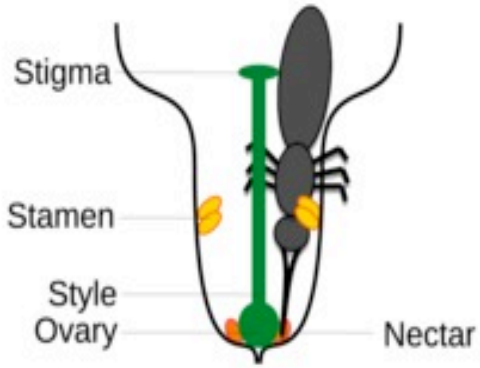
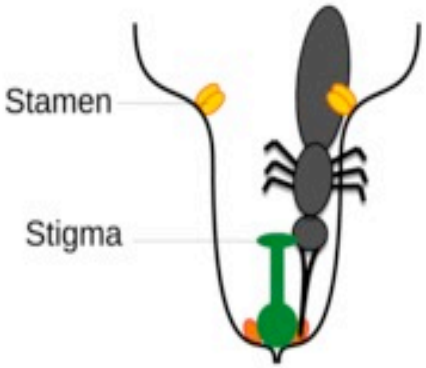
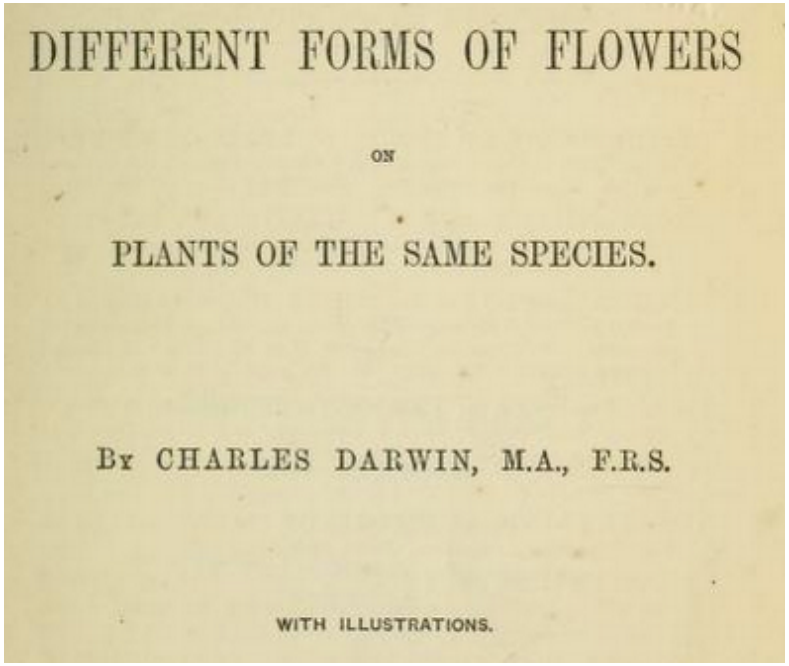
Pannell & Cossard



Pin



Thrum



DIFFERENT FORMS OF FLOWERS

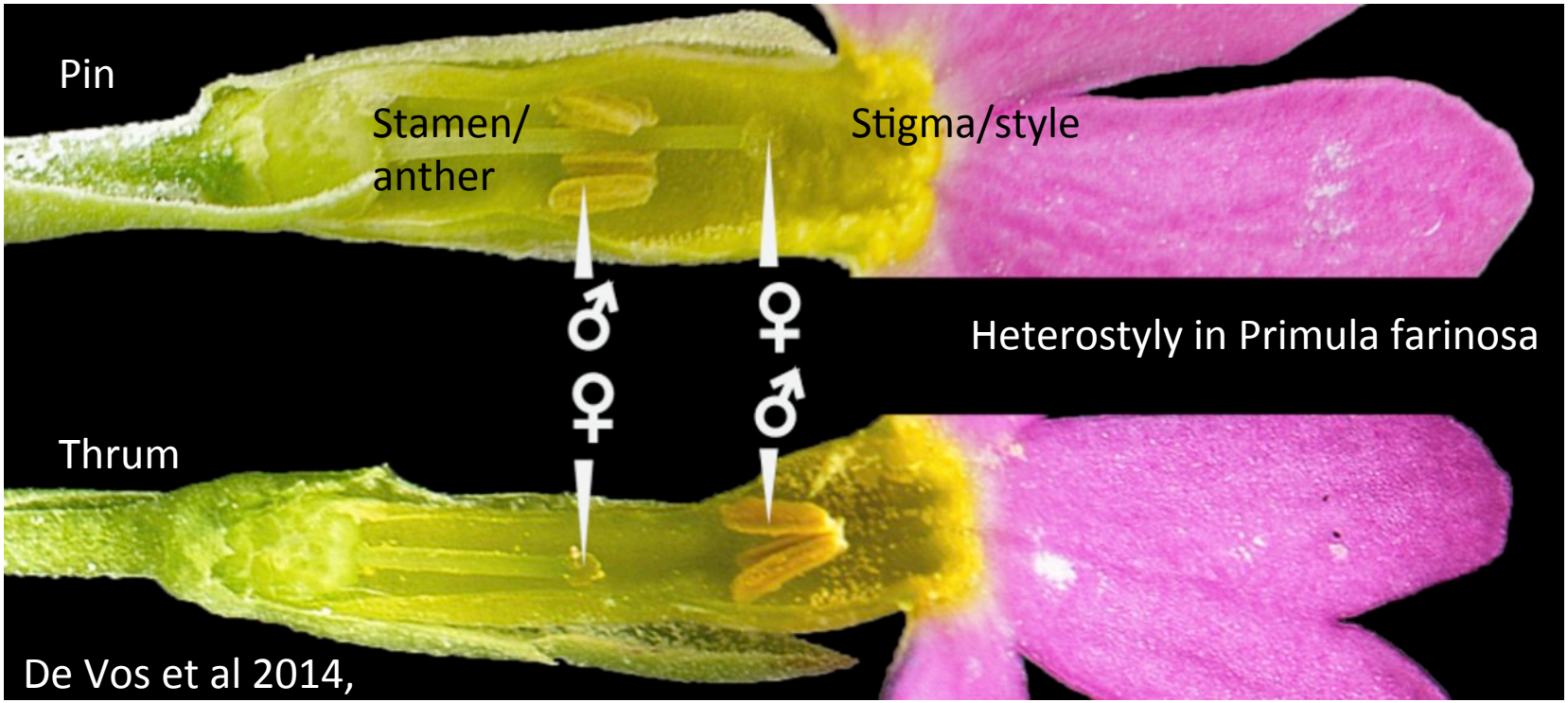
ON

PLANTS OF THE SAME SPECIES.

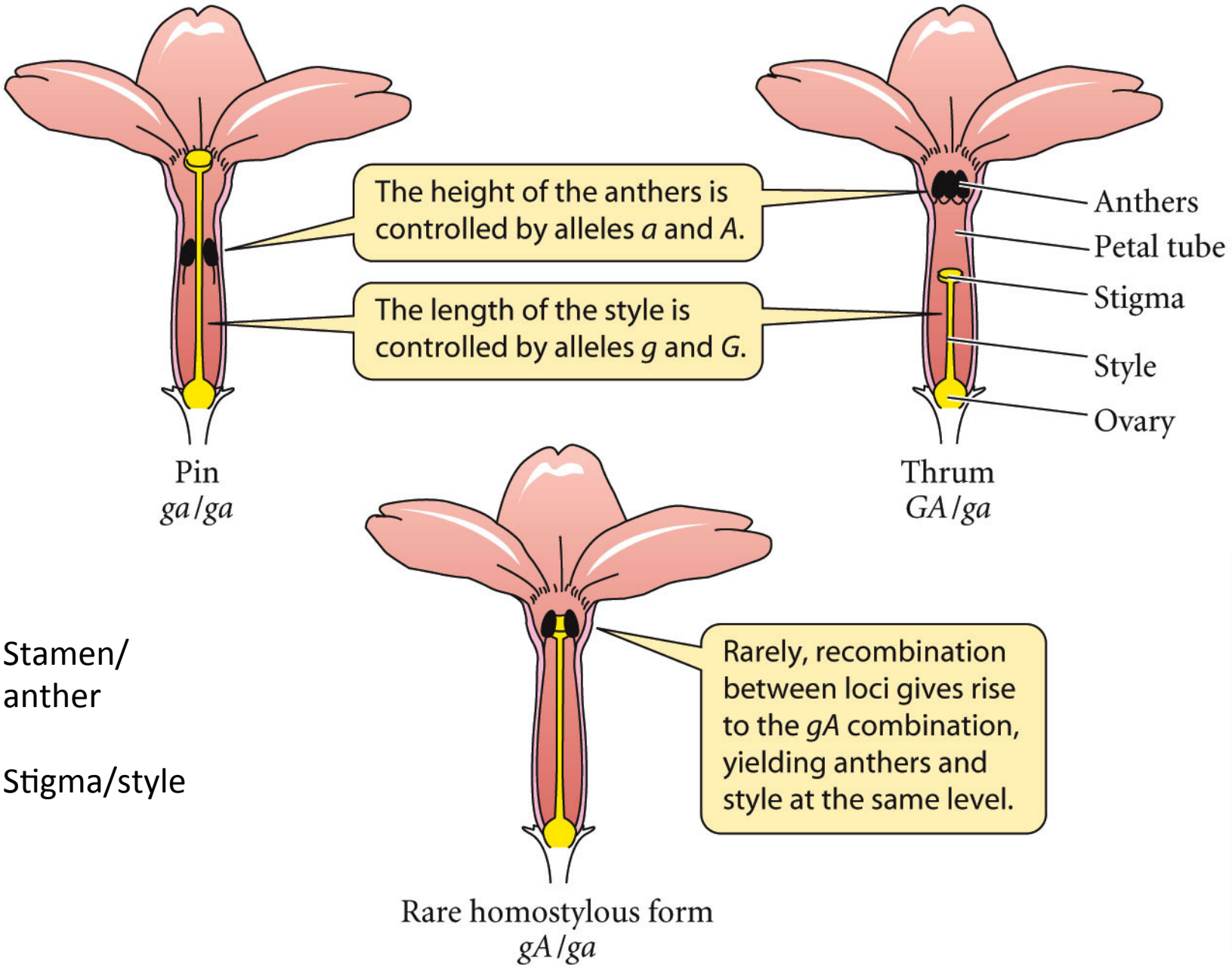
By CHARLES DARWIN, M.A., F.R.S.

WITH ILLUSTRATIONS.

"I do not think anything in my scientific life has given me so much satisfaction as making out the meaning of the structure of heterostylous flowers".-Darwin



