

Phylogeny of the order Tylenchida (Nematoda)

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Accepted for publication 30 November 1992

Summary. The structures of the most value for the macrotaxony of the class Nematoda - amphid, phasmid, deirid, lateral field and head sensory organs are situated on the lateral radii of the nematode body or near them. It is proposed to consider all these organs as a complex structural unit: «the lateral complex». Caudal alae of males (bursa) also belong to the lateral complex. There are 1) the non-phasmidial caudal alae (phasmids are absent from the tail), 2) the pre-phasmidial caudal alae (caudal alae are situated anterior to the phasmids), 3) the phasmidial caudal alae (phasmids are situated on the caudal alae as phasmidial ribs, alae envelop the tail). Phylogeny of the order Tylenchida is analysed by comparison of the lateral complexes of the taxa. *Atetylenchus* is the most primitive taxon. Some amendments are made to the classification by Siddiqi (1986), which is considered closest to the natural order. The order Tylenchida consists of 4 suborders, three of them (Tylenchina, Criconematina, Hexatylina) possess complexes of synapomorphic characters and therefore are considered to be monophyletic. The suborder Hoplolaimina is regarded as being paraphyletic, thus containing the remainder of the taxonomic divisions of the order. Hoplolaimina contains 2 superfamilies: 1) Dolichodoroidea: Psilenchidae, Meiodoridae n. rank: *Meiodorus*, *Brachydorus*, *Neodolichodorus*, *Hirschmanniella* and 2) Hoplolaimoidea: Merliniidae n. rank, including *Pratylenchoidea*, Belonolaimidae, (corresponding to Belonolaiminae *sensu* Siddiqi, 1986), Tylenchorhynchidae and other families of higher plant parasites. Hoplolaimoidea differs from Dolichodoroidea by the structure of the phasmidial caudal alae of males which envelops the tail, and by a lateral field in females and juveniles reaching the hyaline portion of the tail (in Dolichodoroidea the lateral field does not reach the hyaline portion of the tail). Psilenchidae represent a paraphyletic group which is not defined by synapomorphic characters. The most primitive taxa of Tylenchida, including *Atetylenchus*, belong to this group. Keys for the identification of the superfamilies and the families of the suborder Hoplolaimina are given.

Key-words: phylogeny, morphology, evolution, new taxa, Merliniidae n. rank, Meiodoridae n. rank.

The order Tylenchida includes free-living plant feeding and mycophagous nematodes, specialized plant parasites and arthropod parasites with complicated life cycles with an alternation of parthenogenetic and gamogenetic generations. The aim of this paper is an analysis of phylogenetic relations in the order, using a new approach. The author proposes some changes in the order classification on the basis of this analysis.

Many nematologists investigated the phylogeny as well as the classification of the order (Chitwood & Chitwood, 1950; Maggenti, 1971, 1981; Andrassy, 1976; Skarbilovich, 1978, 1980; Sumenkova, 1984; Drozdovsky, 1989). A prominent contribution to the phylogenetic study was made by Filipjev (1934), who

was the author of the first phylogenetic concept for the class Nematoda as a whole. He argued the Rhabditid-Diplogasterid ancestry of the Tylenchida in the modern context (Filipjev, 1934). This point of view was developed by Paramonov (1962, 1970) who proposed the hypothesis of the origin of the higher phytoparasitic tylenchids and of the whole order from primitive fungus feeders. The most important among the more recent phylogenetic papers are: the fundamental monograph by Siddiqi (1986), the joint set of articles by Fortuner, Maggenti, Luc, Geraert and Raski «A reappraisal of Tylenchina» which was later published as a separate volume (Fortuner et al., 1987-1988) as well as the series of articles by Chizhov and co-authors (Chizhov & Berezina, 1988; Chizhov &

Kruchina, 1988, 1992). In general these recent phylogenetic papers consider Tylenchida separately from the general evolution of Nematoda. For this reason the choice of the main characters and evolutionary directions in the transformation series of these characters depend mainly on the point of view of each author and not on detailed comparison of the taxon with all possible «out-liers». Such a comparison should define the choice of the most significant characters. Usually on the basis of the chosen characters the sums of the plesiomorphies and synapomorphies are calculated. Thereafter the phylogenetic diagram with dichotomous branching is constructed, using these calculations.

The proposed approach. In this article the Tylenchida is examined from general nematological taxonomic principles, as Filipjev did, but with much new knowledge of this group. The most important characters for Nematoda macrosystematics are situated on 2 lateral radii of a threadlike body. They are: an amphid (a paired cephalic chemoreceptor), a phasmid, peristomal cephalic sensilla, a lateral field and a cervical papilla (a deirid). The basis of this line is the lateral field - a paired surface structure of two lateral hypodermic chords (Fig. 1. A). These chords are extremely important structures for a basic plan of the nematode anatomy. They are of particular importance in a functional sense: nematode movement proceeds by snakelike undulation in the dorso-ventral plane and the lateral chords act as flexible columns for the tubular nematode body. They support the ventral and dorsal pairs of muscle fields, which are antagonistic. The undulation proceeds owing to the antagonism of these paired sets of muscles. Also there are ventral and dorsal hypodermic chords. However in tylenchids the ventral and dorsal chords are significantly less developed than the lateral cords, similarly in Secernentea and Chromadoria. The new approach here is to investigate the diversity of structure of the lateral complex in the order Tylenchida. The lateral complex here is regarded as a complicated structural unit and not a sum of separate characters. This approach avoids calculations of sums of synapomorphies and plesiomorphies. On the basis

of an analysis of the diversity of the lateral complex it is possible to define: 1) the most primitive taxon of the Tylenchida by comparison with the lateral complexes of closely related orders; 2) the transformations of the initial lateral complex within the order; 3) how the lateral complex transformations are in concordance with alternations in other characters and present a general view of the evolution in the order on the basis of these data. The classification by Siddiqi (1986) is used as the basic one for this analysis as it appears to be closest to the natural order and uses the greatest number of taxonomic characters. The family Myenchidae (parasites of the leech coelom) and the family Myorcytesidae (parasites of amphibian muscles) were excluded from the examination as little information is available on their morphology, especially on the structure of the lateral complex.

Review of lateral complex structures

Peristomial complex of sensilla and the subdivision of the anterior body end. The stomatal opening with a complex of surrounding sensilla are located at the junction of the lateral radii of a body. As in other Nematoda, the first circle of the inner labial sensilla includes 6 pore-like structures; the second and the third circles of sensilla are also located on the head region, the sensilla of the third circle (cephalic sensilla) being situated more laterally than the second circle sensilla (outer lip sensilla) (Fig. 1. G); for examples in *Pratylenchus sensillatus* (Anderson & Townshend, 1985); *Radopholus similis* (Baldwin et al., 1983). Two lateral sensilla of the second circle, which are usually present in other Nematoda, are not detected in Tylenchida. Therefore, the general formula for the arrangement of the anterior end sensilla in Tylenchida is 6 + (4 submedian + 4 submedian), this being a full set of sensilla. A reduction in number of sensilla, a shift of inner labial sensilla (the lateral pair only or all of them) into a prestoma, and other transformations take place in different groups.

It is necessary to compare the terminology used for the lip region in Tylenchida with that used for the

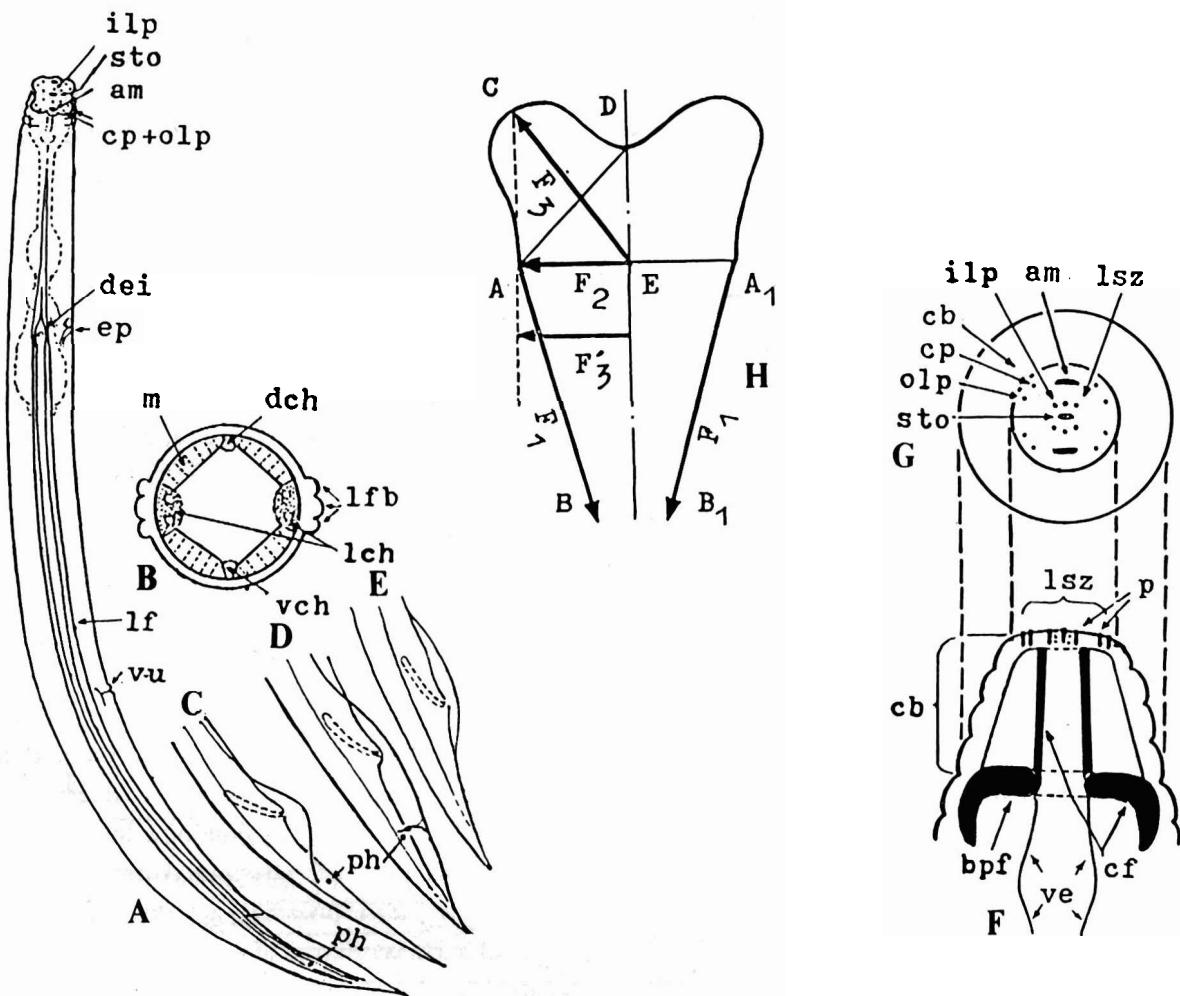


Fig. 1. Morphology of the nematodes of the order Tylenchida.

