Part IV

NEMATA, NEMATOMORPHA, ACANTHOCEPHALA, PENTASTOMIDA

ENDOPARSITIC NEMATODES

48

NEMATA

Introduction to Endoparasitic Nematodes (Phylum Nemata)

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Phylum Nemata

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Chapter 48

Introduction to Endoparasitic Nematodes (Phylum Nemata)

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General Shape and Structure of Endoparasitic Nematodes

Nematodes are relatively small, mostly dioecious, non-segmented worms that generally lack any sort of well-developed external structures for locomotion. Many of the animal parasitic species possess external cuticular structures that enable them to move and maintain their position in the host and—depending on the host—this could include the gut, mesenteries, sub-cutaneous tissues, or other organs. The external structures of parasitic nematodes that enable them to detect their environment include **amphids** on the anterior end, **deirids** (also called **cervical papillae**) near the level of the **nerve ring**, **phasmids** near the tail, and various kinds of **sensory sensillae**. As far as is known, no animal parasitic nematodes have eye spots, and only a few nematodes that live in marine intertidal interstitial environments have eye spots. Some nematodes have complex lips surrounding the mouth (Figure 1) and these lips facilitate feeding. The lips and associated structures posterior to the mouth may enable the nematode to attach to the host intestine. Not all nematodes have all of these structures and different combinations of characters are used for identification and classification into different groups.

Examples of species that attach firmly in the small intestine are species of Ancylostomidae (Figure 2) which, among others, includes the hookworms (genus *Ancylostoma*). Anisakids are also known to attach to the submucosal layer of the gastrointestinal tract of their hosts. This includes various species in the genera *Anasakis*, *Terranova*, and *Pseudoterranova.* These nematodes usually use marine mammals as their definitive hosts.

On the posterior end of nematodes, males of some groups, such as species of the order Strongylida (Figures 3–5), have a well-developed and complex apparatus called the **copulatory bursa** that is used to grasp the female to facilitate mating. Other nematodes, such as species of *Physaloptera*, Oxyurida, and Filarioidea have various combinations of papillae (sensillae) and cuticular ornamentations that serve a similar purpose.

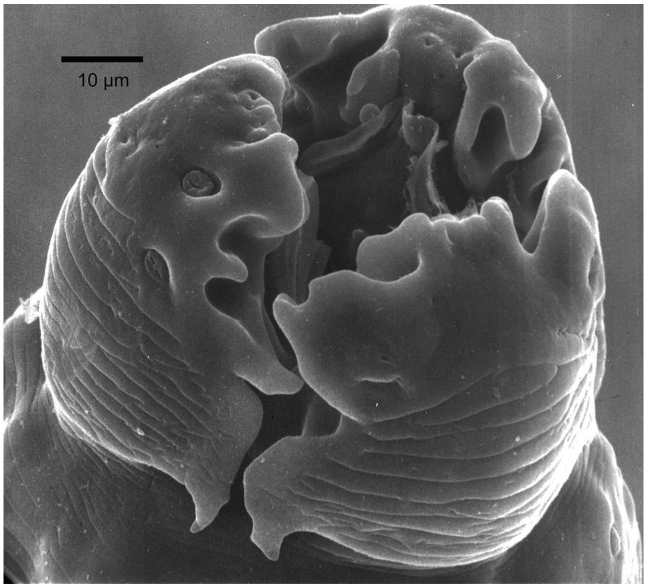

Figure 1. Scanning electron micrograph of the anterior end of a species of *Paraspidodera* from *Ctenomys* in Bolivia showing 3 large lips with sensory papillae, also known as sensillae (plural) or sensillum (singular) on each lip. Source: S. L. Gardner. License: CC BY 4.0.

Figure 2. Image of anterior end of *Ancylostoma ctenomyos*, a parasite of rodents of the genus *Ctenomys* from the eastern lowlands of Bolivia. The stoma with the cutting teeth and plates are clearly visible. The villi of the small intestine are pulled into the stoma and the teeth abrade the villi. Blood then is pumped into the intestine from the abraded villi via the esophagus. Source: S. L. Gardner. License: CC BY 4.0.

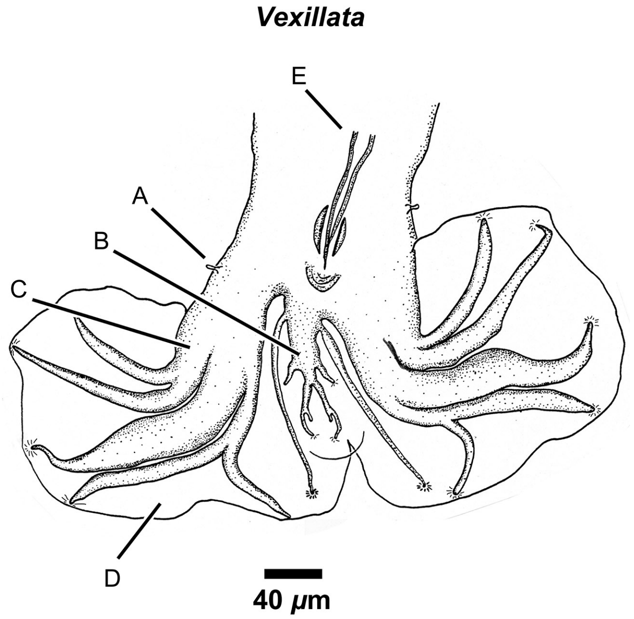

Figure 3. Drawing of the posterior end showing a ventral view of the copulatory bursa of *Vexillata armandae* (order Strongylida, family Ornithostrongylidae), a parasite of the coarse haired pocket mouse (*Chaetodipus hispidus*). Labels: A) Papillae (ray 0); B) Dorsal ray; C) Lateral rays in the 2-1-2 arrangement; D) Vellum (thin cuticular membrane) of bursa; E) Setacous spicules retracted. Source: S. L. Gardner. License: CC BY 4.0.

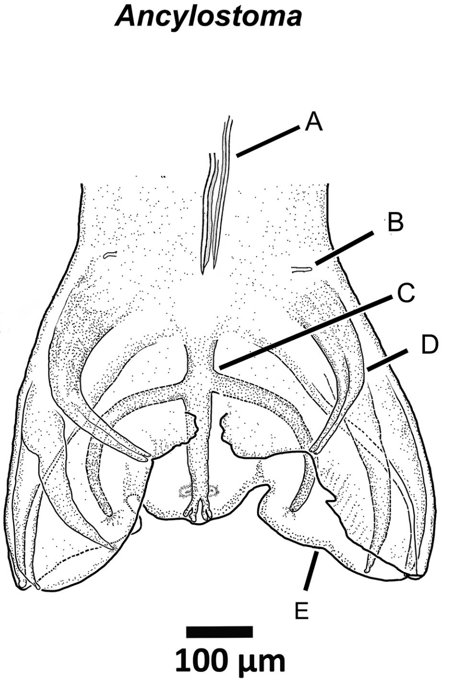

Figure 4. Drawing of the posterior end of a species of *Ancylostoma ctenomyos* a parasite of rodents of the genus *Ctenomys* in lowland Bolivia. Labels: A) Posterior ends of the spicules; B) Ray 0 or pre-bursal ray; C) Dorsal ray; D) Lateral rays; E) Vellum of bursa. Source: S. L. Gardner. License: CC BY 4.0.

Depending on the species, the body of parasitic nematodes usually has a greater diameter (when viewed in transverse section) near the middle of the body of the animal relative to the anterior end. All nematodes have a round shape when viewed from either end of a transverse section through mid-body (Figures 5A–D). The body wall of a nematode is covered with flexible acellular cuticle that is mostly translucent and is secreted by a cellular hypodermis. The circular or round nature of the transverse sections is why these animals are sometimes called roundworms.

The **external cuticle** of the nematode may be smooth, have longitudinal striations, or have well-developed winglike structures called **alae** (= wings; Latin) or ridges that are situated on the lateral surfaces of the body (Figure 5D). Some species have well-developed lateral alae near the anterior end where they are called **cervical alae**. The tiny wings, or alae, can also run the entire length of the body on the lateral cuticle of the body, in which case they are termed **lateral alae**, and if only on the posterior, they are called **caudal alae**. It is thought by some researchers that the alae are utilized by nematodes to orient themselves somehow in the host and there is conclusive evidence that the alae are species-specific, and can be used in identifying and classifying the nematodes.

The cuticle of nematodes can be extremely thin and fragile, or it can be thick and extremely strong and even very resistant to digestion, as shown in those species that live in the acid environment like that found in the stomach of a carnivore. For example, filarioid nematodes have a very thin cuticle. They occur in the tissues of vertebrates and are able to exist only within these osmotically balanced habitats and if they are removed and placed in water, they usually quickly explode due to osmotic pressures.

Nematodes are sometimes casually called **pseudocoelomates** because in most species that have been studied, their body cavity does not appear to be completely lined with cells derived from embryonic mesoderm. All coelomate animals that are termed eucoelomates—or true coelomates—have a peritoneum that lines both the body cavity and the internal organs and the peritoneum is a layer of tissue that is derived from embryonic mesoderm. Most nematodes do not have an obvious or visible lining of the body cavity, although, as Armand Maggenti (1981, p. 10) pointed out: "Nematodes have a well-developed body cavity filled with fluid and with some evidence of mesodermal lining, if one considers the muscle sheath as mesoderm and the epidermal layer around the gonads and the basal lamella of the intestine as being of mesodermal origin."

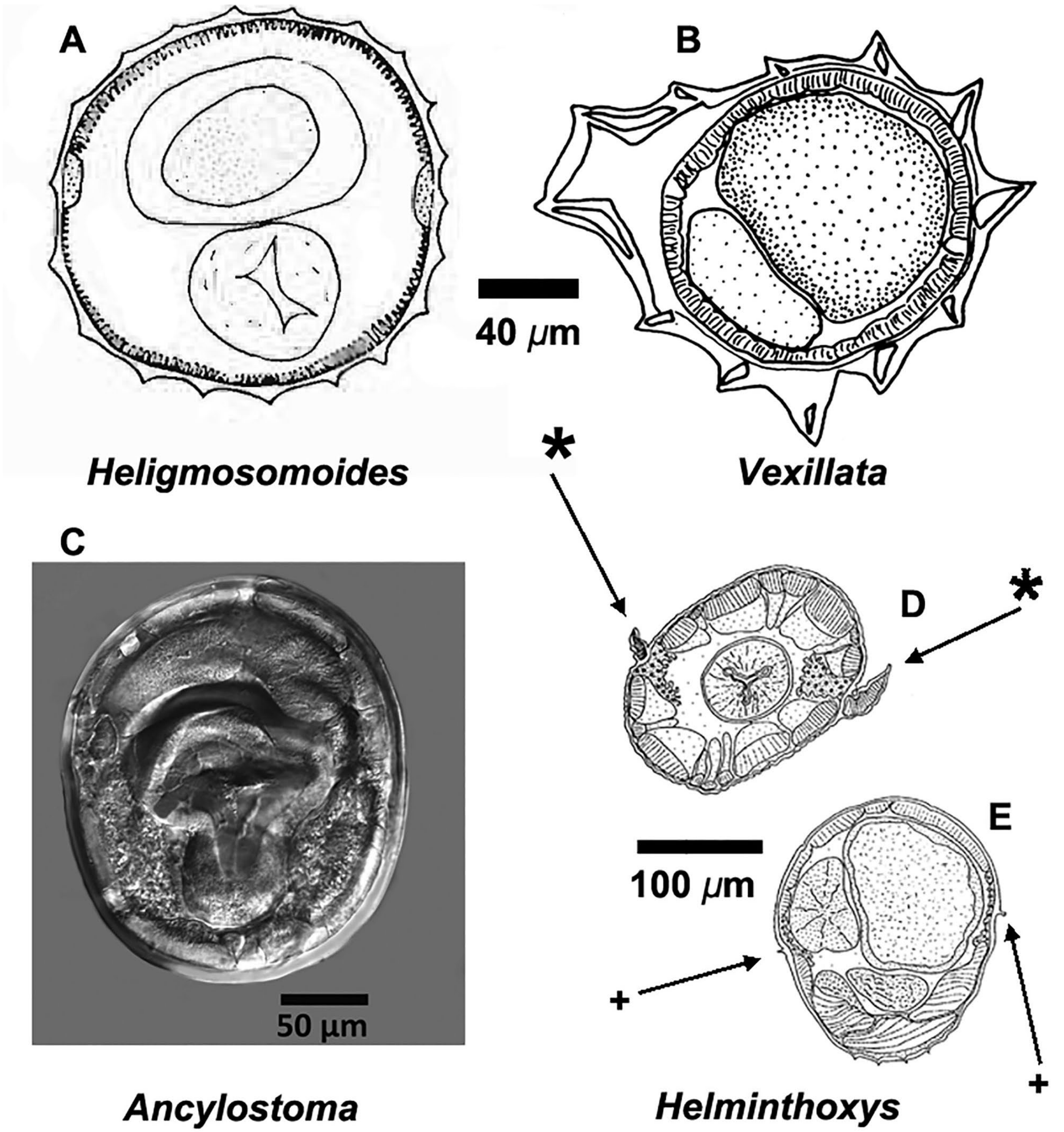

Figure 5. Drawings and photographs of transverse sections from 3 species of order Strongylata (Figures A–C), including: A) Transverse section at midbody of *Heligmosomoides thomomyos* showing the lack of cuticular aretes within the cuticle; B) Transverse section at midbody of a species of *Vexillata* showing the well-developed carene and well-developed cuticular aretes; C) Digital image of a transverse section of *Ancylostoma ctenomyos* showing a relatively smooth cuticle; D and E) Transverse sections through a species of *Helminthoxys* (order Oxyurida) with D) Cephalic alae (*) via a cut through the area of the esophagus. E) Transverse cut through the posterior part of the nematode showing the small lateral alae (+). Source: S. L. Gardner. License: CC BY 4.0.

Another unique feature of all nematodes is the fact that they have no circular muscles. Therefore, movement is accomplished by contraction and relaxation of **longitudinal muscles** in apposition, or antagonistic to, their **hydrostatic skeleton**. The nematode moves as the muscles contract and the cuticle flexes thus enabling nematodes to writhe around, moving through the organs and tissues of their hosts, and in some cases, into the external environment. Nematodes maintain their form in a way analogous to a water balloon because their body fluids are under a positive pressure in the **hydrocoel** relative to their environment.

Individuals of most animal parasitic species of nematodes have a complete **digestive tract** with an anterior **stoma** lined with cuticle, followed by a **pharynx**, then a tri-radiate **esophagus** (Figure 5D) that can be muscular (Figure 6) or glandular in form, or the esophagus may have a combination of both muscular and glandular sections as in some species of the superfamily Filarioidea, and others. The tubular **intestine** (Figure 6F) is usually a single cell in thickness and is lined on the body cavity side with a thin collagen-like material. Internally, the single layers of cells are lined completely with microvilli (Grassé, 1965; Maggenti, 1981; 1991a). The **gastrointestinal tube** extends from the esophagus to the anus, or **cloaca**, with some species possessing out-pouched **cecae** or **diverticulae** near the esophageal end (Figure 7).

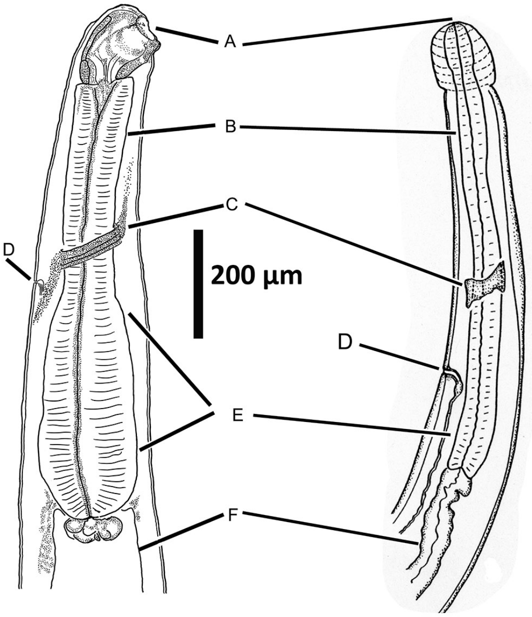

Figure 6. Anterior end of 2 strongylid nematodes showing homologous structures of the anterior end. A) Mouth; B) Anterior end of muscular esophagus; C) Nerve ring, also called the circum-esophageal commissure; D) Excretory pore; E) Base of esophagus; F) Intestine. Source: S. L. Gardner. License: CC BY-NC-SA 4.0.

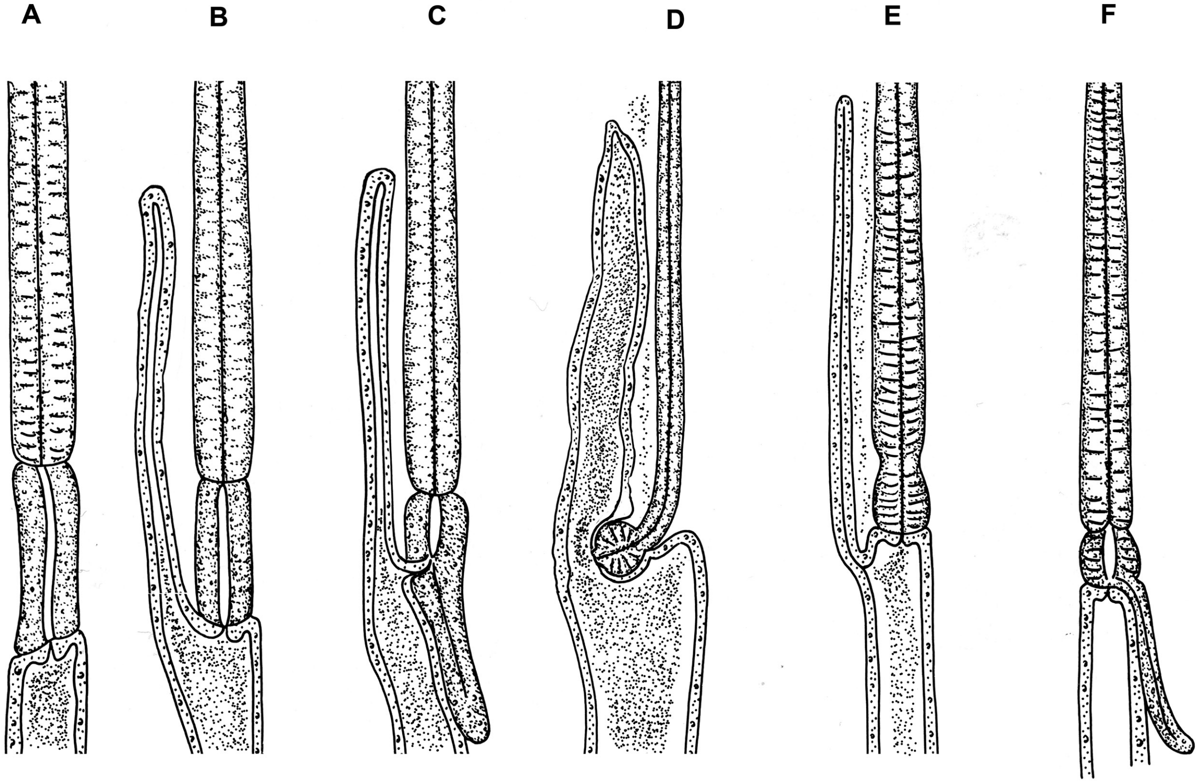

Figure 7. Intestinal cecae or diverticulae that may occur in nematodes of the order Ascaridida. A) *Anasakis*; B) *Porrocaecum*; C) *Contracaecum*; D) *Dujardinia*; E) *Aguticaecum*; F) *Raphidascaris*. Source: Adapted from Maggenti, 1981; Yamaguti, 1961. License: CC BY 4.0.

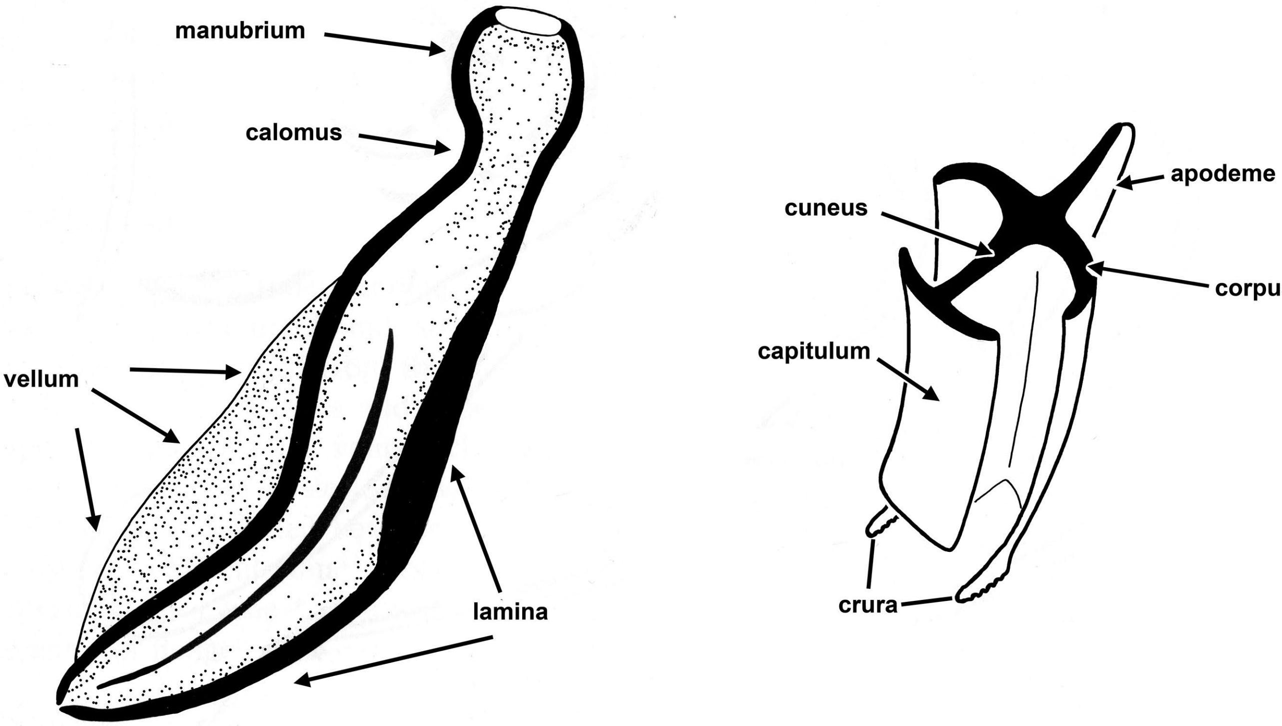

Figure 8. A) Spicule, showing major parts. B) Gubernaculum, transverse section showing how the spicule can slide through the opening between the capitulum and the corpus. Source: Adapted from Maggenti, 1981. License: CC BY-NC-SA 4.0.

Most nematodes are **sexually dimorphic** with definite male and female individuals, and they are usually **dioecious**, meaning that they have to mate to produce viable eggs. In those species that are dioecious, males usually have a pair of cuticularized **spicules** that are used to assist in the transfer of sperm to the females (Figure 8A).

There are some pinworms in which the males have no spicule at all, such as species of *Aspiculuris*. Many male nematodes also have a **gubernaculum** (Figure 8B) that serves to guide the spicules during copulation. Some species are hermaphroditic and in these cases the nematode produces both sperm and ova from the **ovotestis** of the same individual at different times during their life stage, or ontogenetic development (Maggenti, 1981).

A major **synapomorphy** (also called a shared-derived character) for the Nemata is the presence of non-contractile, **myo-neural processes** that extend from the contractile portion of the muscle cell to the neural junctions of the dorsal or lateral **nerve cords** (Figure 9). Figure 9 shows the contractile portion of the muscle below and the neural part with the nucleus above with a laterally extending neural process that extends to the nerve cord.

Nematodes vary greatly in size and the diameter of most species is usually much less than 2 mm, even in the longest of the long nematodes such as *Placentanema gigantissima*, which is a 9 m-long parasitic nematode that lives in the reproductive tract of whales. The thickest ones, or those individuals with the greatest body width of all nematodes known so far, is the giant kidney worm, *Dioctophyma renale.* This nematode lives in mustelids, such as minks, badgers, and weasels, and has a diameter of up to 15 mm with a length of more than 1 m. The eggs of nematodes are also very similar in size with eggs of most species having eggs that range from 50–100 μm-long by 20–50 μm-wide.

External Covering: The Cuticle

An example of diversity in shape and structure of the cuticle is that of the complex cuticular aretes found in most species of the superfamily Trichostrongyloidea that are parasitic in the small intestines of many species of vertebrates, especially mammals, in which the exocuticle is modified into a series of cuticular aretes called the synlophe. In these forms, it is thought that the ridges running down the length of the body of the nematode are used in maintaining their position in the intestine of their hosts (Figure 10). In the latter part of the 1960s and 1970s, an evolutionary schema of nematodes classified in the superfamily Trichostrongyloidea was developed by Marie Claude Durette-Desset and Alain Chabaud in the Laboratoire des vers, Muséum national d'Histoire naturelle in Paris, France (currently named Laboratoire de biol-

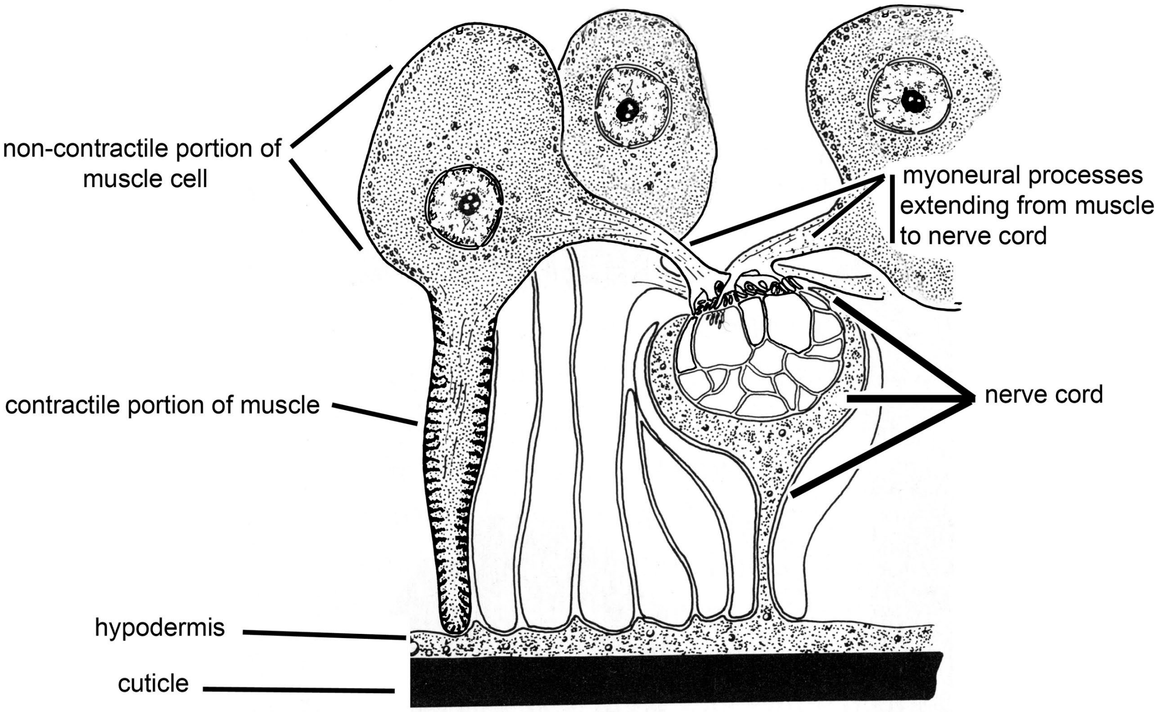

Figure 9. Schematic of the contractile and non-contractile portions of the muscle cells seen in the Nemata. Source: Adapted from Maggenti, 1981. License: CC BY-NC-SA 4.0.

ogie parasitaire, protistologie, helminthologie). They worked out the biogeographical and morphological evolution of these nematodes using a combination of the structure of the **synlophe** (Figure 10) and the rays of the bursa (Figure 3) that allowed an understanding of the evolutionary relationships of one of the most speciose groups of parasitic nematodes (Durette-Desset, 1971).

The external cuticle may be smooth without alae or external lines, or the cuticle may have complex rings. In the posterior part near the cloaca of many male nematodes (Physalopteridae, Filarioidea, and others), and in addition to sensory papillae or sensillae, there may be a rough area of the external cuticle called the **area rugosa**, or the rough area. A hypothesis about why this is found in males is that the rough cuticle may enable the male to locate and attach to the female more easily for mating purposes. Some nematodes have an **exocuticle** (external cuticle) composed of serrated ridges or bumps, or the cuticle may be very smooth. Some groups, such as species comprising the superfamilies Heterakoidea and Subuluroidea, possess cuticularized suckers situated anterior to the cloaca that are surrounded by sensory papillae and evidently enables the male to find and attach to the female in the intestinal tract of the host (Figure 11).

Host Range and Diversity of the Nemata

All species of vertebrates and many species of beetles examined by scientists thus far serve as hosts for at least 1 species of parasitic nematode. Some nematodes have a very **narrow host range**, surviving and reproducing successfully only in a single species of host, or perhaps in a phylogenetically- or ecologically-related group of species. Other nematodes show a wide host range, being much more likely to jump from one suitable host to another during opportune times during their life history, exhibiting what is termed **ecological fitting** (Janzen, 1985; see also Brant and Gardner, 2000; Brooks et al., 2019).

Within a single free-living animal, myriad habitats may be occupied by nematodes. Organs and tissues of a mammal have different hormone levels, different levels of pH, various levels of exposure or isolation from the immune system, and more. To illustrate the diversity of habitats in a single mammal host, for example in humans, *Trichinella* species can occur as juveniles, encysted in various muscles like the diaphragm or the tongue, *Strongyloides* species may be found in the mucosa of the intestine or other tissues, *Ascaris* may be found migrating in blood and lungs, juveniles called microfilariae of filarioid nematodes may be found in blood or lymph, or adult *Ancylostoma*, *Necator*, and *Ascaris* species may be found in the

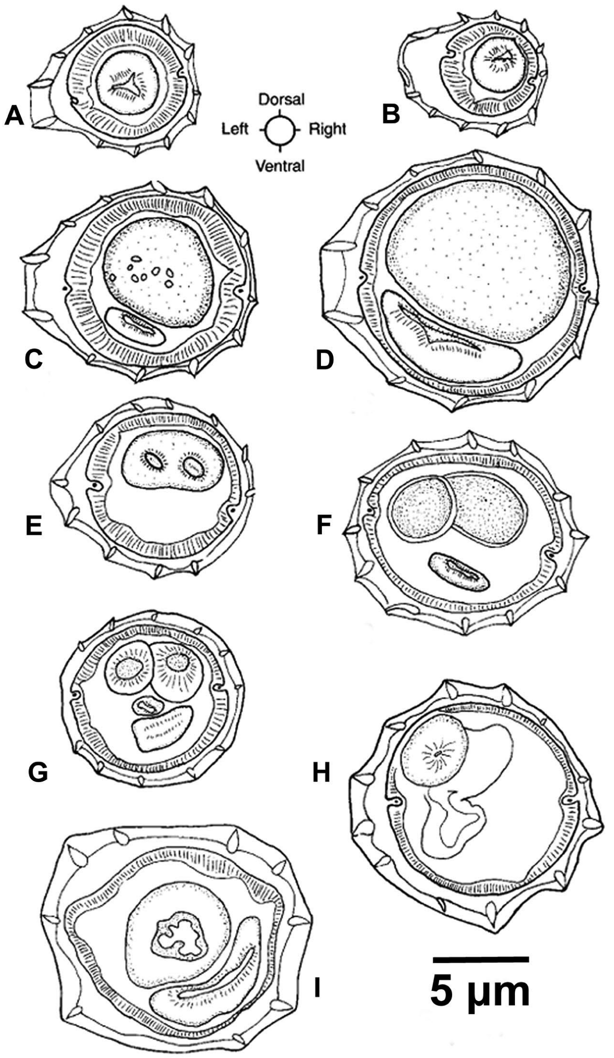

Figure 10. Transverse sections of *Vexillata armandae*. A) Section through esophagus of male; B) Section through esophagus of female; C) Midbody of male; D) Midbody of female; E) Posterior 1/4 of body of male through the spicules; F) Posterior 1/4 of body of female through eggs in the uterus; G) Posterior 1/16 of body of male through the spicules just anterior to the cloaca; H) Posterior section of female at level of ovijector infundibulum I) Posterior section of female at level of ovijector vestibule. Source: S. L. Gardner. License: CC BY 4.0.

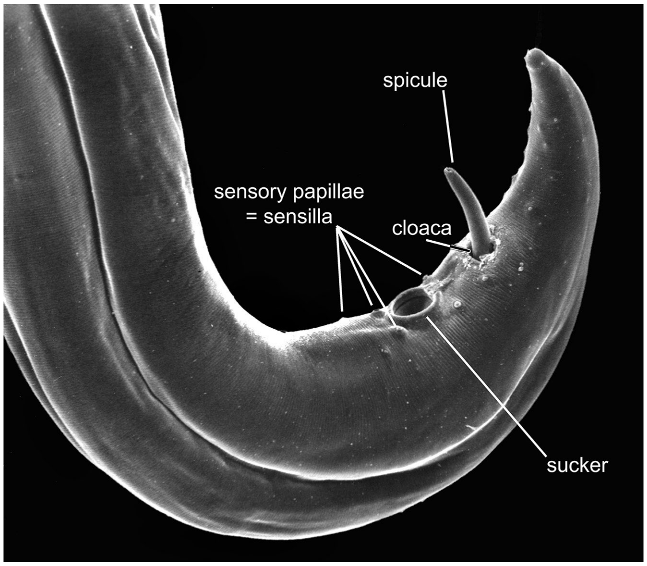

Figure 11. Posterior end (tail) of a male *Paraspidodera* showing the relatively smooth cuticle, a sucker just anterior to the opening of the cloaca, and 1 spicule protruding from the cloaca. Source: S. L. Gardner. License: CC BY 4.0.

small- and large intestines. Individuals of these same species, as well as *Onchocerca, Loa*, and *Wuchereria*, can occur as juveniles in muscle or connective tissues, and as adults in mesenteries and subcutaneous tissues, and *Enterobius vermicularis* may be found in the large intestine and cecum.

In the early part of the 20th century, Nathaniel Cobb (1915) recognized that nematodes are extremely biodiverse. He was well acquainted with animal parasitic nematodes, and his familiarity with the Nemata led him to estimate that well over 80,000 species of nematodes would eventually be found parasitizing vertebrates alone. Falling short of Cobb's estimate, to date only about 20,000 species of parasitic nematodes have been described from all species of 48,000-plus recognized species of vertebrates. The natural history, development, and transmission parameters of more than 550 species of animal nematodes are well known (Anderson, 2000). As parasites of vertebrates, Anderson (2000) estimated that there were about 2,300 described genera distributed among 256 families comprising about 33% of all nematode genera. If each of the approximately 6,526 known species of mammals (as of July 2023; see https://mammaldiversity.org) were each infected with only 2 species of nematodes with narrow host range, there would be expected to be a minimum of 13,052 species of parasitic nematodes only in the class Mammalia.

Pinworms, which are nematodes of the order Oxyurida (Figure 12), have a relatively narrow host-range and it is well known that almost all species of rodents, lagomorphs, and primates have their own species of pinworm. Both recent and historical studies have shown that pinworm nematodes exhibit relatively narrow host range, and many have been shown to have cospeciated with their primate and rodent hosts (Hugot, 1999). Currently, a total of about 900 species of pinworms have been described, with vertebrates hosting about 500 species and invertebrate species hosting only about 400.

Because pinworms tend to have a narrow host range, their numbers correlate approximately with the number of host species there are. By way of example, pinworms that are parasitic in arthropods are classified in the superfamily Thelastomatoidea. There are currently about 4,500 described species of cockroaches with more than 20,000 to 30,000 additional species expected to be eventually described (Ghosh, 2017). There are around 17,000 species of millipedes known with more than 60,000 species expected yet to be described. If each species of cockroach and millipede harbors its own species of pinworm, huge numbers of thelastomatoid pinworms will eventually be described from just these 2 arthropod groups alone.

The greatest diversity in the superfamily Oxyuroidea of vertebrates expected to be found in the future may result from examination of the catfishes of the Amazon basin (Rodrigues et al., 2020). During studies of the catfishes of the Amazon basin, Rodrigues (personal communication, 2020) stated that every fish examined was infected with oxyurids.

It is estimated that approximately 138 species of nematodes have been reported from humans (Crompton, 1999), with 32 to 36 being host-specific. Estimates of the number of human infections in the year 2000 by species of parasitic nematodes are shown in Table 1.

Large numbers of species of Oxyuroidea are also expected to be described from Neotropical rodents of the family Muridae. As of 2022, only around 8 species of pinworms have been described from Neotropical murids, while there may be 400–800 undescribed species of Oxyuroidea, given that 1–2 new species of oxyuroid nematode are found in each new species of rodent examined.

Classification

In this book, the use of the phylum name **Nemata** (= **thread**; German) for the nematodes partially follows Hodda's (2022) work, as well as the older work by Maggenti (1981; 1991a) who considered Chitwood's (Chitwood and Chitwood, 1977) emendation of the name Nemates to Nemata a correct and robust move because this followed the Pearse system for nomenclatural endings (Pearse, 1936). Maggenti (1981) points out that the old phylum name Nematoda is a leftover class level name from previously discarded classifications that were developed when the nematodes were considered to be a class in a larger group called the now-superceded phylum Aschelminthes. However, not all biologists who study nematodes adhere to this system; see, for example, the contrasts in older classifications in the work by Libbie Hyman (Hyman, 1953), the massive work by the French zoologist Pierre-Paul Grassé (1965), and the book General Nematology by Maggenti (1981) for the variations.

Hodda's (2022) work includes an explanation about why the upper-level classification of the Nemata is confusing and difficult. Maggenti (1981) and Anderson (2000) are generally followed for the higher order names for the animal parasitic nematodes and Hodda (2022) is generally followed for the names lower in the classification; however, in this work, no great effort has been made to synchronize the classifications with Hodda (2022) and others since changes are being made daily as more data from genomic sequencing efforts roll into the databases holding information on the Nemata.

All told, above the level of the order, confusion reigns relative to the classification and systematic arrangement of the nematodes, although Hodda's (2022) efforts should bring some measure of stability to the classification of the group. Maggenti (1981) is usually followed in the upper levels of the classification and the phylogeny presented by Anderson (2000; see Figure 12) provides the main groups; however, there are some points of agreement between Maggenti's and Anderson's with Hodda's more recent (2022) classification.

The classes recognized in this book include the Secernentea and the Adenophorea (Figure 13). Recent work shows that these groups are mostly substantiated both in morphological and molecular analyses although competing phylogenetic hypotheses and associated classifications have also been proposed (Adamson, 1989; Dorris et al., 1999; Blaxter et al., 1998; Brooks and McLennan, 1991; Anderson, 2000; Hodda, 2022).

Table 1. Estimated numbers of common nematode infections in humans worldwide. Data from Crompton, 1999.

Species	Number of humans infected	Geographic distribution
Ancylostoma duodenale and *Necator americanu*s	1,298,000,000	Worldwide
Brugia maylayi and *B. timori*	13,000,000	South Pacific, Southeast Asia, and India
Dracunculus medinensis	Estimated to be fewer than 100 human cases	Sub-Saharan Africa
Loa loa	13,000,000	West Sub-Saharan Africa, central Sub-Saharan Africa, and Yemen
Onchocerca volvulus	17,660,000	Central America, South America, and Sub-Saharan Africa
Strongyloides stercoralis	70,000,000	Temperate regions

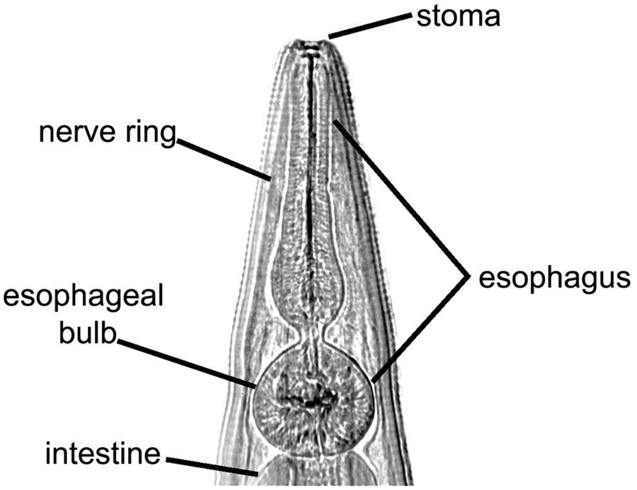

Figure 12. Anterior end of *Didelphoxyuris*, a pinworm nematode of South American marsupials, showing: A) The small stoma at the anterior end, followed by the well-developed muscular esophagus with a large posterior bulb. The esophagus acts as a muscular pumping organ, pumping food into the intestine. Source: S. L. Gardner. License: CC BY 4.0.

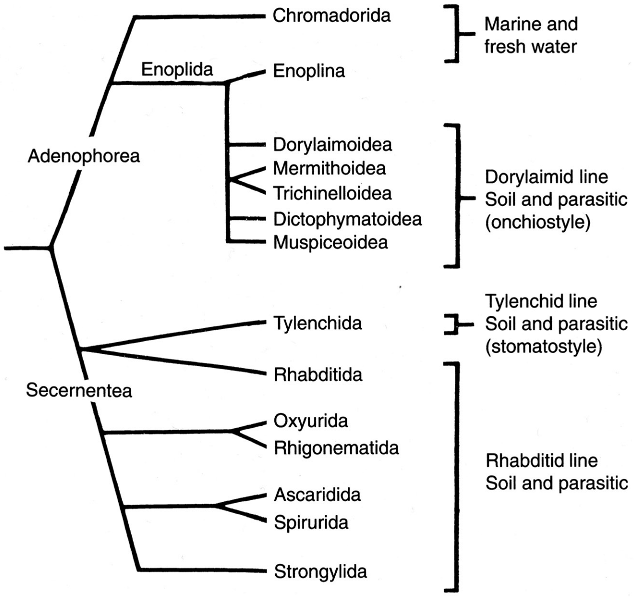

Figure 13. Phylogenetic hypothesis of main groups of the phylum Nemata. Sources: Adapted from Anderson, 2000; Maggenti, 1991. License: CC BY-NC-SA 4.0.

Relation to Other Animal Groups

One analysis grouped the nematodes, gastrotrichs, priapulids, kinorhynchs, and the loriciferans into a superphylum group called the Cycloneuralia based on the circular shape of the nerve ring that loops around the esophagus in most groups and functions as the central part of the nervous system in these animals (Nielsen et al., 1996). Other studies have shown that the Nemata share a common ancestor with the Nematomorpha (see Zrzavy, 1998). Mayer and Whitington (2009) and Nielsen (2012) show that the Nemata share a common ancestor with the Nematomorpha in a different superphylum designation called the Nematoida.

Ancient History of Nemata

The oldest written account of the giant intestinal nematode *Ascaris lumbricoides* in humans dates to approximately 4,750 years ago, from China. In this work, foods to avoid and a description of the symptoms of humans infected with these worms was accurately given (Hoeppli, 1959; Maggenti, 1981). In the area of the Nile River Valley, early Egyptian physicians first recorded the presence of both *Ascaris* and the guinea worm, also called the fire worm, *Dracunculus medinensis*, in an ancient papyrus manuscript written by Egyptian physicians around 3,550 years ago, which was obtained and translated by the Egyptologist Georg Ebers in 1872 (see Chitwood and Chitwood, 1977; Maggenti, 1981). About 2,400 years ago, Hippocrates first wrote about nematodes infecting other animals besides humans when he recorded his finding of pinworm nematodes of horses. In the 13th century, Albertus Magnus and Demetrios Pepagomenos recorded nematodes from falcons (cited in Rausch, 1983; see also Chitwood and Chitwood, 1977).

Physical evidence of nematodes date from much earlier than the written accounts. Eggs of the pinworm of humans, *Enterobius vermicularis*, and the whipworm of humans, *Trichuris trichuria*, occur in coprolites dated to about 7,000 years old from Peru, and eggs of the human-specific hookworm, *Ancylostoma duodenale*, have been reported from coprolites dated to around 7,230 years old, collected from caves in eastern Brazil (Araújo et al., 2008). Eggs of *Ascaris lumbricoides* have been positively identified from coprolites of human origin dated to about 28,000 years old from caves in France, but these are the only occurrence of a record this old (Bouchet et al., 1996). The dearth of other nematodes from human remains older than about 7,000 years appears to be due to the fact that organic material comprising the coprolites themselves do not preserve well enough to last that long (Karl J. Reinhard, personal communication, 2022).

Trace or Fossil History

The only fully fossil nematodes that are known thus far are insect parasitic or plant parasitic forms that occur very rarely in amber inclusions (Poinar et al., 1994). One pinworm egg was found in a fossilized fecal pellet from a cynodont around 250 million years old (Hugot et al., 2014). Because there are no fossil records of nematodes of Cambrian or Precambrian ages, estimates of the age of the Nemata have been only speculation up to the present time and without fossils, it is difficult to calibrate molecular clocks for the nematodes. An estimate of the time of divergence of the nematodes from the rest of the animal groups appears to be about 1,177 ± 79 million years (Wang et al., 1999).

Most authors consider the ultimate origin of nematodes to be from a marine ancestor (Maggenti, 1991; Malhakov, 1994). The tri-radiate esophagus and the tubular body indicate an initial possible primarily sedentary existence of the ancestral forms of the Nemata, with the posterior end attached to the substrate and the anterior end freely encountering the marine environment from all sides, thus the somewhat radial symmetry may be secondarily-derived from selective advantage of the animal experiencing the environment from all sides simultaneously (Armand Maggenti, personal communication, 1992).

Nematode Chapter Organization

In the following sections in this chapter, the superfamilies Trichuroidea and Trichinelloidea will be covered under class Adenophora and several representatives from class Secernentea will be discussed following those, including order Ascarida and superfamily Heterakoidea, and the orders Camallanida, Filariata, Oxyurida, Spirurida, and Strongylida.

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NEMATA

Trichuroidea and Trichinelloidea (Superfamilies)

María del Rosario Robles and Rocío Callejón Fernández

- Phylum Nemata
  - Class Adenophorea
    - Order Trichocephalida
      - Superfamily Trichuroidea
      - Superfamily Trichinelloidea

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Chapter 49

Trichuroidea and Trichinelloidea (Superfamilies)

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Introduction

Maggenti's (1981) classification of nematodes will mainly be followed in this section and will include a description of the morphology and molecular attributes of nematodes of the superfamilies Trichuroidea and Trichinelloidea. In recent years there has been a significant advancement in knowledge on the phylogenetic relationships of many of the species that are included in these superfamilies (see Hodda, 2022 for a summary). These results and others that help illuminate the ecological and epidemiological aspects of these nematodes will be described. The primary species of medical and veterinary importance will also be discussed.

Taxonomy

The upper level classification of this group is still unsettled and several authors have provided different proposals of infraclass hierarchies, such as from the orders Enoplida, Trichinellida, and Trichocephalida, the superfamily Trichinelloidea and Trichuroidea, and different combinations of families and subfamilies, such as Trichinellidae/Trichuridae, Trichurinae/Capillariidae, Capillarinae/Trichosomoididae, and Anatrichosomatidae/Trichosomoidinae (see, for example, Maggenti, 1981; Anderson, 2000; Moravec, 2001a; Roberts and Janovy, 2009; Anderson et al., 2009; Hodda, 2022).

Based on Moravec (2001a), Table 1 includes the genera included in each family considered in this section. Trichuridae includes more than 80 species, Capillariidae includes more than 300 species, Trichosomoididae includes fewer than 10 species, and Trichinellidae is a monotypic family (containing a single genus) and considered for many years to have only 1 species; however, recently 9 species have been identified (Robles et al., 2006; 2008; Fugassa et al., 2014; Krivokapich et al., 2012).

Morphological Characteristics

These nematodes have very few observable differences and, therefore, represent one of the most difficult groups to classify with respect to their taxonomy and systematics, since the genera and species are distinguished only based on their morphology (Moravec, 2001a). For example, their cephalic structures and details of the posterior end are dif-ficult to observe with a light microscope. The details of the anterior ends are too small to observe readily using standard microscopy so, reliable data can only be obtained by the use of scanning electronic microscopy (SEM). Using SEM, features such as the papillae and the stylet of the oral aperture, the bacillary band, and accessory genital organs may have taxonomic value, and these may otherwise be easily overlooked.

Specimens from the class Adenophorea are characterized by their lack of both phasmids and lateral excretory canals.

Table 1. Genera in each family considered in this chapter, based on Moravec (2001a).

Superfamily	Family	Genus/Genera
Trichuroidea	Trichuridae	*Trichuris*
	Capillariidae	*Amphibiocapillaria*, *Aonchotheca*, *Baruscapillaria*, *Calodium*, *Capillaria*, *Capillostrongyloides*, *Crocodylocapillaria, Echinocoleus*, *Eucoleus*, *Freitascapillaria*, *Gessyella*, *Liniscus*, *Paracapillaria*, *Paracapillaroides*, *Paratrichosoma*, *Pearsonema*, *Piscicapillaria*, *Pseudocapillaria*, *Pseudocapillaroides, Pterothominx*, *Schulmanela*, *Tenoranema* (among others, depending on the classification used)
	Trichosomoididae	*Anatrichosoma*, *Huffmanela*, *Trichosomoides*, *Trichuroides*
Trichinelloidea	Trichinellidae	*Trichinella*

Selected Sub-groups of Trichocephalida

Following are descriptions of characteristics that help distinguish specimens among a few select groups of Trichocephalida.

Overview of Superfamilies Trichuroidea and Trichinelloidea

In general the differences in species assigned to either superfamily, as well the families included in Trichuroidea, are based on certain diagnostic characteristics (synapomorphies) that are given in Table 2. The main characters that serve to define the groups include: Relative widths of anterior and posterior portions, sexual dimorphism (body size) (Figure 1), the position of the rows of stichocytes, particular characteristics of the bacillary glands, and the number and positions of the associated bacillary bands (Figure 2). In the realm of reproductive characters, the important synapomorphies here include: Characteristics of accessory genital organs in the male, for example, caudal alae, copulatory bursa, papillae, and caudal lobes (Figure 3), as well

Table 2. Trichuroidea and Trichinelloidae: Comparison of morphological characters.

Maggenti (1981)	**Trichuroidea**			**Trichinelloidea**
Moraveč (2001a)	**Trichuridae**	**Capillariidae**	**Trichosomoididae**	**Trichinellidae**
Width of body	Thin and long anterior portion, shorter and broader posterior portion	Filiform, similar throughout the extension	Filiform, similar throughout the extension	Filiform, similar throughout the extension
Sexual dimorphism	Little difference in size between sexes	Little difference in size between sexes	Large size difference between sexes	Large size difference between sexes, females twice the size of males
Position of stichocytes	Regularly aligned with similar size	Regularly or irregularly aligned with similar size	Irregularly aligned with different size	Regularly aligned with similar size
Number and position of bacillary bands	1 lateral in anterior portion, with cuticular inflations bordering the bacillary band in the proximal part	1–4 with variable positions in anterior and posterior portions	1–4 with variable positions in anterior and posterior portions	Without bacillary band
Male: Characteristics of genital organs	Spicule sclerotized and spicular sheath cylindrical with spines. Caudal papillae present	Spicule sclerotized or not observable and cirrus with morphology and ornamentation. Variable structures: caudal alae, copulatory bursa, papillae, caudal lobes	Spicule and cirrus vestigial or absent	Spicule and cirrus absent
Female: Characteristics and position of the vulva	Opening near the end of the esophagus May have protruding lips and spines	Opening near the end of the esophagus	Opening near the end of the esophagus	Opening in the middle of the esophagus
Eggs	Polar plugs slightly protruding above the shell surface	Polar plugs not protruding above the shell surface, although with variable forms and ornamentations	Polar plugs not protruding above the shell surface, sometimes dark surface	Without eggs

The classification below superfamilies follows Moraveč (2001a). The morphological characterization was obtained from Moraveč (2001a), Anderson et al. (2009), and contributions of authors of this chapter (Figures 1–6).

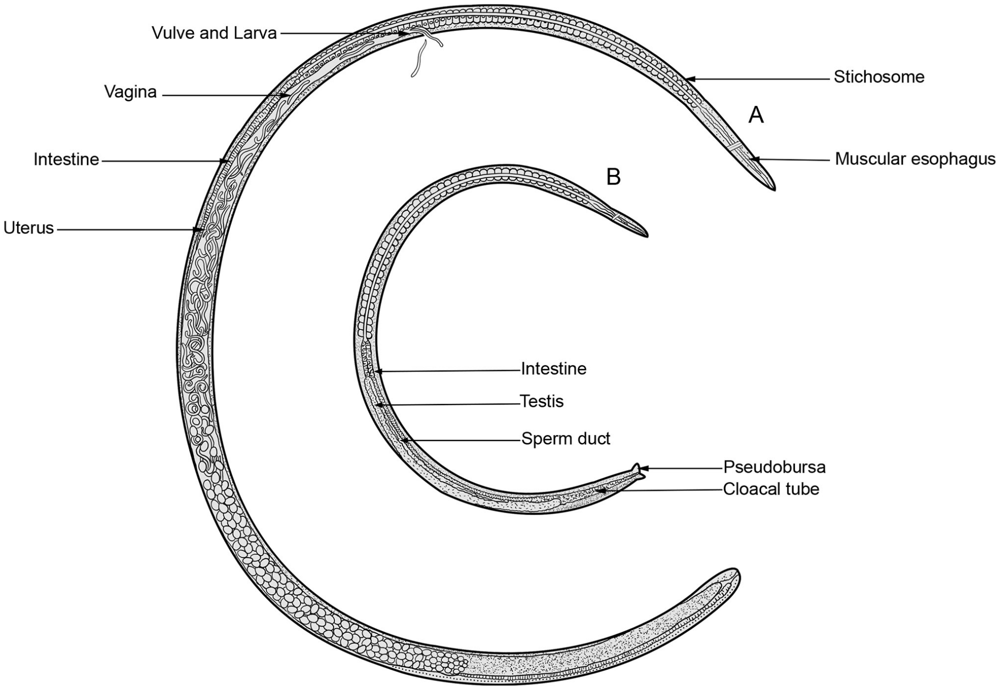

Figure 1. Diagrammatic representation of morphological structures of male and female specimens of *Trichinella spiralis*, as an example of Trichinelloidea. Source: K. Solas. License: CC BY-NC-SA 4.0.

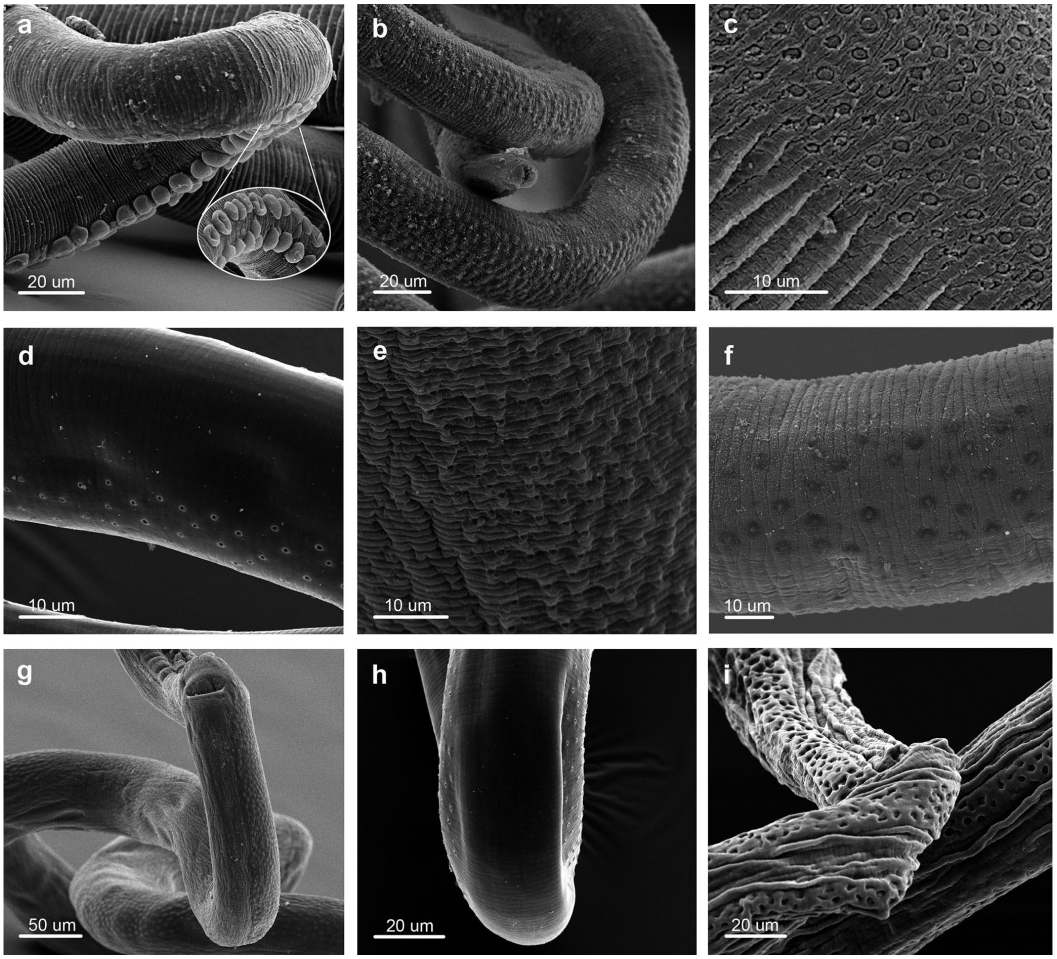

Figure 2. Scanning electron micrographs of bacillary bands from trichuroid species in rodents:

a) Cuticular inflations bordering the bacillary band in *Trichuris navonae* Robles, 2011.

b) Bacillary band located after the inflations, with detail of the oral aperture in *T. laevitestis* Suriano & Navone, 1994. Detail of bacillary glands

(c) in *T. bainae* Robles et al., 2014, (d) in *Eucoleus* sp.,

(e) in *Echinocoleus* sp.,

(f) in *Anatrichosoma* sp. Number and position of bacillary bands,

(g) 1 lateral bacillary band,

(h) 2 lateral bacillary bands,

(i) 1 ventral and 2 lateral bacillary bands.

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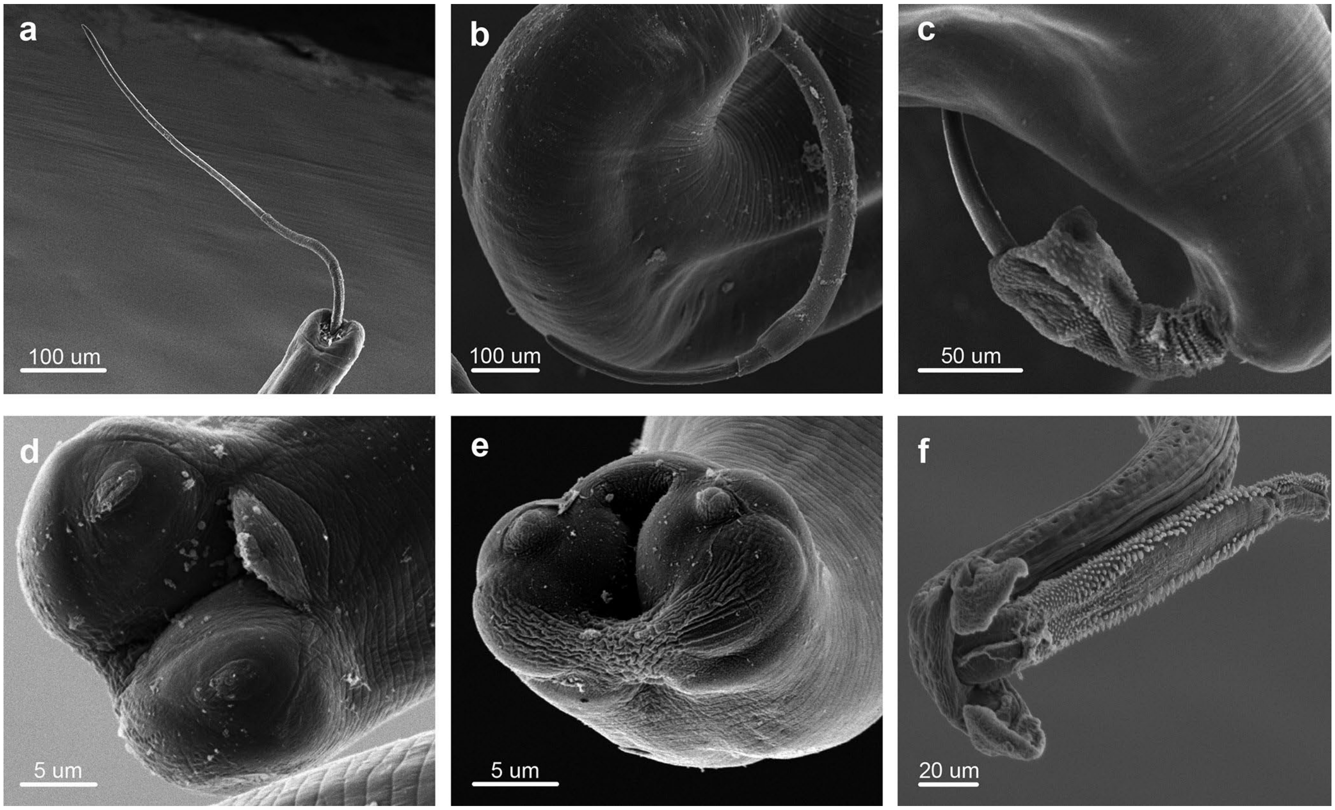

Figure 3. Scanning electron micrographs of accessory genital organs of males from trichuroid species in rodents: a) Ventral view of tail, spiny spicular sheath cylindrical and spicule everted in *Trichuris* sp. b) Lateral view of tail, spiny spicular sheath forming a distal spherical bulge in *Trichuris* sp. c) Ventral view of tail, spiny spicular sheath forming a distal spherical bell in *Trichuris* sp. d) Ventral view of tail, 2 lobes terminally expanded with 2 central papillae in *Pseudocapillaria* sp. e) Ventral view of tail, 2 lobes terminally expanded forming a pseudobursa with 2 lateroventral papillae in *Eucoleus* sp. f) Dorsal view, with spiny cirrus everted and lobes terminally expanded with 2 projections in *Echinocoleus* sp. Source: M. de R. Robles and R. Callejón Fernández. License: CC BY-NC-SA 4.0.

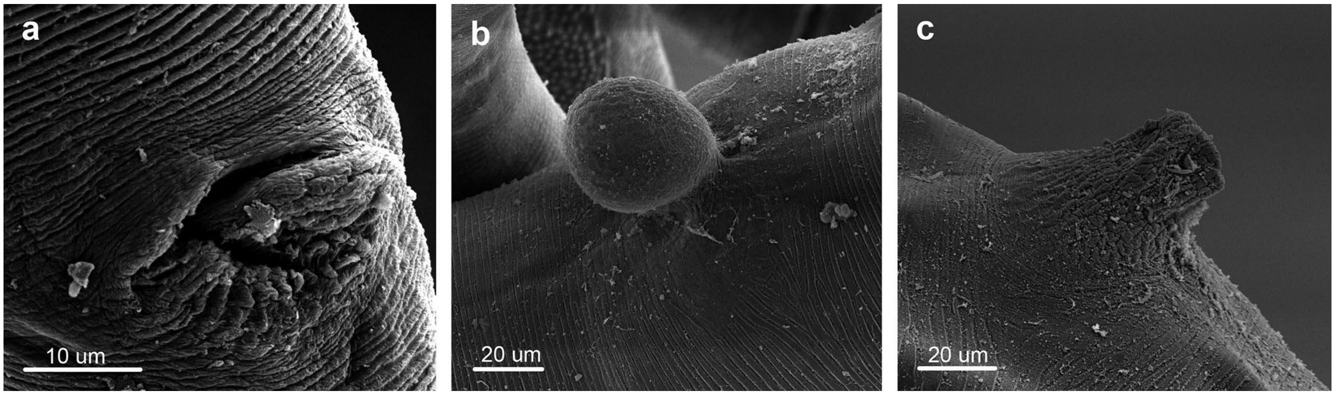

Figure 4. Scanning electron micrographs of characteristics of the vulva of the female from trichuroid species in rodents: a) Detail of non-protusive vulva in *Trichuris navonae* Robles, 2011. b) Detail of spherical protusive vulva in *Trichuris* sp. c) Detail of cylindrical protusive vulva in *Trichuris* sp. Source: M. de R. Robles and R. Callejón Fernández. License: CC BY-NC-SA 4.0.

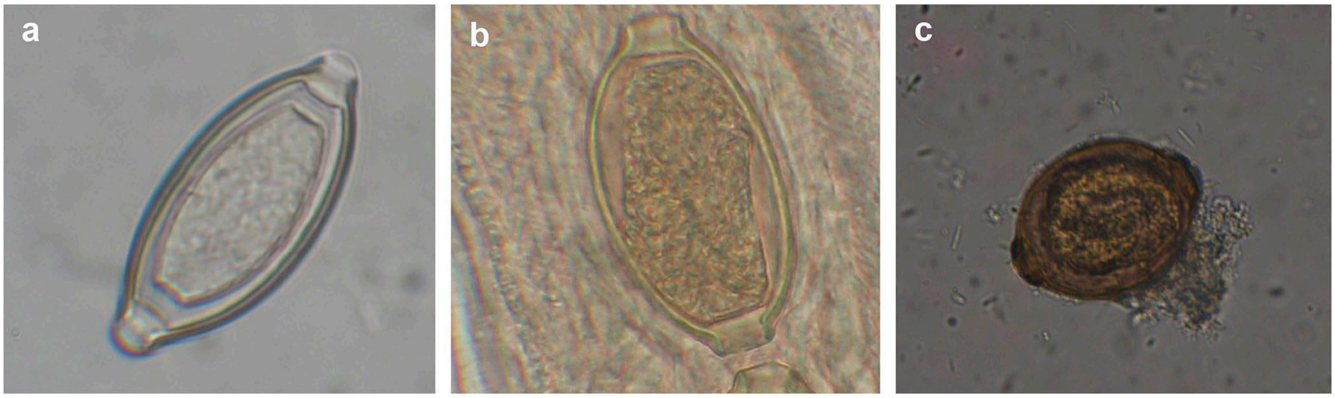

Figure 5. Micrographs of characteristics of eggs from trichuroid species in rodents: a) Detail of *Trichuris* sp. egg. b) Detail of *Eucoleus* sp. egg. c) Detail of *Anatrichosoma* sp. egg. Source: M. de R. Robles and R. Callejón Fernández. License: CC BY-NC-SA 4.0.

Table 3. Comparison of molecular data between the superfamilies Trichuroidea and Trichinelloidea.

Maggenti (1981)	**Superfamily Trichuroidea**			**Superfamily Trichinelloidea**
Moraveč (2001a)	**Family Trichuridae**	**Family Capillariidae**	**Family Trichosomoididae**	**Family Trichinellidae**
Number of studied species by genus	Genus	Genus	Genus	Genus
	Trichuris 20 species	*Aonchoteca* 6 species; *Balluscapillaria* 1 species; *Calodium* 2 species; *Capillaria* 11 species; *Eucoleus* 3 species; *Paracapillaria* 1 species; *Pearsonema* 1 species; *Pseudocapillaria* 1 species	*Anatrichosoma*	*Trichinella* 9 species
Genes studied	SSU rDNA, ITS1, 5.8S, ITS2 rDNA, *cox1* mtDNA, *cytb* mtDNA, TPI rDNA, *16S* mtDNA, mitochondrial complete	SSU rDNA, *cox1* mtDNA	SSU rDNA, *cox1* mtDNA	SSU rDNA, 5S-ISR, ITS rDNA, *cox1* mtDNA, mitochondrial complete

as the characteristics and opening position of the vulva in the female (Figure 4), and the shape of the eggs, especially the characteristics of the polar plugs (Figure 5) (see Maggenti, 1981; Moraveč, 2001a; Anderson et al., 2009; Robles et al., 2012).

Molecular Characteristics

DNA-based methods are powerful tools for synthetic studies, providing a basis for a better understanding of poorly understood aspects of the biology, epidemiology, pathogenesis, and taxonomy of trichocephalid nematodes. Note that the systematic literature often contains references to specific regions of comparable DNA, termed **markers**. Markers indicate any region of DNA sequences that are used across different species and are not always genes, although genes are a type of marker. See Table 3 for a comparison of molecular data between the families of Trichuroidea and Trichinelloidea.

Table 4. Comparison of biological aspects between superfamilies of Trichuroidea and Trichinelloidea.

Maggenti (1981)	**Trichuroidea**			**Trichinelloidea**
Moravč (2001a)	**Trichuridae**	**Capillariidae**	**Trichosomoididae**	**Trichinellidae**
Host groups	Some families of mammals	Fishes, amphibians, reptiles, birds, and mammals	Fishes and mammals	Reptiles, birds, and mammals
Infection location	Cecum	Different tissues and organs	Different tissues and organs	Different tissues and organs
Source of eggs	Feces	Feces, urine, skin, and from predators	Feces and urine	Without eggs
Maturation of the laid eggs	Uncleaved or in morula	Uncleaved, in morula, or larved	Larved	-
Place of hatching of the juveniles	Female lays eggs, juveniles hatch as J_1 (oviparous)	Female lays eggs, juveniles hatch as J_1/J_2 (oviparous), or larvae hatch inside uterus (ovoviviparous)	Female lays eggs, juveniles hatch infective (oviparous)	Female releases juveniles inside uterus (ovoviviparous)
Complexity of the life cycle	Direct (1 host)	Direct and indirect (1 or more hosts). With paratenic hosts	Indirect (more than 1 host)	Autoheteroxenous (same individual is both definitive and intermediate host)
Environment	Terrestrial	Terrestrial and aquatic	Terrestrial and aquatic	Terrestrial

Box 1. Interesting Facts

- Mammals are the most important hosts for the genus *Trichinella*, with infections known to occur in 150 species belonging to 12 orders (Marsupialia, Insectivora, Edentata, Chiroptera, Lagomorpha, Rodentia, Cetacea, Carnivora, Perissodactyla, Artiodactyla, Tylopoda, and Primates).
- Humans are the only species of primate that can be infected in natural conditions by any of the species of the genus *Trichinella*, except for *T. zimbabwensis*.
- Mammals are susceptible to all *Trichinella* species, whereas reptiles are only susceptible to *T. papuae* and *T. zimbabwensis* and birds are only susceptible to *T. pseudospiralis*.
- *Trichinella spiralis* is found in 87% of samples of domestic pigs, 67% of wild boar, 88% of equines, 79% of synanthropic rats, and 100% of synanthropic armadillos (data obtained from the samples from the International Center for Research of Trichinellosis) (Pozio and Murrell, 2006).
- Data have surfaced suggesting that Trichinellidae and Trichuridae diverged from a common ancestor 250–300 Ma (= million years ago) using the variation in 3 genes (SSU rDNA, mitochondrial large subunit rDNA, and cytochrome oxidase I (*cox1*) mitochondrial DNA (mtDNA) (Zarlenga et al., 2006).

Biological Aspects

Trichocephalids occur in various organs of all groups of vertebrates. Species of *Trichuris* occur in various species of mammals, especially, but not exclusively, in rodents, carnivores, and primates while species of Capillariidae occur in all vertebrate groups. Interestingly, species allocated to the Trichosomoididae occur in fishes and mammals, while species of Trichinellidae parasitize reptiles, birds, and mammals.

Direct and indirect life cycles have been observed among nematodes of the families Trichuridae, Capillariidae, and Trichosomoididae. For those species that have complex life cycles, a large number of animal groups have been shown to function as intermediate hosts (for example, molluscs and annelids). Also, in many cases, the life cycles may involve paratenic hosts (Miyazaki, 1991; Anderson, 2000; Moravec et al., 1987; Moravec, 2001a). A paratenic host is a host in which the parasite does not develop further while it is in that host but remains infective to the next definitive, or final, host. The definitive host is the host in which sexual reproduction occurs.

All adult trichurids that have been studied bury a part of the anterior portion of their body (the stichosome) in the base of the cecal villi in the mucosa. The stichosome winds around in this area in a convoluted path. Most species of Capillariidae and Trichosomoididae are able to embed their whole body in different tissues, burrowing through the epithelial and subepethelial tissues and into the organs themselves, such as the stomach, intestine, liver, spleen, musculature, bladder, kidneys, and other organs (Yamaguti, 1961; Anderson, 2000; Moravč, 2001a). See Table 4 for a comparison of biological aspects between the superfamilies of Trichuroidea and Trichinelloidea.

Both superfamilies include species of epidemiological importance, especially *Trichinella spiralis* due to the large number of reported human cases.

Superfamily Trichuroidea

Morphology of Trichuroidea

The body is divided into 2 regions: The narrow anterior part contains the esophagus, with a stichosome (= a series of large gland cells—called stichocytes—attached to the posterior region of the esophagus), and the posterior part

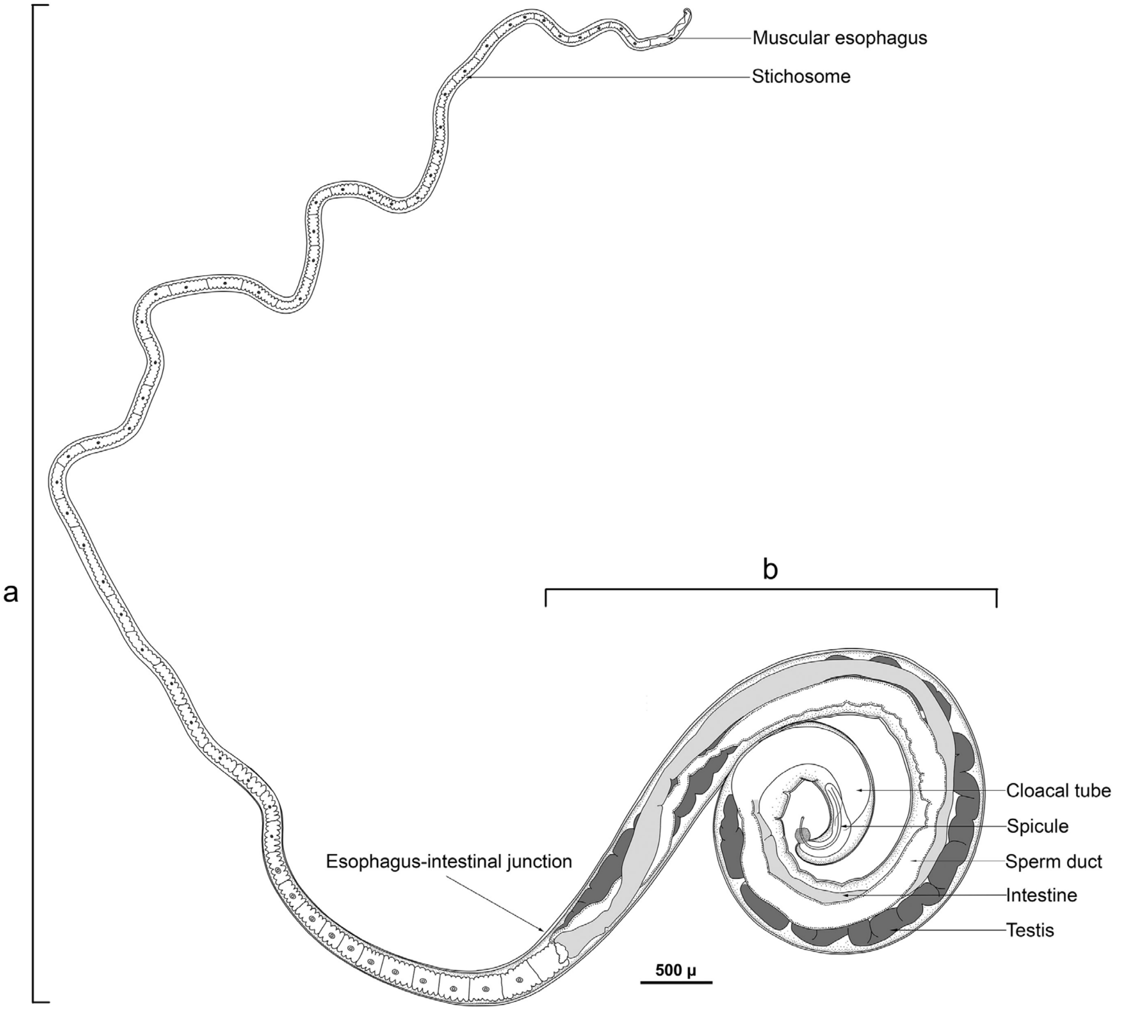

Figure 6. Diagrammatic representation of the morphological structures of a male specimen of *Trichuris muris* as an example of Trichuoidea. a) anterior part, b) posterior part. Source: A. Panti May. License: CC BY-NC-SA 4.0.

of the body contains the reproductive system and begins at esophageal-intestinal junction. A bacillary band is present (= extreme modifications of the hypodermis which can form between 1 to 4 chords of a complex of glandular and non-glandular cells). Males and females each have a single gonad, males with 1 spicule, and females with 1 ovary, and are oviparous. The eggs are bi-operculate, with an opercular plug or opening in each end. The life cycle may be direct or indirect (see Figure 6) (Yamaguti, 1961; Maggenti, 1981; Moravec, 2001a; Anderson et al., 2009).

Molecular Characteristics of Trichuroidea

Within the superfamily Trichuroidea, several ribosomal and mitochondrial DNA markers from around 20 species allocated to the genus *Trichuris* have been identified. The full mitochondrial genomes of *T. trichiura*, *T. ovis*, *T. discolor*, and *T. suis* are available on GenBank (Liu et al., 2012a; 2012b; see also https://www.ncbi.nlm.nih.gov/genbank/). In the case of the Capillariidae, species of a few genera (around 25) have been studied using 2 DNA markers. Conversely, just a few species of *Anatrichosoma* have been reported (members of the family Trichosomoididae) using sequences from 2 markers.

Biological Aspects of Trichuroidea

Adult Trichuroidea are dioecious (having 2 sexes) and, after mating, females produce eggs that are diploid, a result of mating and the combining of gametes. In what appear to be morphological adaptations to increase the probability of dispersal to new hosts, various innovations in the eggs of trichuroids are evident. Host lifestyle is probably one of the main factors in the development of evolutionary innovations in this group as morphology of the eggs varies depends on the kinds of habitats within which the host resides.

Since the site of infection within the host species of adult trichuroids is extremely variable and the eggs are the only means of making it to the next host, it is reasonable to assume that morphological characteristics of the eggs may increase the probability that the eggs will make it to subsequent host individuals. For species of nematodes living in the gastrointestinal or respiratory tract, eggs are naturally passed with the host's feces. Some species inhabit the bladder or kidneys, and so, the eggs pass in the urine. Also, eggs can occur in the epidermis and they are released to the external environment when the outer layers of skin are shed. Other locations include the liver, spleen, and muscles in which the eggs are encapsulated by host tissue. In these cases, the only way to the external environment can be through predation (the eggs are dispersed by a predator's feces) or from the decomposing host's body, which is an interesting way to get around! (Pence and Little, 1972; Anderson, 2000; Moravec, 2001a; Robles et al., 2008; 2012; 2014; Fantozzi et al., 2018).

The degree of maturation of the eggs inside the host is also variable among species in the families and genera of trichuroids. In several cases, the eggs are laid uncleaved (that is, without any development of the blastomeres), requiring a certain period in the environment to reach the development of the juvenile form. However, in other cases, the eggs can hatch when laid, making them instantly infective for another host. First-stage juveniles (J_1), and probably other stages, possess a stylet. Despite the majority of surveys suggesting that trichuroids always infect the final host in the first-stage, some authors have observed the second molt of juveniles (J_2) in their intermediate hosts (Moravec et al., 1987; Moravec, 2001a).

Family Trichuridae

Genus *Trichuris*

The phylogenetic relationships of *Trichuris* species from different host groups have been explored based on rDNA (ITS and SSU) and mtDNA (*cox1* and *cytb*), showing separate clades. In this context, *Trichuris* from rodents are a sister of *T. vulpis* from canids; while *T. trichiura* and *T. suis* form a separate clade. Both clades are the sister of a clade that includes *T. ovis*, *T. leporis*, and *T. skrjabini*, all parasites from herbivores (Cutillas et al., 2009; Callejón et al., 2013) (Figures 7 and 8).

Other analyses have used different markers (ITS2 rDNA, *cox1*, and *cytb* mtDNA), to explore each distinct clade. For example, a series of papers has been published showing dif-

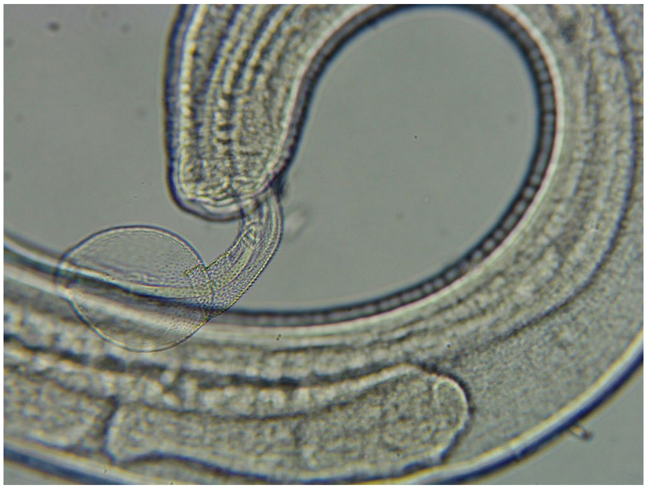

Figure 7. Posterior of a male of the genus *Trichuris* from a rodent. The spicule can be seen inside the spinose spicule sheath. The sheath is expanded at the distal end in this specimen. Source: S. L. Gardner, HWML. License: CC BY.

