



NEMATODE PHYSIOLOGY: SIGNIFICANT DEVELOPMENTS IN THE UNDERSTANDING OF THE BIOLOGY OF SIMPLE EUKARYOTIC ANIMALS

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Early insights

"They occur in arid deserts and at the bottoms of lakes and rivers, in the waters of hot springs and in polar seas where the temperature is constantly below the freezing point of pure water...enormous depths in Alpine lakes and in the ocean...sometimes the eggs and larvae are so resistant to dryness that if converted to dust they revive when moistened...diversity of habitat...inconceivably abundant". Cobb's (1914) (Fig. 1) assertions, the validity of which has stood the test of time, demand reflection on the physiological amplitude and unique characteristics that would facilitate such a range of habitats and activities.

Nematodes parasitize vertebrates, invertebrates, and plants; many are not parasites but are sustained by feeding on other organisms. Yet, there are recent discoveries of nematodes from the benthos that have no mouths but a rudimentary gut filled with chemoautotrophic bacteria (Ott *et al.*, 1982; Miljutin *et al.*, 2006). Even in some soil nematodes, a reduced mouth and esophagus has led to speculation of diffusion across the cuticle of nutrients in solution (Bongers, 1990, Fig. 2). Early developments in nematology were strongly driven by recognition of the causal organisms of the maladies of man and

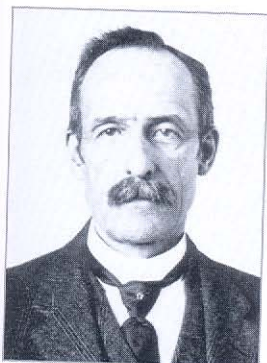


Fig. 1. Nathaniel A. Cobb



Fig. 2. Tom Bongers

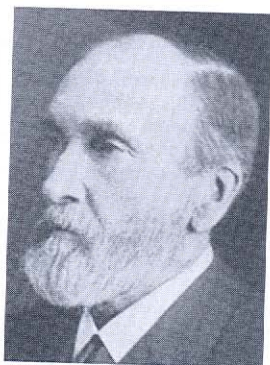


Fig. 3. H.C. Bastian



Fig. 4. Emile Maupas



Fig. 5. Ellsworth Dougherty

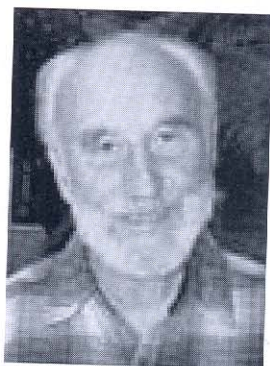


Fig. 6. Warwick Nicholas

domestic animals. Commanded by their size and obvious human impact, vertebrate-parasitic nematodes have been, for centuries, a focus of investigation (W.P. Rogers, Theodor Von Brand, Donald Fairbairn and many others). Consequently, *Ascaris* and other vertebrate-parasitic nematodes have been models for understanding nematode physiology, embryology, and development (Wright, 1998).

Advances in microscopy enabled observation of the micro- and mesofauna of soil and water. Fascination with the biology of the bacterial-feeding nematodes led to an understanding of their life cycles, including the existence of an alternative life stage by such 19th century keen observers as Schneider, Perez and Bastian (Fig. 3). Consider the likely amazement of a reincarnated Emile Maupas (Fig. 4), pioneer of protozoology, were he made aware of the scien-

tific endeavors and advances surrounding *Caenorhabditis elegans*, the nematode that he described from organic soils in Algeria.

