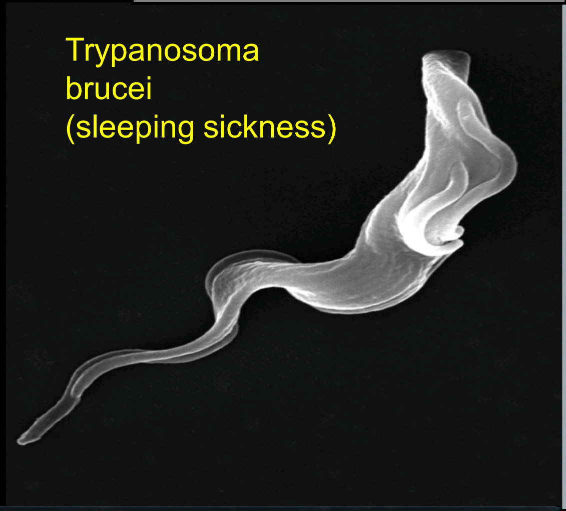
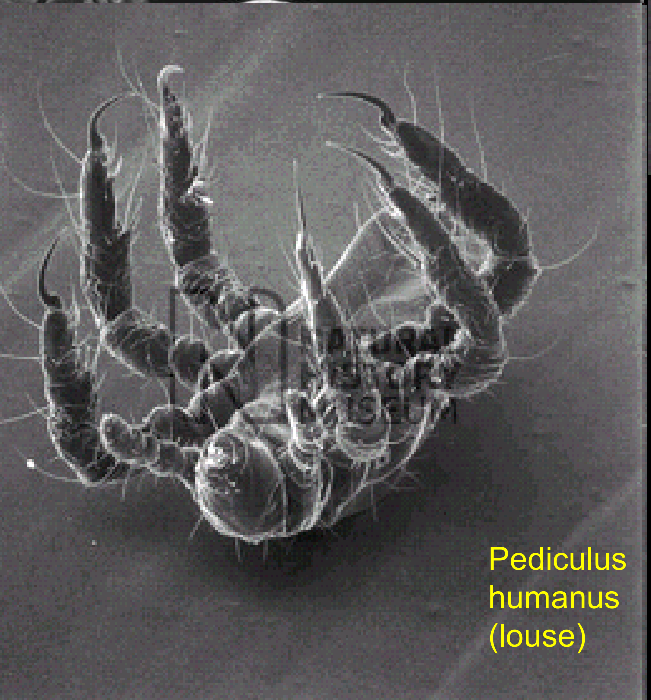
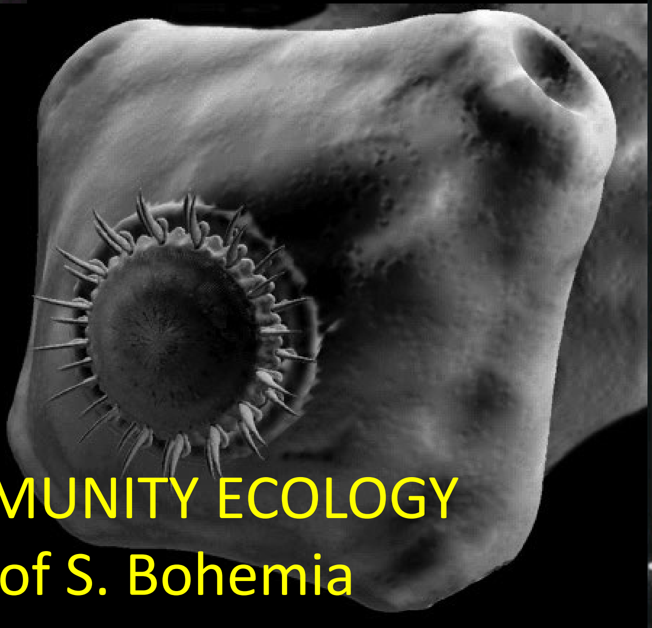
Parasites: an aesthetically pleasing trophic level


Schistosoma mansoni (bilharzia)


Ancylostoma duodenale (hookworm)


Trypanosoma brucei (sleeping sickness)


Pediculus humanus (louse)

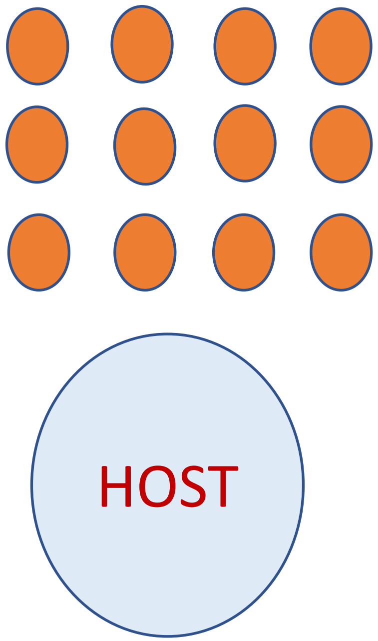

Taenia solium (tapeworm)

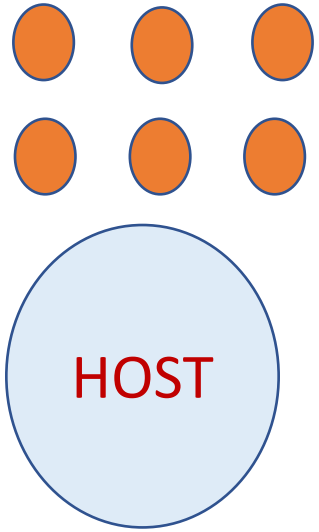

Giardia lamblia (intestinal protozoan)

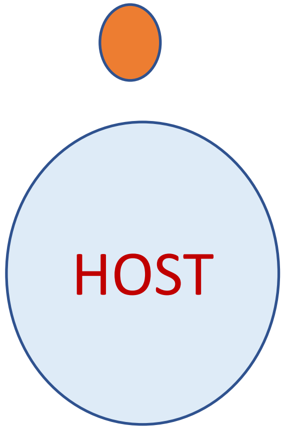
VOJTECH NOVOTNY: COMMUNITY ECOLOGY

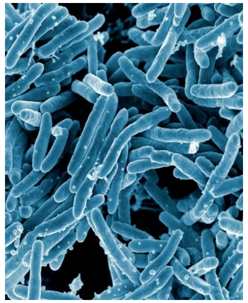
LECTURE NO 1, University of S. Bohemia

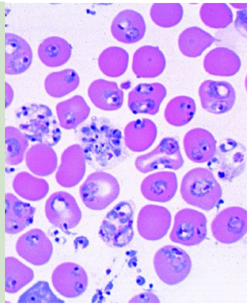
Pathogen – Parasite – Parasitoid

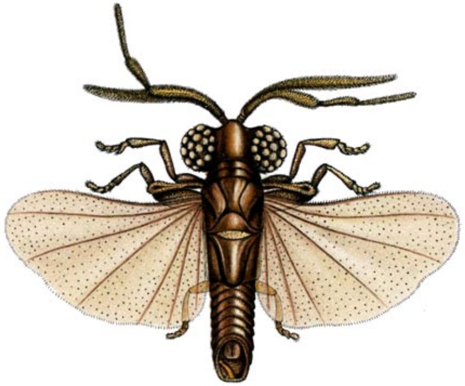






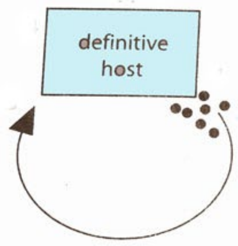






What is fascinating on parasite ecology?

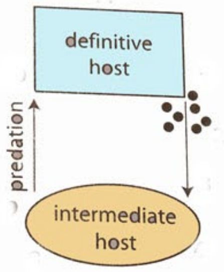
Seemingly insanely complicated developmental cycles, including often obligatory sequence of several host species



simple cycle:

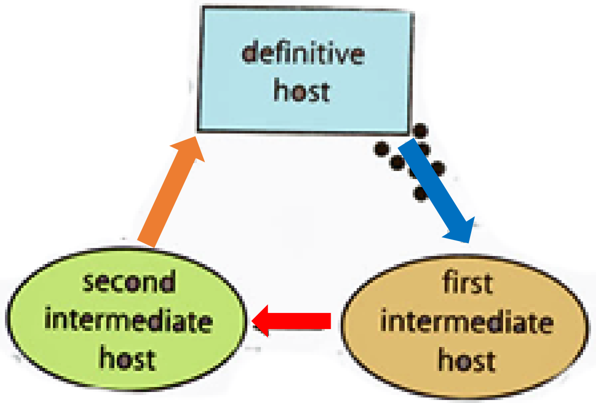
single host species infects itself

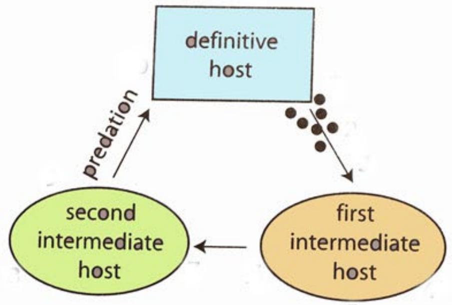
transmissions:
- passive, probabilistic
- active, targeted by parasite
- active, targeted by host or transmission agent



more complicated cycle:

parasite has one intermediate host

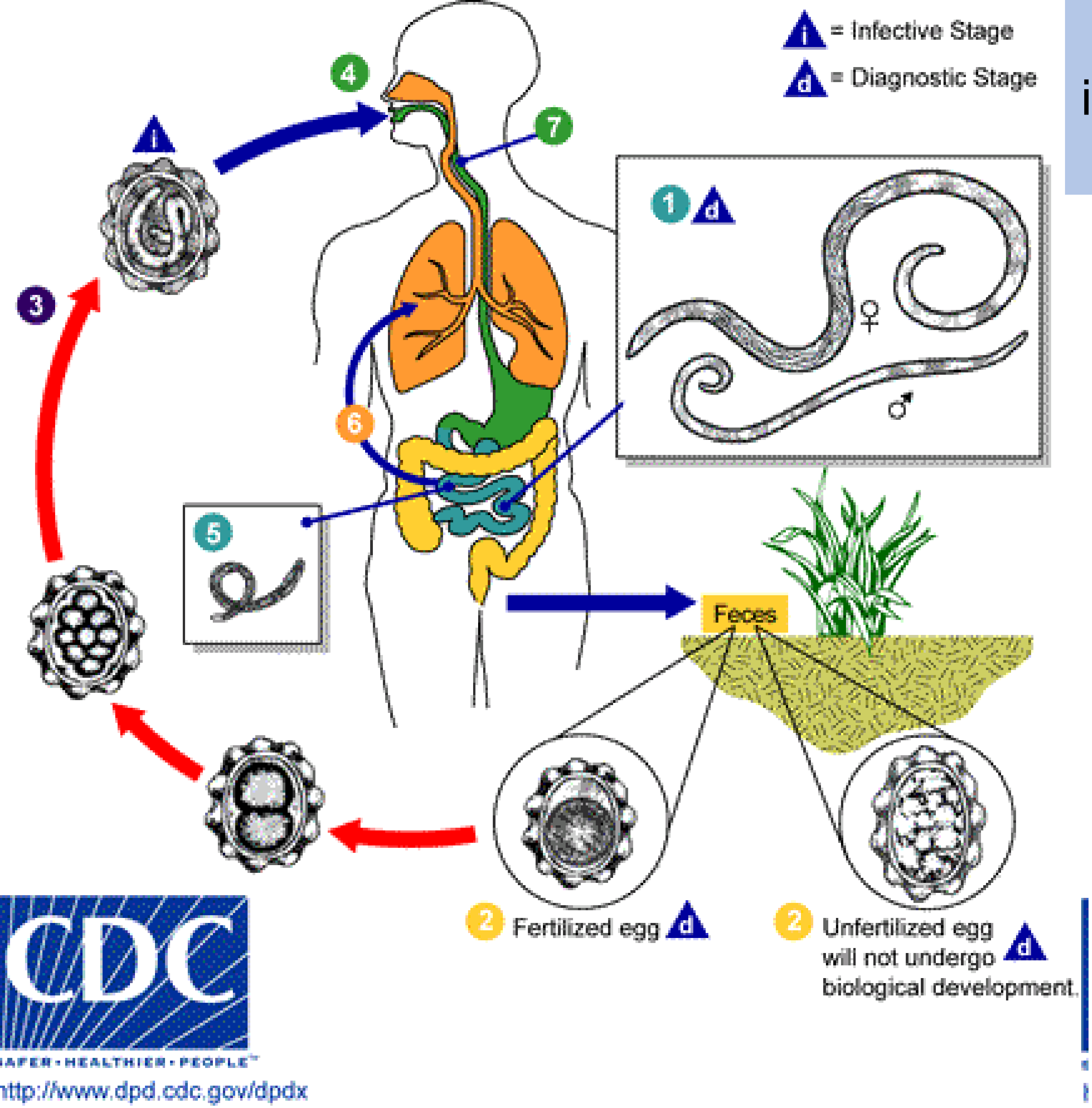




even more complicated cycle:

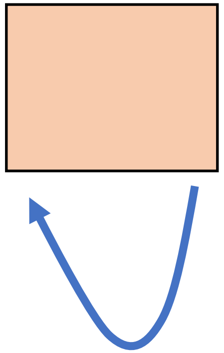
parasite has to pass through more than one intermediate host

Simple cycle: most is infected from conspecific individuals

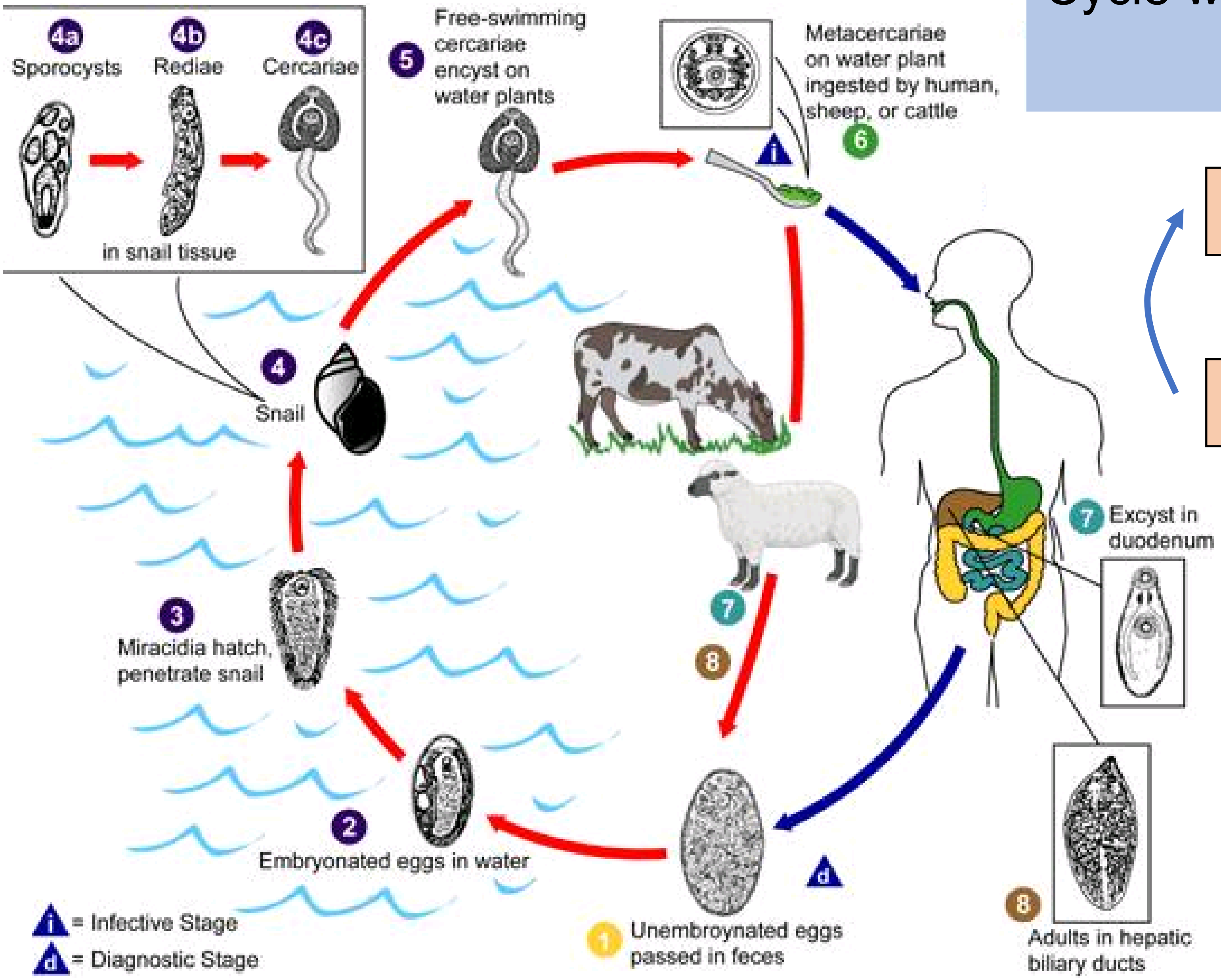


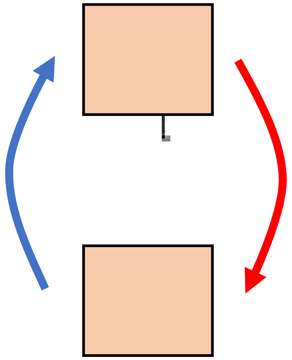
transmissions:
passive, probabilistic
active, targeted by parasite
active, targeted by host or transmission agent

Ascaris lumbricoides: intestinal parasite, eggs in faeces contaminate food



Cycle with one intermediate host

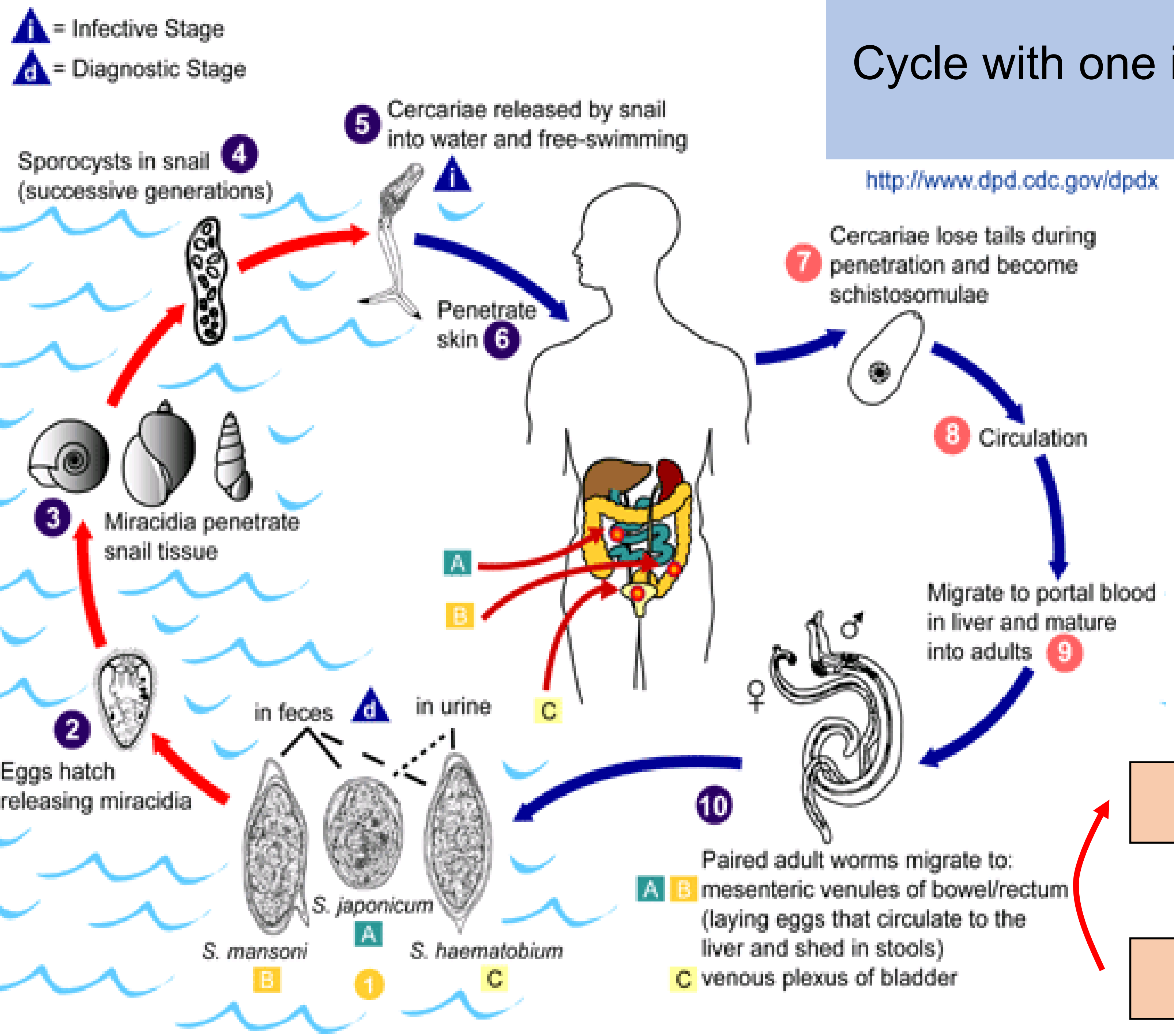




Fluke *Fasciola hepatica*

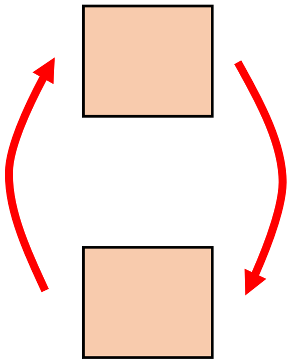
Mature flukes live in hepatic biliary ducts (humans, other mammals), eggs in faeces, active larva (miracidium) emerges in water, attacks snails, where further develops (sporocyst, redia, cercaria). Active cercaria leaves the snail, encysts on water or submerged plants, waits to be eaten by the final host.

Cycle with one intermediate host

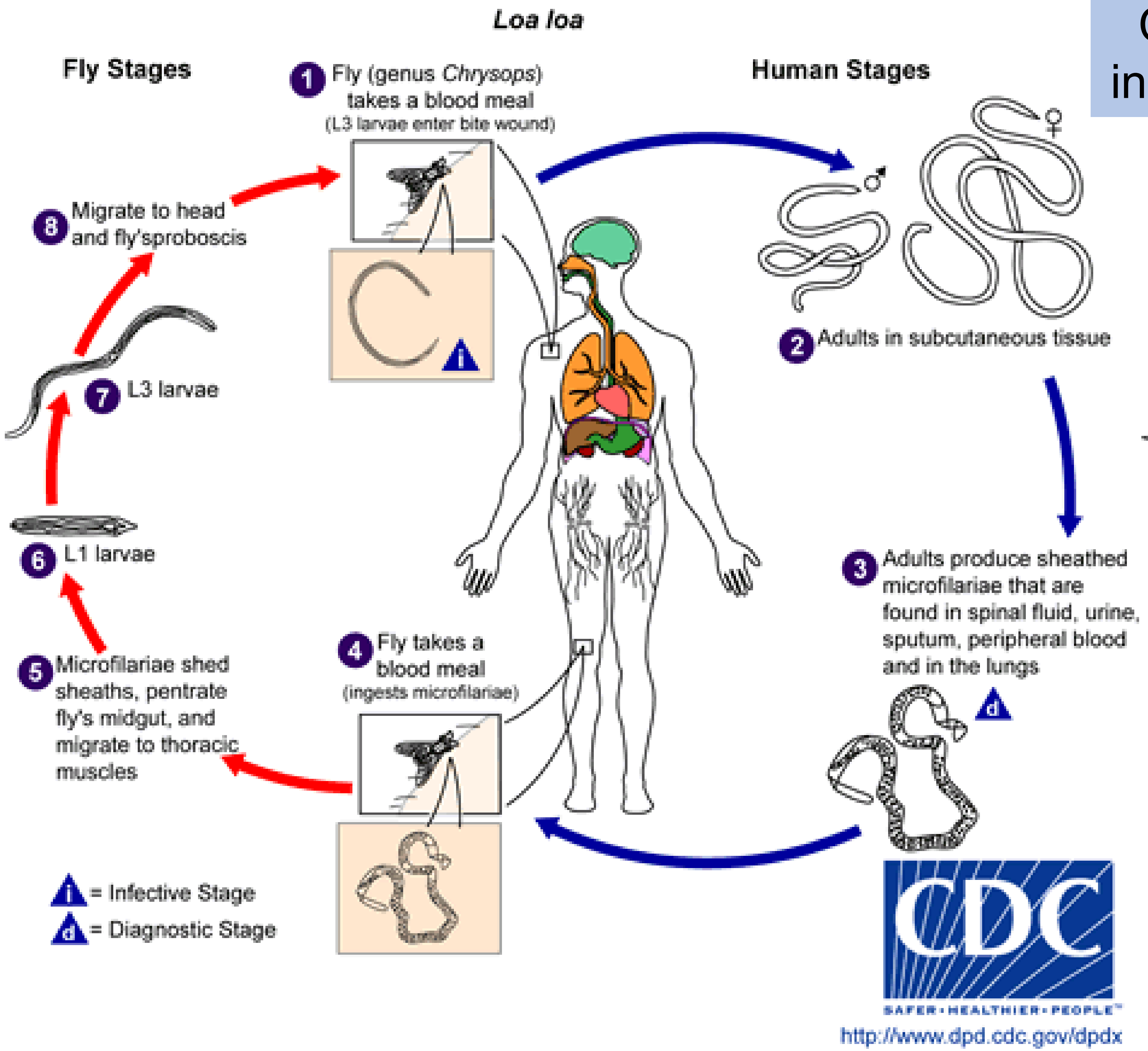


Schistosoma haematobium
(causes bilharziasis)

Mature worms in veins of urinary bladder, eggs released in urine, active larvae (miracidium) emerge in water, attack snails, where undergo further development, leave them as active swimming larvae (cercaria) attacking humans, penetrate their skin and sexually mature in them.

