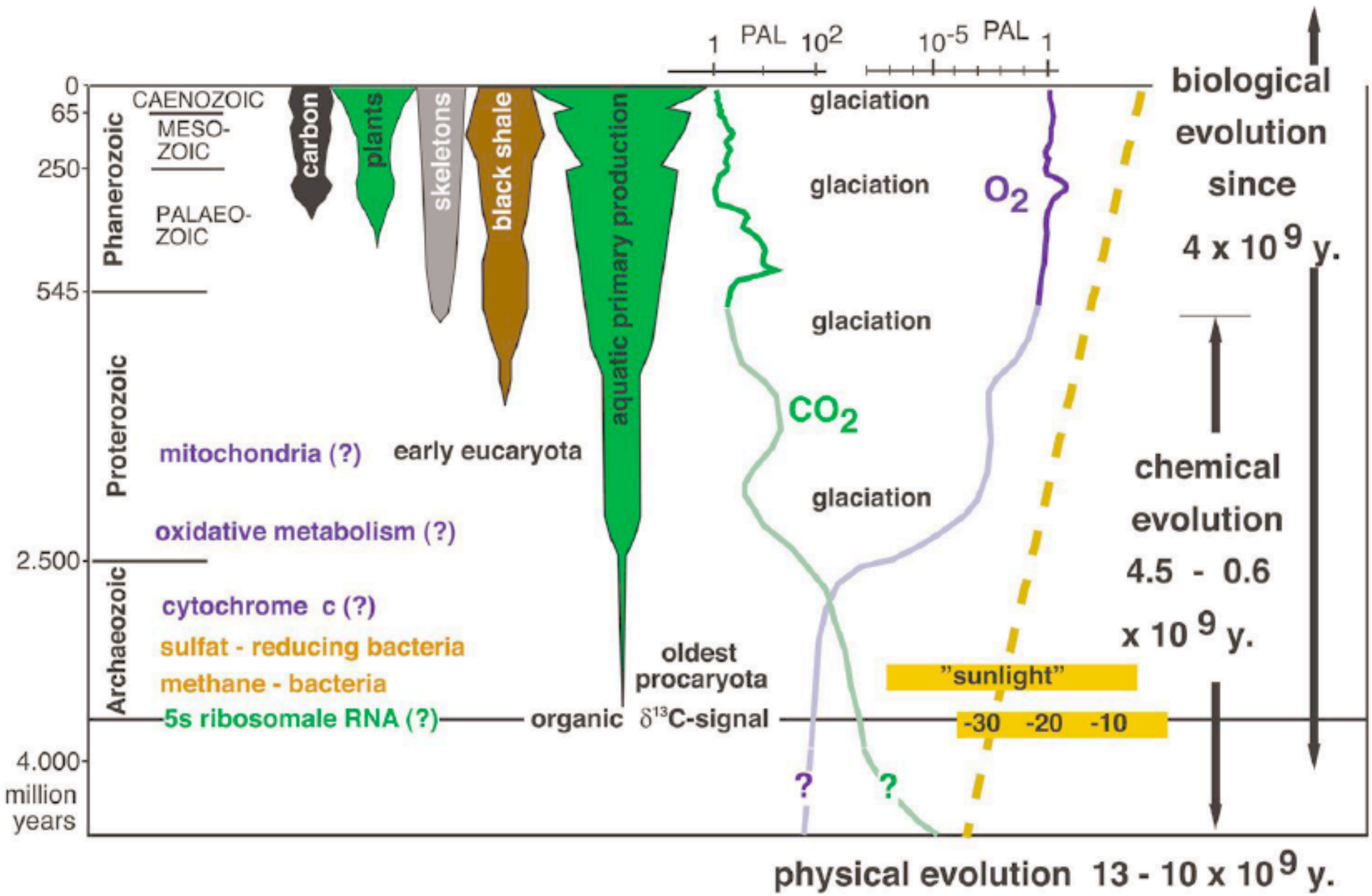
The History of Life and the Nature of the Fossil Record

Douglas H. Erwin

National Museum of Natural History

and

Santa Fe Institute



1 PAL 10^2
10^{-5} PAL 1
0
65
250
545
2.500
4.000
million years
Phanerozoic
CAENOZOIC
MESO-ZOIC
PALAEO-ZOIC
Proterozoic
Archaeozoic
carbon
plants
skeletons
black shale
aquatic primary production
glaciation
glaciation
glaciation
glaciation
O_2
CO_2
biological evolution since 4×10^9 y.
chemical evolution 4.5 - 0.6 $\times 10^9$ y.
mitochondria (?)
early eucaryota
oxidative metabolism (?)
cytochrome c (?)
sulfat - reducing bacteria
methane - bacteria
5s ribosomale RNA (?)
organic δ^{13}C-signal
oldest procaryota
"sunlight"
-30 -20 -10
?
?
physical evolution 13 - 10 $\times 10^9$ y.

How is biological diversity constructed?

- How do organisms/species construct their own environments, and those of other species?
- How have ecological networks been constructed and how have they evolved?
- How has the evolution of gene regulatory networks influenced evolution?

Framework of Lecture 1

- Nature of the fossil record - types of fossils
- Types of biodiversity
- Large-scale patterns
- Resolving time
- Diversity vs. Disparity

Body Fossils

Crinoids

Gogia

Devonian Eurypterids

Soft body Fossils

Opabinia regalis, Burgess Shale, 505 Mya

Soft body Fossils

Waptia

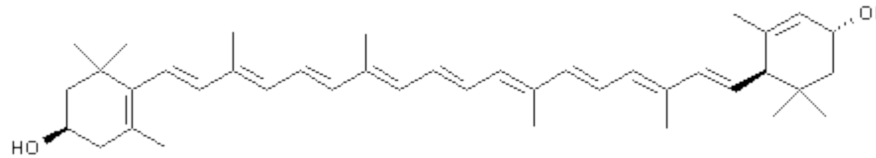
Trace Fossils

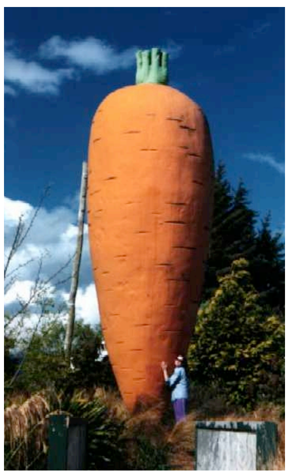
Trace Fossils

Biomarkers

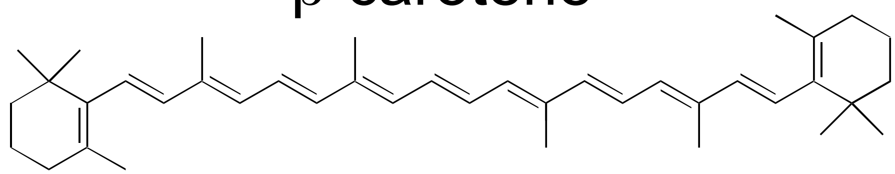
- Carotenoids are usually yellow, orange or red coloured pigments

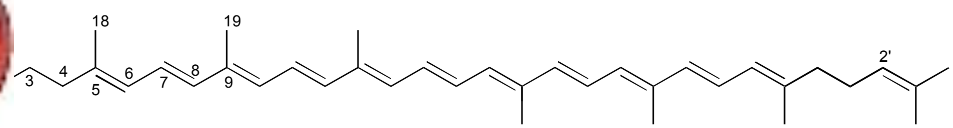
lutein





β-carotene





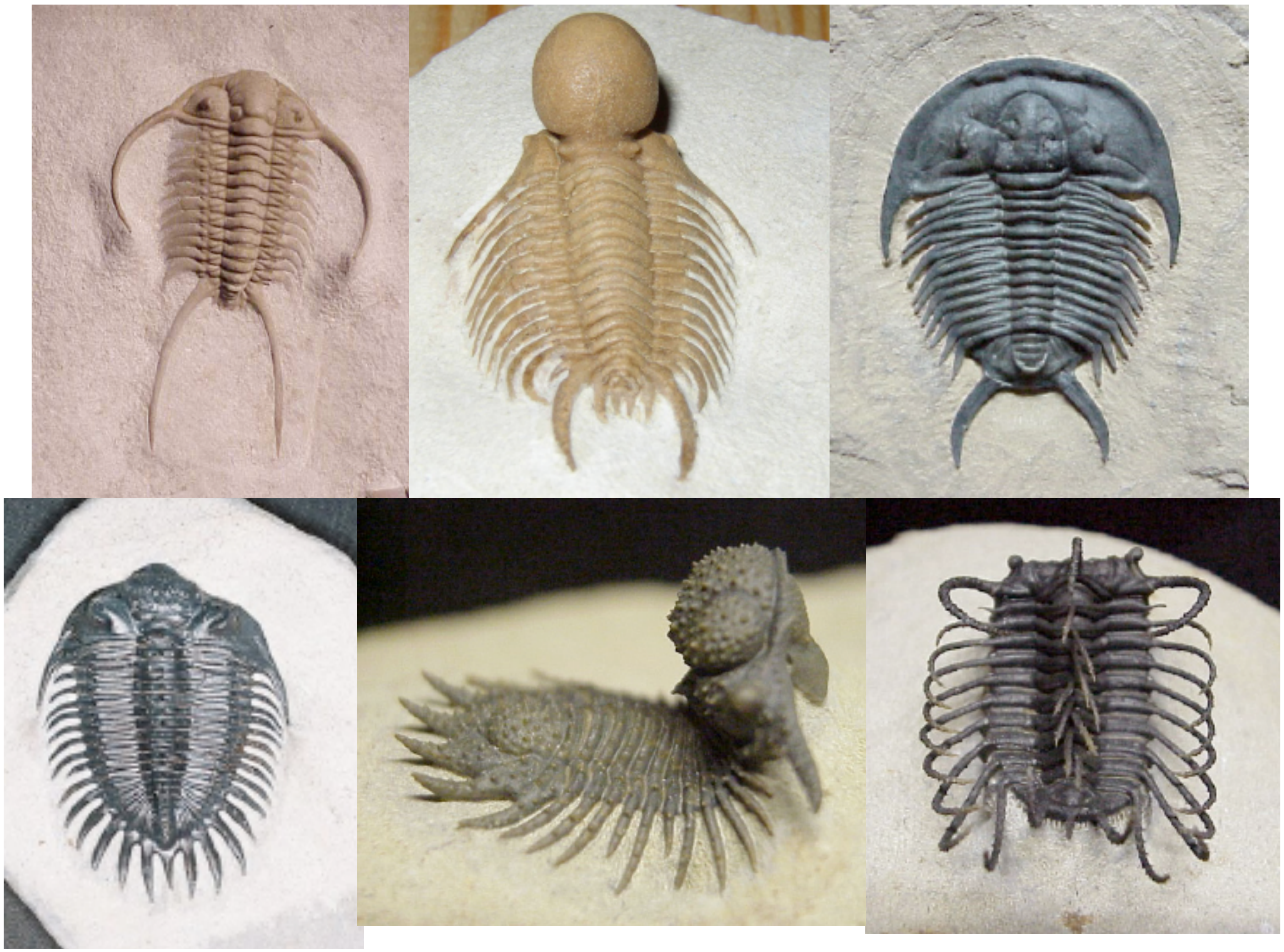
lycopene

Types of diversity:

- Taxic (no. of species)
- Phylogenetic
- Morphologic disparity
- Functional diversity
- Ecospace
- Social/behavioral
- Developmental

Taxic Diversity

Phylogenetic Diversity



Images from /hazen.gl.ciw.edu

Morphologic Diversity (Disparity)

Images from /hazen.gl.ciw.edu

Functional and Ecologic Diversity

Architectural Diversity

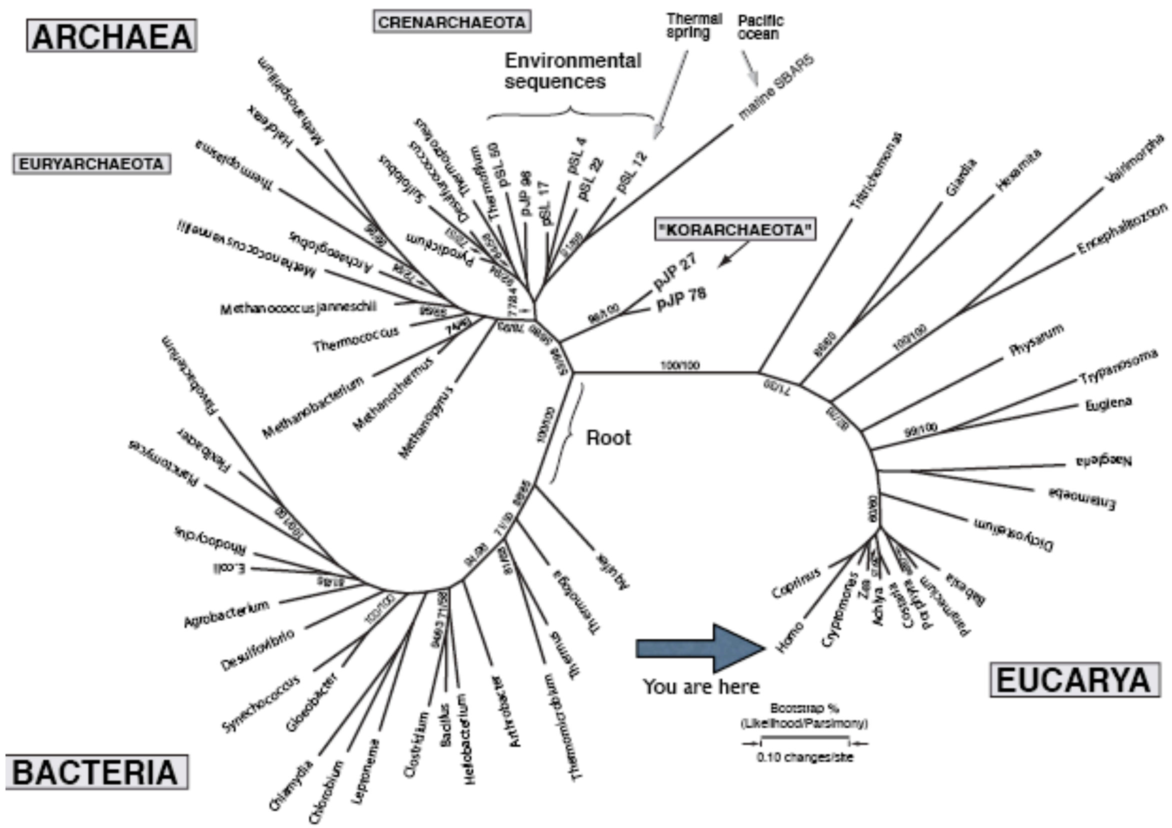
Behavioral Diversity

Developmental Diversity

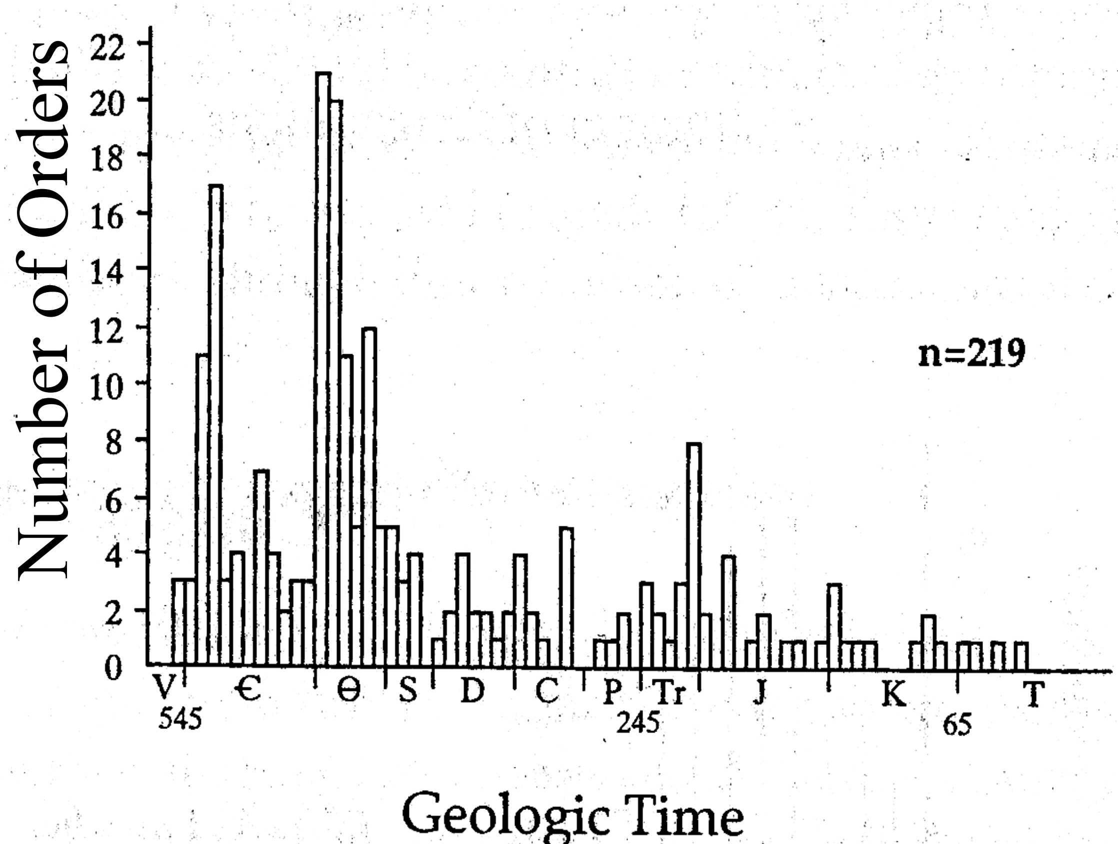
Framework of Lecture 1

- Nature of the fossil record - types of fossils
- Types of Biodiversity
- **Large-scale patterns**
- Resolving time
- Diversity vs. Disparity

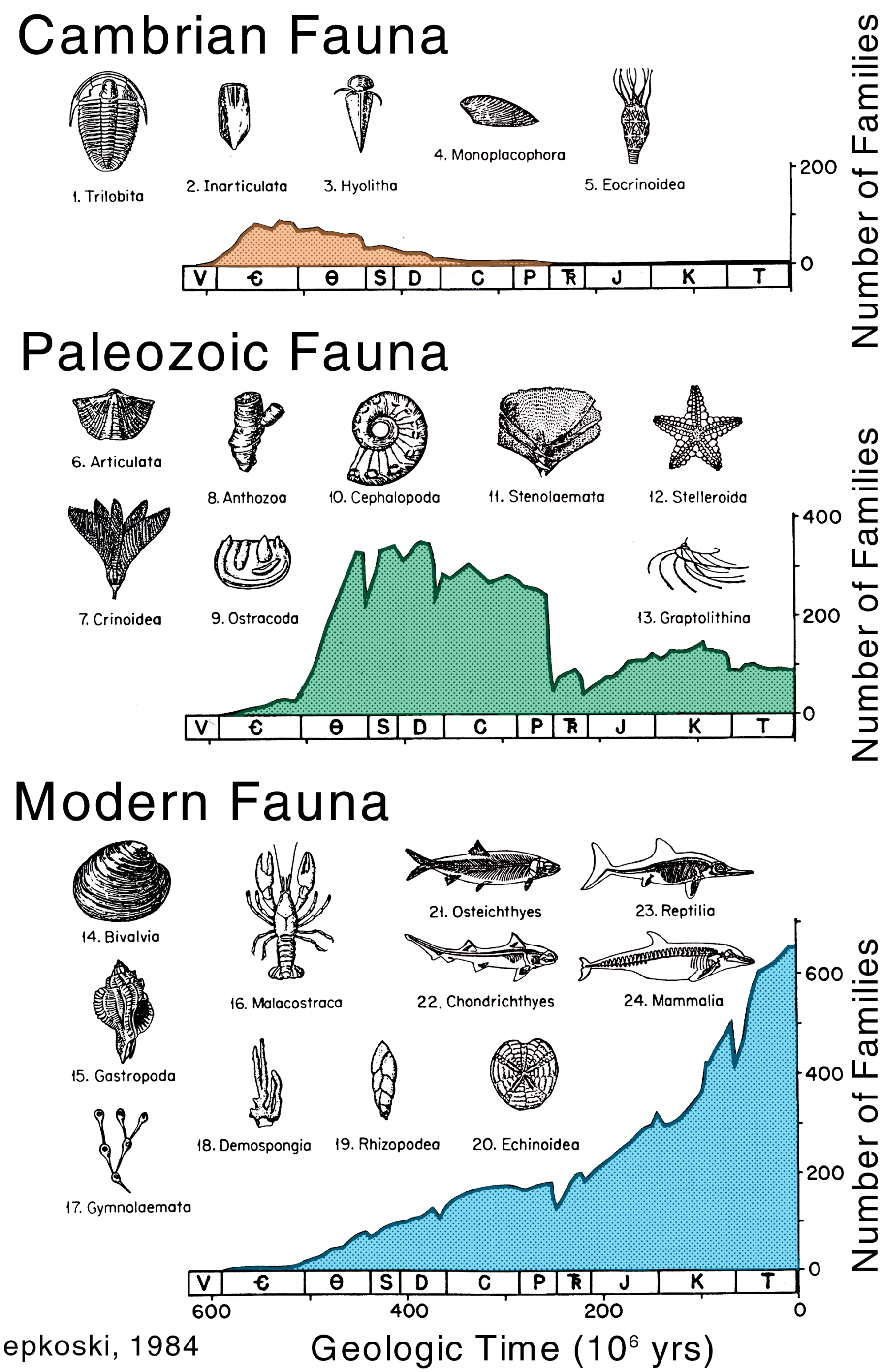
Tree of Life


ARCHAEA
CRENARCHAEOTA
EURYARCHAEOTA
"KORARCHAEOTA"
Environmental sequences
Thermal spring
Pacific ocean
Root
You are here
BACTERIA
EUCARYA
Bootstrap %
(Likelihood/Parsimony)
0.10 changes/site

Phanerozoic history of marine Orders

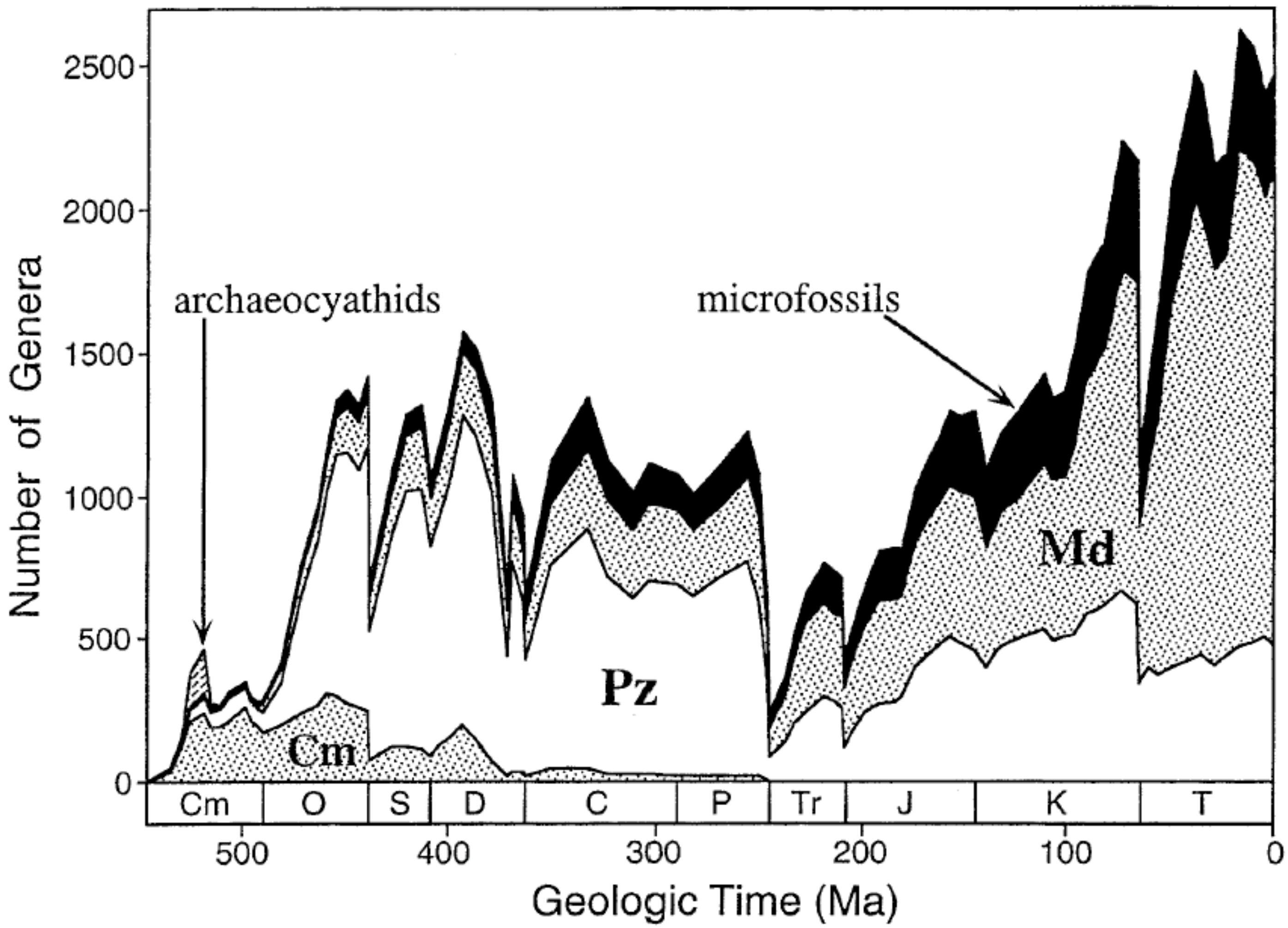


Eble 1998



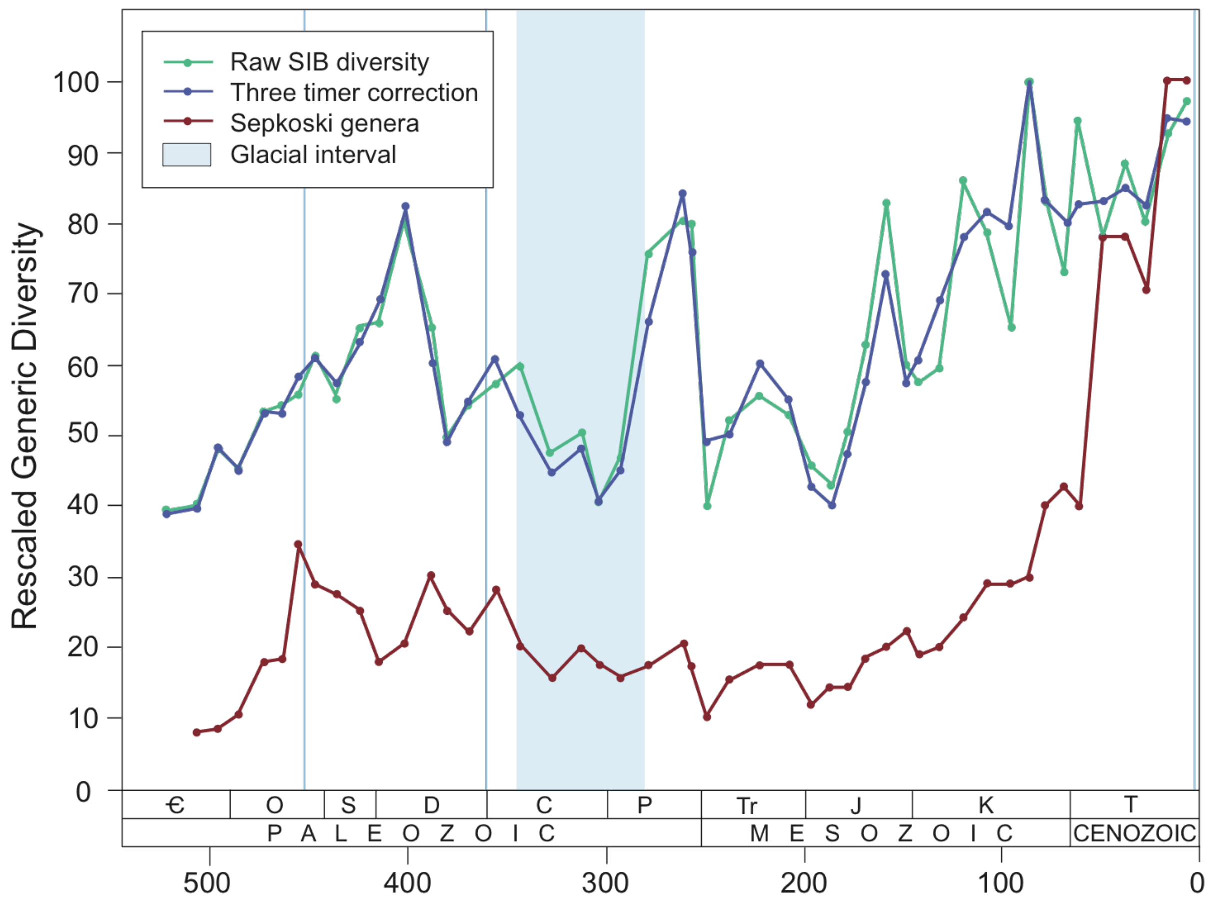
Sepkoski, 1984

Phanerozoic history of marine genera



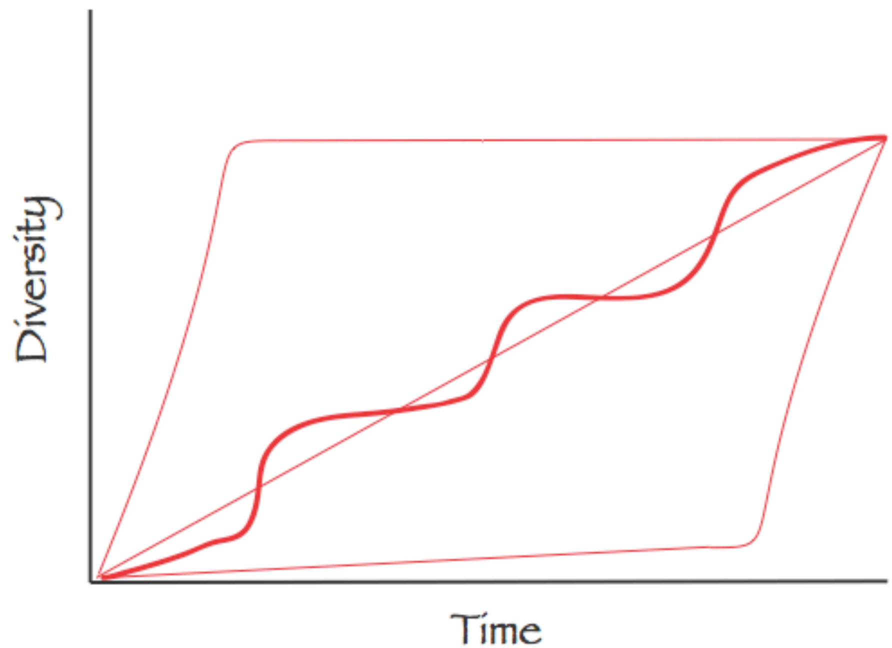
Sepkoski 1999

Phanerozoic Marine Diversity



Erwin in Press *Current Biology* after Sepkoski 1992; Alroy et al 2009

Causes of Increased Diversity

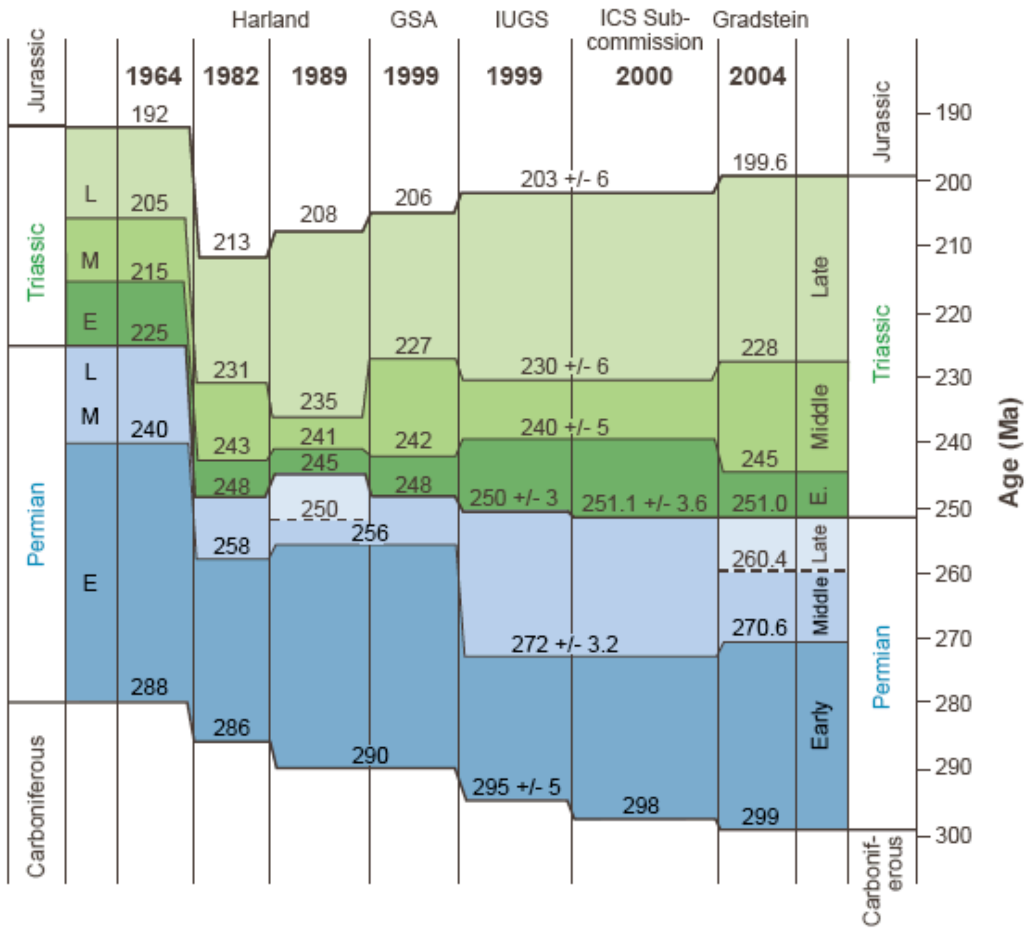


- Niche subdivision?
- Change in environmental conditions?
- Increased nutrient availability?
- Adaptations providing access to new resources?

