

Choanotaenia

(platyhelminth: cestode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Cestodes (tapeworms) have elongate ribbon-like bodies ranging from a few millimetres to several metres in length. Cyclophyllidean tapeworms are usually intestinal parasites of terrestrial vertebrates and have an anterior scolex (hold-fast organ with suckers and sometimes hooks) and a posterior tape (strobila) made up of segments (proglottids). Adult worms lack a gut (they absorb nutrients) and they are hermaphroditic (segments containing both male and female reproductive organs). Eucestodes have indirect life-cycles involving oncospheres (hexacanth embryos) released from ingested eggs to form encysted larval stages (metacestodes) in the tissues of intermediate hosts and their transmission to definitive hosts by predation. Adult dilepidids usually have an armed rostellum and are parasitic in poultry but are rarely pathogenic. The encysted larval stages (cysticercoids) of *Choanotaenia* spp. occur in house flies, beetles and grasshoppers which are consumed during foraging.

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: Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)

Phylum: Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)

Clade: Neodermata (syncytial tegument = neodermis)

Class: Cestoda (tapeworms, gut absent, anterior scolex, proglottid segments, heteroxenous, predator-prey cycles)

Subclass: Eucestoda (larvae hexacanth (with six hooks))

Order: Cyclophyllidea (terrestrial species, scolex with four suckers, often bearing hooks, eggs release oncospheres)

Family: Dilepididae (tapeworms of dog/cat and fowl, scolex usually armed, genital pores alternate, some with paired genitalia, cysticercoid larva)

Genus: *Choanotaenia* (parasitic in small intestines of birds)

Species: various species cause enteritis in chickens

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 do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The cestodes (or tapeworms) lack digestive tracts and have elongate ribbon-like bodies (strobila); most being polyzoic (segmented) divided internally and/or externally into proglottids, although some are monozoic (unsegmented). Serial proglottids may be craspedote (overlapping) or acraspedote. Proglottids are generally hermaphroditic, possessing both male and female reproductive organs (those in which the male system matures first are protandrous, those in which the female system matures first are progynous). Terminal proglottids may detach from the strobila when they are immature (hyperapolytic), mature (euapolytic) or gravid (apolytic), or remain attached until they degenerate (anapolytic). Cestodes possess remarkable anterior attachment organs on the head (scolex): many divided into 4 membrane-bound muscular acetabula evident as suckers or bothridia (stalked, fused or bearing loculi); others bearing two weakly muscular bothria; some possessing a simple apical funnel (monobothriate); and some

with a complex apical organ or rostellum that may be retractable, armed with hooks or bearing tentacles. Fertile tapeworms produce eggs in which larval stages develop as non-ciliated oncospheres or ciliated coracidia or lycophores. These stages possess 6 or 10 hooks which they use to invade the tissues of intermediate hosts where they form encysted metacestode stages: either alacunate forms (proceroid with tail-like cercomer, plerocercus with retracted scolex, plerocercoid with an everted scolex, or merocercoid with an invaginated scolex) or lacunate forms (cysticercoid with cercomer and a retracted scolex, or cysticercus with an invaginated scolex). Two main cestode subclasses are recognized: Cestodaria with decacanth larvae (with 10 hooks) and Eucestoda with hexacanth larvae (with 6 hooks). The Eucestoda are divided into 17 orders on the basis of many morphological and biological differences, many groups being well supported by contemporary molecular characterization studies. Acetabulate orders (with bothridia) include Lecanicephalidea, Tetrphyllidea, Proteocephalidea, Cyclophyllidea, Tetrabothriidea, Phyllobothriidea and Rhinebothriidea; those bearing bothria include Bothriocephalidea, Caryophyllidea, Diphyllidea, Diphyllbothriidea, Haplobothriidea, Spathebothriidea and Trypanorhyncha; while others with apical pads/suckers include Cathetocephalidea, Litobothriidea and Nippotaeniidea.

