TAXONOMIC POSITION OF THE NEMATODE FAMILY NOTHOTYLENCHIDAE (THORNE, 1941) JAIRAJPURI ET SIDDIQI, 1969

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Relationship ties of nematodes of the family Nothotylenchidae (superfamily Neotylenchoidea) with nematodes of the superfamily Tylenchoidea and the possibilities of their transfer as a subfamily of the family Tylenchidae are discussed. The revision being proposed is based on the following factors: 1) The process of cessation of function of the esophageal metacorpus is not restricted to members of the superfamily Neotylenchoidea, but is widespread in the superfamily Tylenchoidea; 2) In Tylenchoidea this process goes with the preservation of all three primary sections of the esophagus which are peculiar to rhabditoid ancestors of this group (corpus, isthmus and cardial section), and with the preservation of the primary compact arrangement of the digestive glands in the tissue of the esophagus and of its characteristic junction with the intestine in the region of the cardia. In the majority of Neotylenchoidea the reduction of the metacorpus is accompanied by the reduction of the isthmus and the cardial section, by the liberation of the glands from the tissue of the esophagus and by its junction with the intestine in the area of the metacorpus; 3) The esophagus in the family Nothotylenchidea is closer in the general plan of structure to representatives of Tylenchoidea than to those of Neotylenchoidea, and is primary in comparison with the esophagus of neotylenchis and other forms in freely arranged glands; and 4) The morphological and ecological resemblance of the type (Nothotylenchus) and of other genera of the family Nothotylenchidae (Boleodorus, Sakia) to genera of the family Tylenchidae (Tylenchus, Aglenchus, Ditylenchus).

Until recently nothotylenchid nematodes were considered by the majority of authors in the constitution of the superfamily Neotylenchoidea (Thorne, 1941; Jairajpuri & Siddiqi, 1969). Analysis of the classification of the neotylenchoids from the position of the structure of the esophagus (Sumenkova, 1974) permits review of the question concerning the inclusion of the nothotylenchids in the composition of this superfamily.

Initially the subfamily Nothotylenchinae was placed within the family Tylenchidae Orley, 1880 (Thorne, 1941). The basic difference from typical tylenchids is the absence of myofibrils and of a cuticular lining in the metacorpal part of the esophagus. In 1949 (Thorne, 1949), nothotylenchids entered into the composition of the family Neotylenchidae together with other subfamilies which also do not have a metacorpal bulb or cuticular lining in it (Neotylenchinae Thorne, 1941; Paurodontinae Thorne, 1941).

Afterwards, when Neotylenchidae began to be considered at the superfamily level (Jairajpuri & Siddiqi, 1969), Nothotylenchinae was raised to the rank of family in the composition of this group.

Then what do nothotylenchids represent? Thorne (1941) gave the following diagnosis of this subfamily. By general shape and external appearance these nematodes resemble species belonging to the genera Tylenchus and Ditylenchus. The corpus of the esophagus is either cylindroid or bears a fusiform basal bulb without a cuticular lining (valvular apparatus) in it. There is a cephalic capsule with six sectors. The ovary is prevulvar, and there is always a posterior uterus. The spicules and gubernaculum are tylenchoid. The type genus is Nothotylenchus Thorne, 1941. Thorne (1941) included in this subfamily two other genera: Boleodorus and Thada, and later (Thorne, 1961), the genera Halenchus Cobb, 1933 and Esphyadophora de Man, 1921. In addition, at different periods, the genera Anguillonema Fuchs, 1938; Nothanguina Whitehead, 1959; Sakia Khan, 1964; Basiliophora Husain & Khan, 1965; and Dorsalla Jairajpuri, 1966 were included in the composition of this group. The latest classification of the family Nothotylenchidae, taking into account the revisions (Jairajpuri & Siddiqi, 1969; Paramonov, 1970; Geraert, 1971) and of our reflections on the position of the subfamily Halenchinae (Sumenkova, 1974) looks as follows:

Superfamily Neotylenchoidea (Thorne, 1941) Jairajpuri & Siddiqi, 1969.

Family Nothotylenchidae (Thorne, 1941) Jairajpuri & Siddiqi, 1969.

Subfamily Nothotylenchinae Thorne, 1941.

Genus Nothotylenchus Thorne, 1941.
Genus Thada Thorne, 1941.
Genus Sakia Khan, 1964.
Genus Dorsalla Jairajpuri, 1966.

