University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Winter 1-1-2013

Worms, Nematoda

Scott Lyell Gardner
University of Nebraska - Lincoln, slg@unl.edu

Worms, Nematoda

Scott Lyell Gardner

University of Nebraska-Lincoln, Lincoln, NE, USA

Glossary

Anhydrobiosis State of dormancy in various invertebrates due to low humidity or desiccation.

Cuticle Noncellular external layer of the body wall of various invertebrates.

Gubernaculum Sclerotized trough-shaped structure of the dorsal wall of the spicular pouch, near the distal portion of the spicules; functions for reinforcement of the dorsal wall.

Hypodermis Cellular, subcuticular layer that secretes the cuticle of annelids, nematodes, arthropods (see epidermis), and various other invertebrates.

Pseudocoelom Body cavity not lined with a mesodermal epithelium.

Spicule Bladelike, sclerotized male copulatory organs, usually paired, located immediately dorsal to the cloaca.

Stichosome Longitudinal series of cells (stichocytes) that form the posterior esophageal glands in *Trichuris*.

Stoma Mouth or buccal cavity, from the oral opening and usually includes the anterior end of the esophagus (pharynx).

Synlophe In numerous Trichostrongylidae, an enlarged longitudinal or oblique cuticular ridge on the body surface that serves to hold the nematodes in place on the gut wall.

Vermiform Worm shaped with tapering form both posteriorly and anteriorly.

What is a Nematode? Diversity in Morphology

General Characteristics and Synapomorphies

Despite numerous assertions that appear in the literature stating that nematodes are morphologically conservative, the contrary is actually true: Species of the phylum Nemata are extremely variable in their morphological

characteristics. Because of this diversity, almost any broad statement regarding their anatomy probably should be tempered or qualified. Nevertheless, in general, nematodes are nonsegmented worms that generally lack external appendages. Most are vermiform, with tapering anterior (**Figure 1**(a)) and posterior ends (Figure 1(b)), cylindrical in cross section, and covered with a usually translucent (Figure 1(c)), flexible acellular cuticle secreted by an underlying cellular hypodermis. The cuticle may be smooth (**Figure 2**) or ornamented with rings (**Figure 3**(a–c)), longitudinal striations, spines (Figure 3(b)), or spikes or it may have well-developed wing-like structures called lateral alae very commonly on the externo-lateral surfaces (**Figure 4**). Some marine species have long setae (genus *Draconema* **Figures 5**(a), (b), and 6), which are modified sensory papillae that are probably used in movement and in detecting their environment. In contrast to all other nematodes some marine species have eye-spots that enable them to detect light in their environment (e.g., genus *Thoracostoma* **Figure 7**).

The fine-structure of the external body-cuticle is complex, acting to protect the animal from the external environment allowing it to remain homeostatic inside. The cuticle can be extremely resistant, and depending on the nematode species and its life-history attributes, for example, the cuticle of the nematode may be able to resist digestion in the most inhospitable stomachs in the vertebrate world. Whereas, nematodes may be extremely delicate, able to exist intact only within the osmotically balanced tissues of other animals (e.g., members of the Order (O) Filaroidea) and if moved from the isosmotic solution to one with fewer salts, they may explode and die in a most amazing display.

Figure 1 (a) Anterior end of *Didelphoxyuris*, the pinworm of South American Marsupials, showing the small anterior stoma at the narrow end, followed by the well-developed muscular esophagus with a large posterior bulb. The esophagus is tripartite and serves as a muscular pumping organ, pumping food into the intestine. **(b)** Whole drawing of a predatory nematode of the genus *Mononchus* showing the general structures of a nematode including the tapering anterior and posterior ends and the ventral vulval opening just posterior to midbody. The stoma is heavily cuticularized and bears a spike or spine that is used to puncture the cuticle of the prey. (c) Confocal microscopic image of the exophageal bulb and posterior part of the esophagus of a species of *Pratylenchus*. The cuticle can be seen as the outer light outline of the nematode with an underlying brighter layer showing the cellular hypodermis. The bulb shaped posterior part of the esophagus attaches via a valve to the single cell thick tubular-intestine, shown here as an optical section just posterior to the esophageal bulb.

(a)

(b)

(c)

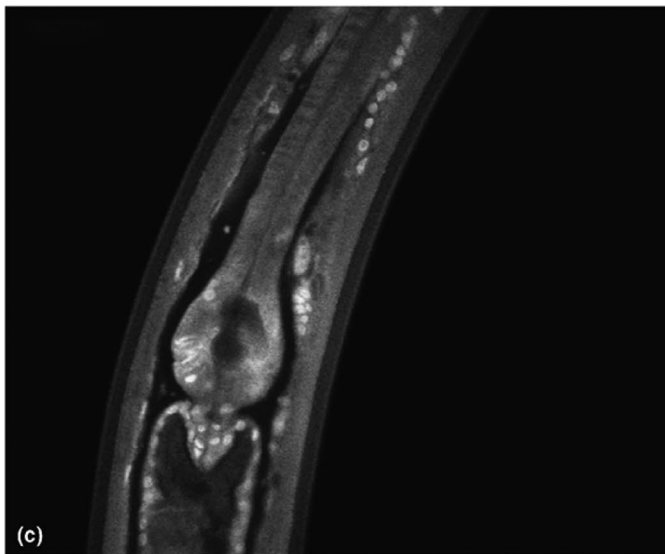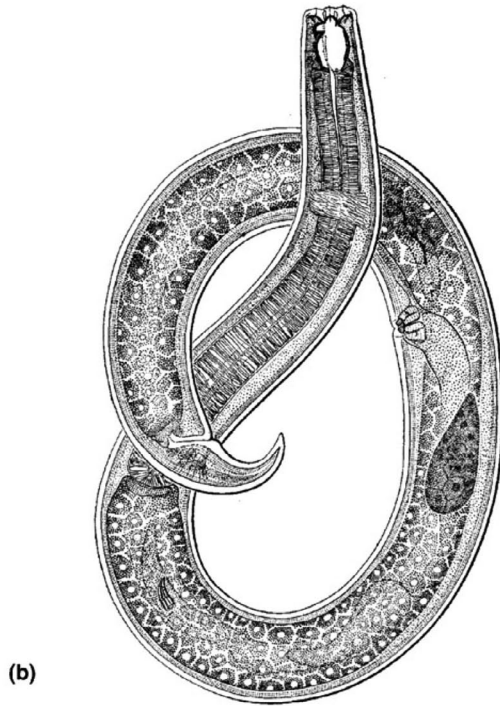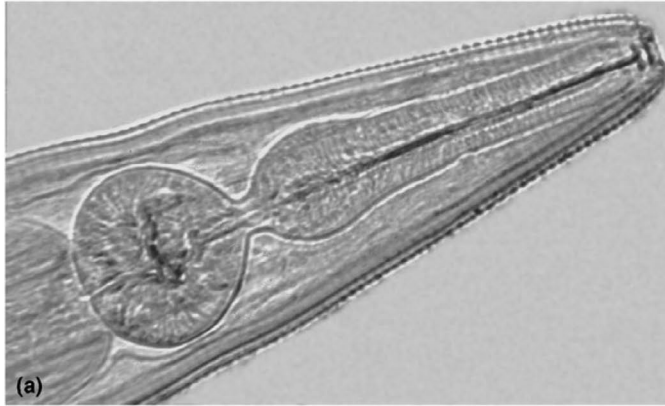**Figure 2** Posterior end (tail) of a male *Paraspidodera* showing the relatively smooth cuticle, a sucker just anterior to the opening of the cloaca, and one spicule protruding from the cloaca.
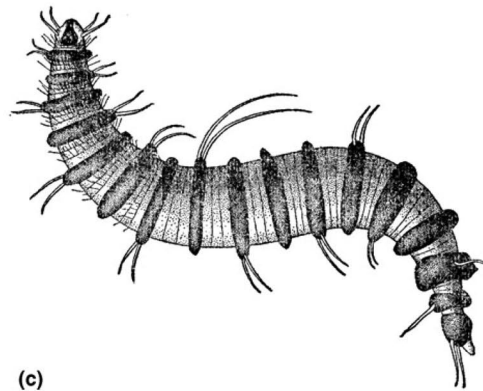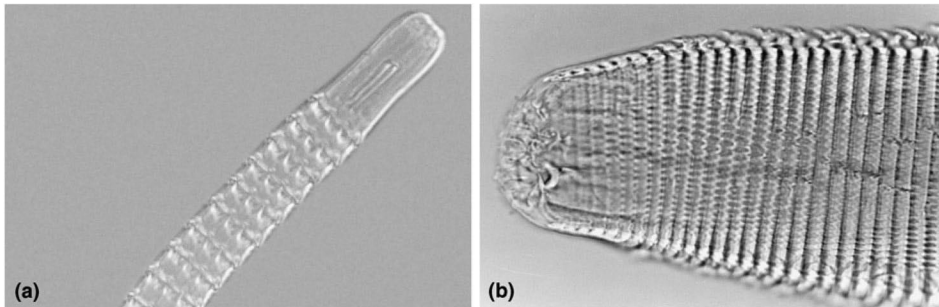
Figure 3 (a, b, c) Anterior ends of marine nematodes showing rings and spines on the cuticle. **(c)** Whole drawing of a marine nematode of the genus *Desmoscolex* showing heavily cuticularized rings and long setae.
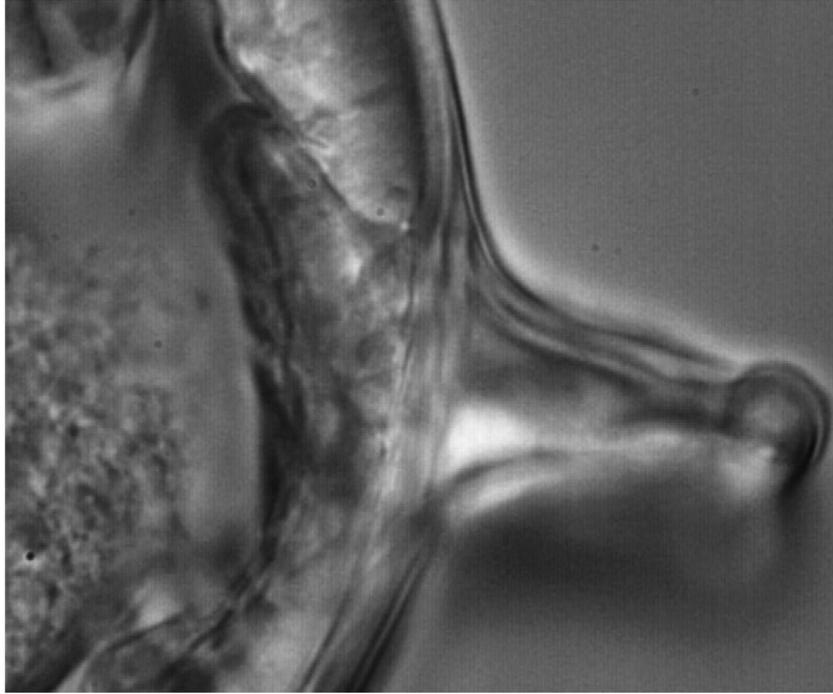
Figure 4 Lateral alae of *Aspidodera*, a parasite of South American xenarthrans, marsupials, and rodents. The ala or wing runs the length of the body possibly providing support for the nematode in the gut of its host. The cellular hypodermis of the nematode can be seen just inside the translucent cuticular layer.
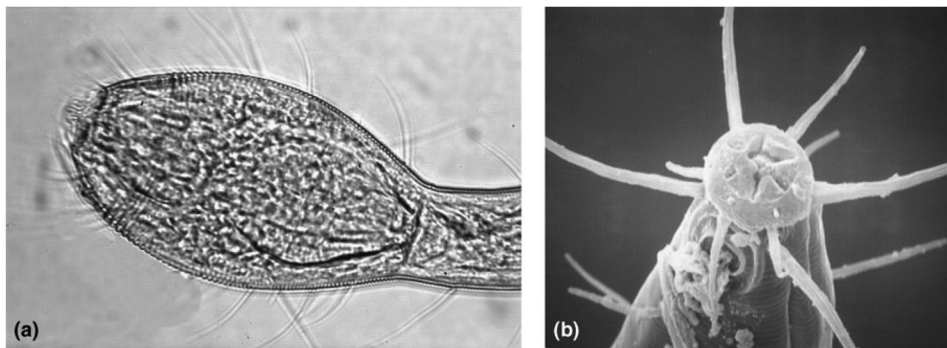
Figure 5 (a, b) The expanded head with visible cuticularized stoma of a species of *Draconema*, a marine nematode. Long setae that are probably used to move and to sense the environment are visible in this photograph. **(b)** Scanning electron micrograph of the anterior end of a marine nematode showing the long setae and a well-developed amphid just ventral and posterior to the lip rings.
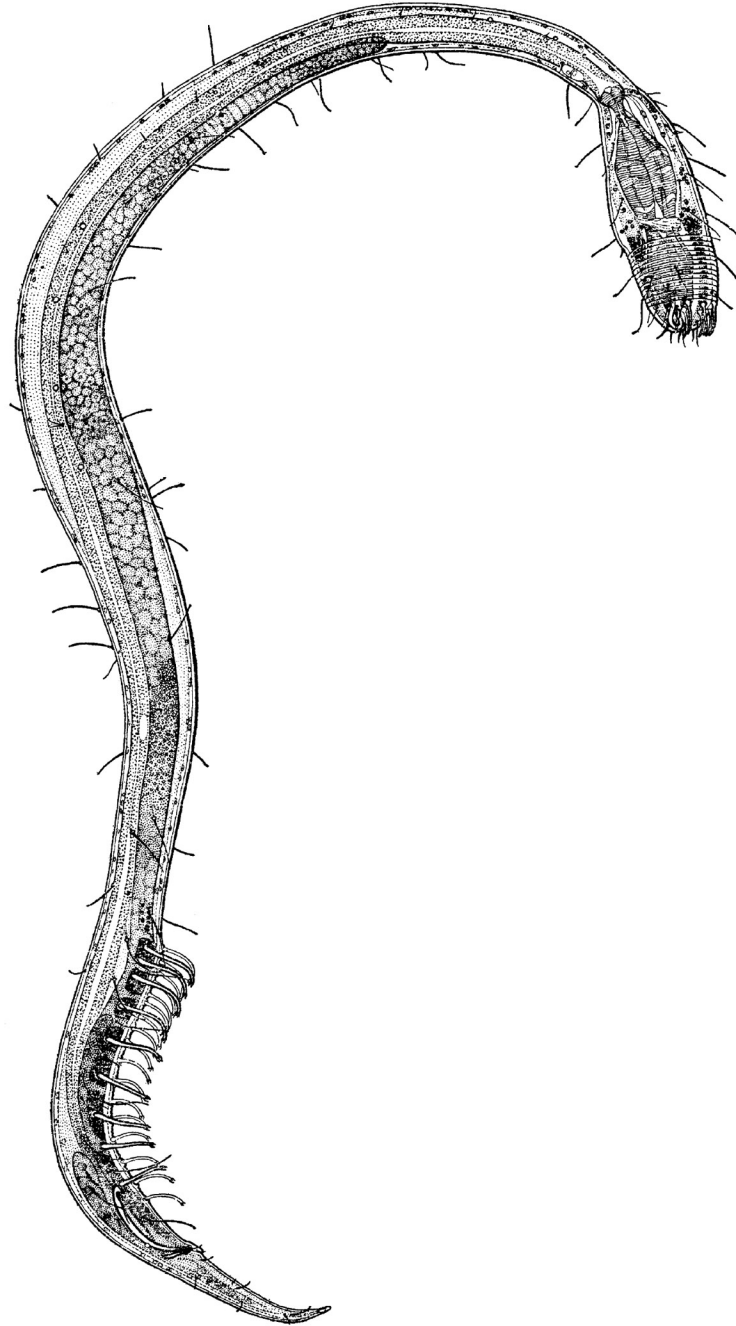
Figure 6 A whole drawing of a male of *Draconema* sp. illustrating the large setae, spicules, testis, and large expanded stoma and head.

