Taxonomy of the plant nematode superfamily Hemicycliophoroidea, with a proposal for Criconematina, new suborder

Mohammad Rafiq Siddiqi

Commonwealth Institute of Helminthology,
103, St Peter's Street, St. Albans, Herts., England.

Summary

Hemicycliophoroidea n. grad. contains Hemicycliophoridae and Caloosiidae n. fam. Caloosiidae n. fam. and Caloosiinae n. subfam. are proposed for the genera *Caloosia* and *Hemicaloosia*. *Caloosia, Hemicaloosia, Hemicycliophora* and *Colbranium* have been re-diagnosed. *Aulosphora* n. gen. and *Loofia* n. gen. are proposed for species formerly under *Hemicycliophora*, largely on the basis of the shape of the vulval and cloacal lips and of the spicules. New combinations proposed are : *Aulosphora penetrans* (Thorne, 1955) (type species), *A. dahomensis* (Germani & Luc, 1976), *A. indica* (Siddiqi, 1961) (Syn. : *Hemicycliophora musae* Khan & Nanjappa, 1972), *A. oostenbrinki* (Luc, 1958), *A. osmani* (Das & Shivaswamy, 1977), *Loofia ferrisae* (Brzeski, 1974), *L. gigas* (Thorne, 1955), *L. robusta* (Loof, 1968), *L. thienemanni* (Schneider, 1925) (type-species), *L. uniformis* (Thorne, 1955), *L. vaccinium* (Reed & Jenkins, 1963) and *Hemicaloosia delpradi* (Maas, 1970). *Hemicycliophora corbetti* n. sp. is described from soil of tomato and Napier grass in Malawi.

A new suborder Criconematina is proposed under the order Tylenchida to accommodate the superfamilies Criconematoidea, Hemicycliophoroidea, Tylenchuloidea and Tylenchocriconematoidea. Criconematina differs from Tylenchina in the structure of the cephalic region and œsophagus in female, absence of phasmids, setaceous spicules and degenerated oesophagus in male. The origin and phylogeny of Criconematina is discussed and a key to its family groups is given.

Résumé

Taxonomie des Hemicycliophoroidea, n. superfam. et proposition du nouveau sous-ordre des Criconematina

L'auteur propose la création de la superfamille des Hemicycliophoroidea n. grad. dans laquelle il classe les Hemicycliophoridae et les Caloosiidae n. fam. ; cette dernière famille comporte une seule sous-famille, les Caloosiinae n. subfam., dans laquelle sont classés les genres *Caloosia* et *Hemicaloosia*. Les diagnoses de ces deux derniers genres, ainsi que celles d'*Hemicycliophora* et de *Colbranium* sont amendéee. Se fondant sur la forme des lèvres vulvaires et cloacales et sur celle des spicules, l'auteur propose également *Aulosphora* n. gen. et *Loofia* n. gen. pour des espèces appartenant précédemment à *Hemicycliophora*. Les nouvelles combinaisons suivantes sont proposées : *Aulosphora penetrans* (Thorne, 1955) (espèce-type), *A. dahomensis* (Germani & Luc, 1976), *A. indica* (Siddiqi, 1961) (syn. *Hemicycliophora musae* Khan & Nanjappa, 1972), *A. oostenbrinki* (Luc, 1958), *A. osmani* (Das & Shivaswamy, 1977), *Loofia ferrisae* (Brzeski, 1974), *L. gigas* (Thorne, 1955), *L. robusta* (Loof, 1968), *L. thienemanni* (Schneider, 1925) (espèce-type), *L. uniformis* (Thorne, 1955), *L. vaccinium* (Reed & Jenkins, 1963) et *Hemicaloosia delpradi* (Maas, 1970). *Hemicycliophora corbetti* n. sp. provenant de la rhizosphère de *Pennisetum purpureum* et de tomate au Malawi est décrit.

Dans l'ordre des Tylenchida l'auteur propose la création des Criconematina n. subord. dans lequel il classe les superfamilles Criconematoidea, Hemicycliophoroidea, Tylenchuloidea et Tylenchocriconematoidea. Le sous-ordre des Criconematina se différencie de celui des Tylenchina par la structure de la région céphalique et de l'œsophage, l'absence de phasmides, la présence de spicules sétacés et l'atrophie de l'œsophage chez le mâle. L'auteur discute l'origine et la phylogénie des Criconematina et présente une clef des diverses familles.

The subfamily Hemicycliophorinae Skarbilovich, 1959 was considered under the family Criconematidae Taylor, 1936 (Thorne, 1949) * until 1966 when Geraert elevated it to the rank of a family and placed it under the superfamily Criconematoidea Taylor, 1936 (Geraert, 1966). The status of the family Hemicycliophoridae Skarbilovich, 1959 (Geraert, 1966) has been upheld by Khan, Chawla and Saha (1976), but the group is considered as a subfamily of Criconematidae by several workers (Golden, 1971 ; Brzeski, 1974 ; Andrássy, 1976, 1979 ; Hooper, 1978).

Two major reviews of this group have recently appeared. One by Brzeski (1974) on the subfamily Hemicycliophorinae and the other by Eroshenko (1976) on the family Hemicycliophoridae. Both deal with the descriptions and keys to the species of *Hemicycliophora* De Man, 1921 and *Caloosia* Siddiqi & Goodey, 1964. Brzeski (1974), for the first time, considered *Hemicriconemoides* Chitwood & Birchfield, 1957, as a member of the Hemicycliophorinae and Hooper (1978) has followed him. Khan, Chawla and Saha (1976) excluded it from the Criconematidae ** and remarked that it is more closely related to the Hemicycliophoridae than the Criconematidae. Andrássy (1979) proposed a new subfamily under Criconematidae, the Hemicriconemoidinae for this genus ; he also proposed the genus *Colbranium* to accommodate the species *Hemicycliophora truncata* Colbran, 1958.

Loof (1976) discussed in detail the morphological differences between the genera *Hemicycliophora* and *Caloosia*. He found that the male tail of *Hemicycliophora typica* was, in fact, the postgenital part of the body and not the postanal part ; a cloaca and male anus being absent in this species. This accordingly accounted for the longer « tail » of the male than the tail of the female. However, a study of the paratype males of *Hemicycliophora penetrans* Thorne, 1955, in various stages of development showed that this is not correct.

A cloaca is formed in this species as in other nematodes and the elongation of the tail takes place after the male emerges from the final juvenile cuticle (see Fig. 1). Loof's (1976) finding, therefore, needs confirmation.

A new genus, *Hemicaloosia*, has been proposed by Ray and Das (1978) for those species of *Caloosia* which have a cuticular body sheath. I propose here Caloosiinae n. subfam. and Caloosiidae n. fam. for the genera *Caloosia* and *Hemicaloosia*, and discuss their relationship with the Hemicycliophoridae. *Aulosphora* n. gen. and *Loofia* n. gen. are proposed under Hemicycliophorinae and the families Hemicycliophoridae and Caloosiidae are assigned to the superfamily Hemicycliophoroidea Skarbilovich, 1959 (n. grad.).

Superfamily Hemicycliophoroidea Skarbilovich, 1959 (n. grad.)

(Fig. 2)

DIAGNOSIS

Criconematina n. subord. : Tylenchida. Moderate to large (female : 0.6-1.9 mm), vermiform, straight to arcuate upon relaxation. Marked sexual dimorphism in which male lacks a stylet and has a degenerate oesophagus. Juveniles and adults with round, coarse, non-retrorse annules, usually numbering over 200. Lateral fields present except in juveniles and females of *Caloosia* and adult females of some genera. Juveniles and females with an extra cuticular sheath enclosing the body, except in *Caloosia* (presence of a four-layered sheath in males of *Hemicycliophora arenaria* has been demonstrated by SEM study by Johnson, Van Gundy and Thomson, 1970). Cephalic region with 1-3 annules (front annule may further be subdivided) ; cephalic framework sclerotized. Oral opening a dorsoventral slit on a labial disc. Amphid apertures close to labial disc. Submedian lobes absent.

* To comply with the Articles 23 (c) and 36 of the *International Code of Zoological Nomenclature* and to incorporate a citation of the authority and the year of the change in the rank of family group names as practised in Nematology and other branches of Zoology, I am adopting this mode of citation in which the family group name is cited exactly as is required by the Articles, followed by the authority and year of the first elevation or reduction of the rank within brackets.

** Andrássy (1979) has pointed out the existence of a senior synonym, Ogmidae Southern, 1914. According ot Article 23 (b) of the I.C.Z.N., Ogmidae should not be used as it is a *nomen oblitum*.

