THE SYSTEMATICS OF THE NEMATODE ORDER TYLENCHIDA (NEMATODA)

V.N. CHIZHOV and S.N. KRUCHINA

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A comparative analysis of different morpho-ecological groups of tylenchids has been carried out based on general data and on the results of original investigations. The main direction of nematode phylogeny in the order Tylenchida is described and rooted. An original classification of Tylenchida with a list of valid taxa and a scheme of phylogenetic relations between the families is proposed.

The discussion on the systematics of Tylenchida based on new information has continued in a great number of publications that appeared during the last few years. As soon as the general principle and theses on the "new system of classification" have been formulated in these publications using the example of the order Tylenchida (Fortuner, Geraert, Luc, Maggenti, and Raski, 1987-1988), the authors of the present article set to define their own position on this problem by making more exact the systematic position of some debatable groups, and to suggest an original classification for the order with a list of valid taxa.

In our previous articles (Chizhov & Berezina, 1988; Chizhov & Kruchina, 1988; 1989) a comparative morphological analysis was carried out. From the results of this analysis we proposed a system of characteristics that permits to create a natural classification of the order based on well-reasoned positions. Besides the morphological characteristics (structure of sexual system, esophagus, head region, sense organs, etc.), biological and ecological characteristics were added to this analysis when permitted by the available information. In our opinion, only by using as many characteristics as possible for the objective evaluation of the different groups of tylenchids, can the creation of a natural system of this rather complex group of nematodes be successful. Recent publications on the embryology of tylenchids also permit to find additional arguments and to use them in this discussion.

Considering the order Tylenchida (without Aphelenchida - Siddiqi, 1980), a monophyletic group of nematodes that historically originated and developed in a soil association and that was primordially and trophically connected with soil hyphomycetes, the primitive structure of the group within the limits of the family Psilenchidae is obvious enough. It was Paramonov (1970) who first paid attention to the fact that the morphological characteristics of psilenchids are similar to the morphology of a hypothetically reconstructed ancestral mycochylolophagist [= organism feeding on the chyle of fungal hyphae]. He marked out the non-adaptive structure of the head region and the didelphy of the genital system as determining features. But it is necessary to note that the initial didelphy of the ancestral forms of tylenchids, typical to this group of nematodes, was recently called in question. Kostyuk (1989) showed that in tylenchids only a single cellular primordium of a genital system is formed during the embryogenesis, while the majority of free-living didelphic groups of nematodes (suborder Enoplia and Chromadoria) have two non-connected single cellular primordia during the embryogenesis. At the same time, it was also noted that if the first division of the cell of a genital primordium occurs during the embryogenesis, then a didelphic system is formed, but if the first division of the genital cell takes place during the postembryonal period, then the female genital system is formed as monodelphic. In our opinion these results testify only to the priority of the didelphic system in tylenchids, because a didelphic female genital system begins to form

begins to form at a earlier stage of ontogenesis and consequently it is more ancient phyletically than a monodelphic one. Apparently, the number of gonads in tylenchid females is not related to the problem of their origin from a single cell primordium during embryogenesis. This characteristic should be considered as one of the distinctive features of this order. Underlining the importance of the characteristics of the embryonal development for building the natural system of the order, the authors focused their attention on the analysis of the initial stages of cell division in the family Tylenchidae (Tylenchidae sensu Andrássy, 1976) by Drozdovskii (1989) who pointed out the radical difference between the representatives of the families Hoplolaimidae and Pratylenchidae (the latter also includes secondary monodelphic forms, or as Siddiqi called (1986), pseudo-monodelphic forms). In our opinion the existence of such radical differences at the initial stages of division in mono- and didelphic groups serves as an additional argument to establish the suborder Hoplolaimina (Chizhov & Berezina, 1988), which groups all the primary didelphic forms and opposes the suborder Tylenchida. The subsequent evolution of the didelphic Hoplolaimidae is related to the formation of plant parasitism and to the colonization of the root system of flowering plants that led to the creation of groups that are primitive in morphology and in the characterisitics of feeding and that are close to modern representatives of Tylenchorhynchidae, having at the same time a combined character of organization. We also think it is of a fundamental importance to note that the transition to feeding on cells of the root system appears to be a determining factor of the subsequent evolution of hoplolaimins, that developed in three directions.