De Vos et al 2014,

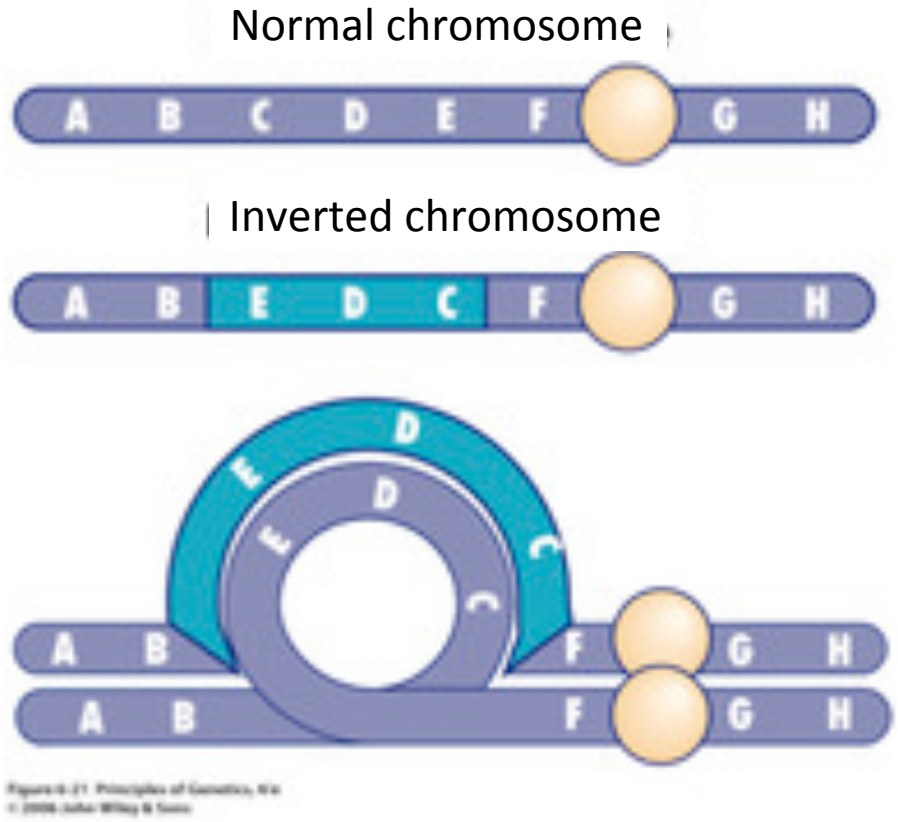


Stamen/
anther

Stigma/style

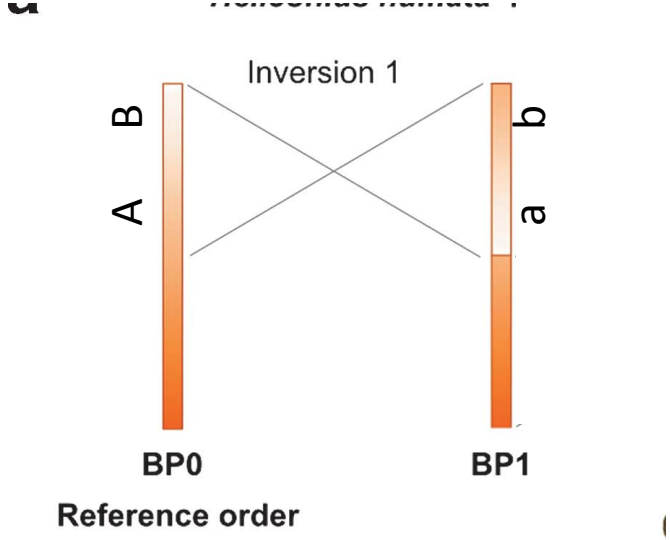
EVOLUTION 2e, Figure 9.19

Inversions block recombination in heterozygotes



Super genes

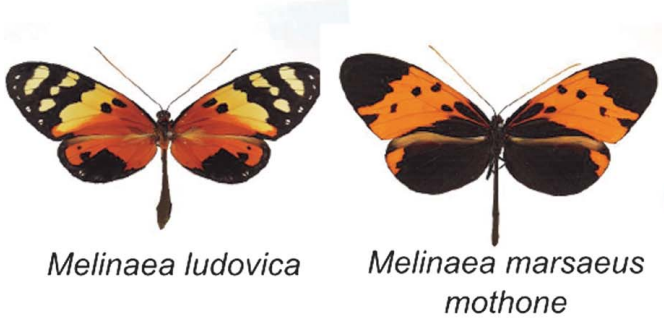
‘coadapted combinations of several or many genes locked in inverted sections of chromosomes and therefore inherited as single units.’
(Dobzhansky, 1970).



Heliconius numata

AB	AB	or	ab
AB	ab		ab

Mimicry model



Supergenes and their role in evolution

M J Thompson[1,2] and C D Jiggins[1]

Faeder-Independent inversion
4Mb

Structural genomic changes underlie alternative reproductive strategies in the ruff (*Philomachus pugnax*)

Sangeet Lamichhaney, Guangyi Fan, Fredrik Widemo, Ulrika Gunnarsson, Doreen Schwochow Thalmann, Marc P Hoeppner, Susanne Kerje, Ulla Gustafson, Chengcheng Shi, He Zhang, Wenbin Chen, Xinming Liang, Leihuan Huang, Jiahao Wang, Enjing Liang, Qiong Wu, Simon Ming-Yuen Lee, Xun Xu, Jacob Höglund, Xin Liu & Leif Andersson

A supergene determines highly divergent male reproductive morphs in the ruff

Clemens Küpper, Michael Stocks, Judith E Risse, Natalie dos Remedios, Lindsay L Farrell, Susan B McRae, Tawna C Morgan, Natalia Karlionova, Pavel Pinchuk, Yvonne I Verkuil, Alexander S Kitaysky, John C Wingfield, Theunis Piersma, Kai Zeng, Jon Slate, Mark Blaxter, David B Lank & Terry Burke

Independent genotype

Satellite genotype

Fredrik Widemo

Faeder genotype

motto555/Thinkstock

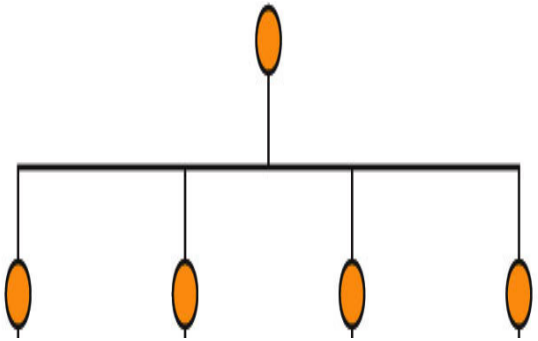
Melissa Hafting

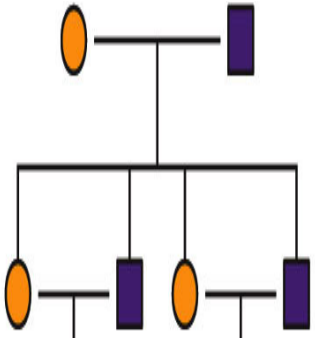
The cost of sex.

Why risk breaking it up a winning genotype.

Finding and attracting a mate are costly and may be impossible, and mating is dangerous

The two fold cost of sex





Sexual organisms only contribute ½ of their genome to their offspring While asexual organisms contribute their entire genome. This is sometimes called the cost of males

Despite this sexual reproduction persists.

- Why have sex?

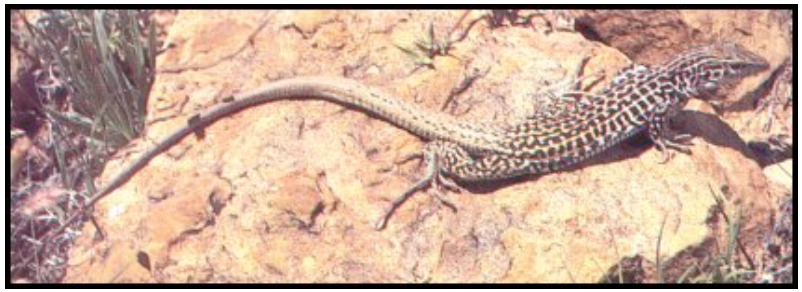
Vast majority of eukaryotic organisms reproduce sexually

Many species are not obligate sexuals and can reproduce clonally (i.e. asexually)

e.g. Vegetative growth in plants.

However, they will only do so for a few generations

Vertebrate asexual species can evolve

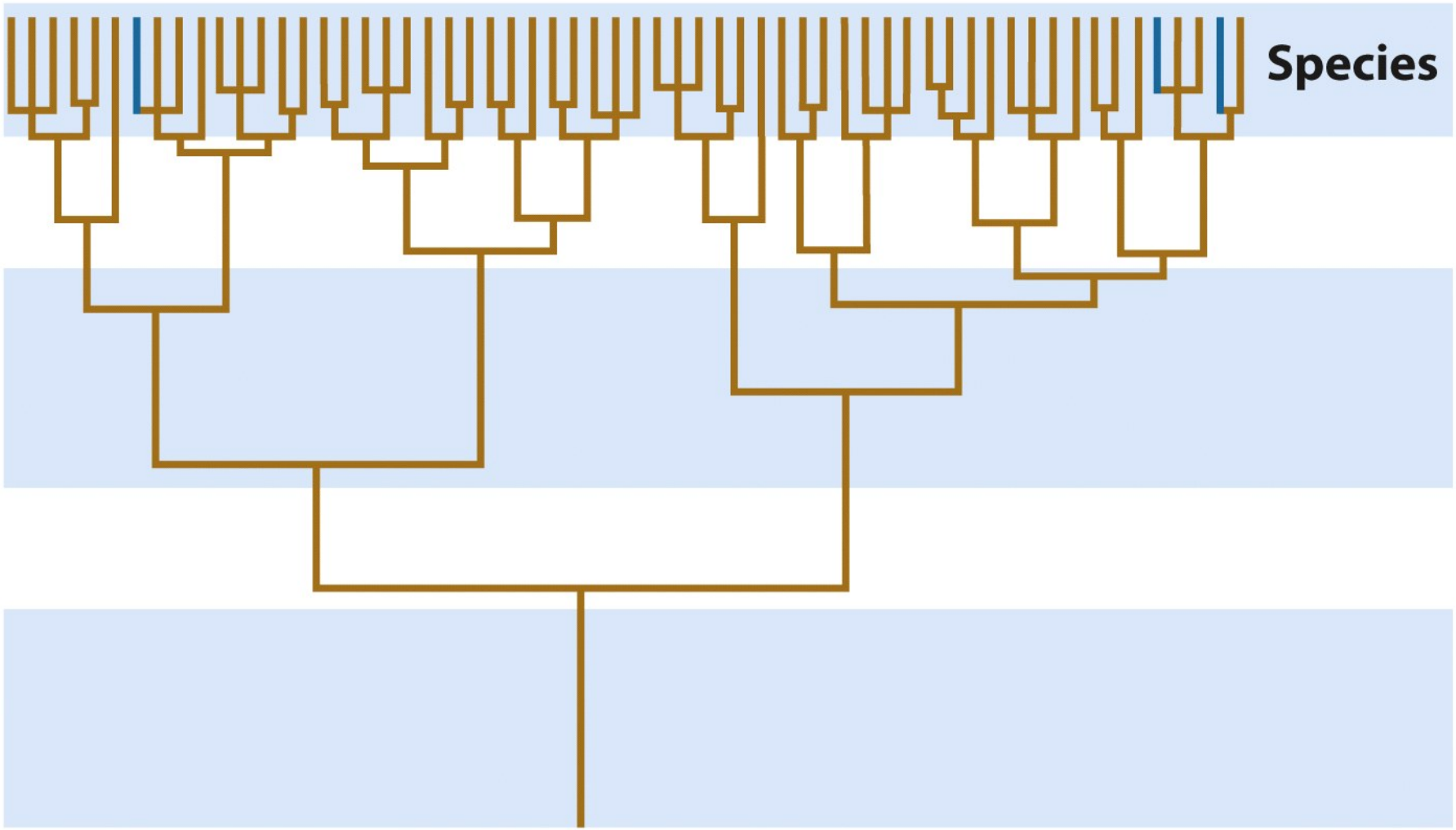


Unisexual Cnemidophorus

Unisexual *P. formosa* (left) sexually parasitizes the sexual *P. latipinna* (right)

Despite this sexual reproduction persists.

Asexual species emerge often in animals/plants but are generally short-lived as species



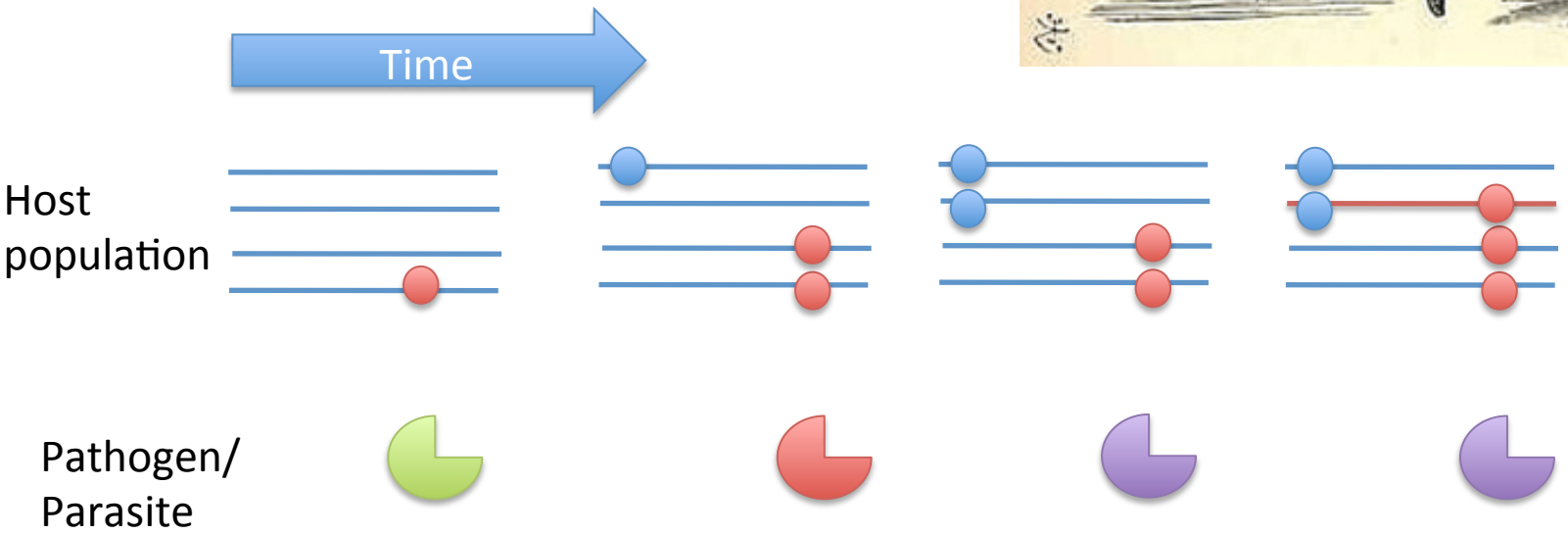
Evolution, 1/e Figure 16.9

Hypotheses for the evolutionary advantage and maintenance of sex

- Asexual species accumulate deleterious mutations
  - Hitchhiking of deleterious mutations
  - Due to Muller's Ratchet
- Asexual species adapt slower
  - forced to fix advantageous mutations sequentially (Clonal interference)
  - Creation of novel haplotypes in asexuals is mutation limited. Hard to keep pace with rapidly evolving pathogens (Red queen hypothesis)