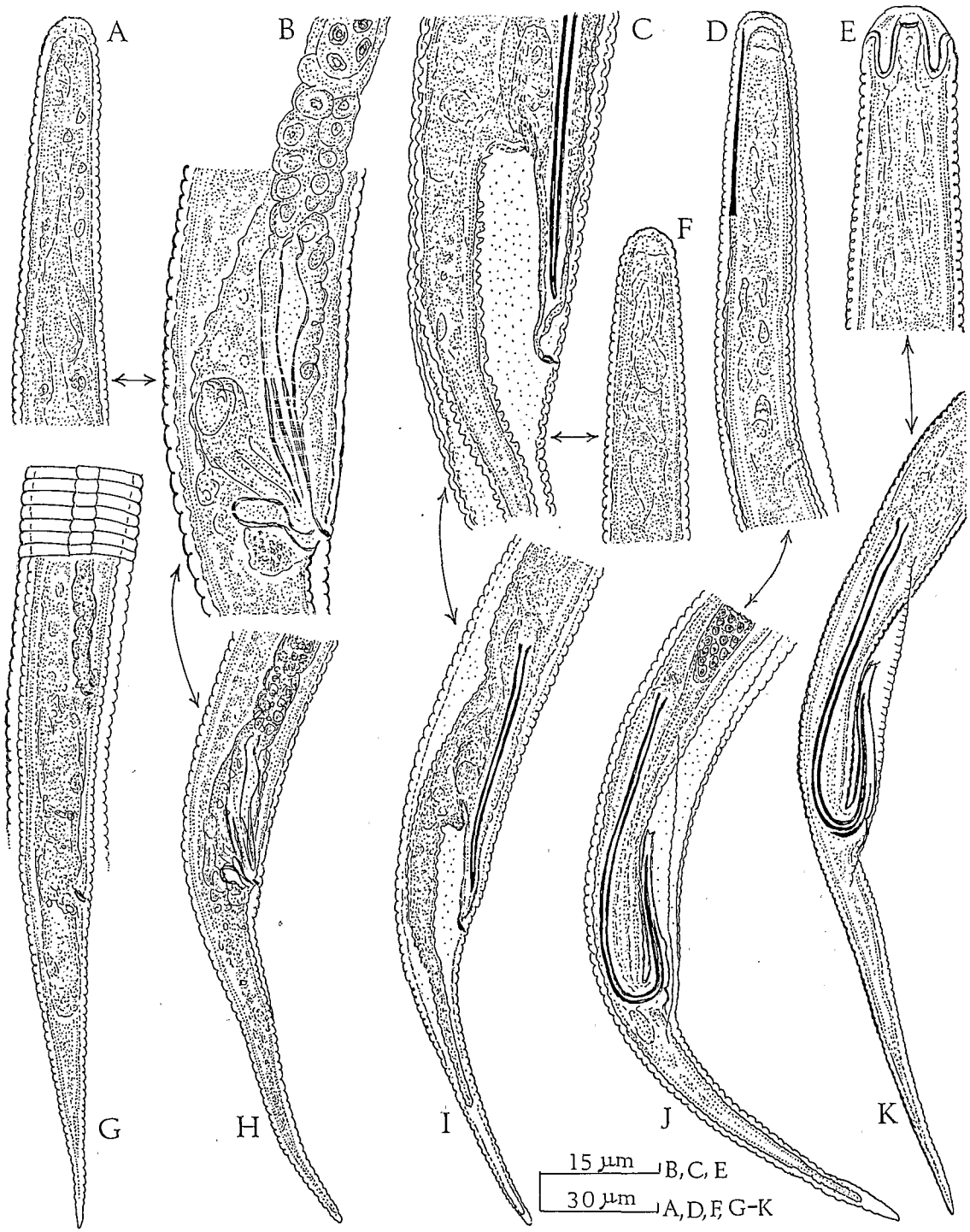

Fig. 1. *Aulosphora penetrans* (Thorne), paratypes. Development of male. (G. IV-stage juvenile is for comparison). A, B & H : A non-stylet bearing IV-stage male juvenile ; note gonoduct and spicule anlage, connecting to rectum. C, F & I : A metamorphosing male still within juvenile cuticle ; note the developing spicule and penial tube attached to the rectum. D & J : Developing male within last two juvenile cuticles ; note in Fig. D the conus of stylet, possibly of III-stage. E & K : Adult male ; note the tail has become alongated once the male is out of the juvenile cuticle (s) (cf. also tail of IV-stage female juvenile in Fig. G.).

Deirids and phasmids absent. Stylet in juveniles (fourth-stage juveniles of some species lack stylet) and females elongated (over 50 µm long in females) ; conus much longer than the shaft ; basal knobs rounded posteriorly sloping. Oesophagus in juveniles (some pre-adult juveniles have degenerate oesophagus) and females with broad precorpus enlarging gradually into a large muscular postcorpus, followed by a short broad isthmus amalgamated posteriorly with a small basal bulb containing the three oesophageal glands. Intestine syncytial, with few widely scattered nuclei ; anteriorly often extending over dorsal side of basal oesophageal bulb and posteriorly into tail cavity ; its lumen and junction with rectum indistinct. Rectum short ; anus pore-like. Vulva transversely oval or slit-like, usually with modified lips, located in posterior region of body, occasionally subterminal. Monodelphic, prodelphic ; no post-vulval uterine sac ; spermatheca offset, ventral or lateral to gonad axis. Tail usually elongated and pointed ; rounded, cylindrical or hemispherical in some species of Hemicycliophorinae. Male tail elongated, tapering, with conspicuous bursa rarely extending beyond its middle. Spicules setaceous and long, weakly cephalated, straight, arcuate, semicircular, U- or hook-shaped. Gubernaculum fixed Cloacal lips forming a penial tube in several genera. Single papilla- or seta-like hypoptygma situated just posterior to claocal aperture.

NOMINATE FAMILY

Hemicycliophoridae Skarbilovich, 1959 (Geraert, 1966).

OTHER FAMILY

Caloosiidae n. fam.

RELATIONSHIP AND DISCUSSION

In having a short and broad isthmus which is amalgamated with the basal bulb Hemicycliophoroidea comes close to Criconematoidea Taylor, 1936 (Geraert, 1966). Members of the Criconematoidea have males with shorter tail and inconspicuous bursa and juveniles and females with shorter, plumper, usually sausage-shaped body, anchor-shaped stylet knobs, body annules fewer in number and usually with cuticular outgrowths, and no sheath (except females of *Bakernema* and *Hemicriconemoides* which have a sheath and round body annules ; these genera are easily differentiated from those of the Hemicycliophoroidea by their smaller body-size in juveniles and adults, sausage-shaped juveniles with spined, retrorse annules and anchor-shaped stylet knobs and by the characters of the male which has a shorter tail and inconspicuous bursa). The round annules and a cuticular body sheath, found among Criconematoidea only in females of *Bakernema* and *Hemicriconemoides*, are adaptive modifications showing only pseudoresemblances to those of the Hemicycliophoroidea because in their juveniles the annules are retrorse and sheath is absent. Here we have an instance of convergence in evolution and not of homology pointing towards a common ancestor.

The round, non-retrorse annules of juveniles and posteriorly sloping stylet knobs relate Hemicycliophoroidea to Tylenchuloidea and Tylenchocriconematoidea. However, the larger body-size, thicker cuticle bearing coarser annules, the shape of the isthmus and a large bursa clearly differentiate it from these superfamilies. The large, vermiform body in juveniles and females, thick cuticle and coarse round annules, posteriorly sloping stylet knobs, elongate tails of juveniles, males and most females and the conspicuous bursa show that the Hemicycliophoroidea represent a different line of development from either that of the Criconematoidea or that of the Tylenchuloidea and Tylenchocriconematoidea. Hemicycliophoroidea n. rank is, therefore, justified.

Family Hemicycliophoridae
Skarbilovich, 1959 (Geraert, 1966)

DIAGNOSIS (amended)

Hemicycliophoroidea. Female and juveniles with two cuticles, the outer one serving as a body sheath which is not membranous. Cephalic annules of female not modified or separated (except in *Hemicycliophora hesperis*). Vulva a transverse slit over half a body-width long and marked by a discontinuity in ventral body con-

