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Nemata

Heterakoidea (Superfamily): Cosmopolitan Gut-Dwelling Parasites of Tetrapods

F. Agustín Jiménez-Ruiz

Phylum Nemata

Superfamily Heterakoidea

Chapter 51

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F. Agustín Jiménez-Ruiz

Department of Zoology, Southern Illinois University Carbondale, Carbondale, Illinois, United States; and Harold W. Manter Laboratory of Parasitology, University of Nebraska State Museum, Lincoln, Nebraska, United States
agustinjz@zoology.siu.edu

Reviewer: Scott L. Gardner, Harold W. Manter Laboratory of Parasitology, University of Nebraska State Museum, Lincoln, Nebraska, United States; and School of Biological Sciences, University of Nebraska–Lincoln, Lincoln, Nebraska, United States

Introduction

Heterakoidea is a superfamily of ascaridid nematodes that occur most often in the cecum and large intestine of amphibians, reptiles, birds, and mammals. Some species are very common with several occurring in galliform birds worldwide, while others may be found commonly in various mammals in both North America and South America. Two genera particularly, *Ascaridia* and *Heterakis*, include important parasites of birds, and both impact rearing of commercial poultry (Jansson et al., 2010).

Heterakoids are characterized by a pre-cloacal sucker in males and an esophagus with a posterior bulb and a muscular anterior corpus. The life cycle of heterakoid nematodes is simple: Eggs containing the infective third-stage juvenile (J_3) are ingested by the definitive host, although for some species, paratenic hosts may be involved.

Phylogenetic analysis of SSU rDNA sequences reveals that, as currently defined, this superfamily is not monophyletic and requires taxonomic revision (Nadler et al., 2007).

Morphology

As noted in the introduction, one of the most conspicuous characters of the heterakoid nematodes is the **precloacal sucker**, which is endowed with a well-developed **cuticular rim**. This character is present in all but a few species that are classified in the superfamily. Notable exceptions include some species of *Lauroia* (see Proença, 1938; Jiménez-Ruiz and Gardner, 2003) and *Ascaridia*. Other important features have been highlighted by Inglis (1967) who described the cuticular ornamentation of the **stoma** (also called the **buccal cavity**) and **lips**, and notes their homology or common origin with the cuticular derivatives of the **esophagus** and **body wall**. The typical stoma of the heterakoid is endowed with a fused **esophagorhabdion** and a conspicuous **cheilorhabdion**. Before the advent of molecular techniques, these characters had been used extensively for the description of genera and the classification of the suprageneric taxa. Other important characteristics of these nematodes include **papillae** in the **precloacal rim** and the **preanal papillae** (see Figure 1).
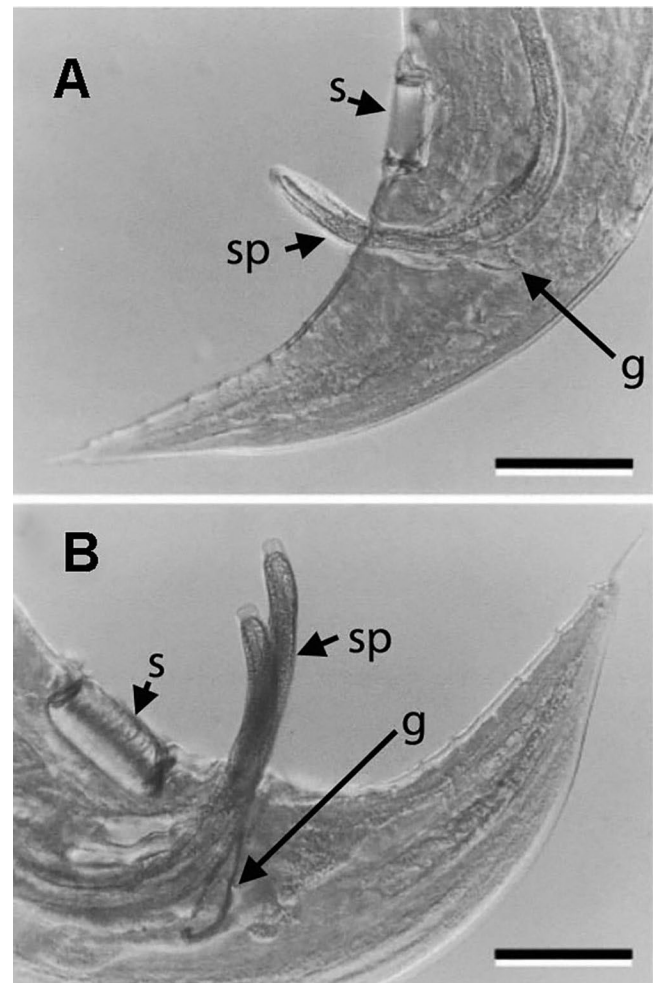

