

A reappraisal of Tylenchina (Nemata).

6. The family Belonolaimidae Whitehead, 1960 ⁽¹⁾

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SUMMARY

The family Belonolaimidae is redefined to include two subfamilies, Belonolaiminae with *Belonolaimus*, *Carphodorus*, *Morulaimus*, *Geocenamus*, and *Sauertylenchus*, and Telotylenchinae with *Tylenchorhynchus* (= *Telotylenchus*), *Trophurus*, *Trichotylenchus*, *Nagelus*, *Paratrophurus*, *Merlinius*, *Triversus*, and *Amplimerlinius*. The following synonymizations are proposed: *Ibipora* = *Morulaimus*, *Hexadorus* = *Geocenamus*, *Uliginotylenchus* = *Trichotylenchus*, *Meiodorus* and *Mulveyotus* = *Triversus*, *Histotylenchus* and *Telotylenchoides* = *Paratrophurus*. The synonymy of *Tylenchorhynchus* includes nine generic names. *Dolichorhynchus* is a junior homonym. *Tetylenchus* is kept in *genera dubia vel incertae sedis*. A tabular key is proposed for identification of the genera in the family.

RÉSUMÉ

Réévaluation des Tylenchina (Nemata). 5. La famille des Belonolaimidae Whitehead, 1960

La famille des Belonolaimidae est redéfinie avec deux sous-familles : Belonolaiminae, comprenant *Belonolaimus*, *Carphodorus*, *Morulaimus*, *Geocenamus* et *Sauertylenchus* et Telotylenchinae, comprenant *Tylenchorhynchus* (= *Telotylenchus*), *Trophurus*, *Trichotylenchus*, *Nagelus*, *Paratrophurus*, *Merlinius*, *Triversus* et *Amplimerlinius*. Les synonymies suivantes sont proposées : *Ibipora* = *Morulaimus*, *Hexadorus* = *Geocenamus*, *Uliginotylenchus* = *Trichotylenchus*, *Meiodorus* et *Mulveyotus* = *Triversus*, *Histotylenchus* et *Telotylenchoides* = *Paratrophurus*. La synonymie de *Tylenchorhynchus* comprend neuf noms génériques. *Dolichorhynchus* est un homonyme plus récent. *Tetylenchus* est classé comme *genus dubium*. Une clef tabulaire est proposée pour aider à l'identification des genres de la famille.

The family Belonolaimidae is here redefined to include two groups of taxa that until now were considered to be distinct : the belonolaimids (Belonolaiminae, Telotylenchinae) with overlapping oesophageal glands, and the tylenchorhynchids (Tylenchorhynchinae, Merliniinae, Trophurinae) with glands abutting and bulb-shaped.

Belonolaimus was placed by Chitwood (1950) in the family Dolichodoridae. Thorne (1949) did not include this genus in his revision of Tylenchida, but Loof (1958), using the system of Thorne and its emphasis on the aspect of the glandular part of the oesophagus, separated *Belonolaimus* from *Dolichodorus* by classifying them into two different subfamilies (Hoplolaiminae and Tylenchinae, respectively).

When Whitehead (1960) proposed a new subfamily, Belonolaiminae, he included in it only genera with glandular overlap (*Belonolaimus* and *Trichotylenchus*).

A few months later, Siddiqi (1960) independently proposed Telotylenchinae for a new genus, *Telotylenchus*, and for *Pseudhalenchus*, both with overlapping glands. The structure of the glandular oesophagus was emphasized again by the same author (Siddiqi, 1971a) when he placed Tylenchorhynchinae and related subfamilies with abutting glands in Dolichodoridae, while Telotylenchinae was placed in Belonolaimidae.

It is our opinion that there is no structural difference between forms with abutting glands (the so-called "bulb"), and forms with glands overlapping the anterior part of the intestine. These forms differ only in the length of the glands, and in the position of the oesophageal lumen relative to the glands (Seinhorst, 1971). The two kinds of arrangements may co-exist in the same family (for example, *Paratylenchus* is a Hoplolaimidae with abutting glands), in the same genus (*Pratylenchoides magnicauda* has abutting glands, while *P. ritteri*

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has a long overlapping lobe) and even in the same species, for example *Ditylenchus myceliophagus* as discussed by Fortuner (1982).

Once admitted that morphology, size, and location of oesophageal glands may vary within any taxa, including families, it becomes evident that belonolaimids, tylenchorhynchids, and related groups belong to the same family.

The family Belonolaimidae

- Belonolaimidae Whitehead, 1960
- = Telotylenchidae Siddiqi, 1960
- = Tylenchorhynchidae Eliava, 1974

DIAGNOSIS

Tylenchoidea. Medium to large sized nematodes, with tail cylindroid to conoid, more than twice as long as wide but never elongate filiform (typically $c' = 2-5$). Phasmids always on posterior half of tail, never enlarged into scutella. Deirids present or absent. Face view as seen with SEM either ancestral (first lip annulus six-sectored) or with lateral sectors regressed and face view evolving towards either a grossly quadrangular shape or a four leaf clover shape. Females typically with two genital branches (except *Trophurus*). Columned uterus with three rows of cells. Males with peloderan caudal alae, rarely lobed or stopping just short of the tail tip. Spicules with or without pronounced velum.

Belonolaimidae are migratory ectoparasites of plant roots. A few species are endoparasitic.

TYPE SUBFAMILY

- Belonolaiminae Whitehead, 1960

OTHER SUBFAMILY

- Telotylenchinae Siddiqi, 1960

COMMENTS

The family Belonolaimidae occupies an intermediate position between Tylenchidae and Hoplolaimidae. It is differentiated from Tylenchidae and Dolichodoridae by its columned uterus with three rows of cells (four rows in the other two families). It differs from Hoplolaimidae by having a longer tail, and by having phasmids always on tail.

Telotylenchinae is accepted only as a subfamily in Belonolaimidae because of the many similarities between belonolaimids and tylenchorhynchids. Face views are often similar amongst various members of both groups (for example, *Morulaimus* is similar to *Merlinius* for this character); the cylindroid tail of belonolaimids is similar to that of *Paratrophurus* and *Amplimerlinius*. The few differences that exist in morphology and

biology of the various genera in the family are best treated at subfamily level. Telotylenchinae are surface grazers feeding on the epidermal cells of plant roots. Belonolaiminae have a long stylet that enables them to reach deeper into the root while the rest of their body remains outside of the plant.

The subfamily Telotylenchinae

- Telotylenchinae Siddiqi, 1960
- = Tylenchorhynchinae Eliava, 1964 (n. syn.)
- = Trophurinae Paramonov, 1967 (n. syn.)
- = Tetylenchinae Siddiqi, 1970
- = Merliniinae Siddiqi, 1971
- = Meiodorinae Siddiqi, 1971 (n. syn.)

DIAGNOSIS

Belonolaimidae. Cephalic framework with weak to medium sclerotization. Stylet 15 to 40 μm long, with cone about as long as shaft. Corpus not enlarged and metacorporal valve of medium development. Labial region continuous or with slight indentation, never bulbous. SEM face view with six lip sectors or with lateral lip sectors regressed. Labial disc lemon shaped or variously fused with lip sectors. Disc and lip sectors sometimes fused together. Sensillae openings often visible on the sub-median lip sectors.

TYPE GENUS

- Tylenchorhynchus* Cobb, 1913
- = *Bitylenchus* Filip'ev, 1934
- = *Telotylenchus* Siddiqi, 1960 (n. syn.)
- = *Quinisulcius* Siddiqi, 1971 (n. syn.)
- = "*Dolichorhynchus*" (primary homonym; n. syn.)
- = *Trilineellus* Lewis & Golden, 1981 (n. syn.)
- = *Divittus* Jairajpuri, 1984
- = *Morasinema* Javed, 1984
- = *Tessellus* Jairajpuri & Hunt, 1984
- = *Neodolichorhynchus* Jairajpuri & Hunt, 1984 (n. syn.)

OTHER GENERA

- Trophurus* Loof, 1956
- = *Clavaurotylenchus* Caveness, 1958
- Trichotylenchus* Whitehead, 1960
- = *Uliginotylenchus* Siddiqi, 1971 (n. syn.)
- Nagelus* Thorne & Malek, 1968
- Paratrophurus* Arias, 1970
- = *Histotylenchus* Siddiqi, 1971 (n. syn.)
- = *Telotylenchoides* Siddiqi, 1971
- Merlinius* Siddiqi, 1970
- = *Scutylenchus* Jairajpuri, 1971
- Triversus* Sher, 1974
- = *Meiodorus* Siddiqi, 1976 (n. syn.)
- = *Mulveyotus* Anderson & Ebsary, 1982
- Amplimerlinius* Siddiqi, 1976

GENUS DUBIUM

Tetylenchus Filip'ev, 1936

COMMENTS ON REJECTED SUBFAMILIES

Tetylenchinae must be rejected after the placement of its type genus in *genus dubium* (see below).

Tylenchorhynchinae is rejected because of the synonymization of *Tylenchorhynchus* and *Telotylenchus*. *Tylenchorhynchus* is the senior synonym at generic level, but Telotylenchinae is the senior subfamily and it should be accepted in accordance with Article 40 (a) of the International Code of Zoological Nomenclature.

Merlinius, the type genus of Merliniinae, is here accepted as a valid taxon. Merliniinae was differentiated by Siddiqi (1971a, 1979) as having six lines in lateral field, spicules cylindroid with distal end rounded and devoid of velum, gubernaculum simple, not protruding from cloaca, median bulb not distinctly offset from procorpus, spermatheca offset, usually with two lobes, and vulva opening small, with distinct epitygma and reduced lateral membranes. Morphology of lateral field is not a primary differentiating character and is at best accepted only as an identification character; shapes of spicules and gubernaculum are accepted as generic characters only; the exact appearance of corpus, vulva, and spermatheca are not well defined in most species in the taxa considered. They cannot be used at this time for definition of systematic relationships. In opposition to these small differences, the close similitude of genera in Telotylenchinae and Merliniinae should be noted. *Merlinius* resembles *Tylenchorhynchus*, *Amplimerlinius* resembles *Paratrophurus*. There are no differences in the biology of all the taxa concerned. It seems best to group them all into a single subfamily.

Trophurus is the only genus in Belonolaimidae with only one female genital branch. Also, it has thickened cuticle on distal end of tail. For this reason, it was grouped with *Macrotrophurus* and *Paratrophurus* in the subfamily Trophurinae. *Macrotrophurus* has been recognized as a Tylenchidae (Geraert & Raski, 1987). The definition of *Paratrophurus* is here enlarged to include species without any thickening of tail cuticle (see below). There exists many species in the family with thickened tail end cuticle, in the genera cited above, but also in *Tylenchorhynchus*, *Trichotylenchus*, *Merlinius*, and *Nage-lus*. The thickening is particularly well marked in *Trophurus*, but it cannot be used as a family criterion. Regression of the posterior genital branch remains the only character that separates *Trophurus* from the rest of the genera in Belonolaimidae. The regression of a single structure is not found to be relevant at subfamily level and Trophurinae is here rejected.

Meiodorinae is rejected after the synonymization of *Meiodorus* with *Triversus*.

The genera in Telotylenchinae

Triversus Sher, 1974

DIAGNOSIS

Telotylenchinae. Body about 1 mm long. Lip region low, flattened. SEM face view with labial disc and first labial annulus fused together; rounded amphid apertures often conspicuous. Stylet 11-25 μm long, robust or with needle-like cone. Labial framework thin, weakly sclerotized, with wide basal ring. Metacorporal bulb fusiform. Lateral field with four or three lines. Female tail conoid, pointed, medium to long ($c' = 3-8$). Deirids absent. Male caudal alae sometimes trilobed.