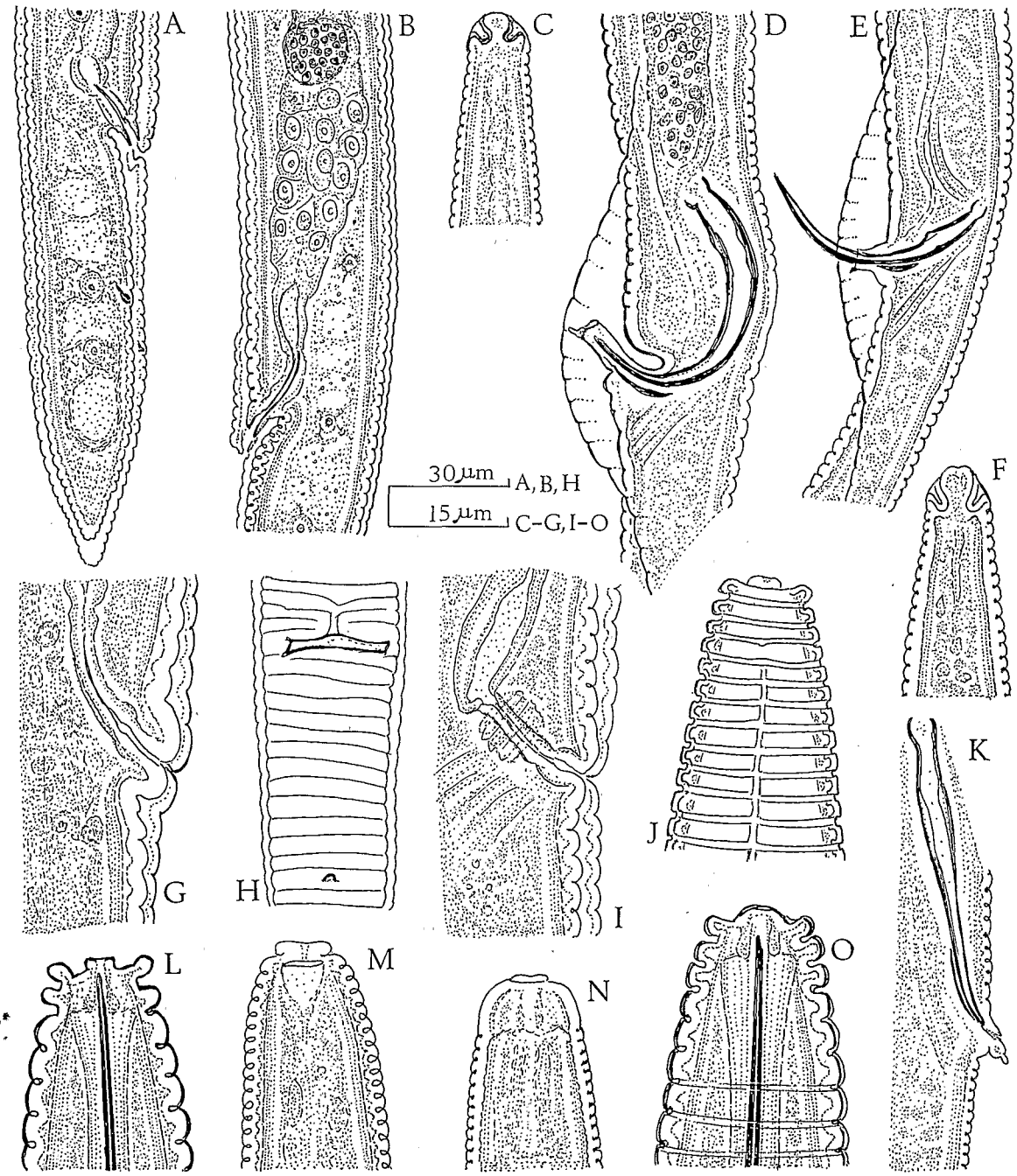

Fig. 2. Organization of Hemicycliophoroidea. A : Posterior end of *Hemicycliophora epicharoides*, paratypes. B-D. *Hemicycliophora typica* from Holland ; B : Vulval region, C : Male head end, D : Spicule region. E, F, and I. *Loofia thienemanni* from Holland; E : Spicule region, F : Male head end, I : Vulval region. G & H : *Loofia robusta*, paratypes, Vulva regions in lateral and ventral view, respectively. J : Female head end of *Hemicaloosia delpradi*, paratype. K-M : *Caloosia paralongicaudata* from Dacca, Bangladesh ; K : Spicule region; L : Female head end; M : Male head end. N : Male head end of *Hemicaloosia paradoxa*, paratype. O : Female head end of *Hemicaloosia nudata*, paratype.

tour (except in *Loofia)* ; vulva lips modified and projecting (except in *Loofia*). Vagina straight or curved but not sigmoid. Male cephalic region marked by a discontinuity in body annulation, usually offset ; frame-work in lateral view appearing as "spectacle mark". Spicules arcuate, semi-circular, U- or hook-shaped. Lips of male gonopore elongated to form a penial tube bearing a single, setose hypoptygma ventrally at its tip. Bursa covering less than one-third of the tail. Male tail longer than that of female which usually is elongate-conoid but may be filiform, cylindroid or rarely hemispherical. Fourth-stage male juvenile without stylet.

NOMINATE SUBFAMILY

Hemicycliophorinae Skarbilovich, 1959 ; with the characters of the family.

NO OTHER SUBFAMILY.

TYPE-GENUS

Hemicycliophora De Man, 1921 ;
= *Procriconema* Micoletzky, 1925.

OTHER GENERA

Aulosphora n. gen.
Colbranium Andrássy, 1979
Loofia, n. gen.

RELATIONSHIP

See under Caloosiidae n. fam.

KEY TO GENERA OF HEMICYCLIOPHORINAE

1. Vulva lips round, low, not modified ; body just behind vulva not recessed ; spicules arcuate 2
   Vulva lips modified, pointed and elongated ; body just behind vulva recessed ; spicules semi-circular, U- or hook-shaped 3
2. Female cephalic region set off by a deep groove ; vulva and anus subterminal ; bursa reaching almost to terminus ... *Colbranium*
   Female cephalic region not set off ; vulva and anus not subterminal ; bursa short, not reaching to terminus ..... *Loofia* n. gen.
3. Vulva lips less than three body annules long ; usually divergent ; spicules semi-circular ; pre- and post-anal stretches of bursa in the ratio of 1 : 1 ..... *Hemicycliophora*
   Vulva lips longer than three body annules, almost parallel ; spicules U- or hook-shaped ; pre- and post-anal stretches of bursa in the ratio of 3-4 : 1 ..... *Aulosphora* n. gen.

Family Caloosiidae n. fam.

DIAGNOSIS

Hemicycliophoroidea. Females and juveniles with or without a body sheath ; if present, sheath membranous, much thinner than the body cuticle and closely adpressed to it. Lateral fields absent in non-sheathed females and juveniles but rarely absent in sheathed females. Cephalic annules of females and juveniles separated, usually modified. Vulva transversely oval, less than half body-width long, depressed and flush with body contour ; no discontinuity of body contour near vulva ; anterior lip of vulva modified, partly overhanging vulva, posterior lip not modified or elevated. Vagina sigmoid. Tails elongate-filiform ; male tail shorter than that of female. Male cephalic region continuous, lacking lateral "spectacle mark". Spicules straight. Lips of cloacal aperture not elongated to form a penial tube, with a single projecting hypoptygma ventrally. Bursa usually covering more than one-third of the tail. Fourth-stage male juvenile with stylet.

NOMINATE SUBFAMILY

Caloosiinae n. subfam. ; with characters of the family.

NO OTHER SUBFAMILY

TYPE-GENUS

Caloosia Siddiqi & Goodey, 1964.

OTHER GENUS

Hemicaloosia Ray & Das, 1978.

RELATIONSHIP AND DISCUSSION

Caloosiidae n. fam. differs from Hemicycliophoridae in the characters of the separated cephalic annules in females and juveniles ; body sheath, if present, being membranous and closely adpressed to the body ; a shorter oval vulva, overhung by its anterior lip and being flush with body contour ; sigmoid vagina ; female tail longer than male tail ; male cephalic region lacking "spectacle mark" ; straight spicules and bursa usually covering more than a third of tail length.

The presence of a cuticular body sheath in *Hemicaloosia* of the Caloosiidae indicates its affinity with Hemicycliophoridae. However, a closer examination shows that the sheath is membranous, much thinner than the body cuticle and sometimes (e.g. *Hemicaloosia nudata*) even difficult to see. It appears that in this genus it is the outermost layer(s) of the cuticle and not the duplication of the whole cuticle, that has given rise to a sheath.

Re-Diagnoses of certain genera of Hemicycliophoroidea

The genera *Caloosia*, *Hemicaloosia*, *Hemicycliophora* and *Colbranium* are re-diagnosed below on the basis of the present study.

Genus **Caloosia** Siddiqi & Goodey, 1964

DIAGNOSIS (amended)

Caloosiidae. Body cuticle thick, strongly annulated and folded between annules. Cuticular body sheath absent. No lateral fields in juveniles and females. Male cephalic region not marked by an interruption of the body annulation.

TYPE-SPECIES

Caloosia longicaudata (Loos, 1948) Siddiqi & Goodey, 1964.
= *Hemicycliophora longicaudata* Loos, 1948.

OTHER SPECIES

Caloosia brevicaudata Khan, Chawla & Saha, 1979.
C. exilis Mathur, Khan, Nand & Prasad, 1969.
C. heterocephala Rao & Mohandas, 1976.
C. paralongicaudata Siddiqi & Goodey, 1964.
C. parlona Khan, Chawla & Saha, 1979.
C. paxi Mathur, Khan, Nand & Prasad, 1969.

Genus **Hemicaloosia** Ray & Das, 1978

DIAGNOSIS (amended) Caloosiidae. Females and juveniles covered by a thin membranous cuticular sheath which is thinner than the body cuticle and closely adpressed to the body ; annules usually separated ; cuticle usually not folded between annules. Lateral fields marked by two incisures usually present on female sheath. Male cephalic region marked by an interruption of the body annulation.

TYPE-SPECIES

Hemicaloosia americana Ray & Das, 1978.

