A CRITICAL REVIEW OF THE SUBORDER TYLENCHINA (FILIPJEV, 1934)
(NEMATODA: SECERNENTEA)

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Geraert (1966) proposed to distinguish a superfamily Criconematoidea Geraert. The question arose consequently concerning a revision of the superfamily Tylenchoidea (Filip'ev, 1934). In this work an attempt is made at another solution of this problem, related to a proposal for the distinction of a superfamily Hoplolaimoidea n. superf. Along with this, the proposal of Geraert (1966) concerning the separation of two suborders of the order Tylenchida Thorne, 1949 is supported.

Identification key of suborders of the order
Tylenchida Thorne, 1949

1. (2) Opening of the dorsal gland displaced to the area of the metacorpal bulb – in its anterior sector; only monodelphic females; caudal alae in males, if present, with bursal ribs; if not, bursal papillae, including terminal ones, present in the tail of males . . . . Aphelenchina (Fuchs, 1937).

2. (1) Dorsal gland opening into the esophagus lumen in the area of the procorpus which is sometimes fused into a common complex with the metacorpal bulb; females mono – and didelphic; the caudal alae have no ribs; bursal papillae absent . . . . Tylenchina (Filip'ev, 1934).

One of the motives for proposing the separation of the suborders named, is belief in the necessity to distinguish two superfamilies in the composition of the suborder of the tylenchids (tylenchatae), the superfamily Tylenchoidea (Filip'ev, 1934), Chitwood & Chitwood, 1937 proposed earlier, and the new superfamily Hoplolaimoidea (Filip'ev, 1934) superf. n. being proposed in this work.

In the process of elaborating the taxonomy of this superfamily I came to the necessity of revising the series of its subordinate groups and to a corresponding reconsideration of the structure of the latter. As a result of the work carried out, the following presentation concerning the taxonomic structure of the order Tylenchida Thorne, 1949 emerged.

Order Tylenchida Thorne, 1949

  Suborder Aphelenchina (fuchs, 1937)

    Superfamily Aphelenchoidea (Fuchs, 1937) Thorne, 1949

      Family Aphelenchidae (Fuch, 1937) Steiner, 1949

Family Aphelenchoididae (Skarbilovich, 1947)*

Family Anomyctidae J. B. Goodey, 1960

Suborder Tylenchina (Filip'ev, 1934)

Superfamily Tylenchoidea (Filip'ev, 1934) Chitwood & Chitwood, 1937

Family Tylenchidae Filip'ev, 1934

Subfamily Tylenchinae Filip'ev, 1934

Subfamily Atylenchinae Skarbilovich, 1959

Subfamily Anguininae Paramonov, 1962

Subfamily Psilenchinae subf. n.

Subfamily Tylodorinae subf. n.

Family Neotylenchidae Thorne, 1941

Subfamily Neotylenchinae Thorne, 1941

Subfamily Nothotylenchinae Thorne, 1941

Subfamily Paurodontinae Thorne, 1941

Subfamily Ecphyadophorinae Skarbilovich, 1959

Family Sychnotylenchidae fam. n.

Superfamily Hoplolaimoidea (Filip'ev, 1934) superf. n.

Tribe Hoplolaimini n. grad.

Family Hoplolaimidae (Filip'ev, 1934) Weiser, 1953

Subfamily Hoplolaiminae Filip'ev, 1934

Subfamily Tylenchorhynchinae Eliava, 1956

Subfamily Rotylenchoidinae Whitehead, 1958

Subfamily Belonolaiminae Whitehead, 1959

Subfamily Trophurinae Paramonov subf. n.

Family Pratylenchidae Siddiqi, 1963

Subfamily Pratylenchinae Thorne, 1949

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*: The structure of this superfamily is not inspected here, remaining on an optional basis in accordance with material published earlier (Paramonov, 1964).

Subfamily Nacobbinae Chitwood & Chitwood, 1950

Family Heteroderidae (Filip'ev, 1934) Skarbilovich, 1949

Subfamily Heteroderinae Filip'ev, 1934

Subfamily Meloidogyninae Skarbilovich, 1949

Tribe Criconematini n. grad.

Family Criconematidae (Taylor, 1936), Thorne, 1949

Subfamily Criconematinae Taylor, 1936

Family Paratylenchidae Raski, 1962

Family Tylenchulidae (Skarbilovich, 1947), Kir'yanova, 1953

Subfamily Tylenchulinae Skarbilovich, 1947

Family Sphaeronematidae (Raski & Sher, 1952) Geraert, 1966

In the following account, the suborder of aphelenchids is not examined inasmuch as only the analysis of the suborder of tylenchids belongs to this work's objectives.

Diagnosis of the suborder Tylenchina seu Tylenchata (Fil., 1934):

Tylenchida: Opening of dorsal ectofermentative gland lumen in the area of the procorpus; females primarily didelphic, secondarily, monodelphic; caudal alae without ribs, or, in the absence of caudal alae, bursal papillae are also lacking; the majority are associated with plants, phanerogamous or cryptogamous; the Neotylenchidae are associated in part with insects, the Sychnotylenchidae entirely with insects. The position of the Allantonematidae Chitw. Chitw. in the system is unclear to me; possibly this is a distinct superfamily. Irrespective of what has been said, I propose to distinguish two superfamilies in the composition of Tylenchina: Tylenchoidea (Filip'ev, 1934) Chitw. & Chitw., 1937 and Hoplolaimoidea superfam. n.

In this work, an attempt is made at characterization of this new superfamily, and its diagnosis and the differential ecologo-morphological features separating the hoplolaimoid group from the superfamily Tylenchoidea (Filip'ev, 1934) Chitw. & Chitw. are offered. A complete analysis of the new superfamily is offered in another work being prepared for publication. Beforehand, it is necessary here to point to the characters and terminology which are used in the present article as the basis of analysis of the new superfamily.

1. Small stylets (8-4 µm), large (15-50 µm) and hypertrophic (up to 100 µm) are distinguished. Stylets of the last type usually reach the anterior edge of the metacorpal bulb and, as a rule, evoke a
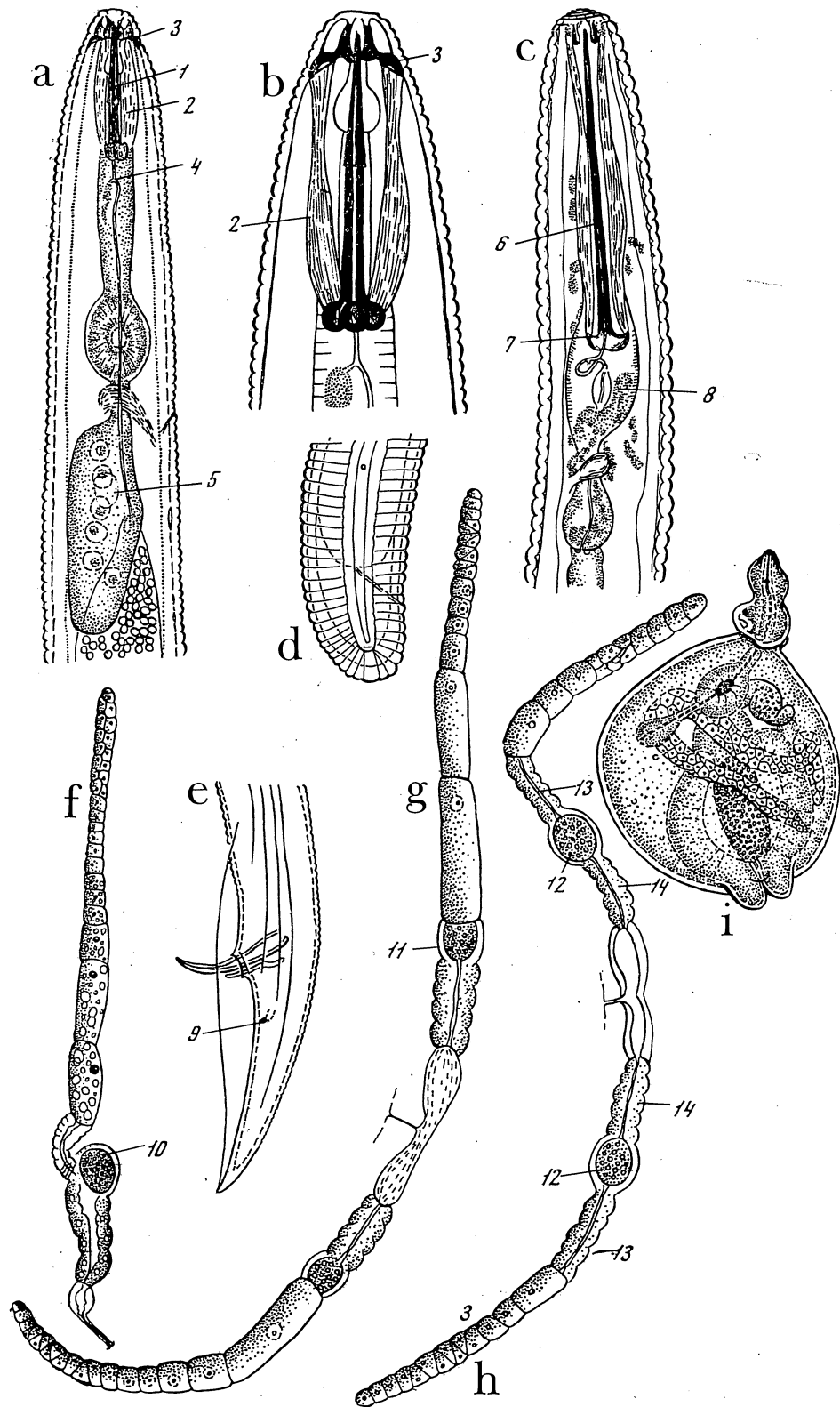
Figure 1. Integration of traits characteristic for the superfamily
Hoplolaimoidea (Filip'ev, 1934) superfam. n.

