

Syngamus

(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 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 syngamids which have large cup-shaped buccal capsules armed with teeth but no leaf crowns. Several species parasitize the respiratory mucosa of birds. They have direct life-cycles, usually involving eggs passed in faeces developing to L3 which are ingested by new hosts and develop to adults. Unlike other strongyloids, the L3 of syngamids develop in eggs before hatching. Infections may therefore occur by ingestion of L3 in eggs, L3 that have hatched or L3 taken up by invertebrate paratenic (transport) hosts. *Syngamus* spp. (gape worms) infect the trachea and bronchi causing obstructive respiratory distress in birds worldwide.

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: Syngamidae (buccal capsule with basal teeth, in respiratory, urinary or digestive tract of mammals/birds)
Subfamily: Syngaminae (gapeworm, in trachea of birds and mammals)
Genus: *Syngamus* (parasitic in trachea of birds)
Genus: *Mammomonogamus* (parasitic in frontal airways of ruminants and cats)
Genus: *Cyathostoma* (parasitic in trachea of waterfowl)
Species: various species cause respiratory distress

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 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)				
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
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
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 <i>per os</i>)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

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 Delectrocephalidae (oral opening hexagonal, dorsal ray with 6 terminal branches, 2 genera in large intestines of birds). The family Syngamidae contains 3 subfamilies: Syngaminae (leaf crown absent, teeth at base of buccal capsule, anterior vulva, 5 genera in trachea of birds and some mammals); Stephanurinae (rudimentary leaf crown, teeth at base of buccal capsule, rudimentary bursa, posterior vulva, 1 genus in urinary system of suids); and Archeostrongylinae (leaf crown absent, teeth absent at base of buccal capsule, 1 genus in intestines of porcupines).

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Worm eggs
Syngaminae					
<i>Syngamus</i> (gape worm)	10	birds	respiratory tract	2-30 mm long, hexagonal cup-shaped buccal capsule armed with teeth, no leaf crowns, small male permanently attached to female vulva imparting Y-shape, L3 develop in eggs before hatching, invertebrate PH	70-100 x 42-62 µm, ellipsoidal, operculate
Stephaurinae					
<i>Stephanurus</i> (kidney-worm)	1	suids	urinary tract	2-5 cm long, stout reddish bodies, white reproductive organs, prominent buccal capsule often armed with teeth, small leaf crowns and external epaulettes, eggs passed in faeces and urine, L3 ingested or percutaneous, earthworm PH	90-136 x 53-70 µm, ellipsoidal, thin-shelled

The subfamily Syngaminae contains 5 genera: *Syngamus* (including subgenera *Syngamus* and *Ornithogamus*), *Cyathostoma* (including subgenera *Cyathostoma*, *Calcaronema* and *Hovorkonema*) and *Boydinema* all of which form adults with buccal capsules with smooth inner walls, eggs with opercula, and are parasitic in birds; while *Mammomonogamus* and *Rodentogamus* form adults with buccal capsules with longitudinal ribs on the inner wall and are parasitic in mammals. [Several early studies suggested that the genus *Cyathostoma* be placed in a separate subfamily Cyathostominae because males and females were not fused *in copula* (as occurs for *Syngamus* spp.), but subsequent studies found this character to be unreliable]. The genus *Syngamus* contains 10 species which infect the trachea of birds causing respiratory distress with birds gaping and struggling for breath (hence the common name of gape worm). The species *S. trachea* occurs worldwide in a range of birds (galliforms, anseriforms, passerines, psittacines, columbiforms, birds of prey), being most evident in gamebirds used for sporting purposes. Many infections have been reported in ground-feeding birds, especially those ingesting invertebrates (earthworms, snails, slugs, coprophagous arthropods) which act as paratenic transport hosts. Infected birds can be found any time in the year, mainly in young birds as older birds apparently gain some protective immunity and shed parasites with age. Species in the other genera may also cause upper or lower respiratory disorders in their hosts, especially in tropical and subtropical regions where climatic conditions favour the survival of larval stages in the external environment.

