

## ***Benedenia***

(platyhelminth: monogenea)

### **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. Monogeneans are elongate to oval flatworms that are ectoparasitic on the skin and gills of fish, although a few are found in the urinary tracts of turtles, frogs and fishes. They have an anterior adhesive organ (prohaptor) and a conspicuous posterior adhesive organ (opisthaptor) armed with hooks or spines, often highly modified for attachment to specific sites. They are hermaphroditic and have direct life-cycles, mostly where eggs hatch releasing a free-swimming larva (oncomiracidium) which actively seeks a new host. Monopisthocotyleans have an opisthaptor that forms a single symmetrical attachment unit lacking haptoral clamps. Capsalids are large oval worms and the opisthaptor has a pair of anterior suckers and two pairs of posterior hooks. Infestations by *Benedenia* spp. have been associated with skin lesions, mortality and reduced productivity in cultured fish populations.

### **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: Monogenea (monoxenous ectoparasites, sac-like gut, direct cycles, oncomiracidium with 3 ciliary bands)  
Order: Monopisthocotylea (posterior haptor comprising a single symmetrical attachment unit, no haptoral clamps)  
Family: Capsalidae (large worms, haptor with pair anterior suckers and two pairs of posterior hooks)  
Genus: *Benedenia* (parasitic in skin/gills of fish)  
Species: various species cause skin lesions in fish

**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 (previously called 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).

Monogeneans and trematodes (flukes) have blind sac-like guts (lacking an anus) while cestodes (tapeworms) lack digestive tracts. Some 3,500 monogenean species have been described: most being ectoparasitic on the skin and gills of fish, although a few are found in the urinary tracts of turtles, frogs, fish and the eye of the hippopotamus. They have an anterior adhesive organ (prohaptor) and a conspicuous posterior adhesive organ (opisthaptor) armed with hooks, hooklets, hamuli (anchors) or clamps, often highly modified for attachment to specific sites. They are monoecious (hermaphroditic) and have direct monoxenous life-cycles mostly where eggs release free-swimming larvae (oncomiracidia with 3 ciliary bands) that actively seek new hosts (gyrodactylids are the exception as they are viviparous and produce live young). While the higher taxonomy of the Monogenea is often disputed with respect to rank, some 67 families have been resolved on the basis of morphological, biological and molecular studies. Three main groups are recognized: 28 families of Monopisthocotylea (opisthaptor with hooks, ectoparasitic on fish skin and gills, feed on epithelia); 37 families of Polyopisthocotylea (opisthaptor with clamps, ectoparasitic on fish gills, feed on blood); and 2 families of Polystomatoinea (opisthaptor with suckers, endoparasitic in tetrapods).

Order	No. families	No. spp.	DH	Characters
Class: Monogenea (= Monogenoidea) (monogenetic life-cycles, ectoparasitic mainly on fish) ~ 3,500 spp.				
Subclass: Monopisthocotylea (= Polyonchoinea) (opisthaptor with hooks, feed on fish epithelia) ~2,500 spp.				
Capsalidea	2	200	mostly marine teleosts, some elasmobranchs	2 anterior suckers, 2 pairs anchors, 14 marginal haptor hooks, some loculi
Dactylogyridea (= Monoaxonematidea)	17	1,000	freshwater and marine teleosts, coelacanth, squala	sperm with single axoneme, 12-14 haptor hooks, 2 pairs anchors, 1 transverse bar
Gyrodactylidea	5	1,500	freshwater and marine teleosts, squid, copepods	16 marginal 'hinged' haptor hooks, 1 pair anchors, dorsal and ventral bars, most viviparous (some nested polyembryony)
Monocotylidea	3	90	marine elasmobranchs	14 marginal haptor hooks, some loculi
Montchadskyellidea	1	10	marine teleosts	14 marginal haptor hooks, gut diverticulate, some endoparasitic in gut
Subclass: Polyopisthocotylea (= Heteronchoinea) (opisthaptor with clamps, most feed on blood of fish) ~1,000 spp.				
Chimaericolidea	1	5	marine holocephalans (chimaeras)	clamps, 1 pair anchors, haptor with 14 marginal hooks (each with domus)
Diclybothriidea	2	70	marine elasmobranchs, holocephalans, freshwater acipenseriform teleosts	clamps open and act as suckers, lateral sclerites absent
Mazocraeidea	34	920	numerous freshwater and marine teleost families	clamps with various structures incl. additional sclerites, hooks, spines; oral sucker a buccal organ, eggs with 2 polar filaments
Subclass: Polystomatoinea (parasitize aquatic tetrapods and lungfish)				
Polystomatidea	2	100	tetrapods (turtles, amphibians, hippopotamus), lungfish	haptor with 3 pairs suckers, egg filaments absent, some endoparasitic in tubular organs

