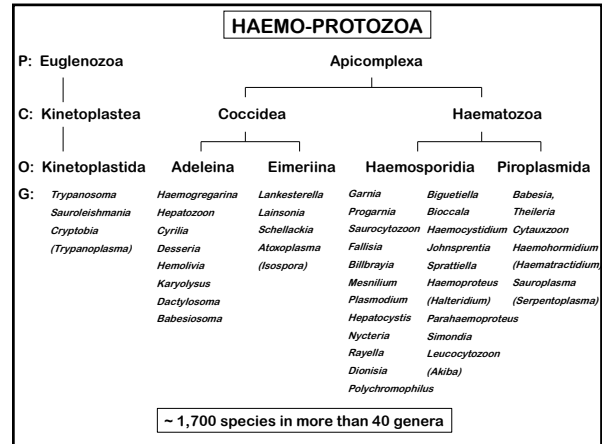
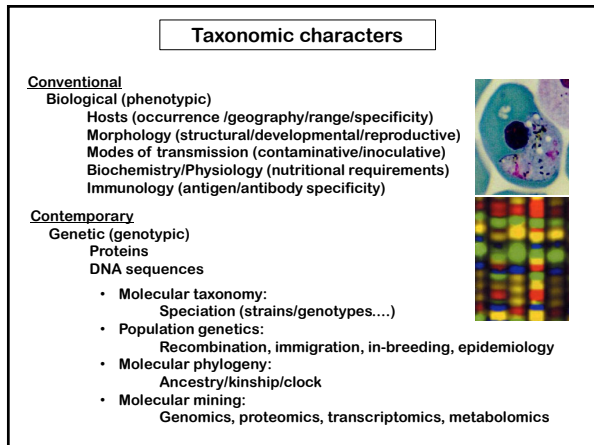


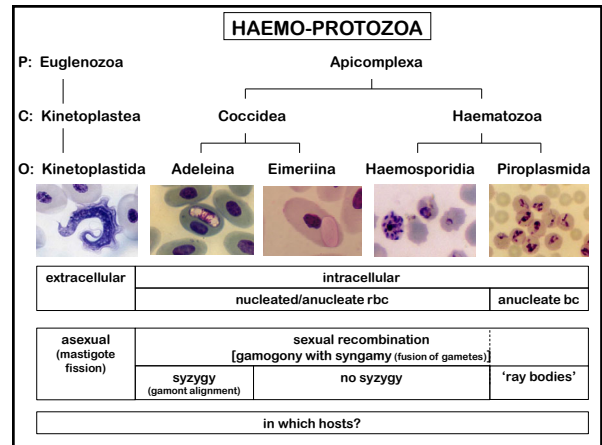
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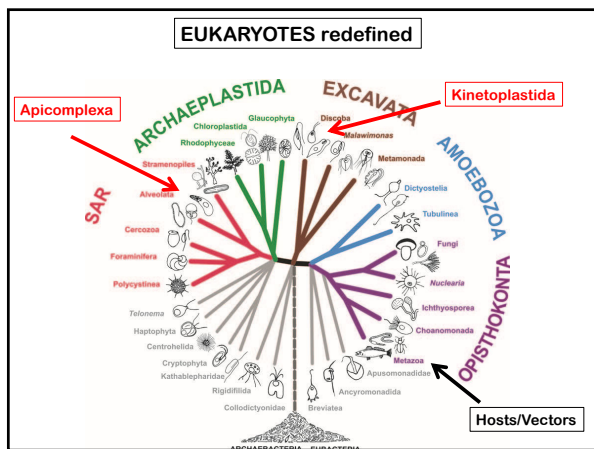
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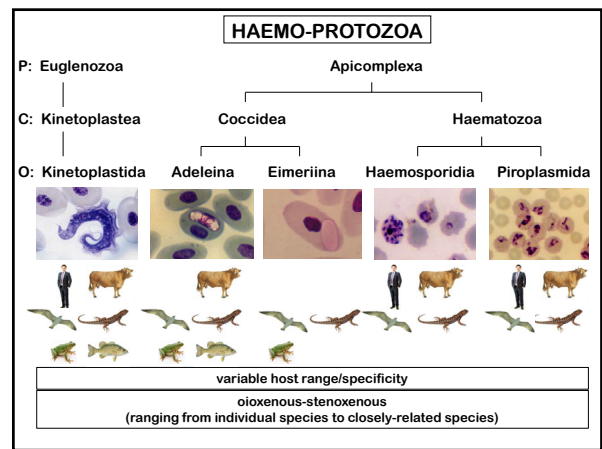
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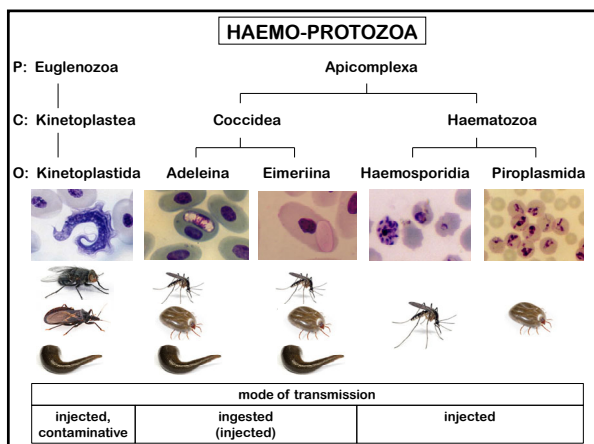
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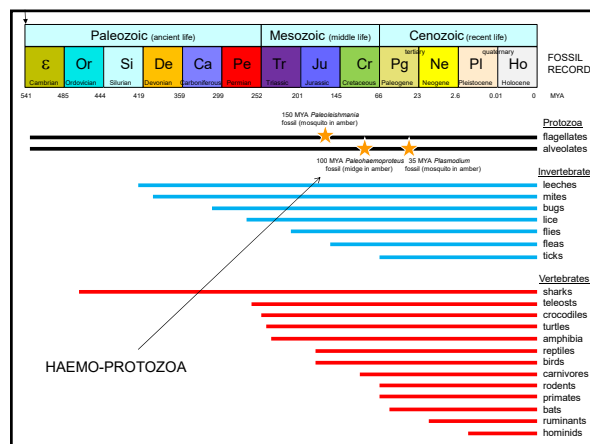
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6



7



10

HAEMO-PROTOZOA

Origins? Evolution?

