

Oslerus

(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including lungworms with small buccal capsules and reduced male bursae. Adult worms are found mostly in the lungs of their hosts, although some inhabit the pulmonary artery, meninges or connective tissues. Five main groups occur: dictyocaulids in ruminants and horses; metastrongyles in pigs; protostrongyles in ruminants; angiostrongyles in carnivores and rodents; and filaroids in dogs. Unlike most lungworms, filaroids have direct life-cycles where adults in the lungs produce eggs which hatch releasing L1 to be swallowed and passed in faeces. L1 are ingested by dogs or, more commonly, transferred to pups by maternal grooming. L2 develop in the intestines and then migrate via the lymphatic-vascular route to the lungs and mature into adults. *Oslerus osleri* infections have been associated with respiratory distress in dogs worldwide.

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: Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class: Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmeida) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family: Filaroididae (direct cycle, infection of carnivores by ingestion of L1)
Genus: *Oslerus* (parasitic in trachea of dogs)
Species: *O. osleri* causes respiratory distress in dogs

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, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the

presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
<i>Incertae sedis</i> Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs)
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasp organ. Many classification schemes group these 'bursate' nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	Characters	Definitive Hosts	Transmission*	No. genera
Metastrongylina (lungworms)				
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	Suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictyocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	Suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes <i>per os</i>)	20

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Lungworms are characterised mostly by their unique location within the respiratory systems of their mammalian hosts, although some species also infect cardiovascular, nervous or intermuscular connective tissues. Adult worms have a small buccal capsule, often reduced to an annulus, and sometimes possessing lips. Male worms have a caudal bursa that is variable in structure (often with reduced lobes and/or rays), spicules and a gubernaculum and telamon that are often not highly developed. Female worms have a median or posterior vulva, sometimes with a sphincter, and they are oviparous (releasing eggs) or ovoviviparous (releasing larvae). Many species have direct cycles involving the ingestion of infective larvae, while others have indirect cycles involving the ingestion of larvae in invertebrate intermediate hosts, and sometimes paratenic hosts. Eight metastrongyline families are recognised: Metastrongylidae (mouth with 2 large lateral trilobed lips, bursa with large lateral lobes and reduced dorsal lobe, oviparous, indirect cycle, earthworms used as intermediate hosts, 1 genus in lungs of suids); Angiostrongylidae (mouth with or without lips, bursa well-developed, oviparous, ovoviviparous, indirect cycle, gastropods used as intermediate hosts, 28 genera in respiratory and vascular systems of marsupials, rodents, insectivores, lemurs, mustelids, viverrids, felids and canids); Dictyocaulidae (mouth small, bursa with large lateral lobes and large dorsal lobe (divided to base), ovoviviparous, direct cycle, 2 genera in airways of ruminants and horses); Filaroididae (mouth small, bursa absent or reduced (rays reduced to papillae), ovoviviparous, direct cycle, 4 genera in respiratory system of canids, mustelids, pinnipeds, primates, and marsupials); Protostrongylidae (mouth small, bursa with large lateral lobes and prominent dorsal lobe, highly developed gubernaculum and telamon, oviparous, indirect cycle, molluscs used as intermediate hosts, 17 genera in lungs of ruminants, felids, canids, leporids, and skeletal muscles and central nervous system of cervids); Pseudaliidae (mouth small, bursa reduced (rays fused but not reduced to papillae), ovoviviparous, direct cycle, 7 genera in respiratory, auditory, circulatory systems of delphinids, phocoenids, monodontids and mongoose); Skrjabinogylidae (mouth small, bursa modified to form lateral fleshy lobes, ovoviviparous, direct cycle, 1 genus in nasal cavities of mustelids); and Crenosomatidae (mouth small, bursa with large lateral lobes and large dorsal lobe (not divided to base), ovoviviparous, direct cycle, 5 genera in respiratory system of canids, felids, pinnipeds, soricids and marsupials).

