Ascaris
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Ascaridomorpha which includes ascaridoid nematodes (roundworms) characterised by their large size, three prominent anterior lips and the absence of a bursa. They occur in the small intestines of many animals (including humans) and most have simple direct life-cycles involving faecal-oral transmission. Female worms produce numerous eggs which are excreted with host faeces and undergo embryonation to contain infective larvae. When ingested, larvae hatch from the eggs and develop into adult worms in the gut. The larvae of ascaridoid species undergo hepato-pulmonary migration before forming adults, whereas those of heterakoid species do not. Two major ascaridoid families are recognised: ascarids in terrestrial mammals; and anisakids in marine mammals. Infections by *Ascaris* spp. are very common in human and pig populations throughout the world, causing unthriftiness and even gut obstruction.

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:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Ascaridomorpha (large roundworms, mouth surrounded by three large lips, numerous caudal papillae)
Superfamily:	Ascaridoidea (ascarids, eggs thick-shelled, direct cycle but larvae undertake hepato-pulmonary migration)
Family:	Ascarididae (large pale roundworms, in terrestrial mammals)
Genus:	*Ascaris* (parasitic in small intestines of humans/pigs)
Species:	*A. lumbricoides* (causes gut obstruction in humans)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and

Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The infraorder Ascaridomorpha is characterised by large roundworms with poorly developed buccal cavity with 3 large lips sometimes separated by interlabia, an undivided oesophagus, numerous caudal papillae, nonbursate males often with pre-anal suckers, and females with complex ovejectors. Five superfamilies (conventionally assigned to the order Ascaridida) are recognised as parasites in vertebrates: Ascaridoidea (cylindrical oesophagus often terminated by swelling without bulb, coelomyarian, eggs thick-shelled); Heterakoidea (oesophagus cylindrical or with claviform corpus, short isthmus and valved bulb, coelomyarian, pre-anal sucker, eggs thick-shelled); Seuratoidea (lips absent, oesophagus short, platymyarian, eggs with delicate shells or hatch *in utero*); Cosmocercoidea (oesophagus with cylindrical corpus, elongate isthmus and valved bulb, platymyarian, eggs with delicate shells or hatch *in utero*); and Subuluroidea (well-developed buccal capsule without lips, coelomyarian, pre-anal sucker, eggs thick-shelled). Adult worms of the superfamily Ascaridoidea inhabit the gastrointestinal tract of vertebrate hosts and generally consume food ingested by the host. They may have simple monoxenous life cycles involving faecal-oral transmission, or more complicated heteroxenous life-cycles involving larval development in vertebrate intermediate hosts and sometimes larval transport in invertebrate paratenic hosts. Female worms produce unembryonated eggs which are passed in host faeces into the external environment where they embryonate to first-stage larvae (L1) which grow and moult to infective L2 or L3. Aquatic species produce thin-shelled eggs which hatch in water releasing sheathed L2 that are taken up by suitable hosts, while terrestrial species produce thick-shelled eggs which hatch releasing L3 when ingested by suitable hosts. Ascaridoid larval stages then undertake unique journeys: most involving pulmonary or somatic migration in their definitive hosts before maturing in the gut, sometimes including

vertical transmission (transplacental and/or transmammary); many migrating into the tissues of intermediate hosts, sometimes involving larval migrans or encapsulation in 'unsuitable' hosts; and a few undergoing precocious development in invertebrate hosts.

Five ascaridoid families are recognised: Ascarididae (lips often with toothed ridge, oesophagus with or without ventriculus, parasites of mammals, birds, reptiles, amphibians, fishes); Anisakidae (lips with tongue-like prolongations with cuticular thickenings, oesophagus with ventriculus with suture-like depressions, parasites of mammals, birds, reptiles and fishes); Crossophoridae (lips semicircular with toothed combs, fimbriated collar, long oesophagus without ventriculus, parasites of hyracoids); Heterocheilidae (lips with tongue-like prolongations with cuticular thickenings, cylindrical oesophagus without ventriculus, parasites of sirenians); and Acanthocheilidae (lips small with teeth or toothed ridges, oesophagus with ventriculus, parasites of elasmobranchs). The family Ascarididae contains 4 subfamilies: Ascaridinae (oesophagus simple, gubernaculum absent, lips hexagonal with anterior region offset from posterior, parasites of terrestrial mammals); Toxocarinae (oesophagus with globular ventriculus without appendices, gubernaculum absent, parasites of terrestrial or marine mammals or birds); Angusticaecinae (oesophagus simple, gubernaculum absent, lips quadrangular and not divided into anterior and posterior regions, parasites of reptiles and amphibians); and Multicaecinae (oesophagus with globular ventriculus usually with appendices, gubernaculum present, parasites of crocodilians or rarely fish). Ascaridid genera of medical and veterinary significance are compared in the following table.

