1 Introduction to Freshwater Nematodes in Ecology: Current Knowledge and Research

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Highlights

- Nematodes are tiny roundworms that abound in most parts of the biosphere.
- They show remarkably diverse life strategies and occupy important positions in food webs.
- Their role in ecosystems has nonetheless been largely ignored by ecologists and nematologists.
- This book offers guidelines for studying the ecology of free-living nematodes, with the aim of increasing interest in this topic in current and future generations of scientists.

1.1 A Short Summary of Nematode Morphology and Reproduction

Nematodes are tiny roundworms, usually elongated, bilaterally symmetrical, and rod- or thread-like in shape. They comprise the 'phylum'

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Nematoda, the name of which derives from a Latinized form of the Greek words *nema-* (meaning thread) and *-eidos* (meaning form or resemblance) (Andrássy, 2005). Most species are microscopic and translucent, with the body lengths of most freshwater species ranging between 0.3 and 5 mm. Parasitic species may be much larger depending on the size of their host. For example, the body length of the largest nematode described so far, *Placentonema gigantissima*, a parasite of sperm whales, may exceed 6–8 m (Gubanov, 1951).

The nematode body wall is composed of an outer non-cellular sheath (the cuticle), an inner syncytial layer (the hypodermis), and the somatic musculature. The body wall determines the shape of the nematode, serves as a barrier to external physico-chemical obstacles, biotic agents, and pathogens, enables direct contact between the worm and its environment, and allows the exchange of fluids and gases into and out of the nematode's body (Andrássy, 2005). The surface of the cuticle may be entirely smooth (as observed by light microscopy) or marked by various transverse or longitudinal structures (Fig. 1.1a,b). During nematode ontogenesis, from egg to adult, the cuticle normally is shed four times (molting or ecdysis).

The general cavity contains an alimentary tract made up of a mouth or oral aperture (Fig. 1.1c–g) and amphid (Fig. 1.1h), followed by an esophagus (Fig. 1.1i,k) and an intestine that opens to the outside via an anus. The excretory system of nematodes is unparalleled among invertebrates because it does not rely on cilia, flame cells, or protonephridia. The nervous system of Nematoda is rather complex. It mainly consists of a central part. The nerve ring ('brain'), and a number of (predominantly six) nerve chords extending anteriorly or posteriorly through the entire body. The longitudinal nerves are then provided with several ganglia.

The female genital system differs substantially from that of the male. In the female, the genital tube or gonad consists of the ovaries, oviducts, uterus (with or without eggs), spermatheca, and vagina (Fig. 1.1l,m). It opens through a separate pore, the vulva, on the ventral side of the body. The male genital system consists of a larger number of sexual characters or structures and is made up of primary and secondary organs. The former includes the testis, seminal vesicle, ejaculatory duct, cloacal chamber, and associated glands, and the latter the copulatory muscles, spicula, gubernaculum, guiding pieces, genital papillae, supplementary organs, and bursa (Fig. 1.1n–p). Most nematode species are bisexual (especially marine nematode species). Sex ratios are variable, but for most free-living nematode species females and males occur in near equal abundance. In other nematode genera and species males are much fewer in number (e.g. *Eumonhystera* spp., *Plectus* spp.). For example, in *Rhabdolaimus* spp. the male:female ratio is typically 1:1000. Moreover, there are several species, such as *Bunonema*, in which only females are found, with males either thus far unobserved because of their rarity or their complete absence. Some of these species are capable of parthenogenesis, a process of monosexual reproduction in which progeny develop from unfertilized ova (eggs), without the participation of male genital cells (spermatozoa). Monosexual reproduction is also exhibited by the few species that are hermaphroditic,

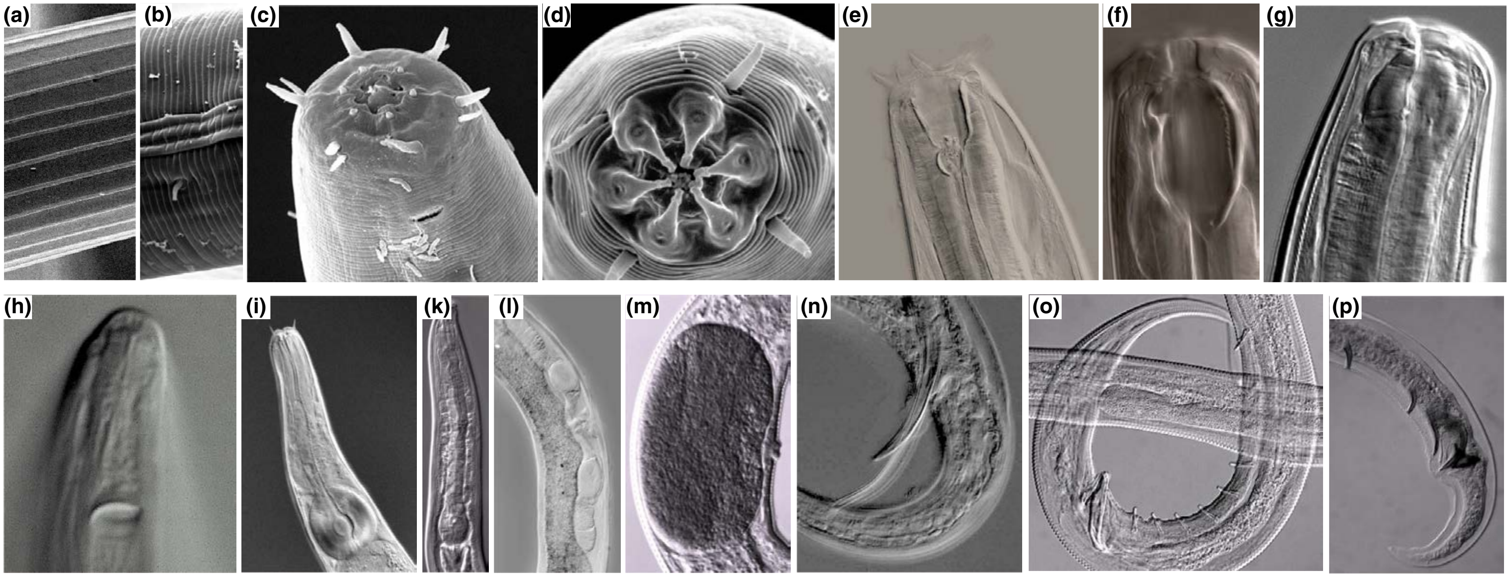

Fig. 1.1. Examples of representative morphological characteristics of freshwater nematodes: (**a**) and (**b**) cuticle ornamentation; (**c**) and (**d**) anterior part showing papillae, lips, and other cephalic setae; (**e**), (**f**), and (**g**) head with inner mouth structures; (**h**) amphid; (**i**) and (**k**) examples of esophagus shape; (**l**) and (**m**) female genital system; (**n**), (**o**), and (**p**) male genital system.

especially those belonging to the Secernentia (Andrássy, 2005). In this case, the hermaphrodite parent, a female-like individual with the usual external (and internal) female characters, produces both eggs and sperm and reproduction occurs through self-fertilization.

1.2 What Is the Role of Nematodes in Freshwater Ecosystems?

1.2.1 A brief history and definition of ecology

Free-living nematodes are widespread in inland waters. Their diverse morphologies and life strategies, as briefly discussed above, reflect their many functions in freshwater ecosystems, the main subject of this book. Although ecology emerged with the Industrial Revolution and the changes in human society that accompanied it, ecological questions were already being posed two millennia earlier. Both Aristotle and Pliny the Elder contemplated the relationship between living beings and their environment as well as the role of humans in the balances of nature. The natural histories developed by these philosophers remained unchallenged until the emergence of the classification system of Linnaeus, the publication of Malthus' *An Essay on the Principle of Population*, the biogeographical reports of Humboldt, the economics of Liebig, and, especially, Darwin's theory of evolution. Together, these works gave rise to the definition of ecology proposed in 1866 by Haeckel: 'Ecology is the science of the relations of living beings, plants and animals, between them and with their environment'. But it was not until the beginning of the 20th century that a more rigorous approach to ecology emerged. Important ecologists, among others, during the past 100 years are: Alfred J. Lotka and Vito Volterra, who, working independently, developed predator–prey models; Vladimir Vernadski, who introduced the biogeochemical concept of 'biosphere'; Arthur G. Tansley, who introduced the concept of ecosystem; and Raymond L. Lindemann, who was among the first to implement the ecosystem concept of Tansley, further defining the key concepts of 'food webs' and 'energy loops'. Indeed, the second half of the 20th century can be considered as the beginning of 'the age of ecology', as later proposed by Donald Worster (1994), as it marked the beginning of an awareness that pollution and its potentially irreversible damage to the environment pose major threats to a sustainable existence. As the list of anthropogenic pressures has grown, ecologists have sought ways to monitor and even protect both ecosystems and the vital services they provide to humankind. Thus, modern ecology is not a self-contained discipline but draws upon genetics, mathematics, modern observational techniques, and computer science in its broad areas of research. Through synergies among these different research fields, ecology is able to consider biological mechanisms at various scales, as summarized schematically in Fig. 1.2. The response of an organism (such as a single nematode) to its global environment (biosphere) can be deconstructed according to the individual ecosystems that compose its biome (e.g. desertic, tropical, Arctic). The temporal and spatial limitations of each ecosystem are reflected in the