Figure 1. Heterakoid nematodes *Aspidodera* spp. A) Posterior end of *A. sogandaresi* showing pre-cloacal sucker (s) and spicules (sp); B) posterior end of *A. fasciata* showing paired spicules (ps) sucker (s) and proximal end of gubernaculum (g). Scale bars = 100 μm. Source: S. L. Gardner, HWML. License: CC BY 4.0.
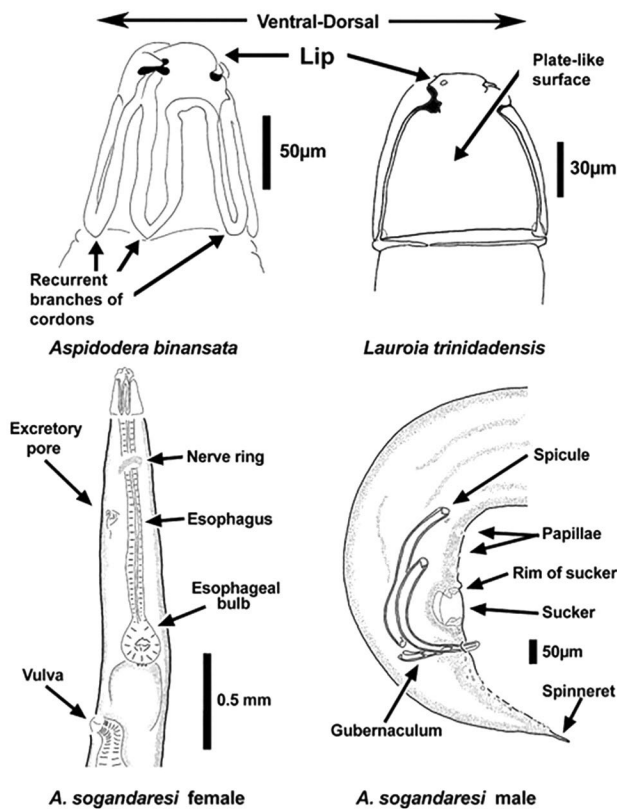
Figure 2. Examples of the structures of the hood in Aspidoderidae (Nemata: Heterakoidea) as seen in the right lip. Source: S. L. Gardner, HWML. License: CC BY 4.0.

Finally, the esophagus is divided into 3 parts, which acquire their final adult configuration in the fourth molt. These include a conspicuous **pharynx**, the **corpus**, and an **esophageal bulb** that is endowed in most species with a **trivalved sphincter** (Figure 2).

Diagnosis

The Heterakoidea are members of the class Secernentea, order Ascaridiomorpha. Three lips are present, with a dorsal lip that is bilaterally symmetrical featuring double papillae and ventral lips, each with a single papilla. There is a conspicuous cheilorhabdion lining the buccal cavity or stoma and a medially located esophagorhabdion. The esophagus is muscular, divided into 3 conspicuous parts, including a pharynx that projects into the lips, corpus, and bulb. There is a heavily cuticularized precloacal sucker with a robust rim, 2 spicules, and a gubernaculum that guides the spicules during copulation. The vulva is usually located at midbody. In the uterus, the eggs are usually unembryonated and the shell is smooth, some with polar pores.

Distribution and Host Associations

Members of the taxon include dwellers of the cecum or large intestine of terrestrial tetrapods, with a single case of infection reported in fish (*Meterakis japonica*, Moravec and Sey). Most of the taxonomic diversity is present in scaled reptiles and birds, followed by several taxa present in frogs and mammals. The heterakoid nematodes have a cosmopolitan distribution being found in the large intestines of reptiles, birds, and mammals on all continents except Antarctica. Very few species appear to be endemic to temperate land masses, with notable exceptions, such as *Hatterianema hollandei* and *Kiwinema gracilicauda*, which appear to be limited to the main islands of New Zealand. Both species occur in endemic tetrapods of these islands such as the tuatara (*Sphenodon punctatus*) and an unidentified species of kiwi of the genus *Apteryx*. Species diversity of these taxa is very low, as only 1 species is known for each genus (Inglis, 1991). This taxon also includes a third genus of limited diversity, since *Mammalakis* includes 2 known species in naked mole rats from South Africa and Europe (Inglis, 1991).

The biogeography and host associations for subfamilies Spinicaudinae and Meteterakinae are in sharp contrast to one another. Prevailing hypotheses posit that Spinicaudinae has a cosmopolitan distribution, yet members of the Meteterakinae show a disjoint and perhaps relictual distribution confined to southeast Asia and the Neotropics (Baker, 1984). These 2 groups are associated with frogs and semiaquatic reptiles. A different pattern is evident in species in the Family Aspidoderidae, for which distribution is chiefly Neotropical with documented dispersions into North America (Jiménez-Ruiz et al., 2012). These parasites chiefly infect mammals of a Neotropical origin and are the only family that predominantly shows this distribution and host association. Interestingly, the relationships of members of the family with other members of the Heterakoidea are yet to be resolved.