OTHER SPECIES

Hemicaloosia delpradi (Maas, 1970) n. comb.
= *Caloosia delpradi* Maas, 1970
H. nudata (Colbran, 1963) Ray & Das, 1978
= *Hemicycliophora nudata* Colbran, 1963
= *Caloosia nudata* (Colbran, 1963) Brzeski, 1974
H. paradoxa (Luc, 1958) Ray & Das, 1978
= *Hemicycliophora paradoxa* Luc, 1958
= *Caloosia paradoxa* (Luc, 1958) Brzeski, 1974

RELATIONSHIP AND DISCUSSION : The above diagnoses of *Caloosia* and *Hemicaloosia* differentiate these genera from each other. An examination of some female paratypes of *Caloosia delpradi* Maas, 1970 made available by P.A.A. Loof, showed the presence of a body sheath bearing lateral fields marked by two closely spaced incisures (Fig. 2, J). This species, therefore, is transferred to the genus *Hemicaloosia*. The females of *Hemicycliophora nudata* are said to possess a cuticular sheath in the tail region only (Colbran, 1963 ; Brzeski, 1974), but an examination of seven females of this species sent by R.C. Colbran shows an extremely thin sheath over the entire body, though at times difficult to see (Fig. 2, O). The juveniles of this species possess a sheath too (Colbran, 1963). The transfer of this species to *Hemicaloosia* by Ray and Das (1978) is justified.

Genus **Hemicycliophora** De Man, 1921

Syn. *Procriconema* Micoletzky, 1925

DIAGNOSIS (amended)

Body just behind vulva deeply recessed. Vulva lips modified, elongated but less than three annules long, usually divergent. Female tail elongate tapering, filiform, cylindrical or rarely hemispherical. Spicules semi-circular. Penial tube well developed but less than body width long, directed outward and forward ; body just in front of penial tube deeply recessed. Pre- and post-anal stretches of bursa almost equal.

TYPE-SPECIES

Hemicycliophora typica De Man, 1921.
= *Procriconema membranifer* Micoletzky. 1925
= *Hemicycliophora membranifer* (Micoletzky, 1925) Loos, 1948

OTHER SPECIES

Hemicycliophora aberrans Thorne, 1955
H. andrassyi Brzeski, 1974
H. aquatica (Micoletzky, 1913) Loos, 1948
= *Tylencholaimus aquaticum* Micoletzky, 1913
H. arcuata Thorne, 1955
H. arenaria Raski, 1958
H. argiensis Khan & Nanjappa, 1972
H. belemnis Germani & Luc, 1973
H. biloculata Colbran, 1969
H. brevicauda Sauer, 1958
H. brevis Thorne, 1955
H. californica Brzeski, 1974
H. chathami Yeates, 1978
(With two subspecies : *H. chathami chathami* Yeates, 1978 and *H. chathami major* Yeates, 1978
H. chilensis Brzeski, 1974
= *H. thienemanni apud* Andrássy, 1967
H. conida Thorne, 1955
H. corbetti n. sp.
H. dhirendri Husain & Khan, 1967
H. diolaensis Germani & Luc, 1973
H. epicharis Raski, 1958
H. epicharoides Loof, 1968
H. eugeniae Khan & Basir, 1963
H. floridensis (Chitwood & Birchfield, 1957) Goodey, 1963
= *Hemicriconemoides floridensis* Chitwood & Birchfield, 1957
= *Hemicriconemoides biformis* Chitwood & Birchfield, 1957
= *Hemicycliophora biformis* (Chitwood & Birchfield, 1957) Goodey, 1963
H. gracilis Thorne, 1955
H. halophila Yeates, 1967
H. hesperis Raski, 1958
H. iwia Brzeski, 1974
H. juglandis Choi & Geraert, 1975
H. koreana Choi & Geraert, 1971
H. labiata Colbran, 1960
H. loofi Maas, 1970
H. lutosa Loof & Heyns, 1969
H. macristhmus Loof, 1968
H. madagascariensis Germani & Luc, 1973
H. mangiferum Misra & Edward, 1971
H. mettleri Jenkins & Reed, 1964
H. micoletzkyi Goffart, 1951
H. minora Wu, 1966
H. nana Thorne, 1955
H. natalensis Loof & Heyns, 1969
H. nigeriensis Germani & Luc, 1973
H. nortoni Brzeski, 1974
H. nucleata Loof, 1968
H. nyanzae Schoemaker, 1968
H. obesa Thorne, 1955
H. obtusa Thorne, 1955
H. ovata Colbran, 1962
H. parvana Tarjan, 1952
H. pauciannulata Luc, 1958
H. poranga Monteiro & Lordello, 1978
H. pruni Kirjanova & Shagalina, 1974
H. raskii Brzeski, 1974
H. ritteri Brizuela, 1963
H. rotundicauda Thorne, 1955
H. salicis Sofrygina, 1972
H. saueri Brzeski, 1974
H. shepherdi Wu, 1966
H. sheri Brzeski, 1974
H. signata Orton Williams, 1978
H. similis Thorne, 1955
H. spinosa Colbran, 1969
H. stralurata Germani & Luc, 1973
H. striatula Thorne, 1955
H. subaolica Jairajpuri & Baqri, 1973
H. tarjani Khan & Basir, 1963
H. tenuis Thorne, 1955

H. tesselata Sauer, 1958
(*H. tesselata* Boonduang & Ratanaprapa, 1974 is a homonym, but it may belong to *Hemicaloosia*)
H. thornei Goodey, 1963
= *H. typica apud* Thorne, 1955
H. transvaalensis Heyns, 1962
H. triangulum Loof, 1968
H. vidua Raski, 1958
= *H. silvestris* Jenkins & Reed, 1964
= *H. vivida* Wu, 1966
H. vitiensis Orton Williams, 1978
H. zuckermani Brzeski, 1963

DISCUSSION

Hemicycliophora as diagnosed here comprises the majority of the species in the subfamily. It appears to be a heterogenous group and further collecting may reveal several generic groups. One of such groups could be the round tailed forms. The species *H. hesperis* having a set off cephalic region with somewhat separated annules and *H. brevicauda* with almost subterminal vulva may represent further groups if more similar species are found.

Genus **Colbranium** Andrássy, 1979

DIAGNOSIS (amended)

Vulva and anus subterminal in a ventral depression of the body. Vulva lips rounded, low, not modified ; body just behind vulva not recessed. Female tail short, rounded ; male tail elongate-tapering. Spicules ventrally arcuate but not semi-circular. Penial tube well developed but less than a body-width long, directed outward and forward. Bursa reaching almost to terminus. Cephalic region set off by a deep groove.

TYPES-PECIES

Colbranium truncatum (Colbran, 1956) Andrássy, 1979
= *Hemicycliophora truncata* Colbran, 1956

DISCUSSION

The above diagnosis of *Colbranium* is based on my study of the specimens of *C. truncatum* supplied by R. C. Colbran. The female cephalic region comprises two rather amalgamated annules of which the basal one is much narrower and larger than the other.

New genera

If one considers the modifications of the vulval lips, spicules, penial tube and bursa in the nominal species of the genus *Hemicycliophora*, four distinct groups are seen : *Hemicyliophora*, sensu stricto ; *Aulosphora* n. gen., *Loofia* n. gen. and *Colbranium*. The two new genera are described below. The basis on which they are erected are good generic characters which are stable and easily recognizable. The elongation of the vulval lips in *Aulosphora* could be considered a functional adaptation to cope with the elongation of the spicules and penial tube in this genus. However, this modification is not dependent upon function alone because a monosexual species, *A. indica* (Siddiqi, 1961) collected from different topographical regions in Northern India has elongated vulval lips.

Aulosphora n. gen.

DIAGNOSIS

Hemicycliophorinae. Body just behind vulva slightly recessed. Vulva lips elongated, over three body annules long, almost parallel and directed backward. Tail elongate-tapering. Spicules often very long (about 100 µm or more), U- or hook-shaped. Penial tube over a body-width long, directed forward and often touching ventral body surface. Body just in front of penial tube not deeply recessed. Bursa mostly pre-anal with pre- and post-anal stretches in the ratio of 3-4 : 1.

TYPE-SPECIES

Aulosphora penetrans (Thorne, 1955) n. comb.
= *Hemicycliophora penetrans* Thorne, 1955

OTHER SPECIES

Aulosphora dahomensis (Germani & Luc, 1976) n. comb.
= *Hemicycliophora dahomensis* Germani & Luc, 1976
A. indica (Siddiqi, 1961) n. comb.
= *H. indica* Siddiqi, 1961
= *H. musae* Khan & Nanjappa, 1972

A. oostenbrinki (Luc, 1958) n. comb.
= *H. oostenbrinki* Luc, 1958

A. osmani (Das & Shivaswamy, 1977) n. comb.
= *H. osmani* Das & Shivaswamy, 1977

RELATIONSHIP

See key to the genera of Hemicycliophorinae.

The name *Aulosphora* is derived from Greek, *aulos* = tube and *phoros* = bearer, and refers to the tubular shape of the vulval lips in lateral view and also to the elongated penial tube of the male.

