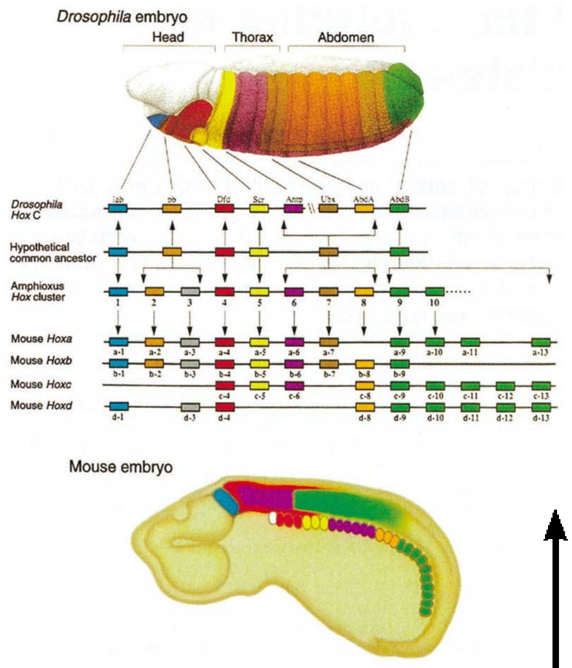
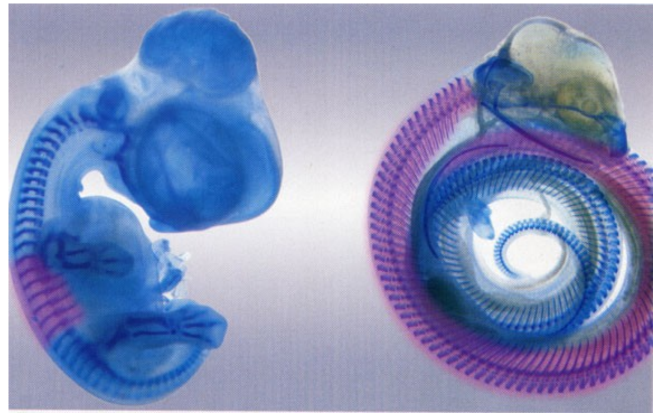
MACROEVOLUTION





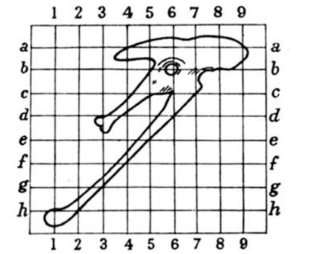


Fig. 161. Pelvis of *Archaeopteryx*.

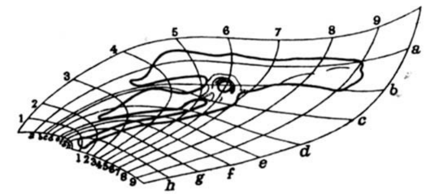
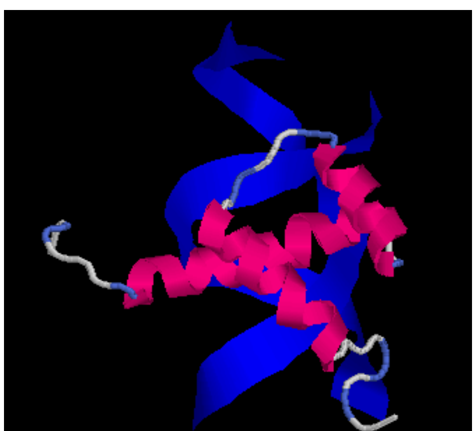
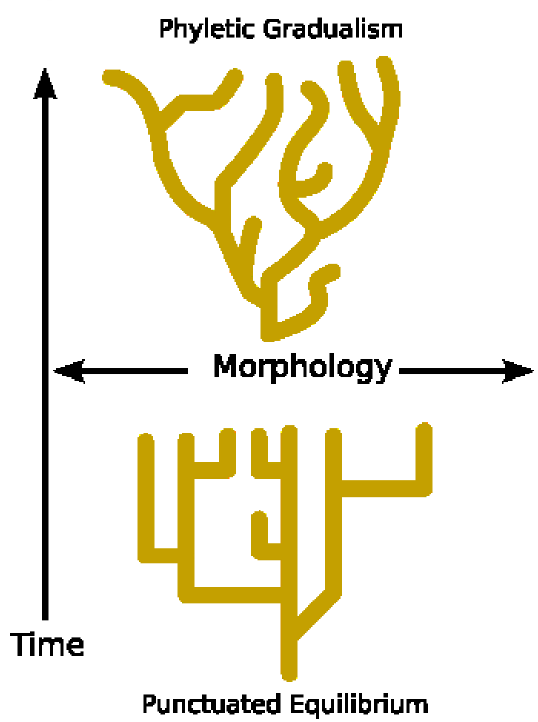
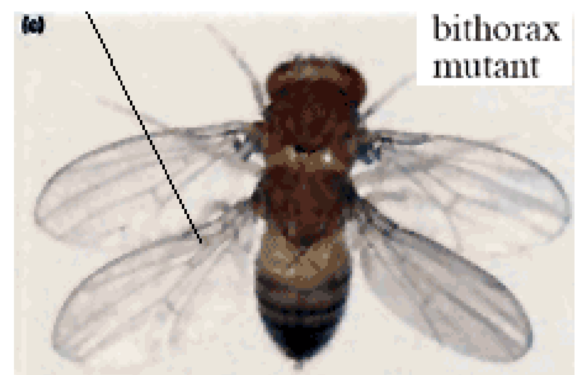


Fig. 162. Pelvis of *Apatornis*.

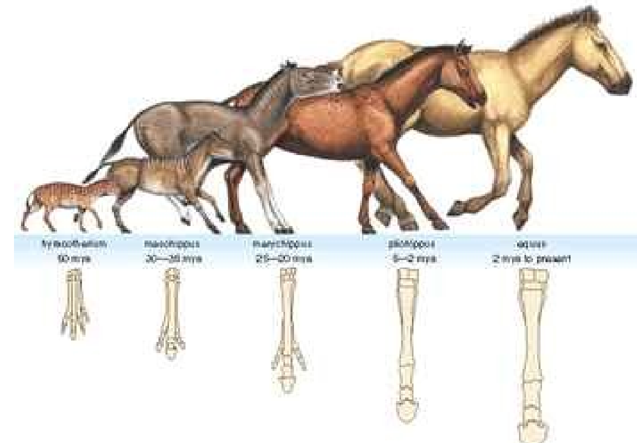






RATE OF EVOLUTION
PUNCTUATED EQUILIBRIA

Rate of evolution:



Haldane (1949)

difference between trait values in time t_2 and t_1

$$r = \frac{\ln x_2 - \ln x_1}{\Delta}$$

time interval t_2 - t_1

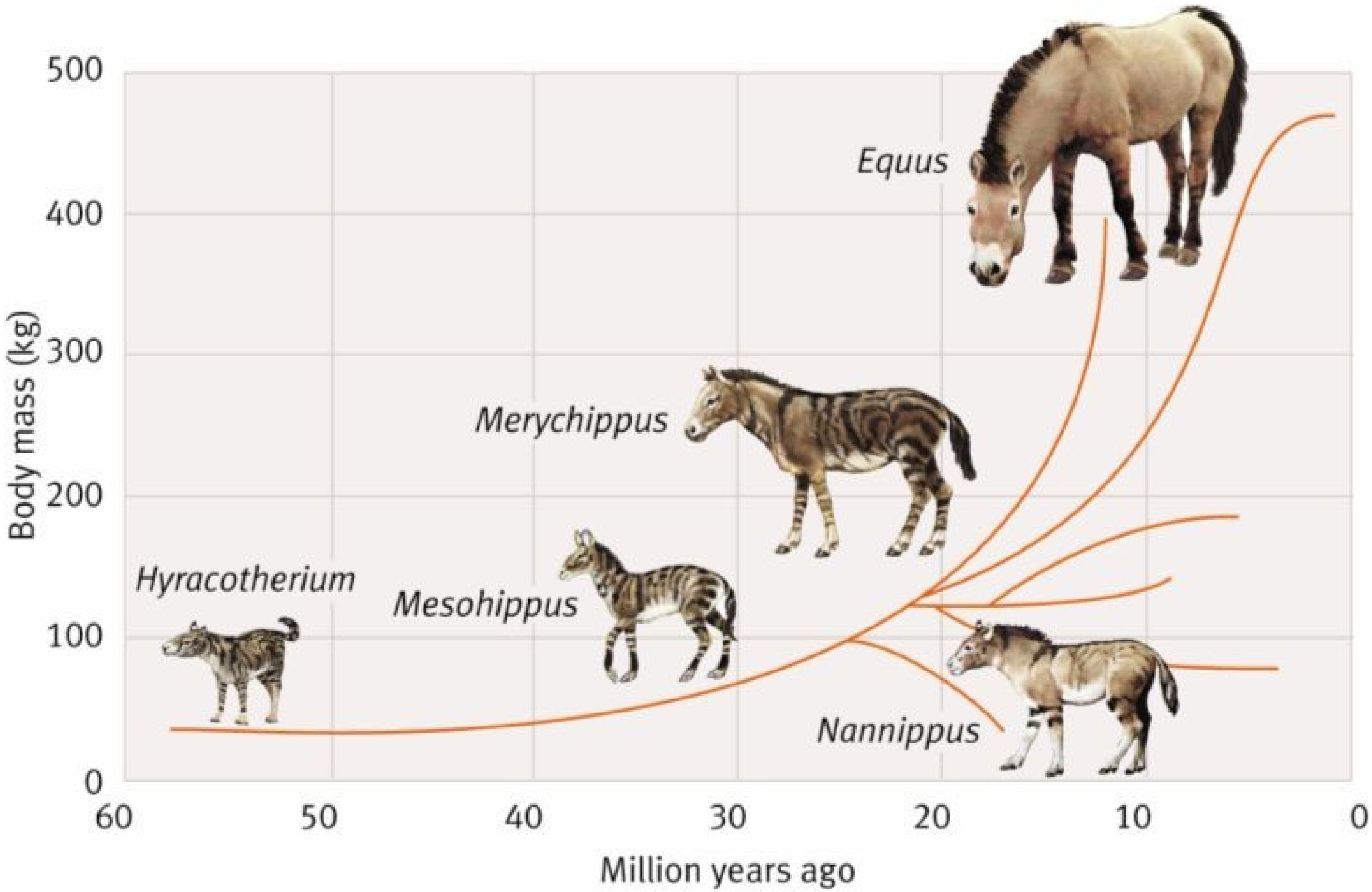
1 darwin = *e*-fold change in a trait over 1 million years

G. G. Simpson:

evoluce bradytelic (slow)

horotelic (standard, eg. horses)

tachytelic (fast)



Haldane (1949): Tertiary horses – 0.04 darwins
domestication – 10^3 darwins

Kuertén (1959): Holocene mammals – 12.6 darwins
Pleistocene mammals – 0.5 darwins
Tertiary mammals – 0.02 darwins

… differences caused by different time intervals

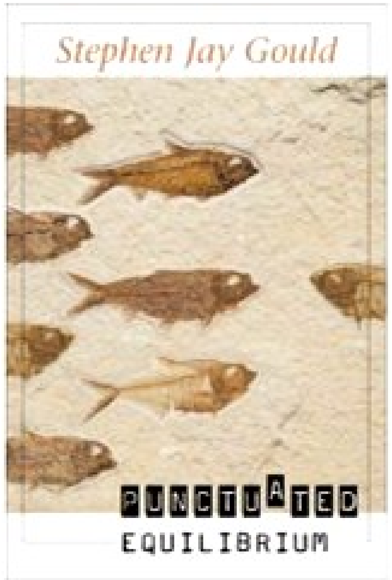
disadvantages:
1. factor *e* is not biologically natural
2. uses absolute time
3. does not take into account measured time interval
4. impossible to compare areas/volumes/linear dimensions

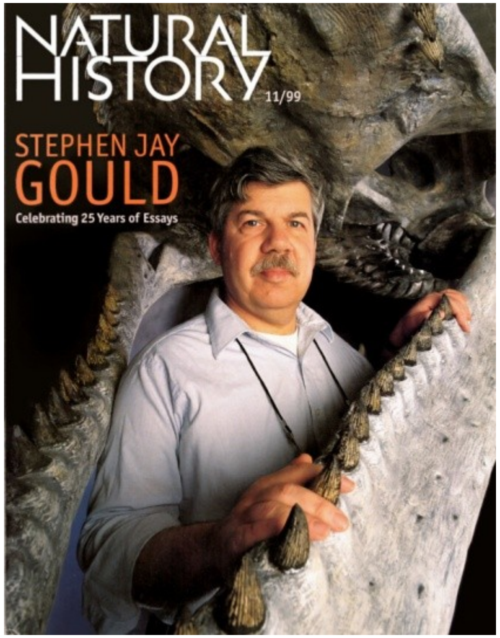
⇒ Haldane (1949), Gingerich (1993): 1 haldane = change measured in units of standard deviation per generation

Theory of punctuated equilibria:

Stephen Jay Gould, Niles Eldredge (1972)

