Heterakis
(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 Ascaridomorpha which includes ascaridoid nematodes (roundworms) characterised by their large size, three prominent anterior lips and the absence of a bursa. They occur in the small intestines of many animals (including humans) and most have simple direct life-cycles involving faecal-oral transmission. Female worms produce numerous eggs which are excreted with host faeces and undergo embryonation to contain infective larvae. When ingested, larvae hatch from the eggs and develop into adult worms in the gut. The larvae of ascaridoid species undergo hepato-pulmonary migration before forming adults, whereas those of heterakoid species do not. Heterakoid worms have a large sucker anterior to the cloaca in males, and two major families are recognised: heterakids having an oesophagus with a rounded terminal bulb; and ascaridiids having one without. Adult heterakids have lateral alae and eggs/L3 may be transported by earthworms (paratenic hosts). Infections by *Heterakis* spp. are common in poultry but are generally asymptomatic, although they can act as a vector for the protozoan *Histomonas meleagridis*, causing blackhead disease.

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:	Ascaridomorpha (large roundworms, mouth surrounded by three large lips, numerous caudal papillae)
Superfamily:	Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by ingestion of eggs)
Family:	Heterakidae (worms with lateral alae, oesophagus with rounded terminal bulb)
Genus:	*Heterakis* (usually parasitic in caeca of birds)
Species:	various species cause asymptomatic infections in poultry

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.

The infraorder Ascaridomorpha is characterised by large roundworms with poorly developed buccal cavity with 3 large lips, an undivided oesophagus, numerous caudal papillae, nonbursate males often with pre-anal suckers, and females with complex ovejectors. Five superfamilies (conventionally assigned to the order Ascaridida) are recognised as parasites in vertebrates: Ascaridoidea (cylindrical oesophagus often terminated by swelling without bulb, coelomyarian, eggs thick-shelled); Heterakoidea (oesophagus cylindrical or with claviform corpus, short isthmus and valved bulb, coelomyarian, pre-anal sucker, eggs thick-shelled); Cosmocercoidea (oesophagus with cylindrical corpus, elongate isthmus and valved bulb, platymyarian, eggs with delicate shells or hatch *in utero*); Seuratoidea (lips absent, oesophagus short, platymyarian, eggs with delicate shells or hatch *in utero*); and Subuluroidea (well-developed buccal capsule without lips, coelomyarian, pre-anal sucker, eggs thick-shelled).

The superfamily Heterakoidea contains worms with prominent pre-anal suckers surrounded by cuticularized rings. Adult worms are parasitic in the gastrointestinal tracts of vertebrates (birds, reptiles, amphibians, mammals) and have direct monoxenous life-cycles where hosts become infected by ingesting larvated eggs and the released larvae do not undertake hepatopulmonary migration. The superfamily contains 4 families: Heterakidae (rounded lips not connected by lateral lobes, short stout oesophagus with rounded trivalved terminal bulb, lateral alae present); Ascaridiidae (large stout lips, slender club-shaped oesophagus without posterior bulb, anterior cuticular flange absent); Aspidoderidae (square lips connected by lateral lobes, long narrow oesophagus with small trivalved terminal bulb, anterior cuticle thickened to form cephalic cap); and Kiwinematidae (shallow rounded lips without distinct margins, oesophagus with trivalved terminal bulb, lateral alae present). Representative genera of significance to animal health and production are tabulated below.

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Heterakidae (worms with lateral alae, oesophagus with rounded terminal bulb)						
Heterakis (caecal worm)	51	birds (esp. galliform), rodents	intestines	4-23 mm long, lateral alae, fine longitudinal striations, 3 anterior lips, oesophageal bulb, abursate males with precloacal sucker, larvae do not undertake hepato-pulmonary migration	63-80 x 35-50 µm, ellipsoidal, thick-shelled	direct (faecal-oral) (sometimes eggs/L3 in earthworm PH)
Ascaridiidae (slender club-shaped oesophagus without rounded terminal bulb)						
Ascaridia	45	birds (esp. galliform), reptiles, fish	intestines	3-12 cm long, poorly developed cuticular alae, 3 large trilobed anterior lips, no oesophageal bulb, abursate males with precloacal sucker, larvae do not undertake hepato-pulmonary migration,	80-90 x 45-50 µm, ovoid, thick-shelled	direct (faecal-oral) (sometimes eggs/L3 in earthworm PH)

