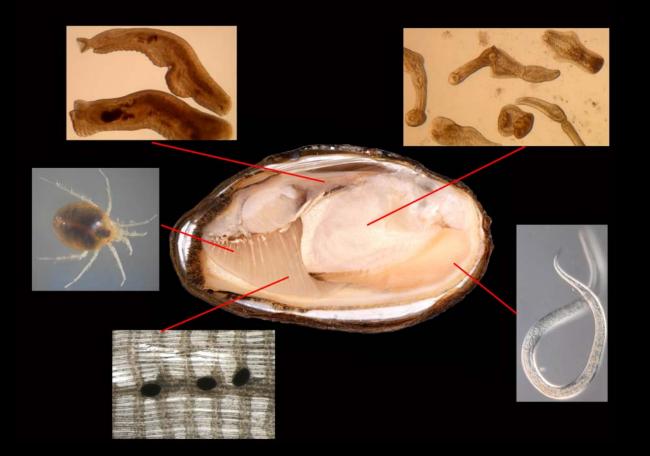
Are Parasites and Diseases Contributing to the Decline of Freshwater Mussels (Bivalvia, Unionida)?



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Outline

- Introduction
- Symbiotes
 - Protists
 - Aspidogastreans
 - Digeneans
 - Bryozoans
 - Nematodes
 - Oligochaetes
 - Leeches
 - Mites
 - Copepods
 - Insects
 - Fish eggs

- Miscellaneous topics
 - Parasite-induced pearl formation
 - Shell deformities
 - Tumors

Introduction

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Infectious Diseases of Freshwater Mussels and Other Freshwater Bivalve Mollusks

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Numerous species of freshwater massets (onler Uninovida) are Imperiled in the wild, and anionids and other freshwater bloabers are important components of many ecosystems. Freshwater massets also are propagated in capibility for production of pearls and enhancement of wild populations. However, infections diseases of these moliasts have received relatively little alterition. Univoldae is the most diverse jamily of freshwater bhahes, and most of the information available for this review is about species in this found. Fiberweit or operating, expectably trenshotder, miles, and Conchoptibility, and some have the potential to decrease the filmess of the host unionid. Several species of potentially pathogenic bacteria have been isolated from freshwater bhahes, but their role in diseases of bhahes potential not been established. Fiberweit have been isolated from freshwater bhahes, but their role in diseases of bhahes potential masset, Hyriopsis cuming). The potential for some pathogens to cause greater harm to freshwater bhahese a Chinese part of substitued. Fiberweit is fiber whether bhahese is alter and adequately. Additional research is also needed to determise whether other parts of potentially pathogenes in the potential for some pathogens to cause greater harm to freshwater bhahese during periods of substitued. Fiberweit is potential for some pathogens to cause greater harm to freshwater bhahese during periods of substituents and the bhahese thark is a solution of the potential treasers.

Keywords unionoida, viruses, bacteria, trematodes, miles, cillates

INTRODUCTION

Freshwater Bivalves

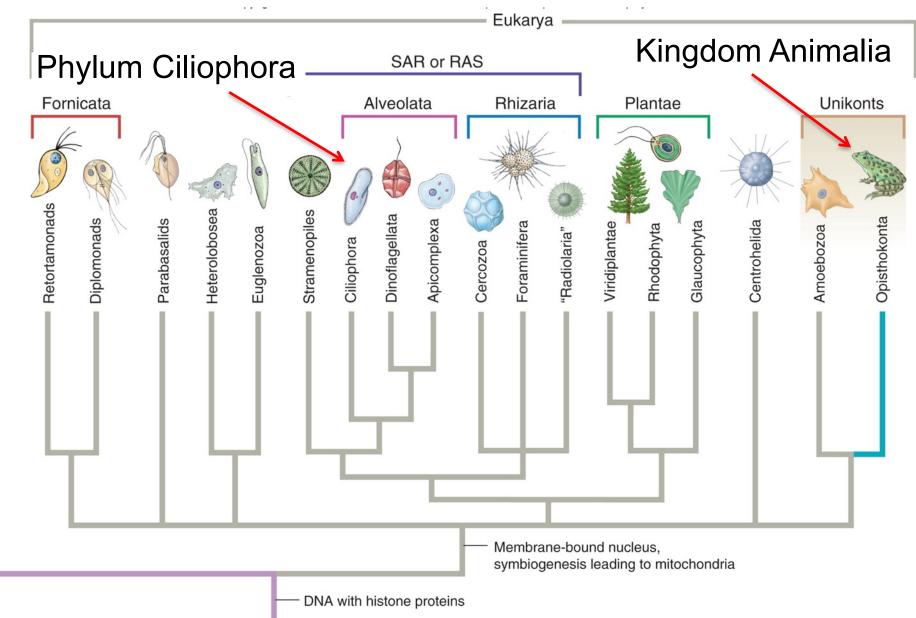
The freshwater mussels (class Bivalvia, order Unionoida) include six families: Unionidae, Margaritiferidae, Hyriidae, Mycetopodidae, Indinidae, and Etheridae (Graf and Cummings, 2007). This order has a worldwide distribution, but about a third of all species are found only in North America. The characteristics that set the order Unionoida apart from other bivalves are restriction to freshwater, parental care of offspring until they are released as larvae, and parasitic larvae (Graf and Cummings, 2006). Adults are relatively sedentary, but the larvae (glochidia) are parasitic on fish or amphibians (Howard and Anson, 1923; Waters, 1997), which provides a mechanism for dispersal. Additional species of freshwater bivalves are in the families Corbiculidae, Sphaeridae, and Dreissenidae (all in

