

Davainea

(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 davaineids usually have an armed rostellum and suckers and are parasitic in birds and mammals, sometimes causing enteric disorders and mortalities. The encysted larval stages (cysticercoids) of *Davainea* spp. occur in snails and slugs 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: Davaineidae (tapeworms of birds, large rostellum with hammer-shaped hooks and spiny suckers)
Genus: *Davainea* (parasitic in small intestines of birds)
Species: various species cause enteritis 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 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 Lecaniccephalidea, 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				
Lecaniccephalidea (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		
Oncoproteocephalidea (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).

The family Davaineidae is characterized by adult tapeworms usually possessing a scolex with small numerous hammer-shaped hooks around the suckers as well as on the rostellum. Over 30 davaineid genera have been described: including *Calostaurus*, *Cotugnia*, *Davainea*, *Fernandezia*, *Fuhrmannetta*, *Houttuynia*, *Idiogenes*, *Ophryocotyle*, *Otiditaenia*, *Paroniella*, *Paspalia*,

Pseudidiogenes, *Raillietina* and *Skrjabinia*. The family Davaineidae is conventionally divided into 2 subfamilies: the Davaineinae (often including the Ophryocotylinae) whose adults do not possess a paruterine organ; and the Idiogeninae whose adults have a paruterine organ. Davaineine tapeworms are commonly found in birds (occasionally mammals) and larval stages develop in insects (such as flies and ants) or gastropod molluscs (slugs and snails). Several taxonomic reviews have attempted to reconcile differences between the davaineine genera, particularly *Davainea* and *Raillietina*. Most *Davainea* spp. are small triangular worms with only 4-9 proglottids, the scolex has rostellar hooks in several rows, the 4 suckers are armed, and the segments have genital pores alternating regularly; while *Raillietina* spp. are generally long tapeworms with numerous proglottids, the scolex has rostellar hooks in 1-2 circular rows, the 4 suckers are sometimes armed, and the segments have genital pores which are unilateral or alternate irregularly. Over 100 *Davainea* spp. have been recorded worldwide from 120 different hosts, but almost half have been synonymized with *Raillietina*. Most *Davainea* infections are asymptomatic although several species have previously been associated with production losses in commercial poultry flocks.

<i>Davainea</i> species	Definitive host [adults in intestines]	Intermediate hosts [cysticercoids in tissues]	Distribution
<i>D. alii</i>	Passeriformes: pycnonotid (red-vented bulbul)		India
<i>D. allagea</i>	Psittaciformes: psittaculid (double-eyed fig parrot)		New Guinea
<i>D. ambajogaiensis</i>	Galliformes: phasianid (chicken)		India
<i>D. andrei</i>	Galliformes: phasianid (grey partridge)		Asia
<i>D. aurangabadensis</i>	Galliformes: phasianid (chicken); Charadriiformes: charadriid (red-wattled lapwing)		India
<i>D. baeri</i>	Piciformes: picid (red-rumped green woodpecker)		Asia
<i>D. balasahebae</i>	Galliformes: phasianid (chicken)		India
<i>D. biroi</i> (syn. <i>Raillietina</i> , <i>Kotlania</i>)	Psittaciformes: psittacid (orange-breasted fig parrot)		New Guinea
<i>D. brachyrhyncha</i>	Cariamiformes: cariamid (red-legged seriema)		South America
<i>D. calva</i>	Galliformes: phasianid (red grouse)		Europe
<i>D. cantaniana</i> (syn. <i>D. oligophora</i>)	Galliformes: phasianid (chicken, common pheasant, turkey), numidid (grey-breasted helmeted guineafowl)		Europe
<i>D. carioca</i>	Galliformes: phasianid (chicken)		South America
<i>D. casuarii</i>	Casuariiformes: casuariid (dwarf cassowary)		New Guinea
<i>D. chauhani</i>	Galliformes: phasianid (blood pheasant, chicken)		India
<i>D. clavulus</i>	Passeriformes: paradisaeid (magnificent riflebird)		Australia
<i>D. columbae</i>	Columbiformes: columbid (common wood pigeon, rock dove, European turtle dove)		Europe
<i>D. difformis</i> sp. inq. (syn. <i>Taenia</i> , <i>T. brevicollis</i>)	Cuculiformes: cuculid (common cuckoo)		Eurasia
<i>D. domesticusi</i>	Galliformes: phasianid (chicken)		India
<i>D. exilis</i>	Galliformes: phasianid (chicken)		India
<i>D. fuhrmanni</i>	Galliformes: phasianid (turkey)		North America
<i>D. guivillensis</i>	Galliformes: phasianid (pheasant); Columbiformes: columbid (wood pigeon)		Europe
<i>D. gunjotinesis</i>	Galliformes: phasianid (chicken)		India
<i>D. hewetensis</i>	Galliformes: phasianid (chicken)		India
<i>D. himantopodis</i>	Charadriiformes: recurvirostrid (pied stilt)		India, Australia
<i>D. isomydis</i>	Rodentia: murid (Abyssinian grass rat)		Africa
<i>D. jalnaensis</i>	Galliformes: phasianid (chicken)		India
<i>D. kekhalensis</i>	Galliformes: phasianid (chicken)		India
<i>D. kramerii</i>	Psittaciformes: psittaculid (rose-ringed parakeet)		India
<i>D. lagopodis</i>	Galliformes: phasianid (grouse)		North America
<i>D. macrorchida</i>	Psittaciformes: psittaculid (Edwards' s fig-parrot)		New Guinea