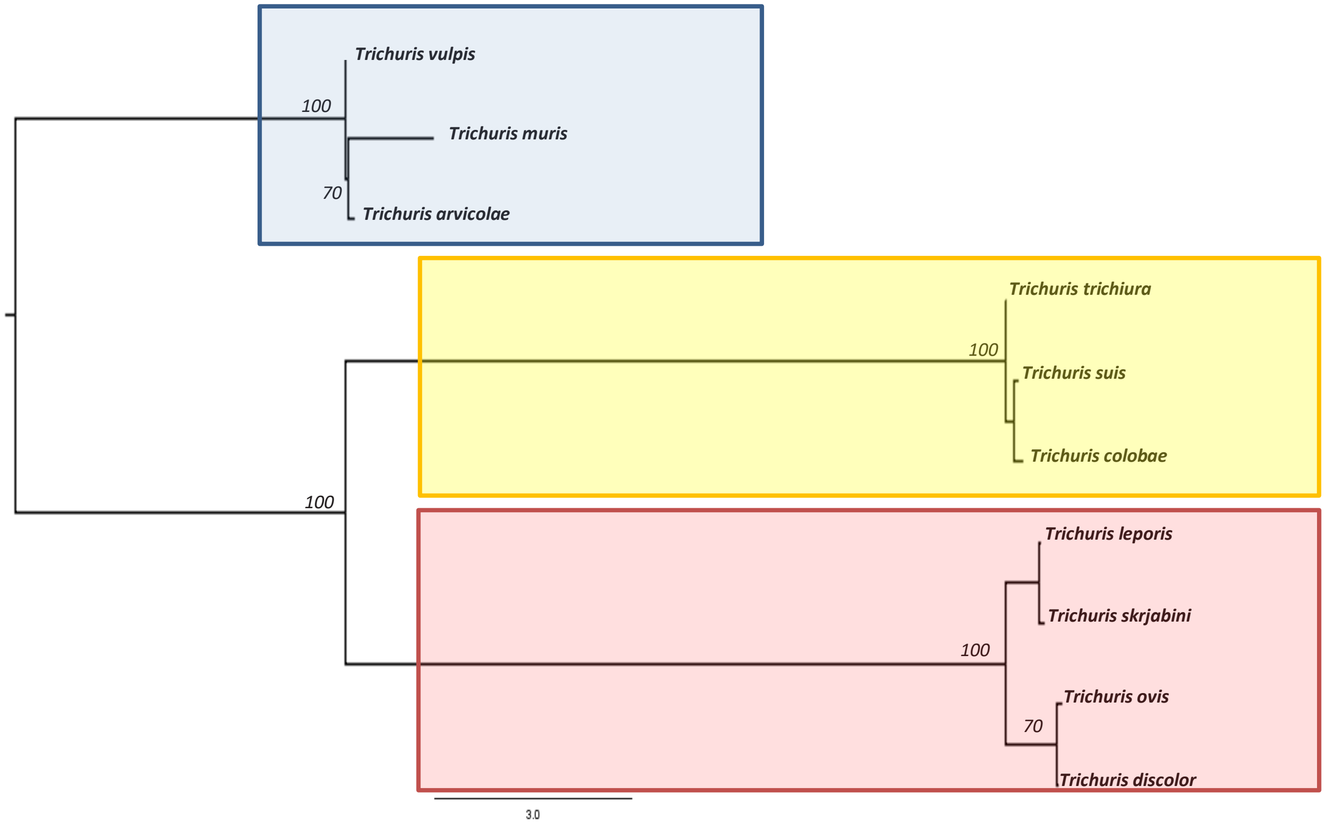

Figure 8. Dendrogram based on ITS1 sequences corresponding to different species of the genus *Trichuris*, with detail of host group. Source: Adapted from Cutillas et al., 2009. License: CC BY-NC-SA 4.0.

ferent phylogenetic hypotheses, including regarding various species of *Trichuris* from rodents of different continents (Robles et al., 2014; 2018; Rylková et al., 2015; Callejón et al., 2016). Notably, species of *Trichuris* seem to accompany their host clades (Robles et al., 2014; 2018); however, some studies also indicate a certain relationship with the history of the geographic areas in which they are now found (Eberhardt et al., 2018).

In a similar way, molecular studies based on ribosomal (SSU, ITS1, ITS2) and mitochondrial (*cox1*, *cytb*) markers have revealed 2 distinct lineages of *Trichuris trichiura* within human and non-human primates (NHP), showing some level of a narrow host range (relationship between each taxonomic level of the host and parasite) (Ravasi et al., 2012; Nissen et al., 2012; Doležalová et al., 2015; Cavallero et al., 2015; Callejón et al., 2017). This is an interesting finding because parasites occuring in many species of hosts versus a parasite species occurring in only 1 host species may have different epidemiological implications, since host reservoirs of the parasites may serve as sources of reinfection for other populations in which the parasite had previously been lost or eliminated. Information on prevalence and occurrence of parasites in hosts in various geographic regions is necessary for design and implementation of effective parasite control systems (Betson et al., 2015).

Family Capillariidae

Genus *Capillaria* sensu lato (s. l.) and other genera

Zhu and colleagues (2000) provided an analysis of genetic variation (*cox1* mtDNA) within and among morphologically-identified species of *Capillaria* s. l. from different host species and from different tissue sites within a host species. Their results showed that, among the species of *Capillaria* s. l. examined, these nematodes showed a relatively high degree of specificity at the level of the host genus.

Little molecular work has been done on species across the genera within the Capillariidae. However, some sequence data are available from capillariids from vertebrates, including sequences of the SSU rRNA gene from birds (Honisch and Krone, 2008; Tamaru et al., 2015), SSU rRNA from capillariids in *Rattus* (Buńkowska-Gawlik et al., 2017), SSU rRNA of human capillariids (El-Dib et al., 2015), *cox1* mtDNA of capillariids from rodents and marsupials (Zhu et al., 2000), and *cox1* mtDNA from capillariids of canine and feline ori-

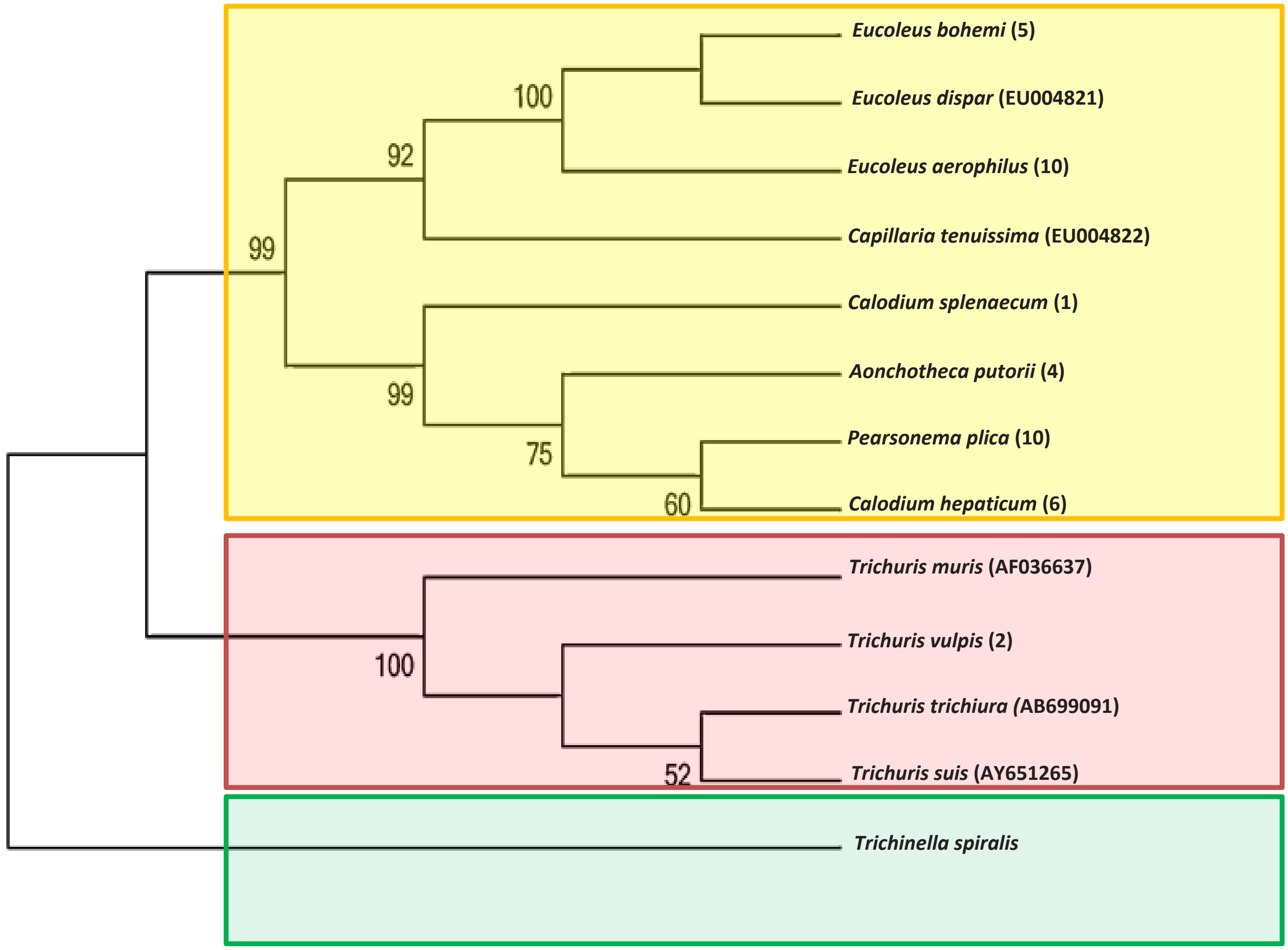

Figure 9. Dendrogram based on the partial sequences of the small subunit rRNA (18S rRNA) gene from species of the families Trichuridae and Capillariidae, with *T. spiralis* as outgroup. Source: Adapted from Guardone, 2013. License: CC BY-NC-SA 4.0.

Box 2. … Building Hypotheses

Many authors have provided phylogenetic hypotheses based on molecular data to try to clarify the relationships of the species in the phylum Nemata including the order Trichocephalida. These molecular analyses mainly have used small subunit ribosomal DNA (SSU rDNA) sequence data.

De Ley and Blaxter (2002; 2004) and Meldal et al. (2007) built trees based on SSU rDNA and based on these data they classified *Trichuris*, *Trichinella*, and *Capillaria* as members of the subclass Dorylaimia (class Enoplea). Holterman et al. (2006) also based on SSU rDNA showed other possible hypotheses in which Trichuris and Trichinella form the sister group of species allocated in the Dorylaimida, Mononchida, and Mermithida. Subsequently, Van Megen et al. (2009) extended the phylogenetic analysis to include members of the Capillaridae, revealing a closer relationship with Trichuridae, and showing both families to be a sister group of Trichinellidae. A recent phylogenetic study has shown that the family Capillaridae seems to be monophyletic and can be clearly separated from Trichuridae (Guardone et al., 2013; Figure 7). In addition, phylogenetic analyses based on mitochondrial DNA suggest that the species included in the genera *Trichuris* and *Trichinella* are members of the order Trichocephalida, separate from other enoplean nematodes including Dorylaimida and Mermithida (Liu et al., 2012; Callejón et al., 2013).

gin (Di Cesare et al., 2012). Guardone and colleagues (2013) show the relationship among different species of nematodes from 5 genera, *Eucoleus*, *Calodium*, *Capillaria*, *Aonchoteca*, and *Pearsonema* (Figure 9).

Many of the early studies must be re-examined since molecular data from species of Capillaridae have not been reconciled with original morphological analyses, and few morphological/molecular voucher specimens have been deposited in recognized parasite collections in established museums. Thus, there appears to be a paraphyletic distribution of species representing genera among different clades that show an incorrect placement of species in phylogenies that are based on an insufficient number of characters. The methods to determine the phylognetics of this group have not been robust enough to include enough data to provide a definitive phylogenetic estimate. More work on the phylogeny combining both morphological and molecular data is necessary to establish well supported trees.

Superfamily Trichinelloidea

Morphology of Trichinelloidea

The body is divided into 2 regions: The anterior part is more slender than the posterior section, the transisition from anterior end to posterior is not clearly visible unless the specimen is cleared in a clearing reagent. The anterior part contains the esophagus with a stichosome comprising stichocytes. The posterior part of the body contains the reproductive system, and the posterior part begins at the esophageal-intestinal junction. This group of nematodes lacks a bacillary band. Both males and females have single gonads and, while males lack spicules and have a large copulatory pseudobursa at the posterior end of the body, in the female, the vulva, or female genital opening, is far anterior in the body, usually just posterior to the region where the stichosome joins the rest of the body. Females are viviparous (Yamaguti, 1961; Maggenti, 1981; Anderson, 2000; Anderson et al., 2009).

Molecular Characteristics of Trichinelloidea

Trichinella spiralis, representing the superfamily Trichinelloidea, has been widely studied using different markers and its full genome is now available. The other 8 species of *Trichinella* in Table 2 have been studied with mitochondrial large subunit rRNA (*lsu* rRNA), *cox1* mtDNA, and ITS rDNA markers (Table 4). Notably, *T. spiralis* occupies a strategic position in the evolutionary tree of nematodes, which helps fill important knowledge gaps in the evolutionary history of this species.

Family Trichinellidae

Biological aspects

Species of Trichinellidae have a very unusual life cycle since the same individual animal serves as both the definitive and intermediate host, with the juveniles and adults located in different organs (Roberts and Janovy, 2009). The transmission of *Trichinella* occurs through a predator-prey cycle and depends on the ability of the juveniles encysted in the muscles to withstand environmental conditions during the interval between host death and ingestion by the next host. Distinct life cycles may be observed in both domesticated and wild animal hosts (Pozio, 2000; Pozio and Zarlenga, 2005).

Genus *Trichinella*.

In general, the members of the genus *Trichinella* are geographically and ecologically restricted to different biogeographic regions. This is due to the adaptations that allow each species to survive in various climates (Pozio, 2016). Eight large areas have been established: *T. nelsoni* (E = encapsulated) and *T. zimbabwensis* (NE = non-encapsulated), and the genotype *Trichinella* T8 in the Afro-Tropical region; *T. britovi* (E) and *T. nativa* (E), and the genotype *Trichinella* T9 in the Palearctic region; *T. nativa* and *T. murrelli* (E), and the genotype *Trichinella* T6 in the Neartic region; *T. papuae* (NE) in the Australasia and Indomalayan region; and *T. patagonienis* (E) in the Neotropical region. *Trichinella spiralis* and *T. pseudospiralis* present a cosmopolitan distribution. The wide localization of *T. spiralis* is evidently the result of anthropogenic activity, while the distribution of *T. pseudospiralis* is linked to spread by birds, except for its presence in the Neotropical region, where it appears to have been introduced though European colonization (Pozio et al., 2009; Krivokapich et al., 2012).

As currently recognized, the genus *Trichinella* comprises a complex of 9 species and 3 genotypes infecting mammals, birds, and reptiles across a broad geographic range (Pozio, 2016). The juvenile stages represented in species of this genus can be distinguished from one another; some are encapsulated (E) and some are non-encapsulated (NE), which refers to the presence or absence of a capsule of collagen around the first-stage juvenile (J_1) that is encysted in the muscle. This stage of the parasite preferentially migrates into striated muscles of different regions of the body of the host and most reports from humans are that the muscles in the diaphram and tongue are first infected. The juvenile nematodes that invade and then encyst in the muscles of the mammal host are the causative agent of the disease **trichinosis** (Zarlenga et al., 2006). Different methods have been developed to enable the correct separation and identification of *Trichinella* genotypes and species, either through employment of variants of conventional single-gene, single-marker PCR, multiplex PCR (which enables amplification of several marker sequences at one time), and variable studies of rDNA and PCR-RFLP (random amplified length polymorphism analysis) of the *cox1* mtDNA gene, or PCR amplification, followed by nucleotide sequencing of DNA in the 5S-intertranscribed spacer region (5S-ISR) region. At the current time, multiplex PCR of sequences from mtDNA is the most popular technique in use for the identification of species of *Trichinella* by the International Trichinella Reference Center in Rome, Italy.

La Rosa and colleagues (2003) published a phylogeny developed from multilocus protein electrophoresis that verified for the first time that those species of *Trichinella* that show unencapsulated juveniles in host muscles form a monophyletic group. The lack of a capsule is thus a morphological synapomorphy, based on the absence of collagen in the muscle cyst, versus those that form a clade and have collegen comprising the cyst of the nematode in the muscle. Also, a sister group of species without capsules has been observed, with species that can infect poikilothermic hosts, and these species grouped separately from parasites of homeothermic animals. A subsequent phylogenetic analysis using molecular markers from the ribosomal D3 rDNA region also grouped species that encyst in the muscules in collagenous capsules and grouped the species that inhabit the Arctic region, indicating that both geographic specificity and morphological synapomorphies are important in determining the patterns of these species over geographic space (Gasser et al., 2004). Another phylogenetic analysis that included the *cox1* mtDNA, the ITS2 rDNA, and the mitochondrial ribosomal major subunit gene (LSU), confirmed results obtained previously, and it was proposed that *T. spiralis* is the species that would have first diversified within the lineage that forms collagenous capsules, and thus is the ancestral form (Zarlenga et al., 2006). This result may be confirmed by using more comparative field-collected samples.

The complete genome of *Trichinella spiralis* was sequenced as a representative of Clade I, a group with encapsulated juveniles in the muscles of their hosts (Mitreva and Jasmer, 2008). The genome sequencing efforts have now been extended to include a non-encapsulated species, *T. pseudospiralis* (Zarlenga et al., 2009).

Trichocephalida Species of Medical and Veterinary Importance

The life cycles of the majority of trichocephalid species are not known. However, species with medical and veterinary importance or species parasitizing economically-relevant hosts have been studied extensively. Therefore, biological data from the majority of species is fragmentary.

Trichuris trichiura is a parasite with a direct life cycle, meaning that it does not require an intermediate host (Figure 7). This whipworm may be present in the cecum and colon of humans and other primates. Fertilizated eggs mature in 10–21 days in the soil. The juveniles do not hatch nor molt until ingestion by a host. There, the first stage juveniles hatch in the upper part of the small intestine, descend the intestinal canal as they develop, repeatedly invading the intestinal mucosa, and arrive at the cecum where they finally settle. The thin anterior part of body is partially inserted into the host's mucosa, the end of which is capable of being drawn into it, and the thick portion of body remains free in the lumen. The complete process requires about 3–4 months. Adults live between 1 to 4 years (Bundy and Cooper, 1989; Miyazaki, 1991). The number of eggs each female produces is estimated to range from about 3,000 to 20,000 per day (Faust et al., 1975).

An intense trichuriasis infection in humans may cause dysentery, anemia, rectal prolapse, and growth retardation. Children are particularly prone to heavy infections (Cooper et al., 1992; Nokes et al., 1992).

Box 3. Doubts … and Mystery Solved

Trichuris suis and *T. trichiura* have been frequently considered to be the same species (see, for example, Schwartz, 1926). However, Soulsby (1982) determined that *T. trichiura* is morphologically similar but biologically distinct from *T. suis*. Furthermore, *T. suis* is not a human parasite, but after ingestion of eggs, the juveniles hatch and are capable of colonizing a human host for several weeks before they are eliminated from the body without any specific therapy (Li et al., 2012). In addition, morphological studies have separated the species based on the existence of 1 pair of caudal papillae, which in fact is present in *T. trichiura* isolated from humans and other primates, but which are absent in *T. suis* (Tenora et al., 1988). In addition, to help clarify the taxonomic status of both species, the ITS1-5.8S-ITS2 fragment of ribosomal DNA was amplified and sequenced by Cutillas et al. (2009; 2014). The morpho-biometric and molecular results support the existence of different species in pigs, humans, and non-human primates.

Trichuriasis is regarded to be the second most common parasitic infection in humans in the tropics (Bundy and Cooper, 1989). This is a cosmopolitan species concerning epidemiological risk, since the appropriate physical conditions exist in several parts of the world, such as a warm climate, high rainfall and humidity, moisture-retaining soil, and dense shade. However, the highest prevalence is observed in populations with poor standards of sanitation (Bundy and Cooper, 1989; Cooper et al., 1992).

Trichuris suis is a parasite with a direct life cycle involving the cecum and colon of pigs. Fertilized eggs mature in the soil between 19 and 21 days, depending on ambient temperatures, and the eggs can survive in the soil for 6 years (Hill, 1957). The juveniles do not hatch nor molt until ingestion by a host, and then they make their way to the cecum, as is similar in all species of *Trichuris*, although different studies have recorded different maturation times (Alicata, 1935; Hill, 1957; Beer, 1973). The complete process requires about 4–5 months.

Common manifestations of *Trichuris suis* infection in pigs include diarrhea, anorexia, and retarded growth. The high prevalence of *T. suis* in pig production systems is one of the major factors constraining global food availability. This severely impacts small scale farmers in developing countries (Li et al., 2012).

Trichuris muris is a parasite with a direct life cycle, present in the cecum and colon of infected mice, rats, and other rodents. Fertilized eggs mature after about 30 days in the soil, depending on ambient temperatures. The juveniles do not hatch nor molt until ingestion by a host, and then they make their way to the cecum as is similar in all *Trichuris* species, although different studies record different maturation times (Shikhobalova, 1937; Fahmy, 1954). This nematode has been extensively utilized as a laboratory model for the study of the human whipworm, *T. trichiura*. This has proven to be an invaluable tool in dissecting the different components involved in immunity to *Trichuris* infection. Moreover, its biology has been used to paradigmatically demostrate cytokine-mediated immunity to gastrointestinal nematodes in general (Cliffe and Grencis, 2004).

Calodium hepaticum (a synonym *Capillaria hepatica*) is a parasite with a special life cycle since it requires no intermediate host, but 2 final hosts are usually needed. This nematode mainly parasitizes the liver of rodents. When this host is eaten by another rat or a carnivore, the eggs are released and passed along with feces of the predator. Also, eggs may be freed when parasitized rodents die and the body degenerates. Notably, the eggs cannot embryonate in the liver; they are embryonated in the soil, and so, are not infective to the predator (Miyazaki, 1991; Roberts and Janovy, 2009; Fantozzi, 2018).

In the life cycle, the female worm deposits eggs in the liver, which become encapsulated within the host tissue. The eggs pass through the digestive tract of the predator with its feces (Roberts and Janovy, 2009). Eggs are susceptible to desiccation or temperatures between 1 ºC and −7 ºC for about 16–19 days, but in temperatures around 25 ºC they can develop in 35–45 days, and new infection occurs by contamination. After hatching in the small intestine, juveniles migrate to the liver, where these mature (Luttermoser, 1938; Spratt and Singleton, 2001).

Humans and other mammals are infected orally through ingestion of contaminated food and beverages containing mature eggs. The presence of this worm in the liver of humans causes serious illness due to necrosis of the parenchyma, and a granuloma is formed eventually as a result of the fibrosis. The afflicted patient may exhibit fever, hepatomegaly, and eosinophilia.

This is a cosmopolitan species with considerable epidemiological risk, since rodents are frequently in the peridomiciliary, and the eggs reach the environment through the decay of the host carcass or when a predator (for example, a dog or cat) ingests the host and releases the eggs through the feces.

Box 4. Curiosities

Eggs of *Calodium hepaticum* have been found in several species of earthworms (Romashov, 1983), resulting in earthworms serving as an important disperser of the eggs.

Calodium hepaticum are a potential biological control agent for rodent populations (Singleton and McCallum, 1990).

Diagnosis of *Calodium hepaticum* infection by molecular techniques has been reported recently (Guardone et al., 2013; Fantozzi et al., 2018).

In the New World, sigmodontine rodents predominate, comprising 381 species (D'Elia and Pardiñas, 2015). Despite the great diversity in species of these rodents, *Calodium hepaticum* has only been recorded in 8 species of this rodent group, and 6 of them from Argentina (Vogelsang and Espin, 1949; Fantozzi et al., 2018). This lack of demonstrated presence within the sigmodontine rodents is probably the result of insufficient sampling in other areas of the Neotropical region.

Box 5. The Importance of Taxonomy with Respect to Medical Aspects

Unfortunately, some taxonomically important morphological features, for example, the structure of the male caudal end, have been inadequately described or are not mentioned at all in studies of the morphology, preventing an appropriate generic assignment of this species in the presently recognized classification system of capillariids. To help rectify this oversight and to correct the systematic status of the medically important capillariid species, the morphology of *Calodium philippinensis* was re-studied by Moravec̆ (2001b). In that study, Moravec̆ (2001b) described the general structure of the male caudal end, particularly the presence of a well-developed membranous bursa supported by 2 lateral, finger-shaped protrusions (rays), each of them bearing a big papilla at its base. These structures are typical among species of *Paracapillaria*, the genus to which *Calodium philippinensis* was transferred.

The eggs then embryonate and may infect a new host. Ingestion of non-embryonated eggs leads to an untrue (or spurious) infection in which the eggs pass through the intestinal tract and exit with the feces without hatching (Juncker-Voss et al., 2000).

However, notably, other studies have shown that people who often eat the liver of wild mammals present a 10-fold higher risk of presenting with spurious infection than those who do not eat the liver of wild animals. There has been speculation by several authors as to the mechanism of transmission, and examination of intradomiciliary rates of spurious infection. In addition, the occurrence of dog feces infected with unembryonated nematode eggs near homes suggests greater risk of new infections without the participation of wild animals in the infection cycle (Wright, 1961; Gonçalves et al., 2012).

Paracapillaria philippiensis has been found to be pathogenic in humans. Its mode of transmission is unknown, but the first human victim (in the Philippines) was known to eat food that contained various internal organs of some small mammals. In *P. philippiensis*, the movement of the worms results in a disruption of the mucosal lining of the small intestine, a degeneration of the lining of the the epithelial cells, and, finally, inflammation of the mucosa. This extensive damage to the intestinal wall induces symptoms resembling malabsorption syndrome. The major symptom is intractable diarrhea that leads to rapid dehydration and emaciation. There is usually some abdominal pain and distension accompanied by a low grade fever. In fatal cases, the loss of nutrition leads to shock, and death is due to this rather than the tissue damage attributable to the parasite.

This highly pathogenic parasite is known to be distributed in eastern, southern, and southeastern Asia, and northern Africa (Philippines, Thailand, Japan, Korea, Taiwan, India, Iran, and Egypt) (for more information on the medical aspects, see, for example, Pradatsundarasar et al., 1973; Hoghooghi-Rad et al., 1987; Chen et al., 1989; Youssef et al., 1989; Lee et al., 1993; Kang et al., 1994; Khalifa et al., 2000). According to Cross (1992), 1,884 confirmed cases of the disease caused by this nematode were documented in humans from 1967 to the end of 1990; 110 cases were fatal.

Anatrichosoma is the genus of nematode parasites known to have an indirect route of infection; however, the life cycle has not been studied in detail. Notably, the eggs have thick-walled and dark shells. These eggs are deposited in tunnels in the epithelium and are presumably released during the sloughing of epithelial cells. These pass out of the host's body in excretory products and are probably infective to the definitive host (Orihel, 1970; Pence and Little, 1972).

Trichinella spiralis is a parasite with an autoheteroxenous cycle; in other words, it is a nematode that is present in an individual animal which serves as both the definitive and intermediate host. It is difficult to know where to begin describing the cycle since it is so complex, and because no stage occurs outside the host (see Figure 10). Transmission occurs when humans or other meat eaters consume raw or undercooked meat of wild animals contaminated with the cysts of *Trichinella*. When raw or rare meat containing cysts is consumed, the infective first-stage juveniles are released from their envelope with the aid of the host's gastric juices. The juveniles then invade the duodenal and jejunal mucosa. In about 36 hours, males and females develop (Gould et al., 1957). Soon after fertilization of the females, the males die. The females subsequently increase to their maximum size and burrow deeper into the mucosa each depositing about 500 juveniles, the majority of which migrate into the intestinal lymphatic and mesenteric veins, eventually reaching the heart and lungs, and then are distributed into the arterial circulation, where they then move to the muscles. The juveniles encyst in the muscles after about 19 days, moving into striated muscles that have low amounts of glycogen and predominantly include the diaphragm, larynx, tongue, abdomen, intercostal spaces, biceps, pectorals, deltoids, and more. Here, the infected muscle cells are transformed into nurse cells (Stewart and Gianini,

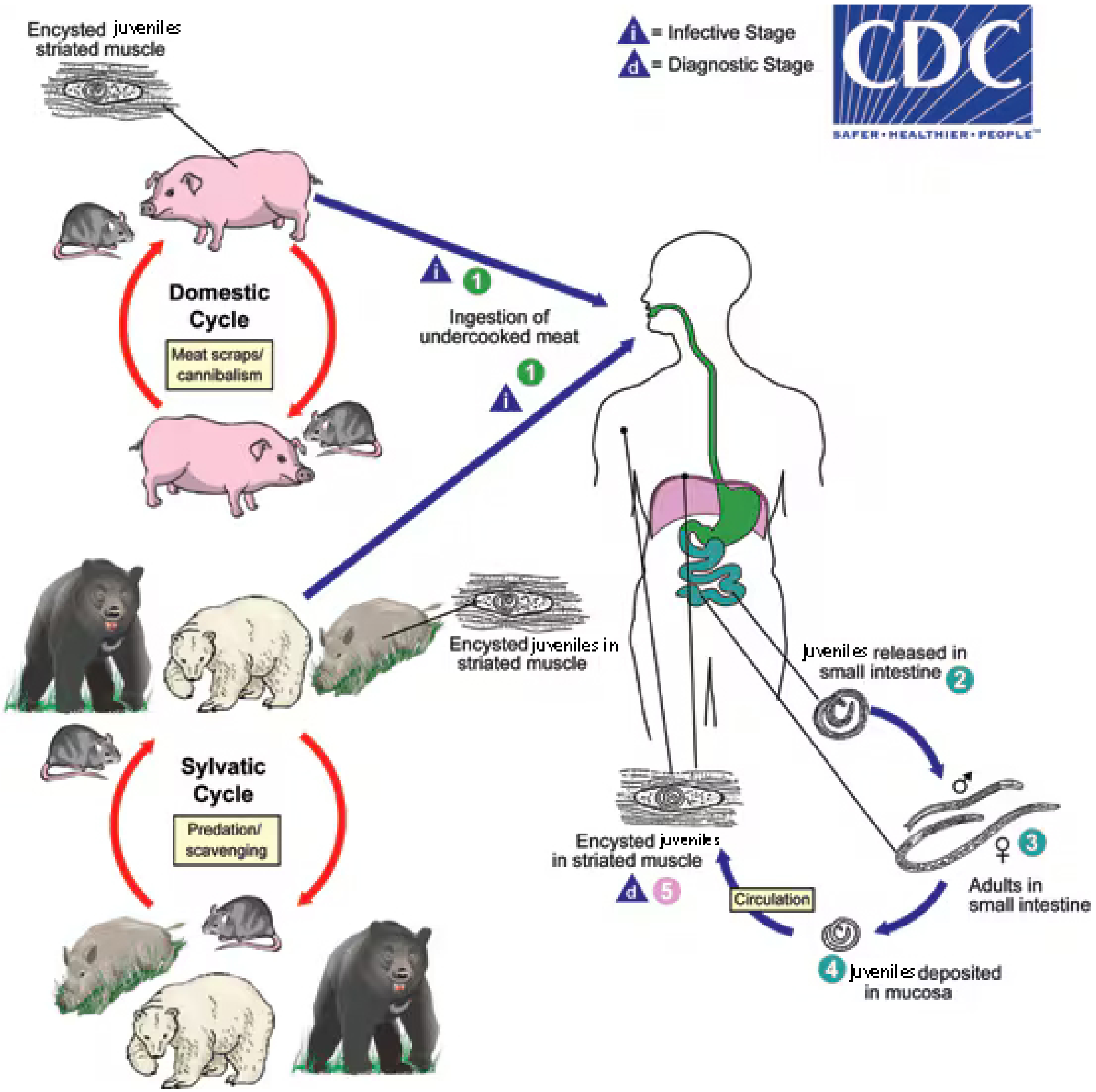

Figure 10. Adult worms and encysted juveniles develop within a single vertebrate host and an infected animal serves as a definitive host and potential intermediate host. A second host is required to perpetuate the life cycle. The domestic cycle most often involves pigs and anthropophilic rodents, but other domestic animals such as horses can be involved. In the sylvatic cycle, the range of infected animals is great, but animals most often associated as sources of human infection are bear, moose, and wild boar. — Life cycle. Trichinellosis is caused by nematodes (roundworms) ingested with undercooked meat containing encysted juveniles of *Trichinella* species (except for *T. pseudospiralis* and *T. papuae,* which do not encyst) (1). After exposure to gastric acid and pepsin, the larvae are released from the cysts (2) and invade the small bowel mucosa where they develop into adult worms (3). Females are 2.2 mm in length; males 1.2 mm. The life span in the small bowel is about 4 weeks. After 1 week, the females release juveniles (4) that migrate to striated muscles where they encyst (5). Diagnosis is usually made based on clinical symptoms and is confirmed by serology or identification of encysted or non-encysted larvae in biopsy or autopsy specimens. — Several species are recognized, including *T. spiralis* (carnivorous and omnivorous animals worldwide), *T. pseudospiralis* (mammals and birds worldwide), *T. nativa* (Arctic bears), *T. nelsoni* (African predators and scavengers), *T. britovi* (carnivores of Europe and western Asia), *T. papuae* (wild and domestic pigs, Papua New Guinea, and Thailand), and *T. zimbabwensis* (crocodiles in Africa), all but the last of which have been implicated in human disease.

1982). In 6 to 9 months the fibrous capsules become calcified. Within the cysts, juveniles may remain viable for more than 5 years. This is the termination of the cycle and the juveniles must await the ingestion of this host to continue.

The list of common hosts is extensive and includes humans, rats, pigs, bears, walruses, seals, and dogs (Maggenti, 1981; Miyazaki, 1991). It has been shown that seal pups can acquire an infection through their mother's milk during the period of parasite juvenile migration. Humans normally become infected by breaking into the pig-rat-pig cycle or by eating uncooked bear meat; and, in North America, bear meat infection is not altogether rare. Five cysts per gram of body weight can be lethal to a human. Therefore, *Trichinella spiralis* is the cause of a serious and often fatal disease in humans known as trichinosis. In mild cases, the symptoms do not differ greatly from the so-called stomach flu, accompanied by stomach upset and general bodily aches and pains. When the invasion is severe, the syndrome includes 3 phases: Invasion, migration, and encystment. Invasion is characterized by stomach flu or food poisoning symptoms. Penetration of the gut by large numbers of juveniles creates symptoms such as vomiting, nausea, dysentery, and colic. Migration and initial invasion and encystment in the muscles is manifested by difficulty in breathing, chewing, swallowing, and speech, and in the limbs there may be spastic paralysis. Encystment is the critical third stage. Often nutritional stress and dehydration are evident. The pulse may at first be fast and strong and then it suddenly drops and cyanosis supervenes; as blood pressure falls, the host collapses as shock ensues. Prior to collapse, nervous disorders include visionary defects, loss of reflexes, disorientation, delirium, and encephalitis. Diagnosis is by biopsy after the juveniles reach the preferred muscle sites (Miyazaki, 1991; Anderson, 2000).

Education is an important part of any control program; however, the most effective measure to avoid becoming infected with these nematodes is by thoroughly cooking meat before ingestion, especially, pork, bear, and rat meat. Freezing is also successful at differing temepratures for different lengths of time. Mainly, prevention requires the cooking of garbage fed to swine, proper freezing and low temperature storage of prepared pork products, and proper inspection. These implementation of pork production and storage regulations have led to a significant lowering of the incidence of trichinosis. Control consists of the destruction of all infected carcasses and viscera, extermination of rats and mice, and heat treating garbage fed to swine (Miyazaki, 1991; Anderson, 2000). However, *Trichinella arctica* has been shown to be infective even after freezing at very low temperatures (Pozio, 2016).

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NEMATA

Ascaridoidea (Superfamily): Large Intestinal Nematodes

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Superfamily Ascaridoidea

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Chapter 50

Ascaridoidea (Superfamily): Large Intestinal Nematodes

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Introduction

Ascaridomorpha includes a diverse group of parasites that live in the alimentary tract of their definitive hosts, and includes species that are of veterinary, medical, and economic importance. The life cycles of these parasites are quite variable, ranging from species with simple direct patterns involving the ingestion of eggs containing infective juveniles, to others that use invertebrates or vertebrates as intermediate or paratenic hosts. Species of Ascaridomorpha are familiar to biologists and laypersons alike as the large intestinal roundworms (although, here preferentially called nematodes) that infect pet dogs and cats; however, a much wider range of vertebrates serves as definitive hosts, including elasmobranchs, teleost fishes, amphibians, reptiles, birds, and mammals.

Ascaridomorpha occurring in mammals are typically large, stout nematodes with 3 large lips; however, there is substantial variation in body size and morphological characteristics among genera and species, even though different taxa are superficially similar in structure. Phylogenetic analysis of SSU rDNA sequences has shown that species allocated to this group are not monophyletic (Nadler et al., 2007), whereas certain families and subfamilies in this group are strongly supported as clades by molecular data (Nadler and Hudspeth, 2000). Of several families in this infraorder, this chapter will emphasize Ascarididae (subordinate within the superfamily Ascaridoidea), which includes many species of medical importance. Representative members of certain other superfamilies will be discussed briefly.

Superfamily Ascaridoidea

Family Ascarididae Baird, 1853

Ascaridids are among the largest nematodes, some species achieving a length of 45 cm or more. They are distinguished by having large rounded or trapezoidal **lips**, and cervical, lateral, and caudal **alae** may be present. **Spicules** are equal in length and rodlike or alate. This family contains the cosmopolitan human intestinal parasite, *Ascaris lumbricoides* Linnaeus 1758 (Crompton, 2001).

Ascaris lumbricoides

Because of their great size and high prevalence, these nematodes may well have been among the first parasites known to humans. The ancient Greeks and the Romans were familiar with them and they were mentioned in the Ebers Papyrus, the 16th century book of medical knowledge from Egypt (Hallman-Mikołajczak, 2004). It is probable that *Ascaris lumbricoides* was either a parasite of pigs that adapted to humans when swine were domesticated and began to live in close association with humans—or perhaps it was a human parasite that humans gave to pigs. Populations of *Ascaris* spp. exist in both humans and pigs, but the extent of genetic isolation between these putative species (*A. lumbricoides* and *A. suum*, respectively) has been the subject of much recent research (Leles et al., 2012).

The two forms are so close morphologically that they are now considered to be the same species. Slight differences in the tiny denticles (small "teeth") on the inner edge of the lips were described between these species (Sprent, 1952), but were later found to reflect age-related wear rather than serve as reliable taxonomic characters (Madden and Tromba, 1976). None of the genetic markers examined to date consistently discriminate between pig- and human-source *Ascaris* spp. Experimental cross-transmission studies show that both putative species can reach maturity in humans and pigs. Genetic studies based on microsatellite markers reveal that there is a low level of hybridization between these species that occurs during co-infection. The distribution of maternally in-

Figure 1. *Contracaecum* sp. (Rhabditida: Anisakidae) in proventriculus and gizzard of a guillemot (*Cepphus* sp.) collected from Scotland, United Kingdom between 1994 and 2013. Source: T. Pennycott, available at Edinburgh DataShare, 2013. License: CC BY 4.0.

herited mitochondrial DNA (mtDNA) haplotypes also reveals patterns that are consistent with low levels of cross-infection, but this interpretation is complicated by the possible retention of ancestral mtDNA polymorphisms between these very recently diverged taxa (Anderson and Jaenike, 1997; Criscione et al., 2007). Leles and colleagues (2012) showed that there are essentially no differences between these two species,so they should be considered to be one species: *A. lumbricoides* Linnaeus 1758.

Morphology

In addition to their great size (Figure 1), *Ascaris lumbricoides* is characterized by having 3 prominent lips each with a dentigerous ridge and no alae. Lateral hypodermal cords are visible with the unaided eye.

Males are 15–31 cm-long and 2–4 mm in diameter at the greatest width. The posterior end is curved ventrally and the tail tip is blunt. Spicules are simple, nearly equal, and measure 2.0–3.5 mm-long. No gubernaculum is present.

Females are 20–49 cm-long and 3–6 mm in diameter. The vulva is about one-third the body length from the anterior end. The ovaries are extensive and uteri may contain up to 27 million eggs with 200,000 being laid per day. When transferred to parasite-naive pigs, female *Ascaris* cease producing eggs after 2–3 weeks (Jungersen et al., 1997). They resume egg production when male worms are transferred into the pig with the females.

Fertilized eggs (Figure 2) are oval to round, 45–75 µm-long by 35–50 µm-wide, with a thick, lumpy outer shell (comprising a mammillated, uterine, or proteinaceous layer) that is contributed by the uterine wall. When eggs are passed in the host's feces, the mammillated layer is bile-stained a golden brown. The embryos within are usually uncleaved when eggs are passed. An uninseminated female, or one in early stages of oviposition, commonly deposits unfertilized eggs (Figure 3) that are longer and narrower than fertilized ones, measuring 88–94 µm-long by 44 µm-wide. Only the

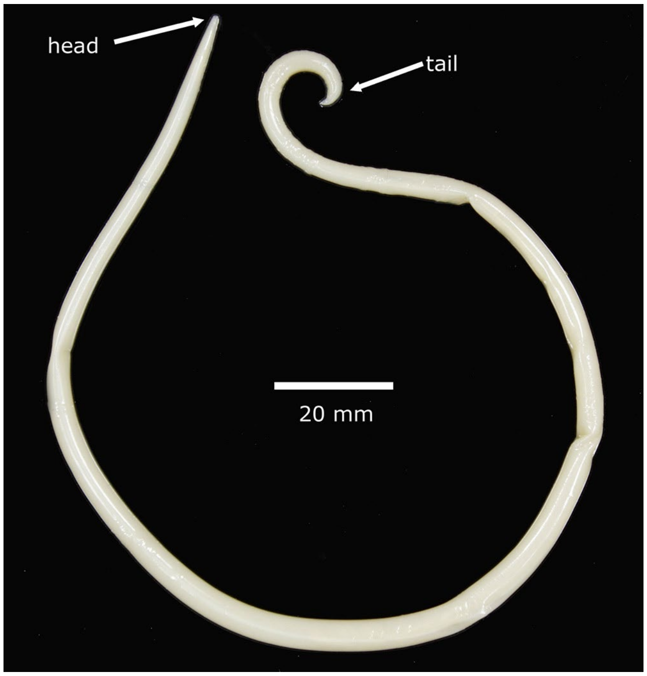

Figure 2. *Ascaris lumbricoides* (Nemata: Ascaridida: Ascarididae), adult male from a human host. Note the tapered head end and the tail that is reflexed (curved) ventrad (meaning, in the ventral direction). These nematodes commonly come out of the anus or the nose of the human host at inopportune times. Source: S. L. Gardner, HWML. License: CC BY.

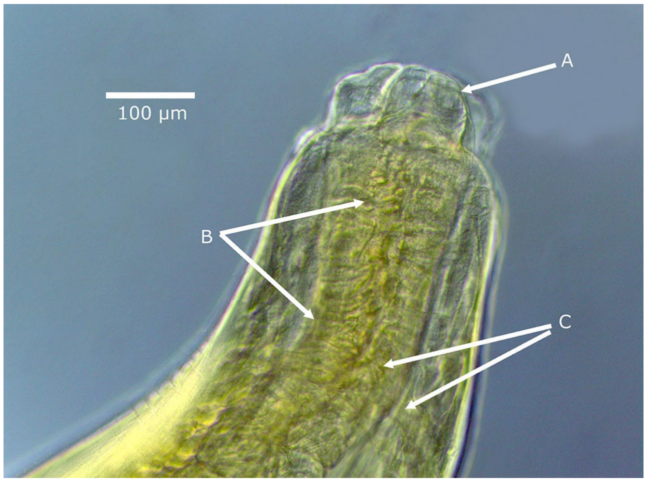

Figure 3. Close up view of the anterior end of an ascarid (Nemata: Ascaridida: Ascarididae) (*Toxascaris procyonis*) showing well, 1 of the 3 lips on the anterior end (A), the anterior part of the esophagus (B), and the nerve ring is seen in arrows pointing from (C). Source: S. L. Gardner, HWML. License: CC BY.

proteinaceous layer can be distinguished in unfertilized eggs because the vitelline, chitinous, and lipid layers of the eggshell are formed only after sperm penetration of the oocyte.

Biology

A period of 9–13 days is the minimal time required for embryos to develop into active first-stage juveniles (J_1s). Embryos are extremely resistant to low temperature, desiccation, and strong chemicals; however, sunlight and high temperatures are lethal in a relatively short time (for example, 2 days at 47 °C). Human ascariasis does not occur where average land temperatures exceed 37–40 °C. Clearly, global warming may change the distribution of ascariasis and other parasitic diseases (Weaver et al., 2010). Juveniles must molt to the third stage to be infective (Geenen et al., 1999) .

Infection occurs when host animals swallow unhatched juveniles with contaminated food and water. They hatch in the duodenum through an indistinct operculum (Figure 4), where the juveniles penetrate the mucosa and submucosa and enter lymphatic tissue or venules (Figure 5). After passing through the right heart of a pig, they enter the pulmonary circulation and break out of capillaries into air spaces. Many worms get lost during this migration and accumulate in almost every organ of the body, causing acute tissue reactions. In contrast to this classical pattern, Murrell and colleagues (1997) report that juvenile *Ascaris* do not penetrate the mucosa immediately after hatching but rather rapidly transit the small intestine and penetrate the mucosa of the cecum and upper colon. Juveniles then accumulate in the liver for up to 48 hours. Incidentally, this research on *Ascaris* in pigs strongly suggests that the actual migration pattern of these nematodes in humans involves the liver, rather than the pattern observed in experiments with abnormal hosts such as guinea pigs and rats (Crompton, 2001).

While migrating through tissues, juveniles molt to the fourth stage (J_4), and during a period of about 10 days grow to a length of 1.4–1.8 mm. They then move up the respiratory tree of the host to the pharynx, where they are swallowed. Many juveniles make this last step of their migration before molting to the fourth stage, but these J_3s cannot survive gastric juices in the stomach. Fourth-stage juveniles (J_4) are resistant to such a hostile environment and readily pass through the stomach to the small intestine, where they molt again and mature. Within 60–65 days of being swallowed, they begin producing eggs. Genetic markers show that *Ascaris* females may be inseminated by more than 1 male in producing offspring (Zhou et al., 2011).

It seems curious that these worms embark on such a hazardous migration only to end up where they began. One hypothesis to account for it suggests that migration simulates an intermediate host, which normally would be required during juvenile development for species with indirect life cycles. Indeed, molecular phylogenetic hypotheses confirm that indirect life cycles are ancestral for ascaridoids, and that the direct (1-host) life cycle of *Ascaris* sp. and *Parascaris* sp. is the derived condition (Nadler and Hudspeth, 2000). After comparing many nematode taxa having tissue migration with closely related taxa that remain in the gut, Read and Skorping (1995) conclude that tissue migration enables faster growth and larger size, thus increasing reproductive capacity.

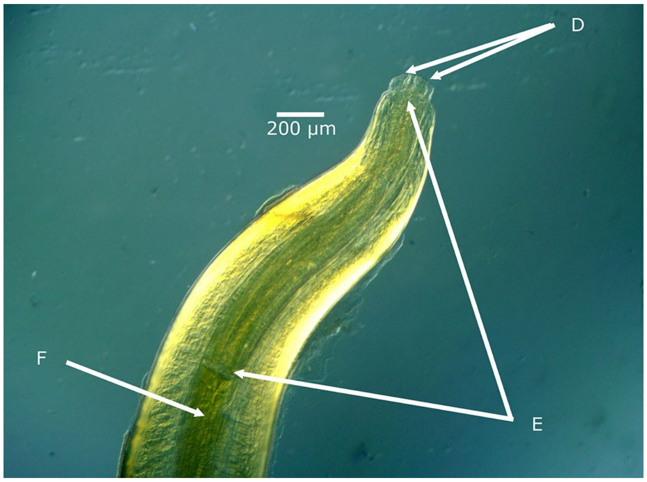

Figure 4. Anterior end of *Toxascaris procyonis* (Nemata: Ascaridida: Ascarididae) showing the three lips on the anterior end (D), the esophagus (E), and the proximal end of the intestine where it attaches to the esophagus (C). Source: S. L. Gardner, HWML. License: CC BY.

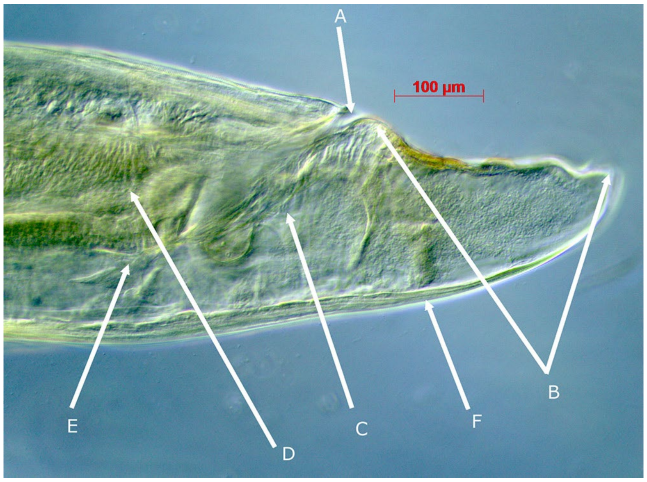

Figure 5. Posterior end of a female *Toxascaris procyonis*. Anus (A), tail (B), muscles that control the rectum and anus (C and E), posterior end of the intestine (D), cuticle (F). Source: S. L. Gardner, HWML. License: CC BY.

Epidemiology

The dynamics of *Ascaris* spp. infection are similar to those of *Trichuris trichiura*. Indiscriminate defecation by hosts, particularly near human or other animal habitations, seeds the soil with eggs that may remain viable for years. Resistance of *Ascaris* spp. eggs to chemicals is in fact legendary. They can embryonate successfully in 2% formalin, in potassium dichromate, and in 50% solutions of hydrochloric, nitric, acetic, and sulfuric acid, among other similar inhospitable substances (Schwartz, 1960). Eggs can survive in anaerobic sewage lagoon sludge for more than 10 years (Rosypal et al., 2007). This extraordinary chemical resistance is a result of the lipid layer of their eggshell, which contains ascarosides.

Longevity of *Ascaris* spp. eggs also contributes to success of the parasite. Brudastov and colleagues (1971) infected themselves with eggs kept for 10 years in soil at Samarkand, Uzbek SSR, Soviet Union. Of these eggs, 30–53% were still infective after all that time. Because of such longevity, it is impossible to prevent reinfection when yards have been liberally seeded with eggs, even when proper sanitation habits are initiated later.

Contamination, then, is the typical means of infection. Children are the most likely to become infected by eating soil or placing fingers and toys in their mouths. Chickens can serve as paratenic hosts (Permin et al., 2000). In regions in which night soil (that is, human excrement) is used as fertilizer, uncooked vegetables become important mechanical vectors of *Ascaris lumbricoides* eggs (Weidong et al., 1998). Experimental support for this hypothesis came from Mueller (1953), who seeded a strawberry plot with eggs. He and volunteers ate unwashed strawberries from this plot every year for 6 years and became infected each year. Cockroaches can carry and disseminate *A. lumbricoides* eggs (Burgess, 1984). Similarly, in some areas, dogs acquire *A. lumbricoides* eggs by coprophagy and spread viable eggs in their feces (Traub et al., 2002). Even windborne dust can carry eggs when conditions permit. Bogojawlenski and Demidowa (1928) found *A. lumbricoides* eggs in the nasal mucus of 3.2% of school children examined in the Soviet Union. Dold and Themme (1949) found *A. lumbricoides* eggs on 20 German banknotes in actual circulation.

Worldwide, 1.27 billion people, about one-quarter of the world population, are infected at any given time (Chan, 1997). Most infections occur in east Asia, China, sub-Saharan Africa, South America, and Central America (WHO, 2006). Morbidity as assessed by disability-adjusted life years (DALYs) totals ~ 10.5 million (Chan, 1997). Severe morbidity occurs in > 100 million cases each year (Chan, 1997); intestinal obstruction, mainly in children, occurs in roughly 1 out of 1,000 infections.

Worms are commonly aggregated in local populations, with a small number of people harboring infections of high intensity. These individuals seem to be predisposed to infection; when they are cured, they tend to become reinfected with large numbers of worms. The reasons for predisposition may be social, behavioral, environmental, and genetic, either alone or in combination. Members of a household tend to have similar infection intensities (household clustering), and individual household risk factors account for much of the variation in household worm counts (Walker et al., 2011).

Pathogenesis

Little damage is caused by penetration of intestinal mucosa by newly hatched worms. Juveniles that become lost and wander and die in anomalous locations, such as the host's spleen, liver, lymph nodes, or brain, often elicit an inflammatory response. Symptoms may be vague and difficult to diagnose and may be confused with those of other diseases. Transplacental migration into a developing fetus is also known. Allergy and immunopathology of ascariasis was reviewed by Coles (1985). The polyprotein allergens (lipid binding proteins) of *Ascaris* spp. are known to elicit IgE antibody responses and appear to be a contributing factor in *Ascaris* pneumonitis (sometimes referred to as Loeffler's pneumonia).

When juveniles break out of lung capillaries into the respiratory system, they cause a small hemorrhage at each site. Heavy infections will cause small pools of blood to accumulate which then initiate edema (swelling) with resultant clogging of air spaces. Accumulations of eosinophils and dead epithelium add to the congestion, which is known as *Ascaris* pneumonitis. Large areas of lung can become diseased, and, if bacterial infections become superimposed, death can result. Once, a student vented his ire on his roommates by seeding their breakfast with embryonated *Ascaris suum* eggs. One roommate almost died before his malady was diagnosed (Newsday, 1970; Phills et al., 1972; Jack Morrison, personal communication, 2023).

Pathogenesis from "normal worm activities"

The main food of *Ascaris* spp. is liquid contents of the small intestinal lumen. In moderate and heavy infections, the resulting theft of nourishment from the host can cause malnutrition, underdevelopment, and cognitive impairment in small children (Crompton, 2001; Levav et al., 1995). Abdominal pains and sensitization phenomena—including rashes, eye pain, asthma, insomnia, and restlessness—often result as allergic responses to metabolites produced by the worms.

A massive infection can cause fatal intestinal blockage (Baird et al., 1986) (Figure 6). Why in one case do large numbers of worms cause no apparent problem, whereas in

Figure 6. Worms recovered from necrotic small intestine, stomach, esophagus, intrahepatic and extrahepatic bile ducts, and gallbladder of a 2-year-old South African girl. Source: Baird et al., 1986. United States public domain.

another worms knot together to form a mass that completely blocks the intestine? The drug tetrachloroethylene, which was formerly used to treat hookworm, can cause *Ascaris* to knot up, but other factors remain unknown. Penetration of the intestine or appendix is not uncommon. The resulting peritonitis is usually quickly fatal. According to Louw (1966), at one time, 35.5% of all deaths in acute abdominal emergencies of children in Cape Town, South Africa were caused by *Ascaris lumbricoides*.

Wandering worms

Overcrowding in high-intensity infections may lead to wandering of adult worms. Downstream wandering may lead to the host's appendix, which can become inflamed or penetrated, or to the anus, with an attendant surprise found in the toilet of an unsuspecting host. Upstream wandering may lead to the pancreatic and bile ducts, possibly occluding them with subsequent grave results. Multiple liver abscesses have resulted from such invasion (Rossi and Bisson, 1983). Worms reaching the stomach are aggravated by the acidity and writhe around, often causing nausea. The psychological trauma induced in someone who vomits up a 45-cm ascarid is difficult to quantify. Aside from any psychological effects, aspiration of a vomited worm can result in death (Darby and Westphal, 1972). Worms that reach the esophagus, usually while the host is asleep, may crawl into the trachea, causing suffocation or lung damage; they may crawl into eustachian tubes and middle ears, causing extensive damage; or they may simply exit through the nose or mouth.

Diagnosis and treatment

Accurate diagnosis of migrating juveniles is impossible at this time. Demonstration of juveniles in sputum is definitive, provided a technician can identify them. Most diagnoses are made by identifying the characteristic, mammillated eggs in feces or by an appearance of the worm itself. Adults can also be diagnosed by ultrasound and other noninvasive radiographic methods (Goyal et al., 2010). So many eggs are laid each day by one worm that direct fecal smears are usually sufficient to demonstrate eggs. *Ascaris lumbricoides* should be suspected when any of the previously listed pathogenic conditions are noted. Most light infections are asymptomatic, and such infections are typically diagnosed only following spontaneous elimination of adults from the anus.

Benzimidazole-based drugs (for example, mebendazole or albendazole) are often effective in a single dose. Benzimidazoles bind to tubulin in the worm's intestinal cells and body wall muscles (Bughio et al., 1994). Emodepside, a novel anthelminthic so far licensed in combination with praziquantel for use in cats, causes relaxation of body-wall muscle of *Ascaris* and inhibits contraction (Willson et al., 2003). Nitazoxanide and ivermectin are also effective (Doumbo et al., 1997; Marti et al., 1996). In regions endemic for many different soil-transmitted nematodes, certain drugs may be preferable to others due to their broader spectrum of efficacy in cases of multiple-species infections.

Toxocara canis

This species is a cosmopolitan intestinal parasite of domestic dogs and wild canids and it is the chief cause of visceral migrans (VM) in humans, discussed later.

As a result of prenatal infections, even puppies in well-cared-for kennels are typically infected at birth and require anthelminthic treatment. It is not uncommon for 100% of puppies to be infected. The owner of a brand new puppy is likely to be startled by the pet's vomiting up several large, active worms. Puppies tend to have the highest infection prevalence. The infective dose of eggs has a large impact on the success of infection in adult dogs where protective immu-

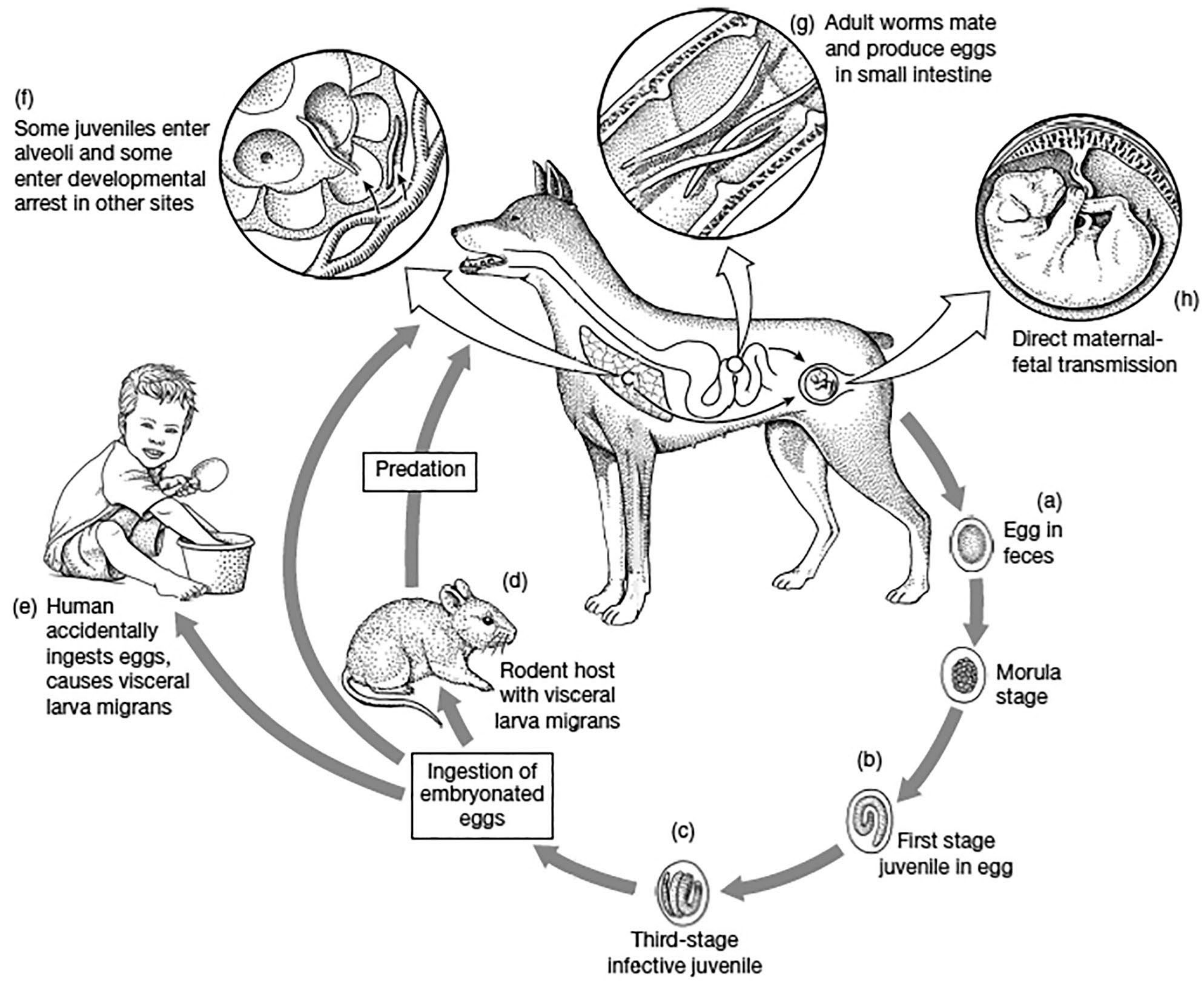

Figure 7. Life cycle of *Toxocara canis*. (a) Shelled embryo passed in feces. (b) J_1 in egg. (c) Infective J_3 in egg. (d) Eggs hatch in rodent host, and juveniles enter developmental arrest in viscera. (e) Eggs hatch in human and juveniles cause visceral larva migrans. (f) After penetration of intestinal wall, some juveniles break out into alveoli, ascend trachea, and finally mature in small intestine. Other juveniles (especially in mature dogs) enter developmental arrest in other sites. (g) Adult worms mate and produce eggs in small intestine. (h) Direct maternal-fetal transmission. Source: W. Ober and C. Garrison in Roberts et al., 2014. License: CC BY 4.0.

nity may have a larger role in the fate of juveniles; a smaller number of eggs administered is more likely to lead to patent infection (Dubey, 1978).

Adult *Toxocara canis* resemble *Ascaris* spp., only are much smaller. Three lips are present. Unlike *Ascaris* spp., however, *T. canis* has cervical alae in both sexes. Males are 4–6 cm-long, and females are 6.5 cm- to more than 15.0 cm-long. The brownish-colored eggs are almost spherical and roughly 75 µm × 85 µm, with surface pits, and are unembryonated when laid.

Biology

Adult worms live in the small intestine of their host, producing prodigious numbers of eggs, which are passed with the host's feces (Figure 7). Development of J_3 within eggs takes 9 days under optimal conditions.

The fate of ingested J_3s depends on host age and immunity. If a puppy is young and has had no prior infection, worms hatch and migrate through the portal system and lungs and back to the intestine, as in *Ascaris lumbricoides*. If the host is an older dog, J_3 fate is variable. Most J_3s will not complete the tracheal migration to become adults, but instead will enter the capillaries and undergo a somatic migration, eventually entering developmental arrest, with most individuals residing in the skeletal muscles.

If a dog harboring encysted, arrested juveniles becomes pregnant, those juveniles are reactivated late in the pregnancy and reenter the circulatory system, where they are carried to the placenta. There they penetrate through to the fetal bloodstream and migrate to the liver where they reside until birth. Juveniles begin migration to the lungs within 30 minutes following birth, and then undergo a tracheal migration. Thus, a puppy can be born with an infection of *Toxocara canis*, even though its mother has shown no sign of patent infection (meaning, not producing eggs). The puppy may also become infected by the transmammary route (that is, in the mother's milk), but this is probably less common than the transplacental route (Gillespie, 1988). If a lactating dog ingests infective juveniles, they can complete migration to the intestine and produce a patent infection.

Another option in the life cycle of *Toxocara canis* is offered when a rodent or other mammal ingests embryonated eggs. In this host the juvenile begins to migrate but then becomes dormant with arrested development. If the rodent is eaten by a dog, the worms promptly migrate through the lungs to the intestine or into tissues to continue their wait, depending on the dog's age. Thus, rodents are paratenic hosts. Although this adaptability favors survival of the parasite, it bodes ill for paratenic hosts, which may undergo behavioral changes as a result of infection that increases their risk of predation (Hamilton et al., 2006).

Visceral migrans

When nematode juveniles gain access to the wrong host species they do not complete the normal migration but undergo developmental arrest and may begin an extended, random wandering through various organs and soft tissues of the body. The resulting disease is known as visceral migrans (VM), in contrast to cutaneous migrans (CM), which occurs only in skin. Visceral migrans can be caused by a variety of spirurid, strongylid, and other nematodes in addition to ascaridoids. However, *Toxocara canis* is the most common species causing VM in humans.

Epidemiology

Many years ago, it was assumed that dog and cat ascaridoids could not infect humans or were not dangerous to them. In the early 1950s it was discovered that this assumption is not true, particularly for nematodes such as *Toxocara canis*. At any one time, about 2.2% of adult dogs and 98% of puppies in the United States are infected with *T. canis*; with the population of pet dogs in the United States, this means that more than 1 million dogs are currently shedding *T. canis* eggs. Thus, risk of human exposure to infective eggs is very high. However, most human infections are covert, and even overt symptoms may go unrecognized and unreported.

Development of a specific immunodiagnostic test, an ELISA using secretory-excretory antigens collected from cultured juveniles, has been a boon to epidemiological studies of VM (Schantz, 1989). This test can distinguish between *Ascaris lumbricoides* and *Toxocara canis*, but does not distinguish *T. canis* from *T. cati* (see Lynch et al., 1993). In the United States, an extensive survey showed an overall seroprevalence of 13.9% (in people > 6 years-old), but was higher for non-Hispanic blacks (21.2%). Other risk factors included low socioeconomic status, living in rural areas, and geographic region (Hotez and Wilkins, 2009; Overgaauw, 1997). A seroprevalence of 34% has been found among Irish school children, and 31% of the children from Croatia with eosinophilia (Holland et al., 1995; Sviben et al., 2009). Seroprevalence among children in developing tropical countries has been much higher, from 50–80%. Visceral migrans is predicted to have a substantial impact on individuals living in poverty worldwide.

Dogs and cats defecating on the ground seed an area with eggs, which embryonate and become infective to any mammal or bird ingesting them. Small mammals are important paratenic hosts; infected mice undergo behavioral changes that increase their risk of predation, which increases the chance to complete the life cycle (Cox and Holland, 1998; 2001; Dold and Themme, 1949; Hamilton et al., 2006). Considering that the crawling-walking age of small children is a time when virtually every available object goes into the mouth for a taste, it is not surprising that the disease is common in children between 1 and 3 years old. In an urban setting, dog owners look upon the city park as the perfect place to walk a dog, while parents bring young children there to play on egg-seeded grass. Thus, of note is the high risk to children by exposure to the environment of puppies (Schantz, 1989). Finally, a factor to contemplate in light of the foregoing is the durability and longevity of *Toxocara canis* eggs, which are comparable to those of *Ascaris* (discussed above).

Pathogenesis

Juvenile *Toxocara canis* provoke a delayed-type hypersensitivity reaction in paratenic hosts and the degree and timing of the reaction depend on the infecting dose (Schantz, 1989). In experimental hosts, most juveniles eventually end up in the brain; it is unclear whether this is because juveniles have a predilection for the brain or because they are destroyed in other sites but remain in the brain. In sites other than the brain, juveniles may be encapsulated by a granulomatous reaction (Figure 8). The most common site of juvenile residence is the liver (as shown in Figure 8), but any organ will do.

Characteristic symptoms of VM include fever, pulmonary symptoms, hepatomegaly, and eosinophilia. The extent of damage usually is related to numbers of juveniles present

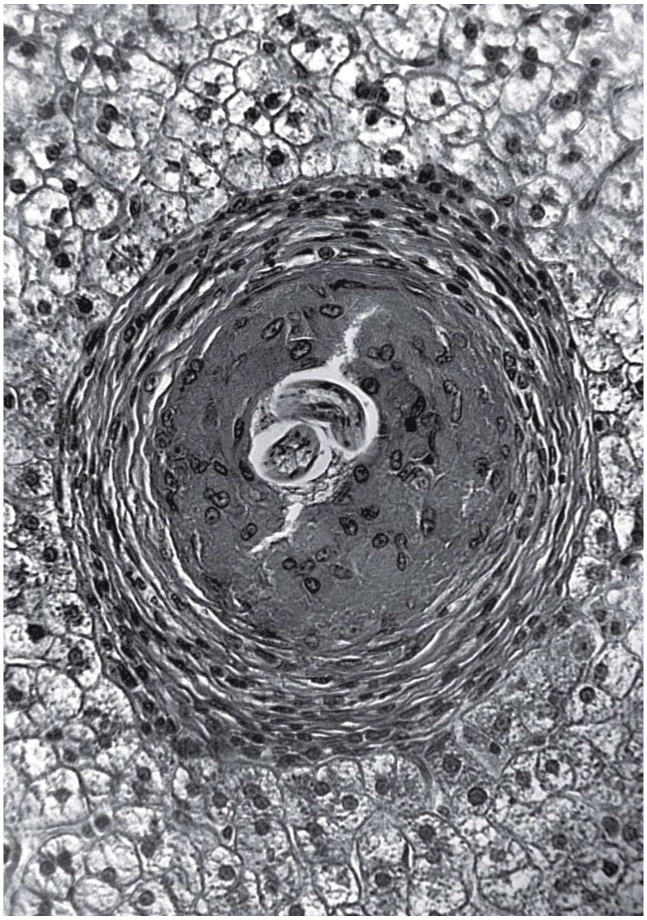

Figure 8. *Toxocara canis* juvenile section in liver of a monkey at 9 months' infection. The juvenile rests in a matrix of epithelioid cells surrounded by a fibrous capsule lacking intense inflammatory reaction. Source: Beaver, 1969 in Roberts et al., 2014. License: CC BY-NC-SA 4.0.

and their ultimate homestead in the host's body. Various neurological symptoms have been reported and deaths have occurred when juveniles were especially abundant in the brain. Presence of juveniles in the spinal cord can lead to inflammatory lesions and sensory or motor dysfunction; treatment with albendazole can yield neurologic improvement in such patients (Jabbour et al., 2011). Rarely, juveniles of *Toxocara canis* cause eosinophilic meningoencephalitis (Vidal et al., 2003). While dire consequences such as these can result from infection, most cases result in rather minor, transient symptoms such as abdominal pain, headache, and cough. This subacute condition is known as covert or common toxocariasis, which is commonly either undiagnosed or misdiagnosed.

Juveniles in a host's eye may cause chronic inflammation of the inner chambers or retina or provoke dangerous granulomas of the retina. These reactions can lead to blindness in the affected eye. The frequency of ocular toxocariasis in the United States is difficult to assess. Ocular toxocariasis was diagnosed in 1% of patients examined for vision loss in Alabama eye clinics in 1987 (Maetz et al., 1987). Generally, ocular damage is the result of invasion of only a single juvenile (Schantz, 1989). It may be that, because heavy infections stimulate a much stronger immune response with low survival rates, juveniles survive longer in light infections, giving them more time to wander into an eye. Other lesions destroy lung, liver, kidney, muscle, and nervous tissues.

Diagnosis and treatment

An ELISA using secretory-excretory antigens has facilitated clinical diagnosis enormously. This test is more sensitive for detecting covert toxocariasis and VM than ocular disease. A high eosinophilia is suggestive of infection with *Toxocara canis*, especially if the possibility of other parasitic infections can be eliminated.

Usually, only patients with severe symptoms are treated (Gillespie, 1988). Diethylcarbamzine and mebendazole appear to be effective treatments (Magnaval, 1995; Smith et al., 2009). An excellent summary of current therapies and preventative measures is given by Magnaval and colleagues (2022). Control consists of periodic deworming of household pets, especially young animals, and proper disposal of the animals' feces. Thus, for toxocariasis, veterinary medicine practices are important to mitigate disease transmission to humans. Some anthelminthics have been reported to be effective against all stages in dogs, including juveniles in arrested development (Altreuther et al., 2009), which presents new options for reducing transmission among dogs. Dogs and cats should be restrained, if possible, from eating available transport hosts. Sandpits in public parks can be protected from contamination by covering them with vinyl sheets when not in use (Uga and Kataoka, 1995; Uga et al., 1996).

Other *Toxocara* Species

Toxocara cati is widely prevalent among domestic cats and other felids (Figure 9). The cervical alae (Figure 10) of *T. cati* are shorter and broader than those of *T. canis*, and the eggs of the two species are slightly different in size. Life cycles are similar, including the use of paratenic hosts, but kittens are infected with *T. cati* only by the transmammary route if mothers are infected during late gestation (Gillespie, 1988). *Toxocara cati* may be an important cause of visceral migrans (VM), but it is difficult to determine the relative importance of each species because the current ELISA test for human infection does not distinguish between *T. canis* and *T. cati*. Adult *T. cati* have occasionally been reported from humans (Eberhard and Alfano, 1998).

Toxocara vitulorum is the only ascaridid that occurs in cattle. Its life cycle is similar to that of *T. cati*, with the young

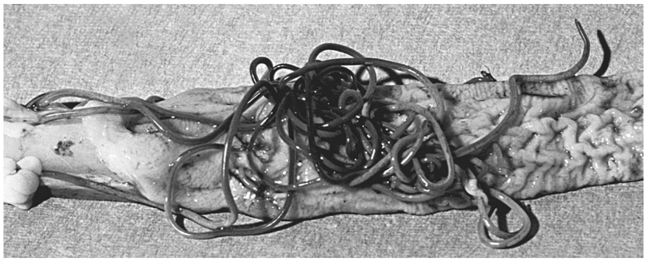

Figure 9. Intestine of a domestic cat, opened to show numerous *Toxocara cati*. Source: R. E. Kuntz in Roberts et al., 2014. License: CC BY-NC-SA 4.0.

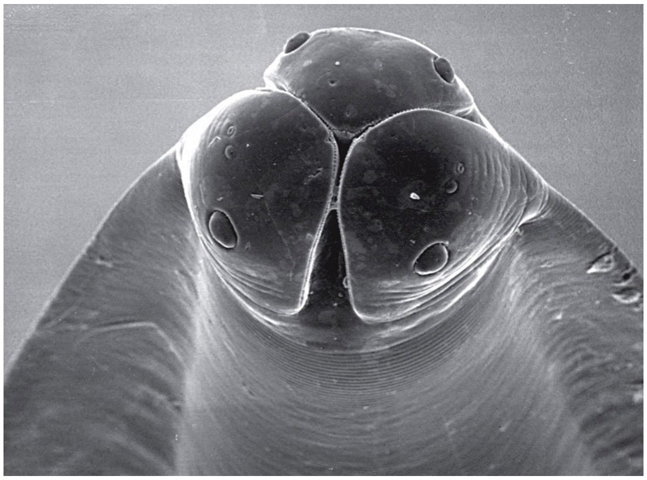

Figure 10. Scanning electron micrograph of *Toxocara cati* en face view. Note the 3 lips with sensory papillae and broad cervical alae on each side. Source: J. Ubelaker in Roberts et al., 2014. License: CC BY 4.0.

being infected by their mother's milk (Roberts, 1990). Adult hosts are refractory to intestinal infection. Young calves may succumb to verminous pneumonia during migratory stages of the parasites. Diarrhea or colic results in economic losses to the animal's human owner.

Parascaris equorum

This large nematode and its congener *Parascaris univalens* are the only ascaridoids found in horses and other equids. *Parascaris equorum* is a cosmopolitan species. It is very similar in gross appearance to *A. lumbricoides* but is easily differentiated by its huge lips, which give it the appearance of having a large, round head. In addition, *Parascaris* spp. individuals are white, whereas fresh *Ascaris* spp. specimens have a reddish color due to their characteristic muscle hemoglobin.

The life cycle is similar to that of *Ascaris lumbricoides*, involving a lung migration. Foals are often infected soon after birth; however, there is no evidence of prenatal or transmammary transmission. Resulting pathogenesis is especially important in young animals, with pneumonia, bronchial hemorrhage, colic, and intestinal disturbances resulting in unthriftiness and morbidity. Intestinal perforation or obstruction is common. Prevalence and intensity of infection decrease with horse age, presumably due to acquired immunity. In several regions *Parascaris equorum* shows strong resistance to the drug ivermectin, although certain other compounds remain viable alternatives for treatment (Lyons et al., 2008). The development and spread of drug resistance in nematodes is of concern because relatively few new anthelminthic drugs are being developed.

Baylisascaris procyonis

This is a very common intestinal parasite of raccoons in North America. Other related species in this genus occur in bears, skunks, badgers, and other carnivores. When embryonated eggs are ingested by a young raccoon, they will hatch in the small intestine, burrow into the intestinal wall, and mature. Older raccoons are typically infected when they eat infected rodent, lagomorph, or bird paratenic hosts that have juveniles encysted in their tissues. More than 90 species of birds and mammals have been reported to be infected (Kazacos, 1986). In these animals, parasite juveniles wander, often invading the central nervous system, resulting in neurological damage and debilitation, or death. This makes infected hosts vulnerable to predation or scavenging by raccoons. Unfortunately, juveniles affect humans in the same way. Neural (juvenile) migrans (NM) caused by *Baylisascaris procyonis* occurs almost exclusively in children younger than 2 years old; risk factors for egg ingestion include geophagia and pica. A substantial fraction of NM cases are fatal. Ocular migrans may occur in association with NM, or independently when it occurs in adult humans. Serological diagnosis of infection in humans has been difficult, but a new ELISA method based on a recombinant DNA antigen appears promising (Dangoudoubiyam et al., 2011).

An important epidemiological factor is close contact between humans and raccoons or raccoon feces. Scavenging raccoons may prowl and feed on pet dog or cat food near human dwellings and outbuildings. Their preferred communal defecation sites are dangerous sources of infection to humans and other animals (Page et al., 1999). Infected raccoons shed approximately 25,000 eggs per gram of feces, and communal raccoon latrines almost always contain infective eggs. Eggs can remain infective for years under ideal conditions, so once an area is contaminated it is nearly impossible to decontaminate using chemical treatments. Methods using heat such as steam generators or a propane flame gun can be effective for small areas (Kazacos, 2001) because juveniles within eggs are killed at 62 °C (Kazacos, 1982; Shafir et al., 2011). Pet kinkajous (another procyonid) sold in the United States have been reported to be infected with *Baylisascaris procyonis* (see Kazacos, 2001). Domestic dogs can also serve as hosts of adult *B. procyonis*, and if such infections were to become prevalent, this could alter factors influencing human infection.

Other species of *Baylisascaris* may have similar pathogenicity, but most hosts are not as likely to come in close contact with humans. Skunks infected with *B. columnaris* are potential hazards, however.

Toxascaris leonina

Toxascaris leonina is a cosmopolitan parasite of dogs and cats and related canids and felids. It is similar in appearance to *Toxocara* spp., being recognized in the following ways: 1) The body tends to flex dorsally in *T. leonina* and ventrally in *Toxocara* spp.; 2) alae of *T. cati* are short and wide, whereas they are long and narrow in *T. canis* and *T. leonina* (Figure 11); 3) the egg surface is smooth in *T. leonina* but pitted in *Toxocara* spp.; and 4) the tail of male *Toxocara* spp. constricts abruptly behind the cloaca, whereas it gradually tapers to the tail tip in *T. leonina*.

The life cycle of *Toxascaris leonina* is simple. Ingested eggs hatch in the host's small intestine, where juveniles penetrate the mucosa. After a period of growth, they molt and return directly to the intestinal lumen, where they mature. Alternatively, juveniles in intermediate hosts such as rodents can infect definitive hosts following predation.

Like for *Toxocara* spp., the pathogenicity of *T. leonina* for the definitive host depends on infection intensity, and in severe cases can involve intestinal obstruction or rupture of the intestine. Visceral migrans involving *T. leonina* has been implicated as a possible cause of human eosinophilia on St. Lawrence Island (Bering Sea), where this nematode commonly infects Arctic foxes, working dogs, and voles (rodent genus *Microtus*) as paratenic hosts (Rausch and Fay, 2011).

Figure 11. Anterior end of *Toxascaris leonina*, an intestinal parasite of dogs, cats, and other canids and felids. Note the narrow cervical alae (arrow) as compared with the broad alae of *Toxocara cati*. Source: J. Georgi in Roberts et al., 2014. License: CC BY-NC-SA 4.0.

Lagochilascaris species

Relatively little is known about the natural definitive host ranges of the 5 described species in *Lagochilascaris*, a genus mainly reported from North America, Central America, and South America. The genus name is derived from the prominent cleft on the inner margin of each lip (Figure 12). These nematodes normally mature in the host's gastrointestinal tract but seem to have a tendency to develop in abscesses outside the gut. The life cycle is indirect, with juveniles developing to the infective stage within rodent intermediate hosts that ingest the eggs. Embryonated eggs are not directly infective for definitive hosts. *Lagochilascaris minor* and *L. major* have often been reported from domesticated cats; *L. minor* is typically found in subcutaneous abscesses in the head or neck of such hosts whereas it localizes in the stomach, esophagus, and trachea of wild cats in South America and the Caribbean. Domestic cats have been experimentally infected with the third-stage juveniles (J_3) of *L. minor* from mice (Barbosa et al., 2007). Experimental infections were patent, suggesting that domestic cats may serve as a reservoir for zoonotic infection. The pharynx of domestic cats appears to be the preferred site for *L. major*; this species has also been reported from wild and domestic canids, and raccoons. Wild cats are believed to represent the natural definitive host for both *L. minor* and *L. major* in South America, but host records are few. In North

Figure 12. *Lagochilascaris turgida.* Note the prominent cleft in the tip of each lip, typical of the genus (lagos (Greek) = hare; cheilos (Greek) = lip). Source: J. Sprent in Roberts et al., 2014. License: CC BY 4.0.

America, *L. sprenti* uses opossums as its definitive host.

Lagochilascaris minor has been reported in humans at least 8 times, usually found in the tonsils, nose, or neck (Sprent, 1971; Volcan et al., 1982). A fatal brain infection has been reported (Rosemberg et al., 1986). When present, worms cause abscesses that may contain from 1 to more than 900 individuals. Juveniles can mature in these locations, and they produce pitted eggs, much like those of *Toxocara* spp. Human infections may last many years or may kill infected people rapidly. How humans become infected is unknown. Humans are unnatural, accidental hosts for this zoonotic infection.

Family Anisakidae Railliet & Henry, 1912

The many species in the family Anisakidae are stomach parasites of fish-eating birds and marine mammals. Species in the genus *Anisakis*, have a life cycle that involves passage of eggs in feces of their definitive hosts, embryogenesis and hatching of J_3s, ingestion of J_3s by a crustacean, development in the hemocoel of the crustacean, and then either, 1) Ingestion by a definitive host, or 2) ingestion by a fish paratenic host, which is ultimately consumed by a definitive host (Deardorff et al., 1991; Sakanari, 1990). Definitive hosts of *Anisakis* spp. are marine mammals.

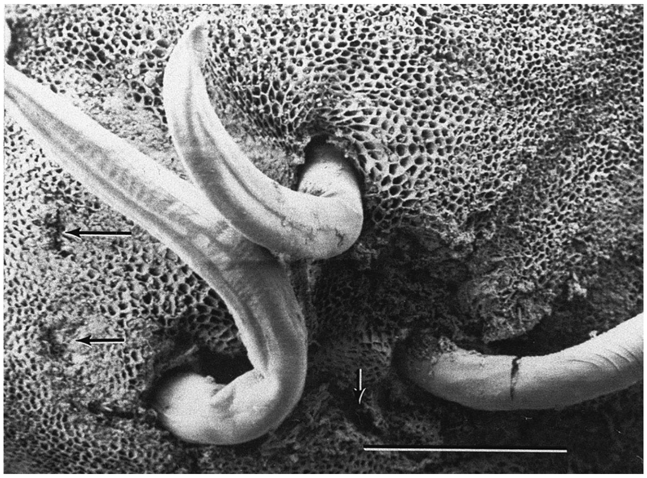

Figure 13. Scanning electron micrograph of *Terranova* sp. juveniles (family Anisakidae) penetrating the stomach of a rat on day three postinfection. Arrows indicate acute lesions caused by juveniles. Scale bar = 1 mm. Source: Deardorff et al., 1983 in Roberts et al., 2014. License: CC BY-NC-SA 4.0.

Living *Anisakis* spp. juveniles can produce pathological conditions in humans who eat them in raw, salted, marinated, smoked, or pickled fish in preparations such as ceviche, sushi, sashimi, lomilomi, and rollmops. Such conditions may be asymptomatic, mild, or severe (Bier et al., 1987). Symptoms generally commence when juveniles begin to penetrate the stomach lining or intestinal mucosa (Figure 13). Gastric involvement may manifest from 1 to 12 hours after ingestion of infected seafood or after up to 14 days in the case of intestinal penetration. Symptoms may include severe epigastric pain, nausea, vomiting, diarrhea, and hives, but the disease may be confused with other disorders, such as peptic ulcers. Sometimes severe IgE-mediated hypersensitivity reactions occur, and because the allergenic substances present may be heat resistant, even cooking may not render them harmless (Caballero and Moneo, 2004).

Diagnosis of gastric anisakiasis by endoscope and removal of worms with biopsy forceps is effective, although catching lively worms with forceps may be challenging (Deardorff et al., 1991). In intestinal anisakiasis, or cases in which the worm has fully penetrated into submucosa or migrated beyond the gastrointestinal tract, diagnosis is more problematic, and symptoms can mimic a number of other, more common conditions. In such cases serodiagnosis can be helpful and recombinant antigens have made detection of IgE antibodies highly specific (Anadón et al., 2010; Sakanari et al., 1988).

