Oxyspirura
(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 both oviparous and viviparous thelazioids (lacking lips). The former are found in the eyes of birds and are transmitted by cockroaches in which L3 develop from ingested eggs. Infections by *Oxyspirura mansoni* have been associated with ophthalmitis in poultry worldwide.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, 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:	Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Family:	Thelaziidae (hexagonal mouth, lacking lips, conspicuous transverse anterior striations, live on surface of eye)
Genus:	*Oxyspirura* (parasitic in eyes of birds)
Species:	various species cause ophthalmitis 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.

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

The superfamily Thelazioidea comprises medium-sized worms with hexagonal or subspherical mouths without pseudolabia infecting the eyes or lungs of mammals, the eyes of birds or the intestines of fish, and using insects as intermediate hosts for larval development. Three families are recognised: Thelaziidae (buccal capsule well-developed, pharynx not elongated, parasites of eyes of birds and mammals); Rhabdochonidae (buccal capsule well-developed, pharynx cylindrical and elongated, parasites of intestines or organs of fish, sometimes other vertebrates); and Pneumospiruridae (buccal capsule small or absent, 6 lips sometimes well-developed or atrophied, cuticle with sheath, gubernaculum often double, parasites of lungs of mammals). The family Thelaziidae (or eyeworms) have hexagonal mouths and conspicuous transverse anterior striations. Two subfamilies are recognised: Oxyspirurinae (inner surface of buccal capsule often armed with teeth, oesophagus divided, vulva near anus, tail pointed in both sexes); and Thelaziinae (inner surface of buccal capsule without teeth, oesophagus not divided, vulva in anterior half of body, tail rounded in both sexes). The subfamily Oxyspirurinae is monotypic and only contains a single genus, *Oxyspirura.*

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs/larvae	Transmission
Subfamily: Oxyspirurinae						
Oxyspirura (eyeworms)	81	birds	eyes	9-20 mm long, smooth cuticle, males with coiled tails, 2 spicules, some with lateral alae, oviparous	eggs 55-60 x 40-45 µm, ellipsoidal, thin-shelled	indirect (L3 in insect IH, esp. cockroaches)
Subfamily: Thelaziinae						
Thelazia (eyeworms)	43	mammals, birds	eyes	14-21 mm long, cuticle with anterior striations, males with coiled tails, 2 dissimilar spicules, ovoviviparous	larvae (L1) 220-280 µm sheathed	indirect (L1 in dipteran IH, esp. muscids)

The genus *Oxyspirura* contains over 80 species of eyeworms described from some 40 families of birds around the world. Female worms are oviparous and their eggs are taken up by insect vectors in which infective larvae develop. Over the years, 6 subgenera have been recognised: *O.* (*Molinospirura*) (buccal capsule undivided, spicules similar but subequal, ovejector dilated, oral opening surrounded by sclerotized ring); *O.* (*Cramispirura*) (buccal capsule undivided, spicules similar but subequal, ovejector not dilated, oral opening without sclerotized ring); *O.* (*Barusispirura*) (buccal capsule undivided, spicules dissimilar and unequal, lateral alae present, gubernaculum absent); *O.* (*Hamulofilaria*) (= *O.* (*Skrjabinispirura*)) (buccal capsule undivided, spicules dissimilar and unequal, lateral alae absent, gubernaculum present or absent); *O.* (*Caballeroispirura*) (buccal capsule divided into anterior and posterior chambers, spicules dissimilar and unequal, lateral alae present, gubernaculum present); and *O.* (*Oxyspirura*) (= *O.* (*Yorkeispirura*)) (buccal capsule divided into anterior and posterior chambers, spicules dissimilar and unequal, lateral alae absent, gubernaculum present or absent). Infections by various species have been associated with clinical disease (primarily conjunctivitis) in poultry and game birds and numerous wild passerine birds.

