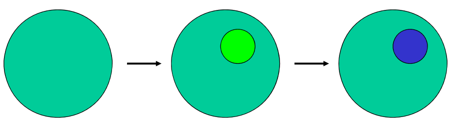
MODELS OF SPECIATION

Sympatric Speciation:

- Speciation without restriction to gene flow.
- Development of reproductive isolation without geographic barriers.
- Requires assortative mating and a stable polymorphism.

MODEL OF SYMPATRIC SPECIATION

ANCESTRAL POPULATION



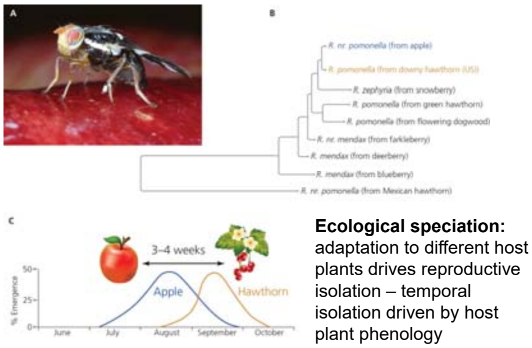
Reproductively isolated, geographically sympatric populations

THE APPLE MAGGOT: A CASE OF SYMPATRIC SPECIATION?

The Apple Maggot

Distribution of “races” of *R. pomnella*

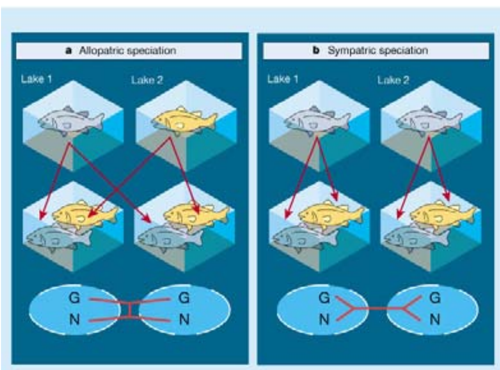
SYMPATRIC SPECIATION IN *RHAGOLETIS*



Ecological speciation: adaptation to different host plants drives reproductive isolation – temporal isolation driven by host plant phenology

Brought to you by the Feder Lab at ND!!!

SYMPATRIC SPECIATION IN CICHLID FISHES FROM NIGARAGUAN LAKES



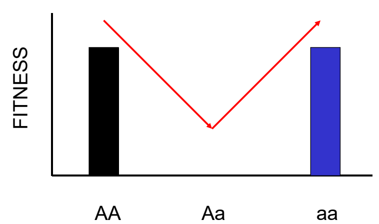
From: Kirkpatrick. 2000. Nature 408:298-299, Wilson et al., 2000. Proc. R. Soc. Lond. B 267:2133-2141

HOW CAN REPRODUCTIVE ISOLATION DEVELOP IN THE ABSENSE OF BARRIERS TO GENE FLOW?

- **Sympatric speciation in animals is a controversial mechanism.**
- **Host-race speciation requires either temporal or ecological isolation.**
- **Both of these mechanisms provide barriers to gene flow. (For example the apple and Hawthorne races of *Rhagoletis* have an effective migration rate of approx. 6%)**

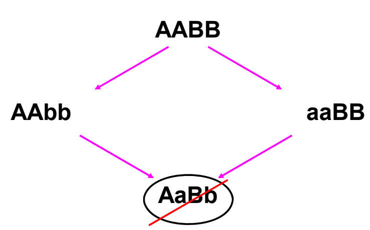
HOW MANY GENES ARE REQUIRED FOR SPECIATION TO OCCUR?

THE PROBLEM WITH A ONE-LOCUS MODEL OF SPECIATION



- In order for a single locus model of speciation to work, populations would have to evolve towards ***lower*** fitness.

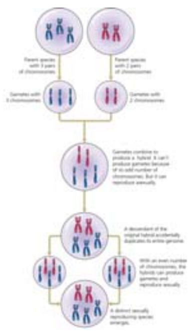
THE BATESON-MULLER-DOBZHANSKY MODEL FOR THE GENETIC BASIS OF POST-MATING REPRODUCTIVE BARRIERS



- This two-locus model relies on ***epistatic*** interactions among genes.

