

## *Raillietina*

(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 *Raillietina* spp. occur in ants and beetles 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: *Raillietina* (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 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 <sup>a</sup>	Scolex	IH1 <sup>b</sup>	Stage <sup>d</sup>	IH2 <sup>c</sup>	Stage <sup>d</sup>
Class: <b>Cestoda</b> (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							
<sup>a</sup> DH = definitive host; <sup>b</sup> IH1 = first intermediate host; <sup>c</sup> 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];							
<sup>d</sup> 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 hammer-shaped hooks around the suckers as well as on the rostellum. Some 14 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 Ophryocotylineae) whose adults do not possess a paruterine organ; and the Idiogeninae whose adults have a paruterine organ. Several taxonomic reviews have attempted to reconcile differences between davaineine genera and many *Raillietina* and *Davainea* spp. have subsequently been synonymized. *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; while *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 which alternate regularly. Several newly erected genera have also previously been recorded as subgenera of the genus *Raillietina*, differentiated as follows: *R. (Raillietina)* (genital apertures unilateral, several oncospheres per egg capsule); *R. (Paroniella)* (genital apertures unilateral, one oncosphere per egg capsule); *R. (Fuhrmannetta)* (genital apertures alternating irregularly, several oncospheres per egg capsule) and *R. (Skrjabinia)* (genital apertures alternating irregularly, one oncosphere per egg capsule). Adult tapeworms occur in vertebrates (birds and mammals) while larval stages develop in insects (such as flies and ants) or gastropod molluscs (slugs and snails). Over 230 *Raillietina* spp. have been recorded worldwide, with some 200 spp. occurring in birds (wild and domestic) and around 40 spp. in mammals (lagomorphs, rodents and occasionally primates).

<i>Raillietina</i> species	Definitive host [adults in small intestines]	Intermediate hosts [cysticercoids in tissues]	Distribution
Subgenus <i>Raillietina</i> (genital apertures unilateral, several oncospheres per egg capsule)			
<i>R. (R.) afghana</i>	Rodentia: cricetid (Afghan vole)		Afghanistan
<i>R. (R.) africana</i> (syn. <i>Davainea</i> )	Carnivora: herpestid (mongoose); Primates: hominid (human)		Africa
<i>R. (R.) alagea</i>	Psittaciformes: psittaculid (double-eyed fig-parrot)		New Guinea
<i>R. (R.) alectorii</i>	Galliformes: phasianid (rock partridge)		Middle-East
<i>R. (s.l.) anatina</i> (syn. <i>Davainea</i> )	Anseriformes: anatid (mallard); Columbiformes: columbid (dove, yellow-footed green pigeon)		Eurasia
<i>R. (R.) angusta</i>	Galliformes: numidid (helmeted guineafowl)		Africa
<i>R. (R.) apivori</i>	Accipitriformes: accipitrid (European honey buzzard)		Russia
<i>R. (R.) aruensis</i> (syn. <i>Davainea</i> )	Psittaciformes: psittaculid (coconut lorikeet, blue-banded lorikeet, black-capped lory, Edward's fig-parrot, double-eyed fig-parrot)		New Guinea
<i>R. (R.) asiatica</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Rodentia: murid (black rat, lesser bandicoot rat, bush rat, striped field mouse, Mayer's brush mouse); Primates: hominid (human)		Asia, Australia
<i>R. (R.) australis</i> (syn. <i>Taenia</i> , <i>Davainea</i> , <i>Ransomia</i> , <i>Kotlania</i> )	Casuariiformes: casuariid (emu)	Hymenoptera: formicid ( <i>Pheidole</i> )	Australia
<i>R. (R.) baeri</i>	Rodentia: murid (black rat, Nile rat, Natal multimammate mouse, Jackson's soft-furred mouse)		Africa
<i>R. (R.) baghdadensis</i>	Columbiformes: columbid (rock dove)		Iraq
<i>R. (R.) bakeri</i>	Rodentia: murid (cotton rat), sciurid (western fox squirrel)		North America
<i>R. (R.) bembezi</i>	Strigiformes: strigid (spotted eagle owl)		Africa
<i>R. (R.) beveridgei</i>	Casuariiformes: casuariid (emu)	Hymenoptera: formicid ( <i>Pheidole</i> )	Australia
<i>R. (R.) boueti</i> (syn. <i>Kotlania</i> )	Galliformes: phasianid (double-spurred spurfowl)		Africa
<i>R. (s.l.) brevicollis</i>	Cuculiformes: cuculid (common cuckoo)		Europe
<i>R. (R.) buckleyi</i> (syn. <i>Ransomia</i> )	Columbiformes: columbid (laughing dove)		Africa
<i>R. (R.) bumi</i>	Strigiformes: strigid (spotted eagle owl)		Africa
<i>R. (R.) bungoensis</i>	Columbiformes: columbid (rock dove)		Japan

<i>R. (R.) bycanistis</i> (syn. <i>Davainea</i> )	Bucerotiformes: bucerotid (black-casqued hornbill, white-crested hornbill, black-and-white-casqued hornbill)		Africa
<i>R. (R.) cacatuinae</i> (syn. <i>Davainea</i> )	Psittaciformes: cacatuid (sulphur-crested cockatoo)		Australia
<i>R. (R.) calcaria</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Musophagiformes: musophagid (great blue turaco); Cuculiformes: cuculid (blue-headed coucal)		Africa
<i>R. (R.) calyptomenae</i> (syn. <i>Ransomia</i> )	Passeriformes: calyptomenid (Whitehead's broadbill)		Indonesia
<i>R. (R.) canabia</i>	Columbiformes: columbid (rock dove)		Middle-East
<i>R. (R.) capillaris</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Tinamiformes: tinamid (tinamou)		South America
<i>R. (R.) cameostrobilata</i>	Galliformes: phasianid (common pheasant, wild turkey)		Russia
<i>R. (R.) carpophagi</i>	Columbiformes: columbid (rock dove, green imperial pigeon)		Indochina
<i>R. (R.) casuari</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Casuariiformes: casuariid (dwarf cassowary)		New Guinea
<i>R. (R.) celebensis</i> [incl. <i>R. c. paucicapsulata</i> ] (syn. <i>Davainea</i> , <i>Ransomia</i> )	Rodentia: murid (trefoil-toothed giant rat, brown rat); Primates: hominid (human)		Indonesia, Myanmar
<i>R. (R.) ceylonica</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Galliformes: phasianid (Indian peafowl); Columbiformes: columbid (Bengal green pigeon, snow pigeon)		India
<i>R. (R.) chilmei</i>	Galliformes: phasianid (snow partridge)		Nepal
<i>R. (R.) chiltoni</i>	Casuariiformes: casuariid (emu)	Hymenoptera: formicid ( <i>Pheidole</i> )	Australia
<i>R. (s.l.) circumcinata</i> (syn. <i>Davainea</i> )	Pelecaniformes: ardeid (little egret)		Egypt
<i>R. (R.) clairae</i>	Piciformes: picid (grey-headed woodpecker)		China
<i>R. (R.) clavicularosa</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Galliformes: phasianid (Clapperton's francolin, crested francolin)		Egypt
<i>R. (R.) clerici</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Anseriformes: anatid (duck); Columbiformes: columbid (rock dove, European turtle dove, Oriental turtle dove)		Eurasia, Africa, Americas
<i>R. (R.) cohni</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Galliformes: phasianid (chicken), numidid (helmeted guineafowl); Pterocliiformes: pteroclid (chestnut-bellied sandgrouse, black-bellied sandgrouse)		Africa, India
<i>R. (R.) colinia</i>	Galliformes: odontophorid (northern bobwhite quail)		North America
<i>R. (R.) columbiella</i>	Columbiformes: columbid (rock dove)		Africa
<i>R. (R.) comitata</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Piciformes: picid (northern flicker, red-headed woodpecker)		North America
<i>R. (R.) congolensis</i>	Passeriformes: estrildid (orange-winged pytilia)		Africa
<i>R. (R.) coreensis</i>	Rodentia: murid (small Japanese field mouse, striped field mouse)		Asia
<i>R. (R.) coturnixi</i>	Galliformes: phasianid (common quail)		Russia
<i>R. (R.) cryptacantha</i> (syn. <i>Ransomia</i> , <i>Davainea</i> )	Columbiformes: columbid (rock dove, European turtle dove, mourning collared-dove, eastern bronze-naped pigeon, laughing dove, ring-necked dove)		Africa
<i>R. (R.) crypturi</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Tinamiformes: tinamid (yellow-legged tinamou)		South America
<i>R. (R.) cyrtus</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Anseriformes: anatid (duck)		South America
<i>R. (R.) daetensis</i>	Columbiformes: columbid (green pigeon)		Philippines
<i>R. (R.) dartevellei</i>	Accipitriformes: accipitrid (palm-nut vulture)		Africa
<i>R. (R.) dattai</i>	Galliformes: phasianid (chicken)		India
<i>R. (R.) debilis</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Ciconiiformes: ciconiid (African openbill)		Africa

