Group, Kin, Species Selection and Punctuated Equilibrium

Joe Felsenstein
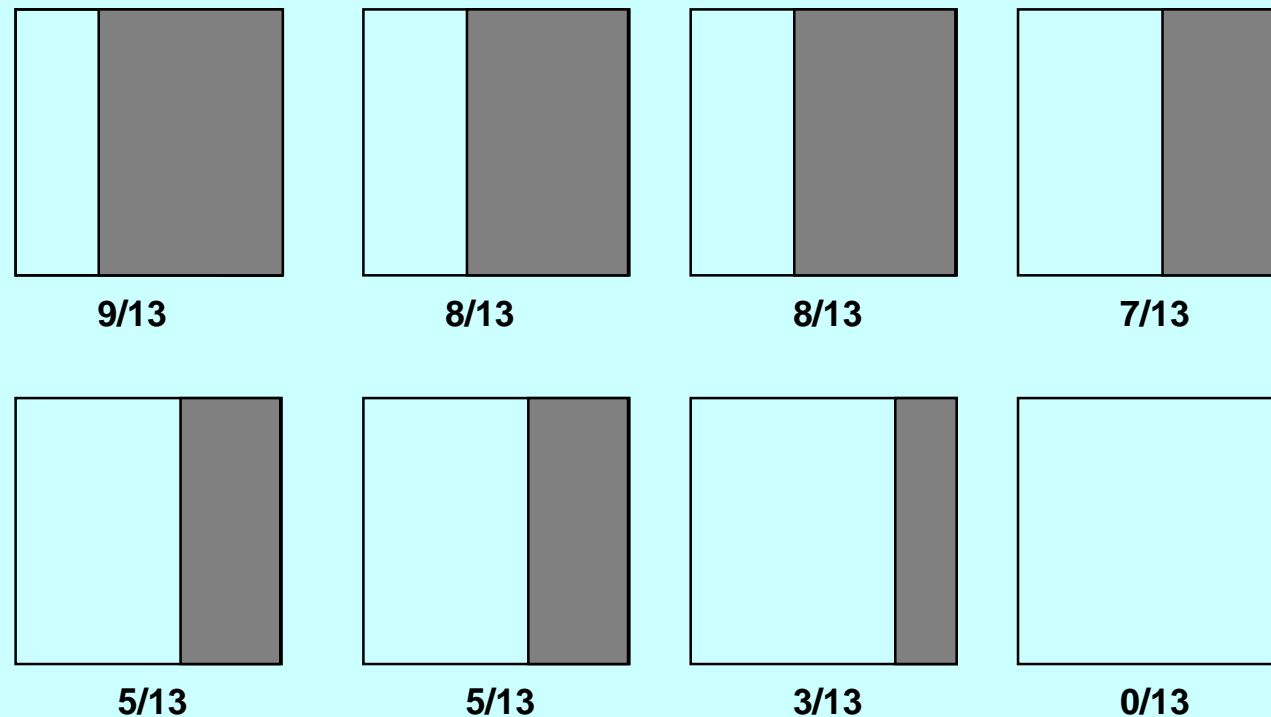
GENOME 453, Autumn 2013

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

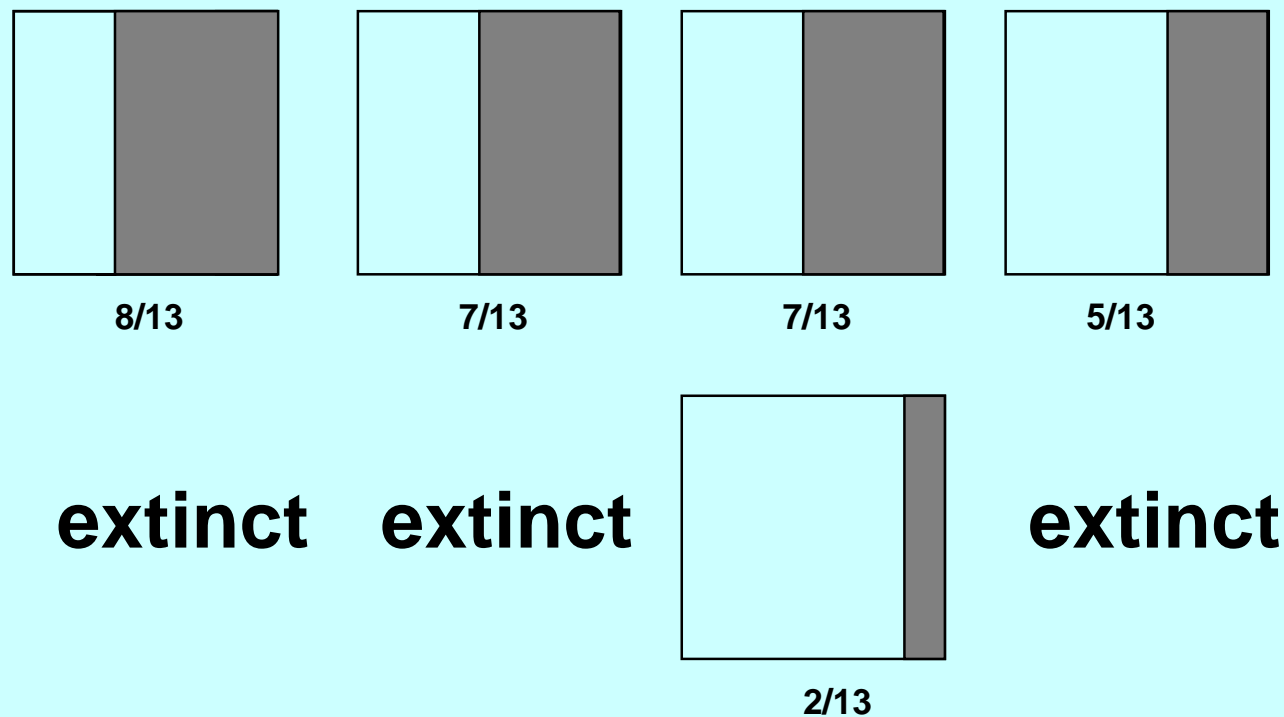| 9/13 | 8/13 | 8/13 | 7/13 |
| 5/13 | 5/13 | 3/13 | 0/13 |

Group selection

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

After: $p = 29/65 = 0.446$

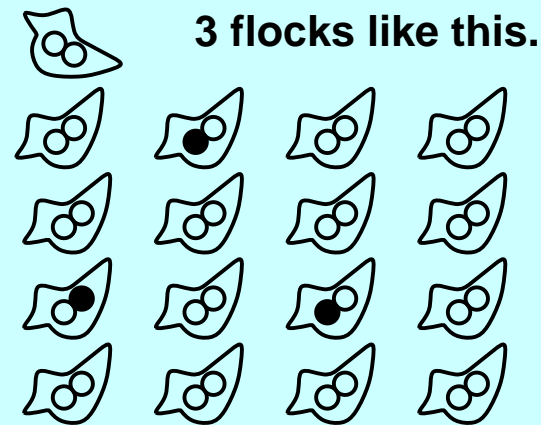Within each population, individual selection against altruists reduces the frequency of the allele.

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

extinct   extinct   **extinct**

2/13

Kin selection: the case of an alarm call

Before   **p = 21/136 = 0.1544123**

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.
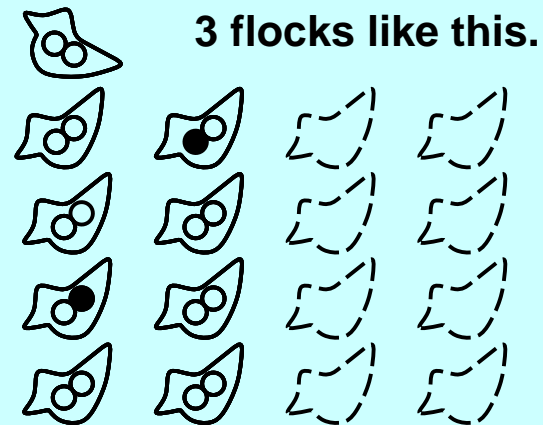
Kin selection: the case of an alarm call

After p = 17/86 = 0.197674

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

cost = 1

benefit = 8

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

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

The mathematics of kin selection

W. D. Hamilton argued on theoretical grounds that an allele predisposing to an altruistic behavior will increase if

$$c < r\,b$$

where (c) is the cost (in fitness) to the altruist

(b) is the total benefit to all recipients

and (r) is the average relatedness of recipients to the altruist.

r is the probability that a (rare) gene heterozygous in the altruist is present in the typical recipient, owing to their relatedness.

Relative	r
Identical twin	1
Brother/sister	1/2
Mother/father	1/2
Offspring	1/2
Half-sibling	1/4
Aunt/uncle	1/4
Niece/nephew	1/4
Grandchild	1/4
First cousin	1/8

W. D. Hamilton 1936-2000
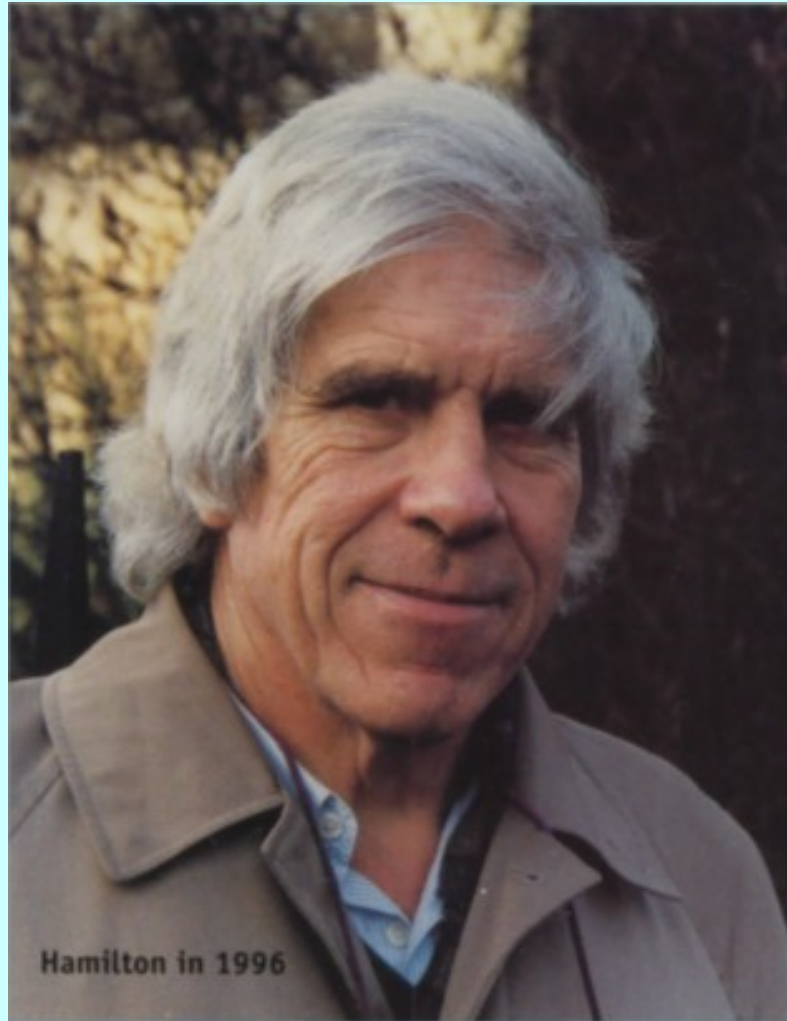
Hamilton in 1996

Cooperative breeding in Florida Scrub Jays

An example is the Florida Scrub Jay, *Aphelocoma coerulescens*. Young scrub jays often stay around the parents' nest for several years, helping raise their full siblings. With a helper about 1.45 offspring are reared, without one, only about 0.5 offspring per year.

Let's calculate the terms of Hamilton's Inequality ...

Cooperative breeding in Florida Scrub Jays

An example is the Florida Scrub Jay, *Aphelocoma coerulescens*. Young scrub jays often stay around the parents' nest for several years, helping raise their full siblings. With a helper about 1.45 offspring are reared, without one, only about 0.5 offspring per year.

Calculation:

Cost	0.5	Offspring foregone
Benefit	0.95	More siblings
Relationship	0.5	As these are full sibs

Note the offspring foregone have only an average of 0.5 copies each of a (putative) gene. So the cost is really 0.25 copies lost.
Since 0.25 < (0.95)(0.5), the behavior is favored.