Address correspondence to John M. Grizzle, Department of Fisheries and Allied Aquacultures, Auburn University, Auburn, AL 36849, USA. E-multgrizzijn Gushurn.edu the order Veneroida). These include the Asian clam Corbicala flaminea and the zebra mussel Dreissena polymorpha, which have received increased attention because of invasion of habitats outside of their original range. Several other bivalve families include a low number of species found in freshwater (Bogan, 2008), but these are not included in our review.

This review includes information about most freshwater bivalves (Table 1), but the emphasis is on the freshwater mussel family Unionidae because information available related to diseases or potential pathogens of freshwater bivalves is primarily about species in this family. Parasites of zebra mussels were reviewed by Molkoy et al. (1997), and some of this information is included in our review. Names of bivalves in our review follow Turgeon et al. (1998).

The conservation status and environmental threats to freshwater mussels have been well documented (Bogan, 1903; Williams et al., 1903; Neves et al., 1907; Bogan, 1908; Neves, 1999; Garner et al., 2004a, 2004b; Lydeard et al., 2004; Strayer et al., 2004; Williams et al., 2008). There are about 300 recent species of freshwater mussels in North America, but many are estinct or imperiled. Among freshwater mussels in the U.S., 37

Evolutionary Relationships of Eukaryotes

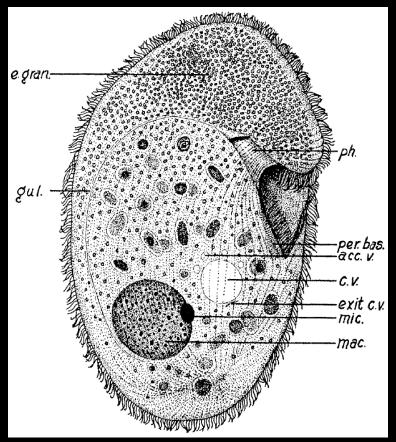


Archaea

From: Hickman et al. (2014)

Phylum Ciliophora ("Ciliates")

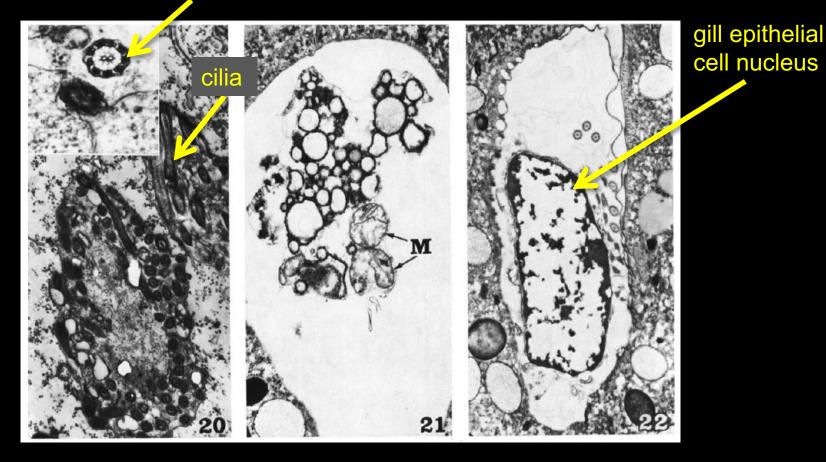
- Conchophthirius or Conchophthirus spp. most frequently reported
- Reported from the mantle cavity
- Cosmopolitan distribution
- Some species are host specific while others are less so
- May attach to tissue
- Food vacuoles may contain bacteria, algae, host cells
- No evidence these ciliates injure their host (commensalism?)
- Asexual reproduction by binary fission, sexual reproduction by conjugation (direct life cycle?)



Conchopthirus anodontae at 600 X (From: Kidder, 1934)

