One minute responses

- Q: Do platypus have more functional genes on their Y's than other mammals?

- A: I wasn't able to find out
  - I did learn that the platypus X's and Y's are not homologous to normal mammal X and Y
  - Some parts match mammal autosomes and some parts match bird Z chromosome!
  - Obviously those parts code for the duck bill :-)

One minute responses

- Q: Do we recognize X and Y (or Z and W) by shared characteristics or are those just arbitrary names for the male-heterogametic and female-heterogametic chromosome systems?

- A: The X/Y and Z/W systems have each evolved several times from different autosomes, so the names are arbitrary

Roadmap

- “Amazon” species
- Meiotic Drive/ Selfish Genes
- Evolution of Sexual Reproduction

“Amazon” species

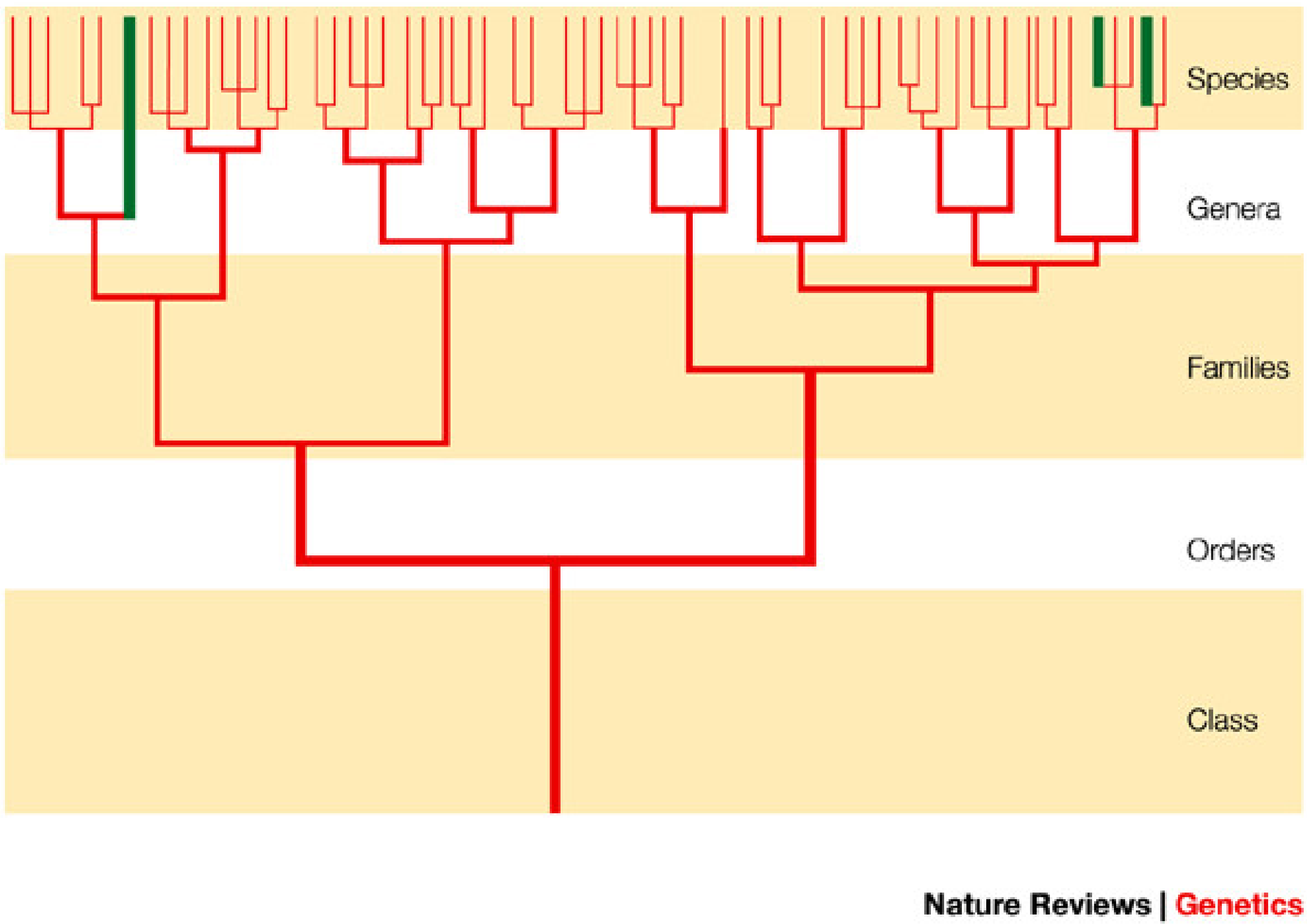
In some lizard and fish species:

