Speciation 2

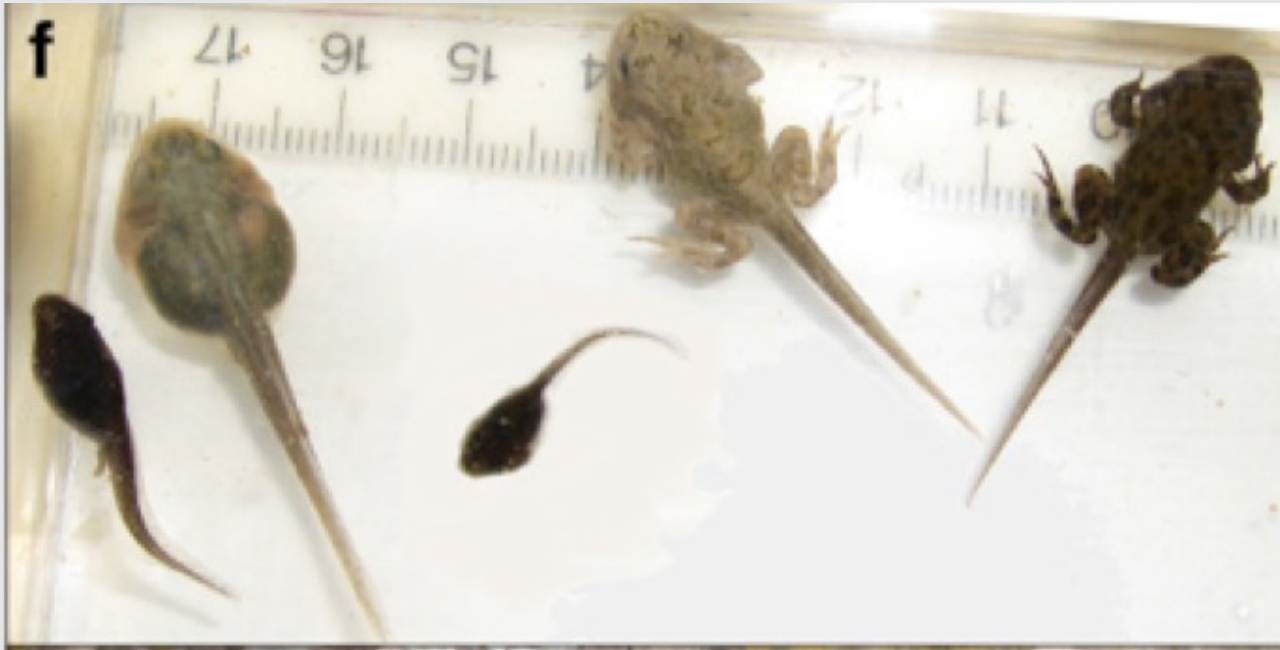http://www.freakingnews.com/Hybrid-Animals-Pictures--563.asp
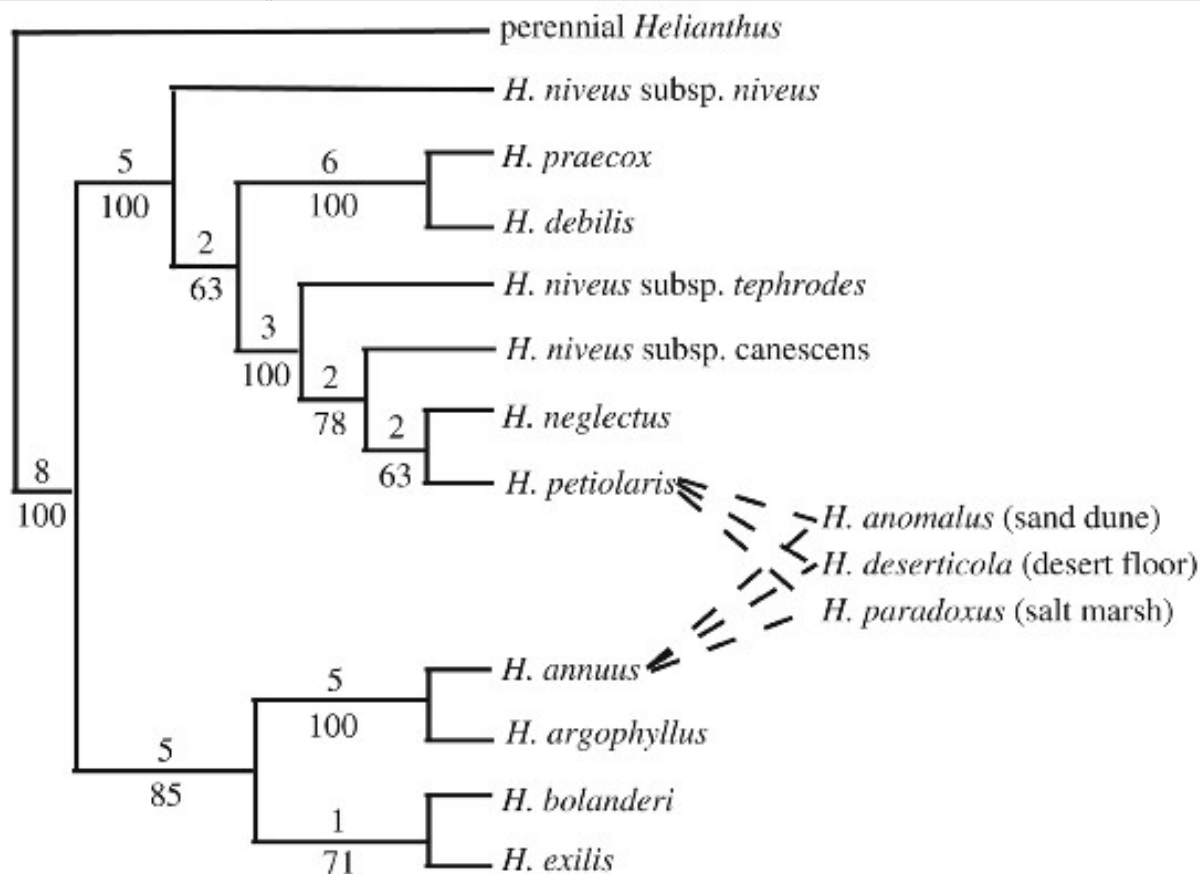
Brian O'Meara
EEB464 Fall 2018

