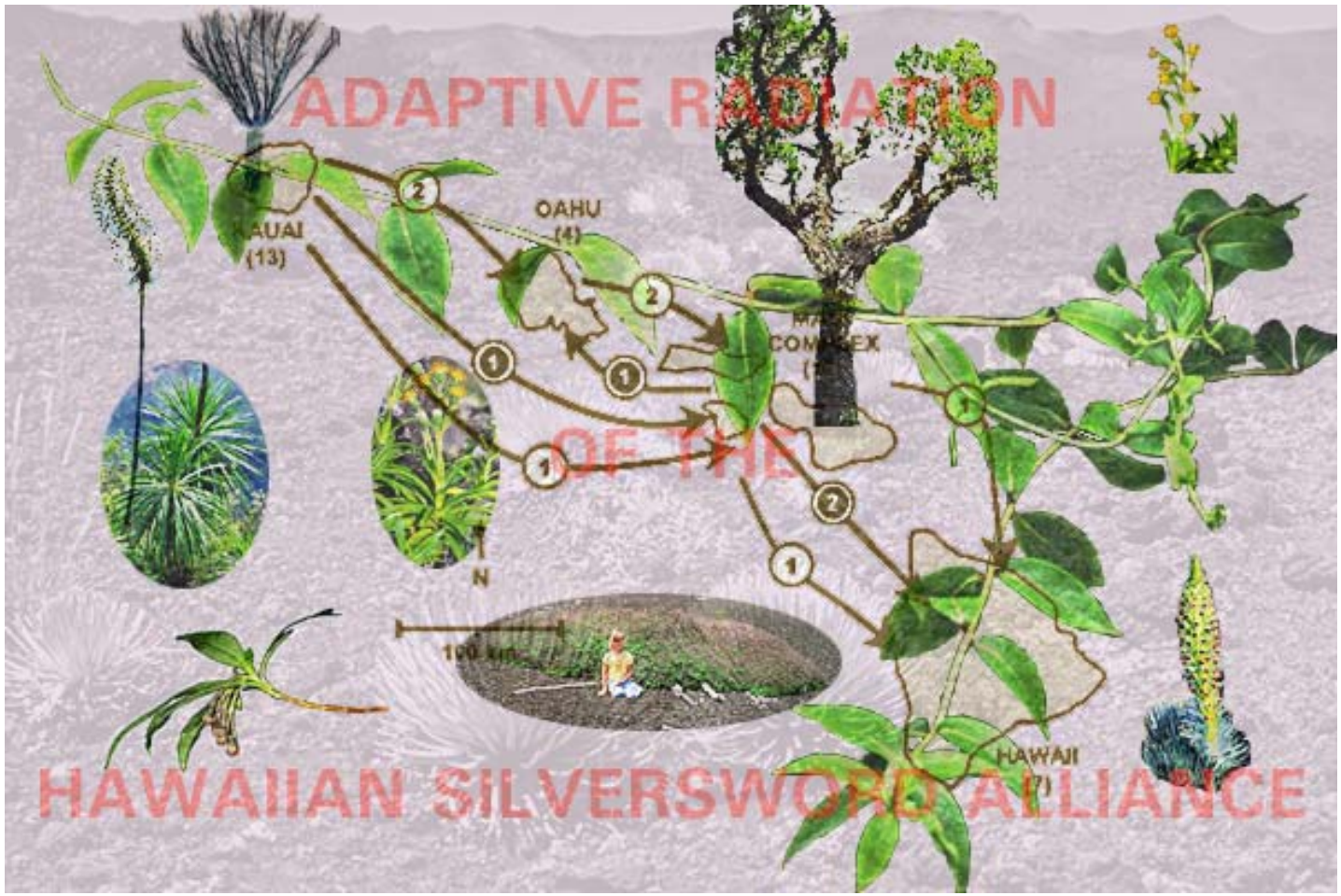
# Adaptive Radiation and Macroevolution in the Hawaiian Silverswords

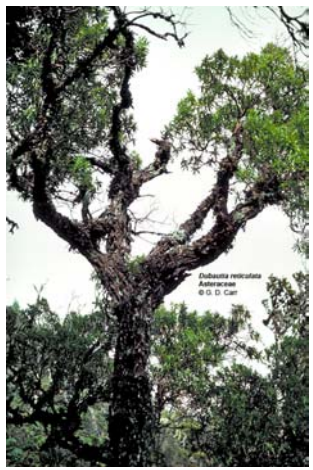
http://www.botany.hawaii.edu/faculty/carr/silversword.htm



