I. Summary of lecture

- Re-cap of pre-Darwinian views on evolution (last lecture)
- The principle of natural selection
- Observations prior to Darwin’s voyage that support evolution:
  - structural and developmental homologies, vestigial structures, the fossil record, geology
- Darwin’s voyage on HMS Beagle:
  - biological richness of tropical forests, fossils in the same area are related, oceanic island species resemble those on the nearest mainland, geographic distribution (the environment per se is not creating the diversity)
- Darwin’s development of the theory of natural selection
- Since Darwin

II. Pre-Darwinian views on evolution

See Fig. 22.2 for major milestones and section below on the fossil record.

The idea of evolution, that living organisms have evolved from other organisms no longer alive on earth, had been proposed by a number of researchers before 1858 when Darwin and Wallace proposed the mechanism, natural selection.

Lamarck: placed fossils in an evolutionary context, including chronological series of older to younger fossils leading to modern species. He also developed the theory of evolution by inheritance of acquired characteristics, which we now know is incorrect.

inheritance of acquired characteristics: organisms change physically as they strive to meet the demands of their environment, and these changes are then passed on to future generations.

III. The principle of natural selection and how this can lead to speciation

1858 Darwin and Wallace independently proposed the mechanism of biological evolution, natural selection.

Darwin defined evolution as descent with modification (see e.g., Fig. 22.7).

One modern definition is change over time in the genetic composition of a population.
Darwin realized that evolutionary change is a two-step process: the first step consists of the production of inherited variation, and the second of the sorting of this variability by natural selection (see Fig. 1.21).

Since there is high mortality amongst all species, and many more individuals are born than needed to maintain the population size, traits that increase the probability that their bearers will survive and reproduce (relative fitness) are more likely to be passed on to their offspring, and to their offspring’s offspring.

In the Darwinian view of the world, organisms evolved their particular features because individuals with those features survived and reproduced better than individuals with different features.

So, the living world is constantly changing, and evolutionary change occurs without any “goals.”

(We now know that chance (genetic drift) also plays a large role in the genetic differentiation of populations, selectively equivalent (neutral) mutations can become established in a population.) Darwin also alluded to this in his writings.

IV. Observations prior to Darwin’s voyage that support evolution

Summary:

• structural homologies: bones of all mammals, also organs, tissues, etc.

• developmental homologies: characteristics are found in the embryo but not at birth which show our ancestry

• vestigial structures: pelvic bones of whales, appendix in humans

• the fossil record: changes in features over time, the older the fossils are the less they look like modern forms

• geology: earth is old (hence time for evolution to produce the huge diversity of living organisms) and accumulation of slow changes over long periods leads to creation of valleys, mountains, etc. (metaphor for natural selection and creation of new species)

• structural homologies that indicate close phylogenetic relationships

homologous structures: a homologous structure is an anatomical, developmental, behavioral, or genetic feature shared between two different organisms because they inherited it from a common ancestor, i.e., same evolutionary origin.

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The feature, e.g., anatomical structure, may now differ in function and there may be structural differences observed, but their evolutionary relationship is apparent.

**Homology** can be described as *similarity between species that is not functionally necessary*.

The closeness of the relationship between two groups of organisms is determined by the extent of homologous features; the more homologous features two organisms share (morphological, developmental, and genetic), the more recent their common ancestor.

For example, although the arms of four-limbed vertebrates externally appear quite different, all have the same basic underlying skeletal and muscular patterns, and developmental patterns (see Fig. 22.14).

**developmental homologies that indicate close phylogenetic relationships**

*ontogeny recapitulates phylogeny*: the developmental history of an organism passes through stages that are shared with the embryonic stages of evolutionary ancestors.

Comparative embryology shows how different adult structures of many animals have the same embryonic precursors. Further, closely related animals show a unity of developmental pattern, particularly in earlier stages, and have more developmental features in common than do more distantly related organisms.

An example of a developmental homology is the “pharyngeal pouches” that nearly all vertebrates acquire to some degree during their development, but which become very different structures in the adults (Fig. 22.15).

Also see chordate characteristics (Fig. 34.3) and how these are seen in the larval stage of tunicates (Subphylum Urochordata) but not in adults.

**vestigial structures**

*vestigial*: occurring in a rudimentary condition, as a result of evolutionary reduction from a more elaborated, functional character state in an ancestor.

The existence of vestigial traits which are no longer of use to the organism show their evolutionary origins, e.g., pelvic bones in whales (see Fig. 22.18 for transitional fossil, and vestigial leg bones in some snakes.

**The fossil record**

From the late 1700’s a large fossil record started to accumulate; changes in characteristics can be seen in fossils. Also, it was observed that species could go extinct, and that new species could appear. The study of fossils led to the realization that major changes had occurred in the earth's history.