Figure 7 Cuticularized "eye-spots" in the marine nematode *Thoracostoma*. Located at about the mid-part of the esophagus, this nematode can detect light in its environment.

Nematodes are called "pseudocelomates" because in most forms, their celom is not completely lined with mesodermally derived cells and they are triploblastic. Possessing no circular body muscles, movement is accomplished by contraction and relaxation of longitudinal muscles in apposition to a hydrostatic skeleton. The body wall, is flexible and very strong. All nematodes maintain their form because their body fluids (in the hydrocoel) are under a positive pressure, relative to their environment, analogous to the way a water balloon maintains its shape. The cross-section in **Figure 8** shows *Vexillata* (a nematode that occurs in rodents of the superfamily Geomyoidea, and recently discovered in other rodents) the round shape of the body under the cuticle supports spines or aretes (the whole structure being called the synlophe). Nematodes have a complete digestive system with an anterior stoma just behind the mouth and usually a tri-radiate or triple muscle-pumping type of esophagus (Figure 1(a) and (c)) that can be muscular or glandular in structure (or both as occurs in certain species of the Filaroidea). The intestine, tubular in form, (Figure 1(c)) is usually a single cell in thickness and is lined on the peritoneal side with a thin collagen-like material and, internally, the cells are lined with microvilli to increase the absorptive surface area of the tubular intestine (Grasse´, 1965; Maggenti, 1981; 1991a). The tubular intestine extends from the posterior of the esophagus straight to the anus or cloaca, sometimes showing out-pouched cecae (blind sacs) or diverticulae near the esophageal–intestinal junction **Figure 9**.
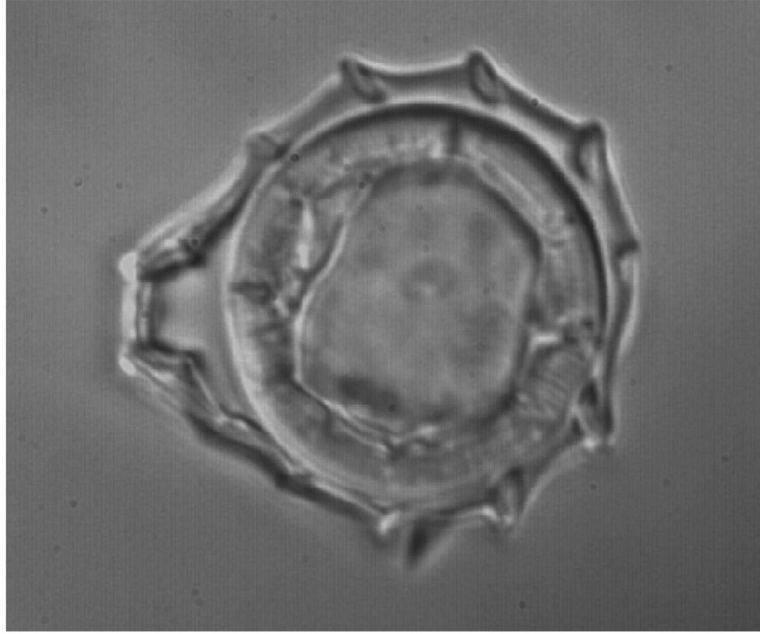
Figure 8 Cross section at midbody of *Vexillata armandae*, a species of nematode parasitic in rodents of the genus *Perognathus* in New Mexico, USA. This photograph shows the spines (aretes) in the cuticle, called the synlophe in Trichostrongyloidea. Inside is the hypodermis lining the body of the nematode. The reproductive tract and the intestine are not visible in this photograph.
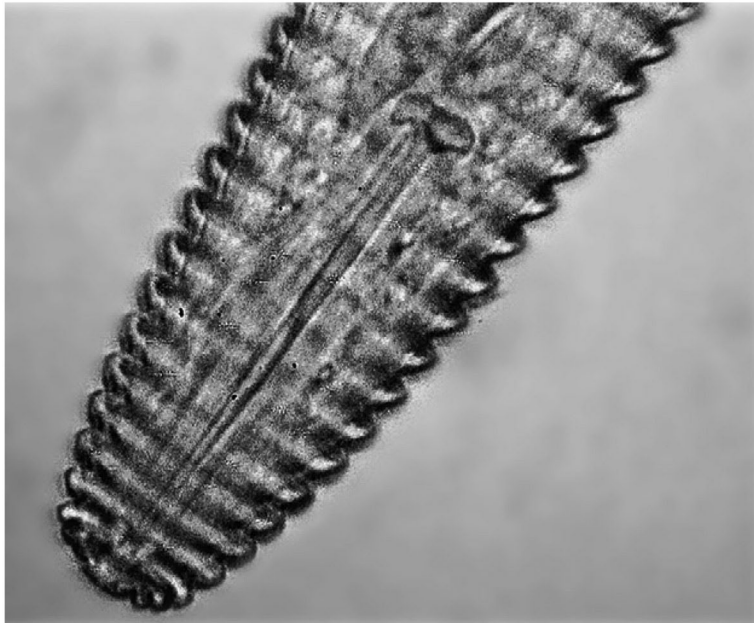
Figure 9 Anterior end of a species of *Criconemoides*, an external root feeding plant parasite. The rings of the cuticle can be seen from the head end posteriad, and the strong cuticularized stomatal spear is clearly visible in this photograph.

Most nematodes are sexually dimorphic with separate sexes (diecious or amphigonus) and oviparous; however, some are ovoviparous and some are viviparous. Males usually have a cuticularized spicule or pair of spicules that are used to assist in the transfer of sperm to the females. Many species also have a gubernaculum (seen extended from the cloaca of a species of *Ansiruptodera* in Figure 23) that guides the spicule during copulation and also eversion of the spicules. Some species are hermaphrodytic and in these cases the nematode produces both sperm and ova from the ovotestis of the same individual at different times during ontogeny (Maggenti, 1991a; Malakhov, 1994).

A synapomorphy of the Nemata is the presence of noncontractile axonlike myoneural processes or extensions that run from the contractile or body portion of muscle cells to the neural junctions of the nerve cords.

Their width is usually less than 2 mm, even when extremely long. However even here there are exceptions, with the giant kidney worm, *Dioctophyma renale* occurring in mustelids and canids sometimes attaining a size of greater than 15 mm by 1000 mm. The eggs of nematodes are also very similar in size with most ranging from 50–100 mm long by 20–50 mm wide with the exception being those of the Antarctic marine nematode *Deontostoma timmerchioi* (40 mm in length of body) that has eggs that range from 870–1100 mm long by 240–350 mm wide (huge by nematode standards).

As mentioned above, nematodes are extremely diverse in size, shape, and structure. The following will only briefly touch on the expansive subject of nematode morphological diversity; for additional reading and exploration see the essential works and references therein of Maggenti (1981); and Grassé (1965 a and b).

