

# INSIGHTS FROM THE TREE OF SEX: WHY SO MANY WAYS OF DOING IT?



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# TREE OF SEX CONSORTIUM



<http://treeofsex.org>



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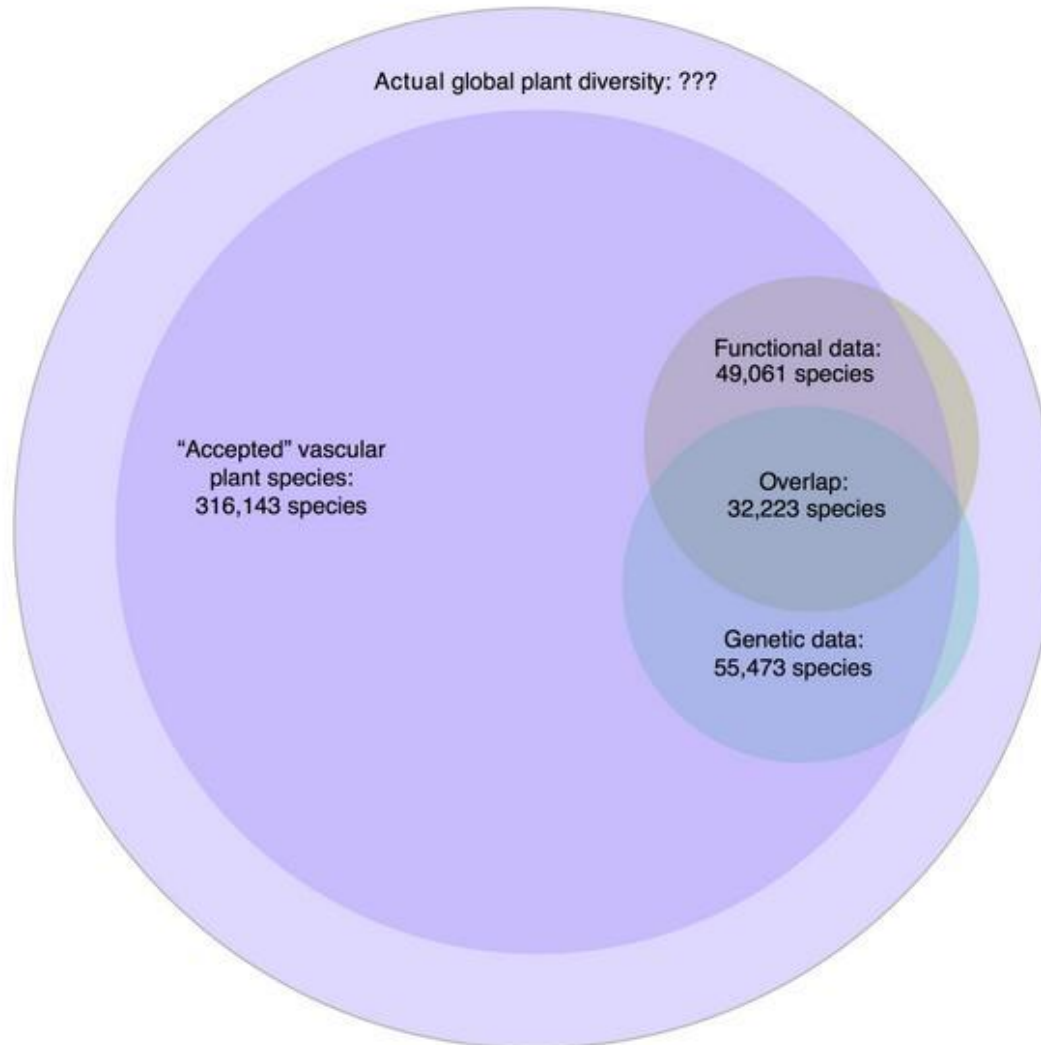
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# STATE OF KNOWLEDGE IN MOST SYSTEMS



Species counts from Smith et al. (2001), Zanne et al. (2014), and the Plant List (v1.1)

## XY sex chromosomes



Female

X X

Male

X Y

## ZW sex chromosomes



Female

Z W

Male

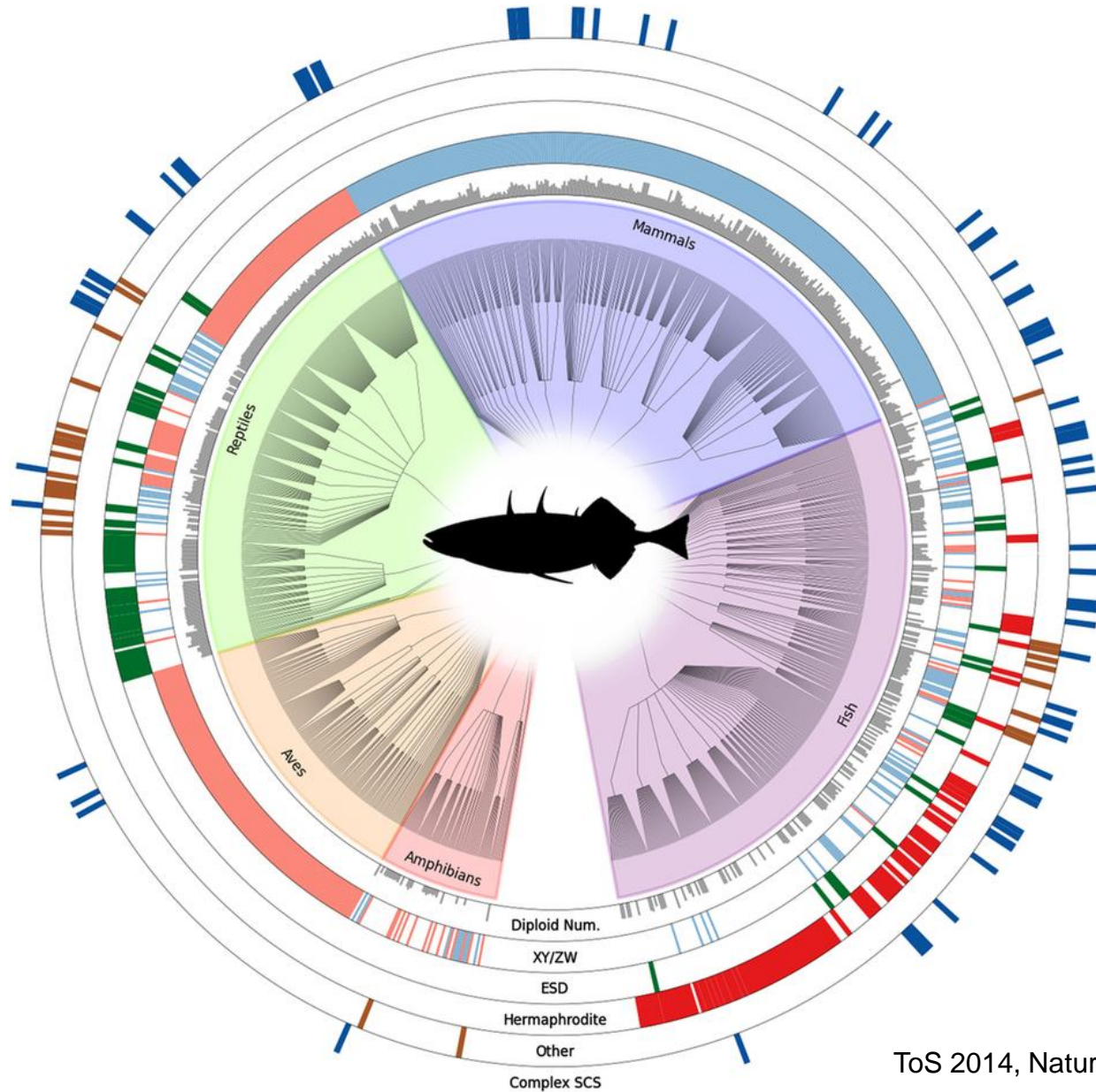
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# INSIGHTS FROM THE TREE OF SEX

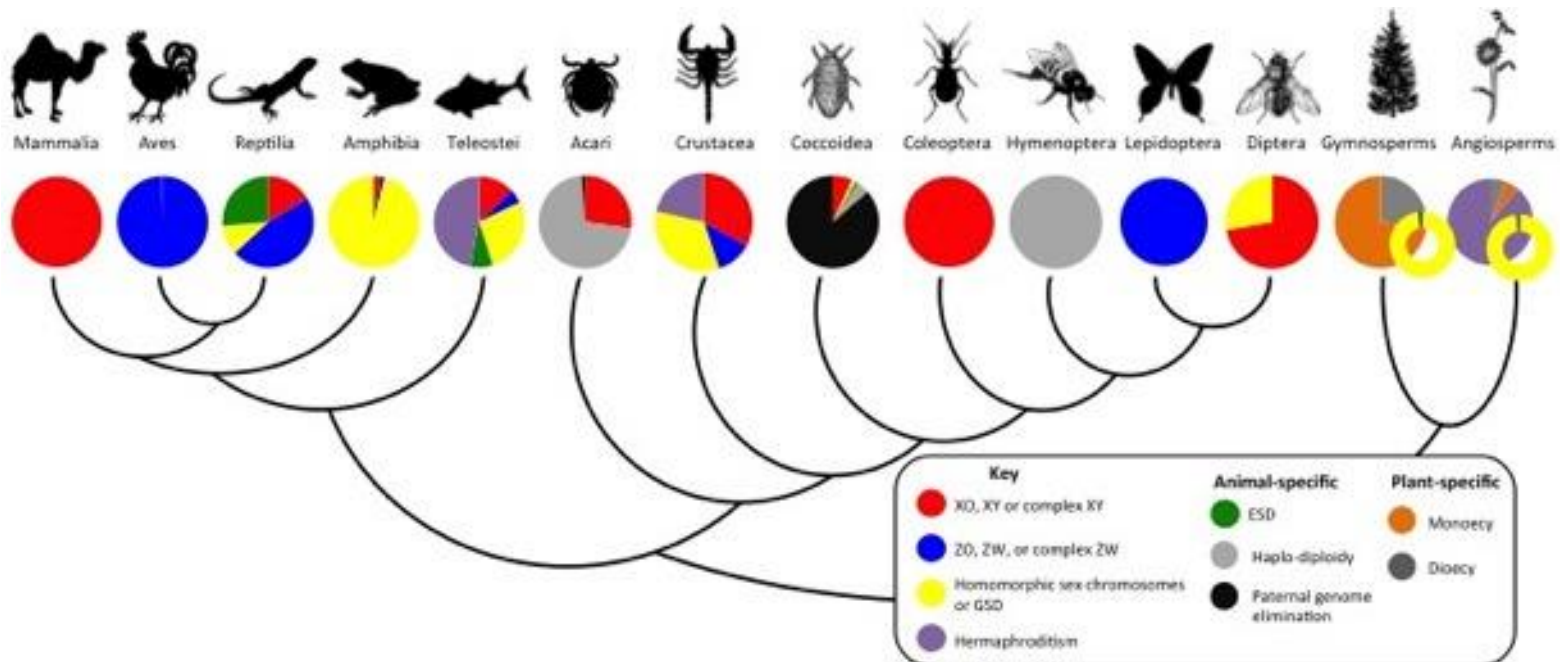
- Variation in sex determination on the Tree of Sex
  - Myths uncovered
- How do transitions in sex determination system occur? Multiple chromosome systems
- Starting fresh. Hermaphroditism to dioecy and back again



