Taenia
(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 carnivorous definitive hosts. Adult taeniids have an armed rostellum (except *T. saginata*), elongate gravid segments and are rarely pathogenic. *Taenia* spp. form encysted larval stages (cysticerci, coenuri or strobilocerci) causing space-occupying lesions and disease in domestic animals and humans.

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:	Taeniidae (scolex often armed, proglottids with single genital pore, fluid-filled cystic metacestodes)
Genus:	*Taenia* (parasitic in intestines/tissues of carnivores/omnivores)
Species:	*T. saginata* (causes cysticercosis in cattle)
	T. solium (causes cysticercosis in pigs and humans)

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 (procercoid 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, Tetraphyllidea, Proteocephalidea, Cyclophyllidea, Tetrabothriidea, Phyllobothriidea and Rhinebothriidea; those bearing bothria include Bothriocephalidea, Caryophyllidea, Diphyllidea, Diphyllobothriidea, Haplobothriidea, Spathebothridea and Trypanorhyncha; while others with apical pads/suckers include Cathetocephalidea, Litobothridea 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
Litobothridea (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
"Tetraphyllidea' relics (6)	104	S,R,M	4 stalked bothridia	C	pro	F,L,C, M	ple, mer
Spathebothridea (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		
Oncoproteocephalidea (2)	562	F,A,P,S,R	4 loculate bothridia, rostellum	C	pro	F	ple
Diphyllobothridea (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 = procercoid, 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). Mature taeniid tapeworms have proglottids with unpaired reproductive organs and a single genital pore, and the scolex is often armed with hooks. Taeniids produce round non-operculated eggs with striated shells, the oncospheres are non-ciliated and they form fluid-filled cystic metacestodes (cysticercus, coenurus, strobilocercus, or hydatid cyst). Several genera (*Taenia* (*Multiceps, Taeniarhynchus*), *Hydatigera,*

Echinococcus, Versteria) have been reported predominantly in carnivorous definitive hosts (canids, felids, primates incl. humans) and herbivorous or omnivorous intermediate hosts (artiodactyls, lagomorphs, rodents, primates).

Over 40 *Taenia* spp. are found in carnivores and herbivores throughout the world. Many species appear to have two scientific names because the larval stages in herbivores were often named (as *Cysticercus*, *Strobilocercus* or *Coenurus* spp.) before it was realized they were developmental stages of adult *Taenia* tapeworms in carnivores. Several workers also proposed new generic names for species forming coenuri (*Multiceps*) or strobilocerci (*Hydatigera*) rather than cysticerci (*Taenia sensu stricto*). Molecular phylogenetic studies have provided some support for the latter proposal (recognizing the genus *Hydatigera*) as well as erecting a new genus *Versteria* for the enigmatic *T. mustelae* (and possibly *T. brachyacantha*). Many classifications continue to use the single genus *Taenia sensu lato* (in the broadest sense) with other genera listed as synonyms or subgenera pending further definitive studies. Three *Taenia* spp. form adult tapeworms in humans which thus act as definitive hosts (*T. solium, T. saginata, T. asiatica*), but humans may also be infected by larval (metacestode) stages of other species (mostly *T. solium*, but occasionally *T. crassiceps, T. multiceps, T. serialis* and rarely *T. taeniaeformis*). *T. solium* infections cycle between humans and pigs in many areas where pork products are common, including regions throughout South and Central America, Eastern Europe, South Africa, China and Indonesia. *T. saginata* infections cycle between humans and cattle in most pastoral (beef and dairy) areas throughout the world. *T. asiatica* (Asian taeniid) cycles between humans and pigs or cattle in several South-East Asian countries and was initially thought to be a strain of *T. saginata* but is now considered a separate species. *T. crassiceps* cycles between canids and rodents in countries in the Northern Hemisphere, although infections by larval stages have been recorded in several humans, mostly immunocompromised individuals. Species forming coenuri in domestic animals and rodents develop mainly in canids, while those forming strobilocerci in rodents develop in many small carnivores, such as felids and viverrids. Several other *Taenia* spp. have been described predominantly from adult worms recovered from wild carnivores throughout Africa, North America and Russia: including *T. polyacantha, T. parenchymatosa, T. ovata* and *T. retracta* from foxes and dogs; *T. acinonyxi, T. gonyamai, T. regis, T. ingwei, T. selousi, T. omissa, T. pseudolaticollis* (syn. *T. laticollis*) and *T. rileyi* from lions, cheetahs, leopards, wildcats, cougars and lynx; and *T. mustelae, T. martis, T. taxidiensis* and *T. secunda* from weasels, martens and badgers.