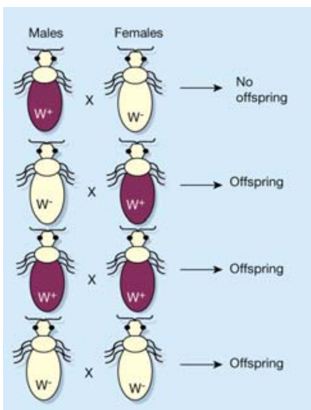
"INSTANTANEOUS SPECIATION"

- **Chromosomal duplications:** As many as 47% of flowering plant species are polyploid.
- Multiplication of the number of chromosomes can occur in at least two ways:
  - **Autopolyploidy** – duplication of the chromosomes of a single species (nondisjunction during meiosis).
  - **Allopolyploidy** – Duplication of a combination of chromosomes from different species.



INFECTIOUS SPECIATION

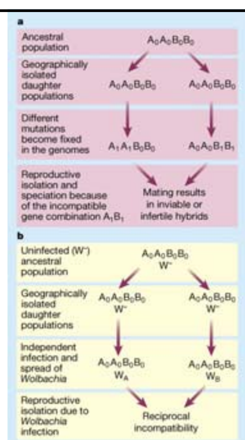
- The bacterium *Wolbachia* can cause *cytoplasmic incompatibility*.
- When infected male hosts (W^+) mate with uninfected females (W^-) no viable offspring are produced.
- Different strains of *Wolbachia* are incompatible.



CONTRASTING THE "CLASSICAL" MODEL OF GENETIC SPECIATION WITH THE 'INFECTIOUS' MODEL

The Classical Model →

The Infectious Model →



EVIDENCE OF THE CLASSIC VIEW OF SPECIATION: ACCUMULATION OF SMALL DIFFERENCES OVER TIME

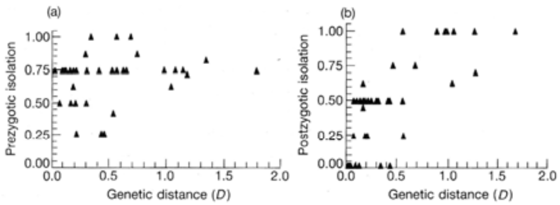


Figure 16.12 Strength of isolation in relation to genetic distance for pairs of species of *Drosophila*. (a) Prezygotic isolation. (b) Postzygotic isolation. Note prezygotic isolation is higher for low distances than is postzygotic isolation. From Coyne and Orr (1989a).

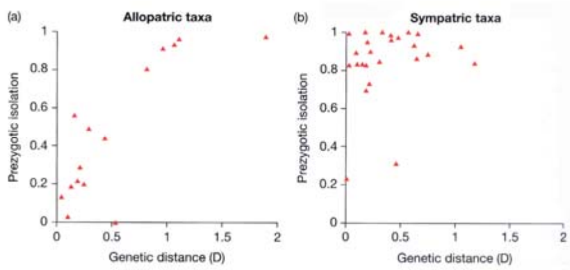
REINFORCEMENT

- Sexual selection on males and natural selection on females may favor indiscriminant mating between populations.
- Without complete pre- and post-zygotic isolating mechanisms, repeated hybridization can fuse gene pools.
- Reinforcement (*i. e.,* selection for positive assortative mating; disruptive selection) can occur if the fitness cost from lost mating opportunities is balanced by a fitness gain in offspring viability.

REINFORCEMENT

- Reinforcement leads to pre-mating isolation.
- Hybridization reduces the strength of reinforcement by homogenizing gene pools.
- Reinforcement must occur sufficiently fast to counter hybridization and complete the speciation process.

PREZYGOTIC REPRODUCTIVE ISOLATION EVOLVES MORE RAPIDLY IN SPECIES THAT ARE SPATIALLY OVERLAPPING:EVIDENCE FOR REINFORCEMENT



FROM: Coyne & Orr 1997

Adaptive radiation is the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage. It involves the differentiation of a *single ancestor into an array of species* that inhabit a variety of environments and that differ in… traits used to exploit those environments.

…It is regarded as the hallmark of adaptive evolution and may well be the most common syndrome in the origin and proliferation of taxa.