# The Hawaiian Silverswords exhibit enormous phenotypic variation (from herbs to trees to vines)..,

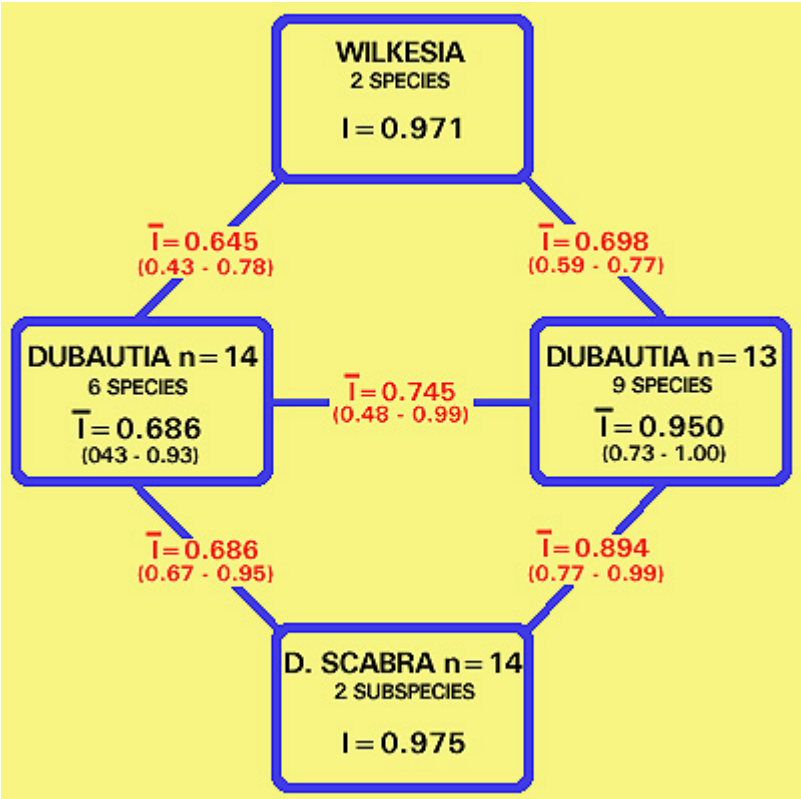
(photos from http://www.botany.hawaii.edu/faculty/carr/silversword.htm)





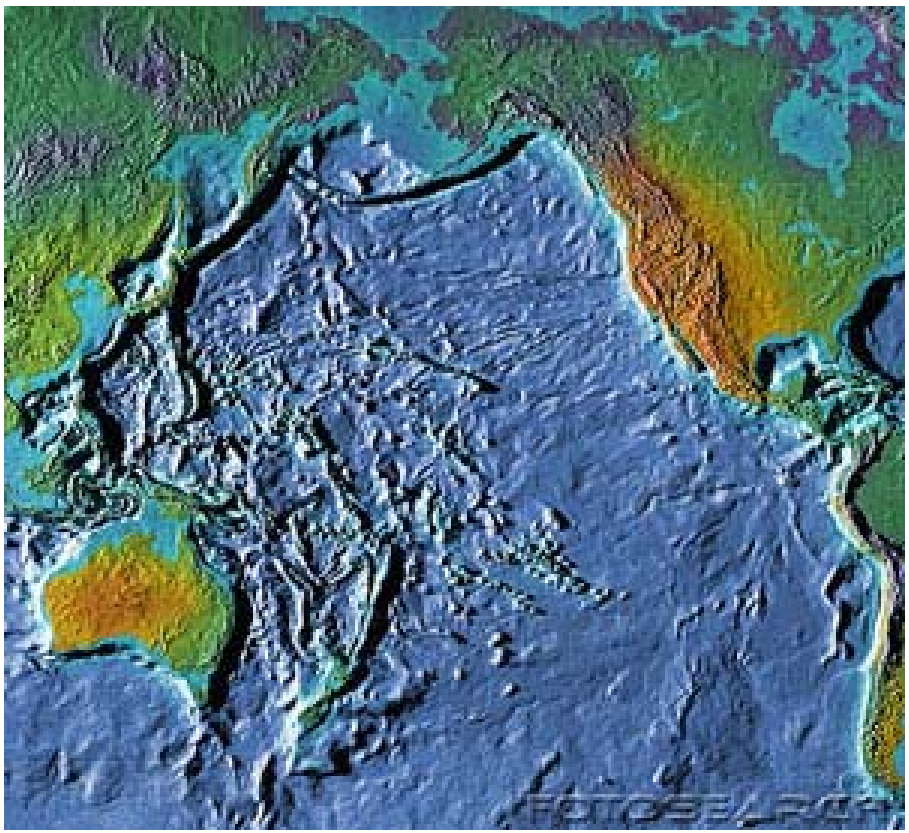

# …yet they have high genetic identity

(http://www.botany.hawaii.edu/faculty/carr/silversword.htm)