Order (+ no. families)	No. spp.	DH ^a	Scolex	IH1 ^b	Stage ^d	IH2 ^c	Stage ^d
Class: Cestoda (tapeworms, without gut, monoecious, endoparasites, heteroxenous, predator-prey cycles)							
monozoic (unsegmented)							
Subclass: Cestodaria (adult lacking scolex, larvae decacanth (with 10 hooks))							
Gyrocotylidea (1)	10	F,S,L	muscular sucker-like organ	-	-	-	-
Amphilinidea (1)	8	F,P	muscular proboscis, or absent	C	pro	-	-
Subclass: Eucestoda ('true' tapeworms, adult with variable scolex; larvae hexacanth (with six hooks))							
Caryophyllidea (4)	122	F	acetabula, loculi, bothria, apical disc or polymorphic	W	pro		
polyzoic (segmented)							
Cathetocephalidea (1)	6	S	apical pad, papillary band				
Diphyllidea (2)	59	S,R	2 bothria; armed rostellum	C,L	ple		
Trypanorhyncha (16)	315	S,R	2 or 4 bothria, 4 tentacles	C	pro	F,C,L	ple, plc
Litobothriidea (1)	9	S	apical sucker, 3-5 segments				
Lecanicephalidea (3)	90	S,R	4 suckers or bothridia, and apical structure or tentacles	C,L,F	pro		
Rhinebothriidea (4)	136	R	4 stalked loculate bothridia	C	pro	F	ple
"Tetrphyllidea" relics (6)	104	S,R,M	4 stalked bothridia	C	pro	F,L,C, M	ple, mer
Spathebothriidea (4)	6	F	undifferentiated or 1-2 bothria	C	ple		
Haplobothriidea (1)	2	F	club-shaped, tentacles, bothria	C	pro	F	ple
Bothriocephalidea (7)	132	F,A	2 bothria	C	pro	F	ple
Nippotaeniidea (1)	6	F	single sucker	C			
Tetrabothriidea (1)	70	B,M	4 muscular bothridia	C,F			
Phyllobothriidea (1)	69	S,R	unarmed bothridia, apical suckers	C,F	ple		
Oncoprotocephalidea (2)	562	F,A,P,S,R	4 loculate bothridia, rostellum	C	pro	F	ple
Diphyllbothriidea (6) (= Pseudophyllidea)	70	M,B,P,A	2 shallow bothria, unarmed	C	pro	F,A,P, M	ple
Cyclophyllidea (16) (incl. Mesocestoididae)	3,034	M,B,P	4 suckers, rostellum, often armed	M,A,B, L,T,I	ccc, ccs	-	-
LEGEND							
^a DH = definitive host; ^b IH1 = first intermediate host; ^c IH2 = second intermediate host;							
[A = amphibian; B = bird; C = crustacean; F = teleost; I = insect; L = mollusc; M = mammal, P = reptile; R = ray; S = shark; T = acarine; W = annelid];							
^d Metacestode: pro = proceroid, plc = plerocercus; ple = plerocercoid, mer = merocercoid; ccc = cysticercoid; ccs = cysticercus, coenurus, strobilocercus or hydatid cyst							

Cyclophyllidean cestodes are polyzoic containing from 2 to > 1,000 proglottids demarcated by external segmentation. They possess an anterior scolex with 4 suckers, many with a rostellum (often armed), and they have compact post-ovarian vitellaria. Adult worms are found in terrestrial vertebrate definitive hosts (mammals, birds, reptiles, amphibians) while larval metacestodes occur in vertebrate (mammal, amphibian, bird) or invertebrate (mollusc, acari, insect) intermediate hosts. Over 3,000 species have been described in 400 genera in 16 families: Acoleidae, Amabiliidae, Anoplocephalidae, Catenotaeniidae, Davaineidae, Dioecocestidae, Dilepididae, Dipylidiidae, Gyrporhynchidae, Hymenolepididae, Mesocestoididae, Metadileptidae, Nematotaeniidae, Paruterinidae, Progynotaeniidae, and Taeniidae (all with lateral genital pores, except the Mesocestoididae).

Over 120 dilepidid genera have been described as intestinal parasites of birds and some carnivores. Adult tapeworms usually possess an armed scolex and the genital pores alternate in their lateral location on consecutive proglottids. Larval stages (cysticercoids) are formed in invertebrate intermediate hosts which are ingested when the definitive hosts feed. The genus *Choanotaenia* contains over 110 nominal species, most parasitizing wild and domestic birds throughout the world, particularly gallinaceous (chickens, turkeys, pheasant, quail) and passerine birds (finches). Cysticercoid stages have been recorded in a diverse range of insects (flies, locusts, beetles, ants, termites). Several attempts have been made to revise generic identities and it was recently proposed that the genus *Choanotaenia* retain only those species with a single crown of rostellar hooks (most species being parasitic in galliform birds) while others with a double crown of rostellar hooks and atrial tufts of bristle-like spines be transferred to the genus *Spiniglans* (most species being parasitic in passeriform birds). Many other genera and species remain to be revised.

