February, 2002
Genetics 453

Evolutionary Genetics

Group, Kin, Species Selection, and Punctuated Equilibrium

Joe Felsenstein

Department of Genome Sciences
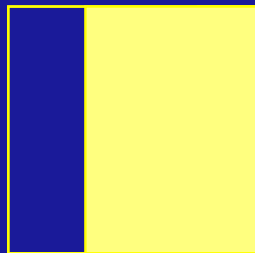University of Washington, Seattle

email: joe@genetics.washington.edu

Group selection

Whole local populations survive or go extinct, in a way that depends on their
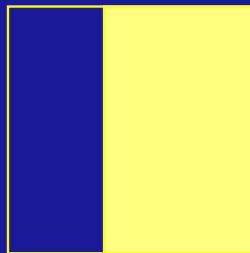
frequency of the altruistic allele
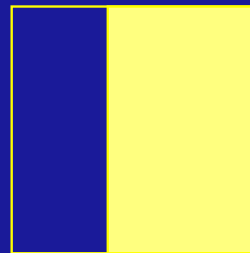
Before $p = 45/104 = 0.4327$

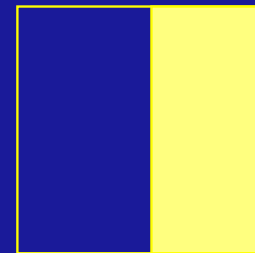local populations, which differ in gene frequency
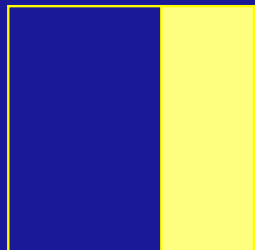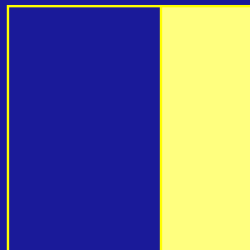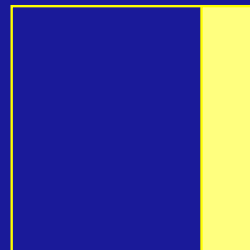

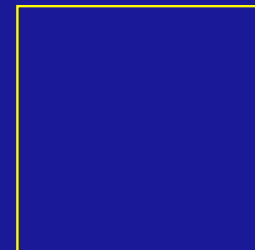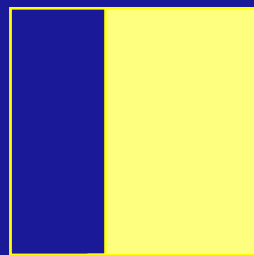| 9/13 | 8/13 | 8/13 | 7/13 |
| 5/13 | 5/13 | 3/13 | 0/13 |

Group selection

Whole local populations survive or go extinct, in a way that depends on their
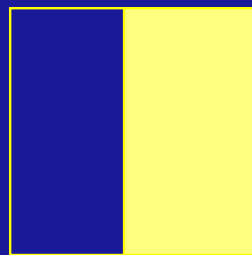
frequency of the altruistic allele

After   p = 29/65 = 0.446

Within each population, individual selection against altruists
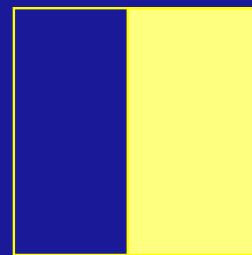reduces the frequency of the allele

8/13   7/13   7/13   5/13

extinct   extinct   extinct

2/13
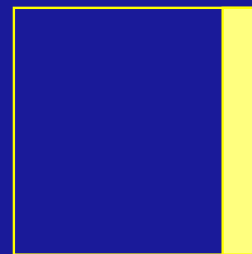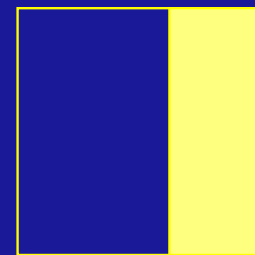
Kin selection –– the case of an alarm call

Before p = 18/136 = 0.132353

1 flock like this.

3 flocks like this.
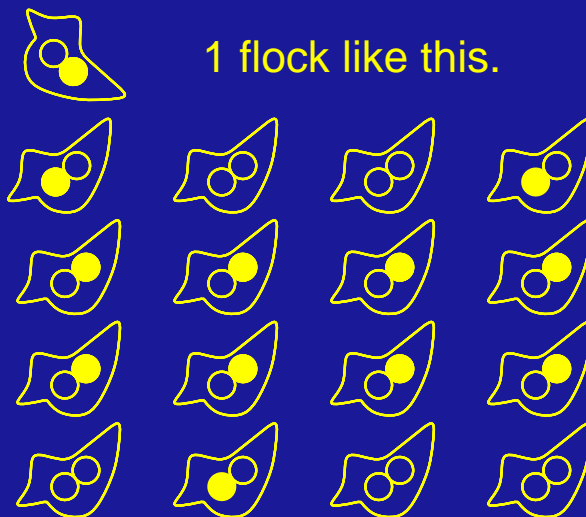
gives alarm call, is eaten
but flock is saved
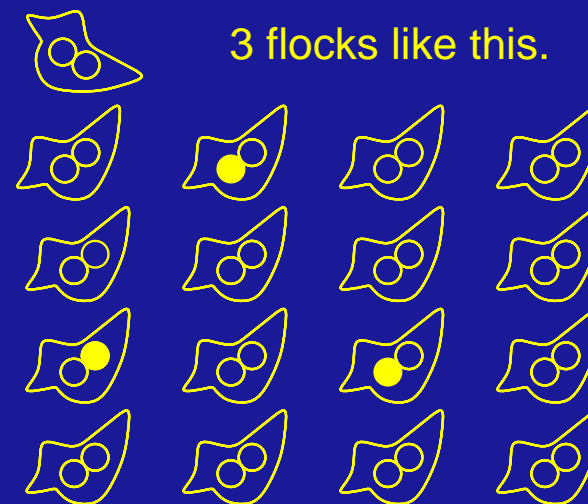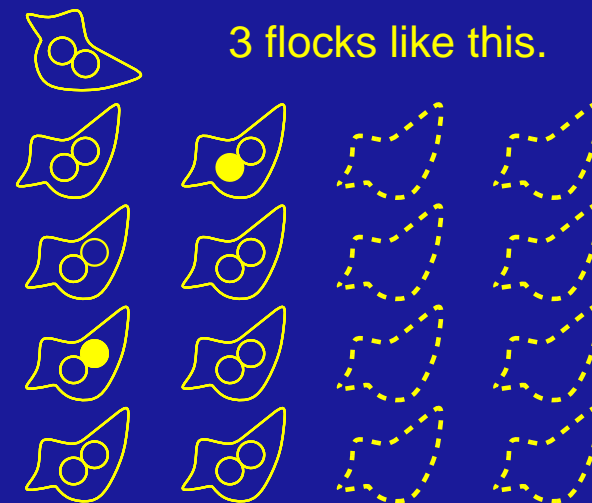
doesn't give alarm call, saves self
half of others eaten

(Note that in the example the other flock members are relatives of the bird that
gives the alarm call, so they tend to have the alleles that it has)

Note –– the numbers shown here are approximately correct at these gene frequencies. Infrequent
occurrences such as homozygotes for the alarm call allele are omitted.

Kin selection –– the case of an alarm call

After   p = 14/86 = 0.16279

1 flock like this.   3 flocks like this.

gives alarm call, is eaten   doesn't give alarm call, saves self
but flock is saved   half of others eaten

cost = 1

benefit = 8

Alarm call allele will increase with any coefficient of relationship > 1/8

Actually, group selection   is a kind of kin selection!

Because ...

1. Groups must vary in gene frequency to have group selection work
    (usually, the gene frequencies differ because, the members of a
      group are related to each other)

2. Having an altruistic behavior reduces the fitness of the individual
    (just as it does in the case of kin selection).

