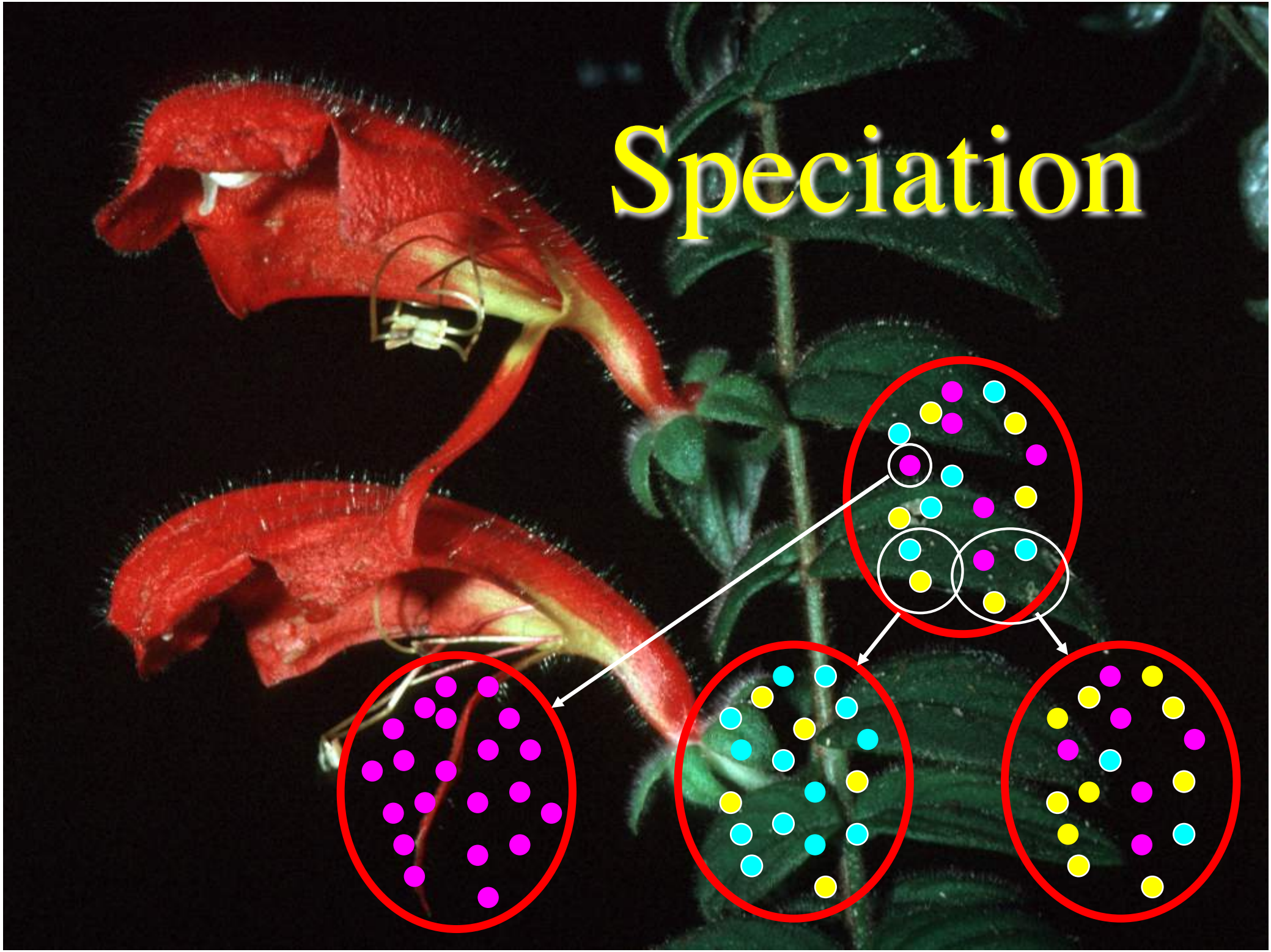
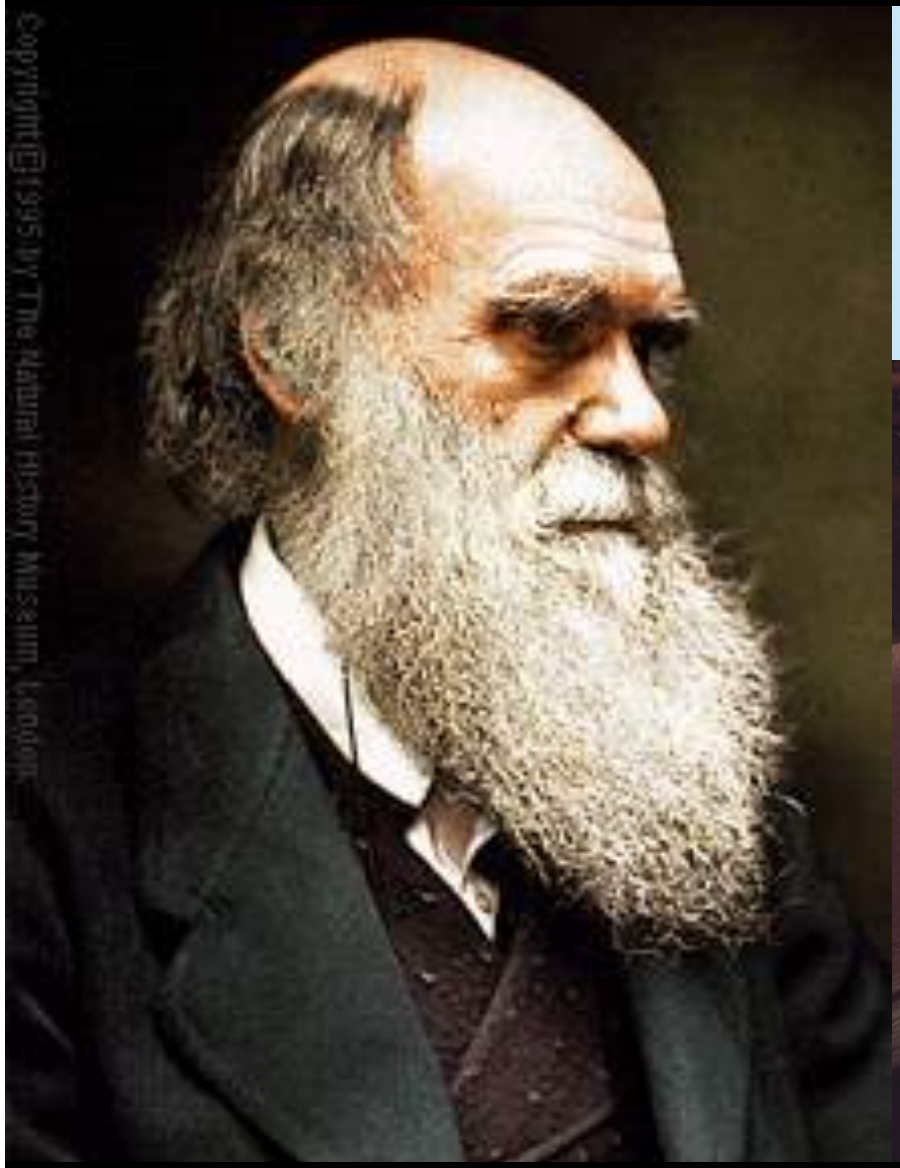
Speciation



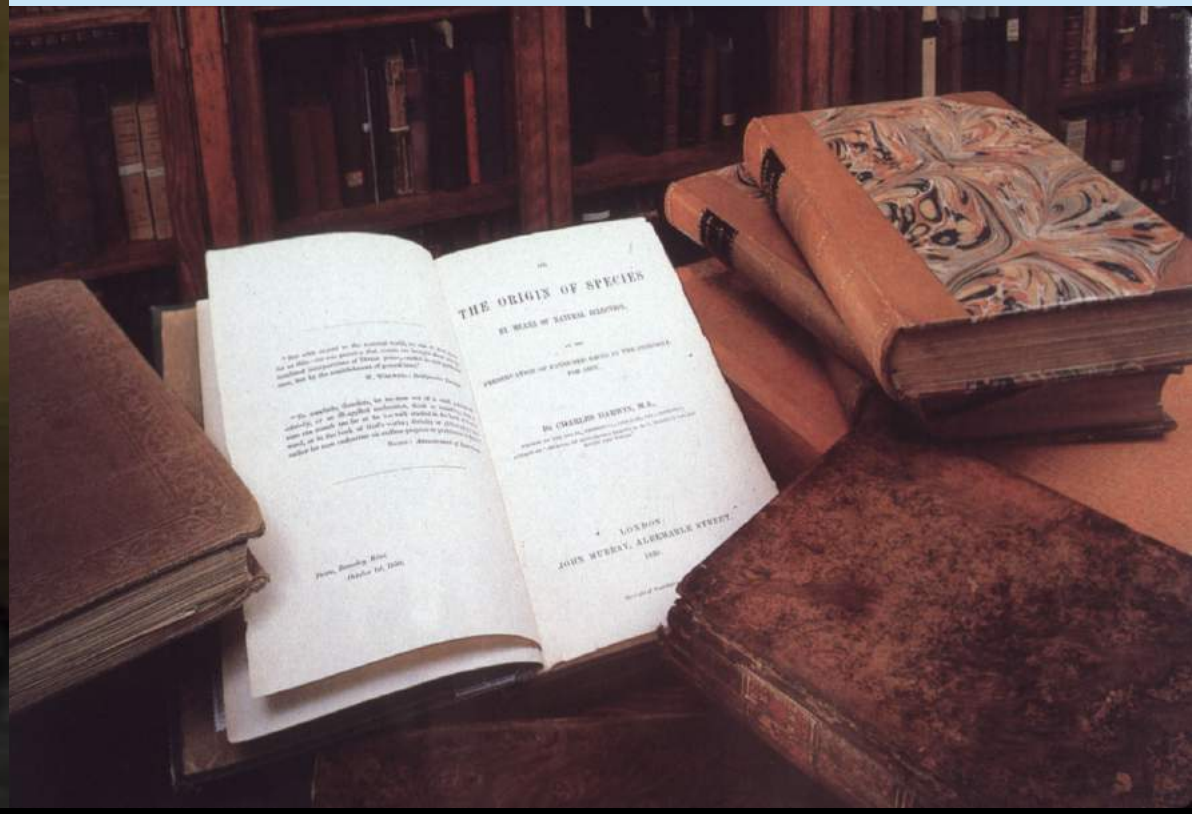
What is Evolution



Darwin himself never uses the word "evolution" in *Origin of Species*.

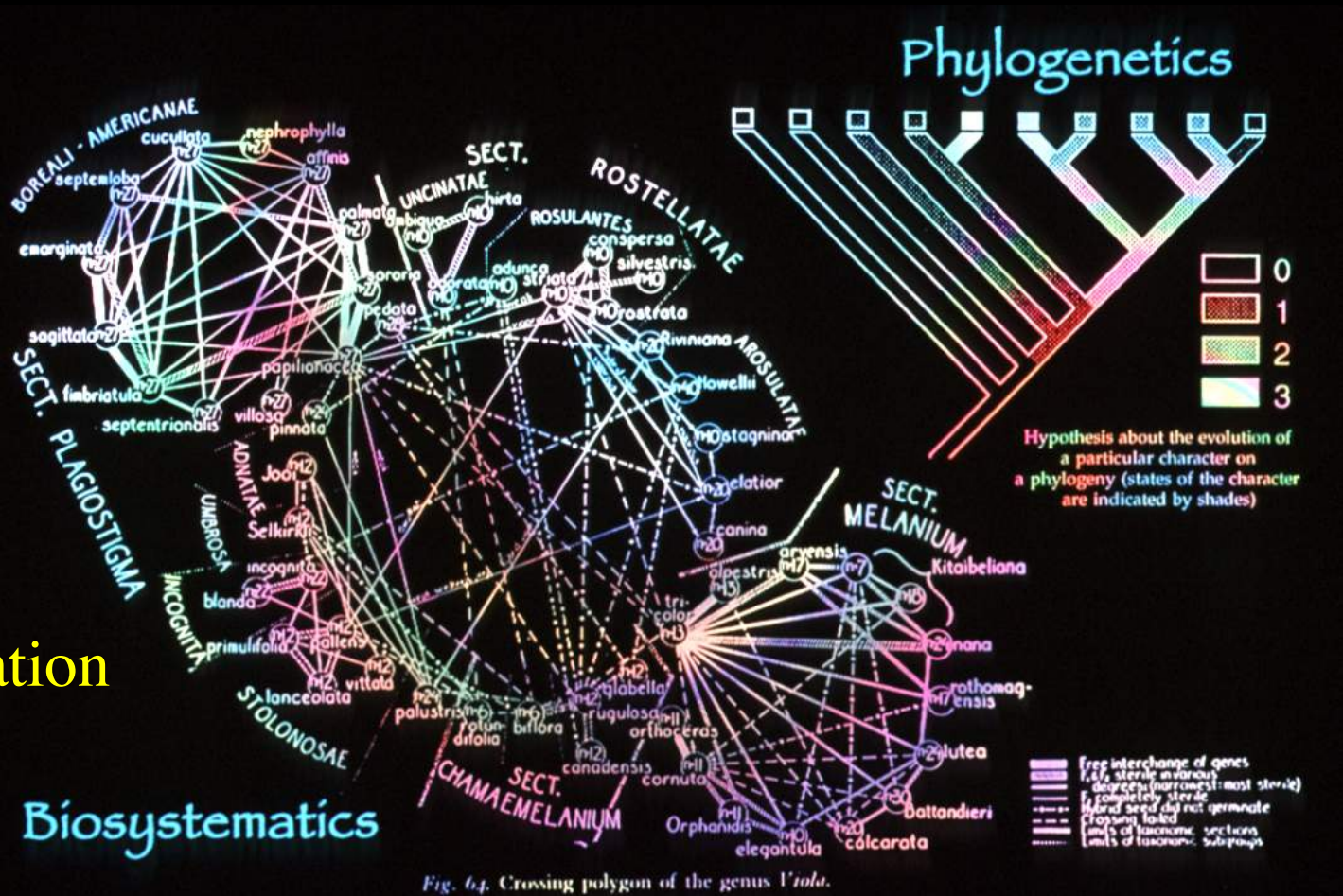
He calls the process

"descent with modification".



What is Evolution

Systematics often divided into two areas: phylogenetics or pattern and biosystematics or process



tree

reticulation

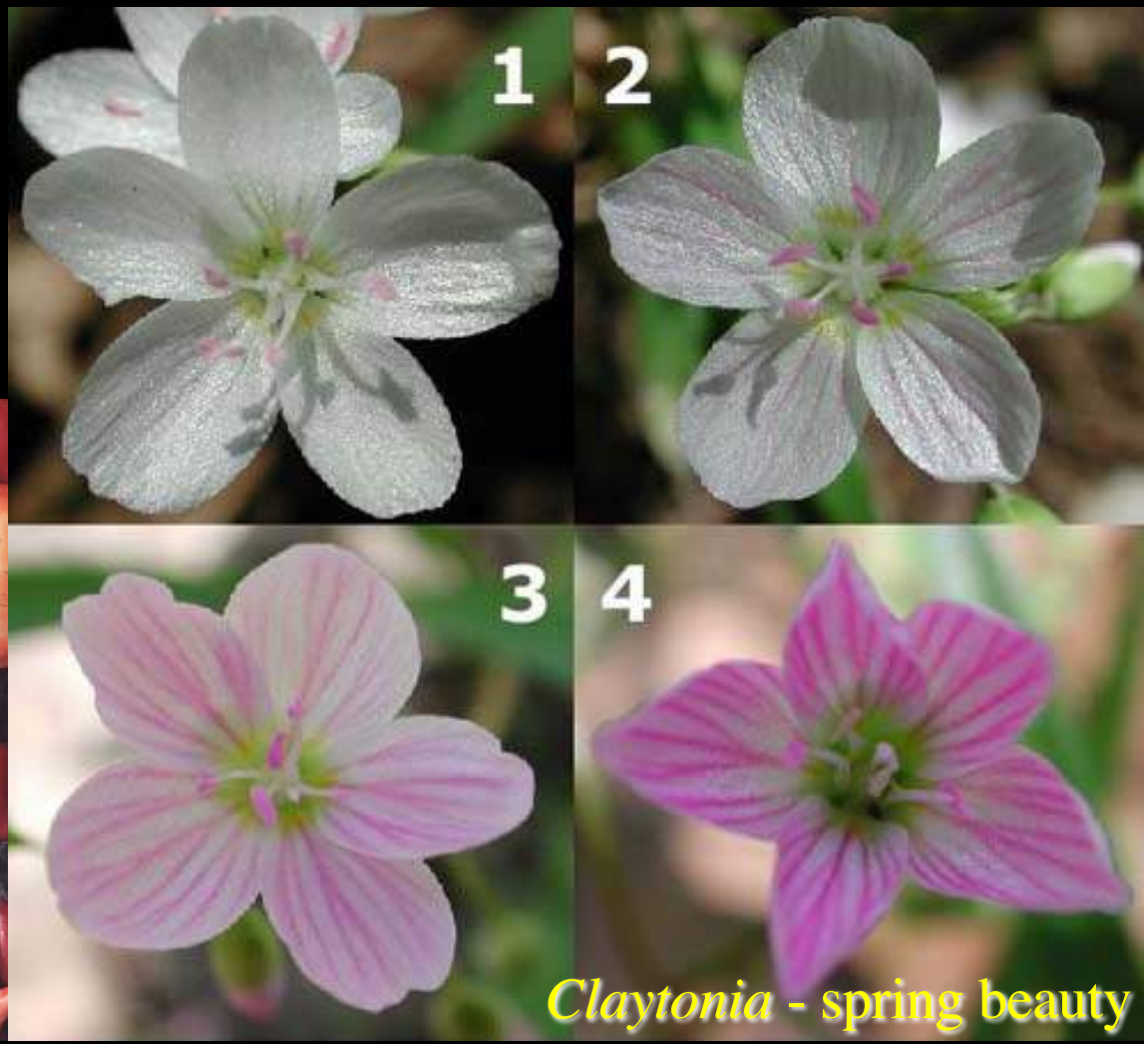
Fig. 64. Crossing polygon of the genus *Viola*.