A: Arrangement of structures of the lateral complex on the nematode body; B: Transverse section of the body with the lateral chords and the bands (ridges) of a lateral field indicated; C-E: Types of male caudal alae (bursa): C - Pre-phasmidial adanal, D - Phasmidial, E - Non-phasmidial adanal; F,G: Cephalic region: F - Lateral view, G - Face view. The corresponding projections are indicated by the dotted line. H: Diagram of vectors of forces in the cephalic regions of nematodes of the families Dolichodoridae and Belonolaimidae when the protractor muscles contract. For explanations see text. am - amphid, bpf - basal plate of inner cephalic framework, dch - dorsal chord, dei - deirid, cb - cephalic base, cf - cephalic framework, cp - cephalic papillae, cp + olp - cephalic papillae and outer labial papillae, ep - excretory pore, ilp - inner labial papillae, lch - lateral chords, lf - lateral field, lfb - bands (ridges) of the lateral field, lsz - labial sensory zone, m - muscle layer, olp - outer labial papillae, p - papillae of cephalic part, ph - phasmid, sto - stomatal opening, vch - ventral chord, ve - vestibulum extension, vu - vulva.

non-Tylenchid Nematoda. The «lip region» in Tylenchida refers to the part of the anterior end of the body, which is situated at the level of the basal plate of the inner anterior end skeleton and anterior to the plate (Fig. 1. F,G). This skeleton is also named a head skeleton, a cephalic framework or an inner skeleton of the lip region. Thus the border of a lip region is defined by the position of an inner cephalic framework. A lip region of the non-Tylenchida is comprised of lips and the labial sensory complex situated on and around

them. The lip region's posterior border is the last (third) circle of the anterior end sensilla (the circle of cephalic sensilla or setae). The reason for this terminology for the lip region of Tylenchida is evident viz. lips of these nematodes are reduced and amalgamated. In connection with the minimization of the stoma, sensilla (besides Atylenchidae) are transformed from setae into papillae usually representing minute pores on the cuticle surface; all the labial sensory complex is shifted, as much as is

possible, closer to the stoma. The smallness of the real lip region have caused taxonomists to regard the basal part of the head skeleton as a posterior border of the lip region. The following terms are used here to characterize the position of the amphids: a) in the labial sensory zone - for the amphids situated at or before the level of the cephalic papillae or corresponding cuticle fields, or more anteriorly; b) in the cephalic basis - for amphids situated posterior to the labial sensory zone (Fig. 1, F,G). In tylenchid terminology the lip region corresponds to the sum of the labial sensory zone and the cephalic base.

The amphids in Tylenchida may be pore-like situated in the labial sensory zone (*Antarctenchus*); slit-like dorso-ventral situated near the cephalic base (*Psilenchus*); slit-like, dorso-ventral, situated in the labial sensory zone (Criconematina, *Pratylenchoidea*, Merliniinae and higher plant parasitic families), or slit-like, stretching longitudinally, ventrally curved, situated near the cephalic base as in *Atetylenchus*. This latter form occurs frequently also within the family Tylenchidae.

Lateral field. As mentioned, a lateral field is a surface structure of the lateral hypodermic chord. The presence and structure of a lateral field and its subdivision into longitudinal bands are the important characters for the macrotaxonomy of Nematoda. For example Enoplia are devoid of a lateral field whereas it is present in Secernentea and Chromadoria possess it.

Deirid (cervical papilla) is present in the lateral field. It is typical for Secernentea and also occurs within the family Plectidae (subclass Chromadoria: order Chromadorida: suborder Leptolaimina, after the classification by Lorenzen (1981).

Phasmid situated in the lateral field, usually in the tail, and is a significant character for the diagnosis of Secernentea (also referred to as the phasmidians, Phasmidia). Phasmid-like structures are present in the tail within the family Teratocephalidae, belonging to the same suborder Leptolaimina. In the suborders

Hexatylina and Criconematina the phasmid is reduced. In the Tylenchina the phasmid is absent in the tail, but phasmid-like structures are present near mid-body, dorsal to the lateral field. The typical tail phasmids are present only in nematodes of the suborder Hoplolaimina.

Structure of the male bursa. The bursa of males (= male caudal alae) is also a part of the lateral complex as the base of the caudal alae are situated on lateral radii and the alae proper are derivatives of the lateral fields. In those nematodes, where caudal alae enclose the tail tip, the phasmids are situated in the caudal alae in the form of bursal ribs (Figs. 1, D & 2). In the bursal rib a characteristic channel extends from the tail and terminates in the phasmidial bulb. Two processes originating from the bulb reach the margin of the caudal ala. This type of caudal alae is here referred to as the «enclosing phasmidial bursa». If the bursa does not enclose the tail tip, it is named adanal. If the phasmid is present in the tail, the bursal ala terminates anterior to the former. This type of a bursa is here referred to as «the pre-phasmidial adanal bursa» (Figs. 1, C & 2). If the phasmids are absent in the tail, the adanal bursa is referred to as «the non-phasmidial adanal» (Figs. 1, E & 2).

The ancestral form of the order Tylenchida

Not only Tylenchida but also other orders of the subclass Secernentea possess all of the previously mentioned structures of the lateral complex: amphid, phasmid, deirid, lateral field and a complete set of cephalic sensilla. The most primitive form of the lateral complex in Tylenchida (= the ancestral form) can be determined by examination of those genera with the fullest set of the lateral complex. There are only a few genera with the complete set of the lateral complex structures: *Atetylenchus*, *Psilenchus*, *Antarctenus*, *Pratylenchoidea* and the genera belonging to the subfamily Merliniinae: *Merlinius*, *Amplimerlinius*, *Hexadorus*, *Nagelus*, *Geocenamus* (Fig. 2). After the comparative anatomical research of Lorenzen (1981), the most primitive form of the amphid of the

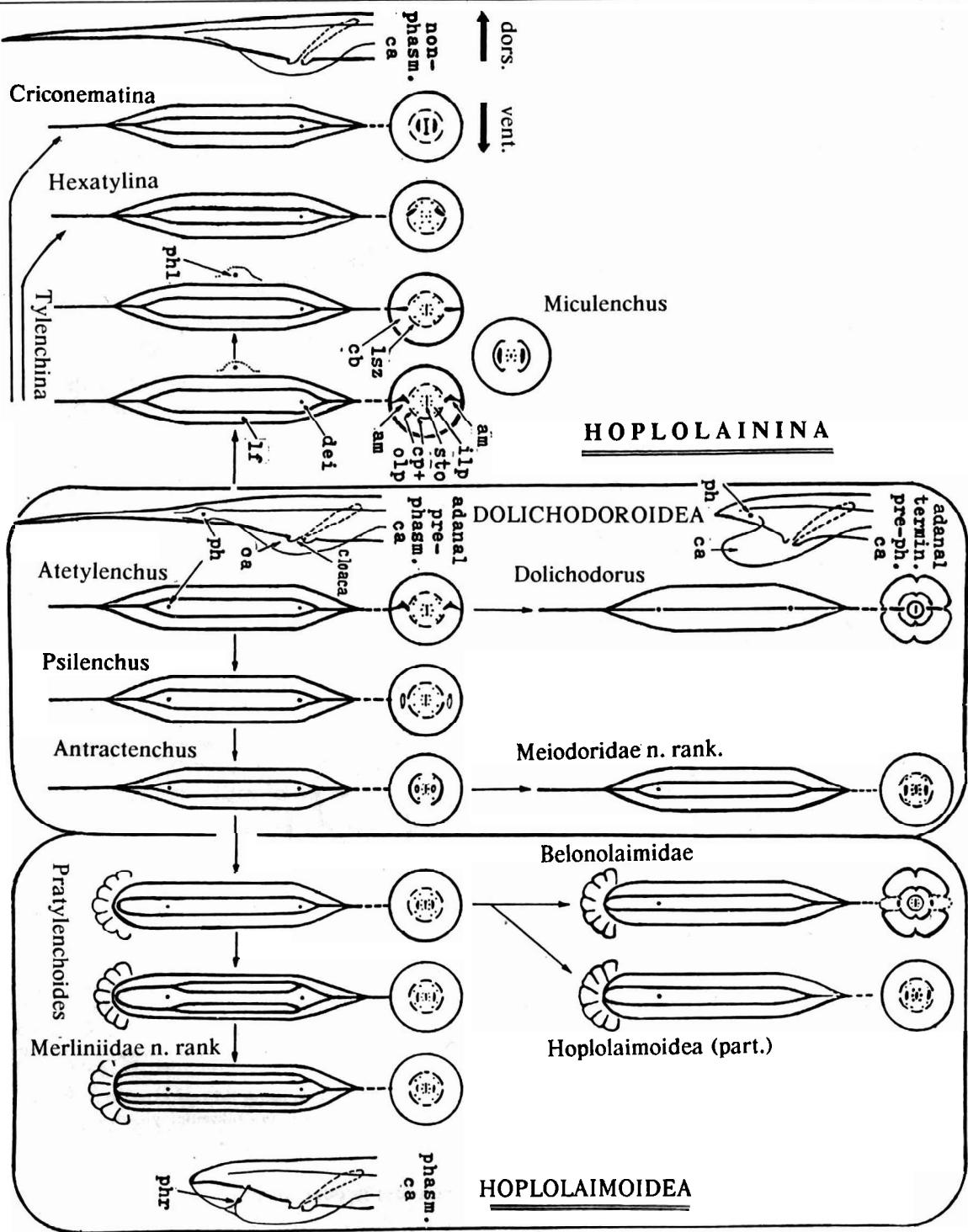


Fig. 2. Primary lateral complexes of the nematodes of the order Tylenchida.

The original lateral complexes, for the corresponding taxa are illustrated. The directions of evolution are indicated by arrows. The diversity of lateral complexes of the suborder Hoplolaimina, consisting of 2 superfamilies - Hoplolaimoidea and Dolichodoroidea (inside the rectangular contours) are illustrated in detail.