# TREE OF SEX COMPILATIONS - VERTEBRATES



# THE ENTIRE TREE OF LIFE

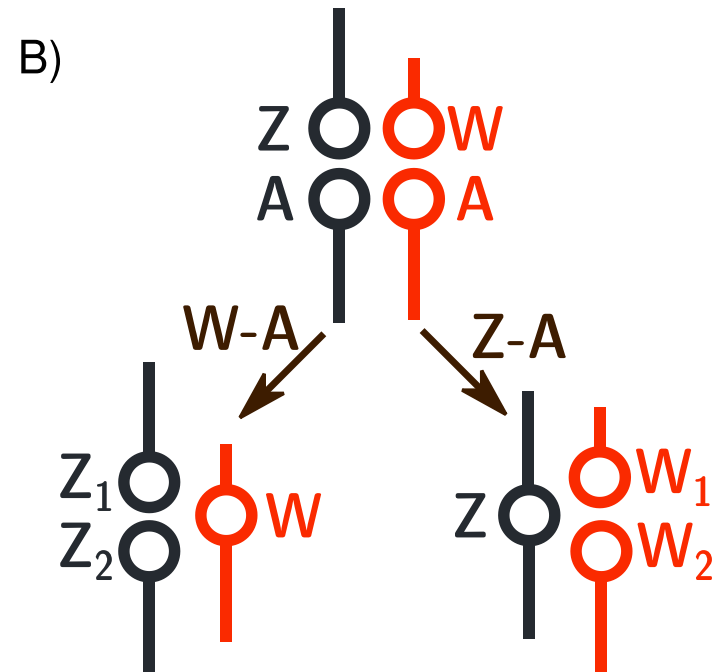
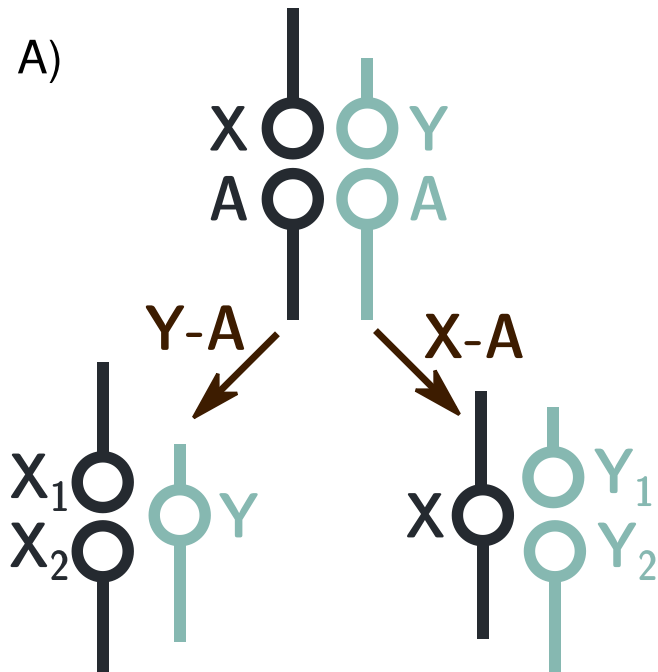


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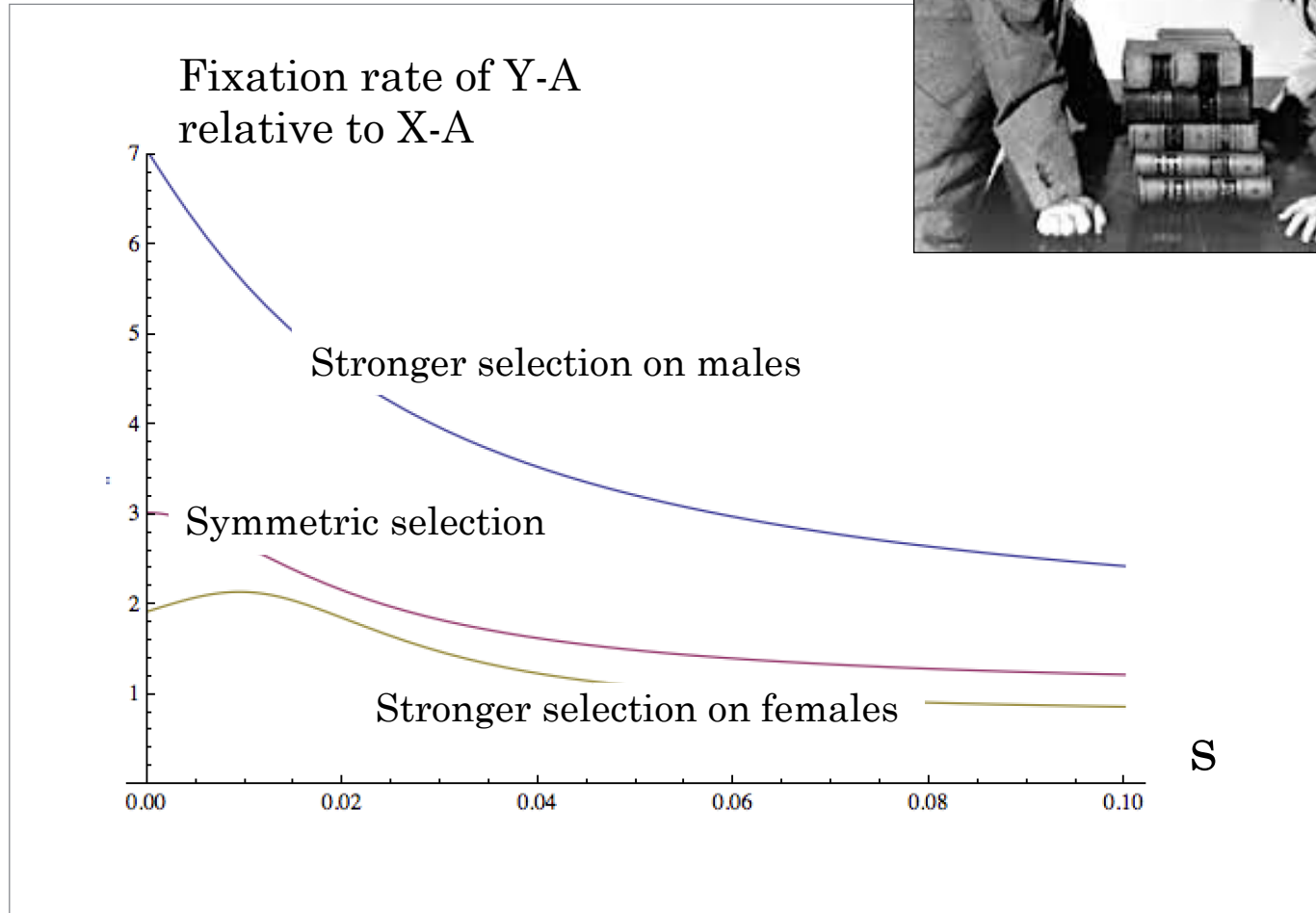
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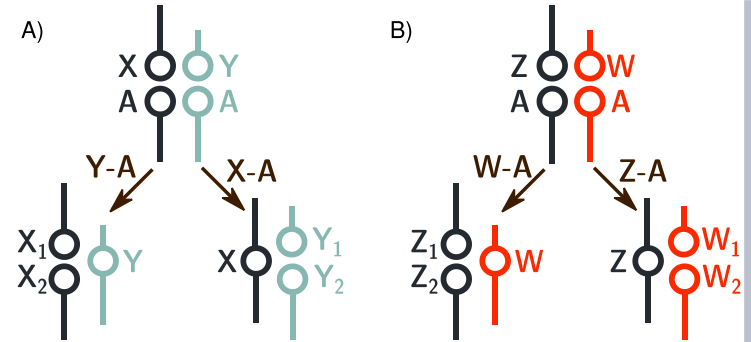
# SEX CHROMOSOME-AUTOSOME FUSIONS



# SEX-ANTAGONISTIC SELECTION



# FUSIONS



- Y-A > X-A has long history
- Sexual antagonism thought to be key
  - males benefit from fusion as it is a mechanism that links Y-chromosomes with autosomal traits upon which sexual selection can act
- Prediction: Should work in ZW systems but pattern should be reversed (Z-A fusions more prevalent)
  - Can now examine in fishes and squamate reptiles



Female

ZW

Male

ZZ

# SEXUAL DIMORPHISM



*Anolis cybotes cybotes*



*Anolis distichus dominicensis*



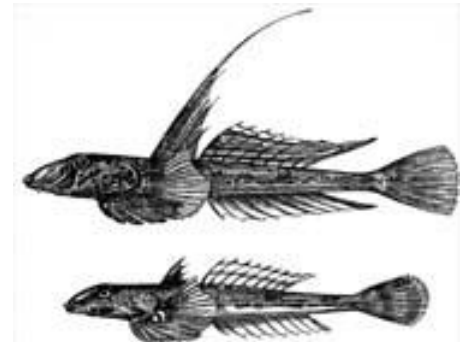
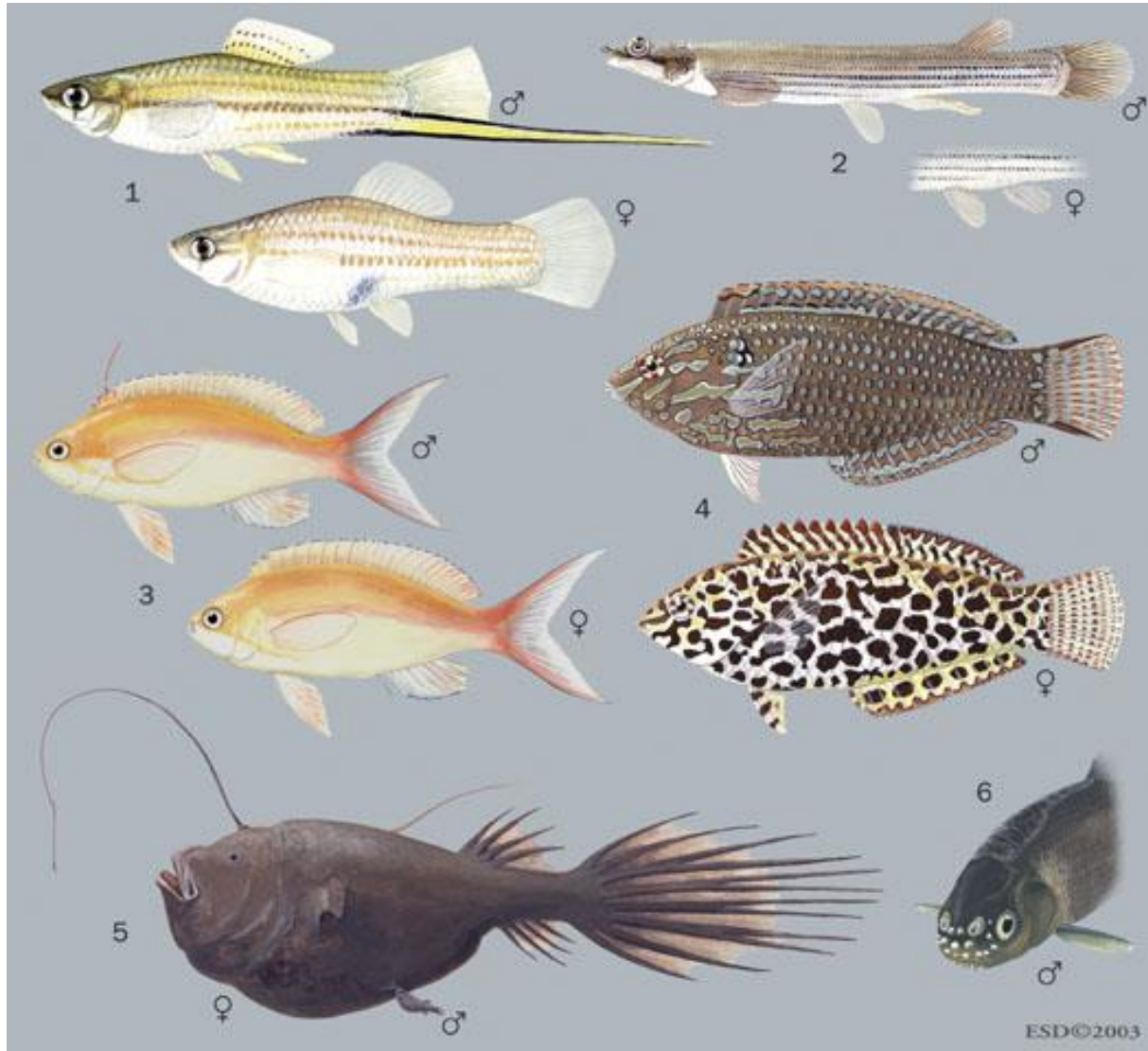
*Anolis evermanni*