The Red Queen Hypothesis

Hosts have to constantly adapt to changing pathogen environment



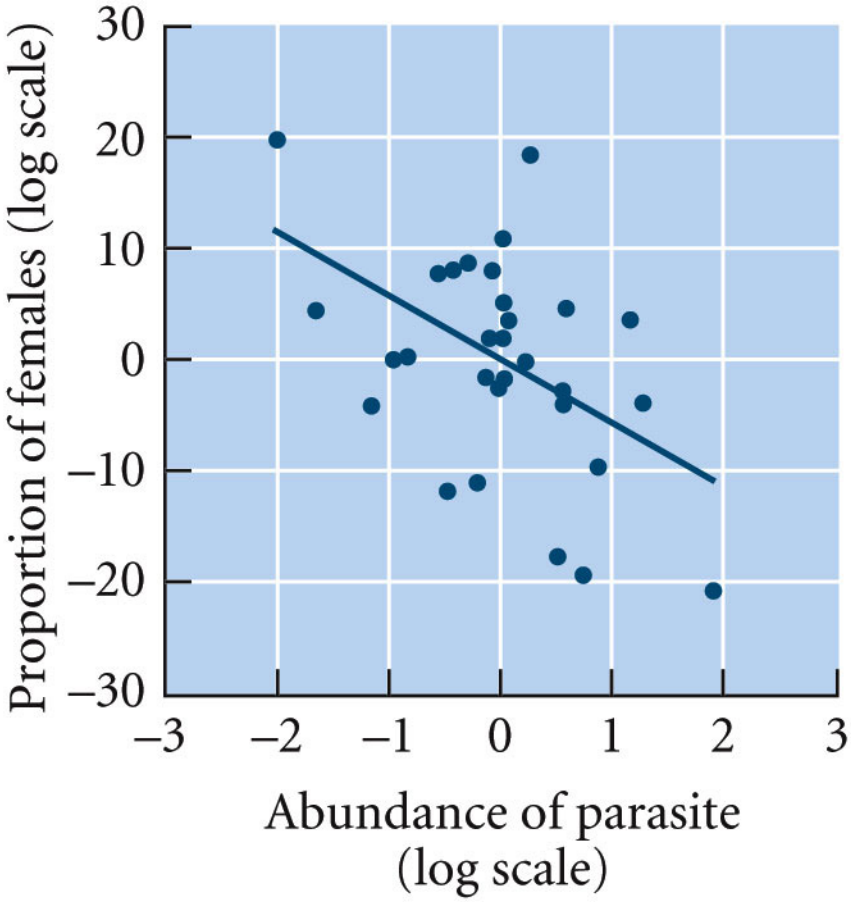
Recombination generates novel combinations of alleles (i.e. haplotypes)

So that sexual species can more rapidly evolve to resist parasites.

Evidence for red queen hypothesis

- Increase in sex with higher parasite load.

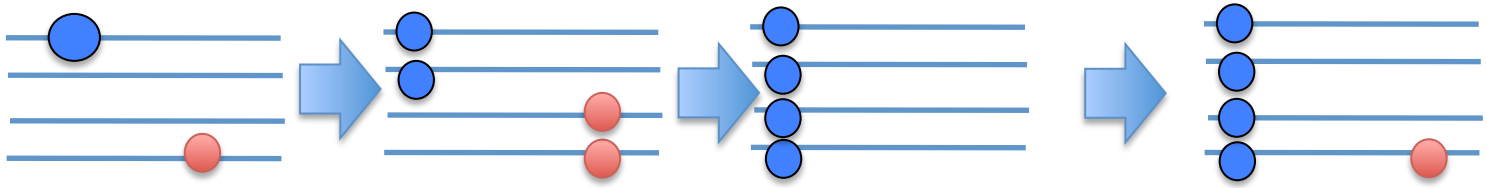
Potamopyrgus antipofarum

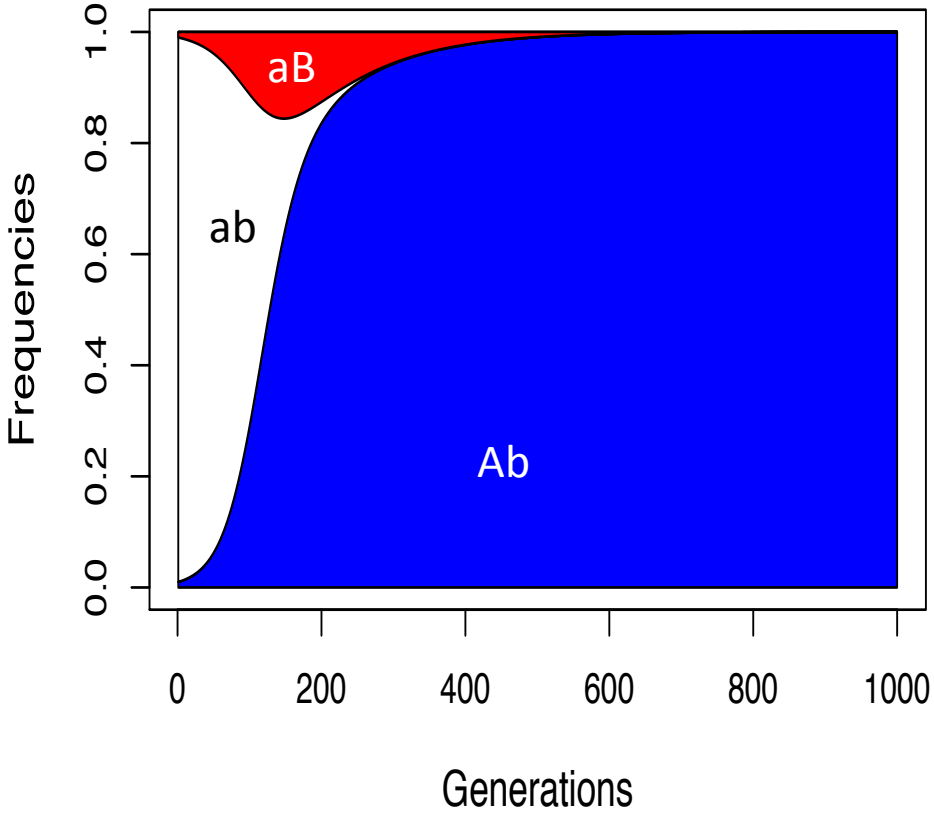


***EVOLUTION 2e*, Figure 15.7**

Clonal interference hypothesis

Selected alleles must fix sequentially in absence of sex

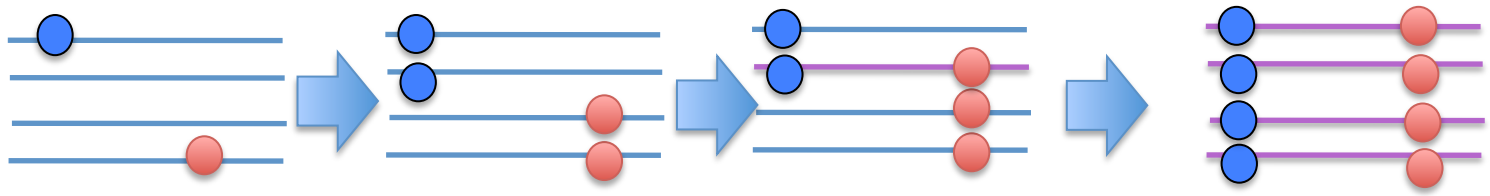


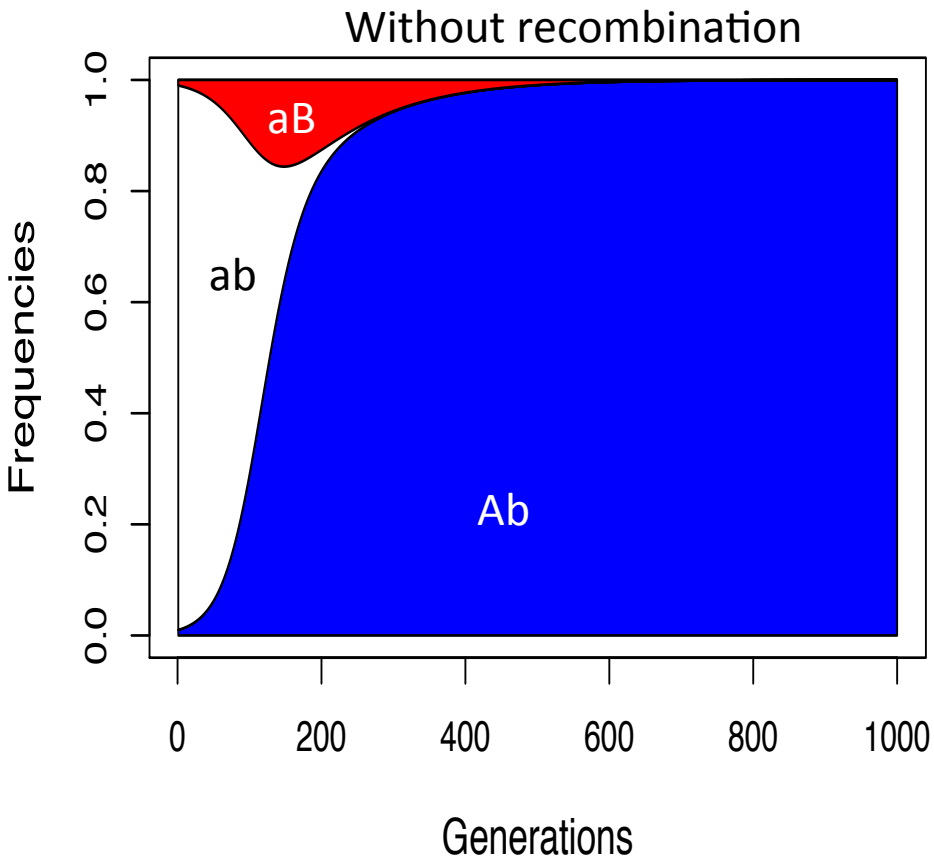


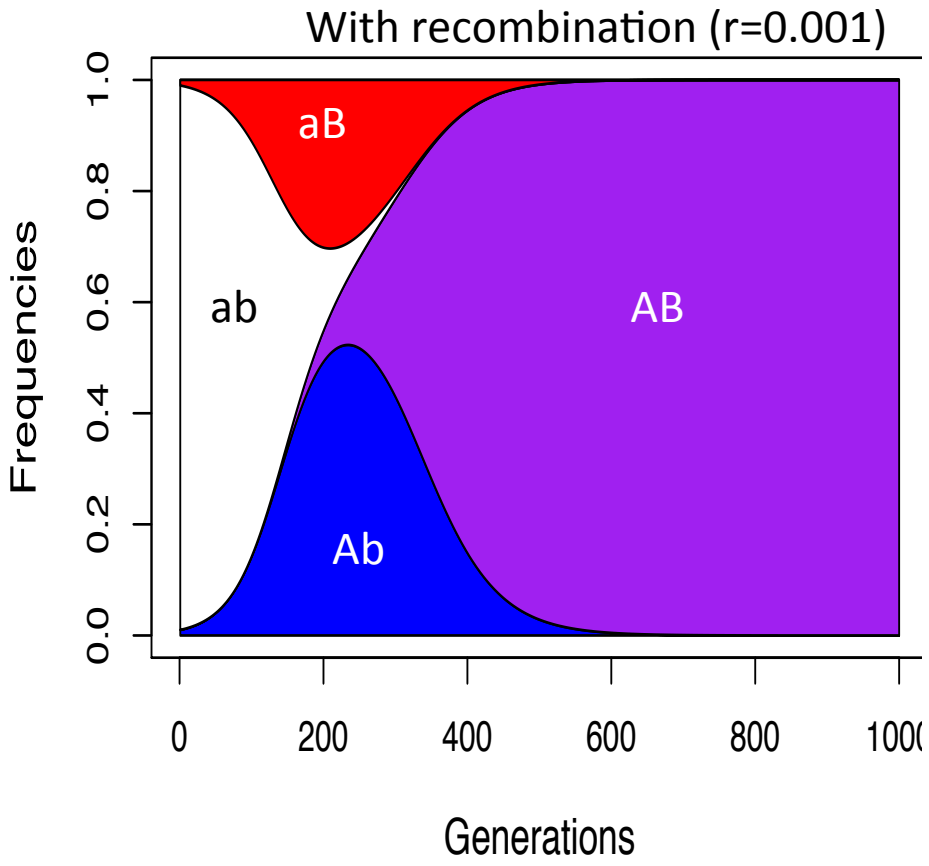
s_A =0.08
s_B =0.06
s_{AB}=0.14

Clonal interference hypothesis

Selected alleles can fix simultaneously in presence of sex.