TYPE SPECIES

Triversus annulatus (Merny, 1964) Sher, 1974
= *Tetylenchus annulatus* Merny, 1964

OTHER SPECIES

T. festonatus (Doucet, 1985) n. comb.
= *Meiodorus festonatus* Doucet, 1985
T. hollisi (Siddiqi, 1976) n. comb.
= *M. hollisi* Siddiqi, 1976
T. hyalacus (Anderson & Ebsary, 1982) n. comb.
= *Mulveyotus hyalacus* Anderson & Ebsary, 1982

COMMENTS

This genus fits the subfamily Telotylenchinae because of the shape of the oesophagus, the two-branched genital system with three rows in columned uterus, and the tail more than three times as long as wide. The tail is pointed, but pointed tails have been reported in other genera in Belonolaimidae (e.g. *Tylenchorhynchus tenuicauda*, *Merlinius joctus*, *M. loofi*, *M. processus*, etc.). *Triversus* is here accepted as a valid genus in Telotylenchinae, differentiated mostly by conspicuous basal ring of the labial framework, low labial region, characteristic SEM face view and male caudal alae often trilobed. *T. annulatus* was said by Sher (1974a) to have three lines in the lateral field but, according to Merny (1964), and confirmed by examination of paratypes, the two ridges that make up the lateral field can be seen as four lines if the ridges are slightly separated.

Meiodorus was proposed by Siddiqi (1976) in Dolichodoridae, Meiodorinae because of pointed female tail and trilobed caudal alae. Siddiqi (1976) commented that the genus was intermediate between Dolichodoridae and Tylenchorhynchinae (here given as synonym of Telotylenchinae).

Meiodorus is quite similar with the genera in the latter subfamily, and particularly with *Triversus*. Both genera have lip area with labial disc and first labial annulus fused together; labial framework very lightly sclerotized but with wide basal ring; corpus fusiform. Also, *Meiodo-*

rus hollisi and *M. festonatus* both have columned uterus with three rows of cells as in Belonolaimidae, instead of four rows as in Dolichodoridae (Geraert, pers. comm.). Pointed female tails are found in *Meiodorus*, *Mulveyotus*, *Triversus*, and some *Tylenchorhynchus* and *Merlinius* species. Lobed caudal alae exist in some species previously placed in "*Dolichorhynchus*" (= *Tylenchorhynchus*). Examination of paratypes of *T. annulatus* proved that the caudal alae is sub-trilobed, with a central lobe thinner and longer than the lateral lobes. In the original description of the species (Merny, 1964) it was said that the caudal alae did not quite reach the end of the tail. In fact, the alae are difficult to observe in lateral view, but in ventral view it can be seen that the central ala extends slightly past the tail tip. There is a definite trend towards lobed caudal alae in Telotylenchinae, and this character should not be used sole criterion for the placement of a taxon in Dolichodoridae. *Meiodorus* is here considered in Telotylenchinae. Within this subfamily, it shows no differences with *Triversus*. The synonymization of *Meiodorus* and *Mulveyotus* proposed by Siddiqi (1986) is accepted and both genera are made junior synonyms of *Triversus*.

Tylenchorhynchus Cobb, 1913

- = *Bitylenchus* Filip'ev, 1934
- = *Telotylenchus* Siddiqi, 1960 (n. syn.)
- = *Quinisulcius* Siddiqi, 1971 (n. syn.)
- = *Dolichorhynchus* Mulk & Jairajpuri, 1974 (n. syn.; junior homonym)
- = *Trilineellus* Lewis & Golden, 1981 (n. syn.)
- = *Divittus* Jairajpuri, 1984
- = *Morasinema* Javed, 1984
- = *Tessellus* Jairajpuri & Hunt, 1984
- = *Neodolichorhynchus* Jairajpuri & Hunt, 1984 (n. syn.)

DIAGNOSIS

Telotylenchinae. Body medium sized. Lateral field with two, three, four, or five lines, sometimes areolated. Longitudinal ridges sometimes present on body. Tail conoid to subcylindroid, about three times as long as wide ($c' = 2-4$), sometimes with thicker cuticle in the distal portion. SEM face view typically with labial disc fused with first lip annulus, and with lateral sectors regressed. The remaining sub-median sectors give a distinctive quadrangular appearance to the face view. Papillae often present on submedian sectors. Head continuous to slightly offset. Stylet 15-30 μm long, thin to slender, with cone about as long as shaft, sometimes needle-like. Deirids often absent. Male with caudal alae rarely lobed. Spicules with well developed velum.

TYPE SPECIES

T. cylindricus Cobb, 1913

OTHER SPECIES

- T. acutooides* Thorne & Malek, 1968
- = *Quinisulcius acutooides* (Thorne & Malek, 1968) Siddiqi, 1971
- T. acutus* Allen, 1955
- = *Q. acutus* (Allen, 1955) Siddiqi, 1971
- T. aduncus* de Guiran, 1967
- T. aerolatus* (Baqri & Jairajpuri, 1969) n. comb.
- = *Telotylenchus aerolatus* Baqri & Jairajpuri, 1969
- = *Telotylenchus areolatus** Fortuner, 1985
- = *Trichotylenchus aerolatus* (Baqri & Jairajpuri, 1969) Jairajpuri, 1971
- nec *Tylenchorhynchus aerolatus* Tobar-Jimenez, 1970
- T. agri* Ferris, 1963
- T. ancorastyletus* Ivanova, 1983
- T. annulatus* (Cassidy, 1930) Golden, 1971
- = *T. martini* Fielding, 1956
- T. antarcticus* Wouts & Sher, 1981
- T. aspericutis* Knobloch, 1975
- T. avaricus* (Kleynhans, 1975) n. comb.
- = *Telotylenchus avaricus* Kleynhans, 1975
- T. badliensis* Saha & Khan, 1982
- T. bicaudatus* Khakimov, 1973
- T. bohrrensis* Gupta & Uma, 1980
- T. brassicae* Siddiqi, 1961
- T. brevilineatus* Williams, 1960
- = *Bitylenchus brevilineatus* (Williams, 1960) Siddiqi, 1986
- = *Tylenchorhynchus indicus* Siddiqi, 1961
- nec *T. indicus* (Siddiqi, 1960) n. comb.
- T. bryobius* Sturhan, 1966
- = *Bitylenchus bryobius* (Sturhan, 1966) Siddiqi, 1986
- T. cacti* Chawla, Bhamburkar, Khan & Prasad, 1968
- = *Q. cacti* (Chawla *et al.*, 1968) Siddiqi, 1986
- T. canalis* Thorne & Malek, 1968
- = *B. canalis* (Thorne & Malek, 1968) Siddiqi, 1986
- T. capitatus* Allen, 1955
- = *Q. capitatus* (Allen, 1955) Siddiqi, 1971
- = *T. acti* Hopper, 1959
- = *T. nilgiriensis* Seshadri, Muthukrisnan & Shunmugan, 1967
- = *T. himalayae* (Mahajan, 1974) n. comb.
- = *Q. himalayae* Mahajan, 1974

* The names *Telotylenchus aerolatus* Baqri & Jairajpuri, 1969, and *Tylenchorhynchus aerolatus* Tobar-Jimenez, 1970, are based on "aerolations", a misspelling of the word "areolations". Emendations were proposed by Fortuner (1985). However, the Secretary of the International Commission of Zoological Nomenclature commented that, when an author deliberately uses a misspelled word to derive the name of a taxon, the scientific name is not in itself a *lapsus calami*, and it should be accepted as valid (Tubbs, *in litt.*). The emendations proposed by Fortuner (1985) are rejected and considered as junior objective synonyms.

- = *T. solani* (Maqbool, 1982) n. comb.
 = *Q. solani* Maqbool, 1982
T. chirchikensis Mavlyanov, 1978
T. chonai Sethi & Swarup, 1968
 = *Divittus chonai* (Sethi & Swarup, 1968) Jairajpuri, 1984
T. clarus Allen, 1955
 = *T. tener* Erzhanova, 1964
T. clathrocutis (Lewis & Golden, 1981) n. comb.
 = *Trilineellus clathrocutis* Lewis & Golden, 1981
T. clavicaudatus Seinhorst, 1963
 = *B. clavicaudatus* (Seinhorst, 1963) Siddiqi, 1986
T. claytoni Steiner, 1937
 = *Tessellus claytoni* (Steiner, 1937) Jairajpuri & Hunt, 1984
T. coffeae Siddiqi & Basir, 1959
T. contractus Loof, 1964
T. crassicaudatus Williams, 1960
 = *Paratrophurus crassicaudatus* (Williams, 1960) Andrásy, 1973
T. cristatus Ivanova, 1983
 = *Dolichorhynchus* (*Neodolichorhynchus*) *cristatus* (Ivanova, 1983) Siddiqi, 1986
T. curvus Williams, 1960
 = *Q. curvus* (Williams, 1960) Siddiqi, 1971
T. cuticaudatus Ray & Das, 1983
 = *B. cuticaudatus* (Ray & Das, 1983) Siddiqi, 1986
T. dactylurus Das, 1960
T. delhiensis Chawla, Bhamburkar, Khan & Prasad, 1968
T. depressus Jairajpuri, 1982
 = *T. (Bitylenchus) depressus* Jairajpuri, 1982
T. digitatus Das, 1960
T. divittatus Siddiqi, 1961
 = *Trilineellus divittatus* (Siddiqi, 1961) Lewis & Golden, 1981
 = *Divittus divittatus* (Siddiqi, 1961) Jairajpuri, 1984
 = *Morasinema divittatum* (Siddiqi, 1961) Javed, 1984
T. dubius (Bütschli, 1873) Filip'ev, 1936
 = *B. dubius* (Bütschli, 1873) Siddiqi, 1986
T. ebriensis Seinhorst, 1963
T. elegans Siddiqi, 1961
 = *T. goldeni* Rashid & Singh, 1982
T. eremicolus Allen, 1955
T. erevanicus Karapetjan, 1979
T. eroshenkoi Siddiqi, 1986
T. ewingi Hopper, 1959
T. flaccidus (Baidulova, 1984) n. comb.
 = *Telotylenchus flaccidus* Baidulova, 1984
T. georgiensis Eliashvili, 1971
T. germanii nom. nov.
 = *Dolichorhynchus* (*Dolichorhynchus*) *elegans* Germani & Luc, 1984
 = *T. elegans* (Germani & Luc, 1984) n. comb.
 nec *T. elegans* Siddiqi, 1961
T. gladiolatus Fortuner & Amougou, 1974
 = *D. (N.) gladiolatus* (Fortuner & Amougou, 1974) Mulk & Siddiqi, 1982
T. goffarti Sturhan, 1966
 = *B. goffarti* (Sturhan, 1966) Siddiqi, 1986
T. graciliformis Siddiqi & Siddiqi, 1983
T. haki Fotedar & Mahajan, 1971
T. hastulatus (Colbran, 1960) n. comb.
 = *Belonolaimus hastulatus* Colbran, 1960
 = *Telotylenchus hastulatus* (Colbran, 1960) Jairajpuri, 1963
T. hordei Khan, 1972
T. huesingi Paetzold, 1958
 = *B. huesingi* (Paetzold, 1958) Siddiqi, 1986
T. impar (Khan & Darekar, 1979) n. comb.
 = *Telotylenchus impar* Khan & Darekar, 1979
T. indicus (Siddiqi, 1960) n. comb.
 = *Telotylenchus indicus* Siddiqi, 1960
T. intervallatus nom. nov.
 = *T. aerolatus* Tobar-Jimenez, 1970
 = *T. areolatus** Fortuner, 1985
 = *Bitylenchus aerolatus* (Tobar-Jimenez, 1970) Siddiqi, 1986
 nec *T. aerolatus* (Baqri & Jairajpuri) n. comb.
T. irregularis Wu, 1969
T. judithae Andrásy, 1962
 = *D. (N.) judithae* (Andrásy, 1962) Mulk & Siddiqi, 1982
T. kashmirensis Mahajan, 1974
T. kegenicus Litvinova, 1946
T. kirjanovae Karapetjan, 1979
T. knoblochi nom. nov.
 = *T. tarjani* (Knobloch, 1975) n. comb.
 = *Q. tarjani* Knobloch, 1975
 nec *T. tarjani* Andrásy, 1969
T. labiatus (Jairajpuri, 1984) Siddiqi, 1986
 = *Divittus labiatus* Jairajpuri, 1984
T. lamelliferus (de Man, 1880) Filip'ev, 1936
 = *D. (D.) lamelliferus* (de Man, 1880) Mulk & Siddiqi, 1982
T. latus Allen, 1955
T. leviterminalis Siddiqi, Mukherjee & Dasgupta, 1982
 = *T. paranudus* Phukan & Sanwal, 1983
T. lineatus (Karapetjan, 1979) n. comb.
 = *Q. lineatus* Karapetjan, 1979
T. madrasensis Gupta & Uma, 1981
 = *Divittus madrasensis* (Gupta & Uma, 1981) Jairajpuri, 1984
T. manubriatus Litvinova, 1946
T. mashhoodi Siddiqi & Basir, 1959
T. maximus Allen, 1955
 = *B. maximus* (Allen, 1955) Siddiqi, 1986
T. mexicanus Knobloch & Laughlin, 1973
T. microconus Siddiqi, Mukherjee & Dasgupta, 1982
T. microphasmis Loof, 1960
 = *D. (N.) microphasmis* (Loof, 1960) Mulk & Siddiqi, 1982
T. minutus Karapetjan, 1979
T. mulki nom. nov.
 = *T. parvus* (Mulk & Siddiqi, 1982) n. comb.
 = *D. (D.) parvus* Mulk & Siddiqi, 1982
 nec *T. parvus* Allen, 1955
T. natalensis Kleynhans, 1984
 = *B. natalensis* (Kleynhans, 1984) Siddiqi, 1986
T. neoclavicaudatus Mathur & Lal, 1979
T. nigericus (Mulk & Jairajpuri, 1974) n. comb.
 = *D. (D.) nigericus* Mulk & Jairajpuri, 1974