- Hybridization

- Reinforcement

- Self-incompatibility & diversity

- Cytoplasmic incompatibility

Hybridization - bad

Colliard et al. Strong reproductive barriers in a narrow hybrid zone of West-Mediterranean green toads (Bufo viridis subgroup) with Plio-Pleistocene divergence. BMC Evol Biol (2010) vol. 10 pp. 232
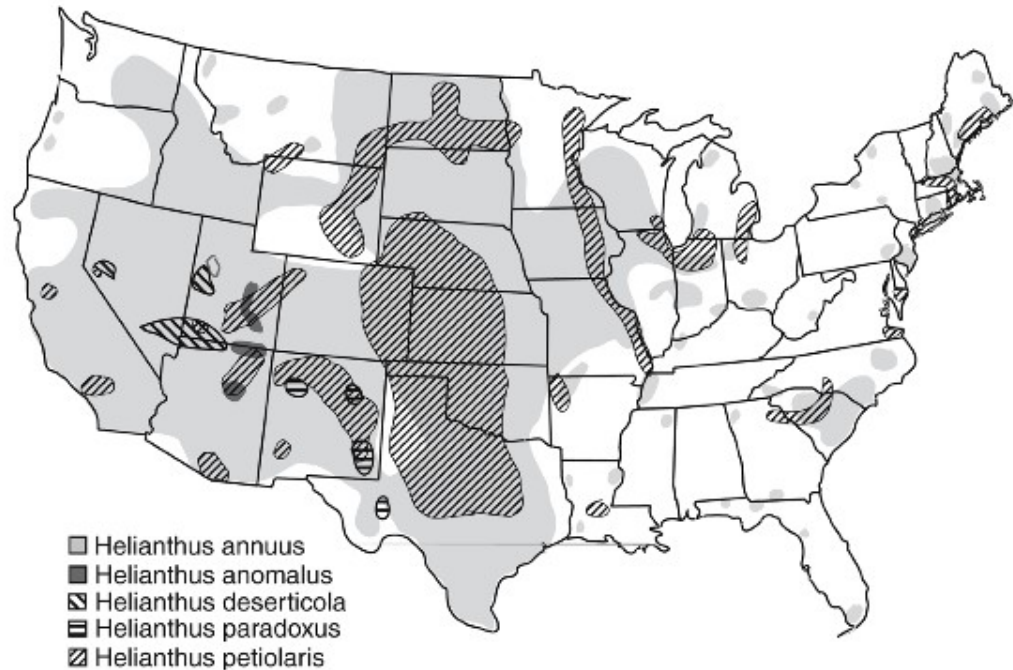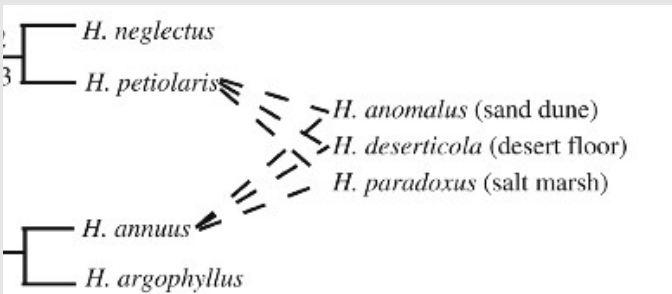
Hybridization - bad?

Fig. 1.

Phylogenetic tree for *Helianthus* section *Helianthus* based on combined chloroplast DNA and nuclear ribosomal DNA data (Rieseberg 1991). The number of mutations are given above and bootstrap percentages below each branch. Dashed lines indicate parentage of homoploid hybrid species
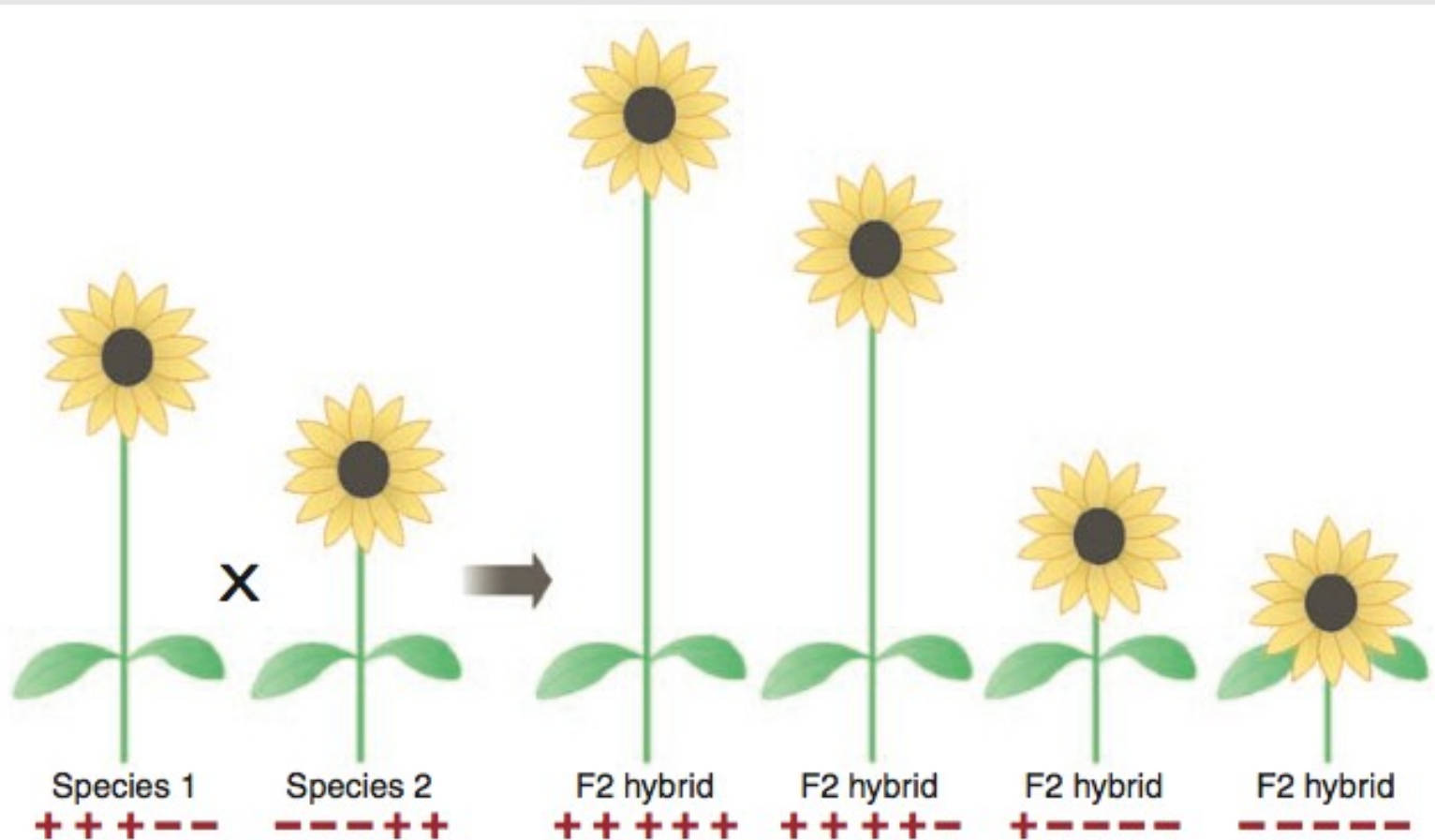
Hybridization - bad?

