

A reappraisal of Tylenchina (Nemata).

2. Classification of the suborder Tylenchina (Nemata : Diplogasteria)

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SUMMARY

The phylum Nemata Cobb, 1919 is accepted as is the class Secernentea and subclass Diplogasteria. Within the subclass the two suborders Tylenchina and Aphelenchina are reunited in the order Tylenchida. The order is subdivided into four suborders : Tylenchina, Aphelenchina, Sphaerulariina and Hexatyliina. This paper focuses on a revision of Tylenchina, here recognized as being composed of two superfamilies : Tylenchoidea and Criconematoidea. Seven families are recognized in Tylenchoidea : Tylenchidae, Anguinidae, Dolichodoridae, Belonolaimidae, Pratylenchidae, Hoplolaimidae and Heteroderidae. Two families are recognized in Criconematoidea : Criconematidae and Tylenchulidae. Within these nine families, fifteen subfamilies are accepted in Tylenchoidea and four in Criconematoidea. A list of the families and their genera is included.

RÉSUMÉ

Réévaluation des Tylenchina (Nemata). 2. Classification du sous-ordre des Tylenchina (Nemata : Diplogasteria)

Le phylum Nemata Cobb, 1919 est accepté, de même que la classe des Secernentea et la sous-classe des Diplogasteria. A l'intérieur de cette sous-classe, les deux sous-ordres des Tylenchina et des Aphelenchina sont réunis dans l'ordre des Tylenchida qui comprend en outre les sous-ordres des Sphaerulariina et des Hexatyliina. Cet article est centré sur une révision du sous-ordre des Tylenchina, considéré comme composé de deux super-familles : les Tylenchoidea et les Criconematoidea. Sept familles sont reconnues dans les Tylenchoidea : Tylenchidae, Anguinidae, Dolichodoridae, Belonolaimidae, Pratylenchidae, Hoplolaimidae et Heteroderidae; et deux dans les Criconematoidea : Criconematidae et Tylenchulidae. A l'intérieur de ces neuf familles, quinze sous-familles sont acceptées dans les Tylenchoidea et quatre dans les Criconematoidea. Une liste des familles et de leurs genres est donnée.

In recent years the concept that nematodes comprise a phylum has been widely accepted by nematologists and invertebrate zoologists alike. What has not been clarified is the phylum name, both Nemata (Cobb, 1919) and Nematoda (Potts, 1932) are being used. We are of the opinion that Nemata should be recognized as the correct designation. Nematoda does not indicate an author's commitment to nematodes as a class or phylum because the name has been used at both levels : when Thorne (1949) proposed the order Tylenchida the included taxa were placed in the subclass Phasmodia (Chitwood & Chitwood, 1933) of the class Nematoda. Rudolphi (1808) proposed Leders' "Rundwurms" (gordians and nematodes) as the group "Nematoidea" along with

Acanthocephala, Trematoda and Cestoidea in the group Entozoa. Therefore there is no reason to credit Rudolphi for the phylum, as Nematoidea included all "thread-like" forms of roundworms, no taxonomic distinction being made. Von Siebold (1843) proposed the order Gordiacea that included *Mermis*. Carl Vogt (1851) placed gregarines, acanthocephalans, nematodes and gordiaceans in the group Nematelmia. Gegenbaur (1859) removed the gregarines and placed Rudolphi's Nematoidea along with acanthocephalans and gordiaceans in the phylum Nemathelminthes. Schneider (1864) added Chaetognatha to Nemathelminthes. Vejdovsky (1866) segregated Nematomorpha (gordiaceans) as a class in Nemathelminthes along with chaetogna-

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thans. Two years later Nematomorpha was removed from Nemathelminthes by Haeckel. It has been assumed that Rudolphi proposed Nematodea for nematodes but as stated above the varied assemblages exclude this; this is also true for Nematelmia, Nemathelminthes and Nematomorpha. The only common characteristic of these nomenclatorial designations is "Nema-". Only one taxon, Nemathelminthes, still remains since it was the only one clearly defined by Vejdovsky (1866). Therefore, none of the others should be used in classification.