External Covering – The Cuticle

An example of diversity in shape is that of the complex cuticular aretes found in species of the O. Strongylida: Trichostrongyloidea (parasitic in vertebrates) in which the exocuticle is modified into a series of cuticular aretes called the synlophe **Figure 12**. In these forms, it is thought that the ridges running down the length of the body of the nematode are used in maintaining their position in the intestine of their hosts (Figure 8). Other forms have an exocuticle composed of serrated ridges (**Figures** 3(a), (b), **10**, and **11**), bumps, or may be very smooth (Figure 2). Some groups (Heterakoidea – parasitic commonly in birds and mammals) possess large cuticularized suckers just anteriad to the cloaca that are surrounded by sensory papillae that evidently allow the male to find the female in the intestinal tract of the host as in *Paraspidodera* of rodents (Figures 2 and **13**) and *Ansiruptodera* from rodents (Figure 23). Marine nematodes of the genus *Draconema* (Figures 5(a)
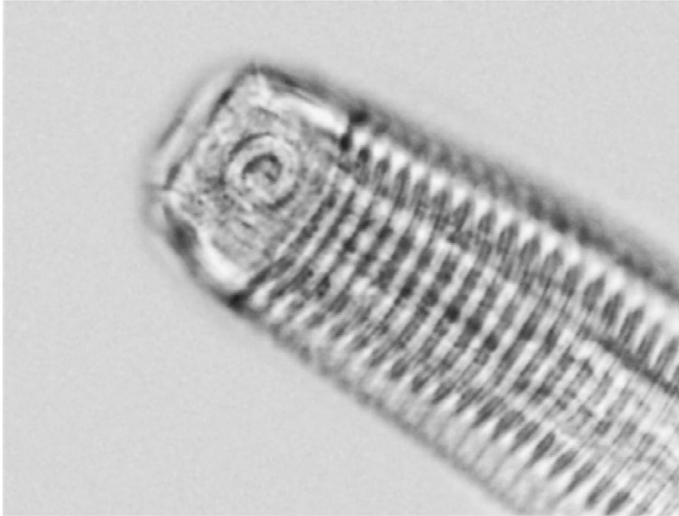
Figure 10 Anterior end of a marine nematode of the genus *Desmodera* showing the rings of the cuticle and a well-developed circular amphid.
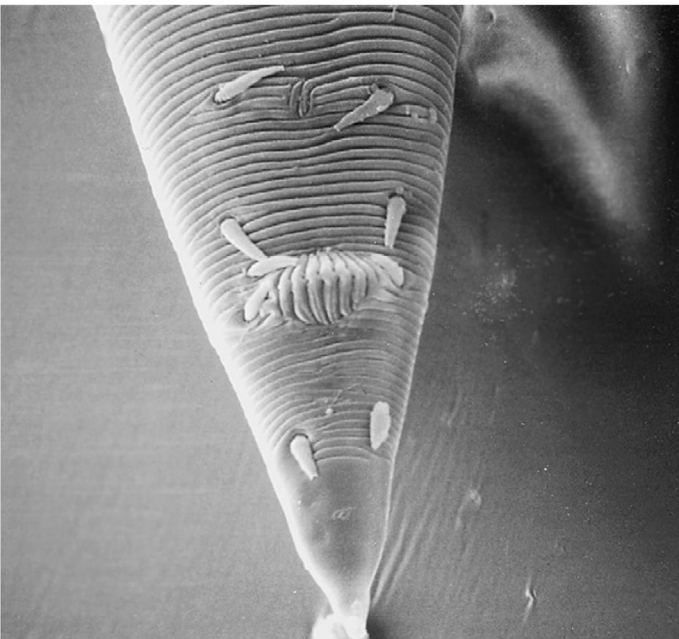
Figure 11 Scanning electron micrograph of the posterior end of a male marine nematode showing rings of the cuticle and small papillae lateral to the cloaca.
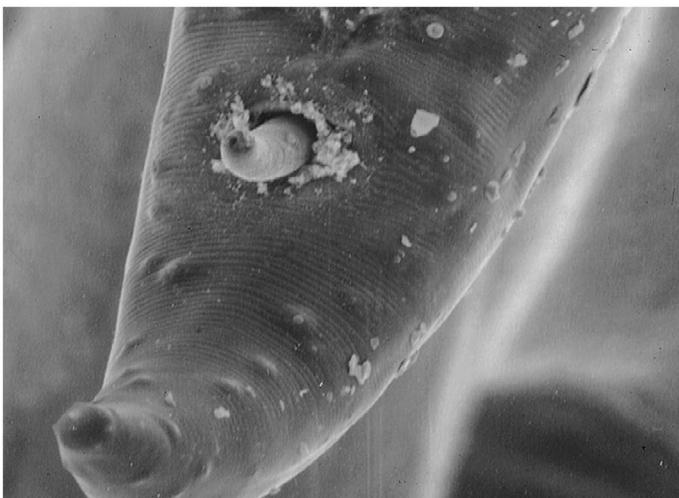
Figure 12 Scanning electron micrograph showing the posterior end of a species of *Paraspidodera* (a parasite of the cecum of rodents of the genus *Ctenomys* in Bolivia) with a spicule everted.

Figure 13 Close up scanning electron micrograph of the sucker and cloacal opening of a species of *Paraspidodera* (a parasite of the cecum of rodents of the genus *Ctenomys* in Bolivia). Numerous sensory papillae can be seen on the cuticle around the cloaca.

and 6) and *Desmoscolex* (3c) have a wildly modified cuticle relative to most nematodes and very large hair-like and segmented cuticular setae that the nematodes use for both movement and detecting its environment (Figures 5(a) and 6). One curious structure that occurs in all Nemata is the amphid, a highly variable sensory organ that can be very obvious as in *Desmodera* (**Figure 10**) or very inconspicuous as in *Chambersiella* (Figure 18).

The Alimentary Canal

The mouth of the nematode (**Figure 14**(a)) provides the anterior opening to the external environment, which connects to the stoma leading posteriad to the muscular esophagus (**Figures 15–18**). The stoma may be quite reduced or absent as in the case of members of the Trichostrongyloidea (O. Strongylida) or they may be well developed such as that found in *Clarkus* (**Figure 16**) and *Mononchus* (Figure 1(b)) and capable of inflicting damage on prey items or it may be modified into horny toothlike structures that are used to attach to the intestinal villi of the host animal (e.g., *Ancylostoma* **Figure 19**). In mammalian gut parasites of the genus *Trichuris* (Adenophorea: Trichuridae) the stoma is lacking and the esophagus is formed of stichocytes comprising a stichosome, which is glandular in function, but many other plant-parasites such as the Adenophorean ectoparasitic, below ground rootfeeders (capable of transmitting viruses between and among plants *Xiphinema, Longidorus*, or *Dorylaimus:* O. Dorylamida: Longidoridae) have a tubular stoma with the posterior parts of the stoma modified into
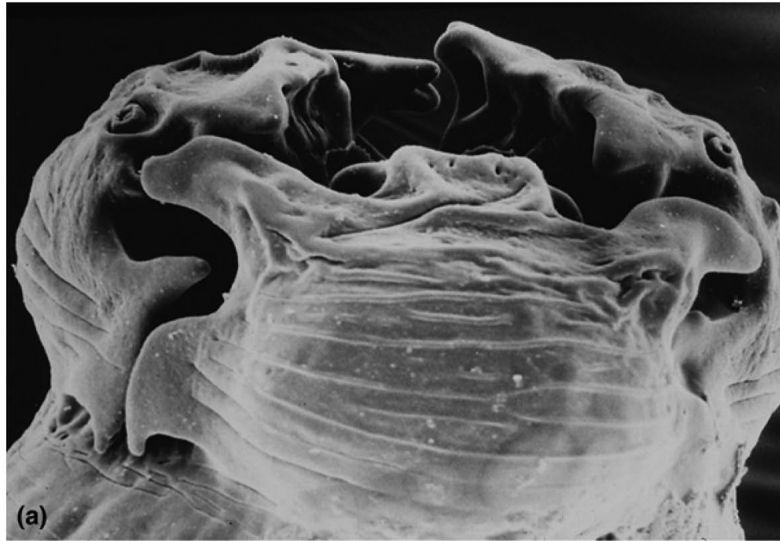
Figure 14 (a) Anterior end of a species of *Paraspidodera* (a parasite of the cecum of rodents of the genus *Ctenomys* in Bolivia) showing three huge lips, the stomatal opening in the middle of the lips and large anteriorly directed sensory papillae on lips 2 and 3 near the outer part of the photograph. **(b)** Head-on-view of a predaceous nematode as might be seen from the perspective of a mild mannered bacterial feeding form such as *Caenorhabditis* just before it is devoured.

Figure 15 Anterior end of a species of *Ansiruptodera* from a rodent from Bolivia showing the anterior end of the muscular esophagus attaching to the partially muscular and cuticularized stoma.
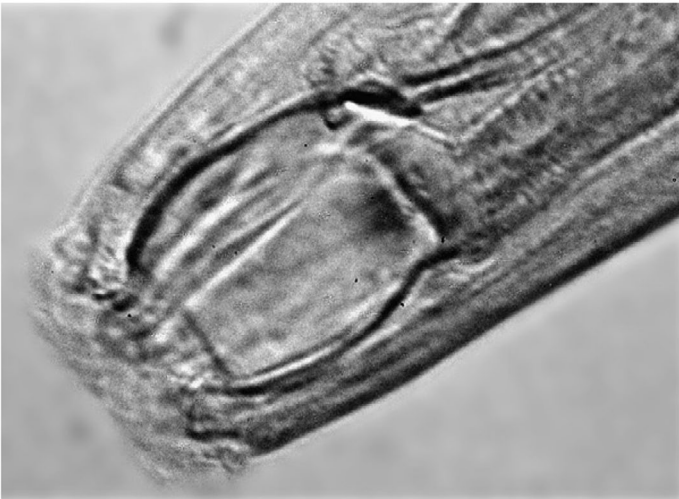
Figure 16 Heavily cuticularized stoma of a predaceous nematode of the genus *Clarkus*. This species
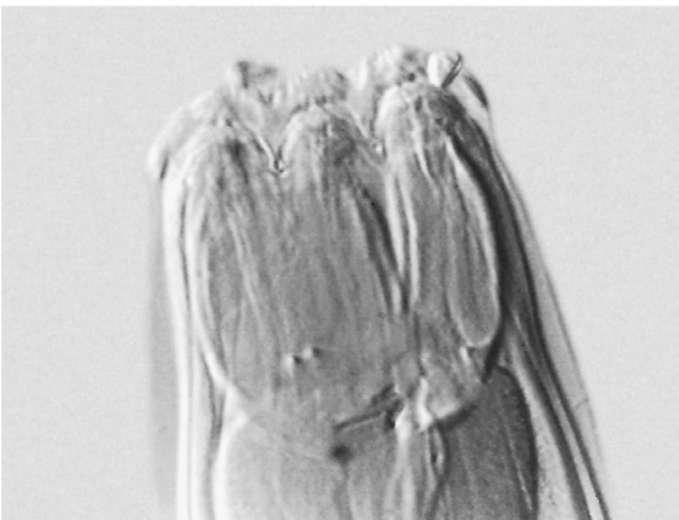
Figure 17 Anterior end of *Miconchus* sp. showing well-developed lips with sensory neurons running posteriad from the anteriorly directed sensory papillae on each lip.
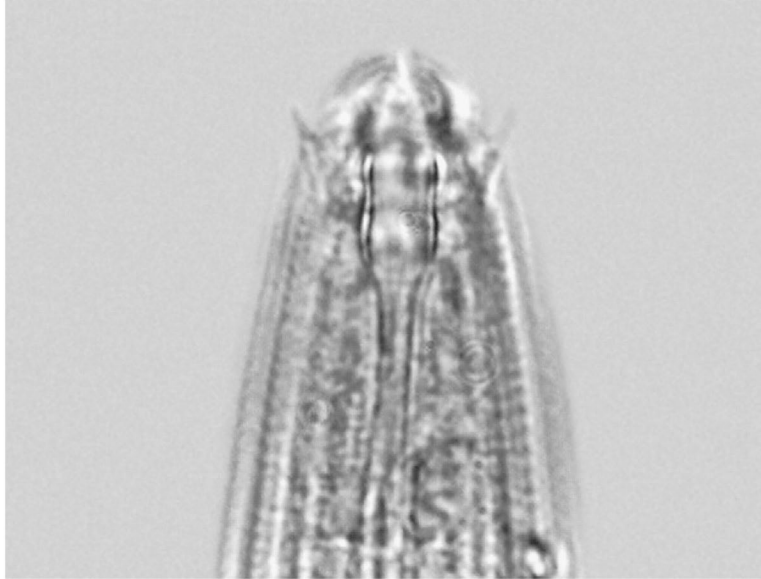
Figure 18 Delicate but well cuticularized stoma of *Chambersiella*.
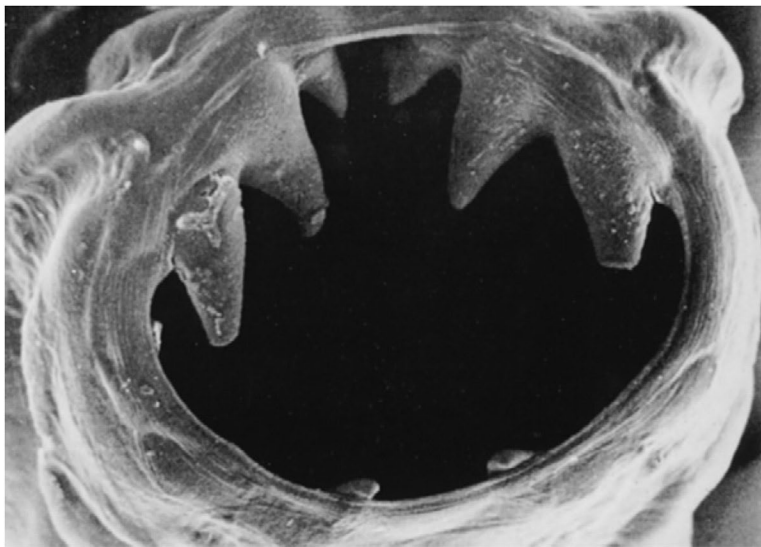
Figure 19 Scanning Electron Micrograph looking into the mouth of a species of mammalian parasite of the genus *Ancylostoma*. The teeth are used to attach to the villi of the host mammal.