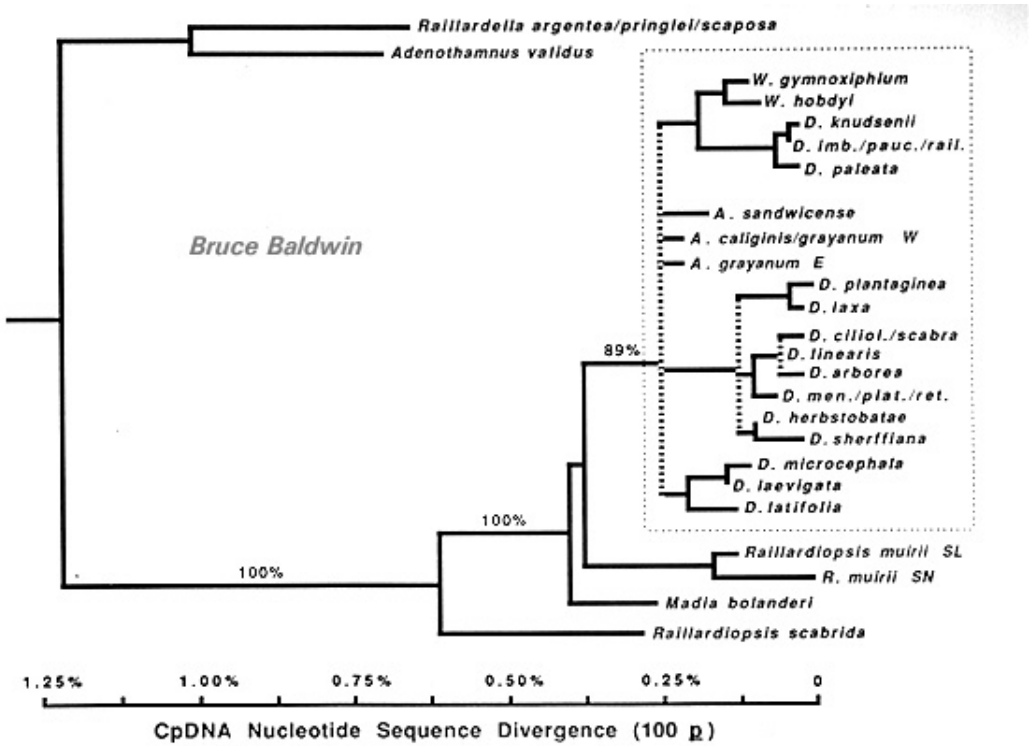

- Despite tremendous morphological and ecological variation among species of the Hawaiian silversword alliance, genetic identities of species pairs based on electrophoretic studies are often very high (I=0.95-1.00), comparable to genetic distances between populations of a single species in continental plants.

# Where Did The Silverswords Come From?



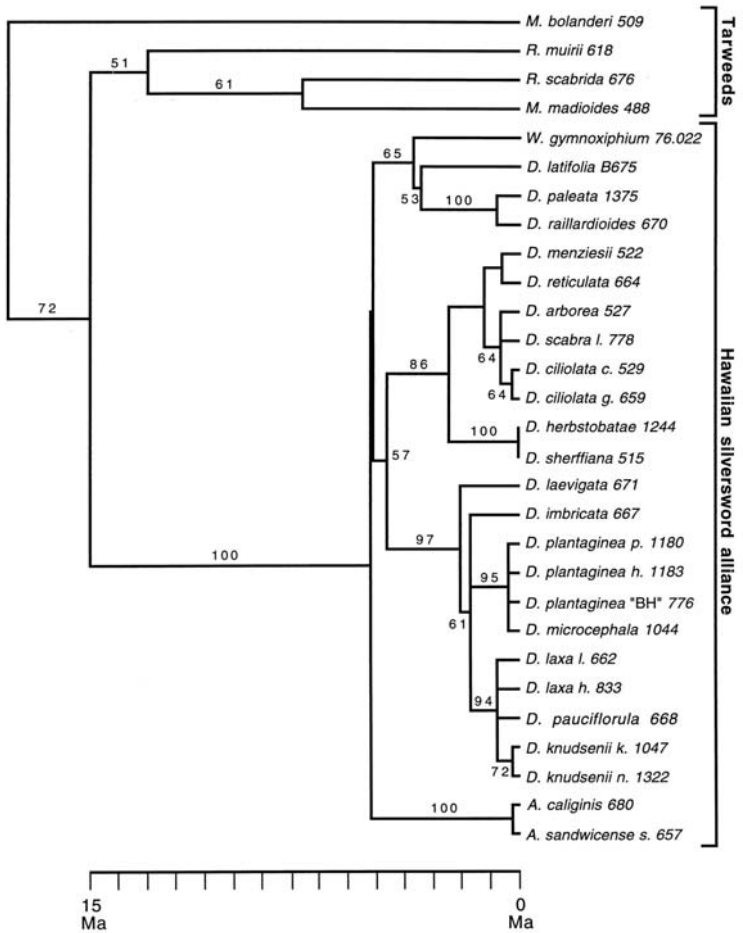
- The Hawaiian Islands are much younger than the continents that form the Pacific Rim
- Construct a phylogeny that includes the Silverswords and all their relatives, and determine which lineages are their nearest relatives

