Habronema/Draschia
(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 tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised; including habronematoids (with pseudolabia and median lips) containing the habronematids which live in the stomachs of horses and are transmitted by muscid flies in which L3 develop. Gastric infections by *Habronema* and *Draschia* spp. are generally asymptomatic, but the larvae may cause granulomatous skin lesions (summer sores).

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:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Habronematoidea (unique head structures with small pseudolabia and median lips)
Family:	Habronematidae (pharynx with dorsal and ventral tooth, indirect cycle involving ingestion of fly)
Genus:	*Habronema* (parasitic in stomach of horses)
Genus:	*Draschia* (parasitic in stomach of horses)
Species:	various species may cause gastritis in horses, while larvae may cause nodular dermatitis

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 (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending

on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
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.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Habronematoidea contains medium-sized worms with unique head structures comprising small pseudolabia and median lips infecting the alimentary tracts of vertebrates and utilizing terrestrial or aquatic insects and crustaceans as intermediate hosts for larval development. Four families are recognised: Habronematidae (large pseudolabia covering median lips, no cephalic papillae on pseudolabia, 8 papillae on median lips, divided oesophagus, female tail not modified as attachment organ, sexual dimorphism not marked, female body not coiled, globular or inflated, parasites of birds and mammals); Tetrameridae (median lips not extending over pseudolabia, no cephalic papillae on pseudolabia, divided oesophagus, female tail not modified as attachment organ, sexual dimorphism marked, female body spirally coiled or globular or with slender extremity with distal end inflated, parasites of mammals and birds); Hedruridae (median lips extending over pseudolabia, cephalic papillae on pseudolabia, undivided oesophagus, female tail modified as attachment organ, parasites of amphibians, reptiles and fish); and Cystidicolidae (small pseudolabia often reduced to appendix, median lips not extending over pseudolabia, 4 papillae at bases of pseudolabia,

divided oesophagus, female tail not modified as attachment organ, sexual dimorphism not marked, female body not coiled, globular or inflated, parasites of fishes).

The family Habronematidae contains 3 subfamilies: Habronematinae (posterior border of pseudolabia without ornamentation, not forming attachment organ, parasites of mammals); Parabronematinae (posterior border of pseudolabia with ornamentation forming attachment organ consisting of cordons, parasites of mammals); and Histiocephalinae (posterior border of pseudolabia with ornamentation forming attachment organ consisting of simple or denticulate leaf-like structures, parasites of birds). The subfamily Habronematinae contains 9 genera (*Chitwoodspirura*, *Cyrnea* (syn. *Seurocyrnea*, *Skrjabinochiona*, *Chenospirura* p.p., *Metacyrnea*), *Draschia*, *Excisa*, *Gendrespirura* (syn. *Chenospirura* p.p., *Cheniellospirura*, *Sinicaspirura*), *Habronema* (incl. subgenera *Habronema*, *Aviabronema*), *Odontospirura* (syn. *Vaznema*), *Procyrnea* (syn. *Aviabronema?*, *Ruschiella*, *Draschearia*), and *Sicarius*) which are differentiated primarily on the basis of differences in adult morphology (esp. cephalic structures), larval morphology (anatomy and ornamentation), modes of transmission, host occurrence/specificity and geographic distribution. Genera of veterinary and medical significance are tabulated below:

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs/Larvae	Transmission
Family: Habronematidae (pharynx with dorsal and ventral tooth, indirect cycle involving ingestion of fly)						
Habronema	32	perissodactyls, birds	stomach	8-35 mm long, cylindrical buccal capsule, 2 large lateral pseudolabia, 2 median lips, bipartite oesophagus, oviparous, some viviparous	eggs, 40-80 x 10-20 µm, elongate, thin-shelled	indirect (L3 in muscid flies)
Draschia	1	perissodactyls	stomach	7-15 mm long, funnel-shaped buccal capsule, 2 large lateral pseudolabia, 2 median lips, bipartite oesophagus, viviparous	larvae (L1) 330-350 µm, anterior tooth	indirect (L3 in muscid flies)
Family: Tetrameridae (extravagant sexual dimorphism, females swollen, coloured bright red)						
Tetrameres	57	birds	proventriculus	3-10 mm, globular body divided into 4 by longitudinal grooves, lateral pseudolabia, 2 median trilobed lips, bipartite oesophagus, oviparous	eggs, 33-62 x 18-30 µm, oval, thick-shelled, operculate	indirect (L3 in crustaceans, amphipods, insects, earthworms)