The rest of the groups in the family, namely Ascaridiidae and Narsingianellinae, show contrasting patterns. The latter appears to be restricted to toads in southeast Asia and the Indian subcontinent (Rao, 1978; Rizvi, 2009), whereas the former is cosmopolitan, with species occurring in birds, and occasionally in mammals and reptiles.

General Biology

The precise dietary requirements of these nematodes have not been determined, although it has long been speculated that because of their habitat they must feed on cecal or gut bacteria. Experimental manipulations show that varying levels of fiber in the host diet induce conspicuous differences in the survival and fecundity on the cecal-dwelling *Heter-*

akis gallinarum (see Daş et al., 2014). Fiber-rich diets increase the volume of the ceca and the fermentation activity induced by bacteria.

Experimental infections that help illustrate their life cycle have been completed for just 6 species, yet they all seem predominantly to feature direct transmission. In some cases, earthworms and other terrestrial invertebrates are used as vectors for the eggs (Ackert, 1917; Frank, 1953). The thin-shelled nature of the eggs, featuring 2 polar pores, may make them prone to prompt dehydration, thus making them highly dependent on humid environments. There is ample evidence, however, that humidity is the key environmental condition that promotes the development of these worms. Experimental work on *Heterakis gallinarum* has been used to characterize the typical life cycle of members of the superfamily. As such, this can be generalized to be monoxenous (without an intervening intermediate host), with females laying unembryonated eggs that complete embryogenesis in the external environment and juveniles undergoing 2 molts (Araújo and Bressan, 1977). The development of the infective stage is temperature dependent; it takes 7 to 12 days to form the infective stages in temperatures ranging between 17 and 29 °C (Graybill, 1921). When temperature is maintained at 27 °C and 33 °C, development completes in 6 and 4 days, respectively. Usually, eggs become infective 24 hours after the second molt (Roberts, 1937).

Experimental approaches to test the animals' endurance in adverse conditions document their resistance to dry environments and drastic temperature and humidity changes, as well as their prolonged retention of infectivity. The eggs can remain infective after being passed through the digestive system of earthworms and grasshoppers (Ackert, 1917; Frank, 1953). The nematodes are able to complete migration to their target organ 48 hours post-infection (hpi).

In contrast, some of the species appear to be able to complete their development optimally while completely submerged in tap water (Petter, 1968; Bain, 1970). In the case of *Spinicauda freitasi* and *S. inglisi*, the development of the infective stage takes between 14 and 15 days when submerged in tap water at 26 °C. Infective juveniles feature a rhabditiform esophagus. When fed to a definitive host, the nematodes reach their target organ typically 40 dpi (Petter, 1968). Experimental infections of larvated eggs of insects showed that the juveniles of *Strongyluris brevicaudata* can migrate and encapsulate in the thorax of cockroaches and occasionally in mosquitoes (Bain, 1970).

As nematodes develop throughout their life, there is a drastic reconfiguration of both internal organs and external appearance. Detailed accounts of this metamorphosis docu-

ment the transformation for *Spinicauda inlgisi*, *Spinacauda freitasi* (see Petter, 1968), *Strongyluris brevicaudata* (in Bain, 1970), and *Heterakis gallinarum* (shown by Dorman, 1928). These juveniles undergo changes and molt twice to develop into infective forms, featuring a rhabditiform esophagus that is devoid of a bulb. During the migration through the digestive system of the definitive host, the nematodes mature with the concomitant development of the characteristic esophageal bulb (Petter, 1968; Bain, 1970).

Evolution

Based on their geographic distribution and the features of their anterior end and cuticular ornamentation, and their association with ectothermic tetrapods, Inglis (1967) offered an interpretation of their evolution with emphasis on their changes of association with vertebrates (specifically, host switching) and major morphological transitions. This notion was further elaborated by Baker (1984) who concentrated on a handful of species in 2 subfamilies and speculated on an origin in the Cretaceous for members of Heterakoidea. Studies on the phylogenetic associations between nematodes of this taxon and their hosts using replicable datasets started with the cophyletic approach for South American species of *Paraspidodera* spp. infecting hystricognath rodents (Gardner, 1991). The historical association among the Aspidoderidae and their wide array of hosts was further addressed in work by Jiménez-Ruiz and colleagues (2006; 2008; 2012). A holistic approach addressing the origin of the Heterakoidea has not yet been produced.