Subfamily Boleodorinae Khan, 1964.

Genus Boleodorus Thorne, 1941.

Representatives of all these five genera are distinctly differentiated from other species of the superfamily Neotylenchoidea mainly by the structure of the esophagus and by the location of the digestive glands. In Nothotylenchidae, the latter join the tissue of the esophagus in its cardial section. The corpus of the esophagus and the isthmus are well expressed. The intestine joins with the esophagus in the cardial section of the latter, which is always clearly designed and has a pear-shaped, sac-like or cylindroid-sac-like form.

In representatives of the family Neotylenchidae, as distinct from nothotylenchids, the esophagus is always strongly reduced, so that with them not only are the myofibrils and the cuticular lining not expressed but the isthmus and the cardial part of the esophagus are practically absent; the intestine joins with the esophagus in the area of the metacorpus, but the digestive glands are arranged freely in the body cavity.

Thus the basic difference between the nothotylenchids and the typical neotylenchids consists of the fact that the first have a normally designed esophagus, consisting of three characteristic parts (corpus, isthmus and cardial section) while with the second, the esophagus is reduced to a significant degree and does not have at least two of the distinctly expressed sections (isthmus and cardial bulb).

If one accepts the hypothesis of Paramonov (1956, 1968) that the ancestral rhabditids were the source of origin of the order Tylenchida (while we do not for the time being have other more convincing evidence of the genesis of the tylenchids), then the type of esophagus which we are observing in the nothotylenchids must be considered primary in comparison with the esophagus of the neotylenchids and other representatives of the tylenchids, in which the glands are separated from the tissues of the esophagus to one or another degree and lie freely in the cavity of the body (Aphelenchidae, Aphelenchoididae, Hoplolaimidae and others). Such a primary esophagus, which is being characterized by the compact arrangement of the esophageal glands in the tissue of the cardial section, as the esophagus of the rhabditids, on the whole is atypical for the superfamily Neotylenchoidea, but is always widespread in the superfamily Tylenchoidea (Orley, 1880) Chitwood & Chitwood, 1937. Free arrangement of the digestive glands within the tissues of the esophagus in Tylenchoidea is rarely encountered (for example, the subfamily Pseudhalenchinae Siddiqi, 1971) and the position of these groups in the classification demands additional investigations. The similarity of the general primary plan or organization of the digestive system of nothotylenchids and Tylenchoidea points, without doubt, to their close relationship.

The nothotylenchids are very close to representatives of the superfamily Tylenchoidea and not only in the organization of the esophagus and the arrangement of the digestive glands. During the revision of the genus Boleodorus it was shown (Geraert, 1971) that its representatives, by the structure of the slanting, slit-shaped amphid openings, by the shape of the head and the esophagus, and by the structure of the female gonads, are very close to species of the genus Psilenchus de Man, 1921. The sole difference consists in the somewhat better development of the middle bulb of the esophagus in species of the genus Psilenchus. Although the above-mentioned author did not make the move, he considered it fully acceptable to remove the subfamily Boleodorinae Khan, 1964 from the Neotylenchidae and to place it after the subfamily Psilenchinae Paramonov, 1967 in the family Tylenchidae.

After having analyzed the differential diagnoses and descriptions of all 28 known species of Nothotylenchus, we arrived at the conclusion that this genus is distinguished from Ditylenchus Filip'ev, 1936, which resembles in design the superfamily Tylenchoidea, by a single characteristic, the absence of a cuticular lining in the metacorpal cavity of the esophagus. In Table 1 comparative data in the morphology of Nothotylenchus and Ditylenchus are represented. This data shows that according to basic morphological criteria (shape of body, head and tail, and general plan of structure of the esophagus and of the genital system of females), these groups of species are practically no different.