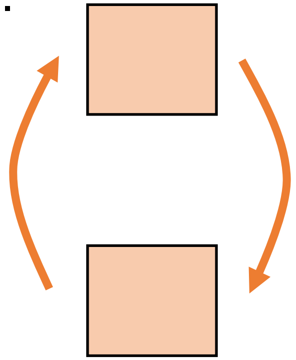


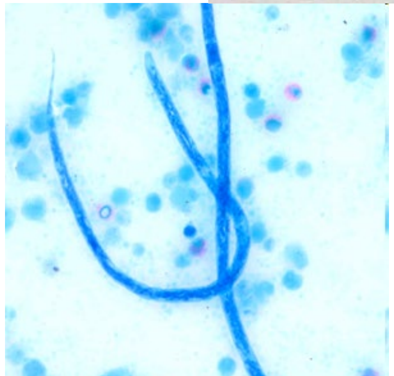
Cycle with one intermediate host



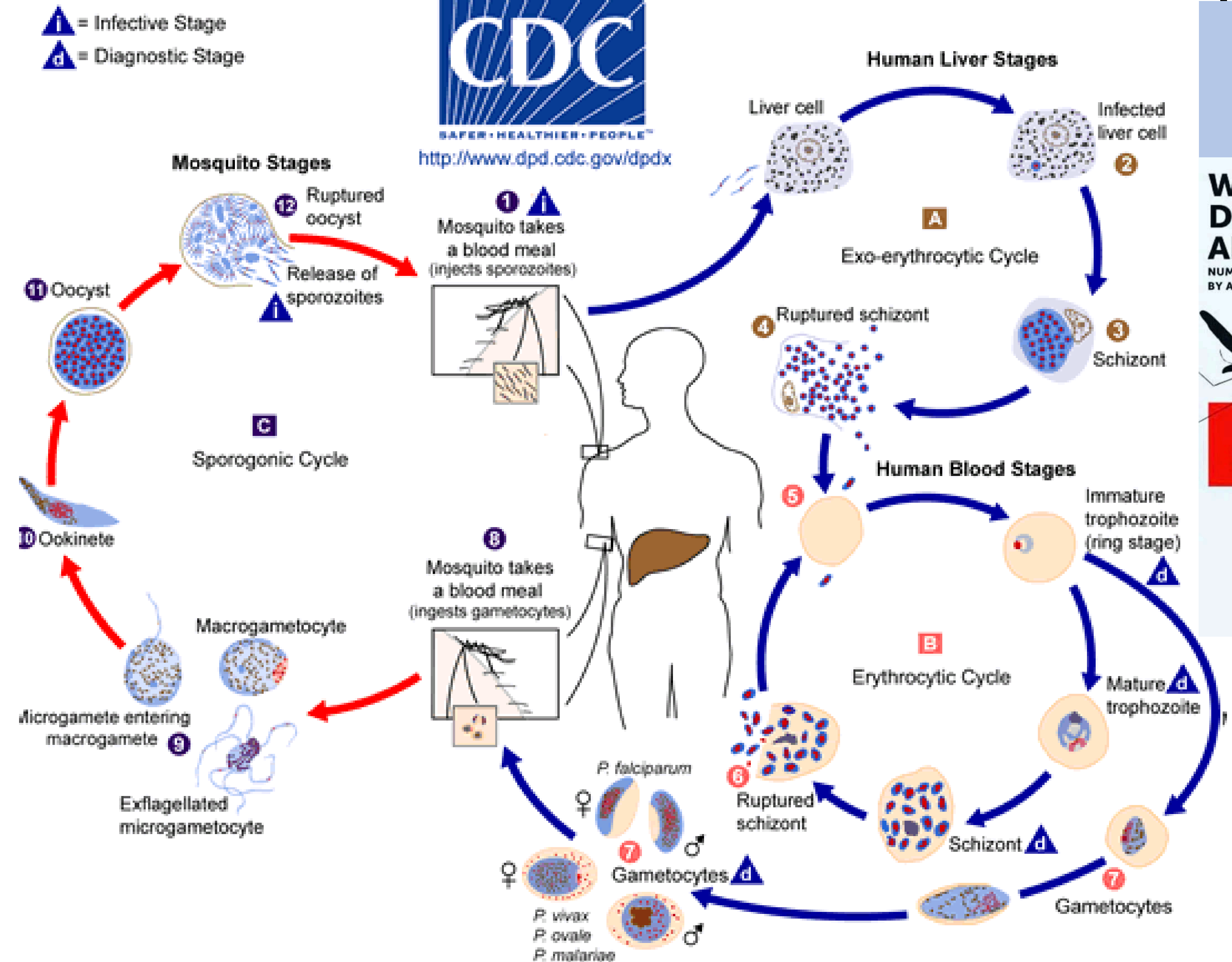
Filaria (*Loa loa*):

Adult parasite in subcutaneous tissue of humans, larvae (microfilaria) with peripheral blood sucked by flies with *Chrysops*, where they develop in thoracic muscles, migrate to salivary glands and infect humans when the flies suck their blood.

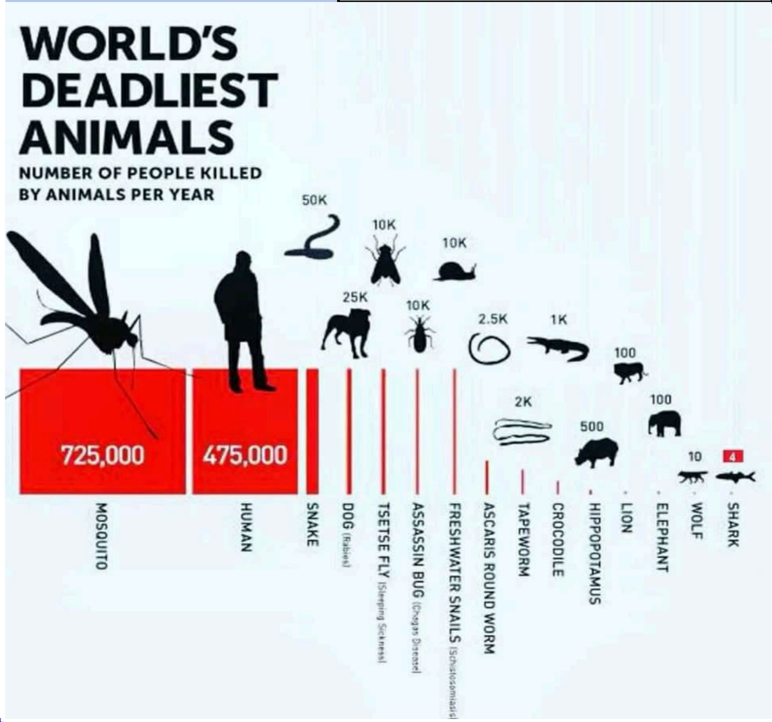




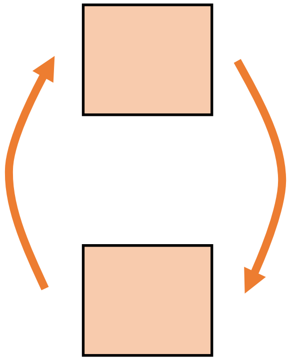
Malaria

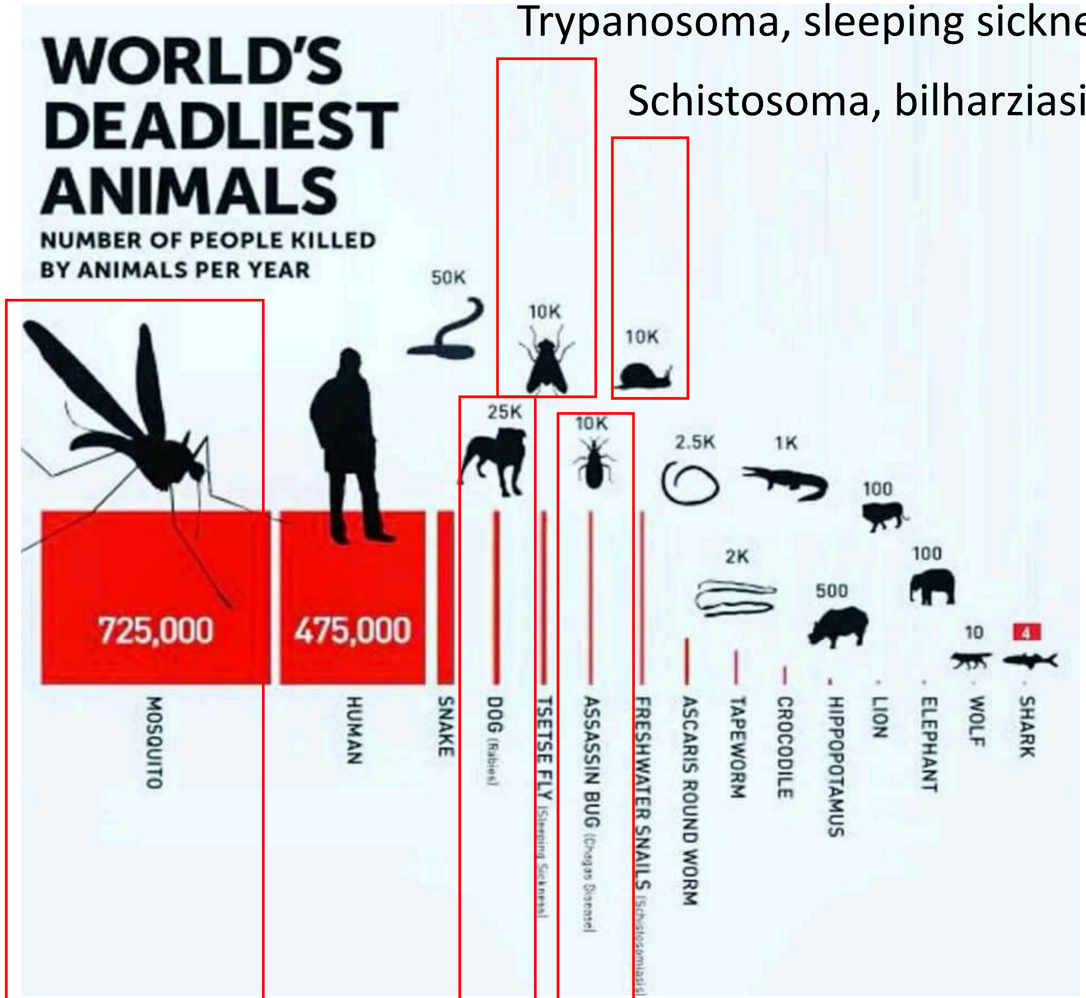


= Infective Stage
= Diagnostic Stage
CDC
SAFER·HEALTHIER·PEOPLE™
http://www.dpd.cdc.gov/dpdx
Human Liver Stages
Liver cell
Infected liver cell
A
Exo-erythrocytic Cycle
Ruptured schizont
Schizont
Mosquito Stages
Ruptured oocyst
Release of sporozoites
Oocyst
Mosquito takes a blood meal (injects sporozoites)
C
Sporogonic Cycle
Ookinete
Mosquito takes a blood meal (ingests gametocytes)
Macrogametocyte
Microgamete entering macrogamete
Exflagellated microgametocyte
Human Blood Stages
Immature trophozoite (ring stage)
B
Erythrocytic Cycle
Mature trophozoite
Ruptured schizont
Schizont
P. falciparum
Gametocytes
Gametocytes
P. vivax
P. ovale
P. malariae



WORLD'S DEADLIEST ANIMALS
NUMBER OF PEOPLE KILLED BY ANIMALS PER YEAR
725,000
475,000
50K
25K
10K
10K
10K
2.5K
2K
1K
500
100
100
10
4
MOSQUITO
HUMAN
SNAKE
DOG
TSETSE FLY
ASSASSIN BUG
FRESHWATER SNAILS
ASCARIS ROUND WORM
TAPEWORM
CROCODILE
HIPPOPOTAMUS
LION
ELEPHANT
WOLF
SHARK





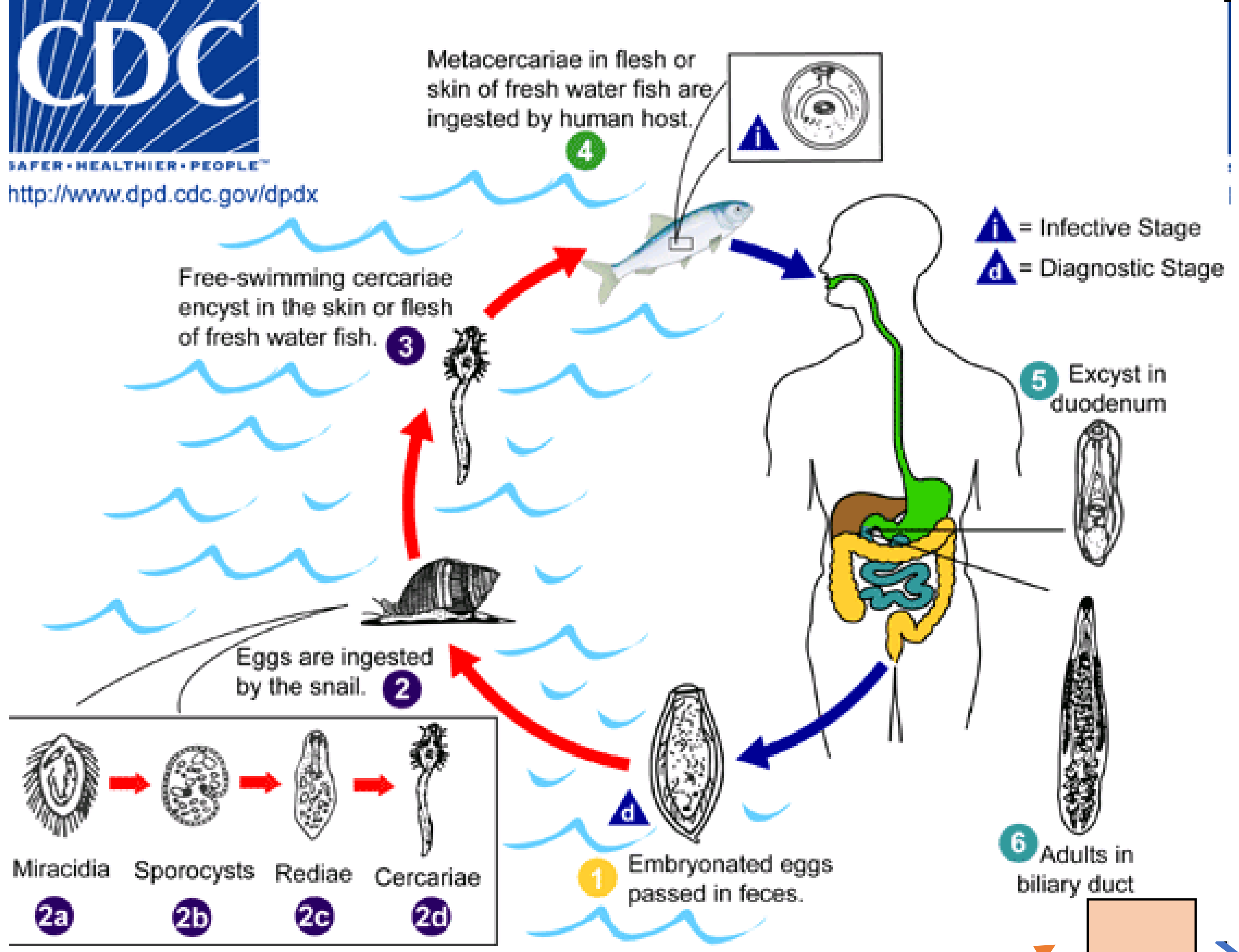
Trypanosoma, sleeping sickness

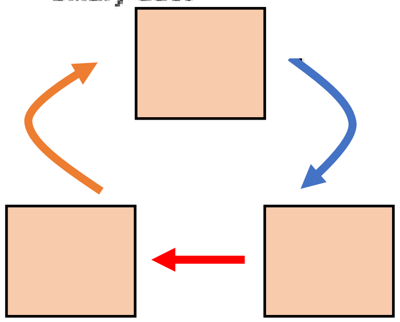
Schistosoma, bilharziasis

Plasmodium
malaria
flavivirus
dengue

Trypanosoma, Chagas disease

lyssaviru, rabies



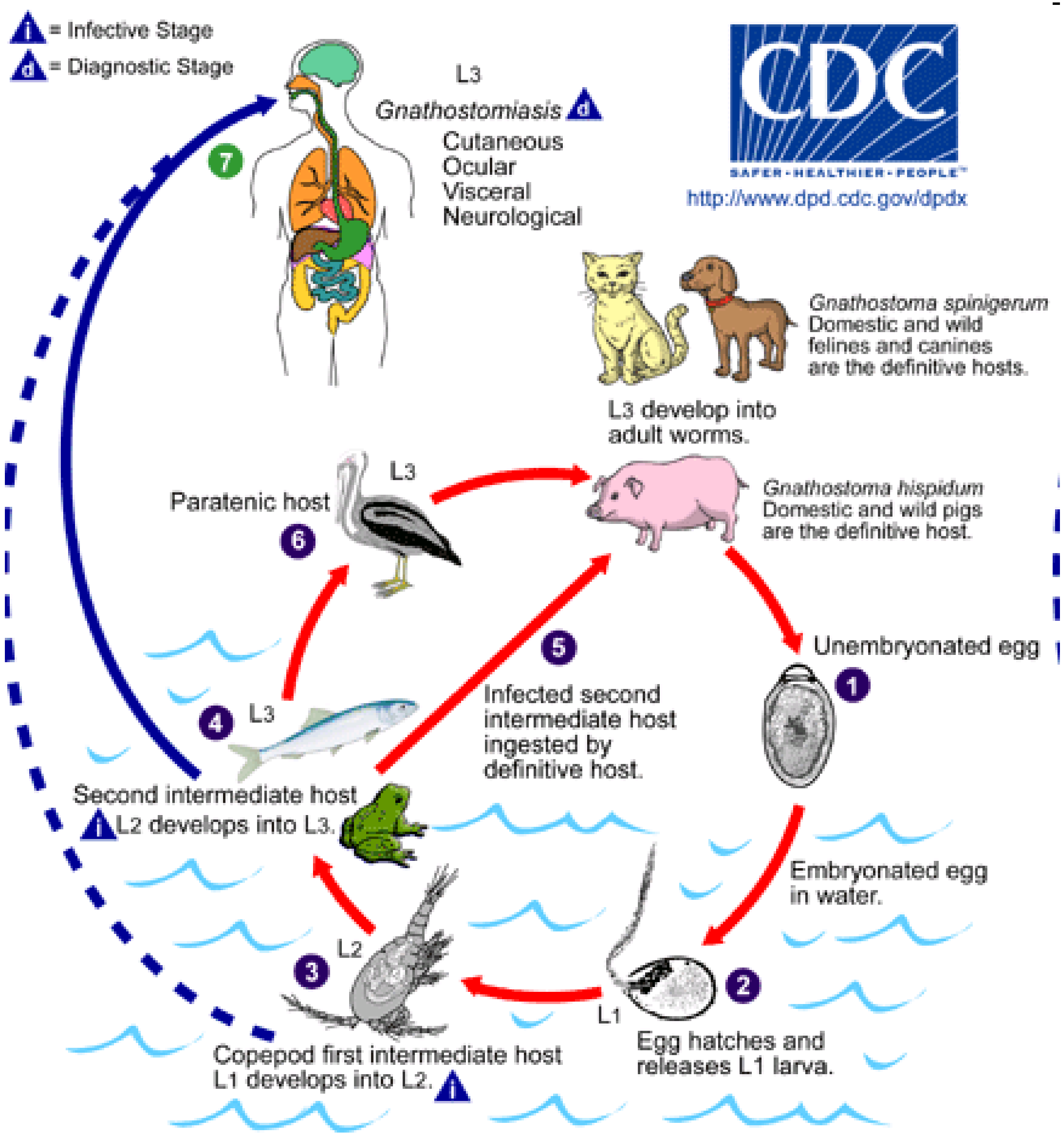


Cycle with two intermediate hosts

Fluke *Clonorchis sinensis*:

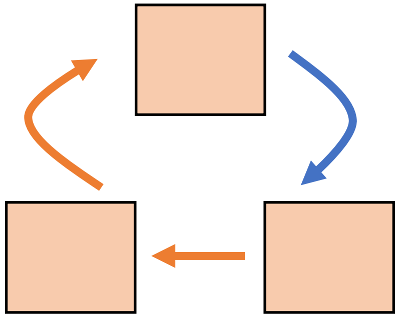
Adult parasite in biliary ducts of the final host (humans), eggs in faeces, in water eaten by a snail, where they develop (miracidium, sporocyst, redia, cercaria). Active larvae (cercaria) leave the snail and penetrate skin of second intermediate host - fish, where they encyst in muscle tissue (metacercaria) and wait to be eaten by the final host, where they mature.

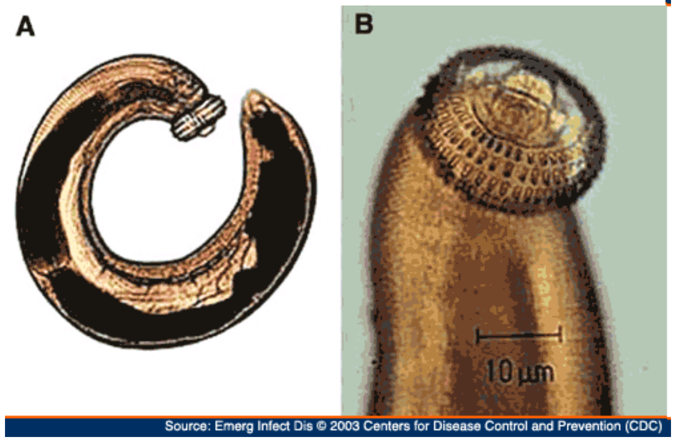

Bithynia sp.



Cycle with two intermediate hosts

Nematode *Gnathostoma spinigerum*:
In final host (canine and feline predators) are embedded in stomach wall, eggs released in faeces, in water emerge larvae which are eaten by the first intermediate host (copepod *Cyclops*). There they wait to be eaten by second intermediate host (fish, frog, snake), which in turn needs to be eaten by the final host. If the second intermediate host is eaten by a bird, parasite can wait in this additional host to be finally eaten by feline or canine predator, but cannot sexually mature in it. Humans are not hosts, if larva is eaten, it cannot mature but wanders in the body (larva migrans).





