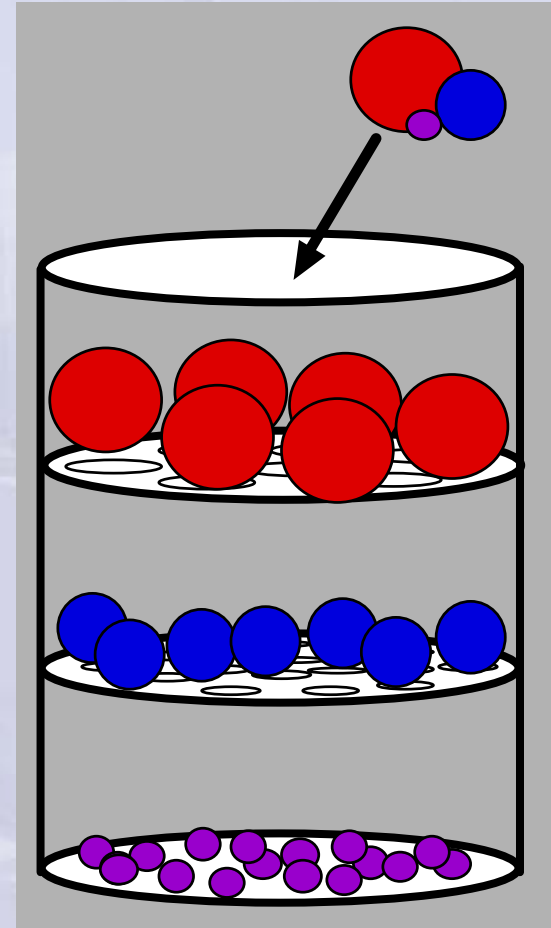




Organisms, Groups, Species

Selection of, Selection for

- Just because something increases in evolution does not mean that it was selected for
- The sorter toy selects balls *of* different colors
- But selection works on size, not color
- Are genes what are selected for?
 - Might selection be blind to genes, as the toy is to color?



Opening to Higher Level Units

- “We reject the whole sexual genome as a candidate replicator, because of its high risk of being fragmented at meiosis. The single nucleotide does not suffer from this problem but ... it raises another problem. It cannot be said to have a phenotypic effect except in the context of the other nucleotides that surround it in the cistron. It is meaningless to speak of the phenotypic effect of adenine. But it is entirely sensible to speak of the phenotypic effect of substituting adenine for cytosine at a named locus within a named cistron. The case of a cistron within a genome is not analogous. Unlike a nucleotide, a cistron is large enough to have a consistent phenotypic effect, relatively ... independently of where it lies on the chromosome...” (Dawkins 1982, pp. 91-92)
- Perhaps levels can be defined in terms of “consistent phenotypic effects”

