Sympatry for the Devil:

More on Speciation Modes

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(For many more studies than can be presented here, check out http://www.talkorigins.org/faqs/faq-speciation.html)

Standard model of speciation

- *Allopatric* speciation
  - An ancestral population is either divided by a barrier (*vicariance*) or disperses to a new habitat (*dispersal*)
  - *Peripatric* speciation is a form of allopatric speciation, caused by isolation of populations on the fringe of the ancestral species' range.

What about *sympatric speciation?*

- Sympatric speciation is speciation without a physical barrier
- Many cases are known that are due to chromosomal causes: *polyploidy* and *hybridization*.
  - These may take only a single generation to act.
- Whether it can happen gradually was debated for a long time. . .
  - It now seems to be accepted that gradual sympatric speciation is not only possible, it's more common than previously suspected.

Instant speciation!

- hybridization
  - two plant species may hybridize to produce a variety that is unlike either parent
  - the new hybrid may not be cross-fertile with either parental species
- polyploidy
  - polyploid races of plants may arise due to errors in meiosis
  - the new polyploid may not be cross-fertile with either parental species

Speciation by polyploidy

Different *Chrysanthemum* species have N=9, 18, 27, 36, 45

C. segetum: 2N=18

C. coronarium: 2N=36

C. indicum: 2N=54

Hybridization: a case study

- In 1928, the Soviet scientist G. Karpechenko crossed radish (*Raphanus sativus*; 2N=18) with cabbage (*Brassica oleracea*; 2N=18)
- Both radish and cabbage belong to the same plant family, the Brassicaceae (mustard family)
- Normally the F_1 hybrid is infertile because the chromosomes can't pair up at meiosis
- However, very rarely, an F_1 hybrid will produce diploid eggs and diploid sperm (called *unreduced gametes*). . .

Hybridization, continued

- This produces a fertile F_2 plant, with two of each chromosome from each species (2N=36). This is known as *allotetraploidy*.
- The result? A fertile plant that could not backcross with either parent, and didn't look like either parent.
- Karpechenko placed it in a new genus, *Raphanobrassica*.

Unfortunately, *Raphanobrassica* was not the "supervegetable" that Karpechenko was hoping for. . .

Case Study: Sunflowers

X

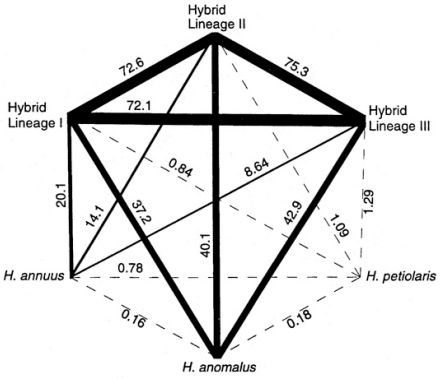
Helianthus annuus
(annual sunflower)

Helianthus petiolaris
(prairie sunflower)

A rare wild species of sunflower, *Helianthus anomalus*, is thought to have arisen from hybrids between *H. annuus* and *H. petiolaris*. It's ecologically specialized (native to sand dunes, whereas its parents are prairie species) and it differs from the parental species through several chromosome inversions, fusions, etc.

Anomalous Sunflowers

- *H. annuus* and *H. petiolaris* almost never interbreed in the wild, but lab-produced hybrid lines can be cultivated and propagated. . .
  - By the way, *H. annuus* and *H. petiolaris* and its hybrids are all *N*=17; hybrids are *monoploid*, not *allopolyploid*.
- Hybrid lineages are interfertile with wild *H. anomalus* but not very cross-fertile with either parental lineage.
- It's possible to recreate a wild hybrid species in the lab!
  - *Source:* Rieseberg, Loren H. 2000. Crossing relationships among ancient and experimental sunflower hybrid lineages. *Evolution* 54 (3): 859.



This diagram from Rieseberg's paper shows the percentage of fertile seed produced in crosses among the three wild species and three different lineages of *H. annuus* x *H. petiolaris* hybrids.

What's *really* odd is that the same parental species seem to have hybridized at least two more times in the wild—giving rise to a total of three *different* species, all of which are ecological and morphological "extremists".

Helianthus deserticola
(desert floor habitat)

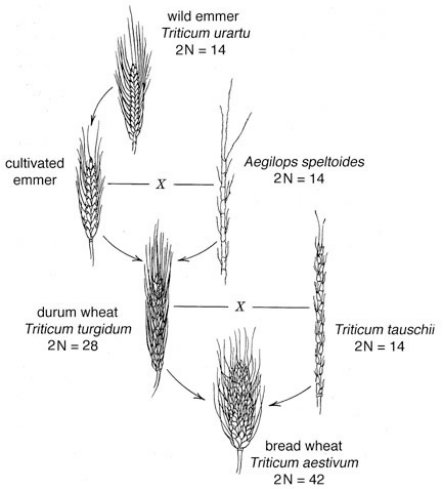
Helianthus paradoxus
(desert salt marshes)

Importance?

