49

NEMATA

Trichuroidea and Trichinelloidea (Superfamilies)

María del Rosario Robles and Rocío Callejón Fernández

Phylum Nemata
  Class Adenophorea
    Order Trichocephalida
      Superfamily Trichuroidea
      Superfamily Trichinelloidea

doi:10.32873/unl.dc.ciap049
2024. *In* S. L. Gardner and S. A. Gardner, eds. Concepts in Animal Parasitology. Zea Books, Lincoln, Nebraska, United States.

Chapter 49

Trichuroidea and Trichinelloidea (Superfamilies)

María del Rosario Robles

Centro de Estudios Parasitológicos y de Vectores
(CEPAVE), La Plata, Buenos Aires, Argentina
rosario@cepave.edu.ar

Rocío Callejón Fernández

Departamento de Microbiología y Parasitología, Facultad
de Farmacia, Universidad de Sevilla, Seville, Spain
callejon@us.es

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 difficult 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 Moravеč (2001a). The morphological characterization was obtained from Moravеč (2001a), Anderson et al. (2009), and contributions of authors of this chapter (Figures 1–6).

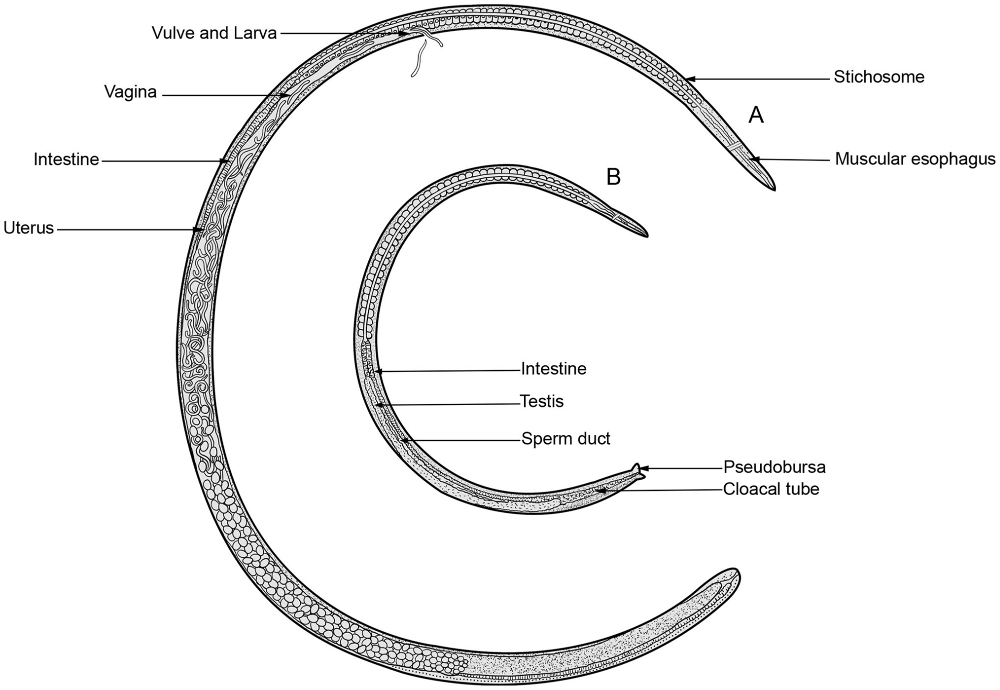

Figure 1. Diagrammatic representation of morphological structures of male and female specimens of *Trichinella spiralis*, as an example of Trichinelloidea. Source: K. Solas. License: CC BY-NC-SA 4.0.

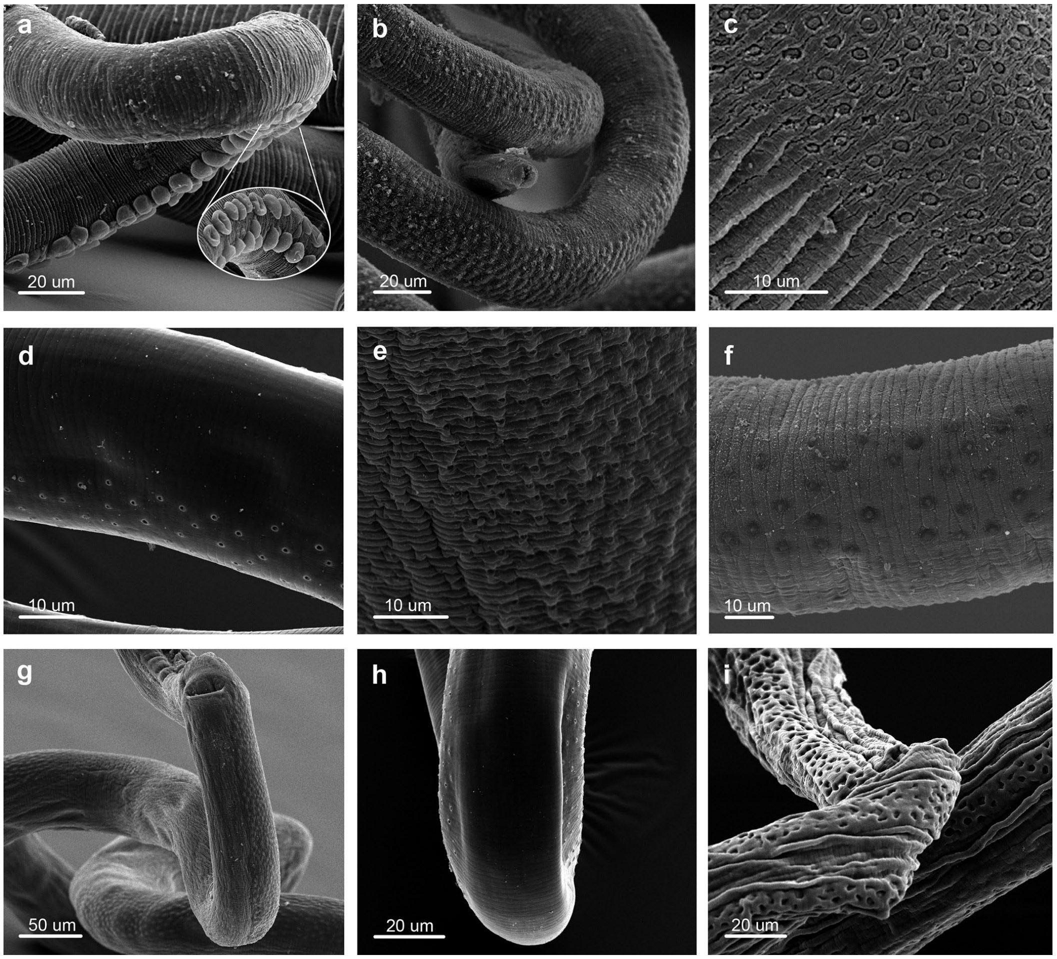

Figure 2. Scanning electron micrographs of bacillary bands from trichuroid species in rodents:

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.

Source: M. de R. Robles and R. Callejón Fernández. License: CC BY-NC-SA 4.0.