3. Being in a group with altruists means you are related to them and
    you benefit from their presence
      (by having a lower chance of group extinction).
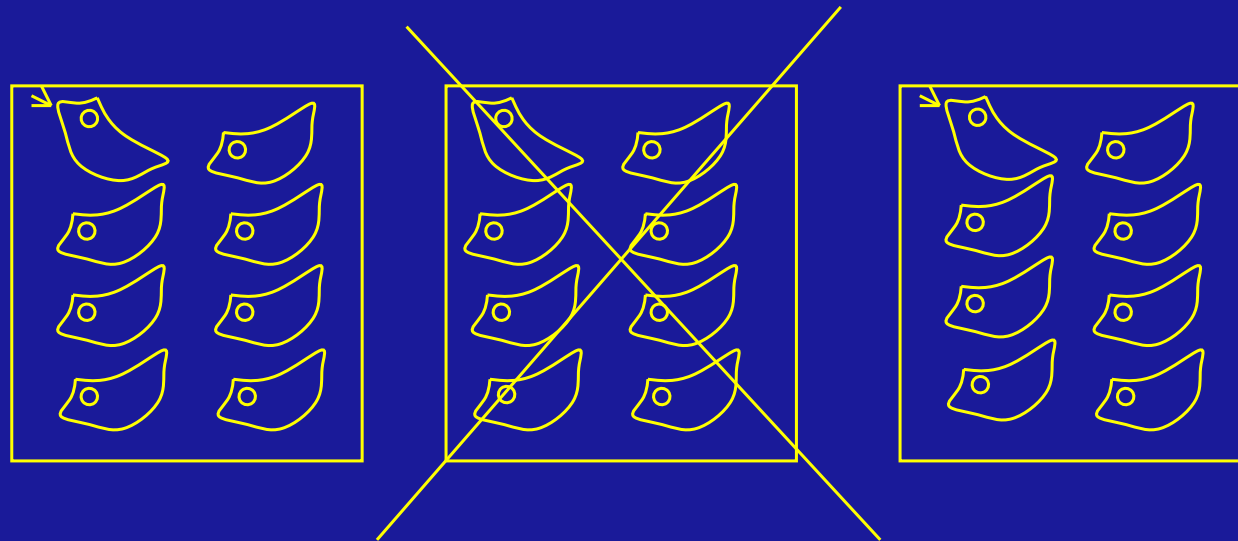
An adaptive trend according to gradualist neo−Darwinians

Time

Phenotype
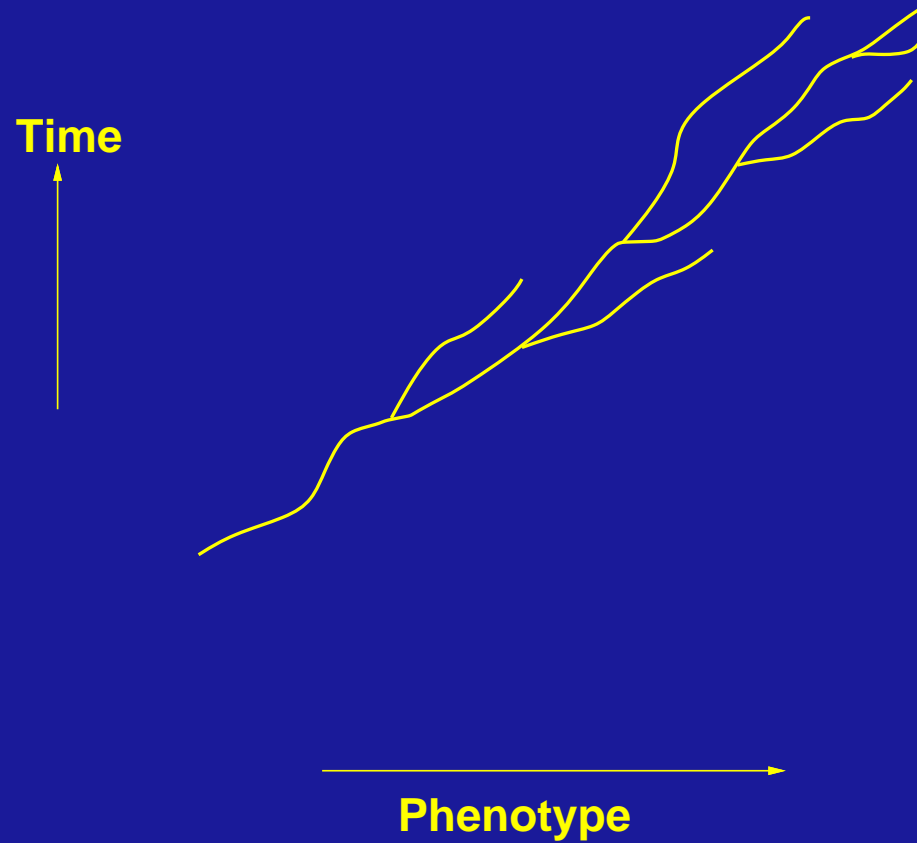
Selection is mostly occurring within species and
not by species selection

An adaptive trend according to punctuated equilibrium
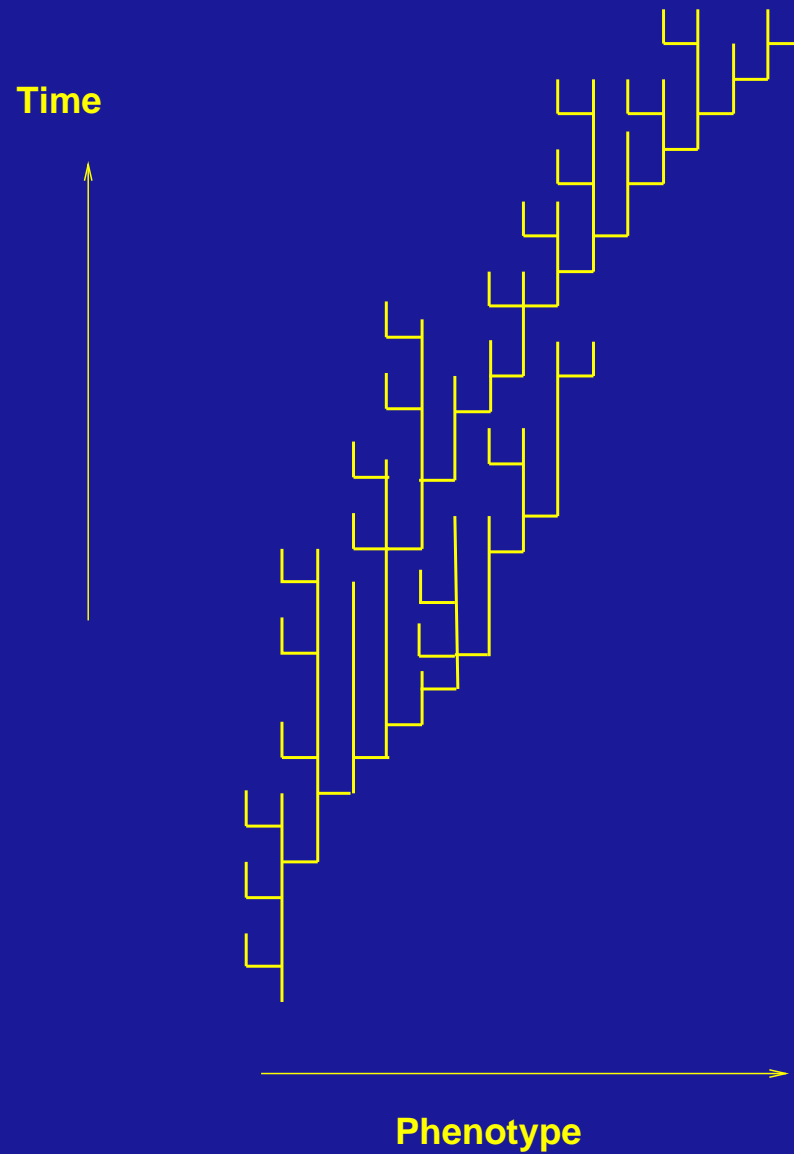
Time

Phenotype

In this hypothetical diagram, 19 speciations leftwards, 21 rightwards

The debate over punctuated equilibrium

Issue 1:   What are typical patterns of evolution

Punctuationists:
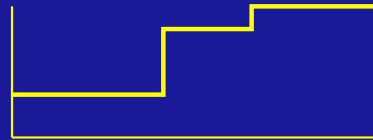
Traditional gradualists:

Gradualists these days:

Issue 2:   Are new evolutionary forces needed to explain these?