Most cases have been reported from Japan, South Korea, Spain, and Scandinavian countries, where raw or marinated fish is consumed regularly. Approximately 2,000 cases per year have been reported from Japan, where it is a major foodborne disease, and the number of cases reported from the United States is increasing (Deardorff et al., 1991; Kagei and Isogaki, 1992). Fatalities due to peritonitis have been recorded (Bier et al., 1987).

Anisakis spp. juveniles are the most frequent cause of anisakiasis, but the name of this disease is a misnomer because other anisakid genera, and even species from other families (such as Raphidascarididae), can be responsible. A common feature of the causative organisms is that they are transmitted through aquatic food chains that involve invertebrates and most typically fish paratenic hosts; these paratenic hosts can be infective for humans.

Cooking kills juveniles, but continued popularity of raw or undercooked fish dishes (some examples of which are listed above) ensures a continued risk of human infection. In many cases, commercial blast freezing causes little change in the texture or taste of fish while effectively killing *Anisakis* sp. juveniles (Deardorff and Throm, 1988).

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NEMATA

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

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Phylum Nemata

Superfamily Heterakoidea

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Chapter 51

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

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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).

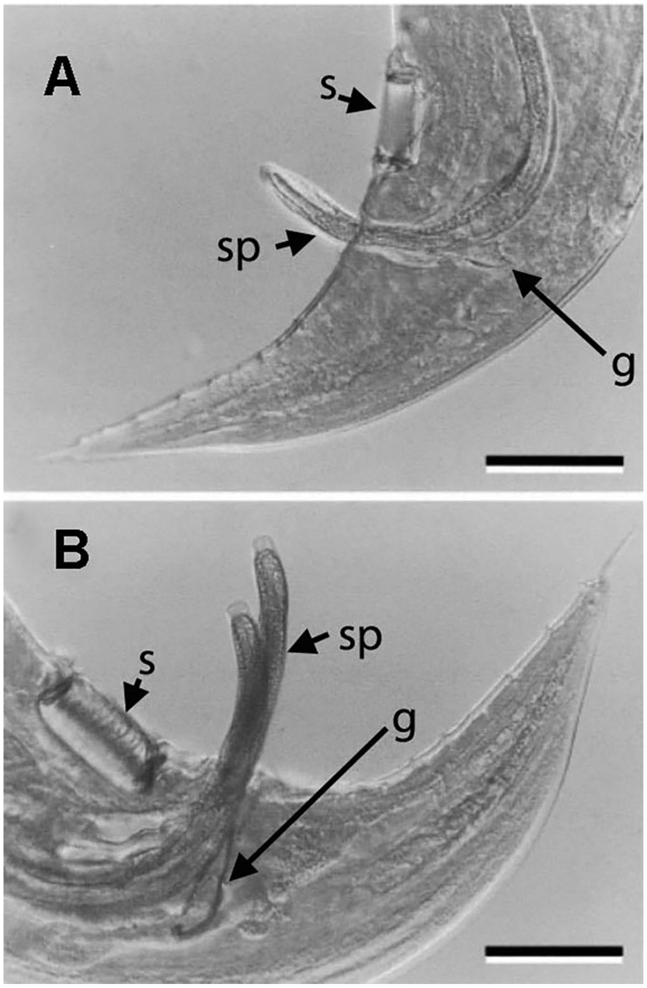

Figure 1. Heterakoid nematodes *Aspidodera* spp. A) Posterior end of *A. sogandaresi* showing pre-cloacal sucker (s) and spicules (sp); B) posterior end of *A. fasciata* showing paired spicules (ps) sucker (s) and proximal end of gubernaculum (g). Scale bars = 100 µm. Source: S. L. Gardner, HWML. License: CC BY 4.0.

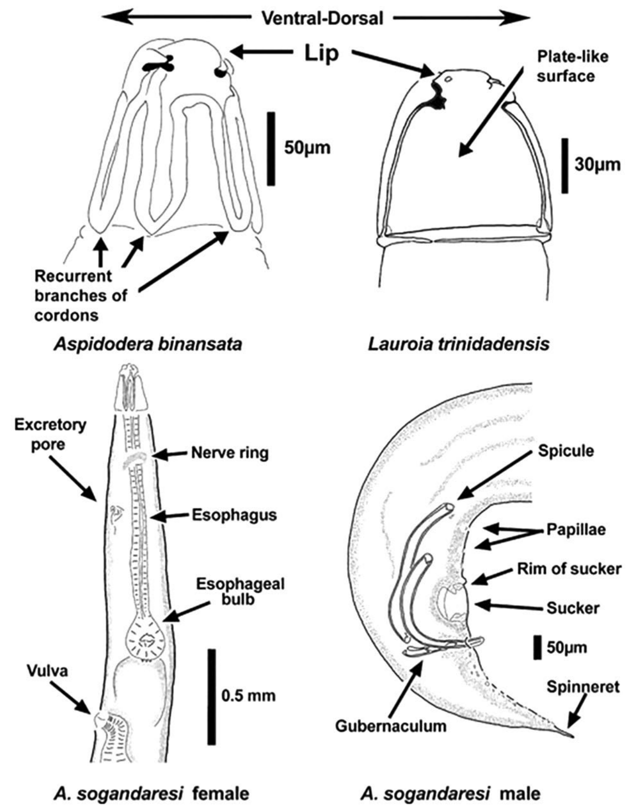

Figure 2. Examples of the structures of the hood in Aspidoderidae (Nemata: Heterakoidea) as seen in the right lip. Source: S. L. Gardner, HWML. License: CC BY 4.0.

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 document 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.

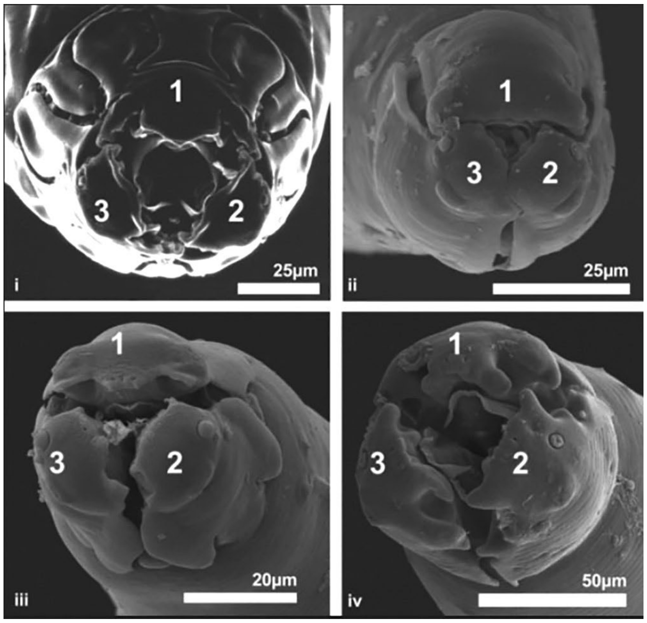

Figure 3. En face view of 4 species of Aspidoderidae showing the positions of the lips. Dorsal lip is labeled 1 in all images; ventral side includes 2 lateroventral lips labeled as 2 (sinistroventral) and 3 (dextroventral). *Aspidodera scoleciformis* (i), *A. bolivari* (ii), *A. scapteromi* (iii), and *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.

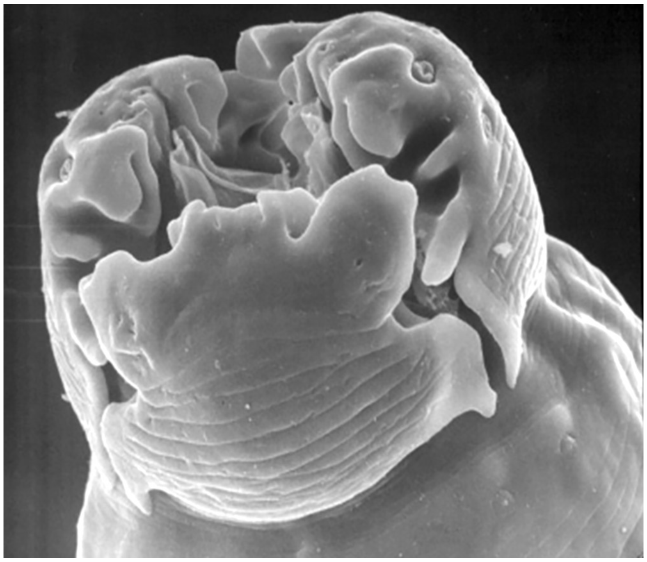

Figure 4. The anterior end of *Paraspidodera* sp. from a rodent from Bolivia, showing the 3 lips. Source: S. L. Gardner, HWML. License: CC BY 4.0.

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.

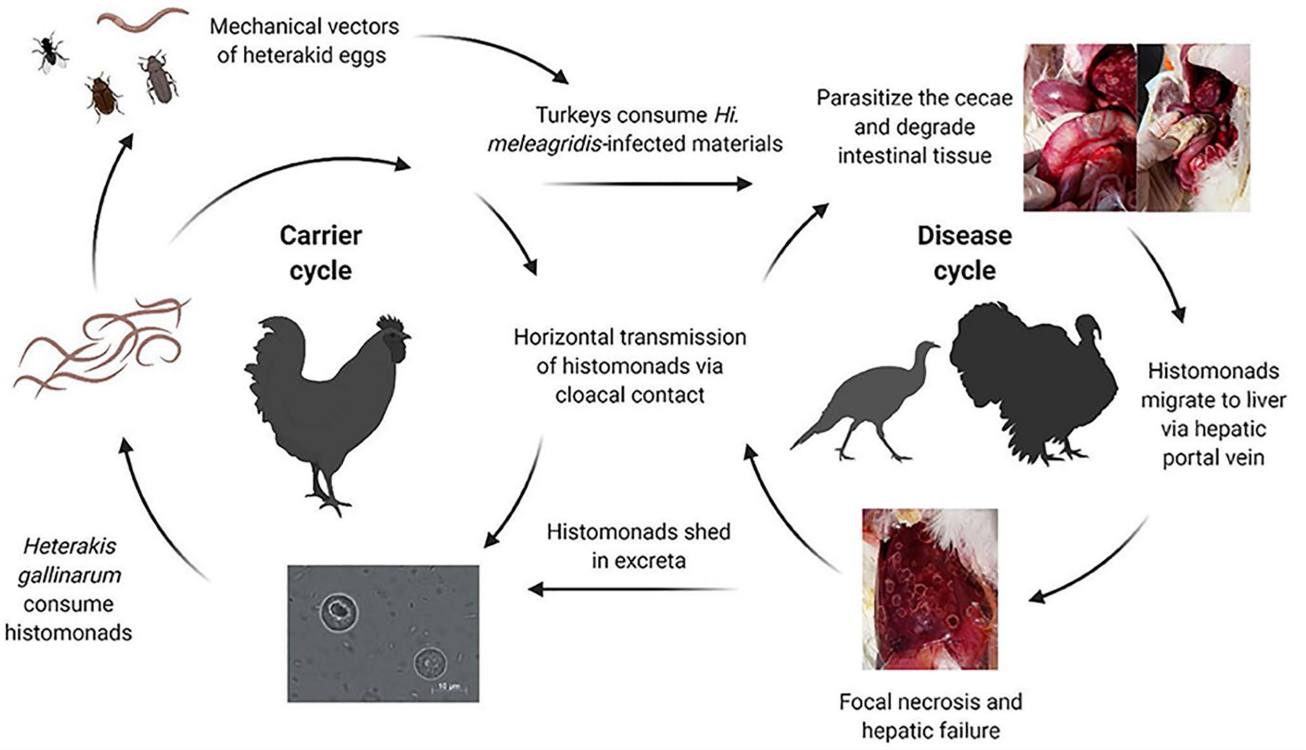

Figure 5. Complex transmission of *Histomonas meleagridis*, a venereal disease of nematodes. In the galliform host, infective eggs of *Heterakis gallinarum* are ingested incidentally as the bird eats earthworms or other soil-dwelling invertebrates from soil contaminated with feces from infected birds. 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

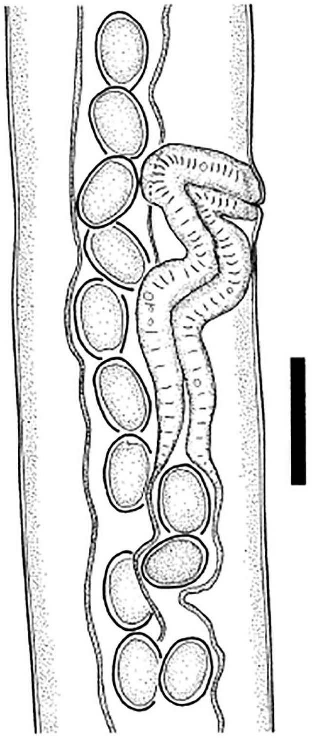

Figure 6. *Lauroia bolivari*. Lateral view of the ovijector with eggs. Scale bar = 100 mm. Source: Adapted from Jiménez-Ruiz and Gardner, 2003. License: CC BY 4.0.

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).

Acknowledgement

A portion of this section was adapted with permission from Roberts et al. (2014, p. 421–422). No byline was included for this contribution at the beginning of this section, so this serves as acknowledgement of the contribution by the authors of that borrowed section.

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52

NEMATA

Oxyurida (Order): Pinworms

Haylee J. Weaver

Phylum Nemata

Order Oxyurida

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Chapter 52

Oxyurida (Order): Pinworms

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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).

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.

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).

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

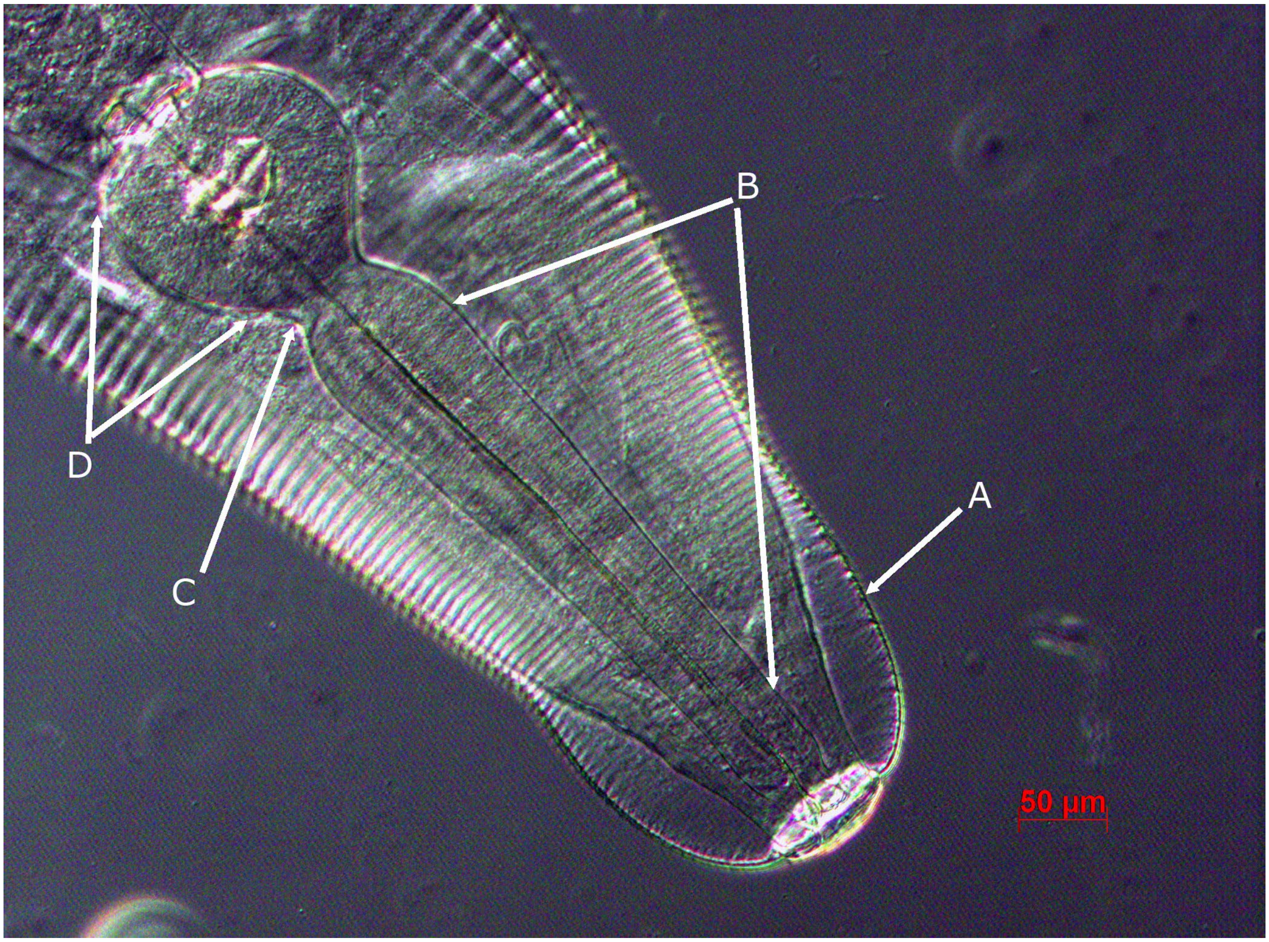

Figure 1. Anterior end of a species of *Syphacia* from rodents of the family Sciuridae (squirrels). Typical of pinworms of rodents, the inflated cuticle near the mouth can be seen (A), in addition, the esophagus expands posteriad (B), narrowing into an isthmus (C), and then expanding into a definite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

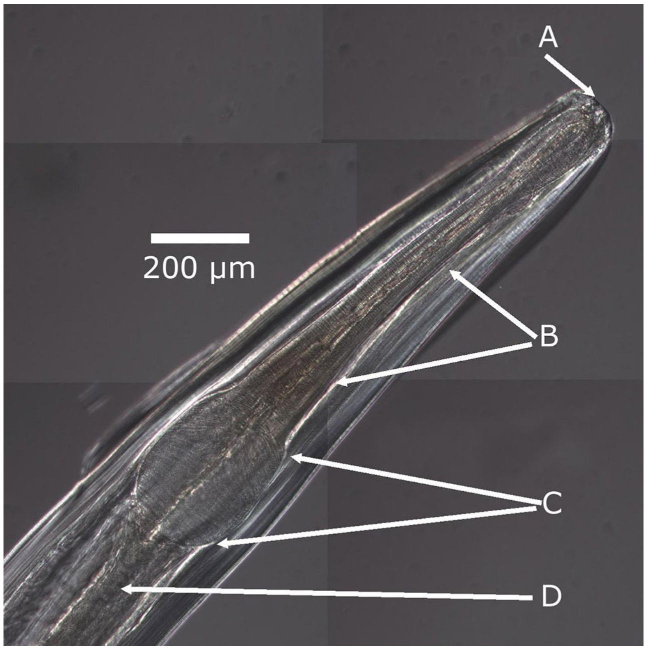

Figure 2. The anterior end of a species of *Passalurus* from the cecum of a rabbit (*Sylvilagus* sp.). The mouth is shown labeled (A), the corpus of the esophagus is marked by arrows (B), the bulb of the esophagus is shown at (C), and the intestine is shown at (D). Source: G. Drabik, HWML, 2016. License: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

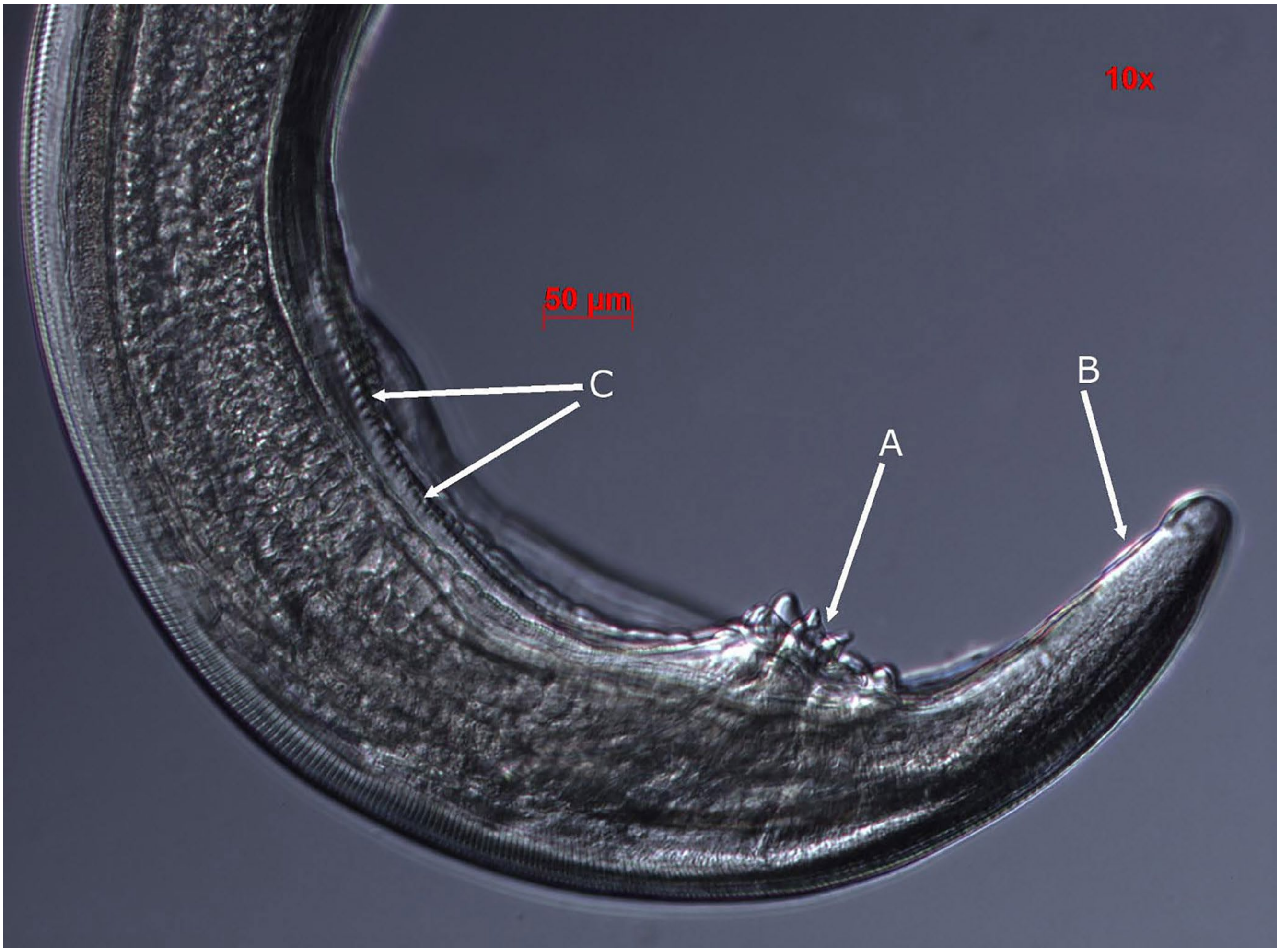

Figure 3. Posterior end of a male *Passalurus* pinworm of rabbit and hares (order Lagomorpha: family Leporidae). The tail (B) is the part of the animal posteriad to the cloaca. The cloaca is shown surrounded by small sensory papillae (A). In male nematodes the exit to the digestive system and the reproductive 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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NEMATA

Spirurida (Order)

Valentin Radev

Phylum Nemata

Order Spirurida

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Chapter 53

Spirurida (Order)

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Introduction

The representatives of the order Spirurida are nematode parasites of fishes, amphibians, reptiles, and mammals. They are some of the most common parasites found in vertebrates. Morphologically and phylogenetically diverse, the order includes 2 suborders, with 12 superfamilies with a large number of families, subfamilies, species, and subspecies that often inhabit a unique site of localization in the host, such as the esophagus, stomach, body cavities, blood vessels, and so on.

Recently their study has involved modern methods, such as scanning electron microscopy, molecular biology, and other techniques. As a result, new conceptions about their classification and complex life cycles are available and are presented here.

Morphology and Locations within the Host

Spirurids are parasites having typical morphological features clearly distinguishing them from other nematodes. Their body is spindle-shaped. The front and back edges can be narrow or tapered. They possess an anterior extremity which is bilaterally symmetrical and they lack lateral, external labial papillae. In some members, the **sexual dimorphism** between males and females is very pronounced. Typically, the **cuticle** of the spiruridis has clear ornamentation. Their body surface may be transverse grooved, having different forms—spikes, teeth, edges, wart-like formations, wrinkles, and others. The **mouth opening** usually is surrounded by 2 lateral 3-section **lips**. In some cases, they possess additional dorsal and ventral lips. Some spirurids have a clearly-differentiated **buccal cavity** or **stoma** which leads into the **pharynx**, which can have different forms. The **esophagus** is divided into 2 parts: The anterior, which is muscular and shorter, and the posterior, which is glandular and longer. Males are without a genital bursa, but sometimes they have **tail-cuticular wings**. The **caudal papillae** are always ventral or ventrolateral in position. There is no pre-anal sucker. There are usually 2 **spicules**, different in shape and length from one another. Normally the right one is shorter and wider. The female **genital opening** is variable in its distance from the anterior end depending on the species (see Figures 1 and 2).

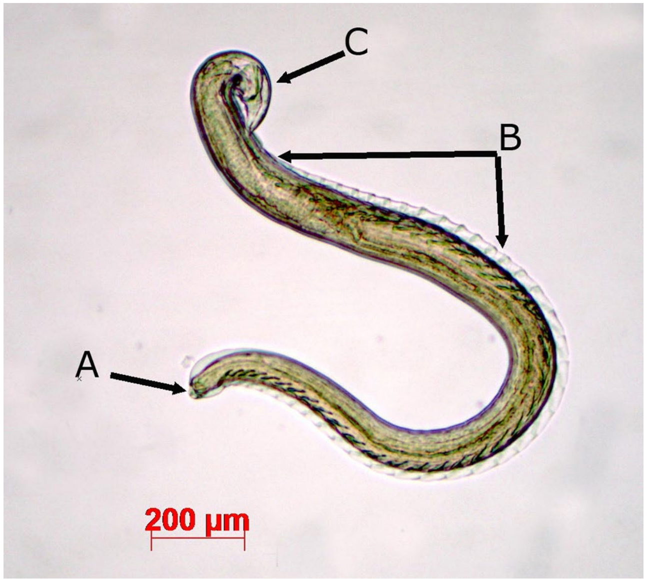

Figure 1. Whole body view of a species of *Pterygodermatites* from a bat. Showing: The mouth is at the anterior end (A), a double row of spines runs the length of body terminating just before the tail (B), and the tail (C). Source: K. Cajiao Mora, 2022. License: CC BY.

Figure 2. Anterior end of a species of spirurid, *Pterygodermatites*, from a bat of the genus *Myotis* collected in eastern Colombia. Small hooks of the cuticle can be seen around the mouth and thin spinose parts of the cuticle can be seen running posteriad. In this species, the spines occur down the body and terminate before the tail. Source: K. Cajiao Mora, 2022. License: CC BY.

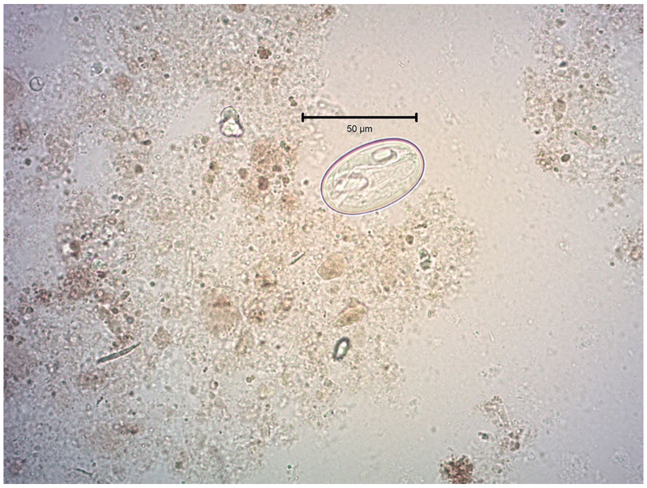

Figure 3. Spirurid egg from a short-eared owl *Asio flammeus*. Source: T. Pennycott, Edinburgh DataShare, https://datashare.ed.ac.uk/handle/10283/2139. License: CC BY.

Females lay eggs (Figure 3) with juveniles already formed. The juvenile stages, which are preinfective in the final or definitive host, develop entirely within an intermediate host, which may be crustaceans, beetles, coprophages, and other insects. Adults are parasites in the host's gastrointestinal tract, nasal cavity, blood vessels, eyes, and conjunctival sacs, under the skin, and in different tissues or body cavities of fishes, birds, and mammals.

Taxonomic Hierarchy with Descriptions

See Table 1 for an aggregated, selective implementation of the higher-level taxonomy for this group with hosts and sites of localization noted (see also Kanchev et al., 2016; Vassilev et al., 1986).

Table 1. Selected superfamilies of nematodes with hosts and sites of localization.

Superfamily	**Intermediate hosts**	**Final hosts**	**Sites of localization**	**Sources**
Acuarioidea	insects	birds, mammals	upper alimentary tract, stomach	Hodda, 2022; Anderson, 2000
Aproctoidea	eyes of small fish	birds	air sacs, nasal cavities, orbits, subcutaneous tissues of the head and neck	Hodda, 2022; Anderson and Bain, 1976; Dubinin, 1949
Camallanoidea	copepods, arthropods	marine, estuarine, and freshwater fishes	gut, deeper tissues, cavities	Ivashkin et al., 1971
Diplotriaenoidea	worms, such as *Diplotrema*, *Quadriplotriaena*	birds	air sacs, nasal cavities, subcutaneous tissues of the head and neck	Hodda, 2022; Anderson and Bain, 1976
Dracunculoidea	cyclopoid copepods	fishes, reptiles, birds, mammals, rarely in amphibians	under the skin	Hodda, 2022; Chabaud, 1975; Petter and Planelles, 1986
Filarioidea	tabanid fly, *Musca domestica*	all classes of vertebrates other than fishes (for example, horses, cattle)	body cavities, blood vessels, lymph vessels, connective tissues	Hodda, 2022; Soulsby, 1965; 1982; Anderson and Bain, 1976
Gnathostomatoidea	copepods	lower vertebrates, mammals	gastric mucosa	Hodda, 2022; Anderson, 2000
Habronematoidea	muscid dipterans	birds, mammals	proventriculus, stomach, causes cutaneous habronemiasis	Hodda, 2022; Anderson, 2000
Physalopteroidea	cockroaches	vertebrates, birds, reptiles,	lumen or wall of the stomach	De Lay and Blaxter, 2004; Cheng, 1973; Anderson, 2000
Rictularioidea	coprophagous insects	carnivores	free in the lumen or firmly attached to the mucosa of the intestine	Hodda, 2022; Witenberg, 1928
Spiruroidea	arthropods	vertebrates	lumen or the wall of the stomach	Hodda, 2022; Soulsby, 1981
Thelazioidea	ovoviviparous and oviparous, *Musca autumnalis*	birds, mammals (such as primates), fishes	eyeworms	Hodda, 2022; Anderson, 2000

Superfamily Acuarioidea

Acuarioidea tend to inhabit the upper alimentary tract or the muscles of the gizzard in birds, or may occur in the stomach of mammals, and are sometimes pathogenic. According to Anderson (2000), most adult acuarioids occur in the gizzard of birds, while a few species are found in both the proventriculus and in the posterior half of the esophagus. Most acuarioids occur in birds living in aquatic habitats and relatively few in birds associated with terrestrial habitats.

Acuarioids can move from one attachment site to another, leaving behind lesions devoid of worms. Cram (1931) reported openings through the gizzard lining associated with *Acuaria hamulosa*. Alicata (1938) found adult *A. hamulosa* mainly in tissues of the gizzard at its junction with the intestine. All acuarioids produce oval, smooth, thick-shelled eggs, each of which contains a small first-stage juvenile (J_1).

Hamann (1893) gave an account of how transmission probably occurs. Piana (1897) showed that *Dispharynx nasuta* of the proventriculus of gallinaceous and passerine birds developed in terrestrial isopods. Cram (1931; 1934), Cuvillier (1934), and Alicata (1938) conducted experiments to investigate the transmission and development of some acuarioids in terrestrial hosts and showed the importance of various insects and isopods as intermediate hosts. Garkavi (1956) investigated the development and transmission of *Streptocara crassicauda*.

Species of acuarioids in terrestrial hosts develop successfully in a great variety of arthropod intermediate hosts, including isopods, grasshoppers, beetles, and even diplopods. Acuarioids which parasitize aquatic hosts develop to the third stage in the haemocoel of aquatic crustaceans or in amphipods. Third-stage juveniles (J_3) vary considerably in morphology especially in the posterior quarter or fifth of the body, which is bent dorsally, and the tail is always armed with spines or tubercles. In other species the tail is unarmed and generally conical. Infections come after ingesting arthropods containing infective third-stage juveniles (J_3). In piscivorous birds, such as cormorants, transmission depends on frog and fish paratenic hosts (Anderson, 2000).

Superfamily Aproctoidea

Aproctoidea include parasites in air sacs, nasal cavities, subcutaneous tissues of the head and neck, and orbits of birds (Anderson and Bain, 1976). Their eggs are thick-shelled and include a fully developed first-stage juvenile (J_1). Little is known about the transmission of any of the species in the Aproctoidea (Anderson, 2000).

Superfamily Camallanoidea

Camallanoidea are parasites of the stomach and intestines of lower predaceous vertebrates (Chabaud, 1975) (see the chapter by Choudhury for a more in-depth summary of the Camallanoidea). Some of them occur in amphibians and reptiles, especially turtles (Baker, 1987), but also in marine, estuarine, and freshwater fishes (Ivashkin et al., 1971). One of the first demonstrations of heteroxeny in the Nemata was by Metchnikoff (1866) and Leuckart (1876) concerning the development of *Camallanus lacustris* of European fishes in copepods. Camallanoids are viviparous nematodes. Their intermediate hosts are crustaceans (Kupriyanova, 1954). Juveniles enter the haemocoel and develop into the third infective stage and they are armed with a few terminal spines. In the paratenic hosts (planktonivorous fishes) juveniles may grow to the fourth stage or become encapsulated in the tissues. Jackson and Tinsley (1998) found juveniles in aquatic toads (Pipidae) in Africa. The paratenic hosts move the juveniles in the food chain. The predator (piscivorous) definitive host can become infected by ingesting copepods or paratenic hosts with juveniles. Linstow (1909) described the juveniles of *Camallanus lacustris* in the isopod *Asellus aquaticus* and Fusco (1980) reported that some juveniles of *Spirocamallanus cricotus* developed successfully in white shrimp (*Penaeus setiferus*). Invasion of predaceous vertebrates is carried out after eating of intermediate or paratenic hosts which contain infective juveniles of camallanids (Anderson, 2000).

Superfamily Diplotriaenoidea

Diplotriaenoidea include spirurids in the air sacs of reptiles and birds (Anderson and Bain, 1976). Chabaud (1955) noted that eggs passed through the respiratory system and out via the feces. Anderson (1957) confirmed these observations experimentally. The female produces oval, smooth, thick-shelled eggs containing a fully developed first-stage juvenile (J_1). Eggs hatch in the gut of their intermediate hosts (grasshoppers and locusts). Their anterior end is surrounded by rows of spines and the tail tip is rounded and also encircled by a row of spines.

Superfamily Dracunculoidea

Dracunculoidea consist of Spiruridae species that occur in tissues and serous cavities mainly of fishes, reptiles, birds, mammals (Chabaud, 1975), and rarely amphibians (Petter and Planelles, 1986) (see the chapter by Choudhury for a more in-depth summary of the Dracunculoidea). According to Anderson (2000), after insemination, the female grows large numbers of first-stage juveniles (J_1). They must be dispersed into the environment where an available copepod may be colonized; these serve as intermediate hosts. In many species, the fully gravid female must be immersed in fresh water, which causes her to burst, thus releasing the juveniles into the environment. The female elicits a skin lesion or migrates into the rectum and protrudes from the body of the host. In some species, juveniles released within the host make their way to the tissues, including the blood. Most dracunculoids occur in hosts which have contact with fresh water.

Superfamily Filarioidea

Filarioidea contain parasites of the tissues and tissue spaces of all classes of vertebrates other than fishes (Anderson and Bain, 1976) (see the chapter by Notarnicola for a more in-depth summary of the Filarioidea). They are all transmitted by haematophagous arthropods. Members of the Filariidae family cause skin lesions and release eggs and/or juveniles in the host. They attract arthropod vectors, mainly individuals in the Muscidae family. The cephalic structures are rather simple. Pseudolabia are absent, but in some groups there may be cuticular elevations or spines. The cephalic papillae are well developed. The buccal cavity usually is considerably reduced. Spicules are variable in length and dissimilar in morphology (Anderson, 2000). Anderson (1957) suggests that the specialized life cycles of onchocercids evolved from those of the orbit-inhabiting *Thelazia* and the subcutaneous filariids (*Filaria* and *Parafilaria*). Other authors have suggested a relationship between some onchocercids and habronematoids like *Draschia* and *Habronema* (Chandler et al., 1941; Bain, 1981).

Superfamily Gnathostomatoidea

Gnathostomatoidea constitute spirurid nematodes characterized by massive, complex pseudolabia, and often spinous cephalic inflations (Chabaud, 1975). They are parasites in gastric mucosa of turtles in eastern North America (Hedrick, 1935). Some species of *Gnathostoma* have been well studied because of their significance to human and animal health. Members of the Gnathostomatoidea separate eggs in an undeveloped state, embryonate to second-stage juveniles (J_2), and hatch in water. Intermediate hosts are copepods or insects of various crustaceans other than copepods (Anderson, 2000).

Superfamily Habronematoidea

Habronematoidea are nematodes with typical head structures. The pseudolabia are not large and median lips are present (Chabaud, 1975). It includes economically important and well-studied groups such as the tetramerids (including *Tetrameres* spp.) of the proventriculus of birds and noted for their peculiar sexual dimorphism, as well as the habronematids (including *Habronema*, *Draschia,* and *Parabronema*) which are transmitted by adult muscid dipterans to horses, certain ruminants, poultry, and other draft animals. They are localized in the stomach of horses and certain ruminants, including camels and elephants. Females, which occur in small tumors in the stomach wall, deposit oval, thin-shelled eggs. The latter usually hatch in the stomach releasing small, poorly differentiated juveniles with an anterior spine-like tooth. Juveniles pass out with the feces of the host. The superfamily also includes aberrant genera such as *Hedruris* (Anderson, 2000). In the United States, Ransom (1913) first discovered that the juveniles of horses developed in juveniles of muscid flies inhabiting nearby dung.

Superfamily Physalopteroidea

Physalopteroidea are parasites in the stomach and intestines of vertebrates. The mouth is encircled by large triangular lips having 1 or more teeth. A buccal capsule is absent. Males include a caudal alae. They usually meet ventrally in front of the cloaca and are supported by at least 4 papillae. The spicules are equal, subequal, or unequal. The female genital atrium is near then anterior or posterior half of body near the anus (Cheng, 1973).

Superfamily Rictularioidea

Rictularioidea consist of many species divided into several genera and subgenera (Quentin, 1969; Chabaud, 1975). They have no pseudolabia and have a denticulate, hexagonal oral opening and a sizeable buccal cavity with teeth. The presence of numerous large body spines is also diagnostic. The eggs are oval, with smooth, thick shells and each contains a fully developed first-stage juvenile (J_1). Eggs hatch in the gut of the insect intermediate host. These worms are parasites in the lumen of the intestine or firmly attached to the mucosa (ileum and in the region immediately posterior to its junction with the Malpighian tubules (Seureau, 1973). Witenberg (1928) fed young dogs the viscera of reptiles in which he had found rictularioid juveniles. The juvenile provokes the formation of a syncytium of epithelial cells which becomes surrounded by a fibrous capsule, which lies between the circular muscles and the epithelium of the ileum (Seureau, 1973).

Superfamily Spiruroidea

Spiruroidea include thelazioids, gnathostomatoids, habronematoids, rictularioids and physalopteroids (Chitwood and Chitwood, 1950). According to Chabaud (1975) the removal and elevation to superfamily status of several groups reduced Spiruroidea to 4 small families.

Spirurids are parasites in the stomach. They hatch thick-shelled eggs containing a fully differentiated first-stage juvenile (J_1) having a cephalic hook and rows of minute spines around the rather blunt anterior end. The tail of the first-stage juvenile (J_1) is often blunt and surrounded by a circlet of minute spines. **Paratenesis** is a common phenomenon in the transmission of spiruroids and the third-stage juveniles (J_3) of several species have been found in tissues of a variety of vertebrates which ingest infected insects, such as dung beetles. Third-stage juveniles (J_3) are generally large and possess some of the cephalic characteristics of adults. Their caudal extremities in some species possess terminal spines or tubercles, but in other species the terminal end is rounded and unornamented at the caudal extremity (Anderson, 2000).

Superfamily Thelazioidea

Thelazioidea consist of families united mainly on the basis of cephalic structures (Chabaud, 1975). The members of Thelazioidea are ovoviviparous and oviparous eyeworms of birds and mammals and the rhabdochonids (*Rhabdochona*) of fishes and primates. Intermediate hosts are different species of muscids.

Some Phylogenies and Molecular Characters

Within Spirurida, the superfamilies Habronematoidea and Thelazioidea are well established groups. Representatives of Cystidicolidae and Rhabdochonidae are widespread and show great diversity, especially in North America, but their phylogenetic relationships remain largely unexplored (Choudhury and Nadler, 2018). Choudhury and Nadler (2018) suggest that Hedruridae appears to be an early branching line of the spirurids.

Wu and colleagues (2008) explored the intra- and interspecific evolutionary variation among species of *Camallanus* collected from different fish species in various regions of China. Phylogenetic analyses of the nematodes suggested that there are 2 main clades, corresponding to different individuals of *C. cotti* and *C. hypophthalmichthys* from different fish species in various geographical locations, although the interior nodes of each clade received poor support.

Černotíková and colleagues (2011) have worked out the phylogenetic relationships of 38 orders, including many among the Spirurida (namely, Camallanidae, Cystidicolidae, Daniconematidae, Philometridae, Physalopteridae, Rhabdochonidae, and Skrjabillanidae) and some among the Ascaridida. The nematode species the authors examined are mostly parasites of marine and freshwater fishes from various locations in New Caledonia, as well as various locations in Africa, Asia, North America, South America, and Europe. Well supported trees allowing the study of phylogenetic relationships among some spirurine nematodes support the placement of Cucullanidae at the base of the suborder Spirurina, but the validity of the genera *Afrophilometra* and *Caranginema* is not supported. It is apparent that geographical isolation is not the cause of speciation in this parasite group and there is no evidence of coevolution with fish hosts (Černotíková et al., 2011).

Classification History

The specialized parasitology literature establishes multiple data which indicate the necessity for and the conduct of taxonomic revisions concerning the order Spirurida. Following are details of taxonomy, type species, and distribution of representatives from the order that were proposed by Gibbons (2010). They differ somewhat from previous views, for instance Chabaud (1975), Anderson (2000), and others, and Hodda's (2022) more recent treatment. The information is presented in a quasi tabular form with nominally narrative descriptions of the groups. Authority names are included and are not truncated. Some groups included here are covered additionally in other chapters within this book.

Order Spirurida Chitwood 1933

The genus *Spiroptera* Rudolphi, 1819 was created by Rudolphi (1819) and originally contained 30 species. The genus has been synonymized in part with *Acuaria* Bremser, 1811 and *Spirura* Blanchard, 1819, and many species assigned to this genus now extend to few genera, such as *Acuaria* Bremser, 1811, *Cosmocephalus* Molin, 1858, *Chevreuxia* Seurat, 1918, *Echinuria* Soloviev, 1912, *Habronema* Diesing, 1861, *Schistorophus* Railliet, 1916, *Sciadiocara* Skrjabin, 1916, *Seuratia* Skrjabin, 1916, *Spirura* Blanchard, 1819, and *Synhimantus* Railliet, Henry and Sisoff, 1912 (Yorke and Maplestone, 1926). The genus listed in Jones and Gibson (1987) is no longer considered valid.

The suborder **Camallanina** Chitwood, 1936 are parasites of the stomach and intestines of lower predaceous vertebrates (Chabaud, 1975). According to Gibbons (2010), Camallanina included the following superfamilies, families, subfamilies, genera, and subgenera: Superfamily **Camallanoidea** Travassos, 1920, with family **Camallanidae** and subfamily **Camallaninae** Railliet and Henry, 1915 constituting the next genera, subgenera, and type species: ***Camallanus*** Railliet and Henry, 1915 (= *Zeylanema* Yeh, 1960) (which is the type genus). These are parasites of fishes and amphibians (Chabaud, 1975), reptiles (Baker, 1987), and estuarine and freshwater fishes (Ivashkin et al., 1971). It includes subgenus ***Zeylanema*** (Yeh, 1960) Moravec and Scholz, 1991. The type species is *Camallanus (Zeylanema) anabantis* Pearse, 1933, which are parasites that live in the intestine of the freshwater fish in the groups Anabantidae, Cyprinidae, Belontiidae, and Clariidae from India. ***Neocamallanus*** Ali, 1957, with type species *Neocamallanus singhi* Ali, 1957, are parasites that live in the intestinae of *Channa striata*, *Hampala dispar*, and *Xenetodon cancila* from Laos. ***Neoparacamallanus*** Bilqees and Akram, 1982, with the type species *Neoparacamallanus sweeti* (Moorthy, 1937) Bilqees and Akram, 1982, are parasites of freshwater fishes.

Another subfamily in Camallanidae is **Procamallaninae** Yeh, 1960. A list of the species in the subfamily has been presented by Petter (1979). The type genus is ***Procamallanus*** Baylis, 1923 and the type species is *Procamallanus laeviconchus* (Wedl, 1862) Railliet and Henry, 1915. They are parasites that live in the stomach and intestine of fishes and amphibians. The life cycle of *P. spiculogubernaculus*, a parasite of fishes, has been investigated by Sinha (1988). *Procamallanus* consist of several subgenera as follows: ***Denticamallanus*** Moravec and Thatcher, 1997, with type species *P. (Denticamallanus) dentatus* Moravec and Thatcher, 1997 are parasites that live in the intestine of characid fish *Bryconops alhurnoides,* from the Uburu River, Amazonas State, Brazil. ***Isospiculus*** Ali, 1957, including *P.* (*Spirocamallanus*) *hilarii* Vaz & Pereira, parasites that live in the intestines of *Acestrorhynchus microlepis* (unspecified), *Astyanax bimaculatus* (adult), *A. fasciatus* (adult), *A. parahybae* (adult), *Hoplias lacerdae* (adult), *H. malabaricus* (adult), *Oligosarcus macrolepis* (adult), *Rhamdia quelen* (adult), *Salminus hilarii* (adult), *Steindachnerina elegans* (adult and juvenile), *Trichomycterus piurae* (unspecified), all from Brazil (Luque et al., 2011). Moravec and colleagues (2003) redescribed *P.* (*S.*) *fulvidraconis* from central China. ***Monospiculus*** Ali, 1957 is a genus with no designated type species. *?Procamallanus (Monospiculus) parasiluri* Fujita, 1927. ***Procamallanus*** (Baylis, 1923 genus) Ali, 1957 with no type species yet proven. *?Procamallanus (Procamallanus) laeviconchus* Baylis, 1923 is a spirurid species and are common parasites of African freshwater fishes. ***Punctocamallanus*** Moravec and Scholz, 1991, with type species *P. (Punctocamallanus) punctatus* Moravec and Scholz, 1991 are parasites that live in the stomach of freshwater fishes in Laos. ***Spirocamallanoides*** Moravec and Sey, 1988 have as a type species *P. (Spirocamallanoides) siluri* Osmanov, 1964. ***Spirocamallanus*** (Olsen, 1952 genus) Moravec and Sey, 1988, with type species *P. (Spirocamallanus) spiralis* (Baylis, 1923), are parasites that live in the intestine of fishes and amphibians. Other genera in the Procamallaninae are: ***Batrachocamallanus*** Jackson and Tinsley, 1995, with type species *Batrachocamallanus xenopodis* (Baylis, 1929) Jackson and Tinsley, 1995, are parasites of African amphibians, *Xenopus* spp. (Jackson and Tinsley, 1995). ***Malayocamallanus*** Jothy and Fernando, 1970, with type species *Malayocamallanus intermedius* Jothy and Fernando, 1970, are parasites in *Fluta alba,* in Malaysia (Jothy and Fernando, 1970). ***Onchocamallanus*** Petter, 1979 is a genus with type species *O. bagarii* (Karve and Naik, 1951) Petter, 1979. They are parasites that live in India in the intestine of *Bagarius bagarius* with an intermediate host of cyclopoid copepods *Mesocyclops leuckarti* and *M. crassus* (De and Maity, 1999). ***Platocamallanus*** Bilqees and Akram, 1982 with type species *P. mehrii* (Agrawal, 1930) Bilqees and Akram, 1982 are parasites of freshwater fishes.

Another subfamily in Camallanidae is **Paracamallaninae** Stromberg and Crites, 1974. Type genus is ***Paracamallanus*** Yorke and Maplestone, 1928 containing the subgenus ***Dentocamallanus*** Moravec and Scholz, 1991 with type species *P.* (*Dentocamallanus*) *sweeti* (Moorthy, 1937), which are parasites that live in teeth on the ribs of the buccal capsule of fishes.

Dracunculoidea is another superfamily in Camallanina. Representatives of this superfamily are parasites in tissues and serous cavities mainly of fishes, reptiles, birds, mammals (Chabaud, 1975), and sometimes in amphibians (Petter and Planelles, 1986). Intermediate hosts are copepods (Anderson, 2000). Dracunculoidea includes the genus ***Lockenloia*** Adamson and Caira, 1991, which is not assigned to a family, consists of parasites that live in the heart of sharks (*Ginglymostoma cirratum*), with type species *Lockenloia sanguineus* Adamson and Caira, 1991. According to Gibbons (2010), Dracunculoidea includes several families, subfamilies, genera, and subgenera, such as: **Dracunculidae** (Stiles, 1907 subfamily) Leiper, 1912 which are parasites of reptiles, birds, and mammals. The family includes several families, subfamilies, genera, and species, which, according to Gibbons (2010) are: ***Fuellebornius*** Leiper, 1926 with type species *F. medinensis* (Linnaeus, 1758) Leiper, 1926, which is a parasite of humans affecting the subcutaneous connective tissues, which then move to the surface of the skin, and provoke the formation of a blister, which bursts, causing the anterior end of the worm to be exposed.

Another family in Dracunculoidea is **Anguillicolidae** Yamaguti, 1935 which are parasites that live in the swimbladder of eels (Laetsch et al., 2012). This family has assigned to it the genus ***Anguillicola*** Yamaguti, 1935 with the subgenus ***Anguillicola*** (Yamaguti, 1935) Moravec and Taraschewski, 1988. The type species is *A. (Anguillicola) globiceps* Yamaguti, 1935. The final hosts are eels of the genus *Anguilla* and the intermediate hosts are planktonic copepods. Another genus in Anguillicolidae is ***Anguillicoloides*** Moravec and Taraschewski, 1988 (Moravec and Taraschewski, 1988) with type species *A. crassus* (Kuwahara, Niimi and Itagaki, 1974) Moravec and Taraschewski, 1988, which are parasites of the swimbladder of eels.

Another family in Dracunculoidea is **Skrjabillanidae** Shigin and Shigina, 1958. They are parasites generally that live in the peritoneal cavity of freshwater fishes. The occurrence of these nematodes in their final and intermediate host (*Argulus foliaceus*) in Hungary has been observed by Molnár and Szekely (1998). This family contains the subfamily **Skrjabillaninae** (Shigin and Shigina, 1958 family) Chabaud, 1965 with several genera, listed in the paragraphs below.

Kalmanmolnaria Sokolov, 2006 (= *Molnaria* Moravec, 1968) are parasites in the subcutaneous tissues of freshwater fishes (*Scardinius erythrophthalmus*) from Lake Balaton, Kis-Balaton, Fish Farms in Hungary. According to Anderson (2000), parasites of this genus can be found also in the serosa of the swimbladder, kidneys, and intestine, as well as on the mesentery of *S. erythrophthalmus* in CIS. Intermediate hosts are crustaceans.

Sinoichthyonema Wu, 1965 is a genus with type species *S. amuri* (Garkavi, 1972) Moravec, 1982. According to Zhokhov and Molodozhnikova (2008) *S. amuri* have been introduced into the Volga basin (Russia) occasionally during the process of introduction of fishes from the Amur River. This species has been also registered in Hungary by Molnár (1989). The systematic status of *S. itenopharyngodoni* Wu, 1973 was put forward by Moravež (1982), including determining that this species is identical to *S. amuri*. Final hosts are *Rutilus rutilus* and *Scardinius erythrophthalmus*.

Garkavillanus Lomakin and Chernova, 1980 is a genus whose type species is *Garkavillanus amuri* (Garkavi, 1972) Lomakin and Chernova, 1980.

Another subfamily in Skrjabillanidae is **Esocineminae** Moravec, 2006 with type and only genus ***Esocinema*** Moravec, 1977 and with the type species *Esocinema bohemicum* Moravec, 1977, parasites that live under the serosa of the air bladder of pike *Esox lucius* in North Bohemia, Czechia.

Another family in Dracunculoidea is **Guyanemidae** Petter, 1975, which includes parasites that live in the peritoneal cavity and tissues of fish. This family includes the subfamilies, genera, and subgenera that are listed in the following paragraphs.

Several of the genera that are included in the subfamily **Guyaneminae** Petter, 1975 (Petter, 1975) include: ***Pseudodelphis*** Adamson and Roth, 1990, with the type species *P. oligocotti* Adamson and Roth, 1990. They are parasites that live in the peritoneal cavity and mesenteries surrounding the intestine of a marine fish species, *Oligocottus maculosus*, in coastal waters of British Columbia, Canada. Another genus is ***Histodytes*** Aragort et al., 2002, with the type species *H. microocellatus* Aragort et al., 2002, which are parasites in the gill, heart, kidney, spleen, and gonad tissues of the elasmobranch *Raja microocellata*. It was described based on material obtained from specimens from the continental shelf of the estuary of Muros y Noia, Spain (off the northwestern costs of the Iberian Peninsula) and is the only guyanemid genus described since the first was found on the European Atlantic coast (Aragort et al., 2002). ***Moravecia*** Ribu and Lester, 2004 are parasites that live in the gill filaments of green porcupine fish or may be found in the blood vessels and body cavity, with the type species *M. australiensis* Ribu and Lester, 2004. This genus was described based on materials obtained from *Tragulichthys jaculiferus* found in Moreton Bay, Queensland, Australia (Ribu and Lester, 2004). Another species of this genus is *Moravecia argentinensis* which was described by Braicovich and colleagues (2007) and are found in the blood vessels and body cavity of the Brazilian flathead, *Percophis brasiliensis*. This is the first species of the genus reported from South American waters.

Another subfamily in Guyanemidae is **Travassosneminae** Moravec, 2006 which according to Gibbons (2010) includes only 1 genus, ***Travassosnema*** De Araujo Costa, Mareira and De Oliveira, 1991, which has the type species *T. travassosi* De Araujo Costa, Moreira and De Oliveira, 1991. They are viviparous parasites that live in tissues behind the eyes of *Acestrorhynchus lacustris*, which may be found in the Tres Marias Reservoir, Mina Gerais State, Brazil. A subspecies, *T. t. paranaensis*, lives in the body cavity of the characid fish *Acestrorhynchus lacustris* from the Paraná River near Guaira in southern Brazil (Moravež et al., 1993; Silva-Souza and Saraiva, 2002).

Another family of Dracunculoidea is **Philometridae** Baylis and Daubney, 1926, and includes the genus ***Afrophilometra*** Moravec, Charo-Karisa and Jirku, 2009. The type species is *A. hydrocyoni* (Fahmy, Mandour and El-Nafar, 1976) Moravec, Charo-Karisa and Jirku, 2009. The genus also includes species which parasitize *Hydrocynus forskahlii* from Lake Turkana, northwestern Kenya (Moravež et al., 2009).

The subfamily **Philometrinae** (Baylis and Daubney, 1926) within the Philometridae includes the following genera: ***Icthyonema*** Diesing, 1861, with a type species that is not clearly determined, but it may be *I. fuscum* Diesing, 1861, parasites of the body cavity of marine fish (Gibbons, 2010). It also contains the genus ***Paraphilometroides*** Moravec and Shaharom-Harrison, 1989, with the type species *Paraphilometroides nemipteri* Moravec and Shaharom-Harrison, 1989. They are parasites found in the dorsal fin and operculum of the marine perciform fish *Nemipterus peronii,* from the coastal waters off Kuala Terengganu, Malaysia (Gibbons, 2010). Moravež (2010) has imaged a gravid female of a paratype specimen of *P. nemipteri* using scanning electron microscopy after which he observed a unique cephalic structure, which clearly distinguishes *Paraphilometroides* from other philometrids. Another genus is ***Margolisianum*** Blaylock and Overstreet, 1999, with the type species *M. bulbosum* Blaylock and Overstreet, 1999, which are found in the southern flounder *Paralichthys lethostigma* from Ocean Springs, Mississippi Sound, Mississippi, United States, and Galveston Bay, Texas, United States. During their maturation, these spirurids have a different localization. Immature females are parasites of the eye, while mature and gravid females can be found in the subcutaneous tissues of the mouth and head, and males may be found in the muscle adjacent to the dorsal fin just posterior to the head (Gibbons, 2010). Another genus is ***Dentiphilometra*** Moravec and Gui Tang Wang, 2002, with the type species *D. monopteri* Moravec and Gui Tang Wang, 2002. These are parasites found in the abdominal cavity of the ricefield eel, *Monopterus albus*, from Hubei Province in central China. This is the second philometrid species recorded from fishes of the Synbranchiformes (Moraveč and Wang, 2002). Another genus is ***Caranginema*** Moravec, Montoya-Mendoza and Salgado-Maldonado, 2008, with the type species *C. americanum* Moravec, Montoya-Mendoza and Salgado-Maldonado, 2008, which are parasites found in the subcutaneous tissue of the crevalle jack *Caranx hippos* from southern Gulf of Mexico. This is the seventh species of Philometrinae recorded from marine and brackish water fishes in Mexico (Moraveč et al., 2008).

Another subfamily in Philometridae is **Alineminae** Moravec, 2006, with the type genus ***Alinema*** Rasheed, 1963 (Gibbons, 2010).

Another subfamily in Philometridae is **Neophilometroidinae** Moravec, Salgado-Maldonado and Aguilar-Aguilar, 2002, with the type genus ***Neophilometroides*** Moravec, Salgado-Maldonado and Aguilar-Aguilar, 2002, whose type species is *N. caudatus* (Moravec, Schulz and Vivas-Rodriguez, 1995) Moravec, Salgado-Maldonado and Aguilar-Aguilar, 2002. These are parasites that live in the swimbladder of Neotropical freshwater catfish and the pimelodid catfish, *Rhamdia guatemalensis* from the Papaloapan River in Tlacotalpan, State of Veracruz, Mexico (Moraveč et al., 2002).

Another subfamily in Philometridae is **Phlyctainophorinae** (Roman, 1965) (Gibbons, 2010), including the genus ***Phlyctainophora*** Steiner, 1921. The type species is *P. lamnae* Steiner, 1921, which are parasites that live in the subcutaneous tissue of *Lamna nasus* from the North Atlantic Ocean. Jones and Delahunt (1995) found the same parasite species in tumor-like lesions on the tail fin and which provoke a chronic inflammatory response in the host, the dogfish *Squalus acanthias*. This is the first record for a member of the genus established in New Zealand and the first record of *Phlyctainophora* adults from the Southern Hemisphere. Another species in this genus is *P. squali*. Dwight, and Murrady, 1969 obtained from *Squalls acanthias* in eastern Pacific Ocean off Los Angeles, California, United States, at a depth of 200 m (Dwight and Murrady, 1969).

The family **Micropleuridae** (Baylis and Daubney, 1926) Travassos, 1960 in Dracunculoidea includes the subfamily **Micropleurinae** Baylis and Daubney, 1926, which are parasites found in fish, amphibians, and reptiles, and includes the following genera (Gibbons, 2010): ***Protenema*** Petter and Planelles, 1986, with the type species *P. longispicula* Petter and Planelles, 1986, which are parasites in the amphibians, *Necturus maculosus* (Proteidae), found in the lakes of Minnesota, United States. ***Granulinema*** Moravec and Little, 1988 with type species *G. carcharini* Moravec and Little, 1988, which are parasites of the bull shark, *Carcharhinus leucas,* found in Lake Borgne, Louisiana, United States. The site of localization in the host is unknown (probably the abdominal cavity). Another species in this genus is *G. simile* Moravec and Little, 1988, for which its localization is also unknown (Moraveč and Little, 1988). ***Kamegainema*** Hasegawa, Doi, Araki and Miyata, 2000, with the type species *K. cingulum* (Linstow, 1902) Hasegawa, Doi, Araki and Miyata, 2000, which are parasites that live in the subcutaneous tissue of amphibians (Hasegawa et al., 2000).

Another family in Dracunculoidea is **Daniconematidae** Moravec and Køie, 1987, which includes viviparous parasites of fish. The type genus is ***Daniconema*** Moravec and Køie, 1987 with the type species *D. anguillae* Moravec and Køie, 1987, which are parasites that live under the serosa of the swimbladder and intestine of eels, *Anguilla anguilla,* found in Lake Esrum, northern Zealand, Denmark. A new family Daniconematidae was established to accommodate it (Moraveč and Køie, 1987). According to Gibbons (2010), another genus in Daniconematidae is ***Mexiconema*** Moravec, Vidal and Salgado-Maldonado, 1992. The type species of this genus is *M. cichlasomae* Moravec, Vidal and Salgado-Maldonado, 1992, parasites that live in the abdominal cavity or viscera, or (rarely) the skin of cichlids, *Cichlasoma* spp., in the coastal lagoons of Celestun, North Yucatán, Mexico. They are parasites that live in the mesentery, swimbladder, liver, spleen, kidney, intestinal lumen, serosal cover of the intestine, or (rarely) in the skin of *Cichlasoma* spp. and other hosts, such as *C. helleri, C. motaguense*, and *C. pearsei* (Moravec, Vidal and Maldonado, 1992). Other habitats in Campeche, Mexico are El Vapor (a freshwater lagoon adjacent to Terminos Lagoon), Palizada, Santa Gertrudis, El Cayo (a saltwater portion within Terminos Lagoon), Pargos, and Rio Champoton. Habitats in Quintana Roo, Mexico include Rio Lagartos (a coastal lagoon) and Noh Beк (a lake). El Vapor, Palizada, Santa Gertrudis, Rio Lagartos, and Noh Beк are truly freshwater localities; all the remaining sites are saltwater or marine localities (Moraveč et al., 1992). Another genus is ***Syngnathinema*** Moravec, Spangenberg and Frasca, 2001. The type species for this genus is *S. californiense* Moravec, Spangenberg and Frasca, 2001, which are parasites that live in the vascular system of the Bay pipefish, *Syngnathus leptorhynchus,* in California, United States. Based on histological studies, the parasites have been found also in other locations, such as in the circulatory system including the sinus venosus, atrium, and renal and hepatic veins.

Another family in Dracunculoidea is **Lucionematidae** Moravec, Molnar and Szekely, 1998, which are viviparous parasites of fish, with the type genus ***Lucionema*** Moravec, Molnar and Szekely, 1998, and with the type species *L. balatonense* Moravec, Molnar and Szekely, 1998. These are parasites that live in the swimbladder of the European pikeperch, *Stizostedion lucioperca* from Lake Balaton in Hungary (Moraveč et al., 1998).

Suborder Spirurina

Moraveč (2007) reviewed the spirurines of fish belonging to approximately 300 species in 4 superfamilies, namely Gnathostomatoidea, Habronematoidea, Physalopteroidea, and Thelazioidea. He has suggested that the classification and taxonomy of species of this suborder in fish requires reevaluation using new techniques, such as scanning electron microscopy and molecular biology (Moraveč, 2007).

In the superfamily **Acuarioidea**, Gibbons (2010) listed 1 family, namely, **Acuariidae** (Railliet, Henry and Sisoff, 1912), with 2 subfamilies: **Acuariinae** and **Schistorophinae**. Also according to Gibbons (2010), **Acquariidae** consists of 3 genera, namely: ***Deliria*** Vicente, Pinto and Noronha, 1980, parasites that live in the stomach of birds. *Pitangus sulphuratus* is found in Rio de Janeiro State, Brazil, of which the type species is *D. gomesae* Vincente, Pinto and Noronha, 1980. ***Paracuaria*** Rao, 1951 are parasites that live in the submucosa of crop in seabirds or the stomach of insectivorous mammals, with the type species being *Pa. adutica* (Creplin, 1946). ***Pseudoaviculariella*** Gupta and Kazim, 1978, are parasites that live in the gizzard of the cattle egret *Egretta garzetta* from Lucknow, India, with the type species *Ps. srivastavai* Gupta and Kazim, 1978. The family Acuariidae consists of 2 subfamilies. One is the **Acuariinae** Railliet, Henry and Sisoff, 1912, which includes the following 10 genera:

1) ***Antechiniella*** Quentin and Beveridge, 1986, parasites that live in Australian marsupials with the type species *A. suffodiax* (Beveridge and Barker, 1975) Quentin and Beveridge, 1986
2) ***Chandleronema*** Little and Ali, 1980, parasites that live in the stomach of raccoons, *Procyon lotor,* and muskrats from the United States and include the type species *C. longigutturata* (Chandler, 1942) Little and Ali, 1980
3) ***Cordonema*** Schmidt and Kuntz, 1972, parasites of birds with the type species *C. venusta* Schmidt and Kuntz, 1972
4) ***Molinacuaria*** Wong and Lankester, 1985, parasites that live under the gizzard lining of birds of the species *Dendragapus obscurus fuliginosus*, *Gallinula chloropus indica*, and *Alcippe brunnea brunnea* from Vancouver Island (Canada), China, and Taiwan, respectively. The type species is *M. bendelli* (Adams and Gibson, 1969) Wong and Lankester, 1985
5) ***Syncuaria*** Gilbert, 1927, parasites that live in the gizzard of birds (grebe, storks, and cormorants) with the type species *S. ciconiae* Gilbert, 1927
6) ***Tikusnema*** Hasegawa, Shiraishi and Rochman, 1992, parasites that live in the stomach and small intestine of the ricefield rat, *Rattus argentiventer,* in Indonesia, with the type species *T. javaense* Hasegawa, Shiraishi and Rochman, 1992
7) ***Voguracuaria*** Wong and Anderson, 1993, parasites that live in the esophagus of the whimbrel *Numenius phaeopus phaeopus* in Vogur, Iceland, with the type species *V. lankesteri* Wong and Anderson, 1993
8) ***Voguracuaria*** Wong and Anderson, 1993, parasites that live in the esophagus of the whimbrel, *Numenius phaeopus phaeopus,* in Vogur, Iceland, with the type species *V. lankesteri* Wong and Anderson, 1993
9) ***Willmottia*** Mawson, 1982, parasites of birds, *Malurus cyaneus*, from Tasmania, with the type species *W. australis* Mawson, 1982
10) ***Xenocordott*** Mawson, 1982, parasites that live in the gizzard of Australian birds, *Phylidonyris novaehollandiae* and *Gymnorhina tibicen*, with the type species *X. patonae* Mawson, 1982

The subfamily in Acquariidae is **Schistorophinae** Travassos, 1918, which according to Gibbons (2010) consists of 3 genera as follows: ***Quasithelazia*** Maplestone, 1932, ***Schistogendra*** Chabaud and Rousselot, 1956, and ***Soboleviceph-alus*** Parukhin, 1964, parasites that live under the gizzard of birds, with the type species *So. chalycyonis* Parukhin, 1964. This genus was listed by Anderson and colleagues (2009) as synonym of *Hadjelia* Seurat, 1916.

The superfamily **Filarioidea**, according to Gibbons (2010), contains the genus ***Avifilaris*** Saunders, 1955, parasites that live in the blood of *Rhodothraupis, Passerina, Pitangus*, and *Empidonax*, with the type species *A. fringillidarum* Saunders, 1955. The family **Filariidae** (Weinland,

1858) Cobbold, 1879 represents a collective group for agamic forms named "***Agamofilaria***" Stiles, 1907. According to Gibbons (2010), Filariidae include a subfamily (**Filariinae** Weinland, 1858) and several genera, including: ***Cystofilaria*** Skrjabin and Shikhobalova, 1948, of which the adults may be found in cysts under the muscular layer of the esophagus in dogs and for which the type species is *C. balkanica* Skrjabin and Schikhobalova, 1948. ***Paracanthocheilonema*** Vladimirov, 1959 in Buliginskaya, Vladimirov and Markov, 1959 are parasites in *Rhombomys opimus, Meriones meridianus*, and *M. erytbrourus* found in the Kashkadarinsk region of Uzbekistan and whose type species is *P. vite* (Krepkogorskaya, 1933) Vladimirov, 1959 in Buliginskaya, Vladimirov and Markov, 1959.

Another family in the Filarioidea is family **Onchocercidae** (Leiper, 1911) which contains the subfamily **Onchocercinae** Leiper, 1911 and several genera (Gibbons, 2010), as follows: ***Bisbalia*** Bain and Guerrero, 2003, which are parasites found in the membranous pocket in the pleural cavity of *Heteromys anomalus* (Rodentia: Geomyoidea) in northern Venezuela and whose type species is *B. vossi* Bain and Guerrero, 2003. ***Cherylia*** Bain, Petit, Jacquet-Viallet and Houin, 1985, parasites of the ventral subcutaneous and perimuscular tissues of the South American marsupial, *Metachirops opossum,* found in French Guiana with the type species *Cherylia guyanensis* Bain, Petit, Jacques-Viallet and Houin, 1985. ***Cercopithifilaria*** (Eberhard, 1980 subgenus), parasites found in primates, ruminants, carnivores, marsupials, and monotremes. *Cercopithifilaria* are transmitted by ticks and the type species is *Cercopithifilaria kenyensis* Eberhard, 1980. ***Chabfilaria*** Bain, Purnomo and Dedet, 1983, parasites of Xenarthra in French Guiana and Guyana, with the type species *Chabfilaria jonathani* Bain, Purnomo and Dedet, 1983. ***Cruorifilaria*** Eberhard, Morales and Orihel, 1976, parasites that live in the renal and pulmonary blood vessels, and (rarely) the coronary vessels of the capybara *Hydrochoerus hydrochaeris* in Colombia with the type species *Cruorifilaria tuberocauda* Eberhard, Morales and Orihel, 1976. ***Dasypafilaria*** (Eberhard, 1982 subgenus), parasites that live in the omentum of Dasypodidae (including the 9-banded armadillo *Dasypus novemcinctus*) found in southern Louisiana, United States, with the type species *Dasypafilaria averyi* Eberhard, 1982. ***Josefilaria*** Moorhouse, Bain and Wolf, 1979, parasites of the ghost bat *Macroderma gigas* found in Australia, with the type species *Josefilaria mackerrasae* Moorhouse, Bain and Wolf, 1979. ***Loxodontofilaria*** Berghe and Gillain, 1939, parasites of elephants in Africa and Burma, Caprinae and Bovidae in Japan, and hippopotamus in Africa, with the type species *Loxodontofilaria loxodontis* Berghe and Gillain, 1939. ***Mansonella*** Faust, 1929, parasites that develop in the subcutaneous tissues of their hosts, and may be found in the Caribbean region, Central America, South America, and Africa, with the type species *Mansonella ozzardi* (Manson, 1897) Faust, 1929. According to Gibbons (2010), there are 6 subgenera as follows ***Cutifilaria*** (Bain and Schulz-Key, 1974 genus) Uni, Bain and Takaoka, 2004, parasites in Cervidae in Europe and Japan, with the type species *Mansonella (Cutifilaria) wenki* (Bain and Schulz-Key, 1974). ***Esslingeria*** (Chabaud and Bain, 1976) Eberhard and Orihel, 1984, parasites of humans, African anthropoid apes, and South American rodents, with the type species *Mansonella (Esslingeria) perstans* (Manson, 1891) Eberhard and Orihel, 1984. ***Mansonella*** (Faust, 1929) Eberhard and Orihel, 1984, parasites of humans, rodents, and carnivores, with the type species *Mansonella (Mansonella) ozzardi* (Manson, 1897) Faust, 1929. ***Sandnema*** (Chabaud and Bain, 1976) Eberhard and Orihel, 1984, parasites of Asian primates and insectivores, with the type species *Mansonella (Sandnema) digitata* (Chandler, 1929) Eberhard and Orihel, 1984. ***Tetrapetalonema*** (Faust, 1935) Eberhard and Orihel, 1984, parasites of platyrrhine primates, with the type species *Mansonella (Tetrapetalonema) marmosetae* (Faust, 1935) Eberhard and Orihel, 1984. ***Tupainema*** Eberhard and Orihel, 1984, parasites of tree shrews in Southeast Asia, with the type species *Mansonella (Tupainema) dunni* (Mullin and Orihel, 1972) Eberhard and Orihel, 1984. Other onchocercid genera according to the author are: ***Molossinema*** Georgi, Georgi, Jiang and Frongillo, 1987, parasites of the cerebral ventricular system of the bat *Molossus ater* in Trinidad, with the type species *Molossinema wimsatti* Georgi, Georgi, Jiang and Frongillo, 1987. ***Strianema*** Eberhard, Orihel and Campo-Aasen, 1993, parasites that live in the subcutaneous tissues of Venezuelan armadillos, *Dasypus* spp., with the type species *Strianema venezuelensis* Eberhard, Orihel and Campo-Aasen, 1993. ***Struthiofilaria*** Noda and Nagata, 1976, parasites which live in the body cavity of the ostrich *Sruthio camelus* found in in Misaki Park Zoo, Osaka Prefecture, Japan, with the type species *Struthiofilaria megalocephala* Noda and Nagata, 1976. ***Yatesia*** Bain, Baker and Chabaud, 1982, parasites that live in the skeletal muscle fascia of capybara *Hydrochoerus hydrochaeris* in Colombia, with the type species *Yatesia hydrochoerus* (Yates, 1980) Bain, Baker and Chabaud, 1982. Another subfamily within the Onchocercidae is **Waltonellinae** Bain and Prod'hon, 1974. According to Gibbons (2010) this subfamily includes several genera, as follows: ***Edesonfilaria*** Yeh, 1960. One of the species in this genus is *E. malayensis* which live in the subserosal connective tissues of the abdominal and thoracic cavities of cynomolgus monkeys (*Macaca fascicularis*) from Indonesia (Nonoyama et al. (1984). ***Foleyella*** Seurat, 1917, parasites that live in the subcutaneous and intermuscular connective tissues and body cavities in chameleonid reptiles, with the type species *Foleyella candezei* (Fraipont, 1882) Seurat, 1917. ***Foleyellides*** Caballero, 1935, parasites of anuran amphibians, mainly Ranidae, with the type species *Foleyellides striatus* (Ochoterena and Caballero, 1932) Caballero, 1935. ***Loaina*** Eberhard and Orihel, 1984, parasites of North American rabbits, with the type species *Loaina uniformis* (Price, 1957) Eberhard and Orihel, 1984. ***Ochoterenella*** Caballero, 1944, parasites that live in the body cavity of anuran amphibians, mainly Neotropical Bufonidae, with the type species *Ochoterenella digiticauda* Caballero, 1944. ***Paramadochotera*** Esslinger, 1986, parasites of *Mantidactylus redimitus,* a racophorid frog in Madagascar, with the type species *Paramadochotera guibei* (Bain and Prod'hon, 1974) Esslinger, 1986 Dirofilariinae Sandground, 1921. ***Pelecitus*** Railliet and Henry, 1910, parasites that live in the tendons, muscles, and (rarely) wings of birds and mammals, with the type species *Pelecitus helicinus* (Molin, 1860).

Another subfamily in Onchocercidae is **Splendidofilariinae** Chabaud and Choquet, 1953 which, according to Gibbons (2010), includes the following genera: ***Splendidofilaria*** Skrjabin, 1923, with 4 subgenera, as follows: ***Amfilaria*** Lopez Caballero and Jimenez Millan, 1979, with the type species *Splendidofilaria (Avifilaria) mavis* (Leiper, 1909) Anderson, 1961. ***Arteriofilaria*** Lopez Caballero and Jimenez Millan, 1979, with the type species *Splendidofilaria* (*Arteriofilaria*) *algonquinensis* (Anderson, 1955) Anderson, 1961. ***Soninella*** Lopez Caballero and Jimenez Millan, 1979, with the type species *Splendidofilaria* (*Soninella*) verrucosa Oschmarin, 1950 and ***Splendidofilaria*** (Skrjabin, 1923 genus) Lopez Caballero and Jimenez Millan, 1979, with the type species *Splendidofilaria* (*Splendidofilaria*) *pawloski* Skrjabin, 1923. Other genera in the Splendidofilariinae are: ***Andersonfilaria*** Bartlett and Bain, 1987, parasites that live in the fossa of the dorsal wall of the pelvic girdle of the common waxbill *Estrilda astrild* (Passeriformes) in Africa, with the type species *Andersonfilaria africanus* Bartlett and Bain, 1987. ***Dessetfilaria*** Bartlett and Bain, 1987, parasites that live in the capsule of the outer wall of the aorta in the heart of toucans in French Guiana and Brazil, with the type species *Dessetfilaria guianensis* Bartlett and Bain, 1987. ***Rumenfilaria*** Lankester and Snider, 1982, parasites in the subserosal connective tissue between the folds of the ruminal wall of moose *Alces alces* from northwestern Ontario, Canada, with the type species *Rumenfilaria andersoni* Lankester and Snider, 1982. ***Serofilaria*** Wu and Yun, 1979 (in Wu et al., 1979), parasites that live in the lymphatic vessels of the serous membrane covering the internal organs of pigs in China, with the type species *Serofilaria suis* Wu and Yun, 1979 (in Wu et al*.,* 1979). ***Splendidofilarioides*** Texeira de Freitas and Nicanor Ibafiez, 1968, parasites of the birds *Mimus longicaudatus* in Peru, with the type species *Splendidofilarioides pachacuteci* Texeira de Freitas and Nicanor Ibanez, 1968. ***Eulimdana*** Founikoff, 1934, parasites of birds, with the type species *Eulimdana clava* (Wedl, 1856). The last subfamily in Onchocercidae is **Lemdaninae** Lopez-Neyra, 1956q, which contains 2 genera, namely, ***Lemdana*** Seurat, 1917, parasites that live in the subcutaneous connective tissue of the head, neck in the vicinity of the trachea, the esophagus, and crop of birds, with the type species *Lemdana marthae* Seurat, 1917. ***Makifilaria*** Krishnasamy, Singh and Iyamperumal, 1981, parasites that live in the peritoneal cavity of the island flying fox *Pteropus hypomelanus* found in Pulau Langkawi, Malaysia, with the type species *Makifilaria inderi* Krishnasamy, Singh and Iyamperumal, 1981.

In the superfamily **Aproctoidea**, Gibbons (2010) listed the following taxa: The family **Aproctidae** (Yorke and Maplestone, 1926 subfamily) Skrjabin and Shikhobalova, 1945, with 1 genus, ***Hovorkonema*** Jurasek, 1977, parasites that live in the stomach of the Carpathian wild boar *Sus scrofa atilla* in Lucenec, Slovakia, with the type species *Hovorkonema gastrofilana* Jurasek, 1977. The subfamily **Aproctinae** Yorke and Maplestone, 1926, with the genus ***Desmidocercella*** Yorke and Maplestone, 1926 and the type species *Desmidocercella (Desmidocercella) numidica* (Seurat, 1920), including the subgenus ***Skrjabinocercella*** Gushanskaya, 1953, with the type species *Desmidocercella (Skrjabinocercella) incognita* Solonitzin, 1932. Furthermore, Gibbons (2010) listed in Aproctidae 4 other genera, as follows: ***Lissonema*** Linstow, 1903, parasites that live in the abdominal cavity of *Otus sunia* from eastern Asia, with the type species *Lissonema rotunda* Linstow 1903. ***Parasaurositus*** Gupta and Johri, 1989, parasites that live in the intrahepatic spaces of the Indian soft shell turtle *Aspideretes gangeticus* found in India, with the type species *Parasaurositus yamagutii* Gupta and Johri, 1989. ***Pseudodiomedenema*** Gupta and Johri, 1988, parasites of the pleural cavity of hoopoe *Upupa epops* found in Lucknow, India, with the type species *Pseudodiomedenema cameroni* Gupta and Johri, 1988 and ***Squatnoftlaria*** Schmerling, 1925.

According to Gibbons (2010), the superfamily **Diplotriaenoidea** includes the family **Diplotriaenidae** (Skjrabin, 1916 subfamily) Anderson, 1958 and the superfamily **Diplotriaeninae** Skrjabin, 1916, with 2 genera, namely: ***Spinodiplotriaena*** Kalyankar and Pallawadar, 1989, parasites that live in the body cavity of the common mynah bird. *Acridotheres tristis* in India, with the type species *Spinodiplotriaena urmilii* Kalyankar and Pallawadar, 1989. ***Versternema*** Bain, Chabaud and Burger, 1992, parasites that live in the body cavity of the ostrich *Struthio camelus* in Botswana, with the type species *Vesternema struthionis* Bain, Chabaud and Burger, 1992.

According to Gibbons (2010), the superfamily **Gnatohostomatoidea** comprises the family **Gnathostomatidae** Railliet, 1895, and the subfamily **Ancyracanthinae** Yorke and Maplestone, 1926, with 2 genera, namely: ***Elaphocephalus*** Molin, 1860, parasites that live in the feet of birds *Psittacus macao* with the type species *Elaphocephalus octocornutus* Molin, 1860. The other genus is ***Metaleptus*** Machida, Ogawa and Okiyama, 1982. *Metaleptus rabuka*, parasites that live in the stomach of *Mustelus griseus*, and *M. manazo*, which have been recorded by Moravec and Nagasawa (2000) in the north Pacific Ocean off Honshu, Japan.

In the superfamily **Habronematoidea**, Gibbons (2010) lists the family **Habronematidae** (Chitwood and Wehr, 1932 subfamily) Ivaschkin, 1961, the subfamily **Habronematinae** Chitwood and Wehr, 1932, and the genus ***Dermofilaria*** Rivolta, 1884, parasites of equids and bovines, with the type species *Dermofilaria irritans* Rivolta, 1884. Furthermore, Habronematidae includes the subfamily **Histiocephalinae** Gendre, 1922, with the genus ***Sobolevicephalus*** Parukhin, 1964 having as the type species *Sobolevicephalus chalcyonis* Parukhin, 1964. It also includes the family **Tetrameridae** Travassos, 1914, with the subfamily **Tetramerinae** (Travassos, 1914), which contains the following genera: ***Acanthophorus*** von Linstow, 1876, which has been accepted as a synonym of *Tetrameres*. ***Ascarophis*** van Beneden, 1871, parasites that live in the gastrointestinal tract of marine fish, with the type species *Ascarophis morrhuae* Beneden, 1871 (Gibbons, 2010). Intermediate hosts are decapods (*Enalus gaimardi*, *Eupagurus pubescens*, *Hetairus polaris*, *Pagurus pubescens*, *Pandalus borealis*, and *Spirontocaris spinus*) from the Bering Sea (Uspenskaya, 1953; 1954), lobster (*Homarus americana*) in North America (Uzmann, 1967), crab, *Carcinus maenas*, from off the coast of Brittany in France (Petter, 1970), crustaceans (*Anisogammarus kygi*, *A. ochotensis*, *A. tiuschovi*, *Idothea ochotensis*, and *Pagurus middendorffii*) from the littoral zone of Big Shantar Island in the Okhotsk Sea (Tsimbalyuk et al., 1970), shore crabs (*Hemigrapsus oregonensis*), porcelain crabs (*Pachycheles rudis*) in California, United States (Poinar and Kuris, 1975), and *Callianassa californiensis*, *Pagurus samuelis*, *P. granosimanus*, *Pachycheles pubescens*, and *Pugettia producta* (Poinar and Thomas, 1976). Moravec et al. (1995) described *Ascarophis mexicana* from the stomach of *Epinephelus morio* and *E. adscensionis* from the Gulf of Mexico and southeastern Mexico in the states of Yucatán and Veracruz. According to the authors, *Ascarophis mexicana* is the second *Ascarophis* species known to parasitize fishes of the genus *Epinephelus* (Moravec et al., 1995). ***Caballeronema*** Margolis, 1977, parasites that live in the alimentary canal of the marine fish*, Scorpaenichthys marmoratus,* found off the Pacific coast of Canada, with the type species *Caballeronema wardlei* (Smedley, 1934) Margolis, 1977. ***Capillospirura*** Skrjabin, 1924, parasites of the digestive tract of sturgeons, with the type species *Capillospirura ovotrichuria* Skrjabin, 1924 (Gibbons, 2010). Based on the characteristics of the cephalic structure of specimens from Old World sturgeons, *Capillospirura* Skrjabin, 1924 (Nematoda: Cystidicolidae) has been redefined.