The family Heterakidae contains 3 subfamilies: Heterakinae (lips not offset from body, caudal alae supported by 3-4 stout papillae or by long thin papillae, head with interlabia or homologues, caudal alae broad supported by long narrow papillae, few sessile papillae present on tail, parasites of birds, rarely mammals); Meteterakinae (lips not offset from body, caudal alae supported by 3-4 pairs of large fleshy papillae, numerous small sessile papillae present on tail, parasites of amphibians, reptiles and mammals); and Spinicaudinae (lips offset from body, caudal alae when present either not supported by papillae or supported by many short stout papillae, parasites of amphibians and reptiles). The subfamily Heterakinae contains 6 genera: *Heterakis* (syn. *Raillietakis*, *Ganguleterakis*, *Inglisakis*), *Gireterakis, Haroldakis, Musserakis, Neohaterakis, Odontoterakis* and *Pseudaspidodera.* The genus *Heterakis* contains some 50 species of small worms with 3 lips without cordons or labial grooves, a complex oesophagus and males with caudal alae, suckers and unequal spicules. Most species are parasitic in the caeca of ground-feeding (mostly grain-eating) birds, particularly Galliformes, although a few species infect mammals. The species *H. gallinarum* is commonly found in domestic and wild poultry around the world. Infections are more prevalent in tropical and subtropical regions than in temperate regions as eggs are unable to develop to the infectious stage at temperatures under 15°C. A variety of invertebrates (earthworms, insects) have also been found to act as paratenic (transport) hosts where larvae may hatch from ingested eggs but they do not undergo further development.

***Heterakis* species**	**Definitive hosts [plus Paratenic hosts (PH)]**	**Location [Clinical signs]**	**Distribution**
Avian hosts			
H. alata (now *Odontoterakis*)	Tinamiformes: tinamid (yellow-legged tinamou, undulated tinamou, red-winged tinamou); Gruiformes: psophiid (dark-winged trumpeter)	intestines	South America
H. arctica	Anseriformes: anatid (greater snowgoose)		Greenland
H. arquata (= *Odontoterakis*)	Gruiformes: psophiid (dark-winged trumpeter); Tinamiformes: tinamid (unspecified tinamou species)	intestines	South America
H. bancrofti (now *Odontoterakis*)	Galliformes: megapodid (Australian brush turkey); Columbiformes: columbid (wonga pigeon)	caecum	Australia
H. beramporia (syn. *H. putaustralis*)	Galliformes: phasianid (chicken, common pheasant, red junglefowl); Anseriformes: anatid (domestic duck, mallard)	caecum [nodule formation]	Asia, Australia
H. bosia	Galliformes: phasianid (Temminck's tragopan, satyr tragopan)		Asia
H. brasiliana sp. dubia	Tinamiformes: tinamid (unspecified tinamou species)		South America
H. brevispeculum	Galliformes: phasianid (chicken), numidid (helmeted guineafowl); Anseriformes: anatid (duck, goose)	caecum, occasionally intestines	worldwide
H. caudebrevis	Galliformes: phasianid (chicken)	caecum	Asia
H. chenonettae sp. inq.	Anseriformes: anatid (Australian wood duck)	caecum	Australia
H. crypturi (now *Odontoterakis*)	Tinamiformes: tinamid (variegated tinamou); Gruiformes: psophiid (dark-winged trumpeter)	intestines	South America