Framework of Lecture 1

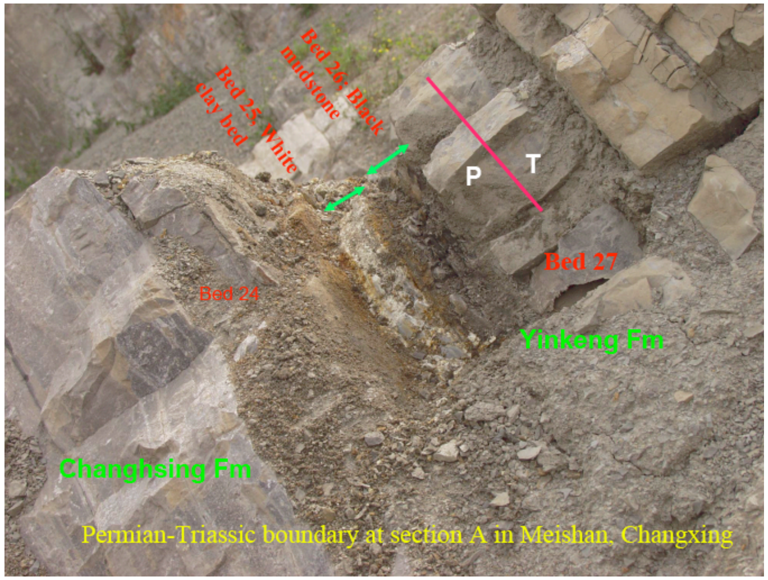
- Nature of the fossil record - types of fossils
- Types of Biodiversity
- Large-scale patterns
- **Resolving time**
- Diversity vs. Disparity

Changing Time Scale

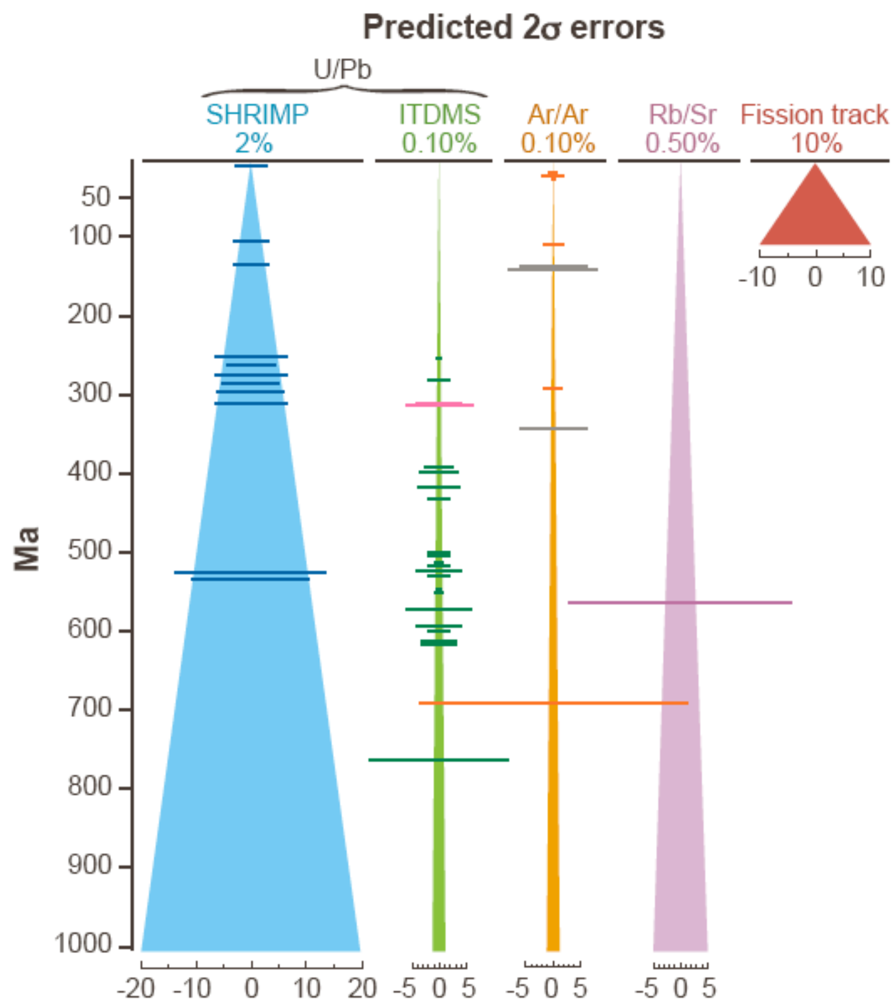


Erwin (2006) Ann. Rev. Earth Planet. Sci

Permo-Triassic Boundary, Meishan

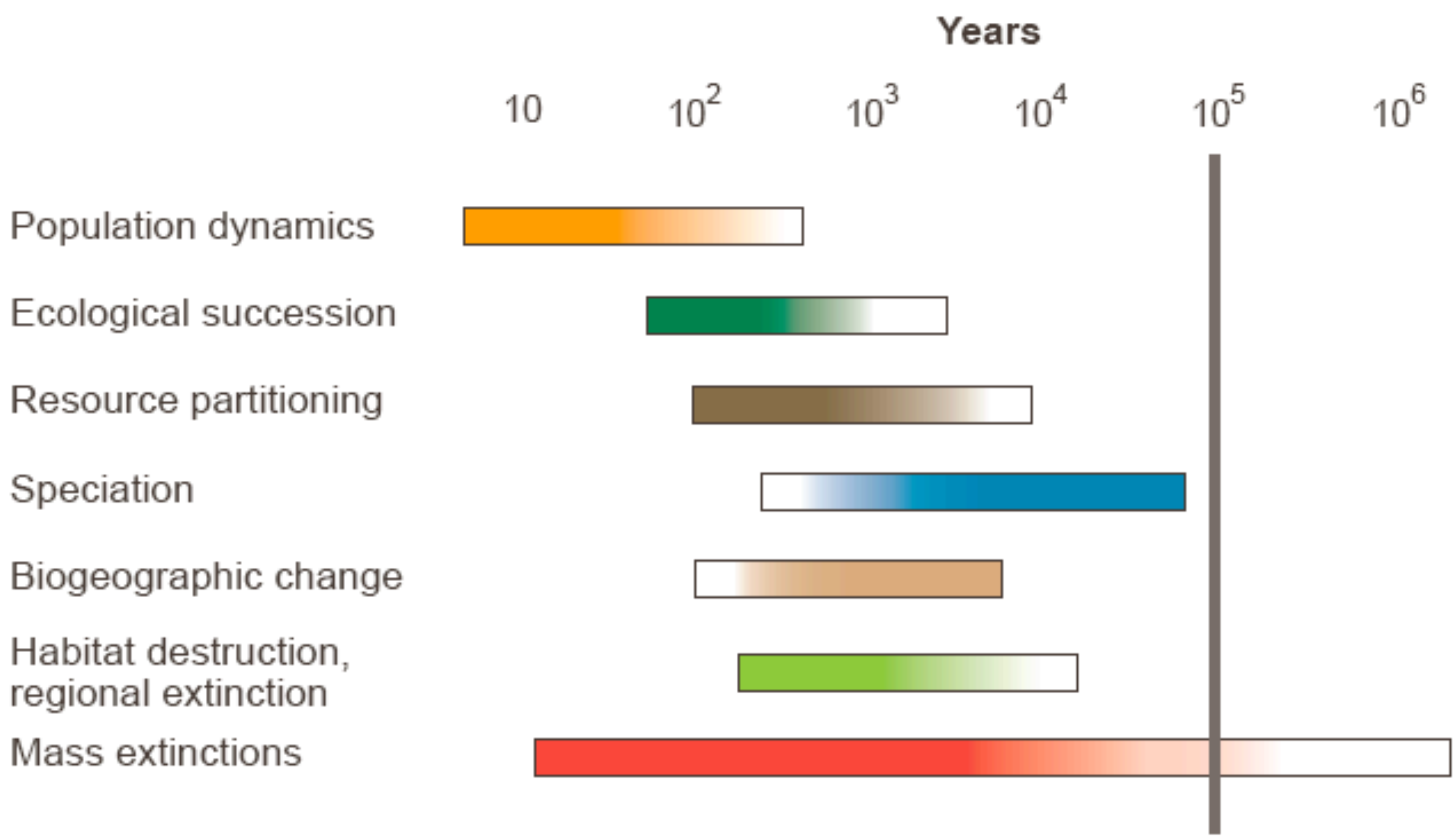


Limits of Geochronologic Resolution



Erwin (2006) Ann. Rev. Earth Planet. Sci

Limits of Paleoecologic Resolution



Erwin (2006) Ann. Rev. Earth Planet. Sci

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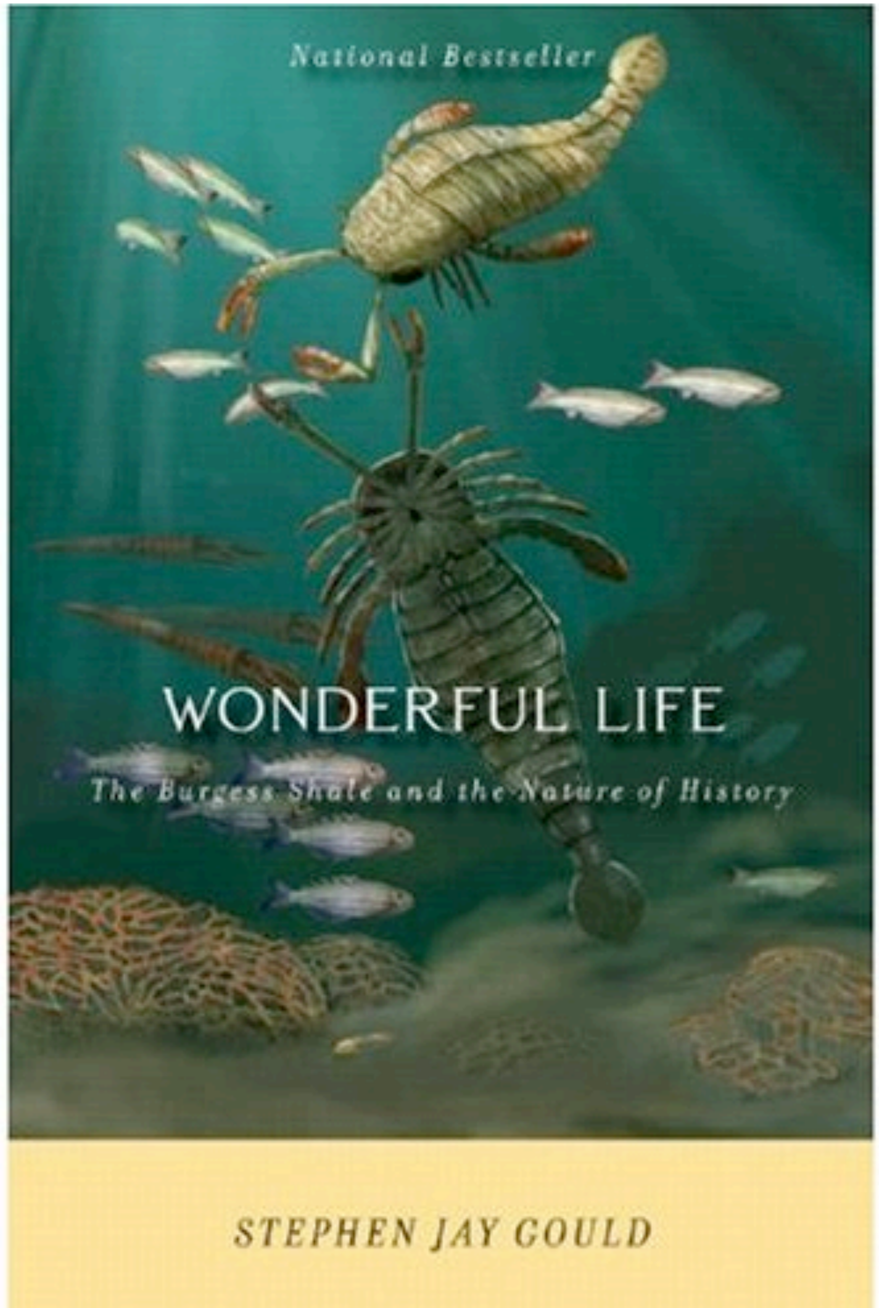
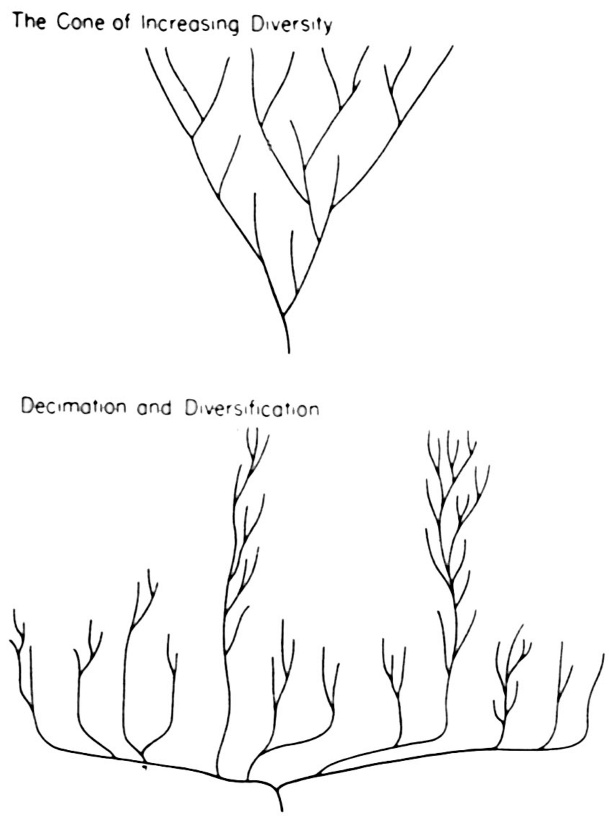


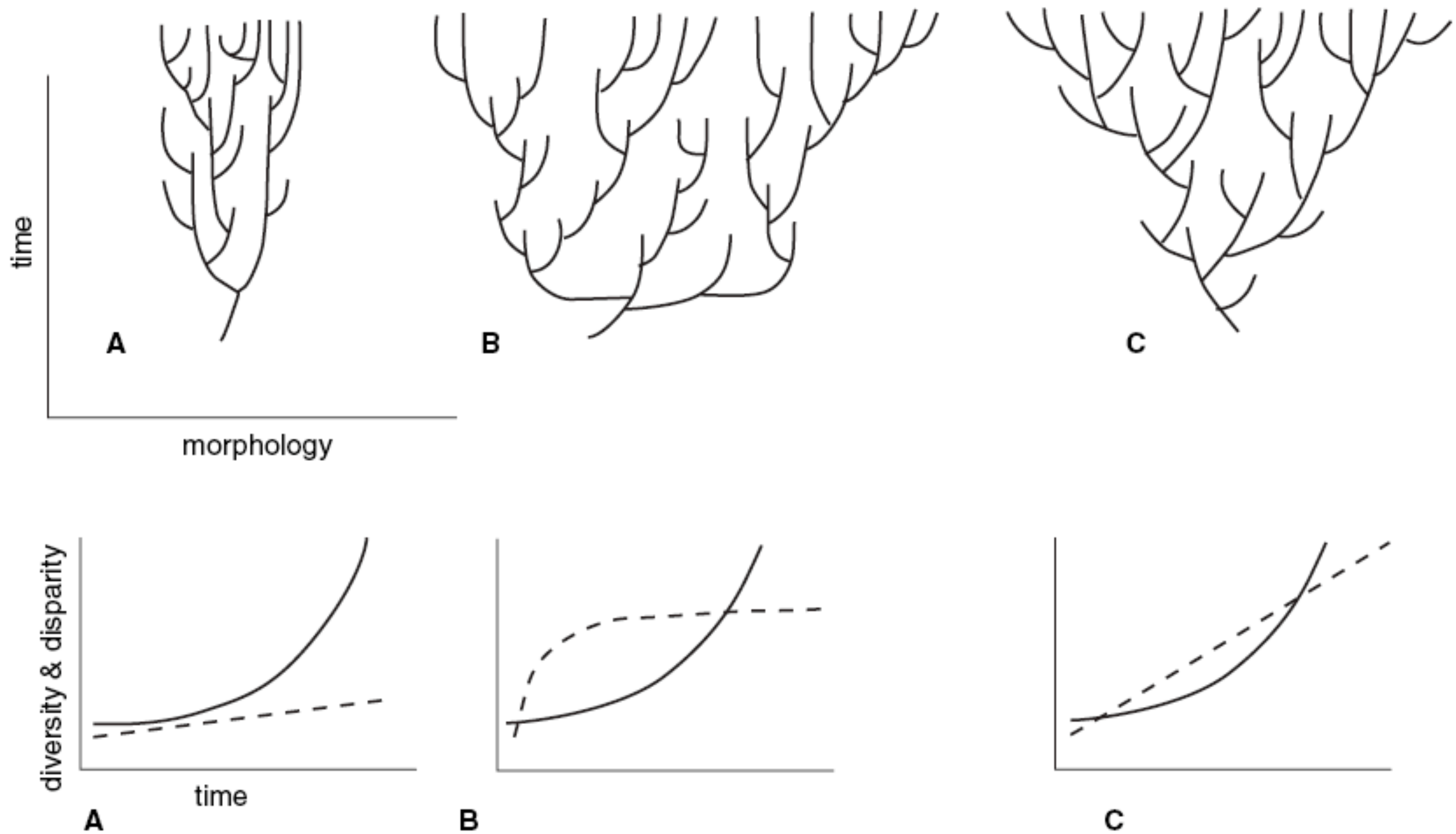
National Bestseller
WONDERFUL LIFE
The Burgess Shale and the Nature of History
STEPHEN JAY GOULD

Cone of Increasing Diversity



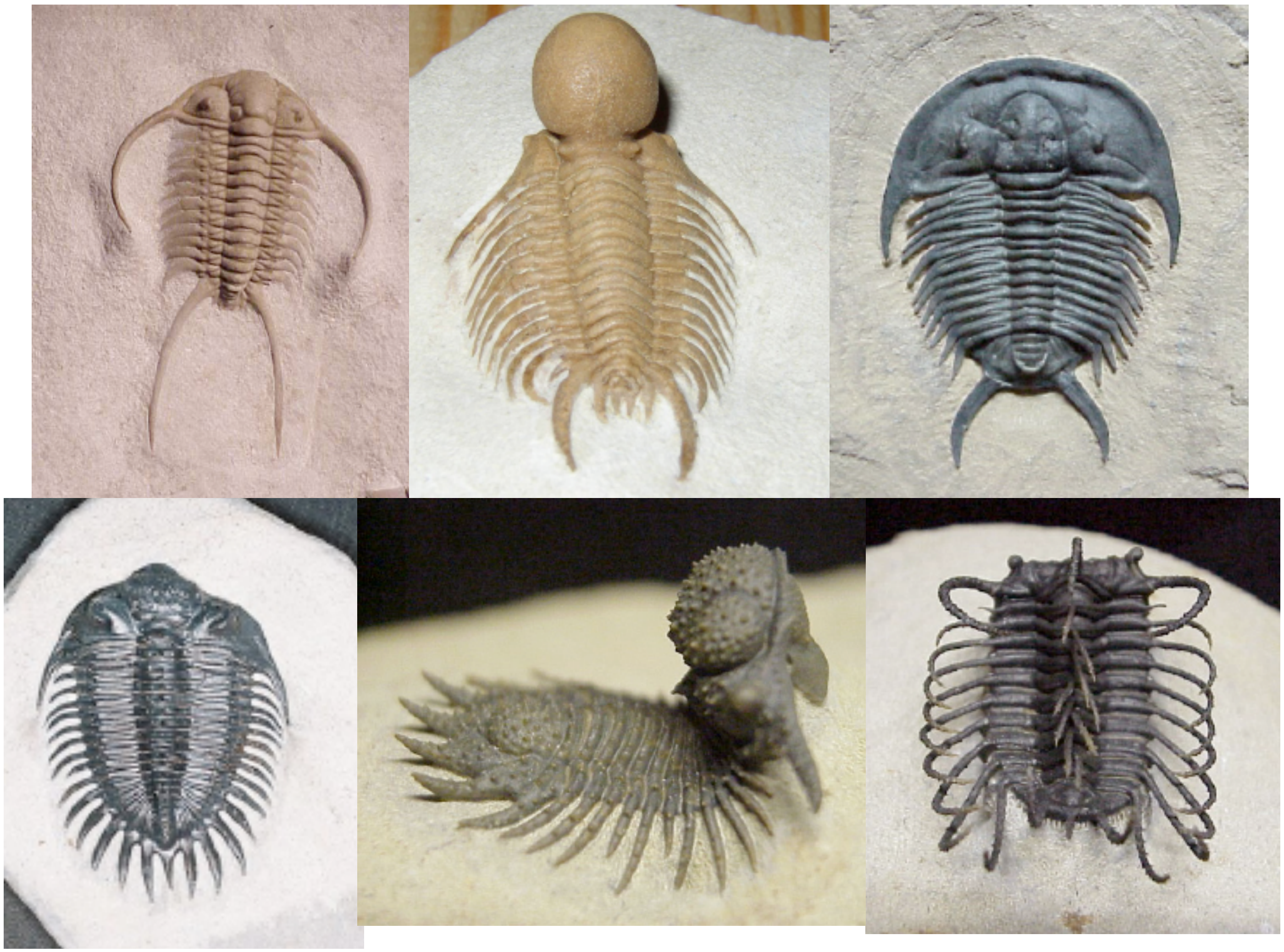
1.17. The false but still conventional iconography of the cone of increasing diversity, and the revised model of diversification and decimation, suggested by the proper reconstruction of the Burgess Shale.

Disparity vs. Diversity



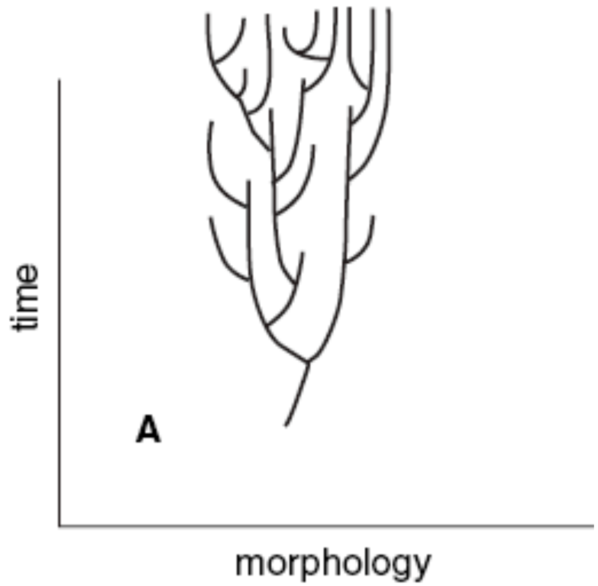
Wesley-Hunt 2005 after Foote 1993

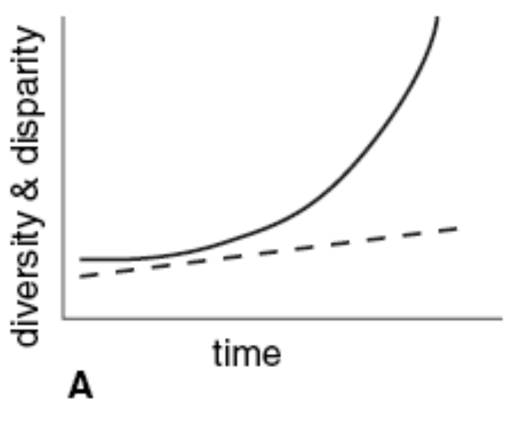
Trilobite Disparity



Images from /hazen.gl.ciw.edu

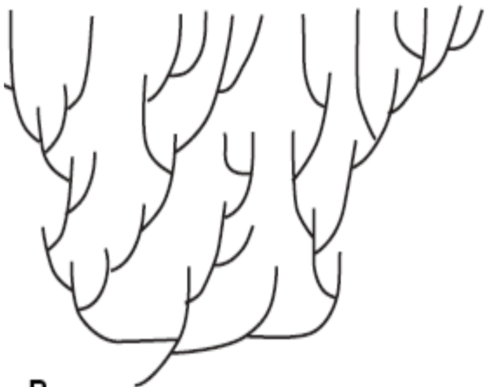
Constrained Disparity



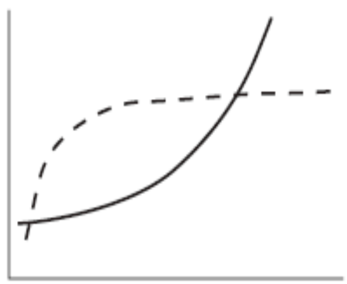


- Diversity exceeding Disparity

Constrained Diversification



B

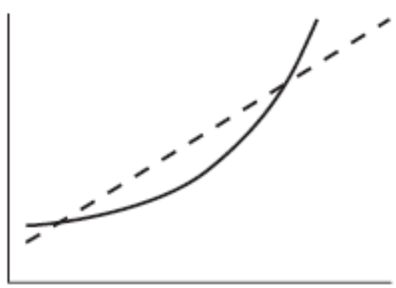


B

- Rapid early increase in disparity
  - Prot/Camb acritarchs
  - Paleozoic gastropods
  - Paleozoic rostroconchs
  - Ord. bryozoans
  - Crinoids
  - Paleozoic blastozoans
  - Ord. trilobites
  - Marine arthropods
  - Insects
  - Angiosperm pollen

Congruent Increases

C



C

- Paleozoic trilobites
- Paleozoic blastoids
- Mes-Cen Aporrhaids
- Cenozoic ungulates
- N. Am Cenozoic carnivores

Least probable when using discrete characters because of character exhaustion

Measurements of Disparity

TABLE 1. A brief description of each measure of disparity is shown below.

