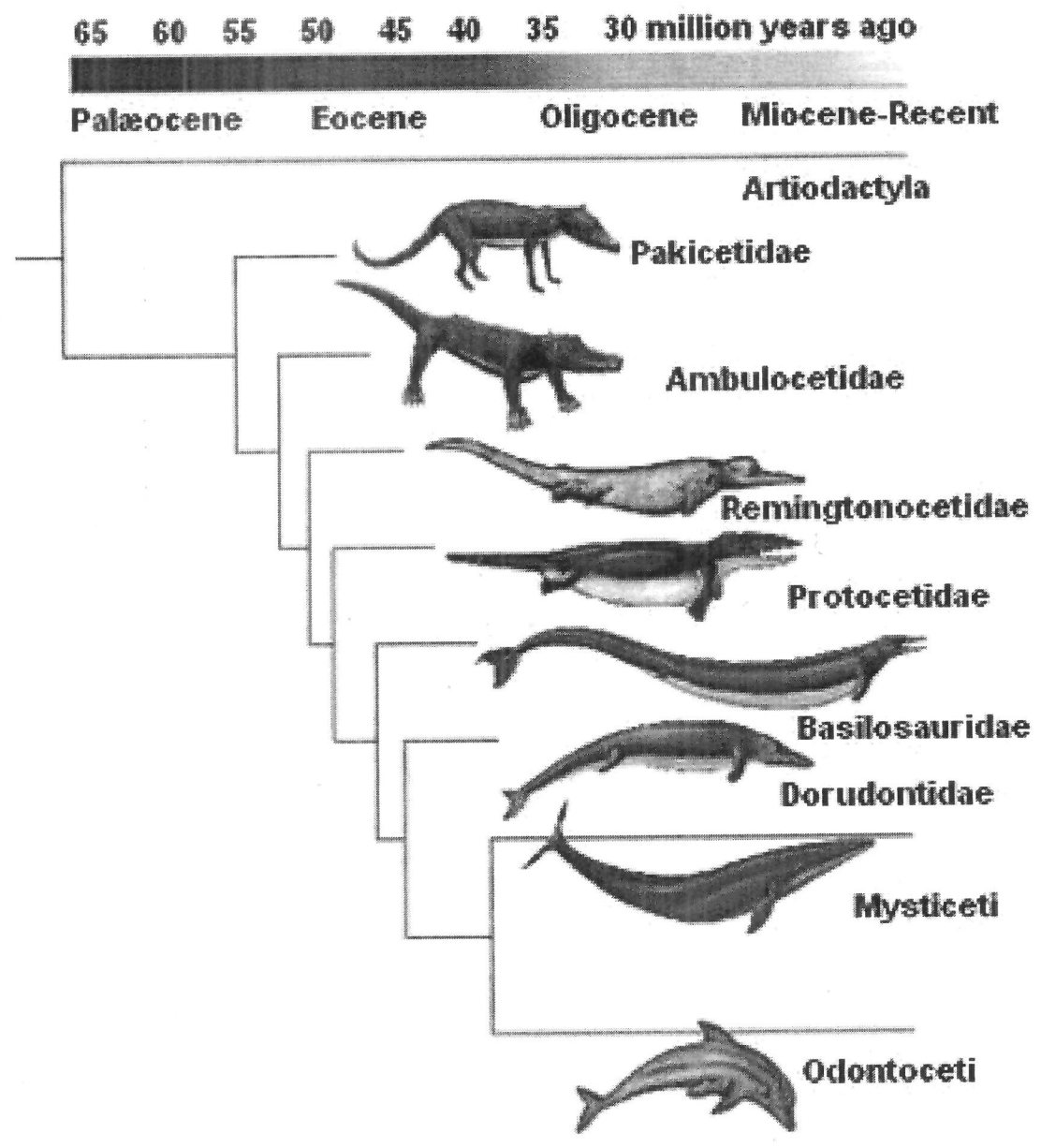# SPECIATION

I. ALLOPATRY x SYMPATRY

The dynamical models we have discussed so far occur at the so-called "ecological" time scale, A sufficiently short time interval where evolutionary changes can be ignored. Now I want to consider systems where the intrinsic characteristics of a species (like its growth rate) can change because it got better adapted to its environment.