Systematics and Phylogeny

Analysis for species included in suprageneric taxa are not clearly defined, and the relationships and even the classification of the families are still in flux (Rao, 1978; Inglis and Harris, 1990; Jiménez-Ruiz et al., 2008; 2012). There are a few proposals of the phylogenetic arrangement for members of the Heterakoidea, yet all of them concentrate on the relationships among species in a genus or a family (Bouamer and Morand, 2008; Jiménez-Ruiz et al., 2013) (see Table 1 for a Linnean classification for the Heterakoidea).

Building on the foundation of the systematic approaches presented by Mozgovoi (1953) and Skrjabin and Shikhobalova (1951), Inglis (1967) proposed an overall classification structure for the group identifying 3 main synapomorphies: 1) Very well-developed **rhabdions** (cuticular structures derived from the esophagus and the body wall that cover the inner lining of the mouth; see Figure 3); 2) **lips**; and 3) a **ventral sucker** with a cuticular rim. This systematic arrangement has survived until the present, although some phylogenetic re-

Table 1. Linnean classification for Heterakoidea (Superfamily) as of 2014.

Heterakoidea
   Kiwinematidae Inglis and Harris, 1990
     Kiwinematinae Inglis and Harris, 1990
       Kiwinema Inglis and Harris, 1990
         Kiwinema gracilicauda Inglis and Harris, 1990
       Hatterianema Chabaud and Dollfus, 1966
         Hatterianema hollandei Chabaud and Dollfus, 1966
     Mammalakinae Inglis, 1991
       Mammalakis Inglis, 1991
         Mammalakis macrospiculum
         Mammalakis spalacis
   Heterakidae Railliet and Henry, 1912
     Heterakinae Railliet and Henry, 1912
       Heterakis Dujardin, 1945
       Pseudaspidodera Baylis and Doubney, 1922
       Odonterakis Skjabin and Schikhobalova, 1947
       Musserakis Hasegawa, Dewi and Asagawa, 2014
         Musserakis sulawesiensis Hasegawa, Dewi and Asagawa, 2014
       Neoheterakis Kumar and Thienpoint, 1974
       Haroldakis Inglis, 1991
     Meteterakinae
       Meteterakis Karve, 1970
       Gireterakis Lane, 1917
       Bufonerakis Baker, 1980
       Cagourakis Petter, Chermette and Vassart, 1988
     Narsingellinae Rao, 1978
       Narsingiella Rao, 1978
     Spinicaudinae
       Spinicauda Travassos, 1920
       Africana Travassos, 1920
       Moaciria Texeira de Freitas, 1956
       Strongyluris Mueller, 1894
       Pseudostrongyluris Guerrero, 1970
   Aspidoderidae Skrjabin and Shikhobalova 1947
     Aspidoderinae Skrjabin and Shikhobalova 1947
       Aspidodera Railliet and Henry, 1912
       Ansiruptodera Skrjabin and Shikhobalova 1947
       Nematomystes Sutton, Chabaud and Durette-Desset, 1980
     Lauroiinae Skrjabin and Shikhobalova 1947
       Lauroia Proença, 1938
       Paraspidodera Travassos, 1914
   Ascaridiidae Travassos, 1919
     Ascaridia Dujardin, 1845

constructions challenge its monophyly (Nadler et al., 2007). The accelerated rate of species descriptions of *Meteterakis* species from the Southeast Asian archipelago seems to suggest the notion that the groups are diverse, yet the taxonomic impediment (that is, a lack of qualified, trained taxonomists) hinders the documentation of biodiversity.
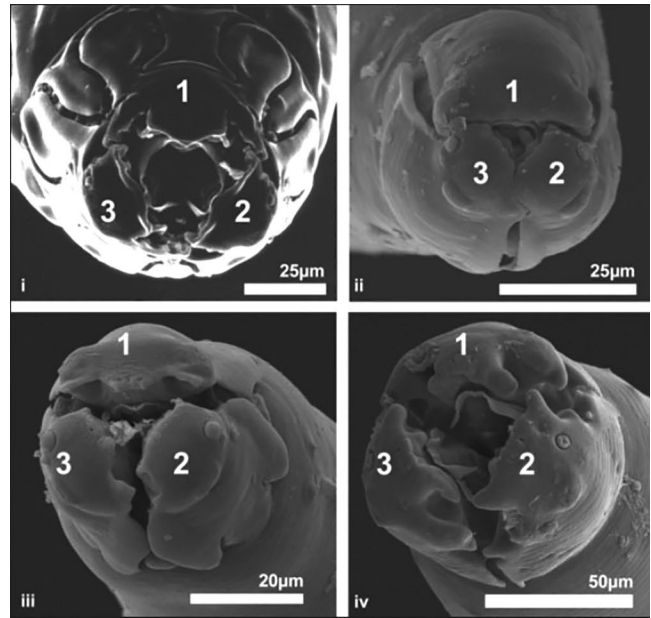

Figure 3. En face view of 4 species of Aspidoderidae showing the positions of the lips. Dorsal lip is labeled 1 in all images; ventral side includes 2 lateroventral lips labeled as 2 (sinistroventral) and 3 (dextroventral). *Aspidodera scoleciformis* (i), *A. bolivari* (ii), *A. scapteromi* (iii), and *Paraspidodera uncinata* (iv). Source: Jiménez-Ruiz et al., 2008. License: CC BY-NC-SA 4.0.