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)

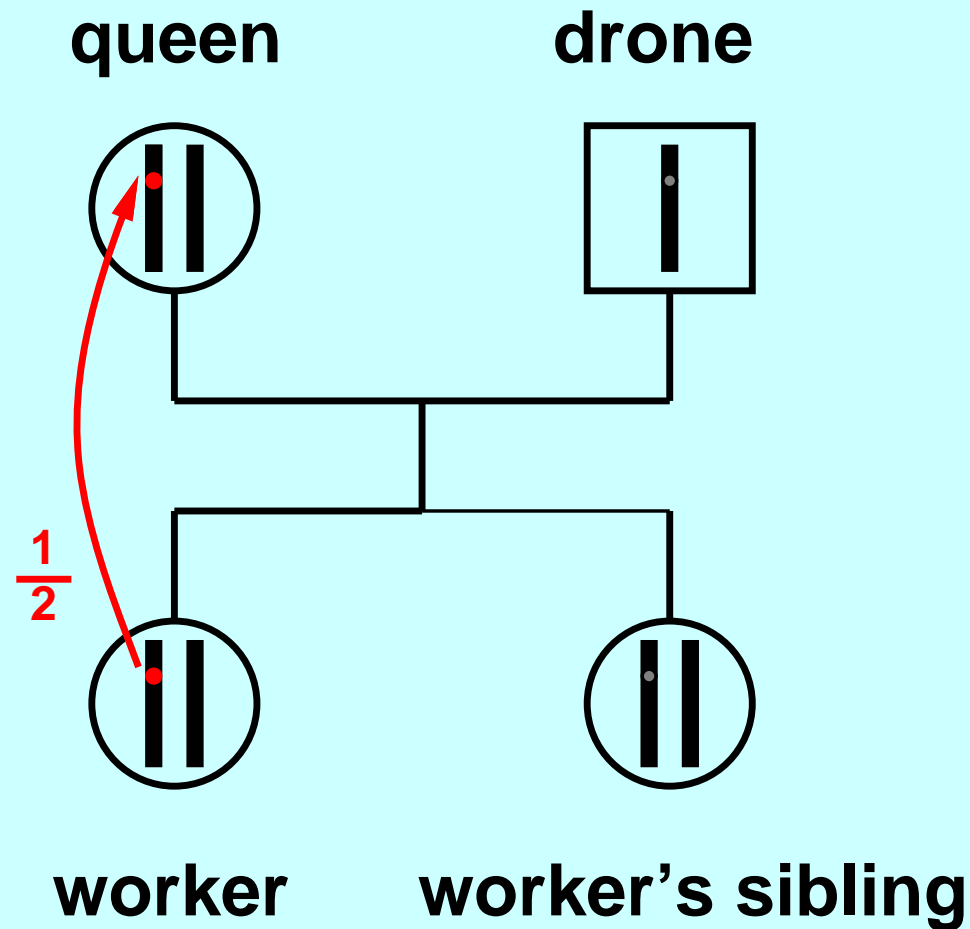3. Being in a group with altruists means you are related to them and you benefit from their presence (by having a lower chance of group extinction)
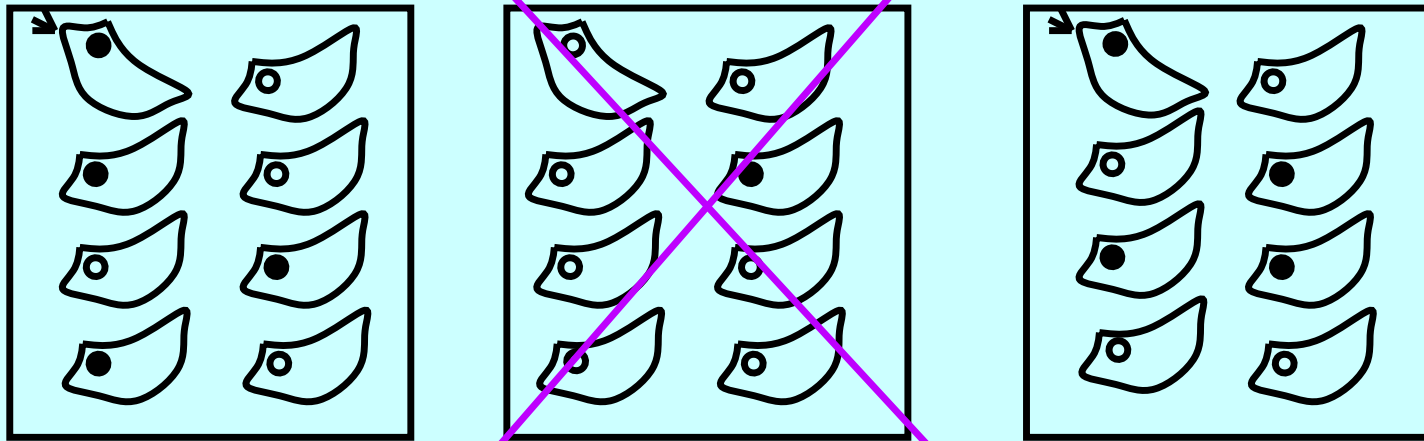
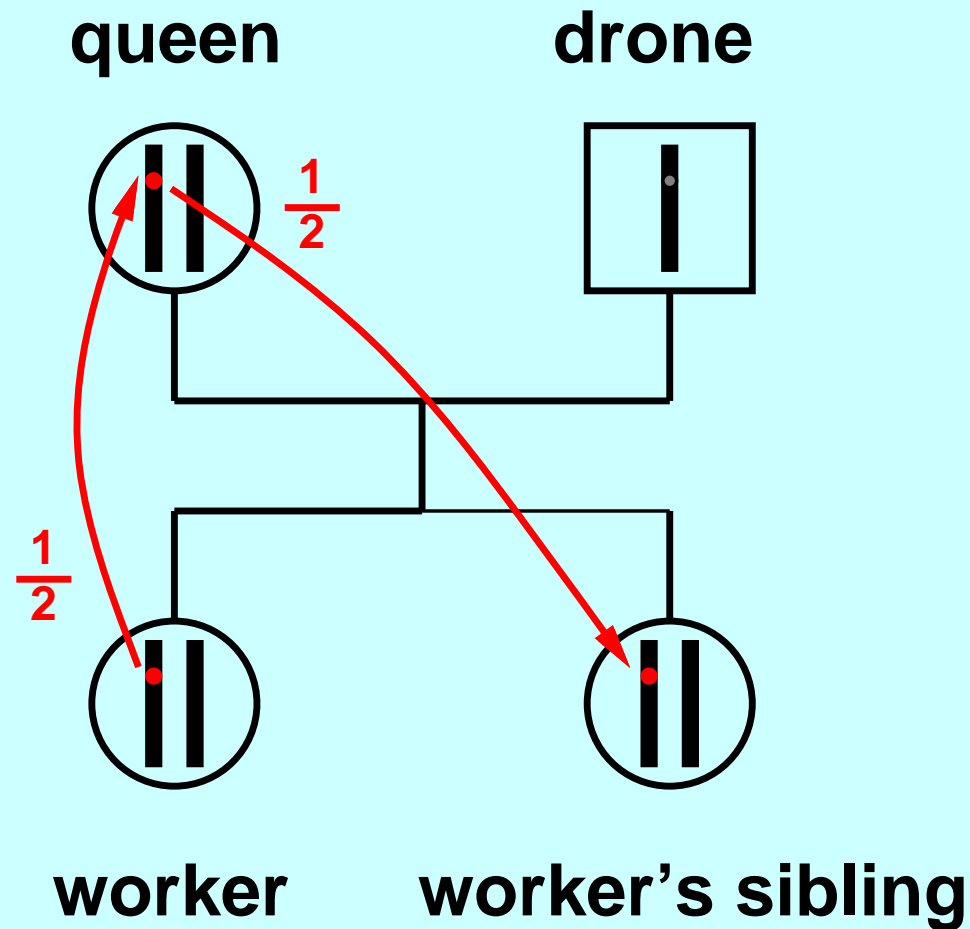# Social insects: Hymenoptera are haplo-diploid
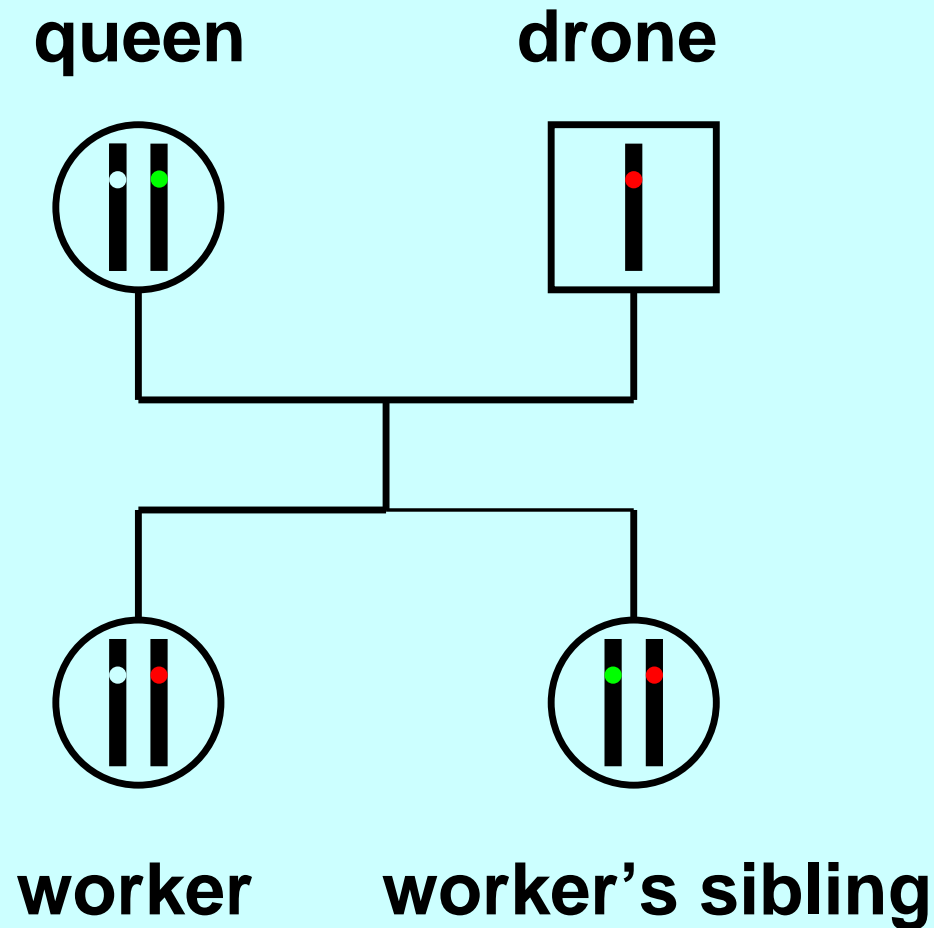
In ants, bees, and wasps, males are haploid, females diploid.

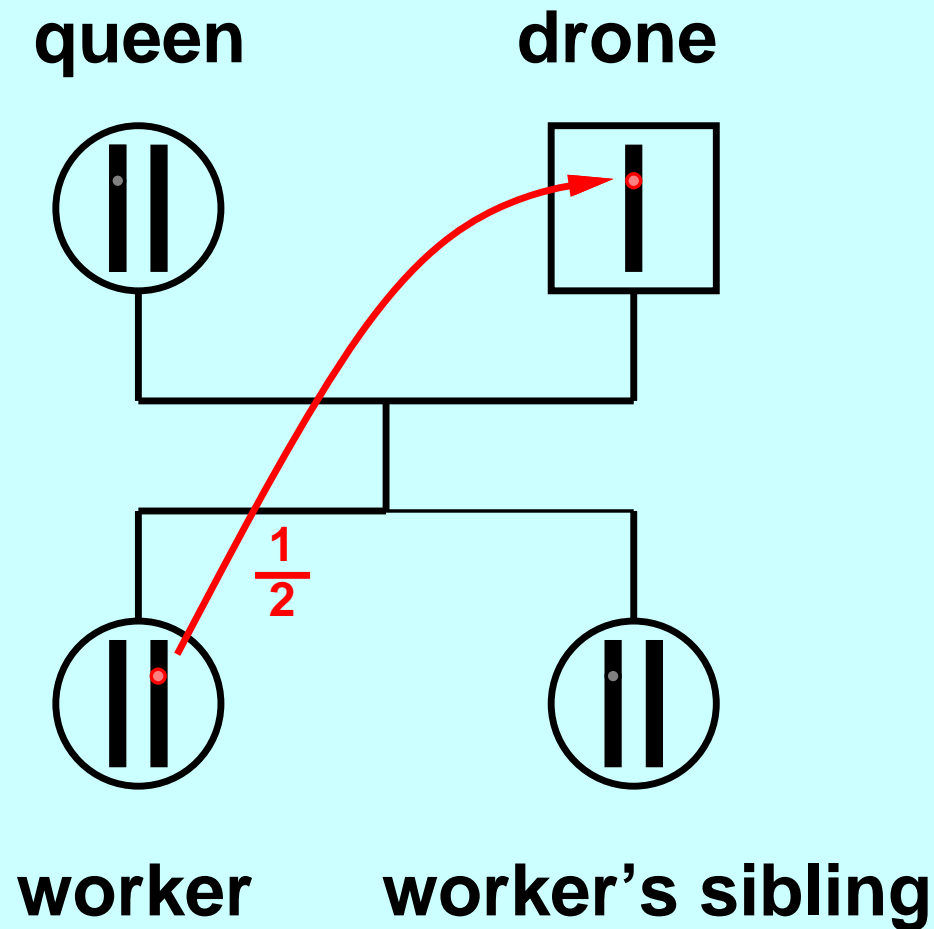# Relatedness between workers and their sibs

queen   drone

worker   worker's sibling

Gene in worker has $\frac{1}{2}$ chance of coming from the queen.

