Anisakis
(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. 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. Adult anisakids are characterised by a post-oesophageal ventriculus and are found in dolphins, whales, predatory teleost fish, sharks and piscivorous birds. Anisakid transmission is unusual in being indirect, involving both intermediate and paratenic hosts. Female worms lay eggs which are passed in host faeces and then ingested by small copepods (intermediate hosts) where they hatch. L3 are passed up the food chain when copepods are eaten by small teleosts (paratenic hosts), which in turn are eaten by larger teleosts before infecting definitive hosts. Infections by larvae may cause enteric disease in humans.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	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:	Anisakidae (large stout worms, in marine mammals/fishes/birds)
Genus:	*Anisakis* (parasitic in gut of dolphins/whales)
Species:	various species cause enteric disease (anisakiasis) 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: Cosmocercoidea (oesophagus with cylindrical corpus, elongate isthmus and valved bulb, platymyarian, eggs with delicate shells or hatch *in utero*); Seuratoidea (lips absent, oesophagus short, platymyarian, eggs with delicate shells or hatch *in utero*); Heterakoidea (oesophagus cylindrical or with claviform corpus, short isthmus and valved bulb, coelomyarian, pre-anal sucker, eggs thick-shelled); Ascaridoidea (cylindrical oesophagus often terminated by swelling without bulb, coelomyarian, eggs thick-shelled); 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 Anisakidae contains 3 subfamilies: Anisakinae (cuticular rings without spines, excretory system ribbon-like, parasites of mammals, birds, reptiles or elasmobranch fish); Goeziinae (cuticular rings with posterior spines, parasites of teleost fishes and rarely reptiles); and Raphidascaridinae (cuticular rings without spines, excretory system not ribbon-like, parasites of fish, occasionally birds). The subfamily Anisakinae contains 8 genera: *Anisakis* (syn. *Capsularia*, *Conocephalus*, *Filocapsularia*, *Peritrachelius*, *Stomachus*), *Phocanema*, *Sulcascaris* and *Terranova* classified in the tribe Anisakinea (oesophagus with oblong to cylindrical ventriculus); and *Contracaecum, Duplicaecum, Galeiceps* and *Phocascaris* classified in the tribe Contracaecinea (oesophagus with reduced globular ventriculus).

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Anisakis	9-24	marine mammals	stomach, intestines	15-82 mm long, 3 anterior lips, post-oesophageal ventriculus, males abursate, larvae undergo hepato-pulmonary migration	45-66 x-35-55 µm, ovoid, thin-shelled	indirect (L3 in crustacean IH) (sometimes in teleost PH)

The genus *Anisakis* contains anywhere from 9-24 species which form adult worms in the gastrointestinal tracts of marine mammals (seals, dolphins, porpoises, whales), particularly in colder temperate and polar waters. Transmission involves larval stages in aquatic invertebrates and fish acting as intermediate and paratenic hosts. Over 100 fish species have been implicated in transmission cycles as transport hosts harbouring L3, which may also be passed up the food chain from fish-to-fish. Development of larval stages have also been reported in some birds, sea snakes and elasmobranchs. Humans may become accidentally infected when consuming raw or improperly cooked fish with larvae causing eosinophilic granulomas in the alimentary tract (but the larvae are unable to complete their development in humans). Infections have been reported throughout Asia, Oceania, Europe and the Americas, often linked to the consumption of popular local delicacies, such as sushi, sashimi, cod livers or fermented herring.

***Anisakis* species**	**Definitive Hosts (adult worms in stomach, intestines)**	**Intermediate Hosts [plus Paratenic hosts (PH)] (larvae in tissues)**	**Distribution**
A. berlandi (= *A. simplex* sp. C)	Artiodactyla: delphinid (long-finned pilot whale, false killer whale), kogiid (pygmy sperm whale)	[PH: Procellariiformes: procellariid (grey petrel)]	Pacific
A. nascetti	Artiodactyla: ziphiid (strap-toothed beaked whale, Blainville's beaked whale, True's beaked whale, Gray's beaked whale)	[PH: Gadiformes: merlucciid (European hake); Perciformes: trichiurid (black scabbardfish); Cephalopoda: onychoteuthid (greater hooked squid)]	Mediterranean, Southern Atlantic
A. paggiae	Artiodactyla: physeterid (pygmy sperm whale, dwarf sperm whale)	[PH: Beryciformes: berycid (splendid alfonsino)]	Atlantic
A. pegreffii (= *A. simplex* sp. A)	Carnivora: phocid (Mediterranean monk seal); Artiodactyla: cetotheriid (pygmy right whale), delphinid (common bottlenose dolphin, striped dolphin, long-finned pilot whale), physeterid (sperm whale), ziphiid (bottlenose whale, Cuvier's beaked whale)	[PH: Anguilliformes: anguillid (European conger, white-spotted conger); Beloniformes: belonid (garfish); Beryciformes: trachichthyid (silver roughy); Carangiformes: carangid (Cape horse mackerel, Mediterranean horse mackerel, Atlantic horse mackerel, bluejack mackerel); Clupeiformes: engraulid (European anchovy), dussumierid (Whitehead's round herring, sardine); Gadiformes: gadid (blue whiting), merlucciid (European hake, Argentine hake, South African hake), morid (red codling); Istiophoriformes: xiphiid (swordfish); Lophiiformes: lophiid (angler, devil anglerfish); Myctophiformes: myctophid (electric lantern fish, spothead lantern fish); Ophidiiformes: ophidiid	Mediterranean, Atlantic, Pacific

