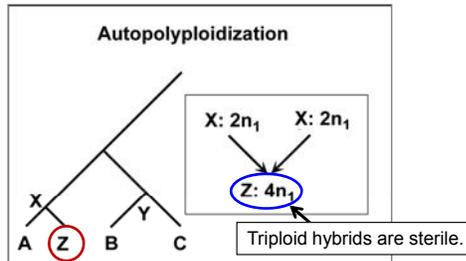


Speciation by **polyploidy** and **interspecific hybridization**

I. **Instantaneous** sympatric speciation via **ploidy changes**

Autopolyploidization: a doubling of the diploid chromosome number in a **single species**.

- Can be considered a type of *bifurcating* (not reticulating) speciation
- Much rarer than allopolyploidization?
- Examples?? (“**stealth speciation**”)



As a result, polyploidy generates immediate reproductive isolation and sympatric speciation

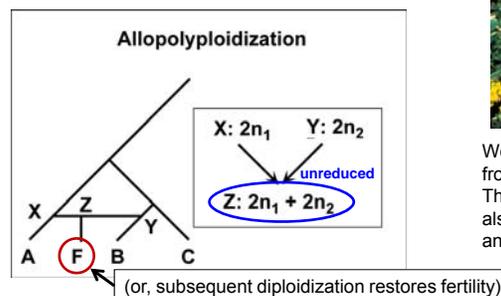


Heuchera grossularifolia (NW USA) on the Salmon River: autotetraploid plants have formed multiple times.

II. **Rapid** sympatric speciation via **hybridization+ploidy changes**

Allopolyploidization: each parent of the **hybrid** contributes its *entire nuclear genome* (usually with uniparental inheritance of the organelles)

- Parents needn't have the same number of chromosomes
- Simplest case is when gametes of both parents are unreduced



Weedy mustard *Brassica napus*, from *B. rapa* x *B. oleracea*. This is found in nature, but can also be produced in the lab (over and over again).

more **allopolyploidy**...

Spartina, S. England:

S. maritima (native) *S. alternifolia* (1870 – USA)

 ↓ ↓

S. townshendii

 ↓ **diploidization**

S. anglica (vigorous!)



Cordgrass

Gilia, California:

G. aliquanta (Cal) *G. minor* (Cal)

 ↓ ↓

G. major

 ↓ **diploidization?**

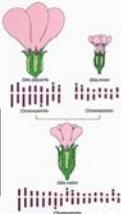


Gilia spp.

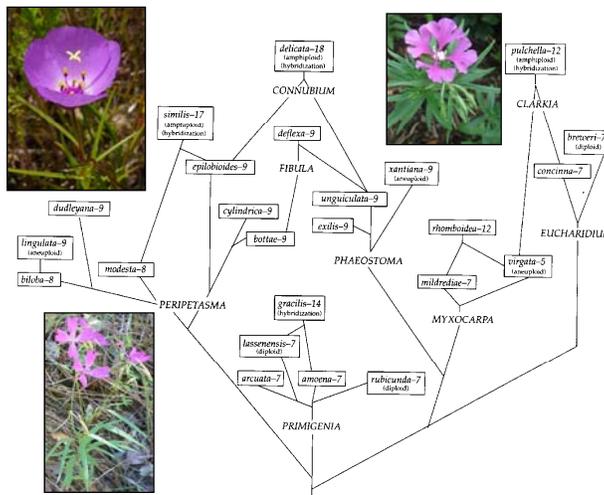
Many other California *Gilia*'s have originated similarly.



Gilia tenuiflora



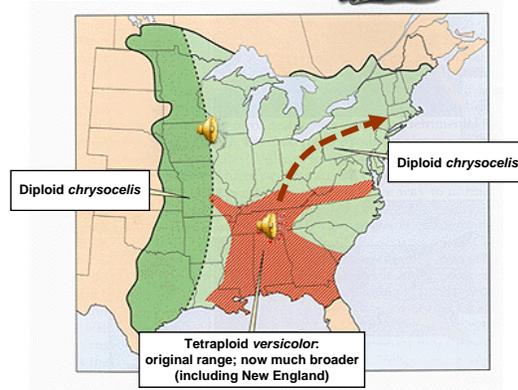
Repeated sympatric speciation by **allopolyploidy** in *Clarkia*, generates **reticulate** evolutionary patterns (after Lewis & Lewis 1955)



Polyphyletic origin of an *animal* species via *autopolyploidy*:

Tetraploid treefrogs (Ptacek et al. 1994, Holloway et al. 2006)

Hyla chrysocelis
and *H. versicolor*



- Physical constraints (**larger cell size**) of tetraploids automatically lower & slow down the male song.
- Apparently, these changes are **matched by female preferences** (Tucker & Gerhardt 2012)
- This makes for very **strong premating reproductive isolation** between diploids and tetraploids, based on songs.
- (**Triploids** are similarly affected, but show intermediate values.)

