macroevolution
Macroevolution - patterns in the history of life

There are several patterns we see when we look at the fossil record over geologic time

1. STASIS

A species’ morphology does not change over time. The classic example of this is the “living fossil” the *Coelocanth*…a fish taxa (genus) that evolved in the Mesozoic, but is still alive today.
2. Characteristics change over time

morphologies change over time, for example, increases in shell thickness or number of ribs on a shell or length/width ratios.

3. Speciation

Constructing phylogenies shows how different species alive at different time intervals are related to one another. These 3 phylogenies show 3 different patterns. Clade A shows that speciation happened at several times in the past. Clade B shows stability in species over long periods of time, and Clade C shows two periods of time when speciation was focused.
One mode of speciation is termed “phyletic gradualism” which is shown in the red line of gradual morphologic change over long periods of time in small, incremental steps. This is the pattern that Darwin was thinking of when he described the ‘transmutation’ or change in species over time.

Another form of speciation is termed “punctuated equilibrium” which is exhibited in all species in this diagram. For example, in species B (green) we see stasis in morphology over long periods of time, with a short interval of time in which morphologic change occurs. What is happening in this interval of time is “invasion” from a geographically isolated population whose gene pool has diverged.
Incremental morphologic change over time. results from changes in the gene pool over time. The graph represents an imaginary distribution of genes in a species (think of the human genome project for all humans!). If an environmental change applies a stress on a species, those having certain genes that enable them to adapt will successfully reproduce and individuals with more of those genes will appear in subsequent generations. Over time the entire gene pool will accumulate these changes and the distribution will change. This type of gradual change in the genotype will result in incremental changes in the phenotype.
4. extinction

Extinction can be frequent or rare within a clade. It can occur simultaneously across several taxa, in which case we may call it a mass extinction (usually defined as 50% of species go extinct). Over 99% of all species that have inhabited the earth have gone extinct. Extinction doesn’t imply “failure” or non-adaptation. It can occur randomly. The average duration of a species is only 1 million years before it experiences extinction.

The 5 major mass extinctions in the history of the earth. Know when these were!
Other Major Issues to Touch On:

1. **Intermediate forms**: how do major new morphologies arise?
   ex, whale evolution...why did mammals return to the sea? How could there be intermediaries to this?

2. **The origin of diversity**
   The photo illustrates a Devonian insect similar to the modern “silverfish.” By the end of the Devonian, this ancestral insect had given rise to two descendents, who subsequently diversified very differently: one into many, many more species than the other. Why did they diversify so differently?
1. Intermediate forms…the search for “missing links”

One strategy for identifying evolutionary relationships, especially of The higher taxonomic orders (= appearance of new traits) is through homology.

Evolution works primarily by modifying pre-existing structures.

“A structure is similar among related organisms because those organisms have all descended from a common ancestor that had an equivalent trait”  Darwin
All tetrapods (= four legged) have limbs with five digits, at least at some stage in development. Certain tetrapods lose some of these digits during development, as in the bird wing shown here. But if the bird wing does not need five digits, why do five initially develop in the growing embryo? The most plausible explanation is that while the five digits are not functionally necessary, they represent a genetic artifact inherited from the ancestors of birds.
Example: Evolution of whales

Land mammal with whale-like teeth

- Had teeth like Mesonychids but an inner ear adapted for water, and nostrils on the top of its skull
- Limbs adapted to swimming and walking on land; shark-like teeth, pelvis like mammal
- Pelvis like whale (not fused to backbone); long snout with whale-like teeth
- Limbs were small flippers, whale-like teeth
- Tiny head, and pointed snout with teeth (modern whales have large heads and blunt snout)

Diversification of baleen whales from toothed whales in the Oligocene; the first baleen whales also had teeth along with their new loose jaw
Movie on whale evolution:


The fossil record preserves several intermediary forms from land-dwelling mammals that forayed into water (for food? To escape predation?) and those with limb, teeth and skull structures which indicate progressively increasing amount of time in - and under-water.

Did whales need to enter the water? Did the ability to stay in water become more well developed with successive generations? 

*or*

Was there a range of variation in ancestral-whale mammals …various tooth structures developed that enabled them to catch and eat fish; nose openings higher on the skull appeared; a re-positioned forelimb appeared (what are the mechanisms by which this variation can occur?)
How can complex structures like a limb develop?

The first fossil that indicates a land-dwelling habitat is a Devonian organism called *Ichthyostega*. How did the structures for this extreme an environmental change (water to land) occur? It must have involved changes in respiration, limb structure, limb orientation and brain neuro-skeletal changes. How could this happen? Discrete stages:

1. The evolution of lungs happened in fish lineages (the lungfish) - this structure was already in place
2. The evolution of a limb that could bear weight
3. The evolution of limbs that could walk (*Acanthostega*)
4. The evolution of structural support for the skull

All of these did not happen at once. Lungs developed early. How did limbs develop from fins? How did limb attachment to the body alter? How did the skull evolve?
The development of bony fins in fish (the Crossopterygii). The bones shown are covered with scales on the fish. Note that the bones consist of the humerus, radius, ulna and only a few phalanges (in fish termed “rays”).