<i>D. marchii</i> (syn. <i>Taenia</i>)	Charadriiformes: scolopacid (common redshank, spotted redshank)		Eurasia
<i>D. meleagris</i>	Galliformes: phasianid (turkey)		North America, India
<i>D. minuta</i>	Charadriiformes: scolopacid (common redshank)		India
<i>D. muktabae</i>	Galliformes: phasianid (chicken); Passeriformes: sturnid (common myna)		India
<i>D. musculosa</i>	Passeriformes: sturnid (common starling)		Europe
<i>D. nana</i>	Galliformes: numidid (guineafowl)		India
<i>D. nitini</i>	Passeriformes: pycnonotid (red-vented bulbul)		India
<i>D. osmanabadensis</i>	Galliformes: phasianid (chicken)		India
<i>D. passerae</i>	Passeriformes: passerid (house sparrow)		India
<i>D. paucisegmentata</i>	Galliformes: numidid (guineafowl)		Africa, India
<i>D. polycalcaria</i>	Passeriformes: corvid (Indian jungle crow)		Sri Lanka
<i>D. polychalix</i>	Psittaciformes: psittaculid (coconut lorikeet)		New Guinea
<i>D. pondicerianusi</i>	Galliformes: phasianid (grey francolin)		India
<i>D. proglottina</i> [incl. <i>D. p.</i> var. <i>dublanensis</i>] (syn. <i>D. varians</i> , <i>Taenia</i>)	Galliformes: phasianid (chicken, turkey); Columbiformes: columbid (pigeon)	Gastropoda: limacid (<i>Limax cinereus</i> , <i>L. agrestis</i> , <i>L. variegatus</i> , <i>Agriolimax</i> , <i>Cepoa</i> , <i>Deroceras panormitanium</i>), physid (<i>Physa heterostropha</i>), arionid (<i>Arion</i>)	worldwide
<i>D. retharei</i>	Columbiformes: columbid (Eurasian collared-dove); Galliformes: phasianid (chicken)		India
<i>D. rhyncota</i>	Piciformes: picid (northern flicker)		North America
<i>D. shindei</i>	Galliformes: phasianid (chicken)		India
<i>D. shrigondaensis</i>	Galliformes: phasianid (chicken)		India
<i>D. sphaerocephala</i>	Charadriiformes: scolopacid (Eurasian curlew)		Eurasia
<i>D. spiralis</i>	Columbiformes: columbid (dove)		New Guinea
<i>D. struthionis</i>	Struthioniformes: struthionid (common ostrich, blue-necked ostrich); Rheiformes: rheid (greater rhea)		Africa, South America
<i>D. tauricollis</i>	Rheiformes: rheid (greater rhea)		South America
<i>D. tetraoensis</i>	Galliformes: phasianid (capercaillie)		India
<i>D. uniuterina</i>	Passeriformes: cotingid (Guianan cock-of-the-rock)		South America
Reassigned species			
<i>D. allomyodes</i> (syn. <i>Raillietina</i>) (now <i>Idiogenoides</i>)	Psittaciformes: psittaculid (Edward's fig-parrot)		New Guinea
<i>D. anatina</i> (now <i>Raillietina</i>)	Anseriformes: anatid (mallard)		India
<i>D. aruensis</i> (now <i>Raillietina</i>)	Psittaciformes: psittaculid (blue-banded lorikeet)		Indonesia
<i>D. australis</i> (now <i>Raillietina</i>)	Casuariiformes: casuariid (emu)		Australia
<i>D. bycanistis</i> (now <i>Raillietina</i>)	Bucerotiformes: bucerotid (black-and-white-casqued hornbill)		Africa
<i>D. cacatuinae</i> (now <i>Raillietina</i>)	Psittaciformes: cacatuid (sulphur-crested cockatoo)		Australia
<i>D. calcaria</i> (now <i>Raillietina</i>)	Musophagiformes: musophagid (great blue turaco)		Africa
<i>D. campanulata</i> (syn. <i>Raillietina</i>) (now <i>Davaineolepis</i>)	Galliformes: phasianid (partridge)		South America
<i>D. capillaris</i> (now <i>Raillietina</i>)	Tinamiformes: tinamid (tinamou)		South America
<i>D. celebensis</i> (now <i>Raillietina</i>)	Rodentia: murid (trefoil-toothed giant rat)		Indonesia
<i>D. centropi</i> (now <i>Raillietina</i>)	Cuculiformes: cuculid (common coucal)		Sri Lanka