Measures of disparity		
Sum of variances	$D = \sqrt{\sum_c V_c}$	V_c is the univariate variance associated with character c
Mean pairwise distance	The mean pairwise distance is defined as the sum of the Euclidean distances in morphospace between all possible pairwise combinations divided by the total number of combinations	
Range	$D = \sqrt{\max_{ss'} \left[\sum_c (X_{s,c} - X_{s',c})^2\right]}$	The range is defined as the maximal Euclidean distance between any two specimens. $X_{s,c}$ equals the value of character c in specimen s
PCO volume	$D = \lambda_1\lambda_2/[N_{sp}]^2$	PCO volume is defined as the product of the two largest eigenvalues of the cross-distance matrix, divided by the square of the number of species
Average pairwise dissimilarity	The version of the average pairwise dissimilarity used in the study differs slightly from previously used versions (Wills et al. 1994; Lupia 1999). The average pairwise dissimilarity is defined as the sum of character-state mismatches between all pairwise combinations of taxa divided by the number of taxon combinations. In this version of the metric we do not distinguish between ordered and unordered characters and we do not normalize by the number of characters used	
Participation ratio	$D = 1\Big/\left[\sum_{u,v} P^2(u, v)\right]$	The participation ratio is similar to the information statistic (M. Foote personal communication 2001). See text and Appendix 1 for a thorough explanation of the measure
Number of unique pairwise characters	$D = \sum_{c_1,t_1} \sum_{c_2,t_2} E(c_1, t_1, c_2, t_2)$	The number of unique pairwise characters is calculated by measuring the number of all possible pairwise combinations of traits that are realized, where c_1, t_1, and c_2, t_2 are character 1 of taxon 1 and character 2 of taxon 2, and where E is zero if none of the specimens possess the combination, and one otherwise

Differences
Between taxa

Measurements of Disparity

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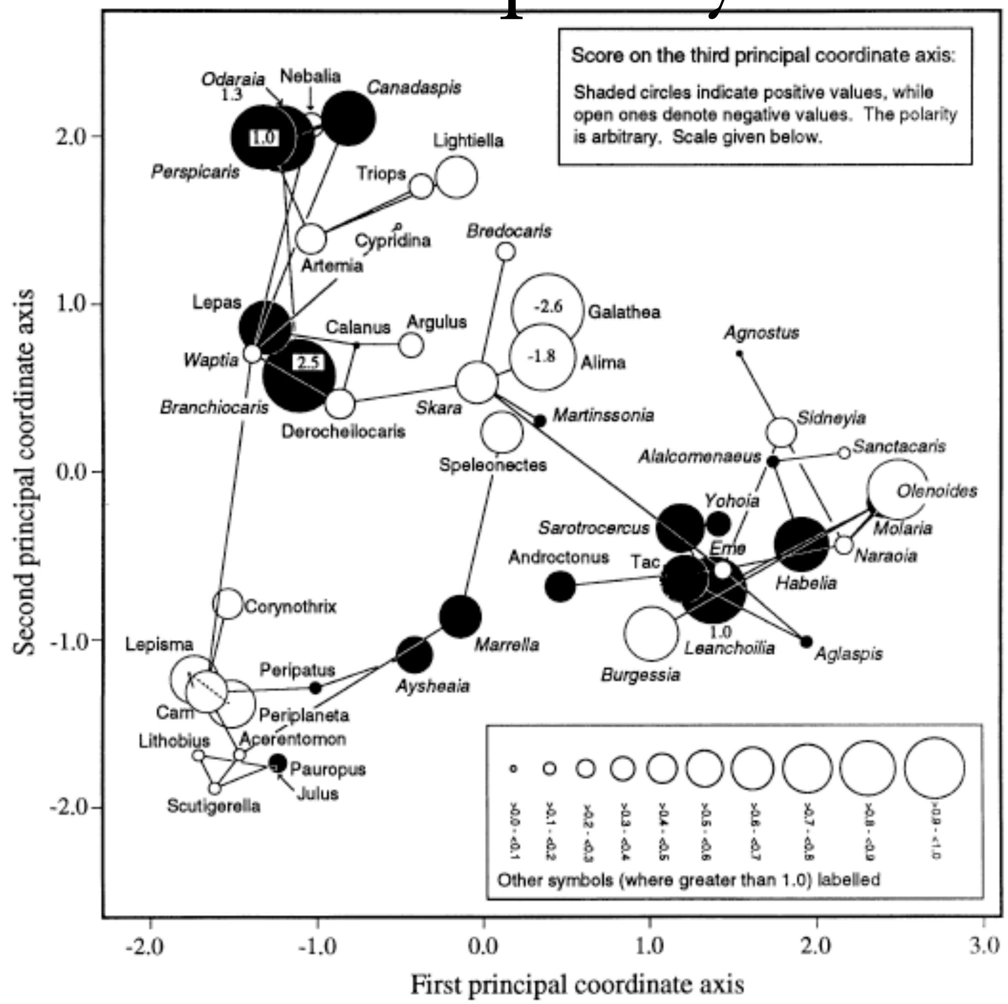
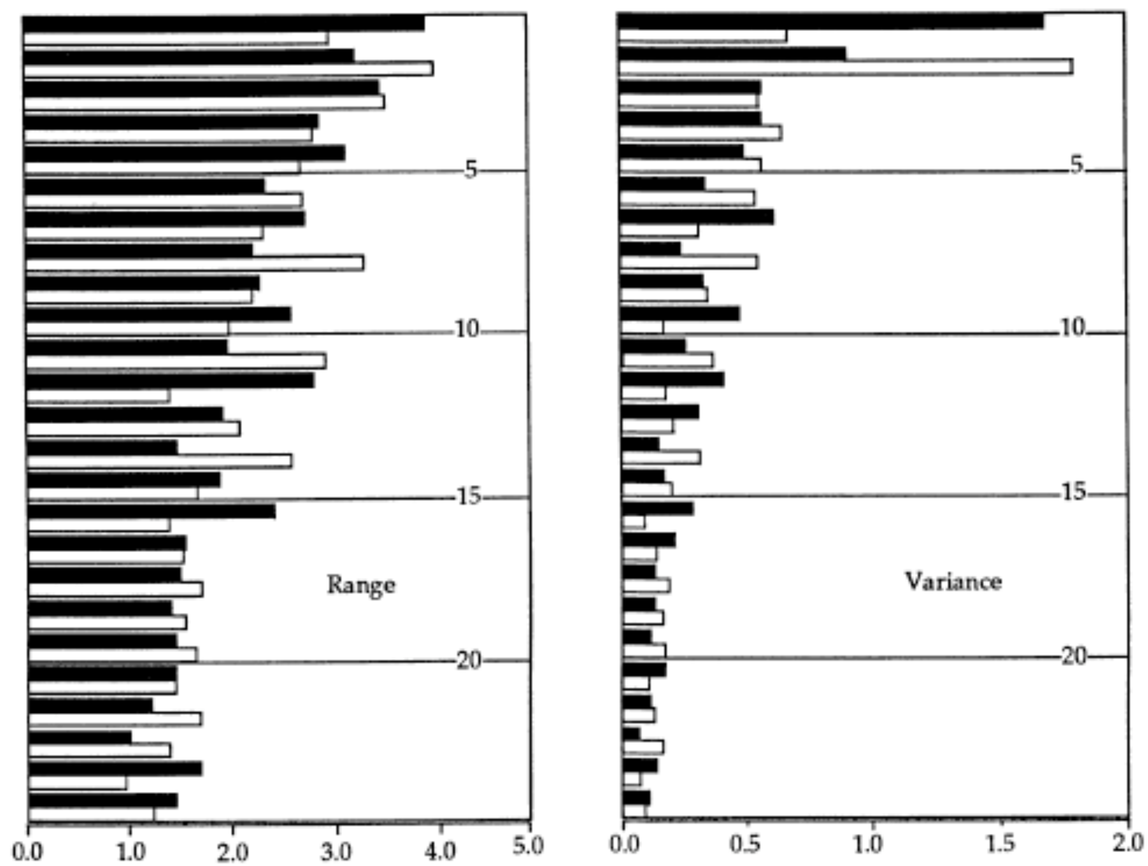
Patterns of Morphospace occupation

Cambrian vs Modern Arthropod Disparity



Wills et al 1994 *Paleobiology*

Cambrian vs Modern Arthropod Disparity



Wills et al 1994 *Paleobiology*

Cenozoic Carnivore Disparity

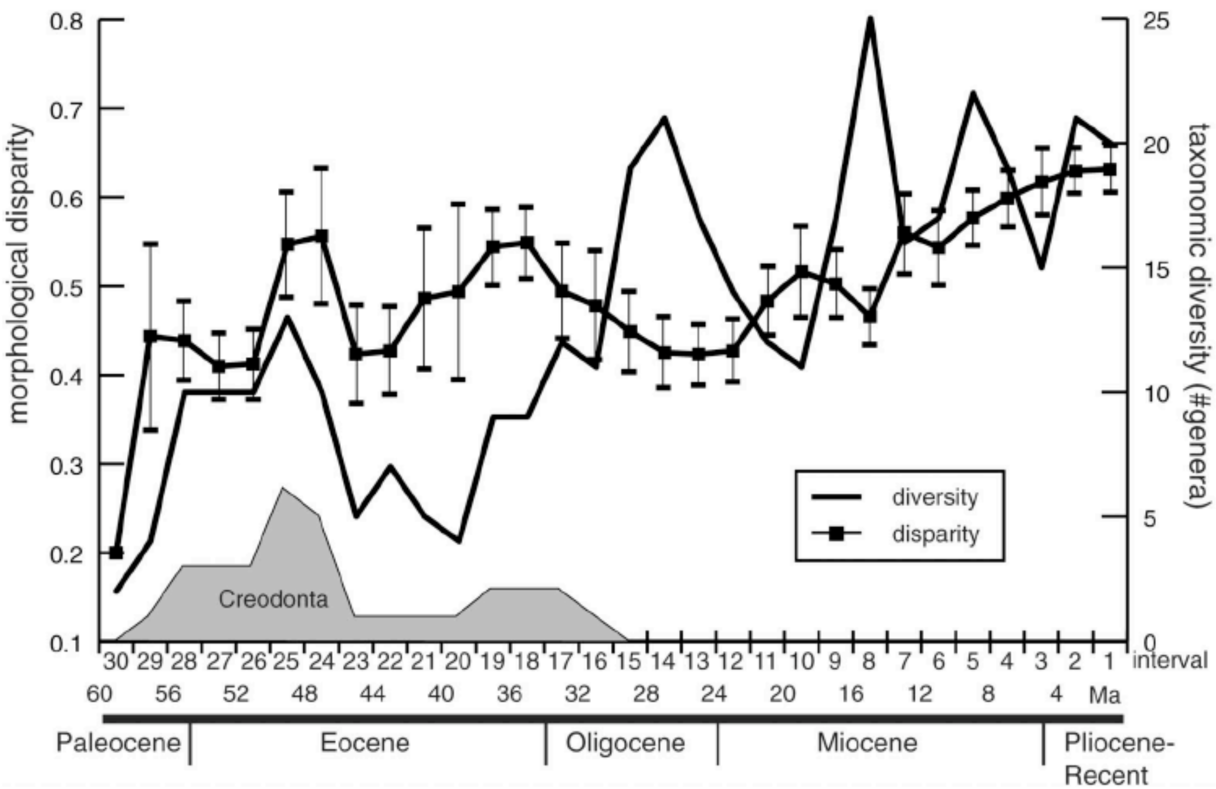
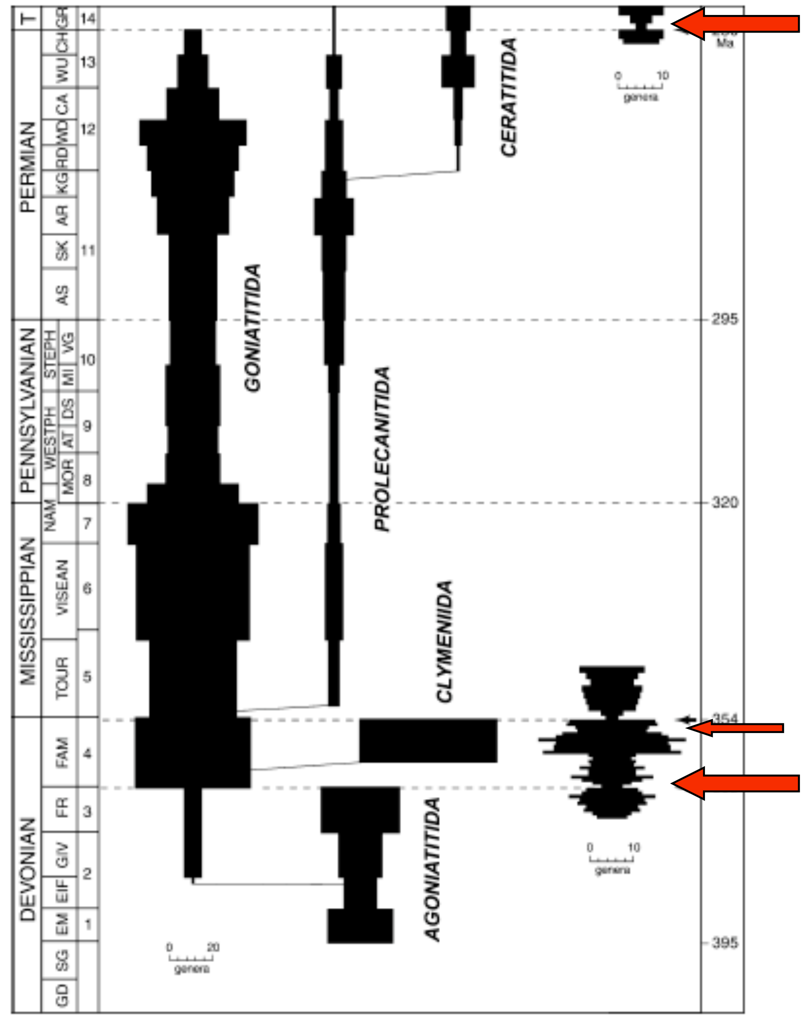


FIGURE 3. Analysis 1: composite of carnivoramorphans and creodonts. Mean pairwise morphological disparity and taxonomic diversity curves over the Cenozoic. Diversity is measured as number of genera sampled. Error bars are based on bootstrap resampling of taxa within intervals and are one standard deviation above and below mean disparity. (Timescale from Berggren et al. 1995.)

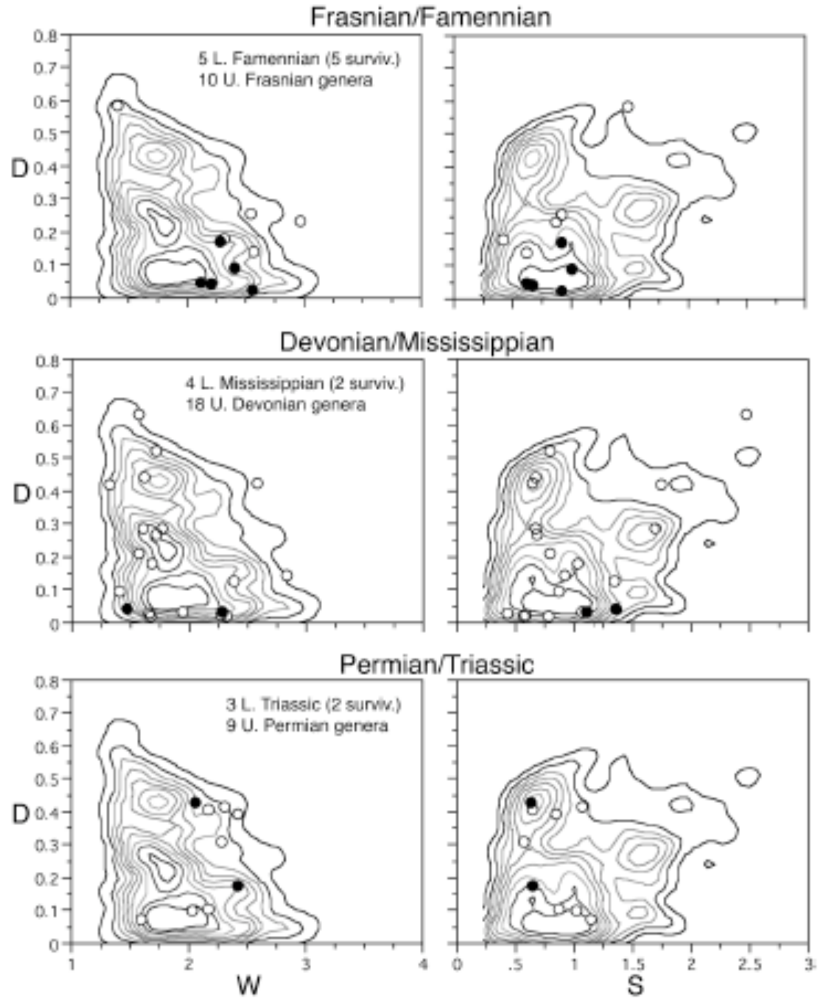
Wesley-Hunt 2005 *Paleobiology*

Ammonoid Diversity



Saunders et al. *Paleobiology* 2004

Ammonoid Disparity



Saunders et al. *Paleobiology* 2004

Results of Disparity Studies

- Disparity generally increases faster than diversity
- This is consistent with diversification into an ecologically undersaturated ecospace
- Disparity studies across mass extinctions do not support claims of increased developmental constraint

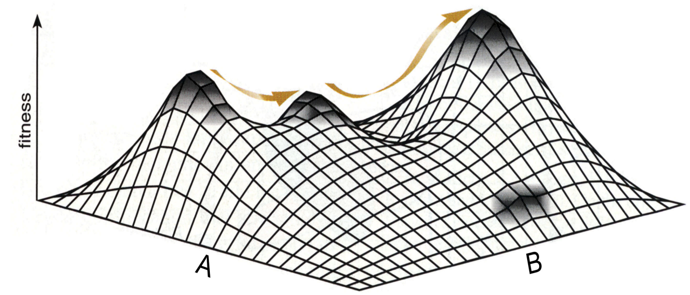
“The real problem for the evolutionist is not to explain the kinds of organisms that have ever existed. The real problem for the evolutionist is how it is that most kinds of potential and seemingly reasonable organisms have never existed”

R. Lewontin, 2003

Why is the distribution of morphology clumpy?

- Winnowing of forms through extinction

- Adaptive peaks



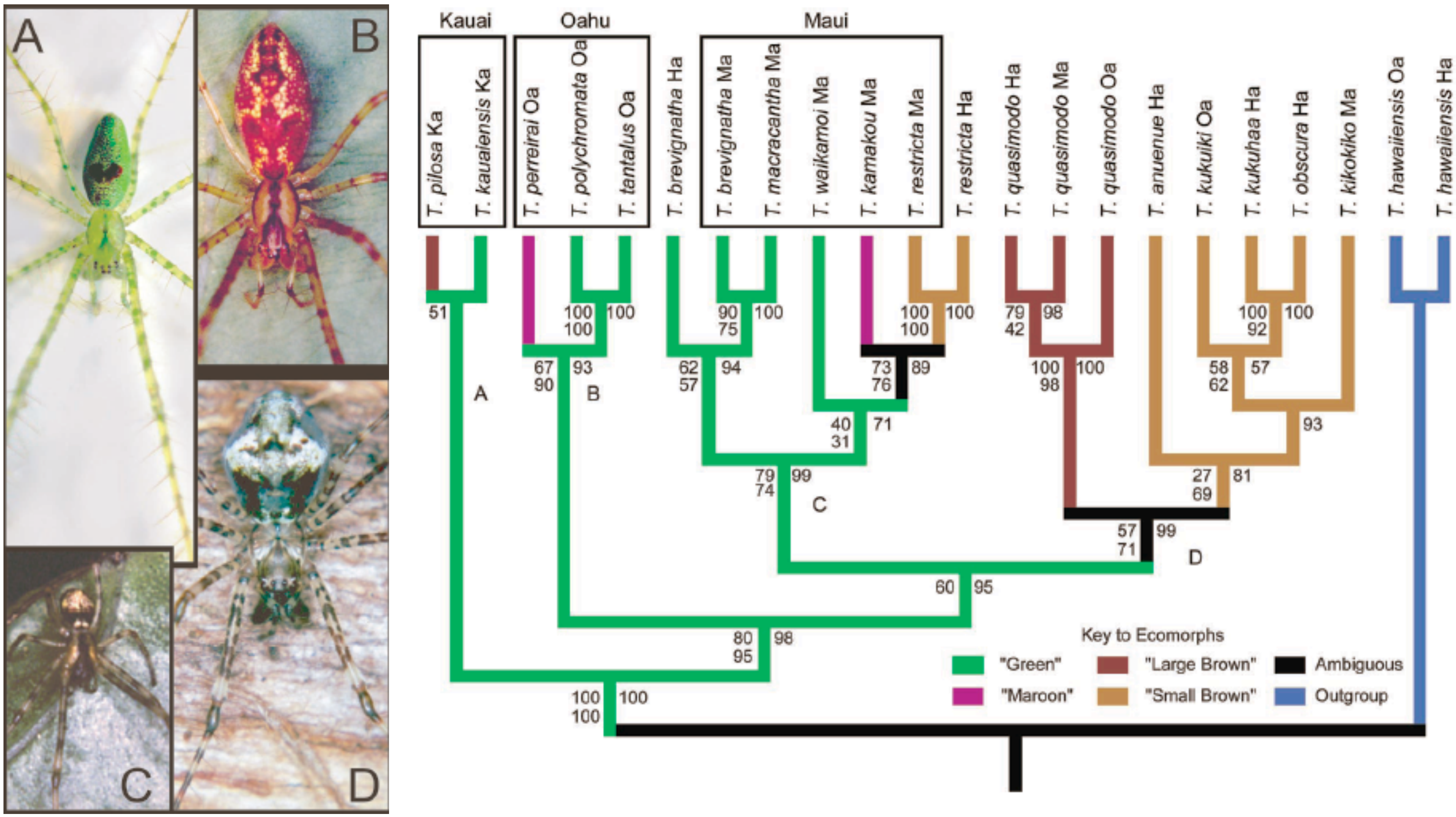
- Structure of developmental networks

- ?

Framework of Lecture 2
Constructing Biodiversity

- Models of Biodiversity
- Ecosystem engineering and Niche construction

Adaptive radiation: Hawaiian spiders



Gillespie, *Science* 2004

PROCEEDINGS
OF THE
NATIONAL ACADEMY OF SCIENCES

Volume 6 JUNE 15, 1920 Number 6

ON THE RATE OF GROWTH OF THE POPULATION OF THE UNITED STATES SINCE 1790 AND ITS MATHEMATICAL REPRESENTATION[1]

BY RAYMOND PEARL AND LOWELL J. REED

DEPARTMENT OF BIOMETRY AND VITAL STATISTICS, JOHNS HOPKINS UNIVERSITY

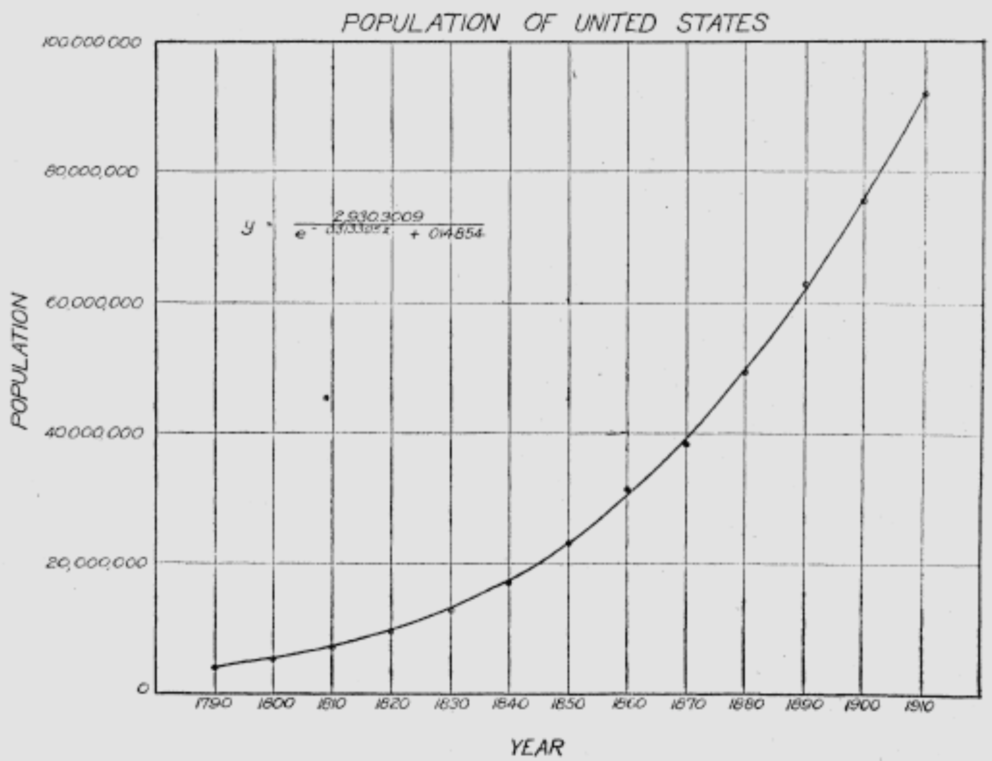


FIG. 3

Showing result of fitting equation (xviii) to population data.

“When did or will the population curve of this country pass the point of inflection, and exhibit a progressively diminishing instead of increasing rates of return? …
It is easily determined that this point occurred about April 1, 1914…. The upper asymptote …has the value
Of 197,274,000 roughly.
- Pearl & Reed, 1920, pgs 284-285

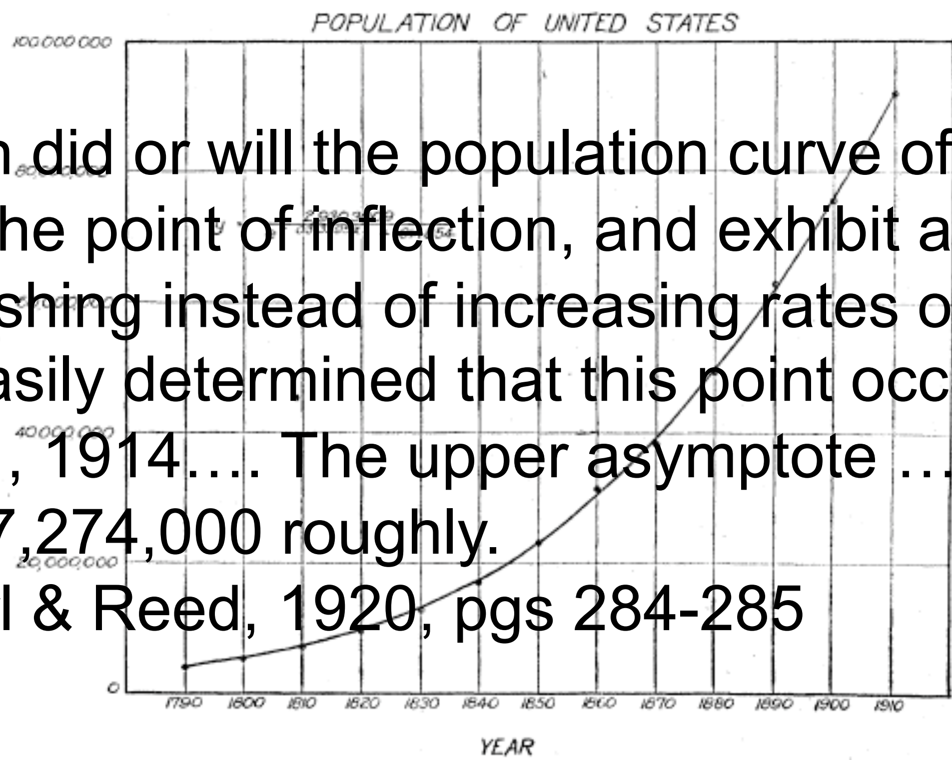
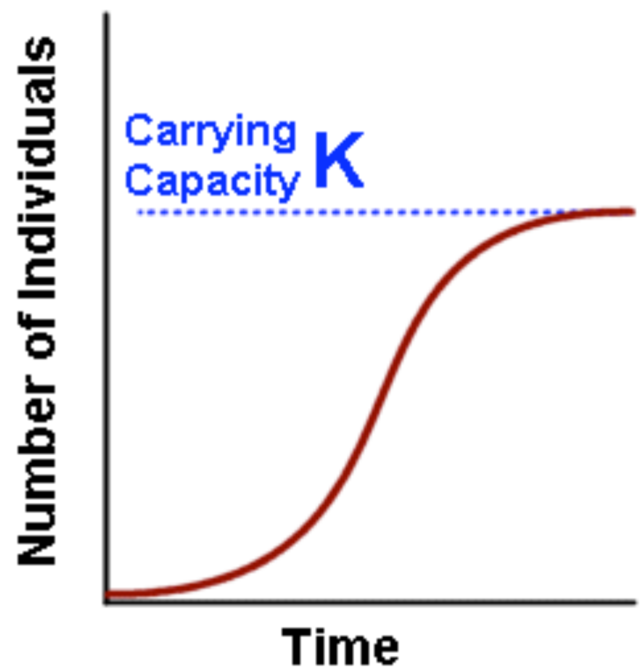


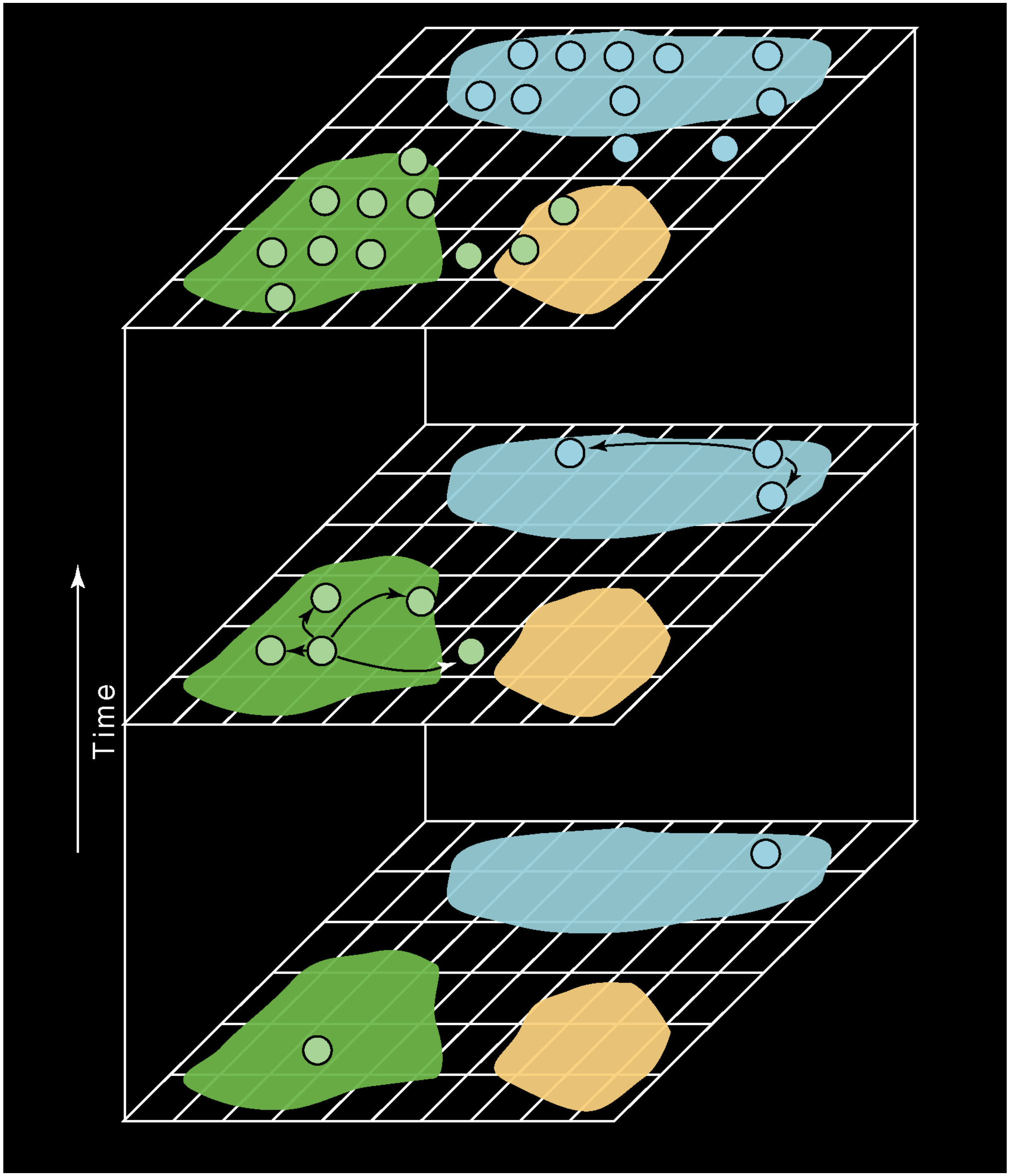
FIG. 3

Showing result of fitting equation (xviii) to population data.