a spear that is used to penetrate plant cell-walls as in *Dorylaimus stagnalis* (**Figure 20**). The Secernentean plant endoparasitic nematode of the genus *Pratylenchus* (**Figure 21**(a)) also has a modified stomatal spear (much more delicate than those found in *Dorylaimus* sp.) with which it penetrates plant cells as the nematode moves through the tissues and cells of the plant (usually below ground).
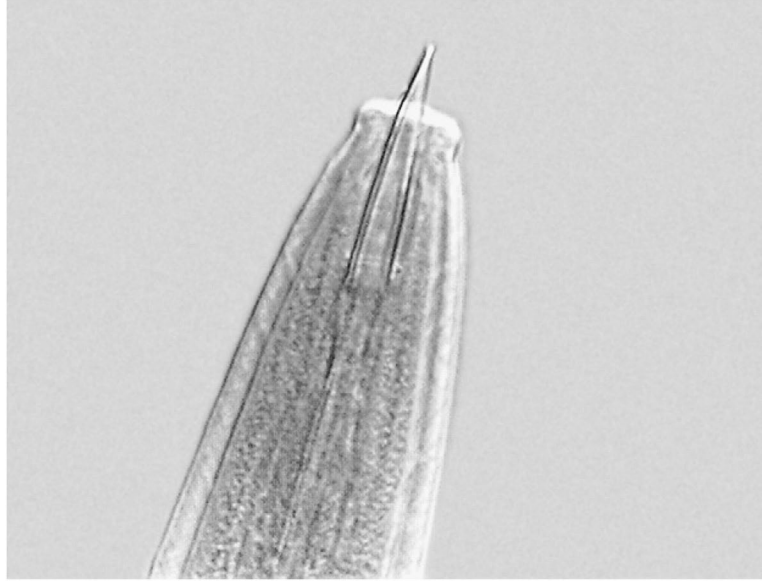
Figure 20 Anterior end of *Dorylaimus stagnalis*, a plant root ectoparasite showing the well-developed stomatal spear that is used to penetrate plant root cells.

The Reproductive System

The reproductive system of most animal parasitic nematodes is adapted to produce extremely large numbers of eggs (e.g., *Ascaris*). Some characteristics of larger animal parasitic nematodes include very large body, two large ovaries, and an equally large uterus. Free-living nematodes generally have much smaller bodies, and are therefore individually less prolific. However, the reproductive systems of most nematodes have the following basic structural similarities: Most females have two ovaries, one anterior (as in *Pratylenchus* Figure 21(b)) and one posterior, each connected to an oviduct and uterus with the uteri connecting to the vagina, terminating in the vulva. Males usually have one testes as in the Secernentea or two as in the Adenophorea, a seminal vesicle and a vas deferens (Maggenti, 1991a) connecting to the outside via the cloaca (Figure 13), which is a joining of the reproductive system and the rectum. Secondary sexual organs in male nematodes are usually much more pronounced and variable than that of the female (**Figures** 2, 6, 11, 12, 13, **22, 23, 24**, and **25**) and most males have one or two spicules (Figure 22), a spicular pouch, sometimes with a spicular sheath (Figure 24), and a gubernaculum. (Figure 23). Some males of the O. Strongylida have a well-developed copulatory bursa (Figure 22).
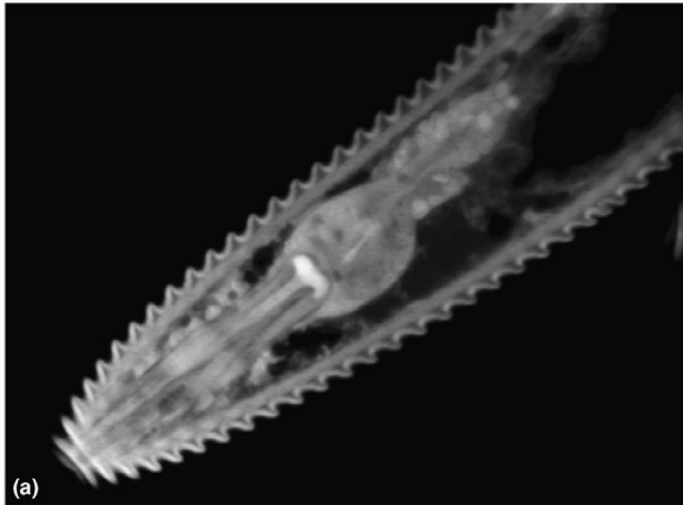
Figure 21 (a) Confocal image of *Pratylenchus* sp. showing the well-developed spear which the nematode uses to penetrate plant cells while moving through the roots of the plant. The muscles and glandular part of the esophagus are also visible. **(b**) Confocal image of *Pratylenchus* showing the anteriorly directed ovary with individual ovocytes and their nuclei visible.
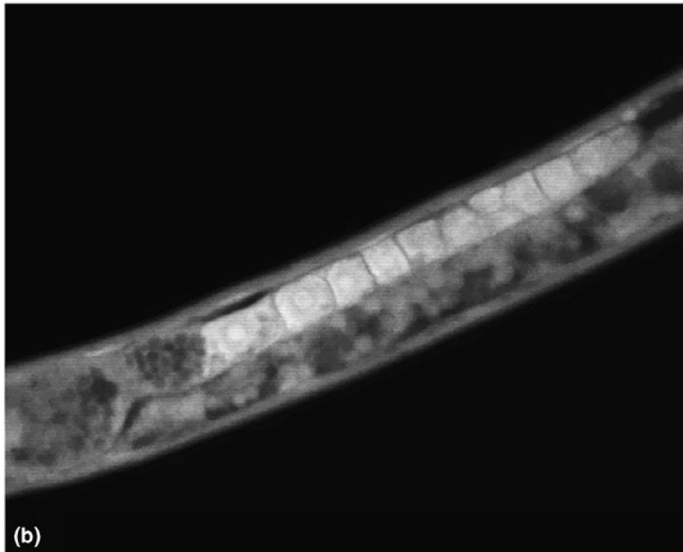
Figure 22 Posterior end of a male trichostrongyloidea showing the well-developed copulatory bursa, bursal rays, and the long thin paired spicules.
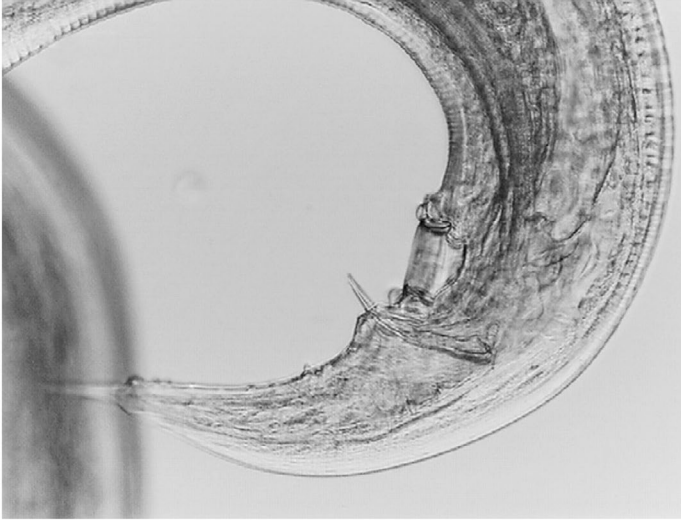
Figure 23 Posterior end of *Ansiruptodera* from a rodent of the genus *Oxymycterus* from Bolivia. The gubernaculum can be seen protruding from the cloaca of this specimen. The cuticularized sucker is also easily visible surrounded by sensory papillae.
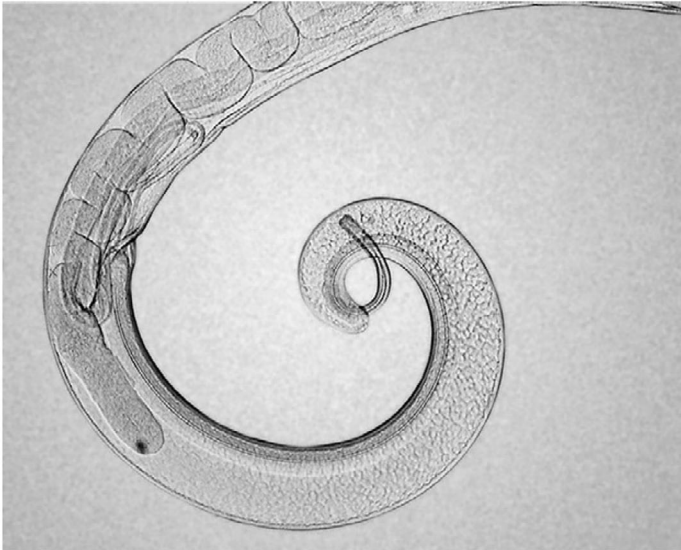
Figure 24 Posterior end of *Trichuris* from a Bolivian species of *Ctenomys*. The long spicule and everted spicular sheath can be seen.

Figure 25 Posterior end of the filaroid nematode *Litomosoides* from *Ctenomys opimus* from high-altitude western Bolivia. Note the dimorphic nature of the spucules in this species one being long and filamentous the other being short and stubby.

Some plant-parasitic nemas produce eggs directly into the plant where the nematode lives (in the case of species of the genus *Pratylenchus,* the female produces eggs that hatch within the tissues of the plant and the juveniles begin feeding), whereas in others such as *Heterodera* (which are ectoparasites) the body of the female fills with eggs, forming a sac that eventually dries and transforms into a resistant cyst with the juveniles within capable of resisting environmental extremes.

The Ubiquitous Nature of Nematodes

There are few habitats on earth unoccupied by nematodes. Over a century of both biological surveys and informal collecting has led many biologists to believe that the Phylum Nemata is probably the most ubiquitous of all animal groups. Early in the history of scientifically based biological investigations, pioneers of microscopy opened a new window into the previously unseen microscopic world of the soils.

