

The Biology of  
**Nematodes**

Edited by Donald L. Lee



# **THE BIOLOGY OF NEMATODES**

This book is dedicated to Alan F. Bird and Kenneth A. Wright in memory of their great contributions to the study of nematodes. They were an inspiration to others and their enthusiasm was unabated up to the time of their deaths.

# THE BIOLOGY OF NEMATODES

Edited by

**Donald L. Lee**

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# CONTENTS

Foreword	vii
Preface	ix
List of Contributors	xi
1 Systematic Position and Phylogeny <i>Paul De Ley and Mark Blaxter</i>	1
2 General Organisation <i>Lynda M. Gibbons</i>	31
3 Life Cycles <i>Donald L. Lee</i>	61
4 Male and Female Gametes and Fertilisation <i>Jean-Lou Justine</i>	73
5 Embryology, Developmental Biology and the Genome <i>Ian A. Hope</i>	121
6 Hatching <i>Roland N. Perry</i>	147
7 Cuticle, Moulting and Exsheathment <i>Donald L. Lee</i>	171
8 Feeding and Digestion <i>Edward A. Munn and Patricia D. Munn</i>	211
9 Feeding Behaviour of Plant-Parasitic Nematodes <i>Urs Wyss</i>	233
10 Metabolism <i>Carolyn A. Behm</i>	261
11 Excretion/Secretion, Ionic and Osmotic Regulation <i>David P. Thompson and Timothy G. Geary</i>	291
12 Neuromuscular Organisation and Control in Nematodes <i>Richard J. Martin, J. Purcell, A.P. Robertson and M.A. Valkanov</i>	321
13 Locomotion <i>Robert McNeill Alexander</i>	345
14 Nematode Sense Organs <i>John Jones</i>	353
15 Behaviour <i>Donald L. Lee</i>	369
16 Nematode Survival Strategies <i>David A. Wharton</i>	389

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17	Ageing <i>David Gems</i>	413
18	Immunology of Nematode Infection <i>Haruhiko Maruyama and Yukifumi Nawa</i>	457
19	Biological Control <i>Brian R. Kerry and William M. Hominick</i>	483
20	Behaviour of Entomopathogenic Nematodes <i>Nobuyoshi Ishibashi</i>	511
21	Chemical Control of Animal-Parasitic Nematodes <i>George A. Conder</i>	521
22	Anthelmintic Resistance <i>Nick C. Sangster and Robert J. Dobson</i>	531
23	Molecular Approaches to Novel Crop Resistance Against Nematodes <i>Howard J. Atkinson</i>	569
24	Epidemiology and Control of Nematode Infection and Disease in Humans <i>Donald A.P. Bundy, Helen L. Guyatt and Edwin Michael</i>	599
	Index	618

# FOREWORD

by Bridget M Ogilvie, DBE, ScD

To most people, nematodes seem dull if not repulsive and their mainly cylindrical, thread like shape does not help their image. Their main uniting feature seems to be their life cycle, an egg followed by 5 stages with moults between. But beneath these rather banal features lies an infinite degree of complexity and variation. This is true both of those which live at least part of their lives as parasites of plants or animals and of the majority that are free living, and are found in all manner of environments, including many that are extreme.

To scientists, the most famous worm today is almost certainly *Caenorhabditis elegans*, used as a model for detailed cellular and molecular studies of a multicellular animal for the past 3 decades, culminating with the publication of the complete sequence of its genome in 1998. These studies have enabled *C. elegans* to be used for the investigation of a variety of biological questions relevant to many species including our own.

The extraordinary depth and detail of our knowledge of *C. elegans* has only just begun to illuminate our understanding of the huge numbers of species that are classified as nematodes. This multi-authored volume edited by Donald Lee is the culmination of his long term commitment to furthering our understanding of these organisms which are ubiquitous in nature and often important parasites of plants and animals. Our understanding of the huge nematode family at the genetic/systematics level does not permit us yet to relate the complexities of these creatures to their environment or their genetic distance from each other. Instead, in this book the vast body of knowledge about nematodes is organised into themes and within each theme, the available knowledge is discussed across the whole arena of nematode variation.

It is 20 years since I too was engaged in research into parasitic nematodes. I am delighted to be asked to write this foreword and thus have the opportunity to see the work of many old friends and even more new scientists engaged in the study of this complex group of animals.

It is particularly pleasing to read reviews that incorporate work done not only at the end of the 20th Century but in some cases, as long ago as the 19th Century. This is a tribute to the scholarship of the participating authors and thus, a commendation of this interesting volume.





# PREFACE

The objective of this multi-author book is to bring together various aspects of the biology of free-living, plant-parasitic and animal-parasitic nematodes in a form that will be suitable for research scientists, academics involved in the teaching of nematodes and some aspects of parasitology, and post-graduates and undergraduates who wish to have the diverse literature available in readily accessible reviews.

Nematodes have tended to be studied because of their medical and veterinary importance and because they are major pests of crops. There is an extensive literature on their structure, systematics, biochemistry, physiology, immunology and molecular biology. However, large numbers of free-living nematodes inhabit marine or freshwater mud and the soil, with several million being found per square metre in the top few centimetres of sub-littoral mud and cultivated soil, and they are being increasingly studied.

The place of nematodes in the early cytological literature is not generally realised. The first description of the formation of polar bodies by sub-division of the nucleus of the ovum; the discovery that both parents contribute equal numbers of chromosomes to the offspring; and the discovery that the cells which eventually form certain organs, such as the reproductive system or the intestine, could be identified as early as the fourth cleavage of the egg, were by scientists who worked on the large ascarid *Parascaris equorum* (syn. *Ascaris megalocephala*) from horses during the 19th century (see Chitwood and Chitwood (1950) *An Introduction to Nematology*, Baltimore: Monumental Printing Co.). Nematodes have again become prominent as model organisms. In 1965 Sydney Brenner chose the free-living nematode *Caenorhabditis elegans* to study the developmental biology, genetics, molecular biology and behaviour of a single organism. Since then its complete cell lineage has been described with every cell being identified and assigned a unique label and the connectivity of its nervous system has been worked out. There is now an extensive literature on all aspects of the biology of this nematode. Information obtained from *C. elegans* is being used in the study of other nematodes and this is reflected in several chapters in this book.

“Larva” instead of “juvenile”, “pharynx” instead of “oesophagus” and “epidermis” instead of “hypodermis” have been used throughout the book. The reasons for this are given in the relevant sections. No attempt has been made to standardise the classification used in the various chapters as this is currently undergoing proposed modification (see Chapter 1).

## Acknowledgements

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# 1. Systematic Position and Phylogeny

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## Introduction

Nematodes are a highly diverse and very important group of multicellular animals, but their systematics have always been volatile and are currently entering a new phase of turbulence. At the moment of writing this chapter, molecular methods and phylogenetic models are bringing new insights that require significant changes in nematode systematics. To provide an overview at this particular time is therefore both an exciting and impossible challenge, since we can roughly predict the extent of the changes to come, but not yet stipulate their precise form.

Several authors have reviewed the complex history of nematode systematics over the past 150 years, and the many individuals that contributed to it (e.g. Micoletzky, 1921; Andr ssy, 1976; Lorenzen, 1983; Inglis, 1983). In this chapter, we therefore do not attempt to present a comprehensive overview of the many different classifications of nematodes proposed in the past. Rather, we will sketch the history of past phylogenetic frameworks for nematodes, briefly discuss how these phylogenies were translated into classifications, and compare them with the first results from molecular phylogenetic analyses. We will also elaborate a first tentative approximation to a classification based on these molecular analyses, combined with morphological data.

Fundamental questions of organismal classification and phylogenetic inference are continuously being debated in ever-growing numbers of books and journals. These debates are becoming ever more specialised and complex, suggesting that a consensus will not be reached any time soon. Our purpose here is not to add our own voice to the chorus, neither by attempting to establish any purported 'supremacy' of molecular phylogenies over morphological data (cf. Moritz and Hillis, 1996 for a sensible assessment), nor by providing the 'one true and definitive' classification for nematodes. Irrespective of all debates about the best

methods and data, we only wish to demonstrate three practical points:

- (i) There is a substantial degree of overall congruence between morphological and molecular phylogenetic analyses of nematodes.
- (ii) Nematode phylogeny is *not* an intractable problem — although certainly not an easy one either.
- (iii) Nematologists must incorporate the latest methods of phylogenetic inference into their repertoire as an integral part of nematode systematics.

We believe the latter point is an essential prerequisite for the continued survival and renewed growth of nematology in the new century (cf. Ferris, 1994). Nematode taxonomy will not be able to assume its proper place within biological systematics unless it catches up with the newest developments of systematic theory and practice, and unless it proves able to estimate nematode diversity, recover nematode relationships, and hierarchically organise nematode classification on a genealogical basis.

## The Higher Classification

### Nemata or Nematoda?

Taxonomic nomenclature provides the basis for recording and communicating classifications. It is therefore an essential biological tool, but not a fundamental axiom underpinning all inferences and assumptions. We consider it of great importance that systematic hierarchies are proposed, compared and rejected, based on the theoretical and relational framework provided by phylogenetic inference. We consider it far less important which names exactly are assigned to the different taxa occurring within such hierarchies, as long as the great majority of users of any given system will understand which taxon is represented by which name.

A good example of a long-lasting nomenclatorial debate about taxon names in nematodes, is the name of the encompassing taxon itself: Nemata or Nematoda? At present, it is nearly universally agreed that nematodes should indeed be ranked as a phylum,

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especially now that the older encompassing taxa Aschelminth(e)s or Nemathelminth(e)s are more and more being questioned (see page 3). Adherents to the name *Nemata* argue that this was the name used in the first proposal (by Cobb, 1919) of phylum rank for nematodes, and that it should therefore be upheld over the corrupted name *Nematoda* (Chitwood, 1957, 1958). The latter was a modification of *Nematodes* as first used at family level by Burmeister (1837), and ultimately derives from *Nematoidea*, an order-level name originally proposed by Rudolphi (1808). On the other hand (see Steiner, 1960), *Nematoda* has been in use longer, and the original proposal of the phylum by Cobb (1919) actually introduced the name *Nemates*, which was only later amended to *Nemata* by Chitwood (1958).

The International Code for Zoological Nomenclature does not rule on taxon names above family level, and for decisions on name validity at lower levels it applies a combination of both chronological priority (arguably favoring *Nematoda*) with rank-specificity (arguably favoring *Nemata*). Hence, there is no obvious official guideline or precedent to be followed — which undoubtedly contributes to the further life of the issue. Since there is no convincing solution in sight, and an ever-growing list of scientifically more interesting questions remain to be answered, we do not wish to devote more time and space to the matter than necessary. We leave it to the reader to apply his or her preferred choice of phylum name as he or she sees fit. In this chapter, we have opted to use the name '*Nematoda*' only for pragmatic purposes, i.e. due to its older and somewhat more widespread usage.

### New Data and Old Questions: The Uncertain Position of Nematodes in Metazoa

#### *The settings*

In the last few decades, molecular approaches to biological systematics have pervaded the field, providing fresh perspectives on a wealth of new and old issues. This transformation is most evident in traditionally popular groups such as vertebrates (Mallat and Sullivan, 1998; Alvarez *et al.*, 1999), vascular plants (Hoot, Magallon and Crane, 1999; Qiu and Palmer, 1999) and arthropods (Eernisse, 1997; Spears and Abele, 1997; Yeates and Wiegmann, 1999), but the practical and theoretical implications and applications of molecular evolution have also drastically redirected research on many other biota (Stenroos and De Priest, 1998; Lang *et al.*, 1999; Sogin and Silberman, 1998; Brinkmann and Philippe, 1999).

Taxonomical studies on microscopic organisms such as nematodes traditionally receive little attention, and have often generated considerable frustration for both their scientific producers and users alike. This is partly due to the severe practical difficulties of obtaining a representative sampling of all relevant taxa. An even greater constraint is formed by observational restrictions on the number of characters available for diagnosis and classification within such groups. In the case of nematodes, this has typically led to textbook

phrases referring to the 'great morphological uniformity of nematodes'. This persistent myth was based on a mere handful of well studied model species and largely ignores the numerous bizarre and perplexing morphologies, ecologies and ontogenies described in specialised literature for over a century (see De Ley, 2000). Nematode morphology is actually rich in potentially useful characters, but an ideal instrument for observation is still missing: light microscopy does not provide enough resolution and requires substantial experience, while electron microscopy (particularly TEM) is far too costly in time and equipment for effective use on a routine basis.

By comparison, modern molecular tools can quickly and affordably provide a wealth of characters, using standardised basic methods applicable in almost any taxon. The systematics of 'morphologically uniform' groups therefore stands to benefit tremendously from these new approaches. In microbiology, for example, prokaryote taxonomy has been revolutionised and is now firmly based on DNA sequence data and the application of the latest methods for computer assisted character analysis (Woese, 1994, 1996; Brinkmann and Philippe, 1999). Sequence analyses of nematode relationships have also begun to appear at a rapidly increasing pace, addressing such issues as the position of nematodes within Metazoa (Sidow and Thomas, 1994; Vanfleteren *et al.*, 1994; Aguinaldo *et al.*, 1997; Aleshin *et al.*, 1998c), relationships among higher-level taxa within nematodes (Vanfleteren *et al.*, 1994; Kampfer, Sturmbauer and Ott, 1998; Blaxter *et al.*, 1998; Aleshin *et al.*, 1998a, b), and relationships within and among previously intractable families and genera (see Fitch, Bugaj-gaweda and Emmons, 1995; Al-banna, Williamson and Gardner, 1997; Nadler and Hudspeth, 1998; Adams, 1998a, b; De Ley *et al.*, 1999).

Another potentially vast source of taxonomic characters is developmental lineage mapping. Like Transmission Electron Microscopy, this technique remains more limited in routine applicability and cost-effectiveness, but lineaging and TEM can nevertheless provide far superior character resolution than light microscopy of preserved material. They are especially powerful when combined with phylogenetic frameworks provided by sequence analyses (cf. Baldwin *et al.* 1997a, b; Goldstein, Frisse and Thomas, 1998; Sommer *et al.*, 1999).

Apart from increasing character resolution as such, alternatives to light-microscopical morphology are of fundamental importance for a second reason: character diversity and divergence in nematode taxa is often quite different depending on the character suites in question. Thus, divergence in ribosomal DNA sequence is remarkably high within certain nematode clades with fairly low morphological diversity, and remarkably low in other clades with much higher morphological diversity (Blaxter *et al.*, 1998). **There is no obvious correlation between rates of morphological evolution and rates of fixation of mutations.** In a developmental analog, nematodes can exhibit substantial diversity in the mechanisms that specify cell fates, even in the absence of any evident differences in ultimate cell fates

themselves, i.e. differences in final morphology (see review by Félix, 1999).

Any classification that claims to represent 'natural relationships' must therefore attempt to combine morphology with other character suites — and this even when relatedness is not directly equated to phylogeny. In this chapter, we assume that classification *should* be based primarily on phylogenetic relationships, even though we are aware that phylogenetic analysis of biological organisms (like any other scientific methodology) is not an infallible approach guaranteed to produce definite answers to all pertinent problems. Rather, our point is that phylogeny provides (a) a neutral ground for analysing, comparing and combining any set of characters reflecting evolutionary history and (b) a theoretical framework for translating that evolutionary history into classification along less arbitrary lines than those followed by individual intuition. Within a phylogenetic framework, new character suites such as molecular data do not replace morphological data, but rather they reduce the number of inconclusive or deficient analyses and thus improve the overall outcome (Patterson, Williams and Humphries, 1993).

Understanding the results obtained with molecular and embryological methodologies requires skills and knowledge that were hardly relevant to nematological systematics before, but which are rapidly becoming essential for both the users and suppliers of nematode classifications. Thus, a new phase is reached in the continuing process of taxonomic revision as driven by advances in accuracy and resolution of characters. Some excellent examples of the concomitant advantages, pitfalls and continuities are provided by recent developments in studies on the phylogenetic position of nematodes within Metazoa, and we will first focus on this issue.

#### *New life for an old debate*

The use of molecular datasets for the analysis of metazoan phylogeny has a short and spectacular history (Field *et al.*, 1988; Christen *et al.*, 1991; Adoutte and Philippe, 1993; Sidow and Thomas, 1994; Halanych *et al.*, 1995; Wray, Levington and Shapiro, 1996; Aguinaldo *et al.*, 1997; Adoutte *et al.*, 1999). The placement of phyla within the radiation of Metazoa has been revised significantly compared to some morphological views, but concurs in many details with re-evaluations based on extant morphology (Nielsen, 1995) and on early Cambrian 'missing link' fossils (Conway Morris, 1993, 1994). In general, few genes have been used for reconstruction of the Metazoan radiation, and particular emphasis is placed on the SSU rDNA gene.

