

Hyostrongylus

(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 stronglyloid 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 trichostrongyles 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 where eggs passed in faeces develop to L3 (L2 cuticle retained as a sheath). Hosts ingest L3 which exsheath, migrate into the mucosa and moult into L4 (some may undergo arrested development, termed hypobiosis) before returning to the lumen to moult into adults. *Hyostrongylus* (red stomach worm) causes diarrhoea and wasting in pigs, but can be readily controlled in intensive piggeries.

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: Trichostrongylidae (hair-like, lips absent/reduced, oesophagus lacking bulb, thin-shelled eggs, direct cycles)
Genus: *Hyostrongylus* (parasitic in stomach of pigs)
Species: *H. rubidus* causes diarrhoea and wasting in pigs

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 Chromadorea 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 IH)
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)				
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
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

The family Trichostrongylidae contains small hair-like worms that infect the gastrointestinal tracts of herbivorous animals, many species causing disease and production losses in ruminant livestock worldwide. Adult worms have a rudimentary buccal cavity with reduced or absent lips but some taxa possessing teeth. Male worms have a well-developed bursa and spicules, and the larger female worms lay thin-shelled eggs that are in the morula stage. Trichostrongyles have direct life-cycles whereby eggs embryonate and hatch in the external environment releasing rhabditiform larvae which grow in soil or on vegetation. These larvae moult to form infective filariform larvae (L3) which are ingested by grazing animals. Various anatomical features have been used to characterize taxa, including patterns of longitudinal ridges (synlophe) on the external cuticular surface as well as structure of the male bursa (arrangement of dorsal, ventral and lateral lobes and supporting rays) and spicules (number, size and shape). Over 50 trichostrongylid genera have been allocated to 8 subfamilies: Trichostrongylinae (reduced synlophe, wide bursa, short twisted spicules, 6 genera in mammals and birds); Amidostomatinae (with buccal teeth or extra-buccal appendages, 8 genera in birds); Filarinematinae (neodont formation, long bursa, 3 genera in marsupials); Haemonchinae (well-developed synlophe, neodont formation, 5 genera in ungulates); Ostertagiinae (well-developed synlophe, modified bursa, 15 genera in mammals); Cooperiinae (symmetrical synlophe, bursa with symmetrical dorsal rays, 12 genera in ruminants); Libyostrongylinae (without synlophe, modified bursa, 5 genera in mammals and birds); and Obeliscoidinae (without synlophe, symmetrical bursa, 5 genera in mammals and birds). Note that some taxonomic classifications have split these 8 subfamilies between 3 separate sister families: with Trichostrongylinae, Amidostomatinae and Filarinematinae allocated to a restricted Trichostrongylidae (cephalic vesicle absent, synlophe reduced or absent, male bursa with short dorsal ray and long lateral lobes); Haemonchinae and Ostertagiinae assigned to the Haemonchidae (cephalic vesicle absent, synlophe present without any specific orientation, male bursa with short dorsal rays, often asymmetrical); and Cooperiinae, Libyostrongylinae and Obeliscoidinae placed in the Cooperiidae (cephalic vesicle present, synlophe bilaterally symmetrical or absent, large male bursa with curved lateral rays). Several other genera have recently been transferred to other taxa

on the basis of cladistic or molecular phylogenetic studies; mostly those in the subfamily Nematodirinae (6 genera in mammals) now classified in the family Molineidae. Specific trichostrongylid genera of veterinary and medical importance are compared in the following table.

