Seeing Evolution — evidence from the past, present, and future.

The evidence is all around us, in the natural world, in our pets, in our food, in our diseases, everywhere you look.

But to start out, a bit of humor:
http://www.youtube.com/watch?v=nfv-Qn1M58I
The Banana — an atheist nightmare! Yeah, right.
More seriously . . .

For a great read, and the possibility of an extra credit book report, check out:

*The Greatest Show on Earth — the Evidence for Evolution*

by Richard Dawkins.
Once more, what’s evolution?

* Evolution is a change in the genetics of populations over time.
* It occurs in a population when some alleles become more common, and other less common, from one generation to the next.
* A population is a group of interbreeding organisms, and an allele is a version of a gene. All populations have many alleles.
* Many explanations have been proposed for life’s diversity. Evolution explains it all!
Buffon – one of first to openly suggest that closely related species arose from a common ancestor and were changing.

Hutton – uniformitarianism – the processes of erosion and sedimentation that act in modern times also occurred in the past.
History, cont.

* Cuvier – catastrophism – brief geological catastrophes are responsible for most geological formations.

* Principle of superposition – lower layers of rocks (and fossils) are older than those above them.

* Fossils represented extinctions, but the organisms are replaced by those from surrounding areas.

* Lamarck – inheritance of acquired characteristics.

* He was the first to suggest that animals could change or become extinct in response to interactions with their environment.

* Lyell – renewed uniformitarianism – natural processes are slow and steady.
This can be seen in places like Arizona's Grand Canyon.

Also see: http://bio.fsu.edu/~stevet/Boating/GrandCanyon/GrandCanyon.html and http://www.bio.fsu.edu/~stevet/VSU/videos/Chapter13/GrandCanyon2010.m4v
And then along came Darwin . . .

- Charles Darwin - five year voyage as naturalist on HMS Beagle.
- Read Lyell and trusted uniformitarianism.
- Tried to reconstruct the past from contemporary observations.
- Noted similarities and differences among organisms.
- Month in Galapagos Islands was the seed of theory of evolution by natural selection.

http://www.bio.fsu.edu/~stevet/VSU/videos/Chapter13/Darwin.mpg

Saturday, January 14, 2012
One particularly striking observation was convergent evolution.

This is the idea that many organisms have similar characteristics, because they evolved in similar environmental conditions, even though they are not closely related.
He returned to England and started thinking . . .

The finches were especially interesting. There were 14 different types, yet all must have originated from one ancestor that made it the islands a very long time ago, i.e. “descent with modification.”
He combined ideas from Malthus' *Essay on the Principle of Population* with this and what he had seen in artificial selection (selective breeding) . . .
To come up with the concept of natural selection:

- Which is the differential reproductive success of individuals with particular genotypes (in modern lingo). Or as he stated “preservation of favourable variations and the rejection of injurious variations.”

- Darwin described his theory of evolution by natural selection in a brief sketch in 1842, and in a longer analysis two years later, but he did not publish either. He submitted his paper with one from Wallace to the Linnaean Society in 1858. And then finally he published *On the Origin of Species by Means of Natural Selections, or Preservation of Favored Races in the Struggle for Life* in 1859.
Table 13.1  
Darwin’s Main Ideas

<table>
<thead>
<tr>
<th>Observations of Nature</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Organisms are varied, and some variations are inherited. Within a species, no two individuals (except identical siblings) are exactly alike.</td>
</tr>
<tr>
<td>2. More individuals are born than survive to reproduce.</td>
</tr>
<tr>
<td>3. Individuals compete with one another for the limited resources that enable them to survive.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Inferences from Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Within populations, the inherited characteristics of some individuals make them more likely to survive and produce fertile offspring.</td>
</tr>
<tr>
<td>2. Because of the environment’s selection against nonadaptive traits, only individuals with adaptive traits live long enough to transmit their genes to the next generation. Over time, natural selection can change the characteristics of populations, even giving rise to new species.</td>
</tr>
</tbody>
</table>

* See http://en.wikipedia.org/wiki/Natural_selection
* We’ll see how natural selection works next time. For now let’s look at some of the evidence for it that has worked over the history of life.
Beautiful cases of diversification by natural selection can be seen in Madagascar and Lake Victoria.