Adoutte *et al.* (1999) point out that the Cambrian radiation may have taken place in a very short period (geologically speaking) with the origin of all modern phyla occurring between 600 My and 550 My BP (Philippe, Chenuil and Adoutte, 1994; but see Conway Morris, 1997). The nature of molecular evolution suggests that very little phylogenetic signal from this radiation may be left in animal genomes, as any gene evolving at a suitable rate at that time may well have diverged so far by now, that any remaining signal has

been obscured by the noise of homoplasy and back-mutation. Some analyses of metazoan evolution using molecular clock models place the divergence of the phyla back to > 1000 My (Raff, Marshall and Turbeville, 1994; Vanfleteren *et al.*, 1994; Doolittle *et al.*, 1996; Wray *et al.*, 1996; Feng, Cho and Doolittle, 1997). While the application of modern molecular clock measures to ancient lineages (and clocks based mainly on the deuterostome Chordata to all phyla) is open to serious question, there is a remarkable consistency in the estimates of the radiation of the phyla (circa 1000 My to 700 My). The metazoan phyla had already diverged at the onset of the Cambrian, as evidenced by the Lagerstatte assemblages of the Burgess Shale and related faunas (Gould, 1989; Foot *et al.*, 1992; Conway Morris, 1993; Conway Morris, 1994). In the absence of informative fossils, the debate must therefore continue. Although nematode fossils are known (mostly preserved in amber), few are older than 30 My and none are informative with regards to the origin of Nematoda (Poinar, 1992; Poinar, Acra and Acra, 1994; Manum *et al.*, 1994). The fossil record is therefore particularly unhelpful in reconstruction of the relationships of the Nematoda (Conway Morris, 1981).

The molecular placement of the Nematoda was initially based on the SSU rDNA sequence from *Caenorhabditis elegans* (Ellis, Sulston and Coulson, 1986). The anomalous behaviour of this sequence (and, ironically, that of the other major protostome model organism, *Drosophila melanogaster*) in molecular phylogenetic reconstruction led to the explicit exclusion of these species from analyses. An example is found in Philippe, Chenuil and Adoutte (1994), where *Drosophila* and *Caenorhabditis* can be robustly placed as sister taxa at the base of the protostomes (while other insect sequences cluster correctly with arthropods deep within the Protostomia). For the arthropods, other SSU rDNA sequences were available that 'behaved better' under various models of sequence evolution and could be used to place Arthropoda within the Metazoa. By contrast, the *C. elegans* SSU rDNA sequence was until recently the only one available for the Nematoda, and the acquisition of SSU rDNA sequences from other rhabditids and from strongyloid or strongyloidid parasites (Putland *et al.*, 1993; Zarlenga, Lichtenfels and Stringfellow, 1994; Zarlenga *et al.*, 1994; Fitch, Bugajgaweda and Emmons, 1995; Fitch and Thomas, 1997) failed to significantly improve inferred branch lengths or resolution. To avoid branch length artefacts, nematodes were often simply left out of reconstructions (Lake, 1990; Philippe, Chenuil and Adoutte 1994; Winnepenninckx, Backeljau and De Wachter, 1995).

In the last few years, the search for less anomalous SSU rDNA sequences was extended to the whole phylum Nematoda, and species from the zooparasitic Spirurida and Trichocephalida proved to have less extreme branch lengths (Halanych *et al.*, 1995; Aguinaldo *et al.*, 1997). Analysis of these sequences with a dataset encompassing the rest of the Metazoa yields a hypothesis of Metazoan evolution substantially different from the accepted models: nematodes are united



with Kinorhyncha, Priapulida, Nematomorpha, Tardigrada, Onychophora and Arthropoda into a clade of moulting animals, the Ecdysozoa (Aguinaldo *et al.*, 1997). Reassessment of other phyla using SSU rDNA has yielded a hypothesis of metazoan relationships where the Protostomia can be split into two major groups: the Ecdysozoa and the Lophotrochozoa. There are several morphological and ontogenetic characters/suites of characters that can be adduced as evidence for these clades (Nielsen, 1995).

Although the proposition of the Ecdysozoa is supported by other characters such as sequence analysis of EF-1 $\alpha$  (McHugh, 1997; Garey and Schmidt-Rhaesa, 1998), moulting, loss of locomotory cilia, trilayered cuticle structure and microvillar epicuticle formation (Nielsen, 1995; Schmidt-Rhaesa *et al.*, 1998), acceptance of such a radical departure from current mainstream thought is slow to accrue. Much of this mainstream opinion derives from Grobbsen's (1910) 'Aschelminthes' concept, and is actually less entrenched in taxonomical tradition than its adherents might assume. Thus, a wide range of different scenarios was proposed by Grobbsen's predecessors and contemporaries, and one of the competing schools of thought specifically argued for close relationship between nematodes, tardigrades and/or insects. Such proposals included the 'Chitinophores' concept of Perrier (1897), as well as the extensive argument by Seurat (1920) for common ancestry of arthropods and nematodes (see review in Chitwood, 1974). Perrier's view was based on the assumption that nematodes originated as a parasitic lineage deriving from arthropod ancestry, and rapidly lost credibility as the anatomy and diversity of free-living nematodes became more evident. Seurat's case for a shared origin was less easily discounted, however: it seems to have been mostly ignored rather than refuted, and should now be given due credit as a largely forgotten forerunner of the Ecdysozoa concept.

#### Future directions

SSU rDNA is a very useful phylogenetic marker, but it is neither the only appropriate choice, nor a consistently reliable one (Hasegawa and Hashimoto, 1993; Sidow and Thomas, 1994), and its support for the Ecdysozoan clade has been questioned by Wagele *et al.* (1999). A wider route to confirmation or rejection of Ecdysozoa is provided by the use of independent sequence datasets for analysis. There is as yet no consensus on any single gene useful for deep analysis of Metazoa in parallel with SSU and LSU rDNA, not least because analyses of proteins and protein genes are also subject to various biases, both at the level of individual sequences (Sidow and Thomas, 1994; Foster and Hickey, 1999) and in comparisons across multiple loci (Guigo, Muchnik and Smith, 1996). Nevertheless, the technologies of sequencing, sequence analysis and sequence database management are developing at such a pace, that it is rapidly becoming possible to analyse multiple loci per organism and thus evaluate the phylogenetic qualities of each locus (see e.g. O'Grady, 1999; Curole and Kocher, 1999).

In this manner, Mushegian *et al.* (1998) performed an extensive analysis of quartets of 42 orthologous proteins encoded by the *C. elegans*, human and *Drosophila melanogaster* genomes, rooted by orthologues from the yeast *Saccharomyces cerevisiae*. They found that 24 different proteins supported a closer relationship between flies and humans (with high mean bootstrap support, >80%), while only 11 supported an arthropod-nematode relationship (with lower overall bootstrap support, mean 61%). This is in apparent conflict with the results derived by Aguinaldo *et al.* (1997) using SSU rDNA, and argues against the 'Ecdysozoa' as a natural group. However, Mushegian *et al.* (1998) pointed out that a larger proportion of slowly evolving genes (where fewer substitutions are inferred in the lineages leading from the respective common ancestors to yeast versus fly, or to yeast versus nematode) supported a nematode + arthropod clade (8 out of 18 protein quartets). In addition, the *C. elegans* protein dataset was shown to have a greater overall substitution rate than the fly dataset, with 25 out of 36 *C. elegans* proteins being more distant from yeast than their fly orthologues (Mushegian *et al.*, 1998). The consensus result, a placement of nematodes basal to a fly + human clade, may thus once again be an artefact of the use of rapidly evolving sequences from *C. elegans*, mirroring the earlier SSU rDNA analyses.

This kind of analysis will undoubtedly benefit from sequence datasets derived from other nematode taxa, particularly those in clades displaying lower substitution rates in SSU rDNA. The inception of EST-based genome projects on nematodes of economic, health and research interest will hopefully yield data sets for such analysis in the near future (Blaxter *et al.*, 1996; Blaxter *et al.*, 1999; Daub *et al.*, 2000; Johnston *et al.*, 1999). An alternative molecular system for phylogenetics is the analysis of gene families that are involved in setting up or executing the body plan of Metazoa. These genes may retain phylogenetic signatures in their sequence and expression patterns that reveal deep relationships. One such family is the homeodomain-containing genes of the HOX cluster (de Rosa *et al.*, 1999). This cluster of paralogous genes, which each contain a short domain involved in binding DNA (the homeodomain), is closely linked in the genomes of many species, and is involved in the core process of specifying and executing anterior-posterior identity during development. Importantly, in most taxa the genes are arranged along the chromosome in the same order as their corresponding sites of activity in specifying tissue/organ fate on the A-P axis.

First discovered in *Drosophila*, the HOX cluster has also been found in mammals, where the general genome duplications evident in the chordate lineages have produced four paralogous HOX clusters. HOX gene datasets, and in some cases demonstration of linkage on the chromosome, have now been acquired for additional taxa, spanning many phyla (de Rosa *et al.*, 1999). The *C. elegans* HOX cluster was described through classical developmental genetics coupled with gene cloning, and is significantly different from both fly and mammal clusters (Costa *et al.*, 1988; Wang *et al.*, 1993; Kenyon, 1994; Salser and Kenyon, 1994). There

appear to be fewer genes in the cluster, which is arranged in a different order and interspersed with non-HOX genes over a large region of chromosome III. These features suggested to early reviewers that the *C. elegans* cluster might be a relic of an ancestral cluster from which the fly and mammal ones were derived. This was based on the assumption that nematodes were basal to arthropods and deuterostomes, an assumption that remains popular (Vanfleteren and Vierstraete, 1999) albeit with increasingly cautious support (see Fitch and Thomas, 1997).

Completion of the *C. elegans* genome project, which revealed additional HOX genes in the cluster, and the proposal of Ecdysozoa have led to reappraisal of the *C. elegans* HOX cluster as a very derived pattern. Analysis of HOX genes from additional phyla from Ecdysozoa and Lophotrochozoa led de Rosa *et al.* (1999) to propose that there is an Ecdysozoan-specific feature of HOX clusters of Priapulida, Arthropoda, Onychophora and Nematoda: the presence of a gene similar to arthropod *Abdominal-B* (AbdB). The arthropod gene *Ultrabithorax* (Ubx) could also be defined in Onychophora and Priapulida, but a nematode (i.e. *C. elegans*) orthologue of Ubx is difficult to define (de Rosa *et al.*, 1999). This model of the metazoan HOX clusters suggests that the Ur-metazoan had nine or ten genes, and that the *C. elegans* cluster has diverged very significantly from this archetypal arrangement. Again, analysis of HOX gene clusters from other nematode taxa will be very informative, particularly from clades known to be less derived in morphology and to have lower substitution rates for the loci in question.

## Early Explorations of Relationships within Nematoda

### *First discoveries of taxa and characters*

With the first taxonomic and anatomical studies of parasitic and free-living nematodes, zoologists of the nineteenth and early twentieth century were given just an inkling of the diversity and complexity of this group. Thus, the earliest taxonomic systems were by necessity limited to very incomplete representation and to excessive emphasis on very few characters. Convergence could not yet be recognised as such, due to limitations of the available microscope optics, and because of the absence of an established framework for accurate description and interpretation. Famous examples of approaches that overemphasized a single character suite and therefore resulted in largely artificial classifications, include the system of Schneider (1866) based on somatic musculature, and the proposals of Cobb (1919) based on stoma armature.

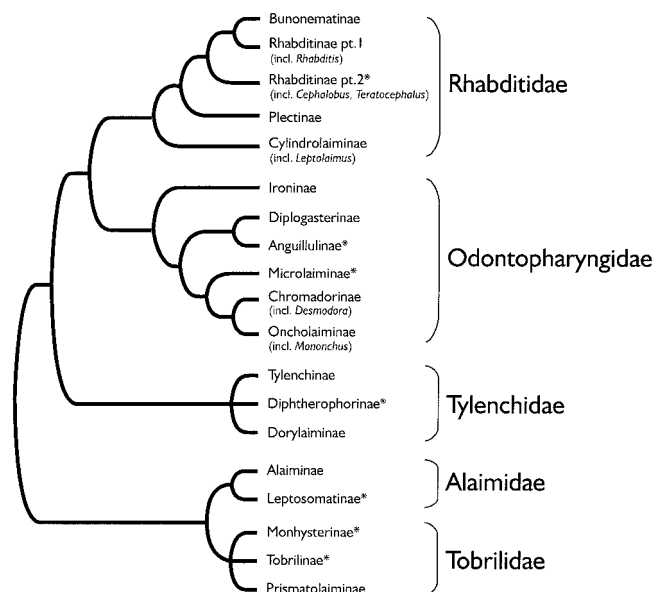
The nematologists and helminthologists of the time were well aware of the exploratory nature of their efforts. At such an early stage in the exploration of the diversity of nematodes, attempts to establish a comprehensive phylogenetic overview were generally recognised as being largely speculative (see de Man, 1876; Micoletzky, 1922). Most classifications of that time were therefore proposed purely on typological

and ecological grounds. Also, although the numbers of known parasitic and free-living species were very limited, synthetic approaches were hindered from the outset by difficulties of comparing the seemingly simple anatomy of microscopic species with the more obviously complex characters of large zooparasites. Combined with the different backgrounds and purposes of different authors, this set a trend for scientific specialisation and fragmentation which was to plague nematology and helminthology throughout their further history. Nevertheless, some attempts were made to integrate all known Nematoda into a single classification, e.g. by simply allocating all zooparasites to a different higher taxon from all other nematodes (Perrier, 1897; Stiles and Hassall, 1926). In effect, this represented an ecological pendant to the morphologically simplistic systems of Schneider and Cobb.

Other authors realised that the affinities between nematode parasites of vertebrates and other nematodes were more complex and required a subtler approach. Thus, Baylis and Daubney (1926) distinguished five encompassing orders within the Nematoda (Ascaroidea, Strongyloidea, Filarioidea, Dioctophymaidea and Trichinelloidea) that contained both zooparasitic and interstitial representatives. Likewise, Filipjev (1929, 1934) rejected a basic division into two groups based on presence versus absence of zooparasitism and proposed no less than eleven orders: Enoplata, Chromadorata, Desmoscolecata, Monhysterata, Anguillulata, Oxyurata, Ascaridata, Spirurata, Filariata, Dioctophymata and Trichurata. Two of these orders, Enoplata and Anguillulata, contained both zooparasitic and non-zooparasitic representatives. Filipjev (1934) also argued strongly in favour of marine nematodes as representing the earliest forms of nematodes. In many respects, his system was highly influential, especially on the subsequent classification of Chitwood (1937). Most of Filipjev's proposed orders remain in use today, albeit with changed endings and with some changes in contents. Filipjev even considered an overall division along the lines of Chitwood's soon-to-follow subclasses Phasmidia/Aphasmidia, but preferred not to group his orders in higher taxa (p. 6 in Filipjev, 1934).

### *An early phylogeny: Micoletzky (1922)*

Those few authors who actually dared to speculate on nematode interrelationships around the turn of the century, were often very cautious about their own phylogenetic and taxonomic inferences. An interesting example of an early system is provided by Micoletzky (1922), who tentatively suggested highly resolved evolutionary trees for 76 genera (see condensed tree in Figure 1.1) of the 167 non-zooparasitic genera known to him at the time. Clearly influenced by Cobb (1919) and Marcinowski (1909), Micoletzky considered stoma structure to be of primary importance and therefore grouped genera into five families based on stomatal characters. This resulted e.g. in the inclusion of all nematodes with teeth in one family (Odontopharyngidae), while all nematodes with a stylet-like organ were united in one other family (Tylenchidae). Both these



**Figure 1.1.** Overview of the phylogenetic relationships among non-zooparasitic nematodes, as cautiously proposed by Micoletzky (1922) on the basis of buccal morphology. Taxa marked with an asterisk were assumed to be paraphyletic. Compiled and modified from figures RW in Micoletzky (1922); see text for details.

groupings later turned out to be extremely artificial. By comparison, his arrangement of plectids, teratocephalids, cephalobids and rhabditids *sensu stricto* (united in one family Rhabditidae) withstood the test of time much better, presaging both the branching order and derived position found for these taxa in much more recent phylogenies (cf. Figures 1.4; 1.6).

### Bipartite Systems and Comprehensive Classifications

#### *The origin of Chitwood's Adenophorea/Secernentea system*

Probably the single most important event in the history of nematode systematics, was the realisation that nematodes with phasmids share numerous other characters and therefore represent a single, highly diversified and yet highly coherent unit (Chitwood and Chitwood, 1933; Chitwood, 1937). As a result of his extensive experience with parasitic and non-parasitic nematodes alike, Chitwood succeeded in cutting across many of the previous simplistic classifications, bringing together in one class most of the important zooparasitic taxa with one of the main free-living groups (rhabditids *sensu lato*), as well as the largest taxon of predominantly phyto- and mycoparasitic nematodes (tylenchids). Sixty years of subsequent research have proven the diagnostic and phylogenetic soundness of this grouping, and Chitwood's system was generally adhered to by many nematologists for over forty years.