Relatedness between workers and their sibs

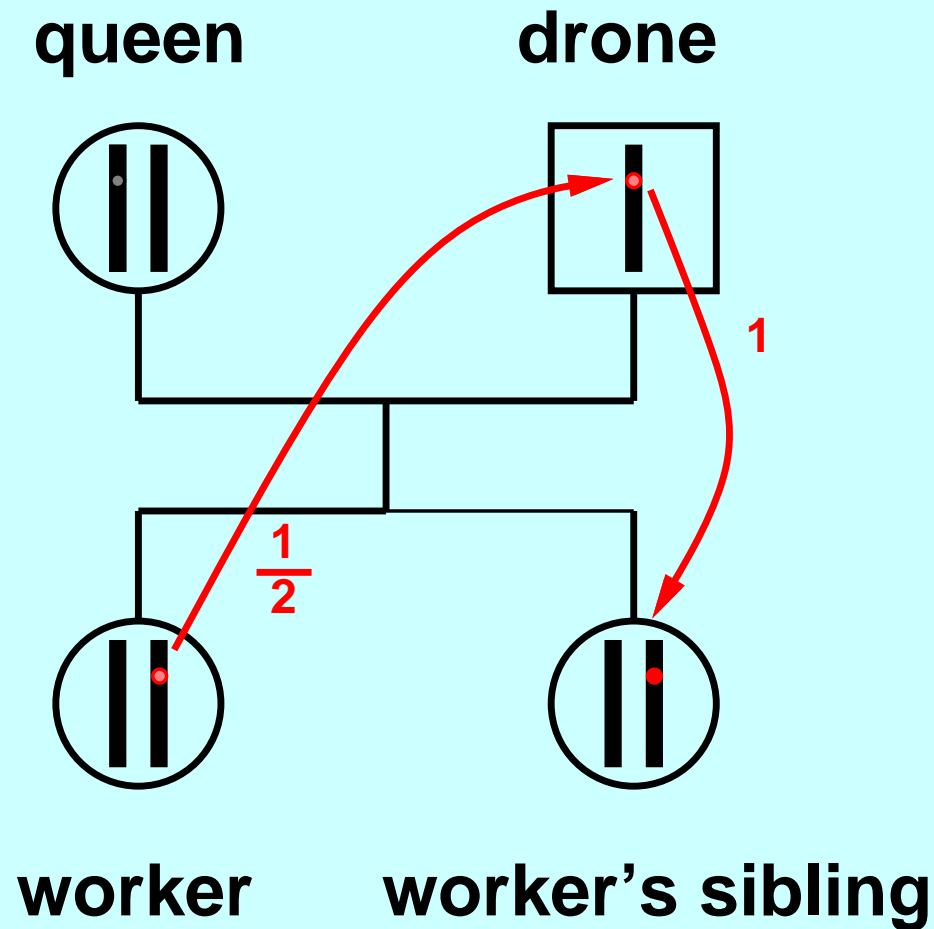**queen**   **drone**

$\frac{1}{2}$

$\frac{1}{2}$

worker   **worker's sibling**

... and that copy has $\frac{1}{2}$ chance of being in the sib, for a chance (so far) of $\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$

Relatedness between workers and their sibs

queen   drone

$\frac{1}{2}$

worker   worker's sibling

also it has $\frac{1}{2}$ chance of coming from the drone.

Relatedness between workers and their sibs

queen   drone

worker   worker's sibling

... and that copy has 100% chance of being in the sib, for a chance of $\frac{1}{2}$.
Result is that total relatedness is $\frac{3}{4}$.

Relatedness if the species were an ordinary diploid

queen   **drone**

$\frac{1}{2}$

$\frac{1}{2}$

$\frac{1}{2}$ $\frac{1}{2}$

worker   **worker's sibling**
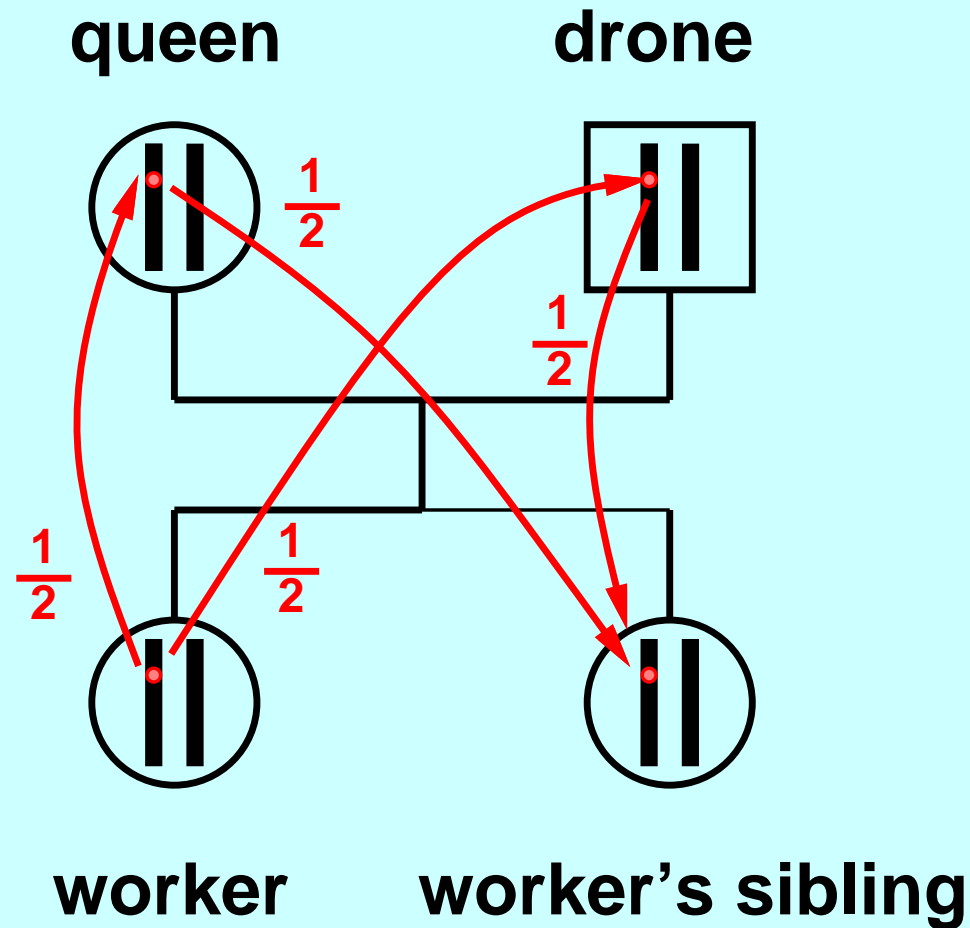
As in termites, the total relatedness is then only $\frac{1}{2}$.