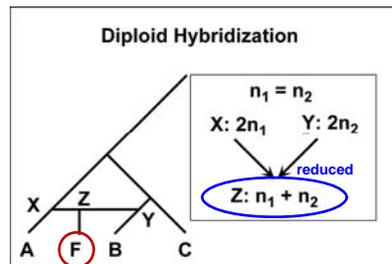
More sympatric speciation via hybridization

Diploid (homoploid) hybridization: each parent contributes **half** of its diploid chromosome set, as it would with normal sex.

- Parents usually have the same chromosome #, but **partially incompatible genomes**.
- Relatively rare, because hybrids are often reproductively compatible with parents.
- Occurs if there's a **good niche available**.



Helianthus deserticola,
homoploid hybrid of *H. annuus* x
H. petiolaris



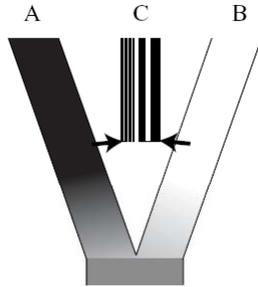
“Homoploid hybrid speciation”
[also called **recombinational speciation** (Rieseberg), **quantum speciation** (Grant 1966), etc.]

Homoploid hybrid speciation (HHS):

Formation of a new hybrid species without change in chromosome number.

1. **Recombinational speciation** (Rieseberg, many papers)

or
**“Mosaic Genome”
 Hybrid Speciation**
 (Jiggins et al. 2008)

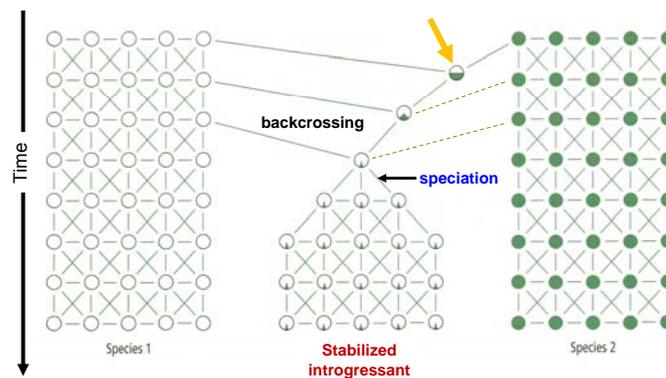


Establishment and stabilization of a recombinant lineage combining compatible regions of the genome in similar proportions from A and B –

SLOW; as reflected in a large signal from neutral markers.

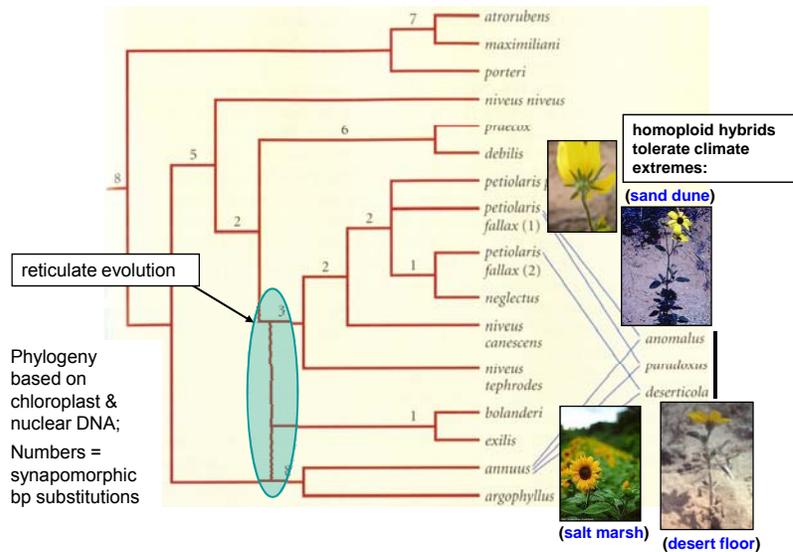
Recombinational speciation may be sympatric, but *not* instantaneous

