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Tribune

A REAPPRAISAL OF TYLENCHINA (NEMATATA) 1. FOR A NEW APPROACH TO THE TAXONOMY OF TYLENCHINA

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During the last three decades plant-parasitic nematodes have received increasing attention. This was due mainly to the discovery during the years between 1943-1953 of the first efficient nematocides, DD, EDB and DBCP. This discovery gave a strong impetus to established nematology laboratories and led to the establishment of laboratories in previously "virgin", or nearly so, territories. As a result, there was an increase in the number of nematologists and taxonomic activity. This is particularly true in those areas new to nematology, because the soil fauna is virtually unknown and taxonomy is one of the few activities fitting with limited material means, that too often is the situation of young laboratories.

As a proof of this impetus to taxonomy, we may refer to Figure 1 where the proposals for new generic taxa of Tylenchina are summed up from 1913 to 1983. One may see that the slope of the curve changes abruptly, in the years 1953-1957.

Some of the recently proposed taxa we may call "valid" taxa because they represent well individualized forms, not at all fitting into heretofore described corresponding taxa. At the opposite end of the spectrum, too many taxa, mainly genera, have been proposed as new when another solution could have been to enlarge the definition of a preexisting corresponding taxon. In some cases one reads statements such as: "the genus C is proposed as new because it is intermediate between genera A and B"; in such cases the first action should have been to examine the possibility of fitting the species of genera A and B together with the species of genus C, in a single genus or, at least to enlarge the definition of either genus A or B to include the species of C.

Multiplication of genera also occurs in taxa containing numerous species and where groups of species can be defined, often using only one character and not of primary importance. Three examples may be cited: in the genus *Hoplolaimus*, some species may have six nuclei (instead of the normal number of three) in the glandular part of the esophagus. All other characters are identical in the two groups of species, taking into account specific variation. Nevertheless, the genus *Basirrolaimus* has been proposed for species having six esophageal nuclei, *Hoplolaimus* being restricted to those species having only three esophageal nuclei. Another example in the genus *Hoplolaimus* pertains to *H. californicus*, in which the two enlarged phasmids are both posterior to the vulva instead of being situated with one anterior to the vulva and the other posterior; here too a new genus, *Hoplolaimoides*, has been proposed, based on this unique character for a single species. In the very homogeneous genus *Radopholus*, in two species out of about 30 the males are described as having a terminal instead of a subterminal bursa as is common to all the other species. This character alone has been used to propose the genus *Neoradopholus* to contain these two species.

These actions may stem from a preconceived idea about the optimal size of a genus. Some taxonomists believe that a genus with more than 50 or 60 species becomes unmanageable and must be split. We assume to the contrary that the number of species in a given genus may vary from one to any number. We agree that in large genera specific identification is difficult; however to facilitate the identification it is often possible to define within the genus, « groups » having no taxonomic value and no nomenclatural status, as did for

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example Geraert (1965) for *Paratylenchus* or Mulvey (1972) for *Heterodera*.

Excessive splitting of genera results in the accommodation in one genus of only those species very close to each other; this leads to « oligomorphic » genera (we will define and discuss this concept below). Then, after division of a genus into several genera, the original genus is often raised to the rank of subfamily to reestablish the relationships between these new genera. In turn subfamilies are raised to family rank, families to superfamily rank, etc. This affects even suborders and orders as four new suborders (Sphaerulariina, Hexatyliina, Myenchina, Criconematina) recently have been proposed within the order Tylenchida [Heteroderina (= Heteroderata) Skarbilovich, 1959 apparently has never been accepted by other taxonomists] and the suborder Aphelenchina has been raised to the rank of order, Aphelenchida.