- Estimated 70% of angiosperm species (flowering plants) are ultimately derived from polyploids or hybrids
  - In ferns, over 90% of species are polyploids
  - Adder's-tongue fern (*Ophioglossum reticulatum*) holds record for chromosome number: $N = 630$.
- Possibility that hybridization allows plants to colonize extreme habitats (because it generates new combinations of traits)
  - The desert sunflowers are being studied further to test this hypothesis.

Importance?

- Many crops are hybrids and/or polyploids
  - *Brassica rapa* (turnip) x *B. oleracea* (cabbage) yielded *B. napus* (rutabaga, canola); *B. rapa* x *B. nigra* (black mustard) yielded *B. juncea* (yellow mustard, edible mustard greens)
  - Cultivated bananas are triploids—either autotriploids of the wild species *Musa acuminata* or allotriploids of *M. acuminata x M. balbisiana*
    - This explains why cultivated bananas have no seeds and can only be propagated asexually, by human intervention).
    - Same for certain apples, other fruits

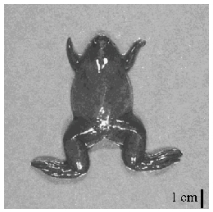


Cultivated wheat is an *allohexaploid*—descended from *two* hybridization events involving *three* ancestral grass species.

And as if *that* weren't enough, bread wheat (2N = 42) has recently been crossed with rye (2N = 14) to form a new *allooctaploid* plant, called triticale (2N = 56).

Polyploidy and hybridization in animals

- These mechanisms are less common in animals, but several cases exist. . .
  - *Xenopus* (African clawed frog) includes twenty species, ranging from 2N to 12N



X. tropicalis: 2N

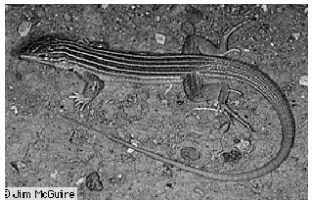
X. laevis: 4N

Polyploidy and hybridization in animals

- Whiptail lizards (*Cnemidophorus*) of the southwestern United States
  - New Mexico whiptail lizard (*Cnemidophorus neomexicxanus*) resulted from a hybrid between the western whiptail (*C. tigris*) and the little striped whiptail (*C. inornatus*)
  - *C. neomexicanus* is reproductively isolated from both parental species—because it is parthenogenetic!
  - Same phenomenon observed in other lizards, such as certain geckos

Cnemidophorus tigris

X



Cnemidophorus inornatus

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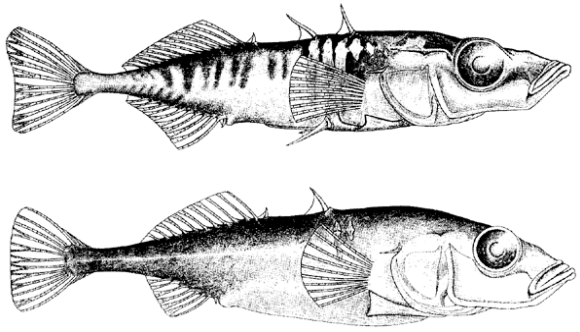
Cnemidophorus neomexicanus (unisexual, parthenogenetic)

By shocking fertile eggs, grass carp (*Ctenopharyngodon idella*) may be forced to develop as sterile triploids. Triploid carp are used for vegetation control in waterways.

It's not a bad idea to remember that chromosome duplications, fusions, inversions and translocations may *accompany* speciation in animals or in any eukaryotes. Whether or not they *cause* sympatric speciation, they may *maintain* it by enforcing hybrid sterility. Remember the two non-interbreeding karyotypes of Kirk's dik-dik (*Madoqua kirkii*). . . .

Other possible cases of sympatric speciation in progress. . .

- Sticklebacks (*Gasterosteus aculeatus*) in British Columbia lakes have speciated in only the last 12,000 years (the time since the last Ice Age)
- The lakes have both *limnetic* (living high in the water column) and *benthic* (bottom-dwelling) strains of stickleback



Top: A male limnetic stickleback
Bottom: A male benthic stickleback

Thanks to Case Studies in Science for images and background info.
Check 'em out for more information. . .

Stickleback speciation in progress

- Benthic and limnetic sticklebacks can potentially interbreed, and the hybrids are viable and fertile. . .
- . . . but courtship behaviors are quite different between the two.
  - In fact, males of one strain attack females of the other
- The strains also look different, feed on different foods, and select different nesting sites.
- Hybridization in the wild is rare (1-2% of Paxton Lake fish appear to be hybrids), and allele frequencies differ between the two forms.
  - Wild hybrids appear to be selected against (*speciation by reinforcement*)

Is this sympatric speciation?

- Sticklebacks live in the oceans as well as lakes, and lake sticklebacks descend from marine ancestors who invaded after the last Ice Age.
- Some suggest that in each lake, the limnetic is the benthic's closest relative. If that's true, then this would be sympatric speciation.
- Alternative hypothesis: "double invasion"—benthics and limnetics result from two separate marine lineages. If that's true, this would be allopatric speciation followed by recontact