- T. nordiensis* Khan & Nanjappa, 1974
= *Tylenchorhynchus aerolatus* Khan & Nanjappa, 1972
nec *T. aerolatus* (Baqri & Jairajpuri, 1969) n. comb.
nec *T. aerolatus* Tobar-Jimenez, 1970
- T. nudus* Allen, 1955
- T. obregonus* (Knobloch & Laughlin, 1973) n. comb.
= *Q. obregonus* Knobloch & Laughlin, 1973
- T. obscurisulcatus* Andrassy, 1959
= *Divittus obscurisulcatus* (Andrassy, 1959) Jairajpuri, 1984
- T. obtusus* (Siddiqi, 1978) n. comb.
= *Telotylenchus obtusus* Siddiqi, 1978
- T. oleraceae* Gupta & Uma, 1981
- T. paaloofi* (Tikyani & Khera, 1970) n. comb.
= *Telotylenchus paaloofi* Tikyani & Khera, 1970
= *Trichotylenchus paaloofi* (Tikyani & Khera, 1970) Jairajpuri, 1971
- T. pachys* Thorne & Malek, 1968
= *Tessellus pachys* (Thorne & Malek, 1968) Jairajpuri & Hunt, 1984
- T. paracti* (Ray & Das, 1983) n. comb.
= *Q. paracti* Ray & Das, 1983
- T. parvus* Allen, 1955
= *B. parvus* (Allen, 1955) Siddiqi, 1986
- T. penniseti* Gupta & Uma, 1980
- T. phaseoli* Sethi & Swarup, 1968
= *D. (D.) phaseoli* (Sethi & Swarup, 1968) Mulk & Jairajpuri, 1974
- T. pini* Kulinich, 1985
- T. prophasmi* (Jairajpuri & Hunt, 1984) n. comb.
= *D. (D.) prophasmi* Jairajpuri & Hunt, 1984
- T. pruni* Gupta & Uma, 1981
= *Divittus pruni* (Grupta & Uma, 1981) Jairajpuri, 1984
- T. punensis* Khan & Darekar, 1979
- T. punici* (Gupta & Uma, 1980) n. comb.
= *Q. punici* Gupta & Uma, 1980
- T. quaidi* Golden, Maqbool & Handoo, 1987
- T. queirozi* Monteiro & Lordello, 1976
= *B. queirozi* (Monteiro & Lordello, 1976) Siddiqi, 1986
- T. rayi* nom. nov.
= *T. impar* Ray & Das, 1983
nec *T. impar* (Khan & Darekar, 1979) n. comb.
- T. robustus* Thorne & Malek, 1968
= *T. robustoides** Thorne & Malek, 1968
- T. sacchari* Sivakumar & Muthukrishnan, 1983
- T. sanwali* Kumar, 1982
- T. sculptus* Seinhorst, 1963
= *Trilineellus sculptus* (Seinhorst, 1963) Lewis & Golden, 1981
- = *Divittus sculptus* (Seinhorst, 1963) Jairajpuri, 1984
= *Morasinema sculptum* (Seinhorst, 1963) Javed, 1984
- T. silvaticus* Ferris, 1963
- T. solani* Gupta & Uma, 1981
= *D. (N.) solani* (Gupta & Uma, 1981) Siddiqi, 1986
- T. spinaceae* Singh, 1976
- T. striatus* Allen, 1955
- T. sulcatus* de Guiran, 1967
= *D. (N.) sulcatus* (de Guiran, 1967) Mulk & Siddiqi, 1982
- T. swarupi* Singh & Khera, 1978
= *B. swarupi* (Singh & Khera, 1978) Siddiqi, 1986
- T. tarjani* Andrassy, 1969
- T. teeni* Hashim, 1984
= *B. teeni* (Hashim, 1984) Siddiqi, 1986
- T. tenuicaudatus* Wouts & Sher, 1981
- T. teres* (Khan & Darekar, 1979) Siddiqi, 1986
= *Telotylenchus teres* Khan & Darekar, 1979
- T. tobari* Sauer & Annells, 1981
= *B. tobari* (Sauer & Annells, 1981) Siddiqi, 1986
- T. tonkiensis* (Mulk & Jairajpuri, 1975) n. comb.
= *Telotylenchus tonkiensis* Mulk & Jairajpuri, 1975
- T. triglyphus* Seinhorst, 1963
= *Trilineellus triglyphus* (Seinhorst, 1963) Lewis & Golden, 1981
= *Divittus triglyphus* (Seinhorst, 1963) Jairajpuri, 1984
= *Morasinema triglyphus* (Seinhorst, 1963) Javed, 1984
- T. trilineatus* Timm, 1963
- T. tritici* Golden, Maqbool & Handoo, 1987
- T. tuberosus* (Maqbool, Ghazala & Fatima, 1984) n. comb.
= *D. (D.) tuberosus* Maqbool *et al.*, 1984
- T. variannus* Mavlyanov, 1978
- T. varicaudatus* Singh, 1971
- T. velatus* Sauer & Annells, 1981
- T. ventralis* (Loof, 1963) n. comb.
= *Telotylenchus ventralis* Loof, 1963
= *Trichotylenchus ventralis* (Loof, 1963) Jairajpuri, 1971
- T. ventrosignatus* Tobar-Jimenez, 1969
= *B. ventrosignatus* (Tobar-Jimenez, 1969) Siddiqi, 1986
- T. verutus* (Kleynhans, 1975) n. comb.
= *Telotylenchus verutus* Kleynhans, 1975
- T. vulgaris* Upadhyay, Swarup & Sethi, 1972
= *B. vulgaris* (Upadhyay *et al.*, 1972) Siddiqi, 1986
- T. wilskii* Kornobis, 1980
= *B. wilskii* (Kornobis, 1980) Siddiqi, 1986
- T. zaeae* Sethi & Swarup, 1968

COMMENTS

* Thorne and Malek (1968) proposed *Tylenchorhynchus robustus*. According to some reports (Smolik, *in litt.*; Siddiqi, *in litt.*) Thorne and Malek later replaced this name with *T. robustoides*, probably because they thought it was a secondary homonym of *T. robustus* (de Man, 1876) Micoletzky, 1922. In fact, the latter species is the type species of the genus *Rotylenchus* since 1936. Since it is not congeneric with the taxon described by Thorne and Malek, the replacement name *T. robustoides* must be rejected. It becomes a junior objective synonym of *T. robustus* Thorne & Malek, 1968.

Tylenchorhynchus is very similar to *Merlinius* in general body shape (shapes of both extremities, oesophagus, etc.). It differs from this genus by SEM face view (*Merlinius* generally has ancestral six sectors still visible or it has a characteristic lemon shape with disc and lateral sectors fused. This derived shape is unknown in *Tylenchorhynchus*), and by spicule shape (without velum in *Merlinius*). The number of lateral field lines (2 to 5 *vs* 6) permits an easy identification of these two genera.

Some species in *Tylenchorhynchus* resemble the genus *Trichotylenchus*, but this latter taxon is restricted to forms with labial region continuous with body contours, stylet slender, and tail long and thin, cylindroid to broadly rounded or clavate end.

Species in *Amplimerlinius* and *Paratrophurus* have labial region continuous with body contours, stylet and labial framework medium to strong, and tails cylindroid, medium to short, thick, with broadly rounded ends.

The species in *Tylenchorhynchus* have several characteristics that are somewhat unusual amongst *Tylenchina* in the sense that they are at the same time easy to recognize and reasonably constant within any given species. These characters (number of lines in lateral field, presence of longitudinal ridges, etc.) can easily isolate groups of species and they are a great help for identification. The temptation was great to give a nomenclatural status to such groups by naming them as genera. Following the action of Siddiqi (1970) who proposed the new genus *Merlinius* for some species in *Tylenchorhynchus*, several authors have made such nomenclatorial moves.

We are opposed to such actions because the differences observed in cuticular features often mask a deeper similarity, or even identity, in the internal organs. Also each cuticular character seems to be evolving independently from the others. For example, the presence of longitudinal ridges is independent of the number of lines in the lateral field, of areolation of these fields, and of the morphology of the anterior region. Using such characters to create genera result in the multiplication of small groups that do not indicate a clear evolutionary trend. In the present article, we will not accept superficial resemblances as generic differentiating criteria. This explains the long list of genera proposed as synonyms of *Tylenchorhynchus*.

Telotylenchus, a genus proposed here as a synonym, is quite different from the genera just discussed in the sense that it was differentiated on much firmer grounds, at least at the time it was proposed (Siddiqi, 1960). It remained valid, if not unchallenged, for a quarter of a century. It was considered to be quite separate from *Tylenchorhynchus* because of an overlap of the intestine by the oesophageal glands. However, Goodey (1963) and Loof (1963) noted that the two genera were in complete agreement except for this one character. Both authors accepted the genus as valid but rejected the subfamily *Telotylenchinae* proposed by Siddiqi together with his new genus. This position has recently been reaffirmed by Loof (1987). Seinhorst (1971) questioned the value of glandular overlap as a criterion for higher level classification. He noted that intermediate forms exist between the two glandular morphologies described as typical in the two genera under discussion. *Tylenchorhynchus brassicae*, *T. clarus*, *T. indicus* and *T. mashhoodi* have glands slightly overlapping, and have the dorsal gland nucleus in the posterior half of the gland. He

concluded that these species might be transferred to *Telotylenchus* if this genus were redefined to include species with oesophageal lumen shifted laterally between the dorsal and one subventral gland, accompanied or not by a glandular overlap. He refrained from making this move because of the great similarity between the species with abutting glands and those with a slight overlap.

