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A NEW DESCRIPTION OF THE PROCESS OF IDENTIFICATION OF PLANT-PARASITIC NEMATODE GENERA

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INTRODUCTION

Accurate identification is a prerequisite to an understanding of the effect of nematodes as parasites of plants. It is obvious that no significant study on plant pests should be initiated until the identity of the parasite has been accurately established. For example, members of the genus *Rotylenchulus* in the past have been erroneously classified in the genus *Helicotylenchus* (*H. elisensis*, *H. parvus*), or they were proposed as new genera (*Spyrotylenchus*, *Leiperotylenchus*). In the first case, potentially dangerous parasites were wrongly identified as members of a relatively innocuous genus. In the second example, costly studies may have been initiated to define the biology of a supposedly new parasite, whereas the biology of *Rotylenchulus* is well known.

As shown by the examples above, errors sometimes are made by nematode taxonomists working within their field of expertise. Nematologists in other branches of the science also may err when they attempt to identify nematodes. The present review investigates the origin of such errors in the hope of defining a better method for more correct identifications.

Identification at the genus level and the species level each has its own problems and difficulties. To limit the scope of this study, it will address only identification at the genus level. Specific identification will have to be studied later

A growing number of researchers are studying new approaches to identification: monoclonal antibodies, nucleic acid probes, characterization of proteins by immunoelectrophoresis, etc.

These methods will allow the identification of a single species or even a race of a species. Similar tests already available for home medical diagnosis (pregnancy test) can be performed by persons with no knowledge of biology. These new techniques will soon provide easy means for identification of selected nematode pests. However, the development of a test for the identification on one species or one race requires lengthy and costly studies. This is economically feasible for important parasites, but it is doubtful that similar tests will ever be developed for all nematode genera, far less for all nematode species. Routine identification will long (or maybe forever) rely on morphological characteristics as seen with light microscopy (for the moment, scanning electron microscopy - SEM - is too complicated and costly for routine use).

Nematode identification, even limited to the genus level, is a difficult process which is not mastered by all plant nematologists. Professional identifiers, taxonomists, farm advisors, workers in private identification labs, employees of regulatory agencies, ecologists engaged in extensive faunistic surveys, etc., identify nematodes daily, or almost daily. Most have an expertise limited to selected nematode groups; a handful are comprehensive experts, able to recognize all genera. It should be noted that even those identifiers with a limited area of expertise can extend this area, if and when necessary, because their knowledge of nematode morphology, and their familiarity with the process of identification, make it easy for them to learn to identify new groups. Other nematologists are occasional identifiers. They only know the "agricultural genera", i.e., the genera that are most commonly found associated with cultivated plants (e.g. *Meloidogyne*, *Pratylenchus*, *Xiphinema*, etc.). They lack the practice for across-the-board identifications, and they have difficulty in learning to identify unfamiliar groups. Those shortcomings are even more obvious for nematologists who are working on a single species (for example Caenorhabditis elegans), and who are unfamiliar with other nematodes. Students are a case apart, at first they may have little or no knowledge of nematodes or of nematode morphology but, in the course of their studies, they are expected to become well acquainted with all nematode taxa.

No matter what their level of expertise and practice may be, most nematologists occasionally have to identify unfamiliar forms. This happens very rarely with the best experts, whereas every specimen presents a new and difficult challenge to the beginner. In such circumstances, the success of identification depends on available identification aids.

TRADITIONAL IDENTIFICATION AIDS

Because of the amount of data related to identification (100 to 150 morphological criteria differentiating 125 to 200 plant nematode genera), it is necessary to use an identification aid when identifying an unfamiliar form. Dichotomous keys are the traditional identification aids in nematology.

With Baylis & Daubney (1926), Tom Goodey (1933), Filip'ev (1936), Thorne (1949), Chitwood (1951), J.B. Goodey (1963), Siddiqi (1971; 1986), Golden (1971), Andrássy (1976), etc., many nematologists have published identification keys encompassing all plant-parasitic nematode genera. Most are dichotomous line keys. Notable exceptions include J.B. Goodey's (1963) tabular keys and Mai's (1975) pictorial key. Traditional identification aids have been used successfully for a hundred years. However it will be shown that their usefulness is greatly reduced when the user has no preconceived idea of the identity of the specimens.

