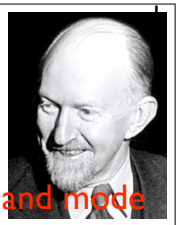
Macroevolution
Introduction



In this lecture we will examine the tempo and mode of evolution, in the words of George Gaylord Simpson.

Simpson studied whether macroevolutionary patterns arise from microevolutionary processes like those we've discussed through the term.

Simpson showed that major evolutionary developments in the fossil record took place in the irregular and undirected manner expected under Darwinian evolution.

Macroevolution
Introduction

TEMPO: Does morphological evolution occur gradually or in fits and starts?

MODE: Is there a tendency for organisms to evolve in a particular direction?

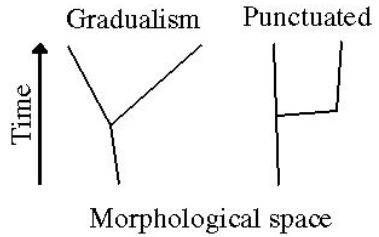
- Towards greater size?
- Towards greater complexity?

Macroevolution
Punctuated Equilibria vs. Gradualism

Following Darwin, the prevailing view of evolution by natural selection held that evolution is gradual.

- Macroevolutionary changes (large changes in morphology that define higher taxonomic divisions) accumulate over long periods of time by gradual microevolutionary processes.

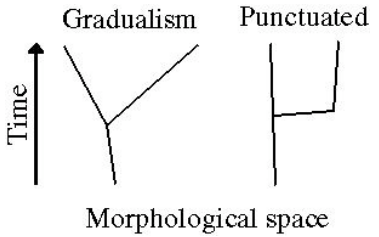
Nevertheless, the fossil record does not always show continuous and gradual changes.



Macroevolution
Punctuated Equilibria vs. Gradualism

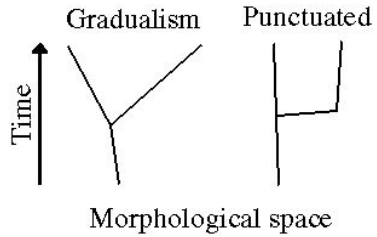
Simpson (1944) noted that higher taxa (e.g. orders of mammals) appear suddenly in the fossil record, describing this pattern as "quantum evolution".

Major morphological innovations sometimes appear suddenly in the fossil record, often preceded and followed by periods of relative stasis.



Macroevolution
Punctuated Equilibria vs. Gradualism

This has historically been interpreted as inaccuracy in the fossil record.

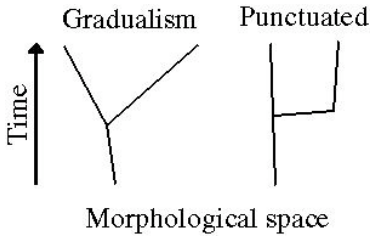


Macroevolution
Punctuated Equilibria vs. Gradualism

Eldredge and Gould (1972) argued otherwise:

1. The pattern was real
2. The pattern reflected a process whereby most evolutionary change happens around speciation events.

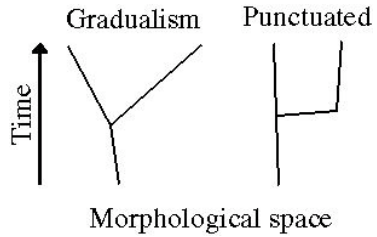
Punctuated equilibrium model of evolution



Macroevolution
Punctuated Equilibria vs. Gradualism

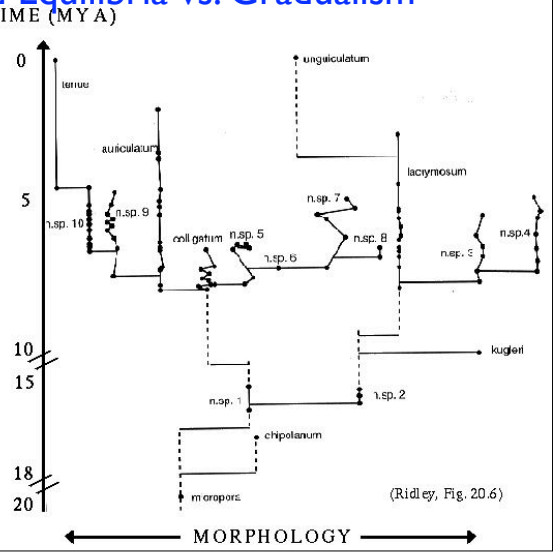
This was an extremely controversial interpretation.

