

## ***Haemonchus***

(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. *Haemonchus* spp. (barber's pole worms) cause acute haemorrhagic anaemia (haemonchosis) markedly impacting production in sheep worldwide. Considerable efforts are made to control infections through chemical interventions (drenching), husbandry and environmental management.

### **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: Trichostrongylidae (hair-like, lips absent/reduced, oesophagus lacking bulb, thin-shelled eggs, direct cycles)  
Genus: *Haemonchus* (parasitic in abomasum of ruminants)  
Species: *H. contortus* causes anaemia and illthrift in sheep

**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 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 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
<b>Trichostrongylina (trichostrongyles)</b>				
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
<b>Strongylina (strongyles)</b>				
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
<b>Ancylostomatina (hookworms)</b>				
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
<b>Metastrongylina (lungworms)</b>				
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 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 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 Ostertagiinae (well-developed synlophe, modified bursa)					
<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
<i>Hyostrongylus</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
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 Haemonchinae was originally erected for genera with one or several teeth in the buccal cavity (neodont formation), large cervical papillae, longitudinal cuticular ridges sometimes restricted to anterior regions, and the male bursa (types 2-2-1 or 2-1-2) with a reduced dorsal lobe and rays 2 and 3 forming a common trunk. The parasites have direct cycles involving faecal-oral transmission whereby eggs voided in faeces contaminate pastures and ultimately produce infective L3 which are ingested and develop in the gastric mucosa. Larval hypobiosis (inhibited or arrested development) in the mucosa is common allowing parasites to persist over adverse seasons. The subfamily Haemonchinae contains 6 genera (*Haemonchus*, *Ashworthius*, *Bigastronema*, *Boehmiella*, *Leiperiatus*, and *Mecistrocirrus*) parasitic in the stomach of artiodactyls (mainly ruminants) and rarely neotropical rodents. The genus *Haemonchus* forms adults with a small buccal cavity containing a single tooth, a well-developed synlophe restricted to the anterior half of the body. Males have 2 spicules with barbed tips and a bursa with an asymmetrical dorsal lobe, while females have a prominent vulval flap. Some 15 species have been described from the abomasum of a range of ungulates (bovids, camelids, giraffids, cervids), with another 13 species synonymised as *H. contortus* (considered to be a highly polymorphic species). *H. contortus* and *H. placei* causes significant diseases in sheep and cattle respectively, mainly in weaners as a protective immunity develops with age. Infections occur mainly in tropical, sub-tropical and warm temperate zones, particularly those with summer rainfall or irrigated pastures. Parasites abound in the wet season due to the high fecundity of mature females and favourable environmental conditions for the survival of larvae on pastures, whereas parasite numbers decline during dry seasons.