# Silversword Phylogeny 1



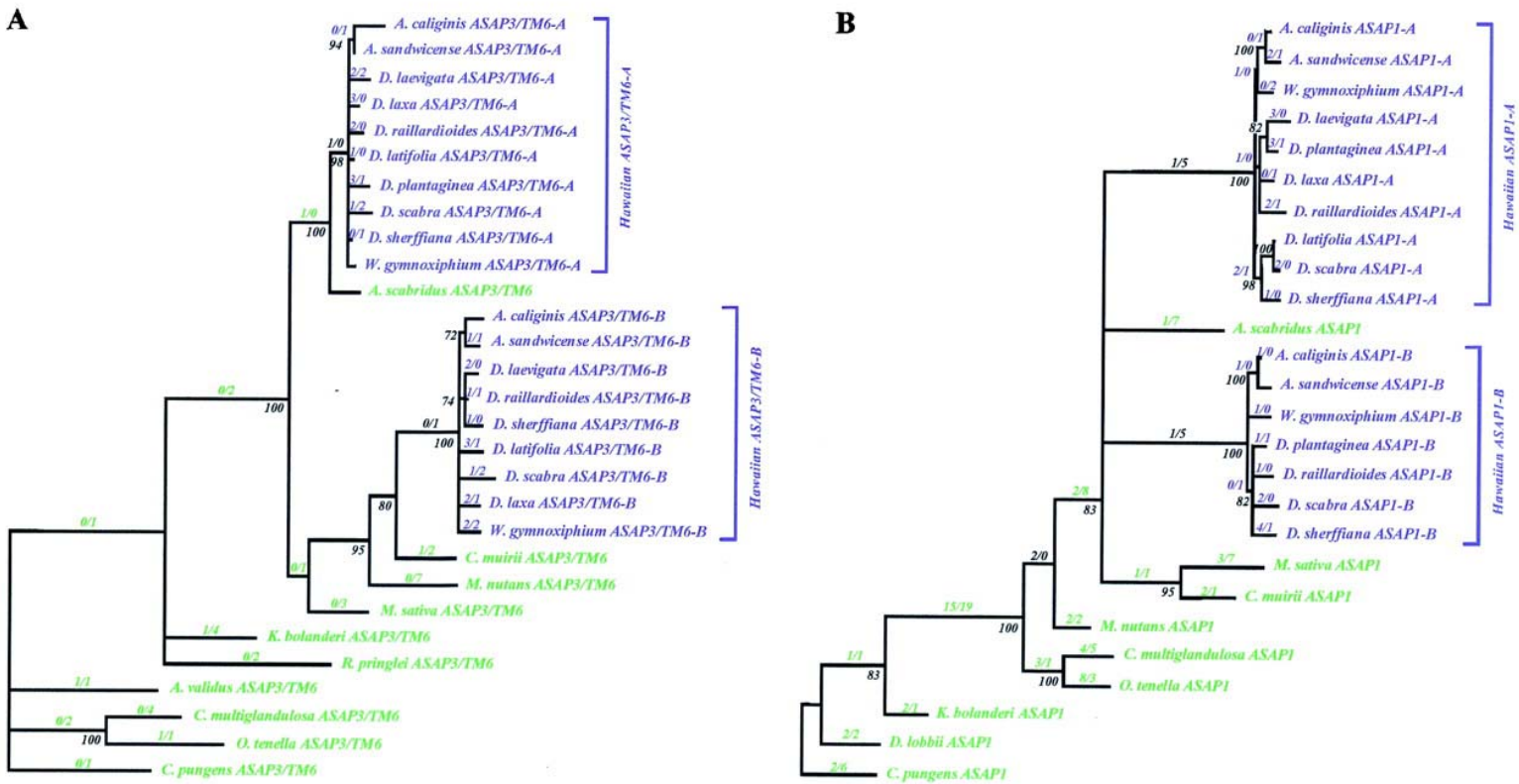

- A phylogeny based on Choroplast DNA suggests that the North American Tarweeds are the nearest relatives to the Hawaiian Silverswords (Baldwin et al 1991)

# Silversword Phylogeny 2




- A phylogeny based on Nuclear Ribosomal DNA also points to the North American Tarweeds as the nearest relatives to the Hawaiian Silverswords
- Using an assumption of a molecular clock, the Silversword radiation is dated to have begun about 5.2 $\pm$ 0.8 million years ago. Kauai, the oldest island, has been geologically dated to 5.1 $\pm$ 0.2 million years old. (Baldwin & Sanderson 1998)

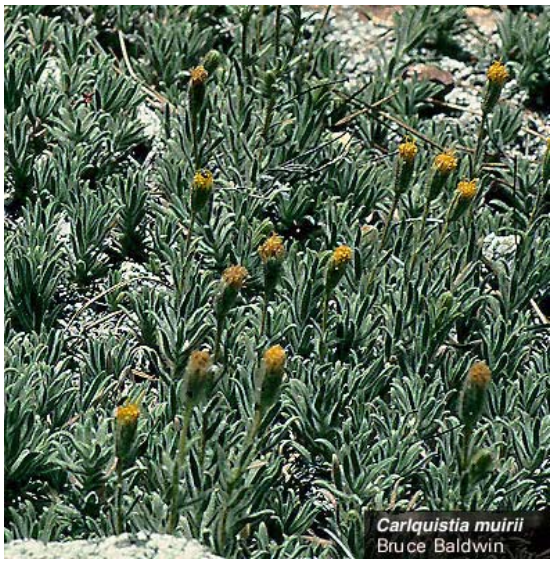
# Silversword Phylogenies 3 & 4



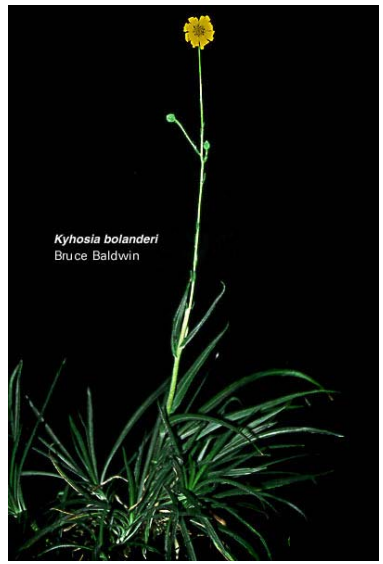

- Two regulatory gene trees based on *ASAP3/TM6* and on *ASAP1* also point to the Tarweeds as the nearest Relatives to the Silverswords (Barrier et al 2001)

