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Nemata

Oxyurida (Order): Pinworms

Haylee J. Weaver

Phylum Nemata

Order Oxyurida

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Chapter 52

Oxyurida (Order): Pinworms

Haylee J. Weaver
Biological Resources Study, Department of the Environment and Energy, Canberra, Australia
weaver.haylee@gmail.com

Introduction

The order Oxyurida, commonly known as pinworms or oxyurids, comprises almost 900 species of parasitic nematodes that inhabit the posterior gut of vertebrates and some arthropods. This diversity of hosts is unique to oxyurids, as no other nematode groups have so successfully parasitized both vertebrates and invertebrates, with species of oxyurids found in all classes of vertebrates and in arachnids, millipedes, insects (beetles, cockroaches, mole crickets, flies), and annelids (Adamson, 1994).

The current higher taxonomy and classification is not used consistently throughout the literature (see the section on systematics and taxonomy below), but the fine-scale taxonomy at the family level and lower is stable and consistent. Oxyurids are strictly parasitic but are microphagous, which distinguishes them from other groups of parasitic nematodes. The group (order Oxyurida, or also known as infraorder Oxyuridomorpha) comprises 3 superfamilies: Oxyuroidea, parasitizing vertebrates, and Coronostomatoidea and Thelastomatoidea, both parasitizing herbivorous arthropods.

Key Features of Oxyurids

Oxyurids are small nematodes that inhabit the posterior gut (cecum and large intestine) of vertebrates and arthropods. Oxyurids display **sexual dimorphism** where females are much larger than males, but both sexes are tapered at both ends with the tail more narrow than the head. They are characterized by having an **esophagus** with a large **terminal bulb**, and in males by having a **single spicule**, or **no spicules** at all (Carreno, 2014). They have 3 **lips** surrounding the **buccal aperture**, and several **cephalic papillae** and **amphids** around the **oral surface**. Males in some taxa have raised **mamelons** on their **ventral cuticle**; other features of the cuticle of both sexes include cervical, lateral, or pre-anal **alae**.

History

Because of its association with humans, *Enterobius vermicularis* (Linnaeus, 1758) was known of long before it was formally named, with the symptoms of enterobiasis described by the ancient Greeks (Moulé, 1911; Hugot et al., 1999). The parasite is considered to be one of the oldest human parasites, with a pre-hominid evolutionary origin (Iñiguez et al., 2003). The oldest record of *E. vermicularis* is from a coprolite dated to 7837 BCE, from what is now Utah, United States (Fry and Moore, 1969). Ancient DNA has been extracted from *E. vermicularis* eggs from coprolites dated between 4000 BCE to 900 CE from Chile and the United States (Iñiguez et al., 2003; 2006), and from 1985 BCE from Brazil (Lino et al., 2018). Evidence of *E. vermicularis* infection has also been found from Roman-occupied Egypt (30 BCE–395 CE) (Horne, 2002), and from Iran from 2500–1500 BCE (Paknazhad et al., 2016).

Despite having no bearing on human health, thelastomatoid oxyurids have been known about since the 1800s when *Cephalobellus cuspidatum* (Rudolphi, 1814) was described from a rhinoceros beetle larva (Carreno, 2014). As more species were described, several workers revised the taxonomy of the Thelastomatoidea, with the family and subfamily status of taxa changing over time (Carreno, 2014). The definitive monographs on the systematics of the Thelastomatoidea were published by Adamson and van Waerebeke (1992a; 1992b; 1992c) and updated by Carreno (2014).

Life History and Ecology

Like many groups of nematodes, oxyurids are monoxenous, and their development and mode of transmission is very similar in vertebrates and invertebrates (Anderson, 2000). In contrast to most other nematodes, however, oxyurids are haplodiploid, where males arise from unfertilized eggs but females form from fertilized eggs (Adamson, 1990). Haplodiploid development is not a common life history trait in nematodes (*Caenorhabditis elegans* notwithstanding) but is common in some groups of rotifers, mites, and some insects.

The life history of oxyurids is fairly similar across the groups that parasitize vertebrates and invertebrates. Females produce thick-shelled eggs that are usually flattened on one side and have an operculum (Anderson, 2000). Eggs are either deposited in an early stage of development with juveniles hatching after they have been passed in feces, or via females migrating to the anus of the host and laying eggs on the host perianal area (Anderson, 2000). The latter method is more common in the Oxyuridae and allows for autoinfection, where the grooming activities will facilitate transfer of eggs to the mouth of the host (Morand and Hugot, 1998). Oxyurids have no free-living or extraintestinal stages, and the infective third-stage juveniles (J_3) hatch directly from eggs following ingestion by the new host and subsequently remain in the posterior gut for their whole life cycle (Adamson, 1994). This combination of traits, combined with the usually low effect on host health, means that oxyurids can have a highly aggregated distribution within host species (Grear and Hudson, 2011).