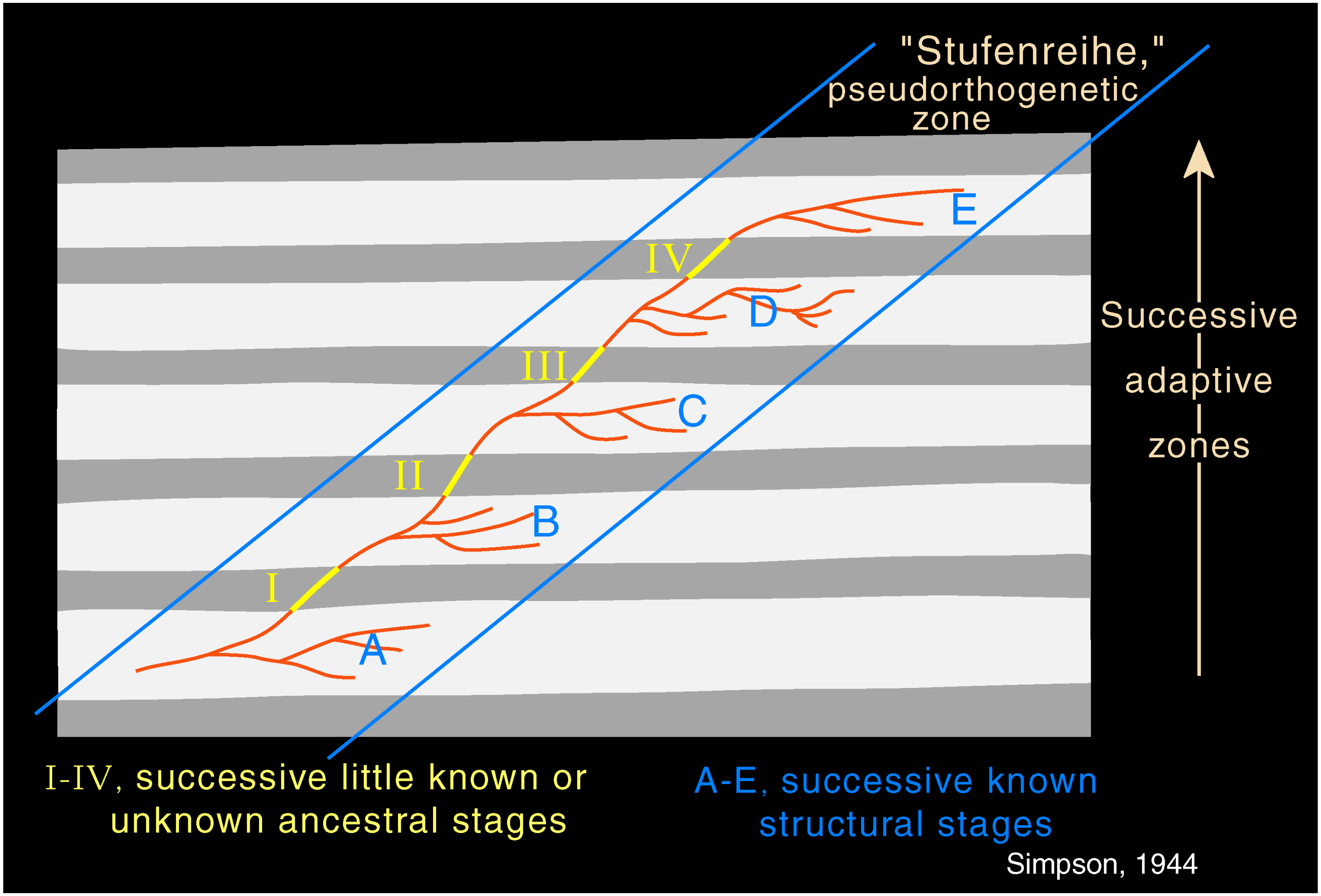
Logistic Growth



$$dN/dT = r\ N\ (1 - N/K)$$

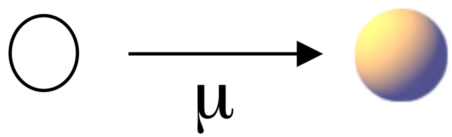

Time

Adaptive Zones



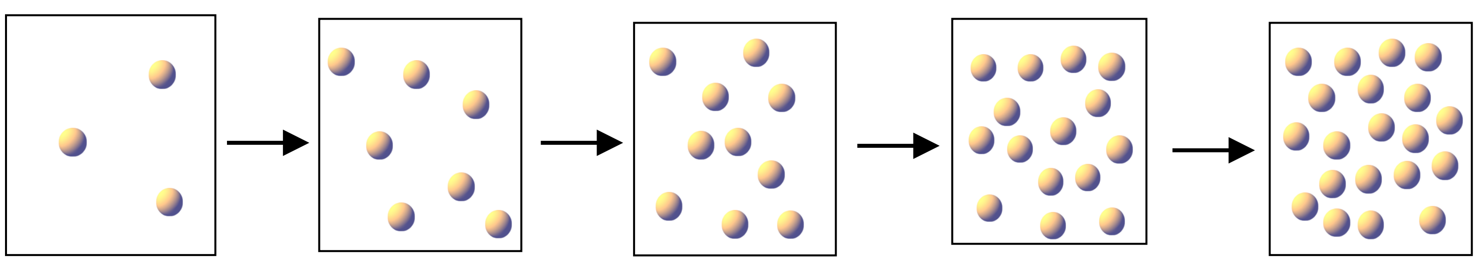
Linear Diversification

Empty niches are filled at random with some probability μ



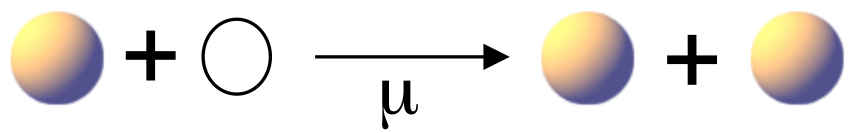
Linear model

$$\frac{dS}{dt} = \mu\,(1 - S)$$



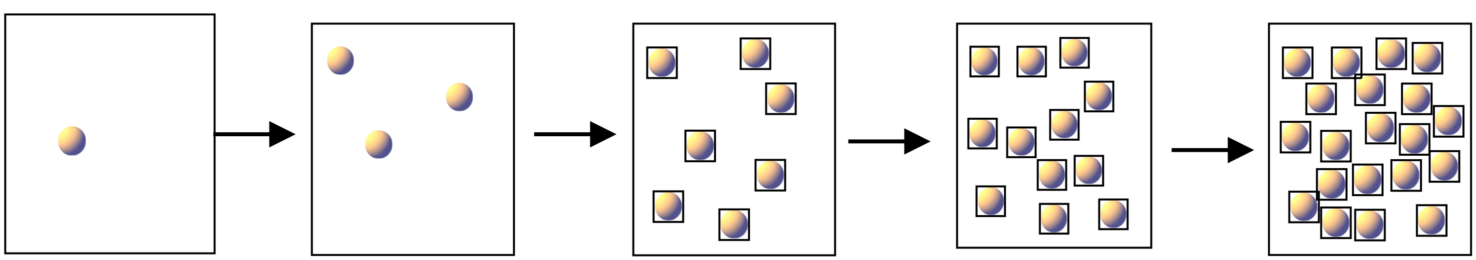
Logistic Diversification

Empty niches are filled at a rate of speciation proportional to the species present

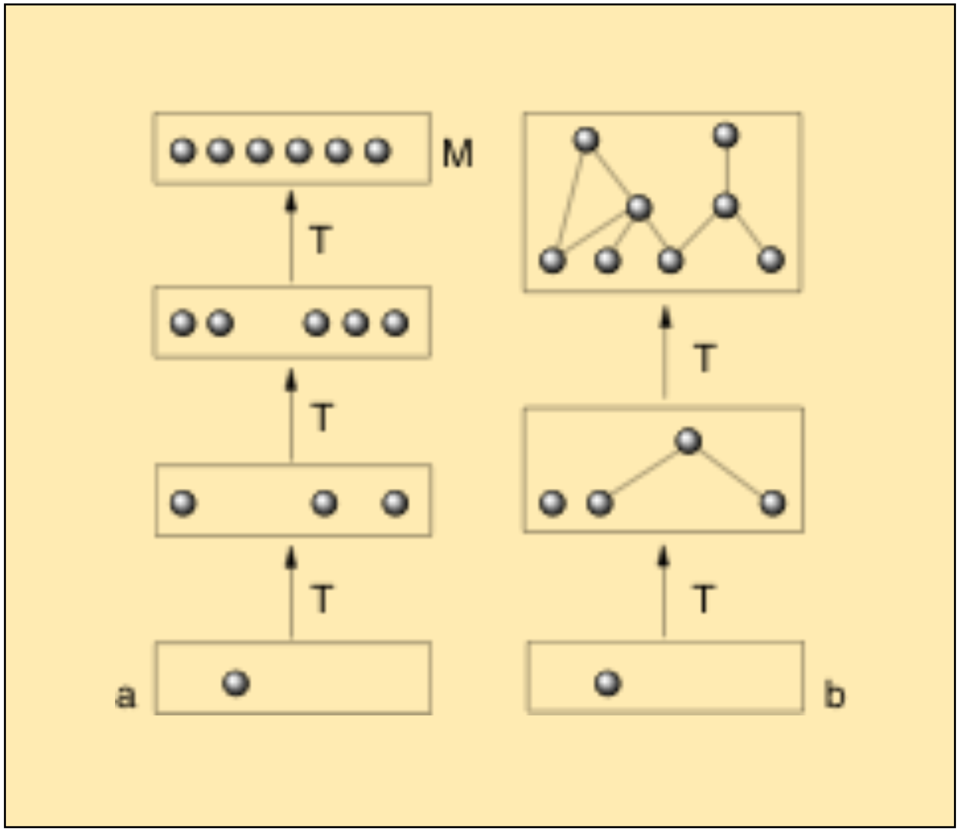


Logistic model

$$\frac{dS}{dt} = \mu S(1 - S)$$



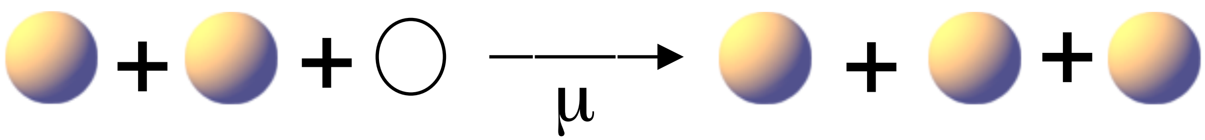
Construction of Biodiversity



Interactions among species allow new opportunities for speciation. Increasing numbers of species interactions allow larger combinatorics, but interactions are difficult to build: delays should be observable, as well as rapid diversity increase once the number of both species and interactions reach a threshold.

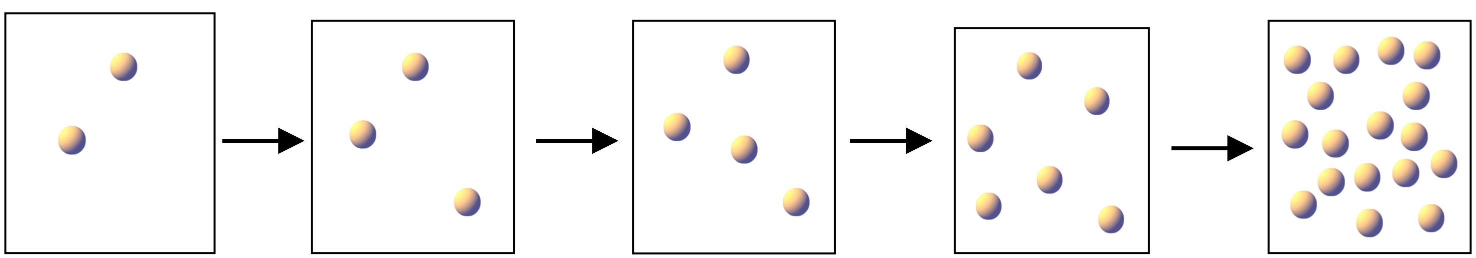
Hyperbolic Diversification

Empty niches are filled at a rate of speciation proportional to the pairs of interacting species. The more the interactions,
the larger the opportunities for filling new, species/based niches



Hyperbolic model

$$\frac{dS}{dt} = \mu S^2(1 - S)$$



Single model : generalized logistic

The three scenarios are included here

$$\frac{dS}{dt} = \mu S^{\beta}(1- S)$$

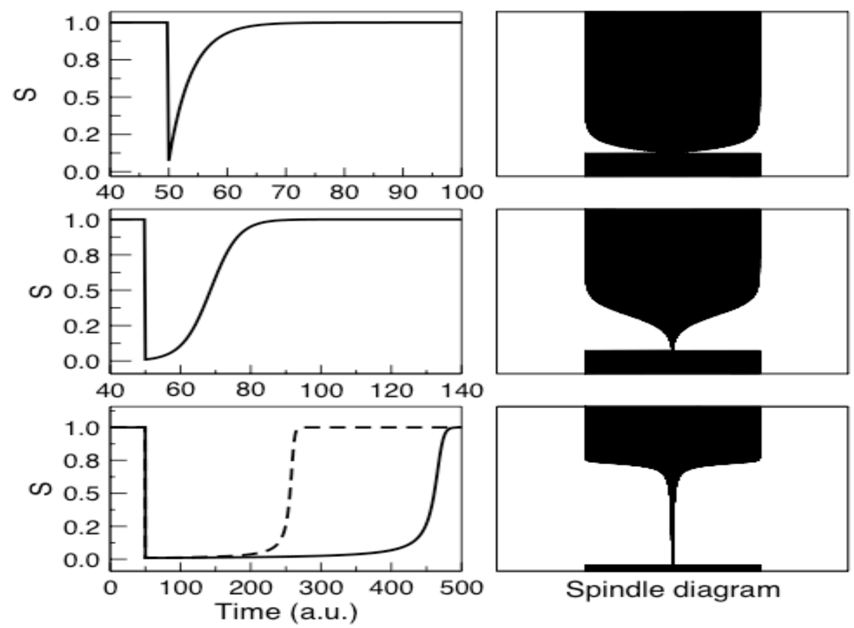
Speciation rate

ecological interactions

Limited resources

Diversification patterns

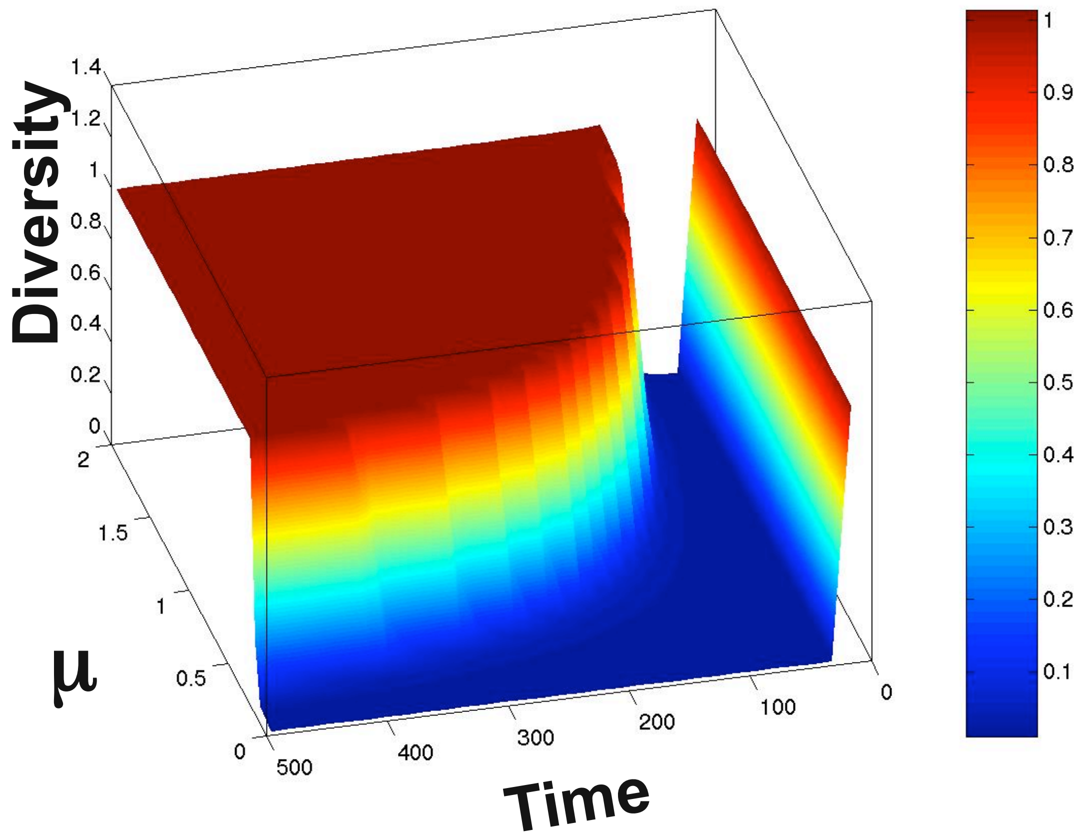
Linear



Logistic

Hyperbolic

Diversification patterns



If species interactions are required in order to increase diversity, a lag is always present, but is shorter as speciation rates become larger.

Approaches to Novelty:

'Genes first' - novelty arises from genetic and developmental changes (supply-driven)

Novelty arises from new ecological opportunities (demand-driven A)

'Environment first' - behavioral changes in a new environment permit success of genetic/ developmental changes (demand-driven B)

Advantages of latest models

- Attempt to incorporate positive feedback through cooperation
- Capturing trophic dynamics

Problems with Models

- Niche construction/ecosystem engineering effects poorly captured

Anabaena - We didn't make the atmosphere, we just made it breathable™

Onion article announcing a cyanobacteria IPO

Problems with Models

- Niche construction/ecosystem engineering effects poorly captured
- Carrying capacity is an exogenous, not endogenous variable

Solow Model of Economic Growth

$$Y \text{ (output)} = K^{\alpha} L^{1-\alpha}$$

Where:

K = capital

L = labor

α = variable between 0 and 1

Technology is exogenous; constant returns to scale

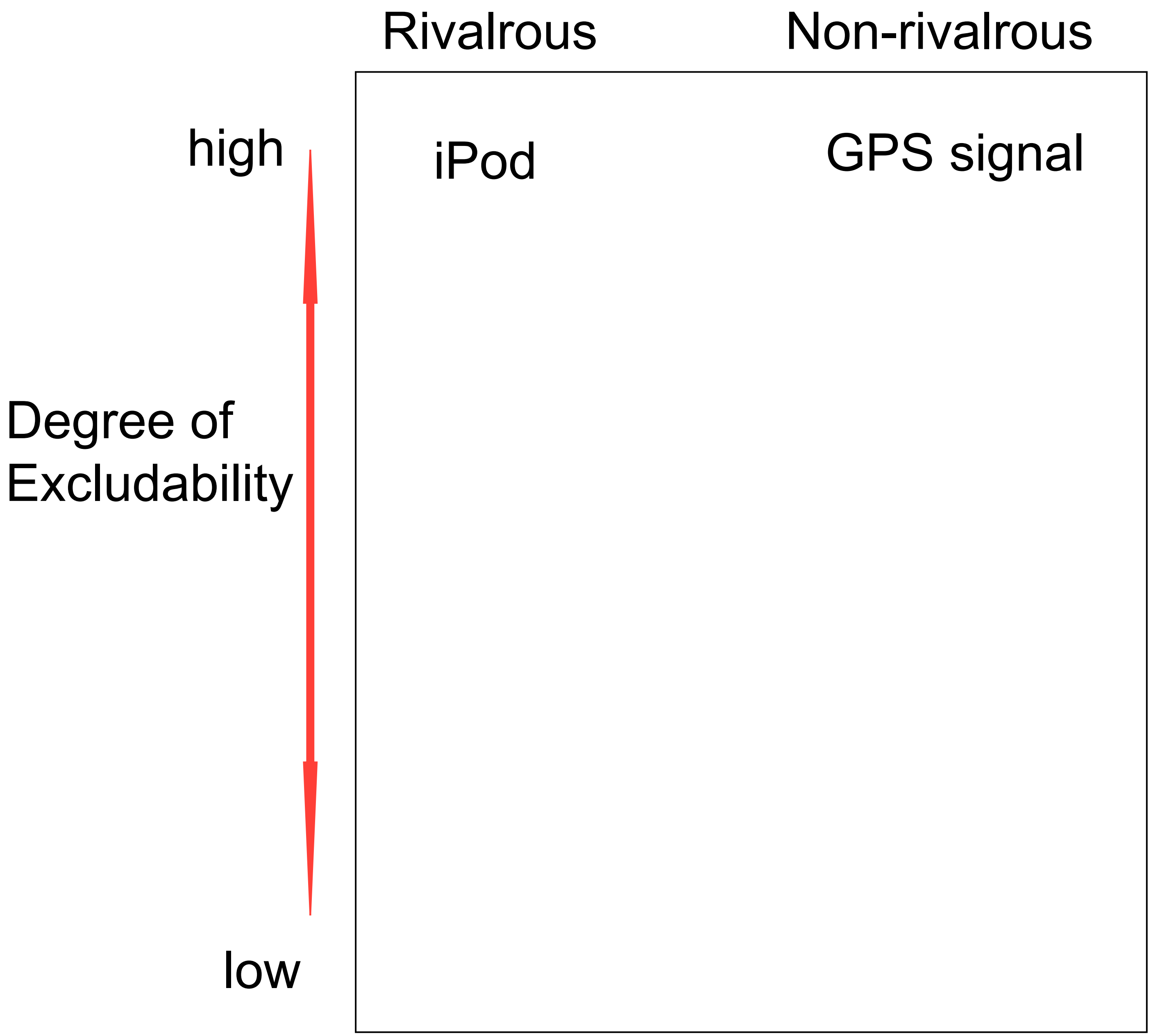
The Solow model will not generate sustained, per-capita growth

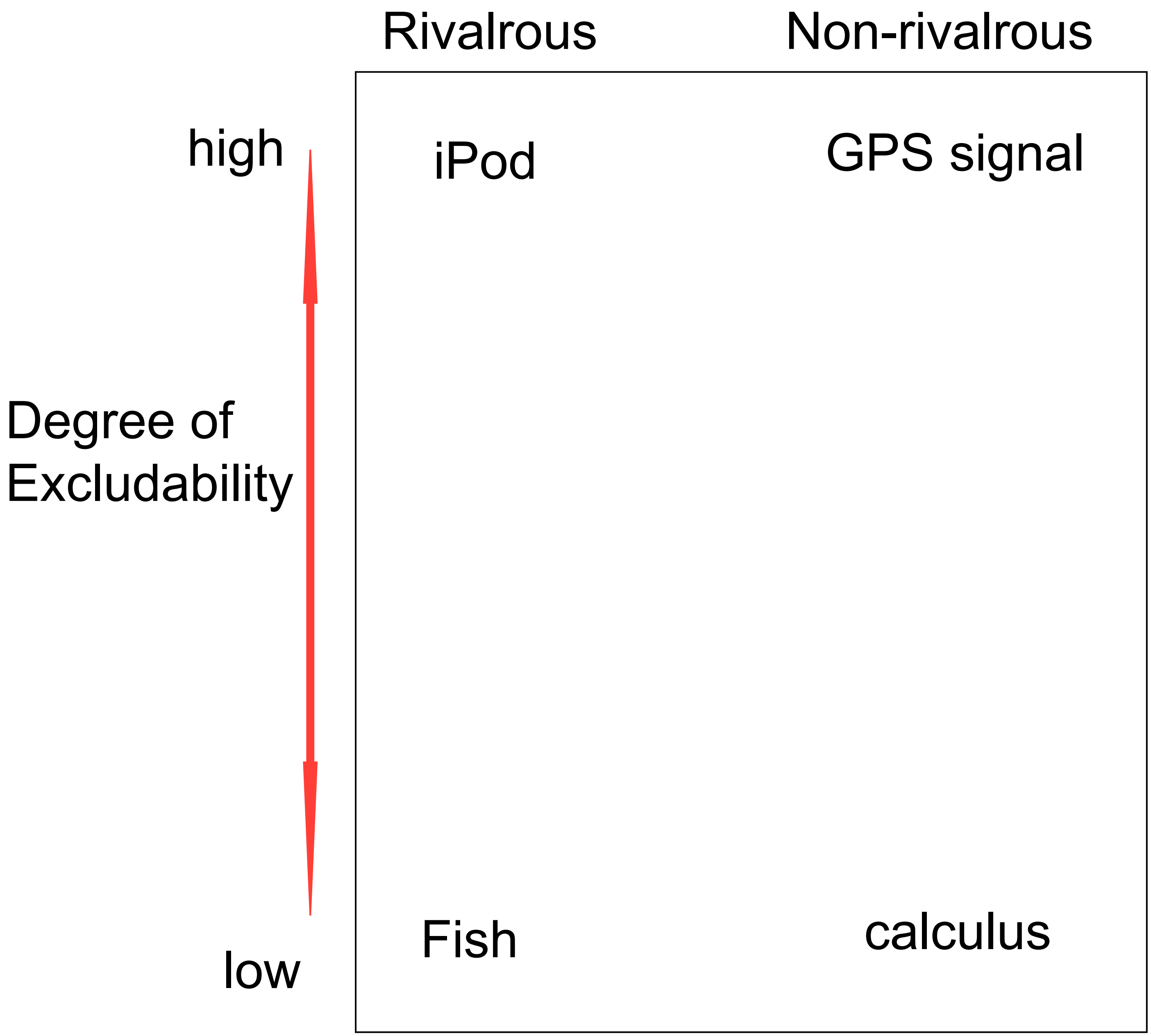
Generating growth requires addition of a technology variable (A):

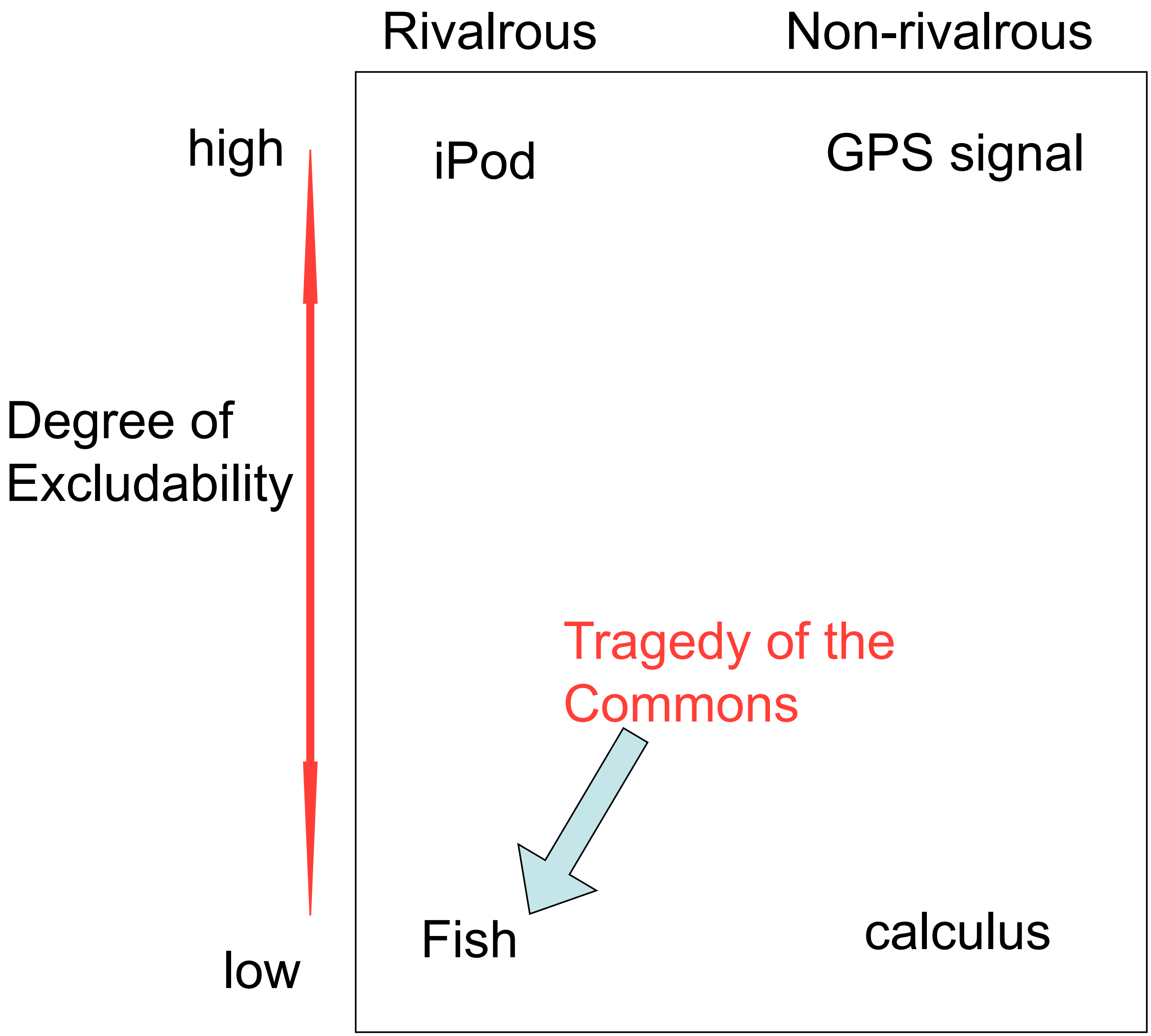
$$Y \text{ (output)} = K^{\alpha} (A L)^{1-\alpha}$$

