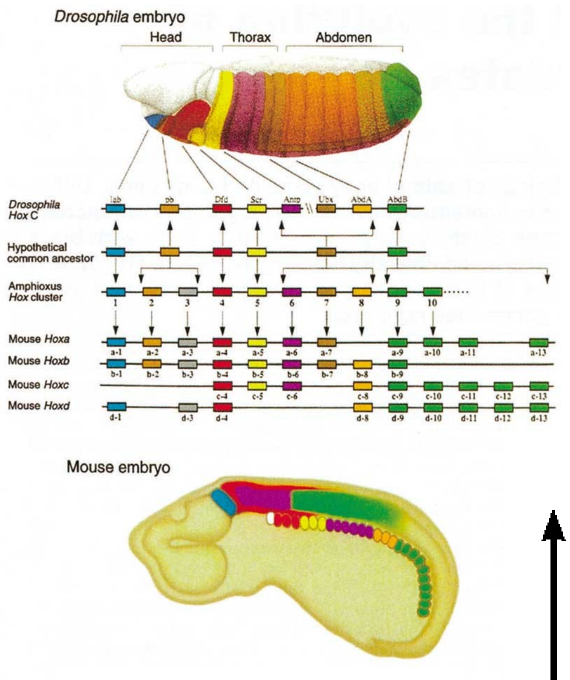
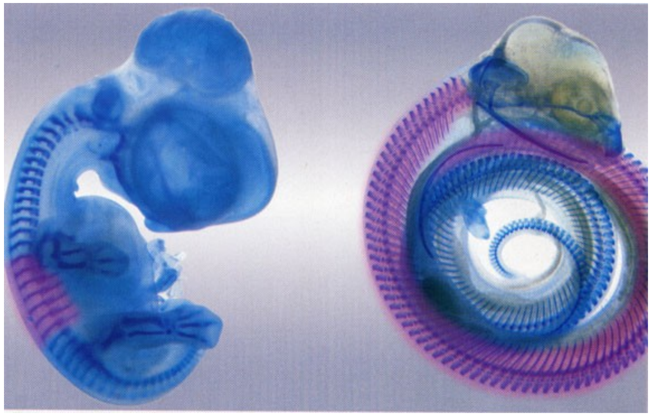
# MACROEVOLUTION





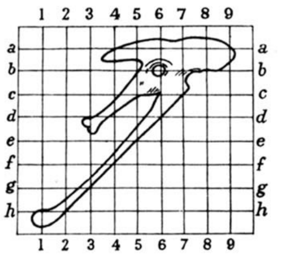


Fig. 161. Pelvis of *Archaeopteryx*.

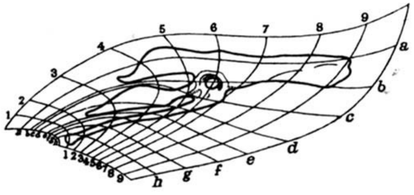
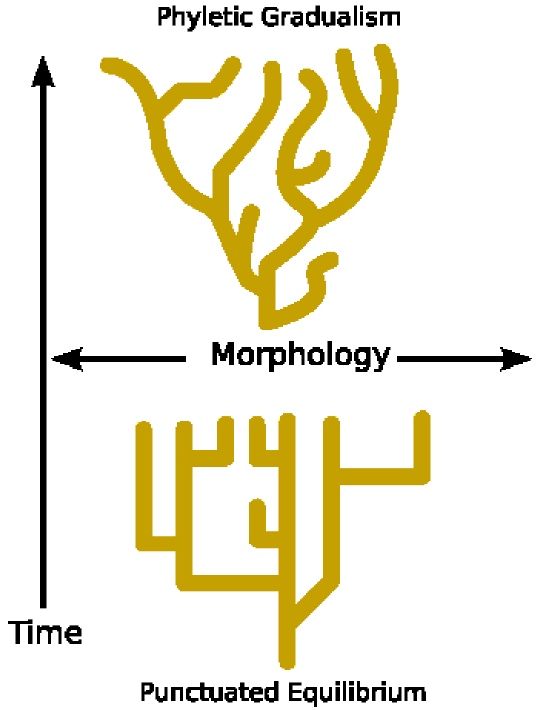
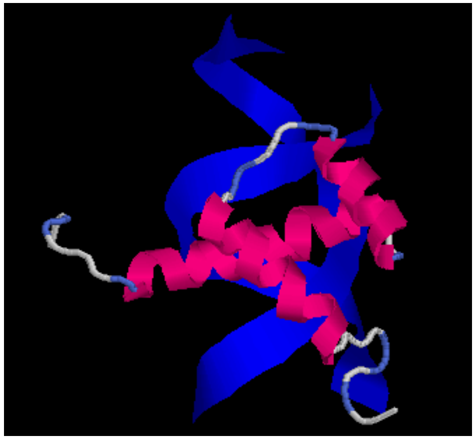
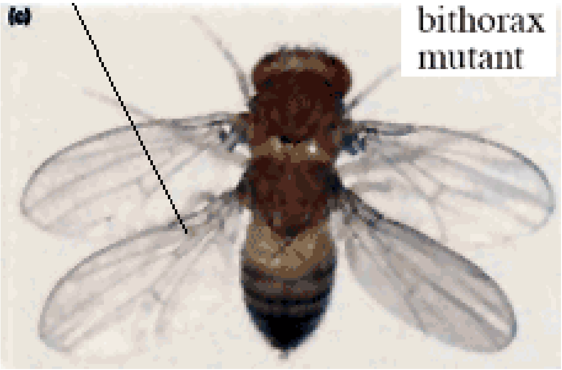


Fig. 162. Pelvis of *Apatornis*.

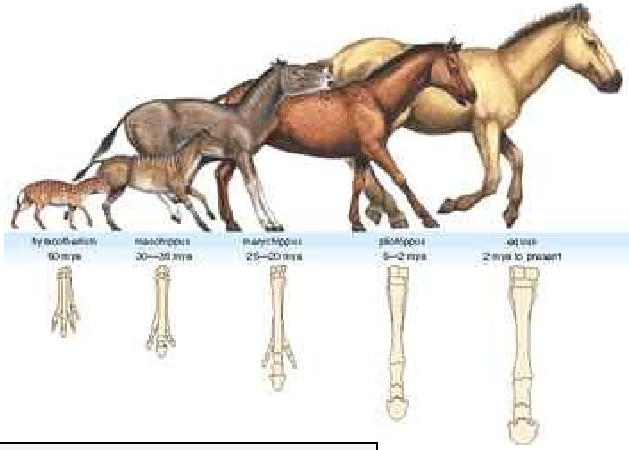






# RATE OF EVOLUTION
# PUNCTUATED EQUILIBRIA

## Rate of evolution:



difference between trait values in time $t_2$ and $t_1$

Haldane (1949)

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

time interval $t_2$ - $t_1$

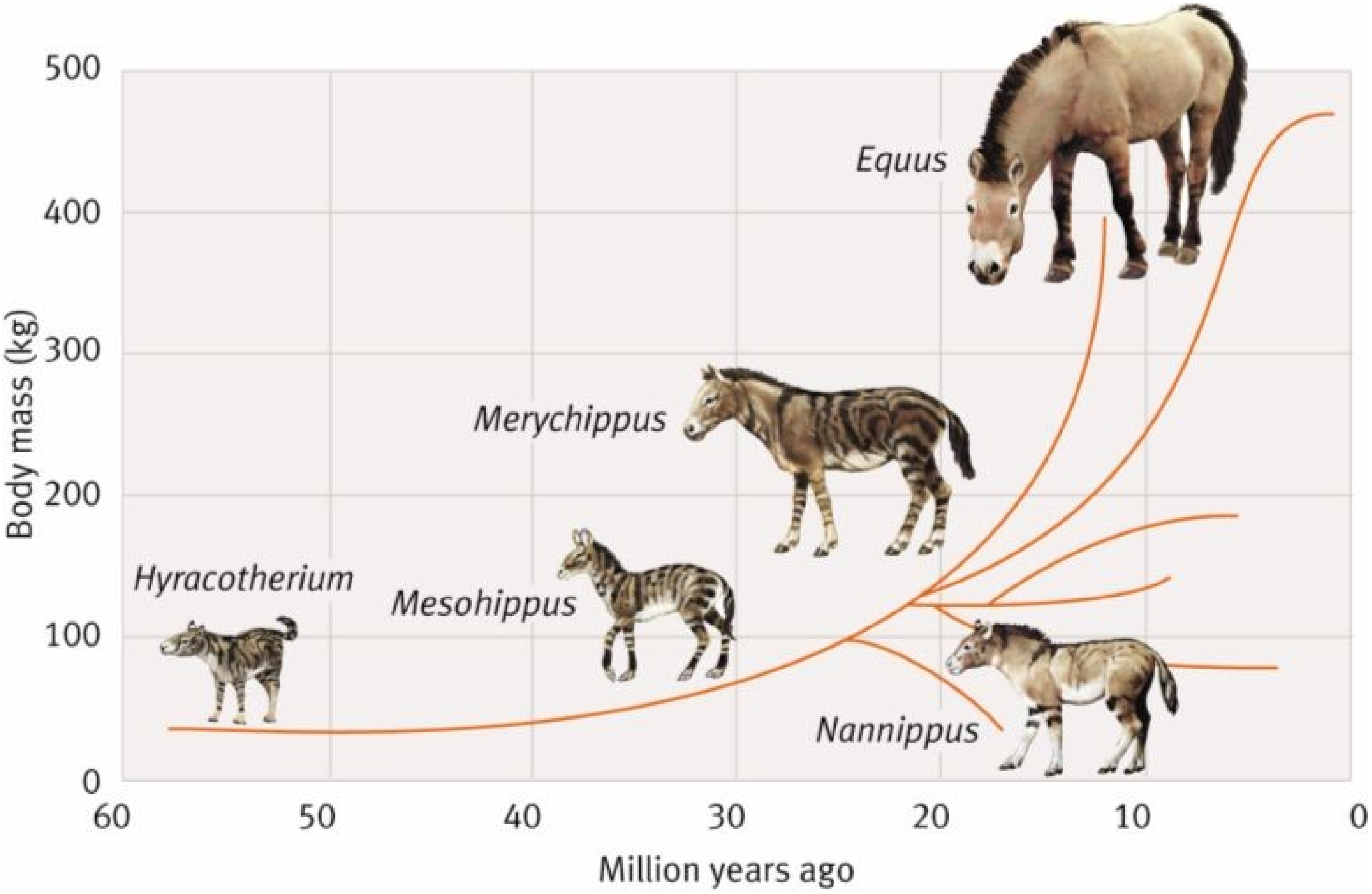
1 darwin = *e*-fold change in a trait over 1 million years

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

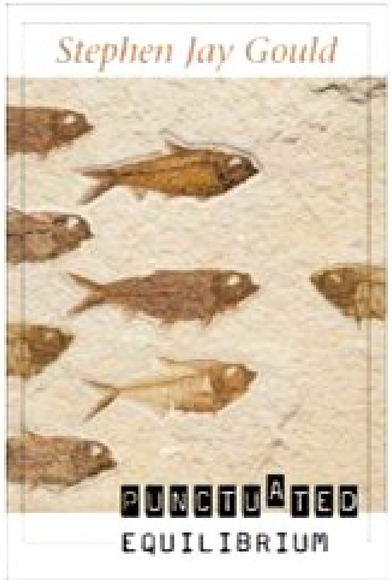
disadvantages:
1. factor *e* is not biologically natural
2. uses absolute time
3. does not take into account measured time interval
4. impossible to compare areas/volumes/linear dimensions

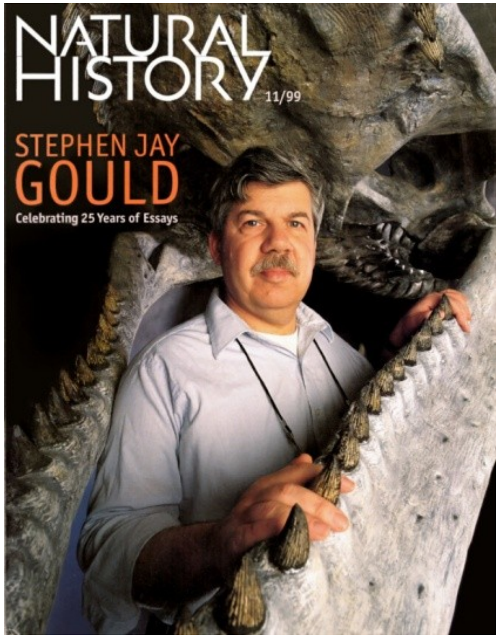
⇒ Haldane (1949), Gingerich (1993): 1 haldane = change measured in units of <u>standard deviation</u> per generation

# Theory of punctuated equilibria:

Stephen Jay Gould, Niles Eldredge (1972)