During the DNA replication mutations can occur as a result of ocasional errors, or due to exposure to radiation, lithium and other chemicals. If this mutations occur on a sex cell they can be transmitted to offspring. Although most mutations are bad, some of them turn out to be useful for the individual at that time, making them "fitter" than others without the mutation, i.e., helping them have more offspring and pass the mutation on.

The mechanism that makes "good" mutations be incorporated in the population and "bad" mutations be discarded is called NATURAL SELECTION, a term coined by Charles Darwin.

Small adaptions can lead to big changes over the years, as illustrated by the evolution of whales:

In several occasions there is more than just big changes: there are bifurcations, or speciation, and new species are formed:

14   7.3 54 2.5   today   (million years)
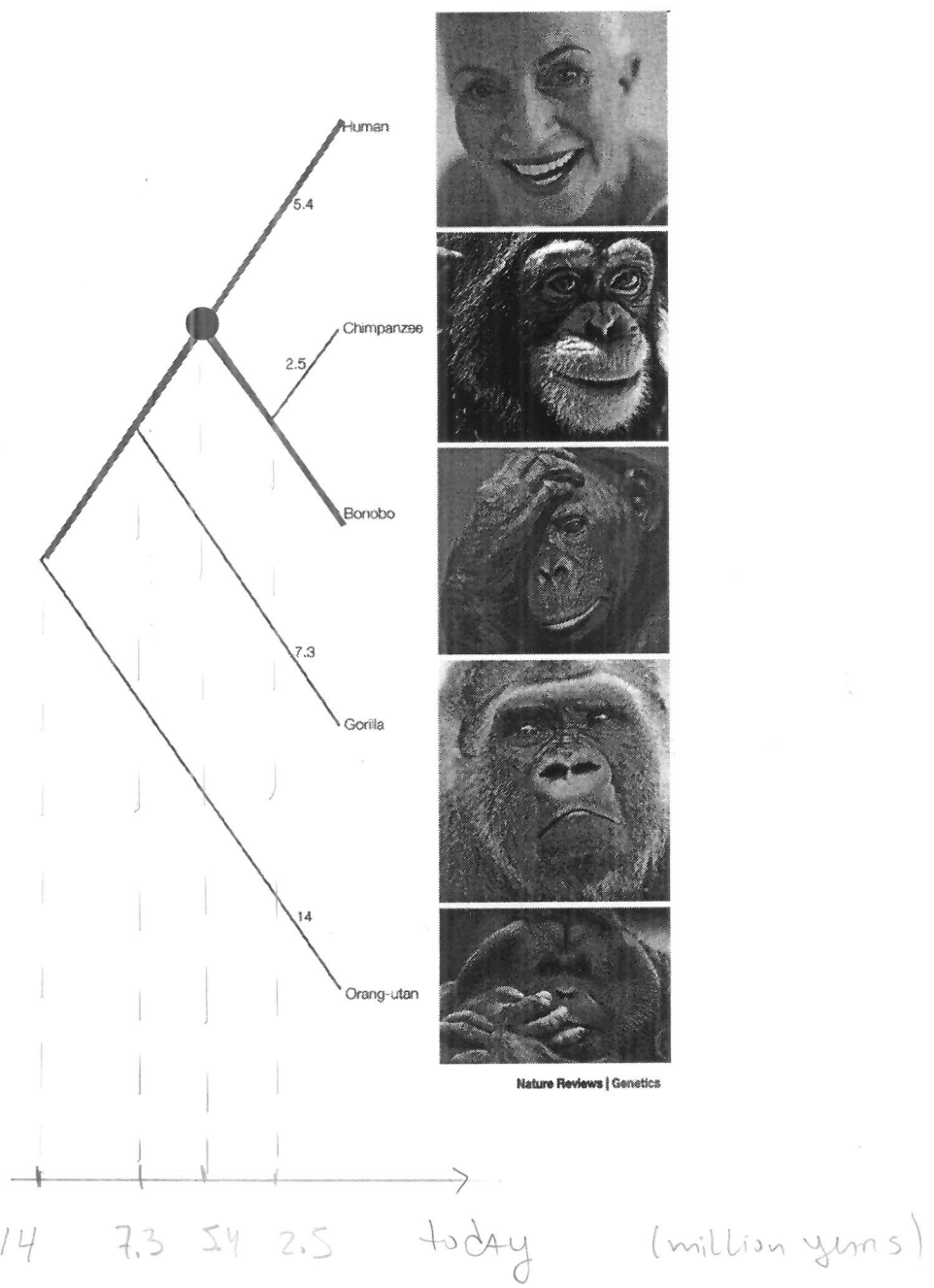
However, if good mutations tend to spread through the population, why is it that some mutations get fixated only in one part of the population and other mutations are fixated in the other part, so that they become different? Won't sexual reproduction pass the mutations around and homogenize the population? In these two lectures I will discuss 3 ways in which this can happen, but there are more.