H. dispar (syn. *H. caudata, circumvallata, hyperborea, monticelliana, stylosa, tenuicauda, H. d. brevispiculatus*)	Galliformes: phasianid (chicken, chukar partridge, rock partridge, grey partridge, red-legged partridge, see-see partridge, Barbary partridge, hazel grouse, common quail, black francolin), numidid (vulturine guineafowl); Anseriformes: anatid (mallard, muscovy, Australian shelduck, domestic goose, greylag goose, greater white-fronted goose, snow goose, swan goose); Strigiformes: strigid (Eurasian pygmy owl)	caecum, occasionally intestines	worldwide
H. fariai (now *Odonterakis*)	Galliformes: phasianid (silver pheasant, spot-winged wood quail)		Asia, South America
H. gallinarum (syn. *H. gallinae, papillosa, parisi, pedioecetes, vesicularis*) (poultry caecal worm)	Galliformes: phasianid (chicken, red junglefowl, Indian red junglefowl, grey junglefowl, Indian peafowl, green peafowl, turkey, black francolin, common pheasant, golden pheasant, silver pheasant, Lady Amherst's pheasant, Mrs Hume's pheasant, Reeve's pheasant, Koklass pheasant, copper pheasant, scintillating copper pheasant, green pheasant, Shikoku green pheasant, Japanese green pheasant, Bianchi's pheasant, Korean pheasant, blue-eared pheasant, brown-eared pheasant, chukar partridge, rock partridge, grey partridge, red-legged partridge, Barbary partridge, Daurian partridge, Chinese bamboo partridge, mountain bamboo partridge, hazel grouse, black grouse, common quail, Japanese quail, northern bobwhite quail, willow ptarmigan, rock ptarmigan, western capercaillie, Altai snowcock, Caucasian snowcock, Himalayan snowcock, Sclater's monal, Cabot's tragopan, Temminck's tragopan), numidid (helmeted guinea fowl); Anseriformes: anatid (domestic duck, mallard, muscovy, domestic goose, greylag goose, Eurasian wigeon); Columbiformes: columbid (pigeon); Coraciiformes: mergid (European bee-eater); Cuculiformes: cuculid (lesser coucal); Gruiformes: psophiid (grey-winged trumpeter), rallid (Eurasian coot, common moorhen); Otidiformes: otidid (Houbara bustard, great bustard, little bustard); Passeriformes: corvid (Cayenne jay); Psittaciformes: cacatuid (Major Mitchell's cockatoo); Strigiformes: strigid (tawny owl); Tinamiformes: tinamid (red-winged tinamou, spotted nothura); Carnivora: felid (cat) [PH: Clitellata: lumbricid (*Allolobophora caliginosa, Eisenia foetida, Helodrilus gieseleri, Lumbricus terrestris*); Diptera: muscid (unspecified house fly); Orthoptera (unspecified grasshopper); Crustacea: porcellionid (*Porcellio scaber*)]	caecum, occasionally intestines [vector for *Histomonas meleagridis*]	worldwide
H. hamulus	Galliformes: phasianid (green peafowl, Indian peafowl)		Europe
H. hefeiensis	Galliformes: phasianid (chicken)		Asia
H. indica (syn. *H. linganensis*)	Galliformes: phasianid (chicken, red junglefowl); Anseriformes: anatid (domestic duck)	caecum	Asia
H. interlabiata	Galliformes: phasianid (long-billed partridge)		Africa
H. isolonche (syn *H. bonasae, hastata, lanei, neoplastica, tragopanis, variabilis*) (caecal worm)	Galliformes: phasianid (chicken, prairie chicken, ruffed grouse, turkey, common pheasant, blood pheasant, golden pheasant, blue-eared pheasant, brown-eared pheasant, copper pheasant, Bianchi's pheasant, Lady Amherst's pheasant, northern bobwhite quail, California quail, grey partridge, Himalayan monal, Temminck's tragopan, satyr tragopan); Anseriformes: anatid (domestic duck);	caecum, occasionally intestines [typhlitis, diarrhoea]	worldwide

