Evolutionary Ecology of Parasites

What is evolutionary ecology of parasites?

1. Evolution of characters in parasite individual, population and community
2. Change of strategy for an organism from free living to parasitic → biological changes
3. Evolution of parasite ability to use one host or most hosts
4. Evolution of life strategy (life traits history) – effects of selection given by host, environment and phylogeny

What is evolutionary ecology of parasites?

5. Evolution of virulence, evolution of manipulation by parasites (to manipulate host behaviour)

6. Speciation and diversification of parasites, host-parasite coevolution

7. Host specificity of parasites – effects of phylogeny, specialization and adaptation

8. Population ecology of parasites – evolutionary causes and ecological consequences of aggregation, dynamics of parasite populations – effect of evolution on population processes

What is evolutionary ecology of parasites?

9. Structure of parasite communities – random or predicted (organized communities)

10. Interactions between parasites – character of interactions, response to interspecific competition, causes and consequences of competition in ecological and evolutionary times

11. Parasite diversity – determinants, biogeographical aspects

12. Immunoecology and evolution of host immunity – trade-off, immunity vs. parasitism, host immune genes and parasite-mediated selection, role of parasites in evolution of host sexual selection

Evolutionarly ecological approach

- Ecological approach – associations in short time
  who harms whom?

- Evolutionary approach – long-termed associations
  host-parasite coevolution
  evolution of immune components

Evolutionary ecology – study of selective pressures from the environment and evolutionary responses to them

Natural selection affects the characters of the individual, the characters of populations and communities

Hierarchical levels of study – individual, population and community

Parasitism from an ecological point of view

- Reciprocal interaction, one gains an advantage, the other is damaged
- Some form of symbiosis (close bilateral interaction), benefit for one species, loss for another species
- Widespread biological phenomenon, high diversity and a large number of niches




Evolutionary success of the parasitism strategy

- Strategy to find a host
- Penetration and attachment strategies
- Adaptation to an unfavorable host environment
- Ability of the parasite to feed on the host
- Ability to defend against the immune system
- Ability to reproduce in the host and ability to disperse

Parasite

- It lives for the whole life or part of its life on the body or inside the body of another organism (= host), it feeds at the expense of the host
- benefit to the parasite, costs to the host
- consumer versus prey
- biotrophic organism

Typical parasite

- One host, very little or no pathological manifestations
- Host survives
- Following Anderson and May this category is separated :
  pathogens – intensity independent models (microparasites)
  typical parasites – intensity dependent models (macroparasites)

!!! Trophically transmissible typical parasite or pathogen - host death necessary

Parasitoid

- One host
- The parasite always causes the death of its host
- Parasitic insect larvae Diptera (Tachinidae) and Hymenoptera (Chalcidoidea, Braconidae), physiological adaptations (endosymbiotic viruses)
- The female lays eggs in the host, hatched larvae are parasitic

Parasitic castrator

- It uses the host's energy for its reproduction
- It kills the host from an evolutionary point of view - it blocks reproduction and reduces fitness
- Partial castrator - a transition between a typical parasite and a parasitic castrator

Micropredator and vector

- Micropredator
- Multiple hosts (more specimens of a given species)
- micropredator does not kill the prey

- Vector transmits diseases
- Flies - mechanical transmission
- *Anopheles* transmits malaria (*Plasmodium*)
- *Phlebotomus* and *Lutzomia* transmit *Leichmania*
- Lice transmits typhus
- Fleas cause encephalitidis and other diseases
- Tse-tse flies (*Glosina*) – sleeping sickness (*Trypanosoma*)

Ecological definition of parasites

- Number of hosts attacked during the life of the parasite
- Influence of the parasite on the biological fitness of the host
- Link between infection intensity and host mortality
- Benefit of host death for parasites

Ecological definition of parasite / prey - effects depending on the number of parasites

Effect on biological fitness	Number of casualties per 1 attacker		
	One victim		More victims
	death disadvantageous	death advantageous	
Less than 100%	Typical parasite	Trophically transmissible parasite	micropredator
100%: victim has zero fitness	Parcial castrator	Trophically transmissible castrator	Social predator

Ecological definition of parasite / prey - effects depending on the number of parasites

<table>
<tr><td rowspan="3">Effect on biological fitness</td><td colspan="3">Number of casualties per 1 attacker</td></tr>
<tr><td colspan="2">One victim</td><td rowspan="2">More victims</td></tr>
<tr><td>death disadvantageous</td><td>death advantageous</td></tr>
<tr><td>Less than 100%</td><td>Monogenea
Ichthyophthirius</td><td>metacercariae of digeneas</td><td>mosquito</td></tr>
<tr><td>100% victim has zero fitness</td><td>Cysticerkoids of Hymenolepis diminuta
Isopoda</td><td>Plerocerkoids of
Schistocephalus</td><td>wolf</td></tr>
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Ecological definition of parasite / prey - effects independing on the number of parasites