- Only females exist
- They must mate so that a sperm can trigger egg development
- They discard the male genome and clone their own
- Reliant on related “normal” species to provide males

Amazon Molly, *Poecilia formosa*, a species which lacks males.

Lonely Amazons

- Males of the sexual species have an incentive not to mate with Amazons:
  - Wastes time and energy
  - Exposed to STDs
- Amazons can go extinct if:
  - Males refuse to breed with them
  - They outcompete species that have males
- This has been observed in artificial ponds
- Species like this arise fairly often, but don't last long


Species
Genera
Families
Orders
Class
Nature Reviews | Genetics

Meiotic Drive

- One allele is transmitted to offspring more often than the other

- t locus in mice:
  - A Tt male transmits t to 85% of his offspring and T to 15%
  - This behaves like very strong selection in favor of t
  - However, tt is lethal

Practice problem

- A Tt male transmits t 85% of the time
- tt individuals all die
- What is the frequency of t in crosses between a Tt male and a TT female?
- What is the frequency of t in crosses between a Tt male and a Tt female (count survivors only)?

Practice problem

- What is the frequency of t in crosses between a Tt male and a TT female? *Offspring are 85% Tt and 15% TT, so t has increased from its original 25% to 42.5%.*

Practice problem

- What is the frequency of t in crosses between a Tt male and a Tt female?

Female	Male	
	T 0.15	t 0.85
T 0.5	TT 0.075	Tt 0.425
t 0.5	Tt 0.075	tt 0.425

So at conception we have 0.075 TT, 0.5 Tt, 0.425 tt. After the tt die, we have 0.13 TT, 0.87 Tt. t has decreased slightly from its initial frequency of 50% to 44%.

- What do you predict long-term?

Meiotic Drive

- There may be group selection against t because a colony with t is less fertile and may go extinct
- However, mice have lots of excess fertility
- At the individual level, the meiotic drive of t balances its selective disadvantage and it is maintained as a polymorphism

Meiotic Drive

- This is called **meiotic drive** because the t chromosome appears "driven to succeed" in meiosis
- The t chromosome sabotages its T partner during meiosis
- Many populations of wild mice have t chromosomes at low frequency
- t chromosomes always have:
  - inversions around the t
  - lethal mutations linked to t inside the inversions

t is a selfish gene

- From the gene's point of view:
  - 2 offspring who both get the gene are as good as 4 offspring half of whom get it
- From the genome's point of view:
  - 4 offspring are better than 2!
- Sperm normally do not express their genome
  - Reduce chance of selfish gene problems?
  - This doesn't stop t because it acts during meiosis

Meiotic Drive

- Why are there lethals on the t chromosome?

- Could be Muller's Rachet:

  - Inversions suppress recombination
  - Without recombination, the t chromosome evolves asexually
  - Muller's Rachet predicts it will accumulate bad mutations

- My theory:

  - Without lethals t would fix almost instantly
  - Without inversions, it would shed its lethals and then fix
  - t without lethals and inversions fixes so quickly we never see it happening

Meiotic Drive on the sex chromosomes

- Imagine a Y mutation that leads to more than 50% transmission of the Y to offspring
- This will spread
- Females will start to become rare
- There is now a selective advantage for any mutation that can either eliminate the meiotic drive of the Y, or bias the sex ratio back toward females
- It's a race–either a second mutation will stop the selfish Y, or eventually the whole population will be male

Y-linked meiotic drive

- The mosquito *Aedes aegypti* has a driver on the Y, called Distorter
- In caged populations Distorter can destroy a population
- Attempts to use this for pest control failed:
  - Wild populations have loci that can suppress Distorter
  - These are rapidly selected when Distorter arrives
  - Wild populations end up with Distorter as a stable polymorphism
  - I bet they've seen it before....
- No human examples are known

A tricky X

Several South American mouse species have a variant X chromosome called X^*

X^*Y is a fertile *female*

Akodon azarae

Things can get complicated

If an X^*Y female mates with an XY male:

	X^*	Y
X	X^*X female	XY male
Y	X^*Y female	YY inviable

This does not cause infertility, because female mice always start more embryos than necessary, and the YY will abort. But it distorts the sex ratio significantly.