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Worm eggs
Subfamily Ostertagiinae (well-developed synlophe, modified bursa)					
<i>Hyostrogylus</i> (red stomach worm)	4	suids, lagomorphs	stomach	4-10 mm long, red coloration, well-developed bursa, gubernaculum, telamon, larval hypobiosis	60-90 x 31-42 µm, ovoid, thin-shelled
<i>Ostertagia</i> (brown stomach worm)	32	artiodactyls	abomasum	6-15 mm long, small buccal cavity, ridged synlophe, small vulval flap, bursa with 5 lateral rays (2-1-2) and proconus, larval hypobiosis	60-100 x 38-50 µm, ellipsoidal, thin-shelled
<i>Teladorsagia</i> (brown stomach worm)	9	artiodactyls	abomasum	10-15 mm long, small buccal cavity, ridged synlophe, small vulval flap, bursa with 5 lateral rays (2-2-1) and proconus, larval hypobiosis	60-100 x 40-50 µm, ellipsoidal, thin-shelled
Subfamily Trichostrongylinae (reduced synlophe, wide bursa, short twisted spicules)					
<i>Trichostrongylus</i> (hairworm, black scour worm)	56	artiodactyls, lagomorphs, rodents, birds	small intestines, stomach	2-10 mm long, rudimentary buccal cavity, distinct excretory notch in oesophageal region, male bursa with long lateral lobes	75-125 x 31-72 µm, ellipsoidal, thin-shelled
Subfamily Haemonchinae (well-developed synlophe, neodont formation)					
<i>Haemonchus</i> (barber's pole worm)	15	artiodactyls	abomasum	10-40 mm long, buccal capsule with tooth, white spiral ovaries, prominent vulval flap, bursa with asymmetrical dorsal ray, larval hypobiosis	62-90 x 40-50 µm, ellipsoidal, thin-shelled
Subfamily Cooperiinae (symmetrical synlophe, bursa with symmetrical rays)					
<i>Cooperia</i> (wire worm)	24	artiodactyls	small intestines, stomach	4-15 mm long, often coiled, bulbous cephalic vesicle, large bursa, large spicules, larval hypobiosis	65-95 x 29-44 µm, ellipsoidal, thin-shelled

The subfamily Ostertagiinae was erected for genera with an accessory bursal membrane and other characters include a head region with a small restricted cephalic vesicle, small cervical papillae and prominent transverse striations, and a body with numerous longitudinal cuticular ridges. Some 23 genera have been reported from ruminants, hippopotami, lagomorphs and suids: namely, *Africanostrongylus*, *Apteragia*, *Camelostrogylus*, *Cervicaprastrongylus*, *Graphidium*, *Grosspiculagia* (syn. *Ostertagiella*), *Hamulonema*, *Hyostrogylus* (syn. *Bergheia*), *Longistrogylus* (syn. *Bigalkea*, *Bigalkenema*, *Kobusinema*), *Marshallagia*, *Mazamastrongylus*, *Orloffia*, *Ostertagia* (syn. *Capreologia*, *Gruhneria*, *Muflonagia*, *Ostertagiana*, *Sjobergia*, *Skrjabinagia*), *Ostertamia*, *Paramecistocirrus*, *Pseudommarshallagia*, *Rinadia*, *Robustostrogylus*, *Sarwaria*, *Spiculoptera* (syn. *Altaevia*), *Spiculopteroides*, *Teladorsagia* (syn. *Paramecistocirrus*, *Stadelmania*), and *Tunisostertagia*. Some members of the Ostertagiinae have been allocated to 2 groups; one characterised by bursal type 2-1-2 (ray 2 grouped with ray 3, isolation of ray 4, ray 5 grouped with ray 6) including *Graphidium*, *Marshallagia*, *Longistrogylus* and *Ostertagia*; and another characterised by bursal type 2-2-1 (ray 2 grouped with ray 3, ray 4 grouped with ray 5, isolation of ray 6) including *Hyostrogylus*, *Spiculoptera*, *Teladorsagia* and *Gazellostrongylus*. The bursal characteristics of members of the genus *Hyostrogylus* also include well-developed lateral lobes, a short dorsal lobe (dorsal ray with 3 branches), a genital cone with 2 small dorsal raylets, and elongate tapering spicules. Several species have been described from the stomachs of mammals (artiodactyls, lagomorphs and primates), where developmental stages may damage the mucosa resulting in gastritis, maldigestion, diarrhoea and poor body condition (particularly in free-range pigs infected with *H. rubidus*). The parasites have direct monoxenous life-cycles involving the faecal-oral transmission of larvae on pastures.