Effect on biological fitness	Number of casualties per 1 attacker		
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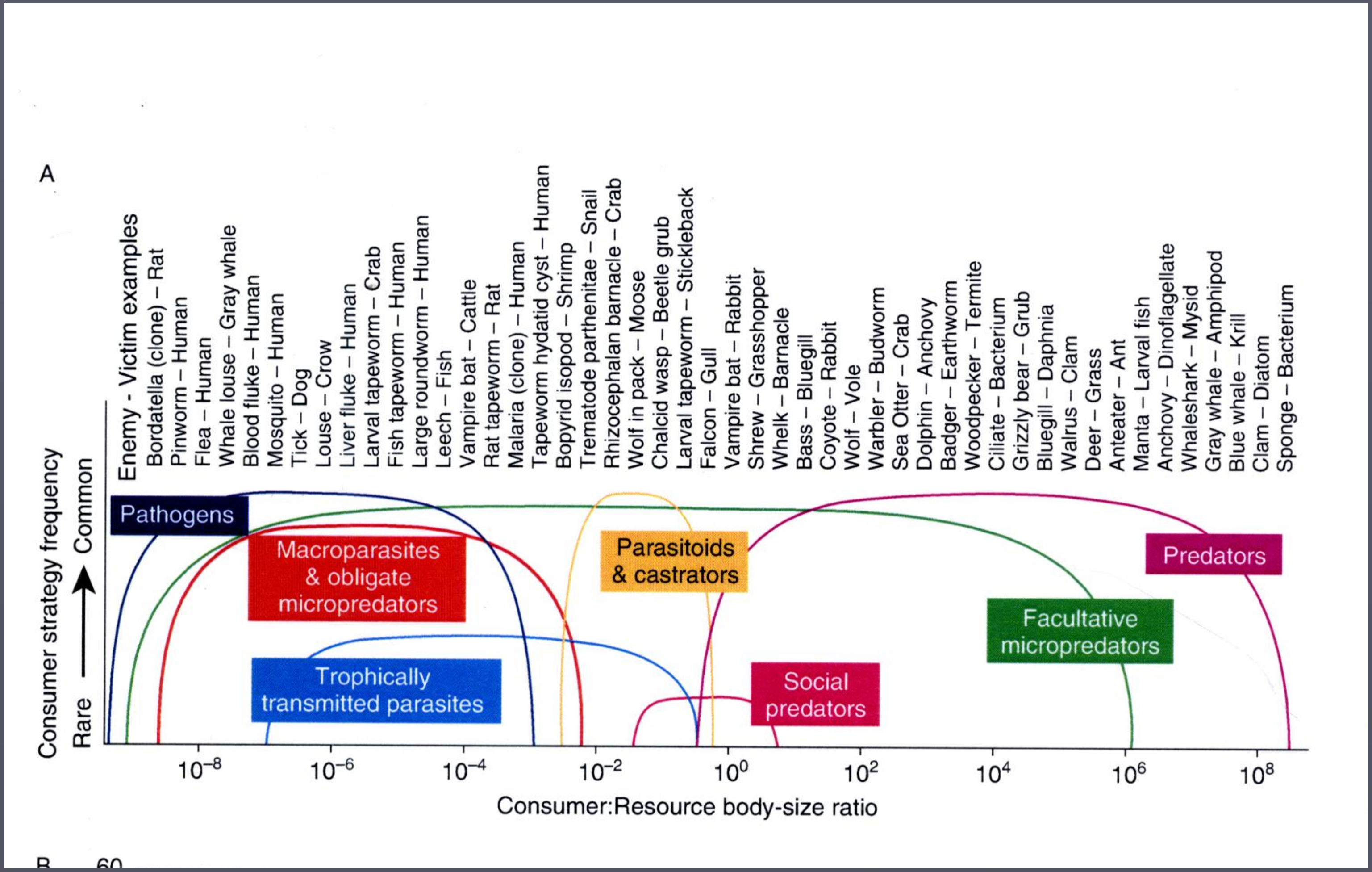
Less than 100%	patogen	trophically transmissible patogen	herbivor
100%: victim has zero fitness	Parasitic castrator	parasitoid	predator

Ecological definition of parasite / prey - effects independing on the number of parasites

Effect on biological fitness	Number of casualties per 1 attacker		
	One victim		More victims
	death disadvantageous	death advantageous	
Less than 100%	*Giardia*, influenza virus	*Toxoplasma*	deer
100% victim has zero fitness	*Sacculina*	lumek	sparrow