TABLE 1

Comparison of the morphology of Nothotylenchus and Ditylenchus

Characters	Nothotylenchus	Ditylenchus
Cephalic capsule	Weakly sclerotized, more often not annulated.	Weakly sclerotized, more often not annulated
Shape of the body	Elongate-fusiform	Elongate-fusiform
Shape of the tail	Conical or elongate-conical slightly bent ventrally, with sharp or blunt tip.	Conical or elongate-conical, curved ventrally with sharp or blunt tip
Lateral fields	From 4 to 6 lines	From 2 to 6 lines
Corpus of esophagus	Cylindroid or with fusiform-oval metacorpus without cuticular lining in it	Shape of metacorpus varies from fusiform to convex-oval and even rounded; cuticular lining present
Isthmus of esophagus	Distinctly expressed	Distinctly expressed
Cardial section of esophagus	In form of pear-shapped or sac-like-cylindroid bulb; glands join tissue of esophagus.	From clavate-broadened, to bulb developed to different degree; sometimes slightly lobular and with dorsal side overlaping anterior intestine section; glands join tissue of esophagus
Length and direction*	Prevulvar, short	Prevulvar, of varying length, often flexed
"V"*	Usually 60-75%	Usually 60-78%, more rarely up to 90%
Arrangement of oogonia*	Mainly in a single row	Mainly in a single row, more rarely in two rows
Spermatheca*	Elongate-sac-like between oviduct and regular pre-uteral gland	Elongate-sac-like between oviduct and regular preuteral gland
Posterior uterus*	With different degree of development from 1 to 3-4 body diameters in length	With different degree of development, more often large, 2-3 body diameters in length
Bursa of males	Peloderan, with different degree of development	Peloderan, with different degree of development

*Genital tract of females

As for differences in the structure of the metacorpus and of the cuticular lining in it, it should be noted that the degree of development of this organ varies noticeably in both genera.

So, a number of species of Nothotylencus (N. allii Khan & Siddiqi, 1968; N. antricolus Andrássy, 1961; N. cylindricollis Thorne, 1941; N. cylindricus Khan & Siddiqi, 1968; N. hexaglyphus Khan & Siddiqi, 1968; N. loksai Andrássy, 1959), possess an esophagus, the corpus of which is almost cylindrical in shape, whereas in other species of this genus, indeed a great deal of them (N. acris Thorne, 1941; N. acutus Khan, 1965; N. attenuatus Mulvey, 1969; N. basiri Khan, 1965; N. buckleyi Das, 1960; N. danubialis Andrássy, 1960; N. exiguus Andrássy, 1958; N. geraerti Kheiri, 1970; N. major Thorne & Malek, 1968; N. tuberosus Kheiri, 1970), is observed a fusiform or tapered-oval swelling of the metacorpus, caused by the development of myofibrils in this part of the esophagus.

Variations in shape and dimensions of the metacorpal bulb are also observed in species of Ditylenchus. Such species as D. ausafi Husain & Khan, 1967; D. cafeicola (S. Stekhoven, 1951); D. convallariae Sturhan & Friedman, 1965; D. destructor Thorne, 1945; D. emus Khan et. al., 1969; D. intermedius (de Man, 1880); D. medicaginis Wasilewska, 1965; D. minutus Husain & Khan, 1967; D. misellus Andrássy, 1958; D. myceliophagus Goodey, 1960; and D. phylobius (Thorne, 1934) have a tapered-oval middle bulb, in some species so weakly developed [D. brevicauda (Micoletzky, 1925); D. dipsacoideus (Andrássy, 1952); D. rarus Meyl, 1954], that the corpus of the esophagus is almost cylindroid. In other ditylenchids the metacorpal bulb differs in shape from convex-oval [D. cyperi Husain & Khan, 1967; D. dipsaci (Kühn, 1857); D. geraerti (Paramonov, 1970); D. nanus Siddiqi, 1963; D. nortoni (Elmiligy, 1971); D. triformis Sasser, 1955] to rounded [D. paragracilis (Micoletzky, 1922); D. phloxidis Kir'yanova, 1951; D. sibiricus German, 1969; Ditylenchus sp. Paesler, 1957; and D. tenuidens Gritzenko, 1971].

Similar examples of variations in the degree of development of the metacorpus exist in the genera Sakia (superfamily Neotylenchoidea) and Tylenchus (superfamily Tylenchoidea), which in our view are also very close. (Table 2).

The data of Table 2 show that these two genera are differentiated only by the sclerotization of the cephalic capsule and the degree of development of the metacorpus as in Nothotylenchus and Ditylenchus; the latter character in both genera is not markedly constant.

In the genus Sakia the corpus of the esophagus varies from almost cylindrical (S. allii Suryawanshi, 1971; S. castori Khan et. al., 1968) to fusiform [S. jonesi (Husain & Khan, 1965)] and tapered-oval [S. indica (Husain & Khan, 1965) and S. propora (Husain & Khan, 1967)].