<i>Hyostrongylus</i> species	Definitive hosts	Location [Clinical signs]	Distribution
<i>H. rubidus</i> (red stomach worm) (syn. <i>Strongylus attenuatus</i> , <i>molini</i> , <i>rubida</i> , <i>Ostertagia</i>)	Artiodactyla: suid (pig), tayassuid (white-lipped peccary), bovid (cattle, sheep, red forest duiker); Lagomorpha: leporid (rabbit); Rodentia: caviid (guinea pig)	stomach [diarrhoea]	worldwide
<i>H. kigeziensis</i>	Primates: hominid (western gorilla, mountain gorilla)		Africa
<i>H. okapiae</i> (syn. <i>Bergheia</i>)	Artiodactyla: giraffid (okapi)		Africa
<i>H. vinnica</i>	Artiodactyla: bovid (sheep, cattle)		Russia
Re-assigned species			
<i>H. gabonensis</i> (now <i>Cervicaprastrongylus</i>)	Artiodactyla: tragulid (water chevrotain)		Africa
<i>H. malviyai</i> (now <i>Cervicaprastrongylus</i>)	Artiodactyla: bovid (blackbuck)		India
<i>H. moreli</i> (now <i>Cervicaprastrongylus</i>)	Lagomorpha: leporid (Cape hare)		Africa

Parasite morphology: *Hyostrongylus* spp. form 3 morphologically distinct stages during their development: membrane-bound eggs; fusiform larvae (4 stages coded L1-L4); and sexually dimorphic adults. Gravid females lay thin-walled ovoid eggs ranging in size from 60-90 x 31-42 µm (note that some texts incorrectly give a smaller egg size (45 x 36 µm) found to be due to a scaling error in the original description). Freshly laid eggs are brown in colour and contain a morula (16-64 cell stage) that almost fills the interior. Eggs hatch releasing free-living (pre-parasitic) first-stage larvae (L1) that initially measure from 280-300 µm but grow up to 550 µm after feeding on bacteria. They have a rounded head, a rhabditiform oesophagus with a posterior bulb, and a slender pointed tail. They moult to form rhabditiform L2 which are similar to L1 but measure up to 700-750 µm in length. L2 moult to form L3 which retain the L2 cuticle as a close-fitting protective sheath. L3 are active but non-feeding free-living stages that are infective to their vertebrate hosts. Infective L3 measure from 715-735 µm in length (sometimes up to 1,000 µm) and have a squared head, a short buccal capsule, a strongyliiform (non-bulbed) oesophagus, intestines comprising 16 cells, a tapering tail with a small digitiform process, and a short tail sheath extension. Following ingestion and exsheathment, L3 invade host tissues and moult to L4 which grow up to 2-3 mm in length and begin to show distinct genitalia (esp. male bursa and female vulva). L4 eventually moult to form young adults (sometimes called L5 or subadults) which then develop into reproductive adults. Mature worms are bright red-pink in colour and slender and hair-like in shape ranging from 4-10 mm in length. They have a small cephalic vesicle with a small buccal cavity lacking teeth (neodont formation absent) and are bound by a well-developed synlophe with numerous (40-45) symmetrical longitudinal ridges. Adults lack an excretory notch (present in the genus *Trichostrongylus*) but they have 2 small cervical papillae projecting above the body surface (smaller than those present in the genus *Haemonchus*). They have a strongyliiform oesophagus leading to elongate intestines ending in a subterminal anus/cloaca. Female worms are larger than males (6-10 mm cf. 4-7 mm) and they have 2 ovaries (didelphic) connected to uteri opening into a posterior vulva surrounded by irregular cuticular inflations (rather than a vulval flap like other trichostrongyles). Mature males have a large copulatory bursa with 2 large lateral lobes and a short symmetrical dorsal lobe (cf. asymmetrical in *Haemonchus*). The lateral lobes have 5 lateral rays (comprising muscular elements following nerve channels to terminal papillae) arranged in a 2-2-1 configuration (ventral rays together, anterolateral and mediolateral rays close together, and posterolateral rays separate) and the dorsal lobe has a single ray which divides into 3 branches. The genital cone has a small proconus (ventral swelling) and a simple rectangular accessory bursal membrane supported by 2 widely-separated dorsal raylets. Males also possess a gubernaculum with a telamon and 2 short tapering spicules with a main stem and 2 slender distal branches (ventral and dorsal).