*Cuvier* was among the first to study fossils with such care that he could distinguish fossils in different layers of sedimentary rocks, which led him and others to the naming of rock strata: the
Paleozoic, Mesozoic, and Cenozoic, and their various subdivisions. He noted that fossils that are progressively less familiar are seen as we go back to older and older rocks (also noted by Lamarck and William Smith) (see layers of rocks of different ages in the Grand Canyon Fig. 22.3). He noted that species went extinct, and that new species appeared. However, he believed in catastrophism (see below) with regions where species went extinct repopulated by species migrating in from other regions.

Lamarck noted that one could connect fossils in layers of rock (strata) in terms of slow changes in appearance as you moved up through the layers, and recognized that evolutionary change explains the fossil record and organisms’ adaptations to their environments. Although the mechanisms of evolution he proposed: 1. use and disuse, and 2. inheritance of acquired characteristics, are incorrect, he made major contributions to the study of evolution.

• geology

gradualism: James Hutton developed the theory of gradualism, which holds that profound changes in Earth’s geologic features is the cumulative product of slow but continuous processes.

This is in contrast to catastrophism where it was assumed that each boundary between strata represents a catastrophe, such as a flood or drought.

uniformitarianism: Charles Lyell incorporated Hutton’s ideas of gradualism and proposed that “the present is the key to the past”: geological processes have not changed throughout Earth’s history. In summary: the forces that build mountains and erode mountains are the same today as in the past. It is important to remember that uniformitarianism does not require that changes always occur at the same rate. There may be abrupt changes, such as volcanic eruptions or impacts of meteorites that are catastrophic, but subsequent changes are the result of known processes such as erosion.

Darwin took Lyell’s book with him on his voyage; two observations of importance to Darwin were that the Earth is very old, and that slow and subtle processes persisting over long periods of time can lead to substantial change.

V. Darwin’s voyage on HMS Beagle

HMS Beagle: Darwin was the naturalist on a 5 year voyage on HMS Beagle (see Fig. 22.5). He spent a lot of time in South America, visited a number of island groups, and saw the unique native animals of Australia.

He was impressed with the biological richness of tropical forests. He studied fossils in South America, and compared the animals living in South America and Australia and on islands (see below).
Observations on the voyage that influenced Darwin's views:

Summary:

• **biological richness of tropical forests:** although not evidence of evolution it got Darwin thinking about the huge diversity of living organisms

• **fossils** related to living animals in the same area

• **oceanic islands species:** related to each other and to species on closest mainland

• **geographic distribution of species:** animals and plants of Australia and South America not related (although may show similarities due to convergences)

• **biological richness of tropical forests**

A huge variety of species are seen in tropical rain forests, and these differ from those seen in say European countries. (This does not by itself imply evolution, but got Darwin thinking about the diversity, and relatedness, of species.)

• **fossils of huge extinct mammals related to those in the same area, and a continuity in changes in characteristics can be seen in fossils across strata in a region**

For example, extinct ground sloths and living sloths are found in South America, also the extinct glyptodont and living armadillos

• **oceanic island species are very often unique and show relatedness to one another, and most closely resemble those of the nearest mainland**

For example, the giant tortoises on the Galapagos Islands are all very similar, but can be distinguished by traits that relate to their environments.

The finches in the Galapagos Islands have diverged to occupy different ecological niches (Figs. 1.23 and 22.6); they all appear morphologically very similar, varying mostly in terms of beak size and behavior.

Darwin did not realize the significance of the finches until pointed out to him on his return to England by John Gould that the birds were all closely related finches. Darwin then noted that the different species of finches were island specific like the other Galapagos animals and suggested that they too were descendants of a mainland ancestor. We now know that they are very much like a species of finch from the mainland of South America.
These so called “Darwin’s finches” of the Galapagos have been extensively studied by other scientists.

• geographic distribution

Lands or islands with similar climates have different types of plants and animals - the environment is not creating the diversity per se (although there may be convergence of traits due to similar ecological conditions (Fig. 22.17).

VI. Darwin’s development of the theory of natural selection

Summary:

• artificial selection as a metaphor for natural selection
• adaptations are not perfect
• species are not fixed
• natural selection as the mechanism of evolution

Influences of Lyell and Malthus

• artificial selection

Darwin was struck by the ability of farmers etc. to breed new varieties of animals and plants (see Fig. 22.10). In particular, he bred pigeons with many diverse traits, and understood that these must all have come from a common ancestral stock.

