

Darwinian Natural Selection

Evidence of Evolution

- Direct observation: species change
- Fossils show intermediate forms
- Extant species show structural, developmental and genetic homology
- Vestigial traits reveal ancestral condition
 - Structural, developmental, genetic
- That is, *descent with modification* becomes fact

But *HOW* does life evolve

- What mechanism(s) account for the fact of evolution?
- Darwin's answer: natural selection

Artificial selection

Evolution by natural selection is an outcome

- If the following are true:
 - Individuals vary (within a species)
 - Some of that variation is genetic
 - More offspring are produced than will themselves reproduce
 - Reproduction is not random

Survival and reproduction

- ‘Survival of the fittest’
- It is reproduction that counts, not survival
- Survival is often necessary for reproduction

Differential Reproduction

- Differential: some more than others
- So if some reproduce more than others, then the traits of those that reproduce more will become more frequent
- Everyone alive today had ancestors that reproduced

Populations change over time

- If some genotypes reproduce more than others,
- THEN the population will change
- That is a necessary outcome, and that is natural selection

This is a testable idea

- Natural selection relies on four things being true
- Each of those things can be independently tested and verified (or refuted)
- No belief or *faith* is required
 - You can simply understand this and think that it is true

Natural selection occurs if:

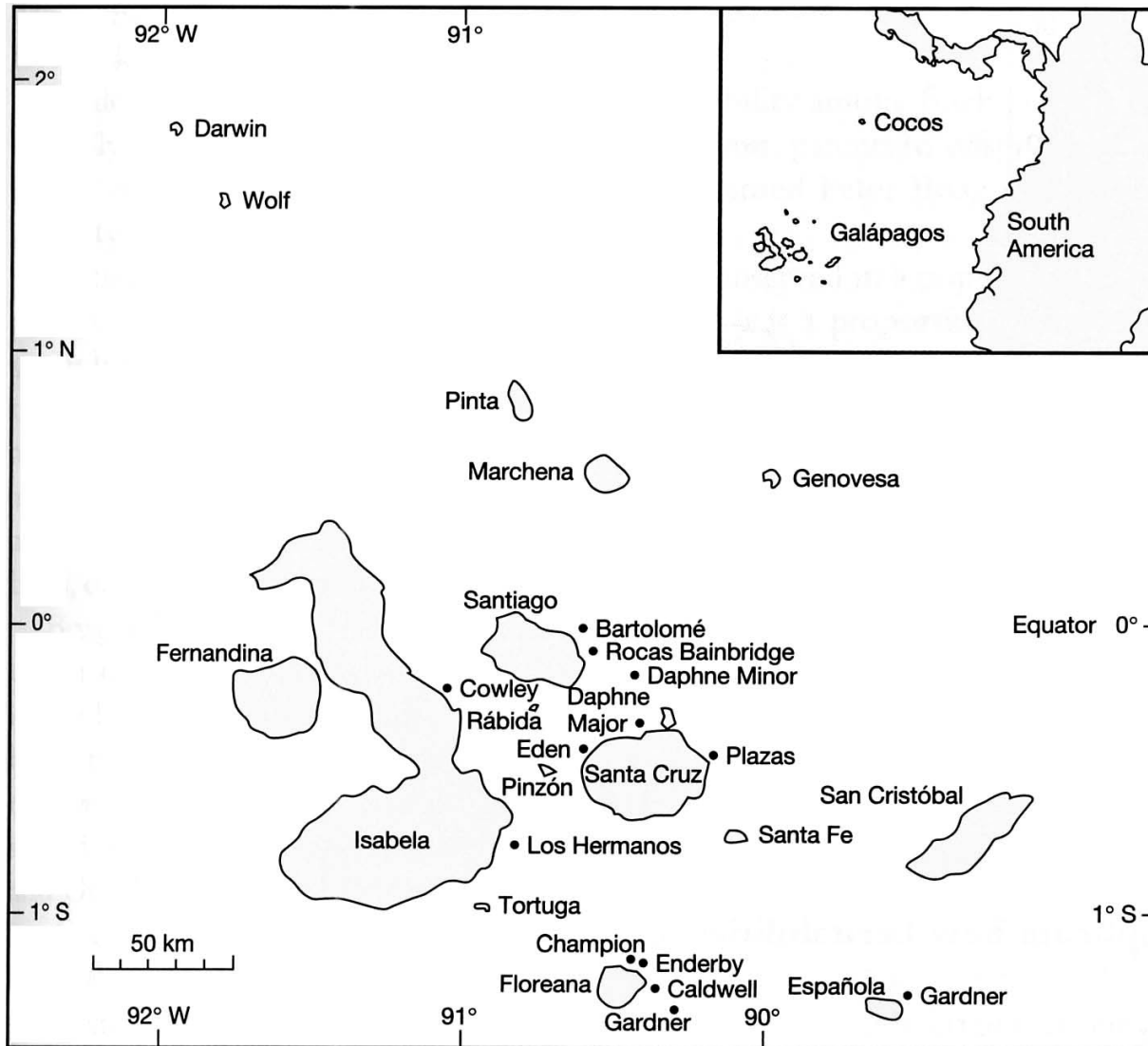
- Individuals within a population vary
- Some of that variation is genetic
- Not everyone survives and reproduces
- Reproduction is not random with respect to traits that vary genetically

An example: Galapagos finches

- Peter and Rosemary Grant have studied finches on the Galapagos islands since 1973



Galapagos Archipelago



Daphne Major

40 hectares

(hectare = 10,000 square meters, or 2.471 acres)