<i>R. (R.) delalandei</i>	Columbiformes: columbid (African green pigeon)		Africa
<i>R. (R.) demerariensis</i> [incl. <i>R. d. trinitae</i> , <i>R. d. venezolanensis</i> ] (syn. <i>R. brumpti</i> , <i>R. davainei</i> , <i>R. equatoriensis</i> , <i>R. halli</i> , <i>R. luisaleoni</i> , <i>R. leoni</i> , <i>R. quitensis</i> )	Rodentia: capromyid (Desmarest's hutia), cuniculid (lowland paca), dasyproctid (red-rumped agouti), echimyid (Guyenne spiny rat), erethizontid (black-tailed hairy dwarf porcupine); Primates: atelid (Guatemalan black howler monkey, Venezuelan red howler monkey), hominid (human)		South and Central America
<i>R. (R.) deweti</i>	Galliformes: numidid (guineafowl)		Africa
<i>R. (R.) douceti</i>	Musophagiformes: musophagid (turaco)		Africa
<i>R. (R.) dromaius</i>	Casuariiformes: casuariid (emu)	Hymenoptera: formicid ( <i>Pheidole</i> )	Australia
<i>R. (R.) echinobothrida</i> (syn. <i>R. grobbeni</i> , <i>R. sinensis</i> , <i>Johnstonia</i> , <i>Taenia infundibuliformis</i> , <i>T. botrioplites</i> , <i>Ransomia botrioplites</i> , <i>Davainea echinobothrida</i> , <i>D. parechinobothrida</i> )	Galliformes: phasianid (chicken, red junglefowl, turkey, grey partridge, rock partridge, common pheasant, common quail), numidid (helmeted guineafowl); Anseriformes: anatid (mallard); Columbiformes: columbid (Oriental turtle dove, rock dove, laughing dove); Accipitriformes: accipitrid (Eurasian sparrowhawk)	Hymenoptera: formicid ants ( <i>Monomorium salmons indicum</i> , <i>Tetramorium caespitum</i> , <i>T. c. jacotti</i> , <i>T. semilaeve</i> , <i>T. simillium</i> , <i>Pheidole bergi</i> , <i>P. fossulata</i> , <i>P. rhombinoda</i> , <i>P. vinelandica</i> )	worldwide
<i>R. (R.) emperus</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Bucerotiformes: bucerotid (hornbill); Cuculiformes: cuculid (Senegal coucal)		Africa
<i>R. (R.) ershovi</i>	Columbiformes: columbid (Oriental turtle dove)		Russia
<i>R. (R.) eupodotidis</i>	Otidiformes: otidid (white-bellied bustard)		Africa
<i>R. (R.) famosa</i>	Psittaciformes: psittaculid (eclectus parrot)		Asia
<i>R. (R.) fausti</i>	Piciformes: picid (grey-headed woodpecker, European green woodpecker)		China
<i>R. (R.) fischthali</i>	Columbiformes: columbid (green imperial pigeon, white-bellied green pigeon)		Philippines
<i>R. (R.) flabralis</i>	Bucerotiformes: bucerotid (great hornbill)		Asia
<i>R. (R.) flaccida</i>	Pterocliiformes: pteroclid (black-bellied sandgrouse)		Asia
<i>R. (R.) flaminata</i>	Columbiformes: columbid (rock dove, western crowned pigeon)		Asia
<i>R. (s.l.) fluxa sp. inq.</i>	Rodentia: murid (brown rat)		Asia
<i>R. (R.) formosana</i>	Primates: hominid (human)		Asia
<i>R. (R.) fragilis</i>	Columbiformes: columbid (pale-capped pigeon)		Asia
<i>R. (R.) francolini</i>	Galliformes: phasianid (black francolin)		Iraq
<i>R. (R.) frayi</i>	Columbiformes: columbid (green imperial pigeon, white-bellied green pigeon)		Asia
<i>R. (R.) friedbergeri</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Galliformes: phasianid (Indian peafowl, turkey, common pheasant, rock partridge, common quail)		Eurasia
<i>R. (R.) frontina</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Piciformes: picid (Syrian woodpecker, great spotted woodpecker, middle spotted woodpecker, green woodpecker, black woodpecker, Campo flicker); Passeriformes: icterid (Baltimore oriole), laniid (great grey shrike)		Eurasia, Americas
<i>R. (R.) fuhrmanni</i> (syn. <i>Davainea</i> ) [incl. subspp. <i>fuhrmanni</i> , <i>idiogenoides</i> , <i>intermedia</i> ]	Columbiformes: columbid (rock dove, Bengal green pigeon, thick-billed green pigeon, African green pigeon, Oriental turtle dove, laughing dove, green spotted wood dove, Namaqua dove); Passeriformes: alaudid (Maghreb lark)		Asia, India, Africa
<i>R. (R.) funebris sp. inq.</i>	Rodentia: murid (brown rat)		Asia
<i>R. (R.) galeritae</i>	Passeriformes: alaudid (Maghreb lark, crested)		Africa, India

(syn. <i>Davainea</i> , <i>Ransomia</i> )	lark), passerid (house sparrow)		
<i>R. (R.) galli</i>	Galliformes: phasianid (chicken)		Japan
<i>R. (R.) garciai</i>	Passeriformes: icterid (greater Antillean grackle)		Central America
<i>R. (R.) garmi</i>	Columbiformes: columbid (pigeon)		Eurasia
<i>R. (R.) gendrei</i>	Columbiformes: columbid (rock dove, thick-billed green pigeon)		Africa
<i>R. (R.) georgiensis</i>	Galliformes: phasianid (turkey, eastern wild turkey)	Hymenoptera: formicid ant ( <i>Pheidole rinelandica</i> )	North America
<i>R. (R.) geraldshmidti</i>	Casuariiformes: casuariid (southern cassowary)		Australia
<i>R. (R.) gevreyi</i>	Strigiformes: tytonid (African barn owl)		Africa
<i>R. (R.) globirostris</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Galliformes: phasianid (grey partridge, common partridge, Barbary partridge, rock partridge, Chukar partridge); Columbiformes: columbid (rock dove)		Eurasia, Africa
<i>R. (s.l.) globocephala</i> (syn. <i>Davainea</i> )	Passeriformes: icterid (red-rumped cacique)		South America
<i>R. (R.) goura</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Columbiformes: columbid (crowned pigeon, Albert's crowned pigeon))		New Guinea
<i>R. (R.) gracilis</i> (syn. <i>Davainea</i> )	Rodentia: murid (eastern spiny mouse), thryonomyid (greater cane rat)		North America, Africa
<i>R. (R.) graeca</i>	Galliformes: phasianid (rock partridge, chukar partridge, Mongolian ring-necked pheasant); Columbiformes: columbid (rock dove)		Russia, India
<i>R. (R.) gvosdevi</i>	Columbiformes: columbid (European turtle dove)		Russia
<i>R. (R.) idiogenoides</i>	Columbiformes: columbid (African green pigeon)		Africa
<i>R. (R.) inda</i>	Columbiformes: columbid (spotted dove)		India
<i>R. (s.l.) infrequens</i> (syn. <i>Davainea</i> )	Casuariiformes: casuariid (dwarf cassowary)		New Guinea
<i>R. (R.) insignis</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Columbiformes: columbid (Oceanic pigeon, mountain imperial pigeon, Mauritius blue pigeon)		Africa, Indonesia
<i>R. (R.) interrupta</i> (syn. <i>Skrjabinotaurus</i> )	Columbiformes: columbid (spotted dove, Oriental turtle dove)		Asia
<i>R. (R.) johri</i>	Psittaciformes: psittaculid (rose-ringed parakeet)		India
<i>R. (R.) joyeuxbaeri</i>	Columbiformes: columbid (red turtle dove)		Asia
<i>R. (R.) joyeuxi</i>	Columbiformes: columbid (rock dove)		Europe
<i>R. (R.) kantipura</i>	Columbiformes: columbid (rock dove)		Nepal
<i>R. (R.) khalili</i>	Musophagiformes: musophagid (Guinea turaco)		Africa
<i>R. (R.) kirghizica</i>	Columbiformes: columbid (rock dove)		Russia
<i>R. (R.) klebergi</i>	Galliformes: odontophorid (northern bobwhite quail)		North America
<i>R. (R.) kordofanensis</i>	Rodentia: murid (African grass rat)		Africa
<i>R. (R.) korkei</i> (syn. <i>R. (Fuhrmannetta)</i> )	Columbiformes: columbid (rock dove, European turtle dove, Oriental turtle dove, rock partridge)		India, Russia
<i>R. (R.) kunisakiensis</i>	Columbiformes: columbid (white-bellied green pigeon)		Japan
<i>R. (R.) lateralis</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Dermoptera: cynocephalid (Sunda flying lemur)		Indonesia
<i>R. (R.) leipoae</i>	Galliformes: megapodiid (mallee fowl)		Australia
<i>R. (R.) leptacantha</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Galliformes: cracid (black curassow, bare-faced curassow, black curassow)		South America
<i>R. (R.) leptosoma</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Psittaciformes: psittacid (turquoise-fronted amazon, hyacinth macaw, golden-collared macaw, scarlet macaw, red-bellied macaw,		Africa, Asia, Australia, Americas

