineata* Whitehead, 1968
- M. deconincki* Elmiligy, 1968
- M. elegans* da Ponte, 1977
- M. enterolobii* Yang & Eisenback, 1983
- M. ethiopica* Whitehead, 1968
- M. fujianensis* Pan, 1985
- M. grahami* Golden & Slana, 1978
- M. graminicola* Golden & Birchfield, 1965
- M. graminis* (Sledge & Golden) Whitehead, 1968
- = *Hypsoperine graminis* Sledge & Golden, 1964
- = *Hypsoperine* (*H.*) *graminis* Sledge & Golden, 1964
- M. hapla* Chitwood, 1949
- M. hispanica* Hirschmann, 1986
- M. incognita* (Kofoid & White, 1919) Chitwood, 1949
- = *Oxyuris incognita* Kofoid & White, 1919
- = *Heterodera incognita* (Kofoid & White, 1919) Sandground, 1923

- = *M. incognita incognita* (Kofoid & White, 1919) Chitwood, 1949  
*M. indica* Whitehead, 1968  
*M. inornata* Lordello, 1956  
 = *M. incognita inornata* Lodello, 1956  
*M. javanica* (Treub, 1885) Chitwood, 1949  
 = *Heterodera javanica* Treub, 1885  
 = *Tylenchus (Heterodera) javanicus* (Treub, 1885) Cobb, 1890  
 = *Anguillula javanica* (Treub, 1885) Laverigne, 1901  
 = *M. javanica javanica* (Treub, 1885) Chitwood, 1949  
*M. jinanensis* Zhang & Su, 1986  
*M. kikuyensis* De Grisse, 1961  
*M. kirjanovae* Terenteva, 1965  
*M. kralli* Jepson, 1984  
*M. litoralis* Elmiligy, 1968  
*M. lordelloi* da Ponte, 1969  
*M. lucknowica* Singh, 1969  
*M. mali* Itoh, Ohshima & Ichinoche, 1969  
*M. megadora* Whitehead, 1968  
*M. megatyla* Baldwin & Sasser, 1979  
*M. megriensis* (Pogosyan, 1971) Esser, Perry & Taylor, 1976  
 = *Hypsoperine megriensis* Pogosyan, 1971  
 = *Hypsoperine (H.) megriensis* Pogosyan, 1969  
*M. microcephala* Cliff & Hirschmann, 1984  
*M. microtyla* Mulvey, Townshend & Potter, 1975  
*M. naasi* Franklin, 1965  
*M. nataliae* Golden, Rose & Bird, 1981  
*M. oryzae* Maas, Sanders & Dede, 1978  
*M. oteifae* Elmiligy, 1968  
*M. ottersoni* (Thorne, 1969) Franklin, 1971  
 = *Hypsoperine ottersoni* Thorne, 1969  
 = *Hypsoperine (H.) ottersoni* Thorne, 1969  
*M. ovalis* Riffle, 1963  
*M. partityla* Kleynhans, 1986  
*M. pini* Eisenback, Yang & Hartman, 1985  
*M. platani* Hirschmann, 1982  
*M. poghossianae* Kir'yanova, 1963  
 = *M. acronea apud* Poghossian, 1961  
*M. propora* Spaul, 1977  
 = *Hypsoperine (H.) propora* (Spaul, 1977) Siddiqi, 1986  
*M. querciana* Golden, 1979  
*M. salasi* Lopez, 1984  
*M. sewelli* Mulvey & Anderson, 1980  
*M. sinensis* Zhang, 1983  
*M. spartinae* (Rau & Fassuliotis, 1965) Whitehead, 1968  
 = *Hypsoperine spartinae* Rau & Fassuliotis, 1965  
 = *Hypsoperine (Spartonema) spartinae* Rau & Fassuliotis, 1965  
*M. subarctica* Bernard, 1981  
*M. suginamiensis* Toida & Yaegashi, 1984  
*M. tadshikistanica* Kir'yanova & Ivanova, 1965

- M. thamesi* Chitwood in Chitwood, Specht & Havis, 1952  
 = *M. arenaria thamesi* Chitwood in Chitwood, Specht & Havis, 1952  
*M. turkestanica* Shagalina, Ivanova & Krall', 1985  
*M. wartellei* Golden & Birchfield, 1978  
 = *M. incognita wartellei* Golden & Birchfield, 1978

## SPECIES INQUIRENDAE

- Meloidogyne marioni* (Cornu, 1879) Chitwood & Oteifa, 1952  
 = *Anguillula marioni* Cornu, 1879  
 = *Heterodera marioni* (Cornu, 1879) Marciniowski, 1909  
 = *Meloidogyne goeldi* Lordello, 1951 *nom. nov.*  
*M. vialae* (Laverigne, 1901) Chitwood & Oteifa, 1952  
 = *Anguillula vialae* Laverigne, 1901  
 = *Heterodera vialae* (Laverigne, 1901) Marciniowski, 1909

## COMMENTS

*Caconema* is a junior objective synonym of *Meloidogyne*.