		(kinglip); Perciformes: bramid (Atlantic pomfret), carangid (horse mackerel, Atlantic horse mackerel, Atlantic mackerel), emmelichthyid (Cape bonnetmouth), sciaenid (redlip croaker), trichiurid (black scabbardfish, silver scabbardfish, largehead hairtail); Pleuronectiformes: paralichthyid (cinnamon flounder), scophthalmid (four-spot megrim); Salmoniformes: salmonid (chum salmon); Scombriformes: gempylid (snoek), scombrid (Atlantic bluefin tuna, chub mackerel, Atlantic chub mackerel, Atlantic mackerel); Scorpaeniformes: scorpaenid (red scorpionfish), sebastid (blackbelly rosefish); Stomiiformes: phosichthyid (slender lightfish); Trachiniformes: pinguipedid (blue cod); Zeiformes: zeid (John Dory); Carcharhiniformes: carcharhinid (blue shark); Cephalopoda: ommastrephid (European flying squid, Angola flying squid, lesser flying squid); Procellariiformes: procellariid (grey petrel); Sphenisciformes: spheniscid (little penguin); Primates: hominid (human)]	
A. physeteris (syn. *A. skrjabini, A. oceanica, A. brevispiculata*)	Artiodactyla: balaenopterid (common minke whale, sei whale), delphinid (Risso's dolphin, short-finned pilot whale, melon-headed whale), kogiid (pygmy sperm whale, dwarf sperm whale), phocoenid (Dall's porpoise), physeterid (sperm whale), ziphiid (bottlenose whale, Cuvier's beaked whale); Carnivora: otariid (brown fur seal)	[PH: Beryciformes: berycid (splendid alfonsino), trachichthyid (silver roughy); Carangiformes: carangid (greater amberjack, Chilean jack mackerel, blue jack mackerel, Atlantic horse mackerel), coryphaenid (mahi-mahi); Gadiformes: gadid (Pacific cod, Alaska pollock), merlucciid (European hake, Patagonian grenadier, common Atlantic grenadier, roughsnout grenadier), gadid (blue whiting); Istiophoriformes: xiphiid (swordfish); Lampriformes: trachipterid (ribbonfish); Perciformes: epigonid (black cardinal fish), nototheniid (Patagonian toothfish), trichiurid (black scabbardfish); Pleuronectiformes: paralichthyid (fine flounder); Scombriformes: scombrid (skipjack tuna, chub mackerel); Scorpaeniformes: scorpaenid (red scorpionfish), sebastid (blackbelly rosefish); Spariformes: sparid (silver seabream); Cephalopoda: loliginid (spear squid), ommastrephid (neon flying squid, purpleback flying squid, Japanese flying squid), onychoteuthid (boreal clubhook squid); Primates: hominid (human)]	Mediterranean, Atlantic, Pacific
A. schupakovi	Carnivora: phocid (Caspian seal)	[PH: Acipenseriformes: acipenserid (sterlet, starry sturgeon, Russian sturgeon, beluga sturgeon); Clupeiformes: clupeid (Caspian shad, Caspian marine shad, Caspian andromous shad, Saposhnikovi shad, anchovy sprat, Black Sea sprat, Southern Caspian sprat, Caspian tyulka); Cypriniformes: cyprinid (common carp, common rudd, ziege, common roach, Caspian roach, tench, Danube bleak, asp, Caspian barbel, vimba bream); Esociformes: esocid (northern pike); Gadiformes: gadid (blue whiting); Gobiiformes: gobiid (monkey goby, bighead goby, round goby, stellate tadpole-goby, Caspian goby); Mugiliformes: mugilid (golden grey mullet, leaping mullet); Perciformes: percid (European perch, estuarine perch, zander); Salmoniformes: salmonid (salmon); Serpentes: colubrid (dice snake); Suliformes: phalacrocoracid (great cormorant)]	Caspian Sea, Black Sea

