

Gongylonema

(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 spiruroids (with prominent lips) containing the gongylonematids which have an unusually broad host range living in the oesophagus and stomach of mammals and the crop of birds. Infections are transmitted by coprophagous beetles and cockroaches in which L3 develop. Adult *Gongylonema* spp. are generally asymptomatic in their definitive hosts, although some species may cause regurgitation in birds.

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: Spiruroidea (two trilobed lips, oesophagus never with bulb, coiled tail in males, two unequal spicules)
Family: Gongylonematidae (anterior cuticle covered with large bosses or irregular scutes arranged in rows)
Genus: *Gongylonema* (parasitic in oesophagus/forestomach of cattle/sheep, crop of birds)
Species: various species cause regurgitation in birds

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)]
<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 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 spirurid 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 Diplotrienoidea (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 Spiruroidea comprises worms with simple non-ornamented heads infecting the stomach (sometimes oesophagus) of mammals and birds and using arthropods as intermediate hosts for the development of distinctive larvae with conspicuous buccal capsules with a left cephalic hook and a rasp of tiny spines. Four families are recognised: Gongylonematidae (body covered with large verruciform thickenings, pseudolabia absent, oral opening octagonal with median lobes, parasites of birds and mammals); Spiruridae (body without verruciform thickenings, reduced pseudolabia, oral opening elongated with lateral elevations, buccal cavity without teeth, parasites of mammals, rarely birds); Spirocercidae (body without verruciform thickenings, reduced pseudolabia, oral opening hexagonal, buccal cavity with teeth, parasites of mammals, rarely birds); and Hartertiidae (body without verruciform thickenings, large pseudolabia subdivided into lobes, parasites of birds). The family Gongylonematidae contains 2 genera: *Gongylonema* (syn. *Gongylomene*, *Misonunus*, *Myzomimus*) with worms having few-many verruciform thickenings (parasites of mammals, marsupials and birds); and *Progongylonema* with worms lacking verruciform thickenings (parasites from mucosa under the tongue of corvid birds) [the latter is considered by some to be a special subgenus of *Gongylonema*].

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Family: Gongylonematidae (anterior cuticle covered with large bosses or irregular scutes arranged in rows)						
<i>Gongylonema</i>	46	mammals, birds	oesophagus, stomach	2-15 cm long, numerous anterior bosses, 2 prominent trilobed lips, bipartite oesophagus	40-70 x 22-35 µm, ovoid, thick-shelled	indirect (L3 in insect IH)
Family: Spirocercidae (stout pink-red worm, well-developed buccal capsule, with 6 rudimentary lips)						
Subfamily: Spirocercinae (weakly-developed lips)						
<i>Spirocerca</i>	5	carnivores	stomach, aorta	3-8 cm long, body pink-red, buccal capsule with thick wall, 2 prominent trilobed lips, bipartite oesophagus	22-38 x 8-15 µm, elongate, thick-shelled	indirect (L3 in insect IH) [sometimes rodent, bird, reptile PH]
<i>Cylicospirura</i> (red worm)	10	mammals	stomach	20-30 mm long, buccal capsule with 6 longitudinal ribs ending in bifid knobs, 6 teeth, bipartite oesophagus	30-40 x 15-25 µm, elongate, thick-shelled	indirect (L3 in insect IH)
<i>Cyathospirura</i> (red worm)	5	mammals	stomach	6-12 mm long, buccal capsule with 6 longitudinal ribs ending in single knob, 8 teeth, bipartite oesophagus	29-38 x 13-22 µm, ovoid, thick-shelled	indirect (L3 in insect IH)
Subfamily: Ascaropsinae (buccal cavity with rugose or annular thickenings)						
<i>Ascarops</i> (thick stomach worm)	10	artiodactyls, rodents	stomach	10-25 mm long, oblique annuli in buccal capsule, 2 prominent trilobed lips, bipartite oesophagus	34-51 x 20-26 µm, oval, thick-shelled	indirect (L3 in insect IH) [sometimes amphibian or avian PH]
<i>Physocephalus</i> (thick stomach worm)	10	artiodactyls, rodents	stomach	6-22 mm long, transverse annuli in buccal capsule, 2 prominent trilobed lips, bipartite oesophagus	31-39 x 15-17 µm, ellipsoidal, thick-shelled	indirect (L3 in insect IH) [sometimes amphibian or avian PH]

