

## *Linguatula*

(arthropod: pentastome)

### Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Crustaceans have a very strong cuticle strengthened by calcium salts; thus their growth must proceed through repeated moults. Most species are aquatic with internal or external gills, two pairs of antennae, mouthparts comprising one pair of mandibles and two pairs of maxillae, and each heteronomous body segment usually bears a pair of ventral biramous extremities (podia). Maxillipods lack appendages on abdominal segments and the nauplius larval stage has a unique maxillipodan eye. Pentastomatids (tongue worms) are unusual endoparasites with elongate worm-like bodies that have lost virtually all their appendages, apart from two pairs of tiny anterior claws near the mouth (collectively accounting for their penta-stome appearance). Most live in the respiratory systems of reptiles, although a few live in the air sacs of seabirds and the nasopharynx of dogs and cats. Eggs passed into the environment release oval larvae with four stumpy legs and an anterior penetration organ used to invade the tissues of an intermediate host (insect, fish, amphibian, reptile or mammal) where it forms a quiescent nymph which is infective to the definitive host. Porocephalids have their mouths between or below the anterior hooks, the hooks have a fulcrum, and the vulva is posterior. Infections by adult *Linguatula* spp. are found in the respiratory passages of carnivores (occasionally humans), and nymphal stages occur in small mammals (occasionally humans) as intermediate hosts.

### Classification:

Domain: Eukaryota (membrane-bound nucleus)  
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)  
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)  
Group: Protostomia (triploblastic, spiral cleavage)  
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)  
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)  
Subphylum: Crustacea (mandibular mouthparts, gills, two pairs antennae, biramous podia, larval nauplius/zoea)  
Class: Maxillipoda (nauplius with maxillipodan eye)  
Subclass: Pentastomatida (tongue worms, anterior end with mouth and two pairs of tiny claws)  
Order: Cephalobaenida (obliquely-paired hooks, medial genital openings)  
Family: Linguatulidae (spatulate adults, parasites of mammals)  
Genus: *Linguatula* (parasitic in respiratory passages of mammals)  
Species: various species cause respiratory problems in carnivores (sometimes humans)

**Parasite biodiversity and host range:** Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Crustaceans have very strong cuticles strengthened by calcium salts, so they moult periodically as they grow and metamorphose through different types of larval stages before forming adults. Most species are aquatic and have internal or external gills, while terrestrial species have internal gills which are kept moist. Crustaceans have mouthparts with two pairs of maxillae (to handle food) and paired mandibles (with opposing biting and grinding surfaces). They have two sets of antennae and each body segment usually gives rise to a pair of ventral biramous appendages (podia). Six crustacean classes are recognized: Brachiopoda, Cephalocarida, Malacostraca, Maxillipoda, Ostracoda and Remipedia. Maxillipods usually have a body plan comprising 5 cephalic, 6 thoracic and 4 abdominal segments followed by a telson. The thoracic segments bear biramous (sometimes uniramous) limbs, but the abdominal segments lack appendages. The carapace is present or reduced, most feed using maxillae, and the nauplius larval stages have unique eyes with three cups, each with tapetal cells (= maxillipodan eye). Six maxillipodan subclasses are recognized: Branchiura, Cirripedia, Copepoda, Mystacocarida, Pentastomatida and Tantulocarida.