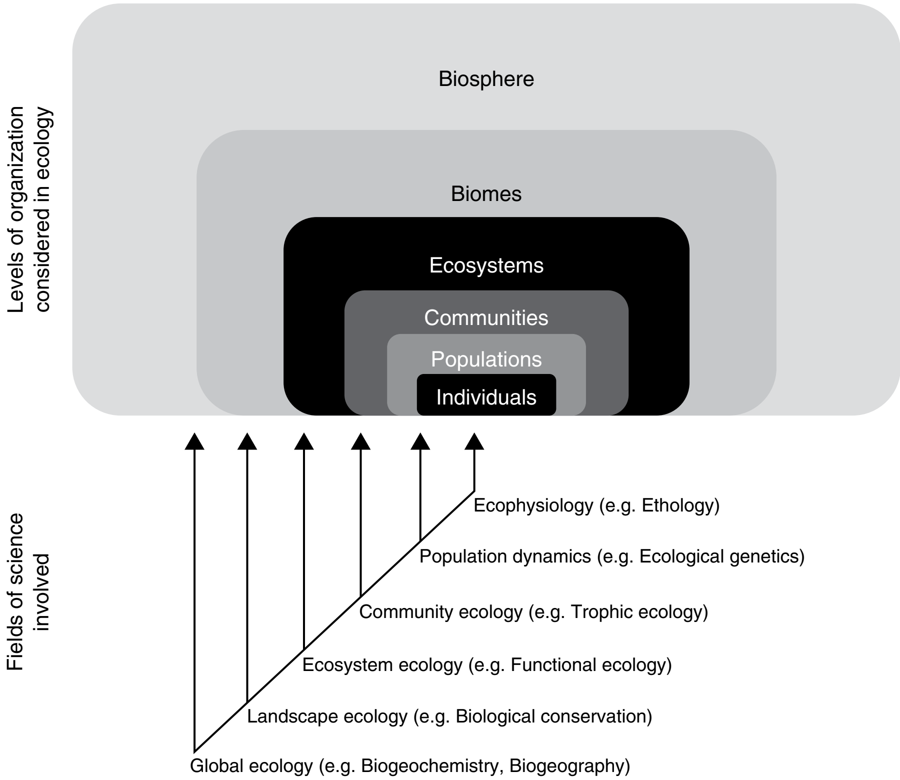

Fig. 1.2. Conceptual scheme of scaling in ecology and the subdisciplines involved in ecology studies. (Author's own figure.)

interactions of coherent assemblages (e.g. algal, nematode, and fish communities may interact within a defined lake ecosystem), each of which is made up of populations of different species made up of individuals of the same species. Because biological interactions may decouple systems and thus hinder direct physico-chemically based determinations of patterns, different observational levels are necessary in ecology to reveal the controls that act on patterns and processes at different scales.

The pioneering ecological concepts developed during the 20th century led to many new questions with respect to species diversity, abundance and biomass patterns, cycles of species co-existence, and the stability and regulation of species numbers. Efforts to answer those questions have given rise to the emergence of unifying research frameworks. One example is the metabolic theory of ecology (Brown *et al.*, 2004), which seeks to explain organismal relationships through coherent correlations between the metabolic rate, body size, and temperature. Sutherland *et al.* (2013) pointed out that, despite growing research activity, many questions and large knowledge gaps remain, as advances have come more slowly than in other scientific disciplines such as chemistry and even astrophysics. Furthermore, the spatiotemporal scale needed to study ecological mechanisms adequately varies widely, depending on the size of the ecosystem, the communities considered, the number of interacting species and individuals, and the nature of their interactions. Problems related to complexity and scaling are the main obstacles hindering the emergence of a unified theory of ecology (Allen and Hoekstra, 2015). In response, ecologists have adopted the approach of first reducing the size and complexity of the ecosystem of interest, by studying community interactions and their mechanisms in laboratory experiments using microcosms as 'micro-ecosystems' before attempting to validate the results in field studies.

1.2.2 Distribution and dispersal of free-living nematodes

Only arthropods have a range of habitats and variety of lifestyles comparable in extent to that of Nematoda. Nematodes outnumber other multicellular animals in the ocean floor, inland waters, and soils, making them essential components of nearly all ecosystems on Earth (Traunspurger, 2002; Danovaro *et al.*, 2008; Van Den Hoogen *et al.*, 2019). An important proportion of nematode species are found globally (Andrássy, 2005; Zullini, 2014), with some being stenotypic (occurring in a few specific habitats) and others eurytopic (occurring in multiple habitats). The reasons for these differences in habitat specificity are poorly understood, but cosmopolitanism seems less common than previously thought (Zullini, 2018).

Studies of nematode ecology and distribution in the biosphere should be approached by taking into account the fundamental difference of scale between our macroscopic world and the microscopic world of nematodes. The human body is thousands of times larger and billions of times heavier than the typical body of nematodes, and human lifespan is also hundreds to thousands of times longer. For a tobrilid nematode, a season in a lake bottom corresponds to an entire life, one that is spent foraging and reproducing within an immense region. From this perspective, how a single nematode species can achieve a global distribution continues to puzzle researchers. However, the scale difference also implies the ability of nematodes to disperse very effectively over long distances. It is also likely that the filter made up of local environmental conditions and species interactions is a stronger constraint to the broader distribution of a species than is the spatiotemporal filter. Once juveniles have hatched, they seek out their food, which drives their active dispersal to favorable patches. Eggs, juveniles, and adults can also be passively dispersed by, for example, water currents, wind, rain, and other animals such as birds (Ptatscheck and Traunspurger, 2020).

1.2.3 Role of free-living nematodes in food webs

Free-living nematodes are an important component of belowground food webs in agro-ecosystems, shrublands, forest (Ferris, 2010; Heidemann *et al.*, 2014; Pausch *et al.*, 2016), and both warm and polar deserts (Liang *et al.*, 2002; Shaw *et al.*, 2018). They are also important contributors to food webs in lake bottoms, streambeds, and microbial biofilms (Majdi and Traunspurger, 2015; Weitere *et al.*, 2018) as well as one of the few links in the food chains in the myriad of karstic environments (Du Preez *et al.*, 2017), pores, and interstices that make up the Earth's crust. In fact, nematodes have even been found in the microbial biofilms that form in the fracture water of a deep mine at a depth of ca. 1 km belowground (Borgonie *et al.*, 2011). The ubiquity, small size, diversity, and abundance of nematodes support their role as intermediaries in food webs, given their ability to exploit essentially all microscopic resources (bacteria, heterotrophic eukaryotes, fungal spores and mycelia, nano- and micro-algae, ultra-fine particulate organic matter and even dissolved organic matter) and in turn serve as food for other invertebrates and many very small vertebrates (Majdi and Traunspurger, 2015). However, the position of nematodes in food webs is complex (e.g. Majdi and Traunspurger, 2017; Wu *et al.*, 2019) because many nematode taxa bear a stylet that allows them to feed and even parasitize plants and animals much larger than themselves. Thus, nematodes are also able to partially exploit the production of higher plants (Pausch *et al.*, 2016) and to serve as 'top predators'. They have also been shown to switch diet opportunistically (Wardle and Yeates, 1993; Moens and Vincx, 1997; Wu *et al.*, 2019). Conversely, relatively large animals such as carp and water fowl can feed massively on nematodes, by filtering them out of the mud (Ptatscheck *et al.*, 2020), thereby reducing both the length of the food chains and energy losses between trophic levels. Interestingly, some common microbial groups, including amoebae, have been shown to pack-hunt and feed voraciously on nematodes (Yeates and Foissner, 1995; Geisen *et al.*, 2015), further challenging the notion that body size determines food web position.

The many pathways through which nematodes in the field acquire their food and, conversely, serve as food for other organisms remain to be fully disentangled, but this is an exciting avenue of research. At the scale of ecosystems, the most important role of nematodes may well be their active participation in carbon and nutrient cycles (Yeates *et al.*, 2009), based on the ability of nematodes to mobilize and package organic matter by burrowing and foraging through microbial mats (Weitere *et al.*, 2018), upgrading the quality of the obtained organic matter by synthesizing essential fatty acids, and then transferring these improved nutrients to higher trophic levels (Menzel *et al.*, 2018). Furthermore, in degraded ecosystems, after a collapse in ecosystem functions (e.g. after organic amendments, Biederman *et al.*, 2008; desertification, Guan *et al.*, 2018; or droughts, Majdi *et al.*, 2020a), nematodes may be among the first organisms in the ecological succession that eventually restore a complex trophic dynamic.