Strepsiptera (Myrmecolacidae): another example of a complex life cycle

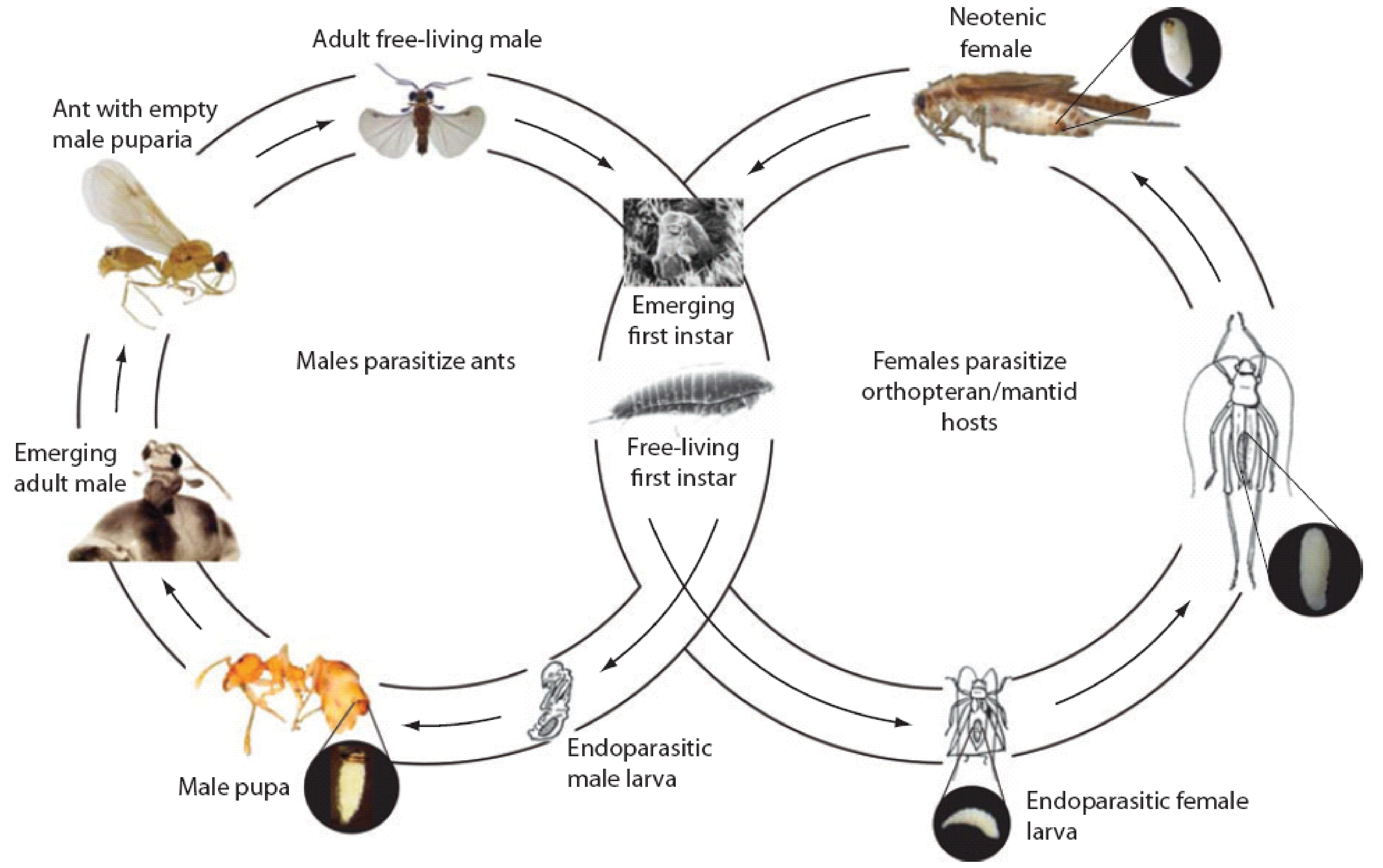
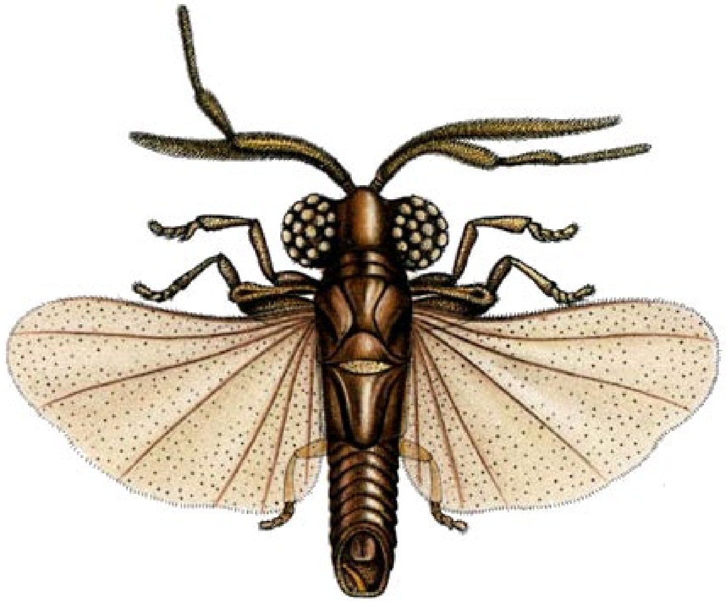


Figure 5

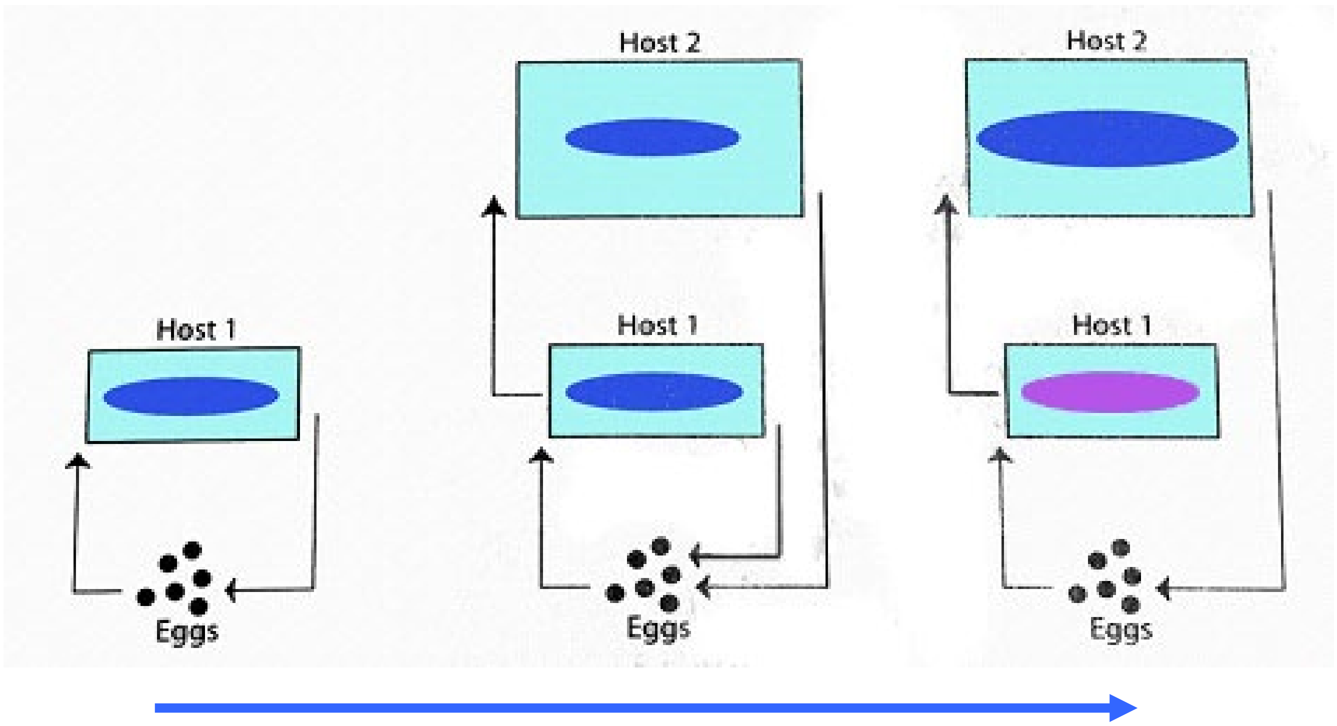
The life cycle of Myrmecolacidae. Males parasitize ants and females parasitize grasshoppers, crickets, and mantids. Modified from

1st instar larvae live freely, male larvae attack ants, female larvae attack grasshoppers, crickets, mantis. Further development is endoparasitic, producing flying males (killing the host) while neotenic females stay as endo-ectoparasites in their host where males find them, and mate with them.



Kathiritamby 2009, Annu. Rev. Entomol. 54: 227

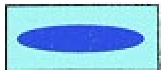
How are new hosts incorporated into the developmental cycle



direction of evolution

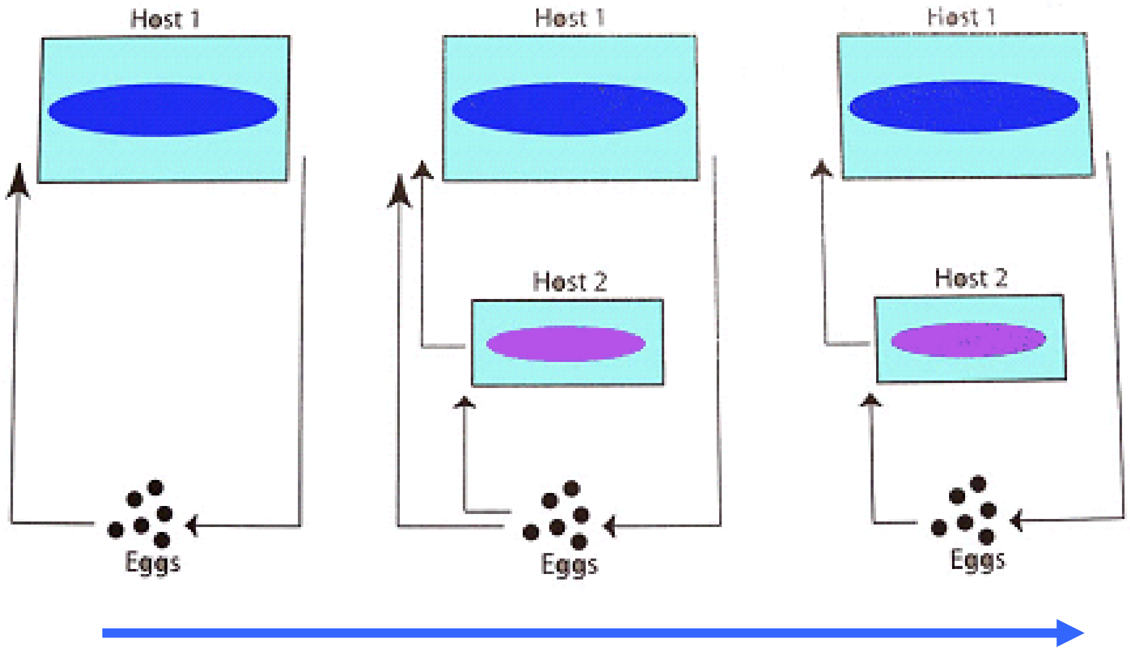
Initially the only host species is often eaten (together with its parasite) by a predator, which becomes initially facultative, later obligatory host. The original host becomes intermediate host as the reproduction of the parasite becomes limited to the newly acquired host.

immature parasites
in intermediate hosts



mature parasites
in final host

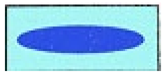
How are new hosts incorporated into the developmental cycle



direction of evolution

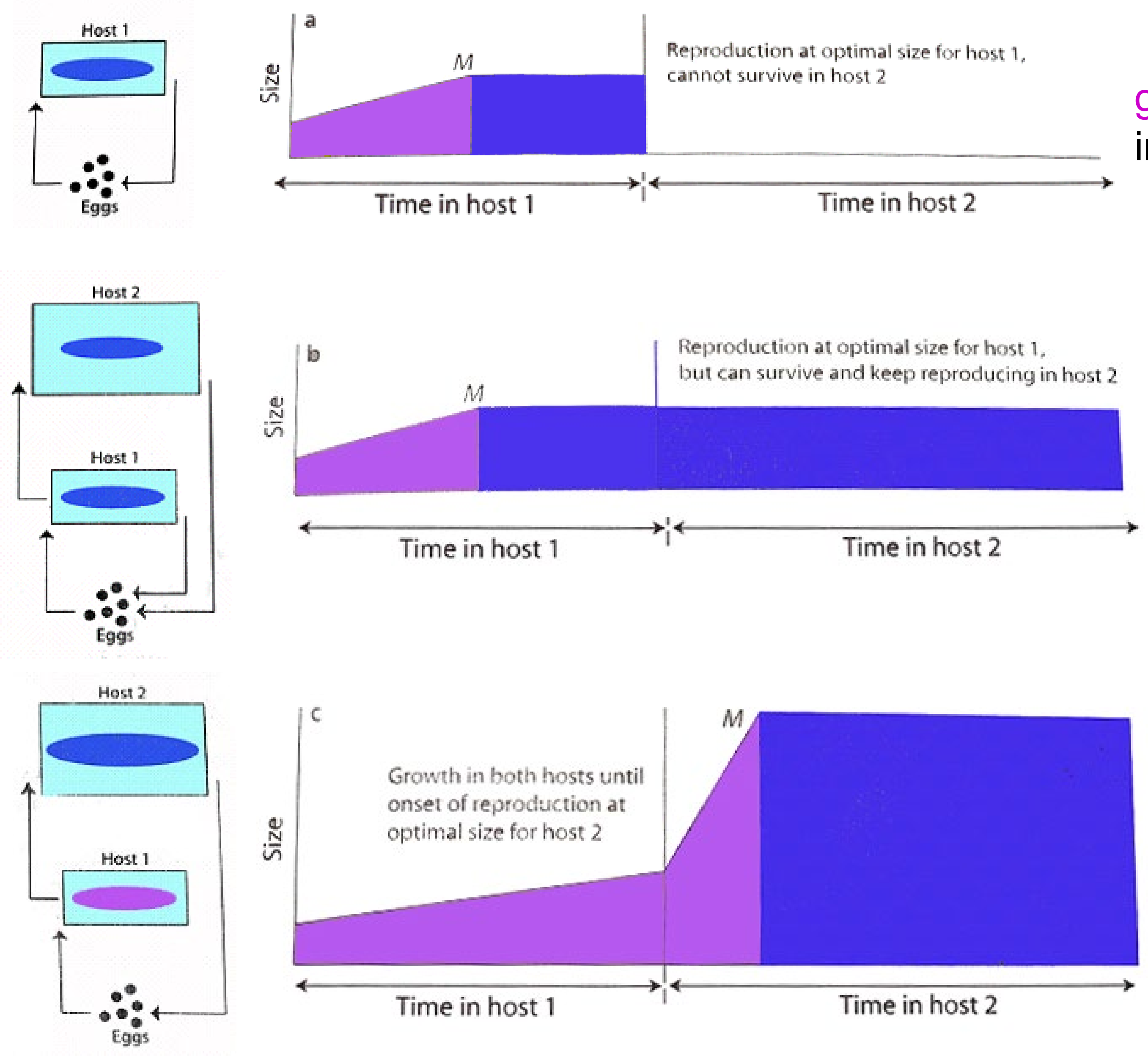
Parasite's eggs released by originally only one host species are often eaten by another species, which then becomes initially only facultative, later obligatory intermediate host of the parasite.

immature parasites
in intermediate hosts



mature parasites
in final host

Benefits from a new host: longer reproduction or growth



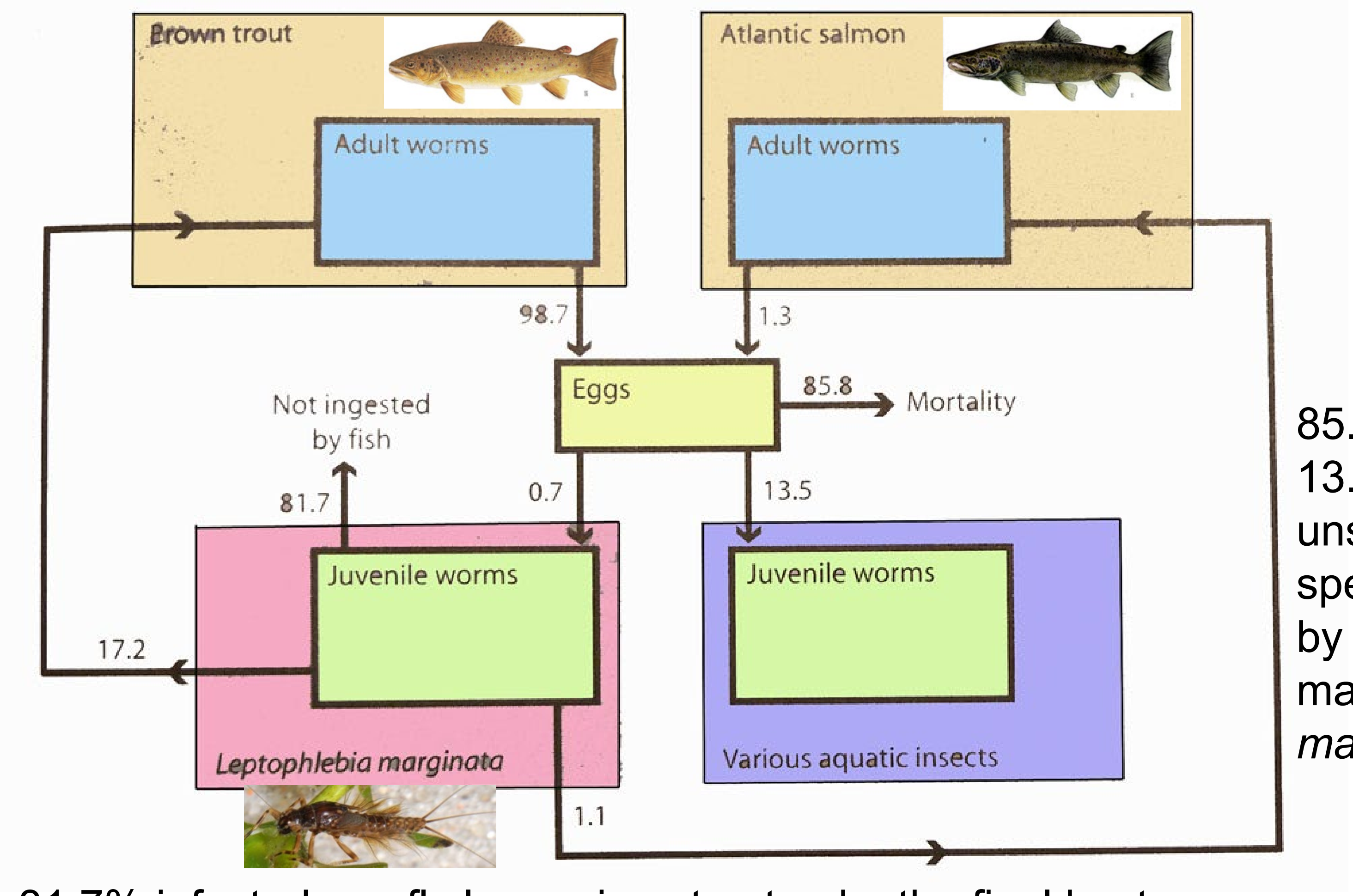
growth and reproduction
in a single host

reproduction
continues in
the new host

growth continues in
the new host

Parasite population dynamics: *Cystidicoloides tenuissima* (Nematoda)

98.7% eggs originates from nematodes living in trout,
1.3% from nematodes in salmon

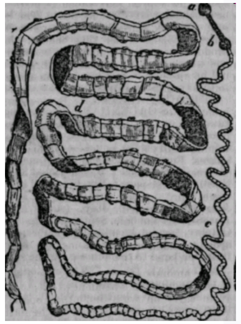


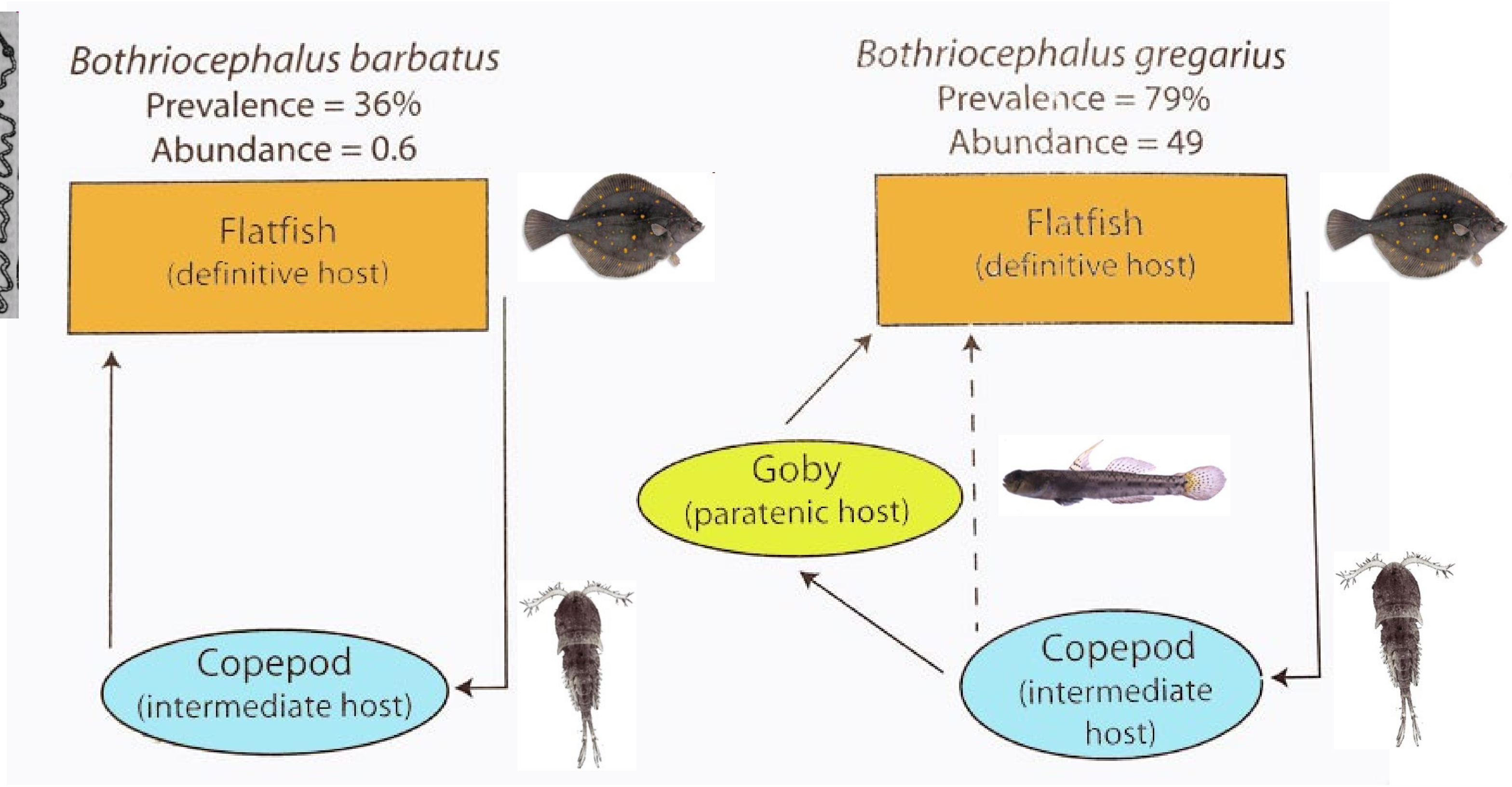
85.8 % eggs dies
13.5% is eaten by unsuitable insect species, 0.7% is eaten by intermediate host, mayfly larva *L. marginata*

81.7% infected mayfly larvae is not eaten by the final host,
17.2% is eaten by trout, 1.1% by salmon

Egg survival: 18.3% from 0.7%, i.e. 1.3 eggs from 1000 develops to an adult

What is the new intermediate host good for?
The case of related tapeworms *Bothriocephalus barbatus* and *B. gregarius*

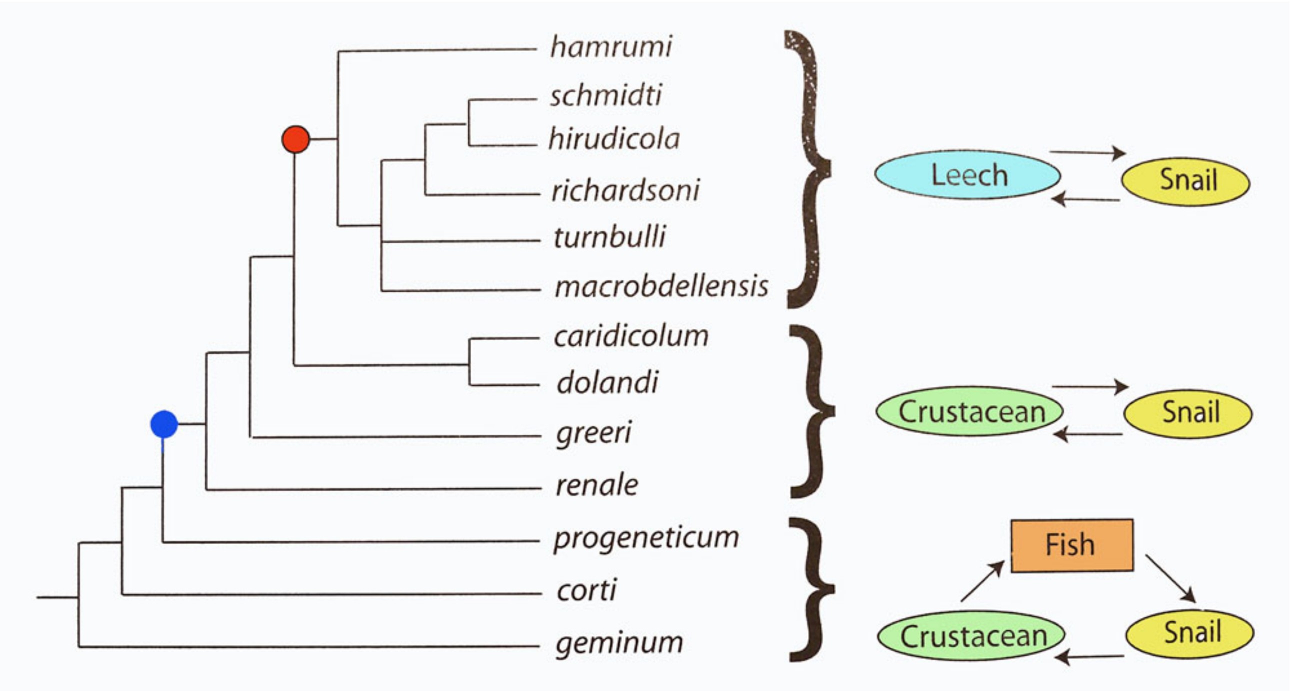




B. barbatus parasitizes flatfish, with a copepod as intermediate host. *B. gregarius* can also include in its cycle goby fish as an optional (paratenic) host where it can multiply and thus better infect the final host.