*Anolis christophi*



# SEXUAL DIMORPHISM





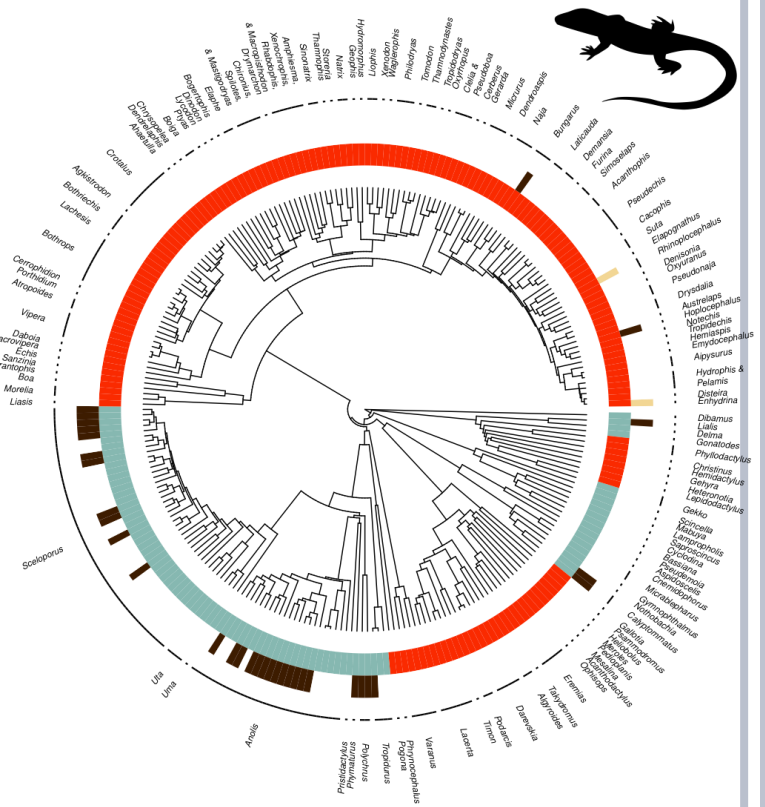
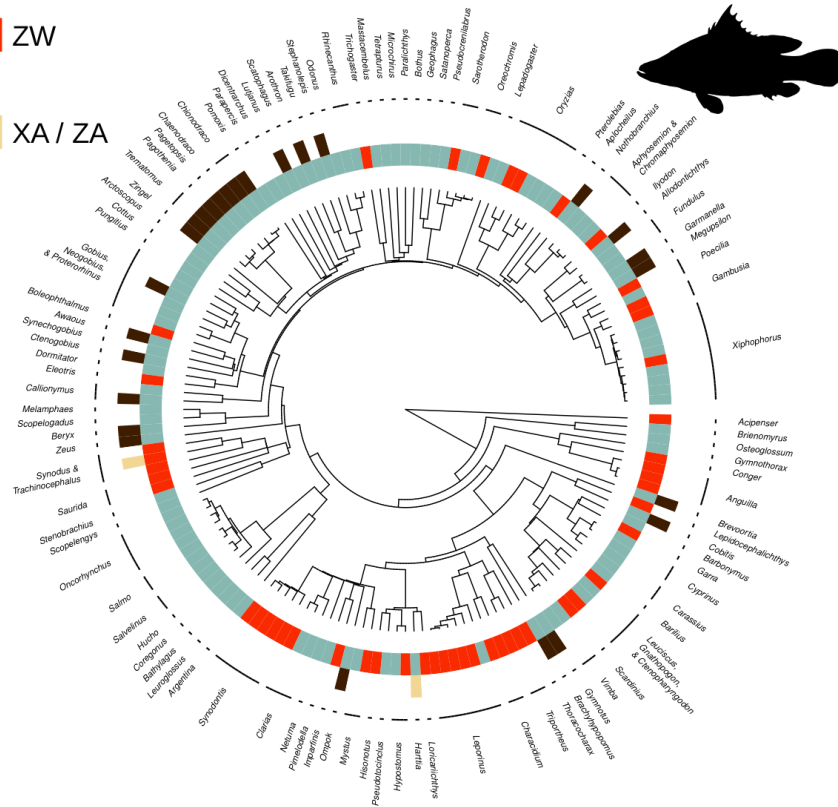
# RESULTS

SD System

XY ZW

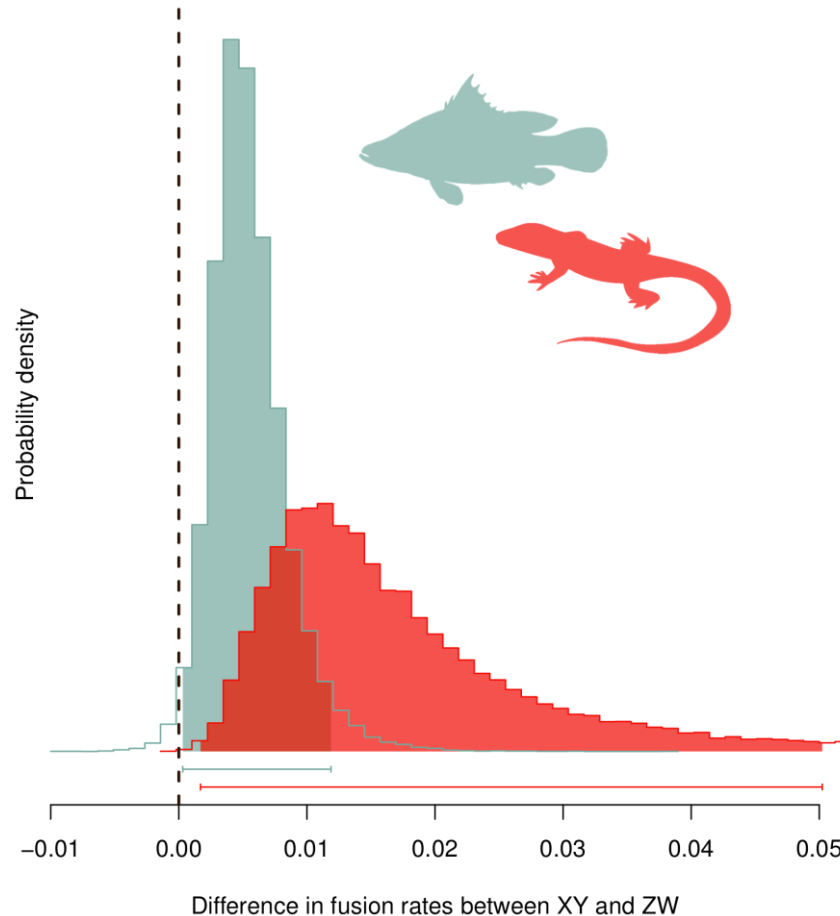
Fusion

YA / WA XA / ZA



In fishes and squamates, fusions in XY lineages were inferred to occur at a higher rate than ZW lineages.

# RESULTS



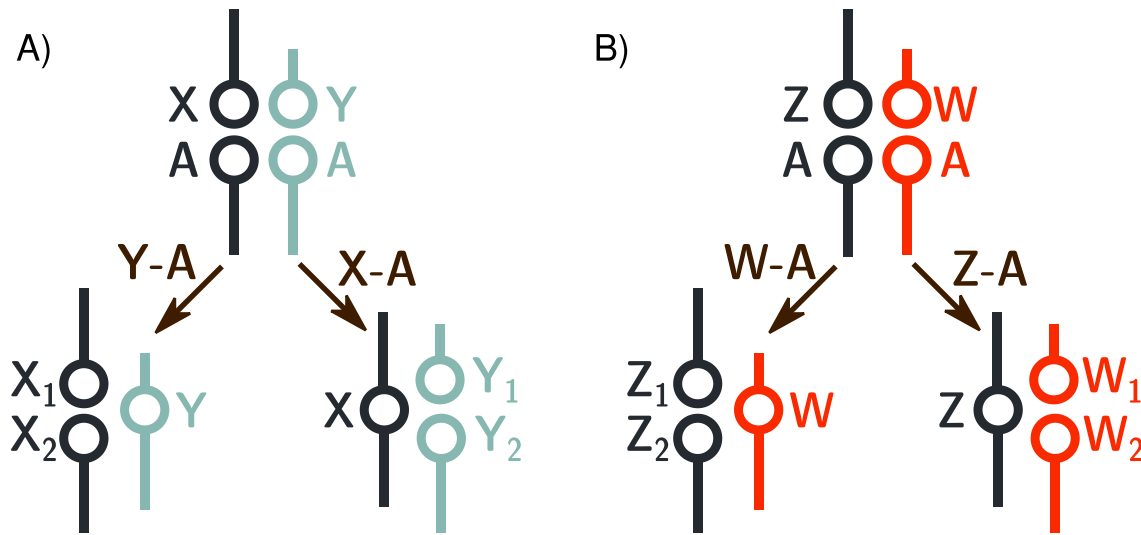
A lot higher: In Fish 99.6% of the posterior probability dist, fusions in XY lineages were inferred to occur at a higher rate than ZW lineages. In squamates, 99.9% fusions in XY > ZW lineages

# Y DO THESE FUSIONS FIX?

Ways that X, Y, Z, and W chromosomes differ:

- The opportunity to fuse
  - E.g.: In XY systems, there are 3 times more X chromosomes available to fuse than Y
- The probability that a fusion fixes/establishes
  - E.g.: The population size of X-A fusions is three times larger than that of Y-A fusions so drift could be a stronger force in Y-A fusions

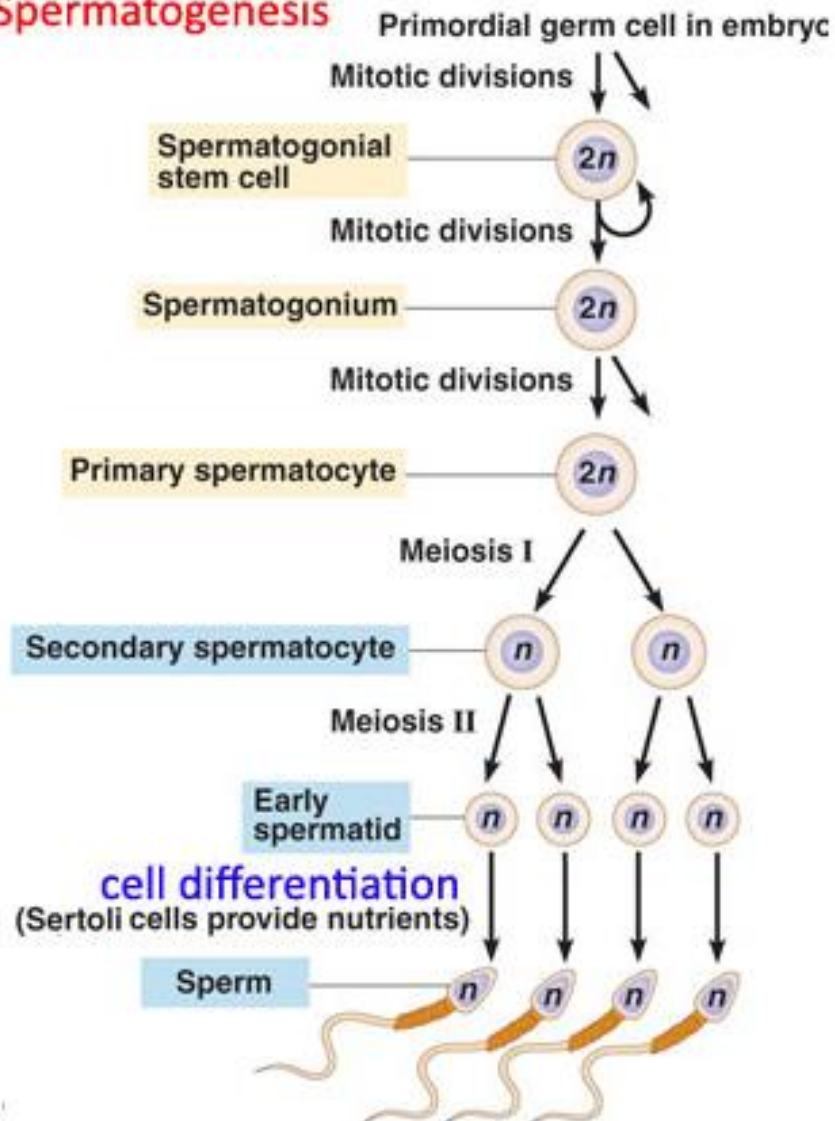
# ARE FUSIONS BENEFICIAL?