1.3 Why This Book?

1.3.1 The relevance of ecology in nematology

As emphasized in the chapters of this book, free-living nematodes are very small, ubiquitous organisms, have a high species diversity and population turnover rate, readily disperse, play multiple trophic roles, and can be cultured in laboratory microcosms. Given these remarkable attributes, nematodes are a nearly ideal model organism for studies in a broad range of research fields. In agricultural science, nematology has moved from a focus on the development of synthetic nematicides to biological control, such as the use of entomopathogenic species of nematodes to impede insect pests or designing solutions to control plant-parasitic nematodes (Webster, 2012). The emergence of molecular technologies has supported investigations based on nematode models (especially *Caenorhabditis elegans*) in medical research and in a variety of other areas of research, including genetics, physiology, neurobiology, and developmental biology (Rankin *et al.*, 1990; Leung *et al.*, 2008; Ferris *et al.*, 2012; Webster, 2012). The 21st century has seen an immense increase in the public's interest in ecology, as the consequences for the planet of decades of urbanization, pollution, and the overuse of natural resources become clear.

We performed a literature search of scientific papers that included the words 'nematode' or 'nematodes' or 'nematoda' in their titles between 1960 and 2019 (analysis last performed on Google scholar 13 October 2020) to get an overview of nematological research during the past 60 years. In general, the number of scientific papers published each year has tended to grow over time (Fig. 1.3), with an average annual rate of 8–9% (Bornmann and Mutz, 2015).

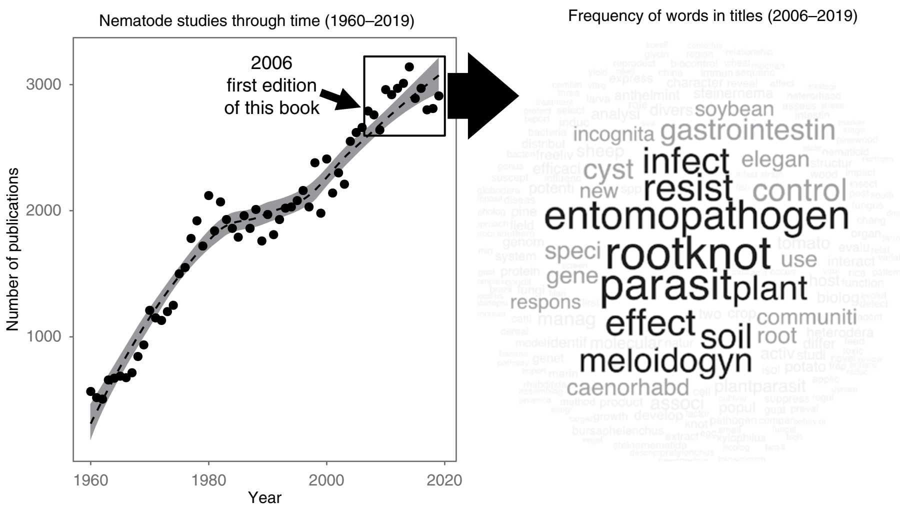

Fig. 1.3. (Left panel) Yearly number of publications with titles containing the words 'nematode' or 'nematodes' or 'nematoda'. The dashed line shows a smoothed conditional means model with the 95% confidence interval (gray). (Right panel) Word cloud representing the relative occurrences of the 200 most frequently used words in publication titles between 2006 and 2019 (*N* = 40,230 titles screened using 'tm' package in R). Words with darker and larger fonts occur more often. The extracted word lists were cleaned by stemming (e.g. 'parasit' instead of 'parasite') before their analysis, by changing all text to lower case, and removing numbers, common English stop words, punctuation, and extra white spaces. (Author's own figure.)

We then used a text-mining approach and focused on the word content of the titles that included ‘nematode’ or ‘nematodes’ or ‘nematoda’ over the period 2006–2019.

Figure 1.3 clearly shows that the recent nematological literature remains heavily focused on parasitic nematodes, especially plant-parasitic species such as *Meloidogyne* spp. (root-knot nematodes). The stem word ‘parasit’ was the second most frequently found across publication titles, whereas ‘freeliv’ ranked 46th. The concentration of research on parasitic nematodes reflects the continued need to mitigate economic losses in agriculture and to improve animal and human well-being, as indicated by the substantial number of publications on gastrointestinal parasites of cattle and humans. In terms of the type of habitats studied, most attention has been devoted to soils (‘soil’ ranked 7th) whereas free-living aquatic nematodes are a relatively marginal field of research, with the stem words ‘marin’ and ‘freshwat’ ranking 185th and 315th, respectively. In the field of ecology, the related stem words were of low (‘ecolog’, 156th) or very low (‘ecosystem’, 375th; ‘web’, 394th; ‘trophic’, 415th; ‘dispers’, 436th) ranking, although generic keywords related to biodiversity and population dynamics fared better (‘communit’, 19th; ‘divers’, 31st; ‘popul’, 38th; ‘distribut’, 66th). Thus, our text-mining analysis sadly demonstrates that nematologists have yet to recognize the potential of nematodes in ecological research. These results are in line with the findings of McSorley (2011), who analyzed topical trends in the *Journal of Nematology* and determined a steady decline in the relative importance of ecological topics in nematology papers published in that journal (22.5% in the 1970s vs. 15.8% in the 2000s), whereas topics associated with biological control increased sharply during the same period (from 1.7% to 12.4%).

1.3.2 An overview of the book’s content

This book is a follow-up of the original, 2006 edition, which was dedicated to the taxonomy and ecology of freshwater nematodes (Eyualem-Abebe *et al.*, 2006), but it takes into account the important books and reviews from the past 15 years that concentrated on free-living nematodes. Among the former, three important volumes on the taxonomy of freshwater nematodes were published by Andrássy (2005, 2007, 2009); Ahmad and Jairajpuri (2010) and both Geraert (2008, 2010, 2011, 2013) and Ghaderi *et al.* (2016) focused, respectively, on Mononchida and the taxonomy of Tylenchida; and Schmidt-Rhaesa (2014) edited a *Handbook of Zoology* covering all taxonomic groups. Other authors have addressed the ecology of freshwater nematodes or, more generally, the ecology of the meiobenthos in books, special issues, and reviews. These include books on nematode behavior (Gaugler and Bilgrami, 2004), nematodes as environmental indicators (Wilson and Kakouli-Duarte, 2009), the second edition of *Meiobenthology* (Giere, 2009), *Perspectives in Meiobenthology* (Giere, 2019), book chapters on the ecology of freshwater nematodes (Traunspurger, 2009, 2014) and on meiofauna in stream ecology (Traunspurger and Majdi, 2017), a special issue of *Hydrobiologia* devoted to the patterns and processes of meiofauna in freshwater ecosystems (Majdi *et al.*, 2020b), reviews of nematodes in aquatic environments (Tahseen, 2012), free-living nematodes in the freshwater food web (Majdi and Traunspurger, 2015) and in aquatic biofilms (Weitere *et al.*, 2018), the biodiversity of aquatic nematodes (Luc *et al.*, 2010; Decraemer and Backeljau, 2015), experimental studies with nematodes in ecotoxicology (Haegerbaeumer *et al.*, 2015), nematodes in caves (Du Preez *et al.*, 2017), and the impacts of plastic particles on benthic invertebrates, including nematodes (Haegerbaeumer *et al.*, 2019).

With this wealth of recent publications, one could ask: why another nematode book? The answer lies in our search of the nematological literature (Fig. 1.3) and a re-occurring take-home message in those publications: despite the recognized importance of nematodes across ecosystems and their undeniable ecological and evolutionary success, many of the world's free-living nematodes have yet to be fully characterized or even discovered. Moreover, important knowledge gaps remain, including studies of the autecology of free-living nematode species, the taxonomic and functional structure of nematode populations and assemblages, the spatiotemporal factors driving nematode dispersal and distribution patterns, the nematode diet, the relevance of nematodes as prey for other organisms, nematode participation in the mineralization of organic matter, and the consequences of habitat degradation on nematode assemblages.

This book focuses on the ecology of free-living nematodes. Our aim is to foster ecological research from the 'perspective of nematodes', as a means to better understand how ecosystems function and thereby devise measures to mitigate current threats to freshwater environments. Because reproducible experimental procedures are the basis for sound science, many chapters offer detailed protocols and case studies. The topics covered by the chapters that follow this Introduction are summarized below.