First, the evolution was directed towards migrating ectoparasitism (the families Belonolaimidae and Dolichodoridae). A possible source of origin for the first group (Belonolaimidae) are primitive representatives of migrating ectoparasites with expressed characters of specialization - a progressive structure of the head region with elongated stylet and developed oesophageal glands, overlapping the anterior part of the intestine, i.e., forms that are close to the structure of telotylenchids. It should be underlined that in the recently published systematics of tylenchids (Maggenti et al., 1987; Fortuner et al, 1987 - 1988) belonolaimids and telotylenchids are considered as subfamilies in the family Belonolaimidae. Primitive tylenchorhynchids with similar tendencies in the development of head region and stylet could serve as a source of origin for the second group of migrating ectoparasites.

The second direction of evolution of didelphic tylenchids is related to the formation of a group of migrating endoparasites, the pratylenchid branch of hoplolaimids. The source of origin for this group of root parasites can be considered to be the forms that are close in their morphology to the primitive tylenchorhynchids of the subfamily Antarctenchinae. The subsequent evolution of this group occurred in two directions: on one hand towards migrating endoparasitism through the formation and fixation of secondary monodelphy (the subfamily Pratylenchinae), and on the other hand towards closer interaction with a plant-host, that led to the origin of sedentary forms, whose ancestors might have separated from the common pratylenchid stem, both at the level of primitive didelphic forms (Nacobboderidae - Meloidogynidae) and after the emergence of monodelphy (Nacobbidae). The discussion on this problem is treated at greater length in Ryss's monograph (1988), whose views on the evolution of pratylenchids are shared by the authors of the present article.

The third direction of evolution in the suborder Hoplolaimina is represented by the semi-endoparasitic forms. The progress in the development of the hoplolaimoid group of species and the formation of the sedentary forms of this evolutionary branch seem to be the least debatable question. The main characters of the hoplolaimoid structure are already formed in a group of migrating ectoparasites close in their structure to the modern representatives of the subfamily Merliniinae. The analysis of numerous publications leads to the conclusion that the origin of sedentary families of Rotylenchulidae and Heteroderidae from hoplolaimoid ancestors seems to be quite well-founded. A *Rotylenchulus* form with its typical morphology, original characteristics of ontogenesis (infective female) and a more primitive nature of interaction with its plant-host is likely to be considered as a intermediate form between semi-endoparasites and specialized heteroderids. At the basis of the heteroderid system, Wouts (1985) places a *Verutus* form that by its morphology and characteristics of pathogenesis is close to rotylenchulids, but that already has a infective larvae of the second stage. This represents the transition from primitive sedentary forms with an infective vermiform female to a infective larval stage, that opens great possibilities for progressive transformations in the process of

postembryonal development, and that is expressed in its final result by a marked increase in the egg productivity. It should also be noted that Wouts's system does not contradict the system by Krall and Krall (1978) based on the idea of co-evolution of heteroderids and plant-hosts.

The position of the only monodelphic representative of the subfamily Acontylinae (*Acontylus vipriensis*) is not at all clear, but considering the availability of a small group of species with an obvious tendency to the reduction of the posterior ovary (genus *Rotylenchoides*), one can suggest that the source of origin of this form is to be found among the family Hoplolaimidae.