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Ascaridinae						
Ascaris (roundworm)	2 (+ 150 *nomen dubium*)	primates, suids	small intestines	15-50 cm long, 3 small lips, striated cuticle, males with curved tail, simple spicules, females opisthodelphic, larvae undergo hepato-pulmonary migration	50-87 x 35-60 µm, ovoid, thick-shelled	faecal-oral
Parascaris	3	equids	small intestines	10-50 cm long, 3 large lips each with transverse groove, cuticle striated, males abursate, simple spicules, larvae undergo hepato-pulmonary migration	90-120 µm, spherical, thick-shelled	faecal-oral
Toxascaris	2	carnivores	small intestines	2-15 cm long, 3 lips, long thin cervical alae, oesophageal ventriculus absent, males lack terminal digitiform appendage, larvae do not undergo hepato-pulmonary migration	70-85 x 60-75 µm, ovoid, thick-shelled	faecal-oral (sometimes ingestion of infected PH)
Toxocarinae						
Toxocara	26	carnivores, ruminants, rodents	small intestines	3-30 cm long, 3 lips, long thin cervical alae, oesophageal ventriculus present, males with terminal digitiform appendage, larvae undergo somatic migration, hypobiosis	64-91 µm, spherical, thick-shelled	faecal-oral, ingestion of PH, transplacental, transmammary

The subfamily Ascaridinae contains 5 genera of large roundworms with well-defined lips and a simple oesophagus: *Ascaris* (syn. *Fusaria*, *Lombricoides*, *Stomachida*), *Baylisascaris, Lagochilascaris*, *Parascaris* and *Toxascaris.* The genus *Ascaris* contains worms whose lips are only separated into anterior and posterior regions by slight lateral indentations (interlabia, cervical alae and lateral flanges absent) and whose cuticles have longitudinal bracket-like bars not reaching the surface. Over 175 *Ascaris* spp. have previously been described from a range of vertebrate hosts (mammals, birds, reptiles, amphibians and fish), but the number of species in the genus is highly contentious. Nowadays, only 2 *Ascaris* species are considered valid: namely, *A. lumbricoides* and *A. suum*. Over 100 species are considered *nomen dubium*, another 40 species are pending detailed characterization studies (*species inquirenda*) and around 35 species have been reclassified to other genera, e.g. those described from reptiles have been grouped into 3 genera: *Polydelphis* (without interlabia, with 4 uterine branches) in pythons; *Travassosascaris* (with interlabia, with 4 uterine branches) in rattlesnakes; and *Hexametra* (without interlabia, with 6 uterine branches) in lizards and snakes.

A. lumbricoides from humans and *A. suum* from pigs are commonly encountered around the world. They have been differentiated on the basis of host occurrence and possibly some minor morphological differences (in the sizes and shapes of labial denticles and copulatory spicules), but more recently by genetic differences (mitochondrial and nuclear gene sequences). *A. lumbricoides* is common in many human populations around the world, particularly in tropical and subtropical countries with high rainfall, as well as in temperate regions with warm summers. Infections are particularly prevalent in impoverished communities with poor environmental sanitary conditions, including households where nightsoil (human faeces) is used to fertilise vegetable crops. It is estimated that almost one quarter of the world population (1.4 billion people) may be infected with soil-transmitted helminths,

with 700 million infected with *Ascaris*. Infections are over-dispersed in local populations, where large numbers of parasites occur in a small number of individuals. Children are most susceptible to clinical infection; although a range of predisposition factors have been reported, involving various combinations of environmental, social, behavioural and genetic factors. *A. suum* is prevalent in pigs, especially in developing countries with free-ranging village or feral pigs. Modern husbandry practices in developed countries have resulted in a significant decline in the incidence of infections in pigs. There is considerable biological and epidemiological evidence to suggest zoonotic transmission of *A. suum* to humans resulting in patent infections, although molecular studies have shown limited gene flow between human and pig ascarid populations. While the whole life-cycle of *A. suum* may not be completed in other non-porcine hosts, their larvae can undergo extensive migration in a number of hosts (cattle, sheep, rodents and lagomorphs) leading to allergic manifestations and/or respiratory distress.

