NEMATODES

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Introduction – Life in a Soil Pore

Few people are aware of the most numerous of all soil-dwelling animals, the nematodes. These minute, unsegmented roundworms are actually aquatic organisms, inhabiting water films (1–5 μm thick) that coat and surround soil particles. (This chapter focuses on nematodes that typically complete their entire life-cycle within terrestrial soils or within plant roots. Numerous parasites of vertebrates have soil-dwelling stages, but their development is dependent on entering an appropriate host species. Vertebrate nematode parasites include hookworms, intestinal roundworms, pinworms, whipworms, and other serious pests of humans and domesticated animals. Information about vertebrate parasites is readily found in textbooks of parasitology.) Their size, typically 0.40–1.0 mm in length, is ideal for navigating this porous matrix. Although fully functional within a water film, they are ultimately bounded by soil structure, restricted in movement within soil pores less than 30 μm diameter.

Nematodes are simple organisms (**Figure 1**). Comprised of approximately 1000 somatic cells in the adult stage, these worm-like organisms are an example of functional and anatomical economy. Lacking eyes, appendages, and true segmentation, nematodes use mechanosensory and chemosensory neurons embedded in the cuticle to orient and respond to a wide range of environmental stimuli. At the nematode's anterior end is a circlet of sensilla arranged around an oral opening. These sensilla, including two larger, laterally placed chemosensory organs called 'amphids,' detect subtle chemical gradients, providing directional information to the nematode (**Figure 2**). Plant-feeding nematodes respond to slight variations in CO_2 and root exudates. A positive chemosensory signal initiates a snake-like sinuous movement characteristic of most nematodes, created by longitudinal body muscles working in apposition to a hydrostatic skeleton. Directional movement more than a few centimeters per day is unlikely in the soil environment. Once they contact the root surface, plant-feeding nematodes will probe with their stylet, a hollow, protrusible, hypodermic needle-like feeding tube (**Figure 3a**). Some plant-feeding nematodes will feed externally to the root surface, using this stylet to puncture cells, withdrawing the cytoplasmic contents. Others will penetrate the root and establish permanent feeding sites within the root cortex, or migrate cell-to-cell, leaving a trail of damaged necrotic tissue.

Free-living nematodes also occupy the interstitial spaces in soil. Unlike the plant-feeders, free-living nematodes are seldom sedentary, continually moving to feed on a diverse array of food, including bacteria, algae, fungi, protozoa, small invertebrates, and other nematodes. They use the same set of sensilla to track their food source; however, their feeding structures are modified to suit their meal. Bacterial-feeders graze using a relatively simple tubular mouthpart,

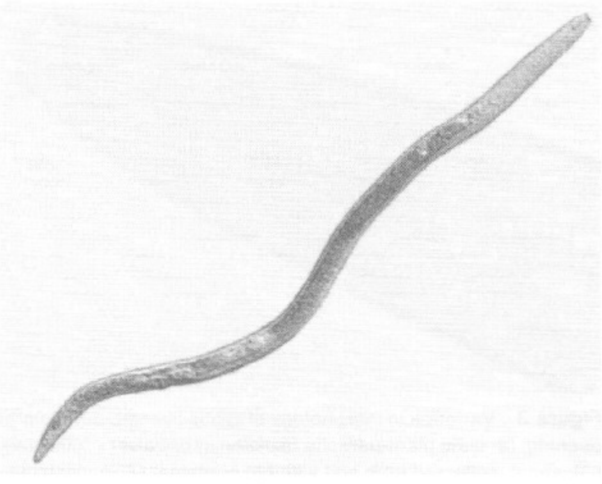

Figure 1 (see color plate 43) Entire body view of a female *Pratylenchus agilis* (×100 magnification), collected on the Konza Prairie (96° W 35′ 39° N 05′) beneath Scribner's panicum (*Panicum scribnerianum*) and bluegrass (*Poa pratensis*) near Manhattan, Kansas. Photograph is provided courtesy of Peter Mullin (2000).

although the cuticle surrounding the oral opening may be modified elaborately to direct food toward the stoma (**Figure 4**). Predators may be adorned with 'teeth,' used to puncture or shred the integument of various invertebrates (**Figure 5**). Fungal-feeders and omnivores have a stylet similar in appearance to that of plant-feeders, distinguished by the lack of stylet 'knobs,' points of muscle attachment for stylet protrusion (**Figure 3b**).