The genus *Gongylonema* contains 2 subgenera: *G. (Gongylonema)* (numerous verruciform thickenings, spicules differ in length, gubernaculum present, parasites of mammals and birds); and *G. (Gongylonemoides)* (few verruciform thickenings, spicules similar in length, gubernaculum absent, parasites of American marsupials). Some 33 species infect mammals and 13 species infect birds. They have indirect life-cycles involving larval development in insect intermediate hosts (especially beetles). Infections are common in a range of animals, including poultry and domestic ruminants, but they rarely cause clinical signs, other than some instances of regurgitation in birds.

<i>Gongylonema</i> species	Definitive hosts	Location [Clinical signs]	Vectors (IH)	Distribution
<i>G. aegypti</i>	Rodentia: murid (mouse)			
<i>G. aequispicularis</i>	Artiodactyla: cervid (roe deer)			
<i>G. alecturae</i>	Galliformes: megapodid (Australian brush turkey); Diprotodontia: macropodid (agile wallaby, eastern grey kangaroo)	oesophagus, stomach		Australia
<i>G. archboldi</i>	Rodentia: cricetid (cotton rat, cotton mouse, Oldfield mouse, Florida mouse, golden mouse)	stomach		North America
<i>G. baylisi</i>	Artiodactyla: tayassuid (collared peccary)			South America
<i>G. beveridgei</i>	Rodentia: murid (bush rat)			Australia
<i>G. brevispiculum</i>	Rodentia: murid (lesser Egyptian gerbil, greater Egyptian gerbil, North African gerbil, Libyan jird, Shaw's jird, fat sand rat)			Africa