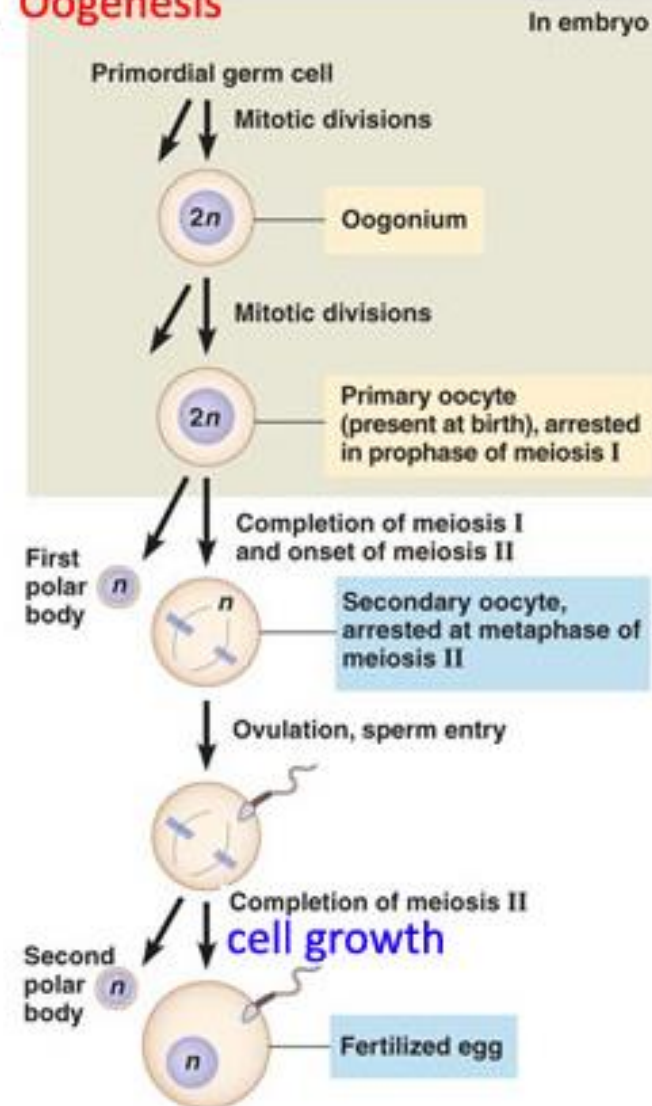
- The most common translocation in humans involves chromosomes 13 and 14 and is seen in about 0.97 / 1000 newborns.
- Carriers have no abnormalities, but there is a risk of unbalanced gametes that lead to miscarriages or abnormal offspring
- Most medical studies indicate they arise disproportionately in males

# SEX DIFFERENCES IN CELL DIVISIONS

## Spermatogenesis

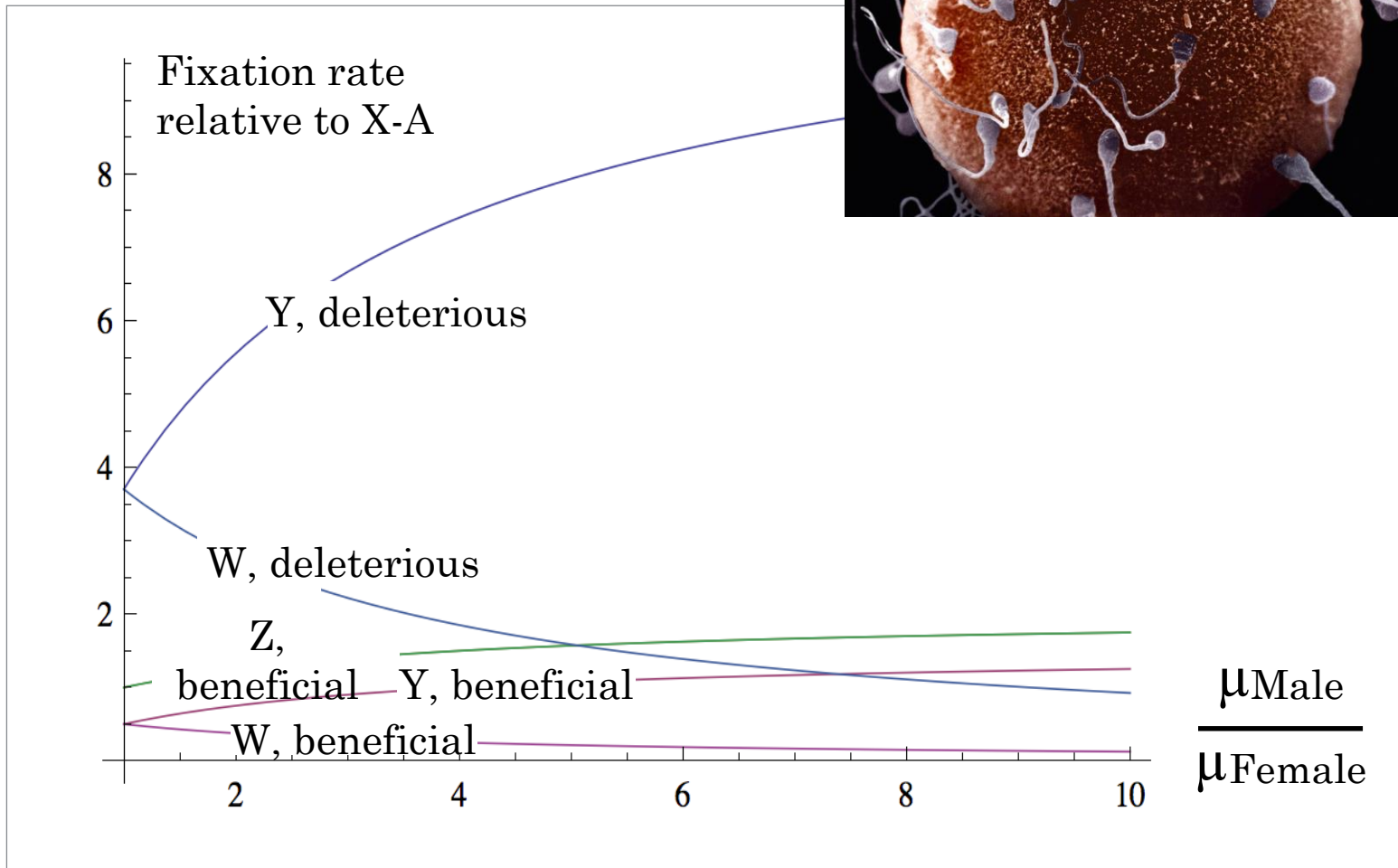


## Oogenesis





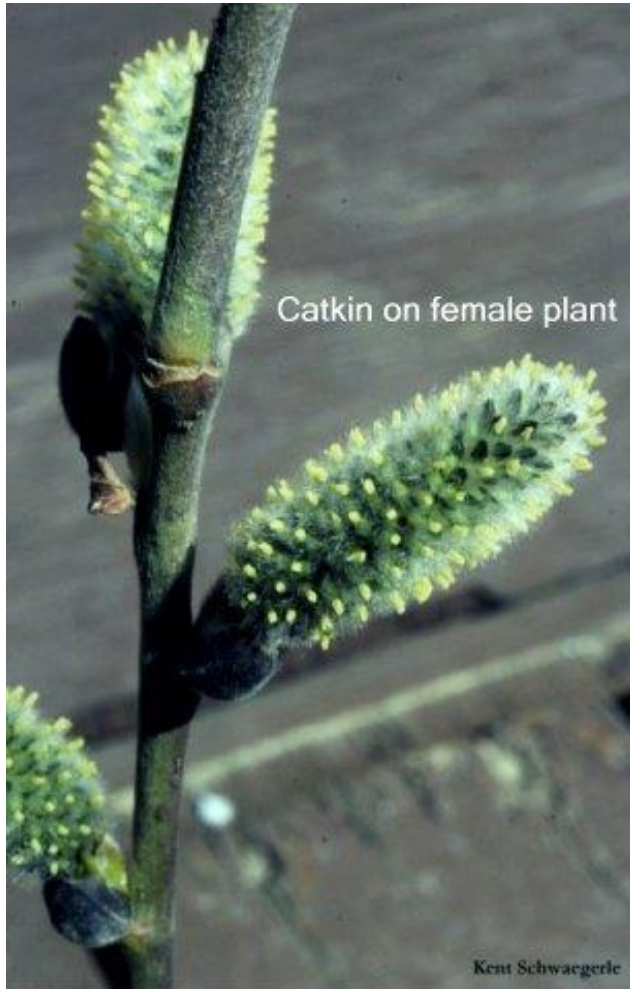
# SEX-BIASED MUTATION



# INSIGHTS FROM THE TREE OF SEX

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- How do transitions in sex determination system occur? Multiple chromosome systems
- **Starting fresh. Hermaphroditism to dioecy and back again**

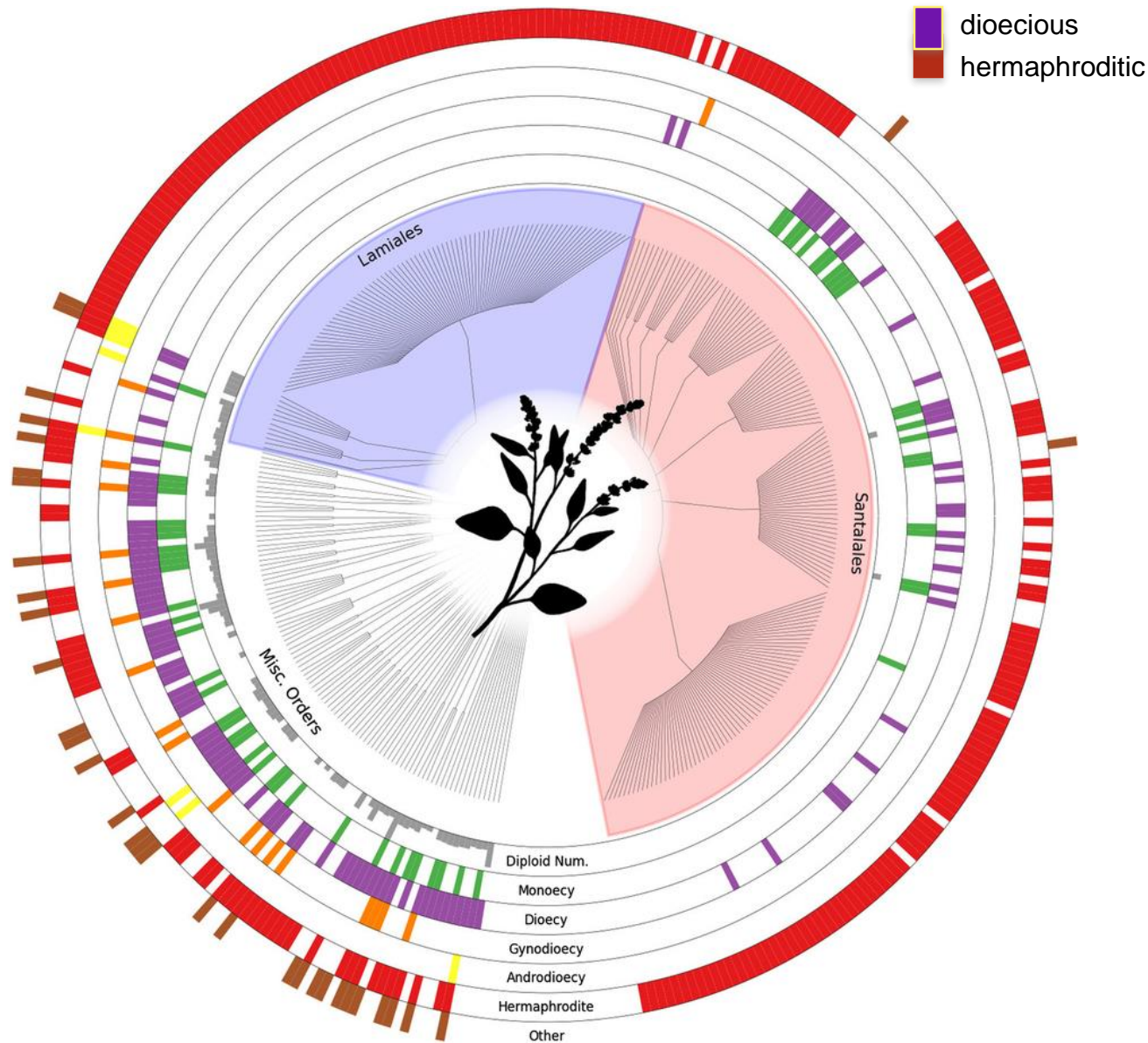
# DIOECY: A SEPARATION OF THE SEXES



# THE RARITY OF DIOECY

- Dioecy represents the sexual system of ~6% of flowering plants
- Reasons for rarity
  - Evolves rarely; Separates sexes reduce inbreeding but may reduce reproductive success if pollen does not transport to stigma
  - Evolves readily but experiences reduced evolutionary success; dioecy represents an “evolutionary dead-end”
  - Evolves readily but transitions back to a nondioecious state quickly.