Major parasitic crustacean families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Class: Maxillipoda					
Subclass: Copepoda (copepods)					
Order: Cyclopoida (open buccal cavity)					
Family: Lernaecidae (anchor worms)	19 genera, 114 spp.	freshwater fishes	copepodids and adults	skin lesions	direct (water)
Former order: Poecilostomatoida (slit-like buccal cavity)[now a "poecilostome" lineage within the Cyclopoida]					
Family: Ergasilidae (gill lice)	27 genera 61 spp.	freshwater and marine fish	adult ♀	gill/skin lesions	direct (water)
Subclass: Branchiura (head with flattened bilobed cephalic fold, carapace expands laterally)					
Order: Argulidea (discoid bodies, attach using hooks, suckers and barbs)					
Family: Argulidae (fish lice)	4 genera 150 spp.	marine and freshwater fish	juveniles, adults	skin lesions	direct (water)
Subclass: Pentastomatida (tongue worms, elongate annulated bodies, 2 pairs tiny anterior claws near mouth)					
Order: Porocephalida (horizontally-aligned hooks)					
Family: Porocephalidae	8 genera, 40 spp.	snakes, lizards (mammal, reptile IH)	adults	lung lesions	indirect (via IH*)
Family: Sebekidae	8 genera, 34 spp.	crocodiles, turtles (fish IH)	adults	lung lesions	indirect (via IH)
Family: Subtriquetridae	1 genus, 4 spp.	crocodiles (fish IH)	adults	lung lesions	indirect (via IH)
Order: Cephalobaenida (obliquely-paired hooks)					
Family: Linguatulidae	1 genus, 4 spp.	carnivorous mammals (mammal IH)	adults	naso-pharyngeal lesions	indirect (via IH)
Family: Cephalobaenidae	1 genus, 1 sp.	snakes (unknown IH)	adults		indirect?
Family: Raillietiellidae	2 genera, 43 spp.	amphibians, snakes, lizards, sugar glider (arthropod IH)	adults	lung lesions	indirect (via IH)
Family: Reighardidae	2 genera, 3 spp.	birds	adults	nasal lesions	direct?

\*IH = intermediate host

Morphological and ultrastructural studies on immature and adult stages suggested that pentastomatids (tongue worms) were related to branchiurans, esp. argulids (fish lice). Analyses of mitochondrial DNA gene sequences indicated unambiguously that pentastomatids are a group of modified branchiurans [the name Ichthyostraca has recently been proposed for a 'Branchiura+Pentastomatida' clade]. Pentastomatids are unusual endoparasites with elongate non-chitinous annulated vermiform bodies that have lost virtually all their appendages, apart from two pairs of tiny anterior claws near the mouth (collectively accounting for their penta-stome appearance). Most live in the respiratory systems of reptiles and amphibians, although a few live in the air sacs of seabirds and the nasopharynx of dogs and cats. Eggs passed into the environment release oval larvae with four stumpy legs and an anterior penetration organ used to invade the tissues of an intermediate host (coprophagous insects, fish, amphibian, reptile or mammal) where it forms a quiescent nymph which is infective to the definitive host. Two orders have been recognized: Cephalobaenida (adults with medial genital openings, and a single oviduct); and Porocephalida (adults with posterior genital openings, and 2 oviducts). The family Linguatulidae has traditionally been placed in the order Porocephalida on the basis of several shared morphotypic characters (especially adult hook structure, reproductive anatomy), but recent molecular studies have suggested that the family be better placed in the order Cephalobaenida. Indeed, linguatulids are flattened spatulate pentastomes with pairs of obliquely-arranged hooks and mammalian final hosts, whereas typical porocephalids are cylindrical with horizontally-aligned hooks and reptilian final hosts. Most linguatulids have heteroxenous (2-host) life-cycles involving cyclic transmission between mammals where adult stages infect the respiratory passages of carnivores (acting as definitive hosts) and larval/nymphal stages infect the viscera of herbivores and omnivores (acting as intermediate hosts). However, one unusual species (*L. arctica*) has been found to have a monoxenous (1-host) life-cycle involving direct transmission between ungulates (reindeer) as the sole hosts. Another genus (*Neolinguatula*) was erected for linguatulid pentastomes with a caudal cleft (namely, *L. nuttali* from lions from Africa and *L. recurvata* from jaguars from South America), but the validity of the genus has been repeatedly questioned.