Parasite species	Definitive Hosts [plus Paratenic Hosts (PH)]	Location [Clinical signs]	Distribution
<i>Syngamus</i> [incl. subgenera <i>S. (Syngamus)</i> (well-developed collar) and <i>S. (Ornithogamus)</i> (rudimentary collar)]			
<i>S. anterogonimus</i>	Charadriiformes: scolopacid (western sandpiper, red-necked phalarope)		Eurasia, North America
<i>S. (Ornithogamus) arcticus</i>	Gaviiformes: gaviid (red-throated loon)	trachea	North America
<i>S. dyki</i>	Passeriformes: turdid (common blackbird)	trachea	Europe
<i>S. (Ornithogamus) gibbocephalus</i>	Charadriiformes: scolopacid (pin-tailed snipe)		Eurasia
<i>S. (Ornithogamus) merulae</i>	Passeriformes: turdid (varied thrush, song thrush, fieldfare, common blackbird, American robin, Naumann's thrush, redwing), muscicapid (blue rock thrush), passerid (house sparrow), corvid (western jackdaw)		Palaearctic
<i>S. palustris</i>	Charadriiformes: scolopacid (ruff, Eurasian woodcock, wood sandpiper)		Eurasia
<i>S. skrjabinomorpha</i>	Galliformes: numidid (helmeted guineafowl), phasianid (chicken); Anseriformes: anatid (goose) [plus PH: Clitellata: lumbricid (<i>Allolobophora caliginosa</i> , <i>chlorotica</i> , <i>jassyensis</i> , <i>Dendroboena faucium</i> , <i>hortensis</i> , <i>mariupoliensis</i> , <i>schmidti</i> , <i>venata</i> , <i>Eiseniella colchidica</i> , <i>Eophila patriarchalis</i>)]	trachea	Palaearctic
<i>S. taiga</i>	Passeriformes: corvid (spotted nutcracker), acrocephalid (sedge warbler, Eurasian reed warbler), motacillid (white wagtail), muscicapid (bluethroat), corvid (rook), alaudid (Eurasian skylark, woodlark); Galliformes: phasianid (hazel grouse, grey partridge)	trachea	Russia
<i>S. tenuispiculum</i>	Passeriformes: turdid (American robin)		North America

<p><i>S. trachea</i> (gapeworm, redworm, forked worm) (syn. <i>S. gracilis</i>, <i>parvus</i>, <i>primitivus</i>, <i>skrjabini</i>, <i>trachealis</i>)</p>	<p>Galliformes: phasianid (chicken, red junglefowl, willow ptarmigan, northern bobwhite quail, chukar partridge, grey partridge, rock partridge, red-legged partridge, hazel grouse, black grouse, western capercaillie, Caucasian woodcock, ring-necked pheasant), numidid (helmeted guineafowl); Anseriformes: anatid (mallard, goose, bar-headed goose); Pelecaniformes: pelecanid (great white pelican), threskiornithid (American white ibis); Suliformes: phalacrocoracid (double-crested cormorant); Gruiformes: gruid (sandhill crane); Piciformes: picid (European green woodpecker); Charadriiformes: scolopacid (dunlin, sanderling, common snipe, ruff, Eurasian woodcock, common greenshank), charadriid (little ringed plover); Coraciiformes: alcedinid (belted kingfisher); Apodiformes: apodid (common swift); Accipitriformes: accipitrid (besra sparrow hawk); Columbiformes: columbid (pigeon); Passeriformes: passerellid (fox sparrow), sturnid (common mynah, common starling), monarchid (black-naped monarch), turdid (song thrush, fieldfare), fringillid (brambling), icterid (red-winged blackbird, common grackle), parulid (northern water thrush), corvid (Eurasian jay, western jackdaw, common raven, hooded crow, carrion crow, large-billed crow, rook, Eurasian magpie, red-billed chough)</p> <p>[plus PH: Clitellata: lumbricid (<i>Allolobophora calliginosa</i>, <i>rosea</i>, <i>Dendroboena platyura</i>, <i>vej dovskiyi</i>, <i>Eisenia foetida</i>, <i>Lumbriculus variegatus</i>, <i>Lumbricus baicalensis</i>, <i>castaneus</i>, <i>rubellus</i>, <i>Nicrodrilus calliginosus</i>, <i>roseus</i>): Diptera: muscid (<i>Musca domestica</i>, <i>Lucilia sericata</i>)]</p>	<p>trachea, lungs [respiratory distress]</p>	<p>worldwide</p>
--	--	--	------------------