Eldredge and Gould did not argue for instantaneous evolutionary change but rather a concentration of gradual evolutionary change near speciation events.



Macroevolution
Punctuated Equilibria vs. Gradualism

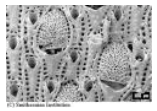
1. Is the pattern real?

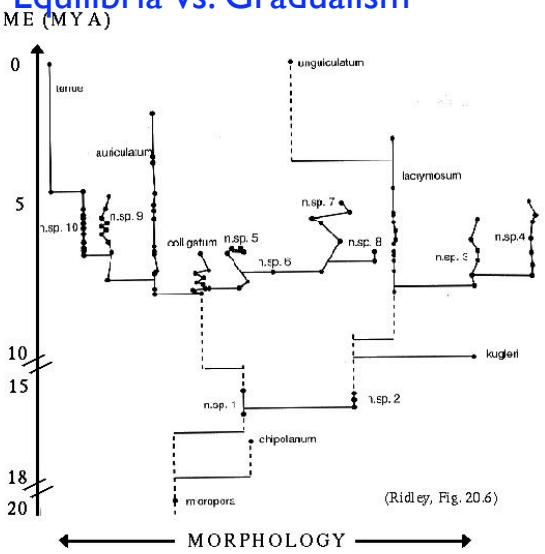


Macroevolution

Punctuated Equilibria vs. Gradualism

Cheetham (1986) examined 1000 fossil specimens from the Bryozoan genus *Metrarabdotos*, an aquatic invertebrate.

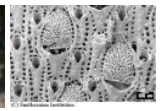



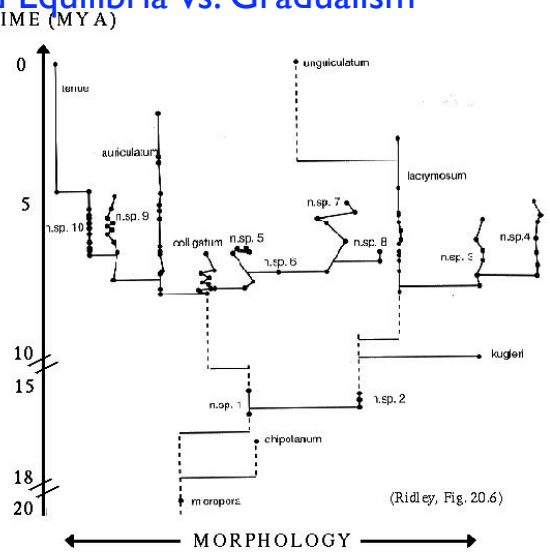


Macroevolution

Punctuated Equilibria vs. Gradualism

Using 46 morphological characters, Cheetham drew a phylogenetic tree connecting the specimens

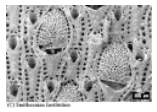



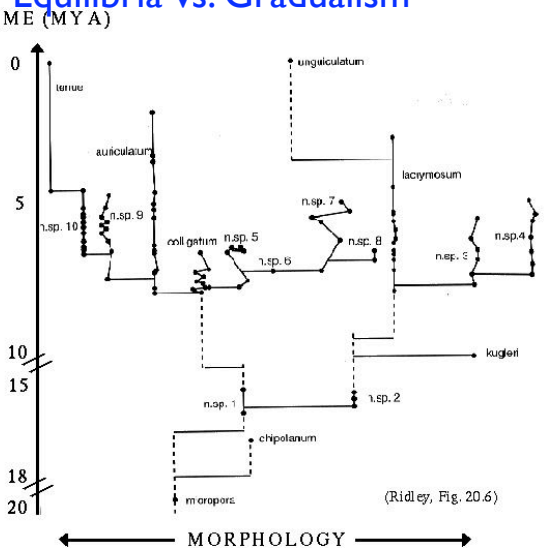


Macroevolution

Punctuated Equilibria vs. Gradualism

Relatively little change occurred within a morphospecies, while large shifts were observed between morphospecies.

