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Life History of *Pelodera strongyloides* (Schneider) in the Orbits of Murid Rodents in Great Britain[1]

GEORGE O. POINAR, JR.

The free-living soil nematode, *Pelodera strongyloides* (Schneider) can be cultivated successfully on artificial media through several generations if adequate numbers of bacteria are supplied as food. Trapido (1965), however, discovered larvae of *Pelodera strongyloides* in the orbits of Muridae in England and Scotland in June, 1963, and brought this association to the attention of the author, then working at Rothamsted Experimental Station in Harpenden, England.

In this association, the nematodes occurred only in lacrimal fluid of the ocular orbit and were never found inside the eyeball.

P. strongyloides has been found in a number of habitats and there are reports of its occurrence in skin pustules of mammals. These findings have been summarized by Chitwood (1932) who examined specimens from the skin of dogs. He concluded that, under rare conditions, this species is capable of secondary invasion into animal tissues.

Stammer (1956) and Osche (1963) found *P. strongyloides* in the orbits of rodents in Germany. Similar larvae were collected by Dr. C. J. Weinmann from the orbits of a specimen of *Microtus californicus* (Peale) in California. Another possible record may be the report by Rausch (1952) who found nematodes in the orbits of lemmings in Alaska.

In England, the nematodes often occurred in large numbers in the corners of the orbits of infected rodents and moved actively through the lacrimal fluid when the eyelid was drawn back. In one instance, 1,293 larvae were removed from the orbits of a bank vole, *Clethrionomys glareolus* (Schreber). More than 90% of *C. glareolus* sampled in the vicinity of Oxford, England, were infected. Specimens of *Apodemus sylvaticus* (L.) were also infected, but to a lesser extent.

LIFE HISTORY: The life history of *P. strongyloides* was studied in the laboratory. Twelve infected specimens of *C. glareolus* were collected from the field and placed in small cages partially filled with moist, sterilized soil. Over a period of several months, soil samples were removed from each cage and the nematodes extracted by a modified Baermann funnel. At the same time, a sample of nematode larvae was removed from the lacrimal fluid for examination.

Two weeks after the infected voles were introduced into the cages, all stages of *P. strongyloides* could be extracted from the soil. When transferred to Nigon's nutrient agar medium (Nigon, 1949), the nematodes went

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through several generations without any association with the voles or vole products. During the following 2 weeks, the soil in several cages became fairly dry and was found to contain a number of "infective" larvae of *P. strongyloides*

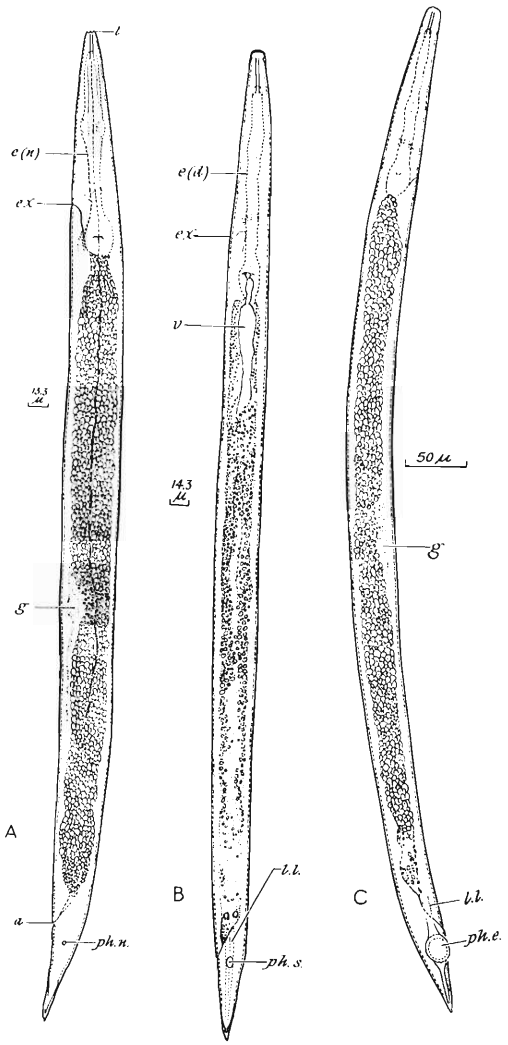

Fig. 1. Comparison of free-living, infective, and parasitic larvae of *Pelodera strongyloides* (Schneider). (A) A free-living larva as developed on Nigon's medium. (B) An "infective" larva recovered from soil in a cage containing infected individuals of *Clethrionomys glareolus*. (C) A mature parasitic larva removed from the lacrimal fluid of *Clethrionomys glareolus*.