Members of the genus *Habronema* have pseudolabia with convex anterior borders and some 32 species have been described from the stomachs of perissodactyls and occasionally from the proventriculus, ventriculus and intestines of birds (mostly non-passerines). Some authors recognize 2 *Habronema* subgenera: namely, *H.* (*Habronema*) (vulva on ventral axis or displaced dorsally, single lateral alae, parasitic in mammals); and *H.* (*Aviabronema*) (vulva on ventral axis, body with or without lateral alae, parasitic in birds); while other authors have synonymized *H.* (*Aviabronema*) with the genus *Procyrnea.* Worms belonging to the genus *Draschia* have pseudolabia with concave anterior borders and the sole species *D. megastoma* is commonly found in perissodactyls. Worms of both genera have indirect life-cycles involving larval development in dipteran flies which deposit infective stages on the mucous membranes of the final hosts where they are ingested. In equids, adult worms develop in the gastric mucosa often causing chronic catarrhal gastritis, sometimes with nodule or tumour formation, while larvae may also cause conjunctival and cutaneous lesions (summer sores).

Parasite species	Definitive Hosts	Location [Clinical signs]	Intermediate Hosts	Distribution
Draschia				
D. megastoma (syn. *Habronema*)	Perissodactyla: equid (horse, donkey, plains zebra, mountain zebra), rhinocerotid (southern black rhinoceros); Lagomorpha: leporid (European rabbit)	stomach [gastritis, nodules, skin lesions (summer sores), conjunctivitis]	Diptera: muscid (*Musca domestica, humilis, sorbens, tempestiva, vicinina, Muscina stabulans, terraereginae, Stomoxys calcitrans, Fannia* spp.)	worldwide
Habronema				
H. (A.) aegotheles	Caprimulgiformes: aegothelid (Australian owlet-nightjar)			Australia
H. (A.) ameerae (= *Procyrnea*)	Falconiformes: falconid (Himalayan kestrel)	proventriculus		India

H. (A.) americanum	Accipitriformes: accipitrid (broad-winged hawk)			North America
H. (A.) asymmetricum	Accipitriformes: accipitrid (pale harrier)			Africa
H. avicedae	Accipitriformes: accipitrid (Indian black-crested baza)			Asia
H. bialatum	Galliformes: phasianid (northern bobwhite quail)			North America
H. (A.) buckleyi	Otidiformes: otidid (northern black korhaan)			Africa
H. bulbosum	Galliformes: phasianid (Indian peafowl)			Asia
H. casuarii	Casuariiformes: casuariid (double-wattled cassowary)			Australasia
H. (A.) chabaudi (= *Procyrnea*)	Falconiformes: falconid (laggar falcon)	proventriculus		India
H. (A.) circi (= *Cyrnea leptoptera*)	Accipitriformes: accipitrid (hen harrier)			Asia
H. (H.) clarki	Perissodactyla: equid (donkey); Rodentia: caviid (capybara, lesser capybara)			South America
H. (A.) colaptes (= *Procyrnea*)	Piciformes: picid (northern flicker)			North America
H. (A.) daleri	Columbiformes: columbid (southern green pigeon)	gizzard		India
H. (A.) diesingi	Galliformes: numidid (vulturine guineafowl)			Africa
H. (A.) dolichocolpos	Accipitriformes: accipitrid (Madagascar cuckoo-hawk, Madagascar harrier-hawk)			Madagascar
H. euplocami	Galliformes: phasianid (kalij pheasant, peacock-pheasant)			Asia
H. (A.) ficheuri (= *Procyrnea*)	Strigiformes: strigid (long-eared owl)			Holarctic
H. hamospiculatum (syn. *H. congolense*, *manidis, zschokkei*) (= *Gendrespirura*)	Pholidota: manid (tree pangolin)			Africa
H. (A.) hrishii	Accipitriformes: accipitrid (black kite)			Eurasia
H. (A.) imbricatum (= *Cyrnea*)	Strigiformes: strigid (oriental scops owl, spotted owlet); Falconiformes: falconid (peregrine falcon)			Holarctic
H. (A.) incertum	Galliformes: phasianid (Gambel's quail)	proventriculus		North America
H. indicum	Coraciiformes: coraciid (Indian roller)			India
H. hyperabadensis	Passeriformes: sturnid (common hill myna)	gizzard		India
H. khalili	Perissodactyla: rhinocerotid (black rhinoceros)			Africa
H. (A.) leptoptera (= *Procyrnea*)	Accipitriformes: accipitrid (Eurasian sparrowhawk); Falconiformes: falconid (Eurasian hobby)			Eurasia
H. longistoma	Perissodactyla: equid (Grant's zebra)	stomach		Africa
H. (A.) longispiculum	Strigiformes: strigid (great grey owl)			Holarctic
H. (A.) longistriata (= *Procyrnea*)	Piciformes: picid (Campo flicker)			South America
H. malani	Perissodactyla: equid (Burchell's zebra, Hartmann's mountain zebra)			Africa
H. (A.) magnilabiatum	Accipitriformes: accipitrid (Himalayan grey-headed fishing			Asia