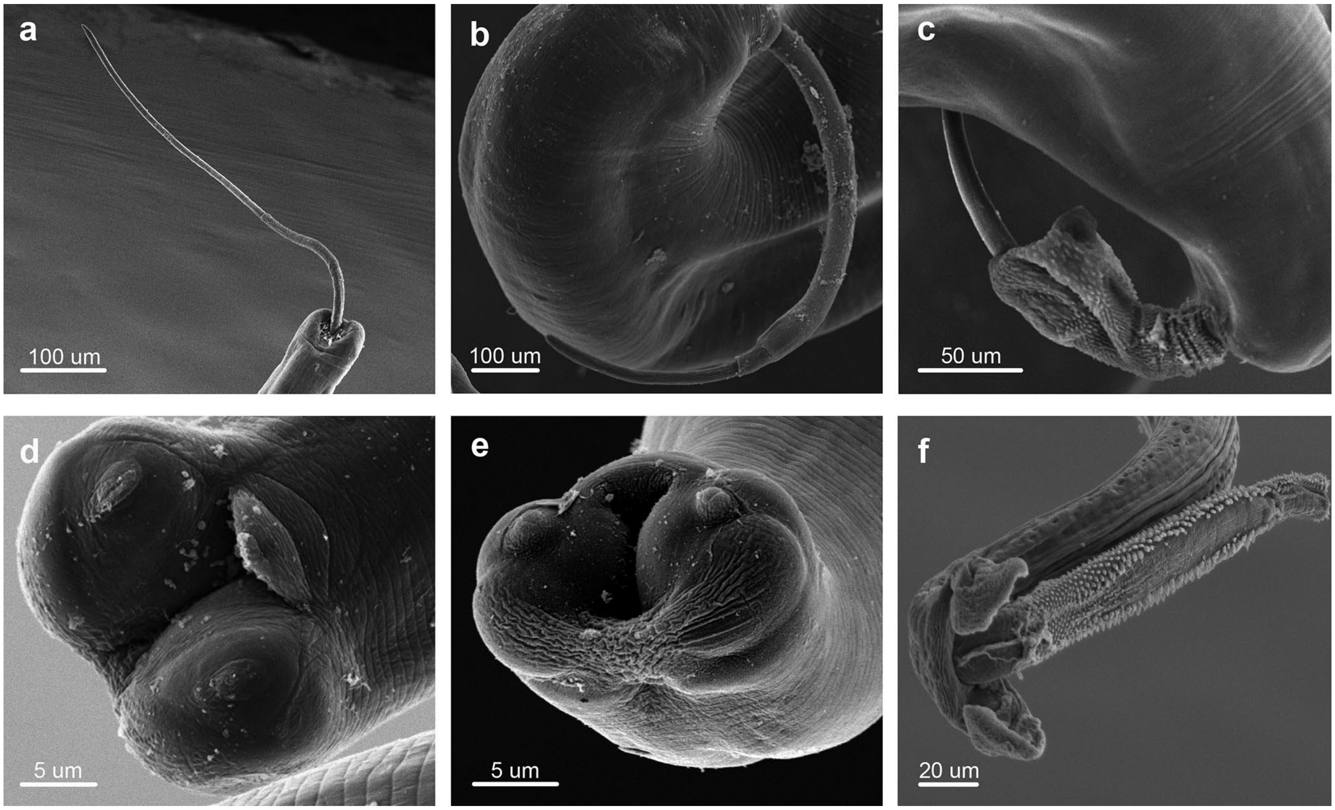

Figure 3. Scanning electron micrographs of accessory genital organs of males from trichuroid species in rodents: a) Ventral view of tail, spiny spicular sheath cylindrical and spicule everted in *Trichuris* sp. b) Lateral view of tail, spiny spicular sheath forming a distal spherical bulge in *Trichuris* 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.

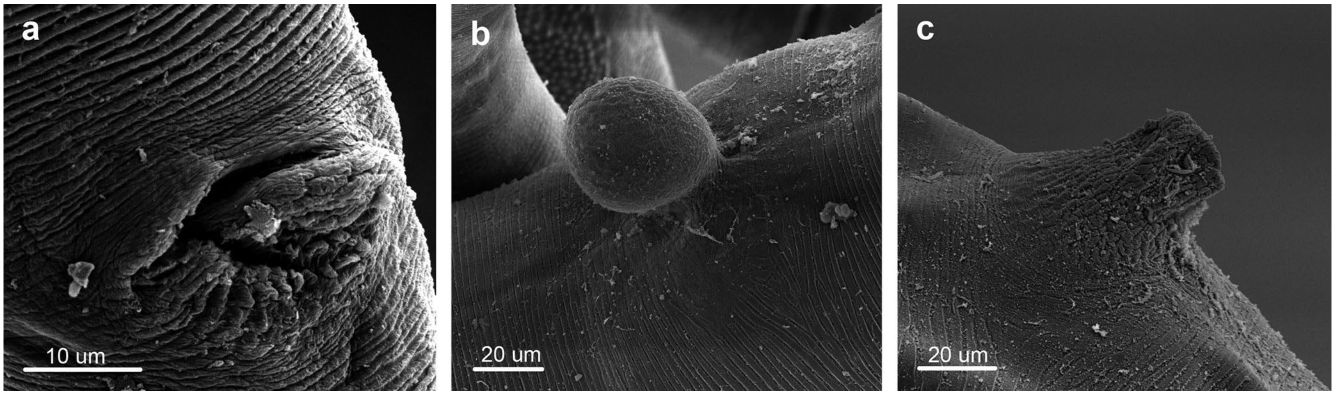

Figure 4. Scanning electron micrographs of characteristics of the vulva of the female from trichuroid species in rodents: a) Detail of non-protusive vulva in *Trichuris navonae* Robles, 2011. b) Detail of spherical protusive vulva in *Trichuris* sp. c) Detail of cylindrical protusive vulva in *Trichuris*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

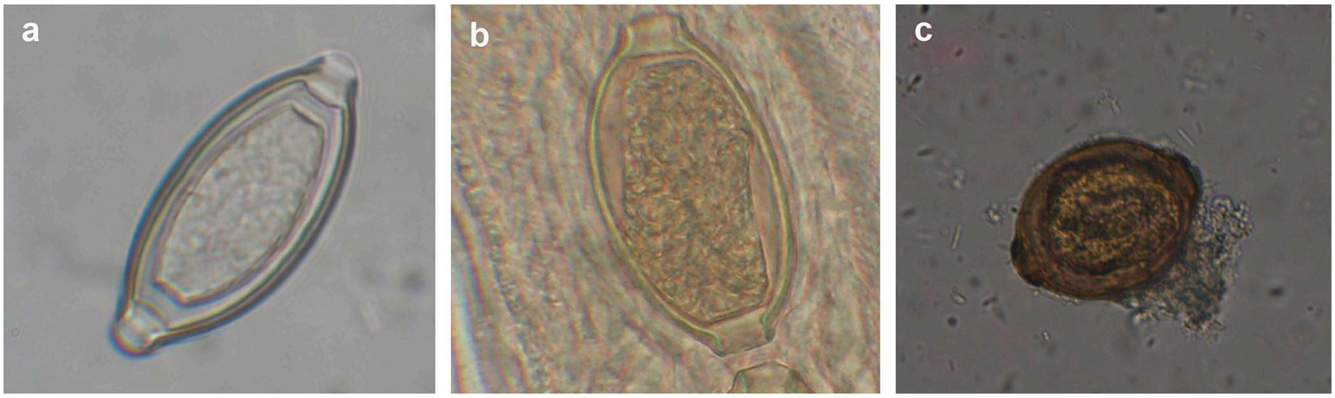

Figure 5. Micrographs of characteristics of eggs from trichuroid species in rodents: a) Detail of *Trichuris* sp. egg. b) Detail of *Eucoleus* sp. egg. c) Detail of *Anatrichosoma* sp. egg. Source: M. de R. Robles and R. Callejón Fernández. License: CC BY-NC-SA 4.0.