Dichotomous and tabular keys rely on an existing classification and require the user to identify successively order, superfamily, family and subfamily before reaching the genus level. This poses several problems:

- Some genera are very similar in some aspects of their morphology to other genera classified in a different family. For example *Amplimerlinius* (Belonolaimidae) resembles *Pratylenchoides* (Pratylenchidae) and *Hoplorhynchus* (the last genus was first described in Hoplolaimidae, but later was synonymized with *Pratylenchoides* by Luc, 1986). When the user is forced to choose one family early in the key, the opportunity is lost to compare the specimen to related genera in other families.

- Higher level categories emphasize systematic relationships. The criteria that characterize these relationships are not always easily visible, e.g. biological features (mycophagy present/absent), life-cycles, ultrastructural details visible only with electron microscopy, or characters that are difficult to see in many specimens.

- Exceptions often must be included in the definition of higher taxa to keep their number to a reasonable level. For example *Aphasmatylenchus* belongs to Tylenchina, a suborder defined by the presence of phasmids; *Pararotylenchus* belongs to Hoplolaimidae in spite of its oesophageal glands not overlapping the intestine. There are many such examples.

- Information about biological variability cannot be included in traditional keys, particularly in dichotomous keys.

As a result, keys are best used as a compendium of information to refresh the memory of knowledgeable experts. They may be very confusing for beginning users who attempt identifying using only the data found in the key. For example see how Siddiqi (1986) used presence/absence of phasmids in the key to families in Tylenchida (an order generally characterized by the presence of phasmids). In this key, the sub orders Hexatylina and Criconematina are given with phasmids absent, while Tylenchina has phasmids present, except *Aphasmatylenchus*. However, the superfamily Tylenchoidea in Tylenchina is said to have "Phasmids not detectable on tail; phasmid-like structures much anterior to tail" and phasmids are "not seen" for the subfamily Thadinae.

For the non-expert (or the expert out of his area of expertise) identification is like trying to find one's way through a swamp on a dark and foggy night. A few patches of high ground with a clearly marked path (i.e., a line or two with an easy answer in the key), but soon he gets to a sign "this way" pointing both directions (because of intra-specific or intra-generic variability), or the sign is lost (criterion not seen). A better approach to identification aid may be achieved by taking a new look at the way an expert identifies forms within his area of expertise.

A NEW APPROACH: DEFINITION OF EXPERT IDENTIFICATION

In practice, expert identification differs from the process described above by two characteristics:

- global approach: the expert makes use of all relevant features simultaneously, instead of considering only one or two features at a time, as does a key;

- direct recognition of specific forms: the expert goes straight to the answer instead of eliminating successive categories.

Keys follow a step by step approach, starting with the entire group (usually at the order level) and eliminating successively whole categories one at a time (sequential process), using one or two characteristics (monothetic process). By contrast the expert uses a simultaneous, polythetic process to "recognizes" at a glance the form to be identified.

For an expert, the "identification landscape" is quite different from the hazy swamp that confronts the beginner. There may still be some patches of fog, and some unknown quicksand may still be lurking here and there, but the identification country is covered with brightly lit, well indicated freeways going directly to the answer ("this is a *Pratylenchus*") or at least in the vicinity of the answer ("this looks like a *Ditylenchus*"; "this belongs to the tylenchorhynchid family of genera"). Or if the expert does not recognize the specimen he can somewhat connect it to a known form ("This looks like a *Dolichodorus*, but with only one genital branch"; i.e., it has all the characteristics of the genus *Dolichodorus*, but it has only one genital branch, instead of two). He can recognize a higher category (family) but narrow down the possible genera by identifying a striking characteristic that exists in only one or a few of the taxa in this family, e.g., this is an hoplolaimid, and it has scutella on body (i.e., it can only be an *Hoplolaimus* or a *Aorolaimus/ Peltamigratus*).

The expert immediate conclusion is often reached at low magnification, either with the dissecting microscope, or with low power objectives of the compound microscope. The dissecting microscope generally is used with live or freshly killed nematodes in a small dish filled with water, before they are mounted on slides. The compound microscope is used either as a second step in the identification of specimens already seen under the dissecting microscope, or it is used directly with specimens previously mounted on permanent slides. It can be noted that the highest magnification attainable with a dissecting microscope (about 40X) is similar to the low power of a compound microscope. Using this material, the expert recognizes at a glance, even before looking at fine morphological details, what is now defined as a promorph.

