



The wild world of Guinea Worms: A review of the genus *Dracunculus* in wildlife



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ABSTRACT

Nematodes are an extremely diverse and speciose group of parasites. Adult dracunculoid nematodes (Superfamily Dracunculoidea) occur in the tissues and serous cavities of mammals, fish, reptiles, amphibians and birds. Of the dracunculid group, perhaps best known is *Dracunculus medinensis*, the human Guinea Worm. Considerable work has been done on *D. medinensis*; however recent infections in peri-domestic dogs and the finding of naturally-infected paratenic hosts (previously unreported for *D. medinensis*) indicate we still have much to learn about these parasites. Furthermore, among eight species in the Old World and six species in the New World there is a lack of general life history knowledge as well as questions on species occurrence, host diversity, and transmission dynamics. Herein, we provide a comprehensive review of the genus *Dracunculus*, in order of a theoretical evolutionary progression from reptilian to mammalian hosts. Species descriptions, where available, are provided but also show where gaps occur in our knowledge of various species. Additionally, many first reports of *Dracunculus* spp. were done prior to the development and use of molecular tools. This is especially important for this group of parasites as speciation based on morphology is only applicable to males of the genus, and males, given their size, are notoriously difficult to recover from definitive hosts. Therefore, we also discuss current molecular tools used in the investigation of this group of parasites. Given recent host-switching events, the dracunculids are of increasing importance and require further work to expand our understanding of this genus.

1. Introduction

Adult dracunculoid nematodes (Superfamily Dracunculoidea) occur in the tissues and serous cavities of mammals, fish, reptiles, amphibians, and birds (Chabaud, 1960; Petter and Planelles, 1986). Many of the species in this group are similar in that females fill with large numbers of first-stage larvae that are released when females come into contact with water. The Family Dracunculidae contains two genera: *Dracunculus*, parasites of mammals and reptiles, and *Avioserpens*, parasites of birds. There are 14 valid species of *Dracunculus* but most knowledge about these parasites stems from research on the medically important *D. medinensis*, also known as the African Guinea worm. Considerable literature and reviews exists for this species (Muller, 1971, 1976; Cairncross et al., 2002; Ruiz-Tiben and Hopkins, 2006; Eberhard et al., 2014). The life cycle of *D. medinensis* has been well

studied and documented, due in large part to the long history of human infections and an eradication campaign initiated by the World Health Assembly in 1981 and spearheaded in 1986 by The Carter Center (Ruiz-Tiben and Hopkins, 2006). However, despite a long history of epidemiologic and public health research, recent infections in peri-domestic dogs in several remaining endemic countries in Africa and the finding of naturally infected paratenic hosts (previously unreported for *D. medinensis*) indicate we still have much to learn about these parasites (Eberhard et al., 2014, 2016a,b; Cleveland unpublished data).

This review focuses on *Dracunculus* species other than *D. medinensis*, with an emphasis on *D. insignis*, which is being used as a model parasite for studies to assist the Guinea Worm Eradication Program.

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1.1. Genus *Dracunculus*

Nematodes in the genus *Dracunculus* are large subcutaneous parasites of mammals and reptiles (snakes and turtles) with most described species being from snakes. The females of *Dracunculus* spp. are some of the longest nematodes with recorded lengths up to 100 cm (Cairncross et al., 2002). Morphologically, female *Dracunculus* spp. are very similar and molecular characterization is needed for definitive identification. Males are considerably smaller (16–40 mm), but they have several morphological features that can be used to distinguish the different parasite species (Crichton and Beverley-Burton, 1973; Cairncross et al., 2002). Unfortunately, males are rarely detected and have never been described for some species. This is particularly problematic for hosts that may be infected with more than one dracunculid (e.g., river otters (*Lontra canadensis*)) or with parasites detected in novel hosts.

1.2. Species of *Dracunculus*

The highest diversity of described *Dracunculus* species occurs in the Old World. To date, eight species have been described with seven occurring in snakes endemic to Europe, Africa, Asia, and Australia (Table 1). Although most *Dracunculus* species described are from snakes, the most widely known and studied species is *D. medinensis*, the human Guinea worm, which also happens to be the only Old World mammalian species (Eberhard et al., 2014). Although *D. medinensis* was historically widespread in Africa and South Asia, through considerable management and eradication efforts, the total number of countries with endemic transmission in either humans or dogs has been reduced from 21 to 3 resulting in a decrease of human cases from 3.5 million in 1986 to 30 in 2017 (Molyneux and Sankara, 2017; https://www.cartercenter.org/health/guinea_worm/case-totals.html). Numerous studies and reviews on recent developments related to this parasite have been published (Eberhard et al., 2014; Eberhard et al., 2016a; b; Cleveland et al., 2017).

In the New World, a lower diversity of *Dracunculus* species has been reported, but more species have been described from mammals (Tables 1 and 2). There are at least 2 species of *Dracunculus* that infect snakes (*D. ophidensis* and *D. braziliensis*), 1 from a snapping turtle (*D. globocephalus*), and 3 from mammals (*D. insignis*, *D. lutrae*, and *D. fuelleborni*).

