The Natural History of Nematodes

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This book is dedicated to
MY PARENTS

Preface

This book has been written as an introduction to the unique group of animals called *nematodes*. Since most existing nematology texts cover specialized topics that are too detailed for the beginning student, the present work provides an overall view of the natural history of nematodes.

Most nematodes, or *roundworms* as they are popularly called, are microscopic in size and have always had little meaning to the general public. Even in the last century, Cobb, a well-known nematologist who wanted to popularize the study of nematodes, at least among scientists, made the following comments about the worthiness of these animals: "The nematodes, poor beasts, do not furnish hides, horns, tallow, or wool; they are not fit for food, nor do they produce anything fit for food; neither do they sing or amuse us in any way; nor are they ornamental—in fact, when they are displayed in museums the public votes them hideous."

It may be true that the public knows little about nematodes, yet to those of us who study them they all have their own personalities and are fascinating in their own ways. What other animal groups have representatives that can evert their uteri through the genital opening and use this structure to absorb nourishment? Or can carry and introduce a pure culture of bacteria into a living host to supply nutrients for their own reproduction? The male of still another nematode, after fertilizing the female, can produce fertile eggs inside his own body.

The more that is discovered about their seemingly simple lives, the

more incredible and amazing nematodes appear. In this book, I have tried to impart some of this wonderment to the reader, who may then understand how biologists can become fascinated with these so-called simple forms of life.

The book covers classification, morphology, development, techniques, control, natural enemies, vector associations, and life cycles. The nematodes are grouped according to their major food sources, i.e., microbotrophic, plant-parasitic, invertebrate-parasitic, vertebrate-parasitic, and predaceous. Each chapter includes a selected bibliography of general and specific readings; a glossary of terms employed in this book appears at the end.

It is hoped that this balanced account of the nematodes as a whole may stimulate the reader to examine some of the additional cited works dealing with more specific aspects of nematode biology.

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PART ONE

Nematode Biology

Chapter One

The Phylum Nematoda

DEFINITION OF NEMATODES

Just what is a nematode? The more one learns the more difficult it becomes to provide a clear answer because of the exceptions encountered. However, nematodes are generally defined as appendageless, nonsegmented, wormlike invertebrates possessing a body cavity and a complete digestive tract. By complete digestive tract is meant a mouth, an alimentary canal, and an anus. There is no specialized respiratory or circulatory system; however, nematodes possess a well-developed nervous system, an excretory system, and a set of longitudinal muscles.

We can only speculate how many species of nematodes exist today. Over 15,000 nematodes have been described, and it has been estimated that there are at least 500,000 species of these animals in the world.

Nematodes vary considerably in size. One of the smallest is the marine form *Greeffiella minutum,* which is only 82 μm in length. In contrast, *Placentonema gigantissima,* the largest nematode known, lives in the placenta of the sperm whale and reaches over 8 m.

Nematodes occur in a variety of habitats, some of which, such as hot springs, ice, or deep ocean trenches, would appear to be uninhabitable. Most nematodes are marine or live in soil and fresh water. But then there are those that parasitize crops, insects, our livestock, and ourselves. Whether an animal be a flea or an elephant, it certainly will have a nematode parasite.

Most scientists study nematodes because of the undesirable effects they produce on plants and animals. It has been estimated that in 1967 nematodes caused a 10 percent reduction of crop yields in the United States and that over 100 million lb of nematicides were used. In 1970 $60 million was spent on treating 1.7 million acres in the United States, and the annual crop loss was estimated at over $1.5 billion. In 1976, it had reached the $4 billion figure.

It is difficult to place a monetary value on the effects of nematode parasites of animals and man. As an example, the nematode responsible for the disease known as "river blindness" or *onchocerciasis* infects some 20 million people in Africa. To find a means of combating this parasite, which is capable of blinding its victim, the World Bank recently granted $150 million for basic and applied research.

However, nematodes do have their desirable sides. Many help to maintain a natural balance in soil and a number parasitize economically important insect pests. Some are being tested and used today as biological control agents. Also, nematodes make good experimental animals for basic investigations in nutrition, physiology, genetics, and aging. Others are being considered as indicators of pollution in our oceans and rivers.

