B242 - MACROEVOLUTION

The topic of macroevolution is controversial and spans many issues linked by asking whether macroevolution a) simply reflects microevolution (within-population changes *e.g.* changes in gene frequency, role of drift *etc*) extrapolated over a long time scale or b) requires new mechanisms?

1) Rates of evolution during and between speciation events?

Can microevolution explain patterns? Evolutionary rates have been measured for many characters, in many species, at many different geologic times. The rates are very variable.
Q. Are the rates of change seen in the fossil record consistent with the mechanisms of evolutionary change studied by population geneticists?
A. Yes. Rates in artificial selection experiments are in fact, far higher than those measured in fossils.
So the magnitude/size of rates isn't a problem for a neo-Darwinist.

2) Relative rates of evolution during and between speciation events?

FOSSIL RECORD? Doesn't show smooth evolutionary transitions. Often a species appears abruptly, persists for a period then becomes extinct. A related species may then arise, but with little sign of any transitional forms between the putative ancestor and descendant.

Darwin's explanation was that the record was incomplete; evolution really was gradual, but most of the record had been lost. Claimed that where a complete fossil record could be found, it would show a gradual morphological change through time in lineages, and where lineages became split, gradual divergence of species: = Evolution by ‘Phyletic Gradualism’.

G. G. Simpson and colleagues (1950's) re-emphasised the role of natural selection. Recognised that rates of evolution can vary because intensities of selection vary. Geologically abrupt changes in morphology in fossil lineages may reflect bouts of pronounced directional selection. Periods of little change may reflect bouts of stabilising selection: = Evolution by ‘Punctuated Gradualism’.

By contrast, **Eldredge and Gould** (1972) argued that the fossil record was an accurate reflection of evolutionary history so that gradualism was an insufficient explanation. They proposed the term ‘punctuated equilibrium’. Their interpretation relies upon assumptions about the speciation process. That new species arise by splitting of lineages and develop rapidly. That small sub-population of the ancestral form gives rise to the new species (often in an isolated part of the ancestral species' geographic range).

If true then the implications for the fossil record?
1) The descendant species will not be preserved at the same site as its ancestor. 2) The new species will only leave fossils at the same site if it re-invades the same area. The transitional forms would be unrecorded because they were produced elsewhere. **Punctuated equilibria model predicts** 1) That most new species make sudden appearances in the fossil record 2) Between speciation events there are long periods of morphological stasis.

Punctuated equilibria versus phyletic gradualism?

Example 1: The Plio-Pleistocene Snails of Lake Turkana

Site (Lake Turkana, Northern Kenya) = very complete sedimentary record. Williamson (1981) documented the changes in snail shell patterns. Measured between 5 and 24 characters in 3300 specimens from 13 species' lineages. Concluded that snails in all 13 lineages showed *no change for prolonged periods, with occasional periods of punctuational change*.

Abrupt changes concentrated in intervals of about 5,000 to 50,000 years, much shorter than the long periods of constancy. Picture (on handout) shows the complex pattern of events. Y-axis shows the passage of time and the level of the lake; picture shows the changes in shell shape for a set of snails and bivalves.

Periods of transition coincide with each other in the various genera; and at times when the sea level changed. As the water level lowered, larger lakes would have fragmented into groups of smaller lakes, and the snails would have had their geographic ranges fragmented into many smaller isolated populations.

This combination of environmental change and isolated populations are the conditions required for allopatric speciation. <u>Potentially these snails show the essential features of the punctuated equilibria model.</u>

However study has been criticised. Some argue that the changes in the snails may not have been evolutionary changes but "ecophenotypic switches" (see my lecture ‘quantitative characters’). A snail's adult phenotype depends upon the environment during development. Perhaps Williamson’s snails haven't speciated and just resemble range of phenotypic variants of modern species.

If Williamson's punctuations are ecophenotypic switches, it would hardly be surprising if (a) *they took place rapidly* and (b) *changes were synchronous across genera*. Then they would not provide support for Eldredge and Gould's theory. So proceed with caution?

Example 2: Ordovician trilobites in Wales

Sheldon's (1987) biometric study of the evolution of trilobites. Extinct arthropods that can be classified by external morphological features such as the number of pygidial ribs. He examined the number of these ribs in 3458 specimens from 8 generic lineages over a period of about 3 million years. *In all 8 lineages the average number of ribs increased and the evolution was gradual*.

Picture (on handout) shows the pattern. A population at any one time was usually intermediate between the samples before and after it. Also a number of reversals in the different lineage which were NOT synchronised in the different lineages. Sheldon interpreted changes as evolutionary (*not ecophenotypic*).

Future research needed to establish which patterns of change are the most common.

Controversial extensions to Eldredge & Gould's basic model:

1) Peripheral population may live under abnormal conditions?

And this causes rapid changes at speciation? Stabilising selection will favour the evolution of homeostatic mechanisms that regulate development = not controversial. However under extreme conditions do these mechanisms break down so that there is a 'genetic revolution'?

No evidence.

2) Macroevolution proceeds via macromutations?

Suggested that most evolutionary breakthroughs could be by macromutations (in regulatory genes and so having multiple effects on the phenotype). The neo-Darwinian response is that developmental macromutations may arise from time to time but will always be **selectively disadvantageous** because they are introducing such a gross change.

Not likely to be important.

3) Stasis reflects developmental constraints?

The neo-Darwinist invokes stabilising selection to explain stasis. Others have suggested that it reflects developmental constraints (defined as "limitations on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system").

In effect, such constraints mean that species do not change because they lack the necessary genetic variation. Williamson argued that his snails showed developmental constraints. But we can test the hypothesis that a character isn't changing because of a lack of genetic variation by looking at modern specimens. Similar shell characters in modern species show substantial heritabilities. This suggests that the trait on fossil snails would have non-zero values arguing against a role for developmental constraints.