Cyathostomum
(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, migrate into the mucosa and moult to L4 before they return to the lumen and moult into adults (some L4 undergo arrested development - termed hypobiosis – in the large intestinal wall). More than 40 species of small strongyles (cyathostomes, cyathostomins, trichonemes or red worms) are found in the large intestines, causing catarrhal and/or haemorrhagic enteritis in horses 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, 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)
Subfamily:	Cyathostominae (small strongyles, cylindrical buccal capsule)
Genus:	*Cyathostomum* (parasitic in caecum/colon of equines)
Species:	various species cause enteritis 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 or 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 (strongylins or migratory strongyles) 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 (trichonemes, cyathostomes, cyathostomines, cyathostomins or non-migratory strongyles) with cylindrical or ring-shaped buccal capsules) found in the large intestines of perissodactyls, elephants, hyracoids, tortoises and occasionally some artiodactyls. Contemporary molecular-genetic 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
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
Strongylinae ('large' strongyles or strongylins)					
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
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

The subfamily Cyathostominae contains small strongyles with single or double corona radiata (leaf crowns) and males with 6 rami in the dorsal ray of their bursa. Some 23-27 genera are recognised in 6 tribes: Cyathostominea (*Caballonema, Coronocyclus, Cyathostomum* (syn. *Trichonema p.p., Ershovinema p.p.*)*, Cylicocyclus, Cylicodontophorus, Cylicostephanus* (syn. *Petrovinema, Schulzitrichinema, Cyclicotetrapedon, Trichonema p.p., Ershovinema p.p.*)*, Cylicostomias, Cylindropharynx, Gyalocephalus, Hsuingia, Parapoteriostomum, Petrovinema, Poteriostomum* (syn. *Hexodontostomum*)*, Skrjabinodentus, Tridentoinfundibulum*) in equids; Eucyathostominea (*Eucyathostomum*) in ruminants; Kilulumina (*Kiluluma*) in rhinoceros and tapir; Murshidiinea (*Khalilia*, *Murshidia*, *Neomurshidia*) in elephants, rhinoceros, warthogs and tapir; Quiloninea (*Quilonia, Theileriana*) in elephants, rhinoceros and hyracoids; and Sauricolinea (*Chapiniella*, *Sauricola*) in tortoises. Members of the tribe Cyathostominea have internal and external corona radiata, females with well-developed parallel ovejectors, males with pick-like spicules and a large gubernaculum with a longitudinal groove and a flanged ventral notch. The genera *Cyathostomum, Cylicocyclus, Cylicodontophorus, Poteriostomum, Cylicostephanus, Coronocyclus* and *Gyalocephalus* are common cosmopolitan parasites in the large intestines of equids, and have been associated with acute catarrhal and/or haemorrhagic enteritis as well as chronic ill-thrift, particularly in young animals but also in equids of other age groups. Infections are transmitted by the faecal contamination of pastures by worm eggs which produce larvae that develop to infective L3 and are ingested by grazing animals.

Parasite species	Definitive Hosts	Location	Distribution
Cyathostomum			
C. alveatum (syn. *Cylichnostomum, Cylicocerus, Cylicostomum, Erschowinema, Trichonema*)	Perissodactyla: equid (horse, donkey, mule, plains zebra)	large intestines	Africa, Europe, Asia
C. catinatum (syn. *Cylichnostomum, Cylicocerus, Cylicostomum, C. pseudocatinatum, Erschowinema, Petrovinema, Trichonema)*	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, tarpan, onager, plains zebra, mountain zebra)	large intestines	worldwide
C. equatoriale	Perissodactyla: equid (Grant's zebra)	large intestines	Africa
C. montgomeryi (syn. *Cylicostomum, Cylicotoichus, Erschowinema, Trichonema*)	Perissodactyla: equid (horse, donkey, mule, plains zebra, mountain zebra, Burchell's zebra)	large intestines	Africa
C. pateratum (syn. *Cylicocerus, Cylicodontophorus, Cylicostomum cymatostomum, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, tarpan, plains zebra)	large intestines	worldwide
C. tetracanthum (syn. *C. aegyptiacum, Cylichnostomum, Cylicostoma, Cylicostomum, Strongylus, Sclerostomum, S. quadridentatum, Trichonema, T. arcuata*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, onager, plains zebra, mountain zebra, Burchell's zebra)	large intestines	worldwide

Species inquirenda			
C. maestrii sp. inq.	Perissodactyla: equid (Grant's zebra)	large intestines	Africa
C. symmetricum sp. inq.	Perissodactyla: equid (Grant's zebra)	large intestines	Africa
C. zavattarii sp. inq.	Perissodactyla: equid (Grant's zebra)	large intestines	Africa