<i>Haemonchus</i> species	Definitive hosts	Location [Clinical signs]	Distribution
<i>H. bedfordi</i>	Artiodactyla: bovid (African buffalo, impala, black wildebeest, blue wildebeest, common tsessebe, sable antelope, kafue lechwe, Limpopo grysbok, Livingstone's eland)		Africa
<i>H. contortus</i> (barber's pole worm, twisted stomach worm, large stomach worm, wire worm) (syn. <i>H. atectus</i> , <i>bangalorensis</i> , <i>bispinosus</i> , <i>cayugensis</i> , <i>cervinus</i> , <i>fuhrmanni</i> , <i>hispanicus</i> , <i>kentuckiensis</i> , <i>lunatus</i> , <i>okapiae</i> p.p., <i>pseudocontortus</i> , <i>tartaricus</i> , <i>uktalensis</i> ) (incl. subspp. <i>contortus</i> , <i>cayugensis</i> , <i>bangalorensis</i> , <i>hispanicus</i> , <i>kentuckiensis</i> , <i>ukatalensis</i> )	Artiodactyla: bovid (sheep, bighorn sheep, mouflon, chamois, Pyrenean chamois, goat, alpine ibex, Iberian ibex, cattle, Bali cattle, zebu, water buffalo, African buffalo, yak, muskox, American bison, addax, impala, blackbuck, bushbuck, water buck, kafue lechwe, common duiker, red forest duiker, blue wildebeest, common tsessebe, Soemmerring's gazelle, Speke's gazelle, nilgiri tahr, sable antelope, Salt's dik-dik, East African oryx, grey rhebok, Cape grysbok, Sharpe's grysbok, southern reedbuck, Bohor reedbuck, Livingstone's eland), antilocaprid (pronghorn), cervid (chital, pygmy brocket, moose, roe deer, red deer, sika deer, sambar deer, fallow deer, marsh deer, white-tailed deer, mule deer, southern mule deer, Columbian black-tailed deer, barasingha, muntjac, Reeve's muntjac), giraffid (Angolan giraffe), camelid (dromedary, llama), suid (pig); Rodentia: hystricid (African brush-tailed porcupine), caviid (guinea pig), murid (Mongolian gerbil, house mouse); Primates: hominid (human); Siluriformes: silurid (helicopter catfish)	abomasum [anaemia, bottle-jaw oedema, illthrift]	worldwide
<i>H. dinniki</i>	Artiodactyla: bovid (dik-dik antelope)		Africa
<i>H. horaki</i>	Artiodactyla: bovid (bontebok, grey rhebok)		Africa
<i>H. krugeri</i>	Artiodactyla: bovid (impala, Cape grysbok, Sharpe's grysbok)		Africa
<i>H. lawrencei</i>	Artiodactyla: bovid (impala, blue duiker)		Africa
<i>H. longistipes</i> (camel stomach worm)	Artiodactyla: camelid (Bactrian camel, dromedary), bovid (cattle, zebu, sheep, goat)	abomasum [anaemia]	Africa, Middle East
<i>H. mitchelli</i>	Artiodactyla: bovid (impala, Sharpe's grysbok, common eland, Livingstone's eland, greater kudu), giraffid (Angolan giraffe)		Africa
<i>H. okapiae</i>	Artiodactyla: giraffid (okapi)		Africa
<i>H. ostertagi</i>	Artiodactyla: bovid (American bison)		North America
<i>H. ovis</i>	Artiodactyla: bovid (goat)		
<i>H. placei</i> (now considered to be a cattle strain adaptation of <i>H. contortus</i> )	Artiodactyla: bovid (cattle, zebu, yak, European bison, muskox, sheep, bighorn sheep, goat, nilgiri tahr, greater kudu), cervid (roe deer, white-tailed deer), antilocaprid (pronghorn), camelid (dromedary)	abomasum [anaemia, illthrift]	worldwide
<i>H. santomei</i>	Artiodactyla: bovid (cattle)		Europe
<i>H. similis</i> (syn. <i>H. bubalis</i> )	Artiodactyla: bovid (cattle, zebu, water buffalo, sheep, goat, common tsessebe, sable antelope, blackbuck), cervid (moose, white-tailed deer)	abomasum [anaemia]	North America, Europe
<i>H. vegliali</i> (syn. <i>vegliai</i> )	Artiodactyla: bovid (impala, sable antelope, suni, Sharpe's grysbok, common duiker, grey duiker, Livingstone's eland, nyala, Cape bushbuck, Limpopo bushbuck, greater kudu)		Africa