(after Rieseberg and Wendel 1993)



The problem of the *initial rarity of hybrids* – and concomitant lack of potential mates – is partially solved if other modes of reproduction are available (asexual reproduction or self-fertilization) (Stebbins 1950)

Recombinational sympatric speciation in *Helianthus* sunflowers: Origin of new diploid species through hybridization (after Rieseberg and Wendel 1993)

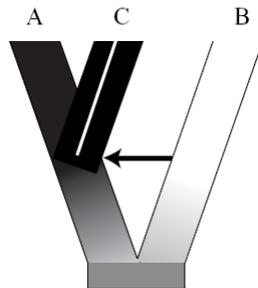


**Another variant of homoploid hybrid speciation:
2. *Hybrid trait speciation*** (Jiggins et al. 2008)

Backcrossing of alleles, i.e. introgression, but limited and unidirectional.

Alleles control a trait with adaptive potential that also causes reproductive isolation (a “magic trait”) –

FAST; little sign from neutral markers.

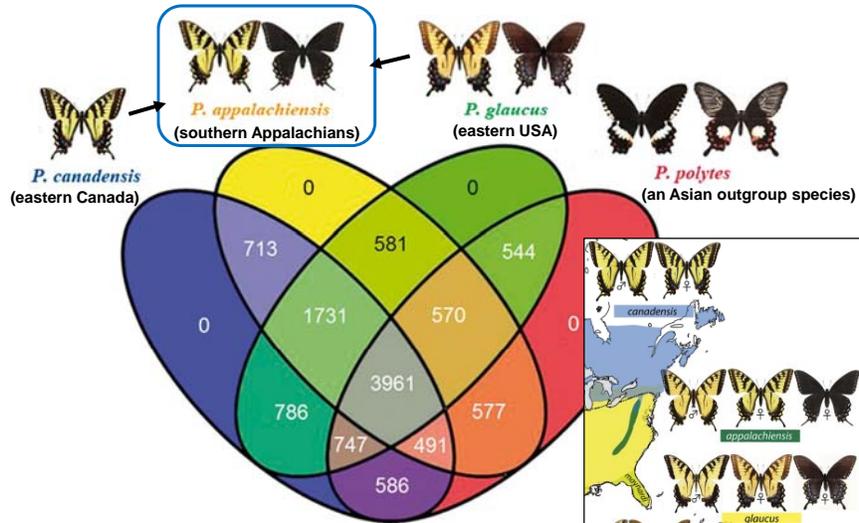


Recent work suggests that homoploid hybrid speciation (either type) is **more common in animals than previously thought**, with evidence from **fishes** (Selz et al. 2014), **birds** (Elgvin et al. 2011; Brelsford 2011), **mammals** (Larsen et al. 2010), & **flies** (Segura 2011; Price et al. 2008).

And **butterflies**:

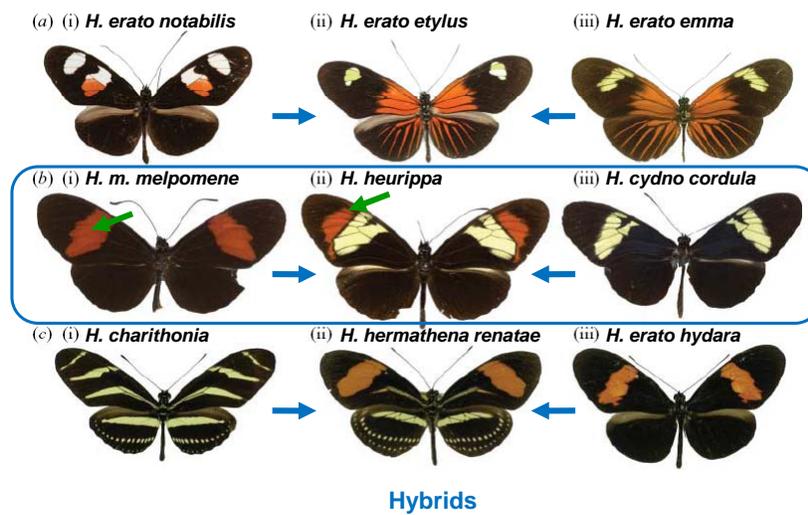
HHS in iconic **tiger swallowtails (*Papilio*)**: Distribution of conserved genomic clusters among four species (Zhang et al. 2013).