(Note : Promorphs and nests of species (below) were originally named protomorphs and nucleus, respectively. Both terms created conflicts, the first because os its shaky etymology (proto means primitive as pointed out by Dr. Coomans), the second because of possible confusion with biological elements (cell nuclei). Following lengthy discussion among the participants , Dr. Doucet proposed promorph, and Dr. Siddiqi proposed nest, and both terms were accepted and are used in the present volume.)

The Concept of Promorph

A promorph (pro before; morph morphology) is a form that can be recognized at low magnification powers, before observation of detailed morphology.

The concept of promorph has no standing with the traditional zoological nomenclature codified in the International Code of Zoological Nomenclature. To clearly mark the difference between names of promorphs and other names, but at the same time to make it easy to associate a promorph name and a well known shape, promorphs will be named by P- and the abbreviated name of a representative genus as given in Table 1.

Table 1 — List of Common Promorphs and Representative Genera

Name of Promorph	Example
P-fil	*Filenchus*
P-dityl	*Ditylenchus*
P-anguin	*Anguina*
P-pratyl	*Pratylenchus*
P-tylencho	*Tylenchorhynchus*
	Merlinius
P-rado	*Radopholus*
P-hoplo	*Hoplolaimus*
P-scutello	*Scutellonema*
P-helico	*Helicotylenchus*
P-rotylulus	*Rotylenchulus*
P-melo	*Meloidogyne*
P-hetero	*Heterodera*
P-crico	*Criconema*
	Criconemella
P-hemicyclio	*Hemicycliophora*
P-paratyl	*Paratylenchus*
	Gracilacus
P-tylulus	*Tylenchulus*
P-aphelus	*Aphelenchus*
P-apheloides	*Aphelenchoides*
P-xiphi	*Xiphinema*
P-longi	*Longidorus*
P-tricho	*Trichodorus*

Recognition of promorph uses quite different characteristics from those found in keys for genus or species identification. Most key identification criteria are seen only with high magnification whereas promorphs are identified at low magnification, where such characteristics are not seen or are fuzzy at best.

Promorph recognition relies on the following characteristics:

overall aspect of the body

- a gross estimate of body length (small, medium, long...)
- gross shape (thin, normal, thick...)
- shape of annuli (body annuli visible in criconematids)
- shape of posterior extremity (filiform, conoid, broadly rounded)
- habitus (straight, C, spiral)
- color of the intestine (light grey, dark grey, almost black, with alternating white and black sections)
- movement (most plant-parasites are sluggish; *Aphelenchoides fragariae* is a good swimmer; movements of *Hirschmanniella* look like the wriggling fingers of a very anxious person, the mononchids are always searching, etc.)
- tendency to float on surface-tension film (mononchids)

anterior end

- very obvious head shape
- stylet size and shape

oesophago-intestinal junction (junction straight and clearly marked, ill-defined, slanted ventrally of dorsally, paraboloid, etc.)

position of vulva (anterior, mid-body, posterior)

special features:
- aphelenchoid bulb,
- double cuticle of *Hemicycliophora*, etc.

Identifications are not conducted in a vacuum, but with knowledge of the origin of the specimens (host, parts of plants, geographical origin of the sample). With this knowledge, an expert expects to find some promorphs, but not others. A sample from a cultivated plant most often will harbor one or a few genera from a list of twenty or thirty "agricultural genera". Furthermore, only a few species are common in each of these genera. These few species are seen much more frequently than the rest of the plant-parasitic nematodes. Their morphology is well known because they are frequently observed and it defines the shape of the promorph. For example, in the genus *Helicotylenchus* very common worldwide, the species *H. dihystera* is the most frequently found. Its characteristic shape defines the well known promorph P-helico/dihystera that many nematologists can recognize at first glance. Many other *Helicotylenchus* species are very similar to *H. dihystera*, and they will be grouped in the same promorph. Others representative of the genus are quite different and they will be recognized as other promorphs such as P-scutello (*H. vulgaris*) or P-hoplo (*H. coomansi*).