Cobb (1919) proposed the phylum Nemata (= Nematodes) and was the first to exclude all but nematodes from the group. Potts (1932) raised Grobben's class Nematoda (Aschelminthes) back to phylum rank but kept the name. Therefore, Cobb's proposal of Nemata has priority, is unequivocal and consequently must be adopted. Also almost universally accepted is the division of the phylum into two classes Adenophorea and Secernentea. However, Andr assy (1976) and Inglis (1983) do not accept this division.

Maggenti (1981, 1982, 1983) proposed that Secernentea be subdivided into three subclasses: Rhabditia, Spiruria and Diplogasteria. Prior to this separation it was not possible, with other than negative characters, to characterize the order Rhabditida that encompassed rhabditids and diplogasterids. The acceptance of the three subclasses allows both morphological and biological separation of the three subclasses.

Among the taxa in Diplogasteria it is possible to understand the phylogenetic and morphologic development towards both insect and higher plant parasitism. This grouping allows us to interpret the development of the metacarpus and valve, the glandular postcorpus and the development of movable mouthparts leading to the tylenchid stylet. Also evident is the shift from mycetophagus forms to tissue absorbers or feeders on higher plant cells. These steps are illustrated by the orders Diplogasterida and Tylenchida.

Siddiqi (1980) and Maggenti (1981) proposed that Thorne's Tylenchida be separated into two orders Aphelenchida and Tylenchida; however, they differ greatly as to the reasons supporting such a division. Siddiqi's 1980 proposal that Tylenchida originated from Oxyurida has been rejected here as it was by Maggenti (1983). Siddiqi's hypothesis demands that we accept that Tylenchida and Aphelenchida represent examples of convergent evolution and that they evolved in separate subclasses. We believe that both originated from Diplogasterida. In this proposal we accept only the order Tylenchida. The order is subdivided into four suborders: Tylenchina, Aphelenchina, Sphaerulariina and Hexatyliina. We recognize that insect parasitism among Tylenchida is closely allied to the development of plant parasitism; however, the evolutionary biology and development are so divergent that separate suborders are warranted. All known members of Sphaerulariina lack

a valved metacarpal bulb. This is significant both taxonomically and phylogenetically. The absence is not a secondary derivation recurring within taxa; it represents a separate line of development among the Tylenchida.

Sphaerulariina is believed to have evolved from forms close to the anguinids. This is not to say that anguinids are the ancestral group for Sphaerulariina but that they still exhibit characteristics and habits that may have been important to the evolution of Sphaerulariina. For example many anguinids can sustain themselves on fungi and genera such as *Sychnotylenchus* are insect associates.

We do not recognize Siddiqi's (1986) concept of the suborder Hexatyliina that encompasses Neotylenchoidea, Anguinoidea, Sphaerularioidea, Iotonchioidea. Neotylenchoidea does not exist in as much as its members are dispersed throughout Tylenchida (Fortuner & Raski, 1987). Geraert (1976) clearly showed the reproductive system and Shepherd and Clark (1976), the head, oesophagus and intestine of *Hexatylys* is different from all other Tylenchida; this included the "Sphaerulariidae-Allantonematoida" complex. Hexatyliina is recognized solely on the genus *Hexatylys* in the family Neotylenchidae.

In this paper we are primarily concerned with the Tylenchina that is here recognized as being divided into two superfamilies: Tylenchoidea and Criconematoidea (Geraert, 1966). The classification presented is based on the proposal of Maggenti (1981); however, one family has been discarded and three reinstated. Seven families are placed in Tylenchoidea and two in Criconematoidea; thus there is a significant condensation as compared to Andr assy (1976), Fotedar and Handoo (1978), and Siddiqi (1986); also the number of subfamilies has been reduced (fifteen in Tylenchoidea; four in Criconematoidea). The rationale behind our proposals has been discussed at length in the first article of this series (Luc *et al.*, 1987).

The suborder, superfamilies and families are characterized as follows:

Suborder TYLENCHINA

Female oesophagus composed of a procorpus, metacarpus and a glandular postcorpus with an intervening isthmus between metacarpus and glandular region, dorsal oesophageal gland orifice opens in the anterior procorpus. Metacarpus generally with valve. Stylet in males and females generally with three basal knobs. Male feeding apparatus atrophied in some taxa. Lip region distinct or undifferentiated from general body contour. Transverse body annulation generally interrupted by longitudinal incisures. Except in aberrant males stoma armed with knobbed axial stylet. Glandular postcorpus shows varying degrees of development; it may join intestine directly or overlap the anterior intes-

tine for some distance. Females with one or two genital branches. Oviduct with two rows of seven cells. Males generally have caudal alae and paired spicules. Deirids present or absent.