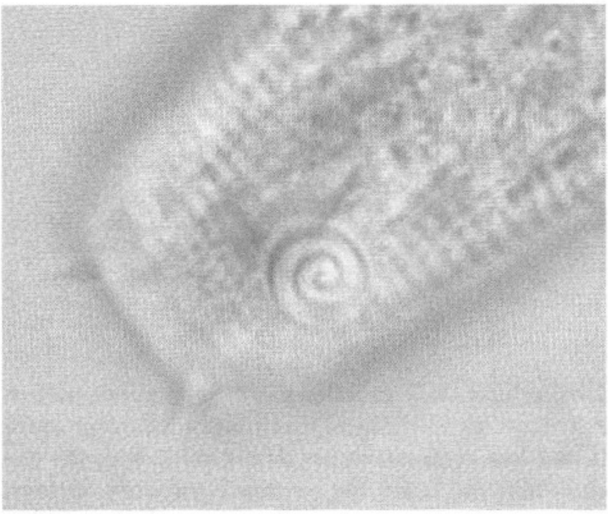

Figure 2 Spiral-shaped chemosensory organs called 'amphids' in an anterior position of *Achromadora* sp. collected from soil of Jumbo Valley fen in Cherry County, Nebraska.

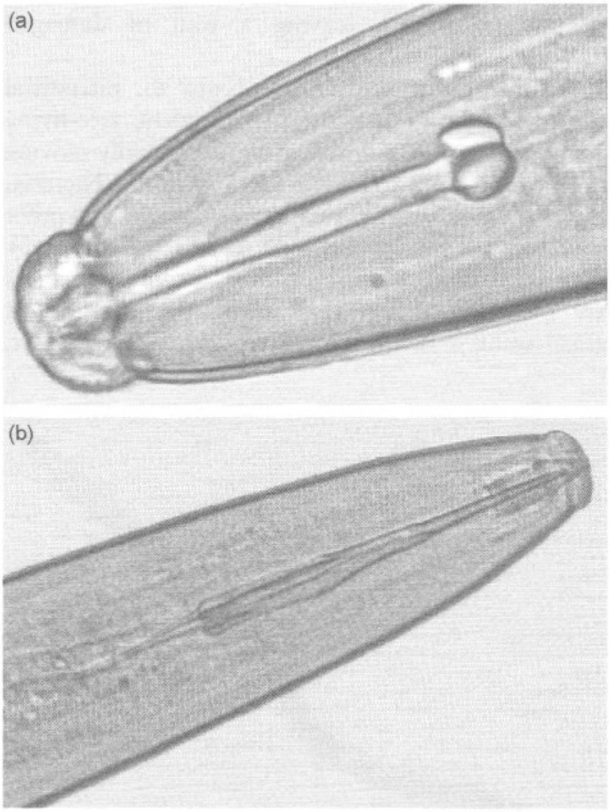

Figure 3 Variation in morphology of spear-like structure in oral opening: (a) male plant-parasite *Hoplolaimus galeatus* (×1000 magnification), collected from soil with big bluestem (*Andropogon gerardii* Vitman) in the Konza Prairie (96° W 35′ 39° N 05′), near Manhattan, Kansas; and (b) female fungivore *Enchodelus hopedorus* (× 400 magnification), collected from the summit of Long's Peak, Colorado (105° W 35′ 40° N 16′). Photographs are provided courtesy of Peter Mullin (2000).

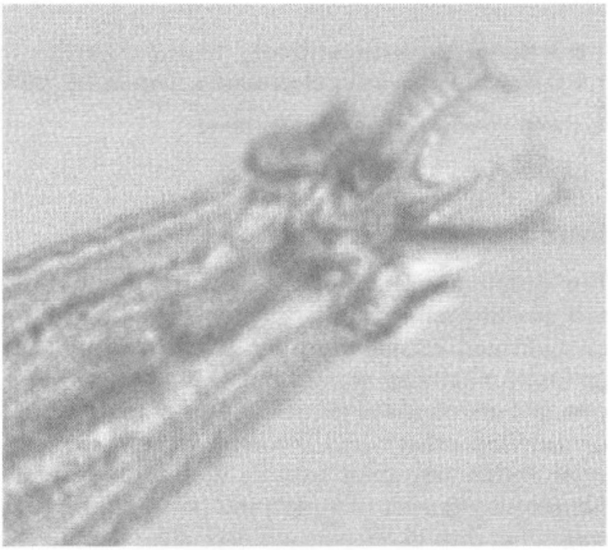

Figure 4 Cuticle ornamentation of oral opening of *Acrobeles ctenocephalus* (×1000 magnification), collected in soil with little bluestem (*Andropogon scoparius*) in the Konza Prairie (96° W 35′ 39° N 05′) near Manhattan, Kansas. Photograph is provided courtesy of Peter Mullin (2000).

