

Anoplocephala, *Anoplocephaloides*, *Equinia*, *Moniezia*, *Thysaniezia*
(platyhelminth: cestode)

Overview

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

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: Anoplocephalidae (tapeworms of hoofed animals, scolex unarmed, cysticercoids in arthropods)
Genus: *Anoplocephala* (parasitic in intestines of herbivores)
Genus: *Anoplocephaloides* (parasitic in intestines of herbivores)
Genus: *Equinia* (parasitic in intestines of herbivores)
Genus: *Moniezia* (parasitic in intestines of herbivores)
Genus: *Thysaniezia* (parasitic in intestines of herbivores)
Species: various species cause enteritis in horses and ruminants

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, Tetraphyllidea, 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))							
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
"Tetraphyllidea" 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). Anoplocephalid tapeworms are parasitic in the small intestines or bile ducts of herbivorous definitive hosts (mammals, birds, reptiles) and they form larval stages

(cysticerci) in arthropod intermediate hosts (oribatid mites). Mature worms range in size from 0.2-5.0 m in length, the scolex is unarmed and bears 4 suckers, some with lappets. Over 400 species have been described in 55 genera.

Four anoplocephalid subfamilies have been described based on differences in their uterine development: Anoplocephalinae with a tubular or reticular uterus that persists in gravid proglottids (230 species in 32 genera, including *Anoplocephala*, *Anoplocephaloides*, *Andrya*, *Aporina*, *Bertiella*, *Cittotaenia*, *Ctenotaenia*, *Diandrya*, *Equinia*, *Gallegoides*, *Genovia*, *Hemiparonia*, *Killigrewia*, *Moniezia*, *Monoecocestus*, *Mosgovoyia*, *Neandrya*, *Paramoniezia* gen. inq., *Paronia*, *Paranoplocephala*, *Parasciurotaenia*, *Phascolecestus*, *Phascolotaenia*, *Progamotaenia*, *Pulluterina*, *Schizorchis*, *Schizotaenia*, *Sciurotaenia*, *Stringopotaenia*, *Sudarikovina*, *Triplotaenia*, *Wallabicestus*); Linstowiinae with a uterus that disintegrates to form capsules around individual eggs (100 species in 13 genera, including *Atriotaenia*, *Cycloskrjabinia*, *Echidnotaenia*, *Gekkotaenia*, *Linstowia*, *Mathevotaenia*, *Oochoristica*, *Paralinstowia*); Thysanosominae with a paruterine organ receiving eggs from the uterus (30 species in 5 genera, including *Avitellina*, *Stilesia*, *Thysaniezia*, *Thysanosoma*, *Wyominia*); and Inermicapsiferinae with complex egg capsules (25 species in 4 genera, including *Inermicapsifer*, *Thysanotaenia*). Anoplocephalines primarily infect herbivorous mammals (ruminants, equids, lagomorphs, phalangerids) which accidentally ingest infected oribatid mites while grazing, but they may also infect other mammals (rodents, flying lemurs, primates (including humans)), and birds (especially parrots). Linstowiines infect insectivorous mammals (bats, rodents, marsupials) and reptiles, and form larval stages in Coleoptera (beetles). Thysanosomines infect ruminants and have Psocoptera (barklice) as intermediate hosts, while Inermicapsiferines infect hyraxes in Africa (IH unknown). The genera of greatest veterinary importance are those that parasitise domestic ruminants and equids; particularly *Anoplocephala*, *Equinia*, *Moniezia* and *Thysaniezia* species, many of which have cosmopolitan distributions along with their hosts, although some are confined to specific areas of Africa, Asia or North America depending on their host distributions. Many anoplocephaline species have also been found to infect rodents and lagomorphs, notably *Paranoplocephala* and *Anoplocephaloides* spp. in voles, lemmings and rabbits in Holarctic regions.

Parasite species	Definitive hosts [adults in gut]	Intermediate hosts [cysticercoids in body cavity]	Distribution
Subfamily: Anoplocephalinae (uterus persisting in gravid proglottids, eggs with pyriform apparatus)			
Moniezia (2 sets of reproductive organs in each segment, 2 reticular uteri)			
<i>M. amphibia</i> sp. inq	Artiodactyla: hippopotamid (hippopotamus)		Africa
<i>M. babai</i>	Artiodactyla: bovid (goat)		India
<i>M. baeri</i>	Artiodactyla: cervid (reindeer)		Europe, North America
<i>M. benedeni</i> (syn. <i>M. alba</i> , <i>M. autumnalia</i> , <i>M. conjugens</i> , <i>M. crassicollis</i> , <i>M. denticulata</i> , <i>M. kuznetsovi</i> , <i>M. latifrons</i> , <i>M. neumanni</i> , <i>M.</i> <i>parva</i> , <i>M. pellucida</i> , <i>M.</i> <i>planissima</i> , <i>M. rupicaprae</i> , <i>M.</i> <i>skrjabini</i> , <i>M. translucida</i> , <i>M.</i> <i>triangularis</i>)	Artiodactyla: bovid (cattle, buffalo, European bison, zebu, sheep, goat, mountain goat, West African dwarf goat, sable antelope, Jackson's hartebeest, greater kudu), cervid (white-tailed deer, mule deer, roe deer, elk), camelid (camel)	Oribatida: achipteriid (<i>Achipteria coleoprata</i>), peloppiid (<i>Ceratoppia</i>), ceratozetid (<i>Ceratozetes</i> , <i>Trichoribates</i>), galumnid (<i>Galumna elimata</i> , <i>G. obvia</i> , <i>Pergalumna</i>), liacurid (<i>Liacarus coracinus</i>), scheloribatid (<i>Liebstadia</i> , <i>Scheloribates laevigatus</i>), oribatulid (<i>Oribatula</i> , <i>Zygoribatula</i>), camisiid (<i>Platynothrus</i>), punctoribatid (<i>Punctoribates</i>)	worldwide
<i>M. bequaerti</i>	Rodentia: capromyid (Desmarest's hutia)		Central America
<i>M. caprae</i>	Artiodactyla: bovid (goat)		Europe
<i>M. chappuisi</i>	Artiodactyla: bovid (roan antelope)		Africa
<i>M. devraoi</i>	Artiodactyla: bovid (goat)		India
<i>M. elongata</i> sp. inq.	Artiodactyla: bovid (goat)		India
<i>M. expansa</i> (syn. <i>M. aishvaryae</i> , <i>M.</i> <i>aurangabadensis</i> , <i>M. bharalae</i> , <i>M. caprai</i> , <i>M. jadhavii</i> , <i>M.</i> <i>jalnaensis</i> , <i>M. mansurae</i> , <i>M.</i> <i>marathwadensis</i> , <i>M. minima</i> , <i>M.</i> <i>murhari</i> , <i>M. osmanabadensis</i> , <i>M. roshanensis</i> , <i>M. shegaonesis</i> , <i>M. shindei</i> , <i>M. sureshi</i> , <i>M.</i> <i>trigonophora</i> , <i>M.</i>	Artiodactyla: bovid (sheep, goat, West African dwarf goat, cattle, zebu, ibex, common duiker, gazelle, scimitar oryx, steenbok, Sharpe's grysbok, bharal), cervid (red deer, white-tailed deer, roe deer, fallow deer), camelid (camel), suid (pig); rarely Primates: hominid (human)	Oribatida (mites): achipteriid (<i>Achipteria coleoprata</i> , <i>A.</i> <i>punctata</i> , <i>Parachipteria</i>), astegistid (<i>Furcoribula</i>), camisiid (<i>Platynothrus</i>), carabodoid (<i>Carabodes</i> <i>minusculus</i>), cepheid (<i>Cepheus</i>), ceratozetid (<i>Ceratozetes</i> , <i>Pelops</i> <i>planicornis</i> , <i>Trichoribates</i>)	worldwide