	blue-winged macaw, red-shouldered macaw, chestnut-fronted macaw, golden parakeet, short-tailed parrot, grey parrot), psittaculid (eastern rosella), cacatuid (galah); Musophagiformes: musophagid (purple-crested turaco)		
<i>R. (R.) loeweni</i>	Lagomorpha: leporid (black-tailed jackrabbit)	Hymenoptera: formicid ant ( <i>Pheiodole sitarches camptestris</i> , <i>P. bicarinata</i> )	North America
<i>R. (s.l.) longicollis</i> (syn. <i>Davainea</i> )	Galliformes: phasianid (chicken)		Europe
<i>R. (R.) lutzi</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Piciformes: picid (chestnut woodpecker, blond-crested woodpecker)		South America
<i>R. (R.) macracanthos</i>	Piciformes: picid (European green woodpecker)		Russia
<i>R. (R.) macrocirrosa</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Musophagiformes: musophagid (red-crested turaco); Cuculiformes: cuculid (Senegal coucal, blue-headed coucal); Galliformes: phasianid (francolin)		Africa
<i>R. (R.) macrarhyncha</i>	Columbiformes: columbid (thick-billed green pigeon)		Asia
<i>R. (R.) macroscolecina</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Psittaciformes: psittaculid (chattering lory, red-capped parrot)		South America
<i>R. (R.) mahonae</i>	Rodentia: thryonomyid (greater cane rat)		Africa
<i>R. (R.) malhotracapoori</i>	Columbiformes: columbid (rock dove)		India
<i>R. (R.) maplestonei</i>	Psittaciformes: psittacid (parrot)		India
<i>R. (R.) mathevossianae</i>	Galliformes: phasianid (see-see partridge)		Russia
<i>R. (R.) mehrai</i>	Columbiformes: columbid (rock dove)	Hymenoptera: formicid ant ( <i>Pheidole rhombinola</i> )	India
<i>R. (R.) melomyos</i>	Rodentia: murid (black-tailed mosaic-tailed rat)		New Guinea
<i>R. (R.) michaelseni</i>	Pterocliiformes: pteroclid (variegated sandgrouse)		Africa, India
<i>R. (R.) micracantha</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Columbiformes: columbid (rock dove, European turtle dove, laughing dove)		Eurasia
<i>R. (R.) microrhyncha</i>	Columbiformes: columbid (spotted dove)		Asia
<i>R. (R.) microscolecina</i> (syn. <i>Davainea</i> , <i>Kotlania</i> , <i>Ransomia</i> )	Psittaciformes: psittaculid (Eclectus parrot, great red parrot, violet-necked lory), cacatuid (salmon-crested cockatoo)		Asia
<i>R. (R.) mitchelli</i>	Casuariiformes: casuariid (emu)	Hymenoptera: formicid ( <i>Pheidole</i> )	Australia
<i>R. (R.) moldavica</i>	Piciformes: picid (European green woodpecker, grey-headed woodpecker, Eurasian wryneck)		Europe
<i>R. (R.) multicapsulata</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Galliformes: phasianid (common pheasant)		Europe
<i>R. (R.) murium</i>	Rodentia: murid (brown rat)		Madagascar
<i>R. (R.) nagpurensis</i>	Columbiformes: columbid (rock dove)		India
<i>R. (R.) namaquensis</i>	Rodentia: murid (Namaqua rock rat)		Africa
<i>R. (R.) neyrai</i>	Otidiformes: otidid (red-crested bustard)		Africa
<i>R. (R.) nripendra</i>	Columbiformes: columbid (rock dove)		Nepal
<i>R. (R.) oitensis</i>	Accipitriformes: accipitrid (Japanese sparrowhawk)		Japan
<i>R. (R.) oligocapsulata</i>	Lagomorpha: leporid (tapeti)		South America
<i>R. (R.) oligorchida</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Psittaciformes: psittaculid (Eclectus parrot)		Polynesia
<i>R. (R.) ortleppi</i>	Columbiformes: columbid (pigeon)		Africa
<i>R. (R.) osakensis</i>	Anseriformes: anatid (duck)		Japan
<i>R. (R.) osipovi</i>	Pterocliiformes: pteroclid (black-bellied sandgrouse)		Russia
<i>R. (R.) palawanensis</i>	Columbiformes: columbid (common emerald dove)		Philippines

<i>R. (R.) parviuncinata</i> (syn. <i>Ransomia</i> )	Anseriformes: anatid (mallard)		China
<i>R. (R.) passeriformicola</i>	Passeriformes: sturnid (hill myna)		Philippines
<i>R. (R.) paucicapulata</i>	Piciformes: picid (great spotted woodpecker)		Europe
<i>R. (R.) paucitesticulata</i> (syn. <i>Davainea, Ransomia</i> )	Columbiformes: columbid (spotted dove, Nicobar pigeon)		India
<i>R. (R.) penelopina</i> (syn. <i>Davainea, Ransomia</i> )	Galliformes: cracid (dusky-legged guan)		South America
<i>R. (R.) penetrans</i> [incl. <i>R. p. nova</i> ] (syn. <i>Davainea, Ransomia</i> )	Galliformes: phasianid (chicken, black-gold pheasant, rock partridge, black grouse); Passeriformes: sturnid (common mynah)		Eurasia
<i>R. (R.) peradenica</i>	Galliformes: phasianid (chicken)		Sri Lanka
<i>R. (R.) permista</i>	Piciformes: picid (green-backed woodpecker); Charadriiformes: scolopacid (common sandpiper)		Africa
<i>R. (R.) perplexa</i>	Columbiformes: columbid (rock pigeon, dove)		India
<i>R. (R.) pici</i>	Piciformes: picid (Japanese green woodpecker, great spotted woodpecker)		Japan, Russia
<i>R. (R.) pintneri</i> (syn. <i>Davainea, Ransomia</i> ) [incl. var. <i>polyorchis, polychalix</i> ]	Galliformes: numidid (helmeted guineafowl, Reichenow's guineafowl, tufted helmeted guineafowl, southern crested guineafowl); Psittaciformes: psittaculid (coconut lorikeet, rosella, rock parrot)		Africa, New Guinea
<i>R. (R.) provincialis</i> (syn. <i>Davainea, Ransomia</i> )	Galliformes: phasianid (red-billed francolin)		Africa
<i>R. (R.) pseudocyrus</i>	Anseriformes: anatid (mallard)		Asia
<i>R. (R.) psittacea</i> (syn. <i>Davainea, Ransomia</i> )	Psittaciformes: cacatuid (triton cockatoo), psittaculid (eclectus parrot)		Polynesia
<i>R. (R.) quadritesticulata</i>	Columbiformes: columbid (red-collared dove)		India
<i>R. (s.l.) rothlisbergeri</i>	Primates: lorisid (Bengal slow loris)		Indonesia
<i>R. (R.) rybickae</i>	Galliformes: phasianid (chicken)		India
<i>R. (R.) saharanpurensis</i>	Galliformes: phasianid (chicken)		India
<i>R. (R.) sartica</i> (syn. <i>Davainea</i> ) [incl. var. <i>massilliensis, mediterranea</i> ]	Passeriformes: corvid (carrion crow), passerid (house sparrow), emberizid (striolated bunting), phylloscopid (Siberian chiffchaff)		Russia, Europe
<i>R. (R.) selfi</i>	Lagomorpha: leporid (desert cottontail)		North America
<i>R. (R.) senaariensis</i> (syn. <i>Davainea, Ransomia</i> )	Columbiformes: columbid (speckled pigeon)		Africa
<i>R. (R.) sequens</i>	Columbiformes: columbid (Philippine collared-dove)		Philippines
<i>R. (R.) shantungensis</i> (syn. <i>R. sinensis</i> )	Galliformes: phasianid (chicken); Rodentia: murid (black rat)		China
<i>R. (R.) sigmodontis</i>	Rodentia: cricetid (hispid cotton rat)		North America
<i>R. (R.) singhi</i>	Columbiformes: columbid (rock dove)	Hymenoptera: formicid ant ( <i>Pheidole rhombinoda</i> )	India
<i>R. (R.) skrabini</i>	Galliformes: phasianid (grey partridge, Indian peafowl)		Russia, India
<i>R. (R.) somalensis</i>	Galliformes: numidid (vulturine guineafowl)		Africa
<i>R. (R.) sonini</i>	Piciformes: picid (black woodpecker, grey-headed woodpecker, great spotted woodpecker); Passeriformes: muscicapid (common rock thrush), turdid (mistle thrush)		Russia
<i>R. (s.l.) sphaeroides</i> (syn. <i>Davainea</i> )	Accipitriformes: accipitrid (black kite, common buzzard, eastern steppe buzzard)		Russia
<i>R. (R.) spiralis</i> (syn. <i>Ransomia</i> )	Galliformes: phasianid (chicken)		India
<i>R. (R.) steinhardtii</i>	Galliformes: numidid (helmeted guineafowl, southern crested guineafowl)		Africa