Superfamily Heterakoidea
Family Ascaridiidae Travassos, 1919

It is important to note that this family name is very similar to the family name Ascarididae Baird, 1853, which is included within the superfamily Ascaridoidea (discussed in another chapter). It is unfortunate that they are so similarly named, but be clear that Ascarididae and Ascaridiidae are absolutely separate groups.

One species within the Ascaridiidae of interest is *Ascaridia galli*, which is a cosmopolitan parasite of the small intestine of domestic fowl and game birds. Males reach a length of 77 mm, and females reach 115 mm. Juveniles within eggs hatch after they are ingested with contaminated food or water. The life cycle does not involve extensive tissue migration. Instead, 8 or 9 days after infection, juveniles molt to the third stage (J_3) and begin to burrow into the mucosa, where they generally remain with their tails still in the intestinal lumen. After molting to J_4 at about 18 days, they return to the lumen, where they undergo their final molt. Probably a majority of worms complete their 2 molts and attain maturity without ever leaving the lumen. However, some juveniles burrow their anterior ends into the intestinal mucosa where they remain for up to 2 months before molting and returning to the lumen to complete development to the adult stage.

Those that attack the mucosa cause extensive damage, and *Ascaridia galli* causes production losses in chickens. High-intensity infections can obstruct the small intestine and cause death. In addition, adult *A. galli* are sometimes found in chicken eggs destined for human consumption. This is obviously of concern to egg producers. Improved management practices to control infection through sanitation are important because in some countries few anthelminthics are approved for use in poultry.

Family Heterakidae Railliet & Henry, 1912

Heterakis gallinarum is cosmopolitan in domestic chickens and turkeys. It was probably brought to the United States in imported ring-necked pheasants. The worms live in the cecum, where they feed on its contents. *Heterakis gallinarum* is unusual because in galliform birds it serves as a vector of the parasitic protozoan, *Histomonas meleagridis*, the causative agent of histomoniasis (blackhead). Hence, the curious phenomenon of one parasite acting as an intermediate host and vector of another is revealed.

Several species of *Heterakis* are known from birds, particularly in ground feeders, and one species, *H. spumosa*, is cosmopolitan in rodents.

Three large lips and an esophageal basal bulb as well as lateral alae are found in this genus. Males are as long as 13 mm and possess wide caudal alae supported usually by 12 pairs of papillae (Figure 4). Their tail is sharply pointed, and there is a prominent preanal sucker. Spicules are strong and dissimilar, and a gubernaculum is absent. Females have the vulva near the middle of their body and a long, pointed tail.

Biology

Eggs of *Heterakis gallinarum* contain a zygote when laid. They develop into the infective stage in 12 to 14 days at 22 °C and can remain infective for 4 years in soil. Infection is contaminative: When embryonated eggs are eaten, third-stage juveniles (J_3) hatch in the gizzard or duodenum and pass down to the cecae. Most complete their development in the lumen, but some penetrate the mucosa, where they remain for 2 to 5 days without further development. Then, returning to the lumen, they mature about 14 days after infection.

If eaten by an earthworm, a juvenile may hatch and become dormant in the worm's tissues, remaining infective to chickens for at least a year. Since these nematodes do not develop further until eaten by a bird, an earthworm is a paratenic host. Grasshoppers, flies, and sowbugs can also serve as mechanical vectors of eggs.
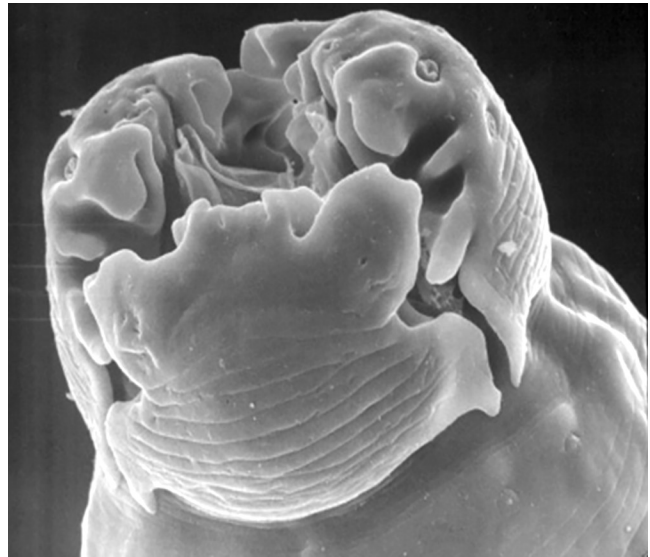

Figure 4. The anterior end of *Paraspidodera* sp. from a rodent from Bolivia, showing the 3 lips. Source: S. L. Gardner, HWML. License: CC BY 4.0.