Parasite size versus host Frequency of strategy



Classification of parasites in ecology

- Microparasite versus macroparasite (Andreson & May, 1979)
- Microparasites - short generation time, high rate of reproduction, reproduction in the host, no infectious stages, acute illness - death or recovering, induction of immunity against reinfection
- Macroparasites - longer generation time, reproduction outside the host, development and growth in the host, produce infectious stages, host immune response (relatively short) depends on the number of parasites, insignificant mortality, frequent reinfection

Classification of parasites in ecology

- Microparasite versus macroparasite

- The size of the parasite is not a determining criterion
- Microparasite – bacteria, fungi, protozoa
- Macroparasite – helminths, arthropods

- Aphids, digenean larvae in snails – microparasite
- *Ichthyophthirius*, *Eimeria tenela,* necrotrophic fungi - macroparasite

Classification of parasites in ecology

- Zooparasite vs. phytoparasite

- Ectoparasite vs. endoparasite
- Endoparasites according to the location:

  - Intestinal *Entamoeba histolytica,* Trematoda, Cestoda

  - In blood plasma *(Trypanosoma),* in blood cells*(Plasmodium)*

  - Intracellular tissue *(Toxoplasma gondii, Leishmania)*

    Epicellular *(Giardia intestinalis)*

    Intercellular *(Myxosporidia)*

  - Cavital *(Entamoeba gingivalis, Trichomonas vaginalis)*
- Ectopic localization: *Paragonimus westermani, Fasciola hepatica* in brain

Classification of parasites in ecology

- According to the link to the host

  obligatory (Monogenea, Digenea, Cestoda)

  optional (facultative) (Nematoda *Micronema*)

  hyperparasite – *Udonella* on parasitic Crustacea
- According to the time period of the parasitism

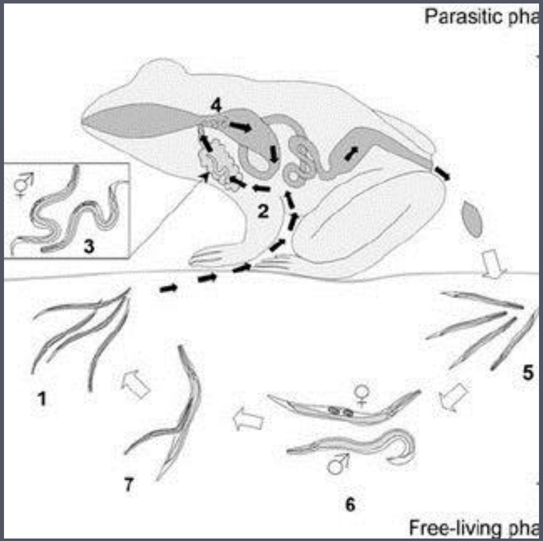
  permanent (*Plasmodium*, *Entamoeba*)

  temporal (*Argulus*, *Ixodes*)

  periodical parasitism

  - stage (glochidia of Mollusca, larvae of Diptera)

  - generation (*Rabdias bufonis*)



Classification of parasites in ecology

- By type of life cycle

  monoxenus (stenoxenous) – life cycle with one host (Monogenea)

  heteroxenous (euryxenous) – life cycle with more hosts (Digenea, Cestoda)

- By type of feeding

  monophagous (stenophagous) – feeding on/in one host (*Eudiplozoon nipponicum*) (strict-specific, species-specific)

  polyphagous (euryphagous) – feeding on/in more hosts (*Trichinella spiralis, Posthodiplostomum cuticola*)

Classification of parasites in ecology

- Host specificity = range of used host species (definitive hosts or intermediate hosts)
- Narrow host specificity (monophagous, specialists, host-specific) – *Taenia solium*, *Schistosoma haematobium* – DH humans
- Wide host specificity (polyphagous, generalists) – *Trichinella spiralis* – DH warm-blooded vertebrates
- Parasites with complex life cycle – different host specificity at the levels of intermediate host and definitive host

Classification of hosts

- Definitive host - a host on/in which the parasite matures sexually and produces eggs or larvae

- Intermediate host – necessary for the development of larval stages of the parasite
  - IH = invasive stage → definitive host
  - one or more intermediate hosts (Digenea, Cestoda)
  - humans as an intermediate host (*Echinococcus*, *Taenia solium*)

Classification of hosts

- Paranthenic (transport) host

  no development of parasite

  parasite survives and retains ability to invade

  not necessary to complete the developmental cycle of the parasite

  important source of infection for IH or DH

  e.g. mollusks for larvae of nematodes with development in short-lived crustaceans

- Reservoir host

  = source of parasite infection for the ecosystem

  - the parasite survives even in conditions unsuitable for a common host

  E.g. Rats and carnivores for *Trichinella*, *Schistosoma japonicum* - eggs into the environment, a source of infection for humans - epidemiological significance