This is type 1, "**Recombinational.**"



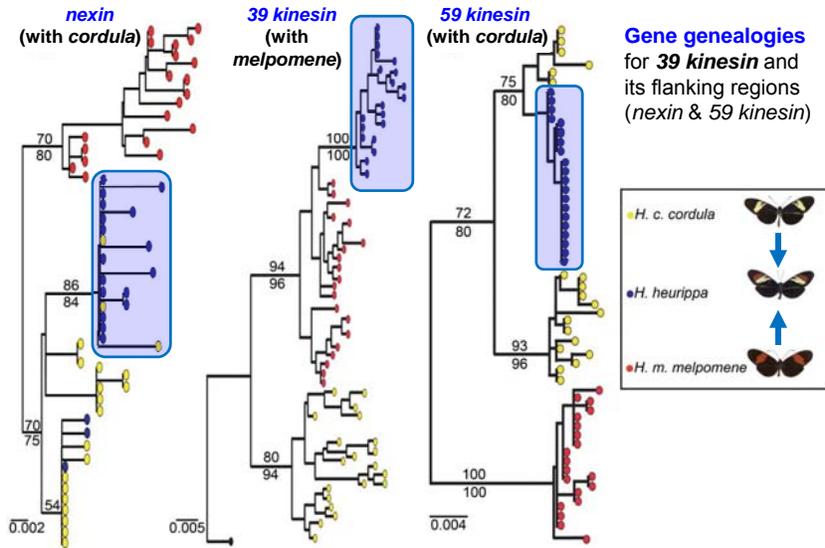
HHS in **Müllerian mimics**? Examples of hybrid patterns in *Heliconius* & their progenitors (Jiggins et al. 2008).

This is type 2, "**Hybrid trait.**"



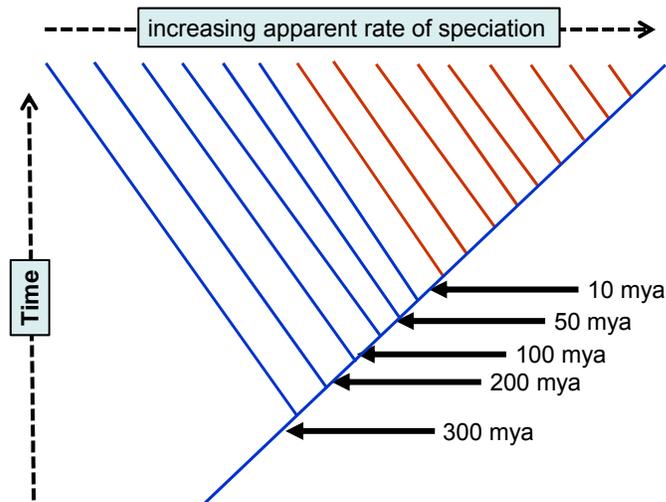
Evidence of hybrid trait speciation in *Heliconius heurippa*

(Melo et al. 2009; Salazar et al. 2010; but see Brower 2011, 2013)

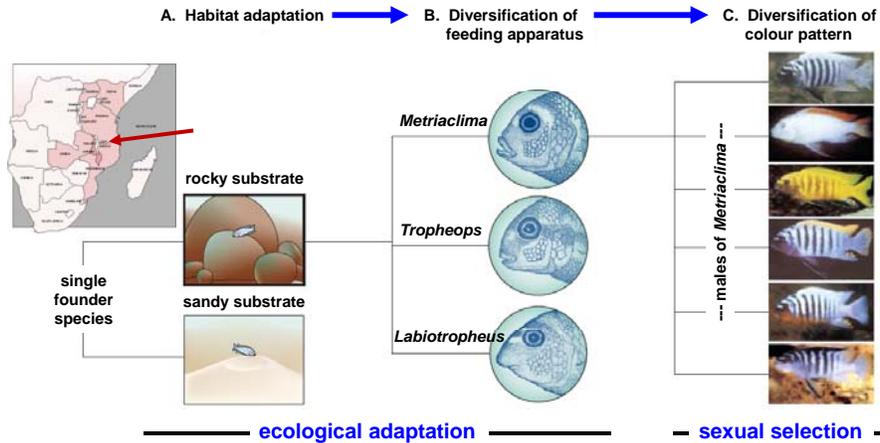


Rates of Speciation: The ubiquitous “Hennigian comb.”