- must consider three organisms (protist – invertebrate – vertebrate)
- presumably free-living protist taken up and became parasitic
- firstly monoxenous, then heteroxenous transfer
- but which host first (invertebrate or vertebrate)?

What evidence?

- fossil record?
- biology (comparative morphology, developmental cycles, host ranges...)
- molecular phylogenies (informative sequences, trees...)
- co-evolution (comparative trees, tanglegrams...)

8

Molecular phylogenies

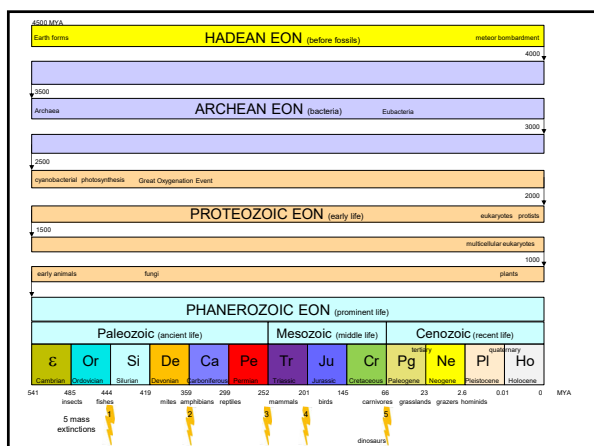
Phylogenetic relationships inferred from DNA sequence comparisons using various algorithms

Genes examined from multiple genomes:

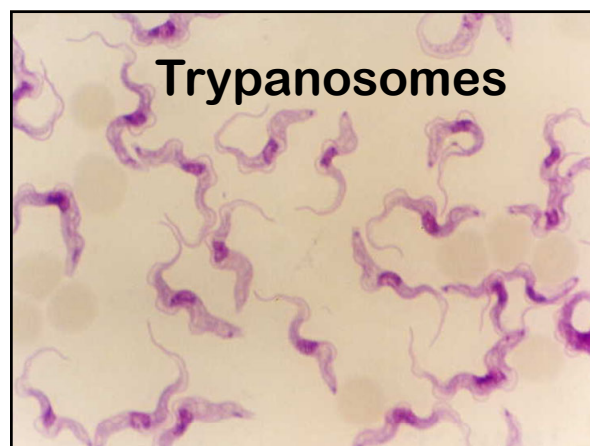
- **nuclear**
 - ssurRNA* (18S ribosomal RNA)
 - gGAPDH* (glycosomal glyceraldehyde phosphate dehydrogenase)
 - hsp70* (heatshock protein 70)
 - polA* (catalytic polypeptide from DNA polymerase A)
 - rpoIIIS* (large subunit RNA polymerase II)
 - gp63* (glycoprotein 63)
 - cpb* (cysteine protease B)
 - asl* (adenylosuccinate lyase)
 - ef2* (nuclear elongation factor 2)
 - cct17* (chaperonin-containing t-complex polypeptide 1) (range of membrane proteins)
- **mitochondrial**
 - cytb* (cytochrome b)
 - cox* (cytochrome oxidase)
- **apicoplast**
 - clpC* (caseinolytic protease C)

look for phenotypic patterns (morphology, biology) in phylogenetic trees

11




9



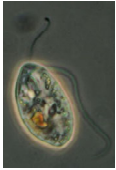
12

Kinetoplastids

- ancient lineages of eukaryotes (among first to contain mitochondria)
- kinetoplast = extranuclear DNA = mitochondrial DNA
- asexual (longitudinal binary fission)



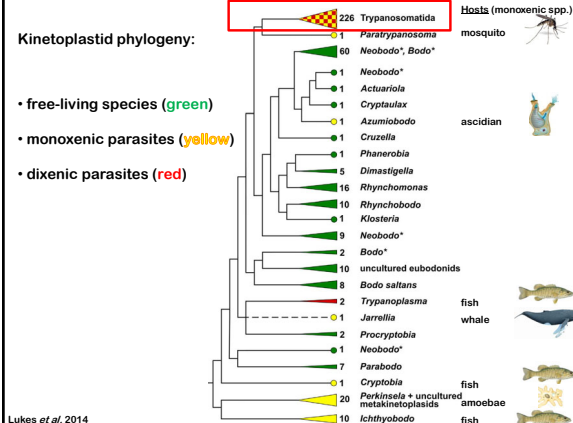
trypanosomes
(single flagellum)
parasites of animals/plants
(monoxenous or dixenous)



bodonids
(two flagella)
most free-living bacterivores
(aquatic/terrestrial habitats)

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Kinetoplastid phylogeny:



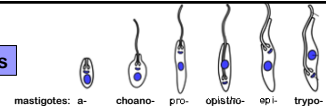
- free-living species (green)
- monoxenic parasites (yellow)
- dixenic parasites (red)

Hosts (monoxenic spp.): mosquito, ascidian, fish, whale, fish, amoebae, fish.

