CLUSTER ANALYSIS OF A GROUP OF MARINE NEMATODES

by

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Australian National University August 1979 This thesis contains no material which has been previously submitted for a degree to any other university.

The research studies described in this thesis, except where due reference is made, was carried out by myself during the period of my candidature.

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ABSTRACT

A preliminary study was made to investigate the phenetic relationships of a group of marine nematodes. Twenty-one nematode genera were selected for an initial study. Each of the genera was scored for thirty morphological attributes. The attribute states were coded and a data matrix was arranged. The matrix was then transformed to standard data type (MULTBET-STYLE), acceptable to the program MULCLAS. The program was executed on the Control Data Cyber 76 at the CSIRO Division of Computing Research in Canberra. The Euclidean metric was computed for all pairs of genera. The classification was performed using the flexible sorting strategy. The subsequent fusions at different levels of similarities were plotted as a "phenogram." The generic list of different phenons were tabulated and the first phenon line was compared with the groupings set by De Coninck, Andrassy and Wieser, based on the identical set of genera. The percent differences were calculated as a measure of intra-group similarities of the phenons compared with the established systems. The results indicated a general agreement between the phenons and Wieser's ecological categories; while De Coninck's and Andrássy's natural groupings showed considerable difference. The initial group was then enlarged by a closely related group of type genera. The phenons indicated significant close generic stability.

It has been concluded that cluster analysis is a useful method to study the taxonomy of marine nematodes.

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ABBREVIATIONS

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am	amphid
В	binary
с	cardia
ca	cuticle annulation
CO	cuticle ornamentation
CS	cephalic setae
b	denticle
h	helmet
ilp	inner labial papillae
ils	inner labial setae
L	literature
m	mandible
Ν	nominal
0	ordinal
oc	ocelli
oe	oesophagus
0-i	oesophagus-intestinal junction
olp	outer labial papillae
ols	outer labial_setae
OTU	operational taxonomic unit
S	specimen
sp	somatic papillae
SS	somatic setae
st	stoma
sty	stylet
t	tooth
v	valve

1. INTRODUCTION

Marine nematodes are all members of the meiofauna, small animals living in or on the bottom sediments, or amongst the fronds of marine plants (Nicholas, 1975). They are the most abundant of all the taxa making up the meiofauna, in littoral, estuarine, coastal, and oceanic sediments, extending from above the high-water mark down into the deepest oceanic trenches.

The significant taxonomic features in marine nematodes are the development of sense organs. The structure of amphids is probably the most useful character for distinguishing higher taxa. The buccal cavity reflects a wide range of structural variations. Many of them have welldeveloped cuticular modifications in form of annulation and ornamentation. Some forms have light-sensitive pigments and ocelli.

The systematic study of marine nematodes began with Filipjev (1918). In later years, a number of nematode taxonomists tried to bring an orderly system of classification or ecology to the systematics of marine nematodes. However, due to extreme versatility, diversity and lack of phylogenetic evidence, the taxonomy of marine nematodes has not yet been stabilized.

The present study is a preliminary attempt to investigate the phenetic relationships of a group of marine nematodes. Cluster analysis was performed using the flexible sorting strategy with the Euclidean metric as a measure of inter-generic similarity. The initial group was then enlarged to examine the stability of the close generic relationships. The aim of the study was to test the hypothesis that: 2

i. The intra-relationships of the group elucidated by cluster analysis reflect a natural or ecological pattern when compared with the established systems.

ii. The close generic relationships remain stable within the group.

2.1 Historical development of the classification of marine nematodes

Borellus in 1656 discovered the first free-living nematode. This was the vinegar eel, *Turbatrix aceti* Peters 1927 (Goodey, 1963). Muller in 1773 described some nematodes, which he associated with bacteria and spirochaetes in the genus *Vibrio*. He later described other members of *Vibrio* including two marine species (*V. gordius* and *V. anguillula*). However, the first scientist to recognise nematodes as a distinct taxon was Dujardin (1845, after Filipjev, 1968). He established the genera *Enoplus*, *Oncholaimus*, *Rhabditis*, and *Dorylaimus*, and described important anatomical features, such as the structure of digestive tract, genital organs, and oral armature. He included them, with some parasitic nematodes, in the group "Enopliens".

According to Filipjev (1968), Leydig (1854) described the caudal glands of free-living nematodes for the first time, and noted the secretion, with which they attach themselves to submerged objects. Bastian's work on taxonomy (1865) described 100 new species of free-living nematodes. His "Monograph of the Anguillulidae" has recently been reprinted (Bastian, 1977). He was the first to divide free-living nematodes into continental (soil and freshwater inhabiting) and marine forms.

In 1886, De Man's magnificent study "Anatomische Untersuchungen über freilebende Nordsee Nematoden" appeared.

He described the entire anatomy of several species of marine nematodes considering the structure of the esophagus and the male and female genital apparatus. However, he did not refer to the nervous system. Between 1888 and 1893 De Man published five papers on the taxonomy of marine nematodes which contain many descriptions of new and old genera and species. Almost all the descriptions are highly detailed, the external features and internal organizations are examined, and in almost all cases detailed drawings are provided. He listed eight families for the free-living nematodes:

Ironidae, Dorylaimidae, Tylolaimidae, Odontaphoridae, Ptychopharyngidae, Tripylidae, Monhysteridae and Odontopharyngidae.

Cobb, who was a contemporary of De Man, described many new species of free-living nematodes. His series of papers "Contribution to a science of Nematology" comprising 26 parts, was the first of its kind in nematology in that he considered nematodes as an independent phylum under the name "Nemata". He proposed that plant parasitic and free-living nematodes be removed from helminthology and be assigned to a new branch of science to be known as "nematology" (Thorne, 1961). He constructed an analytical key to all the genera of free-living nemas - both continental and marine forms. In considering the higher taxa, he based his classification almost entirely on the characteristic of the buccal cavity.

Filipjev (1918) published a monograph which included all free-living marine nematodes known at that time. This important work has recently been republished in an English

translation (Filipjev, 1968). He divided the free-living nematodes into five families:

- Enoplidae, cuticle smooth; esophagus attached anteriorly to cuticle; ovaries reflexed; majority of species marine.
- Chromadoridae, cuticle annulated; esophagus not attached to cuticle; uterus simple; largely marine.
- Desmoscolecidae, cuticle consisting of very thick conspicuous annules; ovaries straight; marine.
- Monhysteridae, lateral organs (amphids) most often round; ovaries straight; marine and freshwater.
- 5. Anguillulidae, esophagus with swelling in middle and having a second enlargement at posterior end; in soil and freshwater; very few marine.

Filipjev and Schuurmans-Stekhoven (1959) combined the system of free-living nematodes with that of the parasites. The grouping of the genera is almost the same as that of Filipjev's earlier classification (1918), but the families were raised to ordinal rank.

Schuurmans-Stekhoven and De Coninck (1933, after Filipjev and Schuurmans-Stekhoven, 1959) made the first attempt to bring a reformed system for the free-living nematodes. They based their classification chiefly on the structure of amphids and composed new orders and families for the free-living nematodes. The formation of their system is based on the following ideas:

- The structure of genital organs gives no sound base for the higher categories.
- The buccal organs present parallel variation in several lines of relationship.
- 3. The amphids afford a conservative feature, do not show such a range of variation and are therefore of great value in the formation of a system.
- 4. The cephalic sense organs, either setae or papillae give likewise essential characters, since they bring about the four - or six - radiate symmetry of the head end.

As a consequence of these ideas Schuurmans-Stekhoven and De Coninck conserved the orders Enoploidea and Anguilluloidea in the sense of Filipjev and have proposed a regrouping of the forms, contained in Filipjev's Chromadorata and Monhysterata by dividing these into three orders:

- 1. Araeolaimoidea, with four cephalic sense organs and the shape of amphid spiral or derived from spiral.
- 2. Chromadoroidea, provided with six cephalic sense organs and spiral or derived from spiral amphid.
- 3. Monhysteroidea, with circular amphid.

The work of the Chitwoods was a turning point in nematode systematics. Their most important work (Chitwood and Chitwood, 1950) has won the appreciation and wide recognition of many students of the nematodes. It has recently

been reprinted (Chitwood and Chitwood, 1974). One essential point of their system was that they divided the Nematoda into two classes Phasmidia and Aphasmidia (later changed to Secernentea and Adenophorea). The two groups were named after the presence or absence of small paired organs, of unknown function, the phasmids which are found on the two sides of the tail of numerous nematodes (or more rarely further foreward adjacent to the lateral cords). Other features of Chitwoods' classification rested on the importance of the cephalic sense organs, and further developed Filipjev's Their classification for marine nematodes includes system. three suborders Monhysterina, Chromadorina, and Enoplina. It considers the shape of the amphids, buccal organs, and the structure and arrangement of the cephalic sensillae to differentiate the following taxonomic categories:

Phylum: NEMATODA

Order: Chromadorida

Suborder: Monhysterina (3 superfamilies and 8 families) Suborder: Chromadorina (3 superfamilies and 6 families) Order: Enoplida

Suborder: Enoplina (2 superfamilies and 6 families)

De Coninck (1965) further developed Chitwoods' system by considering the precise structure and arrangement of sense organs.

De Coninck's key to families of marine nematodes, describing the morphological characters used at each taxonomic level is given (Appendix 1). His classification is outlined:

Class: NEMATODA

Subclass:	Adenophorea
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Superorder: Chromadoria

Order: Araeolaimida (2 suborders and 5 superfamilies)
Order: Monhysterida (1 suborder and 3 superfamilies)
Order: Desmodorida (2 suborders and 5 superfamilies)
Order: Chromadorida (2 suborders and 3 superfamilies)
Order: Desmoscolecida (1 suborder and 2 superfamilies)

Superorder: Enoplia

Order: Enoplida (2 suborders and 3 superfamilies) Order: Dorylaimida (2 suborders and 4 superfamilies)

De Coninck's system has met wide acceptance, though it has been modified in minor way by later publications.

The next major classification of nematodes has been proposed by Andrássy (1976). He used almost the same set of characters that were considered by De Coninck to tabulate a set of different or identical characters for the two major groups of free-living nematodes (Chromadorida and Enoplida). Andrássy indicated that Chromadorida have 10 common characters which **are all** unifying characteristics (regarded as positive features); while Enoplida have 7 such characters, of which 5 are unifying (positive) and 2 are not unifying characters (regarded as negative features). On the basis of the morphological character analysis, Andrássy concluded that the two groups of "Adenophorea" differ from each other in fundamental features, representing distinct evolutionary lines. He proposed that the Adenophorea he divided into two morphologically different groups, the subclasses Torquentia and Penetrantia. They were named after the most characteristic feature of each species group, the shape of the amphid. The Latin "torquere" means "to wind, to twist" and is used for the formation of the new name, Torquentia. In the second group the amphid is pocket-like. The Latin "penetrate" means "to penetrate" and is used for the name Penetrantia. This refers to the big ampoule of the amphid which penetrates the body.

Andrássy extended his quantitative approach to derive the evolutionary trends within each subclass down to family level and further divides them into subfamilies, including their genera. His classification is as follows:

Class: NEMATODA

Subclass: Torquentia

Order:	Monhysterida (2 suborders and 5	superfamilies)
Order:	Desmoscolecida (2 suborders and	3 superfamilies)
Order:	Chromadorida (4 suborders and 7	superfamilies)

Subclass: Penetrantia

Order: Enoplida (3 suborders and 8 superfamilies) Order: Dorylaimida (4 suborders and 11 superfamilies)

The Torquentia are all free-living, and the majority are marine. Among the Penetrantia, only the Enoplida is marine.

Andrássy's new system has yet to be evaluated by nematologists. De Coninck's classification is still regarded as the established one for marine nematodes.

Wieser (1952-59) considered ecological criterion and divided marine nematodes into four categories according to their presumed food. The classification is based on a correlation between the morphology of the stoma and many scattered published observations on their feeding habits (Nicholas, 1975). Wieser's four groups are as follows:

- 1A. Selective deposit feeders. Without stoma, or with reduced stomatal cavity. Food, which must be soft and in suspension, ingested by oesophageal suction. Large and hard particles are not ingested. 97 genera.
 - 1B. Unselective deposit feeders. Stoma with an unarmoured cup-shaped or cylindrical cavity. Oesophageal suction is supplemented by the movements of the lips and stoma in ingesting food. Food, in suspension, includes relatively large hard objects, such as diatoms, as well as finer softer material. 73 genera.
 - 2A. Epigrowth feeders. Stomatal cavity armed with teeth, rods, or plates. Food may be scraped from surfaces for ingestion, or cells may be pierced and the contents sucked out. 104 genera.
 - 2B. Predators and omnivors. Stoma with powerful armature of teeth and plates. Prey may be swallowed whole, or small animals or algal cells may be pierced and the contents sucked out. 87 genera.

2.2 Natural Classification

The nature of a classification depends on its purpose. The central idea underlying "natural" grouping is the great usefulness of a method that can group together entities in such a way that members of a group possess many attributes in common (Gilmour, 1963, after Sneath and Sokal, 1973). He indicated that a classification based on many correlated characters generally possesses a higher predictability than a system based on few characters. A system that considers a restricted number of characters is regarded as a special or artificial classification (Bird, 1971). An example of a special classification is the one given by Cobb (1935) for free-living nemas. The system proposed by De Coninck is "natural" because it considers many shared characters.

Sokal (1966) pointed out that a classification based on one or only a few characters is generally "monothetic"; that is, all the members of any group possess all of the features that are used to define that group. A classification based on many characters are "polythetic", and does not require any one character to be shared by all the members of the group. Hence, no single feature is either essential to group membership or is sufficient to make an individual a member of the group.

2.3 Phylogenetic Classification

This aims to reconstruct the characters of the ancestral organisms to study the evolutionary rates, convergence, and parallelism. The theoretical principle of descent with modification, that is phylogenetic, is clearly responsible for the existence and structure of a natural system of classification. The phylogenetic relationships are generally based on the data from paleontology. Marine nematodes do not have fossil records. Their phylogeny has been guessed by the evaluation of morphological characters.

De Coninck proposed evolutionary relationships among the marine nematodes from trends found in certain features, such as the structure of amphids. Their evolutionary significance has been emphasised in his system by regarding the amphids as a weighted character. He implied that the amphids contribute more than the other characters in classification of marine nematodes. Adrássy, however, made a quantitative approach to explain evolutionary lines within nematodes by considering their morphological features.

2.4 The Development of Numerical Methods in Taxonomy

A new approach to systematics began as early as 1898, when Heincke used a measure of phenetic distance to distinguish between races of herring (Sokal and Sneath, 1963). However, because of computational difficulties, the numerical method had limited success. With the advent of high-speed electronic computers, it became possible to consider large scale data analysis in classification.

Numerical classification was further advanced by the acceptance of equal weights for different characters. Taxonomists, usually, tend to weight the characters in terms of their presumed evolutionary importance. Sokal (1966) pointed out that evolutionary importance is undefinable and generally unknown. He argued that to weight characters according to their value in distinguishing between groups in a classification is a logical fallacy. Since the purpose of employing the characters is to establish a classification, one can not first assume what these groups are, and then use them to measure the diagnostic weight of a character. The idea of equal weighting is further discussed and supported by Sneath and Sokal (1973). The use of many characters, and the application of methods of cluster analysis in building the taxonomic hierarchy, were also major advances in numerical taxonomy (Jardin and Sibson, 1971; Sneath and Sokal, 1973).

2.5 Phenetic Relationship

An important advance in numerical taxonomy was the separation of overall similarity (phenetics) from phylogenetic considerations (Sneath and Sokal, 1973). This was mainly because the phylogeny of the vast majority of taxa is unknown.

Numerical taxonomy bases classification entirely on resemblance, defining natural classification as those yielding taxa whose members are in some sense more similar to one another than they are to members of other taxa. The similarity, or resemblance is based on a set of phenotypic characteristics of the objects or organisms under study. Hence, the taxonomic relationships are evaluated purely on the basis of the resemblances existing now in the material under study. It does not consider the origin of the resemblance found, nor the rate at which resemblance may have increased or decreased in the past.

Sokal (1966) provided a similarity matrix and phenogram to show degree of similarity between a group of nematodes. Moss and Webster (1970) considered phenetics and numerical taxonomy applied to systematic nematology. Bird (1971) recommended the numerical techniques for nematode classification. He suggested the establishment of phenetic clusters. Freudenhammer (1975) provided a phenogram for the smallest order of marine nematodes (Desmoscolecida) that indicates generic relationships similar to Andrássy's system. Decraemer and Coomans (1978) gave a trellis diagram that refers to the degree of affinity of nematode fauna from the Great Barrier Reef.

2.5.1 Operational Taxonomic Units

The objects to be classified are called "operational taxonomic units", or OTU's. They may be individuals representing species, or higher-ranking taxa such as genera

or families.

Moss and Webster (1970) indicated that for an initial study, a group of about twenty OTU's are a reasonable number to elucidate phenetic relationships.

2.5.2 Taxonomic Characters

Each OTU has a number of items of information, called attributes. Phenetic relationship is based on the evaluation of various attributes called taxonomic characters. A taxonomic character of two or more states, which cannot be further subdivided into independent characters within the study at hand, is called a "unit character".

Lance and Williams (1967) distinguished between the following three categories of attributes:

- Quantitative. These are usually measurements or counts. A quantitative attribute has also been called numerical, numeric or metric. In the general case, it may be signed, though earlier it was restricted to all-positive data.
- 2. Ordered Multistate (ordinal). These attributes must be able to exist in more than two states, such that the states are ranked; that is, the order of the states is meaningful. An example is the annulation of the cuticle among nematodes that may be smooth, distinct, coarse or very coarse.

3. Disordered Multistate (nominal). The states are not ranked and no difference is made to the order in which the states are numbered. An example is the shape of the amphids of nematodes that may be circular, spiral or pocket-like.

A special case of the nominal attribute is that with only two states, the presence or absence of a morphological structure. It is often called a binary or qualitative attribute. The meristic attributes are essentially counts, and can only take integral values; an example is the number of teeth of nematodes. In such a case the attribute is coded as nominal, so that the states remain separate (Williams, 1976). There is a further possible distinction within the general class of disordered multistate. It is the situation where attributes are serially dependent in a hierarchic manner such that the secondary character depends on a primary character. An example is the binary character of whether the nematode possessed or did not possess teeth. If a nematode has teeth, there are potentially a considerable number of attributes concerning teeth that can be scored for that nematode; but if it has no teeth, the additional attributes can not be scored. In practice the binary character can be converted into several independent characters (Sneath and Sokal, 1973). Hence, the lack of teeth is scored as one of the discrete states in the nominal attribute.