	Otidiformes: otidid (great bustard); Strigiformes: strigid (Eurasian scops owl)		
H. kotdwarensis	Galliformes: phasianid (chicken)		India
H. kumaoni	Galliformes: phasianid (Indian red junglefowl)		Asia
H. kurilensis	Charadriiformes: alcid (crested auklet, whiskered auklet)		Russia
H. longecaudata (*longicaudata*)	Galliformes: phasianid (chicken, silver pheasant)	caecum	Russia
H. longespiculum	Galliformes: phasianid (crested partridge)		India
H. macroura (syn. *H. altaica*)	Galliformes: phasianid (chukar partridge, grey partridge, rock partridge, Altai snowcock, Caspian snowcock, Caucasian snowcock, Himalayan snowcock, Tibetan snowcock); Anseriformes: anatid (domestic duck, goose)	caecum, intestines	Asia
H. maculosa	Columbiformes: columbid (pigeon, rock dove)		
H. meleagris	Galliformes: phasianid (chicken, turkey)		Asia
H. multidentata (syn. *Odontoterakis*) (now *Haroldakis*)	Tinamiformes: tinamid (variegated tinamou)	caecum, large intestines	South America
H. multipapillata (syn. *Gangulererakis*)	Columbiformes: columbid (pin-tailed green pigeon)		Asia
H. nainitalensis	Galliformes: phasianid (Indian red junglefowl)		
H. nattereri	Tinamiformes: tinamid (solitary tinamou, grey tinamou); Galliformes: cracid (red-billed curassow)	caecum	Americas
H. oscari	Galliformes: cracid (red-billed curassow)	intestine	South America
H. parva	Galliformes: phasianid (chicken, red junglefowl, common pheasant, silver pheasant); Anseriformes: anatid (goose)	caecum	Asia
H. pavonis	Galliformes: phasianid (chicken, peafowl, ring-necked pheasant, green pheasant, copper pheasant); Pelecaniformes: ardeid (black-crowned night heron)		Asia
H. perspicillum	Galliformes: phasianid (chicken)		
H. psophiae	Gruiformes: psophiid (dark-winged trumpeter)	intestines	South America
H. pusilla	Galliformes: phasianid (Ceylon junglefowl, red junglefowl)		Africa
H. rimula	Cuculiformes: cuculid (greater coucal)		Asia
H. silindae	Galliformes: phasianid (red-necked spurfowl, red-necked francolin, hazel grouse)		Africa
H. sinica	Galliformes: phasianid (Temminck's tragopan)		Asia
H. skrjabini (now *Odontoterakis*)	Gruiformes: psophiid (grey-winged trumpeter)		South America
H. spiculatus (incl. *H. inglisi* ex: Vicente *et al.,* 1993)	Tinamiformes: tinamid (yellow-legged tinamou, variegated tinamou, small-billed tinamou, spotted nothura)		Americas
H. valvata (now *Odontoterakis*)	Tinamiformes: tinamid (yellow-legged tinamou, Tataupa tinamou, spotted nothura)	intestines	South America
H. vexans	Galliformes: phasianid (Taiwan partridge)		Taiwan
H. vulvolabiata	Galliformes: phasianid (Taiwan partridge)		Taiwan
H. yamadori	Galliformes: phasianid (chicken, green pheasant, northern green pheasant, copper pheasant, scintillating copper pheasant, Chinese bamboo partridge), numidid (helmeted guineafowl); Pelecaniformes: ardeid (black-crowned night heron)		Asia
H. yani	Galliformes: phasianid (chicken); Anseriformes: anatid (domestic duck)	caecum	Asia
Reptilian/amphibian/piscine hosts			
H. bufonis	Anura: bufonid (Asian common toad)		Asia
H. foveolata	Pleuronectiformes: pleuronectid (European plaice)		Europe
H. govindi (now *Meteterakis*)	Anura: bufonid (Asian common toad); Sauria: varanid (Bengal monitor)	large intestine	Asia
Mammalian hosts			
H. balamukensis	Peramelemorphia: peramelid (common echymipera)		Papua New Guinea

H. dahomensis	Rodentia: cricetid (Gambian pouched rat)		Africa
H. equispiculis sp. inq.	Rodentia: murid (black rat)		India
H. fieldingi	Rodentia: murid (rakali)	caecum, colon	Australia
H. girardi (now *Gireterakis*)	Rodentia: hystricid (Sunda porcupine, Malayan porcupine, crested porcupine)	intestine	Asia
H. inglisi (ex: Gupta & Trivedi, 1982)	Chiroptera: vespertilionid (greater Asiatic yellow bat)		Asia
H. macrospiculum (now *Mammalakis*)	Rodentia: spalacid (mole-rat)		Russia
H. oweni	Peramelemorphia: peramelid (northern brown bandicoot)	large intestines	Australia, Papua New Guinea
H. sirawii	Rodentia: murid (New Guinean rat)		New Guinea
H. spalacis (now *Mammalakis*)	Rodentia: spalacid (lesser mole-rat, greater mole-rat)		Russia
H. spalaxi (now *Mammalakis*)	Rodentia: spalacid (lesser mole-rat, greater mole-rat)		Russia
H. spumosa (syn. *Ganguleterakis, H. rattui*)	Rodentia: murid (house mouse, Algerian mouse, striped field mouse, typical striped grass mouse, small Japanese field mouse, large Japanese field mouse, Himalayan field mouse, Korean field mouse, Natal multimammate mouse, brown rat, black rat, dusky field rat, roof rat, bush rat, Polynesian rat, Australian swamp rat, African grass rat, soft-spined Atlantic spiny rat, rakali, Indian gerbil), cricetid (grey red-backed vole, Japanese red-backed vole, Japanese grass vole, Smith's vole), talpid (Kobe mole); Peramelemorphia: peramelid (northern brown bandicoot); Gruiformes: rallid (slaty-legged crake) [PH: Clitellata: megascolecid (*Pheretima hilgendofi*), lumbricid (*Eisenia foetida*)]	caecum, upper colon	worldwide
H. verrucosa sp. inq.	Rodentia: dasyproctid (agouti)		South America
H. yamagutii (syn. *H. pandei*)	Rodentia: murid (Indian desert jird, black rat)		India