Why does this persist?

- Data:
  - The trait is old (X^* chromosomes are quite diverse)
  - It arose independently several times
  - X^*Y females start breeding at a younger age and continue breeding for a longer time than XX females.
  - X^* has a meiotic drive advantage

- Mathematical modeling of these numbers predicts the observed sex ratio fairly well

Evolution of Sexual Reproduction

1. Defining sex

2. Cost of sex

3. Arguments based on adaptation

4. Arguments based on error correction

5. Arguments based on linkage

Defining sex

I will define sex broadly as anything which creates individuals whose genomes incorporate genes from multiple different sources, with the new genes replacing homologous genes:

- Conventional sexual reproduction
- Transfer of part of a bacterial chromosome via Hfr
- Reassortment or recombination of viruses in a co-infection
- Picking up DNA from environment

Defining sex

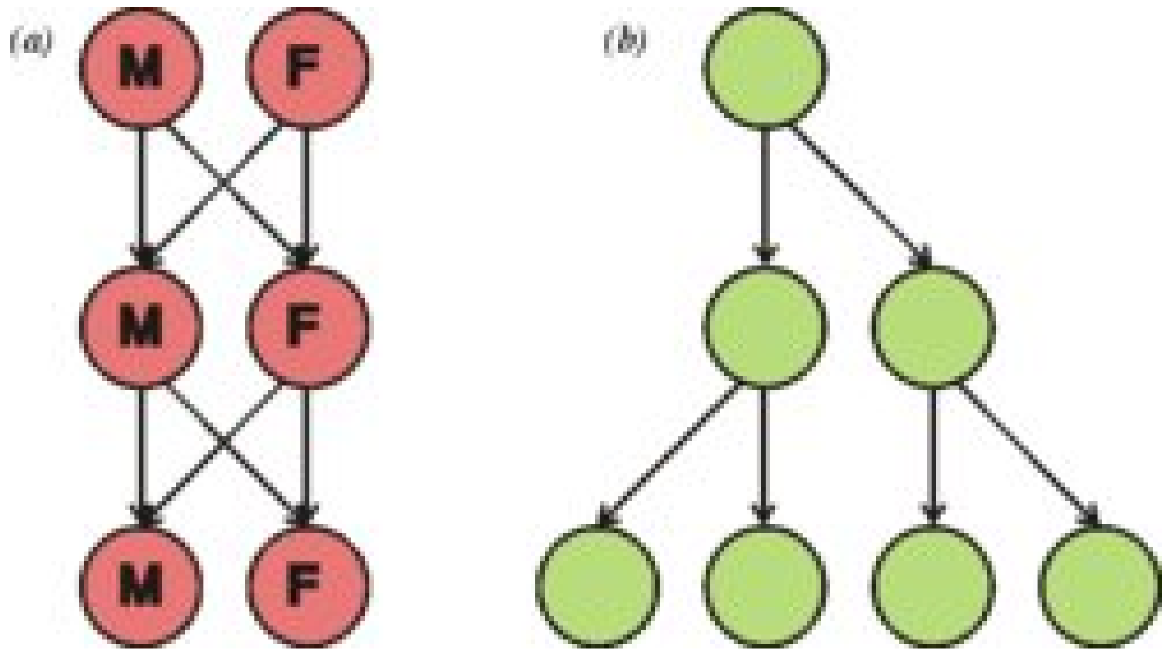
Related but a bit different are cases where there was no homologous gene originally:

- Gain of a plasmid
- Endosymbiosis
- Fusion of multiple different viruses into one
- Horizontal transfer of a gene with no homolog

Consequences of sex

- Many forms of sex create either a temporary or permanent diploid state
  - Error detection by comparing the two copies
  - Dominance/recessiveness
- Sex breaks up linkage disequilibrium
  - Creating beneficial new combinations
  - Breaking up good existing combinations