Genetic Variation within Species

Evolution requires source of genetic variation and a driving force

Genetic variation within species is the rule - human selection or natural selection or random events involved

Capsicum - pepper

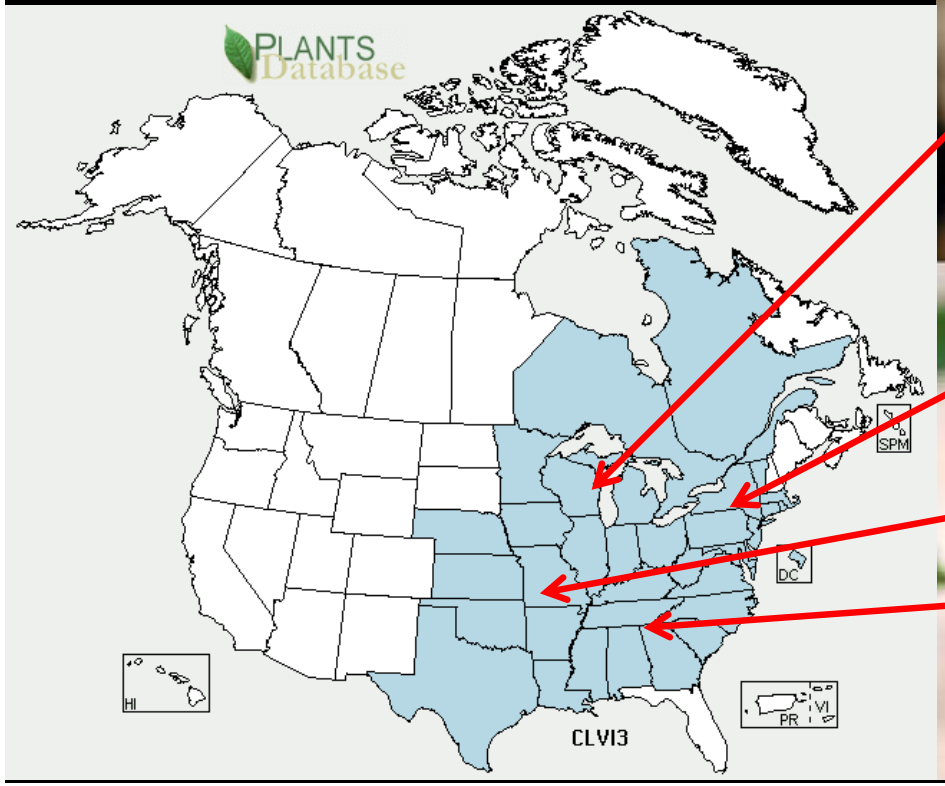


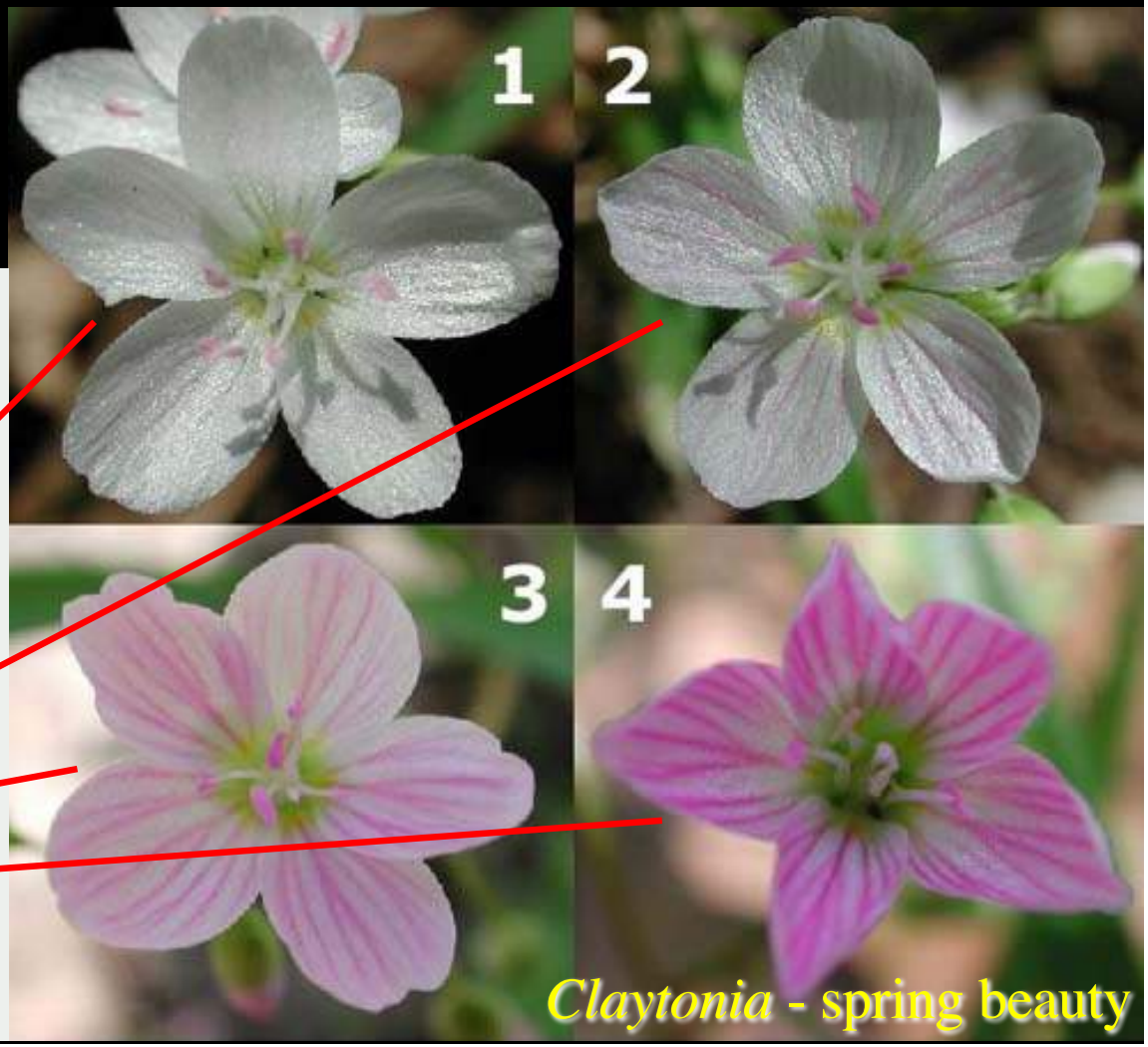
Claytonia - spring beauty

Genetic Variation within Species

Evolution requires source of genetic variation and a driving force

Variation seen in flowers, pollinators, light regimes, moisture regimes, chromosome number





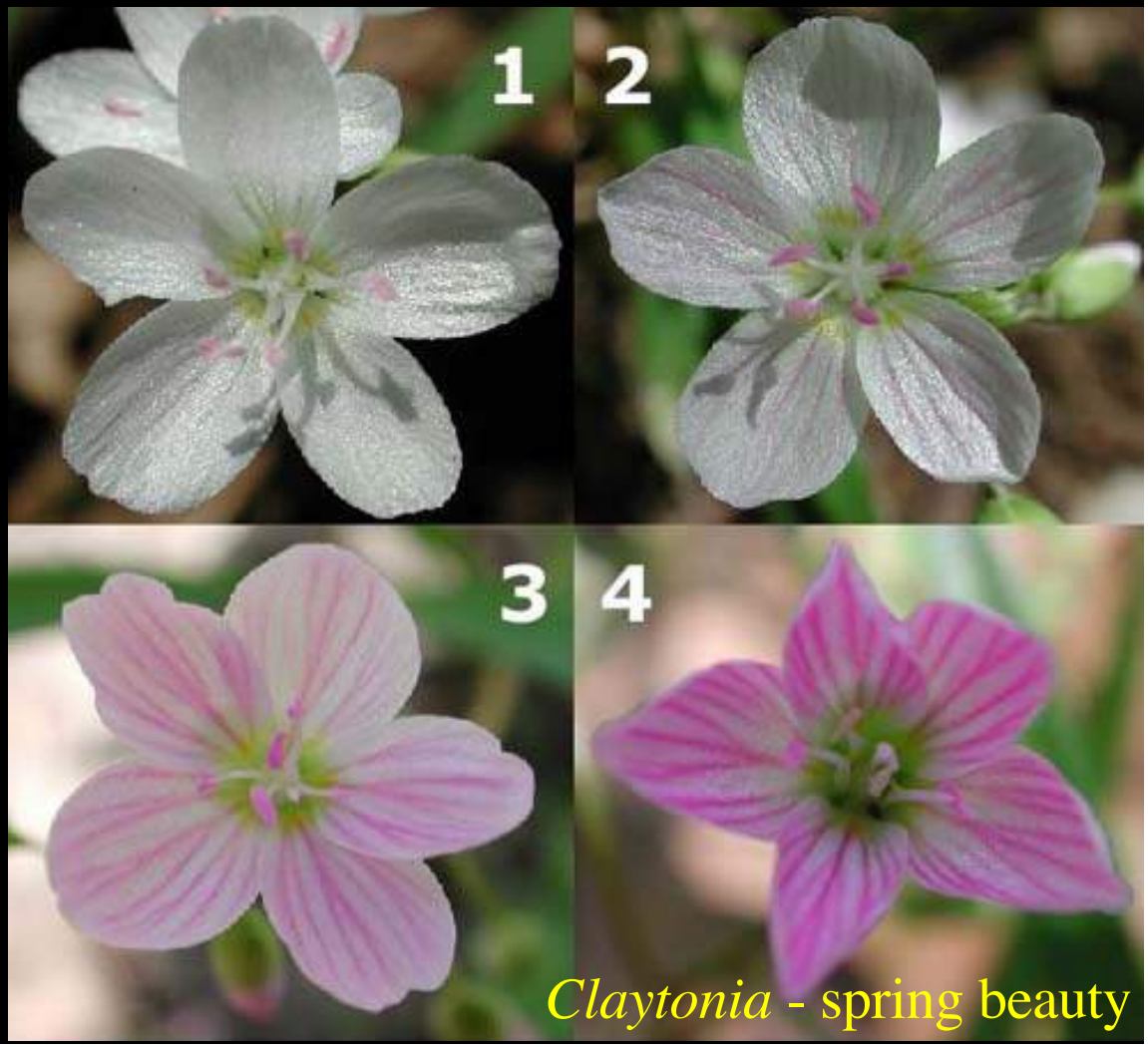
Claytonia - spring beauty

Genetic Variation within Species

Evolution requires source of genetic variation and a driving force

Natural selection - mechanism by which populations become modified in response to the environment

Adaptation - adjustment of the population to the environment



Claytonia - spring beauty

Genetic Variation within Species

- Modern genetic tools indicate substantial genetic variation within and among populations of species – raw material for natural selection or random events to act upon

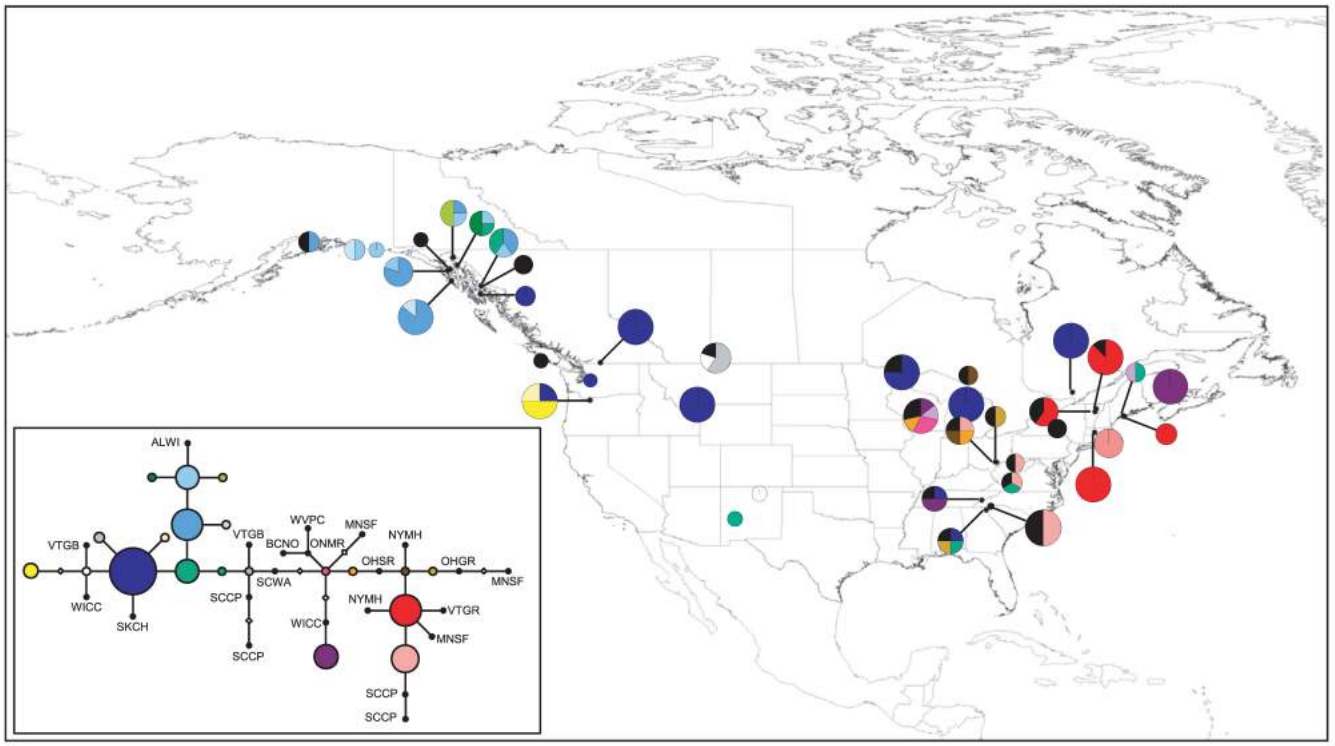


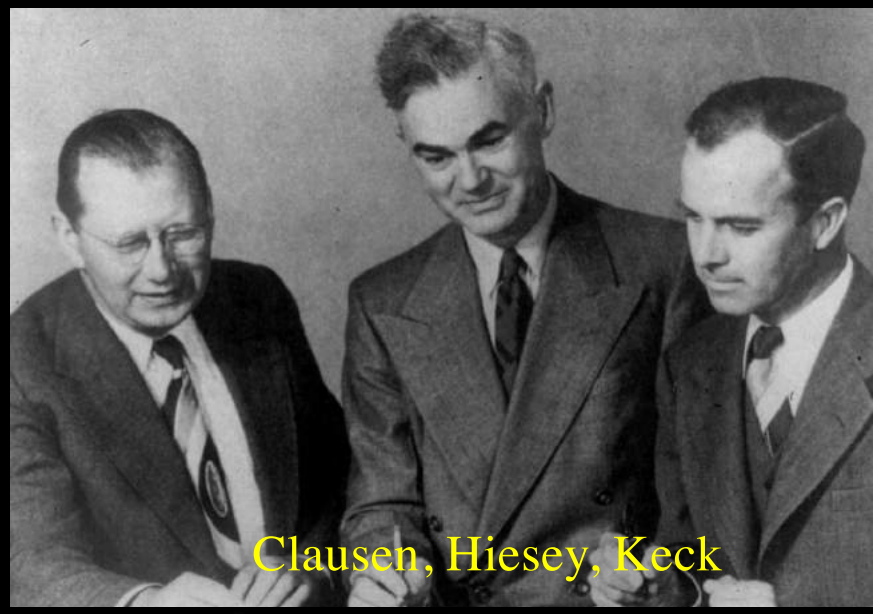
Figure 3 Distribution of chloroplast *rps2* haplotypes of *Monotropa hypopitys*. Pie chart sizes are approximately proportional to sample size, with the smallest circles representing $n = 1$ and the largest representing $n = 8$. The inset shows the phylogenetic relationships between the 42 haplotypes. Open diamonds represent missing haplotypes and small black circles represent unique haplotypes, i.e. those found in a single individual. The population of origin of each unique haplotype is indicated.