Superfamily Tylenchoidea

Lip region generally hexaradiate and distinguished from general body contour. Labial region supported by a cuticularized skeleton that may or may not be well developed. Procorpus generally set off from metacarpus, usually slender and cylindrical. Isthmus narrow and leads to the expanded glandular region almost always wider than the metacarpus. Glandular region consists of three glands ending at the beginning of the intestine or variously overlapping this structure. Phasmids commonly adanal, on the tail or erratically on body.

Family TYLENCHIDAE

Body slender, vermiform; lateral field varies from 0-multiple longitudinal lines. The general body cuticle may be ornamented with longitudinal ridges. Lip region generally elevated, rounded and annulated. Labial framework weakly developed (except. : *Antarctenchus*); stylet usually small and delicate (exceptions : *Campbellenchus*, *Gracilancea*, *Epicharinema*). Amphids vary from small oblique slits to long sinuous clefts longitudinally directed. Deirids present or absent, phasmid-like structures present or absent usually advulval (occasionally typical phasmid on tail : *Tylodorus*, *Atetylenchus*, *Antarctenchus*). Oesophagus divided into slender procorpus, elliptical metacarpus mostly with valve, long slender isthmus followed by symmetrical pyriform glandular region. Females generally with a single anteriorly directed genital branch; twelve celled spermatheca often offset; columned uterus with four rows of cells; post-uterine sac (PUS) length less than one vulval body diameter. Male caudal alae leptoderan. Sperm cells with little cytoplasm. Tails elongate-conoid generally narrowing to filiform outline. Free-living algal and fungus feeders, sometimes parasitic on higher plants.

Family ANGUINIDAE

Body slender, vermiform or somewhat swollen in mature females. Lateral field with either four or six or more lines. Low, flattened anterior end, small delicate stylet; labial framework lightly sclerotized. Amphid apertures small, lateral slits. Female genital system with sixteen-celled tubular spermatheca, in line with genital tract; columned uterus with four rows of cells or it may be a multicelled structure. PUS length variable from very long to none at all. Female tails conoid not elongated. Male caudal alae short, leptoderan, sometimes long and peloderan (*Sychnotylenchus*). Sperm cells with large amount of cytoplasm (exception : *Pseudhalen-*

chus). Deirids and phasmids generally absent. Family contains free-living (fungus feeders) as well as facultative and obligate higher plant parasites, normally parasites of the above ground plant parts.

Family DOLICHODORIDAE

Large slender nematodes with cylindroid bodies. Cuticle distinctly annulated, lateral field with three or four incisures. No deirids. Labial region distinctly off-set and annulated. Amphid apertures small slits laterally or dorso-ventrally directed. Stylet well developed up to 150 µm. Oesophagus with amalgamated pro-metacarpus, short isthmus and pyriform glandular region not overlapping the intestine. Female tail rounded to hemispherical with spike-like extension, rarely elongate-conoid. Females with two genital branches, columned uterus with four rows of cells. Male caudal alae wing-like and lobed. Amphimictic reproduction. Obligate migratory ectoparasites of plant roots.

Family BELONOLAIMIDAE

Body vermiform, slender to robust. Lip region high, rounded, ogival or slightly flattened. Cephalic framework variable from poorly to very well developed (*Carphodorus*). Amphid apertures dorsoventral slits located at the edge of the labial disc. Oesophagus usually with a slender procorpus, rounded metacarpus, slim isthmus and a glandular postcorpus that may or may not overlap the intestine. Lateral field with two to six lines. Body cuticle sometimes with longitudinal ridges. Female tails cylindroid to conoid, more than twice as long as wide, often with thickened terminal cuticle, never elongate filiform. Phasmids always confined to the tail region. Females with two genital branches (exception : *Trophurus*); columned uterus with three rows of cells. Male caudal alae peloderan. Deirids present or absent. Obligate root parasites. Generally migratory ectoparasites but some taxa are capable of feeding as endoparasites.