The lung fish and mudskippers use bony fins for locomotion in muddy shallow water, in other words, a structure that could be used for walking was already formed and only needed to be modified to bear weight (an example of “pre-adaptation”).

How did the bony fin become more fully “digitized” for walking? genetic variation and natural selection: “fine-tuning” structures

http://www.pbs.org/wgbh/evolution/library/03/4/l_034_03.html
How can major structures like limbs develop?

- Work on the genetics of *Drosophila* have documented the existence of a group of genes termed the “homeotic selector genes.” These genes produce proteins that “turn on” other genes by directly bonding to specific DNA sequences, causing these genes to produce proteins: molecular dominoes. Thru the action of these genes (termed “HOX genes) cells are “taught” what they are, where they are supposed to be relative to neighboring cells, and how to be “a team player.” Differences in body shape result from changes in the concentration of HOX genes. Mutation in HOX genes can cause a huge range of very major changes in body plan, for example, the appearance of appendages. Famous ex of *Drosophila* developing an extra set of legs by mutation of HOX genes
Ex: Evolution of complex structures: the jaw

The cartilaginous structures called “gill arches” in fish (blue) support the soft tissue of the gill. The first pair of gill arches (red) rotated forward as did the second pair (green) of gill arches.

How do we know this happened? We can study the genetics of modern lamprey. During embryonic development we actually can trace HOX gene activity that causes changes in the mandible (jaw)
How did a complex structure such as a wing develop? Was there ever a primitive, poorly-functioning wing (a “half-wing”) for some “missing link” organism that later evolved into a functioning wing for flight?

Rotated scapula created a shoulder blade and allowed for increased limb rotation and the creation of the first “arm” Sinosauropteryx – 125 MYA

Development of a small bone called the semi-lunate carpel allowed the phalanges to rotate, in other words, the creation of a “wrist” Velociraptor – 85–80 MYA

All images are from www.dinosaur-world.com/feathered_dinosaurs/wing_evolution.htm
Rotation of the position of the scapula in this ostrich-sized dinosaur increased up and down movement of the arm. *Unenlagia* – 90 MYA

Development of a small sternum (breastbone) provided a site of attachment to muscles that could allow the arm to move up and down rapidly (=flap). *Archaeopteryx* – 150–148 MYA
the first digit, or “thumb” of this dinosaur developed the ability to attach the feathers (alula) that control flight; equivalent to the flaps on a plane wing they allow bank and turn maneuvers. Eoalulavis – 125–130 MYA

Modern birds have small, hollow bones, large wing surface, short tails, large sternum, sophisticated feathers
Modern Birds – 65 MYA to present

Note that this sequence is not linear! Some features developed early in organisms in response to some environmental stress, others developed later. Feathers, for example, evolved in dinosaurs that were entirely terrestrial (not as a precursor to flight). These features evolved and were later modified in response to natural selection (=pre-adaptation).
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Diversification can happen when
* The environment may have offered opportunities for specialization.
* A fragmented environment might make reproductive isolation likely.
* The environment may have provided a release from competition with other insects.

All of these factors can drive diversification—but only if the population has the genetic variation to take advantage of the opportunities presented by the environment.

3. **Adaptive Radiation** - if diversification happens in a short time it is termed an adaptive radiation. The newly evolved lineages have different adaptations than their single ancestor. This reflects the adaptations to exploit new resources. The most famous adaptive radiation in earth history is the “Cambrian explosion” or rapid diversification of life after the Precambrian, followed closely by the radiation following the extinction of the dinosaurs.....
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The adaptive radiation of the mammals - note that this diversification is concentrated between 70 and 50 mya.

Why does adaptive radiation occur?
The earliest mammals evolved from a group of dinosaurs called the therapsids in the Late Triassic. The earliest ID’d mammal is smaller than a cat and is distinguished by its teeth and ear bones. Mammals did begin to diversify before the dinos went extinct at the end of the Cretaceous. One of these mammals was an ancestral primate.

Were mammals superior to dinosaurs?
4. **Extinctions.** The flip side of the adaptive radiation coin. When large numbers of organisms go extinct, niches are made available for adaptive radiations.

Following these mass extinctions were explosions in the diversity of life.

What causes extinction? There is a theory that “extinction happens,” if a species exist for only ~1my, then if you have a mono-phyletic Family, it will go extinct ~1my. If you have a low diversity taxon, for example a Class made up of only 2 or 3 species, then it will go extinct in 2-3 my. Statistically then, extinctions can just “happen.” Another theory: major environmental change (sea level, climate); a third: meteor impacts…not common, but episodic over timespans of Earth history.
5. **Evolutionary trends** - the evolution of “big structures” such as limbs, or a head (= cephalization). Is there a trend toward complexity?

This is a “major issue” that is still being discussed. With our anthropomorphic viewpoint, we think life has gotten more “complex” with us at the pinnacle. HOWEVER, given the abundance of life forms such as bacteria (the original species still exist!), beetles (more species than any other invertebrates!), and bony fish (most vertebrate species!) perhaps this is not true!
Thanks to the Berkeley Museum website for many of these illustrations

http://evolution.berkeley.edu/evosite/evohome.html