Figure 5 Teeth of oral opening of predator *Mylonchulus montanus* (×1000 magnification), collected in soil with big bluestem in the Konza Prairie (96° W 35′ 39° N 05′) near Manhattan, Kansas. Photograph is provided courtesy of Peter Mullin (2000).

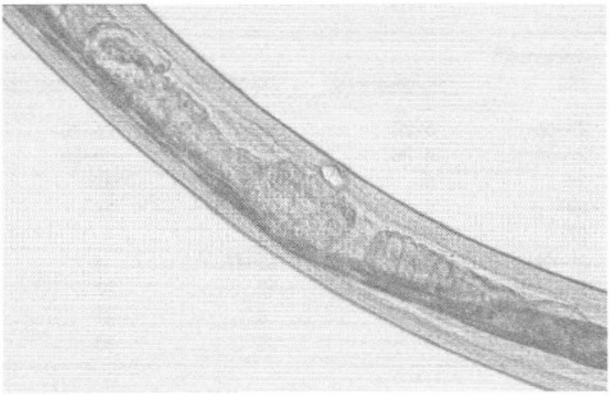

Figure 6 Ovary in reproductive tract of female *Axonchium micans* (× 400 magnification), collected in soil with big bluestem/Scribner's panicum in the Konza Prairie, near Manhattan, Kansas. Photograph is provided courtesy of Peter Mullin (2000).

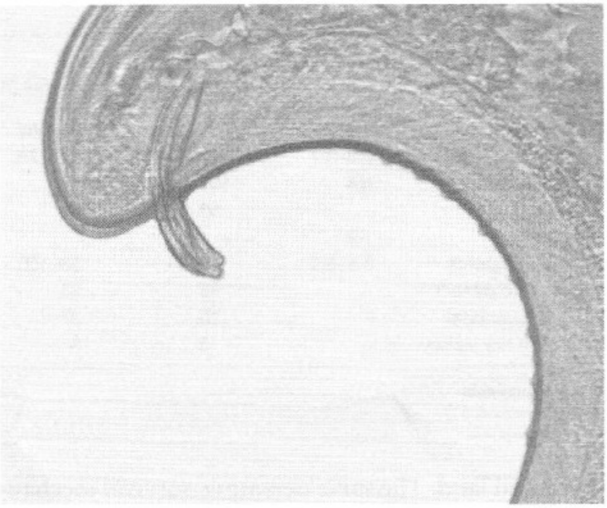

Figure 7 Protrusible modification of male genitalia of *Aporcelaimellus obscuroides* (×400 magnification), collected in soil with big bluestem/Scribner's panicum in the Konza Prairie, near Manhattan, Kansas. Photograph is provided courtesy of Peter Mullin (2000).

Early observations of nematodes by light microscopy led scientists to refer to nematodes as a 'tube within a tube.' Food entering the nematode is channeled quickly into a tubular esophagus and then passed into an intestine that comprises the bulk of the body cavity. Waste products are eliminated through a posterior ventral anus. There is no circulatory or respiratory system within the nematode. In addition to the alimentary system, the reproductive system is a conspicuous feature in the adult nematode (**Figure 6**). Females and hermaphrodites are characterized by a branched genital system, which produces eggs that exit the body via a ventral genital opening in the body wall. Males possess a spicule, a cuticularized, protrusible modification of the genital system that guides sperm into the female for internal fertilization (**Figure 7**). Many nematodes are strictly bisexual, but parthenogenesis and self-fertilizing hermaphroditism are also common among species. Regardless of mode of reproduction, nematodes are prolific animals. Some species complete a life-cycle of 3 or 4 days. Others require several months to go from egg to egg-laying female. *Meloidogyne* spp., an economically important group of plant parasites, will typically begin to produce eggs within 3 weeks of hatching; each female is capable of producing hundreds of eggs during an adult life.