Family PRATYLENCHIDAE

Body slender, vermiform to greatly swollen. Lip region low, less than 0.5 the diameter of basal lip annulus generally with fewer than five annuli. Stylet strong but short, less than 2.5 times longer than the diameter of basal lip region annulus. Cephalic framework well developed especially the basal plate. Esophageal glands overlap the intestine (exception : some *Pratylenchoides*). Deirids rare (*Pratylenchoides*). Phasmids located on tail region. Tails generally more than two anal body diameters long. Male caudal alae peloderan. Females with one or two genital branches, when one the posterior branch is a postuterine sac. Columned uterus composed of three rows of cells. Sexual dimorphism may occur, either male feeding apparatus atrophied or females may be saccate. Obligate endoparasites of higher plant roots, either migratory or sedentary parasites.

Family HOPLOLAIMIDAE

Female vermiform to kidney-shaped. Lip region higher than 0.5 the diameter of the basal lip annulus, with rounded or trapezoidal outline in lateral view. Stylet strong, 2.5-3 times longer than the diameter of the basal lip annulus. Oesophageal glands overlapping the anterior intestine (exception *Pararotylenchus*). Females with two genital branches, posterior branch may be reduced to PUS. Columned uterus with three rows of four cells. Lateral field generally with four lines. Phasmids generally located anterior to anus, rarely on the tail. Tail two body anal diameters long or less, generally curved dorsally, sometimes hemispherical. Eggs layed in a gelatinous matrix in *Rotylenchulinae*. Males may show sexual dimorphism, in some taxa feeding apparatus non-functional. Caudal alae of male leptoderan. Gubernaculum with titillae. Deirids absent. Obligate higher plant parasites with a migratory ecto-endoparasitic habit, sometimes semi-endo-sedentary parasites.

Family HETERODERIDAE

Body vermiform and slender in juvenile, robust in males and always swollen in mature females. Labial region always developed especially in larvae and males. Cephalic framework usually well developed, strongest in larvae and males. Oesophageal metacarpus usually large, postcorpore glands always overlap the anterior intestine. Larval and male bodies annulated; female body ornamentation variable from annuli to reticulation. Females swollen, with two genital branches amphidelphic or prodelphic; columned uterus with three rows of cells; eggs layed in a gelatinous matrix or retained within the female body of which the cuticle may be transformed (cysts). Males lack a caudal alae and the cloaca is nearly terminal (exception : *Bursadera*). Sedentary obligate parasites of roots, forming galls in some cases.

Superfamily Criconematoidea

Labial region poorly developed. Lip region represented by a labial disc often with four submedian lobes. Pro-metacarpus generally amalgamated, postcorpore pyriform and clearly off-set from intestine, no overlap (exception *Sphaeronema whittoni*). Females with single anteriorly directed genital branch with no post uterine extension. Columned uterus not defined. Males with nonfunctional feeding apparatus, rarely with caudal alae. Phasmids absent, deirids mostly absent.

Family CRICONEMATIDAE

Female body sausage-shaped to vermiform. Cuticle thick, in some cases double, lacking lateral field in females; annuli vary from rounded with or without extra cuticular layer to retrorse with lobation, crenation, scales

or spines. Deirids absent. Labial region with or without submedian lobes, framework well developed. Stylet massive, cone much longer than shaft and knobs. Oesophagus generally with amalgamated pro-metacarpus, short isthmus and small pyriform glandular region. Males lack a stylet; caudal alae absent to well developed; lateral field with two, three or four longitudinal lines. Obligate migratory to nearly sedentary ectoparasites of plant roots, some taxa induce terminal root galls.

Family TYLENCHULIDAE

Female body slender, swollen or globose. Cuticle thin and annulated except swollen forms may have fine punctations or minute tubercles. Lateral field present, not visible on swollen forms. Labial framework weak, stylet delicate. Oesophagus with amalgamated pro-metacarpus or with slightly swollen procorpore, distinct metacarpus, isthmus and pyriform glandular region. Male feeding apparatus degenerate, caudal alae absent. Deirids rarely present. Near sedentary to sedentary obligate higher plant parasites.