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**
Moravec (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; Moravec, 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

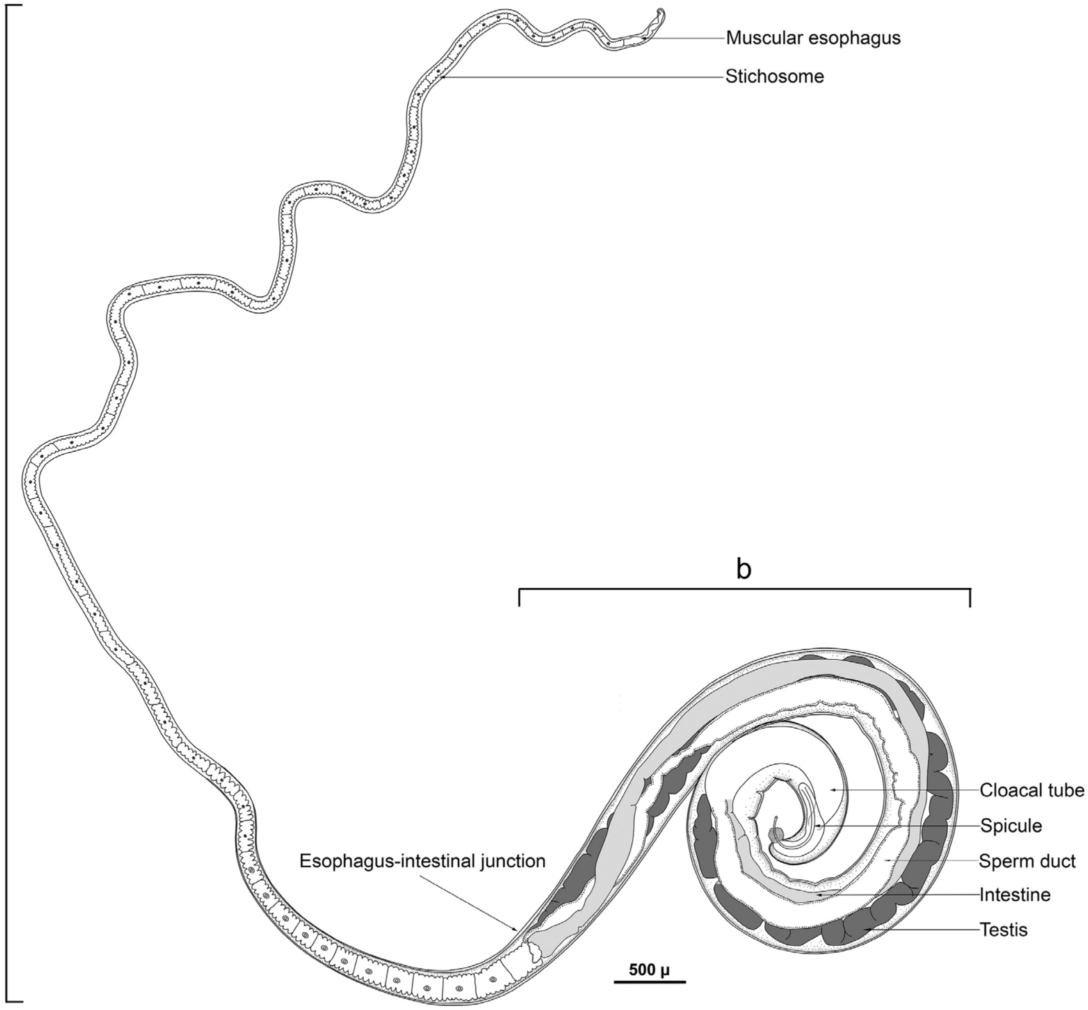

Figure 6. Diagrammatic representation of the morphological structures of a male specimen of *Trichuris muris* as an example of Trichuoidea. a) anterior part, b) posterior part. Source: A. Panti May. License: CC BY-NC-SA 4.0.

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-

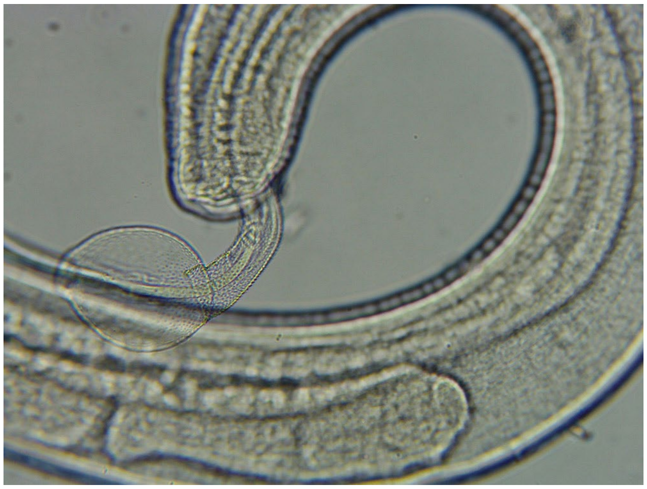

Figure 7. Posterior of a male of the genus *Trichuris* from a rodent. The spicule can be seen inside the spinose spicule sheath. The sheath is expanded at the distal end in this specimen. Source: S. L. Gardner, HWML. License: CC BY.