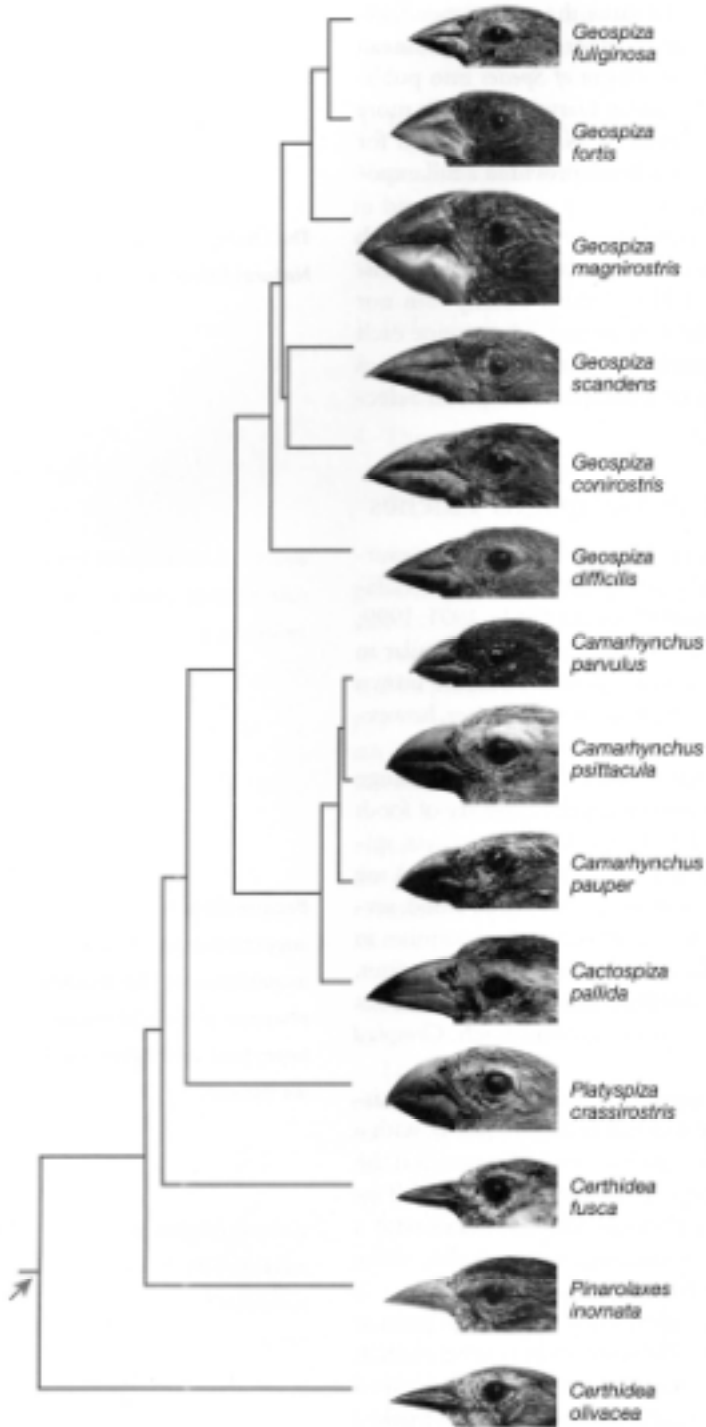
Finches

14 species

Phylogeny based on DNA
sequence variation

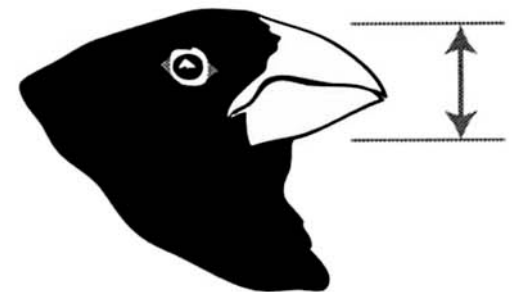
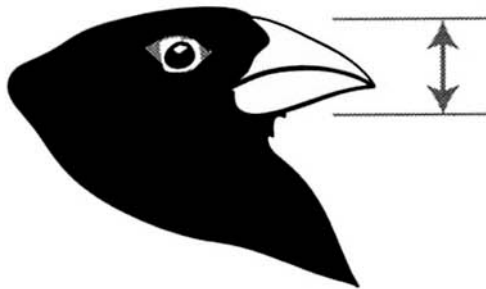
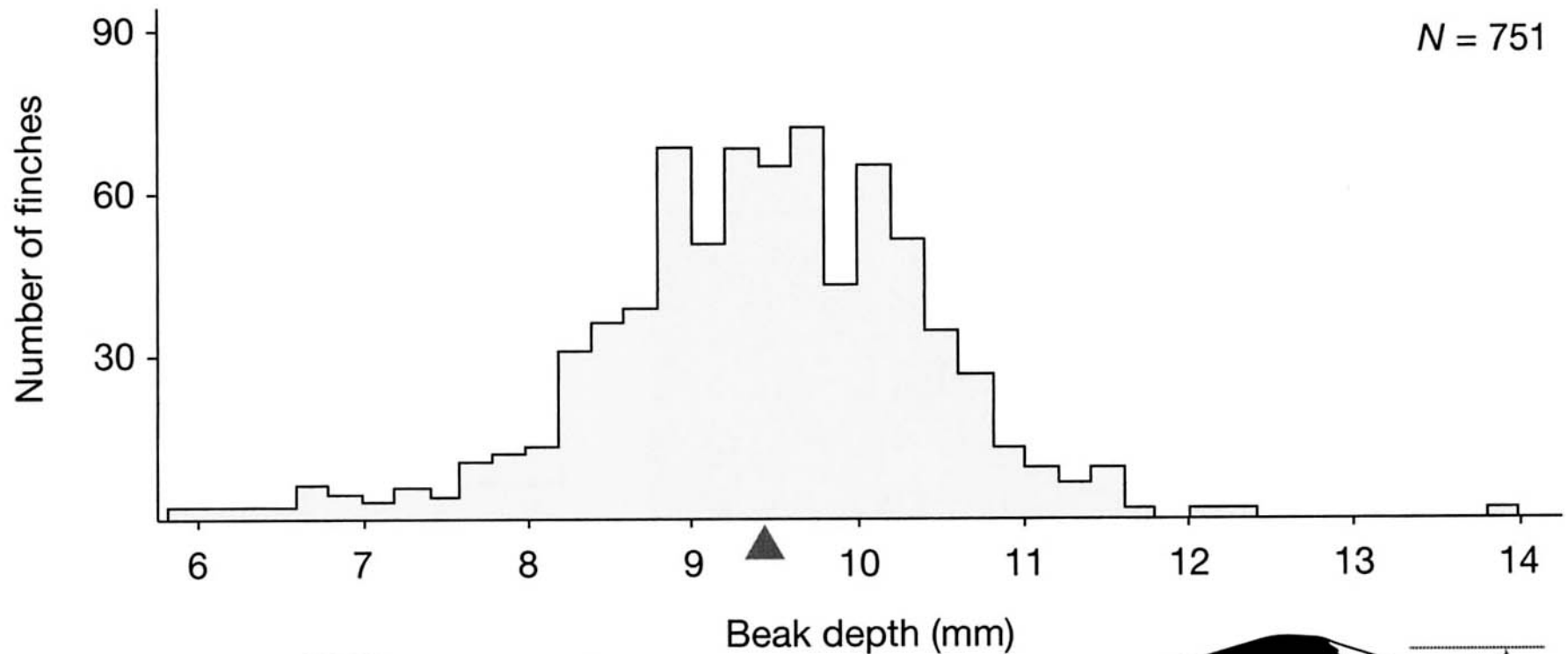
Lots of beak variation
among species

We focus on *Geospiza
fortis*, medium ground
finch



Do individuals in a population vary?

