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DAUER STAGE IN NEMATODES

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ABSTRACT

Nematodes, like many organisms, are adapted to survive in unfavourable environmental conditions and different strategies are used by different species depending on their ecological niche. The free-living model nematode *Caenorhabditis elegans* will enter the dauer stage, a larval stage geared for survival, when unfavourable environmental conditions (such as crowding or lack of food) are encountered. Animal and plant- parasitic nematodes frequently use a survival stage in order to synchronize their life cycle with that of their hosts in order to optimize their chances of successful invasion. Animal parasitic nematodes are frequently activated after the parasite is exposed to conditions found in the gut of animals (high pH, increased CO2), while in the case of some plant-parasitic nematodes, hatching is activated by host root diffusates. The sequence of events from perception of the hatching stimulus to hatching varies considerably between species. This linking of host and plant parasite is a form of quiescence and is restricted to species that are host-specific.

Keywords: *Nematode, C.elegans parasitism, diapauses, daf genes*

INTRODUCTION

Dauer diapause is a stress-resistant, developmentally quiescent, and long-lived larval stage (Alion *et al.*, 2000). Nematode undergo diapauses is a well known fact. The molecular mechanism governing the entry and exit in diapauses has been worked out in a free-living nematode *Caenorhabditis elegans* (Euling and Ambros , 1996). The dauer formation decision is complex, and the outcome greatly impacts the survival of the individual and its progeny. Developing larvae sense cues from their environment (Johnson *et al.*, 1984). Specific neurons interpret these cues, and translate them into modulation of several interconnected signal transduction pathways. Ultimately, this modulation gives rise to a specific outcome to enter dauer or to develop continuously (Lin *et al.,* 1997). Nematodes were once classified with a very large and heterogeneous cluster of animals grouped together on the basis of their overall worm-like appearance, simple structure of an internal body cavity called a pseudocoelom, and the lack of features such as cilia and a well-defined head that are found in most animals.

Diapause in Nematodes

This group, variously known as Aschelminths or Pseudocoelomata, is today no longer recognized as a natural one. It is quite likely that the simple body plan of these organisms has resulted from reduction and simplification from more than one group of ancestral organisms, and so the pseudocoelom is neither a uniquely derived nor useful character. The simplicity is thus a result of secondary simplification from a more complex body design, and not necessarily an indication of primitive or simple origins. Current studies indicate that nematodes are actually related to the arthropods and priapulids in a newly recognized group, the Ecdysozoa. The body of a nematode is long and narrow, resembling a tiny thread in many cases, and this is the origin of the group's name. The word "nematode" comes from a Greek word *nema* that means "thread". The epidermis (skin) of a nematode is highly unusual; it is not composed of cells like other animals, but instead is a mass of cellular material and nuclei without separate membranes. This epidermis secretes a thick outer cuticle which is both tough and flexible (Riddle *et al.*, 1981).

The cuticle is a feature shared with arthropods and other ecdysozoans. As in those other groups, the cuticle is periodically shed during the life of a nematode as it grows, usually four times before reaching the adult stage. The cuticle is the closest thing a roundworm has to a skeleton, and in fact the worm uses its cuticle as a support and leverage point for movement. Long muscles lie just underneath the epidermis. These muscles are all aligned longitudinally along the inside of the body, so the nematode can only bend its body from side to side, not crawl or lift itself. A free-swimming roundworm thus looks rather like it is thrashing about aimlessly (Wallace *et al.*, 1996). The muscles are activated by two nerves that run the length of the nematode on both the dorsal (back) and ventral (belly) side. Unlike other animals, where the nerves branch out to the muscle cells, a nematode's muscle cells branch toward the nerves.

The ventral nerve has a series of nerve centers along its length, and both nerves connect to a nerve ring and additional nerve centers located near the head. The head of a nematode has a few tiny sense organs, and a mouth opening into a muscular pharynx (throat) where food is pulled in and crushed. This leads into a long simple gut cavity lacking any muscles, and then to an anus near the tip of the body. Food digested in the gut is not distributed by any specialized vascular system, and neither is there a respiratory system for the uptake or distribution of oxygen. Rather, nutrients and waste are distributed in the body cavity, whose contents are regulated by an excretory canal along each side of the body (Aboobaker & Blaxter, 2000). Many nematodes are able to suspend their life processes completely when conditions become unfavorable; in these resistant states they can survive extreme drying, heat, or cold, and then return to life when favorable conditions return. This is known as cryptobiosis, and is a feature nematodes share with rotifers and tardigrades.