stasis vs. rapid change

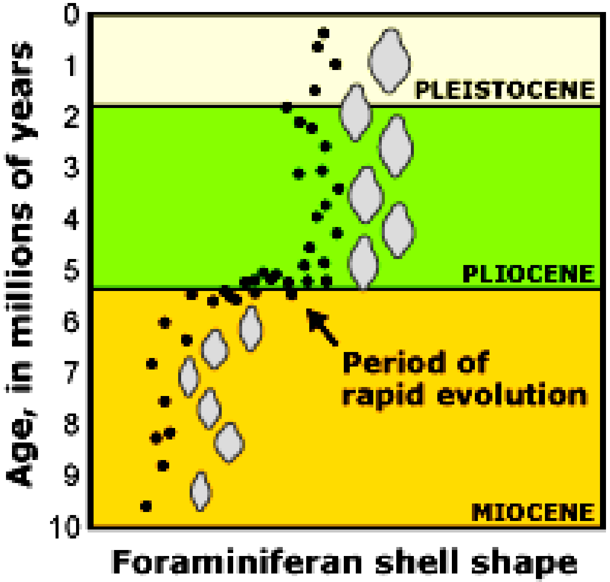


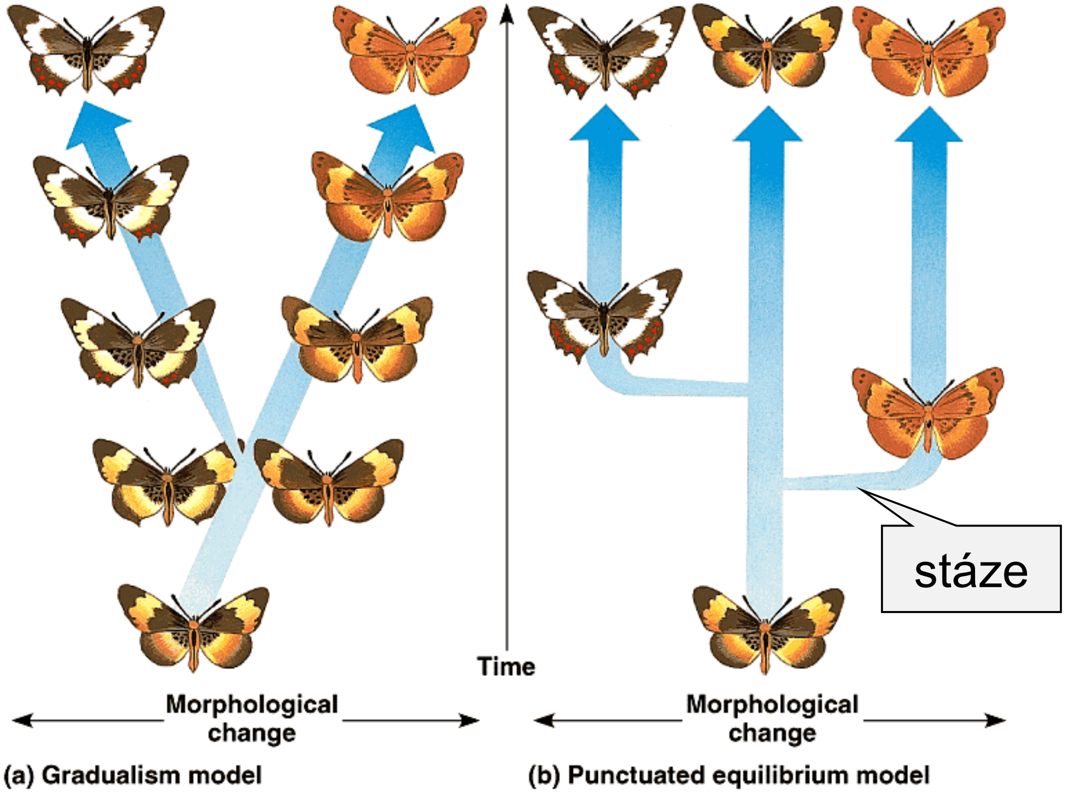


S.J. Gould

N. Eldredge

# stasis vs. rapid change





stáze

(a) Gradualism model

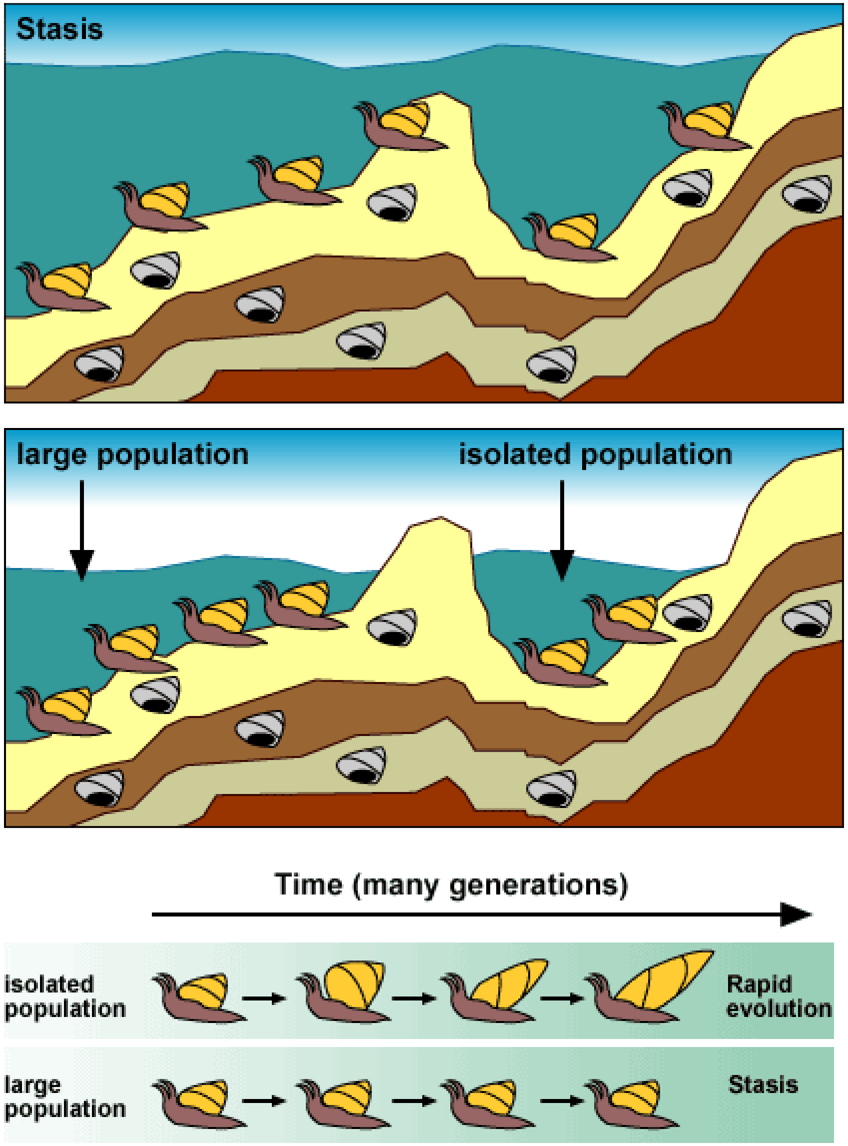
(b) Punctuated equilibrium model

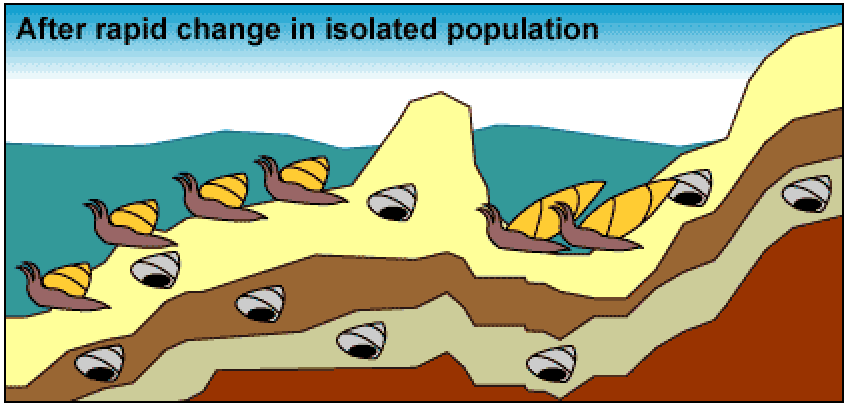
Mechanism?

peripatric speciation

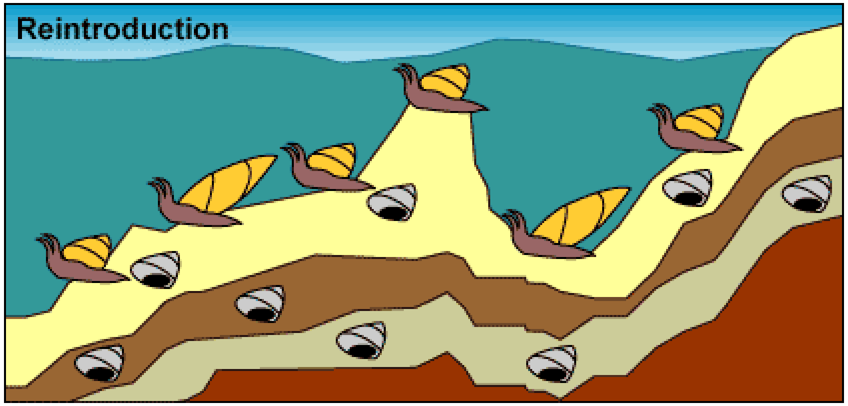
macromutation – R. Goldschmidt, *The Material Basis of Evolution* (1940): „hopeful monsters“

# Peripatric speciation and punctuated equilibria

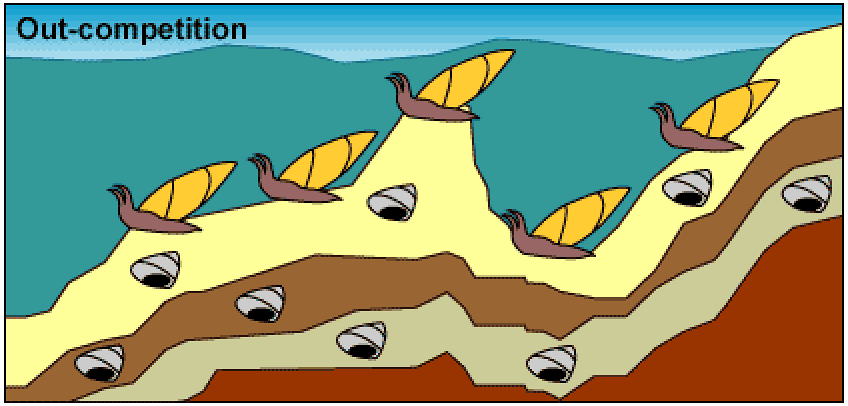




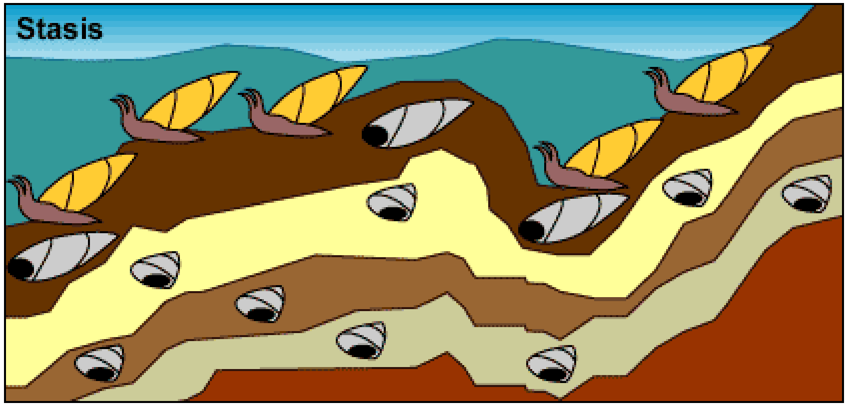
After rapid change in isolated population

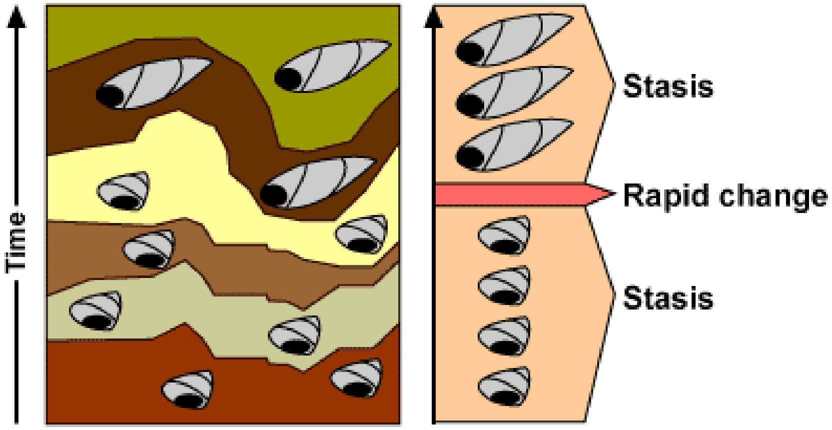


Reintroduction

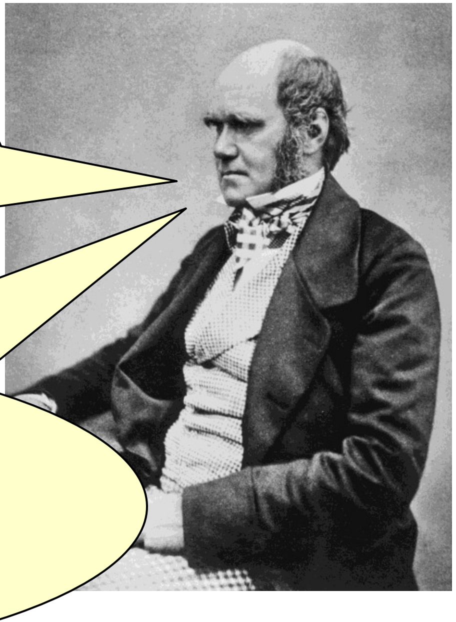


Out-competition

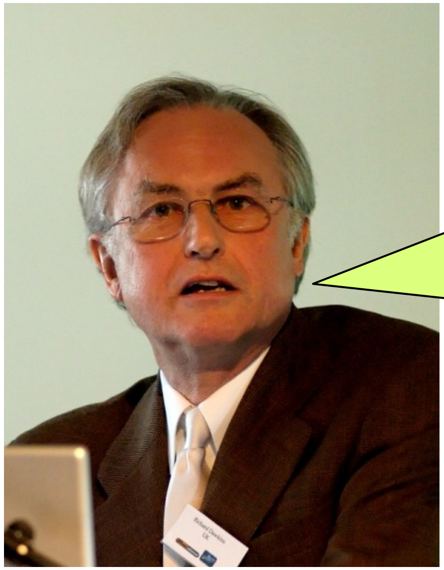

Stasis


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 variable rate – species change either in discrete steps (punctuationism) or gradually. Therefore, stasis is only an extreme case of slow evolution.

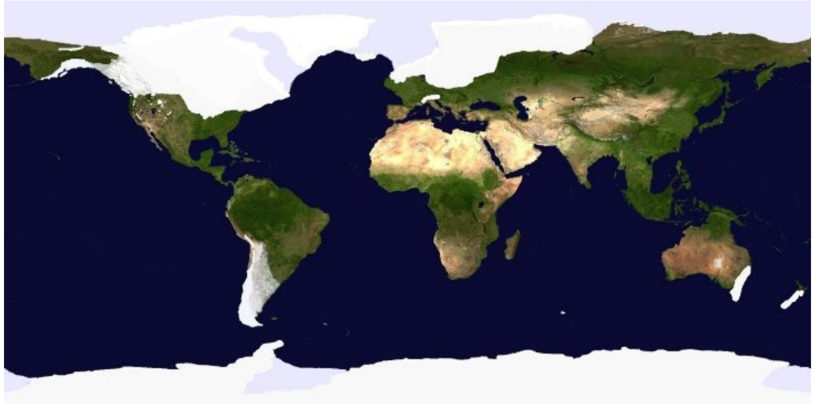
R. Dawkins: Blind watchaker

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“

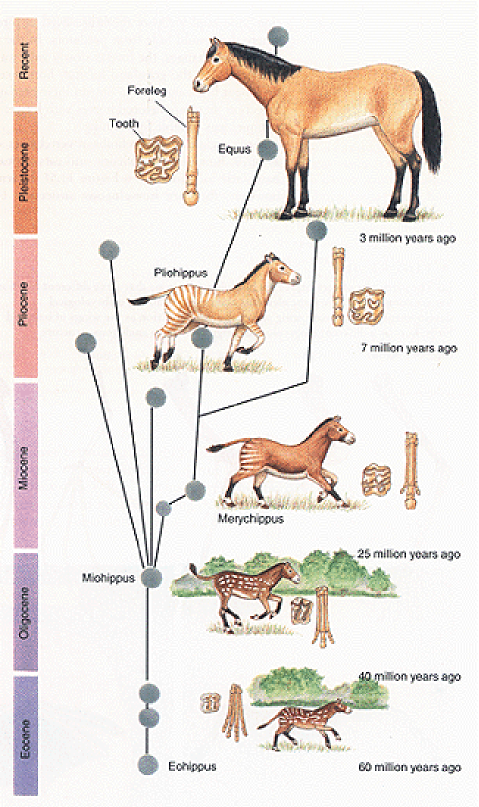
# Evolution of horses:

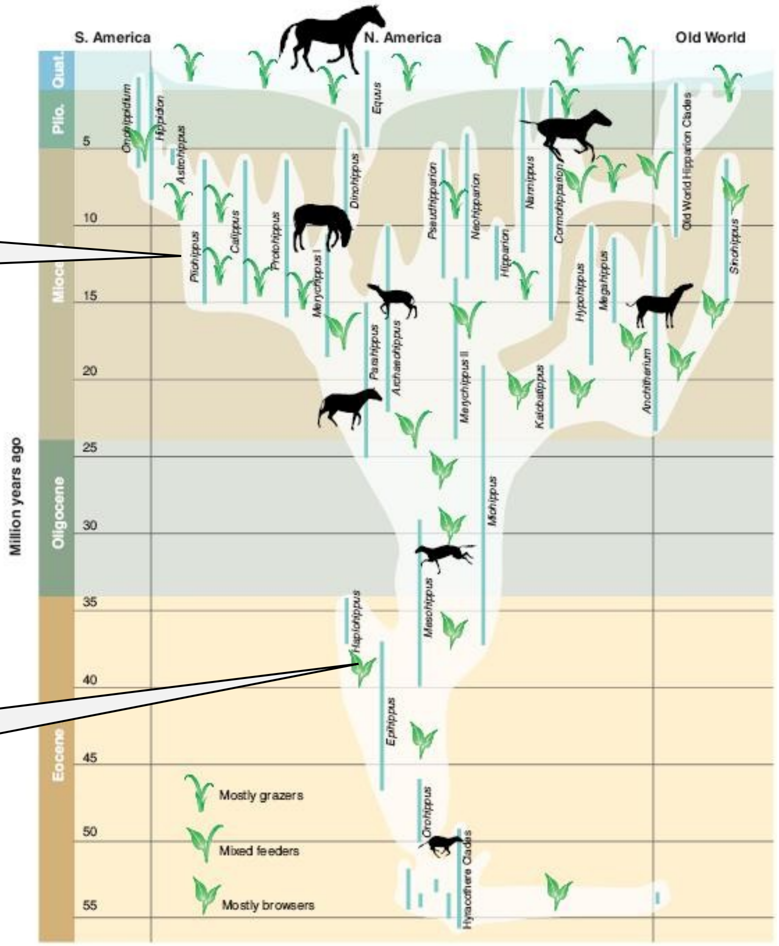
2 dental dimensions

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



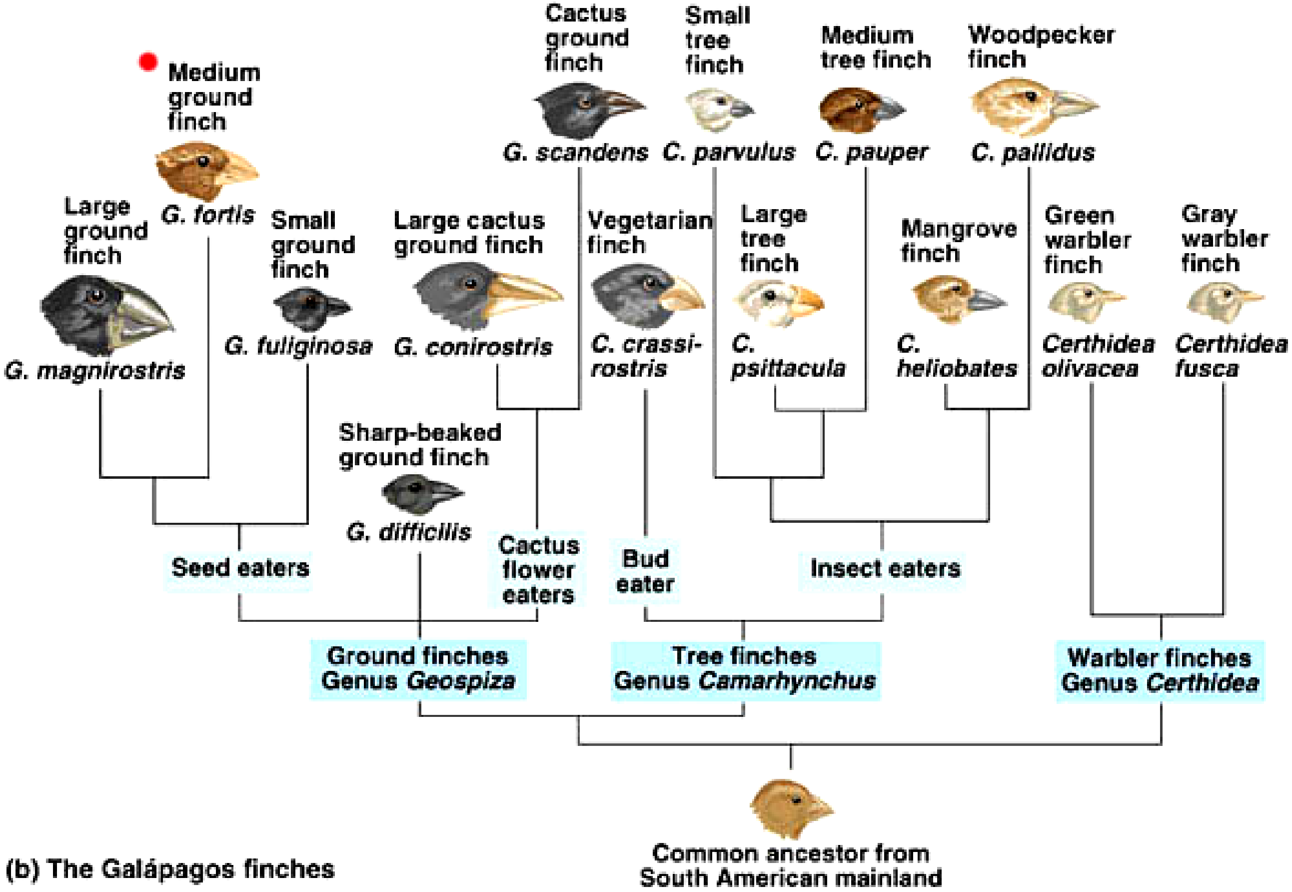


grazing

browsing

# 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)

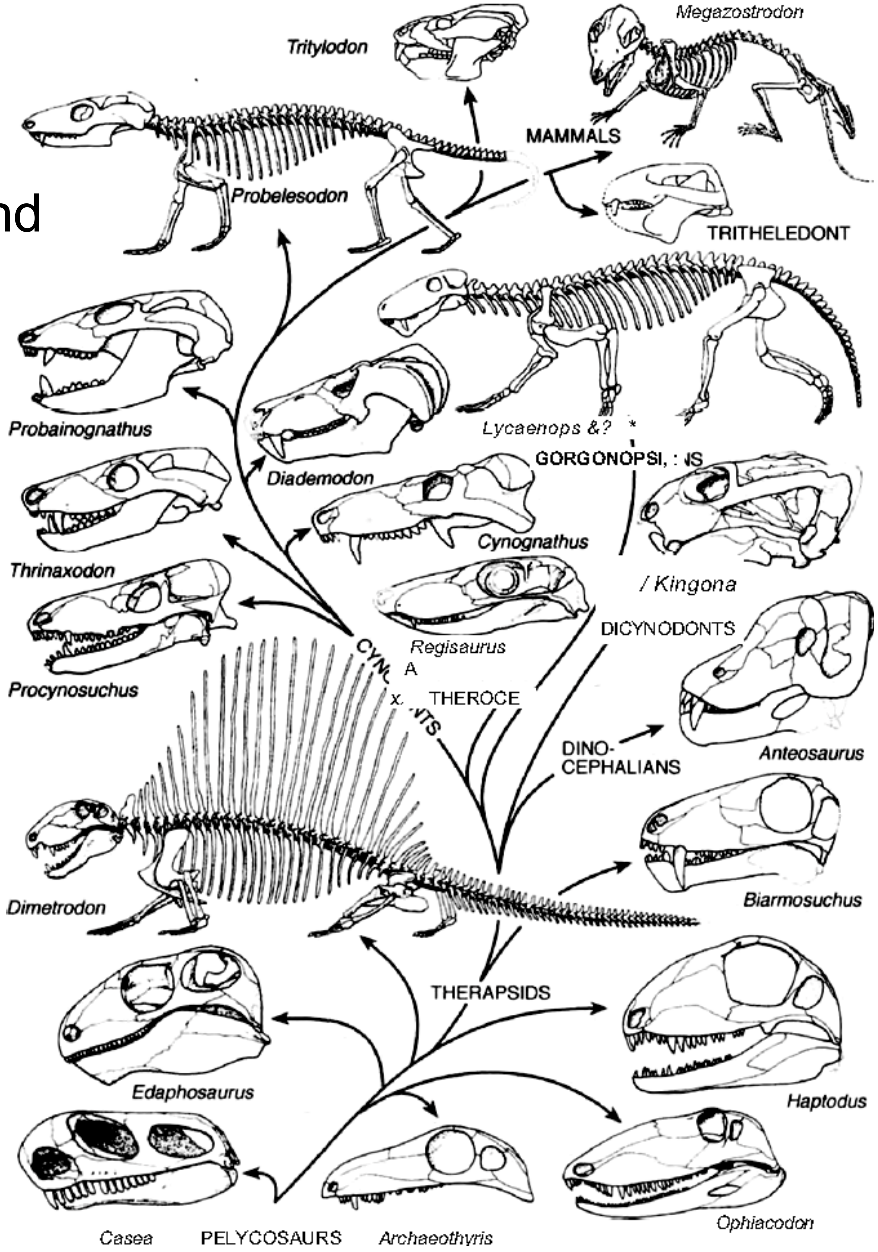


(b) The Galápagos finches

# Evolution of mammals from therapsid reptiles:

changes gradual

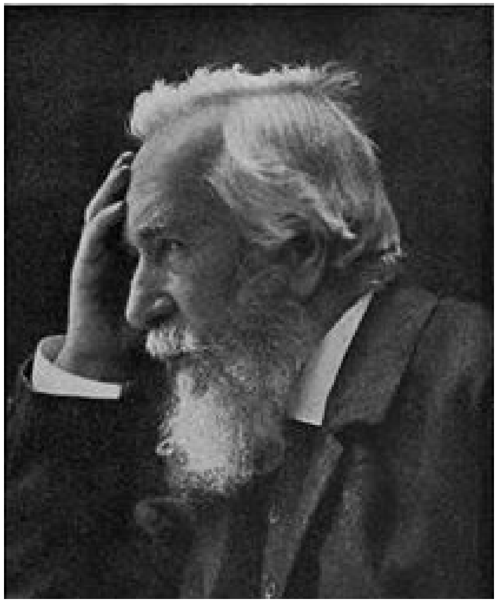
large differences between reptiles and mammals are adaptive in individual links ⇒ same mechanisms as in microevolution

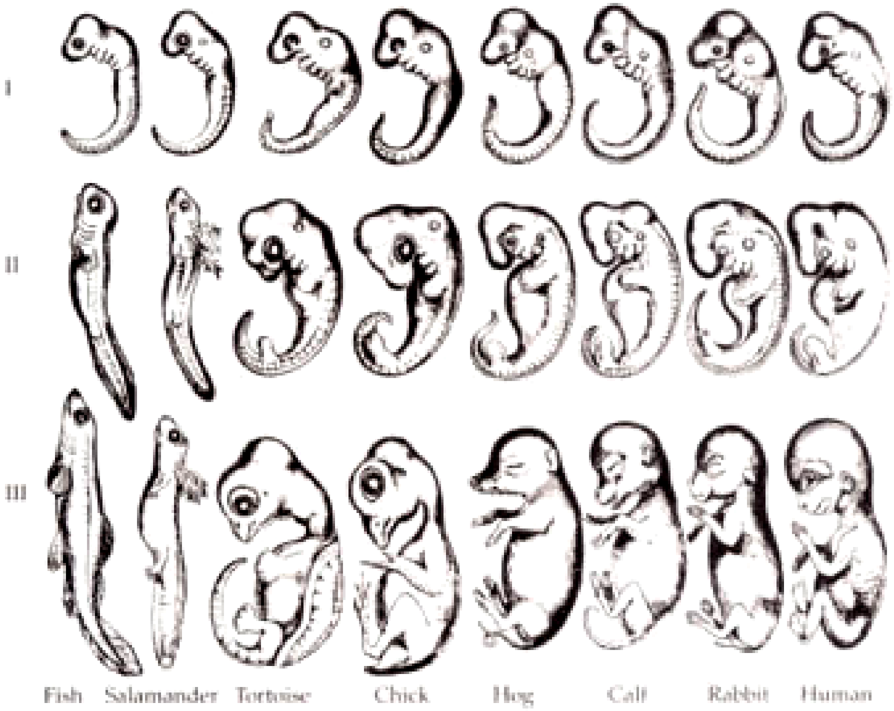


# Relation of macroevolution and ontogeny

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 (?)

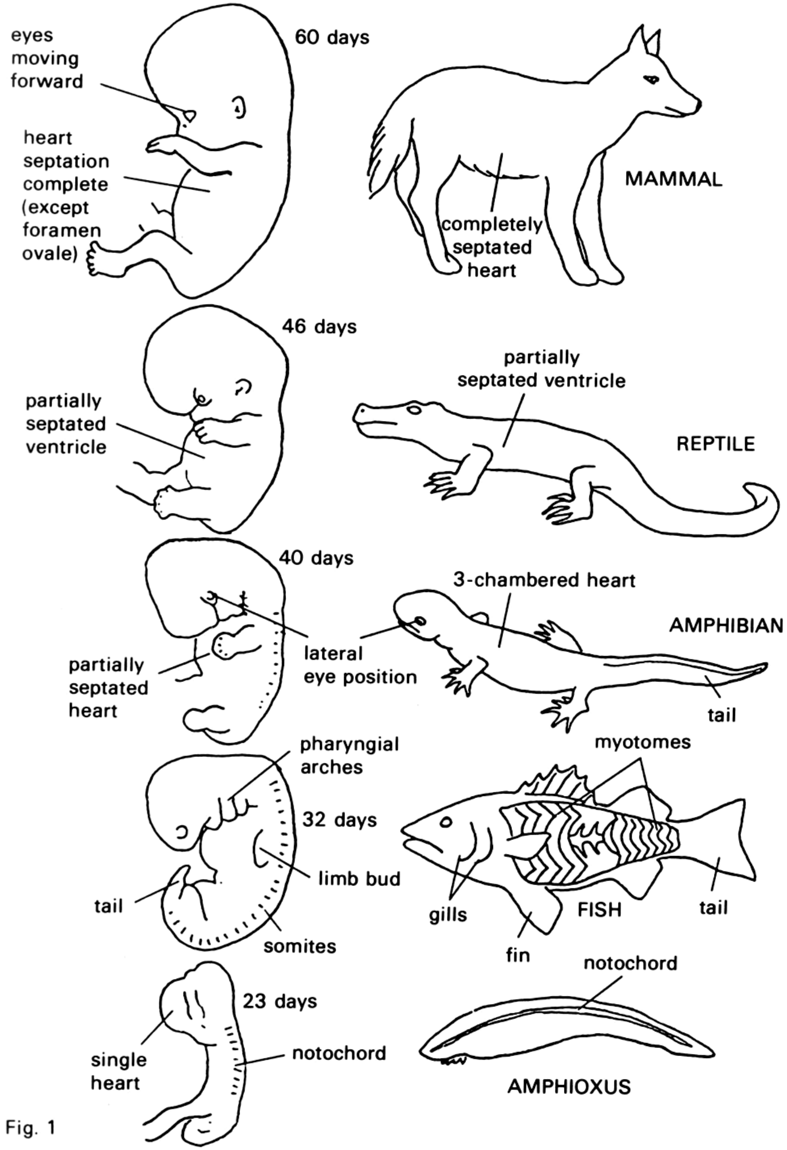
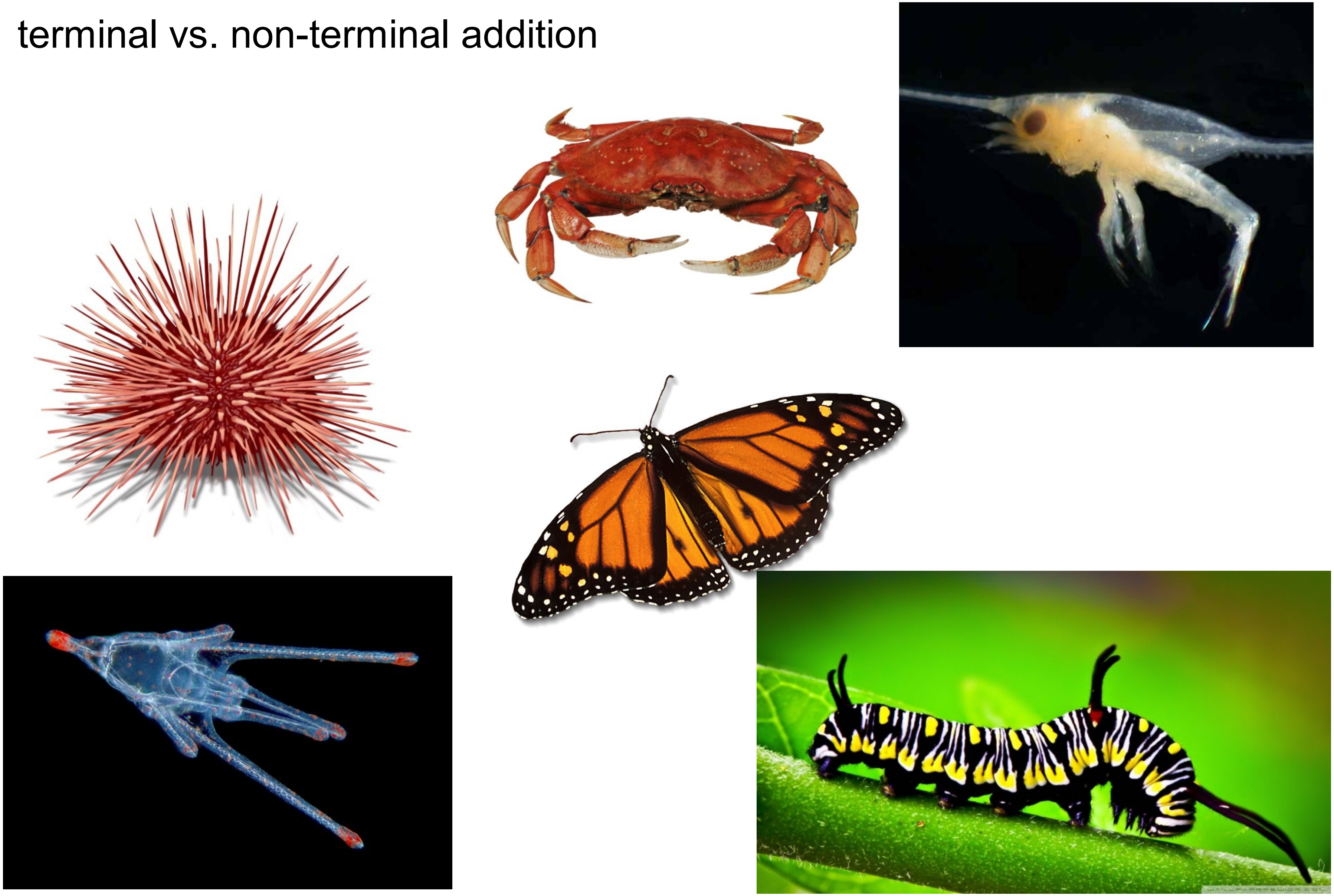