**Parasite morphology:** *Haemonchus* spp. form 3 different morphological stages in their developmental cycles: eggs; larvae (4 stages designated L1 to L4); and adult worms (males and females). Gravid females lay thin-walled ellipsoidal eggs ranging in size from 62-90 x 40-50  $\mu\text{m}$  and containing an embryo in the early stages of cleavage (4-32 blastomeres). Fully embryonated eggs hatch to release free-living rhabditiform L1 which measure around 340-350  $\mu\text{m}$  and have a tubular buccal cavity, an oesophagus with a distal valved bulb, and an attenuated sharply pointed tail. L1 moult to form rhabditiform L2 which are longer measuring from 400-450  $\mu\text{m}$  and have developed lateral alae. L2 moult to form infective filariform L3 which retain the L2 cuticle with its attenuated pointed tail generally kinked at the tip (the tail of the ensheathed larva is less attenuated and conical). L3 measure from 650-866  $\mu\text{m}$  in length and have a bullet-shaped head with an anterior shoulder, an elongate buccal cavity closed anteriorly, prominent lateral alae, an elongate stronglyliform (non-bulbed) oesophagus, intestines comprising 16 triangular cells (arranged alternately giving the lumen a zigzag appearance as opposed to the straight intestinal lumen in hookworm L3), the gut ending in 2 terminal cells, and finely tapering tails (often appearing kinked or offset) with an elongate tail sheath extension (65-119  $\mu\text{m}$ ) of which the last 10-20% is filamentous. Following ingestion and exsheathment, L3 moult to form L4 which escape from the L3 cuticle through a longitudinal slit. L4 measure from 655-840  $\mu\text{m}$  and their buccal capsule opens so they feed and grow, eventually moulting to become young adults (sometimes designated L5). Adult worms are 10-40 mm long and have a rounded head (cephalic vesicle absent) with a small globular buccal capsule containing a single tiny lancet-shaped tooth attached to the dorsal wall (neodont formation used for feeding). They lack the anterior excretory notch present in *Trichostrongylus*, but have a pair of large cervical papillae projecting above the body surface. The synlophe is well-developed with prominent transverse striations at the anterior end followed by numerous longitudinal cuticular ridges restricted to the anterior body. Adult worms are sexually dimorphic with females being larger than males (18-40 mm cf. 10-30 mm in length). Females are characterized by their red-and-white (barber's pole) appearance (white ovaries spiral around the red blood-filled intestines), short vagina, large prominent vulva flap (linguiform in sheep, bulbous in cattle), and short pointed tail without a terminal spine. Females are didelphic and their uteri may contain hundreds of developing eggs. Males have a prominent caudal copulatory bursa with 2 large lateral lobes containing supporting rays (muscular elements following nerve channels to terminal papillae) arranged in a 2-2-1 or 2-1-2 configuration, a smaller asymmetrical dorsal lobe (with a Y-shaped dorsal ray). They also possess a gubernaculum and 2 short thick spicules with distal barbs (left spicule 0.02-0.04 mm, right spicule 0.04-0.06 mm). *H. contortus* in sheep and *H. placei* in cattle were originally distinguished by minor differences in several morphotypic and biological traits (*H. placei* males have longer spicules, females have a knob-like vulva flap, L3 are shorter, and eggs kept at 11°C do not hatch). However, experimental studies succeeded in hybridizing these species with progeny showing some sex-linked dominant traits (notably in vulva morphology and cold resistance of eggs). *H. placei* is now considered by many authorities to be a cattle strain adaptation of *H. contortus*.

**Site of infection:** Fourth-stage larvae (L4) and adult worms infect the fourth stomach (abomasum) of ungulates or the glandular stomach of monogastric animals. L1 and L2 are free-living stages in faecal material and on soil and pasture, while L3 are the infective stages for grazing animals.

**Pathogenesis:** Infections by *Haemonchus* spp. vary in their pathogenicity depending on the parasite species, host susceptibility and intensity of infection. Most species are infective for a small range of artiodactyls and a few are notorious pathogens of domestic livestock, particularly young animals. Worms pierce the abomasal mucosa using their oral lancets causing tissue lacerations and blood loss through active feeding (exacerbated by rapid blood transit through worms) and petechial haemorrhages (exacerbated by anticoagulants secreted by feeding worms). While light infections may remain asymptomatic, they may still contribute to significant subclinical production losses (reduced meat, milk and/or fibre). Heavier infections (> 1,000 worms in sheep, > 8,000 worms in cattle) may cause mild to severe clinical disease (haemonchosis), with high morbidity and mortality in susceptible cohorts. Depending on the course and severity of infection, 3 successive stages of disease are recognised; namely, peracute, acute and chronic stages. Early stage (peracute or hyper-acute) infections occur when developing L4 cause petechial haemorrhages resulting in blood loss and anaemia. The onset of disease may be rapid particularly when young susceptible animals ingest large numbers of infective L3 all at once. Infections by > 20,000 *H. contortus* L3 may cause sheep to lose up to 1 litre of blood per day and die suddenly from haemorrhagic gastritis. Later stage infections by young and maturing adults may cause acute or chronic disease syndromes depending on the intensity of infection. Heavy infections may quickly lead to acute disease when feeding worms cause mucosal lacerations, erosions at attachment sites, frank petechial haemorrhages and significant blood loss. Acute signs include severe anaemia, hypoproteinaemia, ascites, subcutaneous oedema (bottle jaw) and only sometimes scouring with darkened faeces due to blood seepage into the gut lumen. Infections by 2,000-20,000 worms may cause animals to lose 100-1,000 ml blood per day (female worms may ingest 0.05 ml blood per day) with clinical anaemia becoming apparent around 2 weeks after infection. Haematocrit values (packed cell volume) may initially stabilise as homeostatic mechanisms (erythropoiesis through bone marrow hyperplasia) begin to compensate, but the continuing loss of blood, iron reserves and serum proteins (esp. albumin) may prove fatal. The abomasal mucosa becomes hyperaemic with many petechiae, focal erosions and some small ulcers, and the submucosa becomes thickened and oedematous. Animals become weak, listless, lose weight (even when food intake may be increased), stunted in growth and emaciated, with high mortality rates in young susceptible animals. Less severe infections (100-2,000 worms) may not result in acute disease, but their protracted course may cause chronic manifestations, particularly during winter when pastures become deficient in nutrients (protein and iron) thus forestalling efficient recovery. The abomasal mucosa exhibits hyperplasia and metaplasia, the submucosa becomes thickened and folded, and there is chronic red bone marrow hyperplasia with reversion to white bone marrow due to iron depletion. Animals do not develop severe anaemia or submandibular oedema but lose weight progressively