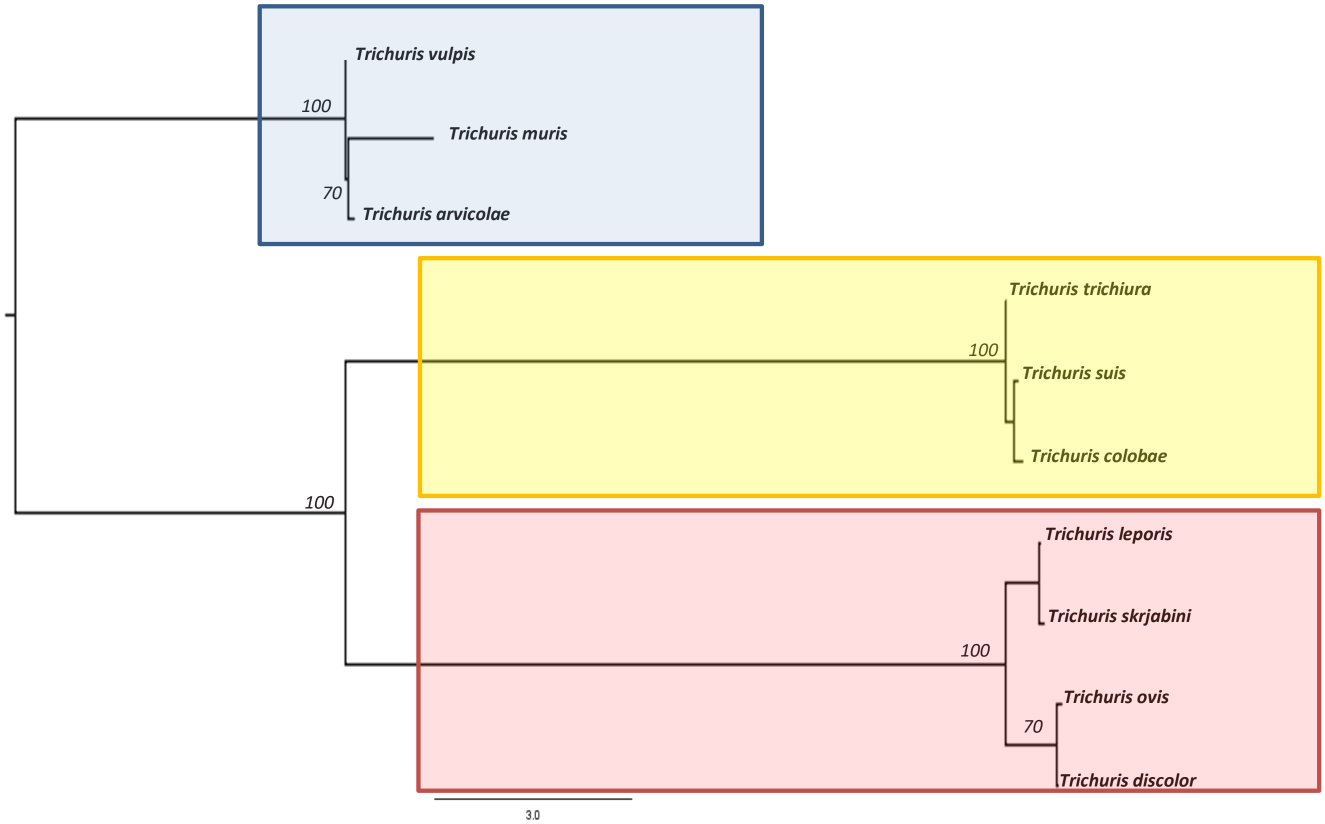

Figure 8. Dendrogram based on ITS1 sequences corresponding to different species of the genus *Trichuris*, with detail of host group. Source: Adapted from Cutillas et al., 2009. License: CC BY-NC-SA 4.0.

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-

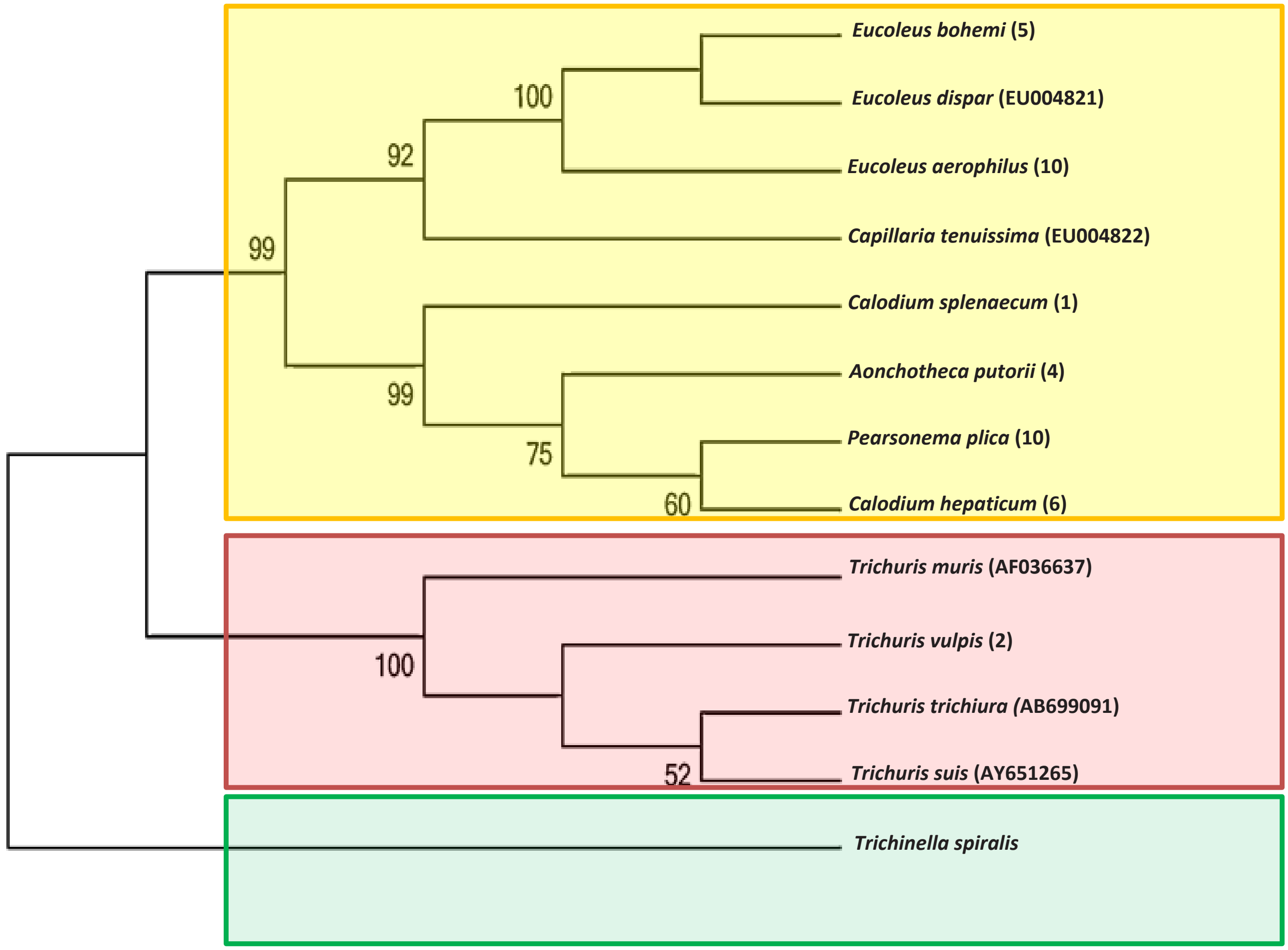

Figure 9. Dendrogram based on the partial sequences of the small subunit rRNA (18S rRNA) gene from species of the families Trichuridae and Capillariidae, with *T. spiralis* as outgroup. Source: Adapted from Guardone, 2013. License: CC BY-NC-SA 4.0.