***Oxyspirura* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Intermediate Hosts**	**Distribution**
O. acuticauda	Passeriformes: sturnid (bank myna)	eye		India
O. alauda	Passeriformes: alaudid (oriental skylark), pycnonotid (red-vented bulbul)	eye		Asia
O. alii	Passeriformes: vangid (common woodshrike)	eye		Asia
O. (*Cramispirura*) *altensis*	Cariamiformes: cariamid (red-legged seriema); Accipitriformes: accipitrid (savanna hawk)	eye		South America
O. anacanthura	Cuculiformes: cuculid (smooth-billed ani, greater ani, guira cuckoo); Piciformes: ramphastid (yellow-ridged toucan, channel-billed toucan)	eye		South America
O. asiatica	Accipitriformes: accipitrid (Eurasian sparrowhawk)	eye		Eurasia
O. basiri	Cuculiformes: cuculid (Jacobin cuckoo)	eye		Asia
O. baskakowi	Passeriformes: muscicapid (European woodland flycatcher, common nightingale), sylviid (lesser whitethroat)	eye		Eurasia
O. bosei (syn. *Chandlerella*)	Passeriformes: corvid (Eurasian magpie)	eye		Eurasia
O. (*O.*) *brasiliensis*	Cuculiformes: cuculid (greater ani); Passeriformes: ploceid (cinnamon weaver, village weaver)	eye		South America, Africa
O. (*O.*) *brevisubulata*	Caprimulgiformes: caprimulgid (pauraque), Strigiformes: strigid (variable screech owl), tytonid (barn owl)	eye		Americas
O. buccosulcata	Passeriformes: sturnid (Brahminy starling, chestnut-tailed starling, pied myna)	eye		India
O. (*Cramispirura*) *buckleyi*	Passeriformes: motacillid (white wagtail)	eye		Eurasia
O. cameroni	Passeriformes: tityrid (black-tailed tityra)	eye		South America

O. (*Molinospirura*) *cassici*	Passeriformes: icterid (red-rumped cacique)	eye		South America
O. cephaloptera	Coraciiformes: momotid (blue-crowned motmot); Passeriformes: icterid (orange-backed troupial)	eyes		South America
O. chabaudi	Passeriformes: motacillid (white wagtail), ploceid (village weaver, red-billed quelea)	eye		Eurasia, Africa
O. chauvancyi	Passeriformes: thamnophilid (northern slaty antshrike)	eye		South America
O. chrysomma	Passeriformes: paradoxornithid (yellow-eyed babbler)	eye		Asia
O. cisticola	Passeriformes: cisticolid (streaked fantail warbler)	eye		Eurasia
O. congolensis	Passeriformes: muscicapid (spotted flycatcher)	eye		North America
O. crami	Otidiformes: otidid (black-bellied bustard)	eye		Africa
O. (*O.*) *crassa*	Strigiformes: strigid (great horned owl)	eye		Americas
O. cruzi	Tinamiformes: tinamid (red-winged tinamou)	eye		South America
O. dendropicosi	Piciformes: picid (cardinal woodpecker)	eye		Africa
O. dicruri	Passeriformes: dicrurid (fork-tailed drongo)	eye		India
O. dicruricola	Passeriformes: dicrurid (fork-tailed drongo)	eye		India
O. dukhunensis	Piciformes: picid (yellow-crowned woodpecker)	eye		India
O. egretta	Pelecaniformes: ardeid (little egret)	eye		Asia
O. elani	Accipitriformes: accipitrid (black-winged kite)	eye		Africa
O. eremopterixa	Passeriformes: alaudid (ashy-crowned sparrow-lark)	eye		Asia
O. fulica	Gruiformes: rallid (Eurasian coot)	eye		Eurasia
O. grandipapillata	Passeriformes: dicrurid (fork-tailed drongo)	eye		India
O. gubernaculata	Passeriformes: motacillid (grey wagtail)	eye		India
O. hexapapillata	Passeriformes: meropid (olive bee-eater)	orbit		India
O. hispanica	Otidiformes: otidid (great bustard)	eye		Europe
O. hyderabadensis	Passeriformes: dicrurid (black drongo)	eye		India
O. (*Cramispirura*) *indica*	Passeriformes: muscicapid (white-rumped shama)	eye		India
O. laharpurensis	Passeriformes: sturnid (common myna)	eye		India
O. leiperi	Passeriformes: leiothrichid (jungle babbler)	eye		Asia
O. lerouxi	Passeriformes: turdid (Indian blackbird)	eye		India
O. lobipluvia	Charadriiformes: charadriid (yellow-wattled lapwing)	eye		India
O. malabarica	Passeriformes: sturnid (chestnut-tailed starling)	eye		India
O. (*Yorkeispirura*) *mansoni* (syn. *O. parvorum*, *Filaria mansoni, Spiroptera mansoni, Microfilaria seguini*) (Manson's eyeworm, tropical fowl worm)	Accipitriformes: accipitrid (northern harrier); Anseriformes: anatid (domestic duck, whistling duck); Columbiformes: columbid (pigeon); Cuculiformes: cuculid (common hawk-cuckoo); Galliformes: phasianid (chicken, red junglefowl, red spurfowl, turkey, ring-necked pheasant, Chinese bamboo partridge, peafowl), numidid (guinea fowl); Passeriformes: icterid (bobolink, red-winged blackbird), laniid (loggerhead shrike), corvid (blue jay, Florida scrub jay); Piciformes: megalaimid (great barbet, black-browed barbet), picid (golden-cheeked woodpecker)	eye, conjunctiva, lachrymal glands [opthalmitis]	Blattodea: blaberid (cockroach, *Pycnoscelus surinamensis*)	worldwide, except Europe
O. mehransis	Pelecaniformes: ardeid (cattle egret)	intestine?		India
O. meropsicola	Coraciiformes: meropid (green bee-eater)	eye		India
O. mirzai	Passeriformes: leiothrichid (jungle babbler)	eye		India
O. myzomelae	Passeriformes: meliphagid (unspecified	eye		Asia