<i>D. ceylonica</i> (now <i>Raillietina</i>)	Galliformes: phasianid (Indian peafowl)		Sri Lanka
<i>D. circumcinata</i> (now <i>Raillietina</i>)	Pelecaniformes: ardeid (little egret)		Egypt
<i>D. clavicularosa</i> (now <i>Raillietina</i>)	Galliformes: phasianid (Clapperton's francolin)		Egypt
<i>D. cohni</i> (now <i>Raillietina</i>)	Galliformes: phasianid (chicken)		Africa
<i>D. comitata</i> (now <i>Raillietina</i>)	Piciformes: picid (northern flicker)		North America
<i>D. compacta</i> (now <i>Raillietina</i>)	Passeriformes: oriolid (Eurasian golden oriole)		Eurasia
<i>D. conopophilae</i> (now <i>Raillietina</i>)	Passeriformes: meliphagid (rufous-banded honeyeater)		Australia
<i>D. contorta</i> (now <i>Dioriraillietina</i>)	Pholidota: manid (Chinese pangolin)	Hymenoptera: formicid (ants)	Indochina
<i>D. crassula</i> (now <i>Raillietina</i>)	Columbiformes: columbid (rock dove)		Eurasia
<i>D. cryptacantha</i> (now <i>Raillietina</i>)	Columbiformes: columbid (rock dove)		Egypt
<i>D. crypturi</i> (now <i>Raillietina</i>)	Tinamiformes: tinamid (yellow-legged tinamou)		South America
<i>D. cyrtus</i> (now <i>Raillietina</i>)	Anseriformes: anatid (duck)		South America
<i>D. debilis</i> (now <i>Raillietina</i>)	Ciconiiformes: ciconiid (African openbill)		Africa
<i>D. elongata</i> (syn. <i>Fuhrmannetta Johnstonia</i>) (now <i>Raillietina</i>)	Tinamiformes: tinamid (tinamou, red-winged tinamou, lesser nothura)		South America
<i>D. emperus</i> (syn. <i>Ransomia</i>) (now <i>Raillietina</i>)	Bucerotiformes: bucerotid (hornbill)		Africa
<i>D. galeritae</i> (now <i>Raillietina</i>)	Passeriformes: alaudid (Maghreb lark)		Africa
<i>D. globirostris</i> (now <i>Raillietina</i>)	Galliformes: phasianid (common partridge)		Europe
<i>D. globocephala</i> (now <i>Raillietina</i>)	Passeriformes: icterid (red-rumped cacique)		South America
<i>D. goura</i> (now <i>Raillietina</i>)	Columbiformes: columbid (Albert's crowned pigeon)		New Guinea
<i>D. gracilis</i> (now <i>Raillietina</i>)	Rodentia: murid (eastern spiny mouse), thryonomyid (greater cane rat)		North America, Africa
<i>D. indica</i> (now <i>Raillietina</i>)	Galliformes: phasianid (chicken)		India
<i>D. infrequens</i> (now <i>Raillietina</i>)	Casuariiformes: casuariid (dwarf cassowary)		New Guinea
<i>D. laticanalis</i> (now <i>Raillietina</i>)	Galliformes: phasianid (grey partridge)		South America
<i>D. leptacantha</i> (now <i>Raillietina</i>)	Galliformes: cracid (black curassow)		South America
<i>D. longicirrosa</i> (now <i>Chapmania</i>)	Accipitriformes: accipitrid (black kite)		Africa
<i>D. longicollis</i> (now <i>Raillietina</i>)	Galliformes: phasianid (chicken)		Europe
<i>D. longispina</i> (now <i>Raillietina</i>)	Piciformes: picid (chestnut woodpecker)		South America
<i>D. lutzi</i> (now <i>Raillietina</i>)	Piciformes: picid (chestnut woodpecker)		South America
<i>D. macrocirrosa</i> (now <i>Raillietina</i>)	Musophagiformes: musophagid (red-crested turaco)		Africa
<i>D. macroscolecina</i>	Psittaciformes: psittaculid (chattering lory)		South America

