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The Systematics and Ecology of Free-living Marine Nematodes

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I Introduction

Nematodes are the most abundant metazoans in marine (littoral, estuarine, coastal and oceanic) sediments, extending from the high-water mark into the deepest oceanic trenches (Nicholas, 1975). All marine free-living nematodes are considered to be members of the meiobenthos; small organisms, mainly metazoans, which are separated from the larger macrobenthos either on a methodological basis (i.e. as all animals passing a 1 mm or a 0.5 mm sieve) or a taxonomic basis (i.e. particular animal groups such as Nematoda, Harpacticoida, Gastrotricha, Kinorhyncha, Tardigrada, Foraminifera etc. which consist exclusively or mainly of small species living in sediments). In most circumstances, nematodes are numerically the dominant group of the meiofauna. In fact, they usually comprise more than 90% of the metazoan fauna (McIntyre, 1971).

That nematodes are ecologically a very successful group is also demonstrated by their high species diversity. The number of species present in any one habitat is usually an order or magnitude greater than for any other major taxon (Platt & Warwick, 1980). In all, about 4000 species of free-living marine nematodes, belonging to some 450 genera, have been described to date, but many more remain to be discovered.

The ecology of marine meiofauna has been reviewed by Swedmark (1964), McIntyre (1969), Coull (1973) and Fenchel (1978). Nicholas (1975) and Platt & Warwick (1980) have considered some general aspects of the biology of marine free-living nematodes.

Ecological research involving nematodes was restricted at first to treating nematodes as a single taxonomic unit of the meiofauna, also considered to be a functional unit. We know now that nematodes are ecologically very heterogeneous and that they occupy different trophic positions in benthic food webs. These differences may be as large between families of marine nematodes as they are between orders in macrobenthic groups. This trophic diversity was first examined by Wieser (1953a) who divided nematodes into four groups according to the structure of the buccal cavity, by postulating that morphological differences are linked to different feeding mechanisms : selective deposit-feeders; non-selective deposit-feeders; epigrowth feeders; predators and omnivores. The validity of this classification has been questioned since several important exceptions exist (Wieser, 1960, Boucher; 1972; Ward, 1975), but Wieser's proposition has remained an important tool in the interpretation of nematode assemblages. However, more direct methods have become available and in the last decade important ecological and systematic advances have been made. Experimental work involving the cultivation of species in the laboratory started in the late sixties and permitted much new information to be obtained on different aspects of nematode ecology. Field work has progressed both in methodology and in the number of habitats and geographical areas which have been investigated. In systematics, the number of people involved was higher in the seventies than ever before and about 42 papers were published each year in the period 1971-1975 by about 50 marine nematologists, describing about 111 new taxa yearly (Gerlach, 1980).

In this paper we attempt to synthesize research on the systematics and ecology of marine free-living nematodes. It is not our aim to evaluate all papers published in the last decades but rather to give an overview of current research and problems.

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† Ranking of authors is at random.

II Systematics

At the Second Symposium on Aquatic Nematodes, Gerlach (1980) mentioned that about 4,000 marine nematode species are known and estimated that more than 20,000 remain undescribed. A review of the development and current status of the systematics of this group thus seems appropriate, especially for novice nematologists who face problems which were elegantly discussed by Hope (1971) who stressed the need for proper study.

Although an historical review of systematic discussions involving nematodes would have to go back to Rudolphi (1819), free-living nematodes were first treated as a separate group by Bastian (1865), who stimulated further work in the field. Only from 1876 onwards did marine nematodes become the target of a series of nematologists.

De Man (1876-1928) was a pioneer in this field and he laid down the basis of modern generic and specific descriptions. His detailed descriptions and fine illustrations, which are still of great value to-day, gave evidence of his clear perceptive sight. Among his contemporaries, only Cobb (1920), considered as one of the greatest nematologists, is comparable to him. Cobb's precise descriptions and figures remain often unsurpassed.

The first classification of all the marine free-living nematode species known at that time was the work of Filipjev (1918/21 in russian; English translation in 1968/70). He constructed a system based on observations of the total morphology, rather than on a single character as others before him had done. Significant new interpretations of this basic classification were proposed by Cobb (1919), Schuurmans Stekhoven & De Coninck (1933), Maggenti (1963, 1970), Gadea (1972, 1973), Andrassy (1976) and most recently by Lorenzen (1981). A comparison of systematic schema of the Nematoda down to orders, by the more outstanding authorities, is given in table 1. Besides these major classifications, other authors also made very useful contributions, but they restricted themselves to taxa found in particular geographic regions such as : the North Sea , Schuurmans Stekhoven (1935); the Baltic Sea, Schneider (1939); North America, Cobb (1920), Chitwood (1951); the Chilean coast, Wieser (1953b, 1954, 1956); the East coast of North America, Wieser & Hopper (1967). Except for the last and Cobb (1920), these works are characterized by an extensive collection of dichotomous keys, which are of incomparable help as long as they remain up to date. A third group of taxonomic works are catalogues or checklists. They reflect the taxonomic hierarchy and/or provide a list of known genera or even species but not necessarily a diagnosis of the taxa : in this category are the catalogues of Stiles & Hassall (1905, 1920), Baylis & Daubney (1926), Hope & Murphy (1972) and the comprehensive Bremerhaven checklist of Gerlach & Riemann (1973/1974). Whereas the others reflect the descending hierarchy of the Adenophorea down to the generic level, the Bremerhaven list is based on the then generally accepted six marine orders down to family, subfamily, genus and species level. To each taxon created in the Bremerhaven list is added a nearly complete chronological outline of the pertinent literature, with special reference to nomenclatorial changes, synonymisations and reviews. From a practical point of view this checklist can be regarded as a milestone, though some changes in classification were made which unfortunately have not been justified.

A new development in marine nematology is the use of pictorial keys, as in the Illustrated Guide of Tarjan (1980), which offers much information for novice nematologists. Unfortunately it is incomplete, several genera being omitted. Also, it is based on the classification of Andrassy (1976), which has already been subject to severe criticism (Coomans, 1977 and Lorenzen, 1981). Special reference must be made to the books of Chitwood & Chitwood (1950) and De Coninck (1965) for their comprehensive study of the external and internal morphology, histology and systematics, provided with many superb illustrations.

1. Evaluation of the different classifications and their characteristics (table 1).

Filipjev (1918/21) distinguished five families based on the structure of the cuticle, the amphids, pharynx, somatic musculature, female gonads and tail. In 1934 he raised these families to the rank of ordines (table 1) and included parasitic forms.

The system of Filipjev was adopted by Schuurmans Stekhoven & De Coninck (1933), who reduced the value of the structure of the buccal cavity "which can be greatly influenced by the environment" and the gonads "which only differ in secondary characteristics". The structure of the amphids and the symmetric relationships of the anterior end seemed to be more conservative. Schuurmans Stekhoven (1935) recognised five orders in the Nematoda errantia, with the Araeolaimoidea as a new order.

Two classes, the Aphasmidea and Phasmidea, differentiated primarily by the presence or absence of phasmids were established by Chitwood (1933, 1937) and by Chitwood & Chitwood (1950). This nomenclature has later been replaced by the terms Adenophorea and Secernentea to prevent confusion with Insects. Some twelve characters were used in differentiating the two classes, but gonads were not considered.

De Coninck (1965) recognized these divisions, as well as the categories Chromadoria and Enoplia first erected by Pearse (1942). His classification was based primarily on the amphid form (especially in the Chromadoria) and secondly on the position and structure of the cephalic sense organs. The position of the outlets of the pharyngeal glands is an important systematic character

Table 1 Diagrammatic representation of the chief interpretations of the classification of nematodes, from class down to order level.

Author	Subclass	Infraclass	Order
FILIPJEV, 1934			Enoplata Chromadorata Desmoscolecata Monhysterata
			Anguillulata Oxyurata Ascaridata Spirurata Filariata Dioctophymata Trichurata
SCHUURMANS-STEKHOVEN, 1935	Nematoda errantia		Enoploidea Chromadoroidea Araeolaimoidea Monhysteroidea Desmoscolecoidea
	Nematoda parasitica		Anguilluloidea
CHITWOOD & CHITWOOD, 1950	Aphasmidia		Chromadorida Enoplida
	Phasmidia		
DE CONINCK, 1965	Adenophorea	Chromadoria	Araeolaimida Monhysterida Desmodorida Chromadorida Desmoscolecida
		Enoplia	Enoplida Dorylaimida
	Secernentea		
HOPE & MURPHY, 1972	Adenophorea		Enoplida Chromadorida Desmodorida Desmoscolecida Monhysterida Araeolaimida
GERLACH & RIEMANN, 1973/74	Adenophorea		Araeolaimida Desmoscolecida Monhysterida Desmodorida Chromadorida Enoplida
ANDRASSY, 1976	Torquentia (=Chromadoria)		Monhysterida Desmoscolecida Araeolaimida Chromadorida
	Penetrantia (=Enoplia)		Enoplida Dorylaimida
	(Secernentia)		
LORENZEN, 1981	Adenophorea	Chromadoria	Chromadorida Monhysterida
		Enoplia	Enoplida Trefusiidae Dorylaimidae
	Secernentea		

within the Enoplia. The classification of De Coninck is considered by most marine nematologists to be one of the most authoritative.

The division Adenophorea-Secernentea was first rejected by Goodey (1963) because phasmids are difficult to distinguish. Moreover, he found a primary division on that basis unacceptable since *Euteratocephalus crassidens*, a species which is clearly Aphasmidian in most respects, also has phasmids. He was followed by Maggenti (1963, 1970) and Gadea (1972, 1973) but their findings were not generally accepted among marine nematologists.

Andrassy (1976) subdivided the nematodes into three subclasses : Torquentia (=Chromadoria), Secernentia (=Secernentea) and Penetrantia (=Enoplia). This division was made after comparison of a set of characters in the Adenophorea and Secernentea, which revealed the Adenophorea as a very heterogeneous group. But, despite the subdivision between Adenophorea and Secernentea being unbalanced and artificial, it continues to be used by some nematologists for the sake of convenience.

Table 2 Characters used in the taxonomy of marine free-living nematodes.

1. **Habitat**
2. **Cuticle : structure**
3. **somatic setae**
4. **Cephalic region**
   a. **general shape**
   b. **cephalic helmet**
   c. **sense organs : number, length and position**
5. **Amphids : shape and position**
6. **Buccal cavity : general structure and dentation**
7. **Pharynx**
   a. **general structure**
   b. **radial canals**
   c. **glands**
8. **Ventral gland**
   a. **position**
   b. **ventral pore**
9. **Cardia : shape**
10. **Female reproductive system**
    a. **number of ovaries**
    b. **structure : outstretched or reflexed ovaries**
    c. **vulva position**
    d. **Demanian system**
    e. **position of ovaries in relation to intestine**
11. **Male reproductive and copulatory system**
    a. **number of testes**
    b. **spicules**
    c. **gubernaculum**
    d. **accessory organs**
    e. **position of testes in relation to intestine**
12. **Tail region**
    a. **general shape**
    b. **caudal glands**
    c. **spinneret**
13. **Metanemes**

Lorenzen (1981) agreed with the subclasses Adenophorea and Secernentea, the latter being a homogeneous group always characterized by the presence of only one anterior testis and the reduction of the caudal glands. Within the Adenophorea, the Enoplia were differentiated from the Chromadoria only by possessing an untwisted spiral amphid. Within the Chromadoria, the Monhysterida were separated by possessing outstretched ovaries. This scheme was based on a careful examination of the phylogenetic impact of twelve characteristics, of which two, the position of the gonads in relation to the intestine and a new organ-system, the metanemes (sense organs), were hitherto unknown. Characters often used in marine nematode systematics are listed in table 2. We will only discuss the Adenophorea (excluding Dorylaimida) down to family level. Although Lorenzen's classification is the most recent, we have used the presently generally accepted categories as proposed by Gerlach & Riemann (1973/74). For each order, a table is given reflecting the evolutionary trends implicit in the various classifications used by marine nematologists. (see tables 3 to 8). The numbers in these tables refer to the characteristics listed in table 2.

