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Nemata

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Phylum Nemata

Suborder Camallanina

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Chapter 54

Camallanina (Suborder): Guinea Worm and Related Nematodes

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Introduction

Including the infamous species *Dracunculus medinensis*, the famed guinea worm of humans that has been known since antiquity, this group contains nematodes that live as adults in the gastrointestinal tracts, body cavities, or tissues of their vertebrate hosts (Anderson, 2000; Moravec, 2006). A common, if not universal, feature of this order is that the embryos develop through ovoviviparity and hatch in utero. In many species, the body of the gravid female ruptures, often upon contact with water, to release these newborn juveniles. The life cycle is aquatic and involves crustacean first intermediate hosts; as such, not surprisingly, the vast majority of these nematodes parasitize fishes, although *D. medinensis* infects humans and other terrestrial mammals.

The group has been classified within the conventional order Camallanida but is now better recognized as a natural (monophyletic) suborder Camallanina (Černotíková et al., 2011). There appear to be no unique morphological features that distinguish the camallinidans as a whole, but each of the 2 superfamilies (see below) have their own typical morphology and biology. Among them, not just *Dracunculus medinensis*, but also several other species cause pathology and disease.

Systematics, Taxonomy, and Phylogenetics

The order Camallanida (or suborder Camallanina) now comprises 2 superfamilies: **Camallanoidea** with 1 family, Camallanidae, and **Dracunculoidea** with the families Daniconematidae, Dracunculidae, Guyanemidae, Lucionematidae, Micropleuridae, Philometridae, Philonemidae, Skrjabillanidae, and Tetanonematidae (Moravec, 2006; Nadler et al., 2007; Černotíková et al., 2011) (Figure 1). Molecular phylogenetic studies have confirmed that many of these camallanids form a natural group, but the relationships of the lesser-known families, namely, Guyanemidae, Lucionematidae, and Tetanonematidae, remain untested (Wijová et al., 2005; 2006; Nadler et al., 2007; Choudhury and Nadler, 2018). Phylogenetic studies have also shown that Anguillicolidae, comprising nematodes of the swimbladder of anguillid eels, belongs with the Gnathostomoidea (Wijová et al., 2006).

Superfamily Camallanoidea

Family Camallanidae

As mentioned above, camallanids are mainly parasites of the gastrointestinal tract of fishes but also parasitize turtles, amphibians, and occasionally aquatic snakes.

Morphology

The camallanids are easily recognizable by their distinctive thick-walled **buccal capsule** that may be ridged on its inner surface, a rounded or slit-like **mouth opening**, mostly without lips, and an **esophagus** with anterior muscular and posterior glandular regions. Females possess a **vulva** near the mid-body. Males are often considerably smaller than females and have caudal **alae** with pedunculate **papillae**. The slender first stage juveniles (J_1) have typically attenuated **tails** that in some species have digitate ends (Moravec and Justine, 2006). The third stage juveniles (J_3) of many species have characteristic **spike-like processes** at the tip of their tails (see Figures 2 and 3).

Distribution

Camallanids are widely distributed in freshwater as well as marine environments. The genus *Camallanus*, in particular, has a worldwide distribution with numerous species in freshwater and marine fishes. The freshwater bodies of the Neotropical region have a rich diversity of camallanids in fishes, mainly in the genus *Procamallanus* (Moravec, 2009). Baker (1987) counted approximately 150 species of camallanids worldwide, of which 40 species were in hosts other than fishes (turtles being the most common among these).

Life cycles

Gravid females presumably release juveniles (J_1) into the intestinal tract of their definitive hosts, but it is not uncommon to see females hanging out of the anus of the fish hosts, in which case, the juveniles are shed directly into the surrounding water. Gravid females of the North American species, *Camallanus oxycephalus*, rupture to shed their juveniles. These shed juveniles are active and attract the attention of copepods that ingest them as food. The juveniles burrow through the copepod gut and enter the copepod's hoemocoel