Clearly, accumulating extinctions have erased the signal of rapid diversification.

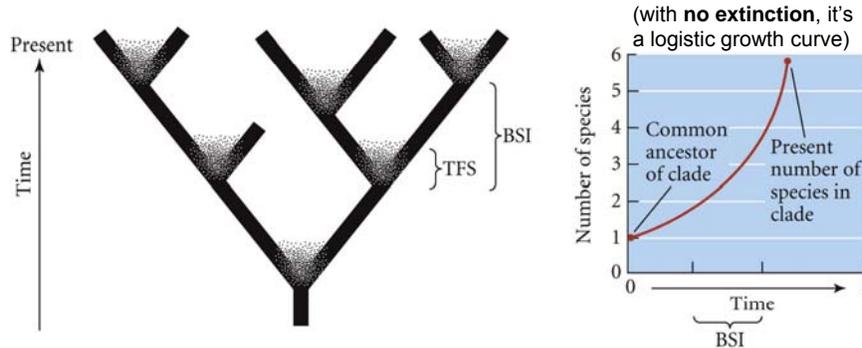


Rapid, recent, and repeated speciation of 1000 Cichlidae in Lake Malawi: ecological, sexually-selected and possibly sympatric? (Kocher 2004)



Age of lake is estimated at 40,000 yrs to 1-2 million yrs → **FAST speciation!**

How does one measure the rate of speciation? Two metrics: **TFS** (time for speciation) and **BSI** (biological speciation interval) (Futuyma 2005)



TFS: the time between the beginning and end of the evolution of reproductive isolation.

BSI: the average time that has elapsed between two sequential bifurcations.

1/BSI: the **speciation rate** (number of species per unit time – usually, *per million years*). (either linear or log scale)

How much time does it take for speciation? (1)

Measuring this involves overcoming several obstacles:

1. How can we tell *when speciation began and ended*, when we can't see it happening?
 - “*Time for speciation*” (**TFS**) is best measure, but it is also the hardest to determine (and therefore rarely used).
 - “*Biological speciation interval*” (**BSI**) is often the best we can do, but it's realistic only for clades that have speciated recently (*unmodified by extinction*)
2. Even if we had evidence of this, *how do we put a date or time span* on the events?
 - **Geological and radiometric dating**? – very inaccurate at these small time scales.
 - **Genetic distances** (Nei, Rogers, or Cavalli-Sforza), based on allozyme or sequence data? – but big assumption is that of a molecular clock.
 - **Sequence divergence**, based on nucleotide data? – but again, must assume clock-like evolution.

How much time does it take for speciation? (2)

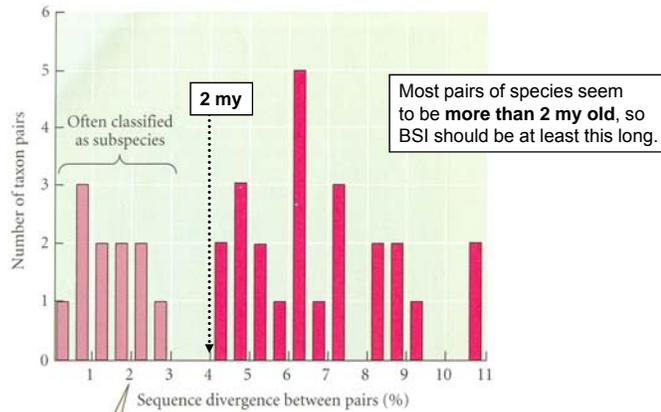
Various bits of indirect evidence:

Genetic distance, D ,* has been shown to measure 0.10-2.00 for different species, and above 1.00 for different genera (note that in theory D can vary from zero to infinity).

1. **Nei** estimated that it takes on average *5 million years* for D to go from 0 to 1.00 (based on many studies)
2. In **Coyne & Orr's** survey of *Drosophila*, average D 's for reproductively isolated species pairs were:
 - **0.54** for pairs that remain **allopatric**.
 - **0.04** for pairs that were always, or become, **sympatric**.
3. **Implication:** “sympatric” *speciation will take less than 1/10 the time of allopatric speciation*. Converted to time, this means:
 - 2.7 million years for pairs that remain allopatric.
 - 200,000 years for pairs that were always or become sympatric.