Evidence of Clonal Interference

doi:10.1038/nature12344

Pervasive genetic hitchhiking and clonal interference in forty evolving yeast populations

Gregory I. Lang[1]*†, Daniel P. Rice[2]*, Mark J. Hickman[3], Erica Sodergren[4], George M. Weinstock[4], David Botstein[1] & Michael M. Desai[2]

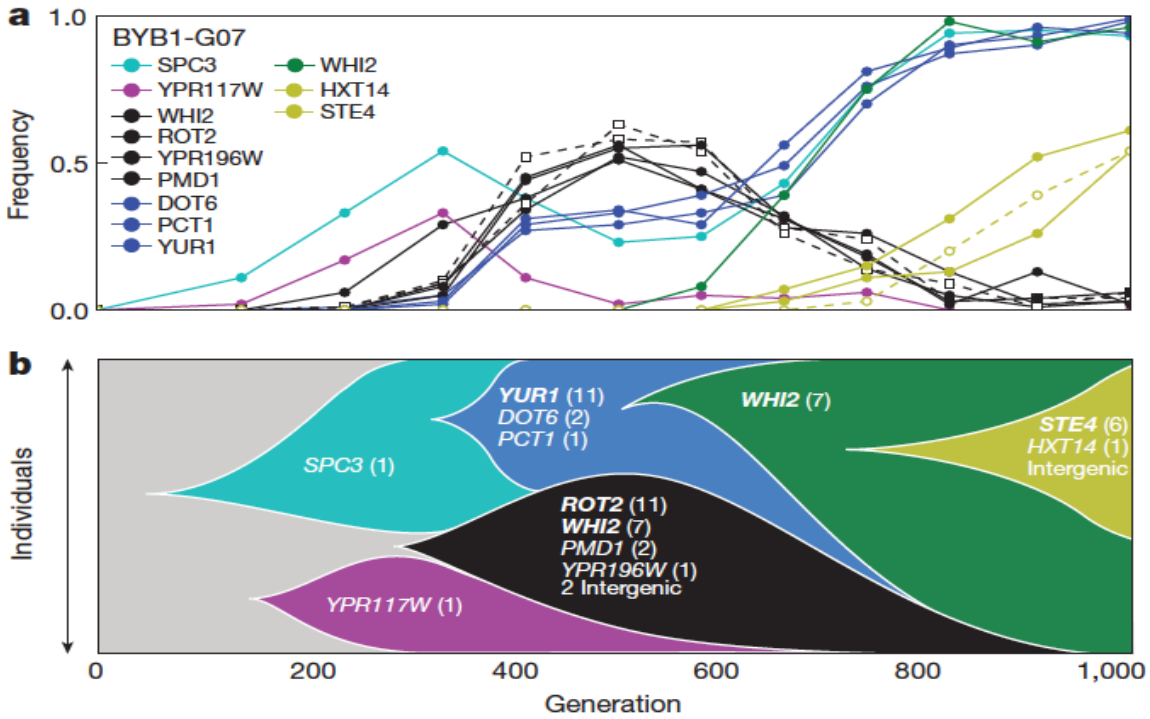


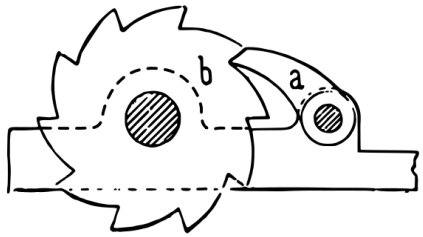
Figure 3 | The dynamics of sequence evolution in BYB1-G07. **a**, The trajectories of the 15 mutations that attain a frequency of at least 30%, hierarchically clustered into several distinct mutation 'cohorts', each of which is represented by a different colour (Methods). **b**, Muller diagram showing the

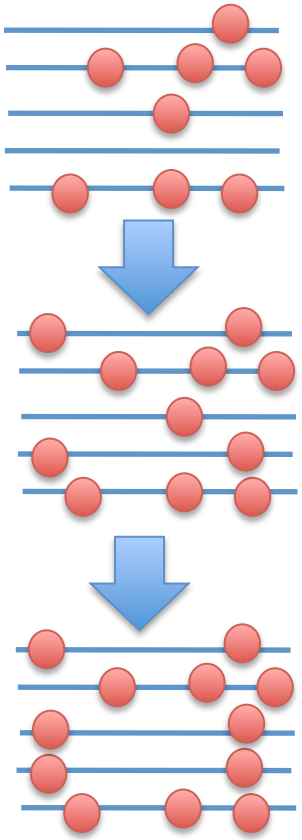
Clonal interference also plays a key role in thinking about evolution of drug resistance in pathogens.

Muller's Ratchet in asexuals

=Deleterious allele

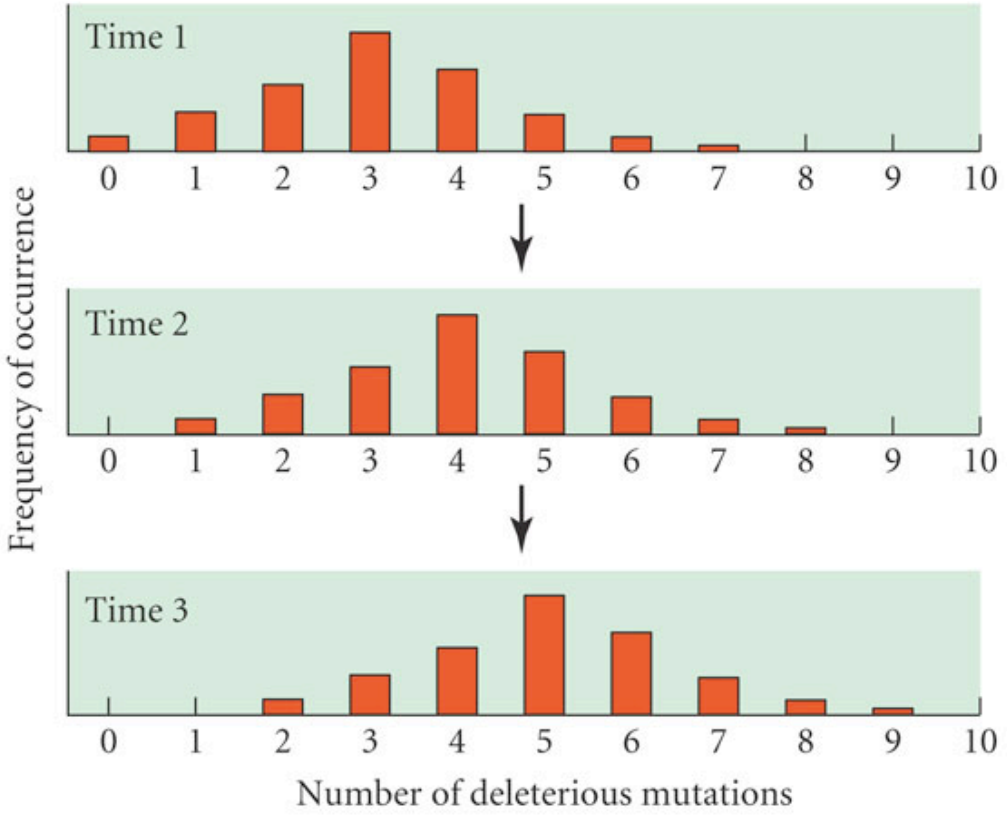
Hermann J. Muller





Loss by drift of haplotype with no deleterious alleles

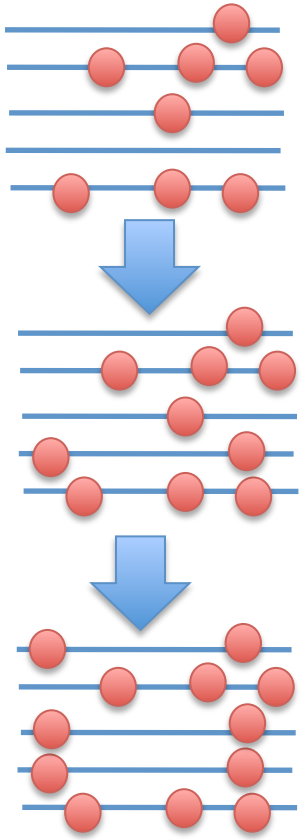
Loss of haplotype w. Only 1 deleterious allele



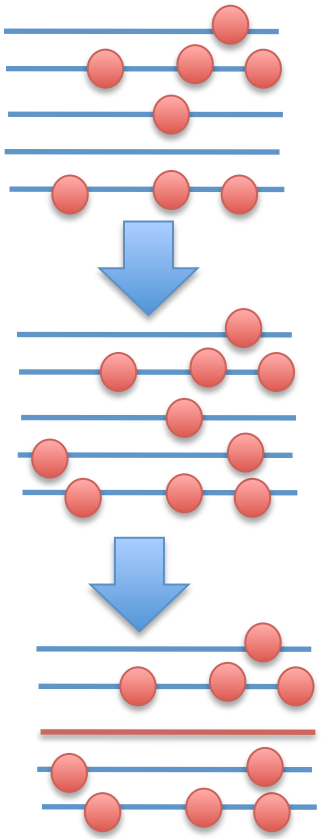
EVOLUTION, Figure 17.20 © 2005 Sinauer Assoc

Muller's Ratchet

Ratchet in asexuals: Progressive loss by drift of haplotype with lowest number deleterious alleles. Lowers fitness of population.



Sexual organisms avoid the effects Of Muller's ratchet.