Hypopitys monotropa - pinesap

Genetic Variation within Species

- three American botanists documented this linkage with their studies on a variety of plant species in California during 1940-1950s

- their work on the *Achillea millefolium* (yarrow) and *Potentilla glandulosa* (sticky cinquefoil) complexes are the best known


Clausen, Hiesey, Keck


Potentilla


Achillea

Genetic Variation within Species

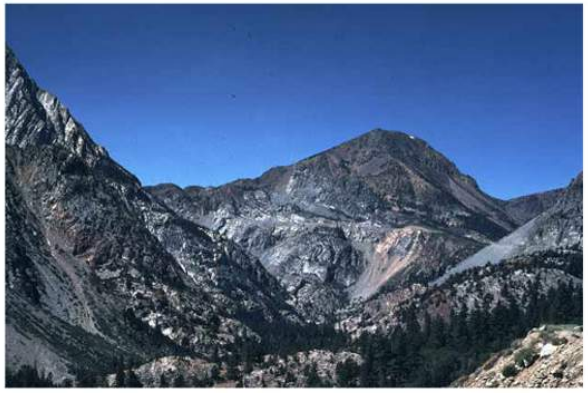
- used a reciprocal transplant design by setting up common garden sites across an elevation gradient from coastal California, through the Coast Range, and up and over the Sierra Nevada

Clausen, Keck & Heisey's California Transect Study Sites

Coastal California, near Big Sur

Coast Ranges, inland from Big Sur

Foothills of the Sierra Nevada



Timberline, east side of Sierra Nevada

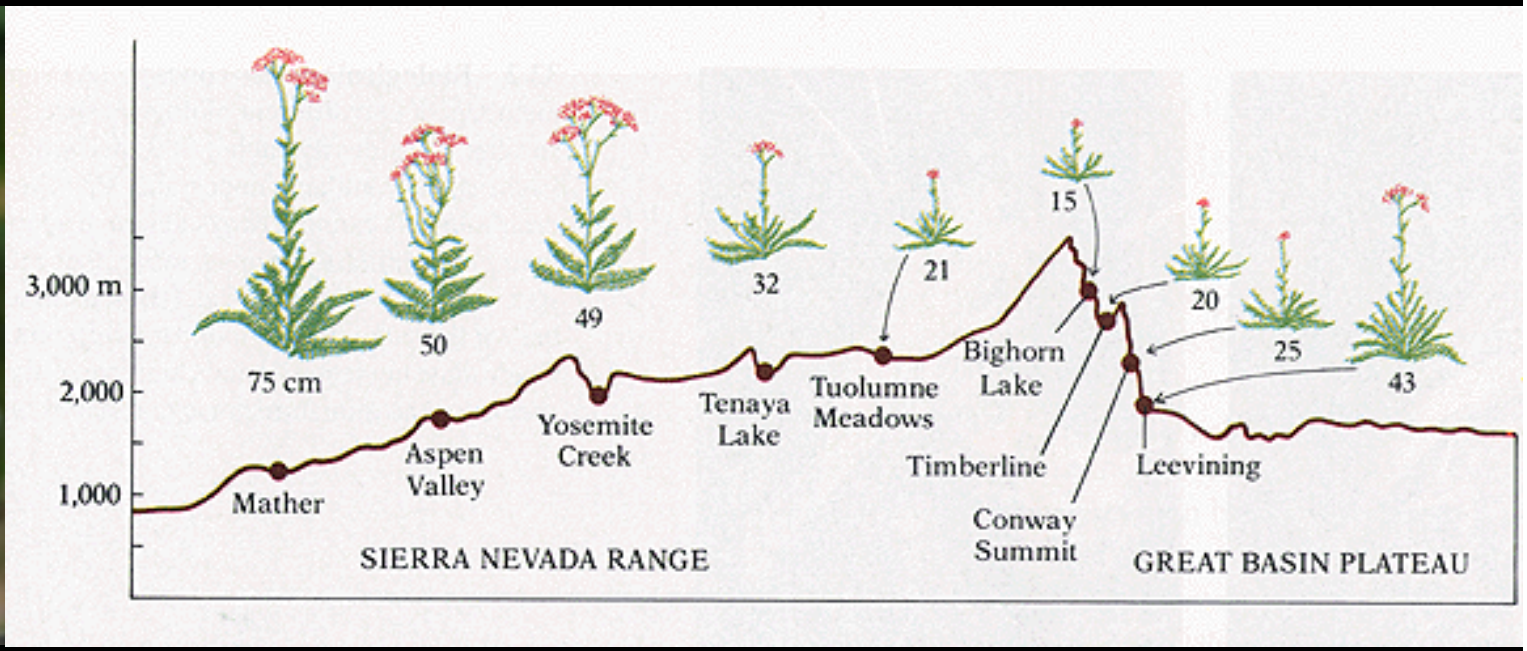
Common garden at Stanford

Common garden at Mather

Genetic Variation within Species

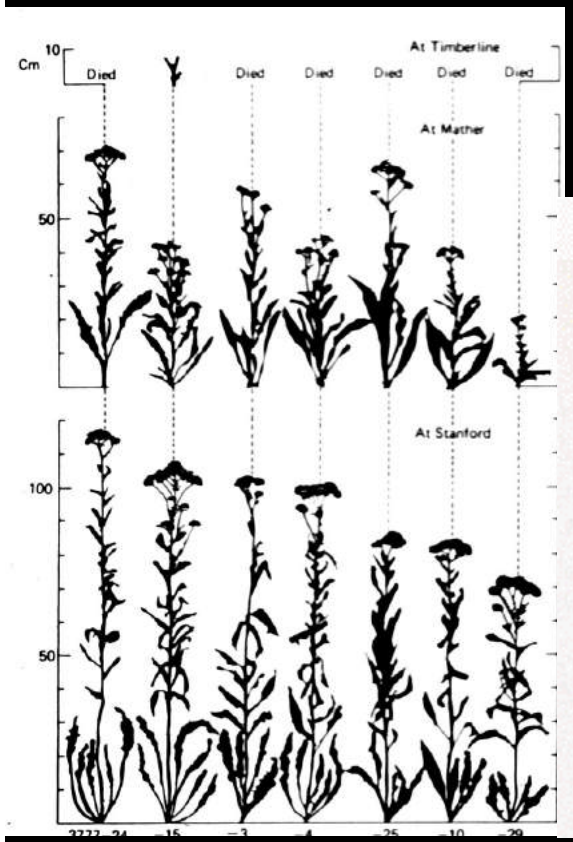
• *Achillea lanulosa* exhibits clinal phenotypic variation in natural populations across the elevational gradient in the Sierra Nevada

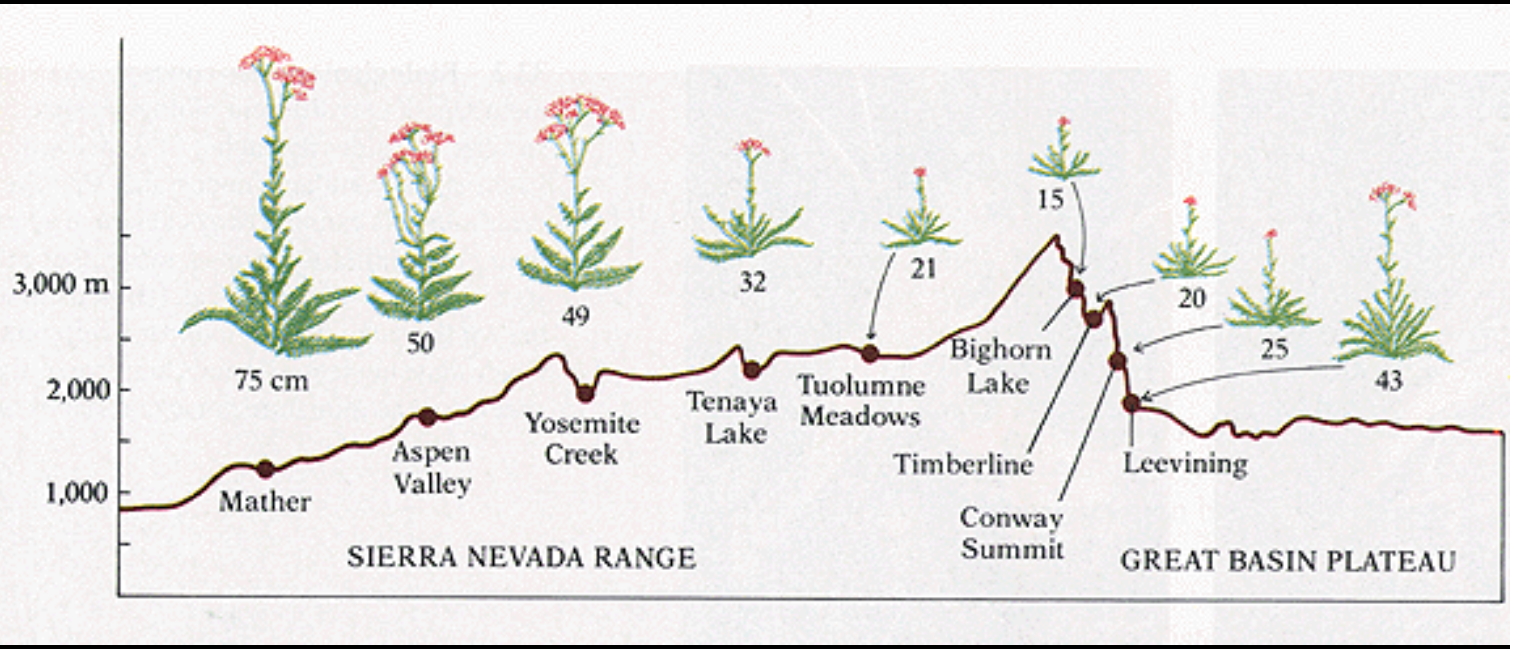

Achillea lanulosa



Genetic Variation within Species

- populations exhibit marked lowering of fitness and adaptation when placed at other sites — clinal genotypic variation or the formation of ecotypes

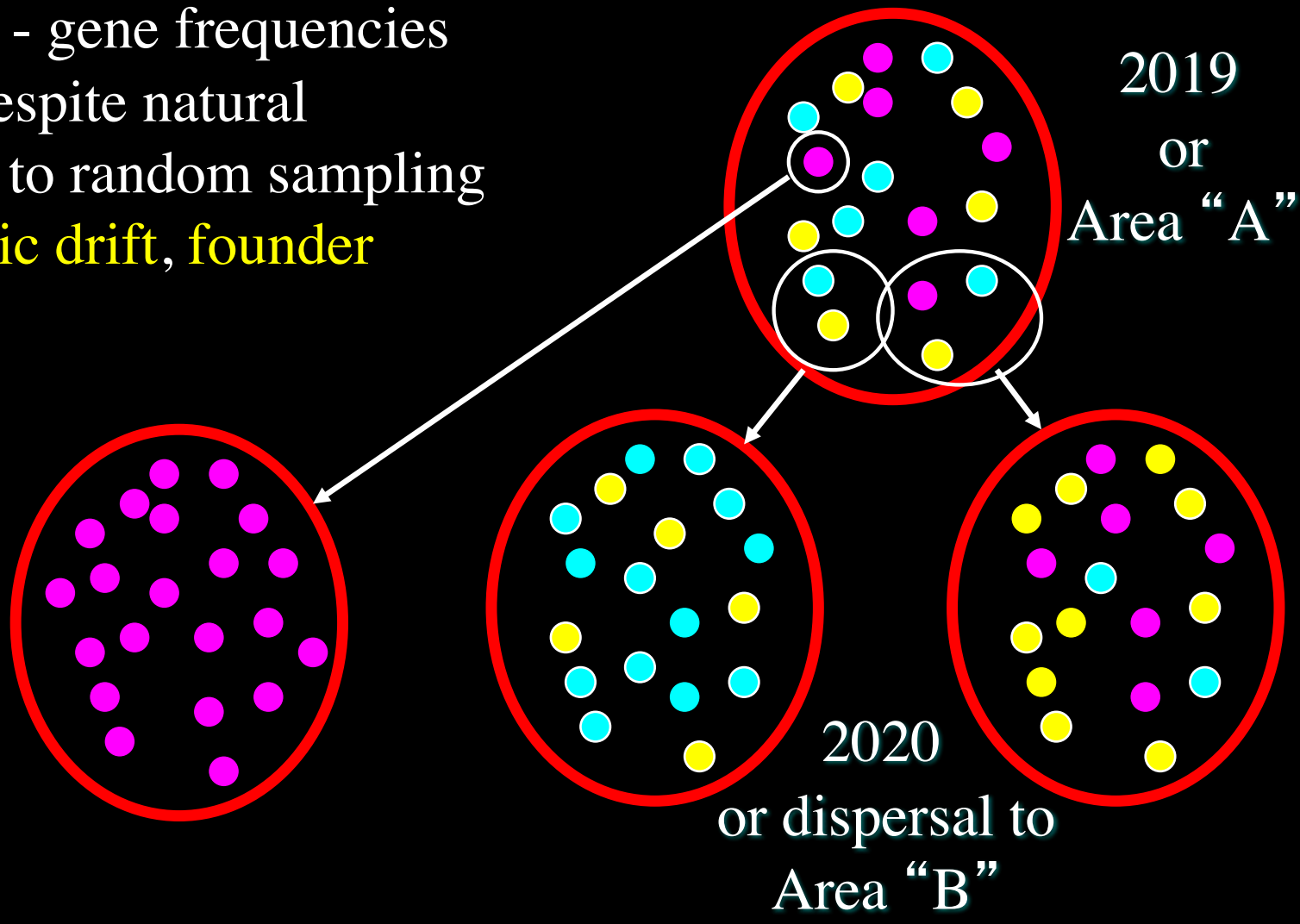




Genetic Variation within Species

Evolution requires source of genetic variation and a driving force

Random Events - gene frequencies may fluctuate despite natural selection owing to random sampling of genes - genetic drift, founder events



Genetic Variation within Species

Evolution requires source of genetic variation and a driving force

Random Events - gene frequencies may fluctuate despite natural selection owing to random sampling of genes - genetic drift, founder events

- effect is greatest in small, isolated populations on "islands" - e.g., cloud forest peaks in central Panama

Genetic Variation within Species

Evolution requires source of genetic variation and a driving force

Random Events - gene frequencies may fluctuate despite natural selection owing to random sampling of genes - genetic drift, founder events

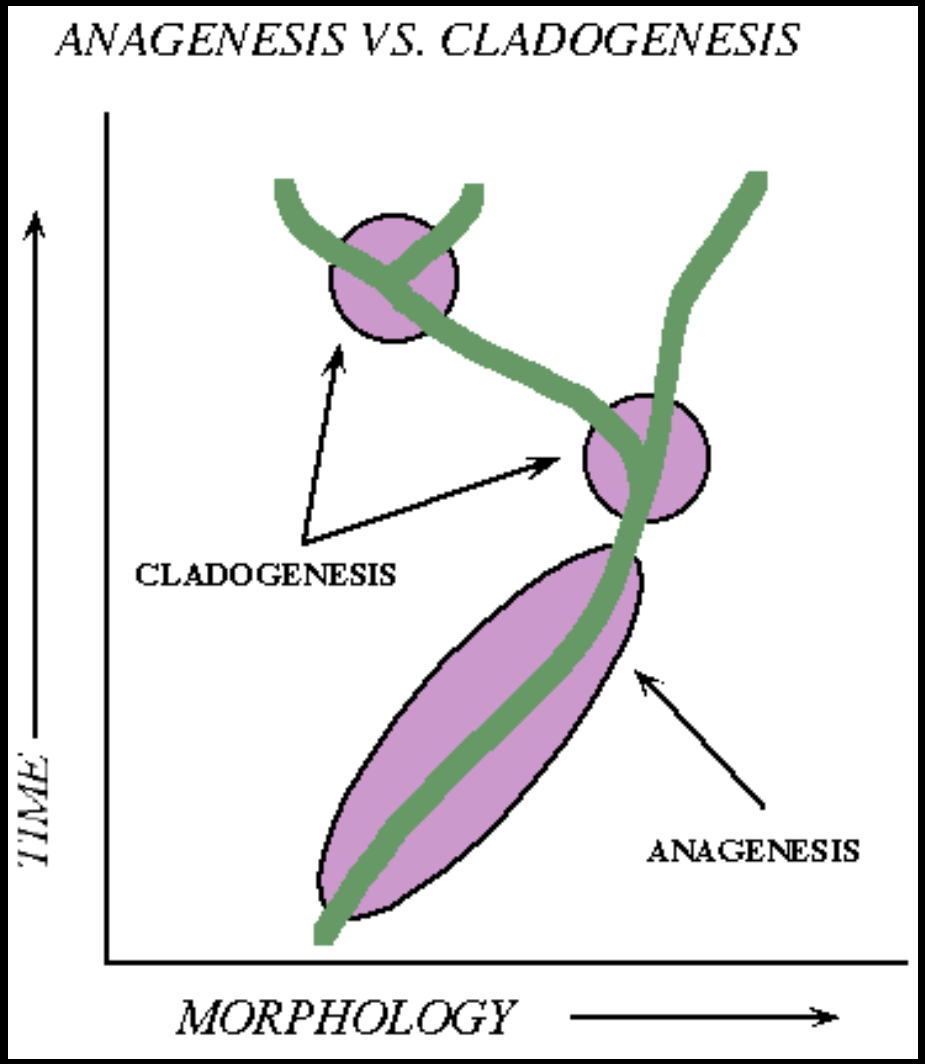
- widespread lower elevation *Lisianthius skinneri* (♦)and isolated cloud forest taxa (♦)

Speciation

Cladogenesis - formation of new species

- anagenesis - evolution within a species lineage — (Darwin's modification)

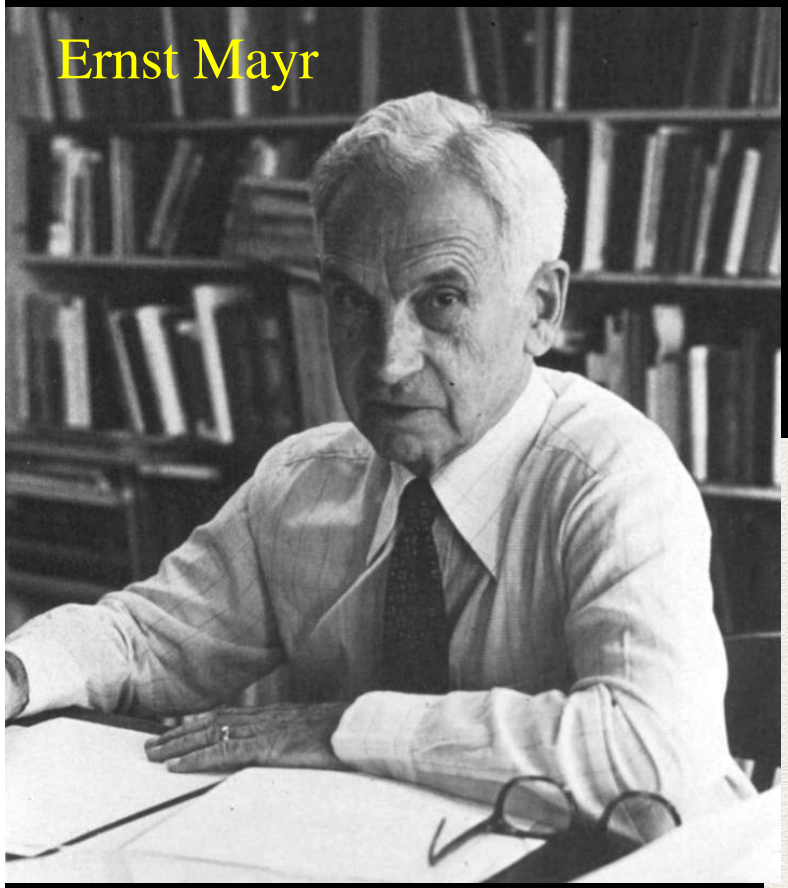
- cladogenesis - evolution to form new species lineages or speciation — (Darwin's descent)



How to Define Species?