* a measure of the dissimilarity of genetic material between different species or individuals of the same species

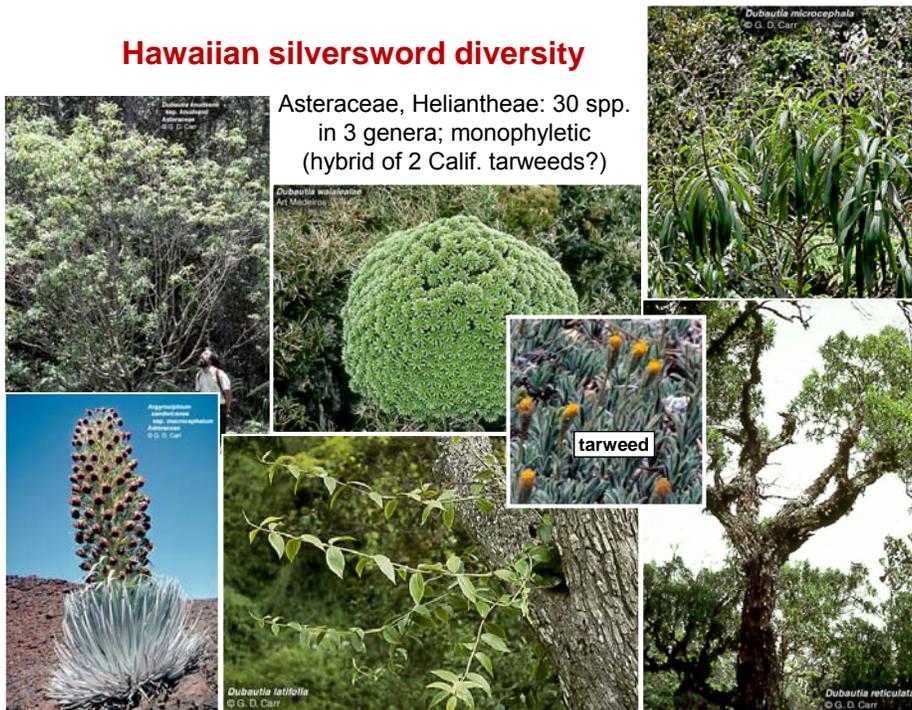
Some data: mtDNA sequence divergence of pairs of North American songbirds (after Klicka & Zink 1997)



Sequence divergence of **2%** (not Nei's D) represents about **1 my** since separation

Note: For **insects**: mtDNA COI barcode value (685 bp) of **2.3%** sequence divergence per MY (Brower 1994).
Or **3.54%/MY** (Papadopoulou et al. 2010).

Hawaiian silversword diversity



Rates of speciation for some plant lineages,
measured as **1/BSI** (from Kadereit & von Hagen 2003)

Table 1
Logarithmic (SR_{log}) and Linear (SR_{lin}) Speciation Rates for *Gentianella*, *Halenia*, and Other Plant Taxa (Ordered by SR_{lin})