Other small strongyle genera and species in equids

Parasite species	Definitive Hosts	Location	Distribution
Caballonema			
C. longicapsulata (syn. *Sinostrongylus*)	Perissodactyla: equid (horse)	large intestines	Asia
Coronocyclus			
C. coronatus (syn. Cyathostomum, Cylichnostomum, Cylicocerus, Cylicostomias, Cylicostomum, Erschowinema, Trichonema, T. subcoronatum)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, tarpan)	large intestines	worldwide
C. labiatus (syn. Cyathostomum, Cylichnostomum, Cylicocerus, Cylicostomias, Cylicostomum, Schulzitrichonema, Trichonema)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, tarpan, plains zebra)	large intestines	worldwide
C. labratus (syn. Cyathostomum, Cylichnostomum, Cylicostomias, Cylicostomum, Schulzitrichonmea, Trichonema)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, mountain zebra)	large intestines	worldwide
C. sagittatus (syn. Cylicostomias, Cylicostomum, Cylicodontophorus, Trichonema)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule)	large intestines	Eurasia
C. ulambajari	Perissodactyla: equid (horse)	large intestines	Asia
Cylicocyclus			
C. adersi sp. inq. (syn. *Cyathostomum*, *Cylicostomum*, *Trichonema*)	Perissodactyla: equid (horse, donkey, mountain zebra, damaraland zebra)	large intestines	Africa, Asia
C. ashworthi (syn. *C. largocapsulatus, C. matumurai, C. zhidanensis, Cylicobrachytus zhidanensis Trichonema largocapsulatus, T. matumurai*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager)	large intestines	worldwide
C. asini	Perissodactyla: equid (donkey, plains zebra, mountain zebra)	large intestines	worldwide
C. auriculatus (syn. *Cyathostomum, Cylichnostomum, Cylicostomum*, *Trichonema*)	Perissodactyla: equid (horse, donkey, mule, plains zebra, mountain zebra)	large intestines	Africa, Americas, Asia
C. brevicapsulatus (syn. *Cylicobrachytus, Cylicostephanus*, *Cylicostomum, Trichonema*)	Perissodactyla: equid (horse, donkey)	large intestines	Eurasia, Americas
C. elongatus (syn. *Cyathostomum, Cylichnostomum, Cylicostomum*, *Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	large intestines	worldwide
C. gyalocephaloides sp. inq	Perissodactyla: equid (donkey, plains zebra, mountain zebra); Proboscidea: elephantid (African bush elephant)	large intestines	Africa
C. insigne (syn. *Cyathostomum, Cylichnostomum, Cylicostomum*, *Cylicostomum zebra, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, onager, plains zebra)	large intestines	worldwide

C. leptostomum (syn. *Cyathostomum, C. bogoriense, Cylichnostomum, Cylicostomum, Cylicotetrapedon*, *Schulzitrichonema*, *Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, tarpan, onager, plains zebra)	large intestines	worldwide
C. nassatus (syn. *C. bulbiferus, Cyathostomum, Cylichnostomum, Cylicostomum*, *Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, tarpan, plains zebra, mountain zebra)	large intestines	worldwide
C. radiatus (syn. *Cyathostomum, Cylichnostomum, Cylicostomum, C. prionodes, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	large intestines	worldwide
C. triramosus (syn. *Cyathostoma*, *Cylicostomum, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, onager, tarpan, plains zebra, Burchell's zebra, Hartmann's mountain zebra)	large intestines	Africa, Asia, North America
C. ultrajectinus (syn. *Cyathostomum, Cylicodontophorus, Cylicostomum, Trichonema*)	Perissodactyla: equid (horse, donkey, onager, plains zebra)	large intestines	worldwide
Cylicodontophorus			
C. bicoronatus (syn. *Cyathostomum, Cylichnostomum, Cylicostephanus, Cylicostomum, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager)	large intestines	worldwide
C. reineckei	Perissodactyla: equid (plains zebra, Hartmann's mountain zebra)	large intestines	Africa
Cylicostephanus			
C. asymetricus (syn. *Cylicostomum, Cylicotetrapedon, Erschowinema, Schulzitrichonema*)	Perissodactyla: equid (horse, donkey)	large intestines	worldwide
C. bidentatus (syn. *Cylicostomum, Cylicotetrapedon, Schultzitrichonema, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	large intestines	worldwide
C. calicatus (syn. *Cyathostomum, Cylichnostomum, Cylicostomum, C. barbatum, Erschowinema, Trichonema, T. tsengi*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, tarpan, onager, mountain zebra, Burchell's zebra)	large intestines	worldwide
C. goldi (syn. *C. ornatus, Cyathostomum ornatum, Cylichnostomum, Cylicocerus, Cylicodontophorus ornatum, Cylicostomias ornatum, Cylicostomum, C. ornatum, C. tridentatum, Cylicotetrapedon, Schultzitrichonema, Trichonema, T. ornatum, T. parvibursatum*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, tarpan, onager, plains zebra)	large intestines	worldwide
C. hybridus (syn. *Cyathostomum, Cylicostomum, Erschowinema, Schultzitrichonema, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, onager)	large intestines	Eurasia, North America
C. longibursatus (syn. *Cylicostomum, C. calicatiforme, C. nanum, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, tarpan, onager, plains zebra)	large intestines	worldwide
C. minutus (syn. *Cylicocyclus, Cylicostomum, Erschowinema, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, tarpan, onager, plains zebra, mountain zebra, Burchell's zebra)	large intestines	worldwide
Cylindropharynx			
C. brevicauda (syn. *C. aethiopica, Cyathostoma aethiopicum*)	Perissodactyla: equid (donkey, mule, plains zebra, Grant's zebra)	large intestines	Africa
C. intermedia	Perissodactyla: equid (plains zebra,	large	Africa

