

Tetrameres

(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including habronematoids (with pseudolabia and median lips) containing the tetramerids which are found in the proventriculus of birds and are transmitted by aquatic crustaceans, amphipods, beetles, cockroaches, grasshoppers or earthworms in which L3 develop. Infections by *Tetrameres* spp. may cause anaemia in domestic and wild 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: Tetrameridae (extravagant sexual dimorphism, females swollen, coloured bright red)
Genus: *Tetrameres* (parasitic in proventriculus of birds)
Species: various species cause anaemia 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, Aprocotoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

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

The family Tetrameridae contains 3 subfamilies: Tetramerinae (body spirally coiled or globular, parasites of the proventriculus (rarely gizzard) of birds); Geopetitiinae (female body with long posterior constriction (in form of elongate peduncle) followed by terminal swelling, parasites of the gizzard of birds); and Crassicaudinae (female body with short posterior constriction (in form of simple narrowing) followed by terminal swelling, parasites of the tissues of whales). The subfamily Tetramerinae contains 3 genera (*Microhadjelia*, *Tetrameres* and *Microtetrameres*) which are differentiated primarily on the basis of adult anatomy, larval characteristics, modes of transmission, tissue tropism, host specificity and geographic distribution. Genera of veterinary and medical significance are tabulated below:

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

The genus *Tetrameres* contains peculiar non-vermiform worms noted for their marked sexual dimorphism with the body of female worms being globular or spirally-twisted and grossly swollen between the head and tail (commonly known as globular stomach worms). Female worms parasitize the proventricular glands of birds while male worms occur on the mucosal surface. Early studies recognised 2 subgenera: namely *T. (Tetrameres)* (body of female globular, male with spines on lateral fields); and *T. (Microtetrameres)* (body of female twisted in tight spiral, male without spines on lateral fields). Subsequent studies, however, considered *T. (Microtetrameres)* to be a separate genus and recognised 3 *Tetrameres* subgenera; *T. (Tetrameres)* (lacking anterior cuticular specializations, body bearing longitudinal rows of cuticular spines); *T. (Gynaecophila)* (lacking anterior cuticular specializations, lacking body spines or bearing only a few poorly-developed spines); and *T. (Petrowimeres)* (bearing anterior cuticular specializations variously described as ‘cordons’, flanges or lateral alae, evident as ridges, wing-like structures, funnel-shaped processes or cleft spines). Some 57 species have been described from a wide range of bird species around the world, some in association with clinical disease, especially in young birds.

<i>Tetrameres</i> species	Definitive hosts	Location [Clinical signs]	Intermediate hosts	Distribution
<i>T. accipiter</i>	Accipitriformes: accipitrid (sharp-shinned hawk, red-tailed hawk)			Americas
<i>T. (G.) aegyptii</i>	Accipitriformes: accipitrid (cinereous vulture)			Eurasia
<i>T. (T.) americana</i> (syn. <i>Tropisurus</i>) (globular roundworm, stomach worm)	Galliformes: phasianid (chicken, red junglefowl, turkey, northern bobwhite quail, ruffed grouse); Columbiformes: columbid (pigeon)	proventriculus [anaemia]	Blattodea: ectobiid (cockroach, <i>Blattella germanica</i>); Orthoptera: acridid (grasshopper, <i>Locusta migratoria</i> , <i>Melanoplus femurrubrum</i> , <i>differentialis</i> , <i>Scyllina cyanipes</i>)	Africa, North America
<i>T. anatis</i>	Anseriformes: anatid (mallard)			
<i>T. (P.) anseranas</i>	Anseriformes: anseranatid (magpie goose)			Australia
<i>T. (G.) aspicula</i>	Ciconiiformes: threskiornithid (white-faced ibis)	proventriculus		South America