A. simplex (whaleworm, herring worm) (syn. *A. marina, A. ivanizkii, A. kukenthalii, A. kogiae, Ascaris*)	Artiodactyla: balaenid (bowhead whale); balaenopterid (common minke whale, sei whale, blue whale, little piked whale, fin whale, humpback whale), delphinid (short-beaked common dolphin, long-beaked common dolphin, common bottlenose dolphin, white-beaked dolphin, dusky dolphin, pantropical spotted dolphin, rough-toothed dolphin, striped dolphin, hourglass dolphin, northern right whale dolphin, Commerson's dolphin, Risso's dolphin, Frasier's dolphin, Atlantic white-sided dolphin, Pacific white-sided dolphin, killer whale, false killer whale, North Atlantic pilot whale, short-finned pilot whale, long-finned pilot whale, melon-headed whale), eschrichtiid (gray whale), kogiid (pygmy sperm whale, dwarf sperm whale), monodontid (beluga whale, narwhal), physeterid (sperm whale), phocoenid (porpoise, harbour porpoise, Burmeister's porpoise, Dall's porpoise, finless porpoise), platanistid (South Asian river dolphin), pontoporiid (La Plata dolphin); ziphiid (Baird's beaked whale, Blainville's beaked whale, Sowerby's beaked whale, Cuvier's beaked whale, True's beaked whale, giant bottlenose whale, northern bottlenose whale); Carnivora: odobenid (walrus), otariid (Steller sea lion, South American sea lion, California sea lion, northern fur seal, brown fur seal, South American fur seal), phocid (common seal, Mediterranean monk seal, grey seal, leopard seal, ringed seal, hooded seal, bearded seal, ribbon seal, harp seal, spotted seal, northern elephant seal, southern elephant seal)	Malacostraca: crangonid (brown shrimp, *Crangon crangon*), euphausiid (krill, *Euphasia nana, pacifica, similis, vallentini*, *Meganyctiphanes norvegica, Nyctiphanes australis, couchii, Thysanoessa inermis, longicauda, longiceps, longipes, raschii*), gammarid (krill, *Gondogeneia antarctica*; amphipod, *Eurymera monticosa*), lysianassid (amphipod, *Waldeckia obesa*), mysid (opossum-shrimp, *Mesodopsis slabberi*), pandalid (caridean prawn, *Pandalus borealis*, *kessleri*), pontageneiid (amphipod, *Bovallia gigantea, Pontogeneiella brevicornis*); Hexanauplia: acartiid (copepod, *Acartia tonsa*), balanid (barnacle, *Balanus*), oithonid (copepod, *Oithona similis*); Polychaeta: polynoid (scaleworm, *Lepidonotus squamata*); Sagittoidea: sagittid (arrow-worm, *Sagitta elegans*) [PH: Acipenseriformes: acipenserid (white sturgeon); Anguilliformes: anguillid (European eel), congrid (European conger), moraenesocid (daggertooth pike conger), ophichthid (snake eel); Argentiniformes: alepocephalid (Agassiz' slickhead), argentinid (great silver smelt); Atheriniformes: atherinid (sand smelt); Aulopiformes: bathysaurid (deepsea lizardfish), synodontid (slender lizardfish, snakefish); Batrachoidiformes: batrachoidid (banded toadfish); Beloniformes: belonid (needlefish, garfish), scomberesocid (Atlantic saury); Beryciformes: trachichthyid (silver roughy); Carcharhiniformes: carcharhinid (blue shark, spadenose shark), scyliorhinid (small spotted catshark); Carangiformes: carangid (cleftbelly trevally, bigeye trevally, Malabar trevally, double-spotted queenfish, African pompano, Japanese scad, torpedo scad, Japanese amberjack, Mediterranean horse mackerel, Atlantic horse mackerel, Japanese horse mackerel, Chilean jack mackerel, blue jack mackerel, Pacific jack mackerel, bigeye scad), echeneid (live sharksucker), menid (moonfish), rachycentrid (cobia); Clupeiformes: clupeid (blueback herring, allis shad, American shad, Twaite shad, alewife, Atlantic herring, Baltic herring, Pacific herring, Chosa herring, Japanese scaled sardine, European pilchard, Japanese pilchard, round sardinella, European spart), engraulid (anchovy, Japanese grenadier anchovy, Argentine anchoita, Japanese anchovy); Cypriniformes: cyprinid (big-scaled redfin); Gadiformes: gadid (polar cod, poor cod, Pacific cod, Atlantic cod, blue whiting, southern blue whiting, navaga, saithe, Norway pout, pouting, haddock, merling, walleye pollock, European pollock, Alaska pollock), lotid (cusk, five-beard rockling, Arctic rockling, common ling, blue ling), macrourid (common Atlantic grenadier, roughsnout grenadier, rock grenadier, ridge-scaled rattail), merlucciid (hoki, blue grenadier, southern hake, silver hake, shallow-water Cape hake, South Pacific hake, North Pacific hake, Argentine hake, European hake), morid (North Atlantic codling), muraenolepid (small-eye moray cod), phycid (hake,	Atlantic, Pacific, Arctic

		white hake, longfin hake, red hake, greater forkbeard); Gasterosteiformes: gasterosteid (three-spined stickleback, nine-spined stickleback); Gobiiformes: gobiid (common goby, sand goby, painted goby, black goby, two-spotted goby), odontobutid (dark sleeper); Istiophoriformes: xiphiid (swordfish); Labriformes: labrid (goldsinny wrasse, Ballan wrasse); Lamniformes: lamnid (salmon shark); Lophiiformes: lophiid (angler, blackmouth angler, black-bellied angler, American angler); Mugiliformes: mugilid (mullet); Myctophiformes: myctophid (lanternfish, small lanternfish, fragile lanternfish, transparent lanternfish, blackhead lanternfish, metallic lanternfish, pearly lanternfish, multi-spotted lanternfish, Warming's lanternfish, Nichol's lanternfish, Reinhart's lanternfish, electron sub-Antarctic lanternfish, belted lanternfish, flaccid lanternfish, Bermuda lanternfish, large-finned lanternfish, noble lampfish, patchwork lampfish); Myliobatiformes: dasybatid (pale-edged stingray); Ophidiiformes: ophidiid (goatsbeard brotula, pink cuskeel); Osmeriformes: osmerid (capelin, European smelt, surf smelt, Arctic rainbow smelt); Perciformes: anarhichadid (Atlantic wolffish), bramid (Pacific pomfret), centropomid (snook), channichthyid (blackfin icefish), epigonid (black cardinal fish), haemulid (saddle grunt), lateolabrid (Japanese sea bass), leiognathid (ponyfish), lutjanid (crimson snapper, bigeye snapper, emperor red snapper), malacanthid (gold tilefish, Argentine tilefish), mullid (deepwater goatfish, sulphur goatfish, red mullet, sur mullet), nemipterid (golden threadfin bream), notothenid (Patagonian toothfish, dusky rockcod, humped rockcod, yellow-belly rockcod, marbled rockcod, Antarctic cod, emerald rockcod, striped rockcod), percid (zander), pholid (rock gunnel), priacanthid (red bigeye, purple-spotted bigeye, Japanese bigeye), sciaenid (meagre, yellow drum, large yellow croaker, redlip croaker, sin croaker), serranid (areolate grouper, yellow grouper), siganid (mottled spinefoot), sparid (bogue, threadfin porgy, common pandora, red seabream, goldlined seabream, black seabream), terapontid (large-scaled terapon, Jarbau terapon), trichiurid (black scabbardfish, silver scabbardfish, largehead hairtail), zoarcid (glacial eelpout, Arctic eelpout, viviparous eelpout, longear eelpout); Petromyzontiformes: petromyzontid (European river lamprey, sea lamprey); Pleuronectiformes: cynoglossid (tongue sole), paralichthyid (large-tooth flounder, bastard halibut), pleuronectid (stone, flounder, arrowtooth flounder, Kamchatka flounder, sohachi, righteye flounder, flathead flounder, yellow-tail flounder, yellow-striped flounder, winter flounder, European flounder, American plaice, Atlantic halibut, Pacific halibut, Greenland halibut, common dab, dusky sole), psettodid (Indian halibut), scophthalmid (megrim, fourspot megrim, windowpane flounder); Rajiformes: arhynchobatid (spinytail skate), rajid (Arctic skate, ocellate spot skate, thorny skate); Salmoniformes: salmonid (sakhalin taimen,	