*Hypsoperine* was proposed by Sledge and Golden (1964) to contain two species, *M. acronea* Coetzee, 1956 and *H. graminis* Sledge & Golden, 1964, which were said to differ from *Meloidogyne s. str.* by the thicker cuticle of the female and mainly the perineal area "situated on a slight protusion". Whitehead (1968) estimated that these two characters were not sufficient to justify a genus. Other characters fit *Meloidogyne*, namely the finger-print like perineal pattern and the incitement of root galling by some. Whitehead's opinion has been generally accepted and *Hypsoperine* species described later have been transferred to *Meloidogyne* by various authors. Nevertheless Siddiqi (1986) resurrected *Hypsoperine* with two subgenera: (*Hypsoperine*) and (*Spartonema*). Siddiqi mentioned, beside the posterior protusion of the female, that the excretory pore is situated posterior to hemizonid in second-stage juveniles of *Hypsoperine* vs anterior in *Meloidogyne*. Siddiqi (1986) separated the two sub-genera by several characters: in (*Hypsoperine*) the female cuticle is thick, eggs are laid in a gelatinous matrix, and the male has a conoid-rounded cephalic region, and second stage juvenile lateral field is four-lined; whereas in (*Spartonema*), represented only by *H. (S.) spartinae*, the female cuticle is thin, eggs are deposited individually, without a gelatinous matrix and the male cephalic region is conoid and the second-stage juvenile lateral field is three-lined. We do not accept that these characters justify different genera, or subgenera. Triantaphyllou (1973) transferred *H. graminis* and *H. ottersoni* to *Meloidogyne* because of their chromosome number (18) and their reproduction by facultative, meiotic parthenogenesis. This left *H. spartinae* to re-

present the genus; however in 1987 Triantaphyllou decided on the basis of anatomy of the oviduct-spermatheca region and most cytogenetic features that *H. spartinae* can be regarded as a *Meloidogyne*. He further stated that the small chromosome number (7) suggests that cytologically *H. spartinae* stands closer to the ancestral form of *Meloidogyne*. The lack of significant morphological, biological or cytological differences dictates that the synonymy of *Hypsooperine* with *Meloidogyne* be upheld.

Concerning *Meloidoderella*, Siddiqi (1986) very convincingly argued that this genus probably was described from a mixed population of *Meloidogyne* and *Globodera*. This would explain the mixture of characteristics it was said to exhibit by its original authors. Despite repeated enquiries, no material could be obtained for study. So we agree with Siddiqi (1986) that *Meloidoderella* should be regarded as a *dubium* and *M. indica* as a *nomen dubium*\*. In such a nomenclatural position, *Meloidoderella* cannot be considered a junior synonym of *Meloidogyne*, as proposed by Siddiqi (1986).

The subfamily NACOBODERINAE  
Golden & Jensen, 1974

= Meloinematinae (Meloineminae) Husain, 1976

### Diagnosis

Heteroderidae. Cuticle not abnormally thick, annulated in all stages of males and females. Cephalic framework strongly sclerotized. Stylet robust. *Female*. Pre-adult female vermiform, free in the substrate, with two opposed immature genital branches, and a short tail. Mature female sedentary, spheroid/pear-shaped, with very long neck and swollen body exposed. Labial area set-off, with irregular annulation (plates) and a reduced non-offset labial disc. Vulva subterminal, well removed from anus; no finger-like print pattern around vulva. Phasmids conspicuous. Remnants of tail present. No cyst stage. Eggs not retained in female body but deposited in a gelatinous matrix. *Male*. Labial area high, annulated set-off. Lateral field with four or five lines. Tail conoid-rounded, without caudal alae (exception: *Bursadera*). Males developing within second-stage cuticle. *Juveniles*. Cephalic sclerotization and stylet robust. Lateral field with four lines.

*Biology*: Sedentary, causing galls on roots.