Pioneering work on nematode nutrition in the 1950s and 1960s, independently and/or collaboratively, by Ellsworth Dougherty (Fig. 5) in California and Warwick Nicholas (Fig. 6), Sydney Brenner (Fig. 7) and others in England, particularly the recognition of *C. elegans* as a potential tool for unravelling the mechanisms of gene expression, are the basis for the enormous importance of *C. elegans* in recent advances in biology (Riddle & Bird, 1985). A landmark in genomics was the completion of sequencing of the genome of *C. elegans* in 1998 by the cumulative and collaborative efforts of scientists in laboratories worldwide, particularly by Jonathan Hodgkin (Fig. 8), the Nobel Prize winning Cambridge cartel of Brenner, John Sulston (Fig. 9), Robert Horvitz (Fig. 10), and the many others whose activity they spawned. Incredibly painstaking cell-lineage studies, mainly through observation of cell division and activity in the nematode egg, by Sulston and colleagues, revealed that 671 cells resulted from divisions that take place in the egg, and most of the rest of the divisions necessary to make up the 959 cells of this nematode occur in later juvenile stages. Among the insights fueled by these studies is a better understanding of the mechanisms and importance of apoptosis, programmed cell death, in development (Riddle, Fig. 11). The tissue and organ functions associated with movement, sensory functions, and reproductive functions are better understood because of the structural and mechanistic insights from nematode model systems. The genome information on "the worm" has stimulated investigations on its plant- and animal-pathogenic relatives.

The classic studies on nematode ecology and migration through soils (Harry Wallace, Fig. 12), chemosensory attraction to mates, food (Noel Greet, Cliff Blake, Chris Doncaster), moulting (Donald Lee, Fig. 13; Ken Davey; Alan Bird, Fig. 14), survival and adaptation (Adrian Evans; Chris Womersley; Seymour Van Gundy, Fig. 15), and on pathogenesis and cellular changes (Alan Bird; Glenn Bergeson; Victor Dropkin, Fig. 16), of the 1940s to the 1970s, provided an important platform for the advances in understanding of plant-nematode interactions.

In this chapter, we will highlight, somewhat anecdotally, some of the important advances made in energetics, vertical gene transfer, moulting and osmoregulation, physio-molecular interactions of nematodes and plants, and ecophysiological adaptation for fitness and survival. While recognizing the names of the contributors and pioneers, we have not been exhaustive in the completeness of our

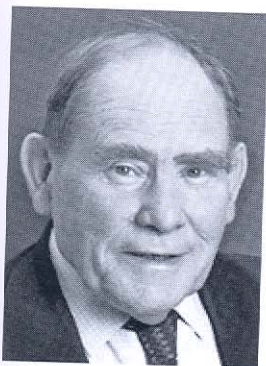


Fig. 7. Sydney Brenner

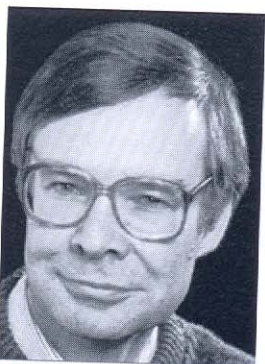


Fig. 8. Jonathan Hodgkin

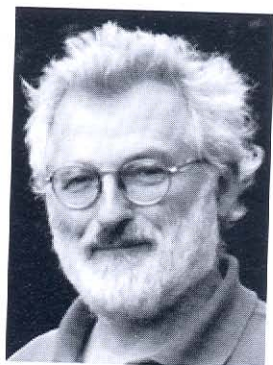


Fig. 9. John Sulston

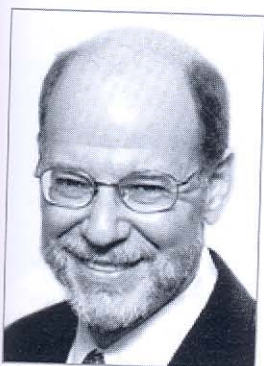


Fig. 10. Robert Horvitz

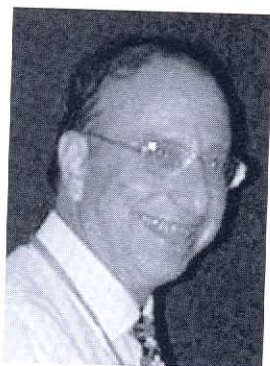


Fig. 11. Donald Riddle



Fig. 12. Harry Wallace

review or in providing citations to sources of the subject matters discussed. In some cases, we are guilty of resorting to familiarity by citing our own papers rather than providing an extensive list of references; we intend no slight and wish to be judged as expedient rather than arrogant in our economy of approach.

