Darwin and the evidence for evolution

Note: Read the section “how to read a tree” on your own

Topic outline:

I. The nature of scientific explanation and proof
- *A. Scientific explanations include statements about patterns and processes*
- *B. Scientific explanations are tested against the empirical evidence*

II. A brief history of evolutionary thought
- *A. The ancient Greeks*
- *B. The Enlightenment*
- *C. Darwin*
- *D. The Modern Synthesis*

III. The evidence for evolution (descent with modification)
- *A. Darwin’s use of hypothetico-deductive reasoning*
- *B. The evidence*
  - *1. Species vary over time*
  - *2. Descent/relatedness explains many kinds of patterns*

I. The nature of scientific explanation and proof

- A. Scientific explanations usually have two components:
  1. a statement of fact (= a description of a pattern): e.g., “species change over time” or “species are related by descent”
  2. a proposed mechanism (= a proposed process) that produces the pattern: e.g., “natural selection causes species to change over time” or “disruption of gene flow can lead to the formation of new species”
- B. To be accepted, scientific explanations must be tested against the empirical evidence (the “real world”) – that means both verifying the pattern and testing the proposed process.
  1. Hypothesis testing follows the basic “scientific method” = hypothetico-deductive reasoning:
     - a. if possible, several possible explanations (hypotheses) for the same pattern are assembled.
     - b. from each hypothesis, generate as many specific predictions as possible
       - i. predictions = statements about what should happen under specific

circumstances if the hypothesis is correct

ii. usually take the form of "if . . . then" statements: "if my hypothesis is correct, then circumstances abc should lead to results xyz"

iii. ideally, alternate hypotheses will lead to different (mutually exclusive) predictions

c. test hypotheses by comparing predictions to the available evidence:

i. "physical evidence" may be the results of experiments in the lab or field, or controlled observations

ii. modes of reasoning are also important – evidence is assessed using inference (reasoning "up" from an observation to its cause) based on two key principles:

a) **uniformitarianism**: processes operating now have operated the same way in the past (i.e., the world "works" the same now as it did millions or billions of years ago, and will work the same way in the future)

b) **parsimony** = Occam's razor: given alternative explanations that fit the available evidence equally well, the simplest explanation is most likely to be correct

d. use results of observations and reasoning to try to disprove as many alternatives as possible; accept as the most likely to be correct the hypothesis with the most predictions met and the fewest falsified (use falsified predictions to alter the hypothesis)

2. Some key points about hypothesis testing, etc.:

a. In strictly logical terms, no scientific hypothesis is ever "100% proven".

i. Rather, rigorous testing increases or decreases the likelihood that a hypothesis is correct

ii. Many scientific explanations have been so rigorously tested that they are likely to be true beyond any reasonable doubt – these may be referred to as "scientific facts".

b. All scientific hypotheses are always subject to revision and change as we accumulate new evidence (which sometimes leads folks critical of science to say that it's all guesswork – but our successes in explaining the natural world suggest otherwise!)
c. Scientists recognize a sort of "hierarchy" of scientific explanations – this is important, because the way scientists use these terms is different from their lay meaning:
    i. **hypothesis** = most tentative explanation, one that has been tested relatively little
    ii. **theory** = a hypothesis that has been repeatedly tested and never falsified – to a scientist, a true "theory" is an explanation that is true beyond reasonable doubt
    iii. so when a scientist speaks of the "theory" of evolution, s/he means something very different than do those who refer to it as "just a theory"!

II. A brief history of evolutionary thought:

The science of biology has a complex past, in large part because living things are much more complex than are non-living things. Among the patterns that were historically difficult to explain were (1) patterns of adaptation (the "fit" between organisms and their environment); (2) patterns of similarity and difference among organisms; and (3) the process of embryonic development – all of which are key to understanding evolution. Here we'll take a brief "snapshot" at several important stages in the development of our understanding of these processes.

