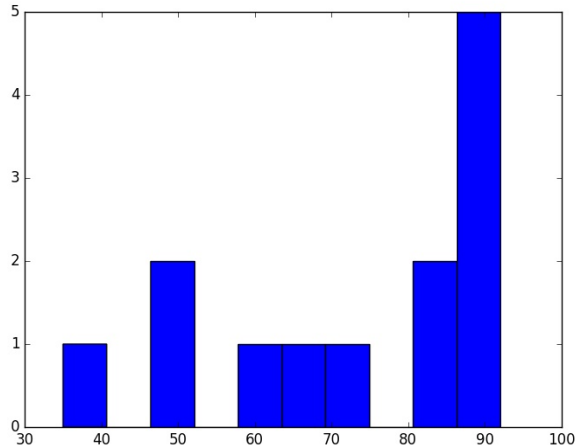
Roadmap

- Finishing up inbreeding
- Evolution of gender
  - Sex ratio – how many males and females?
  - Sex determination – how did they get to be male/female?
  - Some truly weird animals

Midterm

- Mean 72.6
- Range 35-92
- Cause for concern if below 60



What to do?

- Adjust homework strategy? (Passive understanding is not enough)
- Practice problems
- Office hours
- Study group

Inbreeding

$f = 1$ is complete self-fertilization

$f = 0$ randomly mating population

- We can think of inbreeding as dividing the population into two parts:
  - a fraction f which receive their two alleles from a single gene copy in an ancestor
  - a fraction $(1 - f)$ which receive their two alleles at random from the gene pool

- Inbreeding always increases homozygotes

Genotype frequencies with inbreeding

$$\text{frequency}(AA) = p^2 + fpq$$
$$\text{frequency}(Aa) = 2pq - 2fpq$$
$$\text{frequency}(aa) = q^2 + fpq$$

- Inbreeding does not itself change allele frequencies
- Selection on an inbred population:
  - Focuses more attention on homozygotes
  - May have a different outcome because of this

Effects of inbreeding

- Random mating:
  - Any heterozygote advantage leads to stable equlibrium
- Inbreeding
  - Heterozygotes are rare so their advantage matters less
  - At $f = 1$ one allele will fix
  - Intermediate values of f can still have equilibria but they are less stable
  - If too far from the equilibrium frequency, one allele will fix

Do humans avoid inbreeding?

- Most cultures actively avoid brother/sister matings
- Some cultures forbid cousin marriages but others prefer them:
  - About 10% of marriages worldwide are first-cousin
  - Up to 50% in some areas
  - Increases birth defect risk from 3% to 4%
  - This is comparable to the increased risk of having a child at age 40 rather than 30

Is inbreeding "bad for the gene pool"?

- Small population size can be bad for the gene pool because of drift
- Inbreeding itself does not change allele frequencies, only genotype frequencies (pushes away from H-W)
- Homozygosity due to inbreeding disappears after one generation of random mating

Inbreeding and the gene pool

- Inbreeding coupled with selection can be good or bad
  - It allows quicker loss of harmful recessives
  - It loses helpful overdominants
- Inbreeding an outbred population will produce a burst of unpleasant recessive phenotypes
- Long-term inbreeding will eliminate these
- Inbreeding is blamed for many problems actually due to drift

Inbreeding versus small size

- Inbreeding:
  - Increases homozygosity
  - Does not directly change allele frequencies
  - Does not eliminate alleles
  - Reveals recessives to selection
- Small population size:
  - Leads to rapid drift in allele frequencies
  - Can eliminate alleles or make them frequent
  - Diminishes the power of selection

Evolution of the sex ratio

- Many organisms have roughly 50/50 sex ratio
- Not all do
- How does sex ratio evolve? What are the factors?

Harem-keeping

- One breeding male and many breeding females per group:
  - sea lions
  - deer
  - horses
  - lions
- Why do these species normally retain 50/50 sex ratio?
- Somewhere out there are 8 disappointed males–what are they good for?

What if only 1 male was born per 9 females?

- 10 adults must produce 10 offspring to replace themselves
  - Average female produces 1.1 offspring
  - Average male produces 10
  - Gene copy in a male will be in 1/2 his offspring = 5
  - Gene copy in a female will be in 1/2 her offspring = 0.55
- An allele that makes male offspring will be in males, and will increase
- The biased sex ratio is evolutionarily unstable

Equal investment

- Sex-ratio logic was developed by RA Fisher
- Selection favors $equal\ investment$ in sons and daughters
  - If sons and daughters equally expensive, this yields 50/50
  - If one sex is much more expensive, fewer will be produced
- Humans have a slight bias toward male births–105-107 boys per 100 girls

How does that happen?