The punctuated equilibrium controversy
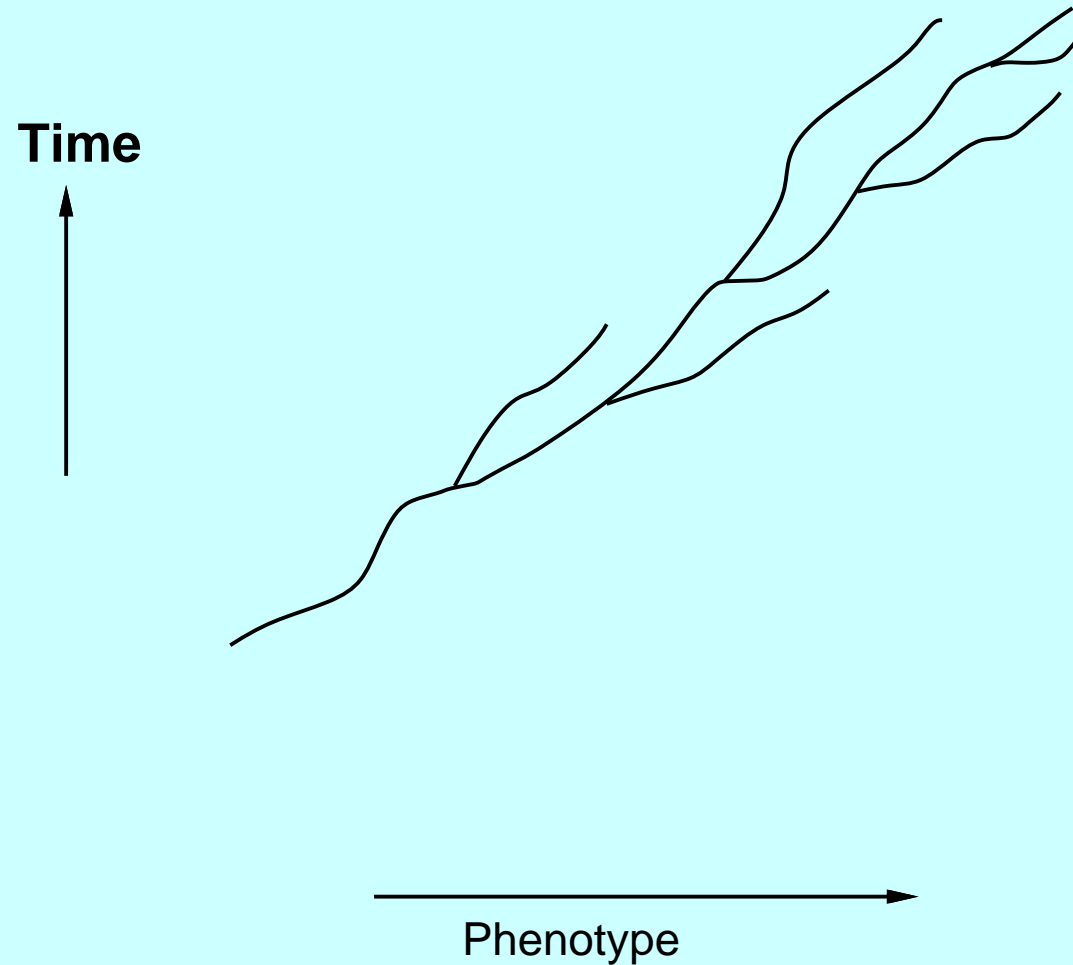

David
Raup

the late
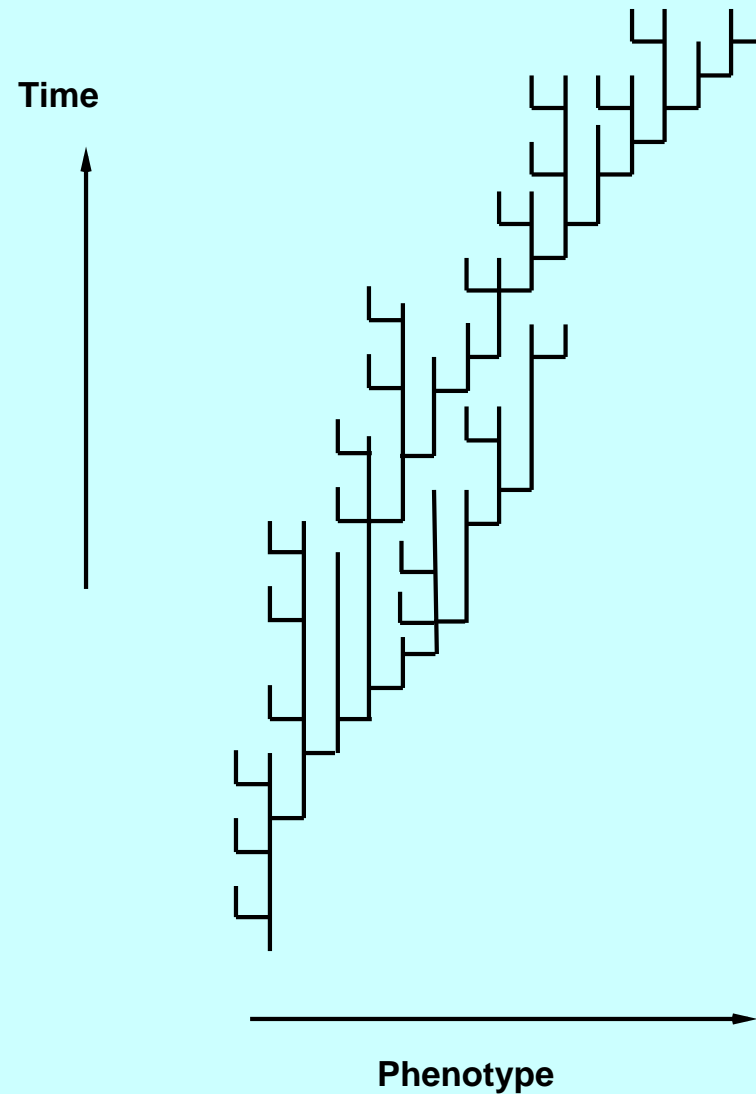Stephen J.
Gould

Niles
Eldredge

the late
Jack
Sepkoski
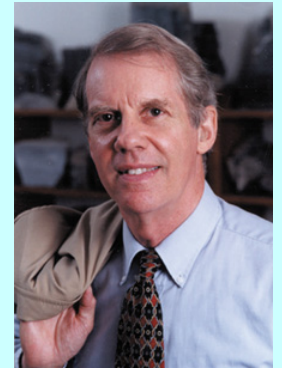
Steven
Stanley

An adaptive trend according to gradualists

Time

Phenotype

Selection is mostly occurring within species and not by species selection
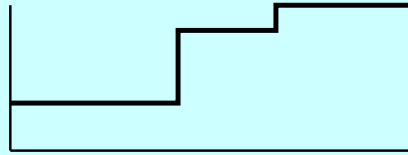
An adaptive trend according to punctuationists

In this hypothetical diagram, 19 speciations leftwards, 21 rightwards

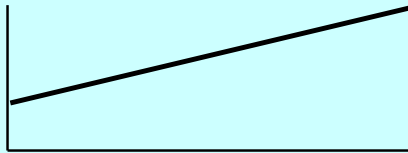**but the rightwards ones survive better**

Issues involving gradualism and punctuationism
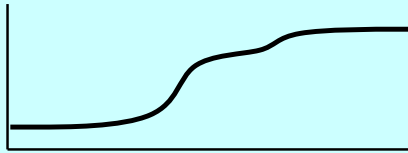
Issue 1: **What are typical patterns of evolution**

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

Gradualist versus punctuationist views

	In: Gradualism	Punctuationalism
What		
Random variation is due to	Mutation ACCTTGA**C**GTTGAA	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

The fossil radiolarian protist Pseudocubus

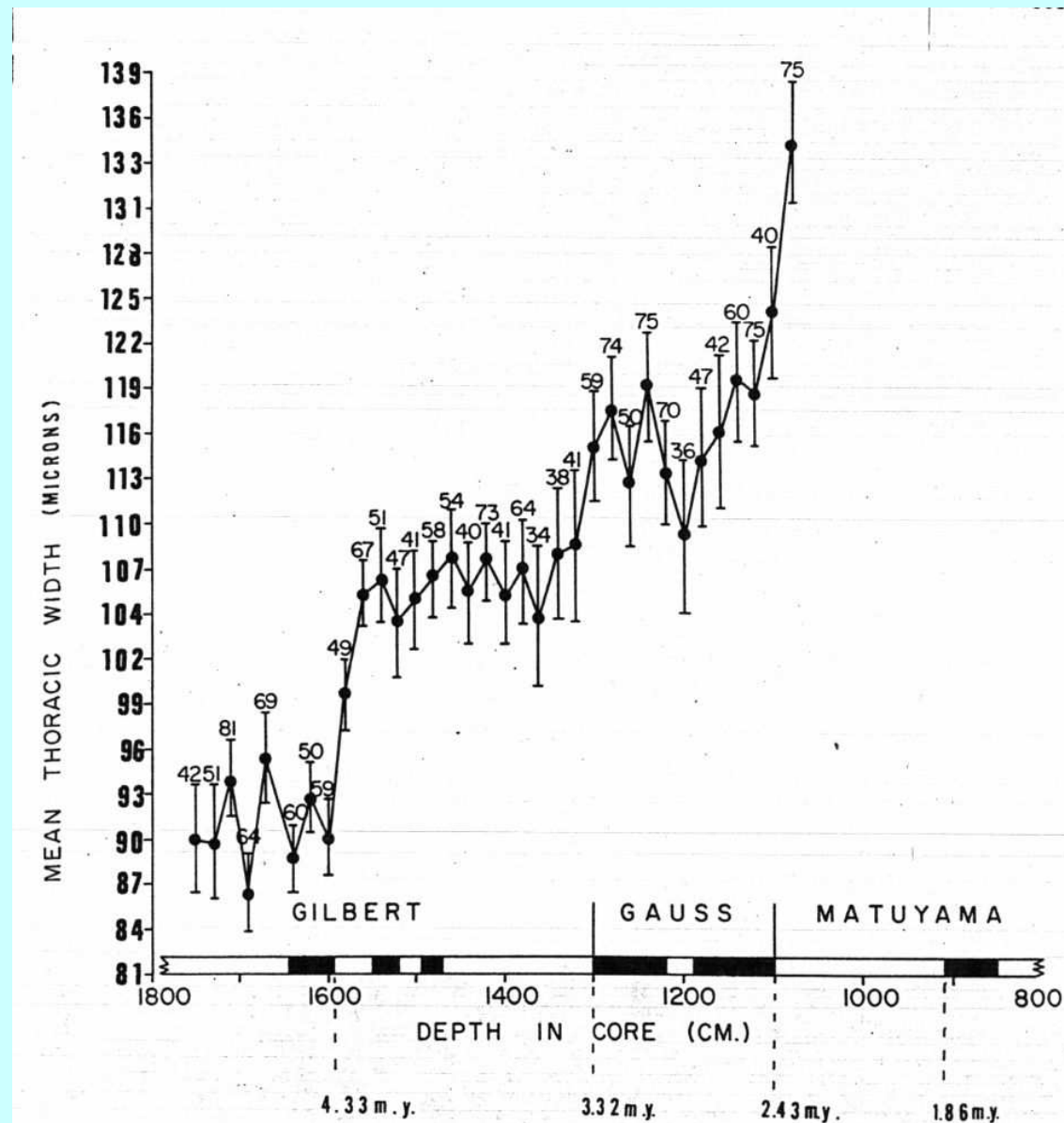# Davida Kellogg's 1975 radiolarian data

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.
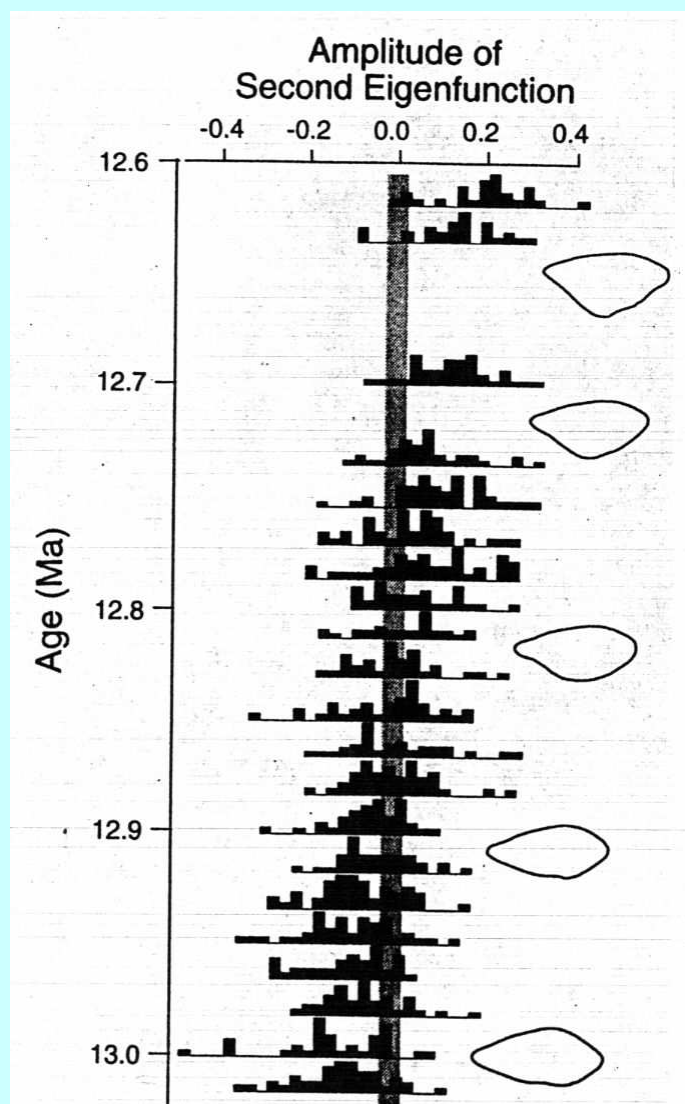
Wei's Globoconella foram data

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 are reconstructed shapes for various positions on the second eigenfunction (from top to bottom): 0.4, 0.2, 0.0, −0.2, and −0.4.
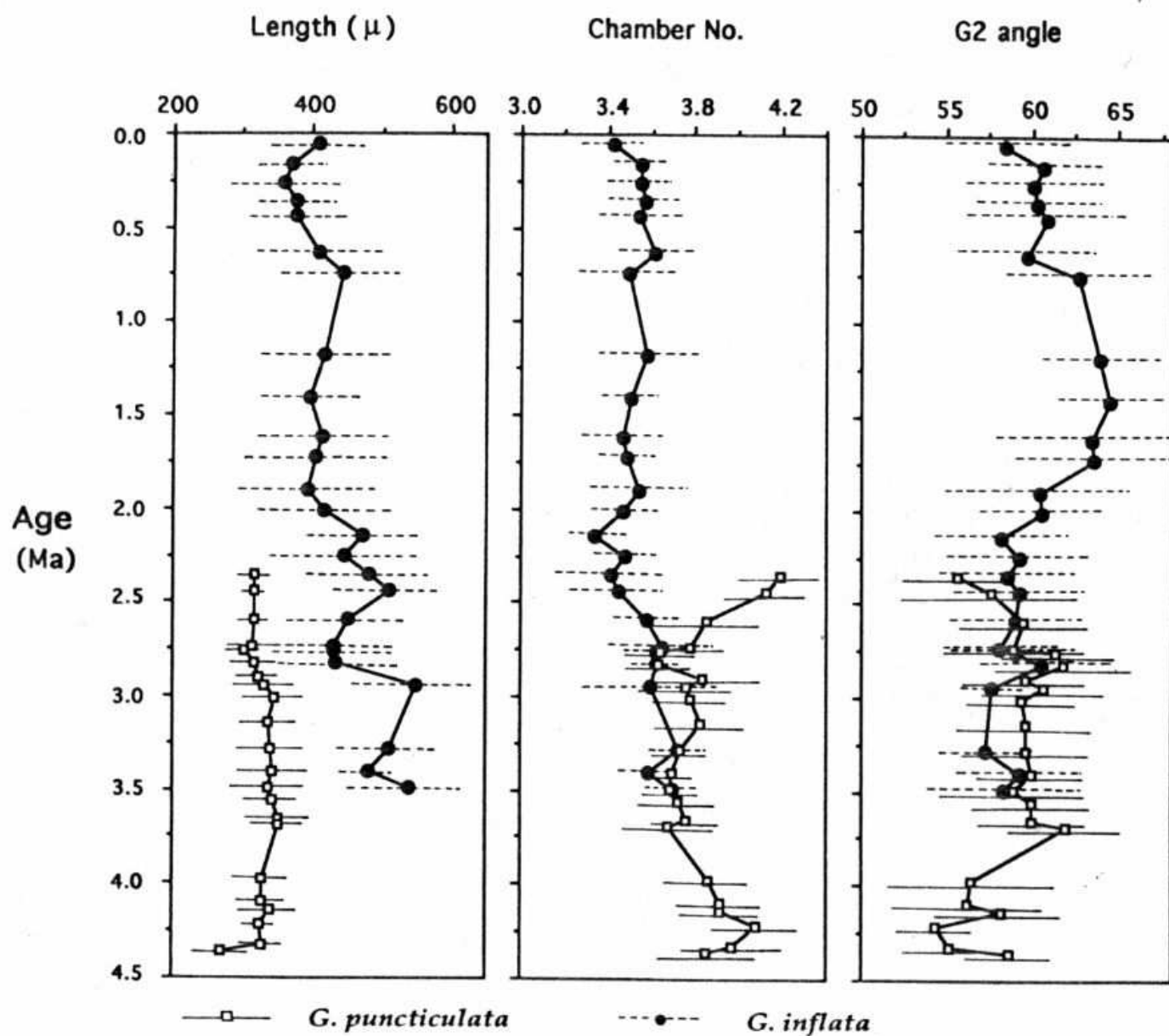
Wei's Globoconella foram data