We call this phenomenon "taxonomic inflation" as taxa are devaluated at each step. As a consequence of this inflation the number of suprageneric taxa becomes excessive in proportion to the number of genera. For example, in the classification of Tylenchida proposed by Fotedar and Handoo (1978), 158 genera in the suborder Tylenchina are distributed into 9 superfamilies, 32 families and 55 subfamilies; this represents ratios of 17.6 genera per superfamily, 4.9 per family, 2.9 per subfamily. In the most recent comprehensive classification (Siddiqi, 1986), the Tylenchida encompass five suborders, eleven superfamilies, 29 families, 64 subfamilies (of which 24 are monogeneric) and 200 nominal genera. It is difficult to believe, when we compare Nematoda to other phyla, that the tylenchids contain such a diversity of structures and forms that so many generic and suprageneric taxa are needed to accommodate them. Tylenchids are very much alike in their anatomy. Maggenti (1981) rejected this inflationary approach, based principally on minute morphologic differences, and accepted only seven families within Tylenchida based on their morphology and biology.

An undesirable consequence of this situation is that the definition of the suprageneric taxa differs according to each taxonomist. It is evident that the concept, and the content, of the family Tylenchidae are very different for Fotedar and Handoo (1978) and for Maggenti (1981) or Siddiqi (1986). It is now impossible to cite a suprageneric taxon, and in some cases a genus, without adding "sensu X" or "following Z".

Therefore, the present status of the taxonomy of tylenchids is unstable and if new taxa continue to be proposed at the rate that has prevailed for the last 20 years, then the situation can only become worse in the future.

We believe that this present unsatisfactory status has resulted from the almost total lack of interest for the evolutionary approach that seeks relationships on the basis of morphology and biology. The disregard of

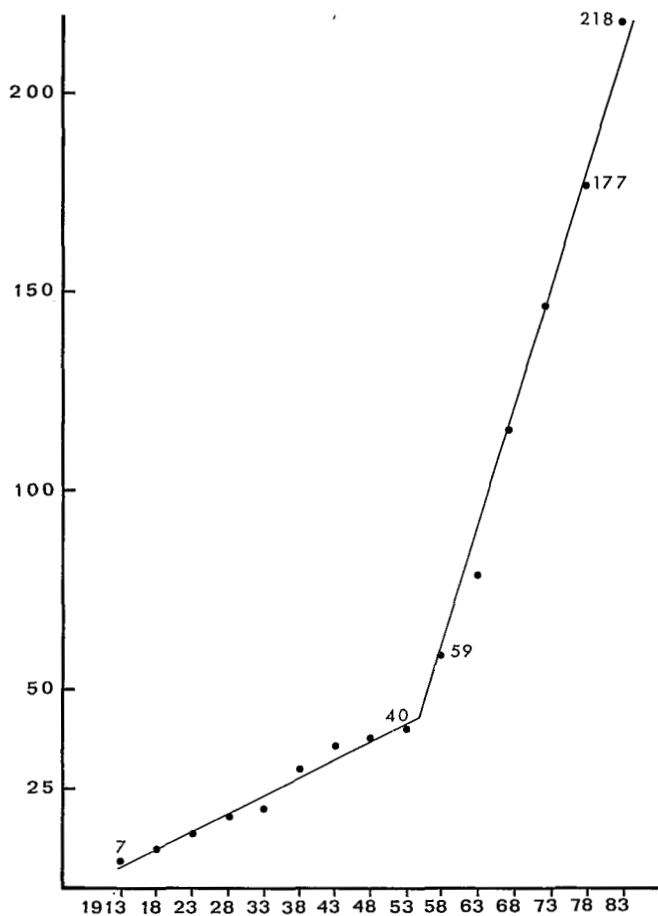


Fig. 1. Cumulative annual number of genera described in Tylenchina from 1913 to 1983.

biology and failure to apply principles of evolution accounts for the inflation of the suprageneric taxa and is most apparent at the generic level where genera are proposed for the sake of identification and nothing else.