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).

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.

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 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 Moravec (2001b). In that study, Moravec (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,

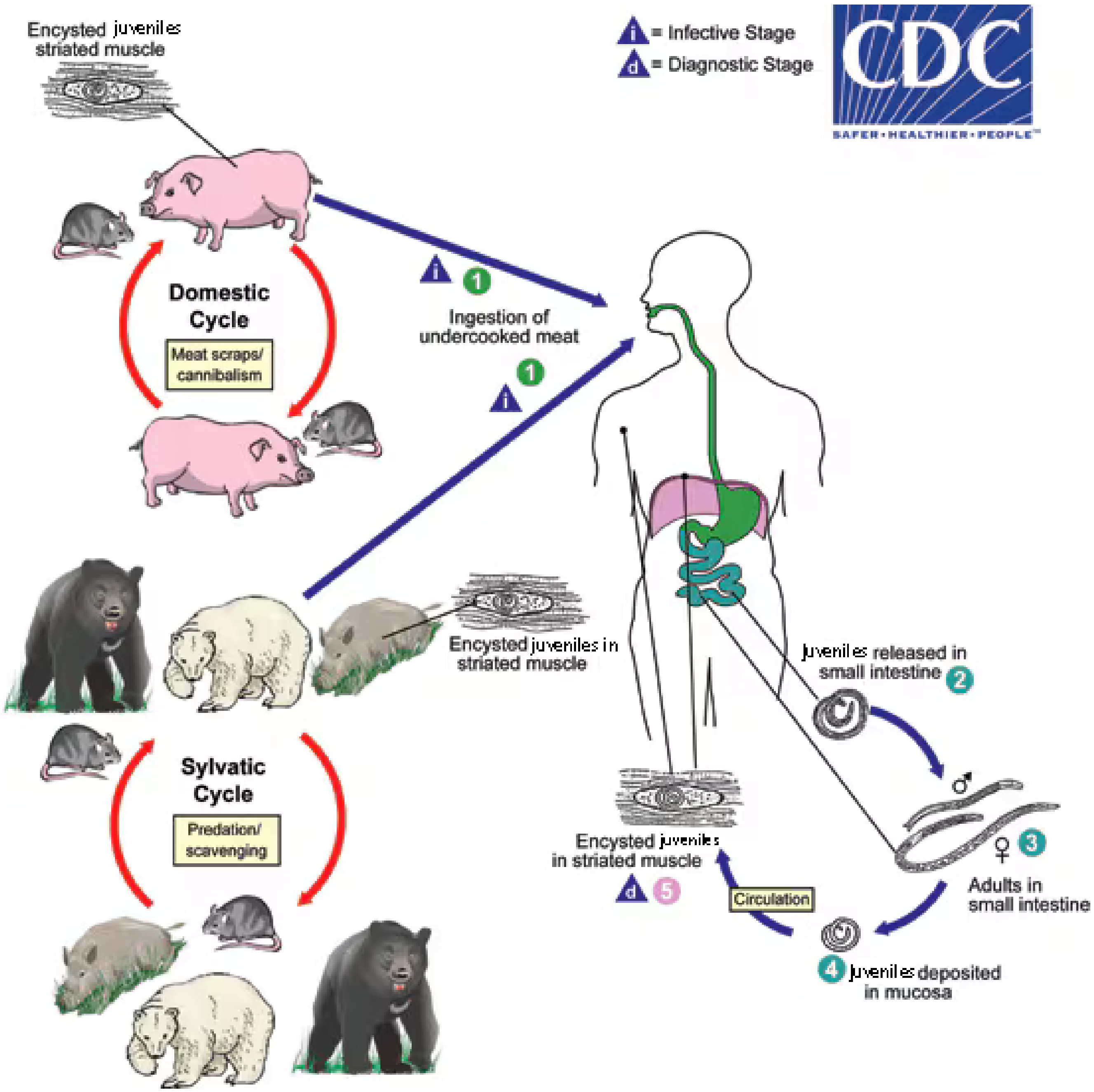

Figure 10. Adult worms and encysted juveniles develop within a single vertebrate host and an infected animal serves as a definitive host and potential intermediate host. A second host is required to perpetuate the life cycle. The domestic cycle most often involves pigs and anthropophilic rodents, but 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).

Literature Cited

Alicata, J. E. 1935. Early developmental stages of nematodes occurring in swine. United States Department of Agriculture, Technical Bulletin 489, 96 p. https://ageconsearch.umn.edu/record/164662/files/tb489.pdf

Anderson, R. C. 2000. Nematode Parasites of Vertebrates: Their Development and Transmission, 2nd edition. CAB International, Wallingford, United Kingdom, 650 p.

Anderson, R. C., A. G. Chabaud, and S. Willmott. 2009. Keys to the Nematode Parasites of Vertebrates, Archival Volume. CAB International, Wallingford, United Kingdom, 463 p.

Beer, R. J. S. 1973. Studies on the biology of the life-cycle of *Trichuris suis* Schrank 1788. Parasitology 67: 253–262. doi: 10.1017/s0031182000046497

Betson, M., M. J. Søe, and P. Nejsum. 2015. Human trichuriasis: Whipworm genetics, phylogeny, transmission and future research directions. Current Tropical Medicine Reports 2: 209–217. doi: 10.1007/s40475-015-0062-y

Bundy, D. A. P., and E. S. Cooper. 1989. *Trichuris* and trichuriasis in humans. Advances in Parasitology 28: 107–173. doi: 10.1016/s0065-308x(08)60332-2

Buńkowska-Gawlik, K., A. Perec-Matysiak, K. Burzyńska, and J. Hildebrand. 2017. The molecular identification of *Calodium hepaticum* in the wild brown rat (*Rattus norvegicus*) in Poland. Acta Parasitologica 62: 728. doi: 10.1515/ap-2017-0087

Callejón, R., A. Halajian, and C. Cutillas. 2017. Description of a new species, *Trichuris ursinus* n. sp. (Nematoda: Trichuridae) from *Papio ursinus* Keer, 1792 from South Africa. Infection, Genetics and Evolution 51: 182–193. doi: 10.1016/j.meegid.2017.04.002

Callejón, R., S. Nadler, M. de Rojas, A. Zurita, et al. 2013. Molecular characterization and phylogeny of whipworm nematodes inferred from DNA sequences of *cox1* mtDNA and 18S rDNA. Parasitology Research 112: 3,933–3,949. doi: 10.1007/s00436-013-3584-z

Callejón, R., M. del R. Robles, C. J. Panei, and C. Cutillas. 2016. Molecular diversification of *Trichuris* spp. from Sigmodontinae (Cricetidae) rodents from Argentina based on mitochondrial DNA sequences. Parasitology Research 115: 2,933–2,945. doi: 10.1007/s00436-016-5045-y