	honeyeater)			
O. (*Yorkeispirura*) *navali*	Accipitriformes: accipitrid (red-tailed hawk)	eye		North America
O. nigerica	Passeriformes: ploceid (weaver, cinnamon weaver, village weaver)	eye		Africa
O. (*Yorkeispirura*) *octopapillata*	Caprimulgiformes: caprimulgid (pauraque); Falconiformes: falconid (northern crested caracara)	eye		Americas
O. opthalmica	Charadriiformes: turnicid (Indian bustard-quail)	eye		India
O. orientalis	Passeriformes: dicrurid (fork-tailed drongo)	eye		India
O. papillosa	Accipitriformes: accipitrid (harpy eagle); Falconiformes: falconid (gray crane hawk)	eye		South America
O. peipingensis (syn. *O. cochlearispiculata*, *lalagea, streparae, yehi*)	Bucerotiformes: upupid (oriental hoopoe); Passeriformes: artamid (black currawong), campephagid (black-headed cuckooshrike), corvid (red-billed chough), emberizid (red-headed bunting), laniid (brown shrike, great grey shrike, lesser grey shrike), leiothrichid (common babbler), ploceid (cinnamon weaver, village weaver, red-billed quelea), sturnid (pied myna), turdid (Naumann's thrush)	eye		Eurasia, Africa
O. petrowi (syn. *O. kaitingensis*, *lumsdeni, matogrosensis, otocompsa*)	Caprimulgiformes: caprimulgid (little nightjar); Coraciiformes: meropid (blue-cheeked bee-eater), momotid (blue-crowned motmot); Galliformes: phasianid (greater prairie chicken, lesser prairie chicken, greater prairie chicken, chukar, Daurian partridge, hazel grouse, black grouse, ruffed grouse, sharp-tailed grouse, greater sage-grouse, ring-necked pheasant, northern bobwhite, scaled quail, harlequin quail); Passeriformes: cardinalid (northern cardinal), corvid (alpine chough, Eurasian magpie, plush-crested jay, purplish jay), hirundid (tree swallow), icterid (common grackle, boat-tailed grackle, purple grackle, eastern meadow lark, red-winged blackbird, brown-headed cowbird), laniid (lesser grey shrike, red-backed shrike, long-tailed shrike, tiger shrike, Turkestan shrike), leiothrichid (white-browed laughing thrush, Chinese hwanei), meropid (blue-cheeked bee-eater), motacillid (water pipit), parulid (common yellowthroat),), ploceid (cinnamon weaver, village weaver, red-billed quelea), pycnonotid (red-whiskered bulbul), turdid (American robin), tyrannid (eastern kingbird, great crested flycatcher), vireonid (white-eyed vireo); Pelecaniformes: ardeid (green heron, cattle egret)	eye	Orthoptera: acridid (grasshopper, *Hippiscus ocelote, Melanoplus differentialis, femurrubrum, ponderosus, Opeia obscura*, *Trimerotropis pallidipenni*s), gryllid (cricket, *Acheta domesticus, Gryllus texensis), romaleid (*plains lubber grasshopper, *Brachystola magna*); *Blattodea: blattid (cockroach, Periplaneta americana), ectobiid (w*ood cockroach, *Parcoblatta)* [plus rare cutaneous larval infection in Primates: hominid (human)]	worldwide
O. pici	Passeriformes: corvid (carrion crow, western jackdaw, Eurasian magpie, red-billed chough, alpine chough)	eye		Holarctic
O. (*Cramispirura*) *popovi*	Caprimulgiformes: caprimulgid (little nightjar); Galliformes: phasianid (prairie chicken, common pheasant, ruffed grouse, sharp-tailed grouse); Passeriformes: artamid (butcherbird), icterid (streak-backed oriole, meadowlark), laniid (lesser grey shrike, Turkestan shrike), motacillid (wagtail),	eye		Eurasia