Twofold cost of sexual reproduction



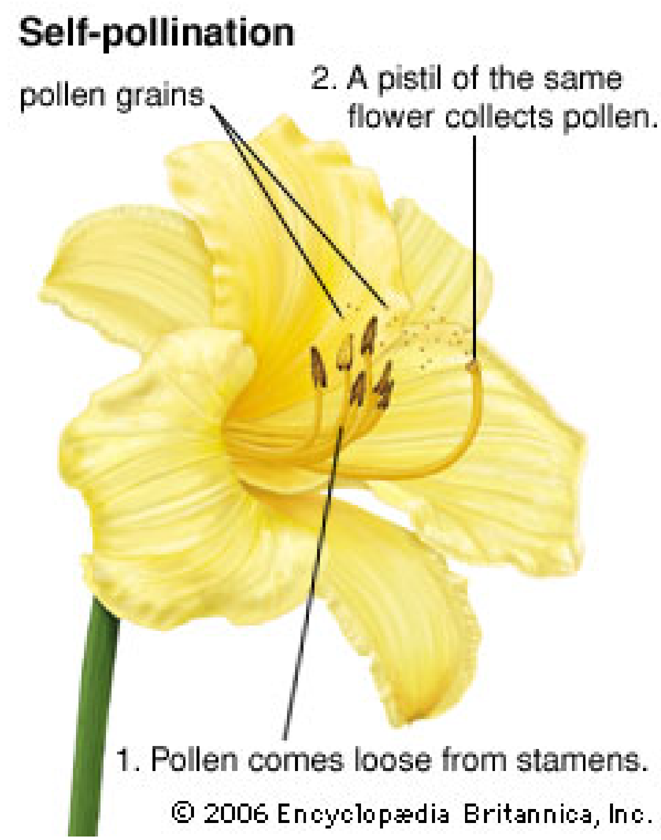
If an asexual offspring is as easy to make as a sexual one, the asexual transmits twice as many copies of your genome

Other costs of sex

- Your alleles work together–why break them up?
- Have to find a partner (if sex is obligatory)
- Have to find a partner of the right sex (if you have sexes)
- Could get an STD or get eaten by potential mate
- Your partner might discard your genes (Amazon Mollies)

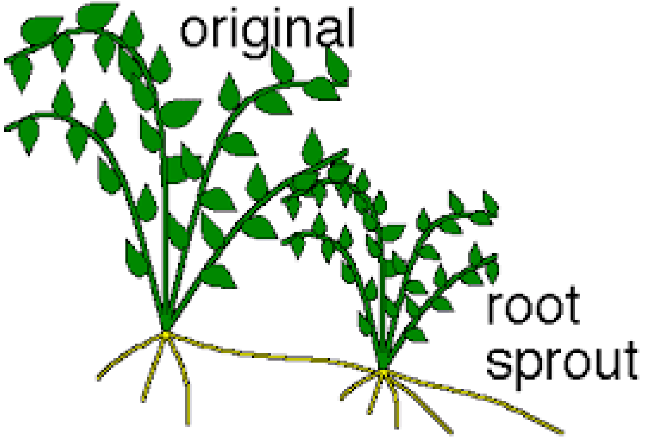
Routes to asexuality: self-fertilization

- An organism could give up sex by becoming self-fertilizing
  - Increases homozygosity
  - Preserves co-adapted gene complexes
  - Reduces fitness in the case of overdominant loci
  - Stops unfavorable gene flow
- Examples: many plants, nematode worms, some ticks