Punctuationists: *Yes, species selection*
and peripheral speciation

Gradualists: *No, can do the same with*

ordinary neo–Darwinian mechanisms

Comparison between gradualist and punctuational views
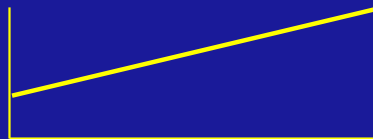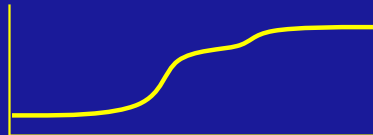
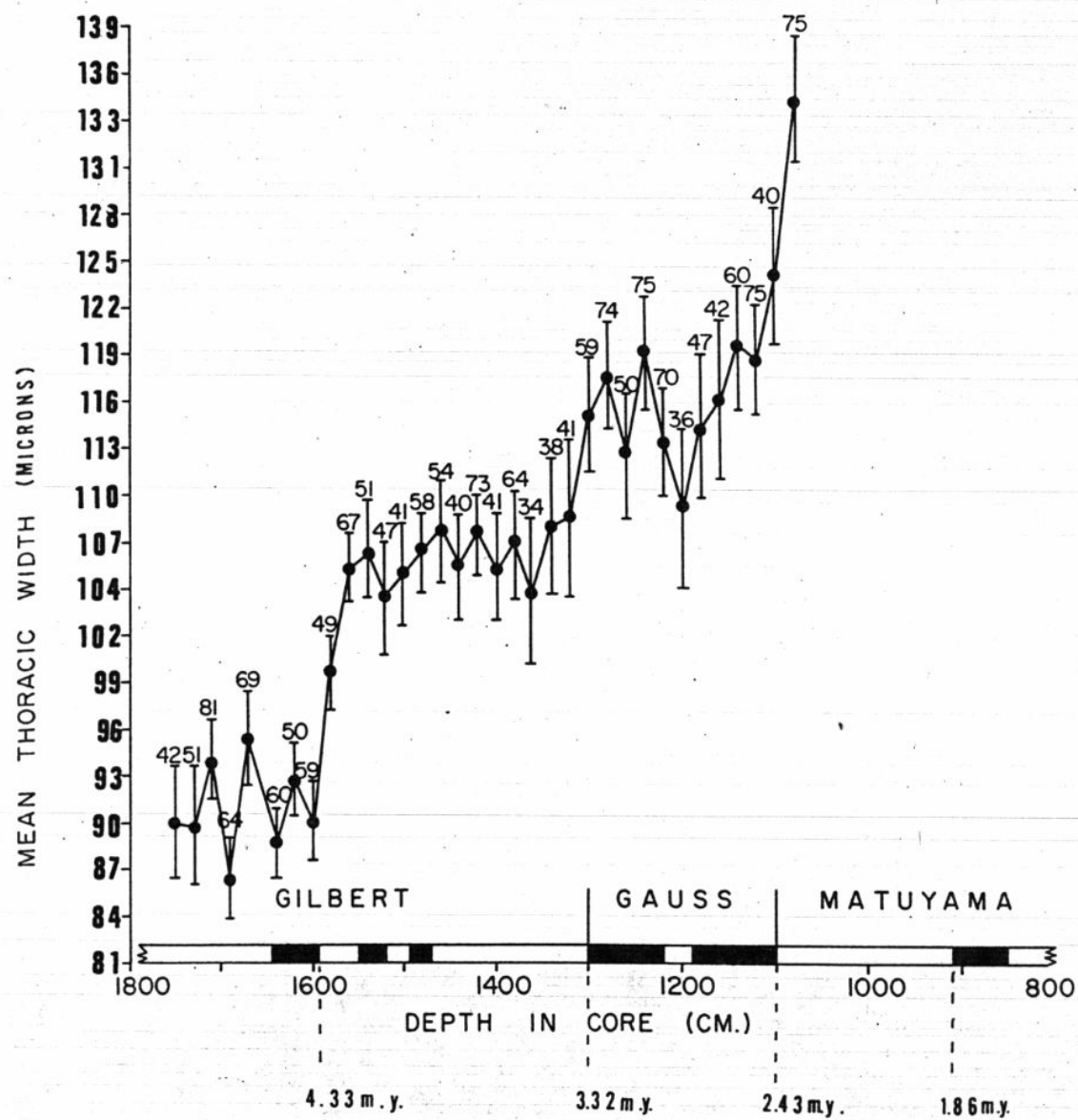| What	In: Gradualism	Punctiuationalism
Random variation is due to	Mutation ACCTTGA cGTTGAA	Genetic drift at the time of formation of a new species
Selection is due to	Individual survival and reproduction	Species selection
Change happens	within populations	between species