<i>T. (G.) aspinosa</i>	Pelecaniformes: ardeid (snowy egret)			North America
<i>T. (P.) australis</i>	Anseriformes: anatid (black swan)			Australia
<i>T. (P.) biziurae</i>	Anseriformes: anatid (musk duck)			Australia
<i>T. (T.) butorides</i>	Ciconiiformes: ardeid (green heron)			Central America
<i>T. cardinalis</i>	Passeriformes: cardinalid (northern cardinal)		Orthoptera: acridid (locust, <i>Locusta migratoria</i>)	North America
<i>T. (T.) cladorhynchi</i>	Charadriiformes: recurvirostrid (banded stilt)			Australia
<i>T. (P.) columbicola</i>	Columbiformes: columbid (rock dove, mourning dove, white-winged dove)			Europe
<i>T. (T.) confusa</i>	Galliformes: phasianid (chicken); Passeriformes: cinclid (brown dipper)	proventriculus [anaemia]	Orthoptera: acridid (grasshoppers, <i>Eutryxalis filata</i> , <i>Orphulella punctata</i>)	South America, Asia
<i>T. (G.) daceioni</i>	Coraciiformes: alcedinid (kookaburra)			Australia
<i>T. (T.) dubia</i> (syn. <i>T. coloradensis</i> , <i>scolopacidis</i>)	Charadriiformes: scolopacid (common snipe, black turnstone, dunlin, sharp-tailed sandpiper, green sandpiper, wood sandpiper, western sandpiper, long-billed dowitcher, bar-tailed godwit, red-necked stint, red-necked phalarope, ruff, Eurasian woodcock)			Australasia
<i>T. (T.) elyi</i>	Pelecaniformes: ardeid (great egret); Accipitriiformes: accipitrid (red-shouldered hawk)	proventriculus		North America
<i>T. (P.) fissispina</i> (syn. <i>Tropisurus</i> , <i>Tropidocerca</i> , <i>Spiroptera pulicis</i> , <i>T. crami</i>)	Anseriformes: anatid (domestic duck, mallard, muscovy duck, mandarin duck, wood duck, falcated duck, ring-necked duck, long-tailed duck, mottled duck, marbled duck, tufted duck, ferruginous duck, harlequin duck, ruddy duck, white-headed duck, black-bellied whistling duck, American black duck, Pacific black duck, Indian spot-billed duck, ruddy shelduck, Australian shelduck, northern pintail, northern shoveler, Eurasian teal, Baikal teal, cinnamon teal, blue-winged teal, Eurasian wigeon, American wigeon, common pochard, red-crested pochard, Baer's pochard, common scoter, velvet scoter, surf scoter, common eider, common merganser, red-breasted merganser, smew, garganey, gadwall, common goldeneye, lesser scaup, greater scaup, canvasback, redhead, bufflehead, greylag goose, bar-headed goose, greater white-fronted goose, lesser white-fronted goose, snow goose, magpie goose, Canada goose, tundra swan, whooper swan, black-necked swan, mute swan); Charadriiformes: larid (common gull, lesser black-headed gull, black-headed gull, European herring gull); scolopacid (common snipe, Eurasian	proventriculus [anaemia]	Branchiopoda: daphniid (water flea, <i>Daphnia pulex</i>); Malacostraca: gammarid (amphipod, <i>Gammarus fasciatus</i> , <i>pulex</i> , <i>lacustris</i> , <i>locusta</i> , <i>maeoticus</i>), hyalellid (amphipod, <i>Hyaella azteca</i> (syn. <i>knickerbockeri</i>)), idoteid (isopod, <i>Idotea balthica</i>); Ostracoda: cypridid (<i>Heterocypris incongruens</i>); Insecta: baetid (mayfly larvae, <i>Cloeon dipterum</i>), ceratopogonid (midge larvae, <i>Culicoides</i>), chironomid (midge larvae, <i>Cricotopus</i> , <i>Polipediis</i> , <i>Prodadius</i> , <i>Tendipes salinarum</i>) [plus PH: Clupeiformes: clupeid (Caspian marine shad); Cypriniformes: cyprinid (common roach, common rudd); Gobiiformes: gobiid (monkey goby, round goby), eleotrid (bigmouth sleeper);	worldwide