Because the two characters used (gland overlap and lumen shift) are at best secondary characters, and because the exact glandular structure is not known for most species, *Telotylenchus* Siddiqi, 1960 is here proposed as a new junior synonym of *Tylenchorhynchus*.

Quinisulcius was proposed by Siddiqi (1971a) for the species in *Tylenchorhynchus* with five lines in the lateral field. Siddiqi added a few other differentiating characters: habitus often well curved, deirids frequently present, small-sized spicule velum, and gubernaculum bent backwards. Tarjan (1973) considered that the number of lines was the only distinctive character. He added two secondary differentiating criteria, i. e. lateral field generally not areolated, and lip region usually offset.

From the descriptions of the fourteen species currently in the genus (*Q. capitatus*, type species, *Q. acti*, *Q. acutoides*, *Q. acutus*, *Q. cacti*, *Q. curvus*, *Q. himalayae*, *Q. lineatus*, *Q. nilgiriensis*, *Q. obregonus*, *Q. paracti*, *Q. punici*, *Q. solani*, *Q. tarjani*), the bent gubernaculum is the only consistent character, and it has been observed in the three species where males are known. However, it should be noted that this character can vary in other taxa, when it is observed from a good number of specimens (*Tylenchorhynchus aerolatus*). Deirids are described in only two species (*Q. acutoides*, *Q. acutus*). The rest of the characters are either variable in the genus (lip region varies from offset to almost continuous, habitus varies from almost straight to spiral), or they are not really different from the characters in *Tylenchorhynchus* (size of spicule, presence of velum, lateral field areolations). All other characters are quite identical in the two genera, including general appearance, tail shape in female and males specimens, digestive and reproductive systems. SEM face views also are similar (compare Figs 4 B and 5 B in Sher & Bell, 1975).

The only real difference remains the number of lines in the lateral field. Siddiqi (1986, page 174) comments that this number is "a character found to be variable in... *Tylenchorhynchus*". In SEM micrograph pictures of *Q. acti* (Vovlas, 1983) and in cross section of *Q. cacti* (Chawla *et al.*, 1968), the fifth, central line is shallower and less marked than the other four lines. The five-line field of *Quinisulcius* can be seen as a slight deviation from the basic four-line field of *Tylenchorhynchus*. The presence of an additional line in the lateral field is certainly an interesting feature for species identification. It has no value for genus differentiation.

Quinisulcius is here proposed as a new junior synonym of *Tylenchorhynchus*.

Dolichorhynchus was differentiated by Mulk and Jairajpuri (1974) from *Tylenchorhynchus* by the notched male caudal alae, head bilobed, and body cuticle marked by prominent longitudinal and transverse striae. It included only two species (*D. phaseoli*, type species, and *D. nigericus*).

Mulk and Siddiqi (1982) rejected the notched alae as a valid generic criterion but they redefined the genus as having prominent longitudinal ridges over entire body, and lateral field with four lines (three ridges). According to this new diagnosis, they transferred five species to the genus (*D. gladiolatus*, *D. judithae*, *D. lamelliferus*, *D. microphasmis*, *D. sulcatus*). Two more species were later described in the genus, *D. elegans* and *D. prophasmsis*.

Notched caudal alae have been described for *Merlinius brachycephalus* and *Tylenchorhynchus lamelliferus*. On the other hand, at least some specimens of *D. nigericus* have non-notched alae, according to Fig. 1M in Mulk and Jairajpuri (1974). We therefore agree with Mulk and Siddiqi (1982) that notched caudal alae is not a valid criterion.

True structure of longitudinal ridges and lateral field can be seen only in cross section or SEM micrographs. Cross sections have been illustrated for a few species in the genus under discussion. Longitudinal ridges are very prominent in *D. elegans*, *D. phaseoli*, *D. parvus*, and *D. sulcatus*. However their structure in the first two species where the ridges are isolated from each other, is very different from the structure in the last two, where they are adjacent. In *D. gladiolatus*, ridges are adjacent and no more prominent than in *Tylenchorhynchus claytoni*.

The lateral fields are composed of three adjacent ridges (forming four lines) in *D. sulcatus* and *D. gladiolatus*; of three ridges forming either four or six lines depending how far apart they are from each other in *D. prophasmsis*; and of only one ridge forming two lines in *D. phaseoli*, *D. parvus* and *D. elegans*.

Because of these widely different structures, and because ridges are attested in several genera where they are associated with lateral fields with two, three, four, and six lines, it is concluded that ridges and lateral field lines cannot be used to differentiate the genus *Dolichorhynchus*.

Bilobed anterior extremities are described for several species in the genus, but only SEM micrographs can be trusted to reveal the true aspect of this character. *D. elegans* SEM face view shows a round labial disc and six well-marked labial sectors. A deeper groove separates each couplet of submedian sectors. *D. prophasmsis* also has grooves between lip sectors, more pronounced between submedian sectors. Similar grooves exist in *T. tobari* (original description) and *T. goffarti* in Sher and Bell (1975). Because the exact morphology of the anterior end is known for only a few species, and because similar shapes exist in *Tylenchorhynchus*, this character cannot be used at this time to differentiate the genus.

Dolichorhynchus Mulk & Jairajpuri, 1974 is here

proposed as a new junior synonym of *Tylenchorhynchus*.

The name *Dolichorhynchus* is an homonym of *Dolichorhynchus* Willey, 1901, a Cephalocordata related to *Amphioxus*. It is here rejected and replaced by an available synonym, *Tylenchorhynchus*, according to Article 60 (b) of the International Code of Zoological Nomenclature. The specific names of the taxa proposed in *Dolichorhynchus* are available according to Article 11 (h) (iii) (1). They are accepted here as new combinations.

The use of shape of labial region and structure of lateral field lines in the definition of the genus *Dolichorhynchus* prompted several authors to propose other genera defined by various combinations of the characters in question (see Tab. 1, summarizing the article of Jairajpuri and Hunt, 1984). The diagnoses of the four

Table 1
Differentiation of four genera related to *Tylenchorhynchus*

Genus	Lateral field : lines/areal.	Labial region : offset/bilobed	Cut. annuli coarse
<i>Trilineellus</i>	3:no	no no	yes
<i>Dolichorhynchus</i>	4:yes	yes-no yes	no
<i>Neodolichorhynchus</i>	4 no or incomplete	yes yes	no
<i>Tessellus</i>	4:no	no no	yes

genera here considered (Tab. 1) are not always consistent with the descriptions of the species included. For example, *Tessellus claytoni* has the lateral field areolated at least partially and the head offset, *Neodolichorhynchus sulcatus* has lateral field completely areolated, *Dolichorhynchus parvus* and *D. elegans* only have two lines (one ridge) in the lateral field, etc. The lateral field of *Trilineellus clathrocutis* is composed of two ridges that form three or four lines depending how close the ridges are from each other. This is evident on the SEM pictures of the field published with the original description of the type species and in Sauer (1986). Also the generic criteria are not consistently used in these related genera. For example, lip region offset *vs* continuous is used to differentiate *Tessellus* from *Neodolichorhynchus*. Lips are offset in *Dolichorhynchus* except in *D. lamelliferus*. If the character "lip region offset" were accepted in the definition of the first two genera, consistency would require creation of another genus for *D. lamelliferus*. Finally species described since the proposal of these genera do not fit well with any of the generic diagnoses. *D. elegans* has caudal alae notched as in *Dolichorhynchus*, and a non-areolated lateral field as in *Neodolichorhynchus*. It becomes evident that all these characters are at best specific characters and should not be used to differentiate genera. Consequently *Tessellus*, *Trilineellus*, and *Neodolichorhynchus* are considered as junior synonyms of *Tylenchorhynchus*.

Siddiqi (1986) treated *Neodolichorhynchus* as a valid subgenus under *Dolichorhynchus*. He differentiated it from *Dolichorhynchus* (*Dolichorhynchus*) mostly by the absence *vs* presence of minute vulval flaps. Vulval flaps are symmetrical outgrowths found on the lateral sides of the vulva. *D. (Dolichorhynchus) phaseoli* (type species of the subgenus) was redescribed by Samsoen and Geraert (1975) from a local population in Cameroon. The latero-ventral ridges (the two longitudinal ridges that are closest to the ventral one) are raised and strengthened at the vulva level to form the flaps. The original description of *D. (Neodolichorhynchus) sulcatus* indicated that the latero-ventral ridges disappear at the vulva level (de Guiran, 1967). Jairajpuri and Hunt (1984) and Siddiqi (1986) failed to indicate what evolutionary significance (if any) they attach to this difference in structure between the two species above. It is easy to define groups of species sharing one or two characteristics, but it takes more to show that these forms are phylogenetically related. Vulval flaps occur in many taxa throughout Tylenchina and this character is of doubtful value as a marker of phylogenetic relationships.

Vulval flaps are mentioned, sometimes with reservations, in the species grouped by Siddiqi (1986) under the subgenus *Dolichorhynchus*. In *D. (D.) elegans* an examination of paratypes revealed the presence of very faint vulval flaps, most probably formed by the division of the ventral longitudinal groove as described in *D. phaseoli* by Samsoen and Geraert (1975). Vulval structures were not described in any of the species placed in the subgenus *Neodolichorhynchus*. It is not proper to infer the absence of a structure in a species because the structure is not mentioned in its description.

Neodolichorhynchus is again rejected.

Divittus Jairajpuri, 1984 and *Morasinema* Javed, 1984 were proposed the same day (20 July 1984) with the same type species *Tylenchorhynchus divittatus*. Jairajpuri (1984), acting as first revisor, rejected *Morasinema* as junior objective synonym.

Divittus was characterized by three lines in the lateral field, and the absence of longitudinal ridges on body. Consistent with the discussions above, these characters are not accepted as diagnostic at the generic level, and *Divittus* is here considered as a junior synonym of *Tylenchorhynchus*. *Divittus* (= *Morasinema*), and *Tessellus* were considered to be synonymous with *Tylenchorhynchus* by Siddiqi (1986).

Bitylenchus was proposed as a subgenus under *Tylenchus* and differentiated from three other related subgenera (*Tylenchus*, *Tylenchorhynchus*, and *Chitinotylenchus*) by the absence of a labial framework and the presence of two genital branches (Filip'ev, 1934).

Jairajpuri (1982) published a study of *Bitylenchus* as a subgenus under *Tylenchorhynchus*, including a short description and a key to its species. He failed to provide a differentiating statement to establish its relationships with other related subgenera. He indicated that a com-

plete discussion for the re-establishment of *Bitylenchus* was to be published in *Nematologia mediterranea*; this article has not appeared in that or any other journal. Siddiqi (1986) formally reinstated *Bitylenchus* as a valid genus with *B. dubius* (Bütschli) as type, a species remarkably similar to *Tylenchorhynchus* in general appearance. Siddiqi differentiated *Bitylenchus* by the areolation of the lateral field outer bands, and the presence of a non protrusible gubernaculum. In the diagnosis of the genus, he also highlighted the presence of a large post-anal intestinal sac, intestinal fasciculi, and he noted that the female tail tip had a relatively thicker cuticle. These characteristics are absent or doubtful in some of the species placed by Siddiqi (1986) under *Bitylenchus*. For example, *B. areolatus* has lateral fields areolated, but it has no post-anal sac, no fasciculi, the cuticle at the female tail tip is not particularly thick, and the gubernaculum protrudes from the cloaca. In *B. tobari* all three bands of the lateral fields are areolated. Post-anal sac is absent from this species and from *B. ventrosignatus*. *B. goffarti* and *B. queirozi* have protruding gubernaculum. Generally speaking, the characters used by Siddiqi to redefine *Bitylenchus* often were not reported by the authors of original species descriptions. Some may be inferred from the illustrations but with a high risk of error when no text backs the figures.