over several weeks becoming pale, weak and emaciated. While animals may exhibit some age-resistance to disease (developing when > 1 year of age), they do not appear to acquire any effective immunity to infection (unlike many other nematode infections). Nonetheless, animals surviving acute and chronic disease may demonstrate a phenomenon known as self-cure when subject to challenge infections. Adult worms are expelled from the gut by immunological mechanisms involving immediate-type hypersensitivity reactions, but this does not necessarily result in protection against reinfection.

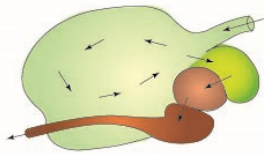
**Developmental cycle and mode of transmission:** *Haemonchus* spp. have direct monoxenous (1-host) life-cycles involving faecal-oral horizontal transmission (faecal contamination of the external environment by worm eggs, oral ingestion of infective larvae by grazing animals). Gravid female worms may lay 5,000-10,000 eggs per day which are voided with host faeces. The eggs embryonate in faecal material and hatch releasing free-living L1 which feed on bacteria before moulting to form another generation of free-living larvae (L2). These larvae then moult but retain their cuticle to form ensheathed L3 which are non-feeding but are infective to hosts. Depending on prevailing environmental conditions, L3 may develop within 5 days in warm moist conditions but their development may be delayed for weeks in cooler conditions. They survive well on improved or irrigated pastures and those with summer rainfall, migrating horizontally (dispersing outwards from faecal pats) and vertically (ascending blades of grass overnight and descending during the day). Infective L3 on herbage are ingested by grazing animals, mostly in late summer and autumn. Inside their hosts, they exsheath in the stomach and burrow into the abomasal glands where they moult to L4 before re-emerging to the lumen to moult and mature as adults. In certain regions scattered throughout tropical, subtropical and temperate areas, L4 may undergo arrested development (hypobiosis) at the beginning of prolonged dry periods, only resuming development with the onset of seasonal rains when conditions are more favourable for the survival of free-living stages. This often results in a spring rise in egg production and pasture contamination which coincides with host reproduction and is thought to be triggered by the periparturient immunosuppression that occurs during pregnancy. Hypobiosis is by no means a universal feature as it does not occur in regions with more frequent rainfall. The prepatent period (time from infection to first excretion of eggs) ranges from 18-21 days for *H. contortus* in sheep and 23-28 days for *H. placei/contortus* in cattle. Patency (duration of egg production) is often continuous year-round, but may exhibit considerable seasonal fluctuations, particularly in areas where hypobiosis occurs (often resulting in high summer burdens in tropical and subtropical areas and severe outbreaks following summer rains).