The heavy arrows indicate the positions of the dorsal (dors.) and ventral (ventr.) sides of the nematode body. adanal pre-phasm. ca - adanal pre-phasmidial caudal alae, adanal termin. pre-phasm. ca - adanal terminal pre-phasmidial caudal alae, am - amphid, ca - caudal alae (bursa), cb - cephalic basis, cp + olp - cephalic papillae and outer labial papillae, dei - deirid, ilp - inner labial papillae, lf - lateral field, lsz - labial sensory zone, non-phasm. ca - non-phasmidial caudal alae, ph - phasmid, phl - phasmid-like structure, phasmidial ca - phasmidial caudal alae, phr - phasmidial rib, sto - stomal opening.

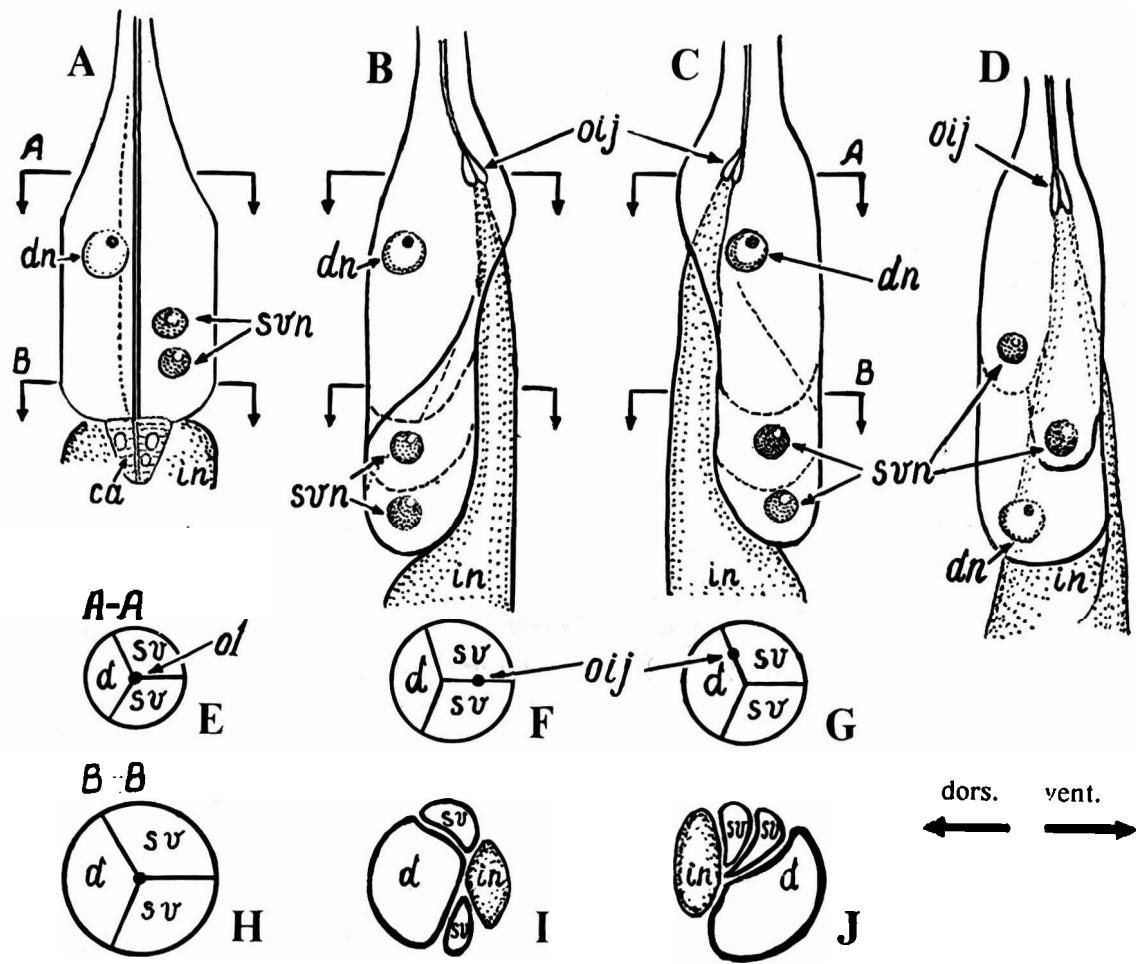


Fig. 3. Diversity of oesophageal gland structure in the nematodes of the order Tylenchida.

A-D: Lateral view; E-G: Transverse section A-A in the anterior part of the glandular body; H-J: Transversal section B-B in the posterior part of the glandular body (levels of sections A-A and B-B are marked in Figures 1-3 by lines with perpendicular arrows). A, E, H: The tylenchoid oesophagus; B, C: The lobed "hoplolaimoid" oesophagus - subventral glands are posterior to the dorsal one; B, F, I: The lobed "hoplolaimoid" oesophagus with an arrangement of the oesophageal-intestinal junction between primary subventral glands (the symmetrical type); C, G, J: The lobed «hoplolaimoid» oesophagus with an arrangement of the oesophageal-intestinal junction between the primary dorsal gland and one of the subventral glands (the asymmetrical type); D: The lobed oesophagus of the family Belonolaimidae and the subfamily Telotylenchinae of the family Tylenchorhynchidae: the dorsal gland is posterior to the subventral ones.

The positions of the dorsal side of the body (dors.) and the ventral one (ventr.) are marked by heavy lines. ca - cardia, d - dorsal gland, dn - dorsal gland nucleus, in - intestine, oij - oesophageal-intestinal junction, ol - oesophageal lumen, sv - subventral gland, svn - subventral gland nucleus.

secernentes is considered to be a slit-like, ventrally curved, postlabial amphid. This amphidial shape is primitive also for the subclass Chromadorea, and is considered to be the most primitive form for the whole class of Nematoda (Lorenzen, 1981). Therefore it is logical also to consider that this amphidial shape is the most primitive in the Tylenchida. Of the above-mentioned taxa only *Atetylenchus* and *Psilenchus* have an amphid situated posteriorly in the cephalic base. In

the other genera the amphid is positioned in the labial sensory zone. Therefore *Atetylenchus* and *Psilenchus* may be considered as representing the most primitive form in the order Tylenchida. The amphid is wide funnel-shaped in *Psilenchus* and slit-like, stretched longitudinally, ventrally curved in *Atetylenchus* (Geraert & Raski, 1987). Geraert and Raski (1987) characterized this general anterior-end shape as being *Filenchus*-like, i.e. the amphid being postlabial, slit-

like, ventrally curved (the structure of the lateral complex of Tylenchidae, to which *Filenchus* belongs, is examined below). Therefore the amphid of *Atetylenchus* is an example of the most primitive amphidial form and position. The transverse slit-like amphid of *Psilenchus* appears to be a development from the ventrally curved amphid of *Atetylenchus*. In SEM micrographs of *Psilenchus* sp. from New Zealand (Sher & Bell, 1975) the ventrally curved slit-like amphids, located in the postlabial zone, were readily apparent. *Atetylenchus* may therefore be considered as the most primitive form in the order Tylenchida by its lateral complex structure. This genus also possesses a weak stylet, lacking knobs and the primitive tylenchoid oesophagus. Within the Tylenchida only *Atetylenchus* and *Psilenchus* possess a stylet without knobs. In other tylenchids this protrusible stoma has 3 knobs, to which the protractor muscles are attached. The stylet of *Atetylenchus* resembles the tubular stoma of the primitive Secernentea (orders Rhabditida, Diplogasterida). A stylet without knobs also occurs in the related order Aphelenchida, i.e. corresponds the out-state for the character. In the tylenchoid oesophagus the glandular part forms a non-lobed compact body followed by the cardia, i.e. oesophageal sphincter (Fig. 3. A). In the more developed specialized genera of Tylenchida the posterior part of the oesophagus is transformed secondarily into the gland lobe and the cardia is displaced anteriorly (Filipjev, 1936; Paramonov, 1970; Seinhorst, 1971; Siddiqi, 1971; Ryss, 1987; - Fig. 3. D). Therefore *Atetylenchus* may be considered the most primitive genus in the Tylenchida by the structure of the lateral complex and other characters.

Evolution of the lateral complex in those genera of the suborder Hoplolaimina which are related to *Atetylenchus*

***Psilenchus* and *Antarctenchus*.** Development of the lateral complex in the line *Atetylenchus* - *Psilenchus* - *Antarctenchus* are evident. The development of the lateral complex concludes in a change of form and position of the amphid. The initial

slit-like amphid of *Atetylenchus* becomes transversal (*Psilenchus*) and is repositioned in the labial sensory zone (*Antarctenchus*; Fig. 2). The stylet in *Psilenchus* is devoid of knobs, as in *Atetylenchus*. Stylet knobs are present in all other genera in the order Tylenchida. Also in *Antarctenchus* only four submedian papillae remain from the peristomial sensilla of the second and third circle (4 + 4) (Fig. 2).

***Doichodorus*.** In *Dolichodorus* the amphid remains longitudinally stretched, postlabial (Fig. 2), but the cephalic region in this genus is transformed into a 4-lobed structure with a strongly developed labial disc. These developments of the lip region are correlated with the enlargement of the stylet in *Dolichodorus*. Nematodes of this genus are ectoparasites of roots. Similar changes of the lip region, - an enlarged stylet, an enlarged labial disc and the presence of a 4-lobed lip region have developed in parallel with the Belonolaimidae, which also are ectoparasites of roots. The parallel development of the lip region shape in *Dolichodorus* and belonolaimids is believed to be the result of similar adaptation to the protraction of the large stylet.

The lip region is the bearing for the stylet protractor muscles. As every bearing, the lip region should be steady to deformation displacements, caused by outer forces. The deformation can be elastic (reversible) or residual. With elastic deformation the body shape is restored to the initial shape after the cessation of loading, but residual deformation is non-reversible. The cephalic framework prevents non-reversible deformation of the lip region arising from contraction of the stylet protractor muscles.

The vector forces in the lip region are presented in Fig. 1. H. The protractor muscles attach to the body wall near the junction of the cephalic framework basal plate with the body wall. This point is marked on the diagram by the letter A. Also the muscles may be attached to the basal plate of the framework or to the vestibulum extension (Fig. 1. F). The protractor muscles contract during protraction of the stylet. The force of the strain F_1 acts along the lines AB and A_1B_1 (Fig. 1. H). Here the outer surface of the lip region (the curved contour ACD) is influenced by an expansion

force, and the base of the lip region (the straight segment AE in the flatness of the cephalic framework basal plate) is influenced by a pressure force. Naturally, the longer and more robust the stylet, the greater are the expansion and pressure forces. It is caused by the enlarged mass of the stylet as well as by the enlarged mass of the stylet protractor muscles.