<i>G. capucinus</i>	Primates: cebid (white-faced capuchin)			India
<i>G. caucasica</i>	Galliformes: phasianid (chicken)			Russia
<i>G. congolense</i>	Anseriformes: anatid (duck, muscovy duck); Galliformes: phasianid (chicken, wild fowl)		Orthoptera: acridid (<i>Locusta migratoria</i>)	Africa
<i>G. crami</i>	Galliformes: phasianid (chicken)	crop [regurgitation]	Blattodea: (unspecified cockroach); Coleoptera (unspecified beetle)	worldwide, except S. America
<i>G. dipodomysi</i>	Rodentia: heteromyid (Merriam's kangaroo rat)			North America
<i>G. dupuisi</i>	Rodentia: murid (multimammate mouse)		Dermaptera: anisolabidid (<i>Anisolabis annulipes</i>)	Africa
<i>G. falconis</i>	Falconiformes: falconid (Eurasian hobby)			Russia
<i>G. fotedari</i>	Rodentia: murid (lesser bandicoot rat)			India
<i>G. freitasi</i>	Galliformes: phasianid (chicken)			South America
<i>G. graberii</i>	Galliformes: phasianid (chicken)			Europe
<i>G. ingluvicola</i> (gullet worm)	Galliformes: phasianid (chicken, turkey, partridge, ring-necked pheasant, mountain quail, northern bobwhite quail); Anseriformes: anatid (domestic duck); Columbiformes: columbid (pigeon)	crop, oesophagus, proventriculus [regurgitation]	Dictyoptera: ectobiid (<i>Blatella germanica</i>); Coleoptera: scarabaeid (<i>Copris minutus</i>)	worldwide
<i>G. ivaschkini</i>	Lagomorpha: leporid (European rabbit)		Coleoptera: tenebrionid (<i>Blaps fausti</i>)	Central Asia
<i>G. longispiculum</i> (incl. subspp. <i>longispiculum</i> , <i>spalacis</i>)	Rodentia: sciurid (little ground squirrel, European ground squirrel, Caucasian mountain ground squirrel), spalacid (greater mole-rat), cricetid (muskrat); Didelphimorphia: didelphid (Virginia opossum)			Holarctic
<i>G. macrogubernaculum</i>	Primates: cercopithecid (Japanese macaque)			Asia
<i>G. madeleinensis</i>	Rodentia: murid (Guinea multimammate mouse)			Africa
<i>G. (Gongylonemoides) marsupialis</i>	Didelphimorphia: didelphid (big-eared opossum, gray four-eyed opossum)	oesophagus		South America
<i>G. mesasiatica</i>	Galliformes: phasianid (ring-necked pheasant)			Europe
<i>G. metopidiusi</i> (syn. <i>G. indicus</i> ?)	Charadriiformes: jacanid (bronze-winged jacana)			India
<i>G. mexicanum</i>	Didelphimorphia: didelphid (common opossum)			Americas
<i>G. minima</i>	Rodentia: murid (Persian jird)			Middle-East
<i>G. monnigi</i> (rumen gullet worm)	Artiodactyla: bovid (sheep, goat)	rumen, reticulum, omasum		Africa
<i>G. mucronatum</i>	Eulipotyphla: erinaceid (North African hedgehog, southern white-breasted hedgehog)	oesophagus	Orthoptera: acridid (<i>Locusta migratoria</i>)	Africa
<i>G. musculi</i>	Rodentia: murid (mouse)			Europe
<i>G. mysciphilia</i>	Rodentia: cricetid (deer mouse)			North America
<i>G. neoplasticum</i> (syn. <i>G. orientale</i> , <i>problematicum</i> , <i>Spiroptera carcinoma</i> , <i>neoplasticum</i>)	Rodentia: murid (mouse, yellow-necked mouse, wood mouse, striped field mouse, large Japanese field mouse, brown rat, black rat, Polynesian rat, Philippine black rat, Asian house	oesophagus, stomach [regurgitation]	Blattodea: blattid (<i>Blatta orientalis</i> , <i>Periplaneta americana</i>); Coleoptera: tenebrionid (beetle, <i>Adesmia biseriata</i> , <i>gebleri</i> , <i>Blaps deplanata</i> , <i>fausti</i> ,	Eurasia