Fig. 1

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

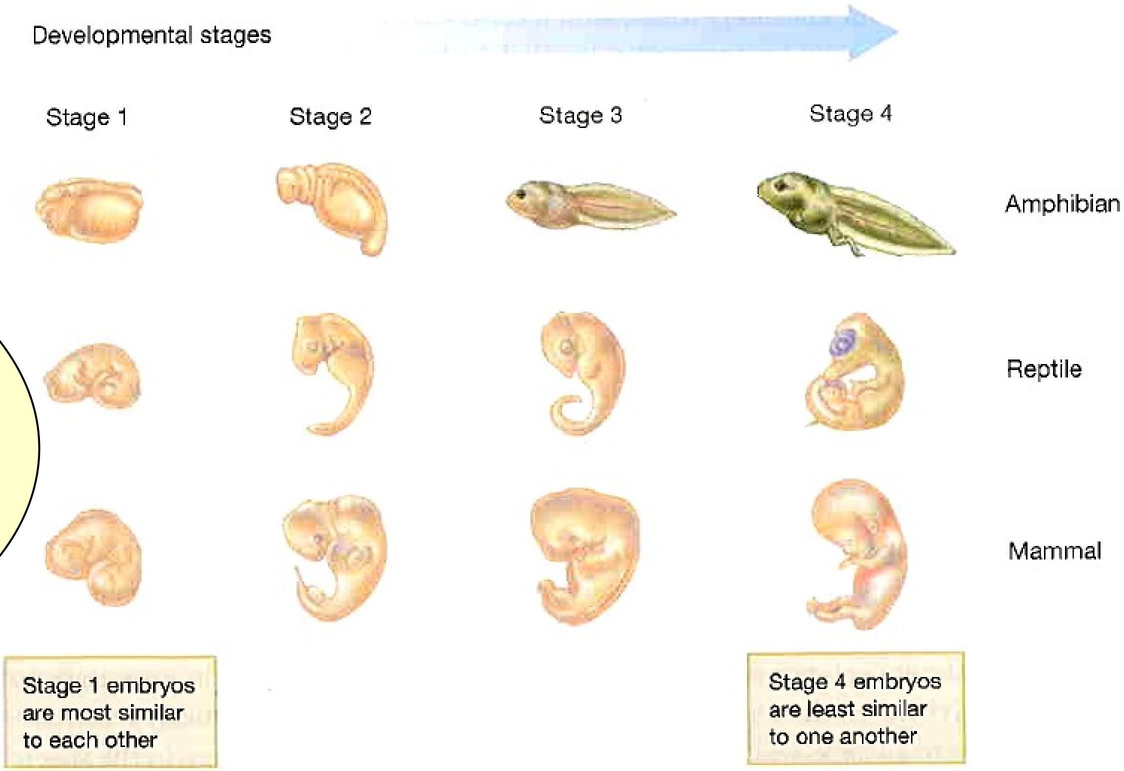
terminal vs. non-terminal addition



# 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.

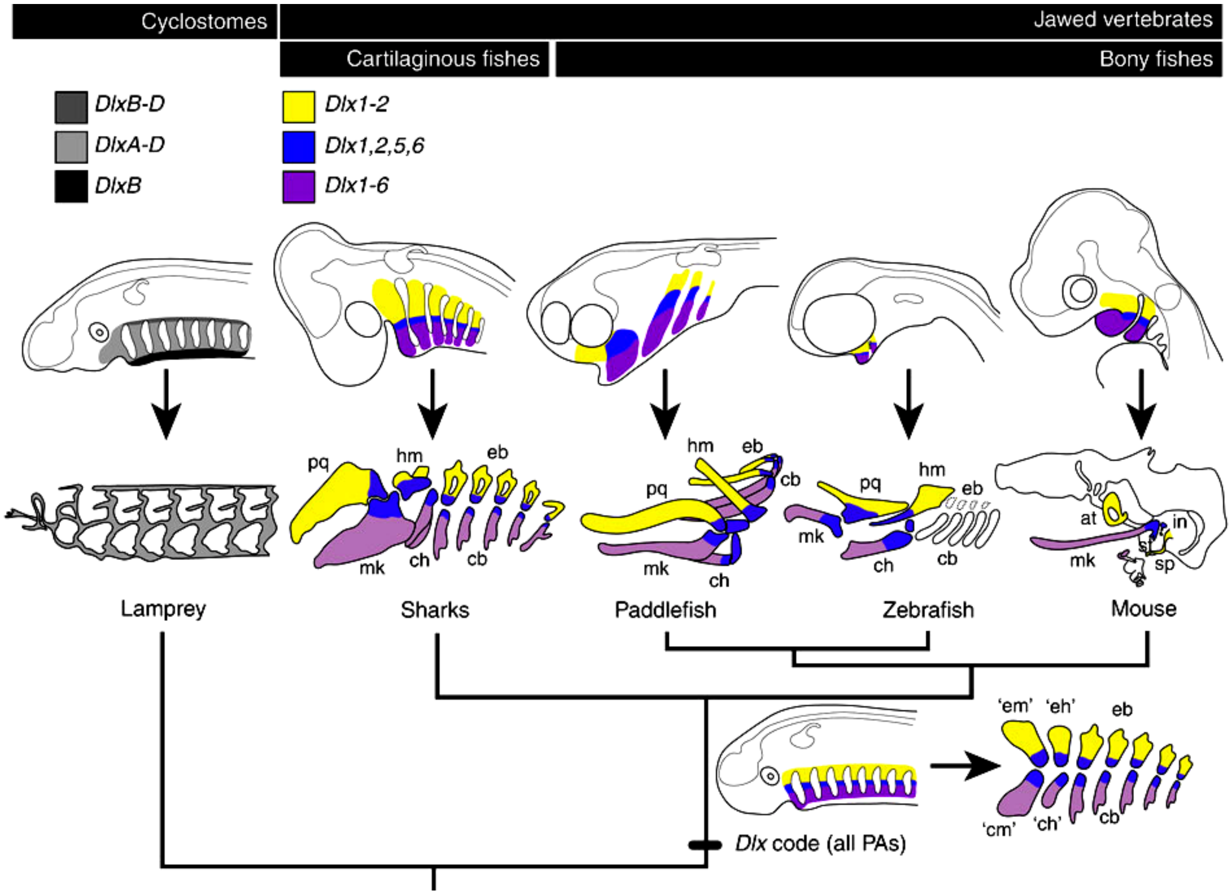


Stage 1 embryos are most similar to each other

Stage 4 embryos are least similar to one another

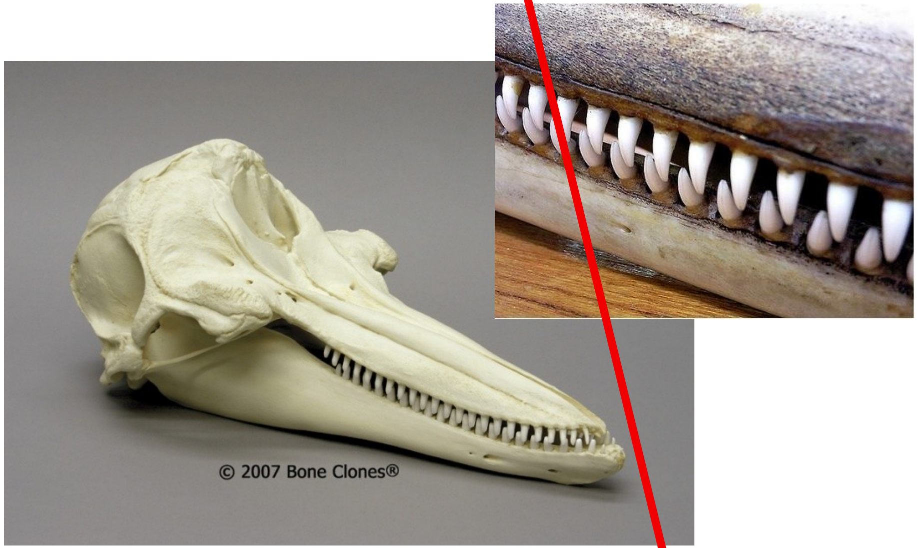
# Karl Ernst von Baer – embryological laws:

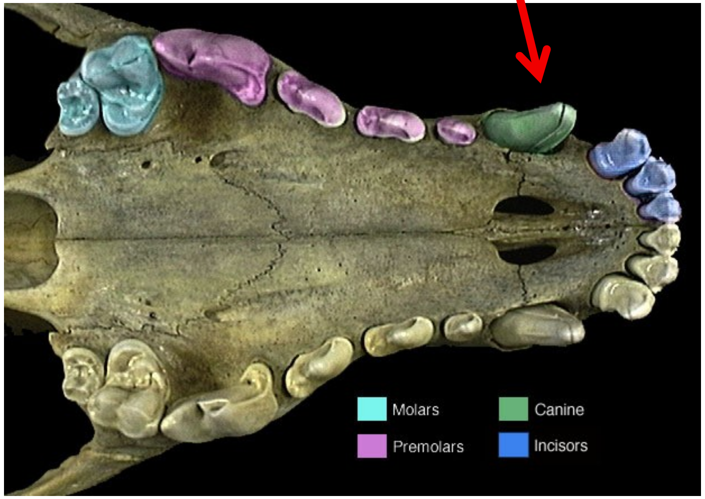
1st law: General traits of a large animal group appear in the embryo earlier than special traits (eg. cartilage in bony fishes).

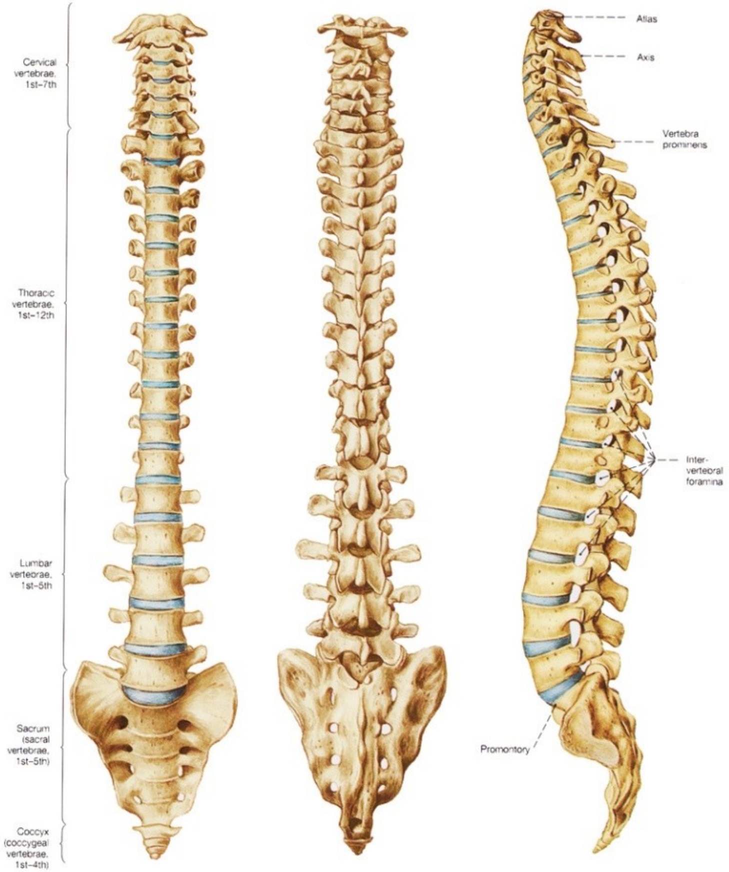


# General principles of ontogeny and evolution:

## modularization and individualization: serial homology and homonymy

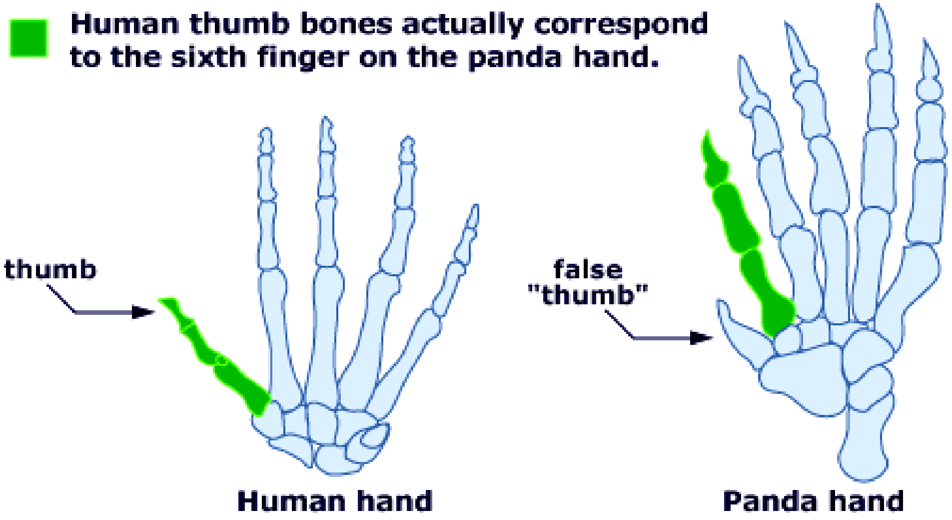


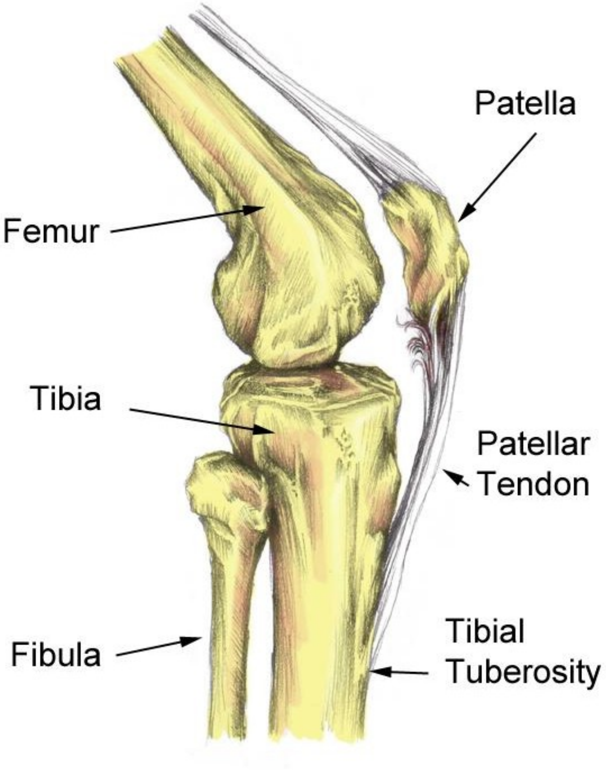




# General principles of ontogeny and evolution:

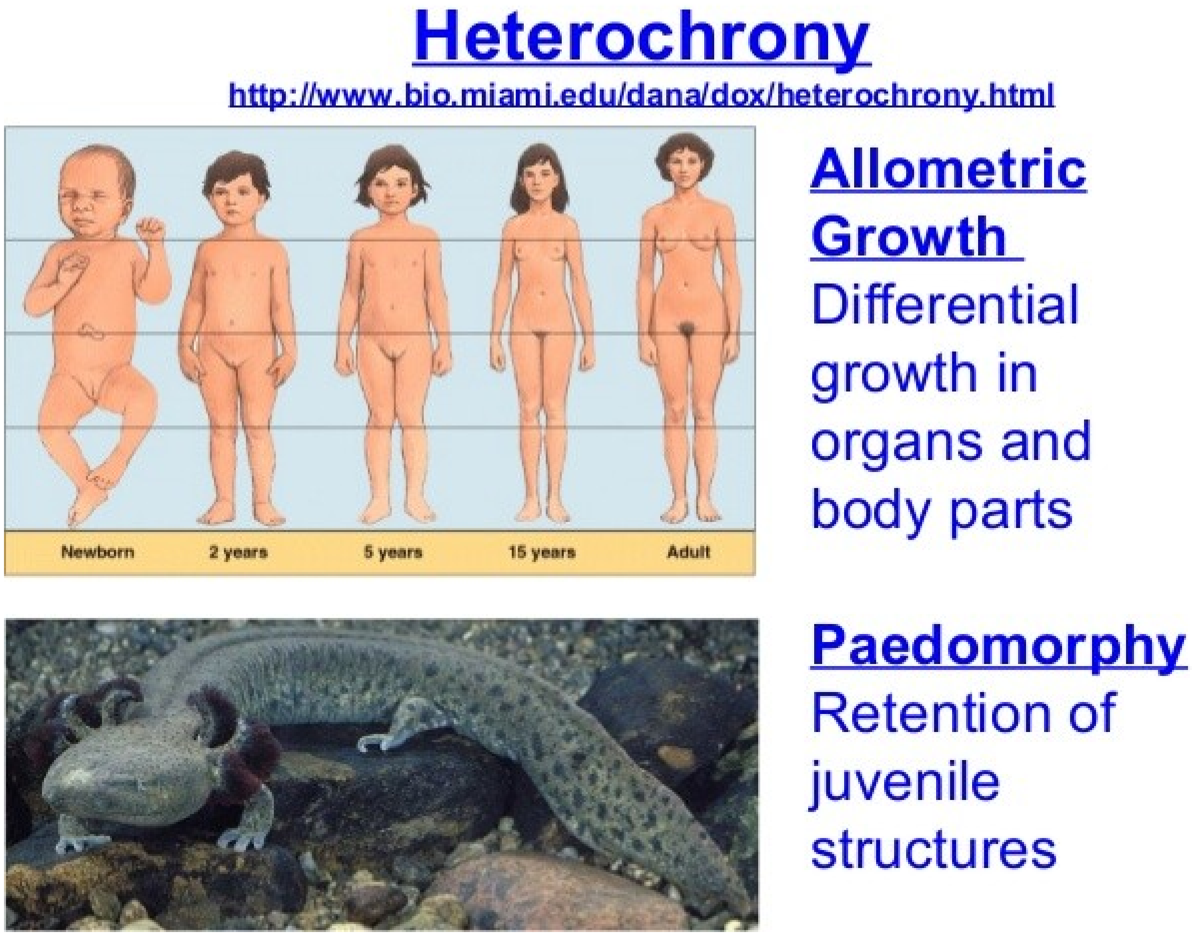
heterotopy = change of the position of a trait phenotypic expression (eg. photosynthesis in succulent stem; sesamoid bones – *patella*, ossified tendons in dinosaur tails, „panda´s thumb“)





# 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:

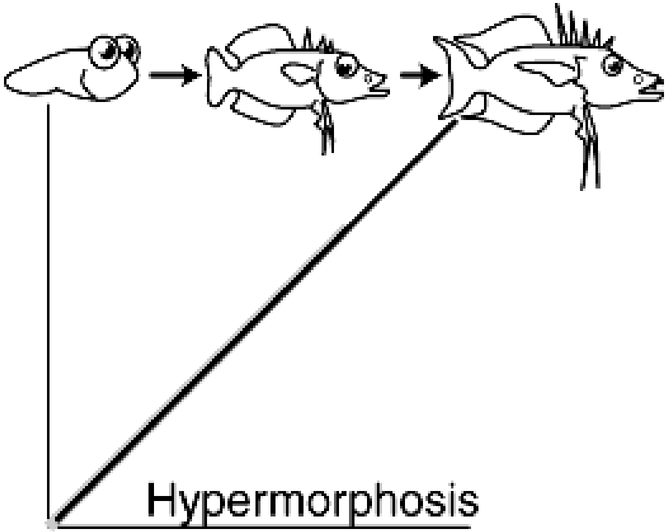
| | | Somatic traits | Reproductive org. |
|---|---|---|---|
| peramophosis | | | |
| | | | |
| paedomorphosis | | | |
| | | | |