***Ascaris* species**	**Definitive hosts**	**Location [Clinical signs]**	**Distribution**
A. lumbricoides (giant roundworm, human roundworm)	Primates: hominid (human, gorilla, chimpanzee, orangutan), hylobatid (gibbon), cercopithecid (rhesus macaque, Barbary macaque, Abyssinian black-and-white colobus), atelid (Guatemalan black howler) [plus miscellaneous reports: Carnivora: canid (dog), ursid (Hokkaido brown bear); Rodentia: castorid (Eurasian beaver), sciurid (black giant squirrel, Indian squirrel, Irrawaddy squirrel, grey squirrel, fox squirrel), murid (mouse), cricetid (muskrat); Lagomorpha: leporid (rabbit, cape jumping hare); Artiodactyla: bovid (cattle, water buffalo, sheep, goat, saiga), cervid (roe deer, moose), suid (pig, wild boar), tayassuid (peccary); Siluriformes: claroteid (bagrid catfish); Gadiformes: gadid (Alaska pollock); Cichliformes: cichlid (blackchin tilapia, Guinean tilapia, Nile tilapia); Diptera: muscid (house fly *Musca domestica*)]	small intestines [illthrift, gut obstruction]	worldwide
A. suum (pig roundworm)	Artiodactyla: suid (pig, wild boar, Sardinian wild boar), Primates: hominid (human) [plus miscellaneous reports: Artiodactyla: bovid (cattle, sheep, goat), cervid (roe deer); Rodentia: murid (mouse); Lagomorpha: leporid (rabbit); Galliformes: phasianid (chicken); Clitellata: lumbricid earthworm *Eisenia foetida*)]	small intestines [production losses]	worldwide

Species awaiting characterization:
A. brevicauda (from crested newt), *brevispiculum* (striped field mouse, wood mouse), *bulbosa* (bearded seal), *casta* (golden dorado), *castoris* (Eurasian beaver), *cebi* (Columbian white-faced capuchin), *circumflexa* (leopard), *columnaris* (black bear, wolverine, Pacific marten, beech marten, European pine marten, fisher, sable, European badger, American badger, striped skunk, spotted skunk, mountain weasel, least weasel, Siberian weasel, stoat, Siberian polecat, European polecat, steppe polecat, raccoon, squirrel, mouse, cotton rat hispid cotton rat), *compar* (willow ptarmigan), *dasypodina* (greater naked-tailed armadillo, six-banded armadillo, striped skunk), *depressa* (Eurasian sparrowhawk, Eurasian eagle-owl, white-tailed eagle, falcon), *devosi* (wolverine, American marten, European pine marten, fisher, stoat, least weasel, European polecat, American mink), *ensicaudata* (common starling, northern lapwing), *eperlani* (European smelt), *equorum* (horse), *ferox* (Syrian rock hyrax), *gestri* (checkered keelback), *gracilis* (long-tailed ground squirrel), *hippopotami* (hippopotamus), *joffi* (little ground squirrel, long-tailed ground squirrel), *laevis* (alpine marmot, hoary marmot, Tarbagan marmot, groundhog, Arctic ground squirrel, long-tailed ground squirrel), *linstowi* (wels catfish), *lotae* (common ling), *marginata* (dog, red fox), *megalocephala* (horse), *meleagrinae* (masked triggerfish, starry triggerfish), *mosgovoyi* (reindeer), *mucronata* (burbot), *osmeri* (European smelt), *ovis* (sheep, saiga antelope), *petiti* (aye-aye), *petromyzi* (European river lamprey), *phacochoeri* (desert warthog, common warthog), *phoxini* (common minnow), *rugosa* (Eurasian eagle-owl), *semiteres* (northern lapwing), *siluriglanidis* (wels catfish), *spalacis* (lesser mole rat), *spilaris* (little owl), *suilla* (pig), *suricattae* (meerkat), *tarbagan* (long-tailed ground squirrel, gray marmot, black-capped marmot, long-tailed marmot, Tarbagan marmot, groundhog), *tentaculatus* (rock hyrax), *thymalli* (grayling), *triquetra* (red fox) and *vimbae* (vimba bream).