Chapter 2 'Sampling and Processing of Freshwater Nematodes with Emphasis on Molecular Methods' is an introduction to current methods of nematode sampling and processing, with the latter including molecular methods as well. **Chapter 3** 'Species Composition and Distribution of Free-living Nematodes in Lakes and Streams' provides an overview of the distributional patterns of nematodes in lakes, rivers, and streams worldwide and of the factors that affect the structuring of nematode communities in the field. **Chapter 4** 'Nematodes from Extreme and Unusual Freshwater Habitats' introduces the reader to the intriguing nematode communities that abound in remote or cryptic habitats as well as those found in extreme environments where multicellular life is pushed to its limits. **Chapter 5** 'Dispersal of Free-living Nematodes' considers the possible reasons underlying the ubiquity of nematodes and their high abundances in nearly all of their habitats. **Chapter 6** 'Feeding Ecology of Free-living Nematodes' details how nematodes acquire their food and interact directly, or not, with microbial processes. **Chapter 7** 'Role of Nematodes in the Food Web:

Nematodes as Predator and Prey' places nematodes in a broader food web context, including their participation in matter and energy fluxes within ecosystems. **Chapter 8** 'Production of Freshwater Nematodes' is a guide to measuring biomass production by nematode communities and to interpreting its ecological significance. **Chapter 9** 'Freshwater Nematodes in Metacommunity Studies' examines the relevance of nematodes as models in theoretical ecology studies of metacommunity. **Chapter 10** 'Single- and Multi-species Toxicity Testing with Nematodes' demonstrates the use of nematode physiological endpoints in analyses of the toxicity of potentially harmful chemicals and heavy metals. **Chapter 11** 'Freshwater Nematodes as Bioindicators in Field Studies – the NemaSPEAR[%]-index' presents an index based on the structure of nematode communities that can be used as a bio-indication tool by conservation ecologists and environmental managers. **Chapter 12** 'Case Studies with Nematodes from the Individual to Ecosystem Level' details four laboratory and field experiments in which nematodes were used to test hypotheses at different ecological scales (individual, population, community, and ecosystem).

Through these chapters, we seek to provide a solid introduction to the ecology of aquatic nematodes for scientists, graduate, and undergraduate students, as well as anyone curious about this evolving field.

1.4 Species Diversity and an Overview of Nematode Classification

Few other groups of animals are likely to harbor so many as yet undiscovered species as Nematoda. Currently, the number of valid species of free-living Nematoda is between 12,000 and 14,000 (Andrássy, 2005; Hodda *et al.*, 2009; Zhang, 2013), such that Nematoda are the fourth most diverse phylum after Arthropoda, Mollusca, and Vertebrata. However, the predicted number of species is at least 500,000 (Andrássy, 1976; May, 1988; Hammond, 1992; Hugot *et al.*, 2001, Blaxter, 2011).

Compared with other groups of animals, the classification of Nematoda is in many respects challenging, as the majority of nematodes are very small and hence difficult to study and identify. Furthermore, nematode classification has itself undergone several revisions, especially since the explosive development of molecular identification, which has opened up new perspectives in systematics (Andrássy, 2005). A gross system of Nematoda classification was compiled in 2005 by Andrássy (2005). In the following we present a short overview of this classification system, but for details of this system (and also other classification systems) the reader should consult Andrássy (2005, 2007, 2009). Among the three main groups of free-living nematodes, of the estimated 1530 known valid genera 33% belong to Torquentia, 29% to Secernentia, and 38% to Penetrantia (Andrássy, 2005). The list below includes several ecological considerations for groups that are major players in limno-terrestrial ecosystems. The number of validated free-living species (freshwater and terrestric), if available, is also reported (in square brackets) and is based on Andrássy (2005, 2007, 2009). Genera and species found in brackish waters are only partly considered in this overview. Some representatives of free-living nematodes are shown in Fig. 1.4.

1.4.1 Torquentia Andrássy, 1974

The species comprising Torquentia are free-living *sensu stricto*, meaning that obligate/facultative plant- or animal parasites are not included. The large majority of the species (~92%) are strictly marine, with the remainder mostly found in continental aquatic environments but a minor proportion adapted to (non-saprobic) terrestrial habitats. In terms of the number of genera and species, Torquentia are nearly as rich as Secernentia and Penetrantia. So far, 673 genera have been established within this class, but how many are 'well-diagnosed' and how many are synonyms (or homonyms) remain to be painstakingly determined. Currently, the decision whether a given genus is valid or synonymous with another is often subjective, such that taxonomic assertions may long remain unchecked. A conservative estimate is that at least three-quarters of the genera (~500–520) are taxonomically valid. Of these, 460–470 are strictly marine and ~50 include but are not limited to continental species. At the species level, there are 3750–3800 'well-diagnosed' species recognized as belonging to Torquentia. Those nematodes are mostly microbivorous or detritivorous, feeding on bacteria, fine particles, protozoans, and algae. Although the feeding preferences of Torquentia have yet to be fully characterized, thus far no predators of other metazoans occur in this group (Andrássy, 2005).

Monhysterida De Coninck & Schuurmans Stekhoven, 1933

Most Monhysterida are aquatic nematodes, predominantly marine, although some species of this group numerically dominate nematode communities in continental waters. Examples of the latter include species from the genera *Eumonhystera* and *Monhystera*, which are systematically found in high numbers in a variety of limnetic habitats.

Monhysterina De Coninck & Schuurmans Stekhoven, 1933
Monhysteroidea de Man, 1876
Xyalidae Chitwood, 1951
Cylindrotheristus [6], Daptonema [5], Mesotheristus [3], Mongolotheristus [1], Penzancia [2], Sacrimarinema [3]
Monhysteridae de Man, 1876
Anguimonhystera [2], Monhystera [20], Eumonhystera [36], Geomonhystera [16], Monhystrella [32], Tridentulus [7], Sinanema [2], Diplolaimelloides and Sitadevinema
Sphaerolaimoidea Filipjev, 1918
Sphaerolaimidae Filipjev, 1918
Hofmaenneria [6]

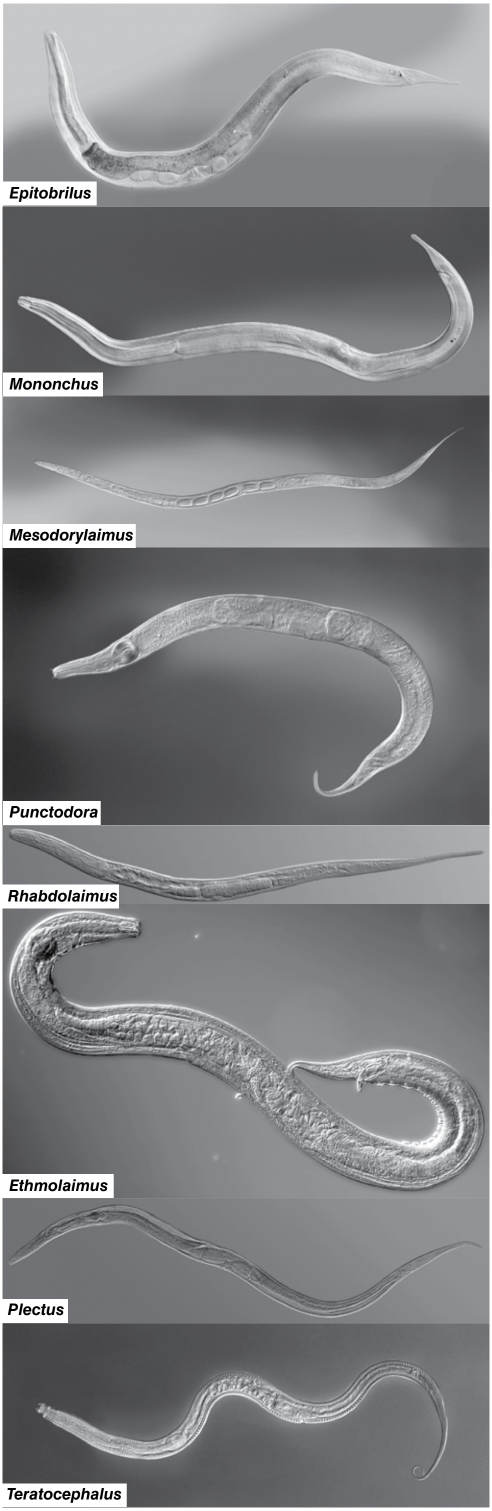

Fig. 1.4. Some representative genera of free-living nematodes. (Photo: Animal Ecology, Bielefeld University.)