# North American Tarweeds

(http://www.botany.hawaii.edu/faculty/carr/silversword.htm)








- These are all small herbaceous plants that lack the phenotypic diversity of the Hawaiian Silverswords

# How did Tarweed like ancestors give rise to Silversword diversity?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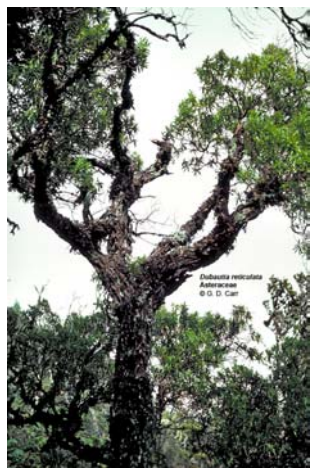
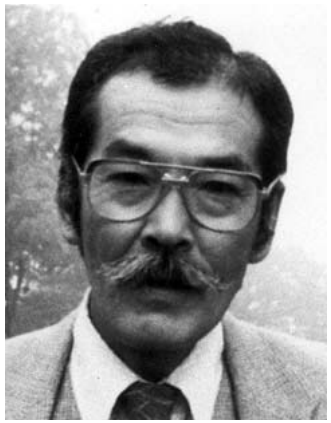
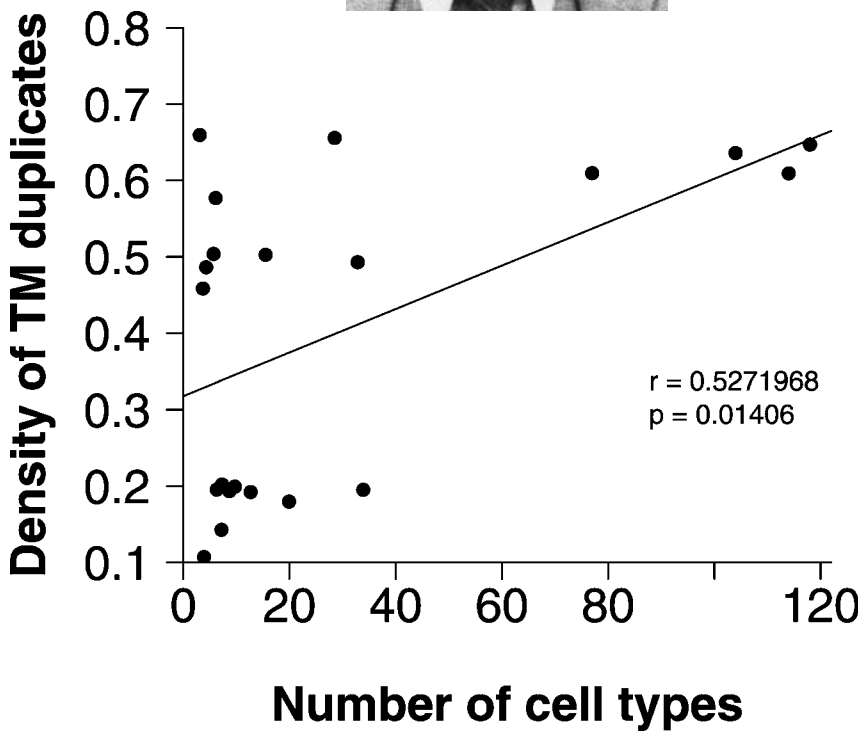


# Gene Duplication And Macroevolution

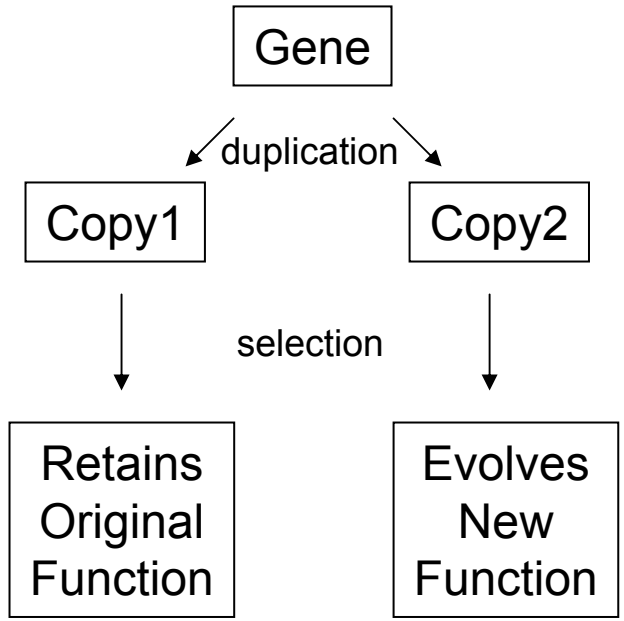





- Susumu Ohno (1970) noticed that episodes of major evolutionary change (e.g. new structures, adaptive radiations) are often preceded by episodes of gene or genome duplication, and hypothesized a connection between the two.
- Ding et al (2006) reported a significant correlation between Number of Cell Types (a measure of complexity or past macroevolution) and gene duplication events, inferred from the fossil record.