		davatchan, pink salmon, chum salmon, coho salmon, masu salmon, sockeye salmon, Atlantic salmon, white-spotted char, rainbow trout, brown trout, brook trout, Dolly Varden trout); Scombriformes: gempylid (snoek), scombrid (Atlantic mackerel, blue mackerel, narrow-barred Spanish mackerel, Japanese Spanish mackerel, chub mackerel, Atlantic chub mackerel, Atlantic bonito, Indian mackerel, bullet tuna, skipjack tuna, mackerel tuna, yellowfin tuna, Atlantic bluefin tuna), sphyraenid (pickhandle barracuda, Japanese barracuda), stromateid (American butterfish); Scorpaeniformes: agonid (dragon poacher), cottid (Altlantic hookear sculpin, longhorn sculpin, great sculpin, shorthorn sculpin), cyclopterid (lumpfish), hemitripterid (sea raven), hexagrammid (green ling, Okhotsk atka mackerel), platycephalid (crocodile flathead, bartail flathead), scorpaenid (plaintail turkeyfish, red scorpionfish, false stonefish), sebastid (Norway haddock, blackbelly rosefish, canary rockfish, silvergrey rockfish, white-edged rockfish, Korean rockfish, Akodai rockfish, Bocaccio rockfish, Steindachner's rockfish, deepwater redfish, Acadian redfish, Norway redfish, golden redfish, osaga), triglid (red gunard, grey gunnard); Siluriformes: ariid (giant catfish); Squaliformes: etmopterid (velvet-belly lanternshark), squalid (spiny dogfish); Stomiiformes: sternoptychid (Mueller's pearlside); Tetraodontiformes: tetraodontid (yellowfin puffer, lunartail puffer, Japanese puffer); Trachichthyiformes: trachichthyid (orange roughy); Trachiniformes: ammodytid (northern sand lance), trachinid (greater weaver); Zeiformes: zeid (John Dory); Cephalopoda: eledonid (curled octopus), gonatid (arrow squid), loliginid (spear squid, long-finned squid, little squid, European squid), myopsid (squid), octopodid (common octopus), oegopsid (commander squid), ommastrephid (Humboldt squid, Argentine shortfin squid, southern shortfin squid, New Zealand arrow squid, red flying squid, purpleback flying squid, lesser flying squid, Japanese flying squid, European flying squid), onychoteuthid (boreal clubhook squid), sepiid (common cuttlefish, golden cuttlefish); Charadriiformes: alcid (Atlantic puffin, thick-billed murre), larid (glaucous gull); Procellariiformes: procellariid (northern fulmar); Testudines: cheloniid (loggerhead sea turtle); Carnivora: mustelid (Eurasian otter); Rodentia: murid (brown rat); Primates: hominid (human)]	
A. typica	Artiodactyla: delphinid (short-beaked common dolphin, dusky dolphin, striped dolphin, common bottlenose dolphin, Fraser's dolphin, pantropical spotted dolphin, spinner dolphin, Atlantic white-sided dolphin, hourglass dolphin, tucuxi, rough-toothed dolphin, short-finned pilot whale, long-finned pilot whale, melon-headed whale, pygmy killer	[PH: Aulopiformes: synodontid (brushtooth lizardfish); Carangiformes: carangid (longnose trevally, bumpnose trevally, imposter trevally, mackerel scad, bigeye scad, bluejack mackerel), coryphaenid (mahi-mahi), echeneid (live sharksucker); Clupeiformes: chirocentrid (Dorab wolf-herring), clupeid (giant herring); Gadiformes: merlucciid (European hake), Perciformes: carangid (horse mackerel), lutjanid (ornate snapper), monodactylid (silver moonfish), mullid (bartailed goatfish), nemipterid (Japanese whiptail, threadfin	Mediterranean, Atlantic, North Sea