Three species have been assigned by Appy and Dadswell (1978) to *Capillospirura*, specifically: *C. ovotrichuria* Skrjabin, 1924 and *C. argumentosa* (Skrjabina, 1966) (= *Ascarophis argumentosus*) from Old World sturgeons and *C. pseudoargumentosa* (= *Caballeronema pseudoargumentosus*) from a New World sturgeon, as has been suggested by Appy and Anderson (1982). ***Comephoronema*** Layman, 1933, parasites that live in the alimentary tract of freshwater fish, with the type species *Comephoronema werestschagini* Layman, 1933. Pereira and colleagues (1993) have described *Comephoronema multipapillatum* from the anterior intestine and cecum of the squirrelfish, *Holocentrus adscensionis*. According to the authors (Pereira et al., 2014), this is the fifth nominal species of *Comephoronema* and the first nematode registered in *H. adscensionis* and the first species of the genus in the Neotropical part of the Atlantic Ocean. ***Crenatobronema*** Solov'eva, 1987, parasites in fish from the Pacific Ocean, with the type species *Crenatobronema guentheri* (Baylis, 1929) Solov'eva, 1987. In his review concerning to the suborder Spirurina, Moravec (2007) considers this genus "inadequately known." ***Cystidicoloides*** Skinker, 1931, parasites of South American freshwater fish, with the type species *Cystidicoloides fischeri* (Travassos, Artigas and Pereira, 1928) Skinker, 1931.

Moravec et al. (2008) have redescribed *Cystidicoloides fischeri* (Travassos, Artigas and Pereira, 1928) noting the localization in the stomach of *Pygocentrus piraya* and *Serrasalmus brandtii* from Três Marias Reservoir, Upper São Francisco River, Minas Gerais state, Brazil. Based on morphological features, the authors (Moravec et al., 2008) accomplished several taxonomic transformations, such as: *Heliconema izecksohni* Fabio, 1982 is transferred to *Cystidicoloides* as *C. izecksohni* (Fabio, 1982). *Cystidicoloides uniseriata* Valovaya and Valter, 1988 is considered a species inquirenda. It has been proposed as a newly erected genus, *Salmonema*, with the type species *S. ephemeridarum*. *Cystidicoloides prevosti* (Choquette, 1951) has been transferred to *Salmonema* as *S. prevosti* (Choquette, 1951). *Sterliadochona savini* Skryabin, 1948 and *Sterliadochona* Skryabin, 1948 are considered as species and genus inquirenda, respectively. ***Echinurioides*** Thwaite, 1926 are parasites of the spurwinged goose, *Plectropterus* sp., in northern Nigeria, with the type species *Echinurioides plectropteri* Thwaite, 1926 (Gibbons, 2010). Skrjabin and Sobolev (1963) list *Echinurioides* as a synonym of *Tetrameres* Creplin, 1846. Alexander and McLaughlin (1997) report the type species as *Tetrameres plectropteri* (Thwaite, 1926), with host *Plectropterus gambensis* in Nigeria. ***Gubernaculomeres*** Oshmarin and Parukhin, 1963 are parasites that live in the proventriculus of *Astur gentilis* and *Aquila clanga*, with the type species *Gubernaculomeres tubocloacis* (Oshmarin, 1956) Oshmarin and Parukhin, 1963 (Gibbons, 2010). ***Moravecnema*** Justine, Cassone and Petter, 2002 is considered to be a parasite of the deep sea hydrothermal fish *Pachycara thermophilum* from the Mid-Atlantic Ridge, with the type species *Moravecnema segonzaci* Justine, Cassone and Petter, 2002 (Gibbons, 2010). This is the first species of parasitic nematode described from a fish endemic to hydrothermal deep sea vents.

The genus ***Prospinitectus*** Petter, 1979 are parasites that live in the intestine of the fish, *Euthynnus affirtis,* off Kuala Lumpur, Malaysia and in the China Sea, with the type species *Prospinitectus mollis* (Mameav, 1968) Petter, 1979 (Gibbons, 2010). The genus ***Pseudascarophis*** Ko, Margolis and Machida, 1985 are parasites that live in stomach of the fish, *Kyphosus cinerascens,* from off the southeastern coast of Japan, with the type species *Pseudascarophis kyphosi* Ko, Margolis and Machida, 1985 (Gibbons, 2010).

Pereira and colleagues (2013) described *Pseudascarophis brasiliensis* found in the stomach of *Kyphosus sectatrix* from off Rio de Janeiro, southeastern Brazil. The genus ***Salmonema*** Moravec, Santos, Brasil-Sato, 2008 are parasites that live in the digestive tract of freshwater fish, with the type species *Salmonema ephemeridarum* (Linstow, 1872) Moravec, Santos, Brasil-Sato, 2008 (Gibbons, 2010). ***Similascarophis*** Munoz, Gonzalez and George-Nascimento, 2004 are parasites of the digestive tract of marine fish off the Chilean coast, with the type species *Similascarophis maulensis* Munoz, Gonzalez and George-Nascimento, 2004 (Gibbons, 2010). Also included is the genus ***Sterliadochona*** Skrjabin, 1948.

A number of genera were discovered in the mid-1900s, namely, *Cristitectus* Petter, 1970, *Salvelinema* Trofimenko, 1962, *Ctenascarophis* Mamaev, 1968 and 1967 Petter, 1969. Rasheed (1965) and Moraveč (1967) have synonymized *Sterliadochona* Skrjabin, 1946 with *Cystidicoloides.* Characters used by Maggenti and Paxman (1971) to re-establish 2 genera have no generic value for nematode parasites of vertebrates (Anderson et al., 2009). The genus ***Tetrameres*** Creplin, 1846 is remarkable for the fact that the mature female is almost spherical in shape, blood-red in color, and lies embedded in the proventricular glands of birds. There are many species in this genus, among which are: *T. americana* Cram, 1927, which occurs in the proventriculus of fowl and turkeys. The final hosts of *T. americana* are the grasshoppers *Scyllina cyanipes* in Puerto Rico and *Melanoplus femurrubrum* and *M. differentialis* in mainland United States, and have been recorded elsewhere from the United States and in South Africa. Intermediate hosts are *M. femurrubrum, M. differentialis*, and *Blatella germanzca. Tetrameres fissispina* (Diesing, 1861) occurs in the duck, pigeon, fowl, turkey, and wild aquatic birds, and has a wide distribution. Intermediate hosts for *T. fissispina* are the water crustacean *Daphnia pulex* and *Gammarus pulex*. *Tetrameres crami* Swales, 1933 occurs in domestic and wild ducks in North America. Its intermediate hosts are the amphipods *G. fasciatus* and *Hvalella knickerbockeri*. *Tetrameres confusa* Travassos, 1919 occurs in the proventriculus of fowl pigeon and other birds in Brazil. Its intermediate hosts are probably similar to those for *T. fissispina*. *Tetrameres mohtedai* Bahlerao and Rao, 1944 occurs in fowl in India and Southeast Asia. Its intermediate hosts are cockroaches and grasshoppers, such as *Spathosternum praszniferum* and *Oxya nitidula*. *Tetrameres pattersoni* (Cram, 1933) occurs in quail, and the intermediate hosts are grasshoppers and cockroaches (Soulsby, 1982). *Tetrameres cardinalis* Quentin and Barre, 1976 has been found in the northern cardinal (*Cardinalis cardinalis* (syn. *Richmondia cardinalis*) in Mexico; its development occurs in *Locusta migratoria*. The intermediate hosts for *T. pattersoni* Cram, 1933 are *Chortophaga viridifasciata* and *Melanoplus femurrubrum* and its final host is *Colinus virginianus* (Anderson, 2000). According to Junker and Boomker (2007), the genus *Tetrameres* also includes *T. coccinea* (Seurat, 1914) Travassos, 1914 from the *Phoenicopterus ruber*, *Bubulcus ibis*, and *Platalea leucorodia* Linnaeus, 1758. *Tetrameres lhuillieri* (Seurat, 1918) is found in *Alectoris graeca* (Meisner, 1804) and *Columba oenas* Linnaeus, 1758 from Algeria. *Tetrameres nouveli* (Seurat, 1914) Travassos, 1914 is found in the black winged stilt, *Himantopus himantopus* (Linnaeus, 1758) in Algeria and Nigeria. *Tetrameres plectropteri* Thwaite 1926 is found in *Plectropterus gambensis*. Both *T. paradisea* Ortlepp, 1932 and *T. prozeskyi* (Ortlepp, 1964) have been described from South African hosts. *Tetrameres paradisea* has been recovered from *Anthropoides paradisea* (Lichtenstein, 1793). *Tetrameres prozeskyi* occurs in *Tockus erythrorhynchus* and *T. leucomelas*. The authors described that and *T. numida* Junker and Boomker, 2007 in *Numida meleagris* from Musina (Messina), Limpopo Province, South Africa.

The superfamily **Physalopteroidea** includes the family **Physalopteridae** (Railliet, 1893 subfamily) Leiper, 1908. According to Gibbons (2010), parasites of the alimentary canal (as well as the esophageal, gastric, or aortic walls) of the selachian *Chlamydoselachus anguineus* from the Pacific coast of central Honshu, Japan, with the type species *Metaleptus rabuka* Machida, Ogawa and Okiyama, 1982.

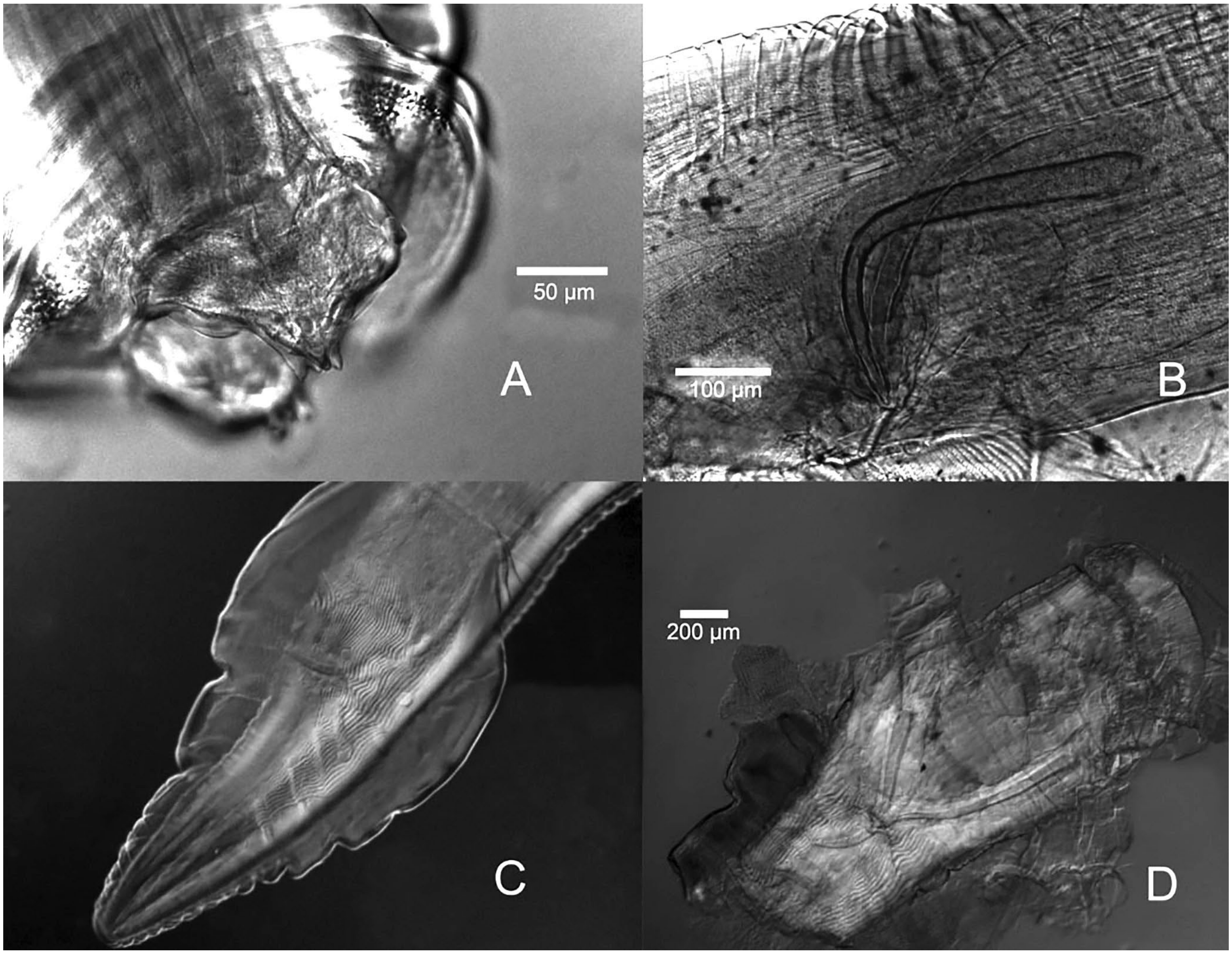

Figure 4. A) Anterior end of *Physaloptera rara* (Nemata: Spirurida: Physalopteridae) from a domestic dog obtained from Iowa, United States. Note the 2 large lips each with 3 small anteriorly-directed teeth (which is typical of *Physaloptera* spp.); B) lateroventral view of the cloacal area showing spicules of *P. rara* from a bobcat in Nebraska, United States; C) ventral view of rays and associated velum of posterior end of *P. rara* from Iowa, United States. Note that the scale bar is the same for both C and D; D) ventral view of a dissected specimen of *P. rara*. Note that this is the same individual as is shown intact in figure C. Source: S. L. Gardner, HWML. License: CC BY.

The subfamily **Physalopterinae** Railliet, 1893 includes the genus ***Kreisiella*** Jones, 1985. According to Gibbons (2010), members of this genus live in the stomach of the Australian lizard *Egernia inornate,* with the type species *Kreisiella chrysocampa* Jones, 1985. Goldberg and colleagues (2008) report finding *Kreisiella chrysocampa* in *Emoia* (Scincidae) from Papua New Guinea. The type species for ***Leptosoma*** Travassos, 1920 is *L. leptosoma* (Gervais, 1848), the adult worms of which live in the stomach or intestine of mammals, birds, reptiles, and amphibians. The genus ***Paraphysaloptera*** Gupta and Kazim, 1979 are parasites of the gizzard lining of the hoopoe *Upupa epops*, with the type species *Paraphysaloptera alii* (Gupta and Kazim, 1978) Gupta and Kazim, 1979. According to Martín-Vivaldi and colleagues (2014), other phisalopterid species in the same final host are *P. indica*, found in the intestine (Gupta and Johri, 1985) and *P. alii*, found in the gizzard (Gupta and Kazim, 1979). Widmer (1970) experimentally infected cats using third-stage *Physaloptera* juveniles (J_3) from the rattlesnake *Crotalus viridis*.

The genus *Paraphysaloptera* possesses 2 subgenera. One subgenus is ***Chlamydonema*** (Hegt, 1910 genus) Gupta and Johri, 1987, with the type species *Physaloptera* (*C.*) *praeputiale* (Linstow, 1888) Travassos, 1917. They are parasites that live in the stomach of *Canis latrans*, *Felis catus domesticus*, *F. pardus*, and *C. familiaris* and are found in Asia, Africa, Europe, North America, and South America. Linstow (1888) described *P. praeputialis* from a wild cat (*F. catus*) from Brazil. Later, Walton (1927) assigned this specimen to the group Mammal.

This is probably the first record of *P. praeputialis* in North America. In the stomach of lynx (*Lynx rufus texensis*) and ocelot (*F. pardalis*) from Mexico the same species has been reported also by Caballero y Caballero and Peregrina (1938).

The other subgenus of *Paraphysaloptera* is ***Physaloptera*** (Rudolphi, 1819 genus) Gupta and John, 1987, with the type genus *Physaloptera* Rudolphi, 1819. *Physaloptera* are common nematodes found in the stomach and muscles of mammals (such as dogs, cats, and humans), reptiles, amphibians, and birds. Physalopterids attach to the walls of the duodenum and stomach (Naem and Asadi, 2013) and are known to have pathological consequences such as catarrhal gastritis, gastrointestinal upset, erosion of the mucosa, ulcers, and vomiting (Soulsby, 1965).

Physaloptera spp. have a complicated life cycle. They have numerous definitive hosts. Intermediate hosts are arthropods, specifically, ground beetles (*Harpalus* spp.) and crickets (*Achetaassimilis* spp.) (Widmer, 1967). Aberrant infections occur at times, and there are possibly second intermediate hosts or paratenic hosts. For example, *Physaloptera* spp. juveniles have been found within the tissues of wild northern bobwhite quail *Colinus virginianus* and it is suspected that quail may serve as paratenic or secondary hosts of these parasites (Kalyanasundaram et al., 2018). Widmer (1970) identified all rodents as potential paratenic hosts for physalopterids. Olsen (1980) used juveniles from rattlesnakes to infect cats. Baughn and Bliznick (1954) found physalopterids in cats in New York, United States. Ackert (1936) and Ackert and Furumoto (1949) found *Physaloptera* spp. in cats in Kansas, United States. In particular, Shoop and colleagues (1991) reported *P. rara* from cats in Arkansas, United States. Marchiondo and Sawyer (1978) recovered *P.* (*Physaloptera*) *clausa* Rudolphi, 1819 specimens from cats in Utah, United States. Using scanning electron microscopy, Chen and colleagues (2017) studied *P. clausa* obtained from the Amur hedgehog *Erinaceus amurensis* in China. Supplementary data on morphological and morphometric characters have been obtained through these additional studies which allows more accurate identification of these species.

Another genus in the Physalopterinae is ***Skrjabinoptera*** Shulz, 1927, which is found in reptiles. According to Anderson (2000), *S. phrynosoma* (Ortlepp, 1922) is a common stomach worm of reptiles that live in Texas, United States, as well as horned toads *Phrynosoma cornutum*. According to Lee (1957), the intermediate hosts are the ants *Pogonomyrmex barbatus* var. *molefaciens*.

Another subfamily in Physalopteridae is **Proleptinae** (Schulz, 1927), including the genus ***Neoleptus*** Ubelaker and Dailey, 1975. According to Specian and colleagues (1975), *Neoleptus* spp. are parasites found in the fish *Heterodontus philippi* and *Mustelus antarticus*, with the type species *Neoleptus australis* (Johnston and Mawson, 1943) Specian, Ubelaker and Dailey, 1975.

According to Gibbons (2010), another subfamily in Physalopteridae is **Mirzalopterinae** Wason and Johnson, 1977, with the type genus ***Mirzaloptera*** Wason and Johnson, 1977. They are parasites that live in the stomach of the bat *Rhinopoma microphyllum* in Jodhpur, India. The type species is *Mirzaloptera barbari* Watson and Johnson, 1977.

Another family in Physalopteroidea is **Rictulariidae** (Hall, 1915 subfamily) Railliet, 1916, and which contains 2 genera. One genus is ***Quentius*** Chabaud and Bain, 1981, which are parasites that live in the duodenum and small intestine of Neotropical marsupials (*Marmosa* spp.) in Cali, Colombia (Chabaud and Bain, 1981). The type species is *Q. kozeki* Chabaud and Bain, 1981. The other genus is ***Shamimana*** Gupta and Masoodi, 1990, which includes parasites that live in the intestine of the marine fish *Plotosus arab* off the Trivandrum coast near Kerala, India. The type species is *Shamimana durdanae* Gupta and Masoodi, 1990.

The superfamily **Spiruroidea** combines the family **Spiruridae** Oerley, 1885, which, according to Gibbons (2010), contains 4 genera.

1) ***Gastronodus*** Singh, 1934, parasites that live in nodules on the stomach wall of the muskrat *Crocidura coerulea* in Hyderabad State, India. The type species is *Gastronodus strasseni* Singh, 1934
2) ***Dollfusnema*** Caballero, 1974, parasites that live in the intestine of the marine fish *Paralabrax clathratus* from Mexico. The type species is *Dollfusnema piscicola* Caballero, 1974
3) ***Isospirura*** Sood and Parshad, 1972, parasites that live in the stomach of *Millardia meltada, Mus musculus bactrianes*, and *Mus booduga* in Ludhiana, India. The type species is *Isospirura meltadi* Sood and Parshad, 1972
4) ***Paracymea*** Gupta and Jaiswal, 1987, parasites that live in the intestine of the birds *Anser indicus* in the Prince of Wales Zoological Gardens, Lucknow, India. The type species is *Paracymea yamagutii* Gupta and Jaiswal, 1987.

Another family in this superfamily is **Gongylonematidae** (Hall, 1916 subfamily) Sobolev, 1949, which, according to Gibbons (2010), contains several genera. ***Gongylonema*** Molin, 1857 embeds in the mucosa and submucosa of the anterior region of the gut of birds and mammals. Usually, the final hosts are sheep and goats, and sometimes also horses, cattle, swine, poultry, dogs, cats, and numerous other wild and domestic mammals and birds. As such, according to

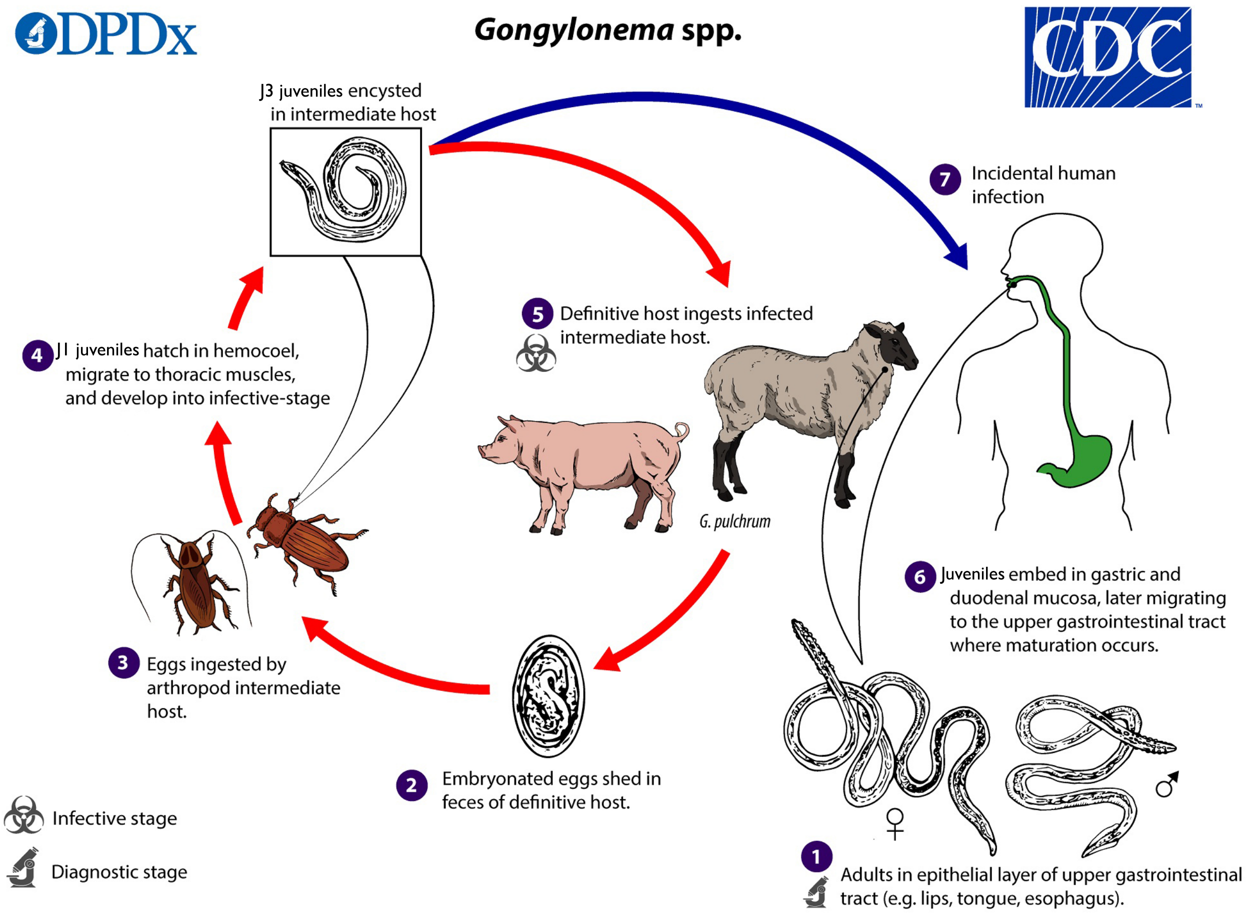

Figure 5. *Gongylonema* is a genus of spirurid nematodes which includes the veterinary parasite *G. pulchrum* (also called the gullet worm or stitch worm) along with several other parasites of mammals and birds. Incidental human infections with *Gongylonema* are rare, and species-level identifications are difficult and seldom confirmed. The life cycle diagram of *Gongylonema* spp. shows: Adult *Gongylonema* inhabit the upper gastrointestinal tract of the definitive host in sites such as the mouth, esophagus, rumen, and stomach (1). The long, thin adults are found in shallow tunnels in the squamous epithelial surfaces of these tissues; the female produces thick-shelled, embryonated eggs containing first-stage (J_1) juveniles. Expelled eggs are released from the tunnels during epithelial desquamation and are carried down the gastrointestinal tract and shed in the feces (2). Intermediate host insects become infected after ingesting eggs in host feces (3). Juveniles develop in the hemocoel of the intermediate host, eventually becoming encapsulated as infective third-stage (J_3) juveniles in the thoracic muscles (4). Suitable definitive hosts become infected after ingesting infected intermediate hosts (5). Juveniles are released in the stomach, which embed in the gastric or duodenal mucosa, and eventually migrate to the upper gastrointestinal tract after 2–3 months (6). Migration of juveniles often creates characteristic zig-zag or sinusoidal tracks in the affected epithelial tissues. Maturation is completed in the upper gastrointestinal tract. Human infections occur following the ingestion of intermediate host arthropods (7), either intentionally or accidentally, in contaminated food or water. In these cases, worms have been found in the mucosal tissues of the lips, cheek, tongue, tonsils, gums, and occasionally esophagus. A few cases of spurious egg passage have been documented, which may be due to the inadvertent consumption of adult *Gongylonema* in certain types of meat (for example, chicken gizzards or pork tongue). Source: Adapted from United States Centers for Disease Control and Prevention, Division of Parasitic Diseases and Malaria, 2019. Public domain.

Soulsby (1982), some gongylonemids can affect the health of humans and domestic animals, for example, *G. pulchrum* Molin, 1857, which can be found in most parts of the world. This parasite species occurs in sheep, goats, cattle, pigs, zebu, buffalo, and (less frequently) horses, camels, donkeys, and wild boar. It may also develop in humans, particularly in the oral epithelium, but also subcutaneously (see Figure 5). The site of localization in non-human animals is the esophagus where *G. pulchrum* embeds in a zigzag pattern in the mucosa or submucosa. In ruminants, it may also appear in the rumen. The intermediate hosts are coprophagous beetles of the genera *Aphodius*, *Onthophagus*, *Blaps*, *Caccobius*, and others (over 70 species). Migrating juveniles root in the wall of the gastroesophageal region. They excyst in the stomach and then migrate anteriorly to the oral cavity and finally reach the wall of the esophagus. The species *G. verrucosum* (Giles, 1892) may be present in the rumen of sheep, goat, cattle, deer, and zebu in India, the United States, and South Africa. *Gonglyonema monnigi* Baylis, 1926 develops in the rumen of sheep and goats in South Africa. *Gonglyonema ingluvicola* Ransom, 1904 and *G. crami* Smit, 1927 occur in fowl in North America, India, the Philippines, Taiwan, Europe, and Australia. *Gonglyonema sumani* Bhalerao, 1933 occurs in the crop of domestic fowl in Uttar Pradesh State, India. The cockroach *Blatella germanica* may be infected with this worm. *Gongylonema verrucosum* embeds in the epithelium, causing just a slight chronic inflammatory reaction with hypertrophy and cornification, but *G. ingluvicola* may burrow into the crop and cause severe lesions in heavy infections.

Bickova and colleagues (2017) report some gongylonematid species that occur in Belarus, such as: *Gongylonema neoplasticum* (Fibiger et Ditlevsen), which occurs in the European water vole *Arvicola amphibius*, forest dormouse *Dryomys nitedula*, and common dormouse *Muscardinus avellanarius*, all from the Brest and Gomel regions (Luninety District). *Gongylonema sorici* Fain, 1955 is found in the common shrew *Sorex araneus* from NP "Belovezhskaya Pushcha" in Belarus. Kinsella and colleagues (2016) describe *G. archboldi* found in tunnels in the gastric mucosa of the cotton rat *Sigmodon hispidus* from Highlands County, Florida, United States. Measurements are also given for specimens from the cotton mice *Peromyscus gossypinus*, oldfield mice *Pe. polionotus*, Florida mice *Podomys floridanus*, and golden mice *Ochrotomys nuttalli* from the same locality. Additional specimens have been collected from the cotton rat and the rice rat *Oryzomys palustris* from Berry Island, San Patricio County, Texas, United States.

Chlamydoprocta Chandler, 1954 are parasites of the skunk *Mephitis mephitis* in Minnesota, United States. The type species is *Chlamydoprocta itascensis* Chandler, 1954, with a subgenus ***Progongylonema*** Hernandez-Rodriguez and Gutierrez-Palomino, 1992. They are parasites that live in the mucosa under the tongue of *Pica pica, Garrulus glandarius, Cyanopica cyanus*, and *Corvus monedula* (Passeriformes, Corvidae) in Córdoba Province, southern Spain. The type species is *Gongylonema (Progongylonema) pacoi* Hernandez-Rodriguez and Gutierrez- Palomino, 1992.

Gibbons (2010) described other genera in Gongylonematidae, which are listed below. ***Mastigonema*** Dailey and Perrin, 1973 are oviparous parasites of the forestomach of Cetacea, *Stenella graffmani* and *S. longirostris,* that are found in the eastern tropical Pacific Ocean. The type species is *M. stellae* Dailey and Perrin, 1973. ***Mazzia*** Khalil and Vogelsang, 1932 are parasites found in dasypodid mammals in Argentina, with the type species *M. mazzia* Khalil and Vogelsang, 1932. ***Paraspiralatus*** Gibbons, Nicholls, Bailey and Samour, 2004 includes a recently discovered species*, P. sakeri*, which was found in the stomach of a wild-caught, female saker falcon in Saudi Arabia (Gibbons et al., 2004). It has been accepted as a type species for the genus *Paraspiralatus*.

Chabaud and colleagues (1983) described *Mazzia bialata*, a parasite of dasypodid mammals (such as *Chaetophractus villosus*) from Buenos Aires, Argentina. According to the authors (Chabaud et al., 1983), this genus is morphologically more specialized than other Neotropical genera that parasitize paleoendemic mammals. Other genera described by this group of researchers includes ***Spirobakerus*** Chabaud and Bain, 1981, which are parasites of the cricetid *Zygodontomys brevicauda* of Colombia. The type species is *Spirobakerus weitzeli* Chabaud and Bain, 1981. Another genus in this group is ***Spirosprattus*** Smales, 2004, parasites found in cysts in the stomach wall of Australian rodents, such as the Cape York rat *Rattus leucopus* (family Muridae). The type species is *Spirosprattus scyphiformis* Smales, 2004.

According to Gibbons (2010), the superfamily **Thelazioidea** contains 3 families, as listed and described here.

Thelaziidae Skrjabin, 1915 includes the genus ***Thelazo*** Pearse, 1933. According to Pearse (1933), *Thelazo* is erected for *T. glossogobii* described from the final host, the tank goby *Glossogobius giurus*. The diagnosis is based on the work of Pearse (1933) who placed the genus in the Thelaziidae, of which the type species is *T. glossogobii* Pearse, 1933, which may be found in marine and brackish waters from the Red Sea, East Africa, South Asia, the Indian Ocean, China, Australia, and the islands of the Pacific Ocean.

The subfamily **Thelaziinae** (Skrjabin, 1915 family) Baylis and Daubney, 1926 contains the genus ***Thelazia*** Bosc, 1819. Members of the genus, such as *T. rhodesi* and *T. skrjabini*, are parasites of the orbits (including under the lids, conjunctiva, and nictitating membrane, and in the lachrymal glands and ducts) of birds and mammals. Other species, such as *T. callipaeda*, are said to develop in the fat body (Anderson, 2000). According to Soulsby (1982), *T. rhodesii* (Desmarest, 1828) occurs primarily in cattle, sheep, goats, and buffaloes, and its habitat is cosmopolitan. *Thelazia gulosa* Railliet and Henry, 1910 appears in cattle in most parts of the world. *Thelazia alfortensis* Railliet and Henry, 1910 occurs in cattle in Europe. *Thelazia lacrymalis* (Gurlt, 1831) develops in the horse in most parts of the world. *Thelazia skrjabini* Ershov, 1928 is found in cattle in Europe, Asia, and North America. *Thelazia callipaeda* Railliet and Henry, 1910 lives under the nictitating membrane of the dog in East Asia and has been reported from rabbits and humans. *Thelazia californiensis* Price, 1930 occurs in sheep, deer, cats, dogs, and humans in the United

States. *Thelazia leesei* Railliet and Henry, 1910 has been reported from dromedary camels in the former Soviet Union and elsewhere in Asia. *Thelazia rhodesi*'s intermediate hosts are *Musca larvipara*, *M. convexifrons*, and *M. amica*. *Musca oseris* transmits *T. lachrymalis* in regions delineated by the former Soviet Union, while *M. autumnalis* appears to be an important vector in the United States (Soulsby, 1982).

According to Gibbons (2010), the genus *Thelazia* consists of 3 subgenera, listed below. ***Isothela*** Railliet, 1925 are viviparous parasites occurring in birds. ***Pericyema*** Railliet, 1925 are ovoviviparous parasites in mammals, with the type species *T.* (*P.*) *callipaeda* Railliet and Henry, 1910. ***Thelazia*** (Bosc, 1819 genus) are viviparous parasites that occur in mammals, with the type species *T.* (*T.*) *rhodesi* (Desmarest, 1827) Railliet and Henry, 1910.

Another family in Thelazioidea is **Rhabdochonidae** (Travassos, Artigas and Pereira, 1928 subfamily) Skrjabin, 1946, parasites that live in the gallbladder of freshwater fish, and is allocated into 6 genera, as listed here. The first is ***Beaninema*** Caspeta-Mandujano, Moravec and Salgado-Maldonado, 2001. Caspeta-Mandujano and colleagues (2001) re-erected this genus and described a new species and new genus. The members of this genus are parasites in the gallbladder of the freshwater fish *Cichlasoma hearli* from the Santiago River, Tepic, Nayarít, Mexico, with the type species *Beaninema nayaritense* Caspeta-Mandujano, Moravec and Salgado-Maldonado, 2001. ***Fellicola*** Petter and Køie, 1993 are parasites that live in the gallbladder of the marine fish *Coryphaenoides rupestris* (a ray-finned fish) from the North Atlantic off the Faroe Islands (Petter and Køie, 1993). According to Petter and Køie (1993), the new genus is close to the genera *Johnstonmawsonia*, *Vasorhabdochona*, and *Pancreatonema* but differs from these genera in having longitudinal thickenings in the anterior dilated part of the pharynx. The type species is *F. longispiculus* Petter and Køie, 1993 (Gibbons, 2010). ***Megachona*** Mejía-Madrid and Pérez-Ponce de León, 2007 was described by Mejía-Madrid and Pérez-Ponce de León (2007) and identified the species *M. chamelensis* from the intestinal cecae of the blue striped chub *Sectator ocyurus* (Kyphosidae, Perciformes) from Chamela Bay, Mexico. According to the authors (Mejía-Madrid and Pérez-Ponce de León, 2007), *Megachona* most closely resembles *Beaninema* Caspeta-Mandujano, Moravec, and Salgado-Maldonado, 2001, F. Petter and Køie, 1993, and *Rhabdochona* Railliet, 1916. The type species is *M. chamelensis* Mejía-Madrid and Pérez-Ponce de León, 2007. The reconstruction of this genus ***Rhabdochona*** Railliet, 1916 was suggested by Moraveč (1975). The members of this group of spirurids are parasites that live in the intestine of fish and they possess 2 subgenera: ***Afrochona*** Puylaert, 1973, which are parasites that live in the intestine of the fish *Aphyosemion cameronensis* in Olounou, Cameroon (Gibbons, 2010). The type species is *A.* (*A.*) *camerounensis* Puylaert, 1973. The other subgenus is ***Globochonoides*** Moravec, 1975. According to Gibbons (2010), they are parasites that live in the intestine of freshwater fishes. The type species is *Rhabdochona* (*G.*) *coronacauda* Belouss, 1965.

Two new species of rhabdochonid nematodes that live in the intestines of freshwater fishes in Chiang Mai Province, northern Thailand were recorded by Moraveč and Yooyen (2011). One of them, *Rhabdochona* (*R.*) *pseudomysti*, is from the catfish *Pseudomystus siamensis* (Regan) (Bagridae, Siluriformes) from Fang Brook, a tributary of the Kok River in the Mekong River basin, Fang District, Thailand. The other is *R.* (*Globochona*) *thaiensis* from the cyprinid *Mystacoleucus marginatus* (Valenciennes) (Cyprinidae, Cypriniformes) in the Ping River in the Chao Phraya River basin, Muang District, Thailand. In accordance with the authors (Moraveč and Yooyen, 2011), these are the first nominal species of *Rhabdochona* reported from Thailand.

Moraveč and Kanda (2012) discovered another new species of nematode, namely, *R.* (*G.*) *rasborae* (Rhabdochonidae), from the intestine of the freshwater cyprinid fish, sidestripe rasbora *Rasbora paviana* from Tirant in the Bangbaimai Subdistrict, Muang District, Surat Thani Province, southern Thailand. According to the authors (Moraveč and Kanda, 2012), this is the third nominal species of *Rhabdochona* Railliet, 1916, and the second species of the subgenus *Globochona* reported from fishes in Thailand. One of the next 2 genera in Rhabdochonidae is ***Johnstonmawsonoides*** Machida, 1975, which are parasites that live in the intestine of the marine teleost fishes *Nemichthys scolopaceus* in Suruga Bay, Japan, with the type species *J. nemichthyos* Machida, 1975. Among the known helminths of meso- and bathypelagic fishes of Norfolk Submarine Canyon, in the western North Atlantic, Gartner and Zwerner (1989) reported nematodes which have been determined to be *Johnstonemawasonia* spp. Another genus in Rhabdochonidae is ***Neoascarophis*** Machida, 1976, parasites that live in the intestine of the marine teleost fishes *Coelorhynchus multispinulosus* and *Bathygadus garretti* in Suruga Bay, Japan, with the type species *Neoascaropbis yarihige* Machida, 1976.

A subfamily of the Rhabdochonidae is **Prosungulonematinae** Skrjabin, Sobolev and Ivashkin, 1967, with the type genus ***Prosungulonema*** Roitman, 1963. It was presented by Chabaud (1975) as a synonym of Rhabdochonidae. Later, Caspeta-Mandujano and colleagues (2001) did not list the genus as valid in the family Rhabdochonidae. McVicar and Gibson (1975) supported the validity of the genus *Prosun-*

gulonema. The members of *Prosungulonema* Roitman, 1963 are parasites of freshwater teleost fishes, with the type species *P. siniperca* (Dogiel and Akhmerov, 1959). According to Chabaud (1975), another genus in Prosungulonematinae is ***Pancreatonema*** McVicar and Gibson, 1975. A new genus and species of nematode, *P. torriensis*, from the pancreatic duct of *Raja naevus* from off the coast of Aberdeen in northwest Scotland has been described and aspects of its biology were discussed by McVicar and Gibson (1975). The type species is *P. torriensis* McVicar and Gibson, 1975.

Another family in the Spiruroidea is **Pneumospiruridae** Wu and Hu, 1938, containing genus ***Pneumospirura*** Wu and Hu, 1938. The type species is *P. hainanensis* Wu and Hu, 1938?. They are parasites of birds and mammals, including some carnivores. Pence and Stone (1977) described a new species, *P. bassarisci*, from the ringtail *Bassariscus astutus* and redescribed 2 species from the bobcat *Felis rufus* in North America. The genus includes the species *P. hainanensis*, *P. capsulata*, and *P. bassarisci*, with site of localization the bronchioles of carnivorous mammals. Wertheim and Giladi (1977) described *P. rodentium* as a lung parasite of *Gerbillus dasyurus* and *Meriones crassus*. Two other species include *P. capsulata*, parasites in the common badger, and *P. rodentium*, found in the lungs of gerbils and birds (Wertheim and Giladi, 1977).

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NEMATA

Camallanina (Suborder): Guinea Worm and Related Nematodes

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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

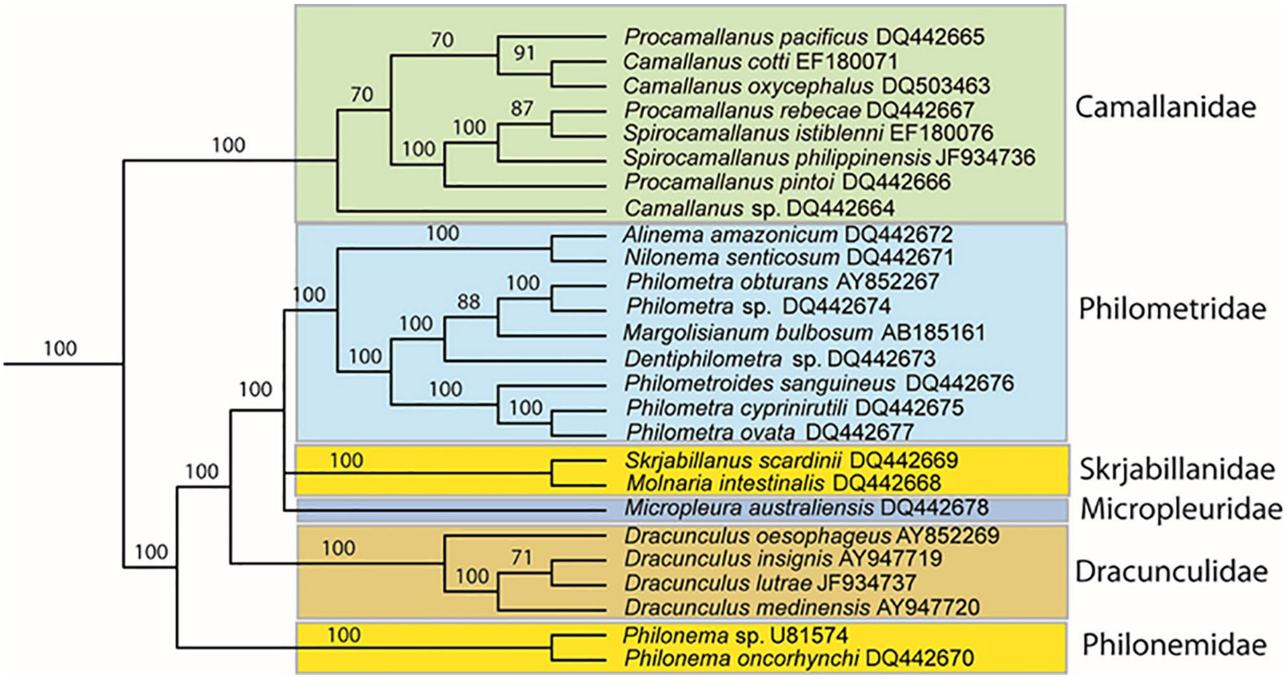

Figure 1. Part of the phylogeny of endoparasitic nematodes based on Bayesian analysis, showing interrelationships of some of the families in suborder Camallanina. Numbers refer to Bayesian Posterior Probability values. Values higher than 90 indicate strong support. Source: Adapted from Choudhury and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

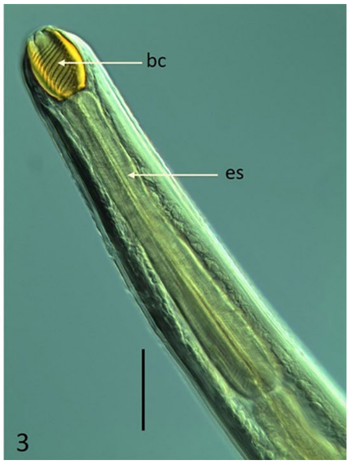

Figure 2. *Camallanus ancylodirus* from quillback (*Carpiodes cyprinus*: family Catstomidae). Source: A. Choudhury. License: CC BY-NC-SA 4.0.

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; Moravec 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 (Moravec, 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 (Moravec, 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. Moravec (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) (Moravec, 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 Moravec (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.

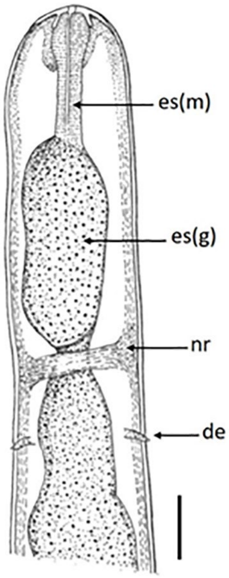

Figure 4. Anterior end of adult male guinea worm *Dracunculus medinensis*; es(m) = muscular esophagus, es(g) = glandular esophagus, nr = nerve ring, de = deirids. Source: Adapted from Moorthy, 1937. License: CC BY-NC-SA 4.0.

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.

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.

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 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.

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).

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-

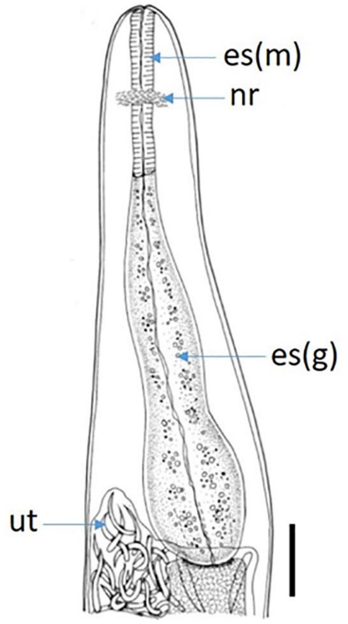

Figure 7. *Philonema agubernaculum*, female, anterior end; es(m) = muscular esophagus, nr = nerve ring, es(g) = glandular esophagus, ut = uterus. Scale bar = 100 µm. Source: Arai and Smith, 2016. License: CC BY 3.0.

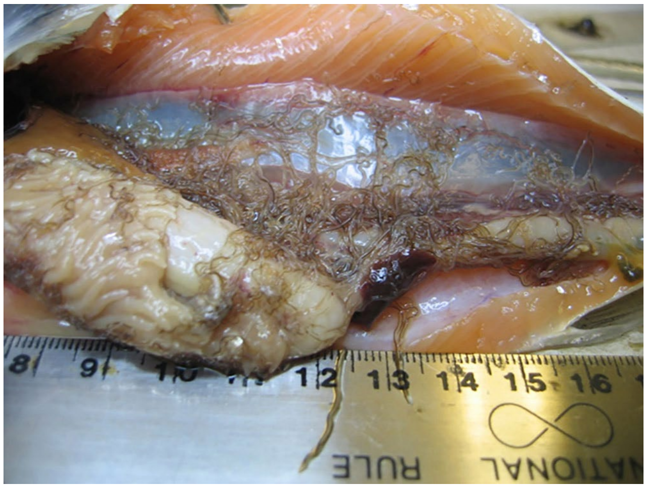

Figure 8. *Philonema oncorhynchi* from a Pacific salmon (*Oncorhynchus* sp.). Source: A. Choudhury. License: CC BY-NC-SA 4.0.

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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Nemata

Filarioidea (Superfamily)

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Phylum Nemata

Superfamily Filarioidea

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Chapter 55

Filarioidea (Superfamily)

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Introduction

Filarioid nematodes are parasites of all classes of vertebrates except fish. Most of the species are parasites of wild animals, however some of them parasitize humans and domestic animals, triggering diseases. The majority of these filarioids are included in the family Onchocercidae. They are tissue-dwelling nematodes, with an indirect life cycle including hematophagous arthropods. Adults have been found in almost all tissues of their hosts; however, they prefer a particular location depending on the species. Usually, they are found parasitizing the body cavity, lymphatic vessels, nodules under the skin, or the right ventricle of the heart. They are viviparous, therefore first-stage juveniles (J_1), also known as microfilariae, are ingested by arthropods from the blood or skin of the definitive host. Later, the J_1s develop into J_2s in different organs of the arthropod, such as the Malpighian tubules in mosquitoes or the muscle cells in ticks, until they molt into J_3s, which migrate near the mouthparts of the vector to be transmitted to a new vertebrate host.

The filarioids have developed unique and highly evolved biological features compared with their parasitic spirurid ancestors. Adults are confined to the internal body of their hosts and have adapted their life cycle to transmission with a motile embryo, the microfilaria, which is accessible to hematophagous arthropods. There are 2 groups of filarioids, one of which is included in the family Filariidae, which includes nematodes that produce skin lesions. In this family, females inhabit the subcutaneous tissue and make a hole in the skin to deposit the eggs and/or juveniles which attract the arthropod vector, such as individuals in the family Muscidae. In contrast, nematodes in the family Onchocercidae have evolved to inhabit a more internal position of adult worms in the body of the hosts. Females deposit their embryos in the connective tissue drained by the initial lymphatic vessels, and the vermiform shape of the embryo or microfilaria allows individuals to reach the peripheral cutaneous lymphatic or blood vessels, thus becoming readily accessible to the vector animal. Microfilaria-like juveniles are an evolved character within the Onchocercidae. In this group, vectors may belong to a variety of arthropods, like biting midges, blackflies, fleas, mosquitoes, lice, mites, and ticks, creating lesions or perforating the skin to suck the infected lymph or blood.

Morphology

Compared to other nematodes, the morphology of filarioids is simple. They are long and slender worms, with **sensing structures** at the anterior extremity which are poorly developed. Their length can be variable from 5 mm to more than 50 cm, with males being smaller than females. Males display a posterior region that is coiled or J-shaped. The anterior extremity of filarioids possesses 2 rings of **papillae**; the internal ring with 4 **labial papillae**, and the external ring with 4 **cephalic papillae** usually located around the **oral opening**. Between them there are 2 lateral **amphids** (Figure 1). However, some species have a smaller number of head papillae. The number and arrangement of the papillae are important characters when identifying members of the species. Filarioids display a small **buccal capsule**. The capsule is constituted of 4 segments: An anterior segment that is transparent and corresponds to the **invaginated cuticle**, and 3 **cuticularized segments** that are more or less developed, depending on the genus. The buccal capsule is sometimes absent in some filarioids, such as specimens in the genus *Mansonella* (Figure 2). The stoma rests on the **esophagus**, which is long and occasionally differentiated in an anterior muscular portion and a posterior glandular

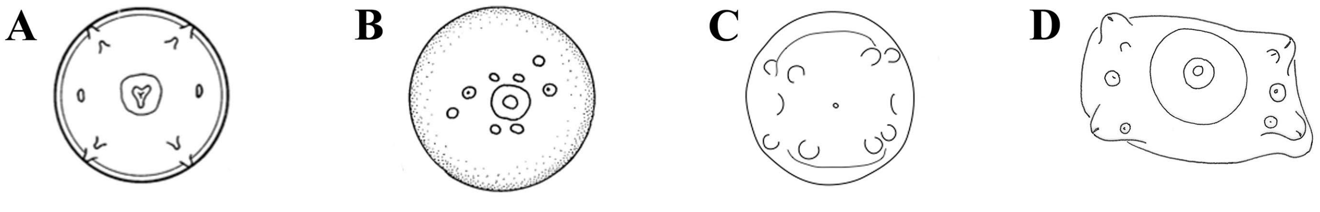

Figure 1. Apical views of some filarioids showing the arrangement of sensitive structures. A) *Brugia beaveri*. B) *Litomosoides odiale*. C) *Mansonela (Tupainema) dunni*. D) *Dipetalonema yatesi*. Sources: A) Adapted from Ash and Little, 1964; B) adapted from Notarnicola and Navone, 2002; C) adapted from Bain et al., 2015; D) adapted from Notarnicola et al., 2007. License: CC BY-NC-SA 4.0.

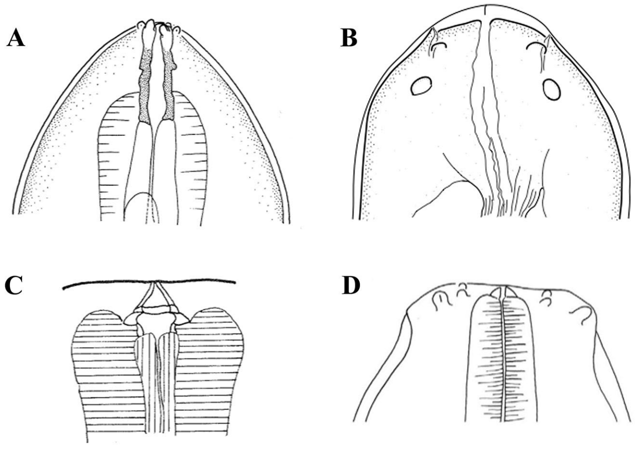

Figure 2. Anterior extremities of some filarioids showing the buccal capsule and the papillae. A) *Litomosoides odilae*, buccal capsule tubular; B) *Mansonella (Mansonella) interstutium*, buccal capsule absent; C) *Litomosa filaria*, buccal capsule constituted by 4 cuticularized segments;D) *Dipetalonema yatesi*, buccal capsule minute. Sources: A) Adapted from Notarnicola and Navone, 2002; B) adapted from Bain et al., 2015; C) adapted from Bain et al., 1966; D) adapted from Notarnicola et al., 2007. License: CC BY-NC-SA 4.0.

portion. Neither the esophagus nor the **intestine** present diverticula. The intestine ends in a **cloaca** in males and in an **anus** in females. Filarioids display a **nerve ring** located anteriorly at the level of the esophagus.

The reproductive system in filarioids is amphidelphic. The male has 2 **testes**, 1 which is anterior and usually visible at the level of the esophagus-intestine junction, and the other that is posterior and visible near the **tail**. This continues with a duct which passes posteriorly without convolutions and opens into the cloaca. The cloaca possesses a **spicular pouch** where the **spicules** and the **gubernaculum** lie. The spicules in filarioids are unequal (meaning different in shape), and dissimilar (meaning different in size). The right spicule usually is shorter than the left spicule (Figure 3). The gubernaculum is sometimes present in some Onchocercinae species. Males also have cloacal papillae placed anterior, around, and/or posterior to the cloacal opening. In some species, there is a cuticle structure called the **area rugosa** all along the median ventral line generally extended into the posterior coiled region of the male. The area rugosa is constituted by **transversal ridges** in *Litomosoides* (Figure 4) or *Dipetalonema*, or by tiny **cuticular bosses**, as in *Litomosa* (Figure 5). Both structures, the papillae and the area rugosa, serve to attach the female during copulation (Figure 6). The length and shape of the spicules, as well as the number of cloacal papillae and the presence or absence of the area rugosa, are characters that help in the identification of the different genera and species.

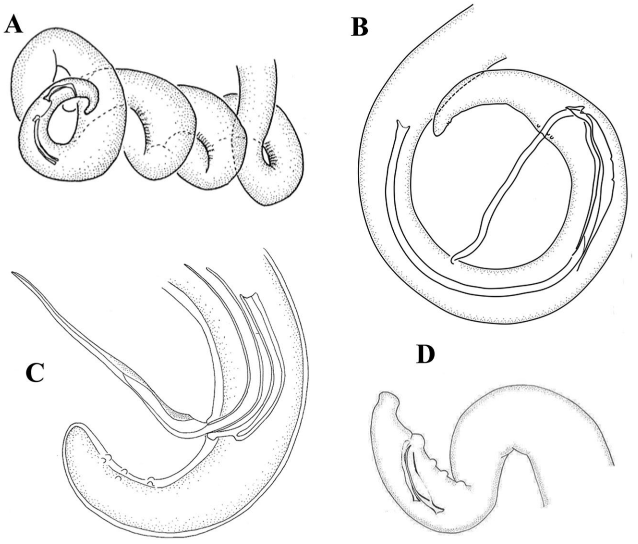

Figure 3. Male posterior ends showing the spicules. A) Posterior extremity of *Litomosoides odilae* showing the coiled region with area rugosa; B) Posterior extremity of *Mansonella (Pseudolitomosa) musasabi* showing the spicules in lateral view. Left spicule longer and different from right; C) Posterior extremity of *Litomosoides salazari* in lateral view; D) *Piratuboides huambensis* posterior region lateral view, with spicules few dissimilar but unequal. Sources: A) Adapted from Notarnicola and Navone, 2002; B) adapted from Bain et al., 2015; C) adapted from Notarnicola et al., 2010; D) adapted from Petit et al., 1983. License: CC BY-NC-SA 4.0.

The reproductive system in the females is convoluted. The anterior **ovary** is located near the level of the esophagus-intestine junction and continues backward in an **oviduct** and the **uterus**. In gravid females, eggs can be observed all along the uterus in different stages of development, such as, in the proximal portion, oval **eggs** containing **blastomera**; in the median portion, oval eggs containing the J_1; and in the distal portion, the extended microfilariae. The uterus continues to be situated within a long muscular **ovijector** and the **vagina**, which in some filarioids is a simple muscular tube (such as in specimens of *Ochoterenella* spp.) while in others it is more complex, differentiated into a **vagina vera** and a **vagina uterine**, as in *Dipetalonema* (Figure 7). The vagina is opened to a vulva at the anterior region, generally at the level of the esophagus or just posterior to it.

Microfilariae can be sheathed or unsheathed or not in the egg membrane, respectively. Females release thousands of microfilariae that migrate to the bloodstream, such as in *Dipetalonema*, or to the skin, such as in *Onchocerca*. Microfilariae are slender and fusiform; the anterior end is rounded usually with a hook, and the posterior end is pointed or blunt. Its length varies from 50 µm to more than 400 µm, depending on the species. The **sheath** is tightly applied to the body.

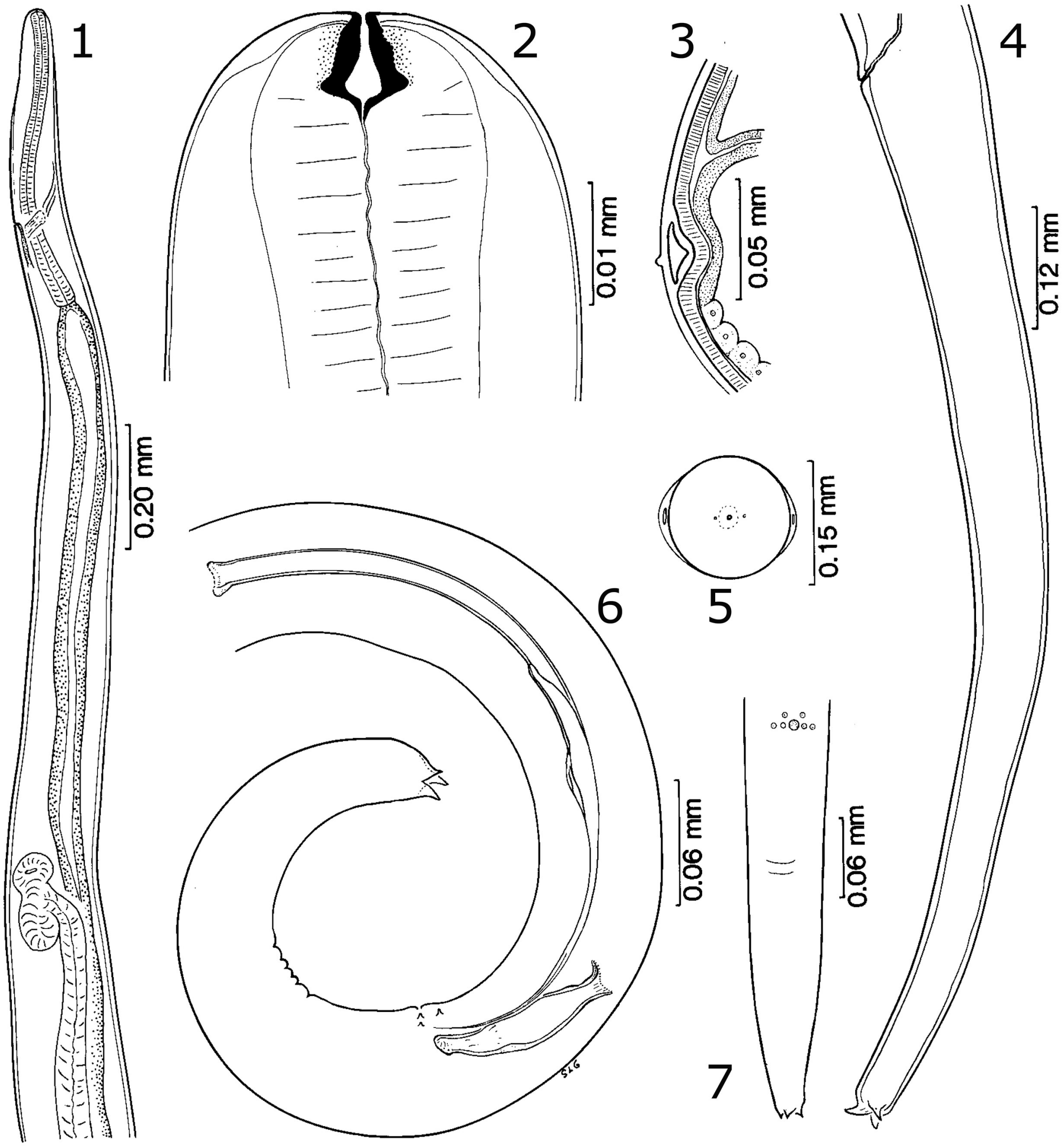

Figure 4. General morphological characters of a filarioid nematode of the genus *Litomosoides* that were obtained from pocket gophers collected in Weld County, Colorado, United States. Plate of *Litomosoides westi*: 1) Anterior end of female showing nerve ring, excretory pore, and vulva; 2) anterior end of female showing degree of development of stoma; 3) cross section of female showing lateral internal cuticular ridge; 4) posterior end of female showing species specific tail with three terminal points; 5) en face view of female; 6) posterior end of male showing coiled aspect, morphologically dissimilar spicules, and small cloacal papillae; 7) posterior end of male showing ventral view. Source: S. L. Gardner, HWML. License: CC BY.

When present, they could be visible at the anterior or posterior ends and appear as a delicate membrane. The internal anatomy of the microfilaria is unique, distinguished by several **internal nuclei** and **primordial organs** (Figure 8). From the anterior to the posterior end, it is possible differentiate the **nerve ring**, the **excretory vesicle** and the **excretory cell**, the inner body composed of few cells, a large stained **G1 cell**, and a row of 3 large, **stained cells** (R2–R4) similar to G1, connected to a clear area called the **anal vesicle** (Figure 8). The function of the G1 cell is unknown, but R2–R4 cells develop in the **rectum** and part of the reproductive system. It has been suggested that the inner body serves as a food reserve (Bain, 1972; McLaren, 1972; Anderson, 2000). The disposition and number of nuclei at the tip of the tail, plus the

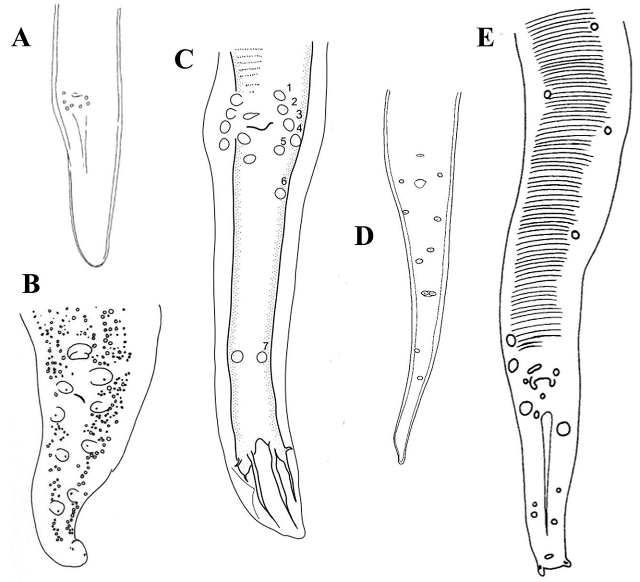

Figure 5. Different arrangements of male cloacal papillae, ventral views. A) *Litomosa goodmani* with a group of pericloacal papillae; B) *Ochoterenella esslingeri* with one precloacal papilla, 4 pairs of large symmetric postcloacal papillae, and ventral ornamentation made of irregular smaller bosses; C) *Mansonella (Mansonella) llewellyni*, precloacal *area rugosa* constituted by a row of small longitudinal ridges, caudal alae present, caudal papillae grouped near the cloaca, phasmids well developed at tip tail; D) *Litomosoides oxymycteri* with an attenuated tail, 1 precloacal papilla, one pair of ad-cloacal, and 4 pairs of asymmetric postcloacal papillae; E) *Orihelia anticlava* presenting precloacal *area rugosa* constituted by a row of small longitudinal ridges, 6 unpaired precloacal papillae, and several asymmetric postcloacal papillae, some larger than others, caudal lappets at tip tail. Sources: A) Adapted from Martin et al., 2006; B) adapted from Souza Lima et al., 2012; C) adapted from Bain et al., 2015; D) adapted from Notarnicola et al., 2000; E) adapted from Notarnicola and Navone, 2003. License: CC BY-NC-SA 4.0.

presence or absence of a sheath, are systematic characters of importance, mostly in species that parasitize humans.

One major characteristic of the Onchocercidae is the periodicity of the microfilariae, which refers to them flooding into the peripheral circulation at certain times of the day or night and disappearing from them at other times. The movement of the microfilariae appears to be associated with physiological changes of the host, as well as with the activity of the vector animals. The other notable characteristic is the longevity of the microfilariae, since they can live circulating in blood for several months after the adults have died. Both features are adaptations of microfilariae that allow them to be transmitted efficiently to the vectors.

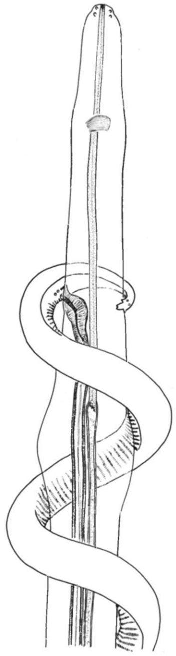

Figure 6. Schema of coupled male and female filarioids. Male cloaca positioned just opposite the female vulva during copulation. The area rugosa and cloacal papillae help for the attachment to female. Source: Adapted from Bain and Chabaud, 1988. License: CC BY-NC-SA 4.0.

Taxonomy of Suborder Filariata

See Anderson (2000) for a good reference to many of the topics following as well as Hodda (2022) for classification also for many life cycles and other important data on treatment and pathology see the web pages of the United States Centers for Disease Control and Prevention (2021).

Family Filariidae

This family includes filarioids parasitizing the subcutaneous tissues of certain mammals. Adults are small to medium-sized, and females possess a vulva located anterior to the nerve ring or near the oral opening, which facilitates the release eggs or juveniles in the skin (Figure 9). Adults and juveniles are located near one another. The family is composed of 2 subfamilies with only 5 genera (Table 1). Filarioids in this family are known to produce diseases clinically characterized by the occurrence of bleeding spots on the surface of the skin, or dermatitis.

Individuals of *Filaria taxideae* (in the subfamily Filariinae), for example, produce inguinal lesions in the skin of American badgers. Females are found in nodules containing embryonated eggs and few first juvenile stages. It is known that females live in the muscle fascia embedded in the dermis of their host and migrate to the epidermis evoking an

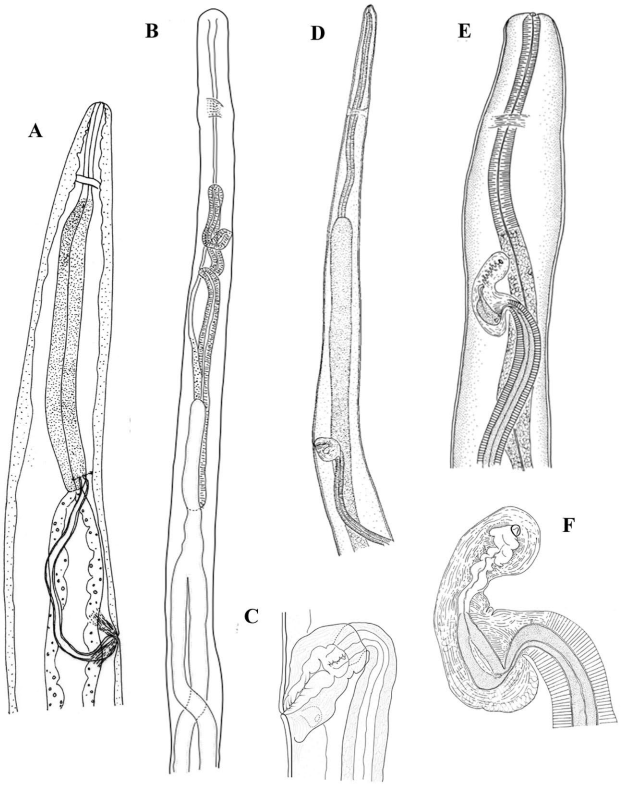

Figure 7. Anterior extremities showing the esophagus, position of the vulva, and shape of the vagina. A) *Ochoterenella esslingeri* possesses an esophagus divided in a short anterior muscular portion and a long posterior portion, the vagina is a simple muscular tube that opens posterior to the esophageal-intestinal junction; B, C) *Mansonella (Mansonella) ozzardi*. B) Anterior end showing a long fibrous esophagus with the vulva at mid-length of the esophagus; C) Vagina uterina simple; D) *Litomosoides oxymycteri* has an esophagus divided and vulva posterior to the esophageal-intestinal junction, vagina globular; E, F) *Dipetalonema robini*. E) Anterior end showing a divided esophagus, vulva at the level of the esophagus near the muscular-glandular division; F) Detail of the vagina, vagina vera conforming a chamber and vagina uterina muscular with a sinuous tube. Sources: A) Adapted from Souza Lima et al., 2012; B, C) adapted from Bain et al., 2015; D) adapted from Notarnicola et al., 2000; E, F) adapted from Vanderhoeven et al., 2017. License: CC BY-NC-SA 4.0.

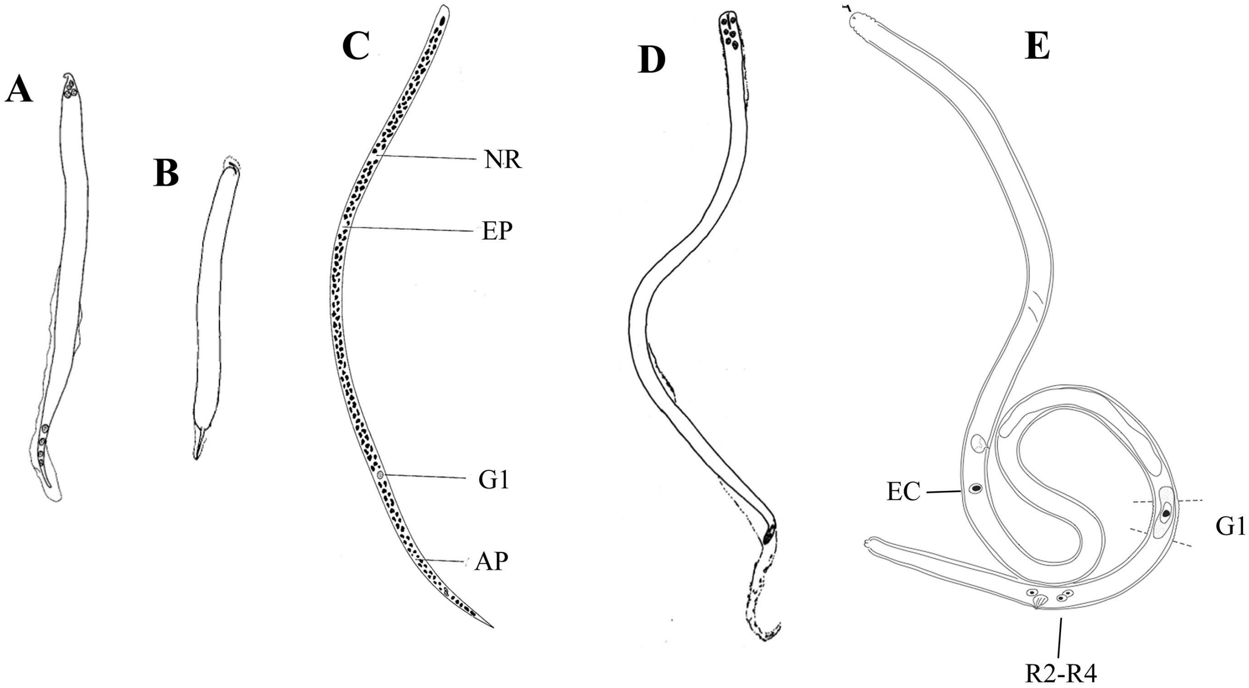

Figure 8. Different shapes of microfilariae. A) Uterine microfilaria of *Litomosoides oxymycteri*, sheath visible at tail; B) Uterine microfilaria of *Litomosoides solari* possessing a tail abruptly attenuated to a sharp point, sheath visible only at tip tail; C) Skin microfilaria of *Onchocerca lienalis*, unsheathed, tip tail with five nuclei aligned in a line; D) Uterine microfilaria of *Ochoterenella esslingeri*, sheathed; E) Blood microfilaria of *Mansonella (Tetrapetalonema) colombiensis*, unsheathed. NR: nerve ring; EP: excretory pore; G1: G1 cell; AP: anal pore; EC: excretory cell; R2-R4: R cells. Sources: A) Adapted from Notarnicola et al., 2000; B) adapted from Guerrero et al., 2002; C) adapted from Eberhard, 1979; D) adapted from Souza Lima et al., 2012; E) adapted from Bain et al., 2015. License: CC BY-NC-SA 4.0.

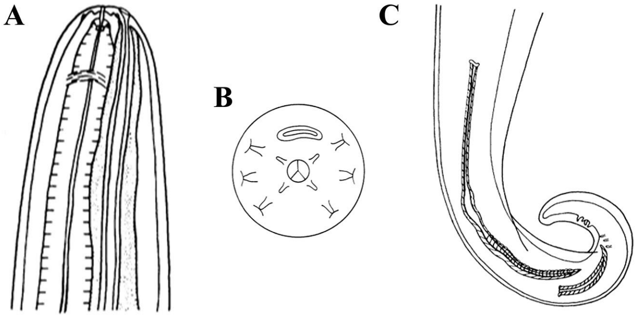

Figure 9. *Filaria taxideae*. A) Female anterior extremity showing the anterior position of the vulva; B) Female apical view, vulva located dorsal to the oral opening, 4 inner labial papillae and 4 external cephalic papillae, 2 lateral amphids; C) Male tail with dissimilar and unequal spicules. Source: Adapted from Keppner, 1969. License: CC BY-NC-SA 4.0.

inflammatory response due to the presence of both adults and eggs (Keppner, 1971). Similarly, species of *Parafilaria* (also in the subfamily Filariinae) have been described from the subcutaneous tissue on the upper parts of the body of horses, cattle, and water buffalo from Eurasia, Africa, and South America. In contrast to *Filaria taxideae*, females of *Parafilaria* migrate from the dermis and settle with their anterior ends immediately below the epidermis where they release embryonated eggs. The females pierce the skin of the nodule, causing bleeding which attracts the dipteran intermediate hosts (Figure 10). The first stage juvenile (J_1) is unsheathed and is carried in blood flowing from the skin. Second stage juveniles (J_2) are found in the body cavity and the fat body of *Musca* and *Haematobia* fly species, and the third stage juveniles (J_3) are found near the mouthparts (Anderson, 2000). Species of *Stephanofilaria* cause dermatitis, such as *S. stilesi* which causes dermatitis along the ventral midline, between the brisket and navel of cattle. In this species, adults are located in the dermis, just beneath the epidermis. The microfilariae are 50 μm-long and enclosed in a spherical sheath.

The development of the parasites coincides with the activity of the vector, that is, during the spring and summer. During these seasons, flies bite parasitized hosts, which become infected in 10 to 15 days, although the prepatent period for these filarioids is variable. Adults grow in 5 to 7 months post infection, depending on the species, and in 8 to 9 months the scratches characteristic of infection appear on the skin of cattle. The bloody spots are distributed in the hump, at the level of the neck, shoulders, withers, back, and rump, depending on the species. In *Parafilaria bovicola*, a parasite from cattle in Europe and Africa, the lesions tend to bleed when exposed to sunlight (Nevill, 1979).

Table 1. Genera included in the family Filariidae**.**

Subfamily	**Genus**	**Hosts**
Stephanofilariinae	*Stephanofilaria*	Parasites of Bovidae
Filariinae	*Filaria*	Parasites of carnivores and rodents
	Suifilaria	Parasites of Suidae
	Parafilaria	Parasites of ruminants and equids
	Pseudofilaria	Parasites of antelope

These worms are not overtly pathogenic; afflicted hosts do not become sick and consequently show no particular clinical symptoms. However, lacerated skin can become infected secondarily with bacteria, fly juveniles, and other pathogens. Moreover, it is known that symbiotic cleaning birds, like oxpecker or cattle tyrant, are also attracted by the spots due to the presence of insects and ticks, making the spots larger.

Several countries in Europe and Asia are endemic for these filarioids. Although the disease is not lethal, the nodules are painful and irritating, and slaughtered carcasses containing the worm are downgraded during inspection. From the point of view of conservation, these parasitoses are important. For example, in the 1960s, and more recently in 2012, there was a filariosis outbreak associated with *Stephanofilaria dinniki* (in the subfamily Stephanofilarinae) in threatened species of white and black rhinoceroses in Meru National Park in Kenya (Round, 1964; Mutinda et al., 2012) (Figure 10).

The therapy recommended for these parasitoses against the adult worms is ivermectin in different doses according to the host (such as cattle or horses), as well as high doses of levamisole and fenbendazole. It is also recommended to control flies and ticks to reduce the entry points of infective juveniles.

Family Onchocercidae

The Onchocercidae includes a diverse group of nematodes with more than 80 genera split among 8 subfamilies. The adult worms are small- to medium-sized. Females possess a vulva situated in the anterior region at the level of the esophagus, although occasionally may be found in the equatorial region. Males have a posterior extremity coiled with or without caudal alae. Microfilariae inhabit the skin, lymph, or blood. Unlike the Filaridae, adults live far away from the juvenile stages, inhabiting the body cavity, heart, skin, muscles, eyes, lymphatic system, and other regions of the host's body.

One of the 8 subfamilies, the Oswaldofilariinae, is confined to reptiles, another 2, the Waltoneliinae and Icosieliinae, to amphibians, while the Splendidofilariinae and the Lemdaniinae are parasites of reptiles, birds, and mammals. The Setariinae are confined to large mammals. Due to their great

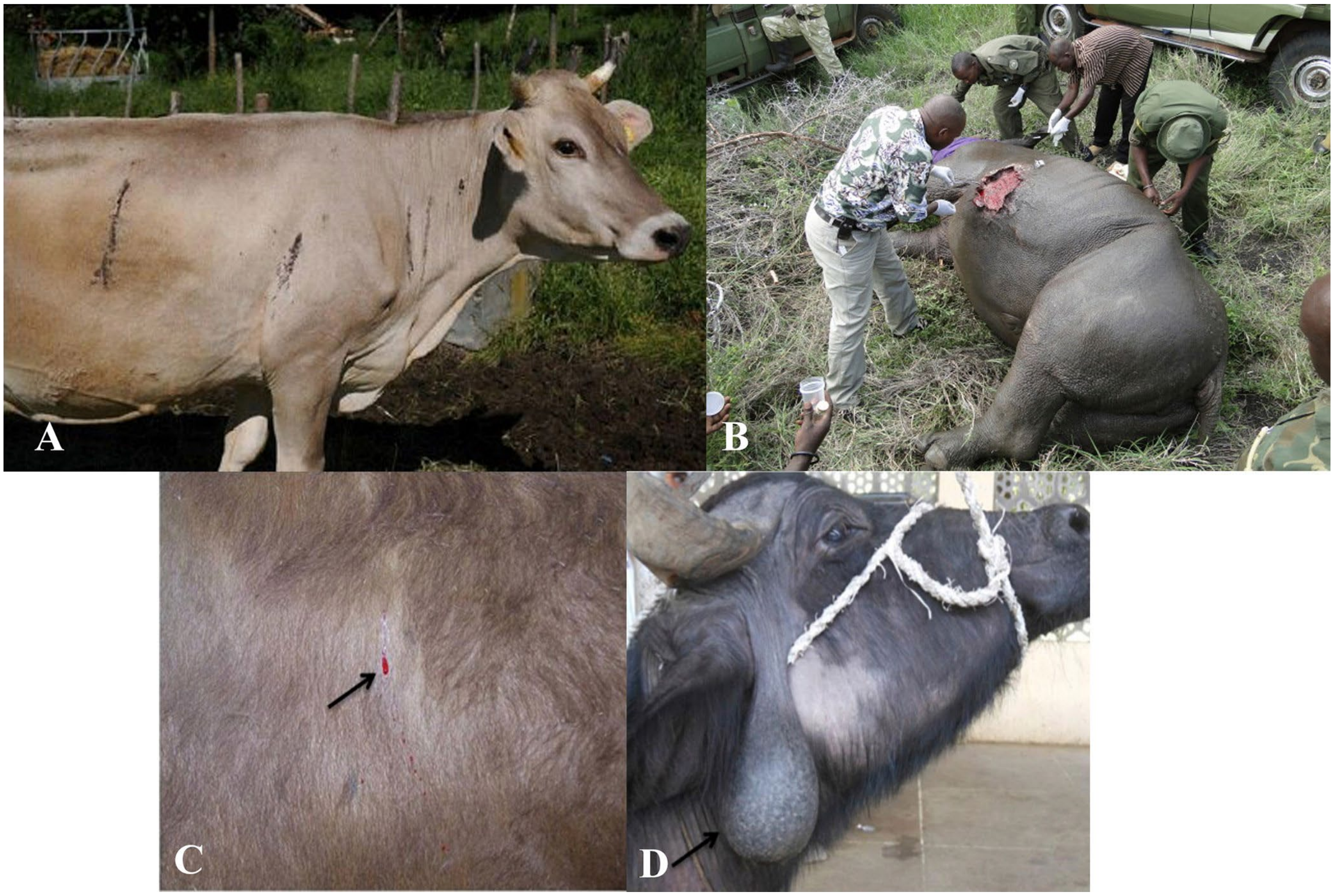

Figure 10. A) Adult female Buffalo from India with a growth below right ear with multifocal bleeding points over the skin; B) Bleeding spot in adult female Buffalo from India caused by *Parafilaria bovicola*; C) Bleeding spot from rhinoceros in Kenya caused by *Stephanofilaria dinniki*. Sources: A, B) Chandratre et al., 2017; B) Mutinda et al 2012. Licenses: A, B) CC BY-NC-SA; C) CC BY 4.0.

diversity and the numerous diseases they cause, the most important subfamilies are the Onchocercinae and Dirofilariinae. Both subfamilies are mainly parasites of mammals, although a few genera occur in birds and reptiles.