FIGURE 8. Time-series of average value (±1 SD) of three morphometric variables in the two *Globoconella* lineages.
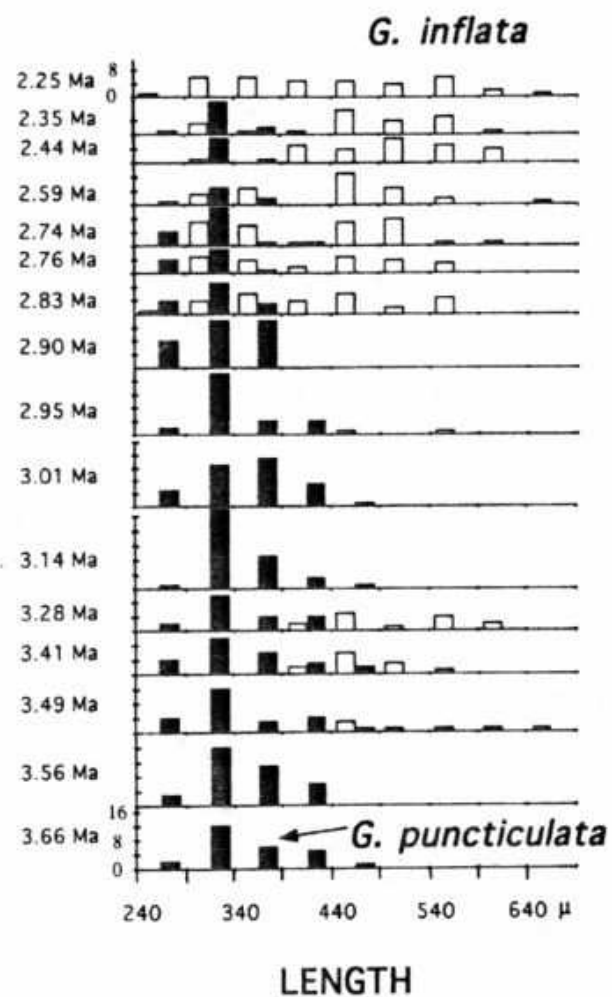
Wei's Globoconella foram data

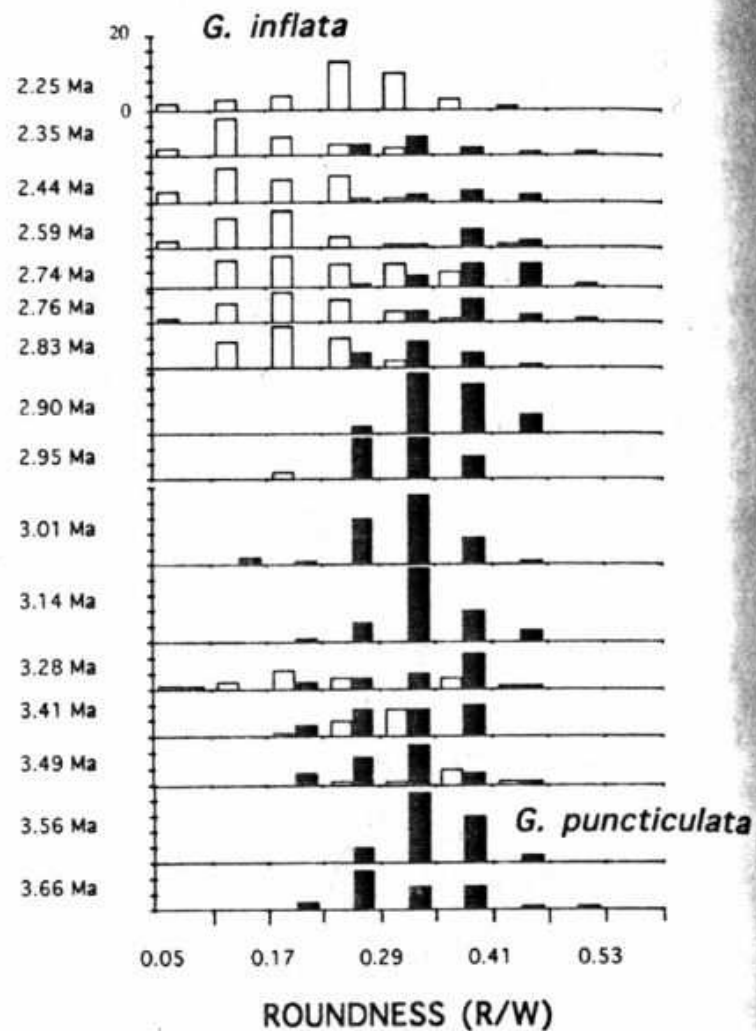FIGURE 9. Stacked histograms of test length (L) of G. inflata and G. puncticulata during 3.66 Ma to 2.25 Ma.

FIGURE 10. Stacked histograms of peripheral roundness (defined as R/W) of G. inflata and G. puncticulata during 3.66 to 2.25 Ma.
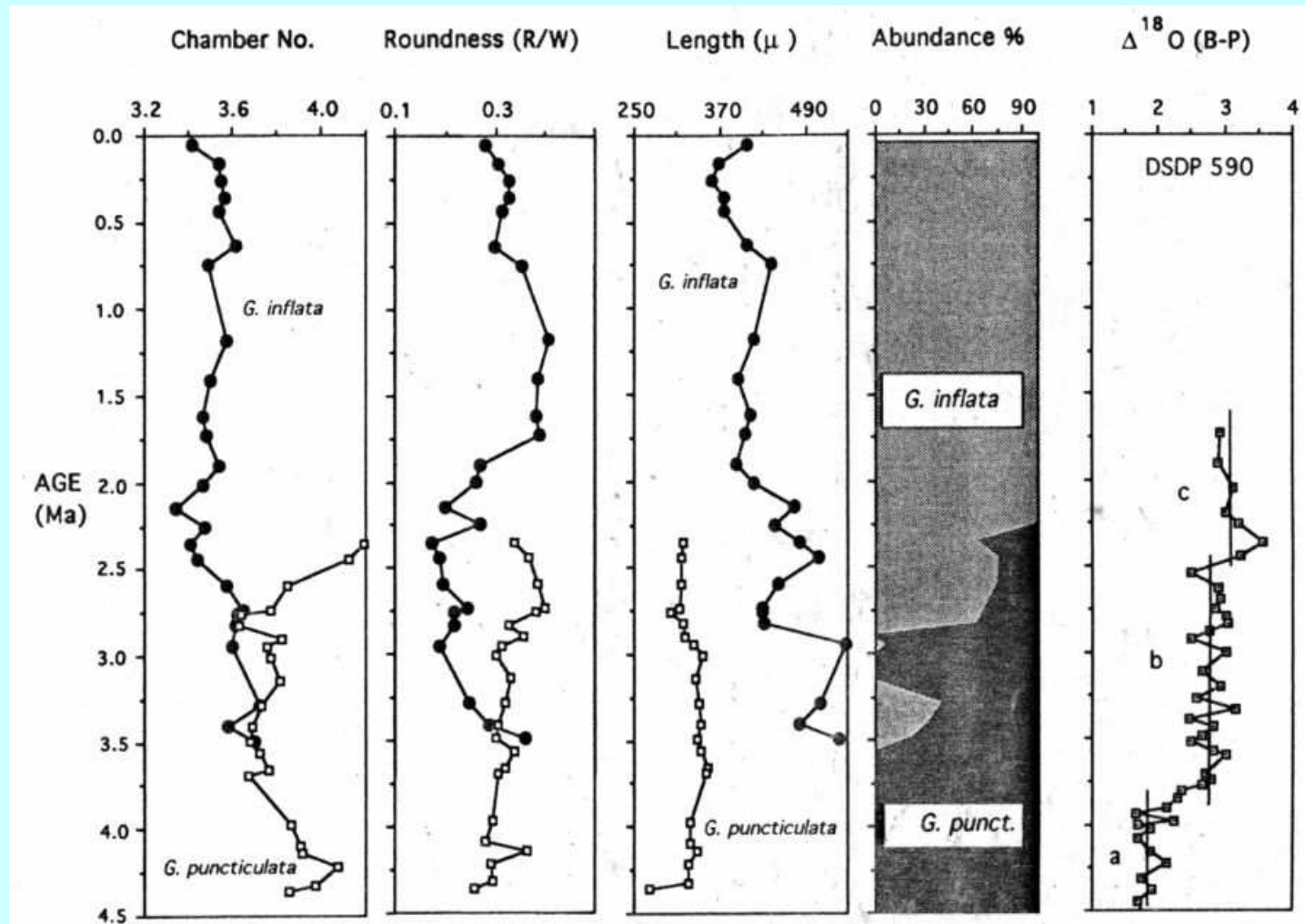
Wei's Globoconella foram data

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.

Gryphaea, a Jurassic oyster
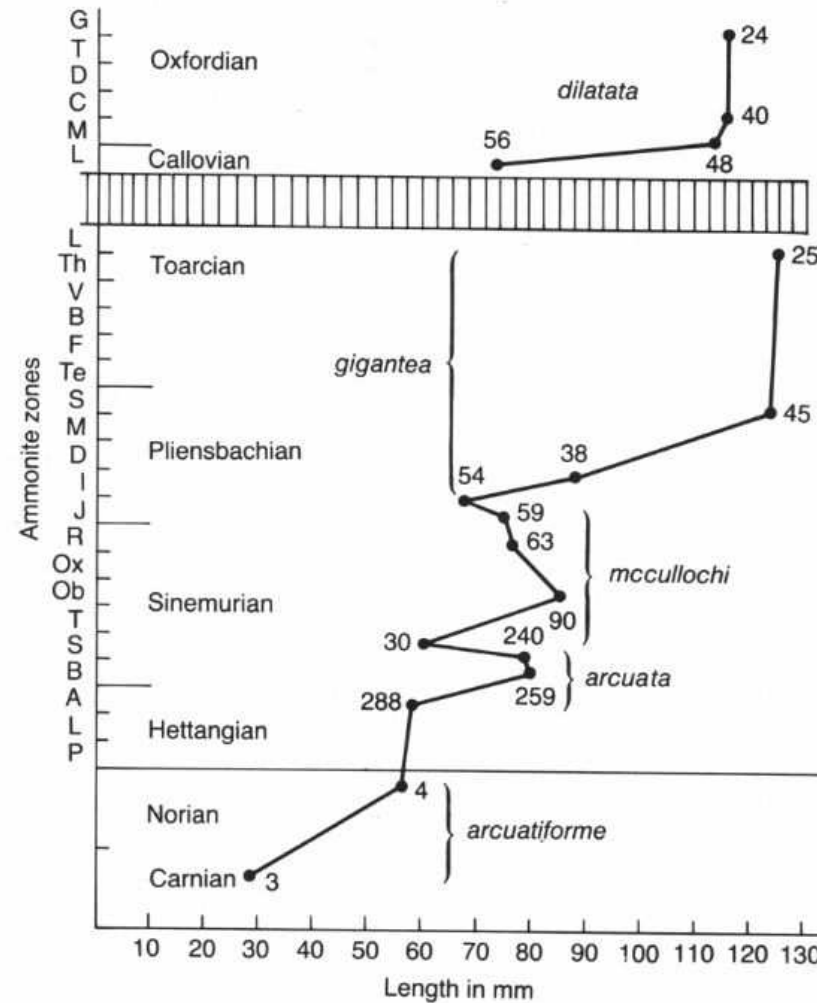
Hallam's Gryphaea Jurassic oyster data

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)

