Bio 1B  Lecture Outline (please print and bring along)  Fall, 2008
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Evolution lecture #6 -- **Tempo and Mode in Macroevolution** -- Nov. 14th, 2008

• **Summary of topics**

  • Define and contrast **adaptation** and **exaptation**
  • Give examples of how **adaptive radiations** lead to diversity within an evolutionary lineage
  • Give examples of how **convergent evolution** shows the action of selection on organisms that are not closely related but have a shared way of life
  • Contrast **punctuated equilibria** and **gradualism**
  • Describe the features of **developmental changes** that can lead to evolution ("evo-devo")
  • Define **macroevolution**

• **Adaptation**

  **Adaptation:** Based on the observation that organism matches environment closely.  Darwin & many Darwinians thought that all structures must be adaptive for something.  But, this has come under severe challenge in recent years.  Not all structures and functions are adaptive.  Some matches between organism and environment are accidental, or the causality is reverse (i.e., the structure came first, function much later).

  • By definition, an adaptation in a formal sense requires fulfillment of four different tests:
    
    **Engineering.** Structure must indeed function in hypothesized sense.
    
    **Heritability.** Differences between organisms must be passed on to offspring.
    
    **Natural Selection.** Difference in fitness must occur because of differences in the hypothesized adaptation.
    
    **Phylogeny.** Hypothesized adaptive state must have evolved in the context of the hypothesized cause.  Think in terms of **problem** (e.g., environmental change) and **solution** (adaptation).  Requires correct phylogenetic polarity (i.e., correct sequence of events on a cladogram).

  • Only something that passes all these tests is a **adaptation.**  If it passes tests 1-3 it could be called an **aptation.**  If it then fails test 4 it could be called as **exaptation.**
The Phylogeny test: polarity

FUNCTIONAL CHARACTERISTICS:

<table>
<thead>
<tr>
<th>TAXON</th>
<th>leaves:</th>
<th>aphid predation:</th>
<th>habitat:</th>
<th>presence of toxic chemical:</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>smooth</td>
<td>no</td>
<td>forest</td>
<td>yes</td>
</tr>
<tr>
<td>B</td>
<td>smooth</td>
<td>yes</td>
<td>forest</td>
<td>yes</td>
</tr>
<tr>
<td>C</td>
<td>hairy</td>
<td>yes</td>
<td>desert</td>
<td>yes</td>
</tr>
<tr>
<td>D</td>
<td>hairy</td>
<td>yes</td>
<td>desert</td>
<td>yes</td>
</tr>
<tr>
<td>outgroup</td>
<td>smooth</td>
<td>no</td>
<td>forest</td>
<td>no</td>
</tr>
</tbody>
</table>

Which of the following adaptive scenarios are supported by these data? Which can be rejected?

a. Hairy leaves evolved to deter aphid predation.  
   (supported)

b. Hairy leaves evolved to insulate leaves in desert environments.  
   (supported weakly)

c. The toxic chemical evolved to deter aphid predation.  
   (rejected)

d. Smooth leaves evolved to gather more light in shady forest environments.  
   (can't say)

• Exaptation

Exaptation (previously called preadaptation): a structure that evolves and functions in one environmental context, but performs an additional function when placed in some new environment. The term is applied when a large change in function is accomplished with little change of structure. It is not called "preadaptation" any longer, because natural selection cannot look ahead and evolve characteristics that will later be useful.

The light honeycombed bones of birds predated flight in their agile, bipedal dinosaur ancestors, who would also have benefited from a light frame.

One question for evolutionary novelties is whether the conditions that favor their maintenance are the same as the conditions that favored their origin. For the eye, they probably did. For the wing, maybe; forerunners of what became wings might have been used for social displays and later co-opted for flight. Therefore, eyes were not exaptations, wings probably were.


• **Adaptive radiations**

  **adaptive radiation**: The evolutionary divergence of members of a single phylogenetic line into a variety of different adaptive forms, usually with reference to diversification in the use of resources and habitats.