	woodcock); Columbiformes: columbid (common wood pigeon, rock dove, stock dove); Falconiformes: falconid (merlin, red-footed falcon); Galliformes: phasianid (chicken, turkey, chukar, rock partridge, grey partridge, Lady Amherst's pheasant, willow ptarmigan), numidid (helmeted guineafowl); Gruiformes: gruid (crane), rallid (corn crake, sora crake, common moorhen, water rail, Eurasian coot); Pelecaniformes: ardeid (grey heron, great egret, black-crowned night heron), threskiornithid (glossy ibis); Podicipediformes: podicipedid (western grebe, horned grebe, great crested grebe, red-necked grebe, black-necked grebe, little grebe); Strigiformes: strigid (tawny owl)		Perciformes: percid (zander); Primates: hominid (human)	
<i>T. (T.) flehartyi</i>	Ciconiiformes: ardeid (little blue heron, Louisiana heron, reddish egret, great blue heron, snowy egret, American bittern)	proventriculus		North America
<i>T. (P.) galericulata</i>	Anseriformes: anatid (wood duck, mandarin duck)			Eurasia
<i>T. (G.) globosa</i> (syn. <i>T. monospicules</i> , <i>pavlovskii</i> , <i>tetrica</i>)	Gruiformes: rallid (American coot, Eurasian coot, common moorhen, American purple gallinule, sora, Baillon's crake)			Holarctic
<i>T. (T.) greeni</i>	Pelecaniformes: pelecanid (Australian pelican)			Australia
<i>T. (G.) gubanovi</i>	Podicipediformes: podicipedid (great crested grebe, red-necked grebe, black-headed grebe, pied-billed grebe, little grebe, Australasian grebe)			cosmopolitan
<i>T. (G.) gynaecophila</i>	Pelecaniformes: threskiornithid (Eurasian spoonbill)			Eurasia
<i>T. (P.) lhuillieri</i>	Galliformes: phasianid (chukar, rock partridge, grey partridge, see-see partridge, Barbary partridge, Daurian partridge, common quail, ring-necked pheasant); Columbiformes: columbid (stock pigeon)			cosmopolitan
<i>T. (T.) megaphasmidiata</i>	Charadriiformes: charadriid (two-banded plover), scolopacid (white-rumped sandpiper)			South America
<i>T. (T.) micropensis</i>	Pelecaniformes: threskiornithid (roseate spoonbill), ardeid (yellow-crowned night heron)			Americas
<i>T. (T.) microspinosa</i> (syn. <i>T. ardamericanus</i> , <i>inermis</i>)	Pelecaniformes: ardeid (great egret, great blue heron, American bittern, yellow-crowned night heron), pelecanid (brown pelican); Suliformes: phalacrocoracid (double-crested cormorant, neotropic cormorant); Accipitriformes: accipitrid (osprey); Strigiformes: strigid (barred owl)	proventriculus		cosmopolitan
<i>T. minima</i>	Passeriformes: passerid (house sparrow)			Europe

<i>T. (P.) mohtedai</i>	Galliformes: phasianid (chicken, red junglefowl); Anseriformes: anatid (domestic duck, mallard)	proventriculus [anaemia]	Orthoptera: acridid (grasshopper, <i>Oxya nitidula</i>); Lepidoptera: tineid (moth, <i>Setomorpha rutella</i>); Coleoptera: scarabaeid (dung beetle, <i>Liatongus cinctus</i>), hydrophilinid (beetle, <i>Sphaeridium quinquemaculatus</i>); Malacostraca: percellionid (woodlouse, <i>Porcellio laevis</i>)	India
<i>T. (T.) nouveli</i>	Charadriiformes: charadriid (lesser sand plover, Kentish plover), recurvirostrid (black-winged stilt, pied stilt, red-necked avocet)			Australasia
<i>T. numida</i>	Galliformes: numidid (helmeted guineafowl)			Africa
<i>T. occinea</i>	Phoenicopteriformes: phoenicopterid (American flamingo)			Americas
<i>T. (G.) oxylabiata</i>	Galliformes: phasianid (hazel grouse)			Europe
<i>T. (T.) paraaraliensis</i>	Charadriiformes: charadriid (white-faced plover, little ringed plover, northern lapwing, American golden plover, Eurasian dotterel)			Asia
<i>T. paradisea</i>	Gruiformes: gruid (Stanley's crane, sandhill crane, hooded crane)	proventriculus		Africa, North America
<i>T. (T.) paradoxa</i> (syn. <i>T. certa</i> , <i>robusta</i> , <i>sobolevi</i> , <i>strigiphila</i>)	Accipitriformes: accipitrid (crested goshawk, swallow-tailed kite, marsh harrier, European honey buzzard); Procellariiformes: diomedeid (wandering albatross, shy albatross); Strigiformes: strigid (Florida barred owl)			Holarctic
<i>T. (G.) pattersoni</i>	Galliformes: phasianid (northern bobwhite quail)		Orthoptera: acridid (grasshopper, <i>Chortophaga viridifasciata</i> , <i>Melanoplus femurrubrum</i>)	North America
<i>T. paucispina</i> (syn. <i>T. quisicali</i>)	Passeriformes: icterid (scarlet-headed blackbird, greater Antillean grackle, common grackle, Cuban blackbird), cardinalid (northern cardinal)			Americas
<i>T. (G.) pjandzhi</i>	Anseriformes: anatid (mallard)			
<i>T. (T.) prozeskyi</i>	Bucerotiformes: bucerotid (red-billed hornbill, southern yellow-billed thornbill)			Africa
<i>T. (P.) ryjikovi</i>	Anseriformes: anatid (mallard, wood duck, falcated duck, blue-winged teal, Eurasian teal, Baikal teal, Eurasian wigeon, northern pintail, northern shoveler, common pochard, Baer's pochard, greater scaup, canvasback, common goldeneye, garganey, gadwall)	proventriculus		Eurasia
<i>T. (T.) salina</i>	Phoenicopteriformes: phoenicopterid (Chilean flamingo)			South America
<i>T. (G.) shaanxiensis</i>	Accipitriformes: accipitrid (cinereous vulture)			Eurasia
<i>T. (T.) skryabini</i>	Charadriiformes: larid (common gull, glaucous gull, little gull, slaty-backed			Eurasia