<i>Choanotaenia</i> species	Definitive host [adults in small intestines]	Intermediate hosts [cysticercoids in tissues]	Distribution
<i>C. abassenae</i>	Passeriformes: sturnid (superb starling)		Africa
<i>C. acridotheresi</i>	Passeriformes: sturnid (common myna, bank myna)		India
<i>C. angolensis</i>	Passeriformes: pittid (African pitta)		Africa
<i>C. arctica</i>	Charadriiformes: scolopacid (sandpiper)		Europe
<i>C. arquata</i>	Charadriiformes: scolopacid (Eurasian curlew)		Europe
<i>C. asymetrica</i>	Caprimulgiformes: caprimulgid (nightjar)		South America
<i>C. atopa</i>	Carnivora: felid (cat)		North America
<i>C. aurantina</i>	Charadriiformes: larid (river tern)		Asia
<i>C. aurti</i>	Charadriiformes: burhinid (Eurasian stone-curlew)		India
<i>C. baicalensis</i>	Eulipotyphla: soricid (long-clawed shrew)		Japan
<i>C. barbara</i>	Passeriformes: passerid (Eurasian tree sparrow)		Europe
<i>C. bhattacharai</i>	Anseriformes: anatid (garganey)		India
<i>C. campanulata</i>	Opisthocomiformes: opisthocomitid (hoatzin)		South America
<i>C. cayennensis</i>	Charadriiformes: charadriid (southern lapwing)		Americas, Africa
<i>C. chandleri</i>	Charadriiformes: charadriid (red-wattled lapwing)		Europe
<i>C. cholodkowskyi</i>	Passeriformes: alaudid (Eurasian skylark)		Eurasia
<i>C. cingulifera</i>	Charadriiformes: scolopacid (common redshank)		Europe
<i>C. constricta</i> (syn <i>Anomotaenia</i>)	Passeriformes: icterid (white-browed meadowlark), turdid (Eurasian blackbird), corvid (grey crow, Eurasian magpie)		Holarctic
<i>C. crassitestata</i>	Piciformes: ramphastid (lettered aracari)		South America
<i>C. croaxum</i>	Passeriformes: corvid (house crow)		India
<i>C. cylindrocephala</i>	Passeriformes: corvid (western jackdaw)		Europe
<i>C. dispar</i> (syn. <i>Dictymetra volvulus</i>)	Charadriiformes: charadriid (yellow-wattled lapwing)		India
<i>C. dogieli</i>	Charadriiformes: scolopacid (great knot)		Eurasia
<i>C. estavarensis</i>	Eulipotyphla: soricid (Eurasian water shrew)		Eurasia
<i>C. falsificata</i>	Charadriiformes: burhinid (Eurasian stone curlew)		Egypt
<i>C. fortunata</i>	Ciconiiformes: ciconiid (white stork)		Europe
<i>C. fotedari</i>	Passeriformes: sturnid (common myna)		Asia
<i>C. fuhrmanni</i>	Accipitriformes: accipitrid (cinereous harrier)		South America
<i>C. galbulae</i>	Columbiformes: columbid (laughing dove); Passeriformes: corvid (house crow)		India, Pakistan
<i>C. globulus</i>	Charadriiformes: scolopacid (green sandpiper)		Africa, Europe
<i>C. gondwana</i>	Columbiformes: columbid (laughing dove); Passeriformes: passerid (common sparrow)		India
<i>C. hypoleucia</i>	Charadriiformes: scolopacid (common sandpiper)		India
<i>C. ibanezi</i>	Charadriiformes: scolopacid (whimbrel)		North America

<i>C. infundibulum</i> (syn. <i>C. infundibuliformis</i>)	Galliformes: phasianid (chicken, turkey, pheasant, common quail, Japanese quail, California quail, rock partridge); Columbiformes: columbid (pigeon, laughing dove); Accipitriformes: accipitrid (black kite, brown hawk)	Diptera: muscid (<i>Musca domestica</i> , <i>Stomoxys calcitrans</i>); Coleoptera: geotrupid (<i>Geotrupes sylvaticus</i>), carabid (<i>Amara fallax</i> , <i>Anaferonia constricta</i> , <i>Cratacanthus dubius</i> , <i>Stenocellus debilipes</i> , <i>Stenolophus conjunctus</i> , <i>Calathus</i> , <i>Hyarpalus indicus</i>), ostomid (<i>Tenebroides mauritanicus</i>), tenebrionid (<i>Alphitophagus bifasciatus</i> , <i>Tribolium castaneum</i>), staphylinid (<i>Apocellus sphaericollis</i>), scarabaeid (<i>Ataenius cognatus</i> , <i>Aphodius granarius</i> , <i>Geotrupes sylvaticus</i>), dermestid (<i>Dermester ater</i>), anthicid (<i>Anthicus confucii</i>); Orthoptera: acridid (<i>Dicromorpha viridis</i> , <i>Melanoplus femurrubrum</i> , <i>Spathosternum prasiniferum</i> , <i>Hieroglyphus nigrorepletus</i>), tettigoniid (<i>Conocephalus pallidus</i> , <i>Hexacentrus munda</i>)	worldwide
<i>C. intermedia</i>	Charadriiformes: scolopacid (giant snipe)		South America
<i>C. intestinalis</i>	Charadriiformes: charadriid (red-wattled lapwing)		India
<i>C. isacantha</i>	Passeriformes: emberizid (bunting)		Europe
<i>C. joyeuxi</i>	Charadriiformes: scolopacid (Eurasian woodcock)		Eurasia, Africa
<i>C. kapurdiensis</i>	Charadriiformes: glareolid (cream-colored courser)		India
<i>C. khadgaonensis</i>	Charadriiformes: charadriid (red-wattled lapwing)		India
<i>C. larimarina</i>	Charadriiformes: larid (great black-backed gull)		Europe
<i>C. littoriae</i>	Strigiformes: strigid (scops owl)		Europe
<i>C. lobipluviae</i>	Charadriiformes: charadriid (yellow-wattled lapwing)		India
<i>C. macrocantha</i>	Charadriiformes: scolopacid (sandpiper)		America
<i>C. macrocephala</i>	Charadriiformes: scolopacid (Eurasian woodcock)		Japan
<i>C. magnicirrosa</i>	Passeriformes: sturnid (common myna)		Myanmar
<i>C. malaconoti</i>	Passeriformes: malaconotid (grey-headed bushshrike)		Africa
<i>C. manocapaci</i>	Cuculiformes: cuculid (groove-billed ani)		Americas
<i>C. manipurensis</i>	Charadriiformes: charadriid (yellow-wattled lapwing), scolopacid (snipe)		India
<i>C. marchali</i>	Charadriiformes: larid (gull)		Eurasia
<i>C. megacantha</i>	Charadriiformes: scolopacid (common sandpiper)		Palaearctic
<i>C. megistacantha</i>	Charadriiformes: burhinid (Senegal thick-knee)		Africa
<i>C. meridionalis</i>	Charadriiformes: larid (kelp gull, brown-hooded gull)		South America
<i>C. microphallos</i> (syn. <i>Anomotaenia</i>)	Charadriiformes: charadriid (northern lapwing), scolopacid (long-toed stint)		Europe, North America
<i>C. mollis</i>	Accipitriformes: accipitrid (black kite)		India
<i>C. multitesticularis</i>	Eulipotyphla: soricid (Chinese mole shrew)		Asia
<i>C. musculosa</i>	Passeriformes: fringillid (common chaffinch),		Europe