CLASSIFICATION

Order TYLENCHIDA Thorne, 1949

Suborder TYLENCHINA Thorne, 1949

Superfamily **Tylenchoidea** Örley, 1880

Family* TYLENCHIDAE Örley, 1880

Subfamily* TYLENCHINAE Örley, 1880

Genera* :

Tylenchus Bastian, 1865

Miculenchus Andrassy, 1959

Filenchus Andrassy, 1954

Malenchus Andrassy, 1968

Irantylenchus Kheiri, 1972

Polenchus Andrassy, 1980

Allotylenchus Andrassy, 1984

Cucullitylenchus Huang & Raski, 1986

Subfamily ECPHYADOPHORINAE Skarbilovich, 1959

Genera :

Ecpthyadophora de Man, 1921

Lelenchus Andrassy, 1954

Ecpthyadophoroides Corbett, 1964

Epicharinema Raski, Maggenti, Koshy & Sosamma, 1980

Mitranema Siddiqi, 1986

* Only valid names for families, subfamilies and genera are listed here. Junior synonyms of these taxa, as well as justifications for new synonymizations, will be given in the subsequent articles dealing with the concerned families.

Subfamily TYLADORINAE Paramonov, 1967

Genera :

Tylogorus Meagher, 1964
Eutylenchus Cobb, 1913
Macrotrophorus Loof, 1958
Cephalenchus Goodey, 1962
Campbellenchus Wouts, 1978

Subfamily ATYLENCHINAE Skarbilovich, 1959

Genera :

Atylenchus Cobb, 1913
Aglenchus Andr assy, 1954
Pleurotylenchus Szczygiel, 1969
Antarctenchus Spaull, 1972
Gracilancea Siddiqi, 1976
Coslenchus Siddiqi, 1978

Subfamily BOLEODORINAE Khan, 1964

Genera :

Boleodorus Thorne, 1941
Psilenchus de Man, 1921
Basiria Siddiqi, 1959
Neopsilenchus Thorne & Malek, 1968
Atetylenchus Khan, 1973
Neothada Khan, 1979
Duotylenchus Saha & Khan, 1982
Basirienchus Geraert & Raski, 1986

Genus incertae sedis :

Luella Massey, 1974

Genera dubia :

Sakia Khan, 1964
Basiliphora Husain & Khan, 1965

Family ANGUINIDAE Nicoll, 1935 (1926)

Genera :

Anguina Scopoli, 1777
Halenchus Cobb, 1933
Ditylenchus Filip'ev, 1936
Thada Thorne, 1941
Sychnotylenchus R hm, 1956
Pseudhalenchus Tarjan, 1958
Subanguina Paramonov, 1967
Cynipanguina Maggenti, Hart & Paxman, 1974
Pterotylenchus Siddiqi & Lenne, 1984

Genus incertae sedis :

Chitinotylenchus Micoletzky, 1922

Family DOLICHODORIDAE Chitwood, 1950

Genera :

Dolichodorus Cobb, 1914
Neodolichodorus Andr assy, 1976

Genus dubium :

Brachydorus de Guiran & Germani, 1968

Family BELONOLAIMIDAE Whitehead, 1960

Subfamily BELONOLAIMINAE Whitehead, 1960

Genera :

Belonolaimus Steiner, 1949

Carphodorus Colbran, 1965

Morulainus Sauer, 1966

Geocenamus Thorne & Malek, 1968

Sauertylenchus Sher, 1974

Subfamily TELOTYLENCHINAE Siddiqi, 1960

Genera :

Tylenchorhynchus Cobb, 1913
Trophurus Loof, 1956
Trichotylenchus Whitehead, 1960
Nagelus Thorne & Malek, 1968
Paratrophurus Arias, 1970
Merlinius Siddiqi, 1970
Triversus Sher, 1974
Amplimerlinius Siddiqi, 1976

Genus dubium :

Tetylenchus Filip'ev, 1936

Family PRATYLENCHIDAE Thorne, 1949

Subfamily : PRATYLENCHINAE Thorne, 1949

Genera :

Pratylenchus Filip'ev, 1936
Pratylenchoides Winslow, 1958
Radopholus Thorne, 1949
Hoplitylus s'Jacob, 1960
Zygotylenchus Siddiqi, 1963
Hirschmanniella Luc & Goodey, 1964
Apratylenchoides Sher, 1973

Subfamily NACOBBINAE Chitwood, 1950

Genus :

Nacobbus Thorne & Allen, 1944

Family HOPLOLAIMIDAE Filip'ev, 1934

Subfamily HOPLOLAIMINAE Filip'ev, 1934

Genera :