Energetics and function

The *C. elegans* developmental studies illuminate the resource conservation dilemma of the plant-feeding nematodes. Assuming that the cell numbers of most plant-feeding nematodes are within a reasonable range of that of *C. elegans*, all of the metabolic energy asso-

ciated with those cell divisions, the differentiation of tissues and most organ systems, hatching, movement, detection of a host, and, in the case of the endoparasites, penetration of the host before feeding commences, is fueled by the resources deposited in the initial single egg cell as it progresses through the oocyte development process. Those resources are finite and must be substantially depleted when partitioned among several hundred cells by the time of emergence from the egg. Thus, energy management strategies that cause the nematode egg, or hatched juvenile, to remain metabolically active prior to access to its food may reduce infectivity.

The metabolic and respiratory energetics of soil-inhabiting nematodes have been studied for populations of several species. Nematode respiration rate per individual decreases with size according to the power dependence of basal metabolism and body weight observed in many organisms, $R = a W^b$, where R is the respiration rate, W is the fresh weight of the individual, and a and b are regression parameters such that b is close to 0.75 for nematodes and other invertebrates (Klekowski *et al.*, 1974; Nicholas, 1975; Apple & Korostyshevskiy, 1980; Atkinson, 1980, Fig. 17). The formula provided by István Andrassy (1956, Fig. 18), in one of the most frequently cited but least read papers in all of nematode ecology, allows calculation of the weight of a nematode as a function of its width and length. It has been an invaluable tool for stepping from the individual to the population and community in studies of nematode energetics.

Estimates and measurements of the coefficients of the metabolic power function have been adopted, with some modifications, for calculating growth and energetics requirements in plant-parasitic nematodes (Melakeberhan & Ferris, 1988; Melakeberhan & Webster, 1992; Reversat, 1987). The calculations highlight the issue of feeding rates and resource partitioning. Unless they have a reliable and sustained food source, as in modified plant host-cell structure, large bodied nematodes often have a smaller gonad:body volume ratio than smaller nematodes. More energy resources are committed to growth and metabolic activity of the somatic tissues than to production of oocytes and eggs. Consequently, populations of larger nematodes that do not have a specialized feeding site grow at a slower rate than those of smaller-bodied organisms.

Respiration rates of adults range between 1.25 and 8.80 nl O₂ h⁻¹ at 20°C among several species studied. Metabolic rates of adults

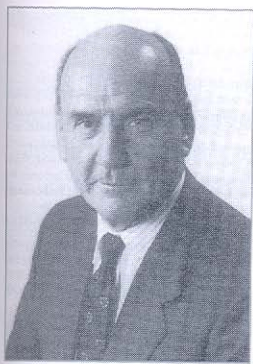


Fig. 13. Donald L. Lee



Fig. 14. Alan Bird



Fig. 15. Seymour Van Gundy

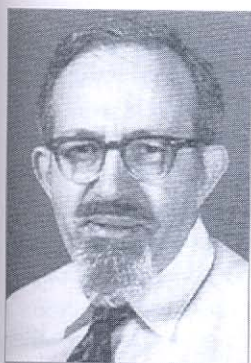


Fig. 16. Victor Dropkin

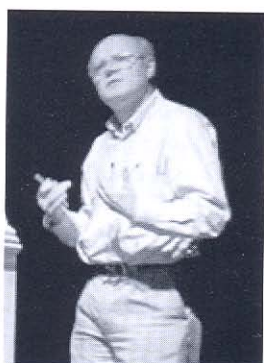


Fig. 17. Howard Atkinson



Fig. 18. István Andrassy

range from $1.15 \text{ nl O}_2 \mu\text{g (f.w.)}^{-1} \text{ h}^{-1}$ for *Rhabditis cucumeris* to $4.43 \text{ nl O}_2 \mu\text{g (f.w.)}^{-1} \text{ h}^{-1}$ for *Mesorhabditis labiata*, at 20°C . At each temperature, metabolic rates of nematodes of similar size vary with thermal adaptation of the species. Metabolic rates of *Cruzanema tripartitum* and *Cephalobus persegnis* were more sensitive to temperature change than were those of *Acrobeloides bodenheimeri*, *A. buetschlii* and *Panagrolaimus detritophagus*. *Cephalobus persegnis* exhibited the greatest total metabolic activity across a range of temperatures, and *P. detritophagus* the least. Observed differences in thermal adaptation may contribute to the predominance of species in the nematode community at different times during the year or at different depths in the soil (Ferris *et al.*, 1995).