**Differential diagnosis:** Infections may be strongly indicated on the basis of clinical symptomatology (black scours, anaemia, bottle jaw, emaciation) in susceptible animals (esp. weaners) during seasons with warm moist conditions. A variety of technical aids have been developed to indicate and even quantify blood loss, including coloured cards to assess the pallor of mucous membranes, dipsticks for occult blood in faeces, and microhaematocrit tubes for determining packed cell volumes. Infections are conventionally confirmed by the direct detection of parasites in host material, usually worm eggs in faecal samples (antemortem) or adult worms in gut samples (post-mortem). A range of coprological tests have been used to harvest and concentrate worm eggs from faeces, usually by alternate sedimentation in water and floatation in high specific gravity sugar or salt solutions. Some tests have been quantitated by counting the number of worm eggs in known volumes of diluted faeces in chambered McMaster or Whitlock slides, and then calculating the number of eggs per gram of faeces (epg). Egg counts provide a rough guide to the level of infection by a range of nematode parasites, with considerable variation found in their correlation with the actual numbers of worms (due to differences in fecundity between species and over time, immunosuppression of egg production, changed rates of passage of digesta, and failure to account for larvae, male worms, immature or senescent females). In the case of *Haemonchus* spp. which are prolific egg producers, there is a relatively good correlation between faecal egg counts and the level of infection, so the technique is often used to indicate the need for chemotherapy as well as to screen for drug resistance (by conducting faecal egg count reduction tests pre- and post-treatment). Nonetheless, it is difficult even for trained technicians to differentiate *Haemonchus* eggs from *Trichostrongylus* and *Ostertagia* eggs. When time permits, specific diagnosis may make recourse to culturing eggs over 1-2 weeks to harvest larvae for differentiation. Faecal samples are incubated in funnels (Baermann technique) or petri-dishes (Harada-Mori technique) until L3 emerge which are then collected and examined microscopically for characteristic features (*Haemonchus* L3 have narrow rounded heads, intestines with 16 cells arranged in a zigzag pattern, and a tapering tail with a medium offset sheath). Infections may also be diagnosed by the detection of adult worms in gut samples collected from deceased, euthanized or sacrificed animals. Both male and female worms can be identified by their morphometric features, notably the barber's pole appearance (white ovaries twisted around red intestines) and the prominent vulvar flap of females, and bursa structure in males. Worm burdens can also be quantitated by counting their numbers in aliquots of saline washes of abomasal and/or intestinal mucosa (sometimes digested in pepsin-hydrochloric acid solutions to release hypobiotic larvae). Research laboratories have developed several serological tests (mostly enzyme immunoassays) to detect specific host antibodies against larval and adult worm antigens, but considerable cross-reactivity was detected with other nematode infections. Modern molecular biological techniques have recently been used to characterize several *Haemonchus* spp. by polymerase chain reaction (PCR) amplification of egg, larval and adult worm DNA (18S, 5.8S and 28S ribosomal DNA and internal transcribed spacer regions I and II).

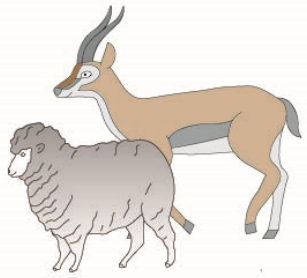
**Treatment and control:** A broad range of anthelmintics have been used to treat infections in livestock, but the emergence of drug resistance has become a widespread problem. When effective, most anthelmintics kill adult worms and some are also active against hypobiotic larvae. Common drug groups include white drenches (benzimidazoles), clear drenches (imidazothiazoles), salicylanilides (closantel) and macrocyclic lactones (ivermectins). Most are available as oral formulations, some as subcutaneous injections and a few as slow-release rumen boluses. Nonetheless, they have little residual activity so animals may be rapidly re-infected if returned