Linhomoeina Andrássy, 1974 (marine)

Desmoscolecida Filipjev, 1929

Desmoscolecoidea Shipley, 1896
Desmoscolecidae Shipley, 1896
Desmoscolex [6], *Pareudesmoscolex [3]*
Greeffiellidae Filipjev, 1929
Cyartonematidae Tchesunov, 1989
Meyliidae De Coninck, 1965

Araeolaimida De Coninck & Schuurmans Stekhoven, 1933

Araeolaimina De Coninck & Schuurmans Stekhoven, 1933
Araeolaimoidea De Coninck & Schuurmans Stekhoven, 1933
Cylidrolaimidae Micoletzky, 1922
Cylindrolaimus [19]
Bastianiidae De Coninck, 1935
Bastiania [11]
Odontolaimidae Gerlach & Riemann, 1974
Odontolaimus [4]
Leptolaimina Lorenzen, 1979
Leptolaimoidea Örley, 1880
Leptolaimidae Örley, 1880
Adelonema [1], *Adenolaimus [1]*, *Deontolaimus [1]*, *Hemiplectus [1]*, *Leptolaimus [2]*, *Leptoplectonema [1]*, *Pakira [1]*, *Paraplectonema [7]*, *Prodomorganus [1]*
Aphanolaimidae Chitwood, 1936
Aphanolaimus [25], *Paraphanolaimus [12]*, *Aphononchus [8]*, *Anonchus [10]*
Haliplectoidea Chitwood, 1951
Rhabdolaimidae Chitwood, 1951
Rhabdolaimus [7], *Udonchus [3]*, *Rogerus [1]*
Aulolaimidae Jairajpuri & Hooper, 1968
Aulolaimus [12], *Pseudoaulolaimus [1]*
Plectoidea Örley, 1880
Chronogastridae Gagarin, 1975
Chronogaster [46], *Keralanema [1]*
Plectidae Örley, 1880
Anaplectus [12], *Arctiplectus [1]*, *Ceratoplectus [8]*, *Chiloplectus [6]*, *Perioplectus [1]*, *Plectus [78]*, *Ereptonema [4]*, *Tylocephalus [10]*, *Wilsonema [4]*, *Wilsotylus [1]*
Metateratocephaloidea Eroshenko, 1973
Metateratocephalidae Eroshenko, 1973
Euteratotecephalus [3], *Metateratocephalus [4]*

Chromadorida Chitwood, 1933

Chromadorida are also mostly marine; however, they further include limnic and, to a lesser extent, terrestrial forms. While mainly they are microbivorous, presumably feeding on fine particles and bacteria, there are reports from marine and freshwater ecosystems of species capable of feeding on diatoms (e.g. Jensen, 1982; Majdi *et al.*, 2012), by using their small teeth to crack the frustules and either swallow the organism in parts or suck out its inner cell contents. Chromadoridae may attain extremely high abundances such that they numerically dominate periphytic algal biofilms of lakes and rivers.

Desmodorina De Coninck, 1965
Desmodoroidea Filipjev, 1922 (marine)
Microlaimoidea Micoletzky, 1922
Microlaimidae Micoletzky, 1922
Microlaimus [60], *Prodesmodora [9]*
Chromadorina Chitwood & Chitwood, 1937
Cyatholaimoidea Filipjev, 1918
Cyatholaimidae Filipjev, 1918
Achromadora [17], *Paracyatholaimus [3]*
Ethmolaimidae Filipjev & Schuurmans Stekhoven, 1941
Ethmolaimus [14]
Chromadoroidea Filipjev, 1917
Hypodontolaimidae De Coninck, 1965
Chromadorita [5], *Dichromadora [2]*, *Neochromadora [1]*
Chromadoridae Filipjev, 1917
Chromadorina [7], *Prochromadora [1]*, *Punctodora [6]*

Draconematina De Coninck, 1965 (marine)

1.4.2 Secernentia Linstow, 1905

This is the second largest taxonomic group and it nearly exclusively consists of nematodes adapted to continental conditions. Thus, Secernentia is the only one of the three classes with essentially no marine members. Specifically, thus far <10 species are known to secondarily occur in marine or brackish habitats. The overwhelming majority of Secernentia are terrestrial, but some members may occur in inland waters. There are at least 440 genera, representing 3300–3400 valid species, according to the classification of Andrássy (2005). Stylet-bearing nematodes are capable of asymmetric predation (i.e. they can feed on prey larger than themselves), with fungal hyphae and the root system of lower or higher plants contributing to their diet. Plant-parasitic nematodes belonging to the Secernentia feed on important crops and are therefore considered to be agricultural pests. Other species are parasites of invertebrates or vertebrates, including humans. Species without a stylet are thought to be microbivorous or mycetophagous, but rarely carnivorous. They occur in various terrestrial habitats but also exhibit varying affinities for saprobic habitats (Andrássy, 2007).

Rhabditida Chitwood, 1933

Rhabditid nematodes occur predominantly in terrestrial environments (e.g. soil, humus, compost, decaying organic matters, dung), where they typically outnumber other nematode groups. Strictly aquatic (limnic and hyaline) species are rare, but the detection of rhabditids in many samples suggests that they are important albeit ephemeral inhabitants of inland waters. The majority of Rhabditida are bacterial feeders but some species are carnivorous.

Teratocephalina Andrássy, 1974
Teratocephalidae Andrássy, 1958
Steratocephalus [1], Teratocephalus [15]

Cephalobina Andrássy, 1974
Cephaloboidea Filipjev, 1934
Cephalobidae Filipjev, 1934
Bunobus, Cephalobus [23], Eucephalobus [12], Heterocephalobellus [2], Heterocephalobus [9], Pseudacrobeles, Acrobeles [21], Acrobeloides [29], Acrobelophis [7], Acroukrainicus, Cervidellus [16], Chiloplacoides, Chiloplacus [29], Nothacrobeles [15], Paracrobeles, Pentjatinema, Placodira, Scottnema, Seleborca [13], Stegelletina, Stegelleta [5], Triligulla, Zeldia [14], Acrolobus [1], Cribonema, Metacrolobus, Panagroteratus, Teratolobus, Panagroteratus, Teratolobus, Metacrobeles
Elaphonematidae Heyns, 1962
Acromoldavicus [2], Kirjanovia, Elaphonema
Osstellidae Heyns, 1962
Panagrolaimoidea Thorne, 1937
Panagrolaimidae Thorne, 1937
Procephalobus [4], Propanagrolaimus [2], Panagrolaimus [44], Panagrobeles [4], Panagrobelium, Brevistoma, Panagrellus [13], Anguilluloides, Tricephalobus [3], Halicephalobus [9], Turbatrix [2], Baujardia
Alirhabditidae Suryawanshi, 1971
Brevibuccidae Paramonov, 1956
Brevibucca, Cuticonema, Plectonchus
Chambersielloidea Thorne, 1937
Chambersiellidae Thorne, 1937
Diastolaimus, Macrolaimellus, Macrolaimus, Catoralaimellus, Chambersiella, Cornilaimus, Geraldius, Bicirronema, Tricirronema, Trualaimus
Alloionematoidea Chitwood & McIntosh, 1934
Alloionematidae Chitwood & McIntosh, 1934
Alloionema, Rhabditophanes [3]

Myolaimina Inglis, 1983
Myolaimidae Andrássy, 1958
Myolaimus [9]

Rhabditina Chitwood, 1933
Rhabditoidea Örley, 1880
Stomachorhabditidae Andrássy, 1970
Rhabditonema [1], Stomachorhabditis [4]
Rhabditidae Örley, 1880
Rhabditis [28], Curviditis [2], Rhabditella [8], Cuticularia [7], Ablechroiulus [10], Cephaloboides [3], Diploscapteroides [5], Discoditis [2], Metarhabditis [1], Oscheius [8], Poikilolaimus [3], Rhitis [9], Rhabditoides [1], Amphidirhabditis [1]
Protorhabditidae Dougherty, 1955
Protorhabditis [13], Prodontorhabditis
Peloderidae Andrássy, 1976
Coarctadera [9], Pelodera [10], Rhomborhabditis [5], Caenorhabditis [15], Dolichorhabditis [10], Pellioditis [16], Phasmarhabditis [6], Xylorhabditis [2], Heterorhabditis
Mesorhabditidae Andrássy, 1976
Crustorhabditis, Cruznema [5], Distolabrellus, Lesjan, Marispelodera, Mesorhabditis [21], Operculorhabditis, Rhabpanus, Teratorhabditis [5], Bursilla [6], Parasitorhabditis
Diploscapteridae Micoletzky, 1922
Diploscapter [13], Carinoscapter
Bunonematoidea Micoletzky, 1922
Bunonematidae Micoletzky, 1922
Bunonema [15], Rhodolaimus [15], Serronema, Rhodonema, Aspidonema [5], Sachsium, Craspedonema
Pterygorhabditidae Goodey, 1963
Pterygorhitis [2], Pterygorhabditis [2]

Diplogastrina Micoletzky, 1922
Cylindrocorporoidea Goodey, 1939
Cylindrocorporidae Goodey, 1939
Cylindrocorpus, Goodeyus, Myctolaimus, Protocylindrocorpus
Longicuccidae Poinar, Jackson, Bell & Wahid, 2003 (parasitic in vertebrates)
Odontopharyngoidea Micoletzky, 1922
Odontopharyngidae Micoletzky, 1992
Diplogastroidea Micoletzky, 1922
Pseudodiplogasteroididae Körner, 1954
Pseudodiplogasteroides
Diplogasteroididae Filipjev & Schuurmams Stekhoven, 1941
Demaniella, Diplogasteroides [4], Demaniella [4], Goffartia [5], Fuchsnema [9], Rhabditidoides, Rhabditolaimus
Diplogastridae Micoletzky, 1922
Acrostichus [13], Anchidiplogaster, Butlerius [10], Cephalobium, Costanemella, Diplogaster [2], Diplogasteriana [2], Diplogasteritus [22], Eudiplogasterium [1], Monobutlerius [5], Parasitodiplogaster, Paroigolaimella [9], Peterngus
Neodiplogastridae Paramonov, 1952

Diplenteron [1], *Fictor [14]*, *Glauxinema [9]*, *Koerneria [29]*, *Micoletzkya*, *Mononchoides [29]*, *Neodiplogaster*, *Oigolaimella [4]*, *Pareudiplogaster*, *Pristionchus [17]*
Heteropleuronematidae Andrássy, 1970
Heteropleuronema
Tylopharynidae Filipjev, 1934
Tylopharynx [2]

Aphelenchida Siddiqi, 1980

Representatives of the Aphelenchida are adapted to a wide range of ecological and biological conditions. Most of these nematodes are free-living in soils, mosses, decaying organic matter, the undersurface of bark, and plant roots, and are mycetophagous or predacious. Some species are phytoparasitic and cause crop losses; however, phytoparasitism is much less well developed in Aphelenchida than in its large sister group, the Tylenchida. The remaining species are associates or obligate ecto- or endoparasites of insects (Andrássy, 2007).