Some of the species left in *Tylenchorhynchus* by Siddiqi (1986) possess some of the criteria he gave as distinctive of *Bitylenchus*. For example, the outer bands of the lateral fields of *T. antarcticus* are areolated; *T. agri* has a large post-anal sac; *T. cylindricus* has intestinal fasciculi; the female tail tip of *T. contractus* has thicker cuticle; *T. claytoni* has a gubernaculum that does not protrude from the cloaca; etc.

Bitylenchus sensu Siddiqi (1986) was defined using very secondary characteristics that are not known for many taxa, and that, when known, do not clearly differentiate this genus from *Tylenchorhynchus*. *Bitylenchus* is again considered as a junior synonym of *Tylenchorhynchus*.

***Trichotylenchus* Whitehead, 1960**
= *Uliginotylenchus* Siddiqi, 1971

DIAGNOSIS

Telotylenchinae. Lip region continuous with body contour. In SEM face views, oral disc lemon-shaped, submedian lobes low and flattened, lateral lobes completely regressed, amphids apertures appears as slits or pores at lateral edge of labial disc. Stylet attenuated, 15-25 µm long, with needle-like cone (somewhat stronger in *T. palustris*). Lateral field areolated, with three lines. Deirids absent. Tail long, three to six times as long as wide, cylindroid, with a broadly rounded or clavate end, sometimes with thicker cuticle at tail tip. Males

spicules with well developed velum, and bent gubernaculum.

TYPE SPECIES

Trichotylenchus falciformis Whitehead, 1960

OTHER SPECIES

- T. astriatus* Khan & Nanjappa, 1971
= *T. trilokiae* Singh, 1971
- T. bifasciatus* (Andrássy, 1961) n. comb.*
= *Tylenchorhynchus bifasciatus* Andrásy, 1961
- T. palustris* (Merny & Germani, 1968) Seinhorst, 1971
- T. papyrus* (Siddiqi, 1970) Seinhorst, 1971
- T. rectangularis* Netscher & Germani, 1969
- T. rhopalocercus* (Seinhorst, 1963) Seinhorst, 1968
- T. uliginosus* (Siddiqi, 1970) Seinhorst, 1971
= *Uliginotylenchus uliginosus* (Siddiqi, 1970) Siddiqi, 1971

COMMENTS

Trichotylenchus was originally characterized by overlapping glands and placed under Belonolaiminae, then Telotylenchinae. Seinhorst (1971) commented on the resemblance between *Trichotylenchus* and those species in *Tylenchorhynchus* that were later placed by Siddiqi (1971a) in the new genus *Uliginotylenchus*. The only difference between the two genera is the absence of a glandular overlap in *Uliginotylenchus*. According to Seinhorst (1971), in all species the oesophageal lumen is asymmetrically shifted between the dorsal and one subventral gland.

Tarjan (1973) rejected the analysis of Seinhorst (1971) because :

1) Glandular overlap is a good classification criterion. It has been argued throughout the present review that it is not.

2) *U. palustris* does not have a slender stylet with needle-like cone. Paratypes of this species have been examined by the present authors. Stylet is not "rather strong" as indicated in the original description, but of a thickness average for tylenchorhynchids. It is true that its cone is not "needle-like", but stronger. Nevertheless, all other character fit comfortably with the generic data.

3) *T. rectangularis* has four lines in the lateral field. Our examination of paratypes showed that there are only three lines, as indicated in the original description.

4) *T. rectangularis* and *T. palustris* have cylindrical tails whereas the rest of the species have tails with clavate extremities. Examination of paratypes showed that *T. rectangularis* tail ends, while not clavate, are more

* Siddiqi (1986) cites Seinhorst, 1971 as the authority for *Trichotylenchus bifasciatus*. Seinhorst (1971) noted that "*T. bifascians*" (*sic*) probably should be placed in *Trichotylenchus*, but he did not made the transfer.

broadly rounded than shown in the original figure. In fact tails of all the species under discussion have the same general shape : long, cylindroid, with a broadly rounded end. Some are more clavate, others are regularly cylindroid, but this should not be considered at generic level.

Following the conclusions of Seinhorst (1971), the basic resemblance between *Trichotylenchus* and *Uliginotylenchus* is here recognized. Consequently, *Uliginotylenchus* Siddiqi, 1971 is proposed as a new junior synonym of *Trichotylenchus*.

Trichotylenchus is characterized among other Telotylenchinae by the shape of labial region, which is elevated and continuous with the body contour and by the tail long, thin, and cylindroid. The slender stylet with needle-like cone is similar to some species in *Tylenchorhynchus*. The lemon shaped disc and lateral sectors are found also in *Merlinius* and *Morulaimus*.

***Paratrophurus* Arias, 1970**

- = *Histotylenchus* Siddiqi, 1971
- = *Telotylenchoides* Siddiqi, 1971

DIAGNOSIS

Telotylenchinae. Body medium sized. Anterior extremity usually bullet shaped, more rarely a little flattened; continuous with body contours, very rarely slightly offset. Face view (SEM) quadrangular. Stylet 20-25 µm long. Lateral field with four lines. Deirids present. Tail short ($c' = 1.5-2.5$), cylindroid with broadly rounded end. Protoplasmic contents of tail often regressed. Oesophageal glands abutting or overlapping the intestine. Male : spicules with velum.

TYPE SPECIES

P. loofi Arias, 1970

OTHER SPECIES

- P. acristylus* Siddiqi & Siddiqi, 1983
- P. anomalus* Kleynhans & Heyns, 1983
- P. baouensis* (Netscher & Germani, 1969) n. comb.
= *Telotylenchus baouensis* Netscher & Germani, 1969
- P. bursifer* (Loof, 1960) Siddiqi, 1971
- P. dissitus* (Colbran, 1969) Siddiqi, 1971
- P. hedys* (Kleynhans, 1975) n. comb.
= *H. hedys* Kleynhans, 1975
- P. histoides* (Siddiqi, 1971) n. comb.
= *H. histoides* Siddiqi, 1971
- P. historicus* (Jairajpuri & Baqri, 1968) n. comb.
= *Telotylenchus historicus* Jairajpuri & Baqri, 1968
- P. housei* (Raski, Prasad & Swarup, 1964) n. comb.
= *Telotylenchus housei* Raski, Prasad & Swarup, 1964
- P. hungaricus* Andrásy, 1973
- P. kenani* Decker & El Amin, 1978

- P. lobatus* Loof & Yassin, 1971
P. sudanensis Decker, Yassin & Al Amin, 1975
P. siddiqii nom. nov.
 = *H. sudanensis* Siddiqi, 1977
 nec *P. sudanensis* Decker, Yassin & Al Amin, 1975

COMMENTS

When Siddiqi (1971*b*) described *Histotylenchus* and *Telotylenchoides*, the former genus was not compared to *Paratrophurus*, and the latter was said to differ from this genus only by its overlapping glands. Both new genera had overlapping glands, but the overlap in *Telotylenchoides* was said to differ from that in *Telotylenchus*, *Trichotylenchus* and *Histotylenchus* in that the dorsal nucleus was close to the oesophago-intestinal junction, with the subventral nuclei anterior to it. However the same author (Siddiqi, 1977) later described *Histotylenchus sudanensis* with subventral nuclei opposite or anterior to the oesophago-intestinal junction. From the illustrations in Siddiqi (1971*b*), the dorsal nucleus lies 5 to 11 μm posterior to the junction in *Telotylenchoides*, 20 μm posterior in *Telotylenchus*, and 36 μm posterior in *Histotylenchus*. This slight difference in measurements is not considered diagnostic at the generic level. The shape of the anterior end is somewhat more rectangular in *Histotylenchus*, and more conoid-rounded in *Paratrophurus* and *Telotylenchus*. This difference seems slight and inconclusive. Lateral fields are said to be areolated over entire body in *Histotylenchus*, but not areolated in the other two genera. Lateral field areolations are at best a specific character as demonstrated once again when Siddiqi (1977) described *Histotylenchus sudanensis* without areolations except in oesophageal region and a few lines in outer bands over rest of body.

The lumen of the stylet cone was said to be asymmetrical near its base in *Histotylenchus*. The stylet lumen is very difficult to observe with the light microscope. In the absence of special preparation techniques, this structure is seen as light refractions that change with focus.

By contrast with these slight differences in details, there are many features in common among the species of all three genera, including their general appearance, SEM face view, etc. *Histotylenchus* and *Telotylenchoides* are here proposed as new synonyms of *Paratrophurus*.

The genus differs from *Tylenchorhynchus* mostly by the shape of the tail, which is short, cylindroid, and has a broadly rounded end. It is interesting to note that, while the relative length of tail is well within the range of values for belonolaimids ($c' = 2$ to 3.5), the protoplasmic contents of the tail, in the species with a thick distal tail cuticle, has a relative length of 1.5 to 2 anal body widths, similar to ratio c' in hoplolaimids. Tails in *Paratrophurus* seem to be experiencing an axial, symmetrical regression that eventually would result in tails as short as those in Hoplolaimidae.

Paratrophurus differs from *Trichotylenchus*, a genus also with cylindroid tail, by the tail being relatively

shorter (c' less than 2.5 vs more than 3 in *Trichotylenchus*), and by SEM face view, quadrangular instead of lemon shaped in *Trichotylenchus*. *Amplimerlinius* resembles *Paratrophurus* in general appearance, but differs from it by SEM face view, and by male spicules without velum. Also, *Amplimerlinius* species all have six lines in the lateral field.

- Merlinius* Siddiqi, 1970**
 = *Scutylenchus* Jairajpuri, 1971

DIAGNOSIS

Telotylenchinae. Body medium sized. Lateral field with six lines (eight lines in *M. koreanus*, though only six are visible in lateral view). Longitudinal ridges sometimes present (*M. koreanus*). Deirids, when present, at a level where the lateral field has only four lines. Tail medium sized ($c' = 2-4$), conoid, never with thickened cuticle in distal portion. Labial region continuous to slightly offset. SEM face view typically with oval labial disc surrounded with six-sectored first lip annulus, submedian sectors somewhat flattened. Labial region annuli interrupted by longitudinal striations or grooves. Stylet generally medium sized, 20-25 μm long, sometimes shorter (10 μm) or longer (up to 40-50 μm), cone sometimes needle shaped. Male spicules without well developed velum, cylindroid, blunt ended. Gubernaculum not protruding from cloaca.