2.5.3 Choice and Number of Characters

Taxonomic characters are expressions of phenotype of the taxon. A general classification should be based on as broad a phenetic spectrum as possible to reduce the differences between classifications based on different sets of characters (Sneath and Sokal, 1973). The criteria for selection of attributes include relevance, that is, the attributes should be relevant in the sense that their corresponding character states should have diagnostic value for the OTU's selected. Gower (1971) referred to the problem of homology, that is, deciding whether a character occurring in one group of organisms also occurs in another group. Bird (1971) indicated that a good taxonomic character must be consistent for all members of a given taxon. The characters chosen need also to be logically uncorrelated, that is, exclude redundancy. Two characters can not be considered when the presence of one will also define or include the other. When there are potentially a vast number of characters, Moss and Webster (1970) recommended sampling experiments to reach a stable classification. They indicated that the basic data structure will tend to come through, once a certain minimum number of characters has been attained. This structure will tend to be maintained as additional characters are added, but may be affected by the addition of characters that may vary randomly, show high variability, or be difficult to measure.

2.5.4 The Data Matrix

The data obtained for cluster analysis is arranged in the form of a $(n \times t)$ matrix X:

The columns represent the t OTU's to be grouped on the basis of resemblances and the rows are n unit characters. Each entry X_{ij} is the score of ith characters for the jth individuals (OTU's) where $0 \le i \le n$ and $1 \le j \le t$.

The data matrix can be examined from at least two points of view (Sneath and Sokal, 1973). The association of pairs of characters (rows) can be examined over all OTU's (columns). This is called R technique. The converse practice, the association of pairs of OTU's over all characters, has been called Q technique. Cluster analysis usually considers Q technique.

2.5.5 The Data Analysis

Sneath and Sokal (1973) mentioned four groups of similarity coefficient that are applied to estimate similarities between all possible pairs of OTU's over all characters. They include association, correlation, distance, and probabilistic similarity coefficients.

Association coefficients are generally used for two-state (qualitative) attributes. Bird (1971) recommended correlation coefficients for morphometric and quantitative attributes. When multistate characters are independent of size, he suggested distance coefficients are useful.

Probabilistic similarity coefficients are used in groups or population studies. They deal with the frequencies of the character states over the classes of OTU's.

2.5.5.1 Distance Coefficients

Williams (1976) considered a variety of metrics that measure the distance between OTU's in a multidimensional space. They include Euclidean and the three Manhattan metric measures (Gower, Bray-Curtis and Canberra). When ordinal attributes are rare, Euclidean metric seems a promising choice among the metrics that could be used (Burr, 1968). Euclidean metric also has useful combinatorial properties in mixed-data case (Lance and Williams, 1967). Considering the nematode genera, majory of attributes are of a nominal nature. Hence, Euclidean metric could be a suitable choice.

2.5.5.1.1 Euclidean Metric

The Euclidean metric regarded as "taxonomic distance" by Sneath and Sokal (1973), is the most commonly used metric. Williams (1976) indicated that for a total of s attributes, the distance between the ith and jth individual denoted by d_{ij} is defined as:

$$d_{ij} = \left\{ \sum_{k=1}^{s} (x_{ik} - x_{jk})^2 \right\}^3$$

where xik is the value of the kth attribute for the ith individual. In practice, the squared Euclidean distance is used,

$$d_{ij}^{2} = \sum_{k=1}^{s} (x_{ik} - x_{jk})^{2}$$

and the value of squared Euclidean distance is generally divided by s, the number of attributes.

2.5.6 Method of Analysis

Lance and Williams (1966) indicated that the methods of classifying the individuals or groups are divided into hierarchic and non-hierarchic methods. The nonhierarchic methods do not exhibit the branching or successive partitions of the taxa. The hierarchic methods involve successive fusion between pairs of most similar individuals ending with the group or successive splitting (fission) of groups into component individuals. The hierarchic methods are usually displayed with a tree-like diagram called a dendrogram, dendrograph or phenogram.

The fission procedure is called "divisive". It is generally applied for population analysis or in cases where large scale data are to be considered.

The fusion procedure is called "agglomerative". It is a common method used for hierarchic classification.

2.5.6.1 Hierarchic Agglomerative System

It may be monothetic or polythetic. As referred to before, the monothetic classification employs few characters that are shared by all the members of the group. It is useful for special or artificial classification and provides a key to identification (de Gruijter, 1977). The hierarchic classification is generally polythetic. It is based on a measure of similarity applied to overall attributes, so that an individual is grouped with those individuals which, on the average, it most resembles (Williams, 1976).

The hierarchic agglomerative system is further divided into combinatorial or non-combinatorial strategies (Lance and Williams, 1967a). The non-combinatorial strategy considers the initial data records (matrix X), while combinatorial strategy employs the inter-individual distance measures that were derived from initial data, for subsequent calculations to elucidate the taxonomic structure of the data. Lance and Williams (1967a) indicated that the combinatorial strategy has computational advantage compared with the non-combinatorial procedure.

2.5.6.1.1 Combinatorial Strategy

If two individuals or groups (i) and (j) fuse to form a group (k) with $n_k (= n_i + n_j)$ individuals, then the distance between (k) and some other individual or group (h) is given by:

$$d_{kh} = \alpha_i d_{hi} + \alpha_j d_{hj} + \beta d_{ij} + \gamma |d_{hi} - d_{hj}|,$$

where the parameters α_i , α_j , β and α define the precise sorting strategy:

i) Nearest-neighbour: $\alpha_{i} = \alpha_{j} = \frac{1}{2}; \quad \beta = 0; \quad \gamma = -\frac{1}{2}$ ii) Furthest-neighbour: $\alpha_{i} = \alpha_{j} = \frac{1}{2}; \quad \beta = 0; \quad \gamma = \frac{1}{2}$ iii) Median: $\alpha_{i} = \alpha_{j} = \frac{1}{2}; \quad \beta = -\frac{1}{4}; \quad \gamma = 0$ iv) Group-average: $\alpha_{i} = \frac{n_{i}}{n_{k}}; \quad \alpha_{j} = \frac{n_{j}}{n_{k}}; \quad \beta = \gamma = 0$ v) Flexible: $\alpha_i = \alpha_j = \frac{1}{2} (1-\beta); \gamma = 0$

vi) Incremental Sum of Squares: $\alpha_{i} = \frac{n_{i}}{n_{k}}; \quad \alpha_{j} = \frac{n_{j}}{n_{k}};$ $\beta = -\alpha_{i}\alpha_{j}; \quad \gamma = 0$

Lance and Williams (1966) mentioned three criteria for strategy assessment:

- The value of the distance measure should change monotonically with successive fusion.
- 2. The process should, as far as the data permits, fuse the individuals or groups into clearlyseparated groups, and not continually add single individuals.
- 3. The metric should define an objective level below which details of individual fusions may be disregarded.

2.5.7 Hierarchic Programs

The CSIRO Division of Computing Research in Canberra holds a variety of programs for hierarchic classification (Williams, 1976). They are stored on a permanent file called TAXON. Two analogous programs, MULCLAS and CLASS, are used for agglomerative polythetic classification with combinatorial strategy. The program MULCLAS was recommended and used in this study.

2.4.7.1 MULCLAS

The program calculates the Canberra, Gower and Euclidean metrics and uses the nearest neighbour, furthest neighbour, median, centroid, group average, flexible and incremental sum of squares' fusion strategies. Lance and Williams (1967) indicated that the flexible sorting strategy with cluster intensity parameter; $\beta = -0.25$ is most commonly used. The magnitude of β determines the extend to which the group is able to separate.

The program accepts any or all the attribute types with provision for missing value. The non-exclusive multistates are permitted, when an individual may exist simultaneously in more than one state.

The sequence of control statements needed for program execution are:

*CY, CHARGE CODE, IDENT MULCLAS (T50) DISPOSE (TAPE 1, *PM) FUSE MULCLAS END OF SECTION CONTROL CARDS DATA CARDS END OF INFORMATION

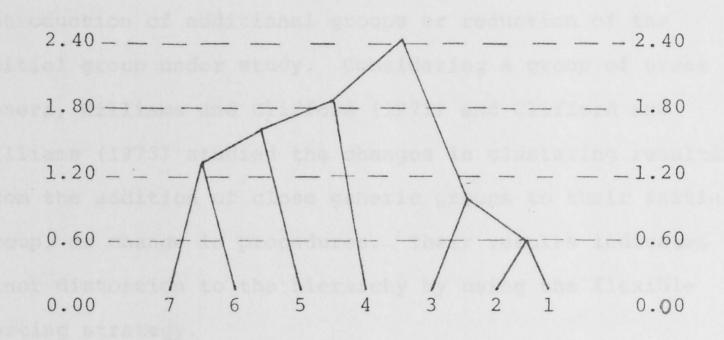
2.5.7.1.1 Results

The Euclidean metric is given for each pair of individual-individual, individual-group, or group-group. The measure are printed in the form:

FUSION		GROUP	SIMILARITY
p + q	=	t	С

where p and q are the individuals (or group) numbers which combined at a value C of the measure in use to give a new group number t.

A visual representation of successive fusions from individuals to the complete group is then produced in hierarchical manner (phenogram):



The X-axis represents the individuals (1-7) that are fused at subsequent level of similarities given in terms of distance units (Euclidean metric) on Y-axis. The distance units increase as the level of similarities decrease. If there are n individuals in the group, there will be (n - 1) fusions (Williams, 1976).

The groups established by cluster analysis are called phenons (Sneath and Sokal, 1973). They are prefaced with a number indicating the level of similarity at which they are formed. The horizontal lines across the above phenogram created four phenon lines. The first phenon line at similarity value of 0.60, has formed six 0.60phenons: 1,2; 3; 4; 5; 6; 7. A given phenon is referred by its first and last number. Phenons are intended to be a general approach to natural taxa and, **like the** term taxon, they can be of any hierarchic rank.

2.5.7.1.1.1 Stability

The stability of the phenons may be examined by the introduction of additional groups or reduction of the initial group under study. Considering a group of grass genera, Williams and Clifford (1971) and Clifford and Williams (1973) studied the changes in clustering resulting from the addition of close generic groups to their initial group, or change in procedures. Their results indicated minor distortion to the hierarchy by using the flexible sorting strategy.

3.1 Initial Group

The nematodes selected for the initial study, were examples taken from twenty-one recognised genera (Appendix 2.1) that were widely distributed along the spectrum of De Coninck's system for classification of marine nematodes. With eighteen of these genera, I used specimens from the southern coast of N.S.W., that were available from the personal collection of my supervisor, Dr W.L. Nicholas at the Zoology Department; while for three genera (*Araeolaimus*, *Draconema* and *Greeffiella*), I relied upon descriptions in the literature. The specimens were identified by Dr W.L. Nicholas, in the first instance, a nematologist, and the identifications were confirmed by Dr R.M. Warwick, a nematode taxonomist (a Visiting Fellow at the Zoology Department).

My observations on the specimens were supplemented with appropriate references which are cited after the name of each specimen. The attributes used in this study were all morphological characters that were easily observable in preserved specimens. They included most of those commonly used and considered by nematode taxonomists of potential value.

Each genus (OTU) was scored for thirty attributes, drawn from seven major morphological structures (amphids, cephalic and somatic sensilla, buccal cavity, armature, oesophagus, and cuticle). The attributes refer only to male specimens. Various states of each attribute were coded and arranged as a data matrix (Table 1).

The data matrix was transformed to the standard data type (MULTBET-STYLE), and arranged for the program MULCLAS. The program was executed on a Cyber 76 Computer at the CSIRO Division of Computing Research in Canberra.

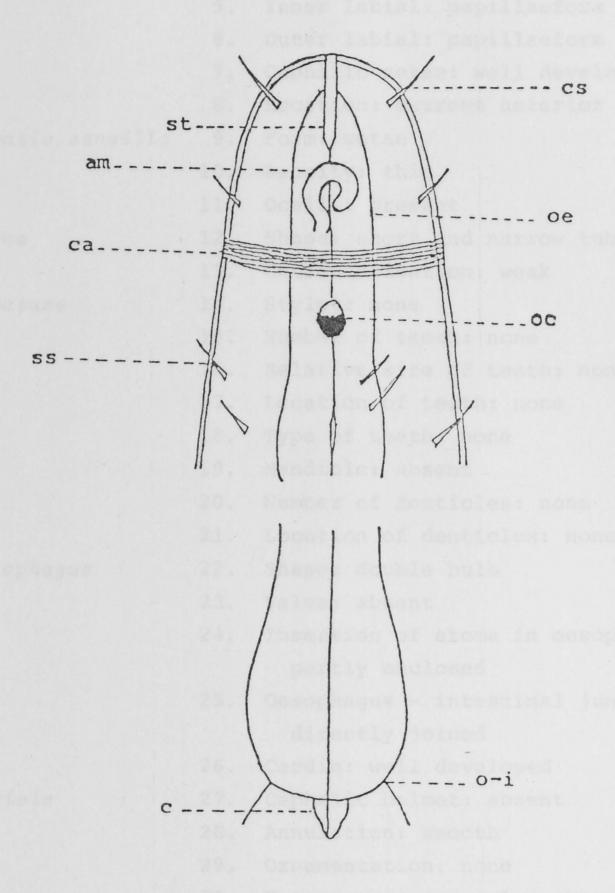
The Euclidean metric was computed for all pairs of genera. The classification was performed using the flexible sorting strategy with parameter, $\beta = -0.25$. The subsequent fusions at various levels of similarities were plotted and given as phenogram. The generic list of phenons were tabulated, and the first phenon line was compared with the groupings set by De Coninck, Andrassy and Wieser, based on the identical set of genera. The percent differences were calculated as:

> no. of genera with different positions in the group with respect to their close neighbours

% difference

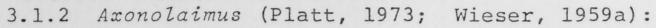
X 100

total number of genera in the group



3.1.1.1 Attributes (Araeolaimus):

Amphids	1.	Shape : question mark
11mp to a co	2.	Size relative to head diameter: medium
	3.	Location: cervical
Cephalic sensilla		Arrangement: (6+6+4)
	5.	Inner labial: papillaeform
	6.	Outer labial: papillaeform
	7.	Cephalic setae: well developed
	8.	Location: extreme anterior
Somatic sensilla		Form: setae
		Density: thin
	11.	Ocelli: present
Stoma	12.	Shape: short and narrow tubular
	13.	Cuticularisation: weak
Armature	14.	Stylet: none
	15.	Number of teeth: none
	16.	Relative size of teeth: none
	17.	Location of teeth: none
	18.	Type of teeth: none
	19.	Mandible: absent
	20.	Number of denticles: none
	21.	Location of denticles: none
Oesophagus	22.	Shape: double bulb
	23.	Valve: absent
	24.	Insertion of stoma in oesophagus:
		partly enclosed
	25.	Oesophagus - intestinal junction:
		directly joined
	26.	Cardia: well developed
Cuticle	27.	Cephalic helmet: absent
	28.	Annulation: smooth
	29.	Ornamentation: none
	30.	Extraneous materials: absent



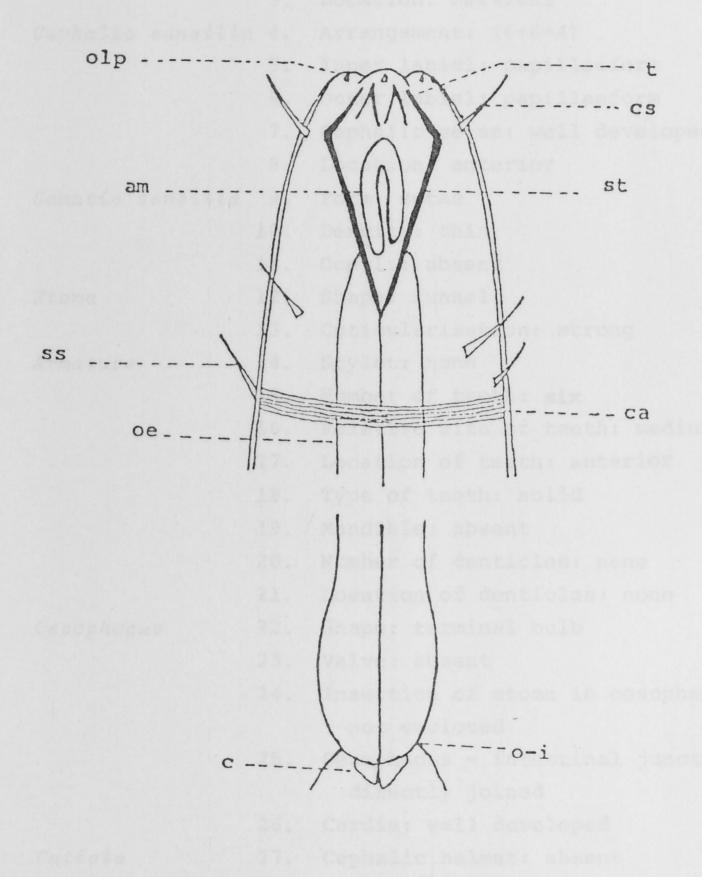


Fig. 2. Anterior end (Axonolaimus)

3.1.2.1 Attributes (Axonolaimus):

Amphids Shape: elongated crook 1. 2. Size relative to head diameter: medium 3. Location: cervical Cephalic sensilla 4. Arrangement: (6+6+4) 5. Inner labial: papillaeform 6. Outer labial: papillaeform Cephalic setae: well developed 7. Location: anterior 8. Somatic sensilla 9. Form: setae 10. Density: thin 11. Ocelli: absent 12. Shape: funnel Stoma 13. Cuticularisation: strong 14. Stylet: none Armature 15. Number of teeth: six 16. Relative size of teeth: medium Location of teeth: anterior 17. Type of teeth: solid 18. Mandible: absent 19. 20. Number of denticles: none 21. Location of denticles: none 22. Oesophagus Shape: terminal bulb 23. Valve: absent Insertion of stoma in oesophagus: 24. not enclosed Oesophagus - intestinal junction: 25. directly joined 26. Cardia: well developed Cephalic helmet: absent Cuticle 27. 28. Annulation: smooth 29. Ornamentation: none 30. Extraneous materials: absent

3.1.3 Leptolaimus (De Coninck, 1965; Jayassee and Warwick, 1977):

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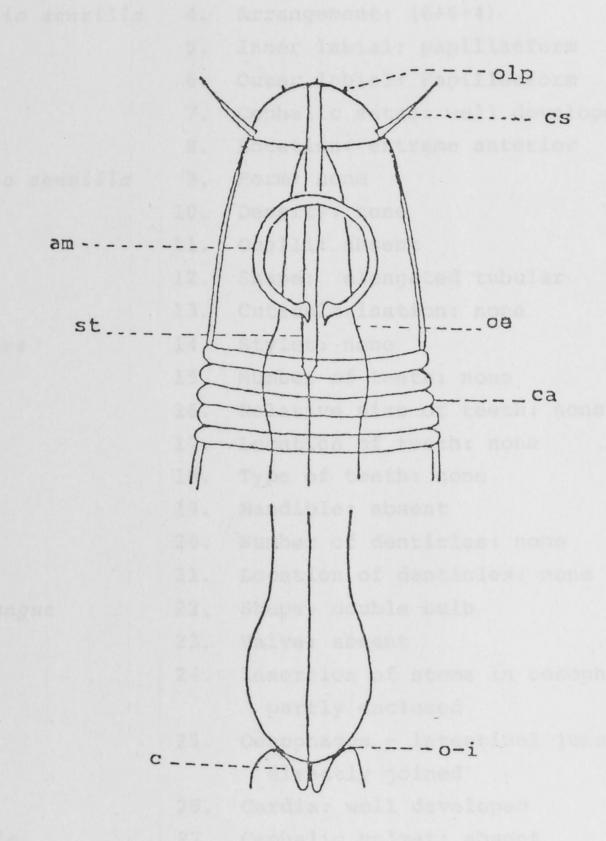