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Worm larvae
Filaroididae					
<i>Oslerus</i> (lungworm)	2	carnivores	trachea	4-64 mm long, small buccal capsule, bursa reduced, L1 voided in faeces, vomitus or sputum, direct cycle (L1 transferred to young during grooming or regurgitative feeding) or indirect cycles (L1 infect gastropods and form infective L3)	230-270 µm, S-shaped tail
<i>Filaroides</i> (lungworm)	17	carnivores, primates	lungs	2-90 mm long, vestigial buccal capsule, bursa absent, L1 voided in faeces, vomitus or sputum, direct cycle (L1 transferred to young during grooming or regurgitative feeding) or indirect cycle (L1 infect gastropods and form infective L3)	220-325 µm, posterior kink

The family Filaroididae contains 4 genera (*Filaroides*, *Filariopsis*, *Oslerus*) parasitic in the respiratory system of canids, mustelids, pinnipeds, primates and Australian marsupials. The family contains delicate worms which are difficult to remove from lung tissues and study intact, but they have been separated from the family Angiostrongylidae in that the males are abursate and the females have a subterminal vulva. Their life-cycles are quite varied: some being direct; while others are indirect and use gastropods or fish as intermediate hosts. The genus *Oslerus* contains 2 spp. separated into 2 subgenera: *O. (Oslerus)* (females with inconspicuous vaginal sphincter) containing the species *O. (O.) osleri* with a direct cycle in canids; and *O. (Anafilaroides)* (females with highly developed vaginal sphincter) containing the single species *O. (A.) rostratus* with an indirect cycle in felids and slugs.

<i>Oslerus</i> species	Hosts	Location [Clinical signs]	Intermediate Hosts (IH) [plus Paratenic Hosts (PH)]	Distribution
<i>O. (Oslerus) osleri</i> [formerly <i>Filaroides osleri</i>] (dog lungworm)	Carnivora: canid (dog, dingo, wolf, coyote, red fox)	trachea, bronchi [cough]	no IH (direct)	worldwide
<i>O. (Anafilaroides) rostratus</i>	Carnivora: felid (cat, wild cat, bobcat, leopard cat)	trachea, bronchi	Gastropoda: limacid (<i>Limax maximus</i>) [plus PH: Rodentia: murid (mouse); Galliformes: phasianid (chicken)]	Americas

Parasite morphology: *Oslerus* spp. form 3 different types of morphological stages during their development: eggs; larvae (4 consecutive stages encoded L1-L4); and adult worms. The eggs are thin-shelled ovoid-ellipsoid stages measuring 80-120 x 50-70 µm and they are fully embryonated when laid. L1 from hatched eggs are thin elongate larvae, those recovered from bronchial mucus measuring 230-270 µm in length while those recovered from faeces measured 326-412 µm long. They had rounded heads, rhabditiform (bulbed) oesophagi, and short wavy S-shaped tails with a prominent constriction. Descriptions of subsequent endogenous larval stages (L2-L4) of *O. osleri* are lacking, while experimental studies on *O. rostratus* have described L3 from slugs as measuring 469-578 x 24-29 µm with pointed tails and small subterminal surface serrations. Adults are pale slender worms measuring 4-64 mm in length and they have striated cuticles with a well-developed tegumental sheath (inflation of outer cortical layer), small buccal capsules, club-shaped oesophagi, and short blunt rounded tails. Adult worms are sexually dimorphic, with males being smaller than females (4-8 cf. 9-15 mm for *O. osleri*, 28-37 cf. 48-64 mm for *O. rostratus*). Mature males are abursate and do not possess a distinct caudal copulatory bursa (the family Filaroididae was separated from the family Angiostrongylidae by the absence of a male bursa). Instead, the male tail has ill-defined lateral and ventral ray vestiges reduced to small single and sessile papillae, and a dorsal ray divided near its tip. Males also have a small gubernaculum and 2 short curved spicules slightly unequal in appearance (90-113 µm long). Mature females are didelphic with 2 ovaries and uteri arranged in a parallel prodelphic formation and connected to a common vulva located posteriorly near the anus. The 2 *Oslerus* subgenera are recognised primarily on the basis of the differences in the vaginal sphincter, being inconspicuous in *O. (Oslerus)* females and highly developed in *O. (Anafilaroides)*. Females of both subgenera produce eggs that are larvated when laid.

Site of Infection: Adult worms infect the upper air passages of their carnivorous hosts, being located in the tracheal and bronchial mucosa adjacent to the carina (cartilaginous ridge at the tracheal bifurcation). Eggs and larvae are voided with host excretions, and invading larvae migrate through the gut to the lungs. Experimental studies on *O. rostratus* have demonstrated L1 may infect terrestrial slugs as intermediate hosts where they develop into L3 which may be spontaneously shed in mucus trails (whereas *O. osleri* do not involve intermediate hosts).