Parasitism less known – parasitic plants

- 1% angiosperm plants (3000 species)
- Presence of chlorophyll – hemiparasites, absence of chlorophyll – holoparasites
- Depending on the connection point to the host – root and stem
- Connection to the host vascular system = haustorium
- i.e. cosmopolitanly expanded *Viscum* (mistletoe)


Parasitism less known – parasitic plants

The course of infection

1) formation of apresorium (organ used to mechanically disrupt cell walls)
2) growth of haustorium (thin fibers), which can exert considerable pressure on the cell wall
3) penetration through the cell wall to the membrane
4) branching without breaking the membrane

Loranthus europaeus
host: *Quercus*

Lathraea squamaria
host: woody plants (roots)

Orobanche (more species)
host: legumes, deafblind, sunflower, hemp

Parasitism less known – nest parasitism

- birds
- Intraspecific parasitism (ducks, songbirds)
- Interspecific (cuckoos…)
- *Cuculus canorus* – about 100 species of songbirds as hosts, host with smaller eggs, of similar colour, strong shell, shorter incubation time

Cowbirds (Icteridae)

Parasitism less known – nest and social parasitism in insects

- Nest parasitism in Hymenoptera
- Social parasitism in ants

  - temporary social parasitism - the new queen kills the host queen
  - slavery - the use of an ant worker of wild species
  - permanent parasitism without slavery - the parasitic species uses the organization to host nests, produces a sexual caste

Polyergus breviceps

Host: *Formica argentea*

Evolution of parasitism

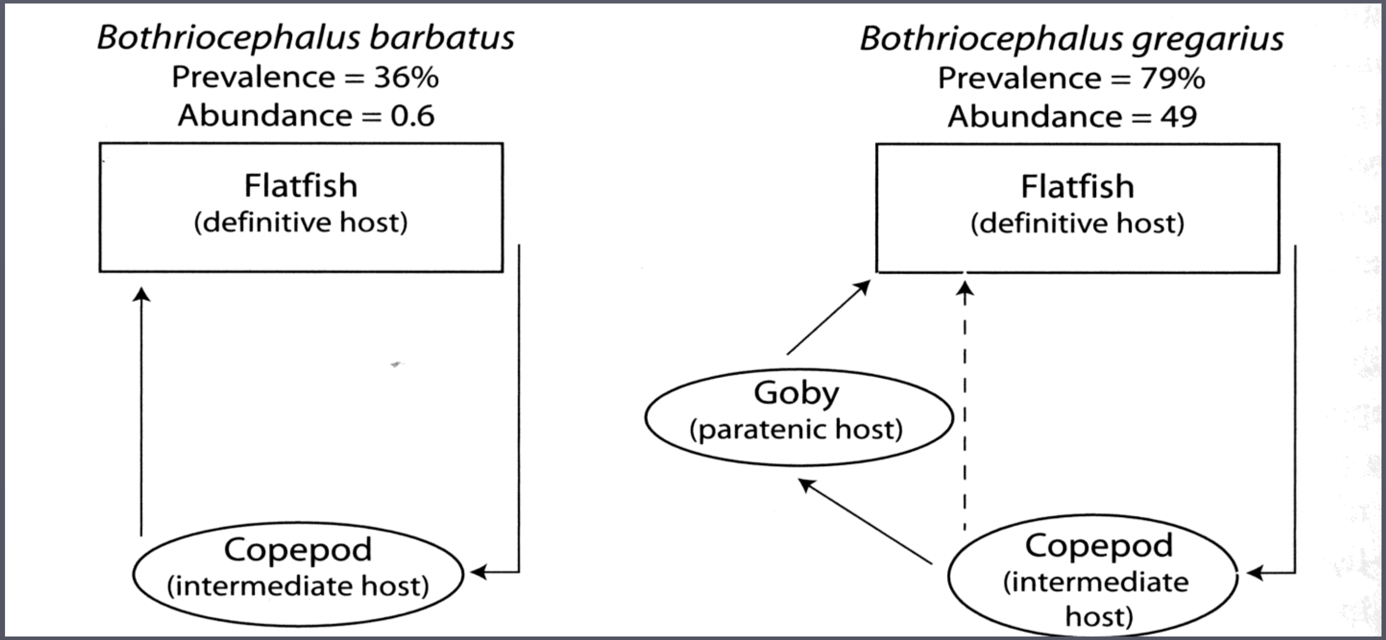
- Independent origin in different groups of organisms – parasitism has multiple origin
- Reversibility of the transition to parasitism (not all)
- It is created on the basis of unique pre-adaptations and historical events
- The transition to parasitism must be beneficial - increase fitness

Origin of parasitism

- at least 50 times in Metazoa
- 1. Free living organisms → a part of the group creates parasitic lineage (e.g. Heteroptera – the two lines switched to a parasitic way of life, Isopoda, Amphipoda, Copepoda, Nematoda – 4 times switched to a parasitic way of life)
- 2. Diversification and evolution of parasitic group – splitting the group and changing the strategy (e.g. Digenea + Monogenea + Cestoda = monophyletic group, Acanthocephala)