The biogeographic distribution of oxyurids is linked with those of their hosts. Coevolution and cospeciation, where the phylogeny of hosts mirrors that of the parasites, was thought to be common among oxyurids (for example, in primates; see Hugot, 1999). More recently, however, evidence for strict cospeciation of oxyurids within host taxa was not found, for example in rodents (Weaver et al., 2016) and in lizards (Mockett et al., 2017). This suggests that speciation of oxyurids is explained by elements of the Stockholm Paradigm, rather than via strict coevolution and cospeciation (see Box 1).

Box 1. The Stockholm Paradigm

The Stockholm Paradigm is a conceptual framework to understand host-parasite evolutionary relationships (see Hoberg and Brooks, 2015 for a detailed discussion.) It includes overviews of: 1) Ecological fitting; 2) the oscillation hypothesis; 3) the geographic mosaic theory of coevolution; and 4) the taxon pulse to explain the suites of parasite and host relationships over time and space. Ecological fitting is the idea that parasites can fit into niches. Switching to a new host is an extremely energy-intensive evolutionary activity for a parasite, so switching to a new host that has the same niche available as the old host (for example, the cecum or hindgut) is possible with relatively low evolutionary effort and thus can lead to speciation of parasites over time (Brooks et al., 2006). This can explain how some species can be found across a wide range of hosts, and/or distributions, and also how, over time, closely-related host species can harbor speciose parasite communities. Taxon pulses are bursts of colonization/radiation and subsequent speciation of taxa (Erwin, 1985), for example when land bridges were exposed during periods of glaciation, for example, for *Syphacia* spp. and their host rodents in Australia (Weaver et al., 2016).

Animal Health/Effects on Hosts

Pinworm life cycles are direct, with autoinfection of hosts common, and do not include any extraintestinal migrations (such as those for hookworm juveniles). Further, pinworms feed on bacteria in the hindgut or cecum, rather than feeding on host tissue. Therefore, the effect on hosts is generally low, with little to no pathogenicity and the only main symptoms in mammals being itching in the perianal area where the females have migrated to lay eggs (Beveridge et al., 2015).

Systematics and Taxonomy

Note that, regardless of any purported establishment of higher-level classifications, the family-level taxonomy is stable and will be used here to avoid any confusion that can result from selective implementation of taxonomies at higher levels.

Formerly grouped as an order within the phylum Nematoda, the Oxyurida was downgraded to be reclassified as the Oxyuridomorpha, 1 of 5 infraorders within the suborder Spirurina (order Rhabditida) along with the Ascaridomorpha, Spiruromorpha, Rhigonematomorpha, and Gnathostomatomorpha (De Ley and Blaxter, 2002; Wijová et al., 2006; Nadler et al., 2007). This group is at times referred to as a member of Clade III nematodes (sensu Blaxter et al., 1998). The Oxyuridomorpha comprises 2 superfamilies, Oxyuroidea and Thelastomatoidea.

Summary of the Main Groups

Superfamily Oxyuroidea

Parasites of mammals, birds, reptiles, amphibians, and to a lesser extent, fish.

Family Oxyuridae

The Oxyuridae is a large family of over 35 genera with a global distribution in a wide range of host mammals, for example, marsupials, rodents, primates, ungulates, and hyraxes (Figures 1–3). Infecting mostly wildlife, some species also affect domestic animals, such as pet rodents, rabbits, and horses. Notable species of this family include *Oxyuris equi*, the pinworm of domestic and wild horses, and *Enterobius vermicularis*, the common pinworm of humans. Neither species is especially pathogenic, but the method of gravid females laying eggs in the perianal region causes itching and irritation to hosts (Beveridge et al., 2015). *Syphacia muris* is a common parasite of wild and domestic black rats (*Rattus rattus*) and *Passalurus ambiguus* is a parasite of wild and domestic rabbits (Leporidae).