A - Hoplolaimoid esophagus of Hoplolaimus seinhorsti: 1 -- large stylet;
2 -- protractors, parallel to axis of stylet; 3 -- developed supporting
skeleton of cephalic capsule; 4 -- pore of the dorsal gland hetero-
typically displaced in back of the basal part of the stylet; 5 -- glands
of the cardial bulb, pressing against the beginning of the intestine;
B - Head end of Rotylenchus sp. of hoplolaimoid type; C - Head end of
Criconemoides annulatus: 6 -- hypertrophic stylet with knobs bearing
outermost protuberances (7); 8 -- typical criconemoid esophagus:
metacorpal bulb greater than cardial bulb which carries intraesophageal
glands; D - Female tail of Tylenchorhynchus sp. of typical hoplolaimoid
form; E - Male tail of Tylenchorhynchus sp. carrying "phasmidial rib" (9);
F-H - Hoplolaimoid ovaries: F -- criconemoid type; G, H -- hoplolaimoid
types: 10-12 -- spherical spermatheca, lying between the proximal (13)
and the distal (14) sections of the preuterine gland; I - Sedentary
females.

Figure 2. Integration of traits characteristic for the superfamily
Tylenchoidea (Filip'ev, 1934) Chitwood & Chitwood, 1937
(see p. 56).

A - Aglenchus costatus (de Man) -- general example of integration of
characteristics: typical tylenchoid esophagus with intraesophageal
glands, oligopropagatory ovary, tubular spermatheca, irregular preuterine
gland and thin tail tip; B - Head end of the same species: annulated
cephalic capsule (hoplolaimoid trait), but slanting protractors of the
stylet, widespread in this superfamily; C - Tail end of Ditylenchus mirus
Andrassy: tail not typical for tylenchoid forms, preuterine gland of
hoplolaimoid type, but typical tubular spermatheca known only in the
tylenchoid forms; D - Front end of Nothotylenchus acris Thorne: the
tylenchoid type of esophagus acquires the characteristics of neotylenchoid
because a bulbar cavity is lacking in the metacorpal bulb; E - Adanal
bursa in Paurodontus gracilis (Neotylenchidae); F - Tail end of Hexatylus
viviparus Goodey: strongly developed irregular preuterine gland;
G - Section of the body of female Ditylenchus dipsaci Kuhn: typical
regular preuterine gland of the quadricolumella type and tubular
spermatheca characteristic only for tylenchoid groups; H - Tail of the
male of the same species with peloderan bursa; I - Tail end of Boleodorus
thylactus Thorne. [Fig. J not described in original. - Editor].

1 -- oligopropagatory ovary; 2 -- irregular preuterine gland; 3 -- quad-
ricolumella or regular preuterine gland; 4 -- preuterine gland of
hoplolaimoid type; 5 -- spherical spermatheca; 6 -- tubular spermatheca.
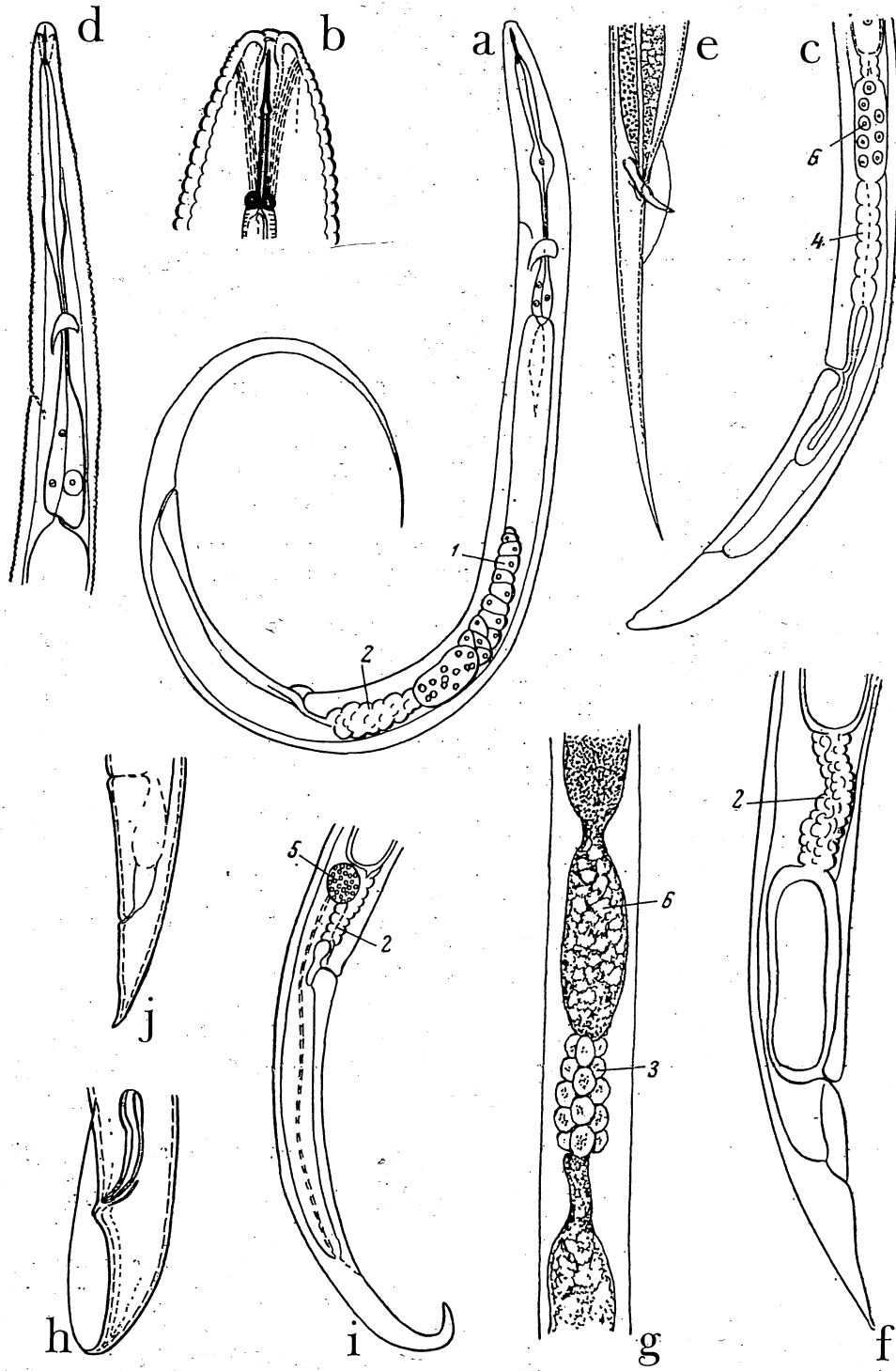
correlated thickening of the procorpus, which in some groups (Criconematidae) merges with the metacorpal bulb. The stylet knobs differ in the following types: small and large spherical knobs; radial knobs drawn out along three radii; turned down knobs, bent back toward the rear end of the body; knobs with protuberances, forwardly directed outgrowths which originated as a result of ergontic correlations between the knob of the stylet as a support and the proximal end of the protrators.

2. Types of esophagus. Hoplolaimoid esophagus: (a) metacorpal bulb usually convex-oval or spherical, with sclerotized internal cavity, (b) cardial (posterior) bulb with glands overlaping the beginning of the intestine in different variants (generic) in the length of its reach and shape. Tylenchoid esophagus: (a) metacorpal bulb varying around a narrow-oval shape, either gripped by processes of cessation of functions, narrowed or made rudimentary, or in a state of reduction but without loss of the internal cavity. Neotylenchoid esophagus: (a) metacorpal bulb regressed with loss of the internal cavity; cardial bulb glands are either in the tissue of the esophagus or overlap the beginning of the intestine, as in the hoplolaimoid esophagus (figures 1 and 2).

3. Types of ovaries. Hoplolaimoid ovary: (a) female sexual system either di- or monodelphic; (b) oligopropagatory (with one row of oogonia), mezopropagatory (two rows of oogonia) or polypropagatory (several rows of oogonia); (c) spermatheca always spherical, sometimes secondarily oval (Pratylenchinae) and either lies proximal from the preuterine gland (quadricolumellae of the authors), or divides it into a proximal part, lying next to the ovary, and a distal part, adjoining the uterus; (d) the preuterine gland long and unique or separated by the spermatheca into two halves (see above). Tylenchoid ovary: (a) always monodelphic; (b) preuterine gland either as in the hoplolaimoid ovary (long), or irregular, consisting of irregular groups of cells, or regular, in the shape of a quadricolumella; spermatheca either spherical or tubular, sometimes not observable in the hoplolaimoid ovary. Neotylenchoid ovary: close either to the hoplolaimoid or to the tylenchoid.

4. Types of caudal alae: (a) the superpeloderan alae continue behind the end of the tail; (b) the peloderan alae reach the end of the tail; (c) the leptoderan do not reach the end of the tail; (d) the adanals only cover the anal area; (e) the caudal alae have a "phasmidial rib," a conditional name referring to a special type of caudal alae, when a short canal, oriented parallel to the plane of the caudal ala to the right and left, originates from the phasmid (figures 1 and 2).