Where:

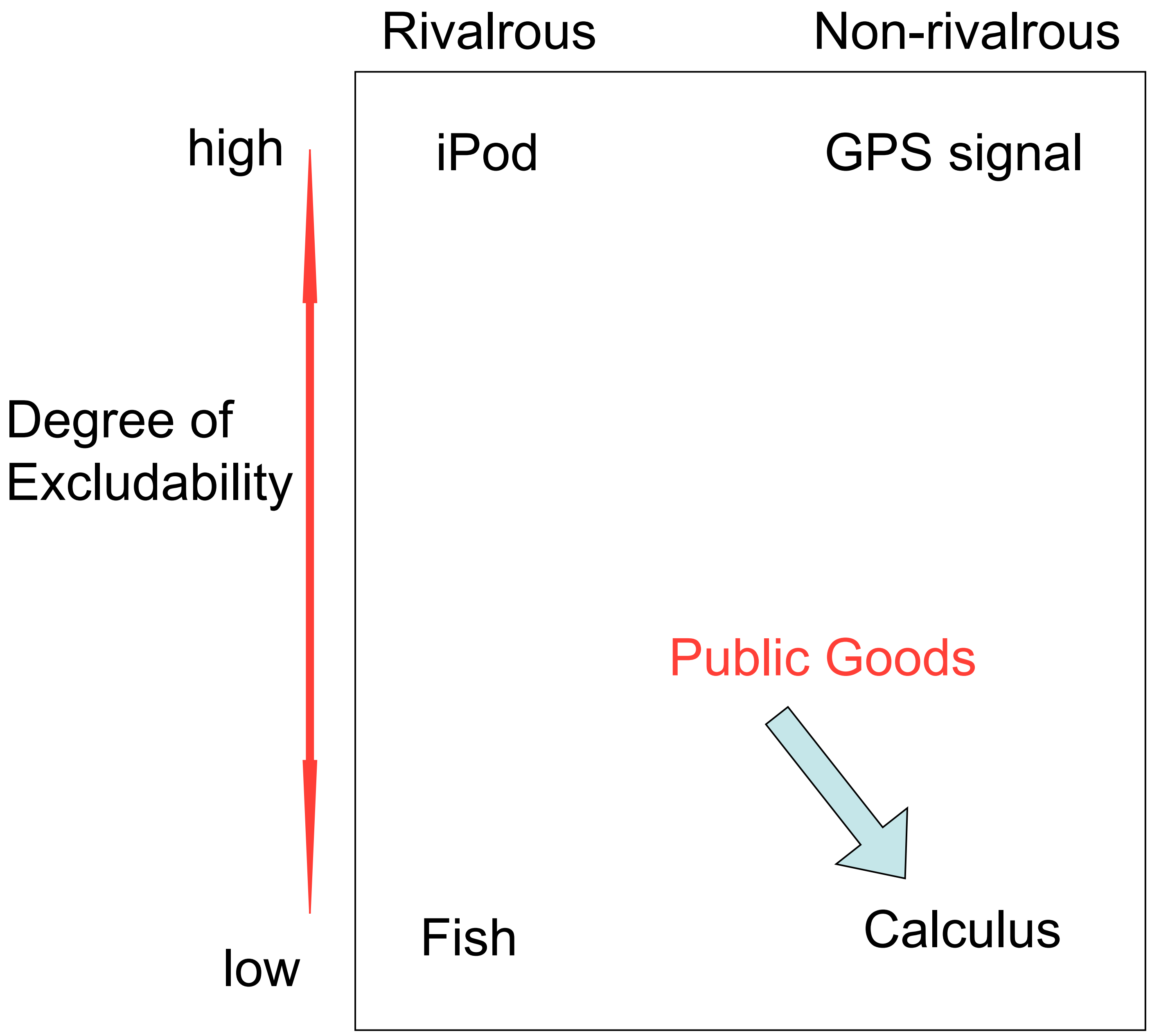
A = Technological variable with technological growth at a constant rate g, where $A = A_0 e^{gt}$

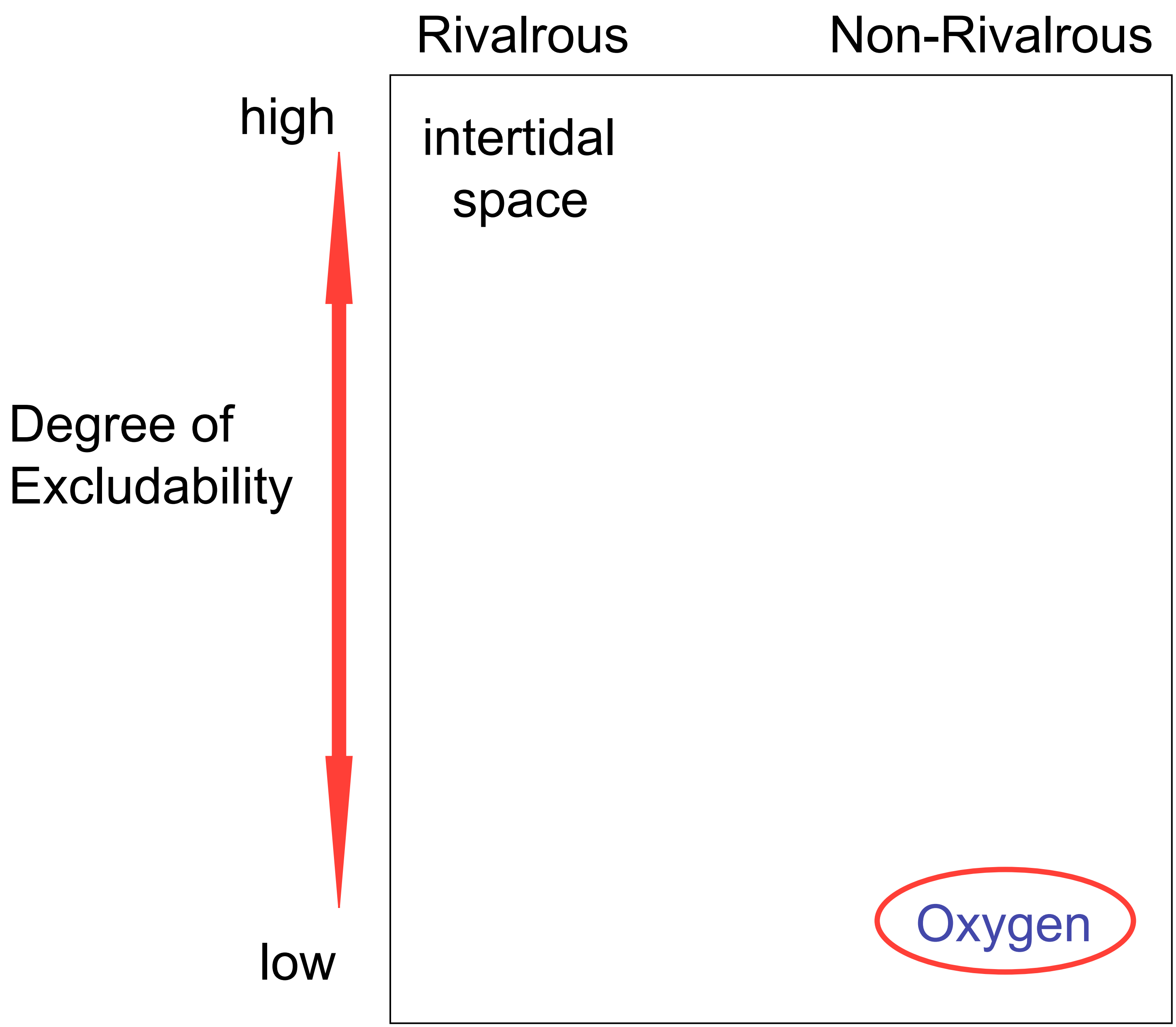

Rivalrous
Non-rivalrous
high
iPod
GPS signal
Degree of Excludability
low

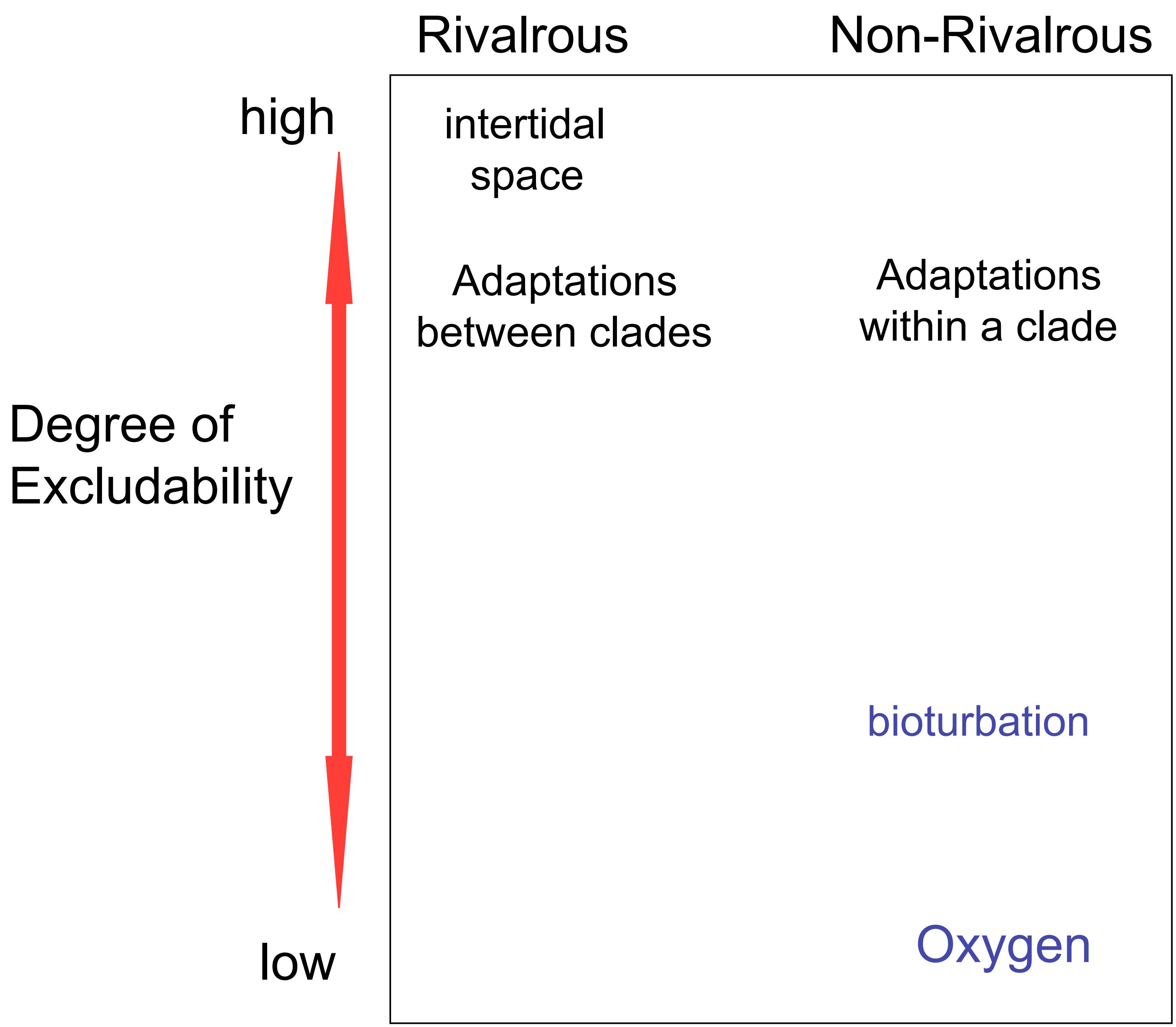

Rivalrous
Non-rivalrous
high
Degree of Excludability
low
iPod
GPS signal
Fish
calculus



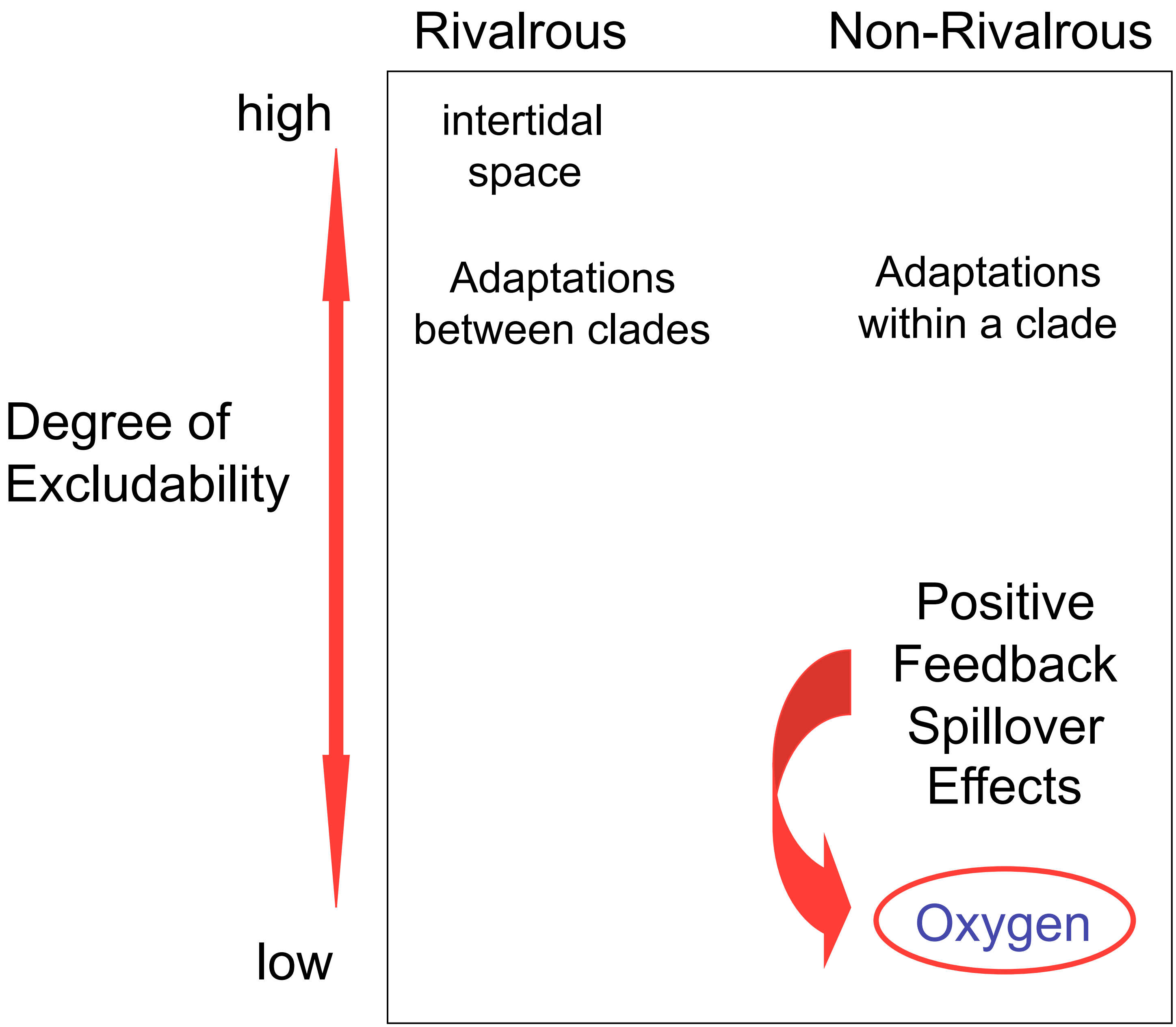
Rivalrous
Non-rivalrous
high
Degree of Excludability
low
iPod
GPS signal
Tragedy of the Commons
Fish
calculus


Rivalrous
Non-rivalrous
high
iPod
GPS signal
Degree of
Excludability
Public Goods
Fish
Calculus
low


Rivalrous
Non-Rivalrous
high
intertidal space
Degree of Excludability
Oxygen
low

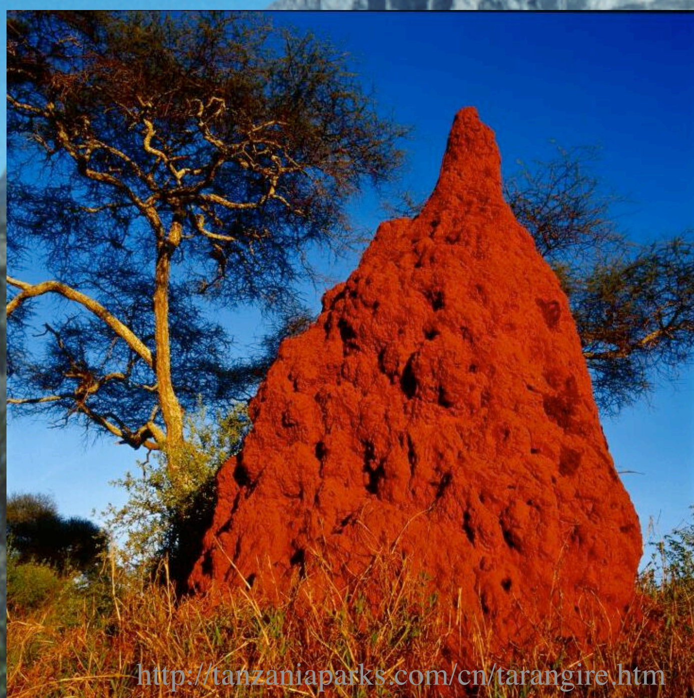


Rivalrous
Non-Rivalrous
high
intertidal space
Adaptations between clades
Adaptations within a clade
Degree of Excludability
bioturbation
low
Oxygen

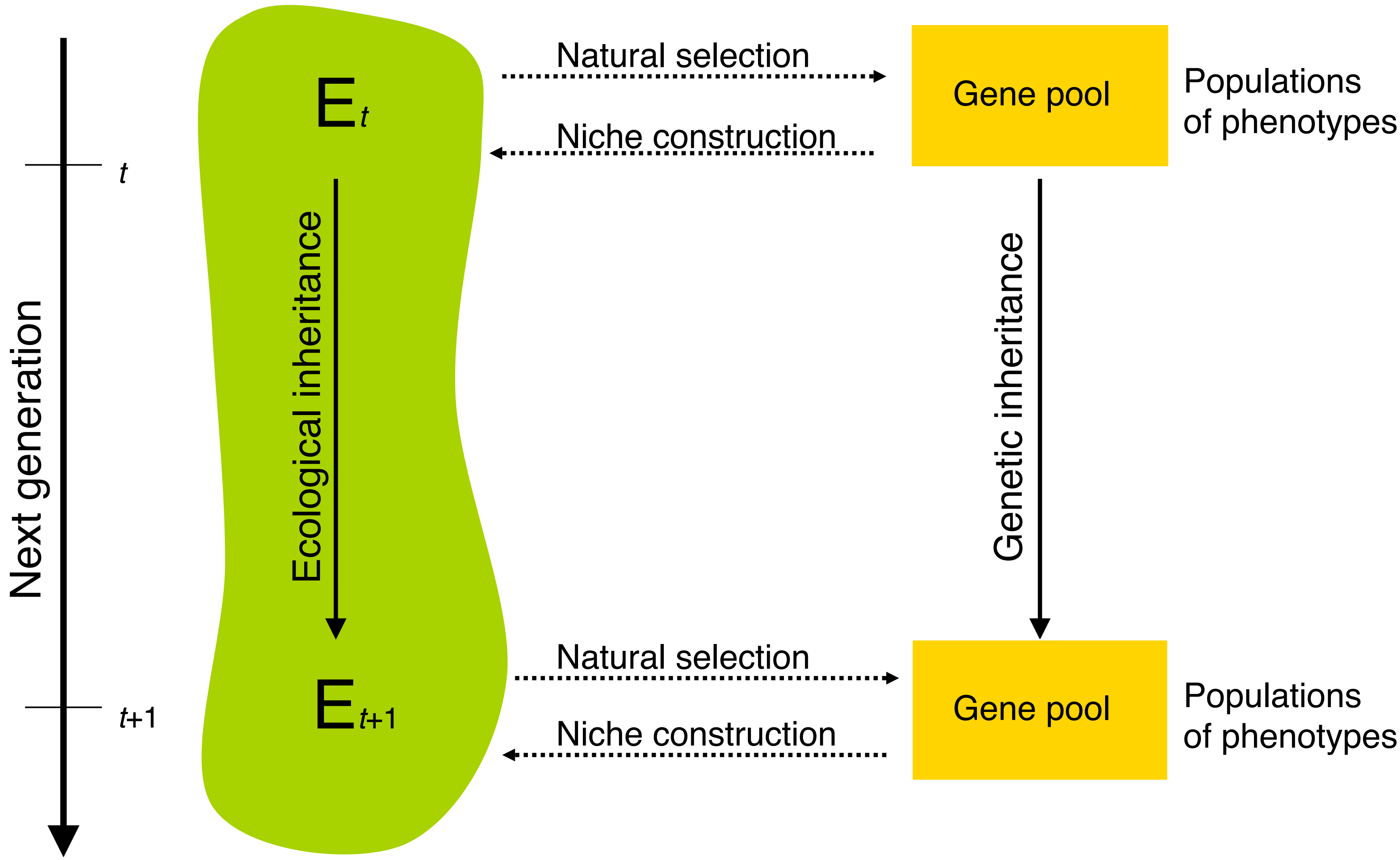

Rivalrous
Non-Rivalrous
high
intertidal space
Adaptations between clades
Adaptations within a clade
Degree of Excludability
Positive Feedback Spillover Effects
Oxygen
low

Non-rivalrous, low excludability settings (low competition) have significant positive feedback effects, facilitating rapid expansions of diversity

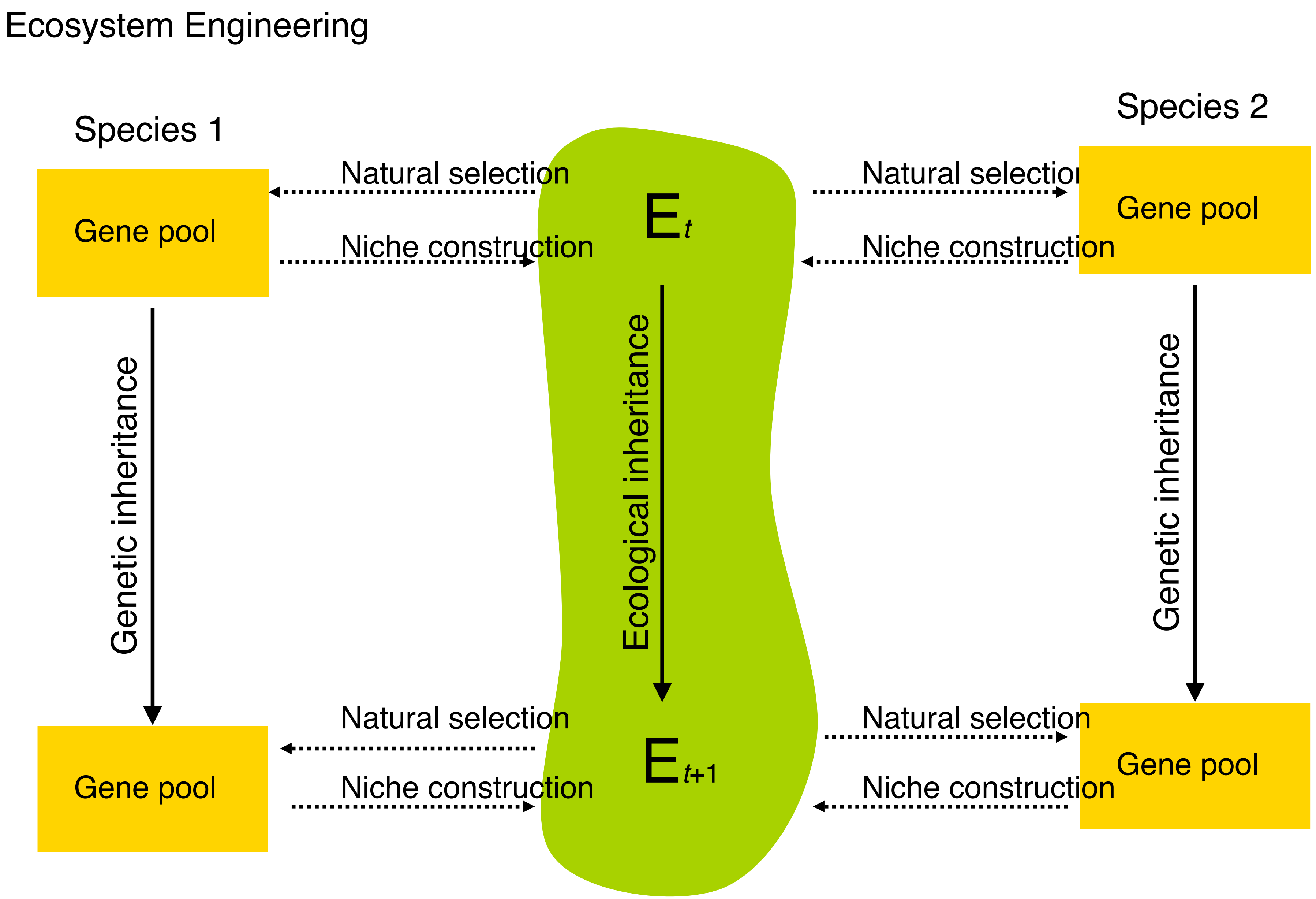
Ecosystem Engineering vs Niche Construction



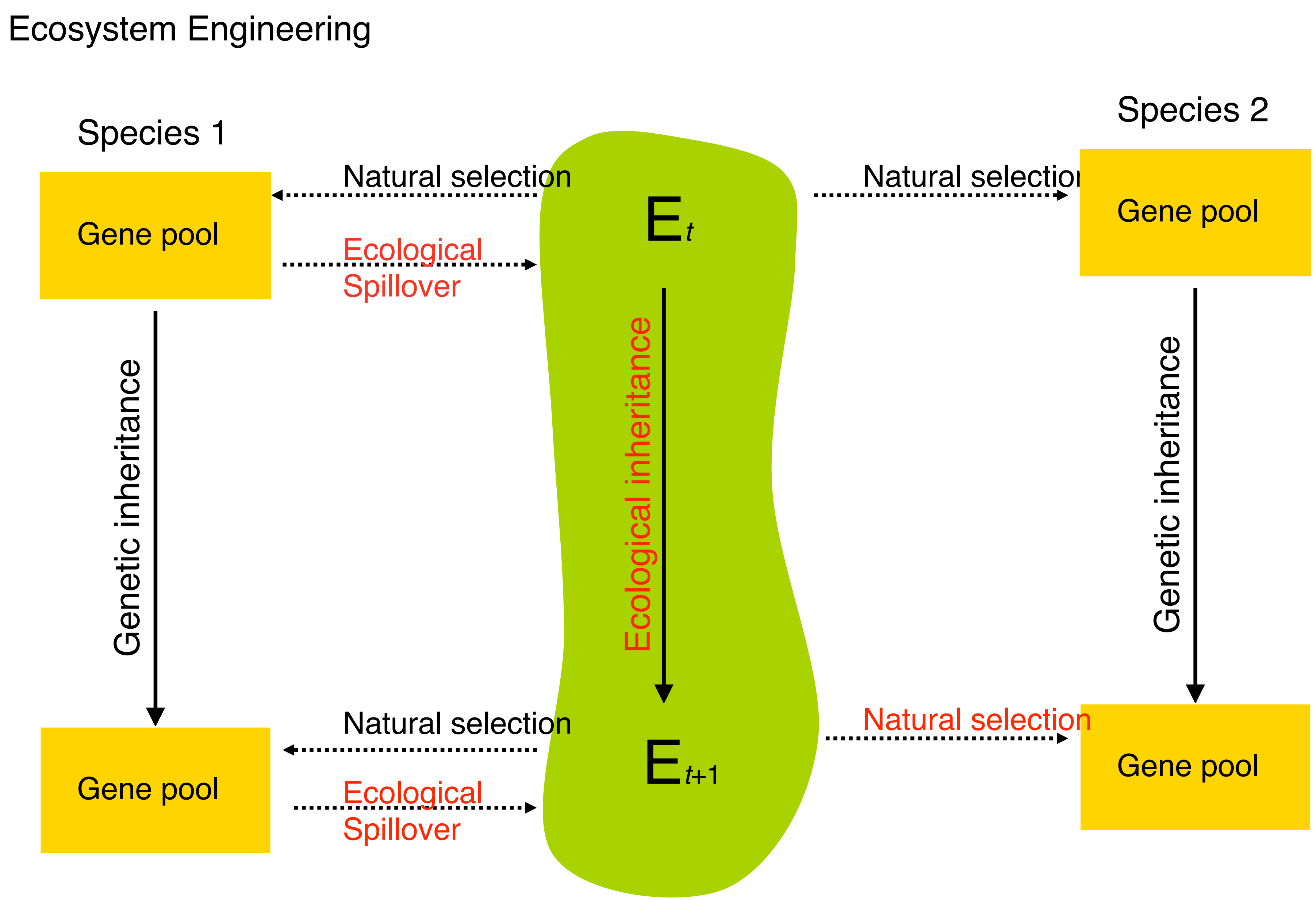
Niche inheritance



Odling-Smee et al.