TYPE SPECIES

- M. brevidens* (Allen, 1955) Siddiqi, 1970
 = *Tylenchorhynchus brevidens* Allen, 1955

OTHER SPECIES

- M. adakensis* Bernard, 1984
M. affinis (Allen, 1955) Siddiqi, 1970
 = *Nagelus affinis* (Allen, 1955) Siddiqi, 1979
M. alboranensis (Tobar-Jimenez, 1970) Tarjan, 1973
 = *N. alboranensis* (Tobar-Jimenez, 1970) Siddiqi, 1986
M. alpinus (Allen, 1955) Siddiqi, 1970
 = *N. alpinus* (Allen, 1955) Siddiqi, 1979
M. apricus (Andrássy, 1980) n. comb.
 = *S. apricus* Andrásy, 1980
M. bavaricus (Sturhan, 1966) Siddiqi, 1970
M. bijnorensis Khan, 1971
M. bogdanovikatjkovi (Kir'yanova, 1941) Siddiqi, 1970
M. capitonis Ivanova, 1983
M. circellus Anderson & Ebsary, 1982
M. conicus (Allen, 1955) Siddiqi, 1970
 = *N. conicus* (Allen, 1955) Siddiqi, 1979
M. curiosus (Wilski, 1965) Sher, 1974
 = *N. curiosus* (Wilski, 1965) Siddiqi, 1986
M. cylindricaudatus (Ivanova, 1968) Siddiqi, 1970
 = *S. cylindricaudatus* (Ivanova, 1968) Siddiqi, 1979
M. falcatus Eroshenko, 1981
 = *N. falcatus* (Eroshenko, 1981) Siddiqi, 1986

- M. gaudialis* (Izatullaeva, 1967) Siddiqi, 1986
M. graminicola (Kir'yanova, 1951) Siddiqi, 1976
M. grandis (Allen, 1955) Siddiqi, 1970
 = *N. grandis* (Allen, 1955) Siddiqi, 1979
M. hexagrammus (Sturhan, 1966) Siddiqi, 1970
 = *N. hexagrammus* (Sturhan, 1966) Siddiqi, 1979
 = *M. berberidis* (Sethi & Swarup, 1968) Siddiqi, 1970
M. hexincisus (Jairajpuri & Baqri, 1968) Siddiqi, 1970
 = *S. hexincisus* (Jairajpuri & Baqri, 1968) Siddiqi, 1979
M. joctus (Thorne, 1949) Sher, 1974
M. koreanus Choi & Geraert, 1971
 = *S. koreanus* (Choi & Geraert, 1971) Siddiqi, 1979
M. laminatus (Wu, 1969) Siddiqi, 1970
 = *S. laminatus* (Wu, 1969) Anderson & Ebsary, 1982
M. lenorus (Brown, 1956) Siddiqi, 1970
 = *S. lenorus* (Brown, 1956) Siddiqi, 1979
M. lineatus (Allen, 1955) Siddiqi, 1970
 = *N. lineatus* (Allen, 1955) Siddiqi, 1979
M. longus (Wu, 1969) Sturhan, 1981
 = *Geocenamus longus* (Wu, 1969) Tarjan, 1973
 = *S. longus* (Wu, 1969) Skwiercz, 1984
M. loofi Siddiqi, 1979
M. macrodens (Allen, 1955) Siddiqi, 1970
 = *N. macrodens* (Allen, 1955) Siddiqi, 1979
M. macrophasmidus Khan & Darekar, 1979
 = *N. macrophasmidus* (Khan & Darekar, 1979) Siddiqi, 1986
M. mamillatus (Tobar-Jimenez, 1970) Anderson, 1977
 = *Scutylechus mamillatus* (Tobar-Jimenez, 1970) Jairajpuri, 1971
M. microdorus (Geraert, 1966) Siddiqi, 1970
M. nanus (Allen, 1955) Siddiqi, 1970
M. neohexagrammus Ivanova, 1978
 = *N. neohexagrammus* (Ivanova, 1978) Siddiqi, 1986
M. niazae Maqbool, Fatima & Hashmi, 1983
M. nothus (Allen, 1955) Siddiqi, 1970
M. paramonovi Volkova, 1972
M. planitierum Eroshenko, 1984
M. plerorbus Anderson & Ebsary, 1982
M. processus Siddiqi, 1979
M. productus (Thorne, 1949) Sher, 1974
M. pseudobavaricus Saltukoglu, Geraert & Coomans, 1976
M. quadrifer (Andrássy, 1954) Siddiqi, 1970
 = *S. quadrifer* (Andrássy, 1954) Siddiqi, 1979
 = *S. ornatus* (Allen, 1955) Siddiqi, 1979
M. quettensis (Maqbool, Ghazala & Fatima, 1984) n. comb.
 = *S. quettensis* Maqbool, Ghazala & Fatima, 1984
M. rugosus (Siddiqi, 1963) Siddiqi, 1970
 = *S. rugosus* (Siddiqi, 1963) Siddiqi, 1979
M. salechardicus Nesterov, 1985
M. semicircularis Luth, 1984
M. siddiqii Mulk, 1978
 = *S. siddiqii* (Mulk, 1978) Skwiercz, 1984
M. sobolevi (Mukhina, 1970) Tarjan, 1973
 = *S. sobolevi* (Mukhina, 1970) Siddiqi, 1979
M. sphaerocephalus (Ivanova, 1982) n. comb.
 = *S. sphaerocephalus* Ivanova, 1982
M. stegus (Thorne & Malek, 1968) Siddiqi, 1970
 = *S. stegus* (Thorne & Malek, 1968) Siddiqi, 1979
M. superbus (Allen, 1955) Siddiqi, 1970
 = *N. superbus* (Allen, 1955) Siddiqi, 1979
M. tartuensis (Krall', 1959) Siddiqi, 1970
 = *S. tartuensis* (Krall', 1959) Siddiqi, 1979
M. tatrensis (Sabova, 1967) Tarjan, 1973
 = *N. tatrensis* (Sabova, 1967) Siddiqi, 1986
M. tessellatus (Goodey, 1952) Siddiqi, 1970
 = *S. tessellatus* (Goodey, 1952) Siddiqi, 1979
M. tetylus Anderson & Ebsary, 1982
M. thomasi (Skwiercz, 1984) n. comb.
 = *S. thomasi* Skwiercz, 1984
M. tortilis Kazachenko, 1980
M. tumensis (Skwiercz, 1984) n. comb.
 = *S. tumensis* Skwiercz, 1984
M. undyferrus (Haque, 1967) Siddiqi, 1970
M. variabilis (Ivanova & Shagalina, 1983) n. comb.
 = *S. variabilis* Ivanova & Shagalina, 1983
M. varians (Thorne & Malek, 1968) Siddiqi, 1970
 = *N. varians* (Thorne & Malek, 1968) Siddiqi, 1986

COMMENTS

Scutylechus was originally proposed for *Tylenchorhynchus mamillatus* Tobar-Jimenez, 1966 and differentiated by the large phasmids, sloping stylet knobs, areolated lateral field, and digitate tail tip. After Anderson (1977) and Hooper (1978) proposed this genus as a junior synonym of *Merlinius*, Siddiqi (1979) revalidated it because of the longitudinal grooves that are divided by transverse striae into small blocks, and by the absence of deirids in *S. mamillatus*.

Because phasmids in *S. mamillatus* are no larger than phasmids in *Merlinius*, because cuticular details are not accepted as diagnostic at generic level, and because the rest of the characters proposed to differentiate *Scutylechus* are common in species of Telotylenchinae, *Scutylechus* is again considered to be a junior synonym of *Merlinius*.

Merlinius is accepted as a valid genus because of the differences in face view, and male spicule structure. The six-line lateral field makes it easy to identify this genus and differentiate its species from those in the related genus *Tylenchorhynchus*.

***Nagelus* Thorne & Malek, 1968**

DIAGNOSIS

Telotylenchinae. SEM face view broadly oval, and laterally elongated, with labial disc partially or completely fused with first lip annulus, lip annulus sectors also partially or completely fused together. Amphids apertures within the structure made by the first annulus and labial disc. The rest of labial annuli without longitudinal grooves or indentations. Deirids present in the lateral field at a level where the field has six lines. Tail irregularly conoid, with a distal hyaline part. Male spicules

without well developed velum, cylindroid, blunt ended. Gubernaculum not protruding from cloaca.

TYPE SPECIES

N. aberrans Thorne & Malek, 1968

OTHER SPECIES

See list in Powers, Baldwin and Bell (1983)

COMMENTS

Powers, Baldwin and Bell (1983) recently reviewed this genus, and differentiated it from *Merlinius* mostly by the structure of the anterior end, as seen in SEM face view, and by the lack of longitudinal lip striations, position of deirids, and hyaline tail extremity. It shares these characters with *Amplimerlinius*, but *Nagelus* can be differentiated from this genus by SEM face view, more oval, slightly offset lip region, and female tail conoid.

***Amplimerlinius* Siddiqi, 1976**

DIAGNOSIS

Telotylenchinae. Body medium to large (1 to 2 mm). Labial region continuous with body contour. SEM face view similar to that of *Nagelus* except that it is more rounded. Lateral field with six lines over most of body. Deirids present, in the six-line area of lateral field. Tail cylindroid with a broadly rounded terminus, with thickened cuticle at distal extremity. Labial framework and stylet robust. Oesophageal glands sometimes overlapping the beginning of the intestine for a short distance. Male spicules without well developed velum, blunt ended. Gubernaculum not protruding from cloaca.

TYPE SPECIES

A. amplius Siddiqi, 1976

OTHER SPECIES

- Amplimerlinius clavicaudatus* (Choi & Geraert, 1975) Siddiqi, 1976
 - = *Merlinius clavicaudatus* Choi & Geraert, 1975
- A. caroli* (Fortuner, 1985) Siddiqi, 1986
 - = *Aphelenchus dubius* Steiner, 1914 in Goodey, 1932
- A. icarus* (Wallace & Greet, 1964) Siddiqi, 1976
 - = *Tylenchorhynchus icarus* Wallace & Greet, 1964
- A. intermedius* (Bravo, 1976) Siddiqi, 1976
 - = *Merlinius intermedius* Bravo, 1976
- A. macrurus* (Goodey, 1932) Siddiqi, 1976
 - = *Aphelenchus dubius* Steiner, 1914
 - nec *Tylenchus dubius* Bütschli, 1873
- A. omentelus* Kleynhans & Heyns, 1983
- A. siddiqii* Mancini, Cotroneo & Moretti, 1982

- A. socialis* (Andrássy, 1962) Siddiqi, 1976
 - = *Tylenchorhynchus socialis* Andrásy, 1962
- A. umbonatus* Ivanova, 1982
- A. viciae* (Saltukoglu, 1973) Siddiqi, 1976
 - = *Merlinius viciae* Saltukoglu, 1973

COMMENTS

Amplimerlinius is somewhat similar to *Paratrophurus* in the large body size with continuous lip region and cylindroid tail with a hyaline distal part. It differs by SEM face view (*Paratrophurus* has a somewhat rectangular SEM face view pattern, similar to *Tylenchorhynchus*) and by the structure of the male spicules. The six-lined lateral field permits an easy identification of this genus.

Amplimerlinius also resembles *Pratylenchoides*, a genus in Pratylenchidae. *Pratylenchoides* has a lower labial region than *Amplimerlinius*, and its labial disc is fused with the sub-median lip sectors only, but the lateral sectors are not modified. *Pratylenchoides* is generally smaller and has a smaller stylet than *Amplimerlinius*. Most of its species have glands overlapping the intestine; some have only four lines in the lateral fields. The sexual dimorphism visible in *Pratylenchoides* (with male stylet and median bulb somewhat atrophied) has not been described in any *Amplimerlinius*. Finally the labial framework is different between the two genera. The basal plate is thinner in *Amplimerlinius* which also has a basal ring longer than *Pratylenchoides*.

***Trophurus* Loof, 1956**

DIAGNOSIS

Telotylenchinae. Body medium sized to large. Lip region bullet-shaped (conoid-rounded), continuous with body contour. SEM face view appears to be smooth, with the labial disc and labial sectors fused in a single structure (Sher & Bell, 1975). Stylet 10-20 µm long. Oesophageal glands abutting, pyriform. Tail cylindroid, with a broadly rounded terminus, sometimes rather short for the family, with thick cuticle at the distal extremity. Females with only one genital branch, posterior branch atrophied to a post-uterine sac. However the vulva is at mid-body.