Cladogenesis - formation of new species

How do you define species?



- difficult, due to continuum of evolutionary processes and products
- emphasis on reproductive isolating mechanisms

Biological Species Definitions

Species represent groups of populations reproductively & potentially reproductively isolated from other such groups

Reproductive Isolation

Many kinds of isolating mechanisms

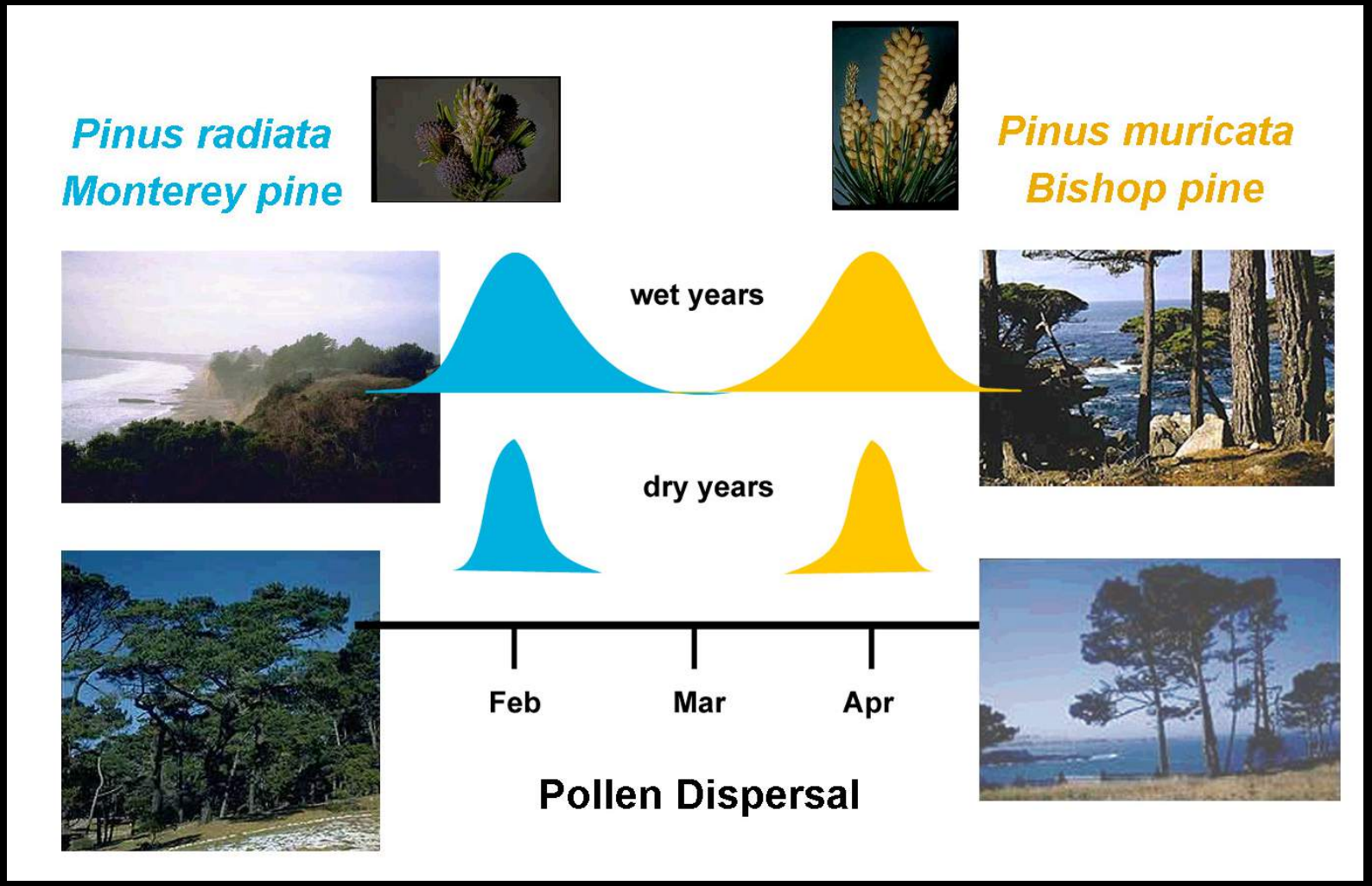
Ecological or habitat isolation

- species adapted to harsh, heavy metal serpentine soils in California ecologically separated from crossing with those that do not

Ceanothus (California lilac) on Catalina Island

Reproductive Isolation

Seasonal or temporal isolation - different times of reproduction



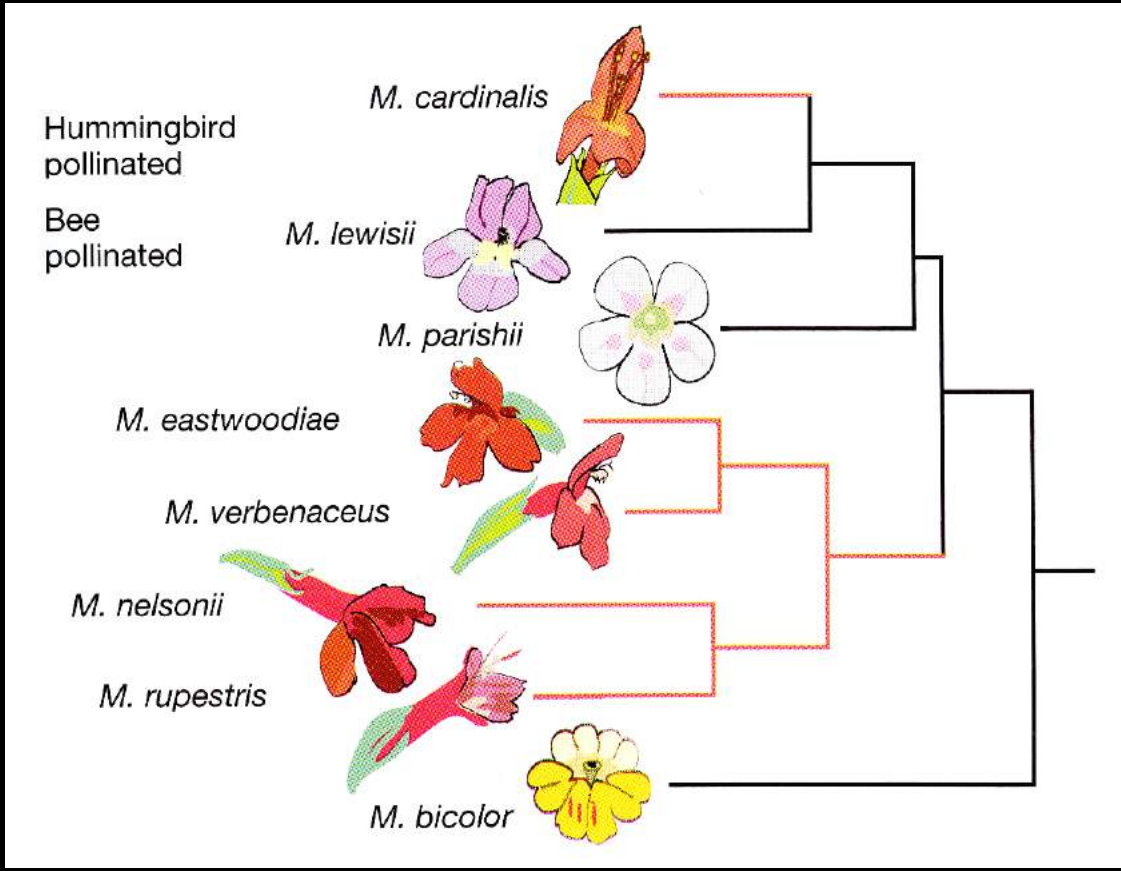
Reproductive Isolation

Mechanical isolation - variation in floral form prevents interspecies pollen movement

- pollen placement or floral form in pseudocopulatory orchids

Reproductive Isolation

Mechanical isolation - variation in floral form prevents interspecies pollen movement



- two western U.S. monkeyflowers *Mimulus cardinalis* and *M. lewisii* — a pair of recently speciated species — are isolated in nature due to different modes of pollination

Reproductive Isolation

Mechanical isolation - variation in floral form prevents interspecies pollen movement

Mimulus cardinalis

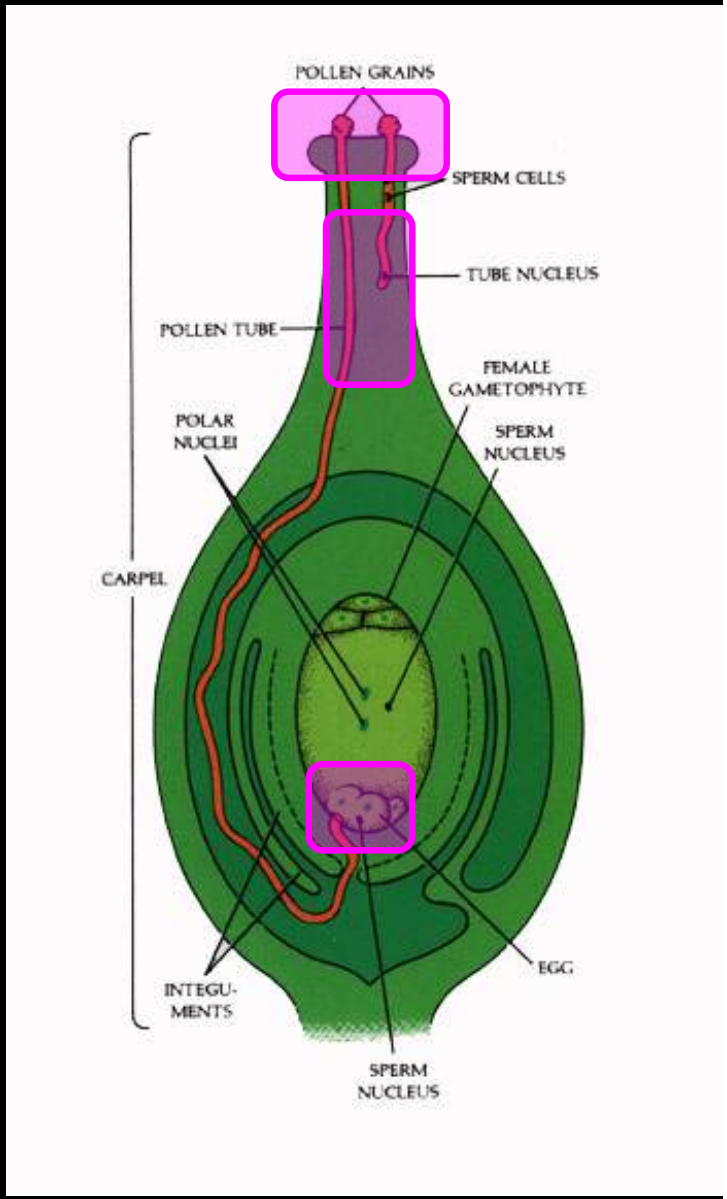
- few genes generated the floral differences that maintain reproductive isolation - however, species can readily hybridize in the greenhouse

Mimulus lewisii

Reproductive Isolation

Gametic incompatability - at three levels in *Heliconia*

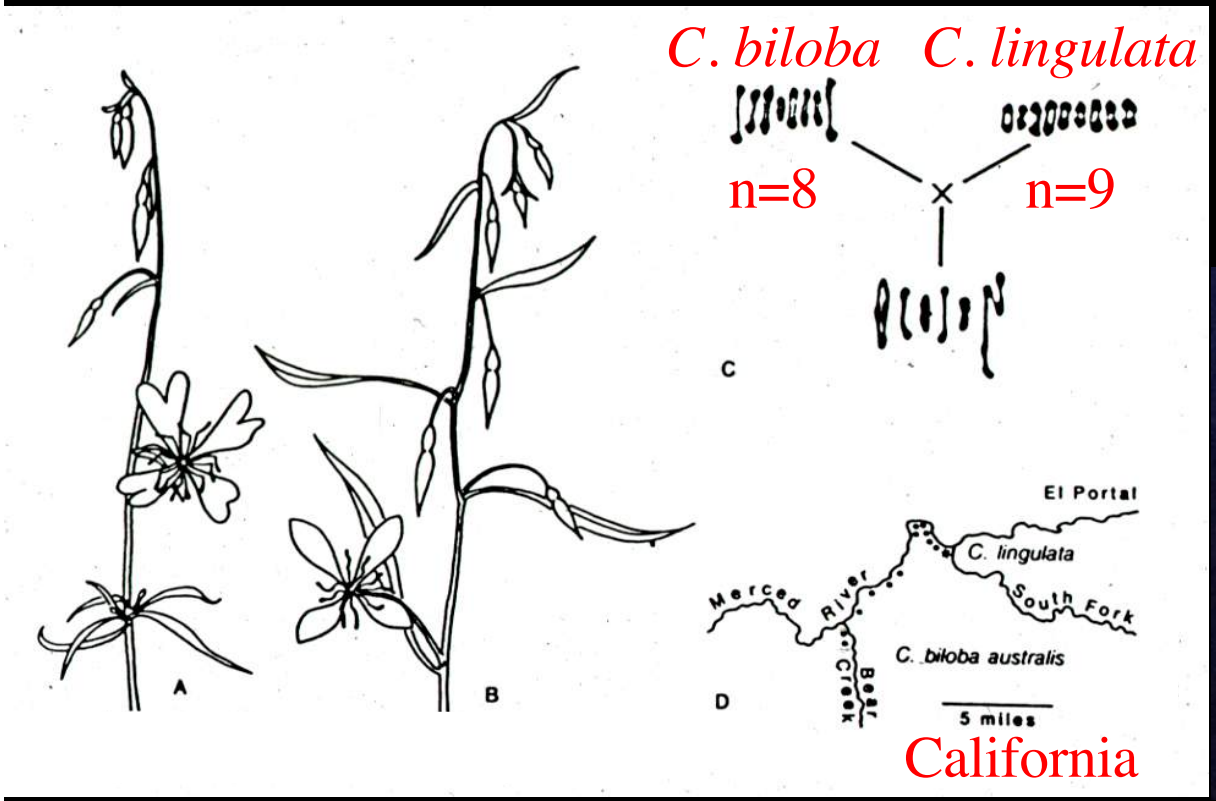
- pollen - stigma: no recognition (lipids)
- pollen tube - style: pollen tube rupture (arabinogalactan protein growth regulation)
- gamete - gamete: sperm-egg rejection

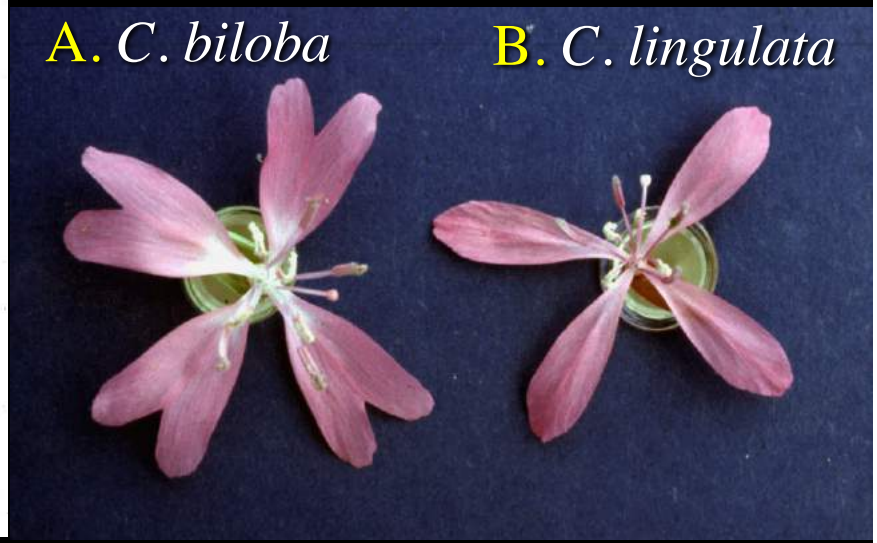


Reproductive Isolation

Hybrid sterility - F_1 sterility

- *Clarkia biloba* & *C. lingulata* - sister species, but differ in chromosome number (n=8 vs. n=9) - intersterile





Reproductive Isolation

F_2 breakdown - F_1 fertile, but subsequent generations show lethal effects

- well studied in cultivated species of cotton (*Gossypium*)

Models of Speciation

Speciation or Cladogenesis - most models or processes of speciation are based on biogeography (‘*patry*’ - homeland)

Allopatric speciation

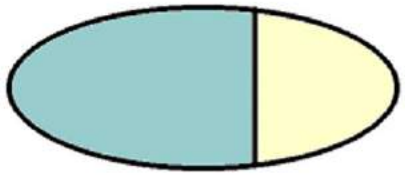
ranges do not touch or overlap

no gene flow

Parapatric speciation

ranges touchbut do not overlap significantly

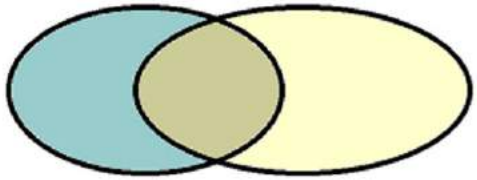
gene flow usually small



Sympatric speciation

ranges overlap significantly

gene flow is not prevented by geography



- geographical
- catastrophic or quantum – will not talk about
- diploid hybrid (homoploid)
- polyploid

Models of Speciation

Speciation or Cladogenesis - most models or processes of speciation are based on biogeography (‘*patry*’ - homeland)