Hyopsodus, an Eocene condylarth mammal
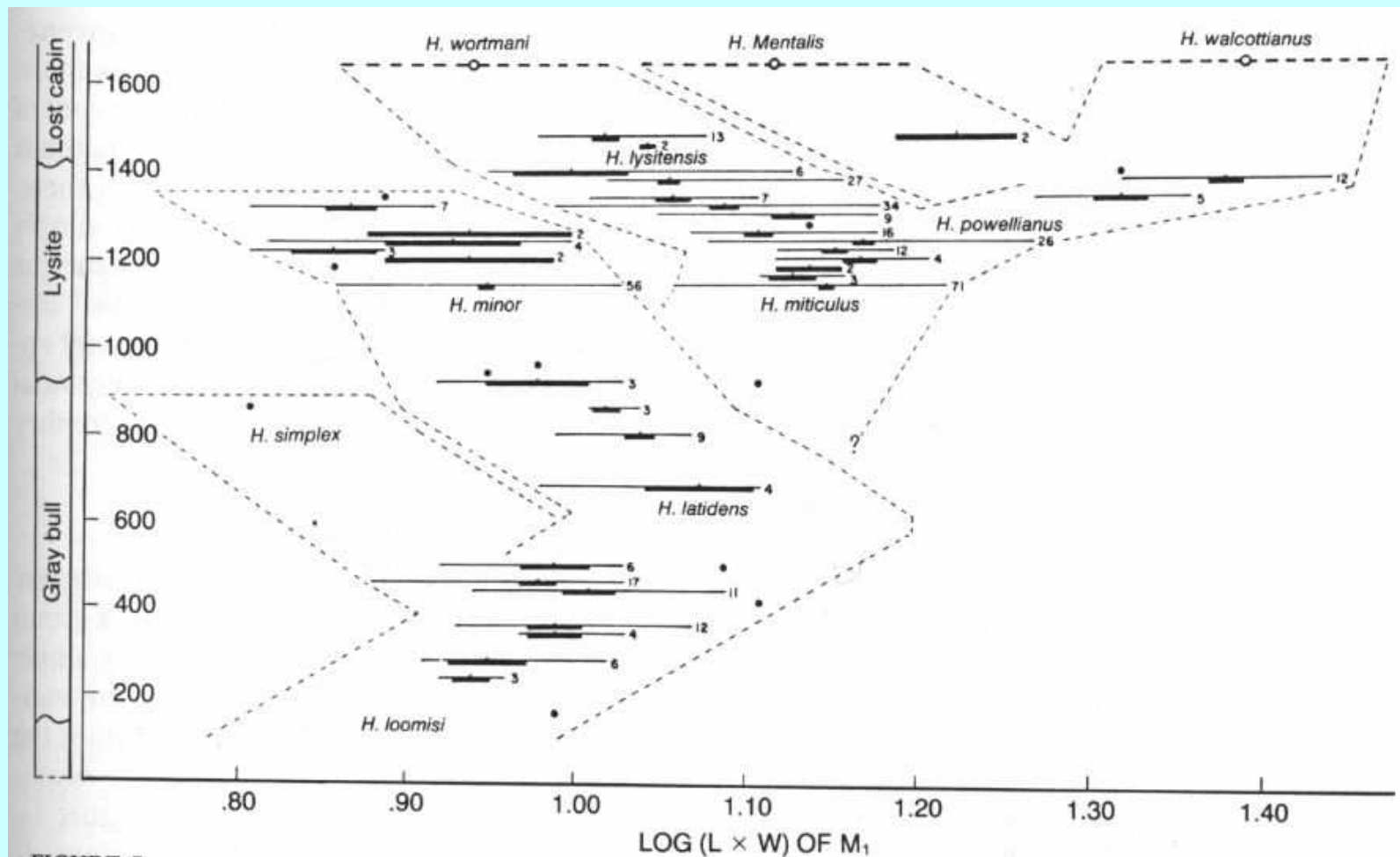
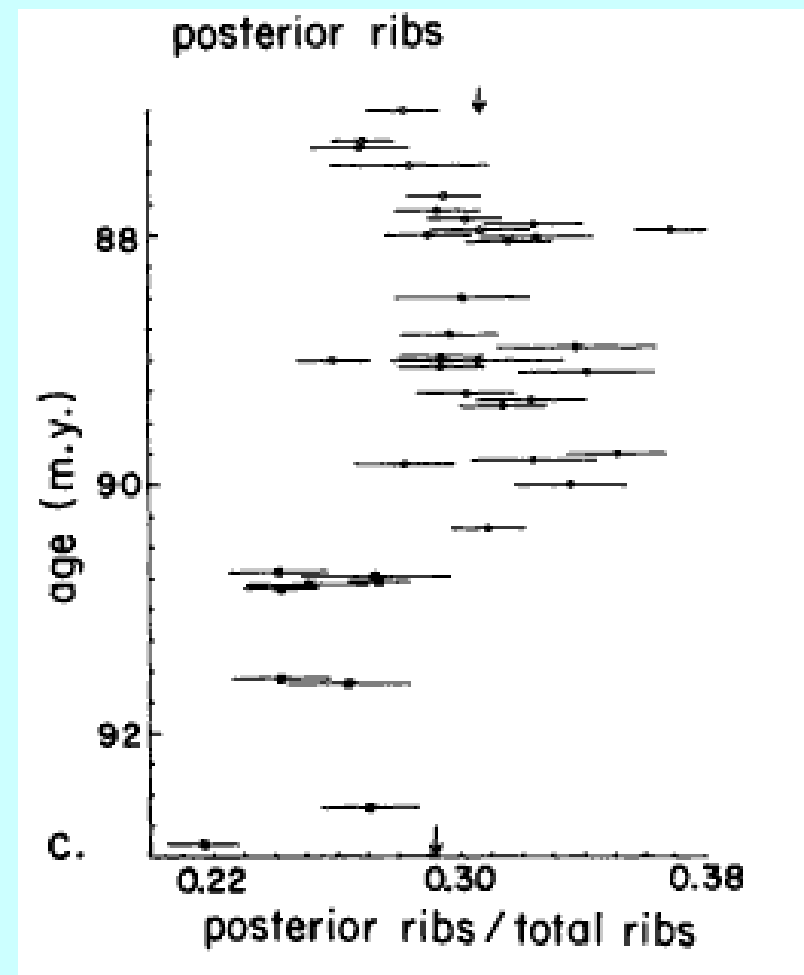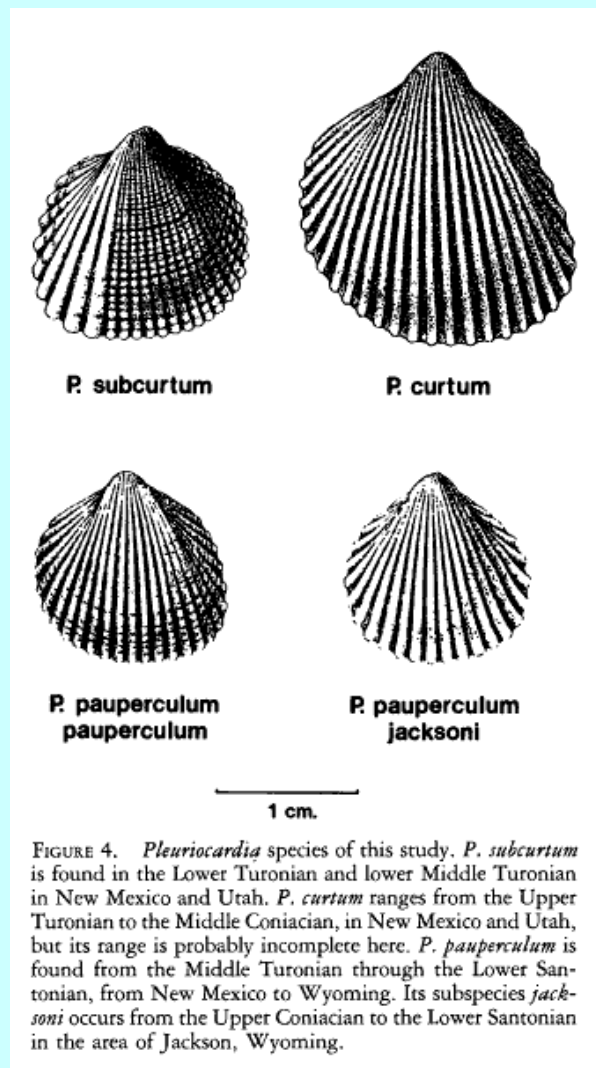# Gingerich's Eocene condylarth data


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)

Pleurocardia **cockles**

P. subcurtum

P. curtum

P. pauperculum
pauperculum

P. pauperculum
jacksoni

1 cm.

FIGURE 4. *Pleuriocardia* species of this study. *P. subcurtum* is found in the Lower Turonian and lower Middle Turonian in New Mexico and Utah. *P. curtum* ranges from the Upper Turonian to the Middle Coniacian, in New Mexico and Utah, but its range is probably incomplete here. *P. pauperculum* is found from the Middle Turonian through the Lower Santonian, from New Mexico to Wyoming. Its subspecies *jacksoni* occurs from the Upper Coniacian to the Lower Santonian in the area of Jackson, Wyoming.

Geary, D. H. 1987. Evolutionary tempo and mode in a sequence of the Upper Cretaceous bivalve Pleuriocardia. *Paleobiology* **13:** 140-151.

Trends through time in some fresh-water cockles
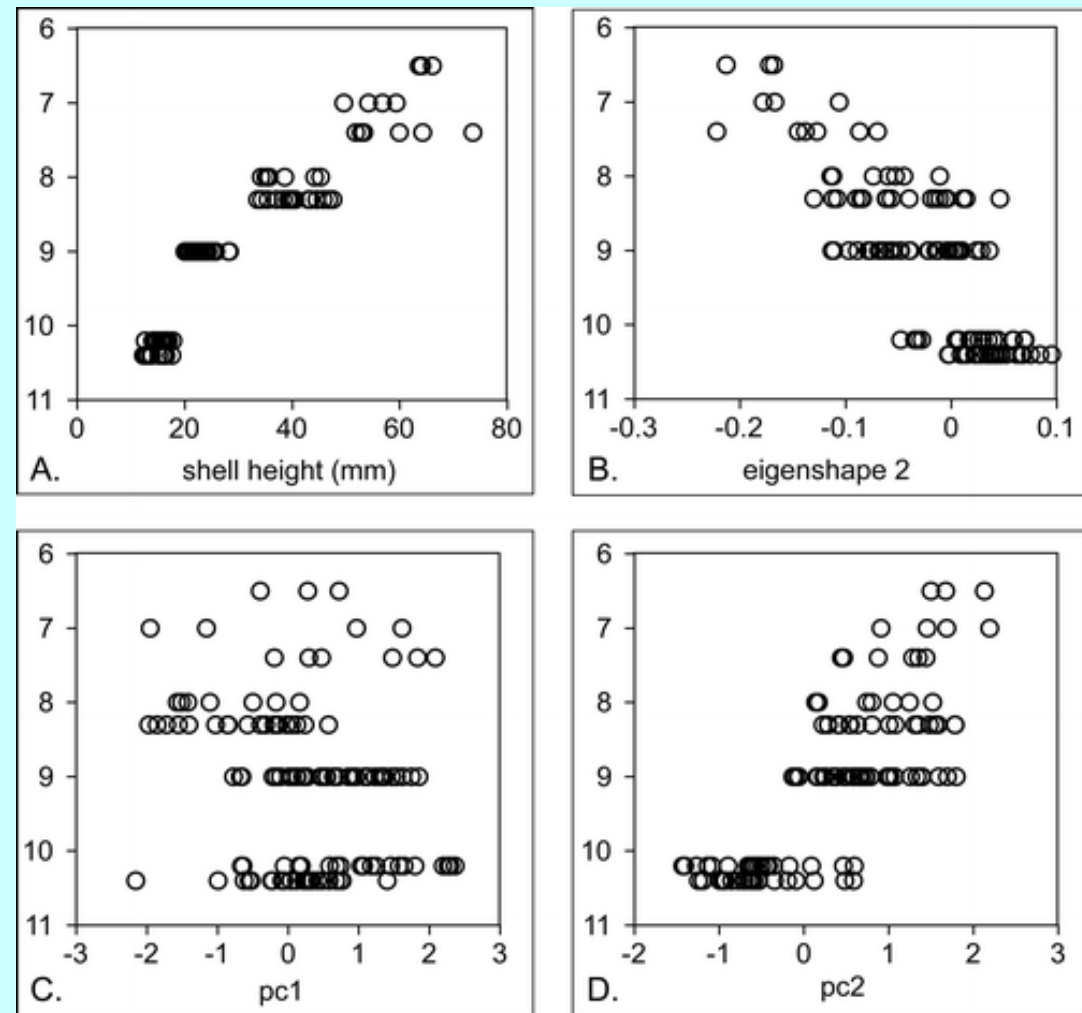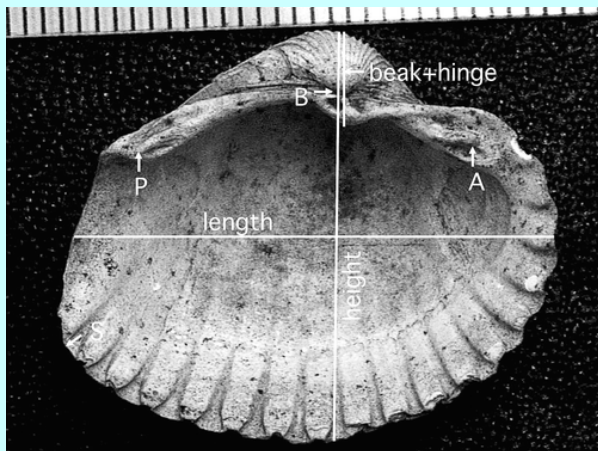
Dana H. Geary, Gene Hunt, Imre Magyar, and Holly Schreiber. 2010. The paradox of gradualism: phyletic evolution in two lineages of lymnocardiid bivalves (Lake Pannon, central Europe). *Paleobiology* **36(4):** 592-614.