This is indeed the case as in the Mediterranean Sea, *B. barbatus* parazitises only 36% of flatfish, while *B. gregarius* 79% of flatfish.

Evolution of host cycle in flukes *Alloglossidium*



replacement of snail by leech

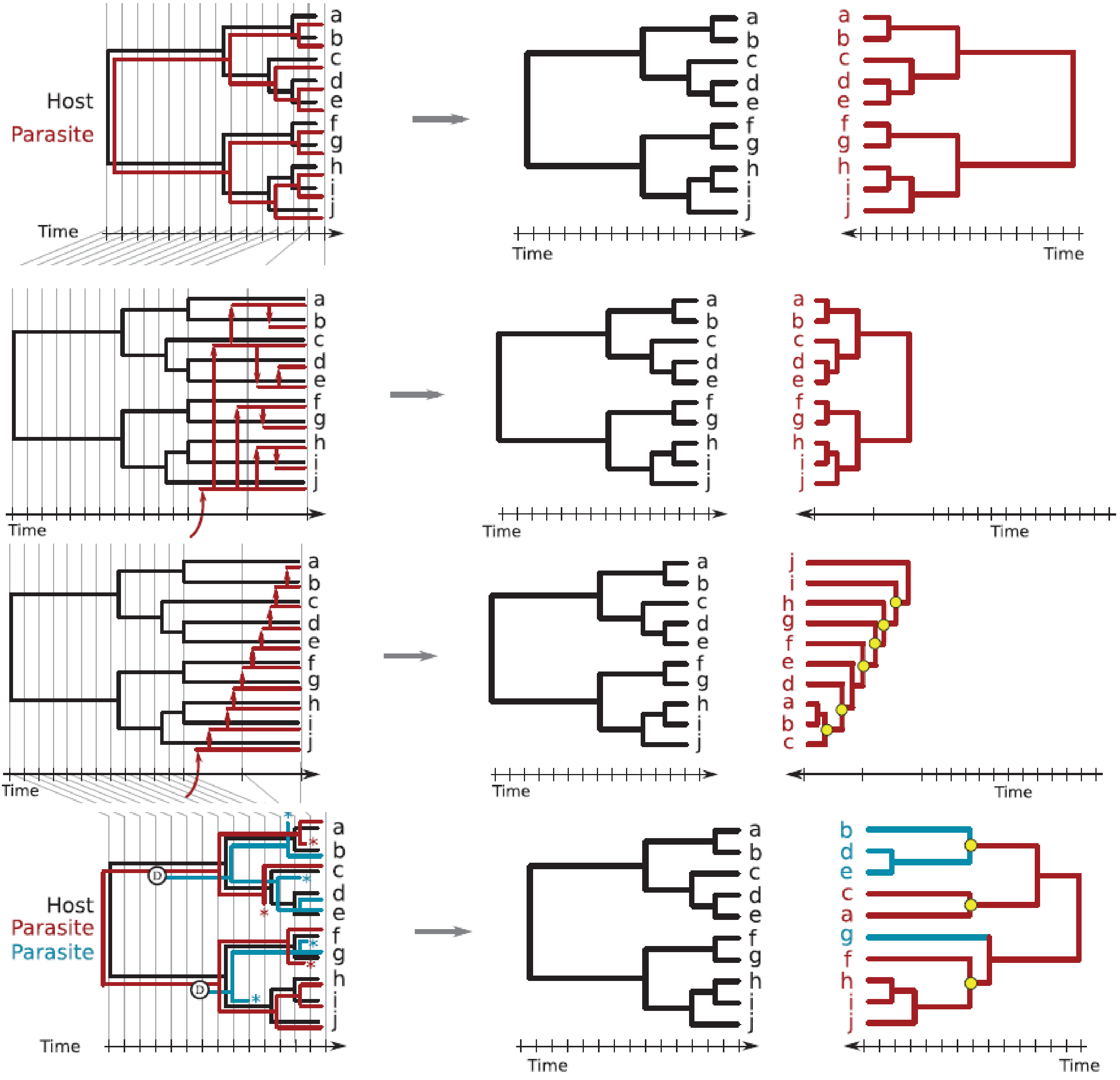
simplified cycle snail - crustacean

initial cycle fish - snail - crustacean

fish host lost

crustacean exchanged for leech

Host-parasite phylogenies

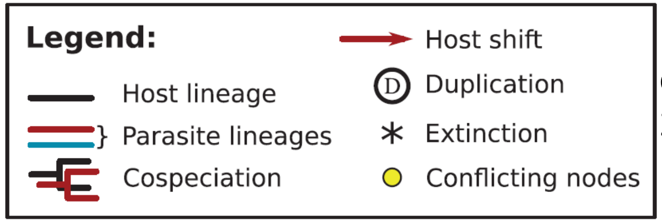


Cospeciation resulting in congruent phylogenies.

Host-shift speciation resulting in congruent phylogenies, but with shorter branches in the parasite lineages.

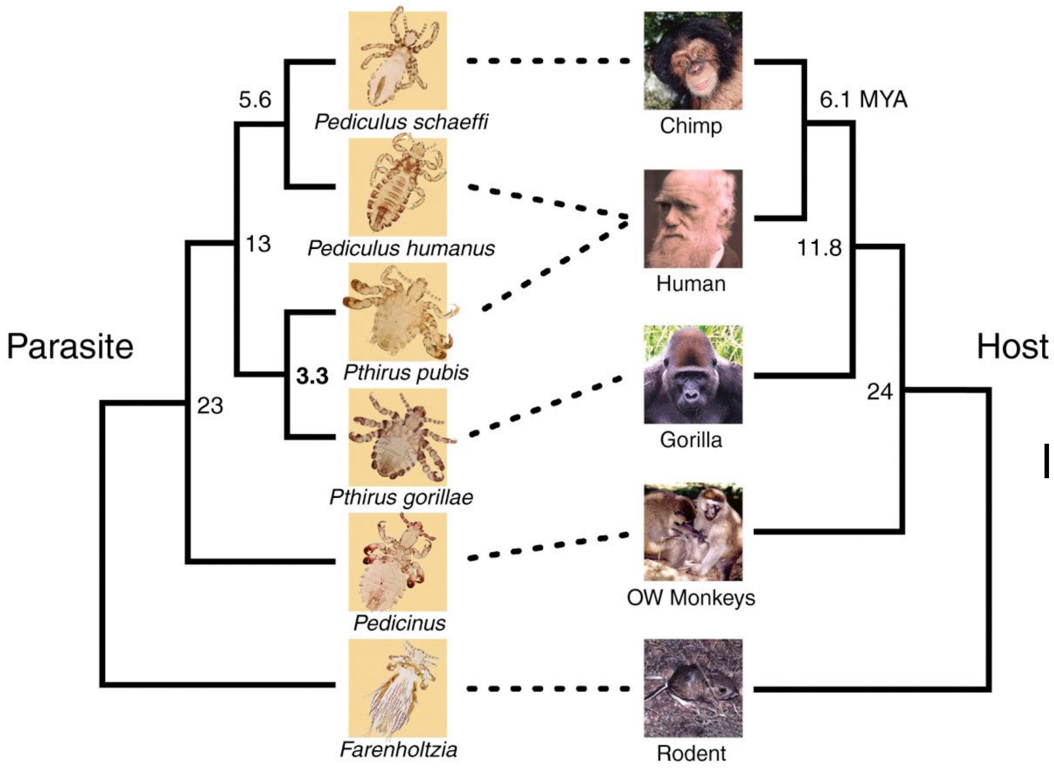
Host-shift speciations, resulting in incongruent phylogenies.

Cospeciation together with intra-host speciation and extinctions, resulting in incongruent phylogenies without any host shift

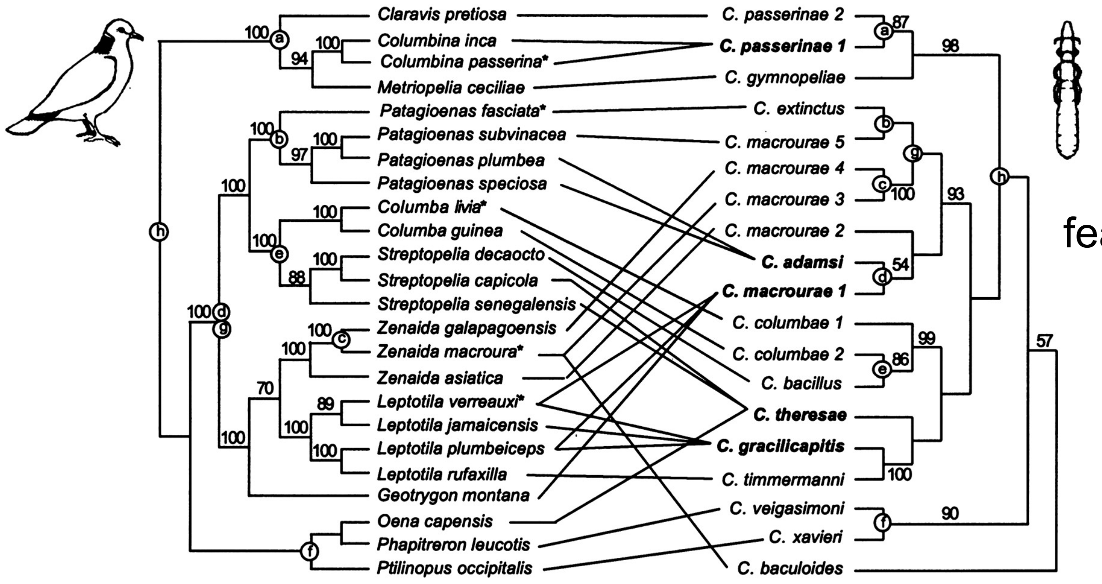


de Vienne et al., 2013, New Phytologist 198: 347

Host-parasite phylogenies

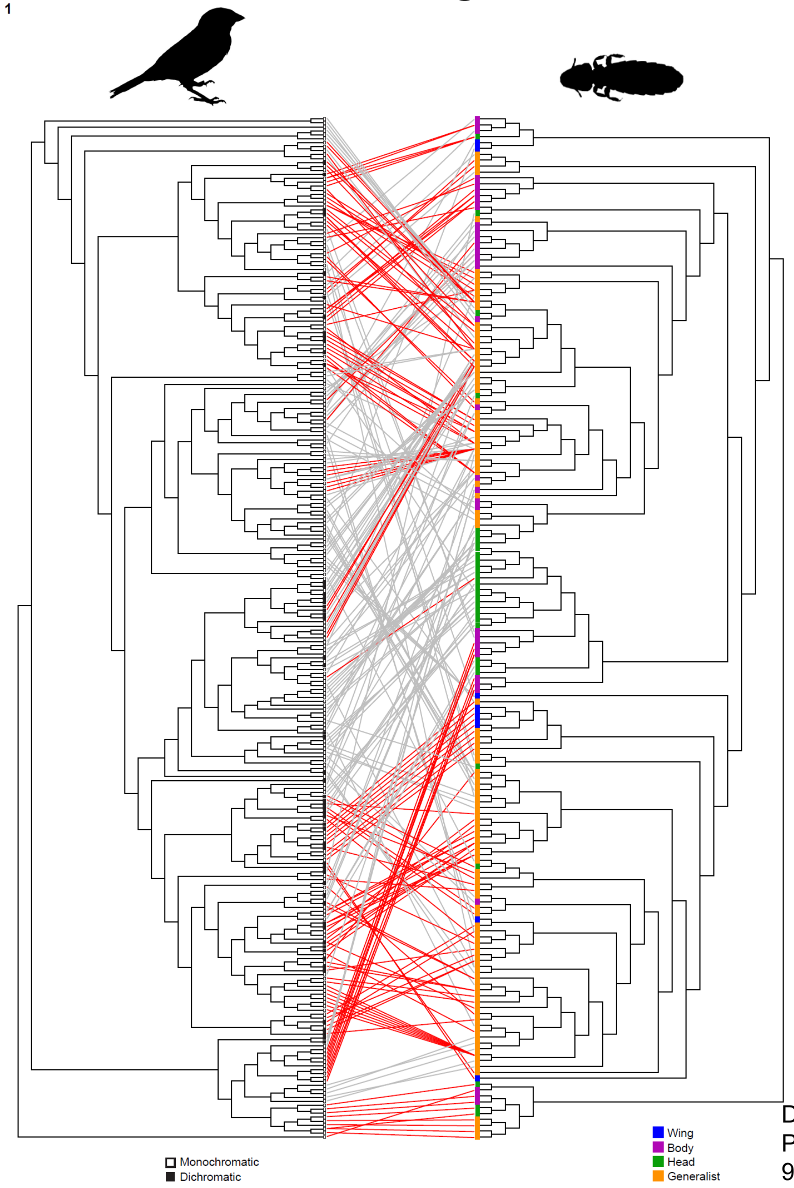


lice x mammals



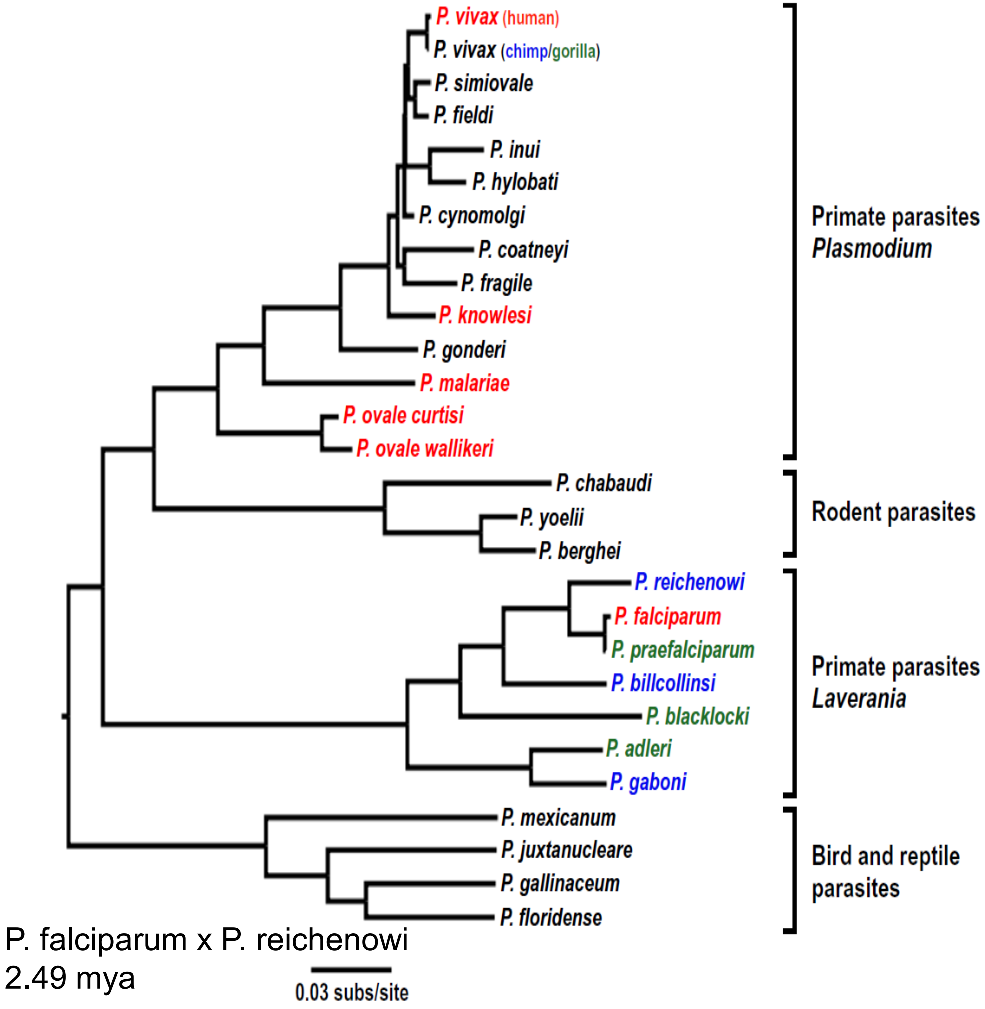
feather lice x pigeons

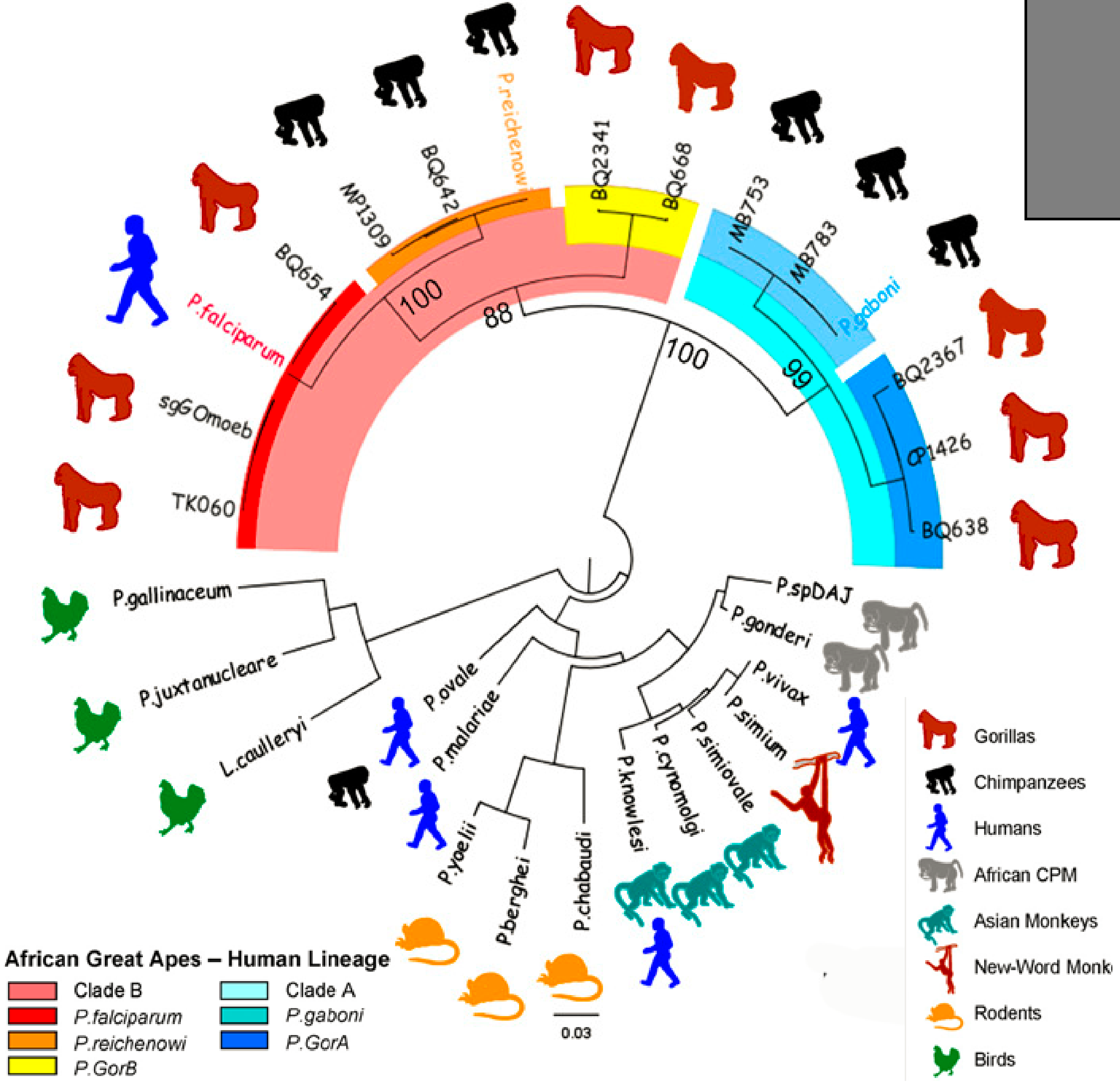
Brueelia feather lice and song birds



Sweet et al., 2918, Int. J. Parasit 48, 641-648

Dale H. Clayton et al. PNAS2003;100:26:156 94-15699





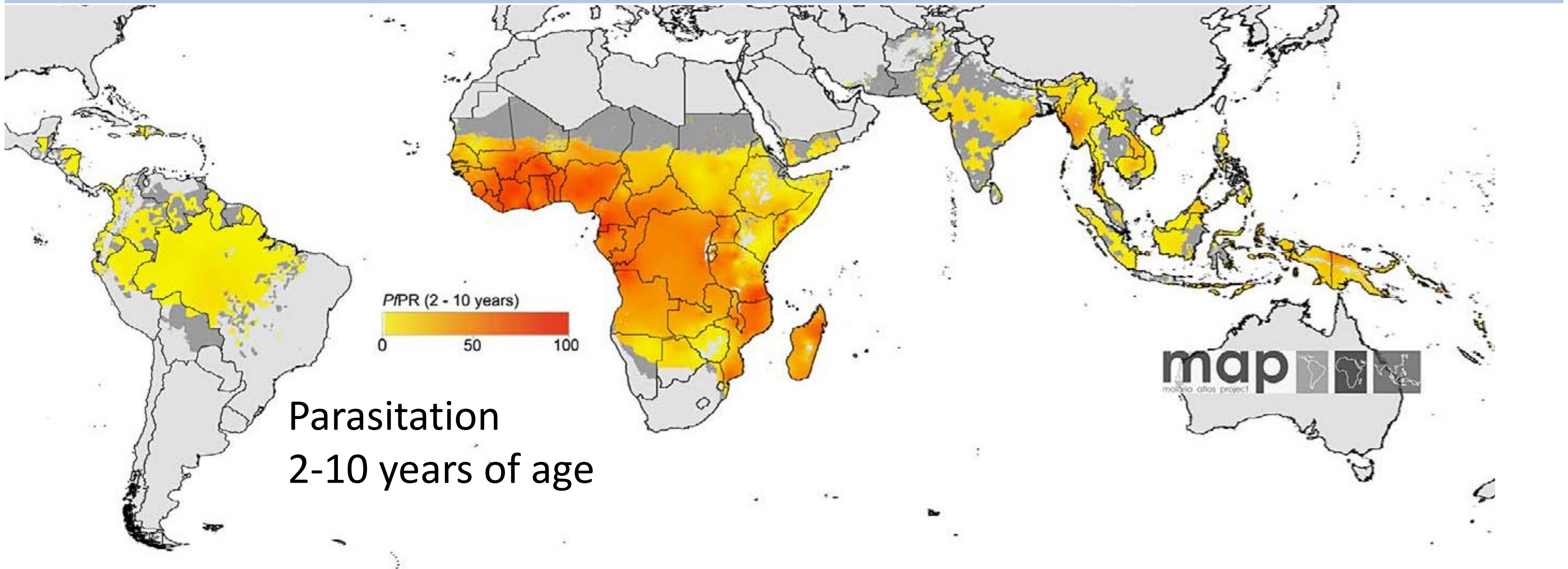
P. falciparum and P. vivax evolved from parasites infecting African apes.
P. falciparum from a recent cross-species transmission from gorilla
P. vivax emerged from parasites of chimpanzees, gorillas and humans

Loy, D.E., et al. Int. J. Parasitol. (2016), http://dx.doi.org/10.1016/j.ijpara.2016.05.008

Ricklefs, R. E., Outlaw, D.C. (2010).. SCIENCE 329: 226-229.