For one hundred years after the publication of Darwin's "Origin" only one school of classification was recognizable, and seemingly the school had not well thought out methodology (Mayr, 1981). The underlying theme of classifications proposed during this period was to base classification on phylogeny and thereby reflect degree of relationship. In the 1950's and 60's, taxonomists began to scrutinize and question the seeming arbitrariness and lack of methodology of the so-called Darwin system. As a result, two new schools of taxonomy emerged. Numerical phenetics first articulated by Sokal and Sneath (1963) and cladistics, whose conceptual spokesman was Hennig (1950). Mayr (1981), during this same period, brought a more explicit articulation to Darwin's methodology, and this system became known as evolutionary taxonomy.

In the so-called numerical taxonomy (phenetics), numerous characters are listed without preconceived choice, then numbered and their relationships and groupings mathematically analyzed. Numerical phenetics has proved largely unsuccessful because the classifications produced varied according to characters or programs of computation chosen. Therefore, the claim that results are objective and repeatable were not always justified (Mayr, 1981). Objectivity for this appraisal is also disclaimed since subjective biological criteria were used to assign variants to operational taxonomic units. However, this method opened the door for the use of mathematics in taxonomic studies; as an example, multivariate analyses can be very useful at specific discrimination.

In the cladistic approach, which is the opposite of the preceding method, a limited number of characters are chosen, their ancestral or derived polarities are defined, and then they are hierarchized. This method is said to be "objective" and/or "scientific", but the choice of the characters, the definition of their polarities (ancestral or plesiomorphic, *versus* derived or apomorphic) and the placement of derived states in evolutionary sequences are mainly subjective for most characters. Therefore, often more than one solution is possible in reconstructing "cladograms" *i.e.* dichotomous phyletic trees based on these sequences of character status. One aspect of the cladistic approach open to criticism is that only anatomo-morphologic data are taken into consideration, and not biological data that also are very important in parasitic groups. Giving a particular taxonomic rank to each branching of the cladogram is also an undesirable consequence of cladistics, *e.g.* Coomans (1979) for Heteroderinae-Meloidogyninae. In that case, it required the introduction of "tribes", a rank intermediate between genus and subfamily. If this is combined with the concept of "superspecies" as defended by Sturhan (1983), there would be five taxonomic ranks between the species and the family! We do not think that such a great number of steps is necessary, nor would it render more evident the relationships between genera; on the contrary, it will increase the risk of discrepancies between different taxonomists concerning the rank to be attributed to any group of nematodes.

Cladistics bases taxa exclusively on genealogy and classifies characters rather than organisms (Mayr, 1981). Mayr points out that the basic weakness of cladistics is the lack of a sensitive method of ranking, the cladist simply gives a new rank after each branching point. The evolutionary taxonomist, following Darwin, ranks taxa by the degree of divergence from the common ancestor, often assigning a different rank to sister groups. An example may well be the family Tylenchidae and the suborder Sphaerulariina.

The philosophy followed here is that of the Mayr evolutionary school. It is our opinion that this school

offers the broadest, most flexible and least restrictive base on which to build a classification that more truly reflects the phylogeny of those nematodes included in the suborder Tylenchina. Both numerical phenetics and cladistics are deemed by us to be too restrictive and limited in retrievable information to be useful in designing a higher classification.

Another problem that must be addressed is that, until now and with few exceptions, the "key characters" used for the practical identification of species and genera, and the "taxonomic characters" that are supposed to reflect phylogenetic relationships between taxa of the same level, have been confused. The result is that the taxonomic value of characters easy to observe and to describe such as the number of lines and the areolation of the lateral field, and other characters linked to the cuticle (longitudinal lines, costation, etc.) more than likely has been overestimated. This situation will be modified with the increased use of the SEM as underlined by Hirschmann (1983). For example, it appears more and more evident that the *en face* view of the lip region as seen by SEM, in many groups of Tylenchina, is an excellent taxonomic character at the family or generic level. In some cases (*Pratylenchus*) variations are useful to define groups of species. Such characters, visible only by SEM, are fundamental to taxonomic diagnosis of genera and species, yet they cannot be used for practical identification purposes.