	eagle)			
H. (A.) magnipapillatum	Accipitriformes: accipitrid (white-eyed buzzard)	proventriculus		India
H. (A.) mansoni (= *Procyrnea*)	Accipitriformes: accipitrid (red-tailed hawk, pallid harrier, common buzzard); Falconiformes: falconid (American kestrel, American peregrine falcon)	proventriculus		North America, Asia
H. (H.) microstoma (syn. *H. majus*) (incl. subspp. *microstoma*, *congolense*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	stomach [gastritis, skin lesions (summer sores), conjunctivitis]	Diptera: muscid (house fly, *Musca domestica,* stable fly, *Stomoxys calcitrans,* buffalo fly, *Haematobia exigua,* horn fly, *Lyperosia irritans*), sarcophagid (flesh fly, *Sarcophaga melanura*)	worldwide
H. (A.) monoptera	Accipitriformes: accipitrid (Asian tawny eagle)	proventriculus		India
H. (A.) murrayi (= *Procyrnea*)	Strigiformes: tytonid (barn owl)			Africa
H. (H.) muscae	Perissodactyla: equid (horse, Przewalski's horse, donkey, onager, mountain zebra); Artiodactyla: bovid (cattle, goat)	stomach [skin lesions, conjunctivitis]	Diptera: muscid (*Musca domestica, humilis, lusoria, terraereginae, ventrosa, Pseudopyrellia* (*Neomyia*)), sarcophagid (*Sarcophaga*)	worldwide
H. numidae (= *Cyrnea*)	Galliformes: numidid (helmeted guineafowl)			Africa
H. (A.) seurati (= *Cyrnea*)	Falconiformes: falconid (Eurasian hobby, red-footed falcon)			Eurasia
H. (A.) singhi	Accipitriformes: accipitrid (common pariah kite)	proventriculus		India
H. (A.) skrjabini	Carnivora: felid (spotted wild cat)			Asia
H. (A.) spinosa (= *Procyrnea*)	Strigiformes: strigid (Eurasian eagle-owl); Falconiformes: falconid (common kestrel, lesser kestrel)			North America
H. (A.) suraiyae (= *Procyrnea*)	Falconiformes: falconid (red-necked falcon)	proventriculus		India
H. tomasi	Perissodactyla: equid (Burchell's zebra)			Africa
H. (A.) tulostoma (= *Procyrnea*)	Accipitriformes: accipitrid (Egyptian vulture)			Africa
H. tyosenense	Perissodactyla: equid (horse)	stomach		Asia
H. (A.) uncinipenis (= *Procyrnea*)	Rheiformes: rheid (greater rhea)			South America
H. unilateralis (= *Procyrnea*)	Piciformes: ramphastid (red-billed toucan, spot-billed toucan)			South America
H. (A.) urophasiana (= *Procyrnea*)	Galliformes: phasianid (greater sage-grouse)	gizzard		North America
H. (A.) waheedae	Accipitriformes: accipitrid (Brahminy kite)	proventriculus		India
H. (H.) zebrae	Perissodactyla: equid (mountain zebra)			Africa