Lukes et al. 2014 *ssurRNA*

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Developmental stages

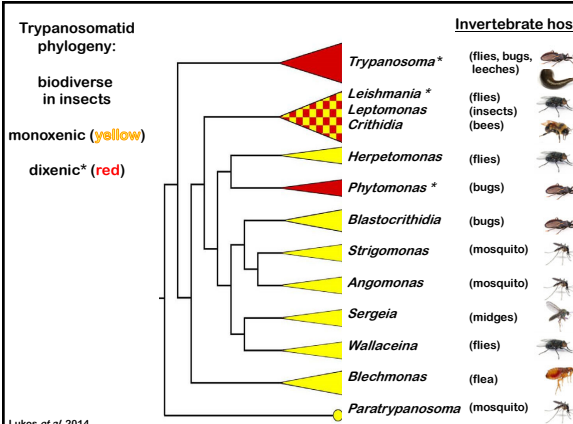


Stage	a-	choano-	pro-	opistho-	epi-	trypo-
Monoxenous (mainly insects)						
<i>Crithidia</i>		a	c			
<i>Leptomonas</i>				p		
<i>Herpetomonas</i>		a		p	o	
<i>Blastocrithidia</i>		a		p		e
Dixenous (invertebrate – animal/plant)						
<i>Phytomonas</i>		a		p		
<i>Leishmania</i>		a		p		
<i>Endotrypanum</i>		a		p		e
<i>Trypanosoma</i>		a		p		e t

increasing complexity

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Trypanosomatid phylogeny:



- Trypanosomatid phylogeny:
- biodiverse in insects
- monoxenic (yellow)
- dixenic* (red)

Invertebrate hosts: flies, bugs, leeches; (flies) (insects) (bees); (flies); (bugs); (mosquito); (mosquito); (midges); (flies); (flea); (mosquito).

Lukes et al. 2014 *ssurRNA*

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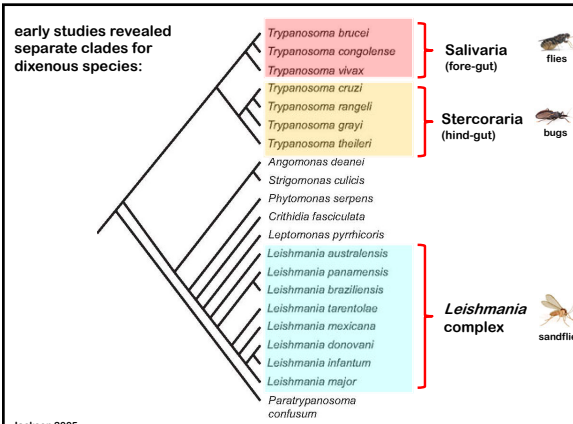
Kinetoplastids of blood

- dixenous (2-host) parasites
 - extracellular in vertebrate blood
 - luminal in invertebrate vector (flies, bugs, leeches)
- some 600 species in 2 families
 - based on host occurrence, vectors, transmission, developmental stages, pathogenicity, culture

Assemblage	Genus	No. species	Vertebrate hosts	Invertebrate vector
F: Trypanosomatidae	<i>Trypanosoma</i>	520	mammals, reptiles, frogs, birds, fish	arthropods, leeches
F: Trypanosomatidae	<i>Leishmania</i>	35	mammals	arthropods
F: Trypanosomatidae	<i>Sauroleishmania</i>	10	lizards/snakes	sandflies?
F: Bodonidae	<i>Cryptobia</i> (<i>Trypanoplasma</i>)	52	fish	leeches

15

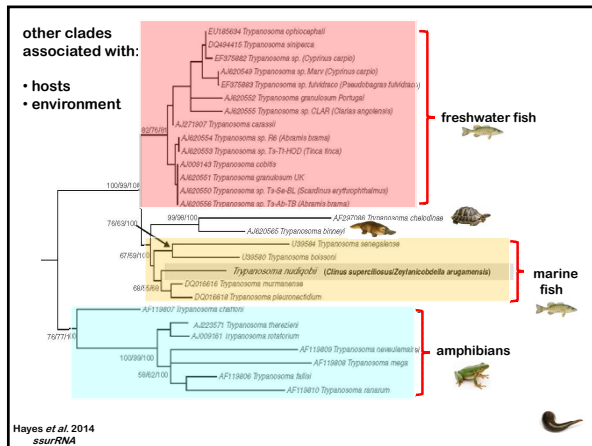
early studies revealed separate clades for dixenous species:



- Salivaria (fore-gut): *Trypanosoma brucei*, *Trypanosoma congolense*, *Trypanosoma vivax*, *Trypanosoma cruzi*, *Trypanosoma rangeli*, *Trypanosoma grayi*, *Trypanosoma theileri*
- Stercoraria (hind-gut): *Angomonas deanei*, *Strigomonas culicis*, *Phytomonas serpens*, *Crithidia fasciculata*, *Leptomonas pyrithicoris*, *Leishmania australensis*, *Leishmania panamensis*, *Leishmania braziliensis*, *Leishmania tarentolae*, *Leishmania mexicana*, *Leishmania donovani*, *Leishmania infantum*, *Leishmania major*, *Paratrypanosoma confusum*
- Leishmania complex: *Leishmania tarentolae*, *Leishmania mexicana*, *Leishmania donovani*, *Leishmania infantum*, *Leishmania major*

Jackson 2005 consensus tree

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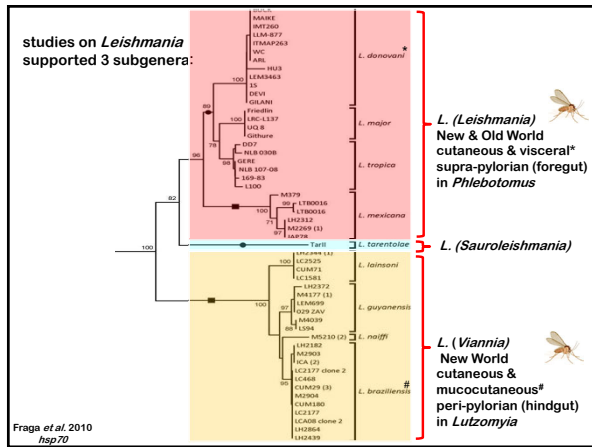
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Apicomplexa

obligative intracellular parasites
 apical complex facilitates host cell invasion (conoid, rhoptries, micronemes...)
 mitochondriate
 apicoplast
 subpellicular alveoli
 Alveolates:

- Dinoflagellates (free-living and symbiotic)
- Ciliates (free-living and symbiotic)
- Apicomplexa (parasitic)