How does X/Y sex determination give a ratio other than 50/50?

- X and Y bearing sperm differ (Y are lighter)
- Implantation of XX and XY eggs may not be identical (not proven)
- Miscarriage of XX and XY differs

If an organism would benefit from a skewed sex ratio there are usually ways for one to evolve even in a chromosomal sex determination system.

Brainstorm

Why might humans have a biased sex ratio?

Some data:

- It's seen in all populations though intensity varies
- It was apparent prior to ways to determine fetal sex in advance
- Males have higher mortality in all age classes after birth

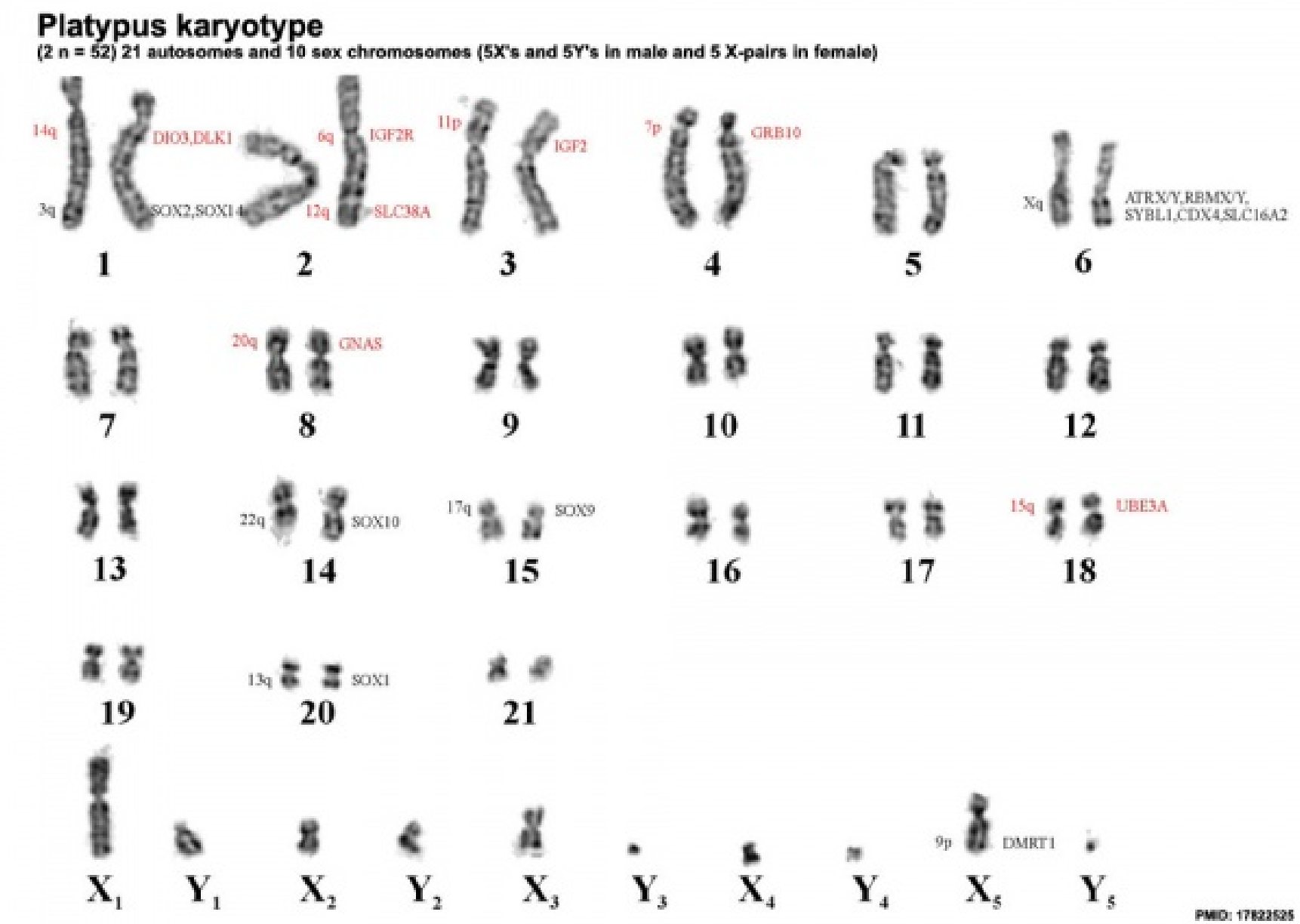
Deer fine-tune their sex ratio

- Big males are more likely to reproduce
- Big sons are expensive for mother
- Mothers tend to have more sons when the mother is:
  - Large
  - Well-fed
  - Socially dominant
- Probably due to sex-specific miscarriage