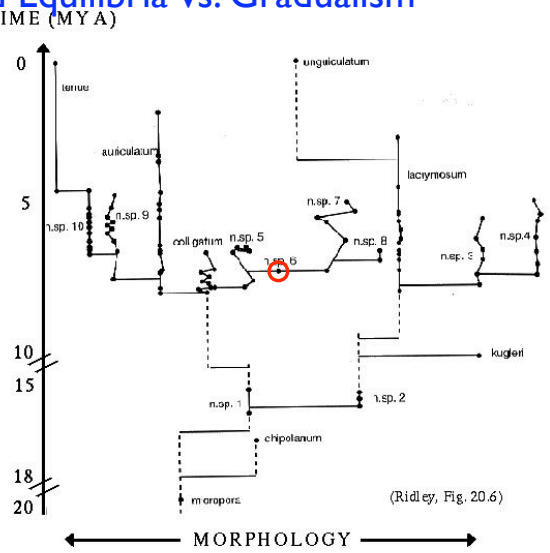





Macroevolution

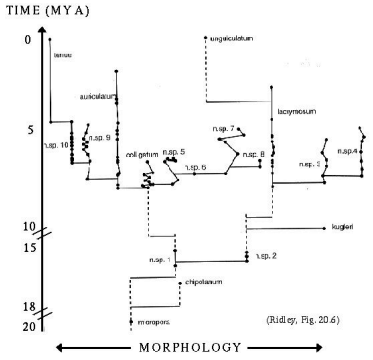
Punctuated Equilibria vs. Gradualism

Almost no intermediates were found in the fossil record between these morphospecies.

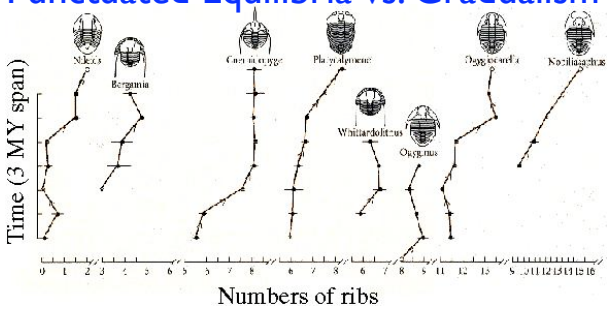


Macroevolution
Punctuated Equilibria vs. Gradualism

Interestingly, Jackson and Cheetham (1990,1994) examined 7 living Bryozoan species from this genus and confirmed that the morphospecies identified differed significantly from one another at a number of allozyme loci.

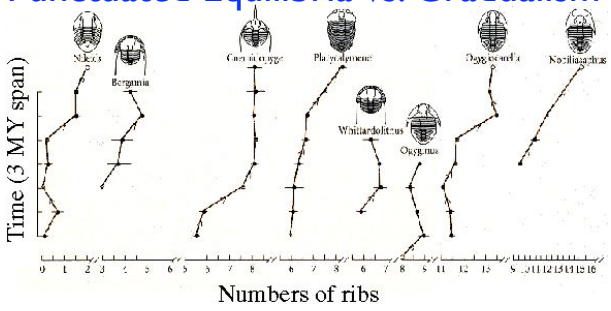


Macroevolution
Punctuated Equilibria vs. Gradualism



Sheldon studied 3458 specimens from eight trilobite lineages.

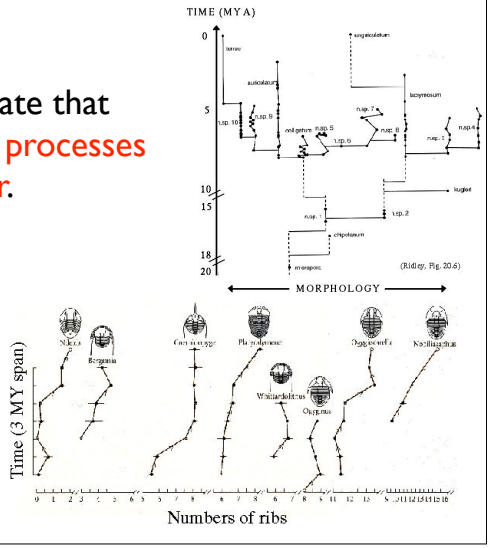
Macroevolution
Punctuated Equilibria vs. Gradualism



These lineages showed gradual change of a sufficiently pronounced nature that the specimens at the beginning and end of each lineage would be classified as different species (and in one case a different genus).