Fossil nematodes have been found in rocks from as early as the Carboniferous. Most living roundworms are microscopic, meaning that their discovery as fossils is likely to be difficult. On the other hand, one species of parasitic nematode can reach 13 meters in length -- it parasitizes the sperm whale. Nematodes also lack any substantial hard parts, again resulting in a spotty chance for fossilization. Despite these problems, fossil nematodes are occasionally found in amber (fossilized tree resin) from the Cenozoic. Because many of their relatives have left fossils dating from the Cambrian, it is likely that the nematodes have been around at least that long in some form. nematode lives not only in almost every geographic location on Earth, but live in such extreme habitats as ice and hot springs, as well as living on or in almost every other kind of animal and plant alive today. Free-living nematodes are extremely abundant in soils and sediments, where they feed on bacteria and detritus. Other nematodes are plant parasites and may cause disease in economically important crops. Still others parasitize animals (including humans); well-known parasitic nematodes include hookworms, pinworms, Guinea worm (genus *Dracunculus*), and intestinal roundworms (genus *Ascaris*).

Dauer is described an alternative developmental stage of nematode worms, particularly rhabditids including *Caenorhabditis elegans* and this phenomenon is reported from certain plant-parasitic nematodes as well whereby the larva goes into a type of stasis and can survive harsh conditions (Dieterich and Sommer, 2009). Since the decision to enter the dauer stage is dependent on environmental cues, it represents a classic and well studied example of polyphenism (Fusco and Minelli, 2010). The Dauer state is given other names in the various types of nematodes such as ‘diapause’ or ‘hypobiosis’, but since the *C. elegans* nematode has become the most studied nematode, the term ‘dauer stage’ or 'dauer larvae' is becoming universally recognised when referring to this state in other free-living nematodes. The dauer stage is also considered to be equivalent to the infective stage of parasitic nematode larvae. As first proposed in 1899-1900, all nematodes have five stages separated by four moults. Under environmental conditions that are favorable for reproduction, *C. elegans* larvae develop through four stages or moults which are designated as *L1*, *L2*, *L3* and *L4*. After L4, animals moult to the reproductive adult stage. However, when the environment is unfavorable, L1 and L2 animals have the option to divert their development from reproduction to dauer formation. Signals such as temperature, food supply, and levels of a dauer-inducing pheromone, a population density cue, influence this dauer decision. Dauer larvae are thus considered an alternative L3 stage larva, and this stage is sometimes preceded by L2d. L2d animals are considered pre-dauer and are characterised by delayed development and dark intestines produced by storage of fat. L2d larvae can either continue normal development or enter dauer stage depending on whether the conditions that triggered their formation persist. Dauer is not, however, a permanent condition. In fact, if the food supply and the population density become optimal for growth the dauer larvae can exit this stage and become L4s and then adults.

Dauer larvae are extensively studied by biologists because of their ability to survive harsh environments and live for extended periods of time. For example, *C. elegans* dauer larvae can survive up to four months, much longer than their average lifespan of about three weeks during normal reproductive development. Two genes that are essential for dauer formation are *daf-2* and *daf-23*. Dauer formation in *C. elegans* requires a nuclear receptor DAF-12 and a forkhead transcription factor *daf-16*. In favorable environments, DAF-12 is activated by a steroid hormone, called Dafachronic Acid, produced by the cytochrome p450, DAF-9. DAF-9 and DAF-12 have been implicated by Cynthia Kenyon and colleagues as being required for extended longevity seen in animals that lack germlines. Kenyon showed that, although the *daf-16* gene is required for life extension in *C. elegans*, the life extension effect can be uncoupled from dauer growth arrest. The lifespan increase was shown to be associated with an increase in stress resistance.

A characteristic of the dauer stage is the pronounced alae which may be implicated in the entering (L1) and exiting (pre adult or L4 in *C. elegans*) of the dauer stage (Golden and Riddle, 1984).

Dauer larvae generally remain motionless, but can react to touch or vibrations. They can stand on their tails, waving their bodies in the air, and attach themselves to any passing animals, particularly insects, enabling them to travel to new food sources. For example, dauer larvae of rhabditids are often found in parallel rows under the elytra of dung beetles, which transport them to fresh supplies of dung. Dauer hypothesis has been shown to play a crucial role in evolution of parasitism among parasitic nematodes (Mitreva *et al.*, 2009).

CONCLUSIONS

Varying degrees of quiescence, particularly anhydrobiosis, enable nematodes to survive a variety of extreme conditions, including desert soils, Antarctic climates, dry fallow soils without hosts, or dispersal in dry seed, plant debris. The phenomenon may be more common in nature than formerly thought. Extreme states of anhydrobiosis appear to be more common in nematodes in water-stressed environments such as drying, above-ground plant parts, but nematodes active at the soil-air inter-face are also vulnerable to desiccation and would benefit from such strategies. Our ability to investigate and understand nematode ecology in these environments will remain limited unless the anhydrobiotic portion of the community is considered. Studies of such marginal and stressful environments have and will continue to yield more information on anhydrobiosis and other nematode survival strategies.

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