Parasite morphology: *Heterakis* spp. form 3 different morphological stages in their developmental cycles: eggs; larvae (4 successive stages encoded L1-L4); and adult worms. The eggs measure 63-80 x 35-50 µm and are oval-ellipsoidal in shape but have sides that are almost parallel (convex in *Ascaridia* spp.). They are bound by thick smooth eggshells (roughened outer surface for *H. spumosa*) with a small clear lenticular body at one pole. Eggs are unembryonated when laid and contain a single central morula. Following embryonation, the eggs contain coiled first-stage larvae (L1) which moult within the egg to form ensheathed L2 (although a few studies suggest another moult to L3 may occur in some eggs). Infective were cylindrical with an anterior boring tooth and lateral alae. Those recovered from dissected eggs measured 231-274 µm while those recovered from earthworms measured 365-387 µm. L3 and L4 are transient parasitic stages and little is known about their morphological characteristics. Adults are robust cylindrical white worms varying in length from 4-23 mm depending on maturity and species. They have sharply pointed tails and are bound by a tough cuticle with fine longitudinal striations and large lateral alae extending along the body. They have anterior mouths with triangular apertures but without cephalic cordons (present in some other genera). The mouth is surrounded by 3 well-defined round lips (one dorsal and two subventral), each with 2 papillae and thickened radial margins. The lips are not offset from the body and they have interlabia, but lack labial grooves and are not connected by lateral lobes. The mouth opens into a complex oesophagus with a small neck (some species with hinged rods) and a long muscular body with a prominent rounded terminal bulb (lacking in members of the ascaridiid family) with 3 well-marked dentate valves. Adult worms are sexually dimorphic, with females being larger than males (8-23 mm cf. 4-18 mm). Mature females are didelphic with 2 ovaries and uteri in an amphidelphic configuration (opposed) and connected to a common vulva opening close to the midbody. Females have narrow straight tails but do not have any special ejaculatory apparatus (ovejectors) but use powerful uterine muscles to pass developing eggs. Mature males are characterised by the possession of a large precloacal sucker (38-150 µm in diameter) surrounded by a chitinous ring, and pointed bent tails with 2 well developed broad caudal alae supported by 12 pairs of caudal papillae. They do not possess a gubernaculum but have 2 equal or unequal spicules ranging in length 0.3-2.8 mm. The spicules of *Heterakis* spp. of poultry fall into several types: *H. gallinarum* type (unequal with a long slender right spicule and a short alate left spicule); *H. dispar* type (with short subequal spicules); *H. isolonche* type (with long equal asymmetrical spicules), and *H. brevispeculum* type (with short equal barbed spicules).

Site of infection: Most species are parasitic in ground-feeding (mostly grain-eating) birds, especially Galliformes, but a few species infect mammals (mostly rodents). Larval stages develop in the large intestines (often near crypts), while adult worms live in the lumen of the caecum of birds (near the tips or blind ends) or the upper colon of rodents. Larvated eggs and freed L2 may also be carried in the alimentary tract or tissues of invertebrate paratenic hosts (notably earthworms).