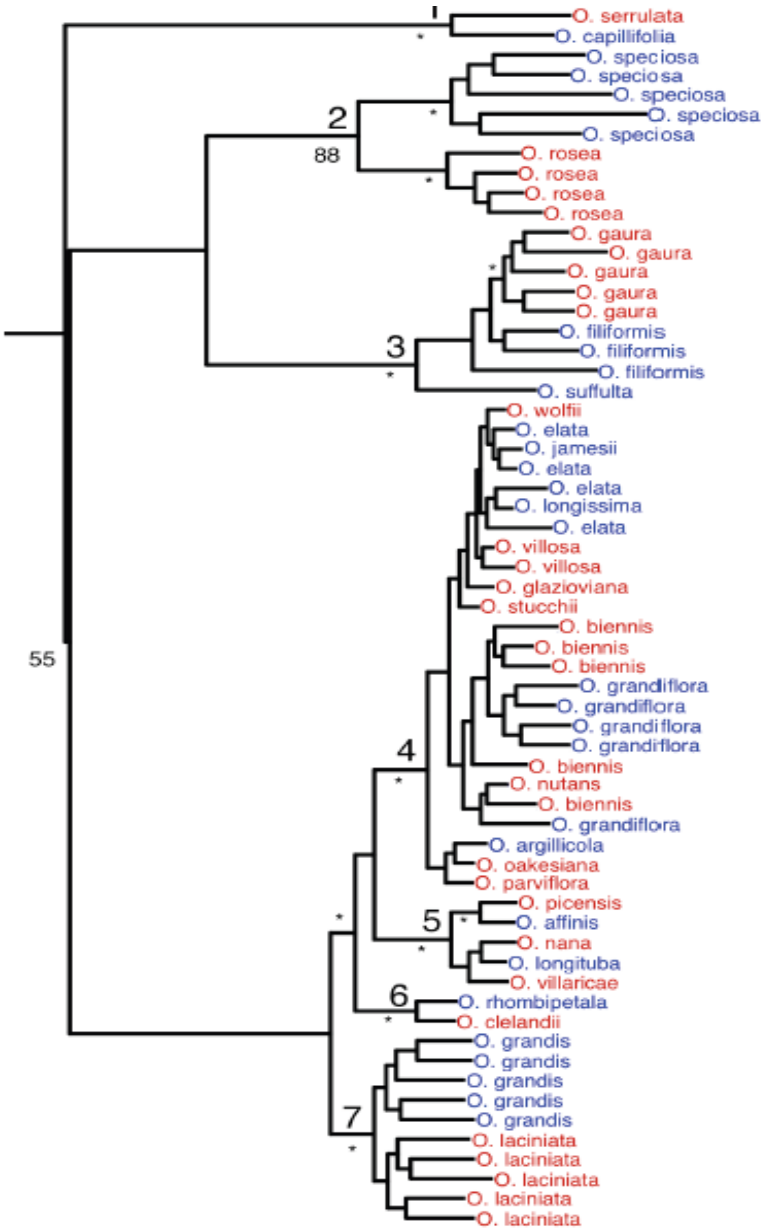


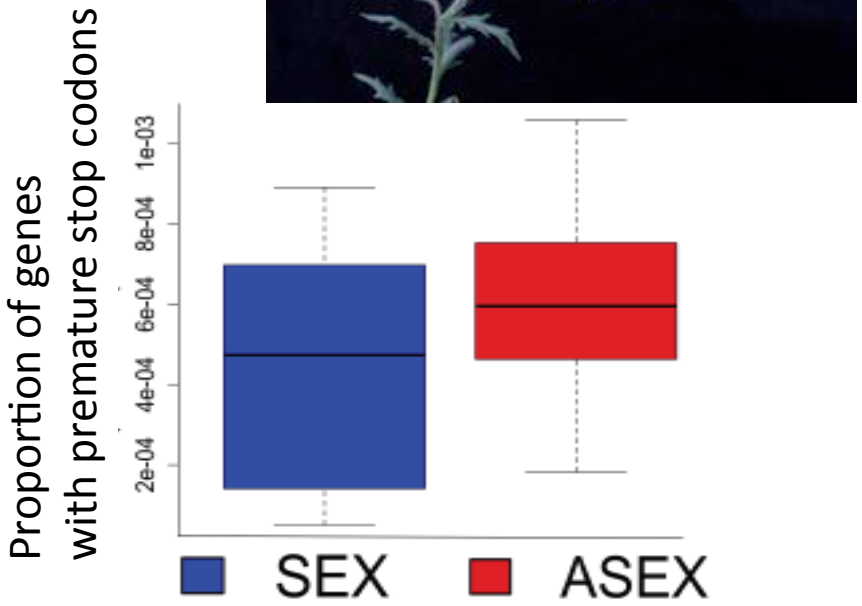
Loss of haplotype With zero deleterious alleles

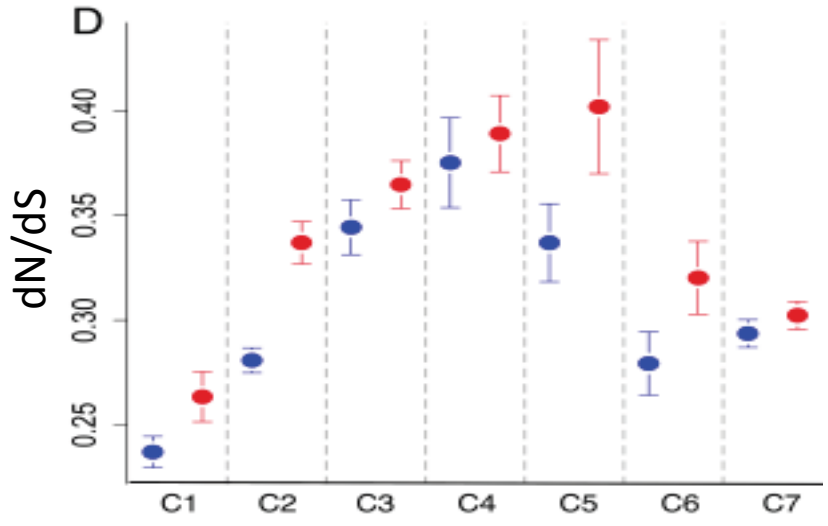
Recombination Can reform that haplotype

Recurrent loss of sex is associated with accumulation of deleterious mutations in *Oenothera*

Jesse D. Hollister[1,2,*], Stephan Greiner[3], Wei Wang[1], Jun Wang[4], Yong Zhang[4], Gane Ka-Shu Wong[4,5,*], Stephen I. Wright[1,6], Marc T. J. Johnson[2,6]

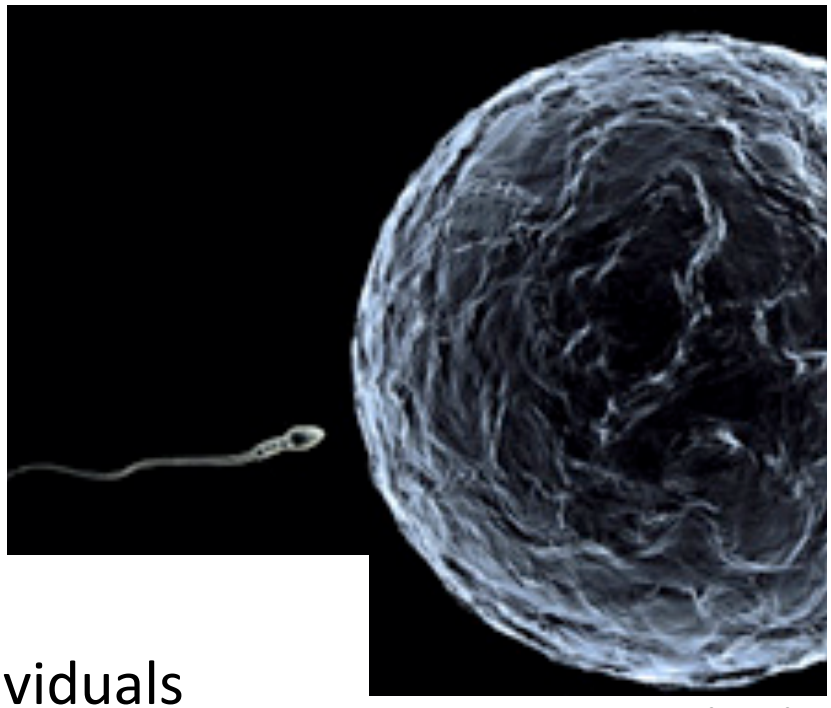






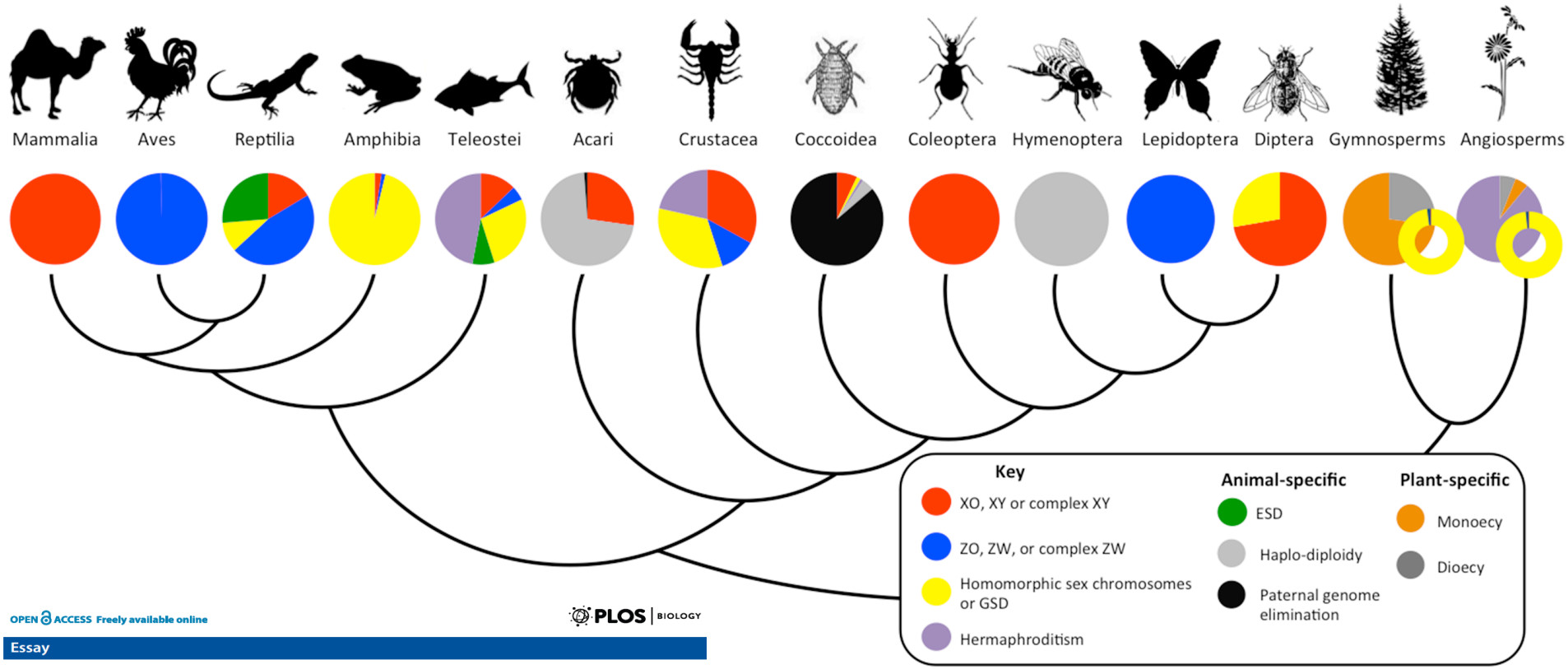
A species having sex is not the same as a species having different sexes

- The fundamental difference between male and female function is Anisogamy (Gametes differ in size)
- Male sexual function:
  - Small mobile gametes
- Female sexual function:
  - Larger less mobile gametes
  - Maternal provisions



Zimmer book

Male and female functions do not necessarily mean sexes are separate individuals
But separate sexes have arisen many times
Perhaps because of:
Selection for specialization
or inbreeding avoidance.



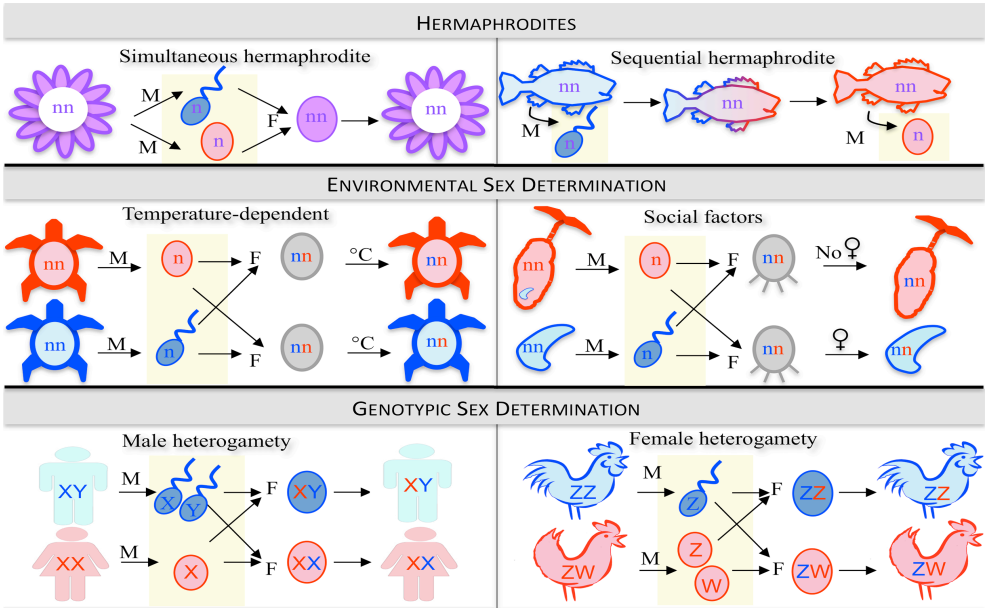
OPEN ACCESS Freely available online

PLOS | BIOLOGY

Essay

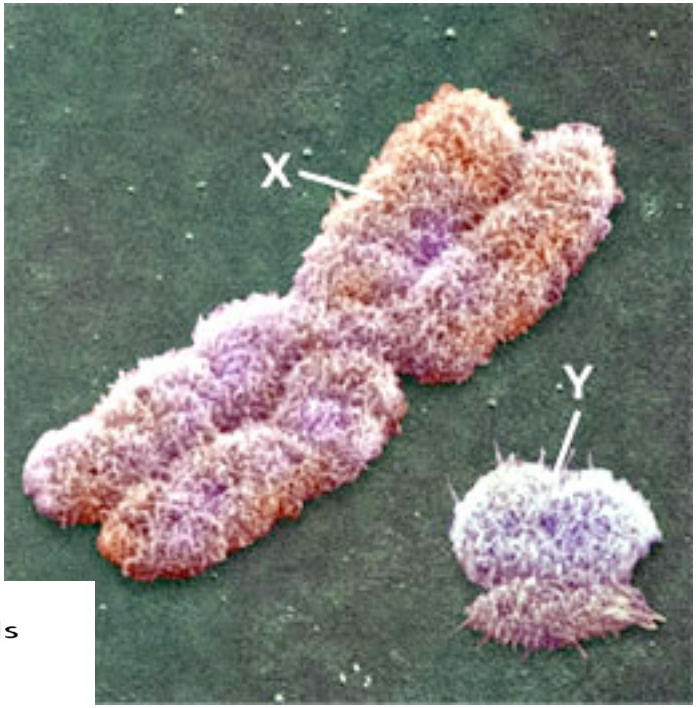
Sex Determination: Why So Many Ways of Doing It?