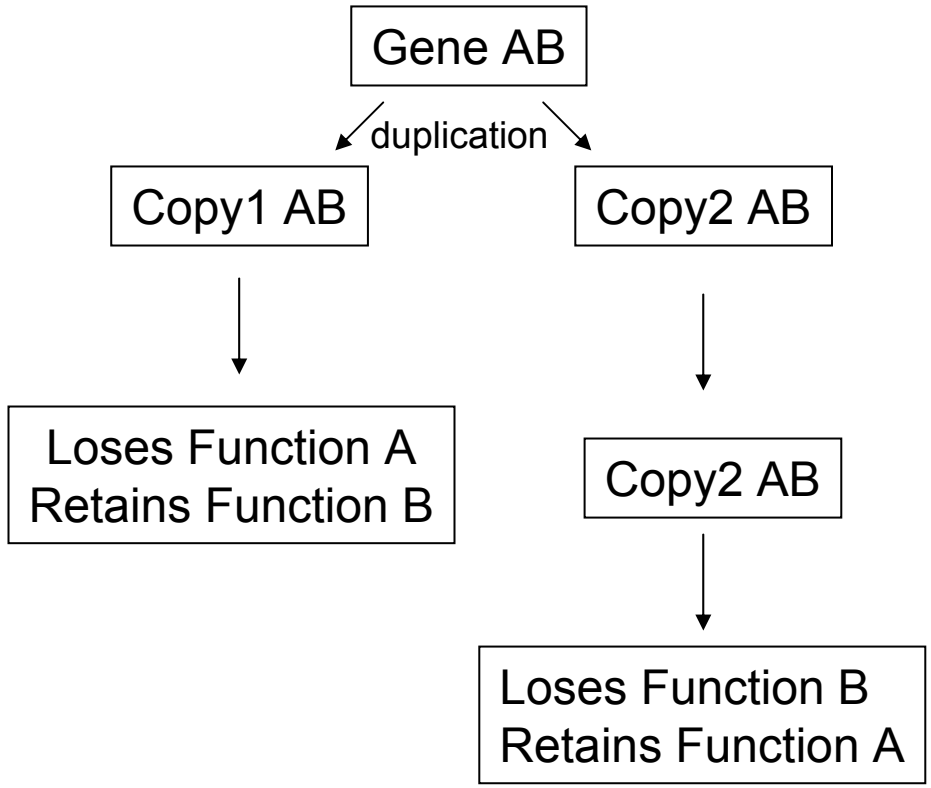
# Gene Duplication Theory

- **Neofunctionalization:**
  - One copy of a duplicate gene is under selection to retain its original function, and the other copy is free to evolve a new function
  - If this process occurs in regulatory genes, then this could lead to the evolution of new developmental pathways and new bauplans