SPECIES — For our purposes species will be defined using the concept of reproductive isolation. A species is a group of individuals that can mate among themselves but not with individuals of other such groups. In an abstract "genetic space" species are islands separated from each other by gaps that are large enough to prevent inter-islands reproduction. We don't require that every male in a species can mate with every female. There might be some incompatibilities inside a species, as long as each individual can mate with a few others in the species.

ALLOPATRIC SPECIATION

A series of empirical observations pointed to the fact that "sister species" — species that are close relatives — were often separated by each other by geographical barriers. Examples:

(A) each side of the Isthmus of Panama has 7 species of shrimp. Each species has its closest relative on the other side

(B) Drosophila's species in Hawaii islands

(C) Darwin's finches in the Galapagos islands

There is also a famous experiment by Dian Dodd where drosophilas were exposed to starch or maltose. After many generations each group adapted to its environment and, when the population were re-mixed together they would only mate with others of the same group.

Is geographic isolation the only way to reach reproductive isolation? Many scientists think so, although less stringent barriers have been considered. The term <u>parapatric speciation</u> was coined to describe situations where partial barrier decrease to contact between subpopulations without completely blocking gene flow.

There are basically two classes of parapatric models

- <u>stepping stone speciation</u>

← sub-populations

local reproduction within each subpopulation
+
exchange of migrants
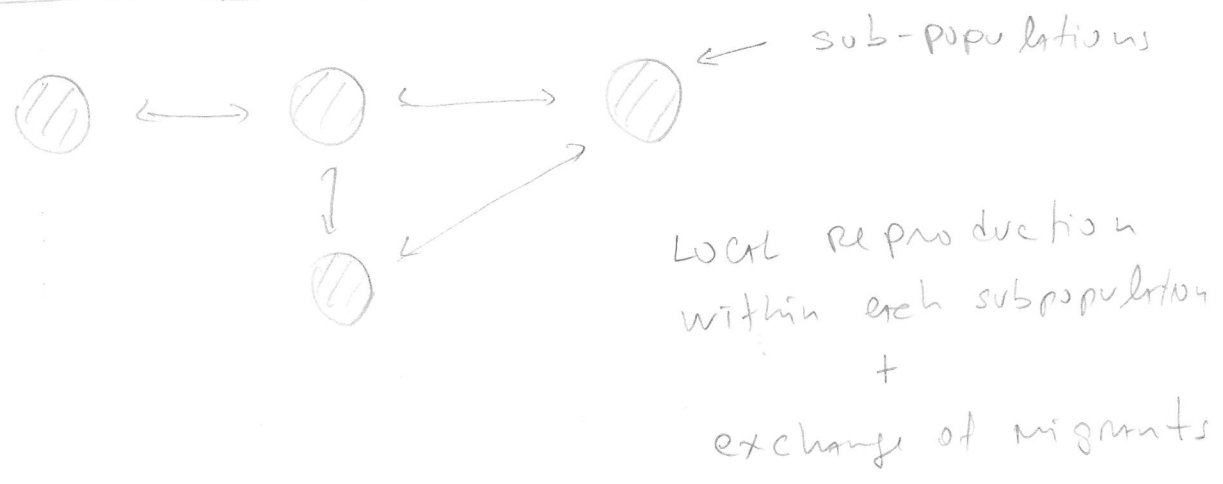
If migration is sufficiently low speciation can still happen.