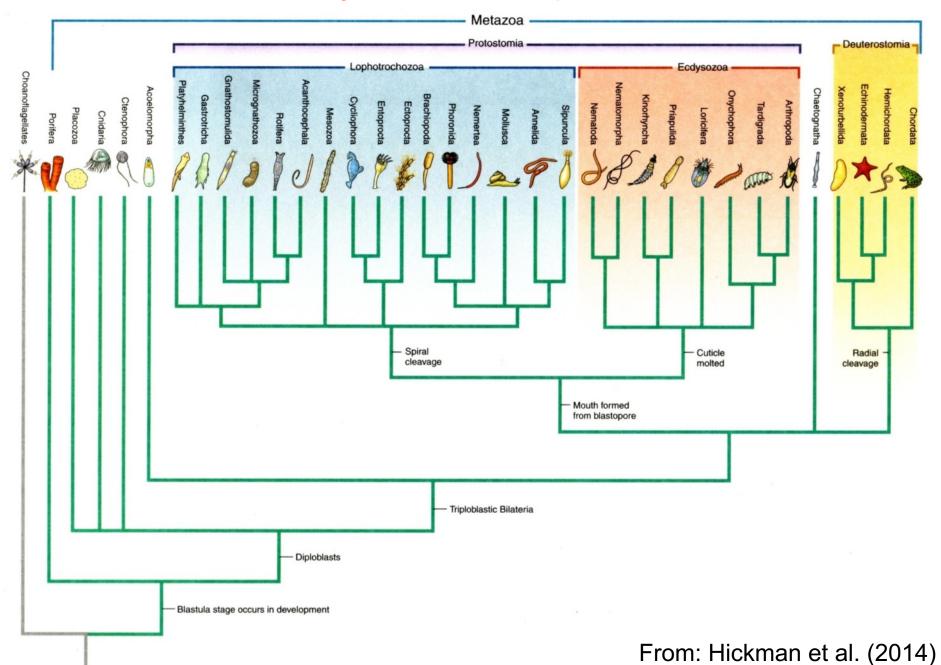
Possible remnants of gill epithelial cells in food vacuoles of *Conchopthirus curtus*

axoneme



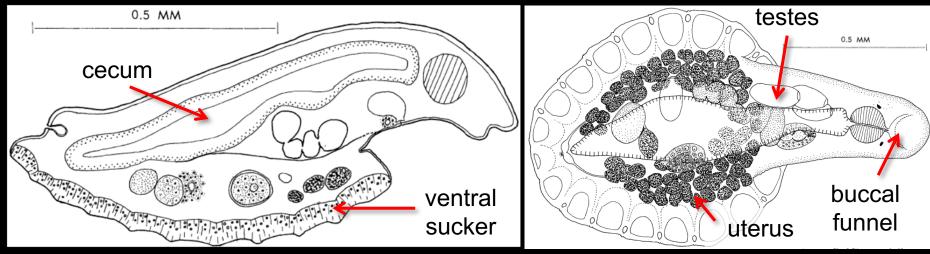
From: Antipa and Small (1971a)

Evolutionary Relationships of Animals



Phylum Platyhelminthes: Class Trematoda: Subclass Aspidogastrea ("Aspidogastreans")

- Reported from mollusks, fishes, turtles
- Basal trematodes or "proto-trematodes"
- Poorly adapted for parasitism
- Complex sensory organs
- Simpler life cycles than digeneans
- Can complete ontogenetic development in a mollusk



Cotylaspis insignis From: Hendrix and Short (1965)

Aspidogastreans reported from unionids

Aspidogaster conchicola

- Infects pericardial cavity, nephridium
- Reported from many unionid spp.
- Widely distributed

Cotylaspis insignis

- Infects gills, suprabranchial cavity
- Reported from many unionid spp. and turtles. Turtles may not be a required host.

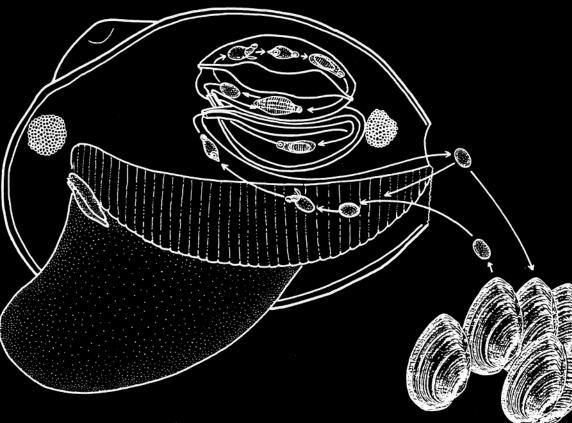
Cotylogaster occidentalis

- Infects intestine
- Reported from unionids, snails, freshwater drum; less common than A. conchicola or C. insignis

Lophotaspis interior

- Only juveniles reported from unionids
- Adults reported from alligator snapping turtles (indirect life cycle?)
- Least common aspidogastrid

Life cycle of Aspidogaster conchicola

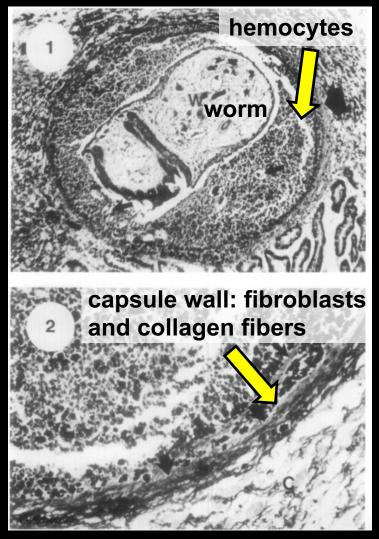


From: Benz and Curran (1996)