	sturnid (common starling), muscicapid (European pied flycatcher)		
<i>C. nebraskensis</i>	Rodentia: cricetid (prairie vole), sciurid (western fox squirrel)		North America
<i>C. nilotica</i>	Charadriiformes: glareolid (cream-colored courser)		Europe, Africa
<i>C. oriolii</i>	Passeriformes: sturnid (common myna)		India
<i>C. pandei</i>	Passeriformes: pycnonotid (red-vented bulbul)		India
<i>C. paranumenii</i>	Charadriiformes: scolopacid (long-billed curlew)		North America
<i>C. passerellae</i>	Passeriformes: passerellid (fox sparrow)		North America
<i>C. pauciannulata</i>	Caprimulgiformes: caprimulgid (nacunda nighthawk)		South America
<i>C. perisorei</i>	Passeriformes: corvid (Siberian jay)		Eurasia
<i>C. peromysci</i>	Rodentia: cricetid (North American deer mouse)		North America
<i>C. platycephala</i>	Passeriformes: alaudid (Eurasian skylark, crested lark), motacillid (tawny pipit, meadow pipit, water pipit, tree pipit, western yellow wagtail), locustellid (river warbler), muscicapid (common redstart, European stonechat, northern wheatear), sylviid (Eurasian blackcap, lesser whitethroat, western Orphean warbler, barred warbler)		Europe
<i>C. plegadis</i>	Charadriiformes: scolopacid (marsh sandpiper)		Eurasia
<i>C. polyorchis</i>	Falconiformes: falconid (lesser kestrel, common kestrel)		Africa, Europe
<i>C. prinopsia</i> (syn. <i>Anomotaenia</i>)	Passeriformes: vangid (straight-crested helmetshrike)		Africa
<i>C. prunellae</i>	Passeriformes: prunellid (alpine accentor)		Japan
<i>C. ratticola</i>	Rodentia: murid (bush rat)		Australia
<i>C. rhynchopis</i>	Charadriiformes: larid (black skimmer)		South America
<i>C. ridibundum</i>	Charadriiformes: larid (black-headed gull)		Europe
<i>C. rostellata</i>	Charadriiformes: recurvirostrid (black-necked stilt)		Americas
<i>C. sciuricola</i>	Rodentia: sciurid (fox squirrel)		North America
<i>C. scolopacina</i>	Charadriiformes: scolopacid (Eurasian woodcock)		Europe
<i>C. scythica</i>	Galliformes: phasianid (pheasant)		Russia
<i>C. shohoi</i>	Galliformes: phasianid (chicken)		China
<i>C. singhii</i>	Charadriiformes: charadriid (red-wattled lapwing)		India
<i>C. skrjabini</i>	Charadriiformes: charadriid (common ringed plover)		Eurasia
<i>C. slesvicensis</i>	Charadriiformes: scolopacid (Eurasian woodcock)		Eurasia
<i>C. sonoti</i>	Passeriformes: sturnid (common myna, jungle myna, Brahminy myna)		India
<i>C. southwelli</i>	Charadriiformes: charadriid (yellow-wattled lapwing)		India
<i>C. spasskii</i>	Eulipotyphla: talpid (large mole)		Eurasia
<i>C. speotytonis</i>	Strigiformes: strigid (western burrowing owl)		North America
<i>C. spermophili</i> (syn. <i>Prochoanotaenia</i>)	Rodentia: sciurid (thirteen-lined ground squirrel, Richardson's ground squirrel)		North America
<i>C. srivastavai</i>	Passeriformes: leiotherichid (black-winged babbler)		India
<i>C. stercoraria</i>	Charadriiformes: larid (gull)		Europe
<i>C. strigium</i>	Strigiformes: strigid (Eurasian scops owl)		Europe
<i>C. sylvarum</i>	Galliformes: phasianid (hazel grouse)		Russia
<i>C. tandani</i>	Passeriformes: muscicapid (blue whistling		India