Descriptions of the "invisible" life seen by pioneers of microscopy such as Antony van Leeuwenhoek evoked images of a wonderfully diverse and dynamic community of worms and other organisms. Subsequent investigations by other early researchers began to open up the unseen world of the nematodes.

Early Views of Nematode Diversity – The Human Perspective

Humans have been parasitized by nematodes from the earliest times. Eggs of the pinworm *Enterobius vermicularis* and the whipworm *Trichuris trichuria* occur in coprolites dated to about 7000 years old (y.o.) from dry areas of Peru and eggs of the hookworm *Ancylostoma duodenale* have been reported from coprolites dated to around 7230 y.o. in eastern Brazil (Arujo *et al.*, 2008). *Ascaris lumbricoides* has been positively identified from human coprolites dated to about 28,000 y.o. from caves in France, but this is the only occurrence of a record this old. The seeming dearth of other nematodes from human remains older than about 7000 years appears to be due to the fact that organic material comprising the coprolites themselves do not preserve well enough to last that long (Karl J. Reinhard, personal communication).

In what is thought to be the oldest surviving written account of *Ascaris* in humans (dated to approximately 4700 y.o. (in China)), foods to avoid and a description of the symptoms of humans infected with these worms were accurately given (Maggenti, 1981). In the area of the Nile River Valley, early Egyptian physicians recorded the presence of both *Ascaris* and *Dracunculus* (the "Guinea Worm") in an ancient papyrus manuscript (written

by Egyptian physicians around 3552–3550 y.o.) which was obtained and translated by the Egyptologist "Ebers" in 1872 (Chitwood and Chitwood 1977; Maggenti, 1981). In the extant literature, the first mention of a nematode from a nonhuman animal was by Hippocrates about 2430 years ago where he described the occurrences of pinworm nematodes of both horses and human females. From that time, little further was discovered until Albertus Magnus and Demetrios Pepagomenos (in the thirteenth century, Rausch, 1983) recorded nematodes from falcons (also see Chitwood and Chitwood, 1977).

With the development of the microscope and the emergence of Europe from the dark-ages, knowledge of nematodes as parasites of plants and animals and of free-living forms expanded rapidly. It was found that nematodes occurred everywhere people looked, in fact, Anton van Leeuwenhoek first recording the presence of vinegar eels "*Anguillula aceti*" in his vinegar stored for personal use in a letter dated 21 April 1676 although he was not aware that others had reported finding nematodes some time earlier (Dobel, 1932).

Recent estimates of infections of humans with common human parasitic nematodes give the following numbers (Crompton, 1999): Of a total human population size of about 6 billion individuals (in the year 2000) the strongylid hookworms, Ancylostoma duodenale and Necator americanus infect about 1,298,000,000 (22%) and the large intestinal nematode, Ascaris lumbricoides occurs in about 1,472,000,000 (25%) people at any one time in the world. Obviously, many people harbor more than one species of nematode at a time, and it is common for people to sport Ascaris, Necator, Trichuris, and Enterobius simultaneously. The author provides the following estimate to indicate just how important these organisms are in the web of life on earth. To put the number of infections of just humans in perspective, the author made the following extrapolations: An adult female Ascaris produces 200,000 eggs per day at an average rate of about 5grams of eggs per year. Actual data for Ascaris in humans that are infected show an average of 18 worms per infected person. Given that ½ of these are females, the author calculated that nine worms per person will produce about 45 grams of eggs in the feces of the host per year. In one year the total population of Ascaris in humans worldwide is conservatively estimated to produce 66,240,000 kg or 66,240 metric tons (72,864 tons (English)) of eggs; this is equal in weight to about 348 large adult blue whales, 8,832 adult male elephants, or 364 fully loaded railroad coal cars.

Estimates of the number of human infections in the year 2000 by other species of parasitic nematodes are shown in **Table 1**. At the present time, approximately 138 species of nematodes have been reported from humans (Crompton, 1999) with 32–36 being host specific.

Table 1. Numbers of common nematode infections in humans worldwide

Species of Nematode	Numbers Infected	Distribution
Ancylostoma duodenale and *Necator americanus*	1,298,000,000	World-wide
Ascaris lumbricoides	1,472,000,000	World-wide
Brugia maylayi and *B. timori*	13,000,000	South Pacific, SE. Asia, India
Dracunculus medinensis	80,000	Sub-Saharan Africa and Yemen
Loa loa	13,000,000	West and Central Sub-Saharan Africa and Yemen
Onchocerca volvulus	17,660,000	Central and South America and Sub-Saharan Africa
Strongyloides stercoralis	70,000,000	Temperate regions
Trichuris trichiura	1,049,000,000	World-wide
Enterobius vermicularis	400,000,000	Temperate regions

Source: Data from Crompton DWT (1999) How much human helminthiasis is there in the world? Journal of Parasitology 85: 397–403.

The Science of Nematode Diversity

Nathan A. Cobb, one of the first scientists in North America to advance nematology, was a student of the renowned German zoologist, Ernst Haeckel. After just a few years of research spanning the globe from Europe, Australia, and North America, Cobb amassed a huge amount of knowledge and came to have a deep appreciation of the immense number of species that existed. With scientific knowledge based on keen observational skills, he understood the nature of both the great numerical density and species diversity of nematodes in all habitats of the globe that he examined. Thus armed, he wrote the following:

> "In short, if all the matter in the universe except the nematodes were swept away, our world would still be dimly recognizable, and if, as disembodied spirits, we could then investigate it, we should find its mountains, hills, vales, rivers, lakes, and oceans represented by a film of nematodes. The location of towns would be decipherable, because for every massing of human beings there would be a corresponding massing of certain nematodes. Trees would still stand in ghostly rows representing our streets and highways. The location of the various plants and animals would still be decipherable, and, had we sufficient knowledge, in many cases even their species could be determined by an examination of their erstwhile nematode parasites.

> *We must therefore conceive of nematodes and their eggs as almost omnipresent, as being carried by the wind and by flying birds and running animals; as floating from place to place in nearly all the waters of the earth; and as shipped from point to point throughout the civilized world in vehicles of traffic."* (From Cobb (1914).

As if challenged by this assertion, scientists have tested Cobb's hypotheses by examining the extremes of the biosphere on earth to evaluate the limits of nematode life. Through these investigations, biologists have now shown that nematodes are living and reproducing everywhere on Earth that water exists in a liquid state even for short periods of time annually.

Diversity of Habitats and Distribution

General

The most obvious ecological character that defines habitats for members of the phylum Nemata is that they all are aquatic animals – to move, live, eat, and reproduce, nematodes must exist in an aqueous environment. This environment includes soils, muds, sands, plants, and animals. They can be found living in soils with moisture contents as low as 5–10%, but in the majority of these cases, the nemas are associated with the roots of plants. It is evident that the environment in which nematodes live constrains their ultimate size. Soil dwelling species live in the water film of the interstices of soil particles. Nematodes, must live and carry out all functions of life in these spaces, thus free-living, or plant-parasitic soil-dwelling forms are usually extremely small. Morphological diversification of nematodes can operate only within the constraints of their life-history parameters, and thus, evolutionary pathways for nematodes living in an interstitial – soil or sediment/sand environment are limited. Thus these forms have limited abilities to diversify into the nonaquatic regions of the earth, and their size is constrained by this fact.

In contrast to the small sizes of plant-parasitic, free-living marine, freshwater, or soil nematodes (some adults can be as small as (*Criconemoides*) with an adult length of around 250 mm), species that occur as parasites of animals are free from the physical constraints on their size and the bodies of species in mammals are, therefore, relatively large. In fact, the largest nematode thus far recorded is *Placentonema gigantissima* from the blue whale with a length of more than 8 meters (Maggenti, 1981). The ratio between the smallest adult nematode to the largest can be calculated as (0.250 mm

(*Criconemoides*)/8,000 mm (*Placentonema*)=0.000031), compared to the ratio between a shrew and a blue whale (50 mm/ 24,4000 mm=0.12), indicating that the size differences in nematodes are three orders of magnitude greater than the mammals.

In the marine-benthic environment Lambshead (1993) has estimated (based on transect data from deep sea benthic samples) that there may be as many as 100 million species of marine infaunal nematodes. As exorbitant as that estimate seems, deep-sea nematodes have been show to be extremely rich in species diversity. One marine sediment sample from the east-Pacific benthos was reported to contain 148 species from a total of only 216 individual specimens examined (Lambshead 1993). At the present time the true extent of species diversity in the marine benthos can only be imagined because fewer than 20 studies of nematode community structure from marine-benthic habitats have been reported (Boucher and Lambshead, 1995). Relatively recent data from Boucher and Lambshead, 1995 shows that in marine environments the highest diversity in nematodes occurs in abyssal benthic sediments.

We now know that great numbers of individuals and species of nematodes live in sediments on the ocean floor distributed from the intertidal continental margins to the benthos of the abyssal zones, even though these marine habitats remain unexplored. Nematodes occur in tissues and organs of all species of vertebrates that have been studied and some, such as *Physaloptera spp.* live, feed, and reproduce in the strongest stomach acids of mammals, birds, and reptiles. Desiccated specimens from both the Arctic and Antarctic have been rehydrated to form viable colonies and living nematodes have been found in the limited meltwater in some of the dry valleys of Antarctica, an area that is probably one of the most extreme biotopes on the earth.

Extreme Biotopes

Some of the most extreme soil habitats on the Earth exist in the Dry-Valleys of the Antarctic where the annual mean air temperature is –20 °C, and soil temperatures at a 5 cm depth for the two "summer months" range from –2.71 to 15.9 °C. In this area, no vascular plants grow and mosses and lichens are rare; this is the only terrestrial soil-system known where nematodes are the final consumers and are at the apex of the food chain (in this case it seems more of a chain than a web). Three nematode species exist in these dry soils, *Scottnema lindsayae*, a microbivore (feeding on bacteria and yeast), *Plectus antarcticus* (a bacterial feeder), and *Eudorylaimus antarcticus*, an omnivorous predator that presumably feeds on individuals of the other two species (Powers *et al.*, 1998). In another biological extreme, Death Valley

in California has recorded some of the highest temperatures in North America and the soils of the valley are teeming with nematodes, many of which have been discovered to possess similar adaptive traits to those found in the cold deserts of Antarctica.

Individuals of some species of Nemata are capable of resisting extended periods of desiccation, for example, 3rd stage juveniles of *Anguina tritici* have been dried for more than 20 years in a state of anhydrobiosis in which all metabolic activities are shut down (Maggenti, 1981). These nematodes have been shown to have specialized proteins that fold into stable/preserved structures as the organism dries. In this state of crypto or anhydrobiosis, individual nematodes can remain viable through incredible extremes of temperature, desiccation, hypoxia, and even synthetic nematicides designed to kill nematodes (of course the regular biochemical processes that nematicides interfere with are not operational, so the nematode does not notice this particular assault). When water again becomes available, the animal in fact comes back to life when the molecular structures rehydrate and the proteins and enzymes spring back into normal operation.

Habitat Diversity

Nematodes occupy every conceivable life-history niche. There are benthic deep-water marine forms that appear to consume mostly diatoms and others such as species of the genus *Draconema* (Figures 5(a), 6) that are mostly associated with marine algae, but it is still unclear what they actually eat. Nematodes of the genus *Dirofilaria* live in the aorta and left ventricles of canids and are transmitted by mosquitoes from dog to dog. Species of nematodes live in the hearts of sharks, and other species occur by the thousands weighing more than one kilogram in the stomach of a pilot whale (SLG pers. obs.), and, as the human consumption of raw marine fish (ceviche and sashimi) has increased, transfer of juvenile *Anasakis, Terranova,* and other anasakines from the fish intermediate host to humans is occurring more commonly and these nematodes are turning up as parasites in the stomach of humans.