That nematode species endemic, and apparently successful, in

the same environment may have different thermal optima (Ferris *et al.*, 1995) is in concurrence with the suggestion of Anderson & Coleman (1982) that temperature-niche breadth mediates competition among species. Differences in temperature-niche breadth determine the predominance of coincident species at different times during the year, or at different depths in the soil. Temporal predominance patterns determine the relative contribution of the coincident species to nitrogen mineralization in managed agricultural systems.

Vertical gene transfer and life history

A.C. "Tasso" Triantaphyllou (Fig. 19) at North Carolina State University has made pioneering contributions to nematode cytogenetics (Evans, 1998). Vertical gene transfer in nematodes is achieved through several mechanisms, including mitotic parthenogenesis, meiotic parthenogenesis, amphimixis, and hermaphroditism. Significant advances have been made in our understanding of how genetic information is transferred and which taxa are amenable to mating experiments that will allow inference of gene function. Mechanisms of sex determination in both parthenogenic and amphimictic species, and sex reversal, were revealed and explained through the studies of Triantaphyllou. It seems likely that sex is determined by the effect of environmental conditions on the degree to which genes from the X chromosome regulate genes on other chromosomes. This would allow for environmentally-mediated sex determination, which is frequently observed. For example, since in sexually reproducing species females are XX and males are XO, one might infer that more X product is required to up- or down-regulate the genetic pathways that result in females than for those that result in males. Consequently, if the signal strength from the X chromosomes is suppressed at high temperature, more males might result. Current studies in the laboratory of Charles Opperman, one of Triantaphyllou's successors, may shed some light on the genetic and molecular basis of sex determination in nematodes <http://www.cals.ncsu.edu/plantpath/>.

Hermaphroditism, an interesting alternative in vertical gene transfer in some members of the family Rhabditidae, was another revelation of the in-depth studies on *C. elegans*. In sequential hermaphroditism, the gonad first produces sperm, which are stored in a spermatheca. The gonad then produces oocytes, which become fer-

tilized eggs as they pass through the spermatheca. In *C. elegans*, about 150 sperm are produced in each arm of the gonad and stored in each spermatheca. The number of sperm produced apparently limits the number of offspring produced by the nematode to around 300 (Gems & Riddle, 1996). True males also occur in a population, but are rare (around 1:1000). However, the frequency of males is enhanced at elevated culture temperature. When a hermaphroditic female is mated with several males, as many as 1400 progeny may be produced (Kimble & Ward, 1988), suggesting that productivity in this form of hermaphroditism, is sperm-limited.

Excretion and osmoregulation

Excretory products of metabolic activity differ in animals of different habitats. Nitrogenous waste products, usually in the form of ammonia, result from metabolic pathways that involve proteins and amino acids. Since ammonia is toxic, terrestrial animals, including arthropods and vertebrates, generally bind the $-NH_3$ group into either urea or uric acid, which are accumulated prior to excretion (Campbell, 1973). Such organisms are termed uricotelic. Nematodes are aquatic organisms, inhabiting marine and fresh water and the water films of soil environments. Like most aquatic organisms, they continually excrete ammonia into the environment as it is produced, thus avoiding the toxic storage problem. Such organisms are termed ammonotelic (Perry, Fig. 20 and Wright, 1998). The excretion of waste nitrogenous products into the soil environment may be a significant contribution to nitrogen availability to plants (Ferris, *et al.*, 1998; Chen & Ferris, 1999). A major difficulty in studying osmotic and ionic regulation of soil-inhabiting and plant parasitic nematodes is their small size, and larger nematodes like ascarids are often used as model systems (Wright, 1998).