Aphelenchina Geraert, 1966
Aphelenchoidea Fuchs, 1937
Aphelenchidae Fuchs, 1937
Aphelenchus [13]
Paraphelenchidae Goodey, 1951
Paraphelenchus [25]
Aphelenchoidoidea Skarbilovich, 1947
Aphelenchoididae Skarbilovich, 1947
Aphelenchoides [150], *Berntsenus*, *Laimaphelenchus [14]*, *Robustodorus [1]*, *Punchaulus [1]*, *Ruehmaphelenchus [2]*, *Schistonchus [9]*, *Sheraphelenchus [2]*, *Tylaphelenchus [7]*, *Bursaphelenchus [80]*, *Rhadinaphelenchus [1]*, *Anomyctus [1]*
Seinuridae Husain & Khan, 1967
Aprutides [2], *Papuaphelenchus [1]*, *Seinura [47]*
Ektaphelenchidae Paramonov, 1964 (semi-parasites of insects)
Parasitaphelenchidae Rühm, 1956 (in bark beetles)
Acugutturidae Hunt, 1980 (ectoparasites of insects)
Entaphelenchidae Nickle, 1970 (parasites of beetles)

Tylenchida Thorne, 1949

Tylenchids are present worldwide, with most species free-living in the soil, usually in association with plants, leaf litter, humus, mosses, or other terrestrial habitats. Unlike aphelenchids, they largely avoid decaying material. Aquatic or semi-aquatic species are rare. A majority of tylenchids live on or inside plants, feeding on their fluid cell contents. Other species are commensal or parasitize insects and other arthropods (Andrássy, 2007).

Tylenchina Chitwood & Chitwood, 1950
Tylenchoidea Örley, 1880
Tylenchidae Örley, 1880

Aglenchus [8], *Allotylenchus [1]*, *Coslenchus [37]*, *Cucullitylenchus [1]*, *Discotylenchus [6]*, *Filenchus [75]*, *Fraglenchus [2]*, *Irantylenchus [1]*, *Polenchus [3]*, *Tylenchus [30]*, *Basiria [42]*, *Boleodorus [25]*, *Neopsilenchus [10]*, *Duosulcius [2]*, *Malenchus [32]*, *Miculenchus [2]*, *Mukazia [1]*, *Ridgellus [1]*, *Silenchus [1]*, *Zanenchus [8]*, *Arboritynchus [1]*, *Campbellenchus [2]*, *Cephalenchus [19]*, *Gracilancea [1]*, *Pleurotylenchus [2]*, *Tylodorus [2]*, *Cervoannulatus [1]*, *Neothada [5]*, *Thada [1]*

Ecphyadophoridae Skarbilovich, 1959

Ecphyadophora [8], *Mitranema [2]*, *Ultratenella [1]*, *Chilenchus [1]*, *Ecphyadophoroides [2]*, *Epicharinema [1]*, *Lelenchus [3]*, *Tenunemellus [6]*, *Tremonema [1]*

Atylenchidae Skarbilovich, 1959

Atylenchus [1], *Eutylenchus [5]*

Anguinidae Nicoll, 1935

Anguina [12], *Diptenchus [1]*, *Ditylenchus [58]*, *Indoditylenchus [1]*, *Nothanguina [1]*, *Nothotylenchus [45]*, *Orrina [1]*, *Pseudhalenchus [4]*, *Pterotylenchus [1]*, *Safianema [6]*, *Subanguina [28]*, *Halenchus [3]*, *Neoditylenchus [24]*, *Sychnotylenchus [6]*

Hoplolaimoidea Filipjev, 1934

Psilenchidae Paramonov, 1967

Antarctenchus [1], *Atetylenchus [6]*, *Psilenchus [17]*

Dolichodoridae Chitwood & Chitwood, 1950

Brachydorus [3], *Dolichodorus [16]*, *Neodolichodorus [10]*

Belonolaimidae Whitehead, 1960

Belonolaimus [5], *Carphodorus [1]*, *Ibipora [4]*, *Morulaimus [8]*

Telotylenchidae Siddiqi, 1960

Bitylenchus [30], *Histotylenchus [6]*, *Neodolichorhynchus [17]*, *Paratrophurus [16]*, *Quinisulcius [15]*, *Sauertylenchus [4]*, *Telotylenchus [17]*, *Trichotylenchus [4]*, *Trophurus [14]*, *Tylenchorhynchus [106]*, *Uliginotylenchus [7]*, *Meiodorus [3]*, *Amplimerlinius [20]*, *Geocenamus [14]*, *Merlinius [30]*, *Nagelus [25]*, *Scutylenchus [21]*, *Macrotrophurus [1]*

Pratylenchidae Thorne, 1949

Hirschmaniella [33], *Pratylenchus [85]*, *Zygotylenchus [2]*, *Achlysiella [6]*, *Apratylenchoides [2]*, *Hoplotylus [7]*, *Pratylenchoides [29]*, *Radopholus [20]*, *Zygradus [2]*, *Naccobus [2]*

Hoplolaimidae Filipjev, 1934

Antarctylus [1], *Aphasmatylenchus [4]*, *Orientylus [4]*, *Helicotylenchus [194]*, *Orientylus [4]*, *Pararotylenchus [15]*, *Rotylenchoides [11]*, *Rotylenchus [75]*, *Varotylus [11]*, *Aorolaimus [7]*, *Basirolaimus [18]*, *Hoplolaimus [14]*, *Peltamigratus [22]*, *Scutellonema [45]*

Rotylenchulidae Husain & Khan, 1967

Acontylus [1], *Rotylenchulus [11]*, *Senegalonema [1]*

Heteroderidae Filipjev & Schuurmans Stekhoven, 1941

Bilobodera [2], *Meloidodera [10]*, *Verutus [2]*, *Atalodera [9]*, *Bellodera [1]*, *Camelodera [1]*, *Cryphodera [6]*, *Ekphymatodera [1]*, *Hylonema [1]*, *Rhizonemella [1]*, *Sarisodera [1]*, *Afenestrata [6]*, *Betulodera [1]*, *Cactodera [12]*, *Dolichodera [1]*, *Globodera [14]*, *Heterodera [71]*, *Punctodera [3]*

Meloidogynidae Skarbilovich, 1959
Bursadera [1], Meloinema [4], Meloidogyne [88], Spartonema [2]

Criconematina Siddiqi, 1980
Tylenchuloidea Skarbilovich, 1947
Paratylenchidae Thorne, 1949
Tylenchocriconema [1], Cacopaurus [1], Gracilacus [45], Paratylenchus [74], Tanzanius [1]
Sphaeronematidae Raski & Sher, 1952
Goodeyella [1], Meloidoderita [3], Sphaeronema [7], Tumiota [1]
Tylenchulidae Skarbilovich, 1947
Trophotylenchulus [14], Tylenchulus [4]
Criconematoidea Taylor, 1936
Criconematidae Taylor, 1936
Criconemoides [38], Discocriconemella [31], Mesocriconema [94], Nothocriconemoides [2], Xenocriconemella [2], Amphisbaenema [1], Bakernema [2], Blandicephalanema [3], Criconema [84], Croserinema [1], Crossonema [30], Lobocriconema [18], Neolobocriconema [21], Ogma [58], Orphreyus [3], Pateracephalanema [8], Hemicriconemoides [49]
Hemicycliophoridae Skarbilovich, 1959
Aulosphora [11], Colbranium [1], Hemicycliophora [126], Caloosia [15]