	whale, false killer whale), kogiid (pygmy sperm whale), phocoenid (common porpoise, Dall's porpoise, harbor porpoise), pontoporid (La Plata dolphin), ziphiid (Sowerby's beaked whale, Cuvier's beaked whale, northern bottlenose whale); Carnivora: phocid (grey seal, harbour seal)	bream), serranid (red grouper, orange-spotted grouper, areolate grouper), trichiurid (largehead hairtail); Pleuronectiformes: paralichthyid (Patagonian flounder, fantail flounder); Scombriformes: scombrid (mackerel tuna, frigate tuna, blackfin tuna, Atlantic bluefin tuna, striped bonito, chub mackerel, bullet mackerel, Indian mackerel, narrow-barred Spanish mackerel), sphyraenid (bigeye barracuda, sawtooth barracuda); Trachiniformes: pinguipedid (sandperch, Namorado sandperch, Brazilian sandperch); Carcharhiniformes: carcharhinid (spinner shark); Serpentes: elapid (blue-lipped sea krait)]	
A. ziphidarum	Artiodactyla: ziphiid (strap-toothed beaked whale, Gervais' beaked whale, Cuvier's beaked whale, Blainville's beaked whale)	[PH: Carangiformes: carangid (bluejack mackerel); Gadiformes: merlucciid (European hake, Atlantic grenadier, roughsnout grenadier); Myctophiformes: myctophid (electric lantern fish, spothead lantern fish); Perciformes: carangid (mackerel), trichiurid (black scabbardfish); Scombriformes: scombrid (chub mackerel); Stomiiformes: phosichthyid (slender lightfish)]	Mediterranean, Southern Atlantic
Species inquirenda			
A. alexandrii	Artiodactyla: delphinid (Chinese white-sided dolphin)		Pacific
A. appendiculata	Procellariiformes: procellariid (short-tailed shearwater)		Australia
A. catodontis	Artiodactyla: physeterid (sperm whale, dwarf sperm whale)		Atlantic
A. delphini	Artiodactyla: platanistid (South Asian river dolphin)		India
A. dussumierii	Artiodactyla: delphinid (long-snouted dolphin, spinner dolphin), physeterid (sperm whale)		Asia
A. goldi	Carnivora: canid (dog)		
A. insignis	Artiodactyla: delphinid (Amazon river dolphin)		South America
A. kuekenthalii	Artiodactyla: monodontid (beluga whale)		Arctic
A. pacificus	Artiodactyla: balaenopterid (common minke whale, sei whale, fin whale), delphinid (killer whale), physeterid (sperm whale); Carnivora: phocid ribbon seal)		cosmopolitan
A. patagonica (syn. *Ascaris*)	Carnivora: otariid (South American sea lion, Steller sea lion), phocid (southern elephant seal)		South America
A. rosmari (syn. *A. bicolor, A. alata*)	Carnivora: odobenid (walrus), phocid (ringed seal)		Arctic
A. salaris		[PH: Gadiformes: gadid (Atlantic cod)]	Atlantic
A. similis (syn. *Ascaris*)	Carnivora: otariid (South American sea lion, California sea lion, South American fur seal, Steller sea lion), phocid (southern elephant seal, northern elephant seal, harbor seal, leopard seal, grey seal)		Southern Ocean, Atlantic, Pacific, Arctic

A. tridentata	Carnivora: otariid (Steller sea lion)		Pacific
A. tursionis	Artiodactyla: delphinid (common bottlenose dolphin)		

Parasite morphology: *Anisakis* spp. form 3 different morphological stages in their developmental cycles: eggs; larvae (4 successive stages designated L1-L4); and adult worms. The eggs are round-oval in shape measuring from 45-66 x 35-55 µm with smooth thin transparent shells and are unembryonated when laid containing a single central morula. The eggs embryonate to form L1 which moult while still within the eggshell to form L2. Emergent L2 are elongate cylindrical stages measuring 220-355 µm in length and they are ensheathed within the L1 cuticle (retained as a protective covering). In crustacean intermediate hosts, the L2 exsheath and grow to 3-6 mm long before moulting to pink-yellow L3 ranging in size from 4-50 x 0.3-2.0 mm. The L3 have a prominent anteroventral boring tooth, an excretory pore located anteriorly, an oesophagus with an anterior muscular portion and a posterior glandular ventriculus (0.15-0.67 mm long) connected to the intestines, and a rounded tail with a terminal spine (mucron). In paratenic hosts, L3 are encapsulated by fibrous connective tissue forming flat cysts (4-5 mm diameter) containing the tightly coiled larvae (watch-spring appearance). L3 dissected from cysts ranged in size from 14-30 x 0.3-0.6 mm and they were bound by a tough cuticle with transverse striations, often appearing wrinkled near the tail. The larvae had rounded heads, an anterior boring tooth, a muscular oesophagus followed by a glandular ventriculus connected to the intestines and ending in a subterminal anus. Four different types of encapsulated larvae have been described from paratenic hosts: type I with an average body size of 28 x 0.5 mm and a long ventriculus, an oblique ventriculus-intestinal junction, and a short rounded tail with a mucron (type often referable to *A. simplex*); type II with an average size of 26 x 0.6 mm and a short ventriculus, horizontal junction, and a long conical tapering tail without a mucron (often referable to *A. physeteris*); type III averaging 29 x 0.8 mm with a short ventriculus and a short rounded tail without a mucron; and type IV averaging 20 x 0.5 mm with a short ventriculus and a short conical pointed tail without a mucron. L4 are transient parasitic stages that range in size from 12-38 x 0.4-1.3 mm and have begun to display developing genitalia. Adults are large white worms measuring 15-82 x 0.4-1.9 mm which possess 3 protruding lips with tongue-like prolongations around the mouth and a single prominent anteroventral boring tooth. The cuticle has fine longitudinal striations, except for the smooth anterior region, but is otherwise devoid of cuticular ornamentations, spicules or spines (characteristic for the subfamilies Anisakinae and Raphidascaridinae). Worms have a distinctive alimentary tract with a glandular ventriculus located between the muscular oesophagus and the intestines (oblong-cylindrical ventriculus in members of the tribe Anisakinea, globular in the tribe Contracaecinea), sometimes with intestinal caeca, but always with a subterminal anus. The excretory system is also unique, being asymmetrical and ribbon-like (also characteristic in the subfamily Anisakinae) with the excretory pore located anteriorly between the subventral lips. Adults worms are sexually dimorphic, with females being slightly longer than males. Mature females are didelphic with 2 ovaries and uteri connected to a small common vulva located in the anterior half of the body. They have conical rounded tails lacking caudal papillae. In contrast, mature males have numerous caudal papillae (1 median, 1 pair proximal, 1 pair double paracloacal, 4 pairs distal) with their patterns of distribution varying between species. Males have 2 stout slightly subequal spicules (0.14–0.32 mm long), an attribute for which the genus was named (*anis* = different, *akis* = spicule).