  • **Adaptive radiations may obscure homologies**, since homologous traits may now differ greatly in how they look and how they function, but their heritage (homology) is seen in their:  
    - **detailed anatomy** (similarity in structure is seen which is not functionally necessary),  
    - **embryonic development** including the same relationship to surrounding characters, and  
    - **fossil history** (the ancestry of the 1 toed modern horse from a 3 toed and the original 5 toed tetrapod ancestor can be traced in the fossil record; Fig. 25.25 (8th), Fig. 24.20 (7th)).

  • **Radiations do not necessarily occur early in the history of a group**: mammals existed throughout most of the Mesozoic;

  • **The appropriate genetic variation must be available to take advantage of an empty niche** – flying insects arose in the Paleozoic, but pterosaurs and birds did not evolve until the Mesozoic.

  • Remember that an **evolutionary trend does not mean that evolution is goal oriented**.

• **Examples of adaptive radiations** are:

  • the so-called Cambrian explosion (all the animal phyla that exist today, plus possibly several that do not, originated in the Cambrian (the first period of the Paleozoic); Fig. 25.10 (8th), Fig. 26.17 (7th)).

  • the development of wings enabled insects to produce thousands of variations on the insect body plan;

  • major adaptive radiation of the mammals in the early Cenozoic, replacing the earlier adaptive radiation of dinosaurs;

  • Silverswords and honeycreepers on Hawaii;

  • finches on the Galapagos Islands; and

  • eucalyptus trees in Australia.

• **Examples of convergent evolution**

  The wing structures of pterosaurs (extinct flying reptiles of the Mesozoic), birds, and bats, are superficially similar, but they are constructed from different materials, and supported by different limb digits.
Other examples of convergent evolution include:

- the streamlined bodies of some marine animals, e.g., sharks, ichthyosaurs (extinct marine reptile of the Mesozoic), and dolphins;
- marsupial and placental mammal resemblances (Fig. 34.34 (8th), Fig. 34.35 (7th)).
- the development of eyes (however, the basic gene involved in eye development is homologous) (Fig. 25.24 (8th), Fig. 24.14 (7th)).
- burrowing animals
- resemblances between anteaters which are not closely related;
- Succulent plants: New World cacti, agaves, and yuccas vs. Old World aloes and euphorbs;
- leglessness in snakes and lizards;

Each of the 3 phyla (divisions) of plants—the brown, red, and green algae, independently evolved photosynthesis through the acquisition of chloroplasts from bluegreen bacteria (Fig. 28.3 (8th), Fig. 28.4 (7th)).

**reversion (reversal):** reappearance of ancestral characters that have been absent in intervening generations. Example: birds can re-express teeth -- a chicken with teeth!

**homoplasy:** possession by two or more species of a similar or identical character state that has not been derived by both species from their common ancestor; embraces convergence and evolutionary reversal

• **Punctuated equilibria and gradualism**

**George Gaylord Simpson:** pointed out that not only does the tempo, or rate, of evolution differ greatly from group to group, but groups apparently have rapid and relatively slow periods in their evolution. He felt new species are created on average every 200,000 years, and new genera every 1-2 million years.

**living fossils:** species that morphologically have changed little from their fossil ancestors in the distant past, e.g., lungfish, horseshoe crabs.

At the DNA level, living fossils usually show as much genetic variation, and molecular evolution, as other species.

**Eldredge and Gould:** proposed theory of punctuated equilibria in 1972.

**punctuated equilibria:** evolution occurring in spurts, creating a "punctuation" in the fossil record; the norm is long periods without change (stasis) punctuated by spurts of relatively rapid evolution (Fig. 24.17a (8th), Fig. 24.13b (7th)).

The hypothesis of **punctuated equilibrium** holds that evolution proceeds relatively rapidly during speciation.
Although the morphological changes are perhaps continuous in the sense of passing through many intermediate stages, the changes when they occur have been so rapid that the fossil record presents the appearance of a discontinuous change.

Between speciation events the population remains relatively constant (a condition Eldredge and Gould called \textit{stasis}), and speciation occurs when a sub-population splits off and evolves rapidly into a new species.