At least 100 species of lemurs in Madagascar. Around 250 different species of Cichlid fishes in Lake Victoria!

And, of course, the well known antibiotic resistance in bacteria phenomenon.
So far we’ve seen how things look:

**Morphology is the study of form — the most ‘primal’ way to classify things.**

- To “morph” is to change shape, e.g. transformer robots (from the Greek morphe meaning form).
- Humans naturally categorize things based on their shape — think, e.g. round versus square versus oblong wooden blocks.
- We saw the differences in the way different critters looked, i.e. their shape and form, and learned which ones to eat, which ones to fear, etc. a very, very long time ago. This is classification.
Aristotle (384-322 B.C.)

"Nothing is more remarkable than [Aristotle's] efforts to exhibit the relationships of living things as a scala naturae" (Charles Singer, 1931)

Aristotle's History of Animals classified organisms in relation to a hierarchical “Great Chain of Being,” placing them according to complexity of structure and function such that 'higher' organisms showed greater vitality and ability to move, "the degree to which they are infected with potentiality." Progressivism!

He believed that “formal cause” (Essentialism) is the Nature-inspired blueprint or plan that guides the existence of all natural and human-made objects. This Plato (428-348 B.C.) inspired, teleological view of the world, nature, and humankind holds that all things stay true to “Form.”
OK. But, what about fossils?!

- They are seen in use as ornaments in Paleolithic sites.
- And were documented at least five hundred years B.C. by Greek philosophers (e.g. Anaximander, 610–540 B.C. and Herodotus, 484–425 B.C.). But then along came Aristotle... and fossils began to be...
- Discounted as “oddly shaped crystals” or “faulty attempts at life that arose spontaneously in rocks” in situ, acting on response to forces known as “vaporous exhalations!”
- Aristotle’s ideas lasted until the Middle Ages when enlightened minds such as Leonardo da Vinci (1452–1519), Gerlamo Fracastoro (1480–1533), and Bernard Palissy (1510–1590) studied the relation of fossils to living counterparts, and argued that they were the remains of organisms that had lived in the distant past.
But Christian religion’s Divine-inspired Creation would rule thought on the topic for a long time.

- This accepts Aristotle’s notion of one and only one Form for all critters, big and small.
- Zealots explained that fossils were remains of organisms killed during the Biblical Noah’s Great Flood . . .
- And proposed that the appearance of progressive change was explained by (1) elevation of habitat, (2) resistance to gravitational settling in the flood waters, and (3) ability to flee the floodwaters. However, . . .
- Geographical clustering of more recent forms with forms from deeper layers that looked like them was a problem. Everything could not have been created in the Garden of Eden. Oh no!
- Extinction was troubling – why would it even happen – but its existence became undeniable. “Progressive creation” explained that indeed extinction had occurred, but so had newer special creations – at least six times. And in more than one place . . .
The rest of the world moved on and saw fossils for what they really are.

As early as 1757, James Parsons and others attempted to deduce the season of the Flood from fossils. If spring, flowers and young fruit should predominate, mature fruit and nuts, if fall. Alas, both were found. It was suggested that mature fruit had been mixed in from the tropics, but if so, then land and ocean animals should be mixed together as well. In fact, they are found in separate deposits, except for some land organisms that floated out to sea.

These and other difficulties led scientists to accept the uniformitarian geology proposed by James Hutton (Theory of the Earth) and Charles Lyell (Principles of Geology). And along came Lamarck, Wallace, and Darwin!
Fossils record forms in evolution.