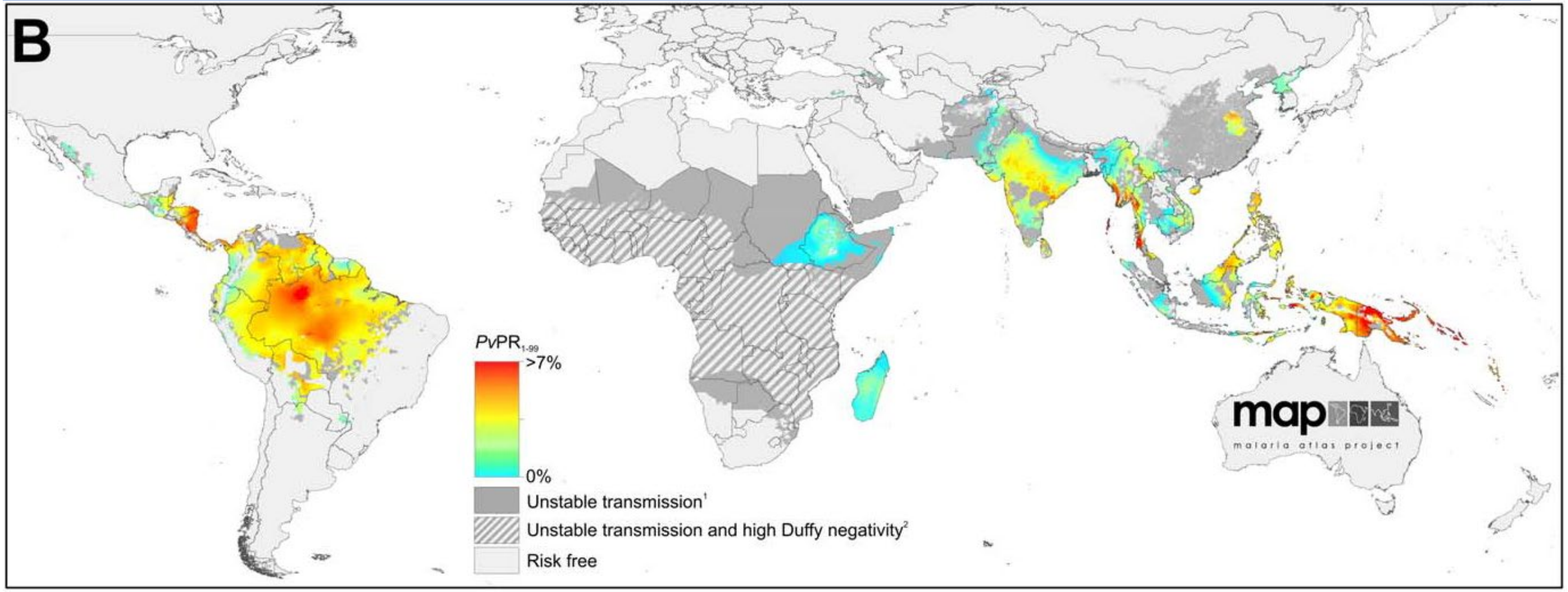
Prugnolle et al. 2010, PNAS 107: 1458–1463

Plasmodium falciparum malaria endemicity



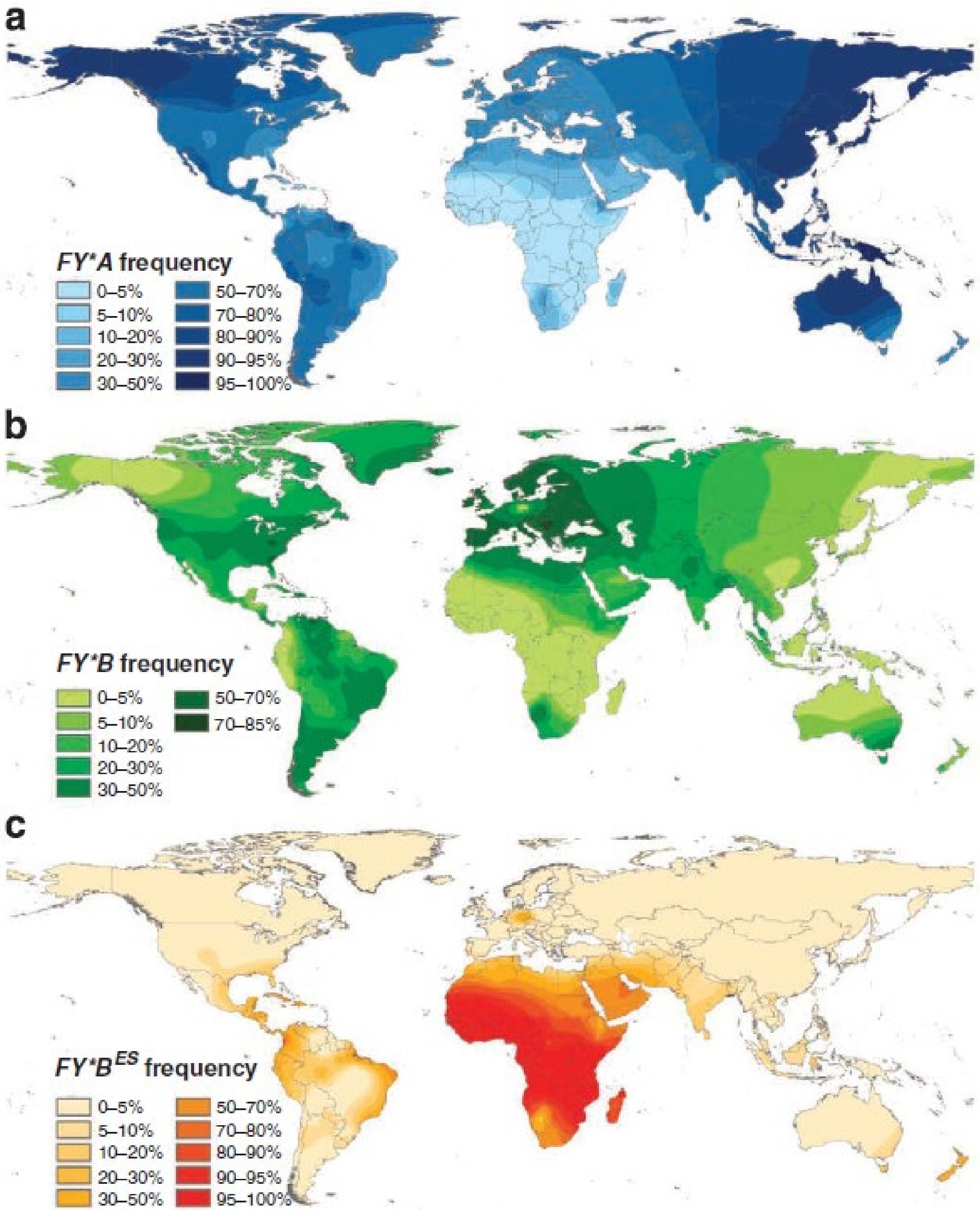
Parasitation
2-10 years of age

Plasmodium vivax transmission: missing from most of Africa

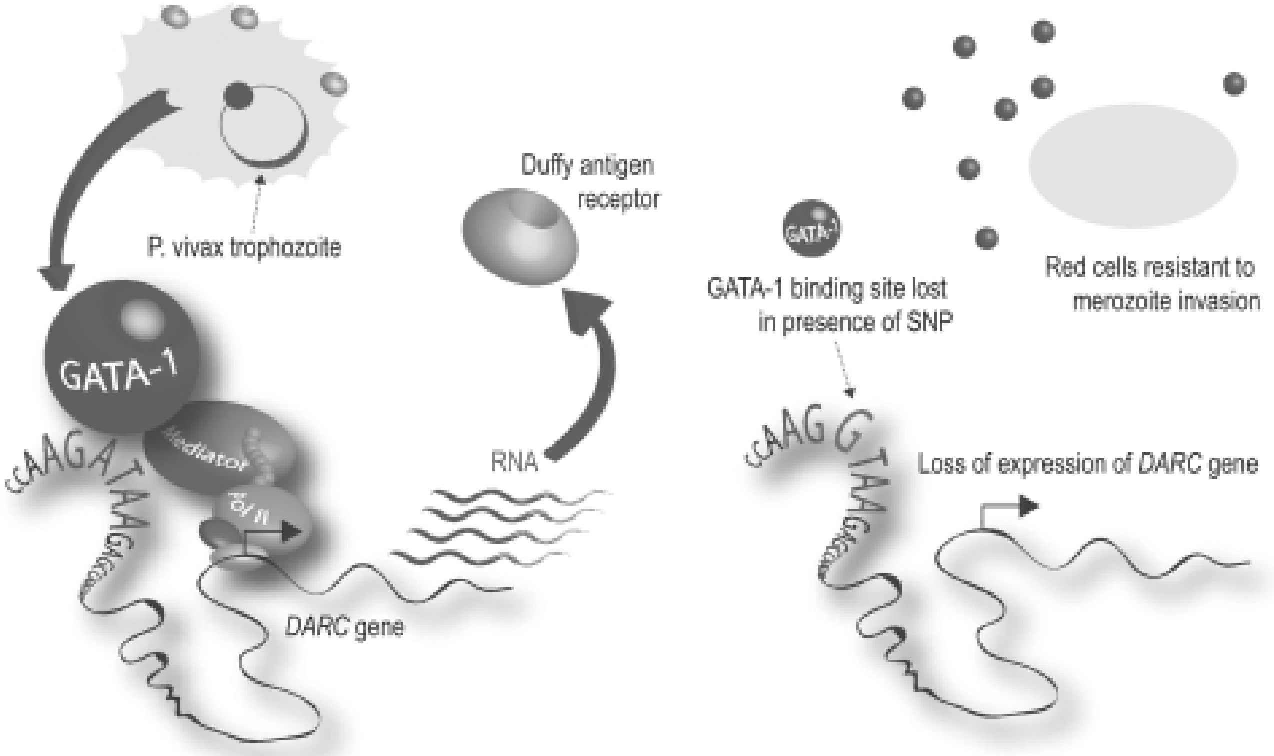


Hay et al. 2009, PLoS Medicine 6, e1000048

Gethink et al. 2012. PLOS Neglected Tropical Diseases 6, e1814



Plasmodium vivax invasion of erythrocytes is dependent on the surface receptor, the Duffy blood-group antigen (Fy) that has two alleles, Fy*A, Fy*B and also FY*B^{ES} alleles, the latter one resulting from a single-point mutation and protecting from vivax.



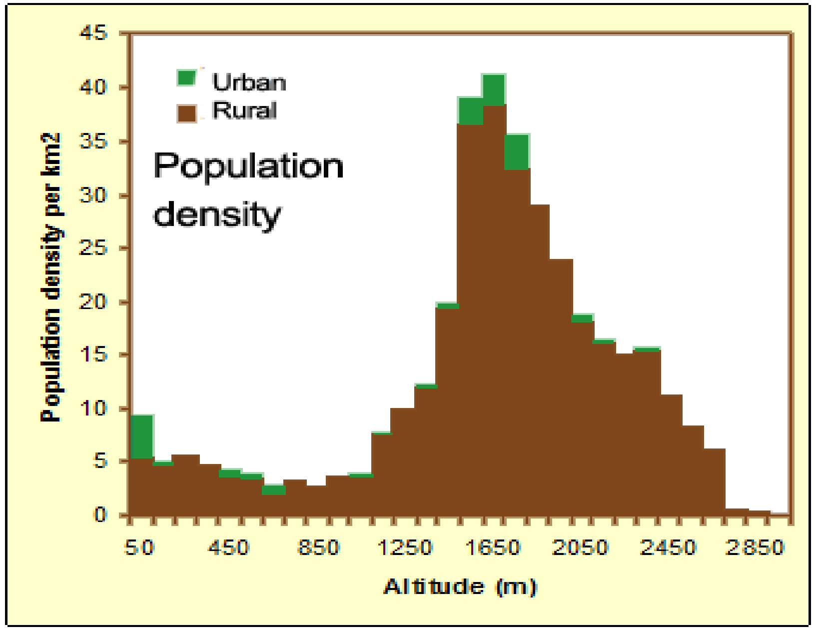
Howes et al. 2011, Nature Communication 2:266 King et al. PNAS 2011, 108:20113

Malaria: an important factor in human evolution

Common Erythrocyte Variants That Affect Resistance to Malaria

Gene	Protein	Function
FY	Duffy antigen	Chemokine receptor
G6PD	Glucose-6-phosphatase dehydogenase	Enzyme that protects against oxidative stress
GYPA	Glycophorin A	Sialoglycoprotein
GYPB	Glycophorin B	Sialoglycoprotein
GYPC	Glycophorin C	Sialoglycoprotein
HBA	α-Globin	Component of hemoglobin
HBB	β-Globin	Component of hemoglobin
HP	Haptoglobin	Hemoglobin-binding protein present in plasma (not erythrocyte)
SCL4A1	CD233, erythrocyte band 3 protein	Chloride/bicarbonate exchanger

- 0–53% population in NG lowlands
- 10% of lowland populations, protects against malaria.
- up to 90% in lowlands, only 5% in mountains. Protects against severe malaria, but increases chances of mild infection, particularly in children.
- relatively harmful, up to 10% in some lowlands
- mild protection against malaria, total protection against cerebral malaria, homozygotes not viable



New Guinea: malaria keeps low population density in the lowlands

Am. J. Hum. Genet. 77:171–192, 2005

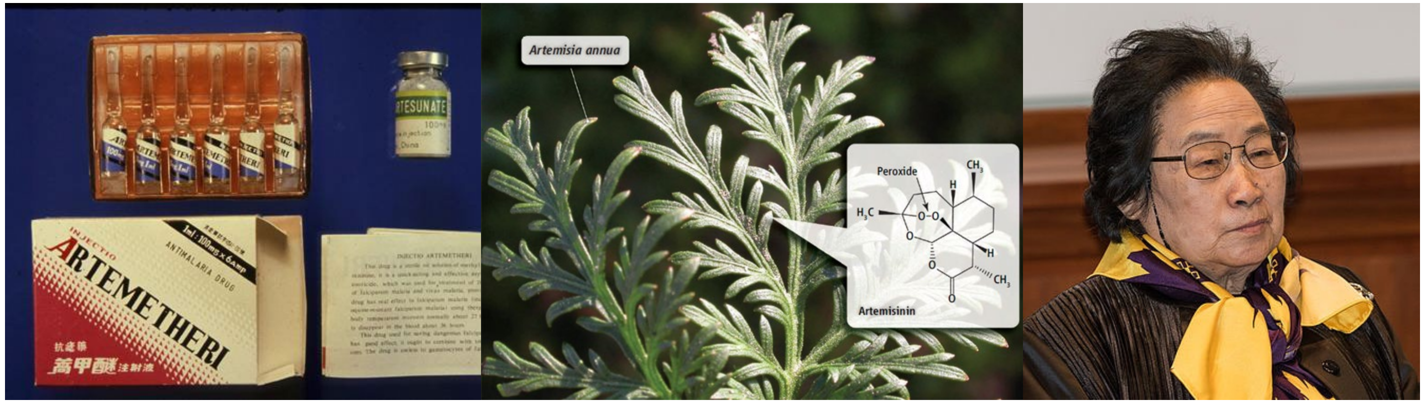
REVIEW ARTICLE
How Malaria Has Affected the Human Genome and What Human Genetics Can Teach Us about Malaria

Two key anti-malarials tied to the US – Vietnam war

USA – Vietnam war

1967 Hi Chi Minh asks Mao to develop an antimalarial drug for Viet Cong troops

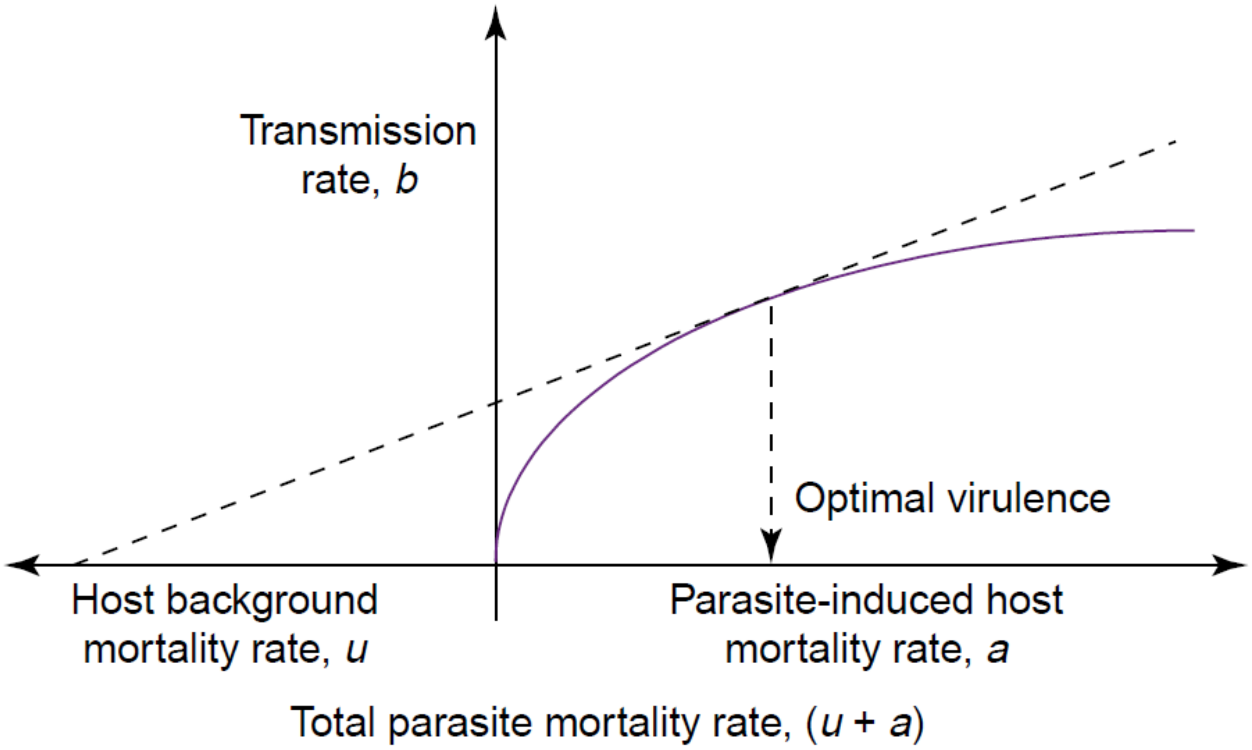
US Government asks the Walter Reed Institute for antimalarial for the troops



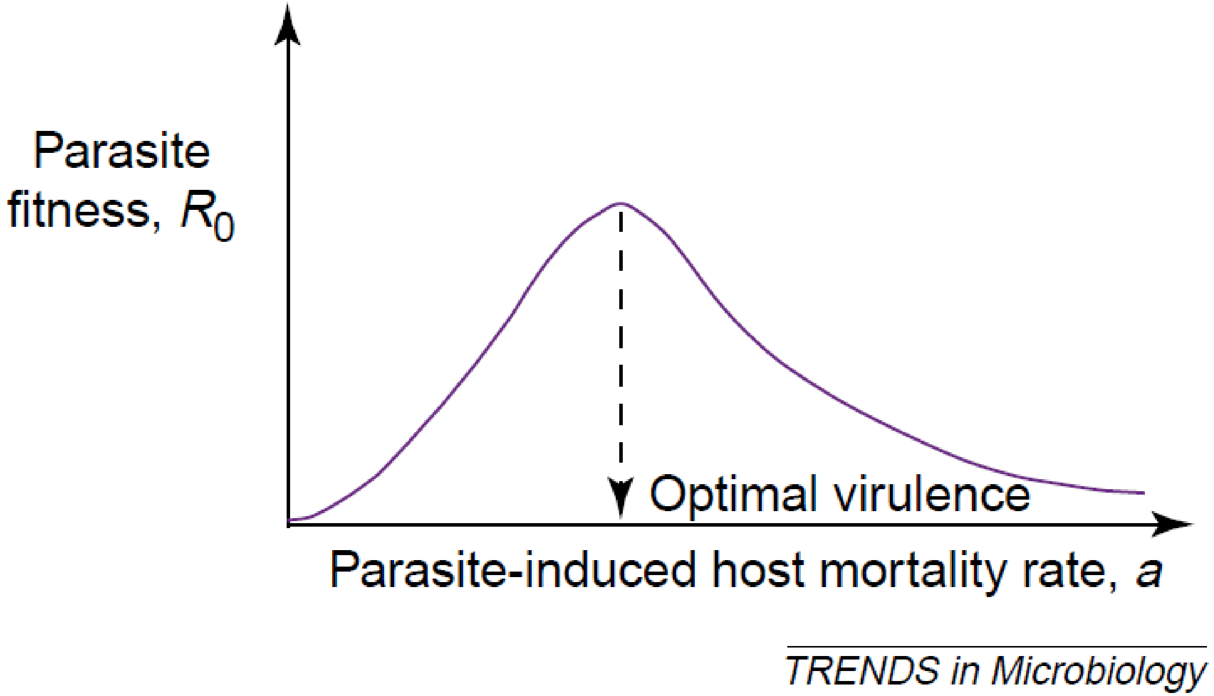
China tested 300 plant species used traditionally against fever and developed Artemether from *Artemisia annua*
2015: Dr Tu Youyou gets Nobel

USA tested 200,000 random compounds and developed Lariam based on the compound no. 142,490
No longer in use, made people crazy

Ability of parasite infect new hosts (infectivity) and negative effect of parasite on its host (virulence) are correlated

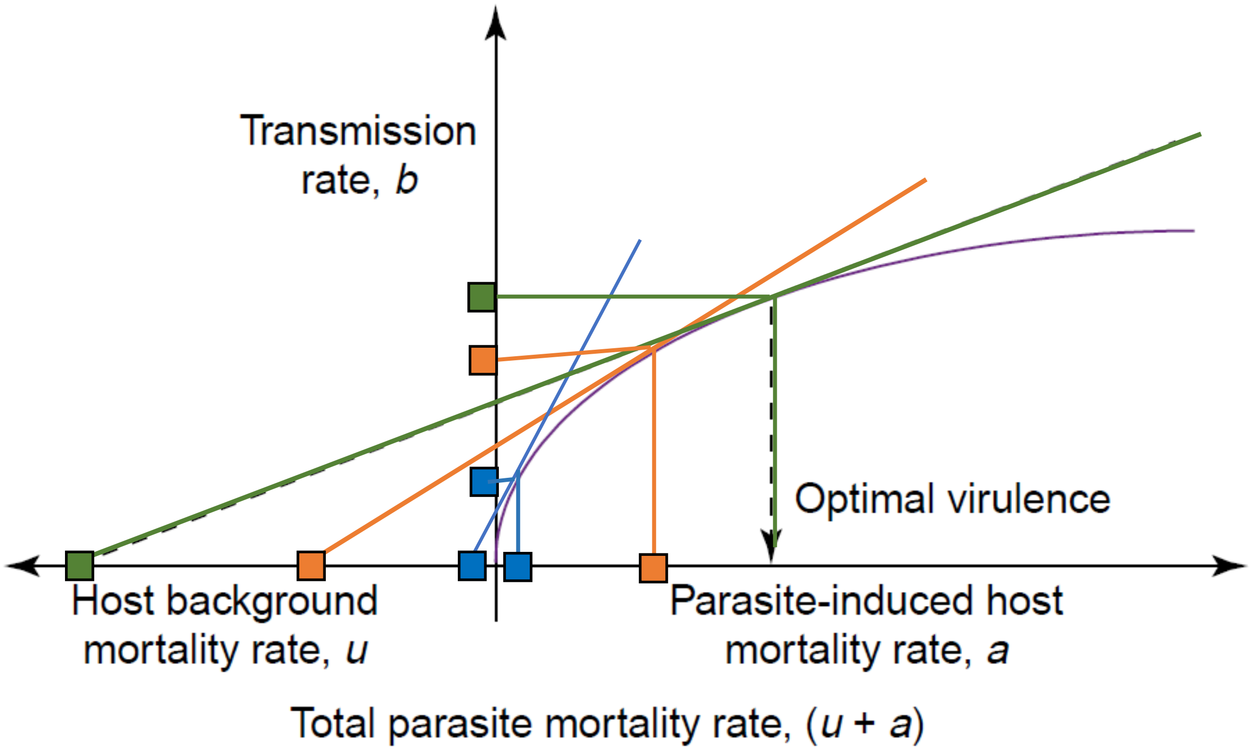


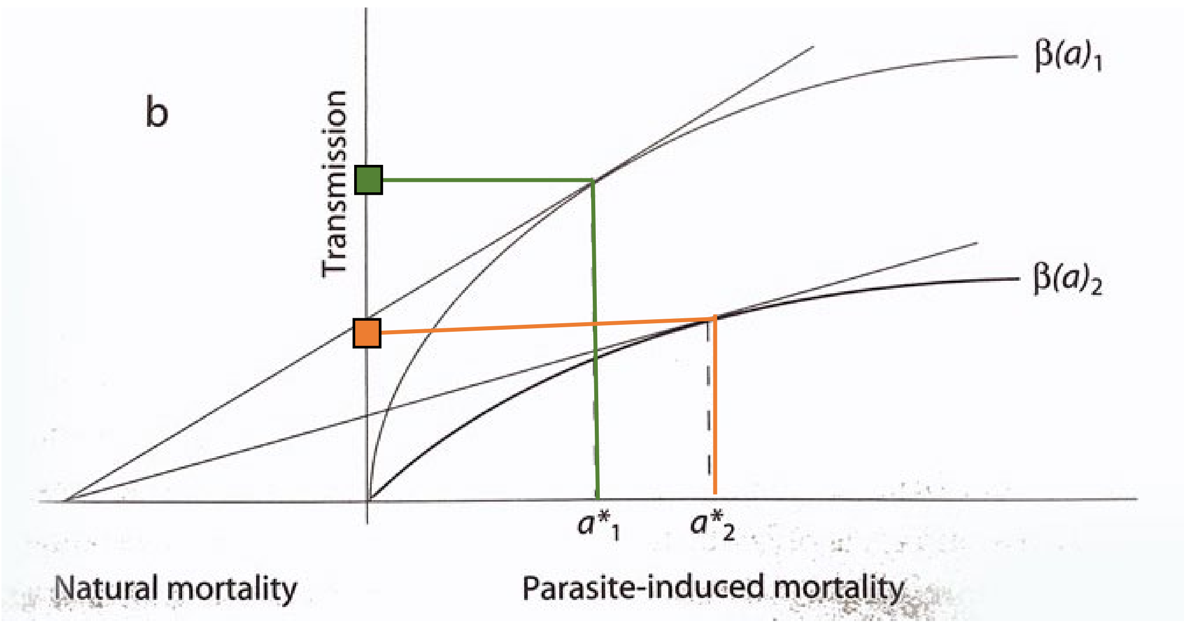
The trade-off model for the evolution of virulence



$$R_0 = b/(u+a)$$ maximum transmission rate to mortality ratio

Ability of parasite infect new hosts (infectivity)
and negative effect of parasite on its host (virulence) are correlated