- <u>CLINAL SPECIATION</u>

continuous habitat with an environmental gradient leading to local adaptations.

The local adaptations might lead to discrete clusters instead of a continuum of phenotypes.

The other extreme of allopatric speciation then is sympatric speciation, where mating is not restricted at all by geographic barriers but might respond to ecological competition.

SYMPATRIC SPECIATION

Here I will use the model by Dieckmann & Doebeli (Nature 400 (1999) 354) to discuss how competition can lead to the break up of population into two reproductively isolated groups in the same spatial location.

Suppose a population of birds lives on area where seeds of several sizes are available. The amount of seeds of size s, $p(s)$, is distributed in such a way that there are lots of "average" size seeds and less big or small seeds. We can think of a normal distribution.

The birds, on the other hand, are characterized by a quantitative trait x which measures beak size. We assume that birds with trait x follow a logistic growth equation with site capacity $K(x)$ whose shape follows the distribution of resources
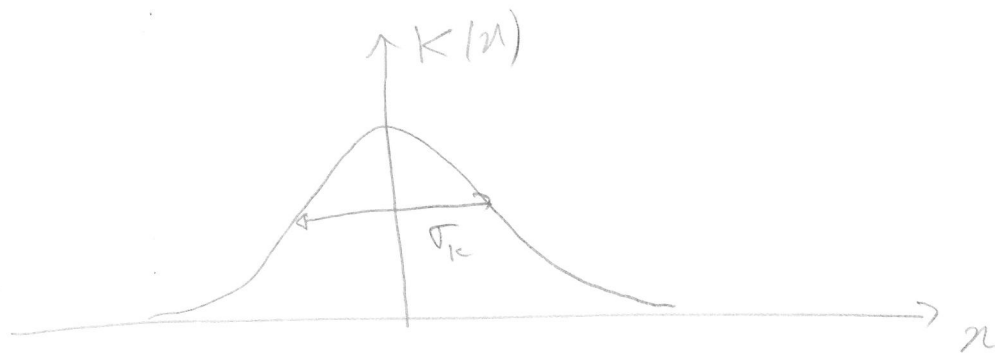
$$K(x) = K_0 \, e^{-x^2/2\sigma_k^2}$$

so that $x=0$ corresponds to beak size adapted to the most abundant seeds.

Birds with similar beaks compete for resources. The strength of competition is

modeled by

$$C(x,y) = e^{-(x-y)^2/2\sigma_c^2}$$

so that the more similar the traits, the more intense the competition.

Assume that initially a small population with trait x colonizes the area. The population growth can be modeled with a logistic equation

$$\frac{dN(x,t)}{dt} = r N(x,t)\left[1 - \frac{N(x,t)}{K(x)}\right]$$

After a time of the order of $1/r$ the population reaches its capacity and

$$N(x,t) \longrightarrow K(x)$$

(see eq. III.(2)).

The question we want to answer is: what happens if a mutant with phenotype

$$y = x + \delta x$$

Appears? Will it "invade" and take over the area? The answer seem pretty obvious: if $K(y) > K(x)$ the mutants should do well, since they can eat more seeds than the residents. We will see that there is more to it than just that.