= 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 | | | |
| | | | |

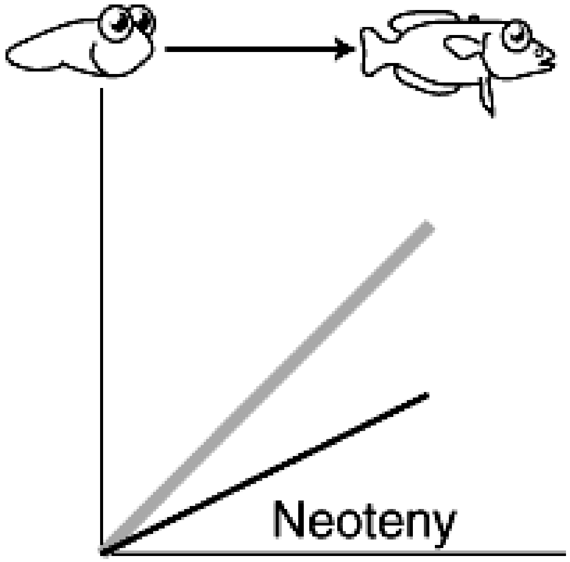



hypermorphosis

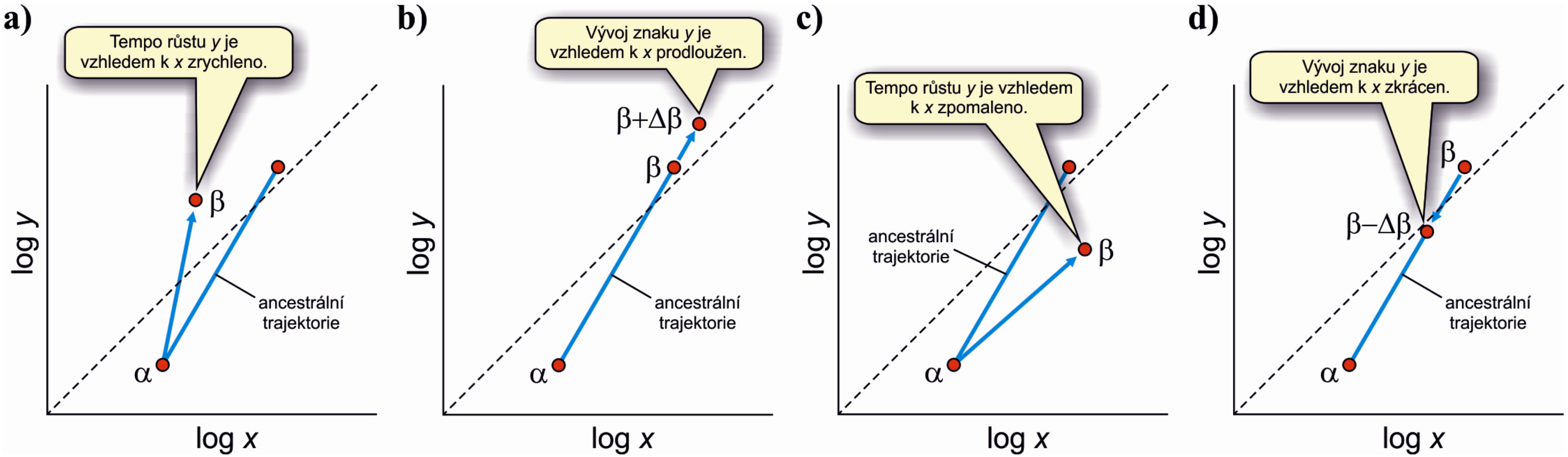
*Megaceros giganteus*

# 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]

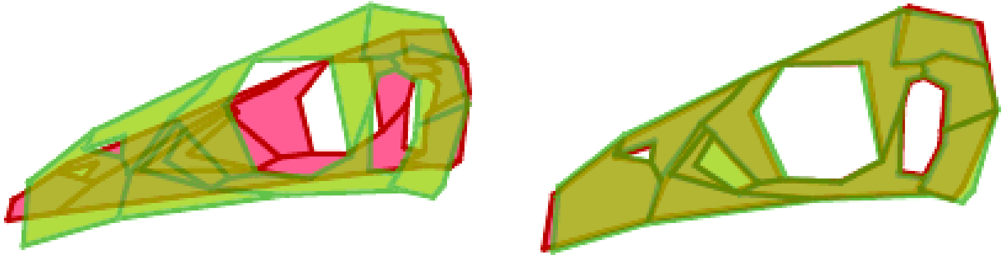
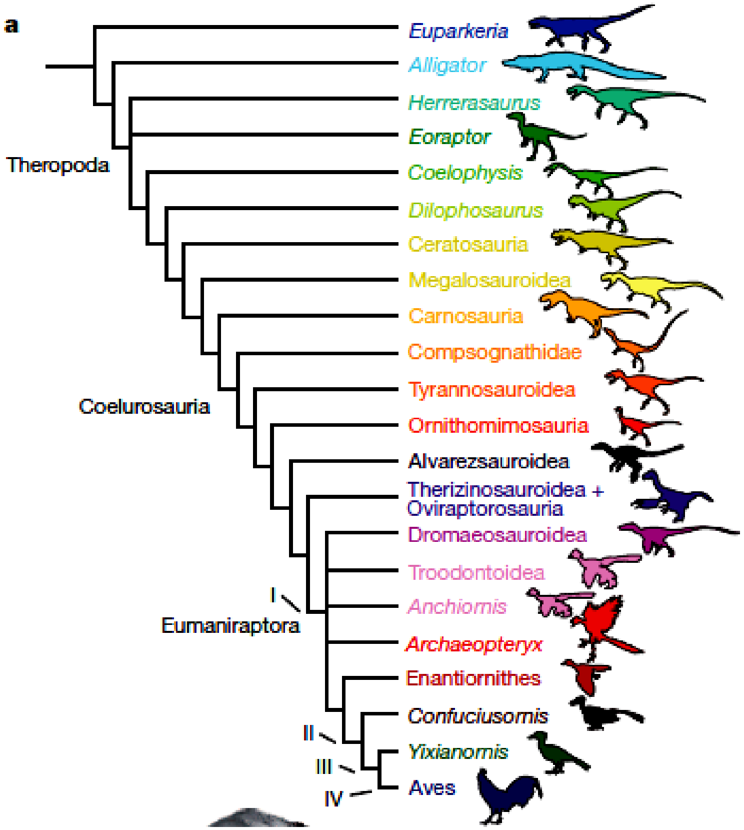


**Figure 4 | Similarity of embryonic *Alligator* and adult *Confuciusornis* skulls.** Superimposition of *Alligator* embryo skull (green) onto *Alligator* adult skull (red, left) and onto *Confuciusornis* adult skull (red, right), showing the nearly identical skull configuration of the latter two and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



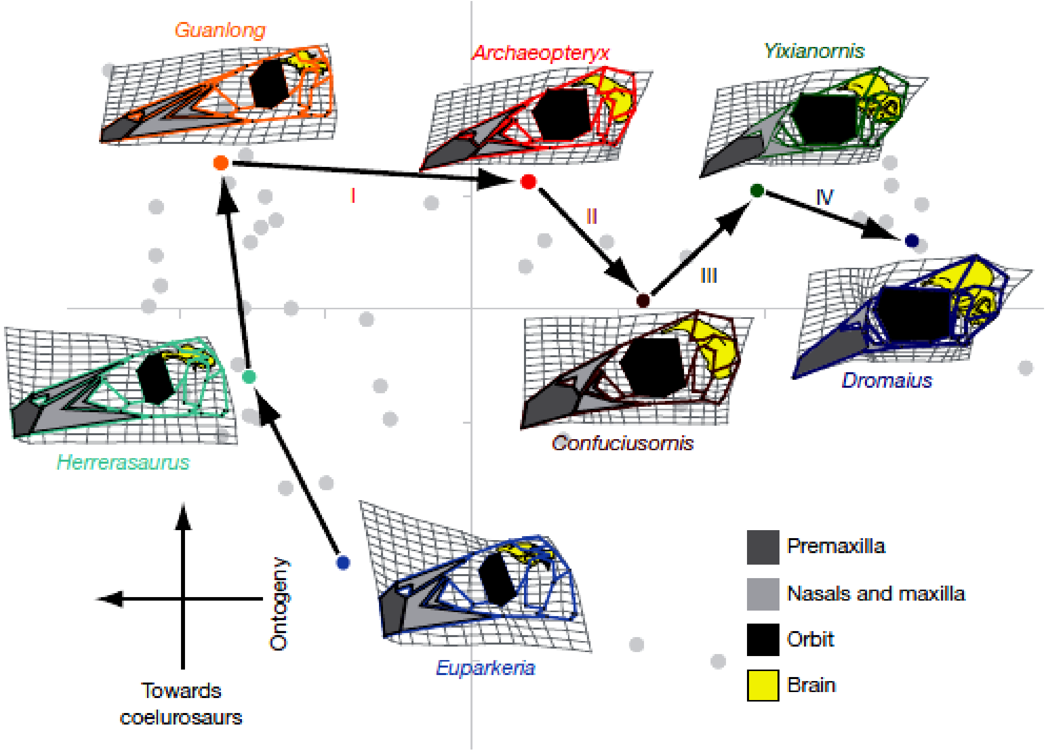
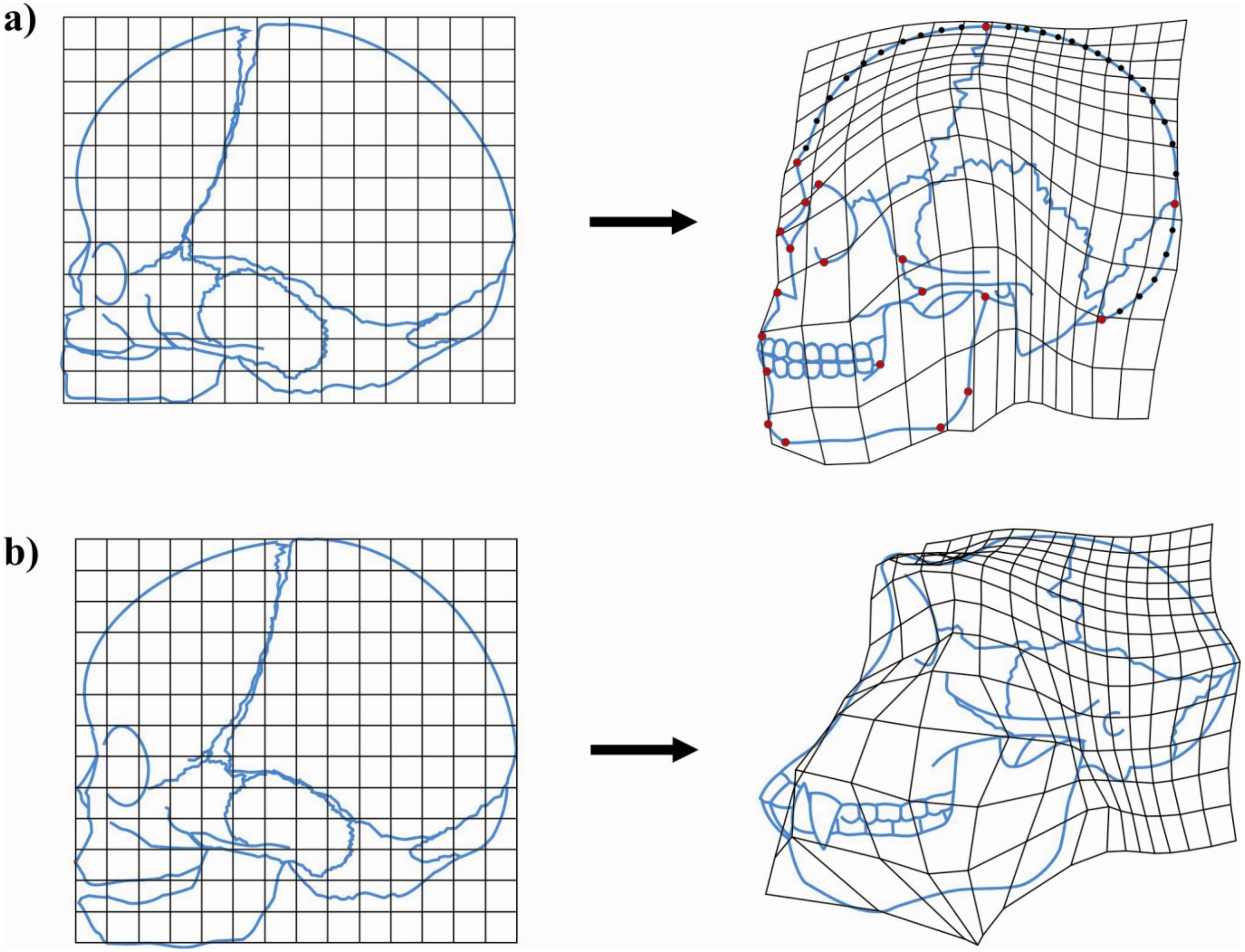


**Figure 5 | Summary of heterochrony and phylogeny in bird skull evolution.** A phylogenetic sequence with skull outlines set on deformation grids is depicted from the primitive stem-group archosaur *Euparkeria* to the modern emu *Dromaius*. Heterochronic transformations referred to in the text are enumerated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

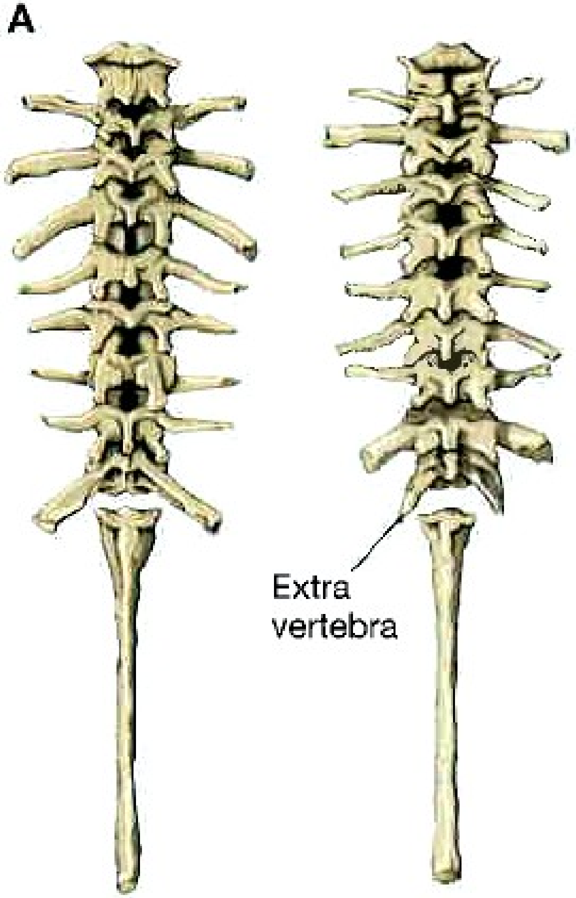
role of gene duplications – more radical changes enabled

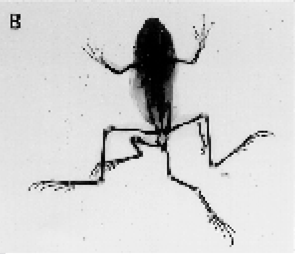
symbiosis, gene transfer (retroviruses)

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)