A. The ancient Greeks: Plato and Aristotle
    1. Plato was a student of Socrates and one of Aristotle's teachers
        a. developed a view of the material world called **idealism** = **essentialism**, sometimes called his **Theory of Forms**
            i. explained in his famous "The Allegory of the Cave" (available on-line!)

ii. basic idea = the material world and everything in it are imperfect manifestations of an ideal world that exists on a metaphysical plane, not a material one
iii. the goal of scholarship is to understand the ideal, not the material
iv. to do so, should ignore the material world and focus on logic, reasoning, etc. to understand the ideal

b. major implication for the history of evolutionary thought:
   i. natural variation represents mistakes/imperfections
   ii. therefore, natural variation should be ignored

2. Aristotle (384-322 BC) modified Plato's Theory of Forms and made other significant contributions:
   a. modified the Theory of Forms by maintaining that the "ideal" or "essence" of material things actually resided within those things
      i. important implication = to study the ideal, the best way is to study the material, i.e., to study the natural world (which he did, to the extent that he's considered the "father of modern biology")
      ii. unfortunately, still held that the material world was an imperfect manifestation of the ideal, so again variation among individuals is ignored
   b. explained adaptation ("fit" between an organism's morphology, behavior, etc. and its environment) by his "**Theory of Causes**"
      i. of the four causes for the fit between organism and environment, the most important is the function or role of the organism – e.g., it's because birds fly that they have wings, feathers, light-weight bones, etc. (the function, "flight", caused the traits to arise)
      ii. Cause-effect relationship analogous to what humans do:
         a) first we conceive of some function (i.e., "we need a way to drive across this river"),

b) then we design a structure that has the right form to match the function (i.e., we build a bridge with a design appropriate to the river and the kind of traffic it must bear)

iii. Although this view makes lots of sense in human terms, it is NOT how the world actually works

a) this view requires that somehow "functions" exist first, and can cause organisms to develop and change to match them

b) unfortunately, because it's so logical in human terms, it remained a major obstacle to the acceptance of natural selection – until as late as the 1940's!

c. To explain the patterns of similarity and difference among organisms, developed the **Scala Naturae** = "ladder of life" or "great chain of being"

i. the scala "connects" all natural things – from inanimate objects through "slime", plants, inverts, verts, to humans and finally to Greeks (surprise!).

ii. the scala represents a pattern of "relationship", but emphatically not a pattern of descent.

iii. Scala also represented, as far as Aristotle was concerned, a scale of values

a) he believed that nature had an inherent property of progressing from the "least perfect" to the "most perfect" things

b) so organisms "higher" on the scala were also "better" or "improved" compared to the lower

c) this thinking is also, unfortunately, still with us today: many continue to believe that evolution is about "progress"

3. During the early Renaissance, the thinking of Plato and Aristotle were incorporated into Western Christianity

a. Plato and Aristotle's "ideal" became "God's plan"

b. imperfections = result of the fall from grace (manifestations of original sin)

c. A divine, intelligent creator is responsible for order and harmony in nature
   i. Scala naturae is a pattern that reflects this order and harmony
   ii. order and harmony is also reflected in adaptation: God creates each species to meet its function/role in nature
d. These, of course, are the ideas that Darwin (and others before and after) challenged

B. The Enlightenment (1700's +) was a major period of scientific growth; important highlights include:
1. establishment of "mechanistic" thinking in the sciences
   a. Although mainstream scientists accepted that God created the world, they sought explanations that didn't rely on the direct action of God, but on "natural" processes (e.g., forces of gravity, electromagnetism, etc.)
   b. Worked very well in the physical/chemical sciences, and to some extent in physiology (explaining, e.g., the flow of blood through the body), but less successful for biology:
      i. processes biology needed to explain -- e.g., development of complex adult from simple single cell -- are far more complex than processes like planetary orbits, electricity, etc.
      ii. living things are incredibly variable:
         a) over time, as during development
         b) from place to place, because of adaptation
   c. Result was that biologists trying to come up with mechanistic explanations came up with what we would now consider extremely strange, implausible ideas – lots of "blind alleys"
2. The industrial revolution had major impacts on the development of science in general, and indirectly on evolutionary biology in particular
   a. need to find new sources of raw material led to major age of exploration, with Western European nations exploring and colonizing the New World, Africa,

Asia, etc.

i. as part of the exploration, naturalists sent/brought back specimens of rocks, fossils, plants, animals
ii. remember that Europe has relatively few species of plants and animals – so all of this new diversity was a very big deal

b. Geology grew rapidly, with some important findings for evolution:
   i. principle of uniformitarianism was established
      a) proposed by James Hutton in 1788
      b) championed and established by Charles Lyell (one of Darwin's teachers) in his Principles of Geology 1830-1833
   ii. fossil record became established and studied, revealing
      a) existence (and extinction) of many, many kinds of organisms, most of which no longer exist
      b) patterns of change over time that were unexplained by Biblical accounts