Taeniid species (synonyms) [metacestode synonyms]	**Definitive hosts (DH) [adults in small intestines] {clinical signs}**	**Intermediate hosts (IH) [metacestodes in tissues] {clinical signs}**	**Distribution**
Species forming cysticerci in IH			
T. acinonyxi	Carnivora: felid (leopard, cheetah)	Artiodactyla: bovid (impala, sable antelope, gerenuk, gemsbok, grey duiker, African buffalo), suid (warthog) [cysticercus in muscles]	Africa
T. arctos	Carnivora: ursid (brown bear)		Europe
T. arvicolae sp. inq.	Rodentia: cricetid (common vole)		Europe
T. asiatica (may be a subspecies of *T. saginata*) [syn. *Cysticercus viscerotropica*]	Primates: hominid (human) {occasionally diarrhoea}	Artiodactyla: bovid (cattle), suid (pig) [cysticercus in muscles] {carcase lesions}	Asia, Africa, Europe
T. brachyacantha (now *Versteria*)	Carnivora: mustelid (white-naped weasel)	Rodentia: murid (rats) [cysticercus in liver]	Africa
T. brevicollis sp. inq.	Carnivora: mustelid (stoat)		Eurasia
T. cervi (syn. *Cysticercus cervi*) (incl. *T. krabbei*) [syn. *Cysticercus tarandi*]	Carnivora: canid (wolf, fox, dog)	Artiodactyla: cervid (deer, reindeer) [cysticercus in muscles] {carcase lesions}	worldwide
T. crassiceps (syn. *T. hyperborea*) [syn. *Cysticercus longicollis*]	Carnivora: canid (Arctic fox, red fox, wolf, coyote, dog), felid (wild cat, lynx), mustelid (beech marten)	Rodentia: murid (mice, rats), cricetid (Arctic lemming, brown lemming, collared lemmings, common vole, northern water vole, Tundra vole, social vole, meadow vole, muskrat, hamster), sciurid (marmot, groundhog, chipmunk, squirrel, sousliks); Eulipotyphla: talpid (common mole); Lagomorpha: leporid (hare); rarely Primates: hominid (human) [cysticercus in abdominal cavity, subcutaneous tissues, muscles]	Northern Hemisphere
T. crocutae	Carnivora: hyaenid (spotted hyaena, brown hyaena)	Artiodactyla: bovid (Ugandan kob, impala, Lelwel hartebeest, hartebeest, blue wildebeest, sassaby, topi, roan antelope,	Africa

		sable antelope, lechwe, gemsbok, southern reedbuck, giant eland, kewel, Grant's gazelle, greater kudu, common duiker, African buffalo); occasionally Primates: cercopithecid (baboon) [cysticercus in muscles]	
T. dinniki	Carnivora: hyaenid (spotted hyaena, striped hyaena)	unknown	Africa
T. gonyamai (syn. *T. hlosei*)	Carnivora: felid (lion, cheetah)	Artiodactyla: bovid (hartebeest, blue wildebeest) [cysticercus in muscles, lymph nodes, lungs]	Africa
T. hyaenae (syn. *T. lycaontis*) [syn. *Cysticercus dromedarii*]	Carnivora: hyaenid (hyaena), canid (African wild dogs)	Artiodactyla: camelid (camel), bovid (cattle, zebu, African buffalo, goat, sheep, kob, Lelwel hartebeest, Grant's gazelle, Thomson's gazelle, Soemmerring's gazelle, roan antelope, common duiker, giant eland, kewel) [cysticercus in muscle, liver]	Africa
T. hydatigena (syn. *T. jakhalsi*) (false hydatid worm) [syn. *Cysticercus tenuicollis*]	Carnivora: canid (dog, red fox, wolf, coyote, black-backed jackal, golden jackal), hyaenid (hyaena), felid (cougar, bobcat, lion), ursid (grizzly bear), mustelid (weasel, stoat, polecat)	Artiodactyla: bovid (sheep, mouflon, goat, chamois, cattle, muskox, blue duiker, goitered gazelle), cervid (deer, moose, mule deer, white-tailed deer, Rocky Mountain elk, roe deer, fallow deer, red deer, reindeer), suid (pig); Perissodactyla: equid (horse); Rodentia: castorid (Eurasian beaver), aplodontid (mountain beaver); Carnivora: ursid (black bear), mustelid (beech marten); Primates: cercopithecid (vervet monkey, African red monkey) [cysticercus in peritoneum, liver]	worldwide
T. ingwei	Carnivora: felid (leopard)		Africa
T. ingwei	Carnivora: felid (leopard)		Africa
T. jaipurensis	Carnivora: felid (lion)		Asia
T. madoquae [syn. *Cysticercus madoquae*]	Carnivora: canid (silver-backed jackal, dog)	Artiodactyla: bovid (Gunther's dik-dik) [cysticercus in muscles]	Africa
T. martis (incl. *T. m. martis* and *T. m. americana*)	Carnivora: mustelid (European pine marten, American pine marten, beech marten, European polecat, American mink, stoat, weasel, fisher), procyonid (ringtail cat), felid (wild cat)	Rodentia: cricetid (bank vole, field vole, Siberian brown lemming, taiga vole, muskrat, European pine vole), murid (mouse, striped field mouse) [cysticercus in body cavity]	Europe, North America
T. melesi sp. inq.	Carnivora: mustelid (European badger)		Europe
T. mustelae (syn. *T. parviuncinatus*) (now *Versteria*)	Carnivora: mustelid (stoat, weasel, Siberian weasel, mountain weasel, Steppe polecat, European pine marten, beech marten, sable, mink, ferret), mephitid (skunk)	Rodentia: murid (house mouse, wood mouse, kleinwuhlmaus, brown rat), sciurid (red squirrel, grey squirrel, fox, squirrel, Daurian ground squirrel, Franklin's ground squirrel, white-tailed prairie dog, groundhog, eastern chipmunk, least chipmunk, Alaska marmot, hoary marmot), cricetid (deer mouse, white-footed mouse, muskrat, common vole, social vole, tundra vole, Major's pine vole, snow vole, field vole, meadow vole, singing vole, Schidlovsky's vole, northern water vole, grey red-backed vole, southern red-backed vole, northern red-backed vole, bank vole, northern bog lemming, southern bog lemming, brown lemming, hamster), dipodid (meadow jumping mouse), aplodontid (mountain beaver)	North America, Europe, Mongolia