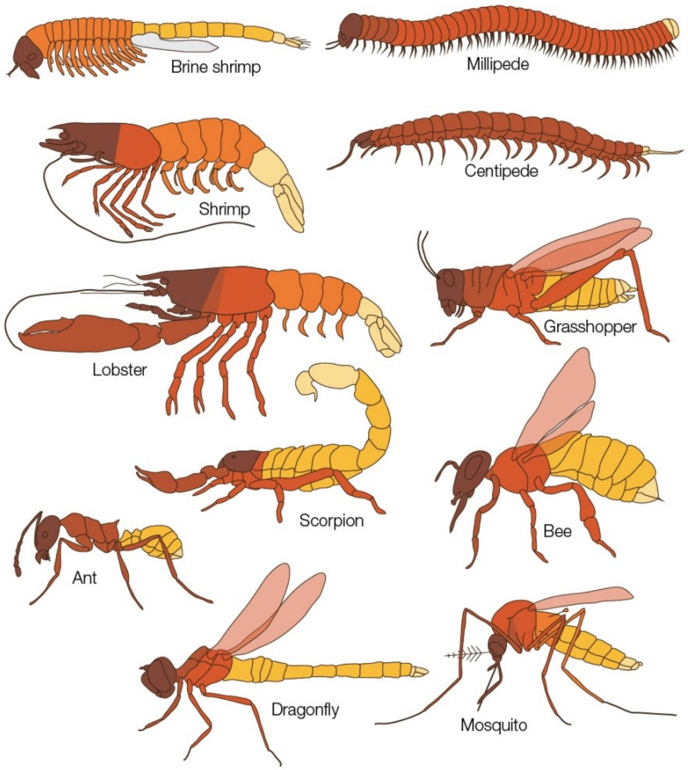
# Homeotic (*Hox*) genes

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>

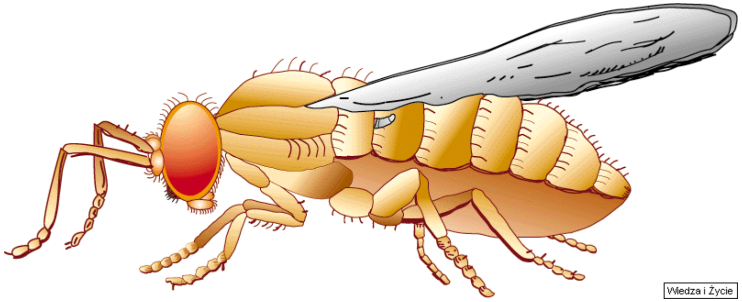
control of transcription of other genes (eg. *Ubx* probably regulates hundreds of „target“ genes)

determination of basic body segmentation

high evolutionary conservativeness

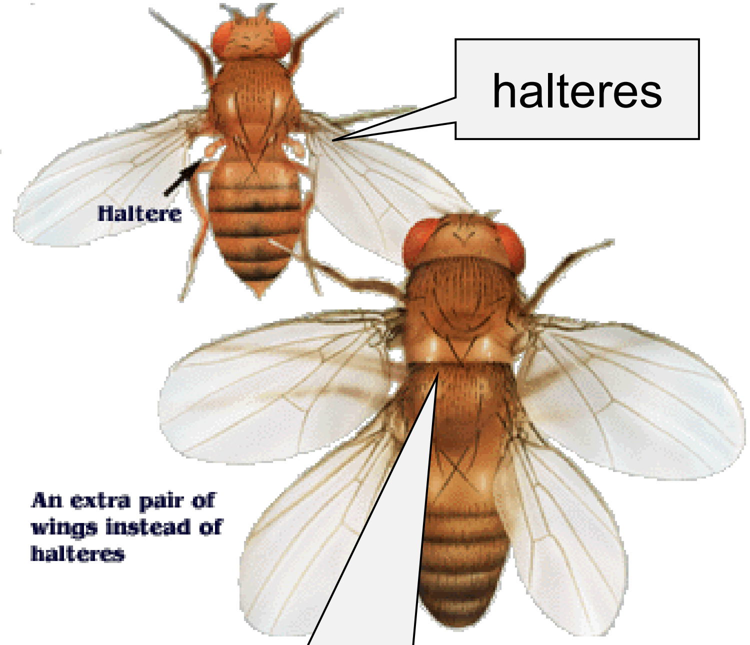


# Homeotic mutation



Wiedza i Życie

*Antennapedia*



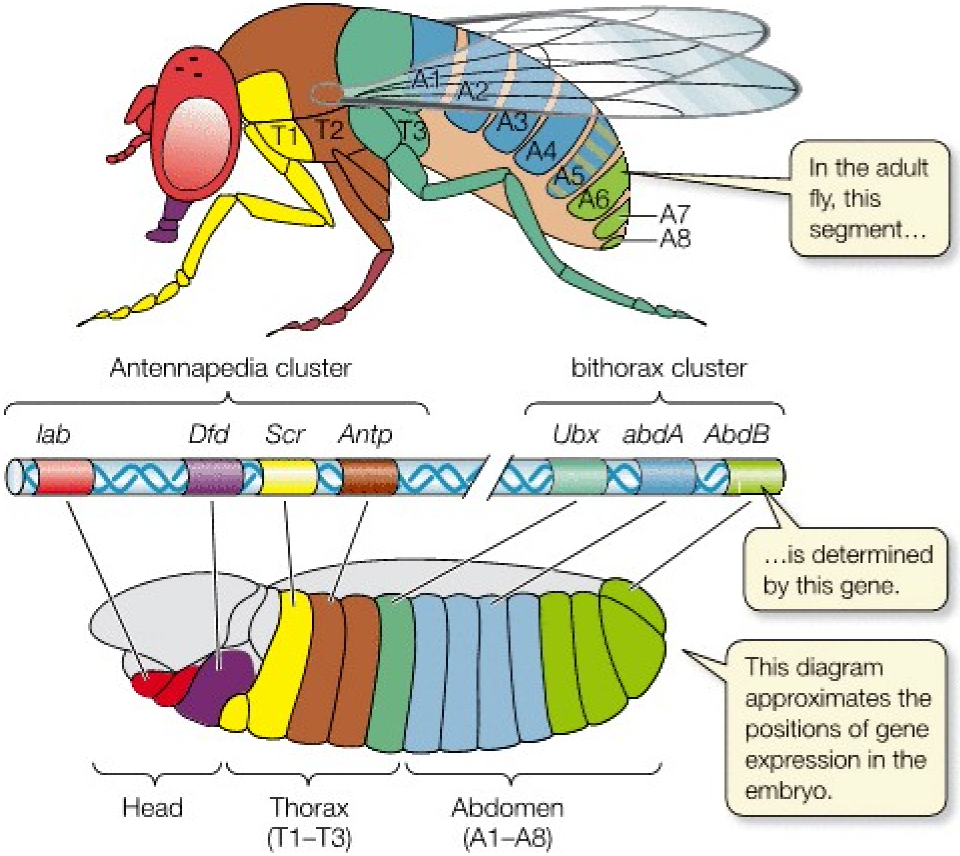
halteres

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

*Bithorax*

# *Hox* genes: basic antero-posterior body segmentation

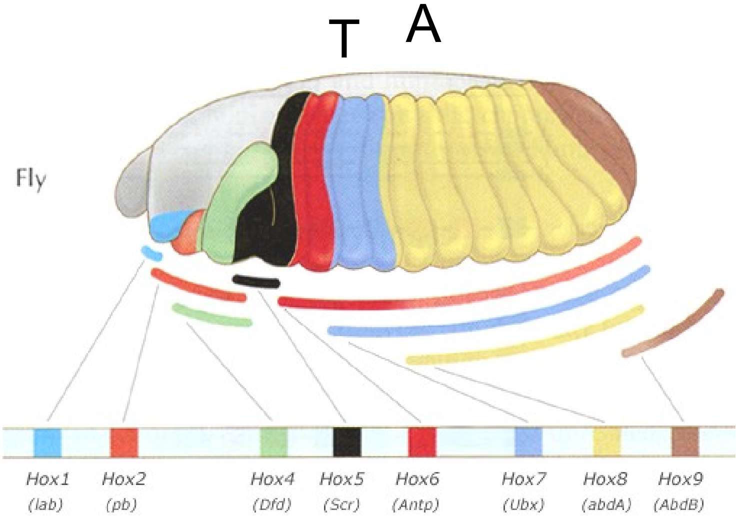
linear clusters, same order as the segments



In the adult fly, this segment…

…is determined by this gene.

This diagram approximates the positions of gene expression in the embryo.



*Hox* gene effects are overlapping

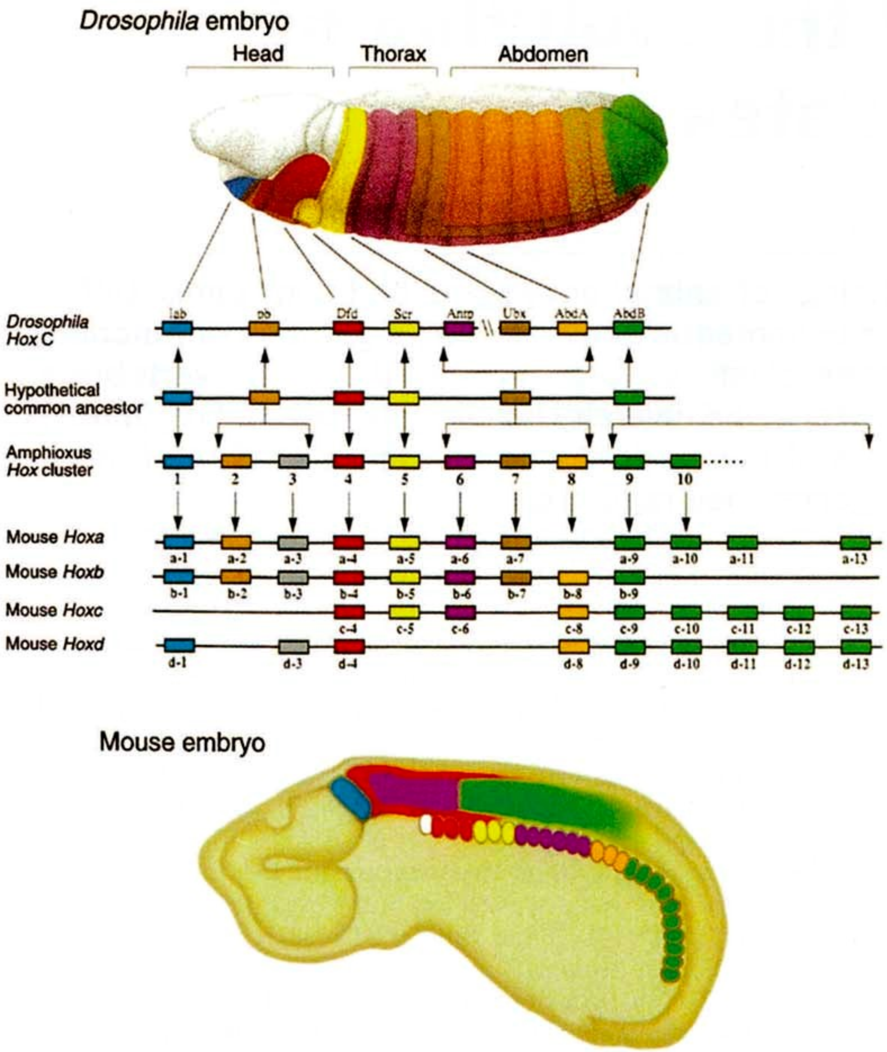
*Drosophila*: 1 linkage group, 2 clusters:

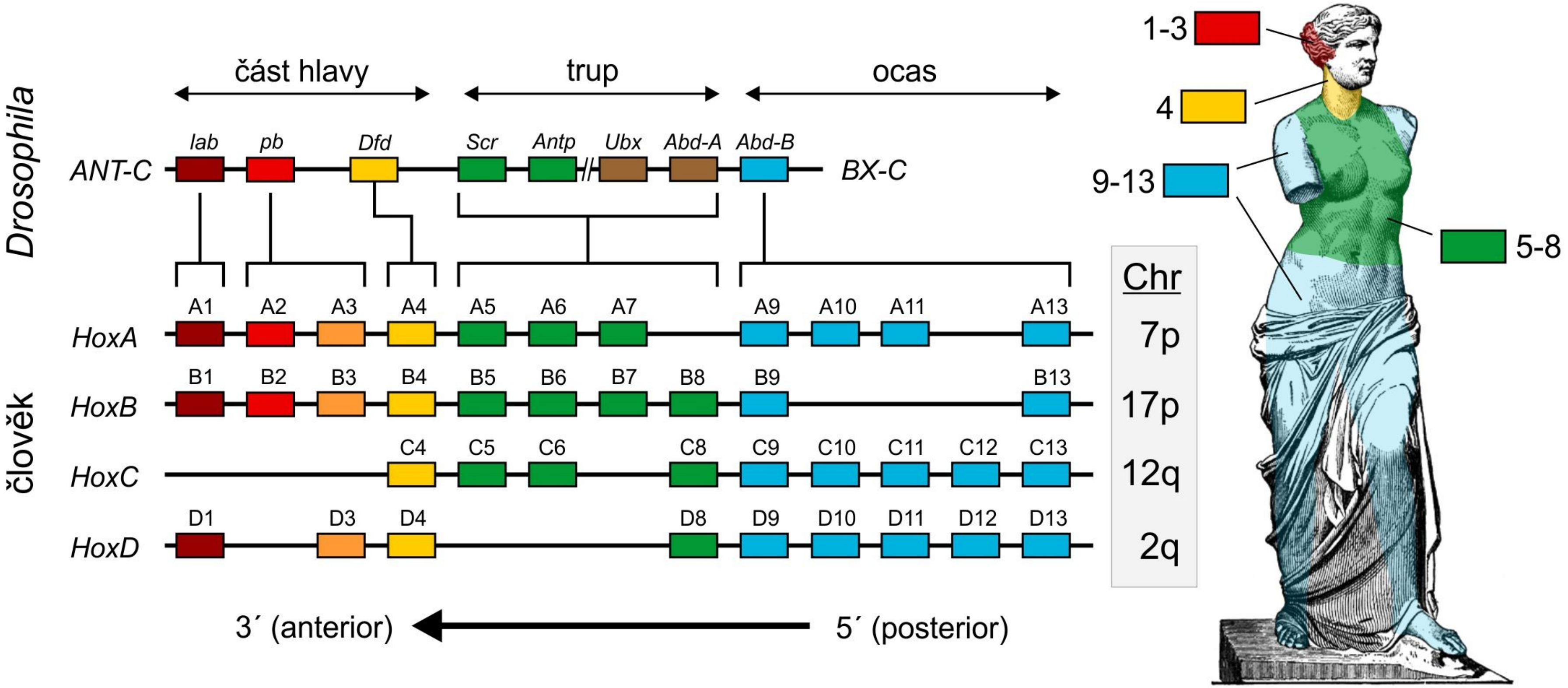
*Antennapedia* (ANT-C)

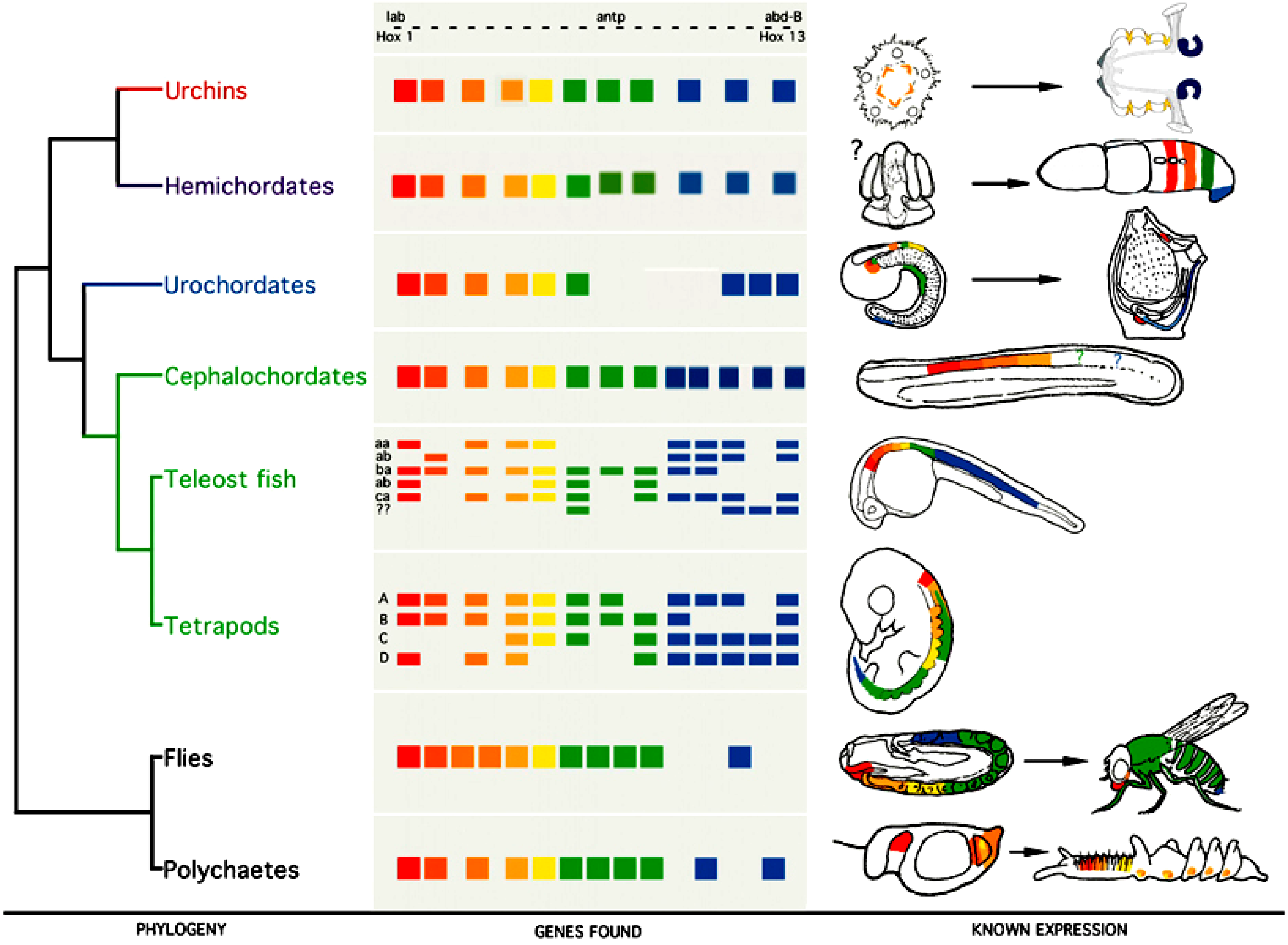
*Bithorax* (BX-C)

vertebrates:

4 linkage groups

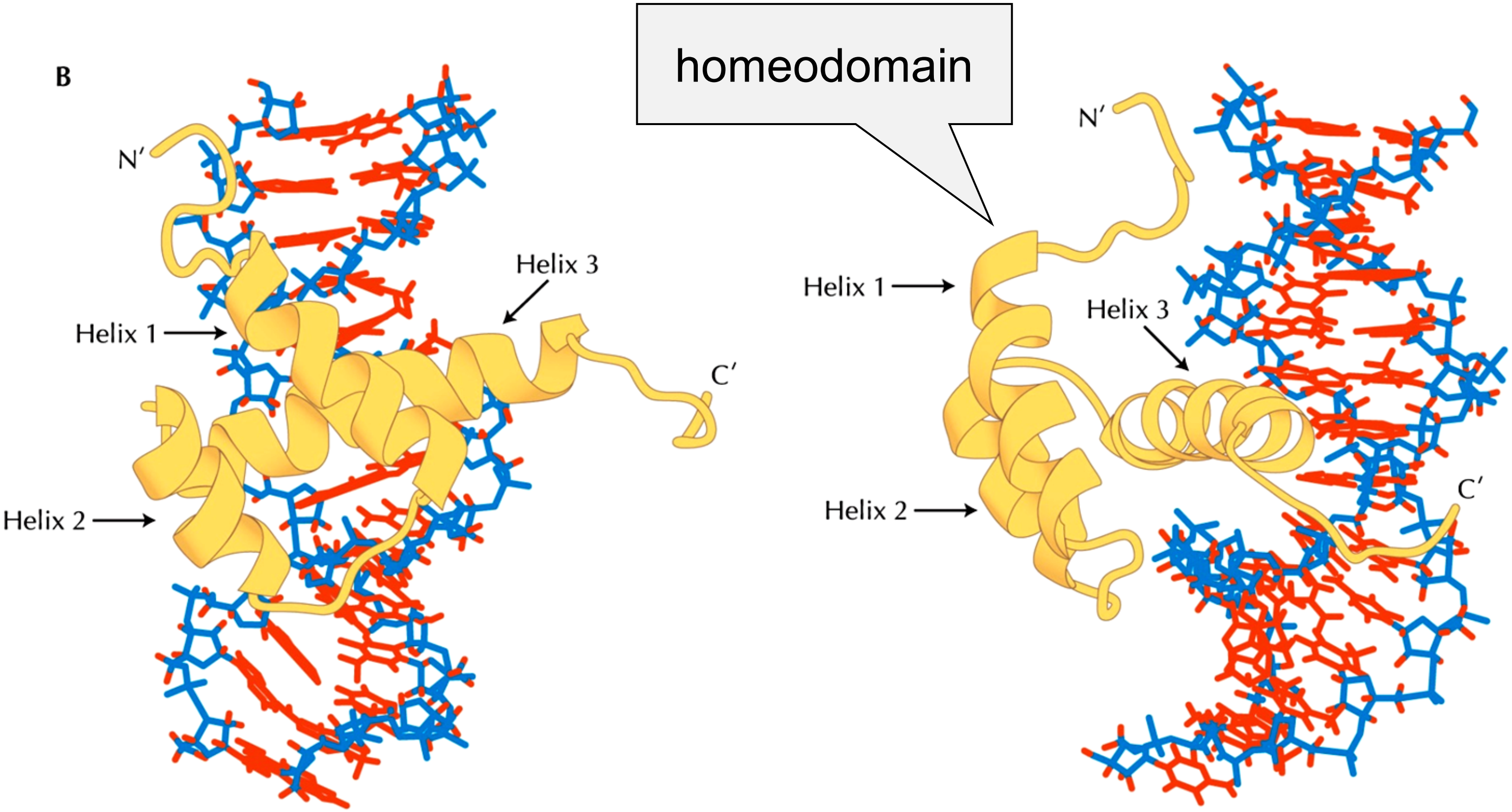



Drosophila
člověk
část hlavy
trup
ocas
ANT-C
lab
pb
Dfd
Scr
Antp
Ubx
Abd-A
Abd-B
BX-C
HoxA
A1
A2
A3
A4
A5
A6
A7
A9
A10
A11
A13
HoxB
B1
B2
B3
B4
B5
B6
B7
B8
B9
B13
HoxC
C4
C5
C6
C8
C9
C10
C11
C12
C13
HoxD
D1
D3
D4
D8
D9
D10
D11
D12
D13
Chr
7p
17p
12q
2q
3´ (anterior)
5´ (posterior)
1-3
4
9-13
5-8