Hexatylina Siddiqi, 1980
Sphaerularioidea Lubbock, 1861
Neotylenchidae Thorne, 1941
Deladenus [22], Hadrodenus [2], Hexatylus [10], Anguillonema [2], Gymnotylenchus [2], Fergusobia [7], Rubzovinema [1]
Sphaerulariidae Lubbock, 1961
Prothallonema [20], Sphaerularia [1], Tripius [2], Bealius [2], Ipiluella [1], Misticius [1], Neomisticius [1], Paurodontella [8], Paurodontoides [2], Paurodontus [9]
Allantonematidae Pereira, 1931
Allantonema [8], Anandranema [1], Bradynema [8], Elaeolenchus [1], Formicitylenchus [1], Howardula [20], Metaparasitylenchus [12], Neoparasitylenchus [27], Parasitylenchoides [8], Pratinema [1], Proparasitylenchus [6], Protylenchus [2], Scatonema [1], Sulphuretylenchus [13], Thripinema [5], Aphelenchulus [1], Bovienema [4], Contortylenchus [29]
Iotonchioidea Goodey, 1953
Iotonchiidae Goodey, 1953
Fungiotonchium [4], Iotonchium [4], Paraiotonchium [6], Skarbilovinema [2]
Parasitylenchidae Siddiqi, 1986
Coprotylenchus [1], Parasitylenchus [9], Kurochkinitylenchus [1], Heterotylenchus [3], Paregletylenchus [1], Wachekitylenchus [4],

Incurvinema [1], Psyllotylenchus [20], Spilotylenchus [8], Heteromorphotylenchus [2]

1.4.3 Penetrantia Andrássy, 1974

Penetrantia contains several important groups of free-living nematodes, but parasites also occur. Roughly 35% of the species are marine, with the rest successfully adapted to continental ecosystems. True saprobiontes are not members of the Penetrantia. Thus far, ~740 genera have been diagnosed. A rough estimate is that among the nominal genera more than 75% (580–590 genera) can be considered as taxonomically validated. At the species level, 4600 valid free-living species have been proposed (Andrássy, 2007). Free-living species likely play a versatile and important role in benthic food webs. They include forms that feed on bacteria, but also species that attain relatively large sizes at maturity such that their diet includes larger prey, such as protozoans, algae, larger organic particles, other nematodes, and other small metazoans. Stylet-bearing species are assumed to be omnivorous, feeding on prey ranging from algal mats to plant roots and other animals. Some species transmit phyto-viruses and thus cause crop damage. There are also species that live as endoparasites in vertebrates. Species with large buccal cavities armed with teeth include predators of small invertebrates and even other nematodes.

Enoplida Filipjev, 1929

Enoplida are a species-rich, mostly marine group of nematodes that mostly include microbivores, bacteria and algae feeders, but also detritivores, and to a lesser degree, carnivores.

Enoplina Chitwood, 1933 (mostly marine)
Leptosomatoidea Filipjev, 1916
Anoplostomatidae Gerlach & Riemann, 1974
Leptosomatidae Filipjev, 1916
Thoracostomatidae De Coninck, 1965
Enoploidea Dujardin, 1845
Anticomidae Filipjev, 1918
Enoplidae Dujardin, 1845
Phanodermatidae Filipjev, 1927
Thoracostomopsidae Filipjev, 1927

Oncholaimina De Coninck, 1965
Enchelidoidae Filipjev, 1918
Belbollidae Andrássy, 1974
Enchelidiidae Filipjev, 1918
Calyptronema [1]
Eurystominidae Filipjev, 1934
Oncholaimoidea Filipjev, 1916

Oncholaimidae Filipjev, 1916
Viscosia [2], *Adoncholaimus [3]*, *Oncholaimus [7]*
Pelagonematidae De Coninck, 1965
Thalassogenus [5]

Ironina Siddiqi, 1983
Ironoidea de Man, 1876
Thalassironidae Andrássy, 1976
Ironidae de Man, 1876
Ironus [21]
Oxystominoidea Filipjev, 1918
Halalaimidae De Coninck, 1965
Leptosomatidae Filipjev, 1916
Oxystominidae Filipjev, 1918
Andrassyidae Chesunov & Gagarin, 1999
Andrassya [2], *Malakhovia [1]*

Tripyloidina De Coninck, 1965 (mostly marine)
Tripyloididae Filipjev, 1928
Tripyloides [1]

Tripylina Andrássy, 1974
Prismatolaimoidea Micoletzky, 1922
Prismatolaimidae Micoletzky, 1922
Prismatolaimus [34]
Onchulidae Andrássy, 1963
Caprionchulus [1], *Limonchulus [3]*, *Onchulus [8]*, *Stenonchulus [1]*, *Kinonchulus [1]*
Tripyloidea de Man, 1876
Tobrilidae De Coninck, 1965

Tobrilids have very successfully adapted to limnetic environments and may be found abundantly in lake bottoms all over the world. Their armed buccal cavity suggests that they can occupy several trophic niches. Adults are probably omnivorous or predators of other nematodes and meiofauna.

Tobrilus [23], *Eutobrilus [27]*, *Epitobrilus [19]*, *Paratrilobus [8]*, *Kurikania [2]*, *Semitobrilus [4]*, *Neotobrilus [19]*, *Macrotobrilus [1]*, *Quasibrilus [2]*, *Asperotobrilus [3]*, *Tobriloides [2]*
Triodontolaimidae De Coninck, 1965 (marine)
Rhabdodemaniidae Filipjev, 1934 (marine)
Pandolaimidae Belogurov, 1980 (marine)
Tripylidae de Man, 1876
Tripyla [24], *Tripylina [6]*, *Tripylella [3]*, *Trischistoma [4]*, *Tobrilia [2]*

Campydorina Jairajpuri, 1983
Campydoroidea Thorne, 1935
Campydoridae Thorne, 1935
Campydora [1]

Trefusiida Lorenzen, 1981 (marine)

Alaimida Siddiqi, 1983

Alaimina Clark, 1961
Alaimoidea Micoletzky, 1922
Alaimidae Micoletzky, 1922
Alaimus [51], *Cosalaimus [4]*
Amphidelidae Andrássy, 2002
Amphidelus [22], *Caviputa [10]*, *Etamphidelus [9]*, *Laxamphidelus [6]*, *Megamphidelus [1]*, *Metamphidelus [3]*, *Paramphidelus [23]*, *Postamphidelus [1]*, *Scleralaimus [1]*, *Scleramphidelus [1]*, *Cristamphidelus [8]*

Diphterophorida Loof, 1991

Diphtherophorina Coomans & Loof, 1970
Diphtherophoroidea Micoletzky, 1922
Diphtherophoridae Micoletzky, 1922
Diphtherophora [33], *Longibulbophora [2]*, *Tylolaimophorus [14]*
Trichodoridae Thorne, 1935
Allotrichodorus [6], *Ecuadorus [2]*, *Monotrichodorus [8]*, *Paratrichodorus [34]*, *Trichodorus [55]*

Mononchida Jairajpuri, 1969

Representatives of Mononchida are free-living and exclusively continental. They are found in a wide range of limno-terrestrial biotopes across the world, but not in saprobic environments. Many species are predators, seemingly with low specificity as exemplified by their ability to feed on protozoans, rotifers, oligochaetes, other small invertebrates, and particularly on other nematodes (Ahmad and Jairajpuri, 2010). Cannibalism also occurs, as some species may also feed upon plant-parasitic nematodes. These carnivorous species are thus potent biocontrol agents that play an important role in maintaining biological balance in agroecosystems (Andrássy, 2009).

Bathyodontina Coomans & Loof, 1970
Cryptonchoidea Chitwood, 1937
Cryptonchidae Chitwood, 1937
Bathyodontus [3], *Cryptonchus [4]*
Mononchuloidea De Coninck, 1965
Mononchulidae De Coninck, 1965
Mononchulus [1], *Oionchus [4]*

Mononchina Kirjanova & Krall, 1969
Mononchoidea Filipjev, 1934
Mononchidae Filipjev, 1934
Actus [5], *Clarkus [12]*, *Coomansus [28]*, *Granonchulus [5]*, *Judonchulus [3]*, *Mononchus [19]*, *Nigronchus [1]*, *Paramononchus [3]*, *Prionchulus [33]*, *Sporonchulus [4]*, *Tectonchus [4]*, *Cobbonchulus [1]*. *Cobbonchus [33]*, *Comiconchus [2]*, *Tricaenonchus [1]*

Mylonchulidae Jairajpuri, 1969
Brachonchulus [1], Crestonchulus [1], Margaronchulus [2], Megaonchulus [1], Mylonchulus [79], Oligonchulus [1], Polyonchulus [2]
Anatonchoidea Jairajpuri, 1969
Anatonchidae Jairajpuri, 1969
Nullonchus [4], Caputonchus [1], Hadronchoides [2],Hadronchulus [3], Hadronchus [3], Iotonchulus [4], Iotonchus [89], Jensenonchus [8], Mulveyellus [5], Parahadronchus [12], Prionchulellus [1], Prionchuloides [1], Crassibucca [4], Doronchus [2], Miconchus [33], Paracrassibucca [1], Promiconchus [3], Anatonchus [15], Micatonchus [3], Tigronchoides [9]

Dorylaimida Pearse, 1942

Members of this group are highly abundant in terrestrial and aquatic habitats extending from the tropics to Antarctica. They include continental and free-living nematodes, but not marine or animal parasitic forms (Andrássy, 2009). Dorylaimida are remarkably diverse in terms of the number of species but also in their roles in ecosystems. This is reflected in their wide range of sizes and their possession of a stylet, which allows these nematodes to feed on a variety of food items, which includes other nematodes (Andrássy, 2009).