As was common practice in pre-Hennigian taxonomy, the remainder of nematodes was also grouped by Chitwood (1937), even though no unifying characters existed for it. At first, he respectively

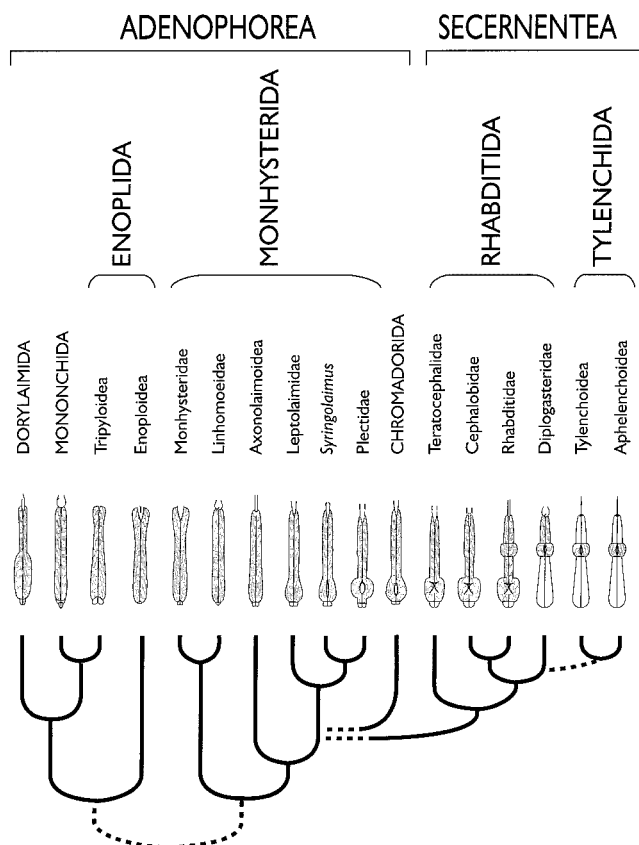
proposed the names Phasmidia and Aphasmdia for the two groups, but subsequently (Chitwood, 1958) suggested replacement with Secernentea (= 'secretors', referring to presence of an excretory system with lateral canals) and Adenophorea (= 'gland-bearers', referring to presence of caudal glands) as modifications of terms coined by von Linstow (1905), in order to avoid confusion with the scientific name already in use for stick-insects.

Chitwood and Chitwood (1933) assumed that bacterial-feeding forms with tubular stoma and valvate basal bulb were closest to the common ancestor of all nematodes. In particular, plectids were presumed to have preserved the morphology of the earliest Adenophorea, while rhabditids were thought to represent the earliest branch within Secernentea. As explained next, these assumptions were later modified or rejected by other authors, and in particular Adenophorea would subsequently be recognised as a paraphyletic group. Most of the major changes to classification proposed after Chitwood (1937) therefore consist of attempts to correct for the lack of phylogenetic and morphological unity of Adenophorea. Thus, our own proposed system (see pages 12 and 13) includes neither the name Adenophorea nor Secernentea as valid taxon, and we will therefore use both names between parentheses throughout the remainder of this chapter.

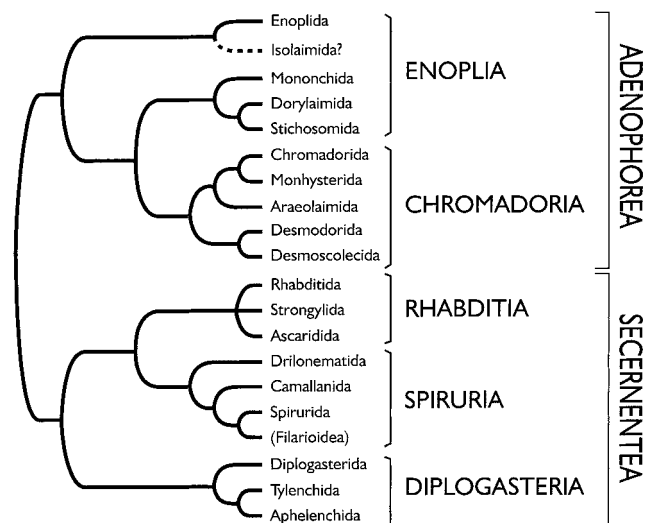
#### *Uprooting the bipartite system: Maggenti (1963–1983)*

Maggenti (1963) elaborated on Filipjev's and Chitwood's observations, focusing particularly on aspects of pharynx structure and excretory system as markers of evolutionary relationships. This led him to the realisation that the pharynx structure of plectids and rhabditids could not arguably be close to that of the common ancestor of all nematodes. Basically, he considered a cylindrical pharynx to be ancestral, suggesting that enoplids and monhysterids were morphologically much nearer to the origin of nematodes than plectids and rhabditids. Furthermore, the origin of rhabditids (and by extension all 'Secernentea') was inferred to lie close to the origin of chromadorids and leptolaimids, implying that 'Adenophorea' were paraphyletic (Figure 1.2).

These observations provided the basis for several later rejections or qualifications of 'Adenophorea' by other authors (see pages 7–9), and thus lie at the root of the eventual replacement of Chitwood's bipartite system by various tripartite systems. However, Maggenti (1963, 1983, 1991) never rejected Adenophorea himself. Although he later stated that classification should be based on phylogeny (Maggenti, 1983), like many evolutionary taxonomists he adhered to the more permissive monophyly criterion of Simpson (1961), where valid taxa should have exclusive ancestry in a single taxon of lower rank, rather than in a single species. He therefore did not apply paraphyly as sufficient cause to invalidate taxa. Even in 1983, Maggenti still maintained 'Secernentea' and 'Adenophorea' as sister taxa (Figure 1.3).



**Figure 1.2.** Overview of the phylogenetic relationships among non-zooparasitic nematodes, as proposed by Maggenti (1963) on the basis of pharyngeal structure and excretory system. Dotted lines represent more tenuous hypotheses of relationship. Enopliida, Monhysterida and Rhabditida were assumed to be paraphyletic. Modified from Maggenti (1963); see text for details.



**Figure 1.3.** Overview of the phylogenetic relationships among all nematodes, as proposed by Maggenti (1983). All taxa were apparently assumed to be monophyletic. Modified from Maggenti (1983); see text for details.

Maggenti rejected close relationships between plectids and rhabditids, arguing that the valve structure in the basal bulb of larger *Plectus* species must be convergent with the 'butterfly valves' of rhabditids, rather than homologous. He may have deemed this necessary to strengthen his case for a basic error in Chitwood's rooting of the nematode tree. However, many of the smaller Plectidae do have butterfly valves (as noted by Lorenzen, 1981, 1994), and a close relationship between plectids and rhabditids is actually quite compatible with a different placement of the root for nematodes. In retrospect, it is therefore ironic that Maggenti actually discarded a strong morphological argument *in favour* of a revised polarisation of pharyngeal characters in nematodes.

### Towards Tripartite Systems: Critical Scrutiny and Fragmented Classifications

*More explicit phylogenies and departures from bipartite systems*

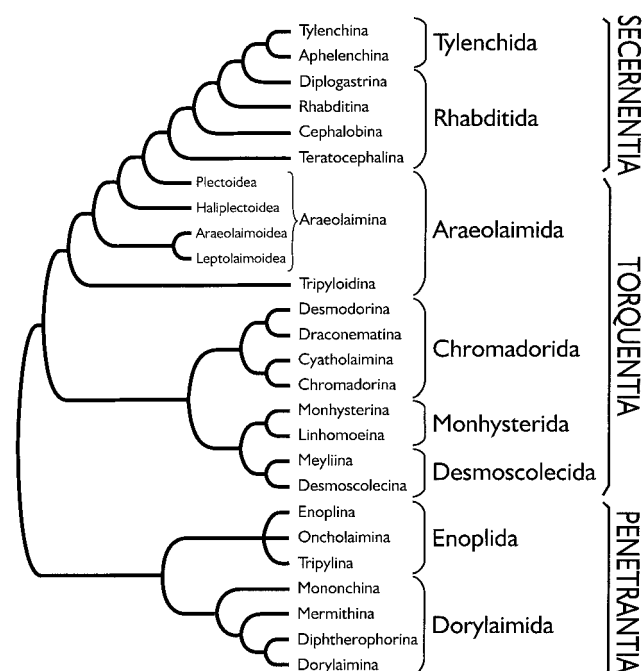
The Adenophorea/Secernentea dichotomy found its way into many textbooks and classifications, but it was never universally accepted. Even while maintaining 'Adenophorea' as a valid taxon, many authors overtly or covertly recognised its lack of monophyly or homogeneity compared to 'Secernentea' (Maggenti, 1963; De Coninck, 1965; Gadéa, 1973; Lorenzen, 1981, 1994; Malakhov, Ryzhikov and Sonin, 1982; Inglis, 1983; Adamson, 1987). More radically, Goodey (1963) simply rejected both classes, *i.a.* on the grounds of the intermediate position of teratocephalids, and instead maintained a multitude of orders as the highest-ranked subphyletic taxa. This proposal did not gain wider acceptance, but more influential were the works of Maggenti (1963) and De Coninck (1965). The latter promulgated the use of the subclasses Chromadoria and Enoplia within 'Adenophorea' to indicate their status as distinct major groups, while the former demonstrated the more derived status of 'Secernentea' and thus spurred later proposals to upgrade the enoplid and chromadorid subclasses to the same rank as their secernentean counterpart (Andrássy, 1974, 1976; Malakhov, Ryzhikov and Sonin, 1982; Inglis, 1983; Adamson, 1987). In some cases these proposals for a tripartite system were grounded in first applications of cladistics, in other cases the inference methods remained intuitive while emphasizing the need for diagnostic coherence of higher taxa. Analysis, depiction and argumentation of evolutionary relationships gained prominence, and it became more important to compile sets of supporting characters, rather than to propose just-so scenarios.

*The system of Andrásy (1974, 1976): typology and paraphyly*

The earliest exponent of a subdivision into three major nematode groups, the phylogeny and system of Andrásy (1974, 1976) provide a highly individual mixture of an explicitly typological outlook combined

with largely implicit evolutionary assumptions and deductions. While his phylogenetic framework followed Maggenti (1963) in depicting Adenophorea as paraphyletic (Figure 1.4), he altogether omitted inclusion of the major zooparasitic groups and attached no noticeable significance to monophyly as a criterion of taxon validity. Thus, he retained both Rhabditida and Araeolaimida as valid orders, despite their perceived paraphyly, and was not at all troubled by discrepancies of rank between presumed ancestral and descendant taxa (he assumed that the Order Rhabditida arose from within the Family Plectoidea, and the Order Tylenchida from Suborder Diplogastrina).

Instead, Andr ssy rejected Adenophorea on the basis of an unweighted count of diagnostic characters: as a group, they could only be defined by 4 'constant characters', versus no less than 17 for Secernentea. He therefore concluded 'that Adenophorea ... cannot possibly be a unified group' (p. 48 in Andr ssy, 1976). By comparison, the enopliid and chromadorid groups were much more homogeneous in their own rights (with resp. 16 and 14 'constant characters') and therefore merited equivalent status to Secernentea. Andr ssy also made unweighted tabular counts of diagnostic characters at lower ranks, to justify taxon validity and separation within his three subclasses at order and suborder level. This primary concern for diagnosis became all the more evident in his subsequently published encyclopaedic key to all known soil and freshwater nematode species (Andr ssy, 1984).



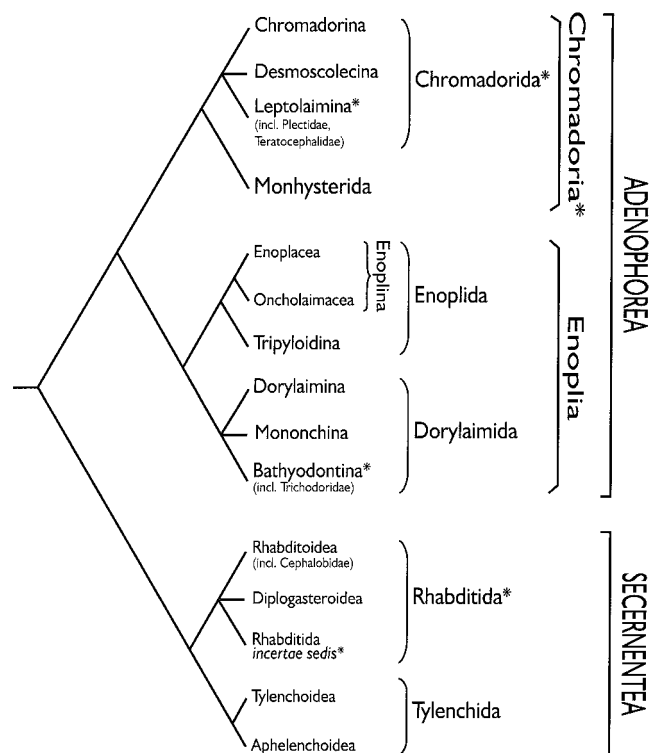
**Figure 1.4.** Overview of the phylogenetic relationships among non-zooparasitic nematodes, as proposed by Andr ssy (1976) on the basis of counts of diagnostic characters. Torquentia, Araeolaimida and Rhabditida are assumed to be paraphyletic. Compiled and modified from figures 21–32 in Andr ssy (1976); see text for details.

Also, since he assumed that Nematoda and Nematomorpha jointly constituted a phylum, Nematoda itself could not be ranked higher than a class, and the three subdivisions within it should therefore be ranked as subclasses. Instead of using subclass names derived from species names, he preferred names referring to characters and therefore proposed Torquentia and Penetrantia (referring to amphidial structure) as replacements for Chromadoria and Enoplia, while modifying the character-based name Secernentea (referring to the excretory system) to Secernentia, so as to match subclass endings.

Despite this heavy emphasis on diagnosis and typology, Andr ssy (1976) did provide a reconstruction of ancestral characters and morphologies, and he also presented a resolved phylogeny of all non-zooparasitic nematode suborders, apparently inferred from an intuitive combination of character counts and reconstruction of so-called 'evolutionary series' of species. His typological/gradistic approach to phylogeny and classification was deemed theoretically and factually flimsy and received extensive criticism (Coomans, 1977; Lorenzen, 1981, 1983, 1994; Maggenti, 1983, 1991). Nevertheless, compared to recent phylogenies as obtained by ribosomal DNA sequencing and a whole battery of highly advanced tree-construction computer algorithms (Figure 1.6), Andr ssy's evolutionary framework was certainly no worse than that of many contemporary schemes claiming a sounder theoretical basis. In many ways, his works epitomize the pragmatic, encyclopaedic, prolific and authoritatively idiosyncratic character of nematode taxonomy in the past century. Although often controversial, the direct connection between diagnostic characters and classification did enable him to formulate identification keys for all groups covered (later extended to species level in his book of 1984), a feat that is unlikely to ever again be repeated. Because of the need for identification tools of many users of nematode taxonomy, his system has become quite influential and will probably remain so for decades to come.

#### *The system of Lorenzen (1981, 1994): intensiveness, cladistics and monophyly*

Lorenzen (1981, 1994) provided the first phylogenetic system with emphatic focus on the 'Adenophorea' and on rigorously cladistic principles (Figure 1.5). His analysis included intense scrutiny of character polarity, and sought to establish monophyly of taxa wherever possible. This yielded many instances of nominal taxa that lacked a defining synapomorphy and were therefore not demonstrably monophyletic. For each such case, Lorenzen amalgamated the groups in question into a single potentially paraphyletic taxon awaiting further resolution. Indeed, absence of evidence does not equate evidence of absence, and it would have been premature for him to reject such taxa outright. However, the unfortunate corollary of his approach was that many separate and distantly related families were effectively being lumped into potentially paraphyletic 'bucket groups'. For instance, within Chromadorida he



**Figure 1.5.** Overview of the phylogenetic relationships among non-zooparasitic nematodes, as proposed by Lorenzen (1981, 1994) on the basis of cladistic analysis of morphological characters. Taxa marked with asterisk are assumed to be paraphyletic. Modified from Lorenzen (1994); see text for details.

included no less than 18 families in the suborder Leptolaimina, among which such disparate taxa as Teratocephalidae, Ceramonematidae and Rhabdolaimidae. In hindsight, this approach led to a paradoxical situation: Lorenzen's analysis most forcefully demonstrated the complete lack of support for 'Adenophorea' as monophyletic taxon, but his classification nevertheless maintained it, for lack of alternative resolution. Thus, he simultaneously demonstrated that cladistics could indeed be applied to such a scientific quagmire as nematode phylogeny — but also that useful morphological characters were too few in number to get sufficient resolution for a well-resolved classification.

A shortage of synapomorphies not only precluded positive proof of paraphyly for 'Adenophorea', but also prevented certain homoplasies from being detected. For example, Lorenzen interpreted the posterior position of the dorsal pharyngeal gland opening in taxa such as trichodorids, alaimids and dorylaimids as synapomorphic, and therefore united the former two with some other taxa in the 'bucket suborder' Bathyodontina. However, more intuitive morphological inferences (Riemann, 1972; Siddiqi, 1974, 1983a, b; Decraemer, 1995) as well as ribosomal data (Blaxter *et al.*, 1997; Vanfleteren and De Ley, unpublished data) show that alaimids and trichodorids belong in or near Enoplida. A posterior displacement of the gland opening may well

be functionally linked to the hydrodynamics of feeding through a very narrow spear and/or mouth opening. If so, the character may easily have arisen repeatedly in unrelated groups. A case in point are the aphelenchids, which are certainly not related to dorylaimids and thus show that the posteriad shift has occurred at the very least twice in Nematoda.