	muscicapid (blue rock thrush, oriental magpie-robin, nightingale), oriolid (oriole), passerellid (seaside sparrow), turdid (thrush); Piciformes: picid (hairy woodpecker)			
O. (*Cramispirura*) *prinia*	Passeriformes: cisticolid (ashy prinia)	eye		India
O. (*Yorkeispirura*) *pusillae*	Passeriformes: cardinalid (northern cardinal), corvid (Florida scrub jay), icterid (purple grackle), mimid (brown thrasher), parulid (common yellowthroat), sittid (brown-headed nuthatch), troglodytid (Carolina wren), turdid (eastern bluebird), tyrannid (great crested flycatcher); Piciformes: picid (red-bellied woodpecker, red-headed woodpecker, hairy woodpecker)	eye		Americas
O. (*Cramispirura*) *rhipidurae*	Passeriformes: rhipidurid (white-throated fantail)	eye		Asia
O. rodriguesi	Passeriformes: icterid (Cuban blackbird)	eye		India
O. rustica	Passeriformes: dicrurid (fork-tailed drongo)	eye		India
O. (*O.*) *rysavyi*	Passeriformes: oriolid (Eurasian golden oriole)	eye		Eurasia
O. schulzi	Cuculiformes: cuculid (Asian koel); Galliformes: phasianid (chukar, grey partridge, Daurian partridge, hazel grouse, black grouse, common quail, western capercaillie); Gruiformes: rallid (Eurasian coot); Passeriformes: corvid (long-billed crow)	eye		Holarctic
O. siamensis	Cuculiformes: cuculid (greater coucal)	eye		India
O. singhi	Passeriformes: motacillid (Richard's pipit)	eye		Eurasia
O. solitaria	Coraciiformes: meropid (green bee-eater)	eye		India
O. stereura	Accipitriformes: accipitrid (spotted eagle)	eye, auditory meatus		Europe
O. sturnia	Cuculiformes: cuculid (sirkeer cuckoo); Galliformes: phasianid (grey francolin); Passeriformes: sturnid (pied myna, bank myna)	eye		India
O. suraiyai	Passeriformes: timalid (Indian scimitar babbler)	eye		India
O. sygmoidea	Passeriformes: corvid (carrion crow, rook, Eurasian magpie, Eurasian jay); Piciformes: ramphastid (Toco toucan, Cuvier's toucan)	eye		Europe, South America
O. (*Yorkeispirura*) *tanasijtschuki*	Passeriformes: icterid (unspecified species)	eye		Russia
O. thanhhoaensis	Passeriformes: leiothrichid (white-crested laughingthrush), muscicapid (blue whistling thrush)	conjunctiva		
O. (*O.*) *toroi*	Galliformes: phasianid (northern bobwhite)	eye		North America
O. (*Yorkeispirura*) *tsingchengensis*	Passeriformes: pycnonotid (black bulbul)	eye		Asia
O. turcottei	Galliformes: phasianid (wild turkey)	eye		North America
O. turdi	Passeriformes: turdid (mistle thrush)	eye		Eurasia
O. (*Yorkeispirura*) *turnicis*	Charadriiformes: turnicid (barred button-quail, common Indian bustard-quail)	eye		Asia
O. wellsi	Passeriformes: ploceid (black-winged red bishop)	eye		Africa
O. youngi	Primates: cercopithecid (Patas monkey)	eye		Russia (zoo)
Species inquirenda				
O. acanthochaerae	Passeriformes: meliphagid (spiny-cheeked	eye		Australia

