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Chris T. McAllister

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Chapter 59

Pentastomida: Endoparasitic Arthropods

Chris T. McAllister

Science and Mathematics Division, Eastern Oklahoma State College, Idabel, Oklahoma, United States
cmcallister@se.edu

Introduction

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

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

Fossil Record

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

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

Evolution

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

Geographic Range

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

History of Pentastomid Research

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

Chief Morphological Characters

The simple body design of pentastomids is surprisingly conservative. All possess an elongate and vermiform-cuticular (chitinous) and porous body (Figures 2A–E), often with a conspicuous abdomen showing distinct annulations (annuli = external segmentation). These are usually strongly united with a rounded cephalothorax possessing, on its ventral surface, a small sucking-type mouth region lacking jaws but bordered by 2 pairs of sclerotized hooks (Figures 2D–E), that can be retracted by specialized locomotor muscles into cu-

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

ticular pockets (Paré, 2008). In some species, these hooks articulate against a basal fulcrum and are controlled by strong muscles used to tear and embed their mouth into host tissues. Males are generally smaller than females and possess copulatory spicules (Figures 2B–C). The conical-shaped pentastomid body, which can range from 2 to 130 mm (0.8 to 5.1 in) in total length, depending on the species, is divided into an anterior forebody and posterior hindbody, which, in some, is bifurcated at its tip. The cuticle of some species is covered with a dense network of chitinous spikes.

Integumentary System

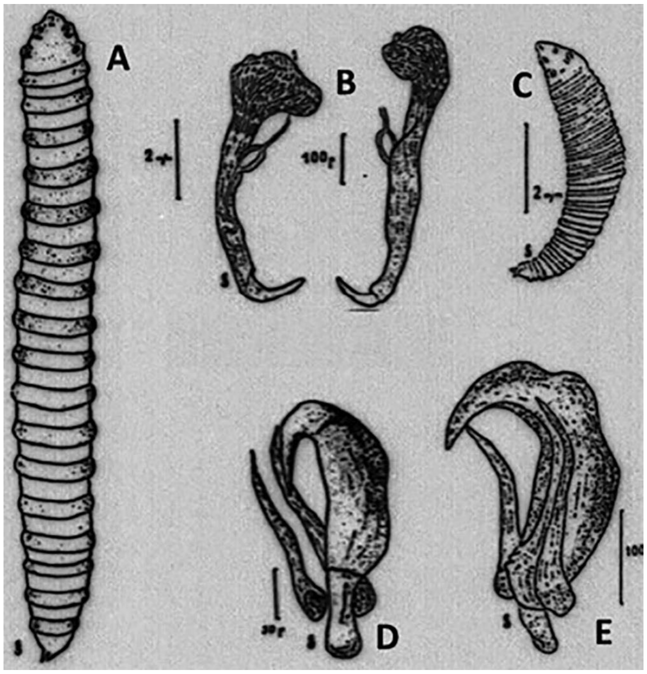
The cuticle of pentastomids is thin and similar to that of other arthropods. It consists largely of 3 layers (subcuticle, endocuticle, and epicuticle) (Riley and Banaja, 1975).

Muscular System

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

Digestive System

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



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

Circulatory, Excretory, and Respiratory Systems

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

Nervous System

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

Reproductive System

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

Pentastomid-Host Relationships

Insects as Hosts

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

Fishes as Hosts

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

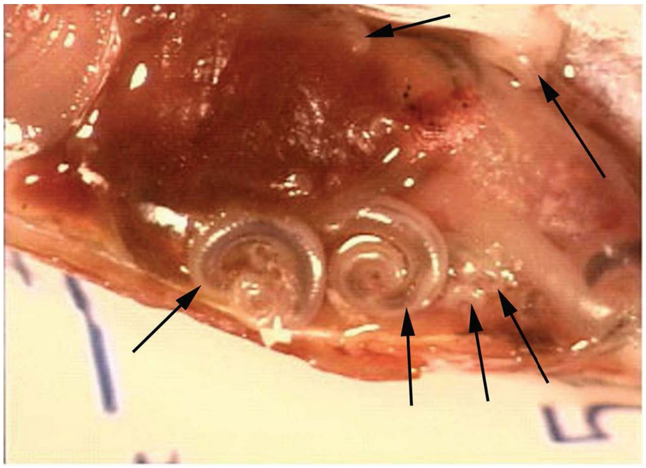


Figure 3. Pentastomid larvae (nymphs; arrows) in the body cavity of a swordtail *Xiphophorus helleri*. Note the varying sizes and locations of the pentastomids. Source: R. P. E. Yanong, 2019. Public domain.