	thrush)		
<i>C. taylori</i>	Passeriformes: malurid (superb fairywren)		Australia
<i>C. tetrastes</i>	Galliformes: phasianid (hazel grouse)		Eurasia
<i>C. thraciensis</i>	Charadriiformes: scolopacid (Eurasian woodcock)		Russia
<i>C. trapezoides</i>	Accipitriformes: accipitrid (great black-hawk)		South America
<i>C. tubirostellata</i>	Eulipotyphla: soricid (Chinese mole shrew)		Asia
<i>C. tugarinovi</i>	Passeriformes: muscicapid (African stonechat)		Africa
<i>C. ululae</i>	Strigiformes: strigid (spotted eagle-owl)		Africa
<i>C. upupae</i>	Bucerotiformes: upupid (African hoopoe)		Africa
Reassigned species			
<i>C. bilateralis</i> (now <i>Laterochites</i>)	Podicipediformes: podicipedid (least grebe)		Americas
<i>C. borealis</i> (now <i>Paricterotaenia</i>)	Anseriformes: anatid (mallard, common shelduck, long-tailed duck, common scoter)		Eurasia
<i>C. brevis</i> (now <i>Liga</i>)	Piciformes: picid (great spotted woodpecker)		Eurasia
<i>C. burhini</i> (now <i>Onderstpoortia taeniaeformis</i>)	Charadriiformes: burhinid (Eurasian stone-curlew)		India
<i>C. centuri</i> (now <i>Liga</i>)	Piciformes: picid (West Indian woodpecker)		Americans
<i>C. chionis</i> (now <i>Anomotaenia</i>)	Charadriiformes: chionid (snowy sheathbill)		Antarctica
<i>C. citrus</i> (now <i>Anomotaenia</i>)	Anseriformes: anatid (velvet scoter) Charadriiformes: scolopacid (common sandpiper, ruddy turnstone, common snipe, great snipe, pin-tailed snipe, dunlin, little stint, wandering tattler, black-tailed godwit, jack snipe, ruff, Eurasian woodcock, wood sandpiper, green sandpiper, Terek sandpiper, common redshank), charadriid (southern lapwing, little ringed plover, Oriental plover)	Gastropoda: succineid (<i>Succinea putris</i>)	Europe, Africa, Americas
<i>C. coronata</i> (now <i>Burhinotaenia</i>)	Charadriiformes: burhinid (Eurasian stone curlew)		Eurasia
<i>C. corvi</i> (now <i>Spiniglans constricta</i>)	Passeriformes: corvid (fan-tailed raven)		Africa
<i>C. crassiscolex</i> (now <i>Molluscotaenia</i>)	Eulipotyphla: soricid (common shrew, Eurasian water shrew, Eurasian pygmy shrew)	Gastropoda: oxychilid (<i>Oxychilus cellarius</i>), discid (<i>Goniodiscus (Discus) ruderatus</i>), gastrodontid (<i>Zonitoides nitidus</i>), succineid (<i>Succinea putris</i>), vitrinid (<i>Vitrina pellucida</i>), cochlicopid (<i>Cochlicopa lubrica</i>), bradybaenid (<i>Eulopa fruticum</i>), pristilomatid (<i>Vitrea contracta</i>), zonitid (<i>Schistophallus orientalis</i>), helcid (<i>Isognomostoma isognomostomos</i>); Coleoptera: scarabaeoid (<i>Geotrupes stercorosus</i>), silphid (<i>Silpha sinuata</i>)	Europe
<i>C. crateriformis</i> (now <i>Liga</i>)	Piciformes: picid (white-backed woodpecker, great spotted woodpecker, middle spotted woodpecker, black woodpecker, Eurasian wryneck)		Europe
<i>C. decacantha</i> (now <i>Fuhrmannolepis</i>)	Charadriiformes: scolopacid (dunlin)		Europe