<i>waranangarensis</i> (sheep tapeworm, double-pored ruminant tapeworm)		<i>trimaculatus</i>), damaeid (<i>Notaspis punctatus</i>), eremaeid (<i>Eremaeus</i>), euzetid (<i>Euzetes</i>), galumnid (<i>Galumna elimata</i> , <i>G. obvia</i> , <i>G. nervosus</i> , <i>G. baloghi</i> , <i>Allogalumna</i> , <i>Pergalumna</i>), haplozetid (<i>Peloribates</i> , <i>Protoribates lophotrichus</i>), hermanniellid (<i>Hermanniella</i>), liacurid (<i>Liacarus coracinus</i> , <i>Xenillus</i>), mochlozetid (<i>Unguizetes reticulatus</i>), oribatellid (<i>Oribatella</i>), oribotritiid (<i>Oribotritia loricata</i>), oribatulid (<i>Oribatula tibialis</i> , <i>O. cognata</i> , <i>O. friziae</i> , <i>Zygoribatula</i>), parakalummid (<i>Neoribates aurantiacus</i>), peloppiid (<i>Ceratoppia</i>), phenopelopid (<i>Eupelops</i> , <i>Peloptulus</i> , <i>Phenopelops planicornis</i>), punctoribatid (<i>Punctoribates punctum</i>), scheloribatid (<i>Schelorbates latipes</i> , <i>S. laevigatus</i> , <i>S. perforatus</i> , <i>S. fimbriatus</i> , <i>Protoschelobates seghetti</i>), scutoverticid (<i>Scutovertex</i>), tectocephid (<i>Tectocephus velatus</i>)	
<i>M. govindae</i>	Artiodactyla: bovid (goat)		India
<i>M. hircusae</i>	Artiodactyla: bovid (goat)		India
<i>M. interproglottina</i>	Artiodactyla: bovid (bharal)		India
<i>M. kalavati</i>	Artiodactyla: bovid (goat)		India
<i>M. lyallpuriensis</i>	Artiodactyla: bovid (goat)		Pakistan
<i>M. madhukarae</i>	Artiodactyla: bovid (goat)		India
<i>M. maharashtrae</i>	Artiodactyla: bovid (goat)		India
<i>M. mathevossianae</i>	Artiodactyla: cervid (reindeer)		Eurasia
<i>M. mettami</i>	Artiodactyla: suid (desert warthog)		Africa
<i>M. mizkewitschi</i>	Artiodactyla: cervid (reindeer)		Eurasia
<i>M. monardi</i>	Artiodactyla: bovid (Ugandan kob, roan antelope, waterbuck)		Africa
<i>M. orientalis</i>	Artiodactyla: bovid (bharal)		India
<i>M. ovisae</i>	Artiodactyla: bovid (bharal)		India
<i>M. pallida</i>	Perissodactyla: equid (horse)		Africa
<i>M. phacochoeri</i>	Artiodactyla: suid (desert warthog, common warthog)		Africa
<i>M. rajalaensis</i>	Artiodactyla: bovid (goat)		India
<i>M. rangiferina sp. inq.</i>	Artiodactyla: cervid (reindeer)		Eurasia
<i>M. rhea</i>	Rheiformes: rheid (greater rhea)		South America
<i>M. rugosa</i>	Primates: atelid (northern muriqui)		South America
<i>M. shivajiraovae</i>	Artiodactyla: bovid (goat)		India
<i>M. sichuanensis</i>	Artiodactyla: cervid (musk deer)		China
<i>M. taimyrica</i>	Artiodactyla: cervid (reindeer)		Eurasia
<i>M. transvaalensis</i>	Rodentia: thryonomyid (greater cane rat)		Africa
<i>Equinia</i> (single set of reproductive organs per segment, arborescent (tree-like) uterus)			
<i>E. mamillana</i> (syn. <i>Paranoplocephala</i> , <i>Anoplocephala</i> ,	Perissodactyla: equid (horse)	Oribatida (mites): achipteriid (<i>Achipteria</i>), ceratozetid (<i>Ceratozetes</i>), galumnid	worldwide