3. Within biology, comparative anatomy and embryology were growing; although investigators didn't understand mechanisms, they documented some very important patterns, including:
   a. similarity in patterns of embryological development among vertebrates
   b. **homology** = structures similar by development, position, arrangement, even when they're superficially different (e.g., bat wing, human arm)
4. Well before Darwin, other biologists began to question the belief that species were fixed and unchanging:
   a. Buffon (1776) suggested that modern horses arose from earlier species, but then recanted (probably for fear of the Catholic church)
   b. Jean-Baptiste de Lamarck (1744 -1829) proposed, in his *Philosophie Zoologique* (1809), a hypothesis to explain both development of new species and patterns of adaptation

i. Lamarck was the father of invertebrate zoology – it's important to remember that he worked primarily on molluscs and other animals with hydrostatic skeletons to understand his thinking
ii. his model was based on ideas that were pretty well accepted at the time:
   a) new, very simple forms of life are constantly generated spontaneously

   b) in any environment, these simple forms of life will adopt behaviors that allow them to survive in that environment (e.g., places where they live, ways of moving, ways of feeding, etc.)
   c) specific behaviors bring about specific patterns of movement of body fluids (remember he worked primarily on invertebrates), which carry the **vital force**
      i) at this time, biologists believed that the quality of "life" was a consequence of a special force (analogous to the force of gravity, or forces generated by electricity), called the vital force
      ii) most believed that this force was carried, somehow, in the circulating fluids
      iii) force was responsible for directing development, though its tendency to cause organisms to "perfect" themselves over time, as well as producing the other characteristics of life
   d) vital force acts on surrounding tissues to change them – some get bigger/stronger, some degenerate, etc., depending on the specific behavior of the organism
      i) variation in behavior –> variation in circulation –> variation in action of vital force on tissues causes organisms to differ from one another
      ii) because behavior is determined by environment, changes caused by the vital force will be adaptive – they will make organisms

better suited to their environment

e) characteristics acquired by adults in their lifetimes are passed on to their offspring, who continue the same process
    i) note that inheritance of acquired characteristics was not Lamarck's ideas – it was widely accepted at the time (and even used by Darwin later!).

f) result = adaptive change over time

iii. Lamarck's ideas were pretty widely rejected at the time, in part because he had no evidence
    a) one of his strongest critics was Lyell, who argued against Lamarck's model in his *Principles of Geology*, which Darwin read while he was on the Beagle . . .
    b) this was probably very important in helping Darwin shape his own ideas

C. Darwin and The Origin
1. A brief outline of Darwin's life:
    a. born 12 Feb 1809 (same day, year as Abraham Lincoln) in Shrewsbury, England
    b. son and grandson of physicians; family was fairly well-off financially:
        i. uncle was Josiah Wedgewood, of Wedgewood china
        ii. eventually married his cousin Emma Wedgewood, so got more money then
        iii. so really didn't need to "work" for a living
    c. basically indifferent student through the equivalent of high school, but always loved "naturalizing" = spending time outdoors hunting, fishing, collecting, etc.
    d. began medical school at University of Edinburgh (at 16), but dropped out; while he was there, though, he studied geology and hunted
    e. changed to study theology at Christ's College, Cambridge, but wasn't really

interested in theology

   i. spent a lot of time with John Henslow, a botanist, learning botany and other natural history
   ii. continued to spend time hunting, collecting