5. Types of organization. Hoplolaimoid types: (a) basic hoplolaimoid type (Hoplolaimidae): cephalic capsule annulated; large stylet, more rarely hypertrophic; strongly sclerotized inner head skeleton of the cephalic capsule often present; hoplolaimoid esophagus; di- or monodelphic hoplolaimoid female sexual system; female tail blunt; caudal alae super-peloderan, peloderan, or leptoderan with a

"phasmidial rib;" esophagus shape sometimes with a tylenchoid structure of the esophageal glands; body shape cylindrical, often curved or spiral; (b) heteroderoid type (Heteroderidae): females bulbous, tail rudimentary, males without caudal alae; other characteristics are hoplolaimoid, but the female genital tracts are polypropagatory, with a large number of oogonia; (c) criconemoid type: cuticle often deeply annulated; stylet hypertrophic; metacorpal bulb merged with the procorpus and larger than the cardial bulb, glands always intraesophageal; single hoplolaimoid ovary; tail pointed or blunt (family Criconematidae); (d) tylenchulid type: female bulbous; metacorpal bulb larger than the cardial bulb; one ovary of the hoplolaimoid type; caudal alae present or not (Tylenchulidae) (figure 1).

Identification key of the superfamilies of the
suborder <u>Tylenchina</u> Geraert, 1966

1.   (2) Cephalic capsule annulated or smooth; females tail conical, and long in many forms or with a thin tip; supporting skeleton of the cephalic capsule weakly developed; metacorpal bulb oval or rudimentary and in this case without a bulbar cavity; stylet usually small, and occasionally hypertrophic; generally, a single ovary; spermatheca tubular or spheroid; preuterine gland regular or irregular; esophageal glands generally in the cardial bulb, and in some instances overlap the beginning of the intestine; ectoparasitic myconematodes and plant nematodes of non-specific and specific effect; endoparasites of stalks and their derivatives and sometimes of roots; parasites of the gametophyte; and parasites of the crypto- and phanerogams . . . . Superfamily Tylenchoidea (Filip'ev, 1934) Chitw. & Chitw., 1937.

2.   (1) Cephalic capsule usually annulated; female tail generally bluntly rouded or pointed and usually short; supporting skeleton of the cephalic capsule distinct or powerful; metacorpal bulb convex-oval or spherical; or it merges with the procorpus into a powerful complex; stylet powerful or hypertrophic; there are two or secondarily a single ovary; spermatheca spherical or spheroid, and sometimes not tubular; esophageal glands generally overlap the beginning of the intestine; they are less frequently enclosed in the cardial bulb; bursa more often peloderan or does not exist; ecto- and endoparasites of roots of phanerogamous; females of root endoparasites are more often swollen and sedentary; there are no mycetophages and no ectoparasitic myconematodes . . . . Superfamily Hoplolaimoidea superf. n.

The substantiation of the proposed new system of the suborder of tylenchids cannot be reduced to a descriptive-morphological analysis. An ecological-morphological analysis has greater significance, since it shows what were the evolutionary directions of the groups of tylenchids being examined here, and what were the causes in forming their morphological organization.

As a preliminary, I should like to underscore that the hoplolaimoid organization is characterized most clearly by an express integration of concrete "hoplolaimoid" features, exhibited in the preceding identification key for the definition of tylenchid superfamilies. The essence of the isolation of the hoplolaimoid groups (the superfamily), does not lie in the fact that its individual traits (esophageal glands enveloping the beginning of the intestine, spherical spermatheca and so forth), are not encountered in the tylenchoid forms - on the contrary, they are encountered in the latter; but the facts are, first, that they are encountered in the latter in other connections (for example, the long, tapered tail), and second, that tylenchoid traits are not observed in the hoplolaimoid forms. Only the cardial section of the esophagus in the hoplolaimoid forms can be "tylenchoid;" however, it is always connected with traits which do not belong to the tylenchoid forms; for example, the "phasmidial rib" or the hypertrophic stylet. I would say that in distinction from the high integration of hoplolaimoid traits in the hoplolaimoid forms, traits in the tylenchoid forms are exposed to disintegration by way of the origin of special organizational traits, connected with a different ecology. It is exactly this aspect of the differences between the two superfamilites that it is very necessary to elucidate further.

Diagnosis and ecological-morphological characteristics of the superfamily Hoplolaimoidea (Filip'ev, 1934), Paramonov, 1966; Tylenchina seu Tylenchata; as a rule cephalic capsule annulated; its skeleton often conspicuous or powerful; stylet more often large or hypertrophic; stylet knobs spherical, radial and drawn down, in various shapes with protuberances; protractors at a small angle or parallel to the stylet axis; cardial bulb usually overlaps the beginning of the intestine; if it does not envelop it, then either the bursa has a "phasmidial rib" or the metacorpal bulb merges with the procorpus and is often larger than the cardial bulb; female gonads primarily didelphic, secondarily monodelphic, and always of the hoplolaimoid type; female tail usually with blunted or conical tip; caudal alae superpeloderan, peloderan, or leptoderan, and sometimes they carry a "phasmidial rib," or if there are none, they are ecto- or endoparasites of the root system of Phanerogamae; none are mycetophagous; some are specialized endoparasites of the roots, they are dimorphic - males are slender; females are swollen and are capable of producing a matrix which functions as an ootheca, and they are partly transformed into cysts carrying eggs and larvae.

Type family: Hoplolaimidae (Filip'ev, 1934) Weiser, 1953. Ectoparasites of the root system of phanerogams prevails within the confines of this family usually with a large stylet or even a hypertrophic one; that is with features of obvious specialization (subfamilies Belonolaiminae, Dolichodorinae and Trophurinae).

Selection on the basis of a large stylet, made by ectoparasitism in roots and retained also in endoparasites of this superfamily, means selection through a loss of capacity for mycetophagia, and correspondingly, to a loss of dependence of phytoparasitism tied to hyphomycetes. In preceding

works (Paramonov 1958), I have developed a viewpoint according to which the tylenchidae became plant parasites as a result of penetrations into plant tissues following phytoparasitic hyphomycetes. This viewpoint is apparently correct with respect to tylenchoid forms (see below), but does not explain the origin of phytoparasitism in hoplolaimoid forms. It is only possible to suppose that the ancestors of these forms were ecto-parasitic myconematodes, the same as for the tylenchid group. The bases of this supposition are examined below. However, the evolution of the hoplolaimoid forms came by way of their liberation from mycetophagia, as this was mentioned above, through the enlargement of the stylet and the loss of that same capacity for mycetophagia. Probably, this is the reason why hoplolaimoid forms cannot be cultivated on fungi in agar. Therefore, the passage from ectoparasitism to endoparasitism was being realized within the limits of Hoplolaimoidea by a completely original route.

In the first stages of this evolution, the endoparasites are very primitive and retain that very organization which the ectoparasitic Hoplolaimidae possess, as for example, species of the genera Hoplolaimus Daday, Scutellonema Andrassy, Rotylenchus Filip'ev, Trichotylenchus Whitehead, and Tylenchorhynchus Cobb. However, within the limits of these species, the development of primitive endoparasitism is already beginning, which is manifest especially clearly in representatives of the genus Helicotylenchus Steiner, although all these forms preserve predominantly ectoparasitic characteristics. On the other hand, the general passage of large-stylet forms of the subfamily Pratylenchinae Thorne to primitive endoparasitism is already observed within the boundaries of the pratylenchids. Pratylenchids, together with the hoplolaimids, are included in the group of migrating root parasites (Pitcher in Southey, 1956). Migrating ecto- and endoparasites cause primitive necrosis in the root system; that last provokes an exodus of nematodes from the necrotized root tissue into the soil with a consequent invasion of new rootlets of plant-hosts. An interesting biological trait of these primitive root parasites already is revealed. Necrosis always becomes a factor which is unfavorable to given individuals of these parasites, but at the same time, it acquires important significance as the factor which provokes the exodus of nematodes from necrotized roots and the invasion of the roots; that is, it becomes a significant factor which promotes an increase in the extensiveness of the invasion. However, this route of development cannot result in perfection of endoparasitism and in increased specialization in a corresponding direction. It is remarkable that hoplolaimoid forms realized the development of endoparasitism in a special direction, connected with the complexity of biochemical relations with plant-hosts.

This special direction of development of endoparasitism is evident in a number of hoplolaimoid groups. First of all, it already originates within the confines of the family of pratylenchids, but only as a representative of the subfamily Nacobbinae. In the species of the genus Nacobbus Thorne & Allen, the females acquire a swollen body shape and become sedentary; that is, they lose the ability to move in space. The eggs and larvae are protected by a matrix secreted by the females which forms an ootheca, the females causing the development of galls on the roots. While reacting to it, the larvae (which, contrary to the female, possesss mobility), abandons the necrotized rootlets, escapes into the soil, and invades new rootlets.

If we compare this process with that which is observed in the ecto- and endoparasitic forms, particularly with the pratylenchids, we can state that the genus Nacobbus possesses a more specialized form of adaptation to endoparasitism. The sedentariness of females in itself increases the "risk of necrosis," since sedentary females cannot leave the necrotized zone of root tissue. However, biochemical relations with the plant-host already arise in the nacobbinids, which delays the time of the beginning of necrosis approximately to the moment when the larvae succeed in carrying out two moultings and by that fact become invaders and react to the beginning necrosis by exiting into the soil from which they penetrate new rootlets. Consequently, some complex adaptation to specialized endoparasitism is already worked out in the nacobbinids, but limited to the origin of biological relationships with the plant, which delays the time of the beginning of necrosis, and the development in this very connection of sedentariness; and equally, of the ability to secrete a matrix which secures the formation of a protected ootheca, together with a swollen shape of the body of females.