Fig. 4.
Present-day distributions of the two parental species, *H. annuus* and *H. petiolaris*, and their three hybrid derivative species, *H. anomalus*, *H. deserticola*, and *H. paradoxus* (based on Rogers et al. 1982)

Hybridization - bad?

Fig. 2. Genetic basis of transgressive segregation showing how segregating hybrids can combine plus and minus alleles from parental species, thereby generating extreme phenotypes or adaptations to extreme habitats.

Rieseberg and Willis. Plant speciation. Science (2007) vol. 317 (5840) pp. 910-4

Hybridization - bad?

Speciation in animals is almost always envisioned as the split of an existing lineage into an ancestral and a derived species. An alternative speciation route is homoploid hybrid speciation[1] in which two ancestral taxa give rise to a third, derived, species by hybridization without a change in chromosome number. Although theoretically possible it has been regarded as rare[1] and hence of little importance in animals. On the basis of molecular and chromosomal evidence, hybridization is the best explanation for the origin of a handful of extant diploid bisexual animal taxa[2–6]. Here we report the first case in which hybridization between two host-specific animals (tephritid fruitflies) is clearly associated with the shift to a new resource. Such a hybrid host shift presents an ecologically robust scenario for animal hybrid speciation because it offers a potential mechanism for reproductive isolation through differential adaptation to a new ecological niche[7]. The necessary conditions for this mechanism of speciation[7] are common in parasitic animals, which represent much of animal diversity[8]. The frequency of homoploid hybrid speciation in animals may therefore be higher than previously assumed.
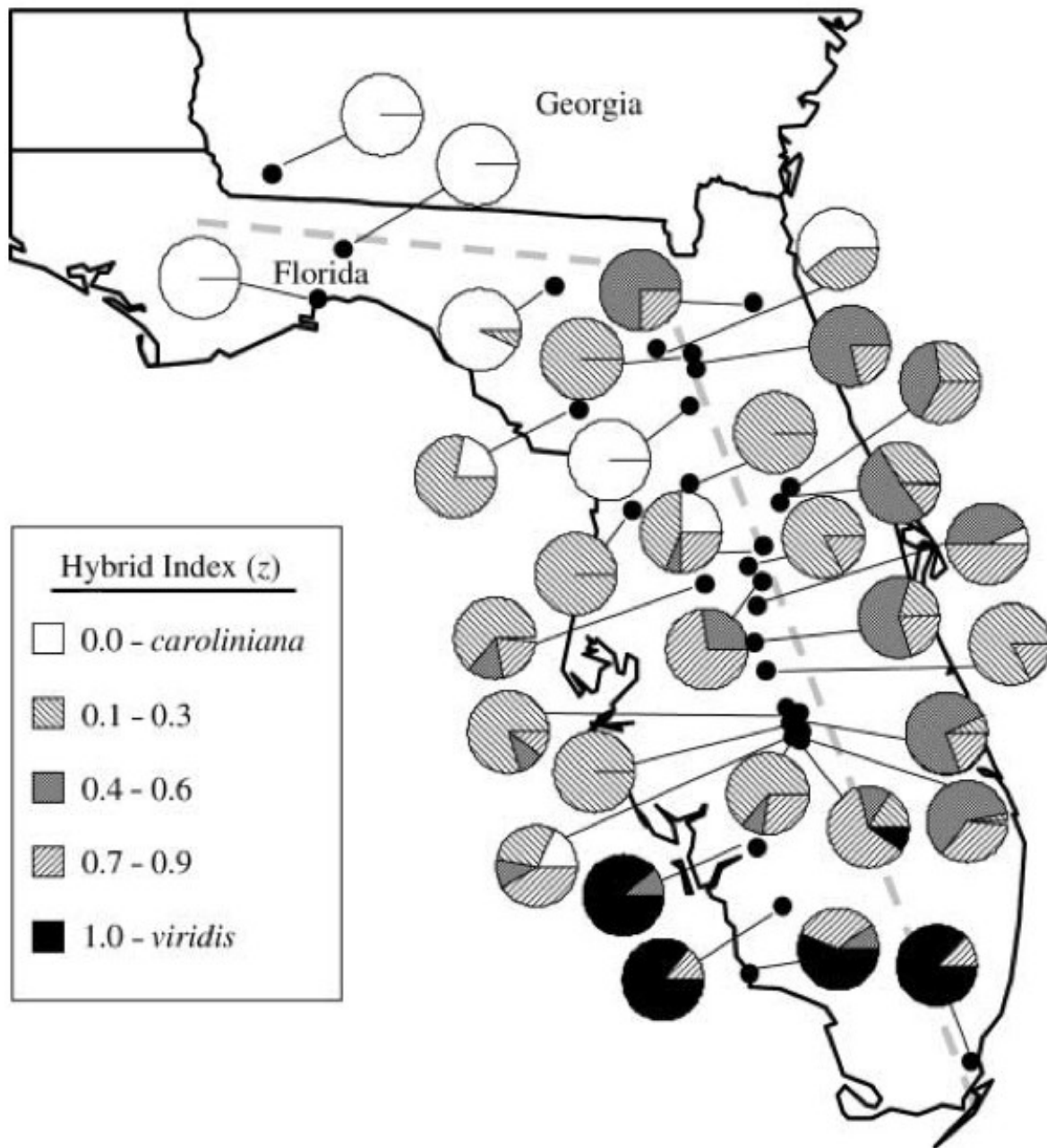
Fig. 1 Distribution of populations and hybrid indices (z-score) for a hybrid zone between the *caroliniana* and *viridis* morphotypes in the *Piriqueta caroliniana* complex in central Florida. The light grey dashed line indicates the position of the transect used to determine the position of each population.