Subfamily Oswaldofilariinae

This subfamily includes filarioids that parasitize lacertilians and crocodiles. The location of adults is variable, being found in the connective tissue, heart, aorta, mesentery, intestinal wall, or body cavity. They are transmitted by mosquitoes. Members of the Oswaldofilariinae are distinguished by a vulva located in the middle or posterior region of the body, an esophagus that is well developed and divided, no caudal alae, sometimes large caudal papillae forming a subterminal group, and spicules that are often stout, unequal, and dissimilar from one another (Figure 11).

The subfamily is composed of 7 genera all parasitizing lizards, with the exception of *Oswaldofilaria*, which has 3 species in crocodiles. *Oswaldofilaria* is the most diverse genus with 13 species distributed in Australia, Africa, and South America (notably, a Gondwanian distribution). *Befilaria* comprises 3 species, 1 in the Neotropical region and 2 in the Ethiopian region; *Piratuboides* is present in South America and Australia only, with 1 and 2 species, respectively. The remaining genera have a restricted distribution. *Piratuba* includes 7 species in the Neotropics, *Conispiculum* includes 2 species, *Gonofilaria* has only 1 species occurring in India, and a single species in *Solafilaria* is found in lizards from Madagascar.

As mentioned above, it has been demonstrated that these filarioids are non-pathogenic to their hosts. A survey carried out in 110 *Tropidurus torquatus* from Brazil revealed that adult filarioids of *Oswaldofilaria chabaudi* were found 35% in the body cavity and 65% in the muscular aponeuroses of which 58% were found in the thighs and 7% at the base of the tail (Pereira et al., 2010). Microfilariae circulate in the blood. Experimental development in different species of *Oswaldofilaria* involved mosquitoes of the genera *Aedes*, *Culex*, and *Anopheles*. Juvenile stages were found in the adipose tissue or muscles of the dipterans.

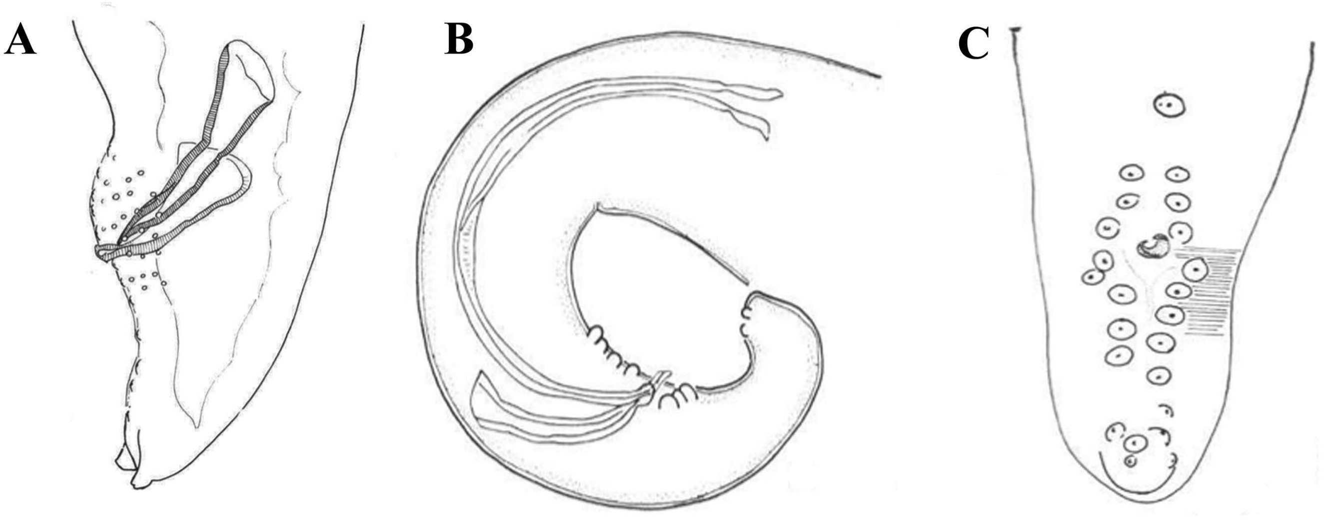

Figure 11. Posterior extremity of males from Oswaldofilariinae. A) *Conispiculum ramachandrani*, lateral view; left spicule slightly longer than right, unequal; numerous minute papillae around the cloaca and lappets at tip tail; B) *Oswaldofilaria versterae*, lateral view, showing pre and postcloacal papillae; left spicule long dissimilar and unequal than right; C) *Befilaria puertoricensis*, ventral view showing 2 lines of cloacal papillae. Sources: A, B) Adapted from Bain et al., 1982; C) adapted from Bain and Chaniotis, 1975. License: CC BY-NC-SA 4.0.

Subfamily Icosielliinae

This subfamily includes a single genus, *Icosiella*, including 9 species parasitizing the subcutaneous aponeurosis of amphibians from Palearctic, Occidental, and Australian realms. Adult worms are short with the posterior end of the body conical and blunt in females and protuberant in males. The buccal capsule is absent, 2 median cephalic spines are present, the esophagus is divided into a short anterior muscular and a long posterior glandular portion, and the anus is subterminal (Figure 12). Nine species were described from subcutaneous tissues from frogs of the family Ranidae, mainly in the genus *Rana*. Vectors in the life cycle of *I. neglecta* were shown to include *Forcipomyia* (biting midges in the family Ceratopogonidae) and *Sycorax* (in the family Psychodidae); these were observed to feed on the head of frogs. Second-stage juveniles (J_2) were detected in the muscles of the flies (Desportes, 1941; 1942).

Subfamily Waltonelliinae

Members of this subfamily are parasites from the body cavity and mesentery of frogs and toads included in the families Bufonidae, Leptodactilidae, Racophonidae, and Ranidae. Adults are characterized by the presence of large cephalic papillae, lateral and caudal alae, and thin and dissimilar spicules (Figure 13). They are distinguished from members of the Icosielliinae by their long tail and the absence of cephalic spines.

There are 5 genera: *Waltonella*, *Ochoterenella*, *Madochotera*, *Foleyellides*, and *Paramadochotera*. Currently, *Ochoterenella* is the only genus reported in Central America and South America. The life cycle is only known for some species of *Waltonella*. They are transmitted by mosquitoes of the family Culicidae allowing microfilariae to develop in the body cavity (in *W. brachyoptera*), in the muscles (in *W. ranae*), or in the fat body (in *W. flexicauda*). Second- and third-stage juveniles (J_2 and J_3) may be found in mosquitoes 15 days post-infection and during the prepatent period in frogs in approximately 7 to 8 months.

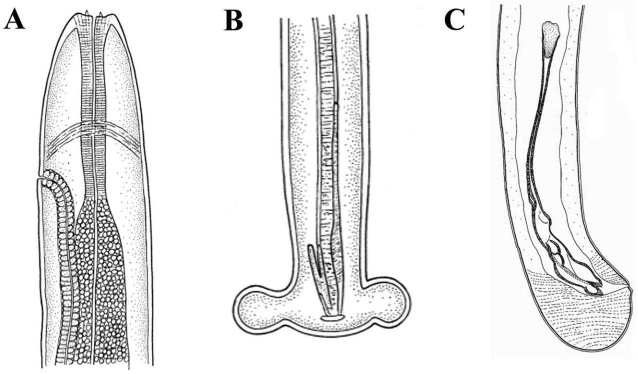

Figure 12. Examples of Icosielliinae species. A, B) *Icosiella turgeocauda*; A) Anterior end of female showing the muscular and glandular esophagus, and the muscular vagina; B) Posterior end of male, ventral view showing two lateral swollen, and dissimilar and unequal spicules; C) Male posterior end of *I. intani,* lateral view showing the spicules. Sources: A, B) Adapted from Bursey et al., 2003; C) adapted from Purnomo and Bangs, 1996. License: CC BY-NC-SA 4.0.

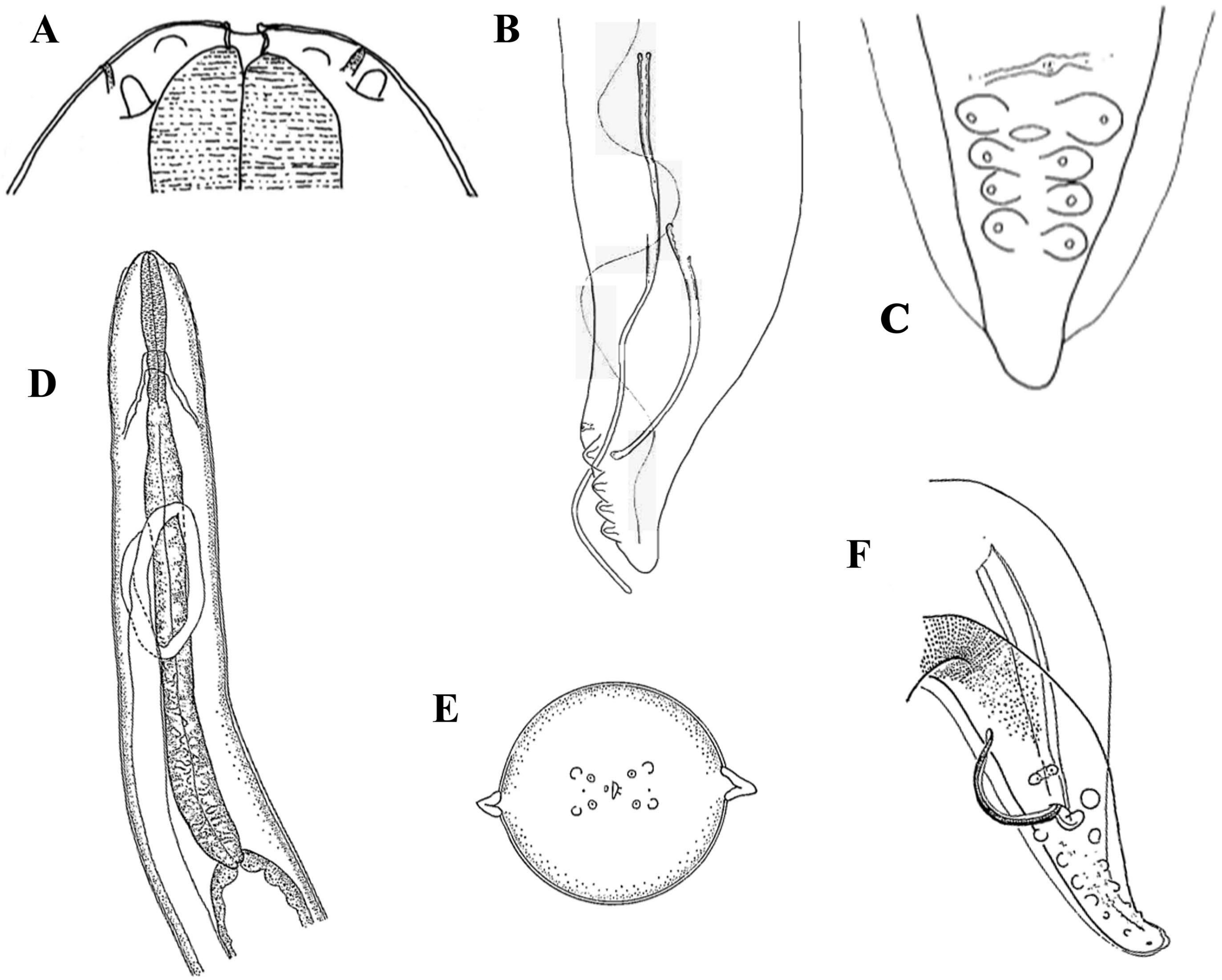

Figure 13. Waltoneliinae species. A) *Ochoterenella esslingeri* anterior extremity showing the buccal capsule and head papillae; B, C) Male posterior end of *Madochotera pichoni*. B. Lateral view showing the spicules and lateral alae; C) Ventral view with large symmetric cloacal papillae; D-F) *Foleyellides striatus*, male; D) Anterior extremity showing the divided esophagus; E) Apical view of the head showing the head papillae and the lateral alae; F) Tail with spicules and caudal papillae. Sources: A) Adapted from Souza Lima et al., 2012; B, C) adapted from Bain and Prod'hon, 1974; D) J. Notarnicola; E) adapted from Esslinger, 1986. License: CC BY-NC-SA 4.0.

Subfamily Setariinae

This subfamily comprises 2 genera: *Setaria* with more than 40 species parasitizing artiodactyls, mainly bovines, hyracoids, and equines; and *Papillosetaria* with only 3 species parasitic in artiodactyls. They are normally found in the abdominal cavity, but also rarely can be found in the eyes, lungs, and skin. Adults are medium- to large-sized, characterized by a complex cephalic structure composed of median or lateral cuticular elevations (spines) and well-developed cephalic papillae. The vulva is near the muscular esophagus, the male tail is rounded without caudal alae, and the spicules are markedly dissimilar from one another (Figure 14). Sheathed microfilariae are 200–231 μ-long; they circulate in the blood until mosquitoes feed on them (*Aedes* spp., *Culex* spp., and *Anopheles* spp.). Microfilariae invade the hemocoel and later the fat body where development takes place. After 12 days, the J_2 is developed and moves again to the hemocoel where it stays for 5 to 12 days more until it reaches the J_3 stage. The infective juveniles are 1.65–2.32 mm-long with numerous tubercules on the tip of the tail. These juveniles then invade a new host and migrate to the final location, the abdominal cavity. The prepatent period varies between 7 and 8 months, and the longevity of adult worms is 1.5 years (Osipov, 1966).

Two species are distributed worldwide: *Setaria equina*, a parasite of the abdominal cavity of horses, and *S. labiatopapillosa* from cattle. *Setaria digitata* parasitizes cattle in Asia. Adults are non-pathogenic, thus, filariasis goes unnoticed unless detected by the presence of microfilariae in blood smears.

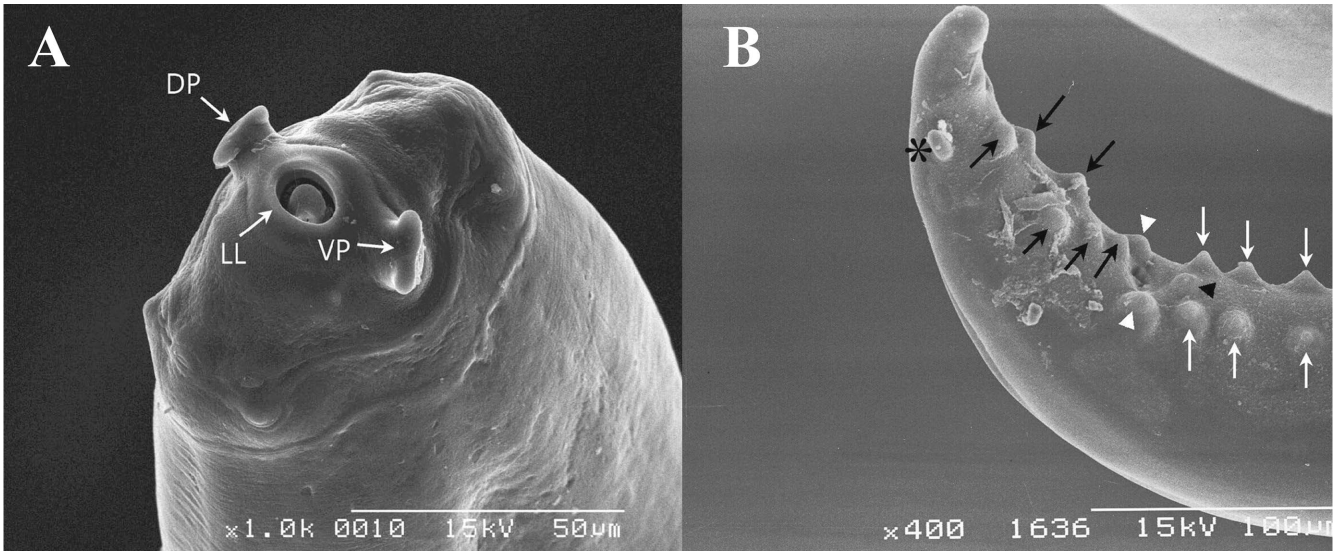

Figure 14. Scanning electron micrograph of *Setaria digitata* found in horse from Korea. A) Anterior end of a male adult showing the anterior structure; DP: Dorsal projection, LL: Lateral lips, VP: Ventral projection; B) Male tail showing the papillae and a pair of lateral appendages near the tip tail (asterisk). Three pairs of precloacal papillae (white arrows), a pair of ad-cloacal papillae (white arrowheads) and 3 pairs of postcloacal papillae (black arrows), plus a central papilla just in front of the cloaca (black arrowhead). Source: Shin et al., 2017. License: CC BY 4.0.

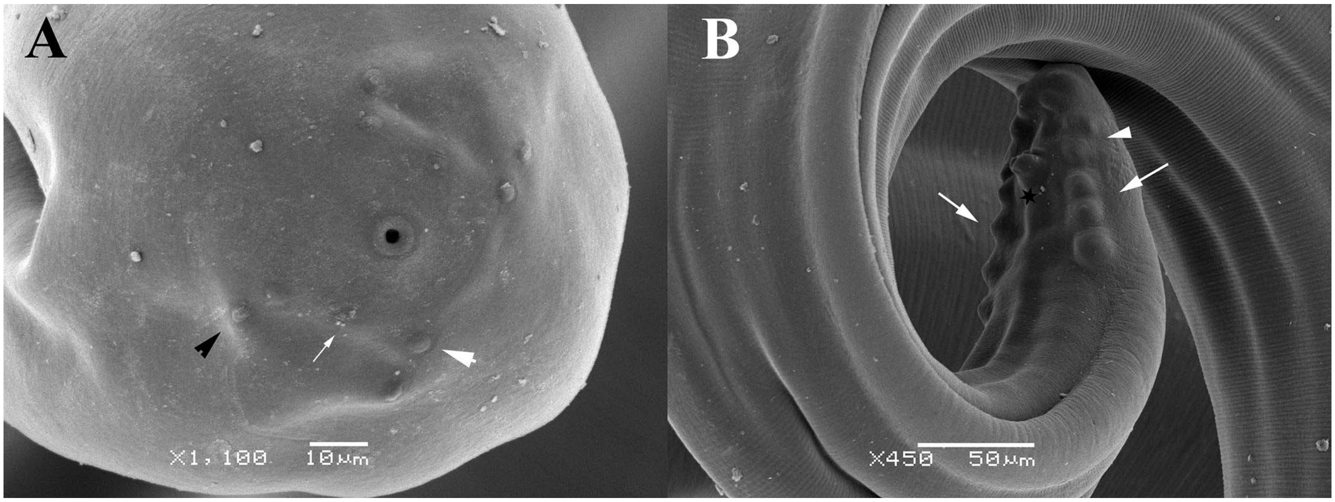

Figure 15. Scanning electron micrograph of *Pelecitus* sp. found in *Arremon flavirostris* (Emberizidae) from Argentina. A) Apical view showing 4 labial papillae (white arrowhead), 4 cephalic papillae (black arrowhead), and amphids (white arrow); B) Posterior extremity of male with protruded cloaca (black asterisk), large precloacal papillae (white arrows), and a group of 2 pairs of postcloacal papillae (white arrowhead). Source: J. Notarnicola. License: CC BY-NC-SA 4.0.

The major pathogenic effect occurs when immature stages migrate erratically in the pleural cavity, central nervous system, urinary bladder, and other organs. *Setaria cervi*, a common parasite of the body cavities from *Alces alces*, *Capreolus* spp., and *Cervus* spp. in Europe and Asia, is frequently found invading the central nervous system with concurrent infections with *Elaphostrongylus cervi* (Metastrongylidae) causing neurological disease (Blažek et al., 1968).

Subfamily Dirofilariinae

Nematodes of this subfamily include males with a short tail and a well-developed caudal alae, which distinguish them from other members of the Onchocercidae. They also have large and pedunculate caudal papillae and spicules that are markedly dissimilar from one another (Figures 15 and 16). Representatives of this subfamily include 1 genus parasitizing reptiles, 1 genus in birds, and 8 in mammals (Table 2)

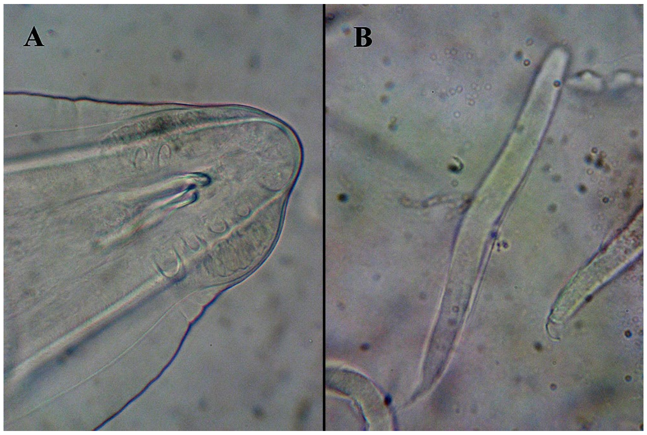

Figure 16. A) Photograph of *Pelecitus* sp. found in *Arremon flavirostris* (Emberizidae) from Argentina, posterior extremity of a male showing symmetrical caudal alae, spicules dissimilar and caudal papillae; B) Photograph of uterine microfilaria of *Pelecitus fulicaeatrae* found in *Podiceps occipitalis* (Podicipediformes) from Argentina. Source: J. Notarnicola. License: CC BY-NC-SA 4.0.

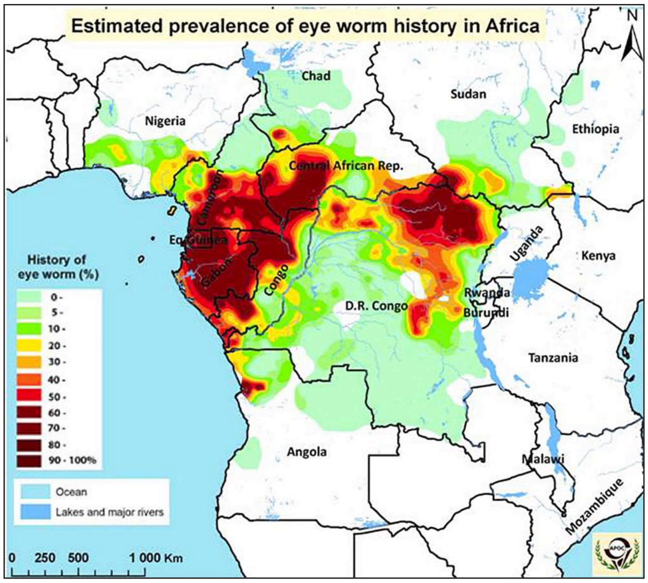

Figure 17. Distribution of *Loa loa* based on prevalence data collected in more than 4,700 villages in 11 African countries. Source: Adapted with data from WHO, 2010, https://www.who.int/apoc/raploa/Africa_EN_map.jpg?ua=1. License: CC BY-NC-SA 4.0.

(Anderson, 2000). Most of the genera are parasites of the subcutaneous tissues or muscles, with the exception of *Edesonfilaria* spp., which is located in the body cavity of arboreal dermopterans, chiropterans, and primates from the Indo-Malaysian region, and the cosmopolitan *Dirofilaria immitis* which parasitizes the right ventricle of the heart and pulmonary artery of carnivorous mammals.

This subfamily includes 2 species that are of epidemiological importance for humans: *Loa loa* and the zoonotic *Dirofilaria immitis*. Adult worms of *L. loa* live in subcutaneous tissues of humans producing edematous swellings on the body known as Calibar swellings or loiasis. Occasionally they migrate through the eyes in the conjunctiva and cornea. The species is endemic of the rainforest of West Africa and equatorial Sudan. Usually, it is diagnosed by the presence of microfilariae in blood smears or adults in the subconjunctiva. It is estimated that between 3 and 13 million people are infected at any one time with filariasis (Klion and Nutman, 2011). Infection is hidden in a large proportion of patients, which are asymptomatic. According to the World Health Organization (WHO, 2022), loiasis (also called African eye worm) is potentially endemic in 11 African countries, recording more than 40% of prevalence in Gabon, Equatorial

Table 2. List of Dirofilariinae genera with their localization and their hosts.

Genus	Localization	Hosts
Bostrichodera	Muscles	Parasites of edentates
Dirofilariaeformia	Pulmonary artery	Parasites of rodents Sciuridae
Edesonfilaria	Body cavity	Parasites of arboreal dermopterans, chiropterans, and primates
Macacanema	Muscles	Parasites of primates
Skjabinodera	Inguinal fascia and renal fat	Parasites of ungulates
Loa	Subcutaneous tissues	Parasites of primates
Foleyela	Subcutaneous and intermuscular connective tissues; body cavity	Parasites of reptiles chameleonids
Pelecitus	Tendons and muscles near leg joints and feet	Parasites of birds and mammals
*Dirofilaria**	Subcutaneous tissue and heart	Parasites of mammals
Loaina	Subcutaneous tissue and muscles	Parasites of lagomorphs

* *Tawila tawila* Khalil 1932 was transferred to *Dirofilaria tawila* by Webber, 1955.

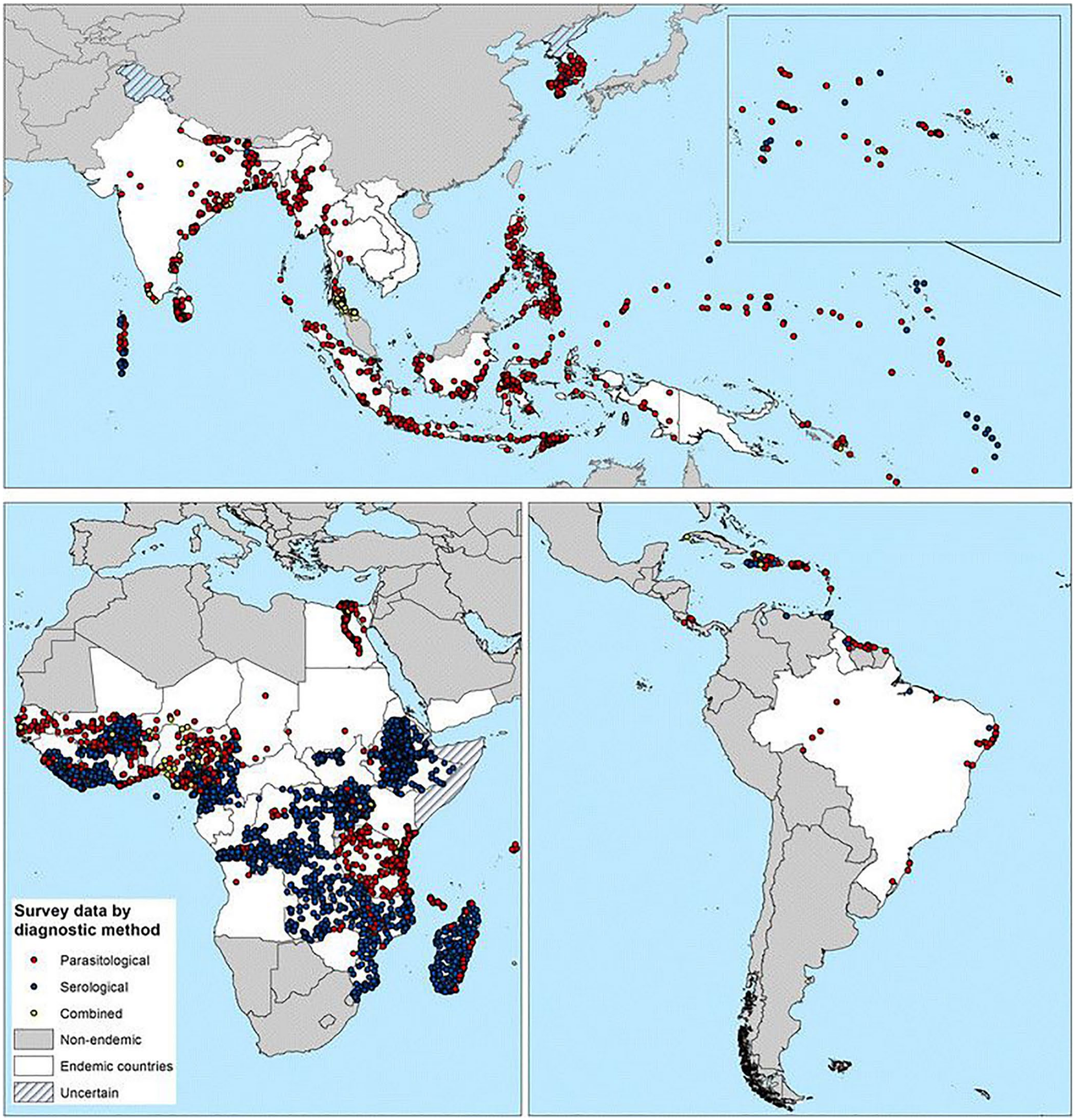

Figure 18. Global atlas of lymphatic filariasis (LF). Global distribution of LF and data points by diagnostic method. Data were identified for 66 of the 72 countries currently endemic and for a further 17 countries where LF is no longer endemic. Red = parasitological methods; blue = serological methods; and yellow = combination of methods. Source: Cano et al., 2014. License: Graphics and text, CC BY 4.0; data, CC0.

Guinea, southern Cameroon, eastern Central African Republic, the Republic the Congo, northwestern Democratic Republic of the Congo, and southwestern Sudan (Figure 17).

The heartworm *Dirofilaria immitis* is a common parasite of dogs and other mammals of several orders, including humans (Artiodactyla, Carnivora, Edentata, Lagomorpha, Perissodactyla, Primates, and Rodentia). Most animals exhibit no signs of disease when infected, however, some of them experience respiratory distress, cough, and other symptoms. Human dirofilariosis has been reported worldwide. Cases presenting with subcutaneous infestations in the Old World are attributed to *D. repens*, a subcutaneous worm from dogs,

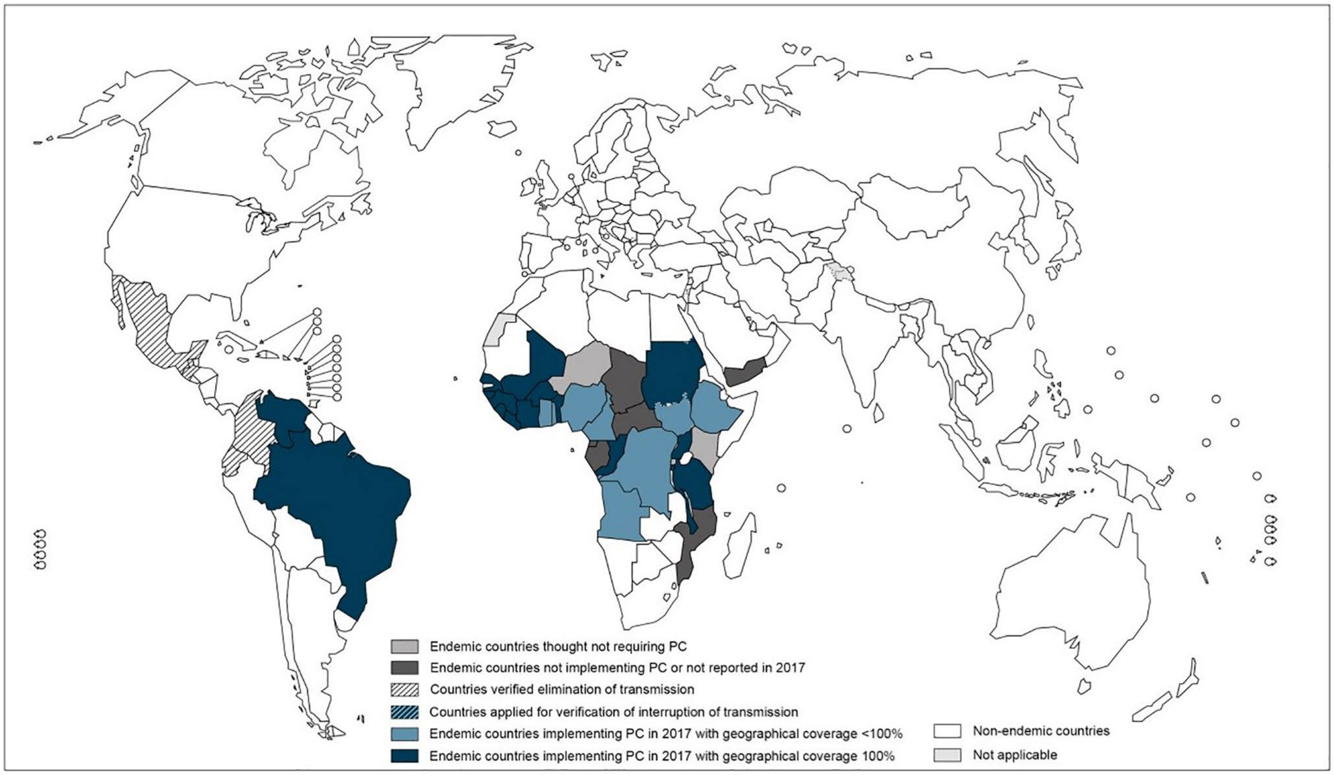

Figure 19. Map of the distribution and status of preventive chemotherapy for onchocerciasis worldwide. Source: Adapted from WHO, https://www.who.int/news-room/fact-sheets/detail/onchocerciasis. Permissions: Cf WHO terms of acceptable uses (non-commercial, educational).

whereas pulmonary dirofilariosis in the New World is associated with *D. immitis* (Dantas-Torres and Otranto, 2013).

The life cycle of filarioids within Dirofilariinae generally includes mosquitoes as intermediate hosts. In *Dirofilaria* spp. juvenile stages develop in Malpighian tubules and, depending on the country and habitat, different genera act as vectors, specifically, *Culex*, *Aedes*, *Anopheles*, *Ochlerotatus*, *Stegomyia*, *Jarnellius*, and *Aedimorphus*. In *Foleyella*, J_2s and J_3s develop in the fat body of mosquitoes, while *Loaina* prefers the hemocoel. In the case of *Loa loa* species, it develops in the horsefly, while *Pelecitus* develops in Mallophaga lice.

As an example of a life cycle, adults of *Pelecitus fulicaeatrae* are found in the tendons near the ankle of coots and grebes. Both male and female *P. fulicaeatrae* worms are short and coiled, and males possess an asymmetrical caudal ala and large pedunculate cloacal papillae. In other species of *Pelecitus*, the caudal alae are symmetrical (Figure 16). Microfilariae are about 92–122 µm-long and occur in the skin and the feathered portions of the lower leg, usually located near the feather follicles (Figure 17). The louse *Pseudomenopon pilosum* (order Amblyocera, suborder Mallophaga) inhabits the base of feathers ingesting tissues of the bird with microfilariae. Second-and third-stage juveniles (J_2 and J_3) of *P. fulicaeatrae* were recovered from the fat body in naturally infected lice. Parasitized lice can be transferred from adult coots to coot chicks, infecting the young birds. Immature adult worms can be found after 20 days post-infection in the ankles, while microfilariae appear in the skin after 7 to 8 months (Bartlett and Anderson, 1989).

Subfamily Onchocercinae: Cause of Several Neglected Diseases in Humans

This subfamily includes more than 30 genera parasitizing mammals. Some of them induce what are termed **neglected diseases** of humans, which is defined by the United States Centers for Disease Control and Prevention (CDC, 2021) as diseases caused by parasites, viruses, or bacteria that cause substantial illness for approximately 15% of the world's inhabitants that results in trapping them in a cycle of poverty.

The worms in this subfamily have a long non-alate tail and dissimilar and unequal spicules (see Figures 3 and 4 above). Adult worms are usually located in the body cavity of the host; however, some species inhabit subcutaneous tissues or the lymphatic vessels and nodes.

Seven species are responsible for infection in humans: *Wuchereria bancrofti, Brugia malayi*, *B. timori*, *Onchocerca volvulus*, *Mansonella (Mansonella) ozzardi*, *M. (Esslingeria) perstans*, and *M. (E.) streptocerca*. Each is described briefly below.

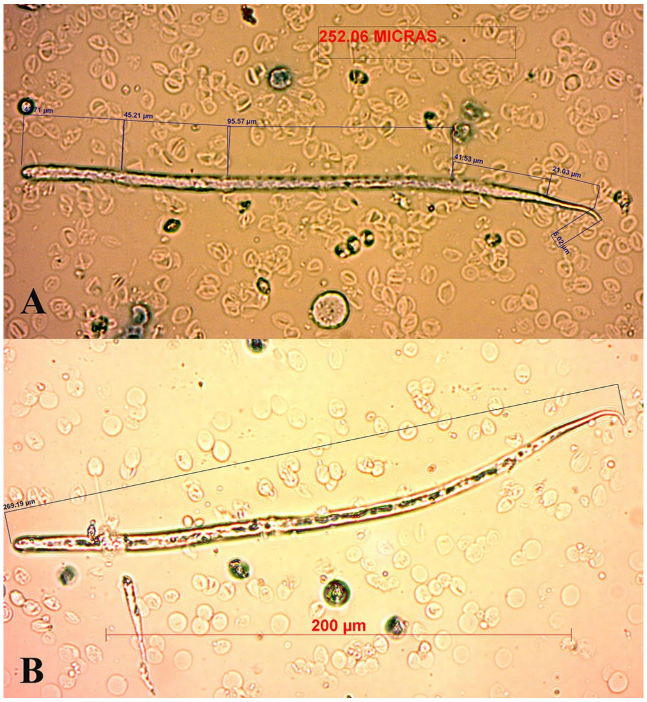

Figure 20. Microfilariae photographs. A) From *Dirofilaria immitis*; B) From *Acanthocheilonema reconditum*. Microfilariae from *D. immitis* is characterized by a cephalic end rounded, straight tip tail, and longer body length; *A. reconditum* possess a cephalic end obtuse, tail J-shaped and shorter body length. Source: S. Costa. License: CC BY-NC-SA 4.0.

Wuchereria bancrofti, Brugia malayi, and *B. timori* cause lymphatic filariasis, or elephantiasis, due to the parasites living in the lymphatic system (vessels and nodes), disrupting the system's normal function. Infection is usually acquired in childhood causing hidden damage to the lymphatic system. Later in life, people develop lymphedema and elephantiasis as well as hydrocele and scrotal elephantiasis. Patients usually suffer physical disability that contributes to poverty (Yonder and Pandey, 2023).

Ninety percent of lymphatic filariasis is caused by *Wuchereria bancrofti*; the remaining 10% by *Brugia malayi* and *B. timori*. Bancroftian filariasis is transmitted by several different species of mosquitoes: *Culex* spp., widespread in urban and semi-urban areas; *Anopheles* spp., mainly found in rural areas; and *Aedes* spp., found on endemic islands in the Pacific. *Brugia malayi* is transmitted by mosquito species of the genus *Mansonia*, whereas *B. timori* is transmitted by *Anopheles* mosquitoes (Anderson, 2000).

Lymphatic filariasis is a major problem in tropical and subtropical countries, extending throughout central Africa, the Nile delta, Turkey, India, Southeast Asia, the East Indies, the Philippine and oceanic islands, Australia, New Guinea, Brazil, Guyana, Venezuela, and some countries in Central America (Figure 18). It is estimated that 120 million people are infected worldwide; of these, almost 25 million men have genital disease and almost 15 million, mostly women, have lymphedema or elephantiasis of the leg (Anderson, 2000).

Onchocerca volvulus specimens are usually found in subcutaneous tissues producing onchocerciasis, or river blindness, which is a filariosis characterized by pruritus, dermatitis, lymphadenopathy, and ocular lesions. It is not a fatal disease; however, it can cause disfigurement of the skin and visual impairment, including permanent blindness. It is transmitted to humans through exposure to repeated bites of infected blackflies of the genus *Simulium*. The WHO (2022) reports that 20.9 million people were infected with *O. volvulus* worldwide in 2020, 14.6 million infected people had skin disease, and 1.15 million had vision loss. Onchocerciasis is distributed in 31 countries of Africa, Yemen, and some countries of Latin America (Figure 19). Implementation of different programs for control, eradication, and treatment of the disease were carried out by the WHO and governments, contributing to Colombia, Ecuador, Mexico, and Guatemala being free of onchocerciasis (WHO, 2022).

Three *Mansonella* species cause mansonellosis. *Mansonella (Mansonella) ozzardi* and *M. (Esslingeria) perstans* reside in body cavities and the surrounding tissues, while *M. (E.) streptocerca* lives in the dermis and subcutaneous tissue. Infections by *M. (E.) perstans* are often asymptomatic, however, are at times associated with angioedema, pruritus, fever, headaches, arthralgias, and neurologic manifestations. Those produced by *M. (E.) streptocerca* can cause skin manifestations, including pruritus, papular eruptions, and skin pigmentation changes. *Mansonella (M.) ozzardi* can cause arthralgias, headaches, fever, pulmonary symptoms, adenopathy, hepatomegaly, and pruritus. Adult filarioids live for several years and reside in various tissues. Biting midges of the family Ceratopogonidae transmit all 3 *Mansonella* species and blackflies of the family Simuliidae play an important role in the transmission of *M. (M.) ozzardi* in Latin America. *Mansonella (E.) perstans* is endemic in Sub-Saharan Africa as well as a northern part of the Amazon rainforest stretching from equatorial Brazil to the Caribbean coast of South America. *Mansonella (E.) streptocerca* is limited to continental Africa, occurring in the tropical rainforest areas of central and west Africa as well as in Uganda, while *M. (M.) ozzardi* has a patchy geographic distribution across Latin America. It has been recorded from southern Mexico to northwestern Argentina, but has not been reported in Chile, Uruguay, or Paraguay. The parasite also occurs on several Caribbean islands and elsewhere in Latin America (Anderson, 2000).

There is a lack of data about the prevalence of the filarioid disease mansonellosis and the morbidity and mortality

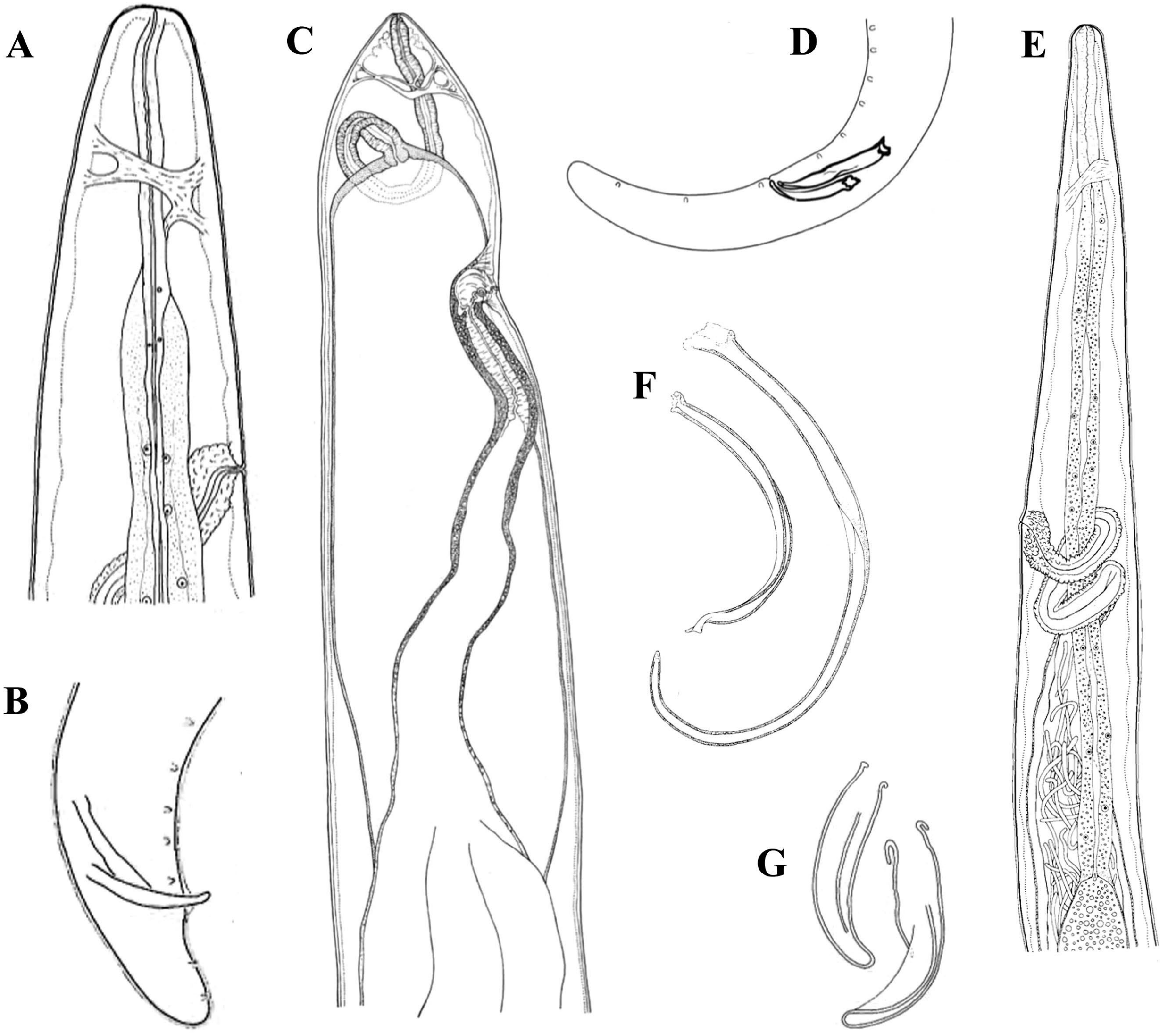

Figure 21. Examples of Splendidofilariinae species. A, B) *Dessetfilaria guianensis*; A) Female anterior extremity showing the muscular and glandular esophagus and the vulva; B) Male tail, lateral view showing the similar and equal spicules; C, D) *Meningonema peruzzii*; C) Female anterior extremity; D) Male tail, lateral view showing the spicules; E, F) *Chandlerella bushi*. E) Female anterior extremity; F) Spicules, dissimilar; G) *Splendidofilaria chandenieri* spicules, similar and equal. Sources: A, B) Adapted from Bartlett and Bain, 1987; C, D) adapted from Orihel and Esslinger; E, F) adapted from Bartlett and Anderson, 1987; G) adapted from Bartlett and Bain, 1987. License: CC BY-NC-SA 4.0.

associated with it. The lack of knowledge of these effects is due in part to a high prevalence of asymptomatic cases, the lack of a clinical profile that makes diagnosis difficult, plus the similarity of the microfilariae to *Mansonella (Esslingeria) streptocerca* (in Africa) and *M. (Mansonella) ozzardi* (in Latin America) with that of *Onchocerca volvulus*. Additionally, mansonellosis parasites have been shown to interfere with some onchocerciasis immunodiagnostic assays, may interfere with the diagnostics used in other neglected tropical disease controls, and negatively affect the efficacy of vaccine programs (specifically, HIV and tuberculosis vaccines) (Ta-Tang et al., 2018).

The method for diagnosing lymphatic filariasis and *Mansonella (Esslingeria) perstans* and *M. (Mansonella) ozzardi* diseases is usually the finding of microfilariae in peripheral blood smears thick- or thin-stained with Giemsa or hematoxylin-and-eosin. Concentration techniques, such as Knott's technique or filtration through a Nucleopore® membrane, may also be efficacious in cases with a low burden of microfilariae. As lymphatic filariasis exhibits a nocturnal periodicity, an accurate diagnosis is best achieved on smears collected at night (10:00 pm–2:00 am). For *Mansonella* this is not necessary because it is a non-periodic filariasis. These

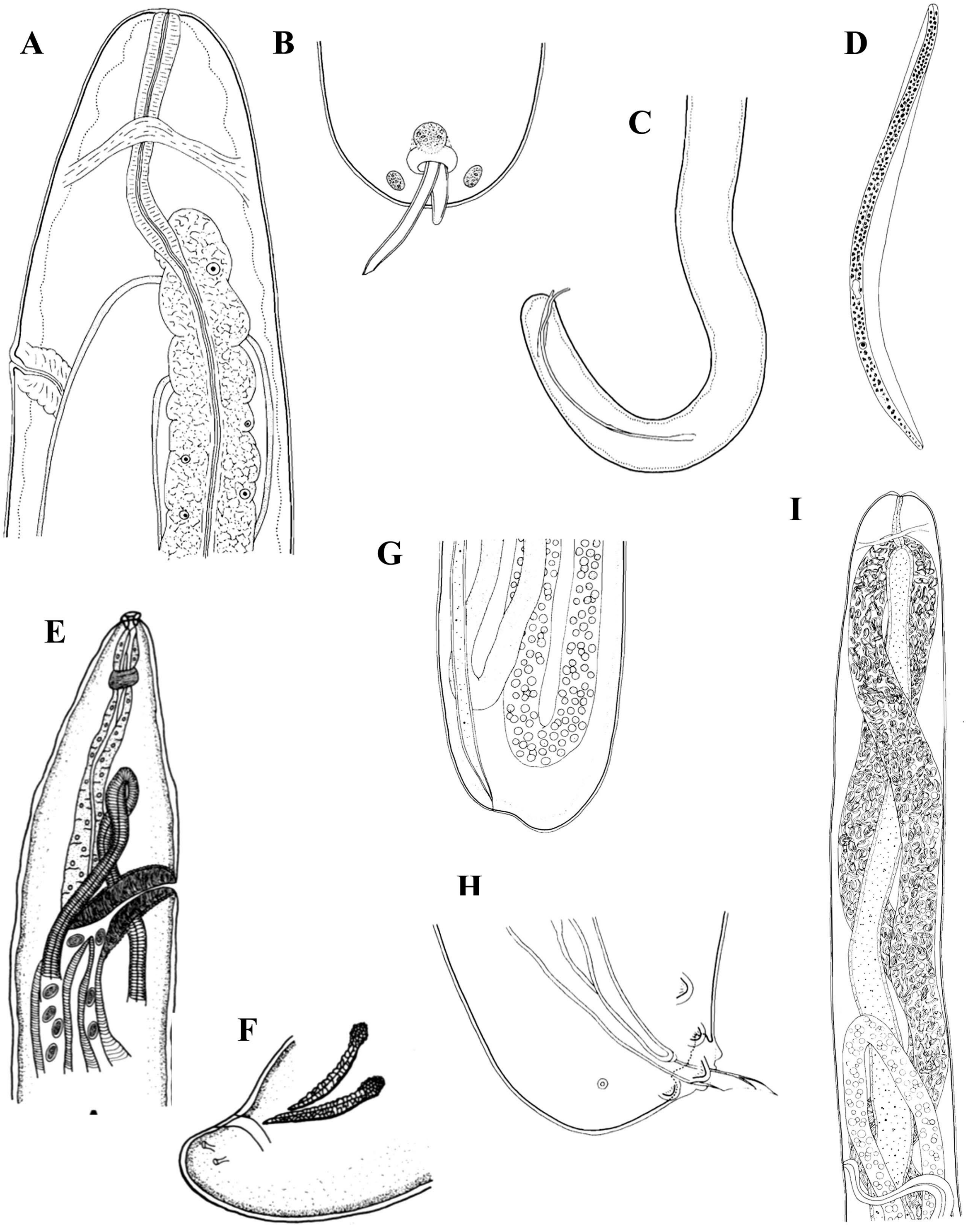

Figure 22. Examples of Lemdaniinae species. A–D) *Lemdana wernaarti*; A) Female anterior extremity showing the differentiation of the muscular and glandular esophagus and position of the vulva; B) Male tail with cloacal papillae; C) Male posterior extremity with dissimilar spicules; E, F) *Aprocta intraorbitalis*. E) Female anterior extremity; F) Male tail with similar spicules and cloacal papillae. G–I) *Eulimdana lari*. G) Female tail showing the anus at tip tail; H) Male tail with similar spicules and cloaca at tip tail; I) Female anterior extremity showing the differentiation of the muscular and glandular esophagus and uterus full of micrifilariae. Sources: A–C) Adapted from Bartlett and Anderson, 1987; E, F) adapted from Hernandez-Rodriguez et al 1986; G–I) adapted from Bartlett et al., 1985. License: CC BY-NC-SA 4.0.

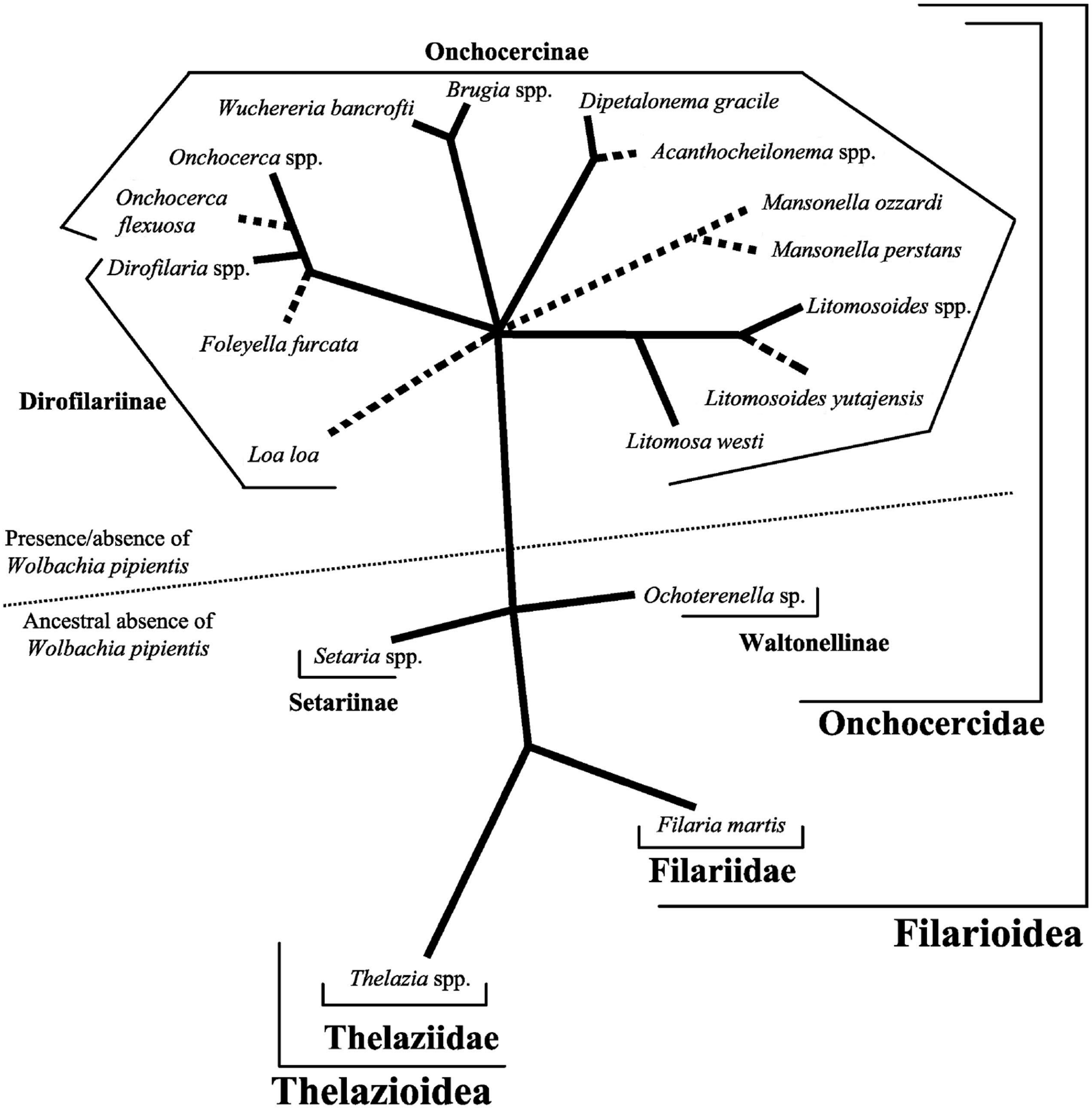

Figure 23. Hypothetical evolution of *Wolbachia pipientis* infection mapped on the phylogenetic tree of Filariae and related nematodes. *Wolbachia pipientis* could have been ancestrally absent from the lineages leading to *Thelazia* spp., *Filaria martis*, *Setaria* spp. and *Ochoterenella* spp. and it could have been acquired on the lineage leading to the Onchocercidae family, and then lost several lineages (*Litomosoides yutajensis*, *Mansonella* spp., *Acanthocheilonema* spp., *Onchocerca flexuosa*, *Foleyella furcata*, and *Loa loa*, dashed lines). The positions of *Mansonella* spp. and *O. flexuosa* are based only on their taxonomic affiliations. Source: Adapted from Casiraghi et al., 2004. License: CC BY-NC-SA 4.0.

methods are cheaper and faster than those using antigen detection, such as the immunoassay for circulating filarial antigens, which can be detected in blood samples collected at any time of day, unlike microfilariae with nocturnal periodicity. However, in many countries, antigen detection diagnosis tests are not licensed, making the diagnosis more difficult due to the similarity of the microfilariae species in areas with several filarioses. Adults may be identified in biopsied specimens of lymphatic tissue. For the pathogens causing onchocerciasis and *M. (E.) streptocerca*, diagnoses are performed by detection of microfilariae in skin snips or adults in biopsy specimens of skin nodules. Microfilariae of *Onchocerca* do not exhibit any periodicity, similarly to *Mansonella* (CDC, 2020).

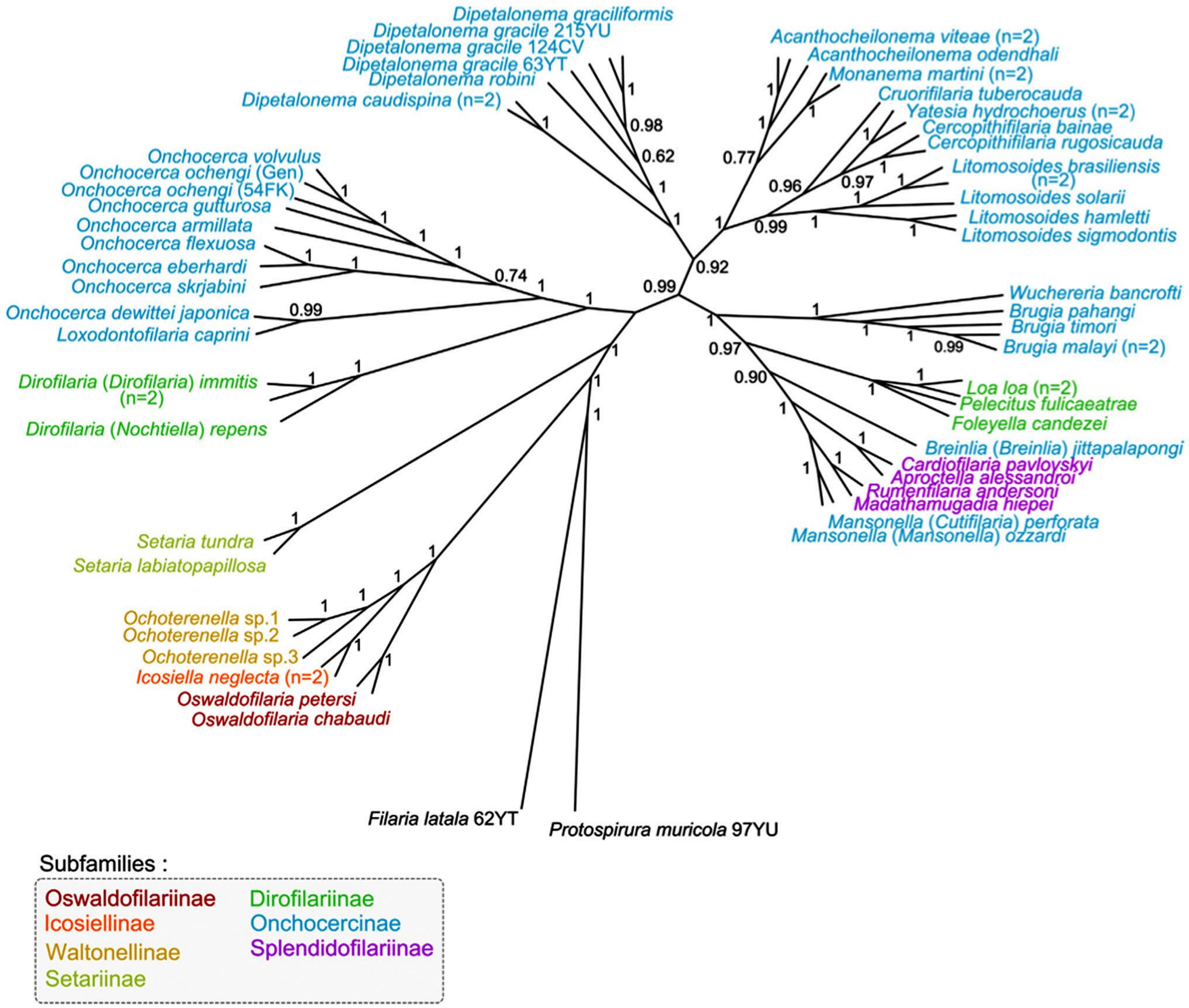

Figure 24. Phylogeny of family Onchocercidae based on partitioned concatenated datasets of 12S rDNA, coxI, rbp1, hsp70, myoHC, 18S rDNA, and 28S rDNA sequences using Bayesian inference. The total length of datasets is approximately 4,950 bp. Sixty onchocercid specimens (representing 48 species) were analyzed. *Filaria latala* and *Protospirura muricola* were used as outgroups. The topology was inferred using Bayesian inference. Nodes are associated with Bayesian posterior probabilities based on one run of 5 million generations. The onchocercid subfamilies are indicated by colors: Blue for Onchocercinae, dark green for Dirofilariinae, purple for Splendidofilariinae, pale green for Setariinae, yellow for Waltonelliinae, orange for Icosielliinae, and red for Oswaldofilariinae. Source: Adapted from Lefoulon et al., 2015. License: CC BY-NC-SA 4.0.

Among filarioids infecting dogs, *Acanthocheilonema reconditum* is a species whose microfilariae have been frequently confused with *Dirofilaria immitis* (Figure 20). This species has also a global distribution. It is important to have a correct identification of the microfilariae since *A. reconditum* is a non-pathogenic species. Adults parasitize the subcutaneous tissues and fascia of canids while microfilariae circulate in blood. The fleas *Ctenocephalides felis* and *C. canis* are the vectors for *A. reconditum*, whereas the role of ixodid ticks (that is, *Rhipicephalus*) as vectors for this filarioid species has been definitively rejected. The full development of microfilariae to the J_3 infective forms occurs in experimental infected fleas in about 15 days. Moreover, the localization and size of developing juveniles inside the infected flea suggest that this arthropod might act as an intermediate host through the ingestion of infected fleas rather than inoculation during a blood meal on dogs. This route of *A. reconditum* transmission is unique, differing from that of other filarioids, which are actively transmitted through the bites of mosquito vectors (Anderson, 2000).

The remaining filarial genera within the Onchocercinae are parasites of mammals, with the exception of *Macdonaldius* which is a parasite of reptiles. Most of the genera display a distribution restricted to a continent. For example, *Litomosoides*, a parasite of the body cavity of bats, rodents, and marsupials represented by 42 species, is distributed on the American continents from the southern United States to central Argentina, while *Dipetalonema* sensu stricto, with 6 species, and *Mansonella (Tetrapetalonema)*, with 13 species, parasitize Platyrrhinii monkeys from Central America to parts of South America. Other genera are monospecific, such as *Orihelia anticlava* which is widespread in South America and is a parasite of the body cavity from armadillos. In contrast, *Filarissima lainsoni* and *Migonella fracchiai* are only known by single unique records from a Brazilian coendou and a Paraguayan bat, respectively (Anderson, 2000).

Subfamily Splendidofilariinae

Members of this subfamily parasitize reptiles, birds, and mammals, including humans. It includes 21 genera with more than 90 species. Females contain a vulva in the anterior region of the body, the tail in both sexes is relatively long, caudal alae are absent, and the spicules are little different in size and morphology (Figure 21). Worms may be found in the body cavity of birds, sometimes in capsules in hidden locations (such as in *Madathamugadia*), while in reptiles they have been found in the mesenteric vessel of the intestine, the heart of turtles (such as in *Cardiofilaria*), or subcutaneous tissues in gecko lizards (such as in *Thamugadia*). In mammals they may be found in the body cavity (as in *Micipsella*) or the central nervous system (as in *Meningonema*) (Anderson, 2000).

The life cycle of these filarioids involves different vectors, such as mosquitoes in *Aproctella* and *Cardiofilaria*, or ornithophilic ceratophogonids in *Chandlerella* and *Splendidofilaria*. *Splendidofilaria fallisensis*, a parasite of the subcutaneous tissues of wild and domestic ducks of North America, utilize ornithophilic simuliids of the genus *Simulium* as vectors. Blackflies crawl under the feathers and engorge on infected blood. Microfilariae penetrate the stomach of the simuliid and develop in the haemocoel. After 7 to 14 days, depending on the temperature, J_3 appears near the mouthpart of the blackfly. Microfilariae appear in the blood of the ducks 30–36 days after they are inoculated with J_3, whereas in *S. californiensis*, a parasite of the heart from California quail, the prepatent period is about 6 months.

The genus *Meningonema* is commonly found parasitizing the central nervous system of African Cercopithecinae, however Boussinesq and colleagues (1995) reported the first human case in 1995. The authors recovered a fourth-stage juvenile (J_4) female from the cerebrospinal fluid of a patient from Cameroon harboring *Loa loa*, but who did not exhibit any neurological symptoms. In another study, microfilariae recovered from patients with cerebral filariasis in Zimbabwe identified as *Mansonella perstans* may have been infected instead with *Meningonema* and not the former species. In fact, microfilariae of *Meningonema* have not been confirmed in humans, although they have been found in the peripheral blood of monkeys; therefore, careful examination of blood samples might reveal that *Meningonema* infection is actually a frequent zoonosis in humans (Boussinesq et al., 1995).

Subfamily Lemdaniinae

Filarioids in this subfamily tend to parasitize birds and, less commonly, reptiles and mammals. Adults are characterized by a subterminal anus in both females and males, an absent buccal capsule, and spicules that are similar in size and form, such as in *Eulimdana*, or may be markedly different, as in *Lemdana* or *Makifilaria* (Figure 22). These filarioids develop in Mallophaga lice, such as *Eufilaria bartlettae*, a parasite of the blackbird (*Turdus merula*) and in mosquitoes of the genus *Anopheles*, such as *Saurocitus agamae*, a parasite of the lizard *Agama agama*.

Wolbachia Bacteria in Filarioids

Intracellular bacteria belonging to the genus *Wolbachia* were discovered in filarial nematodes and arthropods in the 1970s with the advent of electron microscopy (Kozek and Figueroa Marroquin, 1977). In arthropods, *Wolbachia pipientis* generally induces alterations in host reproduction, acting as a tool to manipulate pest insects; while in filarioid nematodes, the evidence shows that these bacteria are required for development and reproduction (Stouthamer et al., 1999). *Wolbachia pipientis* bacteria are typically contained in a host-derived vacuole, inhabiting the hypodermic cells and the reproductive tissues of the female filarioid worm. Bacteria have also been recovered in juvenile filarioid stages, but not in male worms. This suggests a vertical mode of transmission through the cytoplasm of the nematode egg, which parallels observations in *Wolbachia* of arthropods. The bacteria may be present in the tissues alone, in small groups of bacteria, or in large groups that fill their cellular environment.

Data generated through electron microscopy and immunohistochemical examinations have helped to elucidate the presence or absence of *Wolbachia pipientis* in filarial species. In the 1990s, PCR amplification and sequencing of the *Wolbachia* genome showed that *Wuchereria bancrofti*, *Litomosoides sigmodontis*, *Mansonella ozzardi*, and all the species examined in the genera *Dirofilaria*, *Onchocerca*, and *Brugia* harbor *Wolbachia pipientis*.

Phylogenetic analysis by comparison of 16S rDNA sequences from *Wolbachia pipientis* have showed that filarial *Wolbachia* are closely related and form a separate group from the *Wolbachia* of arthropods. *Wolbachia* of filariae segregate into 2 clusters (named C and D), which diverge from the A and B clusters that are recognized for arthropods. Within the C and D filarial *Wolbachia* lineages, the bacterial phylogeny is congruent with the nematode phylogeny. However, in the rodent filaria *Acanthocheilonema viteae*, PCR consistently showed no evidence of *Wolbachia*; this was also the case for *A. reconditum*, microfilariae of *Mansonella perstans* and *Litomosoides yutajensis* (Onchocerciinae); *Loa loa*, and *Foleyella furcata* (Dirofilariinae); *Ochoterenella* spp. (Waltoneliinae); *Setaria equina*, *S. labiatopapillosa*, *S. tundra* (Setariinae), and *Filaria martis* (Filariinae) (Casiraghi et al., 2004).

Mapping the presence or absence of *Wolbachia pipientis* in different species within the subfamilies of the Onchocercidae and Filariidae will support the trees generated by molecular data of filarioids and will help to elucidate the phylogeny of Filariata.

Phylogeny of Filarioid Nematodes

A phylogeny of filarioid nematodes based on morphological characters has been proposed by Anderson and Bain (1976) and Chabaud and Bain (1994). However, due to the convergence of morphological characters among lineages, the phylogenies proposed are not sustainable at all and the proposed evolutionary scenario is weak. The major question regards the classification of the Onchocercidae, and their origin and evolution. Analyses based on molecular characters still are ongoing. A huge amount of sequence data is available for pathogenic filarioids (for example, *Wuchereria bancrofti* and *Brugia malayi*) as well as model filarial parasites (such as *Litomosoides sigmodontis* and *Acanthocheilonema vitae*) than for the remaining filarioids, for which data are scarce. The first phylogenetic analyses were conducted for the Onchocercinae and Dirofilariinae. However, biological material is scarce, impeding broad taxonomic sampling, and the markers used (12S rDNA and coxI genes) are not suitable for resolving the internal nodes which would help elucidate the evolution within the Onchocercidae. Lefoulon and colleagues (2015) proposed a robust phylogenetic hypothesis of the relationships within the Onchocercidae based on 7 loci: 2 mitochondrial and 5 nuclear genes of 48 species belonging to 7 subfamilies. These authors concluded that the tree topology is not congruent with the classic systematic delineations and the present phylogeny neither supports the monophyly of the Dirofilariinae, Onchocercinae, nor Splendidofilariinae (Figure 24) (Lefoulon et al., 2015).

Future studies including other sequence data, the presence or absence of *Wollbachia pipientis*, and more species within the order Filariata are necessary for the elucidation of the phylogeny of this group.

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NEMATA

Strongyloidea and Trichostrongyloidea (Superfamilies): Bursate Nematodes

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Phylum Nemata

- Superfamily Strongyloidea
- Superfamily Trichostrongyloidea

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Chapter 56

Strongyloidea and Trichostrongyloidea (Superfamilies): Bursate Nematodes

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Introduction

The bursate nematodes include those within the superfamilies Strongyloidea Baird, 1853 and Trichostrongyloidea Cram, 1927. Even though there are new data showing various phylogenetic relationships among and between species in these groups, they will be discussed here under the umbrella of bursate nematodes for the sake of simplicity. Bursate nematodes are distinguished by the presence of a copulatory bursa on the posterior end of the male (**bursa** = purse or pouch; Latin).

In general—although with exceptions—bursate nematodes have relatively stout bodies with a muscular **esophagus** that is not divided into various parts but is narrower at the anterior end and more bulbous and expanded toward the posterior end where the esophagus attaches to the **intestine**. There is always an encircling **nerve ring** around the esophagus and—as in almost all nematodes—the nerve ring slants more posteriad on the ventral aspect of the nematode and slants more anteriad on the dorsal aspect. The **excretory pore** exits the **cuticle** in the general vicinity of the nerve ring and is always situated ventrally (Figure 1). A morphological feature—which is in fact a synapmorphy for the bursate nematodes—is the possession of a **copulatory bursa** in males that is composed of muscular **rays** with **cuticular membranes** connecting them (Figure 2). The copulatory bursa consists of laterally-projecting **cuticular extensions** that surround the **tail** of males in species assigned to both superfamilies, and this structure serves as a grasping/sensory organ equipped with **sensory muscular papillae** (Figure 3). The bursa grasps the female during copulation and enables the male to extend the **spicule** or spicules (Figure 4) into the **reproductive tract** of the female thus facilitating the transfer of ameboid sperms to the female reproductive system. The bursa surrounds the spicules and the **cloaca** (which is the joint opening that drains the intestinal and reproductive systems; Gardner et al., 1994b).

Most species of bursate nematodes that are parasites in the intestines of vertebrates have direct life history patterns and only the definitive host is needed for the parasite to reach sexual maturity; however, some species that occur in organs or tissues such as lungs, muscles, or the central nervous system of their vertebrate hosts, have indirect life history patterns. Examples are species of *Angiostrongylus*, which are normally parasites of rodents, but can infect people living in tropical and subtropical regions with devastating neurological consequences. These species use land-dwelling molluscs (snails and slugs) as intermediate hosts (Alicata, 1991).

Following are discussions of the 2 superfamilies and a few of the highly numerous other families. For additional information on other groups of these animals, see Travassos (1937), Anderson (2000), and the CIH keys by Anderson and colleagues (2009).

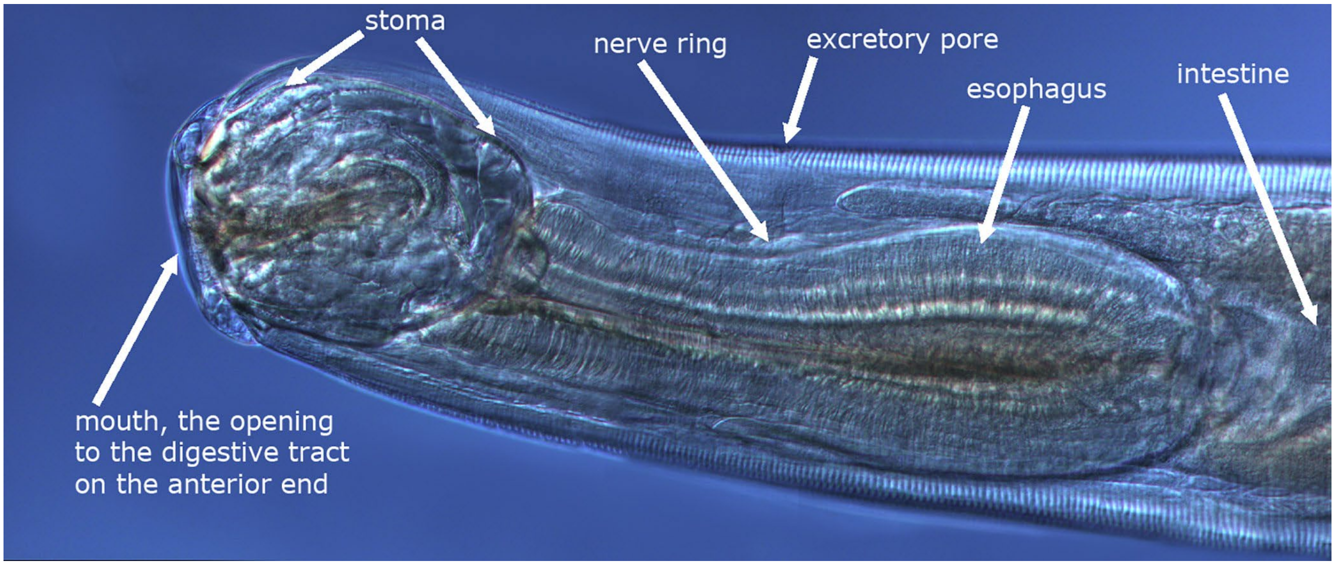

Figure 1. Anterior end of a specimen of *Ransomus rodentorum* with structures labeled. Normarsky micrograph. Source: S. L. Gardner, HWML. License: CC BY 4.0.

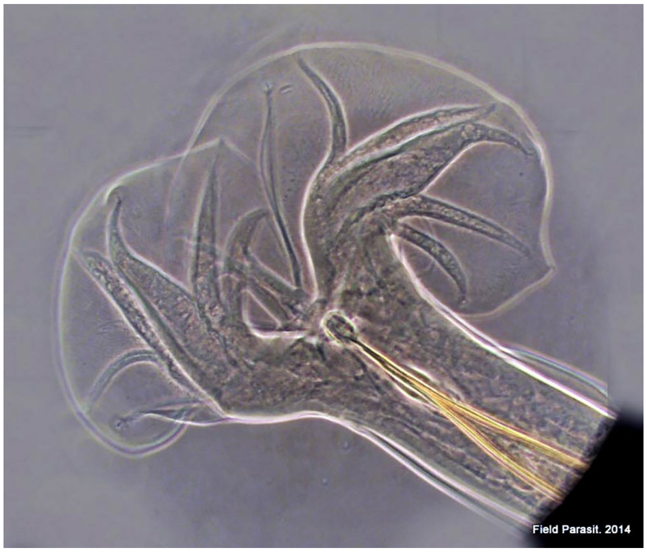

Figure 2. Copulatory bursa of *Vexillata armandae*, a parasite of the small intestine of the coarse-haired pocket mouse *Chaetodipus hispidus*. Collected and imaged at Cedar Point Biological Station, near Ogallala, Nebraska, United States. Source: S. L. Gardner, HWML, 2014. License: CC BY 4.0.

Superfamily Strongyloidea Baird, 1853

The strongyloids (also known as strongyles; superfamily Strongyloidea Baird, 1853) comprise a diverse group of parasitic nematodes with a cosmopolitan distribution in vertebrates. Nematodes classified in the superfamily Strongyloidea are defined by several characteristics that are well-established **synapomorphies** (meaning, shared derived characters) for the group, as listed above.

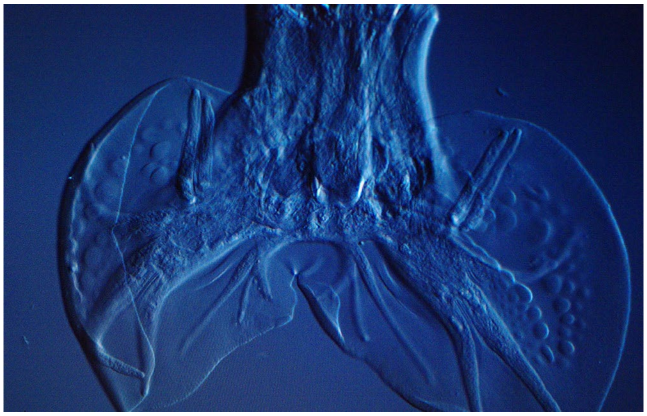

Figure 3. Copulatory bursa of a male of a species of trichostrongyloid nematode from *Ochotona princeps* (order Strongylida, superfamily Trichostrongyloidea) collected in Colorado, United States. Source: D. Tufts, HWML, 2013. License: CC BY 4.0.

Following are discussions of 2 families within the Strongyloidea, families **Ancylostomatidae** and **Strongylidae**, and several species within those. From the standpoint of human health, the more important of these 2 families is the Ancylostomatidae, commonly known as hookworms.

Hookworms: Family Ancylostomatidae

The ancylostomatid nematodes are commonly known as **hookworms** because of the initial name given them by Goeze (1782), who noted membranous expansions with 2 rib-like structures on the tail of the males, which were collected from the intestine of a European badger (*Meles meles*). Frölich (1789) found similar worms in foxes, also with membranous

Figure 4. Posterior end of male *Ransomus rodentorum* showing bursa and twin/paired spicules. Source: S. L. Gardner, HWML. License: CC BY 4.0.

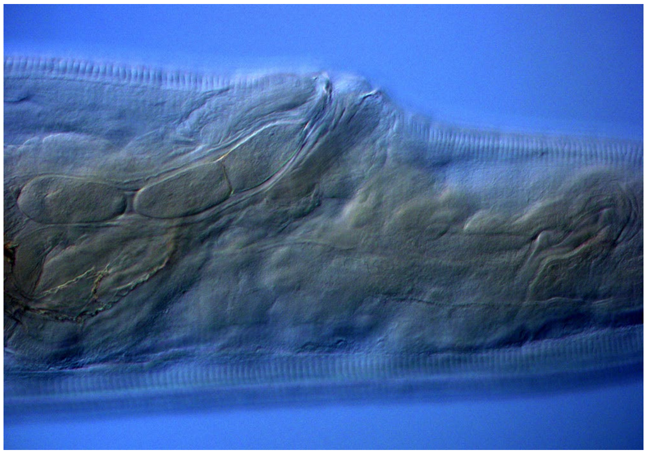

Figure 5. Posterior end showing ovijector of the same individual of *Ransomus* as shown in Figure 1 above. Eggs can be seen being expelled from the body via the muscles of the ovijector. Normarsky micrograph. Source: S. L. Gardner, HWML. License: CC BY 4.0.

expansions in the tails. Frölich called these nematodes Hakenwurm (= hookworm; German).

In their mammalian hosts (including humans), adult hookworms usually live in the duodenum (the anterior part of the small intestine), where they attach to the mucosa, pulling mucosa into their **stomata** and abrading the villi with **cuticularized cutting teeth** or **plates** (Figure 6, left). The cuticularized plates of the stoma rupture the capillaries of the mucosa and the nematode pumps blood rapidly into its intestine with the muscular esophagus. Little of the blood that is extracted from the host is digested or used by the nematode and most of the blood that is pumped out of the capillary beds of the host pass through the intestine of the nematode, out the anus, and directly back into the lumen of the host's gut. As can be seen clearly in the video (available at hookworm.vob (Japan National Institute of Health, n. d.), worms feed heavily on blood, most of which is wasted as it passes directly out of the worms out into the lumen of the intestine, where most of the blood is digested and reabsorbed.

As mentioned above, species in the family Ancylostomatidae are important human pathogens. They generally afflict people in warm-temperate, subtropical, and tropical areas of the world living without access to adequate sanitation facilities and without ready access to shoes (Loukas et al., 2016). Because the main 3 species of hookworms that reside in humans have similar life-histories, pathogenicity, control schemes, symptomatology, and epidemiology, they are treated below as a single topic, with notations where important variations occur. See Table 1 for a list of valid species of *Ancylostoma* (see Drabik and Gardner, 2019). *Necator americanus* is also of concern with respect to human health and will be discussed below, as well.

General Morphology

Ancylostomatid nematodes are robust with the anterior extremity reflexed dorsad. The esophagus is muscular and club shaped with a narrow anterior end and a more swollen posterior part. Esophageal glands are located in the pseudocoel extending posteriad. Cervical papillae or deirids are present near the nerve ring. These nematodes are dioecious with males having a conspicuous and well-developed copulatory bursa, consisting of 2 broad lateral lobes with lateral rays and a smaller dorsal lobe with a multi- or bifurcating dorsal ray (depending on the species) (Figure 6). The bursal rays found laterally are termed the externolateral rays. The dorsal ray is situated in the dorsal part of the bursal lobe. The rays

Figure 6. Left image: Posterior end of a male specimen of *Ancylostoma* from a tuco-tuco (a rodent of the genus *Ctenomys*) in Bolivia. The rays and vellum make up the copulatory bursa. Right image: Anterior end showing the cuticularized hooks of the stoma of the same species of nematode. Source: S. L. Gardner, HWML. License: CC BY 4.0.

Table 1. Species of *Ancylostoma* from mammals including known original hosts, zoogeographic region of occurrence, and nearest approximate geographic collection locality of type specimens. Zoogeographic regions follow Wallace, 1876. Source: Adapted from Drabik and Gardner, 2019. License: CC BY 4.0.