Parasite morphology: *Draschia* and *Habronema* spp. form 3 distinct morphological stages in their developmental cycles: eggs; larvae (4 successive stages designated L1-L4); and adult worms. The thin-shelled eggs are oval, sometimes elongated and cigar-shaped, measuring 40-80 x 10-20 µm, and are larvated when laid. L1 have cylindrical ridged bodies measuring 330-350 µm long with an anterior spine-like tooth. Two types of L2 have been observed, robust sausage-shaped stages measuring 400-500 µm, and elongate slender stages measuring up to 990 µm, many stages apparently enclosed in a sheath of host origin. Infective L3 range in size from 1.5-4.0 mm and have a conspicuous cephalic cone with a hexagonal mouth surrounded by large bilobed dorsal and ventral lips and smaller lateral lips, 4 cephalic papillae and 2 lateral amphids. The cuticle is deeply ridged, transversely and longitudinally, and the tail is conical and studded with small papillae appearing as spiny knobs. Adults are small white-yellow worms measuring from 7-15 mm in length for *Draschia* and from 8-35 mm for *Habronema*. Their bodies are cylindrical with curved conical tails and tapering anterior ends (*Draschia* has a transverse groove or cephalic collar at the anterior end). They have large thick-walled buccal capsules (cylindrical in *Habronema* and funnel-shaped in *Draschia*) with narrow pseudolabia and 2 median lips (ventral and dorsal) with sensory papillae. The buccal capsule may be unarmed (e.g. *D. megastoma, H. muscae*) or armed with teeth (e.g. *H. majus* with 2 teeth). The pseudolabia have convex anterior borders in *Habronema* and concave anterior borders in *Draschia.* The lips may be unlobed (e.g. *D. megastoma*), bilobed (e.g. *H. microstoma*) or trilobed (e.g. *H. muscae*). Worms have one (*Habronema*) or two (*Draschia*) lateral cervical alae, and a bipartite oesophagus (with a short anterior muscular section and a longer posterior glandular section). Adults are sexually dimorphic, with females being slightly larger than males (10-15 cf. 7-10 mm for *Draschia,* 12-35 cf. 8-22 mm for *Habronema*). Mature females are didelphic with 2 ovaries and uteri connected to a short vagina and an ovoid ovejector opening into a common anterior vulva. The body is not spirally twisted nor globular and the caudal extremity is not inflated (in contrast to *Tetrameres*). Mature males have spirally twisted tails with well-developed caudal alae, pedunculate caudal papillae and 2 elongate curved spicules unequal in length (left spicule larger).

Site of infection: Adult *D. megastoma* worms burrow into the gastric mucosa of equids, usually near the junction of the oesophageal and glandular regions. In mammals, adult *Habronema* worms live in the mucus covering the glandular portion (fundus) of the stomach, with their heads attached to the mucosa. In birds, adult *Habronema* worms infect the proventriculus, ventriculus and/or intestines. Larval stages entering the gut complete their development within the lumen, while those entering cutaneous or mucocutaneous tissues are unable to complete their development but nonetheless may cause lesions. Worm eggs release larvae that are taken up by insect intermediate hosts where they form infective larval stages in the haemocoel before invading the mouthparts.

Pathogenesis: Most infections are asymptomatic, although heavy infections by some species may cause gastric signs while larvae infecting superficial tissues may cause cutaneous or conjunctival lesions. Larvae deposited on moist membranes around the muzzle are swallowed thereby reaching the stomach in order to complete their development to adult worms. Most species cause traumatic damage to the gastric mucosa and elicit host inflammatory responses resulting in chronic congestion and mild catarrhal gastritis associated with the secretion of thick tenacious mucus. Some species (e.g. *H. muscae*) have also been associated with petechial haemorrhages and gastric ulcer formation. The species *D. megastoma* is the most pathogenic, however, as worms live in colonies in the fundic submucosa causing large fibrous tumour-like lesions (2-10 cm diameter). The granulomatous nodules have 1-2 central openings and are filled with worms embedded in necrotic and caseous exudate. The nodules project into the lumen but are well tolerated and usually do not produce clinical signs. Infected animals may develop digestive disorders during autumn and winter, with capricious appetite, pica, polydipsia, constipation alternating with diarrhoea, and colic due to pyloric obstruction and severe indigestion. Infections may occasionally cause suppurative gastritis, pyloric stenosis or obstruction, adhesions with adjacent organs and even gastric perforation with subsequent peritonitis, particularly when abscesses are formed due to secondary pyogenic bacterial infections. Different types of disease may arise when larvae invade moist membranes separate from the alimentary tract where they are unable to complete their development to adults but nonetheless may cause severe inflammatory reactions and lesions before they succumb to host immune responses. Larvae deposited on broken skin or open wounds may cause proliferative lesions consistent with nodular granulomatous ulcerative dermatitis. The lesions appear as red-brown cauliflower-like masses (up to 5-15 cm in diameter) that protrude above the surface of the skin and haemorrhage easily (condition known variously as summer sores, jack sores, swamp cancer, bursati, or granular dermatitis). The lesions are intensely pruritic and painful and hosts attempt to relieve the itch by biting, scratching and rubbing thereby causing the wounds to bleed or fester. Summer sores occur mainly due to infection with *D. megastoma* larvae, although some *Habronema* spp. may cause similar lesions which are less severe and transient. The sores are often found on body parts prone to superficial injuries (head, withers, inner lower limbs, coronet above the hoof) and secondary bacterial infections may worsen lesions. As the larvae gradually die, the lesions become fibrous and inactive, but often do not heal until cooler weather commences and fly activity ceases. Larvae deposited around the eyes may burrow in the conjunctivae causing ulcerative weeping lesions at the medial canthus, the nictitating membrane or the eyelid. The lesions become progressively nodular with granulomatous masses (3-4 mm in diameter) causing local irritation, ulceration, conjunctivitis, keratitis, lacrimation with epiphora, photophobia, and squinting. Invading larvae may occasionally be carried to the lungs either via the bloodstream or by migration down the airways. Infections may result in pulmonary granulomas or purulent bronchitis, but they are rarely severe enough to cause clinical signs (cough or nasal discharge). Several instances have also been reported where larvae have invaded the prepuce and glans penis of stallions causing dysuria. In contrast to mammalian infections, those in birds have not been associated with any significant pathological changes, morbidity or mortality.