Doris Bachtrog[1]*, Judith E. Mank[2], Catherine L. Peichel[3], Mark Kirkpatrick[4], Sarah P. Otto[5], Tia-Lynn Ashman[6], Matthew W. Hahn[7], Jun Kitano[8], Itay Mayrose[9], Ray Ming[10], Nicolas Perrin[11], Laura Ross[12], Nicole Valenzuela[13], Jana C. Vamosi[14], The Tree of Sex Consortium[¶]

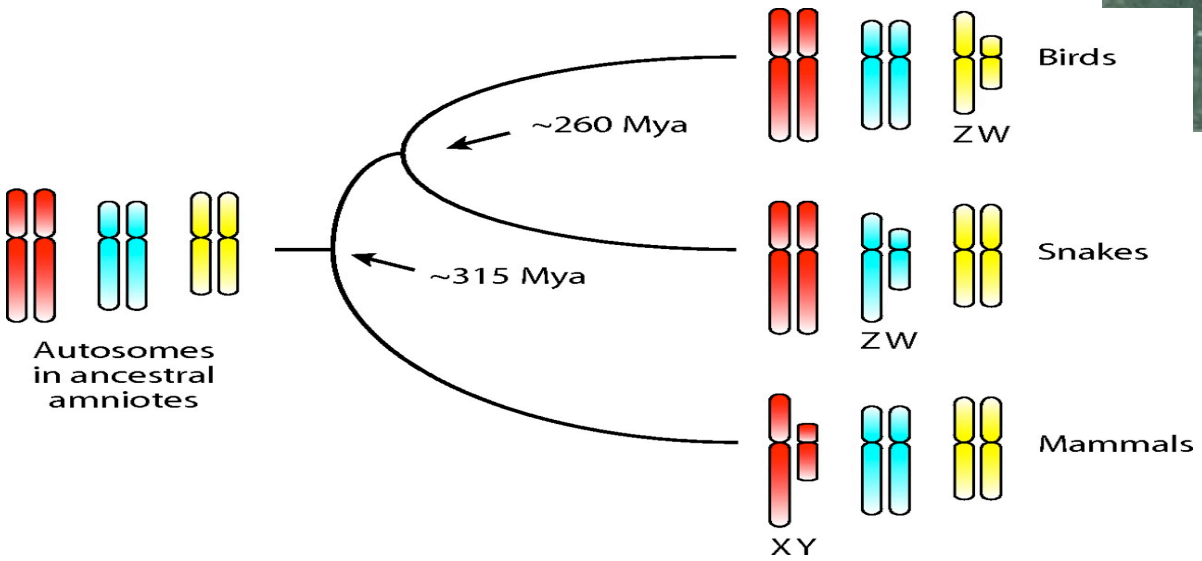


Evolution of sex chromosomes

In species with genetic sex determination
the chromosomes containing the sex determining factors
are often heteromorphic:
One is much reduced in
function and size.
And does not recombine.

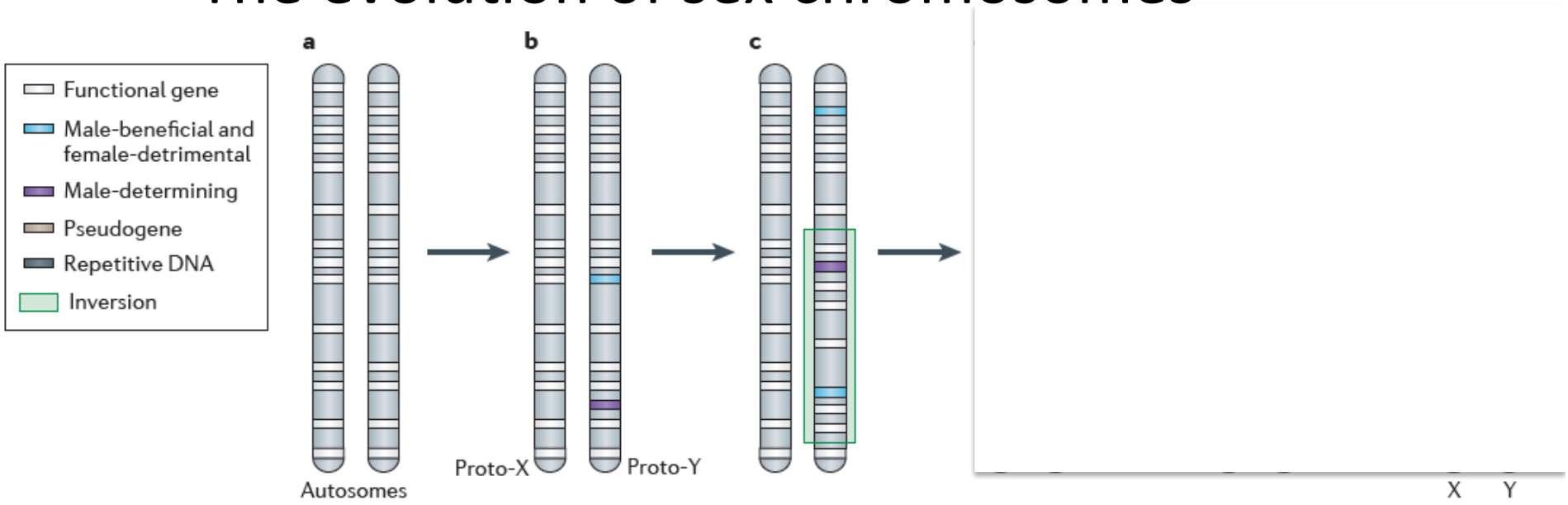


Human Y: 60 Mbp ~80 genes
Human X: 153 Mbp ~2000 genes

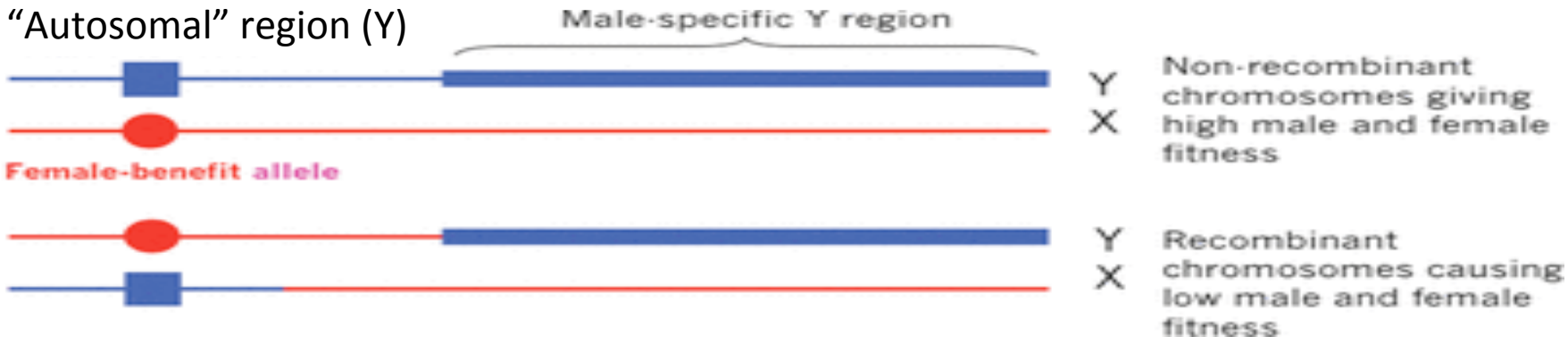


Heteromorphic sex chromosomes have evolved independently many times

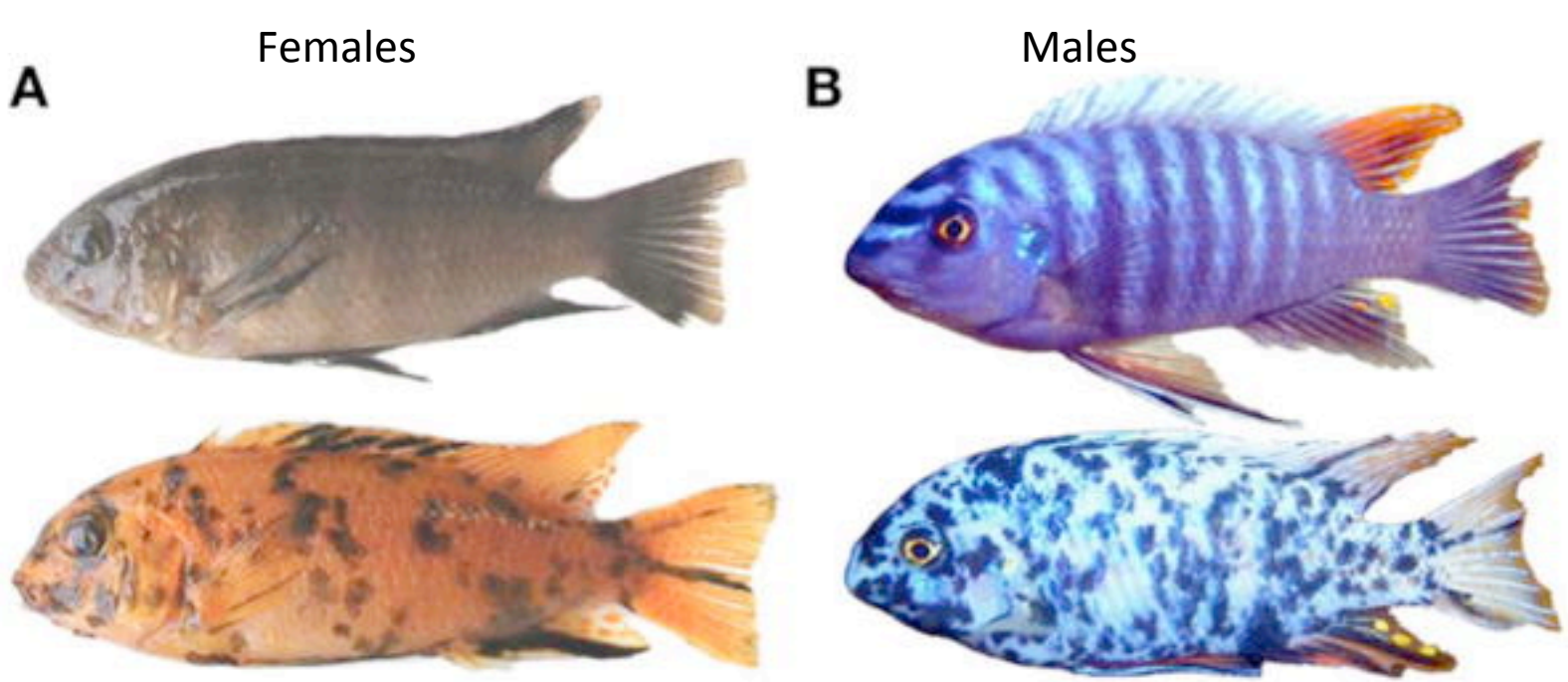
The evolution of sex chromosomes



Sex determining allele arises (e.g. dominant male determining allele)
Recombination between sexually antagonistic allele and male-determining allele have lowers fitness.
Recombination between these loci suppressed by inversion