KEY TO SPECIES OF *Aulosphora* N. GEN.

1. Sheath annules bearing longitudinal striae 2
   Sheath annules not bearing longitudinal striae 5
2. Female and juveniles with hemispherical cephalic region ; spermatheca with sperm ; males present 3
   Female and juveniles with tapering cephalic region ; spermatheca without sperm ; males absent ..... *A. indica*
3. Vulva lips 5-6 body annules long ; spicules 123-125 µm long ..... *A. penetrans*
   Vulva lips less than 5 annules long 4
4. Spicules 98-108 µm long .....*A brzeskii*
   Spicules 38-64 µm long .....*A. oostenbrinki*
5. Female body annules 250-266 in number ; stylet 130-134 µm long ; spicules 160-163 µm long ..... *A. osmani*
   Female body annules 334-365 in number ; stylet 83-95 µm long ; spicules 95 µm long ..... *A. dahomensis*

Loofia n. gen.

DIAGNOSIS

Body just behind vulva not recessed. Vulva lips rounded, low, not modified. Tail elongated, tapering, or anteriorly cylindrical. Spicules arcuate but not semi-circular or hook-shaped. Penial tube short (less than three body annules long), directed outward and forward. Body just in front of penial tube not recessed. Pre- and post-anal stretches of bursa in the ratio of 1 : 1-1.5.

TYPE-SPECIES

Loofia thienemanni (Schneider, 1925) n. comb.
= *Hoplolaimus thienemanni* Schneider, 1925
= *Procriconema thienemanni* (Schneider, 1925) Micoletzky, 1925
= *Hemicycliophora thienemanni* (Schneider, 1925) Loos, 1948.

OTHER SPECIES

Loofia ferrisae (Brzeski, 1974) n. comb.
= *Hemicycliophora ferrisae* Brzeski, 1974

L. gigas (Thorne, 1955) n. comb.
= *H. gigas* Thorne, 1955

L. robusta (Loof, 1968) n. comb.
= *H. robusta* Loof, 1968

L. uniformis (Thorne, 1955) n. comb.
= *H. uniformis* Thorne, 1955

L. vaccinium (Reed & Jenkins, 1963) n. comb.
= *H. vaccinium* Reed & Jenkins, 1963

RELATIONSHIP

See key to the genera of Hemicycliophorinae. The genus is named in honour of P.A.A. Loof.

KEY TO SPECIES OF *Loofia* N. GEN.
(Based on female)

1. Body 1.9 mm long ; stylet 150 µm long ..... *L. gigas*
   Body under 1.5 mm long ; stylet under 120 µm long 2
2. Tail uniformly tapering ..... *L. uniformis*
   Tail not uniformly tapering 3
3. Body annules 206-244 in number ; spermatheca with sperm ..... *L. robusta*
   Body annules over 250 in number ; spermatheca empty 4
4. Inner cephalic cuticle not annulated ..... *L. thienemanni*
   Inner cephalic cuticle annulated 5
5. Lateral fields marked by two incisures ; labial disc elevated ..... *L. ferrisae*
   Lateral fields not marked by incisures ; labial disc not elevated ..... *L. vaccinium*

Hemicycliophora corbetti n. sp.

(Fig. 3)

MEASUREMENTS

See Table 1.

DESCRIPTION

Female

Body arcuate, tapering towards blunt extremities, with a pronounced ventral constriction just behind vulva. Sheath annules slightly flatter than body annules, marked with faint longitudinal striae, about 70 in number at mid-body. Lateral fields marked by two irregular incisures often enclosing a third incisure forming a zig-zag line, areolated ; on one female only a single lateral line was seen. Body annules 4.5-4.8 µm wide, numbering 205-220 (211) and 36-39 (38) in pre-vulval and post-vulval regions of body, respectively. Cephalic region continuous, with two annules on both sheath and body cuticles ; labial disc not elevated ; frame-work

Table 1

Measurements of *Hemicycliophora corbetti* n. sp.

	II - Stage (*n = 2*)	*III - Stage* (*n = 4*)	*IV - Stage* (*n = 8*)	♀♀ (*n = 13*)	*Holotype* ♀
Length (mm)	0.49-0.57	0.66 (0.62-0.68)	0.8 (0.72-0.83)	0.9 (0.77-1.12)	0.9
V	—	—	87.3 (86.3-88.2)	89 (87-91)	89
a	22-25	27 (22-29)	23 (21-25)	26 (25-31)	27
b	4-4.8	4.9 (4.6-5.5)	5.8 (5.5-6.3)	6 (5.7-6.7)	5.8
c	13.5	14 (13.5-15)	15 (14-16)	18 (15.8-22.2)	18
c′	2.3	2.5 (2.4-2.8)	2.3 (2.0-2.6)	2.4 (2.2-2.6)	2.3
Stylet (µm)	(n = 1) 63	76 (73-78)	77.6 (n = 3) (76-80)	86 (78-93)	88
R	251-270	252 (242-259)	258 (250-271)	249 (242-260)	256
Rst	(n = 1) 31	27 (26-29)	25 (n = 3) (23-27)	24 (23-25)	23
Roes	57	49 (47-51)	47 (43-51)	44 (41-46)	43
Rex	51-58	49 (47-50)	52 (51-54)	48 (47-50)	50
RVan	—	—	18 (14-20)	18 (16-21)	21
Ran	29-33	25	24 (21-27)	21 (19-23)	19
Excretory pore from anterior end (µm)	95-121	143 (141-145)	158 (135-166)	156 (143-173)	174

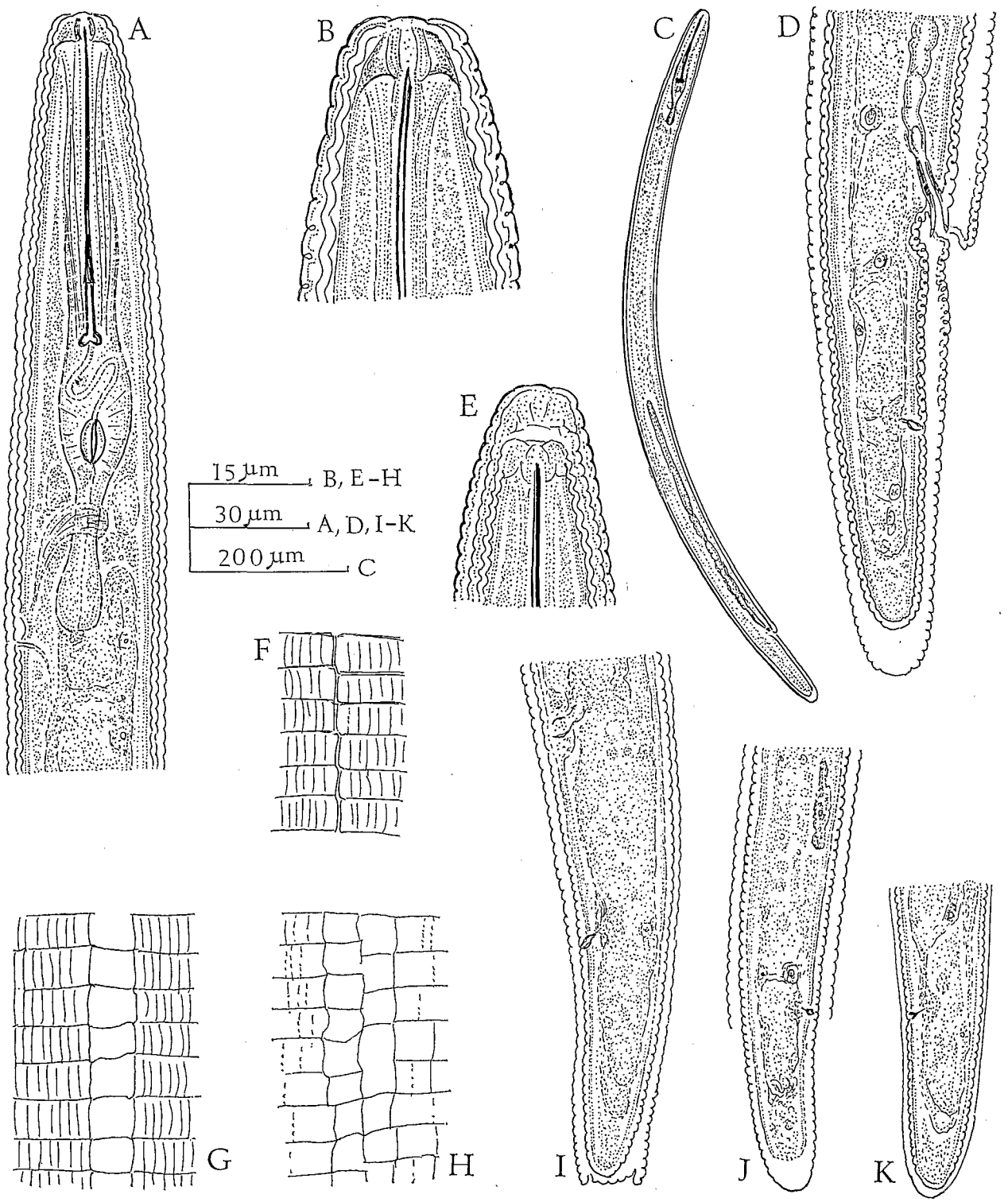

Fig. 3. *Hemicycliophora corbetti* n. sp. B-D : Holotype. A, F-H : Paratype females. E, I : IV-stage. J : III-stage. K : II-stage, paratype juveniles. A : Oesophageal region. B & E : Head ends. C : Entire female. D, I-K : Posterior regions. F-H : Lateral field patterns.

moderately sclerotized. Spear 78-93 µm long, extends through 23-25 (24) annules ; conus (68-75 (72) µm long ; basal knobs backwardly inclined, enclosing a distinct cavity at base, 6-8 (7) µm across. Orifice of dorsal oesophageal gland 8-12 (10) µm behind spear base. Oesophagus typical of the genus with a short amalgamated isthmus crossed by nerve ring ; refractive valve plates of corpus 12-13 µm long by 4.5-6.0 µm wide. Excretory pore one to five annules behind oesophageal base. Hemizonid distinct, two annules long, at the level or two annules anterior to excretory pore.