Ecosystem Engineering
Species 1
Species 2
Gene pool
Natural selection
Niche construction
Natural selectio
Gene pool
Niche construction
E t
Genetic inheritance
Ecological inheritance
Genetic inheritance
Natural selection
Natural selection
Gene pool
E t+1
Gene pool
Niche construction
Niche construction


Ecosystem Engineering
Species 1
Species 2
Gene pool
Natural selection
Ecological
Spillover
E_t
Natural selection
Gene pool
Genetic inheritance
Ecological inheritance
Genetic inheritance
Natural selection
Gene pool
Ecological
Spillover
E_{t+1}
Natural selection
Gene pool

Crassostrea virginica

Image: WHOI

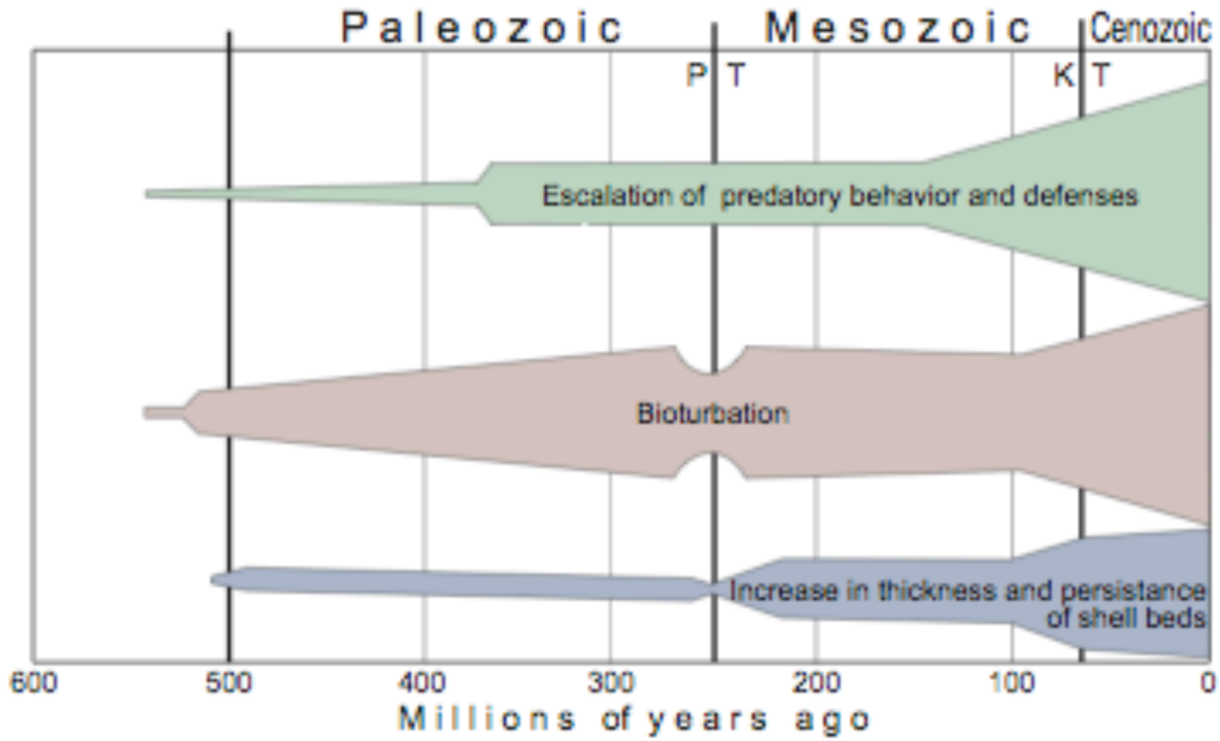
Oysters in Chesapeake Bay

- In 1988 oyster populations could potentially filter the water column above 9m (where they live) in 244 days, and the entire volume of the Chesapeake Bay in 325 days.
- Populations before 1870, when extensive harvesting began, could filter in 2.5-4 and 3-6 days
- This provided a ‘top-down’ control of the pelagic ecosystem.

Oysters in Chesapeake Bay

- The virtual elimination of the oysters has shifted the Chesapeake estuary from an ecosystem with extensive benthic and pelagic primary productivity, high mesozooplankton density and abundant fish stocks, to one dominated by ctenophores, jellyfish, pelagic microbes, and particulate organic carbon.

Ecosystem Engineering & Niche Construction



Problems with Models

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- Carrying capacity is an exogenous, not endogenous variable
- Carrying capacity does not change endogenously over time

Problems with Models

- Niche construction/ecosystem engineering effects poorly captured
- Carrying capacity is an exogenous, not endogenous variable
- Carrying capacity does not change endogenously over time
- Absence of full (toy) model of trophic dynamics
- Adaptations vary in their ecological impact

- *Niche construction* increases species abundance
- *Ecosystem engineering* increases diversity

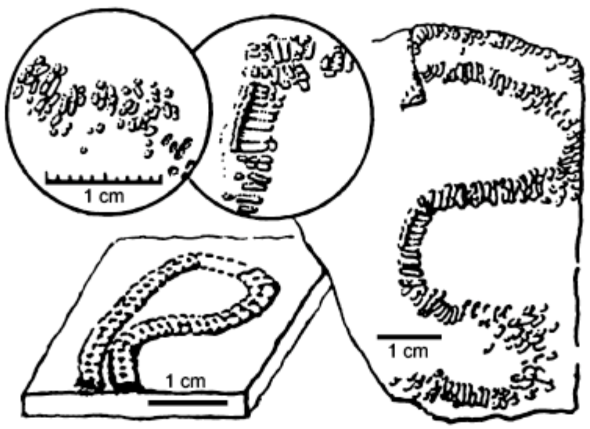
Conceptual Framework for recovery and innovation

- Inclusion of invention and innovation as endogenous parameters
- Positive feedback (spillovers) occur during low competition situations, particularly for non-rivalrous, non-excludable products of *ecosystem engineering*. Diversity increase should slow as increased competition reduces spillovers.
- Contrast this with the empty ecospace approach derived from Simpson and others.

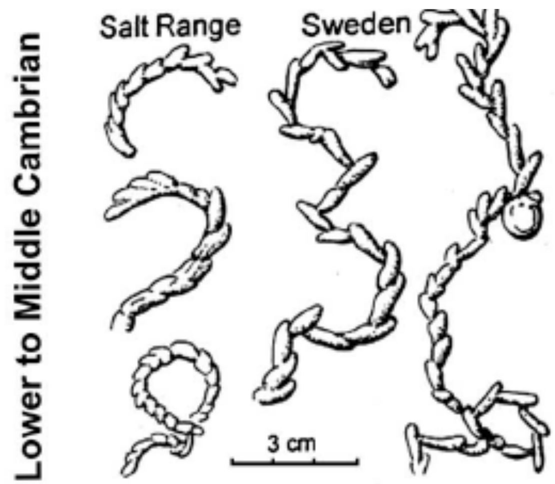
Typical late Neoproterozoic Sediments:
no burrowing

Lower Cambrian Burrows
from Siberia

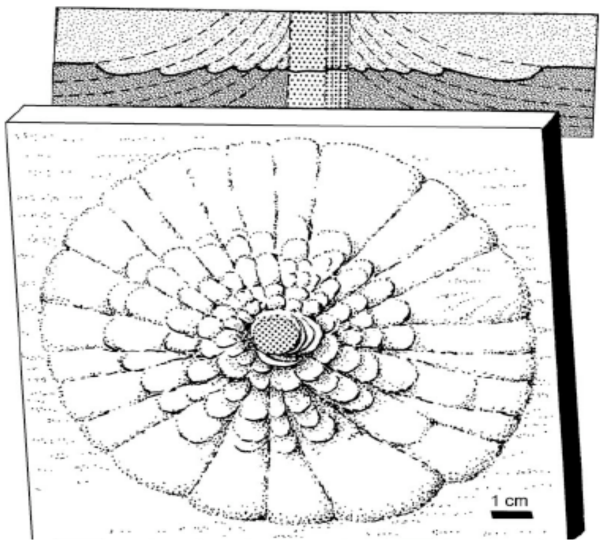
Ediacaran-Cambrian Trace Fossils



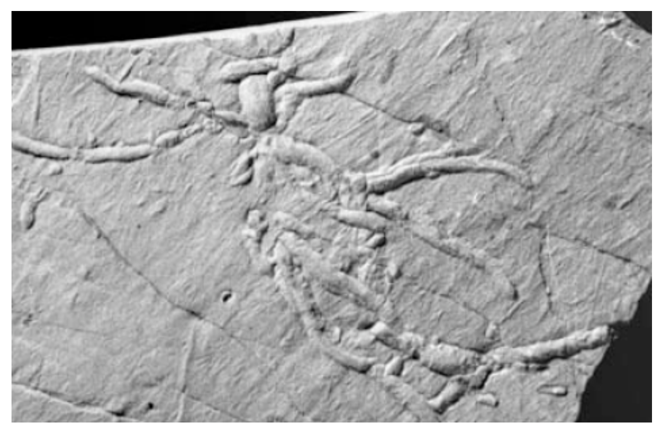
Nenoxites (Ediacaran, Russia)



Tripichnus



Mawsonites



Streptichnus

Ecological Spillovers

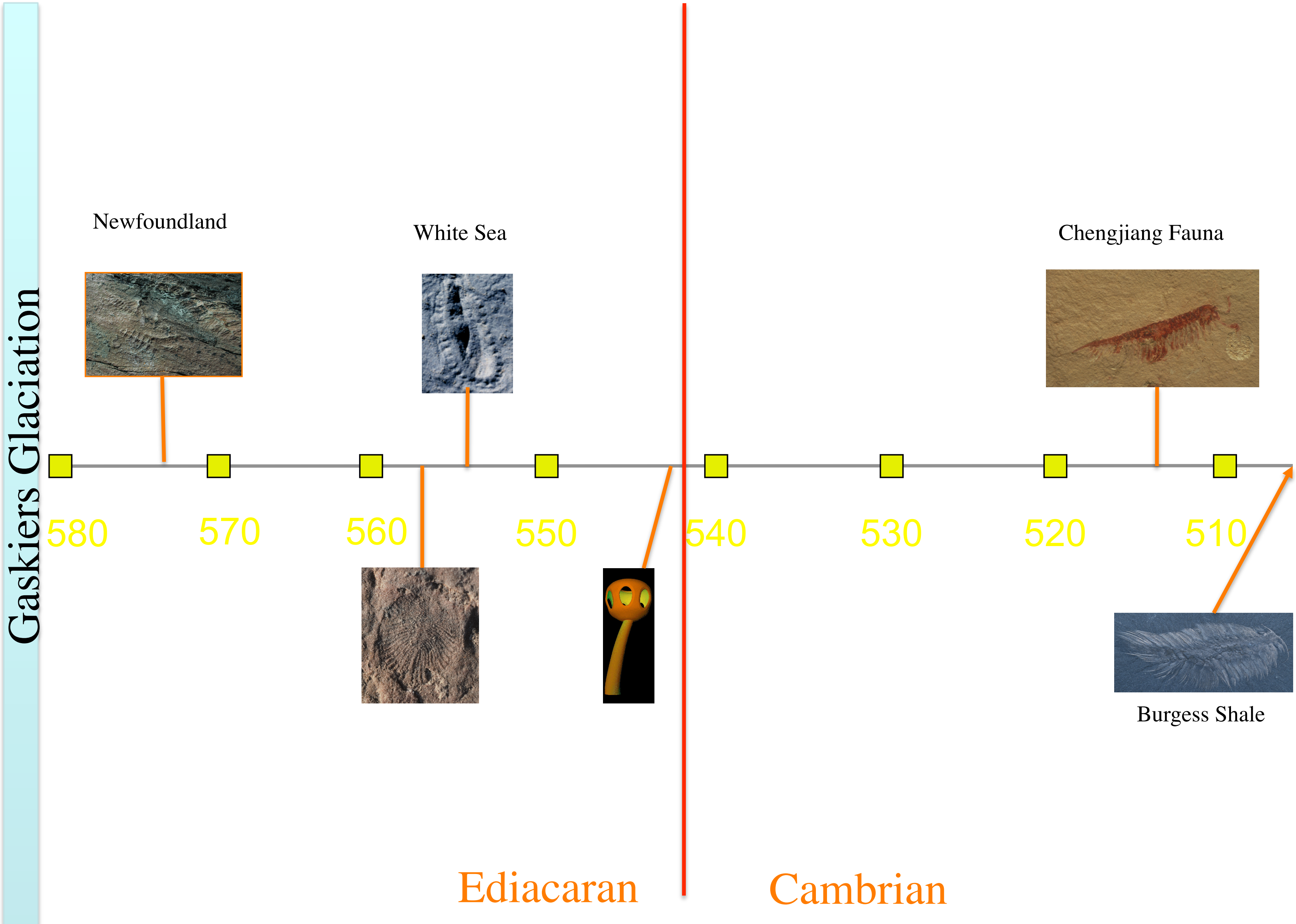
- Sponges: sequestering carbon via filtration. Oxidation of oceans allow increased production of collagen.
- Burrowing: change in S isotopes, enhances primary productivity in seds, increases biodiversity

Ediacaran niche construction

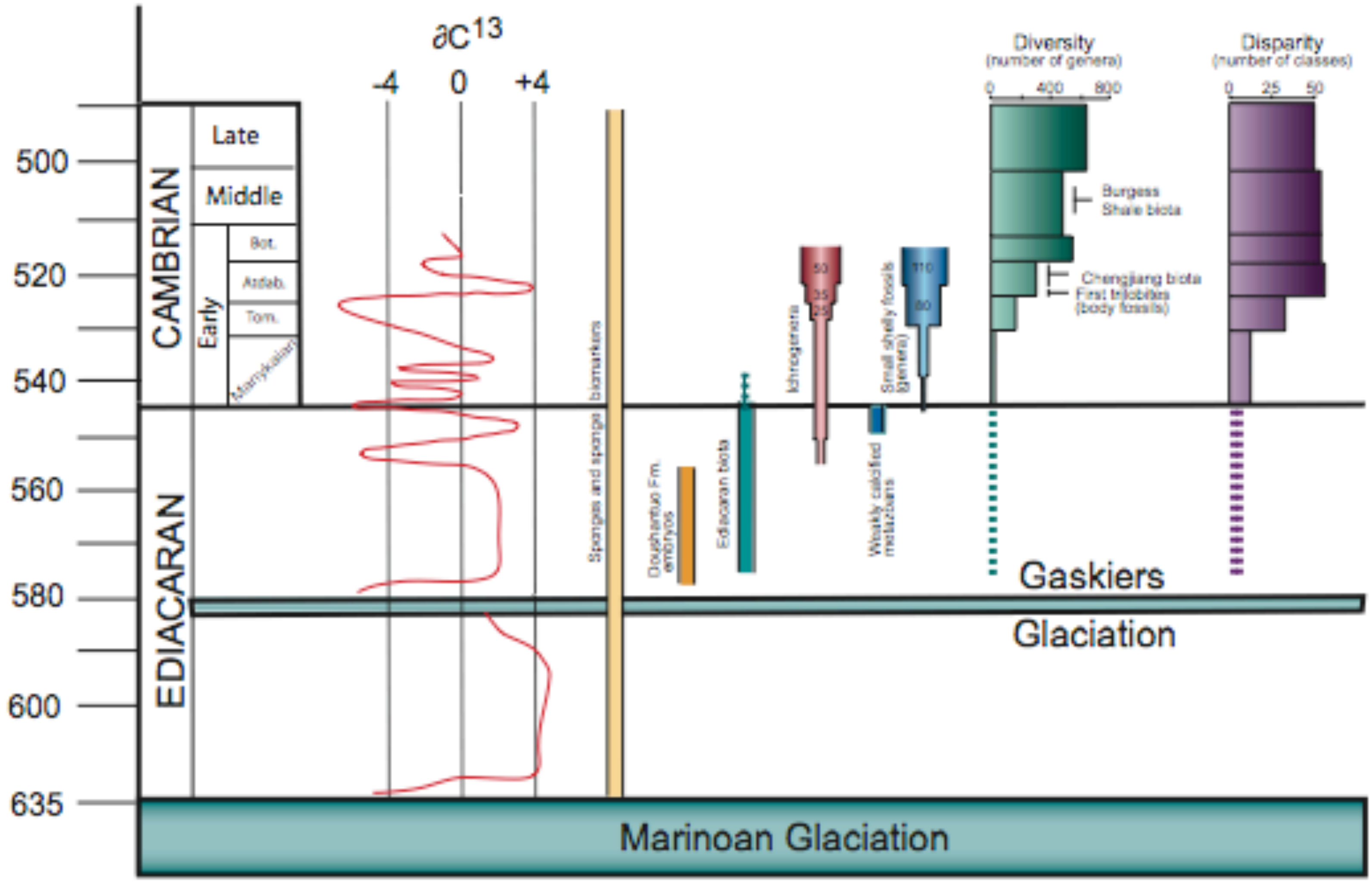
- Microbial substrates
- Grazing (*Kimberella)* (-)
- Osmotrophy (-)

Cambrian Niche Construction

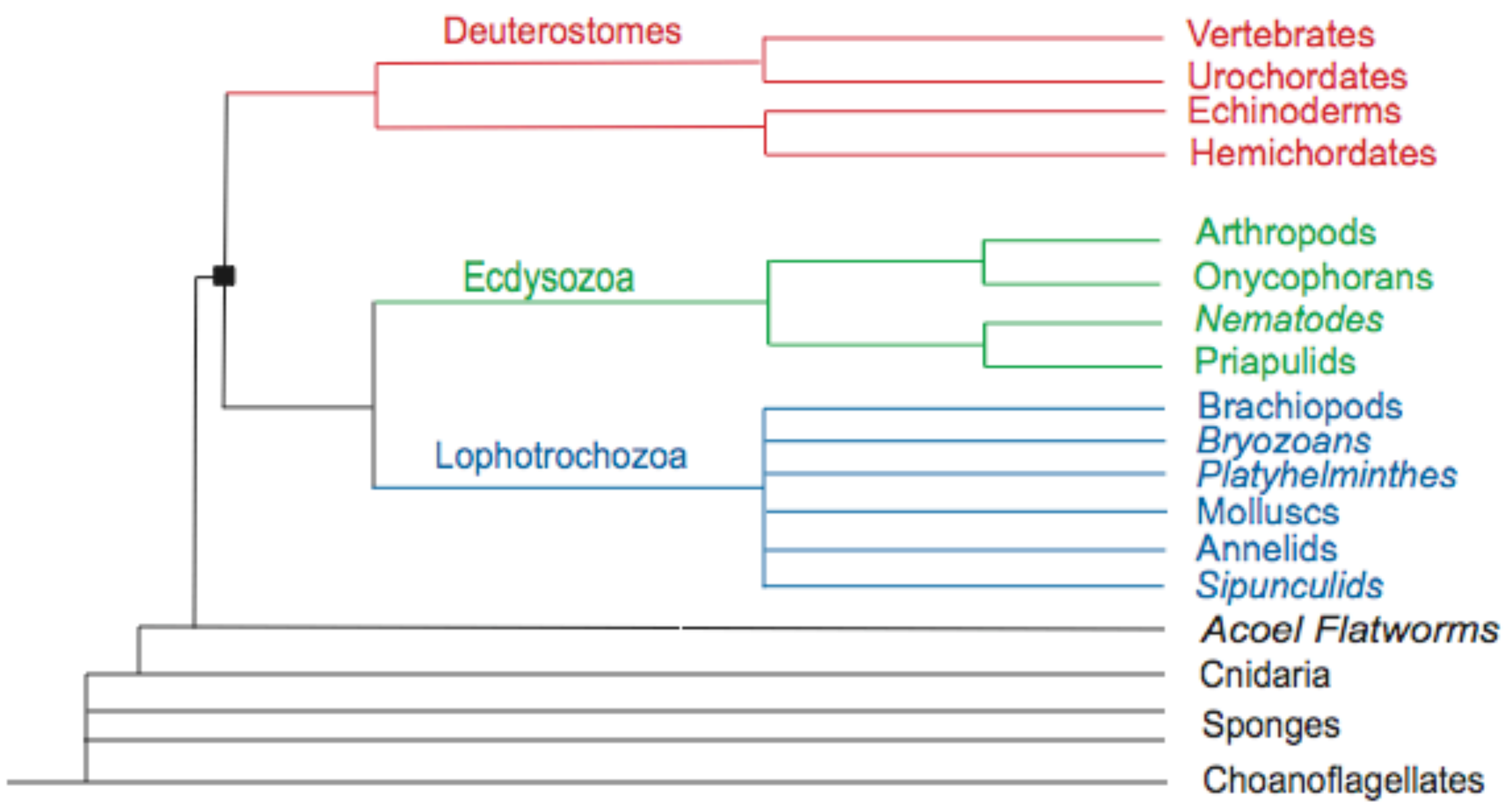
- Archaeocyathid reefs (+)
- Burrowed sediments (+/-)
- Shelly substrates (+)


Gaskiers Glaciation
Newfoundland
White Sea
Chengjiang Fauna
580
570
560
550
540
530
520
510
Burgess Shale
Ediacaran
Cambrian

Metazoan Diversification



Animal Phylogeny

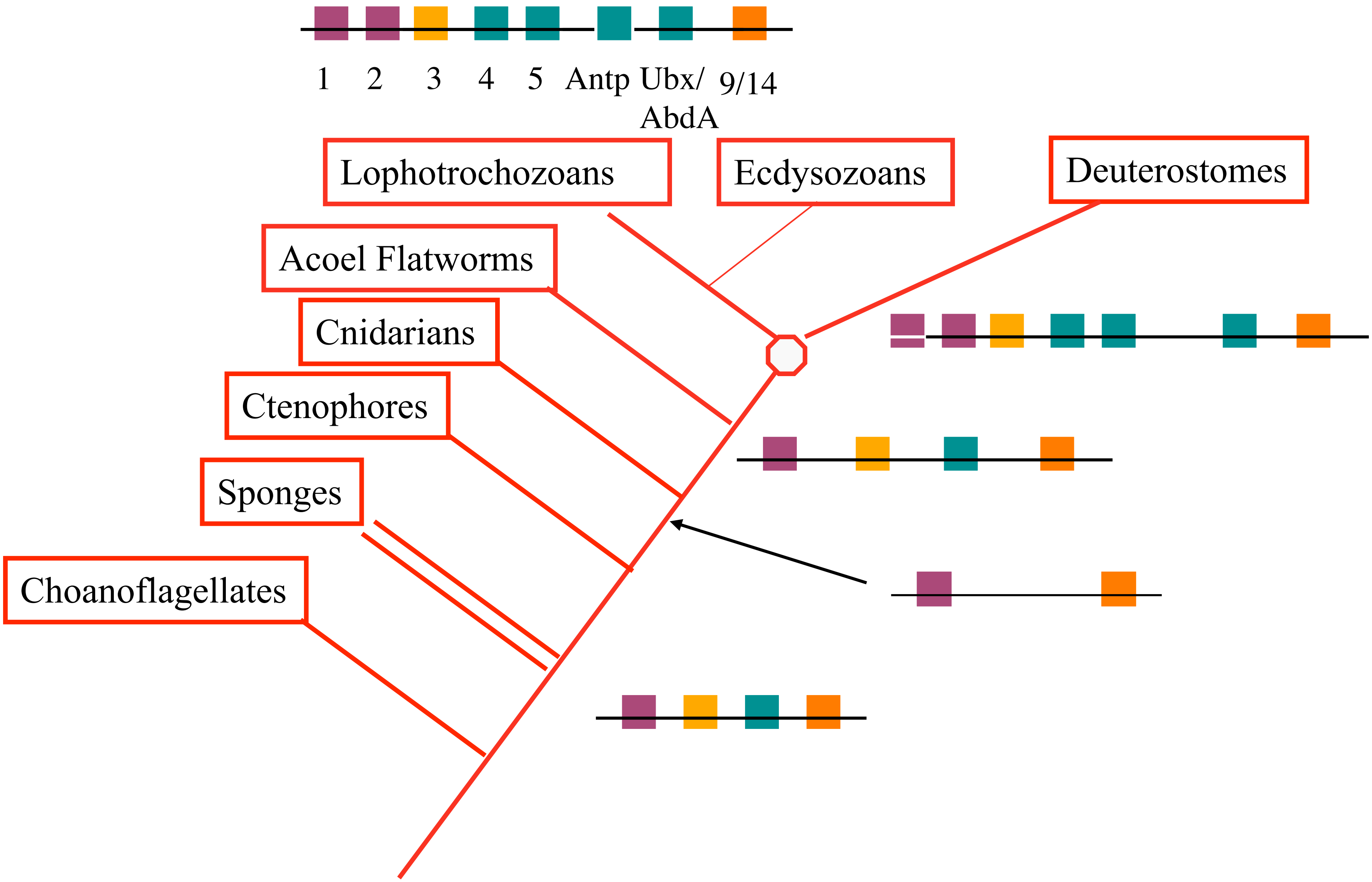


Developmental invention: Eye genes in *Drosophila*

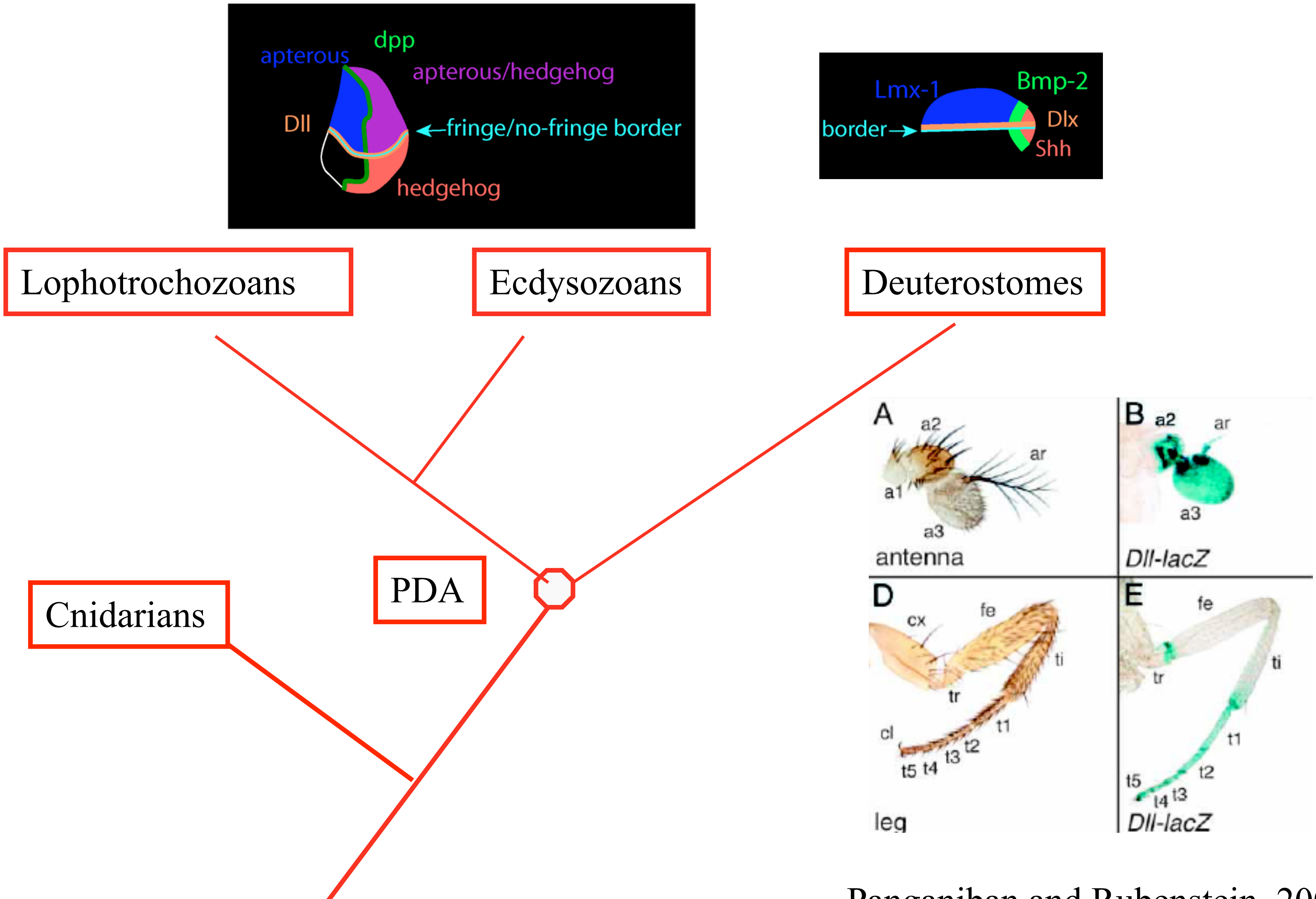
- PAX-6 genes are highly conserved adult expression in vertebrates and *Drosophila*
- *NOT* expressed in adult eyes of cephalopods, polychaetes
- Expressed in 2-cell larval eyes of *Platyneris* (an annelid) supporting an ancestral role in larval eye formation