- Paleontology – the study of fossil remains and other clues to past life.
- Fossil – any evidence of an organism from more than \( \sim 10,000 \) years ago.
- Fossils can form through several methods.
- The fossil record is often incomplete. But some examples of a complete record of transitional forms are well known, e.g. horses and whales!
The whale story

See e.g. http://www.pbs.org/wgbh/evolution/library/03/4/1_034_05.html

Amazingly, the ancestor of this ancient land mammal’s most closely related extant descendant is the Hippo! And molecules tell the same story.
Here's a picture, a phylogeny, of that evolution.

http://www-personal.umich.edu/~gingeric/PDGwhales/Whales.htm
All sorts of fossils going on . . .

Be sure to check out:
http://www.ucmp.berkeley.edu/index.php
This one is in the Grand Canyon and those are my sun glasses!
‘Gaps in the fossil record’ aren’t really a problem . . .

* They should be there:
  * The vast majority of organisms never leave fossils, it’s a rare phenomenon;
  * Geological events destroy fossils; and they . . .
  * May be buried deep underground or even underwater; and maybe . . .
  * We just haven’t found them yet!
They are formed through a variety of processes: Compression, Impression, Cast, Petrification, and Intact preservation, e.g. amber.
We can tell the age of fossils.

* Relative dating – places fossil into a sequence of events without assigning a specific age through the . . .

* Principle of superposition – older is deeper.

* Absolute dating → range of likely dates.

* Radiometric dating uses isotopes as a clock.

* It uses the concept of half-life – the time it takes for half of the atoms to decay, e.g. with their effective date range . . .

* Carbon-14 ($^{14}$C, several 100 to around 60,000 years), potassium-40 ($^{40}$K, 100,000 to 4.5 billion years), and Uranium-238 ($^{238}$U, 1 million to 4.5 billion years).
The principle . . .

Plants incorporate it from CO\(_2\) and it passes up the food chain.

So we just measure the amount of \(^{14}\)C left. But it’ll only work for things less than ~60,000 years old and only for organic materials (i.e. not for inorganic fossils).
What's this have to do with morphology?

* Morphology is the only way to estimate the relationships of fossils among themselves and to extant (present-day) organisms.

* And the dating of fossils allows us to calibrate the phylogenies of extant organisms. Fossil dates must be at or before nodes on the tree where that group appears.

* What about this geographic clustering effect that so troubled early naturalists and didn't fit with Biblical Creation?
Large-scale changes in the Earth's surface influenced evolution, big-time!

* Plate tectonics — the Earth's surface consists of several rigid plates (tectonic plates) that move, really.
* Areas can rise up when plates come together, e.g. the Himalayas! Also . . .
* Subduction zone — one plate goes under the other.
Biogeography:

Where you are matters!

Check out the PaleoMap project: http://www.scotese.com/
Biogeography - study of distribution pattern of species across the planet.

* Marsupials are mammals whose young are born tiny and helpless and complete development in the mother's pouch.

* Australia has many marsupials unlike the rest of the world, which only has a few, e.g. the 'possum.'

* Marsupials were once widespread in Gondwana.

* Then Australia drifted off.

* South America had marsupials but most went extinct when placental mammals moved in.

* Marsupials remained abundant and diversified in Australia due to isolation.
Biogeography works on a much smaller scale too.

- e.g. On island chains:
  - Organisms that can swim, fly, or raft to new habitat colonize an island.
  - They undergo adaptive radiation!
  - And exchange with the mainland is probably quite rare. Therefore, . . .
  - Relocated organisms evolve into new species (small population size, many available niches, no competition . . .)
Homology!

* Probably the most important concept in evolutionary biology.
* Similarities between two structures reflects common ancestry (usually); e.g. . . .
* Different modern vertebrates share many anatomical similarities because they share a common ancestor that originated this organization.
* Homologous structures may not even have the same function; e.g. . . .
* Our middle ear bones and fish jaw bones
Homologous morphological structures

All the same bones — the forelimb of land vertebrates

Copyright © The McGraw-Hill Companies, Inc. Permission required for reproduction or display.
Analogous structures . . .