stasis vs. rapid change

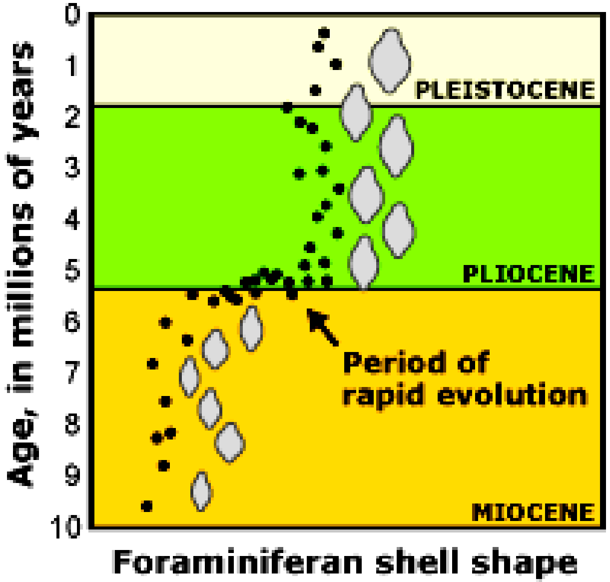


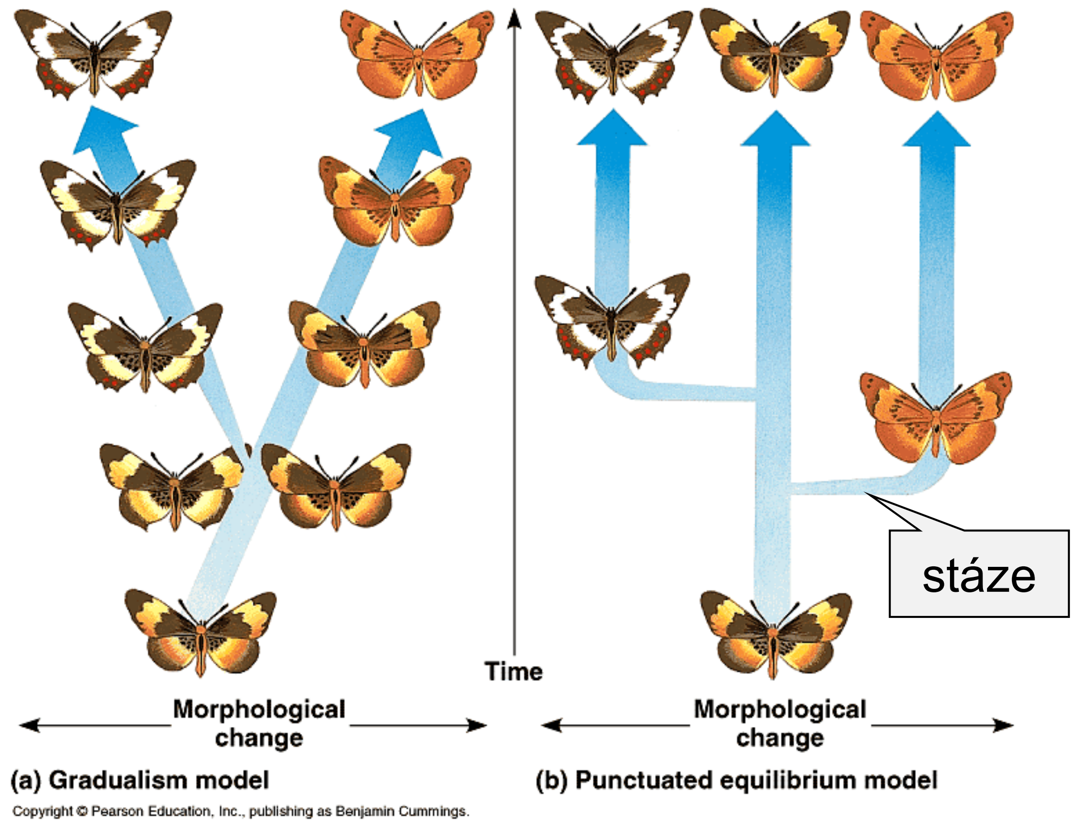


S.J. Gould

N. Eldredge

stasis vs. rapid change



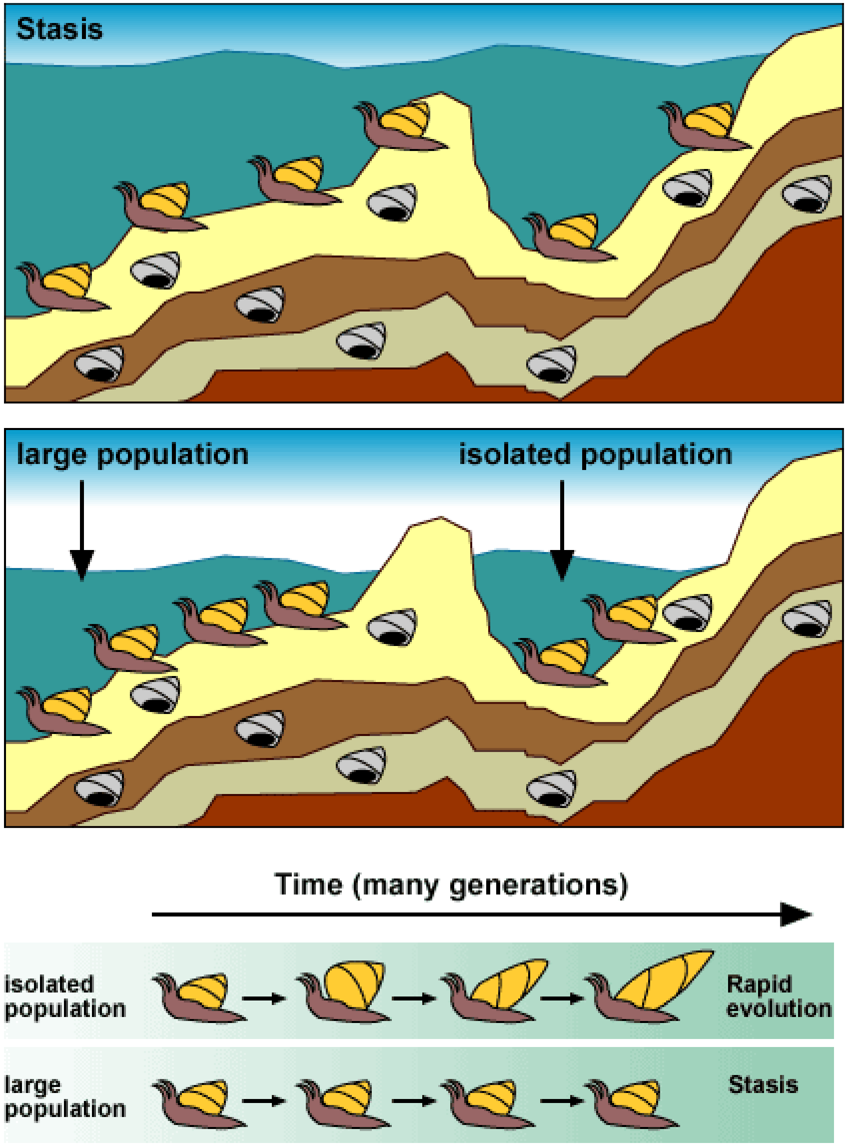


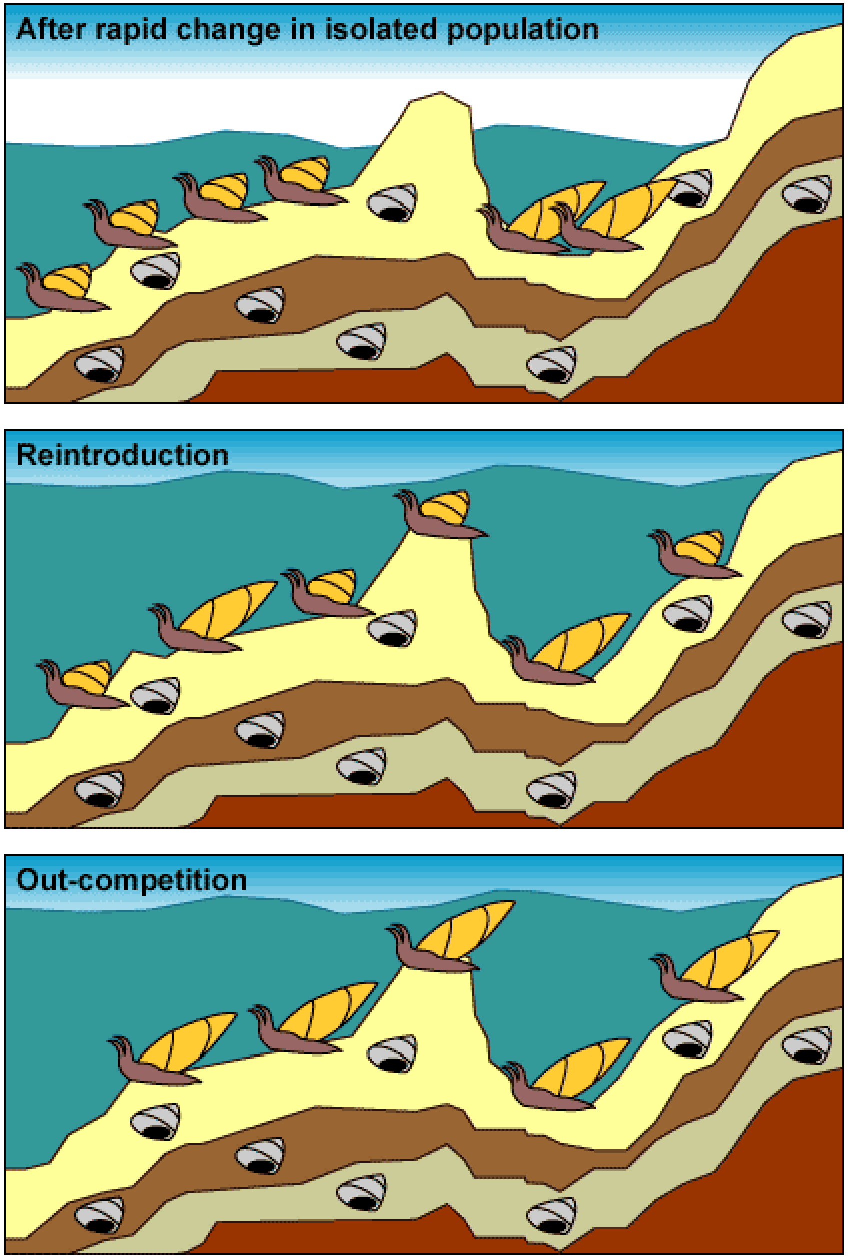
Mechanism?

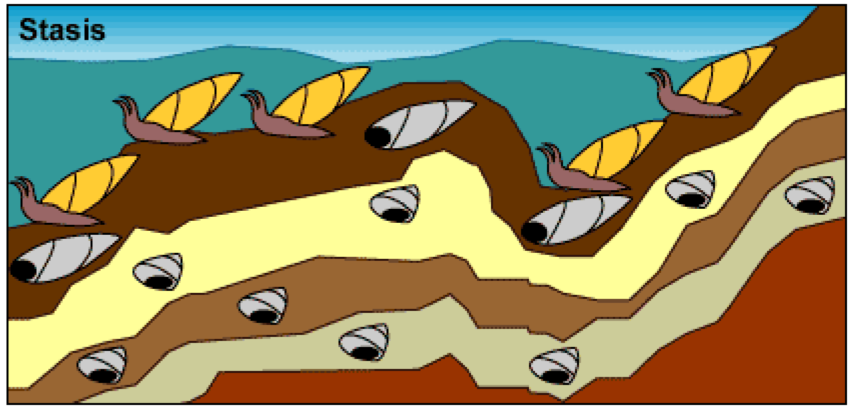
peripatric speciation

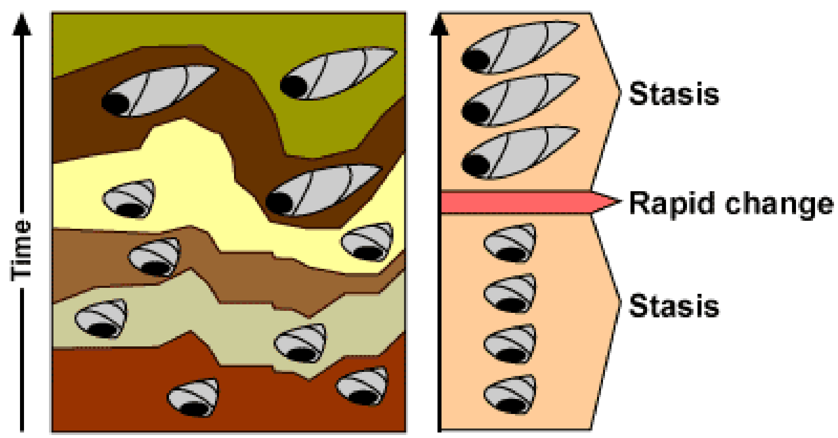
macromutation – R. Goldschmidt, *The Material Basis of Evolution* (1940): „hopeful monsters“

Peripatric speciation and punctuated equilibria

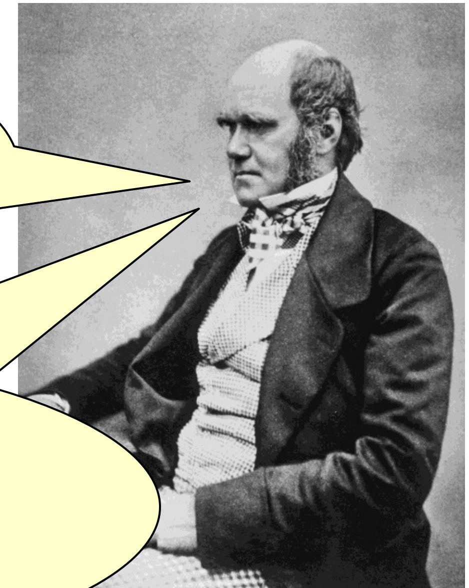



After rapid change in isolated population
Reintroduction
Out-competition

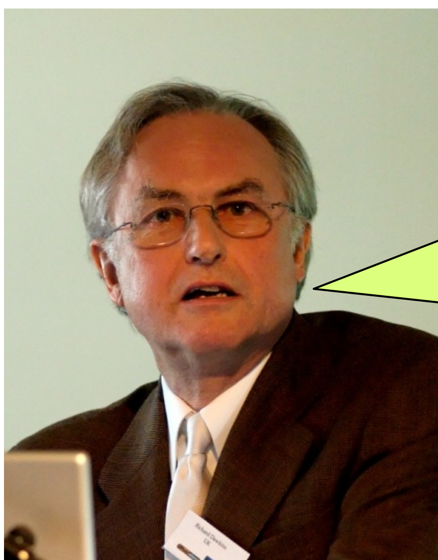

Stasis


Time
Stasis
Rapid change
Stasis

Species of different genera and classes has not changed by the same rate or to the same degree (see „living fossils“).



Periods during which species were changing were short relative to periods during which they stayed unchanged.



Except of (nonexisting) completely constant rate there is only <u>variable</u> rate – species change either in discrete steps (punctuationism) or gradually. Therefore, stasis is only an extreme case of slow evolution.

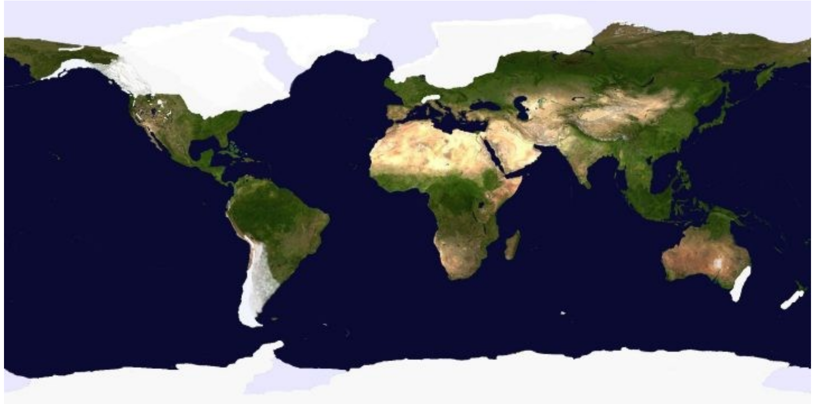
R. Dawkins: Blind watchaker

Punctuational proces typical for language evolution:
changes play an important role in periods of divergence of a new language
Bantu, Indoeuropean and Austronesian group: 10-33% differences connected with language splitting

How to explain stasis?

genetic or ontogenetic constraints

habitat tracking – glacial/interglacial cycles



short-term local divergence – rapid changes spatially limited

Relation between micro- and macroevolution

Steven M. Stanley (1975): macroevolution separated from microevolution

S.J. Gould (1980): „deposition of neo-Darwinism from the throne“, „effective death of neo-Darwinism“

Modern Synthesis narrow, extrapolationistic and reductionistic

Is macroevolution really different from microevolution?

evolution of horses

Darwin´s finches

mammal evolution

evolution as „matryoshka“

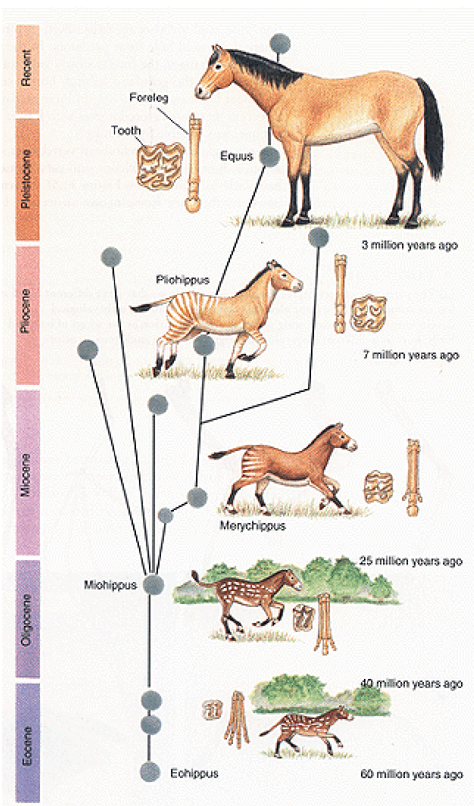
Evolution of horses:

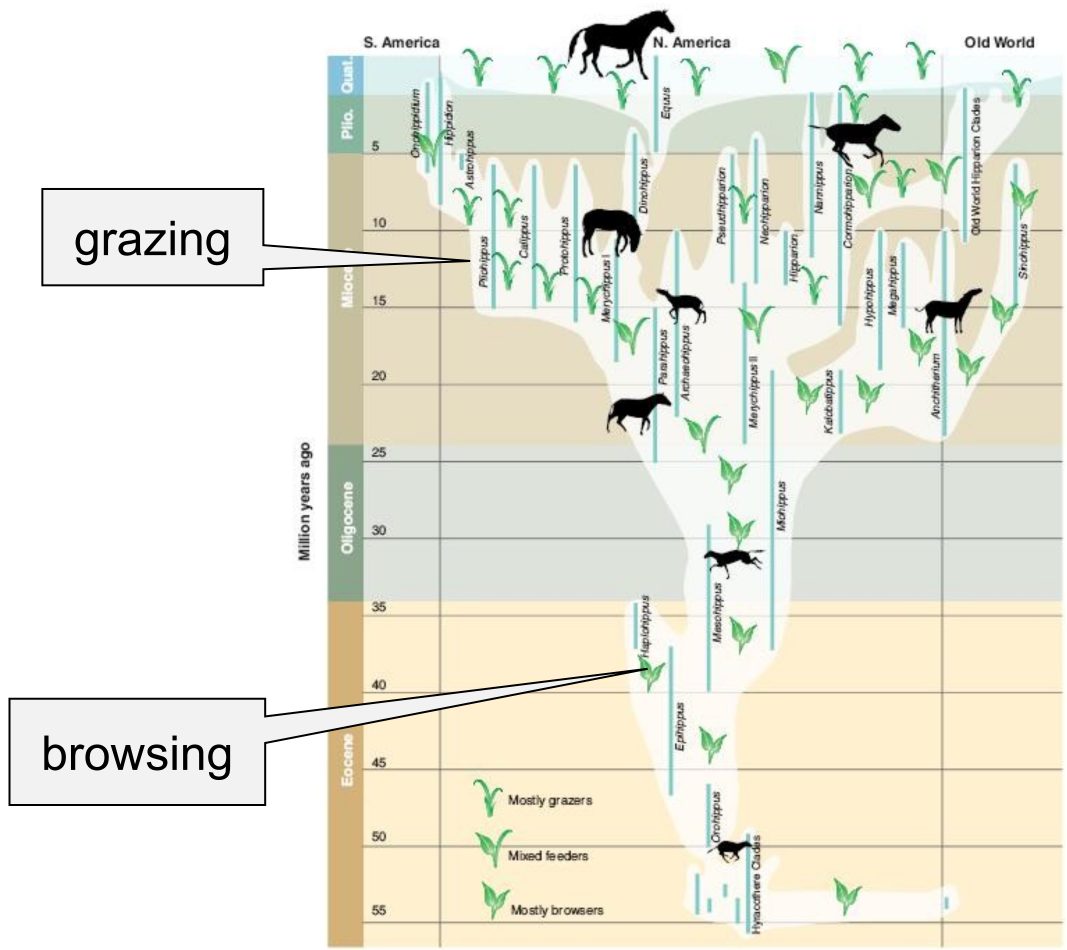
2 dental dimensions

mean rate can be explained by acting of directional selection
(sufficient 2 selective deaths/million of individuals/generation)