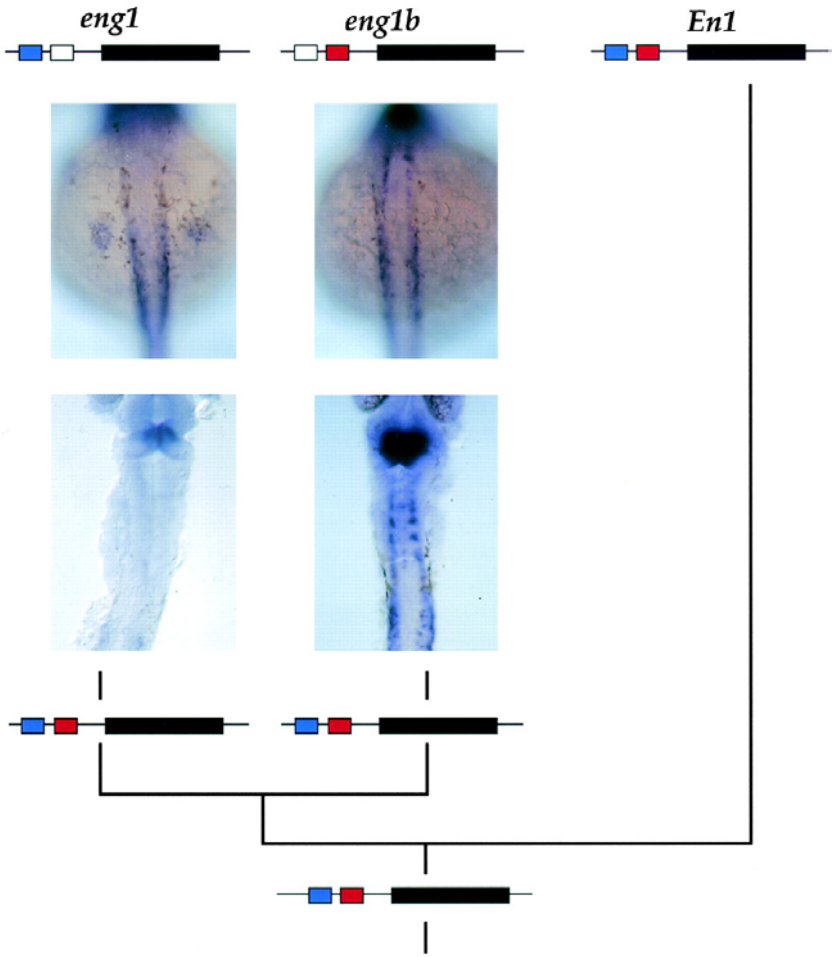


# Gene Duplication Theory

- **Subfunctionalization:**
  - Regulatory genes often have multiple functions (pleiotropy). A variation on the gene duplication hypothesis is that duplicate copies may each evolve to partition the functions of the original gene into discrete subfunctions, and thus allow subsequent independent evolution among subfunctions.
  - May be a bridge to neofunctionalization.

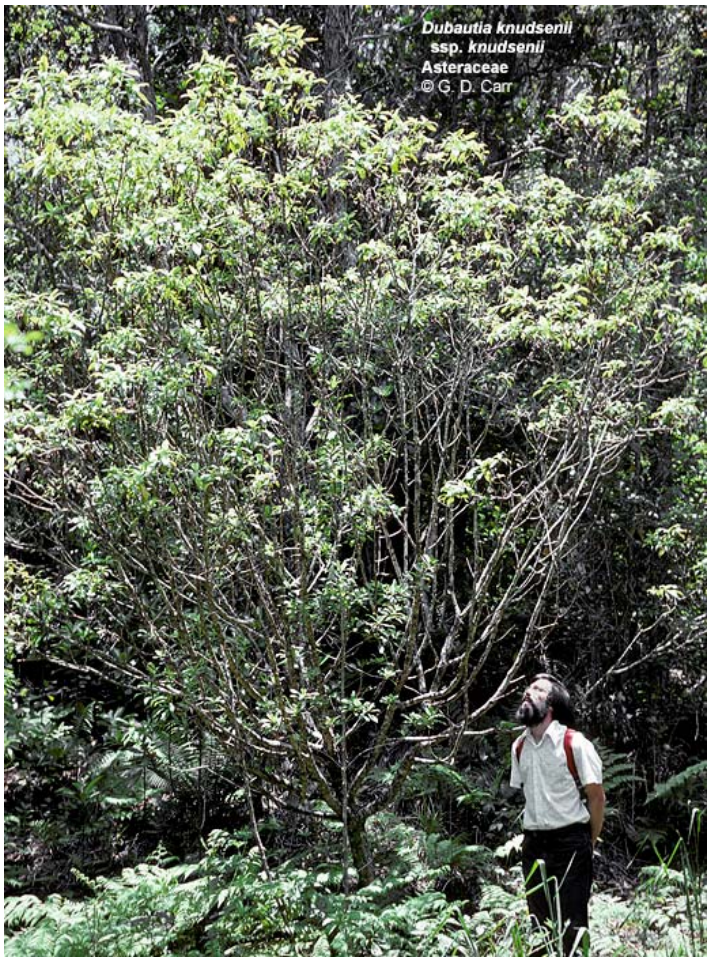


# Subfunctionalization of an engrailed gene in zebrafish




- In mouse, En1 expresses in both pectoral limb buds *and* the hindbrain.
- In zebrafish, eng1 expresses in pectoral limb buds, and eng1b expresses in the hindbrain (Force et al 1999).

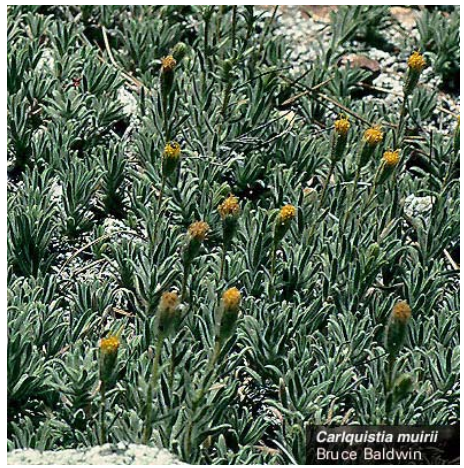
# Evidence for Genome Duplication in the Silverswords

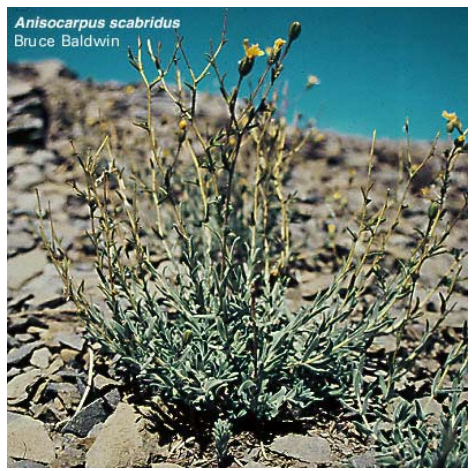



- **Twice the Chromosomes:**
  http://www.botany.hawaii.edu/faculty/carr/silversword.htm
  - Silverswords have roughly twice the chromosome number as Tarweeds, which suggests they're tetraploids
- **Duplicate Genes:**
  (Barrier et al 1999, 2001)
  - Two regulatory genes, *ASAP3/TM*6 and *ASAP1*, and one structural gene, *ASCAB9*, exist as single copies in the Tarweeds, but as duplicate copies in the Silverswords.