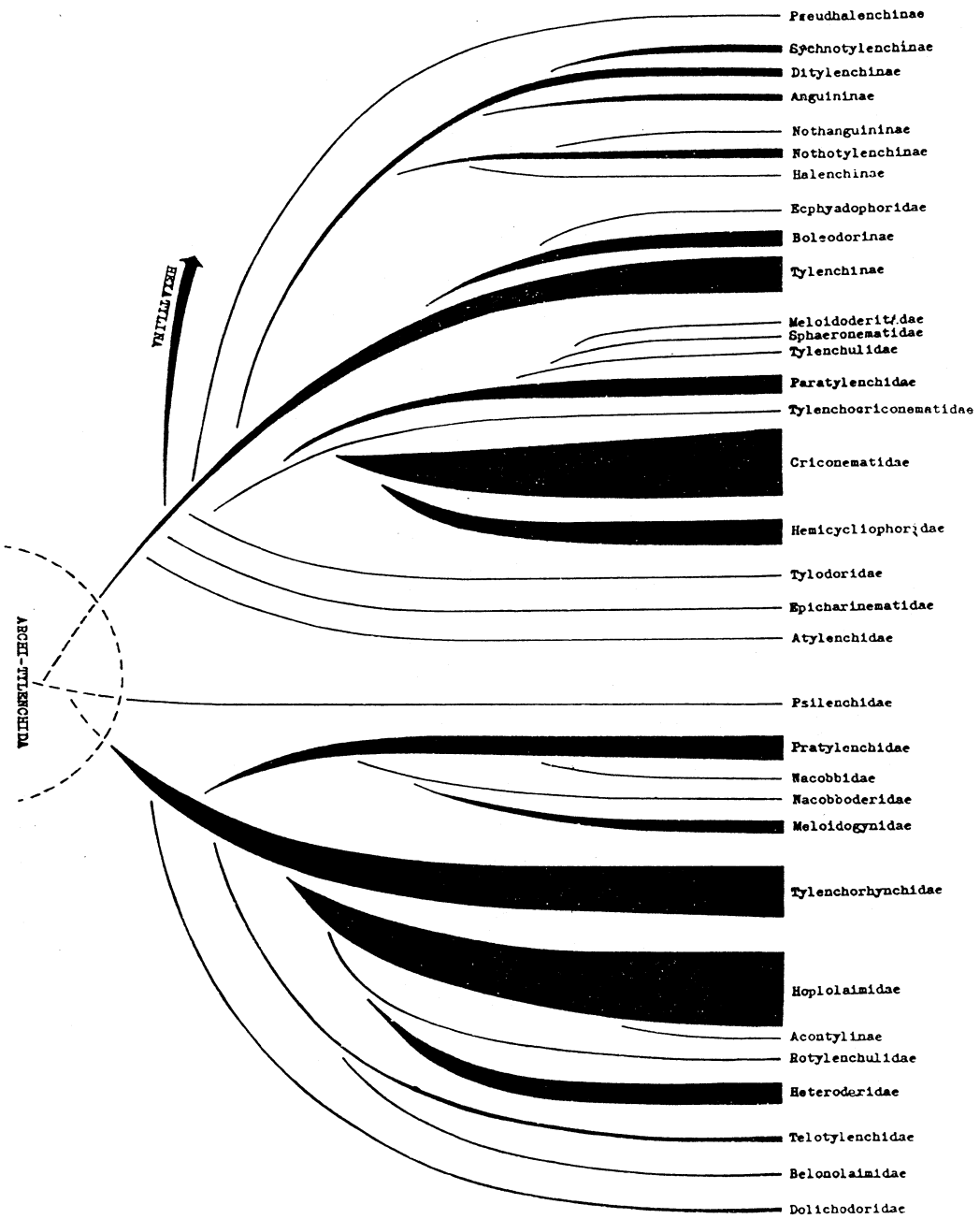
Analyzing the group of monodelphic tylenchids that we have accepted in the suborder Tylenchina (excepted the entomo-pathogenic nematodes), it is necessary in particular to underline that the formation of monodelphy is a direct reflection of the evolutionary processes that have resulted in the formation of a mode of life of mycochylophagy. In our opinion, there is practically no alternative to the mycotrophic theory of the origin of tylenchids by Paramonov (1970). Monodelphy of Tylenchida in all cases (once for all Tylenchina and twice for the suborder Hoplolaimina) was formed by selection on high mobility, which was necessary for a more active search of food sources. It is for this reason that a reduction of the posterior genital branch always takes place, which helps increase the locomotor function of the posterior part of the body. The diversity of monodelphic tylenchids is based on a colossal multiformity of mycoflora - the principal category of the soil community. It is in the mycochylophagous group that were formed the preconditions for the subsequent evolution of plant parasitism within the suborder.

