Triodontophorus/Oesophagodontus
(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 strongylids which are stout worms with a large buccal capsule often armed with teeth and with a leaf crown around the mouth. Small and large species occur in the intestinal or respiratory mucosa of domestic animals and birds. They have direct life-cycles where eggs passed in faeces develop to L3 (L2 cuticle retained as a sheath). Hosts ingest L3 which exsheath, invade the mucosa and moult into L4 before returning to the lumen to moult into adults. *Triodontophorus, Oesophagodontus* and *Craterostomum* species are non-migratory strongyles of the caecum/colon, which can contribute to poor body condition in equids worldwide. These genera were conventionally classified together with *Strongylus* as large strongyles, but molecular-genetic studies found them to group together with the small strongyles.

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:	Strongylidae (strongyles, large buccal capsules, often with teeth/leaf crown, equid hosts) [originally classified as large strongyles in the subfamily Strongylinae on the basis of similar morphotypic features, but recently realigned with the small strongyles in the subfamily Cyathostominae on the basis of molecular studies]
Genus:	*Triodontophorus* (parasitic in caecum/colon of equines)
Genus:	*Oesophagodontus* (parasitic in caecum/colon of equines)
Species:	various species cause unthriftiness in horses

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 microbes 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**
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
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
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

Strongyle worms are characterised by their prominent buccal capsules with lips, leaf crowns or labial collars at the mouth opening, sometimes with teeth or cutting plates. They are parasitic in a variety of organ systems in a range of animals, including the large intestines of mammals (ruminants, suids, elephants, perissodactyls, rodents, marsupials and primates), tortoises and ratite birds, the forestomach of marsupials, the trachea of birds and mammals, and the renal system of suids. Four families are recognised: Strongylidae (buccal capsule globular or cylindrical, oral opening circular, dorsal ray with 6 terminal branchlets, 32 genera in large intestines of mammals, reptiles and birds); Chabertiidae (buccal capsule globular or cylindrical, oral opening circular or oval, with leaf crown or labial collar, with up to 3 teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 22 genera in gastrointestinal tract of mammals); Syngamidae (buccal capsule subglobular, oral opening hexagonal, numerous teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 7 genera in respiratory, urinary and digestive tracts of mammals and birds); and Deletrocephalidae (oral opening hexagonal, dorsal ray with 6 terminal branches, 2 genera in large intestines of birds). The family Strongylidae contains 2 subfamilies conventionally differentiated on worm size and buccal capsule morphology: namely, Strongylinae ('large' strongyles (or strongylins) with globular or funnel-shaped buccal capsules) parasitic in the large intestines of perissodactyls, elephants and ratite birds (sometimes undergoing extra-intestinal migration); and Cyathostominae ('small' strongyles (or trichonemes, cyathostomes, cyathostomines, cyathostomins) with cylindrical or ring-shaped buccal capsules) found in the large intestines of perissodactyls, elephants, hyracoids, tortoises and occasionally some artiodactyls. Contemporary molecular characterization studies, however, do not fully support the separation of these subfamilies as several 'large' strongyles group together with the 'small' strongyles.

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Worm eggs
Strongylinae (‘large’ strongyles or strongylins)					
Triodontophorus, Oesophagodontus, Craterostomum, Bidentostomum	11	equids	large intestines	6-25 mm long, globular or funnel-shaped buccal capsule often with teeth, leaf crowns [*despite their large strongyle features, molecular studies group them with the small strongyles]	66-130 x 33-68 µm. ellipsoidal, thin-shelled
Strongylus (redworms)	13	ungulates, esp. equids	large intestines	10-50 mm long, red colouration, large globular buccal capsule often armed with teeth, leaf crowns, L3 with long filamentous sheath	64-99 x 36-58 µm, ellipsoidal, thin-shelled
Cyathostominae (‘small’ strongyles* or cyathostomins)					
Cyathostomum, etc.	6	equids	large intestines	5-30 mm long, red-grey colouration, cylindrical buccal capsule, with labial collar, some with dorsal gutter, external and internal leaf crowns variable	35-150 x 17-68 µm, ellipsoidal, thin-shelled