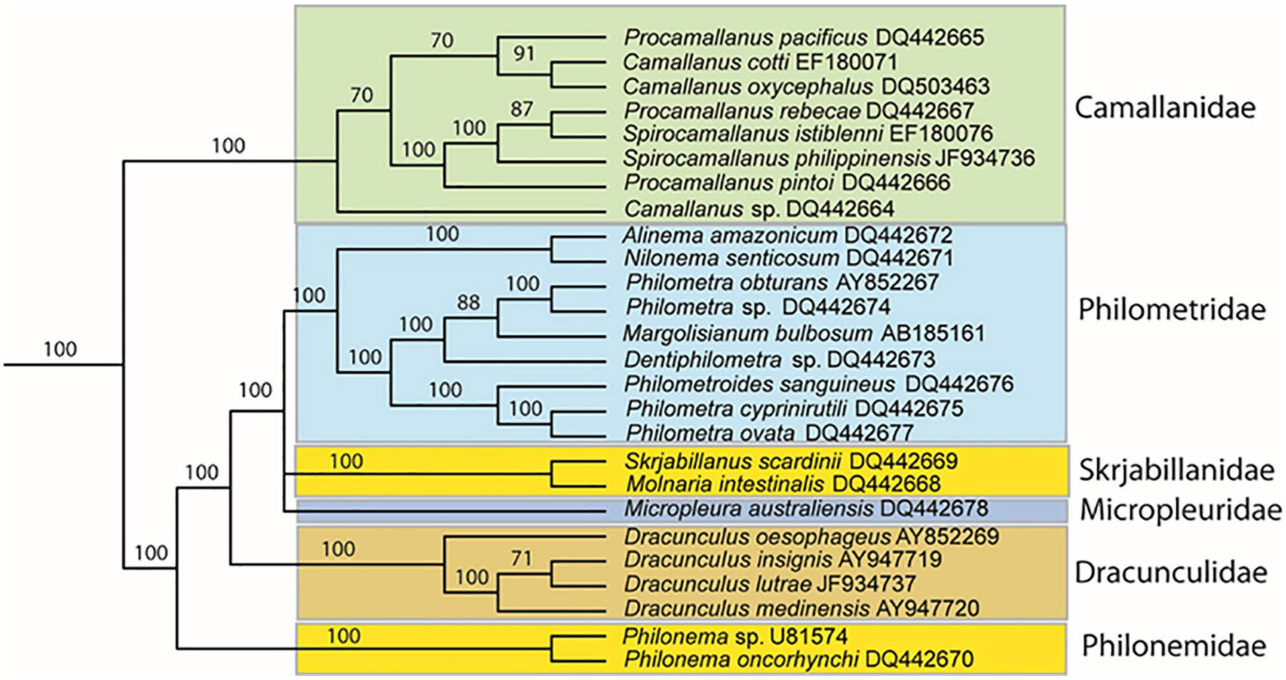

Figure 1. Part of the phylogeny of endoparasitic nematodes based on Bayesian analysis, showing interrelationships of some of the families in suborder Camallanina. Numbers refer to Bayesian Posterior Probability values. Values higher than 90 indicate strong support. Source: Adapted from Choudhury and Nadler, 2018. License: CC BY-NC-SA 4.0.

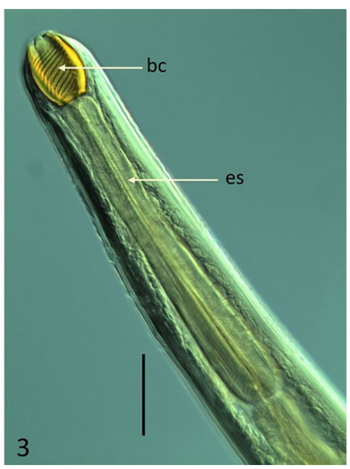

Figure 2. *Camallanus ancylodirus* from quillback (*Carpiodes cyprinus*: family Catstomidae). Source: A. Choudhury. License: CC BY-NC-SA 4.0.

Figure 3. *Procamallanus* sp. from a tetra (*Bryconamericus scleroparius*: family Characidae); bc = buccal capsule, es = esophagus. Source: A. Choudhury. License: CC BY-NC-SA 4.0.