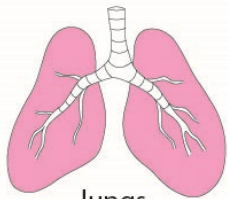
Pathogenesis: Most infections are asymptomatic even though worms produce granulomatous nodules in the trachea and bronchi as early as 2 months after infection. The nodules are located in the submucosa between the supporting cartilage rings near the tracheal bifurcation. They are fibrous and contain tangles of tightly coiled worms (counts ranging from 1-105 worms per nodule). They are covered by intact epithelium except for small pores through which female worms protrude their tails to lay eggs. The nodules appear as grey wart-like masses 2-20 mm in diameter, often flat but sometimes protruding as plaques up to 10 mm into the lumen. Nodules containing live worms may provoke local lymphocytic infiltrations whereas nodules with dead worms elicit strong inflammatory responses with neutrophils and a few giant cells. Heavy infections involving numerous, large or confluent nodules may cause respiratory difficulties, usually chronic in onset with progressive airway obstruction (chronic tracheobronchitis or verminous nodular bronchitis which can appear similar clinically to kennel cough). The main clinical sign is coughing, with spasmodic paroxysmal attacks of a hard dry (non-productive) rasping cough, precipitated by exercise or cold air and unresponsive to antibiotic therapy. Other signs include inspiratory respiratory distress with wheezing and acute onset dyspnoea, exercise intolerance, inappetence, anorexia, weight loss, emaciation, and death. The most severe cases occur in young dogs (6-12 months old), particularly in working dogs rather than household pets.

Developmental cycle and mode of transmission: *Oslerus* and *Filaroides* spp. are unique amongst the metastrongyle lungworms because they may have direct or indirect life-cycles, exemplified by *O. osleri* with direct transmission in canids and *O. rostratus* with indirect transmission between felids and gastropods. *O. osleri* females deposit larvated eggs in the trachea where they hatch. Many of the released L1 are coughed up, swallowed, and shed intermittently in host faeces, but are often sluggish, dead or degenerate (suggesting that faecal-oral transmission via coprophagy would be uncommon, even though it has been demonstrated experimentally). Instead, most infections are transmitted when L1 in sputum, expectorations or saliva are transferred to pups during maternal grooming through licking or when L1 in vomitus are transferred during regurgitative feeding (common in wild carnivores) or scavenging. Ingested L1 moult in intestines and L2 migrate to the lungs via the lymphatic and/or vascular systems where they develop to subadults (often referred to as L5) in alveoli and bronchi before settling near the tracheal bifurcation to mature. The prepatent period (time from infection to first larval excretion) ranges from 63-147 days and infections have been found to remain patent for several years, especially when entrenched in breeding kennels. In contrast, experimental studies with *O. rostratus* from felids have shown that L1 may infect leopard slugs which act as intermediate hosts in which L3 develop. Infective L3 have also been shown to be spontaneously shed by slugs in mucus trails, and they have even survived in mice and chickens as experimental paratenic (transport) hosts.

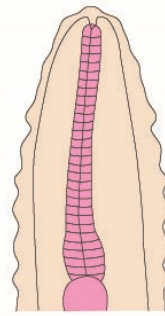
Differential diagnosis: The predominant clinical sign of coughing is nonspecific and physical examination reveals little other than increased tracheal sensitivity (although throat manipulation does not precipitate coughing). Eosinophilia may sometimes be detected by haematology (complete blood count) or cytology (airway washes). Infections are readily detected by endoscopic examination (bronchoscopy) under anaesthesia, which reveals characteristic nodules containing worms in the trachea. Medical imaging techniques (lateral thoracic radiography) may also reveal soft tissue densities (granulomas) in the caudal trachea. Diagnosis may be confirmed by detecting L1 in endoscopic biopsies of sputum, transtracheal washes, bronchoalveolar lavages, and less frequently in fresh faecal samples following floatation or Baermann filtration (but faecal shedding is intermittent). L1 appear as sluggish coiled stages with S-shaped tails. Molecular biological techniques have been used to characterize parasites following the polymerase chain reaction (PCR) amplification and sequencing of nuclear genes (ribosomal RNA).

Treatment and control: A range of anthelmintic drugs have been used in attempts to treat infections, including benzimidazoles (fenbendazole, thiabendazole, oxfendazole) and macrocyclic lactones (ivermectin, doramectin). No single therapy was effective in eradicating infections, but extended treatment with several drug combinations led to symptomatic improvement with the amelioration of clinical signs and nodule shrinkage. Preventive strategies applicable to animal breeding or housing facilities involved better sanitation (regular removal of faeces and vomitus, washing/disinfecting cages), good hygiene (washing soiled animals, providing clean food and water), chemoprophylactic treatment (particularly breeding animals), quarantine and isolation (including separating pups from older infected animals, sometimes requiring hand-raising or foster-rearing), and excluding molluscs and wild animals from facilities (using chemical or physical barriers).