	rat, Libyan jird, Persian jird, Mongolian gerbil), cricetid (social vole, bank vole, European water vole, Major's pine vole, European hamster, Turkish hamster), caviid (guinea pig); Eulipotyphla: erinaceid (European hedgehog); Lagomorpha: leporid (European rabbit)		<i>oblonga</i> , <i>Pisterotarsa gigantea</i> , <i>Trigonoscelis</i> , <i>Tenebrio molitor</i>)	
<i>G. nepalensis</i>	Artiodactyla: bovid (water buffalo)			Asia
<i>G. nitsulescui</i>	Eulipotyphla: erinaceid (northern white-breasted hedgehog)			Europe
<i>G. pacoi</i> (now <i>Progongyilonema</i>)	Passeriformes: corvid (Eurasian jay, western jackdaw, azure-winged magpie, Eurasian magpie)	tongue		Europe
<i>G. peromysci</i>	Rodentia: cricetid (deer mouse)			North America
<i>G. phasianella</i>	Galliformes: phasianid (sharp-tailed grouse)			Europe
<i>G. pithyusensis</i>	Rodentia: glirid (garden dormouse)			Europe
<i>G. pulchrum</i> (syn. <i>G. confusum</i> , <i>contortum</i> , <i>filiforme</i> , <i>hominis</i> , <i>labiale</i> , <i>microgubernaculum</i> , <i>ransomi</i> , <i>scutatum</i> , <i>spirale</i> , <i>subtile</i> , <i>ursi</i>) (gullet worm)	Artiodactyla: bovid (cattle, African buffalo, sheep, argali, goat, mouflon, impala, goitered gazelle, Maxwell's duiker), cervid (roe deer, chital, fallow deer, red deer, sika deer, white-tailed deer), camelid (camel, dromedary, llama), suid (pig, wild boar, Sardinian wild boar); Perissodactyla: equid (horse, donkey, onager); Lagomorpha: leporid (rabbit, cape hare); Rodentia: murid (brown rat), caviid (guinea pig), hystricid (Indian crested porcupine), echimyid (coyppu), sciurid (Sherman's fox squirrel); Eulipotyphla: erinaceid (four-toed hedgehog), soricid (lesser white-toothed shrew); Didelphimorphia: didelphid (common opossum); Carnivora: canid (dog), felid (cat), mephitid (skunk), ursid (American black bear); Galliformes: phasianid (chicken); Anura: bufonid (European green toad); Primates: callitrichid (common marmoset), cercopithecoid (Japanese macaque), hominid (human)	oesophagus, mouth, tongue, stomach	Blattodea: blattid (cockroach, <i>Blattella germanica</i>); Coleoptera: scarabaeid (beetle, <i>Amphimallon</i> , <i>Aphodius elegans</i> , <i>fimetarius</i> , <i>fossor</i> , <i>granarius</i> , <i>haroldianus</i> , <i>lugens</i> , <i>lunifer</i> , <i>luridus</i> , <i>macovski</i> , <i>melanostictus</i> , <i>moestus</i> , <i>pusillus</i> , <i>rectus</i> , <i>satellitius</i> , <i>sordidus</i> , <i>sublimatus</i> , <i>tianshanicus</i> , <i>urostigma</i> , <i>Caccobius jessoensis</i> , <i>schreberi</i> , <i>Chironitis hungaricus</i> , <i>Copris acutidens</i> , <i>hispanus</i> , <i>lunaris</i> , <i>ochus</i> , <i>Gymnopleurus aciculatus</i> , <i>mopsus</i> , <i>Liatongus phanaeoides</i> , <i>Oniticellus fulvus</i> , <i>pallens</i> , <i>pallipes</i> , <i>Ontitis humerosus</i> , <i>Onthophagus amyntas</i> , <i>bivertex</i> , <i>catta</i> , <i>deflexicollis</i> , <i>fracticornis</i> , <i>gibbulus</i> , <i>koshantschikovi</i> , <i>lemur</i> , <i>leucostigma</i> , <i>nuchicornis</i> , <i>pugargus</i> , <i>quadridentatus</i> , <i>ruficapillis</i> , <i>similis</i> , <i>speculifer</i> , <i>tracticornis</i> , <i>verticornis</i> , <i>Oryctes nasicornis</i> , <i>Pentodon</i> , <i>Scarabaeus sacer</i> , <i>Sisphyus schaefferi</i>), dermestid (<i>Dermestes</i>), geotrupid (beetle, <i>Geotrupes impressus</i>), tenebrionid (<i>Blaps deplanata</i> , <i>oblonga</i> ,	worldwide

			<i>Cyphogenia gibba</i> , <i>Pisterotarsa gigantea</i> , <i>Tenebrio molitor</i>); Orthoptera: acridid (grasshopper, <i>Calliptamus barbarus, italicus</i>), gryllid (<i>Gryllus bimaculatus</i>), tettigoniid (bush cricket, <i>Semenoviana tameriana</i> , <i>Tettigonia</i>)	
<i>G. rodhaini</i>	Artiodactyla: giraffid (okapi)			Africa
<i>G. saimirisi</i>	Primates: cebid (Guianan squirrel monkey)			South America
<i>G. sciurus</i>	Rodentia: sciurid (red squirrel)			Russia
<i>G. soricis</i>	Eulipotyphla: soricid (common shrew, greater white-toothed shrew, greater red musk shrew, Fraser's musk shrew)	oesophagus	Dictyoptera: blattid (<i>Periplaneta orientalis</i>)	Africa
<i>G. spalacis</i>	Rodentia: spalacid (lesser mole rat), cricetid (muskrat)			Russia
<i>G. sumani</i>	Galliformes: phasianid (chicken)			India
<i>G. thapari</i>	Galliformes: phasianid (grey junglefowl)			India
<i>G. verrucosum</i> (rumen gullet worm)	Artiodactyla: bovid (sheep, goat, Siberian ibex, cattle, zebu), cervid (white-tailed deer)	rumen, reticulum, omasum	Blattodea: (unspecified cockroach); Coleoptera (unspecified beetle)	Asia, Africa, Americas