Species of *Ancylostoma*	**Host**	**Biogeographic region**	**Type locality**
A. aliuropodae Xie et al., 2017	*Ailuropoda melanoleuca* (David, 1869)	Palearctic	Fengtongzai Nature Reserve, China Brazil
A. bidens Molin, 1861	*Nasua nasu* (Linnaeus, 1766), *Procyon cancrivorous* (Linnaeus, 1766)	Neotropical	Brazil
A. braziliense de Faria, 1910	Canidae, Felidae	Cosmopolitan	Brazil
A. buckleyi Le Roux and Biocca, 1957	*Felis concolor* (Linnaeus, 1771), *Cerdocyon thous* (Linnaeus, 1766)	Neotropical	Leticia Amazonas, Colombia
A. caninum (Ercolani, 1859)	Canidae	Cosmopolitan	Turin, Italy
A. ceylanicum Looss, 1911	Canidae, Felidae, *Homo sapiens*	Ethiopian, Oriental, Palearctic	Sri Lanka
A. conepati (Solanet, 1911)	*Conepatus chinga* (Molina, 1782)	Neotropical	Buenos Aires, Argentina
A. ctenomyos	*Ctenomys steinbachi* Thomas, 1907, *C. boliviensis* Waterhouse, 1848	Neotropical	Bolivia
A. duodenale (Dubini, 1843)	*Homo sapiens* Linnaeus, 1758	Cosmopolitan	Milan, Italy
A. galogoi van der Berghe, 1936	*Otolemur crassicaudatus* (Geoffroy Saint-Hilaire, 1812)	Ethiopian	East Central Africa
A. genettae Macchioni, 1995	*Genetta genetta* (Linnaeus, 1758)	Ethiopian, southeast Palearctic	Scebeli River, Somalia
A. gilsoni Gedoelst, 1917	*Sciurus prevosti* (Desmarest, 1822)	Oriental	Malaysia
A. hescheleri Mönnig, 1938	*Orycteropus afer* (Pallas, 1766)	Ethiopian	South Africa
A. iperodontatum Le Roux and Biocca, 1957	*Acinonyx jubatus* (Schreber, 1775)	Ethiopian	Zambia
A. japonica Fukuda and Katsurada, 1925	*Homo sapiens* Linnaeus, 1758	Palearctic	Japan
A. longespiculatum Mönnig, 1938	*Felis silvestris* Schreber, 1777	Palearctic	South Africa
A. malayanum Alessandrini, 1905	*Ursus* sp.	Palearctic, Oriental	Southeast Asia
A. martinaglai Mönnig, 1931	*Canis mesomelas* Schreber, 1775	Ethiopian	South Africa
A. mephitis Micheletti, 1929	*Ictonyx striatus* (Perry, 1810)	Ethiopian	?
A. minimum (von Linstow, 1906)	*Prionailurus rubiginosus* (Geoffroy Saint-Hilaire, 1831)	Oriental	Sri Lanka
A. mucronatum (Molin, 1861)	*Dasypus novemcinctus* Linnaeus, 1758	Neotropical	Brazil
A. mycetis (Molin, 1861)	*Alouatta* sp.	Neotropical	Brazil
A. paraduodenale Biocca, 1951a	*Leptailurus serval* (Schreber, 1776)	Ethiopian	Zambia—Rome Zoo
A. pluridentatum (Alessandrini, 1905)	*Felis* spp.	Neotropical	Brazil
A. protelesis Macchioni, 1995	*Proteles cristatus* (Sparrman, 1783)	Ethiopian	Scebeli River, Somalia
A. somaliense Macchioni, 1995	*Canis mesomelas* Schreber, 1775	Ethiopian	Scebeli River, Somalia
A. taxidae Kalkan and Hansen 1966	*Taxidea taxus* (Schreber, 1777)	Nearctic	Manhattan, Kansas, United States
A. tubaeforme (Zeder, 1800)	*Felis silvestris* Schreber, 1777	Palearctic	—

are species specific (Drabik and Gardner, 2019). The number and general patterns of rays in the copulatory bursa are also a characteristic found in other male rhabditid nematodes, although they are much reduced in free living and insect parasitic forms (Gardner et al., 1994b). As mentioned earlier, all species of nematodes in the superfamilies Strongyloidea and Trichostrongyloidea have very well-developed copulatory bursae (Gardner et al., 1994a). The paired spicules in these nematodes are setaceous in form with a well-developed vellum (Maggenti, 1981).

Females have a simple, conical tail. The vulva is ventrally located and is usually in the posterior one-third of the body and the uterus is didelphic. About 5% of the daily output of eggs is found in the uteri at any one time; the total production is several thousand per day for as long as 14 or more years for a single female.

Life History

As far as is known, species of *Ancylostoma* and *Necator* mature and mate in the small intestine of their host. Eggs are produced by the thousands and embryos within the thin-shelled eggs develop into 2-, 4-, or several-cell stages by the time they are passed with feces. Species infecting humans cannot be identified by egg structure or size. Eggs that pass out into the environment require warmth, shade, and moisture for continued development. Coprophagous insects may mix the feces with soil and air, perhaps hastening embryogenesis, which is completed within 24 to 48 hours in ideal moist conditions. Newly hatched J_1s have a rhabditiform esophagus with a characteristic constriction at the level of the nerve ring and a basal bulb with a valve. Differentiation of hookworm juveniles from those of *Strongyloides* spp. is difficult for a beginning parasitologist.

First stage juveniles living in the feces deposited by their host feed on bacteria therein and molt their cuticle in 2 to 3 days. Second-stage juveniles (J_2), which also have a rhabditiform esophagus, continue to feed and grow and, after about 5 days, molt to the third stage (J_3) filariform-type of juvenile, which is then infective to a mammal. At this point, the second-stage cuticle may be retained as a loose-fitting sheath until penetration of a new host, or the cuticle may be lost just before the juvenile penetrates. Filariform J_3s have a strongyliform esophagus; that is, with a reduced basal bulb that is not separated from the corpus by an isthmus. It has been shown that the J_3s do not feed and they evidently survive on the stored bacterial soup stored in the intestine. Hookworm J_3s are similar to filariform J_3s of *Strongyloides* spp. but can be distinguished by the tail tip, which is pointed in hookworms and notched in *Strongyloides* spp.

Living in the upper few millimeters of soil, J_3s remain in the water film surrounding soil particles and they never survive freezing or drying out. There is a short, vertical migration in the soil, depending on the weather or time of day. When the ground surface begins to desiccate, they migrate a short distance into the soil, staying ahead of the drying soil. Under ideal conditions, they can live for several weeks using this up and down method to stay alive. When the ground surface is wet, after rain or morning moisture condensation in the form of dew, the juveniles wriggle to the surface, remaining in a resting posture until activated (Haas et al., 2005). They are stimulated into sinusoidal motion called “the dance macabre” by a variety of environmental cues, such as touch, vibration, water currents, heat, light, or carbon dioxide. Warmth and moisture stimulate them to stand upright on their tail, waving to-and-fro in a searching behavior termed **questing** or **nictation**. Warmth and fatty acids in skin induce penetration behavior (Haas et al., 2005).

Infection occurs when J_3s contact a host’s skin and burrow into it, and they resume feeding at about this time (Hawdon et al., 1993). They usually shed the second-stage cuticle as they penetrate, but the presence of a cuticle does not preclude resumption of feeding (Kumar and Pritchard, 1994). Juveniles can penetrate any epidermis, although parts most often in contact with the soil, such as hands, feet, and buttocks, are most often attacked. *Necator americanus* (and probably other skin-penetrating nematodes) secrete a variety of enzymes that hydrolyze skin macromolecules (Brown et al., 1999; Crompton, 1989; Yu et al., 1995).

After gaining entry to a blood or lymph vessel, juveniles are carried to the liver via the hepatic portal vein, and then to the heart and the lungs via the pulmonary artery. In the lungs, the juveniles break from the venous capillary beds into the air spaces of the alveoli where they molt to the fourth stage (J_4), leaving behind the cuticle like an abandoned collapsed space suit. At this point, the fourth stage juvenile (J_4) now has an enlarged stoma. The fourth stage juveniles (J_4) are carried by ciliary action of the ciliated columnar epithelial cellular lining of the bronchi and bronchioles up the respiratory tree to the glottis where they coughed up by the host, and—if they are lucky—they may be swallowed and finally arrive in the small intestine. There they attach to the mucosa with their enlarged stoma, begin to grow, and then molt to the adult stage. After further growth, they become sexually mature and the male grasps the female with his copulatory bursa transferring ameboid sperm into the genital tract of the female (Williamson et al., 2003).

At least 5 weeks are required from the time of infection via penetration through the host’s epidermis to the beginning of egg production in the intestine. However, it has been shown that juveniles of *Ancylostoma duodenale* can undergo developmental arrest for up to 38 weeks, their maturation perhaps coinciding with the seasonal return of environmental conditions favorable to transmission (Behnke, 1987). *Ancylostoma caninum*, a widespread hookworm of dogs and other carnivores, manifests developmental arrest or stasis during its tissue migration and then is reactivated in female dogs when they begin lactation, resulting in transmammary transmission to pups (Arasu, 2001). Reactivation of the juveniles is modulated by estrogen and prolactin (Hotez et al., 2004).

Many species of hookworms across several genera occur in humans and domestic and wild mammals globally (Drabik and Gardner, 2019). Hookworms represented by several species infect approximately 500 million people worldwide and are responsible for much morbidity and mortality globally (Loukas et al., 2016).

Following are more details about of some the species of Ancylostomatidae, including *Necator americanus* (Stiles, 1902), *Ancylostoma duodenale* (Dubini, 1843), *A. ceylanicum* Looss, 1911, and *A. caninum* (Ercolani, 1859), especially the implications of their effect on human health.

Necator americanus (Stiles, 1902)

The Latin name for this species translated literally means American killer. This species is also called the New World hookworm and was first discovered in Brazil and then Texas, United States, but it was later found indigenous in Africa, India, Southeast Asia, China, and the southwest Pacific islands. It probably came to the New World with the trade in enslaved people in the 16th through 19th centuries, with both enslaved individuals and their captors contributing to the importation of the pathogen.

This nematode has caused much human suffering and has had a significant negative impact on the economic development of the southern United States as well as other regions of the world in which it occurs (Loukas et al., 2016). Primarily a parasite of tropical and subtropical regions, *Necator americanus* is the most common species of hookworm in humans in most of the world, accounting for about 85% of recorded infections (Hotez et al., 2010). Prior to effective hookworm control in the United States, about 95% of hookworms in the southern states were this species (Behnke, 1987; Loukas et al., 2016).

Necator americanus has a pair each of dorsal and ventral cutting plates surrounding the anterior margin of the stoma (Looss, 1911). In addition, a pair each of subdorsal and subventral teeth are near the rear of the stoma. The duct of the dorsal esophageal gland opens on a conspicuous cone that projects into the stoma. Males are 5 mm- to 9 mm-long with filariform/needlelike spicules that have minute barbs at their tips and are fused distally. Females are 9 mm- to 11 mm-long and their vulva is located in about the middle of their body with a single individual producing about 5,000 to 10,000 eggs per day (Behnke, 1987; Loukas et al., 2016).

Ancylostoma duodenale (Dubini, 1843)

As noted above, *Ancylostoma duodenale* (Looss, 1911; see Figure 7) has a tropical and subtropical worldwide distribution (Loukas et al., 2016). It is known in mines as far north as England and Belgium. Since Lucretius, in the 1st century CE, it was known to cause serious anemia in miners. Mines offer an ideal habitat for egg and juvenile development because of their constancy in temperature and humidity. The problem is apt to occur whenever miners defecate on the open ground, outside of established latrines (Cumming and White, 1917).

The anterior margin of the stoma of *Ancylostoma duodenale* has 2 ventral plates, each with 2 large teeth that are fused at their bases (Looss, 1911). A pair of small teeth is found in the depths of the capsule. The duct of the dorsal esophageal gland runs in a ridge in the dorsal wall of the buccal capsule and opens at the vertex of a deep notch on the dorsal margin of the capsule.

Adult males are 8 mm- to 11-mm-long and have a bursa characteristic for the species. The needlelike spicules have simple tips and are never fused distally. Females are 10 mm- to 13 mm-long, with the vulva located about a third of the body length from the posterior end. A single female can lay from 10,000 to 30,000 eggs per day (Hotez and Pritchard, 1995).

This is the first hookworm for which the life history was fully studied and understood. To demonstrate this early work on this organism, following is a lengthy excerpt from Arthur Looss (1911) from his monograph on the morphology and life cycle of *Ancylostoma duodenale*, based on his work in Egypt in 1896 he wrote:

> In order to study in greater detail the very earliest changes in the larvae after their arrival in a host, without sacrificing large experimental animals, I had attempted to introduce the larvae into rats and guinea pigs, partly along with food or drink …. These attempts never gave rise to a settlement of the larvae in the intestine of the experimental animals … [but the larvae] evidently remained alive for a long time. The subsequent history of these larvae was not investigated further, since in the meantime my attention was drawn in another direction. While engaged on one of the experiments, … a drop of the fluid fell on my left hand between the roots of two fingers. I paid no attention to this moisture which dried up of itself within a few minutes. At the

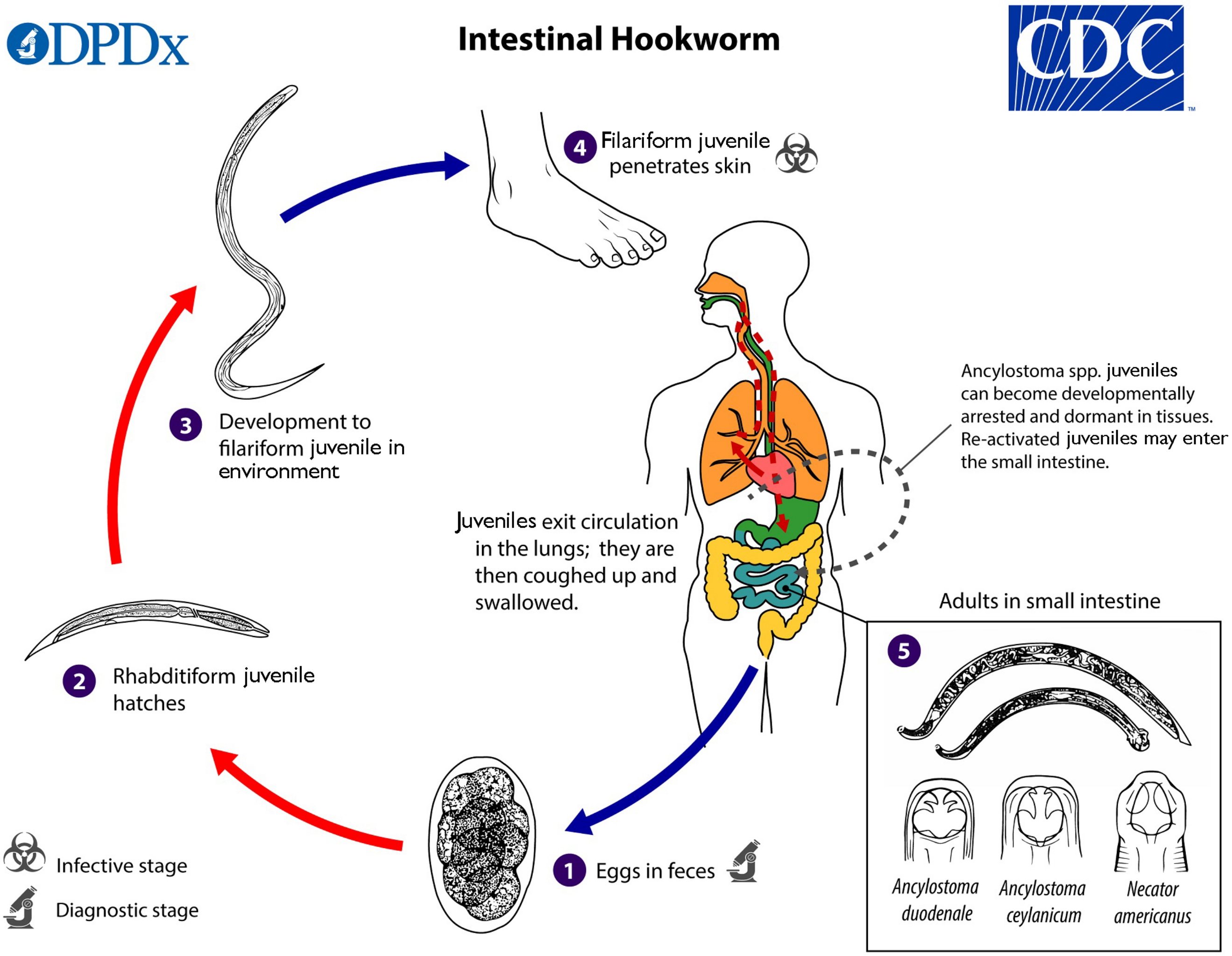

Figure 7. Hookworm (intestinal) causal agents and life cycle. Intestinal hookworm disease in humans is caused by *Ancylostoma duodenale*, *A. ceylanicum*, and *Necator americanus*. Classically, *A. duodenale* and *N. americanus* were considered the 2 primary intestinal hookworm species worldwide, but newer studies show that a parasite infecting animals, *A. ceylanicum*, is also an important emerging parasite infecting humans in some regions. Occasionally juveniles of *A. caninum*, normally a parasite of canids, may partially develop in the human intestine and cause eosinophilic enteritis, but this species does not appear to reach reproductive maturity in humans. Another group of hookworms infecting animals can penetrate the human skin causing cutaneous larva migrans (*A. braziliense*, *A. caninum*, *Uncinaria stenocephala*). Other than *A. caninum*, these parasites do not develop further after their juveniles penetrate human skin. Eggs are passed in the stool (1), and under favorable conditions (moisture, warmth, shade), juveniles hatch in 1 to 2 days and become free-living in contaminated soil. These released rhabditiform juveniles grow in the feces and/or the soil (2), and after 5 to 10 days (and 2 molts) they become filariform (third-stage) juveniles that are infective (3). These infective larvae can survive 3 to 4 weeks in favorable environmental conditions. On contact with the human host, typically bare feet, the juveniles penetrate the skin and are carried through the blood vessels to the heart and then to the lungs. They penetrate into the pulmonary alveoli, ascend the bronchial tree to the pharynx, and are swallowed (4). The juveniles reach the jejunum of the small intestine, where they reside and mature into adults. Adult worms live in the lumen of the small intestine, typically the distal jejunum, where they attach to the intestinal wall with resultant blood loss by the host (5). Most adult worms are eliminated in 1 to 2 years, but the longevity may reach several years. Some *A. duodenale* juveniles, following penetration of the host skin, can become dormant (hypobiosis in the intestine or muscle). These juveniles are capable of re-activating and establishing patent, intestinal infections. In addition, infection by *A. duodenale* may probably also occur by the oral and the transmammary route. *Ancylostoma ceylanicum* and *A. caninum* infections may also be acquired by oral ingestion. *Ancylostoma caninum*-associated eosinophilic enteritis is believed to result following oral ingestion of juveniles, not percutaneous infection. *Necator americanus* does not appear to be infective via the oral or transmammary route. Source: Adapted from United States Centers for Disease Control and Prevention, Division of Parasitic Disease and Malaria, 2019. Public domain.

same time, however, a burning sensation made itself felt on the spot, which grew more intense, while the skin became distinctly reddened. I am still of opinion that the most natural thing was to refer these symptoms to the *Ankylostoma* larvae, which … were present in the drop in great numbers. But the alternative existed that the active agent was either the water, in which the larvae had been kept (in this special case for a long time), and into which they might have discharged irritating products of excretion; or the irritating agency was the *Ankylostoma* larvae themselves. To test this, I let a drop of fluid without larvae fall on to another part of the hand and allowed it to dry. No reaction followed. Then a drop of fluid containing numerous larvae—as at first—was dropped in a third place on the back of the left hand, and was spread out with the handle of the scalpel so gently that the skin was only touched occasionally. Even before the fluid had quite dried up, the burning and reddening of the skin began exactly as before. It was thus clear that the irritating action proceeded from the larvae themselves. In order to see what had become of them I scraped the last remains of the fluid from the skin with the blade of the scalpel, using some pressure, and examined it under the microscope. The *Ankylostoma* larvae, previously so numerous, had disappeared, except for a few specimens; between the epithelial cells which had been scraped off innumerable empty skins were found, burst at the head end, and among them some half desiccated, still feebly motile larvae. The great majority had disappeared, and I saw no better explanation of this disappearance than the assumption that the larvae, casting their envelopes, had penetrated the skin and had thus produced the symptoms described. These symptoms, which were at first local, extended in the course of the next 24 hours over the whole hand, which also swelled considerably. The application of poultices of Goulard's water reduced the swelling in about 3 days, but it completely disappeared only after 6 days. … The fact that the mature *Ankylostoma* larvae not only possessed the power of actively penetrating into the uninjured skin of their host, but that they made energetic use of this power the moment they had an opportunity of doing so was so unusual—from the helminthological standpoint—that to regard it as a mere chance behaviour on the part of the larvae would have seemed to me simply absurd. Its true significance would not perhaps have suggested itself to me so rapidly, had I not become so strongly infected with the parasite in a manner up to that time wholly inexplicable. This infection was a fact; that it had not occurred through the mouth I also regarded as a fact; that the larvae could disappear in the uninjured skin I had just convinced myself on my own person with my own eyes; that this power of penetration into the uninjured skin was accidental and without further significance I considered as out of the question. But if the penetration of the larvae was the starting point of a second path by which they—no matter for the present in what manner—could reach the intestine of their definitive host, then indeed this phenomenon had not only a significance, as was to be expected from the outset, but my own enigmatical infection could be explained. For during my previous investigations I had certainly been careful to keep my hands away from the mouth, or to disinfect them according to the prescribed methods whenever there was the possibility of their coming into contact with the mouth (in eating, etc.); but I had thought nothing of allowing the water permeated with larvae to remain on my hands while manipulating the cultures and the material used for infection. Thus, the larvae had had an ample opportunity to affect an entry from the hands. That their penetration had never produced subjective symptoms is easy to understand; for in the first place the number of larvae entering simultaneously can, under the circumstances, never have been very large, and in the second place, even if a slight itching had been perceptible, there would have been no conceivable reason for seeking its cause in the penetration of *Ankylostoma* larvae into the skin. I may say without exaggeration that I have given earnest and prolonged consideration to all the points here enumerated before coming to a final decision; but in whatever way the facts in question were regarded they all conformed to one theory only, namely that the skin must be another starting point for the larvae from which they could reach the intestine and grow there to sexual maturity.

Ancylostoma ceylanicum **Looss, 1911**

Ancylostoma ceylanicum was first recorded as a parasite of carnivores in Sri Lanka but is now known from people in Southeast Asia, the East Indies, and the Philippines. A morphologically similar species, *A. braziliense*, is considered to be cosmopolitan in the tropics and is found in domestic and wild carnivores. Although this species has been reported from humans in Brazil, Africa, India, Sri Lanka, Indonesia, and the Philippines, the infections reported probably were from *A. ceylanicum. Ancylostoma braziliense* is the most common cause of cutaneous larva migrans (creeping eruption) in the southeastern United States and the tropics in the Western Hemisphere.

Ancylostoma caninum (Ercolani, 1859)

Ancylostoma caninum is the most common hookworm of domestic dogs, especially in the Northern Hemisphere. It has been found in humans on at least 5 occasions, and the worm also is a common cause of cutaneous larva migrans (Figure 8). This hookworm is an important cause of eosinophilic enteritis (EE) in northeastern Australia and is now reported in the United States (Croese, 1998). EE causes abdominal pain with peripheral blood eosinophilia but with no eggs evident in the fecal examinations. Evidently the development to maturity of these nematodes in humans is inhibited, but the presence of even 1 immature worm can cause EE. *Ancylostoma caninum* juveniles have been isolated from human muscle and associated with muscle inflammation (Little et al., 1983). This species is also implicated in other pathology involving invasion of human tissues (Loukas et al., 2016).

Human Hookworm Disease

The distinction between hookworm infection and hookworm disease is important. Far more people are infected with hookworms than exhibit overt disease symptoms. The presence and severity of disease depend strongly on 3 factors: 1) Number of worms present, 2) species of hookworm, and 3) nutritional condition and immune status of the infected person. In general, fewer than 25 *Necator americanus* individuals in a person will cause no symptoms, 25 to 100 worms lead to light symptoms, 100 to 500 produce moderate symptoms and considerable damage, 500 to 1,000 result in severe symptoms and grave damage, and more than 1,000 worms cause very grave damage that may be fatal. Because *Ancylostoma duodenale* individuals suck more blood than *N. americanus* ones, fewer *A. duodenale* worms can cause greater disease; for example, 100 *A. duodenale* worms may cause severe symptoms. However, the clinical disease is intensified by nutritional condition, impairment of host's immune response, and other factors.

The human immune response to hookworm infection is complex, but it is clear that hookworms have evolved to modulate the host's defense system. Survival of hookworms appears to depend upon a balance between host immune responses that ultimately protect the parasite. When attached to the host's mucosa, mature hookworms seem to be protected from the host's immune response. In contrast to established adults, newly recruited juvenile worms appear to cause a strong eosinophilic response that expels them from the small intestine (Croese and Speare, 2006).

In addition, several potential mechanisms for evading the host's defense systems have been discovered. For example, *Ancylostoma* spp. secrete a neutrophil inhibition factor that interferes with activation of neutrophils (Pritchard, 1995). *Necator americanus* directly secretes acetyl cholinesterase, which can inhibit or decrease peristaltic movement of the intestine and possibly acts also as an anti-inflammatory factor. It also secretes glutathione-S-transferase and superoxide dismutase, substances that interfere with antibody-dependent, cell-mediated cytotoxicity (ADCC). Nine genes in *N. americanus* code for proteins similar to neutrophil inhibitory factor (Daub et al., 2000). The details involved in the possible immunomodulation by hookworms is not established definitively and is a hotly debated topic (Mortimer et al., 2006).

Epidemiology

A combination of poor sanitation and conducive environmental conditions is necessary for high endemicity of hookworm in people. The disease is restricted to warmer parts of the world (and to specialized habitats, such as mines in more severe climates) because juveniles will not develop to maturity at less than 17 °C, with 23–30 °C being optimal. Freezing temperatures kill eggs and juveniles. Oxygen is necessary for hatching of eggs and juvenile development because their metabolism is aerobic. Thus, juveniles will not develop in undiluted feces or in waterlogged soil. Therefore, soil that is loose with lots of humus and has reasonable drainage and aeration is favorable to the development and survival of juveniles. Both heavy clay and coarse sandy soils are unfavorable for the parasite, the latter because juveniles are also sensitive to desiccation. Alternate drying and moistening are particularly damaging to juveniles; hence, very sandy soils become noninfective after brief periods of frequent rainfall. However, juveniles live in the film of water surrounding soil particles, and even apparently dry soil may have enough moisture to enable survival, particularly below the surface.

Juveniles are quite sensitive to direct sunlight and survive best in shady locations, such as coffee, banana, or sugarcane plantations. Humans working on such plantations often have preferred defecation sites, not out in the open where juveniles would be killed by sun, of course, but in shady, cool, secluded spots beneficial for juvenile development. Repeated return of people to a defecation site exposes them to continual reinfection. Furthermore, use of preferred defecation sites makes it possible for hookworms to become endemic in otherwise quite arid areas. A higher average number of worms per individual will seed the soil with more eggs, so human defeca-

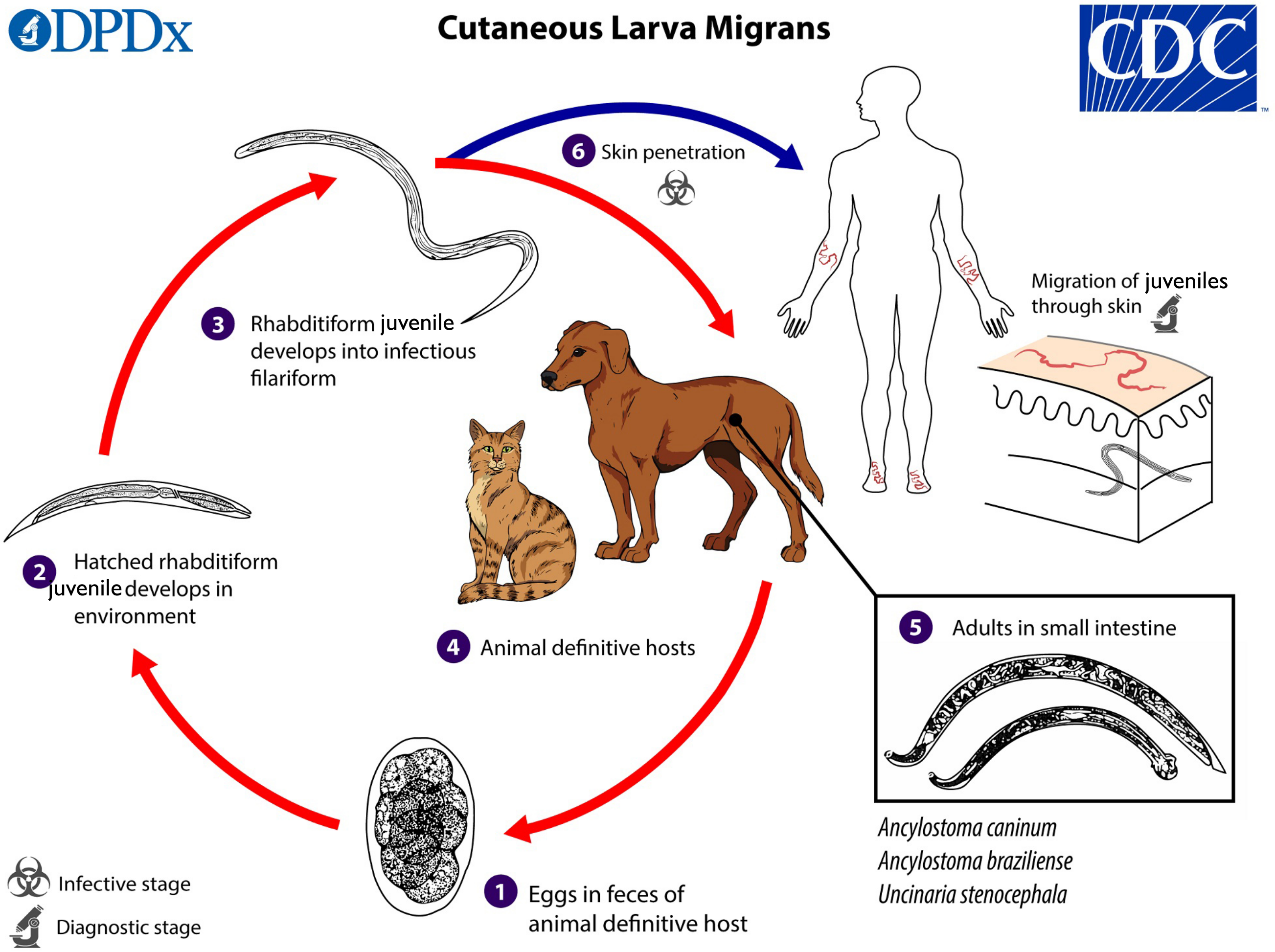

Figure 8. Zoonotic hookworm (extraintestinal) causal agents and life cycle. Some zoonotic hookworm species are capable of infecting humans, but they typically do not develop in the intestine and instead infect extraintestinal sites like the skin. Cutaneous larva migrans (CLM) has been associated with *Ancylostoma caninum*, *A. braziliense*, and *Uncinaria stenocephala*, which are all hookworms of dogs and cats. *Bunostomum phlebotomum*, a cattle hookworm, is also capable of causing short-lived CLM in humans. Cutaneous larva migrans (also known as creeping eruption) is a zoonotic infection with hookworm species that do not use humans as a definitive host, the most common being *A. braziliense* and *A. caninum*. The cycle in the definitive host is very similar to the cycle for the human species, which involves tracheal migration to the small intestine. Some juveniles become arrested in the tissues and serve as the source of infection for pups via transmammary (and possibly transplacental) routes. Mature hookworms reproduce in the small intestine, and eggs are passed in the animal definitive host's stool (1), and under favorable conditions (moisture, warmth, shade), juveniles hatch in 1 to 2 days. The released rhabditiform juveniles grow in the feces and/or the soil (2), and after 5 to 10 days (and 2 molts) they become filariform (third-stage) juveniles that are infective (3). These infective juveniles can survive 3 to 4 weeks in favorable environmental conditions. On contact with the animal host (4), the juveniles penetrate the skin and are carried through the blood vessels to the heart and then to the lungs. They penetrate into the pulmonary alveoli, ascend the bronchial tree to the pharynx, and are swallowed. The juveniles reach the small intestine, where they reside and mature into adults. Adult worms live in the lumen of the small intestine, where they attach to the intestinal wall. Some juveniles become arrested in the tissues and serve as source of infection for pups via transmammary (and possibly transplacental) routes (6). Humans become infected when filariform juveniles penetrate the skin (7). With most species, the juveniles cannot mature further in the human host and migrate aimlessly within the epidermis, sometimes as much as several centimeters a day. Some juveniles may become arrested in deeper tissue after skin migration. Source: Adapted from United States Centers for Disease Control and Prevention, Division of Parasitic Disease and Malaria, 2019. Public domain.

tion on open ground keeps soil contamination high. Use of nightsoil as fertilizer for crops is an especially important factor in parts of East Asia.

Juveniles develop best in near-neutral pH, and acid or alkaline soils inhibit development, as does the acid pH of undiluted feces (pH 4.8 to 5.0). Chemical factors also have an influence. Urine mixed with feces is fatal to eggs, and several strong chemicals that may be added to feces as disinfectants or fertilizers are lethal to free living stages. Salt in the water or soil inhibits hatching and is fatal to juveniles.

Because worms penetrate the epithelial tissues of the host, a habit of going barefoot in tropical countries is an elemental contribution to transmission. The role of skin penetration presumably accounts for a general lack of high correlation of hookworm with *Ascaris lumbricoides* and *Trichuris trichiura* infections, which must be acquired by ingestion (Booth and Bundy, 1992). However, higher egg counts have been reported in instances of hookworm coinfection with *Ascaris lumbricoides*, suggesting a possible synergistic effect (Fleming et al., 2006). This finding may have important implications for control strategies.

Longevity of the worms is important in transmission to new hosts, continuity of infection in a locality, and introduction to new areas. Juveniles can survive in reasonably good environmental conditions for about 3 weeks; in protected sites like mines, they can last for a year. There is some dispute about the life span of adults, but a good estimate is 5 to 15 years. A person who moves from an endemic area loses the infection in about that time. Specifically, *Necator americanus* has been recorded to live up to 15 years and species of *Ancylostoma* have been reported to live from 12 months to 5 years (Nawalinski et al., 1978a; 1978b; Behnke, 1987).

Schad and colleagues (1984) discovered that juveniles will survive in muscles of paratenic hosts. Thus, *Ancylostoma duodenale* can be transmitted through ingestion of undercooked meat, including rabbit, lamb, beef, and pork. Pigs can also serve as transport hosts for *Necator americanus* (Steenhard et al., 2000). Similarly, dogs can be infected with the canid hookworm, *A. caninum*, by ingestion of juveniles in mice, cockroaches, and possibly other paratenic hosts that might be consumed through predation.

Pathogenicity

In addition to causing iron deficiency anemia involving the direct loss of blood from the mucosa of the intestine by the feeding action of adult nematodes, human hookworm disease manifests 3 main phases of pathogenicity: 1) The cutaneous phase or invasion period, 2) pulmonary phase, and 3) intestinal phase. When a juvenile enters an unsuitable host, after the cutaneous phase or invasion period, it may result in cutaneous larva migrans, after which the pathogenic action of the worm is halted. Cutaneous larva migrans is included in the discussion in the section on migration phase or invasion period, below.

Cutaneous phase or invasion period

The cutaneous phase or invasion period begins when juveniles penetrate the host's epithelial tissue. They do little damage to superficial layers, since they seem to slip through tiny cracks between skin scales, or penetrate sweat pores or hair follicles. Juveniles are stimulated to penetrate by host fatty acids and they must remain in a water film for successful penetration (Haas et al., 2005).

Cutaneous larva migrans may occur at this point. See the discussion of this phase, below. At this stage, infection with pyogenic bacteria may result from the nematodes penetrating into the skin and bringing bacteria with them from their previous fecally-laced habitat, causing an urticarial reaction and dermatitis, a condition known as ground itch.

Proteases released by J_3s cause an increase in cellular permeability and disruption of vascular endothelial cell junctions (Williamson et al., 2003). Once in the dermis, however, their attack on blood vessels initiates a tissue reaction that may isolate and kill the worms.

Pulmonary phase

After the cutaneous phase, or invasion period, the worms enter the hepatic portal system, migrate to the liver, then go into the heart, and then to the lungs. More specifically, the pulmonary phase occurs when juveniles break out of the lung capillary bed into alveoli and progress up the bronchi to the throat. Juveniles migrating through the liver, heart, and lungs may cause inflammation in the lungs termed pulmonary pneumonitis (Hotez et al., 2004). Small hemorrhages occur in the alveoli, and in some cases juveniles induce eosinophilic pneumonia, or Loeffler's syndrome. The pulmonary phase is usually asymptomatic, although there may be some dry coughing and sore throat.

Intestinal phase

The intestinal phase is the most important period of pathogenicity. On reaching the small intestine, young worms attach to the mucosa with their strong buccal capsule and teeth, and they begin to feed on blood. Initiation of this phase is accompanied by painful eosinophilic enteritis (see also the discussion about this phase of infection by Looss; 1911). In heavy infections, worms are found from the pyloric stomach to the ascending colon, but usually they are restricted to the anterior third of the small intestine. Worms move from place to place, and blood loss is exacerbated by bleeding at sites of former attachment (Gilman, 2000). Hookworms produce proteins that inhibit host blood clotting factors (Gan et al., 2009), and these molecules may contribute to bleeding at former feeding sites. Ironically, such anticoagulants may have beneficial medical applications (Friedly, 1996). Worms pass substantially more blood through their digestive tracts than would appear necessary for their nutrition alone, but the reason for this is unknown. Blood loss per worm is about 0.03 ml per day for *Necator americanus* and around 0.26 ml per day for *Ancylostoma duodenale.*

Migration phase

After the cutaneous phase, or invasion period, cutaneous larva migrans (also termed creeping eruption) may occur. It is usually caused by invasive juvenile hookworms of species normally maturing in animals other than humans (however, ground itch and larva migrans may also occur with the normal human hookworms). In cases of cutaneous larva migrans, juveniles manage to penetrate the skin of humans, and although they may migrate into and through the stratum germanitivum, they are incapable of successfully completing migration to the intestine. Before they are overcome by immune effectors, they produce distressing, but rarely serious, complications of the skin.

After entering the top layers of epithelium, juveniles are usually incapable of penetrating the basal layer (stratum germinativum), so they begin an aimless wandering. As they tunnel through skin, they leave a red, itchy wound that usually becomes infected by pyogenic bacteria. Juveniles may live for weeks or months. It is known that some can enter muscle fibers and become dormant (Little et al., 1983). Juveniles can attack skin anywhere on the body, but people's feet and hands are more in contact with the ground and so are most often affected. Thiabendazole is used as a treatment for cutaneous larva migrans.

Species of hookworms from cats, dogs, and other domestic animals are likely to come into contact with people. *Ancylostoma braziliense*, a common hookworm of dogs and cats, appears to be the most common agent throughout its geographic range (Schad, 1994). Travelers from temperate regions who acquire this infection by visiting tropical beaches may encounter difficulty obtaining a correct diagnosis and medication upon returning home (Tremblay et al., 2000).

Severe Infections

Patients with severe infections may lose up to 200 ml of blood per day, but around 40% of the afflicted person's iron may be reabsorbed before it leaves the intestine (Layrisse et al., 1961). Nevertheless, a moderate hookworm infection will gradually produce iron-deficiency anemia as body reserves of iron are used up. Severity of anemia depends on worm load and dietary iron intake of a patient. Anemia during pregnancy can cause serious complications, putting both mother and child at risk. In hookworm endemic regions, iron deficiency resulting from hookworm infection during pregnancy is common (Baidoo et al., 2010). Slight, intermittent abdominal pain, loss of normal appetite, and desire to eat soil (geophagy) are common symptoms of moderate hookworm disease. Certain areas in the southern United States became locally famous for the quality of their clay soil, and people traveled for miles to eat it. In the early 1920s, an enterprising person began a mail-order business, shipping clay to hookworm sufferers throughout the country!

In very severe infections, patients suffer severe protein deficiency, with dry skin and hair, edema, and potbelly in children and with delayed puberty, mental disability, heart failure, and even death. Intestinal malabsorption is not a marked feature of infection with hookworms, but hookworm disease is usually manifested in the presence of malnutrition and is often complicated by infection with other worms and/or malaria.

The drain of protein and iron is catastrophic to a person subsisting on a minimal diet. In addition, the staple foods of some countries, such as cassava, rice, and corn, are poor sources of iron. Chronic malnutrition, particularly in the young, often results in stunted growth and intellectual disability, but treatment for the worms can significantly increase fitness, appetite, and growth (Latham et al., 1990; Stephenson et al., 1989). Impairment in ability to produce IgG results in lowered antibody response to hookworms as well as to other infectious agents.

Diagnosis

Demonstration of hookworm eggs or worms themselves in feces is, as usual for gut parasites, is the only definitive diagnosis of the disease. Demonstration of eggs in direct smears may be difficult, however, even in clinical cases, and one of the several concentration techniques should be used. If estimation of worm burden is necessary, techniques are available that give reliable data on egg counts (Cross, 2000). It is not possible to distinguish *Ancylostoma duodenale* eggs from those of *Oesophagostomum bifurcum* or *Ternidens deminutus*, and this is important in the areas of Africa where *O. bifurcum* and *T. deminutus* are widely prevalent in humans. PCR methods have been described for these identifications, and a multiplex real-time PCR test based on DNA from a 200-µl fecal sample can diagnose species in mixed infections and provide quantitative results that correlate with egg counts (Verweij et al., 2001). However, implementing advanced molecular diagnostics for routine testing is sometimes not practical (Schindler et al., 2005; Verweij et al., 2001; De Gruijter et al., 2005).

To rid a person of hookworm infection it is neither necessary nor possible to distinguish *Necator americanus* eggs from those of *Ancylostoma* spp., but care should be taken to differentiate *Strongyloides stercoralis* infections. This is not a problem unless some hours pass between time of defecation and time of examination of feces. Then hookworm eggs may have hatched, and juveniles of *Ancylostoma* spp. must be distinguished from those of *S. stercoralis*.

However, it is necessary to be able to distinguish *Necator americanus* and *Ancylostoma* spp. in studies on the efficacy of various drugs or chemotherapeutic regimens because the 2 species are not equally sensitive to particular drugs: *N. americanus* has low sensitivity to ivermectin, in contrast with *Ancylostoma* spp. (Richards et al., 1995). Differentiation can be accomplished by recovery of adults after anthelmintic treatment, culturing juveniles from feces, or molecular identification based on single eggs.

Treatment

Mebendazole or albendazole are commonly used for treatment, as they kill all nematodes. Single-dose therapy is inexpensive and convenient, but reports of drug failure and decreased efficacy for mebendazole suggest that albendazole later emerged the drug of choice (Albonico et al., 2003; Hotez et al., 2010). There is also evidence that populations of *Necator americanus* are becoming resistant to mebendazole in Africa (De Clercq et al., 1997) and *Ancylostoma caninum* shows evidence of resistance to the anthelminthic pyrantel pamoate (Kopp et al., 2007). It has also been found that routine treatment of pregnant women in areas of high hookworm prevalence significantly decreases incidence of infants with very low birthweight (Larocque et al., 2006).

Treatment for hookworm disease should always include dietary supplementation. In many cases, provision of an adequate diet alleviates symptoms of the disease without worm removal.

Control

Control of hookworm disease depends on lowering worm burdens in a population to an extent that remaining worms, if any, can be sustained within nutritional limitations of people without causing symptoms. Mass treatment campaigns do not eradicate the worms but certainly lower the so-called seeding capacity of their hosts. Education and persuasion of a population in sanitary disposal of feces are also vital. Economic dependence on nightsoil in family gardens remains one of the most persistent of all problems in medical parasitology.

Recognizing these factors, the American zoologist Charles W. Stiles persuaded John D. Rockefeller to donate $1 million in 1909 to establish the Rockefeller Sanitary Commission for the Eradication of Hookworm Disease (Ackert, 1952). (The activities of the commission eventually led to the formation of the Rockefeller Foundation and then Rockefeller University.) Beginning state by state and then extending throughout the southeastern United States, the Commission would first survey an area. Residents of the area were examined for infection and then treated with anthelmintics. Thousands of latrines were provided with instructions on how to use and maintain them. As a result of efforts of this and other similar hygiene commissions, hookworm prevalence is now much lower in some areas of the world. Nevertheless, worldwide prevalence of hookworms is still high; between one-fifteenth and one-tenth of the Earth's human population remains infected (Chan, 1997; Hotez et al., 2010; CDC, 2023).

New molecular methods and technologies hold much promise for advances in understanding hookworm biology and implementing control measures. For example, the transcriptome of *Necator americanus* adults has been analyzed (Cantacessi et al., 2010) revealing 18 potential drug targets that lack homologues in the human genome. By inference, this means that drugs can be applied to a human population to rid the worms from humans while relatively no effect is seen on the host itself. Rapid and specific molecular diagnostic methods that clearly differentiate among different species of hookworms are needed in order to begin to achieve effective control (Clements and Alene, 2022). Deep sequencing of the genome of *N. americanus* has recently been carried out in order to identify potential drug resistant markers. Other newer methods of molecular biology are now being implemented in the ongoing battle against hookworm disease (George et al., 2022).

Family Strongylidae Baird, 1853

Family Strongylidae currently contains 1,126 species in 4 subfamilies (see Hodda, 2022).

Members of Strongylidae Baird, 1853 occur in a variety of mammals, especially herbivores such as horses, in which they are a serious veterinary problem. They are commonly recognized as large strongyles (several species of *Strongylus*, of which *S. vulgaris* is the most important) and small strongyles (mostly the numerous species of *Cyathostomum*) (Herd, 1990). Adults of both are found in the large intestine of equines. Eggs pass out in feces, hatch as J_1s, and develop in soil into infective J_3s; the latter retain the cuticle of the J_2 as a close-fitting sheath. These crawl onto vegetation and are eaten by grazing hosts. All undergo a migration and period of development in various tissues, the details of which vary with species.

Developing juveniles of *Strongylus vulgari*s migrate into the arteries of the host, especially the anterior mesenteric artery, where they cause thrombosis and arteritis. After 3 to 4 months in the arteries, young adults migrate to the intestine where they eventually enter the lumen and reach maturity.

In the past, the arterial stages of *Strongylus vulgaris* were shown to be present in 90% to 100% in horses in the United States, and it was the most feared equine parasite (Herd, 1990). *Strongylus vulgaris* remains sensitive to benzimidazole and ivermectin anthelmintics, but cyathostomes are relatively resistant to these drugs. As a result, *S. vulgaris* has almost been eradicated, and small strongyles such as *Cyathostomum* spp. are instead a much bigger problem with horse owners. To aid in diagnosis, a quantitative real-time PCR test has been developed for *S. vulgaris* (Nielsen et al., 2008).

Oesophagostomum spp. are parasites of primates, rodents, ruminants, and pigs. They are called nodular worms because developing juveniles form nodules in the walls of both the small and large intestines of the host. Adults live in the large intestine. Infections are normally acquired by ingestion of third-stage juveniles (J_3s). Infections in humans are generally considered to be accidentally caused by the zoonotic species of this genus. However, *O. bifurcum* has a high prevalence in humans and nonhuman primates in one small area in Africa (northern Togo and Ghana). Additionally, individuals with infection by species of hookworms have a higher likelihood of also being infected with *O. bifurcum* (Ziem et al., 2006). Infection of humans by these species of nematode typically shows up as a painful abdominal mass that sometimes requires surgical intervention. Eggs of *O. bifurcum* are indistinguishable morphologically from hookworm, but J_3s obtained after fecal culture show clear differences. Although morphologically indistinguishable, *O. bifurcum* from humans and 3 nonhuman primate hosts show relatively high levels of genetic divergence. This observation is consistent with low levels of gene flow between these host-associated populations (Gasser et al., 2006).

Syngamus trachea is the gapeworm of poultry and is called this because adults live in the trachea of their galliform hosts causing the host to gasp and gape with the mouth wide open. The fowl coughs up eggs, swallows them, and then passes them in feces. Juveniles molt twice in the egg to become infective J_3s. Eggs may or may not hatch in soil, and a variety of terrestrial molluscs, earthworms, and arthropods can serve as paratenic hosts.

Syngamus trachea individuals can survive several years in earthworms, and numerous wild bird species serve as reservoirs. Definitive hosts become infected when they swallow embryonated eggs or juveniles. Infective juveniles penetrate the gut wall, are carried by blood to the lungs where they break out into alveoli, and then proceed up to the trachea. At this stage, males remain attached to a female via their copulatory bursa. Young birds are most severely affected and may die with a heavy infection.

Superfamily Trichostrongyloidea Cram, 1927

The superfamily Trichostrongyloidea Cram, 1927 constitutes one of the most diverse and complex taxa within the bursate nematodes (Durette-Desset, 1985; 2009; Hoberg and Lichtenfels, 1994). The group includes more than 1,000 described species approximately 175 genera. These worms have a worldwide distribution and direct life cycle. They occur in the gut and sometimes in the stomach of almost all classes of terrestrial vertebrates (Durette-Desset, 1992).

Some of the species of medical and veterinary importance include *Haemonchus contortus*, *Ostertagia* spp., and *Trichostrongylus* spp., which are discussed briefly below.

Figure 9. Posterior end of a specimen of a trichostrongyloid nematode *Obeliscoides cuniculi*, the stomach nematode of rabbits and hares in North America. This specimen was collected from the stomach of an individual of *Sylvilagus* sp. north of Ogallala, Nebraska, United States. The contracted bursa of this male is visible with small bosses covering the cuticle. Two similar spicules are visible lying parallel which are easily seen in this Normarsky micrograph (NP2380). Source: G. Drabik and S. L. Gardner, HWML, 2018. License: CC BY 4.0.

General Morphology

Trichostrongyloids are usually small, very slender worms, with a small, non-developed **stoma**. Lips around the **mouth** are very reduced or absent, and cuticularized teeth or spines in the stoma are rarely present. The **cuticle** of the **head** may be inflated and some of them are filled with fluid containing hemoglobin that is not host-derived and may be pink when the nematodes are collected alive (Figure 9). Males have a well-developed **copulatory bursa**, and **spicules** vary from simple setaceous to extremely complex falcate or modified hamate in form (see Maggenti, 1981), depending on species and group. Females are usually considerably larger than males. The **vulva** is located anywhere from before the midbody to near the **anus**, depending on the species and group (Figure 10). Worms lay thin-shelled eggs that are in the morula stage (Durrette-Desset et al., 1999).

Life Cycles

Life cycles are similar in all species of trichostrongyloid nematodes. For those that have been studied, no intermediate host is required; eggs hatch in soil or water and develop directly into infective J_3s. Some infections may occur through skin, but as a rule juveniles must be swallowed with contaminated food or water. Many trichostrongyloids undergo exsheathment, where J_3s escape the J_2 cuticle during initial infection. The host stimuli that induce production of exsheathing fluid by the J_3 has been extensively investigated. Enormous numbers of juveniles may accumulate on heavily grazed pastures, causing serious or even fatal infections in ruminants and other grazers. A given host usually is infected with several species since their life cycles are similar, and severe pathogenesis results from the cumulative effects of all the worms. Cost to the sheep industry in Australia, for example, is high (McLeod, 1995).

Following is a brief discussion of the families **Trichostrongylidae, Dictyocaulidae**, **Angiostrongylidae**, and **Protostrongylidae**, as well as a few noteworthy species.

Family Trichostrongylidae Leiper, 1912

Many genera and an enormous number of species comprise the family Trichostrongylidae (Durrette-Desset et al., 1999; Hoberg and Lichtenfels, 1994). They are primarily parasites of the stomach or small intestine of all classes of vertebrates, causing great economic losses in domestic animals, especially ruminants, and in a few cases causing disease in humans.

Haemonchus contortus

Haemonchus contortus lives in the so-called fourth stomach (or abomasum) of sheep, cattle, goats, and many wild ruminants. The species has been reported in humans in Brazil and Australia. It is one of the most important nematodes of domestic animals, causing severe anemia in heavy infections (Flach, 2008).

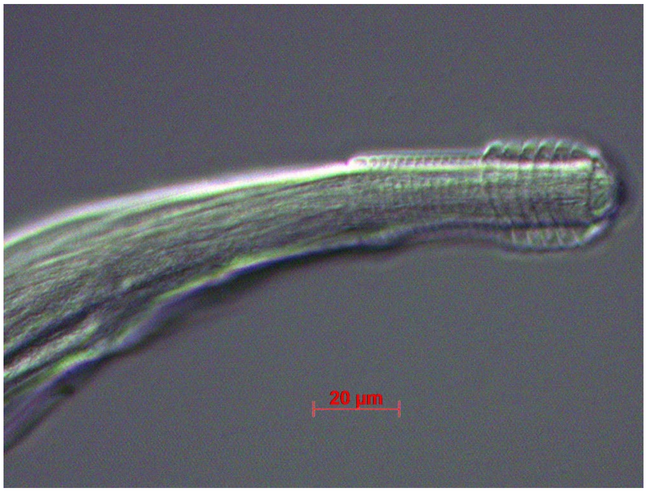

Figure 10. Anterior end of the specimen depicted in Figure 9, a trichostrongyloid nematode *Obeliscoides cuniculi*, the stomach nematode of rabbits and hares in North America. Source: G. Drabik and S. L. Gardner, HWML, 2018. License: CC BY 4.0.

The small stoma contains a single well-developed tooth that pierces a host's mucosa (Emery et al, 2016). The blood this species sucks from this wound gives the transparent worms a reddish color. The large females have white ovaries wrapped around the red intestine, lending it a characteristic red and white appearance and leading to its common names: Twisted stomach worm and barber-pole worm. Prominent cervical papillae are found near the anterior end. The male's bursa is powerfully developed with an asymmetrical dorsal ray. Spicules are 450 µm- to 500 µm-long, each with a terminal barb. The vulva has a conspicuous anterior flap in many individuals but not in all. Frequency of occurrence of the vulvar flap seems to vary according to strain.

Infection occurs when livestock eat forage containing J_3s, which are sheathed in the loosely fitting second-stage cuticle. Exsheathment takes place in the rumen or reticulum of the host animal. Arriving in the abomasum or upper duodenum, worms molt within 48 hours, becoming J_4s with a small buccal capsule having formed. They feed on blood, which forms a clot around the anterior end of the worms. The worms molt for a final time in 3 days and begin egg production about 15 days later. Fourth-stage juveniles can undergo developmental arrest, typically in fall, with maturation to adults occurring in spring. Arrest is considered a mechanism promoting survival and transmission in temperate climates, leading to the spring rise in eggs passed in feces of sheep (Emery et al., 2016).

Anemia, emaciation, edema, and intestinal disturbances caused by these parasites result principally from loss of blood and injection of hemolytic proteins into the host's system. A host often dies with heavy infections, but those that survive usually develop immunity due to specific inflammatory responses in the intestinal mucosa.

Ostertagia Species

Ostertagia spp. are similar to *Haemonchus contortus* in host and location, but they differ in color, being a dirty brown—hence, their common name, brown stomach worm. The buccal capsule is rudimentary and lacks a tooth. Cervical papillae are present. The male bursa is symmetrical. The vulva has a large anterior flap, and the tip of the female's tail bears several cuticular rings.

Their life cycle is similar to that of *Haemonchus contortus* except that J_3s invade gastric glands and elicit nodules. J_3s molt before returning to the lumen, where they feed, molt, and begin producing eggs about 17 days after infection. *Ostertagia* spp. suck blood but not as much as *H. contortus*. Species of *Ostertagia* often undergo developmental arrest as J_4.

Some common species of *Ostertagia* are *O. circumcincta* in sheep, *O. ostertagi* in cattle and sheep, and *O. trifurcata* in sheep and goats. Economic losses in the cattle industry due to *O. ostertagi* and other nematodes probably exceed $600 million per year in the United States alone (Smith and Granfell, 1985).

Trichostrongylus Species

Trichostrongylus spp. are some of the smallest members of the superfamily, seldom exceeding 7 mm in length. Many species parasitize the small intestine of ruminants, rodents, pigs, horses, birds, and humans. They are colorless, lack cervical papillae, and have a rudimentary, unarmed stoma. The male's bursa is symmetrical, with a poorly developed dorsal lobe. Spicules are brown and distinctive in size and shape in each species. The vulva lacks an anterior flap (Anderson, 2000).

Their life cycle is similar to that of *Haemonchus* spp. except that J_3s burrow into mucosa of the anterior small intestine, where they molt. After returning to the lumen, they bury their heads in mucosa and feed, grow, and molt for the last time. Egg production begins about 17 days after infection.

Common species of *Trichostrongylus* are *T. colubriformis* in sheep, goats, cattle, and deer; *T. tenuis* in galliform birds such as grouse, pheasant, chickens, and turkeys; *T. capricola, T. falcatus,* and *T. rugatus* in ruminants; *T. retortaeformis* and *T. calcaratus* in rabbits; and *T. axei* in a wide variety of mammals. Hudson and colleagues (1998) showed that the periodic crashes in populations of British red grouse (*Lagopus lagopus scoticus*) were due to negative impact on fecundity caused by build-up of *T. tenuis* (Cattadori et al., 2005; Hudson et al., 1998).

Approximately 10 species of *Trichostrongylus* have been reported in humans, with records from nearly every country of the world. There are 9 species in Iran alone (Pearson and Schwartzman, 1991). Reported prevalence has varied from very low to as high as 69% in southwest Iran (Sabha et al., 1967) and 70% in a village in Egypt (Lawless et al., 1956).

Pathological conditions are identical in humans and other infected animals. Traumatic damage to intestinal epithelium may be produced by burrowing juveniles and feeding adults. Systemic poisoning by metabolic wastes of the parasites and hemorrhage, emaciation, and mild anemia may develop in severe infections.

Diagnosis can be made by finding characteristic eggs in feces or by culturing juveniles in powdered charcoal. Juveniles are very similar to those of hookworms and *Strongyloides* spp., and careful differential diagnosis is required. Molecular diagnostics are available for the common trichostrongylid species from ruminants (Sweeny et al., 2011).

Treatment and Drug Resistance

Treatment with thiabendazole or with pyrantel pamoate has proven effective. Cooking vegetables adequately will prevent many infections in humans. However, drug resistance in nematodes of livestock has been reported for every class of anthelminthic, and multidrug resistance (MDR) was reported in worms of sheep and goats in the 1980s (Kaplan, 2004; Shoop, 1993). MDR in trichostrongylids infecting small ruminants threatens production throughout the world, but particularly in South America, South Africa, Malaysia, and the United States. Resistance by trichostrongyles to benzimidazole drugs (for example, albendazole, mebendazole, and thiabendazole) is increasing and quite ominous (Conder and Campbell, 1995; Geerts et al., 1997).

Family Dictyocaulidae

Species in this genus are medium-sized nematodes that as adults parasitize the bronchi and trachea and are associated with bronchitis in their hosts. *Dictyocaulus filaria* is an important parasite of sheep and goats, but also infects wild antelope and deer. Adults live in bronchi and bronchioles, where females produce embryonated eggs. Eggs hatch while being carried toward the trachea by ciliary action. First-stage juveniles appear in feces and develop to J_3s in contaminated soil without feeding. Cuticles of both first and second stages are retained by the third stage until the worm is eaten by a definitive host; then cuticles of all these stages are shed together. J_3s penetrate the mucosa of the small intestine and enter mesenteric lymph nodes. There they undergo 2 molts to become small adults (about 500 µm-long), enter the circulation by way of the thoracic duct, and parasitize the trachea and bronchi. They commonly cause death of their host (Anderson, 2000).

Fully-grown adults are slender and long, with males reaching 80 mm and females 100 mm. The bursa is small and symmetrical; spicules are short and boot-shaped in lateral view. The uterus is near the middle of the body. Other species in horses and cattle are similar to *Dictyocaulus filaria* in morphology and biology.

Family Angiostrongylidae

One of the main pathogenic organisms in the family Angiostrongylidae is *Angiostrongylus cantonensis*, also known as the rat lungworm, detailed below. Other worms in the family are also covered briefly.

Rat Lungworm: *Angiostrongylus cantonensis*

Angiostrongylus cantonensis was first discovered in pulmonary arteries and the heart of domestic rats in China in 1935. Later the worm was found in many species of rats and bandicoots, and it may mature in other mammals throughout Southeast Asia, the East Indies, Madagascar, and Oceania, with infection rates as high as 88%. As a parasite of rats, it attracted little attention, but 10 years after its initial discovery it was found in the spinal fluid of a 15-year-old boy in Taiwan. It has been discovered since in humans in Hawaii, Tahiti, the Marshall Islands, New Caledonia, Thailand, Vanuatu, the Loyalty Islands, and other places in the Eastern Hemisphere. It is now known to exist in Louisiana (United States), the West Indies, and the Bahamas (Raccurt et al., 2003).

This is another illustration of the value of basic research in parasitology to medicine, because when the medical importance of this parasite was realized, the reservoir of infection in rats already was known. Surveys of parasites endemic to wild fauna of the world remain the first step in understanding epidemiology of zoonotic diseases.

Morphology

Angiostrongylus cantonensis is a delicate, slender worm with a simple mouth and no lips or stoma. Males are 15.5 mm- to 25 mm-long, whereas females attain lengths of 19 mm to 34 mm. The bursa is small and lacks a dorsal lobe. Spicules are long, slender, and about equal in length and form. An inconspicuous gubernaculum is present. In females the intertwining of intestine and uterine tubules gives the worm a conspicuous barber-pole appearance. The vulva is about 0.2 mm in front of the anus. Eggs are thin-shelled and unembryonated when laid. Eggs are not produced in human infections.

Life Cycle

Eggs are laid in the pulmonary arteries, carried to capillaries, and break into air spaces, where they hatch. Juveniles migrate up the trachea, are swallowed, and are expelled with feces.

Many types of molluscs serve as intermediate hosts, including slugs and aquatic and terrestrial snails. Terrestrial planarians, freshwater shrimp, land crabs, and coconut crabs serve as paratenic hosts. Frogs have been found naturally infected with infective juveniles (Ash, 1968). Experimentally, Cheng (1965) infected American oysters and clams, and Wallace and Rosen (1966) succeeded in infecting crabs. All juveniles thus produced were infective to rats.

When eaten by a definitive host, J_3s undergo an obligatory migration to the brain, which they leave 4 weeks later as subadults. In rats, the time from infection to egg appearance in feces is about 6 weeks.

Epidemiology

Humans or other mammals become infected when they ingest J_3s. There may be several avenues of human infection, depending on the food habits of particular groups of people (Alicata, 1991; Cross, 1987). In Tahiti it is a common practice to catch and eat freshwater shrimp raw or to make sauce out of their raw juices. It is also possible to eat slugs or snails accidentally with raw vegetables or fruit. In Thailand and Taiwan, raw snails are often considered a delicacy. Infective juveniles escape from slugs and can be left behind in their mucus trail on vegetables over which they crawl (Heyneman and Lim, 1967; Ming et al., 2017). Such juveniles have been found on lettuce sold in a public market in Malaysia. Fish can serve as paratenic hosts in some circumstances. Thus, although the epidemiology of angiostrongyliasis is not completely known, ample opportunities for infection exist.

Pathology

For many years a disease of unknown cause was recognized in tropical Pacific islands and was named eosinophilic meningoencephalitis. Patients with this condition have high eosinophil counts in peripheral blood and spinal fluid in about 75% of cases and increased lymphocytes in cerebrospinal fluid. Neural disorders commonly accompany these symptoms, particularly cranial nerve involvement. It is now known that *Angiostrongylus cantonensis* is at least one cause of this condition.

The presence of worms in blood vessels of the brain and meninges, as well as that of free-wandering worms in brain tissue, or subdural and subarachnoid spaces, results in serious damage. Some effects of such infection are severe headache, fever in some cases, muscle paralysis and speech impairment, stiff neck, coma, and death. The clinical symptoms mimic migraine, brain tumor, and psychoneurosis. In nonsusceptible hosts such as mice and guinea pigs, interleukin-5 activates eosinophils that kill the worms (Sugaya et al., 1997).

Diagnosis and Treatment

When the symptoms described appear in a patient in areas of the world where *Angiostrongylus cantonensis* exists, angiostrongyliasis should be suspected. It should be kept in mind that many of these symptoms can be produced by hydatids, cysticerci, flukes, *Strongyloides* spp., *Trichinella* spp., various juvenile ascarids, and possibly other lungworms. Alicata (1963) and Ash (1968) differentiated the juveniles of several species of metastrongylids that could be confused with *A. cantonensis*.

Albendazole shows promise in treating infection, but no anthelminthic appears reliably therapeutic. Dead worms in blood vessels and the central nervous system may be more dangerous than live ones. A spinal tap to relieve headache may be recommended (Ansdell et al., 2018.

Other Species in the Family Angiostrongylidae

Angiostrongylus costaricensis parasitizes mesenteric arteries of many species of rodents in Central America and South America, southern North America, and Cuba (Morera, 1985). Cases in humans have been diagnosed from countries in North America, Central America, South America, and several Caribbean islands. Worms mature in mesenteric arteries and their branches. In humans, most damage is to the wall of the intestine, especially cecum and appendix, which become thickened and necrotic, with massive eosinophilic infiltration. Abdominal pain and high fever are the most evident symptoms. These intestinal disorders are caused by pathogenic changes that affect blood vessels, or pseudo-neoplastic tissue thickening. No symptoms of meningoencephalitis are noted, unlike the symptoms that are typical in infections due to *A. cantonensis*.

Angiostrongylus vasorum is a serious, emerging disease of dogs (Morgan et al., 2005). It has been reported from many countries in Europe, North America, South America, and Africa. Adults localize in the right ventricle and pulmonary arteries of dogs and other canids and causes labored breathing, exercise intolerance, weight loss, abdominal and lumbar pain, heart failure, and sudden death. Snails and slugs can serve as experimental intermediate hosts, and frogs as transport hosts. However, the role of different infection sources for wild and domestic canids remains undetermined (Morgan et al., 2005). Genetic studies indicate that transmission occurs between wild and domestic canids (Jeffries et al., 2010).

Family Protostrongylidae

Protostrongylus rufescens parasitizes bronchioles of ruminants in many parts of the world. Its intermediate hosts are terrestrial snails, in which it develops to the third stage. The definitive host is infected when it eats the snail along with forage. Mountain sheep in America are seriously threatened by this and related species, which take a heavy toll on lambs every spring. Hibler and colleagues (1972) demonstrated transplacental transmission of *Protostrongylus* spp. in bighorn sheep.

Umingmakstrongylus pallikuukensis is a parasite in lungs of muskoxen in the Canadian Arctic. It has a snail intermediate host and its transmission dynamics are being radically altered by global warming (Kutz et al., 2004; 2005).

Other Trichostrongyloidea Species

In addition to species from ruminants already mentioned, *Cooperia curticei* (family Trichostrongylidae), *Nematodirus spathiger*, and *N. filicollis* (family Molineidae) often occur in the same host as other trichostrongyles and, together, cause much damage. *Hyostrongylus rubidus* (family Trichostrongylidae) is a serious pathogen of swine and can cause death when present in large numbers. *Heligmosomoides polygyrus* (family Heligmosomidae, *H. polygyrus* = *Nematospiroides dubius*) in mice and *Nippostrongylus brasiliensis* (family Heligmonellidae) in rats are easily kept in the laboratory, and they serve as important tools for research on nematode biochemistry, immunology, life cycles, and other topics (Anderson, 2000).

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NEMATOMORPHS

57

NEMATOMORPHA

Nematomorpha (Phylum): Horsehair Worms

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Phylum Nematomorpha

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Chapter 57

Nematomorpha (Phylum): Horsehair Worms

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Figure 1. Free-living adult gordiids. A) Adult free-living male *Gordius* sp.; B) A typical Gordian knot containing numerous individuals of *G. terrestris*. Source: M. G. Bolek. License: CC BY-NC-SA 4.0.

Introduction

Nematomorphs are commonly known as horsehair worms because of their resemblance to and the common myth of worms arising from horse tail or mane hairs that fall into water. Additionally, because of their habit of becoming entangled in masses of many individuals while mating, horsehair worms are also known as Gordian worms after the Gordian knot from Greek mythology (Figure 1) (Bolek et al., 2015).

The phylum Nematomorpha consists of species that can be allocated into 2 major classes, the freshwater and terrestrial Gordiida and the marine Nectonematida. These animals are unique in several ways and they are 1 of 3 entirely parasitic animal phyla that include the Cestoda—the tapeworms—and the Acanthocephala—the thorny-headed worms (Hanelt et al., 2005). At the current time, the nematomorphs include approximately 360 species that have been described globally and are included in 19 extant and 2 extinct genera (Poinar, 1999; Poinar and Buckley, 2006; Yadav et al., 2018). The 5 known marine species belong to the genus *Nectonema*, and all infect decapod crustaceans (phylum Crustacea: class Decapoda) (see Schmidt-Rhaesa, 2013). Among the Gordiida, both dioecious and parthenogenetic species are known and at least 1 species occurs in terrestrial habitats (Hanelt et al., 2012; Anaya et al., 2019). The freshwater and terrestrial gordiids have complex life cycles, which means that the life cycle can be completed by using multiple hosts with final free-living larvae and adults. Species of gordiids that infect an insect such as a cricket, appear to influence the cricket to go near or into water where the adult worm then emerges from the insect to continue its life in a free-living phase (Thomas et al., 2002; 2003). After emerging from their host, dioecious species form large mating assemblages, also called gordian knots, where they mate and females deposit egg strings on substrate in the water. Those species that are parthenogenetic immediately deposit egg strings after emerging from their host (Hanelt et al., 2012; Bolek et al., 2013a). Larvae develop in the water and infect various species of aquatic invertebrate animals (Bolek and Coggins, 2002; Hanelt and Janovy, 2003). Some of these infected animals (such as aquatic insect larvae) act as paratenic or transport hosts, and when the insects metamorphose, they can carry the cysts to a terrestrial environment where they may be consumed by omnivorous or predatory arthropods, including millipedes, orthopterans (crickets, grasshoppers, etc.), beetles, cockroaches, and mantids (Figure 2).

Horsehair worms are commonly found in domestic water sources such as swimming pools, toilet bowls, cow troughs, pet water bowls, and more, thus making human interactions with them quite common (Bolek, 2000; Hanelt et al., 2005). However, besides the trauma people experience when they discover nematomorphs in their toilet or pet's water bowl, they have no medical or economic importance, although their potential as biological control agents has been suggested (Schmidt-Rhaesa, 2013). There are a few reports of adult horsehair worms from humans, but all of these observations are most likely the result of people swallowing infected arthropods or arthropod hosts releasing free-living worms into drinking water (Bolek et al., 2015). Additionally, there is one odd report of larval horsehair worms in human facial tissue resulting in orbital tumors (Singh and Rao, 1966). However, this report is questionable because juvenile worms contain few if any morphological characteristics of gordiids (see Schmidt-Rhaesa, 2013).

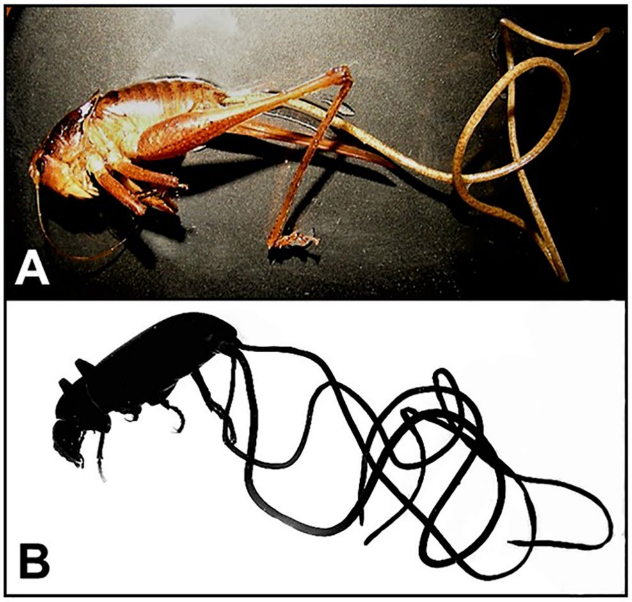

Figure 2. Examples of typical arthropod definitive hosts for gordiids. A) An undescribed species of shieldback katydid *Atlanticus* sp. with an emerging female *Chordodes morgani*; B) an unidentified tenebrionid beetle with 3 emerging individuals of a new species of *Parachordodes*. Source: M. G. Bolek. License: CC BY-NC-SA 4.0.

Chief Morphological Characters

The Nematomorpha belong to the superphylum Ecdysozoa. As with all ecdysozoans (which means molting animals), horsehair worms molt their **cuticle** at least once during their life history. As free-living adults, nematomorphs are very long, cylindrical, and thin, and range from a few cm to over 2 m in length and less than 1 to 3 mm in diameter (Bolek et al., 2015). However, most free-living worms are 20–40 cm in length (Bolek and Coggins, 2002; Schmidt-Rhaesa, 2013).

Among the freshwater and terrestrial gordiids, adult females are usually longer and thicker than adult males (Bolek and Coggins, 2002). Adult free-living worms vary in color from white to shades of dark brown. In some species of *Chordodes*, some individuals have dark patches on a lighter background, producing a leopard-skin pattern, whereas in species of the genus *Gordius* some individuals may have white spots on a darker background (Figure 4C,D). However, color is not a good characteristic for species identification, and most species for which information is available contain various color morphs within and among populations (Schmidt-Rhaesa, 2013).

The anterior end in free-living adults is spheroid or distinctly tapering (Figure 4E,F). The **mouth** may be visible or closed (Figure 4H), and no other structures are present on the anterior end. In some species, there is a distinctly lighter colored area on the anterior end known as a **calotte**, followed by a darkly pigmented ring (Figure 4G). The posterior end is trilobed or unbranched in females and bi-lobed or unbranched in males (Figure 5A–D). In males, the **cloacal opening** is always situated on the ventral side and may contain cuticular structures, such as **circumcloacal spines**. The **cloaca** of males is usually surrounded by either post-cloacal **crescents** or **spines** and/or pre-cloacal **bristles**, and these structures are genus-and/or species-specific (Figure 5E). The cloaca in females is terminal or slightly subterminal and circumcloacal spines have not been reported for females of most species (Bolek and Coggins, 2002; Schmidt-Rhaesa et al., 2003; Bolek et al., 2010; Begay et al., 2012; Schmidt-Rhaesa, 2013).

The marine *Nectonema* species are morphologically similar to the gordiids, wormlike, long, 10–270 mm for males and 30–960 mm for females and approximately 1 mm in diameter (Schmidt-Rhaesa, 2013). The anterior and posterior ends are rounded in females, whereas the posterior end is curved ventrally and distinctly tapered in males. Unlike most gordiids, the cuticle is smooth and does not contain areoles or other surface structures, but instead the dorsal and ventral longitudinal midlines contain natatory bristles (Figure 3). In addition to the ventral longitudinal nerve cord, a dorsal nerve cord is present. The intestine is incomplete and forms a blind gut. Unlike the freshwater gordiids, the anterior end of nectonematids contains a body cavity with conspicuous large cells of unknown function known as **giant cells**. Additional work by Schmidt-Rhaesa (1996a; 1996b) and Restelli and colleagues (2002) indicates that gordiids and nectonematids differ in their muscle cell structure. Freshwater gordiids have thick and thin contractile filaments which are concentrated in bundles as thick sheets and myofibrils enclose the cell body; whereas nectonematid muscle cells are coelomtyarian, as in some nematodes.

General larval morphology. Larvae are 60–100 µm by 14–30 µm in length and width, respectively, cylindrical in shape, and superficially annulated. A septum divides the larval body into 2 regions, the pre-septum and the post-septum (Figure 10). The pre-septum contains 3 rings of cuticular **hooks** and an eversible **proboscis**, supported by 3 internal **stylets** and various sets of **muscles** (Müller et al., 2004). The outer **cuticular ring** contains 6 hooks, 1 of which is positioned ventrally and bifurcated; whereas the middle and inner rings contain 6 hooks, none of which is bifurcated (Figure 11) (Szmygiel et al., 2014). The post-septum contains 1–4 terminal spines among some gordiid genera (Szmygiel et al., 2014). Internally, the post-septum contains the **pseudointestine**, which is subdivided into unequal portions and opens to the outside of the body via a small duct (Hanelt and Janovy, 2002; Szmygiel et al., 2014). The pseudo-intestine is assumed to have a glandular function and empties during cyst formation.

Cuticular Features

In most species of Nematomorpha, the surface of the cuticle is smooth or structured into elevated thickenings called **areoles**. When present these are separated by interareolar furrows; in addition, a variety of short spines and/or bristles may be present on the surface of the cuticle. In most gordiid species, 1 or 2 types of areoles are present. These are known as simple areoles that form a regular pattern on the cuticle (Figure 5F). In species of some genera, such as those in the genus *Gordius*, areoles are lacking or are weakly developed, while in species of other genera, such as those in the genus *Chordodes*, up to 6 different types of areoles can be present and include the characteristic crowned areoles which define the species in this genus (Figure 5I–J) (Schmidt-Rhaesa et al., 2003; Bolek et al., 2013b). Finally, in some species, 2 or more areoles may be fused and form structures referred to as mega-areoles and super-areoles, and these are considered synapomorphies that group species into defined genera (Figure 5G,H).

Sexual dimorphism is common in the areole pattern among gordiids. For proper descriptions and to make firm identifications to the level of species, it is necessary to have examples of and descsribe the characters of both sexes for complete species descriptions (Bolek and Coggins, 2002; Bolek et al., 2010; 2013b).

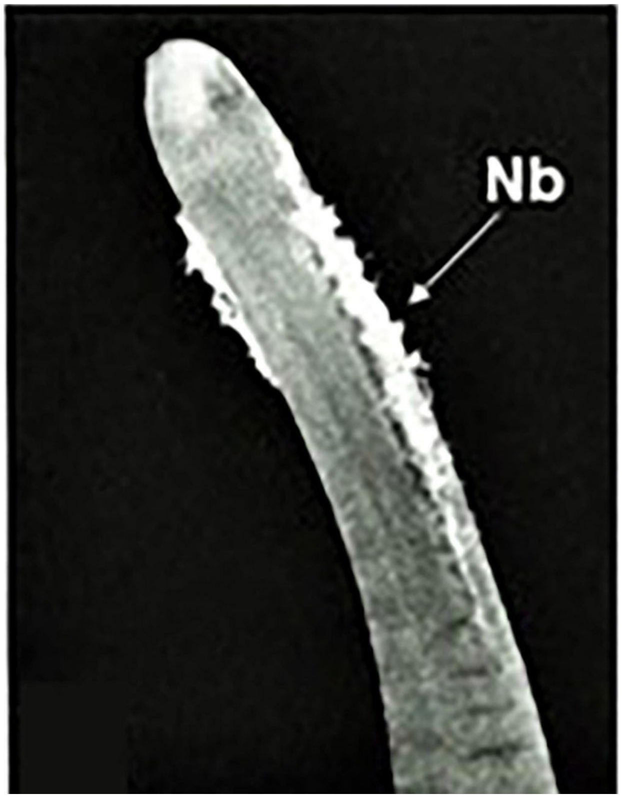

Figure 3. Light micrograph showing natatory bristles (Nb) on the anterior part of a mature fee-living gordiid.

Body Wall

The body wall of adult gordiids is composed of a thick cuticle containing an outer homogeneous region and an inner fibrous region. The fibrous region consists of 25–45 layers of thick **fibrils** that are arranged in a crisscross pattern alternating at an angle of 60–65° (May, 1919; Schmidt-Rhaesa, 1997; 2013). Studies on the chemical composition of the cuticle by Brivio and colleagues (2000) and Protasioni and colleagues (2003) indicate that the makeup of the fibrils is not collagen but some other proteinaceous components. Below the cuticle is a very thin epidermis, which secretes the cuticle layers during development within the definitive host (Schmidt-Rhaesa, 2013). The musculature in all nematomorphs consists of **longitudinal muscles** and, as in species of the phylum Nemata, circular muscles are absent (Schmidt-Rhaesa, 1996a; 1996b; Restelli et al., 2002). The body cavity in free-living adults is mostly filled with **gonads** and vacuolated **parenchyma cells** filled with lipids and glycogen, and the **digestive track** is greatly reduced (Reutter, 1972).

Nervous System

The nervous system consists of a **brain** (basically a circumesophageal **nerve commisure**), a ventral longitudinal **nerve cord**, which emerges from the ventral part of the brain, and a number of peripheral basi-epidermal **nerves**. The brain forms a ring-like structure similar to those possessed by species in the phylum Nemata and surrounds the anterior region of the **alimentary canal** (Schmidt-Rhaesa, 2013). The ventral nerve cord is connected to the epidermis by a thin lamella (Schmidt-Rhaesa, 1997). Simple **sensory organs** in the cuticle are not fully understood, but some studies indicate that integumentary receptors are present. However, it is unclear if these function as mechanoreceptors or if they have other functions (Schmidt-Rhaesa, 2013).

Digestive System

In free-living adults, a **mouth** may or may not be present and, depending on the gordiid species, the **pharynx** can be a cuticularized tube (Figure 4H), cellular in structure, or absent altogether. The **intestine** is located dorsally to the ventral nerve cord and consists of layers of cuboidal cells that manifest **microvilli** on the lumen side of the tissue. Work on *Paragordius varius* indicates that the organization of the intestine changes during development in the definitive host, decreasing in free-living adults compared to parasitic juveniles. In both sexes, the intestine and reproductive system fuse and form the **cloaca**, which is lined with **cuticle** (Schmidt-Rhaesa, 1997; 2005; 2013).

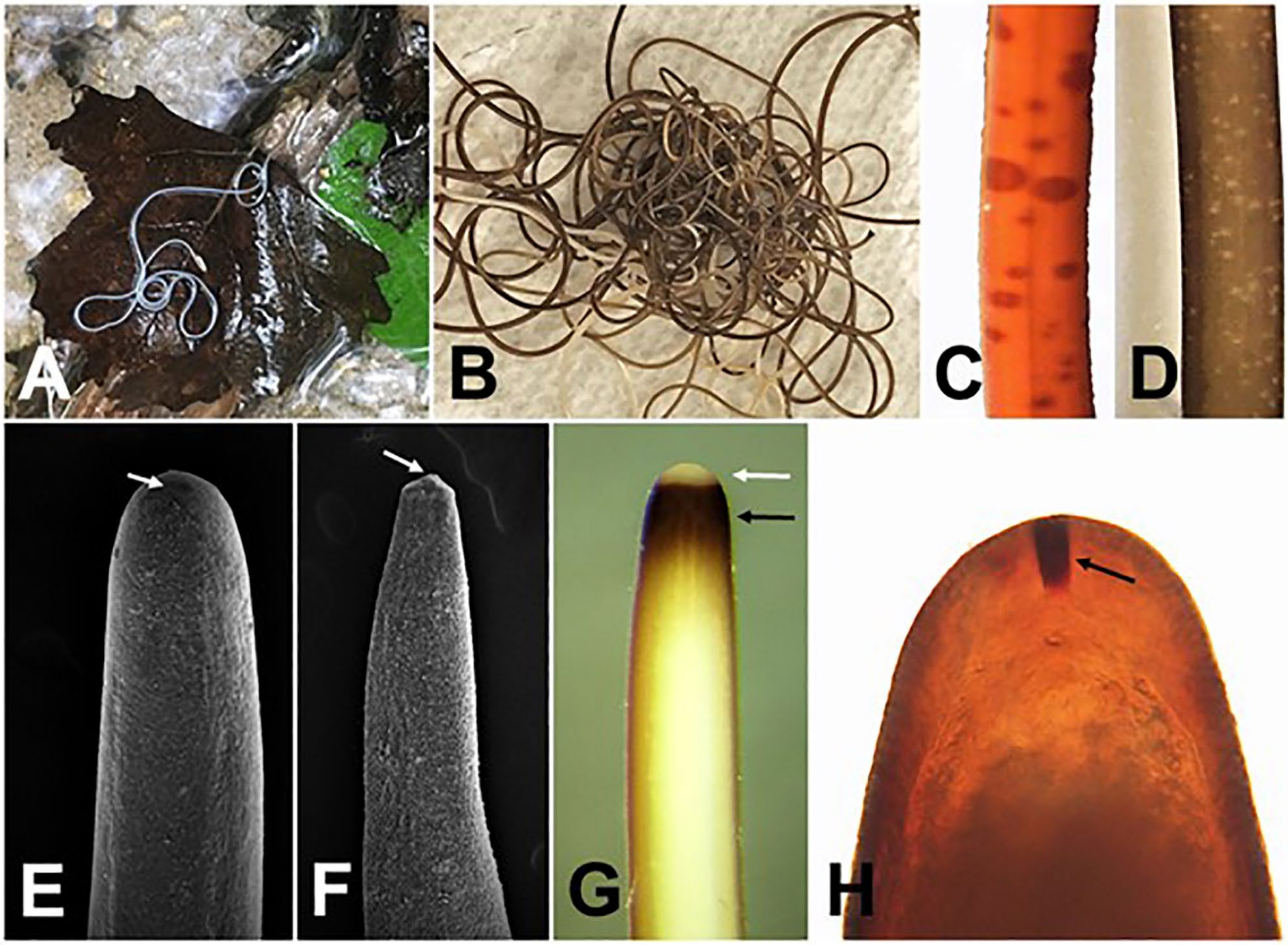

Figure 4. Color and anterior morphology of adult free-living gordiids. A) Typical white color of a female *Gordius difficilis*; B) a Gordian knot of *G. terrestris* showing variation in color of worms ranging from white to dark brown; C, D) mid-body region of a free-living adult female *Chordodes morgani* showing the leopard pattern and the mid-body region of a free-living adult male *G. terrestris* showing white spots on a darker background; E, F) scanning electron micrograph of the E) anterior region being spherical in *G. difficilis* and F) distinctly tapering in *C. morgani*. Note the degenerate mouth (white arrows); G) anterior end of a female *G. terrestris*. Note the calotte (white arrow) followed by a by a dark pigmented ring (black arrow); H) anterior end of a male *C. morgani*. Note the cuticularized pharynx (black arrow). Source: M. G. Bolek. License: CC BY-NC-SA 4.0.