Hoplolaimus von Daday, 1905
Rotylenchus Filip'ev, 1936
Helicotylenchus Steiner, 1945
Scutellonema Andr assy, 1958
Aorolaimus Sher, 1963
Aphasmatylenchus Sher, 1965
Antarctylus Sher, 1973
Pararotylenchus Baldwin & Bell, 1981

Subfamily ROTYLENCHULINAE Husain & Khan, 1967

Genera :

Rotylenchulus Lindford & Oliveira, 1940
Acontylus Meagher, 1968
Senegalonema Germani, Luc & Baldwin, 1983

Family HETERODERIDAE Filip'ev & Schuurmans Stekhoven, 1941

Subfamily HETERODERINAE Filip'ev & Schuurmans Stekhoven, 1941

Genera :

Heterodera Schmidt, 1871
Meloidodera Chitwood, Hannon & Esser, 1956
Globodera Skarbilovich, 1959
Cryphodera Colbran, 1966
Atalodera Wouts & Sher, 1971
Sarisodera Wouts & Sher, 1971
Punctodera Mulvey & Stone, 1976
Cactodera Krall' & Krall', 1978
Hylonema Luc, Taylor & Cadet, 1978
Thecavermiculatus Robbins, 1978
Dolichodera Mulvey & Ebsary, 1980
Verutus Esser, 1981
Rhizonema Cid del Prado Vera, Lownsbery & Maggenti,
1983
Afenestrata Baldwin & Bell, 1985
Bellodera Wouts, 1985

Subfamily MELOIDOGYNINAE Skarbilovich, 1959

Genera :

Meloidogyne Goeldi, 1892
Meloinema Choi & Geraert, 1974
Bursadiera Ivanova & Krall', 1985

Genus dubium :

Meloidoderella Khan, 1972

Superfamily Criconematoidea Taylor, 1936

Family CRICONEMATIDAE Taylor, 1936

Subfamily CRICONEMATINAE Taylor, 1936

Genera :

Criconema Hofmänner & Menzel, 1914
Ogma Southern, 1914
Hemicriconemoides Chitwood & Birchfield, 1957
Bakernema Wu, 1964
Discocriconemella De Grisse & Loof, 1965
Criconemella De Grisse & Loof, 1965
Nothocriconemoides Maas, Loof & De Grisse, 1971
Blandicephalanema Mehta & Raski, 1971
Pateracephalanema Mehta & Raski, 1971

Genera dubia :

Macroposthonia de Man, 1921
Criconemoides Taylor, 1936

Subfamily HEMICYCLIOPHORINAE Skarbilovich, 1959

Genera :

Hemicycliophora de Man, 1921
Caloosia Siddiqi & Goodey, 1964

Family TYLENCHULIDAE Skarbilovich, 1947

Subfamily TYLENCHULINAE Skarbilovich, 1947

Genera :

Tylenchulus Cobb, 1913
Sphaeronema Raski & Sher, 1952
Trophonema Raski, 1957
Trophotylenchulus Raski, 1957
Meloidoderita Pogosyan, 1966

Subfamily : PARATYLENCHINAE Thorne, 1949

Genera :

Paratylenchus Micoletzky, 1922
Cacopaurus Thorne, 1943
Gracilacus Raski, 1972

Subfamily : TYLENCHOCRICONEMATINAE Raski & Siddiqui, 1975

Genus :

Tylenchocriconema Raski & Siddiqui, 1975

DISCUSSION

Our concept of the classification of Tylenchina is based on both comparative morphology and biology. We recognize that categories above the species are subjective; however, up to and including the family there are certain biological parameters that can be applied. The family group, when properly defined should yield more information than any other category in the Linnean hierarchy below it or above it. The family and to a lesser extent the genus should occupy a well defined niche or adaptive zone; to this they owe their origin. If this premise is accepted then there cannot be, at this time, twenty or more families in Tylenchina.

The Tylenchoidea exhibit a broad array of biological and morphological characteristics that set well defined family parameters. Their feeding habits range from so-called free-living forms whose sustenance comes from fungi and algae to obligate parasites of the above and below ground parts of plants. As higher plant parasites they may be ectoparasites, ecto-endoparasites, migratory endoparasites, sedentary semi-endoparasites or sedentary endoparasites.