TYPE SPECIES

T. imperialis Loof, 1956

OTHER SPECIES

- Trophurus impar* Ganguly & Khan, 1983
- T. lomus* Saha, Chawla & Khan, 1974
- T. longimarginatus* Roman, 1962
- T. marathwadensis* Suryawanshi, 1971
- T. minnesotensis* (Caveness, 1958) Caveness, 1959
 - = *Clavaurotylenchus minnesotensis* Caveness, 1958

- T. roigi* Razhivin, O'Reilly & Perez Millan, 1973
T. scognamiglii Talamé, 1974
T. sculptus Loof, 1956
T. similis Khan & Nanjappa, 1971
T. ussuriensis Eroshenko, 1981

COMMENTS

Trophurus is unique among Tylenchina in having the vulva at mid-body while the posterior genital branch is atrophied. As noted by Loof (1956) the ratio V is equal to about 50 in some monodelphic Tylenchidae, but in those cases, it is the long filiform tail that is responsible for this unusual situation. In *Trophurus*, the tail is short, there is no posterior branch to speak of, and the vulva is nevertheless in the middle of the body. This makes it easy to accept *Trophurus* in Telotylenchinae, a subfamily where all other genera have two genital branches. Tails of *Trophurus* species are short (c' under 2), but the slim stylets are quite different from the robust stylets of Hoplolaimidae, a family characterized by its short tails. Also, phasmids are located on the tail. As in *Paratrophurus* and *Amplimerlinius*, the shorter tails accompanied by a thick distal cuticle seems to indicate a regression of tail length in an axial, symmetrical manner. Tail regression in Hoplolaimidae seems to follow either the mode asymmetrical (*Helicotylenchus*) or the mode axial, lateral (*Hoplolaimus*).

Genus *dubium*

Tetylenchus Filip'ev, 1936

Sher (1974a) reviewed the history and status of this genus first proposed in 1936 by Filip'ev with *T. tenuis* (Micoletzky, 1921) as the type species. He found that the type species was not adequately described or illustrated, and that the poorly preserved holotype did not retain sufficient characters to make a specific or generic diagnosis possible. He placed *T. tenuis* in *species dubiae* and the genus *Tetylenchus* in *genera dubia*. The rest of the species in *Tetylenchus* were transferred by Sher (1974a) to *Merlinius*, *Leipotylenchus*, and *Triversus*. Siddiqi (1979), after studying the poorly preserved holotype of *T. tenuis* agreed with the decision of Sher, and noted that there was a possibility that this species might be a *Ditylenchus*. In agreement with Sher's (1974a) opinion, *Tetylenchus* is here considered a *genus dubium*.

The subfamily Belonolaiminae Whitehead, 1960

DIAGNOSIS

Belonolaimidae. Cephalic framework often very weak, sometimes heavily sclerotized. Stylet slender, elongate, usually 60-150 μm long, with cone longer than shaft

($m = 60-80$). In forms with elongate stylets, procorpus enlarged and separated from the median bulb by a constriction. Median bulb strong, muscular, with large valve. Labial region often offset, bulbous in lateral view, sometimes continuous with body contour. SEM face view generally with a well marked, round, labial disc and a first lip annulus with submedian sectors well marked and lateral sectors regressed, almost absent. Rarely, lateral sectors only slightly regressed. In one genus, *Morulaimus*, labial disc and lateral sectors are fused into a lemon-shaped structure. Female tail long, generally cylindroid to broadly rounded end, sometimes more conoid. Deirids always absent.

Belonolaiminae differs from Telotylenchinae by its biology, with a tendency towards an elongation of the stylet to reach inside the roots. SEM face views, with well marked round labial disc are characteristic for most genera.

TYPE GENUS

Belonolaimus Steiner, 1949
= *Ibipora* Monteiro & Lordello, 1977 (n. syn.)

OTHER GENERA

Carphodorus Colbran, 1965
Morulaimus Sauer, 1966
Geocenamus Thorne & Malek, 1968
= *Hexadorus* Ivanova & Shagalina, 1983 (n. syn.)
Sauertylenchus Sher, 1974

The genera in Belonolaiminae

Sauertylenchus Sher, 1974

DIAGNOSIS

Belonolaiminae. Body large sized (1.7 mm in the type species). SEM face view with six sectors present, lateral sectors slightly smaller than submedians. Labial framework weakly developed. Stylet thin, long (37 μm in the type species). Deirids absent. Glands abutting. Male spicules with flanges. Gubernaculum slightly protruding from cloaca.

TYPE AND ONLY SPECIES

S. labiodiscus Sher, 1974

COMMENTS

Sher (1974b) placed *Sauertylenchus* in Tylenchorhynchinae (= Telotylenchinae). However, the bulbous labial region, round labial disc, weakly developed labial framework, strongly valvated median bulb, elongate stylet, link this genus to the belonolaimids. This genus from Australia may be seen as a relict of ancestral forms

from which evolved the present day belonolaimids. Because it shares some derived characters with members of this subfamily (strong valve, elongate stylet), it is now transferred to Belonolaiminae.

***Geocenamus* Thorne & Malek, 1968**

= *Hexadorus* Ivanova & Shagalina, 1983 (n. syn.)

DIAGNOSIS

Belonolaiminae. Body medium sized. Labial region bulbous. SEM face view with well marked round labial disc. First lip annulus divided into six sectors, lateral sectors smaller. Labial framework weakly developed. Lateral field with six lines. Deirids absent (but said to be inconspicuous by Siddiqi, 1986). Stylet slender, 25-130 μm long, cone longer than shaft. Tail conoid to almost cylindroid. Spicules without velum, blunt ended. Gubernaculum not protruding from cloaca.

TYPE SPECIES

- G. tenuidens* Thorne & Malek, 1968
= *Tylenchorhynchus polonicus* Szczygiel, 1970
= *G. polonicus* (Szczygiel, 1970) Sturhan, 1981

OTHER SPECIES

- G. arealoferus* (Razzhivin, 1971) n. comb.
= *Morulaimus arealoferus* Razzhivin, 1971
G. arcticus (Mulvey, 1969) Tarjan, 1973
G. deserticola (Ivanova & Shagalina) n. comb.
= *Hexadorus deserticola* Ivanova & Shagalina, 1983
G. kirjanovae (Sagitov, 1973) n. comb.
= *Dolichodorus kirjanovae* Sagitov, 1973
= *H. kirjanovae* (Sagitov, 1973) Siddiqi, 1986
G. longus (Wu, 1969) Tarjan, 1973
= *T. longus* Wu, 1969
G. tokobaevi (Sultanalieva, 1983) n. comb.
= *Morulaimus tokobaevi* Sultanalieva, 1983
= *H. tokobaevi* (Sultanalieva, 1983) Siddiqi, 1986
G. uralensis Baidulova, 1983

COMMENTS

Geocenamus was originally proposed in Tylenchorhynchinae, and said by Siddiqi (1979) to be related to *Merlinius*. Like *Sauertylenchus*, its bulbous labial region, round labial disc, and sometimes elongate stylet are derived characters that prompted us to move this small genus to Belonolaiminae.

Hexadorus was recently proposed in Belonolaiminae by Ivanova and Shagalina (1983) for a new species, *H. deserticola* and for *Morulaimus arealoferus*. Its general appearance (labial region, tail shape, lateral field, bilobed spermatheca, male spicules of *M. arealoferus*, etc.) is quite similar to *Geocenamus*. Stylet length of *H. arealoferus* (60-70 μm) is similar to that of *G. longus* (56-65 μm). Range of stylet lengths in *Hexadorus*

(60-130 μm) overlaps the corresponding range in *Geocenamus* (27-65 μm). The male of *H. deserticola* was described by Ivanova and Shagalina (1983b). The spicules and gubernaculum correspond well to the definition of *Geocenamus*. *Hexadorus* is here proposed as junior synonym of *Geocenamus*.

Geocenamus differs from *Sauertylenchus* by the smaller body length and the shape of male spicules. The six lines in lateral fields provide an easy way to differentiate the two genera.

***Morulaimus* Sauer, 1966**

DIAGNOSIS

Belonolaiminae. SEM face view with labial disc lemon-shaped; first labial annulus divided into six sectors, lateral sectors smaller, submedian sectors somewhat flattened. Labial region not marked by deep longitudinal indentations. Stylet elongate, 60-100 μm long. Cone 60-80 % of total stylet length. Labial framework always weak. Procorpus thickened to accommodate the long stylet, and separated from the median bulb by a constriction; median bulb with strong valve. Oesophageal glands overlapping beginning of intestine. Tail sometimes short for Belonolaimidae ($c' = 2$ to 3), tail shape varies from cylindroid with a broadly rounded terminus to almost conoid.

TYPE SPECIES

- M. arenicolus* Sauer, 1966

OTHER SPECIES

- Morulaimus geniculatus* Sauer, 1966
= *Scutellonema magnum* Yeates, 1967
M. sclerus Sauer, 1966
M. simplex Sauer & Annells, 1981
M. soldus Colbran, 1969
M. whitei (Fisher, 1965) Sauer, 1966
= *Telotylenchus whitei* Fisher, 1965

COMMENTS

Morulaimus is differentiated from *Belonolaimus* by the lemon shaped labial disc. The species in this genus are generally smaller and proportionally thinner, with a shorter stylet, and with a tail shorter and more conoid than species in *Belonolaimus*. To date, all species described in *Morulaimus* have a four-line lateral field, which helps in their identification.

Morulaimus differs from *Sauertylenchus* and *Geocenamus* by the more regressed lateral lip sectors. It has a longer stylet and the glands overlap the intestine for a longer distance.

***Belonolaimus* Steiner, 1949**

= *Ibipora* Monteiro & Lordello, 1977 (n. syn.)

DIAGNOSIS

Belonolaiminae. SEM face view shows a well marked rounded labial disc, and first lip annulus divided into six sectors, lateral sectors almost completely regressed, seen only as small interruptions of the first one or two labial annuli. Labial region marked by deep longitudinal grooves. Stylet very long, 60-150 μm long, its cone 70-80 % of total stylet length. Corpus as in *Morulaimus*. Oesophageal glands overlapping beginning of intestine. Female tail cylindroid with a broadly rounded terminus. Lateral field with four lines or less.

TYPE SPECIES

B. gracilis Steiner, 1949

OTHER SPECIES

- B. anama* (Monteiro & Lordello, 1977) n. comb.
= *Ibipora anama* Monteiro & Lordello, 1977
- B. euthychilus* Rau, 1963
- B. jara* (Monteiro & Lordello, 1977) n. comb.
= *I. jara* Monteiro & Lordello, 1977
- B. lineatus* Román, 1964
= *I. lineatus* (Román, 1964) Monteiro & Lordello, 1977
- B. lolii* Siviour, 1978
= *I. lolii* (Siviour, 1978) Siviour & McLeod, 1979
- B. longicaudatus* Rau, 1958
- B. maritimus* Rau, 1963
- B. nortoni* Rau, 1963

COMMENTS

Ibipora was proposed as intermediate between *Morulaimus* and *Belonolaimus* because its species have the same face view as the latter and lateral fields with four lines, as in the former. The number of lateral field lines in not diagnostic at generic level. The species in *Ibipora* have a stylet ranging from 65 to 100 μm that is somewhat shorter than species in *Belonolaimus s. str.* (90-150 μm). This small difference does not warrant the recognition of a separate genus. *Ibipora* is here proposed as a new junior synonym of *Belonolaimus*.

Belonolaimus differs from *Morulaimus* mostly in the SEM face view. The characters discussed in the paragraph on *Morulaimus* can help in the identification of these two genera.

***Carphodorus* Colbran, 1965**

DIAGNOSIS

Belonolaiminae. SEM face view with well marked labial disc; first labial annulus divided into six sectors,

with lateral sectors a little smaller than the submedians. Labial region with deep indentations. Labial framework massive, strongly developed. Stylet elongate, about 95 μm long, with cone about 68 % of stylet length. Corpus as in *Belonolaimus*. Oesophageal glands overlap beginning of intestine. Tail relatively short ($c' = 1.7$), cylindroid with a broadly rounded terminus. Lateral field said to be with two lines in original description, but SEM pictures show four lines (Sauer, Brzeski & Chapman, 1980).