(syn. *C. ornata, C. dolfusi sp. inq. C. rhodesiensis sp. inq*.)	Hartmann's mountain zebra)	intestines	
C. longicauda (syn. *C. asini)*	Perissodactyla: equid (donkey, mule, plains zebra, Hartmann's mountain zebra)	large intestines	Africa
Gyalocephalus			
G. capitatus *(syn. G. equi)*	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	large intestines	worldwide
Hsiungia			
H. pekingensis (syn. *Cylicocyclus*)	Perissodactyla: equid (horse, donkey)	large intestines	Asia
Parapoteriostomum			
P. euproctus (syn. *Cylichnostomum, Cylicodontophorus, Cylicostomum, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	large intestines	worldwide
P. mettami (syn. *Cyathostomum, Cylicocercus, Cylicodontophorus, C. zhongweiensis, Cylicostoma, Trichonema, Cylicostomum ihlei*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager)	large intestines	Africa, Eurasia
P. mongolica (syn. *Cylicodontophorus*)	Perissodactyla: equid (horse)	large intestines	Asia
P. schuermanni (syn. *Cylicodontophorus, Trichonema*)	Perissodactyla: equid (plains zebra)	large intestines	Africa
Petrovinema			
P. poculatum (syn. *Cyathostomum, Cylichnostomum, Cylicostephanus, Cylicostomum, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	large intestines	worldwide
P. skrjabini (syn. *Cylicostephanus, Poteriostomum, Trichonema*)	Perissodactyla: equid (horse, donkey)	large intestines	Asia
Poteriostomum			
P. imparidentatum (syn. *P. pluridentatum, Cylicostomum, C. zebrae, Cylichnostomum, Hexodontostomum markusi*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	large intestines	worldwide
P. ratzii (syn. *Craterostomum, Cylicostomum, Cylichnostomum*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	large intestines	worldwide
Skrjabinodentus			
S. caragandicus (syn. *Cylicostephanus*, *Trichonema*)	Perissodactyla: equid (horse, mule)	large intestines	Asia
S. longiconus (syn. *Cylicostephanus*)	Perissodactyla: equid (plains zebra, mountain zebra, Hartmann's mountain zebra)	large intestines	Africa
S. tshoijoi (syn. *Cylicostehanus*)	Perissodactyla: equid (horse)	large intestines	Asia
Tridentoinfundibulum			
T. gobi (syn. *Cylicostephanus, C. torbertae*)	Perissodactyla: equid (horse, mule)	large intestines	Eurasia, North America

Parasite morphology: The small strongyles form 3 different morphological stages in their development: eggs; larvae (4 successive stages designated L1-L4); and adult worms (males and females). Freshly laid eggs are ovoid in shape, bound by smooth thin shells, and contain a morula at the 4-8 cell (blastomere) stage. Eggs produced by small strongyles vary considerably in size, collectively ranging from 35-150 x 17-68 μm, although the range is narrower depending on genus and species (see following table). The first 2 larval stages (L1 and L2) are free-living stages that feed on microbes and have rounded heads, rhabditiform oesophagi (with cuticular valves) and tapering tails. L3 are free-living ensheathed stages (they retain the L2 cuticle) and are arrested in development although motile, do not feed on microbes and are infective to their equid hosts. Cyathostomin L3 range in length from 730-890 μm and have characteristic long filamentous tail sheath extensions (2:1 body to tail-sheath ratio), tapering heads, small tubular buccal