		[cysticercus in viscera]	
T. olnojinei	Carnivora: hyaenid (spotted hyaena, striped hyaena)	Artiodactyla: bovid (hartebeest, blue wildebeest, topi, Grant's gazelle) [cysticercus in sacral epidural space]	Africa
T. omissa	Carnivora: felid (cougar, oncilla, jaguarundi)	Artiodactyla: cervid (white-tailed deer, mule deer, brocket deer) [cysticercus in lungs, pericardium]	Americas
T. ovis (sheep measles worm) (syn. *T. krabbei, T. rangifer*) (incl. *T. o. ovis, T. o. krabbei*) [syn. *Cysticercus ovis*]	Carnivora: canid (dog, wolf, coyote, Arctic fox, red fox), felid (cougar), ursid (black bear, brown bear) {sometimes diarrhoea}	Artiodactyla: bovid (sheep, mouflon, bighorn sheep, goat, goitered gazelle), antilocaprid (pronghorn), cervid (roe deer, red deer, fallow deer, mule deer, reindeer, caribou, elk, moose) [cysticercus in muscles] {carcase lesions}	worldwide
T. parenchymatosa	Carnivora: canid (dog, Arctic fox)	Artiodactyla: cervid (reindeer, red deer) [cysticercus in viscera]	Russia
T. pencei	Carnivora: procyonid (ring-tailed cat)		North America
T. pisiformis (syn. *T. serrata, T. novella, T. utricularis*) [syn. *Cysticercus pisiformis*]	Carnivora: canid (dog, wolf, red wolf, red fox, Arctic fox, grey fox, golden jackal, black-backed jackal, coyote, African wild dog), felid (bobcat, Canada lynx, wild cat, oncilla, lion, leopard), mustelid (polecat)	Lagomorpha: leporid (rabbit, black-tailed jackrabbit, white-tailed jackrabbit, marsh rabbit, snowshoe hare, Cape hare, European hare, Abyssinian hare, Tolai hare, mountain hare, desert cottontail, eastern cottontail, mountain cottontail, New England cottontail, tapeti); Rodentia: murid (house mouse, yellow-necked mouse, brown rat, black rat), sciurid (fox squirrel), cricetid (bank vole, common vole, muskrat), caviid (guinea pig) [cysticercus in peritoneum, liver] {occasionally hepatitis}	worldwide
T. polyacantha (incl. *T. p. arctica, T. p. polyacantha*)	Carnivora: canid (Arctic fox, red fox, wolf, dog)	Rodentia: cricetid (Siberian brown lemming, Steppe lemming, common vole, Tundra vole, singing vole, narrow-headed vole, bank vole, grey red-backed vole); Lagomorpha: ochotonid (Mongolian pika), leporid (European rabbit) [cysticercus in peritoneal cavity, pleura]	Northern Hemisphere
T. regis (syn. *T. bubesei*)	Carnivora: felid (lion, leopard)	Artiodactyla: bovid (hartebeest, blue wildebeest, topi, beisa, gemsbok, sable antelope, waterbuck, southern reedbuck), suid (desert warthog); Perissodactyla: equid (plains zebra) [cysticercus in body cavity]	Africa
T. saginata (syn. *T. africana, T. bremneri, T. confusa, T. cylindrica, T. hominis, T. mediocanellata, T. philippina, T. tonkinensis, Taeniarhynchus saginatus*) (human beef tapeworm, beef measles worm) [syn. *Cysticercus bovis, C. inermis*]	Primates: hominid (human) {occasionally diarrhoea}	Artiodactyla: bovid (cattle, zebu, topi, kob, beisa, harnessed bushbuck, red-fronted gazelle, dorcas gazelle, Mongolian gazelle), cervid (reindeer) [cysticercus in muscles] {carcase lesions, calcification}	worldwide
T. saigoni	Primates: cercopithecid (crab-eating macaque)		Asia
T. selousi	Carnivora: felid (wildcat)	Rodentia: murid (four-striped grass mouse)	South Africa
T. simbae	Carnivora: felid (lion)	unknown	Africa
T. solium (human pork tapeworm, pork measles worm) [syn. *Cysticercus cellulosae*]	Primates: hominid (human) {occasionally diarrhoea}	Artiodactyla: suid (pig, wild boar, bushpig), camelid (camel); Primates: cercopithecid (vervet monkey, moustached monkey, patas monkey, chacma baboon, rhesus macaque), hylobatid (lar gibbon), hominid (human);	worldwide