Cavallero, S., C. De Liberato, K. G. Friedrich, D. Di Cave, et al. 2015. Genetic heterogeneity and phylogeny of *Trichuris* spp. from captive non-human primates based on ribosomal DNA sequence data. Infection, Genetics and Evolution 34: 450–456. doi: 10.1016/j.meegid.2015.06.009

Chen, C.-Y., W.-C. Hsieh, and T.-L. Chen. 1989. Case report of human infection with *Capillaria philippinensis*. Taiwan Epidemiology Bulletin 5: 93. https://www.cdc.gov.tw/En/File/Get/3FAXcsldlTHQh3zzQO3yJQ

Cliffe, L. J., and R. K. Grencis. 2004. The *Trichuris muris* system: A paradigm of resistance and susceptibility to intestinal nematode infection. Advances in Parasitology 57: 255–307. doi: 10.1016/S0065-308X(04)57004-5

Cooper, E., C. Whyte-Alleng, J. Finzi-Smith, and T. MacDonald. 1992. Intestinal nematode infections in children: The pathophysiological price paid. Parasitology 104 (Supplement): S91–S103. doi: 10.1017/s0031182000075272

Cross, J. H. 1992. Intestinal capillariasis. Clinical Microbiology Reviews 5: 120–129. doi: 10.1128/CMR.5.2.120

Cutillas, C., R. Callejón, M. De Rojas, B. Tewes, et al. 2009. *Trichuris suis* and *Trichuris trichiura* are different nematode species. Acta Tropica 111: 299–307. doi: 10.1016/j.actatropica.2009.05.011

Di Cesare, A., G. Castagna, O. Otranto, S. Meloni, et al. 2012. Molecular diagnosis of *Capillaria aerophila*, an agent of canine and feline pulmonary capillariosis. Journal of Clinical Microbiology 50: 1,958–1,963. doi: 10.1128/JCM.00103-12

Doležalová, J., M. Oborník, E. Hajdušková, M. Jirků, et al. 2015. How many species of whipworms do we share? Whipworms from man and other primates form two phylogenetic lineages. Folia Parasitologica 62: 1–12. doi: 10.14411/fp.2015.063

Eberhardt, A. T., M. del R. Robles, L. D. Monje, P. M. Beldomenicoa, et al. 2018. A new *Trichuris* species (Nematoda: Trichuridae) from capybaras: Morphological-molecular characterization and phylogenetic relationships. Acta Tropica 190: 244–252. doi: 10.1016/j.actatropica.2018.11.029

El-Dib, N. A., A. A. El-Badry, T. H. Ta-Tang, and J. M. Rubio. 2015. Molecular detection of *Capillaria philippinensis*: An emerging zoonosis in Egypt. Experimental Parasitology 154, 127–133. doi: 10.1016/j.exppara.2015.04.011

Fahmy, M. A. 1954. An investigation on the life cycle of *Trichuris muris*. Parasitology 44: 50–57. doi: 10.1017/s003118200001876x

Fantozzi, M. C., M. del R. Robles, F. E. Peña, L. R. Antoniazzi, et al. 2018. *Calodium hepaticum* (Nematoda: Capillariidae) in wild rodent populations from Argentina. Parasitology Research 117: 2,921–2,926. doi: 10.1007/s00436-018-5983-7

Faust, E. C., P. C. Beaver, and R. Jung. 1975. Animal Agents and Vectors of Human Disease, 4th edition. Lea and Febiger, Philadelphia, United States, 479 p.

Fugassa, M. H., R. S. Petrigh, and M. del R. Robles. 2014. Reexaminación paleoparasitológica de coprolitos de roedores procedentes de la Patagonia argentina considerando información parasitológica actual. [= Paleoparasitological reexamination of rodent coprolites from Argentinian Patagonia, considering current parasitological data.] Revista Argentina de Zoonosis y Enfermedades Infecciosas Emergentes VIII: 22–23. http://sedici.unlp.edu.ar/handle/10915/118709

Gasser, R. B., M. Hu, Y. G. A. El-Osta, D. S. Zarlenga, et al. 2004. Nonisotopic single-strand conformation polymorphism analysis of sequence variability in ribosomal DNA expansion segments within the genus *Trichinella* (Nematoda: Adenophorea). Electrophoresis 25: 3,357–3,364. doi: 10.1002/elps.200405985

Gomberg, H. J., S. E. Gould, C. S. Hertz, and J. B. Villella. 1957. Studies on *Trichinella spiralis*, VI: Effects of cobalt-60 and X-ray on morphology and reproduction. American Journal of Pathology 33: 79–105.

Guardone, L., P. Deplazes, F. Macchioni, J. M. Mag, et al. 2013. Ribosomal and mitochondrial DNA analysis of Trichuridae nematodes of carnivores and small mammals. Veterinary Parasitology 197: 364–369. doi: 10.1016/j.vetpar.2013.06.022

Hill, H. C. 1957. The survival of swine whipworm eggs in hog lots. Journal of Parasitology 43: 104. doi: 10.2307/3274772

Hodda, M. 2022. Phylum Nematoda: Trends in species descriptions, the documentation of diversity, systematics, and the species concept. Zootaxa 1668: 265–293. doi: 10.11646/zootaxa.5114.1.2

Hoghooghi-Rad, N., S. Maraghi, and A. Narenj-Zadeh. 1987. *Capillaria philippinensis* infection in Khoozestan Province, Iran [Case report]. American Journal of Tropical Medicine and Hygiene 37: 135–137. doi: 10.4269/ajtmh.1987.37.135

Honisch, M., and O. Krone. 2008. Phylogenetic relationships of Spiruromorpha from birds of prey based on 18S rDNA. Journal of Helminthology 82: 129–133. doi: 10.1017/S0022149X08912359

Juncker-Voss, M., H. Prosl, H. Lussy, U. Enzenberg, et al. 2000. Serological detection of *Capillaria hepatica* by indirect immunofluorescence assay. Journal of Clinical Microbiology 38: 431–433. doi: 10.1128/JCM.38.1.431-433.2000

Kang, G., M. Mathan, B. S. Ramakrishna, E. Mathai, et al. 1994. Human intestinal capillariasis: First report from India. Transactions of the Royal Society of Tropical Medicine and Hygiene 88: 204. doi: 10.1016/0035-9203(94)90296-8

Khalifa, R. M., A. A. Sakla, and A. A. Hassan. 2000. *Capillaria philippinensis*: A human intestinal nematode newly introduced to upper Egypt. Helminthologia 37: 23–27.