Other genera in birds

Parasite species	Definitive Hosts [plus Paratenic Hosts (PH)]	Location [Clinical signs]	Distribution
<i>Cyathostoma</i> [incl. subgenera <i>C. (Cyathostoma)</i> , <i>C. (Calcaronema)</i> and <i>C. (Hovorkonema)</i>]			
<i>C. (Hovorkonema) americanum</i>	Accipitriformes: accipitrid (Cooper's hawk, northern goshawk, red-tailed hawk, eastern red-tailed hawk, broad-winged hawk, western marsh harrier, common buzzard, rough-legged buzzard); Strigiformes: strigid (snowy owl, long-eared owl, little owl)	trachea, air sacs	Europe, North America
<i>C. bouharti</i> (syn. <i>Syngamus</i>)	Casuariiformes: casuariid (cassowary)	trachea	Australia
<i>C. brantae</i> (syn. <i>Syngamus</i>)	Anseriformes: anatid (Canada goose, snow goose, mandarin duck); Casuariiformes: casuariid (emu, zoo animal)	trachea	Eurasia
<i>C. (Hovorkonema) brodskii</i>	Accipitriformes: accipitrid (western marsh-harrier); Gruiformes: gruid (black crowned crane)		Eurasia
<i>C. (Hovorkonema) bronchialis</i> (syn. <i>Syngamus</i>)	Anseriformes: anatid (mandarin duck, greylag goose, Canada goose, swan); Casuariiformes: casuariid (emu) [plus PH: Clitellata: lumbricid (<i>Eisenia foetida</i>)]	trachea, bronchi [respiratory distress]	North America, Europe
<i>C. cacatua</i>	Psittaciformes: cacatuid (sulphur-crested cockatoo)	air sacs	New Zealand
<i>C. coscorobae</i> (syn. <i>Syngamus</i>)	Anseriformes: anatid (coscoroba swan, spur-winged goose)	trachea, bronchi	Americas
<i>C. ibisi</i>	Pelecaniformes: threskiornithid (Indian white ibis)	trachea	India
<i>C. lari</i>	Charadriiformes: larid (European herring gull, black-headed gull); Falconiformes: falconid (common	orbital sinuses	Eurasia