<i>R. (R.) streptopeliae</i>	Columbiformes: columbid (red turtle dove)		India
<i>R. (R.) taiwanensis</i>	Columbiformes: columbid (pigeon)		Asia
<i>R. (R.) taylori</i>	Psittaciformes: psittacid (grey parrot)		Africa
<i>R. (R.) tetragona</i> [incl. <i>R. t.</i> var. <i>cohni</i> ] (syn. <i>Davainea</i> , <i>Ransomia</i> )	Galliformes: phasianid (chicken, Indian peafowl, green peafowl, turkey, francolin, great argus, ruffed grouse, rock ptarmigan, willow ptarmigan, grey partridge, rock partridge, common quail), numidid (helmeted guinea fowl, southern crested guineafowl); Columbiformes: columbid (rock dove, European turtle dove); Anseriformes: anatid (duck)	Diptera: muscid fly ( <i>Musca domestica</i> ); Hymenoptera: formicid ants ( <i>Leptothorax</i> , <i>Pheidole rhombinoda</i> , <i>vinelandica</i> , <i>Pachycondyla sennaarensis</i> , <i>Tetramorium simillium</i> , <i>caespitum</i> ); Gastropoda: hygromiid snails ( <i>Helix carthusianella</i> , <i>H. maculosa</i> )	worldwide
<i>R. (R.) tetragonoides</i> (syn. <i>Ransomia</i> )	Galliformes: numidid (helmeted guineafowl)		Africa
<i>R. (R.) thapari</i> (syn. <i>Davainea</i> )	Piciformes: picid (scaly-bellied woodpecker); Galliformes: phasianid (chicken); Passeriformes: pomatostomatid (babbler)		India
<i>R. (s.l.) thryonomysi</i>	Rodentia: thryonomyid (greater cane rat)		Africa
<i>R. (R.) tokyoensis</i>	Columbiformes: columbid (rock dove)		Japan
<i>R. (R.) torquata</i> [incl. <i>R. t.</i> var. <i>rajae</i> ]	Columbiformes: columbid (rock dove)		India, Asia
<i>R. (R.) toyohashiensis</i>	Galliformes: numidid (helmeted guineafowl)		Japan
<i>R. (R.) trapezoides</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Rodentia: murid (typical striped grass mouse, striped mouse, African grass rat)		Africa
<i>R. (R.) trinitatae</i>	Rodentia: dasyproctid (agouti), echimyid (Guyenne spiny rat)		South America
<i>R. (R.) tunetensis</i>	Columbiformes: columbid (rock dove, Oriental turtle dove, European turtle dove, pigeon)		Russia, India
<i>R. (R.) turaci</i>	Musophagiformes: musophagid (Livingstone's turaco)		Africa
<i>R. (R.) turnixae</i>	Charadriiformes: turnicid (yellow-legged buttonquail)		Asia
<i>R. (R.) undulata</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Musophagiformes: musophagid (great blue turaco, purple-crested turaco); Cuculiformes: cuculid (African emerald cuckoo)		Africa
<i>R. (s.l.) vaganda</i> (syn. <i>Davainea</i> )	Accipitriformes: accipitrid (African fish eagle)		Africa
<i>R. (R.) vietnamense</i>	Columbiformes: columbid (spotted dove)		Asia
<i>R. (R.) vinagoi</i>	Columbiformes: columbid (African green pigeon)		Africa
<i>R. (R.) vivieni</i>	Galliformes: phasianid (Japanese quail)		Indochina
<i>R. (R.) vogeli</i>	Columbiformes: columbid (African green pigeon)		Africa
<i>R. (s.l.) voluta</i>	Eulipotyphla: erinacid (four-toed hedgehog)		Africa
<i>R. (R.) volzi</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Galliformes: phasianid (chicken, Indian peafowl); Columbiformes: columbid (rock dove)		Russia, India
<i>R. (R.) waltairensis</i>	Columbiformes: columbid (spotted dove)		India
<i>R. (R.) weissii</i> [incl. <i>R. w.</i> var. <i>valiclusa</i> ] (syn. <i>Ransomia</i> )	Columbiformes: columbid (rock dove, European turtle dove, Oriental turtle dove, laughing dove, yellow-eyed pigeon)		Russia, Africa, Australia
<i>R. (R.) wernerii</i> (syn. <i>Davainea</i> , <i>Ransomia</i> )	Coliiformes: coliid (speckled mousebird)		Africa, Europe, India
<i>R. (R.) williamsi</i>	Galliformes: phasianid (turkey)		North America
<i>R. (R.) zahratis</i>	Columbiformes: columbid (rock dove)		Middle-East