To prevent confusion, we use the terminology suggested in the Round Table Discussions at the First Workshop on the Systematics of Marine Free-living Nematodes (summarized by Coomans, De Coninck. & Heip, 1979): we do not use the terminology of Lorenzen (1981) describing the cephalic sense organs but rather follow De Coninck (1942, 1965). Coomans (1979) is followed for the terminology of the body regions.

2. Araeolaimida (table 3)

The order Araeolaimida was erected by De Coninck & Schuurmans Stekhoven (1933) on the basis of its primitive characters : the amphids are a simple spiral and three separate circles of cephalic sense organs (6+6+4) are present.

According to the position and structure of the cephalic sense organs and the structure of the pharynx, this order was further split up by De Coninck (1965) into two suborders, six superfamilies and ten families.

Members of the Tripyloidina were transferred to the order Enoplida by Gerlach & Riemann (1973/74) but returned to their original position by Andrassy (1976). The suborders established by the latter are based on differences in the number of cephalic sense organs, the structure of the buccal cavity, pharynx and male genital supplements. The latter two characters also served to distinguish the four superfamilies in the Araeolaimina.

After comparing the system of De Coninck (1965) and Gerlach & Riemann (1973/74), Vitiello (1974) considered the systematics of this order as unsatisfactory and suggested some new families.

Recently, this order has been split by Lorenzen (1981): taxa with outstretched ovaries are transferred to the Monhysterida and taxa with antidromous reflexed ovaries to the Chromadorida. A new suborder Leptolaimina was created in the Chromadorida to include all taxa not belonging to the Chromadorina. The new suborder is composed of 18 families which previously belonged mainly to the Araeolaimida.

The Axonolaimoidea, characterized by a spiral or loop-shaped amphid, comprise the Axonolaimidae (six tooth-like structures at anterior end of the buccal cavity), the Comesomatidae (amphids with at least 2 ½ turns), the Diplopeltidae (four cephalic setae dominant and amphid with only one turn) and the Coninckiidae raised to family level for its unique combination of characters.

The new position of the Comesomatidae seems rather peculiar : they were placed within the Axonolaimoidea because of their spiral amphid but are exceptional by the punctated cuticle and the position of the cephalic sense organs; the amphids, spiral with at least 2 ½ turns are unique within the Monhysterida!

3. Desmoscolecida (table 4)

These distinctive marine nematodes with short fusiform bodies and well developed annules were raised to ordinal level by Filipjev (1929). He also differentiated two families : Desmoscolecidae (cuticle coarsely annulated, no 'hairy' coat) and Greeffiellidae (cuticle not coarsely annulated, 'hairy' coat). The superfamily Desmoscolecoidea was established by Schuurmans Stekhoven (1935) and the Greeffielloidea by De Coninck (1965). The latter author added a new family Meyliidae, with spiral amphids, to accomodate the genus *Meylia.*

In a revision of the order, Timm (1970) presented a general introduction to the biology and anatomy of the Desmoscolecida, with a critique on evolutionary trends and keys for all genera. He rejected the distinction between the Desmoscolecidae and Greeffiellidae since he considered *Progreeffiella* and *Hapalomus* as transitional forms. Meyliidae was excluded from the group because it lacks typical characters. There remained only one family : Desmoscolecidae (with one subfamily).

This order was again revised by Freudenhammer (1975), with a comprehensive and detailed study on the morphology and terminology within that group. The systematic analysis was based mainly on two characteristics : the structure and position of the somatic setae and on the structure of the cuticle, desmen and appendages. He also restricted the order to one family (with three subfamilies). That same year, a revision of the Greeffiellinae by Schrage & Gerlach (1975) appeared.

The view of Andrassy (1976) resembles that of the De Coninck (1965), although he raised the Meyliidae to superfamily level.

An extensive review and discussion of the origin and evolution of this order together with work at the generic level was given by Decraemer in a series of papers (1974a, b, c, d; 1976a, b; 1977a, b, c; 1978a, b, c, d). Taxonomic divisions were based upon the type of setal pattern, according to Lorenzen (1969), and upon the male reproductive system.

A quite different view was presented by Lorenzen (1981), who rejected the order and placed the Desmoscolecoidea in the Monhysterida because of their outstretched ovaries. The Meyliidae were reintroduced within this group because of the presence of cephalic setae on peduncles.

4. Monhysterida (table 5)

According to Filipjev (1918/21, 1934) outstretched ovaries are characteristic for nematodes within the Monhysterida. The amphids are always distinctly spiral, horseshoe shaped or circular. Two families were distinguished by the presence (Linhomoeidae) or absence (Monhysteridae) of an apophysis on the gubernaculum.

Members of this order were placed by Chitwood & Chitwood (1950) in the suborder Monhysteroidea of the Chromadorida, characterized by circular amphids, outstretched ovaries and convergent ends of the pharyngeal radii. They recognized three families : Monhysteridae, Linhomoeidae and Siphonolaimidae; the latter differentiated by its styletiform buccal cavity.

De Coninck (1965) distinguished four families by the structure of the buccal cavity : variable (Linhomoeidae), barrel shaped or cylindrical (Sphaerolaimidae, Monhysteridae), small, tubulous or with spear (Siphonolaimidae), and the structure of the amphids, following Filipjev in this character. It is clear that the Linhomoeidae constitute a very heterogeneous group.

Andrassy (1976) recognized eight families. The most important difference is the female genital system being paired in the Linhomoeidae and unpaired in the remaining ones. The latter were further distinguished as by previous authors on the structure of the buccal cavity and on the presence (Diplolaimelloidea) or absence of a bursa. Except for some shifts within the order, no significant changes were made.

The order Monhysterida was extended by Lorenzen (1981) and now unites ten families with outstretched ovaries from different orders. On that basis, all members of the Desmoscolecida were incorporated. The Monhysteroidea, previously revised by Lorenzen (1978c), were characterized by only one (anterior) ovary and were divided into three families based on the position (in relation to intestine) and number of the gonads and the length of the cephalic setae : Monhysteridae (one testis (anterior); testis and ovary on the right), Xyalidae (two testes and two ovaries; anterior gonad on the left, posterior gonad on the right), Sphaerolaimidae (cephalic setae longer than the outer labial setae). New observations within the Xyalidae were discussed in Lorenzen (1977). The close relationship of the Linhomoeidae with the Siphonolaimidae was adopted from Riemann (1977a) : both possess subventral gland ducts in the stomatal region.

5. Desmodorida (table 6)

Species of this group were placed by Filipjev (1934) in the subfamilies Richtersiinae, Desmodorinae, Monoposthiinae, Epsilonematinae and Draconematinae of the order Chromadorata.

Chitwood & Chitwood (1950) gathered them within the superfamily Desmodoroidea of the Chromadorina. They differentiated three families by body form and presence or absence of ambulatory and glandular setae : Desmodoridae, Epsilonematidae and Draconematidae.

De Coninck (1965) erected the Desmodorida to accomodate species which differ from the Chromadorida by the head capsule and cuticle without punctations. Presence or absence of adhesion tubes put them respectively into Draconematina or Desmodorina. The latter is subdivided into seven families on the basis of a set of characters such as : cuticle with or without ridges, presence or absence of the cephalic capsule, structure of the cephalic sense organs, the ovaries, the number and size of the annulations.

Andrassy (1976) did not separate the Desmodorina and Draconematina from the Chromadorida. Species with widely coiled amphids, prominent helmet and reflexed ovaries could belong either to the Metachromadoridae, Desmodoridae or Ceramonematidae; whereas species with narrowly coiled amphids, less prominent helmet and outstretched ovaries could belong either to Microlaimidae, Richtersiidae or Xenellidae. Species with peculiar body form could belong either to the Epsilonematidae or Draconematidae.

Lorenzen (1981) rejected the ornamentation of the cuticle as a criterion to differentiate the Desmodorida and kept the members of this order within the Chromadorida, Chromadorina, the latter being characterized by the twelvefolded vestibulum and a dorsal tooth which is bigger or as large as the two ventrosublateral teeth. The Desmodoridae were included with the Epsilonematidae and Draconematidae as they have only one (anterior) testis.

In his revision of the Microlaimidae, Jensen (1978) erected a new family : Molgolaimidae, based on the structure of the head region, the shape of the pharynx, the position of the ventral pore, the shape of the tail, the structure of the gonads and the ornamentation of the cuticle.

Lorenzen (1981) lowered the rank of the Molgolaimidae to a subfamily in the Desmodoridae, because of the structure of the gonads and its inability to be dyed with cottonblue.

The superfamily Ceramonematoidea, a restricted and homogeneous group, was erected by De Coninck (1965). Haspeslagh (1972, 1973, 1978) considered the very thick cuticle with prominent annulations and longitudinal crests, and the well developed head capsule as important taxonomic characters. According with these, the family Dasynemellidae of De Coninck (1965) was suppressed and the Xenellinae were raised to the family rank. Andrassy (1976) lowered the rank of the Ceramonematoidea and placed them within the Desmodoroidea.

Lorenzen (1981) did not agree with the system of Haspeslagh (1972, 1973) which was based on only two characters. The whole group is transferred : the Xenellidae to the Trefusiida, because of the similar shape of the amphid and the presence of only one posterior ovary; the Ceramonematidae no longer fitted into the Desmodoroidea because the vestibulum is not twelvefolded and they were placed in the Leptolaimina.

A comprehensive monograph of the superfamily Draconematoidea was published by Allen & Noffsinger (1978). The most profound taxonomic feature of this group is the ventral adhesion tubes, responsible for the leech-like movement. Number and size vary between species within different genera and between immature forms and adults. A new family was created : Prochaetosomatidae, closely related to Draconematidae.

Lorenzen (1981) lowered the rank of the Prochaetosomatidae to a subfamily of the Draconematidae. Differences between Draconematidae and Epsilonematidae have been mentioned earlier (Lorenzen, 1974). The earlier taxonomy of Steiner (1931) was based only on the exoskeleton, but Lorenzen (1973) studied the total morphology and postembryonic development of the Epsilonematidae.

6. Chromadorida (table 7)

Filipjev (1934) included taxa of the Araeolaimida, and Chitwood & Chitwood (1950) all other taxa, except the Enoplida, among the Chromadorida, and Filipjev characterized the Chromadoridae as having an annulated cuticle and a twelvefolded vestibulum.

Chitwood & Chitwood (1950) had classified them into four families, gathered within the superfamily Chromadoroidea. The families were distinguished mainly by the shape of the amphid and the cardia : Chromadoridae (amphids kidney to spiral shaped, cardia small), Microlaimidae (amphids spiral with one or two turns, cardia elongate), Cyatholaimidae (amphids uni-to multi-spiral, cardia well developed, triradiate) and Tripyloididae (amphids spiral with one or two turns, cardia well developed, triradiate). Remarkable is the unusual position of the latter family within the Chromadoroidea.

According to De Coninck (1965), the position of the cephalic sense organs and the shape of the amphids were definitely different between the Cyatholaimidae and the Chromadoridae and both gave rise to the creation of two suborders. The whole order consisted of five families : Comesomatidae, Chromadoridae, Cyatholaimidae, Choanolaimidae and Selachinematidae, differentiated from each other by features such as the cuticle, amphid, cephalic sense organs, buccal cavity, pharynx and male supplements.

This order was again extended by Andrassy (1976), who included the species of the Desmodorida (within two suborders). Reviewing the current taxa of the Chromadorida, the general idea of De Coninck (1965) was adopted (also two suborders); four of the five families were raised to superfamily level, but the Comesomatidae were transferred to the Cyatholaimina because of their multispiral prominent amphid, making the Chromadorina a more homogeneous group.