# Evidence for Allotetraploid Hybrid Origin for the Silverswords

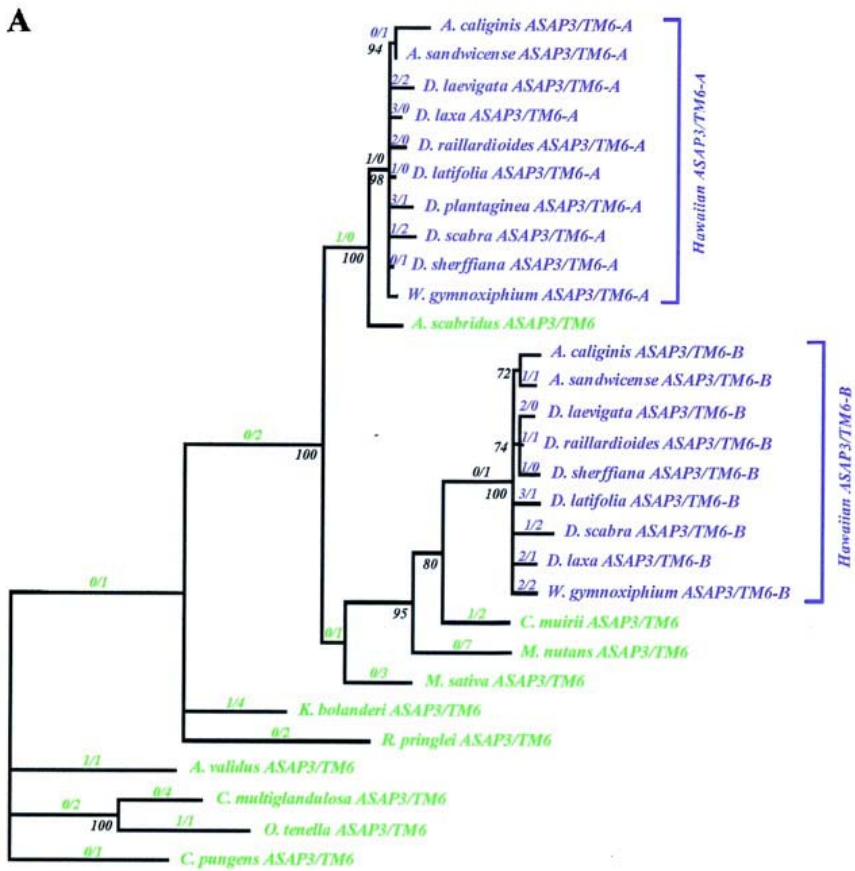
- Preceding evidence for genome duplication
- Two particular tarweeds, *R. muirii* and *R. scabrida*, consistently appear in phylogenies as the nearest relatives to the Silverswords



# Evidence for Allotetraploid Hybrid Origin for the Silverswords

(Barrier et al 1999, 2001)




- One Silversword copy of regulatory gene, *ASAP3/TM6-A*, shows *R.scabrida* to be the nearest Tarweed relative to the Silverswords.
- The other copy, *ASAP3/TM6-B,* shows *R.muirii* to be the nearest Tarweed relative to the Silverswords

# The Silverswords Evolved More Rapidly Than The Tarweeds

(Barrier et al 2001)

| | Regulatory Genes | | | | Structural Gene | |
|---|---|---|---|---|---|---|
| | *ASAP3/TM6* | | *ASAP1* | | *ASCAB9* | |
| Point Mutations | Hawaiian Silverswords | North American Tarweeds | Hawaiian Silverswords | North American Tarweeds | Hawaiian Silverswords | North American Tarweeds |
| Nonsynonymous | 25 | 5 | 28 | 50 | 7 | 3 |
| Synonymous | 15 | 31 | 11 | 64 | 9 | 31 |

- Hawaiian Silverswords vs North American Tarweeds
  - All 3 genes accumulated relatively more nonsynonymous point mutations in the Silverswords than in the Tarweeds
- Regulatory vs Structural Genes
  - Within the Silverswords, the Regulatory Genes accumulated relatively more nonsynonymous point mutations than the Structural Gene

# What do we know about the developmental genetics of *ASAP3/TM6* and *ASAP1*?

- Lawton-Rauch et al 2003, compared partial sequences for both genes for several individuals from 2 silversword species from 2 genera and 2 islands
  - *Argyroxiphium sandwicense* ssp. *macrocephalum* (above), from Maui
  - *Dubautia ciliolata* ssp. *glutinosa* (below) from Hawaii


# What do we know about the developmental genetics of *ASAP3/TM6* and *ASAP1*?

- Both genes showed interspecific differences in haplotype
- *Dubautia ciliolata* showed intraspecific differences between the two copies of *ASAP3/TM6*


The data are consistent with the hypothesis of genome duplication, eventual neofunctionalization, and rapid regulatory gene evolution.