On the other hand, the host-parasite relationship may constitute a source of characters that have received too little attention for the definition of various taxa. As an example, within Heteroderidae it appears that some genera (*Heterodera*, *Globodera*) consistently induce in the host multinucleate coenocytic nutritive cells, whereas other genera (*Hylonema*, *Rhizonema*, for example) induce the formation of a single giant cell provided with a single giant nucleus. Similarly, *Tylenchulus* and *Trophotylenchulus* can be separated on the basis of differences in host reaction.

Our approach in reappraising of the taxonomy of tylenchids has been to try to combine morpho-anatomical data and biological data, and to take into consideration indications given by these characters tentatively to define evolutionary lines. Doing this, our aim is to contribute to the stabilization of, and to clarify the status of, various nematode taxa rather than to propose one more new classification of Tylenchina. We will not hesitate to use question marks when necessary instead of approving or creating taxa with insufficient foundation or justification.

We agree with the biological definition of species and that it is the only natural taxon corresponding biologically to an objective entity. We are fully aware that this concept is difficult to apply in the case of thelytokous species, sibling species, etc. On the contrary, supraspecific taxa are intellectual (subjective) concepts that reflect the human tendency to "put in order" things and

creatures. However, authors of such taxa seldom take into consideration the evolutionary lines that can be traced from all the available data. The genus is the first step of this arrangement or classification and as such, the closest to the natural entities. From the genera are derived all the superior taxa.

Thus our first step was to reconsider generic validity and placement. In order to accomplish this we followed two precepts. The first is that our perceptions of what constitutes a generic or suprageneric taxon, has not to be eternal; they correspond to a moment in systematics and additional data may change our concepts. For example, when the genus *Brachydorus* de Guiran & Germani, 1968, was described from a single species, it was clear that this genus was close to *Dolichodorus*, differing mainly by two characters : a long, regularly effiliated tail and a relatively short stylet, whereas the hitherto described *Dolichodorus* species had a very long stylet and a short, rounded tail, sometimes with a short spicate terminus. Later *Brachydorus swarupi* Koshy, Raski & Sosamma, 1971 was described in which the stylet was longer and the tail shorter than those of the type species; then *Dolichodorus longicaudatus* Doucet, 1981 was described with a stylet shorter than in other *Dolichodorus* species and a long conical tail, intermediate between *Brachydorus* and those *Dolichodorus* species with a spicate tail. Therefore, the original species of *Brachydorus* could represent only the extreme of variability in tail shape and stylet length within the genus *Dolichodorus*.

On the other hand, two genera that have been synonymized, later can be restored when new important differences are discovered. This is the case, for example, of *Tylenchulus* and *Trophotylenchulus* that were synonymized by Maggenti (1962) on the basis of significant morpho-anatomical resemblances. However, a recent study of Cohn and Kaplan (1983) shows significant differences in the host relationship of these two genera, and consequently it now appears that each should be considered as a valid taxon.

The second precept we followed in our reassessment of genera is that the species are not always grouped in the same way in different genera. In one case there is a large or euryomorphic genus, a concept well-known and used in other branches of zoology and other natural sciences; it means that one or more characters can vary progressively from one species to the other (morphocline) within the same genus. In such genera, species are easily identified and separated from each other, but the limits of the genus itself are more difficult to assess. A good example of a euryomorphic genus is *Pratylenchoides* in which the glandular part of the esophagus can vary from abutting bulb-like glands (*P. magnicauda*) to a long overlap over the intestine (*P. ritteri*).

In contrast there are oligomorphic genera in which all the species closely resemble each other (for example,

Pratylenchus, *Rotylenchulus*). Such genera are easily defined, but their species are more difficult to differentiate from each other.

Both kinds of genera can co-exist in the same family or subfamily, as is the case with *Pratylenchoides* and *Pratylenchus*.