Nygolaimina Ahmad & Jairajpuri, 1979
Nygolaimoidea Thorne, 1935
Nygolaimidae Thorne, 1935
Afronygus [1], Aquatides [13], Clavicauda [2], Clavicaudoides [11], Feroxides [1], Laevides [13], Nygolaimus [34], Paranygolaimus [2], Solididens [8], Paravulvus [17], Nygolaimellus [6]
Aetholaimidae Jairajpuri, 1965
Aetholaimus [5]
Nygellidae Andrássy, 1958
Nygellus [6]

Dorylaimina Pearse, 1936
Dorylaimoidea de Man, 1876
Thorniidae De Coninck, 1965
Nygolaimoides [5], Thornia [11], Thorniosa [1], Loofilaimus [1], Sphaeroamphis [1], Thorneella [1]
Dorylaimidae de Man, 1876
Amphidorylaimus [3], Kunjudorylaimus [2], Prodorylaimus [20], Prodorylaimium [6], Protodorylaimus [2], Dorylaimus [29], Halodorylaimus [2], Idiodorylaimus [7], Ischiodorylaimus [11], Laimydorus [43], Baladorylaimus [1], Calcaridorylaimus [5], Calodorylaimus [11], Chrysodorus [5], Crocodorylaimus [10], Fuscheila [2], Kittydorylaimus [1], Mesodorylaimus [145], Miodorylaimus [2], Namaquanema [1], Afrodorylaimus [6], Apodorylaimus [2], Drepanodorylaimus [13], Paradorylaimus [7]
Thornenematidae Siddiqi, 1969

Coomansinema [5], Indodorylaimus [4], Lagenonema [6], Opisthodorylaimus [11], Prothornenema [1], Sicaguttur [3], Thornenema [25], Anadorella [1], Paratimminema [2], Sclerolabia [5], Willinema [7]

Actinolaimidae Thorne, 1939

Trachactinolaimus [3], Trachypleurosum [6], Actinolaimus [6], Afractinolaimus [4], Egitus [22], Mactinolaimus [10], Metactinolaimus [2], Neoactinolaimus [17], Paractinolaimoides [2], Paractinolaimus [27], Scleroactinolaimus [1], Stopractinca [4], Westindicus [6], Actinca [5], Afractinca [4], Brasilaimus [7], Parastomachoglossa [3], Practinocephalus [3]

Qudsianematidae Jairajpuri, 1965

Discolaimium [30], Discolaimoides [16], Discolaimus [41], Filidiscolaimus [1], Latocephalus [9], Mylodiscoides [1], Mylodiscus [1], Salimella [1], Carcharolaimus [20], Caribenema [5], Caryboca [4], Allodorylaimus [28], Amblydorylaimus [1], Baqriella [1], Boreolaimus [7], Crassogula [1], Crassolabium [34], Dorydorella [3], Epidorylaimus [14], Eudorylaimus [95], Kallidorylaimus [1], Kolodorylaimus [1], Labronema [41], Labronemella [11], Microdorylaimus [17], Scalpellus [1], Skibbenema [1], Talanema [7], Torumanawa [2], Arctidorylaimus [3], Ecumenicus [4]

Aporcelaimidae Heyns, 1963

Akrotonus [1], Aporcelaimellus [57], Aporcelaimus [21], Aporcella [2], Epacrolaimus [2], Makatinus [10], Metaporcelaimus [14], Silvallis [1], Tubixaba [5], Nygolaimium [3], Scapidens [2], Sectonema [24], Aporcedorus [2]

Paraxonchiidae Dhanachand & Jairajpuri, 1981

Gopalus [1], Tendinema [2], Parapalus [1], Paraxonchium [13]

Crateronematidae Siddiqi, 1969

Chrysonema [6], Crateronema [2], Oonaguntus [2], Lordellonema [4], Moshajia [5], Poronemella [4], Sicorinema [3], Sicorinemella [3]

Nordiidae Jairajpuri & Siddiqi, 1964

Inbionema [1], Malekus [2], Oriverutoides [1], Oriverutus [27], Actinolaimoides [10], Acunemella [1], Longidorella [39], Thornedia [3], Californidorus [4], Enchodelus [23], Enchodorus [2], Heterodorus [25], Kochinema [8], Lanzavecchia [2], Lenonchium [6], Pungentella [15], Pungentus [21], Rhyssocolpus [10]

Longidoroidea Thorne, 1935

Longidoridae Thorne, 1935

Australodorus [1], Longidoroides [18], Longidorus [150], Paralongidorus [28], Paraxiphidorus [3], Siddiqia [34], Xiphidorus [9], Xiphinema [248]

Belondiroidea Thorne, 1939

Belondiridae Thorne, 1939

Amphibelondira [1], Axonchoides [1], Belaxellus [1], Belondira [3], Belondirella [2], Bullaenema [1], Helicobelondira [1], Immanigula [1], Porternema [1], Probelondira [1], Anchobelondira

[1], Axonchium [33], Dactyluraxonchium [2], Heynsaxonchium [1], Metaxonchium [19], Nimigula [1], Phallaxonchium [5], Syncheilaxonchium [9], Uniqaxonchium [2]

Swangeriidae Jairajpuri, 1964

Durinemella [1], Oxybelondira [4], Oxydirus [13], Paraoxybelondira [1], Paraoxydirus [6], Qudsiella [1], Swangeria [2], Falcihasta [4], Hulqus [3], Mitoaxonchium [1], Paraqudsiella [1], Lindseyus [4], Roqueus [2]

Dorylaimellidae Jairajpuri, 1964

Axodorylaimellus [6], Dorylaimellus [63], Ibadanus [1], Mesodorylaimellus [4]

Tylencholaimoidea Filipjev, 1934

Leptonchidae Thorne, 1935

Apoleptonchus [1], Bertzuckermania [1], Caveonchus [3], Clavigula [1], Funaria [12], Incanema [1], Leptonchus [11], Loncharionema [2], Meylis [3], Paraleptonchus [1], Proleptonchoides [3], Proleptonchus [6], Sclerolaimus [1], Aculonchus [4], Basirotyleptus [26], Glochidorella [6], Sclerostylus [2], Trichonchium [3], Zetalaimus [3], Gymnotyleptus [3], Scalpenchus [1], Tyleptus [8], Utahnema [3], Kantbhala [5], Xiphinemella [15]

Tylencholaimidae Filipjev, 1934

Capilonchus [2], Chitwoodielloides [3], Chitwoodiellus [5], Chitwoodius [8], Cricodorylaimus [2], Meylonema [2], Pseudotylencholaimus [1], Rostrulium [1], Tylenchodoroides [1], Tylenchodorus [1], Tylencholaimus [52], Mumtazium [1], Promumtazium [7], Tantunema [5], Discomyctus [10], Lawtonema [1], Oxydiroides [3], Wasimellus [1], Curvidorylaimus [2], Metadorylaimus [1], Neometadorylaimus [1], Vanderlindia [2], Pachydorylaimus [7], Heynsnema [3]

Mydonomidae Thorne, 1964

Calolaimus [7], Timmus [1], Dorylaimoides [69], Morasia [5], Mydonomus [4]

Tylencholaimellidae Jairajpuri, 1964

Athernema [1], Agmodorus [4], Doryllium [14], Goferus [1], Oostenbrinkella [3], Phellonema [1], Dorella [4], Margollus [2], Tylencholaimellus [36]

Aulolaimoididae Jairajpuri, 1964

Adenolaimus [6], Aulolaimoides [6], Cladocephalus [1], Oostenbrinkia [2]

Encholaimidae Golden & Murphy, 1967

Encholaimus [2], Helmabia [6], Nemabia [1], Acephalodorylaimus [1], Cephalodorylaimus [1], Echinodorus [1]

Mermithida Hyman, 1951

This group includes a few species (isolaimiids) free-living in soils but the vast majority are obligate animal parasites during their larval stages.

They parasitize a wide variety of soil and freshwater invertebrates, such as crustaceans, insects, spiders, slugs, and snails. The final molt, mating, and oviposition of the nematode occur in the soil or in the aquatic habitat of the host.

Isolaimiina Inglis, 1983
Isolaimiidae Timm 1969
Isolaimium [12]

Mermithina Andrássy, 1974 (no free-living genera)

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