	kestrel); Accipitriformes: accipitrid (Eurasian sparrow hawk, common buzzard)		
<i>C. sarcidiornis</i> (syn. <i>Syngamus</i>)	Anseriformes: anatid (knob-billed duck)	trachea	
<i>C. (Cyathostoma) sphenisci</i>	Sphenisciformes: spheniscid (African penguin); Gaviiformes: gaviid (common loon); Pelecaniformes: pelecanid (brown pelican, American white pelican)	trachea, lungs, air sacs	Africa, North America
<i>C. (Hovorkinema) tadornae</i>	Anseriformes: anatid (common shelduck)	trachea	Russia
<i>C. trifurcatum</i>	Ciconiiformes: ciconiid (black stork)	trachea	Europe
<i>C. turemuratovi</i> (syn. <i>C. microspiculum</i> , <i>Syngamus</i> (<i>Ornithogamus</i>), <i>S. hexadontus</i>)	Suliformes: phalacrocoracid (great cormorant, pygmy cormorant)		Asia
<i>C. (Hovorkinema) variegatum</i>	Anseriformes: anatid (mallard, snow goose, bar-headed goose, black swan); Galliformes: phasianid (Indian peafowl); Casuariformes: casuariid (emu); Gruiformes: gruid (whooping crane, sandhill crane, common crane); Ciconiiformes: ciconiid (white stork, black stork); Accipitriformes: accipitrid (northern goshawk, Eurasian sparrowhawk, western marsh harrier, white-tailed sea eagle, common buzzard)	trachea, bronchi [respiratory distress]	Eurasia, Australia
<i>C. (Cyathostoma) verrucosum</i> (syn. <i>Calcaronema</i> , <i>Syngamus</i>)	Pelecaniformes: pelecanid (Dalmatian pelican, great white pelican); Ciconiiformes: ciconiid (white stork)		Asia
Boydinema			
<i>B. alcyone</i> (syn. <i>Syngamus</i>)	Coraciiformes: alcedinid (belted kingfisher)		North America

Other genera in mammals

Parasite species	Definitive Hosts [plus Paratenic Hosts (PH)]	Location [Clinical signs]	Distribution
Mammomonogamus			
<i>M. auris</i> (syn. <i>Syngamus</i>)	Carnivora: felid (cat)	middle ear [otitis interna]	Asia, Americas
<i>M. dispar</i>	Carnivora: felid (cat, cougar)		North America
<i>M. felis</i>	Carnivora: felid (tiger)	lungs	Malaya
<i>M. gangguiensis</i>	Artiodactyla: bovid (cattle)		
<i>M. hippopotami</i>	Artiodactyla: hippopotamid (hippopotamus)		Africa
<i>M. ierei</i>	Carnivora: felid (cat)	nasal cavities [sneezing, discharge]	Caribbean
<i>M. indicus</i> (syn. <i>Syngamus</i>)	Proboscidea: elephantid (Indian elephant)		Asia
<i>M. laryngeus</i> (syn. <i>S. laryngeus</i> , <i>S. kingi</i>)	Artiodactyla: bovid (cattle, water buffalo, sheep, goat); Carnivora: felid (jaguar); Didelphimorphia: didelphid (common opossum); Primates: hominid (human)	larynx [laryngitis, cough]	Asia, Africa, South America
<i>M. loxodontis</i> (syn. <i>Syngamus</i>)	Proboscidea: elephantid (African forest elephant); Primates: hominid (western lowland gorilla)		Africa
<i>M. mcgaughei</i>	Carnivora: felid (cat)	sinuses, pharynx [sneezing, discharge]	Sri Lanka
<i>M. nasicola</i>	Artiodactyla: bovid (cattle, African forest buffalo, sheep, goat), cervid (deer); Primates: hominid (human)	nasal cavities [sneezing, discharge]	Americas, Africa
<i>M. okapiae</i>	Artiodactyla: giraffid (okapi)	bronchi	Africa
Rodentogamus			
<i>R. citelli</i>	Rodentia: sciurid (long-tailed ground squirrel)		Russia

(syn. <i>Syngamus</i>)			
<i>R. microtinae</i> (syn. <i>Syngamus</i>)	Rodentia: cricetid (grey red-backed vole, northern red-backed vole, tundra vole)		Palaearctic
<i>R. ryjikovi</i>	Rodentia: murid (striped field mouse, large Japanese field mouse)		Asia