Epidemiology

As a result of the longevity of the eggs, it is difficult to eliminate *Heterakis gallinarum* from a domestic flock. The many different mechanisms for persistent contamination of poultry farms by eggs remains a challenge to implementing sanitation procedures, such as cleaning and disinfection, without concurrent use of strict hygiene barriers. In addition, wild birds may also serve as sources of infection. Furthermore, as earthworms feed in contaminated soil, they accumulate large numbers of juveniles, which in turn cause massive infections in the unlucky birds that eat them.

Pathogenesis

Generally speaking, *Heterakis gallinarum* is not highly pathogenic in itself. Chickens typically have only minor histopathological lesions when infected, but show localized cellular immune effects, particularly a Th2-dominated response at the site of infection (Schwarz et al., 2011). However, the protozoan, *Histomonas meleagridis*, is transmitted between birds within eggs of *He. gallinarum* (see Long et al., 1987). This protozoan is the etiological agent of blackhead, a particularly serious disease in turkeys where mortality in captive flocks can exceed 85%. Unlike in chickens, blackhead can be directly transmitted between turkeys by fecal contamination. Typically, the protozoan is eaten by the nematode and multiplies in the worm's intestinal cells, ovaries, and finally the embryo within the egg. Hatching of the worm within a new host releases *Hi. meleagridis*. In chickens co-infected with

He. gallinarum and *Hi. meleagridis*, severe ulceration of the cecal mucosa may occur. The protozoan infection elicits a different, Th1-dominated immune response and a higher T-cell infiltration rate than with infection of *He. gallinarum* alone (Schwarz et al., 2011).

Diagnosis and treatment

Heterakis gallinarum can be diagnosed by finding eggs in feces of its host. Birds allowed to roam a barnyard usually are infected. Worms are effectively eliminated with mebendazole. Usually, a flock of birds routinely gets this or other drugs in its feed or water. Other benzimidazole drugs that are effective against juvenile stages, such as albendazole and febendazole, have been shown to be useful for preventing establishment of *Histomonas meleagridis* by preventing nematode infection (Hegngi et al., 1999). Unfortunately, drugs directly effective against *Hi. meleagridis* have been found to be carcinogenic and are no longer registered for use in poultry. Without effective drugs or a vaccine, control of blackhead disease currently relies on management practices, including prophylaxis by regular deworming. In some countries, regulatory bans on keeping laying hens in metal cages have led to husbandry conditions that increase transmission of these nematodes, providing new challenges to their control (Jansson et al., 2010).

Ecology

Heterakoid worms appear to be moderately prevalent in the populations of tetrapods sampled in a systematic manner. Navone (1990) has demonstrated that the prevalence of some species of *Aspidodera* in armadillos from central Argentina was greater than 50% in the wet season and reduced to roughly 30% in the dry season. The prevalence of 2 species of *Aspidodera* in central Florida reach a combined level of 63% (Varela-Stokes et al., 2008). Both *Heterakis gallinarum* and *Ascaridia galli* occur in several wild and domestic galliform birds, posing a problem for wildlife managers in certain regions of the world.

Economic Importance

The species with the greatest known economic impact in the group is *Heterakis gallinarum*, known to infect poultry (domesticated chickens and both wild and domesticated turkeys) and may produce disease from high levels of infection. Yet the pathology induced by these species seldom jeopardizes the survival of the host and the infection by these nematodes alone rarely induces much mortality in a population. Nevertheless, *He. gallinarum* is involved in the transmission of a species of flagellated protozoan of the order Trichomonadida that causes significant mortality in wild and captive flocks of galliform birds. As noted above, *Histomonas meleagridis* is the causative agent of blackhead in chickens. This trichomonad is not known to produce cysts, having only an unflagellated trophozoite stage as well as a flagellated trophozoite stage, thus the trophozoite is the only morphotype in their life cycle. The parasite is transmitted horizontally through cloacal exchange or via contamination with fresh feces. The trophozoites do not live long in feces, and chickens are little affected by this protozoan, but in turkeys it is sometimes 100% fatal to the flock.