		Carnivora: canid (dog, red fox), felid (wildcat), mustelid (polecat), ursid (brown bear), otariid (brown fur seal); Lagomorpha: leporid (mountain hare, European rabbit); Rodentia: sciurid (ground squirrel), murid (mice, black rat), cricetid (golden hamster) [cysticercus in muscles, organs] {lesions, neurological signs}	
T. talicei		Rodentia: ctenomyid (collared tuco-tuco)	South America
T. taxidiensis	Carnivora: mustelid (American badger), canid (coyote)	Rodentia: sciurid (rock squirrel, Wyoming ground squirrel, Franklin's ground squirrel)	North America
Species forming coenuri in IH			
T. (*Multiceps*) *clavifer sp. inq.*		Rodentia: echimyid (coypu)	Europe
T. (*Multiceps*) *endothoracicus* [syn. *Coenurus endothoracicus*]	Carnivora: canid (fox)	Rodentia: murid (rats, mice, gerbils, jirds) [coenurus in muscles, body cavity]	Asia, North Africa
T. (*Multiceps*) *gaigeri* (possible synonym of *T. multiceps*) [syn. *Coenurus gaigeri*]	Carnivora: canid (dog, fox)	Artiodactyla: bovid (goat, sheep) [coenurus in muscle, subcutis] {carcase lesions}	worldwide
T. (*Multiceps*) *multiceps* [syn. *Coenurus cerebralis*]	Carnivora: canid (dog, raccoon dog, Arctic fox, red fox, corsac fox, coyote, black-backed jackal, wolf), felid (cougar)	Artiodactyla: bovid (sheep, mouflon, argali, goat, Caucasian goat, chamois, Pyrenean chamois, cattle, wisent, yak, gemsbok, Siberian ibex, goitered gazelle, roan antelope, saiga antelope), cervid (roe deer, reindeer), camelid (dromedary, Bactrian camel), suid (pig); Perissodactyla: equid (horse); Lagomorpha: leporid (snowshoe hare); occasionally Primates: cercopithecid (gelada), hominid (human) [coenurus in brain, spinal cord, subcutis] {occasionally neurological signs known as gid, sturdy or staggers}	worldwide, except North America, New Zealand
T. (*Multiceps*) *macracantha*	Carnivora: viverrid (genet, Cape genet), herpestid (mongoose), mustelid (striped polecat, weasel), felid (wildcat)	Rodentia: murid (house mouse, wood mouse, African pygmy mouse, African grass rat, red rock rat, Namaqua rock rat, acacia rat, four-striped grass rat, African soft-furred rat) [coenurus in liver]	Europe, Africa
T. (*Multiceps*) *otomys sp. inq.*		Rodentia: murid (South Africa vlei rat)	Africa
T. (*Multiceps*) *serialis* (incl. *T. s. brauni, T. brauni,* syn. *T. laruei, M. glomeratus, M. packi*) [syn. *Coenurus serialis, C. brauni*]	Carnivora: canid (dog, African wild dog, black-backed jackal, red fox)	Lagomorpha: leporid (European rabbit, European hare, snowshoe hare, eastern cottontail); Rodentia: murid (house mouse, typical striped grass mouse, southern multimammate mouse, black rat, thicket rats, Southern African vlei rat, African soft-furred rat, greater Egyptian gerbil), nesomyid (climbing mouse), hystricid (porcupines), spalacid (Rwanda mole-rat); Primates: cercopithecid (blue monkey, purple-faced leaf-monkey), hominid (human) [coenurus in connective tissue, subcutaneous tissue, eyes]	America, Africa, Europe
T. (*Multiceps*) *skrjabini* (possible synonym of *T. multiceps*) [syn. *Coenurus skrjabini*]	Carnivora: canid (dog, fox)	Artiodactyla: bovid (sheep) [coenurus in muscle, subcutis] {carcase lesions}	worldwide
T. (*Multiceps*) *smythi sp. inq.*	Carnivora: canid (wolf)		Europe
T. (*Multiceps*) *twitchelli*	Carnivora: mustelid (wolverine)	Rodentia: erethizontid (North American porcupine), cricetid (muskrat, Siberian brown lemming, meadow vole), sciurid	North America

		(European ground squirrel, American red squirrel) [coenurus in muscles]	
Species forming strobilocerci in IH			
T. (*Hydatigera*) *balaniceps sp. inq.*	Carnivora: canid (wolf)		North America
T. (*Hydatigera*) *kamiyai* (now *Hydatigera*)	Carnivora: felid (European wild cat)		Europe
T. (*Hydatigera*) *krepkogorski* (now *Hydatigera*)	Carnivora: felid (African wild cat, European wild cat, sand cat, jungle cat), canid (red fox)	Rodentia: murid (rats, mice, gerbils); Lagomorpha: leporid (rabbits, hares) [strobilocercus in mesenteries, liver]	Russia, Asia
T. macrocystis [syn. *Cysticercus macrocystis*] (now *Hydatigera*)	Carnivora: felid (oncilla, jaguarundi, margay, Geoffroy's cat, bobcat, Canada lynx)	Lagomorpha: leporid (tapeti, snowshoe hare, jackrabbit, mountain hare); Rodentia: sciurid (red squirrel) [strobilocercus in muscles, mesenteries, liver]	Americas, Russia
T. (*Hydatigera*) *parva* (now *Hydatigera*)	Carnivora: viverrid (common genet)		Africa
T. (*Hydatigera*) *pseudolaticollis* (syn. *T. laticollis*) (now *Hydatigera*)	Carnivora: felid (lynx)		North America
T. (*Hydatigera*) *rileyi* (syn. *T. lyncis*) (now *Hydatigera*)	Carnivora: felid (Eurasian lynx, bobcat, cougar, wildcat)	Rodentia: sciurid (American red squirrel), aplodontid (mountain beaver), cricetid (packrat, marsh rice rat, hispid cotton rat, northern red-backed vole, Tundra vole) [hemistrobilocercus in liver]	Nearctic
T. (*Hydatigera*) *taeniaeformis* (syn. *T. infantis, T. longihamatus, H. himalayotaenia*) [syn. *Strobilocercus fasciolaris, S. crassicollis, Cysticercus fasciolaris*] (now *Hydatigera*)	Carnivora: felid (cat, bobcat, wildcat, lynx, tiger), mustelid (stoat), canid (red fox, coyote-wolf hybrid)	Rodentia: murid (house mouse, spiny mouse, pygmy field mouse, Algerian mouse, brown rat, black rat, African grass rat, lesser Egyptian gerbil), cricetid (muskrat, hispid cotton rat, common vole, field vole, meadow vole, woodland vole, European pine vole, Savi's pine vole, deermouse, yellow-rumped leaf-eared mouse), echimyid (coypu), sciurid (grey squirrel); Lagomorpha: leporid (rabbit); occasionally Strigiformes: strigid (Eurasian eagle-owl); Galliformes: phasianid (common pheasant); rarely Primates: hominid (human) [strobilocercus in liver]	worldwide