Macroevolution
Punctuated Equilibria vs. Gradualism

Such examples illustrate that punctuated and gradual processes can both occur.



Macroevolution
Punctuated Equilibria vs. Gradualism

Reviewing 58 such studies, Erwin and Anstey (1995) conclude:

"Paleontological evidence overwhelmingly supports a view that speciation is sometimes gradual and sometimes punctuated, and that no one mode characterizes this very complicated process."

Macroevolution
Punctuated Equilibria vs. Gradualism

(2) What explains punctuated evolution?

Why might morphological evolution be rapid around speciation events?

Why might morphological evolution be relatively static during other periods of time?

Macroevolution
Punctuated Equilibria vs. Gradualism

(2) What explains punctuated evolution?

Eldredge & Gould's (1972) explanation following Mayr:

- Peripatric speciation of a small isolated population might lead to rapid changes in a daughter population (drift), whereas large parental populations remain relatively unchanged.

Macroevolution
Punctuated Equilibria vs. Gradualism

(2) What explains punctuated evolution?

Gould & Eldredge's (1993) explanation following Futuyma:

- Populations are constantly changing, but genetic mixture across populations prevents sustained differences from accumulating. Speciation "locks up" the changes that a population has undergone.

Macroevolution
Directionality in evolution

"It is absurd to talk of one animal being higher than another...We consider those, where the intellectual faculties most developed, as highest. -- A bee doubtless would [use]...instincts."

Charles Darwin's Notebooks 1833-1844 (B46, 74)

Macroevolution
Directionality in evolution

"Progress" is a thorny concept in evolution, since it implies that there is a goal towards which evolution proceeds.

Natural selection and mutation are "myopic" processes: they act in the present and have no foresight.

Macroevolution
Directionality in evolution

Nevertheless, change does occur and often follows a particular trend (with exceptions).

Directional trends have been argued to occur along the following axes:

- Size
- Complexity

Macroevolution
Directionality in evolution – size

Cope's rule: Body size increases within a lineage over evolutionary time.

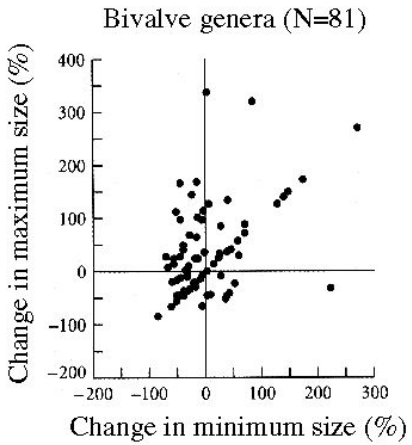
This rule has often been explained by the potential advantages of being large: increased defense, mating success, foraging success, improved homeostasis (sustaining a constant state in a changing environment).

However, we tend to focus on extreme cases where body size has clearly increased. Is Cope's rule generally true?

Macroevolution

Directionality in evolution – size

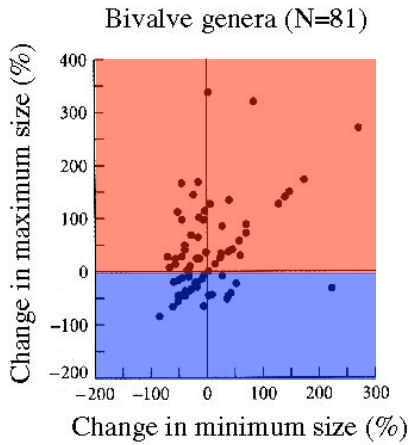
Jablonski (1996) examined 191 bivalve and gastropod lineages over a 16 MY period, in the most extensive study of Cope's rule.



Macroevolution

Directionality in evolution – size

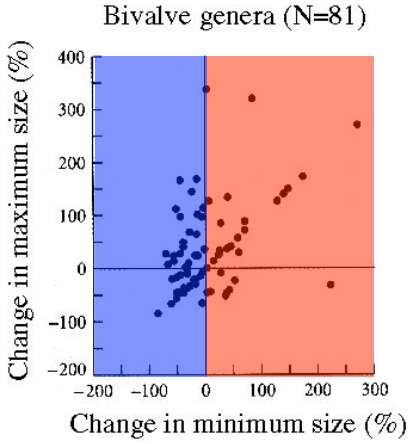
The body size of the largest species within a genus often increased, but also decreased 36% of the time.