# TREE OF SEX COMPILATIONS - PLANTS

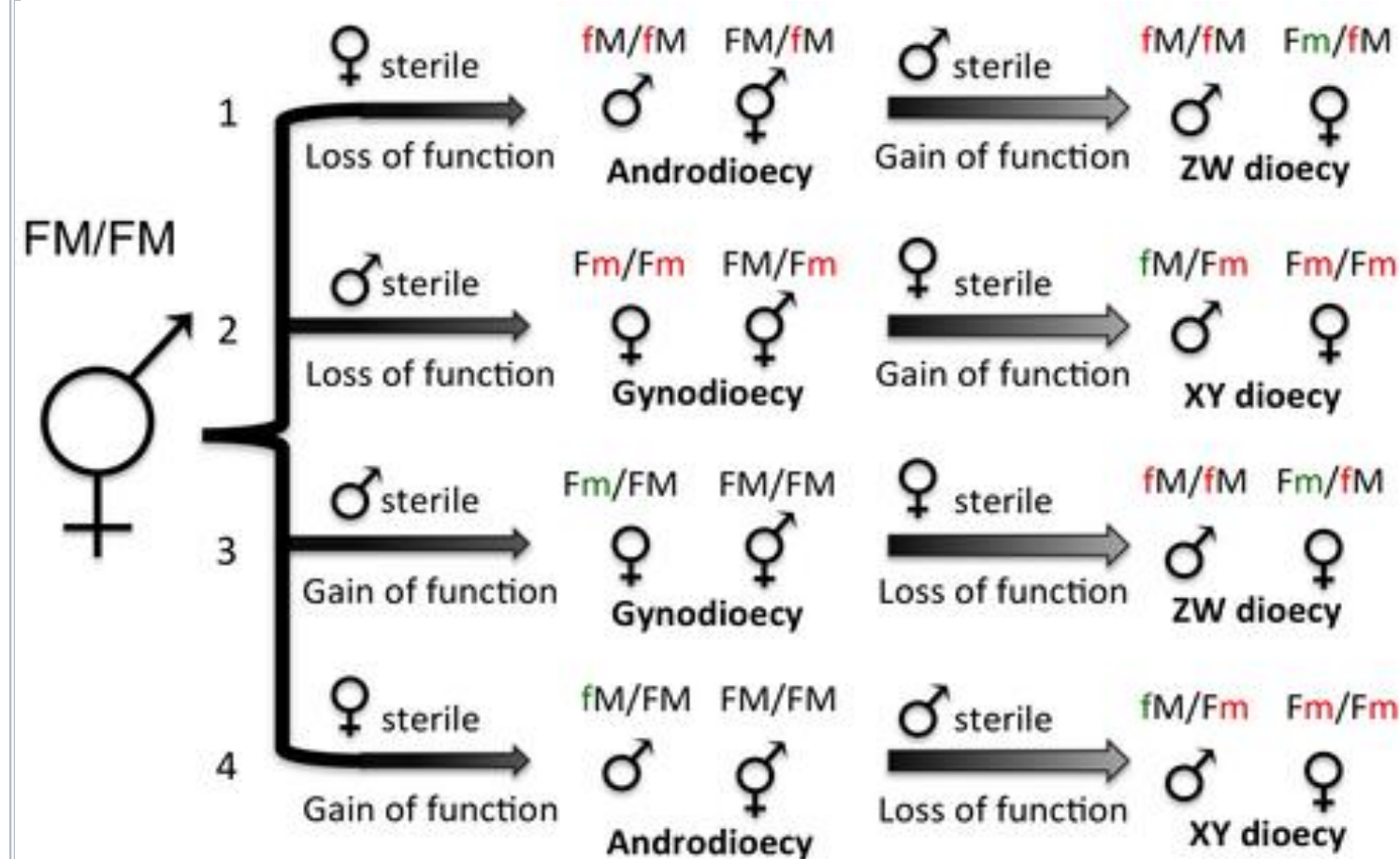




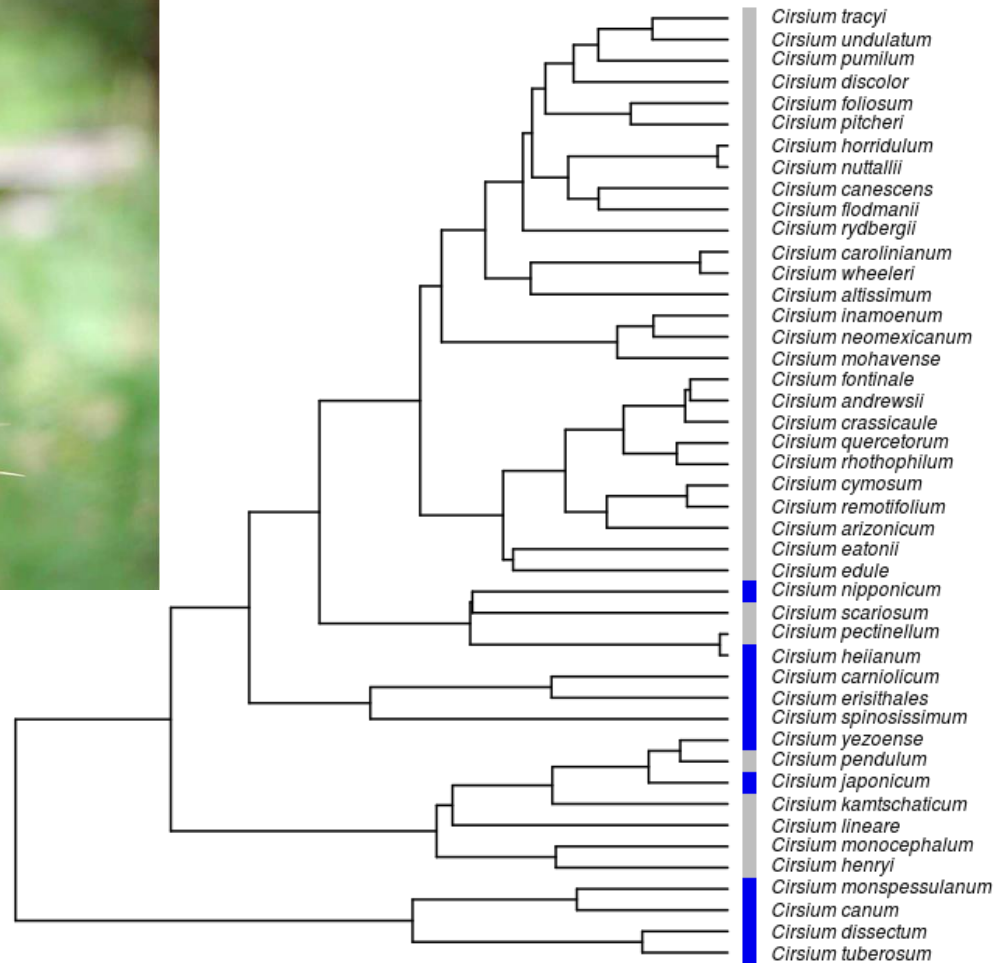
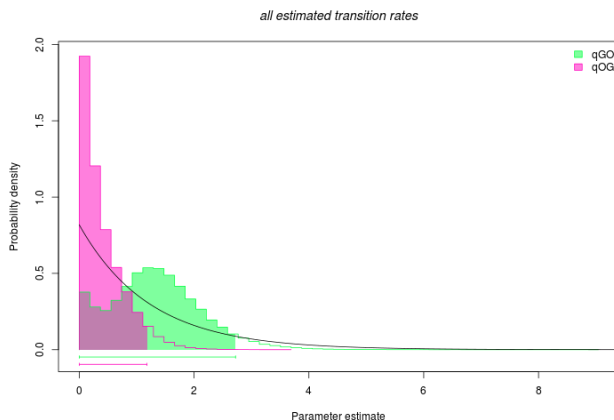
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# PLANTS AND THE EVOLUTION OF SEX CHROMOSOMES



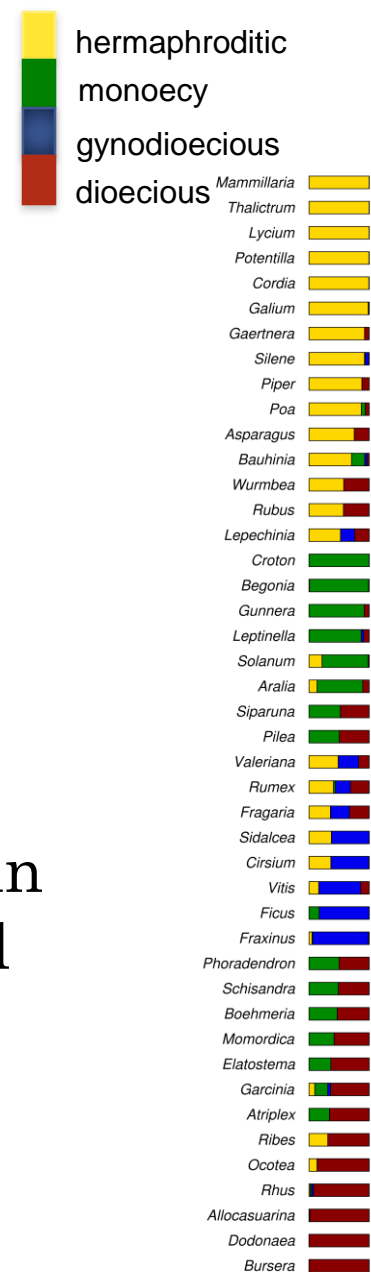
# WITHIN-GENUS ANALYSES



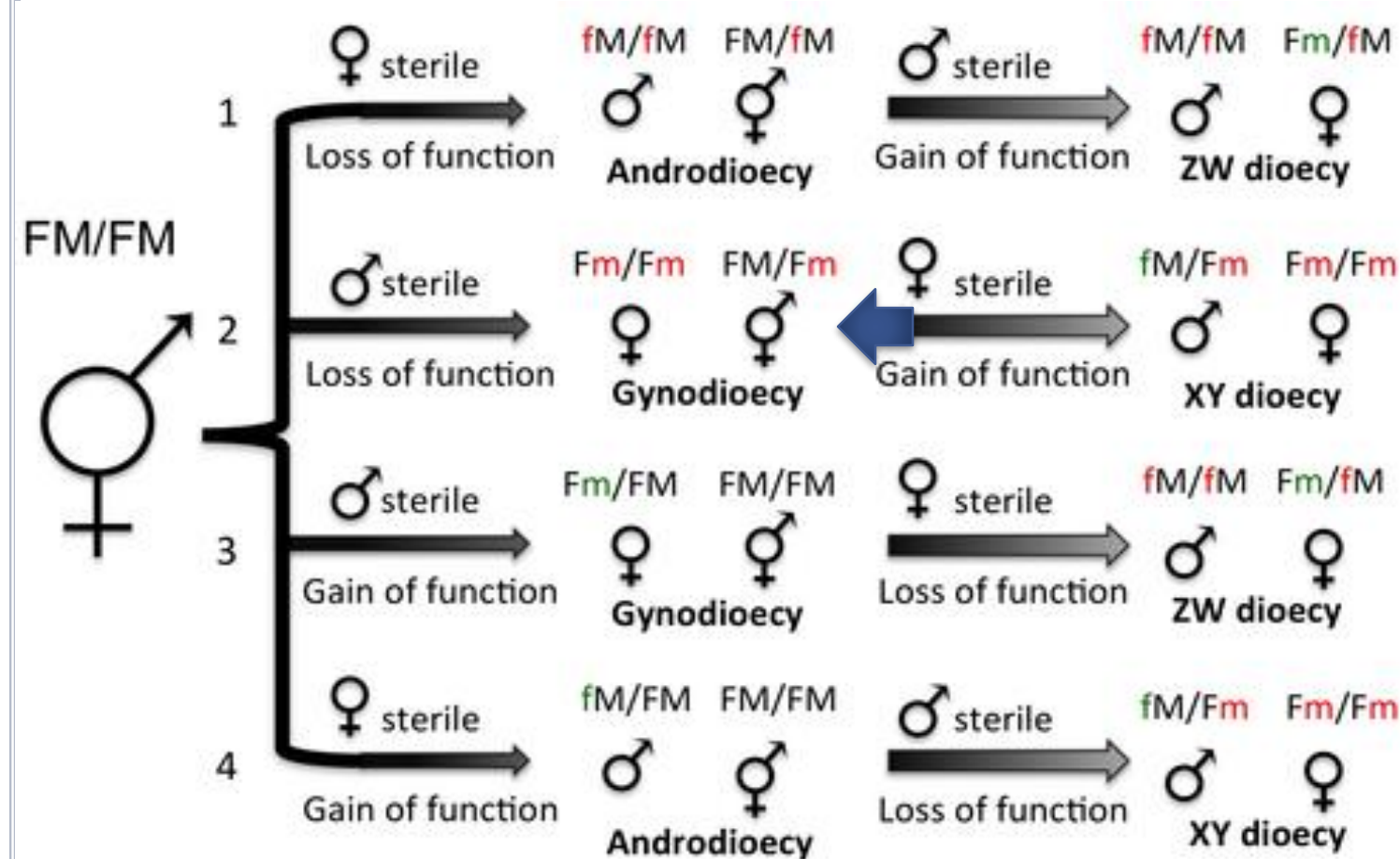
On 44 different genera!