Site of infection: Adult worms infect the stomach and intestines of their definitive (final) hosts (cetaceans and pinnipeds), often embedded in the mucosa. Developing larval stages (L2, L3) are found in the haemocoel of their crustacean intermediate hosts (euphausiids), while L3 may also be found encapsulated in the body cavities and internal tissues of various paratenic hosts (mostly teleost fish and squid). Humans may also act as accidental paratenic hosts for L3 which attach to the wall of the oesophagus, stomach or intestine, sometimes penetrating to extraintestinal sites (abdominal cavity, mesenteries, pancreas, liver, lung).

Pathogenesis: The effects that adult worms have on their final hosts are largely unknown, although clusters have been found in association with small ulcerative lesions and local inflammation usually in the stomach mucosa. Similarly, the effects that larvae have the fitness of their crustacean intermediate hosts are unknown, but the parasites are usually confined to the haemocoel rather than host tissues. In contrast, encysted larvae are often found in the tissues of their piscine paratenic hosts, causing unsightly lesions in many commercial fish species. Most fish appear healthy externally, but encysted larvae may be detected macroscopically either singly or in clusters in the peritoneum, mesenteries, visceral organs and muscles. The larvae are surrounded by fibrous connective tissue, often with melanomacrophage infiltrates in chronic infections. Infected livers appear red-brown due to local haemorrhages or green due to the destruction of bile ducts. In the stomach, infections may also cause crater syndrome whereby the thickened mucosa develops erosive craters up to 10 mm in diameter containing protruding larvae. Many reports have also observed larval migration into the musculature following host death (particularly for *A. simplex*). An increasing number of cases have been described in humans which act as accidental paratenic hosts when they consume L3 in raw or poorly cooked seafood. The larvae attach or migrate in host tissues within a few days of consumption but they cannot complete further development and die after a short period (2-3 weeks) although lesions may persist for several months. The larvae may cause direct tissue damage and provoke strong allergenic responses. The resultant disease may be acute or chronic in presentation and is known as anisakiosis/anisakiasis (terms often restricted to infections by *A. simplex* s.s.) or anisakidosis (more general term including other anisakids, such as *A. pegreffi, Contracaecum* or *Pseudoterranova* spp.). Larvae attach mostly to the stomach mucosa (sometimes the intestines, rarely the oesophagus), where they burrow down to the muscularis mucosae, rarely penetrating the wall and moving to ectopic extra-intestinal locations (abdominal cavity, mesenteries, omentum, bowel). In the mucosa, larvae may often detach and reattach at adjacent sites

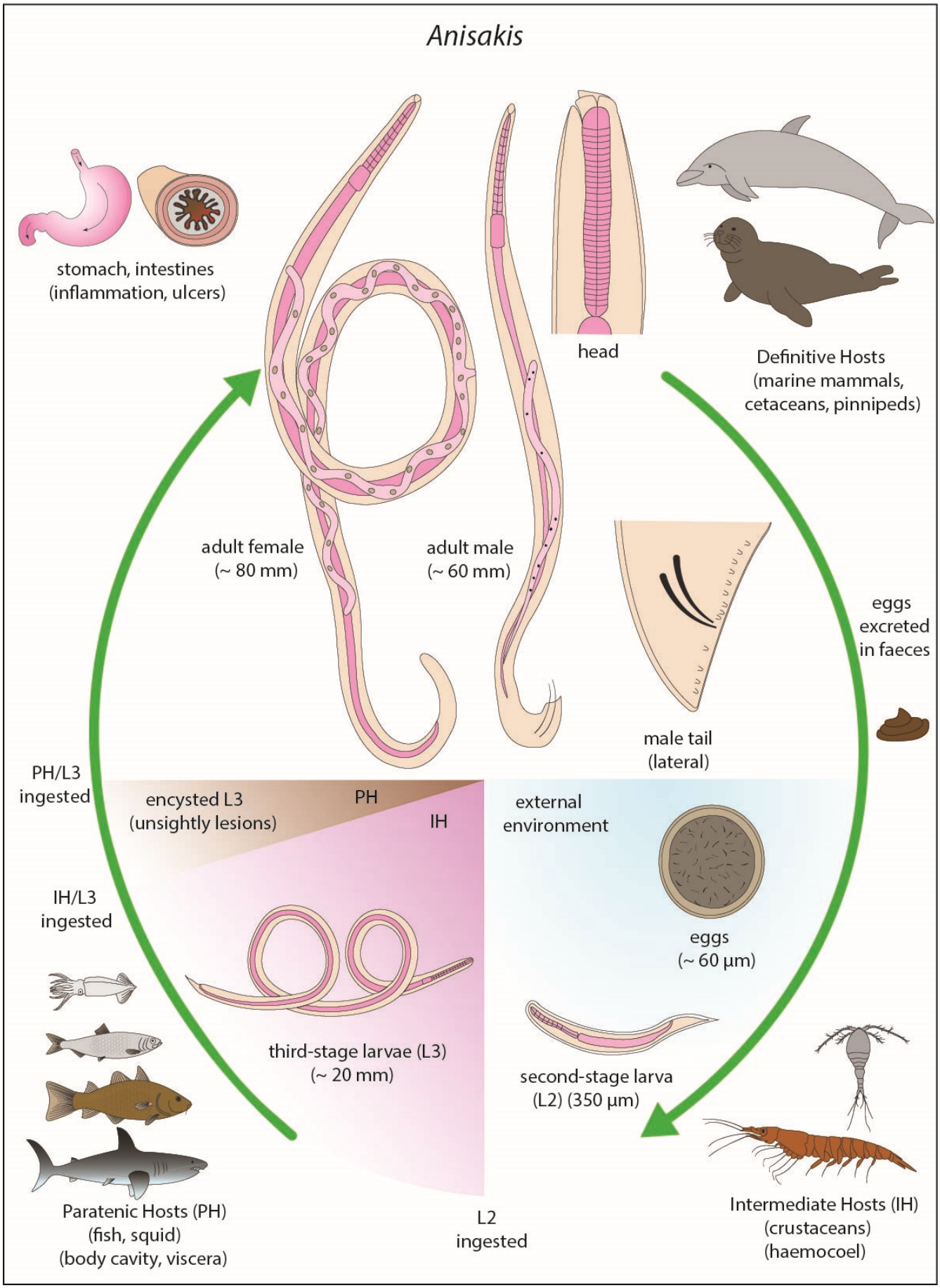
causing small petechial haemorrhages. The larvae elicit host inflammatory responses ranging from local inflammation to abscess/ulcer formation with necrosis and eosinophilia, to localized granuloma formation with encapsulation, cellular infiltrates (especially eosinophils) and larval degradation, to massive eosinophilic haemorrhagic tumour-like growths (pseudo-neoplasms with larvae at centre), particularly when infections involve the large intestines. Clinical signs vary considerably depending on the individual, the number of larvae (often only one), and the site of infection (gastric, intestinal or extra-intestinal). Initial clinical signs may include the sensation of having something between the teeth, tingling throat, dysphagia, mild cough and nasal congestion. Gastric signs may appear as early as 4-6 hours after infection and are often acute in nature, with epigastric pain (rapid and severe), gastric reflux, nausea and vomiting, sometimes with haematemesis due to ulceration. Intestinal signs may appear 7 days after infection with abdominal pain, colic, diarrhoea (sometimes with faecal occult blood), enteritis, leucocytosis, and sometimes with intestinal obstruction and peritonitis due to inflammation, oedema, granuloma and abscess formation. Lastly, many patients exhibit acute allergic (hypersensitivity) reactions to infection, particularly children and atopic individuals. Larval somatic and secretory products are highly allergenic and have been associated with the production of Th2 cytokines, mastocytosis, IgE antibody production and eosinophilia. Clinical signs may vary from mild to severe: with local irritation, inflammation and ulceration occurring at sites in contact with larvae; general urticaria (occurring in 60–70% of gastric cases); and type I hypersensitivity reactions involving airway hyperactivity (anaphylaxis, asthma, bronchospasms, rhinoconjunctivitis), angioedema with hypotension, and dermatitis.