Dolph Schluter, 2000
The Ecology of Adaptive Radiation

…some time after a rather distinctive *new adaptive type* has developed it often becomes highly diversified. …the same sort of diversification follows, and in this case begins almost immediately, when a group spreads to a new and, for it, *ecologically open territory*.

- Simpson, 1953

WHAT PRECIPITATES AN ADAPTIVE RADIATION?

ECOLOGICAL OPPORTUNITY: the invasion of unutilized ecological niches leads to rapid diversification, e.g., colonizing a remote archipelago, surviving a mass extinction.

KEY INNOVATION: the acquisition of a novel adaptive trait (behavioral, morphological, or physiological) allows organisms to exploit previously unavailable ecological niches.

EVIDENCE FOR THE ECOLOGICAL OPPORTUNITY HYPOTHESIS

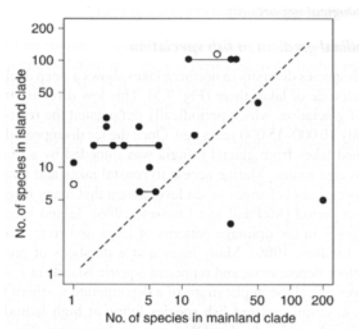


Fig. 7-7 IN: Schluter 2000. *The Ecology of Adaptive Radiation*. Oxford Univ. Press. Oxford

Seeing this graduation and diversity of structure in one small, intimately related group of birds, one might really fancy that, from an original paucity of birds in this archipelago, *one species has been taken and modified for different ends*.

Darwin, 1842

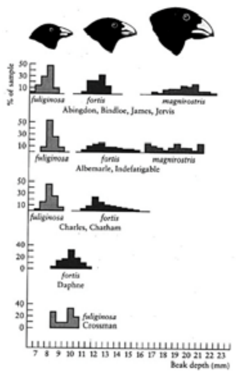
Character Displacement:

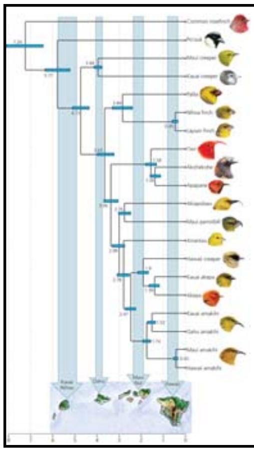
- Members of one lineage constrain phenotypic evolution in members of other lineages

There are two sides to this coin:

1) It may **promote** divergence between closely related species when there are unexploited ecological niches available.

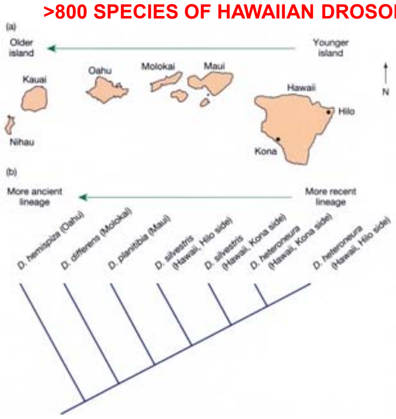
2) It may **constrain** divergence when there are no unexploited niches

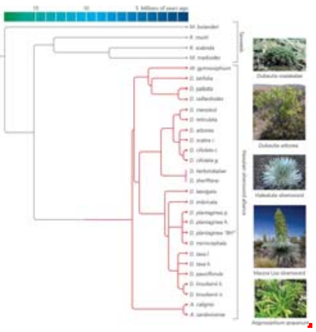




HAWAIIAN HONEYCREEPERS

>800 SPECIES OF HAWAIIAN DROSOPHILID FLIES



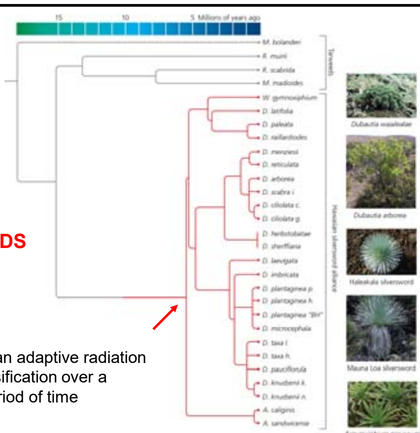


HAWAIIAN SILVERSWORD ALLIANCE

- 28 SPECIES DERIVED FROM A SINGLE COMMON ANCESTOR. THESE PLANTS OCCUPY HABITATS RANGING FROM EXPOSED LAVA TO WET FOREST.