Allopatric speciation

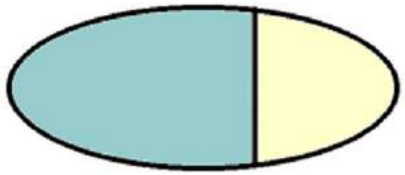
ranges do not touch or overlap

no gene flow

Parapatric speciation

ranges touchbut do not overlap significantly

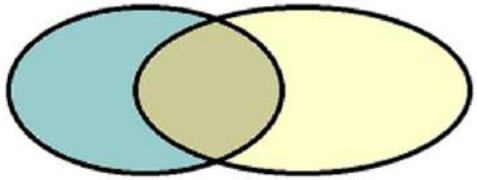
gene flow usually small



Sympatric speciation

ranges overlap significantly

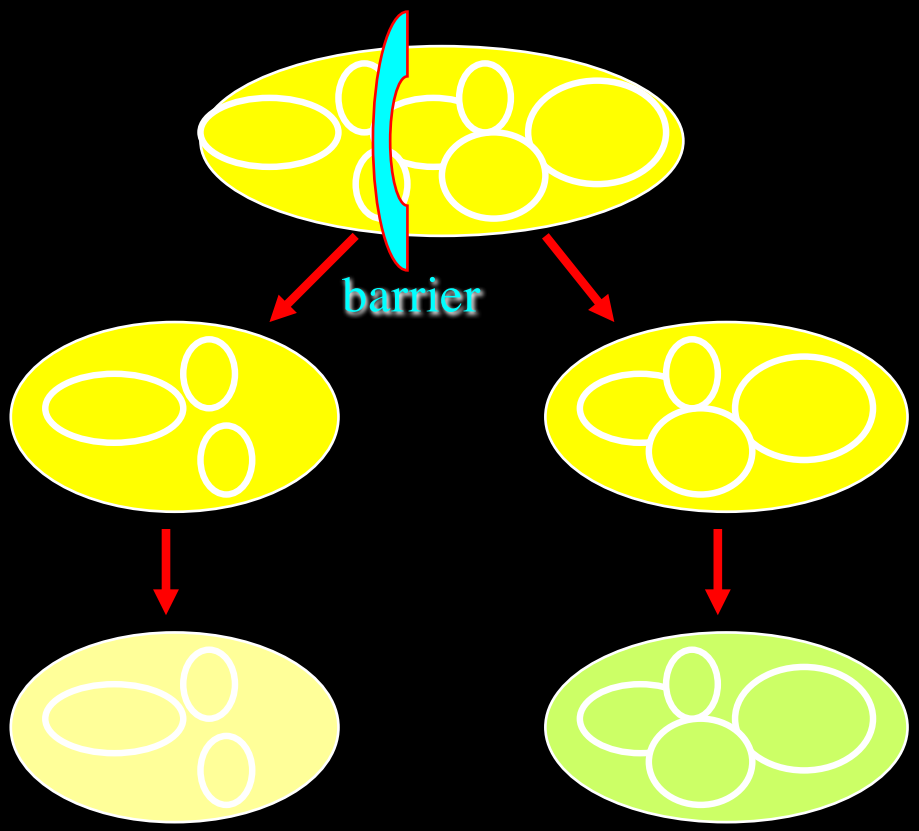
gene flow is not prevented by geography

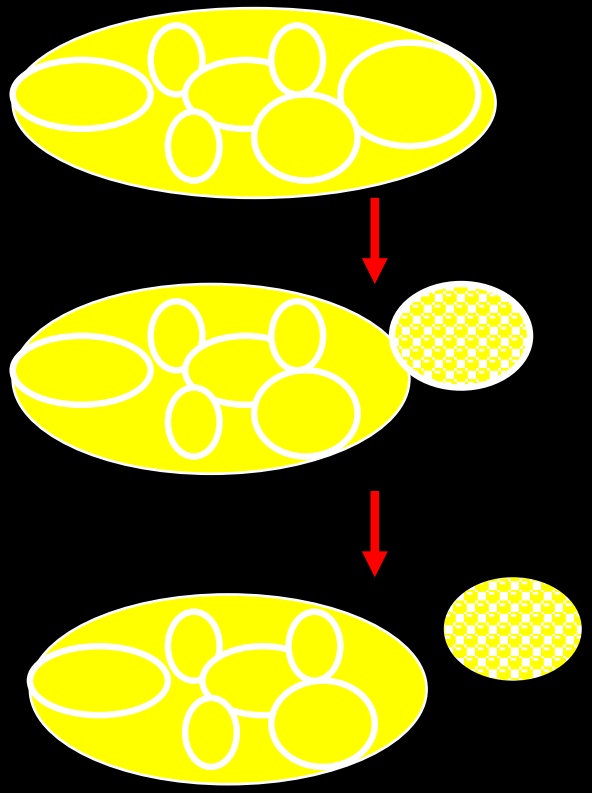


- allopatric speciation refers to lineage splitting facilitated by complete geographical separation

- called the geographical or conventional model of speciation — it is the best documented and most important

Geographic Speciation

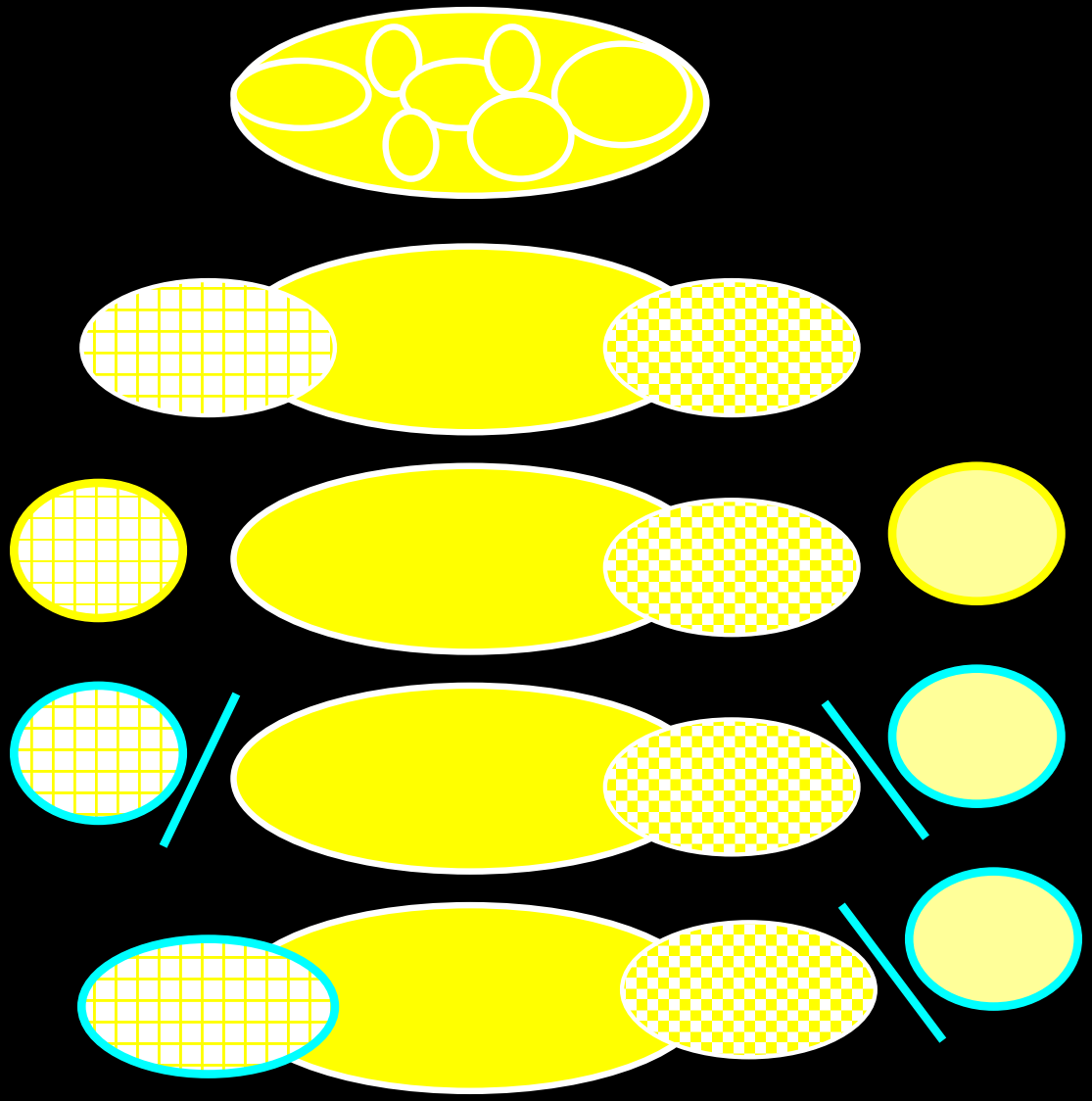




- ‘dumb-bell’ model: ancestral species forms two new species by division

- peripheral isolate model: one new species forms at edge of retained ancestral species

Geographic Speciation

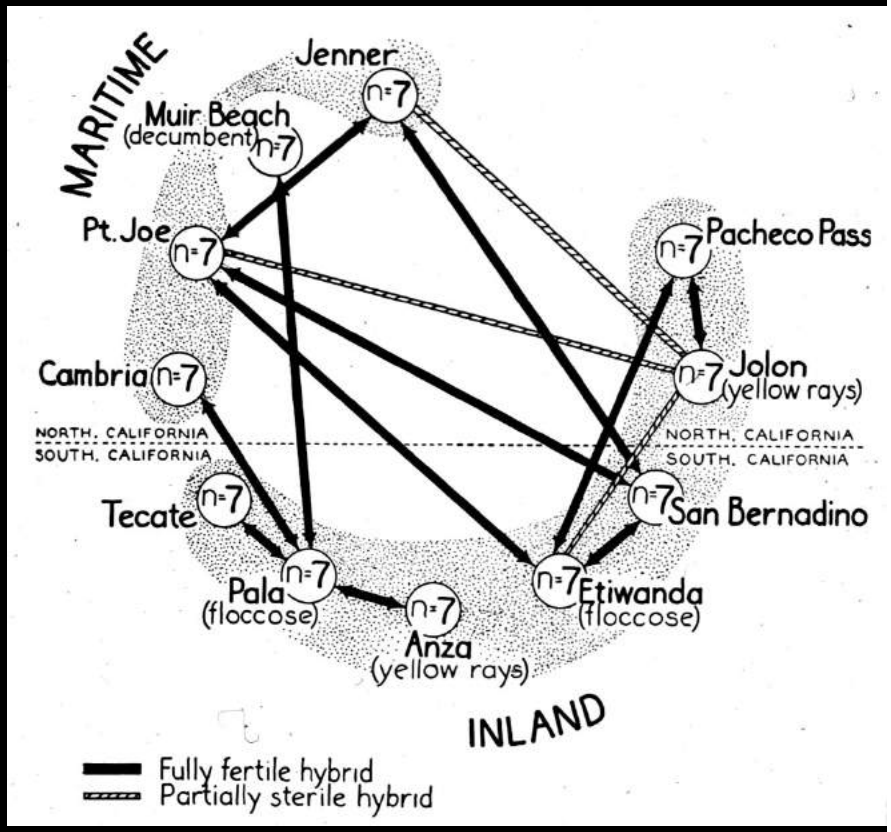


- freely interbreeding series of populations
- races form in response to n.s. and environmental variation
- differentiation and migration lead to geographically isolated races or subspecies
- reproductive isolation forms within or between subspecies and races
- range expansion allows new species to co-exist

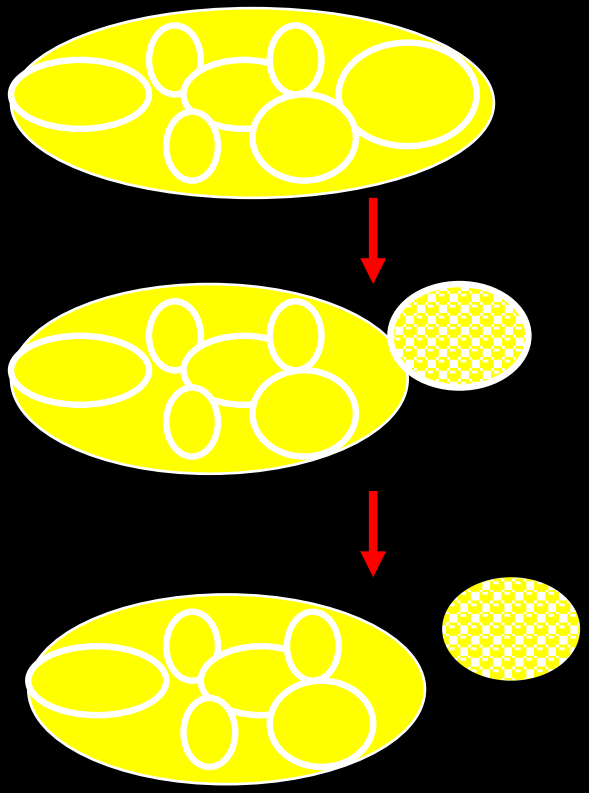
Geographic Speciation

The degree of reproductive isolation among geographical sets of populations within an actively evolving species complex is often tested by crosses

Layia - tidy tips



Geographic Speciation



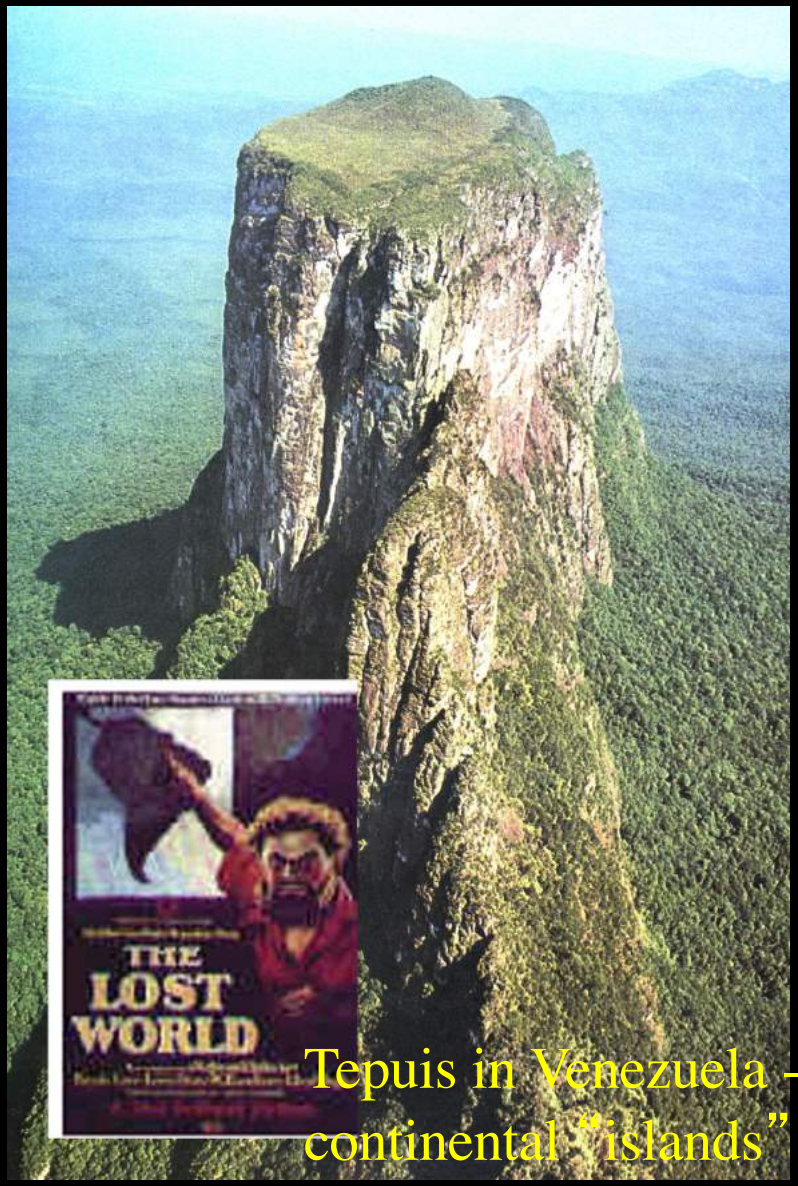
• peripheral isolate model: new species forms at edge of retained ancestral species

"Island" Model of Speciation

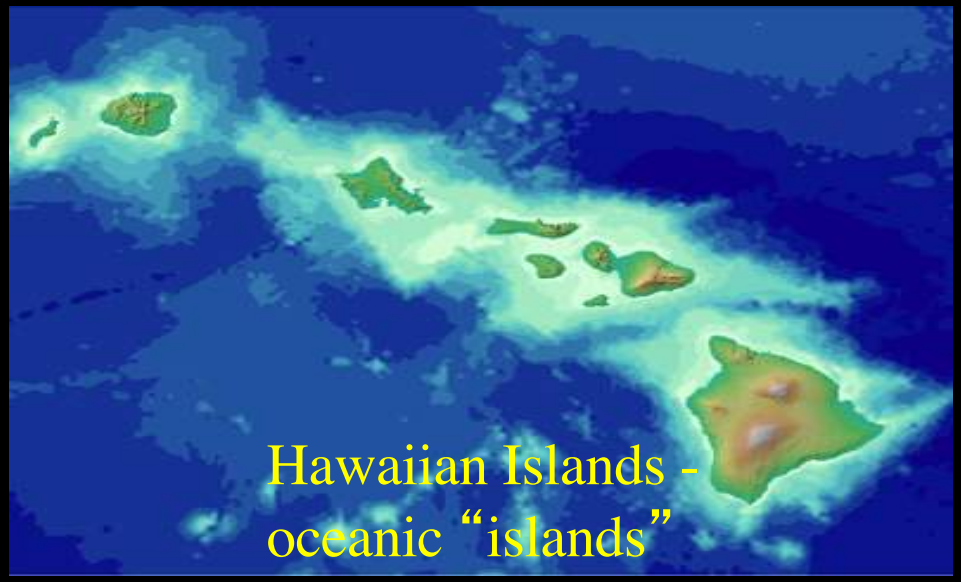
• A rapid form of peripheral isolation and speciation involving "island" like habitats completely separated from contact