If these peculiarities of the biology of the nacobbinids were isolated instances, the question would not have such burning interest. But the fact of the matter is that this type of specialized endoparasitism is clearly demonstrated in different groups of hoplolaimoid endoparasitic forms.

This is very clearly expressed within the boundaries of the family Heteroderidae Skarbilovich. This family is not phyletically connected to the nacobbinids, and forms a special phylogenetic branch of the hoplolaiminids. Nevertheless, within the confines of this family arise convergently similar adaptations, in particular in the genus Meloidogyne Goeldi. When the larva of a root-knot nematode penetrates a rootlet, necrosis does not take place. This is achieved in the first place by the fact that bacterial flora, born by the invading larva into the tissue of root, perishes in it, and the gall, which is formed under the influence of biochemical activity of the developing larva, remains sterile, as Pokrovska's investigations have shown (1961). The gall remains free of necrosis even later, as a result of the peculiar biochemical interrelationships between the developing root-knot nematode (female) and the plant-host. I believe Myuge (1965), has correctly explained the essence of these relationships. In his investigations he came to a conclusion concerning the origin and significance of giant cells which are formed during Meloidogyne or Heterodera infection. The giant cells were considered by the author as trophic intermediaries between the nematode and the plant. According to Myuge's data, the formation of the giant cells (symplasts) is the result of interaction of the nematode enzymes with the glutathione of the plant cell. This gives rise to the well-known rhythm of interaction, expressed by the fact that the plant produces inhibitors of the enzyme of the nematode. The enzyme causes hydrolysis of the tissue, as a result of which the nematode creates a source of nutrition, while devouring the products of hydrolysis. Following this, a pause occurs in the ectoparasitic activity of the nematode. This pause opens up for the plant the possibility of an accumulation of inhibitors and a strengthening of the synthetic processes. It is just in this

connection that the giant cells, while remaining a source of nutrition for the nematode, are characterized by restoration processes and consequently, it is as if they were insured against the rise of premature necrosis.

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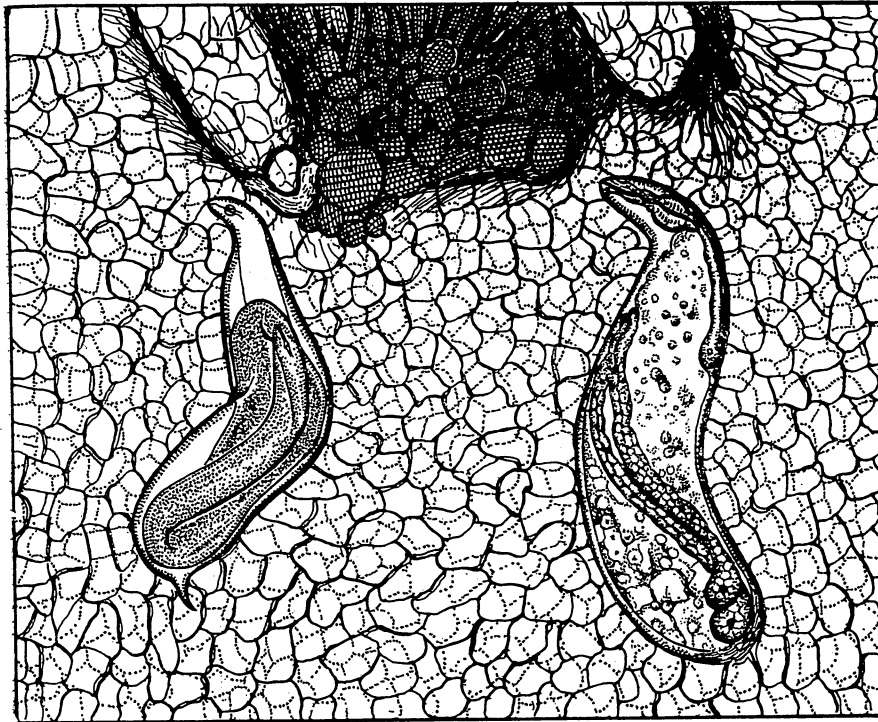
Figure 3.   Cross section of gall tissue of the klin cucumber.   Males inside their cuticles and young females of Meloidogyne incognita (Kofoid & White, 1919) Chitwood, 1949, with their head end turned towards the giant cells.   Gall tissue with no sign of necrosis.   Orig.

These relationships work on the extent of ontogenesis of the nematode (Fig. 3).   But one more protective adaptation is worked out in females of root-knot nematodes.   Maggenti and Allen (1960), showed that there are regular correlations between the secretion of the matrix, at the expense of which the ootheca is formed, and the production of eggs.   A fibrous matrix is secreted from the anal glands of the female of the gall nematode, rhythmically and in portions.   Whenever the perineal area of the body of the female is completely opened by the matrix, the production of the eggs which are thus absorbed in the matrix, begins.   It is perfectly clear that in this instance we have a matter of an adaptive process, mastered by choice (Paramonov, 1962).   These relations confirm the idea that the ootheca (matrix) has protective functions.   Precisely in this connection, the rhythm of the process is such that first the matrix is secreted, and only after this does the laying of eggs begin.   This confirms the opinion of Helsing concerning the protective significance of the ootheca.

Larvae which have left the egg membrane remain at first in the matrix of the ootheca. If the gall is not huge, they later on are freed from the matrix, and if the perineal area of the female sticks out (into the soil), then the larvae exit right there and then, when possible, into new rootlets. However, if the ootheca is deep inside the gall, the larvae can remain in its tissue (see, for example Paramonov, 1954, figure 9, page 1010), while undergoing ontogenesis there and turning into females. So, a complex of females can arise in the tissue of one gall, which correspondingly expands and acquires the significance and organization of a confluent gall. Such confluent galls are also free for some time from necrosis. However, in these confluent galls, biochemical interdependencies between plant tissue and the complex of root-know nematodes (females) cannot be so very rythmical as in a small gall with one female, since ontogenesis of separate individuals are not synchronized, while now forming a series of generations, or more precisely, a population of females and larvae. For some time these primary galls are free of necrosis, but ultimately as the result of the disturbance of a concrete chemical balance which was founded on biochemical interrelations between the root-knot nematodes (females) and the plant (Myuge, 1965) destructive changes originate in the galls and later on necrotic processes originate under the influence of saprobionts, and also under the direct influence of the disturbances mentioned above of the correlations between the nematodes and the plant.

The beginning of necrosis becomes an information which provokes the exodus of the larvae from the gall into the soil with a subsequent invasion of new rootlets and new plants. Usually at these moments an increase in extensiveness of the invasion is observed both in the soil and in greenhouses. From the general biological viewpoint, we can express these relationships with the assertion that necrosis becomes a factor in the expulsion of larvae from the gall (confluent gall), and consequently, a factor in the spread of the invasion. Therefore, in the presence of the described relationships, necrosis is transformed from a factor injurious for the nematode, into a factor useful for it.

On the whole, a legitimate idea comes into existence: that at first (i.e., at the beginning of ontogenesis and in the process of formation of young sedentary females under the influence of biochemical interrelations of nematode and plant), necrosis is delayed until the last stages of development of the gall, when the females manage to produce descendents,* consisting of mobile larvae of the second age. But, the mobility of the larvae removes the "risk of necrosis", since larvae can leave the necrotic zones and penetrate into new rootlets. In these relationships we have the possiblity of seeing a special form of adaptation of a species to the increase of the coefficient of reproduction. We underscore here that while becoming phyletically different branches of the development of the hoplolaimoid forms, the nacobbinids and root-knot nematodes possess similar adaptations to endoparasitism.

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*: The delaying of the onset of approaching necrosis is in fact correlated with significant periods of the ontogenetic cycle.

The hoplolaimidae were the source of development of another group, the subfamily Heteroderinae Skarbilovich. As is well known, females of the heteroderinids also are swollen and sedentary and capable of forming oothecae, as were the preceding groups. With the heteroderinids, however, another type of defensive adaptation arises. Aging females turn into cysts, containing eggs and larvae. In these new connections necrosis loses its significance. The exodus of larvae from the cysts is not determined by its influence, but by their reactions to diffusates of the roots and to other factors.