Subgenus <i>Paroniella</i> (genital apertures unilateral, one oncosphere per egg capsule) (some authors have promoted this subgenus to generic status, thus various synonyms exist)			
<i>R. (P.) acanthovagina</i>	Galliformes: phasianid (chicken)		Malaya
<i>R. (P.) amethiensis</i>	Passeriformes: nectariniid (purple sunbird)		India
<i>R. (P.) assamensis</i>	Galliformes: phasianid (chicken)		India
<i>R. (P.) bargetzii</i>	Piciformes: lybiid (grey-throated barbet)		Africa
<i>R. (P.) barmerensis</i>	Passeriformes: corvid (house crow)		India
<i>R. (P.) beppuensis</i>	Passeriformes: corvid (eastern jungle crow)		Japan
<i>R. (P.) blanchardi</i> (syn. <i>Davainea</i> )	Rodentia: murid (Mentawai long-tailed giant rat, noisy rat, Rajah spiny rat), thryonomyid (greater cane rat)		Africa, Indonesia
<i>R. (P.) bomensis</i>	Piciformes: lybiid (double-toothed barbet)		Africa
<i>R. (P.) boviemi</i>	Pholidota: manid (Sunda pangolin)		Indonesia
<i>R. (P.) bulbularum</i>	Passeriformes: pycnonotid (yellow-vented bulbul)		Philippines
<i>R. (P.) capoori</i>	Galliformes: phasianid (grey francolin)		India
<i>R. (P.) centuri</i>	Piciformes: picid (red-bellied woodpecker)		North America
<i>R. (P.) cirroflexa</i>	Piciformes: picid (sooty woodpecker)		Philippines
<i>R. (P.) compacta</i> (incl. <i>R. c. polytestis</i> ) (syn. <i>Davainea</i> )	Passeriformes: turdid (mistle thrush), oriolid (Eurasian golden oriole, African golden oriole, black-naped oriole), ploceid (orange weaver), parid (Eurasian blue tit)		Eurasia, Africa
<i>R. (P.) conopophilae</i> (syn. <i>Davainea</i> )	Passeriformes: meliphagid (blue-faced honeyeater, rufous-banded honeyeater, garrulous honeyeater, white-throated honeyeater)		Australasia
<i>R. (P.) coronea</i>	Passeriformes: corvid (Philippine crow, common raven, Australian raven)		Philippines, India
<i>R. (P.) corvina</i> (syn. <i>Davainea</i> , <i>D. polycalcarata</i> )	Passeriformes: corvid (Indian jungle crow, large-billed crow, white-billed crow), icterid (Dumont's grackle), artamid (magpie)		Africa, India, Asia
<i>R. (P.) cruciata</i> (syn. <i>Davainea</i> )	Piciformes: picid (lineated woodpecker, grey-headed woodpecker), corvid (magpie)	Coleoptera: kateretid ( <i>Brachypterus aurantiacus</i> )	South America, Russia
<i>R. (P.) culiauana</i>	Passeriformes: oriolid (Philippine oriole)		Philippines
<i>R. (P.) delhiensis</i>	Galliformes: numidid (helmeted guineafowl)		India
<i>R. (P.) dendrocopina</i>	Piciformes: picid (Japanese pygmy woodpecker)		Japan
<i>R. (P.) duosyntesticulata</i>	Piciformes: megalaimid (coppersmith barbet)		India
<i>R. (P.) facile</i> (syn. <i>Davainea</i> )	Galliformes: phasianid (satyr tragopan)		Asia
<i>R. (P.) fecunda</i>	Anseriformes: anatid (duck)		Asia
<i>R. (P.) filiforme</i>	Columbiformes: columbid (European turtle dove)		Cuba
<i>R. (P.) fulvia</i>	Pterocliiformes: pteroclid (black-bellied sandgrouse)		Asia
<i>R. (P.) huebscheri</i>	Pelecaniformes: ardeid (yellow bittern)		China
<i>R. (P.) japonica</i>	Passeriformes: corvid (large-billed crow)		Japan
<i>R. (P.) karatchvili</i>	Passeriformes: corvid (Eurasian magpie)		Asia
<i>R. (P.) kashiwarensis</i>	Galliformes: phasianid (chicken)		Japan
<i>R. (P.) longispina</i> (syn. <i>Davainea</i> )	Piciformes: picid (chestnut woodpecker, blond-crested woodpecker, giant lineated woodpecker)		South America
<i>R. (P.) macassarensis</i>	Galliformes: phasianid (chicken)		Indonesia
<i>R. (P.) magninumida</i>	Galliformes: phasianid (chicken, turkey), numidid (helmeted guineafowl)	Coleoptera: cerabycid ( <i>Solenophorus pedicularis</i> )	Iran, North America
<i>R. (P.) minuta</i>	Galliformes: phasianid (northern bobwhite quail)		North America
<i>R. (P.) molpastina</i>	Passeriformes: pycnonotid (Sri Lankan red-vented bulbul)		India

<i>R. (P.) mothensis</i>	Passeriformes: corvid (large-billed crow)		India
<i>R. (P.) myzomelae</i>	Passeriformes: meliphagid (Micronesian myzomela)		Indonesia
<i>R. (P.) nedumangadensis</i>	Columbiformes: columbid (rock dove)		India
<i>R. (P.) ngoci</i>	Columbiformes: columbid (mountain imperial pigeon)		Indochina
<i>R. (P.) numida</i> (syn. <i>Davainea</i> )	Galliformes: numidid (helmeted guineafowl)		Africa, Americas
<i>R. (P.) paradisea</i> (syn. <i>Davainea</i> )	Passeriformes: paradisaeid (crinkle-collared manucode)		New Guinea
<i>R. (P.) parbata</i>	Galliformes: phasianid (chicken)		Nepal
<i>R. (P.) perreti</i>	Passeriformes: pycnonotid (dark-capped bulbul)		Africa
<i>R. (P.) pinsonae</i>	Piciformes: picid (lesser yellownape, black woodpecker)		Asia
<i>R. (P.) pycnonoti</i>	Passeriformes: pycnonotid (light-vented bulbul)		China
<i>R. (P.) rangonica</i>	Galliformes: phasianid (chicken)		India
<i>R. (P.) rangoonica</i>	Accipitriformes: accipitrid (black kite)		India
<i>R. (P.) retractilis</i> (syn. <i>Davainea</i> )	Lagomorpha: leporid (black-tailed jackrabbit, cottontail rabbit, desert cottontail); Rodentia: murid (black rat)		Africa, North America
<i>R. (P.) reynoldsae</i>	Passeriformes: corvid (house crow, fan-tailed raven)		Africa, Asia
<i>R. (P.) rhynchota</i> (syn. <i>Davainea</i> )	Piciformes: picid (northern flicker, red-headed woodpecker)		North America
<i>R. (P.) siamensis</i>	Piciformes: megalaimid (lineated barbet, green-eared barbet)		Asia
<i>R. (P.) singaporensis</i>	Passeriformes: oriolid (black-naped oriole)		Singapore
<i>R. (P.) southwelli</i>	Galliformes: phasianid (chicken)		Malaya
<i>R. (P.) sphecotheridis</i> (syn. <i>Davainea</i> )	Passeriformes: oriolid (short-billed honeyeater), dicurid (drongo)		Australasia
<i>R. (P.) symonsii</i>	Galliformes: phasianid (Indian peafowl)		India
<i>R. (P.) tenuiformis</i>	Galliformes: phasianid (chicken)		Africa
<i>R. (P.) tinguiana</i>	Galliformes: phasianid (chicken)		Philippines
<i>R. (P.) tragopani</i> (syn. <i>Davainea</i> )	Galliformes: phasianid (satyr tragopan)		India
<i>R. (P.) urogalli</i> (syn. <i>Davainea</i> )	Galliformes: phasianid (grey partridge, rock partridge, red-legged partridge, see-see partridge, willow ptarmigan, white-tailed ptarmigan, rock ptarmigan, red grouse, black grouse, western capercaillie, Himalayan snowcock, Altai snowcock, satyr tragopan); Pelecaniformes: ardeid (little bittern)	Hymenoptera: formicid ants	Eurasia
<i>R. (P.) vigintivassus</i>	Galliformes: phasianid (chicken)		South America
<i>R. (P.) woodlandi</i>	Galliformes: numidid (helmeted guineafowl)		Africa
<i>R. (P.) yaponensis</i>	Piciformes: picid (woodpecker)		Africa
Subgenus <i>Skrjabinia</i> (genital apertures alternating irregularly, one oncosphere per egg capsule) (some authors have promoted this subgenus to generic status, thus various synonyms exist)			
<i>R. (S.) bodkini</i>	Charadriiformes: scolopacid (spotted sandpiper)		South America
<i>R. (S.) boehmi</i>	Galliformes: phasianid (chicken)		Europe
<i>R. (S.) bolivari</i>	Galliformes: phasianid (common quail, rock partridge, red-legged partridge)		Europe
<i>R. (S.) bonini</i>	Columbiformes: columbid (common wood pigeon, Oriental turtle dove); Galliformes: phasianid (chicken); Anseriformes: anatid (duck)		Europe
<i>R. (S.) campetherae</i>	Piciformes: picid (woodpecker)		Africa
<i>R. (S.) caprimulgi</i>	Caprimulgiformes: caprimulgid (Indian nightjar)		India