The characterization of a promorph as common or rare must rely on a clearly defined geographical area. Some promorphs are common worldwide, other are confined to a continent or smaller geographical area. They are considered as rare worldwide, but they may be common in this particular area.

The few well known and very common forms are the most likely candidates for identification: if an hoplolaimid is found in a sample from a cultivated land, then it is most likely to be a P-helico/ dihystera or a P-scutello. Obviously there is also the possibility that it belongs to a different promorph that is not very common, but that is sometimes found in an agricultural sample, such as P-hoplo for example. Also, particular hosts, habitat, or geographical regions may have one or more promorphs common only in these circumstances, but not in the general case. For example P-helico/ multicinctus is common on banana; P-hirsch is common on paddy rice, etc. Finally rare forms are found only in the most exceptional circumstances (*Antarctylus, Carphodorus*, etc.).

Fast expert identification is achieved by first jumping to the most obvious conclusion and assuming that the specimen to be identified belongs to one of the few primary targets according to given circumstances. Obviously, the expert then verifies that this immediate conclusion was correct. If it were not, or if no primary target were obvious, then the expert would investigate secondary targets, then rare forms.

Promorph is an heuristic concept and the various promorphs should not to be defined too rigidly. Each expert recognizes his own promorphs; an error in choosing a promorph is not as crucial as an error in picking a family in a traditional key. Promorphs can be seen as units in a loose networks of superpromorphs and subpromorphs(2) that can provide an alternative answer in case a wrong choice is made during the identification process.

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(2) The use of prefixes, super- and sub-, was rejected during the workshop; see discussion following the lecture of Dr. Siddiqi on identification of dolichodorids.

The concept of superpromorph loosely correspond to the family in traditional classifications. For example, a superpromorph SP-hoplolaimid can be recognized under low magnification by the following characteristics:

body robust, of medium long length, cylindroid;
posterior extremity broadly rounded or quarter rounded;
stylet robust, rather long;
oesophago-intestinal junction not straight;
Vulva at mid-body.

This superpromorph contains several promorphs: P-hoplo, P-scutello, P-helico, etc., that are typical of the group. Subpromorphs can be defined as differing from the typical members of a group by only one or two details. For example, the subpromorph P-rotyloides resembles typical hoplolaimids but it has a posterior vulva. Other promorphs are a mixture of characteristics from two different superpromorphs. For example,the genus *Pararotylenchus i*s intermediate between the superpromorphs hoplolaimid and tylenchorhynchid; the genera *Amplimerlinius, Pratylenchoides*, and the species described as *Hoplorhynchus riparius* are intermediate between these two superpromorphs and the pratylenchids.

The categories are endless, and are limited only by the experience of the expert. They do not need to be clearly defined and listed. The purpose of the concept of promorph for identification is to allow focusing the identification to the most likely candidate, in given circumstances, and also to suggest alternative answers, if this first candidate does not fit the available data. Experts know that if they make a tentative identification as *Amplimerlinius*, they should test the possibility that the specimens may in fact belong to *Pratylenchoides*, in a different family.

The process of identification does not stop with the recognition of a promorph, but it continues to the genus level, then to the species level. Promorphs are made of one or several subunits, that can be said in first approximation to correspond to one or several genera. For example, P-pratyl correspond to the genus *Pratylenchus*, P-tylencho correspond to several genera, whose number and diagnoses depend on conflicting classifications.

Trying to go directly from promorph to genus level raises two problems, namely there is no consensus on genus definitions, and existing genus definitions often use systematic criteria, not identification criteria.

We must by-pass these conflicts because, judging from past history, classification controversies are forever, while identification is a practical and urgent matter, that cannot wait for their resolution. For this purpose, it is necessary to introduce a second new concept: the nest of species.

<u>The concept of nest of species</u>

A nest is a group of species that share the same set of primary identification criteria. To parallel the nomenclature proposed above for promorphs, nests will by named N- followed by the name of a representative genus (e.g. N-pratylenchus).

A primary identification criterion is a morphological characteristic that is both constant and reasonably easy to observe in a given group of species.