<i>Anoplocephaloides</i>		(<i>Galumna</i> , <i>Allogalumna</i>), scheloribatid (<i>Scheloribates</i>)	
<i>Anoplocephala</i> (single set of reproductive organs per segment, uterus elongated sac with pocket-like appendages)			
<i>A. diminuta</i>	Perissodactyla: rhinocerotid (Javan rhinoceros)		Asia
<i>A. gigantea</i> (syn. <i>A. vulgaris</i>)	Perissodactyla: rhinocerotid (black rhinoceros)		Africa
<i>A. gorillae</i>	Primates: hominid (eastern gorilla)		Africa
<i>A. latissima</i>	Perissodactyla: rhinocerotid (Javan rhinoceros)		Asia
<i>A. magna</i> (syn. <i>A. plicata</i>) (equine tapeworm)	Perissodactyla: equid (horse, donkey)	Oribatida (mites): scheloribatid (<i>Scheloribates</i>)	worldwide
<i>A. manubriata</i>	Proboscidea: elephantid (Asian elephant)		Asia
<i>A. perfoliata</i> (syn. <i>A. rhodesiensis</i>)	Perissodactyla: equid (horse, donkey, zebra, Burchell's zebra)	Oribatida (mites): achipteriid (<i>Achipteria</i> , <i>Parachipteria</i>), ceratozetid (<i>Ceratozetes</i> , <i>Trichoribates</i>), galumnid (<i>Galumna</i> , <i>Allogalumna</i>), scheloribatid (<i>Scheloribates</i> , <i>Liebstadia</i> , <i>Urubambates</i>), carabodoid (<i>Carabodes</i>), eremaeid (<i>Eremaeus</i>), hermanniellid (<i>Hermanniella</i>), liacurid (<i>Liacarus</i>), oribatulid (<i>Zygoribatula</i>), camisiid (<i>Platynothrus</i>)	worldwide
<i>Anoplocephaloides</i> (single set of reproductive organs per segment, tubular uterus)			
<i>A. bulmeri</i>	Rodentia: cricetid (southern bog lemming)		North America
<i>A. dentata</i>	Rodentia: cricetid (common vole, European snow vole, Balkan snow vole, European pine vole, Gunther's vole, tundra vole, field vole, singing vole, meadow vole, reed vole, tiaga vole, bank vole), murid (yellow-necked mouse), spalacid (lesser mole-rat)		Eurasia, North America
<i>A. dentatoides</i>	Rodentia: cricetid (gray red-backed vole)		Eurasia
<i>A. kontrimavichusi</i>	Rodentia: cricetid (northern bog lemming)		North America
<i>A. lemni</i>	Rodentia: cricetid (North American brown lemming, Siberian brown lemming)		North America, Russia
<i>A. troeschi</i> (syn. <i>Paranoplocephala infrequens</i>)	Rodentia: cricetid (meadow vole, montane vole), geomyid (plains pocket gopher)		North America
Reassigned species			
<i>A. acanthocirrosa</i> (now <i>Afrobaeria</i>)	Rodentia: murid (southern African vlei rat, Dent's vlei rat)		Africa
<i>A. apodemi</i> (now <i>Hokkaidocephala</i>)	Rodentia: murid (small Japanese field mouse)		Japan
<i>A. arfaai</i> (now <i>Gallegoides</i>)	Rodentia: murid (wood mouse)		Europe
<i>A. baeri</i> (now <i>Hokkaidocephala</i>)	Rodentia: murid (small Japanese field mouse)		Japan
<i>A. floresbarroetae</i> (now <i>Genovia</i> , formerly <i>Leporidotaenia</i>)	Lagomorpha: leporid (tapeti)		Central America
<i>A. indicata</i> (now <i>Flabellloskrjabinia</i>)	Perissodactyla: tapirid (Malaysian tapir)		Asia
<i>A. isomydis</i> (now <i>Afrobaeria</i>)	Rodentia: murid (Abyssinian grass rat, common rufous-nosed rat, tropical vlei rat)		Africa