(fluid filled body cavity); there they develop to a stouter J_3 stage. The J_3 stage is easily identified as a camallanid because it already has the distinctive buccal capsule of the family and its tail has the characteristic terminal spike-like processes. When copepods infected by developed J_3 juveniles are ingested by the definitive hosts, the juveniles develop into J_4s and then adult worms in the host's gastrointestinal tract. However, it is common for camallanids, especially those species with piscivorous definitive hosts, to use another host in their life cycles, most commonly a paratenic host. Such a paratenic host is typically a smaller fish that is also often prey for the piscivorous definitive host. The J_3 juveniles from the ingested copepods consumed by the paratenic host persist in the gut or remain encapsulated in visceral organs. When the correct definitive host consumes an infected paratenic host, the J_3 juveniles develop to adulthood. In some cases, the J_3 juveniles may even develop to the J_4 stage in a much smaller paratenic fish host, but because further development (to the J_4) occurs, such a host may now be arguably considered a true second intermediate host rather than a paratenic host. In these ways, many camallanids bridge an ecological gap in the food web, to reach their piscivorous definitive hosts that would not normally consume copepods directly.

The life cycles of the common European species *Camallanus lacustris* and the equally common North American species *C. oxycephalus* illustrate the principles and phenomena discussed in the foregoing section. Both species use paratenic hosts, and in addition, *C. lacustris* can also re-establish as adults in larger predatory fish hosts (**post-cyclic hosts**) (Moravec, 1994). Partial or full life cycles are also known in species of *Neocamallanus*, *Paracamallanus*, and *Procamallanus* (including *Spirocamallanus*) (Moravec, 1998; Anderson, 2000).

Pathology and disease

Camallanids are capable of causing considerable pathology as adults (Meguid and Eure, 1996; Dick and Choudhury, 1995). For example, *Camallanus oxycephalus* can cause rectal prolapse accompanied by the destruction of the gut epithelium, hyperplasia of underlying tissue, inflammation, vascularization, and infiltration by various leucocytes and fibroblasts (Dick and Choudhury, 1995). *Procamallanus spiculogubernaculus* causes blood loss in the stinging catfish, *Heteropneustes fossilis*, in India (Sinha and Sinha, 1988). The highly successful invasive species *C. cotti* causes visible swelling and inflammation of the anus in poeciliids (for example, guppies) accompanied by hemorrhaging, edema and extensive rectal tissue erosion; it has become the main nematode parasite of poeciliids in aquaculture (Rigby et al., 1987; Menezes et al., 2006; Moravec̆ and Justine, 2006).

Superfamily Dracunculoidea

The dracunculoids are unique in that, unlike most other nematodes, they occupy the various cavities of the body other than the gut, as well as some tissues.

The anatomy of dracunculoids is also peculiar in several ways. Unlike their camallanoid relatives, species of all but 1 order of dracunculoids have no buccal capsule; only species in Skjrabillanidae have a relatively small buccal capsule. The lack of a buccal capsule gives the unique appearance of a muscular esophagus opening directly to a mouth, especially because these worms also lack lips. The vulva and anus of mature females of several species are often atrophied (Moravec̆, 2006).

The dracunculoids include some of the smallest parasitic nematodes, such as the ~ 1 mm-long adults of *Lucionema* spp. as well as some of the longest, such as *Dracunculus medinensis* and some philometrids, that can exceed 1 m in length (Moravec̆, 2006). The males of many species are markedly smaller than the females.

Like their camallanoid cousins, dracunculoids use copepods as first, and often the only, intermediate hosts. They are distributed worldwide and the vast majority of species are parasites of fishes; only species in Dracunculidae are exclusively parasites of tetrapods, including humans.

In fact, the superfamily includes one of the most high-profile nematodes of humans, the guinea worm, *Dracunculus medinensis*, which is discussed in more detail below. Moravec̆ (2006) has provided a thorough review of the morphology and biology of this group, including a key to species. Life cycles have also been reviewed by Anderson (2000).

Family Dracunculidae

The family contains 2 genera, *Avioserpens* and *Dracunculus*. The 4 known species of *Avioserpens* are all parasites of aquatic birds. *Dracunculus* comprises 11 species, of which 6 are in snakes in Asia, Africa, Madagascar, and Australia, as well as 1 found in turtles, and 4 in mammals (including *D. medinensis* of humans) (Moravec̆, 2006; Jones and Mulder, 2007).