FIGURE 4. Mean thoracic width of *P. vema* vs. depth in core E14-8. Vertical lines through points indicate 95% confidence intervals for means. Numbers above lines indicate number of specimens in sample. Time line across bottom shows depth at which magnetic reversals occurred.
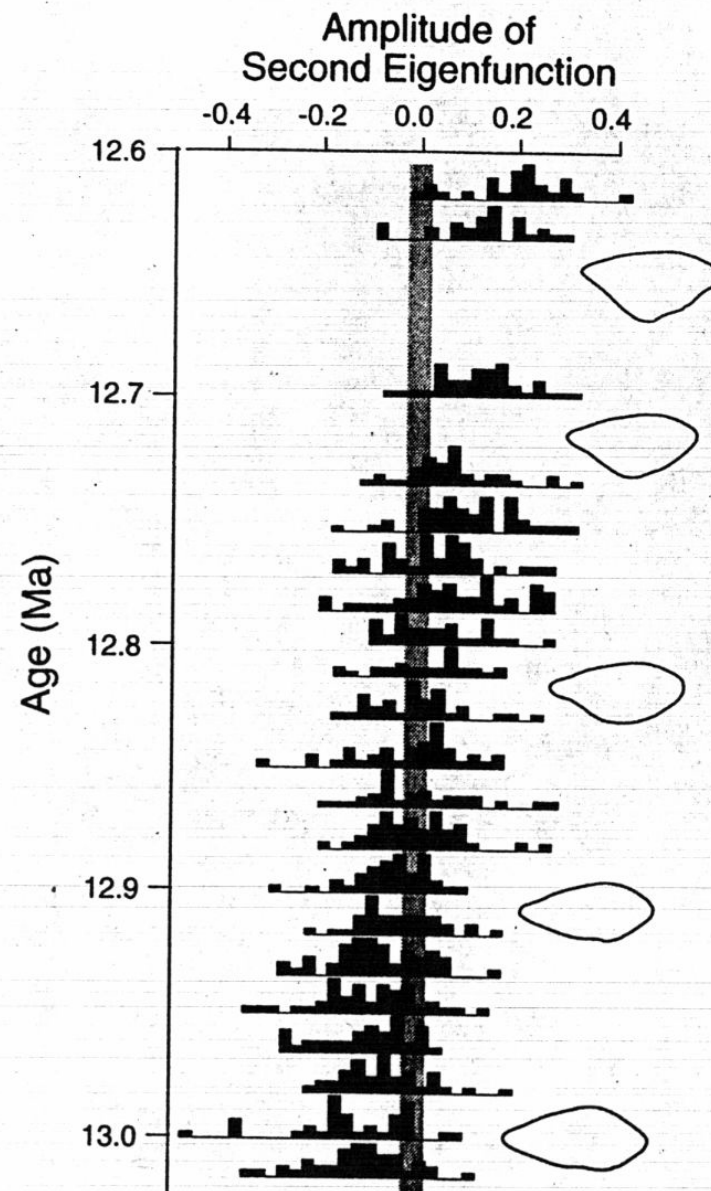
FIGURE 3. Stratigraphic distribution of fohsellids along the second eigenfunction (see also Fig. 5B). Shaded vertical line drawn through the mean shape for the eigenfunction illustrated by the outline at 12.8 Ma. Outlines
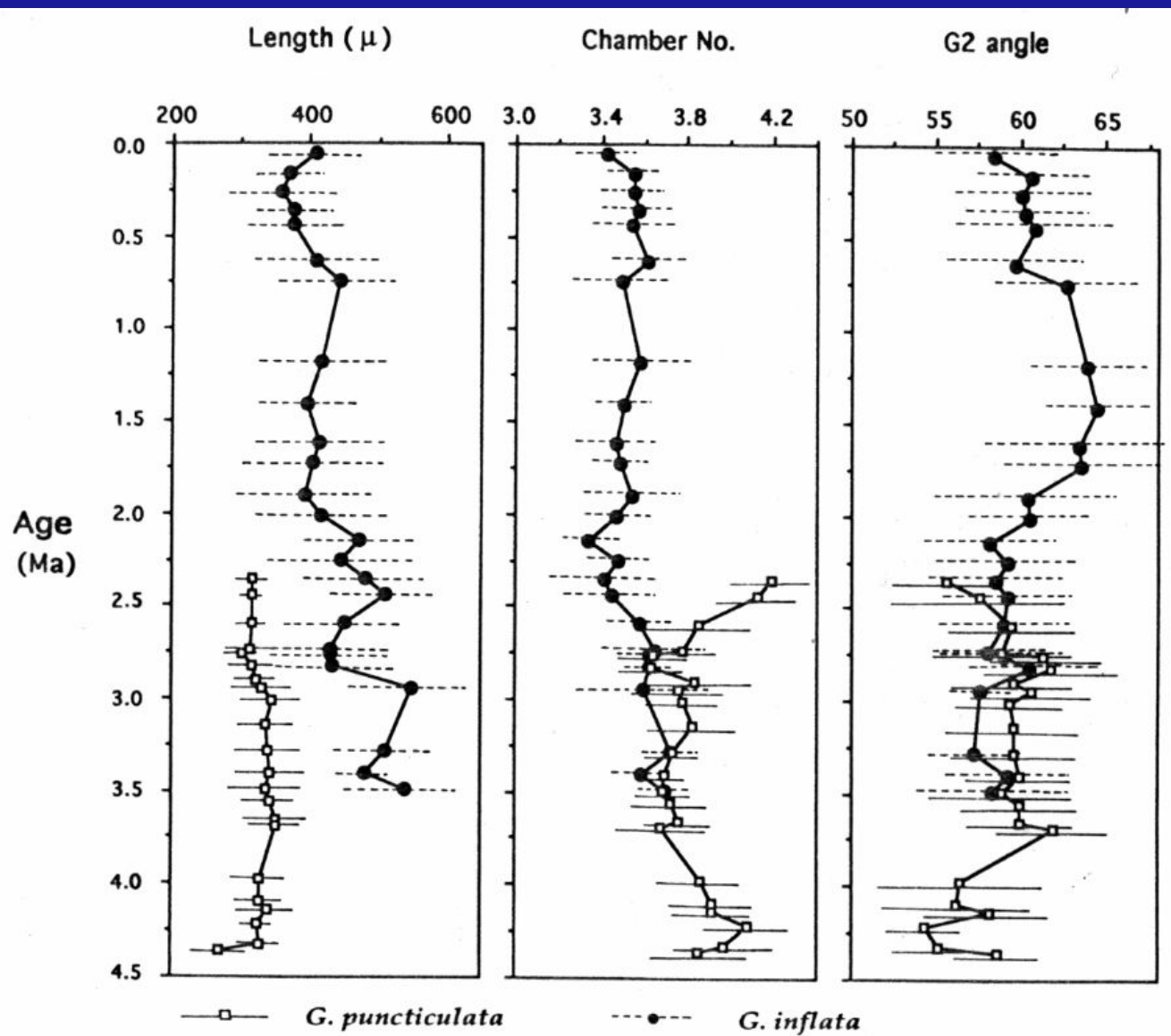
FIGURE 8. Time-series of average value (±1 SD) of three morphometric variables in the two *Globoconella* lineages.
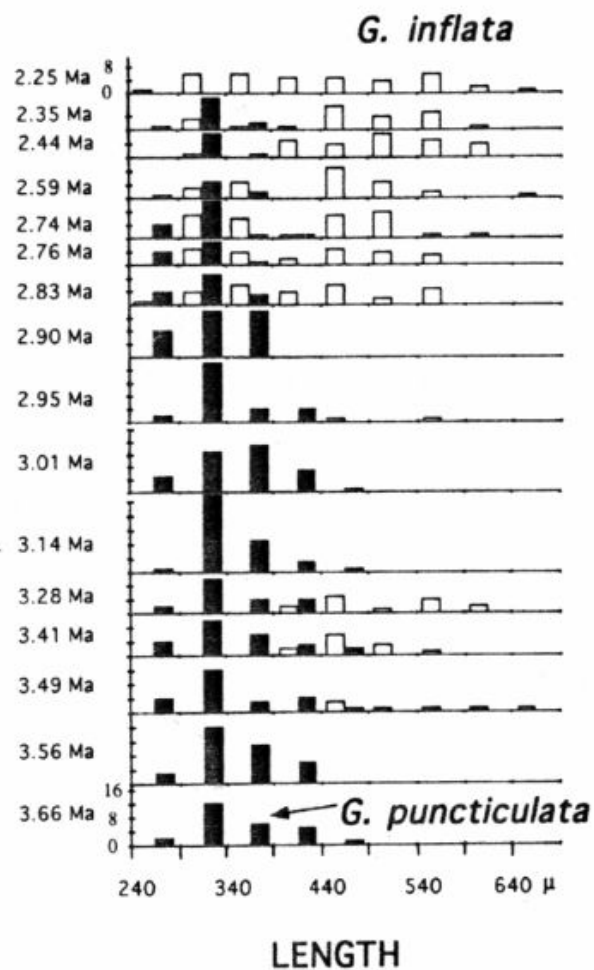
FIGURE 9. Stacked histograms of test length (L) of G. inflata and G. puncticulata during 3.66 Ma to 2.25 Ma.