<i>A. neofibrinus</i> (now <i>Microcephaloides</i>)	Rodentia: cricetid (round-tailed muskrat)		North America
<i>A. pseudowimerosa</i> (now <i>Genovia</i> , formerly <i>Leporidotaenia</i>)	Lagomorpha: leporid (European rabbit)		Europe
<i>A. rauschi</i> (now <i>Paranoplocephala</i>)	Rodentia: cricetid (European snow vole, European pine vole)		Europe
<i>A. romerolagi</i> (now <i>Leporidotaenia</i>)	Lagomorpha: leporid (volcano rabbit)		Mexico
<i>A. ryjikovi</i> (formerly <i>Paranoplocephala</i> , now <i>Parasciuropaenia</i>)	Rodentia: sciurid (gray marmot, Himalayan marmot)		Asia
<i>A. schachmatovae</i> (now <i>Paranoplocephaloides</i>)	Rodentia: cricetid (tundra vole)		Eurasia, North America
<i>A. tapirus</i> (now <i>Flabelloskrjabinia</i>)	Perissodactyla: tapirid (tapir)		Asia
<i>A. tenoramuraiae</i> (now <i>Microcephaloides</i>)	Rodentia: cricetid (European snow vole, European pine vole)		Europe
<i>A. transversaria</i> (now <i>Marmotocephala</i>)	Rodentia: sciurid (long-tailed marmot, gray marmot)		Asia
<i>A. variabilis</i> (syn. <i>Paranoplocephala borealis</i>) (now <i>Microcephaloides</i>)	Rodentia: geomyid (plains pocket gopher, northern pocket gopher), cricetid (meadow vole, singing vole, tundra vole, prairie vole, montane vole, Siberian brown lemming)		North America, Russia
<i>A. wigginsi</i> (now <i>Marmotocephala</i>)	Rodentia: sciurid (Arctic ground squirrel)		North America
<i>A. wimerosa</i> (now <i>Genovia</i> , formerly <i>Leporidotaenia</i>)	Lagomorpha: leporid (European rabbit, mountain hare)		Europe
<i>Paranoplocephala</i> (single set of reproductive organs per segment, reticular uterus, long vagina and cirrus)			
<i>P. batzlii</i>	Rodentia: cricetid (singing vole, insular vole)		Alaska
<i>P. campestris sp. inq.</i>	Rodentia: cricetid (common vole)		Europe
<i>P. communis sp. inq.</i>	Rodentia: cricetid (southern red-backed vole, western harvest mouse, meadow vole, montane vole, long-tailed vole)		North America
<i>P. feodorovi</i> (syn. <i>Parandrya</i>)	Rodentia: cricetid (European water vole, field vole, Maximowicz's vole)		Eurasia
<i>P. forcipata sp. inq.</i>	Rodentia: chinchillid (northern viscacha)		South America
<i>P. freemani</i>	Rodentia: cricetid (taiga vole, muskrat)		Alaska
<i>P. jarrelli</i>	Rodentia: cricetid (tundra vole)		Europe, North America
<i>P. kalelai</i>	Rodentia: cricetid (grey red-backed vole, bank vole)		Palaearctic
<i>P. kirbyi</i>	Rodentia: cricetid (California vole)		North America
<i>P. macrocephala</i> (syn. <i>P. translucida</i>)	Rodentia: geomyid (plains pocket gopher), cricetid (meadow vole)		North America
<i>P. maseri</i>	Rodentia: cricetid (sagebrush vole)		North America
<i>P. microti</i>	Rodentia: cricetid (prairie vole)		North America
<i>P. montana sp. inq.</i>	Rodentia: cricetid (common vole, European snow vole)		Russia
<i>P. omphalodes</i> (syn. <i>P. caucasica</i>)	Rodentia: cricetid (common vole, European water vole, tundra vole, insular vole, singing vole, field vole, bank vole, social vole, grey dwarf hamster), murid (southern African vlei rat, bush vlei rat)		Palaearctic, Africa

Reassigned species			
<i>P. acanthocirrosa</i> (now <i>Afrobaeria</i>)	Rodentia: murid (Southern African vlei rat, Dent's vlei rat)		Africa
<i>P. alaskensis</i> (now <i>Douhittia nordensikoeldi</i>)	Rodentia: cricetid (singing vole)		North America
<i>P. alternata</i> (now <i>Rauschoides</i>)	Rodentia: cricetid (northern collared lemming, Arctic lemming)		Holarctic
<i>P. aquatica</i> (now <i>Rodentocestus</i>)	Rodentia: cricetid (European water vole, muskrat)		Europe
<i>P. arctica</i> (now <i>Rauschoides</i>)	Rodentia: cricetid (northern collared lemming)		Nearctic
<i>P. bairdi</i> (syn. <i>Andrya</i>) (now <i>Douhittia</i>)	Rodentia: cricetid (eastern heather vole, western heather vole, red tree vole, Sonoma tree vole, white-footed vole)		North America
<i>P. blanchardi</i> (now <i>Microticola</i>)	Rodentia: cricetid (common vole, field vole, Skomer vole, European water vole, muskrat)		Palaearctic
<i>P. buryatiensis</i> (now <i>Gulyaevia</i>)	Rodentia: cricetid (grey red-backed vole, reed vole)		Russia
<i>P. dasymidis</i> (now <i>Hunkeleriella</i>)	Rodentia: murid (African marsh rat)		Africa
<i>P. etholeni</i> (now <i>Microticola</i>)	Rodentia: cricetid (meadow vole)		Finland
<i>P. fellmani</i> (now <i>Lemminia</i>)	Rodentia: cricetid (Norway lemming)		Holarctic
<i>P. genovi</i> (now <i>Rodentocestus</i>)	Rodentia: cricetid (muskrat)		Europe
<i>P. gracilis</i> (now <i>Eurotaenia</i>)	Rodentia: cricetid (field vole)		Europe
<i>P. gubanovi</i> (now <i>Lemminia</i>)	Rodentia: cricetid (wood lemming)		Siberia
<i>P. gundii</i> (now <i>Afrojoyeuxia</i>)	Rodentia: ctenodactylid (common gundi)		Africa
<i>P. janickii</i> (now <i>Tenoraia</i>)	Rodentia: cricetid (field vole)		Palaearctic
<i>P. krebsi</i> (now <i>Microcephaloides</i>)	Rodentia: cricetid (northern collared lemming)		Nearctic
<i>P. longivaginata</i> (now <i>Gulyaevaia</i>)	Rodentia: cricetid (red vole, grey red- backed vole), sciurid (red squirrel)		Siberia
<i>P. mascomai</i> (now <i>Microcephaloides</i>)	Rodentia: cricetid (Cabrera's vole)		Europe
<i>P. neotomae</i> (now <i>Andrya</i>)	Rodentia: cricetid (dusky-footed woodrat)		North America
<i>P. neofibrinus</i> (now <i>Microcephaloides</i>)	Rodentia: cricetid (round-tailed muskrat)		North America
<i>P. nevoi</i> (now <i>Microcephaloides</i>)	Rodentia: spalacid (Middle East blind mole- rat)		Syria
<i>P. nordenskoeldi</i> (now <i>Douhittia</i>)	Rodentia: cricetid (northern collared lemming, Arctic lemming)		Holarctic
<i>P. octodonensis</i> (now <i>Andrya</i>)	Rodentia: octodontid (common degu)		South America
<i>P. oeconomi</i> (now <i>Parandrya</i>)	Rodentia: cricetid (bank vole)		Palaearctic
<i>P. nearctica</i> (now <i>Douhittia</i>)	Rodentia: cricetid (southern red-backed vole, northern red-backed vole, long-tailed vole)		North America
<i>P. ondatrae</i> (now <i>Cookiella</i>)	Rodentia: cricetid (meadow vole, montane vole, muskrat)		North America
<i>P. otomyos</i> (now <i>Afrobaeria</i>)	Rodentia: murid (southern African vlei rat)		Africa
<i>P. petuaristae</i> (now <i>Bertiella</i>)	Rodentia: sciurid (Japanese giant flying squirrel)		Japan