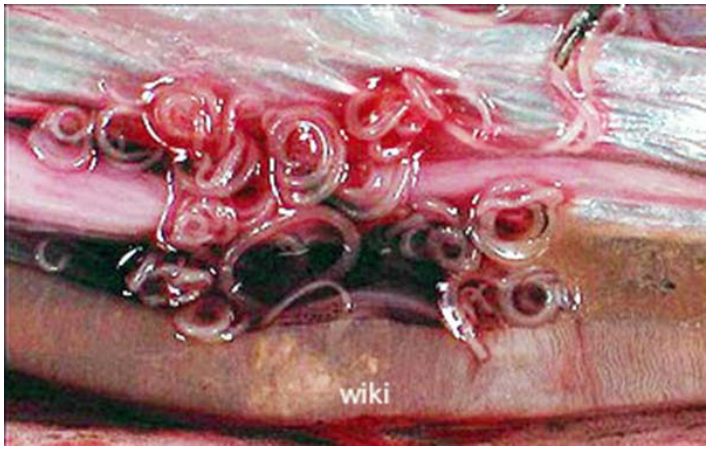
Developmental cycle and mode of transmission: *Anisakis* spp. have indirect heteroxenous life-cycles involving larval development in crustacean intermediate hosts, larval transport in fish or squid paratenic hosts and adult development in piscivorous final hosts (mostly pinnipeds and cetaceans). To date, adult *Anisakis* worms have been detected in 32 species of dolphins (mostly delphinids but including a platanistid and a pontoporiid), 6 species of porpoises (phocoenid), 17 species of toothed whales (ziphiid, physeterid, kogiid, and monodontid), 9 species of baleen whales (balaenopterid, balaenid, cetotheriid, and eschrichtiid), 15 species of seals (phocid), 7 species of sea-lions/fur-seals (otariid) as well as the walrus (odobenid) and dog (canid). Adult worms lay unembryonated eggs in the alimentary tract which are excreted with host faeces. The eggs embryonate in seawater to form L1 which then moult within the egg to form ensheathed L2 (a few miscellaneous reports suggest that L3 may form within some eggs). Eggs are well adapted to cold temperatures, and they embryonate and hatch within 4-8 days at 13-18°C or within 20-27 days at 5-7°C. The released larvae are active stages that swim and drift in seawater surviving for 3-4 weeks at 13-18°C or 6-7 weeks at 5-7°C. The L2 are then ingested by planktonic or pelagic crustaceans which act as intermediate hosts for L3 development. Suitable hosts include euphausiid krill, gammarid, lysianassid and pontageneiid amphipods, crangonid and mysid shrimp, pandalid prawns as well as acartiid and oithonid copepods, balanid barnacles, polynoid polychaetes, and sagittid arrow-worms. Ingested L2 exsheath and penetrate into the haemocoel where they moult and grow to larger L3 which may survive for as long as their hosts. Infections are more prevalent in regions of higher salinity as the juvenile stages of euphausiids favour such conditions for their development. When infected crustaceans are eaten by small teleost fish and cephalopods, the L3 burrow through the gut wall and encyst in fibrous connective tissue capsules usually on the serosa of visceral organs, but occasionally in the muscles or beneath the skin. These hosts act as paratenic (transport) hosts as the L3 are carried in the tissues without undergoing further development. Encysted L3 may also ascend the food chain and establish in larger teleost fish and some elasmobranchs when they consume smaller infected fish. A wide range of paratenic hosts have been reported from 97 families in 35 orders of teleost fish, including many commercially important marine and anadromous species such as herring, mackerel, cod, and salmon, 7 families of squid, 2 families of octopus, 5 families of sharks, and 3 families of rays/skates. Infections by L3 have also been detected occasionally in 2 families of sea-snakes, 1 family of sea turtles, 5 families of sea-birds, 1 family of otters, accidentally in 1 primates (humans) and experimentally in rodents (rats). Final hosts (marine mammals) become infected when they consume infected paratenic hosts. Ingested L3 infect the stomach mucosa where they moult to L4 and then subadults (often called L5) which grow to sexually mature adult worms. Little is known about the prepatent or patent periods of infections in the final hosts (cetaceans or pinnipeds). Humans become infected by the consumption of L3 in fish or cephalopods when eaten raw or semi-raw (lightly cooked, smoked, salted, pickled or fermented) in traditional culinary dishes, such as sushi, sashimi, ceviche, tuna tartare, pickled herring or anchovies, salted or smoked herring, tiradito, gravlax, Chinese kuai, Fijian kokoda, Micronesian kelaguen, or fish tripe.