Species reclassified to other genera:
A. adunca = *Hysterothylacium aduncum*
A. anguillae = *Raphidascaris acus*
A. anoura (syn. *A. attenuata, A. rubicunda*, *A. oculata*) = *Polydelphis anoura*
A. applanata = *Hexametra applanata*
A. aquillae = *Contracaecum haliaeti*
A. bicolor = *Anisakis rosmari* (syn. *Anisakis simplex*)
A. biuncinata = *Hysterothylacium fabri*
A. brachycheilos = *Polydelphis brachycheilos*
A. circularis = *Terranova circularis*
A. clavata = *Contracaecum clavatum* (syn. *Hysterothylacium clavatum, Hysterothylacium aduncum*)
A. decipiens = *Pseudoterranova decipiens*
A. fabri = *Contracaecum fabri* (syn. *Hysterothylacium fabri*)
A. falcigera = *Contracaecum falcigerum* (syn. *Contracaecum radiatum*)
A. filholi (syn. *A. nelsonis*) = *Anisakis simplex* larvae
A. gadi = *Hysterothylacium gadi*
A. gestri = *Hexametra gestri*
A. hexametra = *Hexametra hexametra*
A. leptura = *Kathlania leptura*
A. marina = *Anisakis marina* (syn. *Anisakis simplex*)
A. marina = *Hysterothylacium rigidum*
A. microcephala = *Contracaecum microcephalum*
A. micropapillata = *Contracaecum micropapillatum*
A. multipapillata = *Contracaecum multipapillatum*
A. osculata = *Contracaecum osculatum*
A. ovalis = *Contracaecum ovale*
A. patagonica = *Anisakis patagonica* (syn. *Anisakis simplex*)
A. pedum = *Contracaecum pedum*
A. plagiostomorum = *Contracaecum plagiostomorum*
A. quadrata = *Mawsonascaris pastinacae*
A. quadricornis (syn. *A. quadrangularis, A. quadrilobata*) = *Hexametra quadricornis*
A. radiata = *Contracaecum radiatum*
A. rotundicaudata (syn. *A. brachyura*) = *Hexametra rotundicaudata*
A. scombrica = *Contracaecum scombricum*
A. similis = *Anisakis similis*
A. simplex = *Anisakis simplex*
A. sphaerocephala = *Cucullanus sphaerocephalus*
A. spiculigerum = *Contracaecum spiculigerum* (syn. *Contracaecum rudolphii*)
A. striata = *Ophidascaris* sp.

Nomen dubium:
A. acanthocaudata (from common ling)*, acerinae* (Eurasian ruffe), *aculeati* (three-spined stickleback), *acuta* (tubot, brill, New York flatfish), *affinis* (common smooth hound), *albulae* (maraena whitefish), *alepocephali* (Risso's smooth-head), *anguillae* (European eel), *appendiculata* (Atlantic pomfret, Atlantic bonito), *argentinae* (Mueller's pearlside), *aspidophori* (hooknose), *atherinae* (Mediterranean sand smelt), *balisticola* (triggerfish), *barbatulae* (stone loach), *belonesvulgaris* (needlefish), *blennii* (viviparous eelpout), *boopis* (bogue), *brachyura* (oriental garden lizard), *bramae* (Atlantic pomfret), *capsularia* (allis shad, royal flagfin, European conger, lumpfish, Atlantic cod, silver scabbardfish, oilfish, Atlantic mackerel, ribbonfosh, John Dory), *carpionis* (common carp), *centrisci* (long-spine snipefish), *clupeae* (European sprat, Atlantic herring), *clupearum* (Atlantic herring), *collaris* (turbot), *constricta* (greater weaver), *crassicauda* (East Atlantic peacock wrasse), *cuneiformis* (ziege, ide, monkey goby), *cyclopteri* (lumpfish), *cynaedi* (goldsinny wrasse), *cyprinierythrophthalmi* (common rudd), *dehiscens* (ringed seal), *digitata* (Ballan wrasse), *ecaudata* (European conger, Atlantic salmon), *engraulidis* (European anchovy, European pilchard), *farionis* (Atlantic salmon), *filariformis* (lanternfish), *flesi* (European flounder), *gadiaeglefini* (haddock), *gadibrandti* (Pacific cod), *gadimerlangi* (blue whiting), *gadiminuti* (poor cod), *gasterostei* (three-spined stickleback), *genypteri* (kingklip), *gracilescens* (Atlantic herring, European anchovy, European sprat), *helopis* (starry sturgeon), *heringii* (giant anteater), *hippocampi* (long-snouted seahorse), *hirsuta* (European smelt), *incrassata* (roughtail stingray), *labiata* (European eel, European conger), *labrilusci* (green wrasse), *leucisciidi* (ide), *linguatulae* (spotted flounder), *longestriata* (Atlantic bluefin tuna), *lophiipiscatorii* (angler), *lyrae* (piper gurnard), *macrolabium* (vadigo, dusky grouper), *macruri* (bighead grenadier), *macruroidei* (grenadier), *madagascariensis* (river hog), *maenae* (blotched picarel), *manidis* (Chinese pangolin), *microcerca* (black-bellied angler), *minuta* (brill), *molvae* (blue ling), *morae* (common mora), *mozgovoyi* (reindeer), *mulli* (red mullet), *neglecta* (black-spotted porcupinefish), *novaculae* (pearly razorfish), *ophidiibarbati* (snake blenny), *ophidiiimberbis* (pearlfish), *orthragorisci* (ocean sunfish), *pachyderma* (porbeagle), *papilligera* (bullet tuna, Atlantic mackerel), *phycis* (forkbeard), *pigmentata* (marmot), *prionodora* (moonfish), *rajae* (common skate), *rostrata*