A last general critique of Lorenzen's approach is that he placed the origin of Nematoda in between 'Adenophorea' and 'Secernentea', an assumption that was largely outdated by 1981. Although he correctly criticized Maggenti (1963) for having exaggerated the degrees of difference between the basal bulb in plectids and rhabditids, Lorenzen (1981, 1983, 1994) did not himself address the question of character polarity of the rhabditid/plectid basal bulb. He also did not consider its possible validity as a synapomorphy for a clade comprising of teratocephalids, plectids and 'Secernentea'. Thus, while Lorenzen pointed out that Maggenti's error had actually deprived him of an argument in favour of his tree of pharyngeal character evolution, Lorenzen in turn failed to pick up on a character that could have settled his own uncertainty as to the paraphyly of 'Adenophorea'.

With the wisdom of hindsight, these comments are easily made, but the importance of Lorenzen's efforts should not be underestimated. His work placed a long-overdue emphasis on the taxonomy and phylogeny of marine nematodes, and was therefore extremely influential on subsequent research into ecology and taxonomy of marine nematodes. He also directly influenced the successive papers by Malakhov, Ryzhikov and Sonin (1982), Inglis (1983) and Adamson (1987), in which the names 'Adenophorea' and 'Secernentea' were abandoned altogether. Inglis (1983) proposed the names Enoplaea, Chromadorea and Rhabditea for classes equivalent to the subclasses Enoplida, Chromadorida and Rhabditida in Lorenzen (1981) and Malakhov, Ryzhikov and Sonin (1982), and expressed the view that Chromadorea and Rhabditea were closer to one another than to Enoplaea. Unlike Lorenzen, Inglis assumed an overtly non-cladistic philosophical stance, arguing that monophyly for nematode taxa (and even for the entire phylum Nematoda) was too difficult to ascertain, and therefore of limited relevance to their classification. Partly following and partly disagreeing with Inglis (1983), Adamson (1987) subsequently presented a cladistic analysis at subclass level and proposed that Rhabditea should also include all taxa grouped in Chromadorea by Inglis (1983). Thus, he reverted to a bipartite system, but one that partitioned the nematode orders quite differently from that of Chitwood (1937).

### Developing an updated Linnean Classification

*The latest system is never the last one*

Nematode systematics is inherently prone to controversy and instability. This is probably even more true now than ever before. On the one hand, it is eminently necessary to incorporate the new molecular phylogenies into a comprehensive classification, not least

because this will allow us to reunite parasitic and non-parasitic taxa once again into a comprehensive single framework. On the other hand, molecular sampling of taxonomic diversity within Nematoda is still very limited, especially within 'Adenophorea' and at lower levels of classification. Here too, the greater ease of collection and culture of 'secernentean' species has led to more extensive and intensive analysis, and concomitant taxonomic changes can therefore be proposed with greater confidence and detail for 'Secernentea' than for 'Adenophorea'. Furthermore, phylogenetic analysis is becoming an ever more sophisticated and complex discipline in itself, which nevertheless remains inherently prone to sources of bias and uncertainty, despite the many theoretical and methodological advances of the last decades. Above all, we have hardly begun the collection and comparison of results obtained from multiple character suites, such as those provided by different molecular loci, or by molecular versus morphological versus developmental data.

We may therefore rest assured that any system formulated today will be outdated almost immediately. Nevertheless, some of the phylogenetic relationships supported by molecular analyses are sufficiently robust or surprising to warrant formal representation in classification. At the very least, this will provide a new set of hypotheses for corroboration, and with a little luck it may contribute to more accurate application and interpretation of comparative studies on nematode genetics, biochemistry, development, morphology, ecology and control. With these provisos, a hybrid classification is presented below, derived partly from more recent morphological systems (e.g. Lorenzen, 1981, 1994; Inglis, 1983; Malakhov, 1994) and partly from results obtained with SSU rDNA sequences (Figure 1.6). As a rule of thumb, the latter were given primacy whenever they provided strong bootstrap support (above 85%), while the former were applied in cases where bootstrap values of molecular phylogenies were insignificant (< 65%), or in groups that were not yet included in sequence analyses<sup>1</sup>. In cases of moderate bootstrap support (65–85%), we attempted to reach a consensus between molecular and morphological patterns of relationships, if possible.

#### *Major changes in perspective*

Undoubtedly, our system will receive a mixed welcome, and numerous modifications may still be required before it can eventually be deemed compatible with an accurate phylogenetic framework. Irrespective of the precise nomenclatorial choices made below, we are confident of one important change: a major shift of balance is required, in order to combine parasitic and non-parasitic taxa within a single phylogeny-based hierarchy. Many taxa formerly placed within 'Adenophorea' need to be retained at, or upgraded to

comparatively high rank, while many parasitic taxa within 'Secernentea' must be downgraded to lower rank than has become accepted in recent years. This balancing act is actually well overdue, even on morphological grounds alone, since it follows inevitably from the combination of two earlier hypotheses: the paraphyly of 'Adenophorea' with respect to 'Secernentea', and the assumption that all parasitic nematode taxa derive from free-living ancestry.

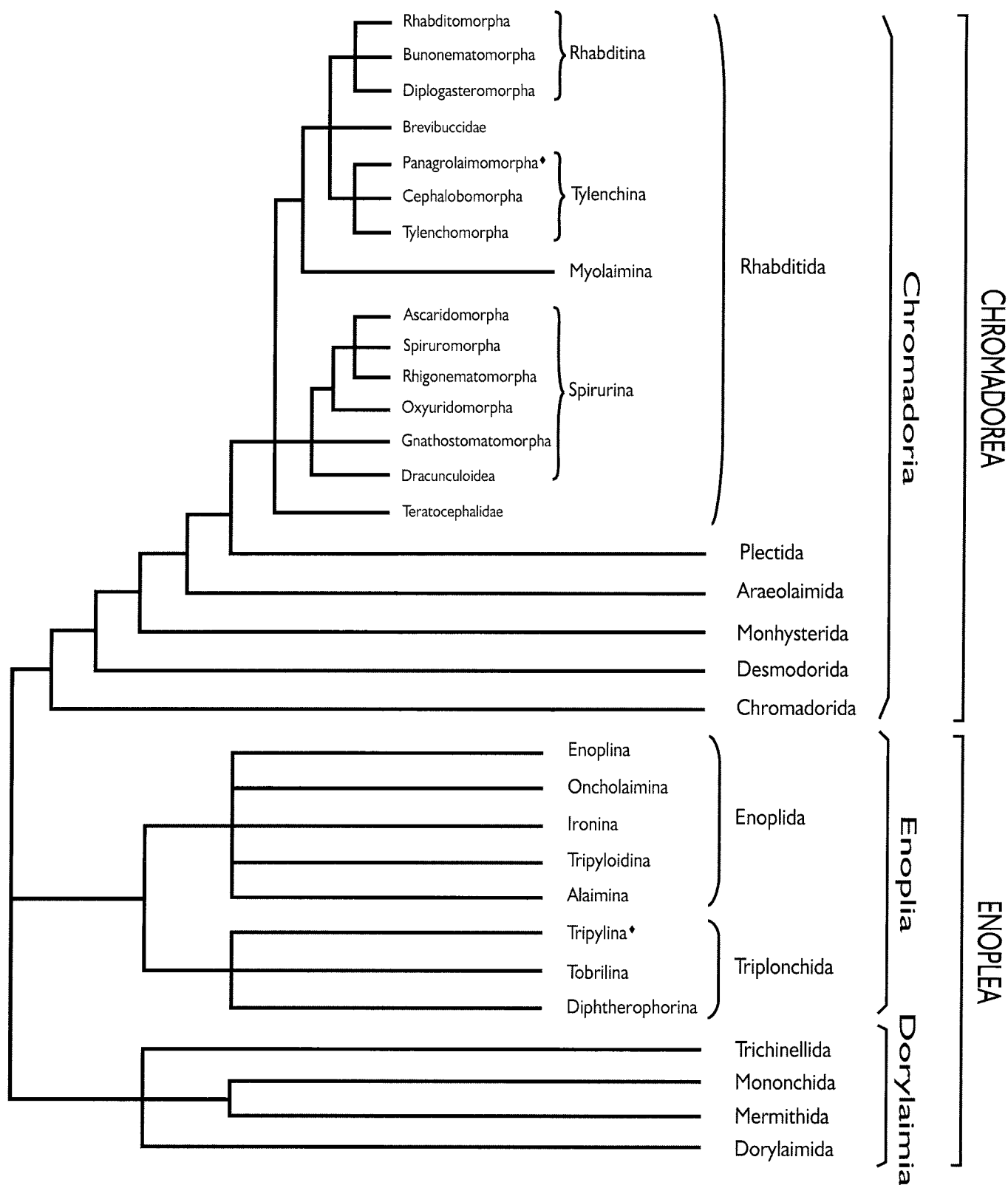
Both hypotheses were previously proposed on the grounds of morphology (Lorenzen, 1981, 1994) and life cycle data (Inglis, 1983; Anderson, 1984), and both are now supported strongly by sequence analysis. Lorenzen (1981, 1994) preserved 'Secernentea' as a class, placing the root of Nematoda between 'Secernentea' and 'Adenophorea'. However, he emphasized that synapomorphies were lacking for 'Adenophorea' and several of its constituent taxa, which were therefore possibly paraphyletic. Sequence data now confirm his suspicions of paraphyly, and place the root of Nematoda somewhere between chromadorids, enoplids and dorylaimids. Thus, although our system differs significantly from Lorenzen's in ranks and names (especially for many chromadorid/'secernentean' taxa), there is nevertheless more agreement in terms of branching orders than meets the eye.

In hindsight, it is evident that previous systems have, by default, overemphasized morphological differences in ranking decisions, at the expense of probable phylogenetic nestedness. This has led to the current tendency to even out morphological ranks across very different nematode groups: individual nematode taxonomists have always tended to either split or lump taxa rather evenly across the board, throughout the entire phylum. Averaging out these trends, this can now be perceived as overemphasis on higher ranks in morphologically highly divergent parasitic taxa such as strongylids and tylenchs, and underemphasis in morphologically cryptic free-living taxa such as enoplids and rhabditids. In this way, molecular phylogenies cut across morphological splitting and lumping approaches, in a way that neither entirely supports nor completely rejects either. Apart from perceived morphological support, numbers of currently known species may provide another source for discomfort with our system. However, in a phylogenetic system species numbers are at best a minor concern<sup>2</sup> in ranking decisions — another respect in which our system diverges from the usual splitting/lumping disputes.

We also introduce a series of infraorders for certain 'secernentean' parasitic taxa, in order to preserve maximum stability at family rank and below. Pearse (1936; 1942) provided no ending for the infraorder rank, but it is fairly often used in e.g. insect systematics, where the most common ending is

<sup>1</sup> These threshold values of 65% and 85% are approximations derived from the simulation studies by Hillis and Bull (1993) of the relationship between bootstrap and probability of correct tree topology.

<sup>2</sup> The comparatively high ranks for 'adenophorean' groups are actually matched by the likelihood that these groups contain a much greater proportion of nematode species richness than currently known. Thus, even if species richness were relevant to taxonomic rank, then it must be noted that future explorations can be expected to make up more than adequately for the relatively few species currently distinguished within 'adenophorean' groups.



**Figure 1.6.** Overview of the phylogenetic relationships among nematodes, derived primarily from published and unpublished analyses of SSU rDNA sequence data (see text for details). Taxa marked with a diamond are positioned on the basis of other criteria (axis determination in the case of Panagrolaimomorpha, spicular musculature in the case of Tripylina). Only those taxa are shown for which SSU rDNA sequence data are known. The differing levels of resolution of the tree primarily reflect the extent to which taxa have been sampled for SSU data, and not the known or suspected diversity of the taxa in question.



-*omorpha* (Barnard, 1999; Yeates and Wiegmann, 1999). In most cases (our suborders Spirurina and Tylenchina) the insertion of infraorders in our nematode classification largely allows preservation of the currently accepted superfamilies (as respectively listed in Schmidt, Roberts and Janovy, 1995 and Maggenti *et al.*, 1987). In the case of our suborder Rhabditina, however, the inclusion of an embedded strongylid group would require an additional ranking level to preserve superfamilies. Rather than introducing a more exotic rank in between infraorder and superfamily (e.g. suprafamily), for which there are few or no precedents in other animal phyla, we have lowered the superfamilies of the former Strongylida (as listed in Schmidt, Roberts and Janovy, 1995) back to family rank, and acted likewise with the similar case of the former Aphelenchina (as listed in Hunt, 1992). We assume that frequent usage of the rank of tribe will be required in future, in order to properly resolve strongylid and aphelench classification below family rank. Analogy can again be made with insects, where the use of tribe rank is quite common in highly diverse and derived taxa such as Diptera (Harbach and Kitching, 1998) and Hymenoptera (cf. Gauld and Bolton, 1988), which typically also contain major parasitic clades.

Finally, it must be noted that some authors argue that Linnean classifications should be abandoned altogether, in favor of truly phylogenetic systems without predetermined taxon ranks or type subtaxa (cf. de Quieroz and Gauthier, 1992, 1994; Ax, 1996). Such an approach would be impractical to introduce here and now, not least because of the firmly Linnean premises of all existing nematode classifications, and the fact that this radical departure from accepted practice still needs to be considered and ratified by the taxonomical community at large (see the preface by Minelli and Kraus in ICZN, 1999). Nevertheless, it does illustrate the extent to which systematics has evolved for other taxa than nematodes, and how radically different all mainstream classifications might eventually be formulated — even for nematodes.

### A Tentative Classification Emphasizing Monophyletic Taxa

The system presented below is a linnean classification derived from phylogenetic analyses and considerations, i.e. it is a hierarchical system of nested, presumably monophyletic taxa assigned to the various ranks commonly applied in zoological classification. A few clarifications are required with regard to form and contents:

- Although derived from trees, this classification does *not* aim to represent a tree in its own right. Thus, the sequential order of subtaxa of equal rank is *not* intended to strictly reflect phylogenetic relationships within a given encompassing taxon, e.g. the first order listed within a subclass is not necessarily the one presumed to have arisen first within that subclass. As a specific example, the order Desmoscolecida is listed first within subclass Chromadoria because its position with respect to other orders of Chromadoria remains unresolved, *not* because we assume that it is closest to order Chromadorida. Taxa that are truly *incertae sedis* (i.e. not only of uncertain position among taxa with rank equal to theirs, but also among several taxa of higher rank) are always listed first, preceding the various higher taxa to which they might belong with equal uncertainty.
- Families are marked with † when SSU rDNA sequence has been obtained from at least one of its species. This provides some idea of the taxonomic extent of sampling obtained so far in our molecular analyses: in most groups, the majority of families have not yet been included. For our classification, the available molecular data are therefore primarily relevant to higher taxa, while the distinction and placement of families remains largely based on existing (morphological) systems.
- Wherever possible, we have attempted to use taxa that are presumably monophyletic on the basis of current data (morphological and/or molecular). However, complete resolution is not always possible, mainly because of the as yet very incomplete molecular sampling. A few taxa are therefore maintained despite strong indications that they are paraphyletic and may in future be greatly restricted in species and genus content. Such families are marked with \*.
- It was not always possible to verify the correct taxonomic author for suprageneric taxa. Some older publications were not available to us, while others often list a different taxonomic author for the same taxon. For order- and class-group taxon names, many older sources do not follow the taxon endings proposed by Pearse (1936, 1942). In those cases, we consider it important that a taxon of a given rank was proposed, but not whether the name of that taxon ended exactly as in the Pearse system. For the taxonomic author of a given order- or class-group taxon, we list the name of the earliest proponent of that taxon name with the relevant rank and etymological stem, regardless of the exact ending of that name as originally spelled. Thus, we list Hyman (1951) as the author of order Mermithida, even though her work actually proposed the order name Mermithoidea.
- For family-group taxa, we have followed the principle of coordination as defined by the International Code of Zoological Nomenclature (Art. 36.1. in ICZN, 1999), where the correct taxonomic author for **all** family-group names based on a given stem, is the earliest author to propose **any** single taxon of family-group rank (subfamily, family or superfamily) with that particular stem. Thus, we now propose a family Mesorhabditidae and superfamily Mesorhabditoidea, but the taxonomic author for both is Andr ssy (1976) because he first proposed the subfamily Mesorhabditinae.