Nevertheless, regularities of the ontogenetic adaptations of the groups named above are convergently similar in many of them, and besides are under the influence of adequate factors as a result of adaptations to endoparasitism in plant roots; that is, under conditions of biocoenetic relationships with the rhizosphere. We can state that the known collection of characteristics recalled above are typical for the endo- parasites studied. Before we sum up their characteristics, we shall examine one more specific hoplolaimoid branch. This branch reveals its history with the families Paratylenchidae (Raski) and Criconematidae (Taylor), represented by specialized ectoparasites with a hypertrophic stylet and a female sexual system of a modified hoplolaimoid type (Fig. 1). Criconematidae underwent considerable radiation (see De Grisse & Loof, 1965). In quality of specialized ectoparasites, the paratylenchids apparently turn out to be the source of develoment of the family Tylenchulidae (Skarbilovich), retaining traits of similarity with the first in the organization of the esophagus, the female sexual tract and the tail of males. The passage of tylenchulids to root endo- parasitism, independently of the nacobbinids and heteroderids, evoked in the tylenchulids adaptations similar to the adaptations of the groups mentioned. The body of tylenchulid females is swollen; they are also always sedentary and capable of producing a matrix. It is remarkable that the matrix is formed, not at the expense of the glands as with the meloidogynids, but from the secretions of the excretory system (Maggenti, 1962). This fact underscores that the formation of the matrix is a biological necessity for producing endoparasites within hoplolaimoid forms. It becomes a necessary link in the integration of the hoplolaimoid organism, connected with the soil and with its biocoenetic system. The development of the matrix determines the nature of the root parasite of sedentary organization. But the matrix, while fulfilling the functions of a protective ootheca (also including protection against necrosis), is correlated with all the other characteristics, with their sedentariness, with the swollen body of females, and with the shift of the time development of necrosis to a period when ontogenetic formation is finished and when an immobile (sedentary) female produces mobile descendents in the form of larvae which are able to leave the zone of necrosis, go out into the soil and invade new rootlets. The biochemical features of this system of adaptation are also subject to their integrated whole, which constitutes the basis of characteristically endoparasitic hoplolaimoid root forms. Root endoparasitism in its soil-biocoenetic connections has created through selection this type of organization and has determined the formation of the superfamily being examined. It is just for this reason that we find within the confines of all the families of Hoplolaimoidea

parallel types of organization, convergently similar. Thus, among ecto-parasitic forms we see similarities in several crucial characteristics of the group (Belonolaiminae, Dolichodorinae, and Trophurinae), in particular in the organization of the stylet and metacorpal bulb, although the hoplolaimid subfamilies mentioned above are phyletically inadequate for the criconematids. We can merely underscore that in the forms of the subfamilies mentioned and in the criconematids, a convergent-similar type of development of specialized adaptations in ectoparasitism is observed at the expense of the root system. This answers our basic thesis concerning the historical unity of all ectoparasitic groups of the hoplolaimoid integration. This conclusion is indeed correct also for endoparasitic groups of the hoplolaimoid plan of organization. We see in particular that within the limits of a series of groups, but particularly Nacobbinae, Heteroderidae and Tylenchulidae, i.e., with three groups of different origin and possessing the significance of different branches of a radiating hoplolaimoid complex, there arise adaptations of the same kind toward specialized root endoparasitism, adaptations which are expressed in the following mutually coordinated characteristics: (a) sedentariness of swollen females, (b) development of specific biochemical relations with plant-host which guarantee the shift of the beginning of necrosis to a period of development of the mobile larvae descendents; and (c) capability to produce a matrix which functions in the capacity of a protective ootheca. At that, the matrix can have a different origin, but always it has an adequate significance which underscores its adaptative significance and its corresponding function.

Thus, we have correctly stated that all the families and subfamilies of the hoplolaimoid group are characterized by similar forms of the adaptive evolutionary process, having pursued its course under the influence of selection on the morpho-physiological integration of vital forms, adapted to nourishment as parasites of the root system of phanerogams. This line of development of a specific root ecto- and endoparasitism is character-ized by a trophism independent of hyphomycetes. Hoplolaimoid forms can further the introduction of fungi into root tissue as a result of perforation of the cell membranes of plant (root) tissues by the stylet, while lowering as well the resistance of plants against mycoses (see Turlygina, 1966), as a result of biochemical activity of the nematodes. Of course, not just the hoplolaimoid groups are responsible for such a process, but here I am discussing only their role. Most important of all is the absence of mycetophagia in the large stylet forms, and in the forms with a hypertrophic stylet as well. Apparently, in this connection, neither the cultivation of Hoplolaimoidea on a fungal medium nor, correspondingly, an elaborated method of cultivation of these nematodes on plant tissue cultures, has been realized (Tyler, 1952; Feder, 1958; Peacock, 1959; Tiner, 1960; and others).

The superfamily Hoplolaimoidea must be examined as an integrated and naturally developed ecological-morphological system, which underwent deep internal adaptive radiation and organic activity within the confines of the root system of the phanerogams by biocoenotic relations with the rhizosphere. These conditions have brought the superfamily Hoplolaimoidea to a biological process and to a very wide distribution, but also to

parasitize the roots of a large number of species of phanerogams. The hoplolaimoid groups of plant nematodes became the dominant representatives of the tylenchs in the root system of phanerogams.

Representative of another superfamily of tylenchs, Tylenchoidea, have incomparably less significance in root parasitism than Hoplolaimoidea.

Diagnosis and ecological-morphological characteristics of the superfamily Tylenchoidea (Filip'ev, 1934), Chitw. & Chitw.:

Diagnosis of the superfamily Tylenchoidea (Filip'ev, 1984), Chitw. & Chitw.: Tylenchida -- cephalic capsule annulated to smooth; its skeleton usually weakly developed; stylet small, but occasionally large or hyper- trophic; protractors often slanting; metacorpal bulb oval or constricted-oval, and either with a cavity or rudimentary and without a cavity; cardial bulb either tylenchoid or with glands overlapping the beginning of the intestine; ovary single with a tubular or spheroid spermatheca; female tail tip generally pointed, very rarely blunted; male with leptoderan or anal alae, rarely peloderan; there is no "phasmidial rib"; female of endoparasites sometimes are not swollen; ecto- and endo- parasites of both crypto- and phanerogams; there are many mycetophagous.

Type family: Tylenchidae Filip'ev 1934.

The tylenchid family forms a natural but complex group of genera and subfamilies. It is necessary to consider the preservation of connections with the cryptogams, and in that group with the hyphomycetes, as the basic ecological feature of this family. Another characteristic ecological trait is parasitism of stalks and their derivatives and of leaves of gametophytes. The connection with gametophytes is a characteristically important element of the tylenchids and even of the entire superfamily Tylenchoidea as a whole. It is important in the determination of the ecological nature of the superfamily under examination and of its ecological characteristics, and in the performance, characteristically, of the tylenchid family. It is striking that in the composition of the genera with typical plant endoparasite nematodes of specific pathogenic effect, species are also known which belong ecologically to a group of forms which are closely connected with hyphomycetes. Thus, within the confines of the genus Ditylenchus (Kuhn), together with typical plant nematodes of specific pathogenic effect such as D. angustus (Butler), D. dipsaci (Kuhn) and D. destructor Thorne, there are known species, ecologically connected with hyphomycetes. Such for example, are D. intermedius (de Man) and D. myceliophagus J. B. Goodey. The first of these species is apparently a mycetophagous, and it was falsely identified by accident with the second of these species, since both feed on the mycelium of fungi (Goodey in Southey, 1965). It is necessary to add to this that plant nematodes of specific pathogenic effect from that very same genus preserve connections with hyphomycetes as was shown for D. dipsaci (Kuhn) and D. destructor Thorne (Turlygina ,& Kosareva, 1962-1963; Baker, Brown & James, 1954; and Turlygina, 1967 -- a general review of the correlations among nematodes, fungi and bacteria). The review of plant hosts of plant nematodes offered by Goodey, Franklin and Hooper (1965), shows that representatives of tylenchid families constitute

a basic mass of forms connected with the cryptogams (Cryptogamae), and in particular with horsetails, mosses and fungi. These groups of hosts remain dominant with respect to forms of the genus Ditylenchus (Kuhn). The proportion of tylenchids parasites of phanerogams (Phanerogamae) is many times less, the vast majority of plant nematodes of specifically pathogenic effect parasitise stalks and their derivatives, but there are comparatively less specialized parasites of roots than among the hoplolaimids. Among root parasites of the tylenchid family one should name here Subanguina radicicola (Greeff) n. comb., which forms galls on the roots of different grasses, including cereals.

The galls are, however, of a different type from those in gall-forming hoplolaimoid forms, and S. radicicola, while residing in roots and soil, maintains mobility and the usual nematode body shape. Consequently, the specifics of its adaptation are of a different type from that of the Hoplolaimoidea. On the whole, the vast majority of phanerogams serve as hosts of the hoplolaimoid forms; this is true in particular for the root systems of these plants.

Another distinctive peculiarity of tylenchids lies in the fact that within their limits endoparasitism in stalks and in the gametophyte of phanerogams acquires great significance, and equally in the leaves of these plants. This feature of theirs distinguishes them well characteristically from hoplolaimoid forms. While studying lists of phanerogams and the distribution of tylenchids according to plant-hosts (Goodey, Franklin, and Hooper, 1965), one must state that the role of tylenchids in comparison with the hoplolaimoid forms is limited with respect to the number of species of phanerogam hosts and to the number of species of tylenchids. Tylenchids are encountered relatively often in plants of the following genera: Agropyron, Agrostis, Allium, Avena, Beta, Calamagrostis, Carduus, Carex, Chionodoxa, Colchicum, Crepis, Elinus, Festuca, Gladiolus, Helianthus, Hiercium, Holcus, Hyacinthus, Medigaco, Narcissus, Phacelia, Phlox, Plantago, Poa, Primula, Ranunculus, Trifolium, Triticum, Tulipa, Veronica and Vicia, and in significantly lesser degrees in other forms. Indeed, the whole basic mass of the phanerogams are objects of agression from hoplolaimoid species. Concerning the number of tylenchid species feeding at the expense of phanerogam, it is a fact that in the list from the authors mentioned, only the following tylenchid species have comparatively great significance: Ditylenchus dipsaci (Kuhn), D. destructor Thorne, and the anguinids. These last are found only in phanerogams whereas D. destructor prevails in cryptogams, particularly in fungi. In mosses the tylenchid also dominate, indeterminate ditylenchids nearly in majority, and among them Ditylenchus askenasyi (Butschli). Such are the general ecological characteristics of the tylenchids. It is quite clear that they are sharply differentiated from the ecological characteristics of hoplolaimoid forms. The latter remain soil forms and parasites of roots, and take possession very completely of the majority of genera and species of phanerogams. The tylenchids play an immensely more modest role in the parasitism of Phanerogamae organs, with reference to the number both of hosts and of species of plant nematodes. Furthermore, they cause completely different diseases, and never acquire those forms of adaptations which were characterized above in relation to the sedentary hoplolaimoid forms.