Other groups of "worms" are frequently confused with nematodes (or roundworms). Those include the flatworms (Platyhelminthes), which lack a body cavity. Tapeworm proglottids moving in animal feces may have a superficial resemblance to nematodes but lack most of the characteristics discussed here. The term *eelworm,* coined earlier as a popular name for nematode, still exists today even though there is no connection with eels or "worms" in their present-day sense, i.e., annelids. Earthworms and their relatives are similar in size, shape, and appearance to many nematodes found in the soil; however their segmented bodies clearly set them apart. *Horsehair* worms, or members of the phylum Nematomorpha, are elongate, dark-colored worms found in fresh water. Again, they have a superficial resemblance to nematodes but their spiny-headed larvae are quite different.

To continue with our definition, nematodes possess bilateral symmetry, four main longitudinal hypodermal cords, a trifid pharynx, circumpharyngeal nerve ring, copulatory spicules (with a few exceptions), and one or two tubular gonads opening at the vulva in the female and into the rectum in the male (forming a cloaca). These characteristics must be revised from time to time as our knowledge grows. For example, nematodes had been considered unique in lacking cilia, but several years ago ciliated elements associated with the nervous system were discovered.

The body cavity of nematodes was long thought to be a pseudo-

coelom rather than a true coelom (in which the mesoderm lines both the ectoderm and endoderm). The significance of the pseudocoelomate condition, which did not isolate the gut from influence of the body musculature and was considered to reveal relationships of nematodes with other animal groups, was much discussed. Recently, however, nematologists have felt that the term *pseudocoelom* has no precise meaning. Membranes found associated with the digestive tract and somatic muscles of some nematodes even suggest that the body cavity is a true coelom.

Another condition frequently associated with nematodes is their eutelic development — also known as *cell constancy*. There is still much discussion as to how constant the cells of various organs are throughout the life of a nematode. In its purest form, this condition means that all somatic cells of the adult exist in the newly hatched juvenile, and growth is due to cell enlargement rather than cell multiplication. In actuality, however, most, if not all, nematodes have cell multiplication after hatching, especially in the intestine and hypodermis (and of course the gonads). So this condition should be understood on a relative basis. Perhaps there are fewer cells which divide in nematodes after hatching than in other animals, proportionally speaking.

The above and other characteristics will be discussed further in the sections on structure and life processes and development.

THE PAST AND THE PRESENT

Just when the first nematode was observed is not known; however, the first recorded roundworms were, not surprisingly, human parasites. Passages in the *Papyrus Ebers* (dated around 1550 B.C.) are said to contain a knowledge of the human intestinal parasite *Ascaris lumbricoides* (Figs. 1-1 and 11-5) and the tissue parasite *Dracunculus medinensis* (Fig. 11-6), both large parasites which may exceed a foot in length.

But it was not until much later that our knowledge of vertebrate parasitic nematodes began to accumulate. In 1835, Owen discovered the juveniles of *Trichinella spiralis,* the causal agent of trichinosis, in human muscles (Fig. 11-18). Studies on the development and life history of these parasites began around this time and continued up to the present. Many of the vertebrate parasitic life cycles are exceedingly complex and it took many years to piece them together. It was not until 1865 that a vertebrate nematode was discovered that spent part of its life in an invertebrate. The early workers Leuckart, Metchnikoff, and Fedtschenko made notable contributions in this area, and in 1878