Hybrid Index (z)

☐ 0.0 – *caroliniana*

▨ 0.1 – 0.3

▩ 0.4 – 0.6

▨ 0.7 – 0.9

■ 1.0 – *viridis*

Bob Peterson
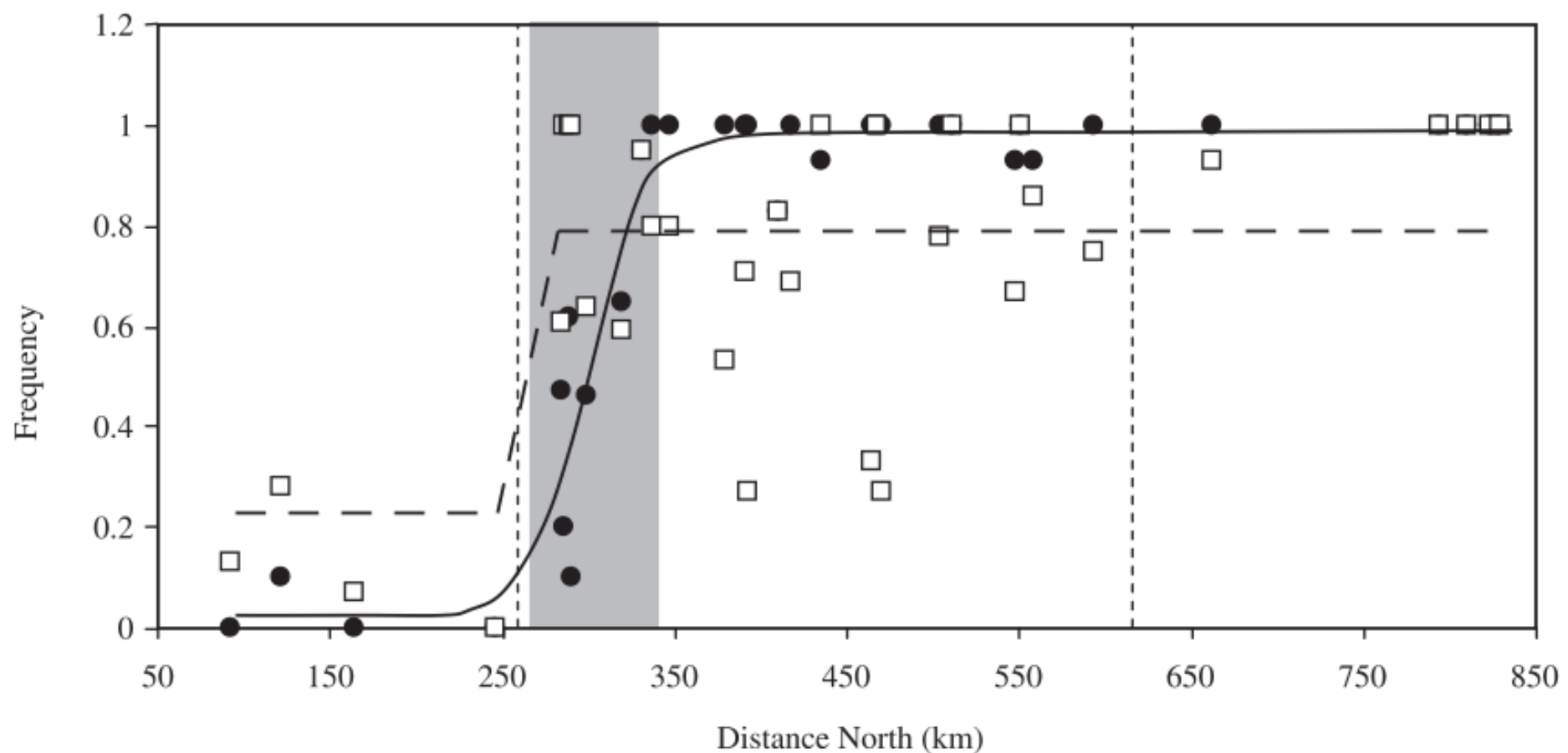
Fig. 3 Position of the c28 (solid line/solid circles) and c59 (dashed line/open squares) clines for the *Piriqueta* hybrid zone in central Florida, USA. Lines are based on the best fit to tanh models (Butlin *et al.*, 1991) using the NLIN procedure of SAS (SAS, 1999). The shaded region indicates the position of the putative tension zone as indicated by the width of these sharp clines. Vertical dashed lines indicate the geographic extent of the hybrid zone. The horizontal axis represents the position of each population along the transect indicated in Fig. 1.