Of the seven families in Tylenchoidea the least derived is Tylenchidae and of the genera within this family *Psilenchus* is the closest to the hypothetical ancestral representative (Luc *et al.*, 1987). Most other members of Tylenchidae have a single anteriorly directed genital branch with few exceptions (*Atetylenchus*, *Macrotriphurus*, *Antarctenchus*, and *Psilenchus* have two opposed branches). Both forms have four rows of cells in the columned uterus. Commonly the spermatheca is specialized as an offset pouch. The amphids in Tylenchidae are for the most part elongate ovals or long sinuous clefts laterally oriented. The family closest to Tylenchidae is Anguinidae most of whose members are characterized by the unusually large sperm. As plant parasites they are distinguished among Tylenchoidea because of their habit of attacking the above ground parts of plants. The columned uterus in Anguinidae basically has four rows but has evolved to the multicelled structure characteristic of *Anguina*.

Dolichodoridae appears to be a remnant of an early attempt at obligate root parasitism. They are all ectoparasites that have adapted to feeding on roots of higher plants. Much is often made of the swollen combined

procarpus and metacarpus; our view is that this is merely an anatomical modification to accommodate the elongate spear. An elongate stout spear seems to be a recurring characteristic among obligate ectoparasites that have no relationship to each other. It occurs in widely divergent groups such as *Xiphinema*, *Longidorus*, *Criconemella*, *Gracilacus*, and in Tylenchoidea in three separate families, Tylenchidae, Belonolaimidae and Dolichodoridae. The long spear is merely correlated with their feeding habits that allows both shallow and deep feeding.

Dolichodoridae retain the four-row columned uterus. The four remaining families of Tylenchoidea have reduced the columned uterus to three rows of cells.

The first time three rows of cells in the columned uterus are seen in Tylenchoidea is in Belonolaimidae. The belonolaimids are primarily ectoparasites of roots; however, there are many species in this family that are well adapted to endoparasitism. *Amplimerlinius* and *Pratylenchoides* appear to be linking genera between Belonolaimidae and Pratylenchidae.

The Pratylenchidae are obligate endoparasites of higher plant roots. It is interesting that their habits range from migratory endoparasites (*Pratylenchus*) to sedentary endoparasites (*Nacobbus*).

The origin of Hoplolaimidae is likely to have been from near the same ancestral stock as Belonolaimidae as shown in *Pararotylenchus*. Their parasitic mode is to function both as ectoparasites and endoparasites with equal facility. There appears to be a relationship between Hoplolaimidae and Heteroderidae. A similarity is seen in the cephalic framework, spear and esophagus. Both families have retained the ancestral two genital branches in the female. Though we do not think the number of lines in a lateral field has evolutionary significance it is interesting to note that most species in Hoplolaimidae and Heteroderidae have four incisures in the lateral field.

The origin of the Criconematoidea is likely also to be from "Tylenchidae-like" ancestors. In this superfamily the most advanced parasites are found in Tylenchulidae. At the same time this family retains more ancestral characters than its sister family Criconematidae. The superfamily has some interesting features, such as, the males all have atrophied feeding apparatuses and the females show no evidence of a second genital branch. This could mean that they diverged from a common ancestor, close to Tylenchidae, very early in the evolution of Tylenchina.

Some of the ancestral characters retained in Tylenchulidae illustrate the antiquity of the included members. The larval stages still exhibit a lateral field with generally two incisures which is unknown in the remainder of the superfamily. Deirids are present and larval oesophagi are similar to those of Tylenchoidea, that is, they lack the amalgamated swollen pro-metacarpus. The morphologically derived Criconematidae are more an-

cestral in their parasitic habit in that, as far as is known, they are migratory ectoparasites that elicit no special plant response. Some of the derived morphological features are the ornate cuticles of the adults and some larvae, the occurrence of extremely long stylets (more than 100 µm). The most unusual development is seen in the somatic musculature that is oblique rather than longitudinally oriented. This enables the accordion-like body movement so characteristic of the subfamily Criconematinae.

It is hoped that this classification will serve as a stable foundation upon which taxonomists can build the future additions to Tylenchina and Tylenchida. Each family is the product of its biology and morphology and represent separate evolutionary entities in the development of Tylenchina.

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Accepté pour publication le 14 mars 1987.