Parasite morphology: *Gongylonema* spp. form 3 different types of developmental stages: eggs; larvae (4 successive stages named L1-L4); and adult worms. The thick-shelled eggs are ovoid measuring 40-70 x 22-35 µm and are fully embryonated when laid. L1 are coiled up within the eggs but when freed they are elongate cylindrical stages measuring 100-300 x 6-13 µm and have rounded heads, conspicuous buccal capsules with a left cephalic hook and a rasp of tiny spines, rhabditoid oesophagus, and rounded tails sometimes bearing a circle of small spines. L2 are larger transient stages found in intermediate hosts, while L3 are larger still (measuring 1.0-4.2 mm long) and already possess most cephalic features of adults as well as lateral alae and rounded tapering tails, often with terminal spines or tubercles. L4 are transient parasitic stages that develop in definitive hosts and they possess developing genitalia. Adults are elongate white worms with slender cylindrical bodies measuring from 20-150 mm in length by 150-300 µm in width. The adults are embedded in the mucosa in an undulating, spiral, zipper or zig-zag fashion (hence the occasional common name of zig-zag worm) usually with their anterior and/or posterior ends protruding into the lumen. *Gongylonema* worms are readily identified by occurrence of large swollen verruciform (round-oval) thickenings or protrusions (often called plaques or bosses) that cover the cuticle, few to many in number, and arranged in several longitudinal irregular rows anteriorly which reduce in thickness posteriorly. Two subgenera are recognised: *G. (Gongylonema)* with numerous verruciform thickenings; and *G. (Gongylonemoides)* with few verruciform thickenings. The cuticles of both subgenera have transverse striations and 2 well-developed cervical alae, festooned in some species (e.g. *G. verrucosum*). The head is rounded with an octagonal mouth surrounded by small inconspicuous lips and some species possess a raised peribuccal rectangular shield (e.g. *G. ingluvicola*). The bipartite oesophagus has an anterior muscular and a posterior glandular portion, the excretory system has lateral canals, and the long tapering tail often displays terminal processes. Adult worms are sexually dimorphic, with females being larger than males (32-55 cf. 17-20 mm long for most species although *G. pulchrum* females may measure up to 150 mm and males up to 62 mm). Mature females are didelphic with 2 ovaries and uteri connected to a common vulva opening posteriorly near the anus. Mature males have 2 unequal narrow caudal alae giving the tail an asymmetric appearance, several pedunculate papillae around the cloaca, a gubernaculum may be present (subgenus *G. (Gongylonema)*) or absent (subgenus *G. (Gongylonemoides)*), and they contain 2 spicules, either unequal (subgenus *G. (Gongylonema)*) or equal (subgenus *G. (Gongylonemoides)*), but quite variable in length depending on species (ranging from 4-180 µm).

Site of infection: Developing larvae and adult worms occur primarily in the subepithelial tissue or submucosa of the oesophagus of their final hosts, but sometimes extending up to the tongue and mouth or down to the stomach(s) of mammals or the crop and proventriculus of birds. Infective larvae develop in the haemocoel and internal tissues of insect intermediate hosts, often becoming encapsulated in the musculature.