Physio-molecular interactions of nematodes and plants

In an era of increasing environmental awareness, it is necessary to find economically and ecologically sustainable nematode management alternatives through an understanding of the physio-molecular and genetic bases of plant nematode interactions from the sub-cellu-



Fig. 19. A.C. Triantaphyllou

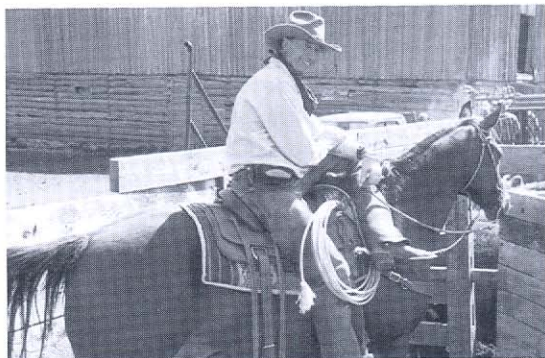


Fig. 21. Richard Hussey

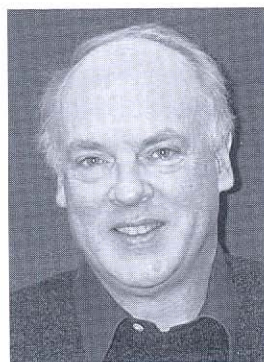


Fig. 20. Roland Perry



Fig. 22. Jaap Bakker



Fig. 23. Valerie Williamson

lar to the ecosystem level. Studies of the physiological changes and formation of specialized feeding sites associated with sedentary plant parasitic nematodes by Alan Bird in Australia and of cellular changes by S.G. Myuge, Glenn Bergeson and Victor Dropkin in the 1960s and 1970s have been the foundation and inspiration for many host parasite studies at the cutting edge of science. The recent activities of several research groups merit high recognition. All are important research programs that are integral to longer-term trajectories from which will emerge novel approaches in nematode management.

First, research spearheaded by Richard Hussey (Fig. 21) at the University of Georgia has characterized the molecular and functional nature of glandular secretions of the root-knot and cyst nematodes, which have very specialized and complex feeding relation-

ships with their host plants. In collaboration with Rick Davis, North Carolina State University, Thomas Baum, Iowa State University, and Jaap Bakker (Fig. 22) and Arjen Schots at Wageningen University, comprehensive profiles have been developed of genes for parasitism that are expressed in the esophageal gland cells of the nematodes (Davis *et al.*, 2000). The potential application of these studies is to target the genes in intervention strategies that will disrupt the host parasite relationship <http://www.plant.uga.edu/faculty/hussey.htm>.

Second, the pioneering work of the Plant Nematode Genetics Group comprising David Bird, Charlie Opperman and collaborators at Rothamsted Research (Rothamsted Experiment Station) in England, which sequenced the *Pasteuria penetrans* (nematode-parasitic bacterium) <http://www.cals.ncsu.edu/plantpath/>. An important goal of that group is to understand the molecular basis of nematode-plant interactions, using *Meloidogyne*, *Heterodera* and *Globodera* spp. as models and employing cellular, genetic and genomic approaches.

Third, Valerie Williamson (Fig. 23) at the University of California, Davis, has, over several decades, made major contributions to our understanding of the molecular and genetic basis of the *Mi*-gene (present in most commercial tomatoes) and other forms of resistance against root-knot nematodes and to the associated host and parasite recognition mechanisms. Isgouhi Kaloshian, now at UC Riverside, and Kris Lambert at the University of Illinois, did their postdoctoral and/or graduate work in Williamson's laboratory and have expanded and extended her studies.

Sterols are among the specific nutritional components that nematodes need from their hosts, and identifying ways to disrupt the sterol supply has been a major focus in the research of US Department of Agriculture's David Chitwood (Fig. 24). Recently, Chitwood & Skanter (2006) identified two genes in *Heterodera glycines* that code for products similar to the 17 α -hydroxysteroid dehydrogenases and are involved in the synthesis of steroid hormones in mammals.