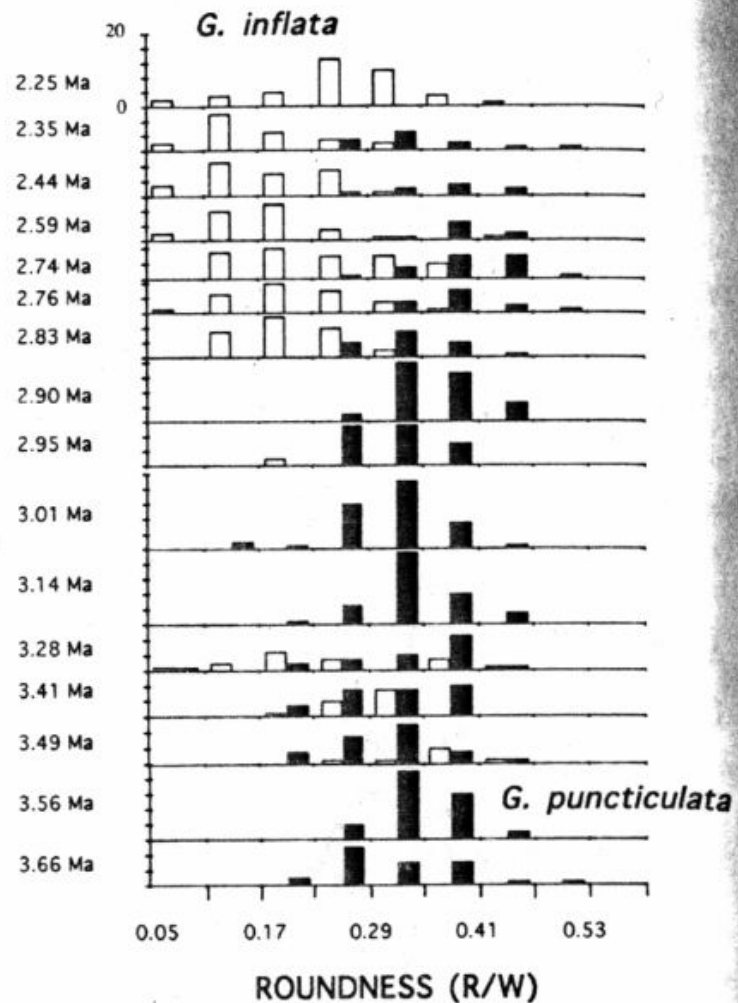FIGURE 10. Stacked histograms of peripheral roundness (defined as R/W) of G. inflata and G. puncticulata during 3.66 to 2.25 Ma.
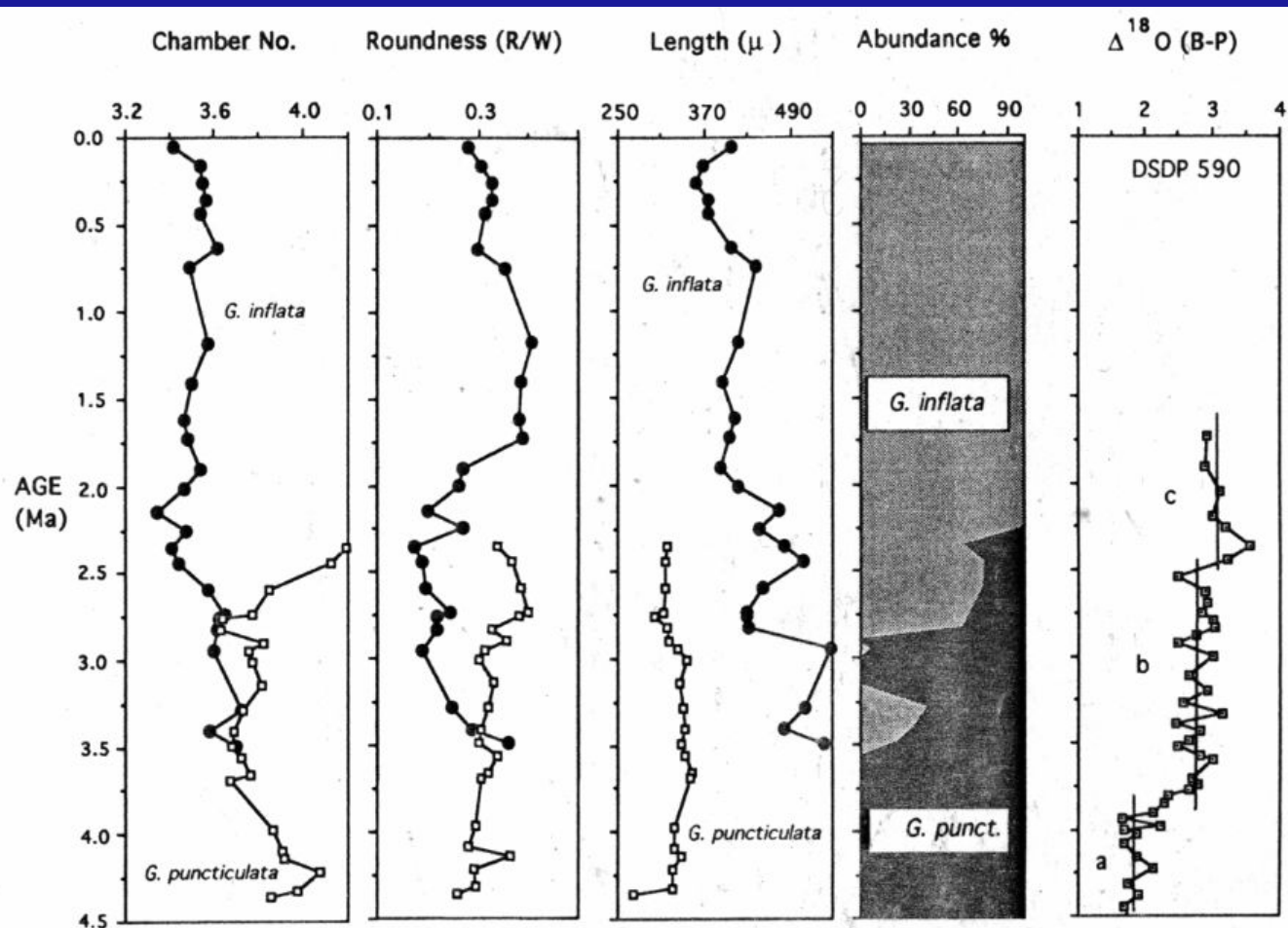
FIGURE 11. Relationships among three morphometric variables, relative abundances of *Globoconella* species in DSDP 588, and the vertical gradient in δ¹⁸O between planktic (*Globigerinoides sacculifer*) and benthic foraminifera (*Cibicidoides kullenbergi*) in DSDP Site 590 (Elmstrom 1985; Elmstrom and Kennett 1986). The benthic foraminiferal δ¹⁸O values are indicative of the paleotemperature/isotopic composition of the Antarctic Intermediate Water Masses in the southwest Pacific. The time-series of the δ¹⁸O gradient exhibits a continuous increase in temperature stratification of the surface and intermediate waters during the Pliocene in three phases. Note that the origination of *G. inflata*, the increasing dominance of *G. inflata* over *G. puncticulata*, and the extinction of *G. puncticulata* correlate with the three-phased history of enhanced stratification of the water column.
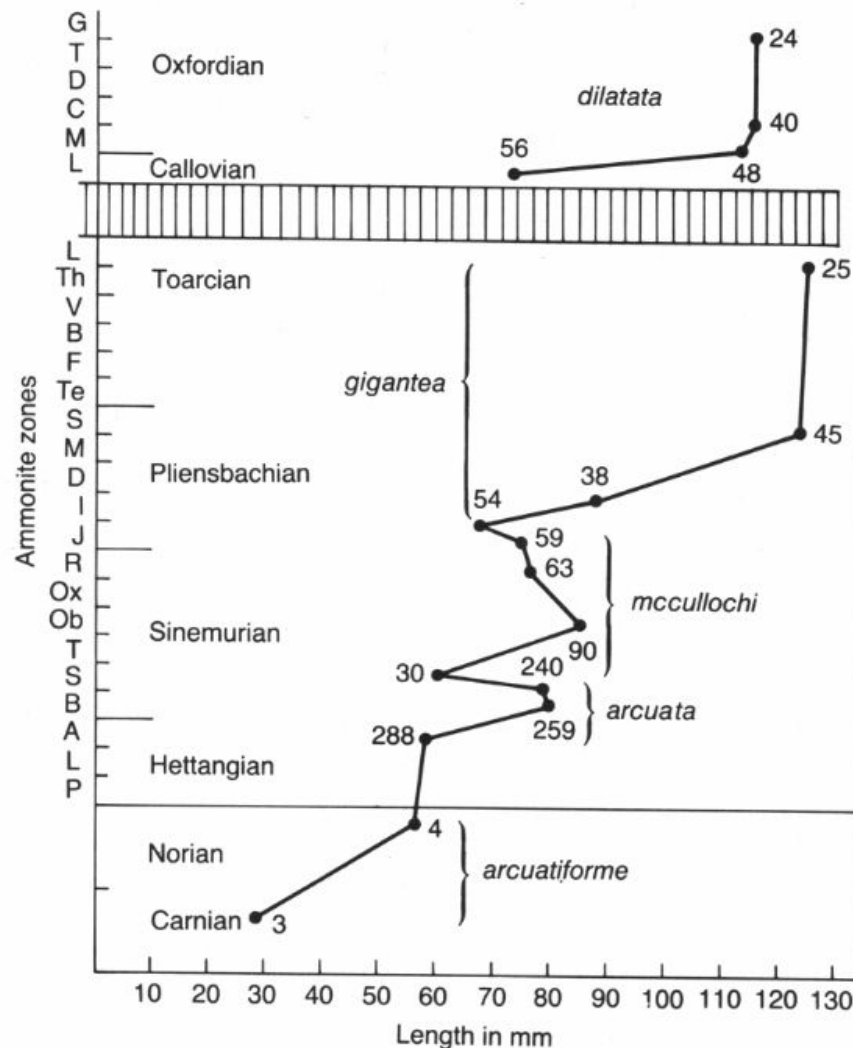
FIGURE 2