**PHYLUM NEMATODA** Potts, 1932**Incertae sedis:****ORDER BENTHIMERMITHIDA** Tchesunov, 1995

Family Benthimermithidae Petter, 1980

**Incertae sedis:****ORDER RHAPTOTHYREIDA** Tchesunov, 1995

Family Rhaptothyreidae Hope and Murphy, 1969

**CLASS ENOPLA** Inglis, 1983**SUBCLASS ENOPLIA** Pearse, 1942**ORDER ENOPLIDA** Filipjev, 1929**Incertae sedis:** Family Andrassyidae Tchesunov and Gagarin, 1999**Suborder Enoplina** Chitwood and Chitwood, 1937

Superfamily Enoploidea Dujardin, 1845

Family Enoplidae<sup>†</sup> Dujardin, 1845

Family Thoracostomopsidae Filipjev, 1927

Family Anoplostomatidae Gerlach and Riemann, 1974

Family Phanodermatidae Filipjev, 1927

Family Anticomidae Filipjev, 1918

**Suborder Oncholaimina** De Coninck, 1965

Superfamily Oncholaimoidea Filipjev, 1916

Family Oncholaimidae<sup>†</sup> Filipjev, 1916Family Enchelidiidae<sup>†</sup> Filipjev, 1918**Suborder Ironina** Siddiqi, 1983

Superfamily Ironoidea de Man, 1876

Family Ironidae<sup>†</sup> de Man, 1876

Family Leptosomatidae Filipjev, 1916

Family Oxystominidae Chitwood, 1935

**Suborder Tripyloidina** De Coninck, 1965

Superfamily Tripyloidoidea Filipjev, 1928

Family Tripyloididae<sup>†</sup> Filipjev, 1928**Suborder Alaimina** Clark, 1961

Superfamily Alaimoidea Micoletzky, 1922

Family Alaimidae<sup>†</sup> Micoletzky, 1922**ORDER TRIPLONCHIDA** Cobb, 1920**Suborder Diphtherophorina** Coomans and Loof, 1970

Superfamily Diphtherophoroidea Micoletzky, 1922

Family Diphtherophoridae<sup>†</sup> Micoletzky, 1922Family Trichodoridae<sup>†</sup> Thorne, 1935**Suborder Tobrilina** Tsalolikhin, 1976

Superfamily Tobriloidea De Coninck, 1965

Family Tobrilidae<sup>†</sup> De Coninck, 1965

Family Triodontolaimidae De Coninck, 1965

Family Rhabdodemaniidae Filipjev, 1934

Family Pandolaimidae Belogurov, 1980

Superfamily Prismatolaimoidea Micoletzky, 1922

Family Prismatolaimidae<sup>†</sup> Micoletzky, 1922**Suborder Tripylina** Andrassy, 1974

Superfamily Tripyloidea de Man, 1876

Family Tripylidae<sup>†</sup> de Man, 1876

Family Onchulidae Andrassy, 1963

**ORDER TREFUSIIDA** Lorenzen, 1981

Superfamily Trefusioidea Gerlach, 1966

Family Simpliconematidae Blome and Schrage, 1985

Family Trefusiidae Gerlach, 1966

Family Laurathonematidae Gerlach, 1953

Family Xenellidae De Coninck, 1965

**SUBCLASS DORYLAIMIA** Inglis, 1983**ORDER DORYLAIMIDA** Pearse, 1942**Suborder Dorylaimina** Pearse, 1942

Superfamily Dorylaimoidea de Man, 1876

Family Dorylaimidae<sup>†</sup> de Man, 1876Family Aporcelaimidae<sup>†</sup> Heyns, 1965Family Qudsianematidae<sup>†</sup> Jairajpuri, 1965Family Nordiidae<sup>†</sup> Jairajpuri and Siddiqi, 1964Family Longidoridae<sup>†</sup> Thorne, 1935Family Actinolaimidae<sup>†</sup> Thorne, 1939

Superfamily Belondiroidea Thorne, 1939

Family Belondiridae Thorne, 1939

Superfamily Tylencholaimoidea Filipjev, 1934

Family Leptonchidae Thorne, 1935

Family Tylencholaimidae<sup>†</sup> Filipjev, 1934

Family Aulolaimoididae Jairajpuri, 1964

Family Mydonomidae Thorne, 1964

**Suborder Nygolaimina** Thorne, 1935

Superfamily Nygolaimoidea Thorne, 1935

Family Nygolaimidae Thorne, 1935

Family Nygellidae Andrassy, 1958

Family Aetholaimidae Jairajpuri, 1965

Family Nygolaimellidae Clark, 1961

**Suborder Campydorina** Jairajpuri, 1983

Superfamily Campydoroidea Thorne, 1935

Family Campydoridae Thorne, 1935

**ORDER MONONCHIDA** Jairajpuri, 1969**Suborder Bathyodontina** Siddiqi, 1983

Superfamily Cryptonchoidea Chitwood, 1937

Family Bathyodontidae Clark, 1961

Family Cryptonchidae Chitwood, 1937

Superfamily Mononchuloidea De Coninck, 1965

Family Mononchulidae De Coninck, 1965

**Suborder Mononchina** Kirjanova and Krall, 1969

Superfamily Anatonchoidea Jairajpuri, 1969

Family Anatonchidae<sup>†</sup> Jairajpuri, 1969

Superfamily Mononchoidea Chitwood, 1937

Family Mononchidae<sup>†</sup> Chitwood, 1937Family Mylonchulidae<sup>†</sup> Jairajpuri, 1969

**ORDER ISOLAIMIDA** Cobb, 1920

Superfamily Isolaimoidea Timm, 1969  
Family Isolaimiidae Timm, 1969

**ORDER DIOCTOPHYMATIDA** Baylis and Daubney, 1926**Suborder Dioctophymatina** Skrjabin, 1927

Family Dioctophymatidae Castellani and  
Chalmers, 1910  
Family Soboliphymatidae Petrov, 1930

**ORDER MUSPICEIDA** Bain and Chabaud, 1959**Suborder Muspiceina** Bain and Chabaud, 1959

Family Muspiceidae Sambon, 1925  
Family Robertdollfusiidae Chabaud and  
Campana, 1950

**ORDER MARIMERMITHIDA** Rubtzov, 1980

Family Marimermithidae Rubtzov and  
Platonova, 1974

**ORDER MERMITHIDA** Hyman, 1951**Suborder Mermithina** Andr ssy, 1974

Superfamily Mermithoidea Braun, 1883  
Family Mermithidae<sup>†</sup> Braun, 1883  
Family Tetradonematidae Cobb, 1919

**ORDER TRICHINELLIDA** Hall, 1916

Superfamily Trichinelloidea Ward, 1907  
Family Anatrachosomatidae Yamaguti, 1961  
Family Capillariidae Railliet, 1915  
Family Cystoosidae Skrjabin, 1923  
Family Trichinellidae<sup>†</sup> Ward, 1907  
Family Trichosomoididae Hall, 1916  
Family Trichuridae<sup>†</sup> Ransom, 1911

**CLASS CHROMADOREA** Inglis, 1983**SUBCLASS CHROMADORIA** Pearse, 1942**ORDER DESMOSCOLECIDA** Filipjev, 1929**Suborder Desmoscolecina** Filipjev, 1934

Superfamily Desmoscolecoida Shipley, 1896  
Family Desmoscolecidae Shipley, 1896  
Family Meyliidae De Coninck, 1965  
Family Cyartonematidae Tchesunov, 1990

**ORDER CHROMADORIDA** Chitwood, 1933**Suborder Chromadorina** Filipjev, 1929

Superfamily Chromadoroidea Filipjev, 1917  
Family Chromadoridae<sup>†</sup> Filipjev, 1917  
Family Ethmolaimidae Filipjev and Schuurmans  
Stekhoven, 1941  
Family Neotonchidae Wieser and Hopper, 1966  
Family Achromadoridae Gerlach and Riemann,  
1973  
Family Cyatholaimidae<sup>†</sup> Filipjev, 1918

**ORDER DESMODORIDA** De Coninck, 1965**Suborder Desmodorina** De Coninck, 1965

Superfamily Desmodoroidea Filipjev, 1922  
Family Desmodoridae<sup>†</sup> Filipjev, 1922  
Family Epsilonematidae Steiner, 1927  
Family Draconematidae Filipjev, 1918  
Superfamily Microlaimoidea Micoletzky, 1922  
Family Microlaimidae Micoletzky, 1922  
Family Aponchiidae Gerlach, 1963  
Family Monoposthiidae Filipjev, 1934

**ORDER MONHYSTERIDA** Filipjev, 1929**Suborder Monhysterina** De Coninck and  
Schuurmans Stekhoven, 1933

Superfamily Monhysteroidea de Man, 1876  
Family Monhysteridae<sup>†</sup> de Man, 1876  
Superfamily Sphaerolaimoidea Filipjev, 1918  
Family Xyalidae<sup>†</sup> Chitwood, 1951  
Family Sphaerolaimidae Filipjev, 1918

**Suborder Linhomoeina** Andr ssy, 1974

Superfamily Siphonolaimoidea Filipjev, 1918  
Family Siphonolaimidae Filipjev, 1918  
Family Linhomoeidae Filipjev, 1922  
Family Fusivermidae Tchesunov, 1996

**ORDER ARAEOLAIMIDA** De Coninck and Schuurmans  
Stekhoven, 1933

Superfamily Axonolaimoidea Filipjev, 1918  
Family Axonolaimidae<sup>†</sup> Filipjev, 1918  
Family Comesomatidae Filipjev, 1918  
Family Diplopeltidae<sup>†</sup> Filipjev, 1918  
Family Coninckidae Lorenzen, 1981

**ORDER PLECTIDA** Malakhov, 1982

Superfamily Leptolaimoidea  rley, 1880  
Family Leptolaimidae  rley, 1880  
Family Rhadinematidae Lorenzen, 1981  
Family Aegialolaimidae Lorenzen, 1981  
Family Diplopeltoididae Tchesunov, 1990  
Family Paramicrolaimidae Lorenzen, 1981  
Family Ohridiidae Andr ssy, 1976  
Family Bastianiidae De Coninck, 1935  
Family Odontolaimidae Gerlach and Riemann,  
1974  
Family Rhabdolaimidae Chitwood, 1951  
Superfamily Ceramonematoidea Cobb, 1933  
Family Tarvaiidae Lorenzen, 1981  
Family Ceramonematidae Cobb, 1933  
Family Tubolaimoididae Lorenzen, 1981  
Superfamily Plectoidea  rley, 1880  
Family Plectidae<sup>†</sup>  rley, 1880  
Family Chronogasteridae Gagarin, 1975  
Family Metateratocephalidae Eroshenko, 1973  
Superfamily Haliplectoidea Chitwood, 1951  
Family Peresianidae Vitiello and De Coninck, 1968  
Family Haliplectidae Chitwood, 1951  
Family Aulolaimidae Jairajpuri and Hooper, 1968

**ORDER RHABDITIDA** Chitwood, 1933

**Incertae sedis:** Family Teratocephalidae<sup>†</sup> Andrásy, 1958

**Incertae sedis:** Family Chambersiellidae Thorne, 1937

**Incertae sedis:** Family Brevibuccidae<sup>†</sup> Paramonov, 1956

**Suborder Spirurina**

**Incertae sedis:** Superfamily Dracunculoidea Stiles, 1907

Family Dracunculidae Stiles, 1907

Family Philometridae<sup>†</sup> Baylis and Daubney, 1926

Family Phlyctainophoridae Roman, 1965

Family Skrjabillanidae Schigin and Schigina, 1958

Family Anguillicolidae Yamaguti, 1935

Family Guyanemidae Petter, 1975

Family Micropleuridae Baylis and Daubney, 1926

**INFRAORDER GNATHOSTOMATOMORPHA**

n. infraord.

Superfamily Gnathostomatoidea Railliet, 1895

Family Gnathostomatidae<sup>†</sup> Railliet, 1895

**INFRAORDER OXYURIDOMORPHA** n. infraord.

Superfamily Thelastomatoidea Travassos, 1929

Family Thelastomatidae Travassos, 1929

Family Travassosinematidae Rao, 1958

Family Hystriognathidae Travassos, 1919

Family Protrelloidiidae Chitwood, 1932

Superfamily Oxyuroidea Cobbold, 1864

Family Oxyuridae Cobbold, 1864

Family Pharyngodonidae Travassos, 1919

Family Heteroxynematidae<sup>†</sup> Skrjabin and Shikhobalova, 1948

**INFRAORDER RHIGONEMATOMORPHA** n. infraord.

Superfamily Rhigonematoidea Artigas, 1930

Family Rhigonematidae Artigas, 1930

Family Ichthycephalidae Travassos and Kloss, 1958

Superfamily Ransomnematoida Travassos, 1930

Family Ransomnematidae<sup>†</sup> Travassos, 1930

Family Carnoyidae Filipjev, 1934

Family Hethidae Skrjabin and Shikhobalova, 1951

**INFRAORDER SPIRUROMORPHA** n. infraord.

Superfamily Camallanoidea Railliet and Henry, 1915

Family Camallanidae Railliet and Henry, 1915

Superfamily Physalopteroidea Railliet, 1893

Family Physalopteridae Railliet, 1893

Superfamily Rictularoidea Hall, 1915

Family Rictulariidae Hall, 1915

Superfamily Thelazoidea Skrjabin, 1915

Family Thelaziidae Skrjabin, 1915

Family Rhabdochondidae Travassos, Artigas and Pereira, 1928

Family Pneumospiruridae Wu and Hu, 1938

Superfamily Spiruroidea Örley, 1885

Family Gongylonematidae Hall, 1916

Family Spiruridae Örley, 1885

Family Spirocercidae Chitwood and Wehr, 1932

Family Hartertiidae Quentin, 1970

Superfamily Habronematoidea Chitwood and Wehr, 1932

Family Hedruridae Railliet, 1916

Family Habronematidae Chitwood and Wehr, 1932

Family Tetrameridae Travassos, 1914

Family Cystidicolidae Skrjabin, 1946

Superfamily Acuarioidea Railliet, Henry and Sisoff, 1912

Family Acuiriidae Railliet, Henry and Sisoff, 1912

Superfamily Filarioidea Weinland, 1858

Family Filariidae Weinland, 1858

Family Onchocercidae<sup>†</sup> Leiper, 1911

Superfamily Aproctoidea Yorke and Maplestone, 1926

Family Aproctidae Yorke and Maplestone, 1926

Family Desmidocercidae Cram, 1927

Superfamily Diplostriaenoidea Skrjabin, 1916

Family Diplostriaenidae Skrjabin, 1916

Family Oswaldofilariidae Chabaud and Choquet, 1953

**INFRAORDER ASCARIDOMORPHA** n. infraord.

Superfamily Ascaridoidea Baird, 1853

Family Heterocheilidae<sup>†</sup> Railliet and Henry, 1912

Family Ascarididae<sup>†</sup> Baird, 1853

Family Raphidascarididae<sup>†</sup> Hartwich, 1954

Family Anisakidae<sup>†</sup> Railliet and Henry, 1912

Superfamily Cosmocercoida Skrjabin and Shikhobalova, 1951

Family Cosmocercidae Railliet, 1916

Family Atractidae Railliet, 1917

Family Kathlaniidae<sup>†</sup> Lane, 1914

Superfamily Heterakoidea Railliet and Henry, 1914

Family Heterakidae Railliet and Henry, 1912

Family Aspidoderidae Skrjabin and Shikhobalova, 1947

Family Ascaridiidae<sup>†</sup> Travassos, 1919

Superfamily Subuluroidea Travassos, 1914

Family Subuluridae Travassos, 1914

Family Maupasiniidae Lopez-Neyra, 1945

Superfamily Seuratoidea Hall, 1916

Family Seuratidae Hall, 1916

Family Cucullanidae<sup>†</sup> Cobbold, 1864

Family Quimperiidae Gendre, 1928

Family Chitwoodchabaudiidae Puylaert, 1970

Family Schneidernematidae Freitas, 1956

**Suborder Myolaimina** Inglis, 1983

Superfamily Myolaimoidea Andrásy, 1958

Family Myolaimidae<sup>†</sup> Andrásy, 1958

**Suborder Tylenchina** Thorne, 1949**INFRAORDER PANAGROLAIMOMORPHA** n. infraord.

Superfamily Panagrolaimoidea Thorne, 1937

Family Panagrolaimidae<sup>†</sup> Thorne, 1937

Superfamily Strongyloidoidea Chitwood and McIntosh, 1934 n.superfam.