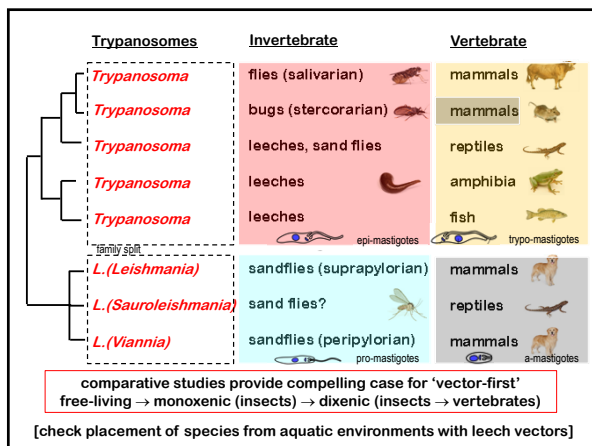
22



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APICOMPLEXA	
Main groups	Hosts
• gregarines	marine worms, insects (gut/body cavity)
• coccidia	marine invertebrates, vertebrates (gut/tissues)
• adeleorine coccidia (incl. haemogregarines)	mostly vertebrates (gut/tissues/blood) (reptiles/amphibia*, leech/arthropod vectors)
• eimeriine coccidia (incl. haemococcidia)	vertebrates (gut/tissues) (reptiles/amphibia*, leech/arthropod vectors)
• haematozoa	vertebrates (blood/tissues)
• haemosporidia	(mammals/birds/reptiles*, dipteran vectors)
• piroplasms	(mammals*, arachnid vectors)

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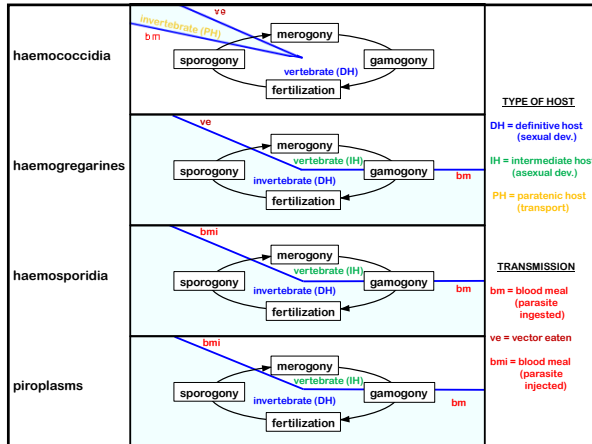
DEVELOPMENTAL CYCLES

Three types of division:

- merogony (= schizogony): asexual multiplication
- gamogony: formation of gametes [fertilization = syngamy, fusion of gametes]
- sporogony: formation of sporozoites

which stage in which host?

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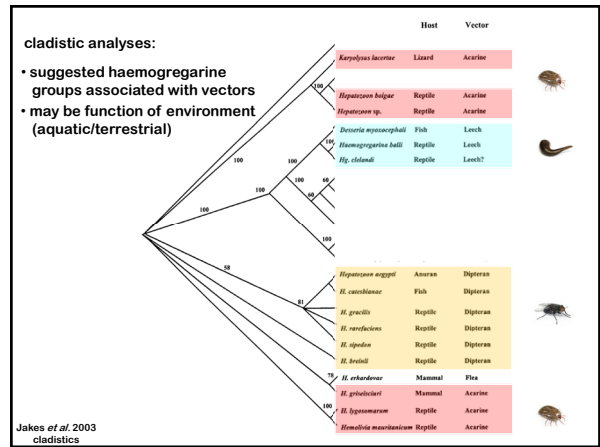
- Some 400 species (taxonomic mess!) (many placements disputed because cycles unknown)
 - *Haemogregarina sensu stricto* (turtles-leeches)
 - *Haemogregarina sensu lato* (crocodiles, snakes, lizards, birds) → *Hepatozoon*
- 4 families recognized (based on pattern of sporogony in vector)
 - Hepatozoidae (sporocysts/oocysts in vector) (some spp. with PH)
 - Karyolysidae (sporokinets in vector eggs) (transovarian)
 - Haemogregarinidae (sporocysts absent, sporozoites in leech tissues)
 - Dactylosomatidae (sporocysts absent, oocysts in leech intestines)

Assemblage	Genus	No. species	Site of development in vertebrate	Site of development in invertebrate	Vertebrate hosts	Invertebrate vector
F: Haemogregarinidae	<i>Cyrtia</i>	4	erythrocytes	erythrocytes	fish	leeches
F: Haemogregarinidae	<i>Desseria</i>	40	erythrocytes	erythrocytes	fish	leeches
F: Haemogregarinidae	<i>Haemogregarina</i>	46	erythrocytes	erythrocytes	turtles	leeches
F: Hepatozoidae	<i>Hepatozoon</i>	300	viscera	erythrocytes, leucocytes	mammals, birds, reptiles, amphibians, fish	leeches, arthropods
F: Karyolysidae	<i>Hemolvia</i>	4	RE cells	erythrocytes	lizards, tortoises, lizards	ticks
F: Karyolysidae	<i>Karyolysus</i>	5	viscera + rbc	erythrocytes	lizards	mites
F: Dactylosomatidae	<i>Dactylosoma</i>	10	erythrocytes	erythrocytes	chameleons, frogs, teleosts	leeches
F: Dactylosomatidae	<i>Babesiosoma</i>	7	erythrocytes	erythrocytes	frogs, fish	leeches