Punctuated change without biological speciation (bifurcation) in Jurassic oysters of the genus *Gryphaea*. Length of the left valve is plotted for samples (number of specimens indicated) in a stratigraphic series of zones of about one million years' duration, distinguished by different ammonite faunas. Sequential members of the same lineage are given different species names (chronospecies). Rapid changes are evident in *dilatata* and in the transition from *mccullochi* to *gigantea*. (From Hallam 1982)
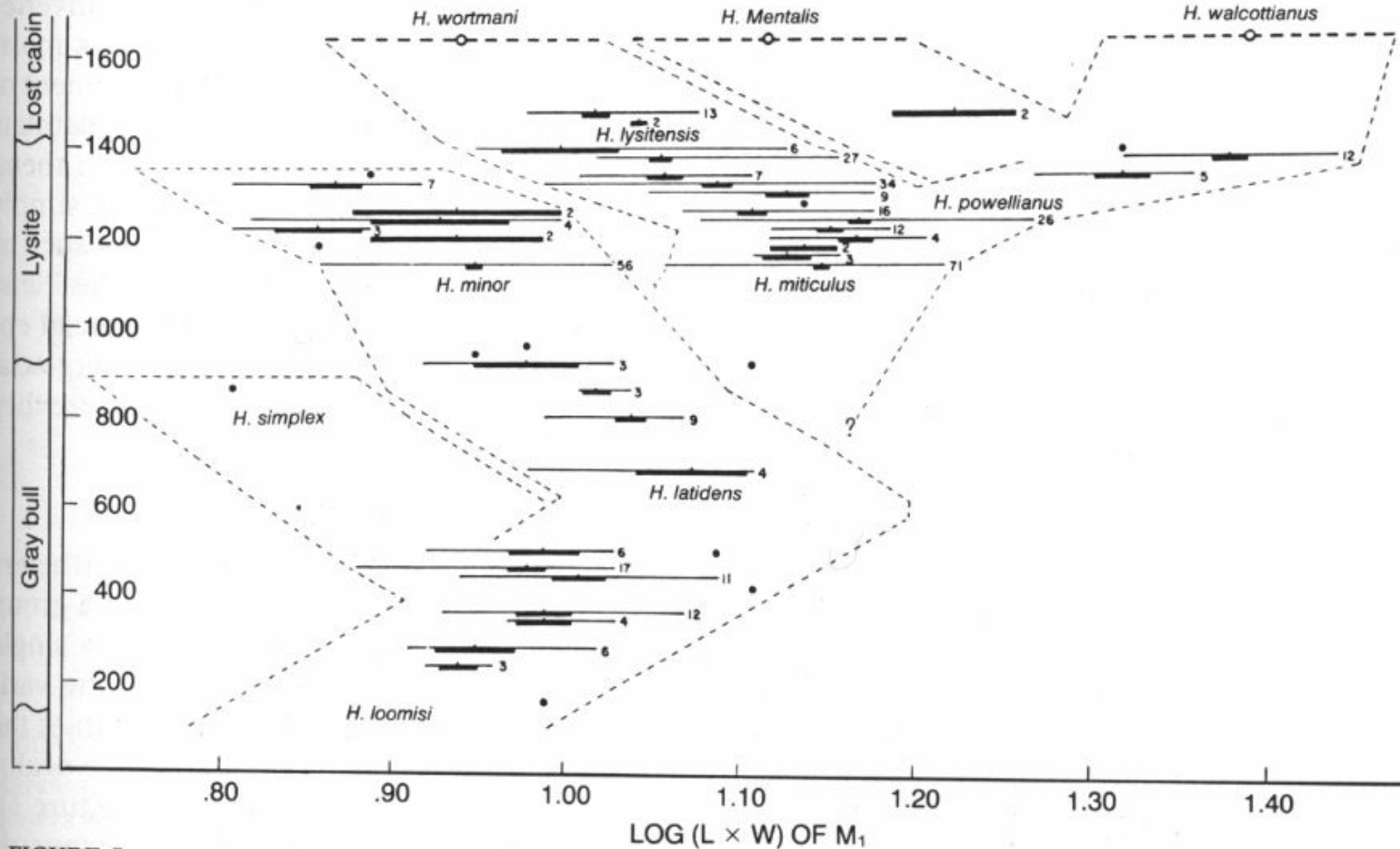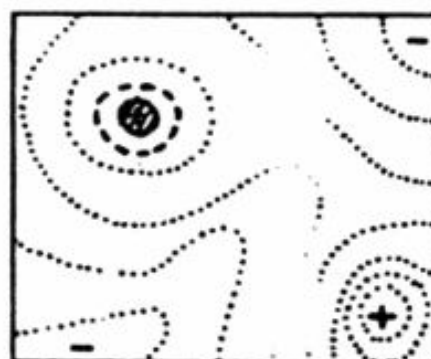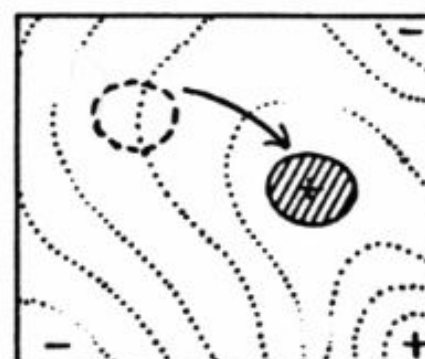
FIGURE 5