Krivokapich, S. J., E. Pozio, G. M. Gatti, C. L. Prous, et al. 2012. *Trichinella patagoniensis* n. sp. (Nematoda), a new encapsulated species infecting carnivorous mammals in South America. International Journal for Parasitology 42: 903–910. doi: 10.1016/j.ijpara.2012.07.009

La Rosa, G., G. Marucci, and E. Pozio. 2003. Biochemical analysis of encapsulated and non-encapsulated species of Trichinella (Nematoda, Trichinellidae) from cold-and warm-blooded animals reveals a high genetic divergence in the genus. Parasitology Research 91: 462–466. doi: 10.1007/s00436-003-0981-8

Lee, S.-H., S.-T. Hong, J.-Y. Chai, W.-H. Kim, et al. 1993. A case of intestinal capillariasis in the Republic of Korea. American Journal of Tropical Medicine and Hygiene 48: 542–546. doi: 10.4269/ajtmh.1993.48.542

Li, R. W., S. Wu, W. Li, K. Navarro, et al. 2012. Alterations in the porcine colon microbiota induced by the gastrointestinal nematode *Trichuris suis*. Infection and Immunity 80: 2,150–2,157. doi: 10.1128/IAI.00141-12

Liu, G.-H., R. B. Gasser, A. Su, P. Nejsum, et al. 2012a. Clear genetic distinctiveness between human- and pig-derived *Trichuris* based on analyses of mitochondrial datasets. PLoS Neglected Tropical Diseases 6: e1539. doi: 10.1371/journal.pntd.0001539

Liu, X., Y. Song, N. Jiang, J. Wang, et al. 2012b. Global gene expression analysis of the zoonotic parasite *Trichinella spiralis* revealed novel genes in host parasite interaction. PLoS Neglected Tropical Diseases 6: e1794. doi: 10.1371/journal.pntd.0001794

Luttermoser, G. W. 1938. An experimental study of *Capillaria hepatica* in the rat and the mouse. American Journal of Hygiene 27: 321–340. doi: 10.1093/oxfordjournals.aje.a118395

Maggenti, A. 1981. General Nematology. Springer-Verlag, New York, New York, United States, 372 p.

Miyazaki, I. 1991. An Illustrated Book of Helminthic Zoonoses. International Medical Foundation of Japan, Tokyo, Japan, 494 p.

Moravec, F. 2001a. Trichinelloid Nematodes Parasitic in Cold-Blooded Vertebrates. Academia, Prague, Czech Republic, 430 p.

Moravec, F. 2001b. Redescription and systematic status of *Capillaria philippinensis*: An intestinal parasite of human beings. Journal of Parasitology 87: 161–164. doi: 10.2307/3285194

Moravec, F., J. Prokopic, and A. V. Shlikas. 1987. The biology of nematodes of the family Capillariidae Neveu-Lemaire, 1936. Folia Parasitologia 34: 39–56.

Nissen, S., A. Al-Jubury, T. V. Hansen, A. Olsen, et al. 2012. Genetic analysis of *Trichuris suis* and *Trichuris trichiura* recovered from humans and pigs in a sympatric setting in Uganda. Veterinary Parasitology 188: 68–77. doi: 10.1016/j.vetpar.2012.03.004

Nokes, C., S. M. Grantham-McGregor, A. W. Sawyer, E. S. Cooper, et al. 1992. Parasitic helminth infection and cognitive function in school children. Proceedings of Royal Society of London 247: 77–81. doi: 10.1098/rspb.1992.0011

Orihel, T. C. 1970. Anatrichosomiasis in African monkeys. Journal of Parasitology 56: 982–985.

Pence, D. B., and M. D. Little. 1972. *Anatrichosoma buccalis* sp. n. (Nematoda: Trichosomoididae) from the buccal mucosa of the common opossum, *Didelphismarsupialis* L. Journal of Parasitology 58: 767–773. doi: 10.2307/3278311

Pozio, E. 2016. Adaptation of *Trichinella* spp. for survival in cold climates. Food Water of Parasitology 4: 4–12. doi: 10.1016/j.fawpar.2016.07.001

Pozio, E. 2000. Factors affecting the flow among domestic synanthropic and sylvatic cycles of *Trichinella*. Veterinary Parasitology 93: 241–262. doi: 10.1016/s0304-4017(00)00344-7

Pozio, E., and D. S. Zarlenga. 2005. Recent advances on the taxonomy, systematics and epidemiology of *Trichinella*. International Journal for Parasitology 35: 1,191–1,204. doi: 10.1016/j.ijpara.2005.07.012

Pozio, E., E. Hoberg, G. La Rosa, and D. S. Zarlenga. 2009. Molecular taxonomy, phylogeny and biogeography of nematodes belonging to the *Trichinella* genus. Infection, Genetics and Evolution 9: 606–616. doi: 10.1016/j.meegid.2009.03.003

Pradatsundarasar, A., K. Pecharanónd, C. Chintanawóngs, and P. Ungthavórn. 1973. The first case of intestinal capillariasis in Thailand. Southeast Asian Journal of Tropical Medicine and Public Health 4: 131–134.

Ravasi, D. F., M. J. O'Riain, F. Davids, and N. Illing. 2012. Phylogenetic evidence that two distinct *Trichuris* genotypes infect both humans and non-human primates. PLoS One 7: e44187. doi: 10.1371/journal.pone.0044187

Roberts, L. S., and J. J. Janovy, Jr. 2009. Foundations of Parasitology, 8th edition. McGraw-Hill, New York, New York, United States, 720 p.

Robles, M. del R., O. Bain, and G. T. Navone. 2012. Description of a new Capillariinae (Nematoda: Trichuridae) from *Scapteromys aquaticus* (Cricetidae: Sigmodontinae) from Buenos Aires, Argentina. Journal of Parasitology 98: 627–639. doi: 10.1645/GE-2991.1

Robles, M. del R., M. C. Carballo, and G. T. Navone. 2008. A new species of *Liniscus* (Nematoda: Trichuridae) from *Oxymycterus rufus* and *Akodon azarae* (Cricetidae: Sigmodontinae) in Buenos Aires Province, Argentina. Journal of Parasitology 94: 909–917. doi: 10.1645/GE-1375.1

Robles, M. del R., C. Cutillas, and R. Callejón. 2018. Morphological-molecular characterization and phylogenetic relationships of a new *Trichuris* species (Nematoda: Trichuridae) parasitic on *Holochilus chacarius* (Cricetidae: Sigmodontinae) from the Chaco ecoregion (Argentina). Infection, Genetics and Evolution, 58: 66–76. doi: 10.1016/j.meegid.2017.11.029

Robles, M. del R., M. C. Cutillas, C. J. Panei, and R. Callejón. 2014. Morphological and molecular characterization of a new *Trichuris* species (Nematoda: Trichuridae), and phylogenetic relationships of *Trichuris* species of cricetid rodents from Argentina. PLoS One 9: e112069. doi: 10.1371/journal.pone.0112069

Rylková, K., E. Tůmová, A. Brožová, I. Jankovská, et al. 2015. Genetic and morphological characterization of *Trichuris* *myocastoris f*ound in *Myocastor coypus* in the Czech Republic. Parasitology Research 114: 3,969–3,975. doi: 10.1007/s00436-015-4623-8

Shikhobalova, N. P. 1937. [Experimental study of the chemotherapy of trichocephalosis, I: Trichocephalosis of white mice.] Meditsinskaia Parazitologiia I Parazitarnye Bolezni 6: 389–400. [In Russian.]

Spratt, D. M., and G. R. Singleton. 2001. *Hepatic capillariasis*. *In* W. M. Samuel, M. Pybus, and A. A. Kocan, eds. Parasitic Diseases of Wild Mammals. Iowa State University Press, Ames, Iowa, United States, p. 365–379.