1.3. General life cycle

Adult female *Dracunculus* mature in the subcutaneous tissues of the definitive vertebrate host where they will form blisters primarily on the distal extremities; however, reports of these lesions are rare in reptile hosts (Crichton and Beverley-Burton, 1977; Brackett, 1938). When the host places the affected area in water the blister will erupt and the female release nearly 500, 000 first stage larvae (L1) into the water column (Muller, 1971). The release of larvae can occur multiple times during different events.

Cyclopoid copepods are a required intermediate host in the life cycle of *Dracunculus* species, although few naturally or experimentally competent species have been identified (Table 1). The intermediate host range appears broad as Old World copepod species can become infected with *D. insignis* and New World copepod species can become infected with *D. medinensis* (Sullivan et al., 1991). However, there was differential mortality among different copepods species following infection with *D. medinensis* suggesting some copepod species are better intermediate hosts than others (Bimi et al., 2005). Once L1s are consumed by copepods they develop to the infective third stage larvae (L3) (Fedchenko, 1871; Crichton and Beverley-Burton, 1975). *Dracunculus medinensis* and *D. insignis* L1 molt to L3 within 21–25 days at 24 °C (Fedchenko, 1871; Crichton and Beverley-Burton, 1975).

Definitive hosts can become infected by ingesting L3s within copepods when drinking water or, for some species, consumption of frog paratenic hosts or fish transport hosts (Fig. 1) (Brackett, 1938; Crichton

and Beverley-Burton, 1977; Eberhard and Brandt, 1995; Anderson, 2000; Eberhard et al., 2016a,b; Cleveland et al., 2017). Once ingested, L3s migrate to subcutaneous and intramuscular connective tissues of the thoracic and abdominal musculature where they undergo an additional 2 molts. Male and female nematodes fully mature to adults after 60–70 days, with fertilization occurring after maturation (Anderson, 2000). Males and unfertilized females remain in subcutaneous musculature of the abdomen and thorax, while fertilized females begin to migrate through the subcutaneous tissues, primarily to the distal extremities. Once fully gravid and larvigerous, females create swelling and an ulcerative-type lesion. This lesion occurs when the female releases uterine fluid (which may contain a few larvae), initiating an immune response from the definitive host and leading to a “thinning” of epidermis through which she can emerge (Muller, 1976; Cairncross et al., 2002).

When these lesions are exposed to water, larvae are expelled from the female into the environment and consumed by the intermediate cyclopoid copepod host (Fig. 1). Female nematodes will then senesce and may be pulled out of tissue by the affected animal or will retreat subcutaneously and calcify. Male and unfertilized female nematodes can survive for 330 days; however, it is proposed that this estimate is conservative (Crichton and Beverley-Burton, 1973, 1974; 1977; Brandt and Eberhard, 1990).

1.4. Diagnostic features

Dracunculus spp. adults are large filiform pale yellow-white nematodes that have marked sexual dimorphism with females being considerably larger than males (Table 1). Both females and males have an atrophied intestine and females have atrophied vulva and vagina. Gravid female worms are almost completely occupied by a uterus distended with L1. The anterior end is rounded, the buccal cavity is reduced, the mouth opening is round and surrounded by variable numbers of papillae, and a thick and clearly defined peribuccal ring is present. Anterior constriction just anterior to the nerve ring may be present. The esophagus is very long with a short muscular portion and a long glandular portion. Tails are generally conical with a sharply pointed tip. Males have either equal or subequal spicules and most species have a gubernaculum (Brackett, 1938; Chandler, 1942a; Crichton and Beverley-Burton, 1975; Cairncross et al., 2002; Moravec and Little, 2004).

First stage larvae released from female worms have extremely long, tapered tails and their overall length can vary between species (i.e., 0.3–0.9 mm), but there is considerable overlap in ranges for many species (Fig. 2). When available, length of L1s for valid *Dracunculus* spp. is provided in Table 1. When larvae develop to the infectious L3 stage in copepods, they lose the long tapering tails, become shorter and broader (i.e., 0.24–0.608 mm, although lengths of most species are unknown), and develop a trilobed tail (Fig. 2) (Anderson, 2000; Muller, 1971).

2. *Dracunculus* species of squamates

Currently there are nine formally described *Dracunculus* species in snakes. The highest diversity has been reported in Eurasia and Africa where *D. coluberensis*, *D. alii*, *D. houdemert*, *D. doi*, *D. dahomensis*, and *D. oesophageus* occur. A single species, *D. mulbus*, has been reported from Oceania. In the Americas, two species (*D. ophidensis* and *D. brasiliensis*) have been described. Also, worldwide, several uncharacterized species have been reported from numerous snake species.

2.1. Squamate *Dracunculus* species by region

2.1.1. *Dracunculus ophidensis* (Brackett, 1938) and other species from North America

Dracunculus ophidensis was first described from garter snakes (*Thamnophis sirtalis*) from southern Michigan and subsequently found in

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