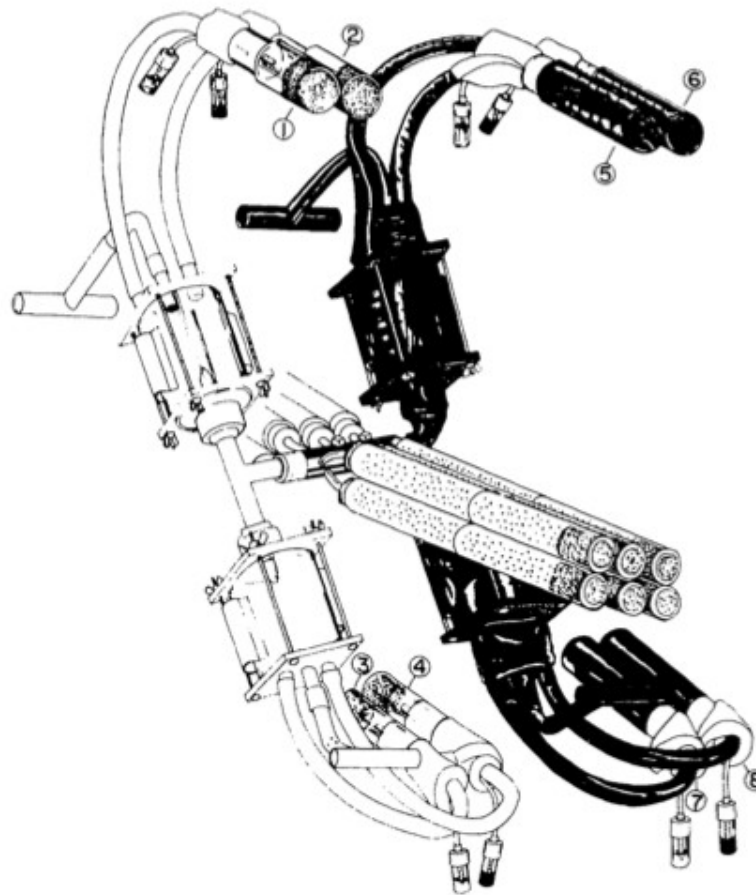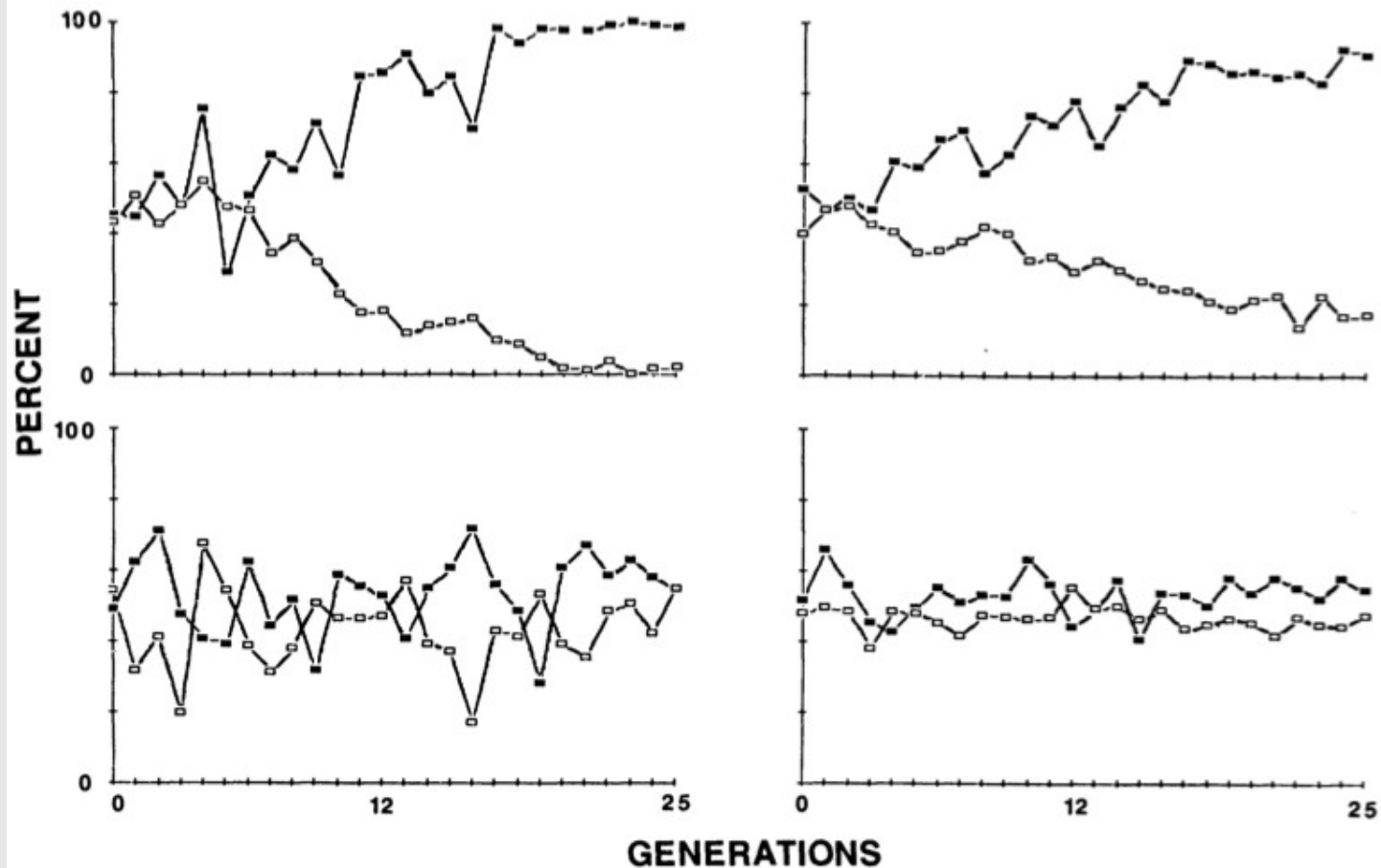FIG. 1.—A drawing of the habitat maze indicating the position of the habitats (labeled 1–8), and the tygon tubes containing the pupae (center). The maze was continuously lighted by fluorescent ceiling lights. The temperature was 25°C and the relative humidity 50%. Chemotaxis vials, attached to each habitat, contained 47.5% ethanol (dark) or 0.5% acetaldehyde (light) and delivered the agents via a wick.

Spatiotemporal   Spatial

FIG. 2.—The percentage of brown-eyed flies in the selected habitats. *Solid symbols*, Data from habitat 5; *open symbols*, habitat 4. *Left*, Spatiotemporal habitat preference; *right*, spatial habitat preference. *Bottom*, Control; *top*, experiment. In calculating percentages, numbers of flies are expressed as the percentage of the total for each eye color to remove variation in the total number of brown- and yellow-eyed flies between generations.
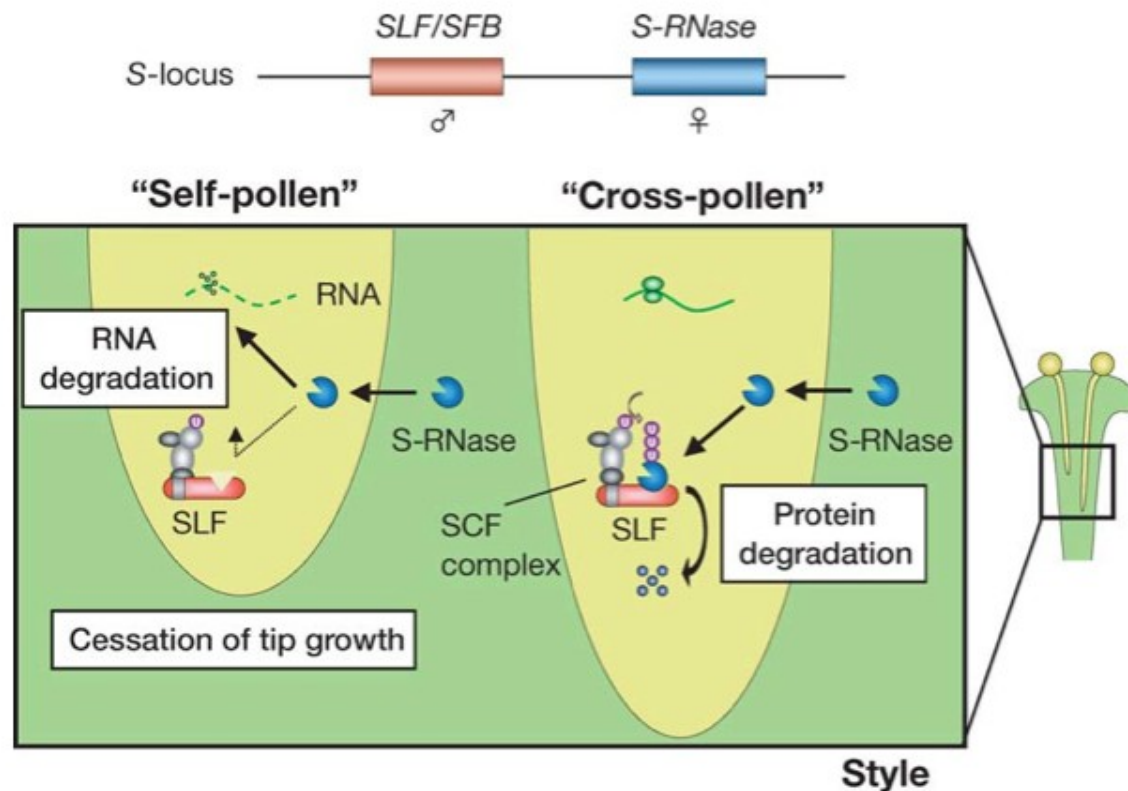
Figure 3