A comparative morphological analysis previously carried out by the current authors (Chizhov & Kruchina, 1989) has shown that a *Neopsilenchus* form combines the greatest quantity of primitive characters and that it can be regarded as an ancestral form within the suborder Tylenchina. It is from this form that the formation of a tylenchid mycochylophagous group took place. In our opinion, the subsequent evolution in the monodelphic group of tylenchids went in the following directions.

The stabilization at the level of mycochylophagy led to the formation of a group with a thin and short stylet and a weakly sclerotized head capsule, and, in some forms, to the reduction of the median bulb that is a character of the deepest specialization to mycochylophagy (Boleodorinae, Ecphyadophoridae).

The other direction in the evolution of monodelphic tylenchs is the formation of a ditylenchoid-anguinoid branch, connected during its development with fungi parasites of flowering plants. The most specialized representatives of this group lost their trophic ties with fungi and reached the level of obligatory parasites of above ground organs of flowering plants. It should be noticed that the use of biological characteristics (Chizhov & Subbotin, 1985; 1990) was a non-traditional way of solving the problem of building the systematics of anguinids. As to the group with a reduced median bulb (Nothotylenchinae and other), the authors think that the display of this character is connected to a deeper specialization at the level of mycochylophagy and that the transition to plant parasitism took place only later; a few forms from the genera *Nothanguina* and *Halenchus* that have reached the level of obligate parasitism can only confirm the supposition of these authors. The authors also consider as quite valid the subfamily Pseudhalenchinae, integrating a small group of forms with a non-typical structure of granular bulb in comparison with the other representatives of the family Anguinidae. It is likely that the type family Tylenchidae should include only two rather related subfamilies: Tylenchinae and Boleodorinae; the latter integrates all the forms that have no median valve and signs of rudimentation of median bulb.

The original criconemoid group of tylenchids should be regarded as an example of a high level of adaptation to root ectoparasitism, and the morphological homogeneity of this group can be used for distinguishing the criconematids as a taxon of the higher rank, up to the suborder level (Siddiqi, 1986). We assume that the description of *Tylenchocriconema alleni* Raski & Siddiqui, 1975 finally solves the problem of the origin of this group from tylenchid ancestors, and the authors consider the formation of the morphological characters common to criconematids (junction of procorpus with median bulb) as a process accompanying the increase of the stylet length and reinforcement of the muscular organs of protractors. The criconematid system suggested by Siddiqi (1986) was based on the structure of the female cuticle, the structure of the head region, the form of the vulva, and other morphological characteristics. The authors agree for the most part with the number of the genera in the family Criconematidae.



A possible scheme of phylogenetic relationships between the families (subfamilies) of the nematode order Tylenchida.

There is no doubt as to the common origin of criconematids and hemicycliophorids and the typical characteristics of the latter, such as a double-layered cuticle, seem to be an original adaptation to specific over humid habitats.

We also think that the proximity of criconematids to the paratylenchoid group looks quite logical. The latter group served as a source of origin for sedentary forms, the most specialized representatives of the suborder Tylenchina.

The figure represents a scheme of possible phylogenetic relationships of the different groups (families and subfamilies) of the order Tylenchida, and each of them corresponds to the exact morpho-ecological criteria.

The authors suggest an original system for the order Tylenchida based on their analysis of, and generalization from, the literature and on the results of their own studies.

THE SYSTEMATICS OF THE ORDER TYLENCHIDA

Order Tylenchida Thorne 1949
- Suborder Tylenchina Thorne, 1949
  - Superfamily Tylenchoidea Örley, 1880
    - Family Tylenchidae Örley, 1880
      - Subfamily Tylenchinae Örley, 1880
        - Genera: *Tylenchus* Bastian, 1865
          - *Aglenchus* Andrássy, 1954
          - *Filenchus* Andrássy, 1954
          - *Miculenchus* Andrássy, 1959
          - *Basiria* Siddiqi, 1959
          - *Cephalenchus* Goodey, 1962
          - *Malenchus* Andrássy, 1968
          - *Neopsilenchus* Thorne et Malek, 1968
          - *Pleurotylenchus* Szczygiel, 1969
          - *Irantylenchus* Kheiri, 1972
          - *Gracilancea* Siddiqi, 1976
          - *Campbellenchus* Wouts, 1978
          - *Coslenchus* Siddiqi, 1978
          - *Discotylenchus* Siddiqi, 1980
          - *Polenchus* Andrássy, 1980
          - *Allotylenchus* Andrássy, 1984
          - *Mukazia* Siddiqi, 1986