if $N_e < 10^4$ individuals, can be explained by drift alone

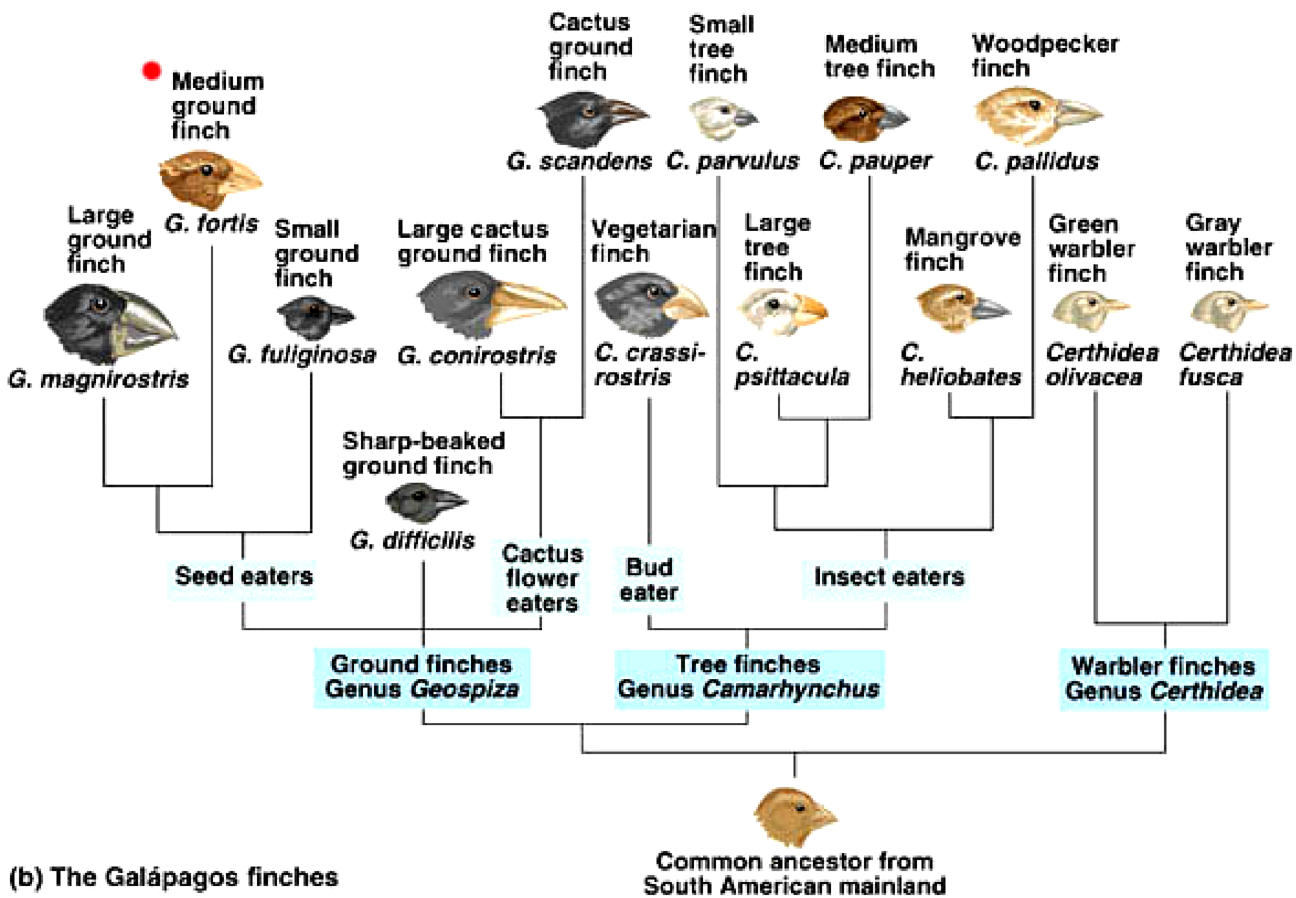
likewise also other fossils





Darwin´s finches:

with known age of Galapágos enough time for diversification to 14 species (in fact more complicated – reversions, possible extinction of some species)

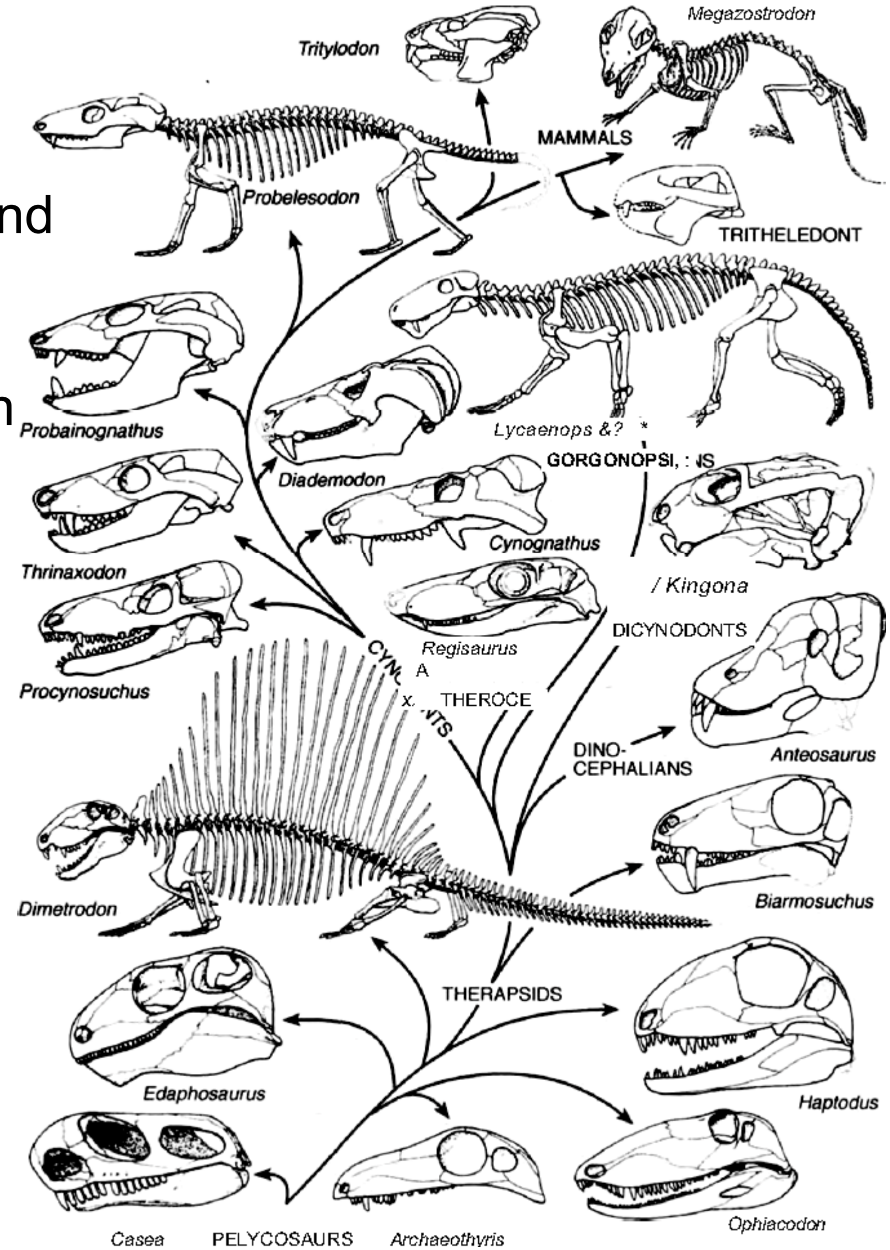


(b) The Galápagos finches

Evolution of mammals from therapsid reptiles:

changes gradual

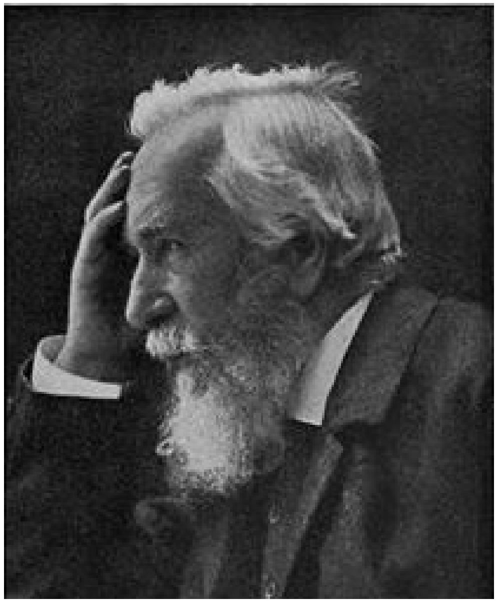
large differences between reptiles and mammals are adaptive in individual links $\Rightarrow$ same mechanisms as in microevolution



Relation of macroevolution and ontogeny

J. F. Meckel, E. Serres: embryos display traits of embryos of species preceding on the *Scala Naturae*

Ernst Haeckel – biogenetic law (= recapitulation l.): ontogeny recapitulates phylogeny (eg. gills during mammal embryonal development)



RECAPITULATION IN MAN (?)

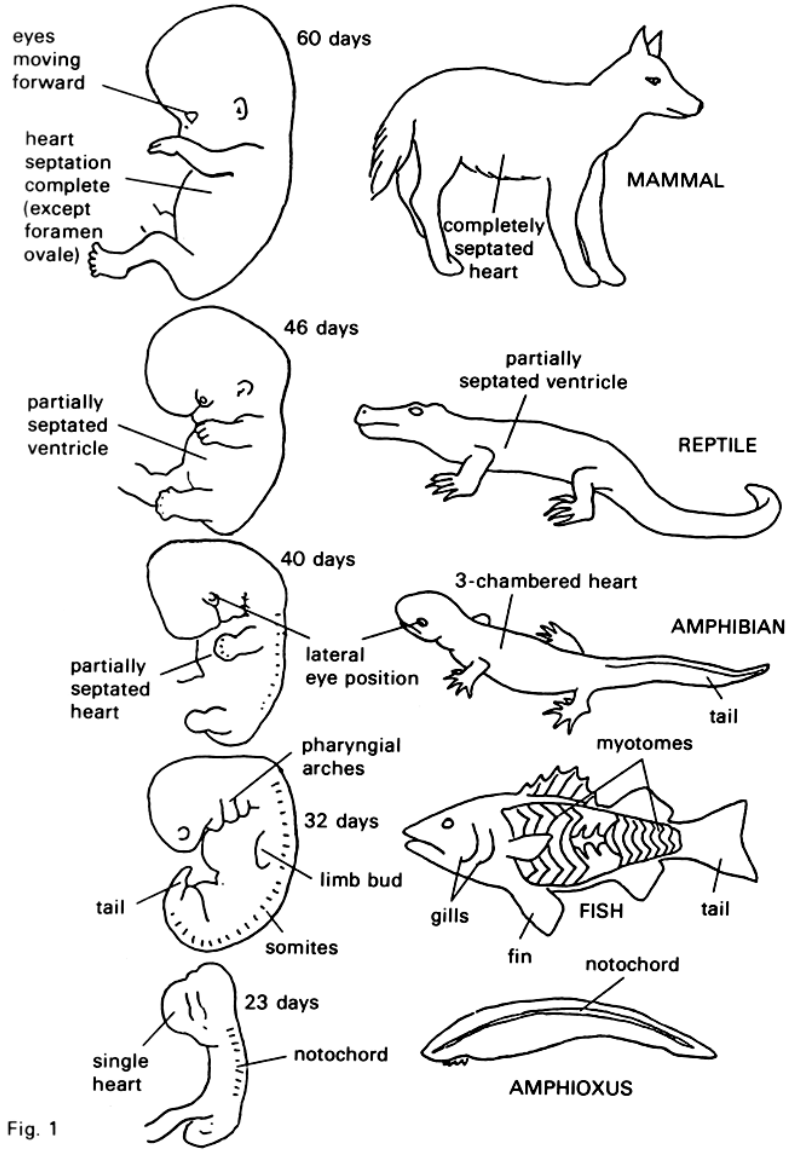
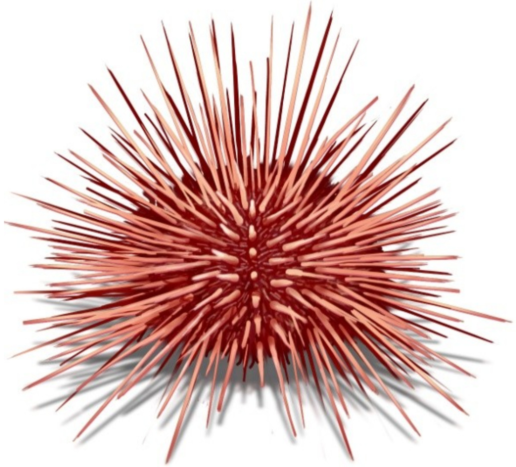
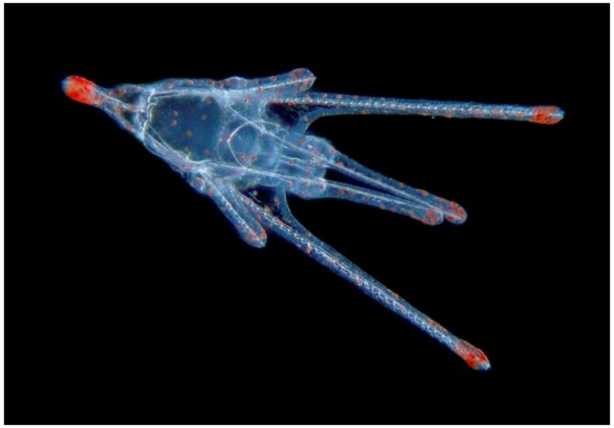


Fig. 1

× specialized larval forms (= non-terminal addition): zoëa of crabs, Müller´s larva of echinoderms, caterpillar of butterflies etc.

terminal vs. non-terminal addition

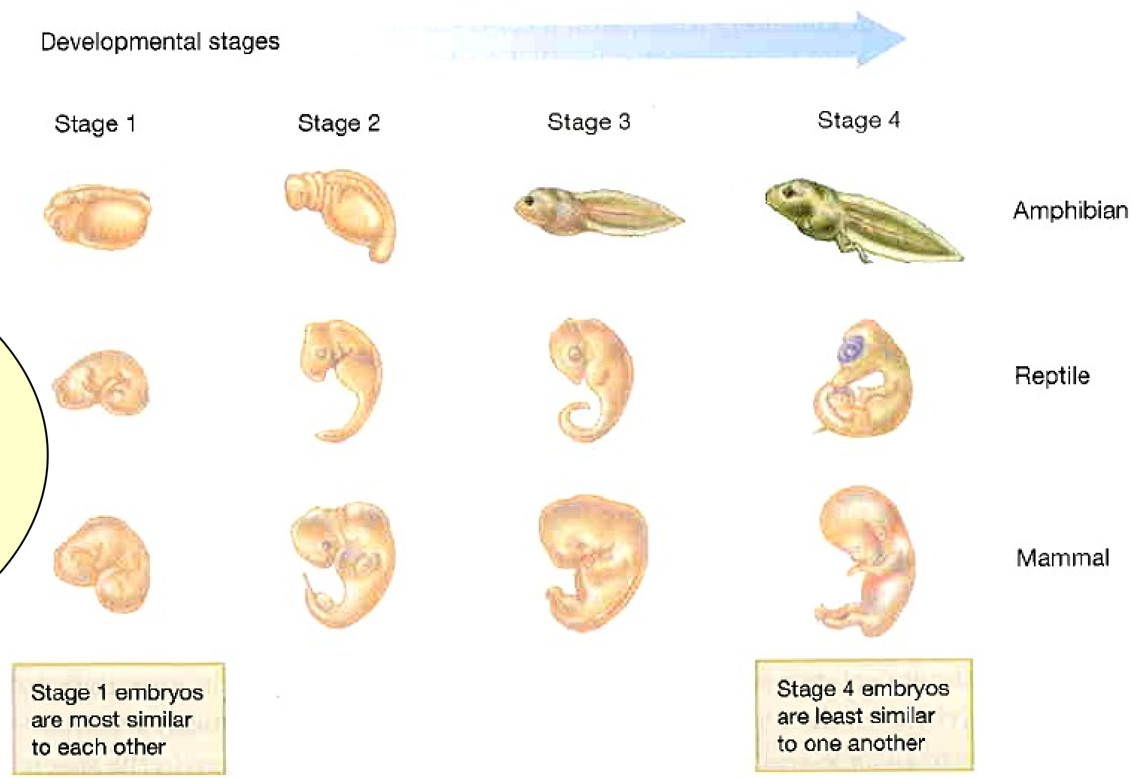




Karl Ernst von Baer – embryological laws:

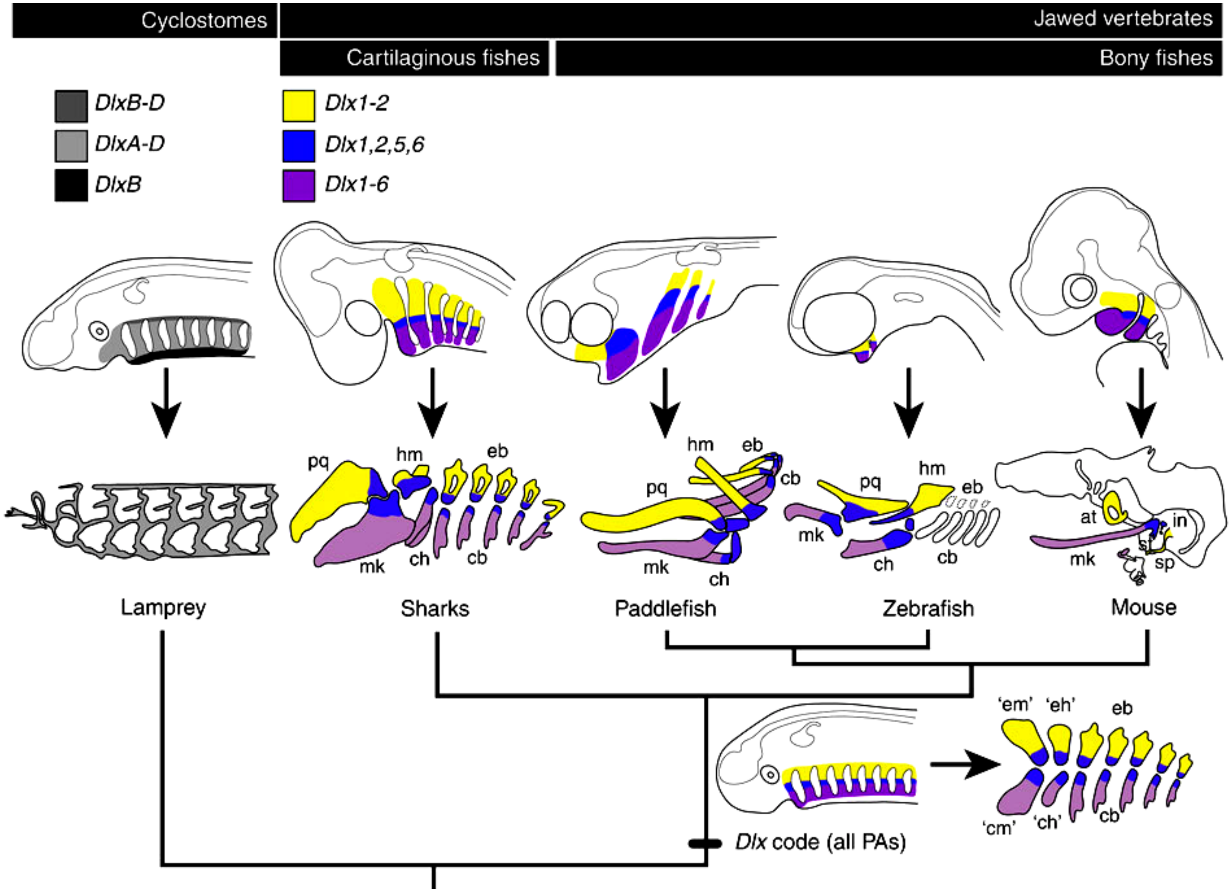
Vertebrate embryos pass through stable stages during their development which are not identical to any animals species.

Embryos of related species are similar to each other and dissimilar to adults of ancestral species.



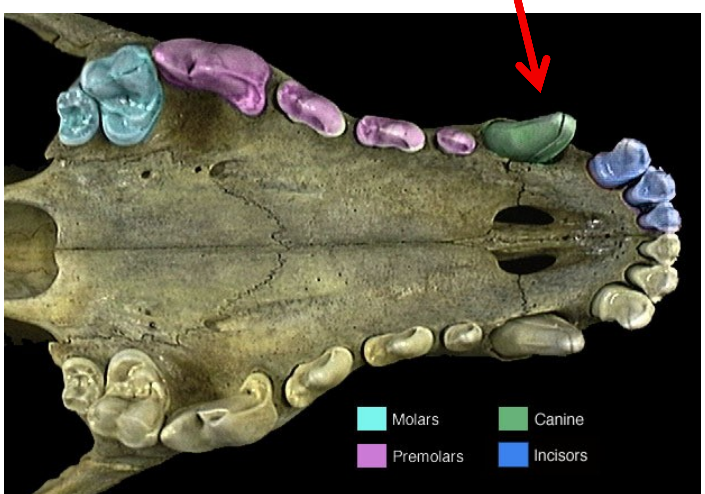
Karl Ernst von Baer – embryological laws:

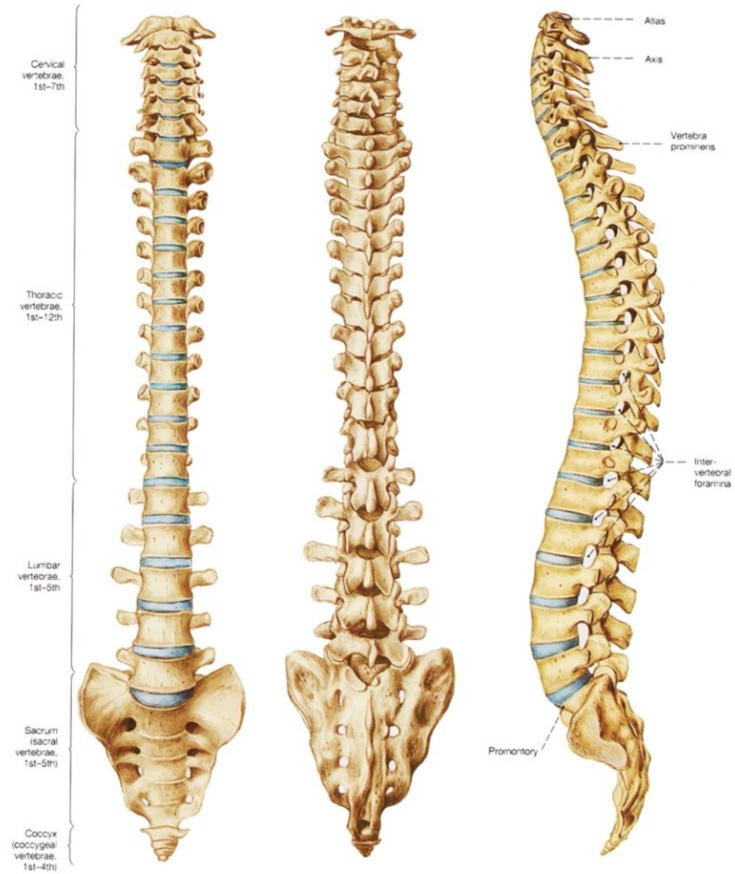
1st law: General traits of a large animal group appear in the embryo earlier than special traits (eg. cartilage in bony fishes).



General principles of ontogeny and evolution:

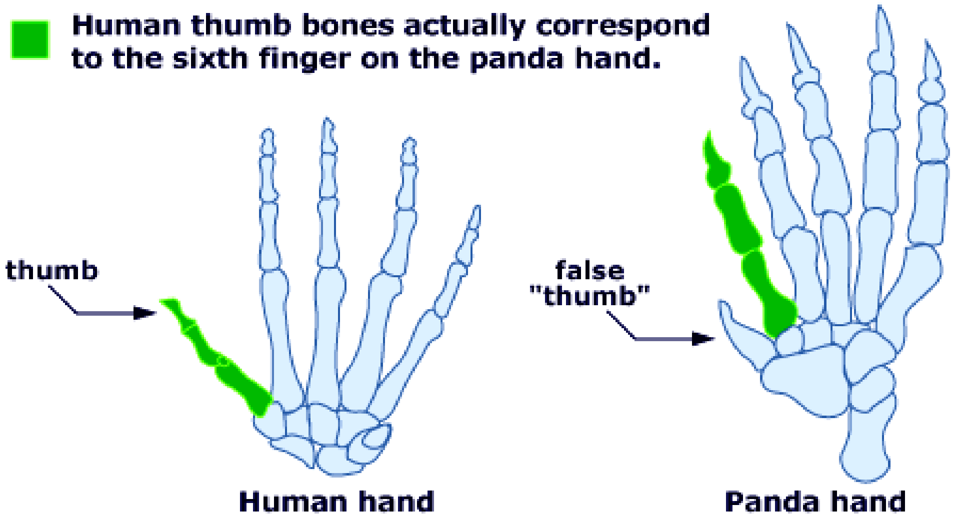
modularization and individualization: serial homology and homonymy

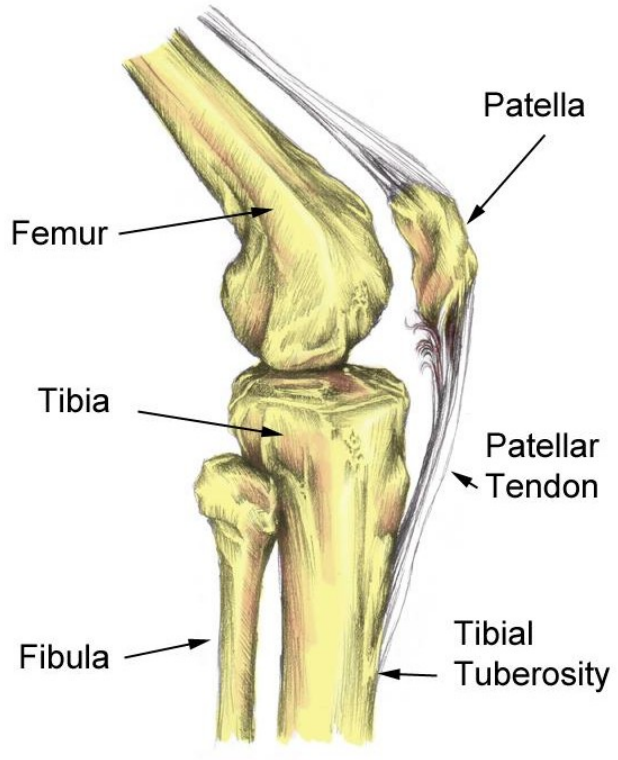




General principles of ontogeny and evolution:

heterotopy = change of the position of a trait phenotypic expression (eg. photosynthesis in succulent stem; sesamoid bones – *patella*, ossified tendons in dinosaur tails, „panda´s thumb“)



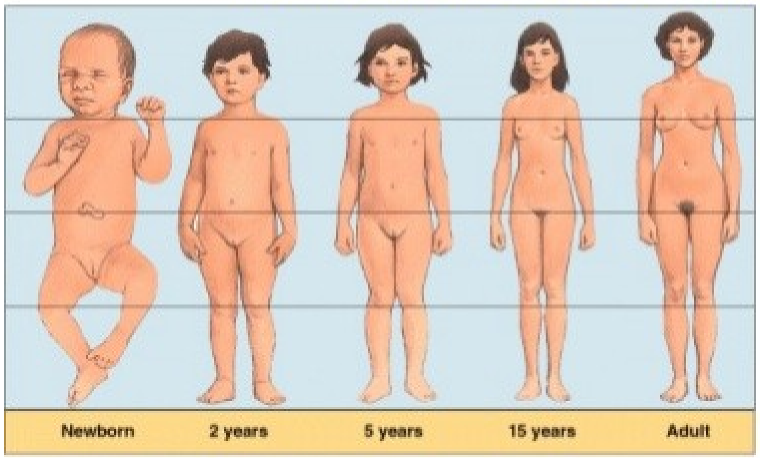


General principles of ontogeny and evolution:

heterochrony and allometry

Heterochrony

http://www.bio.miami.edu/dana/dox/heterochrony.html



Allometric Growth
Differential growth in organs and body parts

Paedomorphy
Retention of juvenile structures

Heterochrony:

		Somatic traits	Reproductive org.
peramophosis			
paedomorphosis			

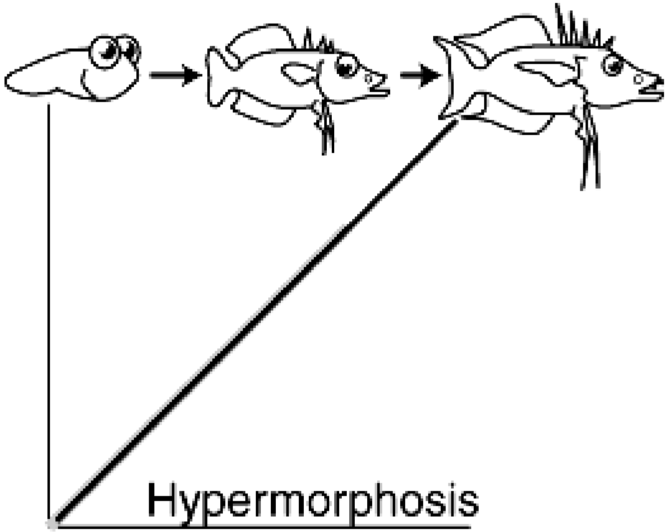
= change of timing of ontogenetic events:

1. speed of the process

2. timing of the process

Heterochronie:

		Somatic traits	Reproductive org.
peramorphosis	hypermorphosis	--	deceleration
	acceleration	acceleration	--
paedomorphosis			

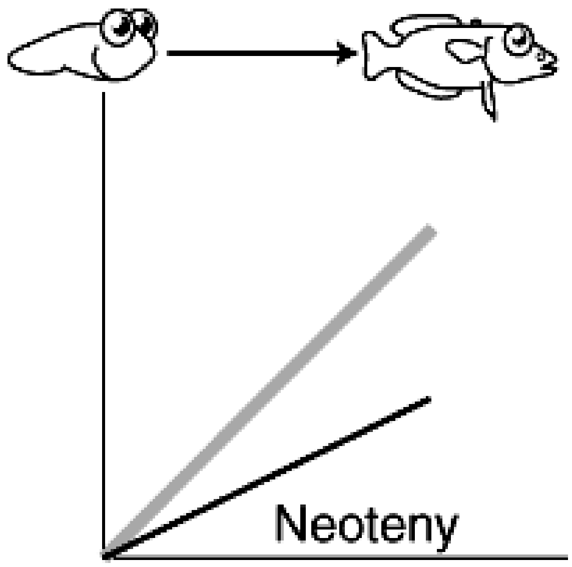


hypermorphosis

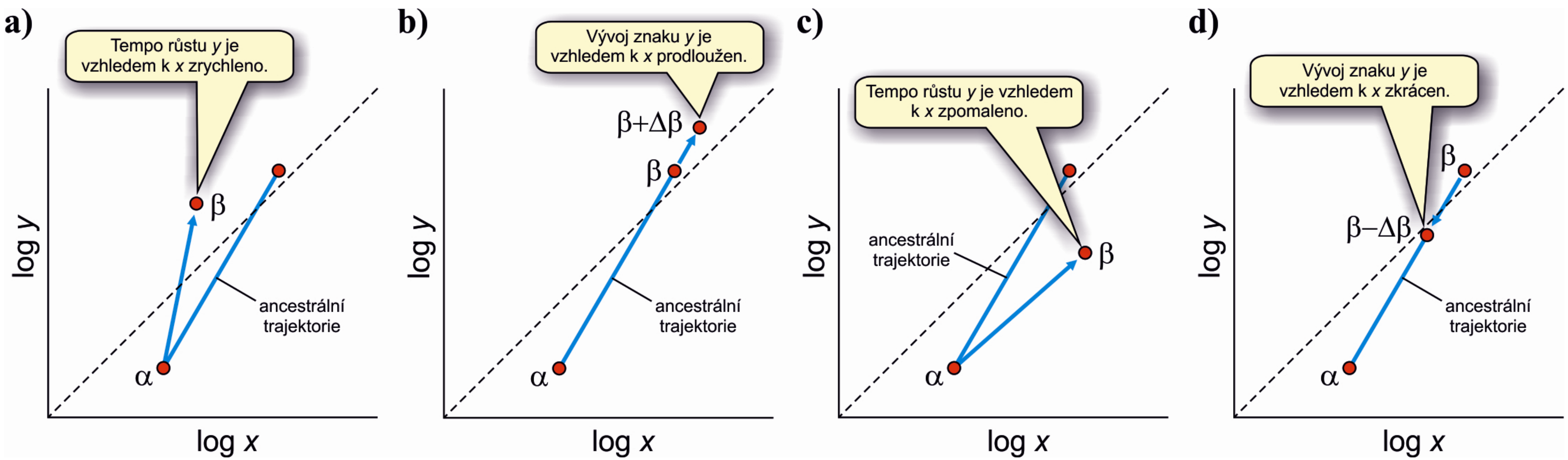
Megaceros giganteus

Heterochrony:

		Somatic traits	Reproductive org.
peramorphosis	hypermorphosis	--	deceleration
	acceleration	acceleration	--
paedomorphosis	progenesis	--	acceleration
	neoteny	deceleration	--



Heterochrony and allometry:



acceleration → peramorphosis

hypermorphosis → peramorphosis

neoteny → paedomorphosis

progenesis → paedomorphosis

neoteny:

Ambystoma mexicanum

LETTER

doi:10.1038/nature11146

Birds have paedomorphic dinosaur skulls

Bhart-Anjan S. Bhullar[1], Jesús Marugán-Lobón[2], Fernando Racimo[1], Gabe S. Bever[3], Timothy B. Rowe[4], Mark A. Norell[5] & Arhat Abzhanov[1]