	gull, European herring gull, Sabine's gull, gull-billed tern, sandwich tern)			
<i>T. (P.) somateriae</i>	Anseriformes: anatid (common eider, surf scoter, velvet scoter)			North America
<i>T. spiculigerum</i>	Suliformes: anhingid (American darter)			North America
<i>T. (P.) spinosa</i> (syn. <i>T. nettatus</i> , <i>pavonis</i>)	Anseriformes: anatid (mallard, tufted duck, ferruginous duck, long-tailed duck, ring-necked duck, ruddy duck, ruddy shelduck, northern pintail, common goldeneye, cinnamon teal, Eurasian wigeon, common pochard, red-crested pochard, bufflehead, velvet scoter, surf scoter, gadwall, greater scaup, lesser scaup, redhead, canvasback, bufflehead, tundra swan, whooper swan); Charadriiformes: larid (lesser black-backed gull), recurvirostrid (black-winged stilt), scolopacid (common redshank); Galliformes: phasianid (Indian peafowl)			Asia
<i>T. (T.) spirospiculum</i>	Ciconiiformes: threskiornithid (buff-necked ibis)	proventriculus		South America
<i>T. (P.) sponsae</i>	Anseriformes: anatid (wood duck)	proventriculus		North America
<i>T. (P.) striata</i>	Anseriformes: anatid (mallard, mottled duck, blue-winged teal)			North America
<i>T. (T.) tarapungae</i>	Charadriiformes: larid (red-billed gull)			New Zealand
<i>T. timopheevoi</i>	Galliformes: phasianid (chukar)			Eurasia
<i>T. (G.) tinamicola</i>	Tinamiformes: tinamid (elegant crested tinamou, pale elegant tinamou)	proventriculus		South America
<i>T. (G.) wetzeli</i>	Sphenisciformes: spheniscid (southern rock-hopper penguin, gentoo penguin)			South America, Antarctica
<i>T. (G.) williamsi</i>	Pelecaniformes: threskiornithid (American white ibis); Gruiformes: gruid (whooping crane)	proventriculus		North America
<i>T. (P.) zakharowi</i>	Anseriformes: anatid (greater white-fronted goose, lesser white-fronted goose, greylag goose, bean goose, brant, tundra swan)			Eurasia
<i>Species inquirenda</i>				
<i>T. (G.) alii</i> <i>sp. inq.</i>	Passeriformes: hirundinid (brown-throated martin)			India
<i>T. araliensis</i> (syn. <i>T. limicollis</i>) <i>sp. inq.</i>	Charadriiformes: recurvirostrid (pied avocet), charadriid (little ringed plover)			Eurasia
<i>T. (G.) ardeae</i> <i>sp. inq.</i>	Pelecaniformes: ardeid (grey heron)			Eurasia
<i>T. asiatica</i> <i>sp. inq.</i>	Anseriformes: anatid (common goldeneye, smew); Gruiformes: rallid (Eurasian coot)			Eurasia
<i>T. avicula</i> <i>sp. inq.</i>	Galliformes: phasianid (chicken)			Europe
<i>T. calidris</i> <i>sp. inq.</i>	Charadriiformes: scolopacid (red knot)			Australia
<i>T. coccinea</i> <i>sp. inq.</i>	Phoenicopteriformes: phoenicopterid (greater flamingo); Pelecaniformes: ardeid (cattle egret), threskiornithid (Eurasian spoonbill)			Africa