Site of infection: Developing larval stages invade the gastric pits and glands in the glandular portion of the stomach, while adult worms occur on the mucosal surface. Free-living stages (eggs and L1-L3) contaminate the external environment and may be found in faecal material, soil or on herbage.

Pathogenesis: Adult worms feed on host blood obtained through the stomach mucosa, while earlier developing larval stages penetrate the mucosa causing structural and functional changes contributing to maldigestion and malnutrition. Light infections are usually asymptomatic, but larger numbers of parasites may damage the mucosa, particularly during the prepatent period when larval stages are prevalent. Larvae penetrating gastric pits and glands cause inflammation (catarrhal gastritis) with excessive mucus production, nodule formation (sometimes confluent), mucosal erosion and ulceration, hyperaemia, haemorrhage, epithelial hyperplasia and metaplasia with loss of acid-producing parietal cells and pepsinogen-producing Chief (zymogen) cells leading to a failure to activate pepsin thereby significantly reducing digestive processes. A breakdown in tight epithelial junctions also results in

fluid and protein leakage into the tissues, circulation and gut lumen, contributing to oedema and hypoproteinaemia. Infected animals lose condition and may exhibit pallor, anaemia, inappetence, poor growth, weight loss or wasting with occasional bouts of diarrhoea. On occasion, adult pigs have died suddenly due to massive blood loss when mucosal ulcers perforate. Clinical disease is uncommon in growing pigs but adults may develop illthrift, particularly when exposed to high levels of infection when placed outdoors on contaminated pastures, or when hypobiotic larvae resume development. Animals do not develop a strong protective immunity and infections tend to accumulate with age. Hosts also seem to be more susceptible to clinical disease when stressed by poor nutrition, extended translocation, pregnancy and lactation. The so-called 'poor-sow' or 'thin-sow' syndrome is often due to persistent *H. rubidus* infection, often concomitantly with *Oesophagostomum* spp.