Family Heteroxynematidae

The 17 genera of the Heteroxynematidae are found in sciurid rodents and lagomorphs (mainly pikas) in Nearctic and Palearctic regions, and birds from the Americas, for example, sandgrouse and tinamou (Petter and Quentin, 1974). Those from birds are thought to be a recent host switch based on the

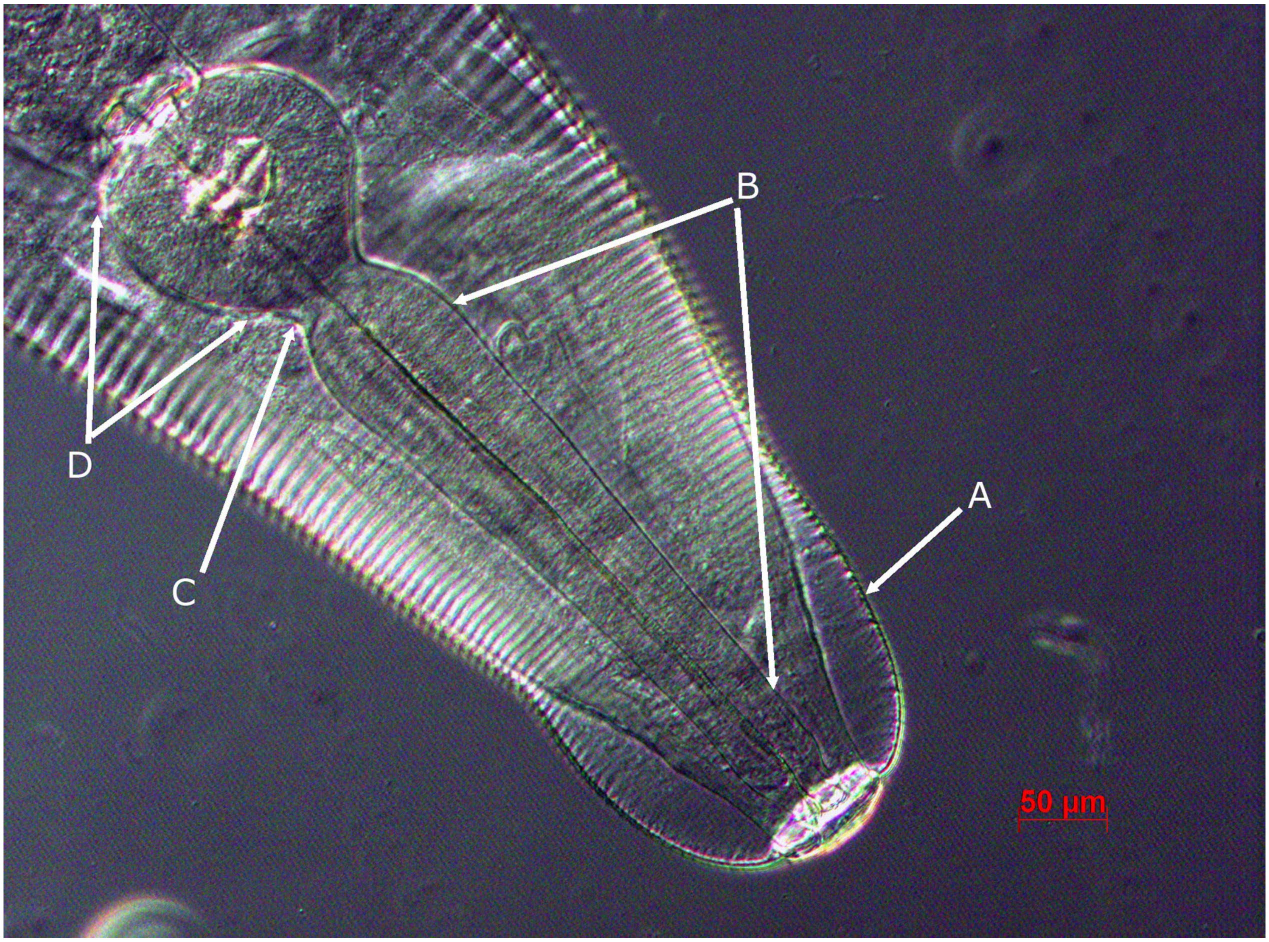

Figure 1. Anterior end of a species of *Syphacia* from rodents of the family Sciuridae (squirrels). Typical of pinworms of rodents, the inflated cuticle near the mouth can be seen (A), in addition, the esophagus expands posteriad (B), narrowing into an isthmus (C), and then expanding into a definite bulb (D). Source: S. L. Gardner, HWML. License: CC BY.