In reviewing genera within Tylenchina we enlarged their definition and accepted a greater intrageneric variability. In several instances, we synonymized genera that had been created by splitting former genera on the basis of few and/or secondary rank characters. This resulted in some cases, in the enlargement of the concept of the family. Subfamilies do not constitute an obligatory taxonomic step; they should be used only when groups of genera can be properly defined and when the subfamily category helps to clarify the relationship between these genera within the family. We do not accept the creation of subfamilies as a kind of routine taxonomic procedure that results in some families, for example, Heteroderidae, in several monogeneric and often monospecific subfamilies.

Evolution and systematics in Tylenchina

Clearly, it is not possible to write on systematics without using words, such as degenerated, evolved, ancestral, regressed, transformed etc... concerning certain characters; and, such words as closer, deriving from, related to, etc... when writing on taxa. As a consequence evolution is always implied when dealing with the classification of living forms. Even the most classical phenetic taxonomists (alpha taxonomy) use these terms, thus weakening the arguments between phenetic and evolutionary (gamma taxonomy) classifications.

When applied to plant-parasitic nematodes, in this reappraisal limited to the Tylenchina, these terms are more often clichés than facts. The problem is complicated by the fact that there are only a few fossil nematodes and of these the most ancient, in amber, are dated about 40 million years, and are quite like those living today (Poinar, 1984). On the other hand, due to the generally wide range of host plants for the same genus or even the same species, and also to the apparent uncertainty of phylogenetic lines in plants, it appears nearly impossible to trace a co-evolution of host and parasite as it has been proposed for some animal parasite groups such as Trichostrongyloidea (Durette-Desset, 1985). Generally speaking, plant parasitic nematodes appear to ignore botanics, and as a consequence render studies of co-evolution of parasite and host often meaningless. However, interesting researches have been carried out (Krall' & Krall', 1970; Stone, 1979) concerning *Heterodera* and related genera. Among Tylenchina, this group apparently is derived (cysts), and peculiar because of their generally narrow range of host

plants. For the most part, hosts are limited to one or only a few close botanical families.

Consequently, any attempt to relate the evolution of plant parasitism within Tylenchina, when all available information and the principles of paleontology are not adhered to is an intellectual game. We must be aware that the forms we are looking at now represent contemporary extremities of numerous lines that have evolved vertically through time, whereas systematic groupings are horizontal. The Tylenchida appear to have their "roots" in Diplogasterida. The search for a "common ancestor" to different groups is a legitimate speculative undertaking. The "horizontal" groupings of nematode classifications often combine forms more convergent than linked phylogenetically. For example the superfamily Heteroderoidea was proposed by Golden (1971) to group within Tylenchina saccate or globose females fixed on or in the roots of plants. This grouping has received little acceptance, because its artificial character is immediately evident. Another example of artificial grouping is the family Neotylenchidae. Other artificial groupings may be present in the classification that are not so easily identified.

These foregoing statements are cautionary and not meant to reject references to evolution in classification. By definition a classification should reflect phylogeny. Phylogenetic trends are apparent within Tylenchida and some will be described below.

In order to accept phylogenetic trends among Tylenchina, one must understand that :

— different states of a character (e.g. one or two ovaries) can be present even in narrow taxonomic divisions (subfamilies or even genera) as well as in superfamilies or suborders;

— each character, or group of characters, even if they are anatomically closely related, have to be assessed separately;

— these trends among characters often are independent and evolved separately; as a consequence, a mixing of ancestral and derived characters in the same taxon must be considered as normal.

Phylogenetic trends

TREND 1. GENERAL TENDENCY AMONG FEMALES, FROM THE ANCESTRAL VERMIFORM STATE, TO BECOME INFLATED, GLOBOSE OR SACCATE

This trend (i) exists in different groups (Anguinidae, Pratylenchidae, Hoplolaimidae, Heteroderidae, Criconematoidea); (ii) is most often correlated with an endo-, semiendo-, or sedentary parasitic existence of the females and often is accompanied by a host response in the vicinity of the stylet (nutritive cells) (see trend 7); (iii) is correlated with an increased production of eggs and sometimes a coincident system of protection for eggs

or juveniles (galls, cysts and/or gelatinous matrix) associated or not with egg diapause.