<i>Linguatula</i> species	Definitive hosts (adults in respiratory passages)	Intermediate hosts (larvae/nymphs in viscera)	Distribution
<i>L. arctica</i>	Artiodactyla: cervid (reindeer/caribou)	none (unusual direct cycle)	Europe
<i>L. multiannulata</i>	Carnivora: canid (spotted hyena)	Artiodactyla: bovid (African buffalo, korrigum, topi, blue wildebeest, hartebeest)	Africa
<i>L. nuttalli</i> (syn. <i>Neolinguatula</i> )	Carnivora: felid (lion, leopard)	Artiodactyla: bovid (water buffalo, blue wildebeest, blue duiker, greater kudu), suid (desert warthog); Primates: cebid (' <i>Cebus defassa</i> '?)	Africa
<i>L. recurvata</i> (syn. <i>Neolinguatula</i> )	Carnivora: felid (jaguar)	Perissodactyla: tapirid (Baird's tapir); Artiodactyla: tayassuid (collared peccary), bovid (harnessed bushbuck); Rodentia: hystricid (crested porcupine); Primates: pitheciid (titi)	Americas
<i>L. serrata</i> (syn. <i>L. caviae</i> , <i>caprina</i> , <i>denticulata</i> , <i>dingoensis</i> , <i>dingophila</i> , <i>ferox</i> , <i>integerrima</i> , <i>lanceolata</i> , <i>rhinaria</i> , <i>taenioides</i> ) (European tongue worm)	Carnivora: canid (dog, dingo, African wild dog, side-striped jackal, black-backed jackal, wolf, maned wolf, culpeo, red fox), felid (cat, lion), procyonid (crab-eating raccoon); Perissodactyla: equid (horse, ass); Artiodactyla: bovid (sheep, goat); Primates: hominid (human)	Rodentia: murid (black rat, brown rat, greater bandicoot rat, Arabian spiny mouse, house mouse, Mongolian gerbil), abrocomid (Bennett's chinchilla rat), caviid (guinea pig, cavy), hystricid (crested porcupine), octodontid (common degu); Didelphimorphia: didelphid (common opossum); Diprotodontia: macropodid (red-necked wallaby); Lagomorpha: leporid (European rabbit, eastern cottontail, European hare, Cape hare, Granada hare); Eulipotyphla: erinaceid (long-eared hedgehog, western European hedgehog); Artiodactyla: bovid (cattle, zebu, African buffalo, water buffalo, sheep, goat, hartebeest, blue wildebeest, impala, nilgai, korrigum, blue duiker, East African oryx, Mongolian gazelle, goitered gazelle), antilocaprid (pronghorn antelope), cervid (roe deer, fallow deer, reindeer/caribou), camelid (dromedary, Bactrian camel, vicuna), suid (pig), tayassuid (collared peccary); Perissodactyla: equid (horse); Carnivora: felid (cat); Primates: hominid (human); Serpentes: viperid (Gaboon viper)?; Charadriiformes: larid (sea gull)?	worldwide

A few other species were also reclassified to other pentastome genera: including *L. armillata* = *Armillifer*; *L. diesingii* = *Armillifer armillatus*; and *L. clavata* = *Porocephalus*.

**Parasite morphology:** *Linguatula* spp. form 4 different types of morphological stages during their development: eggs, larvae (several stages), nymphs (several stages), and adults. The eggs are oval, measuring 90-133 x 70-120 µm and surrounded by a thick eggshell with a yellow inner layer and a transparent membrane-like outer layer (which wrinkles when dry). They are embryonated and contain an ovoid primary larva with 2 pairs of hooks and developing legs. Hatched larvae have elongated club-like transparent bodies up to 200-250 µm in length with 4 distinct legs (each with 2 claws), an anterior penetration apparatus (consisting of a median spine and bifid lateral spines) and a short spiny tail. Different studies have reported that larvae undergo several moults growing in size to 4-6 mm long before metamorphosing into nymphs that lack larval characteristics (lost legs, penetration apparatus, and tail). It has also been reported that nymphs may undergo several moults increasing in size up to 16 mm long. The body has become broadly cylindrical with a somewhat flattened anterior portion tapering posteriorly, eventually becoming recurved and forming a prominent C-shape. Nymphs are segmented with up to 90 circular annulations, each with a row of small spines, and the chitinous cuticle is penetrated by numerous ring-like structures which are the sclerotized openings of subcuticular glands. Mature nymphs become heavily encapsulated in host tissues and are often surrounded by the exuvia of previous stages. They have ventrally located mouths with circumoral jointed chitinous hooks, large acidophilic anterior glands, simple tubular digestive tracts and primordial genitalia. Adult stages have dorsoventrally-flattened bodies that are distinctly spatulate being broadened anteriorly and tapering posteriorly (in contrast to porocephalid adults which are cylindrical). They are often called tongue worms because their shape resembles that of the