cavities, long strongyliform oesophagi (without cuticular valves), and intestines comprising 6 or more cells. The identification of L3 is possible for some genera (e.g., *Poteriostomum* and *Gyalocephalus)* but those of the other cyathostomin genera can only be assigned to larval types (primarily on the basis of intestinal anatomy and cell numbers). *Poteriostomum* form broad L3 with intestines having 16 rectangular or pentagonal cells arranged in a double row, whereas *Gyalocephalus* L3 have intestines formed by 12 rectangular or pentagonal cells (the first 6-10 in a double row, and the remainder in a single row). A total of 8 other cyathostomin L3 types have been described: type A having intestines with 8 cells in a 2+6 configuration (first 2 triangular or rectangular cells in double row, remaining 6 trapezoidal or rectangular cells in a single row) often assigned to *Cyathostomum*, *Cylicocyclus*, *Cylicostephanus* and *Petrovinema* spp.; type B having intestines with 8 cells in a 4+4 configuration (triangular or pentagonal cells in double row) often referred to *Cylicocyclus* and *Cylicodontophorus* spp.; type C having intestines with 8 cells in 2+2+4 configuration (first 4 pentagonal, triangular or rectangular cells in double row, remaining 4 trapezoidal cells in single row) usually referred to *Cylicostephanus* spp.; type D having intestines with 8 trapezoidal or triangular cells in single row; type E having intestines with 6 triangular or trapezoidal cells in different configurations of double and single rows; type F having intestines with 7 elongate triangular or trapezoidal cells in different configurations (often 2-4 in double rows, 2-3 in single rows); type G having intestines with 8 elongate triangular or rectangular cells; and type H having intestines with 9 elongate triangular cells in a 6+3 configuration (first 6 in double row, remaining 3 in single row). The parasitic L4 (encysted and hypobiotic stages) grow up to 3-9 mm in length and sometimes show generic and species-specific cephalic and genital structures.

Genus	**Egg size**	**L3 intestines**
Cyathostomum	76-105 x 36-49 µm	8 cells (type A)
Caballonema	98-112 x 47-54 µm	
Coronocyclus	86-147 x 39-60 µm	
Cylicocyclus	35-130 x 17-65 µm	8 cells (type A or B]
Cylicodontophorus	76-120 x 39-59 µm	8 cells (type B)
Cylicostephanus	53-114 x 34-56 µm	8 cells (type A or C]
Cylindropharynx	84-106 x 44-61 µm	
Gyalocephalus	90-118 x 50-68 µm	12 cells
Hsiungia	114-150 x 54-72 µm	
Parapoteriostomum	80-128 x 50-62 µm	
Petrovinema	61-130 x 32-56 µm	8 cells (type A)
Poteriostomum	95-115 x 48-57 µm	16 cells
Skrjabinodentus	97-128 x 42-64 µm	
Tridentoinfundibulum	114-133 x 57-65µm	

Adult cyathostomins are commonly known as small red-worms due to their small size (5-30 x 1.5 mm) and their bright red colouration (sometimes yellow-grey). They have round mouths and well developed short cylindrical buccal capsules without buccal teeth but possessing elaborate cephalic structures, including mouth collars, cephalic papillae, corona radiata (internal leaf crowns (ILC) and external leaf crowns (ELC)), extra-chitinous supports, septum intracoronae (from anterior edge of buccal capsule to lateral edge of leaf crowns), dorsal gutters, oesophageal funnels and oesophageal teeth. Some 14 cyathostomin genera are recognised by different combinations of these structures. For example, the genus *Cyathostomum* has a high mouth collar divided into inner and outer rings, submedian papillae extending through the collar, a broad cylindrical buccal cavity (wider than deep) without buccal teeth, a nipple-like dorsal gutter, a shallow oesophageal funnel with inconspicuous oesophageal teeth, the elements of the ELC are longer, thicker and fewer than those of the ILC, the ILC insertion line is sinuous, the ELC has extra-chitinous supports consisting of a sclerotized ring anterior to the buccal capsule (sometimes appearing as a continuation of the buccal capsule but usually connected to it by strands of connective tissue), and the ILC has extra-chitinous supports near the anterior edge. The genus *Coronocyclus* is similar but the extra-chitinous support for the ELC is separated anteriorly from the buccal capsule, and the ILC insertion line is straight. The genera *Cylicocyclus, Cylicodontophorus, Gyalocephalus* and *Hsiungia* also have high mouth collars divided into rings; the genera *Cylicostephanus, Cylindropharynx, Petrovinema, Skrjabinodentus* and *Tridentoinfundibulum* have flattened mouth collars divided into rings; and the genera *Poteriostomum, Parapoteriostomum* and *Caballonema* have mouth collars that are not divided. The buccal capsules of several genera are modified, with the genus *Cylicocyclus* having a posterior hoop, *Hsiungia* a basal ring, *Poteriostomum* and *Petrovinema* posterior thickenings, *Parapoteriostomum* anterior thickenings, and *Cylindropharynx* being elongated. The oesophageal funnel may be shallow or elongate, and usually possesses inconspicuous teeth (although those of *Hsiungia* and *Caballonema* are more prominent, those of *Tridentoinfundibulum* are large, and those of *Gyalocephalus* are sickle-shaped).

