Ollulanus
(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 spirurinids, 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 the molineids which are small hair-like worms with a small buccal capsule. Adults are usually found in the stomach/abomasum or small intestines of mammals or birds. They have direct life-cycles, usually involving eggs passed in faeces developing to L3 which are ingested and subsequently form adults. The monotypic genus *Ollulanus*, however, is unique as the females are viviparous (eggs hatch *in utero*) releasing L3 which may undergo auto-infection or be shed in vomitus to be ingested by new hosts. Infections may cause gastritis, vomiting and emaciation in cats, and occasionally pigs.

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, Phasmidea) (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:	Molineidae (reduced buccal capsule, cephalic vesicle, female tail with spine/cusps, direct cycles)
Subfamily:	Ollulaninae (head with spiral coil, female tail with cusps, viviparous (develop to L3 in uterus))
Genus:	*Ollulanus* (parasitic in stomach of cat/fox/pig)
Species:	various species cause gastritis in felids and suids

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)]
Incertae sedis 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 His
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 clasping 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**
Trichostrongylina (trichostrongyles)				
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
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 *per os*)	20
Metastrongylina (lungworms)				
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
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

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

Some authorities recognize a superfamily Molineoidea comprising 4 families: Molineidae in mammals, birds and reptiles; Amphibiophilidae mainly in amphibians; Mackerrastrongylidae in monotremes and marsupials; and Strongylacanthidae in bats. These worms have a buccal capsule reduced to an annulus, most have a cephalic vesicle and a bilaterally symmetrical synlophe, the males have an asymmetrical bursa and females have a tail with a caudal spine or numerous tubercles. The family Molineidae contains 6 subfamilies: Nematodirinae (corona radiata, neodont formation, bursa with short dorsal ray split to base, didelphic, oviparous, 6 genera in herbivorous mammals); Ollulaninae (synlophe absent, cephalic vesicle absent, bursa with short dorsal ray, monodelphic, viviparous, female tail with 3-5 tubercles, 1 genus in felids and occasionally suids); Molineinae (bursa with short dorsal ray not split to base, synlophe with perpendicular ridges, 26 genera in amphibians, reptiles and mammals); Dromaeostrongylinae (bursa with elongate dorsal ray, 1 genus in birds); Merstensinematinae (bursa with short dorsal ray not split to base, synlophe absent, 2 genera in reptiles and amphibians); and Anoplostrongylinae (cephalic vesicle with armature, synlophe with dorsoventral ridges, bursa with short dorsal ray not split to base, 25 genera in edentates and bats). Specific molineid genera of veterinary and medical importance are compared in the following table.

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Worm eggs/larvae
Subfamily Ollulanidae					
Ollulanus	1	carnivores	stomach	0.7-1.0 mm long, small buccal capsule, females with trifid tail, viviparous (eggs hatch *in utero*), larvae shed in vomitus (or auto-infection)	larvae 400-500 µm, tail with terminal cusps
Subfamily Nematodirinae					
Nematodirus (thin-necked intestinal worm)	53	artiodactyls, lagomorphs	small intestines	10-30 mm long, cephalic inflation, thin neck, mid-body spiral coil, female with spiked tail, male with long thin spicules	150-260 x 67-118 µm, eggs ellipsoidal, thin-shelled

The subfamily Ollulaninae contains a single genus (*Ollulanus*) with a single species (*O. tricuspis*) infecting the stomach of felids, and occasionally canids and suids. While infections have been reported sporadically from many countries, they are probably widespread around the world together with their felid hosts. They have unusual cryptic life-cycles as the female worms are viviparous and produce live larvae which are transmitted in host vomitus (rather than being oviparous and laying eggs which are transmitted in host faeces, like many other gastroenteric nematodes).

***Ollulanus* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Distribution**
O. tricuspis (syn. *O. suis, O. skrjabini*)	Carnivora: felid (cat, wild cat, lion, tiger, cougar, cheetah), canid (dog, red fox); Artiodactyla: suid (pig)	stomach [gastritis, emaciation, vomiting]	Europe, Americas, Australasia

Parasite morphology: The species *Ollulanus tricuspis* forms 2 different morphological stages in its developmental cycle; namely, larvae (4 stages designated L1-L4); and adult worms. While female worms do produce eggs, they embryonate and hatch internally (*in utero*). Three sequential larval stages develop coiled up within the eggs; rhabditiform L1 measuring around 350 µm long with round blunt tails; rhabditiform L2 measuring around 340 µm long with tails bearing 3 cusps; and strongyliform L3 measuring from 400-500 µm in length and having short tails with at least 3 terminal cusps. Following hatching, L3 uncoil in the uterus of the female and are then released into the gut lumen of the host. Following infection (or auto-infection) by freed L3, the larvae moult firstly to L4 and then to young adults on the gastric mucosa. L4 measure from 625-650 µm in length and have begun to develop male or female genitalia. Adults are small hair-like worms 0.7-1.0 mm long and are not visible to the naked eye. They are surrounded by a tough cuticle with conspicuous longitudinal ridges and cervical papillae. The anterior end usually coils around on itself but does not possess an anterior inflation (cephalic vesicle). They have a cup-like buccal capsule that does not contain teeth, hooks, cutting plates or other ancillary structures. The elongate esophagus is slightly swollen where it joins the tubular intestine. Mature worms are sexually dimorphic, with females being larger than males (0.8-1.0 x 0.03 mm cf. 0.7-0.8 x 0.04 mm). Males have a well-developed copulatory bursa with 2 large lateral lobes, each supported by 5 rays (comprising muscular elements following nerve channels to terminal papillae) arranged in a 2-1-2 configuration, and a smaller dorsal lobe (supported by a single short dorsal ray). They have 2 stout equal spicules 40-50 µm long, each with a longitudinal split, but they do not have a gubernaculum or telamon. Female worms are readily identified by their characteristic tails bearing 3 major bumps (cusps or tubercles) which are occasionally accompanied by up to 3 minor ones. They are monodelphic with a single ovary and uterus opening into a posterior vulva without a muscular ovejector. Mature females are viviparous as they produce 1-3 large eggs at a time that embryonate and hatch internally releasing L3.