<i>T. cochleare</i> (<i>cochleariae</i>) <i>sp. inq.</i>	Pelecaniformes: ardeid (cattle egret, black-crowned night heron, boat-billed heron)			South America
<i>T. (T.) cordoniferens</i> <i>sp. inq.</i>	Anseriformes: anatid (lesser whistling duck)			India
<i>T. cubana</i> <i>sp. inq.</i>	Ciconiiformes: phoenicopterid (American flamingo)			Americas
<i>T. cygni</i> <i>sp. inq.</i>	Anseriformes: anatid (Bewick's swan, tundra swan, snow goose, Canada goose, mallard, blue-winged teal, lesser scaup, American wigeon)			Eurasia, Americas
<i>T. (G.) deccani</i> <i>sp. inq.</i>	Pelecaniformes: threskiornithid (Indian white ibis)			India
<i>T. diomedea</i> <i>sp. inq.</i>	Procellariiformes: diomedeid (wandering albatross, yellow-nosed albatross)			Australia
<i>T. (G.) fermini</i> <i>sp. inq.</i>	Ciconiiformes: ardeid (green heron)			Central America
<i>T. gigas</i> <i>sp. inq.</i>	Anseriformes: anatid (mallard)			South America
<i>T. (T.) hagenbecki</i> <i>sp. inq.</i>	Anseriformes: anatid (domestic duck); Galliformes: phasianid (chicken); Ciconiiformes: ciconiid (greater adjutant); Gruiformes: gruid (sarus crane)			Asia
<i>T. (P. indiana</i> <i>sp. inq.</i>	Anseriformes: anatid (ruddy shelduck)			India
<i>T. lobibycis</i> <i>sp. inq.</i>	Charadriiformes: larid (silver gull)			Australia
<i>T. (G.) manoji</i> <i>sp. inq.</i>	Psittaciformes: psittacid (plum-headed parakeet)			India
<i>T. (G.) minutes</i> <i>sp. inq.</i>	Ciconiiformes: ardeid (Indian pond heron)			India
<i>T. numenii</i> <i>sp. inq.</i>	Charadriiformes: scolopacid (Eskimo curlew, Eurasian curlew, common sandpiper)			Russia
<i>T. (T.) phaenicopterus</i> <i>sp. inq.</i>	Columbiformes: columbid (yellow-footed green pigeon)			India
<i>T. (P.) plectropteri</i> <i>sp. inq.</i>	Anseriformes: anatid (spur-winged goose)			Africa
<i>T. schigini</i> <i>sp. inq.</i>	Ciconiiformes: ardeid (purple heron)			Russia
<i>T. scolopacis</i> <i>sp. inq.</i>	Charadriiformes: scolopacid (Eurasian woodcock)			Asia
<i>T. (G.) singhi</i> <i>sp. inq.</i>	Ciconiiformes: ciconiid (white stork); Pelecaniformes: ardeid (great egret)			Africa
<i>T. unispina</i> <i>sp. inq.</i>	Passeriformes: corvid (American crow, carrion crow)			Americas
<i>T. uxoria</i> <i>sp. inq.</i>	Charadriiformes: scolopacid (common sandpiper, curlew sandpiper, Terek sandpiper, long-billed dowitcher)			Eurasia
<i>T. vietnamensis</i> <i>sp. inq.</i>	Galliformes: phasianid (silver pheasant)			Asia
Re-assigned species				
<i>T. centuri</i> (now <i>Microtetrameres</i>)	Passeriformes: icterid (eastern meadowlark, western meadowlark), fringillid (canary)		Orthoptera: acridid (grasshopper, <i>Melanoplus</i>)	North America
<i>T. cloacitectus</i> (now <i>Microtetrameres</i>)	Accipitriformes: accipitrid (Himalayan buzzard)			Asia
<i>T. corax</i> (now <i>Microtetrameres</i>)	Passeriformes: corvid (Eurasian magpie, large-billed crow)		Orthoptera: acridid (grasshopper,	Eurasia, North America

			<i>Melanoplus</i>)	
<i>T. cruzi</i> (now <i>Microtetrameres</i>)	Piciformes: picid (yellow-fronted woodpecker), buconid (Guianian puffbird)			Africa
<i>T. helix</i> (now <i>Microtetrameres</i>)	Columbiformes: columbid (pigeon)		Orthoptera: acridid (grasshopper, <i>Melanoplus bivittatus</i> , <i>femurrubrum</i>); Blattodea: blattid (cockroach, <i>Blattella germanica</i>)	
<i>T. inermis</i> (now <i>Microtetrameres</i>)	Passeriformes: leiothrichid (red-billed leiothrix, Chinese hwamei), muscicapid (Siberian rubythroat), ploceid (orange weaver)		Orthoptera: acridid (grasshopper, <i>Locusta migratoria</i> , <i>Tylotropidius patagiatus</i>)	Africa, Asia
<i>T. inflata</i> (syn. <i>T. haemochrous</i>) (now <i>Microtetrameres</i>)	Falconiformes: falconid (peregrine falcon)			
<i>T. oriolus-orientalis</i> (now <i>Microtetrameres</i>)	Passeriformes: leiothrichid (red-billed leiothrix, Chinese hwamei); muscicapid (Siberian rubythroat)			Asia
<i>T. spiralis</i> (now <i>Microtetrameres</i>)	Pelecaniformes: ardeid (cattle egret)			Egypt