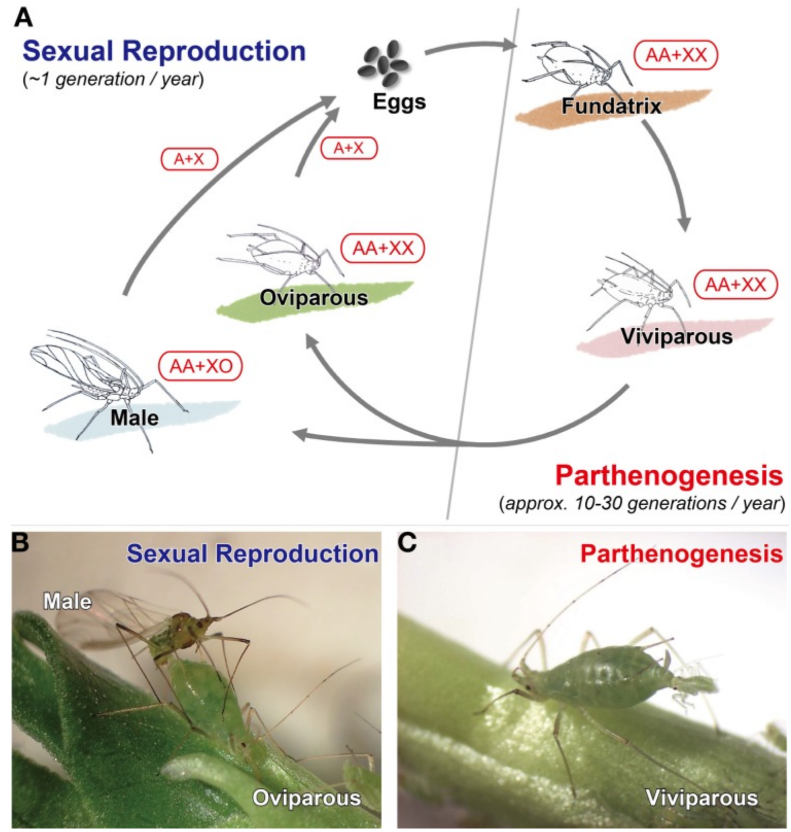
Routes to asexuality: cloning

- Alternatively, an organism could give up sex by cloning itself
  - Short-term, does not increase homozygosity
  - Preserves co-adapted gene complexes
  - Great for overdominant loci – can fix the heterozygote!
  - Long-term, diploidy will be lost
  - Examples: plants that reproduce vegetatively, bdelloid rotifers, Amazon mollies, some lizards, salamanders, many bacteria



Sex for special occasions only

- Aphids clone during summer and reproduce sexually in fall
- “Parthenogenesis” – female produces cloned offspring
- They also switch between live-bearing and egg-laying
- They can be born pregnant



Sex for special occasions only

- Yeast clones when conditions are good and sporulates sexually when they are bad
- Dispersal forms are often sexual
- Many bacteria pick up foreign DNA when starving – do they want sex or are they just hungry?

My favorite paper title of all time: "Bacterial Tranformation: Is Sex With Dead Cells Ever Better Than No Sex At All?" Rosemary Redfield, Genetics 119, 1988.

Sexual reproduction is vulnerable

- Consider a mutation that causes its possessor to go through meiosis and mate
- This allele is passed on to half the offspring
- Alternative alleles that cause cloning are passed on to all offspring
- A cloning allele will spread unless sexual offspring are:
  - Twice as fit
  - Half cost to produce
  - Some combination of those two

How is sexual reproduction maintained?

At least four explanations have been proposed:

- Sex allows production of more diverse offspring
- Sex maintains diploidy:
  - Overdominance
  - Correction of genetic errors
- Sex breaks up linkage disequilibrium

Diverse offspring

Adaptation explanations:

- Sexual offspring contain genetic combinations not found in either parent
- Diverse offspring may be able to inhabit more niches
- If many excess offspring are produced, the good ones are more important than the bad ones
- Evidence: dispersal forms (spores, winged aphids) are often sexual even in mostly-asexual species

Diverse offspring

- Diversity in a family has other advantages:
  - Reduced sibling competition
  - Reduced parent/offspring competition
  - Less vulnerable to each others' diseases and parasites
- Can this really overcome a twofold advantage?

Maintaining diploidy

- Cloning does not initially reduce heterozygosity
- Eventually an asexual will tend to lose its diploidy:
  - Second gene copy is redundant
  - Bad mutations are perfectly hidden from selection
  - Eventually the "backup" goes bad
  - Evidence: bdelloids have only one copy of most genes
- Without diploidy overdominance is impossible
- This may be particularly important in fighting parasites and disease

Maintaining diploidy

- However, once you are a heterozygote for an overdominant locus, cloning looks better than mating!