- Direct life cycle
- Life cycle stages include: Operculated egg, juvenile, adult
- Adults mature in pericardial cavity or nephridium
- Eggs may be released into mantle cavity
- Mussels may acquire eggs while filtering water
- Can complete life cycle without leaving mussel

Pathogenicity of aspidogastreans

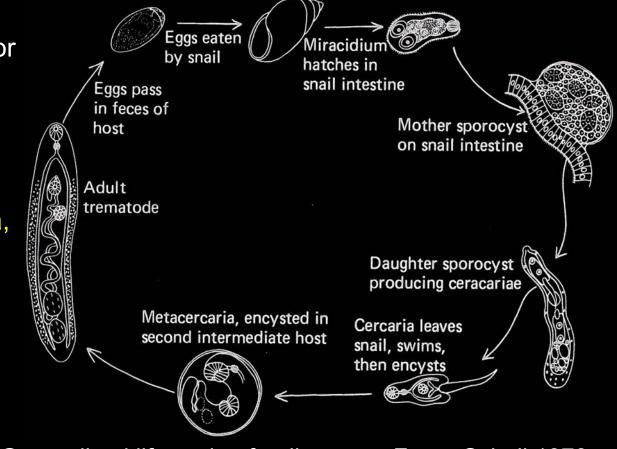
- Most pathology studies focus on Aspidogaster conchicola (Pauley and Becker, 1968; Bakker and Davids, 1973; Huehner and Etges, 1981; Huehner et al., 1989)
- Some studies have not observed lesions
- May injure mussels through attachment and feeding
- Localized cellular changes such as necrosis, metaplasia
- Mussels may encapsulate (encapsulation response or granuloma) aspidogasters if they invade the visceral mass



Figs. 1–2 From: Huehner and Etges (1981) showing encapsulation of *Aspidogaster conchicola*.

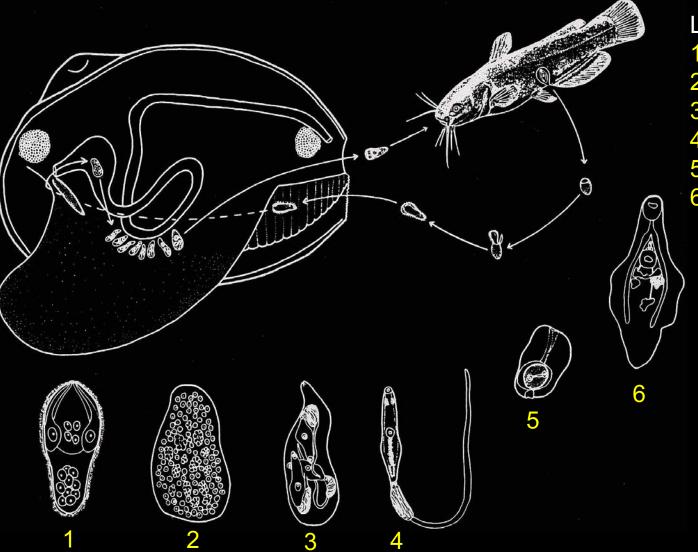
Phylum Platyhelminthes: Class Trematoda: Subclass Digenea ("Digenetic trematodes")

- Indirect life cycle
- Mollusks can be first and or second intermediate host
- Vertebrates are definitive hosts
- Larval stages occur in mollusks: Sporocyst, redia, cercaria, metacercaria
- Cosmopolitan distribution



Generalized life cycle of a digenean. From: Schell 1970.

Life cycle of a trematode



Generalized life cycle of Gorgoderinae. From: Benz and Curran 1996.

Life cycle stages

- 1. Miracidium
- 2. Mother sporocyst
- 3. Daughter sporocyst
- 4. Cercaria
- 5. Metacercaria
- 6. Adult

Digenean families reported from mussels

Bucephalidae

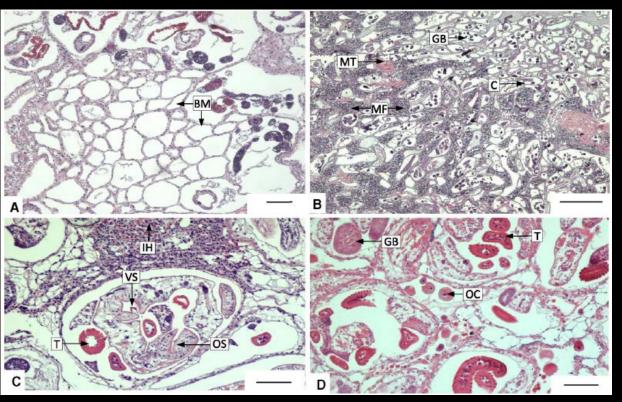
- Unionidae can be 1st intermediate host
- Sporocyst, redia, cercaria
- Gorgoderidae
 - Unionidae can be 1st intermediate host
 - Mother and daughter sporocyst, cercaria

Allocreadiidae

- Unionidae can be 1st or 2nd intermediate host
- Sporocyst, redia, cercaria, metacercaria
- Apocreadiidae
 - Unionidae can be 1st or 2intermediate host
 - Sporocyst, cercaria, metacercaria