Parasite morphology: *Tetrameres* spp. form 3 distinct types of morphological stages during their development: eggs; larvae (4 consecutive stages encoded L1-L4); and adult worms. Each of these stages is quite unique (even peculiar) compared to other nematodes. The eggs are small and ovoid, sometimes elongated, measuring 33-62 x 18-30 µm. They have thick smooth eggshells with polar swellings and delicate circular grooves forming opercula, sometimes adorned with polar ornamentations or tufts of short filaments. The eggs are embryonated when laid and larvated when excreted with faeces. L1 are short stout cylindrical stages measuring 150-220 x 9-13 µm with several circles of tiny spines around the head, a left cephalic hook and rasp, a rhabditiform oesophagus, and a rounded tail with a few subterminal spines. L2 are larger transient stages found within invertebrate intermediate hosts, while infective L3 are larger still (measuring 1.5-4.0 mm long) and most species have crenulated cuticles (with deep transverse striations) and rounded tails often equipped with rugosities, bristles or protuberances. L4 are transient stages parasitic within birds and they have just begun to show genital formation (especially in females where the uteri grow around the intestines). Adult worms are characterised by their extreme sexual dimorphism, with pale white males being cylindrical (filiform) and bright red females being almost spherical (sometimes fusiform). Both sexes have mouths with median lips (dorsal and ventral) and lateral pseudolabia (without cephalic papillae), and an elongate bipartite oesophagus. Species belonging to the subgenera *T. (Tetrameres)* and *T. (Gynaecophila)* have anterior ends lacking specialised cuticular features, whereas those of the subgenus *T. (Petrowimeres)* have anterior specializations (variously described as cordons, flanges, alae, ridges, wings, processes or spines. Mature female worms have a peculiar non-vermiform appearance with bulbous globular bodies, sometimes spirally-twisted, but grossly swollen between the tapering cephalic and caudal extremities (hence their common name as globular stomach worms). Females range in size from 3.5-10.2 mm long but they are 3.0-6.0 mm wide (midbody diameter). They have 4 deep longitudinal grooves (furrows) on their surface cuticle (hence their generic name as 'tetra'-meres'). The body is occupied by expanded uteri containing enormous numbers of eggs and the vulva opens posteriorly near the subterminal anus. In contrast, mature male worms appear vermiform, having slender thread-like bodies measuring 3.0-8.3 mm long by 116-133 µm wide. Males belonging to the subgenus *T. (Tetrameres)* have cuticles bearing longitudinal rows of spines, whereas those of the subgenus *T. (Gynaecophila)* lack spines. Males have 2 unequal slender spicules (left spicule longer) and the tail often has caudal papillae transformed into spines.

Site of infection: Developing larvae and adult worms infect the glandular stomach (proventriculus) of their avian definitive hosts. The bulbous female worms become embedded in proventricular glands while the small filiform males remain on the mucosal surface. Infective larvae develop in the haemocoel and tissues of intermediate hosts (crustaceans and insects) which have consumed worm eggs.

Pathogenesis: Light infections in birds are usually subclinical, but heavy infections can cause morbidity and mortality, particularly in poultry, game birds and waterfowl. Worms develop in the proventricular glands and may cause local traumatic damage, sometimes ulceration, while female worms feed on host blood and may cause anaemia. Most damage occurs, however, when females embedded in the gut wall grow and form large nodules (0.5-2.0 cm in diameter) which act as space-occupying lesions leading to glandular atrophy, proliferative proventriculitis with necrosis and sloughing of the mucosa, and progressive thickening of the gut wall. The lumen fills with thick slimy mucus and sloughed tissues, sometimes becoming partially or even completely