still enclosed in their last-stage cuticle (Fig. 1, B). They were much slower-moving than the free-living larvae (Fig. 1, A) and when placed in water moved slowly back and forth inside their cuticles. These ensheathed larvae were narrower than the larvae of the free-living generation and would often remain motionless in culture plates for a long time. The lips were offset, the stoma long and narrow, and the esophagus appeared degenerate, with both the metacorpus and the basal bulb musculature reduced. Many possessed a viscous material behind the bulb flaps which often extended into the anterior portion of the intestine. The oval-shaped phasmids were slightly enlarged.

Coincident with the appearance of ensheathed larvae in the soil was the finding of identical forms in samples from the lacrimal fluid of caged voles.

The development of the larvae in the lacrimal fluid was studied by periodic sampling of infected *C. glareolus* in metal bottom cages, which prevented reinfection of the orbits from soil.

After several days, the newly introduced ensheathed larvae would exsheath and begin to move slowly through the lacrimal fluid. Development of the exsheathed larva in the lacrimal fluid usually took 2–3 weeks. This is relatively long, considering the life cycle of the free-living generation takes only 5 days on Nigon's medium.

During this developmental period in the lacrimal fluid, the body increased in length and width and gradually became granular from the deposition of food material in the intestine. The lips gradually became less offset.

Most remarkable was the enlargement of the phasmids (Fig. 2). Shortly after the newly introduced larvae exsheathed in the lacrimal fluid, the phasmids, although larger than those of the free-living larvae, appeared as small discs (Fig. 2, A). The phasmidial glands contained secretions which reached the exterior via a phasmidial duct. After 2 days, the contents of the glands increased, enlarging the gland reservoirs and forcing material into the phasmidial ducts (Fig. 2, B). Eventually, each gland enlarged to a point where its inner wall was in contact with that of the opposite pair and at the same time, forced the phasmidial ducts apart and stretched the phasmidial opening (Fig. 2, C). At this time, secretions

could be seen in phasmidial canals, which extended anteriorly into the body cavity. When the larva was fully developed, the phasmidial openings enlarged and appeared as a pair of discs on the tail of the nematode (Fig. 2, D).

Soon after this phase, parasitic larvae were found in the soil under the infected voles (Fig. 1, C). These were postparasitic larvae and when removed to Nigon's medium, they molted to the adult stage and began a free-living existence. I was unable to find any sign of a molt occurring between the period of exsheathment and the final molt in the soil to the adult form. Further studies are now in progress to determine the total number of molts in this species and the stage of the infective form. The phasmidial discs were shed with the last cuticle and the adults, which now had normal phasmids, appeared morphologically identical to free-living adults reared several generations on media in the laboratory. The sexual stages of *P. strongyloides* are illustrated in detail by Chitwood and Chitwood (1937, see p. 8–9), but no mention has been made of enlarged phasmids in previous cases of *strongyloides*–mammal associations.