Polymorphism



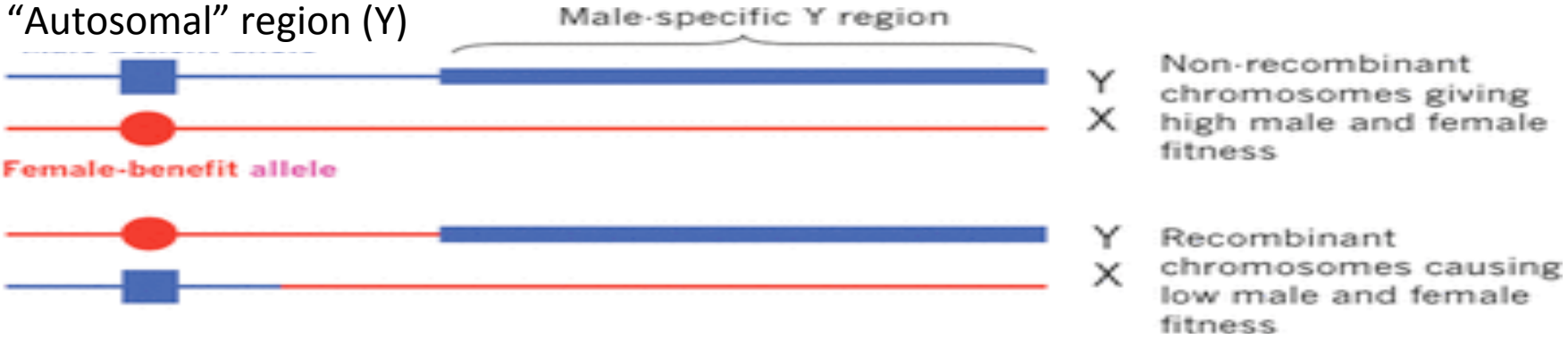
Recessive female advantageous allele

Has deleterious consequences in males

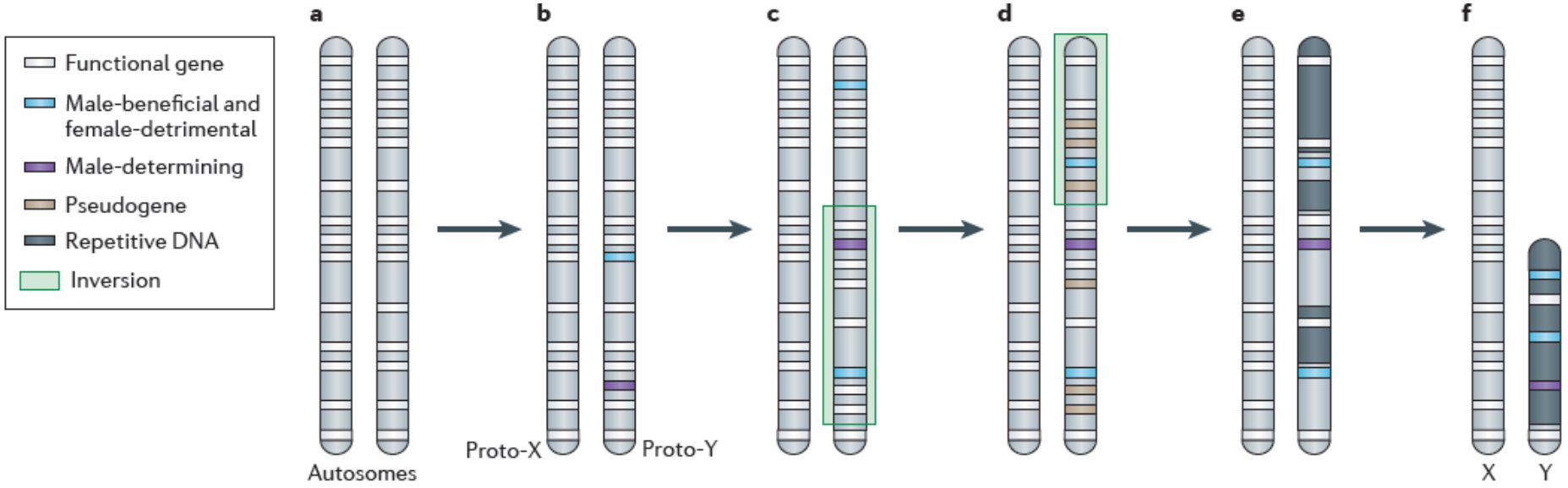
Sexual Conflict Resolved by Invasion of a Novel Sex Determiner in Lake Malawi Cichlid Fishes

Reade B. Roberts, Jennifer R. Ser, Thomas D. Kocher*

Sexual antagonistic alleles and the evolution of reduced recombination on Y chromosomes



The evolution of sex chromosomes

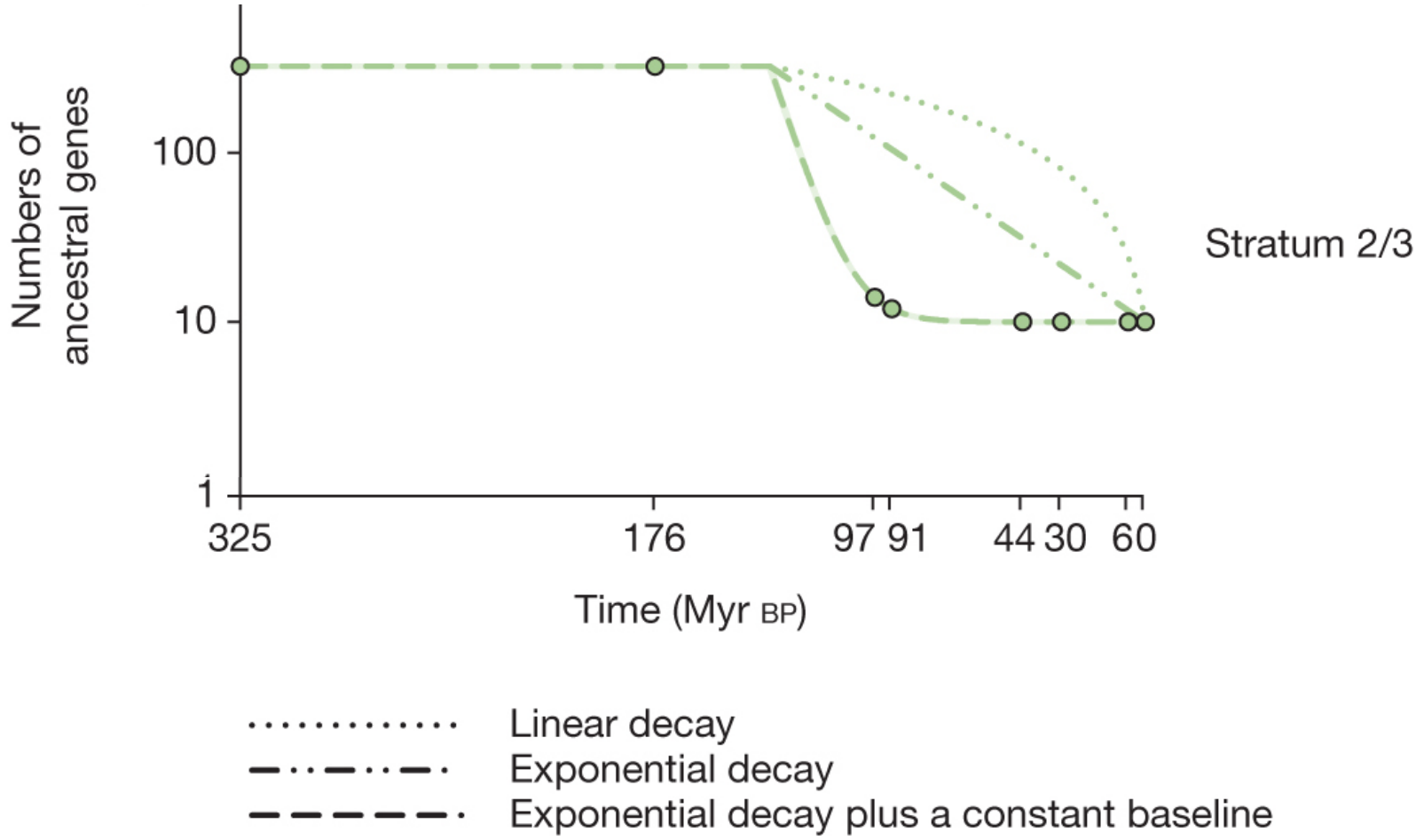


Sex determining allele arises (e.g. dominant male determining allele)
Recombination between sexually antagonistic allele and male-determining allele have lowers fitness.
Recombination between these loci suppressed by inversion

Shutting off recombination now means that this section of Proto-Y no long recombines (note that Proto-X can recombine with itself in females)

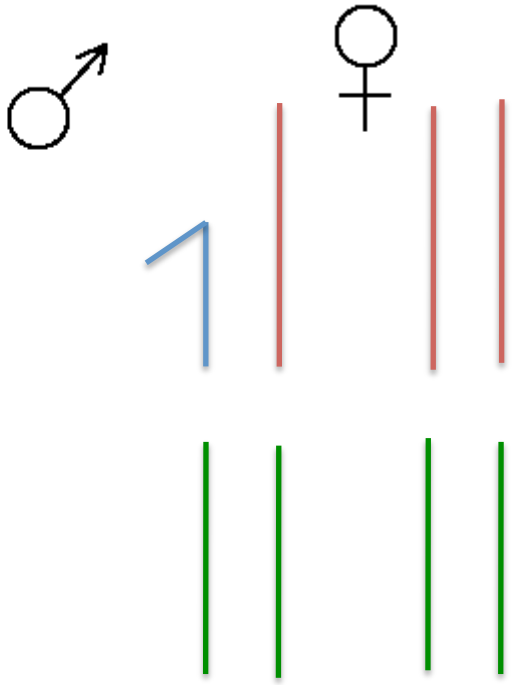
This in turn leads to degeneration of Y sex chromosome genes due to:
Muller's Ratchet
And the hitchhiking of deleterious alleles.
Accumulation of repeats and transposable elements.

Ancestral gene content in section of human Y chromosome



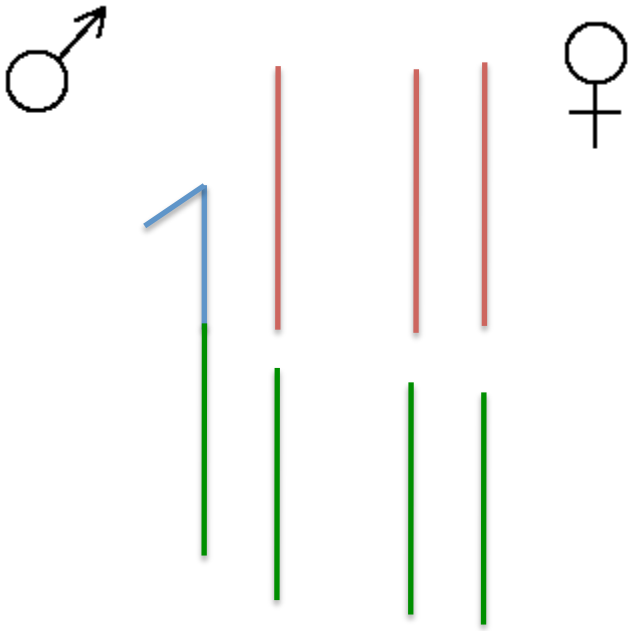
Bellot et al 2015, Nature

Neo-sex chromosomes in Drosophila

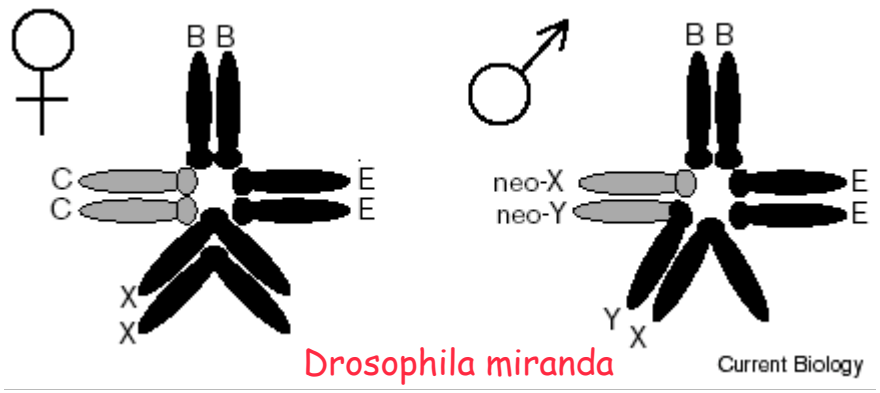


If an autosome fuses to the Y chromosome

Then one copy segregates with the Y and one
With the X this is called a neo-sex chromosome