Monopisthocotyleans have an opisthaptor that forms a single symmetrical attachment unit lacking haptor clamps. Five orders are recognized on the basis of differences in parasite morphology, development and host occurrence; including the order Capsalidea characterized by worms possessing 2 anterior suckers, 2 pairs of anchors and a posterior haptor with 14 marginal hooks and accessory sclerites. A total of 250 species belonging to 2 families (Capsalidae and Enoplocotylidae) have been described mostly from marine bony (teleost) and some cartilaginous (chondrichthyan) fishes. Nine capsalid subfamilies have been erected containing 49 genera and over 220 species; most parasitizing teleost fishes although 2 species are found on sturgeons and 15 species on elasmobranchs. The combination of ancient (shark, ray, sturgeon) and modern (teleost) fish lineages as hosts suggests that capsalid evolution is likely a blend of host-parasite co-evolution and host-switching.

Capsalidae subfamilies	Haptor morphology	Number of testes	Hosts	Genera (number of species)
Benedeniinae	aseptate	2	mostly teleosts, some elasmobranchs	<i>Allobenedenia</i> (2), <i>Allometabenedeniella</i> (1), <i>Ancyrocotyle</i> (2), <i>Benedenia</i> (syn. <i>Tareenia</i> ) (30), <i>Benedeniella</i> (2), <i>Calicobenedenia</i> (1), <i>Dioncoseudobenedenia</i> (1), <i>Lagenivaginopseudobenedenia</i> (2), <i>Menziesia</i> (5), <i>Metabenedeniella</i> (2), <i>Neobenedenia</i> (6), <i>Oligoncobenedenia</i> (1), <i>Pseudallobenedenia</i> (2), <i>Trimusculotrema</i> (4)
Capsalinae	septate	multiple	teleosts	<i>Caballerocotyla</i> (24), <i>Capsala</i> (14), <i>Capsaloides</i> (10), <i>Nasicola</i> (2), <i>Tricotyla</i> (3), <i>Tristoma</i> (8), <i>Tristomella</i> (8)
Dioncinae	septate	2	teleosts, elasmobranchs	<i>Dioncus</i> (11)
Encotyllabinae	septate	2	teleosts	<i>Alloencotyllabe</i> (1), <i>Encotyllabe</i> (17)
Entobdellinae	aseptate	2	elasmobranchs (esp batoids), some teleosts (esp. flatfish)	<i>Branchobdella</i> (1), <i>Entobdella</i> (9), <i>Listrocephalos</i> (2), <i>Neoentobdella</i> (6), <i>Pseudoentobdella</i> (1)

Interniloculinae	septate	4	teleosts	<i>Interniloculus</i> (2)
Nitzschiinae	aseptate	multiple	acipenserids (sturgeons)	<i>Nitzschia</i> (2)
Pseudonitzschiinae	aseptate	multiple	teleosts	<i>Pseudonitzschia</i> (1)
Trochopodinae	septate	most 2, some 4 or multiple	mostly teleosts, some elasmobranchs	<i>Allomegalocotyla</i> (2), <i>Macrophyllida</i> (1), <i>Mediavagina</i> (2), <i>Megalobenedenia</i> (2), <i>Megalocotyle</i> (6), <i>Megalocotyloides</i> (6), <i>Pseudobenedenia</i> (3), <i>Pseudobenedeniella</i> (1), <i>Pseudobenedenoides</i> (2), <i>Pseudomegalocotyla</i> (1), <i>Sessilorbis</i> (1), <i>Sprostonia</i> (2), <i>Sprostoniella</i> (3), <i>Tetrasepta</i> (1), <i>Trilobiodiscus</i> (1), <i>Trochopella</i> (1), <i>Trochopus</i> (15)