(jewfish), *rubicunda* (Indian python, reticulated python), *salmonisomul* (Arctic cisco), *sauri* (Atlantic lizardfish), *scaphirhynchi* (shovelnose sturgeon), *schroederei* (giant panda), *sciaenae* (shi drum), *scombrorum* (chub mackerel), *scorpaenae* (red scorpionfish), *scorpaenaecirrhosae* (scorpionfish, black scorpionfish), *siluri* (wels catfish), *smaris* (picarel), *soleae* (shorthorn sculpin, common sole), *sparoidum* (bogue, sand steenbras, saddled seabream, picarel), *spicrae* (picarel), *squali* (Schmidt's dace), *stictodora* (pink dentex), *succisa* (lumpfish, thornback ray), *tenuissima* (whiting, common ling), *torpedinis* (marbled electric eel), *trigonura* (stone loach), *truncatula* (European perch), *truttae* (Atlantic salmon), *ungulata* (Ballan wrasse), *uranoscopi* (Atlantic stargazer), *velocissima* (ruffe, zander, European perch) and *wedli* (red mullet).

Parasite morphology: The parasite forms several different developmental stages: eggs, larvae [moult from first-stage (L1) through to fourth-stage (L4)], and adults (male and female). Fertilised eggs appear as round-oval tan-coloured (bile-stained) stages measuring from 50-87 µm in length by 35-60 µm in width (*A. lumbricoides* eggs 65-75 x 35-50 µm, *A. suum* eggs 56-87 x 46-57 µm). They are surrounded by a thick albuminous mamillated (lumpy) outer coat. Before insemination or in early stages of oviposition, female worms may also excrete unfertilised eggs which are more elongate (75-95 x 35-50 µm) and decorticated (not mamillated). Fertilised eggs are excreted unembryonated, but then develop L1 which moult twice to form L2 then L3. When infective eggs are ingested by susceptible hosts, they hatch releasing small stout larvae (170-250 µm long) with conical tails. The larvae invade host tissues and grow in size (500-600 µm long) before undertaking hepato-pulmonary migration. Larvae in the lungs grow up to 1.0-1.7 mm long and then migrate up the trachea to be swallowed. They moult in the intestines to form L4 (1.6-2.7 mm long) which then moult to form juvenile worm (17-23 mm long) which grow and mature. Adult worms are tubular, cream-pink in colour and large: female worms measuring 200-500 x 3-6 mm; while males are smaller, measuring 150-300 x 2-4 mm. Adults have a striated cuticle and an anterior mouth with 3 small fleshy lips (one dorsal, 2 ventrolateral) bearing small denticles along their anterior inner margins. They do not possess interlabia and they do not bear cervical or caudal alae. Mature males have a tail that curls ventrally, a single tubular testis and a pair of equal spicules 2.0-3.5 mm long. Mature females have an opisthodelphic reproductive tract, with two coiled branches running posteriad initially from the anterior vulva. The combined uteri may contain millions of eggs at any one time and gravid females lay thousands of eggs daily. The species *A. lumbricoides* and *A. suum* are considered by many to be virtually indistinguishable. While careful examination by some workers indicated that *A. suum* had larger labial denticles and thinner and sharper spicules than *A. lumbricoides*, others have reported considerable pleomorphy in these characters apparently related to the age of the worms. Molecular characterization studies have tended to support their separate classification, but they are apparently not as host specific as previously thought.

Site of infection: Adult worms live in the lumen of the small intestine, where the females lay numerous eggs which are shed in host faeces. Prior to the development of adult worms, the infective larvae undertake a curious circuitous hepato-pulmonary migration (a phenomenon considered to be an evolutionary relict behaviour preserved from ancestral forms). The larvae migrate through the gut wall and are carried via the portal circulation to the liver and then the lungs where they penetrate into air spaces and move up the respiratory tree to the epiglottis where they are swallowed (ending up in the gut from where they started).