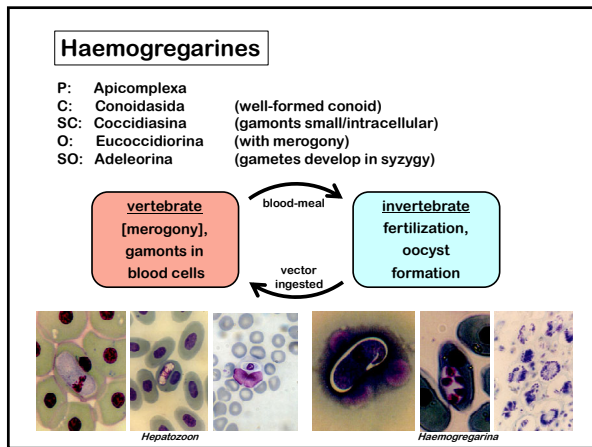
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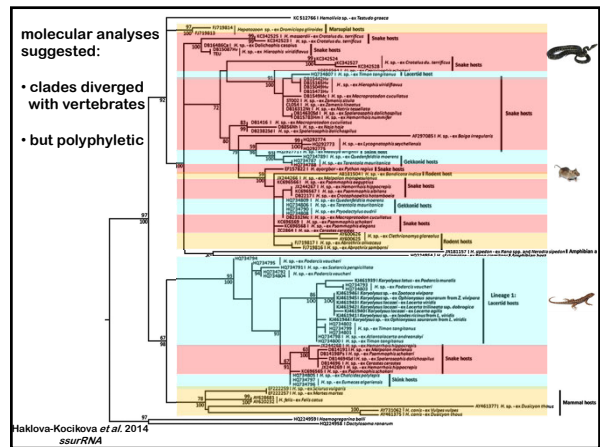
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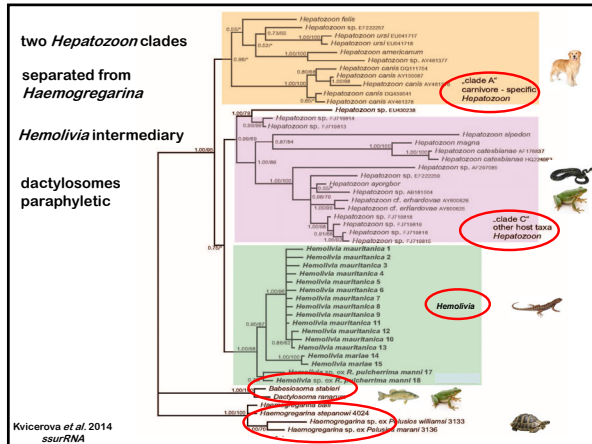
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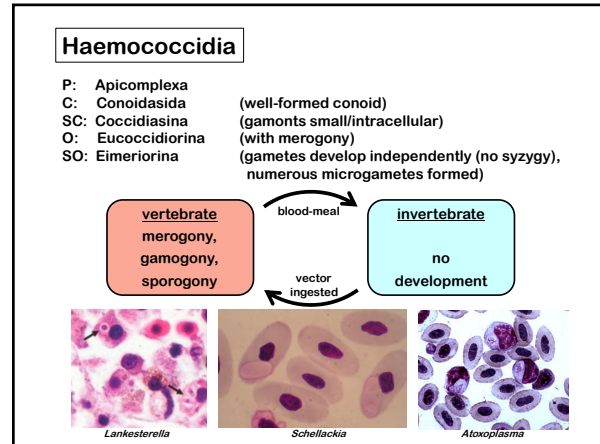
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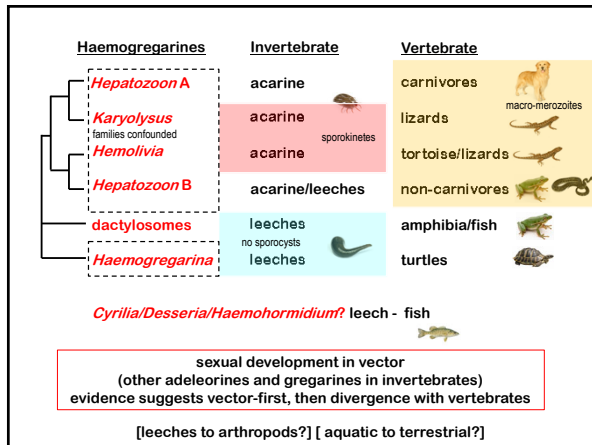
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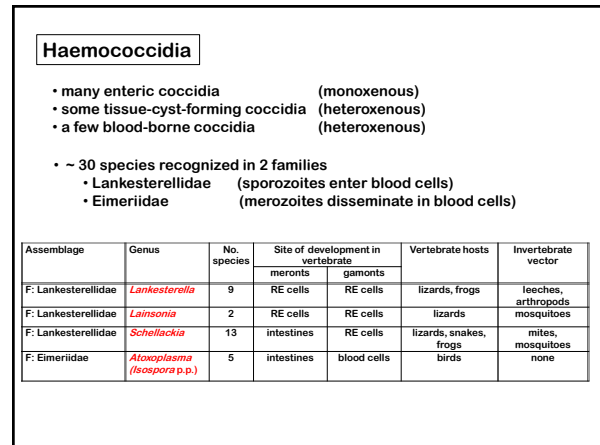
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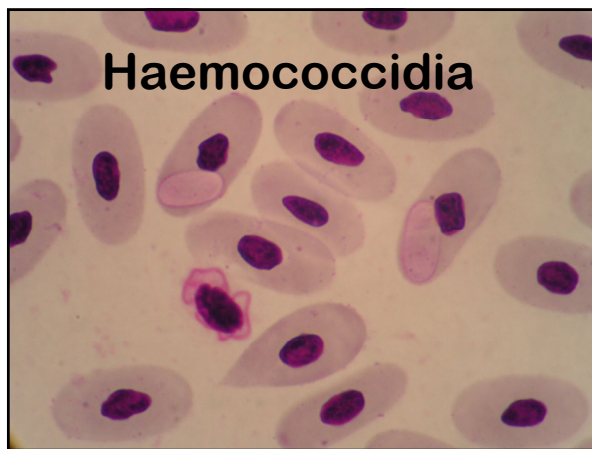
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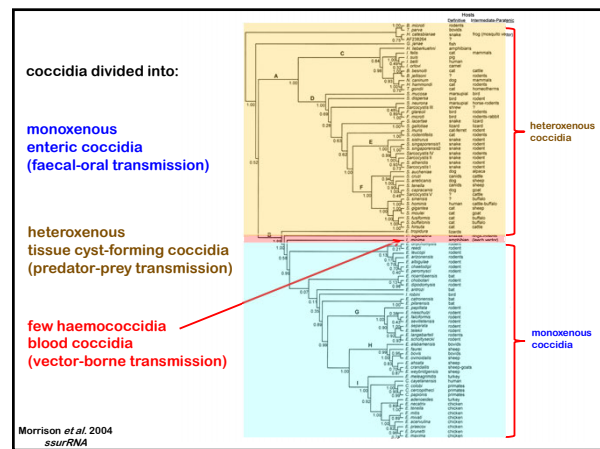
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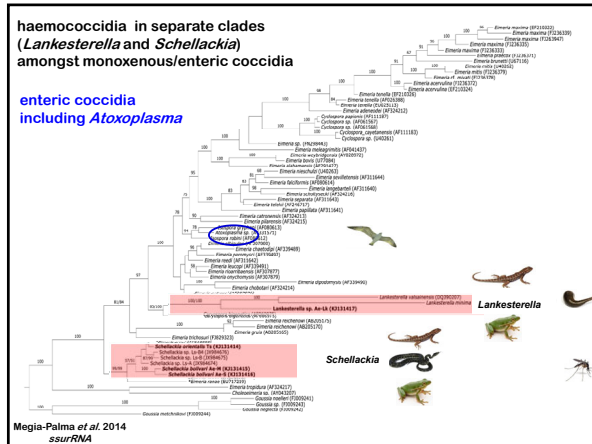
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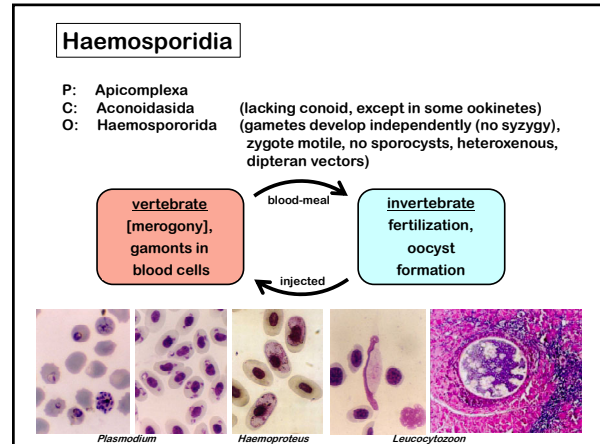
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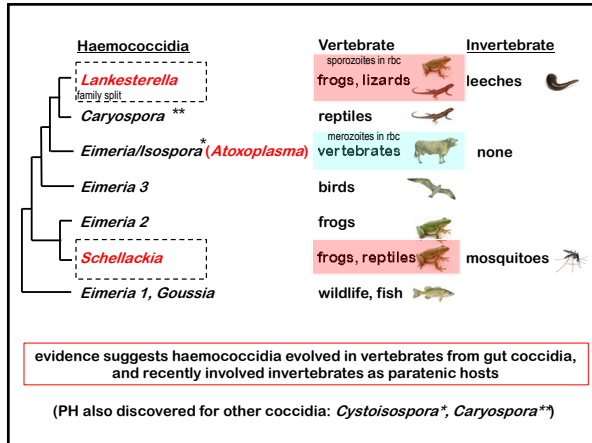
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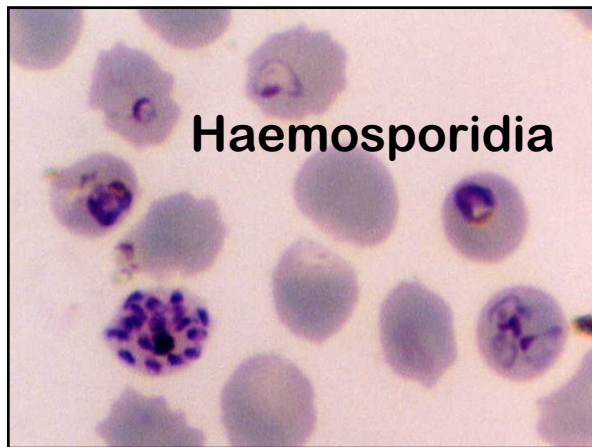
38