# ROOT STATES

- In 44 genera, in only 2 of them are we 95% confident that transitions to dioecy were higher than going backwards
  - Examining transition rates: 70% of genera show no directionality
- Further, if transitions were more often in the direction of Herm->dioecy, we would expect more reconstructed root states would be herm
  - Result: nope. ~1/3 of genera likely to have dioecious root



# PLANTS AND THE EVOLUTION OF SEX CHROMOSOMES



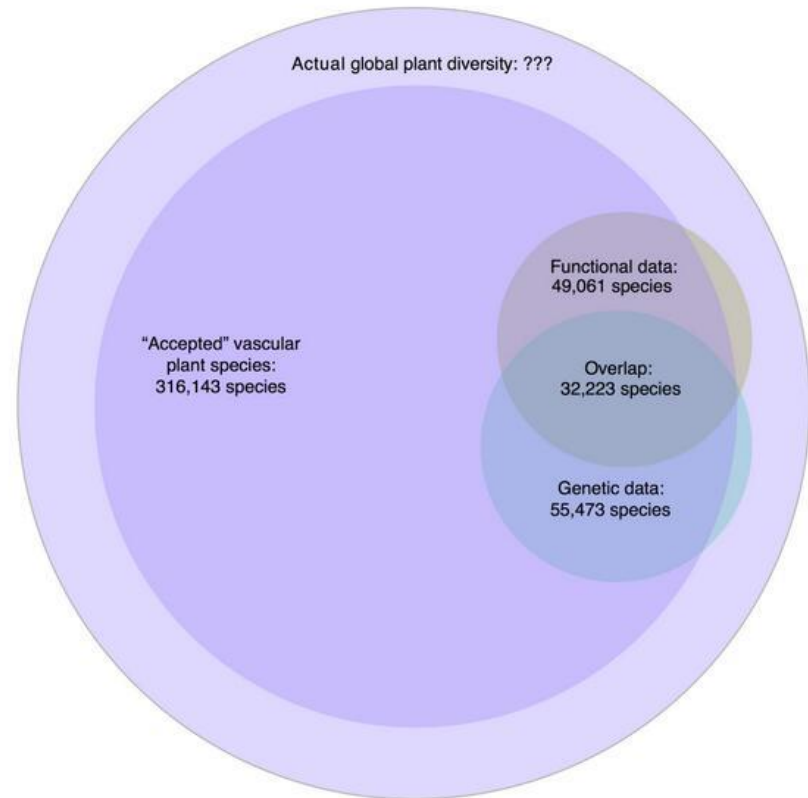


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# CONCLUSIONS

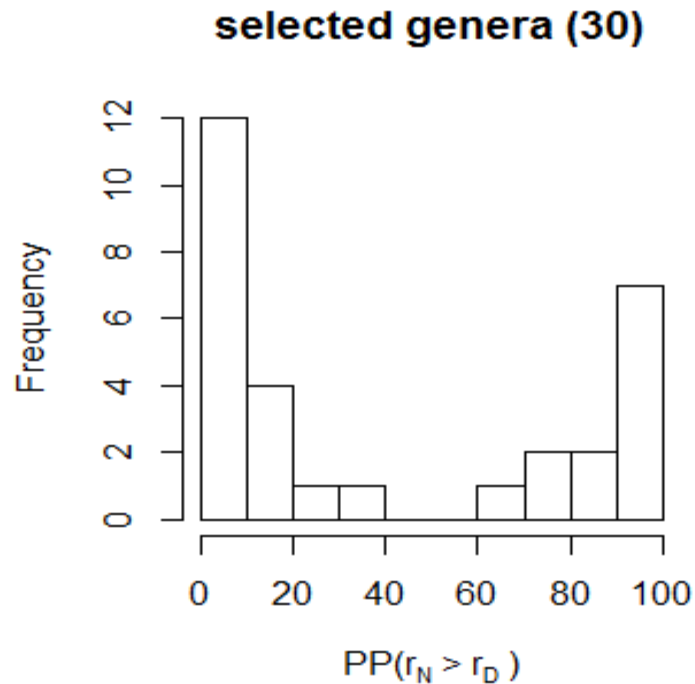
- A broad perspective provides:
  - Alternative hypotheses when model systems take you down the wrong path;
  - A path to understanding the function of traits
    - What is the consequence of having an XY system? Does sex determination alter evolutionary trajectories?
    - Does separate sexes inevitably lead to greater extinction? In XY systems, is male mutation rate the problem?



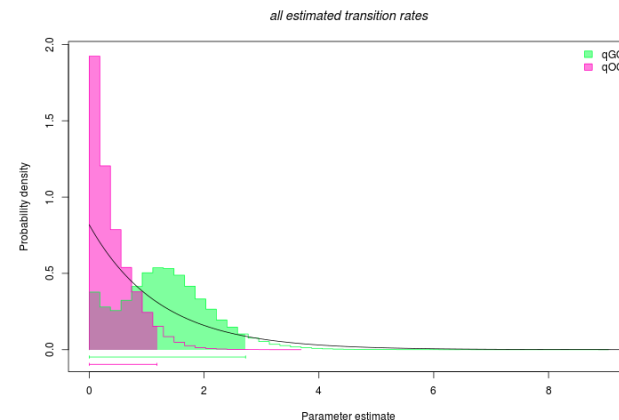
Species counts from Smith et al. (2001), Zanne et al. (2014), and the Plant List (v1.1)

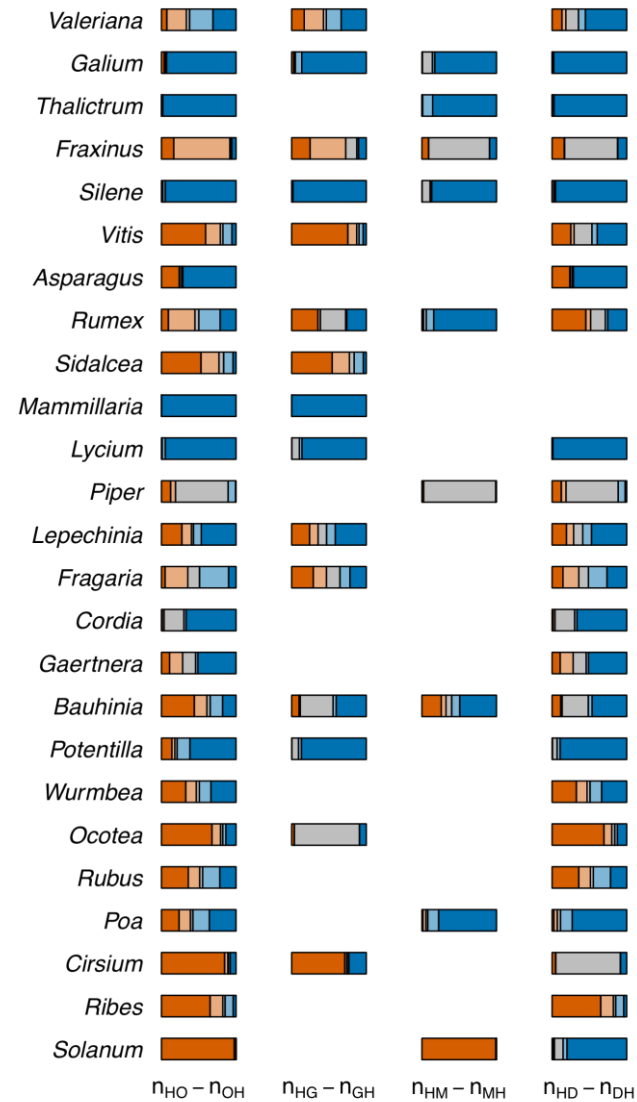
# DIOECY AS AN EVOLUTIONARY DEAD-END

- Can also generate the posterior probabilities (PP) of speciation upon Non-dioecious (N) and Dioecious (D) background



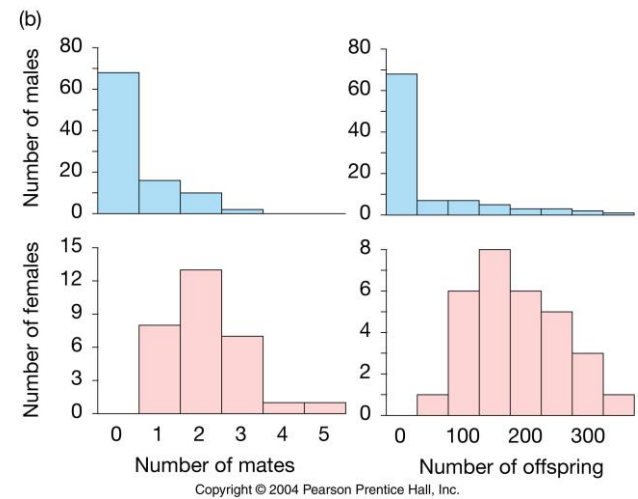
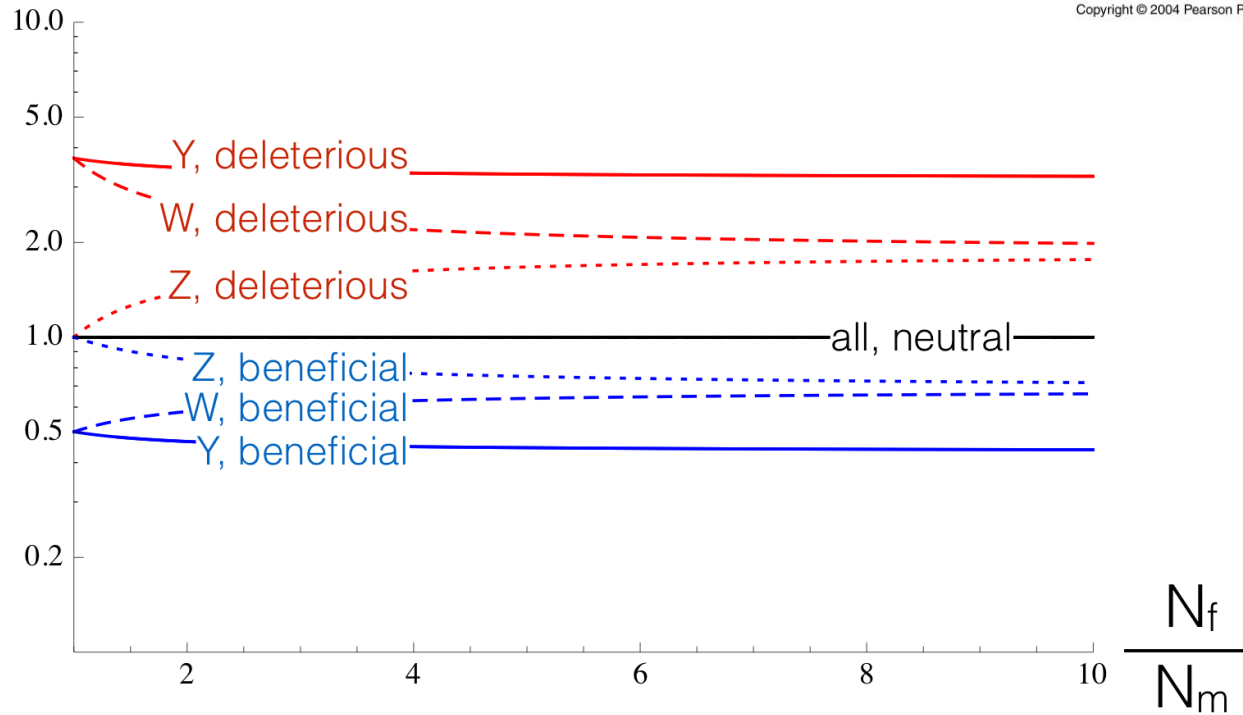
- Bimodal
- In  $\sim 1/2$  of the genera, dioecy experiences higher speciation rates than non-dioecy