- May appear superficially similar, but . . .
- Are similar adaptations in organisms that do not share the same evolutionary history. They are . . .
- Due to convergent evolution; e.g. bird wings and insect wings.
Homology versus Analogy:

At least the bones are; not the flight surface.

No common ancestry of the parts.
What about vestigial structures?

- They have no apparent function in one species, but are homologous to a functional organ in another, e.g. . . .
- Some whales and snakes have vestigial limbs, and the . . .
- Human appendix. Also, . . .
- Humans have muscles that most of us can't use, but in other mammals they are used to move their ears.
Ernst Haeckel (1834–1919) said, “Ontogeny recapitulates phylogeny.” That is, the embryonic development of an individual organism (its ontogeny) follows the same path as the evolutionary history of its species (its phylogeny).

Controversial due to Haeckel’s overly ambitious artistic license! However, we now see that there really are many similarities of form in embryonic structures between different species.
So, what about living, present day, adult critters?

* All the same criteria hold.
* We can compare homologous structures to ascertain phylogeny.
* But the structures have to be homologous!
* Parsimony states that simplest explanation is that organisms that share the same derived structures are related, rather than requiring those structures to be reinvented each time in each organism.
An example in Hemichordata

Fig. 2. Scanning electron micrographs (SEMs; B, D, and F) showing the dorsal epibranchial ridge and gill bars of three enteropneust pharynxes with the anterior to the left. (A) Colour photograph of a 55-cm long enteropneust Glossobalanus polybranchioporus displaying regionalization in the trunk, including gonadal wings, liver sacs, esophagus, and intestine, which is characteristic of the family Ptychodidae. (B) SEM of the gill region of an unidentified species of Ptychodera shows synaptacles, or cross bridges, joining the primary and secondary gill bars. (C) Schizocardium braziliense belongs to the family Spengelidae, a group that lacks gonadal wings, and except for the genus Schizocardium, lacks liver sacs. (D) The gill bars of the genus Schizocardium have synapticles. (E) Saccoglossus pusillus typifies the harrimaniid morphology in lacking liver sacs, genital wings, and synapticles bridging the gill bars. (F) SEM of a 20-day-old specimen of Saccoglossus kowalevskii. The pair of gill pores of enteropneusts develops sequentially, starting at the anterior region of the trunk and adding successive pairs posteriorly (inset). They elongate into a slit shape with the development of the collagenous gill bars. (H) A zooid of the pterobranch Cephalodiscus gracilis that has been removed from its tube. Cephalodiscus gracilis has a single pair of gill pores (inset) that are not heavily ciliated and thus probably do not pump water from the pharynx. (I) SEM of the outer pharynx of the cephalochordate Branchiostoma floridae. The metapleuralfold has been removed to show detail of the gill bars, including synapticles. Collar (c), cephalic shield (cs), gonadal wing (gw), proboscis (p), posterior extension of metasome (pm), primary gill bar (pg), synapticle (s), secondary (tongue) gill bar (sg), and trunk (t). Refer to Fig. 1 for other abbreviations.

Sensitivity analysis

To determine if the branching pattern among the deuterostomes (Fig. 5) was robust, I tested the effects of removing the (i) tunicates and (ii) enteropneust taxa from the matrix (Table 1), and then re-ran the bootstrap analysis. The resultant bootstrap values of five clades in the deuterostome tree are listed in Table 4.

Support for this hypothesis adds an additional 4 steps to the most parsimonious tree (Table 3). The recent hypothesis that the pterobranchs are sister-taxon to the harrimaniid worms (Cameron et al. 2000; Peterson and Eernisse 2001) (i.e., enteropneust polyphyly) is supported by this data, but an additional 6 steps are necessary to fit the data to the tree. Constraining the data to a tree that places the pterobranchs as sister-taxon to the remaining deuterostomes (Jeffries 1986) results in a TL of 165 steps, 7 steps longer than the shortest tree (Table 3).