We return now to the morphological characteristics of the tylenchids. They can be characterized by the following factor: in the tylenchids, different elements of morphological characteristics of hoplolaimoid forms are observed, but in the latter there are characteristically no elements of the tylenchids, or they are encountered as exceptions. These correlations compel one to recognize that the tylenchids are evolved from ancestors common to the hoplolaimoids.

This theoretical position, as it appears to me, explains the fact that in the morphological organization of tylenchids, there are elements different from the morphological organization of the hoplolaimoid type.

These elements are very clearly displayed, in particular, in the organization of representatives of the polytypic genus Tylenchus Bastian. Thus, in the shape of this genus we see an irregular preuterine gland (Figure 2), a spherical spermatheca, and annules on the cephalic capsule. These characteristics do not correspond to a hoplolaimoid morphological system. The plan of organization of the genus Tylenchus remains not hoplolaimoid, but tylenchoid as shown by the typical tylenchoid esophagus and by the organization of the protractors, quite often oriented at a noticeable angle to the long axis of the stylet, although this last bears the stamp of adaptation to the sucking of the rootlets. The metacorpal bulb is usually tapered-oval and within this genus is very often in the beginning or middle phases of regression, although preserving the internal bulbar cavity. Moreover, the genus has a long tail with a sharply thinned tip, and quite often an adanal bursa. The female genital system is always monodelphic. Thus, hoplolaimoid characteristics (spherical spermatheca, and possibly the irregular preuterine gland which is observed in some hoplolaimoid forms), will remain only isolated elements of the tylenchoid type, being retained in some of the species and genera of the tylenchids. The genus Tylenchus is especially interesting, in this respect, and it is possible that it preserved the ancestral characteristics of the phyletic past, in which the hoplolaimoid and tylenchoid forms were close to common ancestors and were not yet differentiated into two groups (two superfamilies). These assumptions find some justification also in the ecology of the tylenchids which, apparently, must be rated as ectoparasites of the root system of phanerogams, capable of perforating and sucking the nourishing rootlets of suitable plants as this was shown by Khera and Zuckermann (1963). Thus, root ecotparasitism of the tylenchids can be considered experimentally proven, although it is not comparable in its pathogenic effect to that produced by representatives of ectoparasitic hoplolaiminids. In any case, characteristics of adaptation to root ectoparasitism are observed in the organization of the stylet of the tylenchids, and probably, in this lies the reason for the similarity of elements of the organization of the cephalic capsule and stylet of the tylenchids to the hoplolaimoid forms. Nevertheless, I shall underscore again, the remaining characteristics of the tylenchids do not leave any question as to their undoubted belonging to the tylenchidae.

Characteristics of organization of root ectoparasites do not have a wide distribution among the tylenchids. As a matter of fact, only Subanguina radicicola (Greeff) can have significance as a pathogenic root parasite of plants. The majority of plant nematodes of pathogenic effect from the

superfamily Tylenchoidea are endoparasites of stalks, of their derivatives (bulbs, tubers), and of the gametophyte of phanerogams. Along with these, as shown above, the tylenchoid forms are closely connected trophically with the hyphomycetes. It is this very factor which is connected with selection of the small stylet. A large sucking power is maintained in small stylets with a thin internal lumen. Hence, comes the reduction of power of the metacorpal bulb, its typical tapered-oval shape, and its distinctive processes of significant immobilization of the radial bulbar myofibrils and of progressive regression of the bulb which we observe in several forms of the tylenchids, although these correlations are not always expressed.

The esophagus in tylenchids is always of the tylenchoid type. I firmly deny that the genera Tetylenchus Filip'ev and Telotylenchus Siddiqi belong to the tylenchids. They have typical hoplolaimoid organization. Among forms with an esophagus enveloping the intestine, the genus Pseudhalenchus Tarjan is noticeable because of these hoplolaimoid characteristics. However, even this genus is nearer to the boundary between tylenchids and neotylenchids than between the latter and the hoplolaimids.

The female genital system of the tylenchids, almost without exception, is monodelphic*. All the didelphic forms which have been included here among them, undoubtedly carry hoplolaimoid characteristics. This also concerns the genera Trophurus Loof and Macrotrophurus Loof. These are, of course, not tylenchids. Characteristically, specific traits appear in the female genital system of the tylenchids. First, in some of the forms several elements of the hoplolaimoid organization are preserved. As such there is the spherical spermatheca being observed in separate species. It is, however, a solitary trait, connected not with other hoplolaimoid characteristics, but with tylenchid traits, in particular with a small stylet, a weak metacorpal bulb (as in several tylenchids), an anal bursa, and a long tail with thinned tip. Second, some traits in the female genital system of the tylenchids are unusual for hoplolaimoid organization -- constant monodelphia everywhere and in all forms, a spread of a primitive tubular spermatheca, and the appearance of a typical quadricolumella, so clearly expressed in the ditylenchids.

Endoparasitic tylenchid forms of the subfamily Anguinae preserve typical traits of the family Tylenchidae. Theoretically, species of the genus Subanguina g. n., produce great interest, in particular S. radicicola (Greeff) n. comb., widespread in Holland, England, Scotland, Norway, Denmark, Finland, Poland, Canada and the U.S.A., but equally well-known in the U.S.S.R. Larvae of the first stage of this subanguinid invade the rootlets of grasses and in the course of approximately three weeks undergo all four moults, reaching sexual maturity after 10-12 days when the females begin to lay eggs. Neither the adult forms nor the larvae of other stages (except the first) are capable of invading roots. The cytological structure of the galls have nothing in common with the galls of heteroderids, although the cells of the galls are abnormally enlarged. In the course of a year (of vegetation) usually only one generation develops. Saprobic nematodes penetrate into the galls, and possibly, the

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*: Didelphic in several species of the genus Psilenchus de Man.

development of subsequent necroses becomes one of the stimuli to the exit of larvae of the first stage from the galls and to the subsequent invasion of new rootlets.

However, the gall does not become the means for development of subsequent generations, as this takes place with Meloidogyne spp. Cavities are formed in the galls of S. radicicola, in which nematodes are also found, and here feeding of the nematodes is also carried out. Here there is no formation, typical for the meloidogynids, of confluent galls containing a population of a number of generations. In the galls of subanguinids there is also no typical giant cells, which in the meloidogynids fulfill the role of trophic intermediaries between the nematodes and the plant.

Thus, except for the fact that S. radicicola (Greeff) develops in rootlets and in soil conditions, its ontogenesis is not similar to the ontogenesis of the heteroderids. This completely different type of development is in fact close to the type of development of the anguinids. At that, life in the gall and in soil conditions does not evoke, in the case being examined, developments of sedentariness as this takes place in meloido-gynids, and this nematode does not form a matrix, although it is found in conditions similar to those which characterize the ecological and biocoen-otic medium typical for the hoplolaimoid forms. This underscores that the hoplolaimoid and tylenchoid groups form two qualitatively different lines of development. As is known, endoparasitic representatives of the tylenchoid group of families use plant organs that are buried in the soil, including gametophytes. And with this, independent of the level of specialization, they never acquire characteristics of the sendentary forms. There is preserved, however, even in the boundaries of tylenchoid organization, a characteristic which is common to all plant nematodes which are connected in particular with the soil -- necrosis. This last maintains the significance of the "moving factor" of invasion, and of the increase in its extensiveness, inasmuch as while reacting to necrosis of the plant tissues, tylenchoid plant nematodes of specific pathogenic effect either move out into the soil or move into the healthy parts of an occupied plant organ.

From what has been said above, it is clear that endoparasitism of the tylenchoid forms does not reach those directions of specialization which are typical for the hoplolaimoid forms. We consider it possible to emphasize that for the tylenchoid forms the directions of evolutionary development which to do not exceed the limits of allomorphoses are typical, while at the same time within the limits of the hoplolaimoid groups, represented by forms of the sedentary type, evolutionary development proceeds within the bounds of a typically enough expressed telemorphic development (Schmalhausen, 1939), connected with a narrow specialization of females who are losing the ability for movement in suioa . These considerations underscore that the hoplolaimoid and tylenchoid groups form completely different phyletic branches. The ontogenesis of the corresponding forms move qualitatively differently within the confines of these two groups of families. We have all the grounds to affirm that sedentary females of the hoplolaimoid groups are the product of qualitatively separate directions of mutation and selection, different from the directions of those very processes within

the confines of the tylenchoid group of families. This also means that indeed the responsible regulatory mechanisms of formation within the limits of the two superfamilies being examined are qualitatively different. These considerations allow me to affirm that the separation of the superfamily Hoplolaimoidea, specific in the respects described, is determined by objective facts and cannot be considered as arbitrary.

In addition to what has been said, I would like to cite several other arguments in support of the view being developed here on the taxonomy of the suborder of the tylenchates (Tylenchinids). The connection of the tylenchids with the hyphomycetes has already been noted above. The distribution among representatives of the tylenchid family of mycetophagia must be considered the most responsible aspect of this connection. I consider mycetophagia as an ancient ecological trait characteristic of the aphelenchoid forms, and continuing to exist also in the tylenchids. This feature has very great significance in the consolidation of the characteristics of the tylenchids, as a specific trait of this family. The fact that mycetophagia is preserved is important, and this was shown above, even in plant nematodes of specific pathogenic effect. It is necessary to deepen the analysis of this question.