Haemosporidia (> 540 species)

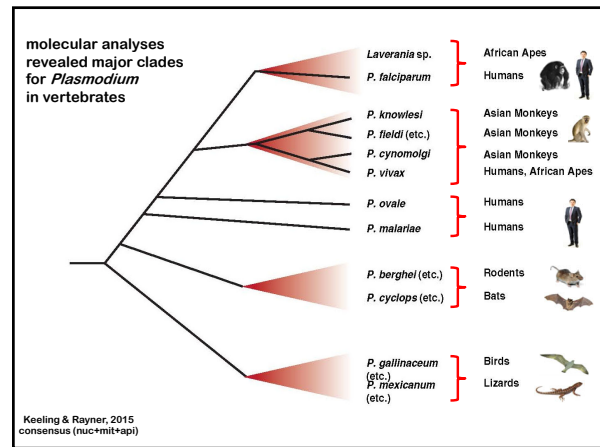
• 21 genera in 4 families recognized on basis of: site of development, host/vector occurrence, haemozoin pigment*

Assemblage	Genus	No. spp.	Site of development in vertebrate		Vertebrate hosts	Invertebrate vector
			meronts	gamonts		
F: Plasmodiidae	<i>Plasmodium</i>	200	liver, blood	erythrocytes*	mammals, snakes, lizards, birds	diptera
F: Plasmodiidae	<i>Haptozycotis</i>	25	liver	erythrocytes*	primates/bats	midges
F: Plasmodiidae	<i>Polychromophilus</i>	6	viscera	erythrocytes*	bats	nycterids
F: Plasmodiidae	<i>Nycteria</i>	7	liver	erythrocytes*	bats	?
F: Plasmodiidae	<i>Biguetiella</i>	1	liver	erythrocytes*	bats	?
F: Plasmodiidae	<i>Bioccala</i>	1	RE cells	erythrocytes*	bats	?
F: Plasmodiidae	<i>Dionisia</i>	1	liver	erythrocytes*	bats	?
F: Plasmodiidae	<i>Rovella</i>	3	liver	erythrocytes*	flying squirrels	?
F: Plasmodiidae	<i>Bilbravia</i>	1	erythrocytes	erythrocytes*	lizards	?
F: Plasmodiidae	<i>Mesnilium</i>	1	RE cells	blood cells*	fish	leeches
F: Plasmodiidae	<i>Haemocystidium</i>	6	RE cells	erythrocytes*	lizards/tortoises	arthropods
F: Haemoproteidae	<i>Haemoproteus</i> (<i>Walteridium</i>)	20	RE cells	erythrocytes*	birds	louse flies
F: Haemoproteidae	<i>Parahaemoproteus</i>	150	RE cells	erythrocytes*	birds	midges