      - Subfamily Boleodorinae Khan, 1964
        - Genera: *Boleodorus* Thorne, 1941
          - *Thada* Thorne, 1941
          - *Sakia* Khan, 1964
          - *Neothada* Khan, 1973
          - *Duosulcius* Siddiqi, 1979
          - *Neomalenchus* Siddiqi, 1979
          - *Duotylenchus* Saha et Khan, 1982

    - Family Atylenchidae Skarbilovich, 1959
      - Subfamily Atylenchinae Skarbilovich, 1959
        - Genera: *Atylenchus* Cobb, 1913
          - *Eutylenchus* Cobb, 1913

    - Family Ecphyadophoridae Skarbilovich, 1959
      - Subfamily Ecphyadophorinae Skarbilovich, 1959
        - Genus *Ecphyadophora* de Man, 1921

Subfamily Ecphyadophoroidinae Siddiqi, 1986
Genera: *Ecphyadophoroides* Corbett, 1964
Mitranema Siddiqi, 1986
Tenunemellus Siddiqi, 1986

Family Tylodoridae Paramonov, 1967
Subfamily Tylodorinae Paramonov, 1967
Genus: *Tylodorus* Meagher, 1964

Family Epicharinematidae Maqbool et Shahina, 1985
Subfamily Epicharinematinae Maqbool et Shahina, 1985
Genus *Epicharinema* Raski, Maggenti, Koshy et Sosamma, 1980

Superfamily Anguinoidea Nicoll, 1935 (1926)
Family Anguinidae Nicoll, 1935 (1926)
Subfamily Anguininae Nicoll, 1935 (1926)
Genera: *Anguina* Scopoli, 1777
Subanguina Paramonov, 1967
Heteroanguina Chizhov, 1980
Mesoanguina Chizhov et Subbotin, 1985

Subfamily Ditylenchinae Golden, 1971
Genera: *Ditylenchus* Filipjev, 1936
Diptenchus Khan, Chawla et Seshadri, 1969

Subfamily Nothotylenchinae Thorne, 1941
Genera: *Nothotylenchus* Thorne, 1941
Hadrodenus Mulvey, 1969
Orrina Brzeski, 1981
Pterotylenchus Siddiqi et Lenne, 1984

Subfamily Nothanguininae Fotedar et Handoo, 1978
Genus: *Nothanguina* Whitehead, 1959

Subfamily Halenchinae Jairajpuri et Siddiqi, 1969
Genus: *Halenchus* Cobb, 1933

Subfamily Sychnotylenchinae Paramonov, 1967
Genera: *Sychnotylenchus* Rühm, 1956
Neoditylenchus Meyl, 1961

Subfamily Pseudhalenchinae Siddiqi, 1971
Genera: *Pseudhalenchus* Tarjan, 1958
Safianema Siddiqi, 1980

Superfamily Criconematoidea Taylor, 1936 (1914)
Family Criconematidae Taylor, 1936 (1914)
Subfamily Criconematinae Taylor, 1936 (1914)
Genera: *Criconema* Hofmänner et Menzel, 1914
Ogma Southern, 1914
Bakernema Wu, 1964

Lobocriconema De Grisse et Loof, 1965
Blandicephalanema Mehta et Raski, 1971
Neolobocriconema Mehta et Raski, 1971
Pateracephalanema Mehta et Raski, 1971
Neobakernema Ebsary, 1981

Subfamily Macroposthoniinae Skarbilovich, 1959
Genera: *Macroposthonia* de Man, 1880
Criconemoides Taylor, 1936
Discocriconemella De Grisse et Loof, 1965
Criconemella De Grisse et Loof, 1965
Nothocriconemoides Maas, Loof et De Grisse, 1971

Subfamily Hemicriconemoidinae Andrássy, 1979
Genus: *Hemicriconemoides* Chitwood et Birchfield, 1957