Pathogenesis: Most infections remain asymptomatic or subclinical, rarely causing morbidity and mortality. Developing larvae and adult worms feed on intestinal content, and only occasionally have larval stages been observed to invade the mucosa for short periods of time (without undergoing histotrophic development). Nonetheless, parasites have been associated with clinical disease predominantly in young chickens and pheasant chicks. Adult birds are more resistant to infection than young birds, and experimental studies have shown that previous exposure confers hosts with some protective immunity. Infections in young birds may cause petechial haemorrhages, inflammation with caecal mucosal thickening, catarrhal or haemorrhagic typhlitis, congestion, and nodule formation, resulting in vague clinical signs including mild diarrhoea (sometimes green), anaemia, decreased appetite, poor growth and weakness. Infections have occasionally been detected in association with neoplastic-like smooth muscle tumours (fibroids or leiomyomas) in the caecal submucosa. Some studies have reported reduced egg production in layers but no differences were observed in weight gains by infected and control birds. In contrast, more severe disease has been recorded in pheasant infected by *H. gallinarum* or *H. isolonche* due to significant inflammation, diffuse or verrucous typhlitis, ulceration, nodule formation, granulomata and fibrous hyperplastic caecal tissues resulting in diarrhoea, progressive emaciation, and high mortalities (up to 50% without treatment)

H. gallinarum may also act as a vector for the transmission of the protozoans *Histomonas meleagridis*, the causal agent of infectious enterohepatitis (blackhead disease) and *Histomonas wenrichi.* Protozoal trophozoites multiply in the worm ovary and penetrate oocytes thus infecting worm eggs and their developing larvae. The protozoa are then transmitted to birds when worm eggs/larvae are ingested (direct or via paratenic hosts), resulting in blackhead disease (usually in turkeys, sometimes chickens) with anorexia, lethargy, listlessness, feather loss, caecal inflammation with cheesy exudates, necrotic livers and high mortality (90%) unless treated.

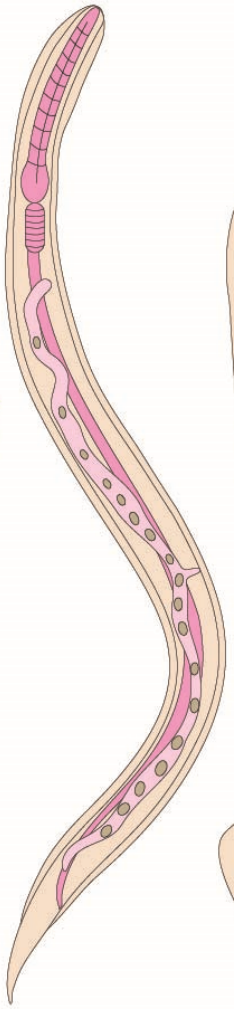
Developmental cycle and mode of transmission: *Heterakis* spp. have direct monoxenous life-cycles that involve the faecal-oral transmission of infective larvae, sometimes within invertebrate paratenic hosts. Gravid female worms lay numerous unembryonated eggs which are excreted into the external environment with host faeces. In warm moist conditions, the eggs embryonate to form L1 which then moult within the egg to form infective L2 in 7-14 days (longer in cooler conditions). The larvated eggs are highly resistant to extremes of temperature and remain infective for long periods (*H. gallinarum* eggs may survive in soil for 1.0-4.5 years, even under snow for 6 months, while *H. spumosa* eggs may survive in faeces at ambient temperature for 120 days). They survive best in well-grassed or densely-vegetated areas with ample moisture and shade, but are susceptible to desiccation in hot dry conditions. Infections are more prevalent in tropical and subtropical regions than in temperate regions as the eggs are unable to develop to the infectious stage at temperatures under 15°C. In addition to egg dispersal by water and wind action, they have also been shown to be mechanically dispersed by various soil invertebrates, including earthworms, grasshoppers, fly larvae and sow bugs. Several earthworm species have also been shown to act as paratenic (transport) hosts when ingested eggs hatch releasing L2 which invade host tissues and remain infective for at least a year without undergoing further development. Final hosts become infected when they ingest infective larvated eggs from the environment or by consuming infective eggs or larvae within paratenic hosts. Following ingestion, eggs hatch in the stomach and small intestines releasing larvae which colonize the caecum in birds or the colon in mammals. The larvae of heterakoid species do not undergo any hepato-pulmonary migration before forming adults (unlike those of ascaridoid species). *Heterakis* larvae develop directly in the lumen into adults, although some may invade the caecal mucosa or caecal glands for 2-5 days before returning to the lumen. The infective larvae moult to L3 in 3-7 days, L4 in 9-10 days, and to preadults (L5) in 14-16 days. The prepatent period (time from infection to first egg excretion) ranges from 21-36 days in birds and 26-47 days in rodents. Adult worms are thought to live for 100-312 days after first producing eggs.