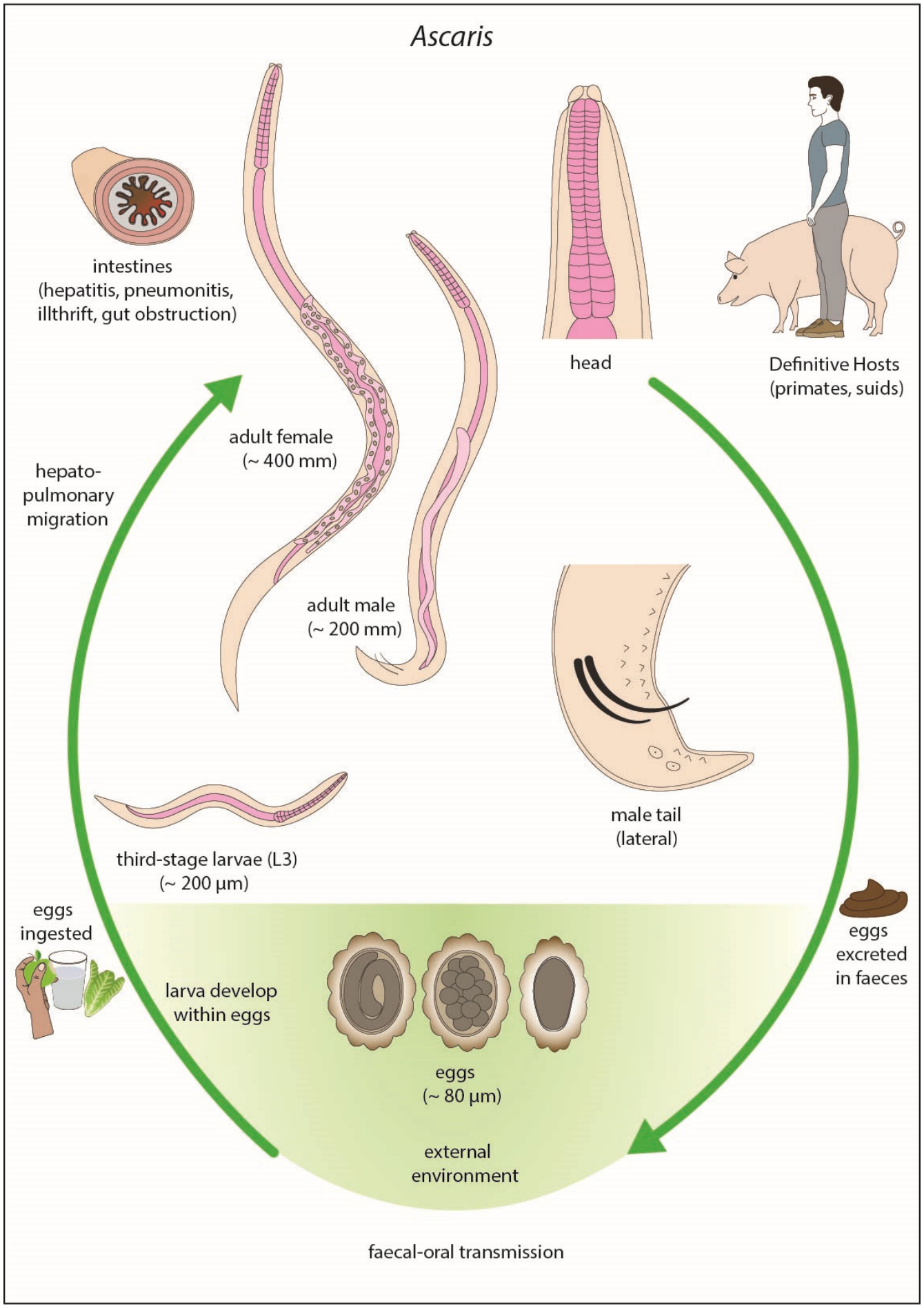
Pathogenesis: Infections by small numbers of worms may remain asymptomatic, although some individuals may develop allergic reactions (urticaria, eosinophilia). Larger numbers of worms, however, can cause significant health problems for the host. Following infection, larvae hatch from eggs in the intestines and invade the intestinal wall to the portal circulation where they pass through the liver and heart to the lungs where L3 are formed. Migrating larvae may cause mucosal haemorrhages in the intestines and white milk-spot lesions up to 1 cm in diameter in the liver (also known as multiple parasitic interstitial hepatitis). Pulmonary migration by larvae may cause petechial haemorrhages, oedema, emphysema, inflammation, and transient pulmonary congestion (pneumonitis, or Loeffler's pneumonia) with cough, chest pain and dyspnoea (difficulty breathing with diaphragmatic thumps or expiratory heaves). Migrating larvae lost or trapped in other tissues often die causing focal inflammation and vague symptoms difficult to diagnose. Adult worms developing in the gut feed on luminal content, they steal liquid nourishment from the host contributing to protein energy malnutrition, impaired carbohydrate absorption and vitamin A malabsorption. Moderate-heavy infections may cause a variety of digestive disorders (abdominal pain, distension, colic, nausea, vomiting, intermittent diarrhoea, anorexia, enterocolitis, mucosal abnormalities) as well as poor growth and development in children with restlessness, insomnia and allergic responses (rashes, asthma). Heavy infections may also cause life-threatening gut obstructions where tangles of worms form a bolus mechanically blocking the gut. To the great consternation of their hosts, worms may also occasionally wander upstream (obstructing biliary or pancreatic ducts, sometimes even being regurgitated) or downstream (infecting the appendix, or being passed in faeces). In pigs, infections by *A. suum* have been associated with reduced productivity through liver damage, reduced feed conversion efficiency, slower live-weight gain, and extended fattening periods. In sheep, and sometimes cattle, grazing on heavily contaminated pastures, migrating larvae may cause eosinophilic granulomas, inflammation and fibrosis in the liver as well as emphysema, oedema and bronchiolitis in the lungs.