The conventional species of the order Chromadorida were classified by Lorenzen (1981) within the superfamily Chromadoroidea (with annulated cuticle), the latter were placed together with the Desmodoroidea and Microlaimoidea in the Chromadorina, Chromadorida. The Chromadorina brought together species with a twelvefolded vestibulum and corresponded closely with the Chromadoridae of Filipjev (1934). The Richtersiidae (synonymized with Selachinematidae) is incorporated within the Chromadoroidea, whereas the Comesomatidae is transferred to the Monhysterida. The classification of the latter family in the Chromadorida has been generally accepted since the work of De Coninck (1965).

The Comesomatidae were first reviewed by Wieser (1954), who established a key to the genera based on the structure of the spicules. Vitiello (1969) added two differential characteristics : the presence or absence of lateral differentiation in the cuticle and the structure of the buccal cavity.

In the revision of Jensen (1979), the family is characterized within the Chromadorida by a copulatory apparatus provided with an apophysis, females with outstretched ovaries, presence of marginal tubes in the pharynx and a non sclerotized and enlarged tail tip. The genera were arranged in three subfamilies : Sabatieriinae, Dorylaimopsinae and Comesomatinae, in agreement with Lorenzen (1981).

The family Chromadoridae was classified by Wieser (1954) primarily on the shape of the amphids, the nature of the dorsal tooth (solid or hollow) and the cuticle (homogeneous or heterogeneous) and its associated lateral differentiations. The difficulty of distinguishing between solid and hollow teeth has led to much confusion (Inglis, 1970).

Wieser (1954) provided a key for the subfamily Cyatholaiminae based on the structure of the male genital apparatus, and particularly of the supplements. In recent papers, emphasis is placed on the position and structure of special body "pores" as a valuable taxonomic character (Hopper, 1972; Sharma *et al.*, 1978). The morphology of the pores has been examined by Inglis (1964) and by Wright & Hope (1968).

7 Enoplida (table 8)

Members of this large order were classified as family Enoplidae consisting of nine subfamilies, within the Enoplata and were characterized by a duplicated head cuticle (Filipjev, 1934).

According to Chitwood & Chitwood (1950) the distinction between the primarily aquatic forms (Enoplina) and primarily soil or parasitic forms is based on the presence of cephalic setae in the former. The aquatic species were grouped into six families, belonging to two main groups in which the cuticle of the head is (Enoplidae, Oncholaimidae) or is not duplicated (Tripylidae, Mononchidae, Ironidae).

Clark (1961) reclassified the order into five suborders utilizing a character proposed earlier by Chitwood : the arrangement of the pharyngeal glands and their ducts. On this basis the Mononchidae were transferred from the Tripyloidea to the Dorylaimina. The Alaimidae were transferred to a newly created suborder : Alaimina, possessing a number of Dorylaimoid and Tripyloid characters as well as some special ones of their own.

The distinction between primarily aquatic and primarily soil or parasitic species was made on a higher level by De Coninck (1965), and from then on the order Enoplida referred mainly to aquatic species. He made a clear distinction between the Enoplidae and the Oncholaimidae on the basis, respectively, of the buccal cavity being surrounded or not by pharyngeal tissue: he reduced both groups to subordinal rank.

According to Andrassy (1976) the lack of a duplicated head cuticle is important enough to remove the Tripylidae from the Enoplina and to create a new suborder : Tripylina. The order Enoplida then comprised 19 families, which can be defined by the typical structure of the head, the buccal cavity, the cephalic sense organs, the pharynx, male supplements and the position of the vulva. The Oxystominidae and Lauratonematidae were transferred from the Enoploidea to the Tripylina without adequate justification.

The order Enoplida is characterized according to Lorenzen (1981) primarily by the presence of a new feature : metanemes. This feature caused a restriction of the Enoplida, with the families Trefusiidae, Onchulidae and Lauratonematidae now forming (table 9) a new order : Trefusiida (without metanemes). Two other new taxa were created based on the position of the ventral gland (which was also a new criterion) : the Enoplacea (in the pharyngeal region) and the Oncholaimacea (postpharyngeal). The Enoploidea comprised forms with gonads at the left of the intestine and with males possessing a preanal tube. Within the Enoplida, 16 families were grouped, their particular characteristics are noted by numbers in table 8.

In a revision published by Platonova (1970), a new superfamily the Leptosomatoidea was distinguished from the Enoploidea by a cylindrical pharynx without crenate walls, buccal cavity indistinct or without obvious division, if teeth are present they are situated in front, the muscles nearly reaching the teeth. This superfamily comprised five families : Leptosomatidae, Anticomidae, Ironidae, Oxystominidae and Triodontolaimidae. Lorenzen (1978) rediscovered the only species of the Triodontolaimidae and concluded that this family is distinguished from the remaining families of the Enoplida by the unique structure of the buccal cavity.

Wieser (1953) provided a short monographic account of the family Enoplidae. He visualized an evolutionary path within the family based on the structure of the buccal cavity.

In his revision of the Enchelidiidae, Wieser (1953) drew attention to a distinct character differentiating the subfamilies Eurystominae and Enchelidiinae : the sexual dimorphism which only occurs within the latter. Exceptionally in marine nematode taxonomy, the female characters become more important than those of the males.

Within the order Enoplida, the family Oncholaimidae has been the most extensively studied. The first monograph on the Oncholaiminae (Kreis, 1934) is a comprehensive study on the morphology of this group, with a summary of the knowledge on the demanian system. This system was later studied in detail by Rachor (1970) for different genera. He considered it as a receptaculum seminis and evaluated it as a taxonomic character proper to the group. A system based on this character was worked out by Belogurov & Belogurova (1977) and a recent key to the genera of the Oncholaimina was presented by Belogurova (1977).

8. New Characters in the description of species.

Whereas the description of species became impoverished in terms of quality and number of characters after the time of de Man and Cobb, recently a change has been seen with new characters being described such as:

- different types and position of body pores in the Cyatholaimidae (Inglis, 1964; Wright & Hope, 1968; Hopper, 1972; Sharma *et al.*, 1978).
- pharyngeal glands opening in front of the nerve ring in the Linhomoeidae (Riemann, 1977) and the Desmoscolecida (Decraemer, 1976).
- two large ventrosublateral glands with long ducts, attached to the excretory ampulla of the ventral gland in *Sabatieria* (Riemann, 1977).
- male ejaculatory glands within the Xyalidae (Lorenzen, 1977).
- occurrence of additional cephalic setae being a sexual dimorphism or intraspecific variation in the Linhomoeidae (Hendelberg, 1977, 1979).
- position of the genital tract in relation to the intestine (Lorenzen, 1977, 1978c, 1981).
- stretch receptor organs (metanemes) in the Enoplida (Lorenzen, 1978b, 1981).
- different types of porids in the Microlaimidae and Molgolaimidae (Jensen, 1978).
- position of the ventral gland: pharyngeal or postpharyngeal (Lorenzen, 1981).
- description of juvenile stages (Lorenzen, 1973, 1974, 1978a, 1981 and Clasing, 1980).

More information is also given on intraspecific variability (Lorenzen, 1973, de Bovee, 1975).

Previously, too much of the classification and recognized groupings was based solely on bibliographic information. An important aspect of future work appears to be the redescription of most species taking into account the newly described morphological characters. In addition, investigations on the variability of the diagnostic characters and description of the juvenile stages should be undertaken.

9. Conclusion

The systematics of marine free-living nematodes is still not stabilized. New systems which try to reflect relationships between the different groups have been proposed about every fifteen years. Bearing in mind the number of new species described every year, this is quite understandable.

Whereas systematics should be based on as many characters as possible, those used in nematode taxonomy are confined to morphology. Although there exist some examples of a numerical approach by nematologists (Moss & Webster, 1970 and Bird, 1971), only Lorenzen (1981) has worked out a phylogenetic system based on cladistic principles. Because fossil records are lacking, this latter approach is more or less speculative, however observations on post-embryonic development provided arguments for the phylogeny.

Within marine nematode systematics there has been a remarkable and unexpected trend towards reduction of the number of characters used in phylogenetic assessment from the period of Filipjev (1918/21) to De Coninck (1965). Reasonable criticism has been made by several authors that the system of De Coninck (1965) was mainly based on two characters (which nevertheless show high validity). Empiricists propose the greatest feasible numbers of characters. This advice is on the whole sound; however, there should be a difference in characterizing species and higher taxa. What is important is not the number of characters but their taxonomic weight. Complexity of structure, synapomorphy, constancy and consistency of characters in a group of species, give a greater weight to characters important for taxonomy.

A significant value of the system of Lorenzen (1981) is the greater number of characters thoroughly analyzed and phylogenetically interpreted : three completely new characters, three known characters with hardly any systematic importance in the past and six known characters of high systematic importance in the past (to which some new aspects were added). But despite the essential validity of this system, many characters will remain "Diskussionspunkte".

III Ecology

1. Nematode Associations

(a) Estuaries and brackish waters

A distinct relationship exists between salinity and nematode assemblages in brackish water biotopes such as estuaries, coastal lagoons and salt marshes, which is reflected in species composition, density, biomass and species diversity. Average population densities of most species decrease towards the head of an estuary and there is usually a decrease in the number of species (Gerlach, 1953; Capstick, 1959; Bilio, 1966; Skoolmun & Gerlach, 1971; Warwick, 1971; Elmgren, 1976; Warwick & Gage, 1975; Saad & Arlt, 1977 and Van Damme *et al.*, 1980).

Capstick (1959) suggested that estuarine nematodes are mainly of marine origin. Down to about $30^{\circ}/_{oo}S$ nematodes are truly marine and they have a widespread distribution in offshore zones as well. This limit is also the lower boundary of occurrence of the Desmodorinae (Riemann, 1966). Gerlach (1953) and Brenning (1973) subdivided nematodes of brackish water areas (exemplified by the Baltic Sea and Kiel Bay) into six groups according to salinity: species which occur from the sea down to the polyhaline, the mesohaline and the oligohaline areas; species which occur in all brackish water areas or in mesohaline and oligohaline areas only; and euryhaline species originally from freshwater. The reality of this subdivision was confirmed by Bilio (1966), Skoolmun & Gerlach (1971), Warwick (1971) and Van Damme *et al.* (1980).

A more subtle division was made by Warwick (1971) who characterized six different habitats along the shore of the Exe estuary, determined by salinity, grain composition and the degree of water retention. Indeed, species distribution is not only related to salinity but to sediment texture, which requires morphological adaptation as well. Species from muddy sediments tend to be small with short setae and are mainly deposit feeders; species from sandy bottoms tend to be predators or epigrowth feeders with long bodies, long setae and a heavily sculptured cuticle.

There is a clear difference in the pattern of species richness along a salinity gradient between macro-and meiofauna. Within the meiofauna, some taxonomic groups may be absent as for instance in the Baltic, (e.g. some kinorhynchs and some ostracods) but there is no obvious overall reduction in species richness. A very rich, truely brackish-water meiofauna exists. The reason for this is not only that estuaries can sustain larger populations (both macro- and meiofauna) but probably also that a well-developed brackish-water meiofauna exists in the coastal ground water along all marine coasts. There thus exists a large pool of species that can invade newly formed brackish water areas such as the Baltic (Fenchel, 1978).

Nematode density is high in estuaries and usually higher intertidally than in the sublittoral (McIntyre, 1969). Salt marshes with a high mud content have extremely high nematode densities : 16 300 ind./10 cm^2 in a *Spartina* salt-marsh in Georgia (Teal & Wieser, 1966) and a record figure of 22 860 ind./10 cm^2 (23 million per square meter!) on a mud flat in the Lynher estuary in England (Warwick & Price, 1979). In a detritus-rich salt marsh along the Western Scheldt river in the Netherlands (the Saaftinge land), Van Damme *et al.* (1980) found very high densities (6 000 ind./10 cm^2), biomass (4.6 g dwt/m^2) and diversity values (2.86 bits/ind.). The adjacent sites in the estuary were much poorer and a decline from the mouth towards the meso-oligohaline zone at the head was found in all parameters: density decreased from 2 160 to 164 ind./10^2, biomass from 980 to 24 mg dwt/m^2 and diversity from 3.01 to 1.63 bits/ind. In general, densities between 200 and 5 000 ind./10 cm^2 are recorded but many data from the literature have to be treated with caution as methodological bias has lead to severe underestimations in much earlier work.