Macroevolution

Directionality in evolution – size

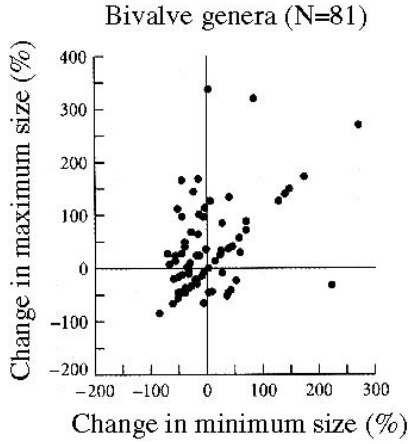
Interestingly, the body size of the smallest species within a genus decreased more often than it increased (36% of the time).



Macroevolution

Directionality in evolution – size

This suggests that the most prevalent pattern is one of increased variability rather than a trend towards larger size.



Macroevolution

Directionality in evolution – complexity

Possibly the most difficult thing about searching for patterns in complexity is defining complexity.

There is a definite risk in defining complexity that we are simply defining "most human-like".

We will discuss two possible definitions of complexity:

- Amount of DNA
- Number of cell types

Macroevolution

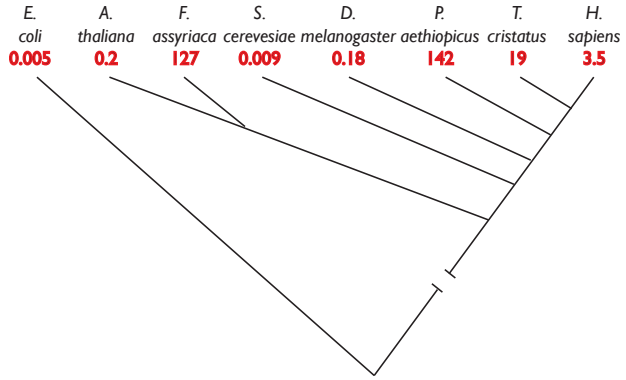
Directionality in evolution – complexity

Species	Genome Size (picograms)*
Escherichia coli (bacteria)	0.005
Saccharomyces cerevisiae (yeast)	0.009
Drosophila melanogaster	0.18
Arabidopsis thaliana (a weed)	0.2
Homo sapiens	3.5
Triturus cristatus (a newt)	19
Fritillaria assyriaca (a monocot plant)	127
Protopterus aethiopicus (a lungfish)	142

*Haploid genome size. 1 pg = ~10^9 base pairs

Macroevolution

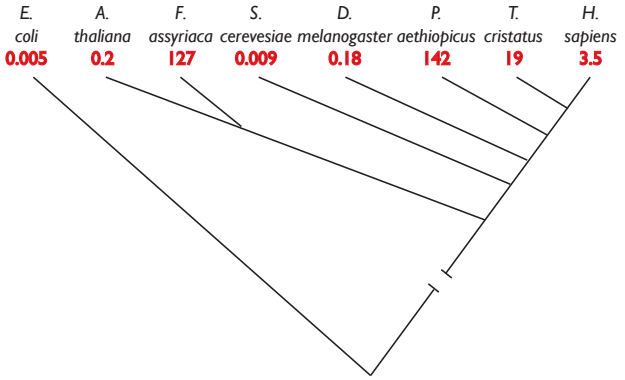
Directionality in evolution – complexity



What may account for these differences?

Macroevolution

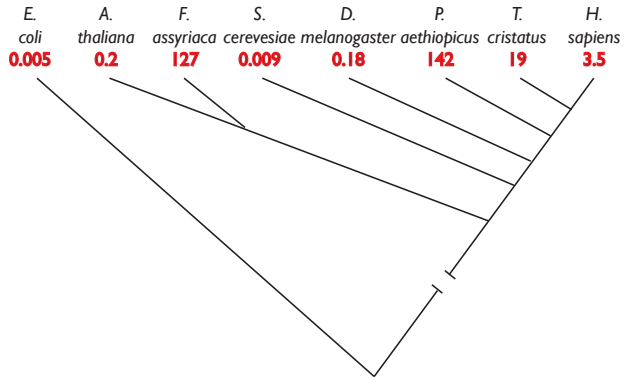
Directionality in evolution – complexity



If organisms started out with small genomes, it would be easier for mutations and selection to increase genome size than the reverse.