During expansion the tensile strength of the lip region surface is important. The curved contour ACD has a reserve of length for the expansion. This reserve is characterized by the difference between the length of the curved segment ACD and the length of the straight segment AD. The more curved the segment ACD, the more stable the lip region is to the expansion force. Therefore, the lip region in the long-stylet tylenchids is highly curved. It can be considered as an adaptation to cope with the increased loads.

During loading the curve ACD tends to become straighter. It means that the lip region undergoes the ring-shaped expansion strains during contraction of the protractor muscles. These strains increase, as the curvature of the corresponding part of the contour ACD increases. The reserve of the cuticular surface in the form of longitudinal folds in the lip region is necessary for the tensile strength of this expansion strain. In the long-stylet tylenchids the lip region has the 4-lobed shape with longitudinal folds (depressions) between lobes. The lobed shape of a lip region can also be considered as an adaptation to the increased loads.

The resistance of the cephalic framework base to pressure depends not only on the solidity of the basal plate of the framework (the vector of the resistance force of skeleton material F_2 along the axis AE is indicated on Fig. 1. H) but also on the projection of the maximum radial line of the cephalic framework (Fig. 1.8), the vector of the resistance force of skeleton material F_3 along the axis EC) on the cephalic framework base (F_3' along the axis AE). Therefore, the greater the maximum radius of a lip region EC, passing through the radial septa (the blade) of the lip region skeleton, (i.e. the more high arched the outer contour of the lip region ACD), the greater the solidity of the skeleton base along the line AE. Also its resistance is increased to possible strains, caused by

the protractor muscles of the stylet. The high arched lobed form of a lip region therefore should be considered as an adaptation to the increased pressure loading in the long-stylet tylenchids.

Thus, the lobed, high arched, shape of a lip region should be optimum for the maximum strains of expansion and pressure arising from the stylet movement outside the body. Probably therefore the 4-lobed shape of the lip region arose independently in *Dolichodorus* and *Belonolaimidae*, the two taxa of ectoparasites with long stylets.

According to the lateral complex, particularly in amphid shape, the genus *Dolichodorus* could be traced from *Atetylenchus* only (Fig. 2). The set of secondary transformations in *Dolichodorus* are: deirid is reduced, lateral field transforms from the 3-band structure (4 incisures) in *Atetylenchus* into a 2-band one (3 incisures) in *Dolichodorus*, tail is shortened and in connecting with it the initial adanal bursa of *Atetylenchus* has been transformed in *Dolichodorus* into the pre-phasmidial adanal-terminal, i.e. into the terminal bursa with a distinct posterior gap between tail and caudal alae (Fig. 2).

Meiodorinae with its pore-like amphid located in the labial sensory zone it evidently may be traced only from *Antarctenchus*. In the *Meiodorinae* the stylet becomes massive and as a result of the tail shortening the pre-phasmidial bursa transforms from adanal into adanal-terminal. The genus *Hirschmanniella* is closely related to *Meiodorinae* by the structure of the lateral complex. Earlier this genus was considered in the family *Pratylenchidae*. *Hirschmanniella* differs however from the *Pratylenchidae* and from other higher hoplolaimoid families by the non-division into sectors of the lip region into sectors (this feature is peculiar to meiodorins as well); and by the lateral field not reaching the hyaline portion of the tail terminus, by the adanal bursa not reaching the terminus and by the phasmids in males not forming ribs on the caudal alae, as occurs in *pratylenchids* and other hoplolaimoid families, but are arranged on the tail as in *Meiodorinae*. These characters suggest that the meiodorins and *Hirschmanniella* be considered as a family *Meiodoridae* n. rank consisting of 2 subfamilies:

Meiodorinae including the genera *Meiodorus* and *Brachydorus* and **Hirschmanniellinae** including the single genus *Hirschmanniella* only.

SEM photographs of the lip region in *Meiodorus festonatus* have been published (Doucet, 1985), of *Hirschmanniella*: *H. miticausa* (Bridge et al., 1983), *H. spinicaudata* (Aubert & Luc, 1985), *H. mucronata* (Siddiqi, 1986). Six inner lip papillae and 4 submedian groups each of 2 papillae are seen distinctly in the photographs of *H. mucronata*. In *Meiodorus festonatus* there are 6 inner lip papillae and 4 submedian papillae. Thus the complete composition of 6 + (4+4) peristomial sensilla may be considered as the primary state for Meiodoridae (Fig. 2).

Pratylenchoides and Merliniinae. With reference to the above taxa which have a fully developed lateral complex, other members of the group i.e. *Pratylenchoides* and *Merliniinae* have a significant transformation of the lateral complex as opposed to that in the line *Atetylenchus* - *Psilenchus* - *Antarctenchus*. In *Atetylenchus*, *Psilenchus*, *Antarctenchus*, *Dolichodorus*, Meiodoridae a lateral field, consisting of several bands (usually 3) at mid-body, becomes narrower towards the body ends and transforms from a wide strip into 1 line on the cuticle surface. This line terminates, before reaching the tail tip, or the tail hyaline level (Fig. 2). In *Pratylenchoides* and *Merliniinae* a lateral field reaches the tail terminus (at least the level of the hyaline zone of the tail) in the form of a wide strip consisting of 3 or 5 bands (Fig. 2). Therefore the lateral chords, of which the surface structures are lateral fields, are combined with a thickened hypodermic hyaline zone at the terminus, forming a joint structure. This structure, with lateral hypodermic chords, appears to represent a single framework. The formation of such a framework possibly improves the flexibility of the tail. The structure of the male tail changes as a consequence of the lateral field displacement to the terminus. Male caudal alae, which help to hold a female during copulation, are derivatives of the lateral fields folds (Fig. 2). In *Atetylenchus*, *Psilenchus* and *Antarctenchus* a lateral field does not reach the hyaline portion of the terminus and consequently caudal alae

also do not reach the tail terminus. The bursa of these taxa is pre-phasmidial, adanal. In *Pratylenchoides* and *Merliniinae* the bursa becomes terminal, caudal alae enclosing the tail tip, - in connection with the lateral field displacement to the terminus. Phasmids, that in *Atetylenchus*, *Psilenchus* and *Antarctenchus* are positioned posterior to the caudal alae on the tail, are situated in *Pratylenchoides* and *Merliniinae* on the caudal alae, forming the so-called «phasmidial ribs». The phasmidial processes extend from the phasmidial bulb to reach the caudal alae margin (the phasmidial bursa - Fig. 1. D). On the basis of the lateral complex structure *Pratylenchoides* and *Merliniinae* may be considered as the single family *Merliniidae* n. rank, possessing the complete composition of a lateral complex and the reaching terminus lateral field of females and the phasmidial bursa of males.

Belonolaimidae and families of the higher plant parasitic Hoplolaimina. The following characters of the lateral complex: terminal bursa with 'phasmidial ribs', reaching terminus lateral field of females, arrangement of transversal and pore-like amphids in the labial sensory zone indicate that belonolaimids and the families of the higher plant parasitic Hoplolaimina: Tylenchorhynchidae, Hoplolaimidae, Rotylenchulidae, Heteroderidae, Pratylenchidae, Nacobidae, Meloidogynidae are related to the Merliniidae and may have arisen from the latter (Fig. 2). In all these families the reduction of a deirid took place. It may be supposed that the Belonolaimidae are the most ancient group among the higher hoplolaimoids, since the amphid remains on the margin of the labial sensory zone. A pore-like amphidial orifice is situated at the margin of a small tube (= the lateral lobe of the lip region according to some terminologies). This tube begins in the anterior part of the cephalic base. Comparison of this amphidial structure with the primitive one for Tylenchida (the amphid of *Atetylenchus*) may suggest that the amphidial tube of the belonolaimids represents the closed longitudinal slit of the amphid of the primitive tylenchs. The orifice of the amphid of belonolaimids therefore represents the anterior part of the initial slit-like orifice of the primitive Tylenchida. Evidently, such an amphid is

more primitive than the transversal or pore-like amphid found in hoplolaimoid families. This suggests an early separation of the belonolaimids from the higher hoplolaimoids. In the present paper the family Belonolaimidae is considered in the context of the subfamily Belonolaiminae *sensu* Siddiqi, 1986 only, i.e. in the following generic content: *Belonolaimus*, *Ibipora*, *Carphodorus*, *Morulaimus*. This family appears to represent a natural taxon. The genera included in it are similar by having a hypertrophied stylet, 4-lobed shape of the lip region, spiculae shape, gubernaculum with titillae and the distal end curved posteriorly and by the presence of an epiptigma at the vulva. Within the Belonolaimidae all genera, apart from *Belonolaimus*, possess 3 bands in the lateral field. Also, in *Carphodorus* there are 3 lateral field bands, of which only the inner one is distinct. In *Belonolaimus* spp. the lateral field has a single incisure only. It is obvious from a comparison of the lateral complexes of the tylenchids that in *Belonolaimus* a secondary reduction in the lateral field structure took place.

Among the above-mentioned higher plant parasitic hoplolaimoid nematodes the most primitive ones are undoubtedly those taxa of the subfamily Tylenchorhynchinae of the family Tylenchorhynchidae with their typically tylenchoid oesophagus (Fig. 3. A, E, H). In the rest of the families and in the subfamily Telotylenchinae of the family Tylenchorhynchidae the heterotopy of the oesophageal glands arises in connection with the increase in the gland volumes and with an intensification of the gland function. The glands could no longer be disposed at the same level in the narrow nematode body as in the primitive tylenchoid type of the oesophageal structure. Therefore, the heterotopy of glands arises at the same time as a reduction in the cardia and its forward displacement (Ryss, 1987, 1988). In higher hoplolaimoids the primary subventral glands (with small nuclei) are the longest. In the family Belonolaimidae, and in the subfamily Telotylenchinae of the family Tylenchorhynchidae, in which similar processes in the gland lobe formation occurred, the dorsal gland (with a large nucleus) is the longest (Fig.

3. D). Detailed investigation of the oesophageal transformations in Tylenchida and of their significance for the systematics of the order were carried out for the first time by Seinhorst (1971) and Siddiqi (1971). The secondary (in comparison with the tylenchoid) lobed structure of the oesophageal glands in Belonolaimidae points to a combination of primitive hoplolaimoid structural peculiarities of the lateral complex and derived characters in the oesophageal gland structure.

Transformations of the lateral complex in Tylenchina

The characteristic feature of the three orders is the absence of phasmids on the tail. The male bursa is usually adanal and devoid of phasmids. The absence of phasmids is secondary as all other orders of the subclass Secernentea possess phasmids.