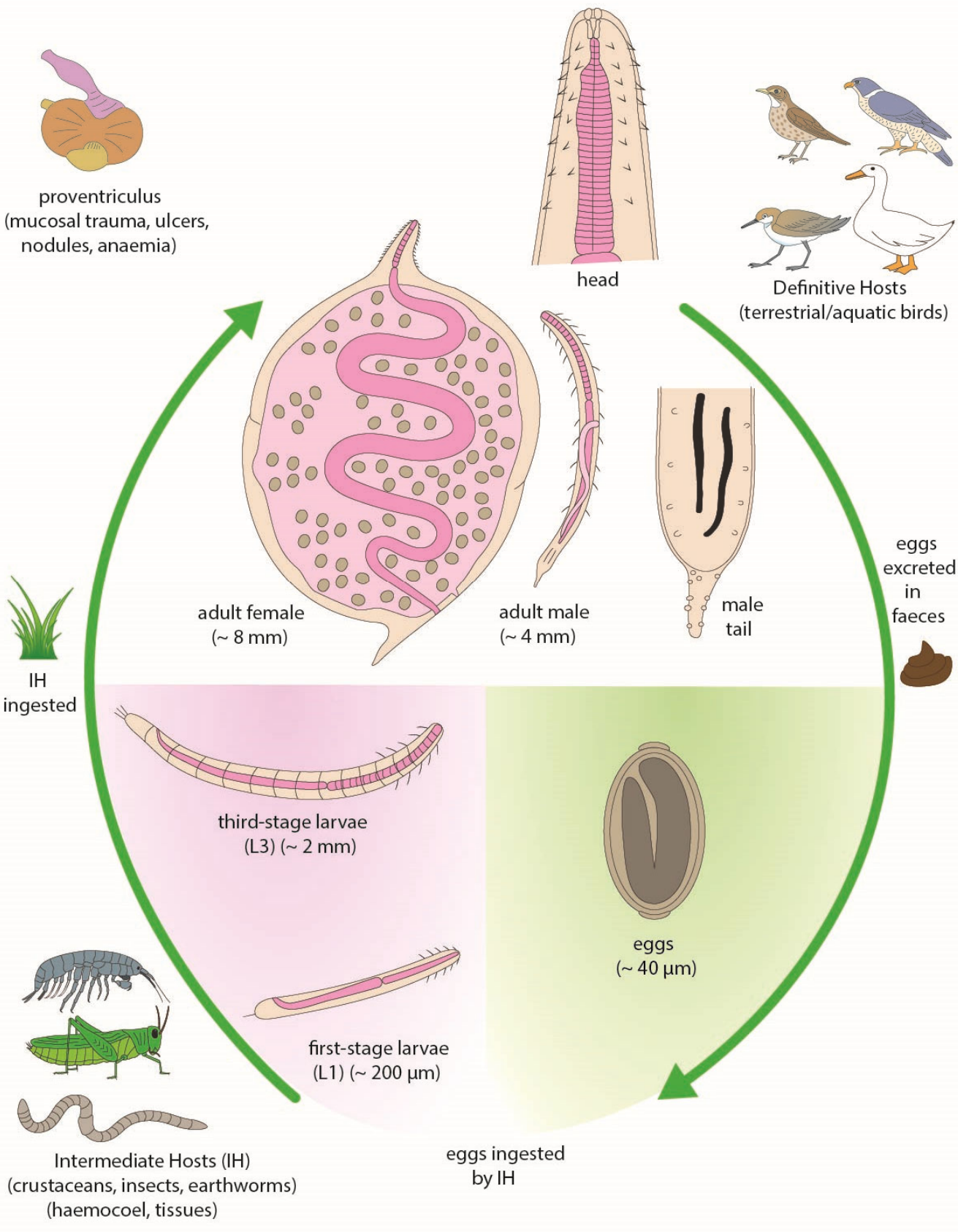
occluded. This prevents food passage with undigested material accumulating in the proventriculus which becomes flaccid and enlarged, sometimes perforating leading to peritonitis. Birds exhibit a range of clinical signs, including anaemia, vomiting, green faeces (due to excess bile), weight loss, weakness and emaciation, with some birds actually dying of starvation. Infections also weaken the immune system, making birds susceptible to other concomitant infections.

Developmental cycle and mode of transmission: *Tetrameres* spp. have indirect heteroxenous life-cycles involving the development of adult worms in vertebrate definitive hosts (terrestrial and aquatic birds) and the development of infective larvae in invertebrate intermediate hosts (terrestrial insects and aquatic crustaceans). Even though female worms are embedded in the proventricular glands of birds, their posterior vulvae and tails are directed towards the lumen so freshly-laid eggs can be carried into the stomach and voided with host faeces. Worm eggs are susceptible to dessication but may survive for several weeks in the external environment in the presence of moisture. The eggs are ingested by various invertebrates which act as intermediate hosts supporting larval development, notably terrestrial insects (grasshoppers, cockroaches), isopods, and earthworms, as well as aquatic crustaceans (amphipods, cladocerans). Ingested eggs hatch in the gut releasing L1 which penetrate the gut into the haemocoel and moult twice to form L3. These larvae remain free in the haemocoel for several days and then gradually encapsulate within host tissues (mostly muscles) becoming infective around 7 weeks. Final hosts become infected when they consume invertebrates containing infective L3 which invade the gastric glands, moult to L4 in 1-2 days and then to subadults (sometimes referred to as L5) in 1-2 weeks. Adult worms mature over 3 weeks and mate, the males then leaving the glands and die, while the female become embedded in fibrous capsules deep within the glands and feed on host blood. The prepatent period (time from infection to first excretion of eggs) ranges from 42-56 days.