Over 30 *Benedenia* spp. have been described as ectoparasites on the skin and fins, and sometimes gills, of marine teleost fishes around the world, mainly in tropical and subtropical regions near coral reefs. Several species have been associated with significant production problems mainly in sea cage aquaculture of marine finfish.

<b><i>Benedenia</i> species</b>	<b>Habitat</b>	<b>Hosts</b>	<b>Distribution</b>
<i>B. acanthopagri</i>	marine	Perciformes: sparid (sea bream, twobar sea bream, Sobaity sea bream)	Middle-East
<i>B. anticavaginata</i>	marine	Perciformes: sparid (yellowfin bream, goldsilk sea bream)	Australia
<i>B. beverleyburtonae</i>	marine	Perciformes: haemulid (slate sweetlip)	Australia
<i>B. bodiani</i>	marine	Labriformes: labrid (saddleback pigfish)	Australia
<i>B. disciliata</i>	marine	Perciformes: haemulid (slate sweetlip)	Australia
<i>B. elongata</i> (syn. <i>kintoki</i> )	marine	Perciformes: lutjanid (lavender jobfish, ruby snapper, flame snapper, bulleye)	West Pacific
<i>B. epinepheli</i>	marine	Perciformes: serranid (redspotted grouper, kelp grouper, convict grouper, Hong Kong grouper, orange-spotted rockcod), cheilodactylid (spottedtail morwong), echeneidid (slender sharksucker), pomacanthid (threadfin butterflyfish); Pleuronectiformes: pleuronectid (Japanese flounder); Anguilliformes: anguillid (whitespotted conger); Tetraodontiformes: monacanthid (unicorn filefish), balistid (clown triggerfish), diodontid (longspined porcupine fish), ostraciid (yellow boxfish, blue-spotted boxfish), tetraodontid (panther puffer, purple puffer, fine-patterned puffer, grass puffer, pear puffer, nashifugu); Labriformes: labrid (Asian sheepshead wrasse); Centrarchiformes: oplegnathid (spotted knifejaw), latrid (spotted-tail morwong); Scorpaeniformes: scorpaenid (Korean rockfish, false kelpfish, red lionfish)	Pacific
<i>B. ernsti</i>	marine	Perciformes: lutjanid (Chinamanfish, emperor red snapper)	Pacific
<i>B. fieldsi</i>	marine	Perciformes: serranid (blue-lined coralcod, blue-spotted rockcod, purple rockcod, blacktip rockcod, specklefin grouper, camouflage grouper, longfin grouper, saddle grouper, greasy rockcod, coral trout, yellowedge coronation trout, red-cheeked fairy basslet)	Pacific
<i>B. hawaiiensis</i> (syn. <i>sargocentron</i> )	marine	Perciformes: priacanthid (glasseye), mullid (yellowstripe goatfish, banded goatfish, doublebar goatfish, sidespot goatfish, whitesaddle goatfish, goldsaddle goatfish), pomacentrid (Hawaiian domino, green damselfish, oval chromis), acanthurid (brown tang, pencil surgeonfish, sleek unicornfish), chaetodontid (millet butterflyfish); Tetraodontiformes: monacanthid (honeycomb filefish, Indo-Pacific dumerili, scribbled leatherjacket filefish, fantail filefish), balistid (Sargassum triggerfish); Aulopiformes: synodontid (banded lizardfish); Beryciformes: holocentrid (yellow-striped squirrelfish, sabre squirrelfish); Labriformes: scarid (bullethead parrotfish)	Pacific, Atlantic
<i>B. haywardi</i>	marine	Perciformes: lutjanid (Chinamanfish)	Pacific
<i>B. hendorffii</i>	marine	Perciformes: coryphaenid (dolphinfish, pompani dolphinfish)	tropics
<i>B. hoshinai</i>	marine	Centrarchiformes: oplegnathid (striped beakfish)	Pacific
<i>B. innobilitata</i>	marine	Perciformes: serranid (comber)	Mediterranean
<i>B. ishikawae</i>	marine	Perciformes: lethrinid (Chinese emperor)	Pacific