An example of a constant criterion would be the low flat head cap of N-pratylenchus. If a genus has species with two or more states of an otherwise very reliable character (i.e., not intraspecifically variable), then it is necessary to split the genus into two or more nests, each defined with only one state of the criterion. Example P-tylencho (i.e.,*Tylenchorhynchus sensu* Fortuner & Luc, 1987) has species with 2, 3, 4, 5, or 6 lateral field lines. Lines is a primary criterion for the definition of five different nests (regardless of how many genera we accept).

There should be a limit to the degree of splitting and the number of nests. For example, the nests N-pratylenchus and N-hirschmanniella are easily differentiated from each other by good primary criteria but the species *Pratylenchus morettoi* has vulva position and genital branches as in *Pratylenchus*, shape of body, labial area, tail and gland overlap as in *Hirschmanniella*. The inclusion of *P. morettoi* in either N-pratylenchus or N-hirschmanniella would introduce variability in groups that were very constant. This species is best kept in a category of its own. To avoid increasing the number of nests, it can be described as a subnest sn-morettoi inheriting its primary criteria from both its parents. The concept of subnests can be used at any time one or a few species are intermediate between two well defined nests (e.g., the Australian species described by Phillips are intermediate between N-rotylenchus and N-scutellonema; the species with a posterior genital branch degenerate but still present are intermediate between N-helicotylenchus and N-rotylenchoides, etc.).

Some genera are defined by systematic characteristics that are not constant in all species. For example, the oesophageal glands of *Pratylenchoides* are a valid systematic characteristic, that justifies the placement of this genus in the family Pratylenchidae. However, the magnitude of the gland overlap is not constant in all the species in this genus, which would make this character a poor identification criterion.

Primary identification criteria should be reasonably easy to observe and unambiguous, avoiding erroneous data as far as possible. The conspicuity of some feature may depend of the specimen where it is observed; for example, the scutella of some hoplolaimids are easy to observe, while the phasmids in some tylenchids or anguinids cannot be used. Clearly visible features may not qualify as primary identification criteria if they present some ambiguity. For example, the lateral field of *Trilineellus* is easy to see, but the number of line is ambiguous and the same specimen may be said to have three or four lines depending on the observer (Fortuner & Luc, 1987).

The concept of nest avoids using genera which are systematic entities. It uses only identification criteria while genera are based on characteristics that demonstrate relationships between forms.

Identification criteria are very practical concepts: if "it works" it can be used, while systematic criteria are shared derived characters (synapomorphies) modified from an ancestral state. Various phenomena, such as parallel evolution, reversal of evolution, secondary regression, homoplasy, must be considered while defining relevant systematic criteria, making it necessary to discard some criteria that nevertheless may be used for identification. It does not matter if the pore-like phasmids of *Meloidodera charis* have a different origin from those in cyst-forming heteroderids (Baldwin, 1986) this characteristic can still be used for practical identification.

Some characteristics that do not qualify as primary identification criteria may be accepted as secondary criteria. Variable characteristics are useful if the range of their variation is well defined in a particular nest. For example, the nest N-basirolaimus is seen with either five or six oesophageal gland nuclei. Other characteristics may be uncertain, i.e., difficult to observe, but may be usable if this uncertainty can be circumscribed. The nest N-trilineellus has either three or four lateral field lines, it certainly does not have two, or five or more lines. Finally, negative characteristics can be very useful. The nest N-diptenchus and a few others have no posterior genital branch at all, and this absence of a feature can help with their identification.

True expertise does not end with the knowledge of morphology. Experts also use rules of thumb that are impossible to include in a formal key, but are very useful for suggesting alternative answers when the first intuition has proved to be false. For example, if a form thought to be a P-melo was later found to have abutting glands, the expert will look for the excretory pore. If it is not visible in the oesophageal region, and if the specimen was obtained from a Citrus, the expert will investigate the possibility that it is a *Tylenchulus semipenetrans*.

Experts also are aware of common errors and pitfalls. If a form is identified as a *Rotylenchulus*, the eventuality should be tested that it may be a *Helicotylenchus*.

A last note about expertise is that it is either visual (the expert recognizes the resemblance between the specimen and a drawing), or it is textual (the expert knows, or finds out in a key, what are the primary criteria for the identification of a particular form). Most often, expertise combines the two approaches: this specimen looks like a P-pratyl (visual expertise) therefore I must check that the glands are overlapping the intestine ventrally (textual expertise).