Molecular model of the self-incompatibility response in the Solanaceae, Rosaceae, and Scrophulariaceae. The *S*-locus consists of two genes, *S-RNase* and *SLF/SFB*. S-RNase is the female determinant and is secreted in large amounts into the extracellular matrix of the style. In a pollinated style, S-RNase is incorporated into the pollen tubes and functions as a cytotoxin that degrades pollen RNA. Although the S-RNase enters the pollen tubes regardless of their *S*-haplotypes, RNA degradation occurs only in self-pollen tubes. SLF/SFB is the male determinant and is a member of the F-box family of proteins, which generally function as a component of an E3-ubiquitin ligase complex. Thus, SLF/SFB is expected to be involved in ubiquitin-mediated protein degradation of nonself-S-RNases.

Goldberg et al. 2010
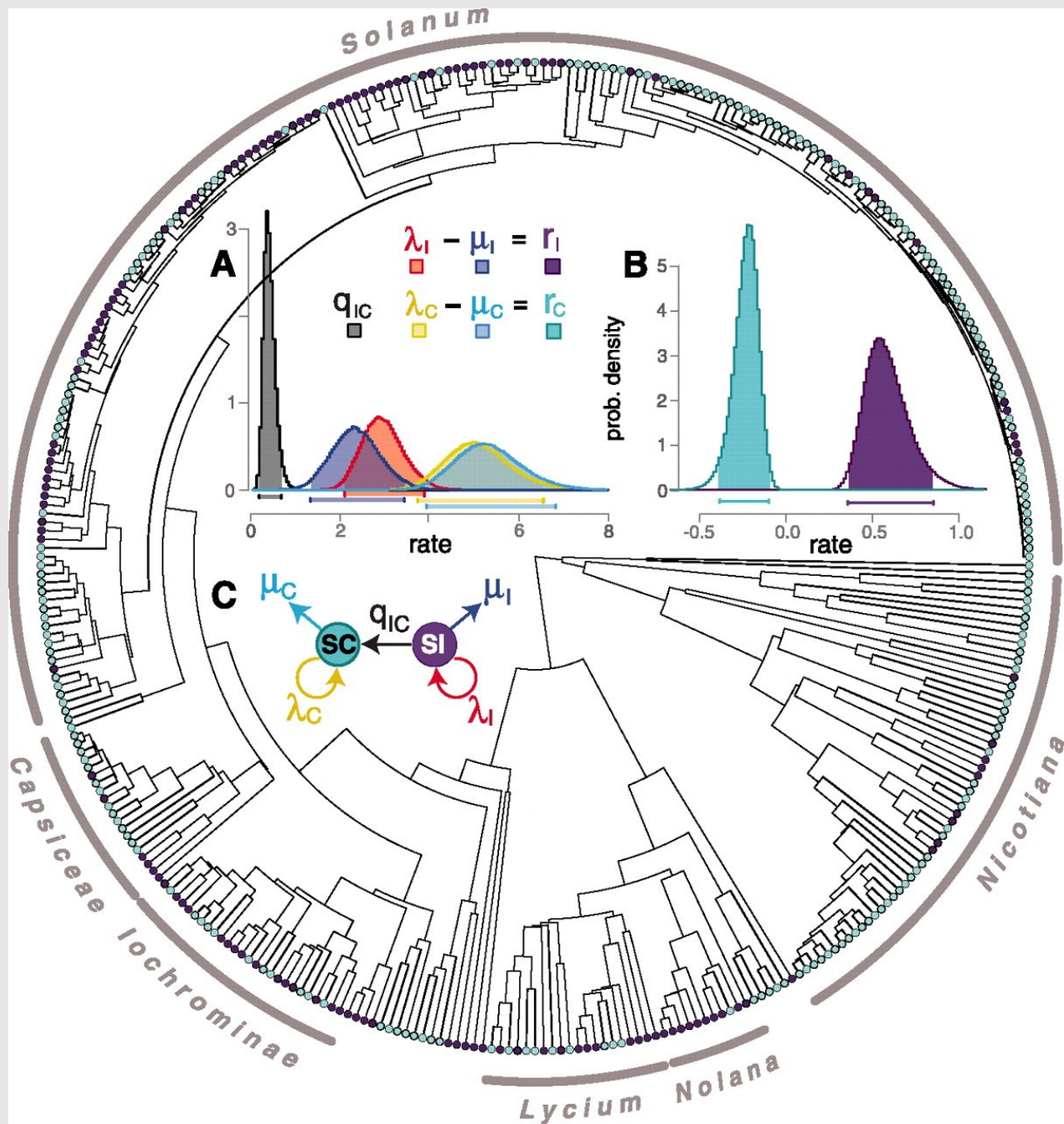
Haldane's rule

Table 1. Observations on interspecific hybridizations[2]

| | One of the two sexes inviable | | Both sexes viable, one sex sterile | |
	Male inviable	Female inviable	Male sterile	Female sterile
Drosophila	**14**[a]	9	**199**	3
Mammals	**0**	1	**25**	0
Birds	2	**21**	0	**30**
Lepidoptera	4	**36**	0	**15**