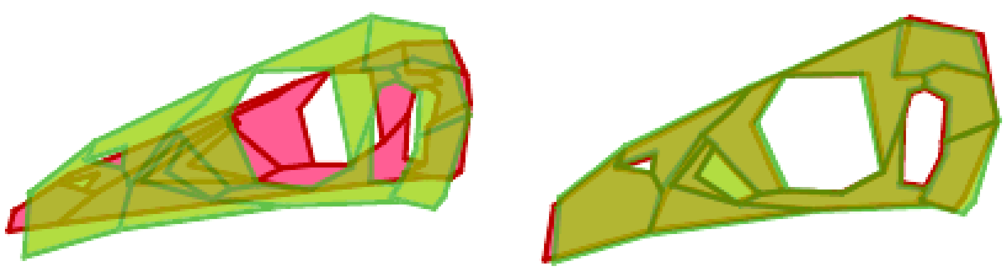
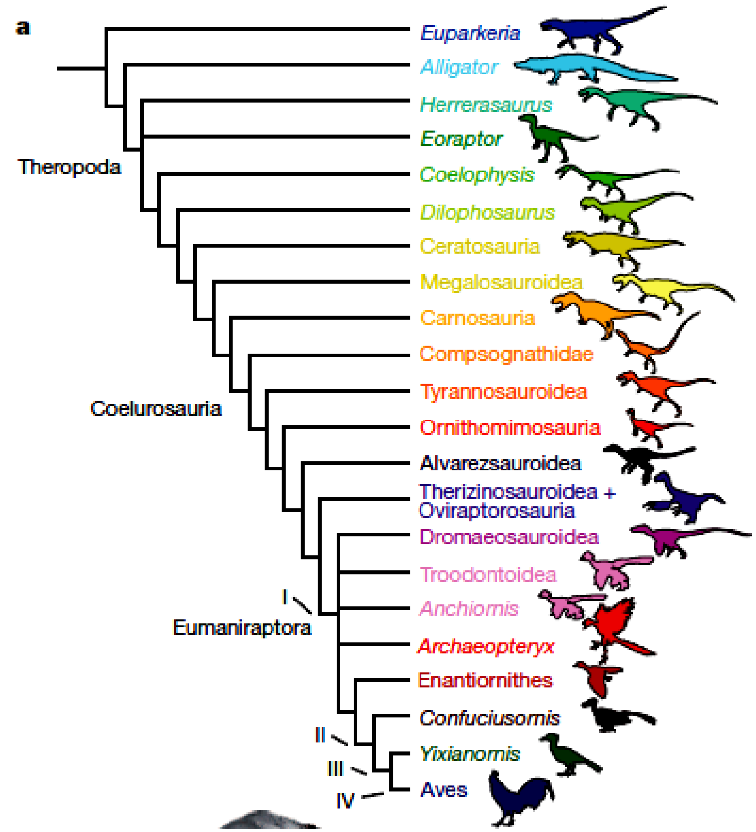


Figure 4 | Similarity of embryonic *Alligator* and adult *Confuciusornis* skulls. Superimposition of *Alligator* embryo skull (green) onto *Alligator* adult skull (red, left) and onto *Confuciusornis* adult skull (red, right), showing the nearly identical skull configuration of the latter two and indicating paedomorphic cranial morphology in *Confuciusornis*.



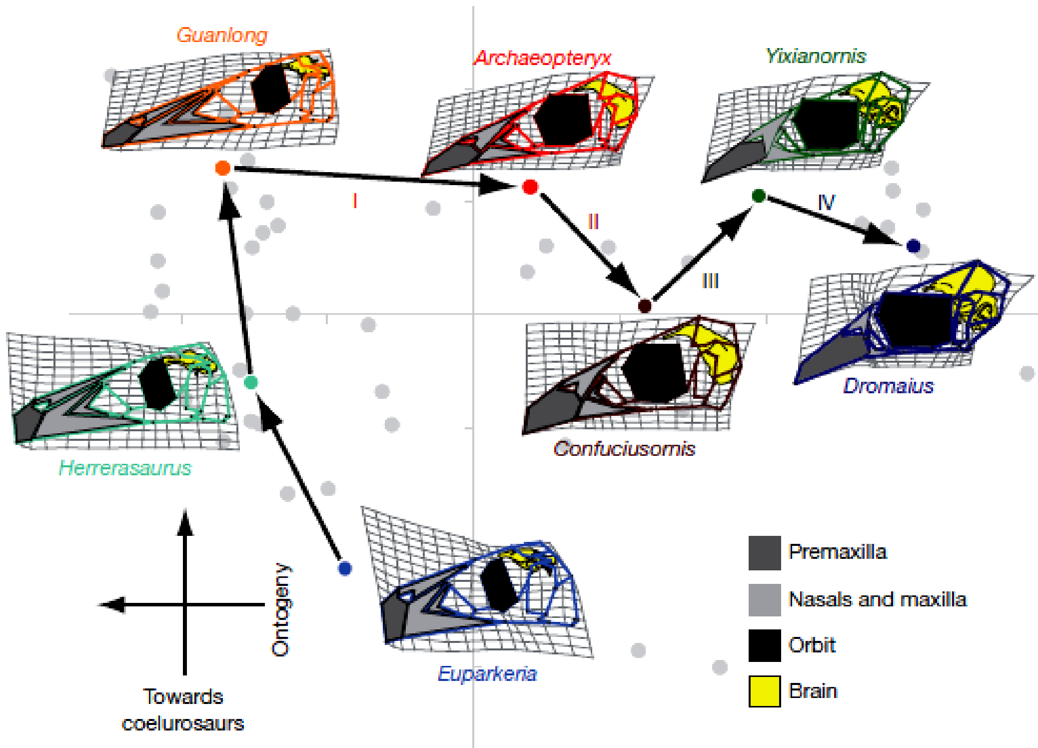
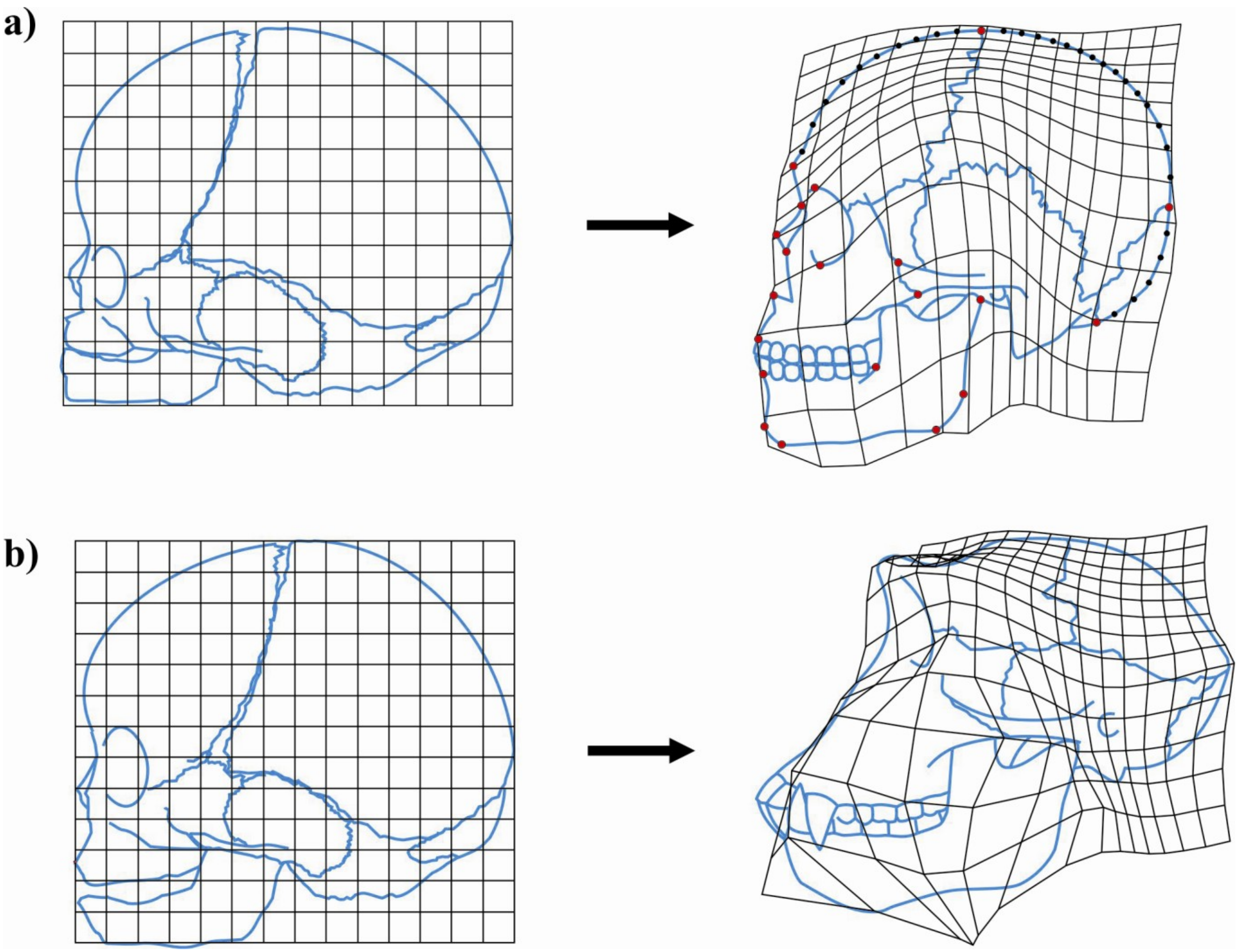


Figure 5 | Summary of heterochrony and phylogeny in bird skull evolution. A phylogenetic sequence with skull outlines set on deformation grids is depicted from the primitive stem-group archosaur *Euparkeria* to the modern emu *Dromaius*. Heterochronic transformations referred to in the text are enumerated with Roman numerals. Major anatomical regions involved in heterochronic transformations are labelled.

Neoteny in humans?



Human neotenic features compared to the chimp*) (Wikipedia):

Head:
- rounded skull
- slender cranial bones
- reduced brow ridges
- large brain
- flat face
- broadened face
- hairless face
- hairs ontop head
- large eyes
- ear shape
- small nose
- small teeth
- small upper and lower jaw

Genitals:
- absence of baculum (*os penis*)
- presence of hymen
- anteriorly oriented vagina

Limbs/posturer:
- legs longer than hands
- foot structure
- upright posture

„Naked“ body

*) some of them are not, in fact, neotenic!

Origin of macroevolutionary novelties:

change of function of a gene product:
pigment producing enzyme → change of coloration
digestive enzyme → change of sexual habits

loss of function:
genes suppressing own pathogenicity
deletion of host proteins recognized by parasites (eg. CCR5-Δ32
deletion in the *CCR5* gene → resistency to the HIV and variola
…. 5-14% of Europeans, in Africans and Asiatics rare)

changes in gene regulation

prions – incorrect translation termination ⇒ bovine spongiform encephalopathy,
scrapie of sheep and goats, kuru, Creutzfeld-Jakob disease in humans

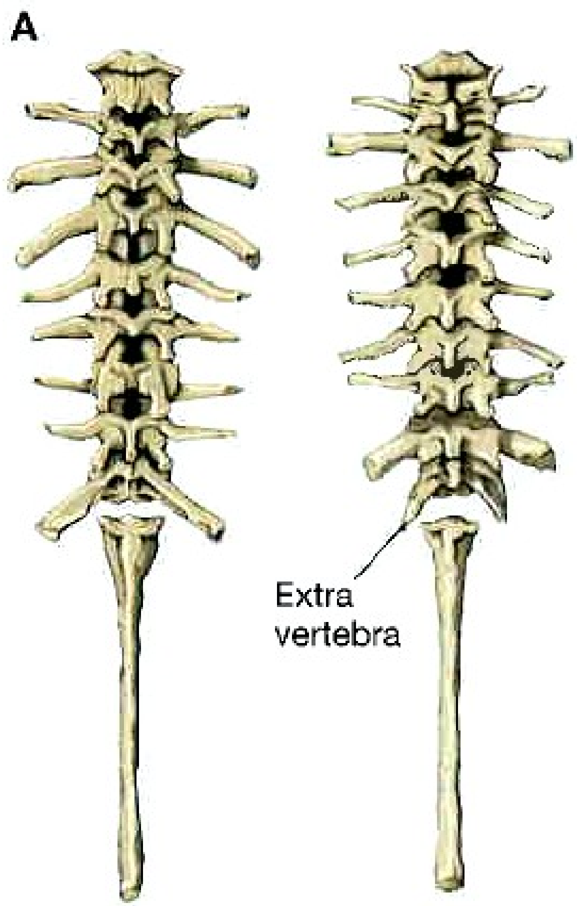
role of gene duplications – more radical changes enabled

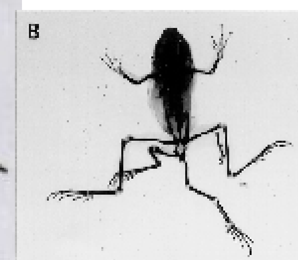
symbiosis, gene transfer (retroviruses)

homeotic genes

Homeotic (*Hox*) genes

William Bateson: „homeosis“ = anatomical changes of large extent (eg. development of an extra finger, cervical vertebra instead of thoracic, limb in ectopic position)





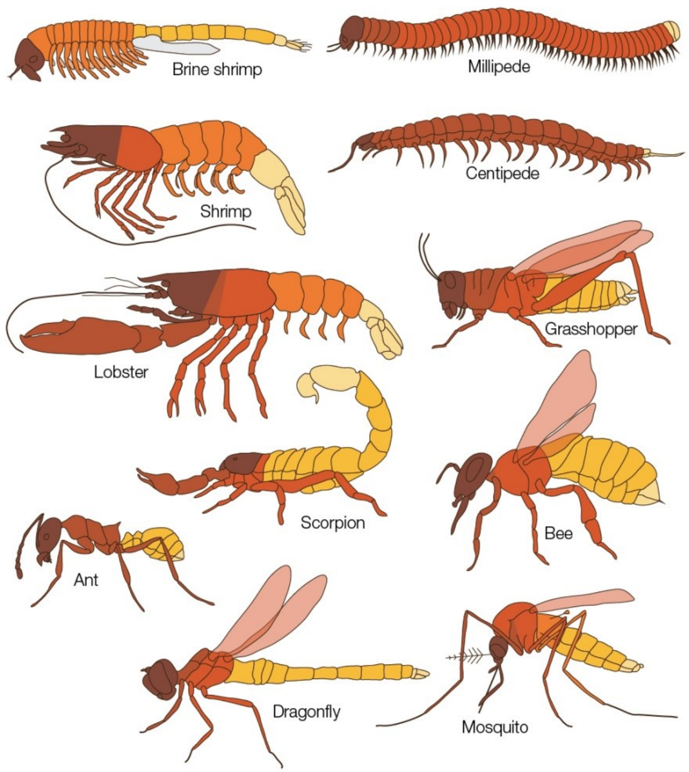
Homeotic (*Hox*) genes

Edward Lewis: homeotic genes = genes responsible for basic segmentation of multicellular animals – <u>homeotic mutations do not change the number of segments but their identity</u>