The final step in the identification process is the attribution of a genus name to the nematode identified. Each expert knows (or he finds out) what genus name is attributed to a nest according to the classification he currently accepts as valid. For example, the nest N-rotylenchoides will be named *Rotylenchoides* by the nematologists following Siddiqi (1986), but it will be named *Helicotylenchus* by those who follow Fortuner (1984). It is unfortunate that two concurrent genus names exist for the same taxon but until a consensus develops among taxonomists, the concept of nest, and the creation of a correspondence table nest namesgenus names according to conflicting classifications, will allow practical identification.

A NEW IDENTIFICATION HELP

To give all nematologists the ability to identify any genus they may observe, they must be given the possibility of emulating the workings of the expert. The identification aid must give them the same knowledge of data as known by the experts (i.e., morphological characteristics and their states; nests/promorphs and their definition; genus names corresponding to each nest), and also it must give them the possibility to use procedures used by the experts (utilization of the data to quickly reach a correct answer).

Well circumscribed domain (identification of plant-parasitic nematode genera), with available experts (nematode taxonomists) using known facts and rules (as explained in the present study), these re the characteristics of problems that fall within a particular area of artificial intelligence: the expert-systems. The implementation of an expert-system NEMISYS (NEMatode Identification SYStem) is being investigated, and its future structure, emulating the processes described in the present study, has been described by Milton and Diederich (1988).

Over thirty nematode taxonomists will collaborate with two computer scientists in a vast project for the development of the ideas presented here, and the creation of the expert-system NEMISYS. It is hoped that this system will allow any nematologist with a basic knowledge of nematode morphology, and with the ability to recognize a few basic forms (promorphs) to identify any plant-parasitic nematode from any origin.

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DISCUSSION

Ferris: You described a nest that had the morphological and anatomical characters of the genus Pratylenchus. Does that nest carry the name of Pratylenchus or some other name that does not give it a label?

Fortuner: The names of nests should resemble the names of related genera because they will be easier to remember. In your example, the nest is identical to the genus Pratylenchus and it is called N-pratylenchus with a little 'p' to differentiate it from the gnus Pratylenchus. Other genera such as Helicotylenchus include several nests. For example, H. dihystera and all similar species belong to the nest H-helicotylenchus-dihystera. Other nest would be H-helicotylenchus-multicinctus and H-helicotylenchus-vulgaris. The latter is very similar to N-scutellonema. At the promorph level it will be identified as P-scutello, then, under the compound microscope, it will be found to have the primary identification characters of N-helicotylenchus.

Jairajpuri: Do you think that your concept of nest corresponds to the concept of superspecies as defined by Mayr?

Fortuner: No. Superspecies are a systematics concept, for true species that are morphologically very similar to each other. Nest have nothing to do with systematics. The same nest can include an Amplimerlinius, a Pratylenchus and an hoplolaimid.

Siddiqi: Why not use the concept of supernest? There could be a supernest SN-helicotylenchus with the several nests you suggested.

Fortuner: In the expert-system, rules will be used to connect related nests. Nests connected by rules can be considered to belong to a supernest. We should not multiply the categories and give names to supernests.

From the discussion section of the chapter by Siddiqi, M.R., Identification of dolichodorids, page 109:

Fortuner: I see a real danger that our project will result in the development of a new classification system, parallel to the traditional Lineaean classification system. I started the trend when I used the concept of superpromorphs, and now Dr. Siddiqi is introducing super nests and family nests. To avoid the confusion that is bound to occur if this trend is not stopped, I propose to call promorph any form that is described using characters seen by the dissecting microscope, and to call nest any form described with characters seen with a compound microscope. If it is found necessary to use promorphs at different levels, each will have its own name, but there will be no different concepts such as superpromorphs. P-hoplolaimid is not a superpromorph, but just another promorph that will be defined in terms more general that those to be used for the promorphs P-hoplo or P-helico. Here, ntylenchoryhnchinae is not a family nest, but just another nest of species that is defined in terms more general than the nests n-tylenchorhynchus, n-bitylenchus, n-leviterminus, etc.