Some species feed on fungi in the soil whereas others are trapped and are themselves consumed by different species of fungi. Still other nematodes like *Mononchus* (Figure 1(b)) and *Clarkus* (Figure 16) are predatory and hunt and eat other nematodes in the soil environment. Free-living bacterial feeding nematodes have been shown to be integral parts in the carbon and nitrogen cycles in healthy soils (Ferris *et al*., 1998) and recent survey work has shown that undisturbed or natural soils in noncultivated habitats can have as many as 20 times more species than soil from similar areas that have been under cultivation (Al Banna and Gardner, 1996).

Abundance – Estimates and Facts

In addition to the large numbers of species that may occur in any given habitat, nematodes also occur in very great densities, for instance, in sheer numerical density of individuals in any given habitat, nematodes exceed even the mites and beetles combined. More than 90,000 nematodes were recorded from a single decomposing apple, and one report showed 1 cc. of marine mud contained 45 nematodes representing 19 species. Nematodes in marine estuaries occur at high numerical densities with reports of 4,420,000 m^{-2} in surface mud and 527,000,000/acre in the top 3 inches of sand in the Massachusetts coast. Counts and extrapolations for relatively moist soils (10–70% moisture content) worldwide show that in the uppermost levels, nematodes occur in mind boggling abundance: 7–9 billion/acre in undisturbed sod in North China; from 800,000,000 to 41 billion per acre (representing just 35 species), in Utah and Idaho and around 3 billion per acre in low-lying alluvial soils of Europe and other areas of North America.

How do Nematodes Affect the Biosphere?

Because of the huge numbers of nematodes that have been shown to occur in plants, animals, soils, and the benthos, there has been much speculation about the role of nematodes in basic biological processes occurring in the soils of the earth. Cobb (1914) speculated that some nematodes "are beneficial" however he also noted that this area of study of this was still in its infancy. In fact, in 2000, this area of study is still just developing and recent work has shown that nematodes can be good indicators of biodiversity (Bongers and Ferris, 1999). Gardner and Campbell (1989) showed that mammalian parasites with complex life cycles may serve as excellent indicators of areas of high biological diversity. Because of the multifarious nature of parasitic nematodes in mammals, it is expected that these kinds of species may provide biologists with additional tools for identification of areas of high biological diversity.

The fact that parasitic nematodes occur in such high prevalence and numerical densities in mammals should give us pause, there is obviously a huge energy drain on any population of mammal that we should care to analyze, and this energy drain probably causes significant decreases in the number of offspring in any given population over long periods of time.

Soils and Plants

Recent studies indicate that nematodes play a substantial role in the cycling of carbon and nitrogen in the soil environment (Bongers and Ferris, 1999)

and it has been shown that the numbers of bacterial feeding nematodes increases as the bacteria increase with annual warming of the soils. In the rainforest of Cameroon, average nematode abundances of $2.04 \times 10^6/m^2$ of rainforest soil were found indicating that these nematodes play a significant role in carbon flux (CO_2 and CH_4) in this rain forest site (Lawton *et al.*, 1996).

Nematodes occur in, on, and around the roots, bulbs, rhizomes, stems, and leaves of plants. They can cause galls in both the somatic and germinal tissues of the plants, where the nematodes can encyst, and dry, waiting for the next stage in their life cycle. There are species that are almost fully endoparasitic, exiting the plant root or stem only as juveniles. Others are fully ectoparasitic, such as species of *Xiphinema* (the vector of grape fanleaf virus). Some species spend part of their life-cycle in a plant and part of it in the soil. As mentioned earlier, seed parasites of the genus *Anguina* may spend most of their existence as juveniles in a dried state, the nematodes rehydrating, molting and then as adults crawling up the outside of the plant during periods of high relative humidity and then laying eggs in the seed head. The seeds are consumed by the developing juveniles, and when they dry, the seed coats protect the also dried nematodes within, and are distributed through the environment as are normal seeds (Maggenti, 1981). Nematodes of the genus *Pratylenchus* use their spear to move through the roots of the plants that they infect, penetrating the plant cells with repeated jabs of their stomatal armature.

Predators, Entomopathogenic Forms, Fungal, and Bacterial Feeders

Many nematodes that are found in the soil are either predaceous forms eating other nematodes, or forms that prey on mites, or other soil macro-organisms. The more spectacular predators such as *Mononchus* and *Clarkus* have specialized buccal structures with which to puncture the cuticles of other nematodes (Figures 1(b), 16). Microbivorous fungal and bacterial feeding nematodes are also extremely abundant with species specializing in their feeding habits on bacteria, fungi, diatoms, and other microscopic organisms. Some, such as juveniles of species of the genera *Heterorhabditis* and *Steinernema* carry special bacterial for the genus *Photorhabdus* in their digestive system. The 3rd stage juveniles wait in the soil until an unwary insect passes nearby, the nematode then homes in on and penetrates the hapless insect, making its way into the hemocoel where it releases the bacteria, which proliferate, killing the host. The nematode then feeds on the bacterial colony and reproduces in the insect, eventually again producing 3rd stage juveniles, which leave the carcass of the insect and disperse into the soil, waiting there for another insect to invade (for more specific details of the lifecycle of these entomopathogenic nematodes see Gaugler and Kaya, 1990).

Bacterial feeding forms occur in the soil in extremely high numbers. In soils that have not been disturbed, and have a good layer of organic matter, large numbers of all kinds of nematodes occur. One of the most well-known groups is the Rhabditida or the rhabditid nematodes. These forms feed on bacteria and yeasts growing in the soil, and are typically found in high numbers in moist soils with high organic content. The most famous of these forms are members of the genus *Caenorhabditis* of which the complete genome of *C. elegans* has recently been sequenced.

Aquatic and Marine Nematodes

This is an area that is wide open for future biologists. How do the trillions upon trillions of individuals and the millions of species that occur in the oceans really affect the biosphere? Nothing is known on the subject at the present time.

How many Species of Nemata?

Estimates of Number Described

Estimates of the numbers of species of nematodes that are known (i.e., described species) vary widely. However, in 1819, Rudolphi summarized what was known of the nematodes and he recorded 11 genera and about 350 species. Just 115 years later in 1934, Filipjev reported that 4601 species of nematodes had been described with about half free-living and the other half parasitic. By 1950, Libbie Hyman estimated that approximately 9000 species were described (based on her analysis of the Zoological record with descriptions being recorded at a rate of about 200 new species being described per year). In 1981, Maggenti's summary showed around 15,000 described species. The author's analysis from counting additions to the Zoological Record shows that in a 5 year period from 1992 to 1996 numbers of descriptions were relatively stable with approximately 776 new species described (average of approximately 155 descriptions per year). From 1996 to 1998 the numbers of descriptions decreased to 118 per year, most likely due to the continued retirement and expiration of taxonomists.

How Many Species of Vertebrate Parasitic Nematodes Exist?

All species of vertebrates examined thus far serve as hosts for at least one species of parasitic nematode. Some mammalian hosts harbor many species of nematodes that are distributed through several orders and families. Some of these nematodes are highly host-specific, surviving and reproducing

successfully only in host individuals comprising a single species or perhaps a closely related group of species. Other nematodes show less specificity, being much more likely to jump from one suitable vertebrate host to another during opportune times during their life-history (Brant and Gardner, 2000).

Within a host, many different types of habitats may be occupied by nematodes. As a species, *Homo sapiens* harbors around 35 species of host-specific parasitic nematodes (Chitwood and Chitwood, 1977). To illustrate the diversity of habitats in a single animal host, humans will be used as an example. In a human, nematodes can occur as juveniles in muscle tissues, usually smooth muscle like the diaphragm or the tongue (*Trichinella*), in the mucosa of the intestine (*Strongyloides*), as migrating forms in blood, and lungs (*Ascaris),* in blood or lymph as microfilariae (Filarioids of humans), as adults in the small and large intestines (*Ancylostoma*, *Necator, Ascaris*), as adults in mesentaries and subcutaneous tissues (*Onchocerca, Loa, Wuchereria)* and *Enterobius* in the large intestine and cecum.

Cobb was well acquainted with animal parasitic nematodes, and his familiarity with host-specificity in the Nemata led him to estimate that as early as 1914, well over 80,000 species of nematodes would eventually be found parasitizing vertebrates alone. Similar estimates could be derived for parasites of invertebrates and plants resulting in totals of free-living and parasitic species numbers far in excess of the approximately 27,000 species of nematodes known today.

> Cobb (1914) stated "*There must be hundreds of thousands of species of nematodes. Of this vast number only a very few thousand have been investigated, and of these, comparatively few with any degree of thoroughness.*"

Present estimates are that only approximately 14,000–16,000 species of parasitic nematodes have been described from all taxa of slightly more than 48,000 currently recognized species of vertebrates. In addition, many species of wild mammals each harbor more than two host-specific species of nematode so the above estimate of 8900 species of nematodes only from mammals can be considered very low.

As of this writing, the natural history, development, and transmission parameters of only around 561 species are known (Anderson, 1992). As parasites of only vertebrates, Anderson (1992) estimated that there were about 2300 described genera distributed among 256 families comprising about 33% of all nematode genera known. This percentage is approximately equal to the percentage of genera of Nemata presently known in marine and freshwater habitats. It is agreed by most workers that this bias is due to the larger number of parasitologists working on selected groups of Nemata relative to the number of specialists working on the free-living marine and freshwater forms.

If each of the approximately 4450 known species of mammals were infected with only two species of host-specific nematodes, we would expect to find a minimum of 8900 species of parasitic nematodes only in the Class Mammalia.

Pinworms, nematodes of the Order Rhabditida Superfamily Oxyuroidea (Figure 1) show high levels of host specificity and it is well-known that almost all species of rodents and primates have one species-specific pinworm, (for instance, *Homo sapiens* harbors *Enterobius vermicularis*). Both recent and historical studies have shown that pinworm nematodes exhibit high levels of coevolution, i.e., concomitant host-parasite speciation (and host-specificity) with their primate and rodent hosts (Hugot, 1999). At the present time, slightly more than 716 species of Oxyuroidea have been described with the vertebrates hosting about 496 species and invertebrates about 217 species. The greatest diversity in the Oxyuroidea to be found in the future is expected to come from examination of the Arthropoda especially beetles, cockroaches (4000 species described and more than 20–30,000 expected to be found) and millipedes (17,000 species described and more than 60,000 species expected to be found). This gives huge numbers of pinworms occurring just in the cockroaches and the millipedes if each species harbors its own species of pinworm. At least two species of pinworms (genus *Thylastoma*) occur in laboratory colonies of *Periplaneta americana* and more are expected to be found in free-living populations (J. P. Hugot, personal communication).

When adequate surveys are completed, large numbers of species of Oxyuroidea are also expected to be described from Neotropical rodents of the family Muridae. Up to the present time, only around seven species of pinworms have been described from Neotropical murids and these rodents potentially host from 400 to 800 undescribed species of Oxyuroidea, (given that only one to two new species of Oxyuroid nematode is found in each species of rodent examined). J. P. Hugot, personal communication.

Recent comparative studies in the Oxyuroidea of rodents shows that the larger the body-size of the rodent, the larger the body size of oxyurid nematodes that it harbors (Morand, *et al.*, 1996).

Comparative Nematode Diversity of New World Subterranean Rodents Geomyidae

Papers on nematode parasites from rodents of the Nearctic family Geomyidae covering the dates from 1857 to the present were reviewed. Combined with field-collected specimens from the early 1970s up to the present time, the author discovered that six of the approximately 11 nematode parasites reported from pocket gophers in North America, are host specific to only the Geomyidae (**Table 2**).