f. graduated in 3 years, then Henslow arranged for him to be offered the position of naturalist/captain's companion on HMS Beagle, which was a surveying ship setting out to circumnavigate the globe and map ports, especially in SA
g. voyage lasted 5 years, during which Darwin (seasick pretty much the whole time) read, collected fossils, plants, animals, and thought a lot about what he was seeing (he studied firsthand what we would now call paleontology, ecology, biogeography, and systematics!)
h. returned to England and started working on his extensive collections; spent the rest of his life engaged in numerous research projects
i. began thinking/writing about the "transmutation of species" in 1837
   i. in 1842 wrote up his preliminary ideas about natural selection in a 35-p notebook entry
   ii. expanded to 242 page draft in 1844; he shared this with Lyell and Joseph Hooker (another botanist), who urged him to publish it
   iii. he wanted to wait until he had more evidence, but directed his wife to publish it posthumously if necessary
j. in 1857, received a letter from Alfred Russell Wallace, a young naturalist working in Malaysia, with whom he had been corresponding
   i. Russell outlined an idea identical to natural selection
   ii. Darwin had just lost a son to scarlet fever, so passed letter on to Hooker and Lyell, urging them to publish it
   iii. Lyell and Hooker knew that Darwin had thought of the idea much earlier, so presented both Wallace's letter and an abstract of Darwin's work to

the Linnaean Society on 1 July 1858

k. Lyell and Hooker pushed Darwin to publish – in 1859, published the Origin
l. Darwin died 19 April 1882; buried in Westminster Abbey

2. Darwin's impact
    a. because of the way in which it was presented, and because of the amount and variety of evidence he used, "The Origin" established the scientific fact of descent with modification (genealogical relatedness + change over time) within about 10 years
    b. the theory of natural selection, however, was not well-received, for several reasons
        i. relies (as we have seen) on understanding pattern and process of variation – which Darwin didn't understand (and no one else did, either)
        ii. natural selection is without goal or progress – and this was very troubling, even for biologists (vestiges of Aristotle still very strong)
3. The Modern Synthesis
    a. As mentioned, although reality of descent well accepted, natural selection ignored for many years. Next major event = Modern Synthesis (=Evolutionary Synthesis = Neo-Darwinism)
    b. 1936 - 1947; represents "fusion" of Mendelian genetics, evolutionary theory, natural history, paleontology, systematics
    c. key was understanding patterns and processes of genetic variation
    d. prior to synthesis, two competing views on variation, genetics (remember Mendelian principles rediscovered ~ 1920):
        i. Mendelians (deVries, T.H. Morgan),
            a) working on lab populations (esp. fruit flies),
            b) focused on large-scale variation (macromutation): after all, these were the kinds of variation that could be seen and shown to conform to Mendelian principles

c) consequently, didn't buy natural selection as major force for change because of reliance on small variations & changes

ii. "Biometricians" studied actual variation in natural populations:

a) saw that small scale, subtle variation very common

b) didn't have mechanism for how this kind of change could be inherited, changed

e. Synthesis began with work by Fisher, Haldane, Sewall Wright: developed statistical models that demonstrated that small scale variation (like seen in natural populations)

i. conformed to Mendelian patterns of inheritance

ii. could, given even slight selective pressure over time, produce substantial change in gene frequencies in population (i.e., could result in evolutionary change)

f. Findings inspired researchers in other fields to look at own studies in lightof natural selection, see if selection fit their data:

i. Dobzhansky studied natural populations of fruit flies; saw how selection could produce new species (Genetics and the Origin of Species, 1937)

ii. Ernst Mayr combined field studies of distribution and variation in birds with selection, systematics, biogeography (Systematics and the Origin of Species, 1942) (1904 - ???)

iii. Geoge Gaylord Simpson demonstrated that natural selection, ideas proposed by Dobzhansky, Mayr, et al., explained fossil record (Tempo and Mode in Evolution - 1944)

iv. G. Ledyard Stebbins did same for plants (Variation and evolution in Plants, 1950)

III. The evidence for evolution (specifically, descent with modification)

A. In The Origin, Darwin used what was then a novel approach to supporting his argument: hypothetico-deductive reasoning as described earlier

1. Competing hypothesis = special creation as viewed in his time:
    a. species created independently of one another (no descent of one species from another)
    b. species do not change over time
    c. species were created recently (within 10,000 years)
    d. species designed by creator for their particular roles/functions
2. Darwin's hypothesis = descent with modification
    a. species arise from previously existing species
    b. species change over time
    c. slow, gradual process (so earth is much more than 10,000 years old)
3. In the Origin, he looked at a variety of evidence and compared it to the specific patterns and predictions made by each hypothesis (which is like what we'll do here).