Tietjen (1969) found marked seasonal changes in nematode species composition in two New England estuaries. Epigrowth feeders reached maximum densities in spring and summer, coincident with an observed increase in benthic microflora production, and deposit- and omnivorous feeders reached a maximum in fall and winter, coincident with increases in organic detritus concentrations.

In the Lynher estuary, where species composition remained rather stable over the year, numbers and biomass were lowest in late autumn and early winter and increased from February onwards to reach a peak in May, followed by a decline to the overwintering level (Warwick & Price, 1979). A similar pattern was observed by Skoolmun & Gerlach (1971) in the Weser-estuary in Germany, where nematodes were most abundant in the top layers of the sediment in summer but most abundant below 5 cm depth in winter.

(b) The littoral zone

The significance of free-living marine nematodes in the littoral zone has recently been reviewed by Platt & Warwick (1980). The coastal subsoil water is the environment of a special interstitial brackish-water fauna, which has been studied intensively along beaches of Europe and North America (Atlantic coast). The littoral zone can be considered as a transition zone between sublittoral truely marine bottoms and the continental subterranean waters with their phreatic freshwater fauna, and salinity influences on the nematode fauna are much the same as discussed in the previous chapter.

Densities of nematodes are highest in muddy salt marshes (cf. estuaries and brackish waters) and lowest in very exposed sandy shores (down to 100 ind./10 cm^2) (Gray & Rieger, 1971). Nematodes numerically dominate the meiofauna of sheltered sandy beaches and muddy coastal areas, but in exposed sandy beaches (usually coarse bottoms) harpacticoid copepods form up 60% of the meiofauna. However, nematode densities recorded in the literature could be underestimated as nematodes penetrate very deeply in these well oxygenated beaches (down to 105 cm, Munro *et al.*, 1978), and usually only the first 20 cm are examined. Intertidal meiofaunal biomass is usually from one fifth to one half of the total animal biomass, depending upon substrate and beach stability, which it is suggested is a dominant controlling factor (Gray & Rieger, 1971).

Ott (1972) examined diversity of nematodes from an intertidal sandflat in North Carolina. He found three patterns: 1) diversity is higher on the sheltered than on the exposed beach in comparable stations in all cases; 2) diversity increases from high tidal level to low tidal level in both beaches; 3) diversity increases with depth into the sediment and even in the lower, anaerobic layers there was an astoundingly high diversity in spite of low density.

In algal communities diversity tends to be lower. Phytal nematode associations have received special attention from only a few authors (Wieser, 1951; 1952; 1959; Ott, 1967; Hopper & Meyers, 1967a & b; Moore, 1971 and Warwick, 1977). Faunal composition is related to the growth form and the texture of the weeds (Warwick, 1977), probably because this in turn influences the kind of epiflora and fauna on which the nematodes feed. There exist annual changes for each nematode species: in spring, carnivore/omnivore and deposit feeders without discrete visual organs predominate, whereas species present in the later part of the year are mainly epigrowth feeders with ocelli or visual pigments. Visual mechanisms may be necessary to maintain the worm's position near the front tips where the light intensity is higher and the epiflora consequently richer (Warwick, 1977).

In nematodes, vertical migration in response to tidal and diurnal cycles is widespread. Boaden & Platt (1971) noticed an overall downward migration of the fauna at periods when the tide crossed the sampling station. Dominant species were concentrated at different depths, with forms possessing strong caudal glands and a strong cuticle occurring in the upper layers. Some species seemed to be adapted to low oxygen tension (or absence of oxygen): *Spirinia laevis, Stephanolaimus elegans* and *Leptonemella aphanothecae*. The meiofauna from or under the redox discontinuity layer separating oxygenated and reduced layers in sediments, was called 'Thiobios' by Boaden & Platt (1971) and the existence of a typical reduced layer nematode fauna was demonstrated by Ott & Schiemer (1973). However, Reise & Ax (1979) dismissed the concept of a true 'Thiobios' and linked deep occurrence of meiobenthic taxa with the presence of burrows where oxygen penetrates much deeper into the sediment. They also remarked that longer nematodes are adapted to living in an environment where oxygen is available only at some distance from food sources in the sediment.

Well-defined vertical gradients exist in the meiofauna which appear to be mainly a response to chemical gradients in the interstitial water (McLachlan, 1978). Oxygen is considered to be the 'super parameter' responsible for these gradients. However, nematodes are less sensitive to decreased oxygen tensions than other meiofauna groups. Hulings & Gray (1976) postulated that biological factors may be important in controlling meiofauna of beaches in summer, whereas in winter physical and chemical factors would be more important. The reverse seems to be the rule in poorly oxygenated sediments (McLachlan, 1978). This is all still speculative, as is the discussion on the trophic importance of meiofauna populations in beaches in general. On exposed beaches, the meiofauna populations may be fuelled by soluble organic matter which is particularized by bacteria, without a significant transfer to higher trophic levels, so that meiofauna would be at the top of the food web (McIntyre & Murison, 1973).

(c) Shallow marine subtidal

McIntyre (1971) summarized published data on quantitative aspects of marine meiofauna from sediments below the low-water line. Most of the studies deal with nematodes.

Before 1960, quantitative data on nematode density had been given by Moore (1931), Krogh & Sparck (1936), Mare (1942) and Bougis (1946; 1950). In none of these studies were nematodes identified to species. Wieser (1953; 1959; 1960) made very important pioneering contributions to both ecology and systematics of marine nematodes.

Even more than on beaches, the small-scale gradients in sublittoral sediments are vertical, whereas variations in exposure to water turbulence, input of organic matter and grain size distribution (factors that are highly correlated) occur over greater horizontal distances and give rise to differences in faunal composition (Fenchel, 1978). Fine sands, muddy sands and sandy muds are the richest habitats in terms of nematode density, whereas coarse sands and gravels have especially low density values (Soyer, 1971; Lorenzen, 1974; Juario, 1975 and Willems *et al.*, in prep.). Average numbers vary from a few to 3 000 ind./cm^2 and biomass values from 100 to 1 500 μg dwt/10cm^2; this represents 90-99% of the total meiofauna numbers and 50-90% of the total meiofauna biomass in most circumstances. Extremely high values have been found in shallow muds in the North Sea off the Belgian coast, where on one station an average density of 42 000 ind./10cm^2 was found (Herman, pers. comm.). In coastal terrigeneous muds off Banyuls-sur-Mer (Mediterranean) very high densities were recorded (average of 4 300 ind./ 10cm^2, maximum of 7 600 ind./10cm^2 in summer, lower in winter). These differences may be related to temperature. In medium well-sorted sands in South Africa, nematode numbers were related to the amounts of nitrogen in the sediment, assumed to indicate the amount of digestible food (McLachlan *et al.*, 1977).

Nematode diversity is correlated with sediment granulometry. Wieser (1960) and Hopper & Meyers (1967a) suggested that more species will be present in a habitat with a larger number of niches, and presumed that marine sediments become more heterogeneous when the silt-clay content decreases and the grain size increases. Diversity is higher in sands where an interstitial fauna exists, than in noncapillary sediments. Species numbers are also higher and sandy sediments contain more 'specialist' species than silty ones (Heip & Decraemer, 1974). That the number of niches is higher in sandy sediments is indicated by the coexistence of closely related species in these sediments indicating the existence of microhabitats. An extreme example of this is the presence of eight species of *Microlaimus* on a sheltered beach found by McIntyre & Murison (1973).

As gradients in sediments occur over a small scale vertically, nematodes should be more sensitive to slight changes in sediment granulometry than most of the macrofauna. Nevertheless, it is possible to characterize different biotopes by means of nematode assemblages. It is even possible to demonstrate, on the family level, that similar sublittoral habitats from the North Atlantic, Mediterranean, North Sea and Baltic Sea are characterized by 'parallel' nematode communities. The first to deal with the community concept in marine nematodes was Wieser (1960) who distinguished two nematode communities in the benthos of Buzzards Bay, USA: an *Odontophora-Leptonemella* community in sandy habitats and a *Terschellingia longicaudata-Trachydemus mainensis* (Kinorhynch) community in a silty habitat. Two basic faunal units have been found repeatedly: a mud unit characterized by high species dominance, low species diversity and low species endemism and a sand unit characterized by low species dominance, high species diversity and high species endemism (Tietjen, 1977).

The coastal muds of most regions are characterized by a few dominant genera showing vicariance, or even by the same species. All the dominant nematodes in these habitats are members of the Comesomatidae, Linhomoeidae and Spiriniidae, with the following genera important : *Sabatieria, Dorylaimopsis, Terschellingia, Spirinia,* etc. These abundant genera may be accompanied by different sub-dominant genera such as *Paramesacanthion, Axonolaimus, Parironus, Longicyatholaimus, Daptonema, Sphaerolaimus* and *Desmolaimus.*

Sandy bottoms are less studied and it is difficult to enumerate a few families or genera which are characteristic since the fauna is much more diverse (Boucher, 1980b). Tietjen (1977) gives habitat preferences on the family level which can be extended to nearly all coastal regions examined: 1) muds: Comesomatidae, Linhomoeidae; 2) muddy sands: Comesomatidae, Monhysteridae, Desmodoridae, Linhomoeidae; 3) fine sands: Monhysteridae, Comesomatidae, Desmodoridae, Axonolaimidae; 4) medium-coarse sands: Monhysteridae, Desmodoridae, Chromadoridae. We can add to this list for clean, coarse sands the family Epsilonematidae and superfamily Draconematoidea which are restricted to these biotopes.

(d) Deep Sea

The qualitative composition of the meiofauna of the deep sea is rather stable: in poor as well as in rich areas nematodes comprise between 85-95% of the meiofauna, when the Foraminifera are excluded. Meiofaunal densities in the deep sea range from a few to 1 500 ind./10m^2 and decrease with increasing depth. This decrease is relatively less than for the macrofauna so that the relative importance of the meiofauna in bottom communities increases with depth (Thiel, 1975). The availability of food is a major factor in explaining the quantitative distribution of meiofauna in the abyssal depths (Dinet, 1979) and highly significant correlations between meiofauna and the ratios C/proteins and N/proteins, which reflect the degree of decomposition, have been found. Similarly, Thiel (1979) explained the higher nematode densities from areas near the coast and from upwelling regions by an increase in food availability.

Only two studies exist in which species composition and diversity of nematodes from the deep sea are discussed (Tietjen, 1976 and Dinet & Vivier, 1979). Tietjen (1976) found that changes in species composition along transects from 50 to 2 500 m depth were correlated with changes in bottom water temperature and changing sediment type. In four sedimentary environments off North Carolina 209 species of nematodes were found, occurring in distinct associations. A sand zone (50-500 m) and a clay-silt zone (800-2 500 m) were recognized, and were separated by a transition zone (500-800 m) with little species endemism. The Enoplidae, Ceramonematidae, Chromadoridae and Desmodorinae have their centers of abundance in sandy sediments; the Leptosomatidae, Oxystominidae, Axonolaimidae, Leptolaimidae, Linhomoeidae, Siphonolaimidae, Sphaerolaimidae and Comesomatidae tended towards increasing abundance in the clay-silts. Dinet & Vivier (1979) found the Monhysteridae, Chromadoridae, Oxystominidae, Desmoscolecidae, Microlaimidae and Axonolaimidae most abundant in the deeper parts of the Bay of Biscay.

The existence of a characteristic deep sea nematode fauna is striking. From the 317 species recorded by Dinet & Vivier (1979) only three could be identified to known species. All the others had affinities with known abyssal genera or were not described at all.