The subfamily Strongylinae conventionally contains 11 genera: 7 typified as large strongyles (*Strongylus* (syn. *Sclerostoma*, *Sclerostomum*, *Alfortia*, *Delafondia*) in equids; *Choniangium, Decrusia, Equinurbia* in elephants; *Codiostomum* in ostriches; *Macropicola* and *Hypodontus* in macropodid marsupials); and 4 other genera (*Triodontophorus* (syn. *Triodontus*)*, Bidentostomum, Craterostomum,* and *Oesophagodontus* (syn. *Pseudosclerostomum*) in equids, originally considered to be large strongyles. However, recent molecular-genetic studies have grouped them together with the small strongyles. The latter 4 genera comprise medium-sized worms with subglobular or funnel-shaped buccal capsules, mouth collars associated with submedian papillae, external and internal leaf crowns with similar or dissimilar elements, males with 3 pairs of branches in the dorsal ray of the bursa, spicules with pick-like or hooked tips, and females with oval or Y-shaped ovejectors. They are parasitic in the large intestines of equids throughout the world and have been associated with poor performance and body condition. Endoparasitic larval stages undergo histotrophic development in the intestinal mucosa but they do not undertake extra-intestinal migration like other large strongyles (*Strongylus* spp.). Infections are transmitted by the contamination of pastures with worm eggs from which infective larvae develop.

Parasite species	Definitive Hosts	Location [Clinical signs]	Distribution
Triodontophorus			
T. brevicauda	Perissodactyla: equid (horse, Przewalski’s horse, donkey, mule, onager, plains zebra)	large intestines [poor condition]	worldwide
T. burchelli	Perissodactyla: equid (donkey, Burchell’s zebra)	large intestines	Africa
T. hartmannae	Perissodactyla: equid (donkey, mountain zebra)	large intestines	Africa
T. minor (syn. Triodontus)	Perissodactyla: equid (horse, donkey, onager)	large intestines [poor condition]	worldwide
T. nipponicus (syn. *T. brochotrilobulatus, T. hsiungi)*	Perissodactyla: equid (horse, Przewalski’s horse, donkey, onager, mountain zebra)	large intestines [poor condition]	Eurasia, Americas
T. serratus (syn. *T. intermedius, Triodontus*)	Perissodactyla: equid (horse, Przewalski’s horse, donkey, mule, onager, plains zebra, mountain zebra); Artiodactyla: suid (pig)	large intestines [poor condition]	worldwide
T. tenuicollis (syn. *T. popovi)*	Perissodactyla: equid (horse, Przewalski’s horse, donkey, onager, plains zebra)	large intestines [poor condition]	worldwide
Oesophagodontus			
O. robustus (syn. *Sclerostomum, Strongylus, Pseudosclerotomum securiferum*)	Perissodactyla: equid (horse, donkey, mule, plains zebra)	large intestines [poor condition]	worldwide
Craterostomum			
C. acuticaudatum (syn. *Cylicostomum, C. mucronatum*)	Perissodactyla: equid (horse, Przewalski’s horse, donkey, mule, onager, plains zebra, Hartmann’s mountain zebra)	large intestines [poor condition]	worldwide

C. tenuicauda	Perissodactyla: equid (horse, plains zebra)	large intestines [poor condition]	Africa, Asia
Bidentostomum			
B. ivashkini	Perissodactyla: equid (horse, mule)	large intestines	Asia

Parasite morphology: These strongyles form 3 different morphological stages in their developmental cycles: eggs; larvae (4 stages designated L1-L4); and adult worms. Gravid female worms lay typical strongyle eggs which are ovoid in shape, surrounded by a smooth thin eggshell and containing a morula at the 4-8 cell (blastomere) stage of development. Eggs range in size from 66-130 x 33-68 µm, with some variation observed among genera (see following Table). L1 and L2 are free-living rhabditiform stages, measuring from 480-700 µm in length, with rounded heads, short cylindrical buccal capsules, bulbed oesophagi, and long slender tails. L3 are ensheathed filariform larvae which are initially free-living, but become parasitic when ingested by suitable hosts. The sheath is formed by retention of the L2 cuticle as a protective covering and it characteristically has a long filamentous tail. L3 are 500-670 µm long and have conical heads with small buccal cavities, a long thin strongyliform oesophagus, and intestines consisting of 16-20 cells. Genera may sometimes be differentiated on the basis of the morphological characteristics of L3: *Triodontophorus* L3 have intestines with 18-20 well-defined rectangular cells; *Craterostomum* L3 have intestines with 16 rectangular cells arranged in a double row anteriorly and a single row posteriorly; and *Oesophagodontus* L3 have intestines with 16-18 elongate or triangular cells in a double row. L4 are parasitic stages that feed on host tissues while growing markedly in size (from 1.2-7.8 mm depending on species) and they have well-developed buccal capsules, 3 stout and pointed oesophageal teeth, and immature genitalia.