Fig. 3. Anterior end (Leptolaimus)

3.1.3.1 Attribute	s (Le	ptolaimus)
Amphids	1.	Shape: circular
-	2.	Size relative to head diameter: large
	3.	Location: cervical
Cephalic sensilla	4.	Arrangement: (6+6+4)
-	5.	
	6.	Outer labial: Papillaeform
	7.	Cephalic setae: well developed
	8.	Location: extreme anterior
Somatic sensilla	9.	Form: none
	10.	Density: none
	11.	Ocelli: absent
Stoma	12.	Shape: elongated tubular
	13.	Cuticularisation: none
Armature	14.	Stylet: none
	15.	Number of teeth: none
	16.	Relative size of teeth: none
	17.	Location of teeth: none
	18.	Type of teeth: none
	19.	Mandible: absent
	20.	Number of denticles: none
	21.	Location of denticles: none
Oesophagus	22.	Shape: double bulb
	23.	Valve: absent
	24.	Insertion of stoma in oesophagus:
		partly enclosed
	25.	Oesophagus - intestinal junction:
		directly joined
	26.	Cardia: well developed
Cuticle	27.	Cephalic helmet: absent
	28.	Annulation: distinct
	29.	Ornamentation: none
	30.	Extraneous materials: absent

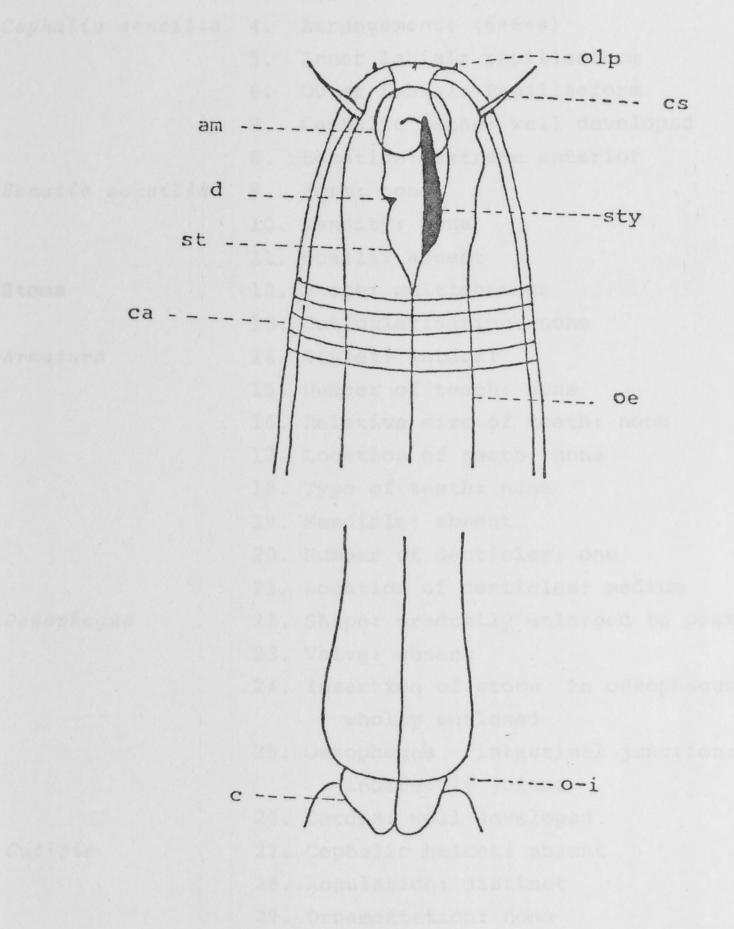


Fig. 4. Anterior end (Procamacolaimus)

1	1	Shape: simple spiral
Amphids	1.	
		Size relative to head diameter: medium
		Location: extreme anterior
Cephalic sensilla		Arrangement: (6+6+4)
		Inner labial: papillaeform
	6.	Outer Labial: Papillaeform
	7.	Cephalic setae: well developed
	8.	Location: extreme anterior
Somatic sensilla	9.	Form: none
	10.	Density: none
	11.	Ocelli: absent
Stoma	12.	Shape: multichamber
	13.	Cuticularisation: none
Armature	14.	Stylet: lateral
	15.	Number of teeth: none
	16.	Relative size of teeth: none
	17.	Location of teeth: none
	18.	Type of teeth: none
	19.	Mandible: absent
	20.	Number of denticles: one
	21.	Location of denticles: medium
Oesophagus	22.	Shape: gradually enlarged to posterior
	23.	Valve: absent
	24.	Insertion of stoma in oesophagus:
		wholly enclosed
	25.	Oesophagus - intestinal junction:
		indirectly joined
	26.	Cardia: well developed
Cuticle	27.	Cephalic helmet: absent
	28.	Annulation: distinct
	29.	Ornamentation: none
	30.	Estraneous materials: absent
P19. 5		

3.1.5 Bathylaimus (Cobb, 1894; Decraemer and Coomans, 1978a; Wieser and Hopper, 1967):

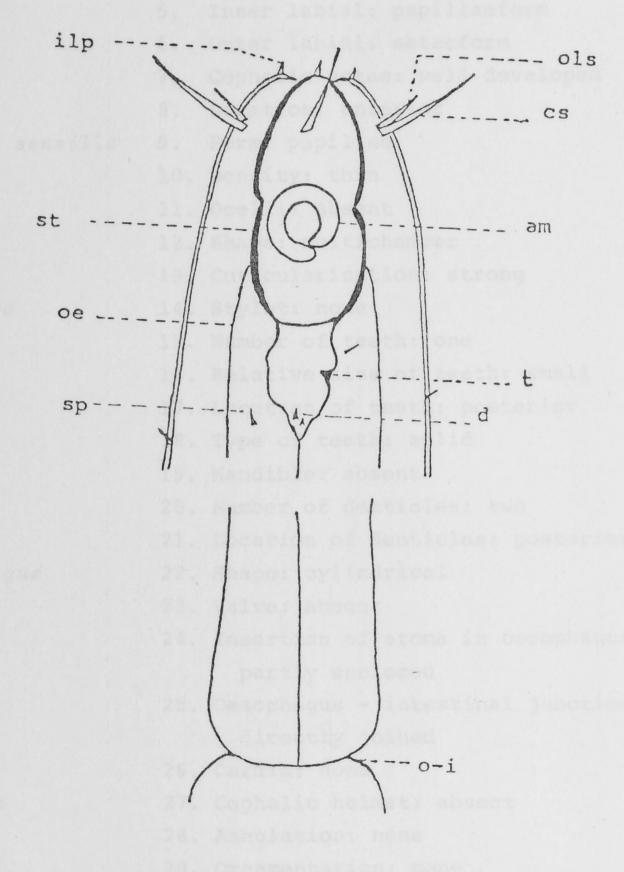


Fig. 5. Anterior end (Bathylaimus)

Amphids	1.	Shape: crook-like
	2.	Size relative to head diameter: medium
	3.	Location: cervical
Cephalic sensilla	4.	Arrangement: $(6 + 10 [= 6 + 4])$
	5.	Inner labial: papillaeform
	6.	Outer labial: setaeform
	7.	Cephalic setae: well developed
	8.	Location: anterior
Somatic sensilla	9.	Form: papillae
	10.	Density: thin
	11.	Ocelli: absent
Stoma	12.	Shape: multichamber
	13.	Cuticularisation: strong
Armature	14.	Stylet: none
	15.	Number of teeth: one
	16.	Relative size of teeth: small
	17.	Location of teeth: posterior
	18.	Type of teeth: solid
	19.	Mandible: absent
	20.	Number of denticles: two
	21.	Location of denticles: posterior
Oesophagus	22.	Shape: cylindrical
	23.	Valve: absent
	24.	Insertion of stoma in oesophagus:
		partly enclosed
	25.	Oesophagus - intestinal junction:
		directly joined
	26.	Cardia: none
Cuticle	27.	Cephalic helmet: absent
	28.	Annulation: none
	29.	Ornamentation: none
	30.	Extraneous materials: absent

3.1.6 Terschellingia (Inglis, 1967; Groza-Rojancovski, 1973; Timm, 1962):

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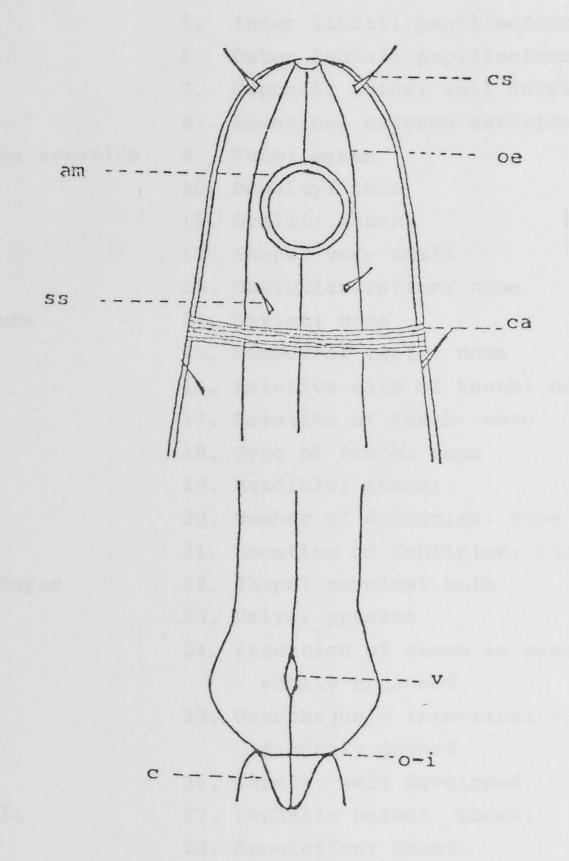
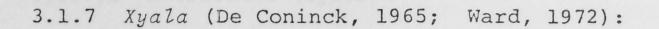
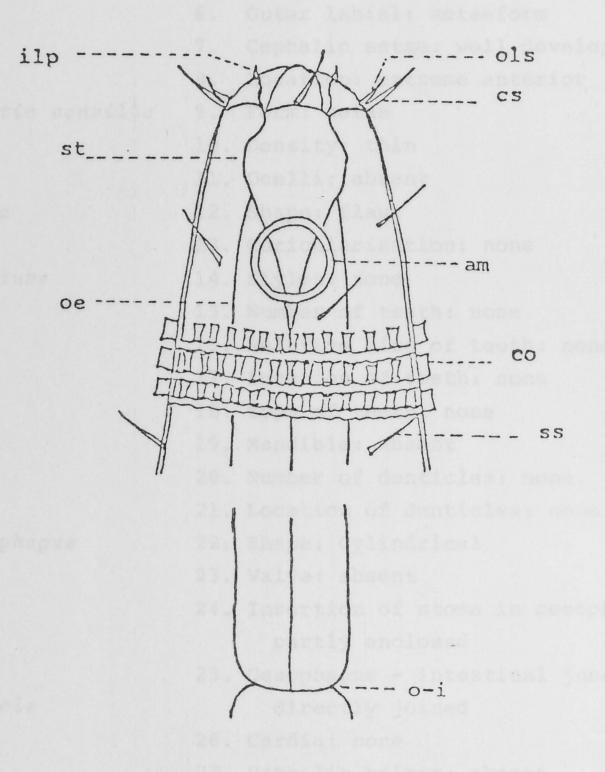


Fig. 6. Anterior end (Terschellingia)

3.1.6.1 Attributes (Terschellingia) Amphids Shape: circular 1. 2. Size relative to head diameter: large Location: cervical 3. Cephalic sensilla Arrangement: (6+6+4)4. Inner labial: papillaeform 5. Outer labial: papillaeform 6. Cephalic setae: well developed 7. Location: extreme anterior 8. Somatic sensilla 9. Form: setae 10. Density: thin 11. Ocelli: absent Stoma 12. Shape: very small 13. Cuticularisation: none Armature 14. Stylet: none 15. Number of teeth: none 16. Relative size of teeth: none 17. Location of teeth: none 18. Type of teeth: none 19. Mandible: absent 20. Number of denticles: none 21. Location of denticles: none Oesophagus 22. Shape: terminal bulb 23. Valve: present 24. Insertion of stoma in oesophagus: wholly enclosed. 25. Oesophagus - intestinal junction: directly joined 26. Cardia: well developed Cuticle 27. Cephalic helmet: absent 28. Annulation: smooth 29. Ornamentation: none 30. Extraneous materials: absent





3.1.7.1 Attributes (Xyala):

Amphids	1.	Shape: circular
	2.	Size relative to head diameter: medium
	3.	LocationL cervical
Cephalic sensilla	4.	Arrangement: $(6 + 10 [= 6 + 4]$
	5.	Inner labial: papillaeform
	6.	Outer labial: setaeform
	7.	Cephalic setae: well developed
	8.	Location: extreme anterior
Somatic sensilla	9.	Form: setae
	10.	Density: thin
	11.	Ocelli: absent
Stoma	12.	Shape: flask
	13.	Cuticularisation: none
Armature	14.	Stylet: none
	15.	Number of teeth: none
	16.	Relative size of teeth: none
	17.	Location of teeth: none
	18.	Type of teeth: none
	19.	Mandible: absent
	20.	Number of denticles: none
	21.	Location of denticles: none
Oesophagus	22.	Shape: Cylindrical
	23.	Valve: absent
	24.	Insertion of stoma in oesophagus:
		partly enclosed
	25.	Oesophagus - intestinal junction:
Cuticle		directly joined
	26.	Cardia: none
	27.	Cephalic helmet: absent
	28.	Annulation: coarse
	29.	Ornamentation: plates
	30.	Extraneous materials: absent

.

3.1.8 Siphonolaimus (De Coninck, 1965; Inglis, 1967; Ott, 1972):

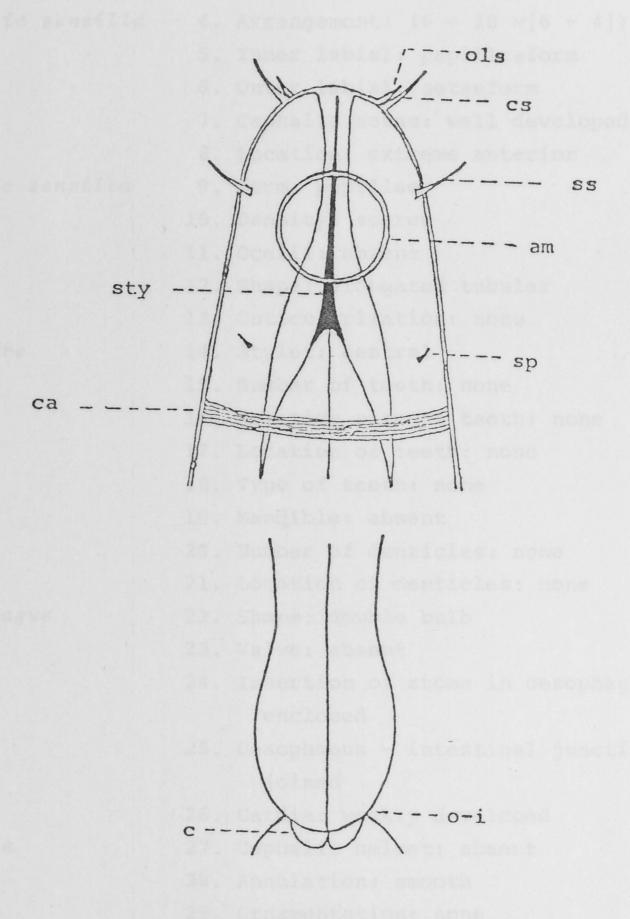


Fig. 8. Anterior end (Siphonolaimus)

3.1.8.1 Attributes (Siphonolaimus)

Amphids

Cephalic sensilla

Somatic sensilla

1. Shape: Circular

- 2. Size relative to head diameter: large
- 3. Location: Cervical
- 4. Arrangement: (6 + 10 = [6 + 4])
- 5. Inner labial: papillaeform
- 6. Outer labial: setaeform
- 7. Cephalic setae: well developed
- 8. Location: extreme anterior
- 9. Form: papillae
- 10. Density: scarce
- 11. Ocelli: absent
- 12. Shape: elongated tubular
- 13. Cuticularisation: none
- 14. Stylet: Central
- 15. Number of teeth: none
- 16. Relative size of teeth: none
- 17. Location of teeth: none
- 18. Type of teeth: none
- 19. Mandible: absent
- 20. Number of denticles: none
- 21. Location of denticles: none
- 22. Shape: double bulb
- 23. Valve: absent
- 24. Insertion of stoma in oesophagus: not enclosed
- 25. Oesophagus intestinal junction: directly joined
- 26. Cardia: weakly developed
- 27. Cephalic helmet: absent
- 28. Annulation: smooth
- 29. Ornamentation: none
- 30. Extraneous materials: absent

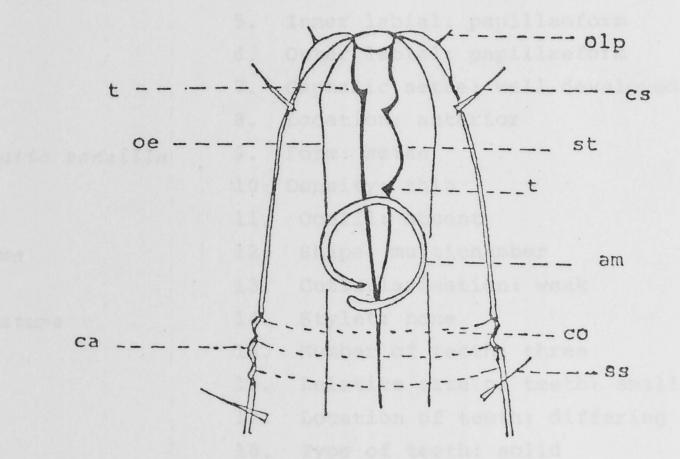
Stoma

Armature

Oesophagus

Cuticle

3.1.9 Microlaimus (De Coninck, 1965; Jensen, 1976; Steiner, 1916):



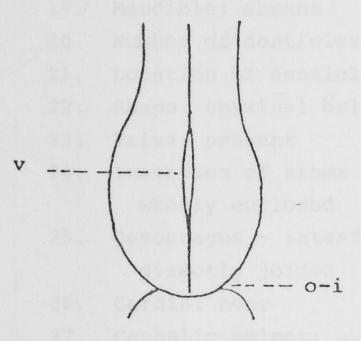


Fig. 9. Anterior end (Microlaimus)