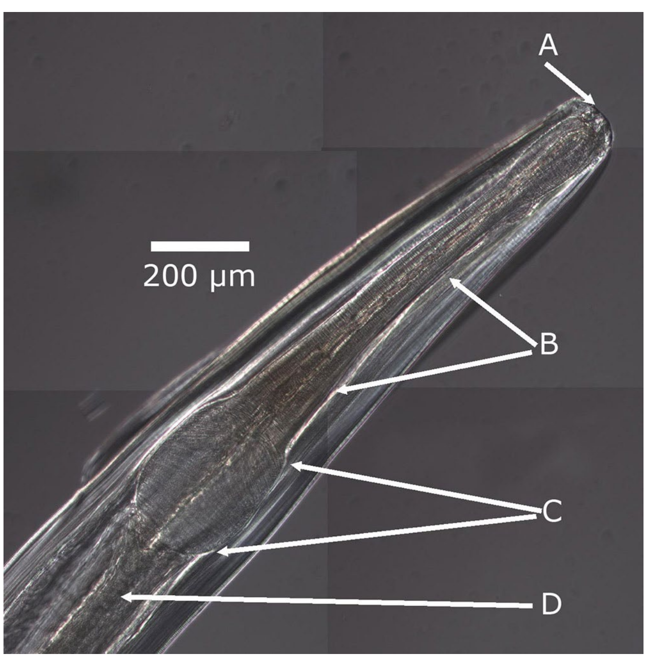

Figure 2. The anterior end of a species of *Passalurus* from the cecum of a rabbit (*Sylvilagus* sp.). The mouth is shown labeled (A), the corpus of the esophagus is marked by arrows (B), the bulb of the esophagus is shown at (C), and the intestine is shown at (D). Source: G. Drabik, HWML, 2016. License: CC BY.