[a]Numbers shown in bold are cases that follow Haldane's rule. It has been argued that because there have been only two changes from male heterogamety to female heterogamety, accompanied by two shifts of the more affected sex of the hybrids from males to females, Haldane's rule would not be significant across metazoans[3] ($P = 0.25$). The central question, however, is why the pattern is so consistent *within* each taxonomic group, for example, 25:0 in mammals. Such consistency implies the existence of physiological, genetical and/or evolutionary mechanisms (see also Ref. 4).
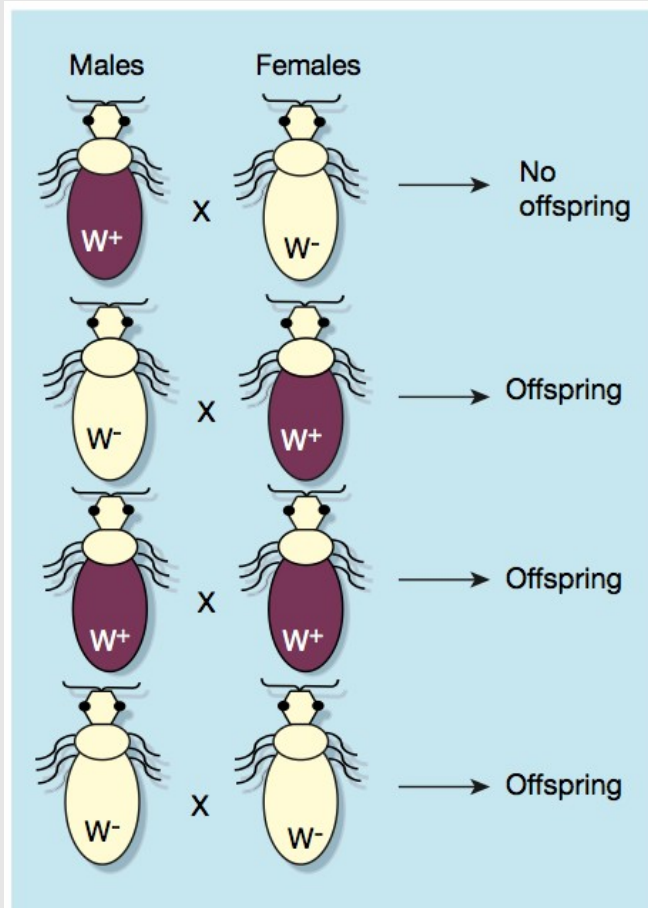
Figure 1 *Wolbachia* and cytoplasmic incompatibility. Cytoplasmic incompatibility means that when a male host infected with *Wolbachia* (W^+) mates with an uninfected female (W^-), no offspring are produced. All other matings are fully compatible and result in the production of offspring. The consequence of this system is that the maternally transmitted *Wolbachia* tend to spread through the host species.

Wade. Infectious speciation. Nature (2001) vol. 409 (6821) pp. 675-677

a

Ancestral population	$A_0A_0B_0B_0$
Geographically isolated daughter populations	$A_0A_0B_0B_0$ $A_0A_0B_0B_0$
Different mutations become fixed in the genomes	$A_1A_1B_0B_0$ $A_0A_0B_1B_1$
Reproductive isolation and speciation because of the incompatible gene combination A_1B_1	Mating results in inviable or infertile hybrids

b

Uninfected (W^-) ancestral population	$A_0A_0B_0B_0$ W^-
Geographically isolated daughter populations	$A_0A_0B_0B_0$ W^- $A_0A_0B_0B_0$ W^-
Independent infection and spread of *Wolbachia*	$A_0A_0B_0B_0$ W_A $A_0A_0B_0B_0$ W_B
Reproductive isolation due to *Wolbachia* infection	Reciprocal incompatibility

Figure 2 **Genetic and infectious models of speciation. a, A standard genetic model in which the initial state is an ancestral population of a species that is homozygous at both of two gene loci, and so is $A_0A_0B_0B_0$. Following geographical isolation, each of two daughter populations is gradually modified as new alleles (A_1 and B_1) arise by mutation and then become fixed in the genome by random genetic drift and natural selection. Because the A_1B_1 gene combination causes complete inviability or sterility in hybrids, the daughter populations are new, descendant species. b, Infectious speciation, which parallels the genetic model. The initial state is an ancestral species, W^-, not infected with *Wolbachia*. Two daughter populations arise which have become infected by different strains of *Wolbachia* (A and B) after transmission from a parasite or parasitoid. The different strains then become fixed in each genome by cytoplasmic incompatibility. Reciprocal cytoplasmic incompatibility between W_A males and W_B females, and W_B males and W_A females, prevents hybridization, so in effect the daughter populations are new species even though they remain genetically identical to one another and to the ancestor.**