The equation for the mutants can be written as follows:

$$\frac{dN(y,t)}{dt} = r N(y,t) \left[1 - \frac{c(x,y) K(x)}{K(y)} \right]$$

since y sees an "effective population" $c(x,y) K(x)$ competing for the same resources.

Because $c(x,y)$ is flat at $y = x$,

$$c(x,y) = e^{-\delta x^2 / 2\sigma_c^2} \approx 1 - \frac{\delta x^2}{2\sigma_c^2},$$

· to first order in δx

$$\frac{dN(y,t)}{dt} = r N(y,t)\left[1 - \frac{K(x)}{K(y)}\right] \equiv R N(y,t)$$

· As expected, if $K(y) > K(x)$ the effective growth rate

$$R = r\left(1 - \frac{K(x)}{K(y)}\right) > 0$$

and the y's thrive. If $K(y) < K(x)$,

$R < 0$ and the mutants die.

Therefore, if mutation is allowed the population shifts towards the optimal fenotype, $x = 0$.

DISRUPTIVE SELECTION

Since the population shifts towards $x=0$ independent of its founder phenotypes, let us consider what happens to a mutant that appears when the residents have $x=0$.

In this case the ratio

$$\frac{K(x)}{K(y)} = \frac{K(0)}{K(\delta x)} = e^{\delta x^2 / 2\sigma_k^2} \approx 1 + \frac{\delta x^2}{2\sigma_k^2}$$

Also differs from 1 by $O(\delta x^2)$ and we cannot discard competition. The full R is

$$R = r\left[1 - \frac{K(x) \, C(x,y)}{K(y)}\right]\Bigg|_{\substack{x=0 \\ y=\delta x}}$$

$$= r\left[1 - e^{\delta x^2 / 2\sigma_k^2 - \delta x^2 / 2\sigma_c^2}\right]$$
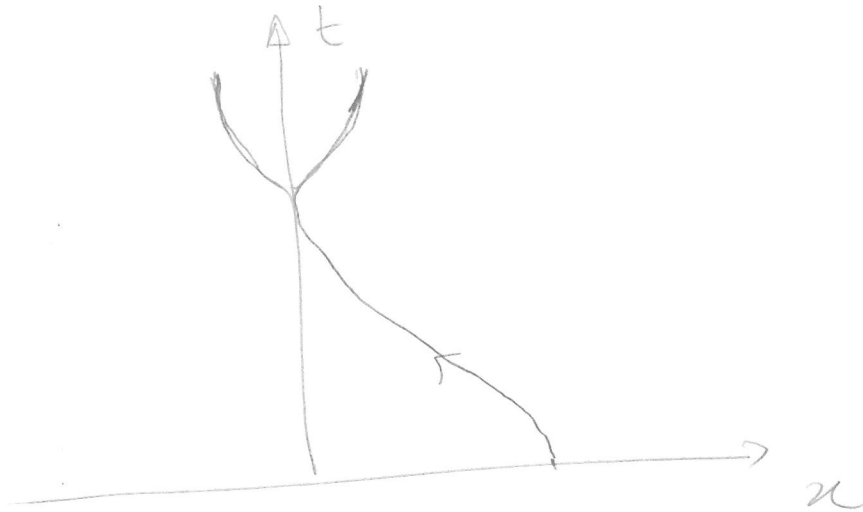
$$= r\left[1 - e^{-\frac{\delta x^2}{2\sigma_k^2 \sigma_c^2}(\sigma_k^2 - \sigma_c^2)}\right]$$

Therefore, if

$$\sigma_k > \sigma_c$$

$R > 0$ and the population of mutant grow.

Moreover, since R depends only on δx^2 we see that $x = 0$ has become unstable and two mutant populations with $x = \delta x$ and $x = -\delta x$ will develop:

Competition splits the population: it is better to have extreme beak sizes, when there is not so much food, but much less competition!

This is very nice. It shows that competition, if sufficiently strong, can be a source of instability and lead to the break up of the population in two.