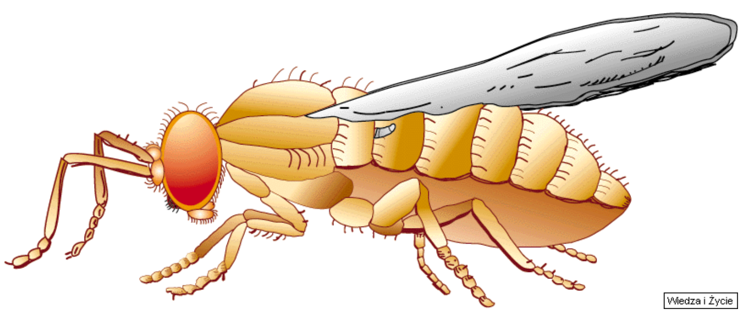
control of transcription of other genes (eg. *Ubx* probably regulates hundreds of „target“ genes)

determination of basic body segmentation

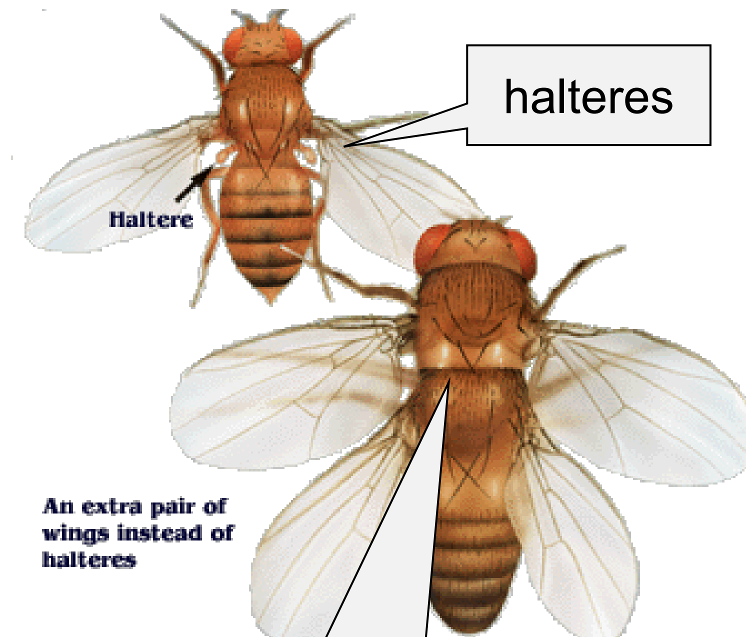
high evolutionary conservativeness



Homeotic mutation



Antennapedia



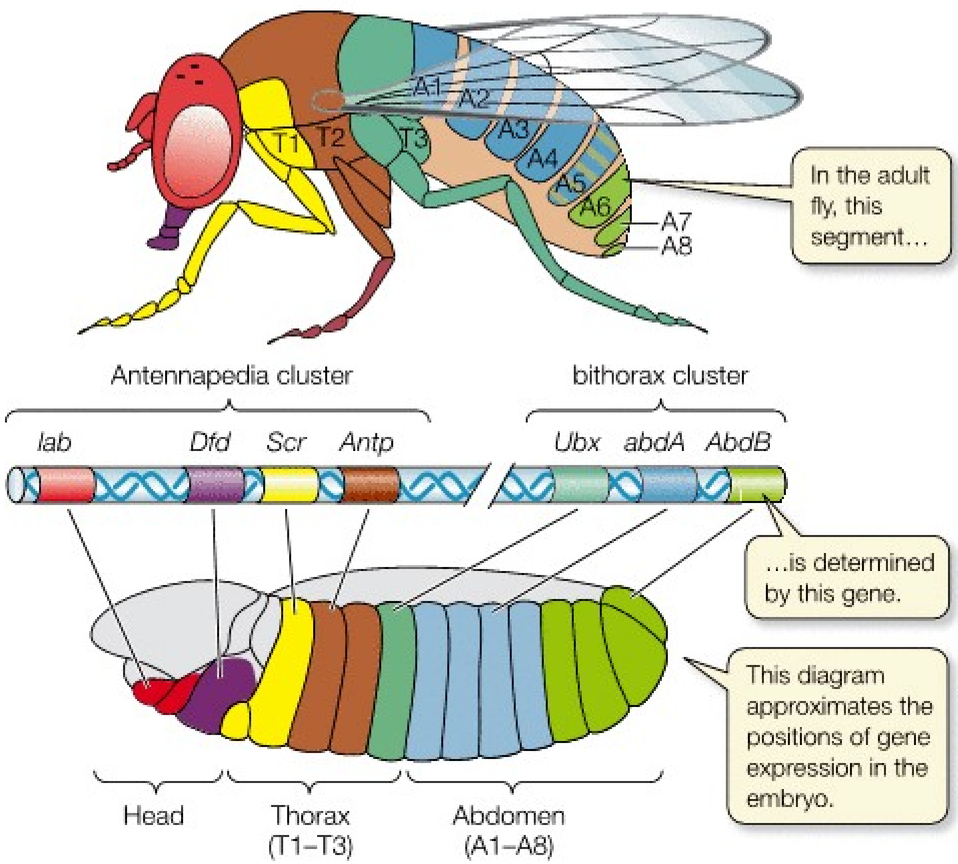
halteres

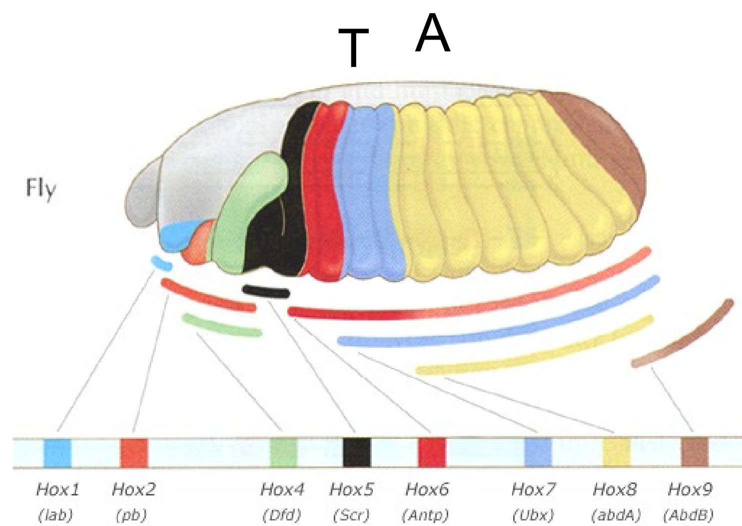
mutation of the *Ultrabithorax* gene: 3rd thoracic segment (T3) → T2

Bithorax

Hox genes: basic antero-posterior body segmentation

linear clusters, same order as the segments





Hox gene effects are overlapping

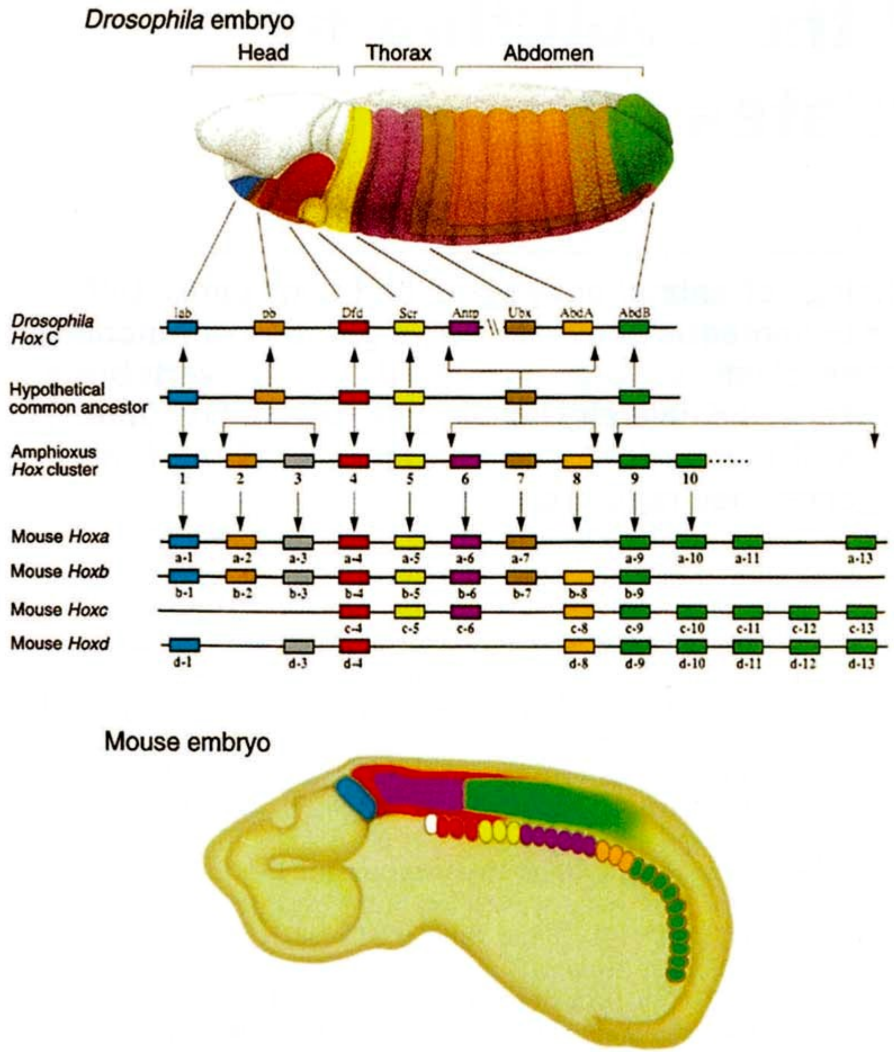
Drosophila: 1 linkage group, 2 clusters:

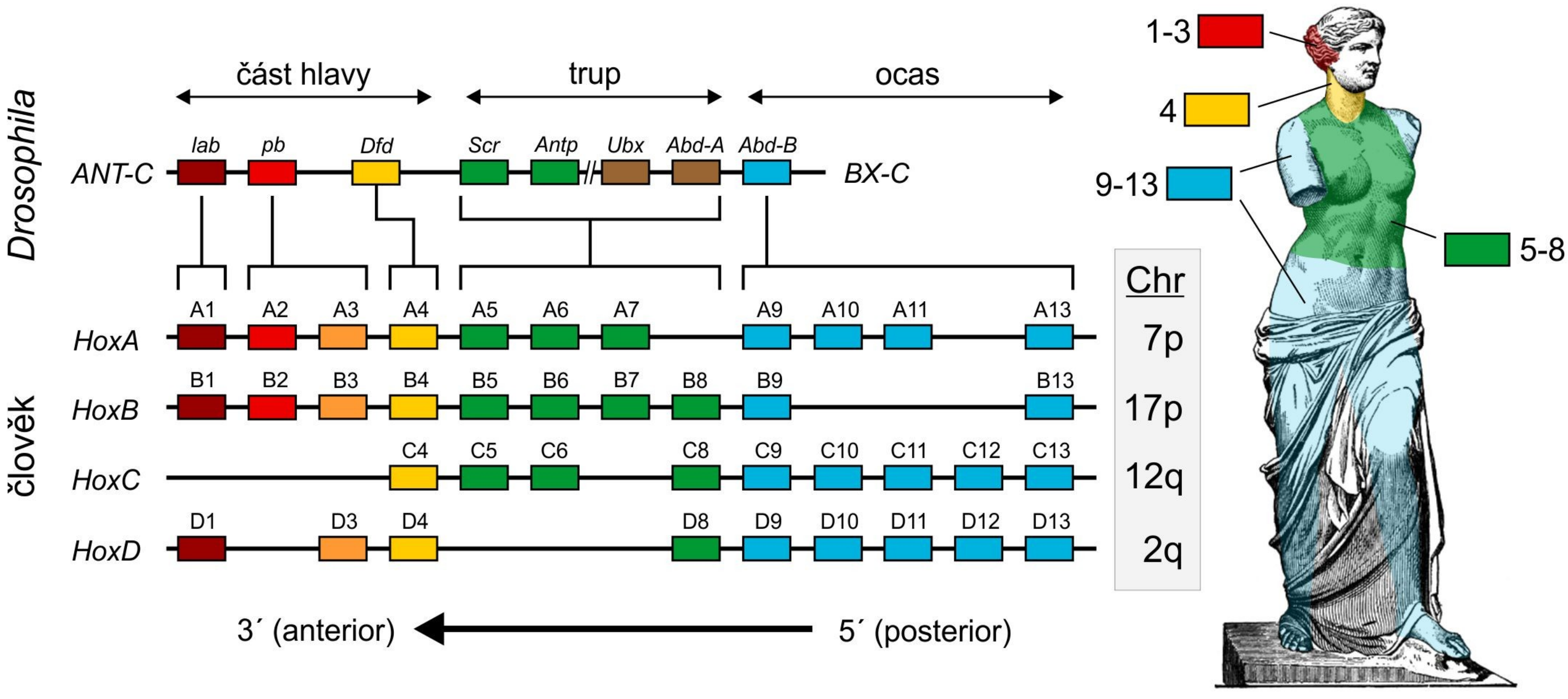
Antennapedia (ANT-C)

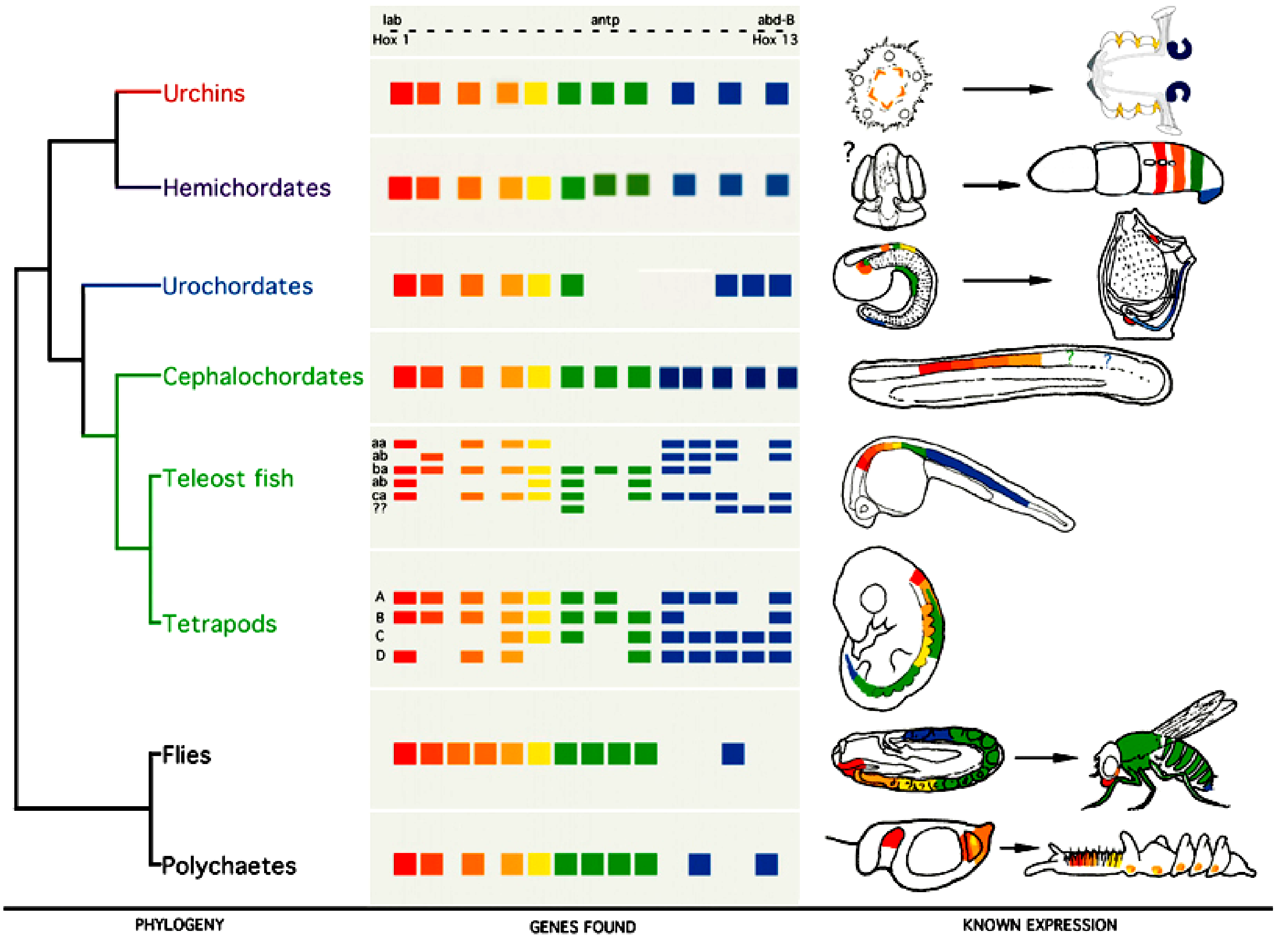
Bithorax (BX-C)

vertebrates:

4 linkage groups

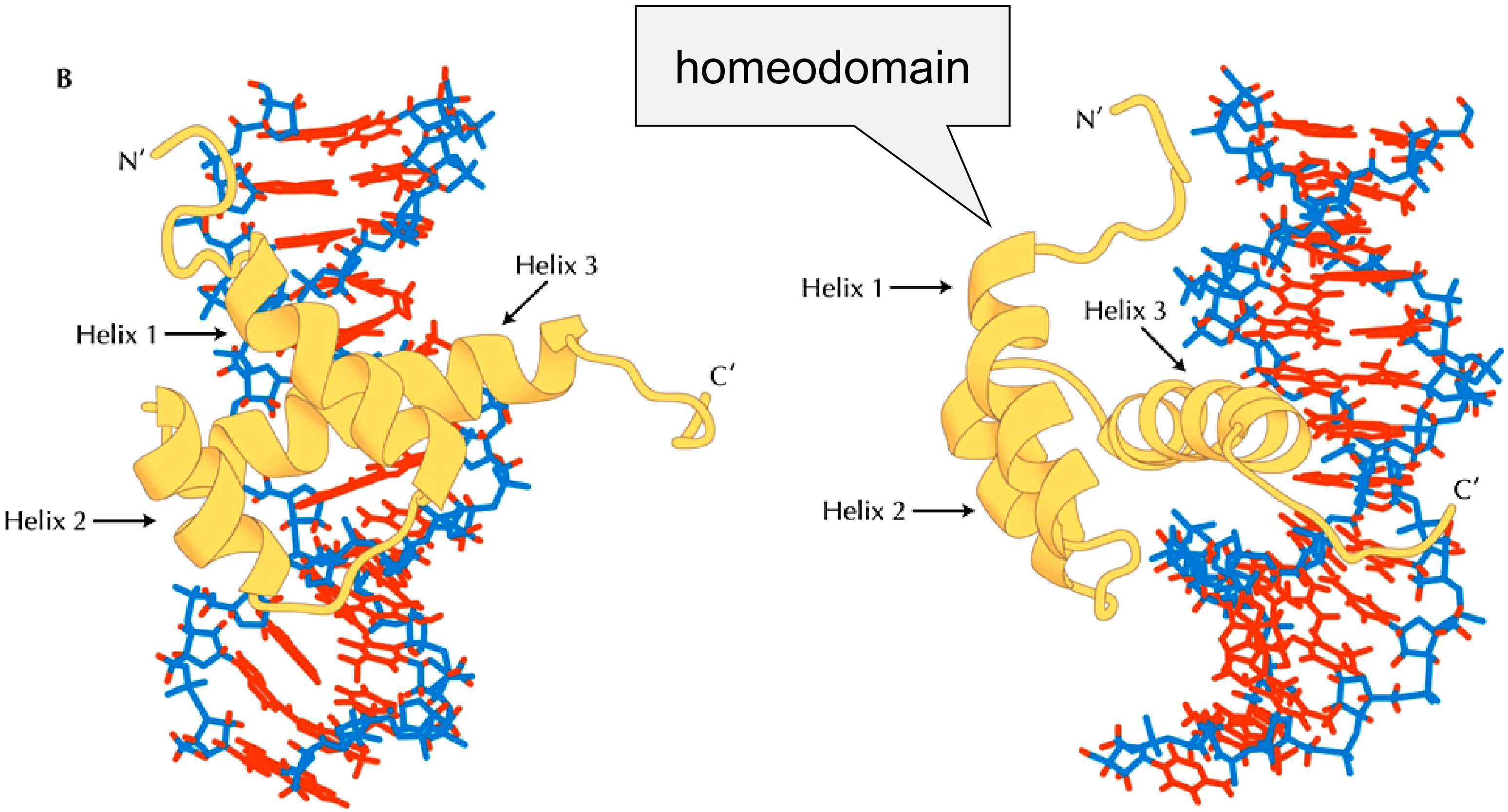



část hlavy
trup
ocas
Drosophila
ANT-C
lab
pb
Dfd
Scr
Antp
Ubx
Abd-A
Abd-B
BX-C
člověk
HoxA
A1 A2 A3 A4 A5 A6 A7 A9 A10 A11 A13
HoxB
B1 B2 B3 B4 B5 B6 B7 B8 B9 B13
HoxC
C4 C5 C6 C8 C9 C10 C11 C12 C13
HoxD
D1 D3 D4 D8 D9 D10 D11 D12 D13
Chr
7p
17p
12q
2q
3´ (anterior)
5´ (posterior)
1-3
4
9-13
5-8


lab
Hox 1
antp
abd-B
Hox 13
Urchins
Hemichordates
Urochordates
Cephalochordates
Teleost fish
Tetrapods
Flies
Polychaetes
aa
ab
ba
ab
ca
??
A
B
C
D
PHYLOGENY
GENES FOUND
KNOWN EXPRESSION