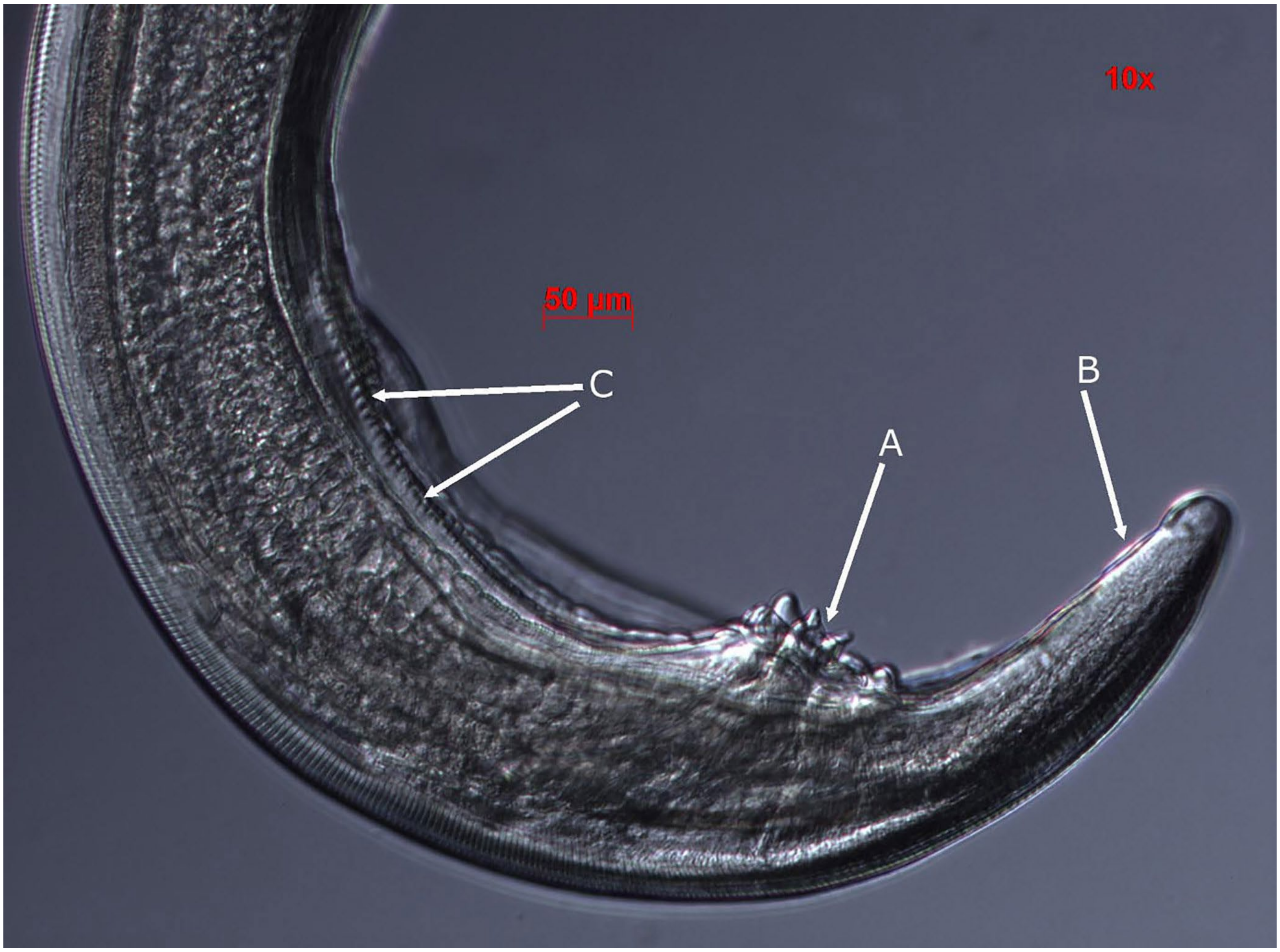

Figure 3. Posterior end of a male *Passalurus* pinworm of rabbit and hares (order Lagomorpha: family Leporidae). The tail (B) is the part of the animal posteriad to the cloaca. The cloaca is shown surrounded by small sensory papillae (A). In male nematodes the exit to the digestive system and the reproductive system share a common duct called the cloaca. Small annulations on the ventral part of the male in species of this genus are evident and are thought to assist the male in mating with the females in the gut of the host. Source: S. L. Gardner, HWML. License: CC BY.

majority of species being found in rodents and lagomorphs (Adamson, 1994). One genus, *Paleoxyuris*, was discovered from a 240-million year-old coprolite from a cynodont (primitive synapsid) (Hugot et al., 2014).

Family Pharyngodonidae

The Pharyngodonidae comprises 30 genera and are parasites of a wide range of vertebrate hosts, including reptiles, amphibians, mammals, and to a lesser extent, fish. One species of monotreme, the short-beaked echidna *Tachyglossus aculeatus* is host to *Parapharyngodon anomalus*, a genus otherwise only found in reptiles (Hobbs, 1996). The relationships between the 7 genera of pharyngodonids occurring in fish and the rest of the family are unresolved, whereas those parasitizing lizards and amphibians show clearer links (Adamson, 1994).

Superfamily Thelastomatoidea

Parasites of arthropods, particularly insects.

Family Thelastomatidae

The Thelastomatide is a large family of over 45 genera with a diverse range of invertebrate hosts (Adamson, 1994; Carreno, 2014). Genera are not limited to insects, with hosts including millipedes, an arachnid, an oligochaete, beetles, cockroaches, flies, and mole crickets (Jex et al., 2006).

Family Hystrignathidae

There are 35 genera in the Hystrignathidae and all are restricted to passalid beetles (Coleoptera: Passalidae) (Adamson, 1994; Carreno, 2014). The family is characterized by having cuticular rods to support the anterior part of the pharynx, elongated eggs that have ornamentation on the shell surface, and at least 1 medial single papilla in males (Adamson and Van Waerebeke, 1992c).

Family Protrelloididae

Members of the 4 genera of Protrelloididae are found in cockroaches only, from North America and South America, India, Madagascar, and Australia (Adamson and Van Waerebeke, 1992b; Jex et al., 2006).

Family Pseudonymidae

The 5 genera of Pseudonymidae are parasites of water scavenger beetles (Coleoptera: Hydrophilidae), except for the genus *Jarryella*, which is found in scarabs (Coleoptera: Scarabeidae) (Adamson and Van Waerebeke, 1992b).

Family Travassosinematidae

Species of the 10 genera of the Travassosinematidae infect mostly mole crickets and are found in India, Madagascar, North America, and South America (Adamson and Van Waerebeke, 1992b).

Superfamily Coronostomatoidea

Superfamily Coronostomatoidea comprises parasites of millipedes and cockroaches.

Family Coronostomatidae

The family Coronostomatidae was erected by Kloss (1961) as part of the superfamily Thelastomatoidea but was moved into its own superfamily, Coronostomatoidea, by Poinar (1977). Both the family and superfamily were subsequently synonymized by Adamson and van Warebeke (1992a) without explanation but were resurrected by Phillips and colleagues (2016). The Coronostomatidae comprises a single genus, *Coronostoma*, with 7 species found in mostly millipedes from Brazil, Burkina Faso, Madagascar, and India, and from a species of cockroach in Australia (Phillips et al., 2016).

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