Parasite morphology: *Syngamus* spp. form 3 different types of morphological stages in their developmental cycles: eggs; larvae (4 stages designated L1-L4); and adult worms. The eggs are elliptical-oval measuring 70-100 x 42-62 µm and are thin-shelled but have 2 thickened polar opercular plugs (except those of *Mammomonogamus*). Freshly-laid eggs contain a morula at the 8-16 cell (blastomere) stage of development. Unlike most other strongyles, larvae develop and moult within the eggs before they hatch (L1 moulting to L2 and then to L3). The early larval stages also lack the rhabditiform (bulbed) oesophagus and filamentous tail common to other strongyles. Following hatching, the emergent L3 measure 278-286 x 13-16 µm and are ensheathed (retain L2 cuticle) and have an elongate oesophagus and a short pointed tail. L4 are transient endoparasitic stages and have not been well described. Adult worms are sexually dimorphic, with female worms being larger than males (5-30 x 0.35 mm cf. 2-10 x 0.2 mm). The adults are highly unusual in that the smaller male attaches permanently to the larger female in permanent copulation (*in copula*) such that they form a characteristic Y-shape (in contrast, *Cyathostoma* males and females are not usually found *in copula*). The worms often appear pink-red in colour due to the presence of host blood in their intestines. Both sexes have large hexagonal mouth openings without leaf crowns but with an orbicular collar, well-developed in the subgenus *S.* (*Syngamus*) but rudimentary in the subgenus *S.* (*Ornithogamus*) (a collar is also present in the genera *Boydinema* and *Rodentogamus*, but absent in *Cyathostoma* and *Mammomonogamus*). *Syngamus* spp. have large subglobular shallow (cup-shaped) buccal capsules with smooth inner walls and 6-10 teeth at the base (the buccal capsules of *Cyathostoma* and *Boydinema* also have smooth inner walls, while those of *Mammomonogamus* and *Rodentogamus* have longitudinal ribs on the inner wall). Mature males have a short asymmetrical copulatory bursa that appears obliquely truncated with supporting rays (muscular elements following nerve channels to terminal papillae) reduced to short thick blunt rami. The dorsal ray is similar in length to the externolateral ray (but is longer in *Cyathostoma*) and it characteristically has 4 terminal branches. Males also have 2 short slender spicules 53-82 µm long, but their distal ends are not connected (whereas they are connected in *Boydinema*). Female worms are didelphic and have 2 ovaries, 2 oviducts and 2 uteri opening into a common vulva located anterior to the midbody in the subgenus *S.* (*Syngamus*) or near the midbody in the subgenus *S.* (*Ornithogamus*). Females have conical tails with pointed processes and they are oviparous and produce numerous thin-walled operculate eggs. While many species display stable uniform morphological characteristics, some species exhibit considerable pleomorphy in certain characters. For example, *S. trachea* isolates from chickens have been found to vary in egg size, worm length, buccal capsule size and shape, number of buccal teeth, and bursa structure; but the differences have not been enough to delineate new or cryptic species.

Site of infection: Adult worms of species infecting birds (*Syngamus*, *Cyathostoma*, *Boydinema*) occur in the lining of the trachea, bronchi and bronchioles, while the preceding larval stages migrate from the gut through the liver to the lungs before forming adults. Adult worms of species infecting mammals (*Mammomonogamus* and *Rodentogamus*) occur in the upper or lower respiratory tract.