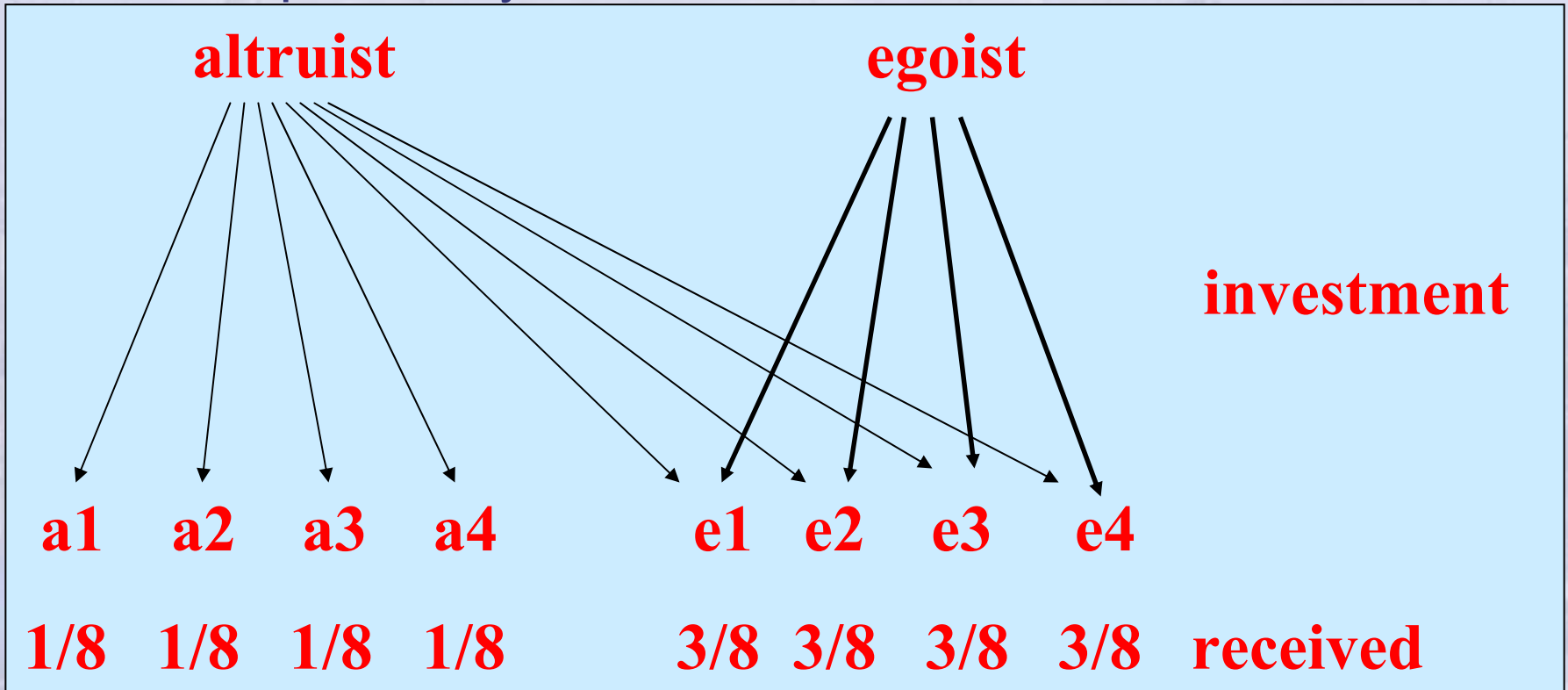


Higher Level Selection

- Cooperative hunting: “When prey have been detected, a wildebeest herd perhaps, the lions start to stalk towards them. As they get close, they take different routes, some going on straight ahead, and some to the sides, so the prey herd is approached by lions stalking them from different directions... Eventually one lion gets close enough to make a rush at a wildebeest, or else a lion is detected by the prey.” Bertram
- Who benefits
 - Individual lions
 - The pride?
 - The species?
 - The genus?
 - The class?

Altruism

- Altruism *ought* to destroy itself
 - Benefits go to the genes of others, who then out reproduce you



- So, why does altruism persist?

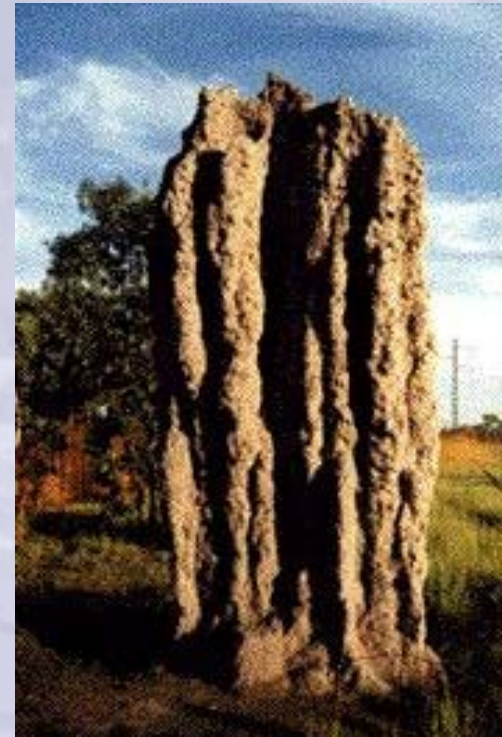
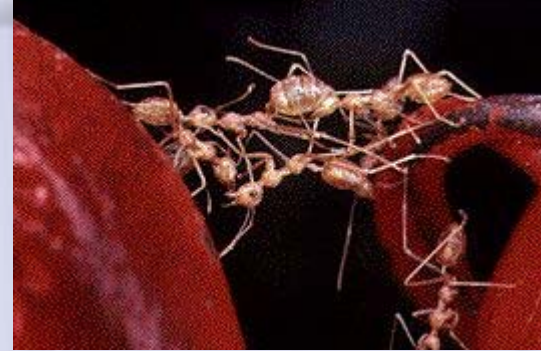
Prisoners' Dilemma

	A Cooperates	A Defects
B Cooperates	A=5/B=5	A=10/B=0
B Defects	A=0/B=10	A=-25/B=-25

- Single round prisoner's dilemma: no coordination possible
- If a community of cooperators existed, they would be subject to invasion by defectors, who should quickly win out
- Iterated version of the game: cooperative solutions possible: "Tit-for-Tat"