mammalian tongue, but they are sometimes called sinus worms after their location in the host. They grow up to 130 mm long and have a translucent white-yellow cuticle with numerous small spines 16-32 µm long. The body is roughly divided into a small rounded head, broad trunk, and elongate blunt tail. The papillar-like head bears an oval mouth that is flanked by 2 pairs of chitinous hooks with double points. The hooks are jointed and have U-shaped campanulate fulcra. The close positioning of the 4 hooks to the mouth is why they were (erroneously) named penta-stomes (meaning 5-mouthed). In *Linguatula* spp., the hooks are arranged obliquely to the mouth (and not horizontally like porocephalids). The digestive system remains simple and tubular with the oesophagus expanding into a saccular stomach, and tubular hindgut and posterior anus. The nervous system consists of a ventral nerve cord with segmental ganglia. While adult pentastomes have a haemocoel, they do not have circulatory, respiratory or excretory organs. The trunk is distinctly annulated (segmented) with 65-92 circular rings, depending on species. The annuli also bear small cup-shaped sensory organs on their lateral margins, and their posterior edges are roughened by numerous tiny spines projecting backwards. The cuticle contains numerous small circular depressions (pores) that are the apical portions of cuticular chloride cells. The trunk lacks limbs but sometimes the caudal trunk has a pair of small outgrowths (vestigial papillae). The tail is usually short and blunt, although 2 species have a bifid posterior extremity with a terminal cleft (characters used by some to erect the new genus *Neolinguatula*, which remains to be validated). Males are smaller than females; e.g. *L. serrata* males are 18-45 mm long while the females are 42-130 mm long. The genital opening in both sexes is flanked bilaterally by papillar (in males) or leaf-like (in females) structures. Males have 2 testes (unlike porocephalids which have one) with tubules leading to ejaculatory bulbs and a long cirrus (penis) in a cirrus sac. The male genital opening is located medioventrally and has copulatory spicules which are not club-shaped. Females have a single ovary but with bifid oviducts opening into a tubular uterus (greatly elongated and irregularly coiled) with diverticula (spermathecae). The female gonopore is located postero-ventrally and separated from the anus by several annulations (heterogyne condition).

**Site of infection:** Larval and nymphal stages occur in the visceral tissues of a wide range of herbivorous hosts (ungulates, rodents, lagomorphs) while adult stages occur in the nasopharyngeal cavities of a small number of carnivores (particularly canids, sometimes humans). Encysted nymphal stages have been detected in the peritoneal lining and mesenteries of the abdomen, the pleural lining of the thorax and on the surfaces of organs, as well as in lymph nodes, spleen, liver, lymph nodes, and sometimes the parenchyma of the lungs. Nymphs have also been detected in the viscera of humans, particularly in lymph nodes. Adult pentastomes have been found in the nasal airways, frontal sinuses, and tympanic cavity of canines and felines, and sometimes in the nasal passages of humans. One species, *L. arctica*, only occurs in the respiratory passages of reindeer and caribou.