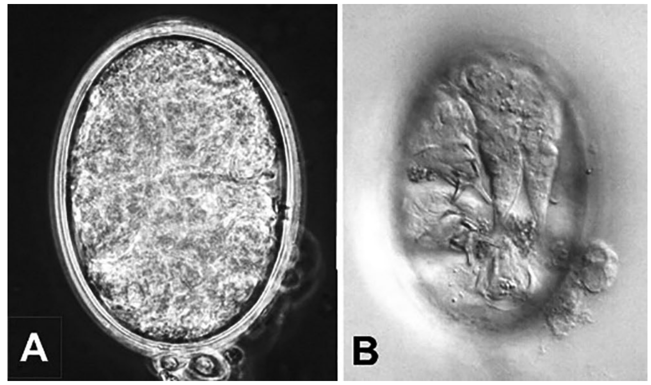


Figure 4. *Raillietiella teagueselfi* eggs from feces of Mediterranean geckos *Hemidactylus turcicus* from Texas, United States. A) Phase contrast microscopy of unembryonated egg; B) Nomarsky-interference contrast microscopy of fully embryonated egg. This pentastomid was described as a new species by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

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

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

Amphibians as Hosts

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

Reptiles as Hosts

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

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

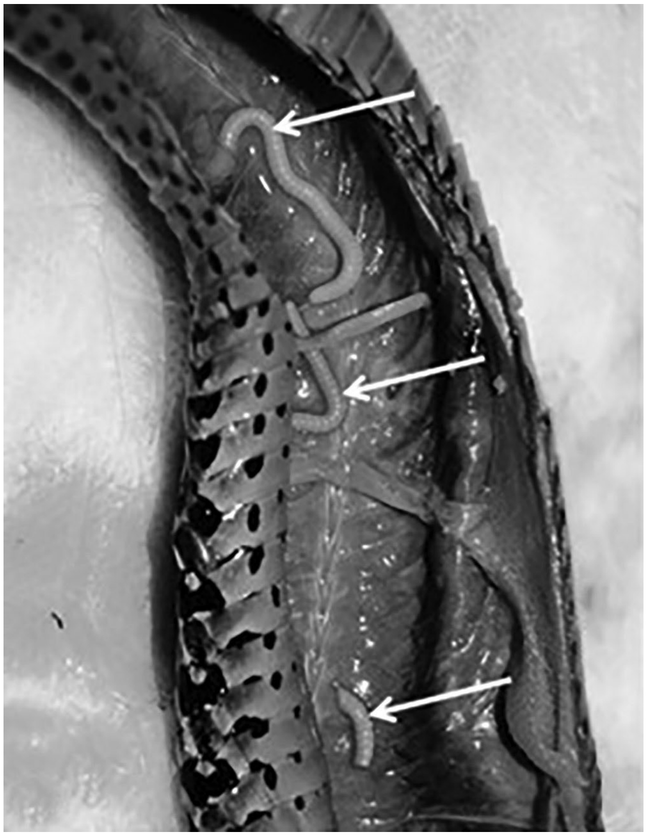


Figure 5. *Kiricephalus* spp. Macroscopic view of in situ *K. coarctatus* (arrows) from an eastern garter snake *Thamnophis sirtalis* from Arkansas, United States. This represents the first report of a reptilian pentastomid from Arkansas. Source: C. T. McAllister. License: CC BY-NC-SA 4.0.