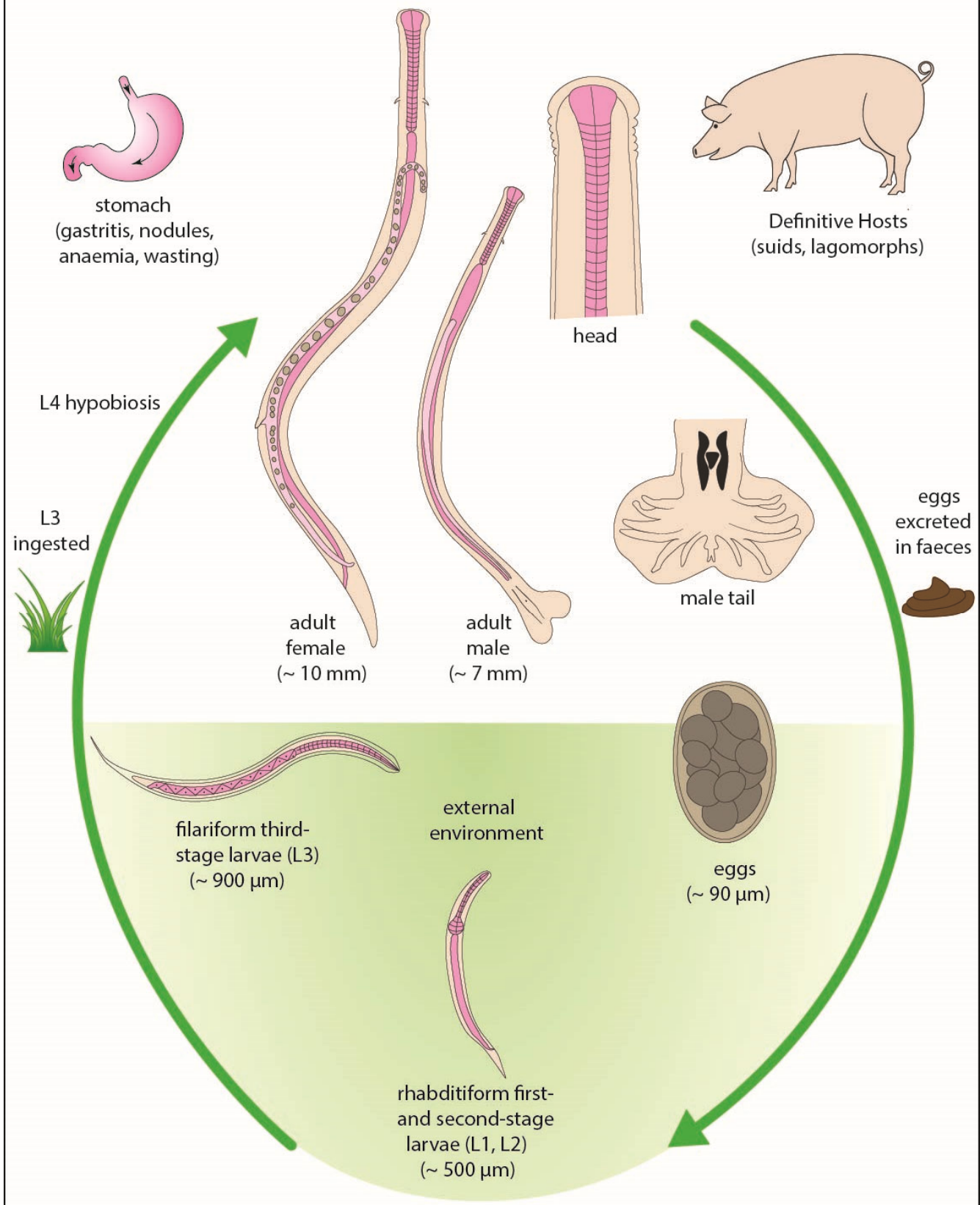
Developmental cycle and mode of transmission: *Hyostromylus* spp. have direct life-cycles with horizontal transmission occurring between individuals by the faecal contamination of pastures by worm eggs from which infective larvae arise to be ingested by foraging animals. Female worms have a low fecundity and only produce 10-50 eggs per day during patency. The eggs are voided with host faeces into the external environment where they embryonate and hatch around 5 days later releasing free-living rhabditiform L1 which feed on bacteria. L1 moult to form rhabditiform L2 which also feed before moulting to L3 which remain enclosed within the L2 cuticle and thus do not feed. Nonetheless, L3 are highly motile stages and they move out of faecal material into the soil and onto vegetation. Infective L3 may develop within 1-2 weeks under optimum conditions (15-20°C, 80-95% relative humidity) although their development may take longer under less ideal conditions and they are highly susceptible to cold and desiccation. Animals become infected by ingesting infective L3 when foraging or grazing. The L3 exsheath in the stomach and penetrate the mucosa where they moult to L4 in nodules in about 2 weeks. These larvae emerge onto the mucosal surface where they moult to young adults (often designated L5) which feed and mature to adult worms which subsequently mate. The prepatent period (time from infection to first egg production) is 18- 21 days, but may be considerably longer if L4 arrested their development for several months (process known as hypobiosis). Inhibition of larval development usually occurs over seasons when external environmental conditions are not conducive to the development and survival of free-living stages on pastures. How endoparasites know prevailing external conditions is unknown but hypobiosis may be induced by repeated infections (occurs more frequently in older animals), seasonal climatic variation (particularly over winter months in temperate regions) and changes in host physiology (larvae resume development when sows begin lactation). Established infections in pregnant animals also show a periparturient rise in egg production, presumably due to a relaxation or partial suppression of immunity. This results in a spring rise in environmental contamination which later places weaning animals at their greatest risk of infection as they begin foraging/grazing. Infections are mostly confined to animals raised outdoors or with access to contaminated pastures, whereas those raised indoors under intensive husbandry are least at risk as their stalls/pens are frequently cleaned. It is common practice in some temperate regions to keep breeding stock (gilts and sows) on pasture, resulting in significantly higher levels of infection.