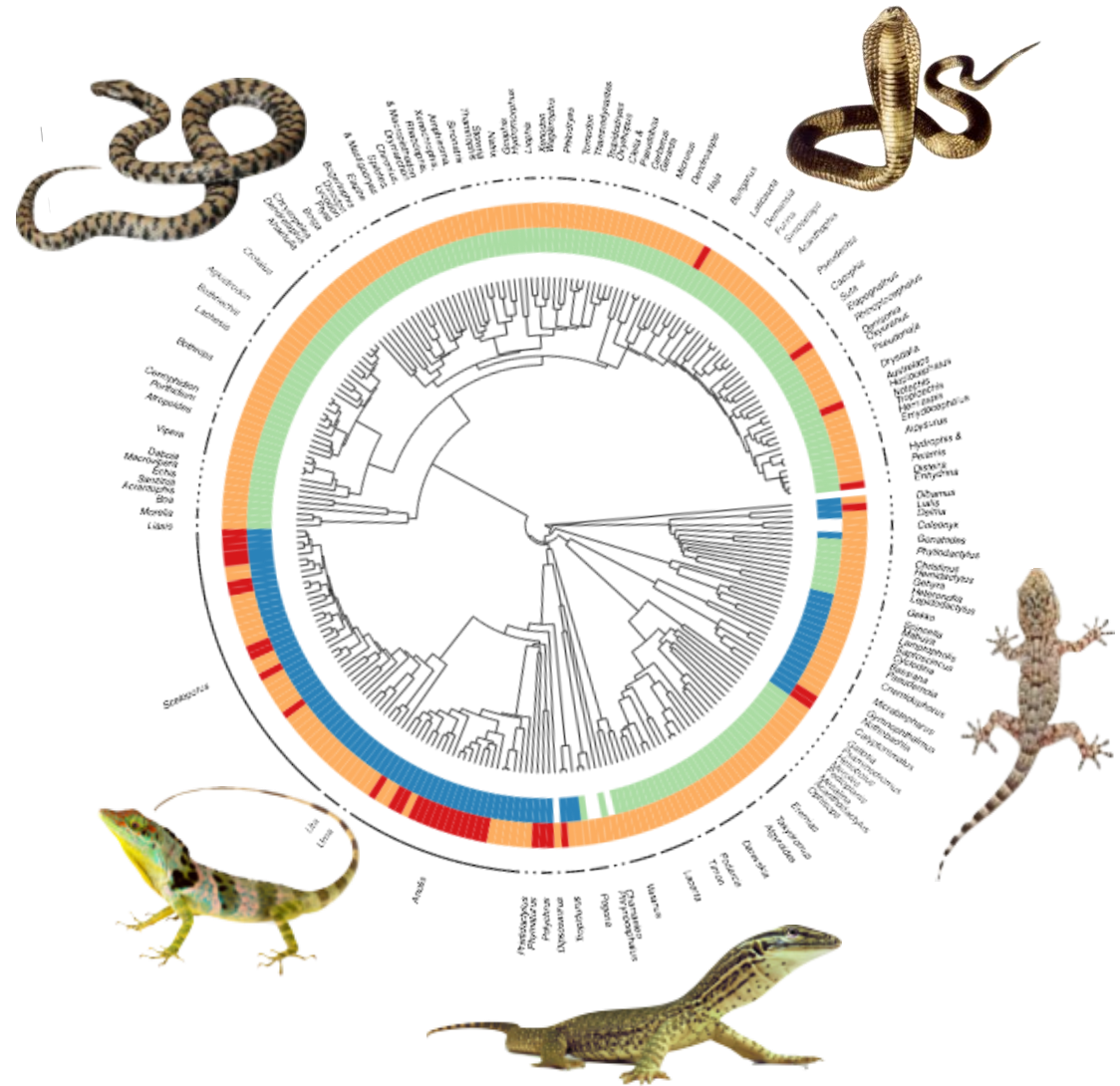
# POPULATION SIZE DIFFERENCES

Establishment rate  
relative to X-A

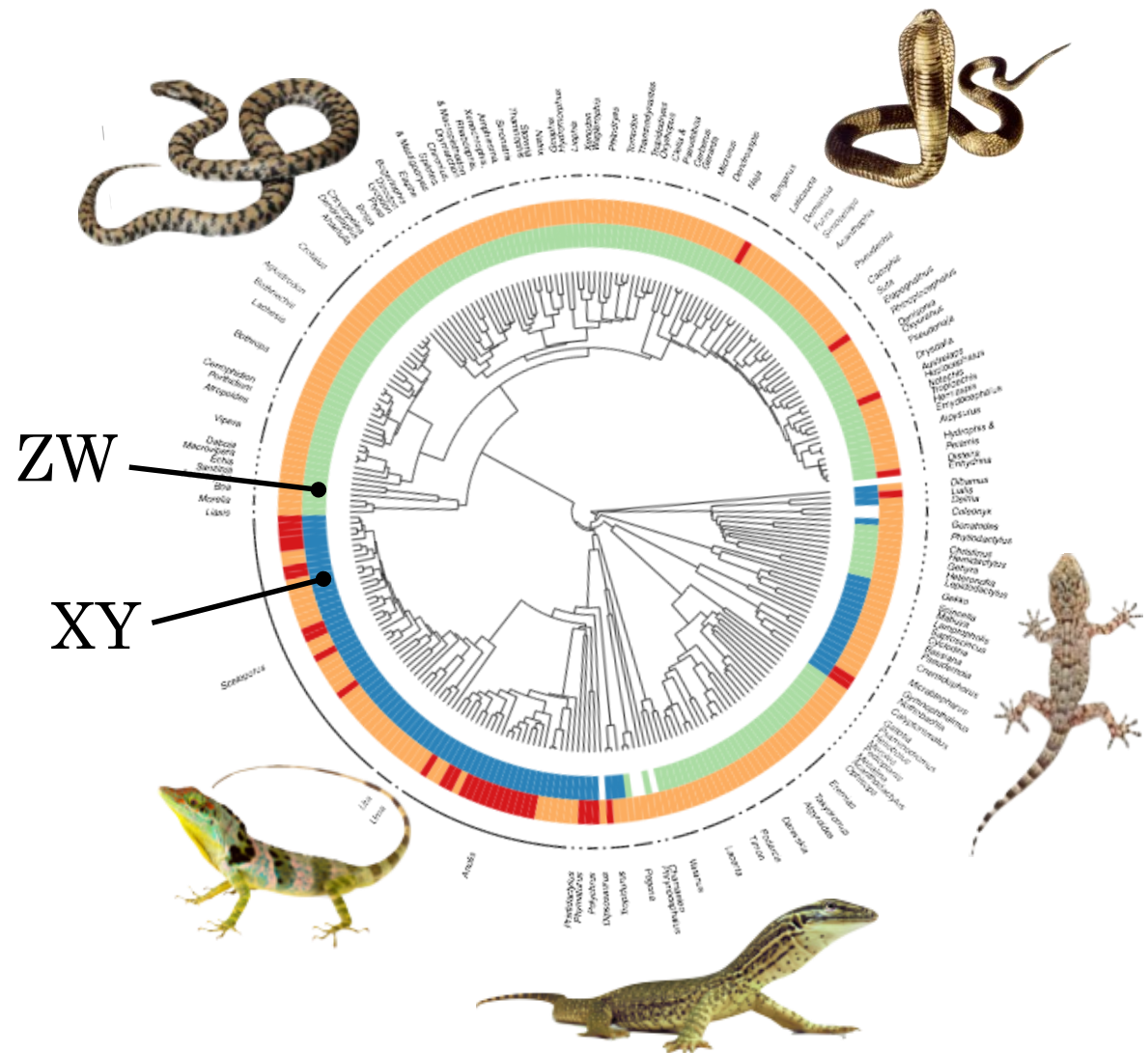




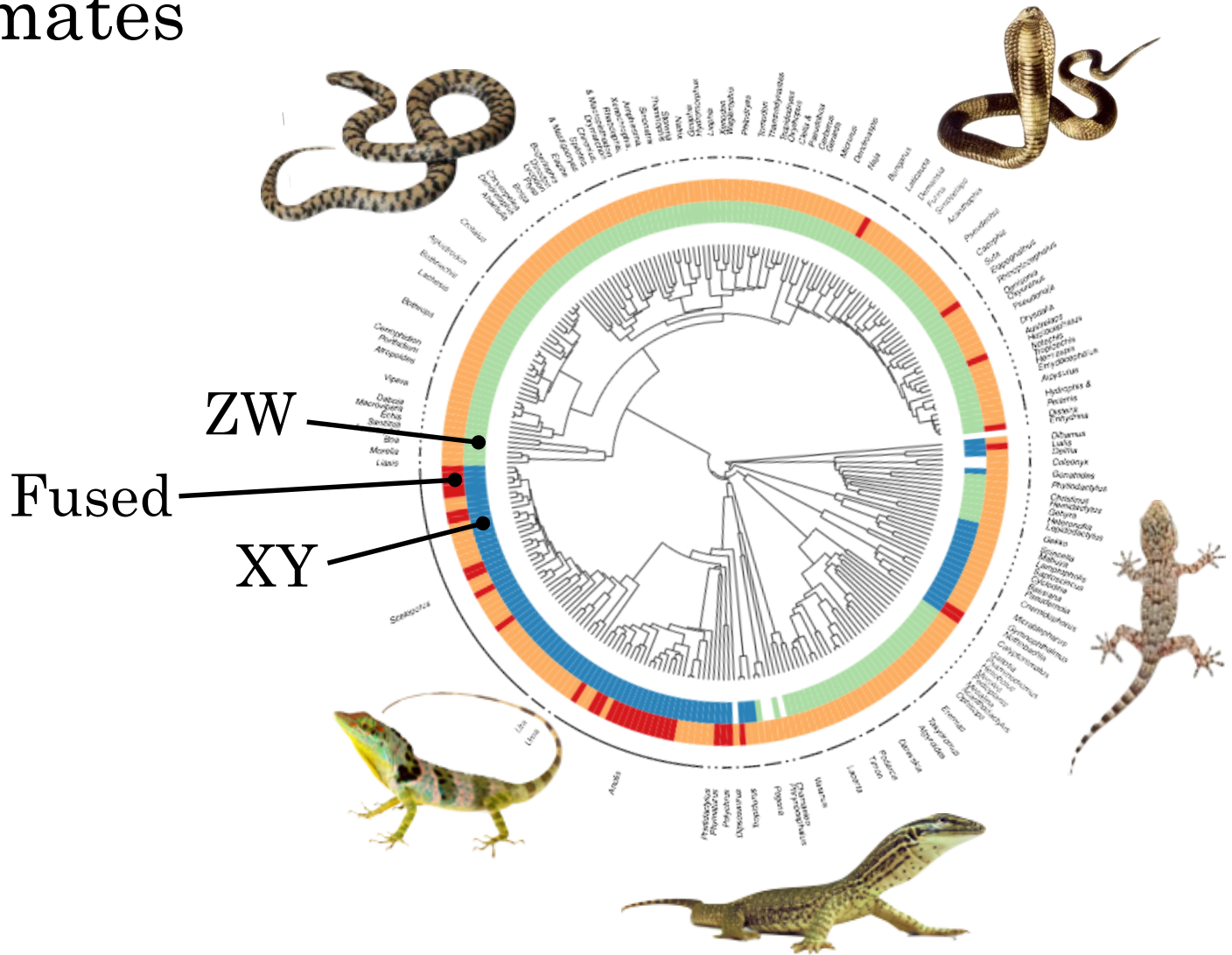
# Squamates



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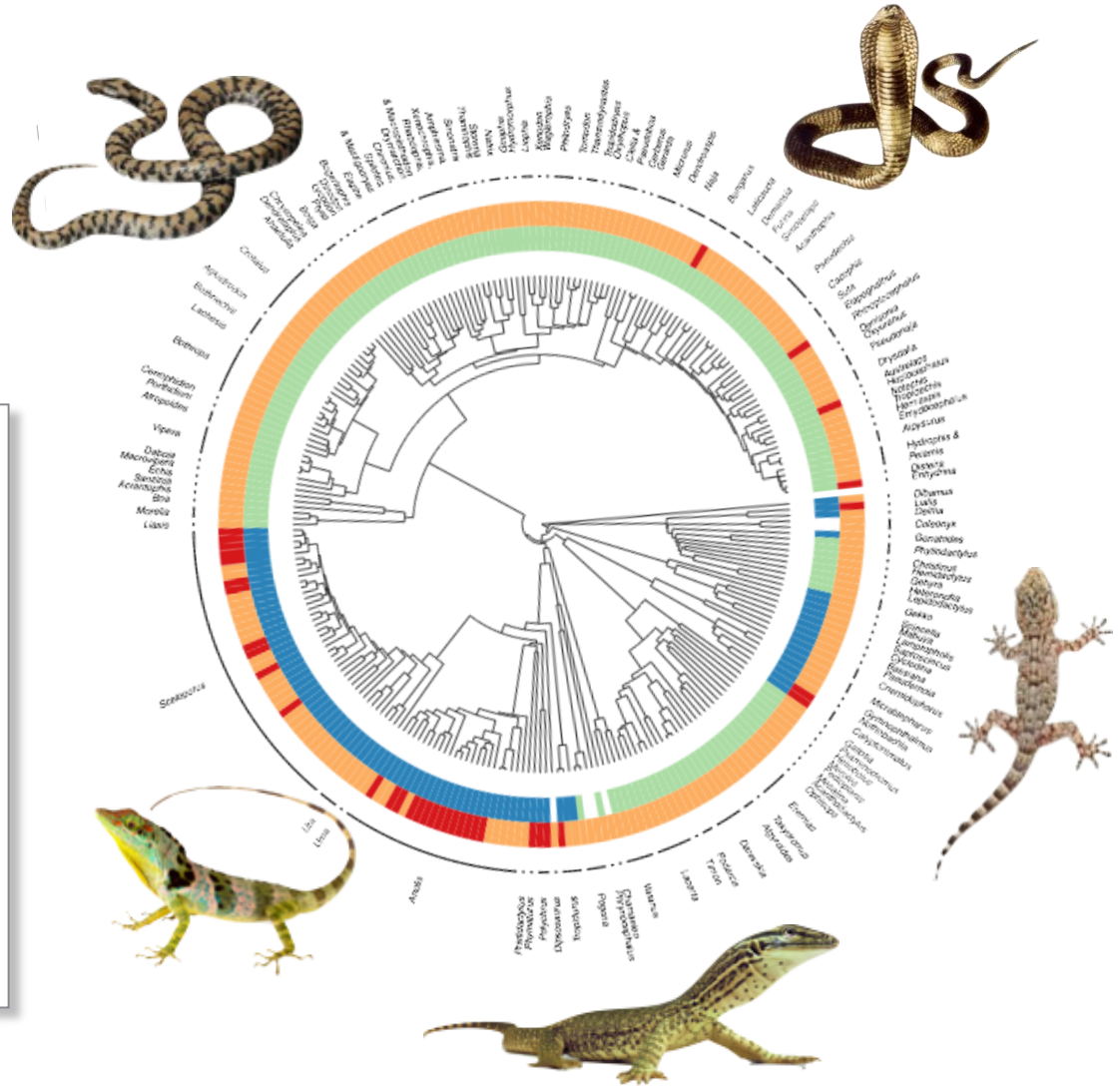
# Squamates