Site of infection: Adult worms infect the fundus of the stomach, and are usually found covered in mucus with their anterior ends partly embedded in gastric crypts. There are essentially no free-living stages as female worms do not produce eggs but release L3 which exit the host in vomitus.

Pathogenesis: Most infections appear to be light and remain asymptomatic, but heavier or prolonged infections have been causally associated with intermittent vomiting in felids, sometimes in suids but rarely in canids. Immature and mature worms bury their heads in the gastric mucosa causing a mild erosive or catarrhal gastritis. The inflammation and excessive mucus production predisposes vomiting, often minutes or hours after eating. Heavy infections may result in severe chronic gastritis with mucosal erosion, hyperplasia, sclerosis and cellular infiltration with lymphoid aggregates and leucocytosis. Animals display recurrent vomiting contributing to dehydration, anorexia, weight loss and emaciation, sometimes culminating in death. Clinical infections have been recorded in domestic and stray cats, as well as in colony-reared cats and captive zoo animals (cheetahs, lions and tigers).

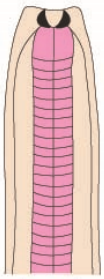
Developmental cycle and mode of transmission: *Ollulanus* has a simple direct monoxenous life-cycle, but its transmission is highly unusual in that infective larvae are transmitted via vomitus (and not by the faecal-oral transmission of worm eggs and the development of infective larvae on pastures). Viviparous females in the stomach mucosa produce and release L3 into the gut lumen which are then passed into the external environment in host vomitus (normally comprising undigested or partly digested food covered in mucus). Infective L3 have been found to survive in vomitus for up to 12 days and horizontal transmission to new susceptible hosts occurs when they ingest contaminated vomitus. The same individual host may also become re-infected by consuming its own vomitus, or when L3 in the stomach directly initiate a new cycle of development. Heavy infections therefore develop in individuals exhibiting regular vomition, although they can also build up by repetitive endogenous auto-infection. Infective L3 moult in the gastric mucosa to L4 and then to subadults (sometimes designated L5) which subsequently mature and mate. The prepatent period (time from infection to first release of L3) was found to range from 28-37 days. Worm burdens in domestic cats may involve only a few worms, although clinical infections often involve several hundred worms (mean intensity of 1,500 reported in several surveys) with occasional reports as high as 11,000 worms. While it has been suggested that long-haired cats may be more likely to transmit infections due to their greater frequency of vomition associated with hairball development after grooming, the most intense and severe infections have been observed in stray cats (that vomit from hunger) and in felids kept in crowded situations (zoos and animal breeding colonies).

Differential diagnosis: Clinical infections may be suspected in animals exhibiting regular vomition and weight loss, but many other gastroenteric pathogens may cause similar nonspecific signs. Diagnosis is usually afforded by the microscopic detection of larvae, sometimes adult worms, in vomitus (natural or following emesis) or in gastric lavages or endoscopic biopsies. Worms may be recovered from digesta and mucus by repeated dilution and sedimentation, or concentrated using sieves and funnels (e.g. Baermann's apparatus) using vomitus instead of faeces (parasites passing posteriad are digested and rarely seen in faeces). Mucosal scrapings can be taken post-mortem from dead or euthanized animals and examined for parasites, often following peptic digestion. In all instances, careful microscopy is required to differentiate larvae and adult worms from a range of other nematode parasites (e.g. *Aelurostrongylus abstrusus*, *Aonchotheca* (*Capillaria*) *putorii*, *Physaloptera* and *Trichostrongylus* spp.) and pseudo-parasites (e.g. oxyurids of small prey animals eaten by felids).

Treatment and control: A range of anthelmintic drugs have been used to treat clinical infections in felids and suids, including macrocyclic lactones (ivermectin), benzimidazoles (fenbendazole, oxfendazole) and imidazothiazoles (levamisole, tetramisole). Repeated treatments were recommended to combat cyclic re-infection and auto-infection, although no endogenous developmental stages (L3, L4 and adults) appeared to be resistant to treatment. Control strategies involve restricting host access to infective material by improving hygiene (removing vomitus, disinfecting pens/cages/runs), isolating individuals (for treatment and to prevent unnecessary interactions) and ensuring housing facilities are secure (particularly against strays).

Ollulanus

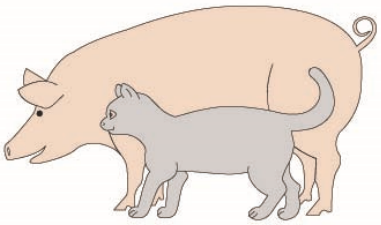
stomach
(gastritis, vomiting,
emaciation)



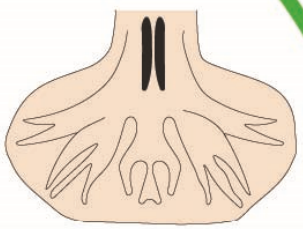
head

adult
female
(~ 1 mm)

adult
male
(~ 0.8 mm)



Definitive Hosts
(carnivores, suids)



male tail

L3 shed
in vomitus

infection by ingestion of L3
(sometimes auto-infection by L3)

females are viviparous
and release L3

third-stage larvae
(L3) (~ 500 µm)

external
environment

Ollulanus adult worm, female

Ollulanus adult worm, male