sp. inq.	honeyeater)			
O. bancrofti sp. inq.	Passeriformes: meliphagid (little friarbird)	eye		Australia
O. brevipenis sp. inq.	Cariamiformes: cariamid (red-legged seriema)	eye		South America
O. conjunctivalis sp. inq.	Primates: lemurid (lemur)	eye		Russia (zoo)
O. heteroclita sp. inq.	Galliformes: cracid (nocturnal curassow), phasianid (Siamese fireback)	eye		Asia
O. podjapolskoi sp. inq.	Charadriiformes: scolopacid (wood sandpiper)	eye		Russia
O. wittei sp. inq.	Passeriformes: corvid (Eurasian magpie)	eye		Africa

Parasite morphology: *Oxyspirura* spp. form 3 different morphological stages in their developmental cycles: eggs; larvae (4 stages designated L1 to L4); and adult worms. The eggs are smooth-shelled, ovoid measuring 55-60 x 40-45 µm, and embryonated when laid. First-stage larvae (L1) freed from eggs have elongate cylindrical bodies measuring 145-235 µm but lack any distinct internal organs. L2 are larger, measuring 625-770 µm, and have a well-developed oesophagus and intestines. L3 are larger still, measuring up to 7.0-8.5 mm, and they have developed 6 lobes around the mouth and distinct cells surrounding the anterior end of the oesophagus. L4 have grown to 10-12 mm in length and the intestines have been laterally displaced by genital primordia, but males have not yet formed spicules and females have only formed incomplete ovaries. Adults are slender white worms measuring 9-20 mm in length with smooth cuticles usually lacking lateral alae (present only in members of the subgenus *O.* (*Barusispirura*)). They have simple mouth openings (surrounded by a sclerotized ring in the subgenus *O.* (*Molinospirura*)), globular buccal capsules (only divided into anterior and posterior chambers in the subgenera *O.* (*Oxyspirura*) and *O.* (*Caballeroispirura*)), tubular intestines, and pointed tails. Adults are sexually dimorphic, with male worms being smaller than females (9-16 cf. 12-20 mm). Mature males have ventrally curved tails, a gubernaculum present only in the subgenus *O.* (*Caballeroispirura*) and sometimes in the subgenera *O.* (*Oxyspirura*) and *O.* (*Hamulofilaria*), and 2 unequal spicules which similar in the subgenera *O.* (*Molinospirura*) and *O.* (*Cramispirura*), but dissimilar in the subgenera *O.* (*Oxyspirura*), *O.* (*Barusispirura*), *O.* (*Hamulofilaria*), and *O.* (*Caballeroispirura*) (right spicule short and stubby, left spicule long and slender). Mature female worms are didelphic with 2 large ovaries and uteri (often filled with eggs) connected via an ovejector (sometimes dilated) to a common vulva located in the posterior half of the body.