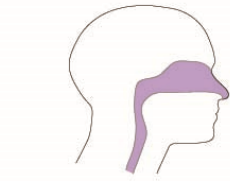
**Pathogenesis:** All larval, nymphal and adult pentastomes are endoparasitic and may migrate and feed on host tissues using their claws, spines, hooks and mouths. All stages feed on host cells, fluids and secretions, with variable reports of blood-feeding (unlike many other pentastomes which actively feed on blood). Infections may cause 2 types of disease depending on the host and stage of infection: visceral disease in intermediate hosts caused by developing larvae and nymphs; or nasopharyngeal disease in definitive hosts caused by developing adults. Most infections by nymphs in intermediate hosts (herbivores and omnivores) are inapparent as the nymphs encapsulate in visceral serosa, but the preceding larval stages may damage host tissues as they migrate through the gut wall into the viscera. Heavy infections may cause transient abdominal signs, enterocolitis, septicaemia, cough, pneumonia, and sometimes death. Encapsulated nymphs may also die and become calcified releasing large amounts of antigenic material which may provoke inflammatory and allergic responses. Adult pentastomes residing in the nasopharynx may grow quite large and cause irritation, respiratory sounds, nose rubbing, sniffing, nasal discharge and obstruction of the upper airways in their definitive hosts (carnivores). Humans may inadvertently act as either intermediate or definitive hosts for *L. serrata*, becoming infected with larvae after consuming eggs contaminating food or water, or becoming infected with adults after consuming encysted nymphs in offal. The occurrence and severity of disease often depends on the precise site of infection, the physiological condition of the host and the intensity of the infection. Visceral linguatulosis may develop when larvae invade tissues (mesenteries, liver, spleen, lungs, eyes) and form nymphs encapsulated in connective tissues. Migration may cause inflammatory tracts and organ perforation, while encapsulation may cause nodular space-occupying lesions with pressure atrophy on surrounding tissues. Viable nymphs are initially encysted in a thin layer of homogenous eosinophilic material with little or no adjacent cellular infiltration. However, they subsequently deteriorate forming necrotic granulomas with thick fibrotic and hyalinized walls and numerous cellular infiltrates (giant cells, macrophages, lymphocytes, plasma cells, and eosinophils), eventually forming granulomatous scars with acellular hyalinized fibrous tissue surrounding amorphous calcified material. Common clinical signs and complications include abdominal pain, enterocolitis, septicaemia, vomiting, bile duct blockage, pneumonitis, bronchitis, lung collapse, night sweats, cough, hepatitis, fibrosis, abdominal pain, headache and uveitis. Nasopharyngeal linguatulosis (regional variations called halzoun or marrara syndrome) occurs when humans eat raw or undercooked offal containing encysted nymphs which subsequently migrate from the stomach up the oesophagus to the pharynx and nasal passages and develop into adults. Migrating stages may cause discomfort and prickling in the throat a few hours after ingestion, whereas developing adults in the nasopharynx cause oedema (larynx, tonsils, fauces, Eustachian tubes, nasal passages, lips, conjunctiva), nasal and lachrymal discharges, episodic sneezing and coughing, dyspnoea, dysphagia, nausea, headache and sometimes abscesses, facial swelling and paralysis, asphyxiation and death. Infections in humans are commonly observed in Africa and Asia, but there are growing numbers being reported in Europe and the Americas, often in travellers.

**Developmental cycle and mode of transmission:** Pentastomes have indirect heteroxenous (2-host) life-cycles and undergo predator-prey transmission involving larval stages in intermediate hosts and adult stages in definitive hosts. *Linguatula* spp. utilize mammalian definitive hosts and the adults reside in the nasopharyngeal cavities (in contrast, porocephalids have reptilian definitive hosts and adults reside in the lungs). Gravid females lay numerous eggs which exit the host in nasal secretions but more usually are swallowed and excreted in host faeces. Eggs may remain viable on the ground on pastures or in water sources for several months. They are fully embryonated and contain an ovoid primary larva (resembling a small mite). Eggs are ingested by mammalian intermediate host when they consume contaminated food or water. A small range of animals serve as intermediate hosts, mostly herbivorous ungulates (especially bovids, some equids) but also smaller omnivores or scavengers (rodents and lagomorphs). Humans and small monkeys may also become accidentally infected. The eggs hatch in the intestines and the primary larvae penetrate the gut wall and migrate for a short time in visceral tissues. They have been reported to undergo several moults before transforming into nymphs which lose their larval characteristics (legs and tail) and encapsulate in host tissues, particularly the mesenteries, lymph nodes and serosa of organs (liver, lungs). There are also a few reports suggesting that the nymphs undergo a few moults before they finally mature to the quiescent but infective final stage. Encysted nymphs persist with host tissues for many months, but ultimately seem to degenerate and calcify. The encysted nymphs are then eaten by carnivorous definitive hosts by predation or scavenging, mostly canids and felids. Humans may also become infected with *L. serrata* by eating raw or undercooked offal (livers, lymph nodes) from sheep and goats. Once ingested, the nymphs excyst in the stomach or intestines and migrate up the oesophagus to the nasopharynx where they attach, feed and grow into adults. Pentastomes mate in their hosts with males traversing tissues to locate females. It is thought that females only mate once as subsequent structural changes in gravid females precludes further mating. Males only live for several months whereas females may live for up to 2 years, producing millions of eggs after 6 months. The infective ova are discharged into the environment along with host respiratory secretions and faeces to complete the cycle.