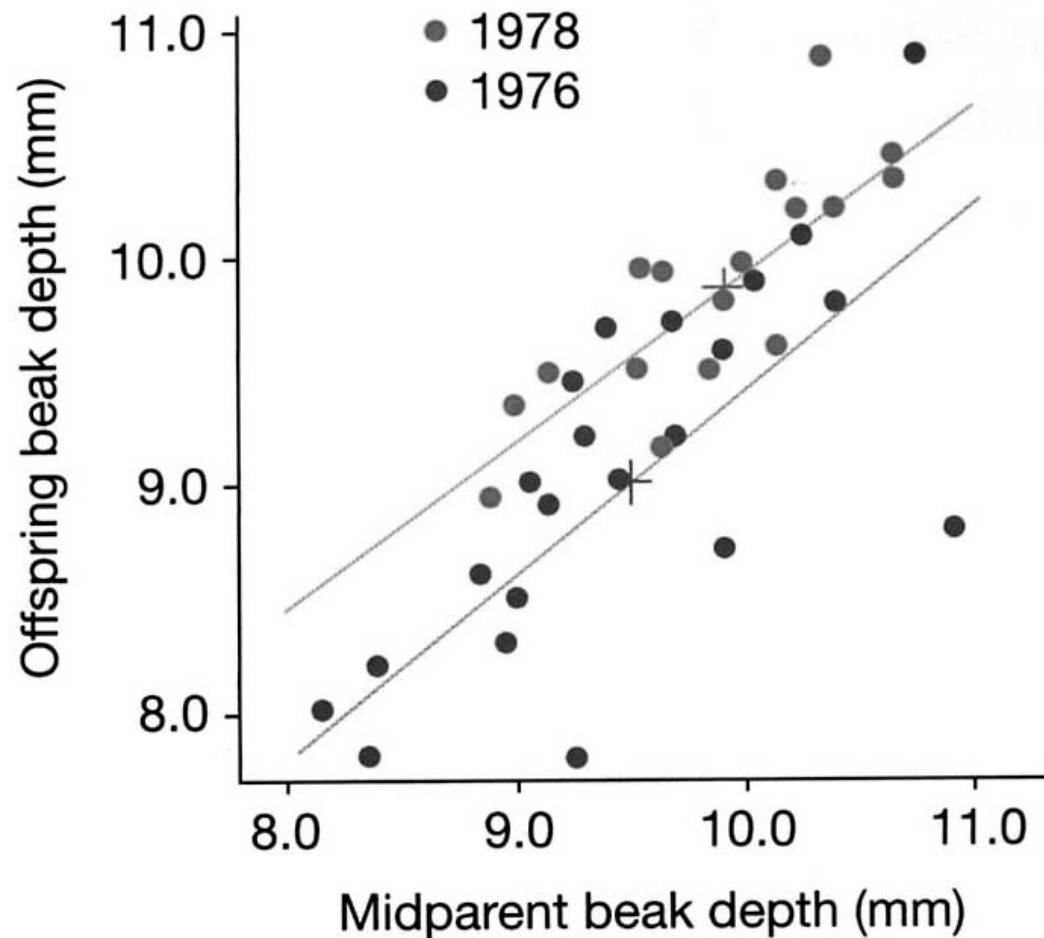
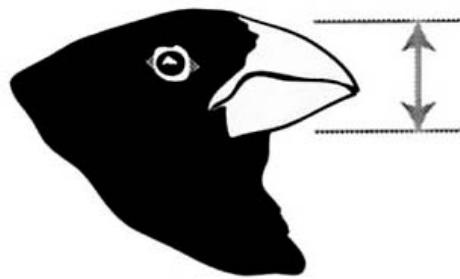
- Population of *G. fortis* averages 1200 individuals
- Almost all have been captured, marked, measured.



Is some of that variation genetic?

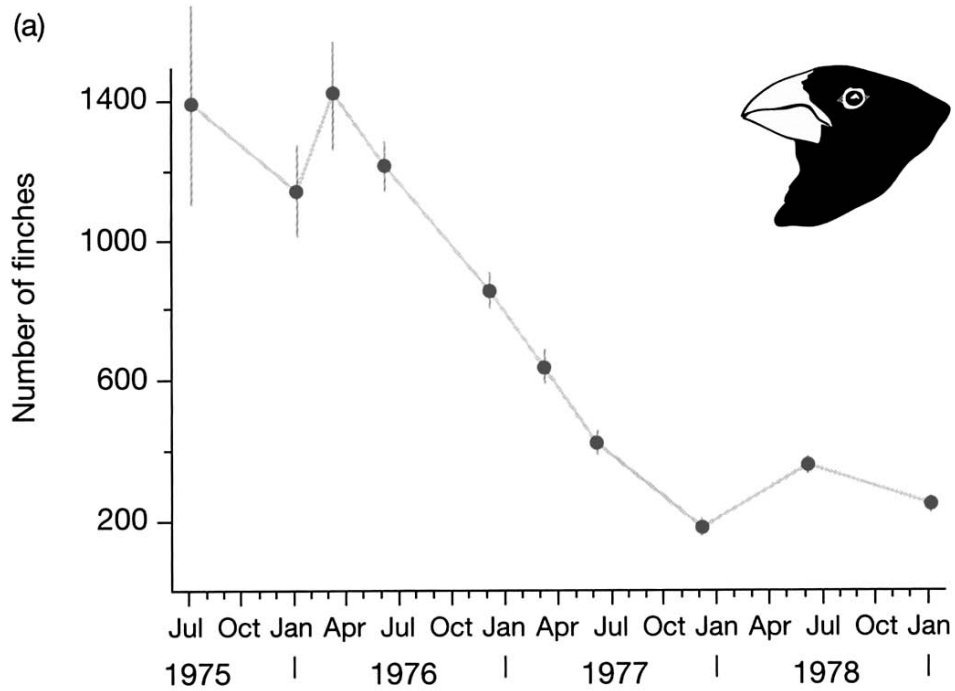
- Heritability: the proportion of phenotypic variation in a population that is due to genetic variation
- Proportion ranges from 0 to 1.
- So variation could be:
 - Completely due to environment: $h^2 = 0$
 - Completely due to differences among genes: $h^2 = 1$
 - Due to both genetic and environmental factors
 - $0 < h^2 < 1$