Nematode Distribution and Abundance

The hallmark of Phylum Nemata is the exceptional abundance and ubiquitous presence of nematodes (**Table 1**). It is a challenging exercise to identify a habitat not occupied by a diverse community of nematodes. Consider the dry valleys of Antarctica, an environment considered so extreme that it is thought to provide the bare minimum for sustaining life on earth. There, in McMurdo Valley, three nematode species occupy the top levels in the soil food chain, two bacterivores and a third species, *Eudorylaimus antarcticus*, that feeds on the two bacterivorous species. Soils of the high Arctic are populated so heavily with nematodes that biologists have searched for explanations for an Arctic nematode biodiversity that exceeds that of the humid tropics. Temperate grasslands appear to sustain the greatest levels of diversity and abundance in the phylum. On Konza Prairie, one of the last remaining large stands of true tallgrass prairie in North America, each handful of soil is likely to contain 50–100 different nematode species. An estimated 1.5 million nematodes can be extracted from a square meter of soil, just within the surface 10 cm. Some researchers have considered the plant-feeding or herbivorous species as 'belowground buffalo,' referring to their impact as grazers of plant roots. Nearly all researchers agree that the approximately 25 000 described species of nematodes represent a small percentage of the species that actually exist in nature.

Finding agreement on those factors responsible for extraordinary nematode abundance and diversity is not so simple. Clearly, the evolutionary age of nematodes has provided considerable time for nematode diversification. Recent molecular studies indicate that the roots of the nematode evolutionary tree are hundreds of millions of years older than the corresponding tree for insects. Marine nematodes, which inhabit even the deepest ocean floors, have a nucleotide diversity that suggests nematodes flourished before life

Table 1 Nematode communities in selected studies

Ecosystem type	*Abundance ($10^6\ m^{-2}$)*	*Genera (n)*	*Species (n)*	*Bacterivore (%)*	*Fungivore (%)*	*Herbivore (%)*	*Predator/ omnivore (%)*
Grassland	2.3–20	30–124	71–384	24–38	5–20	16–41	26–40
Deciduous forest	2.3–3.7	22–81	34–175	27–46	15–25	13–31	5–32
Tropical rainforest	NA	107	204	35	5	29	30
Tundra	–	58	162	55	3	22	19
Heath	1.2	–		57	–	2	–
Agroecosystems	3.5–5.0	19–44	33–100	36–46	13–19	33–41	5–7
Temperate desert	–	18	23	33	22	17	28
Antarctic coastal	–	15	27	47	27	0	27
Antarctic dry valley	–	3	3	67	0	0	33

NA, not available.

colonized land. The same nematode survival mechanisms that allowed them to be among the first colonizers of land most likely contribute to a competitive advantage in current-day harsh environments.

Physiology

Although nematodes depend on free water for normal functioning, under harsh conditions such as freezing or drying many nematodes are capable of entering a cryptobiotic state, essentially a reversible state of suspended animation until favorable conditions return. Anhydrobiotic success, the ability to withstand the lack of moisture, depends on a slow rate of dehydration, rapid decline in cuticle permeability, and accumulation of compounds such as trehalose and glycerol to stabilize phospholipids and proteins. Species including *Acrobeloides* spp., *Aphelenchus avenae*, and *Scutellonema brachyurum* start to enter anhydrobiosis by coiling at gravimetric water contents of 3.7% (−300 kPa), 9% (−30 kPa), and 15% (−10 kPa), respectively. It is unknown how long nematodes may persist in this state and still survive hydration. Specimens of the wheat gall nematode *Anguina tritici* have been revived after more than 30 years in anhydrobiosis.

Nematodes are not alone among invertebrates in their ability to enter a cryptobiotic state. Therefore, additional clues to their successful colonization of soil are found in their physiological versatility. Physiological adaptations have allowed nematodes to invade habitats in which few other animals can survive and avoid interspecific competition and many environmental selection pressures. Nematodes are capable of regulating their uptake of oxygen over a wide range of partial pressures from 100 to 5%. When oxygen falls below 5%, nematodes convert their use of energy reserves. For example, *Aphelenchus avenae* uses reserves of neutral lipids under aerobic conditions and glycogen under anaerobic conditions. Not only does a hydrostatic skeleton facilitate movement, but also an ability to expand or contract body size in response to gradual changes in concentration of solutions containing sodium, calcium, magnesium, and/or potassium ions. The adjustment process, osmoregulation, is possible by modifying the permeability of their cuticle. Furthermore, nematodes can tolerate a wide pH range, with some species capable of withstanding strong acids or bases (pH 1.6–11.0). Nematode tolerance for temperature is equally remarkable. In hot springs, nematodes live at temperatures as high as or higher than any other Metazoa. *Aphelenchoides parietinus*, a cosmopolitan species, has been reported from 58°C springs in Chile and 61°C springs in New Zealand.