Genus	Mouth collar	ELC cf. ILC elements (external cf. internal leaf crowns)	Other	Female length (mm)	Male length (mm)
Cyathostomum	high, divided	longer, thicker, fewer (18-29 cf. 30-90)	sinuous ILC insertion line, extra-chitinous supports connected anteriorly	5-13	4-11
Coronocyclus	high, divided	longer, thicker, fewer (16-28 cf. 40-80)	straight ILC insertion line, extra-chitinous supports separated anteriorly	7-13	5-11
Cylicocyclus	high, divided	longer, thicker, fewer (10-54 cf. 30-150)	buccal capsule (BC) with posterior hoop	7-30	5-17
Hsiungia	high, divided	similar (no. unspecified)	BC with basal ring, prominent teeth	12-17	9-12
Cylicodontophorus	high, divided	shorter, thinner, more (17-30 cf. 15-30)	ILC inserted near anterior edge	11-16	7-12
Gyalocephalus	high, divided	shorter, thinner, more (90-95 cf. 30-34)	3 sickle-shaped teeth	10-11	7-10
Poteriostomum	high, undivided	shorter, thinner, more (60-95 cf. 38-59)	ILC inserted near posterior edge, BC thicker posteriorly	11-21	9-14
Parapoteriostomum	arched, undivided	shorter, fewer (38-60 cf. 25-46)	BC thicker anteriorly	6-16	6-11
Petrovinema	flattened, divided	similar but fewer (28-36 cf. 80-84)	BC thicker posteriorly	10-19	8-15
Cylicostephanus	flattened, divided	longer, thicker, fewer (8-22 cf. 18-42)	depressed mouth collar	5-10	4-8
Skrjabinodentus	flattened, divided	shorter, thinner, fewer (8-16 cf. 16-23)	bursa with 4 branches (rather than 6)	8-13	8-10
Tridentoinfundibulum	flattened, divided	similar no. (30-40) but longer, thinner	3 prominent teeth	13-16	10-12
Cylindropharynx	flattened, divided	dissimilar and fewer (6 cf. 12)	ELC elements triangular, elongate BC	6-11	5-10
Caballonema	flattened, undivided	dissimilar, longer, fewer (8 cf. 16)	ELC elements triangular	12-16	6-13

Adult worms are sexually dimorphic, with female worms being moderately larger than males (5-30 cf. 4-17 mm). Mature males have a well-developed copulatory bursa, the dorsal lobe of which is usually longer than the lateral lobes (except for *Hsiungia* and *Cylindropharynx* where they are equal in length). The lateral lobes are supported by 6 rays (comprising muscular elements following nerve channels to terminal papillae) varying in branching pattern and length, and the dorsal ray typically has 6 branches (except *Skrjabinodentus* which has 4 branches). Males also have a gubernaculum with a dorsal handle (except *Gyalocephalus*) and a ventral notch (except *Petrovinema, Cylindropharynx* and *Skrjabinodentus* which have enlarged distal tips, and *Parapoteriostomum* which has paired ventral prominences). The genital cone is conical and short (except for *Gyalocephalus, Petrovinema, Parapoteriostomum, Skrjabinodentus* and *Cylindropharynx* where it is elongate, the latter also having finger-like appendages). Males have 2 filiform spicules which are equal in length and have pick-like tips (*Cyathostomum, Coronocyclus, Cylicostephanus, Cylicocyclus, Caballonema*), hook-like tips (*Cylicodontophorus, Poteriostomum, Gyalocephalus, Petrovinema, Parapoteriostomum, Skrjabinodentus, Tridentoinfundibulum, Cylindropharynx*) or straight tips (*Hsiungia*). Mature female worms are didelphic with 2 ovaries, 2 oviducts, 2 uteri and 2 well-developed ovejectors connected to an oval or Y-shaped vestibule (except *Cylindropharynx* where the vestibule is T-shaped) leading to long or short vagina which opens to the exterior through a posterior vulva close or distant to the anus (*Cylicodontophorus* also having a prominent anteroventral vulvar bulge). The tails of female worms may be long, short, conical or digitiform, sometimes with a sharp tip. Females are oviparous as they lay partially embryonated strongyle-type eggs.

Site of infection: Free-living larval stages develop from worm eggs deposited on pastures in host faeces. Parasitic larval stages encyst within the large intestinal wall of their perissodactyl hosts within which they continue development or undergo developmental arrest (hypobiosis). Adult cyathostomins are then found in the lumen of the caecum and the ventral and dorsal colon (not the descending colon or rectum).