Heritability estimated from resemblance among relatives

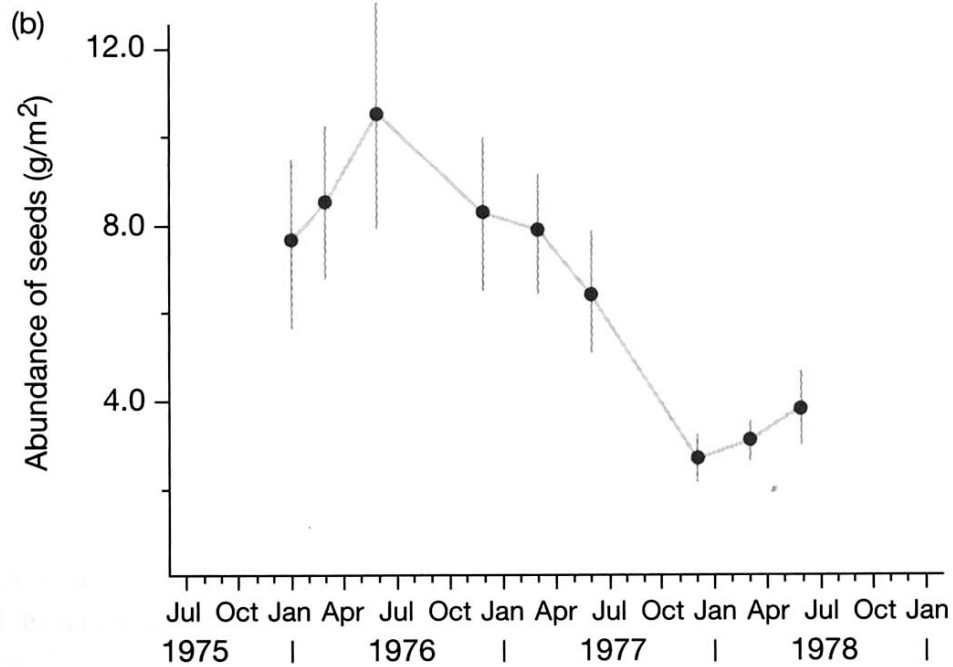


Does everyone survive and reproduce?

- Finch example: 89% of *G. conirostris* die without breeding
- In 1977 severe drought caused crash in *G. fortis* population



Drought, food, and finches



Beyond finches....think

- What would happen to the population size if the average female produced more or less than one surviving reproducing daughter?
 - More than 1 ?
 - Less than 1 ?
- So in sexual species, if each male and female couple produces two surviving reproducing offspring **OVER THEIR ENTIRE LIFE** then the population is stable

Example

- Female cricket mates with a male, lays 100 eggs over her life
- What % of those survive and reproduce (on average) if the population is stable?

- Male and female robin make a nest with four eggs year after year for 7 years = 28 eggs
- On average, only 2 of 28 survive and reproduce
 - One replaces the female, one replaces the male

Potential for reproduction

Table 3.1 Reproductive potential

This table gives the number of offspring that a single individual (or pair of individuals, for sexual species) can produce under optimal conditions, assuming that all progeny survive to breed, over various time intervals. Darwin picked the elephant for his calculations because it was the slowest breeder then known among animals.

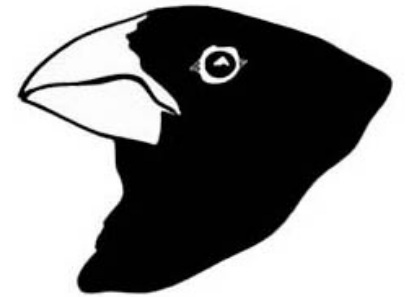
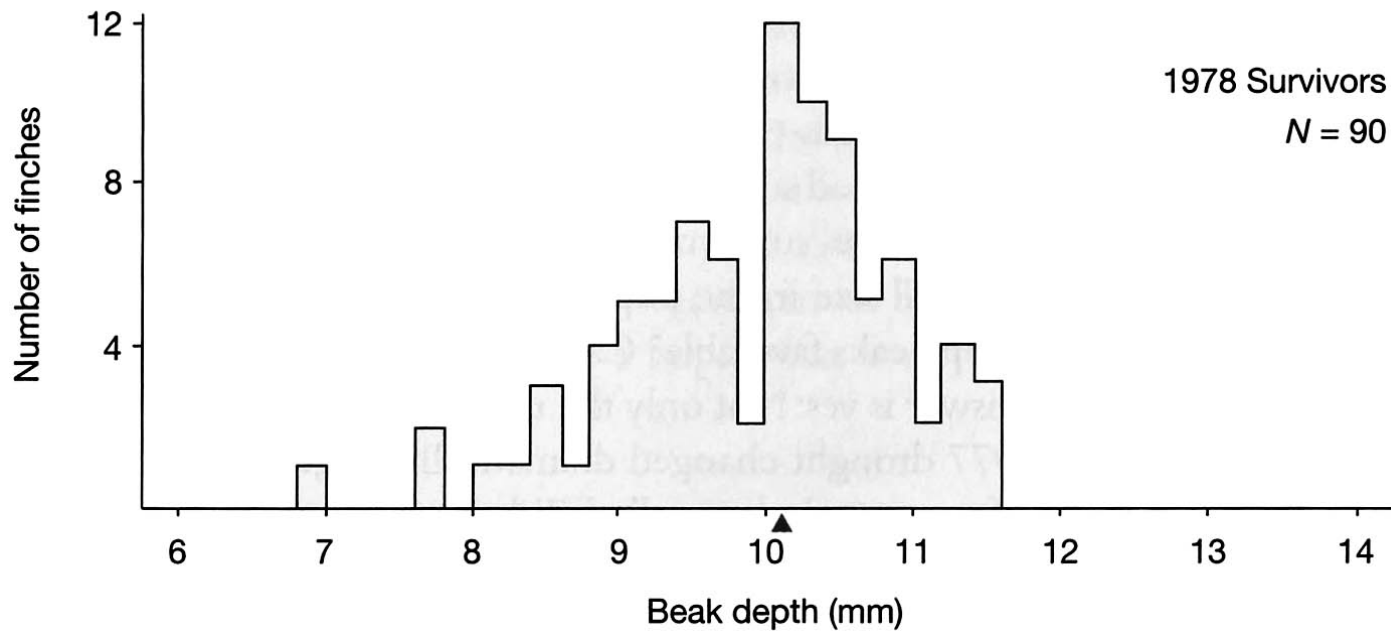
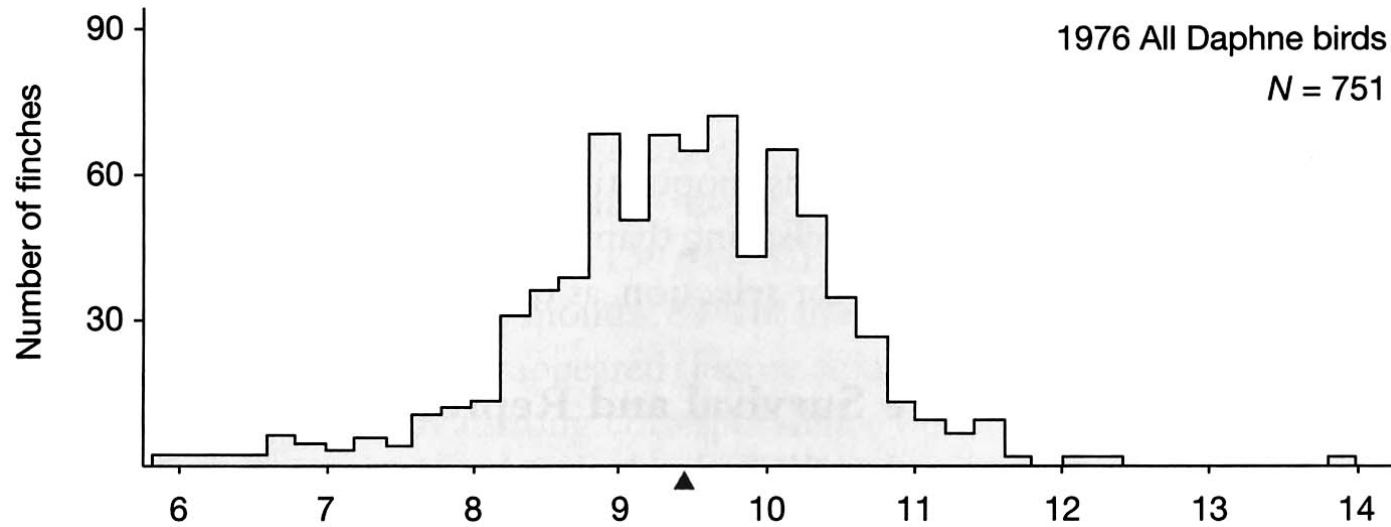
Organism	Reproductive potential	Citation
<i>Aphis fabae</i> (an aphid)	524 billion in one year	Gould 1977
Elephant	19 million in 750 years	Darwin 1859
Housefly	191×10^{18} in 5 months	Keeton 1972
<i>Mycophila speyeri</i> (a fly that feeds on mushrooms)	20,000/square foot in 35 days	Gould 1977
<i>Staphylococcus aureus</i> (a bacterium)	Cells would cover the Earth 7 feet deep in 48 hours	Audesirk and Audesirk 1993
Starfish	10^{79} in 16 years*	Dodson 1960