XX/XY sex determination

Mammals, some amphibians:

- Usually XX female, XY male
- Sex determined by a master gene on the Y
- XO are sterile females
- Weird exception: Platypus have 5 X's and 5 Y's
- Their meiosis involves daisy-chaining all 10 chromosomes


Platypus karyotype
(2 n = 52) 21 autosomes and 10 sex chromosomes (5X's and 5Y's in male and 5 X-pairs in female)
14q
DIO3,DLK1
3q
SOX2,SOX14
6q
IGF2R
12q
SLC38A
11p
IGF2
7p
GRB10
Xq
ATRX/Y,RBMX/Y,
SYBL1,CDX4,SLC16A2
1
2
3
4
5
6
20q
GNAS
7
8
9
10
11
12
22q
SOX10
17q
SOX9
15q
UBE3A
13
14
15
16
17
18
13q
SOX1
19
20
21
9p
DMRT1
X1
Y1
X2
Y2
X3
Y3
X4
Y4
X5
Y5
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Different flavor of XX/XY

Flies:

- XX female, XY male
- Sex determined by ratio of autosomes to X's:
  - 3A/1X – "supermale"
  - 2A/1X – male
  - 3A/2X – intersex
  - 2A/2X – female
  - 3A/3X – female
  - 2A/3X – "superfemale"
- Y is not needed except to improve fertility

ZZ/ZW system and haplodiploidy

- Birds, butterflies, some amphibians:
  - ZW female, ZZ male
- Ants, bees, wasps:
  - Males are haploid (from unfertilized eggs)
  - Females are diploid (from fertilized eggs)
  - Decision to fertilize is up to the mother
  - No sex chromosomes

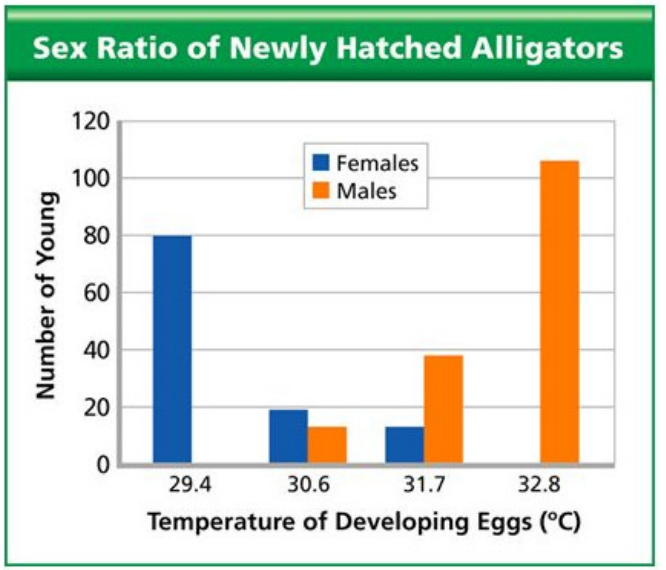
Temperature dependent sex determination

In some reptiles and amphibians:

- No sex chromosomes
- Sex is determined by temperature
- Low temperature is male in some species and female in others
- Parents can influence gender of offspring during egg-rearing

American alligators

- 72% female (1995-1999 in Louisiana)
- Males are high-temperature sex (i.e. this is not global warming)
- Is this stable? If so, how?
- Are cold female babies cheaper to raise than hot male ones?



Evolutionarily unstable?

- Normally ZW/ZZ
- Some ZZ females at extreme temperatures
- Selective breeding at high temperatures lost the W completely leading to a temperature-dependent system with no sex chromosomes
- FAST evolutionary change!