A punctuated change in Ordovician trilobite
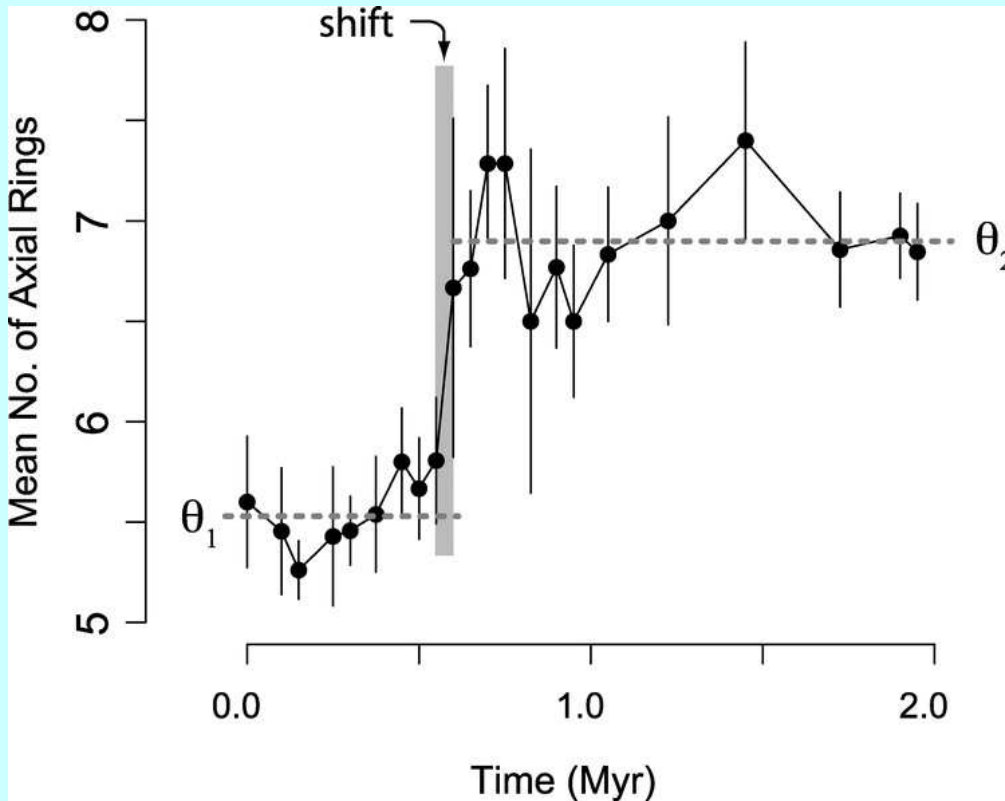
Mean number of pygidial axial rings in a stratigraphic sequence of the trilobite *Flexicalymene* (Cisne et al. 1980). The best-supported model for these data implies an unsampled punctuation event between the ninth and tenth samples (vertical gray rectangle); dashed horizontal lines indicate the estimated stasis optima (θ_1 and θ_2) for this model. Time is measured in millions of years from the first population. Vertical bars show 95% confidence intervals around the sample means.
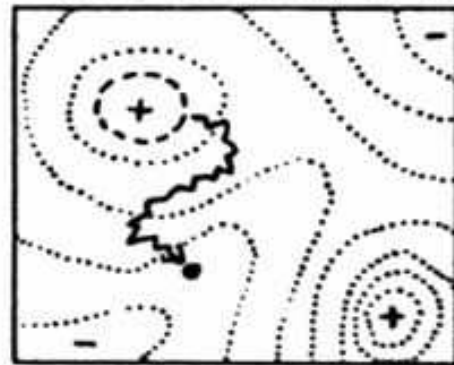
From G. Hunt, 2008, *Paleobiology*.

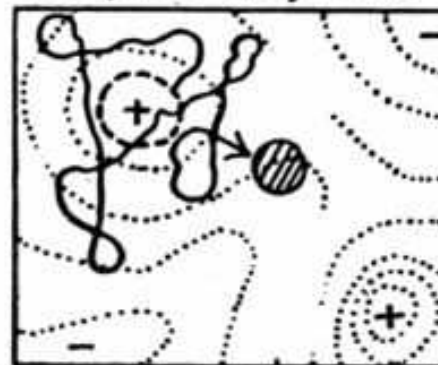# Sewall Wright's (1932) adaptive peaks

A. Increased Mutation or reduced Selection 4NU, 4NS very large

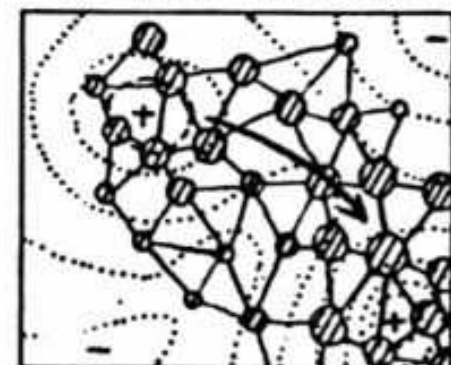B. Increased Selection or reduced Mutation 4NU, 4NS very large

C. Qualitative Change of Environment 4NU, 4NS very large
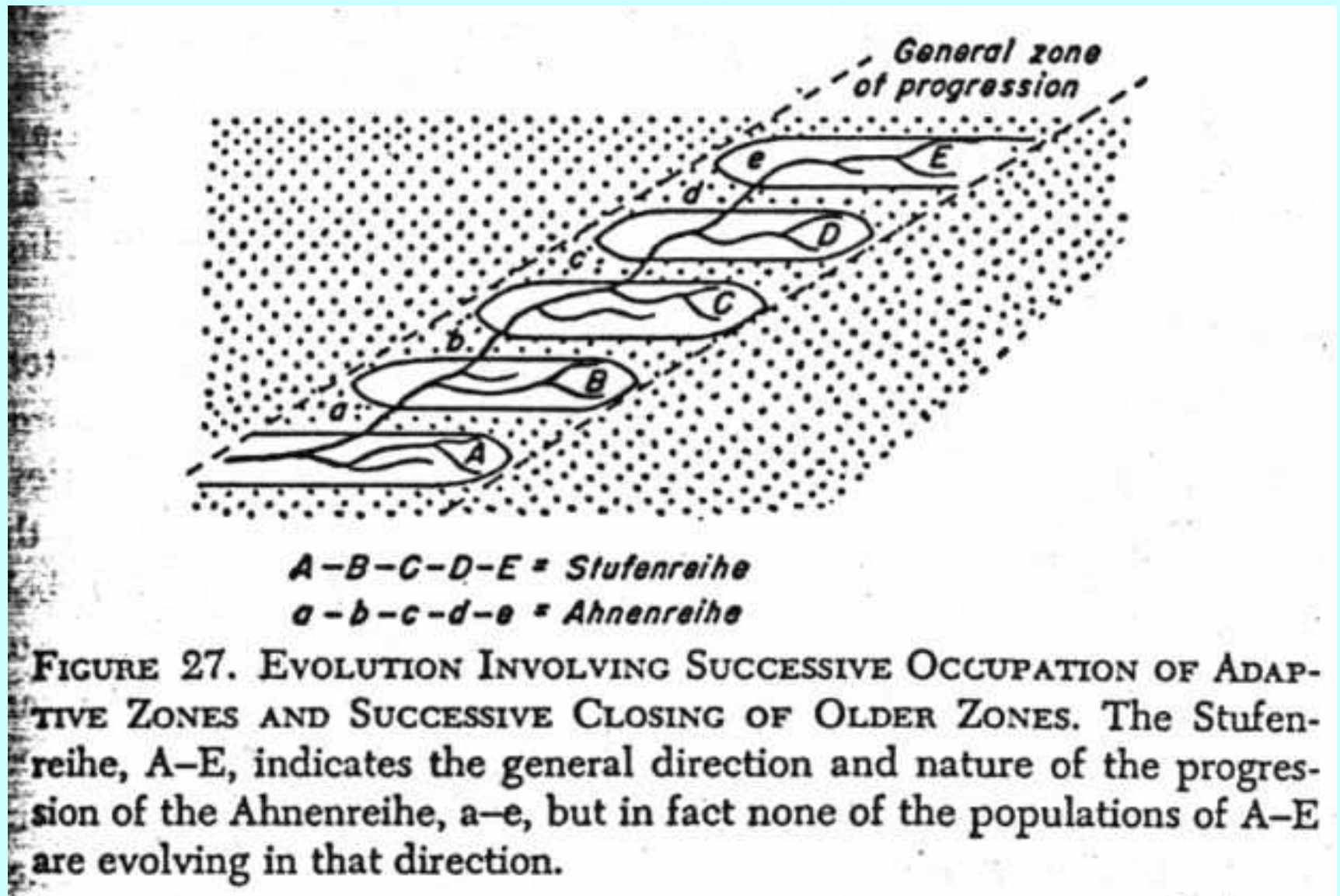
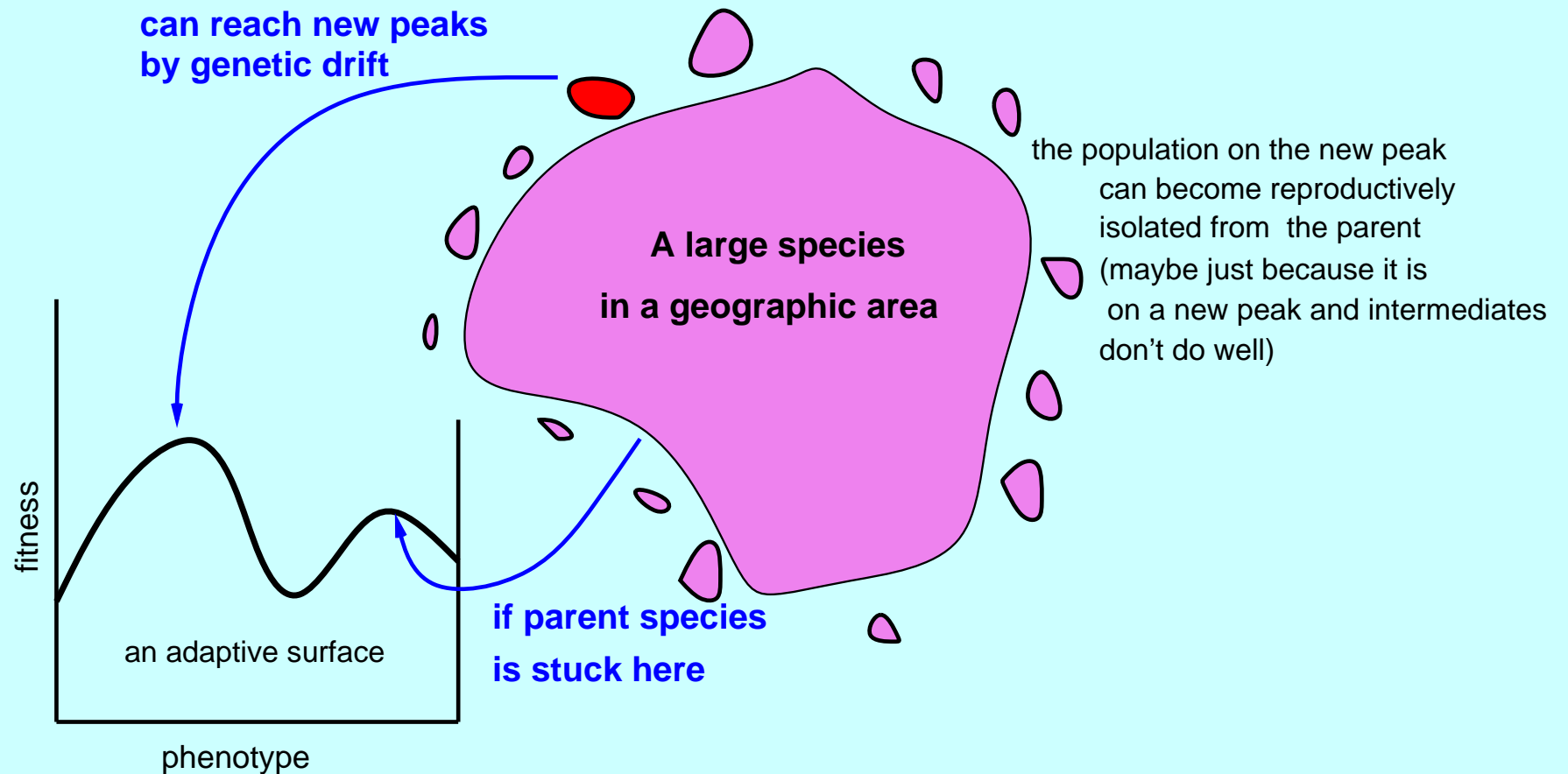D. Close Inbreeding 4NU, 4NS very small