* 10^{79} is the estimated number of electrons in the visible universe.

OK, the majority of reproductive potential is not met

- Death
- Failure to reproduce
- The question is, is the reproduction that does occur random with respect to heritable traits or not?

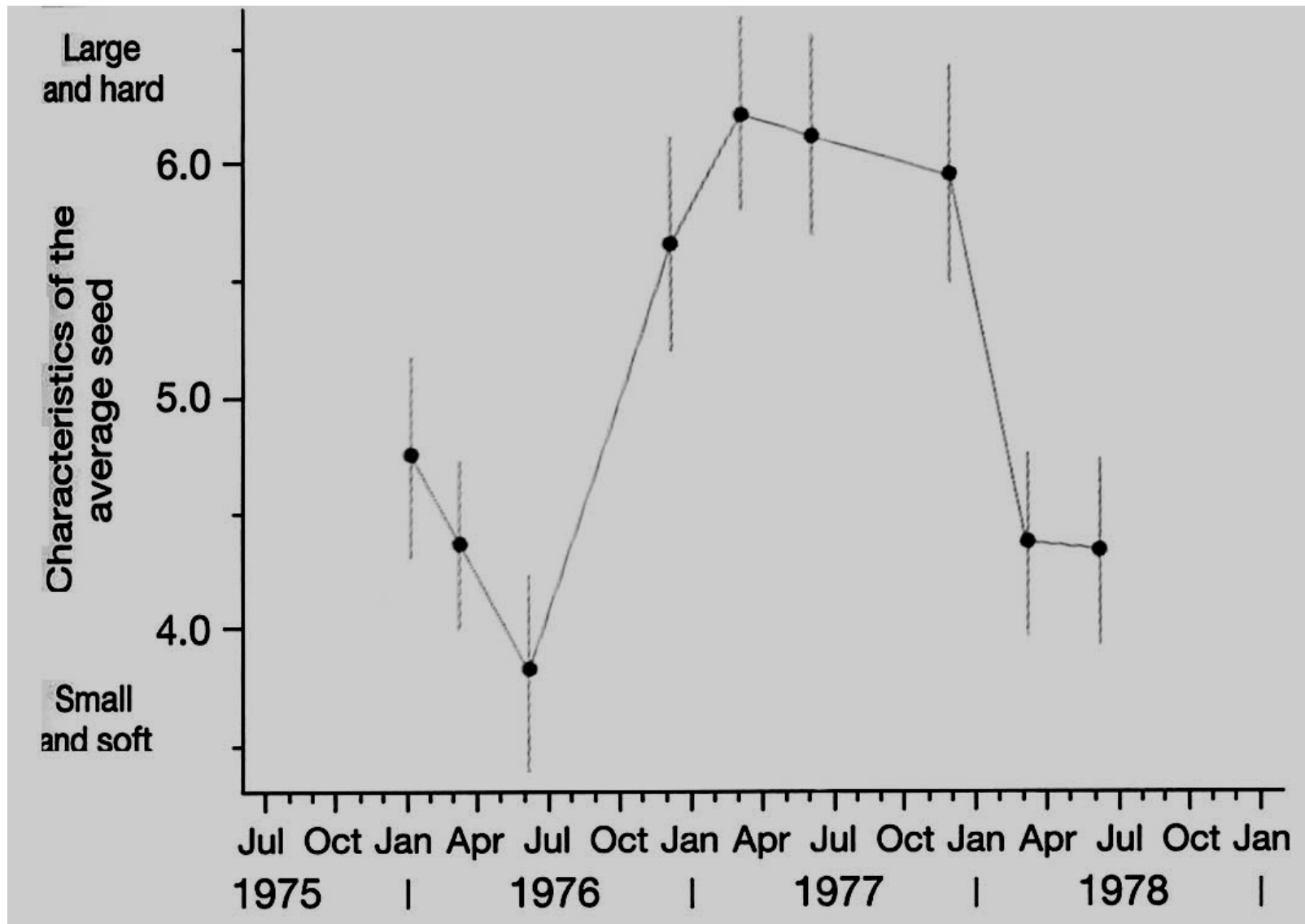
Non-random finch survival 1977



What caused non-random survival?