Family Hemicycliophoridae Skarbilovich, 1959
Subfamily Hemicycliophorinae Skarbilovich, 1959
Genera: *Hemicycliophora* de Man, 1921
Colbranium Andrássy, 1979
Loofia Siddiqi, 1980

Subfamily Caloosiinae Siddiqi, 1980
Genera: *Caloosia* Siddiqi et Goodey, 1964
Hemicaloosia Ray et Das, 1978

Superfamily Tylenchuloidea Skarbilovich, 1947
Family Tylenchulidae Skarbilovich, 1947
Subfamily Tylenchulinae Skarbilovich, 1947
Genera: *Tylenchulus* Cobb, 1913
Trophotylenchulus Raski, 1957
Trophonema Raski, 1957

Family Sphaeronematidae Raski et Sher, 1952
Subfamily Sphaeronematinae Raski et Sher, 1952
Genera: *Sphaeronema* Raski et Sher, 1952
Goodeyella Siddiqi, 1986

Family Meloidoderitidae Kirjanova et Poghossian, 1973
Subfamily Meloidoderitinae Kirjanova et Poghossian, 1973
Genus: *Meloidoderita* Poghossian, 1966

Family Tylenchocriconematidae Raski et Siddiqui, 1975
Subfamily Tylenchocriconema Raski et Siddiqui, 1975
Genus: *Tylenchocriconema* Raski et Siddiqui, 1975

Family Paratylenchidae Thorne, 1949
Subfamily Paratylenchinae Thorne, 1949
Genera: *Paratylenchus* Micoletzky, 1922
Cacopaurus Thorne, 1943
Gracilacus Raski, 1962

Suborder Hoplolaimoidea Chizhov et Berezina, 1988
Superfamily Hoplolaimoidea Filipjev, 1934
Family Hoplolaimidae Filipjev, 1934
Subfamily Hoplolaiminae Filipjev, 1934
Genera: *Hoplolaimus* von Daday, 1905
Scutellonema Andrássy, 1964
Aorolaimus Sher, 1963
Peltamigratus Sher, 1964
Basirolaimus Shamsi, 1979

Subfamily Rotylenchinae Golden, 1971
Genera: *Rotylenchus* Filipjev, 1936
Helicotylenchus Steiner, 1945
Antarctylus Sher, 1973
Pararotylenchus Baldwin et Bell, 1981
Varotylus Siddiqi, 1986

Subfamily Rotylenchoidinae Whitehead, 1958
Genera: *Rotylenchoides* Whitehead, 1958
Orientylus Jairajpuri et Siddiqi, 1977

Subfamily Acontylinae Fotedar et Handoo, 1978
Genus: *Acontylus* Meagher, 1968

Subfamily Aphasmatylenchinae Sher, 1965
Genus: *Aphasmatylenchus* Sher, 1965

Family Dolichodoridae Chitwood, 1950
Subfamily Dolichodorinae Chitwood, 1950
Genera: *Dolichodorus* Cobb, 1914
Neodolichodorus Andrássy, 1976

Subfamily Meiodorinae Siddiqi, 1976
Genera: *Meiodorus* Siddiqi, 1976
Brachydorus de Guiran et Germani, 1968

Family Tylenchorhynchidae Eliava, 1964
Subfamily Tylenchorhynchinae Eliava, 1964
Genera: *Tylenchorhynchus* Cobb, 1913
Bitylenchus Filipjev, 1934
Paratrophurus Arias, 1970
Uliginotylenchus Siddiqi, 1971
Sauertylenchus Sher, 1974
Triversus Sher, 1974
Trilineellus Lewis et Golden, 1981
Doubtful genus: *Tetylenchus* Filipjev, 1936

Subfamily Merliniinae Siddiqi, 1971
Genera: *Geocenamus* Thorne et Malek, 1968
Nagelus Thorne et Malek, 1968
Merlinius Siddiqi, 1970

Amplimerlinius Siddiqi, 1976
Hexadorus Ivanova et Shagalina, 1983

Subfamily Macrotrophurinae Fotedar et Handoo, 1978
Genus: *Macrotrophurus* Loof, 1958