Macroevolution

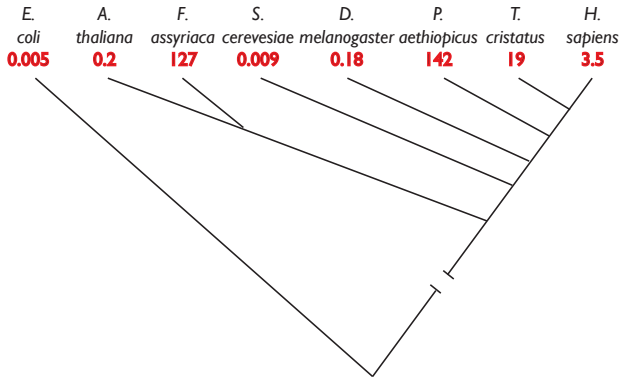
Directionality in evolution – complexity



Junk DNA may accumulate as the result of transposable elements (or other repeat elements) copying themselves throughout the genome.

Macroevolution

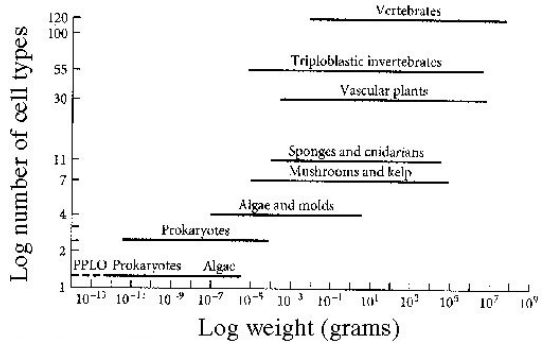
Directionality in evolution – complexity



There are more coding sequences in some organisms than others: *E. coli* have ~4000 genes, *Drosophila* ~13,000 genes, humans ~60,000 genes.

Macroevolution

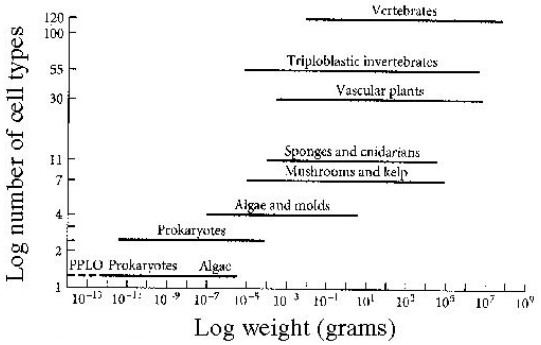
Directionality in evolution – complexity



The total number of recognizably different cell types is much larger in vertebrates than in invertebrates, plants, fungi, etc.

Macroevolution

Directionality in evolution – complexity



Nevertheless, there is no evidence that the number of cell types has increased within any of these phyla since the Cambrian (Futuyma, 1998).

Macroevolution
Directionality in evolution – complexity

Most of the net trend toward an increased number of cell types was established early in evolution (before the Cambrian).

Again, assuming that the common ancestor to all living organisms had one cell, the only direction in which evolution could proceed is up.

Macroevolution
Directionality in evolution – complexity

"Our strong and biased predilection for focusing on extremes...generates all manner of deep and stubborn errors. Most notable of these misconceptions is the false and self-serving notion that evolution displays a central and general thrust towards increasing complexity, when life, in fact, has been dominated by its persistent bacterial mode for all 3.5 billion years of its history on Earth."

-- Stephen J. Gould (1997, Nature 385: 199-200)

Macroevolution
Conclusions(?)

Evolution may occur rapidly…or slowly.

Evolution may increase size…or decrease it.

Evolution may lead to greater complexity…or greater simplicity.

This may seem a bit frustrating.

Yet the resulting view that evolution is a complex process leading to a richness in the forms and varieties of life is, in its own way, satisfying.

Macroevolution
Conclusions(?)

"It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms...have all been produced by laws acting around us....There is grandeur in this view of life."

-- C. Darwin (Origin of Species, 6th edition)