Table 2. *Nematode species*   *Classification and Location in Host*

Trichuris fossor	Sub-Phylum Adenophorea
	Cecum and large intestine
	Sub-Phylum Secernentea
Ransomus rodentorum	Cecum/small intestine
Vexillata vexillata	Duodenum
Vexillata convoluta	Duodenum
Heligmosomoides thomomyos	Duodenum
Litomosoides thomomydis	Mesentaries
Litomosoides westi	Mesentaries

Of members of the vertebrate Class Mammalia, one of the most complete sets of nematode parasite data exists for rodents of the family Geomyidae. Of the approximately 35 known species of pocket gophers (Wilson and Reeder, 1993), at the present time only 15 species have been surveyed for parasitic nematodes. From those 15 species, six species of nematodes are known to be host-specific only to geomyids. Some nematodes such as the strongylid *Ransomus rodentorum* and the heligmosomid *Heligmosomoides thomomyos* and filarioids of the genus *Litomosoides* have been reported from more than one species of gopher, other nematode species such as *Vexillata vexillata* occur only in gophers of the tribe Thomomyini (genus *Thomomys*) but do not appear to be host-species specific.

These mammals occur in an extremely wide and ecologically variable geographic area (from southern Manitoba and British Columbia south to extreme northern Colombia) therefore, there may be many more undescribed or undetected species of nematodes in these hosts than this analysis provides. In addition, no studies on genetic diversity of nematodes (or any endoparasites) in these rodents have been published, therefore, levels of genetic variation in these nematodes are unknown and the true genetic diversity that exists will probably cause an increase in the number of nematode species that are recognized.

There is little if any evidence of phylogenetic coevolution of the nematode parasites and their pocket gopher hosts. However, all species listed are specific to species of the family Geomyidae and both *Litomosoides* and *Vexillata* appear to exhibit some level of phylogenetic host specificity with two closely related North American species of *Litomosoides* being found only in geomyids (Brant and Gardner, 2000) and species of *Vexillata* occurring more generally in members of the Geomyoidea.

Table 3. *Nematode species*

Nematode species	*Classification and Location in Host*
Trichuris (43 spp.)	Sub-Phylum Adenophorea Cecum and large intestine Sub-Phylum Secernentea
Ancylostoma caninum (host capture in synanthropic species of rodents?)	Duodenum
Pudica sp. Host capture from Muroid rodents.	Duodenum
Litomosoides (2 spp.)	Peritoneal cavity and mesenteries
Paraspidodera (46 spp.)	Cecum and large intestine

Nematodes of Tuco Tuco's (Ctenomyidae)

A review of the nematode parasites occurring in Neotropical rodents of the genus *Ctenomys* indicates a considerably more depauperate fauna of nematodes as compared with the Nearctic Geomyidae (**Table 3**). Data collected from 1984 up to the present time indicate that nematodes of the genera *Trichuris* and *Paraspidodera* have cospeciated with their hosts and exhibit different levels of phylogenetic congruence relative to their hosts. In addition, nematodes of the trichostrongyloid (O. Strongylida) genus *Pudica* were encountered only two times from the same species of *Ctenomys* in one locality (from a sample of more than 500 individuals and more than six species of hosts examined). The occurrence of *A. caninum* in *Ctenomys* appears to be a capture, as it only occurred in areas where dogs, humans, and ctenomyids lived in relatively close proximity (banana fields in lowland Santa Cruz, Bolivia).

   Although most of the pocket gophers examined carefully generally harbor from one to several species of nematodes in the small intestine, very few nematodes are found in samples of tuco-tucos. Even though the genus *Ctenomys* contains almost 40 species, comparatively few species of nematodes have been described or reported from them. This lack of parasites in a wide-open group of mammals might be a result of rapid speciation in the mammal group with parasites failing to keep up with the speciation rate of the mammals themselves and actually loosing parasites through time; there is some evidence that the ctenomyids have speciated rapidly in their history (Lessa and Cook, 1998). The lack of a diverse fauna of nematodes in these mammals could also be due to historical accident whereby the ancestor of the ctenomyids had a low diversity of nematode parasites (for whatever reason) thus giving rise to a phylogenetic lineage of mammals lacking a diverse fauna of parasites. But why have they not picked up more parasitic nematodes from other syntopic species of mammals?

There is some evidence of host-switching in nematodes of the genus *Litomosoides* in that two species occur in *Ctenomys opimus* in high-altitude Western Bolivia, but these nematodes have not been reported from any other species of *Ctenomys* from throughout the Neotropics. Superficially this indicates a host-capture event from some other lineage of mammals (Brant and Gardner, 2000). Another example is the fact that nematodes of the genus *Pudica* found in *Ctenomys* have diverse relatives in other species of muroid rodents in South America but none in ctenomyids, leading to the conclusion that most are now found in the tucos because of host-switching events, and not phylogenetic coevolution.

Nematodes of the genus *Paraspidodera* are found only in Hystricognath rodents in the Neotropical Region and these nematodes appear to have had a long historical, coevolutionary association with ctenomyids, showing varying levels of both cospeciation and host-switching. The adenophorean whip worm genus *Trichuris* occurs in many diverse groups of rodents in the Neotropics and at the present time, no analyses have been done to examine the levels of coevolution with ctenomyids.

The multifarious nature of nematode diversity in subterranean mammals in the Nearctic and Neotropical Regions requires at the minimum that phylogenetic hypotheses for each group of mammals and their nematodes be developed and then each host-group can be compared with each parasite group. Much more detailed work needs to be paid to collecting parasites from some of the unknown species of *Ctenomys* throughout the Neotropics. The same can be said about the level of knowledge of parasitic nematodes in the Geomyidae in the northern Neotropics and southern Nearctic regions.

Molecular Diversity in the Nemata

Several molecules have been used to begin to assess phylogenetic and genetic diversity within the Nemata and the number of investigations using molecular methods to try to quantify the diversity of the nematodes is rapidly increasing (Dorris *et al.*, 1999; Blaxter *et al.*, 1998; Al-Banna *et al.*, 1997; Nielsen, 1996). However, because of the extremely large number of species that may exist, examination of levels of molecular or genetic diversity in representatives of the group as a whole can be said as just the beginning even though massive amounts of molecular data on nematodes are now literally pouring into the literature stream. The summary papers by Blaxter *et al.* (1998); Dorris *et al.* (1999); Meldal, *et al.*, 2007; Holterman *et al.* (2006); Van Megan *et al.* (2009); and Bik *et al.* (2010) indicate the utility and power of estimating the molecular–phylogenetic relationships among the Nemata using ribosomal DNA and other molecular sequence data. Initial studies of

the molecular diversity within and among several lineages of the Strongylida show that the genetic diversity among these taxa is relatively low (Chilton *et al.*, 1997). From these works, it is clear that molecular phylogenies will provide robust tests of the hypotheses of morphological relationships among the Nemata. As more regions of DNA are used to examine the relationships among the nematodes, we expect additional clarification of both the deep phylogenetic branches (Bik *et al.*, 2010) that are at present relatively obscure in the molecular phylogeny of the Nemata and the more rapidly evolving branch tips that represent extant species with valuable genetic information

Relationships to other Animal Groups

A recent analysis grouped the nematodes, gastrotrichs, priapulids, kino-rhynchs, and the loriciferans into a group (superphylum) called the Cycloneuralia (**Figure 26**) based on the circular shape of the brains in these groups (Nielsen *et al.*, 1996). The aforementioned study and at least one other (Zrzavy, 1998) using 18s rDNA sequences showed that the Nemata share a common ancestor with members of the phylum Nematomorpha but there was a shuffling of the other groups out of the "Cycloneuralia" (**Figure 27**).

More recently, Lartillot and Philippe (2008) presented a molecular phylogeny of the Bliateria where they show the Nemata as sharing a most recent common ancestor with members of the phylum Tardigrada and are close to the phylum Arthropoda in their final tree (**Figure 28**).
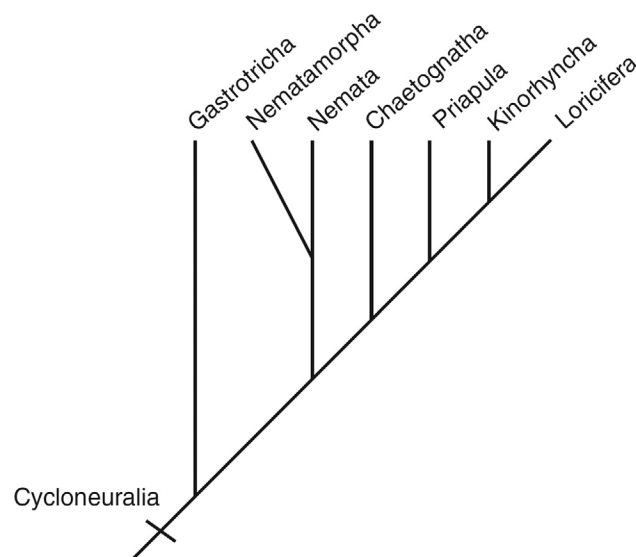

Figure 26 Phylogenetic tree showing the relationships of the Nemata to the rest of the Cycloneuralia.

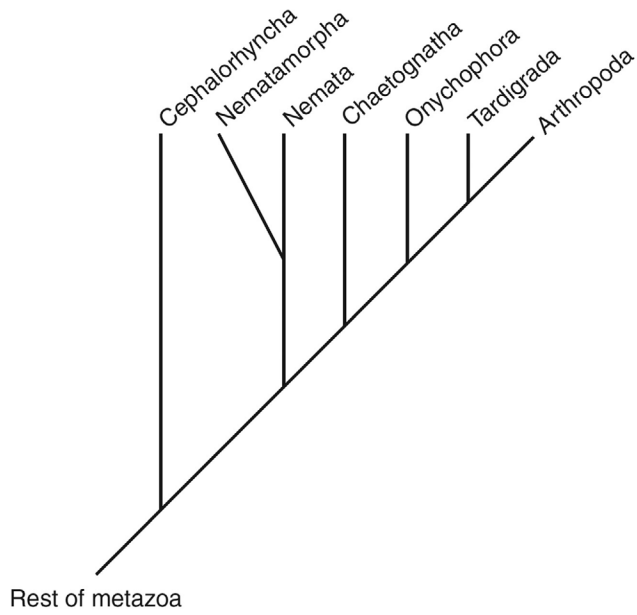**Figure 27** Phylogenetic tree showing the relationship of the Nemata to the rest of the Animalia
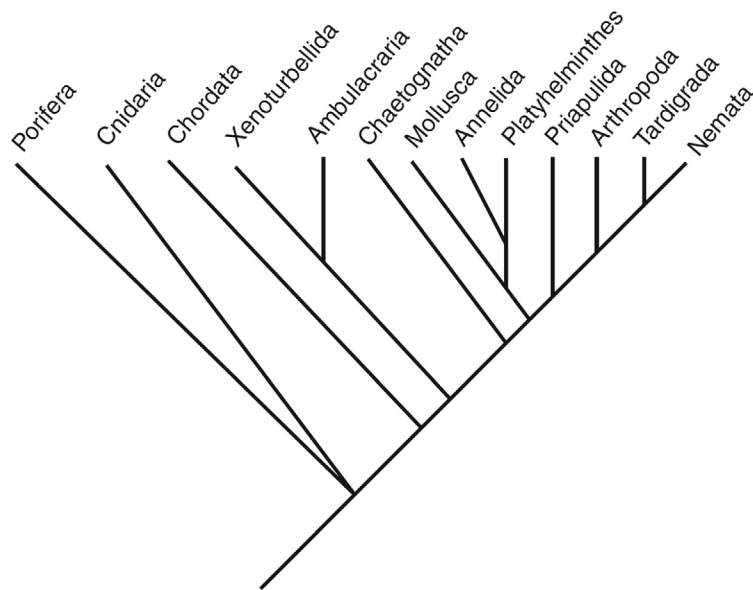

Figure 28 Phylogenetic tree of the Bilateria showing the sister group of the Nemata to be members of the phylum Tardigrada or the moss bears.