Differential diagnosis: Even when infections cause clinical signs, they are vague and nonspecific and may be attributed to many other conditions. Patent infections are conventionally diagnosed by the microscopic detection of worm eggs in faecal samples, either direct in wet mounts or smears, but usually following their concentration by sedimentation in water and floatation in high specific gravity sugar or salt solutions. The intensity of infection may also be determined by counting worm eggs in faecal aliquots in volumetric McMaster or Whitlock chambers and calculating the number of eggs per gram of faeces. *Heterakis* eggs are similar in morphology to those of *Ascaridia*, both being thick-shelled and ellipsoidal, but those of *Heterakis* are slightly smaller and have nearly parallel sides rather than convex sides. Infections may also be diagnosed by the post-mortem detection of adult worms and lesions in the caeca (usually granulomas with necrotic centres, or leiomyomas with haemosiderosis). Parasites may also be detected in mucosal scrapings, squash preparations or caecal digests. Molecular biological techniques have been used to characterize parasites from environmental and clinical samples following the polymerase chain reaction (PCR) amplification and sequencing of nuclear genes (ribosomal RNA and internal transcribed spacers 1 and 2) and the complete mitochondrial genome for several species.

Treatment and control: Clinical infections in young birds (especially chickens and pheasant chicks) have been successfully treated with a range of old and new anthelmintic drugs, including heterocyclic thiazines (phenothiazine, now discontinued), monothiophosphates (coumaphos), benzimidazoles (mebendazole, flubendazole, albendazole, fenbendazole, cambendazole), prebenzimidazoles (febantel), imidazothiazoles (levamisole, tetramisole), diethylenediamines (piperazine) and macrocyclic lactones (ivermectin). Studies on alternative therapies found that extracts of white wormwood, *Artemisia herba-alba*, significantly reduced worm burdens and fecundity in *H. gallinarum* infections, and other plant extracts (aloe, garlic, root bark) and even bee products (propolis) demonstrated some modest anthelmintic effects. Various preventive strategies have been used in the poultry industries to limit parasite transmission by reducing faecal contamination of the environment and minimizing the exposure of susceptible birds to potential sources of infection. Improved sanitation and hygiene have involved the regular removal of litter from poultry houses, not using faecal material as fertilizer on grazing areas, raising birds on hard substrates (wood slats, wire mesh, hardware cloth, concrete), cleaning cages/yards frequently, providing clean food and water, and treating soil areas with insecticides to reduce paratenic host populations. Appropriate bird management has involved separating young birds from adults, not raising chickens and turkeys together (axiomatic amongst poultry producers), avoid overcrowding, instituting quarantine and isolation procedures, and prevent wild birds from entering facilities.

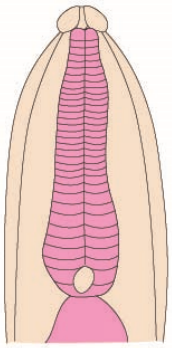
Heterakis

intestines
(enteritis, diarrhoea,
vector for histomoniasis
(blackhead disease))

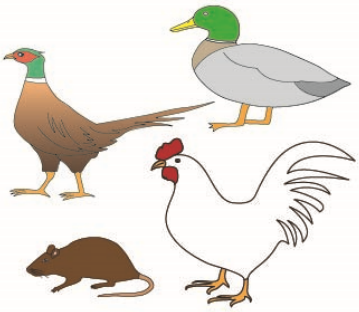


adult female
(~ 20 mm)

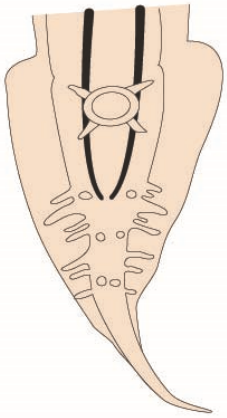
adult male
(~ 15 mm)



head



Definitive Hosts
(birds, esp. poultry,
rodents)



male
tail

eggs/L2/PH
ingested

L2 also carried in PH

second-stage larva
(L2) (400 µm)

external
environment

eggs
(~ 70 µm)

eggs
excreted
in faeces

L2 develop
in eggs

Paratenic Hosts (PH)
(earthworms)
(body cavity, viscera)

	
Heterakis adult worm, head	*Heterakis* worm eggs