Nematode diversity decreases with depth as the sediment becomes finer (Tietjen, 1976). However, the diversity of the deep sea nematode assemblages is significantly higher than that of shallow-water assemblages with the same sediment characteristics. A faunal change occurs around the depth of 4 000 m (Dinet & Vivier, 1979). This increased diversity may be due to the greater stability of the deep sea environment and may on the other hand indicate the possible susceptibility of these populations to man-made disturbances such as dumping or deep sea mining (Thiel, 1975).

2. Horizontal and Vertical distribution

(a) Small-scale horizontal distribution

Many studies have shown that meiofaunal populations are distributed in aggregations, forming patches of high abundance on the sea bottom. For nematodes, this has been demonstrated by Vitiello (1968), Gray & Rieger (1971), Arlt (1973) and Gerlach (1977).

These patchy distributions have often been correlated with patchiness of the environment, though other mechanisms such as reproductive patterns may be involved (Heip, 1975). Gerlach (1977) showed that decaying organisms and the associated microflora may attract certain meiofaunal organisms, such as nematodes, and food in general is thought to be important. Meiofauna was shown to be attracted selectively to patches of some species of algae but not to others, and this selective recruitment may be important when food species are patchily distributed (Lee *et al.*, 1977).

Biogenic structures (e.g. *Uca* or *Arenicola* burrows, or roots of *Spartina*) affect the distribution of meiofauna significantly and must be taken into account when quantifying meiofauna in areas where much structural heterogeneity is present (Bell *et al.*, 1978; Reise & Ax, 1979).

(b) Vertical distribution

The vertical zonation in marine sediments is clearly reflected in the fauna. The depth to which organisms penetrate is correlated with characteristics of the sediment such as oxygen concentration and food availability. In most sediments the surface layers are oxidized and it is improbable that a permanent meiofauna can develop in sediments which are periodically or permanently anoxic. When light is available photosynthesis in the oxidized surface layer is possible, but reduced oxygen tensions will be obvious only after a few centimeters in even well aerated sediments, with the exception of high-energy beaches where the oxidized layer can be several meters deep.

Photosynthesis and possibly chemosynthesis at the boundary between oxidized and reduced layers (the redox discontinuity layer) provide new organic material and the distribution of many meiofauna species in shallow waters is linked to this. Nematodes are often concentrated in the upper-most layers in late spring and summer and extend into deeper sediments in winter. Also 2A species (epigrowth-feeders) tend to dominate in summer and 1B species (non-selective deposit-feeders) later in the year.

In muds, the vertical distribution is not the same as in sands. Salvat & Renaud-Mornant (1969) shows that 2B species (omnivores) decrease with depth in coralligeneous sands whereas 2A species increase. In muddy sediments, Boucher (1972) obtained contrary results, with 2A species decreasing with depth and 1B species increasing.

Perhaps the most important factor regulating vertical distribution is not food but the capability to adapt to stress conditions (McLachlan, 1978). Wieser *et al.* (1974) demonstrated that several species had lethal temperatures close to the maximum temperatures experienced in the habitat. Wieser & Kanwisher (1961) and Teal & Wieser (1966) showed that nematodes that live deepest in the sediments have the lowest metabolism.

Wieser *et al.* (1974) describe how *Paramonhystera wieseri* seems to thrive better in (apparently) oxygen-free environments and therefore considered the species to be an obligate anoxobiont, as at least some of its life functions are irreversibly damaged by normal oxygen tensions.

The evidence for a characteristic nematode fauna of permenently deoxygenated sediments (Ott & Schiemer, 1973) has recently been questioned in general (Reise & Ax, 1979) but the dispute is far from settled.

3. Feeding

Nematodes occupy many very different roles in aquatic ecosystems as consumers of bacteria, as grazers of primary producers and as predators and parasites. *Rhabditis marina* has been reported to take up dissolved organic matter directly (Chia & Warwick, 1969), but these results have been questioned (Tietjen & Lee, 1975; Tietjen, pers. comm.).

As already mentioned, the first approach towards elucidating the role of nematodes was based on the morphology of the buccal cavity (Wieser, 1953a). Wieser (1960) himself conceded that his classification was not as strict as he thought and that many nematodes are omnivorous, not only species with heavily armed mouth cavities but also some species classified as deposit or epistratum feeders on the basis of their mouth morphology.

The feeding behaviour of marine nematodes has been reviewed by Tietjen & Lee (1977a) but quantitative information for marine species is scarce. The daily ingestion rate of algae by *Chromadorina germanica* is equal to its own body weight, and this species consumes significantly more algae than bacteria when offered the choice. This tends to confirm Wieser's views but *Monhystera denticulata* and *Rhabditis marina* show no difference in preference between algae and bacteria in terms of weight, though many more bacteria were consumed in terms of cells available. This suggests that ingestion rate in these species is determined by the size of the food particles. The data of Tietjen & Lee (1977a) also point out that some selection of food occurs, though the mechanism remains unknown.

The food ingestion of three species has been calculated by Tietjen (1980b) to be 144 and 600 ng C per day per animal, or between 9 and 37 ng C per day and per ng C of animal. This is in the range reported for meiofauna in general, i.e. between 0.1 and 10 μg dry-weight per day (about 40 and 4 000 ng C).

Qualitative information on aspects of feeding indicates the often highly complex nature of the interactions between nematodes and the microflora of sediments. Riemann & Schrage (1978) described the continuous production of mucus by nematodes, which produce a slimy trail along which particles adhere firmly. By creeping repeatedly on their traces, burrows are made that may be very important in determining sediment texture. Riemann & Schrage (1978) suppose that small particles such as bacteria and even macromolecules may become trapped in the mucus and are subsequently browsed. A similar mechanism has been advanced by Gerlach (1978): by their activity meiofauna stimulate bacterial growth and thus increase bacterial production to levels which are not attainable without this activity. This process has been called 'gardening'.

The amount to which marine nematodes serve as food for higher trophic levels remains unclear. There certainly are important predators within the meiofauna itself (e.g. hydrozoans such as *Protohydra* or *Halammohydra*, many turballarians, nematodes); there are also known consumers of nematodes among the macrofauna and some fish species. Coull & Bell (1979) suggest that the meiofauna of muds and detritus-rich habitats serves as a significant source of food for higher trophic levels (primarily browsers) whereas in sandy substrates the members of the meiofauna serve primarily as nutrient regenerators.

4. Life cycles

Evaluation of the importance of nematodes in marine ecosystems has centered mainly around the structural characteristics such as abundance and biomass and direct measurement or calculation of production has until now not been achieved. Indirect methods which have been used so far depend on Waters (1969) concept of life-cycle turnover or on respiration data. The first method requires knowledge of the annual number of generations in the field. In most instances this number has been estimated from laboratory experiments and the field data which are available are for large slow-growing species with only one or a few generations annually.

Enoplus communis has only one generation annually in a salt marsh in Massachussetts (Wieser & Kanwisher, 1960), whereas *Enoploides spiculohamatus* (2-3), *Oncholaimus brachycercus* and *Viscosia viscosa* (2) had only two or three generations annually in the Weser estuary (Skoolmun

& Gerlach, 1971). In a four-year study, Smol *et al.* (1980) established that *Oncholaimus oxyuris* had most probably two generations in three years in a remarkable pattern in which overwintering juveniles belong to two different generations. Overwintering large juveniles become adult early in spring and produce another generation in the same year which overwinters as small juveniles. These small juveniles become adult much later in the year and their offspring overwinter as large juveniles.

However, the number of annual generations in most nematode species is probably much higher than one or two, but as in many cases breeding is almost continuous. Laboratory experiments are necessary to obtain information on this aspect of their life-cycles.

The already large amount of literature on cultivation of marine nematodes has been summarized recently by Kinne (1977) who documents culture methods for the following species (original publication mentioned between brackets): *Aphelenchoides marinus* (Meyers *et al.*, 1964), *Chromadora macrolaimoides* (Tietjen & Lee, 1973), *Diplolaimella ocellata* (Chitwood & Murphy, 1964), *Metoncholaimus scissus* (Hopper & Meyers, 1966a; Meyers & Hopper, 1966, 1973; Meyers *et al.*, 1970), *Monhystera denticulata* (Tietjen & Lee, 1972), *M. disjuncta* (Chitwood & Murphy, 1964; von Thun, 1968; Gerlach & Schrage, 1971), *M. filicaudata* (Tietjen, 1967), *Rhabditis marina* (Lee *et al.*, 1970; Tietjen *et al.*, 1970), *Theristus pertenuis* (Gerlach & Schrage, 1971) and *Adoncholaimus thalassophygas, Chromadorina tenuis, Diplolaimella ocellata, Diplolaimelloides oschei* (von Thun, 1968 in Gerlach, 1971). Recent studies have been made by Heip *et al.* (1978) for *Oncholaimus oxyuris* and Vranken *et al.* (1981) for *Monhystera parelegantula.*

A number of these species have been cultured only at room temperature and constant salinity. Under these conditions generation times are often of the order of two to four weeks, though much longer generation times have been observed e.g. for oncholaimids and much shorter generation times such as for *Rhabditis marina* (2.5 days) exist as well. However, temperature has a profound influence on development time and generation time. This effect can be described by a simple power equation $D = aT^b$ relating development (or generation) time and temperature. Values of b vary between -1.05 for *Theristus pertenuis* (Gerlach & Schrage, 1971) and -2.87 for *Diplolaimella ocellata* (Hopper *et al.*, 1973). A modal value is $b = -1.8$, indicating that development accelerates by a factor 2.5 to 3.5 between 10 and 20°C and 1.8 to 2.2 between 20 and 30°C. This modal value is high when compared with other groups such as Calanoida ($b = -1.04$) and Harpacticoida ($b = -1.29$) (Heip & Smol, 1976)., and it therefore appears that temperature has a more profound effect on nematodes than on other meiobenthic groups.

The combined influence of temperature and salinity on development has been studied by Tietjen & Lee (1972, 1977b) on *Rhabditis marina, Monhystera denticulata* and *Chromadorina germanica.* Both *M. denticulata* and *C. germanica* appear to be better adapted for life in the middle and upper portions of their salinity range.

The average number of generations in natural populations with continuous breeding has been estimated from experiments as described above. These estimations vary from 5 for *Monhystera parelegantula* in a lagoon in Belgium (Vranken *et al.*, 1981) to 15 for *Chromadorina germanica* and *M. denticulata* in the New York area (Tietjen & Lee, 1972, 1977b) and 17 for *M. disjuncta* in Germany (Gerlach & Schrage, 1971). As only a few species have been studied, and most of them belong to the same genus, it is too early to give some modal value of the annual number of generations.

5. Production

Estimation of production using the classical method as described by Crisp (1971), based on growth analysis of field populations, has not yet been attempted for marine nematodes. Estimations of this important ecological parameter in the literature are either based on biomass data using a standard figure proposed by Gerlach (1971) or on respiration data using a regression equation proposed by McNeil & Lawton (1970).

Gerlach (1971) based his values on the concept of life-cycle turnover introduced by Waters (1969), which has to be multiplied by the annual number of generations to obtain an estimate of a yearly P/B (production to biomass) ratio and on experiments of von Thun (1968) who studied the life-cycle of the brackish-water species *Chromadorita germanica.* Starting with one male and one female (ww = 1 μg) and assuming a random mortality of 10% per day and 20 eggs per female, he calculated a production of 10 μg during the life-cycle and an average standing stock of 3.3 μg so that life-cycle turnover is around 3.

A mortality of 10% per day may be too high but this factor is relatively unimportant in calculating life-cycle turnover. Although such calculations are rather crude, there is good agreement with estimates based on standard demographic techniques (Heip, unpublished), provided a stable age-distribution is reached, which might be the case for many small species with continuous breeding.