Pathogenesis: Infections by small strongyles (cyathostomins) are commonly found in equids and usually occur as mixed infections involving multiple genera and species. Parasites may cause disease when developing or emerging from the tissues as larvae or when residing and feeding in the intestinal lumen as adults. Small strongyles have small buccal capsules which they use to feed superficially on mucosal tissues (they are not plug-feeders like large strongyles with large buccal capsules). Nevertheless, cyathostomin feeding causes traumatic damage to mucosal tissues with petechial haemorrhages and mild ulceration at feeding sites

leading to a desquamative catarrhal, haemorrhagic and/or fibrinous enteritis (typhlocolitis), with mucosal thickening and oedema. Heavy infections may result in altered bowel function with diarrhoea, anaemia, unthriftiness with lethargy and sudden weight loss, particularly in animals up to 2-3 years of age. However, the most serious clinical manifestations are associated with larval cyathostomins, which can profoundly damage the gut wall not only when they first invade (causing type I cyathostominosis) but later when encysted stages emerge (causing type II cyathostominosis). L3 penetrate the epithelial lining and glands of the caecum and ventral colon, where they grow in fibrous granulomatous nodules (0.5-5.0 mm in diameter), although some may penetrate the muscularis mucosa and develop in submucosa. Heavy infections may involve thousands of encysted larvae covering the mucosa causing structural and functional changes that markedly reduce digestive processes and nutritional metabolism. The developing larvae do not undergo extra-intestinal somatic migration like the large migratory strongyles (*Strongylus* spp.), but they undergo histotrophic development in the tissues which can be extended for up to 2.5 years when larvae inhibit or arrest their development (process known as hypobiosis). The most devastating damage arises when encysted larvae emerge synchronously from the intestinal wall, causing haemorrhages and ulceration and precipitating severe clinical disease - known as larval cyathostominosis (type II). The condition is characterised by severe inflammation and is associated with a sudden onset of severe diarrhoea, fluid seepage with oedema and protein loss, intermittent colic, pyrexia, sudden and progressive weight loss and wasting, and death is common in outbreak situations. The damaged mucosa also predisposes to endotoxaemia when endotoxins in the intestinal contents enter the bloodstream. Disease relates to the synchronous reactivation, excystation and emergence of larval stages from the mucosa, and can be seasonal (late winter or early spring in temperate zones). Young horses are the vulnerable, particularly those reared on continually or progressively contaminated pastures, although horses of all ages are susceptible to cyathostomin infection because these nematodes do not induce protective immunity.