Ecology

Although nematodes have adapted mechanisms to survive extremities of climate, their activity is stimulated by the return of more moderate conditions. For example, communities of nematodes are revived after rain in desert soils or after a relatively warm period in soils of polar regions. Species are found interacting with other organisms in a variety of occupations including competitor, opportunist, parasite, host, predator, or prey. As a competitor, nematodes rival protozoa for access to bacterial food sources. However, differences in size and generation time can alleviate competition by specializing on microhabitats fine-tuned to minute spatial and temporal scales. As opportunists, nematode species are phoretically transported by insects, adhering to their bodies, providing an opportunity to reach food sources at a longer distance than they would be capable of reaching alone. For example, Psychodidae flies carry nematodes to fermenting organic matter; dung beetles carry nematodes to fresh dung; and Scolytidae bark beetles transport Tylenchida and Rhabditida to their tunnels, where they feed on bacteria and fungi. Nematodes that are parasites of plants include both specialists and generalists.

Host ranges may extend to hundreds of plant species or be restricted to a single plant variety. Some nematodes specialize in precise feeding sites along the root. Plant-parasitic nematodes affect primary productivity of plants by altering uptake of water and nutrients. These abnormalities may result from changes in root morphology and/or physiology resulting in reduced productivity. Other nematodes infect insects, killing them within 48 h by releasing insect-pathogenic bacteria into the insect. The insect host dies from the bacterial infection, and nematodes feed on the bacteria and develop and reproduce inside the insect cadaver. In this case, the nematode and bacteria have a mutualistic association. Sometimes, a nematode finds itself in a role reversal, becoming the host or target of fungi specialized for trapping nematodes, using constricting rings, sticky knobs, or hyphal nets. Being in the middle of a food chain, nematodes eventually become prey to higher-order consumers. Nematodes provide a portion of the diet for many kinds of small soil arthropods. For example, a symphylan can hold seven large nematodes in its gut at one time. In 1 day, a mite may consume two large nematodes or several smaller nematodes.

Genetic diversity, nematode abundance, and the variety of niches occupied by nematodes has led to the assessment of nematode communities as a means of making predictions about past or present soil conditions. The species composition and relative nematode abundance of species comprising a nematode community allow nematodes to serve as biological indicators for soil disturbance as well as 'soil health.'

Monitoring

Nematodes contribute directly to biogeochemistry of soils by regulating processes such as decomposition and nutrient cycling. Nematodes do not feed on decaying organic matter directly, but on bacteria, fungi, algae, and actinomycetes that colonize and decompose decaying plant and animal debris. Indirectly, nematodes control availability of nutrients by regulating the abundance or activity of these organisms, releasing nitrogen and phosphorus from microbes they digest, immobilizing nutrients in their live tissues, and excreting excess nitrogen as ammonium. Under field conditions, bacterial-feeding and predatory nematodes contribute 8–19% of nitrogen mineralization in conventional and integrated farming systems, respectively.

Nematode community structure and function are known to change in response to land-management practices such as nutrient enrichment through fertilization by organic or inorganic nitrogen, cultivation, liming, drainage, plant community composition and age, and toxic substances such as heavy metals, pesticides, and polycyclic aromatic hydrocarbons. Disturbance can affect the survival of individuals directly, or indirectly by changing resource levels. For example, a larger ratio of fungal-feeding to bacterial-feeding nematodes suggests less effect by cultivation than a smaller ratio. Any disturbance that results in compaction reduces soil porosity, and the numbers of relatively large-sized nematodes. General biocides such as methyl bromide can nearly eliminate nematodes, returning the ecological succession of soil communities to that assembling a depauperate soil matrix. Although recovery occurs eventually, abundance and diversity of nematode communities may take years to achieve prefumigation levels. Alternatively, some herbicides affect nematodes indirectly by reducing vegetation and smaller additions of organic matter to soil.

The composition of nematode communities may reflect the frequency of disturbance to soil, whether the disturbance is primarily physical and/or chemical in origin. This concept is based on the principle that different species have contrasting levels of sensitivity or tolerance to stress because of unique survival and/or reproductive traits. Smaller values of an index that integrates relative abundance of species within each sensitivity/tolerance class are indicative of a more disturbed environment, and larger values may indicate a less-disturbed environment. Ideally, indicators of soil health would correspond with ecological processes occurring in soil. Because initial experiments have been correlative in nature, it is too soon to claim such an association with great confidence.

The concept of nematodes as indicators of soil condition and their predictive use in soil management represents a tremendous shift in emphasis in the science of nematology. Formerly a science focused on the control of parasitic and harmful species, now nematodes are seen as an integral and potentially useful component of soil systems. In light of this new perspective, it is likely that the study of nematodes will contribute significantly to our understanding of biological processes in the soil.

Further Reading

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