The suborder Tylenchina is considered here to be comprised of the families: Tylenchidae, Atylenchidae, Tylodoridae, Ecphyadophoridae, i.e. its composition corresponds to the superfamily Tylenchoidea *sensu* Siddiqi, 1986. Within the Tylenchina the most close to *Atetylenchus* is the family Tylenchidae. In Tylenchidae there is a longitudinal slit-like ventrally curved amphid situated near to the cephalic base (i.e. posterior to the labial sensory zone) and a complete labial sensory complex (see, for example, SEM photographs in: Sher & Bell (1975); Siddiqi (1986); Fortuner et al. (1987, 1988)). This type of amphid has been designated by Geraert and Raski (1987) as being *Filenchus*- like. By the presence of ventrally curved postlabial amphids it may be concluded that the Tylenchina are the most primitive among the three non-phasmidial suborders. Tylenchina possess a clear-cut synapomorphy: phasmids are absent on the tail, but there is a pair of phasmid-like structures in the postmedian part of the body, dorsal to the lateral field. It is premature to speak about the homology of these phasmid-like structures to phasmids *in situ*, since no investigations on the innervation have been carried out. The position of them outside the lateral field (i.e. outside the typical lateral complex) calls into question such a homology. In other Secernentea such a structure

has not been observed. Siddiqi (1978, 1986) first reported these phasmid-like structures as important taxonomic characters and the synapomorphy for Tylenchoidea. Within Tylenchina the transformation of shape and position of the amphid takes place (Fig. 2). It becomes straight, longitudinal, slit-like, located in a cephalic base, then transforms to pore-like, moving into the labial sensory zone (*Miculenchus*: Geraert & Raski (1987) - see Fig.2.

Taxonomic borders of Tylenchina and Hoplolaimina and the taxonomic division of the order Hoplolaimina

Earlier Tylenchoidea were considered the most primitive group in the order; it had been joined in one suborder with the hoplolaimoid forms. Nevertheless, a secondary absence of the tail phasmids and a secondary synapomorphy in the form of the phasmid-like structure is a basis to consider this group as the monophyletic, secondary specialized taxon in the rank of the suborder Tylenchina. The hoplolaimoid forms: *Atetylenchus* and the groups close to it may be designated as a separate suborder, Hoplolaimina, including the most primitive forms lacking the obligate synapomorphies for the suborder. When a taxonomic subdivision is proposed only one of the two newly established groups will possess a complex of synapomorphies, and the other group represents the remainder of this new taxonomic subdivision. The group possessing synapomorphies is monophyletic and derived and the group lacking synapomorphies group is paraphyletic and includes the primitive forms, and the taxa related to them. For example, when Secernentea, which is the derived taxon possessing synapomorphies, was proposed within Nematoda, the other taxon - Adenophorea was diagnosed as lacking these synapomorphies. Subsequently, in a similar manner the subclass Enoplia was segregated from Adenophorea with the remaining taxa in the subdivision placed in the subclass Chromadoria. Among the latter are the most primitive taxa of Nematoda. Earlier the subdivision to Hoplolaimina and Tylenchina was proposed (Chizhov & Berezina,

1988; Chizhov & Kruchina, 1988, 1992) on the basis of a comparative morphological investigation of the female genital system. However these authors did not present a clear-cut differential diagnosis for the 2 suborders and the characteristics of the complexes of synapomorphies for the most derived from the two taxa. Within Hoplolaimina the forms with reaching terminus lateral fields and the terminal bursa can be segregated as the superfamily Hoplolaimoidea, including all advanced plant parasites and the remaining paraphyletic primitive forms (including *Atetylenchus*) which, not possessing synapomorphies of that rank, can be designated as the superfamily Dolichodoroidea. In the latter the genus *Dolichodorus* can be designated as the monotypic family Dolichodoridae by the shape and position of the slit-like amphid, the 4-lobed lip region and a long stylet. Another monophyletic group of long-stylet nematodes with pore-like amphids are represented by the family Meiodoridae n.rank. The remaining taxa segregated from the dolichodorids and meiodorids represent a paraphyletic group of the most primitive Tylenchida, including the genera *Atetylenchus*, *Psilenchus*, *Antarctenchus*. It is logical to consider these genera as a separate family - Psilenchidae which corresponds with the family suggested by Siddiqi (1986).

By their biotopic characteristics the Hoplolaimina are in general advanced plant roots parasites, inhabiting the mineralized soil levels. The Tylenchina as well as the Psilenchidae under Hoplolaimina inhabit the moss-lichen and the litter layers.

The history of the systematics of Hoplolaimoidea and the significance of the oesophageal gland structure for the determination of the taxonomic limits of the hoplolaimoids

The majority of the Hoplolaimoidea taxa typically possess an oesophageal gland lobe, in which the 2 primary subventral glands are longer than the dorsal gland (Fig. 3. B & C). Only in Belonolaimidae and Telotylenchinae (Tylenchorhynchidae) is the primary dorsal gland longer than the subventral gland (Fig. 3 D). The biological significance of the transformation

of the oesophagus from non-lobed to one containing a gland lobe may be accounted for as follows. Specialization to plant parasitism and the intensification of the oesophageal gland function occurs and the gland volume increases. This is caused by the necessity to dissolve plant cell contents by secretions from these glands injected through the stylet capillar into the host cell. The enlarged glands cannot be arranged at the same level in the narrow nematode body. Their heterotopy evolves so that the gland bodies become arranged in a single row forming a lobe and their primary positions - one large dorsal and two subventral - are changed (Fig. 3). The new arrangement is determined by the lobe position, which may be dorsal or ventrosublateral. The cardia, initially lying posterior to the gland bodies on the boundary of the oesophagus and intestine, moves to the anterior border of the oesophageal glandular part and undergoes a partial reduction of muscle fibers. In the most specialized types of the oesophagus the cuticular oesophageal intestinal valve retains from the cardia. With the cardia the anterior part of the intestine moves forward so that the gland lobe overlaps the intestine (Fig. 3. B-D). This displacement may occur between the subventral glands - in this case the mid-intestine pushes the gland lobe dorsally (Fig. 3. B, F, I) or between the subventral and dorsal gland. In this case the anterior part of the intestine pushes the gland lobe ventrosublaterally (Fig. 3. C, G, J). Thus, the formation of the lobe and the oesophageal gland heterotopy is important for the evolution of forms with the exointestinal digestion, which excrete gland secretions into host tissues to assist in the feeding process. To these nematodes belong the plant feeders since every cell on which a nematode feeds is enclosed into a massive cellulose wall. The biological significance of the oesophageal gland lobe formation in the evolution of the parasitic nematodes was explained by Ryss (1987, 1988). Earlier Ryss and Krall (1981) proposed the use of the structure of the oesophageal glandular part for the segregation of the group of the higher plant parasitic Tylenchida. According to these authors, the higher phytophages are the families possessing a lobe in which 2 subventral glands lie

posterior to the oesophageal-intestinal junction. Using this character, the authors re-established the superfamily of the higher phytophages Hoplolaimoidea, which had been proposed by Paramonov (1967), but in a narrow taxonomic context (without the criconematoïd forms). Proposing the superfamily, Paramonov (1967) did not give a clear differential diagnosis and therefore the name Hoplolaimoidea was used by taxonomists as a junior synonym of Tylenchoidea only. Siddiqi (1980) attempted to re-establish Hoplolaimoidea as a natural group of the advanced plant parasitic forms but again he did not give a clear differential diagnosis for the taxon. Later Siddiqi (1986) used the arrangement of the oesophageal glands for the differentiation of Hoplolaimoidea. According to his diagnosis, the primary subventral glands in Hoplolaimoidea lie posterior to the dorsal gland. It is clear that the oesophageal gland lobe with 2 subventral glands at the end formed more than once in the evolution of Tylenchida. It occurred independently within *Pratylenchoïdes* (the line *P. sheri*, *P. heathi* with an abutting oesophagus - *P. ritteri*, *P. megalobatus* with a large giant lobe) and within Hoplolaimidae (the line *Paratylenchus* with an abutting oesophagus - *Helicotylenchus* - *Hoplolaimus* with a gland lobe). The transformation of the glands of the tylenchoid oesophagus into the oesophagus with a glandular lobe ending by the primary dorsal gland took place in the line: subfamily Tylenchorhynchinae - Telotylenchinae within the family Tylenchorhynchidae, which is closely related to the higher hoplolaimoids (Fig. 3. A & D). The same structure has a gland lobe in the family Belonolaimidae (= subfamily Belonolaiminae *sensu* Siddiqi, 1986) which is very close to the group of higher plant feeders; it evidently developed such an oesophageal structure independently of Telotylenchinae. Oesophageal gland lobe formation therefore evolved in the plant feeders more than once. The formation of the lobe with subventral glands at the end, and the formation of the lobe with the dorsal gland at the end occurred repeatedly in the evolution of the Tylenchida. The classification proposed by Fortuner et al., (1987-1988)

also points to the parallelism in the formation of the gland lobe in different taxa of tylenchids. Heterotopy of glands and the oesophageal gland lobe occurred repeatedly in the parasitic Tylenchida probably because of an intensification of gland cell secretions which were used in the feeding process of these nematodes. Formation of a lobe is connected with reductions in the initial tylenchoïd glandular bulb i.e. reductions in connections between 3 glands and a cardia, cardia reduction and with reductions of connections of the glandular bulb with the body wall. Therefore the gland lobe formation (and its particular types) may be considered as the developmental specialization to phytophagy. This kind of specialization is accompanied by the foregoing reductions and this is typical for the evolution of the parasitic adaptations. Neither the presence of a lobe, nor its peculiar types determine the large monophyletic groups, but only characterize the adaptation trend arising in parallel different phyletic lines. In this paper the lateral complex structure and not the morphology of the glandular part of the oesophagus is used for the differential diagnosis of the Hoplolaimoidea.