As mentioned above, nematodes are soft-bodied and mostly very small organisms, any larger forms that existed in prehistory were probably parasites of vertebrates, however, these left no fossil traces. The only fossil nematodes that are known are insect parasitic or plant parasitic forms that occur very rarely in amber inclusions, but these are also not very old. Because there are no fossil records of nematodes of Cambrian or Precambrian ages, estimates of the age of the Nemata have been only speculation up to the present time and without fossils; it is difficult to calibrate molecular clocks for the nematodes. However, through application of various models of molecular evolution and molecular clock theory, estimates of the time of divergence of the nematodes from the rest of the animal groups appear to be approximately 1177–1179 million years (Wang *et al.*, 1999) (this study showed a basal origin of the nematodes on a phylogenetic tree, in contrast to the relatively derived placement in the analyses shown in Figures 26–28).

Most authors consider that nematodes arose from a Marine ancestor. The tri-radiate esophagus and the tubular body indicate a possible primarily sedentary existence with the posterior end attached to the substrate and the anterior end freely encountering the marine environment from all sides, thus the secondarily derived somewhat radial symmetry (Maggenti, personal communication).

Classification and Groups of the Nemata

Above the level of the order, confusion reigns relative to the classification and systematic arrangement of the nematodes. Maggenti (1991) is usually followed in this regard and his analyses followed corroborated historical analyses in recognizing the two main sub-phyla: the Secernentea and the Adenophorea. Recent work shows that these groups are substantiated both in morphological and molecular analyses although competing phylogenetic hypotheses and associated classifications have also relatively recently been proposed (Dorris *et al.*, 1999; Blaxter *et al.*, 1998; Adamson, 1989). Even more recent work by Meldal *et al.* (2007); Holterman *et al.* (2006); Van Megen *et al.* (2009) and Bik *et al.* (2010) have provided some larger scale analyses of the Nemata using sequencing of ribosomal DNA and other conserved genes.

A systematic treatment of the nematodes was recently undertaken by Hodda (2007) where he reviews the systematics of the group and proposes a classification that incorporates molecular, developmental, and morphological advances. He reviews the classification of the Nemata as a phylum (although he uses Nematoda as the name). Here the author would like to point out that Maggenti (1981, 1991a, and 1991b) used Nemata as the name for the phylum as he often pointed out that "Nematoda" is a class level name left over from the old classification when nematodes were considered a class in

the phylum Aschelminthes. If the nematodes were considered a class under a different phylum name, then Class Nematoda would be appropriate, as it is, Phylum Nemata is more correct (A.R. Maggenti, personal communication).

Since 1949, at least eight authors have provided classifications for members of the phylum Nemata (Malakhov, 1994; Brooks and McLennan, 1993; Maggenti, 1991). Of these, the classifications of Maggenti (1981; 1991) have proven to be the most useful summary of all nematodes (free-living, and parasitic); however, phylogenetic hypotheses have recently been proposed based on both molecular and morphological characteristics. This does not necessarily mean that because a phylogeny has been proposed that a classification from that phylogenetic tree will result (Maggenti, 1991a and Brooks and McLennan, 1993).

At this point in time, the synthetic classification proposed by Hodda (2007), which takes the arrangement down to the level of the family, appears to be the most easily useable and informative new classification. He presents the groups in a table format, and as noted above, uses information from many different fields of study of the Nemata to generate the classification. One of his goals was to minimize the changes in taxonomic rank of well established groups to achieve stability and he generally follows the use of superorders (e.g., Maggenti, 1991).

Future Knowledge of Nematodes

The author hopes that this summary treatment provides readers with sufficient knowledge to allow more in-depth research on nematodes. The group is so large, and so ecologically, morphologically, and phylogenetically diverse that to attempt to discuss the diversity of the group in such an abbreviated way is practically futile at best. N. A. Cobb (1914) stated this clearly on the last page of his famous "Nematodes and Their Relationships" (pp. 490).

 "The foregoing fragmentary sketch may indicate to the student, as well as to the general reader, the vast number of nematodes that exist, the enormous variety of their forms, and the intricate and important relationships they bear to mankind and the rest of creation."

As more data on distribution and function of nematodes throughout the biosphere are obtained, the importance of this group of worms will surely be realized. We are just beginning to explore the oceans, and we are probably losing more species of nematodes from rainforest clearing than will ever be ultimately found, described, and classified.

The author hopes that mankind will generate more interest in the microscopic world of the Nemata, and that this section will provoke the reader into action and disprove what Van Leeuwenhoek stated about his fellow man on 28 September, 1715 in which he said: "... And over and above all, most men are not curious to know: nay, some even make no bones about saying, What does it matter whether we know this or not?" (Dobel, 1932; pp. 324–325).

References

Adamson M (1989) Constraints in the evolution of life histories in zooparasitic nematoda. In: Ko RC (ed.) Current Concepts in Parasitology, pp. 221–253. Hong Kong: Hong Kong University Press.

Al-Banna L, Williamson VM, and Gardner SL (1997) Phylogenetic analysis of nematodes of the genus Pratylenchus using nuclear 26s rDNA. Molecular Phylogenetics and Evolution 7: 94–102.

Al Banna L and Gardner SL (1996) Nematode Diversity of Native Species of Vitis in California. Canadian Journal of Zoology 74: 971–982.

Anderson RC (1992) Nematode Parasites of Vertebrates. Their Development and Transmission, pp. 578. Wallingford, UK: CAB International.

Arujo A, Reinhard KJ, Ferreira LF, et al. (2008) Parasites as probes for prehistoric migrations? Trends in Parasitology 24: 112–115.

Bik HM, Lambshead JD, Thomas WK, et al. (2010) Moving towards a complete molecuar framework of the Nematoda: A focus on the Enoplida and earlybranching clades. BMC Evolutionary Biology 10: 353. 14 pages.

Blaxter ML, De Ley P, Garey JR, et al. (1998) A molecular evolutionary framework for the phylum Nematoda. Nature 392: 71–75.

Bongers T and Ferris H (1999) Nematode community structure as a bioindicator in environmental monitoring. Trends in Ecology and Evolution 14: 224–228.

Boucher G and Lambshead PJD (1995) Ecological biodiversity of marine nematodes in samples from temperate, tropical, and deep-sea regions. Conservation Biology 9: 1594–1604.

Brant SV and Gardner SL (June 2000) Phylogeny of species of the genus Litomosoides (Nemata: Onchocercidae) evidence of rampant host-switching. Journal of Parasitology 83: 545–554.

Brooks DR and McLennan DA (1993) Parascript. Parasites and the Language of Evolution. Washington, DC: Smithsonian Institution Press.

Chan MS (1997) The global burden of intestinal nematode infections – fifty years on. Parasitology Today 13: 438–443.

Chilton NB, Gasser RB, and Beveridge I (1997) Phylogenetic relationships of Australian strongyloid nematodes inferred from ribosomal DNA sequence data. International Journal for Parasitology 27: 1481–1494.

Chitwood BG and Chitwood MB (1977) Introduction to Nematology, pp. 334. Baltimore: University Park Press.

Cobb NA (1914) Nematodes and their relationships. In: Yearbook of Department of Agriculture for 1914, pp. 457–490. Washington, DC: Government Printing Office.

Crompton DWT (1999) How much human helminthiasis is there in the world? Journal of Parasitology 85: 397–403.

Dobel C (1932) Antony Van Leeuwenhoek and His "Little Animals," pp. 435. NY: Harcort, Brace and Co.

Dorris M, De Ley P, and Blaxter ML (1999) Molecular Analysis of Nematode Diversity and the Evolution of Parasitism. Parasitology Today 15: 188–193.

Ferris H, Venette RC, van der Meulen HR, et al. (1998) Nitrogen mineralization by bacterial feeding nematodes: Verification and measurement. Plant and Soil 203: 159–171. Gaugler R and Kaya HK (1990) Entomopathogenic Nematodes in Biological Control, pp. 365. Boca Raton, FL: CRC Press.

Grassé P-P (1965) Traite´ de Zoologie. Anatomie, Syste´matique, Biologie. Ne´mathelminthes (Ne´matodes) Ne´matodes - Gordiace´s - Rotife`res - Gastrotriches - Kinorhynques. Tome IV. Fascicule II, III. pp. 1–1497.

Holterman M, van den Wurff A, van den Elsen S, et al. (2006) Phylum-wide analysis of SSU rDNA reveals deep phylogenetic relationships among nematodes and accelerated evolution toward crown clades. Molecular Biology and Evolution 23: 1792–1800.

Huber JCh (1906) Demetrios Pepagomenos uber die Wurmer in den Augen der Jagdfalken. Zool. Annal. 2: 71–73.

Hugot JP (1999) Primates and their pinworm parasites: The Cameron hypothesis revisited. Systematic Biology 48: 523–546.

Lambshead PJD (1993) Recent developments in marine benthic biodiversity research. Oce´anis 19: 5–24.

Lartillot N and Philippe H (2008) Improvement of molecular phylogenetic inference and the phylogeny of Bilateria. Philosophical Transactions of the Royal Society B 363: 1463–1472.

Lawton JH, Bigtnell DE, Bloemers GF, et al. (1996) Carbon flux and diversity of nematodes and termites in Cameroon forest soils. Biodiversity and Conservation 5: 261–273.

Lessa E and Cook JA (1998) The molecular phylogenetics of Tuco-tucos (genus Ctenomys, Rodentia: Octodontidae) suggests an early burst of speciation. Molecular Phylogenetics and Evolution 9: 88–99.

Maggenti AR (1981) General Nematology, pp. 372. New York: Springer-Verlag.

Maggenti AR (1991a) Nemata: Higher Classification. In: Manual of Agricultural Nematology, pp. 147–187. New York: Marcel Dekker, Inc.

Maggenti AR (1991b) General Nematode Morphology. In: Manual of Agricultural Nematology, pp. 3–46. New York: Marcel Dekker, Inc.

Malakhov VV (1994) Nematodes. Structure Classification and Phylogeny, pp. 286. Washington, DC: Smithsonian Intitution Press.

Meldal BHM, Debenham NJ, De Ley P, et al. (2007) An improved molecular phylogeny of the Nematoda with special emphasis on marine taxa. Molecular Phylogenetics and Evolution 42: 622–636.

Morand S, Legendre P, Gardner SL, et al. (1996) Body size evolution of Oxyurid (Nematoda) parasites – the role of hosts. Oecologia 107: 274–282.

Musser GG and Carleton MD (1993) Family Muridae. In: Wilson DE and Reeder DM (eds.) Mammal Species of the World: A Taxonomic and Geographic Reference, pp. 501–755. Washington, DC: Smithsonian Institution Press.

Nielsen C, Scharff N, and Eibye JD (1996) Cladistic analyses of the animal kingdom. Biological Journal of the Linnean Society 57: 385–410.

Powers L, Mengchi H, Freckman-Wall D, et al. (1998) Distribution, community structure, and microhabitats of soil invertebrates along an elevational gradient in Taylor Valley, Antarctica. Arctic and Alpine Research 30: 133–141.

Rausch RL (1983) Chapter 5. The biology of avian parasites: Helminths. In: Farner DS, King JR, and Parkes KC (eds.) Avian Biology, vol. VII. NY: Academic Press.

Wang D, Kumar S, and Hedges B (1999) Divergence time estimates for the early history of animal phyla and the origin of plants, animals and fungi. Proceedings of the Royal Society of London, Series B 266: 163–171.

Van Megen H, Van den Elsen S, Holtermann M, et al. (2009) A phylogenetic tree of nematodes based on about 1200 full-length small subunit ribosomal DNA sequences. Nematology 11: 927–950.

Zrzavy J, Mihulka S, Kepka P, et al. (1998) Phylogeny of the Metazoa based on morphological and 18S ribosomal DNA evidence. Cladistics 14: 249–285.