Developmental cycle and mode of transmission: The parasite life-cycle is direct and does not involve intermediate hosts or vectors, although paratenic (transport) hosts may sometimes be involved. Infections are passed between definitive hosts by the faecal-oral transmission of eggs containing infective larvae (L3). Freshly-excreted eggs require 9-40 days for embryonation before they become infective. Embryonation occurs faster in warm moist soil (especially clay) and water (~10 days at 30°C). The eggs are

very resistant to external environmental conditions and can survive high temperatures (up to 45°C) and dry conditions (down to 6% humidity). Experimental studies have shown that eggs may remain viable in soil for several years. They are also dispersed in the environment by wind, water, earthworms and insects (cockroaches). Eggs in soil/water may be transferred to the mouth by contaminated hands or ingested with foods (uncooked vegetables, washed salads and fruits) or soil (pica = dirt-eating), especially by young children. Once ingested, the eggs hatch in the small and large intestines releasing infective larvae (previously thought to be L2 but now shown to be L3 covered by a loosened L2 cuticle). The L3 invade the mucosa and migrate via the portal circulation to the liver and then to the lungs over 8-10 days. They break into the airspaces (alveoli) of the lungs and move up the bronchi and trachea to the pharynx where they are swallowed. This pulmonary migration is enigmatic as the parasites end up in the intestines from where they started. It has been argued that such migration by various ascarid species may be a remnant genetic trait derived from a vector-borne ancestor, or that it is an adaptive trait strongly associated with enhanced adult body size and fecundity and maintained by selection. Once back in the small intestines, the larvae moult to L4 around 2 weeks after infection and then to L5 (sub-adults) around 3-4 weeks after infection. Worms mature by 6 weeks after infection and females begin egg production 40-65 days after infection (= prepatent period) and produce huge numbers of eggs (up to 200,000 per day). The adult worms may live for 6 months to 2 years, so the entire parasite life-cycle can range from 2 months up to 5-10 years. It has also been shown that eggs of *A. suum* ingested by earthworms or dung beetles may hatch releasing larvae which may remain in their tissues for some time but can resume development when the paratenic host is ingested by pigs. Suckling piglets have also been found to acquire infections from sows udders contaminated with embryonated eggs and repeated infections have been shown to induce partial immunity.

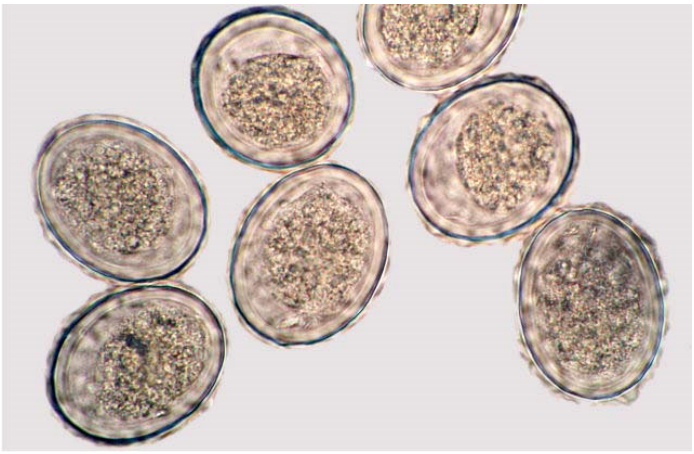
Differential diagnosis: Infections may be indicated by clinical history and symptomatology but are confirmed by the microscopic detection of eggs in faecal material, often using sedimentation and/or floatation concentration techniques. Ascarid eggs are relatively dense and float better in saturated salt solutions with higher specific gravities (e.g. zinc or magnesium sulphate rather than saturated sodium chloride). Occasionally, intact adult worms may be expelled through the anus, mouth or nose. Haematological tests often reveal marked peripheral eosinophilia during infections but it can be quite variable in strength and duration. Imaging techniques (X-ray, ultrasound, magnetic resonance imaging (MRI) and computed tomography (CT) scans) may be used to discern large worms in tubular organs and ducts. At necropsy, tangles of adult worms may be found in the intestines and small white-spot fibrotic lesions may be visible through the liver. The antemortem diagnosis of infections during the larval migration stage is difficult due to non-specific nature of any clinical signs. Larvae have sometimes been detected in sputum samples but are difficult to identify by untrained personnel. Several immunoserological tests (variants of enzyme immunoassays) have been developed to detect host antibodies against infections but they are generally not clinically useful due to persistent antibody responses and cross-reactivity with other helminths. Various molecular biological techniques using polymerase chain reactions (PCR) to amplify specific gene sequences (mitochondrial cytochrome genes, nuclear ribosomal genes and a range of microsatellite markers) have been used to genotype isolates, trace infections, test egg viability after disinfection and even test coprolites.