Taxon	Reference	No. of species	Estimated age of lineage (my)	(expon.) SR _{log} (sp/my)	(linear) SR _{lin} (sp/my)
<i>Cyanea</i> Gaudich. + <i>Rollandia</i> Gaudich./Hawaiian Islands	Givnish et al. 1995	51	17.4 (max) 8.7 (min)	0.23 0.45	2.9 5.9
<i>Robinsonia</i> DC./Juan-Fernandez Islands	Sang et al. 1995	7	4 (max)	0.49	1.8
<i>Silversword</i> alliance/Lawaiian Islands	Baldwin and Sanderson	28	3.2	0.56*	5.4
<i>Schiedea</i> Cham. et Schldl. + <i>Alsinidendron</i> Hl. Mann/Hawaiian Islands	Wagner et al. 1995	29	5.1 (max)	0.66	5.7
<i>Dendroseseris</i> D. Don/Juan-Fernandez Islands	Sang et al. 1994	11	2.6	0.92	4.2
<i>Halenia</i> in Central America	von Hagen and Kadereit, in press	15	ca. 2.7	1.00	5.6
<i>Gentianella</i> s. str./high alpine Andes	von Hagen and Kadereit	170	ca. 3	1.71	56.7
<i>Gentianella</i> s. str./alpine Australia/New Zealand	von Hagen and Kadereit	32	ca. 2	1.73	16.0
<i>Halenia viridis</i> group/high alpine Andes	von Hagen and Kadereit	5	ca. 1.0	1.79	3.0
<i>Dendroseseris</i> (Hauman ex Humbert) B. Nord/ tropical African mountains	Knox and Palmer 1995	11	1	2.40	11.0
<i>Argyranthemum</i> Webb/Canary Islands	Francisco-Ortega et al.	17*	1	2.83	17.0
		24	1.2	2.65	20.0
		39 ^b	1.2	3.05	32.5
<i>Tetramolopium</i> Nees/Hawaiian Islands	Lowrey 1995	11	0.7 (min)	3.43	15.7
<i>Halenia weddelliana</i> group/high alpine Andes	von Hagen and Kadereit, in press	16	ca. 0.8	3.47	20.0
<i>Dianthus</i> , the carnations of temperate Eurasia	Valente et al. 2010	200	1.5	3.80	133.0

BSI = 1.8my (green arrow pointing to Silversword alliance)

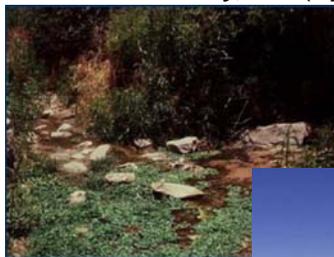
BSI = 0.3my (red arrow pointing to *Halenia weddelliana* group)

BSI = 0.25my (blue arrow pointing to *Dianthus*)

Attributed to innovative nectar spurs & colonization of Andes mountains (a Gentian)

Attributed to Pleistocene aridity

How fast is speciation? **Desert Pupfish**
from Death Valley, etc. (*Cyprinodon* spp.)



> 10,000 yrs ago:
the Mojave Desert
was not a desert



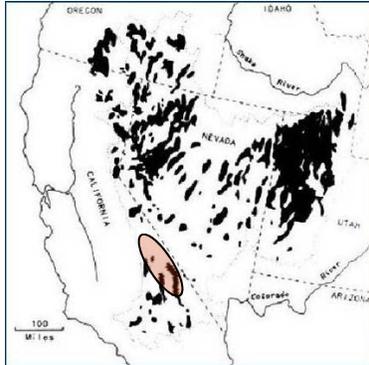
Postglacial climate change in
southwestern North America
led to **allopatric isolation**.



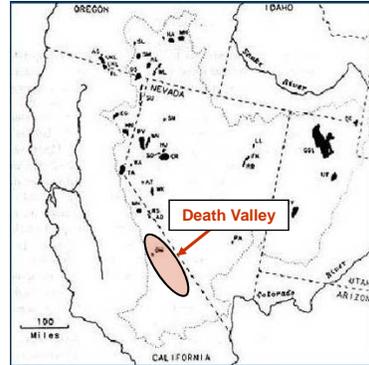
isolated springs



Shrinking and disappearing lakes
over the past 10,000-30,000 years



then...(>10,000 years ago)

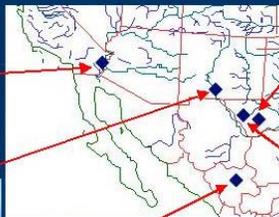


...and now.

There are about **20 desert pupfish** species in all, each restricted to a few springs, streams, or other such refuges (*allopatric speciation*).
Must be only $\approx 10,000$ years old (BSI=0.01my).



C. macularius



C. bovinus



C. pecosensis



C. alvarezi



C. elegans

Rapid speciation: more fishes (and note convergent evolution)