TREND 2. DEGENERATION OF MALE ESOPHAGEAL SYSTEM

Males have a tendency to have less developed, atrophied, non-functional digestive tracts exemplified by degeneration of esophagus, esophageal glands, and, in the ultimate phase, stylet. The first step (male stylet shorter than female stylet, and median esophageal bulb less developed in the male) exists in nearly all groups of Tylenchina, often accompanied with modified (narrower) lip area and weaker sclerotization of the labial framework.

The last step (degeneration of esophagus and of stylet) exists in several groups : all Criconematoidea (stylet present only in some males of Tylenchulinae) and some Pratylenchidae (*Radopholus*) and Hoplolaimidae (*Acontylus*).

If it is obvious that males without stylet and/or with degenerated esophagus cannot feed, this does not mean that all males with « normal » stylet and esophagus feed (allegedly *Meloidogyne* and perhaps *Pratylenchoides*).

TREND 3. REGRESSION AND DISAPPEARANCE OF FEMALE POSTERIOR GENITAL BRANCH. STRUCTURE OF THE CRUSTAFORMERIA

This trend is not observed in Criconematoidea where there is no trace of posterior branch, even as a post-uterine sac. In other groups, the occurrence of this regression is sporadic and nearly always a PUS of variable length and structure remains present.

Within Tylenchina, outside Criconematoidea, we estimate that the regression or the absence of the posterior female genital branch does not characterize any of the families or subfamilies. This is contrary to Andrassy's (1976) concept of families within Tylenchina. Fully developed female genital branches may coexist with a reduced posterior branch in the same family (Tylenchidae), subfamily (Pratylenchinae) or even, but rarely, in the same genus as for example in *Helicotylenchus* (= *Rotylenchoides*). At the subfamily level, couplets of genera exist that closely resemble each other, where one has two complete branches (didelphy) and the other only one, i.e., *Pratylenchoides* and *Apratylenchoides* in Pratylenchidae. One complete (anterior) female genital (monodelphy) branch is the derived character state. Some genera with this character have female J4 bearing a genital primordium with two branches. Studies on cell lineage (Sternberg & Horvitz, 1981; Horvitz & Sternberg, 1982) revealed a short evolutionary distance between mono- and didelphy, since the death loss of a single cell could transform a didelphic into a monodelphic species. Horvitz and Sternberg (1982) concluded that "derivation of monodelphy from didelphy has probably appeared

repeatedly during evolution and hence is a poor taxonomic indicator". We agree with their conclusion.

A more significant difference in the female reproductive system is arrangement of the cells of the columned uterus (= crustaformera, tri- or quadricolumella). Following observations made by Geraert (1986) : in Criconematoida these cells are not arranged in rows; in some families of Tylenchoidea, considered as more ancestral (Tylenchidae and Dolichodoridae), the cells are arranged in four rows (quadricolumella); some Anguinidae also have four rows of cells while other genera in this family show a (secondary?) arrangement in multiple rows. In families considered as more derived (Belonolaimidae, Pratylenchidae and Hoplolaimidae) the cells are arranged in three rows (tricolomella). In *Meloidogyne* and in less derived heteroderids like *Rhizonema*, the cells also are arranged in three rows (Geraert, unpubl.) while in other more derived heteroderids the rows can no longer be seen.

TREND 4. REINFORCEMENT OF STYLET AND OF LABIAL SCLEROTIZATION

This appears to be linked with the evolution from mycophagous habits to active root parasites of higher plants. But a reverse can be observed in some evolved Tylenchoidea (Meloidogyninae, Nacobbiniae) where the female, sessile within the roots, has a stylet weaker than that of the male or even of 2nd stage juveniles. Criconematoida also reiterate this line of evolution; in the more derived Tylenchulinae the sessile females, have a weak stylet and the male stylet is degenerate.