Parasite morphology: These tapeworms form three developmental stages: eggs, larvae and adults. The morphological characteristics of the adults are distinctive; all adults having an anterior scolex (holdfast organ), with four muscular acetabulate (saucer-like) suckers, surmounting a long (up to 10 m) ribbon-like strobila (tape) made up of numerous (as many as 2,000) proglottids (segments). *T. solium* tapeworms are usually 1.8-4 m long (some reported up to 8 m) while *T. saginata* tapeworms are usually smaller ranging from 0.3-0.6 m long (some up to 2.5 m). The anterior scolex is small measuring around 1-2 mm in section: that of *T. solium* is spheroidal and armed with two circles of 22-32 rostellar hooks (alternating in size from long 180 µm to short 130 µm), while that of *T. saginata* is cuboidal and un-armed. Adult worms are hermaphroditic with segments containing both male and female reproductive organs. Anterior segments are usually immature and broader than long, middle segments with fully developed genitalia are square, and posterior segments are gravid (filled with eggs) and longer than broad (especially those of *T. saginata* compared to *T. solium*). Gravid proglottids have a prominent uterus with a medial stem and numerous lateral branches on either side (7-13 for *T. solium* and 15-32 for *T. saginata*). Genital pores are marginal, alternating irregularly. Most *Taenia* spp. were assigned to either of two morpho-groups based on the arrangement of genital ducts: those with ducts passing between the lateral excretory canals (e.g. taeniids of humans, dogs and cats, except *T. taeniaeformis*) or those with ducts passing the canals ventrally (e.g. *T. taeniaeformis* and taeniids of viverrids and mustelids). The eggs of most species are similar in morphology; being spherical, 31-48 µm in diameter, surrounded by a thick radially-striated wall, and containing a hexacanth (six-hooked) nonciliated embryo (oncosphere). The larval stages (metacestodes) are lacunate (internal channel forms during development) and they become encysted within intermediate host tissues. Most *Taenia* spp. (e.g. *T. saginata* and *T. solium*) form distinctive pearly-white cysticerci (*singular* cysticercus) which appear as small (8-10 mm in diameter) fluid-filled bladders (hence the common name of bladder-worms), each containing a single invaginated scolex (infective stage). Other taeniids form different larval stages: those belonging to the subgenus

T. (*Multiceps*) (e.g. *T.* (*M.*) *multiceps*) forming larger coenuri (*singular* coenurus) containing clusters of numerous invaginated scoleces on its internal wall; and those belonging to the genus *Hydatigera* (e.g. *H. taeniaeformis*) forming strobilocerci (*singular* strobilocercus) with an invaginated scolex at the end of a long pseudo-segmented neck.

Site of infection: Adult tapeworms lay in the lumen of the small intestines of their definitive hosts, attached to the mucosa only by their scoleces. Larval stages (metacestodes) may develop in a range of tissues and organs in their intermediate hosts, particularly in muscles, visceral organs and sometimes the brain.

Pathogenesis: Infections in humans by the large adult tapeworms generally involve only 1-2 worms, and often do not result in any distinct symptoms, although there may be vague abdominal pains with mild intermittent diarrhoea or constipation, epigastric pain, nausea and generalized allergic manifestations, including urticaria, anal pruritus and eosinophilia. Infections by the encysted larval stages (cysticerci) do not appear to cause any severe clinical disease in their normal hosts (cattle and pigs) even when present in relatively high numbers. The cysts often occur in skeletal muscles and connective tissues of the skin (reports in the liver appear to be incorrect identifications), and while they may occupy space, they generally do not cause organ enlargement, tissue displacement or untoward pressure on surrounding areas. Degenerating cysticerci tend to calcify and are palpable in the tissues. Heavy infections by live and calcified cysts impart a measly appearance to the flesh and may lead to the condemnation of the carcase. Unfortunately, humans may also be infected with *T. solium* through the process of self-infection when eggs are accidentally ingested (and possibly by retroinfection when eggs carried upwards by reverse peristalsis hatch in the gut). Cysticerci may develop in virtually every organ and tissue of the human body, although they show a particular affinity for the muscles and brain, and less commonly for subcutaneous connective tissue, eye, heart, liver, lungs and coelom. Humans are quite susceptible to pressure necrosis, particularly when cysticerci develop in the brain (neurocysticercosis with cerebral signs, headaches, seizures, epilepsy and coma), eyes (ocular signs, pain, and loss of vision), muscles (myositis, hypertrophy/swelling) or subcutaneous tissues (nodules on the torso and extremities, sometimes painful). Degenerating cysticerci may elicit severe acute, and even fatal, inflammatory responses before their eventual calcification. Similarly, most infections of intermediate hosts by *Taenia* (*Multiceps*) spp. forming coenuri are asymptomatic unless the larval cysts degenerate or become large enough to interfere with vital organs. Coenuri may develop in the brain, eyes, muscles or subcutis causing symptoms ranging from altered neurological status, behavioural changes, irritability, unusual tilting of the head (gid), increased intracranial pressure, hydrocephalus, meningoencephalitis, seizures, paralysis and death. Naive animals are highly susceptible to taeniid infection; heavy infections sometimes causing significant liver damage, and heavy pasture contamination sometimes resulting in focal outbreaks (cysticercosis storms). In contrast, animals in endemic areas may develop premunitive (concomitant) immunity when persistent primary infections provide protection against subsequent re-infection.