Dracunculus medinensis

This is the famed guinea worm afflicting humans, a nematode known since antiquity. The ancient Egyptians, Israelites, Vedic Indians, Persians, Arabs, Greeks, and Romans all seemed to have been aware of this parasite; ancient texts of several of these cultures mention the disease. The fiery serpent Moses speaks of in the Old Testament may refer to the guinea worm because the parasite was common in the Levant. Calcified remains of the guinea worm were found in an Egyptian mummy, and their extraction—by coiling the female worm on a small twig—was described by classical historians. The common emblem in the medical profession, the caduceus, which depicts 2 snakes wound around a staff, may have been inspired by the guinea worm. Linnaeus (1758), in his famous Systema Naturae, gave the worm its first scientific name, *Gordius medinensis*, but taxonomists later placed the worm in its current genus, *Dracunculus*. Muller (1971) and Moravec̆ (2006) provide excellent accounts of the history of this worm's association with humans.

Morphology

The females of *Dracunculus medinensis* are best known and most commonly encountered. Their slender, cylindrical bodies reach lengths of 80 cm in humans. The anterior end is blunt with a small mouth opening surrounded by raised papillae. The tail is curved and conical with a tiny blunt mucron at the tip. The intestine is collapsed. The uterus is voluminous and filled with up to 3 million J_1 juveniles at a time. The vulva is not functional. In stark contrast, the males are slender worms only 3 mm-long, at most. They have a similarly rounded anterior with a tiny mouth opening surrounded by small papillae. They have a conical pointed tail. The males are hardly ever seen by humans. Elements of the morphology of *D. medinensis* are shown in Figure 4.

Distribution

The original range of the guinea worm formed a broad belt across Sub-Saharan Africa, north across the Levant and the Arabian Peninsula, and through Iran into India. However, due to sustained eradication programs, the parasite is now localized only in a few areas in Africa and India.

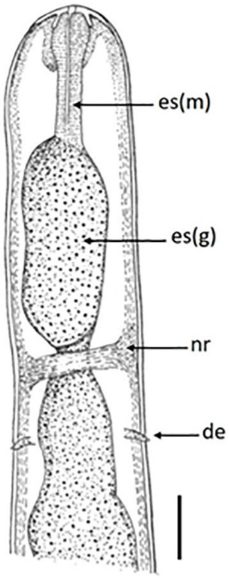

Figure 4. Anterior end of adult male guinea worm *Dracunculus medinensis*; es(m) = muscular esophagus, es(g) = glandular esophagus, nr = nerve ring, de = deirids. Source: Adapted from Moorthy, 1937. License: CC BY-NC-SA 4.0.

Figure 5. Aleksei Pavlovich Fedchenko (1844–1873), Russian naturalist and explorer. Source: Brockhaus and Efron Encyclopedic Dictionary (Энциклопедический словарь Брокгауза и Ефрона). https://upload.wikimedia.org/wikipedia/commons/8/85/Alexei_Fedchenko.jpg. Public domain.

Life cycles

Humans become exposed to the infective J_3 stage in copepods—the first and only intermediate hosts—by drinking unfiltered water contaminated by infected copepods. After a long—10 months or more—period of development in the human body, the gravid female reaches the connective tissue under the skin and begins initiating a localized blister, commonly on the upper part of the foot. The blister grows and eventually bursts; a small portion of the gravid female's body near its anterior end protrudes from the open blister and ruptures on contact with water. The J_1 juveniles are thus shed into the surrounding water, ready to infect copepods. Once that portion of the worm is spent, it dries and the female worm moves a fresh portion of her body into the opening so she can shed more juveniles. The mechanical extraction of the worm from human tissue is facilitated by its behavior (see section below). Eventually, the female sheds all her juveniles and then dies. A variety of cyclopoid copepods in several genera can be hosts of the J_3 juveniles. Eberhard and colleagues (2016) have shown that frogs can serve as paratenic hosts. Dogs can serve as reservoir hosts. As mentioned above, Anderson (2000) and Moravec (2006) provide thorough reviews of the life cycle.

Experimental life cycle studies in cats, dogs, and rhesus monkeys (see review by Anderson, 2000) suggest that infective J_3 juveniles burrow through the duodenum and undertake a month-long journey, first migrating to the mesentery, and then to the abdominal and chest muscles, where they mature. This is also where copulation and fertilization occur in the following 2.5 months. Males die in the musculature. In the 4–6 months following fertilization, females migrate to the extremities, become gravid and initiate the characteristic blisters that prepare them to shed their juveniles (Anderson, 2000). Twenty-seven-year old Russian biologist Aleksei Fedchenko (Figure 5) was the first to describe the life cycle; his work was published in 1871. A number of parasitologists, notably Moorthy, Onabamiro, and Muller (for example, see Muller, 1968; 1971, and references therein) added important details to Fedchenko's pioneering work.