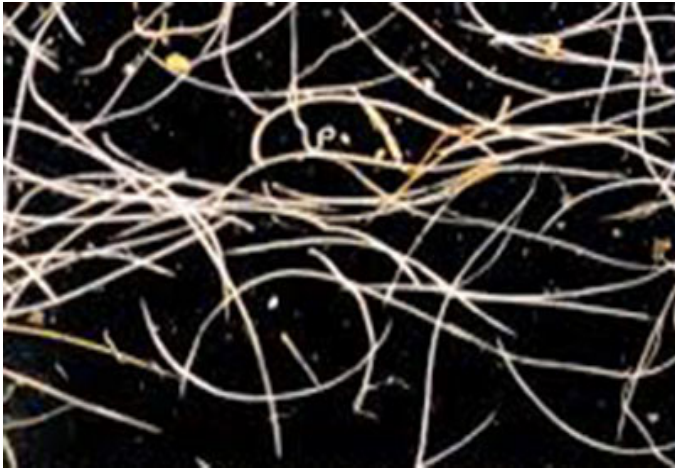
Differential diagnosis: Infections are difficult to diagnose on the basis of clinical symptomatology due to their nonspecific nature (often manifest only as illthrift). Coprological tests are therefore used to detect worm eggs in faecal samples after sedimentation in water and/or floatation in saturated sugar or salt solutions (eggs buoyant in media with high specific gravity). Several techniques are also quantitative in that the number of eggs counted in aliquots of diluted faeces in volumetric chambers (McMaster or Whitlock slides) may be used to calculate the number of eggs per gram of faeces (epg). However, coprological tests frequently demonstrated poor specificity (inconclusive negative results due to irregular egg excretion and low fecundity) and poor correlations with worm burdens (not accounting for developing larvae, males, or females not laying eggs because they are too young or too old). Egg morphology could also not be used for specific or even generic diagnosis, as *Hyostromylus* eggs are remarkably similar to those of *Oesophagostomum* spp. Recourse can be made to coprocultures whereby faecal samples are incubated for several days in funnels or petri dishes in order to harvest L3 for microscopic examination and identification. *Hyostromylus* L3 are slender active stages (often exhibiting a 'swimming' motion) with short tails ending in digitiform processes. In contrast, the L3 of *Oesophagostomum* are shorter, sluggish (do not 'swim') and have long filamentous tails without processes. Infections may also be diagnosed by the recovery and identification of adult worms in gut samples collected at post-mortem from dead or sacrificed animals. The stomach and intestines may be ligated, perfused with saline and the numbers of worms counted in gut washes (or sometimes mucosal digests to release tissue-bound larvae). A range of immunological tests (including precipitation, complement fixation, immunofluorescence, and enzyme immunoassays) have been used to detect specific host antibodies against worm antigens, but many demonstrated cross-reactivity problems with other nematodes. More recently, molecular biological techniques have been used to characterize parasites by polymerase chain reaction (PCR) amplification of specific nuclear gene sequences (ribosomal DNA).