Vulva lips modified, projecting one or two annules, not tubular ; sheath cuticle forming a short sleeve in this region. Vagina thick-walled, dilated, directed inward and forward. Gonad prodelphic. Spermatheca indistinct ; no sperm in genital tract. Uterine egg 104 × 25 µm. Post-vulval part of body 2.7-3.8 (3) times vulval body-width long. Distance between vulva and anus 34-52 (42) µm or 0.74-1.01 (0.84) times tail length.

Tail sub-cylindrical with a broadly rounded tip, 40-55 (49) µm long ; tail annules 19-23 (21) in number, reaching tip but not extending around tip (Fig. 3, D).

Male

Not known.

Juveniles

Similar to female in shape of body, lip region, spear, oesophagus and tail. Lateral field with one to three incisures, variable even on the same individual. Number of body annules (R), Rex and Ran not varying much between stages of development (see Table 1). Double cuticle in all stages, four cuticles in moulting individuals. Spear functional but in several specimens only conus or part of it is seen. Stages can be recognized by the body length. Indication of vulval region is seen in III-stage ; IV-stage juveniles have vulva primordium at about 86-88 per cent of body.

TYPE HABITAT AND LOCALITY

Soil around roots of tomato (*Lycopersicon esculentum)* at Nkhompola I, Namitete Dambo, near Tembwe, Malawi. Also found around roots of *Pennisetum purpureum* at the same locality.

TYPE MATERIAL

Collected by Dr. D.C.M. Corbett (after whom the species is named) on 22nd November, 1962. Holotype female, five female, and 15 juvenile paratypes at Commonwealth Institute of Helminthology, St. Albans, England. Two female paratypes at each of these centres : Rothamsted Experimental Station, Harpenden, England ; Landbouwhogeschool, Wageningen, Netherlands ; Muséum national d'Histoire naturelle Laboratoire des Vers, Paris, France ; USDA Nematode Collection, Beltsville, Maryland, USA.

RELATIONSHIP

Hemicycliophora corbetti n. sp. is related to those species whose females have elongate cylindrical to subcylindrical tails (it should be remarked here that *H. nigeriensis* and *H. obtusa* basically have pointed female tails) : *H. arenaria* Raski, 1958 ; *H. nigeriensis* Germani & Luc, 1973 ; *H. obtusa* Thorne, 1955 ; *H. signata* Orton Williams, 1978 ; and *H. straturata* Germani & Luc, 1973.

From *H. arenaria* it differs in having longitudinal striae on sheath, and lateral fields with incisures, fewer body annules, especially in post-vulval region, inconspicuous labial disc and spermatheca lacking sperm. *H. nigeriensis* has fewer body annules (213-232 ; mean : 220), lateral fields marked only by breaks and anastomoses of annules and female tail, if rounded, is shorter (less than two anal body widths long) and less tapering. It differs from *H. obtusa* in the female having cuticular striae and lateral fields with incisures and a sub-cylindrical tail. *H. signata* and *H. straturata* are closely related to each other. They differ from this new species in having fewer body annules, a shorter spear and a less tapering post-vulval region of the body.

Proposal for the new suborder Criconematina

The order Tylenchida Thorne, 1949 * has two suborders : Tylenchina Chitwood & Chitwood, 1950 and Aphelenchina Geraert, 1966. It belongs to the subclass Secernentea among which it is readily recognized by the protrusible buccal stylet in most juveniles and adults.

The suborder Tylenchina is a large group as compared to the Aphelenchina. Some of its genera are fungal feeders and parasites of insects and other invertebrates, while most are obligate plant parasites. Three lines of phylogenetic development among Tylenchina are evident. The first line represented by the superfamilies Myenchoidea, Sphaerularioidea, and Neotylenchoidea shows a conservation of several ancestral characters, especially a cylindroid, non-muscular corpus, a primitive form of stylet and monodelphy. From a similar but more primitive ancestral group, at least two other branches, with distinct evolutionary trends towards plant-parasitism, split off and developed independently. These are represented by the present day Tylenchina, *sensu stricto*, and Criconematina n. subord. The suborder Heteroderata Skarbilovich, 1957 (see Skarbilovich, 1959) lies on the same line of development as the Tylenchina, *sensu stricto*. The review of Heteroderoidea by Stone (1977) clearly shows that the group does not merit a higher status than that of a superfamily.

Under the suborder Tylenchina *sensu* Geraert (1966), Raski and Siddiqui (1975) recognized seven superfamilies : Tylenchoidea, Atylenchoidea, Neotylenchoidea, Heteroderoidea, Criconematoidea, Tylenchuloidea (emended from Tylenchulidoidea ; the original proposal of this group by Skarbilovich (1947) is Tylenchululinae which has long been emended as Tylenchulinae) and Tylenchocriconematoidea. The last three of these superfamilies share the common characteristics of the precorpus being amalgamated with a large muscular postcorpus, a small basal oesophageal bulb containing three oesophageal glands and males having a degenerate oesophagus. The morphological characteristics of these superfamilies suggest that they have a different organisation than the group represented by the superfamilies Tylenchoidea, Atylenchoidea, Sphaerularioidea, Myenchoidea, Neotylenchoidea, Hoplolaimoidea and Heteroderoidea. The origin and phylogeny of the two groups also appear different as discussed below and thus there is a good justification for the proposal of the suborder Criconematina for the former group.

The Criconematina exhibit several morphological peculiarities not found in the Tylenchina, *sensu stricto*. These include thick retrorse annules that may bear scales, spines and other cuticular configurations, the "crawling" locomotion (Stauffer, 1924 ; Wallace, 1963) assisted by thick "capped" annules having more flexible interannule cuticle (De Grisse, 1972), a cuticular sheath which may be present in juveniles as well as adults, the presence of four sub-median lobes in most families (Geraert, 1966), the characteristic constancy in stylet shaft length being independent of the length of the conus which may exceed 100 µm (Geraert, 1978), a criconematid oesophagus and the production of gelatinous matrix by the excretory system (Maggenti, 1962).

Seshadri (1964) showed that in *Macroposthonia xenoplax* the intestine is syncytial and lacks a lumen ; the same is true for *Tylenchulus* (Maggenti, 1962). I found the intestine in all the genera of Criconematina to be syncytial and lacking a definite lumen. Unlike the Tylenchina, the junction of the intestine with the rectum is inconspicuous and the « solid » mass of the intestine may be pushed anterior to the oesophago-intestinal junction or beyond the anal level, as a diverticulum (see Fig. 3, A & D).

Criconematina n. subord.

CHARACTERISTICS

Tylenchida. Female obligate plant root-parasite, male and some juveniles incapable of tissue feeding. Usually under 1 mm long. Marked

* Authorities for ordinal and subordinal ranks of Tylenchida are cited here according to the first proposal of the name of that rank in a formal manner. Citations such as Tylenchida (Filipjev, 1934) Thorne, 1949 ; Tylenchida (Oerley, 1880) Thorne, 1949 ; Aphelenchina (Fuchs, 1937) Geraert, 1966 are not correct because Filipjev (1934), Örley (1880) and Fuchs (1937) have not erected any definite ordinal ranks. The International Code of Zoological Nomenclature does not cover taxa at ordinal or higher ranks.