Evolution of the first upper molar of the condylarth *Hyopsodus* in early Eocene
deposits in the Big Horn Basin of Wyoming. The mean of each sample is shown
with the standard error (horizontal bar) and the range (horizontal line). Sample
sizes are indicated at the right of each distribution; points are single specimens.
The dotted envelopes show Gingerich's interpretation of the data as reflecting both
gradual anagenetic change and speciation. These data have also been interpreted
by other authors as an example of punctuated equilibrium. (From Gingerich 1976)
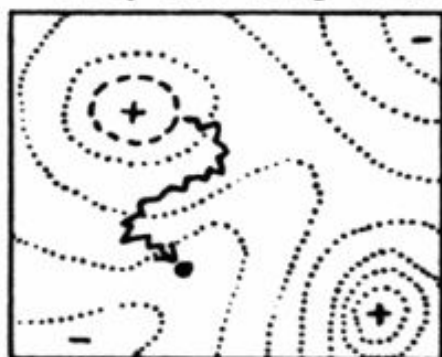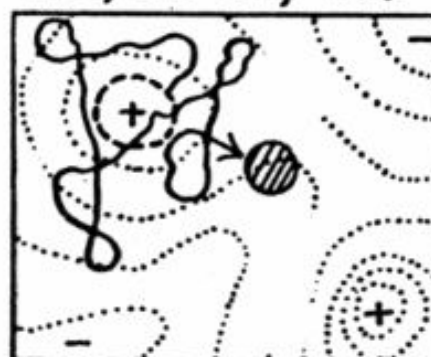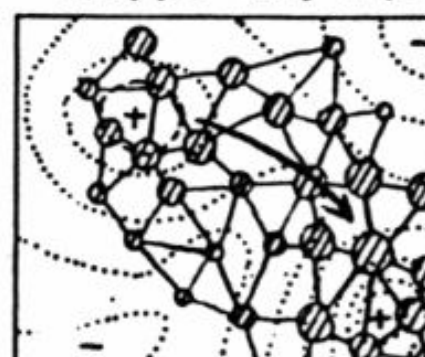
FIGURE 4.—Field of gene combinations occupied by a population within the general field of possible combinations. Type of history under specified conditions indicated by relation to initial field (heavy broken contour) and arrow
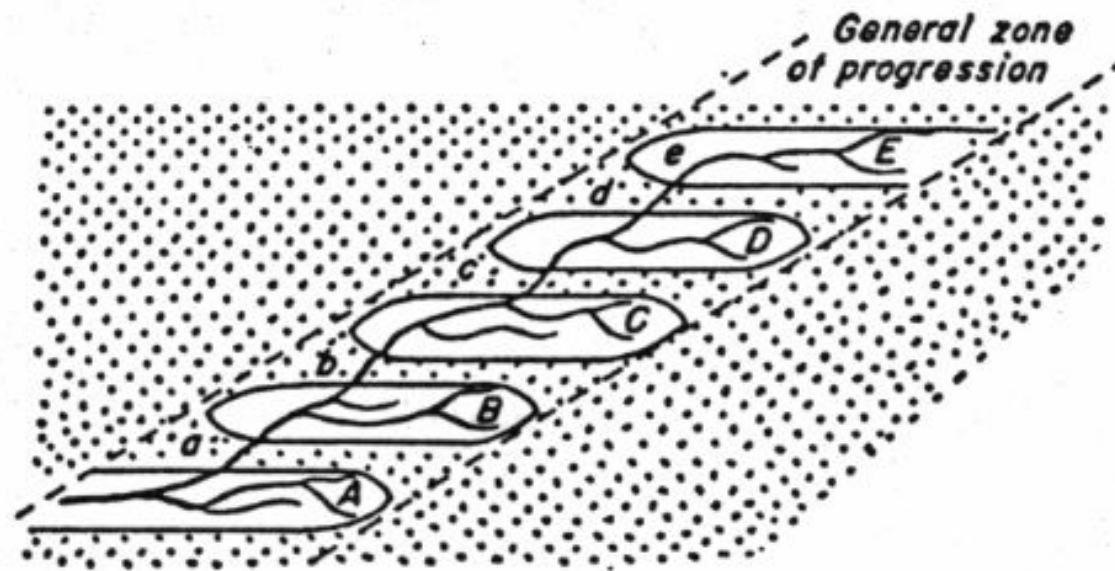
A–B–C–D–E = Stufenreihe
a–b–c–d–e = Ahnenreihe

FIGURE 27. EVOLUTION INVOLVING SUCCESSIVE OCCUPATION OF ADAPTIVE ZONES AND SUCCESSIVE CLOSING OF OLDER ZONES. The Stufenreihe, A–E, indicates the general direction and nature of the progression of the Ahnenreihe, a–e, but in fact none of the populations of A–E are evolving in that direction.
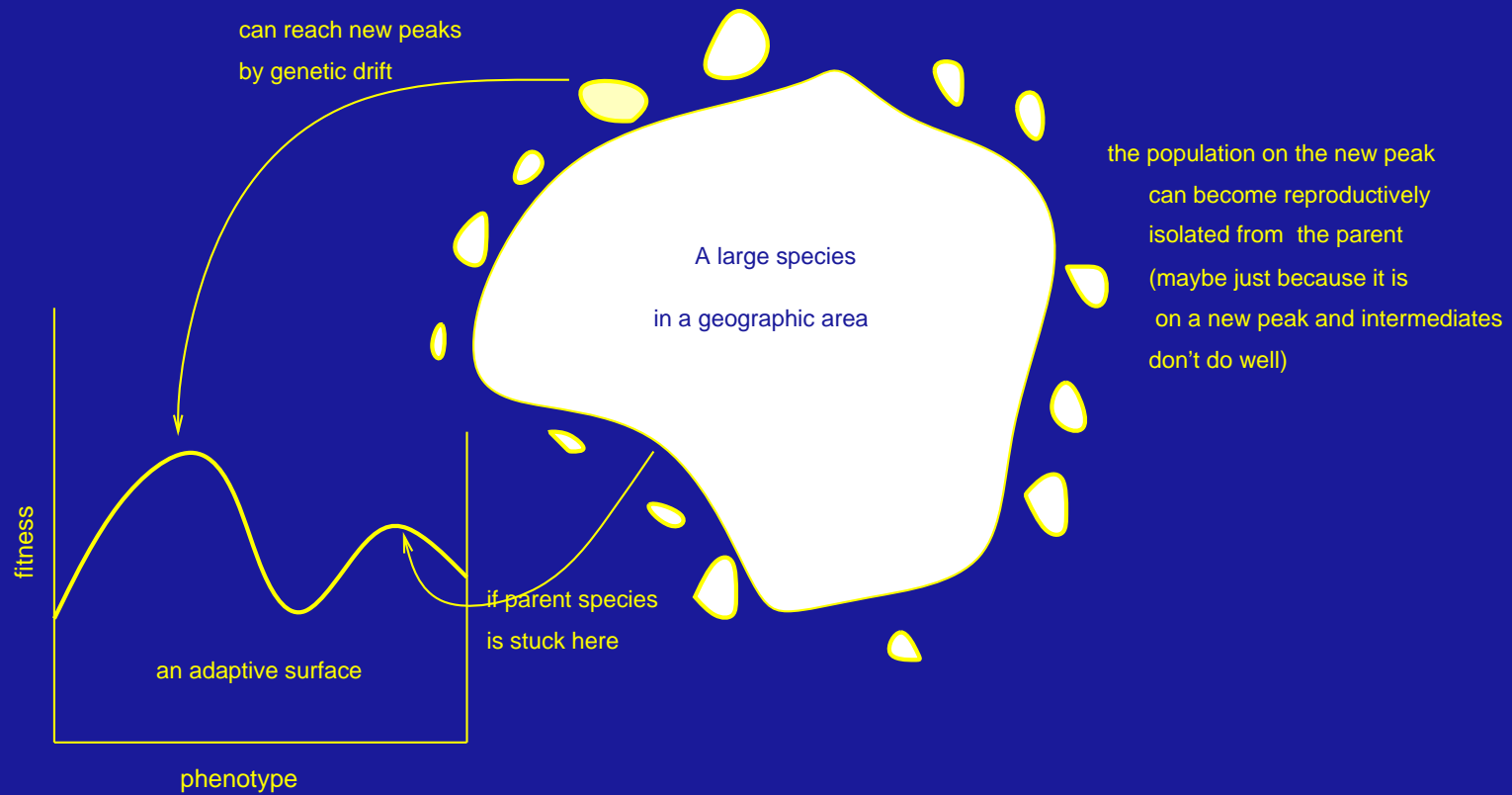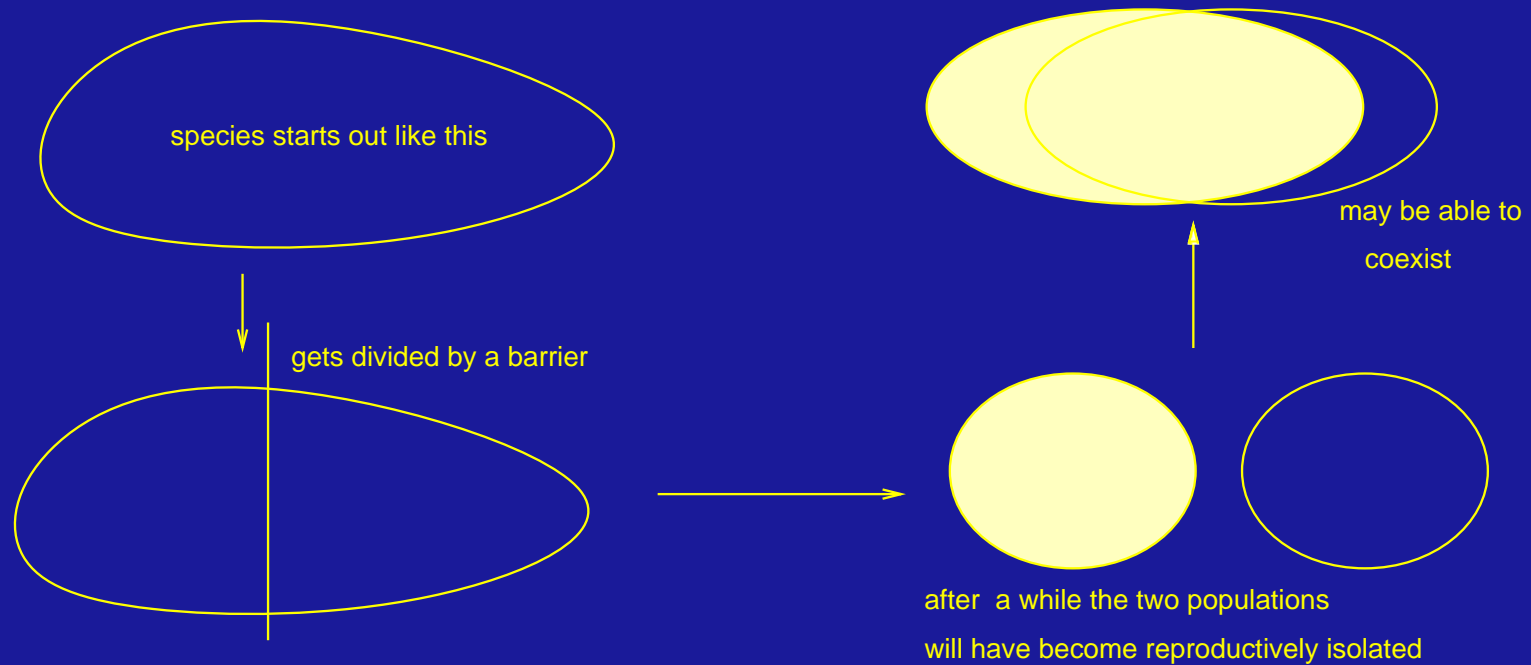
Peripheral speciation (Ernst Mayr)