Homeobox: 180 bp → homeodomain

60 AA (expression regulation)



Hox-genes are highly conservative

A

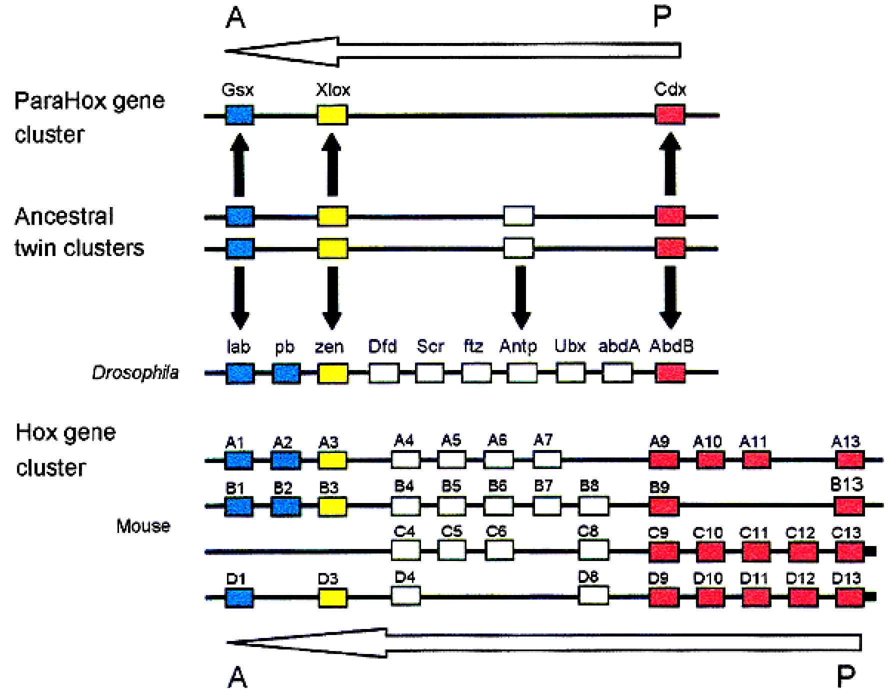
Scr group

Fruit fly	TKRQRTSYTRYQTLELEKEFHFNRYLTRRRRIEIAHALCLTERQIKIWFQNRRMKLKKEH
Grasshopper	TKRQRTSYTRYQTLELEKEFHFNRYLTRRRRIEIAHALCLTERQIKIWFQNRRMKWKKEH
Beach hopper	TKRQRTSYTRYQTLELEKEFHFNRYLTRRRRIEIAHALCLTERQIKIWFQNRRMKWKKEH
Centipede	TKRQRTSYTRYQTLELEKEFHFNRYLTRRRRIEIAHSLCLSERQIKIWFQNRRMKWKKEH
Mite	TKRQRTSYTRYQTLELEKEFHFNRYLTRRRRIEIAHSLCLSERQIKIWFQNRRMKWKKEH
Leech	NKRTRTSYTRHQTLELEKEFHFNRYLSRRRRIEIAHVLNLSERQIKIWFQNRRMKWKKDH
Sea urchin	SKRSRTAYTRYQTLELEKEFHFNRYLTRRRRIEIAHALGLTERQIKIWFQNRRMKWKKEH
Zebra fish	GKRARTAYTRYQTLELEKEFHFNRYLTRRRRIEIAHALCLSERQIKIWFQNRRMKWKKDN
Mouse	GKRARTAYTRYQTLELEKEFHFNRYLTRRRRIEIAHALCLSERQIKIWFQNRRMKWKKDN
Human	GKRARTAYTRYQTLELEKEFHFNRYLTRRRRIEIAHALCLSERQIKIWFQNRRMKWKKDN

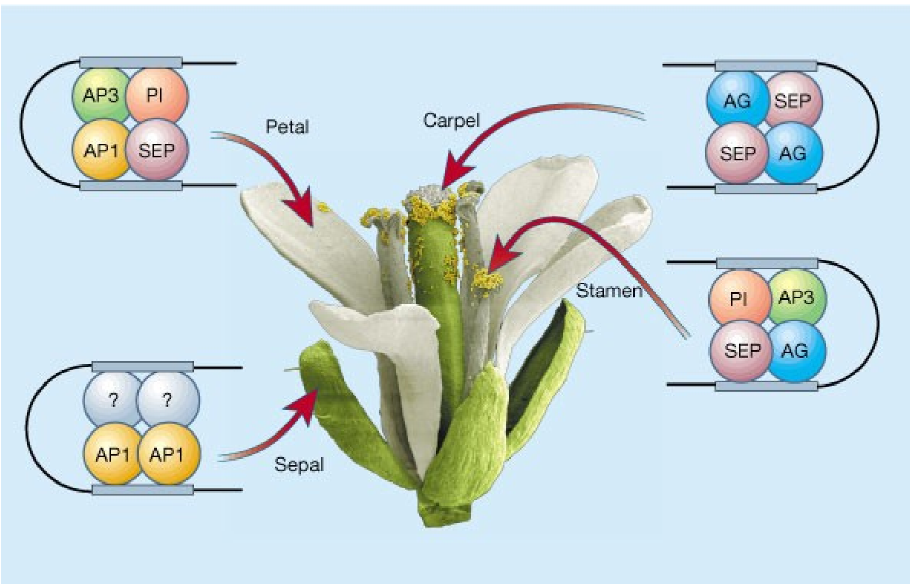
Antp group

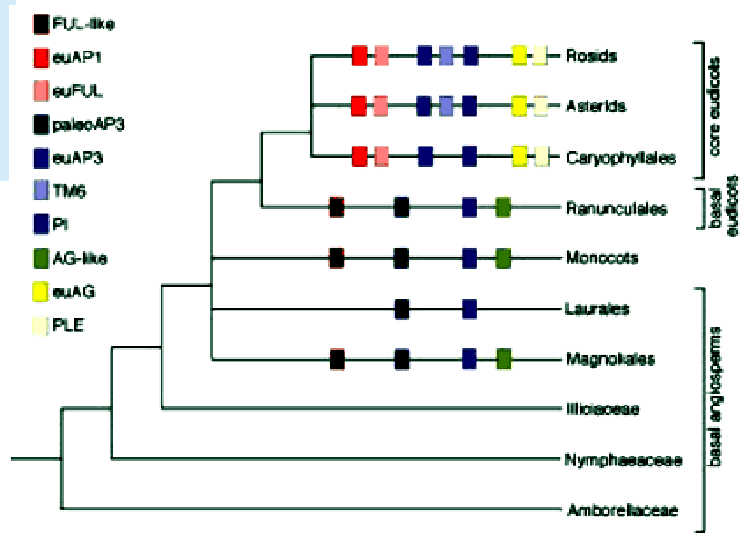
Fruit fly	RKRGRQTYTRYQTLELEKEFHFNRYLTRRRRIEIAHALCLTERQIKIWFQNRRMKWKKEN
Grasshopper	RKRGRQTYTRYQTLELEKEFHFNRYLTRRRRIEIAHALCLTERQIKIWFQNRRMKWKKEN
Beach hopper	RKRGRQTYTRYQTLELEKEFHFNRYLTRRRRIEIAHALCLTERQIKIWFQNRRMKWKKEN
Centipede	RKRGRQTYTRYQTLELEKEFHFNRYLTRRRRIEIAHALCLTERQIKIWFQNRRMKWKKEN
Spider	RKRGRQTYTRYQTLELEKEFHFNRYLTRRRRIEIAHALCLTERQIKIWFQNRRMKWKKEN
Leech	QKRTRQTYTRYQTLELEKEFYSNRYLTRRRRIEIAHSLALSERQIKIWFQNRRMKWKKEN
Sea urchin	GKRGRQTYTRQQTLELEKEFHFSRYVTRRRRFEIAQSLGLSERQIKIWFQNRRMKWKREH
Zebra fish	GRRGRQTYTRYQTLELEKEFHFNRYLTRRRRIEIAHALCLTERQIKIWFQNRRMKWKKEN
Mouse	GRRGRQTYTRYQTLELEKEFHYNRYLTRRRRIEIAHALCLTERQIKIWFQNRRMKWKKES
Human	GRRGRQTYTRYQTLELEKEFHYNRYLTRRRRIEIAHALCLTERQIKIWFQNRRMKWKKES

ParaHox genes

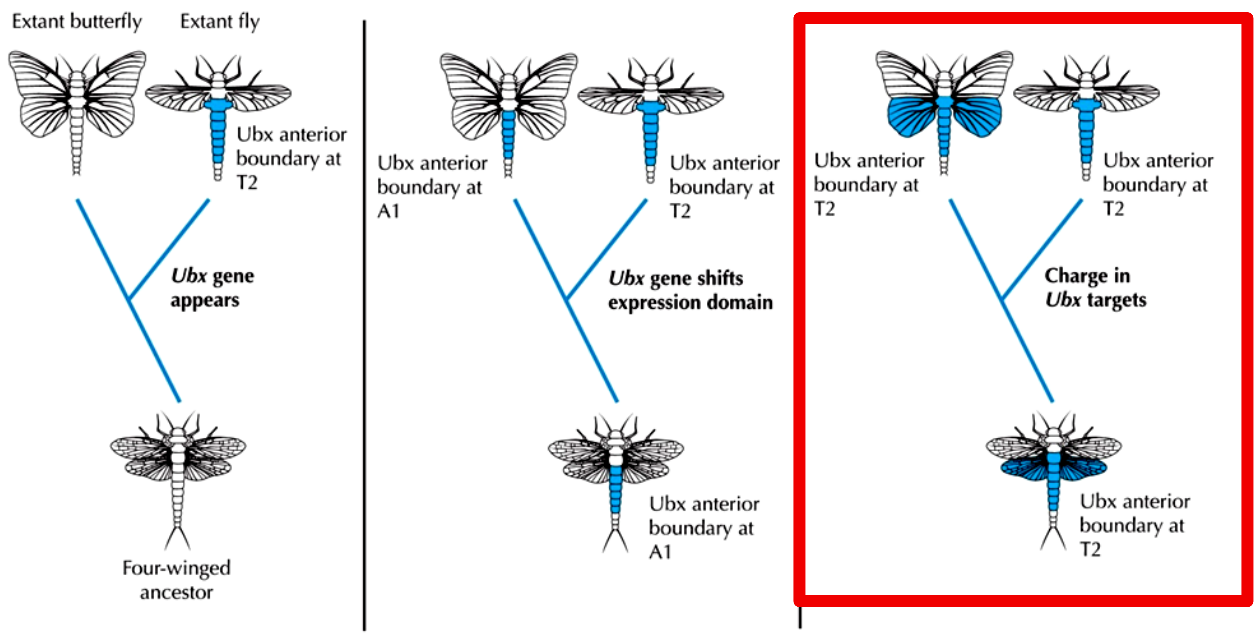


MADS-box genes in plants

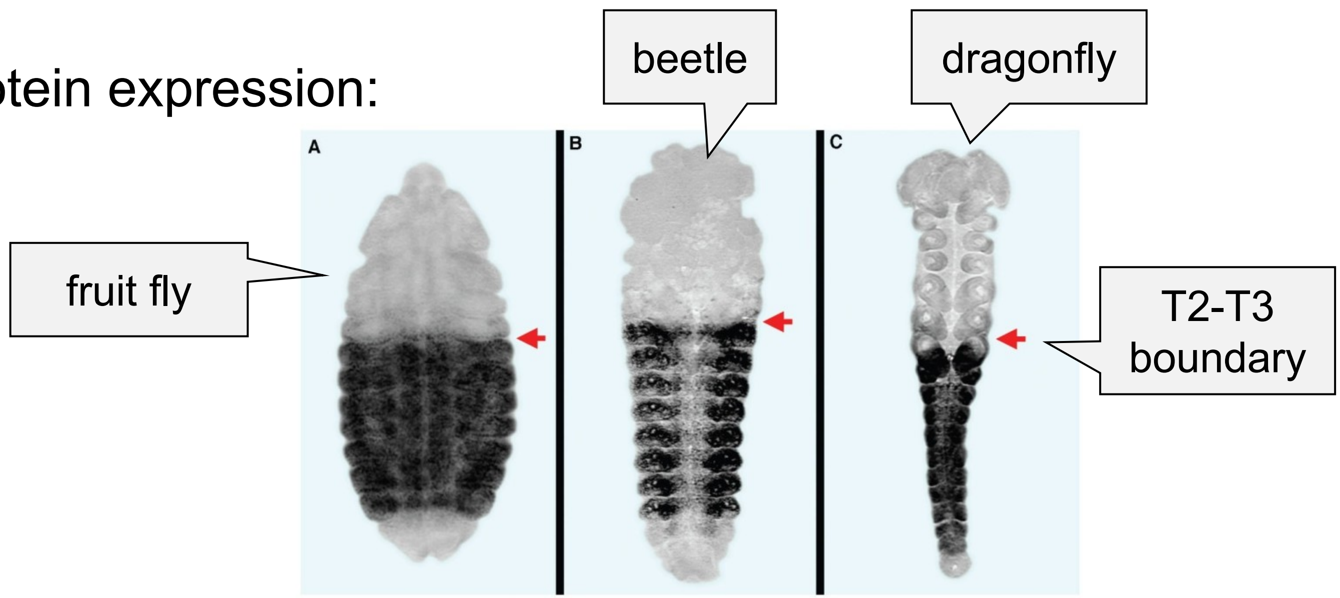


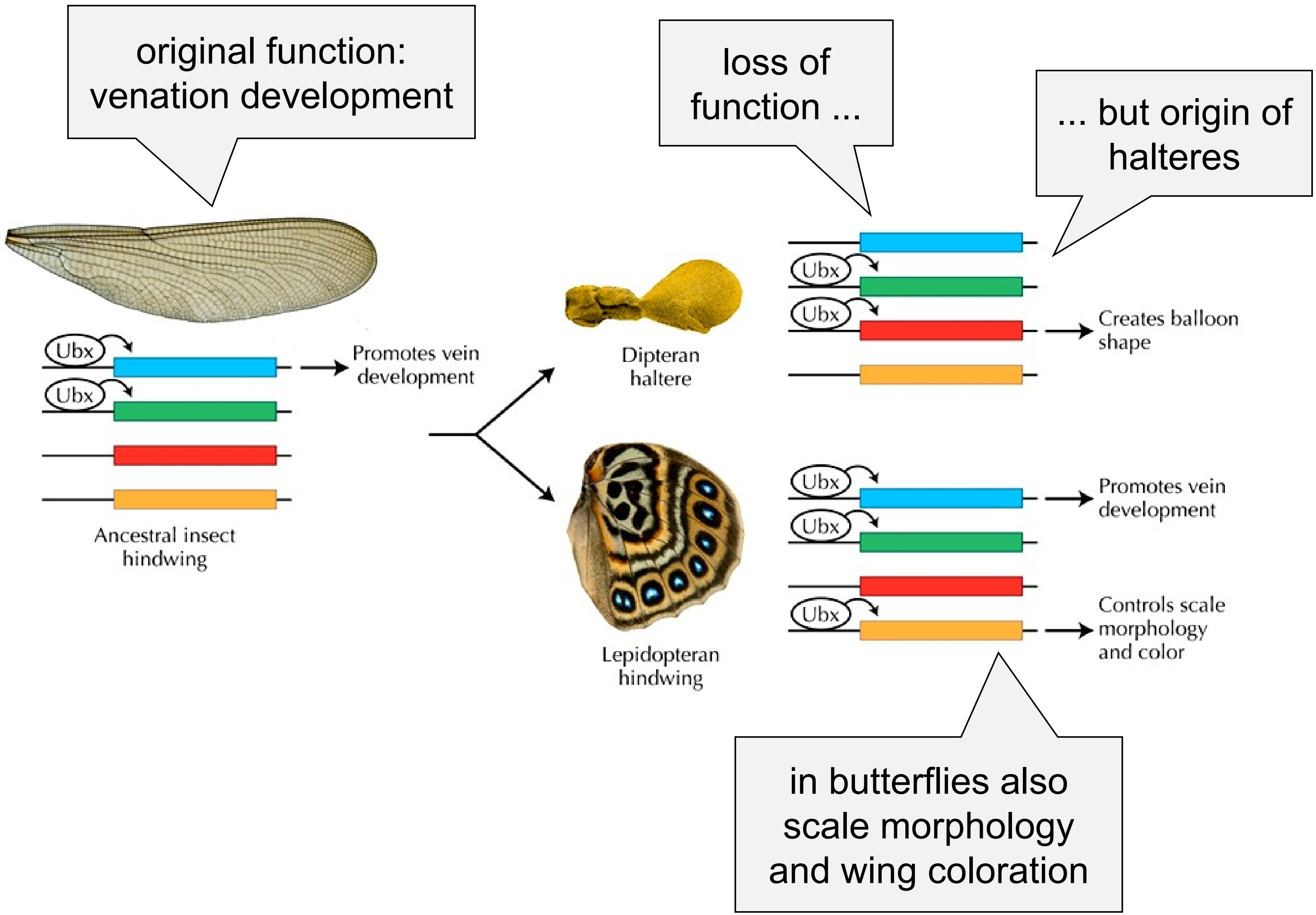


3 hypotheses of the origin of dipteran arrangement:



Ubx protein expression:



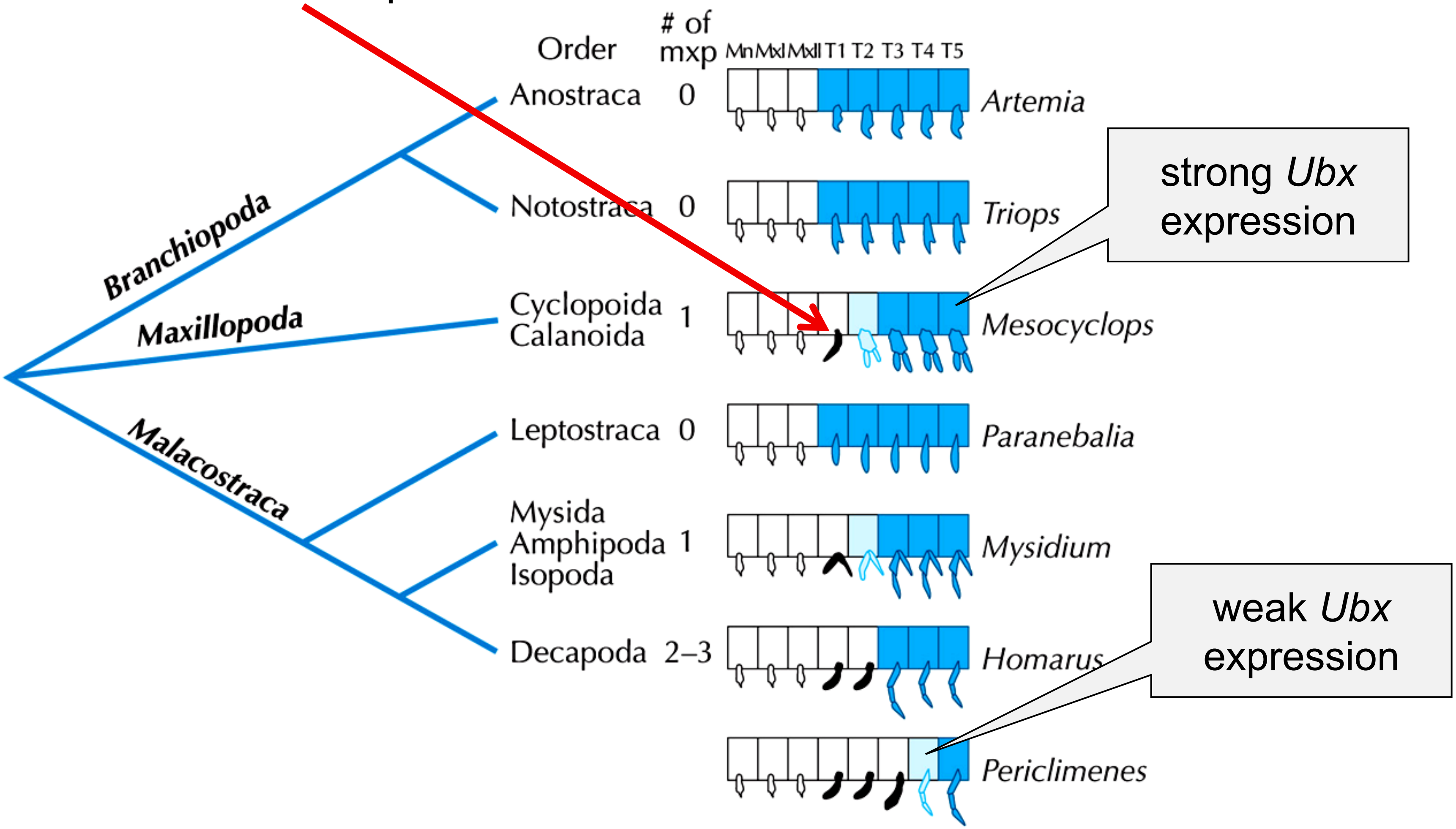


original function: venation development
loss of function ...
... but origin of halteres
Ubx
Ubx
Promotes vein development
Ancestral insect hindwing
Dipteran haltere
Ubx
Ubx
Creates balloon shape
Lepidopteran hindwing
Ubx
Ubx
Ubx
Promotes vein development
Controls scale morphology and color
in butterflies also scale morphology and wing coloration

Evolution of thoracic segments in crustaceans – shift of anteroposterior boundary of expression of the *Ubx* gene:

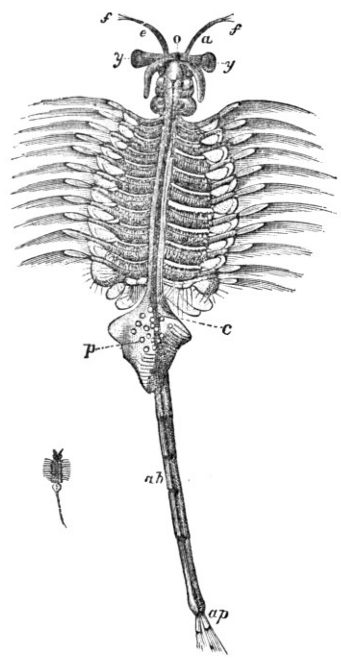
thoracic segments: copepods – 6, lobster – 8, brine shrimps – 11 (ancestral)

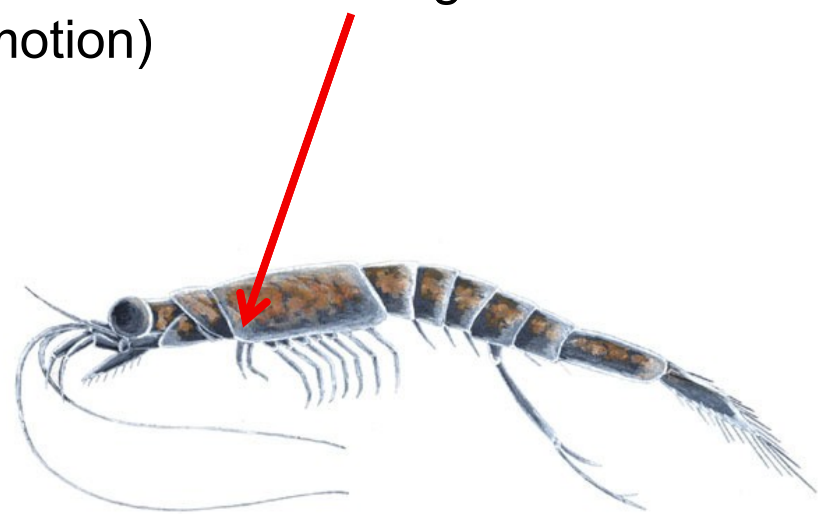
movement → maxillipedes



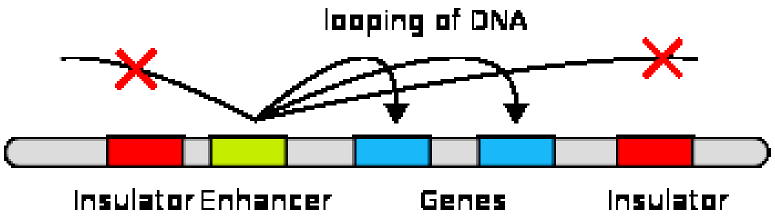
shift of anteroposterior boundary of *Ubx* gene expression = position of transition of locomotory segments and maxillipedes

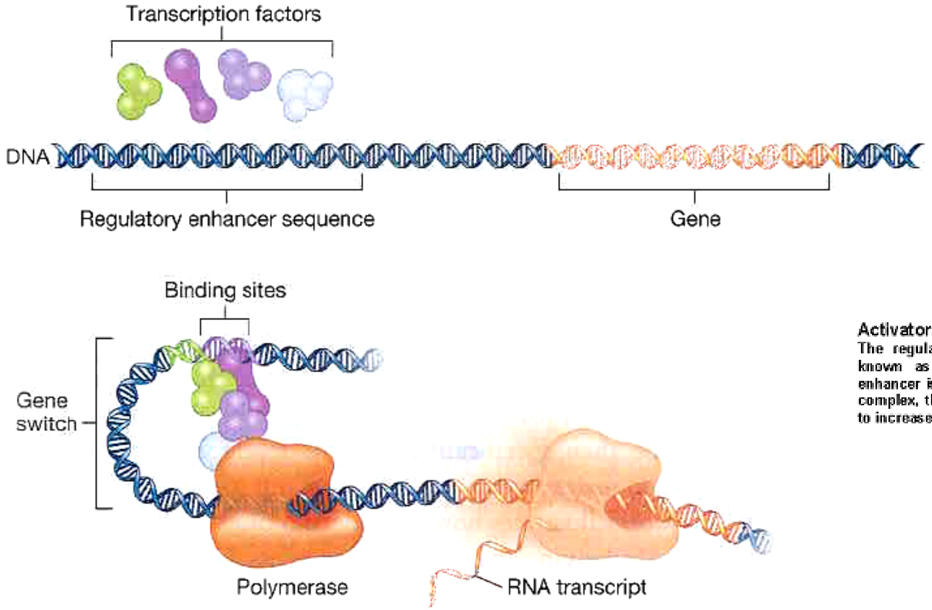
např. opossum shrimps: 2nd segment, prawns: 4th segment
2nd thoracic limb of opossum shrimps = transitional segment between 1st (maxillipede) and 3rd limb (locomotion)

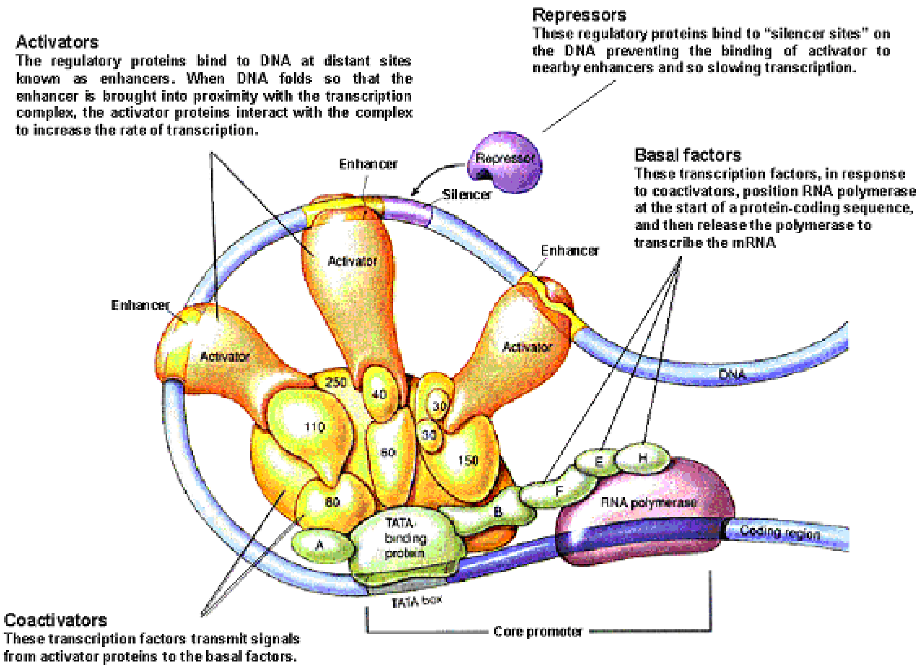




Besides transcriptional factors also regulatory enhancers:







Macroevolutionary trends
species selection

trends: real × passive (eg. wall effect)

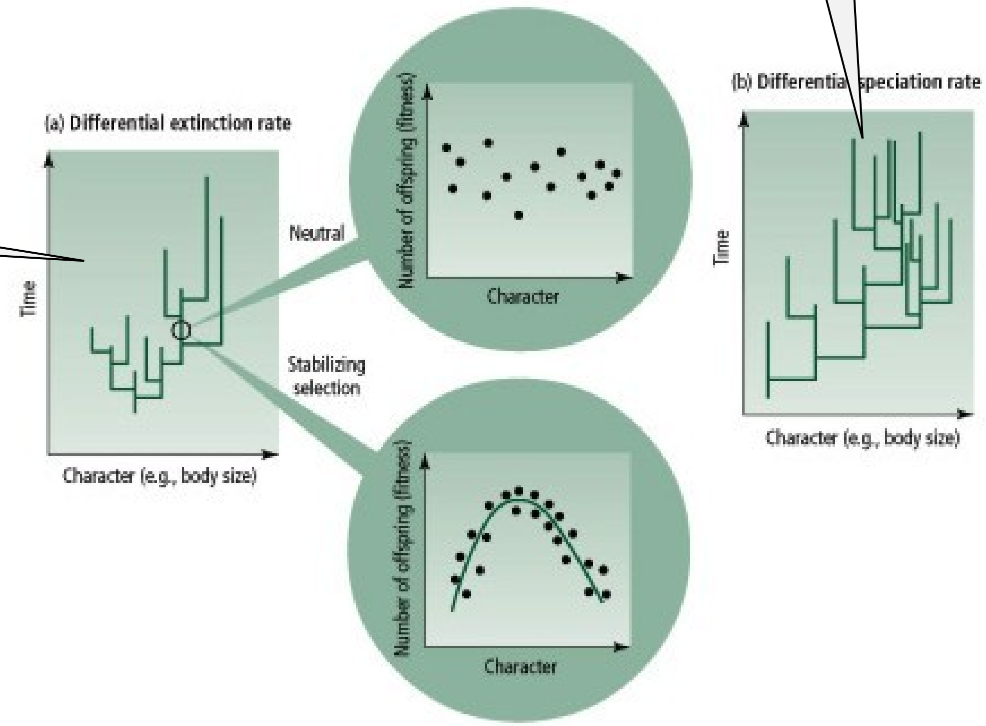
Edward Drinker Cope: trend to bigger size

Species selection:

= preferential survival or proliferation of species

different speciation rates

different extinction rates

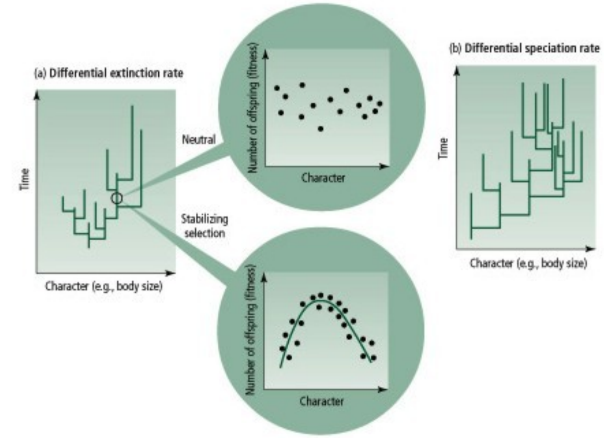


the trait connected with differential survival or speciation

these features independent of natural selection

trait is heritable during speciation

SS favours only nonadaptive trends (otherwise = natural selection)



Necessary to prove:

higher speciation rate/lower extinction rate in lineages which deviate from the average in the direction of the trend

the trend and distribution of varied speciation/extinction rates are not caused by shift in fossil record

the trend and distribution of varied speciation/extinction rates are not caused by natural selection