<i>P. primordialis</i> (now <i>Douthittia</i>)	Rodentia: sciurid (American red squirrel), cricetid (meadow vole, long-tailed vole, singing vole, montane vole, tundra vole, water vole, southern red-backed vole, northern red-backed vole, dusky-footed woodrat, western harvest mouse)		Nearctic
<i>P. sciuri</i> (now <i>Rodentocestus</i>)	Rodentia: sciurid (northern flying squirrel)		North America
<i>P. serrata</i> (now <i>Arctocestus</i>)	Rodentia: cricetid (northern collared lemming, Arctic lemming)		Holarctic
<i>P. threlkeldi</i> (now <i>Monoecocestus</i>)	Rodentia: chinchillid (northern viscacha)		South America
<i>P. yoccozi</i> (now <i>Chionocestus</i>)	Rodentia: cricetid (European snow vole)		Europe
Subfamily: Thysanosominae (paruterine organ receiving eggs from uterus)			
<i>Stilesia</i> (2 sets of reproductive organs in each segment)			
<i>S. ambajogaensis sp. inq.</i>	Artiodactyla: bovid (cattle, zebu)		India
<i>S. aurangabadensis sp. inq.</i>	Artiodactyla: bovid (bharal)		India
<i>S. daulatabadensis sp. inq.</i> (syn. <i>S. thapari</i>)	Artiodactyla: bovid (goat)		India
<i>S. globipunctata</i> (syn. <i>S. alii</i> , <i>S. caprai</i> , <i>S.</i> <i>dhondagae</i> , <i>S. garhwalensis</i> , <i>S.</i> <i>govinda</i> , <i>S. kotdwarensis</i> , <i>S.</i> <i>mehdii</i> , <i>S. ovipunctata</i>)	Artiodactyla: bovid (sheep, goat, cattle, zebu, gazelle), camelid (camel)	Oribatida (mites): galumnid (<i>Galumna</i> , <i>Allogalumna</i>), scheloribatid (<i>Schelorbates</i>), oribatulid (<i>Zygoribatula</i>), hygrobatid (<i>Africacarus</i>)	Eurasia, Africa
<i>S. hepatica</i> (syn. <i>S. sjostedti</i>) (liver tapeworm)	Artiodactyla: bovid (sheep, goat, cattle, Cape bushbuck), cervid (elk, deer, moose) [bile ducts]	Oribatida (mites)	Africa, Asia
<i>S. hircusi sp. inq.</i>	Artiodactyla: bovid (goat)		India
<i>S. marathwadaensis sp. inq.</i>	Artiodactyla: bovid (goat)		India
<i>S. okapi sp. inq.</i>	Artiodactyla: giraffid (okapi)		Africa
<i>S. vittata</i>	Artiodactyla: bovid (sheep, goat), camelid (camel)	Oribatida (mites)	India, Africa
<i>S. wadaensis sp. inq.</i>	Artiodactyla: bovid (goat)		India
<i>S. yavalensis sp. inq.</i>	Artiodactyla: bovid (goat)		India
<i>Thysanosoma</i> (2 sets of reproductive organs per segment, but only single uterus)			
<i>T. actinioides</i> (fringed tapeworm)	Artiodactyla: bovid (sheep, goat, cattle, antelope), cervid (deer, elk) [also bile ducts]	Oribatida (mites)	Americas
<i>T. misrai sp. inq.</i>	Artiodactyla: bovid (goat)		India
<i>Thysaniezia</i> (single set of reproductive organs per segment)			
<i>T. connochaeti</i>	Artiodactyla: bovid (cattle, blue wildebeest)		Africa
<i>T. giardi</i> (Giard's tapeworm) (syn. <i>Helictometra</i>)	Artiodactyla: bovid (cattle, buffalo, sheep, goat)	Oribatida (mites): achipteriid (<i>Achipteria</i>), scheloribatid (<i>Schelorbates</i> , <i>Liebstadia</i>), oribatulid (<i>Zygoribatula</i>), ceratozetid (<i>Trichoribates</i>), puncatoribatid (<i>Puncatoribates</i>)	Eurasia, Africa, Americas
<i>T. ovilla</i> (syn. <i>T. aspinosa</i> , <i>T. himalayai</i> , <i>Thysanosoma ovilla</i>)	Artiodactyla: bovid (cattle, water buffalo, zebu, sheep, goat, dama gazelle, impala, eland, hartebeest), camelid (camel)	Oribatida (mites); Psocoptera: psocid (bark lice)	Africa