Gould and Eldredge claim that punctuation and stasis is the most common pattern in the fossil record, but other researchers disagree. The true situation is probably a mixture of punctuation and gradualism.

\textbf{gradualism:} gradual evolutionary change (Fig. 24.17b (8th), Fig. 24.13a (7th)).

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{gradualism.png}
\caption{A: The gradualist "tree of life", after Weller B: The punctuated-equilibrium "tree of life"}
\end{figure}

\textit{Evolution and Development (Evo/Devo)}

\textbf{allometric growth:} difference in relative rates of growth of various parts of the body (Fig. 25.19 (8th), Fig. 24.15 (7th)).

\textbf{heterochrony:} evolutionary changes in the timing or rate of development. Heterochronic changes can result in the appearance juvenile characteristics of one species in the adults of another species, called paedomorphosis. Heterochrony can thus result in the appearance of several coordinated changes being the result of a single change in development. By looking at the adult phenotype, it is not always easy to decide what character or characters evolved. Large difference might be the result of a simple change, as in the salamander foot.

\textbf{paedomorphosis:} a sexually mature adult retains features that were juvenile structures in its evolutionary ancestors (Fig. 25.20 (8th), Fig. 24.16 (7th)). Humans are thought to be paedomorphic relative to chimps.
**hypermorphosis**: extending development past the ancestral stage

**Hox genes**: are regulatory genes that affect morphological evolution (Figs. 25.21 and 25.22 (8th), Figs. 24.18 and 24.19 (7th)).

They are transcription-regulating factors with spatial and temporal patterns of expression that provide positional information.

Homeotic or Hox genes control where specific structures are formed. For example, one important difference between fish and tetrapods is where on the limb bud a Hox gene is expressed.

Hox genes have been found in all animal phyla investigated. Divergence among Hox genes and their functions in different lineages of animals is thought to underlie many differences in body plans, both among and within phyla.

The Hox gene cluster has been duplicated twice in the history of vertebrates. The first duplication occurred about 520 mya and may have been a critical step in the evolution of vertebrates, and the second, about 425 mya may have permitted an increase in morphological complexity of vertebrates.

**macroevolution**: the major events in the history of life that are revealed by the fossil record. Sometimes referred to as “evolution above the species level.” Macroevolution encompasses such events as the formation of higher taxa (genera, families, orders, etc.); the origin of novel features, e.g., wings, mass extinctions, e.g., of dinosaurs at end of Mesozoic.

**microevolution**: changes in the gene pool of a population over successive generations (more details in later lecture).

- **Large scale macroevolutionary patterns are the result of microevolutionary changes combined with species selection.**

**species selection**: results from differences in the rate of speciation and extinction. Once a species makes or begins to make an adaptive transition, its descendents may have such an advantage that they will increase their geographic range, colonize new habitats, and evolve further very rapidly. The result will be a wide variety of species that share the new adaptation. Powered flight evolved very few times only in vertebrates, in pterosaurs, birds and bats. Bats have become very diverse and abundant because of their ability to fly. They comprise roughly 25\% of the 4000 species of mammals. They have a worldwide distribution and are abundant wherever they are found. Anteater morphology has evolved in mammals a comparable number of times but it does not seem to be such a good idea so there are very few such species.

**Surviving species often do not indicate past levels of diversity or past trends.** Both horses and hominids have only a single surviving species. Without knowledge of the fossil record, we would tend to think of a single directional trend.
Questions relating to lecture on Tempo and Mode of Evolution

1. Do self quiz questions #’s 5 and 7 on page 533 of the textbook (8th edition), or #’s 9 and 10 on page 489 of the 7th edition.

2. All the major groups of land living animals, except the birds, contain species that produce live babies. For animals that mate on land, fertilization within the female is the rule. Retaining fertile eggs within her body long enough for them to hatch there does not require major anatomical or physiological changes. The trait viviparity (giving birth to live young) is believed to have arisen independently a number of times in frogs and reptiles. In these cases, viviparity is

   A. an example of homoplasy
   B. an analogous trait
   C. an example of convergent evolution
   D. all of the above are correct
   E. none of the above is correct