Evolution of parasitism – increase of fitness

The complexity of the life cycle increases the fitness parasite



e.g. two species of parasites living in sympatry

Evolution of parasitism

- Two evolutionary scenarios in Diplomonadida

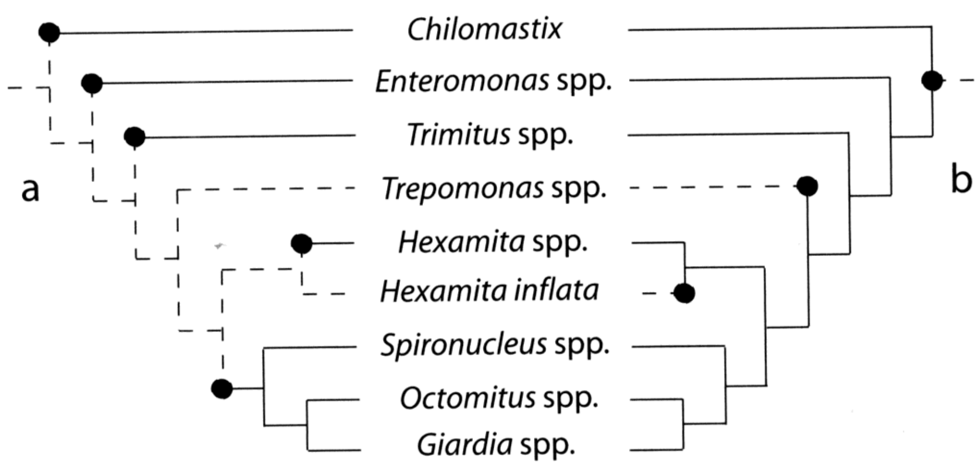


Figure 2.1 Two scenarios for the evolution of parasitism in the protist taxon Diplomonadida. Free-living lineages are indicated by broken lines, parasitic lineages by solid lines; black circles illustrate the proposed transitions between lifestyles. The phylogeny is based on the analysis of twenty-three ultrastructural characters; *Chilomastix* is the outgroup. In scenario (a), the ancestor was free living, and parasitism arose on five separate occasions. In scenario (b), parasitism was the ancestral state in the Diplomonadida, and there were two reversals to a free-living lifestyle. (Modified from Siddall et al. 1993)

Evolution of parasitism

- Regression evolution → lower structural complexity = simplification

- Morphology - loss of some organs

  reduction of some organs (saculinization) - locomotor, nervous and sensory systems

  however, exceptionally complex nervous and sensory organs: Aspidogastrea *Lobatostoma manteri,* Monogenea *Polystomoides malayi*

  larvae 8000 and adult 20.000-40.000 of sensory receptors

- Reduction of genome size (unused parts)

  however, big genome in some parasites

Evolution of parasitism

- **Reducing body size in parasites**

  dependence on the size of the host's body = Harrison´s rule

  12 m didymozoid trematodean species in *Mola mola*

  40 m *Tetragonoporus calyptocephalus* in cetaceans
  Schistocephalus solidus up to 2x heavier than a fish host

- **Optimal virulence**

  evolution towards optimal virulence (depends on the mode of transmission, host availability…) - maximizes fecundity during the life of the parasite