Developmental cycle and mode of transmission: These tapeworms have indirect life-cycles: involving predator-prey transmission where carnivores acquire infections by ingesting larval stages in meat. Adult worms produce thousands of eggs which are released from caudal segments (proglottids) and shed in faeces, or the gravid proglottids themselves break off and are shed as packages of eggs in faeces (sometimes up to 6 segments per day). The eggs are very resistant to desiccation and sewage treatment and can live for weeks on pastures. They are ingested by intermediate hosts with contaminated feed, drinking water, or are physically transferred to the mouth. The eggs hatch releasing the oncospheres which use their hooks and gland secretions to penetrate the gut wall into the circulation where they carried mainly to the skeletal muscles and connective tissues. Over 3 months, they metamorphose into thin-walled cysticerci; each containing a single tiny scolex invaginated into the lumen. Coenuri with several scoleces may take up to 9 months to develop. These encysted larval stages are transmitted to their definitive hosts by carnivory, when infected meat or offal is consumed raw or under-cooked. After ingestion, the outer bladder is digested away releasing the scolex which evaginates, attaches to the small intestinal mucosa and grows into an adult in about 10 weeks. Each segment is hermaphroditic containing both female and male reproductive organs. Cross-fertilization occurs when the segments have matured to a certain point in their development (around the middle of the tapeworm). Mating occurs between adjacent segments when the tapeworm repeatedly folds back on itself. Adult worms may live for as long as 25 years and they will produce billions of eggs in that time. Parasite life-cycles may be inadvertently facilitated by human activities in domestic situations; including poor hygiene and sanitation, intensive husbandry practices with over-crowding, inadequate meat inspection, poor effluent disposal in flood-prone areas and using untreated nightsoil or sewage for fertilizing pastures and crops. In particular, faeces from humans (and canids) may contain taeniid eggs which cause cysticercosis in domestic meat animals (and in humans in the case of *T. solium*). Many sylvatic cycles also occur between wildlife species with natural predator-prey relationships involving carnivores (mainly canids, felids and viverrids) and herbivores/omnivores (particularly suids, ruminants, lagomorphs and rodents).

Differential diagnosis: Intestinal infections in humans are diagnosed by the detection of gravid segments or eggs in faecal samples, the latter being detected best after concentration in high specific gravity salt or sugar solutions. The eggs of *T. saginata* and *T. solium* are identical, but the gravid segments of *T. saginata* are more active than those of *T. solium*, the vaginal opening is guarded by a muscular sphincter, and they have more lateral branches of the uterus (although some overlap in numbers may occur). Infections by cysticerci may be suspected on the basis of clinical symptomatology (especially neurocysticercosis), but the metacestodes often can only be visualized and/or felt when in superficial locations. Modern medical imaging techniques (magnetic resonance imaging (MRI), computerized axial tomography (CAT) and ultrasonography) may detect cysticerci in soft tissues, while

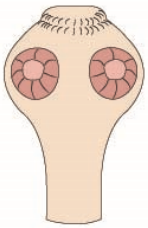
X-rays generally only detect calcified cysticerci. Several immunological tests (enzyme immunoassays, immunoblots) have recently been developed to detect host antibodies or parasite antigens in host samples (serum, cerebrospinal fluid, tissue biopsies/aspirates or faeces); most tests appear to be sensitive and specific although some cross-reactions have been observed with other tapeworm species. Molecular tests are also being developed to characterize parasites, including Southern blot hybridization, restriction fragment length polymorphism (RFLP), single strand conformational polymorphism (SSCP), random amplified polymorphic DNA (RAPD), loop-mediated isothermal amplification (LAMP), multiplex analyses and DNA sequencing, most using polymerase chain reactions (PCR) to amplify specific sequences of nuclear genes (18S and 28S ribosomal RNA (rRNA), internal transcribed spacer (ITS) regions, oncosphere-specific proteins (*Tso31*), cathepsin L-like cysteine peptidase (*clp*), noncoding DNA fragments (HDP1, 2), sequence characterized amplified region (SCAR) markers) or mitochondrial genes (cytochrome c oxidase subunit 1 (*cox1*), cytochrome b (*cob*), ATP synthases (*atp*) and NADH dehydrogenases (*nad*)). In many countries, meat inspection of slaughtered animals is mandatory to screen for various carcase lesions, including larval stages of tapeworms (cysticerci, coenuri). While cysts may be detected in superficial or accessible locations on carcases, usually the masseter muscles, tongue and heart, such screening has low sensitivity.

Treatment and control: Several groups of anthelmintic drugs (isoquinolines, benzimidazoles, salicylanilides, isothiocyanates) may be used to kill adult tapeworms but they are generally not effective against eggs. Single doses of praziquantel or niclosamide can cure infections in definitive hosts, while daily doses of praziquantel given for 1-2 weeks are effective against larval cysticercosis in intermediate hosts. Repeated doses of benzimidazoles (mebendazole, albendazole and fenbendazole) are effective against adult and larval stages. Epsiprantel is poorly absorbed and is most effective against adult stages in the gut. Nitroscanate has been used as a broad spectrum anthelmintic against enteric nematodes and cestodes in dogs. In humans afflicted with neurocysticercosis, surgical intervention may be required to remove cysts from the brain, and treatment of the patient pre- and post-surgery with albendazole or praziquantel has been recommended. The prevention of infections involves breaking the transmission cycle; through stringent meat inspection for ‘measly’ meat, tracing heavy infections back to individual farms, condemnation of infected carcases for human consumption, proper cooking or freezing of meat (pickling meat often does not kill larvae), sanitary disposal of faeces, prohibiting the use of sewage for fertilizing pastures, washing salad vegetables, strict personal hygiene, curbing hunting/scavenging behaviour in dogs, and mounting public awareness and education campaigns. Vaccines developed for *T. ovis, T. saginata* and *T. solium* have proven very effective in clinical trials but they have yet to be released commercially.