B. The evidence:

1. Descent with modification requires an old earth
    a. read about the establishment of the geologic time scale p. 37
    b. applying the principles of uniformitarianism, geologists (Hutton and Lyell, in particular) had established, even by Darwin's time, that the earth was <u>much</u> more than 10,000 years old
    c. current methods of radiometric dating establish conclusively that earth is on the order of 4.5 billion years old and life is at least 3.5 billion years old
    d. note that this conclusion is based on repeated tests: using different radiometric methods and repeating same methods on different rocks, etc.
2. Descent with modification holds that species change over time – which requires variation within species as a precondition
    a. Variation within species is readily observed at the morphological and biochemical levels
        i. most obvious in domesticated plants, animals, where differences among

"varieties" is often extreme

    ii. but also holds in natural populations, where variations in size, shape, color, proteins, DNA, etc., are easily measured and documented (we'll talk more about this later)

b. Change within species over time has also been directly observed over even short time scales:
    i. e.g., soapberry bugs in Florida (fig 2.7): change in size of preferred fruit correlated with change in size of beak over ~ 100 years
    ii. e.g., house sparrows have changed in size, color over ~ 100 generations since their introduction into North America (OH/HO)
    iii. e.g., resistance of HIV to AZT etc.
    iv. e.g., decrease in size of fish in commercial fisheries, etc. etc. etc.
c. Artificial selection can cause major change in structure/function over time, indicating that apparently "uniform" species are "hiding" major amounts of genetic variation
    i. e.g., compare differences in dog breeds (or any other domestic animal)
    ii. e.g., kales (broccoli, brussels sprouts, cabbage all same species)
d. The amount of variation within species, and the amount of change species undergo over time, is sufficient to give rise to new species
    i. note that discussion of new species requires that we define species – traditionally, two definitions are possible (we'll get into this in much more detail later):
        a) morphological species: species are identified by their morphological differences
        b) reproductive isolation: species are identified by their inability to interbreed
    ii. We have experimental evidence from lab studies of plants and some animals (e.g. fruit flies) that artificial selection can, in fact, produce

reproductive isolation

iii. Studies of "ring species" demonstrate that variation within a species can, under the right circumstances, be enough to lead to reproductive isolation -- e.g., *Ensatina eschscholtzii* in CA (see handout)

a) salamanders distributed in "ring" in mountains around the Central Valley

b) morphological variation fairly extensive across species range, with different subspecies recognized based on morphology, genetics, etc.

c) subspecies form "ring", starting in south with *E. e. klauberi*; each interbreeds with adjacent subspecies all the way around the Central Valley to the southeastern most subspecies, *E. e. crocreator*

d) but *E. e. klauberi* and *E. e. crocreator* don't interbreed: they are reproductively isolated from one another

e) demonstrates that variation within a species can, under the right circumstances, lead to reproductive isolation and the formation of a new species

e. Summarize: we have direct and overwhelming evidence that species do vary, that they change over time, and that the amount of variation within species is sufficient to give rise to new species by either morphological or reproductive criteria.

i. this supports Darwin's view of descent with modification

ii. this falsifies the special creation view that species are unchanging

3. Descent (with modification) – the idea that existing species arose from previously-existing species & have changed over time – explains many different patterns in nature.

a. **homology** = features of organisms that share fundamental similarities in terms of the number, kind, and arrangement of structural components, even

a) structures superficially different

b) structures have different functions

i. many, many examples of homology, including
   a) anatomical homologies in animals and plants
   b) developmental homologies even in distantly related animals (e.g., fruit flies and humans!)
   c) biochemical homologies (homologies of proteins, DNA)
      i) e.g., some snake venom proteins are homologous with pancreatic proteins
      ii) e.g., common genetic code among eukaryotes

ii. Special creation doesn't explain homology well: if organisms are specially created to "fit" their function/role in the environment, then predict fundamental differences in development and structure when functions are vastly different (e.g., digging vs. flying vs. swimming vs. running)

iii. Descent with modification predicts two important patterns:
   a) homologies themselves = characteristics inherited from common ancestor; superficial differences are due to different adaptations
   b) concordance of patterns produced by different homologies:
      i) homologies among organisms fall into nested, hierarchical sets: they group organisms based on similarity
      ii) hierarchical patterns produced by one set of homologies (e.g., anatomical) are consistent with those produced by others (e.g., DNA or proteins)
         a) special creation predicts no particular relationship between sets of characteristics, so no reason to expect this consistency
         b) descent with modification predicts exactly this pattern, because all characteristics are reflecting the same pattern of descent