can reach new peaks
by genetic drift

A large species

in a geographic area

the population on the new peak
can become reproductively
isolated from the parent
(maybe just because it is
 on a new peak and intermediates
don't do well)

fitness

if parent species
is stuck here

an adaptive surface

phenotype

There are many other schemes for speciation

a commonly invoked one is allopatric speciation

species starts out like this

gets divided by a barrier

after a while the two populations

will have become reproductively isolated

may be able to

coexist

Fitness

Genetic drift (versus selection)

Phenotype

Time

Phenotype

... followed by selection

Fitness

Phenotype

Time

Phenotype
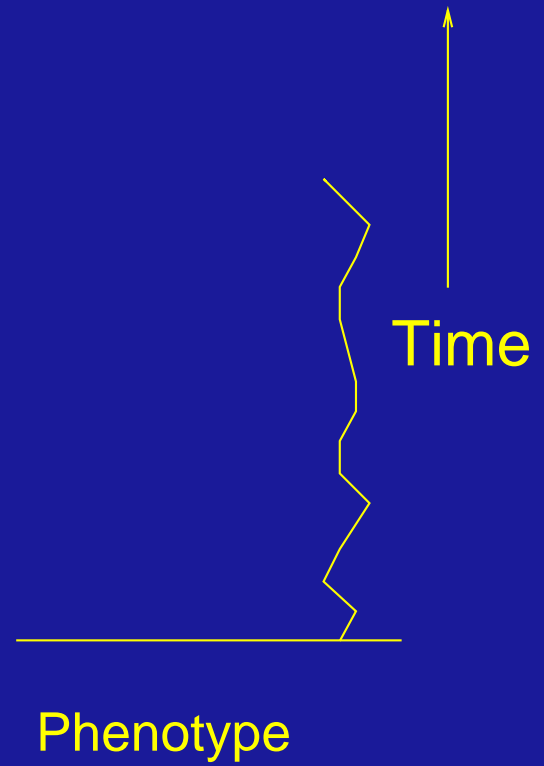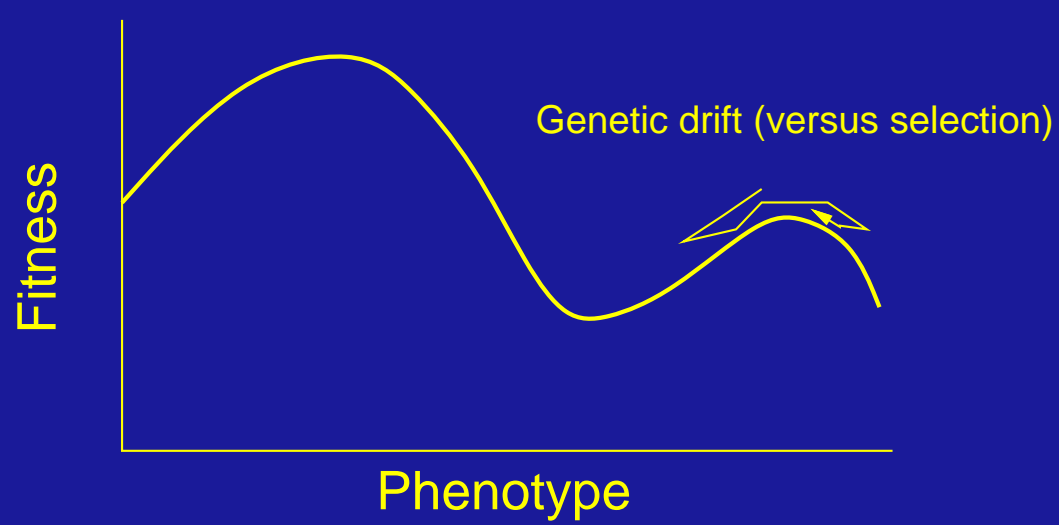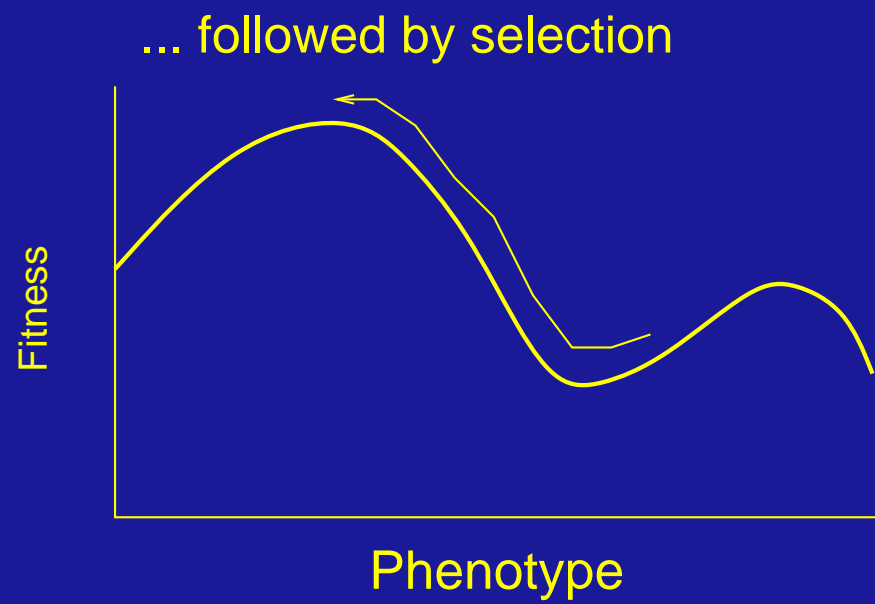
This freeware-friendly presentation prepared with

- Linux (operating system)

- PDFLaTeX (mathematical typesetting and PDF preparation)

- Idraw (drawing program to modify plots and draw figures)

- Adobe Acrobat Reader (to display the PDF in full-screen mode)

(except that we had to use Microsoft Windows to project this as the X server I have in Linux is not too great)