sexual dimorphism, the male slender and with degenerate oesophagus and the female sausage-shaped, spheroidal or cylindrical and with a well developed oesophagus. Female and juveniles bearing thick cuticle either with retrorse annules lacking lateral fields (and in several genera with spines, scales or other cuticular configurations), or with smooth coarse rounded annules that may or may not be covered with a sheath ; those bearing thin cuticle have fine rounded annules and lateral fields often marked with incisures (lateral fields obliterated in swollen stages). Cephalic region in female and juveniles with usually less than three but often modified annules ; oral aperture dorso-ventrally longitudinal, often I-shaped due to two lateral liplets, on a raised area or labial disc (= fused lips ! see Loof and De Grisse, 1973) ; amphidial apertures round to oval, close to labial disc area. Basically there are four submedian pseudolips (each often with lobe-like outgrowths) and two small lateral pseudolips (for definition see Loof and De Grisse, 1973) ; no papillae on surface of lip region. Cephalic frame-work hexa-radiate, with light to heavy sclerotization. Deirids reported in thin-cuticle genera *Tylenchulus* and *Paratylenchus*. Phasmids absent (occasional reports of phasmids doubtful). Stylet in female and most juveniles often very long with conus markedly longer than the shaft which has a constant length of about 8-10 µm ; basal knobs well developed, either sloping backwards or anchor-shaped with outer margins projecting forwards. Males and some juveniles lack stylet or have a degenerated one ; oesophagus in such cases degenerated. Females and most juveniles with well developed stylet. Oesophagus criconematoid, with the postcorpus (= median oesophageal bulb) enormously developed, muscular, containing a large often elongated refractive cuticular valvular apparatus and being anteriorly amalgamated with precorpus which is usually broad and surrounds the basal region of the stylet ; isthmus either slender and offset from basal bulb or short and broad being amalgamated with the basal bulb. Basal bulb small, offset from intestine, contains three oesophageal glands (except in *Sphaeronema whitlloni* and *Meloidoderita kirjanovae* in which the glands are partially free). Orifice of dorsal oesophageal gland at a short distance (usually over 4 µm) behind spear base. Oesophago-intestinal valve small, usually indistinct.

Vulva transversely oval or slit-like, located posteriorly usually at over 75 percent of body length. Gonad monodelphic, prodelphic, outstretched (may be coiled in swollen females). Postvulval uterine sac absent. Spermatheca not well formed or axial when distended with small-sized sperm, round to longitudinally oval, usually offset and inclined laterally or ventrally, several sperm in a row fill its lumen-width. Uterus with a distinct crustaformeria and an ovijector. Vagina leading inward and forward. One or two synchronous eggs in uterus at a time except in *Meloidoderita* in which the uterine walls form a cyst ; numerous eggs may be deposited in a gelatinous matrix produced by the excretory system (e.g. *Tylenchulus*).

Intestine syncytial, lacking a definite lumen, often extends beyond anal level. Junction between intestine and rectum indistinct, without a sphincter valve. Female anus a small pore, rarely absent.

Male monorchic, with degenerated oesophagus, stylet mostly absent but may be represented by a degenerated, non-functional one. Male gonoduct mostly filled with small-sized sperm all of which are usually produced at one stage of male development ; testis in mature males obliterated. Spicules often very long and setaceous, with small narrow head, an elongate-slender shaft (calomus) and a finaly pointed distal end ; variable in shape but often arcuate. Gubernaculum linear or crescent-shaped in lateral view, fixed. Bursa usually low, devoid of phasmidial extension, rarely terminal, may be absent. Cloacal lips usually narrow and elevated, or drawn out as a penial tube. Hypoptygma (a papilla) single, rarely double (e.g. *Tylenchocriconema*), on posterior lip of cloaca, may be absent (e.g. *Tylenchulus*).

Inhabitant of soil; not marine. Female an obligate plant root parasite ; juveniles may or may not feed on plant roots ; males free-living in soil.

TYPE SUPERFAMILY

Criconematoidea Taylor, 1936 (Geraert, 1966).

OTHER SUPERFAMILIES

Hemicycliophoroidea Skarbilovich, 1959 (n. grad.)

Tylenchocriconematoidea Raski & Siddiqui, 1975

Tylenchuloidea Skarbilovich, 1947 (Raski & Siddiqui, 1975).

DIAGNOSIS, RELATIONSHIP AND DISCUSSION

Criconematina n. subord. is recognized by the structure of the cephalic region and the oesophagus, the stylet bearing a long conus and prominent basal knobs, cuticular and annular modifications, sexual dimorphism (in which the male has a degenerate oesophagus and either a degenerate or absent stylet), the shape and structure of the male gonoduct and accessory genital structures, the absence of phasmids, the soil habitat, and the feeding on plant roots.

Criconematina is closer to Tylenchina *sensu stricto*, than to Aphelenchina and differs from the latter because the juvenile and female anus is a small pore, the orifice of the dorsal oesophageal gland is not in the median oesophageal bulb, the spicules are not rose thorn-shaped or derived from that shape and the male tail is not papillate.

From Tylenchina, the new suborder differs in the structure of the cephalic region especially in having four submedian lobes or their derivatives, in the lateral liplets guarding the oral opening which consequently appears I-shaped and the oesophagus of feeding stages having a large muscular postcorpus which is amalgamated with the broad precorpus. A constant monodelphy, the absence of the phasmids and the male having a degenerated oesophagus usually lacking stylet and a bursa devoid of pseudoribs formed by the extension of the phasmids also help in separating it from Tylenchina.

The broad corpus amalgamated with the enlarged postcorpus is characteristic of the Criconematina and so is the stylet with a large conus and a constant shaft length as discussed by Geraert (1978) and mentioned above. Unlike Criconematoidea and Hemicycliophoroidea, the isthmus in Tylenchina is never broad and amalgamated with the basal bulb.

The typical transversely annulated cephalic region of Tylenchina is not seen in Criconematina, except in the males. In the juveniles and females of Criconematina the cephalic region usually comprises one or two annules which are variously modified. The submedian lobes or their derivatives are not seen in Tylenchina. The oral opening in Tylenchina is either circular or oval and devoid of lateral liplets (cf. SEM of cephalic regions in Sher and Bell, 1975).

In Tylenchina the phasmids are usually distinct and the intestine is cellular with distinct lumen and intestinal-rectal junction ; if the intestine extends into the tail it forms a sac. In Criconematina the intestine is a "solid" mass which may show vacuolation but a distinct lumen is absent. The presence of retrorse annules, cuticular spines and other structures and a cuticular sheath is unique for Criconematina among the Tylenchida.

The development of saccate females, the sexual dimorphism and the modification of the male accessory genital structures (bursa, spicules, gubernaculum, hypoptygma) appear to have taken different developmental courses in the two groups. In contrast to the Criconematina, the swollen females of the Tylenchina usually retain their didelphy (in one-ovaried forms a degenerated post-vulval uterine branch is present), the gelatinous matrix is produced either by the rectal glands *(Meloidogyne)* or the gonoduct (Heteroderidae, *Rotylenchulus*, *Aconlylus*) and, in several cases, the entire body wall forms a protective cyst for eggs. The males of such Tylenchina have well developed stylet and oesophagus (Heteroderoidea) and distinct phasmids. The large campanulate, sometimes trilobed, bursa with phasmidial extensions, the distally flanged or notched spicules, a large protrusible gubernaculum, the telamon and gubernacular titillae are peculiarities of the Tylenchina, while the setaceous spicules becoming semi-circular, U- or hook-shaped, single hypoptygma and the development of a penial tube are characteristics of the Criconematina.

KEY TO FAMILIAL GROUPS OF CRICONEMATINA

1. Female and juveniles with fine cuticular annules which are not retrorse ; isthmus of oesophagus slender, not amalgamated with basal bulb 2
   Female and juveniles with coarse cuticular annules which may be retrorse ; isthmus of oesophagus broad, amalgamated with basal bulb 6
2. Female slender (a = about 40), about 500 µm or longer ; male with asymmetrical cephalic region and a terminal bursa .... TYLENCHOCRICONEMATOIDEA.... ..... TYLENCHOCRICONEMATIDAE
   Female not so slender, usually under 500 µm long ; male with symmetrical lip region and a subterminal or absent bursa .... TYLENCHULOIDEA.. 3
3. Precorpus slender ; stylet short (usually under 15 µm) with conus usually equal to or shorter than shaft ; female sub-spherical or elongate saccate with body mostly enlarging dorsally ; male usually with elongate-conoid tail... 4
   Precorpus broad, stylet long (often over 20 µm) with conus much longer than shaft ; female vermiform, if saccate body enlarging on all sides ; male with short sub-cylindroid tail ..... PARATYLENCHIDAE
4. Adult female sub-spherical, body without a post-vulval region ; excretory pore at or near oesophagus, leading into excretory duct directed posteriorly 5
   Adult female not sub-spherical, body with a post-vulval region, excretory pore much posterior to oesophagus, leading into excretory duct directed anteriorly .... TYLENCHULIDAE
5. Uterine wall abnormally thickened to form a cyst on death ; bursa distinct .... MELOIDODERITIDAE
   Uterine wall not forming a cyst on death ; bursa indistinct or absent .... SPHAERONEMATIDAE
6. Female and juveniles spindle- or sausage-shaped with retrorse annules (annules round in females of Hemicriconemoidinae) ; basal knobs of stylet anchor-shaped ; male develops by metamorphosis within a spined juvenile ; male tail short, with low bursa ..... CRICONEMATOIDEA... CRICONEMATIDAE. 7
   Female and juveniles eel-like with non-retrorse annules ; basal knobs of stylet not anchor-shaped ; male develops normally ; male tail long, with high bursa..... ..... HEMICYCLIOPHOROIDEA..... 9
7. Female with two cuticles and non-retrorse annules ..... HEMICRICONEMOIDINAE
   Female with single cuticle and retrorse annules 8
8. Female with body annules bearing spines, scales or other cuticular configurations..... ..... CRICONEMATINAE
   Female with body annules smooth or crenate, not bearing spines, scales or other cuticular configurations ..... MACROPOSTHONIINAE
9. Female and juveniles with a thick cuticular sheath ; spicules arcuate, semi-circular, U- or hook-shaped ... HEMICYCLIOPHORIDAE
   Female and juveniles with a membranous sheath or without it ; spicules straight .... CALOOSIIDAE