Bearded Dragon

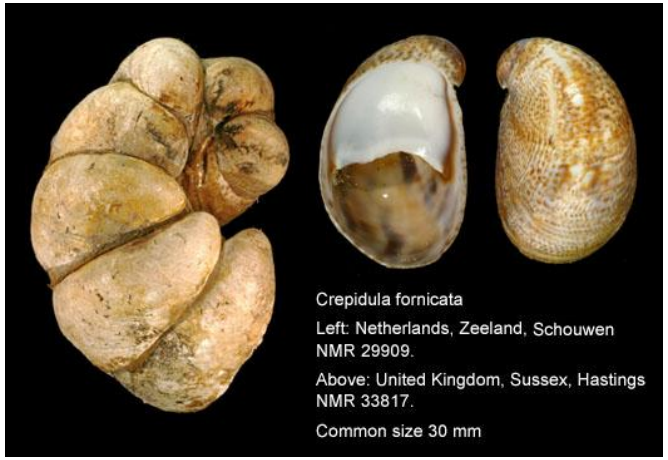
Sex Determination

In some fish and molluscs:

- Sex changes during an individual's life
- Usually male when small and female when large
- Females invest more in their offspring (large egg, small sperm) so it useful to be male if you are small and can't invest much
- Opposite case can happen if there is male/male competition and size matters

Sex Determination

- The mollusc *Crepidula fornicata* lives in stacks
- The bottom animal becomes female; all others become male
- Lowest, largest male fathers 86% of offspring
- I don't know why the others become males...



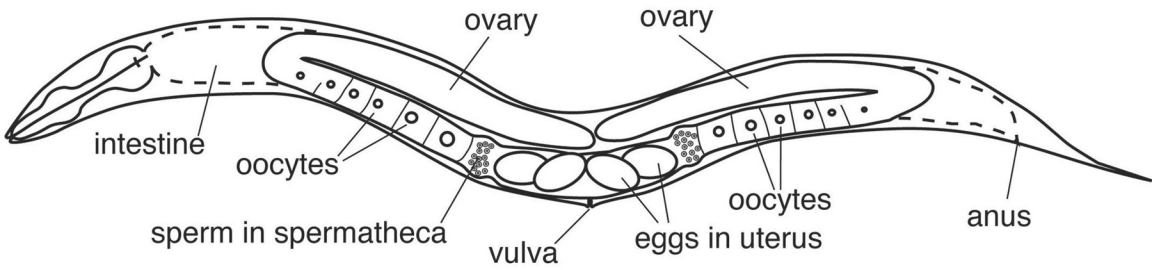
What about plants?

- Males XY, females XX (campion)
- Males and females are haploid: males have Y, females have X (liverwort)
- Choice of male vs. hermaphrodite made based on neighbors' pheromones (fern)
- One gene system: different alleles are male, female, or hermaphrodite (papaya)
- Two gene system: different allele combos are male, female, hermaphrodite or have separate male and female flowers on the same plant (cucumber)

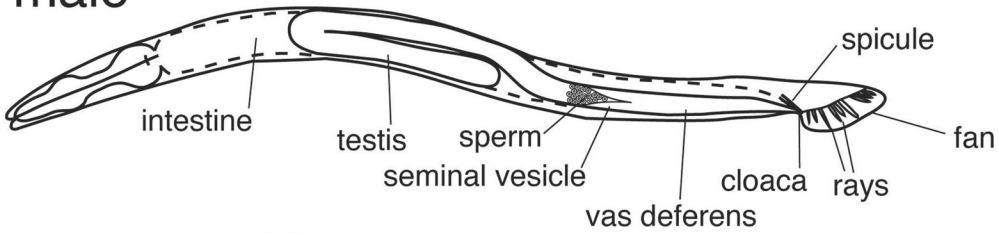
Two sexes but not male and female

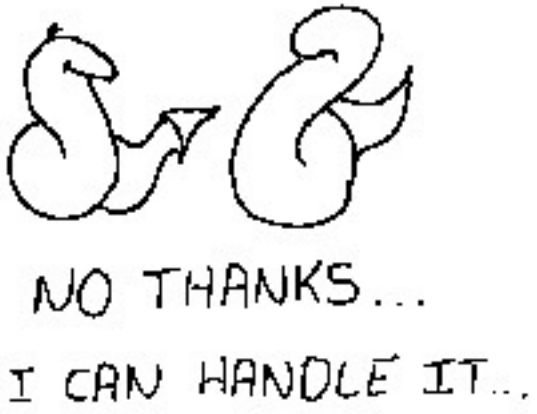
- Nematode *C. elegans* has hermaphrodites and males
  - Hermpaphrodites are XX and can self-fertilize
  - Males are XO and can mate with hermaphrodites
  - (Two hermaphrodites can't mate)
- Equal-ratio argument does not apply as most individuals do not have a male parent
- Males are rare (0.05%) in most lab and wild populations

XX hermaphrodite



XO male





Which one is the female?