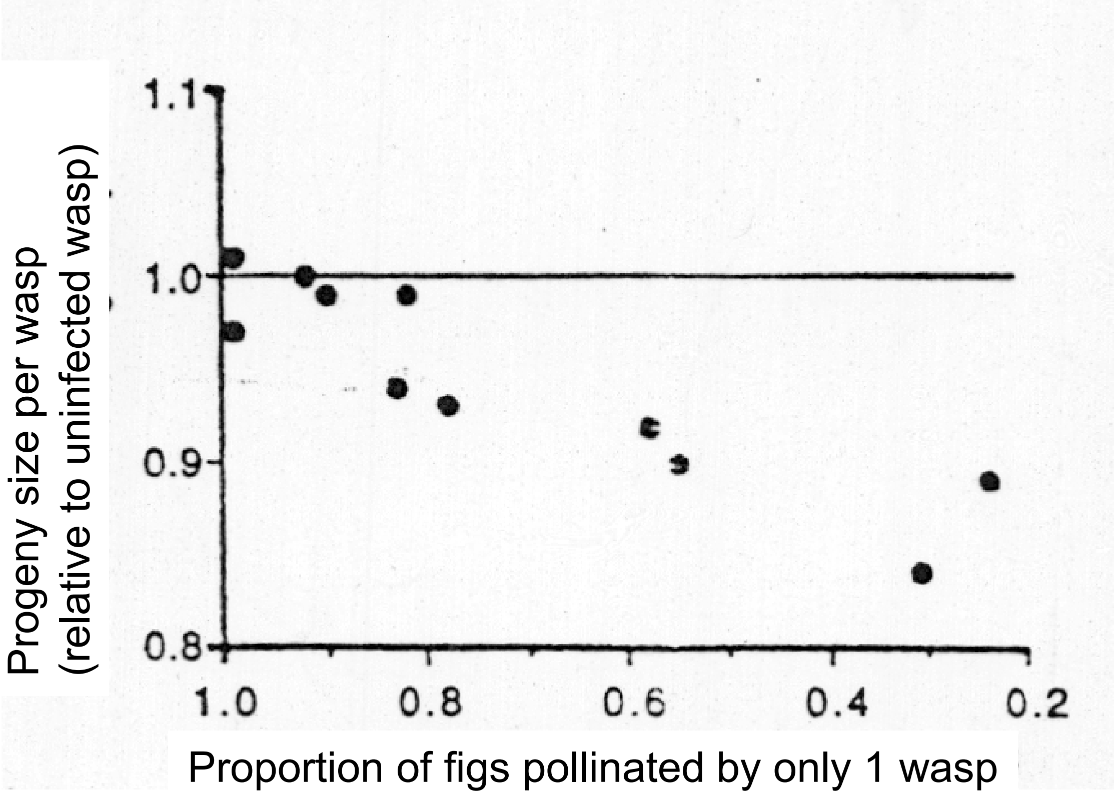




$$R_0 = b/(u+a)$$

Why hospitals are dangerous places: high pathogen-independent mortality rate selects for virulent pathogens than maximise transmission rate even at the expense of high pathogen-induced mortality of their host

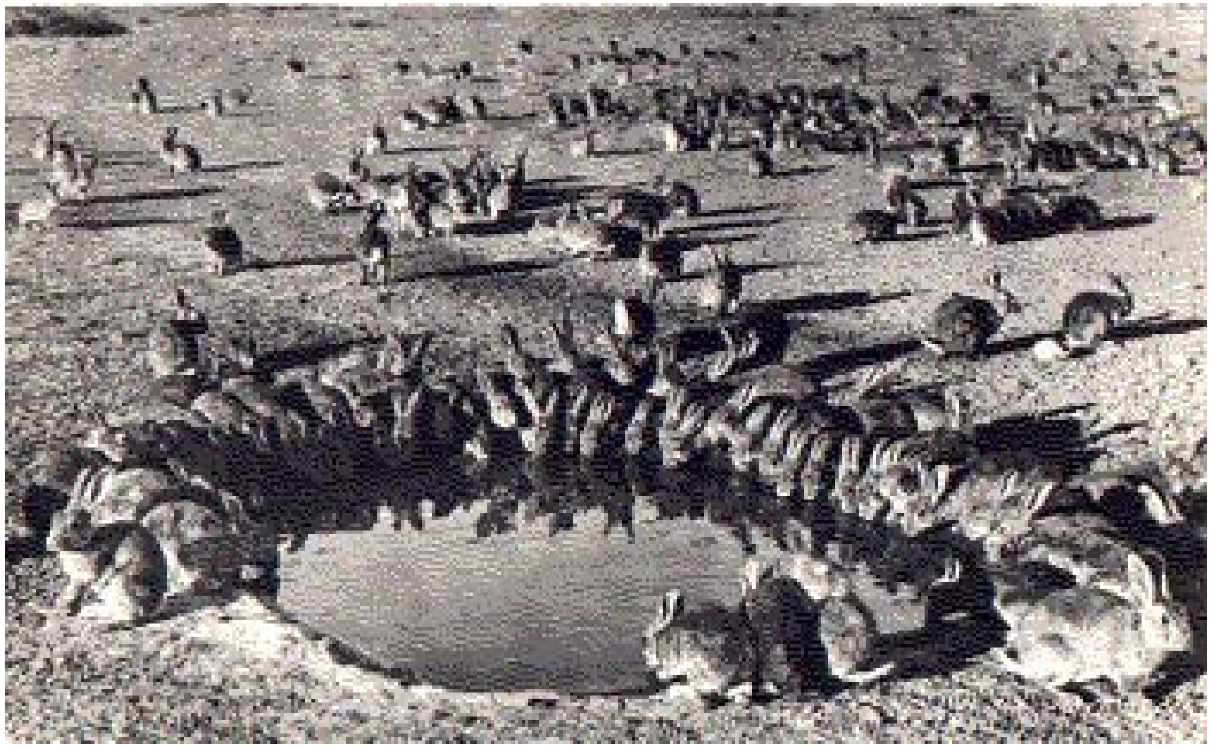
Virulence decreases with the intensity of transfer of parasite from hosts to their progeny (vertical transfer) relative to transfer among unrelated individuals (horizontal transfer)



Figs are pollinated by fig wasps. They enter into a fig, pollinate flowers lay eggs, and die. Eggs hatch into larvae, they develop in adults - wingless males and winged females; they mate, males die, females collect pollen and leave to search for another fig. Parasitic nematodes are transferred from the female to the next generation of fig wasps developing within the fig.

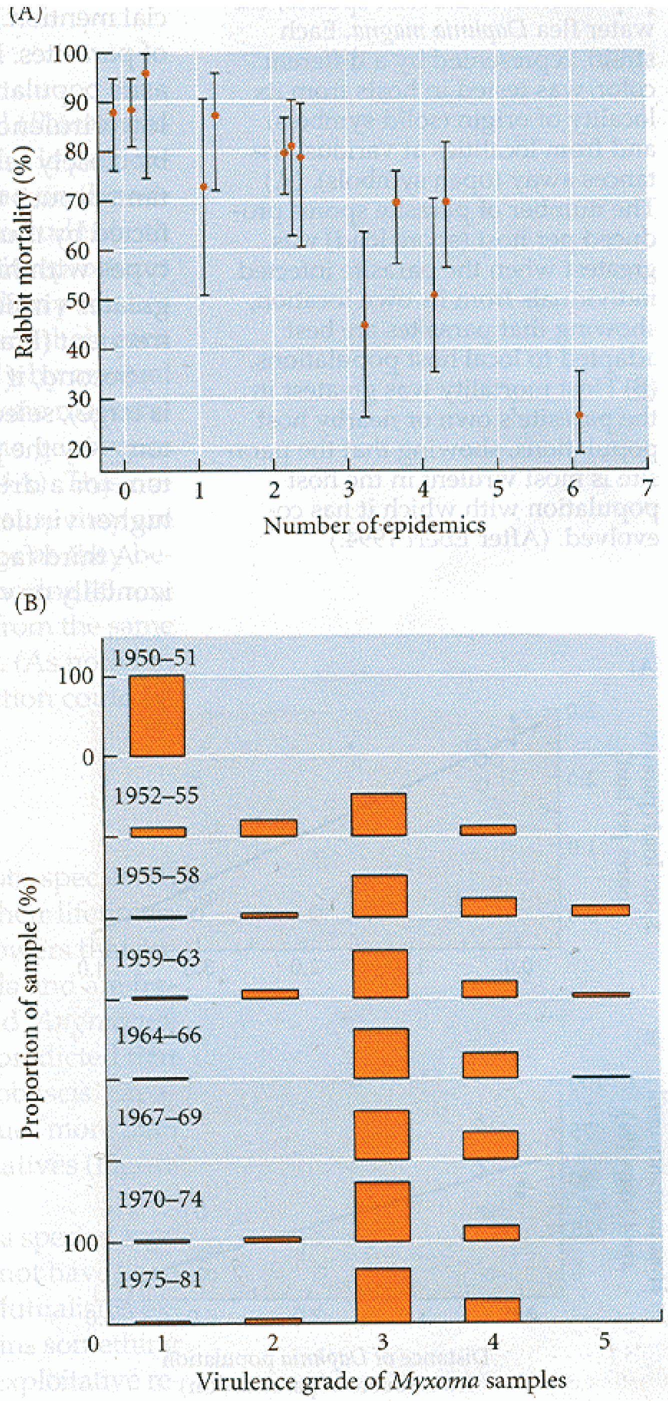
Fig. 1. Relation between virulence, measured as the lifetime reproductive success of nematode-infected relative to uninfected female fig wasps, and the proportion of multifoundress broods encountered in 11 Panamanian species. Increased incidence of multifoundress broods provides increased opportunities for nematode transmission. Those species of wasp characterized by increased opportunities for transmission of their species-specific parasitic nematodes contain more virulent species of nematodes. All statistical tests indicate a significant relation [$P < 0.001$ (*22*)].

Evolution of virulence

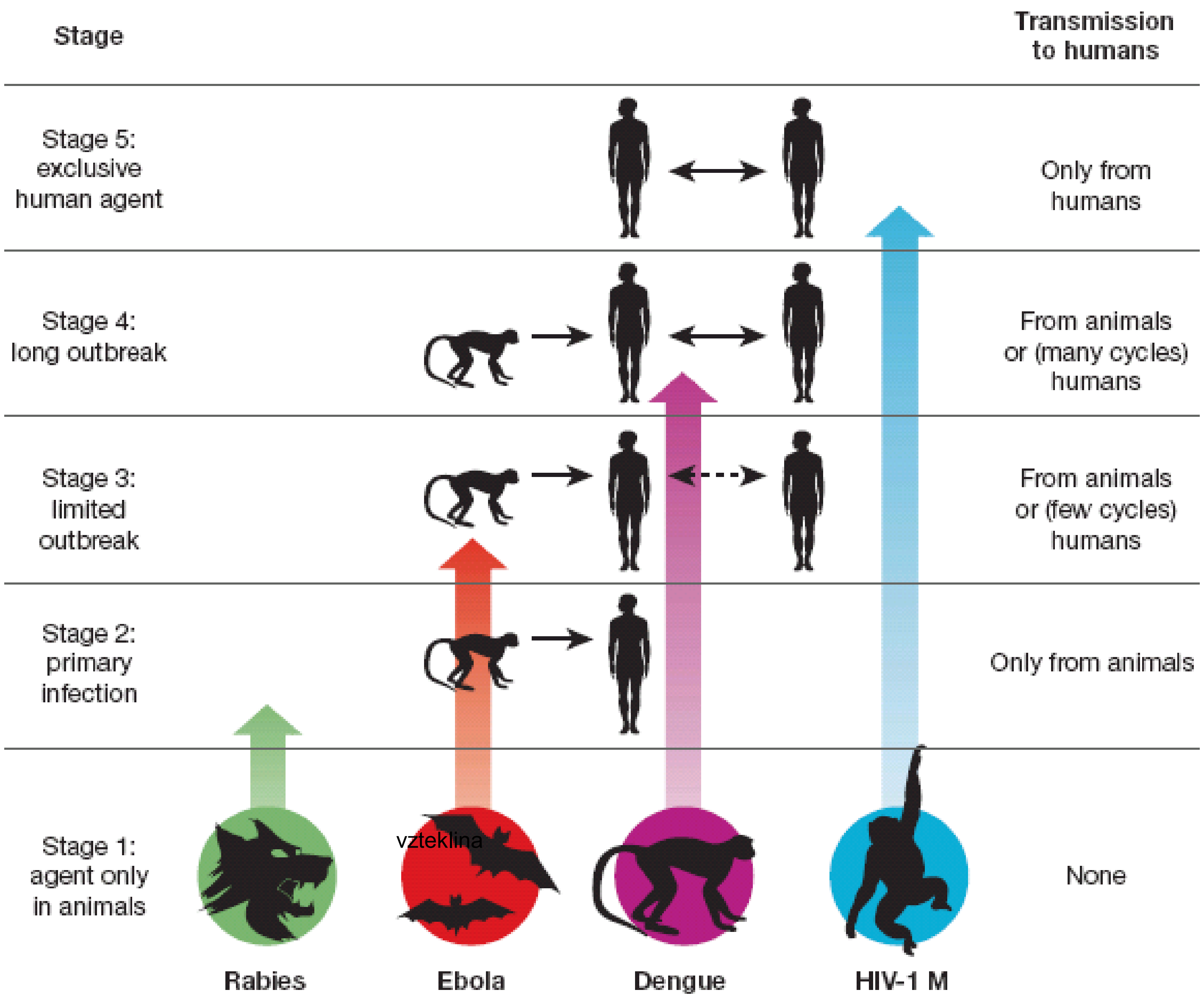


Virulence of species transmitted by a vector (malaria, Anopheles mosquitoes) tends to be higher than in species transmitted by direct contact among hosts (myxomatosis, rabbits).

Myxomatosis, introduced to Australia to control rabbits, evolved steadily towards lower virulence.



Transfer of viral species on humans



circulation only among humans

transfer from animals to humans as well as among humans

transfer from animals to humans, and limited transfer among humans

transfer from animals to humans only

Wolfe et al. 2007. Nature 447: 279

Figure 1 | Illustration of the five stages through which pathogens of animals evolve to cause diseases confined to humans. (See Box 1 for

Parasites and pathogens

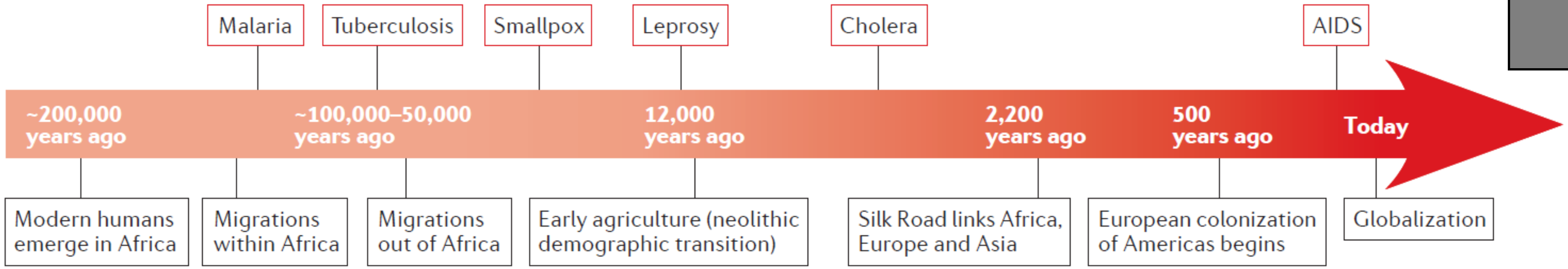
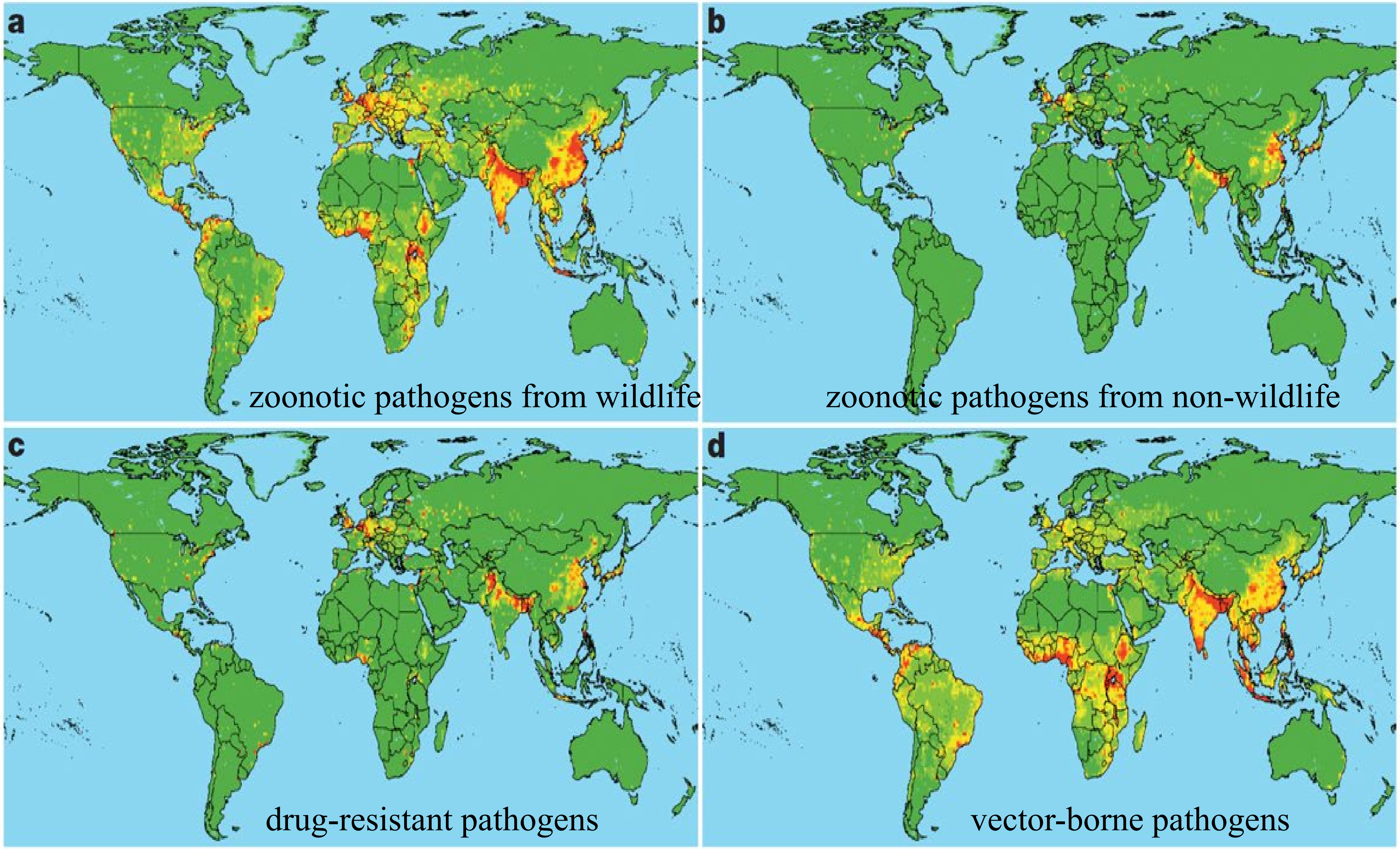


Table 1 | **Age and geographical origin of major human pathogens**

Pathogen	Disease	Pathogen type	Pathogen genome size (kb)	Place of origin	Approximate age of pathogen	Human mortality rate	Length of illness
Plasmodium falciparum	Malaria	Protozoa	24,000	Africa before human dispersal	>100,000 years	2–30% for severe malaria	Variable
Mycobacterium tuberculosis	Tuberculosis	Gram-positive bacteria	4,000	East Africa	40,000 years	10% develop active tuberculosis, of whom ~70% die	Years
Variola virus	Smallpox	DNA virus	186	East Asia or Africa	15,000–70,000 years	1–30%	Weeks
Mycobacterium leprae	Leprosy	Gram-positive bacteria	33,000	East Africa or the Middle East	>10,000 years	Not typically lethal, but chronic infection reduces fertility	Years
Vibrio cholerae	Cholera	Gram-negative bacteria	4,000	Ganges River Delta	>5,000 years	5–50%	Days
HIV-1	AIDS	Lentiviral type of retrovirus	9.2	West and Central Africa	<100 years	100% (without treatment)	Years

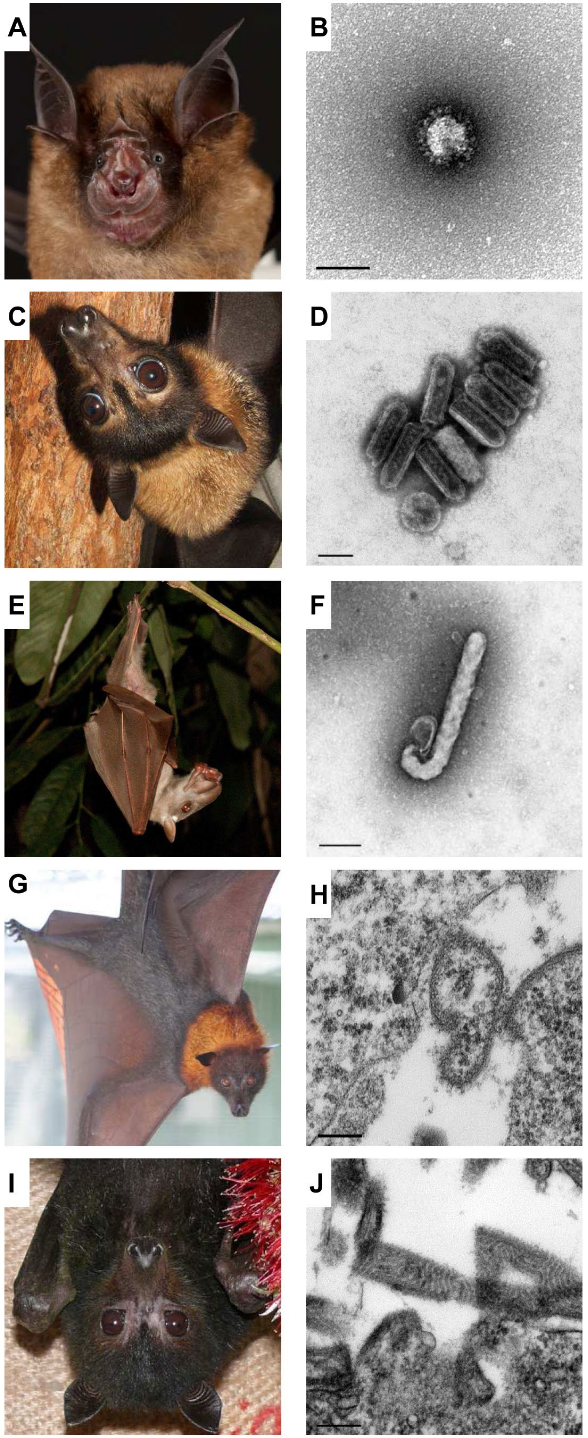
Karlsson et al. 2014
Nature Reviews Genetics

Emerging infectious diseases



Zoonotic viruses:
Bats 61 species
(1.8 per host species)
Rodents 68 species
(1.5 per host species)

Allen et al., NATURE COMM. 8: 1124 Jones et al. Nature 451, 990 Louis et al. 2012 Proc R Soc B 280: 20122753



The Chinese horseshoe bat (A; Rhinolophus sinicus) hosts SARS-like coronaviruses(B).