<i>B. jaliscana</i>	marine	Perciformes: serranid (starry grouper, spotted grouper)	Pacific
<i>B. lolo</i>	marine	Labriformes: labrid (yellowtail coris wrasse, yellowstripe coris, blackeye thicklip wrasse)	Pacific
<i>B. lutjani</i>	marine	Perciformes: lutjanid (Spanish flag snapper)	Australia
<i>B. madai (sp. inquir.)</i>	marine	Perciformes: sparid (red seabream)	Pacific
<i>B. malaboni</i>	marine	Perciformes: serranid (humphead wrasse)	Pacific
<i>B. merinthe</i>	marine	Scorpaeniformes: scorpaenid (ulukau)	Pacific
<i>B. monticellii</i>	marine	Mugiliformes: mugilid (grey mullet, golden grey mullet, thinlip mullet, flathead grey mullet, greenback mullet, keeled mullet, bluespot mullet); Gobiiformes: gobiid (rock goby)	Red Sea, Pacific
<i>B. noblei</i>	marine	Scorpaeniformes: scorpaenid (Bocaccio rockfish)	North America
<i>B. ovalis</i>	marine	Perciformes: lutjanid (deepwater red snapper), priacanthid (bigeye)	Pacific
<i>B. ovata (syn. akaisaki)</i>	marine	Perciformes: serranid (sunrise perch)	Pacific
<i>B. pagrosomi (sp. inquir.)</i>	marine	Perciformes: sparid (red seabream)	Asia
<i>B. pompatica</i>	marine	Perciformes: sciaenid (meagre), carangid (amberjack)	East Atlantic
<i>B. rohdei</i>	marine	Perciformes: lutjanid (Spanish flag snapper)	Australia
<i>B. scari</i>	marine	Labriformes: scarid (bullethead parrotfish)	Indo-Pacific
<i>B. sciaenae (syn. elegans)</i>	marine	Perciformes: sciaenid (meagre, corb, shi drum), serranid (brown spotted grouper)	Europe, Pacific
<i>B. Sebastodis</i>	marine	Scorpaeniformes: scorpaenid (Japanese stingfish)	Pacific
<i>B. sekii</i>	marine	Perciformes: sparid (red seabream)	Pacific
<i>B. seriolae</i>	marine	Perciformes: carangid (yellowtail amberjack, Japanese amberjack, yellowtail kingfish)	Indo-Pacific
<i>B. synagris</i>	marine	Tetraodontiformes: tetraodontid (scribbled toadfish)	IndoPacific

**Parasite morphology:** Capsalid monogeneans have 3 distinct developmental stages: eggs, larvae (oncomiracidia) and monoecious (hermaphroditic) adults. The eggs are tetrahedral, usually 100-200 µm along their long axes and each possesses a pronounced filamentous appendage measuring 0.9-2.3 mm long. The oncomiracidia are elongate measuring 170-400 µm in length and those of most species have patches or zones of epidermal cells bearing locomotory cilia. These larval stages have prominent anterior glandular elements (combinations of lateral and median head glands), pigmented eyes, flame bulbs, and a disc-like posterior haptor with hamuli (sometimes called anchors or hooks), accessory sclerites and marginal hooklets (sometimes called hooks). Adult worms have flattened leaf-like bodies up to 3-12 mm in length with 2 anterior disc-like attachment organs (often hooded or bipartite) and a well-developed posterior saucer-shaped opisthaptor armed with 2 pairs of ventrally directed hamuli, 1 pair of median accessory sclerites, 14 small marginal hooklets and a thin membranous marginal valve which is often scalloped. Some species possess pigmented bodies (black, brown, red, blue, green) producing an overall colouration or fragmented mottled appearance. Mature worms are hermaphroditic, possessing male (2 testes, accessory glands, vas deferens, penis enclosed in muscular sac) and female reproductive organs (germarium with internal chamber, extensive vitellaria, vitelline reservoir, ootype, uterus, vagina) with the male and female genital apertures usually common (sometimes separate). Capsalids are oviparous and usually produce and lay eggs one at a time although some species have been observed with up to 6 developing eggs in or near an expanded uterus.