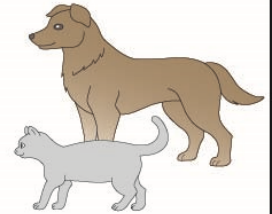
Oslerus



lungs
(nodular bronchitis,
tracheobronchitis)



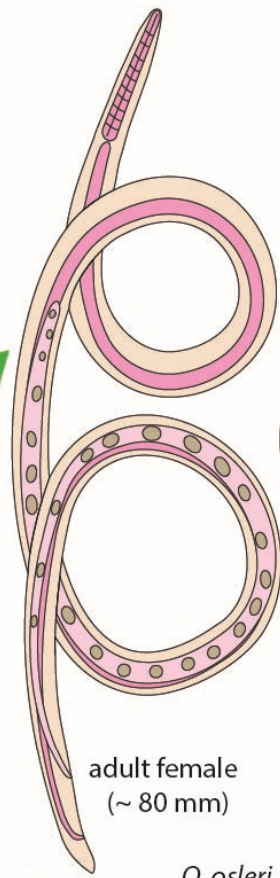
head



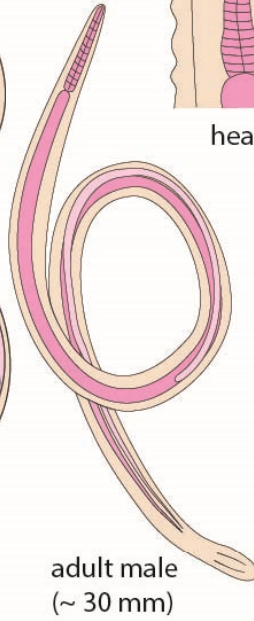
Definitive Hosts
(canids, felids)

somatic migration

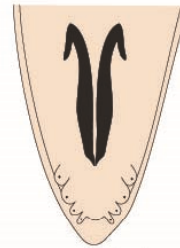
L1 or
L3/IH/PH
ingested



adult female
(~ 80 mm)



adult male
(~ 30 mm)



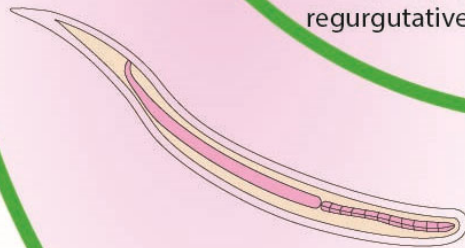
male tail

L1 voided
in faeces,
sputum,
vomitus



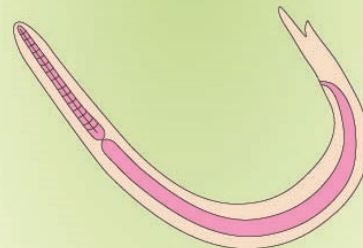
eggs hatch in host

O. osleri
direct transmission via
coprophagy, grooming,
regurgitative feeding



third-stage larvae (L3)
(~ 350 µm)

O. rostratus
indirect transmission
via IH ± PH



first-stage larvae (L1)
(~ 300 µm)

external
environment

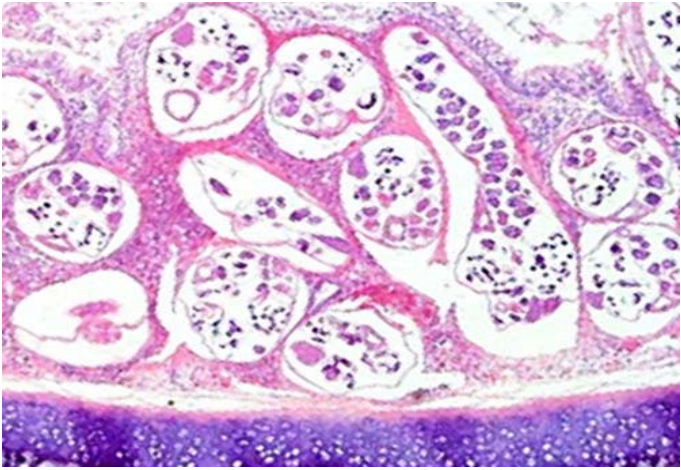


Paratenic Hosts (PH)
(rodents, birds)
(tissues)

L1 ingested or
penetrate dermis



Intermediate Hosts (IH)
(slugs)
(tissues)



Oslerus tracheal lesion