The taxonomic position of *Neodolichodorus*

In classifications by Siddiqi (1986) and Fortuner et al., (1987-1988) *Neodolichodorus* is considered as the most close taxonomically to *Dolichodorus*. In Siddiqi's (1986) classification both genera have been combined in the subfamily Dolichodorinae, family Dolichodoridae. In the classification of Luc and Fortuner (1987) both genera and *Brachydorus* are placed in the family Dolichodoridae (without a subdivision to subfamilies). *Neodolichodorus* and *Dolichodorus* are the nearest with a long stylet and tylenchoïd oesophagus. However the lip region of *Neodolichodorus* is rounded and not 4-lobed as in *Dolichodorus*. In *Neodolichodorus* the prominent labial disc is absent, but the disc is prominently developed in *Dolichodorus*. The main difference is in the form and position of the amphid. In *Dolichodorus*

the amphid is in the form of a longitudinal slit, beginning anteriorly from the labial disc and coming into a cephalic base. In *Neodolichodorus* the amphid is a small dorso-ventral slit, located in the labial zone. In Nematoda the shape of the amphid aperture is very stable and is used as an important character for diagnostics of the higher taxa, up to subclasses. Therefore, the unification of *Dolichodorus* and *Neodolichodorus* into a single supergeneric taxon appears illogical. It is clear from the aforesaid analysis that the form and position of the amphid in *Neodolichodorus* is more derived than in *Dolichodorus* and corresponds to the amphidial form and position in *Antarctenchus* and *Meiodoridae* n. rank. By the pre-phasmidial adanal-terminal bursa and absence of the deirid it is logical to consider *Neodolichodorus* under Meiodoridae and to arrange in the typical subfamily Meiodorinae together with *Meiodorus* and *Brachydorus*. Lateral fields in females of *Neodolichodorus* as distinct from the other *Dolichodoroidea* reach the hyaline part of the tail. This feature is an obligate character in Hoplolaimoidea. In *Neodolichodorus* the displacement of the lateral fields to the terminus is caused by the distinct secondary shortening of the tail, especially by shortening in its ventral side. This has resulted in the phasmids having been moved to the level of the anus or even more anterior. This shortening of the tail and the shift of phasmids took place in parallel with the typical family of the Hoplolaimoidea - Hoplolaimidae - in the genera *Helicotylenchus* and *Rotylenchus*. In the hoplolaimids *Helicotylenchus multicinctus* and *H. vulgaris* the shortening of the tail (in the change of an index c') and the shifting forward of the phasmids were traced in a life history (Zuckerman & Strich-Harari, 1963; Yuen, 1966). In the type-species *Neodolichodorus obtusus* the early stage juveniles have a spicate tail, typical for the Dolichodoroidea (Siddiqi, 1986). The presence of the pre-phasmidial adanal-terminal bursa and shape of the tails in the early stage juveniles suggests the position of *Neodolichodorus* in the superfamily Dolichodoroidea, in the family Meiodoridae is phylogenetically justified.

Lateral complex of Hexatylina

Representatives of this suborder are devoid of phasmids and phasmid-like structures. Their amphids are labial, always located dorso-sublateral (Fig. 2). The main part of the suborder are the specialized entomoparasites which have a complex life-cycle, often including an alternation of generations. In the entomoparasitic Hexatylina there are reductions in the oesophageal structure and the female reproductive system is often hypertrophied. Members of the Anguinidae are the closest family to other suborders of Tylenchida. Anguinids are usually parasites with a simple life-cycle. They are mycophages and agents of combined nematode-fungus infections of plants. The higher anguinids - the genera *Anguina*, *Subanguina*, *Cynipanguina* and others are parasites of the aerial parts of plants, forming galls each with a nematode colony consisting of adults, juveniles and eggs. Higher anguinids have a hypertrophied female reproductive system containing a large number of synchronous eggs and a secondarily transformed oesophagus with a gland lobe. The formation and enlargement of the lobe can be easily seen in the ontogenesis by comparing the second stage juveniles possessing a tylenchoid oesophagus with juveniles of the following stages and adults (Ryss & Krall, 1981). Species closest to other Tylenchida are in the genus *Ditylenchus* and they possess the tylenchoid oesophageal structure and the non-hypertrophied female reproductive system. The lateral complex of *Ditylenchus* shows a resemblance to other Tylenchida with phasmids and phasmid-like structures being absent. The lateral field does not reach the hyaline part of the tail, therefore, the bursa is usually adanal, sometimes subterminal. The lateral field may contain a large number of bands (3-5, sometimes 7) with the initial number probably being 3 bands (4 incisures) as in other Tylenchida (Fig. 2). A deirid is present as in other Hexatylina. The amphid is slit-like, located in the labial sensory zone (see SEM micrographs in Siddiqi, 1986; Raski, Maggenti, 1983). The amphidial slit extends from the margin of the labial zone and passes longitudinally inwards to the oral opening. The slit is orientated the dorso-medially.

There are 6 inner labial papillae around the stoma; in the second circle 4 groups each with 2 pore-like papillae can be distinctly seen in the photographs in the book by Siddiqi (1986). This arrangement seems to correspond to the initial Hexatylina structure of the peristomal sensilla complex: 6 + (4 submedian + 4 submedian). In other micrographs - for example see the face view of *Hexatylus*, *Nothotylenchus*, *Safianema*, *Anguina*, *Cynipanguina* in Raski and Maggenti (1983) only the four submedian papillae could be recognized in the second circle. Four cephalic papillae were indicated by Siddiqi (1986) as a typical and obligate character of Hexatylina.

Homologies following from the structure and position of the amphid in Hexatylina

The dorso-sublateral amphids located on the margin of the labial zone are typical for hexatyls in the primitive *Ditylenchus*, in *Pseudhalenchus* and in *Hexatylus*, *Anguina* and *Cynipanguina* (Raski & Maggenti, 1983); the amphids are stretched in the form of an oblique slit (Fig. 2). In the forerunner to Hexatylina as in other primitive nematodes, the amphid was situated posterior to the labial zone. It is obvious from the shape of this organ in the contemporary Hexatylina that its aperture represented a longitudinally stretched slit. It is difficult to elucidate whether this slit on the lateral surface of the head cuticle was straight or curved ventrally or dorsally. With the shift of the amphid to the labial zone the projection of the amphidial aperture in the frontal plane (or of the lip region plane proper) should be retained, as it is perpendicular to the initial plane of the amphidial aperture position. As the slit-like and pore-like amphids of Hexatylina open always dorso-sublaterally, one can conclude that the terminal part of the amphidial canal was situated in the same position in the ancestral Hexatylina. According to the comparative-anatomical investigations of the whole class Nematoda (Lorenzen, 1981) this feature is characteristic of the primary ventrally curved amphid. Therefore the initial dorso-sublateral labial amphids of hexatyls are suggested to have arisen from the

postlabial longitudinal ventrally curved amphids. It is logical to derive therefore the lateral complex of Hexatylinea from the lateral complex of Tylenchina. The tylenchoid oesophageal shape in the primitive Hexatylinea also points to such relationship. Nevertheless, the structure of the cardia in anguinids is distinct from that in Tylenchina and Hoplolaimina. In anguinids this part has the two anteriormost modified cells of the intestine (Siddiqi, 1986), whereas in hoplolaims and tylenches the cardia is tricellular. The primitive Hexatylinea are supposed to be *Ditylenchus*-like mycophagous nematodes inhabiting the litter. Subsequently they evolved as agents of the complex fungus-nematode infections of the aerial parts of plants (Paramonov, 1962, 1970). The descendants of the mycophages and phyto-mycophages became entomoparasitic hexatylins with complex life-cycles including the alternations of generations (Chizhov & Kruchina, 1988), or higher plant-parasitic gall-forming nematodes inhabiting the aerial parts of plants - *Anguina*, *Subanguina*, *Cynipanguina* (Anguinidae) (Paramonov, 1962, 1970).

Transformations in the lateral complex of Criconematina

The majority of the Criconematina have peculiar scale-like, coarsely annulated, cuticle with a specific musculature. Nematodes of the superfamily Tylenchuloidea are the closest in appearance to the tylenchoids. These are cylindrical nematodes with finely annulated cuticles. On this basis the Tylenchuloidea are considered the most primitive Criconematina. The lateral complex of Tylenchuloidea is similar to that of Tylenchina and Hexatylinea: phasmids are absent, a lateral field does not reach the narrowly conical tail and accordingly the male bursa is usually adanal or absent. A deirid is present. The important differences from other non-phasmidial suborders are in the structure of the labial sensory complex and form of the amphid. The amphid is labial in the form of a dorso-ventral slit (Fig. 2). The sensilla of the labial complex are submerged, openings of the papillae are absent on the surface of the lips, amalgamated around the I-shaped oral opening. Inner

labial sensilla open in the prestoma. In other Criconematina - Hemicycliophoroidea and Criconematoidea the reduction of the deirid and the lateral field took place, evidently caused by the formation of the peculiar coarsely annulated cuticle.

To which of the two non-phasmidial suborders - Tylenchina or Hexatylinea do the Criconematina most closely resemble can be deduced as follows. Hexatylins differ significantly from Tylenchuloidea by the position of the amphidial aperture which is always dorso-sublateral. On the other hand in Tylenchina similar transverse labial amphids occur (*Miculenchus*, *Filenchus chilensis*; Geraert and Raski, 1987). The presence of submerged peristomal sensilla and the criconematooid oesophagus where the procorpus has amalgamated with the metacorpus indicates that Criconematina significantly differ from Tylenchina, more so than Hexatylinea differ from Tylenchina. Therefore it may be concluded that Criconematina separated before Hexatylinea from the Tylenchina (Fig. 5).

Correlation of morphological characters accompanied by transformations of the lateral complex: diversity in the female reproductive system

In contrast to the primitive Hoplolaimina, the tail phasmid of 3 other suborders disappeared. Also the posterior branch of the primitive didelphic female reproductive system became reduced in these suborders. Initially the female genital system in nematodes was didelphic. Among Tylenchida the didelphic system is predominant in the Hoplolaimina. During morphogenesis the didelphic system develops in the form of 2 branches of the genital primordium. There is a germinal cell originating in an ovary at the end of each branch. In rare cases where the genital system of hoplolaims consists of a single anterior branch (*Pratylenchus*), the posterior branch of the genital primordium with the posterior germinal cell does not complete its development (Roman & Hirschmann, 1969; Ryss, 1981, 1988) - see Fig. 4. This is evidence of the didelphic genital tract that remains in ontogenesis (Ryss, 1981).