Harry Wallace's (1973) soil-nematode interface and Alan Bird's (1974) and Victor Dropkin's (1980) nematode feeding behaviour analyses have led to more applied studies. Starting from his graduate research with John Webster, the second author of this chapter acknowledges that the classic work of Harry Wallace on the soil-nematode interface provided the basis for his own work on the manipula-

tion of soil nutrients to adversely affect nematode infective and developmental behaviour (Melakeberhan, 1999). Moreover, Victor Dropkin's (1980) categorizing of plant parasitic nematodes into destructive (host cells killed, *Pratylenchus*), adaptive (cells modified, *Heterodera*), and neoplastic (cells modified and undergoing new growth, *Meloidogyne*) feeding behaviors generated interest in whether nematodes of different feeding behaviour affect host physiology differently. Similarity of effects leads to the possibility that the damage of several nematode species may be offset by a single management option (e.g., nutrient amendment). If effects are different, more situation-specific options will be required (Melakeberhan, 2006).

Ecophysiology: physiological adaptations for fitness and survival

Nematodes occupy many trophic levels and perform many services in the soil food web (Bongers & Ferris, 1999). Plant and soil nematodes have evolved a suite of adaptations that confer fitness in a variety of spatio-temporal niches and that enhance their probability of survival under adverse conditions. The physiological basis and mechanisms of nematode survival, including omnivory, dauer stages, cryptobiosis and dormancy, are reviewed by Womersley *et al.* (1998). Plant-feeding nematodes are primary consumers of incoming resources. They, in turn, constitute a resource for many other organisms in the soil food web through predation by fungi, bacteria, and a diversity of mesofauna. Besides providing ecosystem services of nutrient cycling, the predation involved in the transfer of carbon through the soil community may result in top-down regulation of the primary consumer species, particularly where food resources are limited due to seasonal host phenology or competition at high nematode densities. A brief review of some mechanisms of nematode survival and fitness provides insight into the observational and inferential powers of the scientists who have studied these aspects of nematode biology.

OMNIVORY: Although the feeding habits of many plant and soil nematodes have not been determined, a great deal of information is available from experiments, observations, inferences based on feeding structures, and on organism associations. The classic paper of

Gregor Yeates (Fig. 25) and colleagues (Yeates *et al.*, 1993) summarized feeding habit information available to that time. They categorized six feeding types among soil and plant nematodes: feeding on vascular plants, feeding on fungal hyphae, feeding on bacteria, feeding on animals, feeding on unicellular eukaryotes and omnivorous feeding. They also recognized two other categories, the ingestion of substrate incidental to feeding by open mouthed morphotypes such as bacterial feeders and certain predators, and dispersal or infective stages that may not be feeding,

often in phoretic relationships with insects. The term "omnivore" is usually applied to certain nematodes of the Dorylaimida for which omnivory has been observed or for which feeding habits are unknown. Clearly, some dorylaims are plant feeders (e.g., *Xiphinema*) and some are predators (e.g., *Labronema*). True omnivory is an adaptation to unreliable food sources that may be seasonally or spatially sparse. Besides its occurrence in the Dorylaimida, it has been observed in Mononchida where juveniles may be sustained on bacteria (Yeates, 1987) in certain Aphelenchina (e.g., *Aphelenchoides* spp.) and Tylenchina (e.g., *Ditylenchus* spp.) where survival between plant hosts by feeding on fungi is of obvious adaptive significance.