Taenia solium

intestines
(sometimes abdominal pain, diarrhoea, allergy)

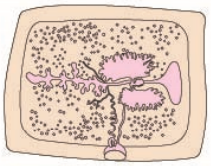
hermaphroditic adults (~ 3 m)



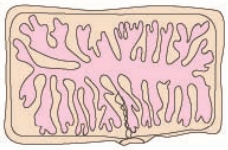
scolex

Definitive Hosts
(humans)

predator-prey transmission through ingestion of infected tissues



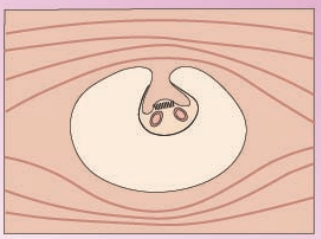
mature proglottid



gravid proglottid

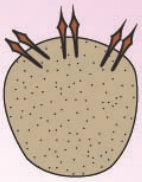
excretion of eggs in faeces

external environment



cysticercus
(~ 8 mm)

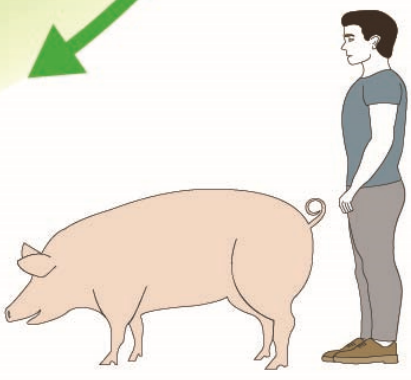
egg
(~ 40 µm)



oncosphere
(~ 40 µm)

neural and muscular tissue
(space-occupying lesions, calcification, cerebral signs)

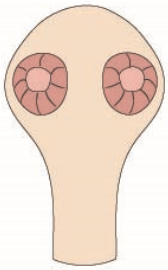
Intermediate Hosts
(pigs, primates, some carnivores, rodents)



Taenia saginata

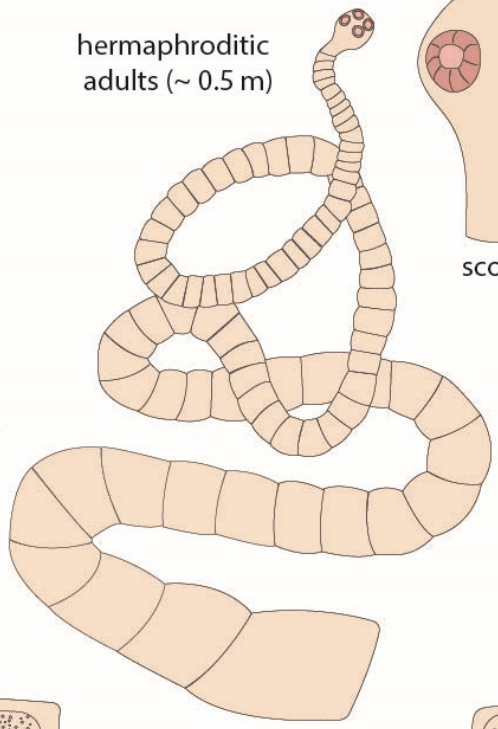
intestines
(sometimes abdominal pain, diarrhoea, allergy)

hermaphroditic adults (~ 0.5 m)

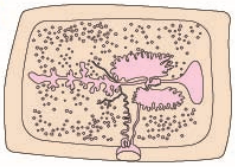


scolex

Definitive Hosts
(humans)

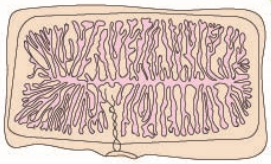


predator-prey transmission through ingestion of infected tissues



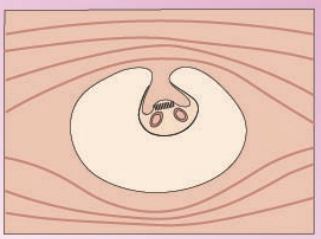
mature proglottid

gravid proglottid



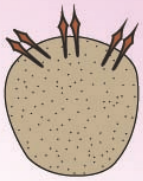
excretion of eggs in faeces

external environment

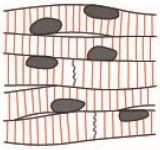


cysticercus
(~ 8 mm)

egg
(~ 40 µm)

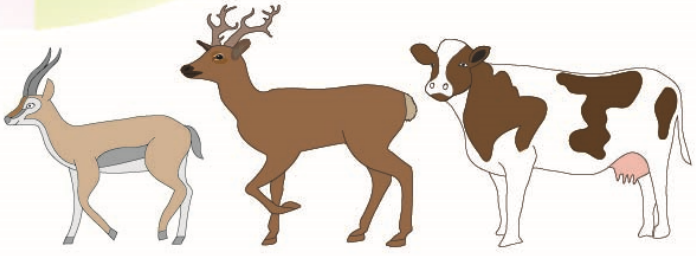


oncosphere
(~ 40 µm)