In taxa of the 3 non-phasmidial suborders the single germinal cell is situated at the end of the single anterior branch of the genital primordium. Therefore specialization to a single tract has gone further and it is probably more ancient in the non-phasmidial suborders. The single female genital tract is widespread not only among tylenchids, but also in other groups of Nematoda. The biological expediency of its acquisition, or more precisely of the reduction of the posterior branch of the primary didelphic genital tract is probably as follows. In females with the primitive didelphic reproductive system the genital opening and the reproductive system sections depositing a completely developed egg are situated in the middle of the so-called trophico-genital part of a body (terminology after Paramonov, 1962), i.e. the mid-body. In nematodes with an unpaired female reproductive system the genital opening and the egg-depositing sections of the genital tract are displaced to the posterior border of the mid-body (Fig. 4. G & H). The trophico-genital section is the main part of the body length, where the main part of the dorso-ventral undulation wave, going along the body, is settled. A nematode proceeds by means of this wave. A completely developed egg in Tylenchida occupies nearly all the body diameter near the genital opening. The flexibility of the mid-body at this point is important for undulation and movement. A displacement of the vulva and the egg-depositing sections of the genital tract to the posterior end of the mid-body section should increase the flexibility of the whole body especially the trophic-genital part. In Tylenchida and in a majority of other Nematoda, with rare exclusions in the order Dorylaimida (families Belondiridae, Longidoridae) the reduction occurs in the posterior genital branch. This has probably developed as a result of it being easier to pull a rigid widened part of the body containing an egg than to push it forward. The latter case would occur if the genital opening would be situated anteriorly from the trophic-genital part, which is the main propulsive undulative agent of the nematode body. A direct analogy may be that of the nematode and a cord. By means of the latter a greater pulling force may be

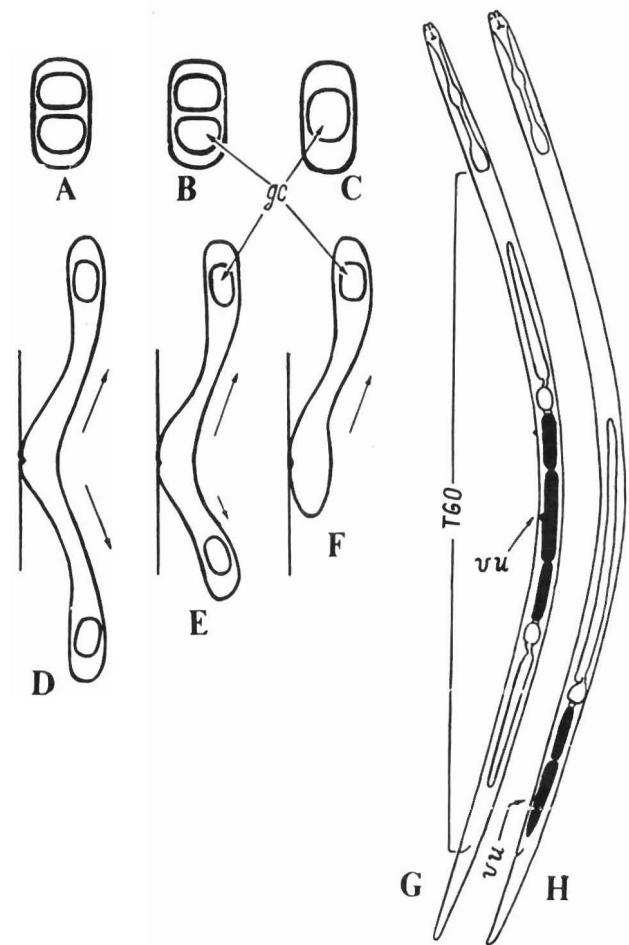


Fig. 4. Types of postembryonic morphogenesis in the female reproductive system of Tylenchida (A-F) and the arrangement of the female genital system and its egg-depositing sections in the nematode body (G, H).

A-C: Types of genital primordium of second-stage juveniles; D-F: Types of development of the genital primordium in ontogenesis. Directions of the morphogenetic movement of the germinal cell in the developing genital primordium are marked by arrows. A, D: Morphogenesis of the female reproductive system of the didelphic Hoplolaimina; B, E: Morphogenesis of the female reproductive system of the monodelphic (pseudomonodelphic) Hoplolaimina (*Pratylenchus*); C, F: Morphogenesis of the female reproductive system of Tylenchina and Hexatylina; G: Position of the reproductive system in didelphic Tylenchida (Hoplolaimina); H: Position of the reproductive system in monodelphic Tylenchida.

Sections of the reproductive tract, depositing a completely developed egg (a preuterine gland - a cristaformaria and an uterine sack) are marked by the black colour. gc - germinal cell, tgo - trophico-genital (the middle) part of a body, vu - vulva.

applied to an object, but the force of a push may be limited.

Earlier the reduction of the posterior branch of the female genital tract has been interpreted by some authors as the deliverance of the posterior part of the

The primitive niche and niche diversity

Following the pattern of phylogenetic relationships developed in the analysis above (Fig. 5) the evolution of the niches for the order Tylenchida may be proposed. It is premature to analyse the evolution of the nutrition requirements and food sources of different taxa. Biotopes colonised by *Atetylenchus*, *Psilenchus*, *Antarctenchus* and *Tylenchina* may be considered primitive niches for the order. These are litter and the above-ground moss-lichen layer. The descendants of the primitive Tylenchida have progressed to parasitism in and on roots of the higher plants from these initial niches. Thus the majority of Hoplolaimina and Criconematina have moved into the mineral soil layers. From the initial niche, more branches, including *Ditylenchus*-like forms, evolved as entomoparasites or parasites in galls on aerial parts of plants i.e. Hexatylina.

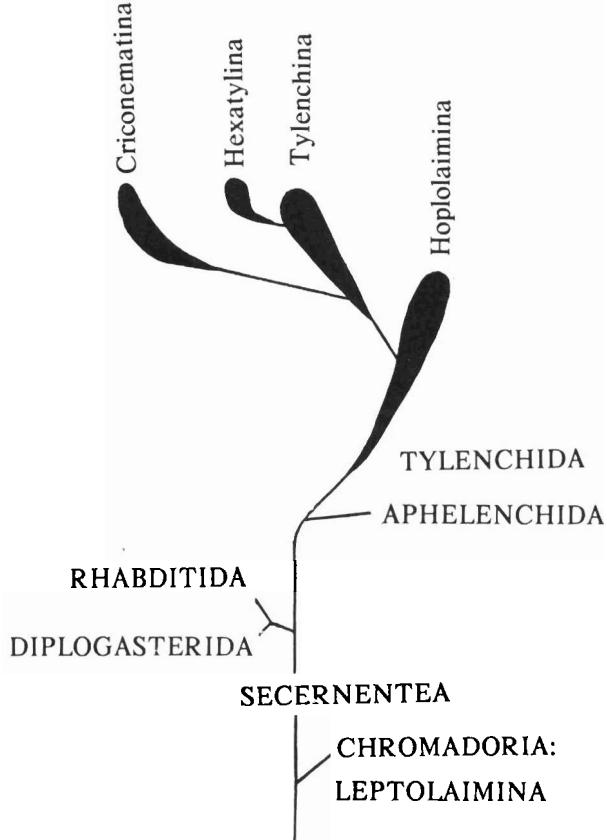


Fig. 5. The diagram of phylogenetic relationships of the order Tylenchida and of the ancestry of the latter.

worm body from an obstacle to a movement. The posterior ovary and oviduct have been considered as the obstacles (Paramonov, 1970; Chizhov & Kruchina, 1988, 1992). But when the vulva is moved to the posterior the posterior body cavity becomes filled again by the anterior genital tract. Therefore, the above-mentioned point of view appears unconvincing.

In three non-phasmidial orders - Tylenchina, Hexatylina, Criconematina reductions in the posterior body part of females are present. The posterior branch of the female reproductive tract and the tail phasmids are reduced. Probably this is connected with an opposition of the more mobile part of the body anterior to the vulva to the less mobile part posterior to the vulva. However in the higher Hoplolaimina (the majority of Hoplolaimoidea) a deirid located in the anterior body part is reduced.

The origin of Tylenchida

The author of the present paper shares the view that Tylenchida and Aphelenchida originated from Rhabditoid-Diplogasteroid ancestors (Fig. 5). These views have been described in classical papers by Filipjev (1934), Chitwood & Chitwood (1950), Paramonov (1970) and Andrassy (1976). The primitive Tylenchida - *Atetylenchus* - correspond to the characters of the lower Secernentea by the structure of the lateral complex: ventrally curved postlabial amphid, presence of a deirid and phasmid, and having 3 bands of the lateral field. According to the opinions of some authors, Secernentea may have originated from the Chromadoria (Andrassy, 1976; Drozdovsky, 1989). The closest to Secernentea taxa among Chromadoria are the Plectidae which possess a deirid and Teratocephalidae which possess phasmid-like papillae in the tail. These two families were related by Lorenzen (1981) to the suborder Leptolaimina in the order Chromadorida, which represents the paraphyletic group located at the base of the phyletic tree of Chromadoria as well as the whole class Nematoda. Thus it may be supposed, based upon the

lateral complex structure of *Atetylenchus* that the origin of the order Tylenchida proceeded very close to the time when Secernentea split from the primitive Chromadoria.

Keys to the suborders, superfamilies and families of the order Tylenchida as well as diagnoses and taxonomic volumes of the groups, whose contents differ from that in classifications by Siddiqi (1986); Fortuner et al., (1987, 1988); Chizhov and Kruchina (1988, 1992), are proposed.

Key to suborders of the order Tylenchida

1. Phasmids present on tail (except *Aphasmotylenchus*), female reproductive system usually paired...
..... Hoplolaimina
 - Phasmids absent, phasmid-like structures may present in postmedian body part lying dorsally from lateral field, female reproductive system unpaired.....
..... 2
 - 2. Phasmid-like structures present dorsally from lateral field in postmedian body part (usually at level of vulva) Tylenchina
 - Phasmid-like structures in postmedian body part absent..... 3
 - 3. Oesophagus criconematoïd: metacorpus fused with procorpus, stylet usually occupies whole procorpus (in redrawn up state), amphids lateral, slit-like, dorso-ventral, oral aperture I-shaped; parasites of plant roots Criconematina
 - Oesophagus non-criconematoïd, metacorpus not fused with procorpus, amphid dorso-sublateral, slit-like or pore-like, oral aperture rounded pore-form. Mycophages and entomoparasites, parasites of aerial organs of higher plants..... Hexatylina

Suborder Hoplolaimina Chizhov & Berezina, 1988 (syn. Heteroderata Skarbilovich, 1959)

Diagnosis. Tylenchida. Amphid postlabial: longitudinal, ventrally curved, V-shaped or dorso-ventral; or labial: dorso-ventral, sometimes pore-like. Deirid present (*Psilenchidae*, *Merliniidae* including *Pratylenchoidea*) or absent (*Dolichodoridae*,

Meiodoridae and the group of higher hoplolaimoid families: *Tylenchorhynchidae*, *Hoplolaimidae*, *Pratylenchidae*, *Rotylenchulidae*, *Nacobidae*, *Meloidogynidae*, *Heteroderidae*). Phasmid present (except *Aphasmotylenchus* in *Hoplolaimidae*). Lateral field with 4, more rarely 1, 3, 6 incisures reaching hyaline part of tail terminus (superfamily *Hoplolaimoidea*) or not reaching it (superfamily *Dolichodoroidea*). Bursa pre-phasmidial: adanal, adanal-terminal or phasmidial terminal.