Differential diagnosis: Infections are rarely indicated by clinical signs as they are relatively nonspecific (anaemia, digestive disorders) and often slow in onset. Infections are conventionally diagnosed by the microscopic detection of worm eggs in faecal samples, either in wet mounts, smears or concentrates (floats). The eggs are unique in morphology, often being cigar-shaped and bearing polar adornments. Infections may also be diagnosed at post-mortem by the visual detection of discoloured lesions (red spots) below the proventricular mucosa. Adult worms may be recovered from lesions by dissection (teasing or squeezing with forceps). Molecular biological techniques have recently been applied to phylogenetic analyses of adult worms following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit ribosomal RNA).

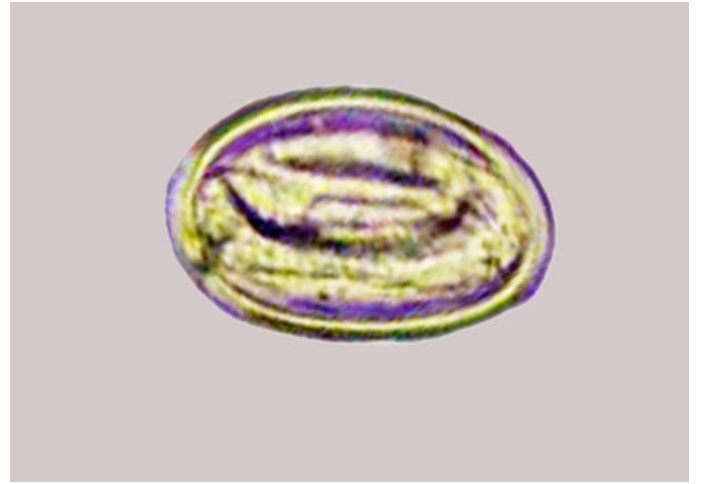
Treatment and control: A range of broad spectrum anthelmintics have been used to treat clinical infections in birds, including benzimidazoles (albendazole, fenbendazole, flubendazole, mebendazole, oxfendazole), imidazothiazoles (levamisole), diethylenediamines (piperazine) and macrocyclic lactones (ivermectin). Repeated or sustained treatment is generally required to eliminate deeply embedded worms and to prevent re-infection, with most medications added to food or water in the poultry industry. Clinical infections usually do not develop in birds confined to indoor areas (poultry sheds, aviaries) but they can become problematic when birds have outdoor access where they can encounter invertebrate intermediate hosts. In these situations, attempts should be made to reduce contamination by worm eggs through improved sanitation and hygiene (regular removal of faeces, litter, bedding) and to minimise transmission through insects and crustaceans (provision of clean food and treated water, prevention of foraging, and judicious use of arthropodicidal chemicals in the environment, around holding facilities or on birds).

Tetrameres

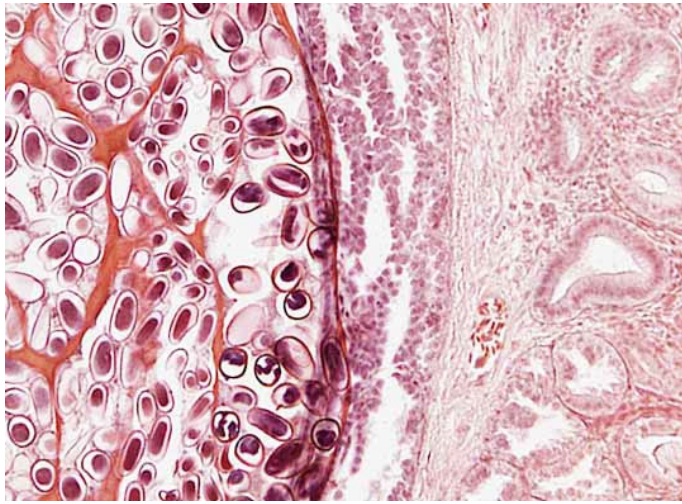




Tetrameres adult worms



Tetrameres worm egg



Tetrameres nodule