**Site of infection:** Adult worms infect the external surfaces of their fish hosts, being found on the skin, fins, buccal cavities (lip folds, tooth pads), branchial chamber and gills (lamellae, arches, rakers) of euryhaline and marine teleosts and elasmobranchs. Oncomiracidia are free-swimming within their aquatic environments before attaching to hosts.

**Pathogenesis:** Capsalid monogeneans attach to the body surface and feed on epithelial cells and mucus, sometimes causing haemorrhages, ulcers, partial fin loss, decreased growth rate and mortality. Skin lesions are erosive and lead to excessive mucus production and wound sites are prone to secondary bacterial infection. Skin damage may be exacerbated by fish scratching on substrates (incl. nets) to alleviate skin irritation. Infections may cause serious economic losses in mariculture (esp. marine finfish in semi-open systems) with production losses (due to death and disease), reduced market value (remaining product with unsightly lesions) and increased production costs (for labour and treatment).

**Developmental cycle and mode of transmission:** Like most monogeneans, most capsalids have direct life-cycles with transmission occurring between fish hosts by free-swimming larvae. Mature hermaphroditic adults lay eggs with long sticky filamentous threads which become entangled on substrates and in organic material (including mucus). The eggs hatch after several days at water temperatures around 20°C, but hatching may be delayed for several months at lower water temperatures. Hatching also depends on photoperiod duration and intensity, with hatching rates being greater during the day and under intense light. The eggs release larvae (oncomiracidia) which are ciliated and swim about seeking new hosts. Larvae attach to the external surfaces of susceptible fish using their haptors and hooks, shed their cilia and begin to feed and mature to adult worms. Depending on the ambient water

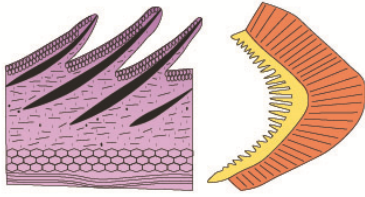
temperature, the whole life-cycle may be completed in days to months. The combination of direct transmission, short generation times, and moderate fecundity can facilitate rapid increases in parasite population densities in susceptible host populations, especially those kept in crowded culture conditions.

**Differential diagnosis:** Infections are diagnosed by the direct demonstration of parasites on fish in biopsy or necropsy tissue samples. Worms are best fixed and mounted as flattened preparations to better observe anatomical features. In some species, however, internal morphology can be obscured by extensive pigmentation and/or vitellaria. Generic identification is made on the basis of morphotypic features, especially the configuration of the opisthaptor and its hooks, the male genitalia and the anterior attachment organs.

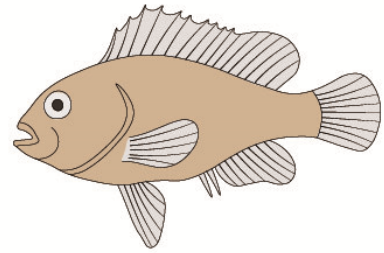
**Treatment and control:** In mariculture, infected fish are conventionally treated by immersion in freshwater baths or dilute hydrogen peroxide. The anthelmintic praziquantel is also effective as a bath or orally via medicated feed (although it reduces feed palatability). The eggs are resistant to these treatments so repeated treatments are required for parasite control. Environmental management is difficult because the eggs entangle on equipment and local substrates. Reducing stocking densities in net pens has met with limited success as the eggs still hatch releasing free-swimming larvae that actively seek whatever hosts are available.