The social insects

- Worker castes do not reproduce—they benefits of their labor go to those who are fertile
- Why does selection not eliminate the sterile classes?
- Distinctive genetics of social insects:
 - Haploidy-diploidy
 - Females are diploid—have both a mother and a father
 - Males are haploid—only have a mother
 - Result: sisters are more closely related to each other than to their daughters
 - Raising their sister's children very likely to produce copies of their own genes



Kin Selection and Inclusive Fitness

- Hamilton's Rule: perform altruistic act when
 - $rb > c$
 - relatedness x benefits > costs of altruistic act
- You can gain direct fitness benefits through producing and raising your own offspring
- You can gain indirect fitness benefits through helping to raise offspring of related individuals (kin selection)
- Direct fitness + indirect fitness = total fitness

Altruism towards non-kin

- Reciprocal altruism—advantageous for an individual to perform actions that benefit another if they in turn do things that benefit that individual
 - I scratch your back if you scratch mine
- Problem: cheaters—receive the advantages of others helping them but don't do anything to help other
 - Rather, direct efforts to promoting own reproduction
- Cheaters would seem to be favored by natural selection

Michael Wade and Tribolium

- Select between groups for those with low fecundity
 - Within groups greater fecundity wins
 - But overall fecundity goes down

Why?

- Within a given group, fecundity more likely to rise
- But there is variability between groups, and those groups with lower fecundity leave more offspring



Simpson's Paradox

- Partitioning a population into two parts can result in a reversal in the direction of relation between two variables
 - The death rate from tuberculosis for African Americans was *lower* in Richmond than in New York.
 - The death rate from tuberculosis for Caucasians was *lower* in Richmond than in New York.
 - The death rate for the total combined population of African Americans and Caucasians from tuberculosis was *higher* in Richmond than in New York.

Simpson's Paradox

Population	New York	Richmond
White	4,675,174	80,895
Black	91,709	46,733
Combined	4,766,883	127,628
Deaths	New York	Richmond
White	8,365	131
Black	513	155
Combined	8,878	286
Mortality rate	New York	Richmond
White	17.9%	16.2%
Black	56.0%	33.2%
Combined	18.6%	22.4%

Group Selection for Altruism

Selfish Group	Selfish Individuals	Altruistic Individuals
Before	40	5
After	20	0
Altruistic Group	Selfish Individuals	Altruistic Individuals
Before	5	40
After	8	40
Combined	Selfish Individuals	Altruistic Individuals
Before	45	45
After	28	40

Group selection as selection for a trait group

- Trait group is a group of organisms that share a trait AND that trait influences the reproductive success of the others
- Group as a whole is an interactor
- Sober and Wilson: kin selection is a version of selection for trait groups

Alternative Account: Frequency Dependent Individual Selection

- Individual and gene selectionists insist we should keep the focus on individuals (and their genes).
 - Treat what appears to be group selection as frequency dependent selection
 - In environments where altruism is high, altruists themselves are favored
- Two equivalent descriptions of the same process?

Superorganisms?

- Interactors that are at a larger scale than organisms
 - “we claim that organisms are objectively interactors, and that some collective individuals are enough like organisms in their crucial respects to be real superorganisms. Hence, they too are objective interactors” (Sterelny and Griffiths, p. 175).
- Key: is there a boundary to the superorganism: “Termite mounds, beehives, ant colonies, and een more obviously, the colonial marine invertebrates have boundaries. They have an inside and an outside” (p. 176).
- What sort of boundary is needed to make a superorganism?

Species—What are they?

- Traditional views of species: species had essences
 - which enabled specifying the conditions necessary and sufficient for species membership
- Darwin's account of gradual change between species seems to undercut the reality of species
- But species seem to be real and the concept seems indispensable to evolutionary theory
 - What to do?

Some Candidate Accounts of Species

- Phenetic species concept: species are groups defined in terms of overall similarity
- Biological species concept: species are populations that are reproductively isolated
- Phylogenetic species concept: species are lineages of ancestral/descendant populations between speciation events
- Others:
 - Cohesion species concept
 - Ecological species concept

Problems with the Phenetic Species Concept

- What is *similarity*?
 - Any two objects in the universe are similar in an unlimited number of respects
 - Must specify dimensions and metrics for determining similarity
- Members of a species can vary significantly (especially in polytypic species) and members of different species may appear more similar to each other than members of the same species