An interesting aspect of the biology of the nematode and the protozoan is that the trophozoites of *Histomonas meleagridis* are able to infect the sexual organs of both female and male nematodes. In the body of the females the trophozoites migrate through the uterus and reach the ovary. In that organ they are able to infect the developing embryos before the proteinaceous shell is formed. In this way, the trophozoites colonize a structure that will act as an exterior casing for the trophozoites, isolating them from the external environment outside both the avian host and the parasitic nematode. Several species of earthworms may serve to help complete the life cycle by ingesting nematode eggs and passing the infected eggs on to chickens or turkeys. The earthworms can pick up the eggs of the heterakoid nematodes from deep in the soil. The trichomonads are then able to hatch from the egg once consumed by the definitive host, then to reach the cecum and continue growth (Figure 5). In combination, these unique biological characteristics hinder the efforts to prevent and control the disease caused by these organisms.

Conservation

Prominent conservation biologist Gerardo Ceballos encourages biologists to frame their studies as a conservation activity (Rojas-Bracho et al., 2018). He suggests that there is value in documenting the distribution of all species to establish the consequences of species interactions in the function of any ecosystem. A challenge for future parasitologists is to frame the study of any group of nematodes (and, in fact, all parasites) from this perspective. Although most efforts in the conservation of parasites deal with the problem of the stress maintained on the hosts (including the pathological consequences of the effects that these parasites have on their hosts), there are more possibilities including using parasites with indirect life cycles as probes for biodiversity, which refers to the fact that discovery of a single species of parasite that uses a complex life cycle in a host immediately reveals several layers of biological complexity (Gardner and Campbell, 1992) or listing the parasites that cycle through sympatric animals and identifying the factors that determine this distribution.
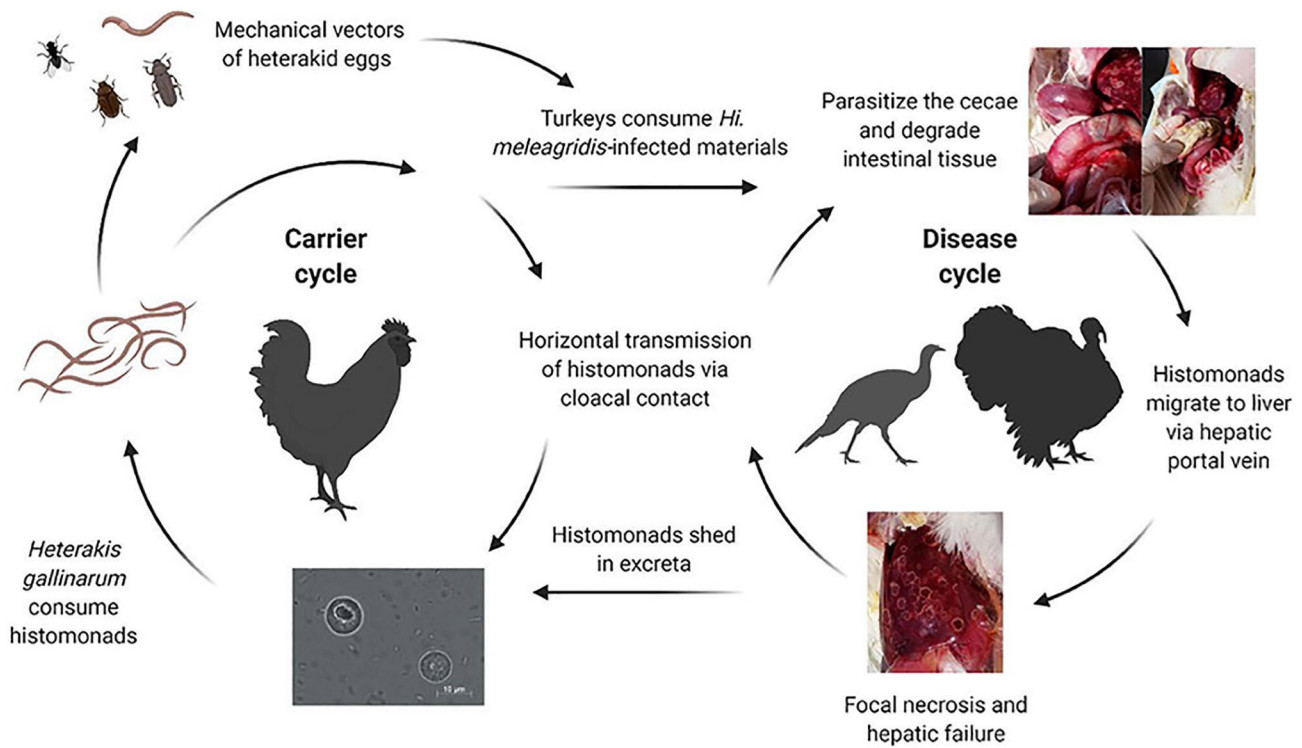
Figure 5. Complex transmission of *Histomonas meleagridis*, a venereal disease of nematodes. In the galliform host, infective eggs of *Heterakis gallinarum* are ingested incidentally as the bird eats earthworms or other soil-dwelling invertebrates from soil contaminated with feces from infected birds. The eggs hatch in the intestine and juvenile nematodes move to the cecae in the lower part of the gastrointestinal tract of the bird where they feed on cecal contents, grow, molt to adults, mate, and produce eggs. Histomonid protozoans living and reproducing in the cecae of the bird invade the nematode via the vulva and move through the ovijector and uterus up to the ovary of the female nematode hosts (*Heterakis gallinarum*) where they proliferate, utilizing the germinal zone of the ovary of the nematode as nutrients. As the protozoans increase their numerical density in the ovary of the nematode, some penetrate the developing oocytes and are encased in the newly formed eggs. *Histomonas meleagridis* can also invade the cloaca and vas deferens of male *Heterakis* and may act as a venereally-transmitted protozoan. In the bird host, the protozoan escapes when the egg hatches and establishes in the cecae of the intestine. Source of image: Beer et al., 2022. Created with BioRender.com. License: CC BY 4.0. | Source of caption: Adapted from Anderson, 2000. License: CC BY 4.0.