• The founder event often involves a very small subset of the original genetic pool of the ancestral species — thus differences accumulate rapidly

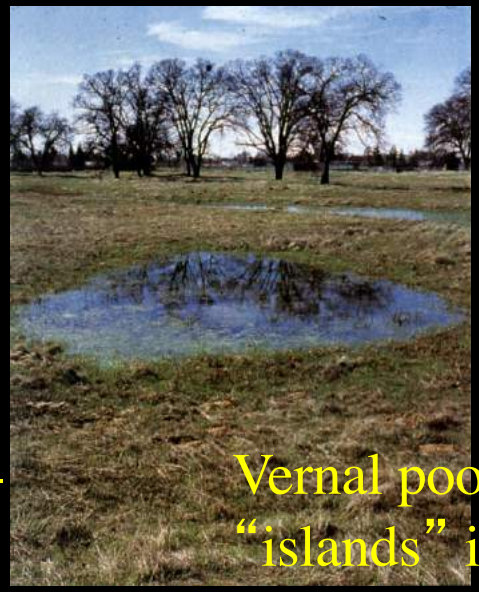
Geographic Speciation

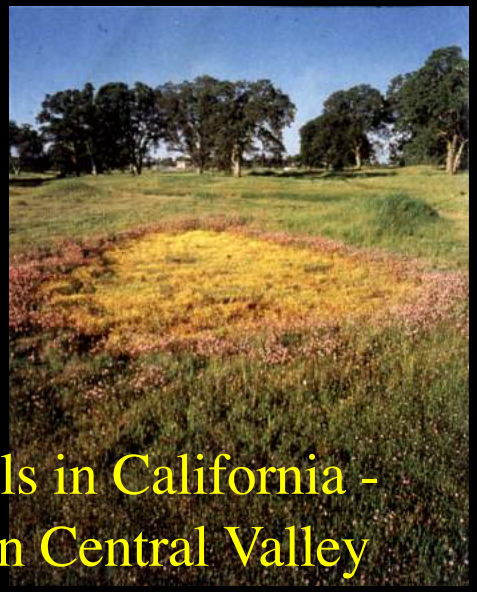


Tepuis in Venezuela -
continental "islands"



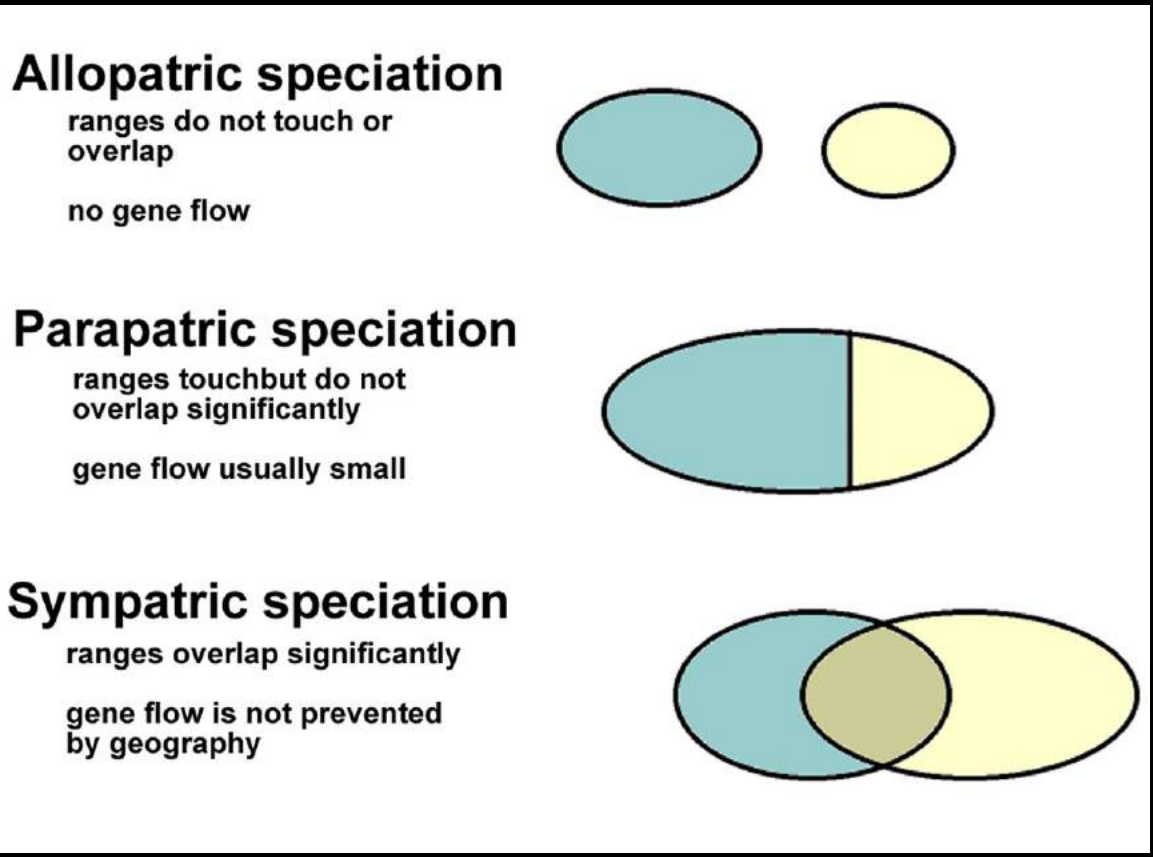
Hawaiian Islands -
oceanic "islands"





Vernal pools in California -
"islands" in Central Valley

Sympatric Speciation



Two types of sympatric speciation where gene flow is not prevented by geography are:

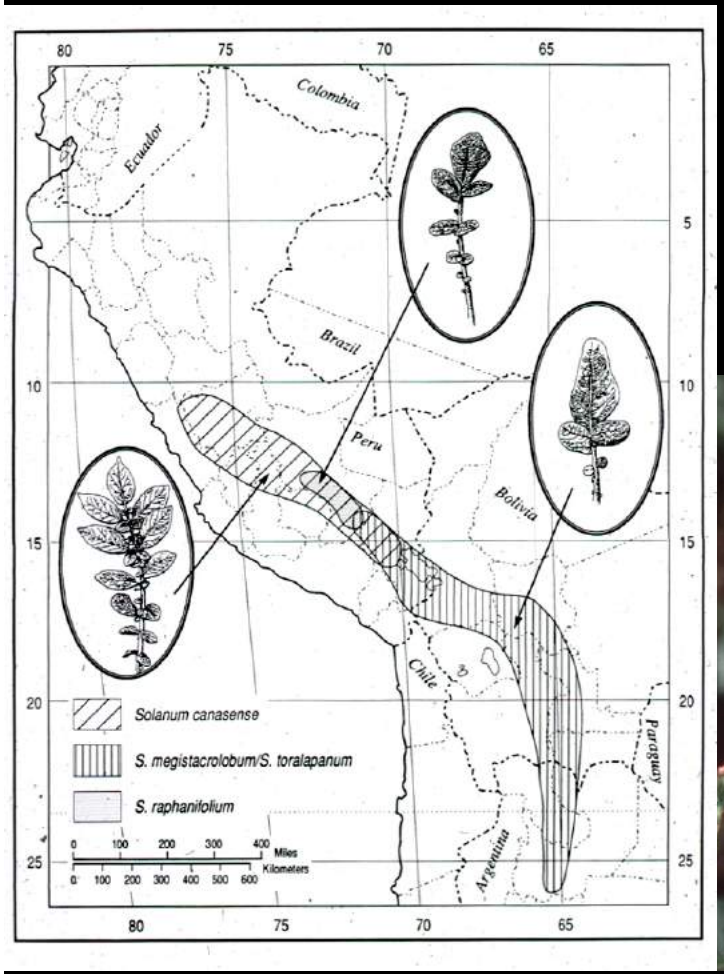
(1) diploid or homoploid hybrid speciation

(2) allopolyloid speciation

Homoploid Hybrid Speciation

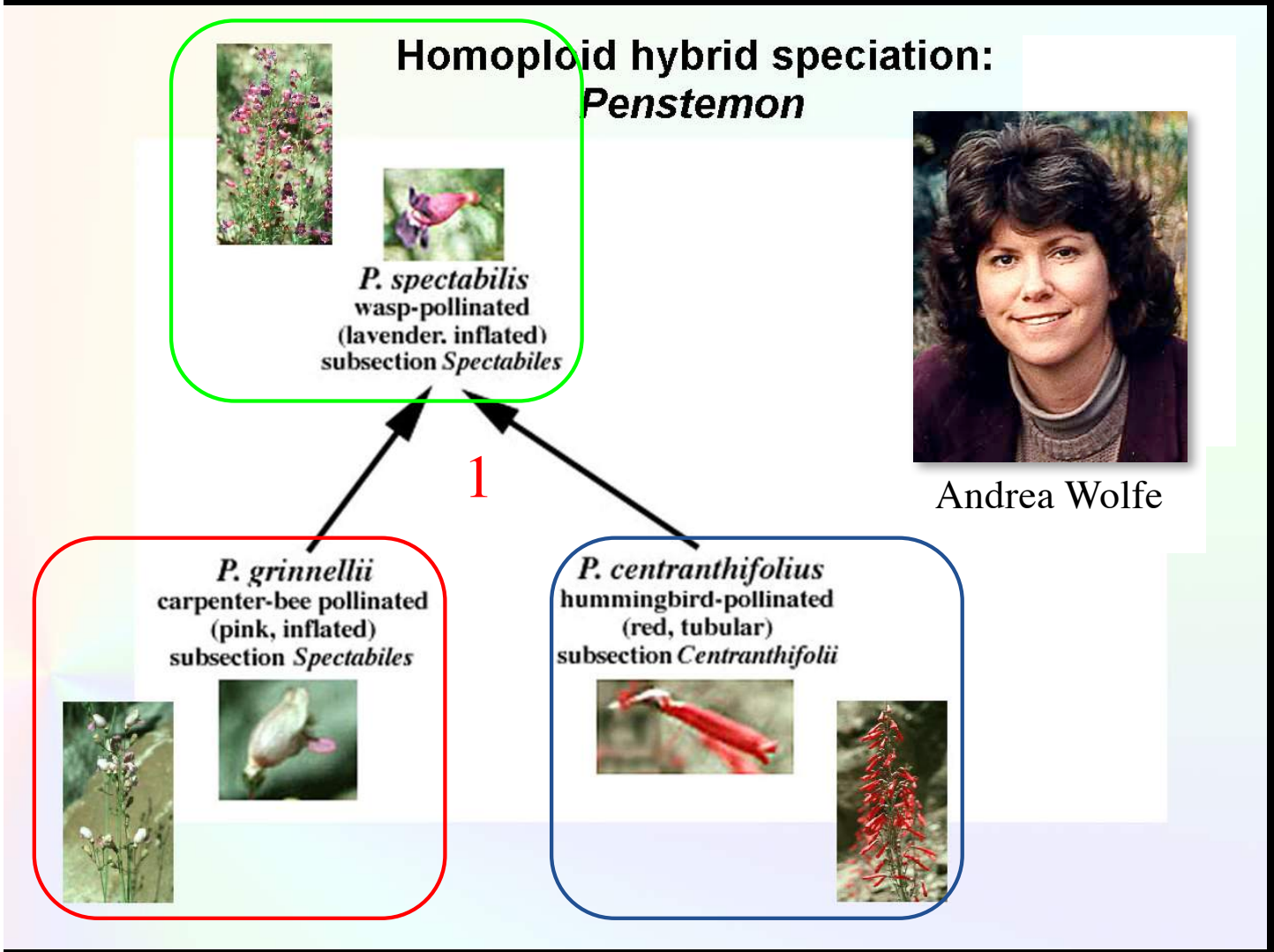
S. canescens X *S. megistacrolobum* → *Solanum raphanifolium*

Spooner, Smith, Sytsma 1991



- ranges overlap
- morphologically intermediate
- DNA says NO! Just an unrelated species

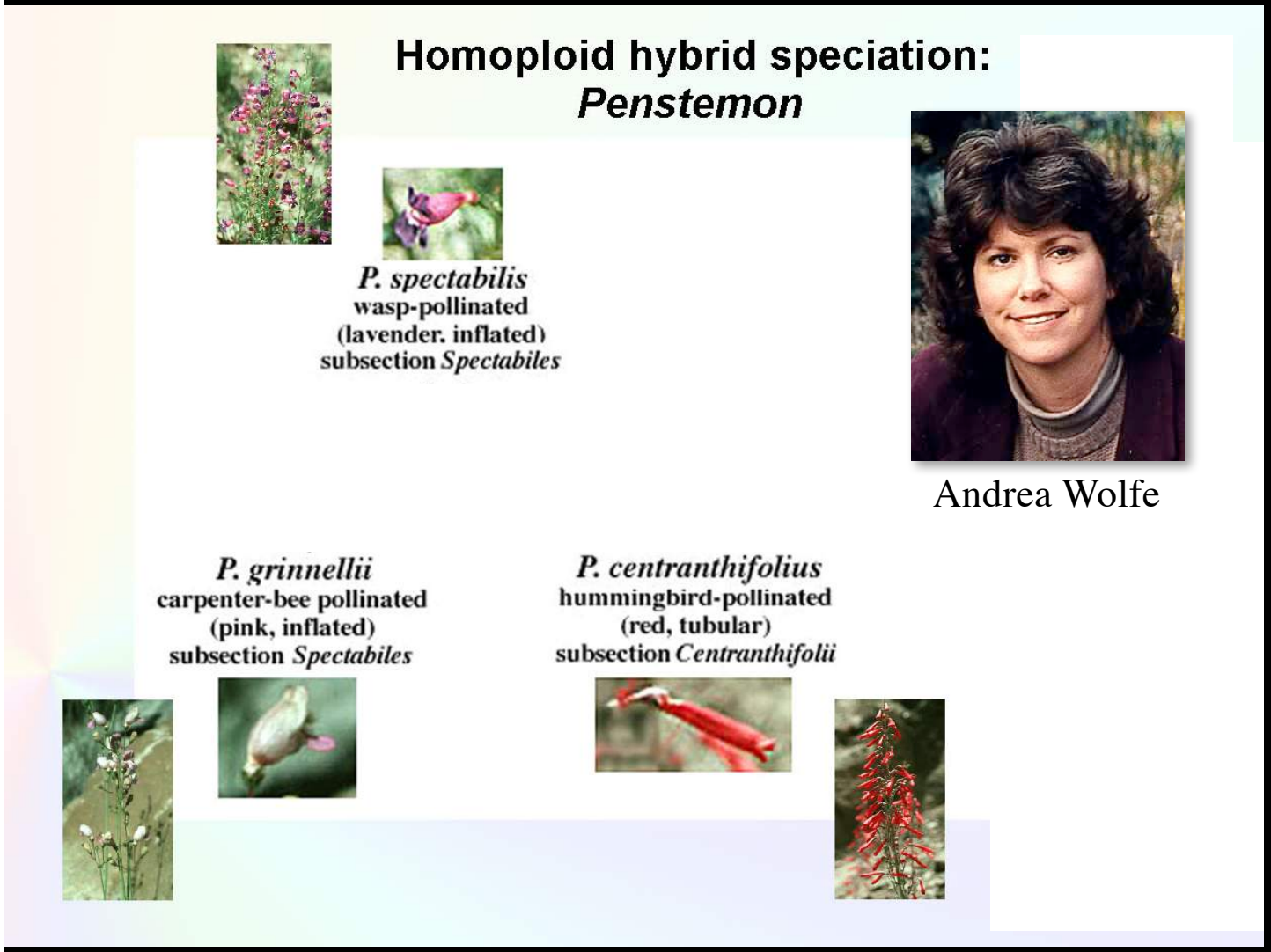
Homoploid Hybrid Speciation



Andrea Wolfe

- two parental species differ in habitat, floral form, pollinators
- *P. spectabilis* is intermediate in habitat, floral form, and isolated by new pollinator