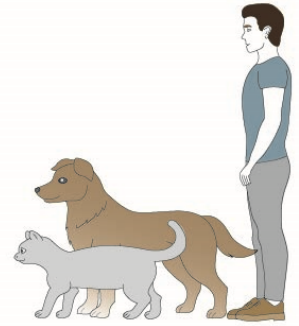
**Differential diagnosis:** Infections by pentastomes are difficult to diagnose on clinical grounds, as many patients are asymptomatic, infections may persist for many years without ill-effect, and even when clinical signs become apparent they are non-specific. Most infections are found fortuitously during medical or veterinary consultation, on surgery or at necropsy. Patent infections may be detected by the detection of pentastome eggs in faecal samples or nasal/sinus washes (gravid females produce millions of distinctive eggs containing small ovoid mite-like embryos). Various medical imaging technologies (radiology, computed tomography, ultrasonography) may be used to assist diagnosis through the detection of internal foreign bodies. Calcified nymphs are conspicuous in mesenteries and soft tissues, but are rarely found in striated muscles (unlike the calcified cysticerci of tapeworms). Adult pentastomes may be detected as soft spatulate tissue masses in nasal passages. Endoscopy may also be used on larger hosts to examine major passages for the presence of segmented adults. Infections are usually confirmed by gross and histopathological studies on specimens collected on biopsy or necropsy (their cuticular annulations remain recognizable). Several studies have developed an enzyme-linked immunosorbent assay (ELISA) to detect specific host antibodies against parasite excretory/secretory (ES) and somatic (S) antigens. Molecular biological studies have also been used to identify and characterize pentastome species by polymerase chain reaction (PCR) amplification of nuclear (18S ribosomal RNA) and mitochondrial (cytochrome c oxidase subunit 1) gene sequences.

**Treatment and control:** There is no particular treatment advocated for pentastome infections. Long-term monitoring of asymptomatic cases have observed that both nymphs in the viscera and adults in the nasopharynx tend to degenerate over 2 years, slowly being absorbed by host cellular reactions or becoming calcified. However, clinicians often intervene in clinical infections to alleviate symptoms and remove or kill parasites. Recourse may be made to the surgical removal of adults from the sinuses, often aided by endoscopy. Care should be taken not to damage the parasites as the sudden release of copious antigenic material may provoke inflammation and allergic reactions. Several studies have also used anti-parasitic drugs in attempts to kill parasites in humans and animals, including diethylenediamines (diethylcarbamazine), isoquinolines (praziquantel), imidazothiazoles (levamisole), and benzimidazoles (mebendazole), but they were not always effective as the parasites were partly protected (nymphal stages are highly encapsulated and adult stages are bathed in copious excretory/secretory material). The use of glucocorticoids is not recommended to moderate inflammatory responses. Recent studies have shown that treatment with macrocyclic lactones (ivermectin) were effective against some animal infections, including the enigmatic *L. arctica* in reindeer (which has an atypical direct cycle not involving intermediate hosts). A range of preventive procedures may be employed to help break the parasite life-cycle, usually involving water treatment (filtration and disinfection to remove and kill eggs), improved sanitation (disposal of faeces and avoiding nasal secretions from pets, burning or burying carcasses), maintaining personal hygiene (wash hands after handling pets and preparing meat), and adopting suitable food hygiene protocols (cook meat and do not feed raw meat or offal). Education campaigns have been developed in several countries in attempts to break culturally-embedded eating habits (e.g. the consumption of raw liver and lymph nodes in certain parts of Africa).