We turn in this connection to the family Neotylenchidae (Thorne, 1941). It is necessary first of all to emphasize that this family has a completely different character. If the tylenchids contain a series of endoparasitic plant nematodes of specific pathogenic effect, then the neotylenchids are plant nematodes of predominantly nonspecific pathogenic effect. Several authors have affirmed that different neotylenchids species are pathogens of serious significance. Separate observations and experiments show that some neotylenchids cause symptoms of pathogenic processes in plants. Thus, Nishizawa and Iyatomi (1955), have shown that Nothotylenchus acris Thorne causes disease of the strawberry, similar in characteristics to the disease of this same plant, provoked by the strawberry aphelenchid.

However, the importance of the neotylenchids as pathogens hardly constitutes a great problem. Thus, in the Technical Bulletins of the Ministry of Agriculture, Fisheries and Food of Great Britain, there is not a single word about the economic significance of the neotylenchids, not counting the vague observation that "some of them (A. P.) are defined as parasites." At that, a reference is made to Nothanguina which forms galls on the stalks and flowers of plant. There is not a word about other neotylenchids, although in the newest bulletin (Southey, 1956), there is much data concerning other plant nematodes. Apparently, the neotylenchids do not cause particular concern. This is true for the overwhelming majority of the huge mass of plant nematode publications.

Nevertheless, in general theoretical and in practical plans, the neotylenchids represent a great interest, since they are closely connected with the hyphomycetes and bacteria, and evidently they also represent a practical interest in these very connections as this is known with respect to the aphelenchids of the strawberry.

The vividly expressed duality of morphological organization must be considered the most striking peculiarity of the family. This concerns a series of characteristics. Thus, the cardial bulb in Neotylenchus Thorne, Nothotylenchus Thorne, Boleodorus Thorne, Thada Thorne, Anguillonema Fuchs, Nothanguina Whitehead, Paurodontus Thorne and Stictylus Thorne is characterized by the intraesophageal location of the ectofermentative glands and by their separation from the beginning of the intestine; that is, it is constructed approximately as in the typical ditylenchids. However, this characteristic is not universal for all the family, since in Hexatylus T. Goodey, Deladenus Thorne, Halenchus Cobb, and Ecphyadophora de Man, the glands of the cardial section of the esophagus are exoesophageal and envelop the beginning of the intestine; that is, they are located just as in the typical hoplolaimoid forms. Moreover, even "hoplolaimoid" variants of this location of the esopageal glands are observed. Further, the same "aggregation" or duality of organization is observed in the structure of the organs of the female reproductive system. So, the spermatheca in several genera is tubular, as for example, in Halenchus Cobb; in others it is spherical, as in Boleodorus Thorne. That same "aggregation" is manifested also in the organization of the preuterine gland. It can be irregular, consisting of groups of cells of indeterminate arrangement as in Hexatylus viviparus T. Goodey, or "hoplolaimoid" as in Boleodorus tylactus Thorne and B. pakistanensis Siddiqi. Further, this same manifestation of "aggregation" of characteristics of the neotylenchids is noted also with respect to the organization of the caudal alae of males, beginning from peloderan in Neotylenchus Steiner and continuing so regularly in the species of Deladenus Thorne to the sharply expressed adanal alae in Halenchus Cobb, Paurodontus Thorne and Boleodorus Thorne, and their complete regression in Gymnotylenchus Siddiqi. The regression of the myofibrils of the metacorpal bulb always serve as the sole absolute taxonomic criterion (Paramonov, 1937) for Neotylenchidae, and in this connection, there are regression and reduction of the bulb itself, and of its internal bulbar cavity as well. This is the most precise diagnostic characteristic of the neotylenchids. The preservation in the neotylenchid group of ancient connections with hyphomycetes should be specially emphasized, and along with this the preservation of some "hoplolaimoid" characteristics (the esophageal glands which envelop the beginning of intestine in some genera, the "hoplolaimoid" preuterine gland, the special spermatheca which "slips by" in some forms, and the peloderan caudal alae). All this speaks of past connection with the hoplolaimids, referring probably to the distant phyletic past which seems to me to be a heterogenically diverging group of ancestral ectoparasitic myconematodes; one of the groups of these myconematodes crossed over to ectoparasitism at the expense of the nourishing rootlets of plants (later including, the phanerogams), which brought into consolidation the hoplolaimids, which were losing the connection with the hyphomycetes. Another group, on the contrary, preserved its connections with the hyphomycetes, the small stylet and other "aggregated" characteristics which resulted in the formation of the neotylenchids. Connections with the hyphomycetes extended the development of characteristics typical for the neotylenchids. It is probable that the development of specialization in the direction of mycetophagia furthered the strengthening of the capillary-suctorial power of the stylet and the corresponding reduction of the suctorial function of the metacorpal bulb.

Therefore, its myofibrils underwent a process of phyletic immobilization of function (Severtsov, 1939), which resulted in regression and even in full reduction of the metacorpal bulb, which is very characteristic of the neotylenchids. All of this fixed the connections with the hyphomycetes. When the latter conquered the tissues of the phanerogams, the ancestral tylenchids, right after the hyphomycetes, penetrated the tissues of the higher plants, and Tylenchidae and Neotylenchidae crossed over from elementary mycetophagia to nourishment at the expense of cells of plant tissues. Tylenchidae partially won trophic independence, and many of them became plant nematodes of specific pathogenic effect. The neotylenchids did not attain this, and as a rule are characterized by a dependent nutrition which remains at the level of plant nematodes of unspecific pathogenic effect. Thus, Tylenchidae and Noetylenchidae form two branches of a common trunk, from which only one has achieved specific pathogenicity which one must take into consideration. The neotylenchids have not reached this level of parasitic organization.

Preliminary observations on the phyletic interrelations of Hoplolaimoidea.

I stipulate that in this article the present question cannot be examined completely. It is necessary, however, to outline precisely the basic status of this problem.

I seems to me that the hoplolaimoid families form an integral, historically developing group. I consider that this group emerged from ancient ectoparasitic myconematodes, as did also the families belonging to Tylenchoidea. Thus, the history of development for all groups is common. However, both the groups named (superfamilies) diverged very early in two directions: (a) ectoparasitic myconematodes, which crossed over to an existence at the expense of the root system of seed plants, with the loss in the final phyletic branches of the capacity for mycetophagia; and (b) ecotoparasitic and endoparasitic forms which preserve the capacity for mycetophagia. The first group (a) became the source of development of Hoplolaimoidea; the second (b) of Tylenchoidea. Such an assumption is based on the fact that both superfamilies undoubtedly are contiguous phylogenetically, but at the same time demonstrate the two divergent directions of development which have been mentioned above. It has been shown that the hoplolaimoid superfamily is characterized by the most complete and typical integration of morphological traits. This is expressed in the fact that the forms of this superfamily are characterized by an integral "hoplolaimoid" organization, connected with a didelphic female genital system. A tylenchoid organization of the cardial bulb which carries intraesophageal glands, remains the only characteristic of the tylenchoid type which has considerably widespread distribution in the hoplolaimoid superfamily. This characteristic is observed very often in hoplolaimoid families. Thus, it is characteristic of the subfamily Dolichodorinae Chitwood & Chitwood, the subfamily Trophurinae Paramonov, and the families Criconematidae and Tylenchulidae. However, this tylenchoid characteristic is always correlated within the limits of these groups with typical hoplolaimoid complexes of other characteristics on which I cannot dwell in this article after merely having recalled them briefly: (a) hoplolaimoid forms of procorpus and metacorpal bulb, (b) hoplolaimoid types of stylet and its knobs, and equally, of the

protractors, (c) hoplolaimoid organization of internal skeleton (d) hoplolaimoid types of female genital system, phyletically conservative. These references allow one to recognize that both superfamilies are historically connected. However, the chief argument in favor of this position remains the fact that the hoplolaimoid characteristics are very widespread within the precincts of tylenchoid groups and, at that, always against the common background of typical tylenchoid organization.

To such hoplolaimoid characteristics in tylenchoid forms belong: (a) the presence of esophageal glands which envelop the beginning of the intestine (in many neotylenchids); (b) the presence, in a series of forms, of a spherical spermatheca which is obligatory for hoplolaimoid forms and is "casuistic" for tylenchoid forms; (c) the presence in some tylenchoid forms of peloderan and superpeloderan caudal alae, widespread in typical hoplolaimoid forms; and (d) the presence among tylenchoid forms of some species in which there are females with a didelphic genital system, not typical on the whole for corresponding superfamilies. These correlations show that hoplolaimoid and tylenchoid forms (groups) have a common origin and that hoplolaimoid groups are closer to the general root of origin of the suborder of tylenchates (tylenchinids), than tylenchoid forms. The latter can be defined as a group within which arose a secondary disintegration of hoplolaimoid characteristics. The transfer from didelphia to monodelphia remains the sharpest characteristic of this disintegration of the complete primary organization. For the rest, the tylenchoid forms are characterized by some disintegration of the female hoplolaimoid genital tract and at the same time by retention of some ancient characteristics of the mycetophagous. Here belong the tubular spermatheca, the small stylet and mycetophagia, widespread within the confines of the tylenchoid groups.