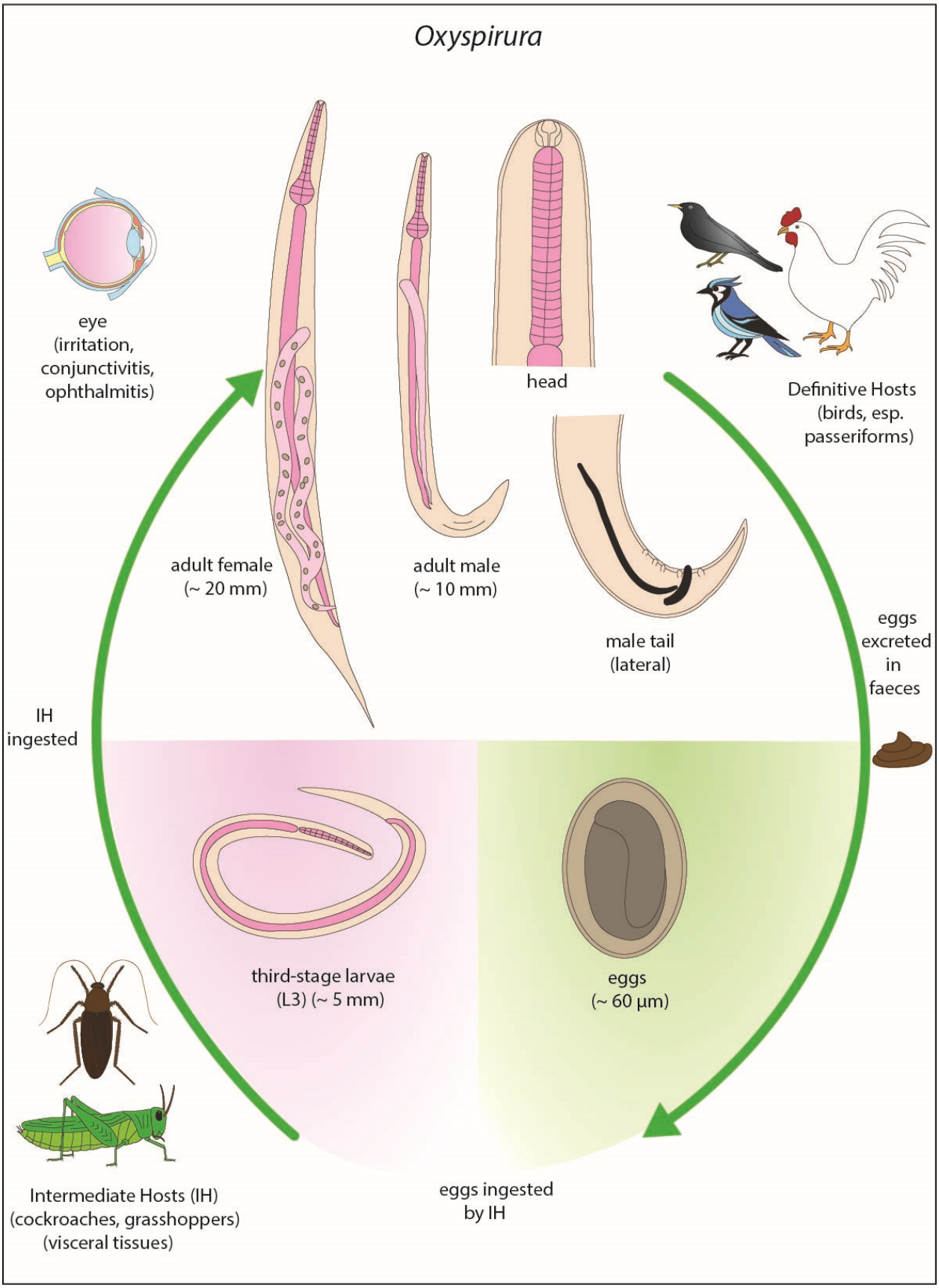
Site of infection: Adult eye-worms infect the eyes of their avian hosts, being found around the orbit on the corneal surface under the nictitating membrane, and in conjunctival sacs, nasolacrimal ducts, and sometimes nasal sinuses. Larval stages develop in capsules in the tissues of invertebrate intermediate hosts (insects, especially cockroaches).