TYPE AND ONLY SPECIES

C. bilineatus Colbran, 1966

COMMENTS

Carphodorus was originally described in Dolichodorinae, but it is considered to be closer to *Belonolaimus* because of the overlapping glands, face view, female and male tails, caudal alae, etc. Its massive labial framework is reminiscent of the corresponding structure in Dolichodoridae, but Sauer, Brzeski and Chapman (1980) have shown that only the external edges and the internal lining of the labial arches are heavily sclerotized, while the basal plate remains thin. This also is observed in *Morulaimus sclerus* and *M. whitei*. The superficial resemblance of labial framework in *Carphodorus* and dolichodorids is due to convergent evolution, but it helps identify *Carphodorus* among Belonolaiminae. *Carphodorus* can be differentiated from the species in *Morulaimus* with a heavily sclerified labial framework by its labial disc that is rounded as in *Belonolaimus* and not lemon-shaped as in *Morulaimus*.

Discussion

Belonolaimidae as defined here is a large family grouping together a number of forms that have followed divergent paths of evolution.

When compared to the ancestral tylenchid (as defined in Luc *et al.*, 1987), or to Tylenchidae and related families, the belonolaimids can be seen as having completed the first step on the road to underground obligate parasitism of higher plant roots. All members of Belonolaimidae are phytoparasites. The alternate life styles such as above ground plant-parasitism and insect association well represented in Tylenchidae and Anguinidae, are unknown among the belonolaimids which also are unable to survive on a fungal diet.

With few exceptions (e. g. semi-endoparasitism of *Tylenchorhynchus acti* (= *Quinisulcius acti*) described by Vovlas, 1983) Belonolaimidae remained migratory ectoparasites. It will be for the Hoplolaimidae to become migratory or sedentary semi-endoparasites, for the Pratylenchidae to develop migratory endoparasitism and semi-endoparasitism, and for Heteroderidae to succeed fully in sedentary endo-parasitism.

Genus	Labial region Shape	SEM Face view Longit. grooves	Labial framework	Corpus	Stylet length (μm)	Cone ratio m (= cone/ stylet)	Incisures on body	at deirids	Deirids	Female tail ratio c'	Tail end shape	Tail end cuticle	Female genit. branches	Male spicule velum	
<i>Triversus</i>	continuous low, flat	no	Labial disc and first ann. fused	weak. Basal ring wide	fusiform	11-25	$m = 50$	3 or 4	absent	3 to 8	pointed	sometimes thick	2	?	
<i>Tylenchorhynchus</i>	continuous to slightly indented	no	lab. disc and sub- med. sect. fused in a quadrangular struct. lat. sect. regressed	weak to medium	fusiform	15-30	sometimes needle-like	2 to 5	often absent	2 to 4 (often 3)	conoid smt. pointed smt. subcyl.	sometimes thick	2	present	
<i>Trichotylenchus</i>	continuous ogival	no	disc. and lat. sect. form lemon- shaped structure	weak	fusiform	15-30	thin. needle-like	3	absent	3 to 6	cylindroid with rounded end	often thick to very thick	2	absent	
<i>Paratrophurus</i>	continuous rarely slightly offset		quadrangular as in <i>Tylenchorhynchus</i>	weak to medium	fusiform	20-25		4	present	1.5 to 3	cylindroid to rounded end	often thick to very thick	2	present	
<i>Merlinius</i>	continuous or slightly offset	yes	lemon-shaped	weak to medium	fusiform	20-25 (rarely 10 to 40-50)	often slender to needle-like	6	4	often present	2-4	conoid (rarely cylindr.)	sometimes thick		
<i>Nagelus</i>	continuous or slightly offset	no	disc. and lab. sectors all fused together. Face view broadly oval	weak to heavy	fusiform	20-30		6	6	present	2 to 4	conoid	sometimes thick	2	absent
<i>Amplimerlinius</i>	continuous	no	disc. and lab. sectors part. or total. fused. Face view broadly rounded	medium to heavy	fusiform	20-40	strong	6	6	present	1.5 to 3	cylindroid with rounded end	mostly very thick	2	absent
<i>Trophurus</i>	continuous	no	?	weak	fusiform	10-20		4		absent	1.5 to 3	cylindroid with rounded end	very thick (10-13 μm)	1	present
<i>Sauertylechus</i>	offset bulbous		disc rounded, six sectors equally developed	regressed	fusiform strong valve	37	$m = 50$	4		absent	2.5 to 3.5	cylindroid		2	present
<i>Geocenamus</i>	offset bulbous		disc rounded, lat. sectors smaller	regressed	fusiform	25-130		6		absent		conoid to cylindroid		2	absent
<i>Mornlaimus</i>	continuous to offset, bulbous	no	lemon shape as in <i>Merlinius</i>	regressed to heavy	procorpus thick, with constriction	60-100	$m = 60-80$	4		absent	2-3	conoid to cylindroid		2	present
<i>Belonolaimus</i>	continuous to offset, bulbous	yes	disc rounded 4 sub-med. sect. well dev. lat. sectors regressed	regressed	procorpus thick with constriction	60-150	$m = 70-80$	4 or less		absent	3-5	cylindroid		2	present
<i>Carphodorius</i>	offset, bulbous	no	disc rounded lat. sectors smaller	massive	procorpus thick with constriction	95	$m = 68$	4		absent	1.7	cylindroid		2	absent

Morphologically, the passage to obligate parasitism of higher plants is associated with lengthening of the stylet, usually longer than in Tylenchidae and Anguinidae. The reduction of the tail that seems to be associated with plant parasitism is already well attested in Belonolaimidae where the filiform tail of the Tylenchidae is unknown. The oesophageal glands begin to increase in size, overlapping the intestine in many species. The columned uterus has three rows of cells (instead of four rows in the less derived families).

The belonolaimids still possess many ancestral, non-derived features, e. g. genital system with two branches (with the exception of *Trophurus*), absence of sexual dimorphism, presence of a strong oesophago-intestinal valve, presence of deirids in many species, and amphimictic reproduction more frequent than parthenogenesis. On the other hand, several evolutionary trends characteristic of Tylenchina (Luc *et al.*, 1987) are visible in the family but, because of multiple parallelisms, they are difficult to arrange into a coherent phylogenetic picture. These trends will be discussed for four relevant features : stylet, labial framework, tail, and face view.

STYLET

Stylets evolved in at least three directions : *i*) a gradual lengthening and strengthening of the stylet from the most basic forms (stylet = 20 μm ; $m = 50$; cone and shaft slender but not modified, knobs small and sloping backwards) to forms close to hoplolaimid stylets (stylet = 40 μm ; $m = 50$; cone and shaft robust; knobs anteriorly flattened; example : *Amplimerlinius amplius*); *ii*) a great elongation of the stylet and particularly of its cone but no other modifications (stylet = 100-150 μm , $m = 60-80$; example *Belonolaimus* spp.); *iii*) a modification of the cone to a thin, needle-like structure (many *Tylenchorhynchus*, *Trichotylenchus*, and *Merlinius* species).

The first trend can be used to explain the structure of the stylets in the more derived families, Pratylenchidae, Hoplolaimidae and Heteroderidae. The second one is associated with an adaptation to "external endoparasitism" where the body of the nematode remains outside the plant while the elongate stylet can reach deep inside the roots. Conversely the third trend shows an adaptation to surface grazing, where the thin needle-like stylet can easily penetrate cells at the periphery of the root.

LABIAL FRAMEWORK

In most species in Belonolaimidae, the labial framework is thin, lightly sclerotized, and the basal plate extends posteriorly in a very thin annular extension (= basal ring) close to the cuticle. Some species of *Amplimerlinius* have a labial framework more strongly sclerotized, somewhat similar to the framework in Pratylenchidae. Similarly, the anterior part of the framework

in *Carphodorus* and in some *Morulaimus* species is heavily sclerotized and resembles the structures observed in Dolichodoridae. However, in *Amplimerlinius*, *Morulaimus* and *Carphodorus*, as in all other belonolaimids, the labial plate and the basal ring remain thin and lightly sclerotized, and quite different from the heavy structures observed in Dolichodoridae and Pratylenchidae. There exists a trend towards a reinforcement of the labial framework in Belonolaimidae, but it follows an original path, quite distinct from the trends observed in other families.

TAIL

Tails in Belonolaimidae probably originated from forms similar to present day *Psilenchus*. The tail of *P. aestuarius* (as illustrated by Siddiqi, 1986) might be seen as an intermediate form with a long, thin, hyaline extremity and a conoid first half. Except for the hyaline part, the tail is somewhat similar to conoid tails in many Belonolaimidae (*Tylenchorhynchus*, *Merlinius*, *Morulaimus*, etc.). Thick terminal cuticle in tails of many species of these genera may be seen as remnants of a similar regression that may have occurred in the past.

Trichotylenchus tails represent what may well be a different path of tail regression. Tails in this genus are long and thin, but they have a cylindroid shape. They may have originated from filiform tails after an axial regression.

Many belonolaimids have thickset, short tails, with a cylindroid shape and a broadly rounded end. Such tails may have originated from either one of the two forms above, or they may have evolved independently from the ancestors of the family. It is significant to note that many among this third category of tails seem to be in the process of an axial regression in which the protoplasmic contents of the tail regress first, being replaced by an extra-thick cuticle at tail tip. A similar regression may have contributed to the formation of the short, cylindroid to hemispherical-ended tails found in many hoplolaimids.

LABIAL REGION

Many Belonolaimids have a labial region similar to that in Tylenchidae, high, ogival, and continuous with the body contour. Two main evolutions seem to have occurred from this ancestral shape; *i*) labial region globose, bulbous, which occurs in many species in Belonolaimidae; and *ii*) labial region with a small indentation that resembles the labial region of hoplolaimids. Face views can only be resolved using SEM photographs. In the most ancestral shape, a roundish or ovoid labial disc is associated with a first lip annulus divided into six sectors equally developed. In Belonolaimidae, amphids are dorso-ventrally directed slits at the edge of the labial disc; the sub-median sectors are always somewhat flattened; and the lateral sectors are smaller. From this

ancestral shape, three lines of evolution can be identified; *i*) the labial disc and reduced lateral sectors are often fused together in a lemon shaped structure (*Merlinius* and *Morulaimus* for example); *ii*) in many forms in Belonolaiminae, the labial disc keeps its identity and becomes quite round and prominent, the submedian sectors enlarge while the lateral sectors regress and almost disappear; the whole structure resembles a four leaf clover that is similar to the face view in Dolichodoridae (but with amphids dorso-ventrally directed instead of lateral slits as in this latter family); *iii*) in *Tylenchorhynchus*, the lateral sectors have completely disappeared, while the disc and submedian sectors are fused into a quadrangular structure. The amphids remain at the lateral edges of this quadrangle. In a further evolution, the labial disc and first labial annulus are completely fused together, leaving the amphid and oral openings as the only structures recognizable in an otherwise plain structure limited by the second labial annulus (*Nagelus* for example; in *Triversus* the amphid openings are enlarged).

It is relatively easy to propose hypotheses on the evolution of characters within Belonolaimidae. It is much more difficult to establish phylogenies of the taxa themselves without running the risk to classify characters rather than taxa.

Only two subfamilies are accepted here because they correspond to clearly distinct biological characteristics. Monophyly of these subfamilies is questionable. *Morulaimus* because of its conical tails and lemon shaped SEM face views, probably originated from an ancestor different from that of the other members of Belonolaiminae with cylindroid tails and four-leaf clover SEM face view. In Telotylenchinae, at least two paths of evolution can be recognized. One goes towards genera closest to Pratylenchidae and Hoplolaimidae (*Amplimerlinius* and *Paratrophurus*); the other followed a divergent way towards typical *Tylenchorhynchus* and *Merlinius* with superficial root-grazing habits.

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