TREND 5. DIFFERENTIAL ELONGATION OF ESOPHAGEAL GLANDS (INTESTINAL OVERLAPPING)

In the ancestral state the three glands are in a definite bulb-like structure, not overlapping the intestine and generally there is a well developed esophago-intestinal valve (= cardia). Transitional cases are present in some families, for example, *Pararotylenchus* (Hoplolaimidae), with "bulb", where an intestinal overlapping is the rule. Even in a genus (some species of *Pratylenchoides*, within the Pratylenchidae) this lack of an overlap can be observed. Moreover, we have included in the family Belonolaimidae (= Tylenchorhynchidae) genera with and without intestinal overlapping of the esophageal glands.

This enlargement of the esophageal glands may affect primarily the subventral glands (most frequently) or the dorsal gland.

TREND 6. SHORTENING OF TAIL

Long tails are considered as ancestral. In this trend Tylenchidae and Belonolaimidae have to be considered retaining the more ancestral state as opposed to Hoplolaimidae, Pratylenchidae and Heteroderidae. But in

some groups, as for example Dolichodoridae, short and long tails may coexist.

When the male tail is shortened, the caudal alae envelop the tail (peloderan type); when tail is long, the alae are adanal (leptoderan). Within derived groups (Heteroderidae, Tylenchulidae) the caudal alae are very weakly developed or even absent.

TREND 7. EVOLUTION OF PLANT PARASITIC HABIT FROM ECTOPARASITIC TO ENDOPARASITIC, AND MIGRATORY TO SEDENTARY

This is correlated with Trend 1 in which the females have a tendency to become obese.

This biological character can have significance at the family level, for example Tylenchidae (primarily ectoparasitic), Belonolaimidae and Hoplolaimidae (ecto-endoparasites), Pratylenchidae (migratory endoparasites) and Heteroderinae-Meloidogyninae (sedentary endoparasitic).

TREND 8. EVOLUTION FROM AMPHIMIXIS TO PARTHENOGENESIS

This is difficult to evaluate, because for many species the data are lacking : often no males have been described in a species, but the original population is composed only of a few females and it is not always reported if their spermathecae contain sperm or not. Nevertheless, it appears that in the more ancestral families (Tylenchidae, Dolichodoridae, Belonolaimidae) the various genera can be assumed to contain a very large majority of amphimictic species, whereas, for example in Hoplolaimidae and Pratylenchidae, more derived, some genera (*Helicotylenchus* in Hoplolaimidae, *Pratylenchus* in Pratylenchidae) contain a majority of parthenogenetic species. In the derived family Heteroderidae, the ancestral subfamily Heteroderinae contains a majority of amphimictic species, whereas the derived subfamily Meloidogyninae is primarily parthenogenetic.

TREND 9. EVOLUTION OF AMPHIDIAL APERTURES

Among Nemata the evolutionary development of the amphid aperture appears to proceed in the direction of increased surface area, probably to enhance sensitivity. Within Tylenchina two lines are evident, one that dead-ends (Tylenchidae) and one that proceeded along with other adaptations to plant parasitism. The amphid aperture among ancestral Tylenchidae is pore-like, whereas, the derived aperture is sinuous, longitudinally elongate and slit-like. Since this form of aperture is limited to the family, it is considered an evolutionary dead-end that did not contribute to the further development of plant parasitism. In the remainder of Tylenchina the pore-like aperture undergoes a steady enlargement becoming more and more cavernous.

TREND 10. EVOLUTION OF THE "FACE"

In the ancestral state, it is represented by a distinct oral disc surrounded by six lip sectors well individualized and equally developed. This structure has been transformed in various ways : fusion of the lip sectors together, fusion of the oral disc with lip sectors, regression and disappearance of the lateral lip sectors, etc...