Pathogenesis: Despite the size and location of *Gongylonema* worms in their definitive hosts, infections are generally nonpathogenic and seldom cause clinical signs. Larvae and adults embedded in the mucosa of the upper digestive tract may cause some traumatic damage and inflammation (oesophagitis) with progressive epithelial cornification, but they rarely cause functional problems as their

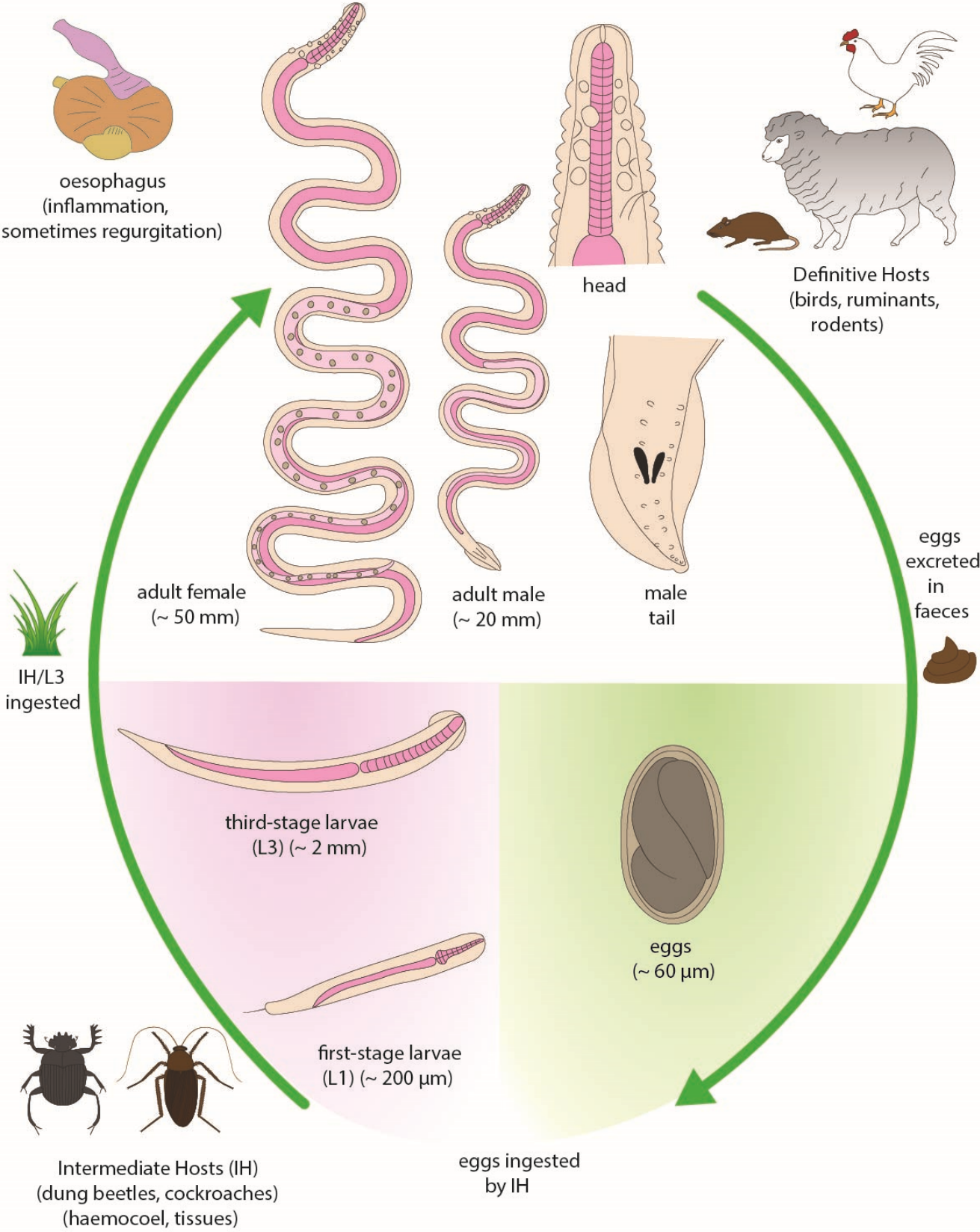
elasticity and zig-zag configuration allows them to expand and contract along with oesophageal peristalsis. Inflammatory changes in birds may sometimes cause oesophageal sensitivity and dysphagia with occasional regurgitation. Infections by *G. neoplasticum* in rats were initially thought to cause gastric tumours, but the lesions are now considered to be non-malignant and associated with vitamin A-deficiency. Incidental infections in humans are generally noticed when young adult worms migrate beneath mucocutaneous membranes causing discomfort (foreign body sensation) in the buccal, oral or gingival regions. Symptoms take around 6 weeks to develop and may continue for months. Patients often report pulling worms from their gums, tongue, lips and inner cheeks after protracted discomfort.