F: Haemoproteidae	<i>Johnspretia</i>	1	RE cells	erythrocytes*	flying foxes	?
F: Haemoproteidae	<i>Simondia</i>	1	RE cells	erythrocytes*	turtles	insects
F: Haemoproteidae	<i>Sprattiella</i>	1	RE cells	erythrocytes*	bats	?
F: Leucocytozoidae	<i>Leucocytozoon</i> (<i>Atiba</i>)	100	RE cells	blood cells	birds	blackflies
F: Leucocytozoidae	<i>Saurocytozoon</i>	2	viscera	leucocytes	lizards	mosquitoes
F: Garniidae	<i>Garnia</i>	7	leucocytes	leucocytes	lizards	arthropods
F: Garniidae	<i>Prozania</i>	1	blood cells	blood cells	crocodiles	?
F: Garniidae	<i>Fallisia</i>	8	leucocytes	leucocytes	lizards	arthropods

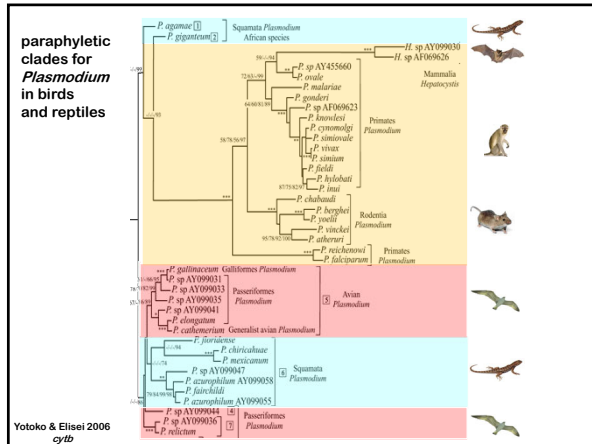
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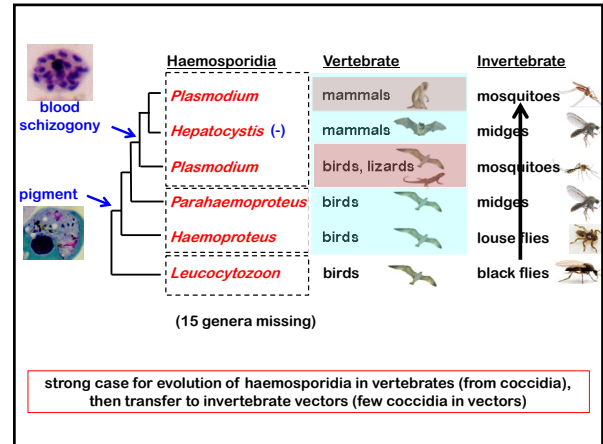
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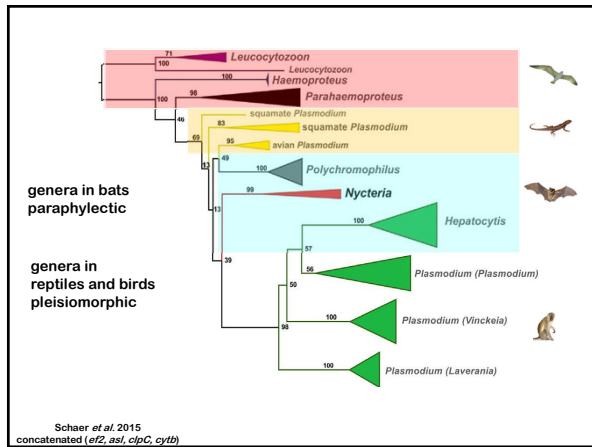
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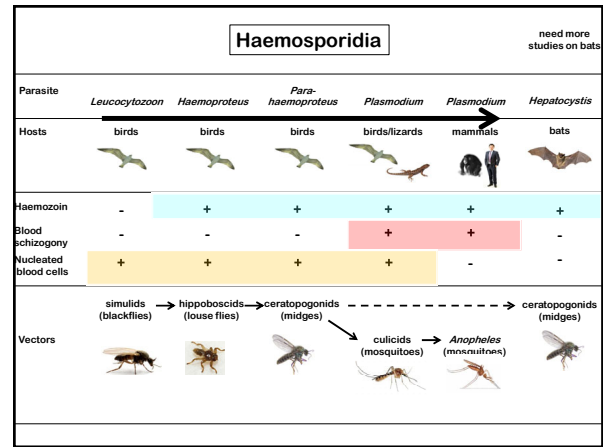
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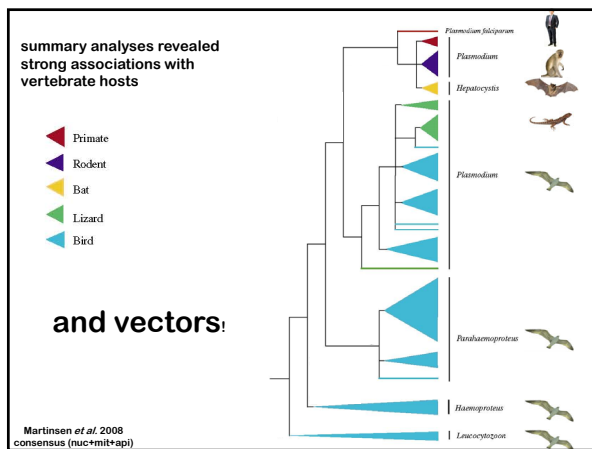
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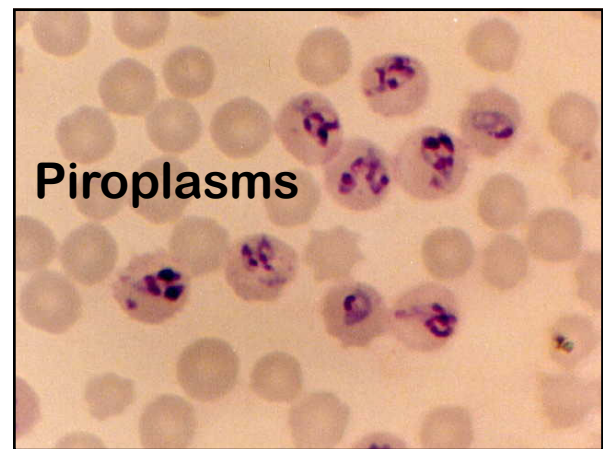
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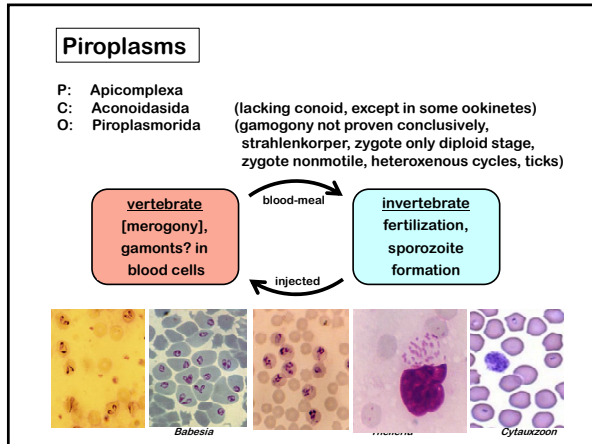
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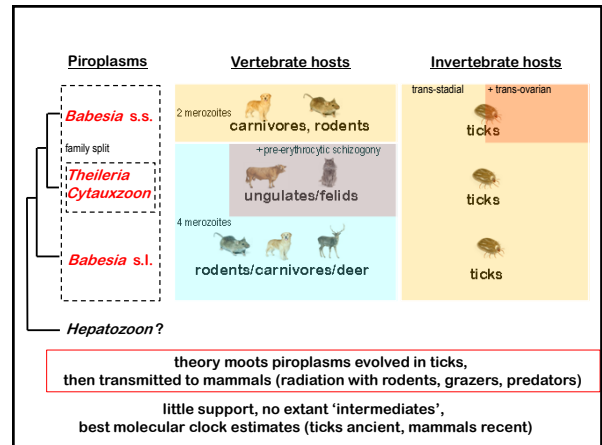
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Piroplasms