# Benedenia

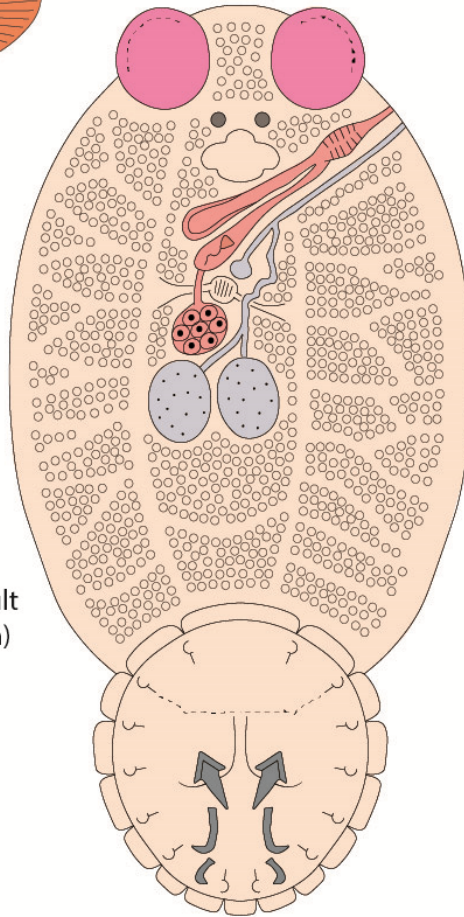
aquatic cycle



skin, fins, gills  
(traumatic damage,  
skin lesions, ulcers)

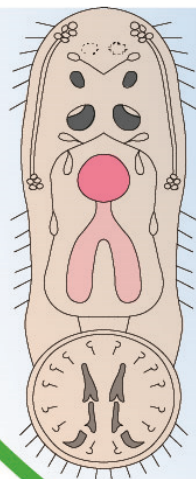


Definitive Hosts  
(marine fish,  
esp. perciforms)

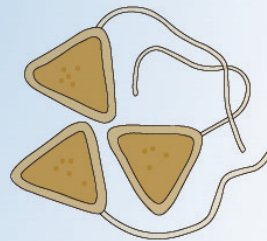


ectoparasitic adult  
(ventral) (~ 9 mm)