- That is, why were finches with bigger beaks favored by selection?
- Average seed size increased
 - Large hard fruits of *Tribulus cistoides* became important for survival

Available Seed Size



Summary of Finch Example

- Individuals within a population vary
 - True for about everything ever measured
- Some of that variation is genetic
 - Also true for hundreds of traits measured
 - Morphological traits typical $h^2 \sim 0.5$
 - Behavioral traits typical $h^2 \sim 0.3$
 - Life history traits typical $h^2 \sim 0.2$

Summary of Finch Example

- Not all individuals survive and reproduce
 - Also true for all stable populations with potential reproduction greater than 1 daughter per female
- Survival and reproduction not random
 - Finches: birds with thicker beaks favored because environmental conditions changed
 - Also true in hundreds of documented cases

Evolution by natural selection results

- What a simple idea!
- T. H. Huxley reported to have said ‘How stupid not to have thought of that before’

Natural Selection recap

- Evolutionary change via the mechanism of natural selection is a necessary result of
 - Variation among individuals within a population
 - A genetic basis to that variation
 - Excess reproductive potential
 - Non-random reproduction (entailing survival)
- Clarifications

Selection versus evolution

- Selection is differential reproduction, it:
 - Occurs within a generation
 - Acts on individuals
 - Acts on phenotypes (expressed traits)
- Evolutionary change
 - Occurs across generations
 - Within a population
 - Is change in genotype frequency

Selection within a generation

- Finches
 - Some birds in 1977 lived some died
- HIV virus
 - Some virions with AZT resistant RT active site mutations reproduced, others without the mutation did not

Evolutionary change across generations

- Finches
 - 1978 population of finches bigger and with deeper beaks than 1976 finches
- HIV
 - The *population* of virions late in infection is AZT resistant, whereas few virions are resistant in the early virion population

Selection acts on individuals

- Some *individual* finches died without reproducing
- Some individual virions could not transcribe RNA to DNA using reverse transcriptase in the presence of AZT so *those individual virions* did not reproduce (but others did)

Selection depends on phenotype

- It is the interaction with the environment that causes success or failure
- That interaction is mediated through the phenotype.....
- But the change in the *population* as a whole *over time* is *genotypic*

Alternatively

- Within a generation, individuals either reproduce or not depending on their phenotype
- Across generations, population changes in genotypic frequency result

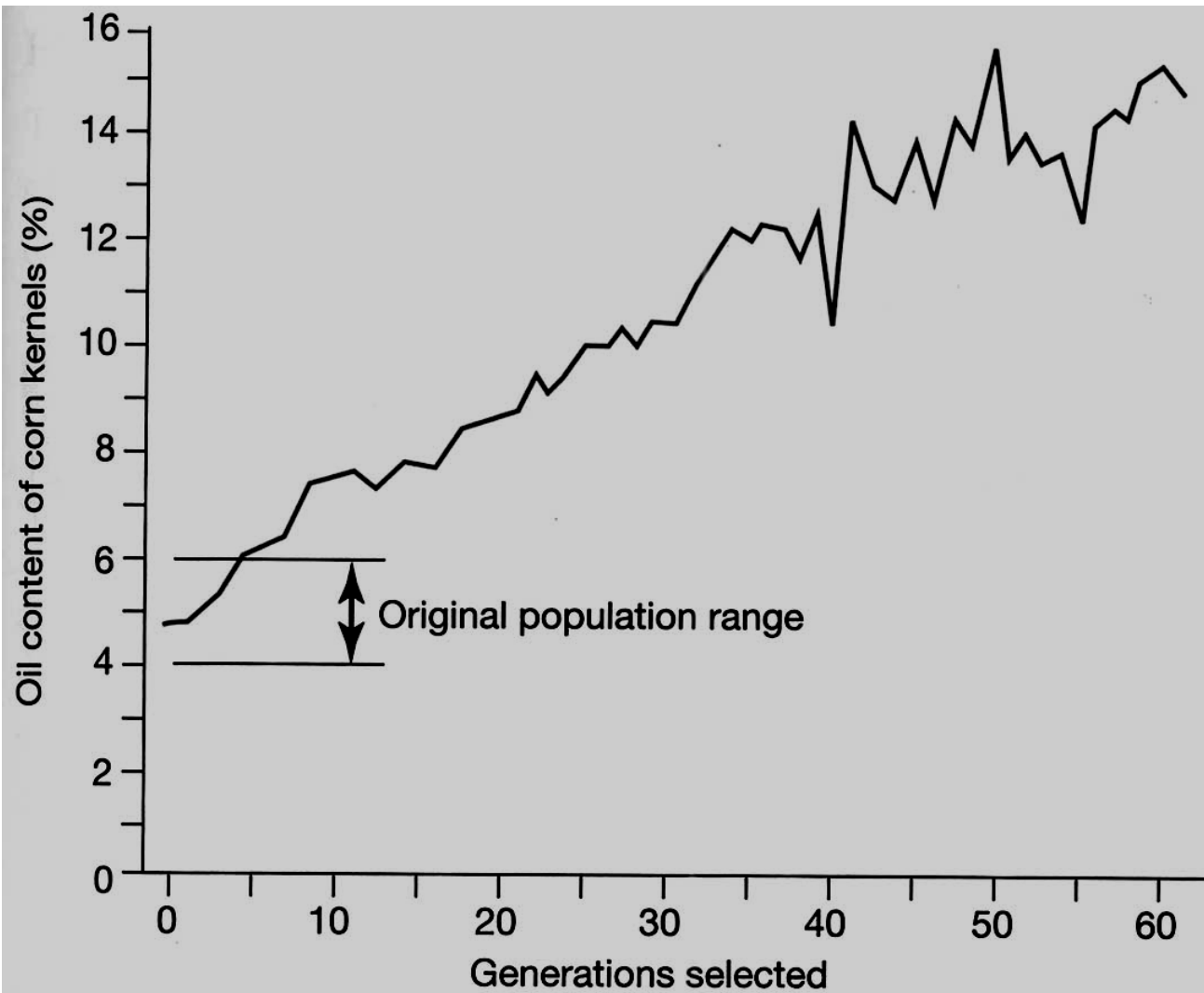
Natural selection is not predictive

- Evolution by natural selection is a *consequence* of the fitness of phenotypes in preceding generations
- It is impossible for organisms to forecast useful mutations
- Natural selection does not *directly* create populations composed of well adapted individuals, it does it *indirectly* by killing off less fit alternatives

How can new traits appear

- Selection acts to weed out less successful variants based on existing phenotypes....so how do new traits arise?
- Selection removes variation
- Mutation adds variation

Change over time



- 60 generations of artificial selection
- Produced new trait values beyond natural range

What about new traits?