Estimates of clade ages range from 2,000 – 4,000,000 years

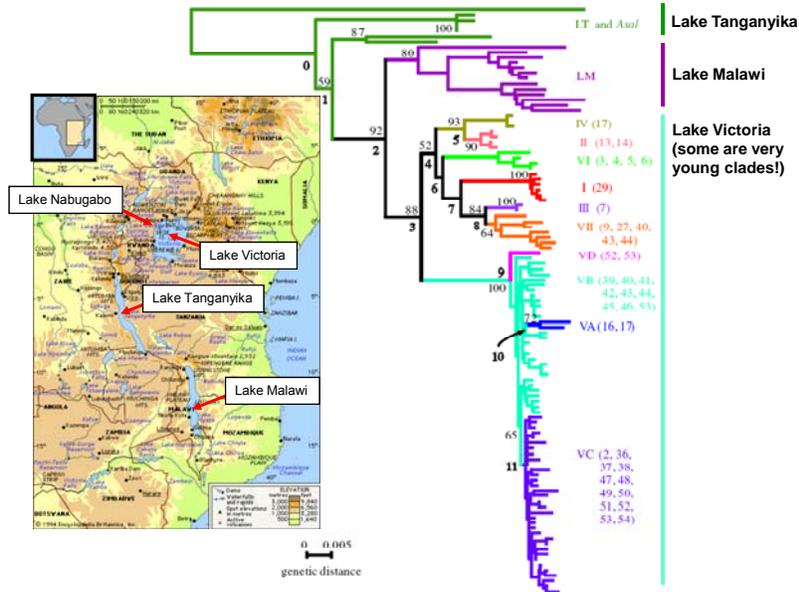
<p>Lake Tanganyika (oldest):</p>  <p><i>Julidochromis ornatus</i></p>  <p><i>Tropheus brichardi</i></p>  <p><i>Bathybates ferox</i></p>  <p><i>Cyphotilapia frontosa</i></p>  <p><i>Lobochilotes labiatus</i></p>	<p>Lake Malawi (younger):</p>  <p><i>Melanochromis auratus</i></p>  <p><i>Pseudotropheus microstoma</i></p>  <p><i>Ramphochromis longiceps</i></p>  <p><i>Cyrtocara moorei</i></p>  <p><i>Placidochromis milomo</i></p>	 <p>Lake Nabugabo (new): Five cichlids derived from Lake Victoria (youngest), radiocarbon dated at precisely 4,000 years ago (Martens 1997).</p> <p>Allopatric or sympatric? – not determined.</p>
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Lake Victoria: 500 species of Cichlidae in 14,500 years
(Genner et al. 2007)

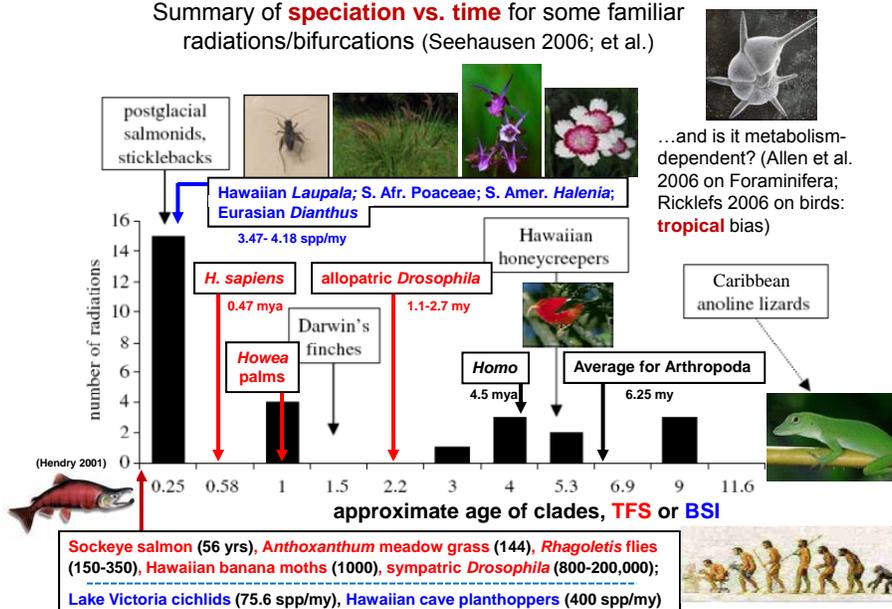


(but note **uncertainty**: maybe as much as 200,000 yrs., and 3 or more founders)

Neighbor-joining phenogram of 670 species of **African Lake Cichlidae**, based on mtDNA control region sequences (Nagl et al. 2000)



Summary of **speciation vs. time** for some familiar radiations/bifurcations (Seehausen 2006; et al.)



Effect of time and niche heterogeneity on speciation:
 Evidence from multiple African cichlid radiations (Seehausen 2006)