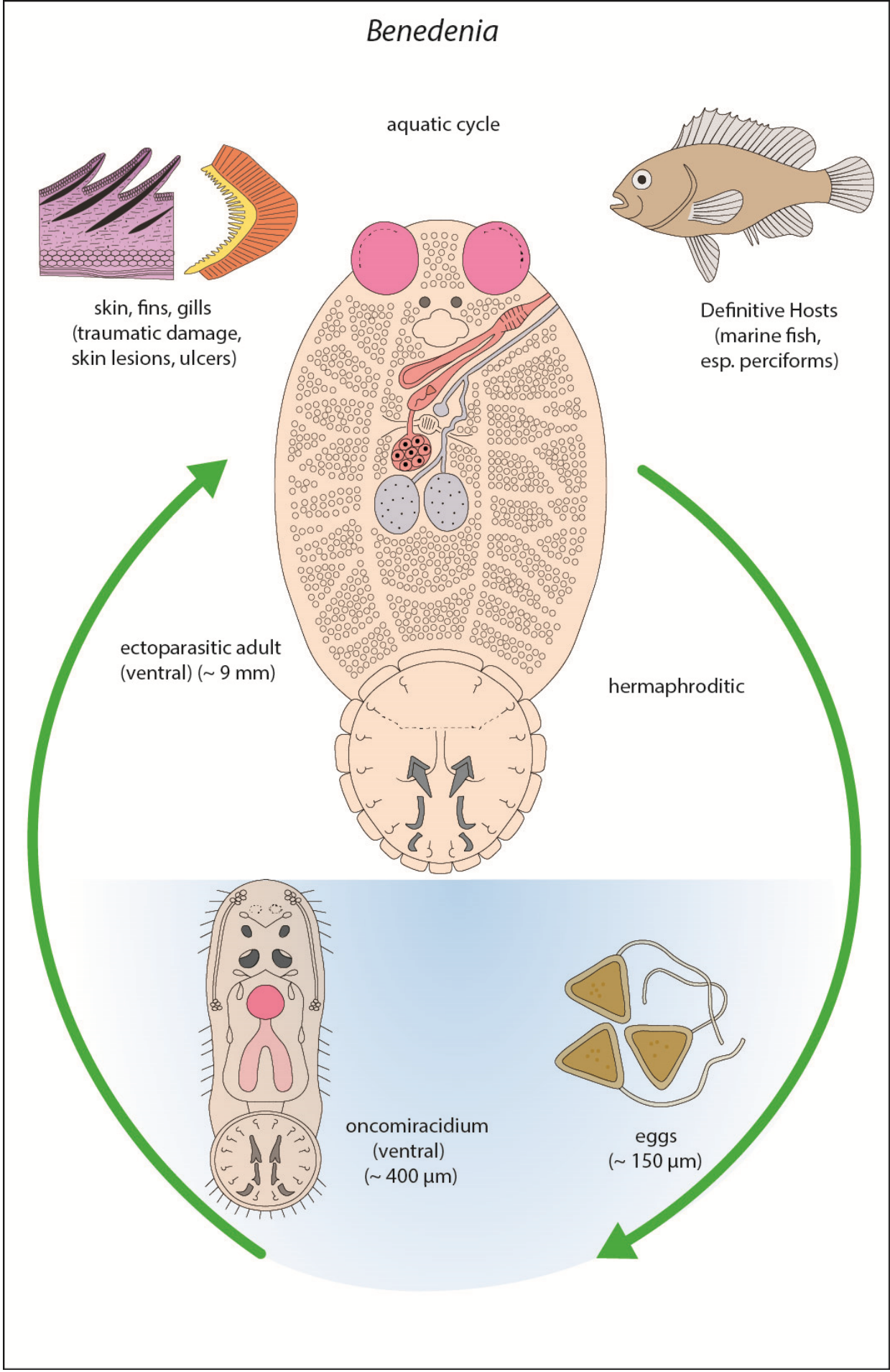
hermaphroditic



oncomiracidium  
(ventral)  
(~ 400  $\mu$ m)

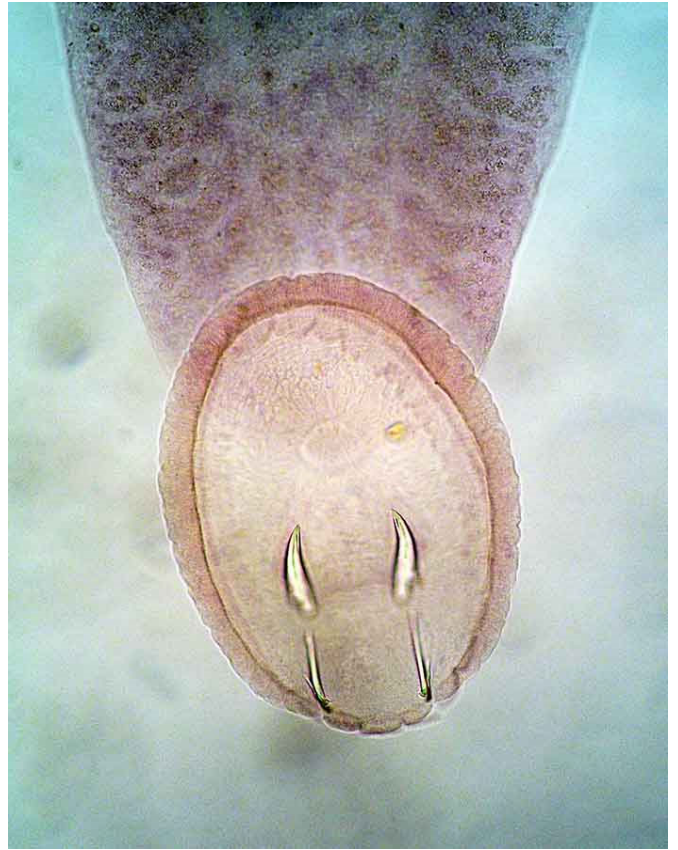


eggs  
(~ 150  $\mu$ m)





*Benedenia* adult worm



*Benedenia* opisthaptor



*Benedenia* oncomiracidia