Reproductive System

The **gonads** are arranged as 2 long dorsolateral tubes, surrounded by **parenchymal cells**, and extend almost the entire length of the body. In mature males, the 2 **testes** are full of spermatozoa but may be empty after males complete mating with several females. In developing females, the 2 dorsolateral tubes contain **ovarial ducts** with numerous extensions called **ovaries** (Schmidt-Rhaesa, 1997).

Little information is available about the structure of gonads in the marine Nectonema species, including no information on mature spermatozoa (Schmidt-Rhaesa, 2013).

Reproduction

Once worms enter water, in dioecious species, male and female worms must find each other to mate. Observations on *Paragordius varius* in the laboratory indicate that male worms begin mating with females even before they completely exit their arthropod definitive host (Hanelt and Janovy, 2004b). However, field studies indicate that most arthropods that are shown to be infected by horsehair worm larvae are infected with a single worm and these individuals must somehow find the opposite sex for copulation after they emerge from their hosts (Bolek and Coggins, 2002; Looney et al.,

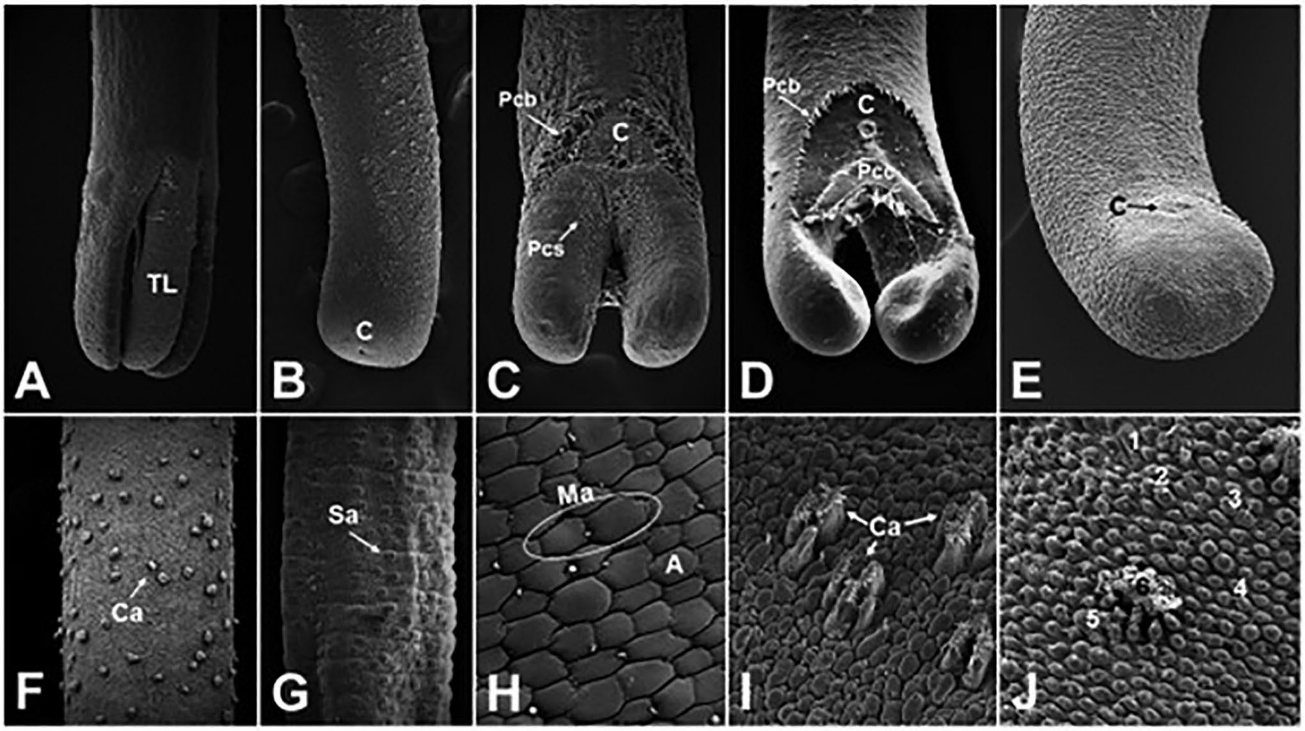

Figure 5. Scanning electron micrographs of the posterior ends and cuticle structures of adult free-living gordiids. A) Posterior end of a female *Paragordius* sp. Note the 3 tail lobes (TL); B) posterior end of a female *Chordodes* sp. showing a round posterior end and a terminal cloaca; (C); C) posterior end of a male *Parachordodes* sp. showing 2 tail lobes, cloacal spines surrounding the ventrally located cloaca (C) and rows of precloacal bristles (Pcb), and postcloacal spines (Pcs); D) posterior end of a male *G. difficilis*. Note the ventrally located cloaca (C), precloacal bristles (Pcb), and postcloacal crescent (Pcc); E) a male *Neochordodes* sp. Note the absence of distinct tail lobes and the cloacal opening (C); F) mid-body region of an adult free-living female *Chordodes* sp. Note the distinct crown areoles (Ca) among simple areoles; G) mid-body region of an adult free-living male *Parachordodes* sp. showing characteristic super-areoles (Sa); H) higher magnification of the mid-body cuticle of a male *Neochordodes* sp. Note the simple (A) and mega-areoles (Ma); I, J) higher magnification of the mid-body cuticle of 2 species of *Chordodes* showing interspecies variation in crown areoles (Ca and 6). Note the 6 types of areoles (1–6) on the cuticle of the *Chordodes* species in (J). Source: M. G. Bolek. License: CC BY-NC-SA 4.0.

2012). Currently, it is unknown whether both sexes find each other by the use of attractants, such as pheromones, or simply by chance. However, field studies using daily collections of individual female *Gordius difficilis* indicate that most females mate within a day of emerging from their host (Bolek and Coggins, 2002).

Both field and laboratory observations indicate that male and female worms initiate typical Gordian knots within hours to days of being placed together (Bolek and Coggins, 2002; Bolek et al., 2013b). During mating, males move up and down the female's body with their coiled posterior end. In genera with bi-lobed posterior ends, such as *Gordius*, a male will spread its tail lobes and glide along the female's body (Figure 8). Once a male's cloaca is in proximity of the female cloaca, the male deposits a mass of sperm referred to as a **sperm drop** or **spermatophore** (Figure 8). Field studies on *Gordius difficilis* indicate that sperm drops can remain on the posterior region of females for at least a week (Figure 8) (Bolek and Coggins, 2002).

The spermatozoa of gordiids are unique and change shape during sperm transfer between a male and a female. They contain a **nucleus** and compartments, which have been named the **acrosomal tube**, **acrosomal sheath**, and **multivesicular complex** (Figure 8). It is unclear if and how these spermatozoa move because they lack a flagellum or pseudopods (Schmidt-Rhaesa, 2013).

After dioecious species mate, females produce up to 8 million eggs during their 2-week to 2-month adult life span (Bolek and Coggins, 2002; Hanelt, 2009). Females in the genus *Gordius* and *Acutogordius* deposit short pieces of **egg strings** approximately 1–2 cm in length on the substrate or while within Gordian knots. In contrast, females of species of *Euchordodes*, *Chordodes*, and *Neochordodes* deposit their egg strings in a zigzag pattern to objects such as sticks or

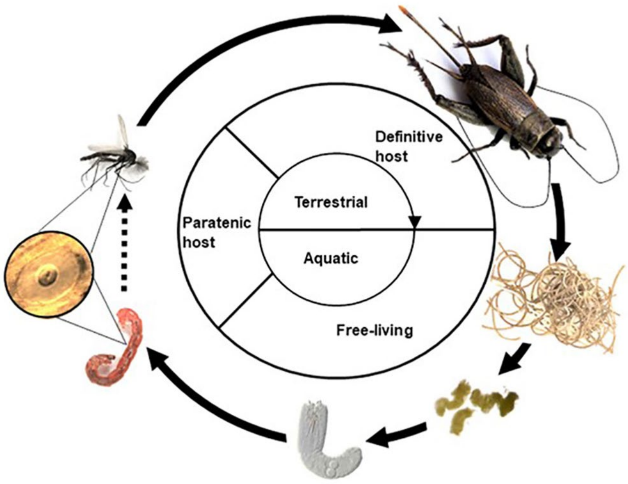

Figure 6. Diagram of a typical gordiid life cycle. The life cycle takes 4–8 weeks to complete in the laboratory depending on the species of nematomorph involved. Source: M. G. Bolek. License: CC BY-NC-SA 4.0.

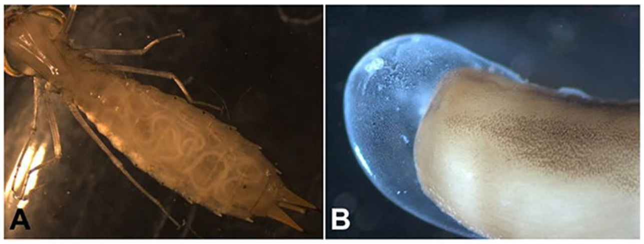

Figure 7. Development of gordiids in their arthropod definitive host. A) An infected larval comet darner *Anax longipes*, showing developing *Neochordodes* species within the hemocoel; B) a developing worm removed from the hemocoel of an arthropod host, showing the thin larval cuticle. Source: M. G. Bolek. License: CC BY-NC-SA 4.0.

rocks in water. Finally, females of *Paragordius* species deposit a single long egg string approximately 1–5 times the length of the worm's body in the water column and/or in algal mats (Figure 9) (Poinar, 2010; Szmygiel et al., 2004; Bolek et al., 2015; Chiu et al., 2017).

Eggs are elliptical to round in shape, with a distinct shell and a thin inner membrane surrounding the developing larva. This inner membrane is relatively thin in aquatic species but is much thicker in gordiids that reproduce in terrestrial habitats (Figure 10) (Anaya et al., 2019). After hatching, the free-living gordiid larvae are semi-sessile and not capable of moving great distances.

In order for aquatic gordiid larvae to reach their terrestrial arthropod hosts, 3 transmission strategies have been proposed. These include: 1) Direct consumption of larvae by the definitive hosts while drinking water; 2) larvae encysting on vegetation/detritus and being ingested accidently while the definitive host ingests vegetation/detritus; and 3) larvae entering and encysting within a paratenic host, which is preyed on or scavenged by the definitive hosts (Hanelt et al., 2005; Bolek et al., 2015). A number of studies show that when definitive arthropod hosts ingest suspended larvae when they drink water, the definitive host becomes infected (May, 1919; Inoue, 1962; Hanelt and Janovy, 2004b). However, comparative work by Inoue (1962) and Hanelt and Janovy (2004a) strongly suggests that prevalence and intensities of these infections in definitive arthropod hosts are much lower compared to those that occur when definitive hosts are exposed to gordiid cysts in paratenic hosts. Finally, observations on gordiid larvae of European and North American *Gordius* species

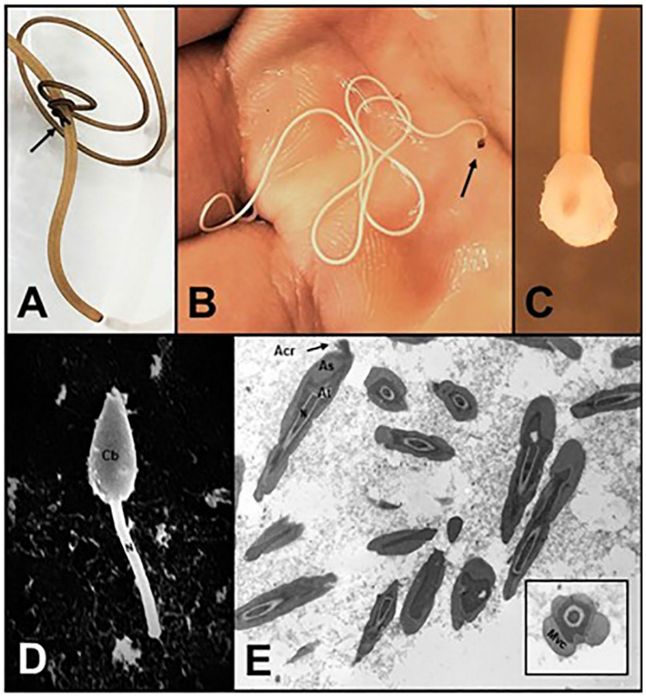

Figure 8. Mating behavior and the morphology of the sperm drop and sperm of gordiids. A) A male *Gordius terrestris* in the process of initiating mating with a female. Note the thinner size and bi-lobed posterior end (arrow) of the male; B) a field-collected female *G. difficilis* with a sperm drop (arrow) on the posterior end; C) a higher magnification of the posterior end of a female *Paragordius varius* with a deposited sperm drop; D) a single sperm on the posterior region of the cloaca of a female *G. difficilis*. Note the round end (Cb) and rod-shaped end (N) where part of the nucleus is located; E) cross- and longitudinal sections of a spermatozoon from the reproductive system of a *Gordius* sp. Note the numerous compartments and organelles, including Acr = acrosome, As = acrosomal sheath, At = acrosomal tube, Mvc = multivesicular complex, and N = nucleus. Sources: A–C) M. G. Bolek; D) Bolek and Coggins, 2002; E and insert) A. Schmidt-Rhaesa. License for all: CC BY-NC-SA 4.0.

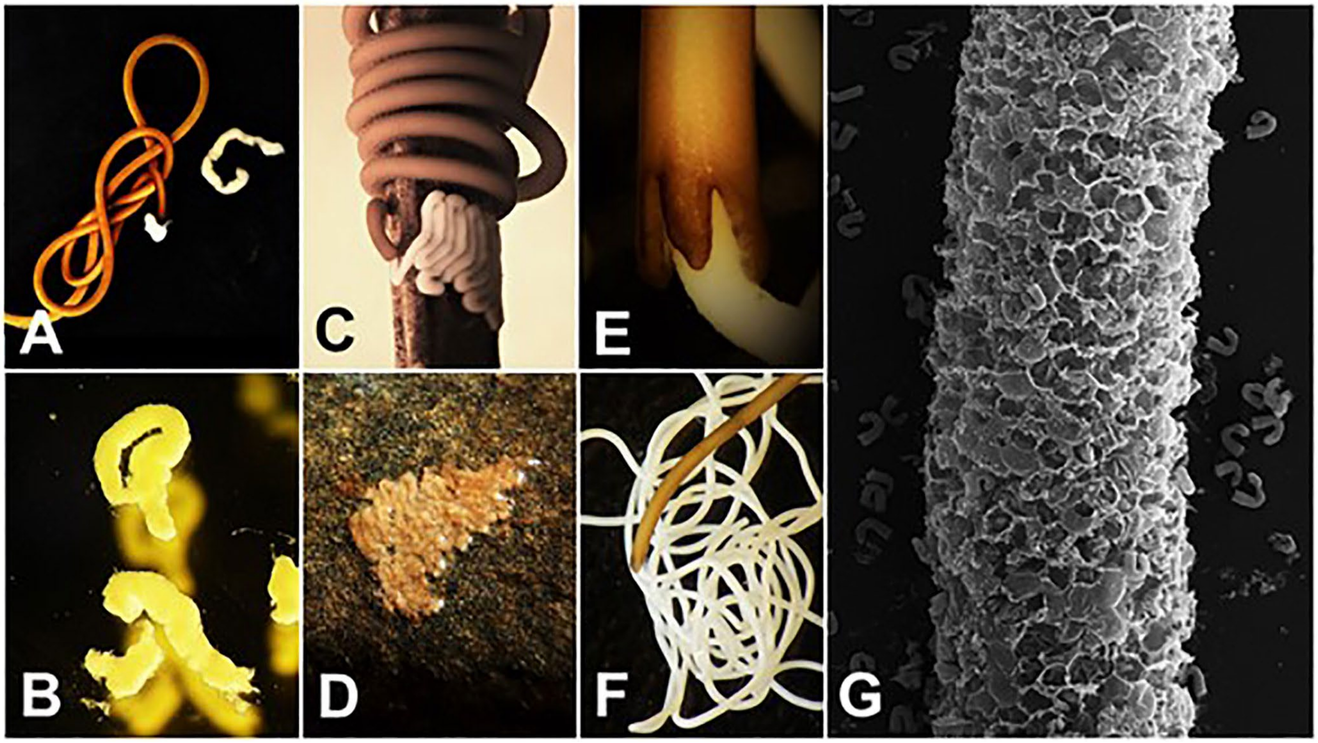

Figure 9. Examples of gordiid egg strings and eggs. A) A female *Gordius terrestris* (brown) in the process of depositing short pieces of egg strings (white); B) higher magnification of pieces of *G. terrestris* egg strings; C) a female *Chordodes kenyaensis* in the process of laying an egg string on a stick. Note the zigzag pattern of the egg string; D) egg string of *Chordodes* sp. deposited on a rock in a zigzag pattern; E) posterior end of a female *Paragordius varius* showing an egg string (white) excreted from between the 3 tail lobes; F) posterior end of a female *P. varius* (tan) in the process of depositing a single and very long egg string (white); G) a scanning electron micrograph of a partial egg string (ES) of *P. varius*, with hatched larvae scattered around the periphery of the egg string. Source: M. G. Bolek. License: CC BY-NC-SA 4.0.

and Asian *Acutogordius* species indicate that these larvae can encyst freely on the surface of aquatic vegetation, or within the egg strings deposited in the environment, but the role of these cysts in transmission is unclear (Dorier, 1930; Bolek et al., 2015; Chiu et al., 2017).

Studies on larvae of other gordiid species indicate that larvae of these species never encyst on vegetation or detritus (May, 1919; Inoue, 1960; Hanelt and Janovy, 2002; Bolek et al., 2010; Hanelt et al., 2012; Bolek et al., 2013a; Szmygiel et al., 2014). In fact, most reports of gordiid cysts have been reported from aquatic metazoan animals including molluscs, annelids, arthropods, fish, and amphibians (Harkins et al., 2016; Chiu et al., 2016; Yamashita et al., 2017). More importantly, experimental studies by Hanelt and Janovy (2004a) demonstrate that 3 phylogenetically distinct species of gordiids indiscriminately infect and form cysts in a variety of aquatic invertebrates and fish. These authors also demonstrated that within non-biting midge paratenic hosts, gordiid cysts survived metamorphosis of these aquatic insects, and when these insects were fed to crickets, the crickets became infected and released adult worms. Taken together, the numerous reports of gordiid cysts infecting a variety of aquatic animals, their ability to survive insect metamorphosis and their ability to infect terrestrial arthropod hosts, supports the paratenic host strategy in the life cycles of gordiids.

Once paratenic hosts ingest larvae, the larvae penetrate the gut and begin forming cysts within the tissue of their paratenic host. During cyst formation, larvae empty the contents of their pseudo-intestine. Laboratory studies by Dorier (1930), Poinar and Doelman (1974), Hanelt and Janovy (2003), Hanelt et al. (2012), and Bolek et al. (2010; 2013a; 2013b) report that during cyst formation, larvae secrete a jelly-like material from the pseudo-intestine and a clear halo-like structure appears around the folded larva (Figure 11). Transmission electron microscopy studies of gordiid cysts in tadpole paratenic hosts indicate that the clear halo-like cyst wall is multilayered (Poinar, 2010). Cyst development can take a few days up to a few months (Hanelt and Janovy, 2002; De Villalobos and Ronderos, 2003). More importantly, if an animal other than a definitive host ingests a paratenic host, the cysts are digested out and the larvae re-penetrate into the

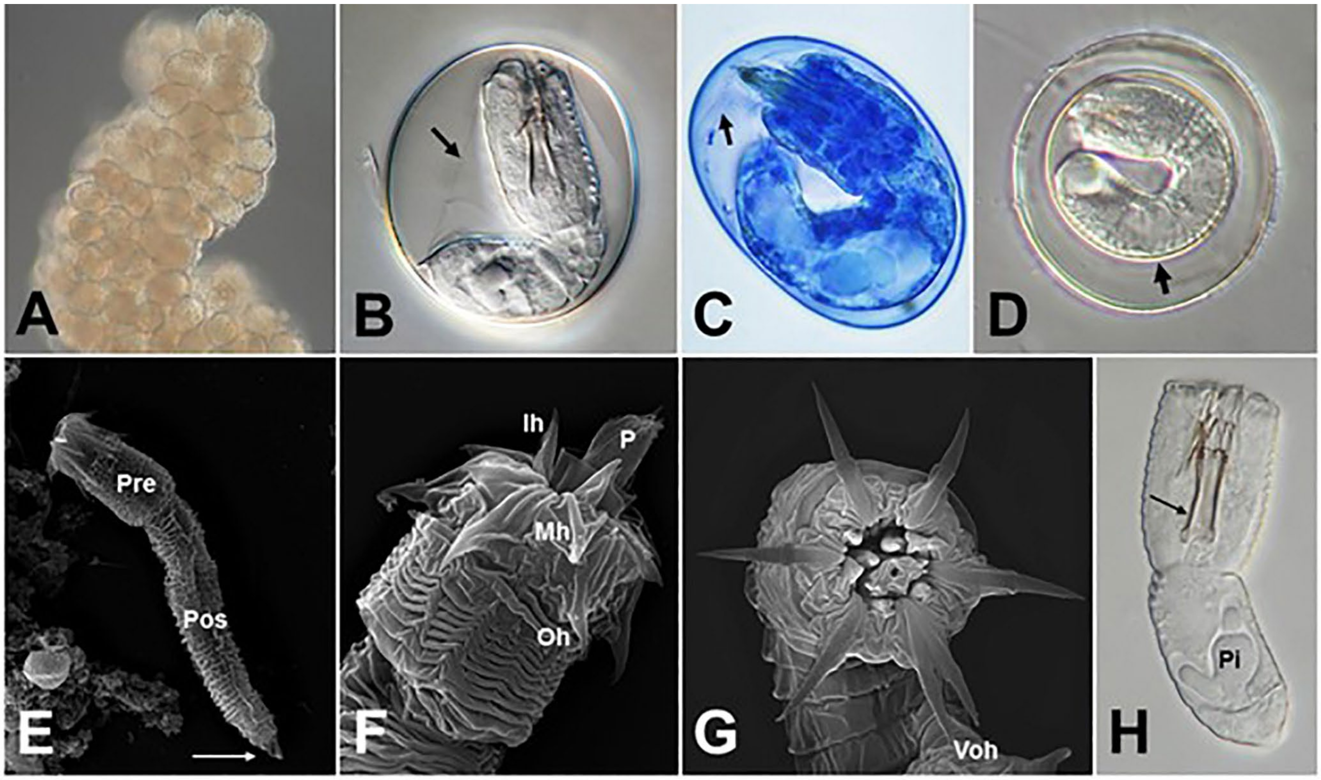

Figure 10. Eggs and larvae of gordiids. A) Higher magnification of pieces of *Gordius difficilis* egg strings showing the concentration of eggs; B, C) typical eggs of freshwater gordiids. Note the developed larva surrounded by a thin inner membrane (arrow) in each egg; D) an unusual egg of *G. terrestris*, a gordiid that lays eggs in the soil. Note the outer shell separated by distinct space from a thick inner membrane (arrow) surrounding the larva; E) scanning electron micrograph of a typical *Gordius* larva. Note the pre-septum (Pre), post-septum (Pos), and terminal spine (arrow) on the post-septum; F) scanning electron micrograph of the anterior end of a *Gordius* larva. Note the proboscis (P) and 3 rings of cuticular hooks including the inner, middle and outer hooks (Ih, Mh, Oh); G) scanning electron micrograph of the anterior end of a *Paragordius varius* larva. Note the dorsoventrally compressed proboscis in relationship to the ventral outer hooks (Voh); H) larva of *Chordodes kenyaensis.* Note the 3 internal stylets (arrow), and V-shaped pseudo-intestine (Pi). Source: M. G. Bolek. License: CC BY-NC-SA 4.0.

second paratenic hosts and re-encyst (De Villalobos and Ronderos, 2003; Hanelt and Janovy, 2003).

It is unknown if nematomorph larvae have any impact on mortality of paratenic hosts in nature. However, several laboratory studies and field observations indicate that insect paratenic hosts mount some type of immune reaction to horsehair worm larvae and cysts (Poinar and Doelman, 1974; De Villalobos and Ronderos, 2003; Hanelt and Janovy, 2003). Host reactions usually involve humoral mediated melanization of larvae (Figure 11) and/or cysts. Melanization of gordiid larvae and cysts have been reported in a variety of aquatic larval insects including mosquitoes, chironomids, caddisflies, mayflies, stoneflies, as well as larval beetles (Poinar and Doelman, 1974; Poinar, 1991; Hanelt and Janovy, 2003; Bolek et al., 2015).

Most definitive hosts for gordiids are predaceous or omnivorous arthropods, which capture infected paratenic arthropod hosts after they metamorphose from an aquatic habitat or scavenge on dead infected paratenic hosts (Figures 2, 6, and 7). Laboratory studies indicate that the maturation of gordiids within the definitive host takes several months. For example, the development within the definitive arthropod hosts can take as long as 8 months for *Gordius tolosanus* (Svábeník, 1925), 2 to 3 months for *Chordodes japonensis*, *C. kenyaensis*, and *Paragordius obamai* (Inoue, 1962; Hanelt et al., 2012; Bolek et al., 2013a), to as short as 1 month for *P. varius* (Hanelt and Janovy, 2004b).

Field studies indicate that after worms emerge from their hosts, only the gut remains within the host's body cavity (Linstow, 1891; Thorne, 1940), whereas, other studies indicate that the production of eggs by female definitive hosts is inhibited or absent altogether (Tanner, 1939; Baker, 1985; Studier et al., 1991; Chiu et al., 2015). Only 1 report found that naturally infected female hosts might be capable of reproducing (Poulin, 1995). A more recent experimental study by Biron et al. (2005b) using naturally infected crickets showed

Figure 11. Cysts of gordiids. A) A larval *Gordius terrestris* in the process of folding into a cyst in its earthworm paratenic host; B, C) typical *Gordius* type cyst, not the folding pattern of the larva; D) fully developed *Gordius* type cyst. Note the clear halo-like structure surrounding the folded larva; E) 2 types of gordiid cysts (arrows) in the hemocoel of a non-biting midge larva; F) a *Paragordius varius* cysts in the tissue of an aquatic snail. Note the prominent spines on the folded larva within the cyst, which are characteristic for the genus *Paragordius*; G) a *Chordodes* like larva on the outside gut wall of an aquatic beetle larva in the process of being melanized (orange-brown pigment). Source: M. G. Bolek. License: CC BY-NC-SA 4.0.

that female crickets were capable of producing eggs only after they released worms and were provided with food ad libitum. However, all female crickets that released worms and produced eggs had difficulties mating with male crickets and/or ovipositing. In contrast, all infected male crickets were castrated by horsehair worms and did not regain the ability to produce sperm after they released worms.

Life Cycle

One fascinating aspect of gordiid biology is their complex life cycle which includes both free-living and parasitic phases (May, 1919; Inoue, 1962; Hanelt and Janovy, 1999; 2004b; Hanelt et al., 2012; Bolek et al., 2013b; Swanteson-Franz et al., 2018) (Figure 6). As juveniles, gordiids are parasites of terrestrial arthropod hosts from which free-living adults emerge into aquatic or semi-aquatic environments, such as waterlogged fields, streams, rivers, and lakes (Hanelt et al., 2005; Anaya et al., 2019). Three species of gordiids (*Paragordius varius*, *P. obamai*, and *Chordodes kenyaensis*) have been domesticated in the laboratory including dioecious and parthenogenetic species (Hanelt and Janovy, 2004b; Hanelt et al., 2012; Bolek et al., 2013a; 2013b). Studies on these domesticated nematomorphs indicate that life cycles of gordiids involve 5 distinct life stages (Figure 6) including: 1) Egg strings, 2) free-living larvae, 3) parasitic cysts, 4) parasitic juveniles, and 5) dioecious or parthenogenetic free-living adults (Hanelt and Janovy, 2004a; 2004b; Hanelt et al., 2012). Juvenile gordiids are obligate parasites of predominantly terrestrial arthropods, whereas a number of species of aquatic animals serve as paratenic hosts for the cyst stage (Hanelt et al., 2001; Bolek and Coggins, 2002; Hanelt and Janovy, 2003; 2004a).

As noted above in general, gordiids commonly infect 4 major groups of terrestrial arthropods, including beetles, orthopterans, praying mantids, and cockroaches. Additional confirmed records exist from earwigs (Dermaptera) and aquatic larval trichopterans and larval dragonflies (Schmidt-Rhaesa, 2013). All gordiids develop in the hemocoel of their arthropod host where they grow from a small length of 60–100 µm to a length of over 2 m for some species (Schmidt-Rhaesa, 2013) (Figure 7). During development in the arthropod definitive host, 2 cuticles are present, a thin white larval cuticle which is replaced by a robust dark adult cuticle (Figure 8) (Schmidt-Rhaesa, 2005). Before emergence from their host, adult gordiids form an open wound on the posterior end of the host's abdomen and once the infected arthropod enters water, the worms emerge head-first (Hanelt and Janovy, 2004b; Hanelt et al., 2012; Bolek et al., 2013a).

As noted, field observations indicate that infected terrestrial arthropods, such as crickets and beetles, deliberately enter water, suggesting that worms may be manipulating the behavior of their arthropod hosts (McCook, 1885; Müller, 1926; Jolivet, 1945; 1948). More recently, Thomas and colleagues (2003) discovered differences in the brains and concentrations of neurotransmitters among infected and uninfected field-collected crickets. Additional studies by Biron and colleagues (2005a; 2005b; 2006) show that several brain proteins are altered in crickets infected with gordiids. It is not known whether the gordiids' mere presence or something emitted by the gordiids affects the hosts' behavior.

Distribution and Diversity

Within the freshwater/terrestrial Gordiida, approximately 360 species of horsehair worms have been described worldwide from 18 extant and 2 extinct genera (Poinar, 1999; Poinar and Buckley, 2006; Yadav et al., 2018). In addition, 5 species of marine horsehair worms have been described from a single genus (Schmidt-Rhaesa, 2013). However, current estimates suggest that only 18% of the horsehair worm diversity has been documented across the world, with another 2,000 species awaiting discovery (Poinar, 2008). The earliest reported and credible fossil Nematomorph, was described from 100 million year-old Lower Cretaceous Burmese amber and belongs to the extinct species *Cretachordodes burmitis* (Poinar and Buckley, 2006). Additionally, 2 individuals of the fossilized species *Paleochordodes protus* (Poinar, 1999) emerging from a cockroach have been described from Dominican amber dated between 15 and 45 million years-old (Figure 12). However, obtaining knowledge on the diversity of horsehair worms has been difficult due to their unusual life cycles, where free-living adult worms exit their hosts, and the lack of reliable ways of collecting the free-living adults over large geographic areas from aquatic and terrestrial habitats (Bolek and Coggins, 2002; Bolek et al., 2013a; Bolek et al., 2015).

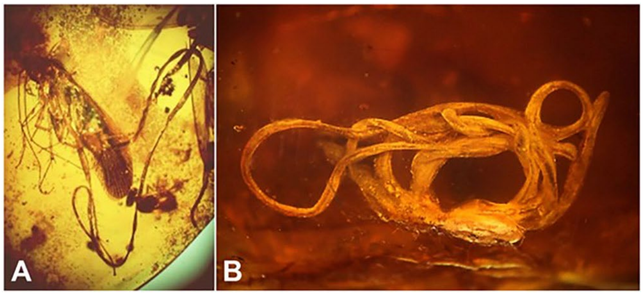

Figure 12. Fossil nematomorphs. A) Two specimens of *Paleochordodes protus* in the process of emerging from a cockroach host in Dominican amber, 15–45 Ma (= million years old); B) the oldest known hairworm fossil *Cretachordodes burmitis* recovered from Early Cretaceous amber, 100 Ma, from Myanmar. Source: G. Poinar. License: CC BY-NC-SA 4.0.

The freshwater and terrestrial horsehair worms have been reported from all continents except Antarctica; whereas the marine genus *Nectonema* is known from several locations worldwide including both coasts of the northern Atlantic Ocean, as well as the Indian Ocean, and the Pacific Ocean from the southern coast of New Zealand (Poinar and Brockerhoff, 2001; Hanelt et al., 2005; Bolek et al., 2015). The fauna of North American, European, and Argentinean nematomorphs has been relatively well studied. However, nematomorph diversity in Africa, Asia, and most of South America has received comparatively little attention (Hanelt et al., 2005; Schmidt-Rhaesa, 2013; Bolek et al., 2015; Schmidt-Rhaesa et al., 2016; Swanteson-Franz et al., 2018; Anaya et al., 2019; Zanca et al., 2020). Among the Nearctic freshwater and terrestrial horsehair worms, 24 species from 7 genera have been described (Schmidt-Rhaesa et al., 2003; Poinar and Chandler, 2004; Begay et al., 2012; Swanteson-Franz et al., 2018; Anaya et al., 2019). However, evidence from molecular barcoding techniques indicates there are numerous hidden, cryptic species. For example, the common Nearctic species *Gordius robustus* represents a large species complex composed of at least 8 distinct genetic lineages (Hanelt et al., 2015). These recent molecular studies indicate the importance of genetic data and limitations of morphological characters in determining some gordiid species within the phylum.

Taxonomy and Phylogeny

The phylum Nematomorpha consists of 2 subphyla, the marine Nectonematida and the freshwater and terrestrial Gordiida comprising 1, and 18 extant and 2 extinct genera, respectively (Schmidt-Rhaesa, 2013). Nematomorphs have few morphological characters that can be used by taxonomists for species determination. Macroscopic characters include the shape of the posterior end being bilobed or round in males, and trilobed or round in females. In addition, the presence of cuticular structures such as crescents near the cloacal opening and/or areas of dense bristles and/or spines on the posterior region of worms are useful for some genera delimitations

(Figure 4) (Schmidt-Rhaesa, 2013). All other characters, including areoles and intra-areoles spaces are found on the cuticle, many of which are so small that scanning electron microscopy (SEM) is necessary to visualize these characters. As such, SEM has become the standard protocol for nematomorph identification (Hanelt et al., 2005; Bolek et al., 2015).

Horsehair worms are placed in the superphylum Ecdysozoa and are considered the sister phylum to the phylum Nemata (Hanelt et al., 2005). However, and unlike nematodes, cephalic papillae, lateral epidermal cords, secretory-excretory systems, amphids, and spicules are lacking in horsehair worms. Other differences between horsehair worms and nematodes include genital openings located on the posterior end of female horsehair worms instead of near the middle of the body as in nematodes. Additionally, and unlike nematodes, these animals have a true larval stage that undergoes drastic morphological tissue reorganization during development in their host (Schmidt-Rhaesa, 1997; 2013).

Of 3 phylogenic hypotheses based on molecular (DNA) sequencing discussed here, the ancestor-descendant relationships of multiple genera and species within the Nematomorpha were analyzed (Bleidorn et al., 2002; Chiu et al., 2017; Tobias et al., 2017). Bleidorn and colleagues (2002) uses a combination of morphological and molecular (18S rRNA gene) data indicating a sister-group relationship between the marine genus *Nectonema* and the freshwater Gordiida. However, within the Gordiida, all species within the basal genus *Gordius* and all species within the sister genus *Paragordius* are monophyletic. The remaining derived genera are not well supported, and some appear as polyphyletic. For example, the more derived *Neochordodes occidentalis* is nested within species of *Chordodes*. More recent molecular phylogenetic analyses using mitochondrial markers (*CO1*) and/or nuclear markers (8S rRNA) indicate that the freshwater genus *Paragordius* is basal to the remaining freshwater and terrestrial gordiids. More importantly, these molecular phylogenetic hypotheses are in agreement with the traditional morphological relationships of freshwater and terrestrial gordiids including the genera *Gordius* and *Acutogordius* within the family Gordiidae and the remaining genera within the family Chordodidae (Chiu et al., 2017; Tobias et al., 2017).

Ecology and Behavior

The ecology of nematomorphs is closely tied to the biology of their arthropod definitive hosts and the aquatic or terrestrial habitats of the adult free-living worms. However, few studies have sampled for free-living adult worms throughout the year and even fewer studies have examined multiple arthropod species for nematomorph infections (Bolek and Coggins, 2002; Poinar and Weissman, 2004; Looney et al., 2012). As a general rule and depending on the gordiid species, nematomorphs vary in their definitive host specificity, and free-living adults are seasonal and have a male-biased sex ratio (Hanelt et al., 2005; Bolek et al., 2015).

Host specificity for most nematomorph species is poorly understood, and most host records are based on field observations (Schmidt-Rhaesa, 1997; 2013; Schmidt-Rhaesa et al., 2003). Field studies indicate that some, but not all, nematomorph species appear to be host-specific at the definitive arthropod host level (Poinar, 1991; Bolek and Coggins, 2002; Schmidt-Rhaesa et al., 2003; Chiu et al., 2011; Looney et al., 2012). For example, the North American *Chordodes morgani* has been reported from 4 phylogenetically distinct orthopteran and cockroach species, suggesting that some horsehair worms are generalists at the definitive host level (Schmidt-Rhaesa et al., 2003). However, other species, particularly in the *Gordius* cf. *robustus* complex, appear to be more specific at the definitive host level and are restricted to a single or a few closely related species of arthropod hosts (Hanelt et al., 2015). Molecular evidence from mitochondrial (*CO1* and *cytB*) and nuclear (partial 28S, ITS1, 5.8S, and ITS2) DNA suggests that at least 8 species occur across North America. However, this group is paraphyletic, since the European *G. aquaticus* and *G. balticus* group among the *G. robustus* lineages form 2 distinct clades, A and B (Figure 13B). When all known arthropod definitive hosts are mapped onto this phylogeny it appears that species within clade A infect various species of orthopterans; whereas species in clade B infect millipedes and ground beetles (Figure 13).

Once emerged from their arthropod hosts, free-living adult worms are seasonal (Bolek and Coggins, 2002; Schmidt-Rhaesa et al., 2005; Salas et al., 2011; Anaya, 2019). For example, Bolek and Coggins (2002) reported the occurrence of free-living adults of *Gordius difficilis* in Wisconsin, United States from June to October; whereas Anaya (2019) reported *G. terrestris* (incidentally, the only known species of gordiid consistently collected from terrestrial habitats) from Oklahoma, United States during October through March. Additionally, Salas and colleagues (2011) examined the seasonal occurrence of free-living individuals of 4 species of sympatric gordiids over a 1-year period from a stream in Argentina. In their study, free-living worms of all 4 species occurred in the stream during the fall, winter, and spring. However, *Noteochorododes cymatium*, *N. talensis*, and *Pseudochordodes dugesi* were most abundant during the winter and spring; whereas *Chordodes brasiliensis* was most abundant during the fall.

The explanation for these seasonal patterns includes the short life span of free-living adult worms (2–8 weeks) and the abundance of their arthropod definitive hosts. For example, in a 3-year study, Schmidt-Rhaesa and colleagues (2005)

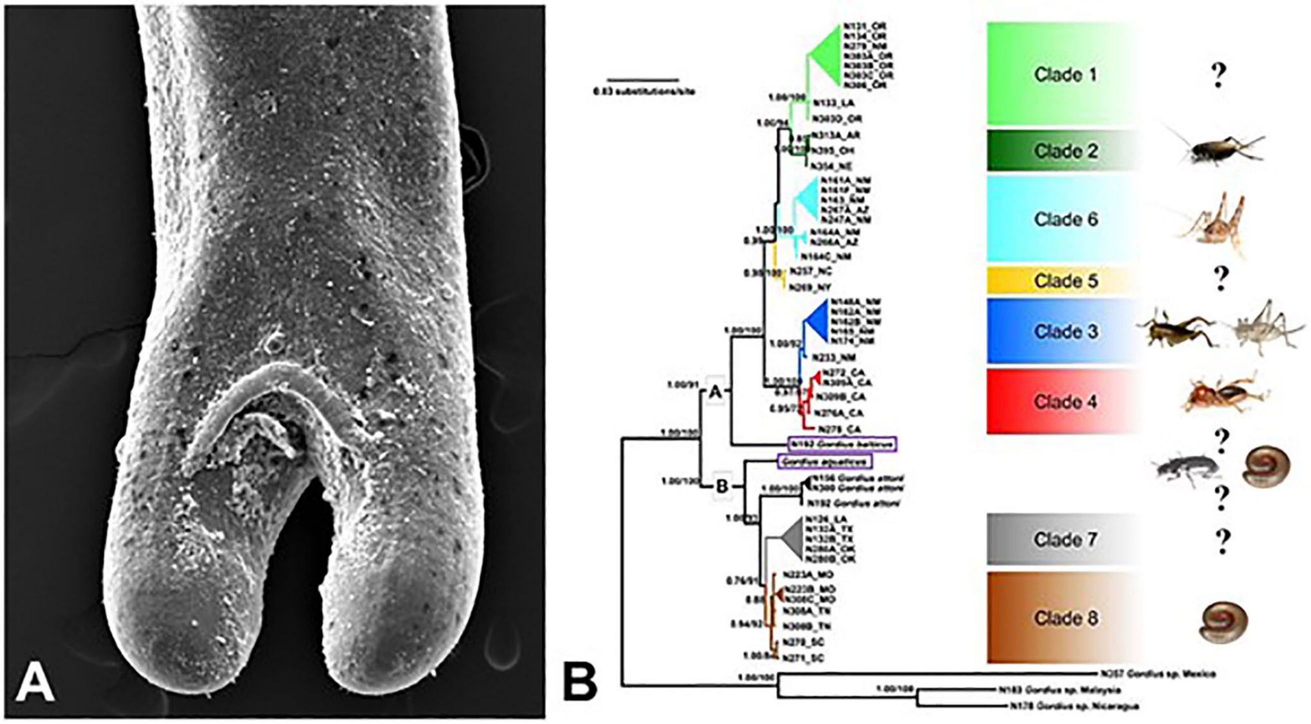

Figure 13. Hosts and phylogenetic relationships of the *Gordius* cf. *robustus* complex. A) Posterior end of a male *Gordius* cf. *robustus*, with the characteristic bilobed end, post cloacal crescent, and poorly developed areoles on the cuticle; B) phylogenetic hypothesis (partial CO1 and cytB sequences) of the *Gordius* cf. *robustus* group and diverse group of arthropod definitive hosts. Note that the *Gordius* cf. *robustus* linages are paraphyletic with European species (purple brackets) group among the *G. robustus* lineages and form 2 distinct clades A and B. Species in clade A appear to infect orthopteran arthropod hosts, whereas, species in clade B infect ground beetle and millipede arthropod hosts. Sources: A) M. G. Bolek; B) adapted from Hanelt et al., 2015. License: CC BY-NC-SA 4.0.

collected data on recently emerged adults of 2 species of nematomorphs and their definitive arthropod hosts around a swimming pool in southern France. Most adults of *Pseudochordodes tricuspidatus* emerged from their hosts during June through August, whereas most adults of *Spinochordodes tellinii* emerged from their hosts during August through September. At their study site, both gordiid species infected different species of definitive hosts and their occurrence was correlated with the abundance of these hosts.

Free-living adults do not feed and are found in various aquatic habitats including water sources in caves, puddles, ponds, lakes, and small and large streams and rivers (Reeves, 2000; Hanelt et al., 2005; Schmidt-Rhaesa, 2013; Bolek et al., 2015). Within these habitats, free-living worms can be located in the sediment, among moist fallen leaves, under rocks, in algal mats, and/or on aquatic vegetation where they form Gordian knots and mate (Hanelt et al., 2005; Bolek et al., 2015). Additionally, free-living adults of *Gordius terrestris*, a terrestrial species, appear during rain events on wet lawns and pools of water on streets and sidewalks, where the worms copulate. After the rains stop, adult free-living worms can be found entangled in the roots of grasses and in the soil where females deposit egg strings (Anaya, 2019; Anaya et al., 2019; Figure 14).

The sex ratio of free-living adult gordiids is usually but not always male biased, with a few field studies indicating equal sex ratios (De Villalobos and Camino, 1999; Valvassori et al., 1988; Salas et al., 2011). For example, Cochran and colleagues (1999) reported that of 1,391 individuals of *Gordius difficilis* collected during a 32-year period in 6 Midwestern states of the United States, 1,205 were males. In contrast, Watermolen and Haen (1994) reported 67 individuals of *G. robustus* from Wisconsin of which 66 were females. These field-skewed sex ratios are in contrast to laboratory life cycle studies on dioecious nematomorph species. Hanelt and Janovy (2004b) and Bolek and colleagues (2013b) each found no statistically significant differences in the sex ratios of *Paragordius varius* or *Chordodes kenyaensis* emerging from laboratory-reared and -infected cricket definitive hosts.

A few hypotheses have been proposed for this strongly skewed sex ratio in the field, including differences in the development times of male and female worms in their final hosts,

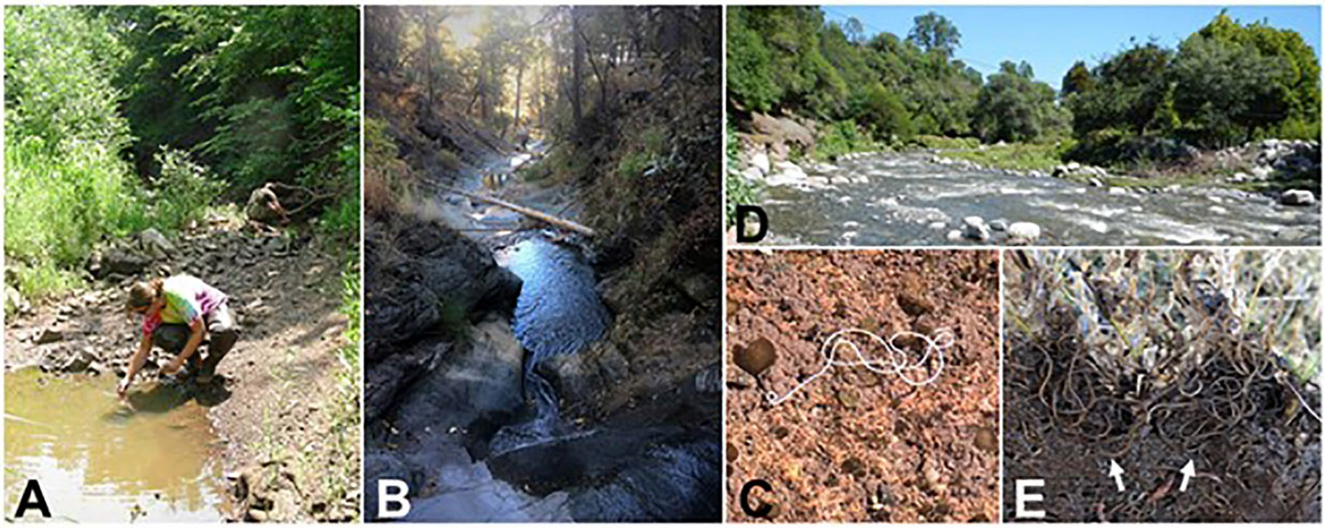

Figure 14. Typical habitat for free-living adults, larvae, and cysts of freshwater and terrestrial gordiids. A) Second-order stream in Payne County, Oklahoma, United States; B) a typical first-order stream in the Chiricahua Mountains, Arizona, United States; C) a white free-living adult male *Gordius* sp. on the bottom of a first-order stream in the Chiricahua Mountains, Arizona, United States; D) a third-order stream in the Córdoba, Argentina. Many of the nematomorphs glue their egg strings on rocks in this habitat; E) adult free-living *G. terrestris* entangled in grass roots under the soil, in a suburban environment, Stillwater, Oklahoma, United States. Source: M. G. Bolek. License: CC BY-NC-SA 4.0.

and/or behavior differences among free-living males and females (Poulin, 1996; Bolek and Coggins, 2002). More recently, Anaya (2019) documented behavioral differences among male and female *Gordius terrestris*, a species with an extremely male biased sex ratio (5.4:1.0) observed in the field. In the laboratory, when male and female worms are placed on the surface of the soil, significantly more females burrow into the soil than males. Once females burrow, they begin ovipositing. This observation is important and provides a plausible explanation for the extremely male-biased sex ratio observed for *G. terrestris* in the field. Taken together, these observations suggest that unlike males, after mating female horsehair worms may be moving to specific locations in the environment to oviposit and be more difficult to locate than males.

Little information is available on the physiological constraints of free-living stages of horsehair worms to their external environment. However, Bolek and colleagues (2013b) indicate that in laboratory cultures adult free-living *Chordodes kenyaensis*, worms die within 24 hours if they emerge from their hosts in cages without a water source, suggesting that adult free-living worms must remain moist to survive. In addition, Achiorno and colleagues (2008) examined the survival of eggs, larvae, and free-living adults of *C. nobilii* to extreme temperatures. They demonstrated that all eggs, most larvae, and all adult gordiids die at a high temperature of 40.5 °C, and all eggs and most adult worms (89%) die at a low temperature of −3 °C. In contrast, larvae frozen at −3 °C for 48 hours survived freezing and are capable of infecting mosquito larva paratenic hosts. Finally, Bolek et al. (2013a) evaluated the survival of larvae and cysts of North American and African gordiids in the genus *Paragordius* when super cooled and/or frozen at −20 °C or −80 °C for up to 7 months. Their work demonstrates that post-frozen larvae and cysts of these species have the ability to infect and develop in the next host in the life cycle. It is currently unclear why larvae and cysts of gordiid species from Africa have the ability to survive super cooling and/or freezing for such periods.

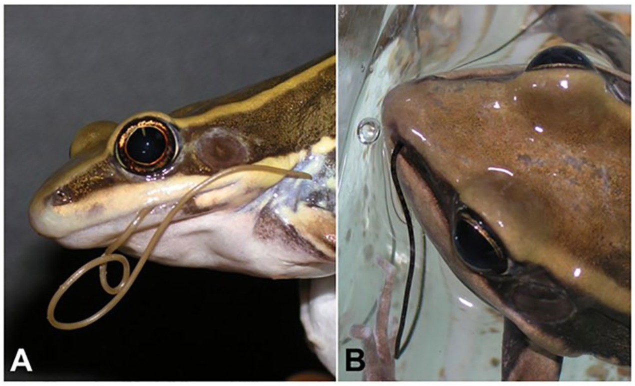

Figure 15. Predators and epibionts of gordiids. A, B) A free-living *Paragordius tricuspidatus* escaping from the mouth (A) and nose (B) of the common green frog (*Rana erythraea*) after it ingested an infected cricket. Source: F. Thomas. License: CC BY-NC-SA 4.0.

Finally, birds, fish, and frogs occasionally eat free-living adult nematomorphs and their infected hosts (Cochran et al., 1999; Bolek and Coggins, 2002; De Villalobos et al., 2008; Fair et al., 2010). However, work by Sato and colleagues (2008; 2011) in Japan indicates that gordiids are only found in the stomachs of trout (*Salvelinus leucomaenis japonicus*) when those fish also consume their camel cricket hosts. As a result, Sato and colleagues (2011) hypothesized that horsehair worm infections and their manipulations of terrestrial arthropod hosts can increase energy inputs into aquatic ecosystems. Using estimates of seasonal prey abundance, they argue that, during worm peak emergence times, infected orthopterans account for 60% of the annual energy intake of Japanese trout (Sato et al., 2011). Other studies by Ponton and colleagues (2006a; 2006b) indicate that when trout and frogs consume orthopterans infected with these nematomorphs, 18–35% of the ingested nematomorphs can escape the predators of their hosts, through the mouth or nose of frogs and the mouth or gills of fish (Figure 15).

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ACANTHOCEPHALA

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Acanthocephala (Phylum)

Scott Monks

Phylum Acanthocephala

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Chapter 58

Acanthocephala (Phylum)

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Introduction

Members of the phylum Acanthocephala are parasitic worms generally referred to as thorny-headed or spiny-headed worms because both larvae and adults have an invertible proboscis at the anterior end. However, this common name is incorrect because acanthocephalans do not have heads! Although some consider the term head as only a general concept, it is not particularly useful in the area of invertebrate biology, except with those groups (such as Arthropoda) that actually have heads. For example, Maggenti and colleagues (2017) define a head as "The anterior body region." which is not very useful to a biologist; however, in the same entry for head, 3 more definitions are included: Definition 2, referring to the polychaete annelids: The prostomium and the peristomium; definition 3, referring to the Arthropoda: Bearing the eyes, antennae, and mouth parts; definition 4, referring to the Nemata: Comprising the lips and sensory organs, oral opening, and supporting head skeleton. Here, each definition is slightly more specific, focusing on the presence of particular structures and sensory organs as part of a head; these are more applicable to biology.

Why get so involved with definitions before acanthocephalans have even been described? There are several reasons, but only one very important reason is mentioned here. It is a complete theme in itself, namely, the concept of **homology**, meaning that 2 characteristics (structures, features, behaviors, and so on) are derived (evolved directly) from the same origin. Or, features, such as organs or structures in 2 or more taxa that can be traced back to the same feature in the common ancestor of these taxa. The concept of homology is in play every day when structures or characters or features are called by the same name, indicating that they are the same thing, having similar features. Because what a name—such as head—means to us, we expect that it is similar to all other heads by having those important, recognizable features, such as having sensory organs clustered in that particular structure. Other obvious misnomers are the uterus, vagina, and penis of acanthocephalans, which are all names borrowed from vertebrate organs. Nevertheless, because they have been used since the first studies of acanthocephalans, scientists must use them or risk confusion.

To bring this back to animals that are known as belonging to the phylum Acanthocephala, the anterior ends of species in this group do not have a concentration of sensory organs—there are no eyes, no mouth, or any other elaborate sensory structures. Thus, to reiterate, the name spiny-headed worm is not appropriate because they have no heads! These conundrums of homology are problematic when trying to discover the relationships of this group to others, but is discussed as the phylogenetic relationships among the acanthocephalans, and the hypotheses about which groups might be close relatives, are considered.

Morphology of the Acanthocephala

Compared to the bodies of members of many phyla of invertebrates, acanthocephalans are rather simple. However, the terminology relating to simple versus complex and primitive versus advanced are relative terms that are not often used by modern biologists for comparisons. This is because of the very nature of this comparison. For example, an acanthocephalan may be considered simple compared to a more complex annelid, but that same annelid is simple compared to most species of vertebrates. Thus, defining a species of organism as simple without context relative to the comparative morphological complexity of other species is futile.

With respect to simplicity versus complexity, this applies to acanthocephalans in relation to presence and absence of sensory structures and organs. First, consider what all species of the Acanthocephala don't have: First, there is no digestive system, second, there are no sensory structures related to light detection and there are no sensilla (as in the Nemata) for pressure detection that have yet been found. They have no organs or organ systems for the exchange of oxygen and carbon dioxide and the majority of species investigated do not have protonephridia for excretion or water regulation. What they do have is discussed in the following sections.

When it is said that acanthocephalans do not have elaborate sense organs, this does not mean that they cannot detect their environment. For instance, the larvae of many species are known to break out of their cysts in the stomach or anterior region of the small intestine of their vertebrate host, the region where bile empties into the intestine. However, this is not necessarily the site where they will establish themselves to begin to mate and produce eggs (Leadabrand and Nickol, 1993; Esch, 2000). One of the better-studied species is *Leptorhynchoides thecatus*, a parasite of the green sunfish *Lepomis cyanellus*. Detailed studies have shown that the young worms migrate through the intestine to the cecae of the fish (Richardson and Nickol, 1999; Richardson et al., 2008). They sense their surroundings, probably following chemical cues in the intestine and its contents and move anteriad and enter the cecae.

Hypotheses concerning how the Acanthocephala came to exist without these structures is discussed in a later section. Suffice it to say for now that the lack of common, or homologous, morphological structures or characters makes it difficult to estimate the phylogenetic relationship of species in this phylum with other groups of invertebrates.

Superficial External Features

Adult worms of most species of Acanthocephala are fairly small—about 1 cm in length—but some individuals of many species are much smaller and individuals of some species may be really huge and can reach lengths of 70 cm (Miller and Dunagan, 1985a). Unstained by their surroundings, they are white, although some species can be colored yellow to orange by the carotenoids ingested by the intermediate (Figure 1) or the definitive host (Nickol, 1985). In the host, the body of most species is somewhat flattened, but when the specimens are killed and fixed for study the osmotic pressure of this process fills the body cavity with liquid and it assumes a more cylindrical shape (Pritchard and Kruse, 1982).

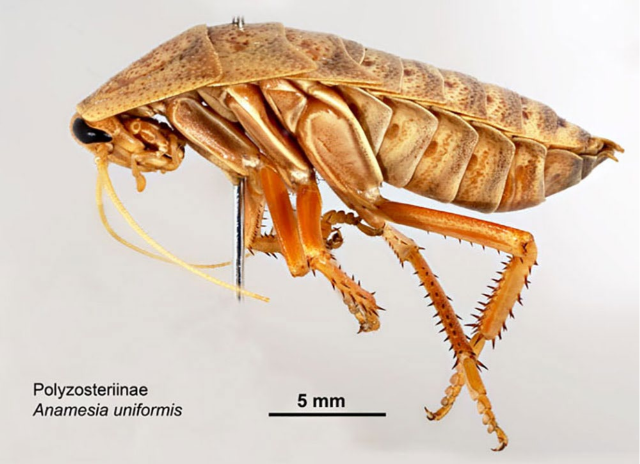

Figure 1. *Anamesia uniformis* (Blattoidea: Blattidae: Polyzosteriinae) cockroach from Barrow Island, Western Australia. Cockroaches may serve as intermediate hosts for acanthocephalans. Scale bar = 5 mm. Source: L. Gibson and S. McCaffrey, Museums Victoria, Australia, 2006. License: CC BY-NC 4.0.

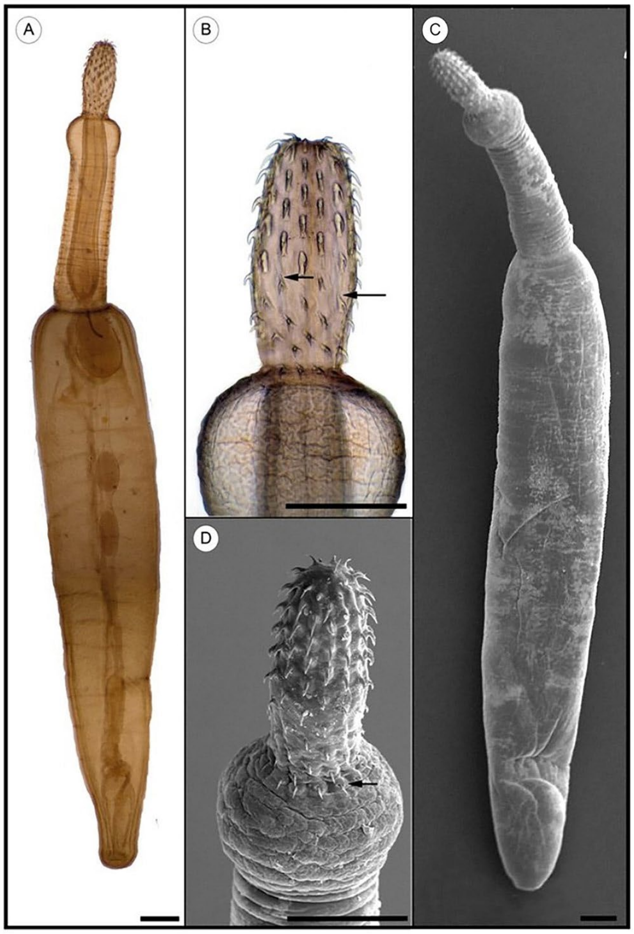

Figure 2. Larval stage (cystacanth) of the fish parasite *Pomphorhynchus tereticollis* isolated from the paratenic host *Neogobius melanostomus*. A, C) Habitus of *Pomphorhynchus tereticollis*, light- and scanning electron microscopy; B, D) detail of proboscis. Number and species specific structure details (arrows) of the proboscis hooks are clearly visible. Scale bar = 500 µm. Source: S. Emde et al., 2012. License: CC BY 4.0.

Cystacanths (the larval stage infective to the definitive host, specific to acanthocephalans, see Figure 2) are similar to adults except that the internal structures (reproductive organs and so on) are not fully developed. The cystacanths have developed into a form that is infective to the definitive host and then the development stops. Instead of being flattened, like adults of many species, the body of a cystacanth is more cylindrical in cross section. Mature cystacanths that are infective to the definitive host can be identified when the proboscis is completely inverted into the proboscis receptacle; the proboscis stays inverted until the definitive host ingests the cystacanth.

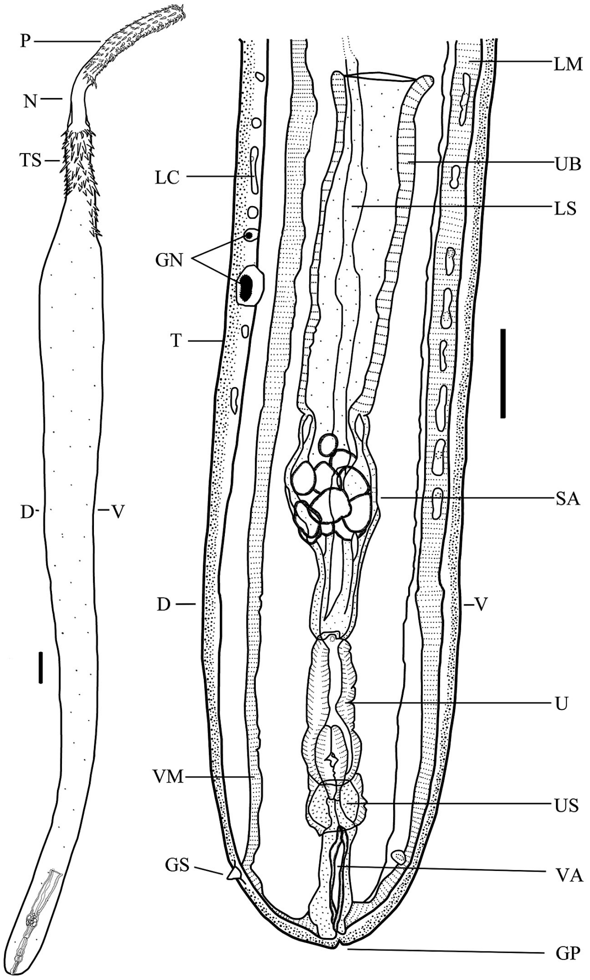

Figure 3. Drawing of the body and reproductive system of a typical female Palaeacanthocephala, *Dollfusentis* sp. D = Dorsal side of worm; GP = genital pore; GS = genital spine; LC = lacunar canal; LM = longitudinal muscles; LS = ligament sac; N = neck; P = proboscis with hooks; SA = sorting apparatus; T = tegument; TS = trunk spines; U = uterus; UB = uterine bell; US = uterine sphincter; V = ventral side of worm; VA = vagina; and VM = vestibular muscle. Source: S. Monks. License: CC BY-NC-SA 4.0.

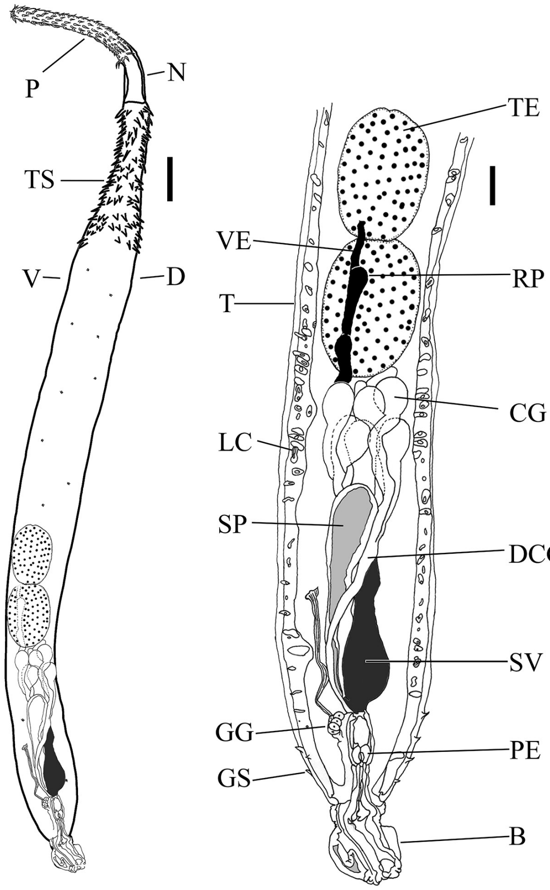

Figure 4. Drawing of the body and reproductive system of a typical male Palaeacanthocephala, *Dollfusentis* sp. B = Copulatory bursa (partially invaginated); CG = cement glands (8) (nuclei not visible); D = dorsal side of worm; DCG = ducts of cement glands; GG = genital ganglion; GS = genital spines; LC = lacunar canals; N = neck; P = proboscis; PE = penis; RP = pouch reservoir containing sperm; SP = Saeftigen's pouch (gray color represents liquid in pouch); SV = seminal vesicle (black color represents sperm); T = tegument; TE = anterior testis; TS = trunk spines; V = ventral side of worm; and VE = vas eferens (black color represents sperm). Source: S. Monks. License: CC BY-NC-SA 4.0.

The outer surface of the body (called the **trunk**) of acanthocephalans can either be smooth or can have **spines** in the tegument. Spines are similar to hooks in composition but lack a root, which, in acanthocephalans, is an important taxonomic character. The spines generally are in the more anterior part of the body, but in some species they also occur in the posterior part of the trunk in the area around the **genital pore** (Monks and Pérez-Ponce de León, 1996; Monks, et al., 1997). The distribution of the spines can be continuous or in various patterns. These patterns are often characteristic for a species and can be used for identification (see the key in Amin et al., 2011).

General Structures of the Body

All acanthocephalans are quite similar in the general structure of the body (Figures 3 and 4). The body of all acanthocephalans is composed of either 2 or 3 sections depending on whether the classic or modern designations are used.

In classic terminology, the **body** (also called the **trunk**; see Figure 5) is considered to be divided into 2 major regions, the **praesoma** and the **metasoma**. The praesoma comprises the armed (containing **hooks**) **proboscis**, **proboscis receptacle**, **cerebral ganglion** (Note: This should not be called a brain! Only vertebrates have brains), **lemnisci**, associated **muscles**, and the unarmed region be-

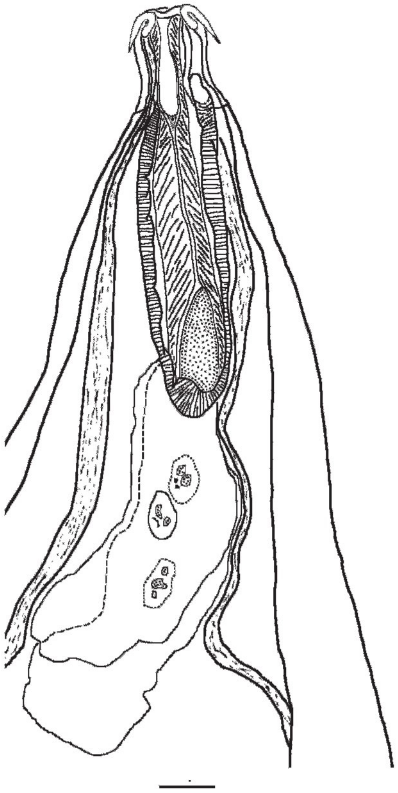

Figure 5. Anterior region of the body of a specimen of *Neoechinorhynchus brentnickoli*. Source: S. Monks. License: CC BY-NC-SA 4.0.

tween the proboscis and the rest of the body that is referred to as the **neck** (also, not a very good name for this region of the body). The metasoma is the hollow trunk of the body. The body wall, or **tegument**, of the metasoma encloses the body cavity.

The tegument was previously called a pseudocoel (Miller and Dunagan, 1985a) but is now referred to as a persistent **blastocoel**, based on more recent studies of development (Brusca and Moore, 2016). A blastocoel is the hollow cavity that forms during embryonic development comprising a ball of cells. One part of this ball of cells then **invaginates**, forming a mouth or an anus (depending on which group of animals are being discussed); this is called **gastrulation** and the larval form is called a **gastrula**. The body cavity of an acanthocephalan is the remnant of this hollow ball of cells that did not completely become lined with mesodermally-derived tissues during embryogenesis.

The tubular channels that constitute the **lacunar system** infiltrate the entire tegument of the metasoma and 2 major canals extend from the anterior to the posterior end of the trunk. Species included in some groups have **spines** that are distributed over the trunk in various patterns. These spines are similar to hooks but are smaller and do not have roots. Within the body cavity are the **proboscis receptacle**, the associated muscle bands mentioned above, and the reproductive organs.

Acanthocephalans are **gonochoristic**. Associated with the reproductive organs of males are **cement glands**, **Safftigen's pouch**, an evertible/retractable **bursa** at the posterior end, associated ducts, among other structures. Females lack these structures. Each group of structures and organs is discussed separately.

Tegument is living tissue that is a syncytium of cells without nuclei which includes dense fibers and connective tissue. The body of acanthocephalans is covered by a multilayered tegument, the overall structure of which resembles that of rotifers (Herlyn et al., 2003; Weber et al., 2013; Sielaff et al., 2016; but see Dunagan and Miller, 1991 for a traditional interpretation). Underneath the tegument are circular and longitudinal muscles, many of which are tubular rather than a dense solid mass. The outer surface of the tegument contains numerous **micropores** that connect to fine canals leading to a complex system of tubes that extend throughout the tegument in patterns specific to particular groups of acanthocephalans. As mentioned above, the system of tubules is called the lacunar system. Finally, the tegument may contain **nuclei**, called **giant nuclei** in some taxa. There can be a few very large/giant nuclei or more numerous **branched nuclei** (for examples of giant nuclei see figures in Monks et al., 2011, and branched nuclei in those of Monks et al., 1997).

Morphology of the Praesoma

Proboscis

The proboscis is one of the distinctive structures of acanthocephalans. The **armament** (**hooks** and **spines**; Figure 6) is a distinctive feature of the proboscis. It can be withdrawn into the **proboscis receptacle** (within the body cavity) by turning it inside out. The hooks make the invagination process necessary.

The hooks somewhat resemble the thorns on the stem of a rose. In most species the hooks are curved, although in some, the more posterior hooks may extend almost perpendicular to the proboscis rather than be curved posteriad (see the figures in Amin et al., 2011). Some species, such as *Koronacantha mexicana*, have rootless spines posterior to the hooks (see the figures in Monks et al., 1997). Each hook consists of a **root** (the part which anchors the hook to the proboscis) and the **blade** (the pointed part of the hook). The root is only an anchor for the hook, not to be confused with the root of a plant. That is, there are no other structures or muscles that might enable the movement of the hook. Spines on the proboscis do not have roots; those on the trunk also don't have

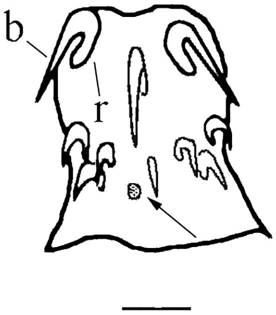

Figure 6. Proboscis and neck of a specimen of *Neoechinorhynchus brentnickoli*. b = blade of hook; r = root of hook; arrow indicates lateral sensory pore. Scale bar = 25 µm. Source: S. Monks. License: CC BY-NC-SA 4.0.

roots. This distinction, that hooks have roots and spines do not have roots, seems clear, but in real life the difference often is blurred. Finally, some prefer to call the spines on the proboscis rootless hooks (Muñoz and George-Nascimento, 2002), leaving the term spines for the armament on the trunk.

When the hooks are fastened into the intestinal wall of the definitive host of the worm, there is no way to dislodge the hooks. This is why the process of invagination of the proboscis is necessary. To visualize the retraction of the proboscis back into the body cavity of the acanthocephalan, if one imagines that a hand is inserted into a tight-fitting glove, it is obvious that the hand is not easily withdrawn from the glove. The easiest way to remove the glove is to turn the glove inside out, removing it by pulling the part nearest the wrist distally toward the fingers and finally over the fingers and off the hand, leaving the glove inside out. The folding inside out of the glove is similar to what happens to the proboscis in invagination.

In the definitive host, the worm forces its proboscis into the tissue of the wall of the host's intestine. Once inserted, the hooks prevent removal and protect the worm from being dislodged by movements of the intestine or its contents. However, acanthocephalans move and migrate within the host's intestine (Leadabrand and Nickol, 1993; Richardson et al., 2008) so they need to be able to unhook themselves. Long strands of inverter muscles extend from inside the body cavity anteriorly to the most anterior point of the proboscis. Normally they are relaxed, permitting the proboscis to remain inserted firmly into the wall of the host's intestine. When an individual acanthocephalan prepares to move, the inverter muscles contract and pull the proboscis inside of the receptacle, disconnecting each ring of hooks as the proboscis is invaginated. This smoothly removes the hooks opposite the way they went in rather than by forcibly tearing them out.

The proboscis of acanthocephalans has different shapes in the different members of the phylum. In general, the proboscis is cylindrical or spherical. In a phylogenetic analysis of members of the phylum, Monks (2001) identified different shapes of the proboscis of the species included in his analyses, including: Round, elliptical to oval, elongate to fusiform, clavate, and cone-like. These shapes were sufficient to differentiate between the taxa in those analyses. Although other shapes are known, such as, spindle-shaped, meaning, wide in the middle and tapering toward each end (see the figures in Richardson et al., 2010, for an example) that would be needed if more species had been included in the analyses by Monks (2001).

The function of the proboscis is to provide attachment to the intestinal wall of the definitive host by penetrating the intestinal wall. To date there is no hypothesis that relates the qualities of the intestinal wall to a particular shape of proboscis. One might think that the length and shape of the proboscis would be related to the structure of the host's intestinal wall—that is, thickness, muscularity, presence of thick connective tissue, and so on—but this does not seem to be true. For example, the proboscis of *Macracanthorhyncus hirudinaceous*, which is a parasite of pigs, has a relatively small and round proboscis (similar to that of *Neoechinorhynchus brentnickoli*). In contrast, species of *Pomphorhynchus*, which are parasites of fish, have a medium-sized, cylindrical proboscis and a long neck that penetrates the relatively thin intestinal wall and extends into the body cavity (see photos and discussion at http://alchetron.com/Pomphorhynchus-laevis).

Other than the hooks, the extent of which marks the posterior margin of the proboscis, few other structures are included in the proboscis (Miller and Dunagan, 1985a). Internally, at the anterior end of the proboscis is a small group of cells called the **apical organ** (Miller and Dunagan, 1983; 1984). The apical organ varies in shape depending on the group, and in some there is a small pore leading outside of the proboscis (Dunagan and Miller, 1983). Note that the apical organ discussed here is not homologous with the apical organ that is found in all species of tapeworms of the genus *Hymenolepis*. In all species of Acanthocephala that have been examined there are 2 large nuclei in the posterior area of the apical organ).

Located opposite each other on the lateral sides of the proboscis, usually near the posterior-most ring of hooks, is a pair of **sensory pores** (Figure 6), or **lateral sense organs** (Herlyn et al., 2001), that open on the surface of the proboscis. Internally, the pores are connected to the sensory support cell complex (Miller and Dunagan, 1983; 1984; 1985a). The function of these cells is not well understood and it is not known what they detect.

Neck

The neck is relatively featureless and there are no hooks or spines present. The posterior margin of the proboscis includes the posterior-most hooks or spines, and thus is not the neck. The neck is tubular, hollow, and connects the proboscis to the trunk. Structures (muscles, nerves, and in some cases the proboscis receptacle) pass through the hollow center of the neck, but they are not fastened to it. Species of *Pomphorhynchus*, which are parasites of adult fish, are one exception (see the photographs and life cycle diagrams available at https://alchetron.com/Pomphorhynchus-laevis). These species have the neck enlarged to form a bulb. The proboscis penetrates the intestinal wall of the host fish, often extending into the body cavity, and the bulb expands to prevent the proboscis from being dislodged.

Morphology of the trunk (metasoma)

The proboscis may be the most notable structure of acanthocephalans, but the trunk, which constitutes the rest of the body, contains the majority of structures. The trunk is divided from the neck by the attachment of the proboscis receptacle.

The **lacunar system**, which is the canal system of the trunk, starts anteriorly at the neck-trunk junction and extends to the posterior end of the body. Longitudinal canals run dorsally and ventrally, or laterally to link circular canals (Miller and Dunagan, 1985a; 1985b). It is thought that the liquid in the canals circulates as a result of body movements.

As mentioned above, many species have spines on the surface of the trunk, distributed in various patterns. Only recently, studies of the manner of attachment to the intestinal wall by species of *Corynosoma* have shown that the spines assist in providing a secondary attachment (Aznar et al., 2002; 2016).

The **proboscis receptacle** is attached to the anterior portion of the trunk. The receptacle, as the name implies, is a structure in which the proboscis is retracted into when it is inverted, but this seems to be only a secondary function because the proboscis could just as well be drawn into the body cavity. The receptacle is a sac, open at the anterior end and most commonly attached at the neck-trunk junction. However, in some taxa the receptacle is attached at the posterior ring of proboscis hooks (see the figures in Amin et al., 2017), or, in a few groups, in the middle of the proboscis (see the figures in Richardson et al., 2010). The wall of the receptacle is composed of 1 or 2 layers of muscle. The muscles of each layer have fibers that are circularly, longitudinally, or spirally oriented (Monks, 2001).

Long **retractor muscle bands** attach to the anterior end of the proboscis and they extend posteriad through the posterior end of the receptacle and are attached to the inner surface of the body wall. When these bands contract, they pull the proboscis into the receptacle. There are no antagonistic muscles that can pull the proboscis back out. Eversion of the proboscis is accomplished by contraction of the muscular receptacle walls, evidently forcing the proboscis out by hydrostatic pressure. Several other muscle bands pass through the receptacle, but most importantly, the **cerebral ganglion** is found in the receptacle. The cerebral ganglion hangs from nerves that run anteriad from it. These nerves exit the receptacle and attach to the inner wall of the trunk, running posteriad. The ganglion is composed of a small number of neurons (around 100 of them), although this knowledge is based on studies of just a few species (Miller and Dunagan, 1985a).

The paired **lemnisci** are connected anteriorly at the neck/trunk junction. Each is a long, spongy organ with a few **giant nuclei**. The function of the lemnisci is unknown, leading some investigators to associate them with the lost digestive system, and possibly with the salivary glands of rotifers (Miller and Dunagan, 1985a). Moore (1946) observed that the lemnisci develop as evaginations of the hypodermal layer of the trunk in *Moniliformis moniliformis*. To date, the best interpretation of the function of the lemnisci is derived from observations of the lemniscal **plasmalemma membrane** that has numerous infoldings that greatly amplify the free surface area exposed to the metasomal (body) cavity (Wright, 1970). Thus, it is thought to have an important physiological role in transporting material relative to the metasomal cavity. However, the precise nature of the materials being transported has not been investigated.

Morphology of the reproductive organs

As in all parasitic worms, the reproductive organs are well-developed structures and are obvious in stained, cleared, and mounted specimens. In acanthocephalans, this is especially true because in the majority of species, the trunk cavity is almost empty except for the presence of the reproductive system. As mentioned above, these animals are **dioecious** or **gonochoristic**, meaning that the sexes are separate, with male and female individuals.

Associated with the reproductive system are the **genital ganglia** and the **protonephridia**. The genital ganglion is a small nexus of neurons that is presumed to control the male reproductive organs (Dunagan and Miller, 1978; Dunagan and Price, 1985); however, in most descriptions of species, the genital ganglia are not mentioned. Most species of acanthocephalans do not have protonephridia, but in a few species, females possess protonephridia comprising **flame cells** (Miller and Dunagan, 1985a).

Female reproductive organs.

The main reproductive organs of females are, from anterior to posterior: **Ovary**, **uterine bell**, **sorting apparatus**, **uterus**, **vagina**, and **gonopore**. The **ligament sac** is associated with the reproductive system and is a hollow, membranous tube—in some groups there are 2 sacs—that runs from the proboscis receptacle to the uterine bell. As the worms mature, the sacs persist in species classified in the Archiacanthocephala but they rupture in species of both Palaeacanthocephala and Eoacanthocephala. In some species almost no remnants can be found. The ovaries develop within the ligament sac. The evolutionary origin of the ligament sac is uncertain, but the presence of the ovaries within the lumen of the sac precludes identifying them as the missing intestine.

When female acanthocephalans are immature, they first have 1 ovary that fragments into groups of cells called **ovarian balls**, which subsequently continue fragmentation into ova (unfertilized eggs) and finally, when fertilized in mature females, into shelled eggs, which are also called **shelled acanthors** because the embryo is called an **acanthor**. The unfragmented ovary can only be seen in female cystacanths or very immature adults. Asaolu (1980) and Asaolu and colleagues (1981) completed detailed studies of this process, including scanning electron micrographs.

While developing, fertilized ova circulate within the unbroken ligament sac or within the body of those species in which they do not persist. Eventually, eggs with shells, both immature and mature, enter the uterine bell. Note that the eggs are mature when they are infective to the intermediate host and only mature eggs are passed into the intestine and then out into the external environment; this is the function of the sorting apparatus. The chemical or physical indicators of maturity are unknown, but the apparatus has 2 openings, one leading back to the body cavity and one leading to the uterus. Based on whatever clues are used, the sorting apparatus sorts the eggs, with the immature ones being routed back to the body cavity for further development and the mature ones being sent on to the uterus.

Mature eggs in the uterus pass to the vagina and then, one by one, out to the environment (which comprises the fecal material in the intestine of the definitive host). Although not a part of the reproductive system, all females have muscles located near or around the gonopore (see Monks and Pérez-Ponce de León (1996) for drawings of the vestibular muscle of *Koronacantha mexicana*). Monks (2001) identified 10 different types of muscle of what has been called the genital vestibule. The acanthocephalans have not been studied sufficiently to identify patterns of the evolution of the different forms of vestibular muscles, but these structures may be important in protecting females of one species from being inseminated by males of a different species. Despite the many different forms, all appear to have the same function—to change the shape of the region around the genital pore in order to prevent copulation until the female is ready or not to permit the bursa of males to fit over the posterior end of females, which, in turn, prevents the penis of males from connecting to the genital pore (see figures in Monks et al., 2008).

Male reproductive organs.