Genus	***Triodontophorus***	***Oesophagodontus***	***Craterostomum***	***Bidentostomum***
Egg size	66-122 x 33-68 µm	88-130 x 40-60 µm	120 x 60 µm	101-107 x 51-52 µm
L3 intestines	18-20 rectangular cells	16-18 elongate/triangular cells in a double row	16 rectangular cells	?
Adult mouth collar	inflated round tube	flattened, sharp peripheral ridge	flattened, divided into 2 rings	flattened, divided into 2 rings
Adult oesophageal teeth	3 large projecting teeth	3 lancet non-projecting teeth	3 small non-projecting teeth	3 large projecting teeth
ELC cf. ILC elements (external cf. internal leaf crowns)	equal no. (44-73) but longer	similar but fewer (18 cf. 34-48)	longer, thinner, fewer (8 cf. 23-24)	similar but fewer (8 cf. 16)

Adult worms measure from 6-24 mm in length, being smaller in size than *Strongylus* spp. and similar in size to the small strongyles (cyathostomins). Although molecular-genetic studies group these genera with the small strongyles, they possess morphological features consistent with large strongyles (*Strongylus*), notably a globular buccal capsule (funnel-shaped in *Oesophagodontus*) armed with 3 oesophageal teeth (see Table). Adult worms also have distinctive arrangements of complex cephalic structures, comprising mouth collars, cephalic papillae, corona radiata (external leaf crowns (ELC) and internal leaf crowns (ILC)), extra-chitinous supports, dorsal gutters, and oesophageal funnels. The genus *Triodontophorus* has a mouth collar resembling an inflated round tube, whereas the genera *Oesophagodontus*, *Craterostomum* and *Bidentostomum* have flattened mouth collars, with those of the latter 2 genera divided into inner and outer rings. The buccal capsule of *Triodontophorus* has a thickened anterior rim and is surrounded by 6 plate-like structures, that of *Oesophagodontus* has a posterior collar, and those of *Craterostomum* and *Bidentostomum* are thickened anteriorly. The dorsal gutter is elongate in *Triodontophorus* and *Craterostomum,* button-like in *Bidentostomum,* and inconspicuous in *Oesophagodontus.* The elements of the ELC and ILC may be similar in appearance but fewer in number (*Oesophagodontus, Bidentostomum*), dissimilar and fewer (*Craterostomum*) or dissimilar and equal in number (*Triodontophorus*). The oesophageal teeth of *Triodontophorus* and *Bidentostomum* project up into the buccal capsule, but those of *Oesophagodontus* and *Craterostomum* do not. Adult worms are sexually dimorphic, with female worms being larger than males (*Craterostomum* females 6-11 mm cf. males 6-10 mm; *Bidentostomum* 9-10 cf. 8-9 mm; *Triodontophorus* 10-20 cf. 8-20 mm; and *Oesophagodontus* 19-25 cf. 15-20 mm). Males have a well-developed copulatory bursa consisting of 2 lateral lobes and a long dorsal lobe. The lateral lobes are supported by 6 rays (comprising muscular elements following nerve channels to terminal papillae) where the ventral rays are shorter or equal to the lateral rays, and the externodorsal rays begin at the junction of the dorsal and lateral lobes. The dorsal lobe is supported by an elongate dorsal ray with 6 branches arising from 3 bifurcations. Males also have a narrow gubernaculum with a small handle and an enlarged distal tip (sometimes with a ventral notch or groove), an elongate genital cone extending beyond the bursal edge, and 2 filiform equal spicules with hook-shaped tips (*Triodontophorus*, *Bidentostomum*) or straight tips (*Oesophagodontus*, *Craterostomum*). Female worms are didelphic with 2 ovaries, 2 oviducts, 2 uteri and 2 ovejectors connected through an oval or Y-shaped vestibule to a common vagina leading to a vulva located in the posterior body but anterior to the anus. Females have tails that may be long, short, conical or pointed. Mature females are oviparous in that they produce and lay partially-embryonated eggs.

Site of infection: Adult worms infect the large intestines of their hosts, and are found in the lumen of the caecum and colon, whereas larval stages migrate into and develop within the intestinal mucosa. Free-living larval stages emerge from worm eggs deposited on pastures in host faeces.