(now <i>Raillietina</i>)			
<i>D. magnicoronata</i> (now <i>Raillietina</i>)	Caprimulgiformes: caprimulgid (<i>Nacunda nighthawk</i>)		South America
<i>D. micracantha</i> (now <i>Raillietina</i>)	Columbiformes: columbid (European turtle dove)		Europe
<i>D. microscolecina</i> (now <i>Raillietina</i>)	Psittaciformes: psittaculid (<i>Eclectus</i> parrot)		Asia
<i>D. multicapsulata</i> (now <i>Raillietina</i>)	Galliformes: phasianid (common pheasant)		Europe
<i>D. numida</i> (now <i>Raillietina</i>)	Galliformes: numidid (helmeted guinea fowl)		Africa
<i>D. oligacantha</i> (now <i>Raillietina</i>)	Tinamiformes: tinamid (red-winged tinamou)		South America
<i>D. oligorchida</i> (now <i>Raillietina</i>)	Psittaciformes: psittaculid (<i>Eclectus</i> parrot)		Indonesia
<i>D. paradisea</i> (now <i>Raillietina</i>)	Passeriformes: paradisaeid (crinkle-collared manucode)		New Guinea
<i>D. parva</i> (syn. <i>Raillietina</i> (<i>Skrjabinia</i>)) (now <i>Mathevotaenia</i>)	Eulipotyphla: erinaceid (hedgehog)		Europe
<i>D. paucitesticulata</i> (now <i>Raillietina</i>)	Columbiformes: columbid (<i>Nicobar</i> pigeon)		
<i>D. penelopina</i> (now <i>Raillietina</i>)	Galliformes: cracid (dusky-legged guan)		South America
<i>D. penetrans</i> (now <i>Raillietina</i>)	Galliformes: phasianid (chicken)		Africa
<i>D. polycalceola</i> (now <i>Raillietina</i>)	Rodentia: murid (<i>Muschenbrock's</i> mouse)		Indonesia
<i>D. polyuterina</i> (now <i>Raillietina</i>)	Galliformes: phasianid (grey partridge)		Europe
<i>D. psittacea</i> (now <i>Raillietina</i>)	Psittaciformes: cacatuid (triton cockatoo)		Indonesia
<i>D. retusa</i> (now <i>Raillietina</i>)	Galliformes: phasianid (black grouse)		Russia
<i>D. sphaeroides</i> (now <i>Raillietina</i>)	Accipitriformes: accipitrid (common buzzard)		Russia
<i>D. sphecotheridis</i> (now <i>Raillietina</i>)	Passeriformes: oriolid (short-billed honeyeater)		Australia
<i>D. tragopani</i> (now <i>Raillietina</i>)	Galliformes: phasianid (satyr tragopan)		India
<i>D. trapezoides</i> (now <i>Raillietina</i>)	Rodentia: murid (striped mouse, African grass rat)		Africa
<i>D. undulata</i> (now <i>Raillietina</i>)	Musophagiformes: musophagid (great blue turaco)		Africa
<i>D. vaganda</i> (now <i>Raillietina</i>)	Accipitriformes: accipitrid (African fish eagle)		Africa