Amphids	1.	Shape: simple spiral
	2.	Size relative to head diameter : large
	3.	LocationL cervical
Cephalic sensilla	4.	Arrangement: $(6 + 6 + 4)$
	5.	Inner labial: papillaeform
	6.	Outer labial: papillaeform
	7.	Cephalic setae: well developed
	8.	Location: anterior
Somatic sensilla	9.	Form: setae
	10:	Density: thin
	11.	Ocelli: absent
Stoma	12.	Shape: multichamber
	13.	Cuticularisation: weak
Armature	14.	Stylet: none
	15.	Number of teeth: three
	16.	Relative size of teeth: small
	17.	Location of teeth: differing locations
	18.	Type of teeth: solid
	19.	Mandible: absent
	20.	Number of denticles: none
	21.	Location of denticles: none
Oesophagus	22.	Shape: terminal bulb
	23.	Valve: present
	24.	Insertion of stoma in oesophagus:
		wholly enclosed
	25.	Oesophagus - intestinal junction:
		directly joined
	26.	Cardia: none
Cuticle	27.	Cephalic helmet: absent
	28.	Annulation: distinct
	29.	Ornamentation: punctation
	30.	Extraneous materials: absent

3.1.10 Desmodora (Luc and De Coninck, 1959; Steiner, 1916):

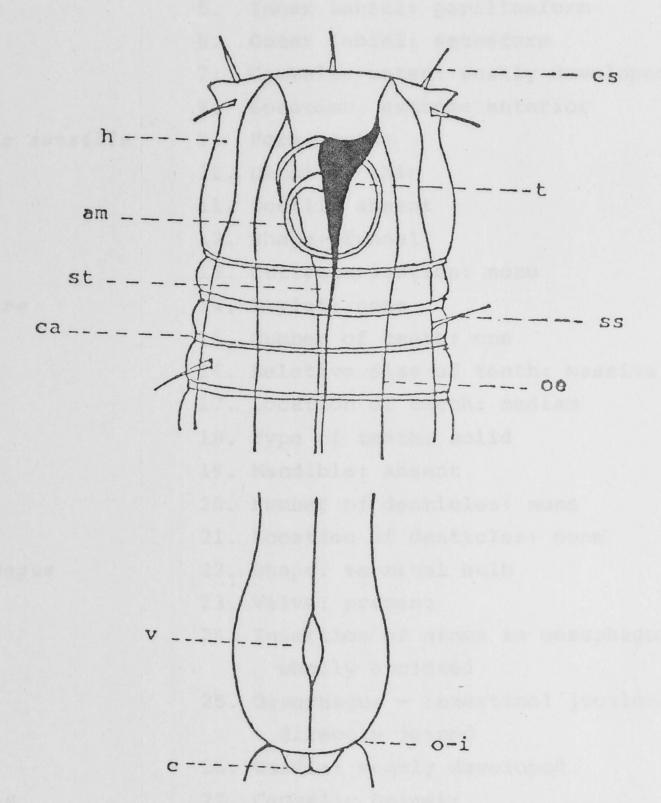


Fig. 10. Anterior end (Desmodora)

Amphids	1. Shape: multispiral
	2. Size relative to head diameter: large
	3. Location: cervical
Cephalic sensilla	4. Arrangement: $(6 + 6 + 4)$
	5. Inner labial: papillaeform
	6. Outer labial: setaeform
	7. Cephalic setae: weakly developed
	8. Location: extreme anterior
Somatic sensilla	9. Form: setae
	10. Density: thin
	ll. Ocelli: absent
Stoma	12. Shape: funnel
	13. Cuticularisation: none
Armature	14. Stylet: none
	15. Number of teeth: one
	16. Relative size of teeth: massive
	17. Location of teeth: mediam
	18. Type of teeth: solid
	19. Mandible: absent
	20. Number of denticles: none
	21. Location of denticles: none
Oesophagus	22. Shape: terminal bulb
	23. Valve: present
	24. Insertion of stoma in oesophagus:
	wholly enclosed
	25. Oesophagus - intestinal juction:
	directly joined
	26. Cardia: weakly developed
Cuticle	27. Cephalic helmet:
	28. Annulation: very coarse
	29. Ornamentation: none
	30. Extraneous materials: absent

3.1.10.1 Attributes (Desmodora):

3.1.11 Ceramonema (Vitiello and Haspeslagh, 1972; Wieser, 1959):

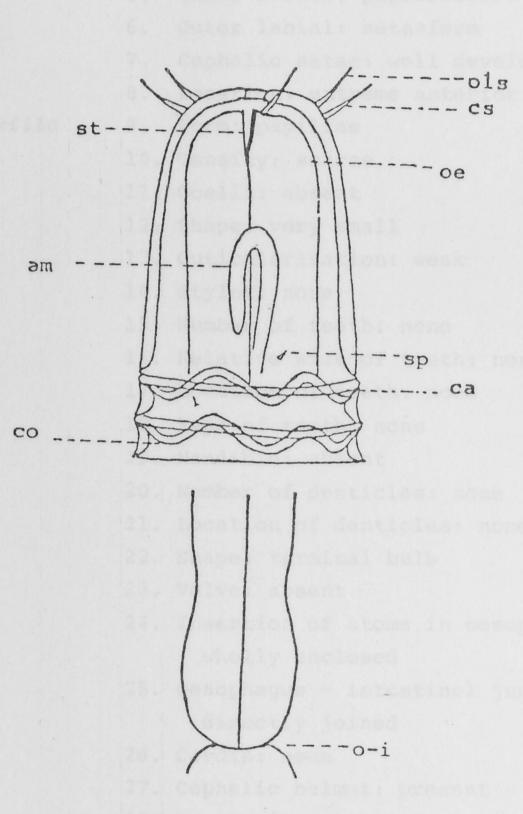
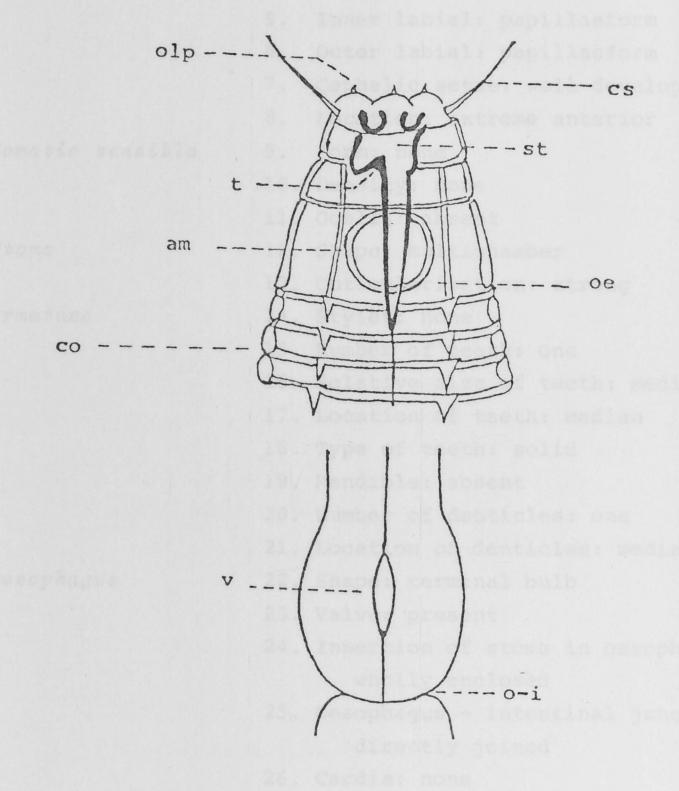


Fig. 11. Anterior end (Ceramonema)

3.1.11.1 Attributes (Ceramonema):

Amphids	1.	Shape: elongated crook
	2.	Size relative to head diameter: medium
	3.	Location: cervical
Cephalic sensilla	4.	Arrangement: $(6 + 10 = [6 + 4])$
	5.	Inner labial: papillaeform
	6.	Outer labial: setaeform
	7.	Cephalic setae: well developed
	8.	Location: extreme anterior
Somatic sensilla	9.	Form: papillae
	10.	Density: scarce
	11.	Ocelli: absent
Stoma	12.	Shape: very small
	13.	Cuticularisation: weak
Armature	14.	Stylet: none
	15.	Number of teeth: none
	16.	Relative size of teeth: none
	17.	Location of teeth: none
	18.	Type of teeth: none
	19.	Mandible: absent
	20.	Number of denticles: none
	21.	Location of denticles: none
Oesophagus	22.	Shape: terminal bulb
	23.	Valve: absent
	24.	Insertion of stoma in oesophagus:
		wholly enclosed
	25.	Oesophagus - intestinal junction:
		directly joined
	26.	Cardia: none
Cuticle	27.	Cephalic helmet: present
	28.	Annulation: coarse
	29.	Ornamentation: overlapping scutes
	30.	Extraneous materials: absent
-		



3.1.13.1 Attributes	(Monoposthia)
Amphids	1. Shape: circular
	2. Size relative to head diameter: medium
	3. Location: cervical
Cephalic sensilla	4. Arrangement: $(6 + 6 + 4)$
	5. Inner labial: papillaeform
	6. Outer labial: papillaeform
	7. Cephalic setae: well developed
	8. Location: extreme anterior
Somatic sensilla	9. Form: none
	10. Density: none
	11. Ocelli: absent
Stoma	12. Shape: multichamber
	13. Cuticularisation: strong
Armature	14. Stylet: none
	15. Number of teeth: one
	16. Relative size of teeth: medium
	17. Location of teeth: median
	18. Type of teeth: solid
	19. Mandible: absent
	20. Number of denticles: one
	21. Location of denticles: median
Oesophagus	22. Shape: terminal bulb
	23. Valve: present
	24. Insertion of stoma in oesophagus:
	wholly enclosed
	25. Oesophagus - intestinal junction:
	directly joined
	26. Cardia: none
Cuticle	27. Cephalic helmet: absent
	28. Annulation: coarse
	29. Ornamentation: scutes
	30. Extraneous materials: absent

Steiner, 1916):

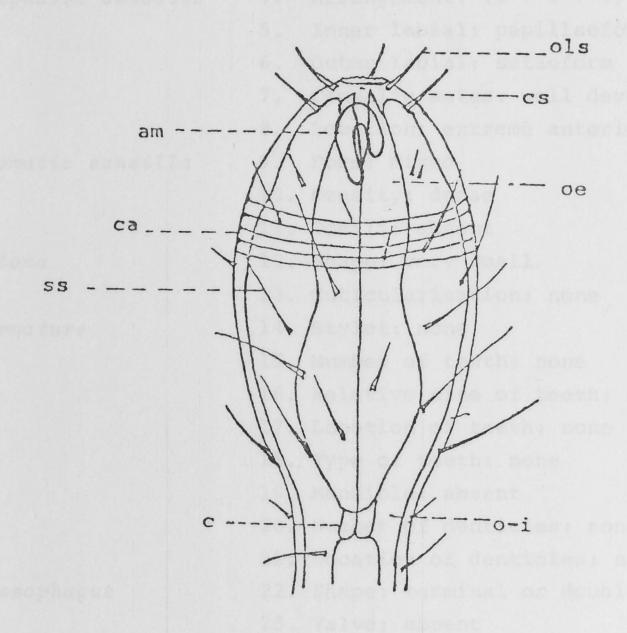
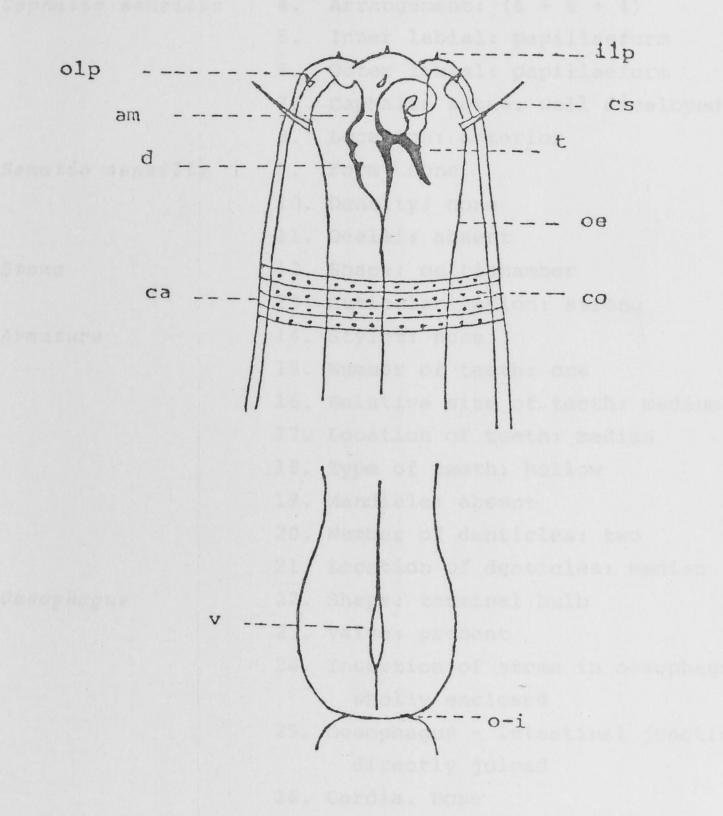
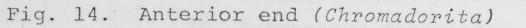


Fig. 13. Anterior end (Draconema)

Amphids	1.	Shape: mostly spiral, also round
	2.	Size relative to head diameter: medium
	3.	Location: estreme anterior
Cephalic sensilla	4.	Arrangement: $(6 + 6 + 4)$
	5.	Inner labial: papillaeform
	6.	Outer labial: setaeform
	7.	Cephalic setae: well developed
	8.	Location: extreme anterior
Somatic sensilla	9.	Form: mixed
	10.	Density: dense
	11.	Ocelli: absent
Stoma	12.	Shape: very small
	13.	Cuticularisation: none
Armature	14.	Stylet: none
	15.	Number of teeth: none
	16.	Relative size of teeth: none
	17.	Location of teeth: none
	18.	Type of teeth: none
	19.	Mandible: absent
	20.	Number of denticles: none
	21.	Location of denticles: none
Oesophagus	22.	Shape: terminal or double bulb
	23.	Valve: absent
	24.	Insertion of stoma in oesophagus:
		wholly enclosed
	25.	Oesophagus - intestinal junction:
		indirectly joined
	26.	Cardia: well developed
Cuticle	27.	Cephalic helmet: absent
	28.	Annulation: distinct
Tig. 14. A	29.	Ornamentation: none
	30.	Extraneous materials: absent

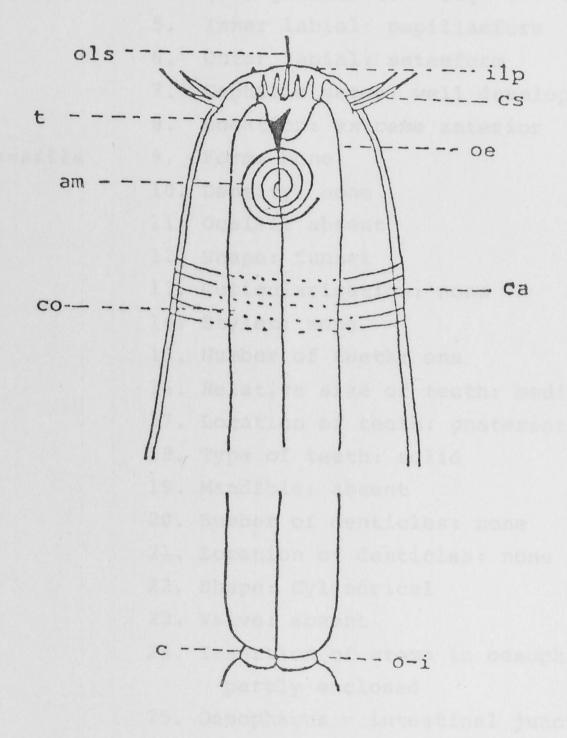


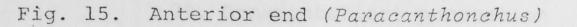


3.1.14.1 Attributes (Chromadorita):

Amphids	1. Shape: Crook-like or slit
	2. Size relative to head diameter: medium
	3. Location: extreme anterior
Cephalic sensilla	4. Arrangement: $(6 + 6 + 4)$
	5. Inner labial: papillaeform
	6. Outer labial: papillaeform
	7. Cephalic setae: well developed
	8. Location: anterior
Sematic sensilla	9. Form: none
	10. Density: none
	ll. Ocelli: absent
Stoma	12. Shape: multichamber
	13. Cuticularisation: strong
Armature	14. Stylet: none
	15. Number of teeth: one
	16. Relative size of teeth: medium
	17. Location of teeth: median
	18. Type of teeth: hollow
	19. Mandible: absent
	20. Number of denticles: two
	21. Location of denticles: median
Oesophagus	22. Shape: terminal bulb
	23. Valve: present
	24. Insertion of stoma in oesophagus:
	wholly enclosed
	25. Oesophagus - intestinal junction:
	directly joined
	26. Cardia. None
Cuticle	27. Cephalic helmet: absent
	28. Annulation: distinct
	29. Ornamentation: punctation
	30. Extraneous materials: absent

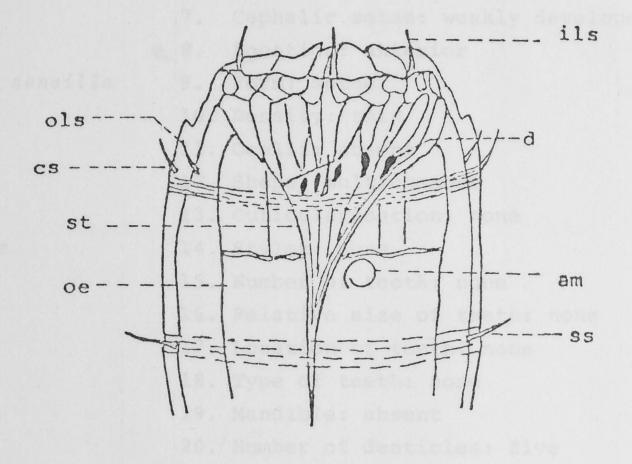
3.1.15 Paracanthonchus (Timm, 1952 and 1957; Vitiello, 1970; Wieser and Hopper, 1967):

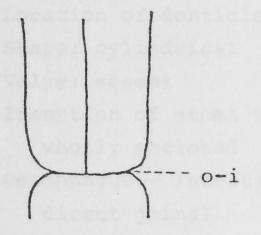


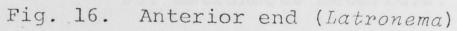


3.1.15.1 Attributes (Paracanthanchus)

Amphids	1. Shape: multispiral
	2. Size relative to head diameter): medium
	3. Location: cervical
Cephalic sensilla	4. Arrangement: $(6 + 10[= 6 + 4])$
	5. Inner labial: papillaeform
	6. Outer labial: setaeform
	7. Cephalic setae: well developed
	8. Location: extreme anterior
Somatic sensilla	9. Form: none
	10. Density: none
	11. Ocelli: absent
Stoma	12. Shape: funnel
	13. Cuticularisation: none
Armature	14. Stylet: none
	15. Number of teeth: one
	16. Relative size of teeth: medium
	17. Location of teeth: posterior
	18. Type of teeth: solid
	19. Mandible: absent
	20. Number of denticles: none
	21. Location of denticles: none
Oesophagus	22. Shape: Cylindrical
	23. Valve: absent
	24. Insertion of stoma in oesophagus:
	partly enclosed
	25. Oesophagus - intestinal junction:
	indirectly joined
	26. Cardia: weakly developed
Cuticle	27. Cephalic helmet: absent
	28. Annulation: distinct
	29. Ornamentation: punctation
	30. Extraneous materials: absent