Family Steinernematidae<sup>†</sup> Filipjev, 1934

Family Strongyloididae<sup>†</sup> Chitwood and McIntosh, 1934

Family Rhabdiasidae<sup>†</sup> Railliet, 1916

#### INFRAORDER CEPHALOBOMORPHA n. infraord.

Superfamily Cephaloboidea Filipjev, 1934

Family Cephalobidae<sup>†</sup> Filipjev, 1934

Family Elaphonematidae Heyns, 1962

Family Osstellidae Heyns, 1962

Family Alirhabditidae Suryawanshi, 1971

Family Bicirronematidae Andr ssy, 1978

#### INFRAORDER TYLENCHOMORPHA n. infraord.

Superfamily Aphelenchoidea Fuchs, 1937

Family Aphelenchidae<sup>†</sup> Fuchs, 1937

Family Aphelenchoididae<sup>†</sup> Skarbilovich, 1947

Superfamily Criconematoidea Taylor 1936

Family Criconematidae<sup>†</sup> Taylor, 1936

Family Hemicycliophoridae Skarbilovich, 1959

Family Tylenchulidae<sup>†</sup> Skarbilovich, 1947

Superfamily Sphaerularioidea Lubbock, 1861

Family Anguinidae<sup>†</sup> Nicoll, 1935

Family Sphaerulariidae Lubbock, 1861

Family Neotylenchidae Thorne, 1941

Family Iotonchidae Goodey, 1935

Superfamily Tylenchoidea  rley, 1880

Family Hoplolaimidae<sup>†</sup> Filipjev, 1934

Family Meloidogynidae<sup>†</sup> Skarbilovich, 1959

Family Tylenchidae  rley, 1880

Family Belonolaimidae<sup>\*†</sup> Whitehead, 1959

Family Pratylenchidae<sup>\*†</sup> Thorne, 1949

Superfamily Myenchoidea Pereira, 1931

#### INFRAORDER DRILONEMATOMORPHA n. infraord.

Superfamily Drilonematoidea Pierantoni, 1916

Family Drilonematidae Pierantoni, 1916

Family Ungellidae Chitwood, 1950

Family Homungellidae Timm, 1966

Family Pharyngonematidae Chitwood, 1950

Family Creagrocercidae Baylis, 1943

#### Suborder Rhabditina Chitwood, 1933

#### INFRAORDER BUNONEMATOMORPHA n. infraord.

Superfamily Bunonematoidea Micoletzky, 1922

Family Bunonematidae<sup>†</sup> Micoletzky, 1922

Family Pterygorhabditidae Goodey, 1963

#### INFRAORDER DIPLOGASTEROMORPHA n. infraord.

Superfamily Cylindrocorporoidea Goodey, 1939

Family Cylindrocorporidae<sup>†</sup> Goodey, 1939

Superfamily Odontopharyngoidea Micoletzky, 1922

Family Odontopharyngidae Micoletzky, 1922

Superfamily Diplogasteroidea Micoletzky, 1922

Family Pseudodiplogasteroididae<sup>†</sup> K rner, 1954

Family Diplogasteroididae<sup>†</sup> Filipjev and

Schuermans Stekhoven, 1941

Family Diplogasteridae<sup>†</sup> Micoletzky, 1922

Family Neodiplogasteridae<sup>†</sup> Paramonov, 1952

Family Mehdiinematidae Farooqui, 1967

Family Cephalobiidae Filipjev, 1934

#### INFRAORDER RHABDITOMORPHA n. infraord.

**Incertae sedis:** Family Carabonematidae Stammer and Wachek, 1952

**Incertae sedis:** Family Agfidae Dougherty, 1955

Superfamily Mesorhabditoidea Andr ssy, 1976 n. superfam.

Family Mesorhabditidae<sup>†</sup> Andr ssy,

1976 n. superfam.

Family Peloderidae<sup>†</sup> Andr ssy, 1976 n.fam.

Superfamily Rhabditoidea<sup>\*</sup>  rley, 1880

Family Diploscapteridae<sup>†</sup> Micoletzky, 1922

Family Rhabditidae<sup>\*†</sup>  rley, 1880

Superfamily Strongyloidea Baird, 1853

Family Heterorhabditidae<sup>†</sup> Poinar, 1975

Family Strongylidae<sup>†</sup> Baird, 1853

Family Ancylostomatidae<sup>†</sup> Looss, 1905

Family Trichostrongylidae Witenberg, 1925

Family Metastrongylidae Leiper, 1908

#### Brief characteristics of major groups:

The following paragraphs expand on various taxa listed above, and particularly on those for which the diagnosis and/or contents are changed substantially in our classification compared to previous systems.

– **CLASS ENOPLA:** SSU rDNA analysis strongly supports distinction of three basal clades in Nematoda: dorylaids, enoplids and chromadorids (resp. clade I, II and C+S in Blaxter *et al.*, 1998). Relationships between these clades cannot be resolved clearly at present, but some analyses do support sister taxon status of dorylaids and enoplids. Since this agrees with all previous systems, we therefore retain dorylaids and enoplids for the present within the encompassing class Enopla.

– **SUBCLASS ENOPLIA:** Lorenzen (1981, 1994) distinguished two orders within Enoplia: Enoplida and Trefusiida. He deduced monophyly of Enoplida from the presence of metanemes. Analysis of the few available SSU rDNA sequences does not resolve higher taxa within Enoplia very well, but disagrees significantly with Lorenzen's system in at least one respect: alaimids, prismatolaimids and diphtherophorids are firmly placed within the enoplid clade, even though they are not known to have metanemes, and the latter two groups are found to be surprisingly close to tobrilids. In order to combine patterns of metaneme presence and SSU rDNA affinity, we therefore transfer the order Triplonchida to Enoplia and expand its contents. We assume for the time being that metanemes do indeed represent a synapomorphy for Enoplia, but also that these structures were lost secondarily in several of its member taxa.

– **ORDER ENOPLIDA:** Lorenzen (1981, 1994) distinguished two suborders within the order: Enoplina and Tripyloidina. The latter taxon was presumed to be paraphyletic, while the former was considered monophyletic on the basis of one synapomorphy (caudal glands usually extending well anterior to anus). SSU rDNA data do not clearly resolve relationships among various relevant taxa, and in particular do not support a single clade for taxa with preanal caudal gland extensions. However, sequence data do strongly suggest that Enoplida *sensu* Lorenzen (1981) are paraphyletic with respect to Triplonchida *sensu* Siddiqi (1983b). By transferring tobrilids and relatives from Enoplida to Triplonchida (see below) we eliminate the obvious paraphyly of Enoplida — at least for the time being: SSU rDNA analysis still does not positively group the remaining member taxa of Enoplida into a monophyletic clade. More extensive sampling is definitely required, and may well lead to further changes in rank and/or composition of this group.

– **Suborder Oncholaimina:** Lorenzen (1981) classified oncholaims within Enoplina<sup>3</sup> on the basis of a single character: the shared presence of preanal caudal gland extensions. However, he noted that this character is variable in at least two other taxa of Enoplina: Enoploidea and Ironidae. Such variability indicates that the extent of the caudal glands must have been subject to homoplastic evolution, through multiple independent origins of the character and/or secondary reversal of the derived condition to its ancestral state. In the absence of other synapomorphies for Enoplina *sensu* Lorenzen, it is impossible to distinguish between these two types of homoplasy, and the monophyly of the taxon is therefore dubious. SSU rDNA analysis does not confirm exclusive common origin of extended glands in oncholaims and enoplids, but instead yields a moderately supported clade grouping oncholaims with the suborder Tripyloidina. Additional morphological synapomorphies need to be recognised and more unequivocal molecular analyses need to be obtained using a wider range of taxa. For the time being we therefore classify oncholaims at equal rank with both Enoplina and Tripyloidina, i.e. as a separate suborder.

– **Suborder Ironina:** SSU rDNA data firmly place ironids in Enoplina, but do not provide clues on their affinities to other member taxa of this subclass. Superfamily Ironoidea *sensu* Lorenzen (1981) includes both species with and without preanal extension of the caudal glands, and also species with or without metanemes. Lorenzen (1981) placed this taxon within his rankless taxon Enoplacea, on the basis of synapomorphies with respect to cervical gland position and muscular connections between the anterior pharynx and the body wall. Both characters are variable within Ironidae, and the muscular connections in Enopliidae

are not obviously homologous, neither structurally nor positionally, to the retractor muscles occurring in some Ironidae (e.g. compare Figure 2 in Inglis, 1964 with Figure 1A in Van Der Heiden, 1974). The affinities of ironids within Enoplida therefore remain unclear, and we place them as a separate suborder until more data become available.

– **Suborder Alaimina:** SSU rDNA analysis unequivocally places alaimids within Enoplina, and not in Dorylaimida, where Lorenzen (1981) placed them on the basis of the posteriorly located dorsal gland opening. As discussed more fully in the text, this character may well be homoplastic. We therefore include alaims in Enoplida and rank them as a separate suborder, since they appear to lack caudal glands and current SSU data do not further resolve their position.

– **ORDER TRIPLONCHIDA:** Trichodorids and their relatives were traditionally placed with dorylaims because of the shared presence of a protrusible, piercing feeding structure. This resemblance was later found to be rather superficial, and several authors suggested closer affinity with enoplids (see review in Decraemer, 1995). Lorenzen (1981, 1994) maintained them within Dorylaimida on the basis of the posteriorly located pharyngeal gland openings. In view of the strong support of SSU rDNA data for inclusion in Enoplina, we assume that this character is convergent (see page 9).

Sequence analysis very robustly positions a clade of nematodes without protrusible spear (tobrilids and prismatolaimids) as sister taxon to triplonchs. We therefore expand the contents of Triplonchida to include the free-living taxa in question, thereby removing a component from Enoplida which would otherwise render the latter order paraphyletic with respect to Triplonchida. This action is not entirely without morphological grounds. Some free-living Enoplina resemble Trichodoridae in several respects (Siddiqi, 1983b). Most notably, the spicule protractor muscles are modified into capsule-like structures that surround the anterior half of each spicule and which appear to squeeze out the spicules rather than simply pulling them backwards. Although this character needs further study, it may represent a synapomorphy for Triplonchida as expanded here.

– **Suborder Tobrilina:** SSU rDNA sequence emphatically unites Tobrilidae and Prismatolaimidae into a separate clade that represents a sister taxon to trichodorids and relatives. A close relationship between these free-living and plant-parasitic taxa is not evident from any morphological character, and Prismatolaimidae were placed in Chromadoria rather than Enoplina by Lorenzen (1981). Given the robustness of the sequence data, we unite tobrilids with prismatolaimids into a suborder

<sup>3</sup> Within Enoplida, Lorenzen (1981) proposed the taxa Enoplacea and Oncholaimacea at unspecified ranks in between order and superfamily. Inglis (1983) criticized this proposal because he considered it unnecessary to introduce an additional ranking level in classification, and because the —acea ending of both names was reserved for the rank of tribe in the nomenclatorial system of Pearse (1936; 1942).

Tobrilina, and presume that this suborder also includes several families that have not yet been included in molecular studies. Distinct spicule protrusion capsules do not occur in any of these families, but the anterior end of the spicules is embedded in muscle tissue in at least some *Prismatolaimus* (cf. Figure 3J,K in Coomans and Raski, 1988) and *Tobrilus* species (personal observation), suggesting that this group may contain muscle arrangements intermediate between completely separate protractors *versus* true capsules. Ultrastructural studies are needed to prove or disprove this hypothesis.

– **Suborder Tripylina:** Tripylids and tobrilids are traditionally classified closely to one another, and Lorenzen (1981) classified them as families within the suborder Tripyloidina. Only a single sequence has been obtained so far from Tripylidae *sensu* Lorenzen (1981), and this sequence provides no resolution other than placement in Enoplia. Despite the absence of any definite support from sequence data, we propose to include Tripylidae in Triplonchida, on the strength of the prominent spicule protrusion capsules found in this family. Another family with prominent capsules is Onchulidae, and we therefore classify it with Tripylidae in suborder Tripylina.

– **SUBCLASS DORYLAIMIA:** Dorylaids and relatives are traditionally classified in the same order, subclass or class as enoplids and relatives (De Coninck, 1965; Andr  ssy, 1976; Lorenzen, 1981; Inglis, 1983; Maggenti, 1983; Adamson, 1986; Malakhov, 1994). SSU rDNA does not resolve the position of dorylaids with respect to chromadorids and enoplids *sensu lato*. This unresolved position hints at the intriguing possibility that dorylaids and relatives might actually represent a full-blown third class of nematodes. This possibility has not been considered seriously in previous systems, nor do we consider it appropriate until definite resolution is obtained at the base of the nematode tree.

Nevertheless, when we consider that none of the free-living taxa within Dorylaimia occupy truly marine habitats, an interesting point is raised: a putative position of the dorylaimid clade as sister taxon to Enoplia + Chromadorea might require us to reconsider the ecology of the common ancestor of all nematodes. Was this ancestor really a marine organism, as proposed by Filipjev (1929, 1934) and now generally assumed, or could it instead have been an inhabitant of freshwater sediments — or even terrestrial deposits? At present, this still seems unlikely and indirectly pleads against a separate class for dorylaids.

In defining Dorylaimia and allocating taxa to it, Lorenzen (1981, 1994) placed great emphasis on posteriorly placed pharyngeal gland openings as an autapomorphy. As discussed on page 9, we strongly suspect this derived character to have arisen more frequently in

nematodes than allowed for in Lorenzen's system. Sequence analysis strongly supports a less comprehensive dorylaim clade, agreeing much more with some of the arguments of Siddiqi (1983b) in that Triplonchida and Alaimina are excluded. Because this clade is well-supported and so clearly separated from the enoplid clade, we agree with Inglis (1983) in allocating to it the rank of subclass.

– **ORDER DORYLAIMIDA:** The order Dorylaimida may well constitute the most diverse order of soil and freshwater nematodes, and particularly so in the tropics. Could this diversity be due to very early origins, rather than/in addition to rapid speciation? The presence of a protrusible spear in dorylaids undoubtedly represents an apomorphy, presumably resulting from a complex evolutionary pathway. However, SSU rDNA divergence within the suborder Dorylaimina is minimal, suggesting either that this locus has evolved at a very slow rate, or that the origins of Dorylaimina are relatively recent. Several key taxa with less derived buccal morphology were not yet sampled (Nygolaimina, Campyodorina) and these issues must therefore remain speculative for the time being.

– **ORDER DIOCTOPHYMATIDA:** No dioctophymatids have yet been sampled for sequence data, but all modern authors agree on a placement within the dorylaim clade (Anderson and Bain, 1982; Skrjabin, 1991).

– **ORDER TRICHINELLIDA**<sup>4</sup>: Only two taxa, from two different families, have been sampled through sequencing thus far, and these place the Trichinellida at or near the base of the Dorylaimia (Blaxter *et al.*, 1998). This placement may be due to long-branch attraction artefacts, and additional sequences from other taxa, particularly capillarid and cystoosid species may in future resolve both the placement of this group and its relation to the other zooparasitic Dorylaimia, the Mermithida and Dioctophymatida (Anderson and Bain, 1982; Skrjabin, 1991).

– **CLASS CHROMADOREA:** In our classification, Chromadorea contains the bulk of taxa within Nematoda, entirely including the 'Secernentea', as strongly supported by molecular data. 'Secernentea' is not a sister taxon of Chromadorea (as allowed by Inglis, 1983, where 'Rhabditea' replaces 'Secernentea') and must therefore receive a lower rank than its encompassing clade. Unlike Adamson (1986), we prefer to use the name Chromadorea for this encompassing clade, because it has line precedence over Rhabditea in Inglis (1983: p. 244) and because it better represents the fundamental split between the enoplid and chromadorid lineages.

<sup>4</sup> To our knowledge, Hall (1916 in Baylis and Daubney, 1926) was the first to propose an order-level taxon for trichurids, trichinellids and their relatives. He used the name Trichinelloidea for this order, preceding by at least ten years the order names Trichocephalida, Trichosyringida or Trichurida, each of which subsequently became popular in different parts of the world. We emend his order name here to Trichinellida and consider this name to have priority over the other three.

Furthermore, SSU rDNA strongly indicates that the stem of the chromadorid clade consists of a comb-like sequence of monophyletic groups, culminating in the 'secernentean' radiation. As a result, 'Secernentea' cannot just be downgraded to subclass, unless we either maintain a paraphyletic subclass for all stem taxa within Chromadorea, or propose a separate subclass for each of these stem taxa. Neither option is acceptable, and we therefore downgrade 'Secernentea' to ordinal rank. There are numerous order names available within the former 'Secernentea' and we have chosen the one with chronological priority, *i.e.* Rhabditida (see below).

– **SUBCLASS CHROMADORIA:** This subclass already existed in previous systems. We therefore preserve it here, but it is only of nominal importance since we do not recognize any other subclasses within Chromadorea.

– **ORDER DESMOSCOLECIDA:** This group of unusual nematodes has long puzzled taxonomists, and no sequence data have as yet been obtained. We therefore follow Lorenzen (1981, 1994) in classifying it within Chromadorea, but as an order rather than a suborder, because of the higher ranks accorded to other components of Chromadorea.

– **ORDER CHROMADORIDA:** Unlike Lorenzen's analysis, SSU rDNA phylogenies strongly support a monophyletic clade of chromadorids *sensu stricto*, as sister taxon to all other hitherto sequenced Chromadorea. In order to allow a reasonably high rank for all other clades within Chromadorea, this taxon must therefore receive ordinal rank (it corresponds to the superfamily Chromadoroidea in Lorenzen, 1981, 1994!).

– **ORDER DESMODORIDA:** Within Chromadorea, this group does not share exclusive common ancestry with chromadorids *sensu stricto*. It is instead the next separate lineage to diverge from the stem of Chromadorea, and must therefore also receive order rank.