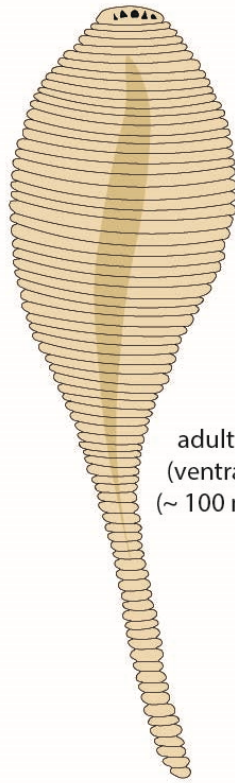
# Linguatula



respiratory tract  
(nasopharyngeal irritation,  
discharge, obstruction)

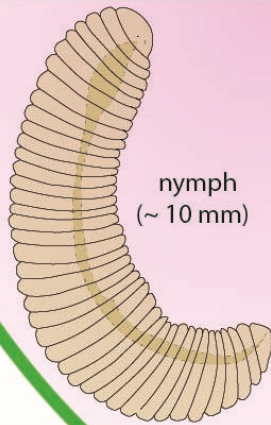


Definitive Hosts  
(carnivores,  
occasionally humans)

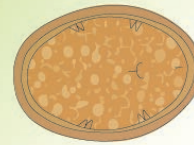


adult  
(ventral)  
(~ 100 mm)

ingestion  
(predation,  
scavenging)

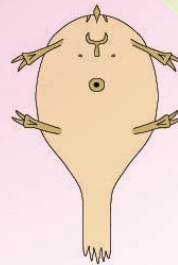


nymph  
(~ 10 mm)



egg  
(~ 100  $\mu$ m)

eggs passed  
in faeces  
(sometimes  
respiratory  
secretions)

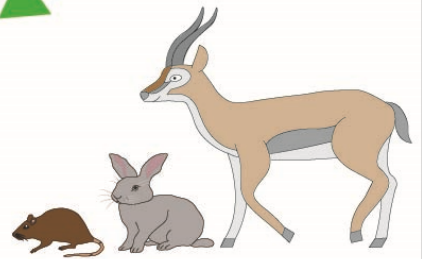


larvae (ventral)  
(~ 200  $\mu$ m)

ingested



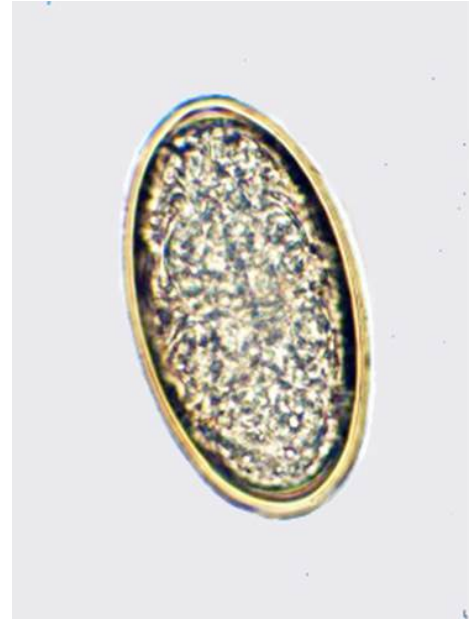
viscera  
(space-occupying lesions,  
granulomas, calcification)



Intermediate Hosts  
(herbivores, omnivores,  
esp. rodents)



*Linguatula* adult



*Linguatula* egg