<i>C. delachauxi</i> (now <i>Burhinotaenia</i>)	Charadriiformes: burhinid (stone curlew)		Europe
<i>C. discoidea</i> (now <i>Anomotaenia</i>)	Ciconiiformes: ciconiid (white stork)		Europe
<i>C. dodecakantha</i> (now <i>Paricterotaenia</i>)	Charadriiformes: larid (little gull)		Eurasia
<i>C. fieldingi</i> (now <i>Cracticotaenia</i>)	Passeriformes: artamid (grey butcherbird)		Australia
<i>C. filamentosa</i> (now <i>Rodentotaenia</i>)	Eulipotyphla: soricid (Eurasian water shrew), talpid (European mole)		Europe
<i>C. glareoli</i> (now <i>Kowalewskiella</i>)	Charadriiformes: scolopacid (wood sandpiper)		Sri Lanka
<i>C. guarti</i> (now <i>Panuwa</i>)	Charadriiformes: charadriid (little ringed plover)		Eurasia
<i>C. hepatica</i> (now <i>Rodentotaenia</i>)	Eulipotyphla: soricid (common shrew)		Europe
<i>C. hydrochelidonis</i> (now <i>Laritaenia</i>)	Charadriiformes: larid (black-headed gull)		Eurasia
<i>C. iola</i> (now <i>Sobolevitaenia</i>)	Passeriformes: turdid (American robin), icterid (western meadowlark, red-winged blackbird)		North America
<i>C. magnihamata</i> (now <i>Burhinotaenia</i>)	Charadriiformes: charadriid (yellow-wattled lapwing)		India
<i>C. meliphagidarum</i> (now <i>Ptilolepis</i>)	Passeriformes: meliphagid (New Holland honeyeater, white-cheeked honeyeater, white- eared honeyeater, yellow-eared honeysucker)		Australia
<i>C. micracantha</i> (now <i>Anomotaenia</i>)	Passeriformes: corvid (western jackdaw)		Eurasia
<i>C. microsoma</i> (now <i>Spiniglans</i>)	Passeriformes: emberizid (crested bunting), ploceid (Heuglin's masked weaver)		India
<i>C. mutabilis</i> (now <i>Cuclincola</i>)	Pelecaniformes: ardeid (black-crowned night heron)		Europe
<i>C. numenii</i> (now <i>Dictymetra</i>)	Charadriiformes: scolopacid (long-billed curlew)		North America
<i>C. parina</i> (now <i>Monosertum</i>)	Passeriformes: passerid (Eurasian tree sparrow), parid (great tit)		Europe
<i>C. passerina</i> (now <i>Icterotaenia</i>)	Passeriformes: passerid (common sparrow, Eurasian tree sparrow), parid (great tit)		Europe
<i>C. picusi</i> (now <i>Liga</i>)	Piciformes: picid (scaly-bellied woodpecker)		India
<i>C. pirinica</i> (now <i>Spiniglans</i>)	Passeriformes: corvid (Eurasian magpie)		Russia
<i>C. porosa</i> (now <i>Paricterotaenia</i>)	Charadriiformes: larid (black-headed gull, common gull, slender-billed gull); Passeriformes: sturnid (common starling)		Eurasia
<i>C. ransomi</i> (now <i>Paricterotaenia</i>)	Charadriiformes: larid (European herring gull, laughing gull, ring-billed gull, Bonaparte's gull, tern, kittiwake); Gaviiformes: gaviid (common loon)		Eurasia
<i>C. ricii</i> (now <i>Dictymetra</i>)	Ciconiiformes: ciconiid (Abdim's stork)		Africa
<i>C. scutigerum</i> (now <i>Monopylidium</i>)	Eulipotyphla: soricid (common shrew, greater white-toothed shrew)		Europe
<i>C. secunda</i> (now <i>Anomotaenia</i>)	Charadriiformes: charadriid (southern lapwing)		Americas
<i>C. sinensis</i> (now <i>Birovilepis</i>)	Passeriformes: eurylaimid (long-tailed broadbill)		Indochina
<i>C. soricina</i> (now <i>Molluscotaenia</i>)	Eulipotyphla: soricid (common shrew)		Eurasia
<i>C. spinosocapite</i> (now <i>Sobolevitaenia</i>)	Passeriformes: sturnid (common starling)		Europe
<i>C. stagnatildis</i>	Charadriiformes: scolopacid (marsh		Eurasia

(now <i>Kowalewskiella</i>)	sandpiper)		
<i>C. sternina</i> (now <i>Paricterotaenia</i>)	Charadriiformes: larid (common tern)		Holarctic
<i>C. triganciensis</i> (now <i>Fuhrmanolepis slesvicensis</i>)	Charadriiformes: scolopacid (Eurasian woodcock)		Eurasia
<i>C. tringae</i> (now <i>Onderstepoortia</i>)	Charadriiformes: scolopacid (sandpiper)		Africa
<i>C. uncinata</i> (now <i>Pseudochoanotaenia</i>)	Charadriiformes: scolopacid (lesser yellowlegs)		Americas
<i>C. unicoloronata</i> (now <i>Sobolevitaenia</i>)	Passeriformes: turdid (mistle thrush, common blackbird), muscicapid (northern wheatear)		Europe
<i>C. variabilis</i> (now <i>Anomotaenia</i>)	Charadriiformes: charadriid (northern lapwing, grey plover), scolopacid (common redshank, curlew sandpiper, dunlin, common snipe, American woodcock)		Holarctic
<i>C. zoniferae</i> (now <i>Polycerus</i>)	Charadriiformes: charadriid (banded lapwing)		Australia

Parasite morphology: *Choanotaenia* spp. form 3 different developmental stages: eggs, larvae (metacestodes) and adults. The eggs are ovoid measuring 35-54 µm in diameter and they contain a nonciliated hexacanth (6 hooked) embryo (oncosphere) surrounded by a non-striated shell (embryophore) and a delicate outer membrane with elongate polar processes (filaments which recede as the embryophore develops). Larval metacestodes appear as ovoid encysted stages (cysticercoids) measuring 120-600 µm in diameter. Cysticercoids are lacunate (with internal cavity) and they possess an anterior retracted scolex complete with rostellar hooks and a tail-like cercomer. Adult tapeworms appear as elongate white ribbons measuring from 4-25 cm long by 1-3 mm wide. The strobila (tape) is usually composed of not more than 30 proglottids, which are wider than long. The margins of the worm also have a saw-tooth appearance as the segments are wider posteriorly than anteriorly. The anterior scolex is small (150-500 µm long) and has 4 unarmed suckers (85-120 µm in diameter) surmounted by a large rostellum (130-230 µm long) armed with a single row of 16-22 thorn-shaped hooks (25-30 µm long) with long slender blades. There is still some debate as to the taxonomic classification of *Choanotaenia*-like species with other configurations of rostellar hooks (e.g. species with a double crown of rostellar hooks have recently been transferred to the genus *Spiniglans*). Adult tapeworms lack digestive tracts and each segment has specialized excretory cells known as flame cells (protonephridia). The tapeworms are hermaphroditic and each segment has one set of male and female reproductive organs with a common opening (genital pore) located at the anterior lateral margin. Genital pores of consecutive segments alternate sides irregularly. Proglottids have multiple testes (20-60), a cylindrical cirrus pouch, a lobed ovary and a saccular uterus that eventually form egg capsules each containing only one egg. The hindmost proglottids are gravid, bell-shaped and filled with eggs.