Parasite morphology: *Davainea* spp. form 3 different sequential stages in their developmental cycles: eggs, larvae (metacystodes) and adults. Mature eggs are usually grey in colour and ovoid-spherical in shape measuring 28-40 µm in diameter. They each contain a single nonciliated hexacanth (6 hooked) embryo (oncosphere) enclosed within an extraembryonic envelope which is nonstriated and without a distinctive membrane. Cysticeroid larvae are white in colour, mostly ovoid in shape measuring from 120-250 µm in diameter, lacunate (with internal cavity) and contain an anterior scolex (retracted into a small double-walled cavity) and a posterior tail-like cercomer, all enclosed within a wrinkled gelatinous coat. Adult *Davainea* tapeworms are small and triangular in shape, only measuring up to 3 cm long and comprising 4-9 segments (proglottids) ranging from 1.4-2.0 mm in length by 0.4-0.6 mm in width. The worms have a small anterior scolex with 4 suckers and a rostellum approx. 80 µm long. The suckers and rostellum are armed with numerous (60-100) small hammer-shaped hooks, the rostellar hooks occurring in 3-10 rows (cf. those of *Raillietina* spp. in 1-2 rows). Adult worms are hermaphroditic, with anterior proglottids being immature (lacking gonads), middle proglottids being mature (containing both male and female gonads) and posterior proglottids being gravid (containing numerous eggs). The eggs are scattered throughout the parenchyma enclosed singly in egg capsules and are shed individually or in short chains through the single genital pore located at the lateral margin (side alternating regularly in consecutive proglottids).

Site of infection: Adult *Davainea* tapeworms infect the small intestines (duodenum) of their avian definitive hosts, mostly galliform birds. Metacestodes (cysticercooids) infect the body cavities of their invertebrate intermediate hosts, presumed to be gastropods (slugs) for most species, although insects (ants) have been implicated for some species.

Pathogenesis: Adult tapeworms lack digestive tracts and do not feed on host tissues but rather absorb nutrients from the gut lumen. Worms attach to the intestinal wall using their armed scoleces and this may cause traumatic damage, inflammation and reduced gut function (poor absorption). While light to mild infections by most species do not cause overt clinical disease, some species have been associated with subclinical production losses in poultry resulting from poor feed conversion efficiencies, retarded growth, reduced weight gain and decreased egg production. In contrast, heavy infections may cause severe disease in birds, particularly when they have ingested large numbers of larval cysticercooids in infected slugs. Birds may experience enteritis, intestinal haemorrhages, bloody diarrhoea, lethargy, dull plumage and ruffled feathers, progressive weight loss, emaciation and eventually difficulty in breathing, leg paralysis and death. Despite its small size, *D. proglottina* is one of the most pathogenic tapeworms of poultry penetrating deeply into the mucosa and causing intense inflammation and mucosal thickening, particularly in chronic cumulative infections. Histopathological changes include vacuolation of epithelial cells, villous atrophy and desquamation, congestion of submucosal glands, granuloma formation and catarrhal enteritis. Heavy infections also lower host resistance to other infectious agents. Infections in poultry are common throughout tropical regions where poor housing and husbandry practices as well as favourable climatic conditions are conducive to parasite survival and transmission.

Developmental cycle and mode of transmission: *Davainea* spp. have indirect heteroxenous (2-host) life-cycles with avian definitive hosts becoming infected when consuming larval stages in invertebrate intermediate hosts. Gravid proglottids containing eggs are passed in bird faeces, often at a rate of one per day. The proglottids migrate out of droppings into adjacent vegetation of soil. The eggs may survive in the external environment for several days in the presence of moisture, but desiccate rapidly. Terrestrial gastropods (slugs) feed on the proglottids and eggs resulting in the release of the contained oncospheres which penetrate the gut wall using their hooks and penetration gland secretions. The oncospheres develop into encysted larvae (cysticercooids) in the body cavity (coelom) of the slugs. Multiple cysticercooids often occur within individual slugs (over 1,500 detected once) and they remain infective for up to 11 months. Foraging birds become infected when they ingest infected slugs and the contained cysticercooids break down releasing the larvae which attach to the gut wall and develop into adult tapeworms. Infections are not multiplicative but cumulative (ingestion of 1 cysticercooid leads to development of 1 tapeworm). Because slugs may harbour multiple cysticercooids, birds often become infected with multiple tapeworms (up to 4,000 recorded in one heavily infected fowl). The time from infection until the first release of gravid proglottids (i.e. the pre-patent period) is around 2-3 weeks, and adult tapeworms have been found to live for up to 3 years.