Gehring 2004

Hox Gene Evolution

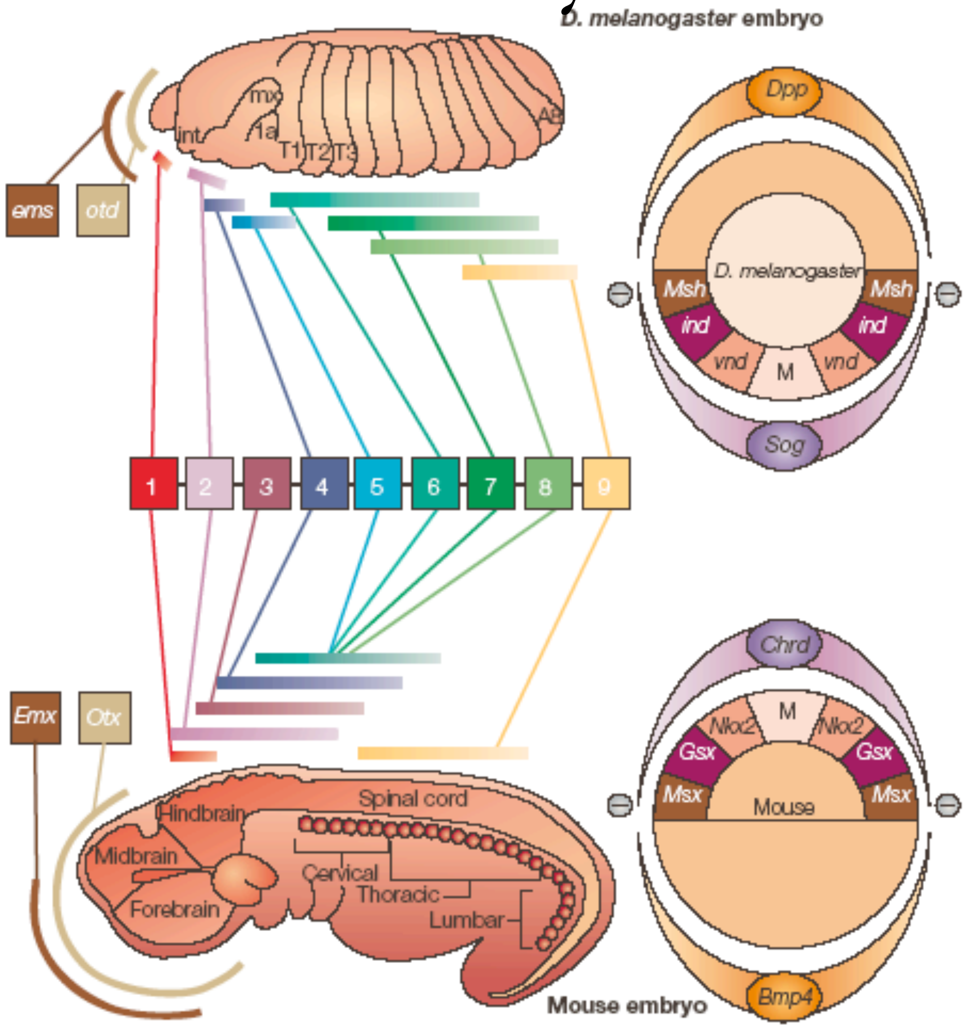


PDA Development: Appendage Development



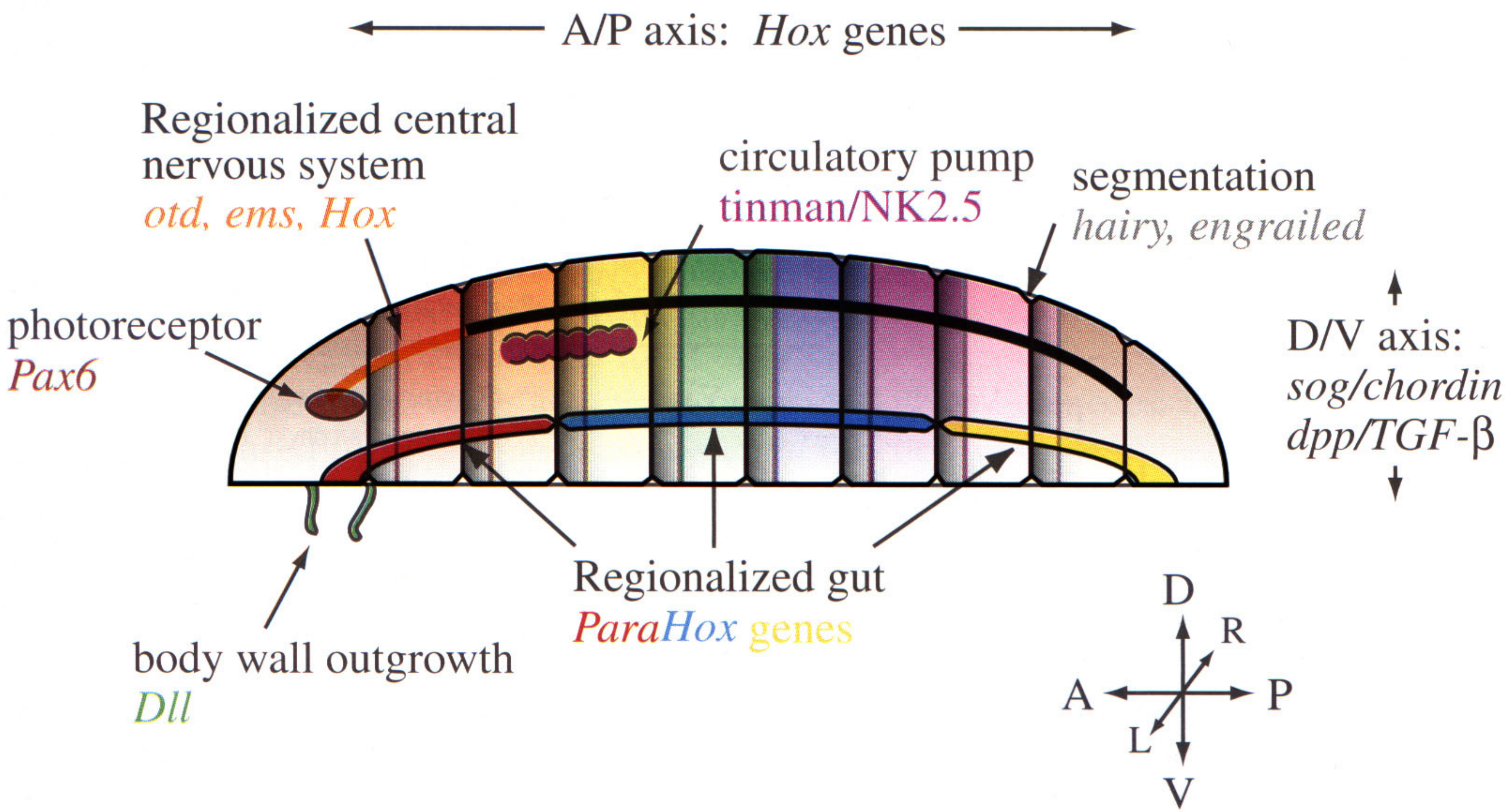
Panganiban and Rubenstein, 2002

Comparison of *Drosophila* and mouse embryos



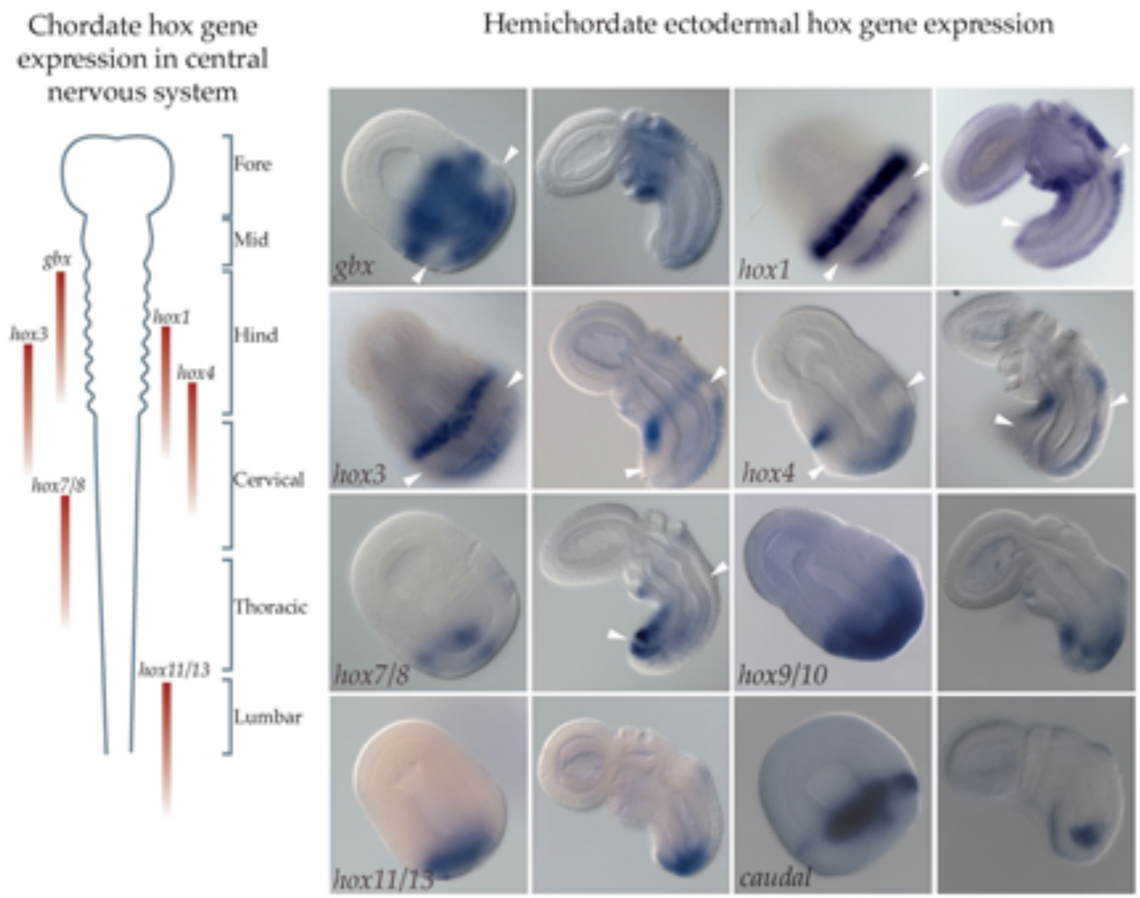
Ball et al 2004

Hypothetical Urbilaterian



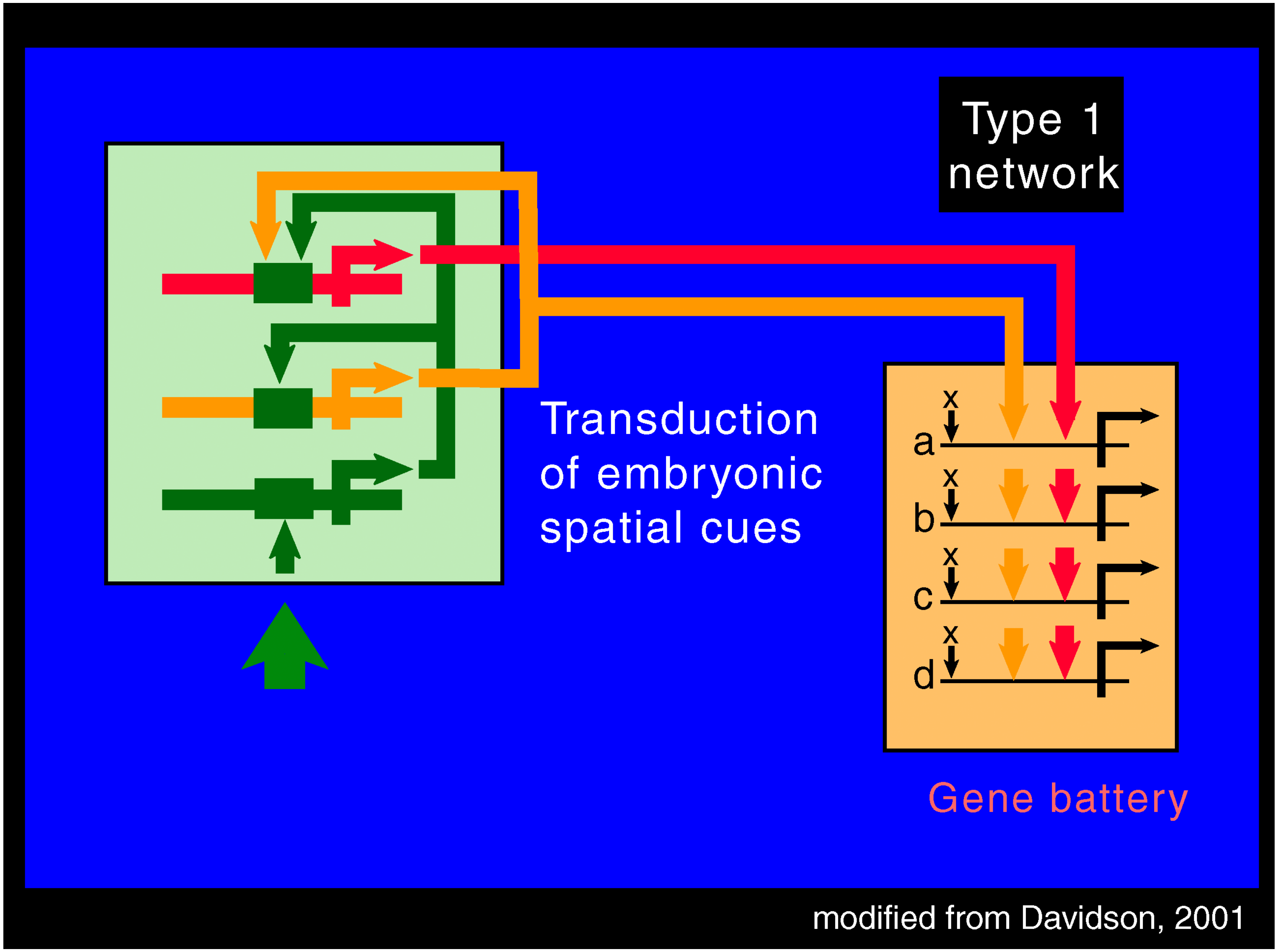
After Carroll et al 2001

Hemichordate ectodermal gene expression

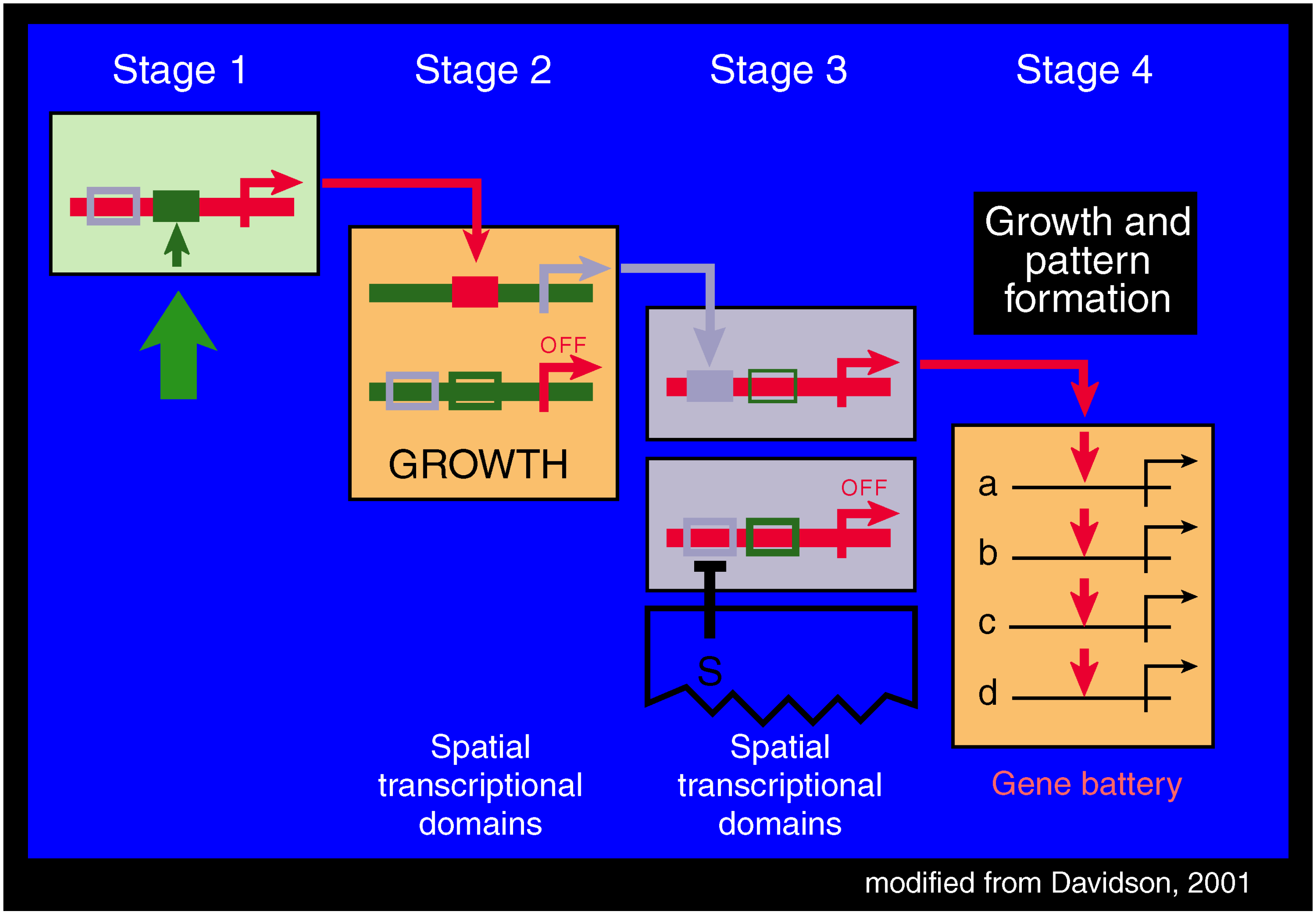


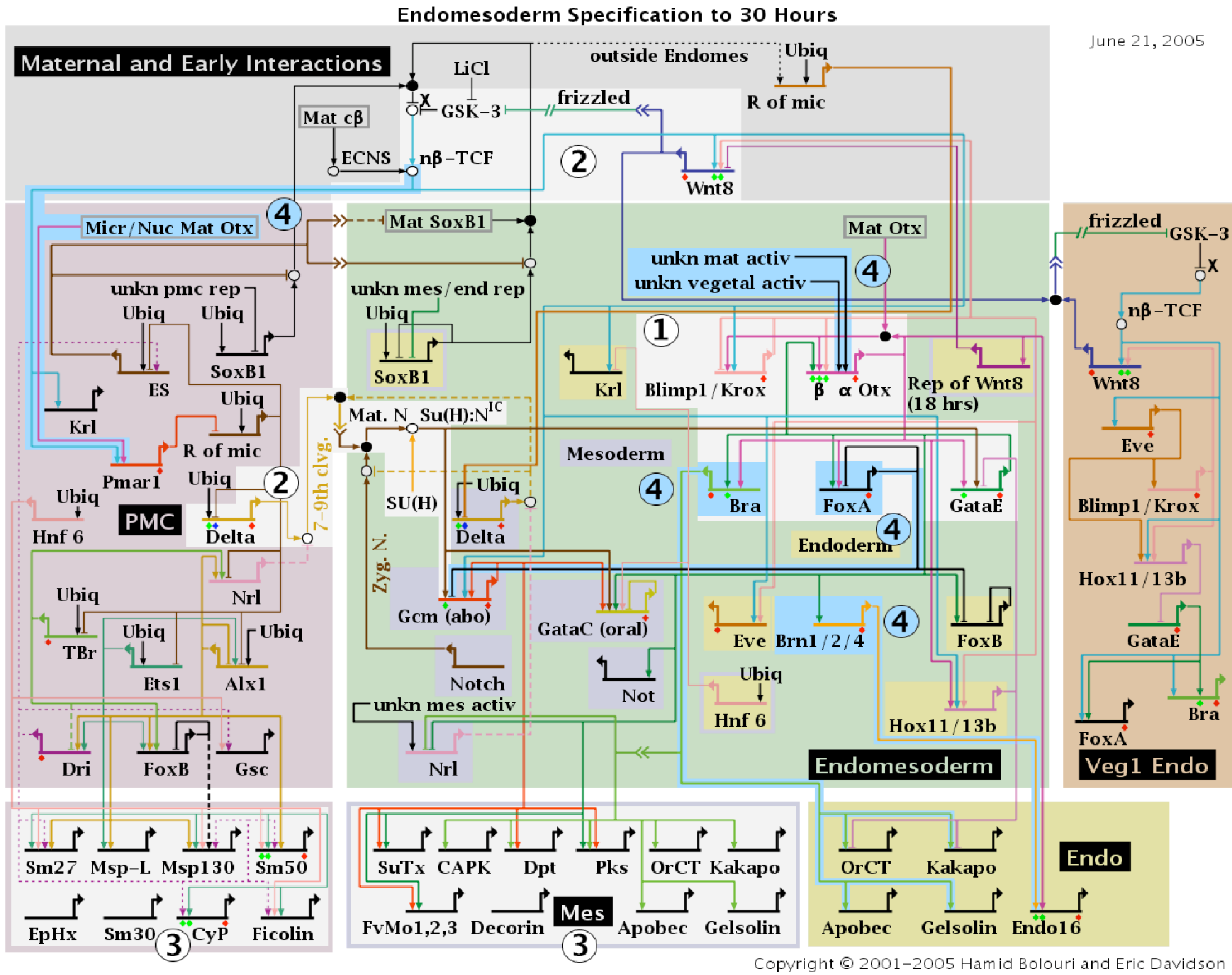
From Chris Lowe, U Chicago

Evolution of Gene Networks



Evolution of Gene Networks





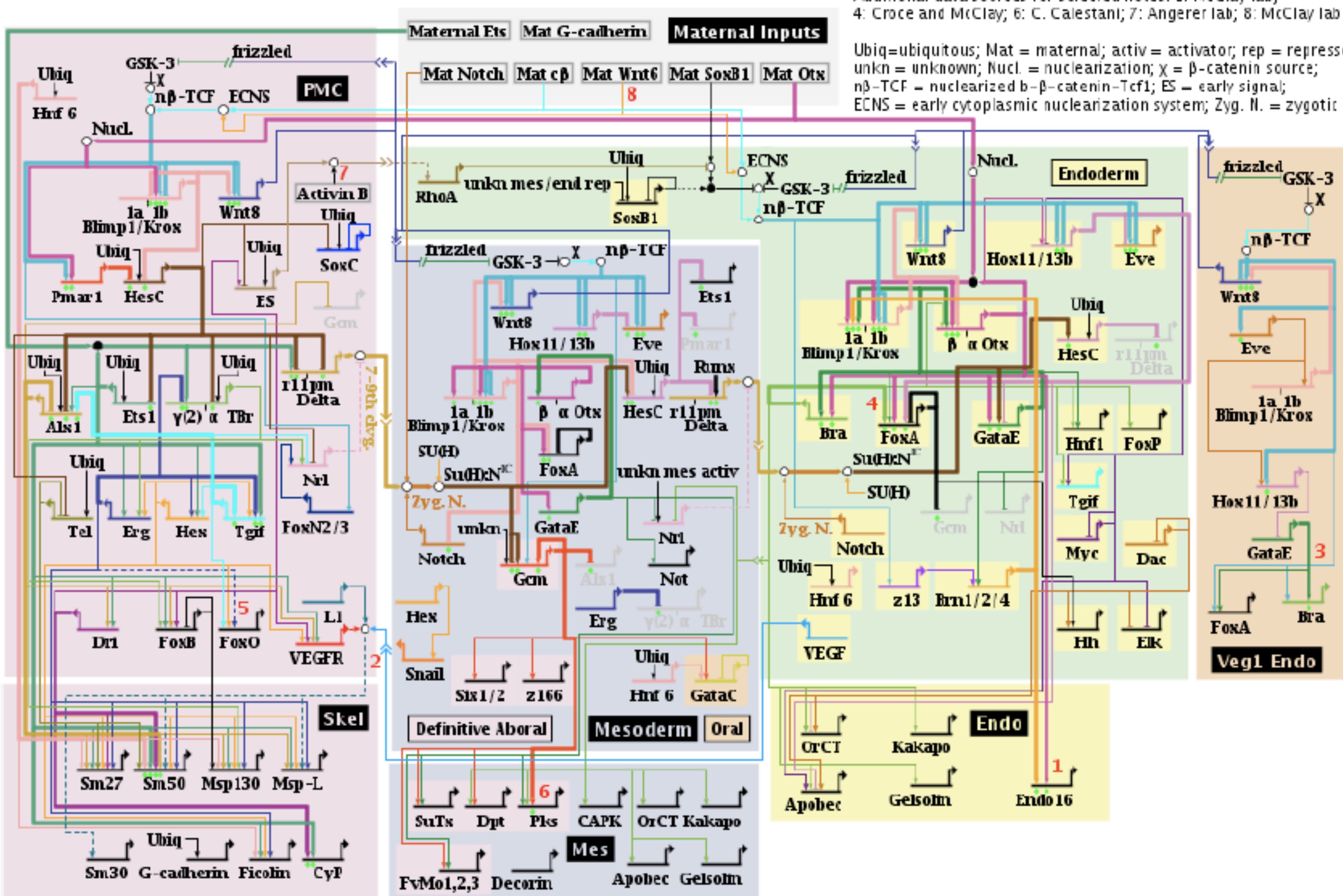
Sea Urchin endomesoderm GRN

Endomesoderm Specification to 30 Hours

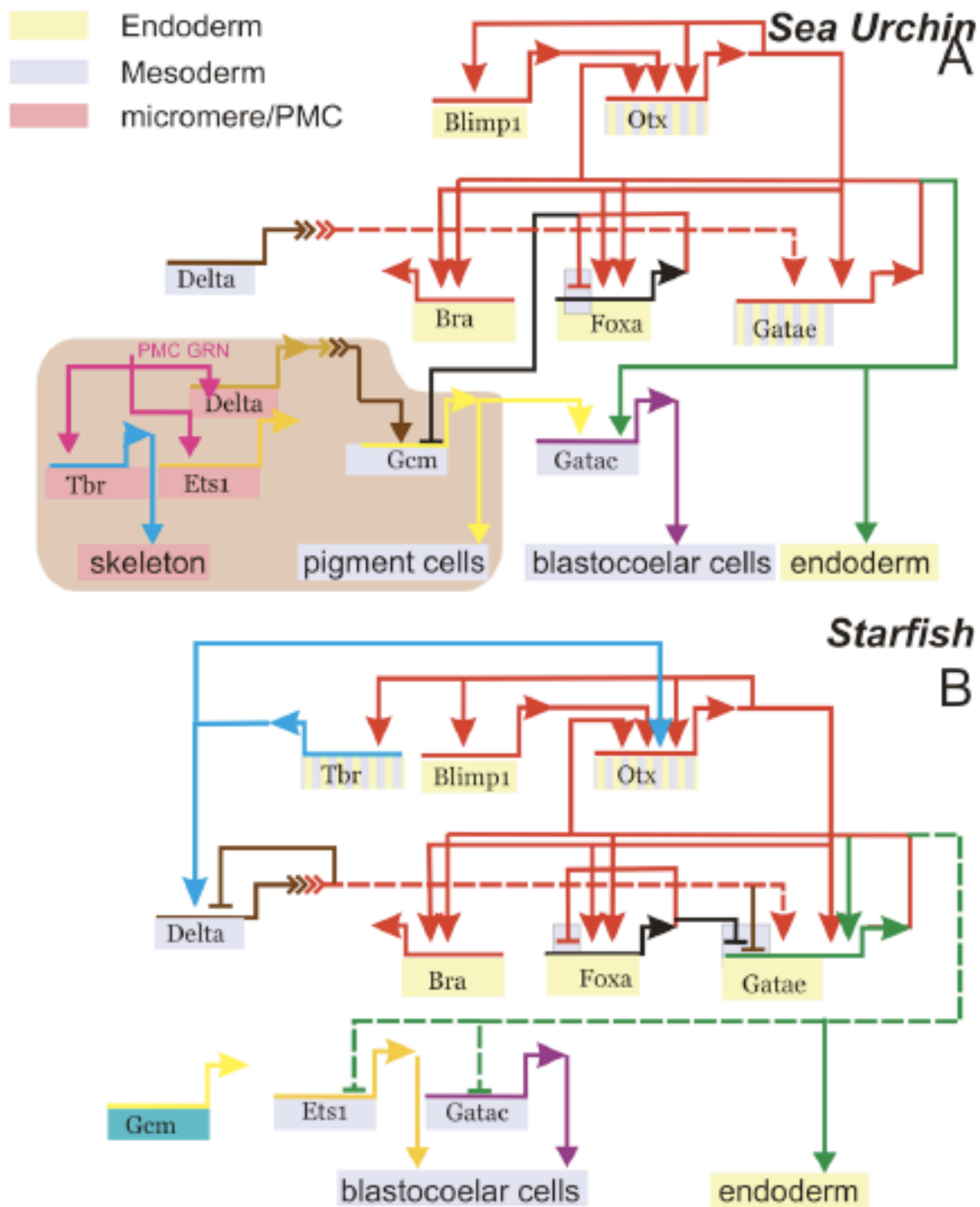
May 06, 2009

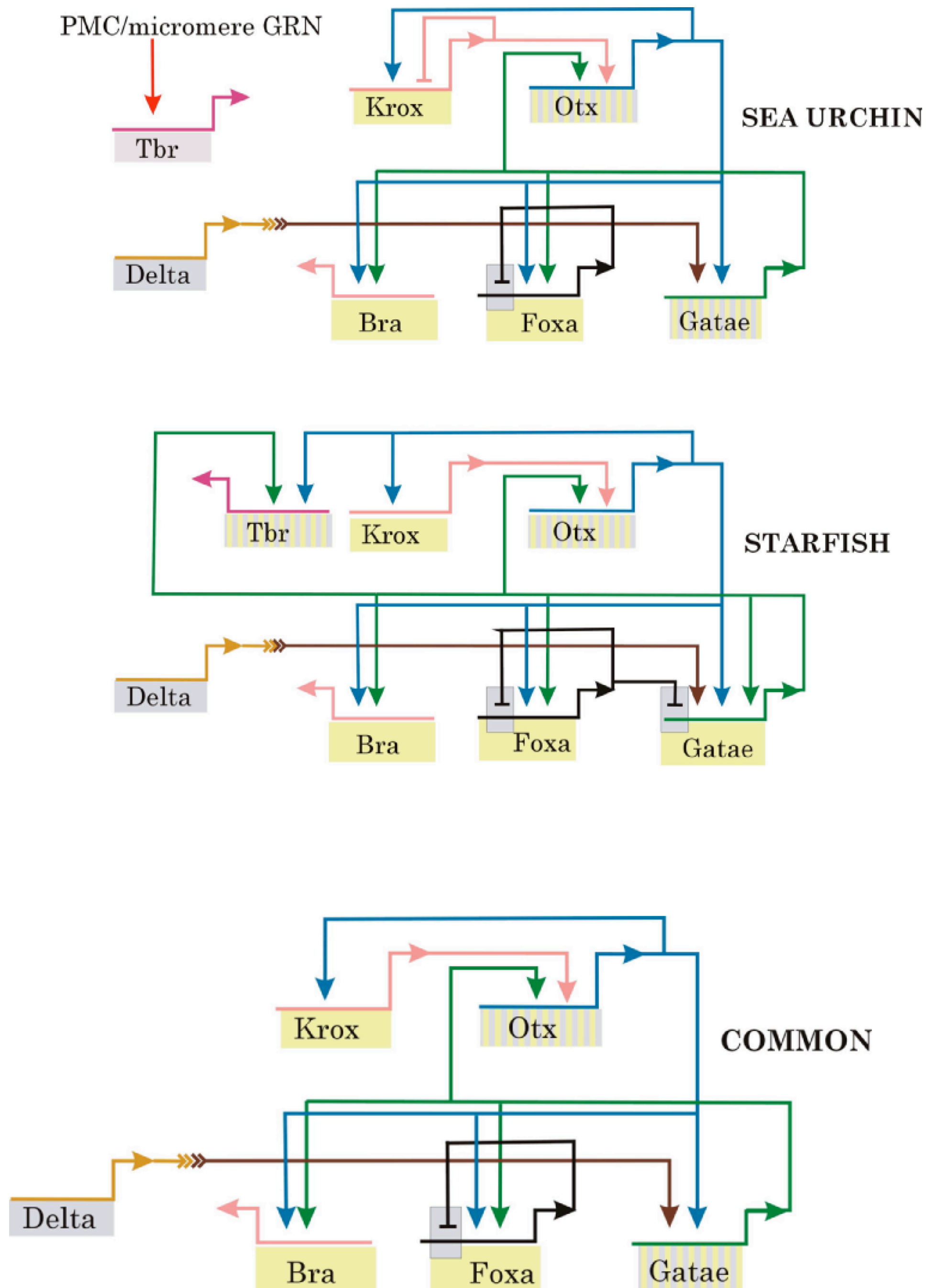
Additional data sources for selected notes: 2: McClay lab; 4: Croce and McClay; 6: C. Calestani; 7: Angerer lab; 8: McClay lab