The principle reproductive organs of males are (from anterior to posterior): **Testes**, **sperm ducts**, **sperm reservoir**, and **penis**. Associated structures are: **Cement glands**, **cement reservoirs** (if present), **Saeftigen's pouch** (also spelled Seftigen), **genital ganglia**, and **bursa**. A thorough study of the morphology of the reproductive system of males is provided by Asaolu (1981).

Male acanthocephalans have 2 testes, variable in location but always located some distance anterior to the remaining organs. As noted by Monks (2001), they are located generally in tandem with one another but they can be almost in line or more diagonal, distant from each other, or somewhat overlapping, but they are never opposite one another. Each testis is connected by the **vas efferens** to either the **vas deferens** or directly to the **seminal vesicle**, depending upon which group they belong to. A duct connects the seminal vesicle to the penis. The vasa efferentia may be expanded in some region to provide additional storage for sperm. Occasionally, males may only possess a single testis, a **monorchia**, although it is not common. Miller and Dunagan (1985a) provide a list of reports of monorchidism in various species.

The male members of many invertebrate phyla, and some females of those phyla, possess **cement glands**. Typically, the cement is used to bond an organism to a substrate, anchoring the organism so it is not dislodged. The cement from the glands of male acanthocephalans also is used for anchoring, but not to a substrate; instead, it is used to glue them temporarily to a female during copulation. The cement also serves to close the gonopore of females, although it is only temporary and it subsequently deteriorates, allowing females to mate again at a later time.

Several types of cement glands are known: A single syncytial gland, usually with 8 giant nuclei; a small number (usually 2–8) of glands, each with a single giant nucleus; or a small number of glands that have numerous fragments of nuclei in each (Van Cleave, 1949).

Contrasting views of the evolution of the cement glands have been suggested, but modern phylogenetic analyses indicate that separate glands with single nuclei are plesiomor-

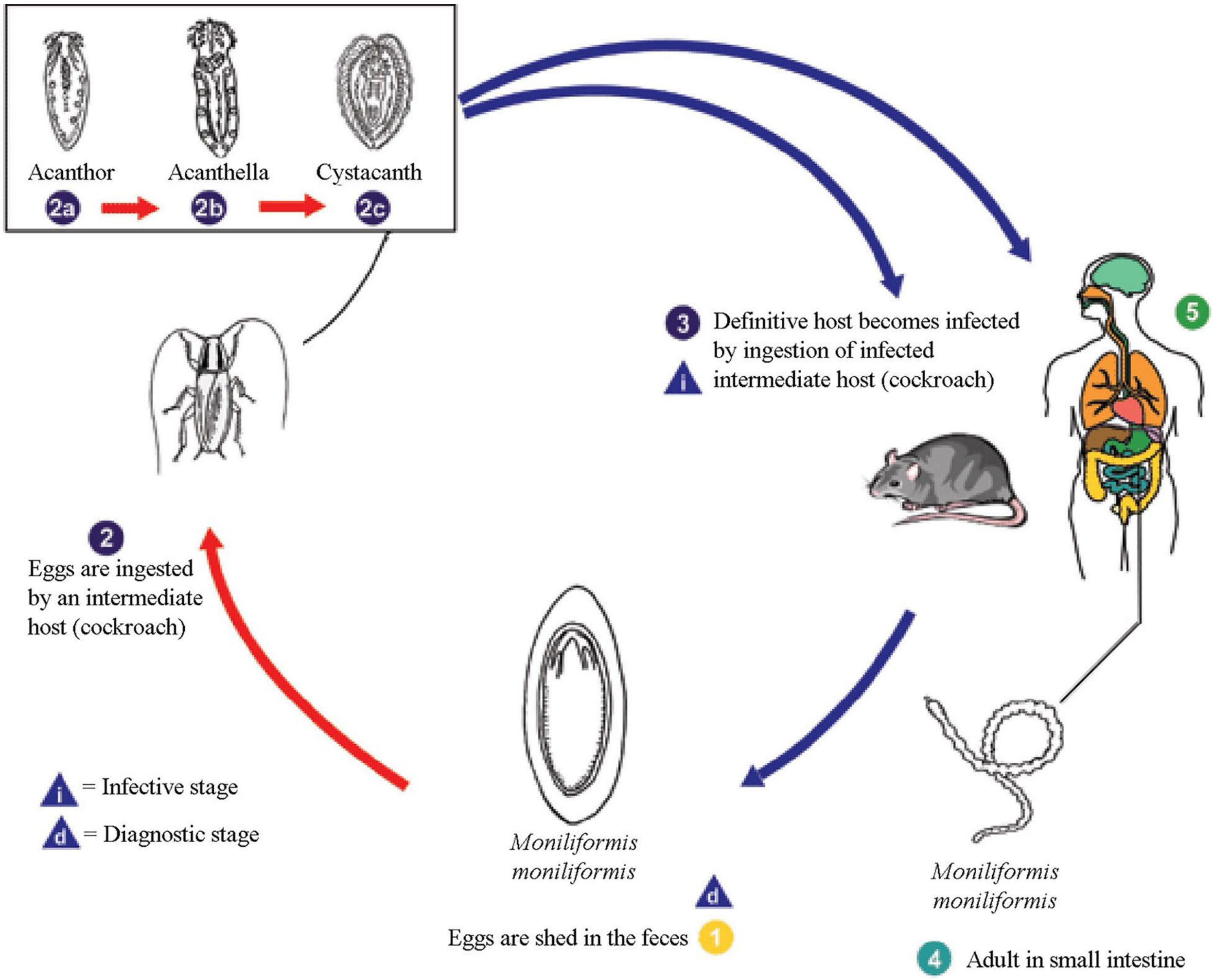

Figure 7. Life cycle of *Moniliformis moniliformis*. 1) Eggs are shed in the feces of the definitive hosts, which are usually rats for *M. moniliformis*, although carnivores and primates, including humans, may serve as accidental hosts. The eggs contain a fully-developed acanthor when shed in feces. 2) The eggs are ingested by an intermediate host, which is an insect (cockroaches, *Periplaneta americana,* for *M. moniliformis*). Within the haemocoel (persistent blastocoel) of the insect, the acanthor (2a) molts into a second larval stage, called an acanthella (2b). After 6–12 weeks, the worm reaches the infective stage, called a cystacanth. The definitive host becomes infected upon ingestion of intermediate hosts containing infective cystacanths (2c). Note that the proboscis is inverted. 3) The definitive host becomes infected by consuming an infected intermediate host. In the definitive host, larvae are liberated from their cysts and they attach to the wall of the small intestine. 4) Here they mature and mate in about 8–12 weeks. 5) In humans, the worms seldom mature, or, when they do mature, will rarely produce eggs. Source: Adapted from DPDx, United States Centers for Disease Control and Prevention, 2019. Public domain.

phic and a syncytial gland has been shown to be a synapomorphy for the species included in the Eoacanthocephala (see Monks, 2001).

Saeftigen's pouch is an expandable vesicle that is connected to the **bursa**. The bursa normally is inverted within the posterior body cavity of males. The muscular Saeftigen's pouch contains liquid that is pumped into the bursa, forcing the bursa out into the form of a cuplike structure that covers the posterior of females and aligns the penis with the vagina. Cement is then released into this area to seal the two individuals in copula.

Although the exact modes of neural communications are not known, the **genital ganglion** probably controls the performance and sequences of the various genital organs. However, it is interesting that a similar organ has not been reported in females.

Life Cycles

Compared to other groups of helminths (that is, Digenea, Cestoda, Nemata, and others) a typical life cycle of acanthocephalans is relatively simple to learn—the definitive host is always a vertebrate and the intermediate host is always an arthropod. A typical life cycle, that of *Moniliformis moniliformis*, is shown in Figure 7. Acanthocephalan life cycles are linked to trophic relationships. This means that a definitive host becomes infected by ingesting its normal food that has a larval acanthocephalan that is infective to that particular species of definitive host.

For this reason, many species of Acanthocephala have very narrow host ranges. Using the previous example, a bird that feeds on insects that eats a cockroach infected with *Moniliformis moniliformis* will not become infected. Likewise, neither will a rodent feeding on pillbugs (*Armadillidium vulgare*) infected with cystacanths of *Plagiorhynchus cylindraceus*, which normally occurs in the robin (*Turdus migratorius*) (see Coady and Nickol, 2000 for a study of this type of interaction). However, this elucidates one curiosity of acanthocephalans. In this latter case, upon ingestion, the helminths would migrate out of the intestine into the body cavity of the rodent. While there, the cystacanth does not develop further; however, it may re-encyst in the rodent where it remains, in a kind of stasis, until a proper host comes along that it can infect, which in this case is probably never, unless of course the rodent dies and an isopod feeds on the dead rodent then becoming infected, ready to transfer the infection on to the avian final host.

As mentioned above, all parasite life cycles are trophically linked and in the cases discussed here, only arthropods can function as intermediate hosts. This would preclude any species that does not eat arthropods from being infected with acanthocephalans. However, there are cases in which the definitive host (such as a hawk or an owl) does not eat arthropods but those species can become infected naturally—here enters the **paratenic host.** The paratenic host is an ecological bridge between the arthropod intermediate host and the definitive host that does not eat arthropods. Usual paratenic hosts are small, insect-eating vertebrates, or in the case of fish, small fish that eat very small aquatic crustaceans; that is, frogs, toads, small lizards, snakes, rodents, and other small fish.

One would never think of a noble eagle or hawk eating insects, but they still can be infected with acanthocephalans. An example of a life cycle of species that involves paratenic hosts is that of the owl dwelling acanthocephalan called *Centrorhynchus* (of which there are several species). Insects become infected when they ingest eggs in the feces of the definitive host (owl or hawk). Snakes, frogs, and/or toads eat the insects, and a lot of them. The cystacanths in the infected insects excyst in the intestinal lumen and migrate to the body cavity where, as mentioned above, they re-encyst. They stay there, alive but in a type of hibernation, until a predatory bird captures the paratenic host, whereupon the cystacanths excyst again and develop within the bird. As an example of the complexity of the situation, Tavares dos Santos and Amato (2010) studied a life cycle in Brazil involving a species of *Centrorhynchus* and a toad, *Rhinella fernandezae*. The definitive host has not yet been identified, but several species of *Centrorhynchus* occur in Brazilian birds.

Finally, it is important to note again that there is no development of cystacanth larvae in paratenic hosts. If the definitive host, such as an eagle or the fish mentioned above, was fed an infected insect or crustacean, respectively, it would become infected with the acanthocephalan, just as it does when it eats the paratenic host.

Before leaving life cycles, one might wonder why there is relatively little precise information on more acanthocephalan life cycles. To give an example, when J. R. Crook was a graduate student, he captured specimens of *Peromyscus maniculatus* (commonly called a deer mouse) and found them to be infected with adult acanthocephalans, *Moniliformis clarki*. Imagine the difficulty in figuring out what arthropods the mouse might be eating, particularly because it is an omnivore. Eventually, Crook discovered that the mice were catching and eating crickets, *Ceuthophilus utahensis*, the Utah camel cricket, that lived in the underground tunnels that the mice made in which to live. The mice set aside a space in the tunnel where they defecated, and the crickets would go there and eat the feces, some of which carried eggs of *Moniliformis* that were passed in the feces of the mouse. The mice would then catch and eat infected crickets, completing the life cycle. This is not the most obvious place to look to find insects on which the mouse was feeding, unless the general life cycle of Acanthocephala was known and if the natural history of the mouse itself was known (Crook and Grundmann, 1964).

Searching out the participants in a life cycle is difficult and often might be the result of luck! This points out a second problem. The parasitologist, who might be a specialist in helminths, must also be a specialist in the vertebrate species that are definitive hosts for the helminths they study, and must know where they live and what they eat. In the case of acanthocephalans, the parasitologist must also know the arthropods, where to find them, and how to identify them. Much of this is not obvious when one reads the description of a life cycle. Today, molecular techniques often are used to match up the identity of cystacanths with adult worms, which often cannot be identified using only morphological details of the cystacanth larvae. Such a study was carried out by Lorenti and colleagues (2018).

Classification and Phylogenetic Relationships

The classification of the members of the phylum Acanthocephala has been relatively stable for some time, but understanding of the phylogenetic relationships of acanthocephalans and relationship to other invertebrate taxa has been in flux significantly. This is largely because the classification of the phylum is still grounded upon classical inductive interpretation of how acanthocephalans should be grouped based on particular characteristics. A list of classical characteristics is presented in Table 1 (Bullock, 1969). These and, of course, other characters have been thought to be indicators of similar ancestry. Thus, species with these characters were placed in the same group (classes are indicated in the table).

A phylogenetic hypothesis, on the other hand, is the result of an analysis of data without the a priori decisions that classical reasoning might give (even though the two might be consistent). It is a provisional conjecture to guide further investigation, although it can be accepted as highly probable based on sound analyses, in view of established facts (data). Instead of using similarity, the hypothesis of relationships is based on characters that are homologous. However, the same classical data might be used in a phylogenetic analysis but the methodology is completely different (see Monks, 2001, for a partial list of the type of data that are useful for this type of analysis).

Because of the different methodology, classifications are rarely 100% consistent with phylogeny, although it would be advantageous if they were consistent. However, thanks to the intellectual acuity of the classical experts who studied acanthocephalans, the classification and recent phylogenetic hypotheses for the higher taxa are relatively similar.

Several works provide complete classifications of the Acanthocephala (Amin, 1985; 2013; Golvan, 1994). Each recognizes the 3 classical classes, **Archiacanthocephala**, **Eoacanthocephala**, and **Palaeacanthocephala**, and some add a fourth class, **Polyacanthocephala** (though others view it as a part of Palaeacanthocephala). Interestingly, the 3 names are tied to early views that one or the other was the most ancient taxon. For those interested in classical classification of the phylum it would be worthwhile to consult the works of Petrochenko (1956; 1958) and (Yamaguti, 1963). The most recent compendium discussing all aspects of acanthocephalan biology, including classification, is Crompton and Nickol (1985). For a list of higher taxa and the number of species known from each at the time of publication, see Monks and Richardson (2011).

Phylogenetic hypotheses of the Acanthocephala are largely consistent with the arrangement of higher taxa, with a continuing greater resolution of relationships and changes in placement as studies have advanced. The first phylogenetic hypothesis for a partial group of genera representing the 3 classes using molecular data were Near and colleagues (1998) and García-Varela and colleagues (2000). The first hypothesis based on molecular data was Monks (2001). Despite some differences in the inclusion of taxa and the methodology, the results of the 3 are similar. In each, Eoacanthocephala and Palaeacanthocephala are designated to be monophyletic sister taxa, meaning, 2 taxa that descended from the same most recent common ancestor. Archiacanthocephala is the most basal class in both cladograms, but in one (Figure 8A) it is a monophyletic clade and the members do not form a monophyletic

Table 1. Characterization of the 3 orders in the Acanthocephala. Adapted from Bullock, 1969.

Character	Archiacanthocephala	Eoacanthocephala	Palaeacanthocephala
Body size	Mostly large	Small	Small to large
Host habitat	Terrestrial	Aquatic	Mostly aquatic
Lacunar system, main longitudinal vessels	Dorsal and ventral or dorsal only	Dorsal and ventral, at least anteriorly	Generally lateral
Cement glands	Usually (always?) 8 uninucleate	Usually 1, syncytial, with giant nuclei; distinct cement reservoir	From 2 to 8, multinucleate
Trunk spines	Absent	Present or absent	Present or absent
Subcuticular nuclei	Few, elongate or branched, or with fragments remaining close together	Very few giant nuclei	Numerous amniotic fragments or few highly branched
Proboscis receptacle	Single muscle layer, often modified by ventral cleft or accessory muscles	Closed sac with single muscle layer	Closed sac with 2 muscle layers, except in Polyacanthorhynchinae
Ligament sac	Dorsal and ventral, persistent, with dorsal sac attached to uterine bell	Dorsal and ventral; disappear in adult; ventral sac attached to uterine bell	Single, ruptured in mature worms; posterior attachment inside uterine bell
Nephridia	Present or absent	Absent	Absent
Embryonic membrane	Usually thick	Thin	Usually thin
Intermediate host	Insects (and millipedes)	Crustacea	Crustacea

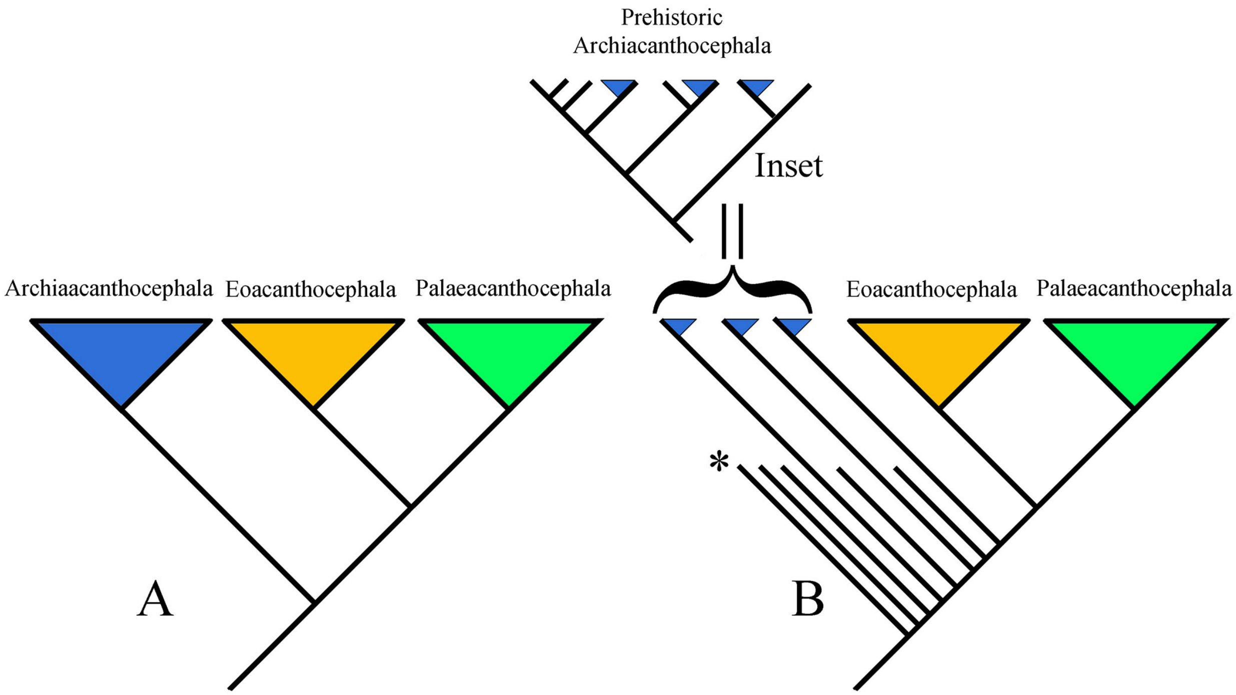

Figure 8. Hypotheses of the phylogenetic relationships of the Acanthocephala. A) Cladistic representation of the general results of 2 molecular analyses; B) Cladistic representation of the general results of another morphological analysis. Inset: Hypothetical clade of prehistoric archiacanthocephalans that in nature represented a monophyletic clade. The asterisk (*) indicates extinct taxa, represented by shorter lines. In the inset, the lines without triangles represent extinct taxa. The clade shown is a hypothetical monophyletic clade including extinct taxa. In this clade none of the extant taxa are closest relatives; the sister groups of each are extinct. Synapomorphies for this putative clade have not been identified; thus, the 3 branches with blue triangles (extant archiacanthocephalans) cannot be identified as a monophyletic clade. Sources: A) Adapted from García-Varela et al., 2000; Near et al., 1998; B) adapted from Monks, 2001. License: CC BY-NC-SA 4.0.

group (Figure 8B) (see the cladograms in García-Varela et al. (2000), Near et al. (1998), and Monks (2001), respectively).

The failure of the methodology to recognize the class Archiacanthocephala as a monophyletic group was interpreted by Monks (2001) as an artifact caused by the very old origin of acanthocephalans. Monks suggested that present day taxa (Figure 8B) are only a relict of the original species in the group (Brooks and Bandoni, 1988); that is, many of the original species (and their hosts) are extinct (Figure 8B, inset) and their absence from the analysis hindered the ability of the methodology to identify synapomorphies for the clade.

Interestingly there are studies that have been interpreted that indicate that acanthocephalans are a part of the phylum Rotifera. One of the first was by Herlyn and colleagues (2003). To continue to explore this interpretation, refer to that study and the subsequent works, both pro and con, which cite this study. Earlier studies (Conway Morris and Crompton, 1982) postulated the phylum Priapulida as a sister group to Acanthocephala, but this idea mainly was based on similarity of fossil priapulids with present-day acanthocephalans.

This summary is far from providing a complete picture of this fascinating group. For more information there are numerous published papers available on the internet or in university libraries, only a very few of which were cited here. Many of these are descriptive taxonomic works, but there are also studies on physiology, behavior, ecology, and more on the subjects mentioned above.

The information and interpretations presented here are based on a phylogenetic perspective. For more information on phylogenetics, terminology, and methodology, a great source is The Compleat Cladist (Wiley et al., 1991; available as a free PDF download at https://kuscholarworks.ku.edu/handle/1808/24957). For further information on phylogenetic hypotheses of different groups of helminth parasites, see Brooks and McLennan (1993; 2002). For sources which bring ecology, behavior, biogeography, and other areas of biology together in a phylogenetic perspective, see Brooks and McLennan (1991). Searching in the Web of Science or Google Scholar for sources that cite these works will provide more recent sources of information.

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PENTASTOMIDS

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Pentastomida: Endoparasitic Arthropods

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Chapter 59

Pentastomida: Endoparasitic Arthropods

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Introduction

The name Pentastomida comes from the Greek: **pente** (five), and **stoma** (mouth), so chosen due to the 5 protuberances that are found on the anterior end of the body; however, only 1 of which is a mouth (also called the snout) (Bush et al., 2001). This cosmopolitan phylum encompasses a homogeneous and distinctive systematic assemblage of over 130 taxa of worm-like dioecious obligate endoparasites that, as adults, inhabit the respiratory tract (bronchi, lungs, and nasal passages) and coelomic cavity of various freshwater and terrestrial vertebrates, with the overwhelming majority (~ 90%) maturing in reptiles (Riley, 1986).

Although there appears to be some disagreement surrounding the classification of pentastomids (Abele et al., 1989), many researchers are content to designate Pentastomida as its own phylum, whereas others (Kelehear et al., 2014) consider it a class. For the purposes of this chapter, pentastomids (also known as tongue worms or linguatulids) will be considered to belong to the phylum Crustacea, subphylum Pentastomida Huxley, 1863, and class Eupentastomida Waloszek, Repetski, and Maas, 2006.

Fossil Record

Pentastomids are the oldest metazoan endoparasites known to science (Kelehear et al., 2014). Fossils occur in the Cambrian and Ordovician marine strata of Canada and Sweden. There are at least 8 Paleozoic fossil species, including species allocated to 4 genera as follows: *Aengapentastomum* Waloszek, Repetksi, and Maas 2006, *Boeckelericambria* Walossek and Müller 1994, *Haffnericambria* Walossek and Müller 1994, and *Heymonsicambria* Walossek and Müller 1994. A fifth genus, *Invavita* Siveter, Briggs, Siveter, and Sutton, 2015, is from Silurian-aged marine strata of England (Siveter et al., 2015) and fossil specimens of *Invavita* were found firmly attached to their ostracod (class Crustacea: order Ostracoda) hosts (*Nymphatelina gravida*). It is probable that these ancient pentastomids have been associated with their hosts since the Mesozoic Era. Prehistoric larvae closely resembling extant primary larvae appeared in the fossil record approximately 100 million years prior to the vertebrates they now parasitize (Riley, 1996), but the identity of the fossil pentastomids' hosts remains an enigma. Today, the higher vertebrates which are infected by tongue worms were basically not present in the early Ordovician period (500 Ma = million years ago) and while the limestone strata were formed in ancient seas in which the fossils were found, modern pentastomids occur only in freshwater or terrestrial vertebrates. However, one possible explanation is that ancient pentastomids attached themselves as ectoparasites to the gills of some of the large marine arthropods which were common in the Ordovician. These include the trilobites, and a lesser-known group called the anomalocarids, voracious predators which could grow up to 2 m-long. Riley and colleagues (1978) suggested that the pentastomids must have made the hurdle from marine invertebrates to freshwater and terrestrial vertebrates, and so were able to survive when their former hosts became extinct.

Extraordinarily well-preserved, 3-dimensional and phosphatized fossils from the Cambrian–Ordovician boundary of Canada and the Upper Cambrian Orsten fauna of Sweden, have been identified by Walosek and colleagues (2006) as pentastomids. These fossils suggest that pentastomids evolved very early and raise doubts about whether these organisms were actually true parasites at that time, and if so, on which hosts. A possible host in this venue is the Conodont (an extinct agnathan chordate).

Evolution

Evolutionarily speaking, knowledge of the relationships of pentastomids are in a state of flux as they share characters with the phylum Annelida, but most evidence suggests that they are more closely related to members of the phylum Arthropoda. As introduced above, some researchers have even proposed that the Pentastomida be regarded as an order of the crustacean class Brachyura, while others (Wingstrand, 1972; Riley et al., 1978; Abele et al., 1989) essentially agree that pentastomids be deemed a subclass of Crustacea (Pancrustacea), closely allied with the Brachyura. In addition, analyses of the mtDNA gene arrangements and sequences have indicated unambiguously that pentastomids are a group of modified crustaceans, probably related to brachyuran crustaceans (Lavrov et al., 2004). Using morphological characters as well as molecular techniques (such as 18S rRNA sequences) some advocates retain the Pentastomida as a separate phylum (Abele et al., 1989), although others recommend supporting their inclusion in the Crustacea. Therefore, pentastomids may be most closely related to brachyuran lice, which are ectoparasitic on fish. For the purposes of this chapter, the designation of the species is retained in this group at the phylum level (the Pentastomida).

Geographic Range

Pentastomids are considered cosmopolitan in distribution, but as a rule, occur more commonly in hosts found in subtropical and tropical regions of the world. Some geographical hotspots for potential hosts include those from equatorial Africa, Australia, the Middle East, and Southeast Asia; they occur less often in vertebrates of the Americas and southeastern Europe. In addition, only 4 species have been reported from the Iberian Peninsula and Macaronesian Islands (Christoffersen and de Assis, 2015).

History of Pentastomid Research

Almeida and Christoffersen (1999) provided a summary of the history of pentastomid research and here additional information is added to their account. Evidently, the first to report a genuine pentastomid was the French veterinarian Philibert Chabert (1737–1814). In 1787, he discovered what he called a worm, which he mistook for the tapeworm *Ténia lancéolé* (now referred to as *Drepanidotaenia lanceolata* (Bloch, 1782) which is actually a member of the Hymelolepididae) in the nasal cavities of dogs and horses. Pioneer descriptions and further efforts to understand pentastomids were made during the next century by Josef Aloys von Frölich (1789), Alexander von Humboldt (1812), Pierre-Joseph van Beneden (1849), and Karl Moritz Diesing (1850), culminating with the account of the *Linguatula* (in 1860) by the German zoologist, C. G. F. Rudolph Leuckart (1822–1898). More recently, meaningful works were written by Richard Heymons (1867–1943) (see Figure 1) of the Berlin Museum, Konstantin von Haffner (1895–1985) of the University of Hamburg, and J. Teague Self (1906–1995) of the University of Oklahoma. One of the most prolific writers of all time on pentastomid biology was John Riley of the University of Dundee, Scotland, United Kingdom.

Figure 1. Historical specimen of a female *Armillifer armillatus* Wyman, 1848 (4 cm-long) collected from an African rock python *Python sebae* from an unknown site. Source: R. Heymons; specimen deposited in the Museum für Naturkunde, Berlin, Germany. Photographer: José Grau de Puerto Montt, 2008. License: CC BY-SA 3.0 Unported.

Chief Morphological Characters

The simple body design of pentastomids is surprisingly conservative. All possess an elongate and vermiform-cuticular (chitinous) and porous body (Figures 2A–E), often with a conspicuous abdomen showing distinct annulations (annuli = external segmentation). These are usually strongly united with a rounded cephalothorax possessing, on its ventral surface, a small sucking-type mouth region lacking jaws but bordered by 2 pairs of sclerotized hooks (Figures 2D–E), that can be retracted by specialized locomotor muscles into cuticular pockets (Paré, 2008). In some species, these hooks articulate against a basal fulcrum and are controlled by strong muscles used to tear and embed their mouth into host tissues. Males are generally smaller than females and possess copulatory spicules (Figures 2B–C). The conical-shaped pentastomid body, which can range from 2 to 130 mm (0.8 to 5.1 in) in total length, depending on the species, is divided into an anterior forebody and posterior hindbody, which, in some, is bifurcated at its tip. The cuticle of some species is covered with a dense network of chitinous spikes.

Integumentary System

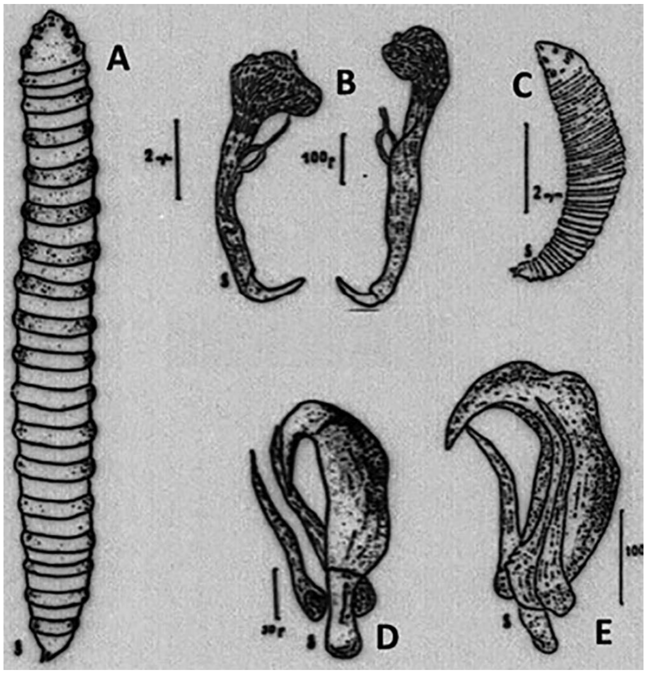
The cuticle of pentastomids is thin and similar to that of other arthropods. It consists largely of 3 layers (subcuticle, endocuticle, and epicuticle) (Riley and Banaja, 1975).

Muscular System

Longitudinal and circular muscles of pentastomids are arthropodan biologically and are cross striated and segmentally arranged.

Digestive System

The gut of pentastomids is a simple straight tube, with the anus opening at the posterior end of the abdomen. Their mouth is held open permanently by a sclerotized lining, the circular, ovoid, or U-shaped cadre; this structure is a significant taxonomic character. Adult pentastomids are hematophagous feeders, breaking lung capillaries and ingesting tissue fluids and blood cells of their hosts.



Figures 2A–E. *Raillietiella chamaelionis* Gretillat and Brygoo, 1959, from *Chamaeleo* sp. from Madagascar showing general characters of pentastomids. A) Female; B) male copulatory spicules; C) male; D) female anterior hooks; E) female posterior hooks. Source: Gretillat and Brygoo, 1959. License: CC BY.

Circulatory, Excretory, and Respiratory Systems

Although the body of pentastomids possess a hemocoel containing blood or hemolymph (Paré, 2008), there are no definitive circulatory, excretory, or respiratory organs.

Nervous System

The nervous system of Pentastomida is similar to that of other arthropods (Doucet, 1965). Their sensory organs are arranged in a definitive pattern and appear to be very simple structurally (Heymons, 1935), which may be due to their parasitic mode of life. The nervous system includes a ventral nerve cord with ganglia in each segment. Mechanosensitive sensilla are present throughout larval development on the anterior head region and positioned in characteristic patterns, increasing in number to the infective stage; the majority of anterior sensilla are located on sensory papillae (Storch and Böckeler, 1979; Winch and Riley, 1986). A subterminal or terminal anus might be flanked by a pair of terminal papillae (Haffner, 1977).

Reproductive System

Riley (1983) provided an excellent review of the reproductive biology of pentastomids. They are dioecious (having males and females) and exhibit distinct sexual dimorphism, with females usually being larger than males (Junker, 2002). Males have a single, tubular testis; however, there are 2 present in the genus *Linguatula*. The testis is continual with a seminal vesicle, which, in turn, connects to a pair of ejaculatory organs. The male genital pore is mid-ventral on the anterior abdominal segment, close to the mouth. Female pentastomids possess a single ovary that extends almost the entire length of the body cavity and may bifurcate at its distal end to become 2 oviducts that unite to form the uterus (Nørrevang, 1983). The uterus terminates as a short vagina that opens through the female gonopore. Fertilization is internal and females mate only once, while the males may be polygamous. Females are capable of producing several million fully embryonated eggs per day, which pass up from the lungs to the trachea of the host and are then either swallowed passed out with the feces or coughed up to the outside.

Pentastomid-Host Relationships

Insects as Hosts

Four species of pentastomids are known from intermediate host insects (3 coprophagus cockroaches and 1 coleopteran) (Lavoipierre and Lavoipierre, 1966). For example, cephalobaenid pentastomids *Raillietiella frenatus* and *R. gehyrae* employ geckos as definitive hosts and cockroaches as intermediate hosts (Ali and Riley, 1983). For some other raillietiellid definitive hosts that do not ingest insects, intermediate hosts may be amphibians, lizards, or snakes (Ali et al., 1982).

Fishes as Hosts

Despite the fact that pentastomids are potentially important endoparasites of subtropical and tropical fishes, comparatively little is known about the occurrence and distribution of pentastomid larvae in freshwater fish and information on this particular host-parasite relationship in the scientific literature is lacking (Giesen et al., 2013). Two families of pentastomids, Sebekidae and Subtriquetridae, use various freshwater fish species as intermediate hosts (Fain, 1961; Overstreet et al., 1985; Winch and Riley, 1986; Boyce et al., 1987; Junker et al., 1998). Most of these fishes (including cichlids and barbs) are common intermediate hosts for pentastomids occurring in crocodilians and piscivorous chelonians, and rarely for some species of snakes. Nymphs (Figure 3) develop in the viscera and muscle tissue of various fishes. Sebekiid and subtriquetrid pentastome larvae have been recovered from the body cavity or swim bladder of several fish species from various localities in South Africa (Luus-Powell et al., 2008). For example, 3 genera found in crocodilians as adults are found in

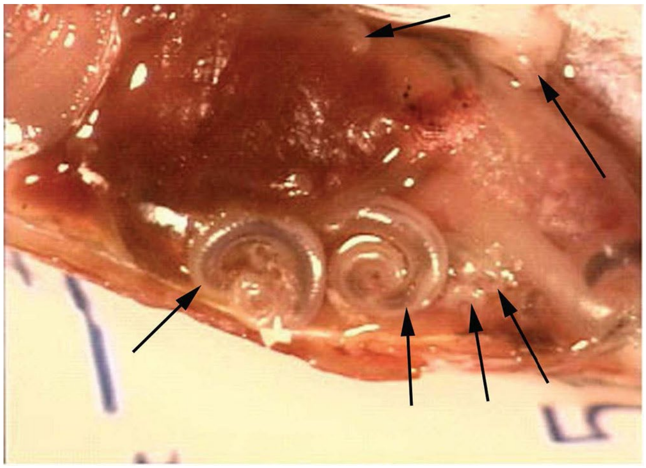


Figure 3. Pentastomid larvae (nymphs; arrows) in the body cavity of a swordtail *Xiphophorus helleri*. Note the varying sizes and locations of the pentastomids. Source: R. P. E. Yanong, 2019. Public domain.

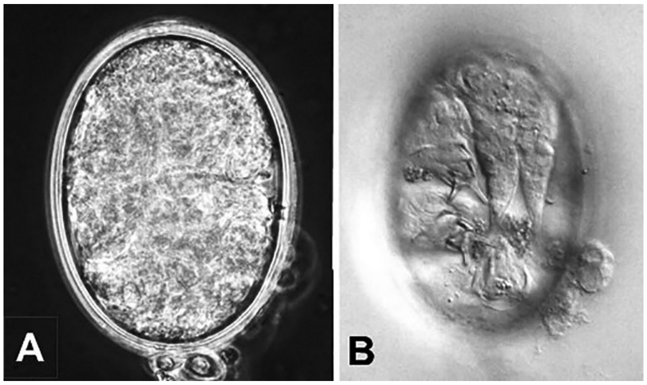


Figure 4. *Raillietiella teagueselfi* eggs from feces of Mediterranean geckos *Hemidactylus turcicus* from Texas, United States. A) Phase contrast microscopy of unembryonated egg; B) Nomarsky-interference contrast microscopy of fully embryonated egg. This pentastomid was described as a new species by Riley and colleagues, 1988. Source: S. J. Upton. License: CC BY-NC-SA 4.0.

intermediate host fish that they eat. To date, several fish species belonging to a number of families worldwide have been recorded as intermediate hosts of sebekiids, namely *Sebekia oxycephala* in cichlids and *Sebekia mississippiensis* in North American *Amia calva*, *Gambusia affinis*, *Fundulus grandis*, *Lepomis gibbous*, *L. macrochirus*, *L. megalotis*, *L. microlophis*, *Micropogonias undulatus*, *Micropterus salmoides*, *Pimephales promelas*, *Pomoxis nigromaculatus*, *Ameiurus natalis*, and *Xiphophorus helleri* (Hoffman, 1999; Luus-Powell et al., 2008). Fain (1961) and Reichenbach-Klinke and Landolt (1973) list *Alestes macrophthalmus*, *Bathybates ferox*, *Chrysichthys brachynema*, *C. mabusi*, *Lates microlepis*, *L. niloticus*, *Mastacembelus* sp., and *Oreochromis niloticus* as intermediate hosts of *Leiperia cincinnalis* in Central Africa.

Experimental transmissions conducted by Riley (1989) with *Subtriquetra* of small fishes (30 to 50 mm-long) caused deaths even before parasite larval development was completed (around 30 to 40 days after infection). However, larger fish (*Aequidens* sp., 70 mm-long) survived infections with 7 (2.5 mm-long larvae), which were already infective.

Amphibians as Hosts

Gedoelst (1921) was the first to report a cephalobaenid pentastomid, *Raillietiella indica*, in the lungs of an amphibian (Asian spined toad *Duttaphrynus melanostictus*; earlier referred to as *Bufo melanostictus*). A few years later, Larrousse (1925) reported a larval linguatulid from the Berber toad (*B. mauritanicus*). Since then, there have been other reports of amphibians as hosts including *Raillietiella bufonis* from Puerto Rican crested toad (*Peltophryne* [= *Bufo*] *lemur*) in Puerto Rico, United States (Ali et al., 1982), cane toad *Rhinella marina* from Hawaii, United States (Barton and Riley, 2004), and *Raillietiella rileyi* from *D. melanostictus* from Malaysia (Krishnasamy et al., 1995). Transmission of pentastomids to amphibian hosts has been reported by Nadakal and Nayar (1968) and Ramachandran (1977). To date, there are apparently no reports of pentastomids from salamanders (Caudata) or caecilians (Gymnophiona).

Reptiles as Hosts

About 90% of adult pentastomids are known from carnivorous reptiles, including lizards, turtles, snakes, and crocodilians (Kelehear et al., 2014). Reptiles become infected by ingesting an intermediate host containing nymphal stages and then pass the eggs (Figure 4) in feces to the environment or the infected reptiles are eaten by another host. The most common genera of reptilian pentastomids are *Armillifer* (Figure 1), *Kiricephalus* (Figure 5), *Porocephalus*, *Raillietiella* (Figure 4), *Sebekia*, and *Waddycephalus* with the majority found as adults in the buccal cavity, trachea, bronchi, and lungs of snakes, lizards, and crocodilians. They also can occur in the heart or the brain of these hosts. Of all reptiles, snakes appear to be the most common hosts, and as Kelehear and colleagues (2014) reported in a survey of tropical Australian snakes, 59% of the specimens they surveyed were infected with at least 1 species of pentastomid. Pentastomids of the genera *Raillietiella* and *Waddycephalus* infect a suite of host taxa, including 7 snake taxa from 3 snake families (Colubridae, Elapidae, and Pythonidae).

A study by Miller and colleagues (2017) revealed that invasive Burmese pythons (*Python vittatus*) in Florida, United States, host 2 species of pentastomids, *Raillietiella orientalis* and *Porocephalus crotali*. Both species also infect some

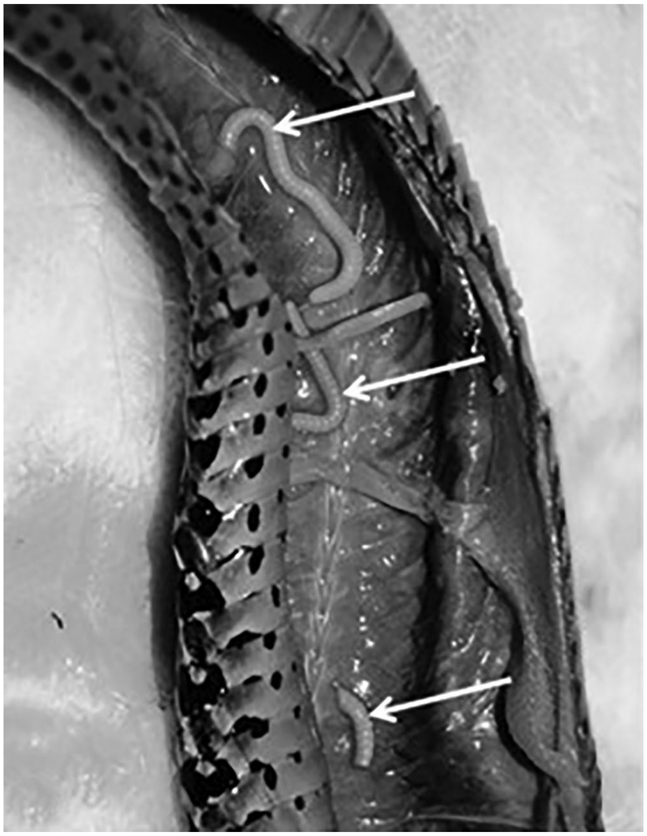


Figure 5. *Kiricephalus* spp. Macroscopic view of in situ *K. coarctatus* (arrows) from an eastern garter snake *Thamnophis sirtalis* from Arkansas, United States. This represents the first report of a reptilian pentastomid from Arkansas. Source: C. T. McAllister. License: CC BY-NC-SA 4.0.

native snakes in Florida, United States. These researchers determined that the former parasite (whose native range is Southeast Asia and Australia) did not originate in Florida but had arrived as a fugitive in the lungs of Burmese pythons. In addition, wherever *Python vittatus* occurs, native snakes in the surrounding areas of the state are also infected with *R. orientalis*.

The following examples of pentastomids in reptiles are provided by Reichenbach-Klinke and Elkan (1965): *Cephalobaena tetrapoda* in South American snakes of the genera *Bothrops*, *Lachesis*, and *Leptophis*; *Raillietiella* spp. in agamid, gekkonid, and varanid lizards, and colubrid and elapid snakes from both the Old World and New World; *Sebekia* spp. in African, South American, and North American crocodiles; *Diesingia megastomum* in Geoffroy's side-necked turtle *Phrynops geoffroanus* from South America; *Alofia platycephalum* from South American crocodiles; *A. indica* from crocodilians from India; *Leiperia* spp. from South American crocodiles and Nile crocodile *Crocodilus niloticus*; *Subtriquetra* spp. in South American and Indian crocodiles; *Elenia australis* in Australian varanids; *Waddycephalus* spp. in Asian, Australian, and Indonesian tree and ground-dwelling snakes and Asian house geckos (*Hemidactylus frenatus*) in Australia; *Porocephalus* spp. in North American and African boid and viperid snakes; *Kiricephalus* spp. in North American, Indian, Madagascan, and Australian snakes; *Armillifer* spp., in Asian and Australian boid, colubrid, and viperid snakes; *Cubirea annulata* in African snakes; and *Gigliolella brumpti* in Madagascan snakes. To date, there are no reports of pentastomids from amphisbaenians (suborder Amphisbaenia).

Birds as Hosts

There are 2 species of pentastomids found in the air sacs (Figures 6A–B) of sea birds (guillemots, gulls, puffins, skuas, and terns) and another in the trachea of white-backed vultures. The majority are found in hosts from the subpolar and polar latitudes in the Holarctic (Nicoli and Nicoli, 1966). For example, the larid pentastomid *Reighardia sternae* occurs in the body cavity and air sacs of about 13 species of gulls and terns and is the only pentastomid species known to use these avian waterfowl as hosts (Riley, 1973). The life cycle of *R. sternae* is unique among pentastomids as it includes an obligate (monoxenous) life cycle with 1-host parasite and an intermediate host phase in the egg (Thomas et al., 1999). The hatching stage directly infects the respiratory system of the avian definitive host.

Non-Human Mammals as Hosts

Adult and/or nymphal pentastomids have been reported to infect captive and natural populations of marsupials, canines, felines, rabbits and hares, antelopes, reindeer calves, camels, cattle, sheep, goats, monkeys, rodents, and many others (Spratt, 2003; Paré, 2008). Those species found in felids and canids typically occur in the nasopharynx. Most of these reports concern *Armillifer armillatus* or *Linguatula serrata*. Dechkajorn and colleagues (2016) reported a case of visceral pentastomiasis in a captive striped hyena (*Hyaena hyaena*) in Thailand.

Humans as Hosts

Humans are rarely infected by adult pentastomids and represent dead-end hosts, meaning that they play no role in the natural cycle of this parasite. However, visceral pentastomiasis caused by nymphal specimens is an emerging zoonotic infection (meaning that they can be passed between humans and animals) and is sometimes observed in individuals in rural western and central Africa and some parts of Asia. African pythons (Pythonidae) and large vipers (*Bitis* spp.) act as definitive hosts for *Armillifer armillatus*

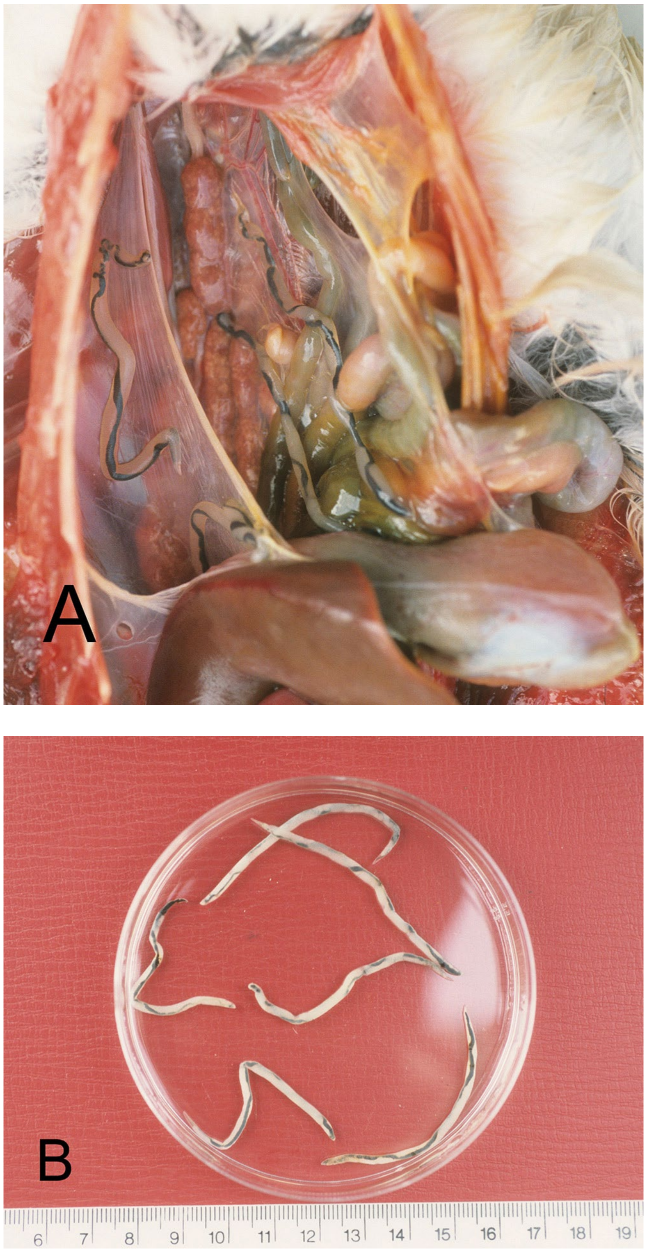


Figure 6A–B. Pentastomids (*Reighardia* sp.) from airsacs of an unknown species of guillemot. A) Worms (arrows) in situ; B) worms removed from airsacs. Source: T. Pennycott, 2016. License: CC BY.

and *A. grandis* in the Congo Basin. Snakes in the bushmeat market have gradually increased over the years and human pentastomiasis has become an important emerging zoonotic disease (Hardi et al., 2017). The mucus from the lungs of infected reptiles (especially snakes) and carnivorous mammals can also cause infection in humans. Humans can also be infected via food or water contaminated with host feces containing pentastomid eggs, by consumption of undercooked snake flesh (including the prized gallbladder), or indirectly through contaminated hands, kitchen tools, or washing water (Fain, 1975; Yapo Ette et al., 2003; Lai et al., 2010; Ibinaiye et al., 2011; Hardi et al., 2013; 2017). Several human infections have been reported from Cameroon, the Democratic Republic of the Congo, and Nigeria (Vanhecke et al., 2016). The majority (99%) of human infections are caused by 2 species, *Linguatula serrata* or *Armillifer armillatus* (Paré, 2008). The adult worm is found in the nasal passages of dogs and sheep, and goats are infected by ova from infected dogs. A syndrome known as Halzoun (also known as nasopharyngeal linguatulosis, present in the eastern Mediterranean) is the common name for the infection of *L. serrata* of the buccopharyngeal mucosa and nasopharyngeal tract of humans (Cannon, 1942; Dabick, 1987; Yagi et al., 1996). This hypersensitivity disease is also known as **Marrara syndrome** in Sudan, named after a dish of raw stomach, lung, trachea, rumen, and liver of sheep, goats, or camels, infected with larvae of *L. serrata*, which is often responsible for the transmission of the parasite to humans. Interestingly, a nymph of *Leiperia cincinnalis* (which usually is found as adults in the lungs of African crocodiles) was found in the feces of a woman in Zaire (Fain, 1960; 1961). This patient was likely infected by larvae from eating some type of fish (Fain, 1975). The possibility of a carcinogenic action of pentastomids has also been suggested (Fain, 1975); however, the arguments for this association are unsubstantiated.

Although pentastomiasis is mostly asymptomatic in humans and usually not a primary health threat, the clinical presentation is quite varied and depends on infected tissues. Nymphs are often located in the abdominal cavity, including the liver and thoracic cavity (including the lungs and pleura) and abdominal emergencies from severe systemic symptoms have been reported; infections of the eyes (ocular pentastomiasis) are rare (Sulyok et al., 2014).

Diagnostic delays are inevitable, and diagnosis focuses on the patient's lifestyle and living environment. It is mainly based on the morphological description of the parasite's calcified cuticle, the site of the lesion, and the parasite's region of origin. Those patients who present symptoms have fever, abdominal pain, diarrhea, and weight loss. When blood samples are obtained, eosinophilia, anemia, and an elevated serum immunoglobulin (IgE) level is sometimes present. Ultrasound, conventional X-ray, computerized tomography (CT) and magnetic resonance imaging (MRI) scans, and a laparoscopic approach might also be helpful for the diagnosis of pentastomiasis. Deworming treatments using praziquantel (Biltricide) and mebendazole (Emverm) are often prescribed for patients infected with certain types of worms causing pentastomiasis. However, most patients do not require any major or invasive treatment.

Human infections have been confirmed for the following pentastomids, including *Linguatula serrata*, *Armillifer agkistrodontis*, *A. armillatus*, *A. grandis*, *A. moniliformis*, *Leiperia cincinnalis*, *Porocephalus crotali* (syn. *A. moniliformis*), and *P. taiwana* (Fain, 1975; Tappe et al., 2009; 2016; Sulyok et al., 2014; Mehlhorn, 2015). In addition, adults of *A. grandis* have frequently been observed in the lungs of rhinoceros vipers (*Bitis nasicornis*) and nymphal infections in humans have been reported in Africa from this species. The nymphs encyst in the omentum, the mesenteries, and even the eyelid of humans (Fain and Salvo, 1966).

Effect on the Host

In the most common hosts (reptiles), pentastomes are hematophagous (meaning that they feed on blood), but even in heavily infected lizards or snakes, anemia has not yet been documented. Host death is often associated with larval and nymphal migration and molting, and by pathological damage caused to the pulmonary lining by the hooks and mouths of feeding adults, which often leads to secondary bacterial infection or fungal pneumonia. Mortality associated with progressive pneumonia from infection with adult *Raillietiella* has been reported in wild geckos from Nigeria, suggesting that pentastomes may act as regulators of wild reptile populations. Imported wild-caught reptiles in private collections and zoos may also develop overt disease from pentastome infection.

Larval Development

Larval and nymphal pentastomid development ranges from indirect, with up to 10 stages, to direct. Development of the embryo ceases with a pre-hatching within the eggshell, which is now termed the primary larva or nymph. Larval migration occurs through the body cavity and after several molts, the larvae become infective in the respiratory tract of the definitive host (Riley, 1986; Buckle et al., 1997).

Life Cycles

A typical pentastomid indirect life cycle (Figure 7) begins when eggs are ingested by a suitable intermediate host and develop into minute larvae or nymphs that penetrate the definitive host's intestinal tract and migrate casually to multiple tissues (usually those of the respiratory tract). These suitable intermediate hosts bridge diverse taxa, including mammals, reptiles, amphibians, fish, and insects. However, for most species the intermediate host has yet to be discovered (Riley, 1986; Paré, 2008). Interestingly, the life cycle of *Raillietiella sternae* involves an obligate 1-host parasite that has shifted its intermediate host phase into the egg. Therefore, the hatching stage directly infects the respiratory system of the definitive host, which is unique among pentastomids.

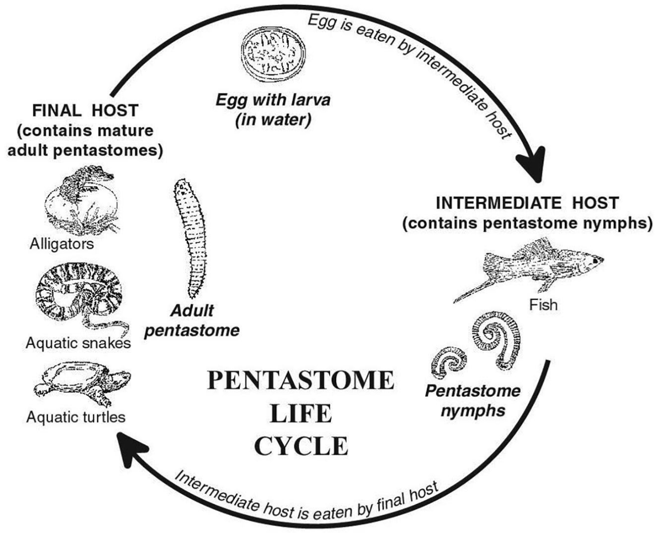


Figure 7. Generalized life cycle of pentastomids. Source: R. P. E. Yanong, 2019. Public domain.

Pentastomid larvae infect the definitive host when the host ingests a suitable intermediate host. These larvae burrow out of the host's digestive system and through to the lungs, where they can cause lesions and scars along their migration path (Jacobson, 2007). In intermediate or accidental hosts, these larvae can establish widespread visceral infections (Brookins et al., 2009; Haddadzadeh et al., 2010; Mätz-Rensing et al., 2012; Yakhchali and Tehrani, 2012). The adult pentastomids feed primarily on blood from host capillary beds in the lungs and are capable of causing severe pathologies resulting in death (Paré, 2008). Large adult pentastomids (up to 15 cm-long) can physically occlude the respiratory passages and induce suffocation. The 2 pairs of hooks they use for attaching to lung tissue can cause perforations and hemorrhaging and disintegrating molted cuticles shed into the lumen of lungs by maturing pentastomids can induce putrescent pneumonia (Jacobson, 2007).

When the life cycle involves a reptilian definitive host, ingestion of an intermediate host containing nymphs are then infective to the definitive host by penetrating the wall of the stomach or intestinal tract using its hooks. The nymphs migrate into the lungs and air passages, where they mature into tongue-shaped adults that can be up to 160 mm-long. In addition, pentastomid adults containing mature eggs may be expelled from the trachea and eliminated from the definitive host through oral expulsion. These adults may also be swallowed, resulting in eggs appearing in the feces. Autoinfection can also occur in some species.

Ecology

Adult pentastomids are mostly restricted to the respiratory tracts of tetrapods, primarily reptiles; larval stages may occur in fish. Several species cause visceral and respiratory infections termed **pentastomiasis** in vertebrates.

As is common with many other parasites, pentastomids may serve an ecological role as regulators of community size and may be considered regulators of host populations. They may even be found in threatened and endangered species and could represent a problem in conservation efforts of those hosts. Since they are often recovered from captive animals in zoos during necropsies, they may also be considered a health problem. In some cases, the death of any given host may be directly or indirectly attributable to an infection with pentastomids. For humans, pentastomids typically infect those people living in impoverished parts of developing countries, such as some in the arid Middle East, Southeast Asia, and Latin America (Riley, 1986). Here, people rely on native reptiles as a food source which can enable transmission of infective nymphs (Almeida and Christoffersen, 2002). However, despite an occasionally high number of nymphal individuals that cause visceral pentastomiasis in humans, most infections are asymptomatic and are often only diagnosed incidentally during surgery or postmortem.

Taxonomic Study

The pentastomids are sometimes classified in their own phylum and class, referred to as phylum Pentastomida Huxley, 1869, class Eupentastomida Walosek, Repetski, and Maas, 2006. In this chapter, pentastomids are considered to belong to the phylum Crustacea, subphylum Pentastomida Huxley, 1863, and class Eupentastomida Waloszek, Repetski, and Maas, 2006.

Descriptions of new species of pentastomids traditionally have been based on various morphological features of the adult worm, with emphasis placed on body size, number of body annuli, and morphology and measurements of the 2 pairs of retractile hooks, the buccal cadre, and the male copulatory spicules, the latter particularly helpful in determination of raillietiellids (Riley, 1986). However, due to 5 main factors and a high level of intraspecific variation, there is potential for misidentifications, including: 1) The small numbers of specimens generally recovered, 2) method of fixation used on those specimens, 3) state of the preserved type or voucher specimens, 4) whether there are both males and females present, and 5) intraspecific variation in the previously mentioned morphological traits. Some species erroneously described as new were eventually categorized as species inquirenda, as in the case of *Raillietiella frenatus* (= *R. frenata*) from alien Mediterranean geckos (*Hemidactylus turcicus*) from Texas, United States (Pence and Selcer, 1988). However, based on the morphological study of Sakla and colleagues (2019), *R. frenata* was discovered actually to be *R. indica* and the host range included a native species, the green anole (*Anolis carolinensis*). Interestingly, morphological features used in pentastomid taxonomy vary as the parasite goes through different developmental stages in the definitive host, especially the morphology of the hooks, which can transition strikingly and progressively. Indeed, data on hooks can be meaningful only when compared between fully mature specimens and much of the morphological variation in hook measurements, the primary diagnostic traits of raillietiellid pentastomids, is due to development or instar stage (Kelehear et al., 2011; Sakla et al., 2019). In addition, type specimens in museum collections are usually fixed as permanent mounts in 10% formalin and/or without using DNA-grade (methanol-free) ethanol as a preservative. In this respect, specimens cannot be described using molecular techniques, a major concern in resolving the taxonomic status of already-described pentastomid species. In the future, it is suggested that taxonomic work should involve a combination of morphological techniques, integrating a consideration of body size, and a quantitative measurement of hook bluntness with complementary molecular techniques (Mätz-Rensing et al., 2012) to assist in the authentication of descriptions of new pentastomid taxa. In general, one needs to account for developmental- and host-induced morphological variation to accurately identify pentastomid species (Sakla et al., 2019).

The classification of the Pentastomida given here follows the works of Almeida and Christoffersen (1999), Junker (2002), Poore (2012), and Christoffersen and de Assis (2013) as well as the more recent classification of Walldorf (2015). There are 7 families within 4 orders, **Cephalobaenida** (1 family), **Raillietiellida** (1 family), **Reighardiida** (1 family), and **Porocephalida** (4 families).

Order Cephalobaenida Heymans, 1935

Cephalobaenid pentastomids possess an anterior mouth with hooks that lack a fulcrum and females possess a vulva at the anterior end of their abdomen. Hosts in this order include amphibians and reptiles (lizards and snakes). There is a single species of Cephalobaenida Heymons, 1922 within the family, Cephalobaenidae Heymons, 1922.

Order Raillietiellida Almeida and Christoffersen, 1999

This order includes 44 species and subspecies of parasites of amphibians, lizards, and snakes, including 1 family (Raillietiellidae Sambon, 1922) and 2 genera, *Raillietiella* Sambon, in Vaney and Sambon, 1910 with 43 species, and *Yelirella* Spratt, 2010 (monotypic). Poore (2012) provides an excellent discussion on the taxonomy of the genus *Raillietiella*.

Order Reighardiida Almeida and Christoffersen, 1999

Species of this order lack abdominal annuli and the poorly developed hook-bearing podia. They are parasites of marine birds and include a single family, Reighardiidae Heymons and Vitzhum, 1936, including the genera *Reighardia* Ward, 1899 (with 2 valid species) and *Hispania* J. Martínez et al., 2004 (monotypic).

Order Porocephalida Heymans, 1935

The Porocephalida is the largest order with 4 families, 11 genera, and 84 species. They have a mouth between or below the level of the anterior hooks with fulcrum (hooks bifurcate in the larvae), a single lamina in the adults, a spirally coiled abdomen in the females, with comparatively large radial coils, and a vulva near the posterior end of the body (Rego, 1984; Riley and Huchzermeyer, 1996; Junker et al., 2000). The number of annuli is usually a consistent and reliable diagnostic criterion in differentiating porocephalid genera (Riley and Self, 1979; 1980; 1981).

The families included in the order Porocephalida Heymans, 1935 include the following: **Linguatulidae** Leuckart, 1860 (with 6 species) are parasites of mammals, with 2 genera, **Linguatula** Frölich, 1789 (with 5 species), and **Neolinguatula** Haffner (in Haffner, Rack and Sachs, 1969) (monotypic). **Subtriquetridae** Fain, 1961 (with 4 species) are parasites of crocodilians with a single genus, *Subtriquetra* Sambon, 1922 (with 4 species). **Sebekidae** Sambon, 1922 (with 34 species) are parasites of chelonians and crocodilians and include 8 genera as follows: *Agema* Riley, Hill and Huchzermeyer, 1997 (monotypic); *Alofia* (Giglioli in Sambon), 1922 (with 7 species); *Diesingia* Heymons, 1935 (2 species); *Leiperia* Sambon, 1922 (with 3 species); *Pelonia* Junker and Boomker, 2002 (monotypic); *Sambonia* Noc and Giglioli, 1922 (with 4 species); *Sebekia* Sambon, 1922 (with 12 species); and *Selfia* Riley, 1994 (monotypic). **Porocephalidae** Sambon, 1922 (with 41 species) are parasites of snakes, with 8 genera as follows: *Armillifer* Sambon, 1922 (with 11 species); *Cubirea* Kishida, 1928 (with 2 species); *Elenia* Heymons, 1932 (monotypic); *Gigliolella* Chabaud and Choquet, 1954 (monotypic); *Kiricephalus* Sambon, 1922 (with 5 species); *Parasambonia* Stunkard and Gandal, 1968 (with 2 species); *Porocephalus* Humboldt, 1812 (with 9 species); and *Waddycephalus* Sambon, 1922 (with 10 species).

Pentastomid Clades (Apomorphies)

It is usually not too challenging, with some practice, to place a given unknown pentastomid specimen within a certain genus; however, identification to the specific level can be rather problematic as well as frustrating. Because many pentastomid taxa generally do not have very good diagnostic morphological benchmarks, it renders them frustratingly difficult to identify. There have only been 2 phylogenetic analyses of the group (Almeida and Christoffersen, 1999; Junker, 2002) as well as some other traditional diagnoses.

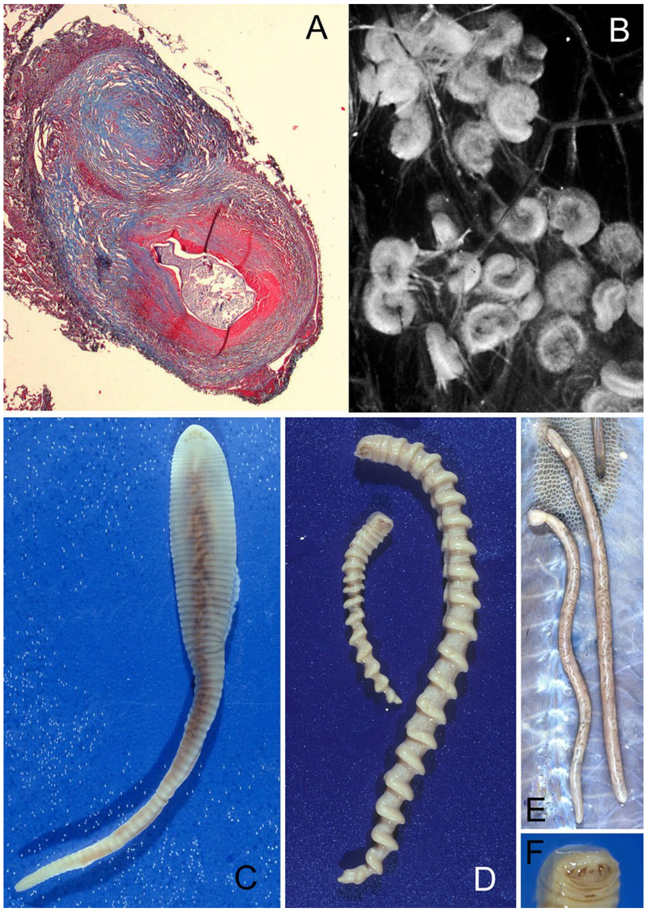


Figure 8A–B. Nymphal and adult pentastomids. A) Excised nodule on the pleural surface of the lung showing nymphal *Linguatula serrata*; B) coiled nymphs of *Armillifer* sp. in simian omentum; C) adult female *L. serrata*; D) adult male (small) and female (large) of *Armillifer* sp.; E) adult *Porocephalus crotali* in snake lung; F) anterior part of *Armillifer* with central mouth and 4 oral hooks. Source: D. Tappe and D. W. Büttner, 2009. License: CC BY.

Some Interesting Pentastomids

Porocephalus crotali (Humboldt, 1811) was originally described from a Venezuelan rattlesnake, *Crotalus durissus terrificus*, by Von Humboldt (1808). Since then, adults have been reported from the lungs (Figure 8E), trachea, and nasal passages of various North American rattlesnakes (*Crotalus* spp.), cottonmouths (*Agkistrodon piscivorus*), and Burmese pythons (*Python bivittatus*), with nymphs in the viscera of rodents that act as intermediate hosts (Penn, 1942; Riley and Self, 1979; Paré, 2008; Yabsley et al., 2015; Miller et al., 2017). It has also been reported from the Indian rat snake (*Ptyas mucosus*) in India (Bino Sundar et al., 2015). Adults have a cylindrical, segmented body with hooks arranged in the form of an arc or a trapeze. The internal organs occupy the entire abdomen. The nymphs are about 8–14 mm in length with a cylindrical and smooth annulated body. There are 2 unequal pairs of hooks that are located at the anterior ventral end around the mouth (Soulsby, 1982).

The life cycle of *Porocephalus crotali* was demonstrated experimentally by Esslinger (1962) and further studied by Riley (1981). When passed by the female parasite in the lung of a snake, eggs are fully developed and infective to the intermediate host. They are subsequently carried to the pharynx, swallowed, and passed out in the feces. Infection is typically without pathology in lung tissues or other tissues generally, either in the snake or the intermediate host, but very heavy infections may lead to death of the definitive host.

The adult *Linguatula serrata* (Fröhlich, 1789) (Figure 8B) is an unusual type of cosmopolitan pentastomid, as it is restricted to mammals and lives in the nasal passages, frontal sinuses, and tympanic cavity of meat-eating definitive hosts, such as domestic and wild canids and felids (such as, dogs, cats, foxes, and wolves) and other carnivores. Most herbivores, including domestic ruminants, serve as intermediate hosts. It has become cosmopolitan and has been recorded from humans in Africa, Europe, the Middle East, North America, South America, and some Caribbean islands. Rarely, severe nasopharyngeal linguatulosis appears in the Middle East when people ingest the nymphs of *L. serrata* in undercooked liver or lymph nodes from goats or sheep. The parasite then attempts to attach in the person's throat or nasopharynx resulting in halzoun or Marrara syndrome (Schacher et al., 1969). Some minor complications from this infection include frontal headaches, pain in the ears, nasal discharges, sneezing, and coughing; major physical difficulties include auditory canal abscesses, breathing difficulty, hemorrhages, facial paralysis and swelling, and occasionally asphyxiation and even death (Roberts and Janovy, 2012). In North America, nymphs of *L. serrata* have also been recovered from human mesenteric lymph nodes, the brain, lungs, and in the anterior chamber of the eye (Hunter and Higgins, 1960; Rendtorff et al., 1962).

Female *Linguatula serrata* can potentially grow up to 13 cm, while males only reach 2 cm (Figure 8C). They attach to the wall of the respiratory system by means of their mouth hooks. Females excrete thousands of eggs per day, up to 5 million (Hobmeier and Hobmeier, 1940). Certain stages are infectious for humans, where the larvae migrate into different organs away from the intestine. If the larvae are eaten by the final host, the larvae invade the nasal system and reach maturity within 6 to 7 months and live for about 15 months (patency period).

In the Old World, eating undercooked goat or sheep liver and mesenteric lymph nodes or the visceral organs of sheep, goats, cattle, and camels is the usual causation of the infection. Many of the snakes sold for human consumption at the rural bush meat markets in the Democratic Republic of the Congo are hosts of *A. armillatus* (Hardi et al., 2017).

Visceral pentastomiasis results when eggs are eaten and nymphs develop in visceral organs, causing pathology such as hepatic granuloma (Gardiner et al., 1984; Baird et al., 1988). Other complications include abscesses in the auditory canals, facial swelling, paralysis, and even asphyxiation and death.

Another unusual infection in humans of tropical Africa occurs when ***Armillifer armillatis*** Wyman, 1848 (Figure 1) infects visceral organs. Its typical definitive hosts are reptiles, mostly pythons, such as the reticulated python *Python reticulatus* and African rock python *P. sebae* while rodents are presumed to act as intermediate hosts (Christoffersen and de Assis, 2013; Murvanidze et al., 2015). Humans may become accidentally infected by the eggs, particularly if consuming (or otherwise contacting) infected snakes. Ingested eggs develop into nymphs that invade different visceral organs (especially the liver) causing a disease called porocephalosis. Most human infections are asymptomatic, whereas some can be debilitating, causing mechanical damage or hemorrhage (Boyce and Kazacos, 1991) or (though rarely) can even be lethal.

Main Sources of Information

A great deal of information on the Pentastomida can be found in the works of Heymons (1935), Hill (1948), Self and Kuntz (1966), Self (1969), Riley (1983; 1986), Almeida and Christoffersen (1999), Junker (2002), Kelehear and colleagues (2011; 2014), Poore (2012), and Christoffersen and de Assis (2013; 2015). These papers formed the basis of this chapter.

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Two very important people, the late J. Teague Self and John Riley were instrumental in mentoring the author and helping him understand the wonders of the Pentastomida. All of Self's specimens were sent to the American Museum of Natural History (New York, New York, United States). The literature in Self's library was sent to the Harold W. Manter Laboratory of Parasitology, University of Nebraska State Museum, Lincoln, Nebraska, United States.

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Preface

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IMPETUS FOR PREPARING THIS BOOK

The United Nations (UN) has declared education as a basic human right. One of the UN's sustainable development goals is a call to ensure "inclusive and equitable quality education and promotion of lifelong learning opportunities for all" (United Nations, 2023; see also WOERC, 2012). Depending on the specifics of their implementation, financing, and dissemination models, open educational resources (OERs) have the potential to help in the effort to achieve equitable learning across the globe (Orr et al., 2015; Lee and Lee, 2021; see also Bali et al., 2020).

Open educational resources are "teaching, learning, and research materials in any medium that reside in the public domain or have been released under an open license that permits their free use and re-purposing by others" (Creative Commons, 2014). Wiley (2020) cites the Creative Commons' framing of OERs as providing explicit permission to "retain, re-use, revise, remix, and redistribute" openly-accessible educational material.

Aside from the obvious benefit of saving students money, OERs have been shown to promote equity among students. Their use has been shown to contribute to maintenance or improvement of student success, especially with respect to retention in school, course completion, grade point average, and subsequent educational attainment (Colvard et al., 2018; Griffiths et al., 2022; Fischer et al., 2015).

HOW TO USE THIS BOOK

Scope

This is a textbook covering concepts in animal parasitology. It is meant to be used by students, teachers, professors, researchers, and members of the public who are interested in learning about animal parasite biology, systematics, taxonomy, zoogeography, and ecology. The primary intended audience is upper-level undergraduate or graduate university students who have knowledge of basic biology and, particularly, basic animal biology.

Organization of the Book

This textbook was conceived to fill a gap in educational materials about parasitology. One of the main goals in both teaching and learning about parasites and parasitology is to understand the diversity of parasites and of parasitism as a way of life on Earth. With this in mind, the editors made a decision to treat the organization of the book as though led by the organisms themselves—a sort of bottom-up approach—and present the parasitic organisms as a parasitologist will first find them in nature, as in: Where they tend to exist in relation to their host, and more specifically, whether inside or outside the host animal. Therefore, the book includes sections covering a few taxonomic groups representing just some of the millions of extant endoparasite (Greek: **endo** = inside; **para** = beside; **sitos** = food) and ectoparasite (Greek: **ektos** = outside) species.

Examples of endoparasites are parasitic trematodes or nematodes that live inside the respiratory systems or gastrointestinal tracts of their hosts. Ectoparasites include lice and ticks, almost all fleas, many mites, a few platyhelminths that live on echinoderms, and even some chordates like the lamprey and vampire bat. Some groups of animals, such as monogeneans and mites, are not neatly categorized and may live part of their lives as endoparasites and part of their lives as ectoparasites or as free-living animals. Despite these myriad variations, the editors believe that the basic division between endo- and ecto- serves well enough to organize the chapters.

In approaching the organization in this way, the focus of the book is primarily at the level of species and other lower level taxonomy as opposed to higher-level groupings which are notoriously constantly in flux. The classification of parasites based on phylogenies is useful and necessary to understand the diversity, diversification, and evolution of parasites, but classification does not dictate the book's primary organization. Instead, the concept of biodiversity of parasites and their animal hosts is the main factor that motivates the research and teaching in the Harold W. Manter Laboratory of Parasitology (University of Nebraska State Museum, Lincoln, Nebraska, United States) where editor Scott L. Gardner conducts his work. It is this push toward understanding biological diversity of parasites that overarchingly informs the organization of this book.

Note about Bibliographical References

The citations in the book are formatted to promote finding usable copies, they are not meant to serve as an archival resource. As such, and to save space, only the first four authors are listed for each resource. A digital object identifier (doi) is included whenever one could be found; but the dois are not hot linked since these links would often take readers to paywalled versions. Readers are encouraged instead to attempt to locate free, legal versions of the resources included in the references whenever possible. For example, free-to-read versions (and sometimes also open access versions) of the papers may be available in institutional repositories, on authors' personal websites, or from academic social media sites.

Note about Images

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Accompanying Glossary

A supplemental glossary is in the process of preparation. Until the glossary is completed, a work that may be used in its stead for many of the terms found in the book is the Dictionary of Invertebrate Zoology (Maggenti et al., 2017) available online for free: https://digitalcommons.unl.edu/zeabook/61/

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Although students of pre-medical studies, medical studies, or veterinary studies may use this text to learn foundational concepts in animal parasitology, it is not a medical or veterinary text. Further, it is not meant for any medical- or veterinary-related purposes whatsoever. When medical or veterinary topics are touched upon in the text, this is for educational purposes for those studying or interested in the biological sciences generally. *No medical or veterinary advice of any kind is offered or implied anywhere in this textbook. No* medical or veterinary diagnoses, treatments, or conclusions of any kind may be construed using the knowledge offered herein.

For studies specifically related to medical parasitology, readers may consult any of a number of qualified texts in the subject, including Medical Parasitology: A Textbook (Mahmud et al., 2017), Medical Parasitology (Satoskar, 2009), and Modern Parasitology: A Textbook of Parasitology, 2nd edition, (Cox et al., 2009), among others. Numerous medical periodicals are also appropriate sources of knowledge about medical parasitology. For medical diagnoses, qualified practitioners of medicine may be consulted directly.

For studies specifically related to veterinary parasitology, readers may consult any of a number of qualified texts in the subject, including Veterinary Parasitology, 4th edition, (Taylor et al., 2015) and Georgis' Parasitology for Veterinarians, 11th edition, (Bowman, 2020), among others. Numerous veterinary parasitology periodicals are also appropriate sources of knowledge about veterinary parasitology. For veterinary diagnoses, qualified practitioners of veterinary medicine may be consulted directly.

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Invitation to Review and Give Feedback

If any qualified readers would like to serve as a reviewer for any of the sections, you are invited to please contact one of the editors to discuss the possibility of being assigned the task of reviewing. You will be credited in revisions if you ultimately serve as a selected reviewer. In addition, if readers discover factual or typographical errors in the content, please contact one of the editors.

HOW THE BOOK WAS DEVELOPED

Origin of the Book

The concept for this book arose in 2018 around the time there was a concerted push to create open educational resources in universities (Austin, 2018; Sennott et al., 2015). This push seemed well-timed to the editors. In fact, the rising costs of textbooks has become a major problem for students to the point where it is basically untenable to expect students to pay for them anymore. The editors reasoned that it would be a good time to call on their esteemed and accomplished colleagues in academia to help create a new textbook in a massively collaborative endeavor, if they were willing to participate.

Also driving the idea of a new textbook, the seminal English-language parasitology textbook of our time, Gerald R. Schmidt and Larry S. Roberts' Foundations of Parasitology, 9th edition (Roberts et al., 2012), has recently gone out of print and there are no plans to update it. John J. Janovy, Jr., the lead author of the last several editions of the Schmidt and Roberts book, agreed that the creation of a new textbook was a good and timely idea.

Contributing to the decision to attempt the creation of a large-scale textbook project was the public access/open access platform available to the editors, namely, the Zea Books imprint of the University of Nebraska–Lincoln Libraries. In line with the OER ethos driving the creation of the content, this publishing imprint operates under a diamond open access model, such that neither the authors nor the readers have to pay to publish nor to read any work published as a Zea Book.

Development of the Book

At the time of the conception of the book idea, the edi-tors capitalized on the availability of visiting scholars in the Harold W. Manter Laboratory of Parasitology (Lincoln, Ne-braska, United States)—Griselda Pulido-Flores, Scott Monks, and Donald Gettinger, as well as local colleagues John J. Janovy, Jr. and Gabor Rácz, and student-colleagues Auggie Tsogtsaikhan Dursahinhan and Guin Drabik—and called to-gether a couple of meetings to discuss their idea with the group. They asked them to envision what they would like to see in a new textbook, one that would be available online for anyone with a computer connection to access for free. Among many other good ideas they shared, they suggested that the book could possibly include numerous links to other sources and interactive modules, and pointed out that the information may be kept more current than was possible with a printed volume. Colleagues Paul Royster, Linnea Fredrickson, Catherine Fraser Riehle, and Mary Bolin in the University of Nebraska–Lincoln Libraries (Lincoln, Nebraska, United States) also provided encouragement and expertise that helped the project on its way.

When preparing to solicit manuscripts for this project, based on the preliminary conversations with colleagues, the editors first prepared an outline of the concepts desired to have covered and then created streamlined style requirements (the instructions for authors and references style guide are available online here: https://digitalcommons.unl.edu/parasittext/). They then asked numerous colleagues—all experts in their subareas of parasitology—to contribute one or more sections based on the outline. So many of them agreed to write sections that it seemed that it really might be possible to create a high-quality work with the input of so many fine experts. Every one of them submitted manuscripts quickly.

The editors gave the authors quite a bit of latitude regarding how to approach their assignment to write sections. They provided an optional template to work from (available here), but use of this format was optional. They wanted the authors to be able to express themselves in the way they each felt was best to demonstrate knowledge of their respective areas of interest within the larger subject of animal parasitology. This liberal approach naturally resulted in some variation in presentation styles, which is perhaps a plus for the reader. It breaks up the tone and emphases from section to section, and the reader gets a sense of each author's different voice and approach. The editors have worked to retain much of each author's preferred style of presentation, but with normalizing of typography and other style elements to help the manuscript finally cohere as a unified whole.

Some of the sections were sent out for review. This review process was open, so the authors knew who was reviewing their work and the reviewers were aware that the authors knew they were reviewing. Reviewed sections are marked as such with the reviewer's name and affiliation. Whether reviewed or not, all of the sections were editor-reviewed by both editors: Sue Ann Gardner edited primarily for bibliographic details and style elements, and Scott L. Gardner edited primarily for content.

Delayed Publication

With best-laid plans, the editors started to review and edit the sections as soon as they were submitted. Then a great number of both quite-dire and less-dire issues arose that interfered with the ability to complete the editing and production in as timely a manner as intended (selected challenges include: The SARS-CoV-2 pandemic requiring remote teaching, a computer crash, a death in the family that then required weeks away from work and home, radical changes in administrations at the university, and other issues). With those issues finally receding in impact, five years after the project began, the book will be published at long last.

Demographic Data About the Authors

With editor Scott L. Gardner's large network of expert parasitologist colleagues, it was possible to seek out scholars who are experts in their field. While the first consideration when deciding who to invite to participate was expertise, the editors further worked toward the desired goal of equity and inclusion in the selection of authors. One result was a 1:2 ratio of women to men. While this does not represent parity, it is an improvement over days past when the majority of authors would likely have been men. Another result of efforts at equity and inclusion was the participation of many au-thors from outside the United States. Approximately 40% of authors are US-American and the remaining 60% are from one of 14 other countries (Argentina, Brazil, Australia, Japan, Mongolia, Bulgaria, Czechia, Germany, Hungary, Norway, Russia, Spain, Mexico, or Canada). Almost half of the authors (44%) do not have English as their first language.

Spanish-Language Version

In late 2018, the Office of the President at the University of Nebraska–Lincoln (Lincoln, Nebraska, United States) issued a call for proposals for Inclusive Excellence Development at the university. The editors were awarded funds to go toward translation of the textbook. With this, the editors partnered with a local professor of Spanish-language translation, Yoanna Esquivel Greenwood, who has created Spanish-language versions for numerous chapters in the book. Thanks to her work, and perhaps with the added input of some of the Spanish speakers among the authors, a comprehensive Spanish-language translation is forthcoming.

Acknowledgement of Authors' Contributions

From the Editors, Scott L. Gardner and Sue Ann Gardner

We sincerely thank all of the authors of this collaborative work. Your excellent contributions and dedication to the ad-vancement of knowledge of animal parasitology have the po-tential to positively change the lives of countless students and teachers worldwide.

While we were grappling with challenges and distractions that delayed the editing of the manuscript of this book, we lost a few of our esteemed author colleagues. We wish to posthumously acknowledge Bernie Fried, Akira Ito, and Robin M. Overstreet for what turned out to be some of their truly late-career contributions. We miss them, and we feel so fortunate to have benefitted from their long-acquired knowledge and their willingness to join in on this project.

Dedication

From the Editors, Scott L. Gardner and Sue Ann Gardner

This book is dedicated to **all** of our academic forebears and mentors who made this effort possible—some of whom are authors* of sections of the book! We can't list everyone, but we can provide a truncated list to commemorate some people especially.

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