In order to obtain the annual turnover or P/B-ratio this figure has to be multiplied with the annual number of generations. On the basis of the literature Gerlach (1971) suggested that a modal figure might be three generations annually, and the subsequent result $P = 9B$ has found wide acceptance to estimate production for nematodes and indeed for meiofauna as a whole. As already mentioned, this figure seems to be an underestimate for many species but it may be too early to put another figure in its place, if indeed such a general number exist.

New work along the same line is that of Zaika & Makarova (1979) who preferred to calculate daily turnover rates (or specific production), $C = P/B$, from the literature. In theory $C = b$, the instantaneous birth rate (and not the intrinsic rate of increase r as stated in the paper) but to evaluate C in this way r has to be known and r can be calculated exactly only when a life-table is available, which is not the case for any marine nematode.

Also, in this as in Gerlach's work, an average of 20 eggs per female is probably too low. It therefore seems that the equation proposed by Zaika & Makarova (1979) relating specific production with temperature $C = 0.008\ T^{0.96}$ (not 0.08 as stated in the paper) must be treated with caution. On a yearly basis $P/B = 27$ for a mean water temperature of 10°C using this equation, and this may well be too high.

As indirect approach to calculate production has been used by Warwick & Price (1979) who used the empirical relationship calculated between production and respiration of short-lived poikilotherm animals proposed by McNeil & Lawton (1970) $\log P = 0.8262 \log R - 0.0948$ (in k cal. $m^{-2}.yr^{-1}$). By measuring respiration of 16 species they found an average of $P/B = 8.4$, surprisingly close to a value of $P/B = 8.7$ calculated by accepting a net growth efficiency of $P/P{+}R = 0.38$ (as found by Marchant & Nicholas (1975) for the freshwater species *Pelodera*); and, of course, also surprisingly close to Gerlach's older figure of $P/B = 9$. Though this adds some strength to this figure, it seems to us that it remains too low and that the resemblance is largely coincidental.

The validity of such an approach depends amongst other things on a functional relationship between P and R. It is interesting to note in this context that Schiemer *et al.* (1980) in experiments with the freshwater species *Plectus palustris* found that both parameters depended on food concentration, but production more so than respiration. Below a threshold density of 10^8 cells/ml of *Acetinobacter* growth and reproduction ceased. As these bacterial densities are not attained in oligotrophic and mesotrophic lakes, this also indicates that food density may be limiting this species in nature.

6. Respiration

Respiration of individual or batches of nematodes has been measured as oxygen consumption using oxygen electrodes (Atkinson, 1973) or Cartesian Diver Respirometry (see Lasserre, 1976, for a review of techniques). The available information has been summarized by Warwick & Price (1979) who published data on 48 species representing all trophic categories.

Respiration (in nl $0_2.ind^{-1}.h^{-1}$) is traditionally expressed in units of body weight such as volume (in nl) using a power equation $R = aV^b$. The coefficients a and b are calculated by regressing log R against log V. As in other poikilotherms $b = 0.75$ on average, though Atkinson (1976) suggested a somewhat higher value $b = 0.79$ and Zeuthen (1953) even believed that metabolism in nematodes is weight-independent. This is certainly not true, but it is interesting to note that Laybourn (1979) found a varying value of b according to temperature in the freshwater species *Anonchus*, with b approaching the value of one at temperatures of 20-25°C.

The value of a is considered to be an indication of metabolic intensity (Schiemer & Duncan, 1974). Warwick & Price (1979) recalculated a from existing data using $b = 0.75$ throughout and could distinguish four groups of nematodes according to values of log a. In general the predator/omnivore and non-selective deposit feeders have faster respiration rates than the epigrowth feeders and selective deposit feeders. Also larger species have a higher metabolic intensity than smaller species and species from well-oxygenated habitats have a higher respiration rate than species from poorly oxygenated habitats. This may be due to a partly anaerobic respiration as suggested by Schiemer & Duncan (1974).

A typical value is around $\log a = -0.1$ which is equal to a respiration of $\pm\ 0.8$ nl $0_2.h^{-1}$ for a volume unit of a respirating nematode. Thus, for a 'typical' nematode, with $\delta = 1.13$ and dwt = 0.25 ww, we have $R\ (\text{nl}\ 0_2.h^{-1}) = -0.1 + 0.75 \log 3.54\ W$ (in ug dwt) or $\log R = 0.42 + 0.75 \log W$, an equation which could be used with caution in the absence of other information.

Community respiration has been evaluated from laboratory measurements by Wieser & Kanwisher (1961), Teal & Wieser (1966) and Warwick & Price (1979). It has been noted by the last of these authors that in these three studies respiration per g ww is very similar and an average value of 6 1 $0_2.m^{-2}.yr^{-1}\,g^{-1}$ is therefore proposed by Warwick & Price (1979) as of possible use when drawing energy budgets when respiration data are not available. Such general values do not take temperature properly into account.

The effect of temperature on respiration has been investigated by Price & Warwick (1980) for *Sphaerolaimus hirsutus* and for *Trefusia schiemeri* and *Theristus floridianus* by Wieser & Schiemer (1977). By plotting the log respiration per unit body weight $R_c = R/W$ against temperature, Q_{10} values can be simply obtained as $Q_{10} = 10\ d$ from $\log R = c + d.T$ Q_{10}-values were 1.17 for *S. hirsutus* between 5 and 25°C, but outside this range the relationship was non-linear. Q_{10} was about 2 for *Trefusia schiemeri* and based on this and some data on other meiofauna animals Price & Warwick (1980) suggested that animals with stable food supplies might have

$Q_{10}\sim1$ whereas animals with a more variable food supply might have $Q_{10}\sim2$. With the scarce data at our disposal it is difficult to see if this generalisation really holds.

7. Pollution biology

The possible use of nematodes as tools in monitoring the biological effects of pollution has been discussed by Heip (1980). Benthic organisms in general are probably the best all-round biotic component to monitor (Gray *et al.*, 1980) and nematodes in particular possess some characteristics such as a short life-span and high diversity which makes them potentially useful.

The influence of pollution on nematodes have received comparatively little attention. Oil pollution has been most thoroughly studied. Nematodes from intertidal habitats appear to be vulnerable to oil pollution and even seven months after the Amoco Cadiz spill, nematode abundance was generally decreased (Boucher, 1980a). However, sublittoral nematode communities showed no such decrease in diversity, rather following the increase of tolerant species such as *Anticoma ecotronis, Sabatieria celtica, Paracyatholaimus occultus* and *Microlaimus conspicuus* which achieved densities 2-4 times higher after pollution occurred. A similar increase in nematode density was observed by Renaud-Mornant & Gourbault (1980), who also found little permanent damage to the meiofauna in general. After the Tsesis spill in the Baltic Sea all meiofauna groups except nematodes were drastically reduced (Elmgren *et al.*, 1980).

That the nematodes as a group are more resistant to different forms of pollution than other benthic groups has also been demonstrated by Van Damme & Heip (1977) in the Southern Bight of the North Sea. In an area with a mixed type of pollution, nematodes were often the only animal group present in the samples.

The effects of heavy metal pollution have been studied by Lorenzen (1974b). He found no short-term effects of industrial wastes containing 10% H_2SO_4 and 14% $FeSO_4$ on the nematode assemblage of the dumping area. Tietjen (1977, 1980a) related nematode distribution with pollution in the New York Bight area and found significant differences between stations with an elevated organic carbon or heavy metal load and clean medium sand stations. *Sabatieria pulchra* and *Tripyloides gracilis,* usually restricted to silty bottoms, were dominant in a contaminated sandy station with a high organic content. It appears that the complex of species that normally inhabits medium sands may be especially sensitive to elevated loads of heavy metals and/or organic matter. Species belonging to the Chromadoridae, Desmodoridae and Monoposthiidae may be reduced or even eliminated and species normally associated with finer sediments such as *Sabatieria* may increase.

The use of nematodes in monitoring thus requires at least some knowledge of nematode systematics, as the response of different species may be very different whereas overall parameters such as density may remain unaffected as some species decrease whereas others increase. However, it appears possible that analysis to species level, which is particularly difficult, may not be necessary and that higher taxonomic groups are as a whole similar in their response. This needs elaboration.

IV Concluding Remarks : On the Importance of Nematodes in Marine Ecosystems

It has been stated many times by meiofauna workers that nematodes must be important in marine ecosystems. The arguments have centered mainly around their enormous abundance, with an order of magnitude of tens of millions per square meter in estuaries and salt marshes, millions per square meter in the shallow subtidal and still hundreds of thousands per square meter in the deep sea. However, the message has still not reached a large part of the scientific community and whereas nearly everybody concerned with the sea is aware of the importance of copepods in the plankton this is certainly not so for the importance of nematodes in the benthos.

There are several reasons for this. Firstly, nematology is a relatively young science and the number of active nematologists is small. Ecological research on nematodes started only a few decades ago and workers were isolated. Not until the start of the International Meiofauna Conferences (Tunis, 1969; York, 1973, Hamburg, 1977 and Columbia, 1980) and the Workshops on Aquatic Nematodes (Gent, 1977; Bremerhaven, 1979; Plymouth, 1981) has there been a growing exchange between nematologists of different nations. Whereas plankton research has a long tradition, benthic research is younger. Earlier workers in the beginning of the century used large mesh sieves and so lost nearly all the nematodes present in the sediment. Because nematodes are indeed small, many species measuring only a few hundred micrometers in length, they are consequently difficult to study in the field or even in laboratory experiments. They have to be examined under the microscope and identification to the species level is tedious and difficult for the inexperienced. A final reason may be that they are inconspicious animals, thriving mostly in the muds, and muds have little research appeal for many people.

All these reasons have hindered research on nematodes for a long time and will probably continue to do so in the future. There are only a few centres actively engaged in the study of marine nematodes and as the number of new ideas in any discipline is roughly proportional to the number of people working in it, it is clear that marine nematology will continue to progress only slowly, and continue to suffer inadequate or diminishing funding.

Nevertheless, all the evidence obtained in recent years clearly demonstrates that nematodes are important in marine ecosystems. Most of the arguments have been summarized recently by Platt & Warwick (1980) and partially by Tietjen (1980). We will illustrate this with two examples: the intertidal mud flat of the Lynher estuary in Cornwall (Warwick & Price, 1979) and the Southern Bight of the North Sea (Heip *et al.*, 1979).

In the Lynher estuary nematodes are extremely abundant, though roughly the same abundance will be found in many other estuaries. Their average density over the year is 12.5 million ind./m^2, their average biomass 1.97 g dwt/m^2; this indicates that the Lynher species are small, with an average individual biomass of only 0.16 μg dwt or roughly 0.64 μg ww. Their respiration amounts to 11.2 g C metabolized per year and their contrasts with the figure of 21.6 g C metabolized for the entire macrofauna. Consumption may be even more astounding: when calculated as the sum of production and respiration it amounts to 29.7 g C per year, again about half the total consumption of the macrofauna. But assuming that nematodes eat about their own body weight daily, total consumption would be 2.9 kg ww per m^2 and per year. This figure seems totally unrealistic, but it should be remembered that nematodes increase their food supply through several mechanisms stimulating bacterial growth.

In the area near the Belgian coast of the Southern Bight of the North Sea average nematode abundance is 1.65 million ind./m^2 and average biomass is 0.99 g dwt/m^2; although there are fewer nematodes than in the Lynher estuary, their total biomass is not much lower as these are larger species with an average individual biomass of 0.60 μg dwt or 2.40 μg ww. Their respiration has been estimated at about 7 g C per m^2 and per year, whereas macrofauna in the same area metabolizes only 3.4 g C per m^2. Thus nematodes alone respire twice as much as the entire macrofauna.