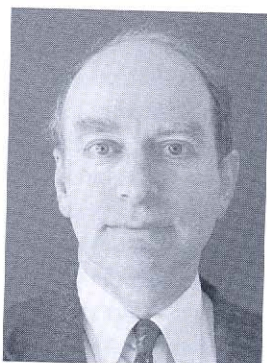


Fig. 24. David Chitwood

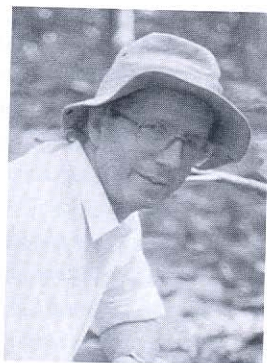


Fig. 25. Gregor Yeates



Fig. 26. David Viglierchio

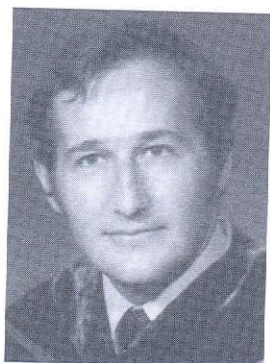


Fig. 27. Neil A. Croll

DAUER STAGES: Many soil nematodes, particularly bacterial feeders of the Rhabditidae, Panagrolaimidae and Diplogasteridae, have a metabolically-suppressed specialized survival stage. Schneider (1866) reported the existence of a life stage of rhabditid nematodes with a cuticle differing from that in other stages; he considered this form to be a moulting stage but was uncertain of its role. According to Maupas (1899), Pérez (1866) recognized an "encysted" stage in *Rhabditis teres* and indicated that larvae easily encysted at the end of the second stage. Experimentally, Maupas (1899) determined that always the same life stage entered encystment when nutrients were lacking. He showed that emergence from the encysted stage occurred with enrichment and noted that encysted nematodes survive for weeks and are often a dispersal stage. Later, Fuchs (1916), in his description of rhabditids associated with bark beetles, coined the term "dauerlarva" for the persistent or enduring stage of these nematodes. Many of the nematodes that have phoretic relationships with insects are in a dauer stage during the phoresy. Likewise, entomopathogenic rhabditids await their insect hosts in a dauer stage. Dauerlarva induction in *C. elegans* is mediated by the ratio between a dauer-inducing pheromone, which is constantly produced by the nematode, and the magnitude of a carbohydrate signal from the bacterial prey (Riddle, 1988). The ratio provides a measure of population size in relation to food availability. When the dauer-inducing pheromone is significantly greater than the food signal, dauer formation commences (Ferris & Bongers, 2006).

CRYPTOBIOSIS: An attribute (literally, hidden life) of certain nematodes that enables their survival without detectable metabolic activity. The most commonly recognized forms of cryptobiosis include anhydrobiosis, cryobiosis, anoxybiosis and osmobiosis in response to dehydration, cooling, low oxygen, and osmotic shock, respectively (Womersley *et al.*, 1998). The first record of anhydrobiosis, although not recognized as such at the time, was that by Needham (1744), when he opened the seed galls of *Anguina tritici* on wheat. Anhydrobiosis is a common attribute of nematodes that are successful in habitats subject to seasonal drying and to those that feed on the above ground parts of plants. For example, fourth stage juveniles of *Ditylenchus dipsaci* enter anhydrobiosis, usually in large masses, on or below the surface of plant tissue, and the term "eelworm wool" describes the appearance of these dried nematodes.

Similarly, the second-stage juveniles of *Aphelenchoides besseyi* enter anhydrobiosis under rice hulls. Many nematode species are capable of anhydrobiosis when subjected to slow drying. However, if the drying is rapid, there is insufficient time for the necessary physiological and membrane structural changes to take place.

DORMANCY: The term is applied to the condition of lowered metabolism and various categories have been recognized in nematodes (Womersley *et al.*, 1998): Facultative quiescence: dormancy under unfavorable conditions with development readily resumed as conditions become favorable. Obligate quiescence: required dormancy for a life stage with development readily resumed under favorable conditions. Facultative diapause: dormancy initiated by environmental factors with delayed resumption of development under favorable conditions. Obligate diapause: dormancy initiated by endogenous factors with delayed resumption of development under favorable conditions after specific requirements are satisfied (e.g., in *Meloidogyne naasi*). Zheng & Ferris (1991) described the delayed development of some eggs in *Heterodera schachtii* despite favorable conditions. They recognized eggs in four categories: the non-dormant condition of eggs that hatch rapidly in water; eggs that hatch rapidly in host root diffusate; eggs that hatch slowly in water over a long period of time; eggs that hatch slowly over a long period of time in host root diffusate. The combination of these categories of egg development results in distribution of hatch over a considerable period and enhances the probability that some of the emerging juveniles will encounter a host plant under conditions conducive to infection, and thus species survival.