Pathogenesis: Infections by these strongyles have been implicated in loss of condition and ill-thrift in equids, but their contribution is unclear, as they usually occur in mixed infections with other large and small strongyles. Adult worms feed on host mucosa causing traumatic damage, petechial haemorrhages, inflammation and ulceration contributing to anaemia, diarrhoea, weakness and poor condition. *Triodontophorus* worms may cause deep ulceration in the right dorsal colon resulting in significant haemorrhage and blood loss. However, the preceding larval stages do not undertake extensive somatic (extra-intestinal) migrations and appear not to cause severe pathological changes like *Strongylus* spp. Instead, they invade the intestinal mucosa where they encyst and undergo histotrophic development before being released back into the gut lumen. They are often referred to as the large non-migratory strongyles and infections have not been associated with acute morbidity or mortality, but rather with cumulative deleterious health effects attributable to mixed strongyle infections.

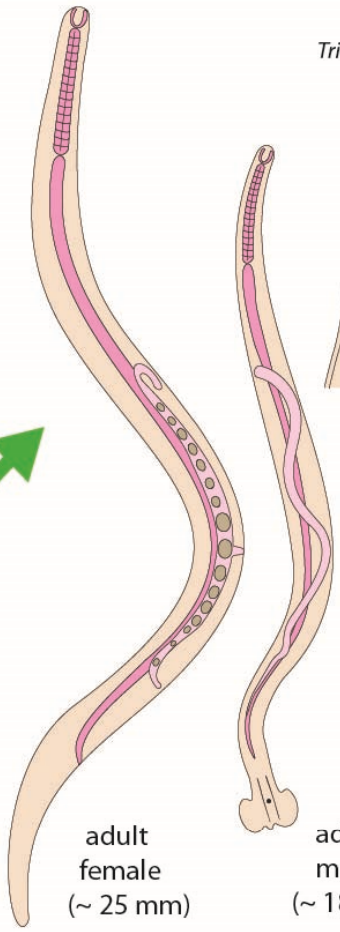
Developmental cycle and mode of transmission: These parasites have direct monoxenous life-cycles involving faecal-oral transmission. Gravid female worms lay eggs that are passed into the external environment with host faeces. The eggs embryonate and hatch after several days releasing free-living L1 which feed on microbes before moulting to L2 which also feed. Eventually they moult to L3 but retain the L2 cuticle as a protective sheath which prevents them from feeding. Development from egg to infective L3 usually takes around 2 weeks in temperate zones, but may be more rapid in warmer regions. L3 exhibit both horizontal migration (dispersal from faeces) and vertical migration (ascending vegetation), particularly in moist conditions. Hosts become infected when they ingest infective L3 on pasture when grazing. The ingested L3 exsheath in the gut and invade glands in the wall of the large intestines where they undergo histotrophic development (the larvae migrate into the intestinal wall but do not undergo extra-intestinal migration). L4 are released into the lumen of the intestines where they moult to young adults (sometimes designated L5) which feed, mature and mate. The prepatent period (time from infection to first release of eggs) is around 9 weeks.

Differential diagnosis: Infections are conventionally diagnosed by the direct detection of parasites, usually by the coprological detection of worm eggs in faecal samples following their concentration by sedimentation in water and floatation in saturated sugar or heavy metal salt solutions, and sometimes by the microscopic detection of larvae in faecal samples. Strongyle eggs cannot be identified reliably to species or genus because of their similar morphologies. Faecal samples may be cultured to yield L3 which allows some genera to be identified on the basis of larval morphology (notably gut anatomy involving the number, shape and configuration of intestinal cells). Unfortunately, coprocultures usually take 2 weeks to perform, and they usually yield numerous larvae of different species, which cannot be identified accurately to genus and species. Infections may be diagnosed by the microscopic identification of worms from gut samples collected at post-mortem, with *Triodontophorus* worms reported to cluster together around colonic ulcers. Molecular biological techniques have been used to characterize large non-migratory strongyles following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (ribosomal RNA), with the results showing clear phylogenetic relationships with small strongyles (cyathostomins).

Treatment and control: A range of anthelmintic drugs have been used to treat infections in horses, including benzimidazoles (e.g., fenbendazole, oxfendazole), tetrahydropyrimidines (pyrantel salts), and macrocyclic lactones (ivermectin, moxidectin, abamectin) which have been effective against gut stages of the parasites (in the absence of drug resistance). It has been recommended that drugs be used judiciously to avoid the development and spread of drug resistance in worm populations, including strategic drenching of particular age groups (e.g., foals) and considering time of the year (season, depending on climatic zone), rotation of anthelmintic classes and rotational grazing with species other than horses (e.g. sheep or other ruminants – which only have *Trichostrongylus axei* (parasite of the stomach) in common with equids). Levels of anthelmintic resistance to particular compounds (classes) can be monitored using faecal egg count reduction tests (FECRT), conducted according to internationally accepted guidelines (cf. World Association for the Advancement of Veterinary Parasitology (WAAVP)). At the farm level, integrated control strategies may also include the reduction of environmental contamination by worm eggs and free-living larvae in the environment (by removing and composting faeces, mixed grazing or pasture spelling).