TABLE 2

Comparison of the morphology of Sakia and Tylenchus

Characters	Sakia	Tylenchus
Cephalic capsule	Weakly sclerotized, apparently not annulated	Predominantly annulated
Shape of the body	Elongate-fusiform	Elongate-fusiform, sometimes weakly bent ventrally
Shape of the tail	Extended-conical with blunted tip	Elongate-conical with blunt or sharp tip
Lateral fields	4 lines	4 lines
Corpus of esophagus	From almost cylindrical to constricted-oval in the region of the metacorpus; cuticular lining in the metacorpus absent	Metacorpus from almost cylindrical or slightly fusiform to convex-oval and almost rounded; cuticular lining present
Isthmus of esophagus	Distinctly expressed	Distinctly expressed
Cardial section of esophagus	Mainly pear-shaped-oval; digestive glands join bulb; glands join tissue of esophagus	From pear-shaped and pear-shaped-oval to elongated-sac-like; glands join tissue of esophagus
Length and direction*	Prevulvar, short	Prevulvar, mainly short, almost never reaches esophagus
Arrangement of oogonia*	In a single row	Mainly in a single row
"V"*	Predominantly 55-60%	Usually 60-75%
Spermatheca*	Always present, from rounded to short-oval	The spermatheca, if it exists, is then in the shape of a rounded-oval offshoot
Spermatozoids*	Small	Small
Posterior uterus*	Less than 1 body diameter or equal to it	Less than one body diameter
Bursa of males	Small, adanal	Short, adanal, up to 3 body diameters in length

*Genital tract of females

In the genus Tylenchus Bastian, 1865 it is possible to distinguish at least three forms of metacorpus: almost cylindrical or slightly fusiform, convex-oval, and almost rounded (Table 3).

TABLE 3

Variations in shape of the metacorpus of the esophagus in species of Tylenchus

Corpus almost cylindrical or slightly fusiform	Metacorpus convex-oval	Metacorpus almost round
T. aquilonius, Wu, 1969	T. ditissimus Brzeski, 1963	T. andrassyi Szczygiel, 1969
T. baloghi Andrássy, 1958	T. cylindricaudatus Wu, 1969	T. arcuatus Siddiqi, 1963
T. facultativus Szczygiel, 1969	T. hagenensis Wu, 1965	
T. goodeyi Das, 1960	T. neodavainei Wu, 1969	T. cerealis Kheiri, 1970
T. hageneri Elmiligy, 1971	T. sandneri Wasilewska, 1965	T. davainei (Bastian, 1865)
T. helenae Szczygiel, 1969	T. striatus Das, 1960	
T. quartus Szczygiel, 1969	T. vesiculosus Knobloch & Knierim, 1969	T. ritai Siddiqi, 1963
T. stylolineatus Wu, 1969 1969	T. vicinus Szczygiel, 1969	T. vulgaris Brzeski, 1963

The cited examples of variations in shape and dimensions of the metacorpus are a reflection of the process of cessation of the functions of the metacorpal bulb in the suborder Tylenchina which took the attention of Paramonov at one time in 1970. More than this, Paramonov showed that this process took place and takes place not in one such group of tylenchids but in parallel fashion in a series of groups (for example, in the families Tylenchidae, Anguinidae, and Neotylenchidae). The wide extent of this process demonstrates the possibility of the existence of a bulbless esophagus not only in neotylenchids but also in nematodes of other groups of the order Tylenchida. In connection with this, the taxonomists are forced to evaluate more carefully than has been done up to this time the diagnostic significance of such a charateristic as the absence of a metacorpus and the cuticular lining in it. Until recently it was considered that this characteristic was important enough for enrolling

the nematodes in the superfamily Neotylenchoidea and for substantiation of the nature and validity of this superfamily. Paramonov, who always dismissed the integrity of Noetylenchoidea, was himself the first who showed the artificiality of this group when he proved that the genus Nothanguina, which possesses a bulbless esophagus, is, according to all the other morphobiological characteristics, a representative not of Neotylenchidae but of Anguinidae.

Establishment of the morphological similarity of the genera Boleodorus and Psilenchus (Geraert, 1971) and the results of our comparative analysis of the genera Nothotylenchus - Ditylenchus and Sakia - Tylenchus permit proposing that Nothotylenchinae also is artificially included in the superfamily Neotylenchoidea, and that its transfer to the superfamily Tylenchoidea would correspond better to their natural ties of relationship.