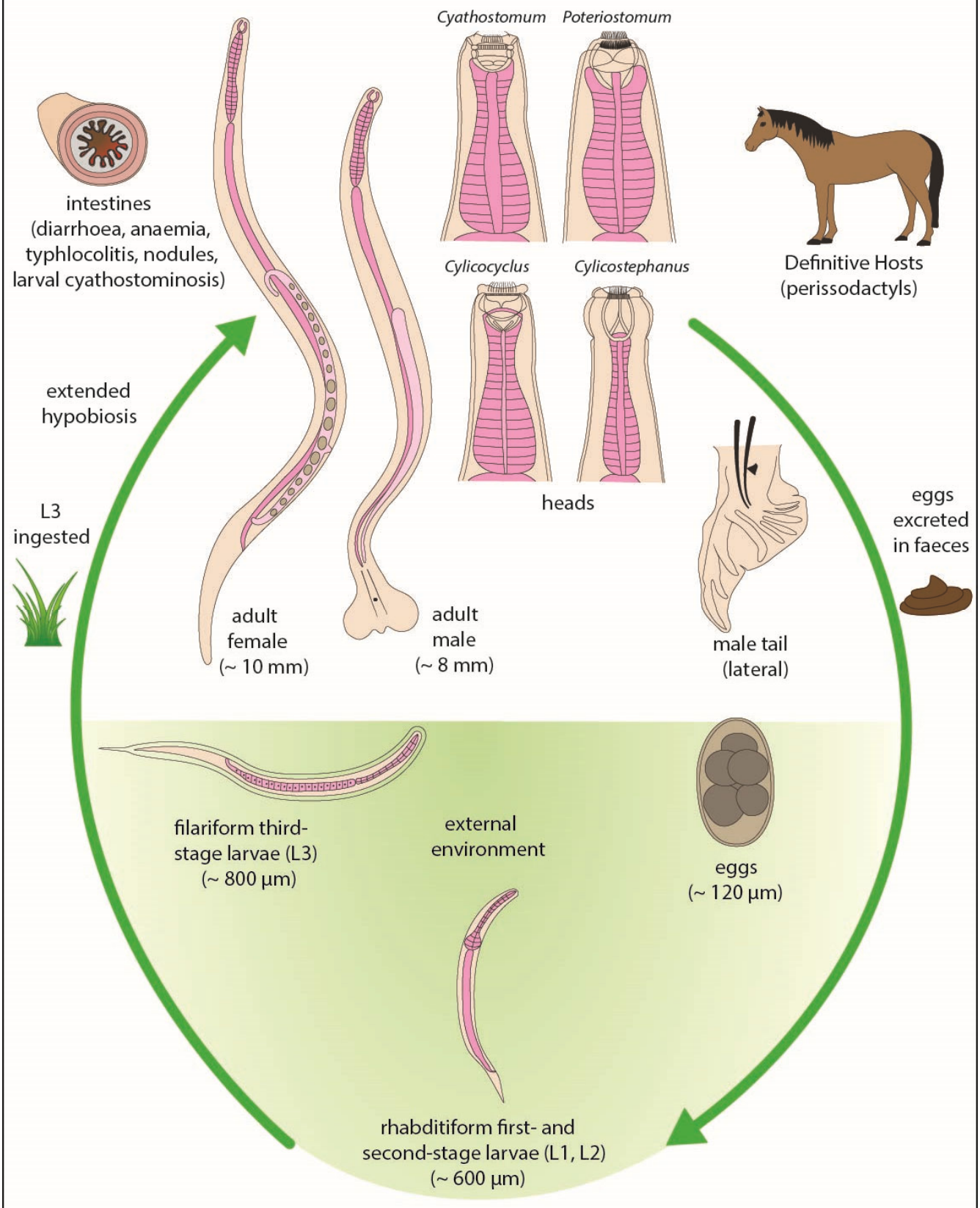
Developmental cycle and mode of transmission: Cyathostomins have direct monoxenous life-cycles involving faecal-oral transmission between hosts. Mature female worms lay eggs in the large intestinal lumen and they are excreted with host faeces into the external environment. The eggs hatch after several days releasing free-living rhabditiform L1 which feed on bacteria before moulting to similar but larger L2 that also feed. These larvae then moult to form filariform L3 which retain the L2 cuticle as a protective sheath and are thus unable to feed. The time taken from egg hatching to the development of L3 varies depending on the prevailing environmental conditions, but it usually takes 1-2 weeks under favourable conditions (warm and moist in temperate climatic regions). Ensheathed L3 can survive for extended periods even under unfavourable, and given adequate moisture, they exhibit horizontal migration (dispersing from faecal pats) and vertical migration (ascending vegetation). Hosts become infected when they ingest infective L3 on pastures whilst grazing. Ingested larvae exsheath in the stomach and the freed early L3 (EL3) may remain in the intestinal lumen for several weeks before invading the mucosa of the caecum and colon where they become encysted in fibrous capsules (and do not undertake extra-intestinal migration). The EL3 develop over several months to late L3, moult to developing L4 (DL4) and then emerge as late L4 (LL4) – the process of emergence is often referred to as excystment. In the intestinal lumen, the LL4 moult to young adults (sometimes designated L5) which then mature into fecund adults. The prepatent period (time from infection to the first release of eggs) varies from 5-14 weeks, but may be considerably longer if EL3 undergo inhibited or arrested development (hypobiosis). It has been estimated that up to 90% of encysted cyathostomins undergo hypobiosis for periods ranging from 3-4 months up to 2 years. Larval hypobiosis appears to be triggered by a variety of factors, involving host physiological responses to stressors (metabolic and reproductive), adverse environmental conditions, and even pre-existing infections. It is often seasonal in occurrence, usually over winter in temperate regions and over summer in tropical regions, thereby causing outbreaks of larval cyathostomosis in spring or autumn, respectively. Despite such periodicity, comparative studies involving breeding and nonbreeding animals has not provided any evidence for a periparturient rise in worm egg production (as occurs for some trichostrongyle nematodes of some ruminant hosts).

Differential diagnosis: Although infections by small strongyles may be suspected on the basis of symptomatology and pertinent history, most clinical signs are relatively nonspecific (diarrhoea, anaemia, loss of condition). Similarly, changes in various clinical parameters may be suggestive but not definitive: including serum biochemistry (hypoalbuminaemia, hyper-beta-globulinaemia, increased alkaline phosphatase, reduced glycated fructose amines) and haematology (neutrophilia, anaemia with or without eosinophilia and/or lymphocytosis). Infections are conventionally diagnosed by the detection of characteristic (ovoid) worm eggs in faecal samples following their concentration by floatation in saturated sugar or salt solutions (specific gravity > 1.3). Quantitative techniques are usually employed, so that eggs can be counted in aliquots of diluted faeces in volumetric chambers (McMaster or Whitlock slides) and then extrapolated to the number of eggs per gram of faeces (epg). However, faecal egg counts do not correlate well with worm burdens, because they do not consider the stage of infection, the developmental stages that do not produce eggs (e.g., mucosal larval stages, males and immature or senescent females) and the fact that different species of worms commonly present have variable reproductive indices (rates). In addition, most strongylin and cyathostomin eggs appear similar in size and appearance and cannot be unequivocally differentiated even to genus. Recourse is sometimes made to larval coproculture where faecal samples are incubated for at least one week in funnels or petri dishes to harvest L3 for microscopic examination. While several cyathostomin genera can be identified on the basis of L3 characteristics (*Poteriostomum* and *Gyalocephalus*), those of the other 12 genera can only be assigned to larval types (A-H), primarily on the basis of gut anatomy (number, shape and configuration of intestinal cells). Infections can be diagnosed at post-mortem by the detection of adult worms and larvae in the gut lumen, in mucosal scrapings following pepsin-acid digestion, or the detection of encysted larvae in the gut wall via transillumination using a light box. Several serological techniques have been developed to detect serum antibodies to larval antigens (cyathostomin gut-associated larval antigen-1) or parasite copro-antigens. However, the kinetics and dynamics of serological responses to