to contaminated areas (thus requiring repeat treatments and giving rise to the conventional adage of 'drench and move' to pasture not recently grazed). Many agricultural authorities recommend that drug-resistant testing (faecal egg count reduction tests) be performed to select the most effective formulations for mass treatments, that drugs be used in cyclic rotation or in combination, and that treatments be conducted periodically (around weaning or seasonally) or strategically (only as required). More recently, studies have counter-intuitively shown that leaving some animals untreated may delay the onset of drug resistance (by providing 'refugia' for drug-susceptible worms). Control programmes for gastrointestinal nematodes should also include management practices designed to limit host exposure and minimise the contamination, development and survival of parasites on pastures. Weaners are most at risk due to their increased grazing frequency, their exposure to high numbers of larvae (the result of the periparturient spring rise in worm egg production), the physiological stress accompanying dietary changes (from milk to grass), and their relative immunological immaturity. It is usually recommended that pregnant animals be treated before birth and that weaners be treated before moving onto safe pastures. Studies have shown that some individual hosts (and some native breeds) have an innate resistance to clinical infection and experimental breeding trials have succeeded in selectively breeding resistant sheep without sacrificing production parameters. Pasture contamination can also be minimised by adopting rotational grazing and/or mixed grazing practices, or spelling pastures over dry summers as worm eggs, free-living L1 and L2, and infective L3 are susceptible to adverse environmental conditions (especially lack of moisture).

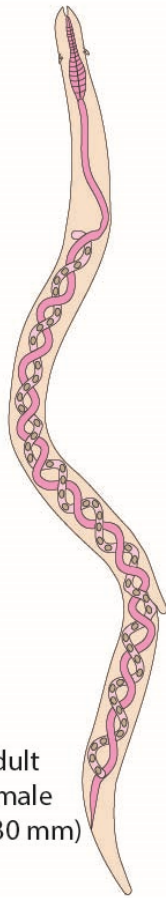
# Haemonchus



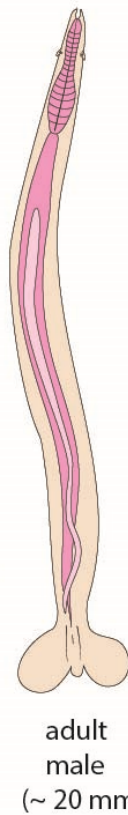
abomasum/stomach  
(haemorrhagic anaemia,  
black scours, bottle jaw,  
emaciation)



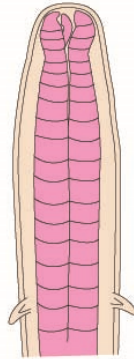
Definitive Hosts  
(artiodactyls, esp.  
ruminants)



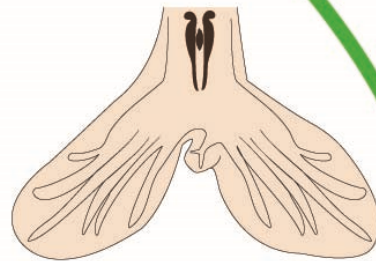
adult  
female  
(~ 30 mm)



adult  
male  
(~ 20 mm)



head



male tail

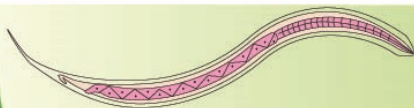
eggs  
excreted  
in faeces



L3  
ingested



L4 hypobiosis



filariform third-  
stage larvae (L3)  
(~ 800  $\mu$ m)

external  
environment



rhabditiform first-  
and second-stage  
larvae (L1, L2)  
(~ 400  $\mu$ m)



eggs  
(~ 60  $\mu$ m)



*Haemonchus* adult worms



*Haemonchus* adult worms



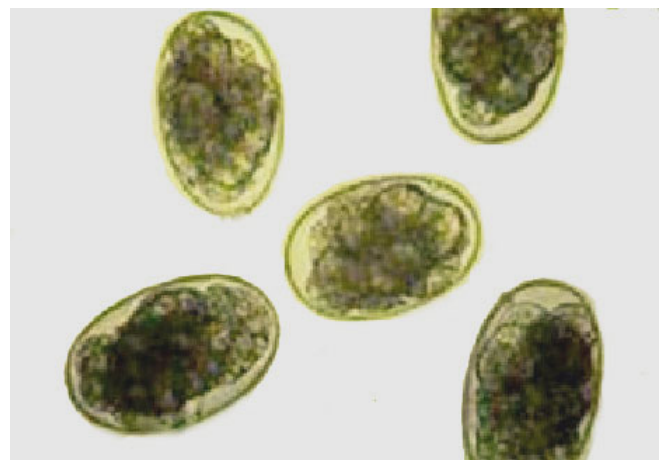
*Haemonchus* adult worm, head



*Haemonchus* adult worm, female vulval flap



*Haemonchus* adult male worm, male bursa



*Haemonchus* worm eggs