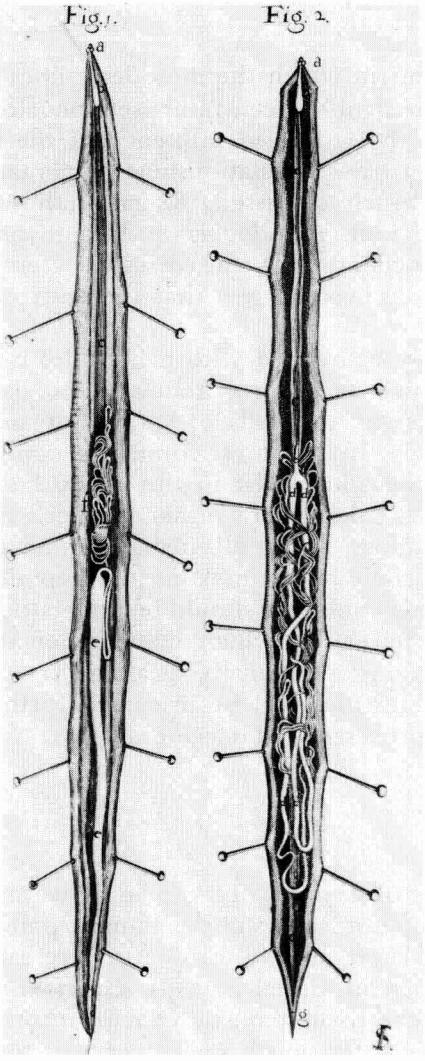

Figure 1-1. From an early study on the anatomy of the human ascarid nematode (*Ascaris lumbricoides*). Dissecting pins expose the body cavities of a male and female parasite. Published by E. Tyson in 1683. (Courtesy of the Bancroft Library, University of California, Berkeley.)

Sir Patrick Manson made the stunning discovery that the nematode causing human filariasis (elephantiasis) is transmitted by a mosquito. Around the turn of the century, Looss discovered that certain nematode parasites could penetrate human skin. Today most of the life cycles of the common vertebrate parasites are known and these and other nematodes are now being scrutinized by chemists, biophysicists, molecular biologists, geneticists, immunologists, nutritionalists, and behaviorists for specialized studies.

The discovery of the first free-living, microbotrophic nematode has been attributed to Borellus in 1656. This nematode was the "vinegar eelworm," *Turbatrix aceti,* which used to be relatively common in

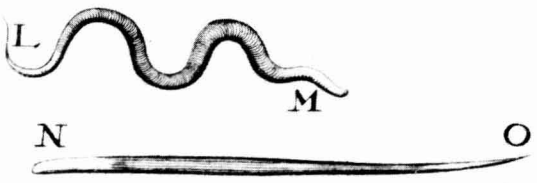

Figure 1-2. Two drawings of the "vinegar eelworm" (*Turbatrix aceti*), a microbotrophic nematode found in vinegar. Published by A. van Leeuwenhoek in 1685. (Courtesy of the Bancroft Library, University of California, Berkeley.)

home-made vinegar, being able to multiply under acidic conditions and feed on microorganisms present during the fermentation process. Because of its common occurrence, it was the object of many early studies (Fig. 1-2). It was discovered later that fruit flies carried the nematodes from one source to another.

The first invertebrate-parasitic nematode was recorded by the French naturalist Réaumur in 1742 during his investigation of bumblebees. While opening the body cavity of a queen to observe egg production, he noted some strange structures that he drew and described, but he had no idea what they were (Fig. 1-3). Much later, it was discovered that they were nematodes, now known as *Sphaerularia bombi,* a widespread parasite of queen bumblebees.

The first plant-parasitic nematode was reported in 1743 by the Englishman Needham, who was examining some dry, diseased wheat kernels. These kernels contained the resistant juveniles of *Anguina tritici,* which Needham described as "fibrous objects in water which after a time came to life" (Fig 1-4).

During this period various workers attempted to classify these relatively new and strange groups of organisms. Nematodes were lumped together with all the other kinds of worms under the kingdom