Evolution of parasite fecundity

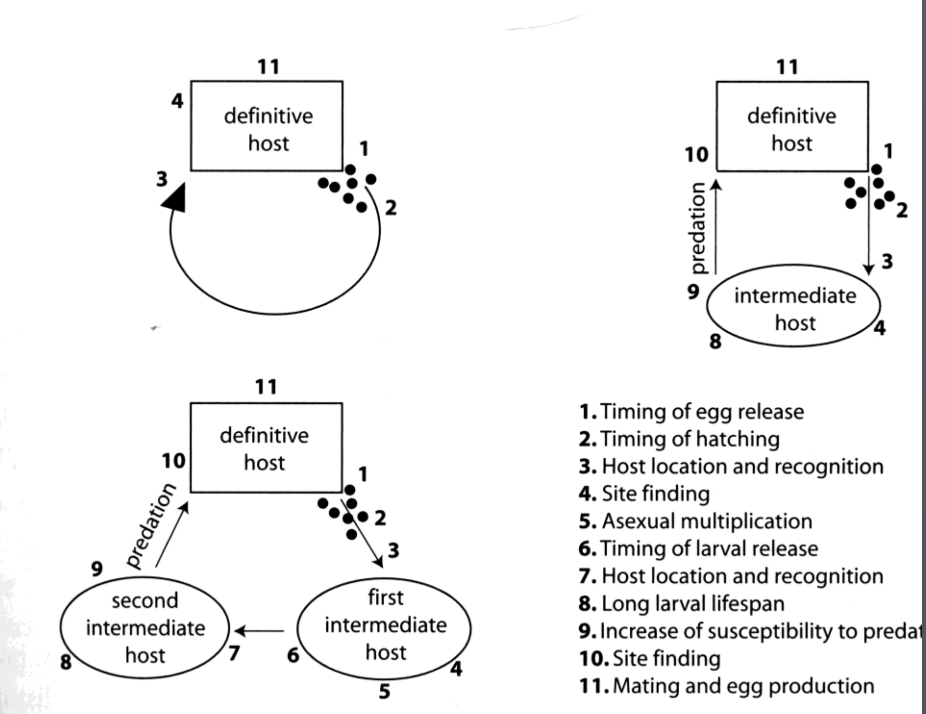
- High fecundity

	Number of eggs during an individual's lifetime	Multiplication of larval stages
Turbellaria (free living)	10	1
Monogenea (ectoparasites)	1000	1
Digenea (endoparasites)	10 milions	≥1000
Cestoda (endoparasites)	10 milions	1-1000

- some parasites have behavior that does not require high fecundity (modify host behavior)

Evolution of life cycle

- Free living way of life → parasitic way of life – simple life cycle and sexual reproduction → complex life cycle – sexual and asexual reproduction, changes of parasite phenotypes, hermaphroditism, parthenogenesis