SOME SPECULATIVE REMARKS ON THE ORIGIN AND PHYLOGENY OF CRICONEMATINA

Andrássy (1976, p. 79) considers Cephalobina as the first "true" Secernentea, followed by Rhabditina and Diplogasterina, with Diplogasterina showing a smooth transition to Tylenchida. He (1976, p. 81) believes that Tylenchida is a monophyletic group that originated from a Diplogasterina-complex. This idea is the same as that of Paramonov (1964, 1968, 1970). Maggenti (1971, 1978) also followed Paramonov's idea that the Aphelenchoidea and Tylenchoidea evolved from a common Diplogasteroidea-like ancestor, and he (1971) speculated that the two branches (i.e. Aphalenchoidea and Tylenchoidea) split off in the Devonian era, some 400 million years ago.

The reasons used by Paramonov, Andrássy and Maggenti (above cit.) in suggesting a Diplogasterina-type ancestor for the Tylenchida refer mostly to the character states of the Aphelenchina. The characters of papillate male tail, the structure of the sperm and spicule (Shepherd & Clark, 1976), a large offset median oesophageal bulb even in the smallest *Cryptaphelenchus*, the

anus in the form of a large crescent-shaped slit and the predatory behaviour (e.g. *Seinura*, *Laimaphelenchus*) of the Aphelenchina do lend support to the view that the Aphelenchina and Diplogasterina have a common origin. But, unlike Diplogasterina, Aphelenchina have the orifice of the dorsal oesophageal gland within the median oesophageal bulb and outstretched female gonad. The suborders Criconematina and Tylenchina, however, stand apart from these groups on the basis of lacking a papillate male tail, rose thorn-shaped spicules, and a tendency towards predatory behaviour and having a small pore-like anal aperture, and hence, following Hennig's (1966) assertion that an ancestral character is of wide occurrence within a group, we have to look elsewhere for their possible ancestor.

Present forms cannot be derived from the contemporary forms as during the evolution over millions of years these perishable small creatures must have had innumerable modifications, successions and extinctions. However, we must try to point out likely origins and establish the probable lines of development for the Criconematina and Tylenchina, on the information and knowledge of the inter-relationships of the nematode groups in order to build a sound classification. The discussion on the origin of the Tylenchina is beyond the scope of this paper. A few points are made here about the likely origin and phylogeny of the Criconematina.

The Criconematina appear to have evolved (independently of the Tylenchina) from ancestors which were somewhat similar to the contemporary Myenchoidea, Sphaerularioidea and Neotylenchoidea. These ancestors were probably fungal feeders and had a tendency to attack lower plants and animals. The alternation of free-living and parasitic generations and the resultant di- tri- or even tetra-morphic females in *Fergusobia*, *Heterolylenchus*, *Deladenus* etc. clearly demonstrate the variability in the anatomy and biology of those ancestral forms.

The key to the origin of the Criconematina lies in the development of a large robust stylet and, correlated with it, in the transformation of a broad corpus into a muscular organ. In fact, similar changes can be seen to occur in the present day forms. The free-living neotylenchid-type females of *Deladenus* spp. possess a stylet about 10 µm long, but the insect-parasitic infective-stage female acquires a stylet about 20 µm long and a broad allantonematid-type oesophagus (Bedding, 1968, 1974). The allantonematid genus *Robleus* Massey, 1974 has a typical criconematid stylet measuring 19 µm in length and having a conus longer than the shaft and rounded, posteriorly sloping basal knobs, as illustrated by Massey (1974). The parthenogenetic female of *Fergusobia curriei* is remarkably similar to thin-cuticle bearing Criconematina (Fisher & Nickle, 1968) and an examination of these females by J. B. Goodey led Siddiqi and Goodey (1964) to believe that the oesophagus of *Fergusobia* was similar to that of criconematids.

Other characters that point towards a common origin of Criconematina and the group represented by superfamilies Myenchoidea, Sphaerularioidea and Neotylenchoidea are given below :

(1) Short body size. Body of female with thin cuticle tends to swell to accommodate the growing reproductive organs, gravid females becoming saussage-or bean-shaped in both groups

(2) Phasmids not seen in either group.

(3) Low cephalic region, at top showing four distinct submedian areas and lacking prominent annulation. Male lip region asymmetrical, directed ventrally in *Tylenchocriconema* and *Iotonchium* (Neotylenchoidea), both having degenerated oesophagus and almost no stylet.

(4) Monodelphy. One ovary which has a tendency to grow, even becoming convoluted, to occupy most of the body cavity. Oviduct not pronounced. Uterus becomes extremely large and thick-walled to form a protective bag or cyst in members of both groups (cf. *Meloidoderita* (Criconematina) vs. *Sphaerularia* and Allantonematidae).

(5) Male and some juveniles with degenerated oesophagus and degenerate or absent stylet in both groups. In fact a degenerated oesophagus of male Criconematina, with or without a pseudostylet reverts back to the original primitive neotylenchid type. Conversely, this could also mean that the development of a robust stylet and the changed mode of feeding contributed to the arrival of a Criconematina-type oesophagus.

(6) Similar pointed spicules, similar gubernaculum and similar small-sized sperm all produced at one stage of male development.

(7) The absence of a bursa in several genera of both groups: The bursa is absent in the genera *Heterotylenchus* and *Gymnotylenchus*. The terminal bursa of *Tylenchocriconema* is low and lacks phasmidial ribs and thus is indistinguishable from the basic type of bursa prevalent among Sphaerularioidea and Neotylenchoidea.

(8) In both groups, the male's only function is to inseminate the female and then die. For this and also for further development to infective stage, which is the young female, the juveniles of both groups need a soil environment. Examples are commonly found of non-feeding males and juveniles and of juveniles not able to develop in the host environment in these two groups.

Some of these resemblances apply equally well to several members of the Tylenchina and this is to be expected because both Criconematina and Tylenchina appear to have a common origin but to have different lines of development towards obligate plant-parasitism. The Criconematina have attained their goal of obligate plant-parasitism "en masse", but whether they are as successful plant parasites as the Tylenchina is disputable.

In the contemporary Criconematina, two main lines of development are evident, as shown in Figure 4.

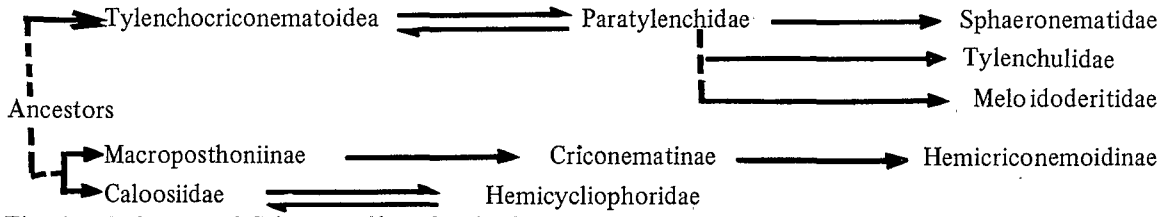

Fig. 4. Phylogeny of Criconematina. See text.

The first line is represented by the superfamilies Tylenchocriconematoidea and Tylenchuloidea. It is characterised by the thin body cuticle showing fine annulation but no other modifications and the slender isthmus of the oesophagus which is not amalgamated with the basal bulb. The second line comprising Criconematoidea and Hemicycliophoroidea has members with thick cuticle with coarse annulation and various modifications (spines, sheath, etc.) and a broad isthmus which is amalgamated with the basal bulb. Inter-relationships between members of the Criconematoidea have been discussed by Loof and De Grisse (1973) and those of the Hemicycliophoroidea have been dealt with in this paper. For the inter-relationships between the members of the Tylenchocriconematoidea and Tylenchuloidea refer to Raski and Siddiqui (1975), Raski (1962), Raski (1973) ; Geraert (1966) ; Kirjanova and Poghossian (1973).

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ADDENDUM

While this paper was in press, the author claimed that other species be added to those enumerated above for each genus. They are listed below :

Caloosia parapaxi Phukan & Sanwal, 1980

Hemicaloosia luci Dhanachand & Jairajpuri, 1980

Hemicycliophora italiae Brzeski & Ivanova, 1978

Hemicycliophora pseudochiliensis Barbez & Geraert, 1980

Aulosphora brzeskii (Barbez & Geraert, 1980) n. comb.

= *Hemicycliophora brzeskii* Barbez & Geraert, 1980