The Heterakoidea include some species that are associated with relictual groups of animals, including *Hatterianema hollandei* present in the tuatara *Sphenodon punctatus*. Although the species is not listed as threatened by the International Union for Conservation of Nature (IUCN; Yeates et al., 2012), it includes a unique group of animals that serves as the only known host for this species of heterakoid. Furthermore, their phylogenetic relationships appear to be blurred by the combination of characters shared with other heterakoids present in southern continents and the potential extinction of ancient lineages of scaled reptiles, birds, and lisamphibians that could have harbored them (Chabaud and Dollfus, 1966; Inglis and Harris, 1990; Inglis, 1991). The association of the parasite with its host and its geography is the result of the optimal factors that make infection possible, including the chance encounter and the compatibility among hosts (Combes, 1991).

The use of different and novel hosts depends on the evolutionary distinctiveness of both parasites and hosts. Parasites would be able to hack the immune system of hosts that may be closer biologically to their original hosts (Park et al., 2018) although there is abundant evidence of the ability of parasites to infect widely disparate hosts due to deep phylogenetic historical signals (Brooks et al., 2019).

Conservation biologists have urged identification of clades with unique genetic diversity. This genetic diversity can be evaluated as to how rare the genetic information is in the members of the group. Between any 2 sister clades, the one of critical conservation importance would be the one that holds the rarest species and includes unique genetic information that would be lost with the extinction of the species that features it. Consequently, the most relictual distribution of a species of nematode in addition to a high specificity suggest
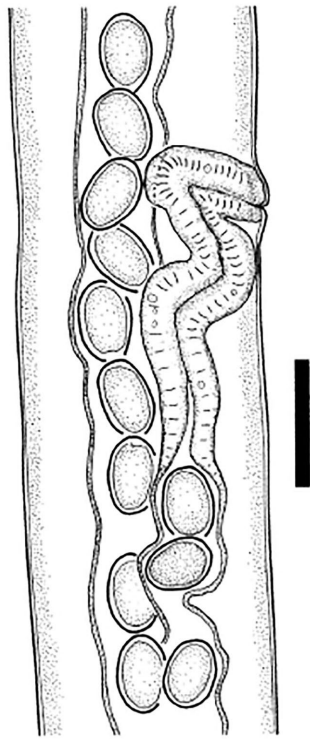
Figure 6. *Lauroia bolivari*. Lateral view of the ovijector with eggs. Scale bar = 100 mm. Source: Adapted from Jiménez-Ruiz and Gardner, 2003. License: CC BY 4.0.

that the species lineage of nematodes is particularly unique. Invoking the earlier example, *Hatterianema hollandei* would be a very important species worthy of extraordinary efforts at conservation (Yeates et al., 2012) since it holds unique information that summarizes an evolutionary lineage in which most of the descendants have become extinct. This evolutionary lineage includes another relict, *Kiwinema gracilicauda*, a parasite of kiwis. The conservation of these lineages will allow scientists to identify the important factors that regulated the interactions of biological associates, including parasites and mutualists of the earliest tetrapods (Boast et al., 2018).

Further evidence of the relevance of heterakoids in the fields of conservation and evolution is provided by the eggs of some heterakoids. In some cases, these structures have been preserved in coprolites that document the associations of recently extinct organisms (Sardella and Fugassa, 2009; Boast et al., 2018). The preservation of some of these eggs has enabled researchers to identify them based on the unique morphology of the eggs (Figure 6) and has enabled the extraction and amplification of small fragments of DNA that allow scientists to identify the egg as coming from a unique species with marked distinctiveness with species currently present in the area (Boast et al., 2018).

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