Treatment and control: Various anthelmintic drugs have proven effective for the treatment of infections. On a population level, mebendazole and albendazole appear to be the drugs of choice in communities endemic for ascariasis, with chemoprevention targeting school-aged children. Repeated doses of benzimidazoles for individual cases increases efficacy, although it sometimes may cause some worms to wander. Suitable alternatives include pyrantel and levamisole, while ivermectin and moxidectin have also recently been trialled in humans. Piperazine was commonly used but has now been substantively withdrawn due to adverse side-effects. In pigs, suspect ascarid pneumonia may be treated with injectable levamisole or ivermectin. For routine deworming, doramectin, ivermectin, flubendazole, fenbendazole, pyrantel and morantel are effective against ascariasis and have a broader spectrum of activity that piperazine. Although most infections can be successfully treated, the individual often returns to the same heavily contaminated environment and quickly becomes re-infected. Environmental decontamination is difficult because the eggs are very resistant to chemicals; they can embryonate in dilute formalin, potassium dichromate, acid solutions and many commercial disinfectants. Because infections accumulate in their hosts (worms do not multiply in hosts), control measures involve avoiding behaviours conducive to the uptake of eggs; such as improving personal hygiene, maintaining sanitary conditions, and proper disposal of excreta. Fresh faecal material should not be used to fertilise edible crops, but it can be processed by microbial biocomposting before use (high temperature processing destroys egg viability). In piggeries, parasite control should include drenching sows prior to farrowing, regularly treating piglets, maintaining strict hygiene in pens/sties, and proper effluent disposal. Control in free-range operations may be problematic due to the high levels of contamination and the longevity of infective eggs, so paddock rotation/spelling may be necessary.

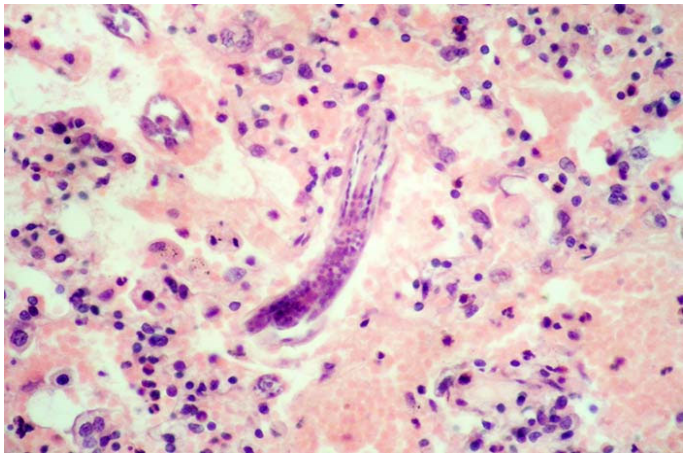

Ascaris
intestines
(hepatitis, pneumonitis,
illthrift, gut obstruction)
adult female
(~ 400 mm)
adult male
(~ 200 mm)
head
Definitive Hosts
(primates, suids)
hepato-
pulmonary
migration
male tail
(lateral)
third-stage larvae (L3)
(~ 200 µm)
eggs
ingested
larva develop
within eggs
eggs
excreted
in faeces
eggs
(~ 80 µm)
external
environment
faecal-oral transmission

Ascaris adult worms

Ascaris adult worms



Ascaris worm eggs



Ascaris larva in lung