- DIVERSE FORMS INCLUDE, VINES, TREES, ERECT SHRUBS, ROSETTES, AND HERBACEOUS MATS

SILVERSWORDS



One signature of an adaptive radiation is a burst of diversification over a relatively short period of time

CICHLID FISHES IN AFRICAN RIFT VALLEY LAKES:

- **LAKE TANGANYIKA: 140 SPP.**
- **LAKE MALAWI: >500 SPP.**
- **LAKE VICTORIA: 250 SPP.**

Lake Malawi Cichlids

Photos by Fredrik Hagblom

INVITED REVIEW

Speciation in rapidly diverging systems: lessons from Lake Malawi

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Abstract

Rapid evolutionary radiations provide insight into the fundamental processes involved in species formation. Here we examine the diversification of one such group, the cichlid fishes of Lake Malawi, which have radiated from a single ancestor into more than 400 species over the past 700 000 years. The phylogenetic history of this group suggests: (i) that their divergence has proceeded in three major bursts of cladogenesis; and (ii) that different selective forces have dominated each cladogenic event. The first episode resulted in the divergence of two major lineages, the sand- and rock-dwellers, each adapted to a major benthic macro-habitat. Among the rock-dwellers, competition for trophic resources then drove a second burst of cladogenesis, which resulted in the differentiation of trophic morphology. The third episode of cladogenesis is associated with differentiation of male nuptial colouration, most likely in response to divergent sexual selection. We discuss models of speciation in relation to this observed pattern. We advocate a model, divergence with gene flow, which reconciles the disparate selective forces responsible for the diversification of this group and suggest that the nonadaptive nature of the tertiary episode has significantly contributed to the extraordinary species richness of this group.

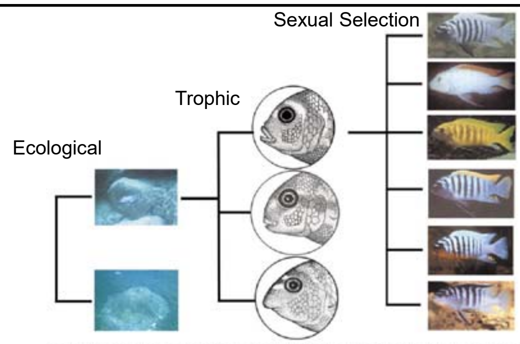
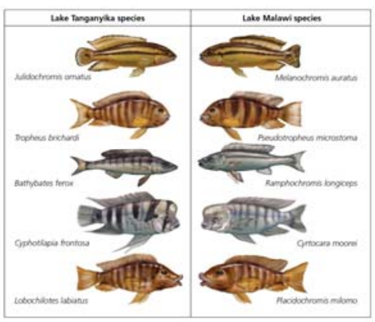


Fig. 1 A proposed phylogenetic history of Lake Malawi's rock-dwelling cichlids based on several molecular phylogenies of Lake Malawi cichlids (Meyer *et al.* 1990; Kocher *et al.* 1993; Meyer 1993; Moran *et al.* 1994; Moran & Kornfield 1995; Albertson *et al.* 1999). Lake Malawi is presumed to have been invaded by a riverine generalist closely allied with Lake Tanganyika's haplochromine tribe approximately 700 000 years ago. This common ancestor subsequently diverged during the primary radiation into the sand-dwelling and rock-dwelling lineages. The rock-dwelling lineage diverged during the secondary radiation into the 10–12 currently recognized mbuna genera. These genera are distinguished primarily on the basis of trophic morphology suggesting the importance of trophic competition during this period of the radiation. The spectacular species richness of the mbuna principally arose during the tertiary radiation. During this period, as many as 25 species per genus diverged presumably in response to sexual selection via female choice for male secondary sexual characteristics such as colour pattern. Line drawings courtesy of R. C. Albertson, colour images courtesy of Konings (1990).