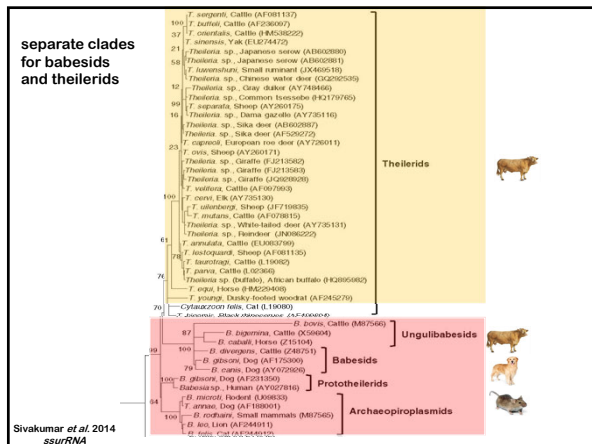
- > 130 species
- 3 families of blood parasites in mammals, and some birds and reptiles (based on site of development in vertebrate host)
 - Babesiidae (erythrocytes, mammals, some birds)
 - Theileridae (lymphocytes then erythrocytes, mammals)
 - Haemohormidiidae (nucleated erythrocytes, reptiles)
- vectors include 1-, 2- and 3-host ticks, involving
 - horizontal (trans-stadial) transmission in ticks
 - vertical (trans-ovarian) transmission in ticks (Babesiidae)

Assemblage	Genus	No. spp.	Site of development in vertebrate		Vertebrate hosts	Invertebrate vector
			meronts	gamonts		
F: Babesiidae	<i>Babesia</i>	100	erythrocytes	erythrocytes	mammals, birds	ticks
F: Theileridae	<i>Theileria</i>	15	lymphocytes	erythrocytes	mainly ruminants,	ticks
F: Theileridae	<i>Cytauxzoon</i>	4	vascular endothelia	erythrocytes	carnivores	ticks
F: Haemohormidiidae	<i>Sauroplasma</i> (<i>Sarpanthoplasma</i>)	3	erythrocytes	erythrocytes	lizards/snakes	ticks?
F: Haemohormidiidae	<i>Haemohormidium</i> (<i>Haematracidium</i>)	12	erythrocytes	erythrocytes	tortoises, frogs, fish	leeches

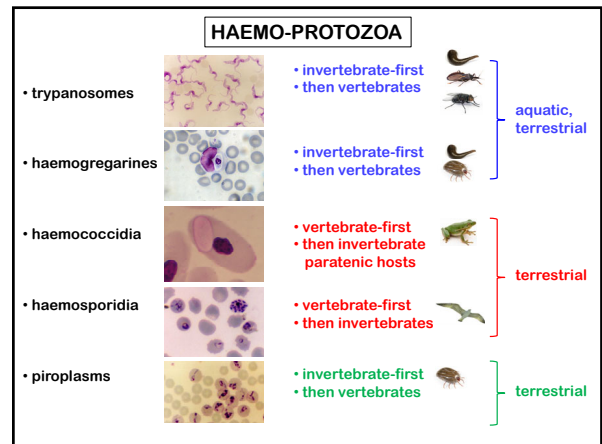
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Future studies

MORE of everything

- more parasites (missing taxa)
- more 'relatives' (free-living & monoxenous species)
- more hosts (better representation)
- more locations (better representation)
- more genes (consensus trees)
- more bioinformatics (coevolution/host-switching)

- more biology (need to determine vectors for most species)