Site of infection: Most *Choanotaenia* spp. are found as adult tapeworms in the small intestines of birds belonging to over 12 orders, particularly Passeriformes and Charadriiformes, but also including domestic poultry. A growing number of species have been found in the intestines of mammalian hosts (shrews, rodents and felids). Larval metacestodes (cysticercoids) have been detected in the body cavities of many insects (flies, locusts, beetles, ants, termites).

Pathogenesis: Infections by most *Choanotaenia* spp. are not considered to be pathogenic as the tapeworms absorb nutrients from the gut lumen rather than feeding on host tissues. Nevertheless, several species have been associated with subclinical production losses in poultry enterprises by reducing feed conversion efficiency, retarding growth, reducing weight gain and decreasing egg production. Heavy infections by a few species have also been found to cause mild to severe clinical disease typified by enteritis, diarrhoea, weight loss, lethargy, apathy, depression and death, notably in poultry and aviary birds (e.g. finches). Histopathological changes have included catarrhal enteritis, vacuolation of epithelial cells, desquamation and atrophy of villi, inflammation and congestion of submucosal glands, and granuloma formation. Heavy infections are also thought to predispose towards concomitant infections by other infectious agents by lowering host resistance.

Developmental cycle and mode of transmission: Dilepidid tapeworms have indirect life-cycles alternating between 2 types of hosts; vertebrates acting as definitive hosts (infected by adult stages), and invertebrates (insects) acting as intermediate hosts (infected with larval stages). Mature tapeworms shed gravid proglottids which are passed with host faeces. These segments are highly motile and rapidly migrate from droppings into the surrounding environment. Here they are eaten by insects and digestive processes break down the proglottids releasing the contained eggs. The eggs hatch and the freed oncospheres actively penetrate host tissues to form larval cysticercoid stages in the insect body cavity. A diverse range of insects (flies, beetles, grasshoppers, locusts, ants, termites) have been found to act as intermediate hosts for *Choanotaenia* spp. When infected insects are eaten by birds or

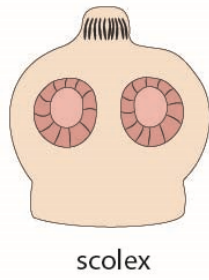
insectivorous mammals, the cysticercoids excyst and attach to the gut wall where they develop into adult tapeworms. The prepatent period (= time between infection and shedding of first eggs) is about 2-4 weeks and adult tapeworms generally do not live longer than one year. Infections are common in many bird species throughout the tropics where climatic conditions are conducive to parasite survival and the abundance of insect populations.

Differential diagnosis: Infections by *Choanotaenia* spp. are conventionally diagnosed by the detection of gravid segments in host faeces, preferably fresh droppings as the motile proglottids migrate out rapidly. Faecal concentration techniques (sedimentation and/or floatation) usually do not recover freed eggs as they remain within excreted segments. Adult tapeworms may be detected upon post-mortem examination of the intestinal mucosa.

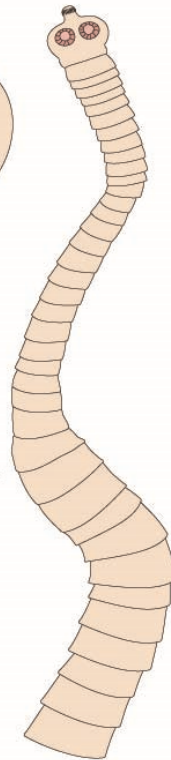
Treatment and control: Individual birds or flocks at risk may be treated for infections using specific cestodocides (niclosamide, praziquantel) or broad spectrum anthelmintics proven to be effective against cestodes, notably the benzimidazoles (albendazole, febantel, fenbendazole, mebendazole, oxfendazole). These drugs are often available as additives for drinking water or feed, but careful attention should be given to any contra-indications (e.g. niclosamide is toxic for geese, praziquantel plus pyrantel tartrate is toxic for chickens). Some measure of parasite control may also be afforded in domestic flocks or aviaries by improving bird housing conditions to exclude potential insect intermediate hosts, disposing of faecal material in a sanitary manner, storing feed in insect-proof containers, and reducing insect populations (using barriers, chemicals or biological control options). Obviously, few of these management strategies can be applied to wild bird populations, and the widespread use of insecticides should be discouraged for ecological reasons.