Parasite morphology: Anoplocephalid tapeworms form 3 different developmental stages: eggs, larvae (cysticercoids) and adults. Gravid proglottids containing eggs are passed in host faeces: those of anoplocephaline species retain their uteri and the eggs possess a unique pyriform apparatus, while thysanosomine species have eggs grouped together within special paruterine organs. The eggs range from triangular to square in shape, some having a distinctive D-shape (flattened on one side), and they measure from 50-80 µm in diameter. They are surrounded by a heavy hyaline capsule comprising an outer vitelline membrane and a thick albuminous layer. Mature eggs are embryonated and contain a hexacanth (6-hooked) non-ciliated embryophore (oncosphere). In anoplocephaline species, the oncosphere is surrounded by the pyriform apparatus, which is pear-shaped, chitinous, refractile and bears 2 finger-like projections. The larval metacystode stage is an encysted cysticercoid into which the scolex has been retracted. Cysticercoids range in size from 100-180 x 90-140 µm and possess a retracted scolex, 3 pairs of hooks, germinal cells, an excretory

pore and a tail-like cercomer. Adult tapeworms range considerably in size from 0.2-10.0 m in length depending on the species. Most *Anoplocephala* spp. are large measuring from 5 cm to 1 m in length by 1-2 cm in width. *Moniezia* spp. are larger and elongate measuring up to several metres in length. Tapeworms have flat ribbon-shaped white-yellow bodies comprising an anterior scolex (holdfast organ) and posterior tape (strobilia) made up of numerous segments (proglottids). The scolex is circular and bears 4 large muscular suckers, some species also possessing 4 basal flaps called lappets (e.g. *A. perfoliata*). The proglottids are wider than they are long, have lateral genital pores and their posterior borders are lined with interproglottid glands (often linear or rosette arrangements of glandular cell clusters in some species of *Moniezia*). Tapeworms do not possess mouth parts or an intestinal tract but absorb nutrients through their body surface (tegument). Mature worms are hermaphroditic and possess male and female reproductive organs in each proglottid, some genera even having two sets of reproductive organs per segment (e.g. *Moniezia*). Individual sets comprise numerous testes and compact ovaries with 2 lobes which produce eggs that are fertilized and mature in the uteri. Posterior proglottids become sac-like as they mature and become gravid filling with numerous eggs. Anoplocephaline species have a tubular or reticular uterus that persists in gravid proglottids, while thysanosomine species have a special paruterine organ that receives eggs. Gravid segments detach and are passed with host faeces, whereupon eggs are discharged into the environment.

Site of infection: Anoplocephalid genera infect the gastro-intestinal tracts and bile ducts of their definitive hosts, mainly ruminants. Adult *Anoplocephala* occur in the small and large intestines, *Moniezia* and *Thysaniezia* in the small intestines, *Equinia* in the small intestines and occasionally the stomach, and *Stilesia* and *Thysanosoma* in hepatic bile ducts. Different species may exhibit some tissue tropism within these regions, e.g. *A. perfoliata* is found in clusters along the ileocecal junction. The larval metacestodes (cysticercoids) are found in the body cavities of their invertebrate intermediate hosts, mostly oribatid mites.

Pathogenesis: These tapeworms occur commonly in domestic livestock, especially ruminants and horses. Infections are rarely associated with clinical disease, even when large numbers of worms may be present. Adult worms attach to mucosal surfaces using their unarmed muscular suckers but do not feed on host tissues (they absorb nutrients across their body walls). Attachment and detachment causes traumatic damage to the mucosa, becoming cumulative as worm numbers increase but often not resulting in overt clinical signs. The exception is the species *Anoplocephala perfoliata* which can be very pathogenic in horses. Chronic infections by large numbers of worms (hundreds) may cause severe enteritis, intestinal obstruction (blockage of ingesta flow in the caecum, terminal ileum or ileocaecal junction), ileocaecal colic (severe abdominal discomfort/pain), reduced gut motility and intussusception (telescoping of the gut, usually of the small intestine into the caecum), caecal perforation leading to peritonitis, and death. At or near attachment sites, there is hyperaemia, erosion and necrotic ulceration of the mucosal epithelium, often with diphtheritic membrane formation and sometimes with focal haemorrhages, villous atrophy, inflammation, epithelial and goblet cell hyperplasia and muscular layer hypertrophy. Large numbers of eosinophils and lymphocytes are present in the tissues with oedema, extensive fibrosis (resulting in mucosal thickening, polyps or raised verrucous granulating masses), and neurological changes (degeneration of neurons and mesenteric ganglia). The risk of colic (spasmodic and acute) increases with higher parasite burdens. Other clinical signs observed have included chronic diarrhoea, fever, increased heart rate, poor growth and unthriftiness. Disease is more severe in young horses but older horses may also show signs. There is also some evidence that heavy infections by *A. magna* in the small intestines of horses may cause enteritis and possibly duodenal rupture. Contradictory results have been observed with respect to *Moniezia* infections in calves and lambs, with some studies finding no ill-effects and others reporting diarrhoea, anaemia, mucosal inflammation, anorexia and reduced weight gain and wool growth.