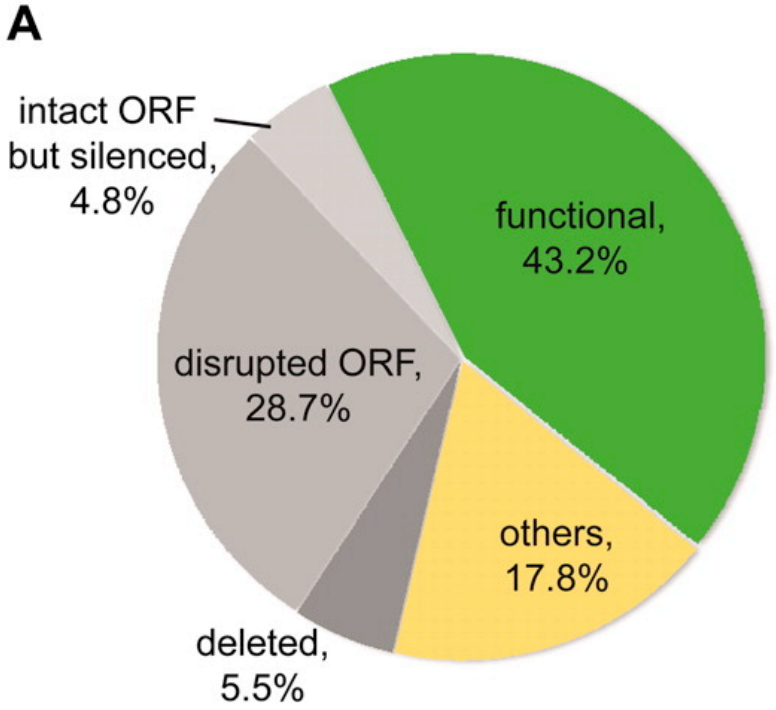
The autosome fused to the Y
does not experience recombination



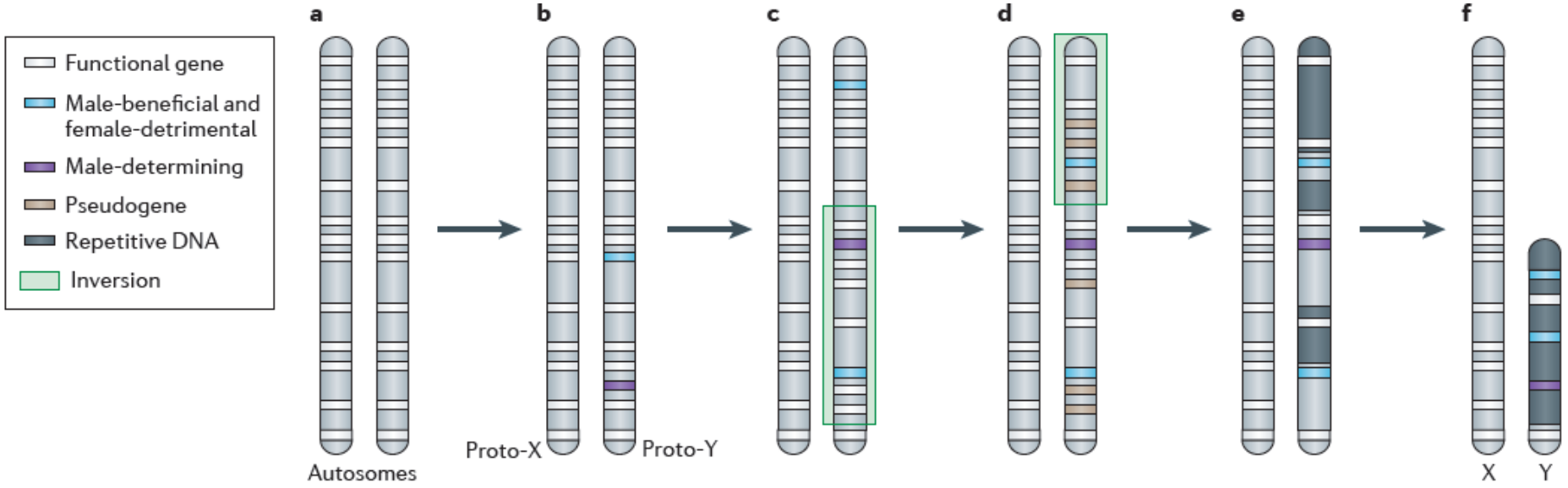
A neo-Y chromosome region was formed in *Drosophila miranda* 1.25 Myrs ago and has rapidly decayed

Majority of genes (open reading frames, ORFs)
In neo-Y region have become non-functional

degeneration of Y sex chromosome genes due to:
Muller's Ratchet
And the hitchhiking of deleterious alleles.
Accumulation of repeats and transposable elements.



The evolution of sex chromosomes



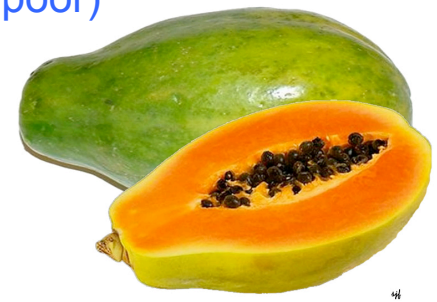
Convergent evolution and different ages of sex chromosomes

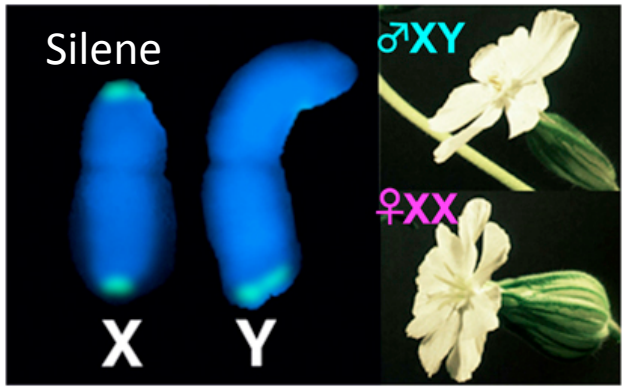
Corresponding X

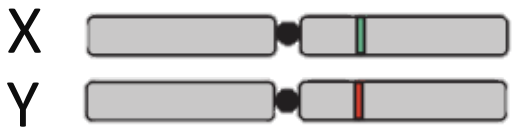
Non-recombining Y (gene poor)

Asparagus

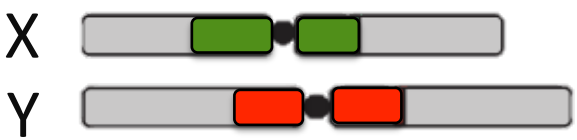
Papaya



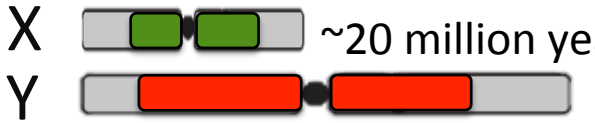




~2 million years old



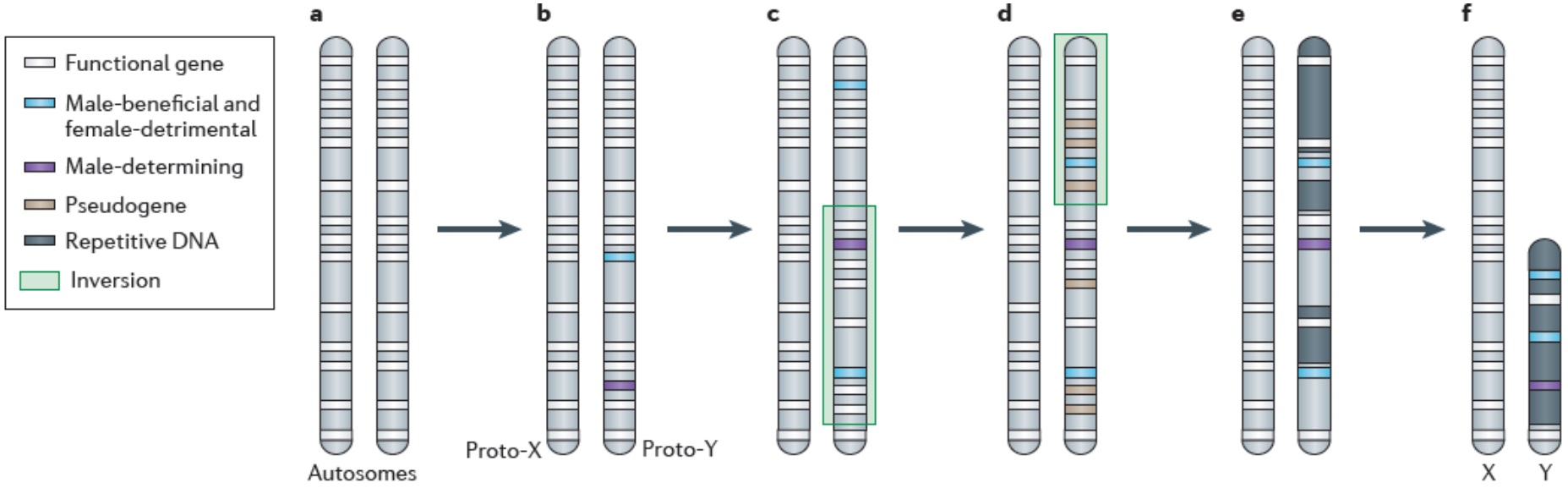
~10 million years old

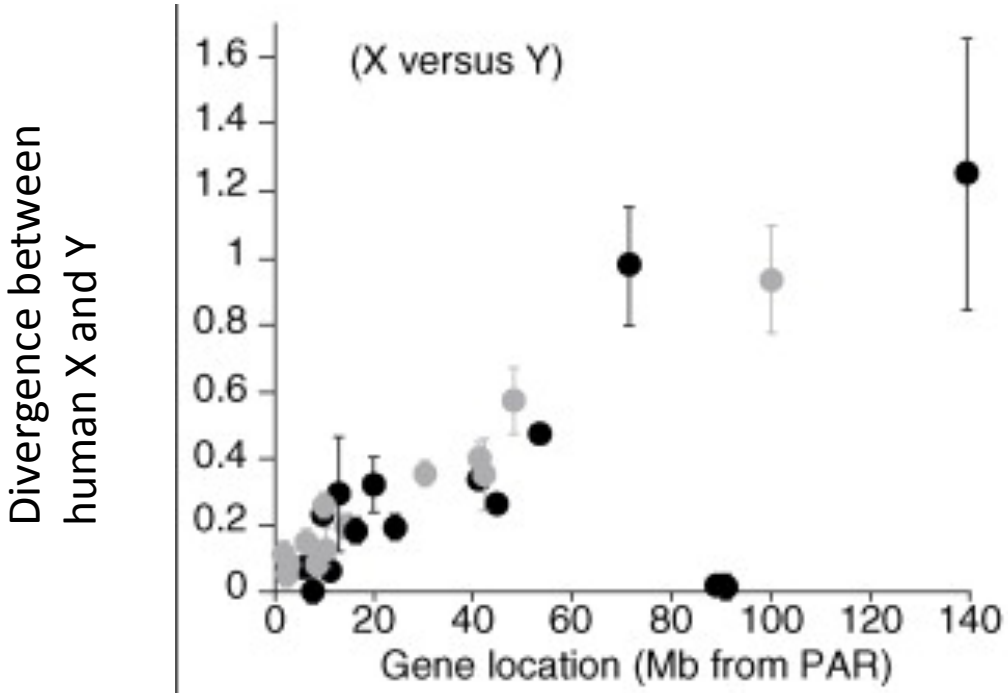


~20 million years old

Cannabis also has old XY

The evolution of sex chromosomes





Our own X and Y have different Evolutionary strata corresponding to different ages that recombination ceased between X and Y (different Inversions & transpositions)

Genes on Y in these different strata are in different states of decay.

Bergero, Charlesworth 2009