Triodontophorus, Oesophagodontus

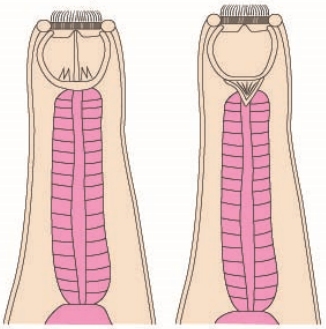
intestines
(diarrhoea, anaemia,
unthriftiness)



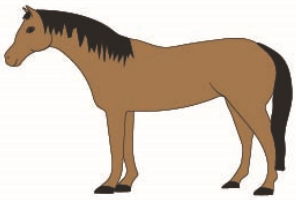
adult
female
(~ 25 mm)

adult
male
(~ 18 mm)

Triodontophorus *Oesophagodontus*



heads

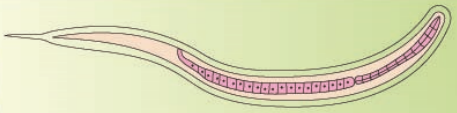


Definitive Hosts
(perissodactyls)

male tail
(lateral)

L3
ingested

eggs
excreted
in faeces

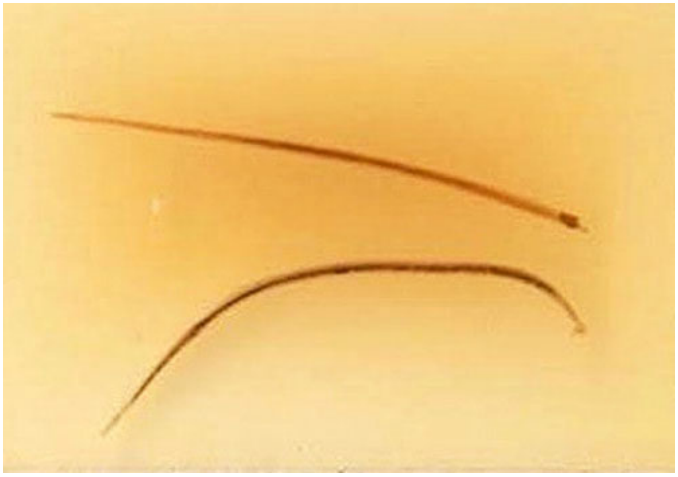


filariform third-
stage larvae (L3)
(~ 600 µm)

external
environment

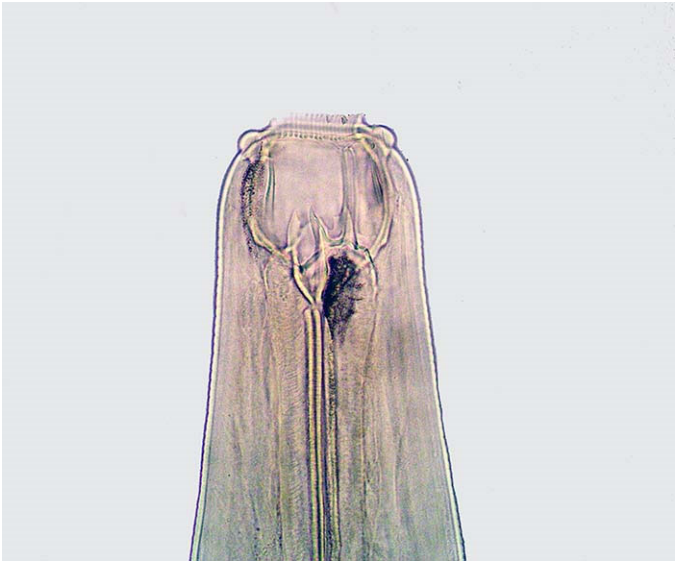
eggs
(~ 100 µm)

rhabditiform first- and
second-stage larvae (L1, L2)
(~ 500 µm)



Triodontophorus adult worms

Triodontophorus worm egg



Triodontophorus adult worm, head