The paraphyletic group, lying at the base of the phylogenetic trunk of the order Tylenchida.

Type family: *Hoplolaimidae* Filipjev, 1934.

Key to superfamilies of Hoplolaimina

1. Male caudal alae enclosing tail tip, phasmidial: phasmids form phasmidial ribs on alae, lateral field of larvae and females reach hyaline part of tail terminus...
..... Hoplolaimoidea
 - Male caudal alae adanal or adanal-terminal, pre-phasmidial: phasmids posterior to caudal alae on the tail, lateral fields of larvae and females do not reach hyaline part of terminus at significant distance (in *Neodolichodorus* only in juveniles of the youngest free stages) Dolichodoroidea

Superfamily Hoplolaimoidea Filipjev, 1934 (Paramonov, 1967)

Diagnosis. Hoplolaimina. Male caudal alae phasmidial, enveloping tail. Phasmids form phasmidial ribs on tail. Lateral fields of females and larvae reach hyaline part of tail terminus.

Type family: *Hoplolaimidae* Filipjev, 1934.

Key to families of Hoplolaimoidea

1. Deirid present.....
..... Merliniidae Siddiqi, 1971 (n.rank).
 - Deirid absent 2
2. Lip region 4-lobed. Amphidial apertures on the end of longitudinal non-annulated lateral tubes, situated in the anterior part of annulated lip region.....

- Belonolaimidae Whitehead, 1960.
- Lip region truncated, conical or rounded, amphids are small slits directed dorso-ventrally or pore-like, located on the lip sensilla zone 3
 - 3. Female body lemon-shaped or saccate 4
 - Female elongate, cylindrical 8
 - 4. Oesophageal glands in the form of lobe, lying on the anterior part of intestine dorsally 5
 - Oesophageal glands in the form of lobe, lying on the anterior part of intestine ventrally 6
 - 5. Female reproductive system paired, lip region of males hemispherical, oesophagus and stylet in males degenerated, gubernaculum protrusible
..... *Achlysiella* Hunt, Bridge & Machon, 1989
(Pratylenchidae Thorne, 1949).
 - Female reproductive system unpaired, lip region of males truncated, conical, stylet and oesophagus of males well-developed, gubernaculum non-protrusible.
..... Nacobidae Chitwood in Chitwood & Chitwood, 1950 (*Nacobbus* Thorne & Allen, 1944).
 - 6. Orifice of dorsal gland at the distance equal to the stylet length from stylet base or more
..... Rotylenchulidae Husain & Khan, 1967.
 - Orifice of dorsal gland at the distance shorter than stylet length from stylet base 7
 - 7. Excretory pore anterior to median bulb
..... Meloidogynidae Skarbilovich, 1959.
 - Excretory pore posterior to median bulb
..... Heteroderidae Filipjev & Schuurmans Stekhoven, 1941.
 - 8. Oesophageal glands in a bulb abutting intestine with cardia lying posterior to glands; if glands form a lobe extending over intestine then the dorsal gland (with large nucleus) is the longest
..... Tylenchorhynchidae Eliava, 1964.
 - Oesophageal glands forming a lobe extending over intestine, subventral glands (with small nucleus) are the longest 9
 - 9. Lip region low, broad, the ratio of stylet length to lip region width not more than 2.5
..... Pratylenchidae Thorne, 1949.
 - Lip region high, narrow, the ratio of stylet length to lip region width 3 or more
..... Hoplolaimidae Filipjev, 1934.

Family Merliniidae Siddiqi, 1971 (n.rank).

Diagnosis. Hoplolaimoidea. Deirid present. Amphids labial, small dorso-ventral slits or pore-like. Lateral field with 4 or 6 incisures. Terminal tail cuticle abnormally thickened. Vulva usually with epiptygma. Spicules usually tubular.

Type-genus: *Merlinius* Siddiqi, 1970.

Other genera: *Pratylenchoides* Winslow, 1958 (included in the family for the first time), *Amplimerlinius* Siddiqi, 1976, *Geocenamus* Thorne & Malek, 1968, *Hexadorus* Ivanova & Shagalina, 1983, *Nagelus* Thorne & Malek, 1968, *Scutylenchus* Jairajpuri, 1971.

Family Tylenchorhynchidae Eliava, 1964

Diagnosis. Hoplolaimoidea. Deirid absent. Amphids labial, small dorso-ventral slits or pore-like. Lateral field with 4, rarely 3 incisures. Oesophageal glands in a bulb, abutting intestine, cardia lying posterior to glands; or glands form a lobe, a dorsal gland (with a large nucleus) lying at the end of a lobe.

Type-genus: *Tylenchorhynchus* Cobb, 1913.

The family includes only subfamilies *Tylenchorhynchinae* Eliava, 1964, *Trophurinae* Paramonov, 1967, *Macrotrrophurinae* Fotedar & Handoo, 1978 (3 subfamilies with a non-lobed glandular part of an oesophagus) and *Telotylenchinae* Siddiqi, 1960 (with a lobe of oesophageal glands, in which the dorsal gland is the longest). Contents of all these subfamilies are considered in the sense of Siddiqi (1986).

Superfamily Dolichodoroidea Chitwood in Chitwood & Chitwood, 1950 (Siddiqi, 1986)

Diagnosis. Hoplolaimina. Male caudal alae pre-phasmidial (phasmids outside the caudal alae, on the tail), adanal or adanal-terminal. Lateral field of females and juveniles (in *Neodolichodorus* - in juveniles of early stages) does not reach the hyaline

part of terminus; if it reaches, so in the form of a single incisure.

Type-family: Dolichodoridae Chitwood in Chitwood & Chitwood, 1950.

Other families: Psilenchidae Paramonov, 1967, Meiodoridae Siddiqi, 1976 (n. rank).

Key to families of Dolichodoroidea

1. Deirid present Psilenchidae
- Deirid absent 2
2. Amphid longitudinal slit-like, coming outside the labial zone into cephalic basis, lip region 4-lobed with prominent labial disc.....
..... Dolichoridae (*Dolichodorus* Cobb, 1914)
 - Amphid pore-like, on the anterior margin of labial zone, indistinct, lip region truncated, conical to rounded, with insignificant labial disc or without disc
..... Meiodoridae Siddiqi, 1976 (n. rank)

Family Dolichoridae Chitwood in Chitwood & Chitwood, 1950

Diagnosis: Dolichodoroidea. Amphids longitudinal slit-like, coming outside the labial zone into cephalic basis, lip region 4-lobed with prominent labial disc. Male caudal alae pre-phasmidial, adanal-terminal, -i.e, there is a gap at the posterior side of ala, separating terminus from bursal ala.

Type-genus: *Dolichodorus* Cobb, 1914.

No other genera.

The monotypic group, differing from other families by shape of lip region and amphidial aperture form.

Family Meiodoridae Siddiqi, 1976 (n. rank)

Diagnosis: Dolichodoroidea. Amphid pore-like, on the anterior margin of labial zone, lip region truncated, conical to rounded, with insignificant labial disc or without disc. Male caudal alae pre-phasmidial: adanal, adanal-terminal, subterminal.

Type-subfamily: Meiodorinae Siddiqi, 1976

Other subfamily: Hirschmanniellinae Fotedar & Handoo, 1978

Subfamily Meiodorinae Siddiqi, 1976

Diagnosis: Meiodoridae. Glands in posterior bulb abutting intestine. Male caudal alae adanal-terminal.

Type-genus: *Meiodorus* Siddiqi, 1976.

Other genera: *Brachydorus* de Guiran & Germani, 1968, *Neodolichodorus* Andrassy, 1976.

Subfamily Hirschmanniellinae Fotedar & Handoo, 1978

Diagnosis: Meiodoridae. Glands in the form of lobe extending over intestine. Male caudal alae adanal to subterminal.

Type-genus: *Hirschmanniella* Luc et Goodey, 1964.

No other genera.

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Рысс А.Ю. Филогения нематод отряда Tylenchida (Nematoda).

Резюме. Структуры, наиболее важные для макротаксономии класса Nematoda: амфид, фазмид, дейрид, боковое поле, окоротовой комплекс сенсилл – расположены на боковых лучах тела или вблизи от них. Предлагается рассматривать их как единую сложную структуру и присвоить ей название «латеральный комплекс». К латеральному комплексу Tylenchida относится и бурса самцов, которая может быть бесфазмидальной (на хвосте отсутствуют фазмиды), предфазмидальной (бурсальные крылья расположены перед фазмидами) и фазмидальной (фазмиды расположены на бурсальных крыльях в виде бурсальных ребер, бурса охватывает хвост). Филогения отряда Tylenchida проанализирована путем сравнения латеральных комплексов. Нематоды рода *Atetylenchus* следует рассматривать как наиболее примитивные. Наиболее близка к естественной система нематод, предложенная Siddiqi (1986). В рамках отряда Tylenchida рассматриваются 4 подотряда, из которых три: Tylenchina, Criconematina, Hexatylina обладают комплексами синапоморфий (монофилетичны), а Hoplolaimina представляет собой парафилетический остаток таксономического группирования отряда. Hoplolaimina включает два надсемейства: Dolichodoroidea (*Psilenchidae*, *Meiodoridae* n. rank.: *Meiodorus*, *Brachydorus*, *Neodolichodorus*, *Hirschmanniella*, *Dolichodoridae*: *Dolichodorus*) и Hoplolaimoidea (*Merliniidae* n. rank., включающее *Pratylenchoides*, *Belonolaimidae*, соответствующее *Belonolaiminae* sensu Siddiqi, 1986, *Tylenchorhynchidae*, *Hoplolaimidae* и другие семейства высших фитопаразитов). Hoplolaimoidea отличается от Dolichodoroidea охватывающей хвост фазмидальной бурской самцов и достигающим гиалиновой зоны хвоста боковым полем личинок и самок (у Dolichodoroidea бурса предфазмидальная, боковое поле не достигает гиалиновой зоны хвоста). *Psilenchidae* представляет собой парафилетическую группу, не объединяемую синапоморфиями, куда относятся наиболее примитивные Tylenchida, включая *Atetylenchus*. Представлен ключ для определения подотрядов, а также надсемейств и подсемейств подотряда Hoplolaimina.
