53

Nemata

Spirurida (Order)

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Phylum Nemata

Order Spirurida

doi:10.32873/unl.dc.ciap053
2024. *In* S. L. Gardner and S. A. Gardner, eds. Concepts in Animal Parasitology. Zea Books, Lincoln, Nebraska, United States.

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).

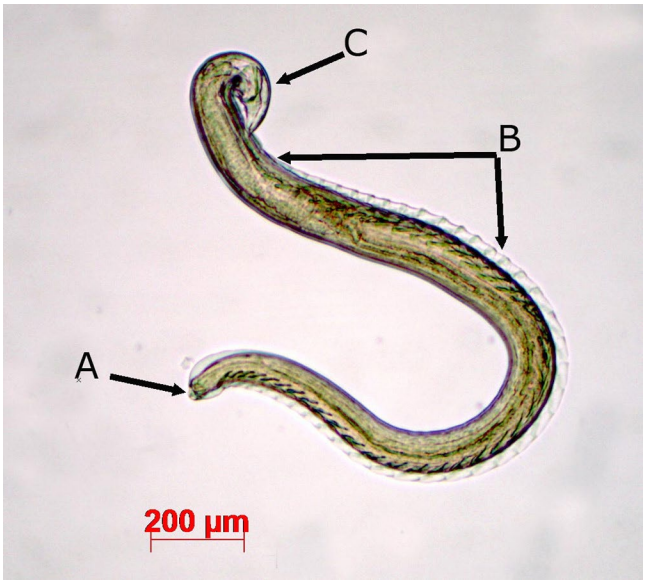

Figure 1. Whole body view of a species of *Pterygodermatites* from a bat. Showing: The mouth is at the anterior end (A), a double row of spines runs the length of body terminating just before the tail (B), and the tail (C). Source: K. Cajiao Mora, 2022. License: CC BY.

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.

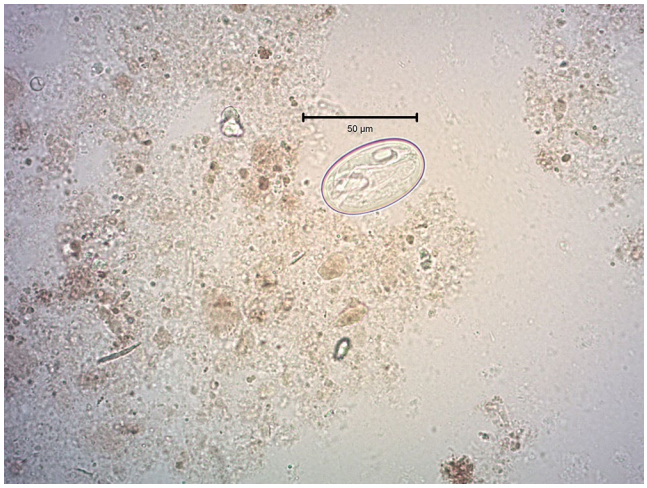

Figure 3. Spirurid egg from a short-eared owl *Asio flammeus*. Source: T. Pennycott, Edinburgh DataShare, https://datashare.ed.ac.uk/handle/10283/2139. License: CC BY.

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 *Carranginema* 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). Moraveč 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 Moraveč (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 (Moraveč 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 (Moraveč 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). Moraveč (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 Bек (a lake). El Vapor, Palizada, Santa Gertrudis, Rio Lagartos, and Noh Bек 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 ***Sobolevicephalus*** 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 subcutane-

ous 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 **Gnathostomatoidea** 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 Moraveč 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). Moraveč 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, Moraveč (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.

Moraveč 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 (Moraveč 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 prasznferum* 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.