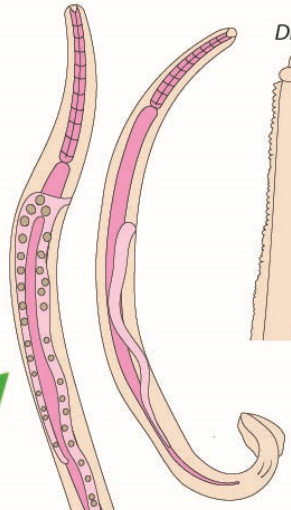
Developmental cycle and mode of transmission: The parasites have indirect heteroxenous life-cycles involving the development of infective larvae in dipteran intermediate hosts which are transmitted to vertebrate definitive hosts in which adult worms form. Gravid female worms lay embryonated eggs in the stomach which hatch in transit through the intestines or immediately after their excretion in faeces. Several reports have suggested that some species (e.g. *D. megastoma, H. microstoma*) may even be viviparous and give birth to live larvae rather than eggs. L1 survive for some time in faecal material (6-7 days at 25-30°C, 28 days at 5°C) and they are active, exhibiting positive hydrotropism and thermotropism. Embryonated eggs and free L1 are ingested by dung-inhabiting dipteran larvae (biting and non-biting muscid flies) which act as intermediate hosts supporting the development of infective L3. Transmission occurs primarily during the warmer months of the year when flies are active and breeding on pastures. The L1 penetrate the gut of the fly larvae, enter the haemocoel and invade tissues (Malpighian tubules or fat bodies) where they moult to L2 after 3-4 days. These stages encapsulate in the tissues during the fly pupal stage and their further development to L3 is synchronised to coincide with the emergence of the adult fly from the pupa. L3 form over several days (faster at higher temperatures) and migrate to the head of the fly invading the labium within 1-2 weeks. Infective L3 break out of the mouthparts when flies feed on suitable definitive hosts, thus becoming deposited on moist membranes or secretions around the mouth, nostrils, conjunctiva, genitalia, broken skin or open wounds. Infective L3 are very susceptible to dessication and die within a few minutes if deposited on dry substrates. Final hosts may also be infected by ingesting infected flies (live or dead) in feed or water. Larvae that are able to access the alimentary tract are swallowed and develop directly to adults in the stomach (they do not undertake any local, somatic or extra-intestinal migrations). The prepatent period (time from infection to first excretion of eggs/larvae) is around 8 weeks. Larvae that are deposited at sites without access to the gut (e.g. skin, eyes, genitals) may invade local tissues but are unable to develop into adults.