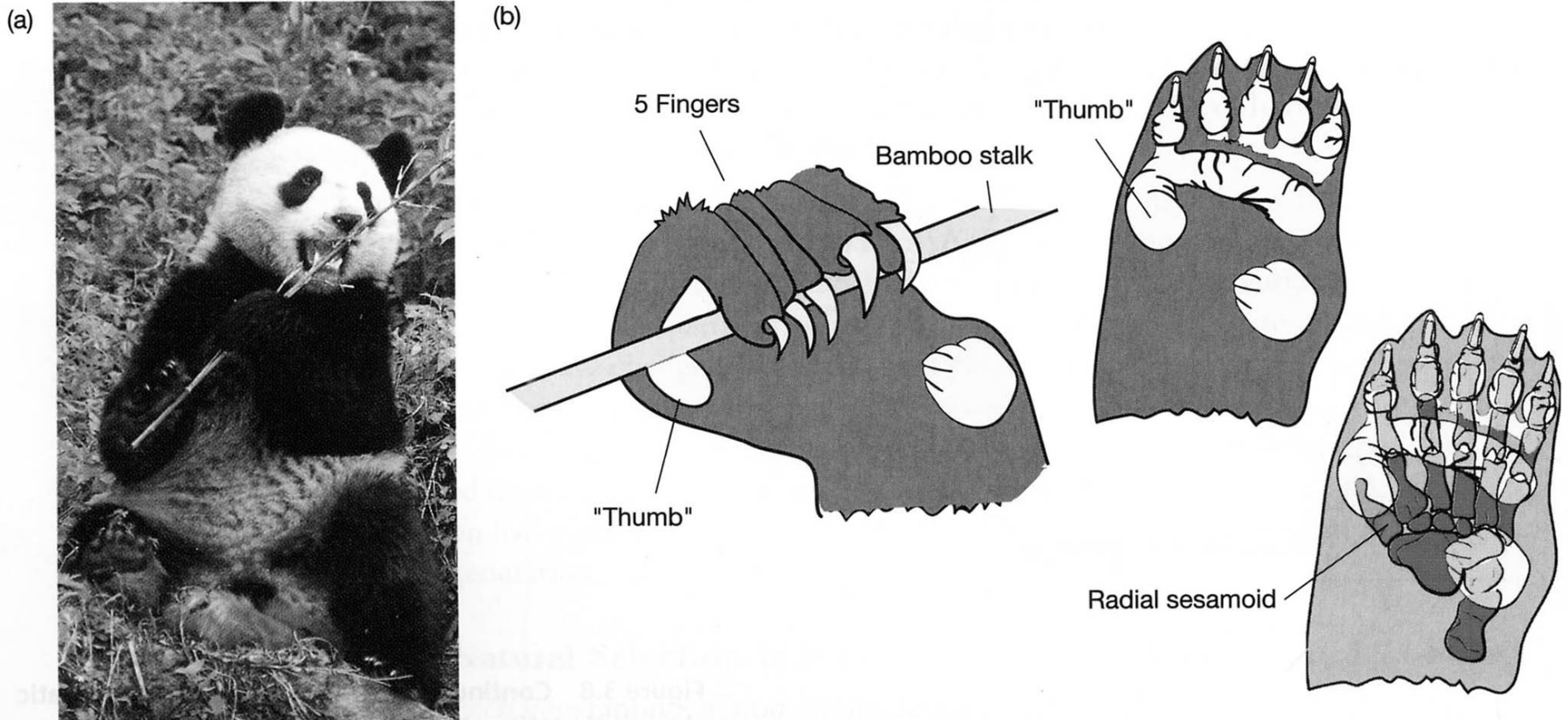


Figure 3.9 The panda's thumb (a) Giant pandas strip the leaves from bamboo by passing the stalk through their hands. (Bill Kamin/ Visuals Unlimited) (b) This drawing shows how the panda's "thumb" forms a slot for bamboo stalks to pass through. After Endo et al. 1999.

Producing imperfection

- Natural selection maximizes reproduction
- Takes what it can as starting material
- Optimizes individual features subject to constraints
- Constraints may be
 - Developmental
 - Correlated characters
 - Trade-offs