TREND 11. REGRESSION OF ESOPHAGO-INTESTINAL VALVE

A well-developed, conspicuous esophago-intestinal valve appears characteristic of ancestral groups with bulb-like esophageal glands (Tylenchidae, Belonolaimidae) and may be retained in some ancestral genera of more derived families (*Pratylenchoides*, *Apratylenchoides* in Pratylenchidae, *Antarctylus* in Hoplolaimidae) where the esophageal glands overlap the intestine. In other genera of these families, the valve is much reduced. In Criconematoidea, despite the bulb-like structure of these glands, no esophago-intestinal valve has been reported.

TREND 12. DISAPPEARANCE OF DEIRIDS

The presence of deirids appears to be ancestral; they are recorded only in Tylenchidae, Anguinidae, some Belonolaimidae, and a single genus (*Pratylenchoides*) of Pratylenchidae. Deirids generally are said to be absent in Criconematoidea although they have been observed on second stage juveniles of *Tylenchulus semipenetrans*, *Trophotylenchulus mangenoti* and *T. floridensis* (Maggenti, 1962).

TREND 13. EVOLUTION OF PHASMIDS

The ancestral position of the phasmid is caudal. In some Tylenchidae a phasmid-like structure occurs erratically along the body. Another evolution leads from the normal punctiform phasmid to the large scutellum present in some genera of Hoplolaimidae. Phasmids are absent in Criconematoidea and in one genus of Hoplolaimidae (*Aphasmatylenchus*), and in females and males of some Heteroderidae.

The « prototylenchid »

From the study of evolutionary trends in Tylenchina, we can imagine the prototylenchid. This hypothetical ancestral form combines the ancestral state of every character studied above.

Female and male vermiform, closely resembling each other; no sexual dimorphism; body short to medium size; tail elongated to filiform; lip area not offset, six discrete lip sectors, amphids pore-like, labial framework weakly developed; stylet thin, short, with small basal

knobs; esophagus with DGO close to stylet base, median bulb fusiform with small valve; esophageal glands short and abutting; cellular intestine with a well-developed esophago-intestinal valve; deirids present; phasmids punctiform, and caudal; female gonads didelphic, amphidelphic, outstretched, equally developed, with a quadricolumellar crustaformeria; male gonad mono-orchic; caudal alae leptoderan, small; amphimictic re-production; mycophagous.

No contemporary nematode fits entirely with such a description : although *Psilenchus*, a representative of Tylenchidae, appears the closest form to the prototylenchid, differing from it only by the shortening of the tail and the structure of the face, as seen with SEM.

Conclusion

The diversity of the arrangement between the different state of the various characters led us to consider that these characters, constituting the trends, have evolved separately, i.e. not at the same rate, with arrests and sometimes reversals. As a consequence ancestral and derived characters may be found together in the same animal. To describe a given species as more derived than another species means that the number and/or weight of the derived characters are greater in the former than in the latter. This is true for taxa at every level.

Conflicting views of the evolution of one group can result from giving more weight to one character than another. For example, within *Heterodera s. lato*, Green (1975) takes into consideration vulval area morphology and estimates that the *H. cruciferae* group is more ancestral and the *Globodera* group more derived, the *cacti* group (= *Cactodera*) being intermediate. Stone (1979) had a contrary opinion when taking into consideration the structure of the 2d stage juvenile face as seen with SEM. This constitutes a very clear illustration of differing interpretation of the evolution of different characters in the same group.

In the series of articles which will constitute the body of our Reappraisal of Tylenchina (excluding by the fact Sphaerulariina and Aphelenchina) we will apply the principles of these " trends " to the individual families and the classification of Tylenchina.

We are conscious that no taxonomy can be a definitively established one, but our aim is to propose an approach permitting to reduce the taxonomic inflation which actually deserves the final aim of the taxonomy, i.e. to present a clear picture of the ordered relationships in a group of living organisms.

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