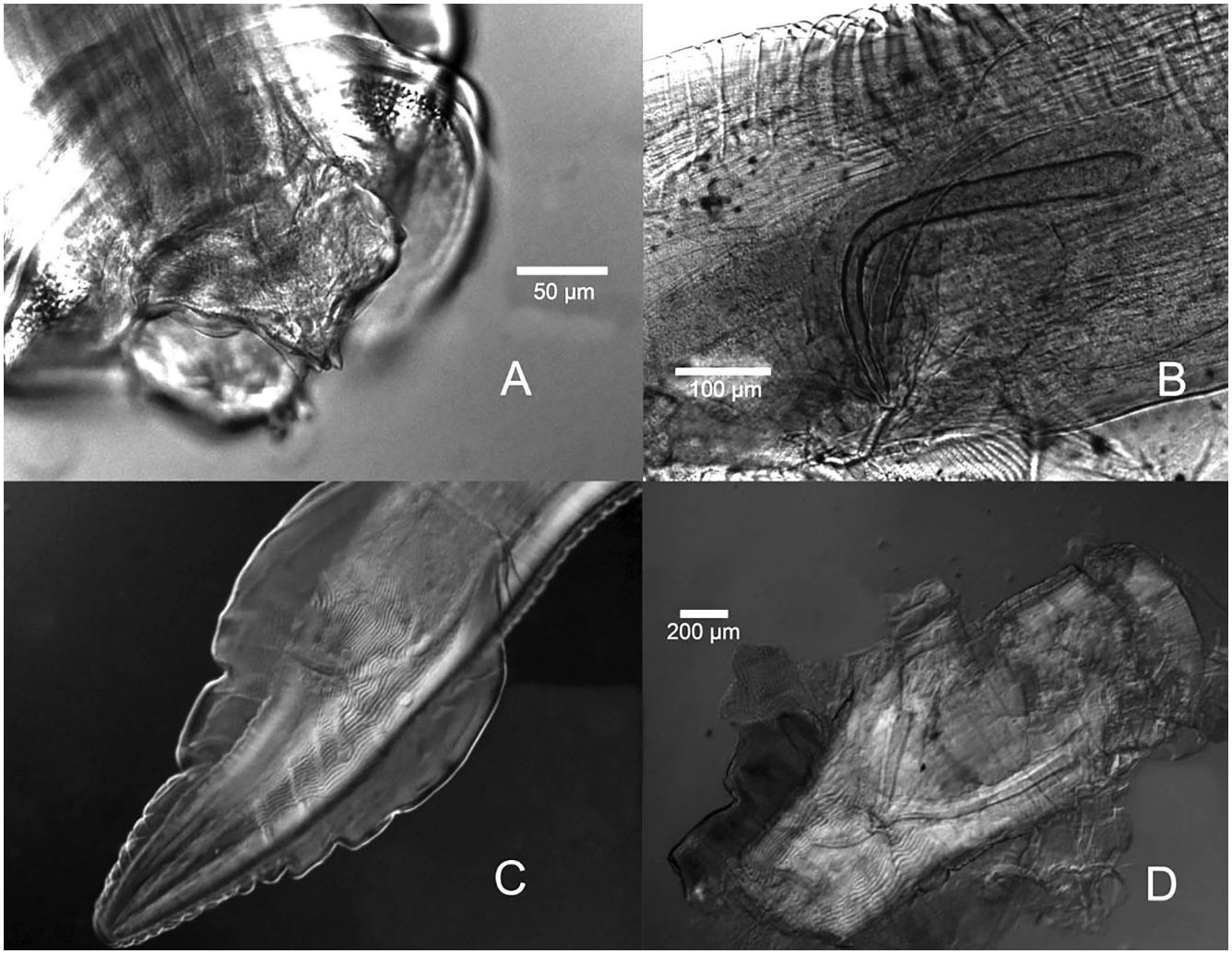

Figure 4. A) Anterior end of *Physaloptera rara* (Nemata: Spirurida: Physalopteridae) from a domestic dog obtained from Iowa, United States. Note the 2 large lips each with 3 small anteriorly-directed teeth (which is typical of *Physaloptera* spp.); B) lateroventral view of the cloacal area showing spicules 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