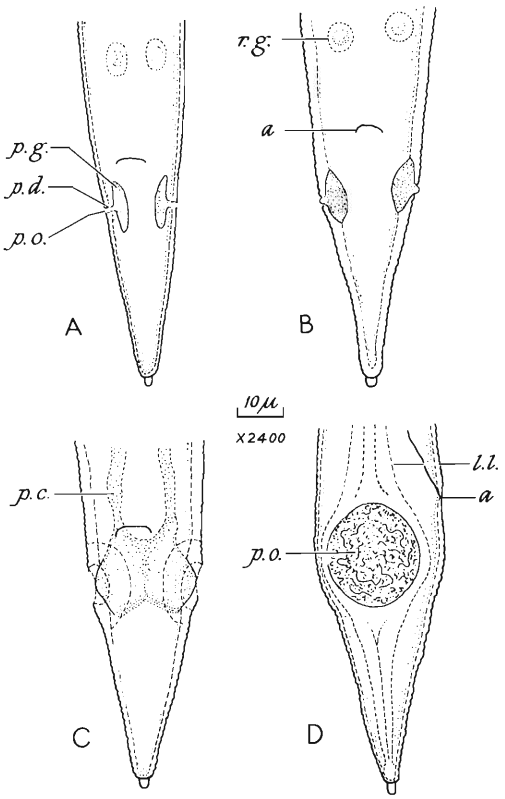

Fig. 2. Phasmidial development in a recently exsheathed parasitic larva of *Pelodera strongyloides* (Schneider). (A) Ventral view of larval tail in an individual which had recently exsheathed. (B) Ventral view of larval tail showing initial swelling of phasmids. (C) Ventral view of tail of an older parasitic larva. (D) Lateral view of tail in a mature parasitic larva showing how the enlarged phasmidial opening has distended the lateral line.

DISCUSSION

The larvae of *Pelora strongyloides* (Schneider) gain entrance into the lacrimal fluid of Muridae through the development of special infective larvae which are formed in the soil. Low humidity stimulates the formation of "infective" larvae, which withstand extremes of temperature and drought that often kill the remainder of the population.

The actual manner of entrance into the orbit is not known, but observations indicate that the infective larvae may be picked up on the feet of the rodents and transmitted to their orbits while the rodents are grooming.

Shortly after entrance, the ensheathed nematode exsheaths and begins development in the lacrimal fluid. During this period, the body size increases and phasmids enlarge. When fully developed, the larvae leaves the orbit and enters the soil where it molts to the adult stage.

One rodent can serve as "host" for several generations of nematode larvae. The death of the vole is not necessary for the completion of nematode development. In fact, when experimental voles died, most of the nematode larvae also died and only a few larvae entered the soil.

The enlargement of the phasmids in larvae living in a somewhat hypertonic environment suggests a possible function of these structures. Thorne (1961) states that the function of phasmids in nematodes is not known, but thinks that in some cases fluid may be expelled from them for the purpose of leaving a scent trail which would attract other members of the same species. Wallace (1963) states that the phasmids in plant parasitic nematodes are probably sensory. This view is also shared by Hyman (1951) who mentions that they are best developed in parasitic forms.

Stephenson (1942) found that the phasmids of *Rhabditis terrestris* Stephenson become enlarged when nematodes are placed in a 0.34 M solution of NaCl. This hypertrophied condition is frequently seen during the recovery process 20–30 hours after immersion in the salt solution when the larvae were adjusting to the hypertonic environment.

From my findings and Stephenson's, it seems that the phasmids may be connected with maintaining the correct osmotic balance in the body, since lacrimal fluid contains about 1.30% inorganic salts.

Throughout the entire study, I have found no obvious pathological effects from the presence of *strongyloides* in the orbits of *C. glareolus*. In cases where hundreds of nematode larvae occur in each orbit, there may be a mechanical obstruction of vision, but inflammation of the eye or associated tissues was never observed. Possibly the nematode larvae obtain their nourishment from solutes in the lacrimal fluid and may also ingest bacteria or debris introduced into the orbit.

I have not been able to restore development of free-living populations of *strongyloides* from the infective larvae. When these "dauer" forms are transferred from dry soil to rich bacteria-laden agar cultures they do not feed or develop but remain quiescent.

The movement of larvae into the orbits of rodents may benefit *strongyloides* (1) by carrying the nematode over periods of adversity, (2) by providing a relatively unexploited ecological niche resulting in little competition for food, and (3) by providing an excellent means of distribution.

SUMMARY

Pelodera strongyloides (Schneider) is capable of forming an infective, ensheathed larva which can develop in the lacrimal fluid of murid rodents. After a developmental period of 2–3 weeks, the larvae leave the orbits and molt to the adult stage in the soil.

While in the lacrimal fluid, the larvae develop enlarged phasmids which may be associated with the excretion of salts, thus regulating their osmotic balance.

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Abbreviations used: a—anus; e(d)—degenerative esophagus; 3(n)—normal esophagus; ex—excretory pore; g—primordial gonad; l.—lips; l.l.—lateral line; p.c.—phasmidial canals; p.d.—phasmidial duct; p.g.—phasmidial gland; p.o.—phasmidial opening; ph.e.—enlarged phasmid; ph.n.—normal phasmid; ph.s.—slightly enlarged phasmid; r.g.—rectal glands; v—viscous material.