### Type genus:

*Nacobbodera* Golden & Jensen, 1974

\* The subfamily Meloidoderellinae Husain, 1976 and the tribe Meloidoderellini Coomans, 1979 are rejected for evident reasons.

### Other genera

*Meloinema* Choi & Geraert, 1974  
*Bursadera* Ivanova & Krall', 1985

### Comments on Nacobboderinae

Golden and Jensen (1974), when proposing the genus *Nacobbodera*, placed it in the family Nacobbidae (Chitwood & Chitwood, 1950) Golden, 1971 and in the subfamily Nacobboderinae Golden & Jensen, 1974. Siddiqi (1986) moved the subfamily Nacobboderinae to the family Meloidogynidae. At this time he synonymized *Nacobbodera* with *Meloinema* Choi & Geraert, 1974.

In this paper we recognize Nacobboderinae as a subfamily in Heteroderidae containing the three genera *Nacobbodera*, *Meloinema*, and *Bursadera*. These three genera have characters common to both Hoplolaimidae and Heteroderidae. On the hoplolaimid side there is the mobile non-reproducing female with the vulva far removed from the anus and a bluntly rounded tail. In *Nacobbodera* and *Meloinema* the male body is twisted as in heteroderids (the description of *Bursadera* does not address this point). The male tail is more hoplolaimid in that it is conoid, ventrally flattened, near bursate to bursate. On the heteroderid side, *Nacobbodera* and *Meloinema* females have the excretory pore located at the metacarpus or anterior to it, whereas *Bursadera* is more hoplolaimid-like in having the excretory pore located posterior to the metacarpus.

It is our policy, that when a genus or subfamily is intermediate between two families, to place the genus or subfamily as ancestral in the more derived family. For this reason Nacobboderinae is placed in Heteroderidae.

### The genera in Nacobboderinae

*Meloinema* Choi & Geraert, 1974

#### DIAGNOSIS

Nacobboderinae. Oesophageal glands in vermiform young female, male and second stage juveniles very long (50-60 % of body length). Excretory pore on female anteriorly situated, half a stylet length behind basal knobs; on male excretory pore at level of metacarpus. Male without caudal alae.

#### TYPE AND ONLY SPECIES

*M. kerongense* Choi & Jensen, 1974

*Nacobbodera* Golden & Jensen, 1974

#### DIAGNOSIS

Nacobboderinae. Oesophageal glands in all stages and



adults overlapping intestine a short distance only. Excretory pore on second stage juvenile and female situated at anterior level of metacarpus; on male excretory pore situated posterior to isthmus. Male without caudal alae.

## TYPE AND ONLY SPECIES

*N. chitwoodi* Golden & Jensen, 1974  
= *Meloinema chitwoodi* (Golden & Jensen, 1974)  
Stone, 1978

*Bursadera* Ivanova & Krall', 1985

## DIAGNOSIS

Nacobboderinae. Oesophageal glands in all stages and adults overlapping intestine a short distance only. Excretory pore in all stages and adults at level of posterior end of metacarpus or posterior to the metacarpus. Male tail bluntly rounded, with well developed caudal alae.

## TYPE AND ONLY SPECIES

*B. longicollum*\* Ivanova & Krall', 1985

## Comments on genera of Nacobboderinae

We have removed *Nacobbodera* from synonymy with *Meloinema* because of the differences between the position of the excretory pore in female and the length of the overlapping oesophageal glands. In both immature and mature females, the excretory pore is located at level of anterior part of metacarpus in *Nacobbodera*, whereas far anterior (half stylet length from stylet base) in *Meloinema*, thus similar to *Meloidogyne*. Also of significance are the overlapping oesophageal glands: in *Nacobbodera*, as well as in *Bursadera*, the extent of the overlap is not unusual, whereas, in *Meloinema* the overlap extends to 50% or more of the body length in the juveniles as well as the vermiform female.

*Bursadera* is distinguished among Nacobboderinae by the presence of the well-developed caudal alae in the male. It is differentiated from *Meloinema* by the length of the oesophageal overlap, i.e., not unusual *vs* extremely long. Two other characteristics may further separate *Bursadera* when confirmed. According to the illustrations the vermiform females have only one ovary; however, this feature is not mentioned in the text. The authors further fail to comment on whether or not the male body has the typical heteroderid twist.

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\* The species name, modified into *longicolla* by Siddiqi (1986), is reestablished here as *longicollum* : *collum*, i, n. (= neck) being a substantive in apposition.

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Accepté pour publication le 25 septembre 1987.