The spectacled flying fox (C; Pteropus conspicillatus) is reservoir for the lyssavirus (D).

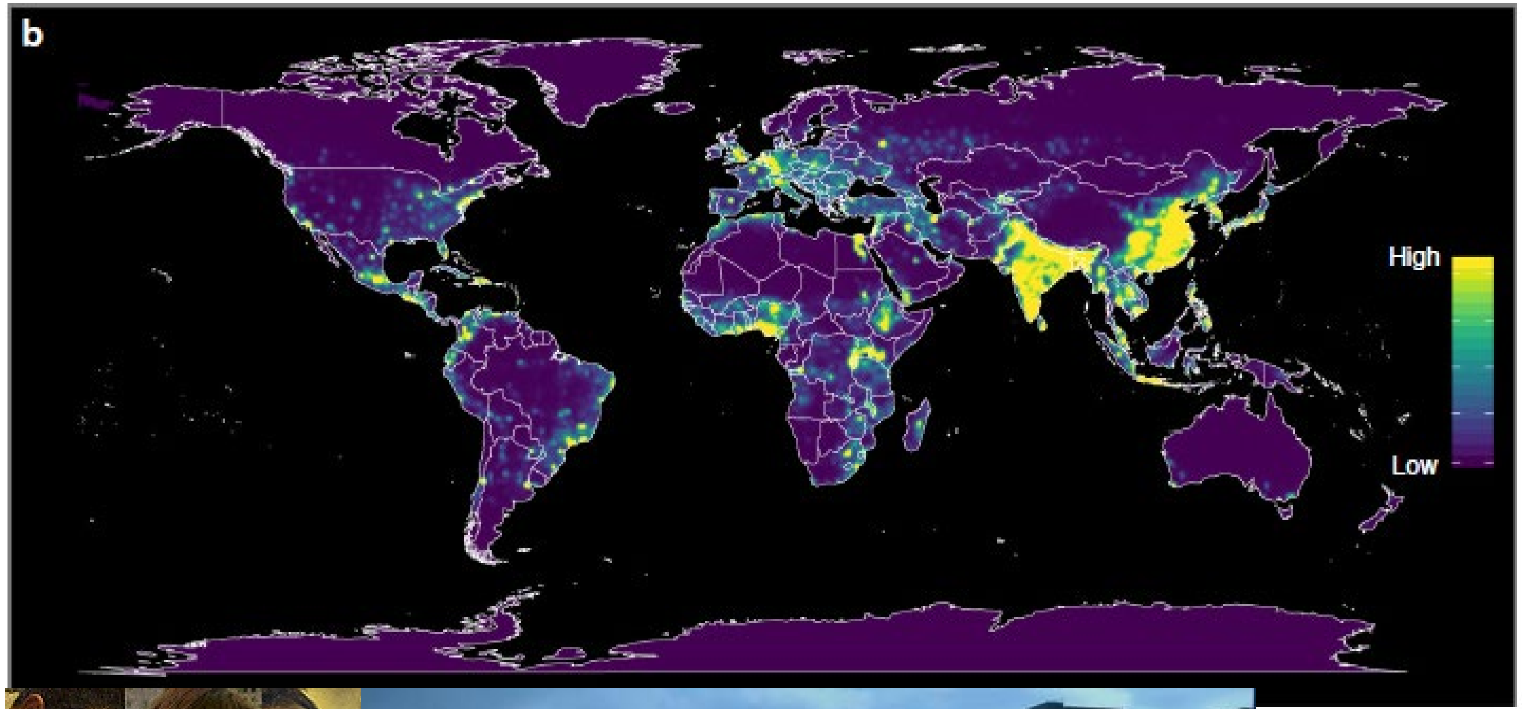
African fruit bats including Hypsignathus monstrosus (E) host Ebola virus (F).

The Malayan flying fox (G; Pteropus vampyrus) is the host of Nipah virus (H).

Pteropid Australian bat species including Pteropus alecto (I) carry Hendra virus (J).

Wynne JW, Wang LF (2013) Bats and Viruses: Friend or Foe? PLoS Pathog 9(10): e1003651. doi:10.1371/journal.ppat.1003651

Emerging infectious diseases

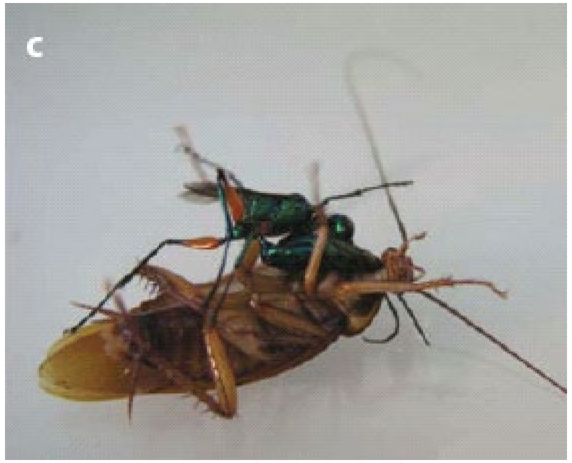


Probability of a new zoonotic infection

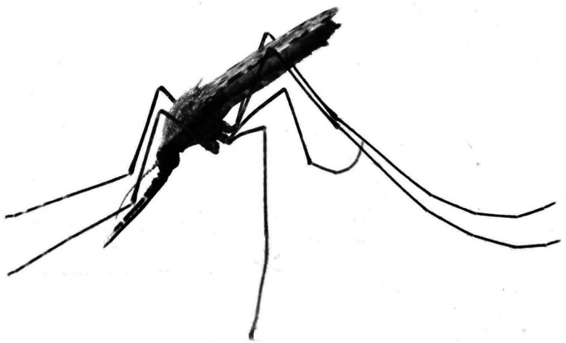
Allen et al., NATURE COMM. 8: 1124 Jones et al. Nature 451, 990

How parasites manipulate their hosts

Ant (*Camponotus*) infected by fungus (*Cordyceps unilateralis*) dies with its mandibles locked onto a plant, ensuring good conditions for the spread of fungal spores by wind



Cockroach (*Periplaneta americana*) is stung into head ganglion and paralysed by wasp (*Ampulex compressa*) so that it serves as a life storage of food for its larvae



Open access, freely available online PLoS BIOLOGY

Malaria Infection Increases Attractiveness of Humans to Mosquitoes

Renaud Lacroix[1], Wolfgang R. Mukabana[2], Louis Clement Gouagna[3¤], Jacob C. Koella[1*]

1 Laboratoire de Parasitologie Evolutive, Université P. and M. Curie, Paris, France, 2 Department of Zoology, University of Nairobi, Nairobi, Kenya, 3 Mbita Point Research and Training Centre, International Centre of Insect Physiology and Ecology, Mbita Point, Kenya

Cricket (*Nemobius sylvestris*) throws itself into water so that parasitic hairworm (*Tellinii spinochordodes*) can emerge from it.

Examples of fatal interactions between parasites and their insect hosts. (*a*) The *Camponotus* ant, mandibles locked onto a leafstalk, with *Hirsutella*, the anamorph of *Cordyceps unilateralis*, emerging from the cuticle (courtesy and copyright of L. Gilbert). (*b*) The hairworm *Tellinii spinochordodes* emerging from a host cricket, *Nemobius sylvestris*, after inducing suicidal behavior in the host (courtesy and copyright of F. Thomas). (*c*) The cockroach *Periplaneta americana* stung in the brain by *Ampulex compressa* (courtesy and copyright of R. Gal).

Manipulation of Host Behavior by Parasitic Insects and Insect Parasites

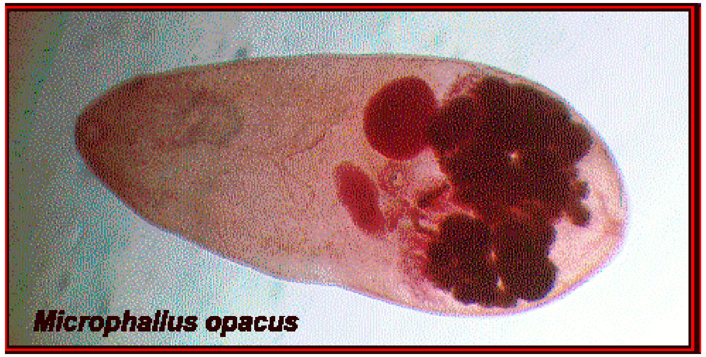
Frederic Libersat, Antonia Delago, and Ram Gal

Annual Review of Entomology, Annu. Rev. Entomol., ento, **2009**, 54 (189-207 • DOI: 10.1146/annurev.ento.54.110807.090556

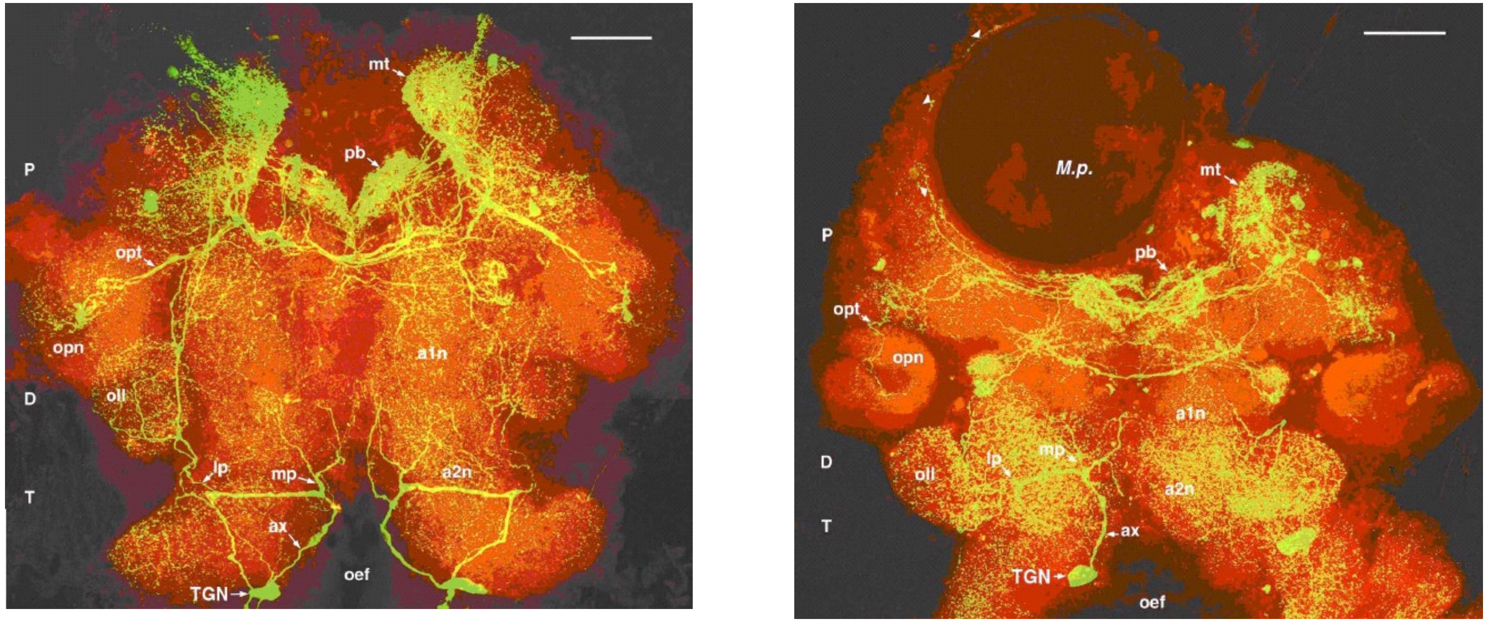
How parasites manipulate their hosts

Larvae (metacercaria) of fluke *Microphallus papillorobustus* encyst in head ganglion and abdomen of their intermediate host, copepod *Gammarus insensibilis*. Metacercaria in the head cause positive phototaxis in their host so that it swims towards the water surface where it is more likely to be eaten by water birds - the final host of the parasite. Metacercaria in the head are intensely attacked by the host and 17% of them are encapsulated and killed, while among the metacercaria in the abdomen only 1% are killed.

Gammarus insensibilis



Fluke *Microphallus*



Healthy brain of copepod *Gammarus insensibilis* (left)
and encysted fluke *Microphallus papillorobustus* (right)

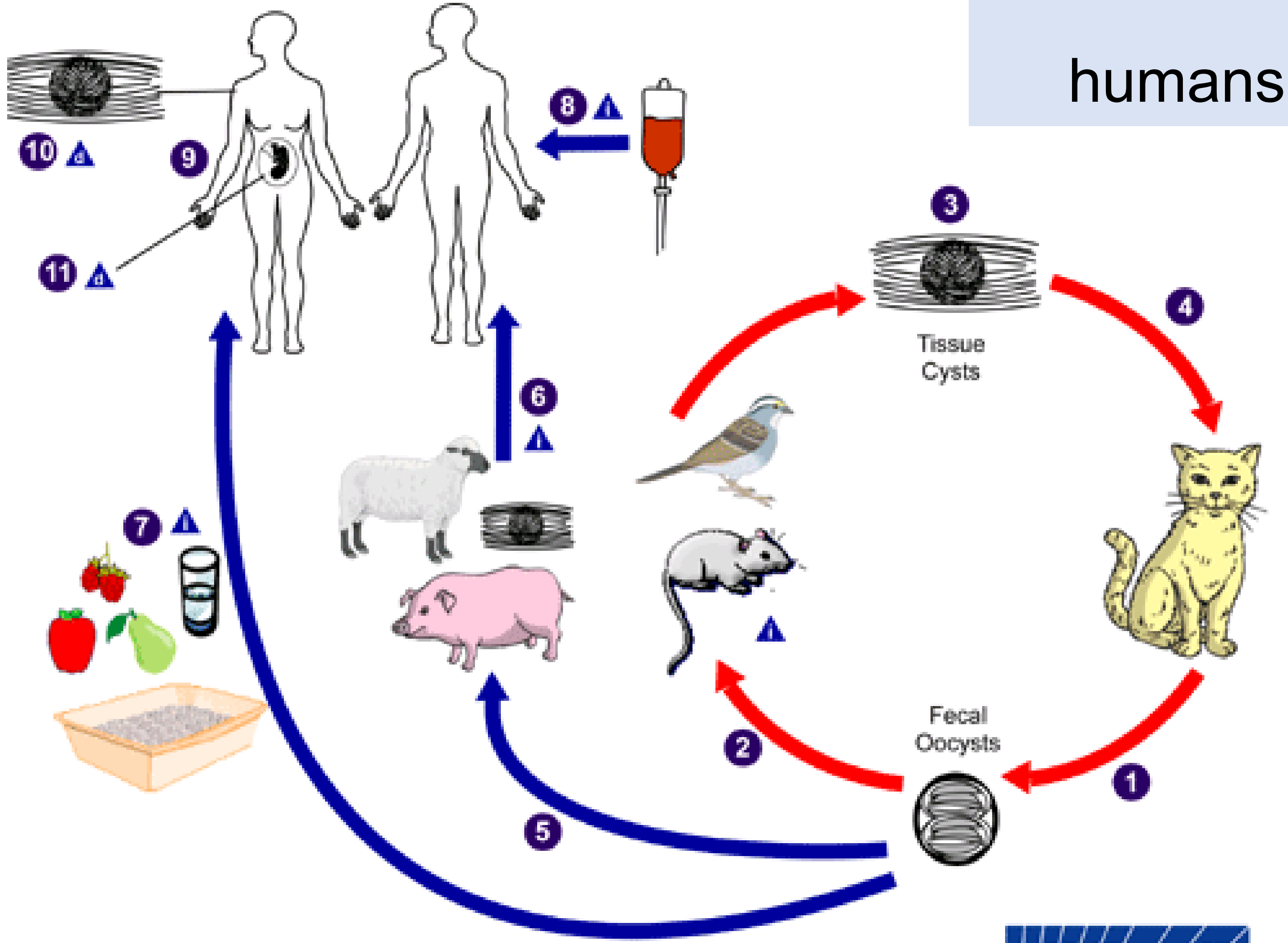
THE ROYAL SOCIETY
Received 8 October 2002
Accepted 6 November 2002
Published online 31 January 2003

Effects of *Microphallus papillorobustus* (Platyhelminthes: Trematoda) on serotonergic immunoreactivity and neuronal architecture in the brain of *Gammarus insensibilis* (Crustacea: Amphipoda)

S. Helluy[1*] and F. Thomas[2]

Figure 1. Brain of *G. insensibilis*. Montage of four stacks of 32 confocal scans showing immunoreactivity for serotonin (greer label) and synapsin (red outline of neuropils). Anterior is at the top. Abbreviations: ax, axon of TGN; a1n, antenna 1 neuropil; a2n, antenna 2 neuropil; D, deutocerebrum; lp, lateral projections of TGN; mp, medial projections of TGN; mt, medulla terminalis; oef, oesophageal foramen; oll, olfactory lobe; opn, optic neuropil; opt, optic tract; P, protocerebrum; pb protocerebral bridge; T, tritocerebrum; TGN, tritocerebral giant neuron. Scale bar, 100 μm.

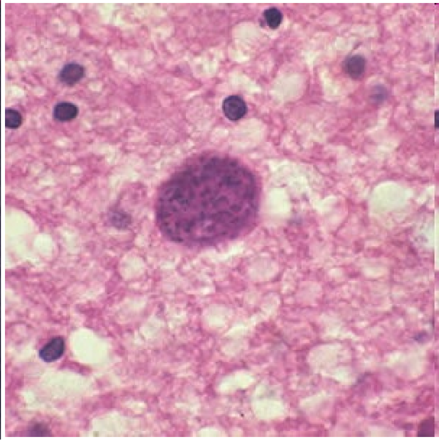
Toxoplasmosis:
humans are not the target hosts



CDC
SAFER·HEALTHIER·PEOPLE™
http://www.dpd.cdc.gov/dpdx

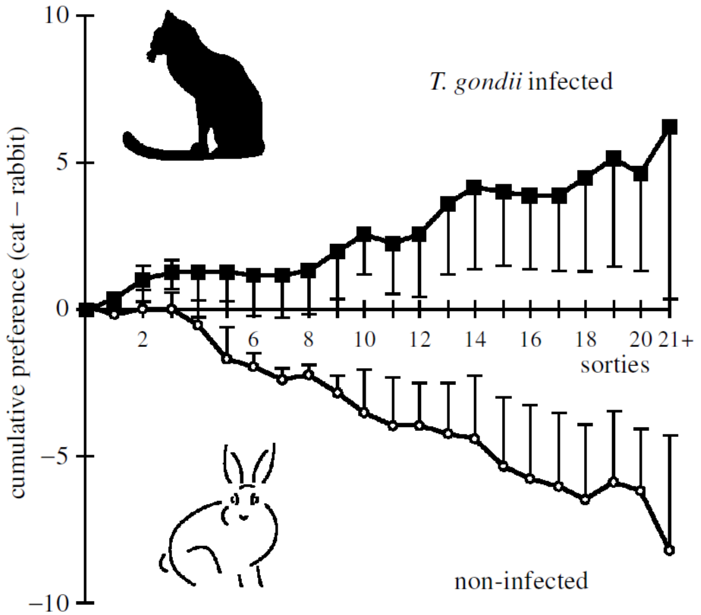
Toxoplasma gondii (Apicomplexa)

final hosts are cats, eggs (oocysts) are released in faeces, further develop in intermediate hosts (birds, rodents, pigs etc.) and encyst in their muscles, waiting to be eaten with their intermediate host by their final host, feline predators. Humans can get infected by oocysts from cat faeces, of cysts in meat.



How parasites manipulate their hosts

Toxoplasma manipulates behaviour of its intermediate hosts (mouse) so that they become more likely to be caught by a cats, its final host. Infected mouse become attracted to (instead of repelled by) the smell of cat urine and have longer reaction time to threats.



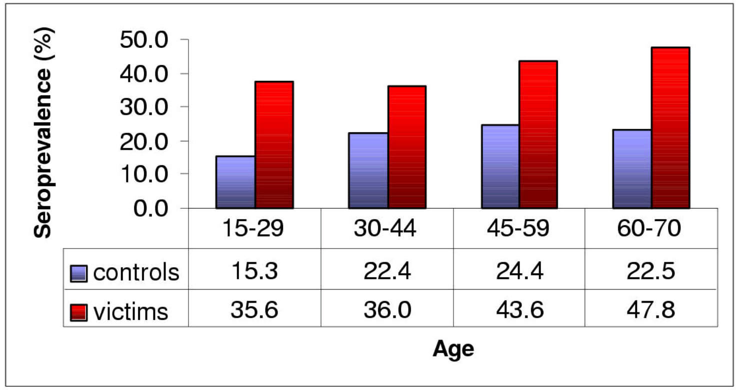
uninfected rats show avoidance of cat-scented area while *T. gondii*-infected rats exhibit a preference for predator-scented areas.

THE ROYAL SOCIETY

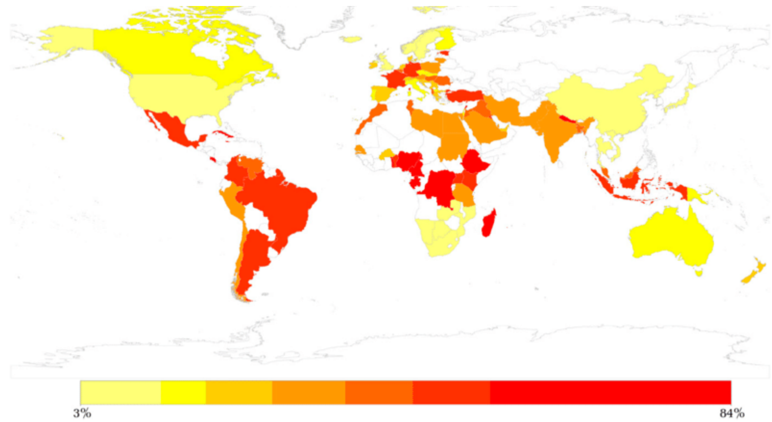
Fatal attraction in rats infected with *Toxoplasma gondii*

M. Berdoy[1,3*], J. P. Webster[2] and D. W. Macdonald[3]

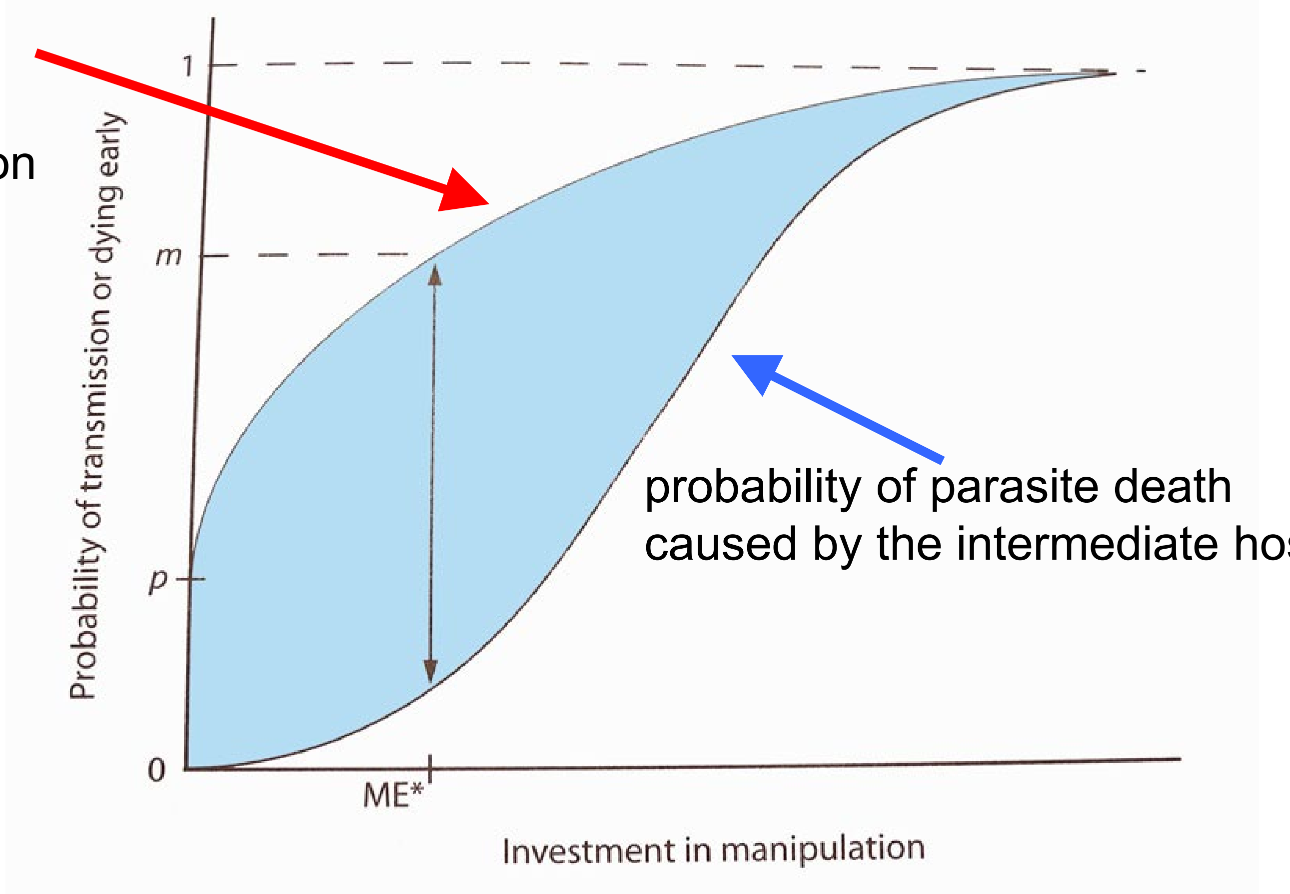
Flegr: people infected by Toxoplasma are more likely to be involved in traffic accidents - perhaps longer response time?