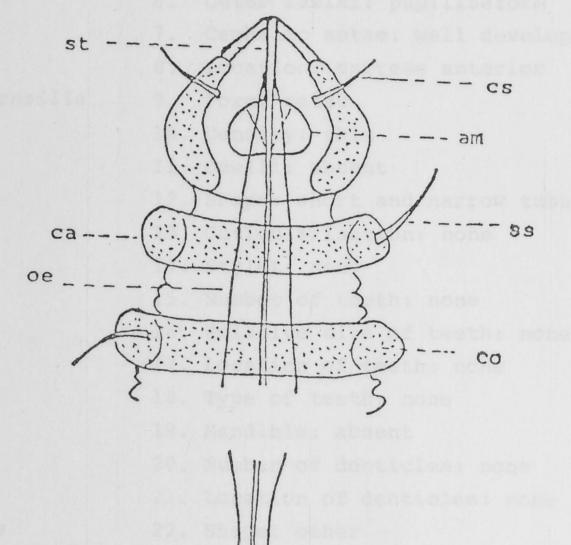




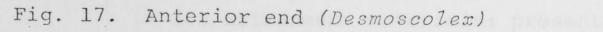


3.1.16.1 Attributes (Latronema):

Amphis	1.	Shape: simple spiral
	2.	Size relative to head diameter): small
	3.	Location: cervical
Cephalic sensilla	4.	Arrangement: $(6 + 10[=6 + 4])$
	5.	Inner labial: setaeform
	6.	Outer labial: setaeform
	7.	Cephalic setae: weakly developed
	8.	Location: anterior
Somatic sensilla	9.	Form: setae
	10.	Density: thin
	11.	Ocelli: absent
Stoma	12.	Shape: multichamber
	13.	Cuticularisation: none
Armature	14.	Stylet: none
	15.	Number of teeth: none
	16.	Relative size of teeth: none
	17.	Location of teeth: none
	18.	Type of teeth: none
	19.	Mandible: absent
	20.	Number of denticles: five
	21.	Location of denticles: median
Oesophagus	22.	Shape: cylindrical
	23.	Valve: absent
	24.	Insertion of stoma in oesophagus:
		wholly enclosed
	25.	Oesophagus - intestinal junction:
		direct joinal
	26.	Cardia: none
Cuticle	27.	Cephalic helmet: absent
	28.	Annulation: smooth
	29.	Ornamentation: punctation
	30.	Extraneous materials: absent



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3.1.17.1 Attributes (Desmoscolex):

Amphids	1.	Shape: vesicular
	2.	Size relative to head diameter): medium
	3.	Location: Cerivcal
Cephalic sensilla	4.	Arrangement: $(6 + 6 + 4)$
	5.	Inner labial: papillaeform
	6.	Outer labial: papillaeform
	7.	Cephalic setae: well developed
	8.	Location: extreme anterior
Somatic sensilla	9.	Form: setae
	10.	Density: thin
	11.	Ocelli: absent
Stoma	12.	Shape: short and narrow tubular
	13.	Cuticularisation: none
Armature	14.	Stylet: none
	15.	Number of teeth: none
	16.	Relative size of teeth: none
	17.	Location of teeth: none
	18.	Type of teeth: none
	19.	Mandible: absent
	20.	Number of denticles: none
	21.	Location of denticles: none
Oesophagus	22.	Shape: other
	23.	Valve: absent
	24.	Insertion of stoma in oesophagus:
		partly enclosed
	25.	Oesophagus - intestinal junction:
		directly joined
	26.	Cardia: none
Cuticle	27.	Cephalic helmet: Absent
	28.	Annualtion: Very coarse
	29.	Ornamentation: punctation

30. Extraneous materials: present

3.1.18 Greeffiella (Cobb, 1922; De Coninck, 1965):

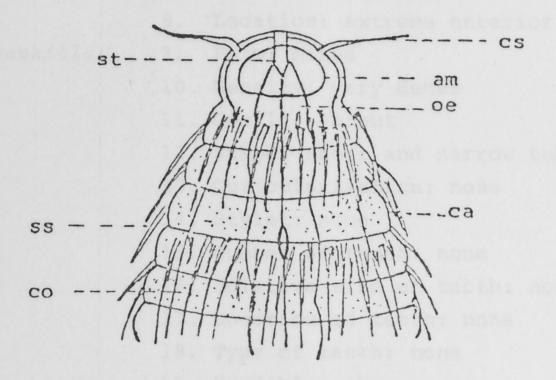


Fig. 18. Anterior end (Greeffiella)

3.1.18.1 Attributes (Greeffiella):

Amphids	1.	Shape: vesicular
	2.	Size relative to head diameter): large
	3.	Location: extreme anterior
Cephalic sensilla	4.	Arrangement: $(6 + 6 + 4)$
	5.	Inner labial: papillaeform
	6.	Outer labial: Papillaeform
	7.	Cephalic setae: well developed
	8.	Location: extreme anterior
Somatic sensilla	9.	Form: mixed
	10.	Density: very dense
	11.	Ocelli: Absent
Stoma	12.	Shape: short and narrow tubular
	13.	Cuticularisation: none
Armature	14.	Stylet: none
	15.	Number of teeth: none
	16.	Relative size of teeth: none
	17.	Location of teeth: none
	18.	Type of teeth: none
	19.	Mandible: absent
	20.	Number of denticles: none
	21.	Location of denticles: none
Oesophagus	22.	Shape: multichamber
	23.	Valve: present
	24.	Insertion of stoma in oesophagus:
		not enclosed
	25.	Oesophagus - intestinal junction:
		directly joined
	26.	Cardia: none
Cuticle	27.	Cephalic helmet: absent
	28.	Annulation: very coarse
	29.	Ornamentation: punctation
	30.	Extraneous materials: absent

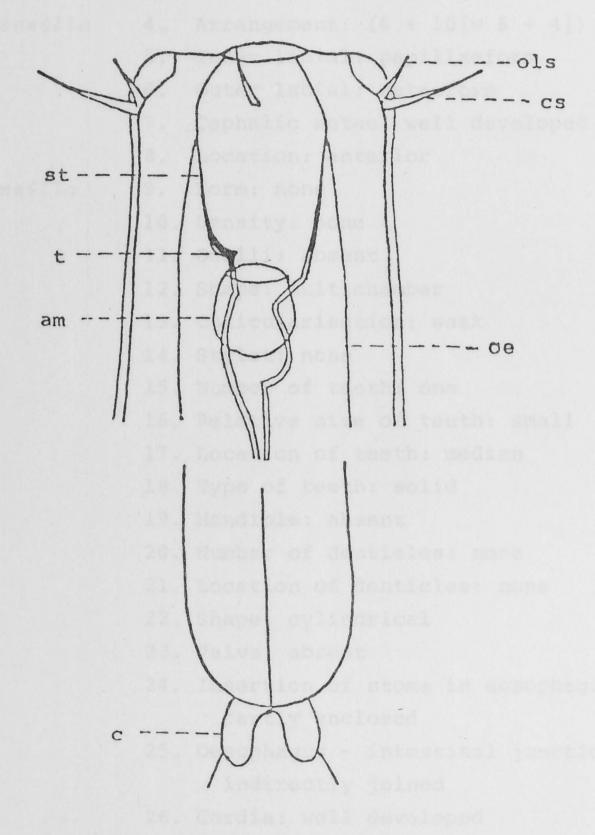
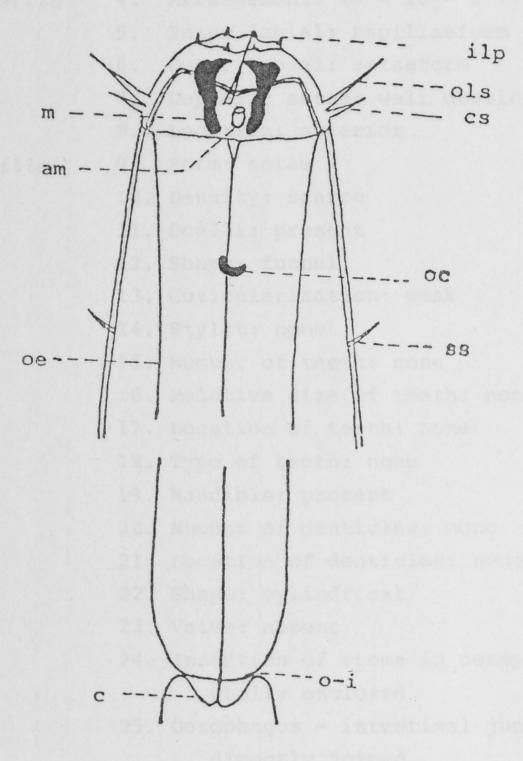
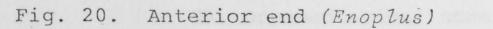


Fig. 19. Anterior end (Tobrilus)

3.1.19.1 Attributes (Tobrilus):

Amphids	1.	Shape: pocket-like
	2.	Size relative to head diameter): medium
	3.	Location: cervical
Cephalic sensilla	4.	Arrangement: $(6 + 10[= 6 + 4])$
	5.	Inner labial: papillaeform
	6.	Outer labial: setaeform
	7.	Cephalic setae: well developed
	8.	Location: anterior
Somatic sensilla	9.	Form: none
	10.	Density: none
	11.	Ocelli: absent
Stoma	12.	Shape: multichamber
	13.	Cuticularisation: weak
Armature	14.	Stylet: none
	15.	Number of teeth: one
	16.	Relative size of teeth: small
	17.	Location of teeth: median
	18.	Type of teeth: solid
	19.	Mandible: absent
	20.	Number of denticles: none
	21.	Location of denticles: none
Oesophagus	22.	Shape: cylindrical
	23.	Valve: absent
	24.	Insertion of stoma in oesophagus:
		partly enclosed
	25.	Oesophagus - intestinal junctions:
		indirectly joined
	26.	Cardia: well developed
Cuticle	27.	Cephalic helmet: absent
	28.	Annulation: none
	29.	Ornamentation: none
	30.	Extraneous materials: absent





3.1.20.1 Attributes	(Enoplus):
Amphids	1. Shape: pocket-like
	2. Size relative to head diameter): indistin
	3. Location: extreme anterior
Cephalic sensilla	4. Arrangement: $(6 + 10[= 6 + 4])$
	5. Inner labial: papillaeform
	6. Outer labial: setaeform
	7. Cephalic setae: well developed
	8. Location: anterior
Somatic sensilla	9. Form: setae
	10. Density: scarce
	11. Ocelli: present
Stoma	12. Shape: funnel
	13. Cuticularisation: weak
Armature	14. Stylet: none
	15. Number of teeth: none
	16. Relative size of teeth: none
	17. Location of teeth: none
	18. Type of teeth: none
	19. Mandible: present
	20. Number of denticles: none
	21. Location of denticles: none
Oesophagus	22. Shape: cylindrical
	23. Valve: absent
	24. Insertion of stoma in oesophagus:
	wholly enclosed
	25. Oesophagus - intestinal junction:
	directly joined
	26. Cardia: well developed
Cuticle	27. Cephalic helmet: present
	28. Annulation: none
	29. Ornamentation: none
	30. Extraneous materials: absent

3.1.21 Oncholaimellus (Chitwood and Chitwood, 1974;

Timm, 1967):

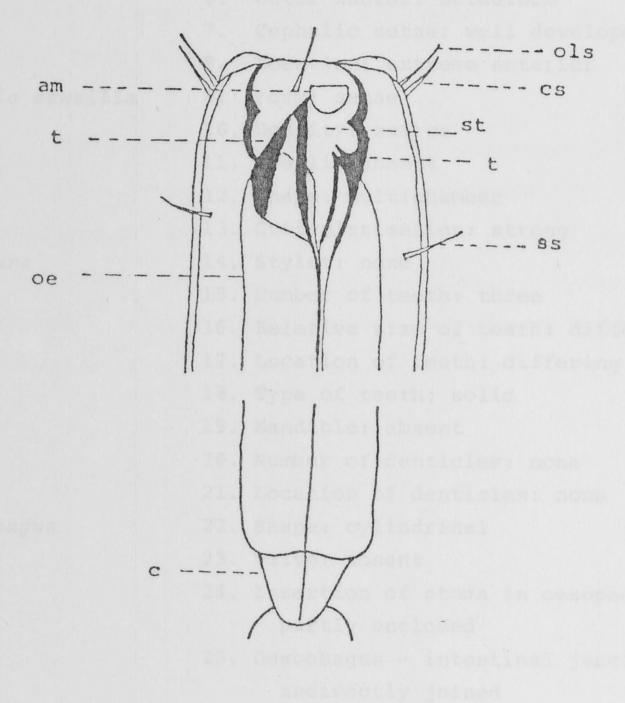


Fig. 21. Anterior end (Oncholaimellus)

Amphids1. Shape: pocket-like2. Size relative to head diameter: small3. Location: extreme anterior4. Arrangement: (6 + 10[= 6 + 4])5. Inner labial: papillaeform6. Outer labial: setaeform7. Cephalic setae: well developed8. Location: extreme anterior9. Form: setae	3.1.21.1 Attributes	icholaimellus):
 3. Location: extreme anterior 4. Arrangement: (6 + 10[= 6 + 4]) 5. Inner labial: papillaeform 6. Outer labial: setaeform 7. Cephalic setae: well developed 8. Location: extreme anterior 	Amphids	Shape: pocket-like
Cephalic sensilla 4. Arrangement: (6 + 10[= 6 + 4]) 5. Inner labial: papillaeform 6. Outer labial: setaeform 7. Cephalic setae: well developed 8. Location: extreme anterior		Size relative to head diameter: small
 5. Inner labial: papillaeform 6. Outer labial: setaeform 7. Cephalic setae: well developed 8. Location: extreme anterior 		Location: extreme anterior
6. Outer labial: setaeform7. Cephalic setae: well developed8. Location: extreme anterior	Cephalic sensilla	Arrangement: $(6 + 10[= 6 + 4])$
 Cephalic setae: well developed 8. Location: extreme anterior 		Inner labial: papillaeform
8. Location: extreme anterior		Outer labial: setaeform
		Cephalic setae: well developed
Somatic sensilla 9. Form: setae		Location: extreme anterior
	Somatic sensilla	Form: setae
10. Density: scarce		Density: scarce
ll. Ocelli: absent		Ocelli: absent
Stoma 12. Shape: multichamber	Stoma	Shape: multichamber
13. Cuticularisation: strong		Cuticularisation: strong
Armature 14. Stylet: none	Armature	Stylet: none
15. Number of teeth: three		Number of teeth: three
16. Relative size of teeth: differing size		Relative size of teeth: differing sizes
17. Location of teeth: differing locations		Location of teeth: differing locations
18. Type of teeth: solid		Type of teeth: solid
19. Mandible: absent		Mandible: absent
20. Number of denticles: none		Number of denticles: none
21. Location of denticles: none		Location of denticles: none
Oesophagus 22. Shape: cylindrical	Oesophagus	Shape: cylindrical
23. Valve: absent		Valve: absent
24. Insertion of stoma in oesophagus: partly enclosed		
25. Oesophagus - intestinal junction:		
indirectly joined		
26. Cardia: well developed		
Cuticle 27. Cephalic helmet: absent		
28. Annulation. None		Annulation. None
29. Ornamentation: none		Ornamentation: none
30. Extraneous materials: absent		Extraneous materials: absent

3.2 Enlarged Group

A second group of genera was taken, drawn from a group of type genera (Appendix 2.2), all of which have been described by De Coninck in Traité de Zoologie (1965). The attributes related to this additional group were listed and their taxonomic data were added to the initial data matrix, to form an enlarged matrix representing the enlarged group (Table 2).

The same procedures as already described for the initial group, were used to obtain a phenogram for the enlarged group. The generic list of the related phenons were tabulated, and the first phenon line was compared with De Coninck's intra-groups. Percent differences were used as a measure of intra-group (close generic) stability.

3.2.1 Attributes (Haliplectus)

Amphids	l.	Shape: circular or simple spiral
	2.	Size (relative to head diameter): small
	3.	Location: cervical
Cephalic Sensilla	4.	Arrangement: $(6 + 6 + 4)$
	5.	Inner labial: papillaeform
	6.	Outer labial: papillaeform
	7.	Cephalic setae: ?
	8.	Location: ?
Somatic sensilla	9.	Form: none
	10.	Density: none
	11.	Ocelli: absent
Stoma	12.	Shape: elongated tubular
	13.	Cuticularisation: none
Armature	14.	Stylet: none
	15.	Number of teeth: none
	16.	Relative size of teeth: none
	17.	Location of teeth: none
	18.	Type of teeth: none
	19.	Mandible: absent
	20.	Number of denticles: none
	21.	Location of denticles: none
Oesophagus	22.	Shape: double bulb
	23.	Valve: present
	24.	Insertion of stoma in oesophagus: wholly enclosed
	25.	Oesophagus-intestinal junction: directly joined
	26.	Cardia: none
Cuticle	27.	Cephalic helmet: absent
	28.	Annulation: distinct
	29.	Ornamentation: none
	30.	Extraneous materials: absent

3.2.2 Attributes	(Lin	homoeus)
Amphids	1.	Shape: circular or simple spiral
	2.	Size (relative to head diameter): large
	3.	Location: cervical
Cephalic sensilla	4.	Arrangement: $(6 + 10 [= 6 + 4])$
	5.	Inner labial: papillaeform
	6.	Outer labial: setaeform
	7.	Cephalic setae: well developed
	8.	Location: extreme anterior
Somatic sensilla	9.	Form: setae
	10.	Density: thin
	11.	Ocelli: absent
Stoma	12.	Shape: cup
	13.	Cuticularisation: none
Armature	14.	Stylet: none
	15.	Number of teeth: one
	16.	Relative size of teeth: medium
	17.	Location of teeth: posterior
	18.	Type of teeth: solid
	19.	Mandible: absent
	20.	Number of denticles: none
	21.	Location of denticles: none
Oesophagus	22.	Shape: terminal bulb
	23.	Valve: absent
	24.	Insertion of stoma in oesophagus: partly enclosed
	25.	Oesophagus-intestinal junction: directly joined
	26.	Cardia: weakly developed
Cuticle	27.	Cephalic helmet: absent
	28.	Annulation: none
	29.	Ornamentation: none
	30.	Extraneous materials: absent

3.2.3 Attributes	(Mon	hystera)
	7	Shaper simple spiral
Amphids	1.	Shape: circular
	2.	Size (relative to head diameter): small
	3.	Location: cervical
Cephalic sensilla		Arrangement: $(6 + 10 [= 6 + 4])$
	5.	Inner labial: papillaeform
	6.	Outer labial: setaeform
	7.	Cephalic setae: weakly developed
	8.	Location: extreme anterior
Somatic sensilla	9.	Form: setae
	10.	Density: thin
	11.	Ocelli: absent
Stoma	12.	Shape: very small
	13.	Cuticularisation: none
Armature	14.	Stylet: none
	15.	Number of teeth: none
	16.	Relative size of teeth: none
	17.	Location of teeth: none
	18.	Type of teeth: none
	19.	Mandible: absent
	20.	Number of denticles: none
	21.	Location of denticles: none
Oesophagus	22.	Shape: cylindrical
	23.	Valve: absent
	24.	Insertion of stoma in oesophagus: partly enclosed
•	25.	Oesophagus-intestinal junction: directly joined
	26.	Cardia: none
Cuticle	27.	Cephalic helmet: absent
	28.	Annulation: distinct
	29.	Ornamentation: none
	30.	Extraneous materials: absent