Species as Individuals



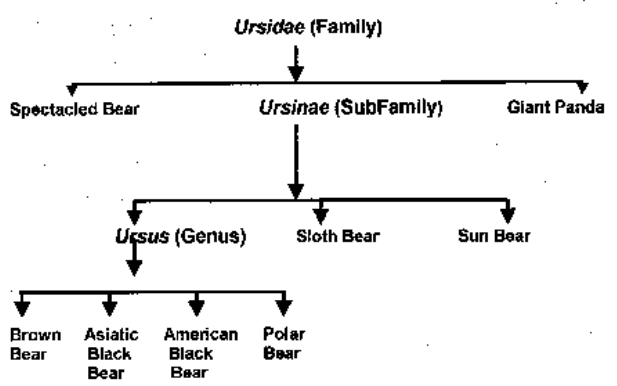
- David Hull and Michael Ghiselin
 - Traditionally species have been construed as types or sets
 - But species are historical entities—they are born and they go extinct
 - In this, they are *individuals*—spatially, temporally extended entities
- Need to know which sorts of lineages count as species: a ranking criterion

Problems with the Biological Species Concept

- Challenge temporally: depending on which organisms you start with, set the forward and backward limits of the species
- Groups that might not interbreed by easily could and groups that are different despite gene flow
 - Might try *potential* interbreeding, but no way to spell that notion out
- Problems with plants and single-celled organisms
 - Especially asexual organisms: Is each individual a different species?

Problems with the Phylogenetic Species Concept

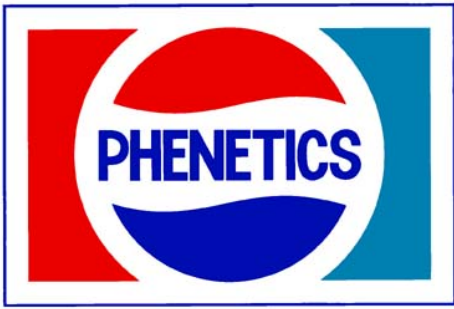
- Need a means of identifying speciation events and so must use something like break in interbreeding or cohesiveness
- “the most plausible account of species is that they are lineages between speciation events. The biological species concept, perhaps supplemented by the ecological species concept or by something else, reemerges as an account of speciation” Sterelny and Griffiths, p. 192).



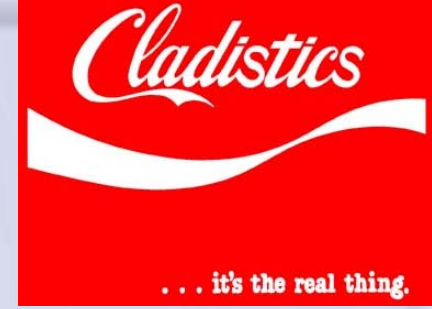
Higher Taxa



- Linnaean Hierarchy
- Three desiderata of a classification system:
 - Position in hierarchy should convey maximal information about the traits of an item
 - Should reflect differences and evolutionary change
 - Reflect phylogeny
- Incompatible desiderata