ADAPTIVE RADIATION AND CONVERGENT EVOLUTION



CONVERGENT EVOLUTION IN THE CICHLID RADIATION

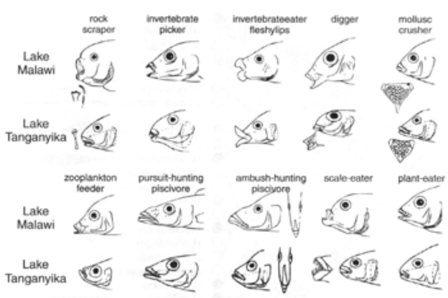
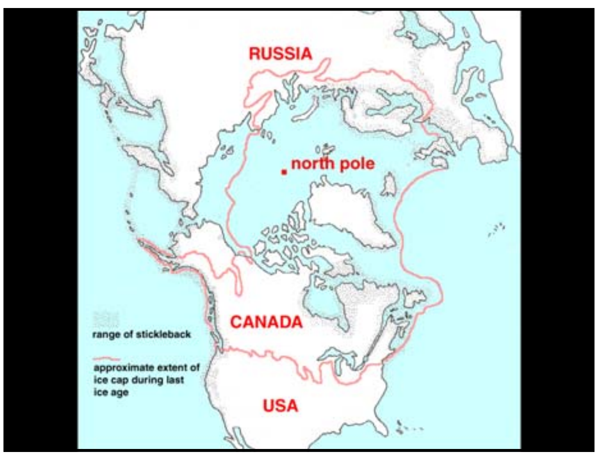


Fig. 1.3 Similar phenotypes in the cichlid fish radiations of Lake Malawi and Lake Tanganyika in East Africa. Images are from Fryer and Iles (1972; Malawi) and Liem (1991; Tanganyika) and are reprinted with kind permission of G. Fryer and Kluwer Academic Publishers, respectively.


Konrad P. Schmidt


RUSSIA
north pole
CANADA
USA
range of stickleback
approximate extent of
ice cap during last
ice age

CHARACTER DISPLACEMENT IN STICKLEBACKS

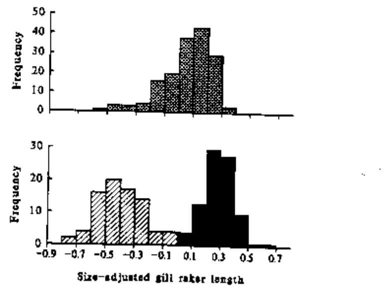
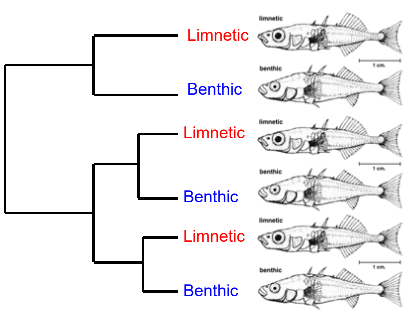


FIG. 3.—Frequency distributions of size-adjusted gill raker length in lakes with one species (Cranby: *upper graph*) and two species (Paxton: *lower graph*). *Shading* in lower figure indicates benthic (*hatched*) and limnetic (*solid*) forms. Gill raker distributions in other one-species lakes were similar to Cranby's, and distributions in other two-species lakes were similar to Paxton's.



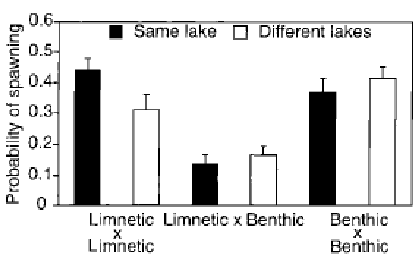


Fig. 1. Uncorrected probability of spawning in no-choice mating trials for various combinations of populations. Error bars are ±1 SE and represent the amount of variation in spawning rate among the various combinations.