– **ORDER MONHYSTERIDA:** Likewise, monhysterids do not share exclusive common ancestry with Chromadorida *sensu* Lorenzen (1981, 1994), but rather represent the next lineage in a nested series within Chromadorea. Also, their position does not agree with the assumption that their morphology represents an ancestral grade (cf. Maggenti, 1963). Lorenzen (1981) defined Monhysterida on the basis of the presence of the outstretched female reproductive branch(es), a credible apomorphy compared with the reflexed condition found in Chromadorida and Desmodorida. On the basis of this character, he therefore included the superfamilies Monhysteroidea, Siphonolaimoidea and Axonolaimoidea within Monhysterida. However, SSU rDNA data clearly show that Axonolaimoidea are sister taxon to a clade of nematodes with reflexed female reproductive branches, suggesting that this character has reverted at least once within Chromadorea. We therefore classify Axonolaimoidea within the order Araeolaimida instead of Monhysterida, similar to the systems of Malakhov,

Ryzhikov and Sonin (1982), Inglis (1983) and Maggenti (1983). Lorenzen noted that autapomorphies could neither be found for Axonolaimoidea, nor for Siphonolaimoidea, and the latter have not yet been sampled for SSU rDNA sequence data. For the time being we maintain the equivalent of Lorenzen's Siphonolaimoidea as suborder Linhomoeina within Monhysterida.

– **ORDER ARAEOLAIMIDA:** Ever since its proposal by De Coninck and Schuurmans Stekhoven (1933), this order has been used as a 'bucket taxon' for numerous families of uncertain affinities. In the system of Lorenzen (1981, 1994) it was rejected and its components were subdivided over the Monhysterida and Chromadorida: Leptolaimina, which constituted the single largest and least resolved suborder in his analysis. Although only two SSU rDNA sequences are available to date from superfamily Axonolaimoidea *sensu* Lorenzen (Félix *et al.*, 2000; Vanfleteren and Moens, unpublished data), these data show that the superfamily clearly does not belong in Monhysterida (contrary to Lorenzen, 1981, 1994), but rather that it constitutes the sister taxon of a clade including Plectidae and all 'Secernentea'. We therefore consider Axonolaimoidea to be a part of an order separate from both monhysterids and plectids. The correct name for this order is Araeolaimida, because *Araeolaimus* is currently classified in Axonolaimoidea (Lorenzen, 1981, 1994). The wider contents of Araeolaimida remain entirely unclear for the present, since known morphological data do not include clear apomorphies shared with other putative relatives of axonolaimids, and more sequence data are not yet available (see below). Araeolaimida *sensu nobis* therefore largely matches the contents and contents specified for the order by Malakhov, Ryzhikov and Sonin (1982), with the important addition of an outstretched female reproductive system as diagnostic character shared with Monhysterida.

– **ORDER PLECTIDA:** The position of the family Plectidae was not resolved in the analyses of Blaxter *et al.* (1998), where it sometimes grouped with Spiruromorpha *sensu nobis*, while ending up as sister taxon to all 'Secernentea' at other times. The latter position is much more in agreement with morphological characters, and is also given stronger support by analyses including additional taxa (Félix *et al.*, 2000; Vanfleteren and De Ley, unpublished). This implies that Plectidae require ranking equivalent to that of Araeolaimida and Rhabditida *sensu nobis*, consistent with the proposal of the order Plectida by Malakhov, Ryzhikov and Sonin (1982). However, a large number of families sharing characters with Araeolaimida and/or Plectidae remain excluded from SSU rDNA analysis. Most of these families correspond with Lorenzen's suborder Leptolaimina, which he characterised as a presumably paraphyletic taxon lacking resolution of internal relationships (Lorenzen, 1981, 1994).

We consider it likely that this unresolved group constitutes a mixture of paraphyletic and/or misplaced



families, and provisionally attempt to classify them by combining the systems of Malakhov, Ryzhikov and Sonin (1982) and Lorenzen (1981, 1994). Thus, the equivalent of Lorenzen's Leptolaimina is placed here as superfamily Leptolaimoidea within the order Plectida. Unlike Lorenzen (1981, 1994), we maintain a separate superfamily Ceramonematoidea, including in it the putatively related but problematic families Tarvauidae and Tubolaimoididae, and unlike Malakhov, Ryzhikov and Sonin (1982) we provisionally place this group within Plectida rather than Desmodorida.

- **ORDER RHABDITIDA:** In our system the order Rhabditida is equivalent with all of 'Secernentea' in most previous classifications, a major change that will undoubtedly meet with ample criticism. Nevertheless, this is a logical monophyly-based alternative to current covertly or overtly paraphyletic systems, and it follows inexorably from the application of Linnean ranks to the strongly supported pattern of relationships provided by SSU rDNA. Morphology has not (yet) yielded sufficient synapomorphies to recognise the series of monophyletic clades preceding 'Secernentea' in evolution, so that past emphasis on diagnosis and typology has allowed an escalation of increasingly higher ranks, without any correction for probable evolutionary relationships. We believe that phylogeny must be the basis for classification, and therefore propose corrections compatible with sound phylogenetic resolution.

- **Family Teratocephalidae:** The genus *Teratocephalus* is morphologically intermediate between 'Adenophorea' and 'Secernentea' and has received a different position in nearly every classification. SSU rDNA sequence analysis also does not clearly resolve its position, variously placing it near Plectidae and/or Spiruromorpha. Until better resolution is obtained, we consider the genus to be the only known member of a family *incertae sedis*. The family Metateratocephalidae used to be classified together with *Teratocephalus* in one superfamily (cf. Andr  ssy, 1984) but it exhibits characters that are much closer to those of Plectida (cf. Karegar, De Ley and Geraert, 1997) and sequence data have not yet been obtained.

- **Family Chambersiellidae:** No member of this family has as yet been included in sequence analysis. Chambersiellid species are characterised by presence of liplets, setiform labial sensilla and relatively posteriad amphids. All these character states may well be plesiomorphic. As far as known, no species have offset spermathecae. Andr  ssy (1984) included chambersiellids in his suborder Teratocephalina, but since the supporting characters may be symplesiomorphic we do not consider it appropriate to unite the two relevant families.

- **Family Brevibuccidae:** SSU rDNA sequence analysis does not resolve the position of *Brevibucca* sp., placing it variously with panagrolaims, rhabditids or near the

base of Rhabditida *sensu nobis* (F  lix *et al.*, 2000). Morphological data on *Brevibucca* and related genera do not suffice to assign it to any suborder or infraorder, still requiring e.g. ultrastructural studies of the buccal cavity to verify presence and structure of the stegostom.

- **Suborder Spirurina:** The molecular analyses of Blaxter *et al.* (1998) suggest that the four zooparasitic orders Spirurida, Ascaridida, Oxyurida and Rhigonematida are very closely related and comprise a clade (clade III) nested within Rhabditida but distinct from other groups included therein. In some analyses, Plectida are the sister group of this clade III within Rhabditida, but, as explained above, a basal position of Plectida is favoured. Linking of Ascaridida with Spirurida and Oxyurida with Rhigonematida has been suggested previously by several authors, but clade III has emerged only from molecular analyses. To conform to the schema presented here, the orders have been reclassified as infraorders. In analysis of SSU rDNA sequences, the Dracunculoidea is placed either basal to these groups, or has its origin in an unresolved polytomy (Blaxter, unpublished). We therefore consider the superfamily as of uncertain position within the suborder. As with the Gnathostomatoidea discussed below, Dracunculoidea may need to be elevated in status (e.g. to infraorder).

- **INFRAORDER GNATHOSTOMATOMORPHA:** The traditional order Spirurida is not monophyletic by molecular criteria, with Gnathostomatoidea being placed basal to clade III, and thus outside the derived group of other spirurids, Oxyuridomorpha, Rhigonematomorpha and Ascaridomorpha (Blaxter, unpublished). They are therefore elevated to infraorder rank.

- **INFRAORDER OXYURIDOMORPHA:** The Oxyuridomorpha is represented by a single heteroxurid taxon in molecular analyses. This is placed robustly in clade III, but additional taxa would improve understanding, particularly from insect-parasitic Thelastomatoidea. The taxonomy of Oxyuroidea is taken from Petter (1976).

- **INFRAORDER RHIGONEMATOMORPHA:** Classification within Rhigonematomorpha basically follows Hunt (1996). Only one species of this infraorder has so far been included in sequence analyses, and it is therefore not yet possible to address the (in)validity of classifying Rhigonematoidea and Ransomnematoida as sister taxa.

- **INFRAORDER SPIRUROMORPHA:** Sequence data is thus far available for only one superfamily within the Spiruromorpha, the Filarioidea, and this group is monophyletic. In the absence of conflicting evidence we maintain the remaining superfamilies within Spiruromorpha, although Anderson, Chabaud and Willmont *et al.* (1974) and Chabaud and Bain (1994) suggest that the Physalopteroidea and Camallanoidea may be similarly distanced from the 'crown spirurids'. Classification follows Chabaud (1975a, 1975b), Anderson (1976) and Anderson and Bain (1976).

– **INFRAORDER ASCARIDOMORPHA:** This taxon is monophyletic by molecular and morphological criteria (Nadler, 1995; Blaxter *et al.*, 1998; Nadler and Hudspeth, 1998). Classification is based on Hartwich (1974) and Chabaud (1978), except for classification of Ascaridoidea which is based on the morphological analysis of Fagerholm (1991) and compatible with the molecular phylogenies obtained by Nadler and Hudspeth (1998).

– **Suborder Myolaimina:** This suborder was first proposed by Inglis (1983) for the families Myolaimidae, Carabonematidae, Agfidae and Chitwoodiellidae. The family Myolaimidae only contains the genus *Myolaimus*, of which all known species are free-living and are characterized by a detached outer cuticular layer, complete absence of spicules and presence of a bursa-like structure on the posterior end of the male body. The other three families all contain very poorly known zooparasitic species with normal cuticle and of which the males have spicules and a more typical rhabditid bursa. SSU rDNA data suggests that *Myolaimus* represents a sister taxon to the combined clade of suborders Tylenchina and Rhabditina *sensu nobis*, and must therefore be placed in a separate suborder. However, we do not agree with Inglis (1983) that the three zooparasitic taxa are demonstrably related to *Myolaimus*. The few data available suggest to us that these three families belong somewhere within Rhabditina (see below), and we place them there as *incertae sedis*.

– **Suborder Tylenchina:** SSU rDNA strongly supports exclusive common ancestry for the morphologically disjunct tylenchs and cephalobids, confirming the varied arguments by Siddiqi (1980 and 1985) against a derivation of tylenchs from diplogasterid ancestry. Blaxter *et al.* (1998) reported moderate support for the inclusion of panagrolaims, steinernematids and strongyloidids in one clade with tylenchs and cephalobids, but this support dwindles with the addition of more sequences (Félix *et al.*, 2000). Nevertheless, an independent synapomorphy supporting inclusion was identified by Goldstein, Frisse and Thomas (1998), who found a similar pattern of embryonic axis specification in early development in these five taxa. We therefore place them together for the time being.

Some important characters of the hypothetical most recent common ancestor of Tylenchina *sensu nobis* include: stegostom without epithelial interrational cells or glottoid part, median bulb absent, mono-prodelphy, bursa absent. All these could well be ancestral to the entire order Rhabditida as defined here. In other words: no obvious morphological synapomorphies for the suborder are known at present.

– **INFRAORDER PANAGROLAIMOMORPHA:** Most taxa sequenced from this clade exhibit relatively long branch lengths in SSU rDNA phylogenies, as well as AT-rich SSU sequences. Both of these features are symptomatic of potential artefacts in phylogenetic resolution of the sequence data. Thus, both the composition and resolu-

tion of this infraorder are much more dubious than that of its presumed sister taxon Cephalobomorpha + Tylenchomorpha. Within Panagrolaimomorpha, we propose a grouping of steinernematids and strongyloidids in a superfamily Strongyloidea, because these taxa share didelphy, zooparasitism/zoopathogenicity and presence of a discrete Dauer stage in the life cycle as putative synapomorphies within Tylenchina. We also include Rhabdiasidae within this group, based on sequence analysis of *Rhabdias bufonis* (Blaxter and Dorris, unpublished) and shared characters as above. However, the position of *Steinernema* does not resolve clearly with SSU sequence data, and the above character polarisations are therefore tentative.

– **INFRAORDER CEPHALOBOMORPHA:** All cephalobid SSU rDNA sequences determined so far (Blaxter *et al.*, 1998; Goldstein, Frisse and Thomas, 1998; Félix *et al.*, 2000; Vanfleteren and De Ley, unpublished data) are derived from within the family Cephalobidae. This taxon is both morphologically and genetically homogeneous compared to other families within the superfamily Cephaloidea, which have not yet been included in molecular studies. It is therefore possible that one or more of these will later turn out to be basal taxa within Tylenchina.

– **INFRAORDER TYLENCHOMORPHA:** Sequence analysis within this taxon is as yet largely restricted to the superfamily Tylenchoidea *sensu* Maggenti *et al.* (1987). It is evident from these preliminary analyses that the families Belonolaimidae and Pratylenchidae are not demonstrably monophyletic, and that cyst nematodes are closely related to Hoplolaimidae while excluding root-knot nematodes (Szalanski, Adams and Powers, 1997; De Ley *et al.*, unpublished). Considering the morphological support for an affiliation of cyst nematodes with Hoplolaimidae and root-knot nematodes with Pratylenchidae (Geraert, 1997), we consider it appropriate to include Heteroderinae as a subfamily within Hoplolaimidae, and conversely to classify Meloidogininae as a fully separate family.

Blaxter *et al.* (1998) included *Aphelenchus avenae* and *Bursaphelenchus* sp. in their analysis, and found conflicting results in terms of resolution of the aphelenchs: *Aphelenchus* was consistently placed as sister taxon to all tylenchs, while *Bursaphelenchus* was usually placed at the base of the clade named here as Panagrolaimomorpha. Additional tylench or panagrolaim sequences do not change this pattern (unpublished data), and our attempts to sequence more Aphelenchoidea *sensu* Hunt (1992) have failed so far. We assume that the positioning of *Bursaphelenchus* sp. in Blaxter *et al.* (1998) is an artefact of branch length and/or elevated AT-contents, and that it is closer to *Aphelenchus avenae* than suggested by current SSU data.

Both genera are traditionally placed in separate superfamilies (resp. Aphelenchoidea and Aphelenchoidea) within a suborder Aphelenchina or an order Aphelenchida, which is characterised i.a. by

aspects of the median bulb structure that are undoubtedly apomorphic (most notably: the median bulb contains the dorsal gland opening). We maintain this clade, but as a superfamily instead of a (sub)order, and comprising of only two families: Aphelenchidae (presumed autapomorphy: males with bursa with rays) and Aphelenchoididae (presumed autapomorphy: isthmus strongly or completely reduced). For the sake of overall rank balancing, the families previously classified within Aphelenchoidoidea *sensu* Hunt (1992) are better classified as subfamilies within Aphelenchoididae *sensu nobis*, and previously recognised subfamilies (Hunt, 1992) can instead be ranked as tribes.

– **INFRAORDER DRILONEMATOMORPHA:** Drilonematids share the presence of an offset spermatheca with Cephaloboidea, and some genera are particularly similar to the cephalob family Osstellidae in pharyngeal and stomatal characters. Neither drilonematids nor osstellids have as yet been included in molecular studies, and the precise position of both remains unclear. For the time being, we therefore classify the former Drilonematida as an infraorder within Tylenchina, on the as yet unverified assumption that they constitute a sister taxon to Cephalobomorpha or to Cephalobomorpha + Tylenchomorpha.

– **Suborder Rhabditina:** Compared to other changes proposed in the classification of taxa formerly grouped in Secernentea, the suborder Rhabditina more or less retains the composition allocated to it by Andr ssy (1984), i.e. it includes diplogasterids (contrary to Maggenti, 1983 and Inglis, 1983) and bunonematids (contrary to Inglis, 1983). However, a minor change is the transfer of Alloionematidae to Panagrolaimomorpha, and a truly major change is the inclusion of all strongylids in Rhabditina. This inclusion of strongylids is not only supported very emphatically by SSU rDNA sequence data (Baldwin *et al.* in Fitch and Thomas, 1997; Blaxter *et al.* 1998; Aleshin *et al.*, 1998a; Sudhaus and Fitch, in press) but also consistent with two morphological character complexes: (a) muscular part of stegostom short, consisting of less than four muscle sets in at least the juvenile stages; (b) presence of a bursa with rays in the males. Both character complexes are credible synapomorphies when compared to the corresponding conditions in Teratocephalidae as outgroup for the suborders Myolaimina, Tylenchina and Rhabditina *sensu nobis* (De Ley *et al.*, unpublished).

– **INFRAORDER BUNONEMATOMORPHA:** Bunonematids are enigmatic creatures with a strongly modified symmetry of all external structures. This modified symmetry is distinctly autapomorphic for the taxon, and therefore does not provide clues on their relationship with other Rhabditida. However, males do have one bursal wing with rays, and the extent of muscularisation of the stegostom looks basically similar to that of Rhabditomorpha. Contrary to the unresolved position obtained by Blaxter *et al.* (1998) with a single *Bunonema* SSU rDNA sequence, inclusion of more species results

in placement basally within Rhabditina (Fitch *et al.*, unpublished).