Males   Females

W_A   X   W_B   →   No offspring

W_B   X   W_A   →   No offspring

W_A   X   W_A   →   Offspring

W_B   X   W_B   →   Offspring

Modified from Wade. Infectious speciation. Nature (2001) vol. 409 (6821) pp. 675-677
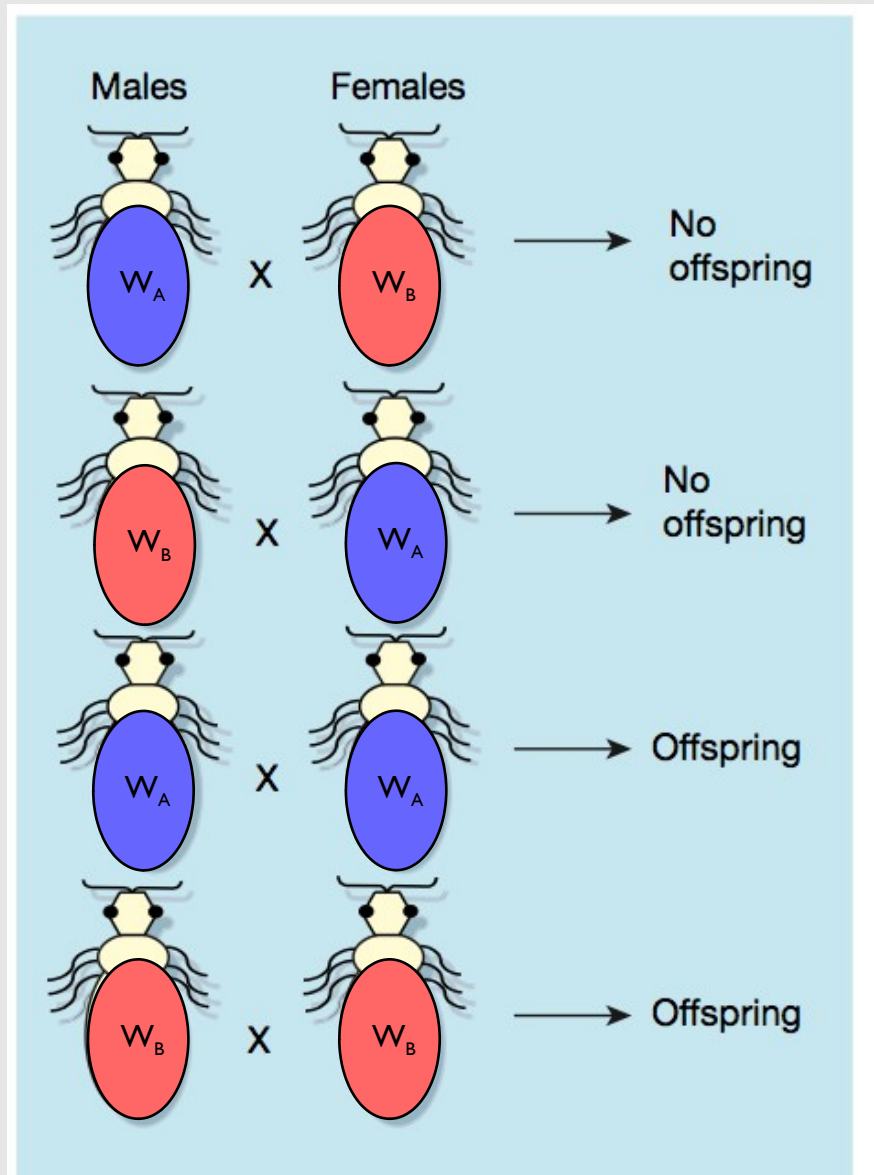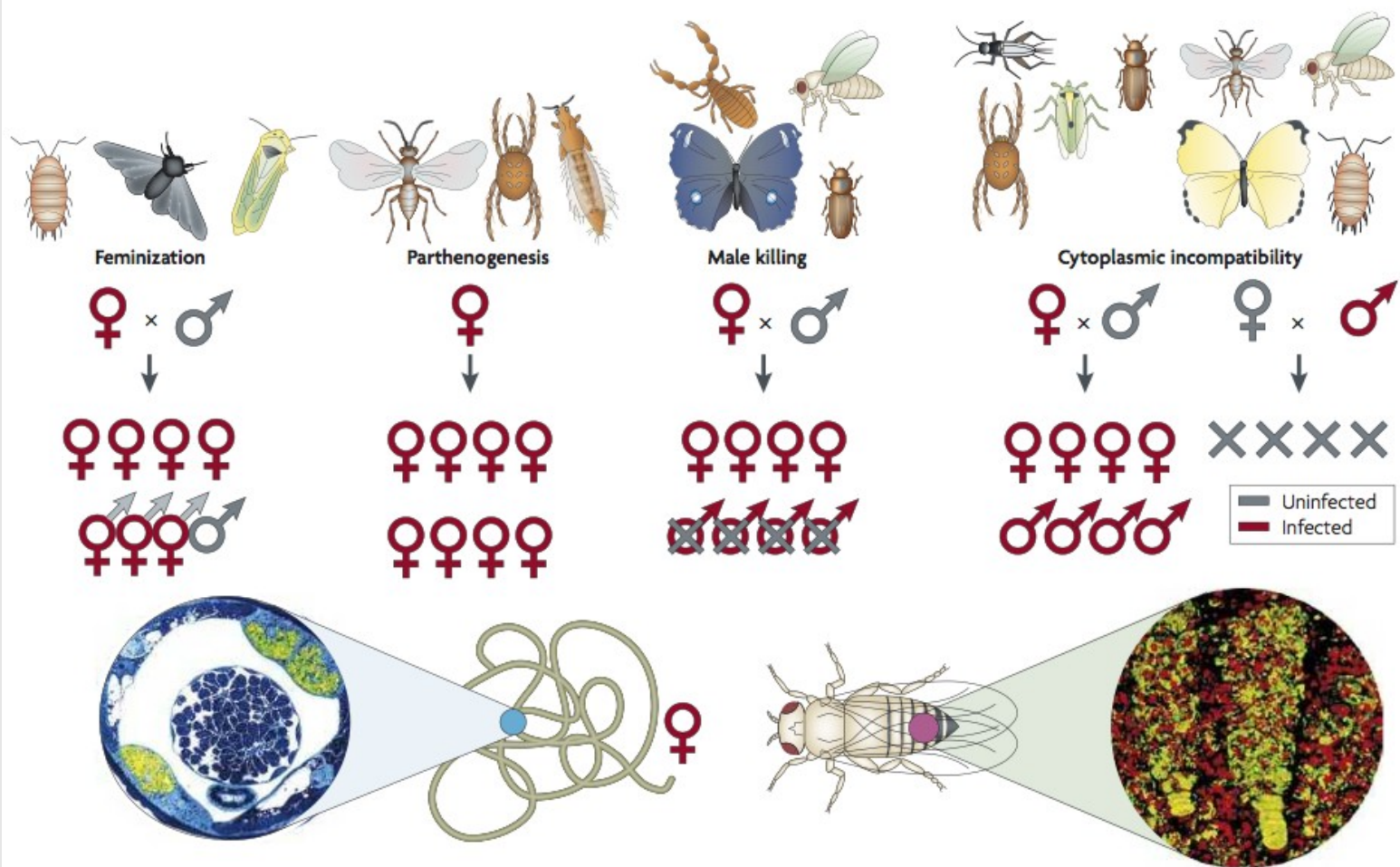
Figure 2 | **Wolbachia-induced phenotypes.** *Wolbachia* cause four distinct reproductive phenotypes in a range of arthropod orders (top). Feminization results in genetic males that develop as females (in the Hemiptera, Isopoda and Lepidoptera orders). Parthenogenesis induction eliminates males from reproduction (in the Acari, Hymenoptera and Thysanoptera orders). Male killing eliminates infected males to the advantage of surviving infected female siblings (in the Coleoptera, Diptera, Lepidoptera and Pseudoscorpiones orders). Cytoplasmic incompatibility prevents infected males from successfully mating with females that lack the same *Wolbachia* types (in the Acari, Coleoptera, Diptera, Hemiptera, Hymenoptera, Isopoda, Lepidoptera and Orthoptera orders). A cross section of a male filarial nematode, *Onchocerca ochengi*, that contains *Wolbachia* is shown (bottom left), in which *Wolbachia* are falsely coloured yellow and fill three of the four syncytial lateral cord cells. *Wolbachia* (yellow) are also shown within the ovaries of a female *Drosophila simulans* (bottom right). The image on the bottom left is courtesy of M. Taylor, Liverpool School of Tropical Medicine, UK. The image on the bottom right is courtesy of M. Clark, University of Rochester, New York, USA.