AUSTRALIAN MARSUPIALS DEMONSTRATE AN ADAPTIVE RADIATION IN THE ABSENSE OF *COMPETITIVE INTERACTIONS* WITH PLACENTAL MAMMALS

THE AMNIOTIC EGG:

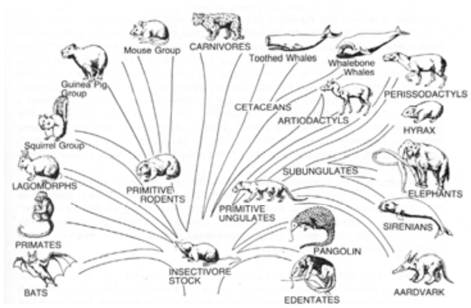
- **Perhaps one of the greatest *key innovations* of all time**

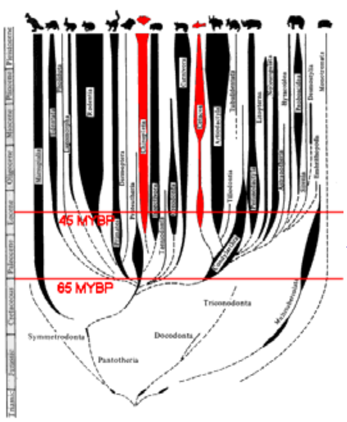
DINOSAUR EGG (Protoceratops) cast replica
This cast is an example of a dinosaur egg found in a nest containing 18 eggs arranged in three circles, one inside another. Protoceratops means "first horn-face".

ANOTHER KEY INNOVATION:

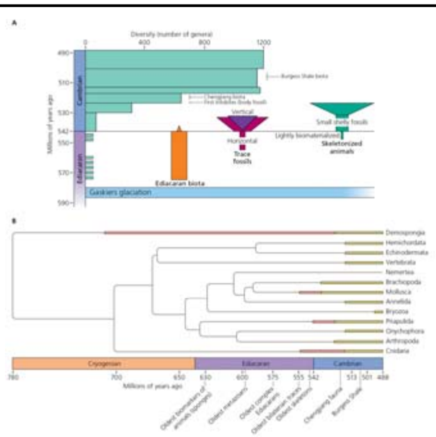
WINGS

ADAPTIVE RADIATION OF MAMMALS

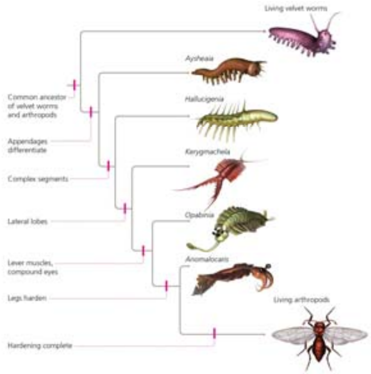




Diversification of the major Mammalian lineages occurred in a relatively short period of time.



ADAPTIVE RADIATION OF ANIMALS



Rapid diversification of animals corresponds to major environmental changes

- Warming and retreat of glaciers
- Oxygenation of ocean
- Increased availability of phosphorous
- Niche expansion

Cambrian Community

Evidence of Predation

TABLE 14.1 Examples of Adaptive Radiation, and the Circumstances Thought to Have Generated Ecological Opportunity in Each Case

Taxa/clade	Mechanism	Opportunity
Cambrian radiation of animals	Environmental change; key innovations (genetic toolkit, body segments, skeletal structures)	Increased O_2 availability; increased developmental capacity to diversify in form; colonization of new lifestyles (e.g., predators), habitats (mobile)
Devonian radiation of plants	Key innovations (seeds, vascular tissue)	Colonization of terrestrial environments
Cretaceous radiation of angiosperms	Key innovation (flowers)	Initiation of mutualistic coevolution with insects
Devonian radiation of insects	Key innovation (wings)	Colonization of the air
Cenozoic radiation of mammals	Extinction of dinosaurs, large reptiles	Undercontested resources/niches
Radiation of Darwin's finches	Colonization of Galápagos archipelago	Undercontested resources/niches
Radiation of silver-swords, fruit flies, honeycreepers	Colonization of Hawaiian archipelago	Undercontested resources/niches
Radiation of cichlids	Colonization of African Great Lakes	Undercontested resources/niches

ADAPTIVE RADIATIONS AND RAPID EVOLUTION

Adaptive radiations are often characterized by:

- Ecological opportunity
- Acquisition of novel adaptive traits
- Competitive interactions among closely related taxa
- Convergent/Parallel evolution
- Rapid phenotypic diversification