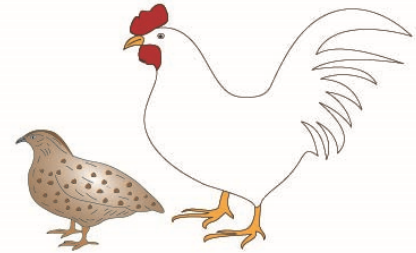
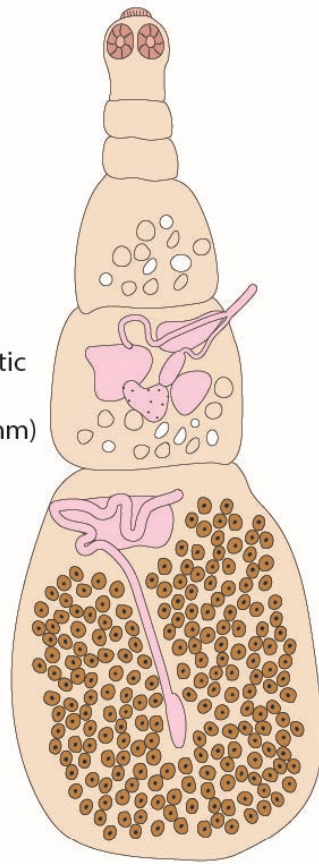
Differential diagnosis: Infections may be diagnosed ante-mortem in birds by the detection of characteristic gravid proglottids in faecal samples. Motile proglottids may be detected by visual examination while their internal morphology is best revealed by microscopic examination. The detection of egg capsules containing single eggs may be facilitated by dissecting or squashing proglottids or by differential staining. Alternatively, infections may be diagnosed post-mortem by the detection of characteristic adult tapeworms in intestinal mucosal preparations (scrapings, smears or digests). Some urgency is required in examining mucosal preparations as the small tapeworms autolyse rapidly over 24 hours.

Treatment and control: Clinical infections in poultry have been successfully treated using a range of anthelmintics effective against cestodes; including isoquinolines (praziquantel), benzimidazole-methylcarbamates (flubendazole) and halogenated hydrocarbons (butynorate, in conjunction with piperazine or phenothiazine). Treatment is often applied as a feed additive in commercial flocks. Control programmes should also target transmission to and from molluscs, either by minimizing faecal contamination of the environment (hygienic waste disposal and/or effluent treatment), eliminating or reducing slug populations (using physical barriers, molluscicides or manipulating environmental conditions by alternate grazing, soil rotovation or weed control), and by curbing bird foraging behaviours (by providing better housing or clean free-range conditions).

Davainea



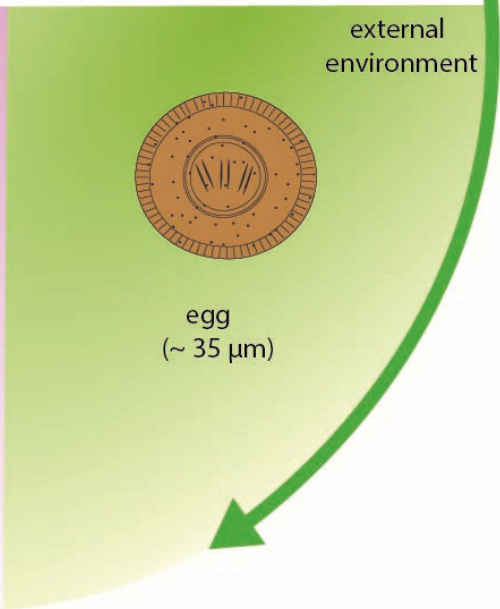
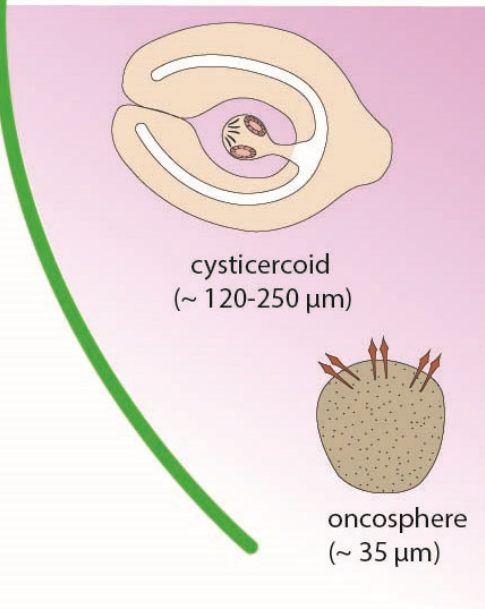
hermaphroditic
adults
(~ 10-30 mm)



transmission
through
ingestion
of infected
slugs

gravid
proglottid

excretion
of eggs in
faeces



Intermediate Hosts
(slugs)
(body cavity)



Davainea adult worm



Davainea adult worm