- Not clear how the long-term benefits of sex can overcome the short-term disadvantages

- An ex-diploid could fine-tune its two copies of each gene to two related functions

- Parasites themselves often lose sex (they may have trouble finding mates)

Another use for diploidy

Error-correction explanations:

- Having two copies of your genes allows correction of errors that arise in replication
- Sexuals allow selection to keep both copies functional
- Again, how can a long-term advantage overcome the short-term cost of sex?
- Are error-corrected offspring really twice as good?

How is sexual reproduction maintained?

Linkage explanations:

- Positive form:
  - An asexual cannot combine favorable mutations that occur in two different individuals
  - A sexual can, and can increase its fitness that way
- Negative form:
  - An asexual genome will accumulate harmful genes that are linked to beneficial ones (Muller's Rachet)
  - A sexual genome can shed them by recombination

In organisms where fathers help out

- If I clone myself, males have no evolutionary reason to help raise my offspring (unless they are my kin)
- If I mate, the male has a reason to help raise our offspring
- If we can raise more than 2x as many offspring together as separately, sex is favored
- This doesn't apply to species without paternal care (a lot of sexual species have none)

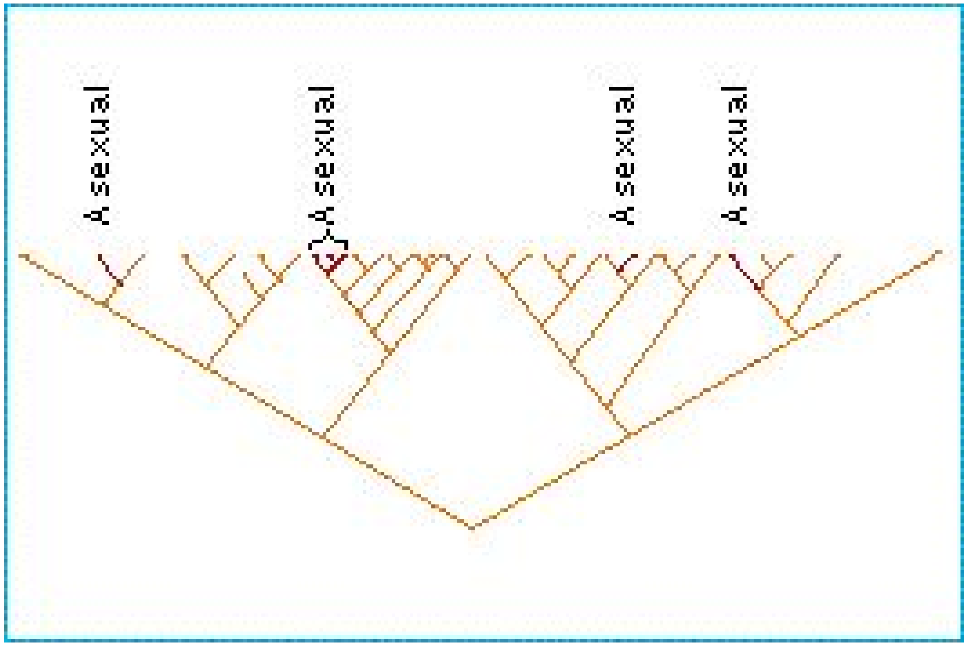
How is sexual reproduction maintained?

- Some of these look like group selection–sex helps the species but not individuals

- The situations under which group selection work in simulations are very limited

- If you are crowded out by asexuals today, it is cold comfort that in a million years they will have troubles....

Evidence for long-term problems with asexuality



Asexual species appear evolutionarily short-lived (bdelloids are the one huge exception)

How is sexual reproduction maintained?

- One of the most debated points in evolutionary biology
- Human need for tidy answers may be a problem
- Perhaps multiple theories are partially correct under different circumstances
- A kind of species "genetic drift" may also be involved:
  - Sub-optimal species may persist by chance
  - If they have better long-term prospects, eventually species of their type will predominate

How is sexual reproduction maintained?

- It is difficult to do adequate computer simulations because the situation is so complex
  - environmental interactions
  - host-parasite interactions
  - relative frequency of helpful and harmful mutations
  - relative intensity of helpful and harmful mutations
  - frequency of overdominant and underdominant mutations
  - cost of sex

One-minute responses

- Tear off a half-sheet of paper
- Write one line about the lecture:
  - Was anything unclear?
  - Did anything work particularly well?
  - What could be better?
- Leave at the back on your way out