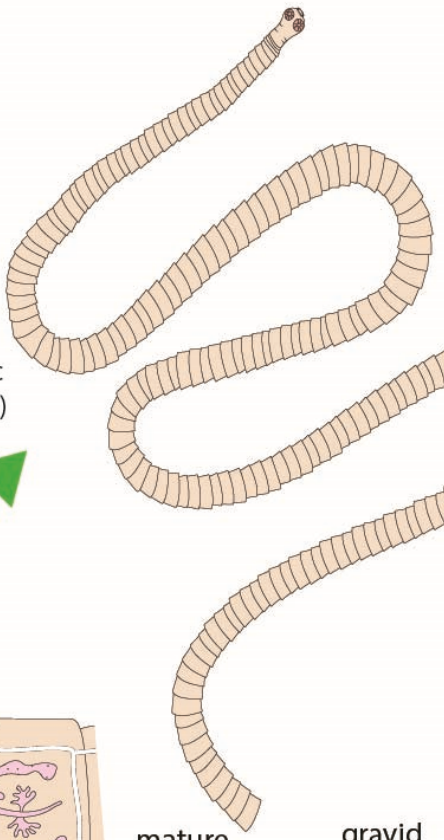
muscular tissue
(space-occupying lesions, calcification)

Intermediate Hosts
(ruminants)

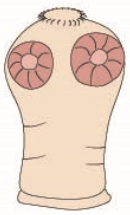


Taenia multiceps

intestines
(sometimes discomfort.
possibly diarrhoea)



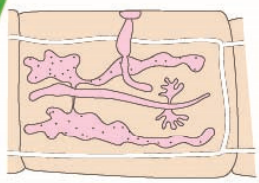
hermaphroditic
adults (~ 0.5 m)



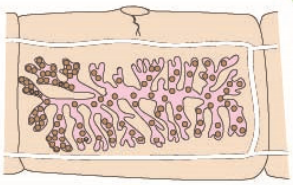
scolex

Definitive Hosts
(canids)

predator-prey
transmission
through
ingestion
of infected
tissues



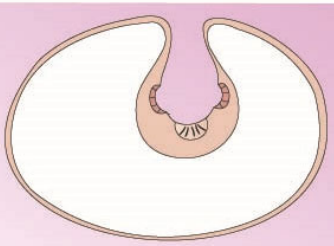
mature
proglottid



gravid
proglottid

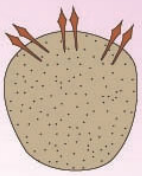
excretion
of eggs in
faeces

external
environment

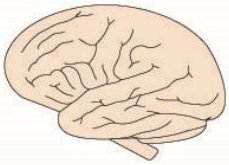


coenurus
(~ 20 mm)

egg
(~ 40 µm)

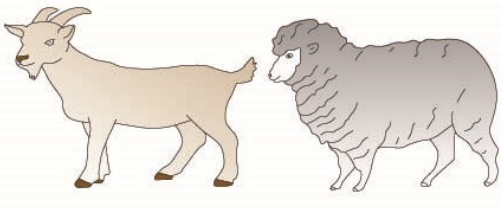


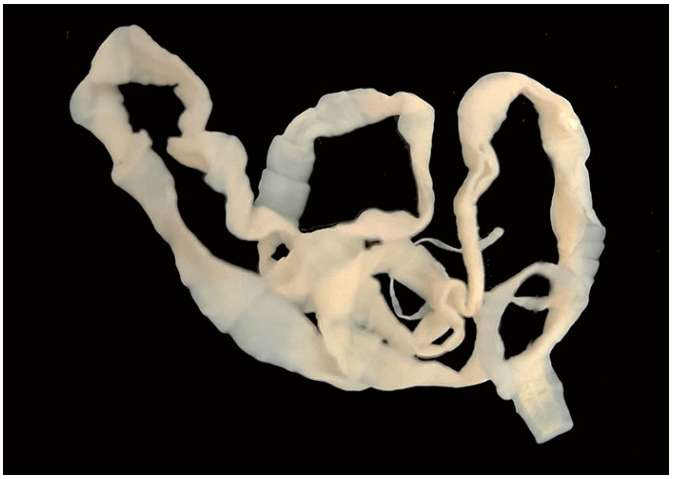
oncosphere
(~ 40 µm)



neural tissue
(space-occupying lesions,
cerebral signs (gid))

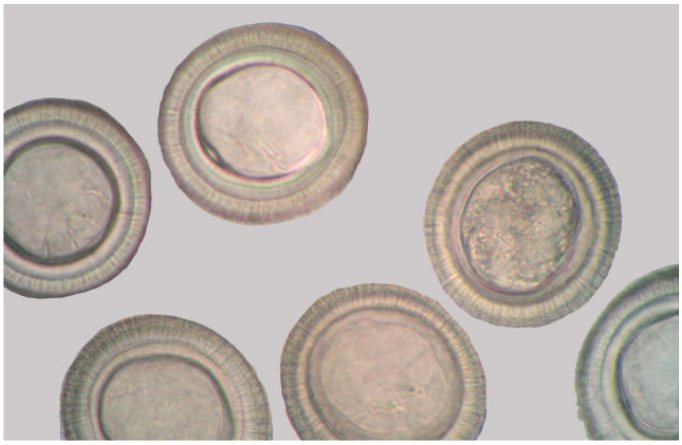
Intermediate Hosts
(ungulates, primates)





Taenia adult worm

Taenia adult worm segments



Taenia worm eggs

Taenia cysticercus

	
Taenia saginata scolex	*Taenia solium* scolex
	
Taenia saginata segment	*Taenia solium* segment