Developmental cycle and mode of transmission: *Gongylonema* spp. have indirect heteroxenous life-cycles with cyclic transmission between vertebrate definitive hosts (in which adult worms develop) and invertebrate intermediate hosts (in which infective larvae develop). Female worms lay embryonated eggs which pass posteriorly and are shed in host faeces into the external environment where they may survive for up to 4 months in favourable warm moist conditions. The eggs are eaten by coprophagous insects (dung beetles, cockroaches) which act as intermediate hosts as they support further larval development. Ingested eggs hatch in the gut of the insects releasing L1 which migrate into the haemocoel within 1-2 days, and then moult twice to form L3 which encapsulate with host tissues (especially the muscles) by 29-32 days. L3 survive for several months (overwinter) in insect tissues, and experimental studies have also shown that L3 dissected from insects may survive for several days in favourable moist conditions. Final hosts become infected when they consume infective L3, usually contained within insects eaten during grazing or foraging, but the possibility of freed L3 being ingested in contaminated food or water cannot be entirely dismissed. All subsequent larval and worm development occurs within the upper digestive tract (larvae do not undertake any somatic or hepatopulmonary migration). L3 migrate upward from the stomach to the oesophagus where they moult to L4 by 11 days and then to subadult stages (often referred to as L5) by 36 days after infection. The worms mature over several weeks and the prepatent period (time from infection to first excretion of eggs) ranges from 56–85 days. Humans become infected accidentally by the ingestion of infected insects or contaminated food and water. Larvae infect the upper oesophagus and migrate into the buccal cavity where some may moult to subadults, but they do not mature nor produce eggs (humans are dead-end hosts).

Differential diagnosis: Infections are generally detected incidentally at post-mortem when adult worms are discovered in the oesophageal mucosa upon dissection. Worm eggs may be detected in faecal samples following their concentration by floatation techniques, but the eggs are similar in morphology to those of some strongyles and spirurids. Infections in humans may be misdiagnosed on clinical grounds as delusional parasitosis, but are convincingly confirmed when motile young worms are detected beneath the buccal mucosa by either the patient or the doctor. Molecular biological techniques have been applied to the characterization of parasites from birds and mammals (including humans) following the polymerase chain reaction (PCR) amplification and sequencing of nuclear genes (ribosomal RNA) and mitochondrial genes (cytochrome oxidase I).

Treatment and control: No specific chemotherapeutic treatment has been recommended as many conventional and modern anthelmintics were found to be relatively ineffective. Some infections responded well to treatment with imidazothiazoles (levamisole), benzimidazoles (mebendazole, albendazole, fenbendazole), and macrocyclic lactones (ivermectin), but drug levels needed to be sustained by repeated systemic administration. Infections in humans are generally treated by surgical extraction of worms from submucosal buccal tissues, often guided by endoscopy and followed by albendazole prophylaxis. Control strategies designed to prevent infections generally consist of reducing contamination of the environment with worm eggs (through improved sanitation, faecal collection and disposal) and preventing transmission to and from insect intermediate hosts (using insecticides to control vector populations). While these strategies may be practicable in domestic or intensive-farming enterprises (generally those involving indoor holding facilities), they are unsuited to farming practices involving extensive pastures and rangelands, and should be contra-indicated in natural situations involving wildlife (the indiscriminate use of insecticides against coprophagous insects may have serious environmental consequences). Human populations in endemic regions should also be advised of the risks of accidentally or purposefully ingesting insects, especially dung beetles.

Gongylonema





Gongylonema adult worms



Gongylonema worm eggs