Choanotaenia

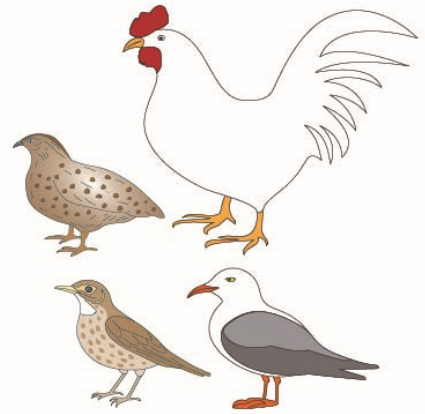
intestines
(rarely enteritis,
diarrhoea, depression)



scolex

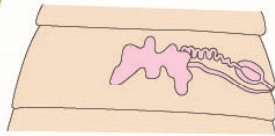


hermaphroditic
adults
(~ 4-25 cm)

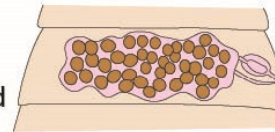


Definitive Hosts
(birds, esp. passeriforms,
charadriiforms and
galliforms)

transmission
through
ingestion
of infected
insects

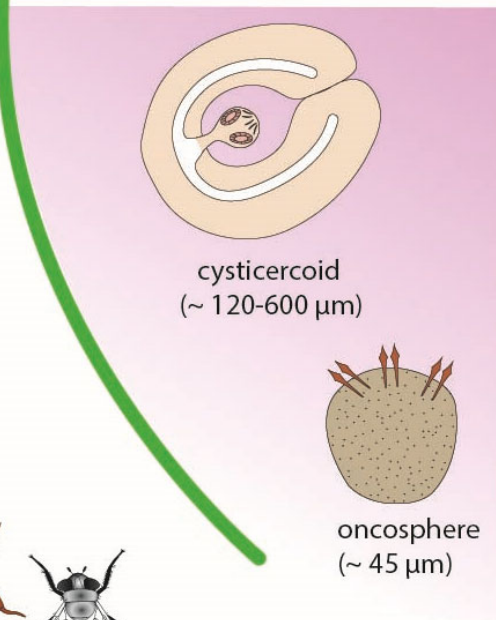


mature
proglottid



gravid
proglottid

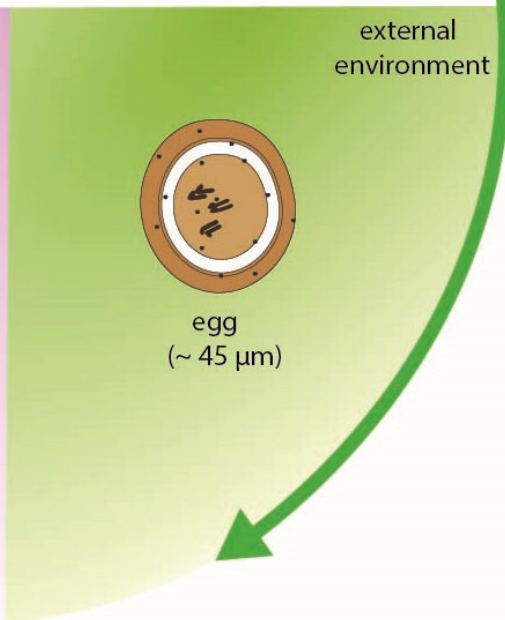
excretion
of eggs in
faeces



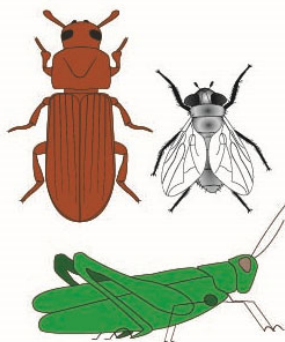
cysticercoid
(~ 120-600 μm)



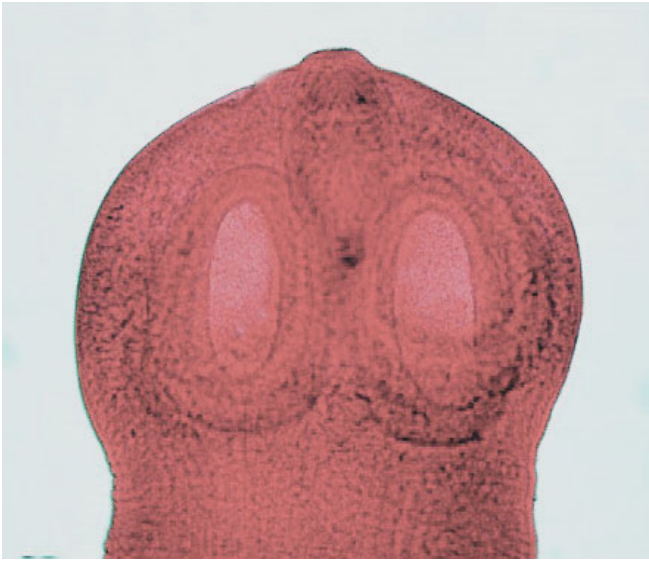
oncosphere
(~ 45 μm)



egg
(~ 45 μm)



Intermediate Hosts
(insects)
(body cavity)



Choanotaenia scolex



Choanotaenia worm egg