One should consider the presence of "aggregated" types of organization as a very important feature, which has the value of an argument in favor of the interpretation of the correlations between both superfamilies. Such "aggregated" types can be obstacles for the taxonomist, but at the same time they are valuable for the phylogeneticist. I am dwelling here on one example of such "aggregated" types. I mean the subfamily Psilenchinae subfam. n., suggested by me. Here, one genus is to the point, Psilenchus de Man. The genus is characterized by the presence of a simple stylet devoid of basal knobs, and having protractors oriented at a slant, making a wide angle from the long axis of the stylet. These are undoubtely primitive characteristics, which draw together this genus with the mycetophagous among which a similar organization is not a rarity. We can consider that the psilenchids retain an ancestral organization in the characteristic considered. At the same time, one peculiarity of organization of the psilenchids brings us closer to this idea; namely, the structure of the female genital tract. The genital tract in the psilenchids is sometimes of two types, "tylenchoid" and "hoplolaimoid." In the first instance, for example in the organization of the genital tract in Psilenchus hilarulus de Man, the spermatheca belongs to the tubular type, a fact which is characteristic for "tylenchoid" organization. In other species, including Psilenchus minor Siddiqi and P. hilarus Siddiqi described by Siddiqi (1963), the female genital tract is constructed according to the hoplolaimoid type, with spherical spermatheca of inserted type included in the system of a double preuterine gland.

Further, in the psilenchids, there is still one important "hoplolaimoid" characteristic -- heterotopy of the pore of the dorsal gland, the duct of which, as in hoplolaimoid forms, opens into the lumen of the esophagus at a distance from the base of the stylet equal to more than 1/3 the length of the stylet (Siddiqi, 1963). Thus, in the psilenchids, there are elements of "aggregated" organization, combining some hoplolaimoid and tylenchoid characteristics. I consider that the psilenchids, while undoubtedly being considered as a family of the tylenchids, can serve as a rough standard of organization of the ancient tylenchates, combining characteristics of the tylenchoid and the hoplolaimoid type. Elements of a similar "aggregation" in organization are observed also in other groups. Such, for example, is the tylenchoid cardial bulb in Tylenchorhynchinae Eliava. All these are traces of the commonness of origin of the hoplolaimoid and tylenchoid groups. Later, adaptive radiation emerged, resulting in integration of hoplolaimoid and tylenchoid organizations. Hoplolaimoid integration of characteristics is associated with selection in the adaptation to root ecto- and endoparasitism and to an elaboration of specific organization of specialized sedentary endoparasites. Tylenchoid integration involves partial disintegration of the hoplolaimoid system and the development of adaptation to plant parasitism, connected with the preservation of mycetophagia.

It is perfectly clear that both directions of development -- "hoplolaimoid" and "tylenchoid" -- are associated not only with different directions of natural selection in corresponding organization, but with the fact that simultaneously these branches become the product of qualitatively different directions of genetic development and of different forms of mutagenic processes. Therefore, the tracing of the formative ontogenetic processes shows a different development of the phyloembriogenetic changes in these groups. Within the confines of the hoplolaimoid organization, the mutagenic process in its connections with selection, result in phyloembriogeneses, which guarantee the formãtrerrp falaehinz; prnjf , whereas within the limits of tylenchoid organization this is not so. This evidently accounts for the fact that within the limits of the hoplolaimoid group of families the tendency toward sedentariness is regulary shown, a tendency that is lacking within the limits of the tylenchoid group.

These facts confirm with full evidence that the hoplolaimoid families (Hoplolaimidae, Pratylenchidae, Heteroderidae, Tylenchulidae, Paratylenchidae, Criconematidae, and Sphaeronematidae), are one complex, whereas the tylenchids and neotylenchids are another complex. I have tried to bring these facts to light and to give evidence of them, while proceeding from a deep belief that natural taxonomic groups are not created, but discovered. The question is merely how successfully this is done.

Thus, we come to the following basic conclusions: (a) both groups of families arose from a common root, represented by ancestral ectoparasitic myconematodes; (b) one of the branches of the last was adapted exclusively to root parasitism and in this connection resulted in the development of large-stylet forms which lost the ability to be nourished by hyphae of fungi and resulted in the formation of the hoplolaimoid organization;

and (c) the other branch, on the contrary, preserved small stylets and the capacity for mycetophagia which played a leading role in the formation of the tylenchoid organization.

It must be remembered that under the conditions of tylenchoid organization endoparasitic specialization is most typically expressed in the development of endoparasitism in plant organs originating from the stem and in the gametophyte.

Phyletic relations between subordinate groups of

Tylenchina

Superfamily Hoplolaimoidea superfam.n. The type family Hoplolaimidae is seen as a group originating directly from ancestors of this superfamily. Such an appraisal of this family results from the following facts: (a) the hoplolaimids are characterized by the most complete and most primitive organization, being noted at the same time for the most clearly expressed integration of hoplolaimoid characteristics; (b) in the boundaries of this family in particular we see forms adapted to ectoparasitism and preserving a predominatly allomorphic type of development without narrow specialization; (c) at the same time, as a result of allomorphic evaluation within the confines of this family, adaptive radiation emerges with departures towards telemorphic reorganizations and endoparasitism. The telemorphic direction of development results in the isolation of the subfamilies Trophurinae, Belonolaiminae and Dolichodorinae in the composition of which forms are observed with a hypertrophic stylet, a correlatively enlarged metacorpal bulb and a strengthened procorpus of the esophagus. It is necessary to consider forms of the families Paratylenchidae and Criconematidae as another specialized branch, originating from Hoplolaiminae. The paratylenchids preserve the hoplolaimoid plan of organization of the female genital tract, but bear traits of specialization expressed in monodelphia, of development of a hypertrophic stylet, and of reinforcement merged in a general complex of procorpus and metacorpal bulb. The criconematids bear these same characteristics, along with traits of further specialization.

Endoparasitism also originated in the core of the Hoplolaiminae. Such first of all are the Pratylenchidae, represented by the subfamily Pratylenchinae migrating root endoparasites. Further, a complex of sedentary forms originating from the pratylenchids Nacobbinae and from the hoplolaimid Heteroderidae which is differentiated into two subfamilies — Heteroderinae and Meloidogyninae. Within the limits of these groups integration of sedentary organization reaches the most specialized degree of development.

A third sedentary branch, the family Tylenchulidae, originates from the family Paratylenchidae. Within its confines, the regularities of morphogenesis are altered and, convergent with typical hoplolaimoid sedentary groups, the process of development of adaptations to sedentariness acquires a different character. This is already apparent from the fact that, although the matrix for eggs is necessary here, it is formed

from another source than in the meloidogynids as has already been pointed out. Nevertheless, the tylenchulids must be seen as a special modified branch of the diverging stream of hoplolaimoid forms.

Such are the preliminary data which describe the phyletic interrelations among hoplolaimoid familes.

As for the superfamily Tylenchoidea, within its limits differentiation into three groups took place very early. One of them - the family Sychnotylenchidae - is undoubtedly very close to the common root of origin of the tylenchates (tylenchinids). In this very connection, several hoplolaimoid traits of organization are preserved in forms of the genus Neoditylenchus Meyl, in particular the heterotopic displacement of the pore of the dorsal gland behind the basal part of the stylet, and the preservation of the superpeloderan alae, and equally the preservation of the blunt tail in females. The families Tylenchidae and Neotylenchidae came into being by other branchings, also ancient, from the common root of the tylenchates. With that, the tylenchids and neotylenchids preserved mycetophagia and the small stylet and correspondignly, connections with the hyphomycetes. On this basis evolves the specific endoparasitic direction of development which is partially connected with parasitism in organs of cryptogams, but at the same time ancient connections are also maintained with the crytogams, in particular with fungi (hyphomycetes).

CONCLUSIONS

1. In this work a critical review of the superfamily Tylenchoidea (Filip'ev, 1934) Chitw. & Chitw. 1937 has been carried out.

2. As a basis of the analysis of this superfamily, the idea has been put forth concerning two types of morpho-physiological integration, connected with different directions of mutagenesis and selection, and with stipulated differences in the ecological characteristics of families which are members of the superfamily named.

3. The analysis has led the author to the necessity of distinguishing two suborders - Aphelenchina (Fuchs, 1937) and Tylenchina (Filip'ev, 1934). Within the boundaries of the suborder (tylenchinids), the author proposes to distinguish two superfamilies - Hoplolaimoidea (Filip'ev, 1934), superfam. n. and Tylenchoidea (Filip'ev, 1934), Chitw. & Chitw., 1937. In this work an identification key of these superfamilies is offered.

4. As a basic factor in the differentiation of the suborder of tylenchates (tylenchinids) into the two superfamilies named, the author considers their differences in ecologo-morphological character-istics, conditioned by different directions of formative processes, always proceeding under the control of selection. In their sources, both superfamilies originated, according to the author, from ancient ectoparasitic myconematodes. With this, Hoplolaimoidea crossed over to parasitism, at first in the capacity of ectoparasites in the root system of Phanerogamae, and became the source of development of

Hoplolaimidae, Pratylenchidae, Heteroderidae, Paratylenchidae, Tylenchulidae and Sphaeronematidae after having achieved high parasitic specialization connected with the formation of sedentary root endoparasites.

This direction of development is connected with the reorganization of ancient (ancestral) ectoparasitic myconematodes in the large-stylet hoplolaimoid forms, adapted to nourishment at the expense of the root system of plants (phanerogams). The other branch preserved the ancient connections with hyphomycetes, and by means of them and right after them was adapted to ecto- and endoparasitism in the root system and chiefly in above-soil organs, while including gametophytes of a series of species of phanerogams and cryptogams, and after having preserved a small stylet and trophic connections with hyphomycetes (Tylenchoidea).

5. To Hoplolaimoidea the author attributes the tribe Hoplolaimini n. grad. (Hoplolaimidae, Pratylenchidae and Heteroderidae) and the tribe Criconematini (Criconematidae, Paratylenchidae, Tylenchulidae and Sphaeronematidae). I suggest here treating the superfamily Criconematoidea Geraert as a new tribe.

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