Pathogenesis: Most infections in birds show few signs of clinical disease as only a few worms may be involved. However, heavier infections by a number of *Syngamus* and *Cyathostoma* spp. may cause serious problems in poultry and game bird production. The parasites are known as gapeworms because they partially block the respiratory tree causing birds to gape (open their mouths wide and stretch their necks to gasp for air) and lose condition. Disease severity is dependent on parasite pathogenicity (some species are highly virulent), the intensity of infection (worm burden), host susceptibility (particularly young galliform birds), host size (small birds with small trachea are more severely affected) and the stage of infection (disease due to migrating larvae or adult worms). Clinical respiratory signs that become apparent during the prepatent period (before adults have matured and produced eggs) are due to the migration and development of larvae and young adults through the lungs, causing pulmonary lesions, inflammation, emphysema and oedema which may lead to pneumonia with dyspnoea and depression. Clinical disease that manifests during the patent period (when eggs are being produced) are due to adult worms attaching to the tracheal mucosa to feed on host blood causing haemorrhagic tracheitis with excess mucus production (often bloody) leading to anaemia, tracheal obstruction, dyspnoea, and respiratory distress (agitated coughing, sneezing, head shaking, gaping, and hissing). Birds stop feeding, rapidly lose weight and body condition becoming weak, depressed, emaciated and may die due to asphyxia (suffocation) and/or starvation. Infections are most severe in young birds, particularly domestic chickens < 2-3 months old, game chicks and turkey poults, especially in breeding or rearing enterprises with outdoor pens or runs. Infections by other genera in mammals (including humans) have occasionally been associated with respiratory signs (coughing, haemoptysis, sneezing, nasal discharge) and poor condition when adult worms infect the upper respiratory tract.

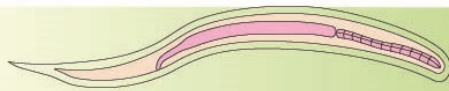
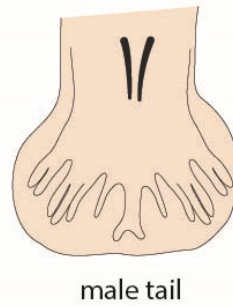
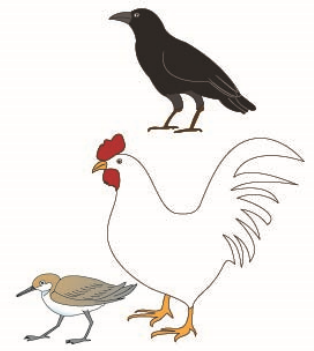
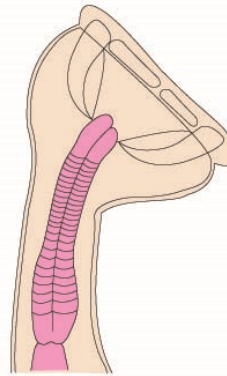
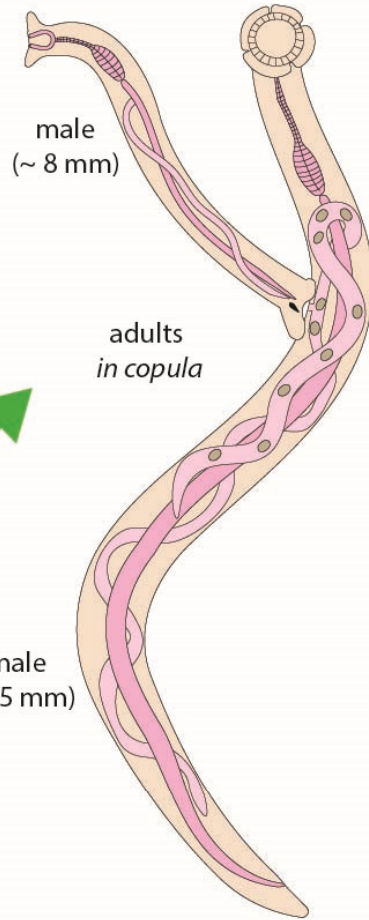
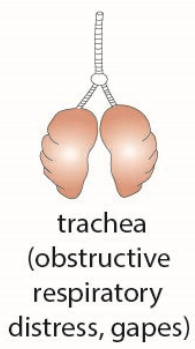
Developmental cycle and mode of transmission: Syngamids usually have direct monoxenous life-cycles involving the faecal-oral transmission of infective larvae (sometimes still in eggs), but they may also have indirect life-cycles involving infectious stages being transported in invertebrate paratenic hosts. Female worms deposit partially-embryonated eggs in the respiratory tract where they are carried up the trachea by the mucociliary escalator to be swallowed and excreted with host faeces. Infective L3 develop