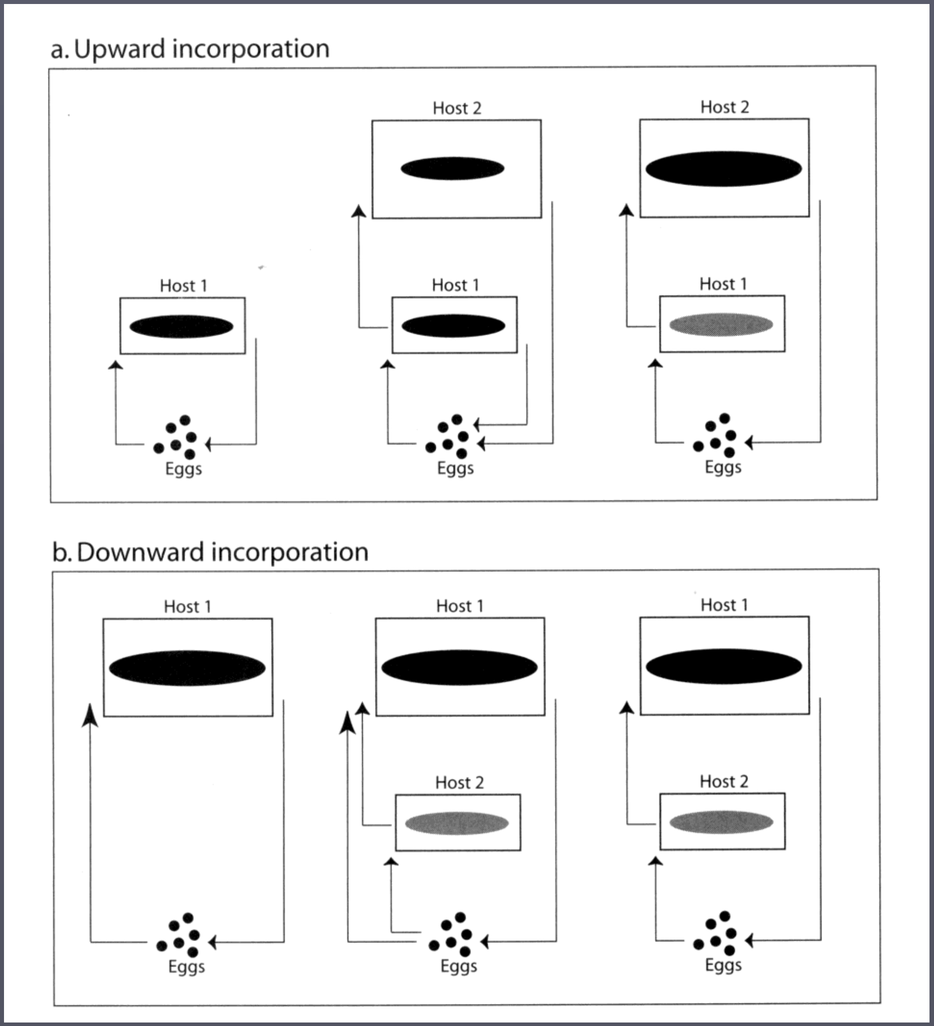


Evolution of life cycle in parasites: increasing complexity of development

- 2 ways of changes

upward incorporation

downward incorporation

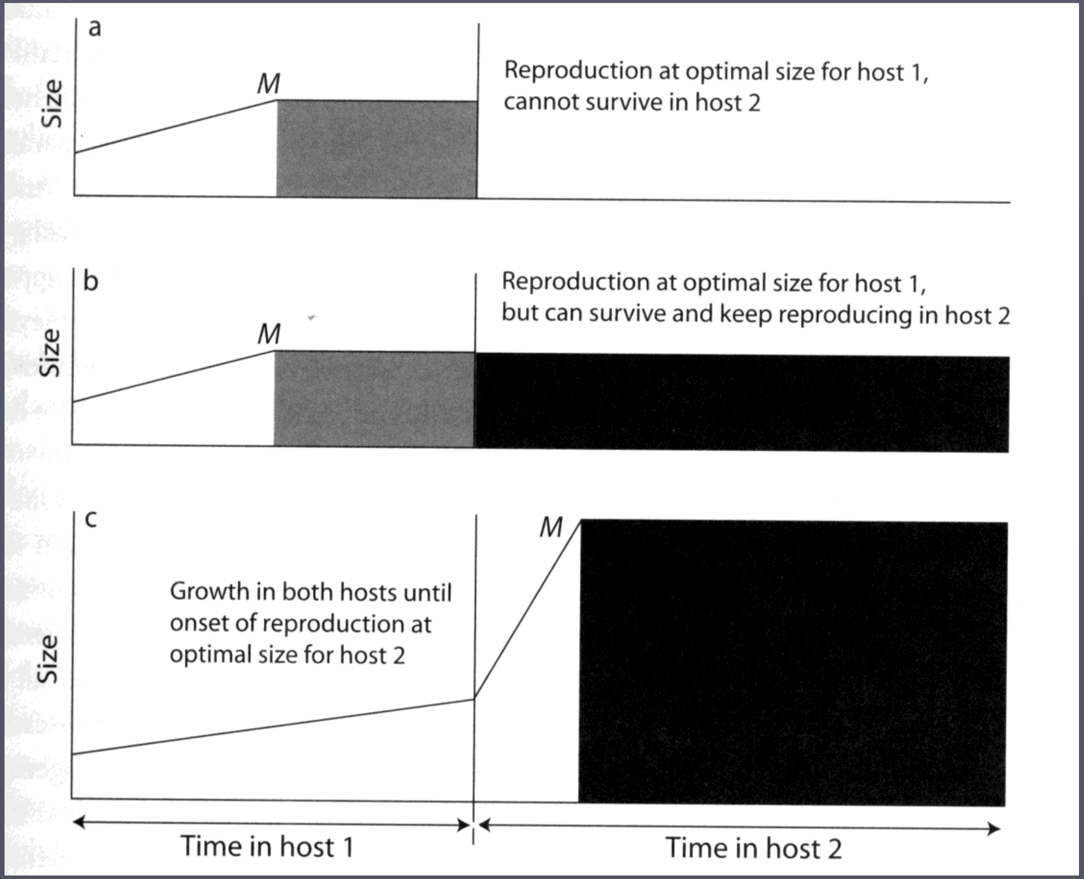


Evolution of life cycle in parasites: increasing complexity of development

- Survival and growth in the new host generates selection to shift sexual maturity and reproduction

upward incorporation of new host

M – sexual maturity



Evolution of parasitism: shortening the development

- Advantageous under certain conditions
- E.g. Sangunicolidae, Spirorchidae and Schistosomatidae (Digenea)