Pathogenesis: Infections are mostly benign and have not been associated with disease in domestic or wild birds (somewhat counter-intuitively when relatively large worms are found in such small eyes). In poultry flocks, a few individual birds tend to be infected, rather than large numbers of birds. Nonetheless, clinical disease may occur in heavy and/or chronic infections. The worms are secretophagous and consume ocular secretions and their movements cause local irritation, exacerbated as birds attempt to relieve the discomfort by scratching. The resultant inflammation produces watery inflamed eyes with excessive lachrymation, conjunctivitis and ophthalmitis. The nictitating membrane may become swollen and flicker constantly, or the eyelids may become stuck together with thick viscous material which may also occlude the nasal passages. Birds become restless and exhibit photophobia. In severe cases, ulceration and erosion of the eyeball may destroy sight completely. Chronic infections are also thought to predispose to secondary bacterial infections.

Developmental cycle and mode of transmission: *Oxyspirura* spp. have indirect heteroxenous life-cycles whereby infections in birds are transmitted via insect intermediate hosts. Gravid female worms lay embryonated eggs in lachrymal secretions which pass through the lachrymal duct to the oral cavity and are swallowed and excreted in host faeces. The eggs survive in moist environments for short periods and are ingested by insects (cockroaches, grasshoppers) which act as intermediate hosts supporting larval development. Ingested eggs hatch in the insect gut releasing the L1 which penetrate the gut wall and enter the haemocoel around 10-14 days. The larvae become encysted in 17-18 days within insect tissues, mainly fat bodies but also Malpighian tubules and intestines, where they moult twice to form L3 by 42-52 days. Birds become infected when they eat insects containing infective L3 which are released in the gut and migrate along the oesophagus, pharynx and mouth to the lachrymal duct and then the eyes (this migration has been observed to be very fast and may occur within 20 minutes). The larvae moult to L4 after 3-5 days and then to subadults (sometimes referred to as L5) around 15-19 days. They mature to sexually reproductive adult worms in several weeks and the prepatent period (time from infection to first excretion of eggs) ranges from 21-48 days for most species, but can be extended up to 86 days in other species.

Differential diagnosis: Infections in birds may be suggested by clinical ocular signs (lachrymation, conjunctivitis), but most diagnoses are made by the direct detection of adult worms under the nictitating membrane or in the conjunctival sac during observation or handling. In the absence of visible adult worms, lachrymal secretions and faecal samples may be examined microscopically for eggs/larvae, although detection rates are often low. Molecular biological techniques have been used to examine parasite phylogeny by polymerase chain reaction (PCR) amplification of nuclear gene sequences (internal transcribed spacer region 2 of ribosomal RNA).

Treatment and control: Infections have conventionally been treated by the physical removal of eye-worms using fine forceps under local anaesthesia, and then the topical application of antiseptics, antibiotics, and sometimes steroidal anti-inflammatory drugs. Although few detailed chemotherapeutic studies have been conducted, several anthelmintic drugs have proven effective when applied topically or orally, including imidazothiazoles (levamisole, tetramisole) and macrocyclic lactones (ivermectin). Preventive strategies appropriate to poultry and aviary industries involve breaking transmission cycles through improved sanitation and hygiene (removal of faeces/litter, cleaning cages, providing dry bedding) and controlling insect vector populations (using exclusion barriers/screens, insect repellents, insecticides), However, care should be taken to only use approved products in poultry facilities.


Oxyspirura
eye
(irritation,
conjunctivitis,
ophthalmitis)
adult female
(~ 20 mm)
adult male
(~ 10 mm)
head
male tail
(lateral)
Definitive Hosts
(birds, esp.
passeriformes)
eggs
excreted
in
faeces
IH
ingested
third-stage larvae
(L3) (~ 5 mm)
eggs
(~ 60 µm)
Intermediate Hosts (IH)
(cockroaches, grasshoppers)
(visceral tissues)
eggs ingested
by IH

Oxyspirura adult worms in eye of bird

Oxyspirura worm eggs

Oxyspirura adult worm, head