**Y-A >>**

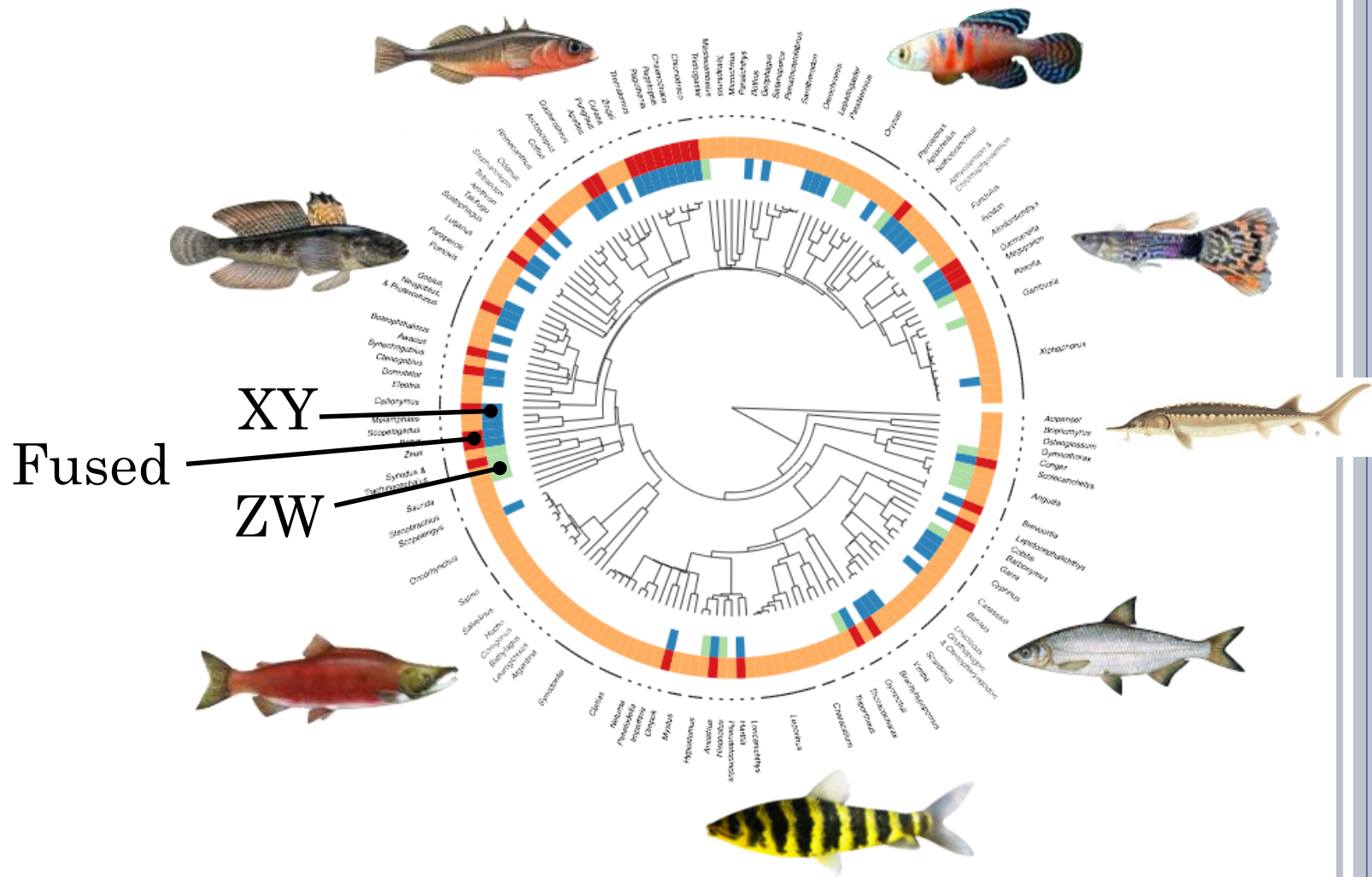
**X-A, Z-A, W-**

A

$$p \ll 0.05$$



# Fish





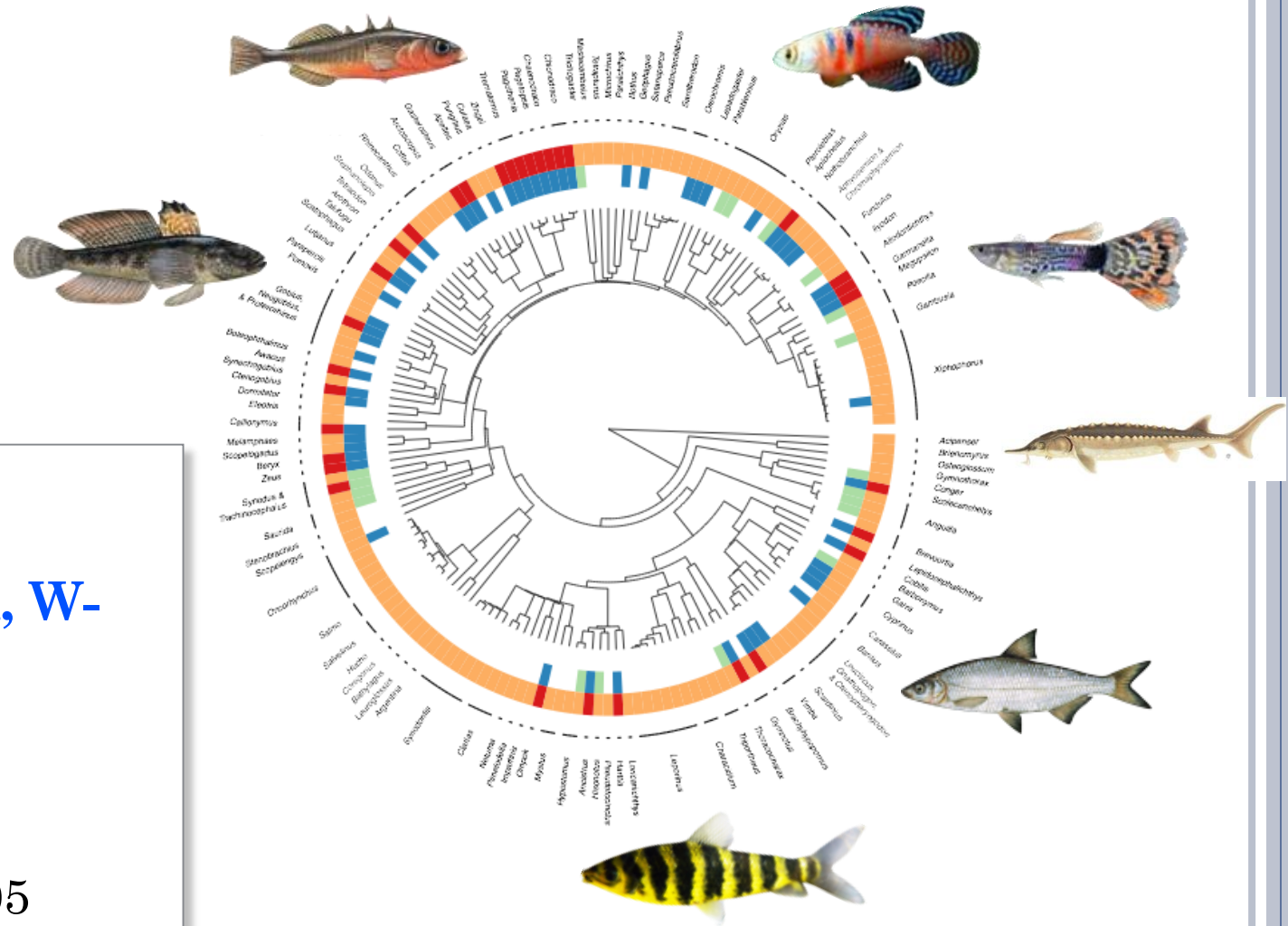
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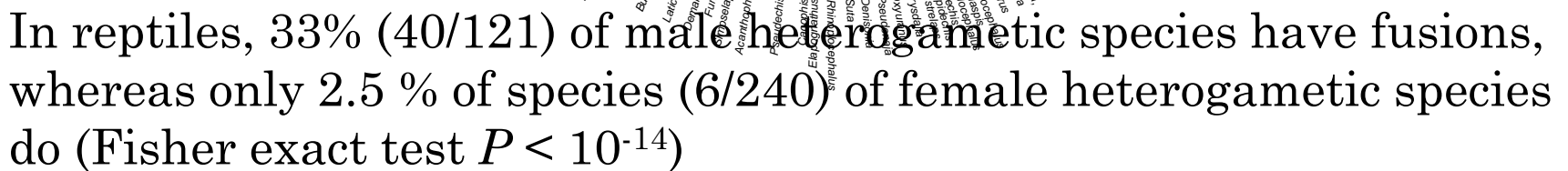
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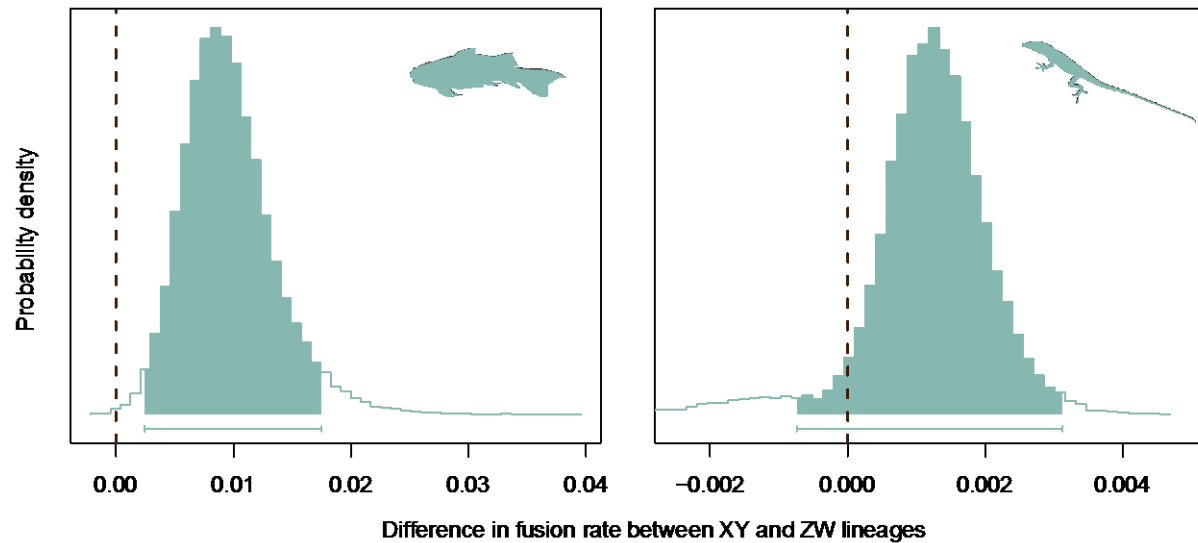
A

$$p \ll 0.05$$









In fish, in 99.6% of the posterior probability distribution, fusions in XY lineages were inferred to occur at a higher rate than ZW lineages (Fig. S1). In squamates, 99.9% of the posterior distribution favored higher rates of fusions in XY lineages than in ZW lineages