Differential diagnosis: Clinical infections often present with characteristic cutaneous and/or conjunctival lesions during the warm fly season (summer sores) or vague gastric signs (usually involving colic) during cooler non-fly seasons. In either case, other aetiological agents need to be discounted. Scrapings and biopsies of proliferative skin lesions and lachrymal fluid may be examined for parasite larvae, but they are usually difficult to find and identify. Infections are conventionally diagnosed by the microscopic detection of worm eggs and/or larvae in faecal samples, usually following egg concentration by floatation or larval recovery by Baermann filtration, although neither technique is highly sensitive. Worm eggs have sometimes been detected by gastric lavage collected by stomach tube. Infections may be diagnosed at post-mortem by the detection of nodular lesions containing adult worms in samples recovered from the stomach mucosa. Histological examination of sections of cutaneous, ocular or pulmonary tissues may sometimes reveal larval stages. Modern molecular biological techniques have been used to characterize parasites from definitive and intermediate hosts (horses and flies, respectively) by polymerase chain reaction (PCR) amplification of nuclear gene sequences (ribosomal RNA and internal transcribed spacer regions).

Treatment and control: A small range of anthelmintic drugs have been used to successfully treat clinical infections, including the macrocyclic lactones (ivermectin, moxidectin), organophosphonates (dichlorvos), diethylenediamines (diethylcarbamazine) and benzimidazoles (oxibendazole, oxfendazole, cambendazole). Ivermectin is most effective against both larval and adult worms, although repeated treatments are required to prevent re-infection. Ocular disease has responded reasonably well to treatment with various concoctions of topical ophthalmic antibiotics, anthelmintics and corticosteroids (involving combinations of nitrofurazone, trichlorphon, ivermectin, diethylcarbamazine, echothiophate iodide and dexamethasone). Most infections occur in horses kept outdoors on pastures (where dung-inhabiting fly vectors abound, albeit seasonally) rather than in horses stabled indoors (where the insect vectors rarely venture). It is difficult to implement effective preventive strategies in extensive outdoor operations, but some initiatives have helped reduce infection rates by minimizing environmental contamination (regular collection and disposal of faeces), managing fly populations (regular application of insecticides to livestock and fixtures) and limiting opportunities for transmission (timely treatment of skin lesions/wounds so they do not attract flies). Similar strategies may be used around stables to safeguard against infections.

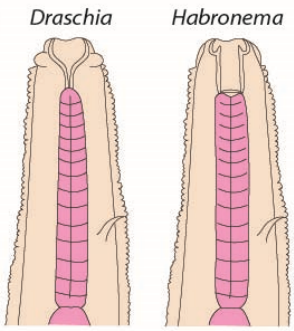
Draschia, Habronema

stomach
(larval dermatitis,
chronic catarrhal gastritis,
sometimes nodule formation)



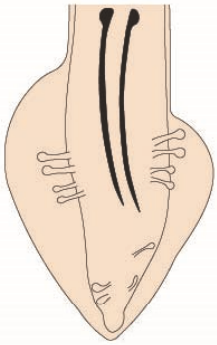
adult female
(~ 15 mm)

adult male
(~ 10 mm)



heads

Definitive Hosts
(perissodactyls, birds)



male tail

eggs hatch in
host or faeces

L3 develop in larvae/pupae
and then invade adult mouthparts

L3
deposited
on hosts

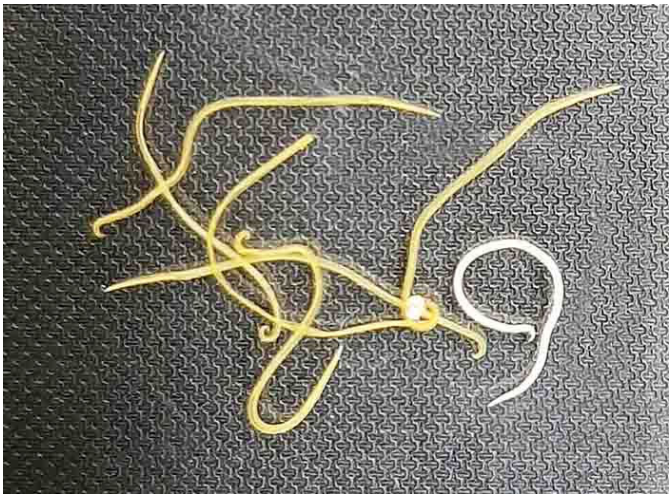
eggs
(~ 80 µm)

eggs/L1
excreted

third-stage larvae
(L3) (~ 2 mm)

Intermediate Hosts
(muscid flies)
(haemocoel, then mouthparts)

eggs/L1 ingested
by fly larvae



Habronema adult worms

Habronema worm egg

Habronema adult worm, male tail

Habronema adult worm, head