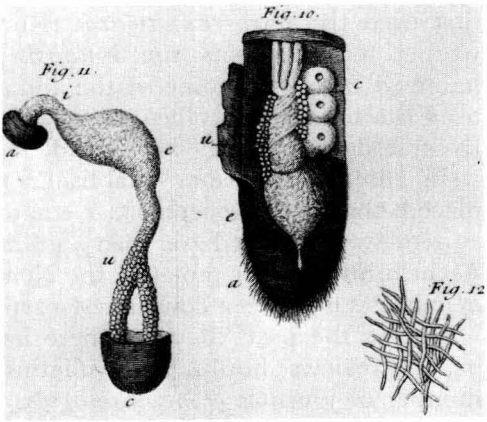

Figure 1-3. Illustrations of the bumblebee parasite *Sphaerularia bombi.* Published by R. A. F. Réamur in 1742. Reamur's Fig. 11 shows the hosts' internal organs covered with juvenile nematodes and the lower forked portion represents the everted uterus of the female parasite. His Fig. 10 shows the everted reproductive sac of the female behind host tissue covered with juvenile nematodes. Figure 12 depicts some of the juvenile nematodes removed from the body cavity of a parasitized bumblebee. (Courtesy of the Bancroft Library, University of California, Berkeley.)

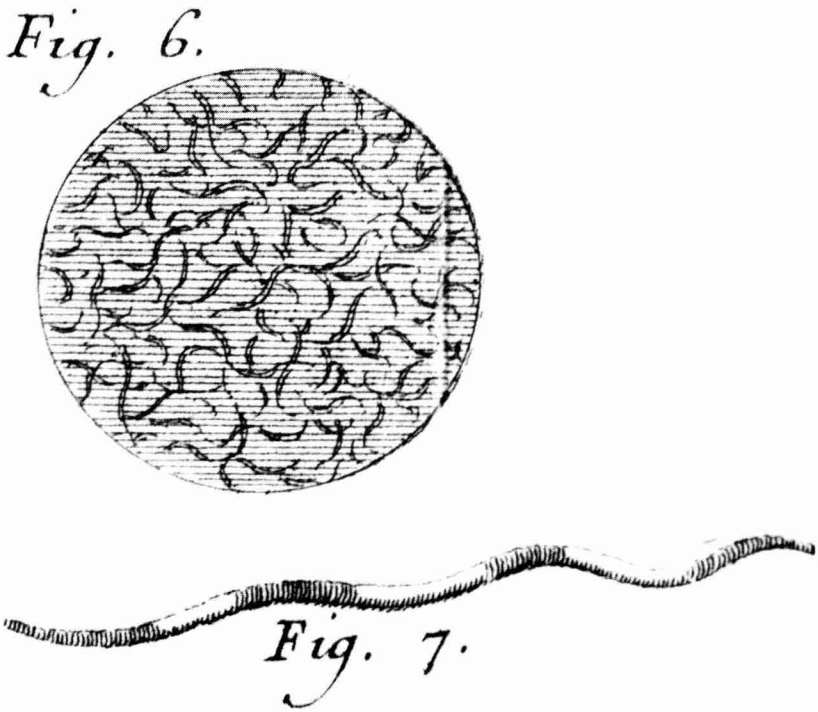

Figure 1-4. Juveniles of the wheat nematode, *Anguina tritici*, observed and published by T. Needham in 1743. His Fig. 6 shows a general view of the nematodes in the field of the microscope lens. One of the resistant juveniles removed from a diseased wheat kernel is illustrated in Needham's Fig. 7. (Courtesy of the Bancroft Library, University of California, Berkeley.)

Vermes by Linnaeus in his *Systema Naturae* (1758). Zeder in 1800 first used the term *roundworm* (Rundwürmer) as a class of parasitic worms. In his *Entozoorum Synopsis* published in 1819, Rudolphi gave latinized names to some of the animal parasitic roundworms and first used the term Nematoidea, from which we derived the name Nematoda (Nematodea) (Greek *nema* 'thread,' *eidos* 'form').

In 1859, Gegenbauer established the Nemathelminthes in which he placed the Acanthocephala, Nematodea, and Gordiacea. This basic system was followed for many years by zoologists although the term Aschelminthes later replaced the Nemathelminthes. More recently, the nematodes have been considered a separate phylum, the Nematoda.

During the past 20 years there has been an explosion of scientific papers, reviews, books, and bulletins on all aspects of nematology. A number of journals – *Nematologica, Journal of Nematology, Revue de*