Disease, pathology, and treatment

The disease caused by these organisms is called dracunculiasis, or sometimes dracunculosis. In the older literature it has also been called draconitis. The localized blister caused by the adult females, most commonly on the legs and feet, causes a burning sensation and is painful. The blister is itself an acute inflammatory response to a relatively small number of juveniles released under the skin by a localized rupturing of the female worm when it is ready to shed its juveniles. Neutrophils, eosinophils, lymphocytes, and macrophages infiltrate the area and are part of the blister fluid. Once the blister bursts, and the female begins shedding juveniles to the outside, the open blister turns into an inflamed ulcer that becomes larger with time and affects the surrounding skin, especially while the worm is being mechanically extracted from the opening over a period of weeks. During this time, there is a risk of secondary infection, which may lead to septicemia, gangrene, and death. Once the worm is extracted, the lesion usually heals quickly. If the infection/ulcer is near joints, secondary complications such as arthritis and fibrous ankyloses can occur and the effects can be crippling. Infections of other areas of the body cause pathology and complications in those locations, such as inflammation of the scrotum and testes, or general cellulitis.

Chemotherapy, surgery, and mechanical extraction have been used to treat guinea worm infections. The drug metronidazole is often used in dracunculiasis; it does not kill the worm but makes it easier to remove, presumably because the drug acts as an anti-inflammatory agent. The age-old, crude, but effective technique of wrapping the spent portion of the worm on a short, slender twig or stick and extracting it manually is still common. Cool water is applied to the open blister so that the worm ruptures and sheds its eggs; this induces the worm to move a fresh portion of its body into the opening and the spent portion of the body can be wound around the twig (see Figure 6). The process is repeated over days or weeks until the entire worm is extracted. Usually only a few centimeters of the worm can be extracted at a time and the afflicted person must take care not to break the worm in the process. Large numbers of juveniles released under the skin by a ruptured worm can cause severe allergic and inflammatory responses and even anaphylactic shock.

Guinea Worm Eradication Program

The guinea worm provides a remarkable example of how philanthropy, education, and tireless volunteering may converge to improve public health outcomes since this human parasite has been nearly eradicated in Africa (Tayeh et al., 2017). In 1981, the World Health Organization (WHO) initiated the guinea worm eradication program in Africa as a key desired outcome of its overall strategy to improve drinking water supply and sanitation. Five years later, in 1986, the Carter Center began its partnership with WHO and UNICEF (also known as the United Nations Children's Fund) to lead philanthropic efforts to eradicate the disease (see information from the WHO on eradicating dracunculiasis at https://www.who.int/activities/eradicating-dracunculiasis.) As a result of the coordinated network of field volunteers, health workers, various WHO and UNICEF branches, the United States Centers for Disease Control and Prevention (CDC), and the Carter Center, the number of cases dropped from 3.5 million

Figure 6. Image of adult female guinea worm being extracted from the leg of an infected person by a health care worker in Africa. Source: World Health Organization. Informed consent as per WHO protocols. License: Cf. WHO terms of acceptable uses (non-commercial, educational).

in 1986 to fewer than 2 dozen per year today. A WHO situation report from January 2022 noted that there were a total of 27 human cases of dracunculiasis in Africa reported in 2020, from Chad, Ethiopia, Angola, Mali, and South Sudan. In addition to these human cases, it was reported that 1,520 infected dogs were identified in Africa, and 71 cats and 4 baboons were also reported to be infected during this same period. The persistence of the guinea worm in reservoir hosts like dogs, even in countries where new cases of dracunculiasis are no longer reported (for example, Mali and Ethiopia), illustrates the need for vigilance and continued control measures to prevent the re-emergence of the disease in humans.

There is an acclaimed documentary on guinea worm, How to Slay a Dragon, which first aired on Al Jazeera on November 19, 2014 as part of its series Lifelines: The Quest for Global Health. It features the biology of the parasite, the efforts of health care workers, and the philanthropy led by former United States President Jimmy Carter. It is available for viewing at https://www.aljazeera.com/program/lifelines/2014/11/19/how-to-slay-a-dragon.