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

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

Birds as Hosts

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

Non-Human Mammals as Hosts

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

Humans as Hosts

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

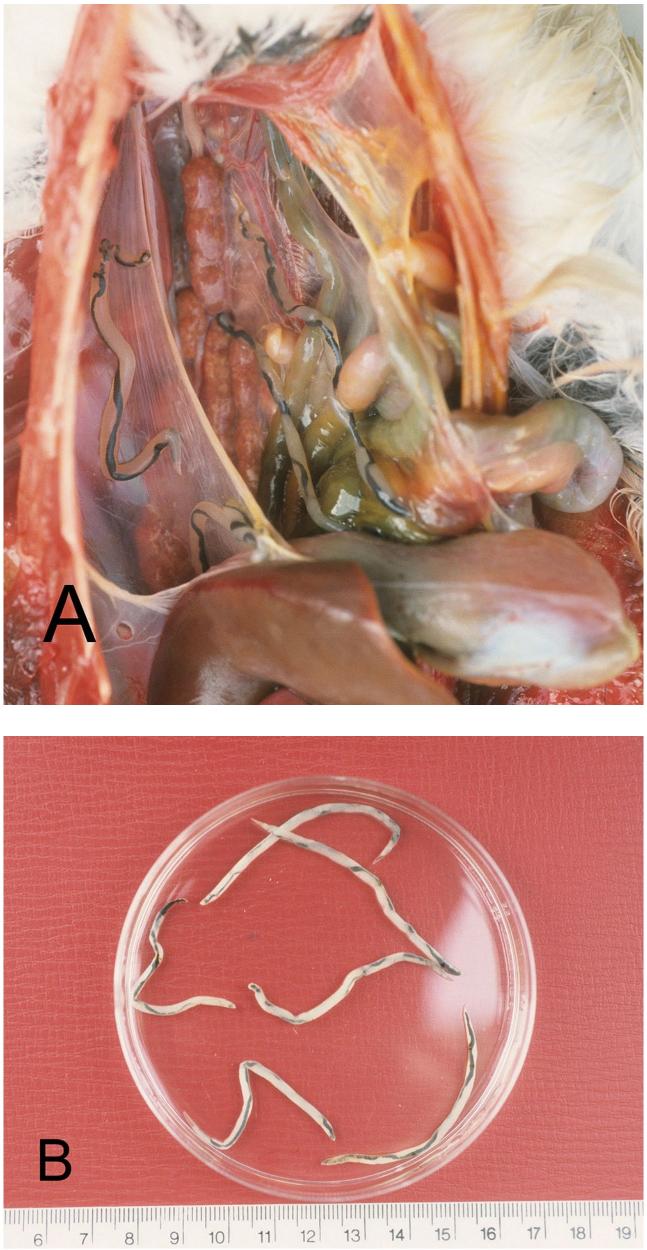


Figure 6A–B. Pentastomids (*Reighardia* sp.) from airsacs of an unknown species of guillemot. A) Worms (arrows) in situ; B) worms removed from airsacs. Source: T. Pennycott, 2016. License: CC BY.

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

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

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

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

Effect on the Host

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

Larval Development

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

Life Cycles

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

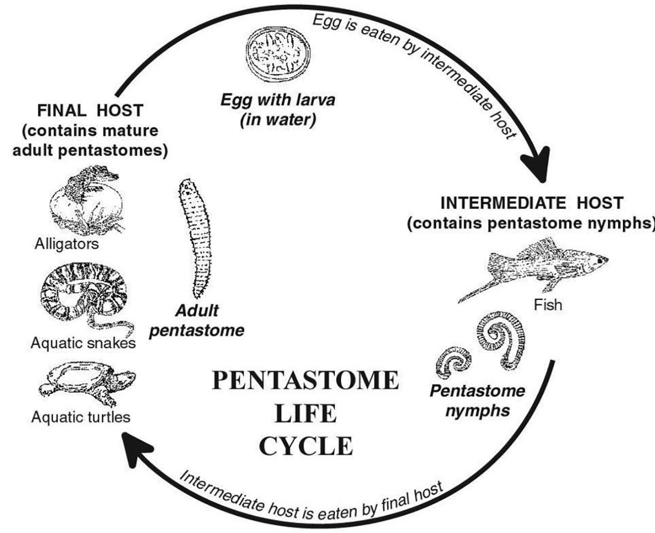


Figure 7. Generalized life cycle of pentastomids. Source: R. P. E. Yanong, 2019. Public domain.

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

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

Ecology

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

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

Taxonomic Study

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

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

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

Order Cephalobaenida Heymans, 1935

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

Order Raillietiellida Almeida and Christoffersen, 1999

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

Order Reighardiida Almeida and Christoffersen, 1999

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

Order Porocephalida Heymans, 1935

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

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

Pentastomid Clades (Apomorphies)

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

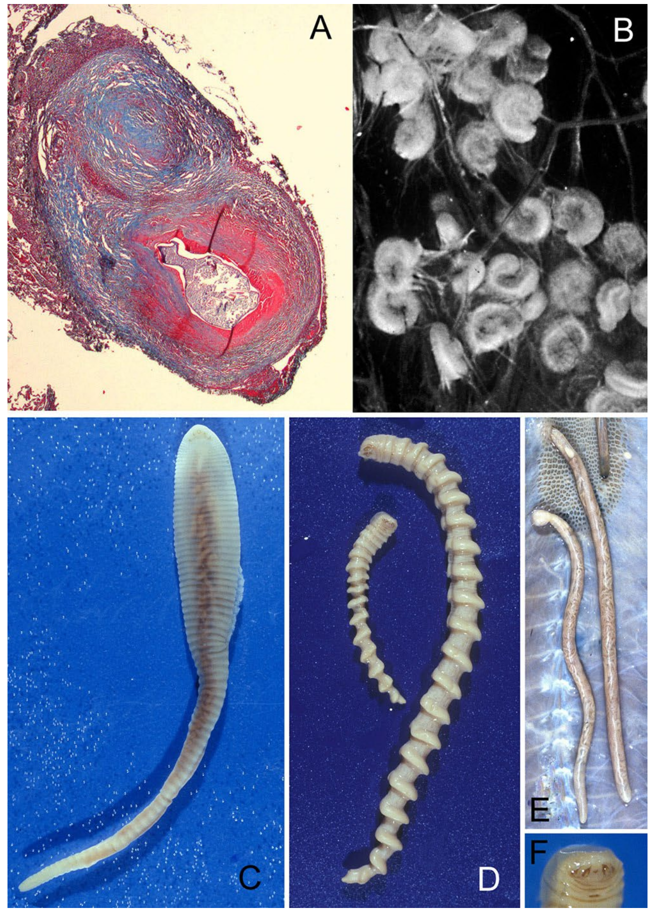


Figure 8A–B. Nymphal and adult pentastomids. A) Excised nodule on the pleural surface of the lung showing nymphal *Linguatula serrata*; B) coiled nymphs of *Armillifer* sp. in simian omentum; C) adult female *L. serrata*; D) adult male (small) and female (large) of *Armillifer* sp.; E) adult *Porocephalus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

Some Interesting Pentastomids

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

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

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

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

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

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

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

Main Sources of Information

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

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