<i>R. (S.) caucasica</i>	Galliformes: phasianid (chicken, turkey)	Hymenoptera: formicid ant ( <i>Tetramorium caespitum</i> )	Russia
<i>R. (S.) centroceri</i>	Galliformes: phasianid (greater sage-grouse)		North America
<i>R. (S.) centropi</i> (syn. <i>Davainea</i> )	Cuculiformes: cuculid (common coucal)		India
<i>R. (S.) cesticillus</i> (syn. <i>Davainea</i> , <i>Ransomia mutabilis</i> )	Galliformes: phasianid (chicken, grey junglefowl, turkey, grey partridge, Daurian partridge, rock partridge, common quail, willow ptarmigan, red grouse, black grouse, hazel grouse, common pheasant, western capercaillie), numidid (helmeted guineafowl), odontophorid (northern bobwhite quail); Anseriformes: anatid (mallard); Otidiformes: otidid (Houbara bustard); Passeriformes: fringillid (canary)	Coleoptera: carabid ( <i>Agonoderus</i> , <i>Amara basillaris</i> , <i>fallax</i> , <i>laticollis</i> , <i>muscula</i> , <i>obesa</i> , <i>Anaferonia constricta</i> , <i>substriata</i> , <i>Anisodactylus</i> , <i>Anisotarsus agilis</i> , <i>subvirens</i> , <i>Bradycellus</i> , <i>Bradytus</i> , <i>Calathus opaculus</i> , <i>Chalenius tomentosus</i> , <i>Cratacanthus dubius</i> , <i>Discoderus</i> , <i>Harpalus faunus</i> , <i>herbivagus</i> , <i>pennsylvanicus</i> , <i>Poecilus</i> , <i>Pterostichus permudus</i> , <i>chalcites</i> , <i>constricta</i> , <i>torvus</i> , <i>Rhagadus</i> , <i>Selenophorus pedicularis</i> , <i>Stenocellus</i> , <i>Stenolophus</i> , <i>Tachys</i> , <i>Triplectrus rusticus</i> , <i>Zabrus</i> ), ostomid ( <i>Tenebroides mauritanicus</i> ), tenebrionid ( <i>Alphitobius</i> , <i>Tenebrio</i> , <i>Tribolium confusum</i> ), anthicid ( <i>Anthicus</i> ), scarabaeid ( <i>Aphodius granarius</i> , <i>Choeridium histeroides</i> ), histerid ( <i>Carcinops pumilo</i> , <i>Epierus pulicarius</i> ), dermestid ( <i>Dermestes</i> ), cantharid ( <i>Podabrus modestus</i> ); Diptera: ichneumonid ( <i>Stenophorus</i> ); Sauria: agamid ( <i>Gonocephalus</i> )	worldwide
<i>R. (S.) circumvallata</i> (syn. <i>R. fedjuschini</i> , <i>R. c. cadarachensis</i> , <i>R. c. siberica</i> , <i>Davainea</i> , <i>Ransomia</i> , <i>Johnstonia</i> )	Galliformes: phasianid (chicken, turkey, common quail, grey partridge, Barbary partridge, black grouse)		Eurasia
<i>R. (S.) crepidocotyle</i>	Passeriformes: leiothrichid (black-throated laughingthrush)		Indochina
<i>R. (S.) cryptocotyle</i> (syn. <i>Davainea</i> )	Galliformes: phasianid (common quail)		Africa
<i>R. (S.) daviesi</i>	Galliformes: phasianid (rock partridge)		India
<i>R. (S.) dendrocopina</i>	Piciformes: picid (Japanese pygmy woodpecker)		Japan
<i>R. (S.) dhuncheta</i>	Galliformes: phasianid (Kalij pheasant)		Nepal

<i>R. (S.) fatalis</i>	Rodentia: murid (lesser bandicoot rat, brown rat)		Asia
<i>R. (S.) hiyodori</i>	Passeriformes: pycnonotid (brown-eared bulbul)		Japan
<i>R. (S.) indica</i> (syn. <i>Davainea</i> )	Galliformes: phasianid (chicken, chukar partridge)		India, Africa
<i>R. (S.) kakia</i>	Passeriformes: corvid (house crow)		India
<i>R. (S.) lavieri</i> (syn. <i>Davainea</i> )	Cuculiformes: cuculid (coucal)		Africa
<i>R. (S.) magnicoronata</i> (syn. <i>Davainea</i> )	Caprimulgiformes: caprimulgid (Nacunda nighthawk)		South America
<i>R. (S.) maroteli</i>	Galliformes: phasianid (turkey)		Europe
<i>R. (S.) metacentropi</i>	Cuculiformes: cuculid (greater coucal)		Asia
<i>R. (S.) microcotyle</i> (syn. <i>Davainea</i> )	Anseriformes: anatid (mallard)		Europe
<i>R. (S.) oligacantha</i> (syn. <i>Davainea</i> )	Tinamiformes: tinamid (red-winged tinamou)		South America
<i>R. (S.) petrovi</i> (syn. <i>Davainea</i> )	Galliformes: phasianid (chicken)		Europe
<i>R. (S.) polyhamata</i>	Charadriiformes: scolopacid (Siberian whimbrel)		Japan
<i>R. (S.) polyuterina</i> (syn. <i>Davainea</i> )	Galliformes: phasianid (grey partridge, rock partridge, common quail, black grouse, western capercaillie)		Eurasia, Africa
<i>R. (S.) progenesia</i>	Galliformes: phasianid (black grouse, grey partridge)		Russia
<i>R. (S.) pterocleti</i>	Pterocliiformes: pteroclid (black-bellied sandgrouse, Pallas's sandgrouse)		Russia
<i>R. (S.) ransomi</i> (syn. <i>Davainea</i> )	Galliformes: phasianid (chicken, turkey)		North America
<i>R. (S.) retusa</i> (syn. <i>Davainea</i> )	Galliformes: phasianid (black grouse, hazel grouse, western capercaillie)		Russia
<i>R. (S.) spinosissima</i> (syn. <i>Davainea</i> )	Passeriformes: turdid (common blackbird, redwing)		Europe
<i>R. (S.) sudanica</i>	Galliformes: phasianid (chicken)		Africa
<i>R. (S.) variabilis</i>	Galliformes: phasianid (greater prairie chicken)		North America
Subgenus <i>Fuhrmannetta</i> (genital apertures alternating irregularly, several oncospheres per egg capsule) (some authors have promoted this subgenus to generic status, thus various synonyms exist)			
<i>R. (F.) bandicotensis</i>	Rodentia: murid (greater bandicoot rat)		China
<i>R. (F.) birmanica</i>	Galliformes: phasianid (chicken); Anseriformes: anatid (duck)		Eurasia
<i>R. (F.) bucerotidarum</i>	Piciformes: lybiid (double-toothed barbet)		Africa
<i>R. (F.) caballeri</i>	Columbiformes: columbid (Zenaida dove, grey-fronted quail-dove)		Central America
<i>R. (F.) crassula</i> (syn. <i>Davainea</i> , <i>Johnstonia</i> )	Columbiformes: columbid (rock dove, European turtle dove, Oriental turtle dove, laughing dove, lemon dove); Galliformes: phasianid (creek partridge, rock partridge, common quail)		Eurasia, Americas
<i>R. (F.) elongata</i> (syn. <i>Davainea</i> , <i>Johnstonia</i> )	Tinamiformes: tinamid (tinamou, red-winged tinamou, lesser nothura)		South America
<i>R. (F.) globocaudata</i> (syn. <i>Davainea</i> , <i>Johnstonia</i> )	Galliformes: phasianid (western capercaillie, hazel grouse, willow grouse)		Eurasia
<i>R. (F.) hertwigi</i> (syn. <i>Davainea</i> , <i>Johnstonia</i> )	Accipitriformes: accipitrid (Bonelli's eagle, red kite)	Sauria: lacertid (common wall lizard)	Eurasia
<i>R. (F.) jurubatensis</i>	Rodentia: cricetid (Goytaca mouse)		South America
<i>R. (F.) laticanalisis</i> (syn. <i>Davainea</i> , <i>Johnstonia</i> )	Galliformes: phasianid (chicken, red junglefowl, common quail, grey partridge)		Europe, South America