Treatment and control: A range of anthelmintic drugs have been used to treat infections, with benzimidazoles (e.g. fenbendazole), probenzimidazoles (e.g. febantel), organophosphonates (e.g. dichlorvos) and macrocyclic lactones (e.g. doramectin, ivermectin) being effective against larval and adult worms, including hypobiotic larvae. Most drugs are available as oral formulations (drenches) although some may be administered percutaneously (injectables). Unfortunately, they do not have any persistent residual activity and animals quickly become re-infected when returned to contaminated pastures, so repeated treatments are required. Pregnant animals are treated to avoid periparturient rises in worm egg production, weaners are treated when they first begin to forage/graze,

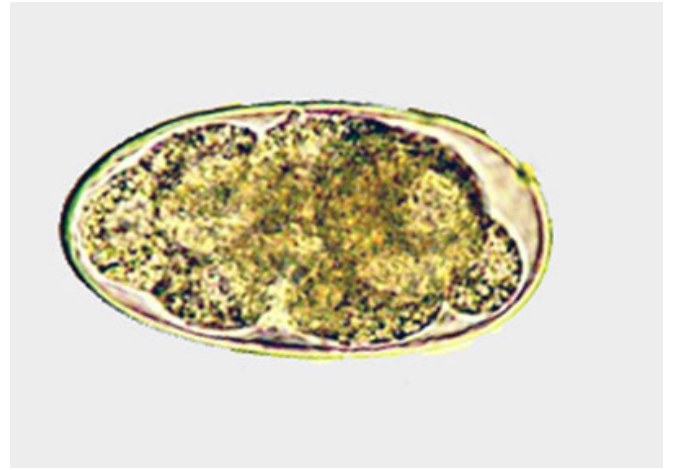
young adults are treated after seasons in which larval hypobiosis may have occurred (end of winter), and adults on pastures (especially sows) are regularly treated as they acquire little protective immunity and infections accumulate with age. Some drug resistance has been detected in parasite populations in pigs, so it is often recommended that drug resistance testing be conducted to select the most efficacious drug and that drenches be used strategically (as required) or in rotation to curb the development of drug resistance. Because the transmission of infections requires hosts to have access to pastures contaminated with free-living stages, control programmes should integrate stock and pasture management practices shown to minimise environmental contamination by worm eggs and reduce the development and survival of larvae on pastures. Animals should be moved to clean areas (spelled or recently ungrazed pastures) after treatment, but this is often difficult in small holdings and backyard situations where set-stocking on few pastures are involved. Stocking rates should be kept low, new livestock should be treated in quarantine and, if possible, pastures should be rotated with other livestock species or crops, or spelled periodically, particularly over adverse seasons (e.g. hot summers). Studies on biological control options have also shown that supplementary feeds laced with the nematophagous fungus (*Duddingtonia flagrans*) resulted in significant reductions in pasture larvae thus contributing to reduced worm burdens.

Hyostrongylus

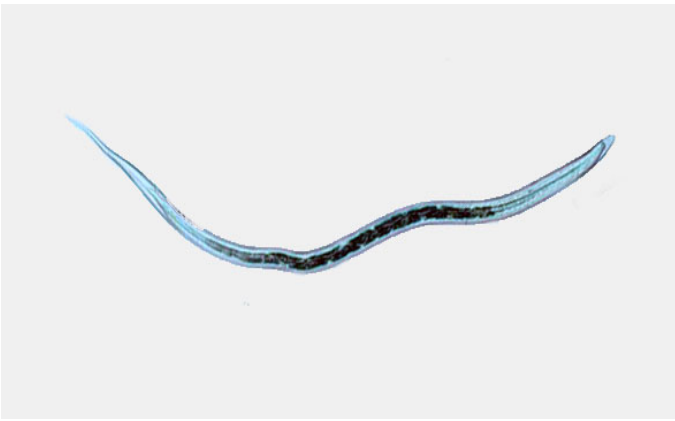




Hyostrongylus adult worms



Hyostrongylus worm egg



Hyostrongylus third-stage larva