b. **vestigial structures** = "functionless or rudimentary homolog of a body part that has an important function in closely related species"

i. again, many, many examples of these, including:
   a) reduced or absent eyes in cave-dwelling animals
   b) reduced wings in flightless birds, insects
   c) human tail bones
   d) vestigial legs in snakes
   e) pseudogenes = lengths of DNA that don't code for functional proteins – e.g., øá ("false alpha") locus of human hemoglobin rsembles the normal á locus, but doesn't produce functional protein
   f) developmental vestiges – e.g., notochords, pharyngeal pouches in humans

ii. special creation predicts that vestigial structures shouldn't happen at all because species are intelligently designed for specific functions

iii. descent with modification predicts vestigial structures as features inherited from a common ancestor and changed over time

c. **Biogeographical patterns** (patterns in the geographic distribution of organisms)

i. special creation predicts that organisms will be most similar in habitats with similar environments (think why)

ii. descent with modification predicts that organisms will be most similar in regions representing places of origin and subsequent dispersal

iii. evidence supports descent – e.g.:
   a) comparing faunas of Africa with those of SA:
      i) special creation predicts that organisms in African tropics will be more similar to organisms in SA tropics than they will to organisms in African deserts (because of similarities/differences in environment)
      ii) descent with modification predicts that organisms in African

tropics will be more similar to organisms in African deserts than to organisms in SA tropics – because they are more likely to share a common ancestor

iii) African organisms are more similar to each other, as are SA organisms (Darwin observed this and similar patterns)

b) patterns of similarity in island chains
   i) special creation predicts no particular pattern of similarity/difference from island to island, or between island and mainland
   ii) descent with modification successfully predicts two patterns:
      a) island forms are more similar to mainland forms, even when environments differ, than they are to island forms from other regions (even when environments the same)
      b) patterns of similarity among island forms within chain often conform to patterns of origins and distributions of islands – i.e., patterns of similarity among organisms follow those predicted based on when islands originate, when they could be colonized, etc.

d. The fossil record: four specific patterns provide important evidence for descent with modification:
   i. **environmental change**: the discovery of, e.g., fossil snails in the Alps and whales in Egypt demonstrate that the earth's environments are not fixed and unchanging (contrary to special creation)
   ii. **extinction** problematic for special creation
      a) aside from Biblical catastrophe, no prediction made that extinction would happen (if perfect creator makes perfect creation, why would things go extinct?)
      b) by Darwin's time, patterns known well enough to prove that multiple

extinction events had taken place over time – not just one, as predicted from Old Testament

iii. The "**law of succession**" = fossil and living organisms in the same region are more similar to each other than they are to organisms from other regions
   a) e.g., Darwin studied armadillos in Argentina, found they were more similar to fossils (glyptodonts) from the same region than to living or fossil organisms from anywhere else
   b) this is exactly the pattern predicted if fossil species represent ancestors of extant forms
   c) pattern not predicted by special creation, because that hypothesis doesn't allow for change over time (which record clearly indicates)

iv. **transitional forms** = organisms with characteristics of both "ancestral" and "descendant" forms
   a) not predicted at all by special creation, but predicted by descent with modification
   b) examples are very numerous, especially in vertebrates – we have well-documented transitional forms, e.g.:
      i) between fish and amphibians
      ii) between amphibians and reptiles
      iii) between reptiles and birds
      iv) between reptiles and mammals
   c) fairly recent e.g. = transitional whale fossils showing change from terrestrial to fully aquatic form

C. Summarize/conclusions:

1. Because of the amount of evidence he presented and because of the way he presented it, Darwin convinced the scientific community of the historical fact of descent with modification within about 10 years of publication of The Origin.

2. Evidence in support of descent has increased dramatically (especially since the development of modern genetics) since that time – descent with modification is true beyond any reasonable doubt.
3. In spite of this, the theory of natural selection – as the mechanism to explain how modification takes place – was basically ignored until the Modern Synthesis of the 1930's, 40's and 50's, when a better understanding of genetic variation allowed the reconciliation of genetics, selection, and patterns of natural variation and adaptation.