3.2.4 Attributes (Spirina)

Amphids	1.	Shape: simple spiral
	2.	Size (relative to head diameter): medium
	3.	Location: extreme anterior
Cephalic sensilla	4.	Arrangement: $(6 + 6 + 4)$
	5.	Inner labial: papillaeform
	6.	Outer labial: papillaeform
	7.	Cephalic setae: well developed
	8.	Location: extreme anterior
Somatic sensilla	9.	Form: setae
	10.	Density: thin
	11.	Ocelli: absent
Stoma	12.	Shape: multichamber
	13.	Cuticularisation: weak
Armature	14.	Stylet: none
	15.	Number of teeth: three
	16.	Relative size of teeth: small
	17.	Location of teeth: differing location
	18.	Type of teeth: solid
	19.	Mandible: absent
	20.	Number of denticles: none
	21.	Location of denticles: none
Oesophagus	22.	Shape: terminal bulb
	23.	Valve: present
	24.	Insertion of stoma in oesophagus: wholly enclosed
	25.	Oesophagus-intestinal junction: directly joined
	26.	Cardia: well developed
Cuticle	27.	Cephalic helmet: absent
	28.	Annulation: smooth
	29.	Ornamentation: none
	30.	Extraneous materials: absent

3.2.5 Attributes (Dasynemella)

Amphids	1.	Shape: simple spiral or crook-like
	2.	Size (relative to head diameter): medium
	3.	Location: cervical
Cephalic sensilla	4.	Arrangement: $(6 + 10 [= 6 + 4])$
	5.	Inner labial: papillaeform
	6.	Outer labial: setaeform
	7.	Cephalic setae: well developed
	8.	Location: extreme anterior
Somatic sensilla	9.	Form: setae
	10.	Density: scarce
	11.	Ocelli: absent
Stoma	12.	Shape: very small
	13.	Cuticularisation: none
Armature	14.	Stylet: none
	15.	Number of teeth: none
	16.	Relative size of teeth: none
	17.	Location of teeth: none
	18.	Type of teeth: none
	19.	Mandible: absent
	20.	Number of denticles: none
	21.	Location of denticles: none
Oesophagus	22.	Shape: terminal bulb
	23.	Valve: absent
	24.	Insertion of stoma in oesophagus: not or
	0.5	wholly enclosed
	25.	Oesophagus-intestinal junction: directly jointed
	26.	Cardia: none
Cuticle	27.	Cephalic helmet: present
	28.	Annulation: coarse
	29.	Ornamentation: overlapping scutes
	30.	Extraneous materials: absent

3.2.6 Attributes (Comesoma)

	1	Change multipuinel
	1.	
Amphids	2.	
	3.	Location: cervical
Cephalic sensilla		Arrangement: $(6 + 6 + 4)$
		Inner labial: papillaeform
	6.	Outer labial: papillaeform
		Cephalic setae: well developed
	8.	Location: cervical
Somatic sensilla	9.	Form: setae
	10.	Density: thin
	11.	Ocelli: absent
Stoma	12.	Shape: very small
	13.	Cuticularisation: none
Armature	14.	Stylet: none
	15.	Number of teeth: none or other
	16.	Relative size of teeth: none or other
	17.	Location of teeth: none or other
	18.	Type of teeth: none or other
	19.	Mandible: absent
	20.	Number of denticles: none or other
	21.	Location of denticles: none or other
Oesophagus	22.	Shape: gradually enlarged to posterior
	23.	Valve: absent
	24.	Insertion of stoma in oesophagus: partly or wholly enclosed
	25.	Oesophagus-intestinal junction: directly joined
	26.	Cardia: none or weakly developed
Cuticle	27.	Cephalic helmet: absent
	28.	Annulation: smoothe
	29.	Ornamentation: punctation
	30.	Extraneous materials: absent

•

3.2.7 Attributes (Cyatholaimus)

Amphids	1.	Shape: multispiral
	2.	Size (relative to head diameter): medium
	3.	Location: cervical
Cephalic sensilla	4.	Arrangement: $(6 + 10 [= 6 + 4])$
	5.	Inner labial: papillaeform
	6.	Outer labial: setaeform
	7.	Cephalic setae: weakly developed
	8.	Location: extreme anterior
Somatic sensilla	9.	Form: papillae
	10.	Density: scarce
	11.	Ocelli: absent
Stoma	12.	Shape: cup
	13.	Cuticularisation: none
Armature	14.	Stylet: none
	15.	Number of teeth: none or other
	16.	Relative size of teeth: none or other
	17.	Location of teeth: none or other
	18.	Type of teeth: none or other
	19.	Mandible: absent
	20.	Number of denticles: none
	21.	Location of denticles: none
Oesophagus	22.	Shape: cylindrical
	23.	Valve: absent
	24.	Insertion of stoma in oesophagus: partly enclosed
	25.	Oesophagus-intestinal junction: directly joined
	26.	Cardia: none
Cuticle	27.	Cephalic helmet: absent
	28.	Annulation: distinct
	29.	Ornamentation: punctation
	30.	Extraneous materials: absent

3.2.8 Attributes (Ironus)

Amphids	1.	Shape: pocket-like
	2.	
	3.	Location: cervical
Cephalic sensilla		Arrangement: $(6 + 10 [= 6 + 4])$
1	5.	
	6.	
	7.	Cephalic setae: well developed
	8.	Location: anterior
Somatic sensilla	9.	Form: none
	10.	Density: none
	11.	Ocelli: absent
Stoma	12.	Shape: elongated tubular
	13.	Cuticularisation: strong
Armature	14.	Stylet: none
	15.	Number of teeth: three
	16.	Relative size of teeth: small
	17.	Location of teeth: posterior or anterior
	18.	Type of teeth: solid
	19.	Mandible: absent
	20.	Number of denticles: none
	21.	Location of denticles: none
Oesophagus	22.	Shape: cylindrical
	23.	Valve: absent
	24.	Insertion of stoma in oesophagus: wholly enclosed
	25.	Oesophagus-intestinal junction: directly joined
	26.	Cardia: well developed
Cuticle	27.	Cephalic helmet: absent
	28.	Annulation: none
	29.	Ornamentation: none
	30.	Extraneous materials: absent

3.2.9 Attributes (Phanoderma)

Amphids	1.	Shape: pocket-like
	2.	Size (relative to head diameter): indistinct
	3.	Location: extreme anterior
Cephalic sensill	a 4.	Arrangement $(6 + 10 [= 6 + 4])$
	5.	Inner labial: papillaeform
	6.	Outer labial: setaeform
	7.	Cephalic setae: well developed
	8.	Location: anterior
Somatic sensilla	9.	Form: setae
	10.	Density: scarce
	11.	Ocelli: present
Stoma	12.	Shape: very small
	13.	Cuticularisation: none
Armature	14.	Stylet: none
	15.	Number of teeth: none
	16.	Relative size of teeth: none
	17.	Location of teeth: none
	18.	Type of teeth: none
	19.	Mandible: absent
	20.	Number of denticles: none
	21.	Location of denticles: none
Oesophagus	22.	Shape: gradually enlarged to posterior
	23.	Valve: absent
	24.	Insertion of stoma in oesophagus: wholly enclosed
	25.	Oesophagus-intestinal junction: directly joined
	26.	Cardia: none
Cuticle	27.	Cephalic helmet: present
	28.	Annulation: none
	29.	Ornamentation: none
	30.	Extraneous materials: absent

30. Extraneous materials: absent

3.3 Coding

- i) Amphids:
 - Shape (N). Code: pocket-like, 1; circular,
 2; simple spiral, 3; multispiral, 4; crooklike, 5; elongated crook, 6; question mark, 7; vesicular, 8.
 - 2. Size relative to head diameter (0). Code: indistinct, 1; small, 2; medium, 3; large, 4.
 - 3. Location (B). Code: cervical, (O); extreme anterior, 1.
- ii) Cephalic sensilla:
 - 4. Arrangement (B). Whether inner, outer labial and cephalic sensilla are in three circles, or the outer labial and cephalic sensilla comprise one circle. Code: (6 + 6 + 4), 0; (6 + 10 [= 6 + 4]), 1.
 - 5. Inner labial (B). Code: papillaeform, 0; setaeform, 1.
 - 6. Outer labial (B). Code: papillaeform, 0; setaeform, 1.
 - 7. Cephalic setae (B). Code: weakly developed, 0; well developed, 1.

- 8. Location (B). Code: Anterior, 0; extreme anterior, 1.
- iii) Somatic sensilla:
 - 9. Form (N). Code: none, 1; papillaeform, 2; setae, 3; mixed, 4.
 - 10. Density (0). Code: none, 1; scarce, 2; thin,
 3; dense, 4; very dense, 5.
 - 11. Ocelli (B). Code: absent, 0; present, 1.
- iv) Stoma (Buccal cavity):
 - 12. Shape (N). Code: very small, 1; short and narrow tubular, 2; elongated tubular, 3; funnel, 4; flask, 5; multichamber, 6; cup, 7; other, 8.
 - 13. Cuticularisation (0). Code: none, 1; weak, 2;
 strong, 3.
 - v) Armature:
 - 14. Stylet (N). Code: none, 1; lateral, 2; central,
 3.
 - 15. Number of teeth (N). Code: none, 1; one, 2; three, 3; other, 4.
 - 16. Relative size of teeth (N). Code: none, 1; small, 2; medium, 3; massive, 4; differing sizes, 5.

- 17. Location of teeth (N). Code: none, 1; posterior, 2; median, 3; anterior, 4; differing locations, 5; other, 6.
- 18. Type of teeth (N). Code: none, l; hollow, 2; solid, 3; other, 4.
- 19. Mandible (B). Code: absent, 0; present, 1.
- 20. Number of denticles (N). Code: none, 1; one, 2; two, 3; more, 4; other, 5.
- 21. Location of denticles (N). Code: none, 1; posterior, 2; median, 3; other, 4.

vi) Oesophagus:

- 22. Shape (N). Code: cylindrical, 1; gradually enlarged to posterior, 2; terminal bulb, 3; double bulb, 4; multi-bulb, 5; other, 6.
- 23. Valve (B). Code: absent, 0; present, 1.
- 24. Insertions of stoma in oesophagus (N). Code: not enclosed, 1; partly enclosed, 2; wholly enclosed, 3.
- 25. Oesophagus-intestinal junction (B). Code: indirectly joined, 0; directly joined, 1.
- 26. Cardia (N). Code: none, 1; weakly developed, 2; well developed, 3.

vii) Cuticle:

- 27. Cephalic helmet (B). Code: absent, 0; present, 1.
 - 28. Annulation (0). Code: none, 1; smooth, 2; distinct, 3; coarse, 4; very coarse, 5.
- 29. Ornamentation (N). Code: none, 1; punctation,
 2; plates, 3; scutes, 4; overlapping scutes, 5.

30. Extraneous materials (B). Code: absent, 0; present, 1.

7	6	2	3	5	2	2	2	3	4	6	2	1.0.0	-				1	1	1	
											•	2,3		4	3	8	8	1		1
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1	0	1	1	0	1	1	1	0	1	1	1	1	Ö	1	0	1	1	0	0	1
3	3	1	1	2	3	3	2	3	3	2	1	4	1	1	3	3	4	1	3	3
3	3	1	1	3	3	3	2	3	3	2	1	4	1	1	3	3	5	1	2	2
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1	1	1	2	1	1	1	3	1	1	1	1	1	1	1	1	1	1	1	1	1
1	3	1	1	2	1	1	1	3	2	1	2	1	2	2	1	1	1	2	1	3
1	3	1	1	2	1	1	1	2	4	1	3	1	3	3	1	1	1	2	1.	5
1	4	1	1	2	1	1	1	5	3	1	3	1	3	2	1	1	1	3	1	5
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1	1	1	3	2	1	1	1	1	1	1	3	1	3	1	3	1	1	1	1	1
4	3	4	2	1	3	1	4	3	3	3	3	3.4	3	1	1	6	5	1	1	1
0	0	0	0	0	1	0	0	1	1	0	1	0	1	0	0	0	1	0	0	0
2	1	2	3	2	3	2	1	3	3	3	3	3	3	2	3	2	1	2	3	2
1	1	.1	0	1	1.	1	1	1	1	1	1	0	1	0	1	1	1	0	1	0
3	3	3	3	1	3	1	2	1	2	1'	1	3	1	2	1	1	1	3	3	3
0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
2	2	3	3	1	2	4	2	4	5	4	4	3	3	3	2	5	5	1	1	1
1	1	1	1	1	1.	3	1	2	1	5	4	1	2	2	2	2	2	1	1	1
0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	1	0	0	0	0

Table 1. Data matrix of "initial group".

																	1	ų.			0.01	2 2	~	2 1	2 1				
7	6	2	3	5	2	2	2	3	4	6	2	2.3	- 5	4	3	8	8	1 1	1	1	2,3	2,3		3	3.5	4	4	1	1
3	3		3	3	4	4	4	4	4	3	4	3	3	3	2	4	4	3	1	2	2	4	2	3	3	3	3	3	1
0	0		1	0		0	0	0	_0	0	0	1	_1	0	0		1	0	1	1	0	0	0	1	0	0	0	0	1
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0	0	0	0	1	0	1	1	0	1	1	0	1	0	1	1	0	0	1	1	1	*	1	0	1	1	1	0	1	1
1	1.	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	0	1	1	0	1	0	1	1	1
1	0	1	1	0	1	1	1	0	1	1	1	1	ó	1	0	1	1	0	0	1	•	1	1	1	1	1	1	0	0
3	3	1	1	2	3	3	2	3	3	2	1	4	1	1	3	3	4	1	3	3	1	3	3	3	3	3	2	1	3
3	3	1	1	3	3	3	2	3	3	2	,1	4	1	1	3	3	5	1	2	2	1	3	3	3	2	3	2	1	2
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
2	4	3	6	6	1	5	3	6	4	1	6	1	6	4	6	2	2	6	4	6	3	7	1	6	1	1	7	3	1
2	3	1	1	3	1	1.	1	2	1	2	3	1	3	1	1	1	1	2	2	3	1	1	1	2	1	1	1	3	1
1	1	1	2	-1	1	1	3	1	1	1	1	1	1	1	1	1	1	1	11	1	1	1	1	1	1	1	1	1	1
1	3	1	1	2	1	1	1	3	2	1	2	1	2	2	1	1	1	2	1	3	1	2	1	3	1	1.4	1,4	3	1
1	3	1	1	2	1	1	1	2	4	1	3	1	3	3	1	1	1	2	1	5	1	3	1	2	1	1,6	1,6	2	1
1	4	1	1	2	1	1	1	5	3	1	3	1	3	2	1	1	1	3	1	5	1	2	1	5	1	1,6	1.6	2,4	1
1	3	1	1	3	1	1	1	3	3	1	3	1	2	3	1	1	1	3	1	3	1	3	1	3	1		1,4		1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0		0	0	0
1	1	1	2	3	1	1	1	1	1	1	2	1	3	1	4	1	1	1	1	1	1	1	1	1	1	1.5	1	- 1	1
1	1	1	3	2	1	1	1	1	1	1	3	1	3	1	3	1	1	1	1	1	1		1	1	1			1	1
4	3	4	2	1	3	1	4	3	3	3	3	3.4	3	1	1	6	5	1	1	1	4	3	1		3	2		1	2
0	0	0	0	0	1	0	0	1	1	0	1	0	1	0	0	0		0	0	0		1							
2		2	3	2	3			3	3		3	3	3	2	3	2	1	2	3	******	1	0	0			0		0	
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3		3	3	1	3			1		1	1	1	1	2		1		3			1	1	1	1	1	1	1	1	1
0		10	0		0	1		0		.1		0	0		0	0	0	0		0	0	2	1	3		1,2	1	3	1
						1					1	1		1				1		1									
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1	1	1	1	1	1	1	1		1	5	4	1		2	2	2	1	1	1		1	1			5	2	2		1
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Table 2. Data matrix of "enlarged group".

4. RESULTS

4.1 Phenons of the Initial Group

The horizontal phenon lines across the phenogram plotted for the initial group of marine nematodes (Fig. 22), established four phenon lines at the level of 0.60, 1.20, 1.80, and 2.40 values of similarity measure (Euclidean metric).

The first phenon line at 0.60 level, created seventeen 0.60-phenons that their generic list were tabulated (Table 3). The second, third, and fourth phenon lines formed nine, five and two phenons respectively, that their generic lists were also tabulated (Table 3).

The genera of the initial group were arranged according to De Coninck's, Andrássy's and Wieser's system of classification (Tables 4-6).

The first phenon line (0.60-phenons) were compared with De Coninck's, Andrássy's and Wieser's groupings (Tables 7-9).

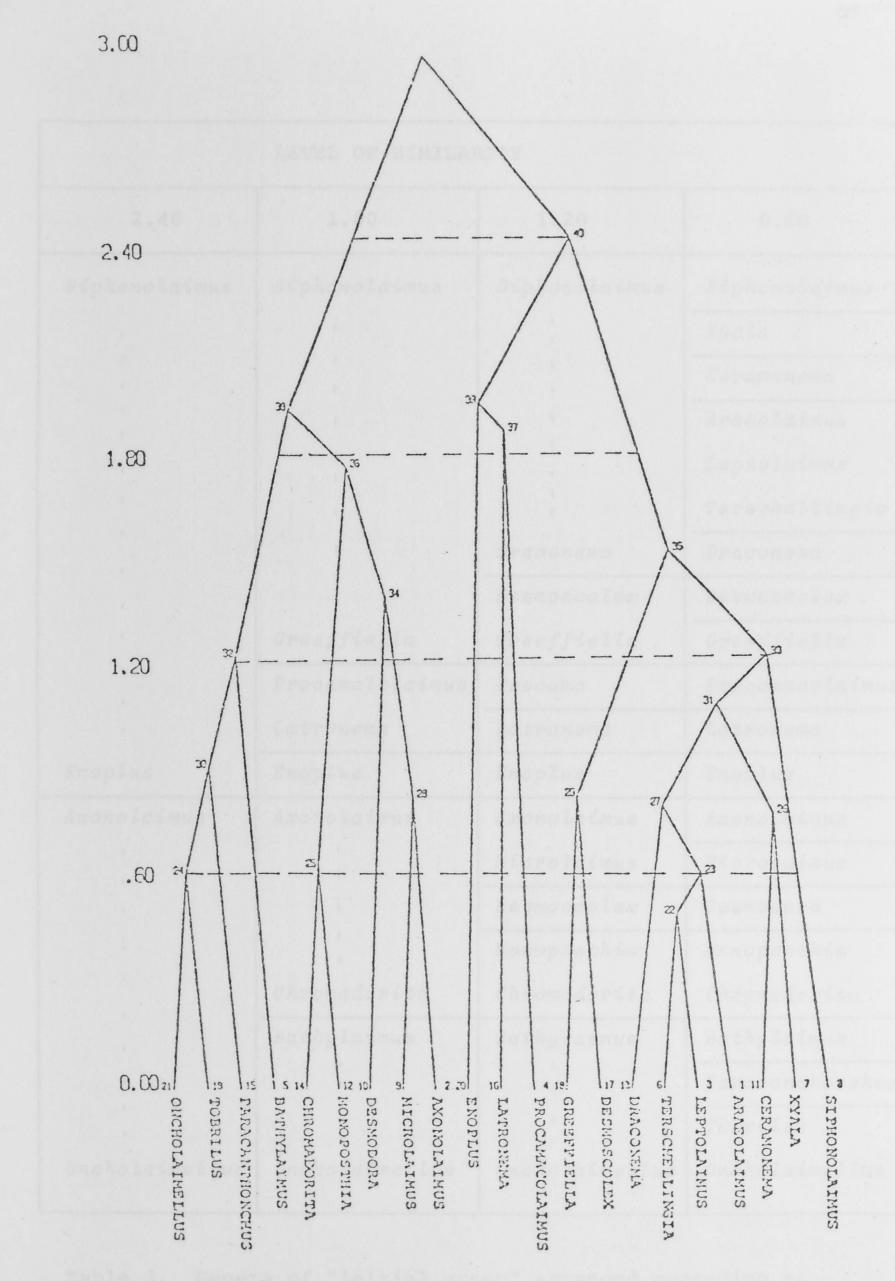


Figure 22. Phenogram of 21 genera of "initial group".