Sources: Cribb et al. (2001); Grizzle and Brunner (2009), and literature therein

Pathogenicity of sporocysts and rediae



Damage to the gonad of *Anodonta anatina* caused by *Rhipidocotyle campanula* (A–B) and *Phyllodistomum* sp. (C–D). From: Müller et al. 2015

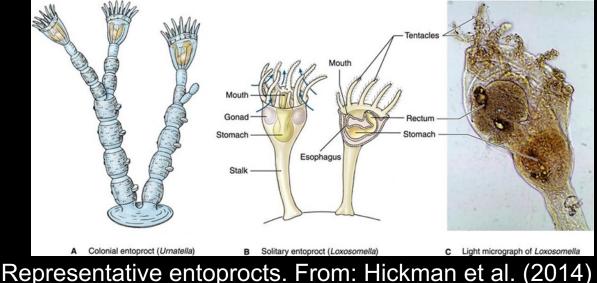
- Sporocyst and redia stages can damage the digestive gland and or gonad and potentially castrate the host
- Sporocysts, rediae,
 cercariae, metacercariae
 may sometimes induce
 pearl formation
- Pathology described by: (Kelly, 1899; Fischthal, 1951; Kniskern et al.
 1952; Jokela et al. 1993; Chittick et al. 2001; Müller et al. 2015)
- Sometimes hemocytes surround or infiltrate digenean infections and sometimes no host response is apparent

Bryozoans: Phyla Ectoprocta and Entoprocta

- "Moss animals"
- Solitary or colonial
- Reported from the exterior shell of unionids
- Reported from exterior shell of "baldies" from Tennessee River (Fuller 1974)
- Bryozoans generally feed on particulate matter using their lophophore (ciliated tentacles)
- Relationship with mussels is unclear, probably commensalistic



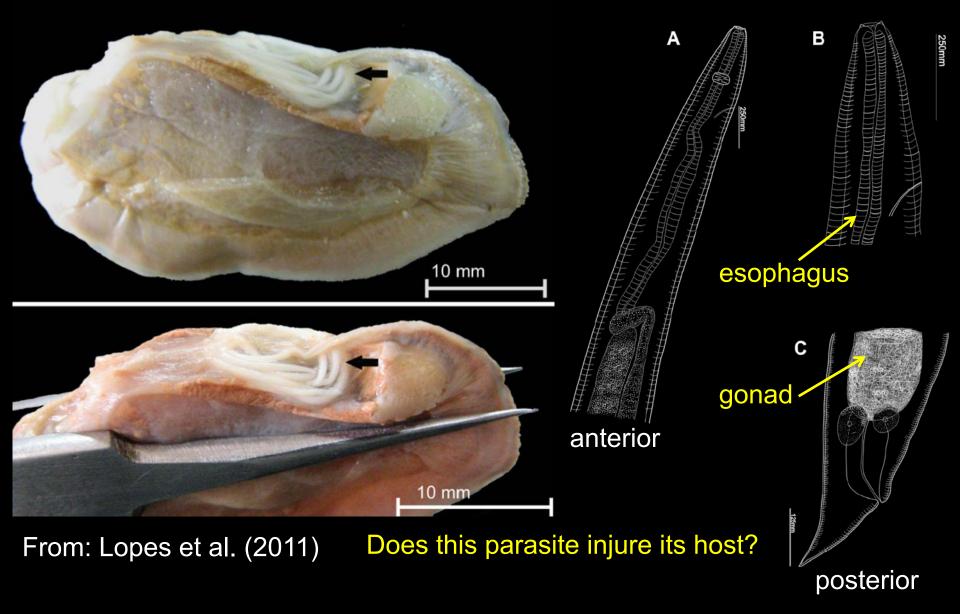
Pectinatella magnifica attached to a submerged branch



Phylum Nematoda

- "Roundworms" mostly reported from marine bivalves
- Marine bivalves reported as intermediate hosts
- Clark and Wilson (1912), Wilson and Clark (1912), Coker et al. (1921) reported Ascaris sp. or Ascaris-like worms from the digestive tract of unspecified unionids
- No species descriptions from freshwater mussels
- Did worms occur in the lumen of the gut or if they were embedded in tissue?
- Lopes et al. (2011) reported 3rd stage larvae of *Hysterothylacium* sp. (Anisakidae) from the pericardial cavity of *Rhipidodonta suavidicus* (Hyriidae)

Hysterothylacium larvae (Anisakidae) in pericardial cavity of Diplodon suavidicus (Hyriidae)



Phylum Annelida: Class Oligochaeta

- Chaetogaster limnaei may occur inside the mantle cavity, gills or kidney of mollusks
- Reported from mantle cavity and kidney of unionids

Some records portray *C. limnaei* as a parasite or predator of mollusks:

- Feeds on juvenile mussels (Coker et al. 1921)
- Kidney cells and concretions of *Lymnaea pereger* observed in the gut (Gruffydd, 1965)
- Reported to feed on subepithelial cells of Physa acuta (Gamble and Fried, 1976)
- Occurred in mantle cavity of Corbicula fluminea that appeared emaciated and diseased (Sickel and Lyles, 1981)
- Some invaded mantle, gill, visceral mass where they may feed on tissue of *Dreissena polymorpha* (Conn et al. 1996)



Chaetogaster limnaei limnaei from *Sinanodonta woodiana*. From: Cichy et al. (2016)

Phylum Annelida: Class Hirudinida

- Unspecified leeches observed in unspecified North American mussels by Kelly (1899), Clark and Wilson (1912), Coker et al. (1921)
- Leeches attach to mantle of some mussels, especially Anodonta spp. may feed on mucus and may feed on mussels as a scavenger (Coker et al. 1921)
- Records of *Placobdella* from unionids
- *Placobdella motifera* may occur in the mantle cavities unspecified mussels (Moore 1912)
- *P. motifera* and *P. parasitica* may occur in the mantle cavities of unspecified mussels (Fuller, 1974)
- *P. motifera* reported from 8 unionid spp. from Louisiana by Curry and Vidrine (1976)
- *P. motifera* reported from *Anodonta cat*aracta in Delaware by Curry (1977)
- No observations of leeches feeding on live mussels

Phylum Arthropoda: Acari

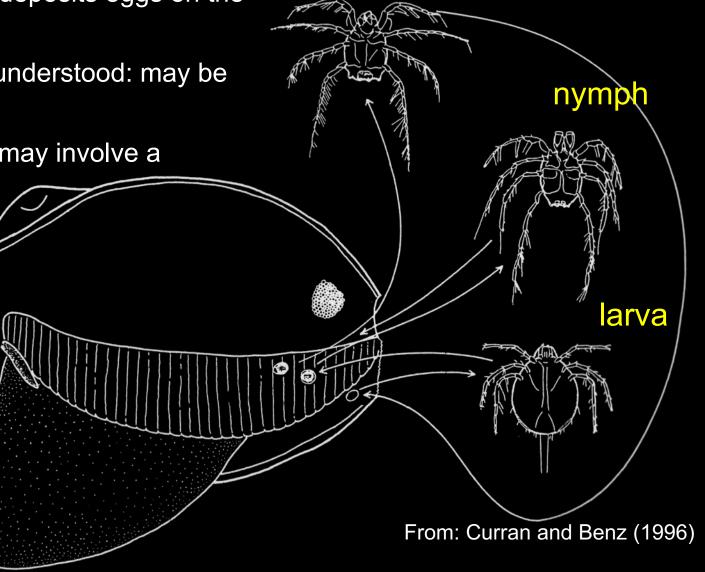
Mites that associate with or infect mussels:

- Hygrobatidae, *Dockovdia* = 2 spp.
- Pionidae, Najadicola = 1 sp.
 - Najadicola ingens infects 30 mussel spp.
- Unionicolidae, *Unionicola* = 244 spp.
 - Unionicola spp. infect 137 mussel spp. representing Unionidae, Hyriidae, Mycetopodidae
- For a review see Edwards and Vidrine (2013)
- Mites may injure mussels through attachment, feeding, ovipositing, encystment of larvae and nymphs (McElwain and Bullard, 2016)
- Najadicola ingens may lay eggs inside the water tubes of mussels and obstruct the passage of ova (Humes and Jamnback, 1950; Humes and Russell, 1951)

Generalized life cycle of Unionicola spp.

- Unionicola spp. oviposit into tissue
- *Najadicola ingens* deposits eggs on the surface of tissue
- Life cycles poorly understood: may be direct or indirect
- Indirect life cycles may involve a chironomid host

adult



Eggs of Unionicola sp. in the gill of Strophitus connasaugaensis

1 mm



A nymph and an egg of Unionicola sp. in the gill of Strophitus connasaugaensis

chrysalis

50 µm

gill filament

nymph

50 µm

Mite remnants in the visceral mass of Strophitus

50 µm

connective tissue

infection

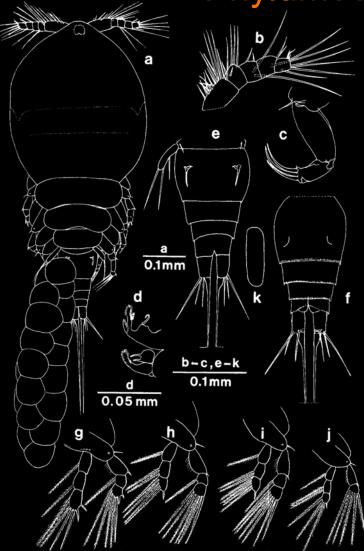
ANY

intestine

50 µm

mite remnants

Phylum Arthropoda: Copepoda

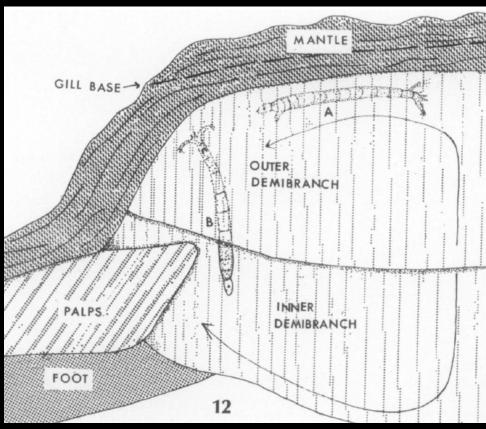


Paraergasilis rylovi from Anodonta piscinalis (Chernysheva and Purasjoki, 1991)