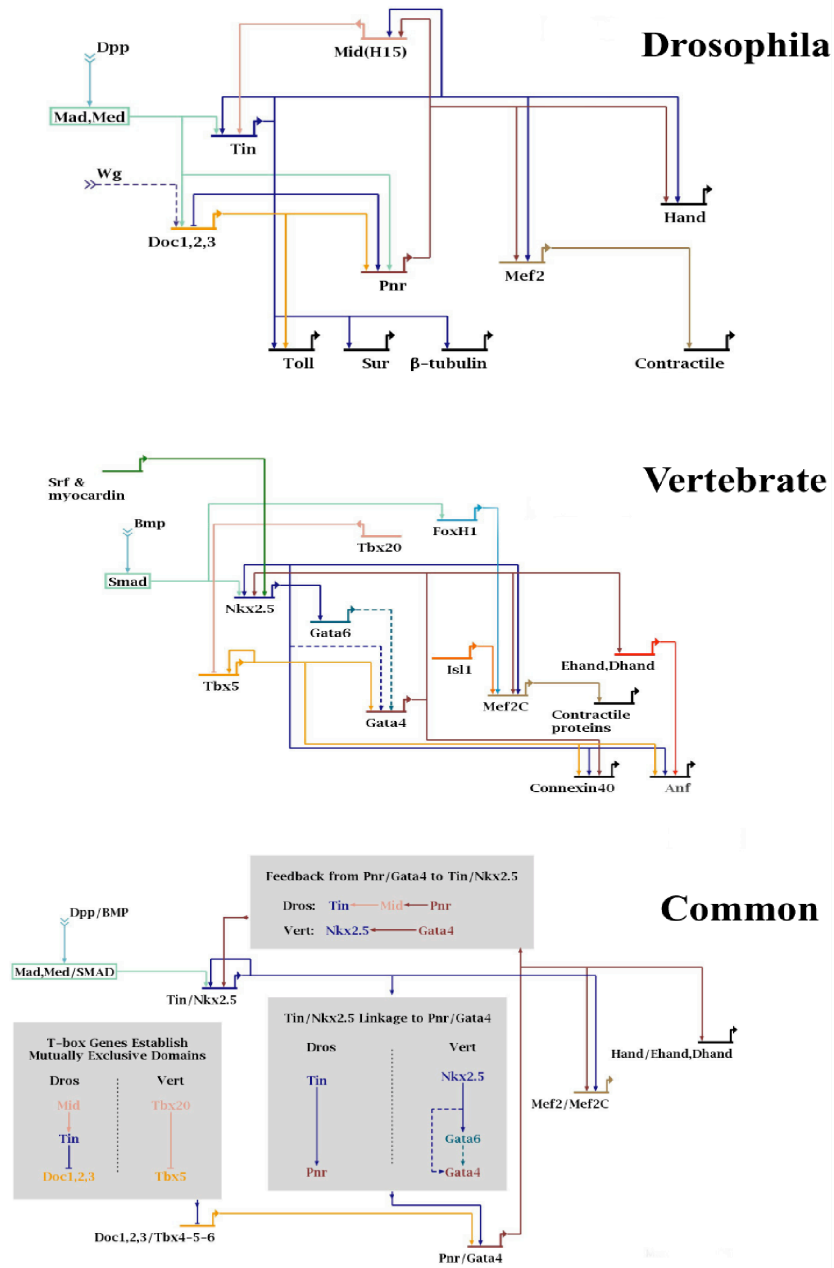
Ubiq=ubiquitous; Mat = maternal; activ = activator; rep = repressor; unkn = unknown; Nucl. = nuclearization; χ = β-catenin source; nβ-TCF = nuclearized b-β-catenin-Tcf1; ES = early signal; ECNS = early cytoplasmic nuclearization system; Zyg. N. = zygotic Notch

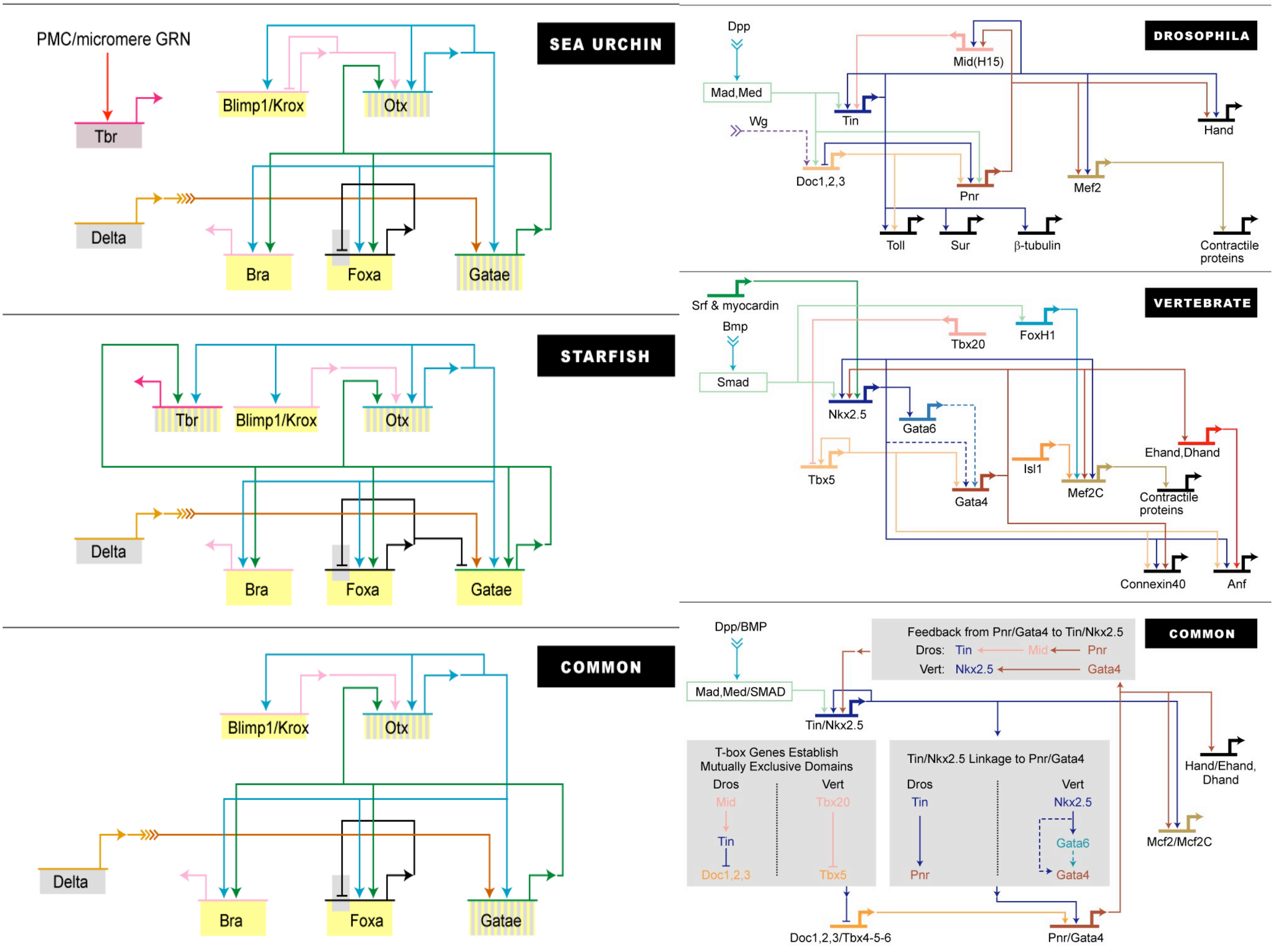


This model is frequently revised. It is based on the latest laboratory data, some of which is not yet published.


Endoderm
Mesoderm
micromere/PMC
Sea Urchin
A
Blimp1
Otx
Delta
Bra
Foxa
Gatae
PMC GRN
Delta
Tbr
Ets1
Gcm
Gatac
skeleton
pigment cells
blastocoelar cells
endoderm
Starfish
B
Tbr
Blimp1
Otx
Delta
Bra
Foxa
Gatae
Gcm
Ets1
Gatac
blastocoelar cells
endoderm


PMC/micromere GRN
Tbr
Krox
Otx
SEA URCHIN
Delta
Bra
Foxa
Gatae
Tbr
Krox
Otx
STARFISH
Delta
Bra
Foxa
Gatae
Krox
Otx
COMMON
Delta
Bra
Foxa
Gatae


Drosophila
Dpp
Mad,Med
Mid(H15)
Tin
Wg
Doc1,2,3
Pnr
Mef2
Hand
Toll
Sur
β-tubulin
Contractile
Vertebrate
Srf &
myocardin
Bmp
Smad
FoxH1
Tbx20
Nkx2.5
Gata6
Tbx5
Gata4
Isl1
Mef2C
Ehand,Dhand
Contractile proteins
Connexin40
Anf
Common
Dpp/BMP
Mad,Med/SMAD
Tin/Nkx2.5
Feedback from Pnr/Gata4 to Tin/Nkx2.5
Dros: Tin Mid Pnr
Vert: Nkx2.5 Gata4
T-box Genes Establish Mutually Exclusive Domains
Dros
Vert
Mid
Tin
Doc1,2,3
Tbx20
Tbx5
Tin/Nkx2.5 Linkage to Pnr/Gata4
Dros
Vert
Tin
Pnr
Nkx2.5
Gata6
Gata4
Hand/Ehand,Dhand
Mef2/Mef2C
Doc1,2,3/Tbx4-5-6
Pnr/Gata4


SEA URCHIN
PMC/micromere GRN
Tbr
Blimp1/Krox
Otx
Delta
Bra
Foxa
Gatae
STARFISH
Tbr
Blimp1/Krox
Otx
Delta
Bra
Foxa
Gatae
COMMON
Blimp1/Krox
Otx
Delta
Bra
Foxa
Gatae
DROSOPHILA
Dpp
Mad,Med
Wg
Mid(H15)
Tin
Hand
Doc1,2,3
Pnr
Mef2
Toll
Sur
β-tubulin
Contractile proteins
VERTEBRATE
Srf & myocardin
Bmp
Smad
Tbx20
FoxH1
Nkx2.5
Gata6
Ehand,Dhand
Isl1
Tbx5
Gata4
Mef2C
Contractile proteins
Connexin40
Anf
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Dpp/BMP
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Feedback from Pnr/Gata4 to Tin/Nkx2.5
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Dros
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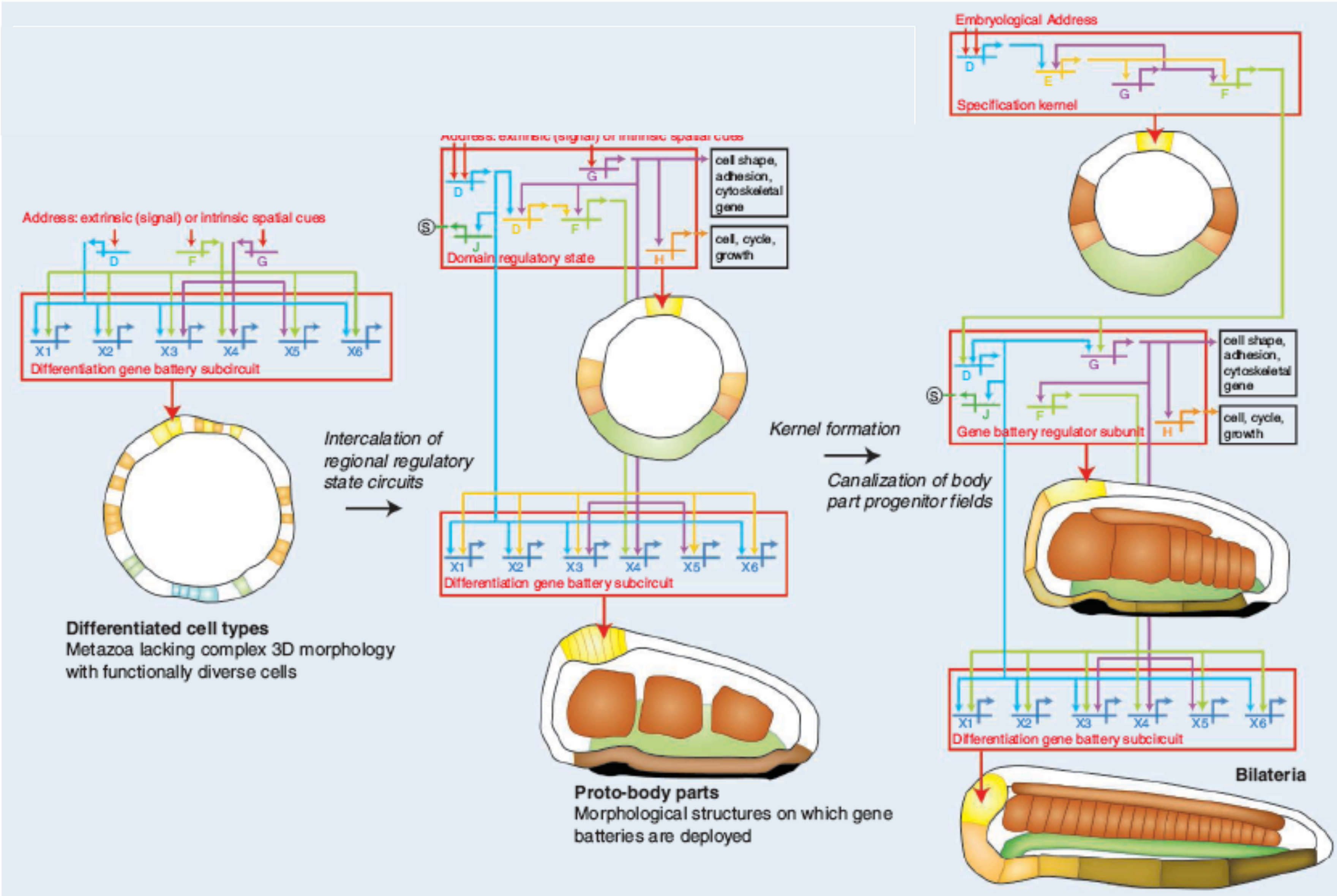
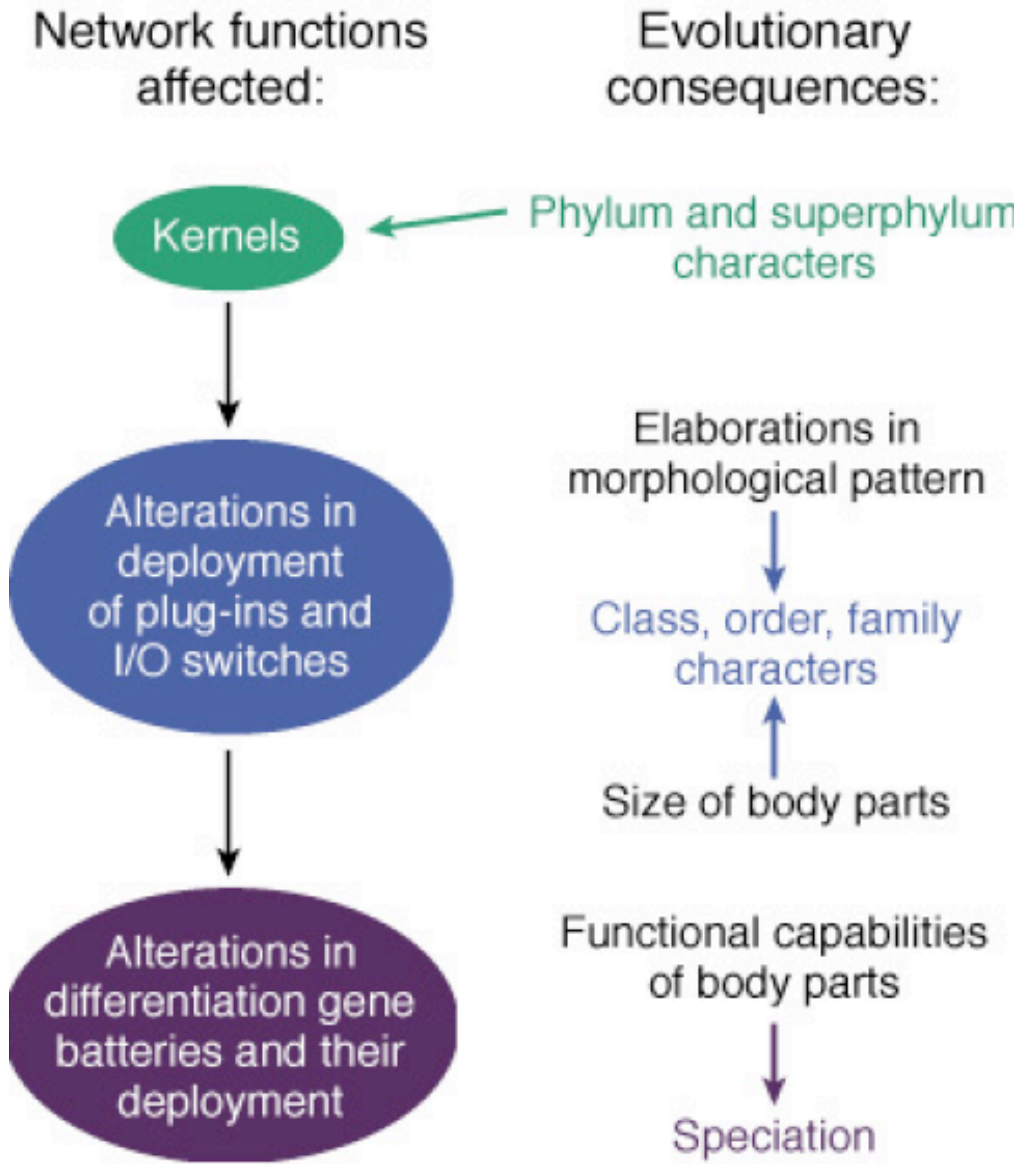
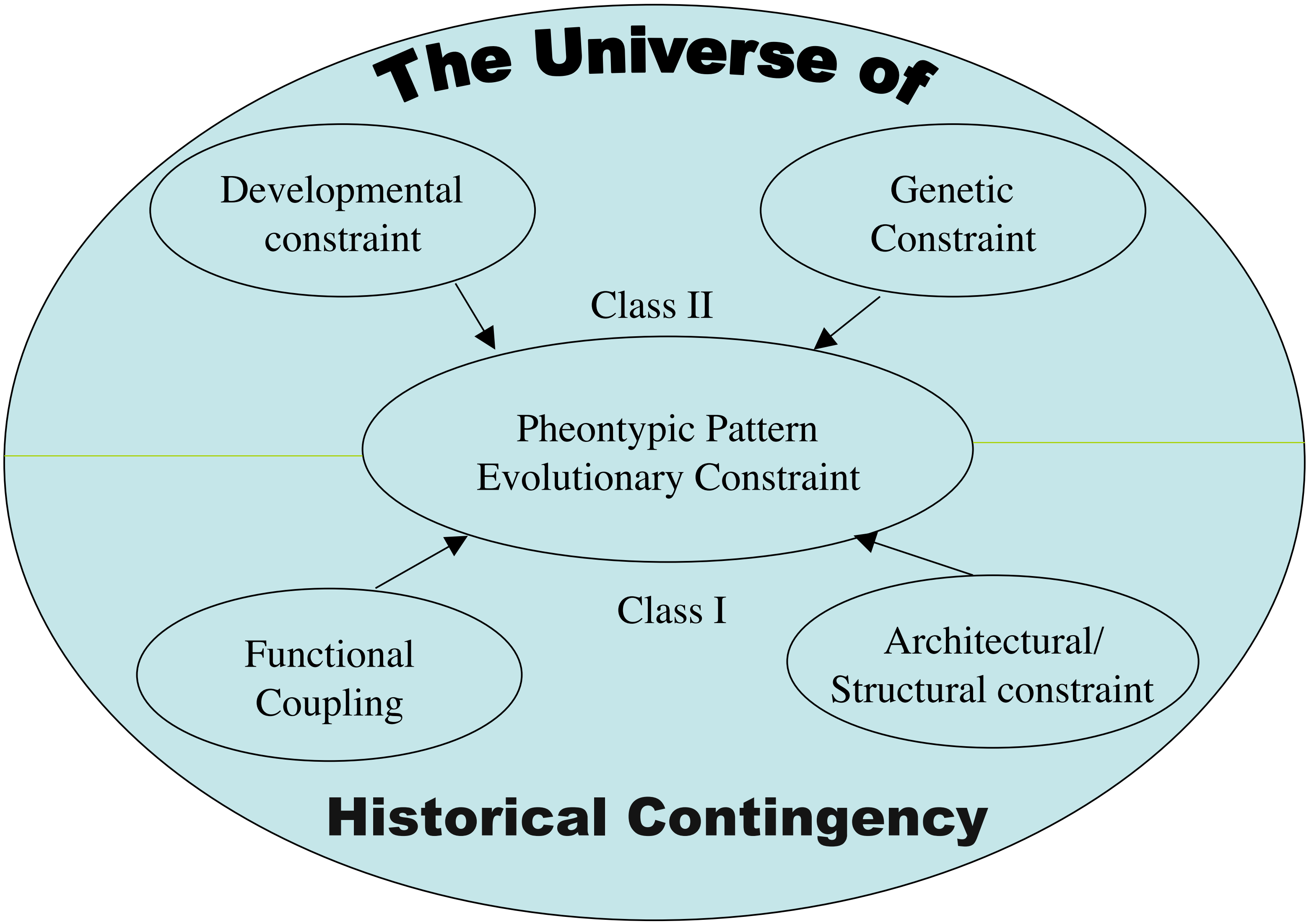
Mid
Tbx20
Tin
Doc1,2,3
Tbx5
Tin/Nkx2.5 Linkage to Pnr/Gata4
Dros
Vert
Tin
Nkx2.5
Gata6
Pnr
Gata4
Hand/Ehand, Dhand
Mcf2/Mcf2C
Doc1,2,3/Tbx4-5-6
Pnr/Gata4



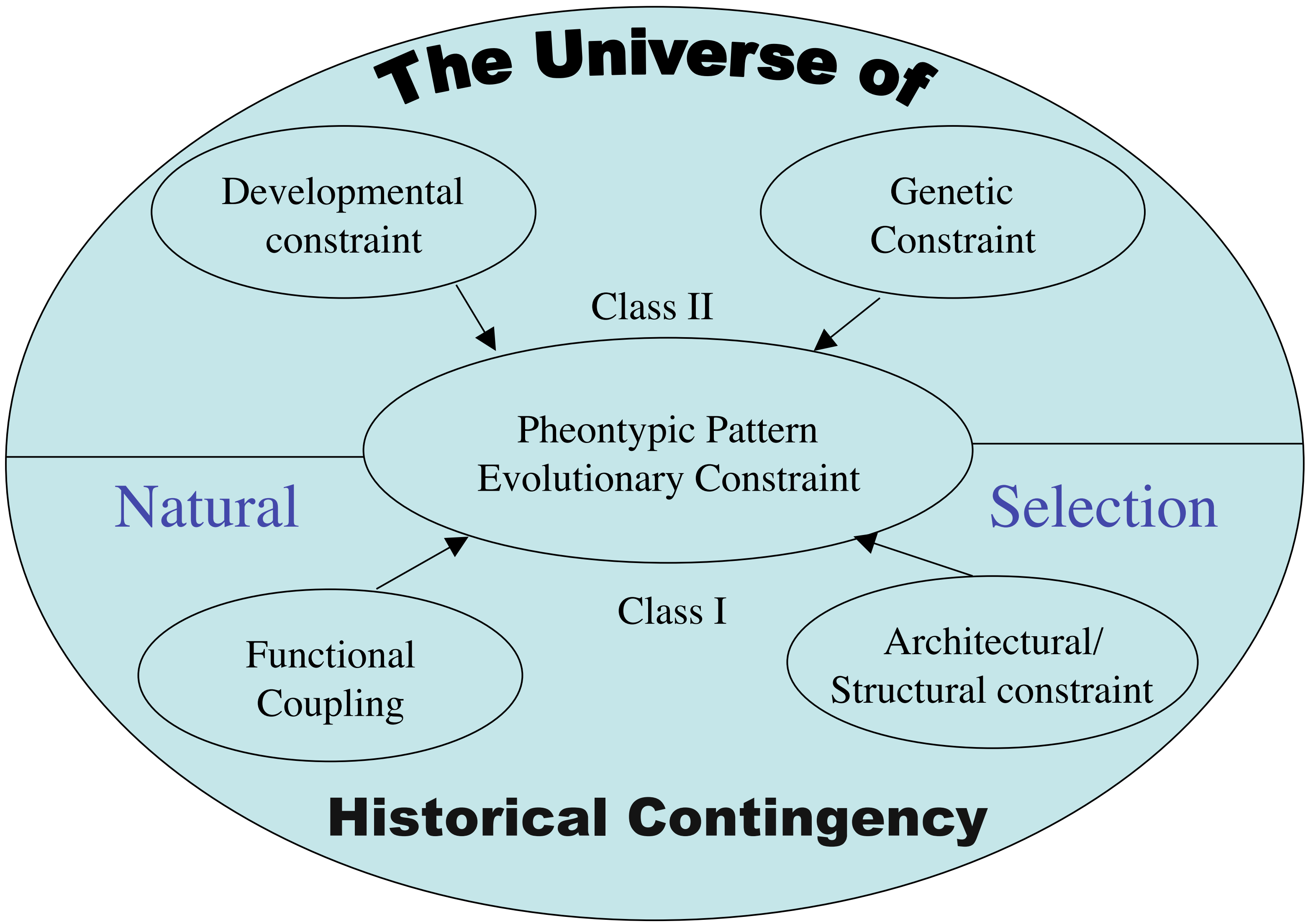
Arendt 2006 after Davidson 2006



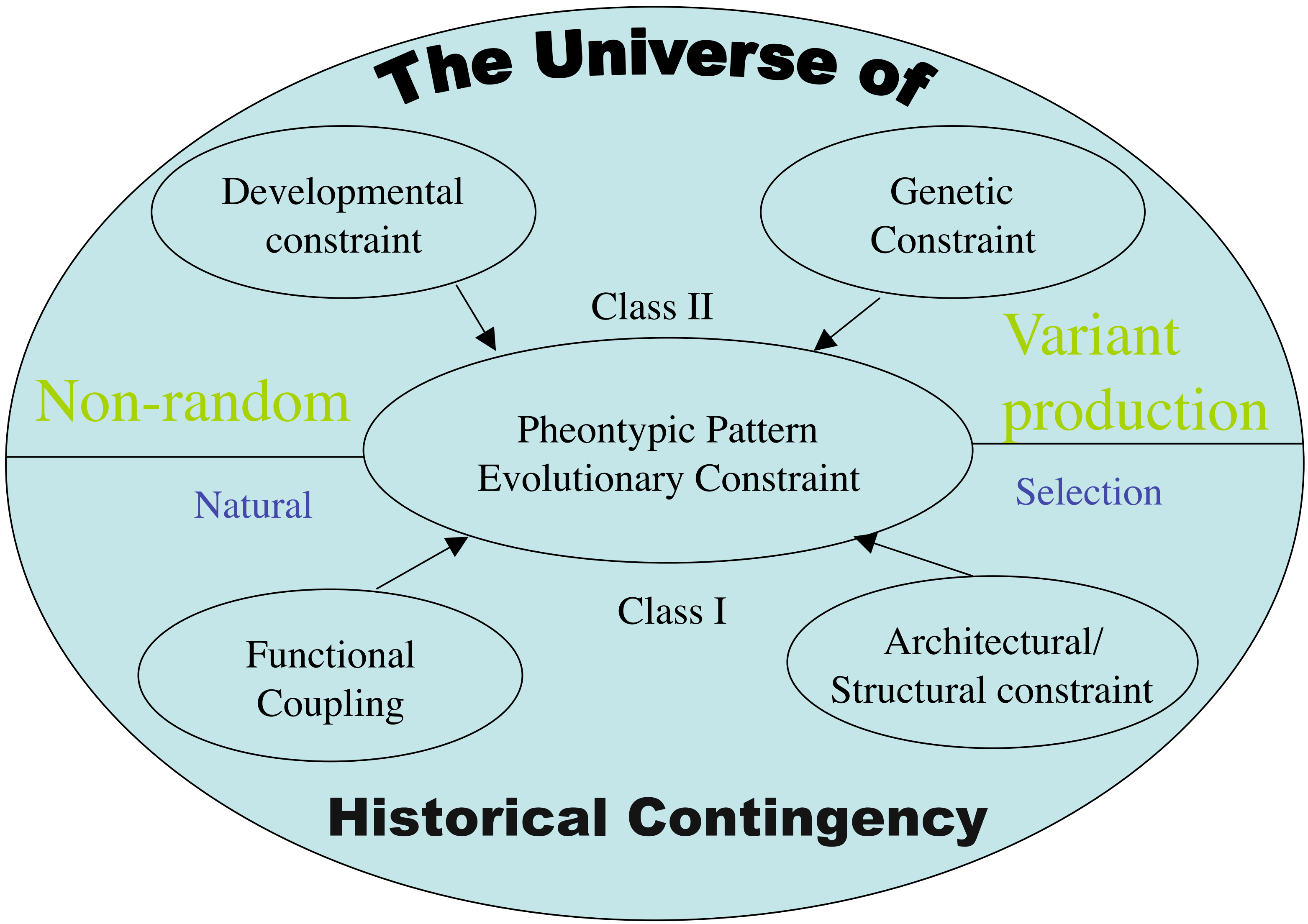
Network functions affected:
Evolutionary consequences:
Kernels
Phylum and superphylum characters
Alterations in deployment of plug-ins and I/O switches
Elaborations in morphological pattern
Class, order, family characters
Size of body parts
Alterations in differentiation gene batteries and their deployment
Functional capabilities of body parts
Speciation



Schwenk 1995



Schwenk 1995



Schwenk 1995