• adaptations

The fact that organisms are well adapted to their environments argues for the action of natural selection (see Figs. 22.6, 22.11). The fact that they are not perfectly adapted was an important point to Darwin, in that it can show descent with modification. (If one were to design an animal or plant from scratch, why not have it perfectly adapted to its environment.)

• species are not fixed

Observations during his trip, especially on the Galapagos Islands, later led Darwin to accept the idea that species are not fixed.

• natural selection as the mechanism of evolution

Lyell: ’Principles of Geology’: the earth is very old and constantly changing. (There is sufficient time for natural selection to cause evolutionary changes.)
Malthus: 'Essay on the Principles of Populations': nature acts to limit population numbers. (More offspring are produced than survive.)

**natural selection (survival of the fittest):** those individuals that possess superior physical, behavioral, or other attributes are more likely to survive and reproduce than those that are not so well endowed.

**Structure of Darwin’s Theory (see Fig. 1.20)**

1. Fact: Populations grow exponentially if unchecked.
2. Fact: Population sizes in nature are usually stable.
3. Fact: Resources in nature are usually limited.

**INFERRENCE:** There will be competition for resources; i.e., a ‘struggle for existence” and only a small number will survive in each generation.

4. Fact: Individuals in a population show variations in their traits or features.
5. Fact: Many variations are passed from parent to offspring.

**INFERRENCE:** Unequal survival and reproduction will lead to the accumulation of favorable (selected) traits over a series of generations.

**1859:** Darwin published 'On the Origin of Species'.

Progressive adaptation by natural selection is responsible for evolutionary changes within a species. When these changes accumulate, they lead to the creation of new species (see Fig. 22.7).

Random genetic variation is sifted by natural selection. Evolutionary change occurs without "goals." Chance (genetic drift) also plays a role in determining the genetic structure of populations and changes over time.

**Darwin:**

1. Earth is very old, and organisms have been changing steadily throughout the history of life.
2. All organisms are descendants of a common ancestor - that is, life arose only once on Earth.
3. Species multiply by splitting into daughter species, and such speciation has resulted in the great diversity of life found on Earth.
4. Evolution proceeds via gradual changes in populations, not by the sudden production of individuals of dramatically different types.

5. The major agent of evolutionary change is natural selection.

6. Thus variation is a creative force, not a smokescreen hiding the truth as thought by the Greeks Darwin closed *The Origin of Species* with the following: "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."

VII. Since Darwin

Summary:

- the fossil record
- organs of extreme perfection
- genetics
- molecular biology
- evidence of selection
- evidence of speciation

• The fossil record since Darwin: a tremendous number of new fossils have been and continue to be found, and all support the evolutionary process.

Many have clarified relationships between groups (transitional fossils, see Fig. 22.18); others have helped date the first appearance of a group of animals, etc.

Precambrian fossils have been found.

• Organs of extreme perfection: to the argument that it is impossible to evolve organs of extreme perfection such as the eye ("what use is half an eye")? Darwin argued that any ability to ‘see’ is better than none, and so a complex organ can develop.

We now know that the same gene is involved in eye development in all organisms (homology), giving the signal to develop an eye. However the eye has evolved independently over 20 times (convergent evolution) in different lineages, and different genes are involved in what type of eye develops.
• **Heredity and the source of genetic variation:** although Gregor Mendel discovered and published the laws of genetic inheritance in 1865, Darwin was unaware of these. Mendel’s laws were rediscovered in the early 1900’s.

With the advent of molecular biology in the last 50 years we understand that mutations in DNA lead to **genetic variation** which may be advantageous, neutral, or deleterious to the organism.

• **Molecular biology:** all the molecular features of life support evolution and the unitary origin of life.

The more closely related two species are, the more similar their DNA and proteins (see Fig. 22.16).

• **Evidence of selection:** many instances of natural selection have been documented, many relate to resistance to malaria (these will be discussed in the lecture on selection); also see Fig. 22.12 on predation pressure and selection for size and age at maturity in guppies, and Fig. 22.13 on evolution of drug resistance in HIV).

• **Evidence of speciation:** we now understand a lot more the processes of speciation (more later in the course).

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**Questions relating to lecture on Darwin**

1. Describe and contrast catastrophism and uniformitarianism.

2. Which of the following is **incorrect** in describing Lamarck:
   
   A. Observed lines of descent of fossils with a chronological series of older to younger fossils leading to a modern species
   B. Developed the concept of inheritance of acquired characteristics
   C. Recognized that the earth was very old
   D. Explained adaptations to the environment as a primary product of evolution
   E. All of the above are correct.

3. List the two types of homologies discussed in the textbook and how these are used to draw the 'tree of life.'

4. Do self quiz questions for Chapter 22 in the textbook.