Global infection rate 30%



Manipulation of intermediate host increases the probability of transition to the final host, but also the probability that the parasite will be killed by the intermediate host, which defends itself against manipulation

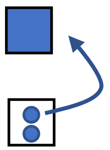


p = probability of transmission to the final host without manipulation
m = probability of transmission at optimum intensity of manipulation
ME = optimum investment by the parasite into host manipulation

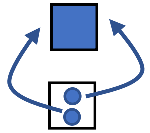
Inter-specific interactions between parasites and host manipulation

When intermediate host is infected by two parasites at the same time, they can be:

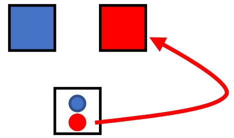
- species with the same final host, one of which manipulates the intermediate host, the other is passive but still benefits from the manipulation



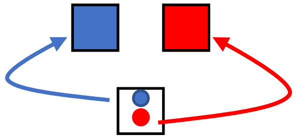
- species with the same final host, both (or none) of them manipulate the intermediate host



- species with different final hosts, one of them manipulates the intermediate host, the other is passive and suffers from the manipulation

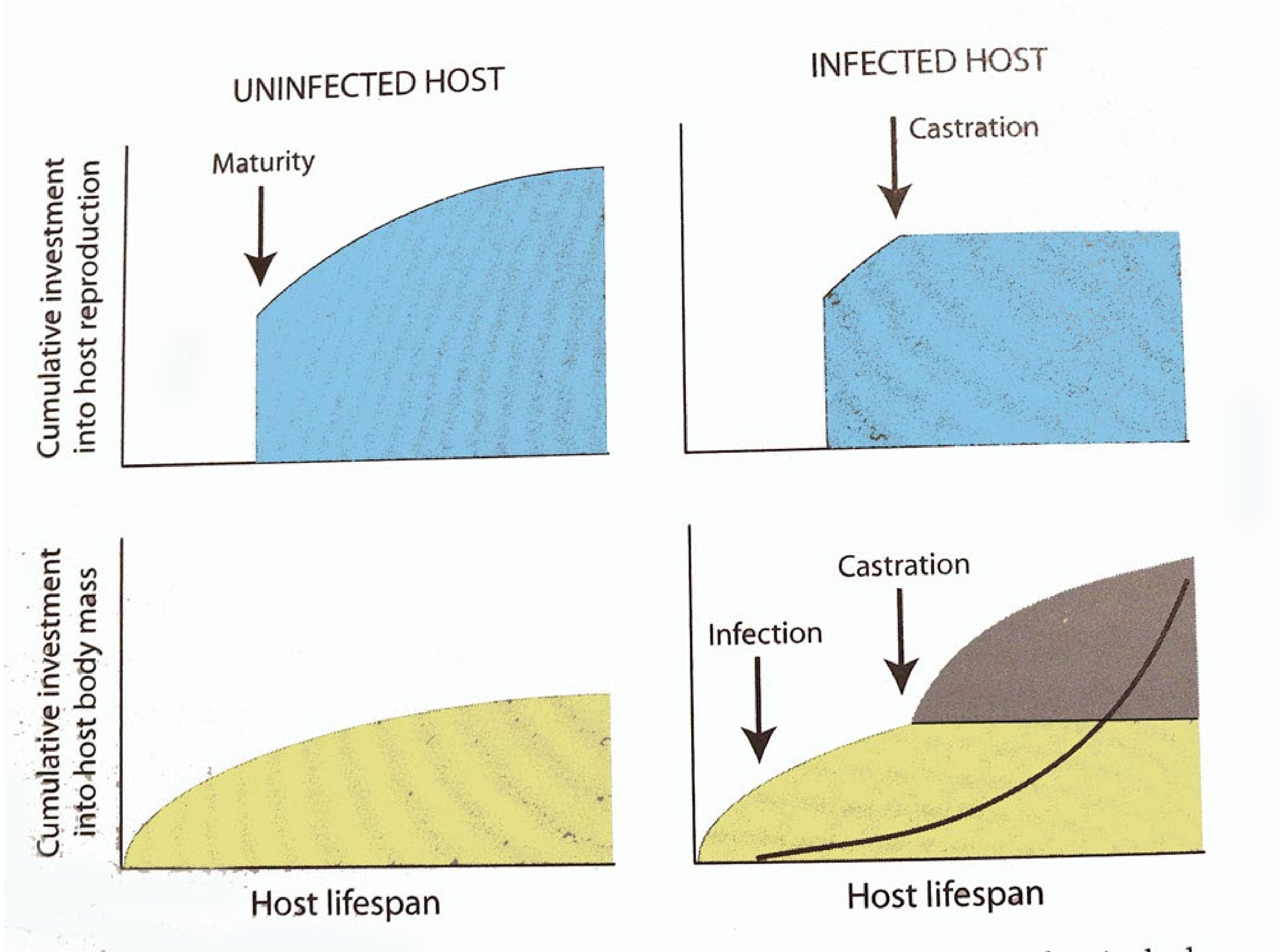


- species with different final hosts, both manipulate the intermediate host and thus compete one with the other for the final outcome



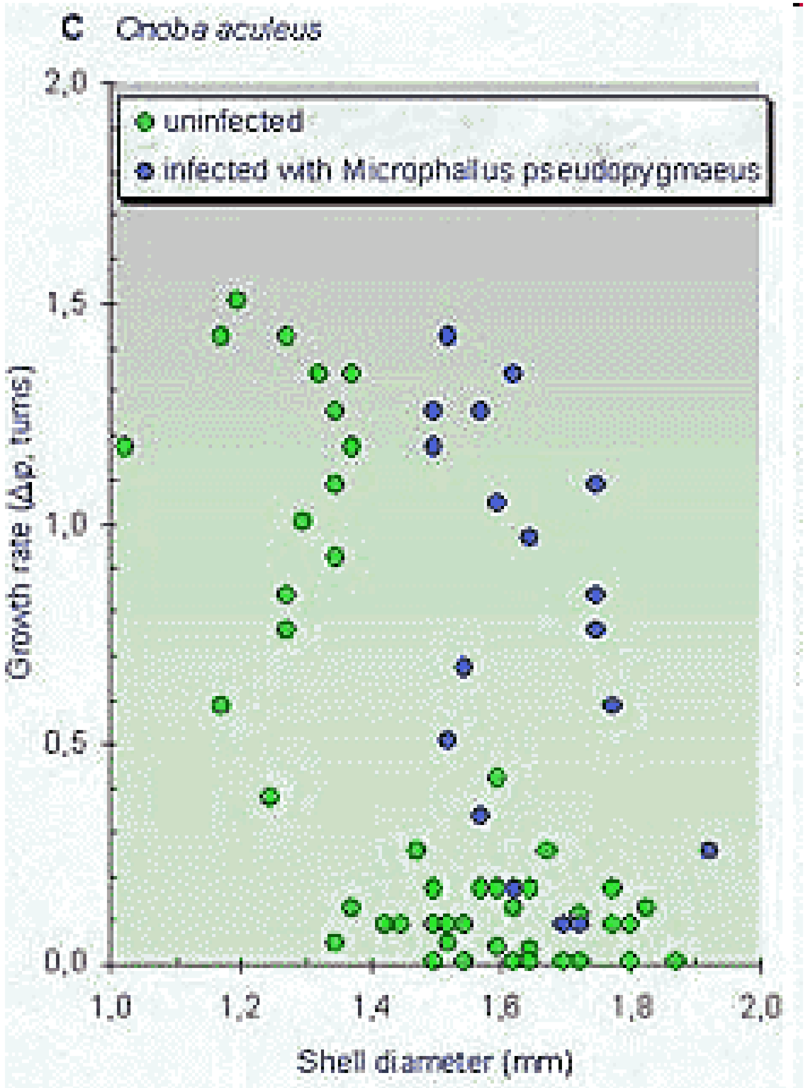
Why should parasites castrate their host?

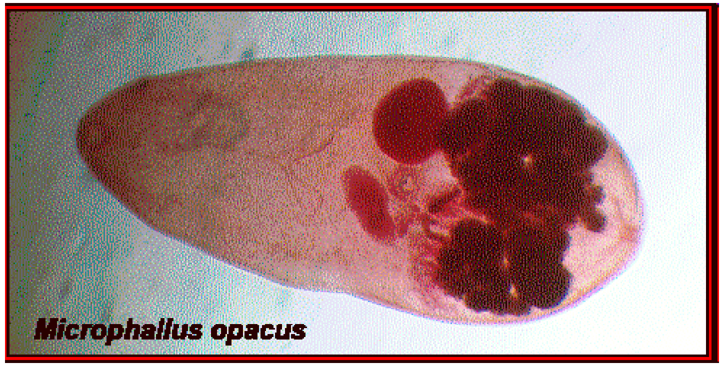
Castrated host no longer invests in reproduction, which means higher investment to its body, which is the parasite's resource

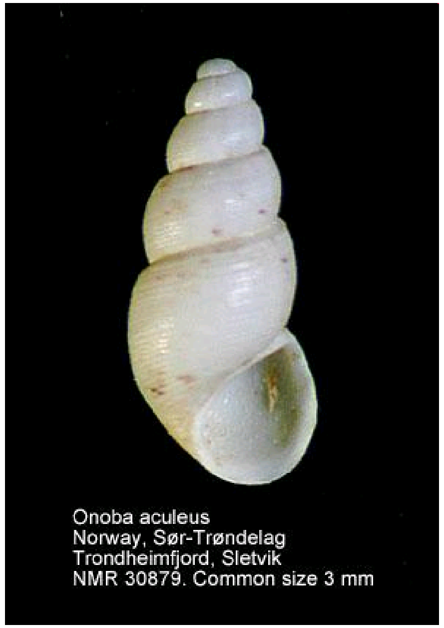


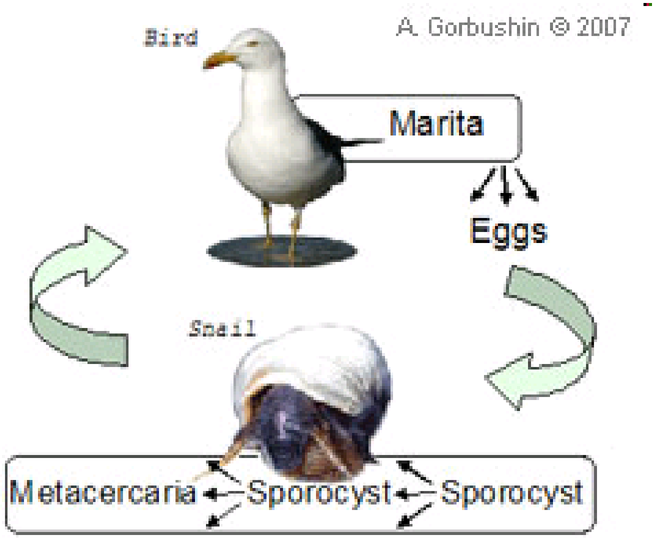
Fluke *Microphallus pseudopygmaeus* chemically castrates its intermediate host, snail *Onoba aculeus* accelerating thus its growth rate

snails castrated by the parasite (blue) grow faster than healthy snails of the same size (green)







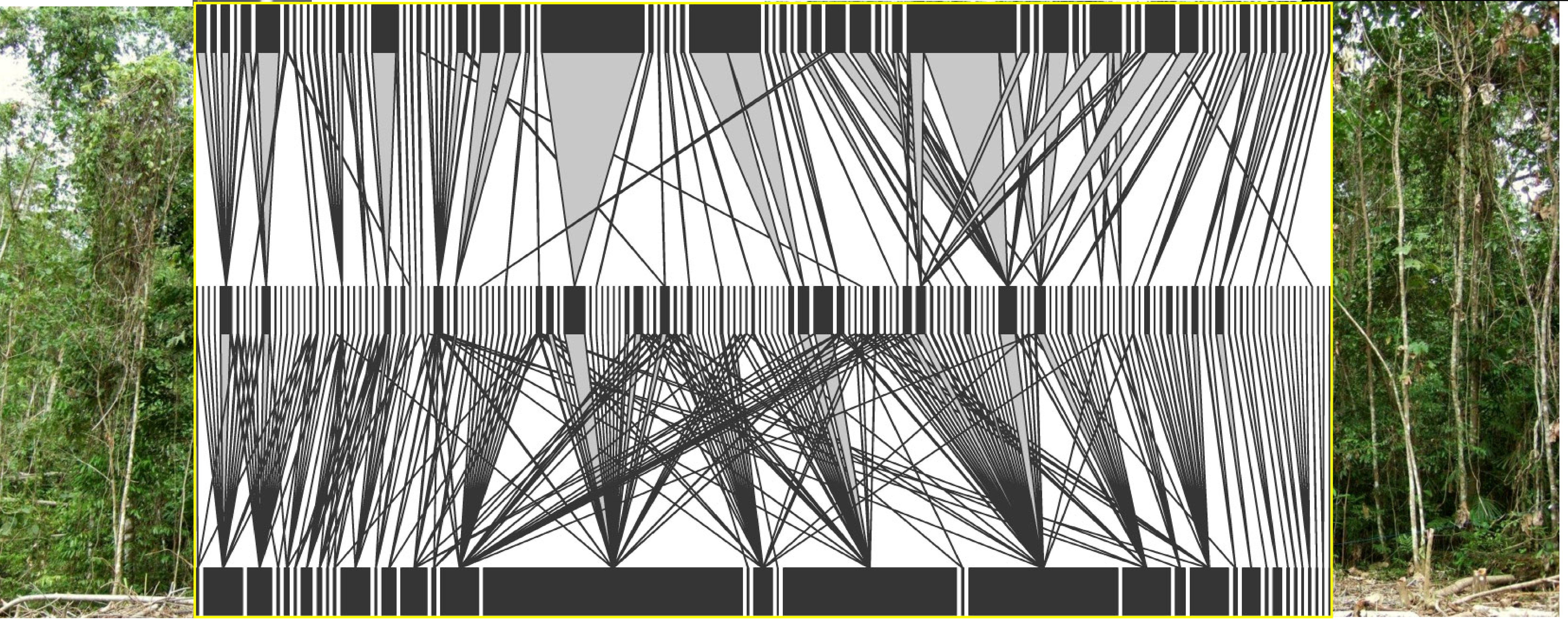


developmental cycle

Autor: A. Gorbushin

Complex host-parasitoid food webs in insect communities

1,523 Hymenoptera and Diptera parasitoids from 166 species



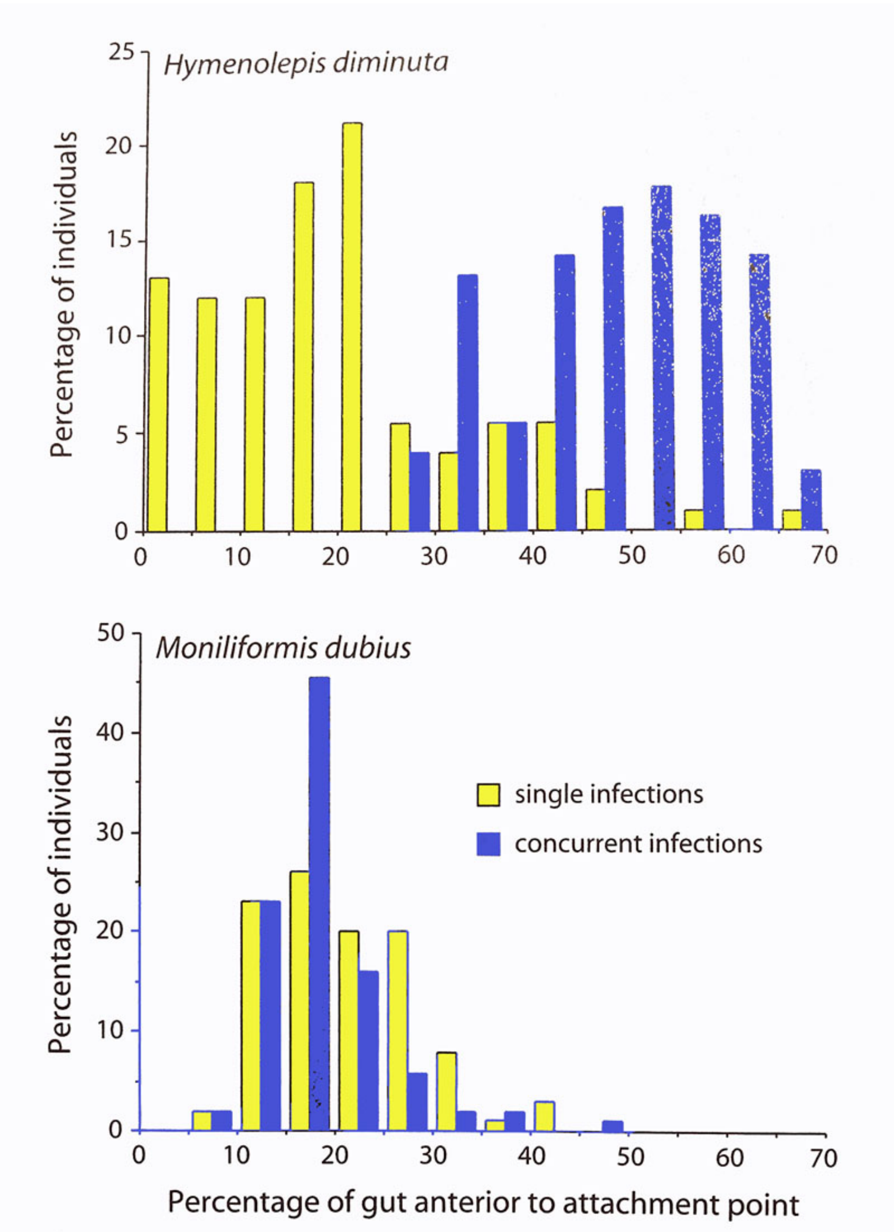
38 tree species - 11,621 caterpillars from 267 species

Lowland secondary rainforest vegetation in Papua New Guinea

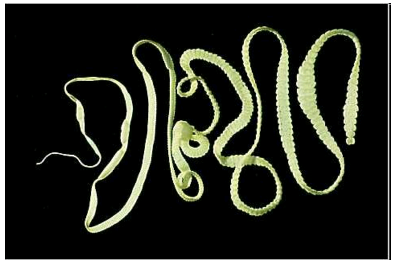
Jan Hrcek et al. 2013 *Oecologia* **173**: 521

Interspecific competition in parasites sharing the same host

distribution of tapeworm *Hymenolepis* and *Moniliformis* in the intestine of rats



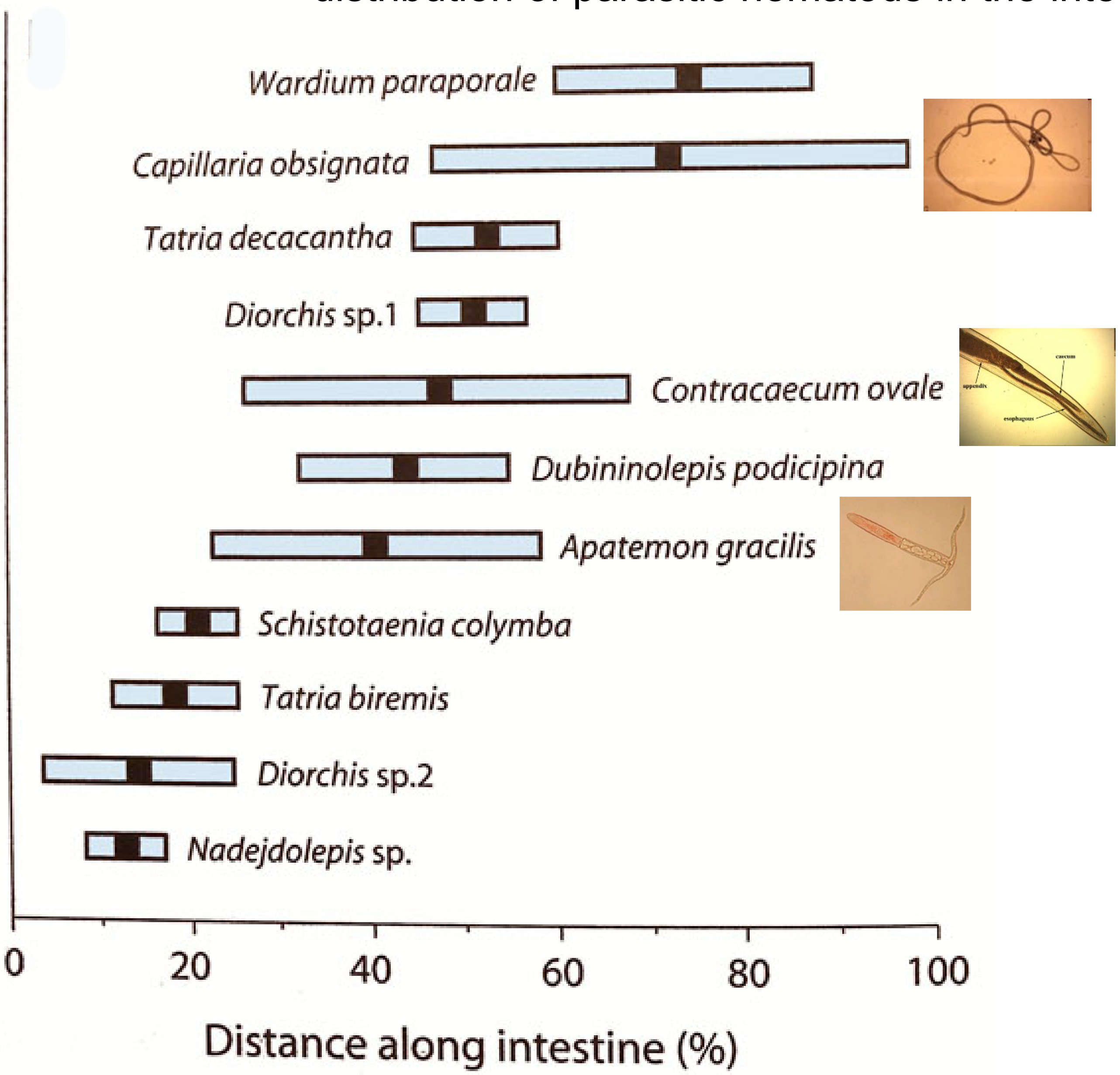
Each species exhibits its optimum in single infections, changes during simultaneous infections are due to inter-specific competition



Hymenolepis prefers anterior part of gut but is displaced by Moniliformis during simultaneous infections

Niche segregation in communities of parasites

distribution of parasitic nematods in the intestine



THE END