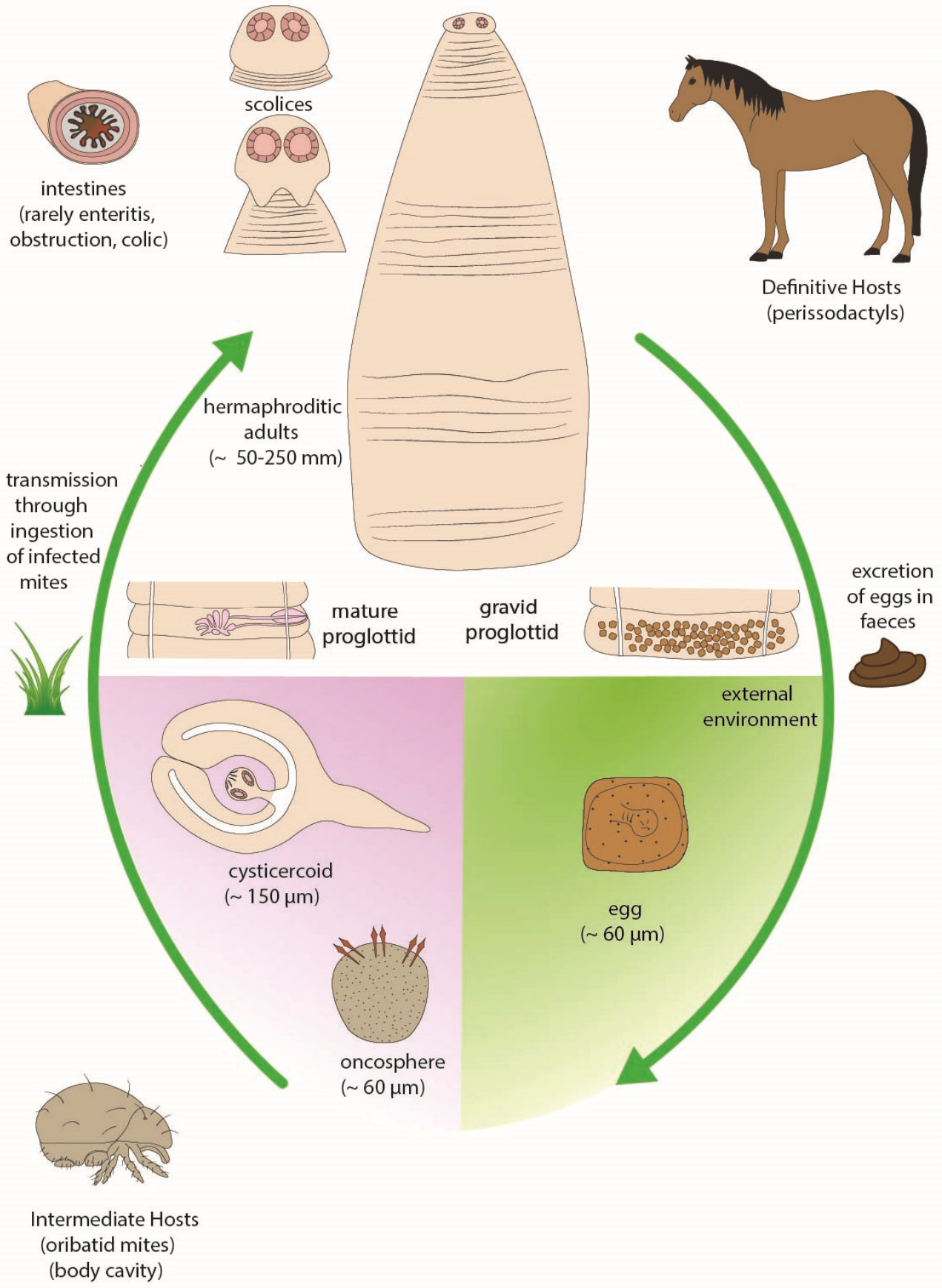
Developmental cycle and mode of transmission: Anoplocephalid species have indirect heteroxenous life-cycles involving cyclic transmission between vertebrate definitive hosts (herbivores infected with adult tapeworms) and invertebrate intermediate hosts (pasture mites infected with larval metacestodes). Parasite species exhibit high host specificity for both definitive and intermediate hosts. Eggs released from gravid proglottids (either in the intestines or in faeces) contaminate pastures and are dispersed by faecal decomposition and rainfall. The embryonated eggs survive for several days although this depends on ambient conditions with eggs surviving up to several months in moist cool environments. The eggs are ingested by pasture-dwelling arthropods, mostly oribatid mites (especially achipteriid, ceratozetid, galumnid, haplozetid, liacurid, oribatulid, phenopeloid and schelorbitid families) for anoplocephaline eggs, psocopteran insects (psocid booklice) for thysanosomine eggs, and coleopteran insects (beetles) for linstowiine eggs. Many infections exhibit seasonal patterns of infection as most of these arthropods feed and breed in particular micro-environments at particular times of the year (pasture mites are more active and prevalent over summer). The eggs hatch within the arthropods releasing the contained embryos (oncospheres) which burrow through the gut using their hooks and glandular secretions. Oncospheres encyst in the body cavity (haemocoel) and develop into cysticercoid stages over 2-4 months. Definitive hosts acquire infections by ingesting infected arthropods on vegetation when grazing. Once ingested, the larval cysticercoid extends its retracted scolex and uses its suckers to attach to mucosa where it develops to a sexually-mature adult over 6-10 weeks (prepatent period). Adult tapeworms are thought to live for several years and progressive maturation of proglottids can ultimately produce thousands of eggs.

Differential diagnosis: Many anoplocephalid tapeworm species do not shed most of their eggs in host faeces but pass gravid proglottids from which eggs are subsequently released. Infections are therefore usually diagnosed in livestock by the detection of motile (writhing) segments (looking like rice grains) in faeces or moving around the anus. Nonetheless, faecal samples may be