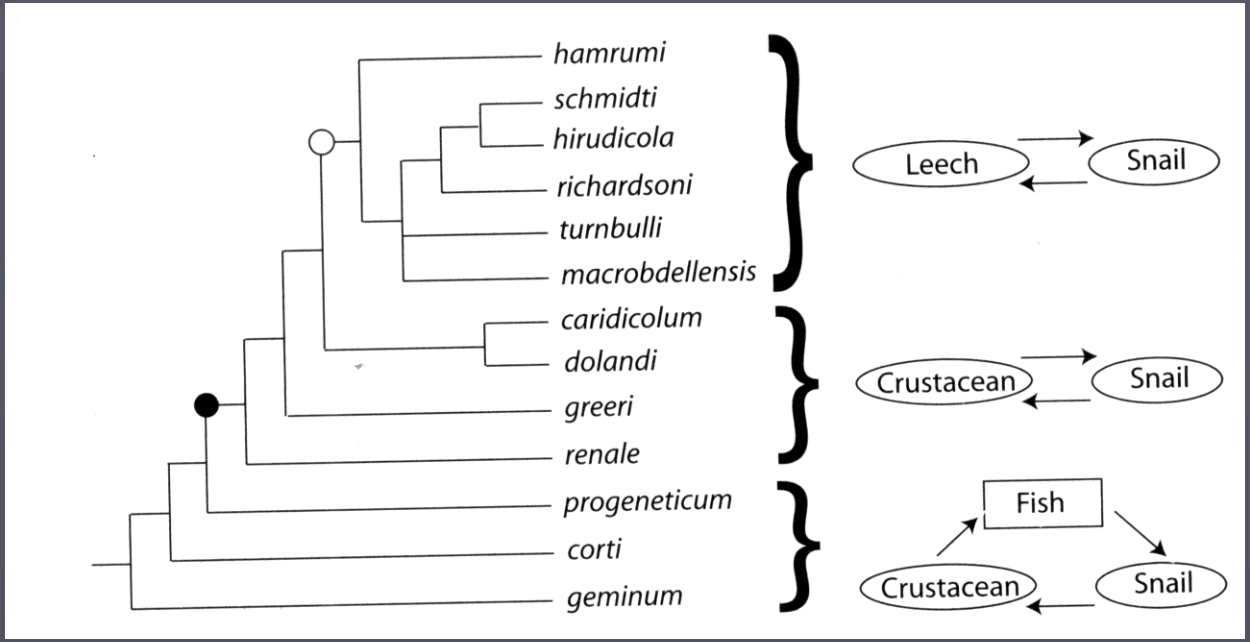


Figure: Trematoda of the genus *Alloglossidium*

Evolution of parasitism: shortening the development

- Three-host life cycle is reduced to two-host or single-host life cycle (several ways)

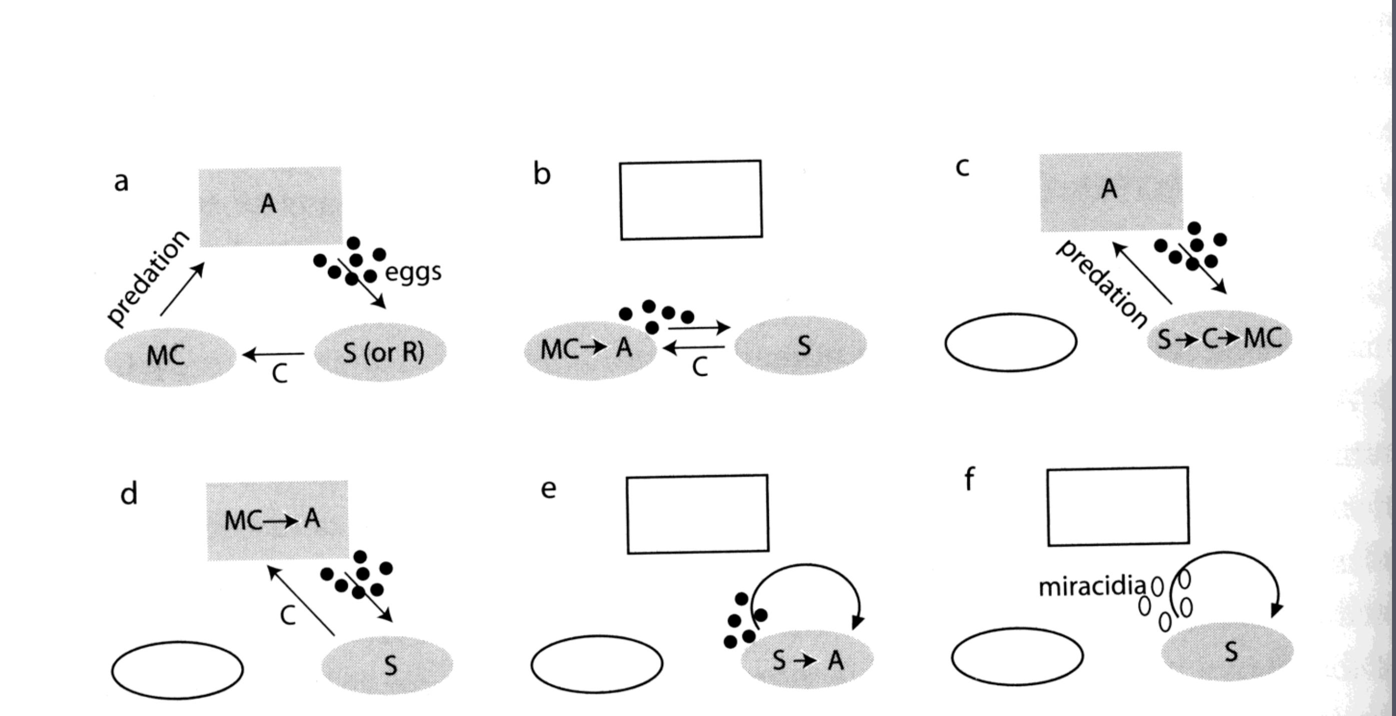


Figure: Trematoda, A – adult, MC – metacercaria, S – sporocyst, R - rediae