Cnidaaria
Polychaeta
Sipuncula
Crinoidea
Asteroidea
Ophuroidea
Echioidea
Holothuroida
Rhabdopleura
Cephalodiscus
Protoglossus
Saccoglossus
Stereobalanus
Xenopleura
Saxipendium
Spengelia
Schizocardium
Glandiceps
Willeyia
Balanoglossus
Psychoderidae
Glossobalanus
Tunicata
Cephalochordata
Vertebrata
As I said molecular evidence corroborates.

* The main principle:

* It is very unlikely that two unrelated species would evolve precisely the same DNA and protein sequences by chance. It is way . . .

* More likely that similarities are due to common ancestry and that the differences are due to mutation after divergence (parsimony).

* Therefore, the more closely related two species are, the more alike their DNA or proteins are.
This can roughly be seen in data like Cytochrome C.

But it’s a huge oversimplification!

At first it was highly criticized – “molecules vs. morphology” – but as data accumulated, corroboration did as well.

Hemoglobin was perhaps the first molecule used in deciphering phylogeny (Zuckerkandl and Pauling, 1965 – way before DNA sequencing).
But we still have to compare homologs!

* The concepts of common ancestry and homology extend beyond anatomy, and physiology, on to genes, and even down to the smallest heritable unit of life, the individual base pairs of DNA.

* And now we have to concern ourselves with more than one type of homology – at least with paralogy and orthology.
Orthologs vs. Paralogs

* Paralogs are the result of gene duplication and subsequent divergence within a lineage; orthologs result from speciation events between lineages. So both tell the story of gene evolution, but only orthologs specifically let us know about speciation.

* Take for instance the following example . . .
The true tree – an ancient gene duplication, prior to the divergence of frogs and humans, produced two copies of hemoglobin.

The confusing tree – due to lack of full representation of orthologs and paralogs – frogs are more closely related to humans than mice!
Fortunately, this is less and less a problem as we learn more, and as the databases get bigger and better.

- However, there is one huge problem — we can only see present day sequence differences, but . . .
- Not all the mutations that have occurred in the past.
- If we truly knew the actual number of events that had occurred in evolutionary history then we could always get the correct tree! But we don’t . . .
‘Shit happens’ phenomenon . . .

This situation necessitates the use of models!

The model of evolution itself –

How much evolution we don’t see because of ‘multiple hits,’ e.g.

\[ A \rightarrow G \rightarrow C \rightarrow G, \]  three events yielding one observed substitution, or

\[ A \rightarrow G \rightarrow A, \]  two events yielding no observed substitutions.
Evolutionary models...

* Are beyond the scope of this course, but...

* Suffice it to say that they attempt to estimate that ‘missing’ evolution we can’t see by inferring:

1) The probabilities of the exchange of one character (either DNA base or protein amino acid) into another;

2) The initial frequencies of those characters; and...

3) The relative rates of change of one part of the sequence compared to another.
All molecular phylogenetic inference methods start with an alignment!
Based on that alignment, and the inference methods that we’ll leave a ‘black box’ for now, we can come up with molecular phylogenies.
So let’s run through a bunch of examples . . .

* Some will be from textbooks,
* Most will be from my own and my colleagues’ research, as was the previous example. These will include:
  * Back to Evo-Devo,
  * Return to the whale,
  * What about those lemurs? And . . .
  * The vertebrate radiation.
Let’s start with Evo-Devo.

* Remember, Evo-Devo is Evolutionary Developmental biology. It is the . . .

* Study of genes and nongenic elements that regulate development and give rise to new body forms;

* Often this involves gradients in different proteins during development that mold the shape of the embryo.

* New phenotypes arise from changing the timing or locations of these signals.