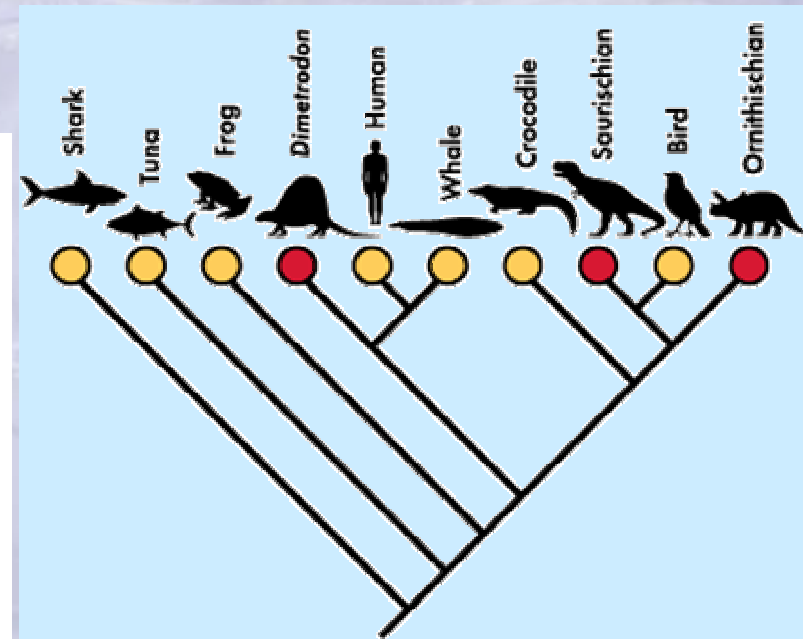
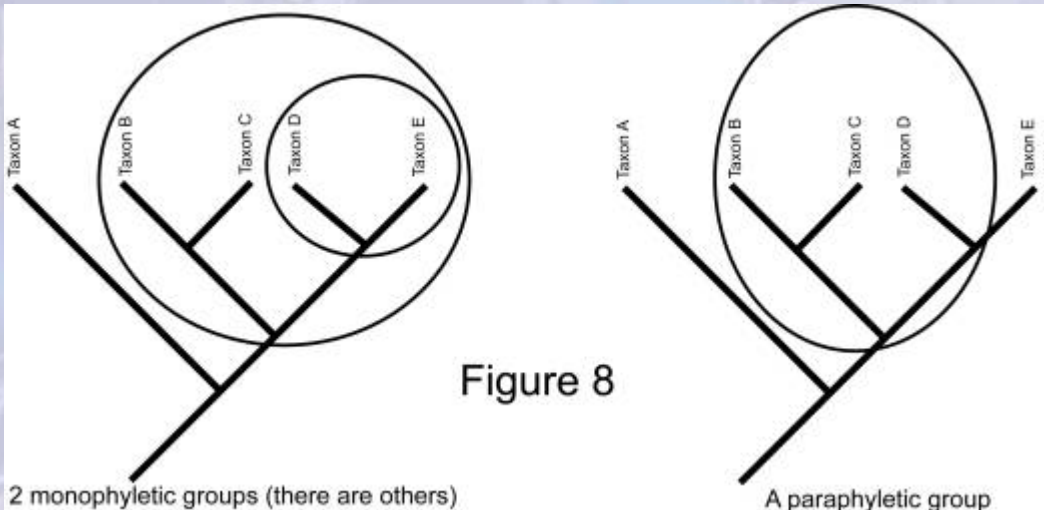
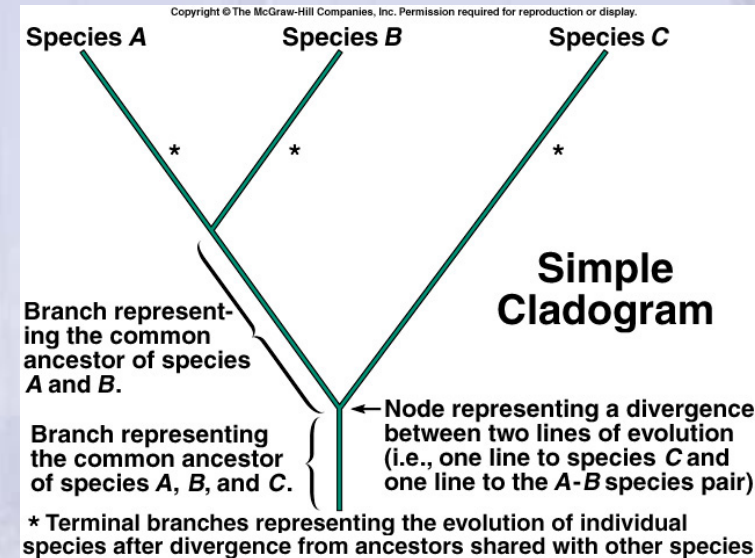
Taxonomy Wars



- Phenetics (numerical taxonomy)
 - Attempts to provide an atheoretical taxonomy (neutral between theories)
 - Start with traits and compute similarities
 - Variety of mathematical/statistical techniques recruited to create trees--phenogram
- Cladistics
 - Make phylogeny the key to taxonomy
 - Show order in which different species split from one another
 - Insist on monophyletic groups: A phyla consists of all and only the descendents of a species

Cladograms

- Represent species at terminal nodes
- Nodes represent splitting of a common ancestor
- Ancestor species ends at the split
- Higher phyla all monophyletic



Species Selection

- Can species be units of selection over and above selection on individual members of a species?
- Require:
 - Species traits that are not just organism traits
 - These traits must be causally salient
 - Some way species traits result from cumulative selection

Evolution of Sex

- Sex is costly: Dilution of genes, whereas asexual reproduction maintains genes
- But on a longer time scale, asexual reproduction faces costs:
 - Sex allows advantageous mutations to come together
 - Sex reduces Red Queen problem (need to constantly adapt just to keep up with changes in environment)
 - Muller's Ratchet: without recombination, chance events in small populations may eliminate the most fit asexual, leading to declining mean fitness

Species Selection and Sex

- Sex might be maintain by selection for sexually reproducing species
 - Asexual species at a disadvantage vis a vis sexual species