- Copepoda contains many free-living and parasitic species
- Parasitic copepods best known from gills and skin of fishes
- Direct life cycle with egg, nauplius, copepodid stages, adult
- Paraergasilis rylovi reported from gills of Anodonta spp. and olfactory sacs of fishes from Europe (Chernysheva and Purasjoki, 1991; Pekkarinen, 1993)
- May attach to mussel gills, but the relationship is unclear

Phylum Arthropoda: Insecta

- Many records of chironomids (Diptera, Chironomidae) from North American unionids (e.g., Roback et al. 1979; Vidrine 1990)
- Probably more common and widely distributed than literature indicates (Forsyth and McCallum, 1978; Roback et al. 1979; Pekkarinen, 1993)
- Chironomid spp. may occur between mantle and gill, *Ablabesmyia* sp. (*A. janta*?) most frequently reported (Roback et al. 1979; Roback 1982; Vidrine, 1990)
- Chironomids may get between mantle and shell whether the shell is breached or not (Beedham 1971; Forsyth and McCallum, 1978; Cichy et al. 2016)



Diagrammatic representation of Ablabesmyia sp. attached to unionid gills (Roback et al. 1979)

Injuries associated with insect larvae

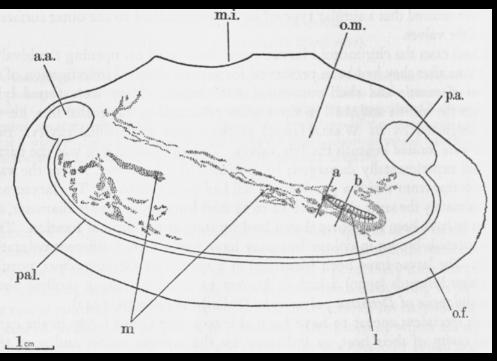
Diptera, Chironomidae:

- Glyptotendipes sp. (G. paripes?) from between mantle and shell of Anodonta cygnea (Unionidae). Histopathological changes including damage to mantle and influx of amoebocytes reported (Beedham, 1971).
- Baeoctenus bicolor larvae and pupae inhabit tubes of particulate matter attached to gills near labial palps of Anodonta cataracta (Unionidae). Larvae feed on gill tissue, as much as 50% of gill missing in some mussels (Gordon et al. 1978).
- Xenochironomus canterburyensis from of Hyridella menziesi (Hyriidae). Chironomid larvae occurred between old shell growth and new shell growth, in mantle cavity, and between mantle and shell. Chironomids associated with blister pearls (Forsyth and McCallum, 1978).

Odonata, Gomphidae:

 Gomphus miliataris fed on gills of Poponaias popeii (Unionidae), some individuals were missing the entire outer gills or all four gills (Levine et al. 2009).

Histopathological changes associated with *Glyptotendipes* sp. in *Anodonta cygnea*



Above: Diagrammatic representation of the outer mantle of *Anodonta cygnea* showing marks made by *Glyptotendipes* sp.

Right: Histology of the outer mantle of *Anodonta cygnea* showing damage and hemocytes associated with *Glyptotendipes* sp.

hemocytes a chironomid arva h hemocytes

From: Beedham (1971).

Phylum Chordata: Actinopterygii

- European bitterling, *Rhodeus sericeus* (Cyprinidae) oviposits into the mantle cavity of mussels in Unionidae and Margaritiferidae in Europe, Asia and North America (For a review, see Smith et al. 2004)
- Bitterling embryos may become lodged between interlamellar spaces in the gill, may compress gill tissue, obstruct water flow through gills of *Unio rostratus* (Stadnichenko and Stadnichenko, 1980)
- Bitterling embryos compete with developing glochidia for oxygen (Smith et al. 2001)
- Bitterling embryos may reduce growth rates of mussels (Reichard et al. 2006)

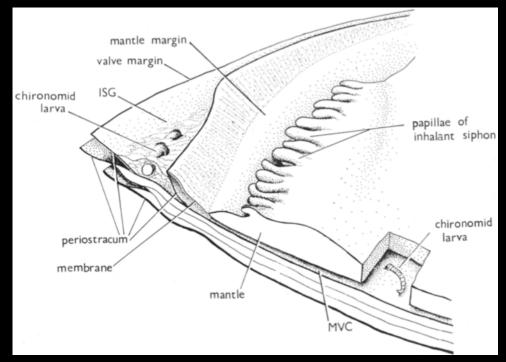
Parasite-induced pearl formation

Records of parasite-pearls in mussels:

- Digeneans: Clark and Wilson (1912), Wilson and Clark (1912), Genter and Hopkins (1934), Hopkins (1934); all records from Unionidae
- Mites: Kelaart and Möbius (1856), Baker (1928); Edwards and Vidrine (2013); all records from Unionidae
- Midge larvae:

Forsyth and McCallum (1978), Pekkarinen (1993)

Right: Diagrammatic representation of chironomids between mantle and shell and chironomid-induced pearls from Forsyth and McCallum (1978).