* The text shows a couple of cases.
One mentions the subtle developmental cues coded in minor differences in regulatory DNA that differentiate chimpanzees from humans. Depending on how you measure it, chimp and human DNA differs by only 5 to 1%. One of these regulatory regions that controls brain development is named HAR1 (Haussler’s group @ UCSC)
Another well known Evo-Devo case are HOX genes. These genes control development in all sorts of ways and mutation in them can cause really weird things! See http://www.pbs.org/wgbh/evolution/library/03/4/l_034_04.html.
A friend, Axel Meyer, works on these in fishes. He looked at the evolution of the HOX cluster of homeotic genes and postulated that their duplications were responsible for the huge diversification of form seen in fishes.
The molecules totally agree, including IRBP and VWF gene sequences (Montgelard et al. 1997), y-Fibrinogen gene sequences between cytochrome b and 12S rRNA sequences (Montgelard et al. 1997), y-Fibrinogen gene sequences, the ancient ancestor of the hippo also leading to the whale. Well... based on lots of characters.

Remember that we have complete fossil representation for whales with tons of intermediate forms, the ancient ancestor of the hippo also leading to the whale. Well... based on lots of characters.

...
What about those lemurs?

Based on all sorts of genes, including ancient DNA from “subfossils,” there was only one colonization event and it happened around 62 million years ago! What else happened then – the end of the ‘Age of Dinosaurs.’

Extinct & Extant lemurs form a clade

The aye-aye remains as the basal lineage

Karanth et al., 2005; PNAS
And the vertebrate radiation?

* This has to do with the diversification of the vertebrates after the split from critters with only a notochord, as exemplified by Amphioxus, seen here in juvenile form:

* This group diverged from a common ancestor of the vertebrates 520 million years ago!
This has been studied in a number of systems, many of which are the regulatory Evo-Devo type we talked about earlier.

For example, with Pax genes (important in many organs' development), Bassham, et al. 2008.

The ‘total evidence’ approach is reviewed by Swalla and Smith, 2008.
So where do all these dates come from?

Based on known event dates, such as fossils, we can use the “molecular clock” to date our phylogenies. Here are the ‘known’ divergence times in Ann Yoder’s lemur study.

C1: Human/Gorilla (8-12 Ma)
C2: Monkey/Ape (32-38 Ma)
C3: Basal Primate (63-90 Ma)
C4: Perrisodactyla (50-58 Ma)
C5: Whale/Whale (33-40 Ma)
C6: Whale/Hippo (51-60 Ma)
C7: Canid/Felid (45-65 Ma)
C8: Loris/Galago (38-42 Ma)
Molecular clocks? Huh!

- Based on the predictions of the Neutral Theory (next time), evolution should proceed at a relatively clock-like manner. Therefore, . . .
- If biologists know the average mutation rate for a particular system, plus the amount of evolution that has happened between any two species (from the tree and the model), then . . .
- Molecular sequences can be used to estimate the time when organisms diverged from a common ancestor.
- Mitochondrial DNA (mtDNA) is nice for newer divergences, because it’s clock runs 5-10 times faster than most nuclear DNA clocks.
But the molecular clock isn’t perfect . . .

Different lineages evolve at different rates — time is ‘squishy.’
Therefore, the best modern methods . . .

* allow for violation of the molecular clock (rate variation) in different parts of the tree;
* compensate for multiple hits (hidden evolution) via models of molecular evolution;
* allow for the use multiple fossil (or other, e.g. clinical isolates) calibration points, and . . .
* accommodate uncertainties in the fossil record (via upper and lower bounds).
Then, great things can then happen!

Such as tracking the spread of Influenza A (from A. Drummond @ MBL MolEvol Workshop, 2009)!
And the H1N1 Swine flu outbreak!

Also from A. Drummond @ MBL MolEvol Workshop, 2009, and see http://tree.bio.ed.ac.uk/groups/influenza/.
The out of Africa hypothesis is based on the diversity, biogeography, and phylogeny of human mtDNA.

mtDNA is maternally inherited. Work has also been duplicated with similar results using the Y chromosome, which, of course, is paternally inherited.
Are you convinced now?

* The evidence in incontrovertible.
* Evolution is real, and happening all around us, all the time.
* Next time we’ll go more into natural selection, not too far, just far enough that you’ll be able to understand the process a bit better. It’s not magic.