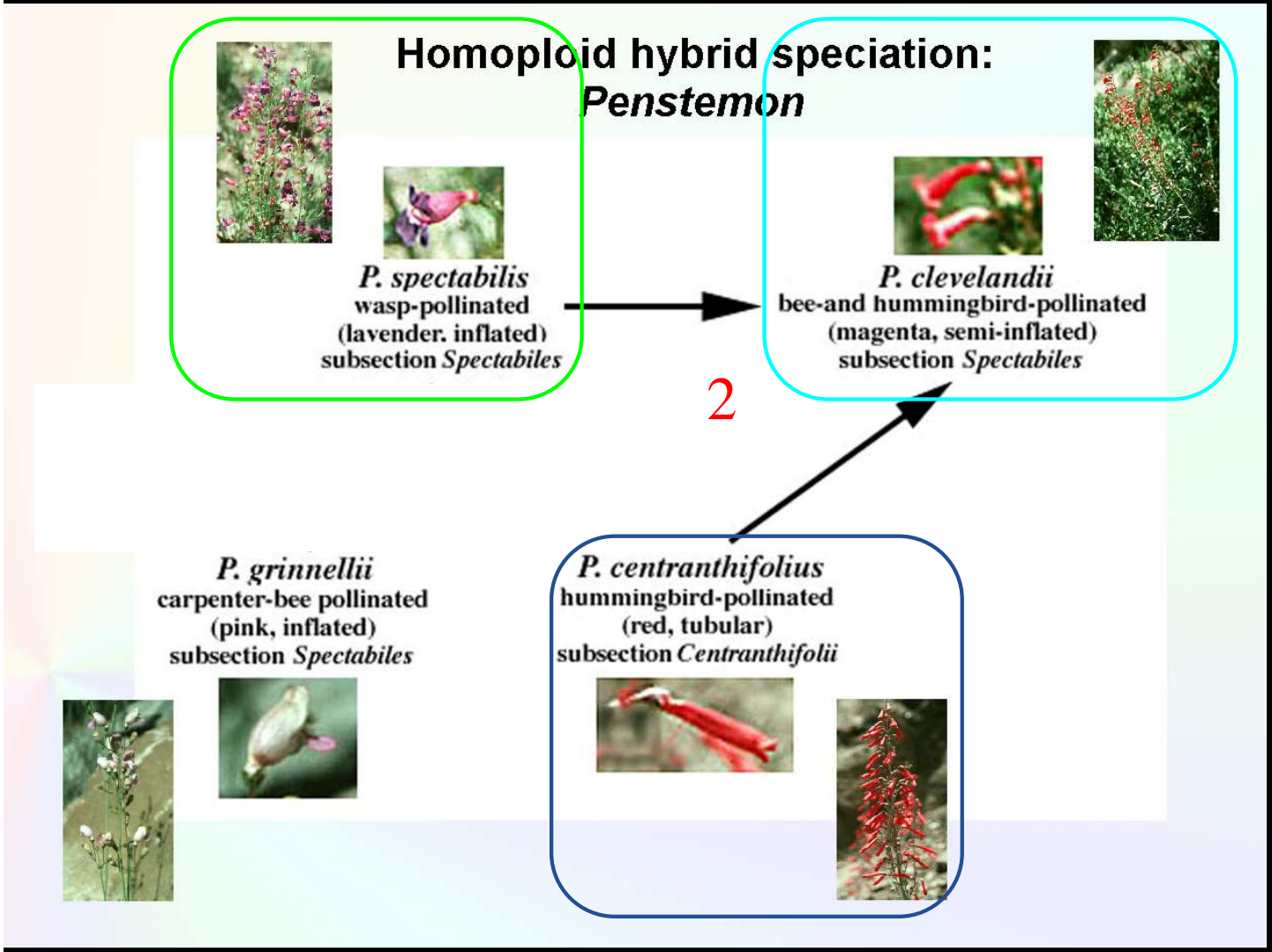
Homoploid Hybrid Speciation



Andrea Wolfe

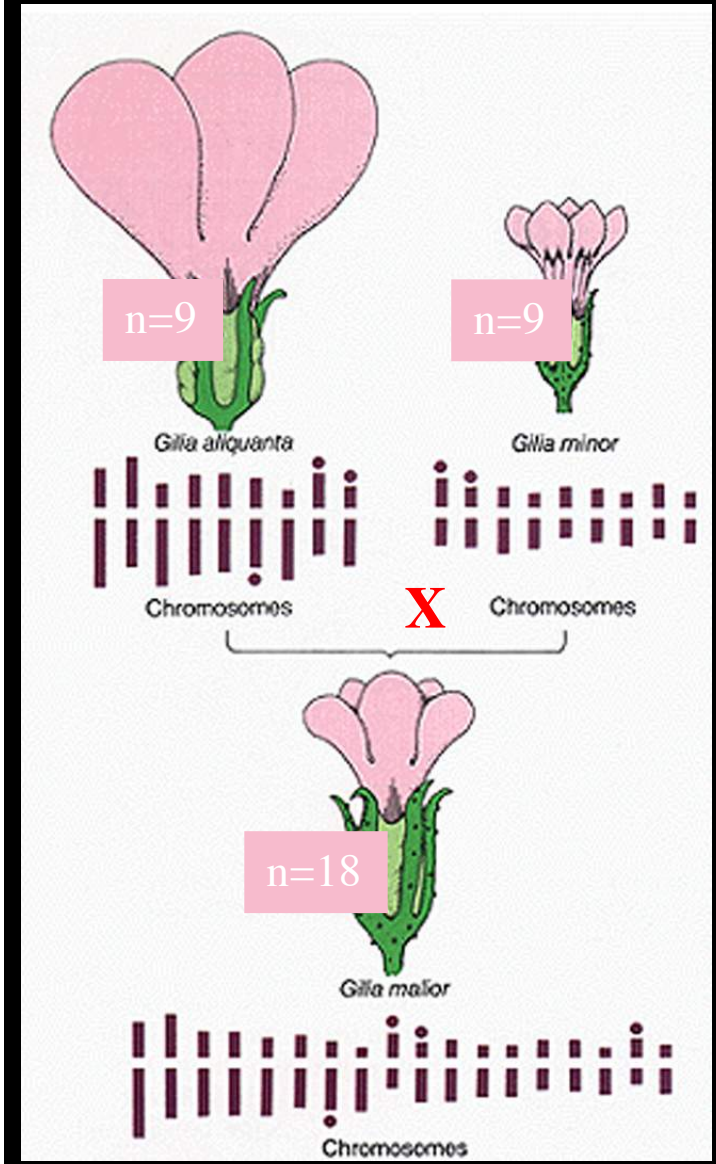
- two parental species differ in habitat, floral form, pollinators
- *P. spectabilis* is intermediate in habitat, floral form, and isolated by new pollinator
- DNA says no! not a hybrid species

Homoploid Hybrid Speciation



- but supports example #2
- *P. clevelandii* is a diploid hybrid species

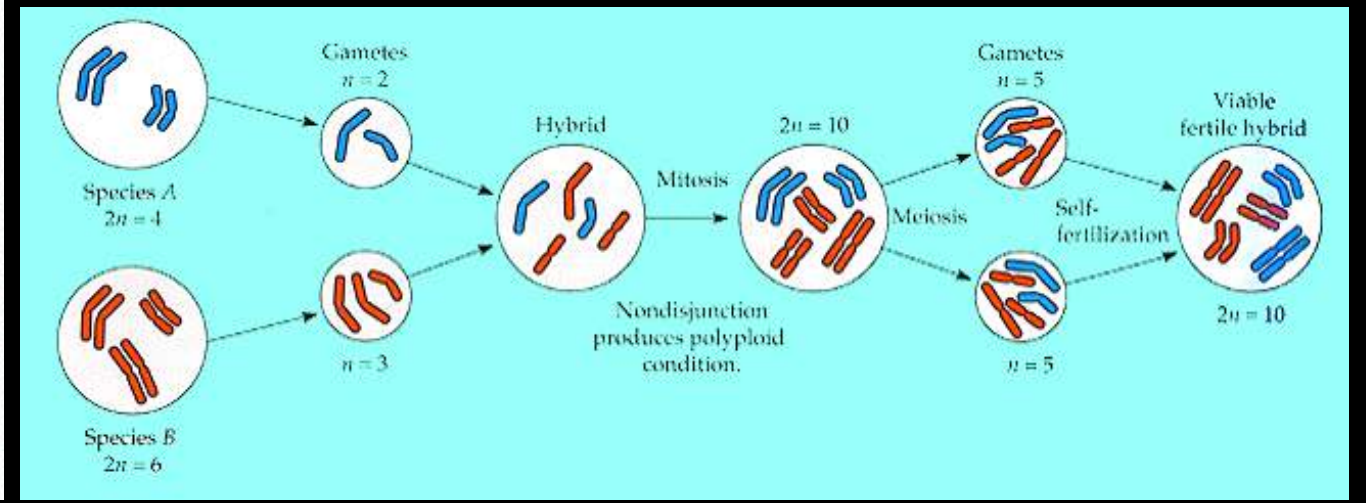
Polyploid Speciation



2 species with same "n"

A very common and instantaneous form of speciation in plants (and a few animals) is allopolyploidy.

- hybridization occurs between two species
- meiotic incompatibilities makes hybrid sterile
- doubling of chromosomes occurs (polyploidy)
- allopolyploid is fertile and reproductively isolated from both parental species

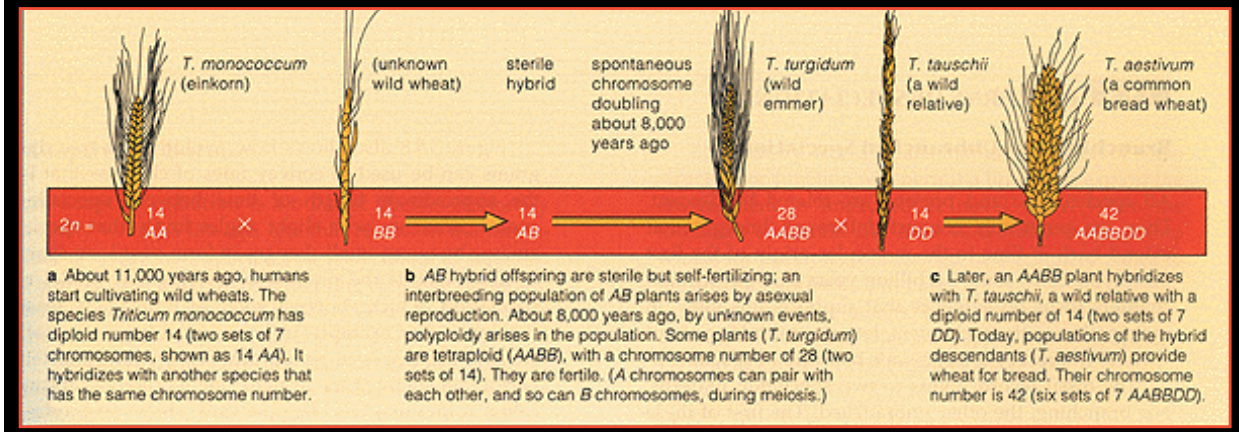


2 species with different "n"

Polyploid Speciation

Under human selection in the Middle East, bread wheat (*Triticum aestivum*) has evolved in about 11,000 years.

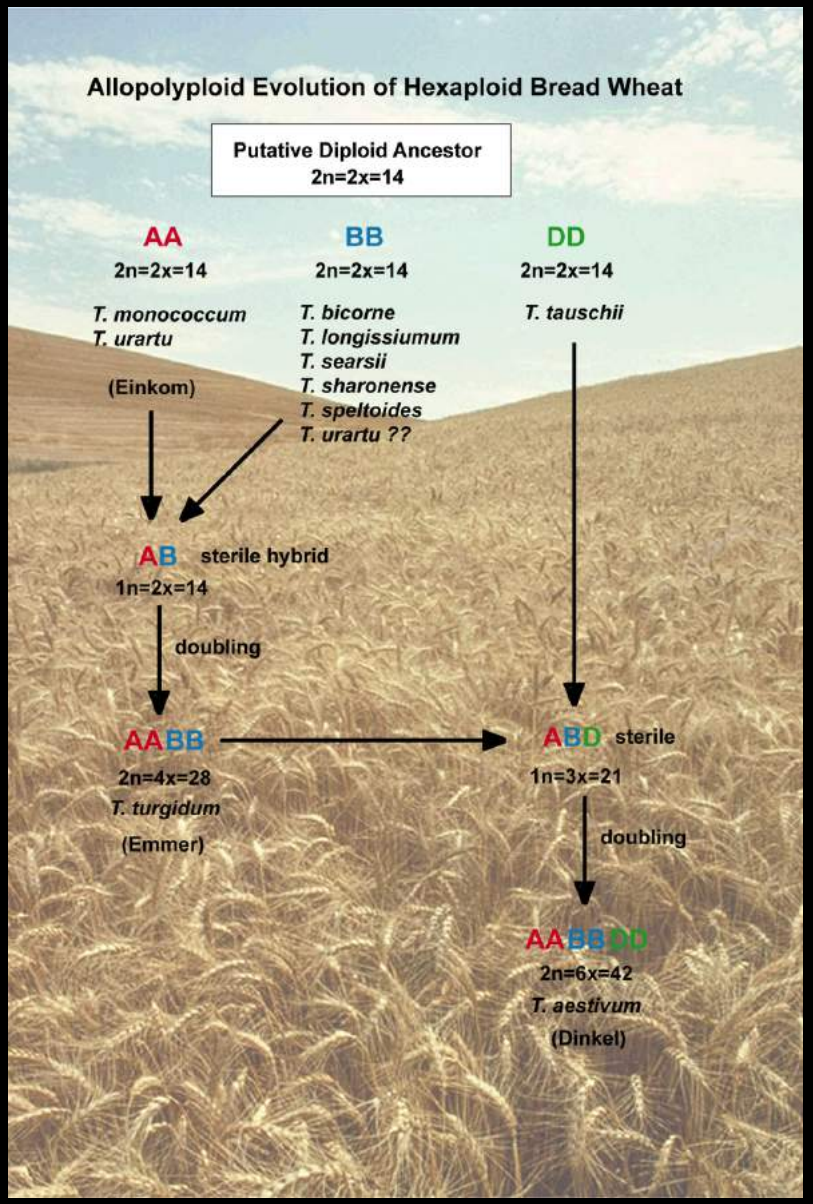
Two successive rounds of hybridization followed by polyploidization have given bread wheat the genomes of three diploid species — it is a hexaploid (6 sets of chromosomes, or 2 from each diploid parental species).



a About 11,000 years ago, humans start cultivating wild wheats. The species *Triticum monococcum* has diploid number 14 (two sets of 7 chromosomes, shown as 14 *AA*). It hybridizes with another species that has the same chromosome number.

b *AB* hybrid offspring are sterile but self-fertilizing; an interbreeding population of *AB* plants arises by asexual reproduction. About 8,000 years ago, by unknown events, polyploidy arises in the population. Some plants (*T. turgidum*) are tetraploid (*AABB*), with a chromosome number of 28 (two sets of 14). They are fertile. (*A* chromosomes can pair with each other, and so can *B* chromosomes, during meiosis.)

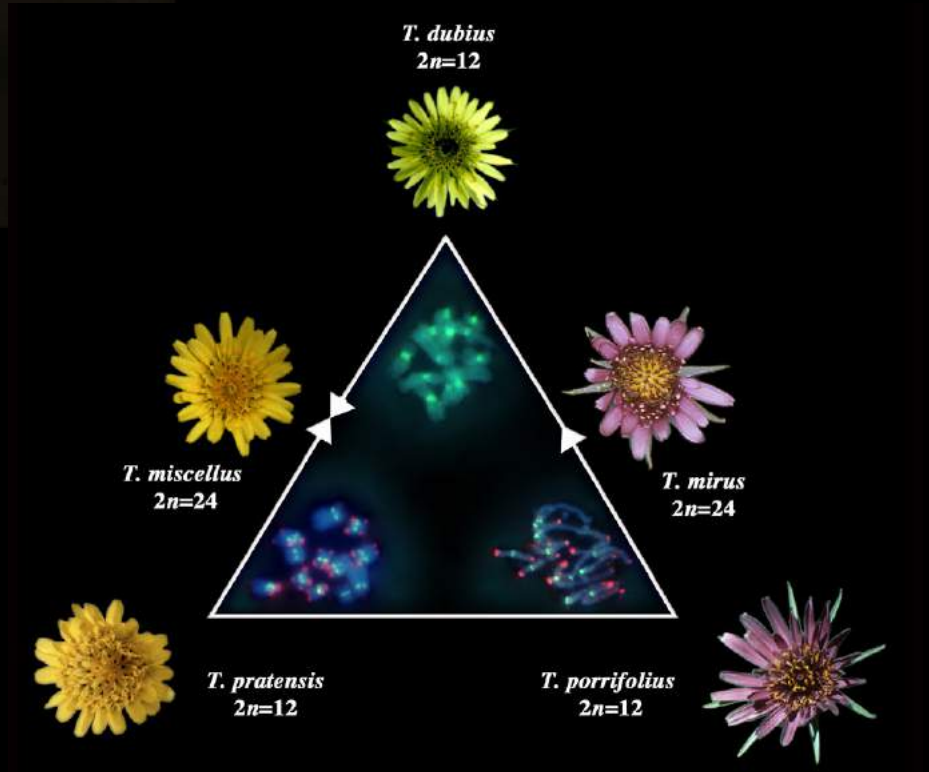
c Later, an *AABB* plant hybridizes with *T. tauschii*, a wild relative with a diploid number of 14 (two sets of 7 *DD*). Today, populations of the hybrid descendants (*T. aestivum*) provide wheat for bread. Their chromosome number is 42 (six sets of 7 *AABBDD*).



Polyploid Speciation

Even more recent speciation has occurred in the goat's-beards in North America.

Tragopogon - goat's beard

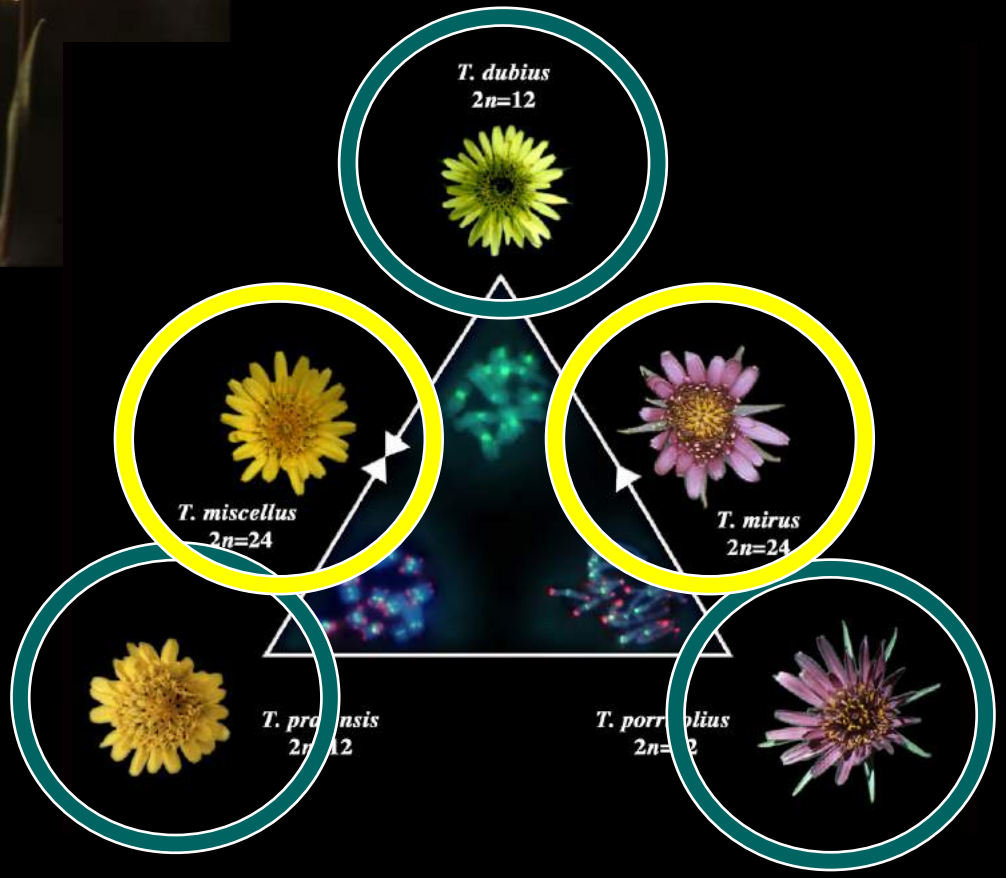


Pam & Doug Soltis

Polyploid Speciation

Even more recent speciation has occurred in the goat's-beards in North America.