Subfamily Trophurinae Paramonov, 1967
Genus: *Trophurus* Loof, 1956

Subfamily Antarctenchinae Spaull, 1972
Genus: *Antarctenchus* Spaull, 1972

Family Telotylenchidae Siddiqi, 1960
Subfamily Telotylenchinae Siddiqi, 1960
Genera: *Telotylenchus* Siddiqi, 1960
Trichotylenchus Whitehead, 1960
Histotylenchus Siddiqi, 1971
Telotylenchoides Siddiqi, 1971

Family Belonolaimidae Whitehead, 1960
Subfamily Belonolaiminae Whitehead, 1960
Genera: *Belonolaimus* Steiner, 1949
Carphodorus Colbran, 1965
Morulaimus Sauer, 1966
Doubtful genus: *Ibipora* Monteiro et Lordello, 1977

Family Psilenchidae Paramonov, 1967
Subfamily Psilenchinae Paramonov, 1967
Genera: *Psilenchus* de Man, 1921
Atetylenchus Khan, 1973

Family Pratylenchidae Thorne, 1949
Subfamily Pratylenchinae Thorne, 1949
Genera: *Pratylenchus* Filipjev, 1936
Radopholus Thorne, 1949
Pratylenchoides Winslow, 1958
Hoplotylus s'Jacob, 1960
Zygotylenchus Siddiqi, 1963
Radopholoides de Guiran, 1967
Apratylenchoides Sher, 1973

Subfamily Hirschmanniellinae Fotedar et Handoo, 1978
Genus: *Hirschmanniella* Luc et Goodey, 1964

Family Nacobbidae Chitwood, 1950
Subfamily Nacobbinae Chitwood, 1950
Genus: *Nacobbus* Thorne et Allen, 1944

Subfamily Bursaderinae Chizhov et Kruchina, 1989
Genus: *Bursadera* Ivanova et Krall, 1985

Family Meloidogynidae Skarbilovich, 1959
Subfamily Meloidogyninae Skarbilovich, 1959
Genus: *Meloidogyne* Goeldi, 1892
Doubtful genera: *Hypsoperine* Sledge et Golden, 1964
Meloidoderella Khan et Hussain, 1972

Family Nacobboderidae Golden et Jensen, 1974
Subfamily Nacobboderinae Golden et Jensen, 1974
Genus: *Meloinema* Choi et Geraert, 1974
Doubtful genus: *Nacobbodera* Golden et Jensen, 1974

Family Heteroderidae Filipjev et Schuurmans Stekhoven, 1941
Subfamily Heteroderinae Filipjev et Schuurmans Stekhoven, 1941
Genera: *Heterodera* Schmidt, 1871
Hylonema Luc, Taylor et Cadet, 1978
Bidera Krall et Krall, 1978
Ephippiodera Shagalina et Krall, 1981
Afenestrata Baldwin et Bell, 1985

Subfamily Ataloderinae Wouts, 1973
Genera: *Atalodera* Wouts et Sher, 1971
Sarisodera Wouts et Sher, 1971
Sherodera Wouts, 1973
Thecavermiculatus Robbins, 1978
Bellodera Wouts, 1985
Camelodera Krall, Shagalina et Ivanova, 1988
Ekphymatodera Baldwin, Bernard et Mundo-Ocampo, 1989

Subfamily Punctoderinae Krall et Krall, 1978
Genera: *Punctodera* Mulvey et Stone, 1976
Globodera Skarbilovich, 1959
Cactodera Krall et Krall, 1978
Dolichodera Mulvey et Ebsary, 1980

Subfamily Cryphoderinae Wouts, 1985
Genera: *Cryphodera* Colbran, 1966
Zelandodera Wouts, 1973

Subfamily Meloidoderinae Golden, 1971
Genus: *Meloidodera* Chitwood, Hannon et Esser, 1956

Subfamily Verutinae Esser, 1981
Genus: *Verutus* Esser, 1981

Family Rotylenchulidae Husain et Khan, 1967
Subfamily Rotylenchulinae Husain et Khan, 1967
Genera: *Rotylenchulus* Lindford et Oliveira, 1940
Senegalonema Germani, Luc et Baldwin, 1984

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Moscow Agricultural Academy

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