***Dracunculus* in Wildlife**

Two North American species, *Dracunculus insignis* in raccoons and *D. lutrae* in otters, and the South American species *D. fulleborni* in opossums, are examples of species of *Dracunculus* that parasitize terrestrial wild mammals. The life cycle of *D. insignis* is very similar to that of the human guinea worm, *D. medinensis*, which occurs as follows: The first intermediate host is a copepod and juveniles ingested with infected copepods in contaminated water migrate and mature in the mammal host; the females reach the skin and release their juveniles to the external environment by an open blis-

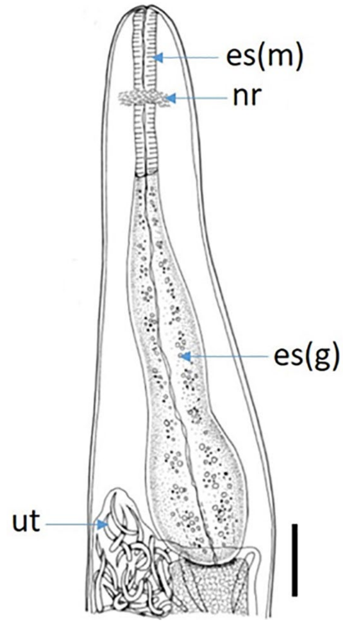

Figure 7. *Philonema agubernaculum*, female, anterior end; es(m) = muscular esophagus, nr = nerve ring, es(g) = glandular esophagus, ut = uterus. Scale bar = 100 µm. Source: Arai and Smith, 2016. License: CC BY 3.0.

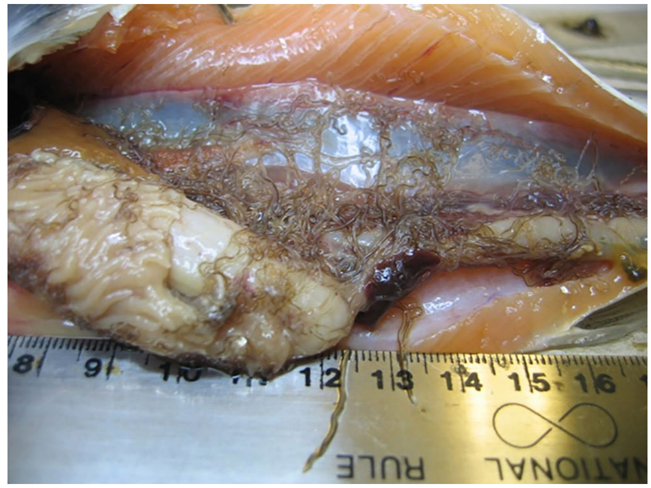

Figure 8. *Philonema oncorhynchi* from a Pacific salmon (*Oncho-rhynchus* sp.). Source: A. Choudhury. License: CC BY-NC-SA 4.0.

ter or abscess on the skin of the animal's lower leg. Inflammation of the blister area occurs in wild and experimentally infected animals. One may assume that the life cycles of the other species are similar. As with *D. medinensis* in Africa, dogs can serve as reservoir hosts for *D. insignis* in North America across a considerable range (Cleveland et al., 2018).

Family Philometridae

Philometrids are widely distributed parasites of fishes (Hoffman, 1999; Moravec and de Buron, 2013). Like their dracunculid relatives, the gravid females of many species are large, packed with juveniles, and reside under the skin, often of the extremities such as the fins (for example, *Philometroides huronensis*), cheeks (*P. nodulosa*), or even in nodules in the eye socket (*P. fulvidraconi*). The female releases its juveniles when its body makes contact with water through a rupturing of the host's skin. Most species have copepod intermediate hosts. Several freshwater and marine species cause pathologies (see Choudhury and Cole, 2011).

Family Philonemidae

Philonemids are typically parasites of the body cavity of salmonid fishes. *Philonema agubernaculum* and *P. oncorhynchi* (Figures 7 and 8, respectively) are common species in salmonids. Gravid females release their juveniles in the body cavity of their fish hosts. The juveniles are carried into the water along with the eggs and milt of spawning fish. Copepods are the first intermediate hosts. Smaller prey fish such as smelt can be paratenic hosts. Infection with *Philonema* spp. may cause visceral adhesions in infected fish (see Choudhury and Cole, 2011).

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