It is clear from these two examples that a very significant portion of the energy flow through the benthic system passes through the nematodes. However, one of the main reasons why marine nematodes have remained unpopular research objects is that it has not been clearly shown that they are of direct benefit or nuisance to man. It has been a popular viewpoint to consider the meiofauna as a whole as something of a closed system, a trophic dead end, in fact a system that is competitive with the macrofauna with its obvious importance to man. Although there is little concrete evidence suggesting important direct consumption of meiofauna by species which are directly important to man, in recent years considerable indirect evidence has become available suggesting that nematodes do indeed pass up the food chain (Platt & Warwick, 1980; Coull & Bell, 1979). Crustaceans and perhaps some fish species such as mullet are expected to be the main predators of nematodes, and a lot of macrofaunal deposit feeders will at least partly depend on them as a food source.

Nematodes certainly play an important indirect role in the marine ecosystem. Their role in stimulating bacterial metabolism is well documented (Tenore *et al.*, 1977; Tietjen, 1980b) and they must have an important and direct influence on the productivity of shallow waters by enhancing nutrient regeneration in the sediments. Their influence on sediment texture has also been documented (Cullen, 1973) and the extensive production of mucus by animals in such density will certainly change the physical characteristics of sediments, which will have significance for dredging and dumping operations.

In conclusion, although it has become clear during the last decade, that free-living nematodes are ecologically the most important animal taxon in all marine sediments, much work remains to be done, both on the ecology and the systematics of this group, before an appreciation of their role in the marine environment will become as recognised as it presently is for many planktonic groups.

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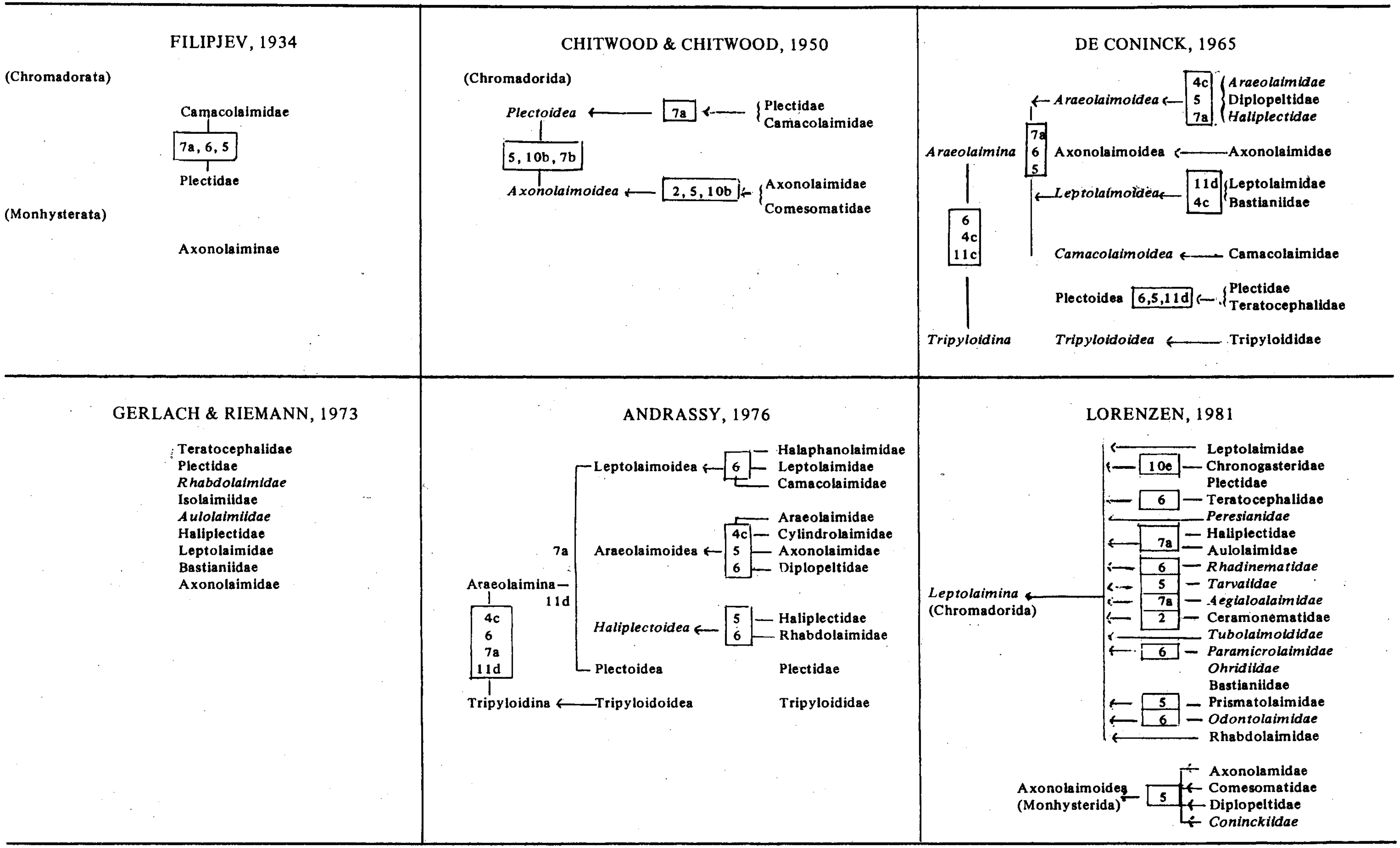
Table 3 : Araeolaimida



Evolutionary trends in the classification of the different orders (newly introduced taxa are in italics). In this table and the following five, characters by which members of a taxon are related and differentiated are presented by numbers (corresponding with characters listed in table 2). The numbers below Lorenzen (1981) refer to holapomorphic characters of the corresponding taxon as established by this author; those under the other authros indicate differentiating characters between the taxa.

Table 4 : Desmoscolecida

FILIPJEV, 1934

$\boxed{2}$ ← Desmoscolecidae
← Greeffiellidae

CHITWOOD & CHITWOOD, 1950

(Chromadorida)

Desmoscolecoidea ← $\boxed{2}$ ← Desmoscolecidae
← Greeffiellidae

DE CONINCK, 1965

Desmoscolecina ← $\boxed{2 \; 3}$ ← Desmoscolecoidea ← $\boxed{5}$ — *Meyliidae*
— Desmoscolecidae
← *Greeffielloidea* : Greeffiellidae

TIMM, 1970

Desmoscolecidae

GERLACH & RIEMAN, 1973

Meyliidae
Desmoscolecidae

FREUDENHAMMER, 1975

Desmoscolecidae

ANDRASSY, 1976

Meyliina : Meylioidea : Meyliidae
$\boxed{5}$
Desmoscolecina ← $\boxed{2}$ ← Greeffielloidea ← $\boxed{2,3}$ ← *Calligyridae*
← Greeffiellidae
← Desmoscolecoidea : Desmoscolecidae

DECRAEMER, 1977

Desmoscolecina : Desmoscolecoidea : Desmoscolecidae

LORENZEN, 1981

(Monhysterida)