<i>R. (F.) leptotrachela</i> (syn. <i>Davainea</i> , <i>Johnstonia</i> )	Pteroclitiformes: pteroclid (Namagua sandgrouse)		Africa
<i>R. (F.) lophoceri</i>	Bucerotiformes: bucerotid (red-billed hornbill, yellow-billed hornbill)		Africa
<i>R. (F.) malakartis</i>	Galliformes: odontophorid (northern bobwhite quail, California quail)		Egypt
<i>R. (F.) nepalis</i>	Passeriformes: passerid (house sparrow)		Nepal
<i>R. (F.) pluriuncinata</i> (syn. <i>Davainea</i> , <i>Johnstonia</i> )	Galliformes: phasianid (common quail, Barbary partridge)		Europe
<i>R. (F.) pseudoechinobothrida</i>	Galliformes: phasianid (chicken, turkey, common quail)		Indochina
<i>R. (F.) salmoni</i> (syn. <i>R. stilesiella</i> , <i>R. stilesiella</i> , <i>Davainea</i> , <i>Johnstonia</i> )	Lagomorpha: leporid (eastern cottontail rabbit, black-tailed jackrabbit)		North America
<i>R. (F.) srbuhiae</i>	Galliformes: phasianid (chukar partridge)		Russia
<i>R. (F.) talourensis</i>	Galliformes: phasianid (chicken)		India
<i>R. (F.) vandenbrandeni</i>	Psittaciformes: psittacid (grey parrot)		Africa
Reassigned species			
<i>R. (R.) allomyodes</i> (syn. <i>Davainea</i> ) (now <i>Idiogenoides</i> )	Psittaciformes: psittaculid (Edward's fig-parrot); Columbiformes: columbid (pink-necked green pigeon)		New Guinea, South America
<i>R. (R.) alouttae</i> (syn. <i>R. multitesticulata</i> ) (now <i>Buginetta</i> )	Primates: atelid (Guianan red howler, Venezuelan red howler, Columbian red howler), hominid (human)		South America
<i>R. (R.) anoplocephaloides</i> (now <i>Baerfainia</i> )	Pholidota: manid (tree pangolin)		Africa
<i>R. (s.l.) biroi</i> (syn. <i>Kotlani</i> ) (now <i>Davainea</i> )	Psittaciformes: psittacid (orange-breasted fig parrot)		New Guinea
<i>R. (s.l.) campanulata</i> (syn. <i>Davainea</i> ) (now <i>Davaineolepis</i> )	Galliformes: phasianid (partridge)		South America
<i>R. (S.) columbae</i> (now <i>Davainea</i> )	Columbiformes: columbid (rock dove)		Europe
<i>R. contorta</i> (syn. <i>Paroniella</i> , <i>Davainea</i> ) (now <i>Diorirailletina</i> )	Pholidota: manid (Chinese pangolin)	Hymenoptera: formicid (ants)	Indochina
<i>R. cubensis</i> (syn. <i>R. loechenesalavezi</i> , <i>R. (F.) kouridovali</i> , <i>Thysanotaenia</i> ) (now <i>Inermicapsifer</i> )	Primates: hominid (human)		Cuba
<i>R. (P.) macropa</i> (now <i>Calostaurus</i> )	Diprotodontia: macropodid (dusky pademelon)		Australia
<i>R. (R.) madagascariensis</i> (syn. <i>R. garrisoni</i> , <i>R. siriraji</i> , <i>Davainea</i> , <i>Ransomia</i> , <i>Taenia</i> ) (now <i>Inermicapsifer</i> )	Rodentia: murid (brown rat, black rat); Primates: hominid (human)		Africa, Asia
<i>R. (S.) parva</i> (syn. <i>Davainea</i> ) (now <i>Mathevotaenia</i> )	Eulipotyphla: erinaceid (hedgehog)		Europe
<i>R. (S.) polycalceola</i> (syn. <i>Davainea</i> ) (now <i>Delamuretta</i> )	Rodentia: murid (Abyssinian grass rat, Musschenbroek's mouse)		Africa, Indonesia
<i>R. (R.) rahmi</i> (now <i>Manitaurus</i> )	Pholidota: manid (tree pangolin)		Africa

**Parasite morphology:** *Raillietina* spp. form 3 sequential developmental stages: eggs, larvae and adults. Mature worm eggs are oval in shape and vary considerably in size depending on species, most ranging from 25-50  $\mu\text{m}$  long but some forming larger eggs (60-90 x 45-80  $\mu\text{m}$ ). Each egg contains a single nonciliated hexacanth (6 hooked) embryo (oncosphere) surrounded by a non-striated shell (embryophore) and a delicate membrane. Cysticercoid larvae are milky white in colour and elliptical in shape measuring 180-450 x 125-325  $\mu\text{m}$ . They are lacunate (with internal cavity), surrounded by a thick cyst wall (18-25  $\mu\text{m}$ ) and have a tail-like cercomer and an anterior scolex retracted into an internal bladder. Adult tapeworms have an anterior knob-like everted scolex, a short flattened neck region and an elongate highly-segmented ribbon-like whitish body (strobila) measuring 10-12 cm long (some up to 25 cm) by 1-4 mm wide. The scolex measures up to 300  $\mu\text{m}$  long and has an elongate rostellum (50-150  $\mu\text{m}$  in diameter) armed with several hundred hammer-shaped hooks arranged in 1-2 circular rows. The scolex also has 4 oval suckers (85-200  $\mu\text{m}$  in diameter) often armed with numerous (usually 8-12) hooks (5-15  $\mu\text{m}$  long). Adult worms are hermaphroditic and each segment possesses male and female reproductive organs with a common genital pore located at the margin either unilaterally or alternating irregularly for consecutive segments. The uterus in mature segments breaks down into small capsules containing either 1 or several (6-12) eggs and gravid proglottids detach from the strobila. The location of the genital pores and the structure of egg capsules have been used to recognize 4 subgenera (some authorities recognize them as separate genera), as follows: *R. (Raillietina)* with unilateral genital pores and egg capsules containing several oncospheres; *R. (Paroniella)* with unilateral genital pores and egg capsules containing one oncosphere; *R. (Fuhrmannetta)* with genital pores alternating irregularly and egg capsules containing several oncospheres; and *R. (Skrjabinia)* with genital pores alternating irregularly and egg capsules containing one oncosphere.

**Site of infection:** *Raillietina* tapeworms occur in the small intestines of vertebrate definitive hosts, predominantly birds, but also some mammals (rodents, lagomorphs, primates, insectivores). Infections in birds are commonly found in the posterior small intestine, but some may extend from the stomach to the cloaca. Larval stages (cysticercoids) develop in the body cavities of invertebrate intermediate hosts; mostly insects (beetles, ants, flies) but sometimes including gastropods (slugs and snails). Several species may also form cysticercoid stages in connective tissues of second intermediate hosts such as lizards.