within the eggs in 2-7 days depending on prevailing environmental conditions (particularly warm moist conditions). The L3 may remain in the eggs for long periods or they may hatch spontaneously after 8-14 days. Both eggs and larvae have been shown to survive in damp soil for up to 9 months. Definitive hosts become infected following the oral ingestion of infective L3 either when larvated eggs are eaten, when released larvae are eaten, or when an invertebrate paratenic host carrying eggs or larvae is eaten. Many infections have been reported in ground-feeding birds, especially those ingesting invertebrates (mainly earthworms, but also including snails, slugs, beetles, and some flies) which act as paratenic hosts in which infective L3 may survive encysted in their tissues for many months (up to 4 years). Ingested L3 exsheath in the duodenum and penetrate the intestinal wall migrating via the venous circulation through the liver to the lungs as early as 4-6 hours after infection. The larvae develop in the lungs over 5-7 days moulting twice to form adults. Males and females copulate after the final moult in the larger bronchi and mated pairs migrate *in copula* to the trachea by day 11. The prepatent period (time from infection to first egg excretion) ranges from 12-21 days and adult worms may live for up to 9 months.

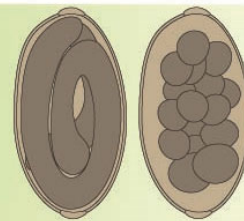
Differential diagnosis: Clinical infections in birds are often diagnosed on the basis of symptomatology when affected birds exhibit the classical signs of gaping for breath and hissing to dislodge obstructions. On rare occasions, dark red worms may be observed in the throat. Coprological techniques can be used to detect worm eggs in faecal samples, either in wet mounts, smears or concentrates (usually faecal floats). The thin-walled operculate eggs can be readily identified but they need to be differentiated from those of *Capillaria* (which are smaller, more robust, have thicker shells, and usually contain a single-celled morula). Adult worms may also be recovered ante-mortem by endoscopic biopsy or post-mortem by dissection, and identified by their red colouration and Y-shaped paired (*in copula*) configuration. Modern molecular biological techniques have recently been used to determine phylogenetic relationships between various taxa following the polymerase chain reaction (PCR) amplification of nuclear genes (large and small subunit ribosomal DNA, internal transcribed spacers 1 and 2) and mitochondrial genes (cytochrome c oxidase I).

Treatment and control: Infections in birds have been successfully treated with a range of anthelmintics administered by individual oral doses, in-feed or in-water medications or by subcutaneous injection, including benzimidazoles (thiabendazole, albendazole, mebendazole, flubendazole, fenbendazole, cambendazole), imidazothiazoles (levamisole, tetramisole), halogenated monophenols (nitroxylnil) and macrocyclic lactones (ivermectin), although the latter was not very effective. Caution is advised in treating heavy infections as birds may be unable to expel numerous dead worms and may suffocate. Repeated treatments may also be required to prevent larval stages from re-establishing infections. Many different control strategies have been used to break transmission cycles in domestic, game and aviary bird facilities, principally involving improved sanitation (removing litter and faeces, cleaning pens/cages), hygiene (clean food and water) and isolation (quarantining new stock, segregating birds of different ages, excluding wild birds as potential carriers, preventing foraging for invertebrate paratenic hosts, and restricting access to contaminated yards and open grounds). Various attempts have been made to treat range soils with chemicals to eliminate worm eggs and larvae and to reduce invertebrate populations, but most were only partially effective and had adverse environmental effects depending on the toxicity of the disinfectants and insecticides. Intensive indoor industries generally do not have problems with gapeworms, although recent trends towards free-range poultry production may experience a resurgence of infections.

Syngamus



external
environment



first- and second-stage larvae
develop within eggs



Occasional Paratenic Hosts
(earthworms)
(tissues)



Syngamus adult worms in copula



Syngamus adult worms in copula



Syngamus worm eggs