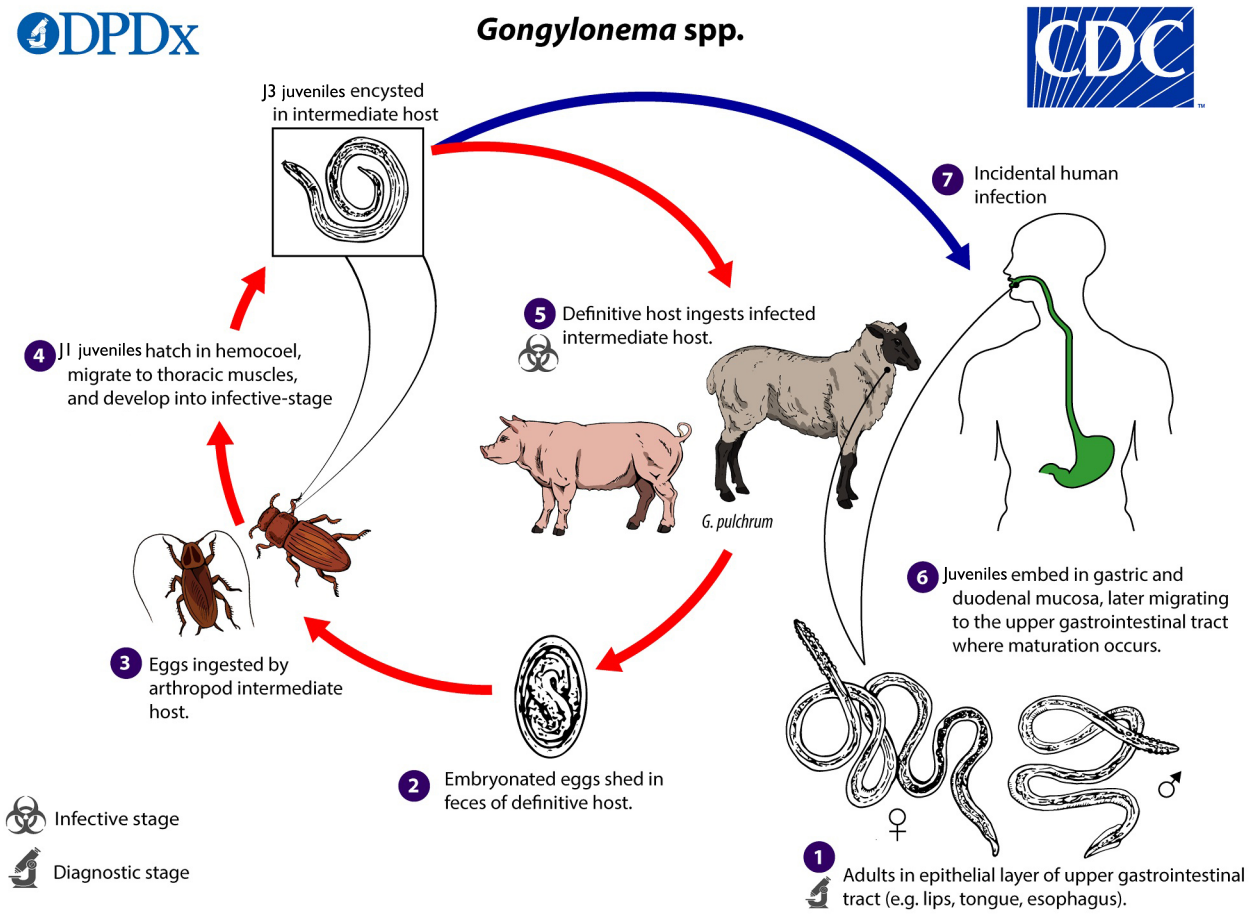

Figure 5. *Gongylonema* is a genus of spirurid nematodes which includes the veterinary parasite *G. pulchrum* (also called the gullet worm or stitch worm) along with several other parasites of mammals and birds. Incidental human infections with *Gongylonema* are rare, and species-level identifications 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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