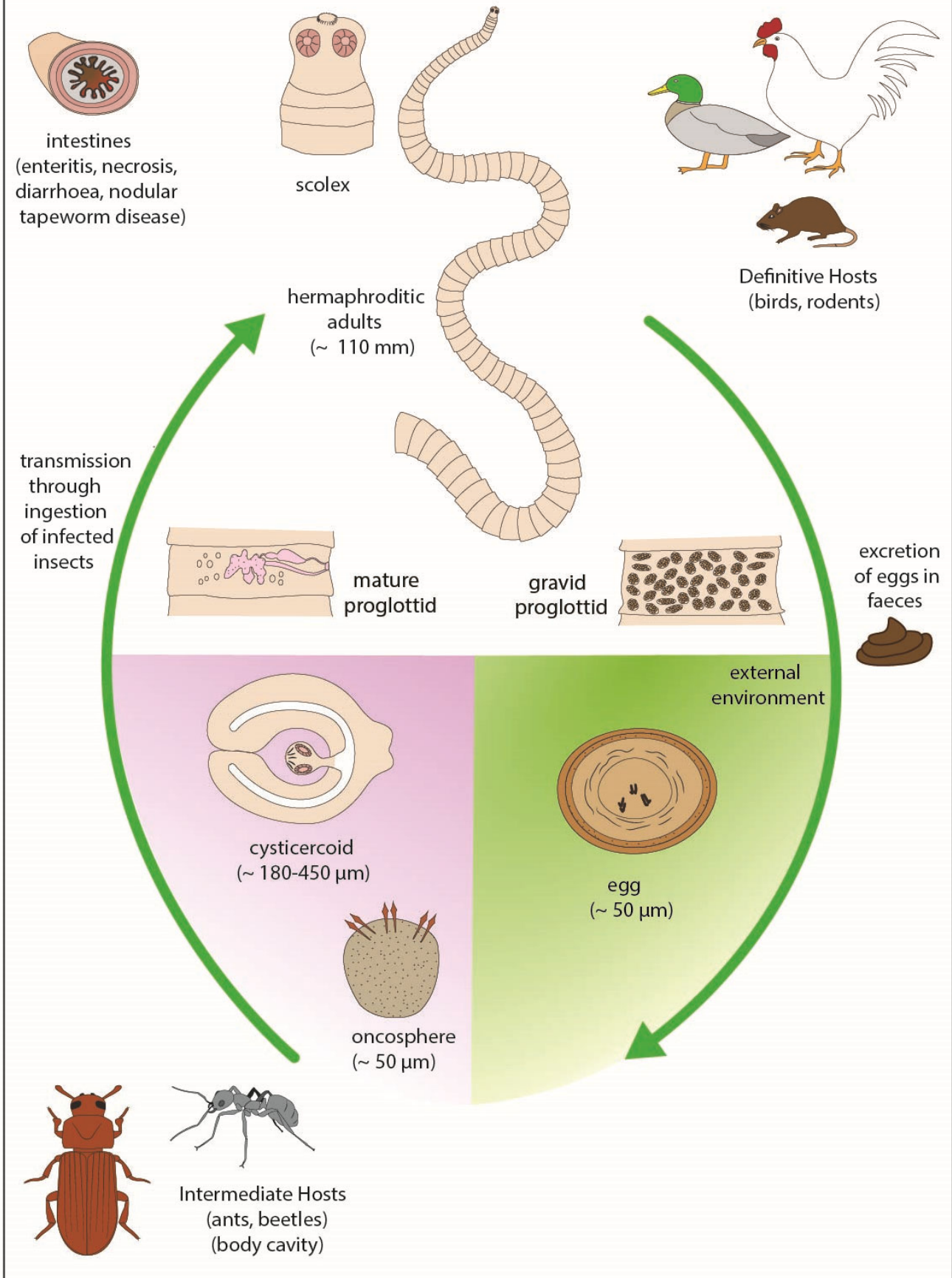
**Pathogenesis:** Adult tapeworms attach themselves to the intestinal wall using their anterior attachment organs (scolex with suckers and armed rostellum). They can insert their scoleces through mucosal layers with the rostellum buried deeply in the muscularis mucosae, thereby causing traumatic damage and eliciting inflammatory reactions. The worms lack digestive tracts and do not feed on host tissues but absorbing nutrients from partly digested food (chyme) in the gut lumen. Light infections in healthy well-fed birds are mostly asymptomatic, although there is mounting evidence that subclinical infections may reduce production parameters in poultry, including growth retardation, reduced weight gain and decreased egg production. Heavy infections markedly reduce feed conversion efficiencies (parasites compete with host for nutrition) which can result in weight loss and stunted growth in juvenile birds and emaciation in adult birds. Severe infections may lead to the formation of intestinal granuloma/nodular lesions (pinhead to pea-sized) around attachment sites due to leucocytic cellular infiltrates (neutrophils, eosinophils, mononuclear cells) and connective tissue encapsulation. The disruption may be so extensive that not only villi and underlying layers (mucosa, submucosa and muscularis) may be affected but intestinal secretory glands may be replaced or undergo significant proliferative (atrophy, hyperplasia) and degenerative (necrosis, desquamation) changes. The disease caused by the species *R. echinobothrida* has been termed "nodular tapeworm disease" in poultry. Collectively, the pathological changes may result in enteritis and diarrhoea leading to emaciation and death, occasionally involving intestinal obstruction and/or perforation. Patechial haemorrhages at attachment sites may also lead to the presence of blood in faeces. Perturbations in clinical parameters have included reductions in haemoglobin concentrations, haematocrits (packed cell volumes), total serum proteins and total erythrocyte counts as well as increases in total leucocyte counts. Chronic infections are thought to lower host resistance to other infectious agents. Infections in poultry are common in tropical regions where climatic conditions and husbandry practices are more favorable for parasite survival and transmission.

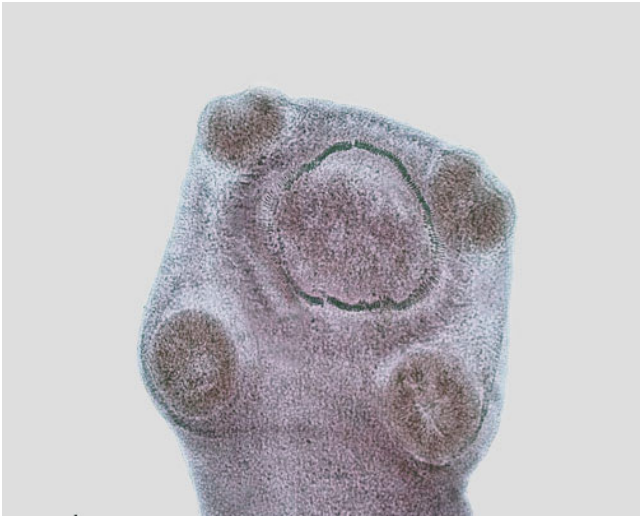
**Developmental cycle and mode of transmission:** Like all tapeworms, *Raillietina* spp. have indirect heteroxenous life-cycles whereby adult tapeworms infect vertebrate definitive hosts and larval metacystode stages infect invertebrate intermediate hosts. Cyclic transmission between hosts involves faecal-oral transmission to intermediate hosts and predator-prey transmission to definitive hosts. Gravid segments containing egg capsules are passed in faeces into the external environment where they remain viable for extended periods depending on moisture and temperature conditions (survival longer in mild moist conditions). These stages are ingested by a range of invertebrates which may act as intermediate hosts for larval development, particularly insects (ants, beetles, flies) and sometimes gastropod molluscs (slugs, snails). Oncospheres released in the invertebrate gut migrate through tissues to the body cavity where they encyst as larval cysticercoids. In the case of ants, foraging workers collect and transport food to their nests to feed their larvae, which are therefore probably the developmental stages that become infected with cysticercoids. These encysted larvae lay dormant until ingested with the invertebrate host by foraging definitive hosts (birds or insectivorous mammals) whereupon they emerge, attach to the gut wall and develop into adult tapeworms. Segments from adjacent worms cross-fertilize (rarely self-fertilize) and gravid proglottids containing eggs within egg capsules are shed some 13-21 days later (= prepatent period).

**Differential diagnosis:** Patent infections are diagnosed by the detection of gravid proglottids containing eggs in faecal samples, usually by direct visual examination of droppings or by microscopic examination of faecal smears (sometimes faecal floats). Several staining techniques have been employed to highlight anatomical features, including Ziehl Neelsen (acid-fast), periodic acid-Schiff (PAS), Scheider's (acetic alum carmine) and Gram's (crystal violet) stains. Infections may also be detected at necropsy by the detection of adult tapeworms and/or nodules in the small intestinal mucosa. Species may be differentiated on the basis of structural features, notably egg capsule configuration, genital pore position, scolex morphology, rostellar hook arrangements, proglottid morphometrics and genital anatomy. More recently, molecular techniques have been used to characterize different species by polymerase chain reaction (PCR) amplification of specific sequences in nuclear (internal transcribed spacer regions of ribosomal RNA) and mitochondrial (nicotinamide adenine dinucleotide dehydrogenase subunit 1, ND1) genes.

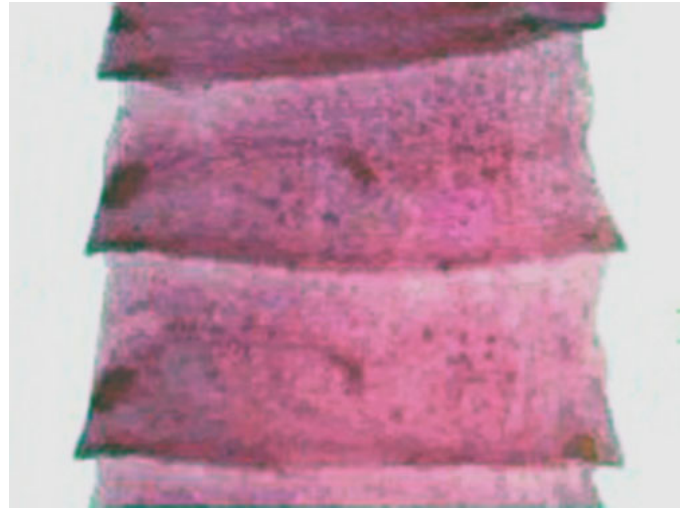
**Treatment and control:** Clinical infections may be treated with a range of anthelmintics, particularly broad-spectrum drugs exhibiting cestodicidal activity, including isoquinolines (praziquantel), benzimidazole-methylcarbamates (albendazole, fenbendazole, oxfendazole) and salicylanilides (niclosamide). Other treatment options using natural plant extracts are currently being investigated in India. Various strategies have also been developed to control transmission to and from invertebrate intermediate hosts near poultry enterprises, involving limiting faecal contamination of the environment (by proper waste disposal/treatment), reducing intermediate host populations (using physical barriers, chemical treatments or biological control agents) and preventing bird foraging behaviours (by indoor confinement or providing clean free-range conditions).

# Raillietina





*Raillietina* scolex



*Raillietina* segments



*Raillietina* egg



*Raillietina* cysticercoid