Tragopogon - goat' s beard



- Three diploid (2n=12) species were introduced into North America about 200 years ago

- By early 1900s, these species had hybridized with each other and then formed two different allopolyploid (tetraploid) species

- These two new allopolyploid species have evolved numerous times (!) in areas where the diploid species overlap in geographical range in North America

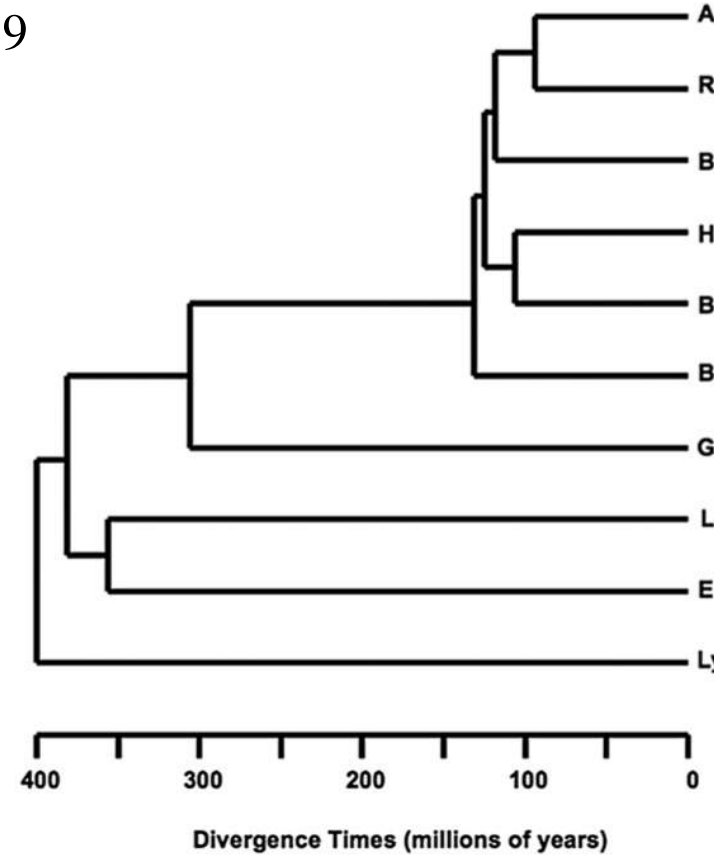
Polyploid Speciation

Loren Rieseberg

The frequency of polyploid speciation in vascular plants

Troy E. Wood[a,b,1], Naoki Takebayashi[c], Michael S. Barker[b,d], Itay Mayrose[e], Philip B. Greenspoon[d], and Loren H. Rieseberg[b,d]

2009



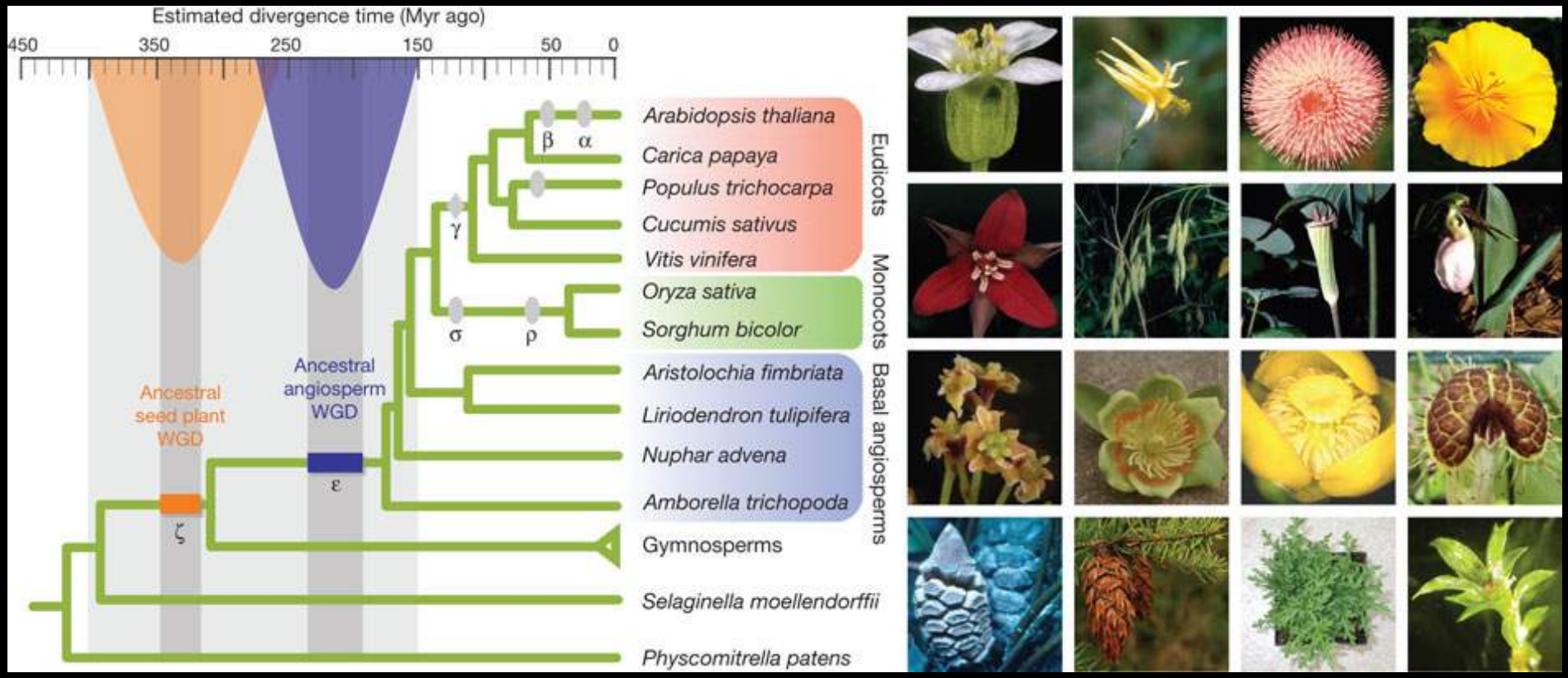
	No. Species	Infrageneric Polyploid Incidence	Polyploid Speciation Frequency
Asterids	106,150	35.05 ± 1%	12.45 ± 1%
Rosids	58,700	31.91 ± 2%	20.63 ± 2%
Basal Eudicots	24,950	37.24 ± 2%	14.11 ± 2%
Higher Monocots	28,150	46.58 ± 2%	21.43 ± 5%
Basal Monocots	33,180	29.94 ± 2%	25.74 ± 4%
Basal Angiosperms	9,250	37.57 ± 6%	1.64 ± 2%
Gymnosperms	830	4.04 ± 3%	– – –
Leptospor. Ferns	11,000	32.86 ± 2%	34.01 ± 4%
Eusporangiate Ferns	380	24.00 ± 7%	19.36 ± 7%
Lycophytes	1,200	33.61 ± 10%	30.77 ± 9%

15.00%

31.37%

Polyploid Speciation

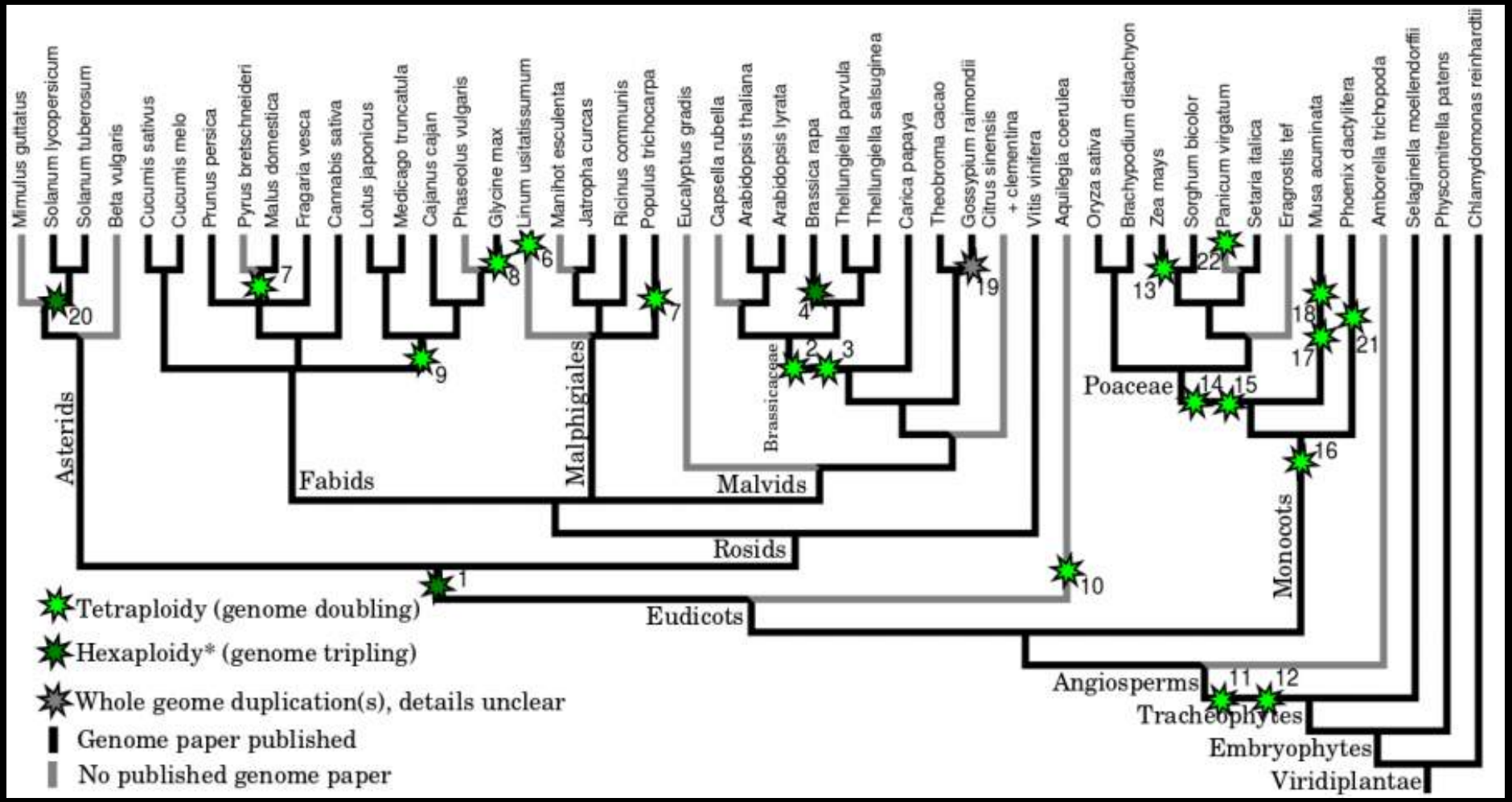
Ancestral polyploidy events in seed plants and angiosperms.



Y. N. Jiao *et al*. *Nature* (2011)

Polyploid Speciation

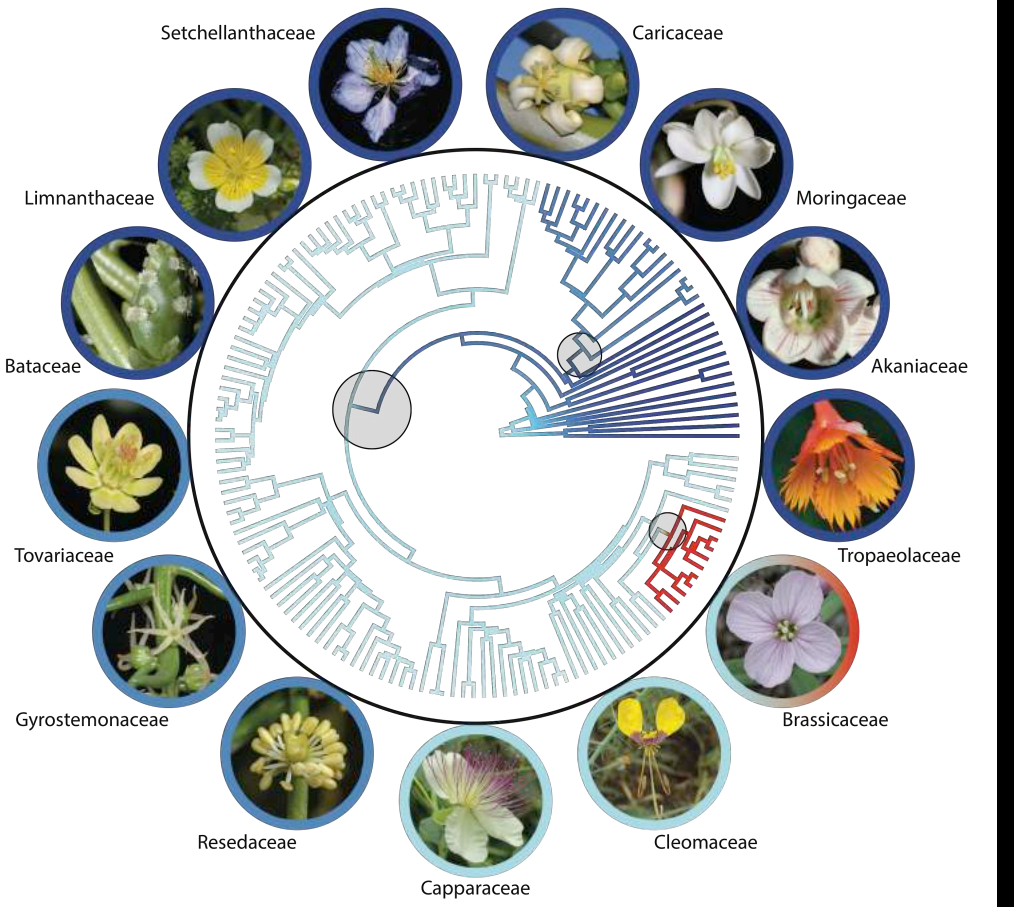
Ancestral polyploidy events in seed plants and angiosperms.

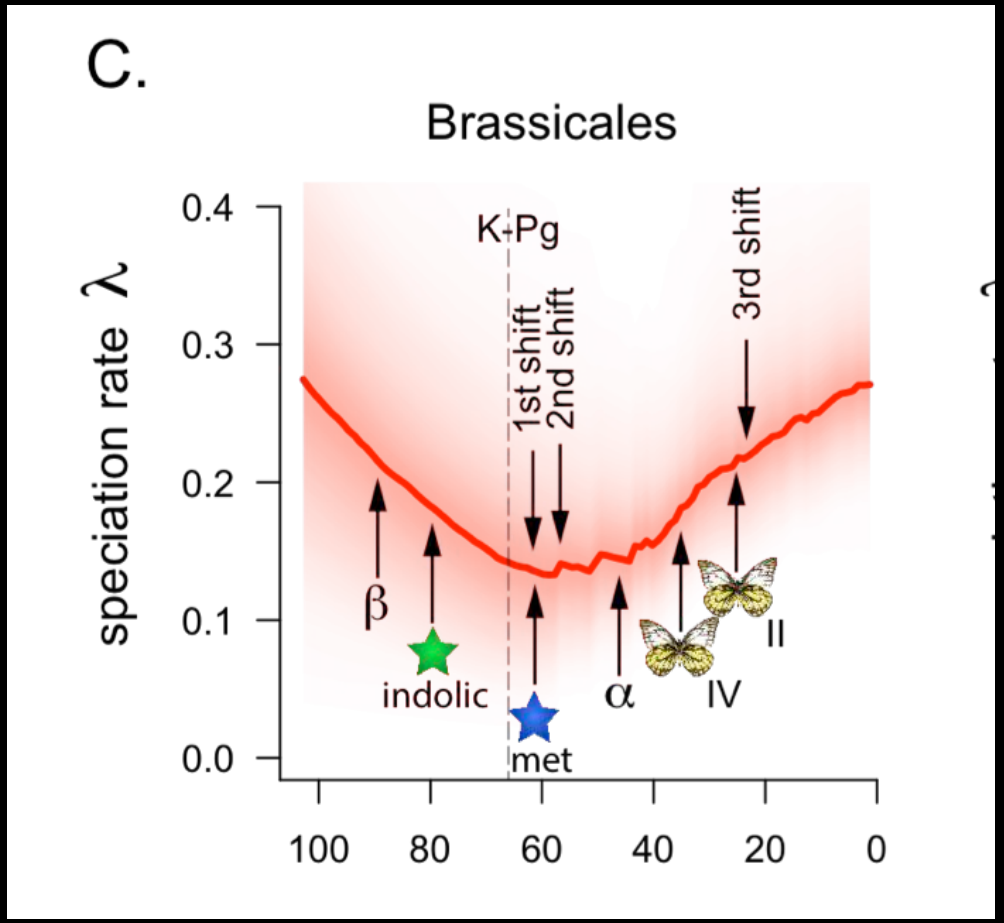


www.genomevolution.org

Polyploid Speciation

Ancestral polyploidy events in seed plants and angiosperms.





Cardinal-McTeague, W. M., K. J. Sytsma, J. C. Hall. 2016. Biogeography and diversification of Brassicales: a 103 million year chronicle. Molecular Phylogenetics and Evolution 99: 204-224