Desmoscolecoidea ← $\boxed{11a, 3}$ ← Desmoscolecidae
$\boxed{3}$ ← Meyliidae

Table 5 : Monhysterida

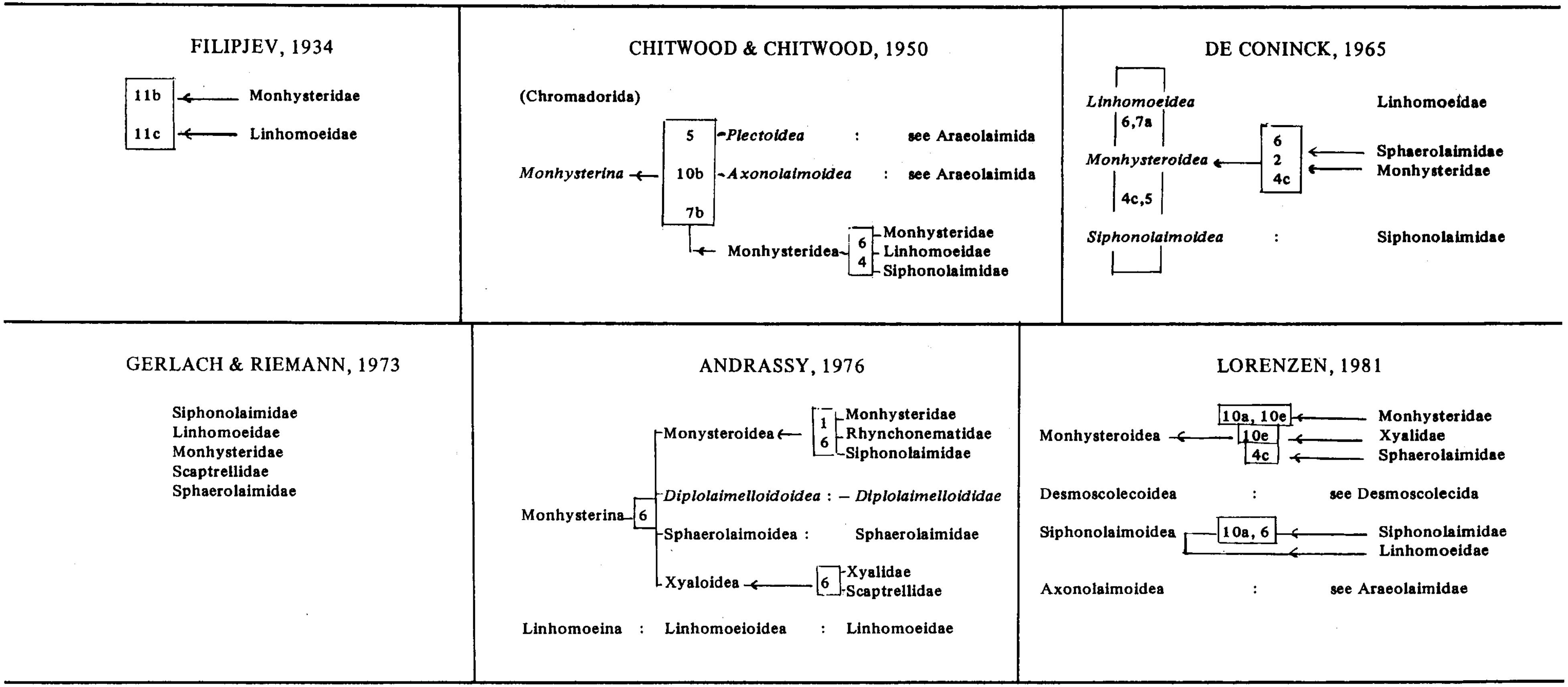


Table 6 : Desmodorida

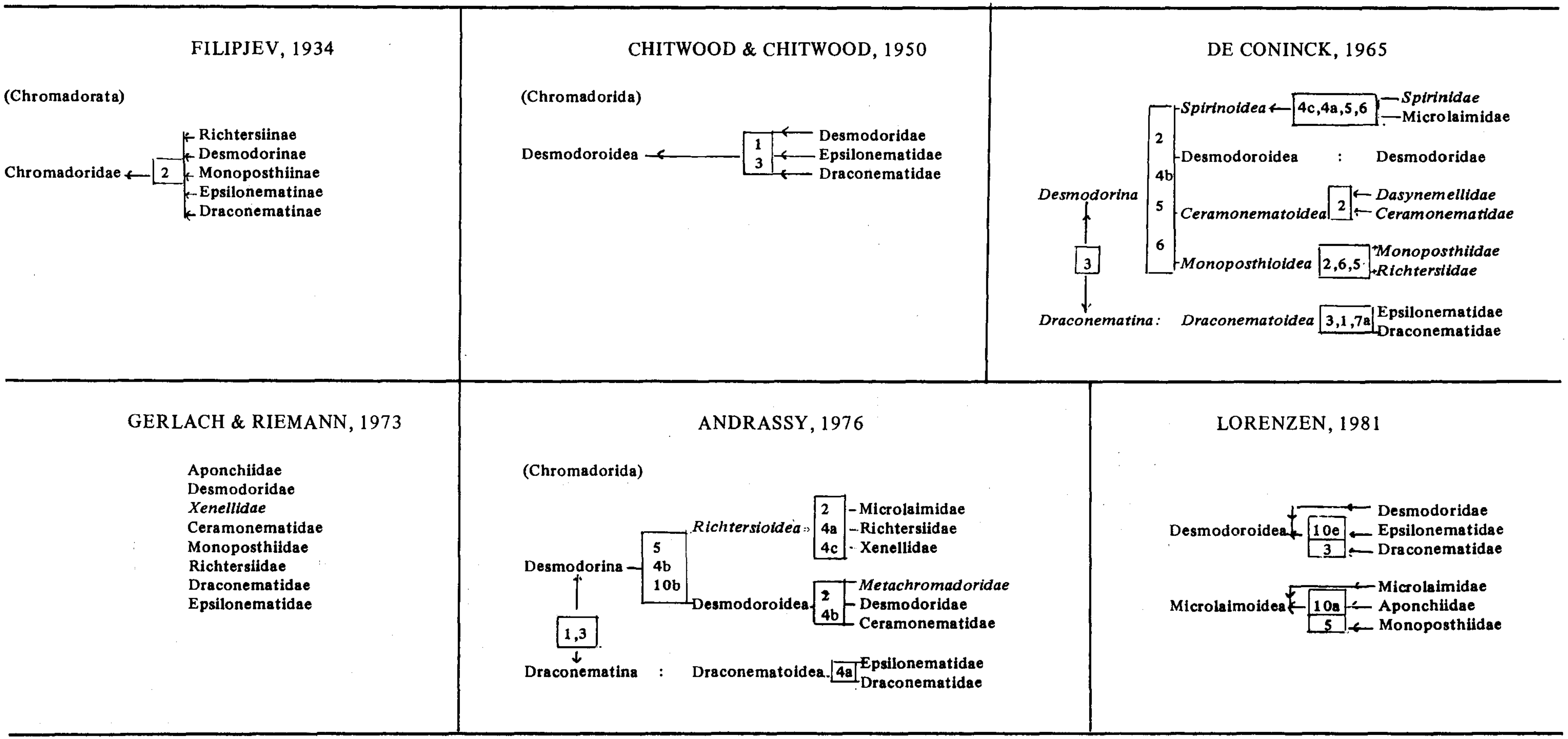


Table 7 : Chromadorida

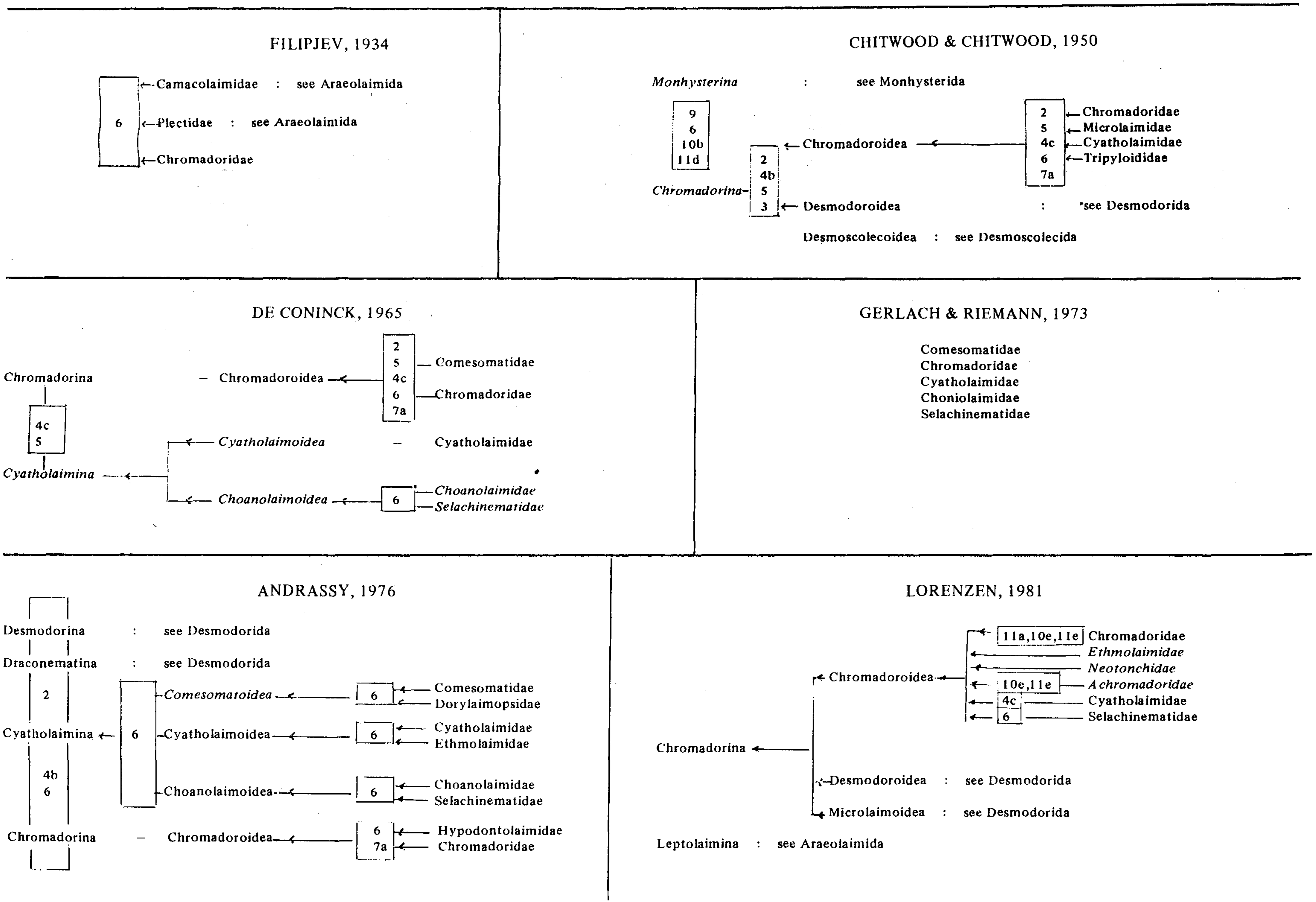
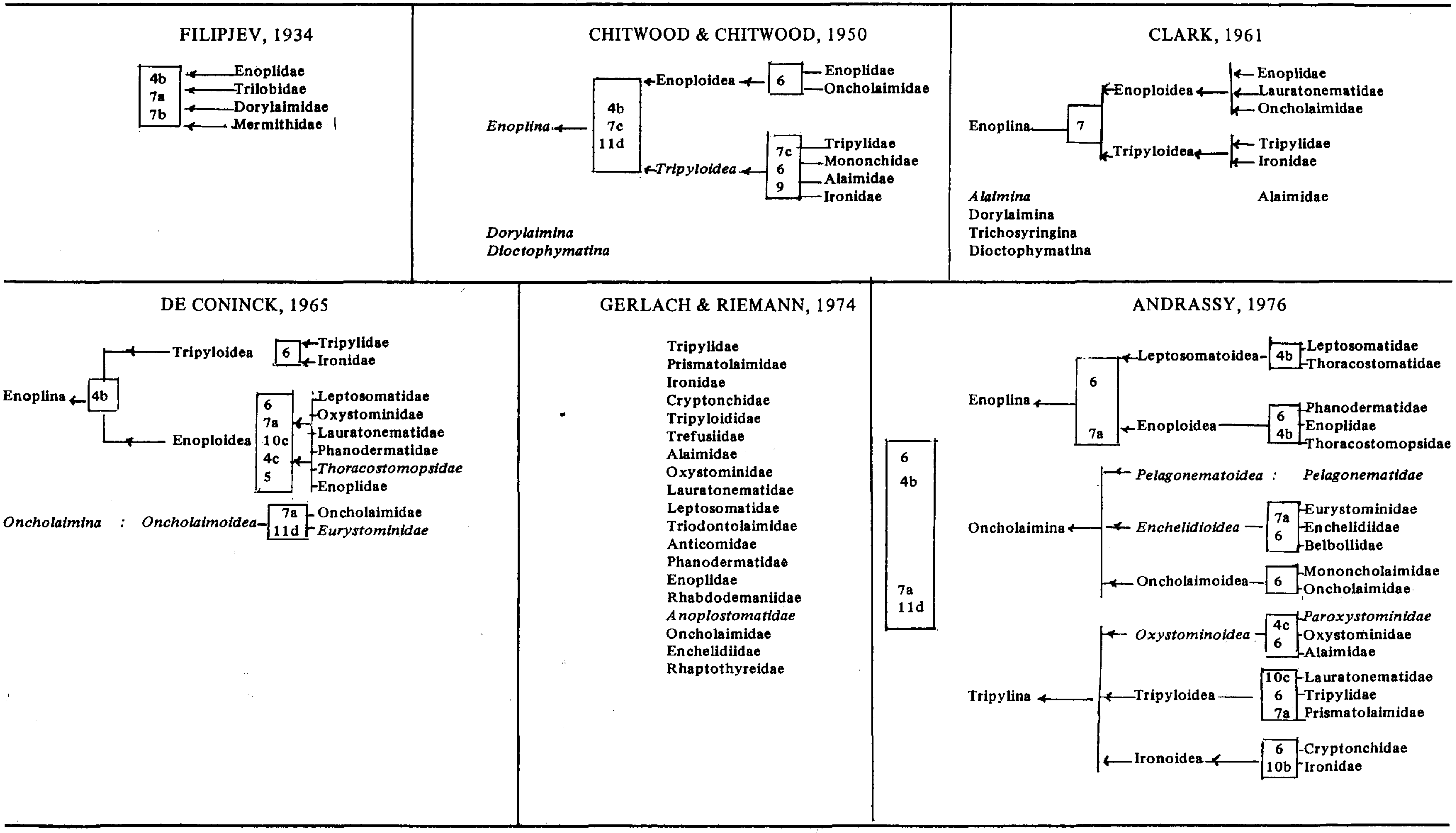


Table 8 : Enoplida



FILIPJEV, 1934

CHITWOOD & CHITWOOD, 1950

CLARK, 1961

DE CONINCK, 1965

GERLACH & RIEMANN, 1974

ANDRASSY, 1976

Table 8 : Enoplida (continued)

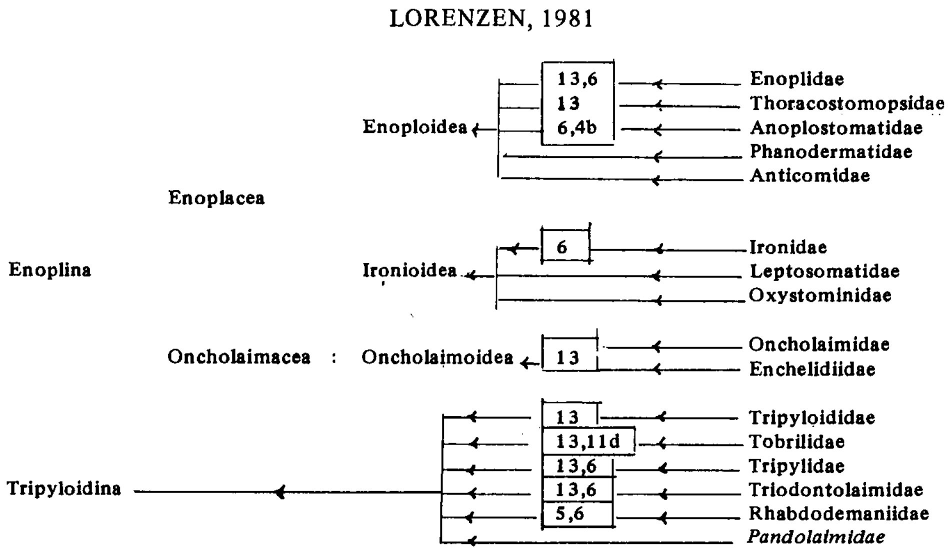


Table 9 : *TREFUSIIDA* nov. ordo