The data concerning the ecology of nothotylenchids also testify in favor of this proposal. If the superfamily Neotylenchoidea is examined on the whole, then all its known families after exclusion of Nothotylenchidae contain a large number of genera and species associated with insects, living parasitically in the body cavities of insects or in their fatty tissues, or dwelling in the rotten frass of the galeries of bark beetles. All species of the family Sphaeulariidae are insect nematodes; in the family Paurodontidae the subfamily Misticiinae and the genus Stictylus from the subfamily Paurodontinae all are associated with insects; so is the genus Deladenus in the family Neotylenchidae. Also, the family Nothotylenchidae contains forms which dwell exclusively in soil and in the rhizosphere and tissues of different plants. Out of 51 known species of this family only N. drymocolus Ruhm, 1956 has been observed in typical dwellling places of insects - in the damp rotten dust of fir and pine stumps. Inhabitance of soil, as well as its morphological peculiarities, very strongly links nothotylenchids together with typical representatives of Tylenchoidea.

Taking into account all that has been said, we propose that nothotylenchids should be considered in the constitution of the superfamily Tylenchoidea; it is possible, until the relationships with other taxa have been established more precisely, to place them for the time being in the family Tylenchidae with the rank of subfamily just as Thorne did originally (Thorne, 1941). One can think that a deeper investigation of the morphology, physiology and biology of all these nematodes will permit to judge more precisely their position in the classification of the superfamily Tylenchoidea.

We did not dwell on the peculiarities of morphology of the genera Thada Thorne, 1941 and Dorsalla Jairajpuri, 1966 inasmuch as they are poor in species and have not been very well described. According to the structure of the esophagus both the one and the other can be included in the family Tylenchidae.

In conclusion we shall not dwell on the possible causes for the cessation of function of the metacorpal bulb in different groups of the suborder Tylenchina. Judging by the data presented, it is possible to think that the reductions of the metacorpus in nothotylenchids and neotylenchids are not equivalent processes inasmuch as this process in the first case goes with the preservation of the common primary form of the esophagus, while in the second it goes in paralles fashion with the reduction of the cardial section and the isthmus and even leads to full atrophy of the esophagus and of its functions in sphaerulariids.

The regression of the esophagus in nothotylenchids is similar to this process in the superfamily Tylenchoidea and, possibly, is caused by the adaptation to feeding on easily absorbed food, when its ingestion through the lumen of the esophagus can be practically almost exclusively realized by the sucking power of the stylet, which is strong in Nothotylenchidae and Tylenchidae since this organ represents a very thin capillary. In connection with this, partial atrophy of the sucking function of the esophagus takes place and, accordingly, reduction of myofibrils and of the thickened cuticular lining of the metacorpus.

As regards the typical Neotylenchoidea, in this group there are clearly expressed traits of full atrophy of the esophagus and of its function. And if in neotylenchids we observe as it were the early stages of this process, then it is expressed in full measure in the family Sphaerulariidae with typical parasites of insects. Usually parasitic females, which feed by osmosis in the body cavity of insects or in fatty tissue, do not have an esophagus and even their digestive glands are weakly developed. Functional digestive glands are observed in these nematodes only in larvae or in generations which feeds on the mycelium of fungi.

All what has been said permits one to think that Neotylenchoidea is undoubtedly a natural group of nematodes, but it is necessary to seek its entire monolithic nucleus among forms associated with different insects or with the conditions of their habitat.

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SYSTEMATIC STATUS OF THE FAMILY NOTHOTYLENCHIDAE (THORNE, 1941) JAIRAJPURI ET SIDDIQI, 1969 (NEMATODA)

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Summary

The wide distribution of the process of immobilization of the oesophagal metacorpal bulbus functions in the suborder Tylenchina and the peculiarity of this process in the superfamilies Neotylenchoidea and Tylenchoidea have been shown. On the basis of morphology (general primary plan of oesophagus structure, mainly) and ecology (soil dwelling, occurrence in rhizosphere and plant tissues), relationships between the family Nototylenchidae (superfamily Neotylenchoidea) and the superfamily Tylenchoidea are considered and the possibility of inclusion of the former in the family Tylenchidae as a subfamily is discussed.