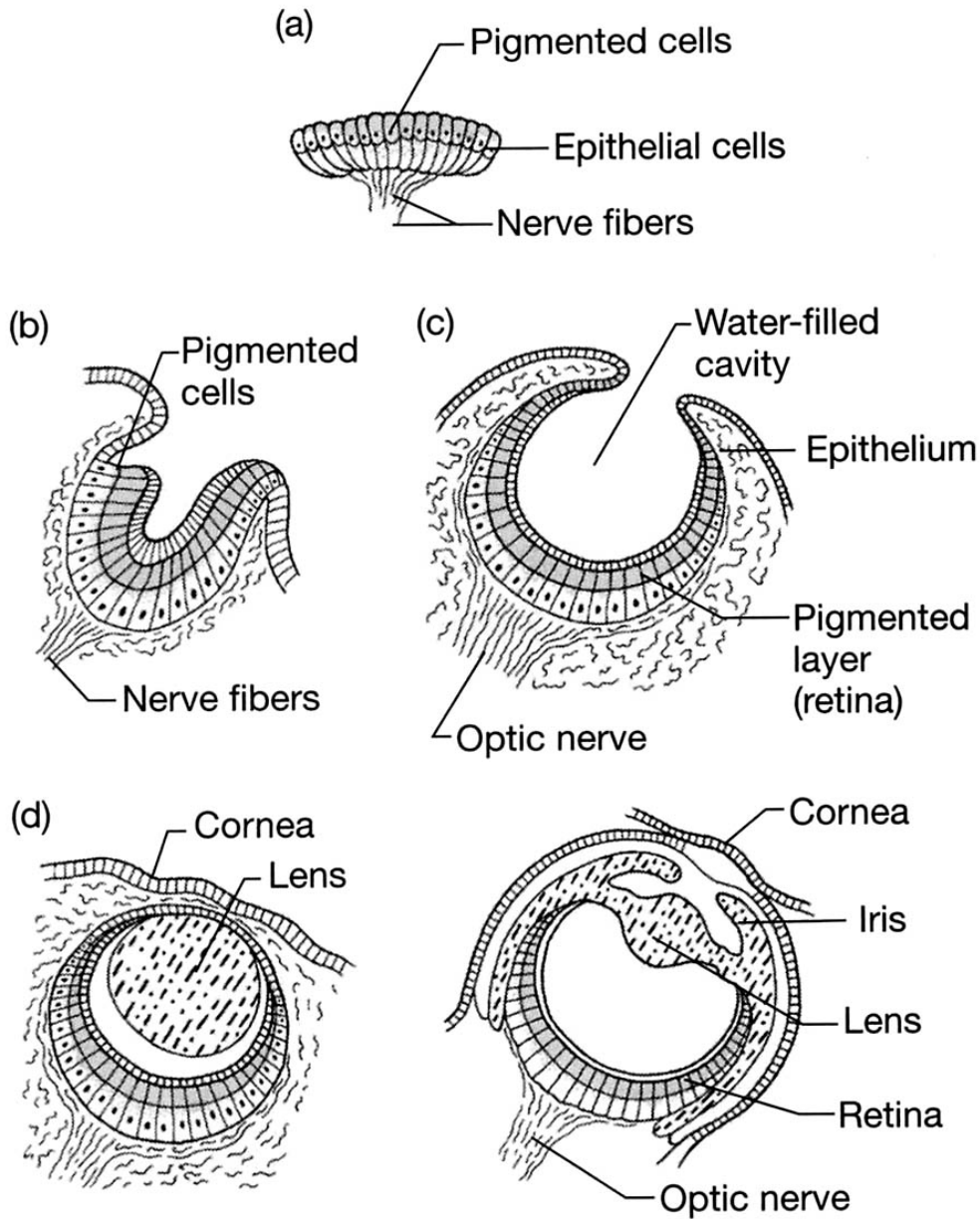
Producing complex adaptation

- Objection of some religious groups
 - How can a random process create complex adaptations?
 - Valid point is that intermediate steps need to be favored by selection as well
- A complex adaptation can not originate because it will be useful once it is formed
 - Evolution does not anticipate
 - Intermediate forms need explanation

What good is an imperfect eye?

- Biologists answer on several fronts:
 - Who has perfect eyes?
- An intermediate eye needs function
 - But it is competing with non-eyes
 - An intermediate eye may well be worse than a good eye, but it isn't competing with good eyes (yet)
- First eyes may simply sense light

Mollusc eyes



a) Pigment spot

b) Pigment cup

c) Optic cup (abalone)

d) Complex eye with lens
(snail *Littorina* and
octopi)

There is no such thing as evolutionary progress

- There is no goal
- All organisms currently alive had each and every one of their ancestors survive long enough to reproduce
- There is no purpose to evolution
- Life has no extrinsic meaning

fitness

- Means *reproductive success*
- Not stronger, faster, smarter
- Not longer lived
- Just producing more surviving offspring than the alternative

- ‘Survival of the fittest’ means that *genes* that promote reproduction will survive, *genes* that reproduce less will disappear

Levels of Selection 1: Not Species

- Evolution by natural selection is NOT different species competing for survival
 - Cheetahs chase, sometimes catch and eat gazelles
 - Selection by cheetahs favors faster gazelles
 - Faster gazelles selectively favor faster cheetahs
 - Gazelles compete for survival with gazelles
 - Cheetahs compete for survival with cheetahs

Levels of Selection 2: Not Groups

- Groups are not a significant evolutionary unit (for most purposes)
 - Selection acts on individuals within a population
 - So selection does not produce adaptations that are “good for the group” or “good for the species”
 - If a trait promotes the reproduction of the individual that has it, then it is favored

Problems with Darwin's formulation

- In 1859, the genetic basis of inheritance was unknown
 - Darwin could not provide mutation as a mechanism adding variation depleted by selection
 - Darwin could not explain how beneficial traits can be inherited intact rather than be lost
 - Mendel's experiments showing independent segregation and assortment unknown to Darwin
 - Traits thought to be mixed, or blended together
- Lord Kelvin calculated the earth to be 15-20 million years old
 - Based on assumption of radiant cooling

The Modern Synthesis

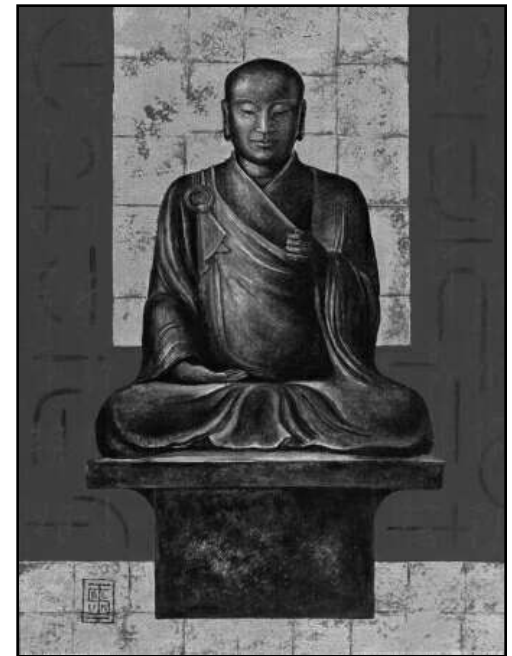
- Integration of genetic understanding
 - Individuals differ because mutation creates new alleles which are found in novel combinations because of independent assortment and segregation
 - Individuals pass alleles to offspring
 - In most generations more offspring produced than will themselves reproduce
 - The individuals that do reproduce have a non-random subset of alleles that make them well adapted to their environment

Why is evolution controversial?

- It isn't....scientifically that is.
- Some religious fundamentalists object to the idea of evolution.
- There is a basic difference between science and religion.

The bases of science and religion

- Science is fundamentally skeptical
 - Evidence is required
 - Constantly questioning
 - Modifies views in light of evidence
- Religion is fundamentally faith based
 - Belief is required, evidence is not



Darwin's outlook (1859, p. 490)

“There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and wonderful have been, and are being, evolved.”