cyathostomins (as a group) and the different developmental stages present during the course of infection remain to be determined. A microchip-based capillary electrophoresis technique has been used to differentiate several cyathostomin species, as have polymerase chain reaction (PCR) amplification techniques for nuclear genes (ribosomal DNA, transcribed spacer regions (ITS) 1 and 2, and intergenic spacer (IGS)).

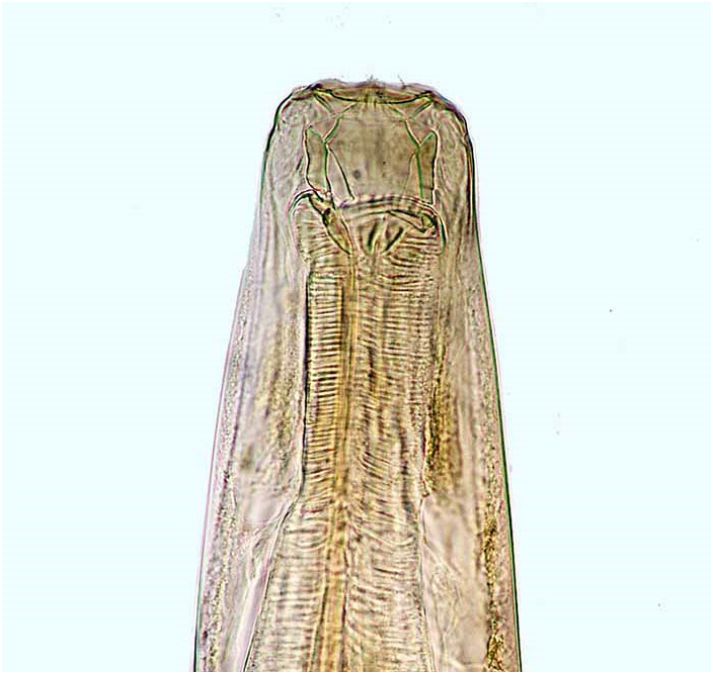
Treatment and control: The widespread application of anthelmintics has been spectacularly successful in treating large strongyle infections in horses, but the drugs have been less effective against small strongyles due to the limited efficacy of numerous drugs against encysted larval stages and the rapid emergence of drug resistance in cyathostomins. Infections are best treated with macrocyclic lactones (ivermectin, moxidectin, and abamectin). In susceptible worms, these lactones are effective against adults, but only moxidectin was 70-80% effective against inhibited/encysted larvae. In the absence of drug resistance, treatments with benzimidazoles (fenbendazole), tetrahydropyrimidines (pyrantel) and diethylenediamines (piperazine salts) were effective against adult worms but less so against encysted larvae and not against inhibited larvae. Recent treatment may also precipitate disease as killing adult stages may stimulate encysted (hypobiotic) stages to emerge from the gut wall. Some treatments have also caused serious side-effects involving severe inflammation of the colonic mucosa. Numerous veterinary health agencies recommend that anthelmintics be used prudently, with faecal egg count reduction tests used to monitor for drug resistance and to select the most appropriate anthelmintic for strategic dosing (usually seasonal, before and after winter) or selective dosing (treat those with high egg counts, as parasites are over-dispersed with the majority occurring in a small number of hosts). Continuous dosing with in-feed pyrantel has been discontinued due to the high levels of resistance induced, and regular-interval ('suppressive') dosing may also induce resistance and/or interfere with the development of natural protective immune responses (but is still practiced widely, especially in yearlings). Various control strategies may also be implemented to limit the faecal-oral transmission of infections, mainly by reducing the contamination on pastures with worm eggs and larvae (drench and move to clean pastures, collect and compost faeces, avoid overstocking, quarantine new animals, separate age groups, rotational grazing of cohorts so that nursing mares and foals do not graze the same area in consecutive years, mixed or alternate grazing with other non-susceptible herbivores, or pasture spelling, particularly over hot dry periods). Several studies have also demonstrated the utility of biological control using nematophagous fungi to reduce larval contamination on pastures.

Cyathostomum and other small strongyles



Cyathostomum adult worms

Cyathostomum worm eggs



Cyathostomum adult worm, head