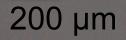
Blister pearls on the nacre (left) and pearls from the mantle (right)



Embedded mite larva

200 µm

Pearls that were embedded in tissue Are parasites inside?

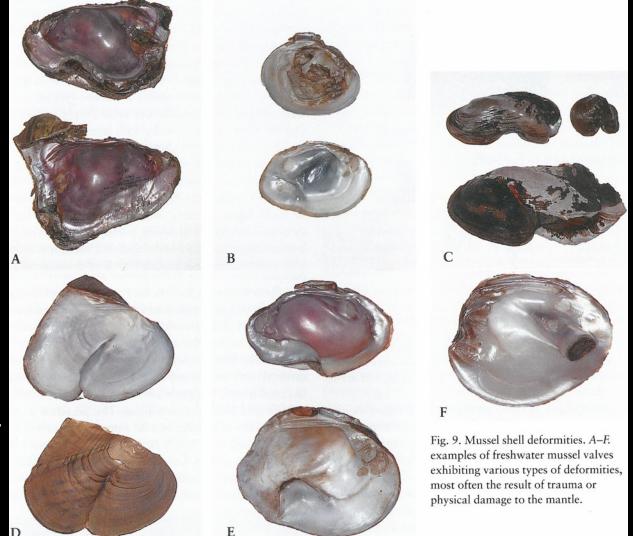


Shell anomalies or deformities

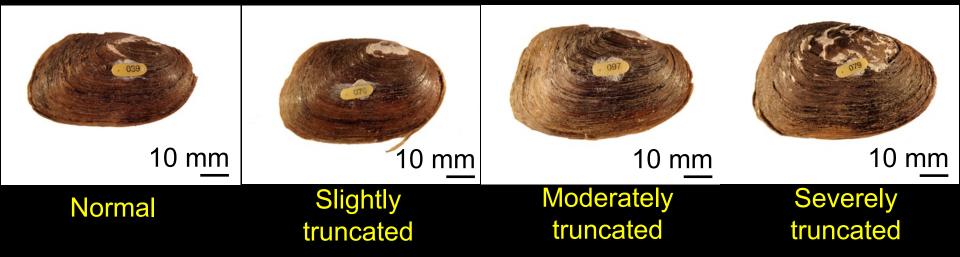
Anomalies or deformities reported include:

- Protuberances
- Infoldings
- Erosion
- Misshapen shells
- For a review, see Strayer (2008)

Examples of shell deformities. From: Parmalee and Bogan (1998).



Normal and truncated right valves of Elliptio complanata

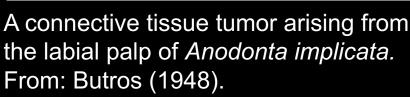


- Occurs among 3 species representing Unionidae as well as *Margaritifera margaritifera* in several rivers in Massachusetts
- Reported from 5 unionid species among rivers in the Southern Tier and Hudson River Valley in New York (Strayer 2006)
- The cause of these deformities is presently indeterminate
- Impact of shell deformities on mussel physiology (feeding, reproduction) is poorly understood

Neoplasms or tumors

Records of tumors in mussels:

- Williams (1890): Adeno-myoma of the mantle of *Anodonta cygnea*
- Collinge (1891): Tumor arising from the mantle-outer gill junction in *A. cygnea*. This mussel lacked nacre in the posterior portion of the shell.
- Butros (1948): Connective tissue tumor arising from the labial palp of *A. implicata*
- Pauley (1967a, 1967b): Adenomas from the foot of *A. californiensis*
- Prevalence of tumors is 1% or less



Are parasites and diseases associated with mussel declines?

- Some parasites such as digeneans, mites, insects can directly reduce fecundity by damaging gonad or by damaging or obstructing marsupial gill
- Prevalence of high infections tends to be low (<20%)
- Are parasitized mussels more susceptible to environmental stress?
 - Jokela et al. (2005) found that Anodonta piscinalis may be more susceptible to Rhipidocotyle spp. (Digenea) under anoxic conditions (eutrophication and ice cover)
 - Choo's dissertation work (2015) suggests rising water temperatures expected with global climate change may increase *Rhipidocotyle* cercarial shedding, and unionid host mortality
- Are parasitized mussels more susceptible to contaminants?
 - Heionen et al. (2001) found that *Pisidium amnicum* infected with Bundodera luciopercae (Digenea) were more likely to survive exposure to pentachlorophenol than uninfected clams
 - NOAA Sentinel Bivalve Program [e.g. Kim et al. (1998)] inconsistent results/typically no correlation to parasites in marine bivalves and specific contaminants; correlations that were observed were usually negative