	LEVEL OF SIMILAF	RITY	
2.40	1.80	1.20	0.60
Siphonolaimus	Siphonolaimus	Diphonolaimus	Siphonolaimus
	1	:	Xyala
	1	Area Lafrina	Ceramonema
		1	Araeolaimus
	1	1	Leptolaimus
ı	1	1	Terschellingia
1	1	Draconema	Draconema
•	Ronkyeberida	Desmoscolex	Desmoscolex
1	Greeffiella	Greeffiella	Greeffiella
•	Procamalolaimus	Procama	Procamacolaimu
•	Latronema	Latronema	Latronema
Enoplus	Enoplus	Enoplus	Enoplus
Axonolaimus	Axonolaimus	Axonolaimus	Axonolaimus
•	1	Microlaimus	Microlaimus
	1	Desmoscolex	Desmodora
•	1	Monoposthia	Monoposthia
	Chromadorita	Chromadorita	Chromadorita
•	Bathylaimus	Bathylaimus	Bathylaimus
	1	Test	Paracanthonchu
	1	1	Tobrilus
Oncholaimellus	Oncholaimellus	Oncholaimellus	Oncholaimellus

Table 3. Genera of "initial group" arranged according to different phenon lines.

	TAXA		
SUBCLASS	ORDER	SUBORDER	SUPERFAMILY
Chromadoria	Araeolaimida	Araeolaimina	Araeolaimus Axonolaimus Leptolaimus Procamacolaimus
		Tripyloidina	Bathylaimus
	Monhysterida	Monhysterina	Terschellingia Xyala Siphonolaimus
	Desmodorida	Desmodorina	Microlaimus Desmodora Ceramonema Monoposthia
		Draconematina	Draconema
		Chromadorina	Chromadorita
	Chromadorita	Cytholaimina	Paracanthonchus Latronema
	Desmoscolecida	Desmoscolecina	Desmoscolex Greeffiella
Enoplia	Enoplida	Enoplina	Tobrilus Enoplus
	-	Oncholaimina	Oncholaimellus

Table 4. Genera of "initial group" arranged according to De Coninck's system of classification.

	TAXA	f BA			
SUBCLASS	ORDER	SUBORDER	SUPERFAMILY		
	Monhysterida	Monhysterina	Siphonolaimus Xyala Terschellingia		
	Desmoscolecida	Desmoscolecina	Greeffiella Desmoscolex		
	Araeolaimida	Araeolaimina	Leptolaimus Procamacolaimus Araeolaimus Axonolaimus		
. <i>7</i>		Tripyloidina	Bathylaimus		
Torquent	ida	Desmodorina	Microlaimus Monoposthia Desmodora Ceramonema		
	ador	Draconematina	Draconema		
	Chromadorida	Cyatholaimina	Paracanthonchus Latronema		
		Chromodorina	Chromadorita		
		Enoplina	Enoplus		
Penetrantia	Enoplida	Oncholaimina	Oncholaimellus		
		Tripylina	Tobrilus		

Table 5. Genera of "initial group" arranged according to Andrássy's system of classification.

GROUP		GENERA	
GROIPS		Ceramonema	
Argoo admus		Araeolaimus	naar-neishbs
Azono ainus		Leptolaimus	
1 - A	Cel	Terschellingia	different
Propostatoplatimo		Draconema	near-ceiteib:
Bathy olaus		Desmoscolex	
Seres ellingia .		Greeffiella	dden Losi
1 - B		Axonolaimus Bathylaimus Xyala	
008802020			
		Microlaimus Desmodora	
2 - A		Monoposthia	
Chromedorica		Chromadorita	need met gebo
Paradathonehus	Des	Paracanthonchus	
Catronoma	all and a	Procamacolaimus	
Deenoa		Enoplus -	
Great keile		Oncholaimellus	
2 – B		Tobrilus	
Onenologianoilue		Siphonolaimus Latronema	

Table 6. Genera of "initial group" arranged according to Wieser's system for classifying nematodes based on their method of feeding and type of food.

.

DE CONINCK'S GROUPS	0.60-PHENONS	INTRA-GROUPS
Araeolaimus	Siphonolaimus	near-neighbour
Axonolaimus	Xyala	п п
Leptolaimus	Ceramonema	different
Procamacolaimus	Araeolaimus	near-neighbour
Bathylaimus	Leptolaimus	п п
Terschellingia	Terschellingia	identical
Xyala	Draconema	different
Siphonolaimus	Desmoscolex	near-neighbour
Microlaimus	Greeffiella	н н
Desmodora	Procamacolaimus	different
Ceramonema	Latronema	н
Monoposthia	Enoplus	n
Draconema	Axonolaimus	11
Chromadorita	Microlaimus	near-neighbour
Paracanthonchus	Desmodora	н н
Latronema	Monoposthia	н н
Desmoscolex	Chromadorita	different
Greeffiella	Bathylaimus	11
Tobrilus	Paracanthonchus	п
Enoplus	Tobrilus	near-neighbour
Oncholaimellus	Oncholaimellus	identical
% differen	ce	42.8

Table 7. Comparison of first phenon line (0.60-phenons) with De Coninck's groupings.

ANDRÁSSY'S GROUPS	0.60-PHENONS	INTRA-GROUPS
Siphonolaimus	Siphonolaimus	identical
Xyala	Xyala	н
Terschellingia	Ceramonema	different
Greeffiella	Araeolaimus	near-neighbour
Desmoscolex	Leptolaimus	11 11
Leptolaimus	Terschellingia	different
Procamacolaimus	Draconema	н
Araeolaimus	Desmoscolex	near-neighbour
Axonolaimus	Greeffiella	11 11
Bathylaimus	Procamacolaimus	different
Microlaimus	Latronema	н
Monoposthia	Enoplus	п
Desmodora	Axonolaimus	п
Ceramonema	Microlaimus	near-neighbour
Draconema	Desmodora	и и
Paracanthonchus	Monoposthia	11 11
Latronema	Chromadorita	different
Chromadorita	Bathylaimus	- н
Enoplus	Paracanthonchus	п
Oncholaimellus	Tobrilus	near-neighbour
Tobrilus	Oncholaimellus	н п
% differe	47.6	

Table 8. Comparison of first phenon line (0.60-phenons) with Andrássy's groupings.

WIESER'S GROUPS	0.60-PHENONS	INTRA	-GROUPS		
Ceramonema	Siphonolaimus	differ	ent		
Araeolaimus	Xyala	п			
Leptolaimus	Ceramonema	near-n	eighbou		
Terschellingia	Araeolaimus	п	н		
Draconema	Leptolaimus	"	11		
Desmoscolex	Terschellingia		п		
Greeffiella	Draconema	11	н		
Axonolaimus	Desmoscolex	"	н		
Bathylaimus	Greeffiella	II	н		
Xyala	Procamacolaimus	different			
Microlaimus	Latronema	near-n	near-neighbou		
Desmodora	Enoplus	"	11		
Monoposthia	Axonolaimus	differ	ent		
Chromadorita	Microlaimus	near n	eighbou		
Paracanthonchus	Desmodora		11		
Procamacolaimus	Monoposthia	н	п		
Enoplus	Chromadorita	н	11		
Oncholaimellus	Bathylaimus	differ	ent		
Tobrilus	Paracanthonchus	·· - 11			
Siphonolaimus	Tobrilus	near-n	eighbou		
Latronema	Oncholaimellus	п	11		
% differe	nce	28.	5		

Table 9. Comparison of first phenon line (0.60-phenons) with Wieser's groupings.

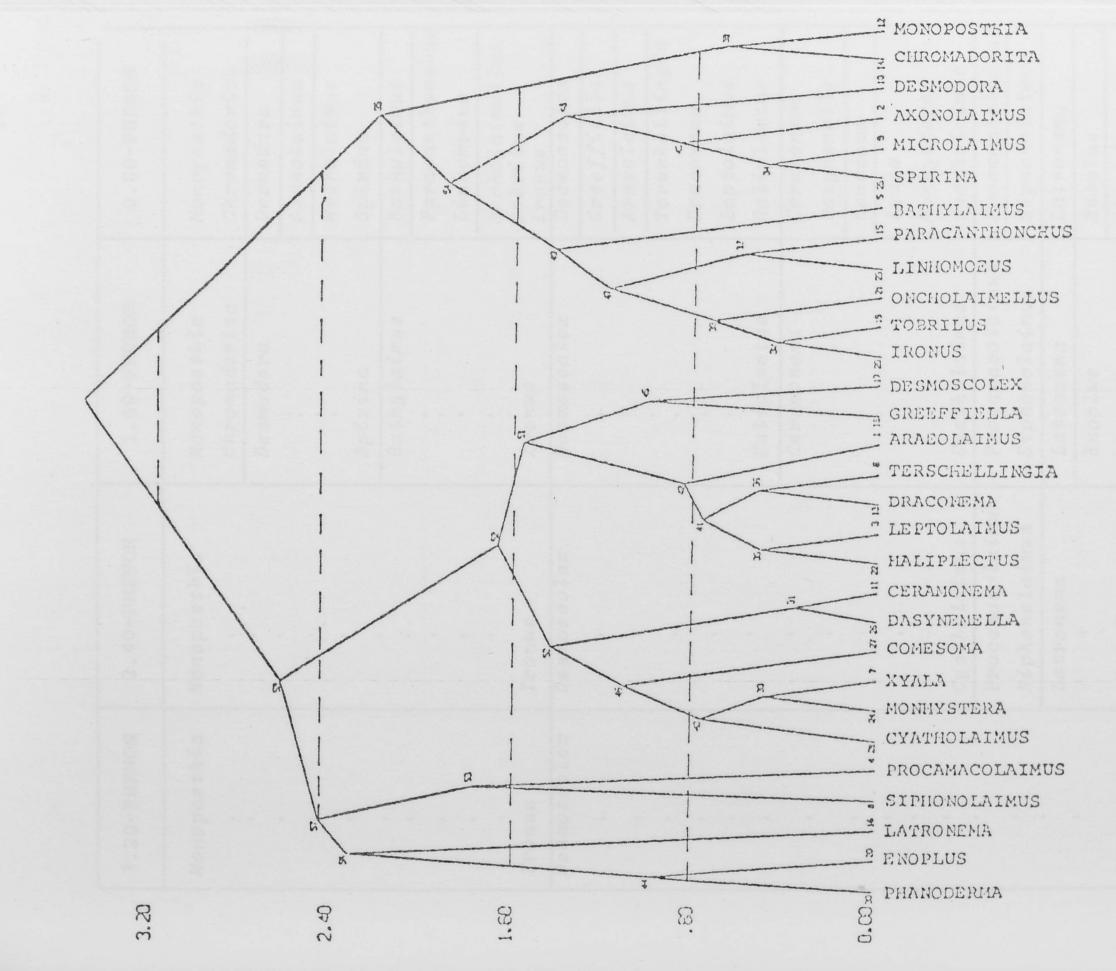
4.2 Phenons of the Enlarged Group

The phenon lines across the phenogram plotted for the enlarged group (Fig. 23), established four phenon lines at the level of 0.80, 1.60, 2.40 and 3.20 values of similarity measure.

The first phenon line at 0.80 level, created nineteen 0.80-phenons that their generic list was tabulated (Table 10). The second, third and fourth phenon lines formed eight, four and two phenons respectively, that their generic lists were also tabulated (Table 10).

The genera of the enlarged group were arranged according to De Coninck's system of classification (Table 11).

The first phenon line (0.80-phenons) was compared with De Coninck's groups of close genera (Table 12).



group". enlarged = 41 0 genera 30 44 0 Phenogram \sim 2 gure E H

3.20-PHENON	2.40-PHENON	1.60-PHENON	0.80-PHENON
Monoposthia	Monoposthia	Monoposthia	Monoposthia
		Chromadorita	Chromadorita
1		Desmodora	Desmodora
ı	1 as maile	Pako indina Aco	Axonolaimus
1	·	:	Microlaimus
I		Spirina	Spirina
·	1	Bathylaimus	Bathylaimus
1	1		Paracanthonchus
1			Linhomoeus
		annye, amina parta 124 m	Oncholaimellus
Ironus	Ironus	Ironus	Tobrilus Ironus
Desmoscolex	Desmoscolex	Desmoscolex	Desmoscolex
t.		•	Greeffiella
1		•	Araeolaimus
			Terschellingia
1	Geomodo et da	eenolorine Doo	Draconema
	•		Leptolaimus
• • • • • • • • • • • • • • • • • • • •	L	Haliplectus	Haliplectus
	ι -	Ceramonema	Ceramonema
		and the second	Dasynemella
	1	······	Comesoma
		aroma dopt na	Xyala
	Cheon dorida		Monhystera
	Cyatholaimus	Cyatholaimus	Cyatholaimus
•	Procamacolaimus	Procamacolaimus	Procamacolaimu
	Siphonolaimus	Siphonolaimus	Siphonolaimus
•	Latronema	Latronema	Latronema
		Enoplus	Enoplus
Phanoderma	Phanoderma	Phanoderma	Phanoderma

Table 10. Genera of "enlarged group" arranged according to different phenon lines.

SUBCLASS	ORDER	SUBORDER	SUPERFAMILY
	Araeolaimida	Araeolaimina	Araeolaimus Haliplectus Axonolaimus Leptolaimus Procamacolaimus
		Tripyloidina	Bathylaimus
Enoplia	Monhysterida	Monhystrina	Terchellingia Linhomoeus Monhystera Xyala Siphonolaimus
	Desmodorida	Desmodorina	Spirina Microlaimus Desmodora Dasynemella Ceramonema Monaposthia
		Draconematina	Draconema
	Chromadorida	Chromadorina	Comesoma Chromadorita
		Cyatholaimina	Cyatholaimus Paracanthonchus Latronema
	Desmoscolecida	Desmoscolecina	Desmoscolex Greeffiella
	Enoplida	Enoplina	Tobrilus Ironus Phanoderma Enoplus
	a one an Laca of the	Oncholaimina	Oncholaimellus

Table 11. Genera of "enlarged group" arranged according to De Coninck's system of classification.

DE CONINCK'S GROUP	0.80-PHENONS	INTRA-GROUP
Araeolaimus	Monoposthia	different
Haliplectus	Chromadorita	11
Axonolaimus	Desmodora	Le 3, " may be equal
Leptolaimus	Axonolaimus	11
Procamacolaimus	Microlaimus	near-neighbour
Bathylaimus	Spirina	пп
Terschellingia	Bathylaimus	different
Linhomoeus	Paracanthonchus	н
Monhystera	Linhomoeus	П
Yyala	Oncholaimellus	near-neighbour
Siphonolaimus	Tobrilus	u and u and
Spirina	Ironus	п п
Microlaimus	Desmoscolex	11 11
Desmodora	Greeffiella	пп
Dasynemella	Araeolaimus	different
Ceramonema	Terschellingia	Den Constrait in grad
Monoposthia	Draconema	н
Draconema	Leptolaimus	near-neighbour
Comesoma	Haliplectus	11
Chromadorita	Ceramonema	11 11
Cyatholaimus	Dasynemella	п п
Paracanthonchus	Comesoma	different
Satronema	Xyala	near-neighbour
Desmoscolex	Monhystera	n n
Greeffiella	Cyatholaimus	-different
Tobrilus	Procamacolaimus	п
Ironus	Siphonolaimus	п
Phanoderma	Latronema	n
Enoplus	Enoplus	near-neighbour
Oncholaimellus	Phanoderma	пп
% diff	erence	50.0

Table 12.

Comparison of first phenon line (0.80-phenons) with De Coninck's intra-group.

5. DISCUSSION

5.1 Initial Group

The formation of groups called phenons at different levels of resemblance (Table 3), may be equated with the usual rank categories such as family, suborder, order and subclass. However, phenons are objectively designed according to particular strategy, and their groups are **less integrated than the taxa of the Linnean** nomenclatural scheme, introduced to the classification of marine nematodes by De Coninck (Table 4) or Andrássy (Table 5).

5.1.1 Comparison of 0.60-phenons with De Coninck's groups

A comparison of the first phenon line (0.60-phenons) with De Coninck's groups (Table 7), showed considerable differences. This may be because De Coninck's system has been based on the interpretation of weighted characters; while this study used equally weighted attributes. It may further be due to the use of a slightly different set of characters.

5.1.2 Comparison of 0.60-phenons with Andrássy's groups

A comparison of the first phenon line with Andrássy's groups (Table 8), resulted in almost the same degree of difference to that observed with De Coninck's groups. The system proposed by Andrássy was based on the analysis of phylogenetic significance of the morphological characters. However, the present study merely depended on the phenetic relationships, regardless of any hypothetical evolutionary effects.

The system given by De Coninck (Table 4) and Andrássy (Table 5), also shows considerable differences between each other, reflecting the limitations of **a phylogenetic** approach to classification of marine nematodes.

5.1.3 Comparison of 0.60-phenons with Wieser's groups

A comparison of the first phenon line with Wieser's ecological groups (Table 9), indicated considerable agreement between two systems. This may be referred to adequate incorporation of attributes related to the buccal cavity in this study.

Wieser's ecological groupings were in part a phenetic approach by considering the relationships between the structure of buccal cavity and feeding habits among the marine nematodes. This criterion falls within the general concept of structure-functional relationships, and apparently is a practical and viable approach to classify the marine nematodes.

Although, Wieser's feeding categories were later modified by Boucher (1972-73), the nematode genera considered in this study did not fall in Boucher's new sub-divisions.

5.2 Enlarged Group

The addition of the new group (type genera), to the initial group, resulted in formation of new phenons (Table 10). A comparison of the first phenon line (0.80phenons) with De Coninck's groupings (Tables 11, 12) indicated that the type general had generally fused with their close generic neighbours. Given the preliminary nature of this study, the phenons reflected considerable intra-group (close generic) stability.