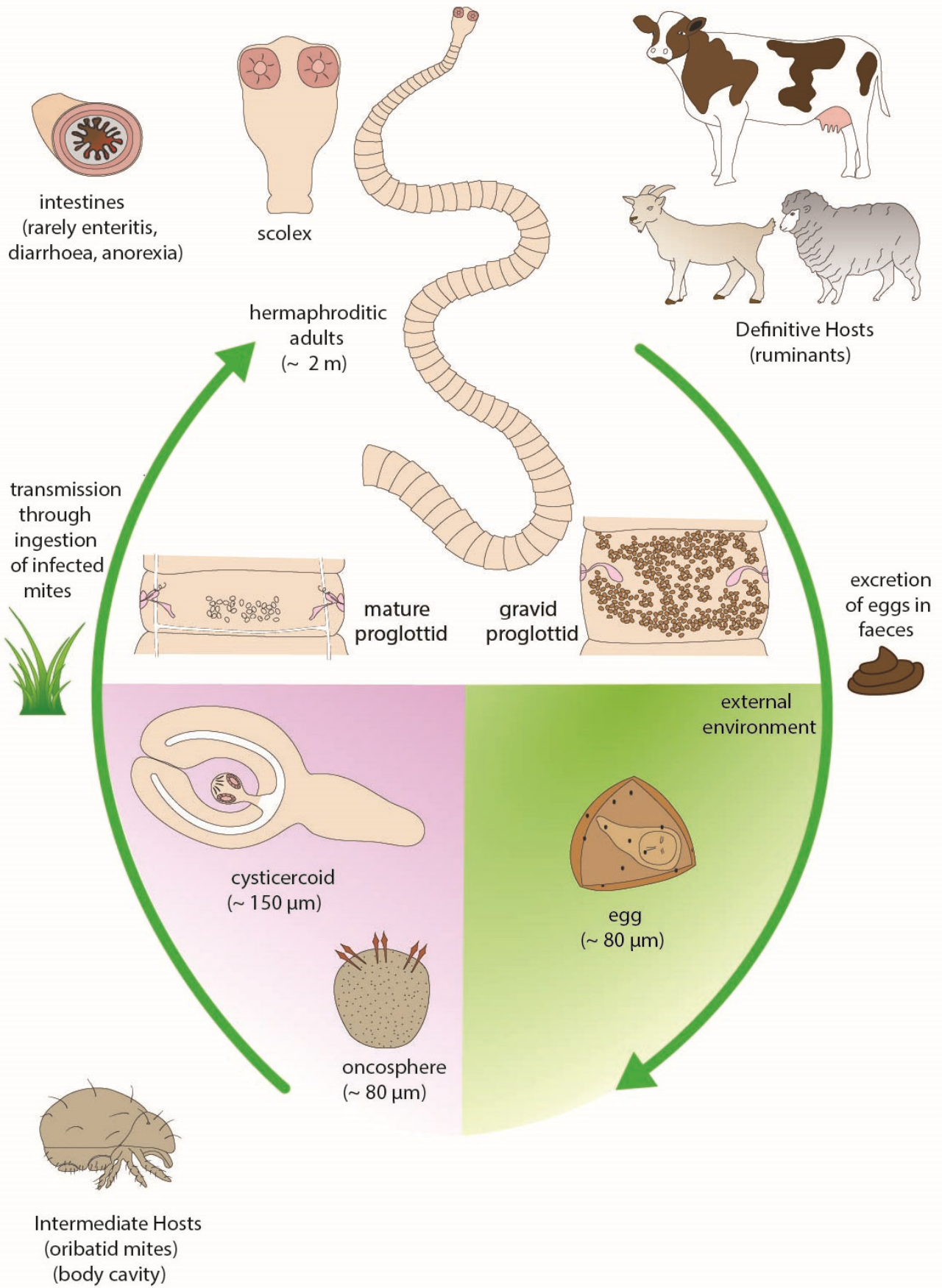
examined microscopically for the presence of characteristic eggs, but the standard McMaster chamber floatation technique shows low sensitivity which may be improved by employing centrifugal floatation. Post-mortem examination commonly reveals the presence of species forming large tapeworms in gut samples, but small species may be overlooked by cursory visual examination. Enzyme immunoassays have been developed to detect host antibodies (serum or saliva) against somatic or excretory/secretory (ES) products from *A. perfoliata* in horses, and an immunoassay was recently developed to detect parasite antigens in faecal samples. However, host antibody responses to infection were found to vary greatly as was antigen shedding. Isoenzyme electrophoresis has been used to characterize several *Moniezia* spp., and molecular techniques based on polymerase chain reaction (PCR) amplification of parasite DNA (nuclear genes for ribosomal RNA and internal transcribed spacers, and mitochondrial genes for proteins, rRNA and tRNA) have been used to discriminate equine anoplocephalids.

Treatment and control: Infections in livestock have been successfully treated using a range of anthelmintics, including praziquantel, niclosamide, albendazole, fenbendazole, oxfendazole, dichlorophen and sometimes pyrantel or morantel. Other modern anthelmintics commonly used on horses, such as macrocyclic lactones (ivermectin, moxidectin), have no effect. Treatment should be conducted strategically to eliminate tapeworms and reduce pasture contamination when intermediate hosts are most active, usually over summer. Re-infection from contaminated pastures can easily occur so regular preventive treatments may be required (every few months for horses). Environmental management procedures can also be instituted to curb infections by reducing contact between parasite eggs, pasture arthropods and grazing animals. Stabling horses overnight limits contact with arthropods which climb pastures during cooler periods and hide during hotter periods. Grazing management strategies can be instituted so definitive hosts can be rotated between pastures (e.g. periodic swapping of horses and cattle). Other extreme methods of pasture management to reduce contamination and arthropod populations include cropping or ploughing, but such interventions are laborious and costly.

Anoplocephala



Moniezia





Anoplocephala adult worms



Anoplocephala worm egg



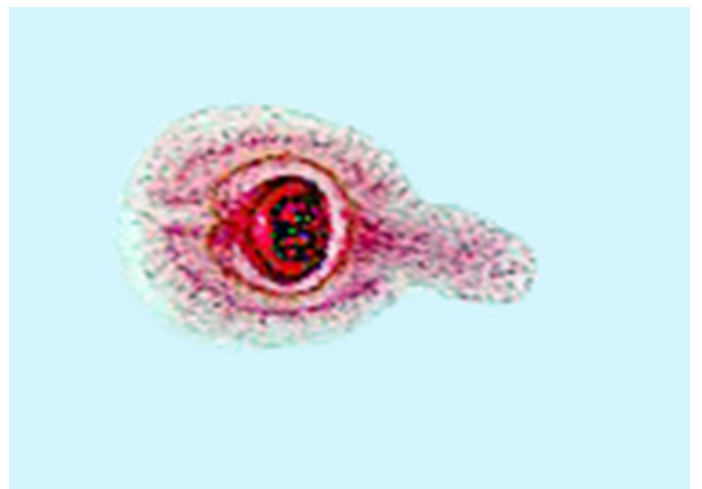
Moniezia adult worm



Moniezia worm egg



Moniezia scolex



Moniezia cysticercoid