HOST RANGE AND HOST RECOGNITION: Many plant-feeding nematodes that are successful in annual crop agriculture have wide host ranges. There is a high probability that they are able to feed on a variety of the plants provided in cropping sequences. However, there are other successful strategies. Some nematodes with quite narrow host ranges are successful because they remain in a dormant state until stimulated to emerge by root exudate signals recognized from a host plant (e.g., *Globodera rostochiensis*). The non-feeding dormant stage might technically be considered a dauer stage without the morphological features of extra cuticle and a closed mouth (Bird & Opperman, 1998). In some cases, the dormant stage is the second

stage juvenile retained in the egg (e.g., *Heteroderinae*) whereas, in other cases, it may be a pre-adult juvenile (e.g. *Paratylenchus* spp.).

RESPONSE TO HOST STIMULI: The soil-root interface and nematode sensory and response behaviour have been the subjects of many investigations over the past several decades (Viglierchio, 1961, Fig. 26; Klingler, 1965; Prot & Van Gundy, 1980; Riddle & Bird, 1985; Pline & Dusenbery, 1987; Robinson, 1995). However, as the always ebullient and insightful Rolo Perry (1996; 2006) of Rothamsted Research points out, many information gaps remain when explaining the physiological basis and mechanism of the interactions.

In a career cut short by his untimely death, the debonair Neil Croll (Fig. 27) synthesized the available information on a range of physiological aspects across the Nematoda in several books. With regard to nematode behavior, Croll recognized that taxes, directed movement towards or away from a stimulus, and kineses, change in the rate of activity or frequency of turning in the presence of a stimulus, are both observed in nematodes (Croll, 1970; Perry, 1996). Resource-locating behavior in nematodes probably consists of a combination of taxes and kineses (Lee, 2002; Rodger *et al.*, 2003; Young *et al.*, 1998), and electrophysiological analyses indicate that reduced activity or more frequent turning can result in aggregation near the stimulus (Perry & Riga, 1995). Taxis and kineses are characterized according to the nature of the stimuli, which may include CO₂, pH, temperature gradients and root diffusates. CO₂, expected to be in higher concentrations in the rhizosphere than in bulk soil, is a strong attractant in a certain concentration range to some nematodes (Klingler, 1965; Pline & Dusenbery, 1987; Robinson, 1995). Interestingly, given the choice of plant roots and insect larvae in an olfactory tube, bacteriophagous entomophilic nematodes moved to plant roots (Boff *et al.*, 2002). However, prior to invading the host, nematodes must sense additional factors to differentiate between the sources of general signals (Rühm *et al.*, 2003). CO₂ may provide a directional stimulus and stimulate a taxis response. However, once the nematode is near the resource, plant signature compounds, such as flavonoids or alkaloids, may precipitate kinesis responses by the nematode resulting in their localization of individuals around food sources.

Although both attraction and repellency of host plants to nematodes have been the subject of several investigations, only a few host- or nonhost-specific compounds have been identified that

mediate the responses (Chitwood, 2002). In a critical assessment of the spatial and temporal nature of the chemoattraction and nematode orientation in soil, Perry (2006) concluded that CO₂ and root diffusates followed by temperature are major nematode behaviour modifying factors.

Outlook

In a relatively short period, significant advances have been made in our understanding of the biology and physiology of nematodes, and we are on an exciting trajectory. Three of the driving forces are evident. First, the success of each new set of researchers in stepping off from the platform erected by earlier workers, in effect embodying the Chinese concept of "standing on the shoulders of the great man". Second, the wonderful advances in technology that have allowed the scaling-down of sensors and the amplification and conversion of the signals necessary for the equipment (developed for rats and guinea pigs) to measure the physiological processes and secretions of the nematodes. Third, the serendipitous selection of *Caenorhabditis elegans*, of all the organisms in the world, as the model system for developmental biology and for genomic characterization. If, as asserted by Lorenzen & Platt (1994), four out of every five multicellular animals on the planet are nematodes, they provide the potential for providing model and assay organisms for advancing science at a multitude of levels, from subcellular biology to the monitoring of global climate change.

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