5.3 Conclusions

This study has shown that cluster analysis based on the similarity measure of Euclidean distance, using flexible sorting strategy, is a viable and potential method that can be used to elucidate the phenetic relationships of the marine nematodes.

The inter-relationships of classifications currently in use for marine nematodes show considerable difference and instability. This is probably because of phylogenetic speculations, which in the case of marine nematodes may not be a practical approach.

Increasing the number of nematode genera contained in the initial group has shown that the close generic relationships remain significantly stable. Taxonomy of marine nematodes could reach a phenetic stability by considering different sets of attributes and systematic increases in the number of genera that would sufficiently represent an overall generic spectrum of the marine nematodes.

> or of other form, but renely a small pore: post and planning abuent. Caudal and hypodernal cland protent fearcept Dorylainida and Dioctochymatinal. Caphalle sensilla setaerorm or papillaeform, often sensilla present on other parts of body, usually mataerorm. Usually male without burse (except honologiana, Oncholaimallus, Diplolaimeila, and

Angenine bestally difficult to distinguish, open h a pose, lebial lexcept in some Diployasteridaely Phasaids present. Candal and hypodermel slands appent. Cophalle semille debally papiliseform.

APPENDICES

 Adapted from De Coninck's Key to Families of Marine Nematodes (excluding Dorylaimida).

Amphids usually well developed, open spiral, pocket or of other form, but rarely a small pore; post anal phasmids absent. Caudal and hypodermal glands present (except Dorylaimida and Dioctophymatina). Cephalic sensilla setaeform or papillaeform, often sensilla present on other parts of body, usually setaeform. Usually male without bursa (except Anoplastama, Oncholaimellus, Diplolaimella, and Longidorus).

Adenophorea].

Amphids usually difficult to distinguish, open by a pore, labial (except in some Diplogasteridae). Phasmids present. Caudal and hypodermal glands absent. Cephalic senilla usually papillaeform, rarely setaeform. Usually no somatic papillae or setae, except in caudal region of male. Secernentea

 Amphids spiral, circular, vesicular, or derived from spiral. Caudal glands usually present. Chromadoria 2 Amphids subepithelial pockets with opening usually in form of horizontal slit, tubeform or forming a pore. Caudal glands present or absent.

Enoplia 31

2. Amphids without transparent turgescent membrane. When the cuticle is coarsely annulated extraneous material is not present. When there are glandular setae they are sub-ventral, not submedian dorsal.

Amphids cephalic with a turgescent transparent membrane (except Meylia spinosa). Cuticle distinct, often coarsely annulated, with extraneous material adhering. Usually dorsal surface with two submedian rows of glandular setae. Sometimes numerous, more or less irregular, cuticular protuberances, sometimes very numerous cuticular spines.

Desmoseolecida 29

3. Amphids usually a single spiral, or circular, or elongated crook or question mark. Cuticle usually smooth, sometimes annulated, but never coarsely so, and very rarely with punctation or other design. Never cephalic helmet. Amphids simple or multiple spiral, kidney shaped or with transverse slit. Cuticle always annulated, sometimes coarsely, often with punctations forming transverse lines. Often cephalic helmet present. 16

Amphids a simple spiral, elongated crook, question mark, rarely circular. Cephalic sensilla usually in 3 circles (6 + 6 + 4), rarely with posterior 2 combined (then head has 3 double lips and a well developed stoma).

Araeolaimida 5

ales with tubular preanal accessivy organs, o

Amphids circular, sometimes more or less evidently formed from closed spiral. Cephalic sensilla usually in 2 circles (6 + 10 [= 6 + 4]) sometimes 3 (6 + 6 + 4).

Monhysterida 14

5. Six lips. Cephalic sensilla in 3 circles, the posterior usually well developed. Gubernaculum not cyatholaimoid.

Araeolaimina 6

Three double lips. Cephalic sensilla in two circles, the latter from combination of posterior two (6 + 10 [= 6 + 4]). Gubernaculum cyatholaimoid, stoma nearly always well developed. Marine and freshwater.

Tripyloidina, Tripyloidoidea, one family: Tripyloididae, Type genus: Tripyloides de Man 1886. Oesophagus without posterior bulb containing valves (of Rhabditid form). Ovaries usually not reflexed.

Oesophagus with posterior bulb with valves (of Rhabditid form). Ovaries reflexed. Plectoidea 13

 Males without tubular preanal accessory organs or numerous papillaeform accessory organs.

Males with tubular preanal accessory organs, or numerous papillae which reach the oesophagus region. Or, if these organs are absent, dorsal wall of stoma forms a stylet.

11

8

8. Stoma feeble, more or less cylindrical, cheilostome not re-inforced; amphids simple spiral, elongated crook, or sometimes circular (derived from closed spiral); sometimes on a cuticularised base. Araeolaimoidea 9

Stoma distinct, conical, usually with re-inforced cheilostome. Amphids a simple spiral, or more or less elongated crook, or circular.

Axonolaimoides, one family: Axonolaimidae, Type genus: Axonolaimus de Man 1889

9. Cephalic sensilla well developed, even when papillaeform. Oesophagus with corpus, isthmus, and terminal bulb, but the latter not very muscular, nor with strong internal cuticularisation.

Cephalic sensilla very reduced, stoma very narrow, elongated. Amphids circular, formed from closed spiral. Oesophagus with small median bulb with central cuticularisation, and with large terminal bulb, muscular with internal cuticularisation. Family: Haloplectidae, Type genus: Haliplectus Cobb 1913

10. Amphids simple spiral, or more or less elongated crook, or circular without circular supporting base. Family: Araeolaimidae, Type genus: Araeolaimus de Man 1880

Amphids very well developed, usually supported by cuticular base, an elongated elipse or crook with an elongated ventral arm.

Family: Diplopeltidae,
Type genus: Diplopeltis Cobb 1905

11. Male with tubular preanal accessory organs, or with very many papillaeform accessory organs reaching oesophagus.

109

10

Leptolaimoidea 12

Male rarely with tubular preanal accessory organs, but if this is so the dorsal wall of the stoma forms a stylet. Amphids simple spiral. Camacolaimoidea, one family: Camacolaimidae, Type genus: *Camacolaimus* de Man 1889

12. Males with preanal tubular accessory organs, often preceeded by long series of non-tubular accessory organs, beginning in oesophagus region. Cephalic sensilla in 3 circles. Marine, freshwater and soil. Family: Leptolaimidae,

Type genus: Leptolaimus de Man 1876

Males without preanal tubular accessory organs, but with a series of non-tubular accessory organs beginning in oesophageal region. Cephalic sensilla in 2 circles (6 + 10 [= 6 + 4]).

Family: Bastianiidae, Type genus: Bastiania de Man 1876

13. Lips normal, without strongly re-inforced borders, sometimes cuticular expansions, more or less branched, which can cover mouth. Amphids form question mark. Males with or without preanal tubular accessory organs. Cuticle annulated.

Family: Plectidae, Type genus: *Plectus* Bastian 1865

Lips jointed, strongly developed, with cuticularised borders. Amphids circular, spiral origin more or less evident, or very reduced in form of pore. Pro-, meso- and metastome cuticularisation not fused (Cephaloboid). Male without tubular preanal accessory organs. Cuticle annulated sometimes with rows of points.

Family: Teratocephalidae, Type genus: *Teratocephalus* de Man 1876

14. i) Stoma very variable, but not funnel-shaped or cylindrical, more or less long and wide. Oesophagus usually enlarged posteriorly, often distinct bulb, sometimes corpus, isthmus, and terminal bulb. Amphids usually a simple spiral, when circular formed from closed spiral. Cephalic sensilla in 2 or 3 circles. If 3 circles there is a well developed oesophagus with bulb or a cylindrical stoma of variable depth. Linhomoeoidea, one family: Linhomoeidae, Type genus: Linhomoeus Bastian 1865

ii) Stoma funnel-shaped, with little re-inforcement of the walls. Sometimes stoma has cuticularised walls, but then there are numerous subcephalic setae or the cuticle ornamented with rows of fine striae. Sometime stoma cylindrical and elongated, but then the anterior end of the body is drawn out and narrow. Amphids circular, very rarely spiral. Cephalic sensilla two circles, third row (cephalic of setae combined with second row (outer labial) of setae, or absent. Oesophagus cylindrical, gradually enlarged towards base, never with bulb.

Monhysteroidea 15

iii) Stoma very narrow, tubular, forming stylet. Oesophagus with elongated terminal bulb, sometimes with "free" oesophagus glands. Amphids large, circular. Cephalic sensilla variable, with 4 or 10 cephalic setae.

Siphonolaimoidea, one family: Siphonolaimidae, Type genus: Siphonolaimus de Man 1893

15. Stoma spaceous, more or less globular, with strong walls, partly "roughened". Cuticle annulated with rows of setae, which in sub-cephalic region are numerous and well developed.

> Family: Sphaeralaimidae, Type genus: Sphaerolaimus Bastian 1865

Stoma of various forms, a feeble funnel-shape, or barrel-shaped, with re-inforced walls, but never "roughened", or a relatively wide elongated cylinder, or two small successive chambers. Amphids circular, very rarely spiral. Cephalic sensilla in 2 circles, often joined by variable number of sub-cephalic setae. The second circle of 6, 10 or more setae. Cuticle smooth, or annulated, often with rows of sensory setae of variable length, or rarely with annulation ornamented with rows of small longitudinal striae, Exceptionally male possess a bursa,

Family: Monhysteridae, Type genus: *Monhystera* Bastian 1865

16. Amphids simple or multi-spiral, never kidney-shaped, sometimes elongated crook on cephalic area with helmet. Cephalic sensilla in 3 circles, sometimes multiple sub-cephalic setae, rarely in two circles (in which case a helmet is present and cuticle has wide annulic with "keels".) Cuticle without punctuations.

Desmodorida 17

Amphids simple or multi-spiral, kidney-shaped, never elongated crook. Cephalic sensilla in 2 or 3 circles. Never with helmet. Cuticle always ornamented with punctations or other designs forming rows.

Chromadorida 25

17. Without sub-ventral preanal ambulatory setae.

Desmodorina 18

19

With preanal sub-ventral ambulatory setae, Draconematina 24

18. Cuticle annulated, finely or distinctly, without longitudinal "keels". Annuli never very wide.

19. No cephalic helmet.

Spirinoidea 20

With distinct cephalic helmet. Desmodoroidea, one family: Desmodoridae, Type genus: *Desmodora* de Man 1889

20. First circle of cephalic sensilla (labial papillae) poorly developed, second and third circle more distinct, the third usually setaeform, close to anterior tip of head. Cephalic region devoid of annuli, generally not as wide as high. When as wide or wider than high, amphids are at very anterior tip of head and sub-cephalic setae found on cephalic region. Ovaries usually double, reflexed.

Family: Spirinidae, Type genus: Spirina Bastian 1865

Cephalic sensilla in 3 distinct circles, first two usually papillaeform, third circle setaeform. Cephalic region marked by absence of annuli, nearly as high as wide, often somewhat globular. Ovaries paired, not reflexed.

Family: Microlaimidae, Type genus: *Microlaimus* de Man 1880

Ceramonematoidea 22

No cephalic helmet, cephalic region differentiation limited to enlarged anterior cuticular annulus. Amphids circular, or simple or multi-spiral. Stoma armature present or absent.

Monoposthoidea 23

22. Cuticular plates very wide (100 or less along body) numerous (more than 400) with longitudinal "keels". First circle of cephalic sensilla papillaeform, second and third setaeform, separated or in single circle of 10 setae.

> Family: Dasynemellidae, Type genus: Dasynemella (Cobb 1920) Gerlach 1956

Cuticular plates less numerous (less than 300) wider (15 to 100 or more along length of body), with longitudinal "kells" and excressences overlapping adjacent plates.

Family: Ceramonematidae, Type genus: Ceramonema Cobb 1920 23.

Cuticular annulation very distinct, with longitudinal rows of spines in form of V. Stoma small, with dorsal and sub-lateral teeth. Anterior plates enlarged. Amphids circular. One or two spicules. Family: Monojosthiidae, Type genus: *Monojosthia* Bastian 1865

Cuticle annulation not very distinct, with numerous (20 or more) longitudinal rows of short setae. Stoma present or absent. Amphids spiral, simple or multiple. Dumpy.

Family: Richtersiidae, Type genus: Richtersia Steiner 1916

24. Glandular ambulatory setae usually in middle third of body, no setae at anterior end. Middle of body in S shape, preceeding ambulatory setae. Oesophagus and sometimes posterior part of body somewhat or distinctly enlarged. Amphids spiral.

Family: Epsilonematidae, Type genus: Epsilonema Steiner 1927

Glandular setae usually in posterior third of body, also present in cephalic region. Oesophageal region enlarged. Oesophagus with very strong anterior and posterior bulb, separated by very short isthmus. Amphids spiral, crook or horse-shoe, displaced to dorsal side of head.

Family: Draconematidae

Type genus: Draconema Cobb 1913

25. Amphids spiral or kidney-shaped. Cephalic sensilla in 3 circles.

Chromadorina 26

Amphids spiral. Cephalic sensilla in 2 circles. Cyatholaimina 27

26. Cuticle smooth with internal punctation. Amphids in multiple spiral. 4 cephalic setae, well developed. Stoma little developed, sometimes with denticules, rarely with tooth forming stylet. Oesophagus enlarged posteriorly.

Family: Comesomatidae, Type genus: *Comesoma* Bastian 1865

Cuticle annulated, with punctation forming rows or other designs. Amphids indistinct, spiral or more or less flattened kidney-shaped, sometimes distinct spiral and a little posterior.

Family: Chromadoridae,

Type genus: Chromadora Bastian 1965

27. Stoma hollow, with or without teeth, mesostome not developed. Sense organs extreme anterior in 2 circles (6 + 10 [= 6 + 4]). Amphids spiral.

Family: Cyatholaimidae,

Type genus: Cyatholaimus Bastian 1865

Choanolaimoidea 28

28. Stoma without strong mandibles, but prostome and mesostome well developed.

> Family: Choanolaimidae, Type genus: *Choanolaimus* de Man 1880

Stoma with 2 or 3 mandibles, usually strong. Family: Selachinematidae, Type genus: Selachinema Cobb 1915

29. Cuticle distinctly annulated, not completely covered in setae, often coarsely annulated, with extraneous material present.

Desmoscolecoidea 30

Cuticle annulated but completely covered with setae of various forms.

Family: Greeffiellidae, Type genus: *Greeffiella* Cobb 1922

30. Amphids spiral not on cephalic region between cephalic setae. Head of Desmoscolecid type.

Family: Meyliidae,

Type genus: Meylia Gerlach 1956

Amphids vesicular, without visible spiral structure, never sub-cephalic.

Family: Desmoscolecidae, Type genus: Desmoscolex Claparede 1863

31. Stoma entirely enclosed by oesophageal tissue. Enoplina 32

Stoma mostly free, only basal part enclosed by oesophageal tissue.

Oncholaimina 39

32. Cephalic cuticle simple. Oesophagus large, more or less cylindrical. Oesophago-intestinal valve (Cardin) well developed.

Tripyloidea 33

Cephalic cuticle double, with or without internal helmet. Oesophagus enlarged posteriorly. Enoploidea 34

33. Stoma more or less short, more or less cylindrical or barrel-shaped, sometimes walls not cuticularised and contiguous. Stoma armed with median or more or less posterior teeth.

> Family: Tripylidae, Type genus: Tripyla Bastian 1865

Stoma elongated, prismatic, armed with 3 small teeth at anterior extremity, or small denticles at extreme

posterior.

Family: Ironidae,

Type genus: Ironus Bastian 1865

34. Stoma lacks 3 massive longitudinal mandibles, neither hooked anteriorly nor forming a delicate framework with median mandibular tooth.

35

Stoma armed with 3 massive longitudinal mandibles each with two anterior hooks, or forming more or less a delicate framework with median tooth. Mandibles set off by cuticular ring. Sometimes stoma armature reduced. Sensilla (6 + 10 [= 6 + 4]). Amphids pockets.

Family: Enoplidae, Type genus: Enoplus Bastian 1865

35. Oesophagus more or less enlarged posteriorly, muscular not vesiculated and without crenellated contour.

36

Oesophagus with posterior enlarged, vesicular, with crenellated outline.

38

36. Female gonad opens normally by vulva some distance from anus.

Female gonad opens in rectum (or by vulva very close to anus, less than 3 diameters a part). Cuticle finely but distinctly annulated. Cephalic sensilla in 2 circles (6 + 10 [= 6 + 4]); amphids often indistinct.

Family: Lauratonematidae, Type genus: Lauratonema Gerlach 1953

37. Cephalic sensilla usually in 2 circles, six papillae or setae and a second of ten papillae or setae (6 + 6 + 4). Amphids a pocket. Family: Leptosomatidae,

Type genus: Leptosomatum Bastian 1865

Cephalic sensilla usually in 3 circles (6 + 6 + 4), rarely the last two little separated. Amphids usually wide open, with opening elongated longitudinally; rarely with narrow transverse slit.

Family: Oxystomatinidae, Type genus: Oxystomina (Buetschli 1874) Filipjev 1921

38. Stoma weakly developed; well developed lips, cuticularised, supported by internal helmet. Family: Phanodermatidae, Type genus: Phanoderma Bastian 1865 Stoma with dorsal stylet, elongated and pointed, carried by a large hollow basal part. Internal cephalic helmet well developed.

Family: Thoracostomopsidae, Type genus: Thoracostomopsis Ditlevsen 1919

39. Oesophagus cylindrical, never crenellated.

Family: Oncholaimidae, Type genus: Oncholaimus Dujardin 1845

the second s

Oesphagus enlarged gradually to posterior, sometimes crenellated or with multiple bulbs. Family: Eurystominidae, Type genus: Eurystomina Filipjev 1918

2. Alphabetic List of Nematode Genera

2.1 Initial Group

- (L) Aracolaimus de Man 1888
- (S) Axonolaimus de Man 1889
- (S) Bathylaimus Cobb 1894
- (S) Ceramonema Cobb 1920
- (S) Chromadorita Filipjev 1922
- (S) Desmodora de Man 1889
- (S) Desmoscolex Claparede 1863
- (L) Draconema Cobb 1913
- (S) Enoplus Dujardin 1845
- (L) Greeffiella Cobb 1922
- (S) Latronema Wieser 1954
- (S) Leptolaimus de Man 1876
- (S) Microlaimus de Man 1880
- (S) Monoposthia de Man 1889
- (S) Oncholaimellus de Man 1890
- (S) Paracanthonchus Micoletzky 1924
- (S) Procamacolaimus Gerlach 1954
- (S) Siphonolaimus de Man 1893
- (S) Terschellingia de Man 1888
- (S) Tobrilus Andrassy 1959
- (S) Xyala Cobb 1920

2.2 Type Genera:

Comesoma Bastian 1865

Cyatholaimus Bastian

Dasynemella Gerlach 1956

Haliplectus Cobb 1913

Ironus Bastian 1865

Linhomoeus Bastian 1865

Monystera Bastian 1865

Phanoderma Bastian 1865

Spirina Filipjev 1918

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