E. Slight Inbreeding 4NU, 4NS medium

F. Division into local Races 4nm medium

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
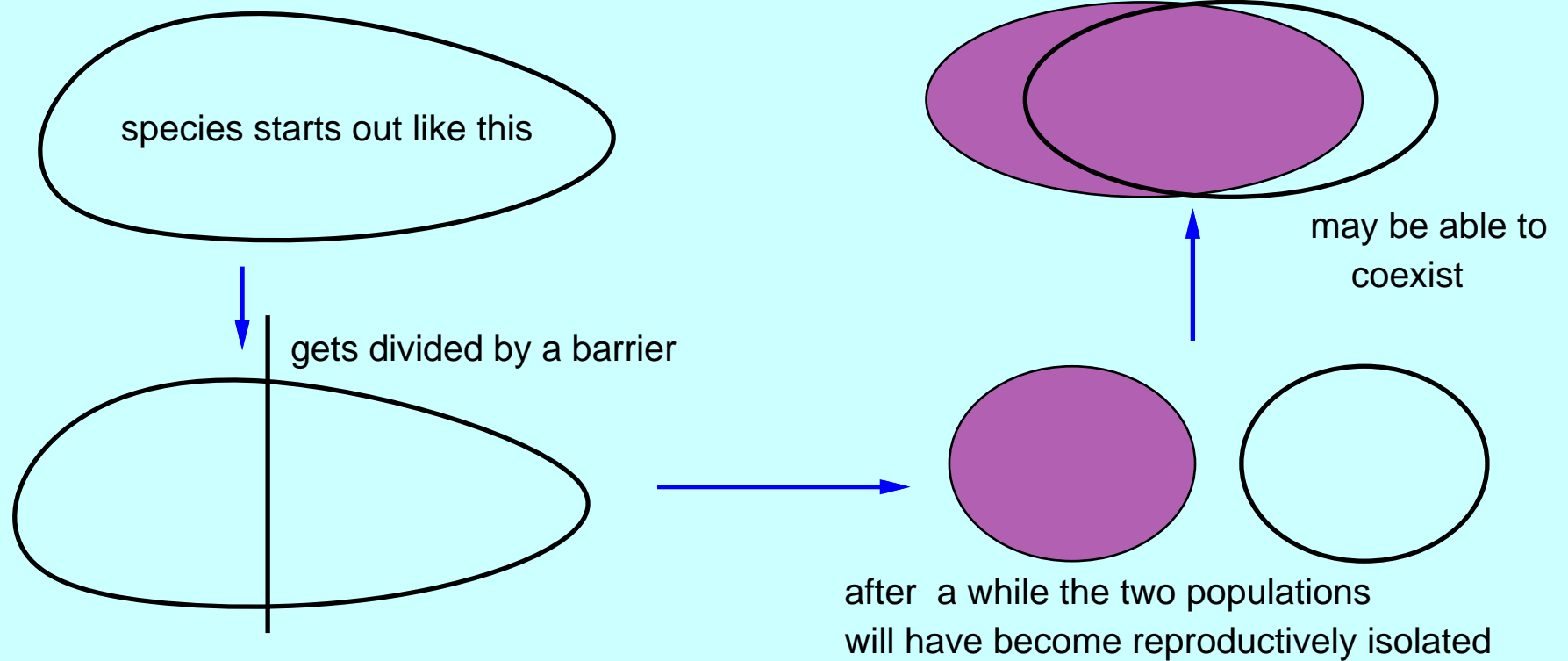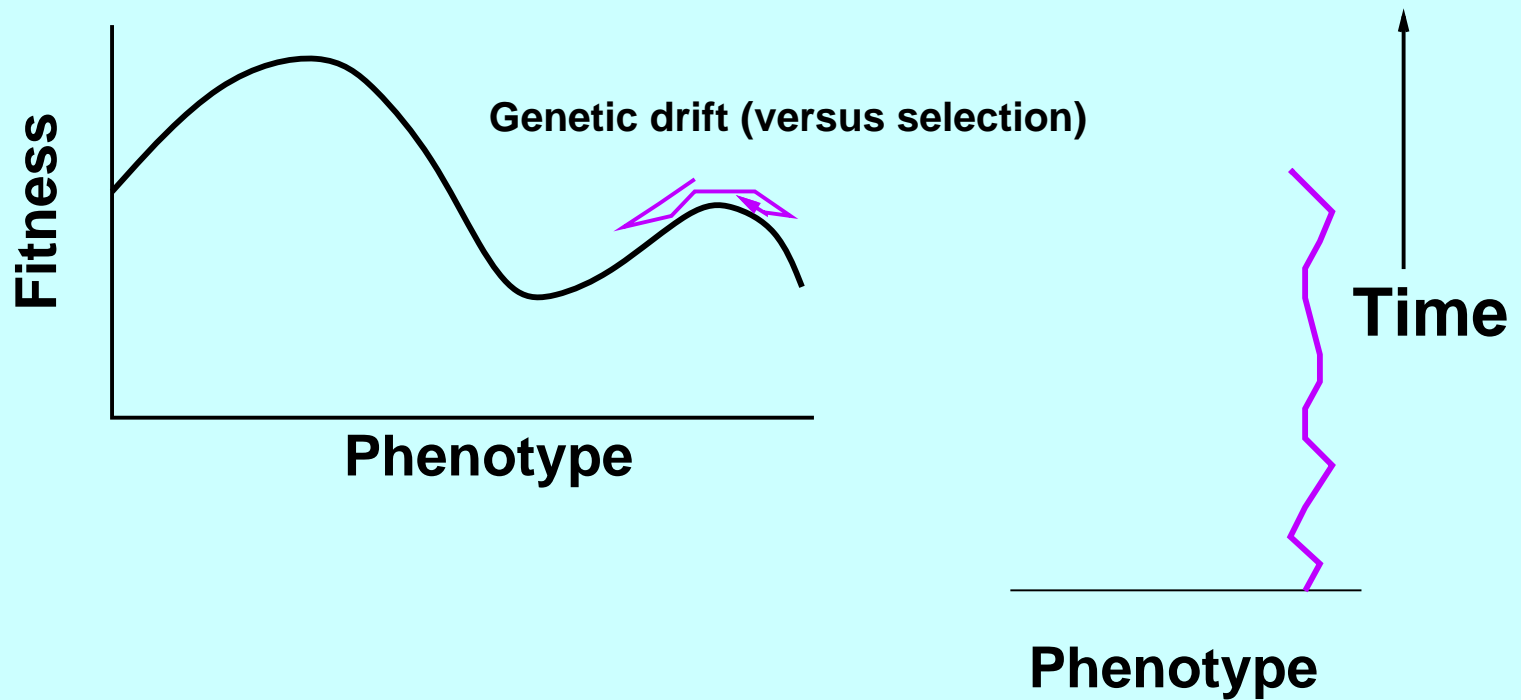
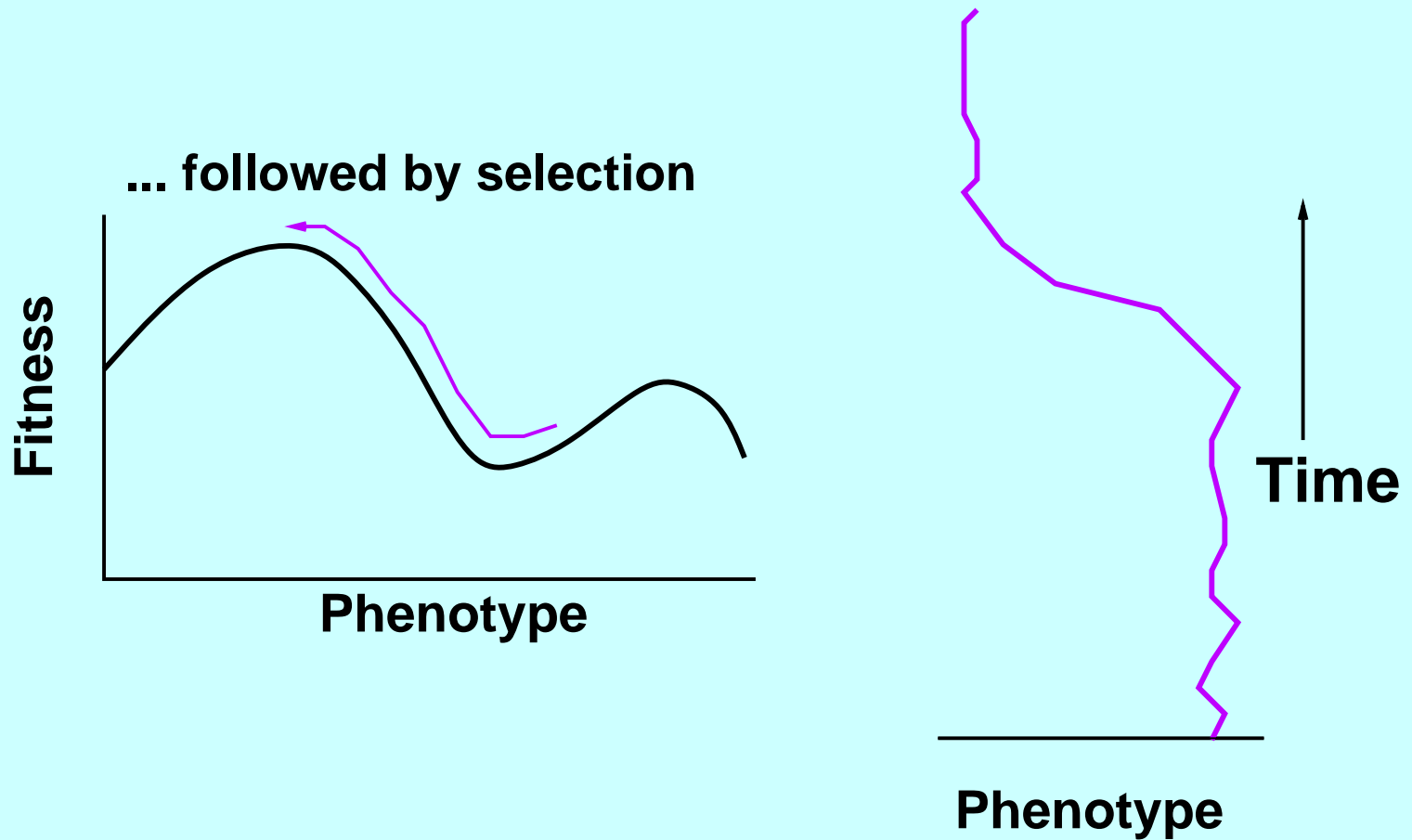# George Gaylord Simpson's 1944 adaptive zones

General zone of progression

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.

Ernst Mayr's view of peripheral speciation

**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

an adaptive surface

**if parent species
is stuck here**

phenotype

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

Punctuated change by gradual mechanisms

Fitness / Phenotype — Genetic drift (versus selection)

Time / Phenotype

Punctuated change by gradual mechanisms

... followed by selection

Fitness

Phenotype

Time

Phenotype

Punctuation by gradual rise of a peak

phenotype

Punctuation by gradual rise of a peak

phenotype

Punctuation by gradual rise of a peak

phenotype

Punctuation by gradual rise of a peak

phenotype

Punctuation by gradual rise of a peak

phenotype