Stewart, G. L., and S. H. Giannini. 1982. *Sarcocystis*, *Trypanosoma*, *Toxoplasma*, *Brugia*, *Ancylostoma*, and *Trichinella* spp.: A review of the intracellular parasites of striated muscle. Experimental Parasitology 53: 406–447. doi: 10.1016/0014-4894(82)90083-2

Tamaru, M., S. Yamaki, L. Angsinco-Jiménez, and H. Sato. 2015. Morphological and molecular genetic characterization of three *Capillaria* spp. (*Capillaria anatis, Capillaria pudendotecta*, and *Capillaria madseni*) and *Baruscapillaria obsignata* (Nematoda: Trichuridae: Capillariinae) in avians. Parasitology Research 114: 4,011–4,022. doi: 10.1007/s00436-015-4629-2

Wright, K. A. 1961. Observations on the life cycle of *Capillaria hepatica* (Bancroft, 1893) with a description of the adult. Canadian Journal of Zoology 39: 167–182. doi: 10.1139/z61-022

Yamaguti, S. 1961. Systema Helminthum, Volume 3: The Nematodes of Vertebrates. Interscience, New York, New York, United States, 1,261 p.

Youssef, F. G., E. M. Mikhail, and N. S. Mansour. 1989. Intestinal capillariasis in Egypt: A case report. American Journal of Tropical Medicine and Hygiene 40: 195–196. doi: 10.4269/ajtmh.1989.40.195

Zarlenga, D. S., B. Rosenthal, E. P. Hoberg, and M. Mitreva. 2009. Integrating genomics and phylogenetics in understanding the history of *Trichinella* species. Veterinary Parasitology 159: 210–213. doi: 10.1016/j.vetpar.2008.10.061

Zarlenga, D. S., B. M. Rosenthal, G. La Rosa, E. Pozio, et al. 2006. Post-Miocene expansion, colonization, and host switching drove speciation among extant nematodes of the archaic genus *Trichinella*. Proceedings of the National Academy of Sciences of the United States of America 103: 7,354–7,359. doi: 10.1073/pnas.0602466103

Zhu, X., D. M. Spratt, I. Beveridge, P. Haycock, et al. 2000. Mitochondrial DNA polymorphism within and among species of *Capillaria* sensu lato from Australian marsupials and rodents. International Journal for Parasitology 30: 933–938. doi: 10.1016/s0020-7519(00)00076-x

Supplemental Reading

Cutillas, C., M. de Rojas, A. Zurita, R. Oliveros, et al. 2014. *Trichuris colobae* n. sp. (Nematoda: Trichuridae), a new species of *Trichuris* from *Colobus guereza kikuyensis*. Parasitology Research 113: 2,725–2,732. doi: 10.1007/s00436-014-3933-6

D'Elía, G., and U. F. J. Pardiñas. 2015. Subfamily Sigmodontinae Wagner, 1843. *In* J. L. Patton, U. F. J. Pardiñas, and G. D'Elía, eds. Mammals of South America, Volume 2: Rodents. University of Chicago Press, Chicago, Illinois, United States, p. 63–70.

De Ley, P., and M. L. Blaxter. 2004. A new system for Nematoda: Combining morphological characters with molecular trees, and translating clades into ranks and taxa. *In* R. Cook and D. J. Hunt, eds. Nematology Monographs and Perspectives, Volume 2: Proceedings of the Fourth International Congress of Nematology (June 8–13, 2002, Tenerife, Spain), p. 633–653.

De Ley, P., and M. L. Blaxter. 2002. Systematic position and phylogeny. *In* D. Lee, ed. The Biology of Nematodes. Harwood Academic, Reading, United Kingdom, p. 1–30.

Gonçalves, A. Q., C. Ascaso, I. Santos, P. T. Serra, et al. 2012. *Calodium hepaticum*: Household clustering transmission and the finding of a source of human spurious infection in a community of the Amazon region. PLoS Neglected Tropical Diseases 6: e1943. doi: 10.1371/journal.pntd.0001943

Holterman, M., A. Van der Wurff, S. Van den Elsen, H. Van Megen, et al. 2006. Phylum-wide analysis of SSU rDNA reveals deep phylogenetic relationships among nematodes and accelerated evolution toward crown clades. Molecular Biology and Evolution 23: 1,792–1,800. doi: 10.1093/molbev/msl044

Meldal, B. H., N. J. Debenham, P. De Ley, I. De Ley, et al. 2007. An improved molecular phylogeny of the Nematoda with special emphasis on marine taxa. Molecular Phylogenetics and Evolution 42: 622–636. doi: 10.1016/j.ympev.2006.08.025

Mitreva, M., and D. P. Jasmer. 2008. Advances in the sequencing of the genome of the adenophorean nematode *Trichinella spiralis*. Parasitology 135: 869–880. doi: 10.1017/S0031182008004472

Pozio, E., and K. D. Murrell. 2006. Systematics and epidemiology of *Trichinella*. Advances in Parasitology 63: 367–439. doi: 10.1016/S0065-308X(06)63005-4

Robles, M. del R., G. T. Navone, and J. Notarnicola. 2006. A new species of *Trichuris* (Nematoda: Trichuriidae) from Phyllotini Rodents in Argentina. Journal of Parasitology 92: 100–104. doi: 10.1645/GE-GE-552R.1

Romashov, B. V. 1983. [*Hepaticola hepatica* (Nematoda, Capillariidae): Details of the life cycle. *In* Parasitological Studies in Nature Reserves]. TsNIL Glavokhoty RSFSR, Moscow, Soviet Union, p. 49–58. [In Russian.]

Schwartz, B. 1926. A possible new source of infection of man with *Trichuris*, with a consideration of the question of physiological varieties among helminths. Archiv für Schiffs- und Tropen-Hygiene 9: 544–577.

Singleton, G. R., and H. I. McCallum. 1990. The potential of *Capillaria hepatica* to control mouse plagues. Parasitology Today 6: 190–193. doi: 10.1016/0169-4758(90)90354-7

Soulsby, E. J. L. 1982. Helminths, Arthropods, and Protozoa of Domesticated Animals, 7th edition. Bailliere Tindall, London, United Kingdom, 809 p.

Tenora, F., I. Hovorka, and D. Hejlková. 1988. A supplement to the scanning electron microscopy of some *Trichocephalus* spp. (Nematoda). Helminthologia 25: 227–234.

Van Megen, H., S. van den Elsen, M. Holterman, G. Karssen, et al. 2009. A phylogenetic tree of nematodes based on about 1,200 full-length small subunit ribosomal DNA sequences. Nematology 11: 927–950. doi: 10.1163/156854109X456862

Vogelsang, E. G., and J. Espin. 1949. Dos nuevos huespedes para *Capillaria hepatica* (Bancroft, 1893) Travassos 1915; nutria (*Myopotamus coypus*) y el raton mochilero (*Akodon venezuelensis*). Revista de Medicina Veterinaria y Parasitologia 8: 73–78.