Differential diagnosis: Most infections by adult worms have been detected incidentally during post-mortem examinations of whales, dolphins or seals following their death in captivity or following boat-strike, strandings or hunting. Infections in crustacean hosts may be detected by their dissection and microscopic examination of the haemocoel for developing larvae, but their identity is difficult to establish. Infections in fish hosts are more frequently detected during processing or food preparation by the discovery of encapsulated coiled larvae in the viscera and muscles (larvae of several species often migrate post-mortem from viscera to muscles). Microscopic studies conducted on larvae recovered from a range of fish species have identified at least 4 major morpho-types (I-IV). Molecular biological studies have used polymerase chain reaction (PCR) amplification, restriction fragment length polymorphism (RFLP) analyses and sequencing of nuclear genes (18S, 5.8 S and 28S ribosomal RNA, internal transcribed spacers 1 and 2) and mitochondrial genes (cytochrome oxidase 2, small subunit ribosomal RNA) to identify a clade of 6 species referable to larval type I (*A. simplex* s.s., *A. berlandi* (= *A. simplex* C), *A. nasceti, A. pegreffi, A. typica, A. ziphidarum*) and another clade of 3 species referable to larval type II (*A. brevispiculata, A. paggiae, A. physeteris*). In humans, infections are difficult to diagnose by symptomatology due to their nonspecific clinical manifestations, even when there is a solid history of the consumption of raw or undercooked fish within the last few days. Many other conditions present with similar clinical signs, such as ulcers, tumours, cholecystitis, appendicitis, peritonitis, Crohn’s colitis, diverticulitis, intestinal intussusception, obstruction, various food allergies,

and other gastrointestinal infections (viral, bacterial, protozoal and helminth). On occasion, larvae may be coughed up or excreted in faeces, but most infections are detected by invasive techniques such as endoscopy (gastroscopy, colonoscopy), laparoscopy or explorative surgery. Medical imaging technologies may help focus explorations by revealing mucosal thickenings, luminal constrictions and/or inflammatory foci by radiography, ultrasonography or computed tomography. A range of immunodiagnostic tests have been developed to detect specific antibody-antigen interactions by immuno-diffusion, immuno-electrophoresis, intradermal skin-prick tests, immuno-fluorescence, haemagglutination, enzyme immunoassays, Western blots and radioallergosorbent tests. Most tests demonstrated good sensitivity but reduced specificity due to antigenic cross-reactivity with other helminths, but some improvements have been achieved using defined antigens, monoclonal antibody reagents and specifically testing for IgE antibodies in cases involving hypersensitivity reactions.

Treatment and control: Given that most anisakid infections in their normal hosts (marine mammals, crustaceans, fish and cephalopods) are cryptic and asymptomatic, little information is available about possible treatments. Infections in humans are accidental and frequently transient, many involving just a few larvae that live for several weeks before succumbing to host responses, although lesions and symptoms may persist for months. Most human infections resolve spontaneously without treatment, but the anthelmintic albendazole has been used to kill larvae, often in combination with supportive therapy to reduce inflammatory and allergic reactions. Accessible larvae may also be removed by endoscopy or laparoscopy, or by surgery usually conducted when intestinal obstructions occur. Many countries have developed education campaigns to warn consumers about the dangers of eating not only raw seafood but also improperly processed dishes (many marinating, brining, salting, pickling, fermenting and smoking techniques may not kill encysted larvae). Larvae are rendered nonviable when cooked at 60°C or above for more than one minute, or by freezing at -35°C or below for 16 hours, at -20°C for at least 24-48 hours, or at -10°C for over 7 days. Some success has also been reported treating seafood with high hydrostatic pressures to kill parasites and increase the shelf-life of produce. While stringent food inspection may be used in fish processing plants, it is advisable to remove the viscera of fish shortly after capture to remove sources of infection and to prevent their post-mortem migration from the viscera to the muscles.


Anisakis
stomach, intestines
(inflammation, ulcers)
head
Definitive Hosts
(marine mammals,
cetaceans, pinnipeds)
adult female
(~ 80 mm)
adult male
(~ 60 mm)
male tail
(lateral)
eggs
excreted
in faeces
PH/L3
ingested
encysted L3
(unsightly lesions)
PH
IH
external
environment
IH/L3
ingested
eggs
(~ 60 µm)
third-stage larvae (L3)
(~ 20 mm)
second-stage larva
(L2) (350 µm)
Paratenic Hosts (PH)
(fish, squid)
(body cavity, viscera)
L2
ingested
Intermediate Hosts (IH)
(crustaceans)
(haemocoel)



Anisakis larvae in herring