- Yeast have two genders a and α
- Mating involves the whole organism (they fuse to make a diploid)
- Some can switch gender by targeted gene conversion
- Why does an organism that can switch gender at will bother to have gender?

inactive a gene	active a gene	inactive α gene	**"a" individual**

inactive a gene	active α gene	inactive α gene	**"α" individual**

"Amazon" species

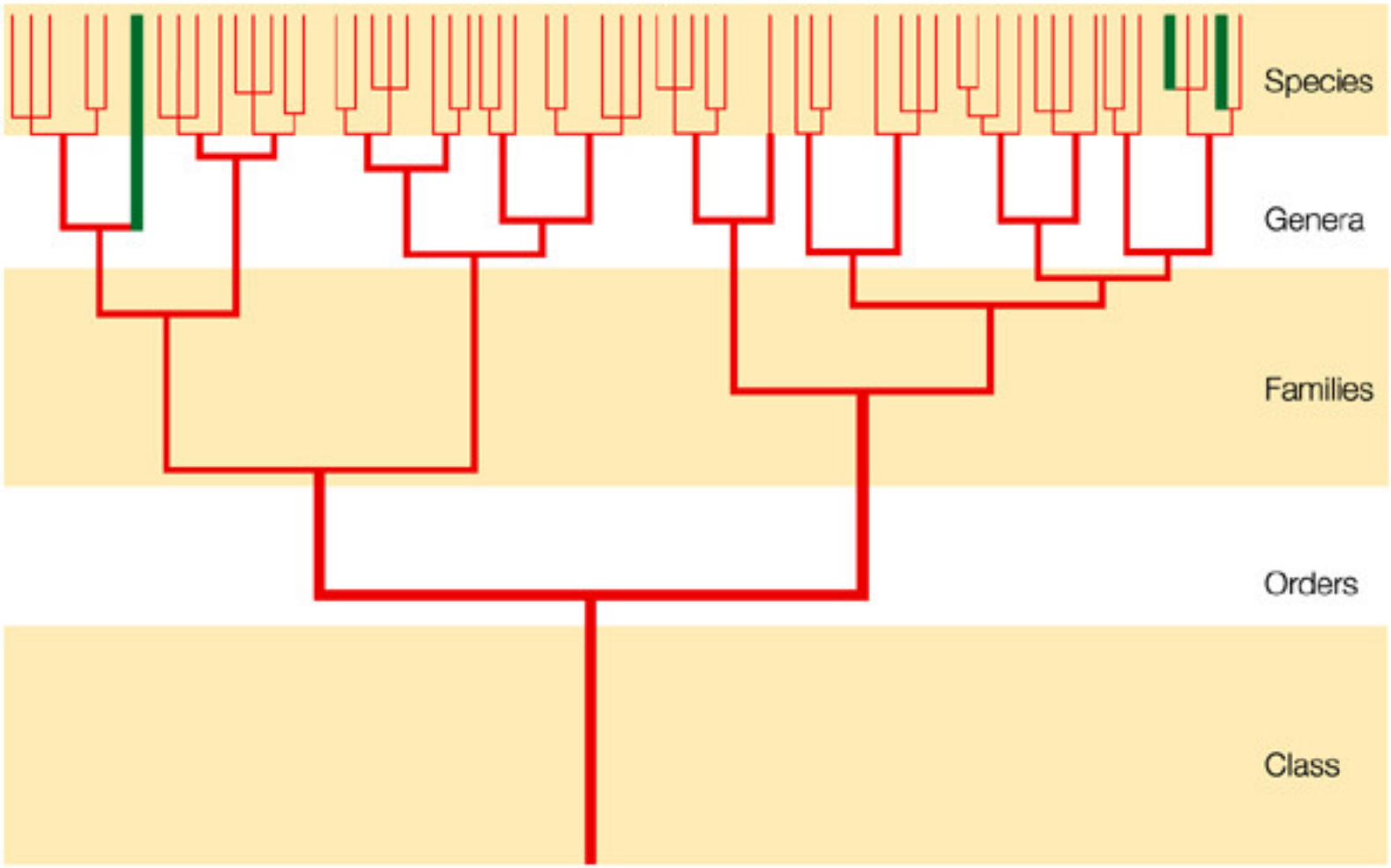
In some lizard and fish species:

- 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



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Why have sex in the first place?

- Not as obvious as it sounds
- Bdelloids went 40 million years without getting any
- A wide variety of explanations–not necessarily mutually exclusive

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