– **INFRAORDER DIPLOGASTEROMORPHA:** Diplogasterids are extremely diverse in buccal morphology, but only one species has been studied in sufficient detail to resolve the arrangement of the musculature of the stegostom (cf. Baldwin *et al.*, 1997a). This study supports placement of diplogasterids as sister taxon to, or basal taxon within Rhabditina. Also, most species of diplogasterids have an at least partially developed bursa with rays. SSU rDNA sequence analysis supports a basal position of this taxon within Rhabditina (Baldwin *et al.* in Fitch and Thomas, 1997; Blaxter *et al.*, 1998; Sudhaus and Fitch, in press) and the study with most extensive representation of Rhabditina suggests a close affinity between *Rhabditoides* species and diplogasterids (Sudhaus and Fitch, in press). Molecular relationships within diplogasterids are not yet clearly resolved, but preliminary analyses by Luong *et al.* (1999) do not lend particular support to the gradistic classification of Andr ssy (1984). For lack of a well-resolved alternative, we maintain for the present most families recognised by Andr ssy (1984), while adding the zooparasitic taxa Cephalobiidae and Mehdinematidae (for the latter, see Luong *et al.* 1999).

– **INFRAORDER RHABDITOMORPHA:** Excluding some *Rhabditoides* species, this infraorder more or less combines the subfamily Rhabditinae *sensu* Sudhaus (1976) or superfamily Rhabditoidea *sensu* Andr ssy (1976, 1983, 1984) with Heterorhabditidae and Strongylida. Andr ssy (1976) proposed subfamilies within Rhabditidae on the basis of a combination of the number of female reproductive branches and the extent of the bursa on the tail. Considering subsequent developmental and molecular data (Sommer and Sternberg, 1994; Fitch, Bugaj-gaweda and Emmons, 1995; Fitch, 1997), both characters were presumably subject to significant amounts of parallelism within the group. Nevertheless, a clade including modified versions of Andr ssy's subfamilies Mesorhabditinae and Peloderinae is supported by SSU rDNA analysis (Sudhaus and Fitch, in press) and is retained here as a separate superfamily Mesorhabditoidea. Its sister taxon is the superfamily Rhabditoidea *sensu nobis*, which is distinguished from Mesorhabditoidea by the autapomorphy of having the male phasmid posterior to all other bursal rays (Kiontke and Sudhaus, in press). As listed above, Rhabditoidea is undoubtedly paraphyletic, since strongylids and heterorhabditids are actually embedded within this taxon, despite their being classified here as a separate superfamily (see below). We resort to this paraphyletic status as a temporary measure pending further phylogenetic resolution within Rhabditoidea, and to avoid further lowering of the rank of the strongylid taxon.

– **Superfamily Strongyloidea:** As with tylenchs and aphelenchs, balancing ranks across the entire phylum also requires significantly lower ranks for the suprageneric taxa of the former order Strongylida. The entire

order must be reallocated to superfamily level, the superfamilies within Strongylida are brought back to family level, and families or subfamilies of previous systems may need to be accorded subfamily and tribe ranks, respectively. This will undoubtedly meet with criticism from specialists of strongylids, but it is a necessary consequence of the derived position of strongylids within the wide radiation of free-living rhabditids. Once again it needs to be emphasized that taxonomic ranks are not proportional to species richness. Instead, they are determined by degrees of nestedness within a given system.

In nematodes, many free-living taxa are very poorly known in terms of character resolution, and current classification of these taxa therefore requires relatively few ranks. By comparison, zooparasitic taxa provide more readily accessible characters, and the nestedness of zooparasitic taxa within radiations of free-living taxa therefore requires more ranks at lower levels for the former than for the latter. The strongylids are particularly well studied (Lichtenfels, 1980; Beveridge and Durette-Desset, 1994; Durette-Desset *et al.*, 1994; Hoberg and Lichtenfels, 1994; Ben Slimane *et al.*, 1996; Durette-Desset *et al.*, 1999), and the richness of characters available for morphological analysis has led to the proposal of strong and apparently robust phylogenetic hypotheses for the group.

Within Strongyloidea there is, in contrast to the morphological diversity, little diversity in SSU rRNA sequence (Zarlenga *et al.*, 1994a,b; Blaxter *et al.*, 1998; Dorris, De Ley and Blaxter, 1999), and thus other genes, particularly the ribosomal cistron internal transcribed spacer region (ITS) are being used to reveal phylogenetic patterns (Campbell, Gasser and Chilton, 1995; Chilton, Gasser and Beveridge, 1995, 1997; Chilton, Beveridge and Andrews, 1997; Chilton *et al.*, 1997, 1998; Hoste *et al.*, 1995; Stevenson, Chilton and Gasser, 1995; Stevenson, Gasser and Chilton, 1996; Hung *et al.*, 1996, 1997; Romstad *et al.*, 1997a,b, 1998; Gasser *et al.*, 1998; Monti *et al.*, 1998; Newton *et al.*, 1998). For clarity's sake, we should specify that we do not consider measures of SSU rRNA sequence divergence relevant to decisions on appropriate ranking of taxa: our lowering of the strongylid taxon to superfamily level is *only* based on nestedness of the obtained phylogenetic tree, and *not* on the uniformity of SSU rDNA sequences among strongylids.

## The Lower Classification

### Species Concepts in Nematodes

#### *Typology and trade-offs*

Because of the medical, veterinary or agricultural importance of many parasitic nematodes, one of the main tasks of nematode taxonomists is the identification of potentially harmful species. In practice, such identifications used to rely largely on light microscopical observation of fixed specimens, and were often based on characters that are barely visible at the limits of optical resolution, are prone to individual variation and fixation artefacts, and which often

require subjective interpretation skills based on years of experience. Furthermore, it was realised that autotokous reproduction occurs widely in nematodes, and that different reproductive strategies can occur in related species, or even within one species (Triantaphyllou and Hirschmann, 1964 and 1980; Poinar and Hansen, 1983). As a result, decisions on validity and diagnosis of nematode species have traditionally been constrained to largely typological methods, and nematode taxonomists have rarely been able or even willing to participate in theoretical debates about species concepts, or in experimental studies of population dynamics, dispersal and vicariance (but see Ferris, 1983).

Instead, debates about taxonomy of nematode species usually focus mainly on issues of splitting vs. lumping of populations into species, and of species into higher taxa. Arguments typically revolve around questions such as the number and extent of differences required for considering two populations as separate species, preferable size versus ease of use of genera and families, diagnostic relevance of variability studies, etc. Those concerned with accurate characterisation of individual species are often required to devote all available time to disentangling overlapping patterns of variability (Anderson and Hooper, 1970; Fortuner and Quénehervé, 1980) and chasing the relevant type material (De Ley, Siddiqi and Boström, 1993; Karssen and Van Hoenselaar, 1998) while those who dare to attempt constructing larger overviews (Andrássy, 1984; Siddiqi, 1985; Jairajpuri and Ahmad, 1992) must of necessity trade specific detail for taxonomic scope, resulting in typological keys and classifications bearing little connection with actual patterns of relatedness and variation.

#### *Morphology does not suffice — even for morphospecies*

At present, there is ample evidence to suggest that light microscopical evidence alone simply cannot provide the diagnostic resolution required for consistent species identification in many of the larger genera and families of nematodes. On the one hand, it is known (but not necessarily acknowledged) that individual species may vary considerably, to such an extent that one species may include character combinations supposedly differentiating between multiple species or even genera (Anderson and Hooper, 1970; Fortuner and Quénehervé, 1980). On the other hand, few or no morphological differences may occur between nematode populations with clearly different reproductive, developmental and/or molecular characters (Sudhaus, 1978; Butler *et al.*, 1981; Sommer *et al.*, 1996; Karssen, 1996; De Ley *et al.*, 1999).

Furthermore, intraspecific polymorphism in diagnostically important characters occurs in certain groups of nematodes, and offspring of heteromorphic parents can display character states different from either parent (Hirschmann, 1950). Finally, and perhaps most frustratingly, some of the commonest nematoda genera contain large numbers of poorly known nominal species, of which the only available data are those found in the original description, which often lacks

many characters that are considered essential by present standards. For instance, Hunt (1993) listed 138 'valid' species for the genus *Aphelenchoides*, but immediately cautioned that many are inadequately characterized for reliable recognition. And in a similar vein, the rapidly deteriorating situation in *Xiphinema* led Heyns (1983) to comment that, paradoxically, morphological characters are insufficient to distinguish morphospecies in the *X. americanum* group!

In view of the already abundant methodological complications of defining species, very little is known about the frequency of hybridisation in nematodes. However, it has been suggested that hybridisation has occurred naturally in the genus *Meloidogyne* (Triantaphyllou, 1985), and evidence was found recently for at least two independent hybrid lineages (Hugall, Stanton and Moritz, 1999): conflicting patterns of sequence diversity in the Internal Transcribed Spacer (ITS) region and in mitochondrial DNA (mtDNA) suggest reticulate origins for certain populations that were identified morphologically and electrophoretically as *M. hapla*, or as one of the species belonging to the *M. incognita*/*M. arenaria*/*M. javanica* complex. While it is at present impossible to evaluate the overall frequency of hybridisation events in nematode phylogeny, we should clearly keep in mind that reticulate evolution probably does indeed occur in nematodes.

### Beyond Morphospecies: Integration of Diverse Kinds of Data

#### New tools

While the light microscope remains the primary instrument for most nematode taxonomists, the past three decades have brought us a panoply of new tools capable of providing many new characters for the diagnosis of species. Some of these require availability of live specimens, while others can be applied to material fixed and preserved by traditional means. Thus, it has finally become possible to make meaningful departures from purely typological approaches, and to adopt and adapt new methods and theoretical frameworks.

In many groups of nematodes, SEM observations have quickly become an essential requirement for accurate interpretation and description of external features, and especially those found on or near the anterior end (Corbett and Clark, 1983; Hirschmann, 1985; Sauer and Annells, 1985; Stewart and Nicholas, 1994; Neuhaus *et al.*, 1997; Hunt and Moore, 1999). Methods have also been developed to study sclerotized internal structures such as stylets (Eisenback, 1993), buccal cavities (Borgonie, Van Driessche and Coomans, 1995) and male reproductive organs (Nguyen and Smart, 1997).

A wide range of molecular and biochemical methods has been adapted for use in nematodes. Because of its apparently uniform structure, the intestine is largely ignored in traditional procedures for description and diagnosis. However, immunofluorescence techniques and vital stains reveal substantial diversity in biochemical properties of intestinal cells of bacterial-feeding

Rhabditida (Borgonie *et al.*, 1995), suggesting that taxonomic applications could be developed with relative ease. Allozyme analysis through electrophoresis is now a common approach to the characterisation of problematic taxa, often allowing separation between morphologically cryptic species (Jagdale, Gordon and Vrain, 1996; Mattiucci *et al.*, 1998; Tastet *et al.*, 1999). PCR-RFLP characterisation of selected loci (usually the ITS region) has been applied extensively (Gasser *et al.*, 1996; Powers *et al.*, 1997), particularly in some of the most challenging taxa such as *Xiphinema* (Vrain, 1993), Heteroderidae (Ferris *et al.*, 1995; Subbotin *et al.*, 1999) and the entomopathogenic genera *Steinernema* and *Heterorhabditis* (Reid, Hominick and Briscoe, 1997). Sequence analysis of selected variable loci provides a potential plethora of diagnostic characters (Thomas *et al.*, 1997), and also allows phylogenetic analysis of at least some of the relationships between analysed species (Adams, Burnell and Powers, 1998; De Ley *et al.*, 1999). Sequence divergence among related species depends greatly on both the locus and species in question, and it is therefore important to choose the right locus for a given taxon. Thus, ribosomal loci such as the ITS region or the D2/D3 expansion segment of the LSU rDNA gene generally work well to distinguish among congeneric species, but in some taxa such as strongylid nematodes it is better to compare more rapidly evolving loci such as the mitochondrial ND4 gene (Anderson, Blouin and Beech, 1998; Blouin *et al.*, 1998).

Some highly specialised tools were developed for embryological studies of *Caenorhabditis elegans*, and these can be applied with relative ease to any other nematode with sufficiently rapid development and transparent embryo. Four-dimensional microscopy can be used to record and analyse development of the entire cell lineage during early development (Schnabel *et al.*, 1997). Microscopy with Nomarski/DIC optics can also yield information on postembryonic characters such as male tail development (Fitch, 1997; Nguyen *et al.*, 1999) and vulva development (Sommer *et al.*, 1999). These studies often reveal substantial differences between closely related species, which are not only directly relevant to taxonomy as new character suites, but also indirectly important in the evaluation of the final morphological characters. For example, within the exceedingly confusing genus *Acrobeloides*, one species displays an autapomorphy with respect to chirality of the second division of the AB blastomere (Félix *et al.*, 1996; De Ley *et al.*, 1999), while another species (or species complex) appears to be autapomorphic with respect to the cell fate of ventral cord cells P9.p and P10.p (Félix *et al.*, 2000). Thus, developmental characters provide a potentially vast source of characters, and this not only in patterns of cell lineages in normal development, but also with respect to artificially induced alterations due to cell ablation, dislocation or other types of manipulations.

#### New concepts

Not surprisingly, such a wealth of new data also allows for the formulation and application of more sophisti-

cated species concepts. In a recent essay that looks set to become highly influential, Adams (1998) advocated a combination of diagnostic procedures borrowed from the Phylogenetic Species Concept of Rosen (1978), and the theoretical concept of 'largest integrating lineages' adapted from the Evolutionary Species Concept of Simpson (1961). He proposed to use the presence *versus* absence of autapomorphies as a basis for deciding on the status as valid species of related populations. Although Adams did not specifically restrict the relevant source of characters to sequence analysis, it has first been applied to sequence data (Adams, Burnell and Powers, 1998; De Ley *et al.*, 1999). At least a minimal amount of phylogenetic analysis is required to demonstrate whether a given character is autapomorphic or not, and in nematodes sequence data are often more directly amenable to such analysis. Furthermore, molecular phylogenies can also be used to polarise other characters (Fitch, 1997; Goldstein *et al.*, 1998; Nadler and Hudspeth, 1998; Sommer *et al.*, 1999; Félix *et al.*, 2000) and thus to pinpoint non-molecular autapomorphies indirectly. In the coming years, we may expect more (and more extensive) datasets to be constructed for developmental and morphological characters alike, which will undoubtedly allow wider experimentation with phylogeny-based species concepts such as that of Adams.

### Population Dynamics, Gene Flow and Genetic Structure of Nematode Species

#### *From diagnosis to dynamics*

Almost nothing is known about the movements of mutations and alleles between conspecific populations of free-living or phytoparasitic nematodes. Population dynamics in natural conditions remain unknown even for *Caenorhabditis elegans*, probably the single best-known metazoan organism in terms of DNA sequence, embryology and neurology. Plant parasites have received greater attention (Vrain *et al.*, 1997) but these studies tend to be strictly limited to monitoring of nematode densities. Some data are available on their molecular population biology (Hyman, 1996; Hyman and Whipple, 1996), but no comprehensive studies have as yet been published. This major gap in our knowledge has direct implications for many fundamental assumptions about speciation and other evolutionary processes in nematodes. Until we know how related populations behave through time and space, no sound inferences are possible about e.g. the taxonomic significance of observed differences between those populations. Even at higher levels of classification, it is important to have quantitative and qualitative insights into population dynamics, for example, in order to interpret observed differences in genetic divergence within and between related higher taxa (see pages 2 and 23).

#### *From dynamics to diversity*

By comparison, studies of zooparasitic nematodes have already produced interesting precedents for applications throughout the phylum. For example, there is

evidence for extensive gene flow between populations of certain nematode trichostrongylid species parasitising domestic animals (see review by Anderson, Blouin and Beech, 1998), suggesting that human transportation of these animals has basically removed all geographical barriers between the parasite populations, and that it encourages rapid spreading of resistance to anthelmintics among these parasites. In contrast, populations of the deer parasite *Mazamastrongylus odocoilei* appear to be more strongly isolated from one another (Blouin *et al.*, 1995).

Furthermore, strong correlations with effective population size and life cycle have been detected. Thus, the low effective infrapopulation sizes of the amphimictic pig parasite *Ascaris suum* may explain why greater genetic differentiation occurs among infrapopulations of this species than in trichostrongylids, despite intensive movement of the hosts by humans (Nadler *et al.*, 1995; Nadler, 1996). And as another example, the alternately hermaphroditic and amphimictic entomopathogen *Heterorhabditis marelatus* displays a combination of low genetic diversity with clearly subdivided population structure (Blouin, Liu and Berry, 1999). In this case, population sizes and gene flow are presumably both quite low, and the species may exemplify dynamics similar to those of specialised microhabitat-colonizers among free-living nematodes.

These studies illustrate that it is now possible — at last — to quantify previously intractable properties of nematode populations, and open up prospects for applications in measurements of dispersal and species turnover. Thus, the coming decades may not only provide us with a factual understanding of population dynamics and genetics, but also with the first objective methods for estimating and comparing nematode species diversity on local, regional and global scales.

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## Systematic Position and Phylogeny

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## Male and Female Gametes and Fertilisation

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## Embryology, Developmental Biology and the Genome

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## Cuticle, Moulting and Exsheathment

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## Feeding and Digestion

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## Feeding Behaviour of Plant-Parasitic Nematodes

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## Nematode Sense Organs

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## Behaviour

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## Nematode Survival Strategies

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## Immunology of Nematode Infection

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## Epidemiology and Control of Nematode Infection and Disease in Humans

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