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

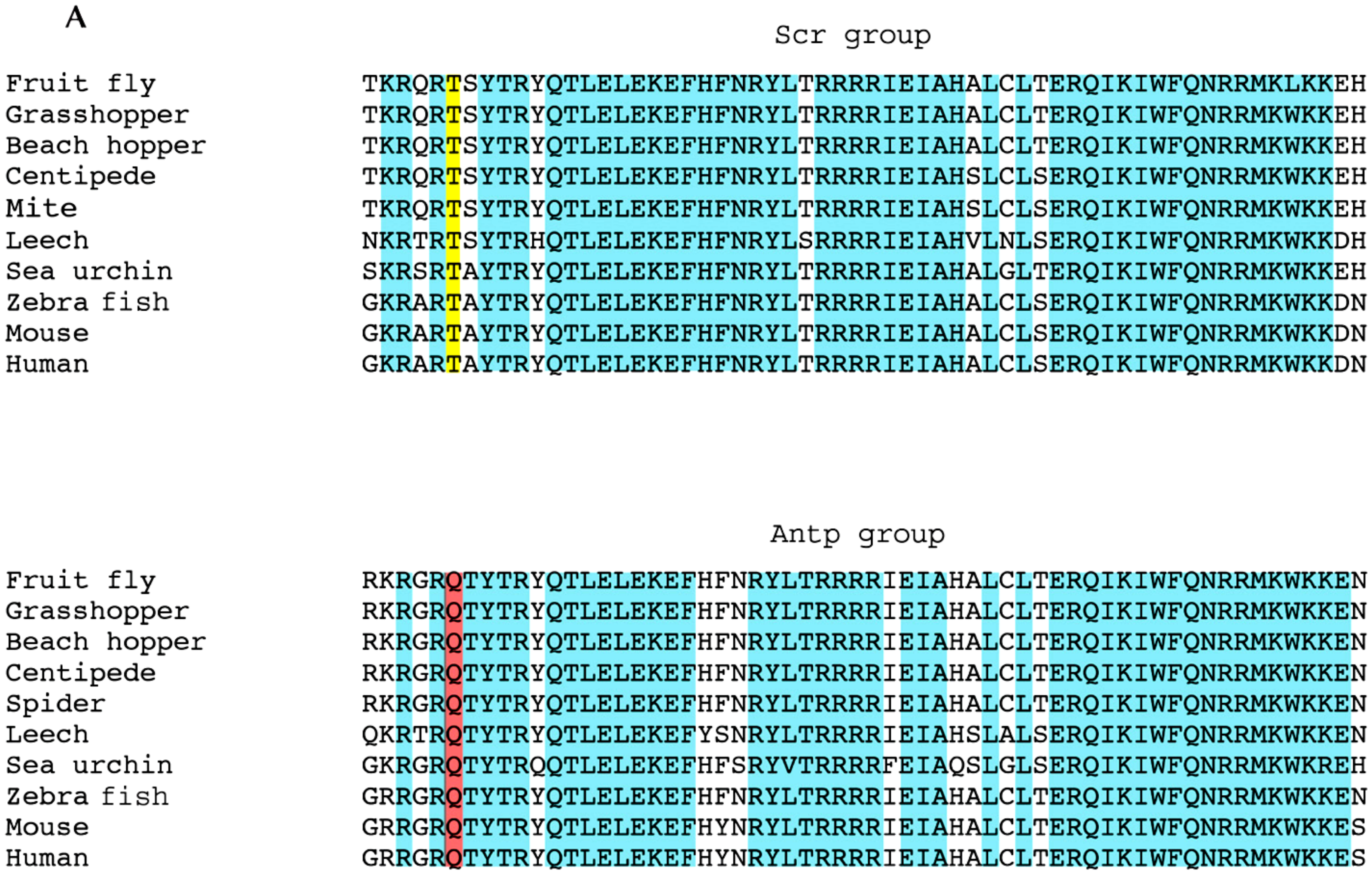
# Homeobox: 180 bp → homeodomain

60 AA (expression regulation)



homeodomain

# *Hox*-genes are highly conservative



A

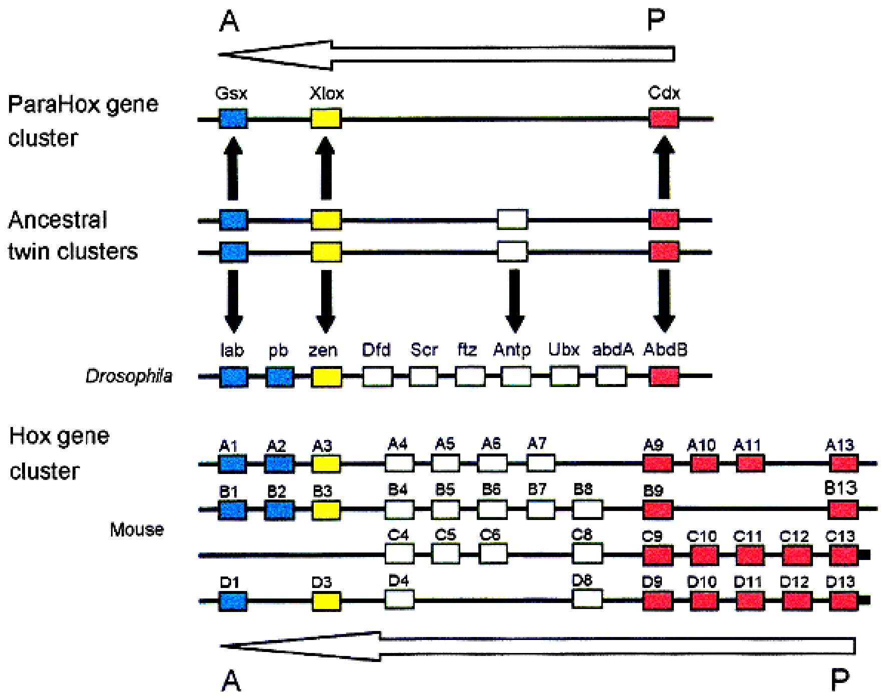
Scr group

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

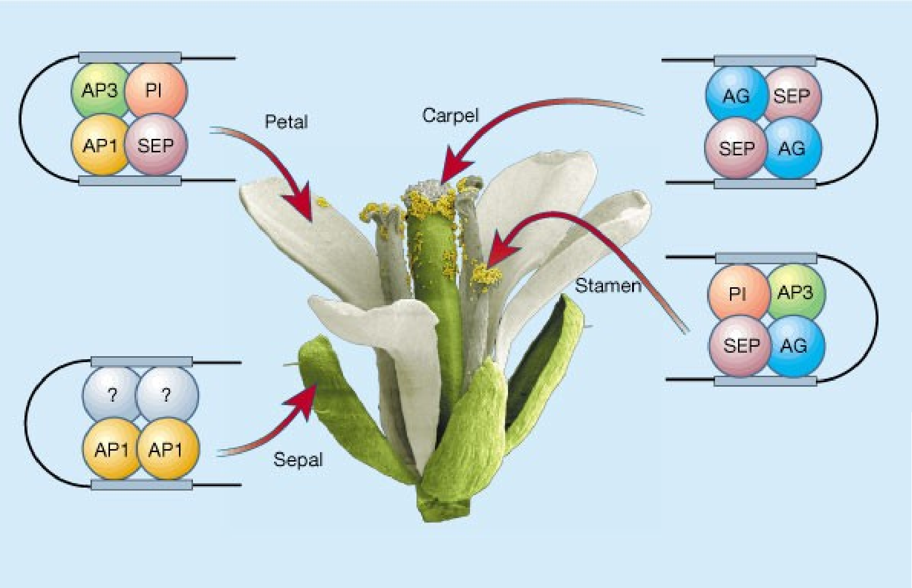
Antp group

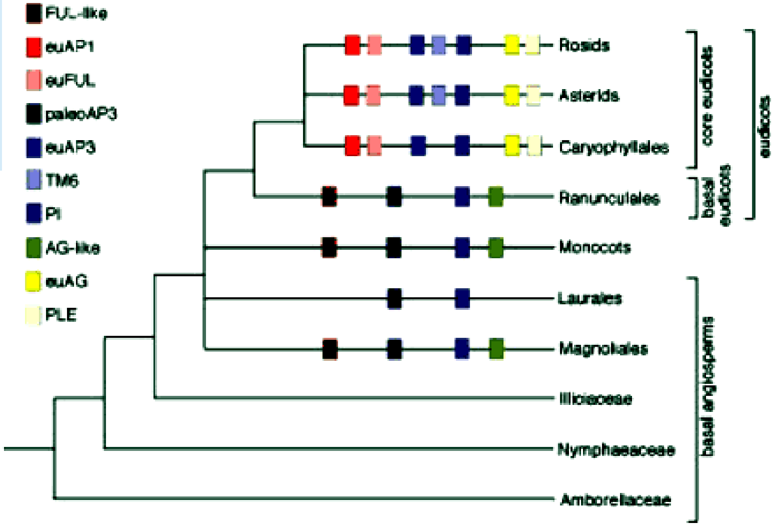
```
Fruit fly       RKRGRQTYTRYQTLELEKEFHFNRYLTRRRRIEIAHALCLTERQIKIWFQNRRMKWKKEN
Grasshopper     RKRGRQTYTRYQTLELEKEFHFNRYLTRRRRIEIAHALCLTERQIKIWFQNRRMKWKKEN
Beach hopper    RKRGRQTYTRYQTLELEKEFHFNRYLTRRRRIEIAHALCLTERQIKIWFQNRRMKWKKEN
Centipede       RKRGRQTYTRYQTLELEKEFHFNRYLTRRRRIEIAHALCLTERQIKIWFQNRRMKWKKEN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

# *ParaHox* genes

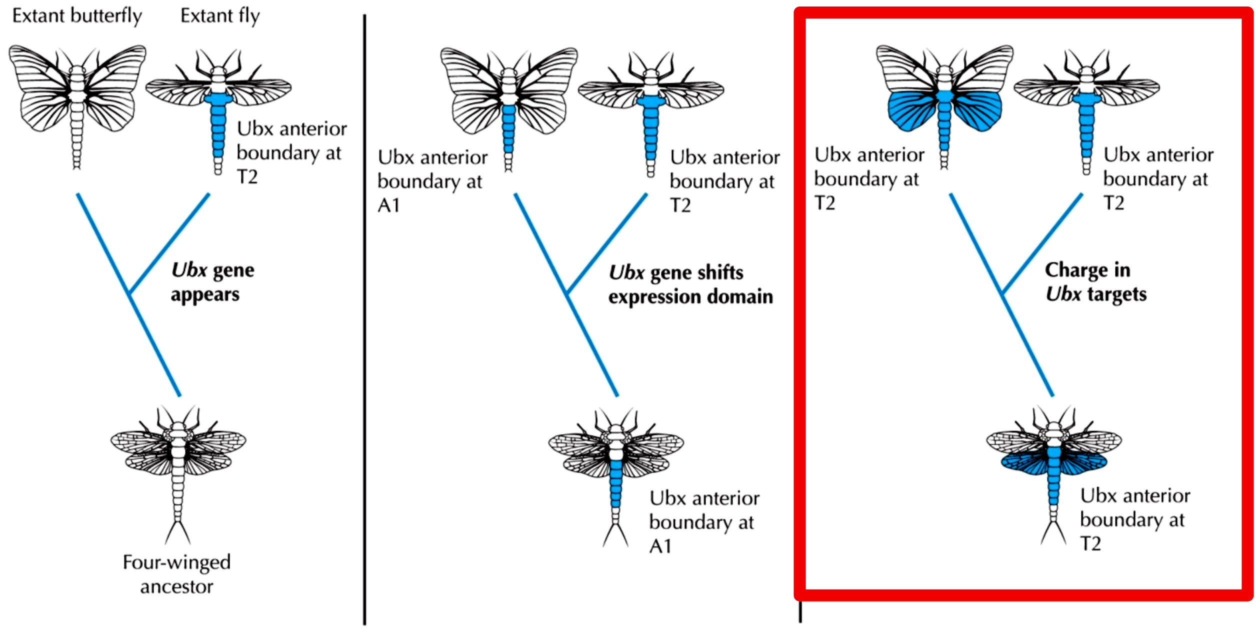


# MADS-box genes in plants

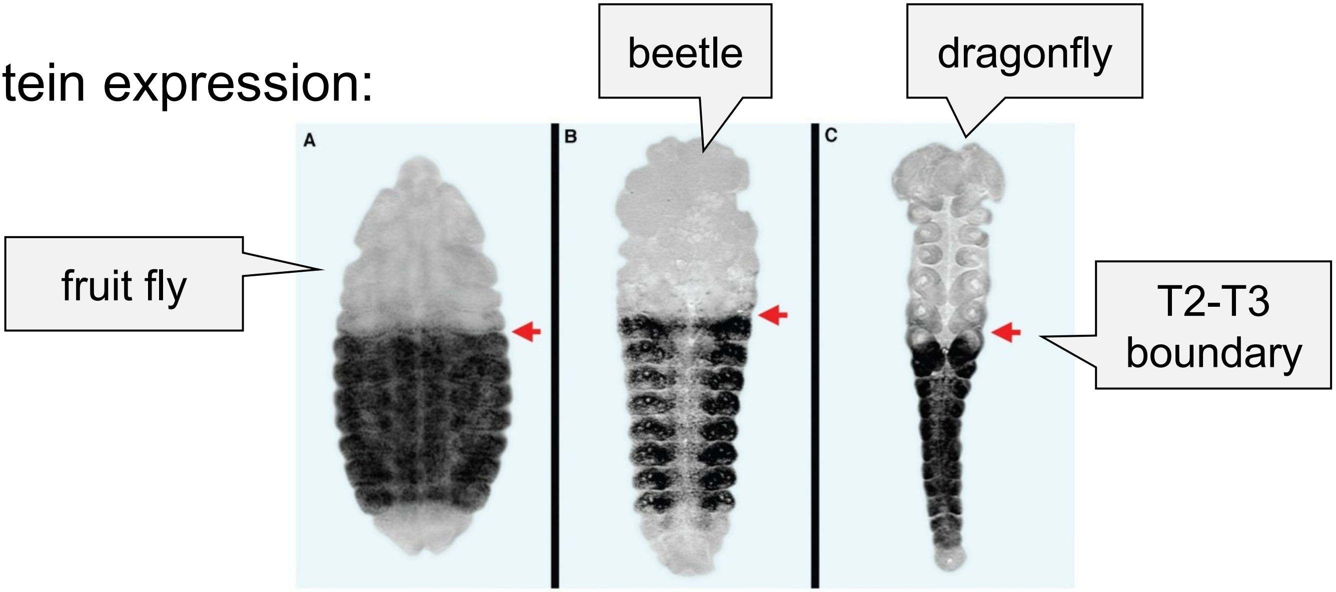




# 3 hypotheses of the origin of dipteran arrangement:



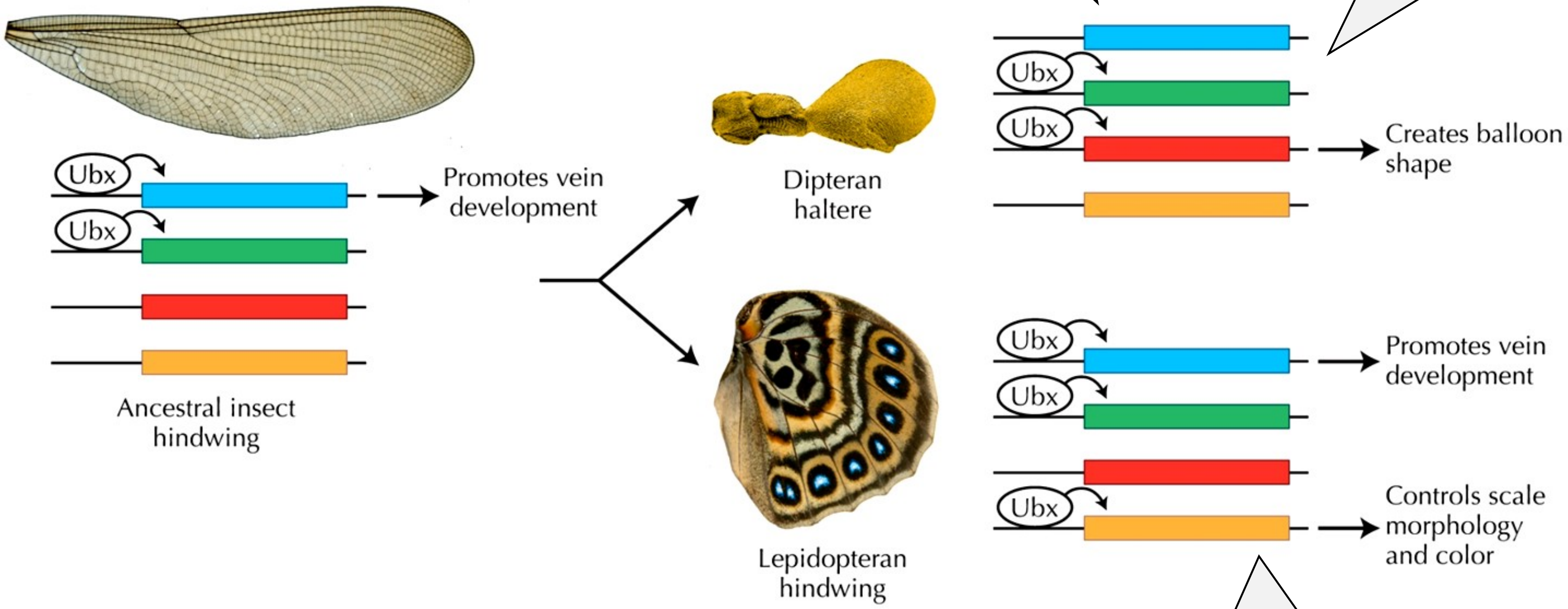
## Ubx protein expression:



original function:
venation development

loss of
function ...

... but origin of
halteres

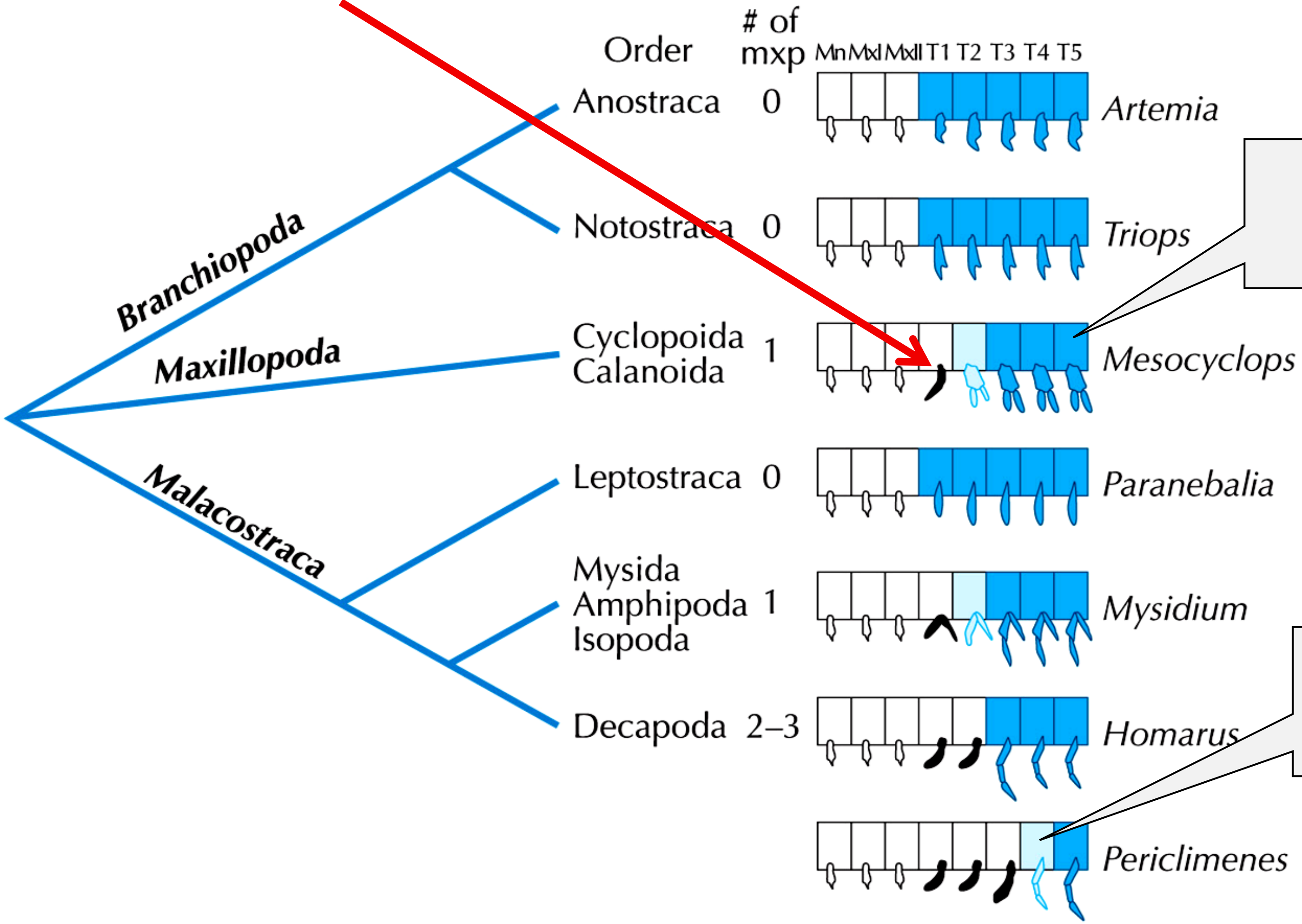


in butterflies also
scale morphology
and wing coloration

# 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

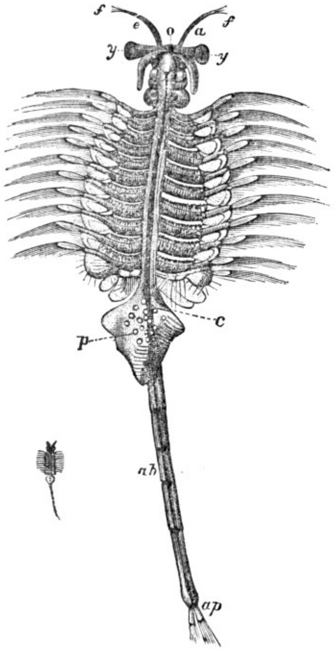


strong *Ubx* expression

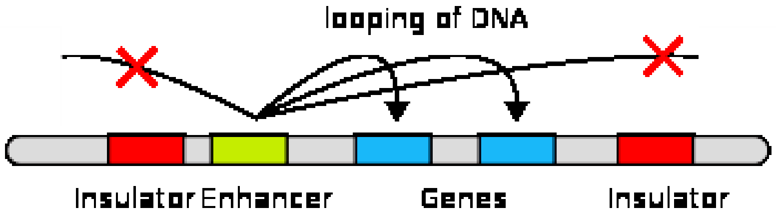
weak *Ubx* expression

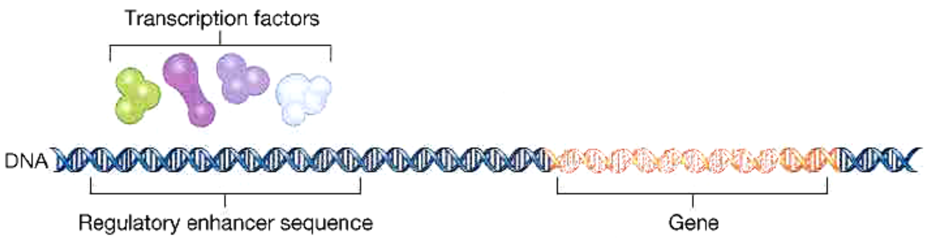
shift of anteroposterior boundary of *Ubx* gene expression = position of transition of locomotory segments and maxillipedes

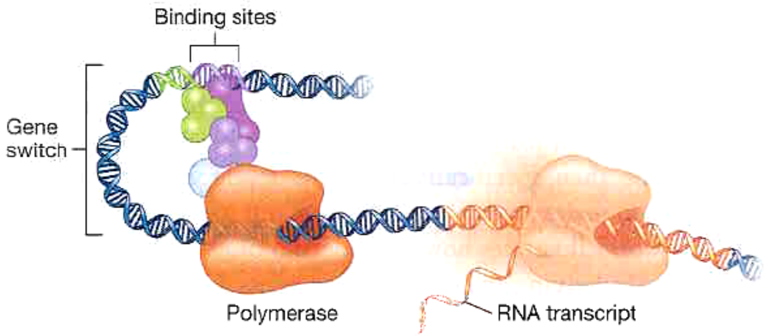
např. opossum shrimps: 2nd segment, prawns: 4th segment
2nd thoracic limb of opossum shrimps = transitional segment between 1st (maxillipede) and 3rd limb (locomotion)

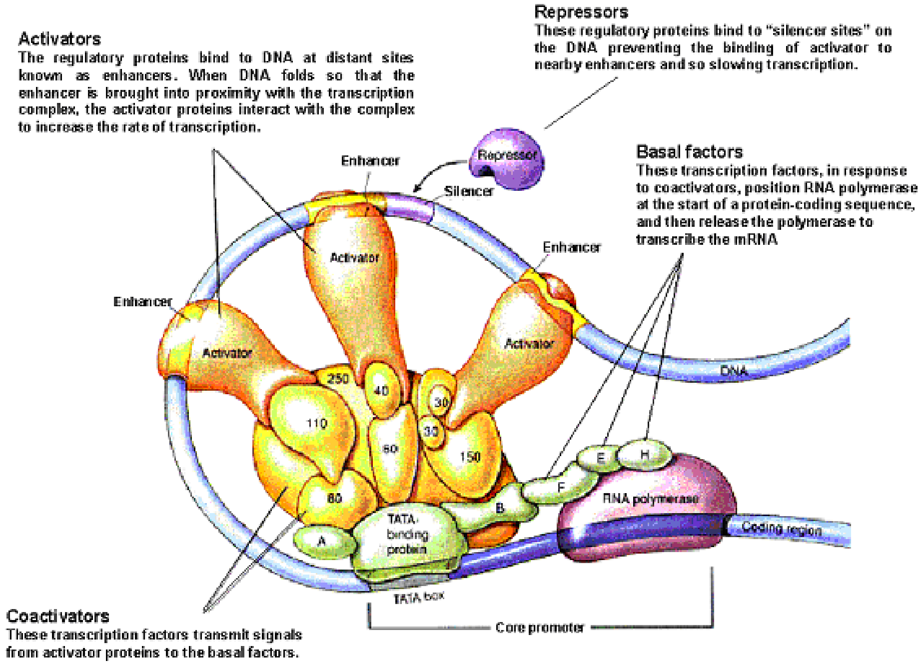


# Besides transcriptional factors also regulatory enhancers:








**Activators**
The regulatory proteins bind to DNA at distant sites known as enhancers. When DNA folds so that the enhancer is brought into proximity with the transcription complex, the activator proteins interact with the complex to increase the rate of transcription.

**Repressors**
These regulatory proteins bind to "silencer sites" on the DNA preventing the binding of activator to nearby enhancers and so slowing transcription.

**Basal factors**
These transcription factors, in response to coactivators, position RNA polymerase at the start of a protein-coding sequence, and then release the polymerase to transcribe the mRNA

**Coactivators**
These transcription factors transmit signals from activator proteins to the basal factors.

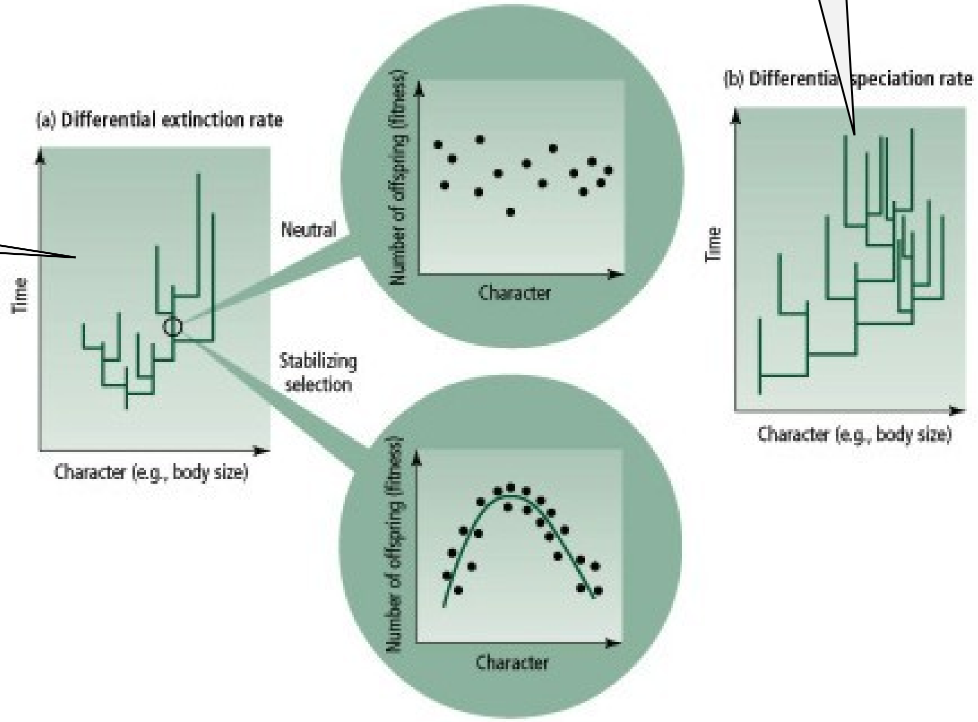
# Macroevolutionary trends species selection

trends: real × passive (eg. wall effect)

Edward Drinker Cope: trend to bigger size

Species selection:

= preferential survival or proliferation of species



different extinction rates

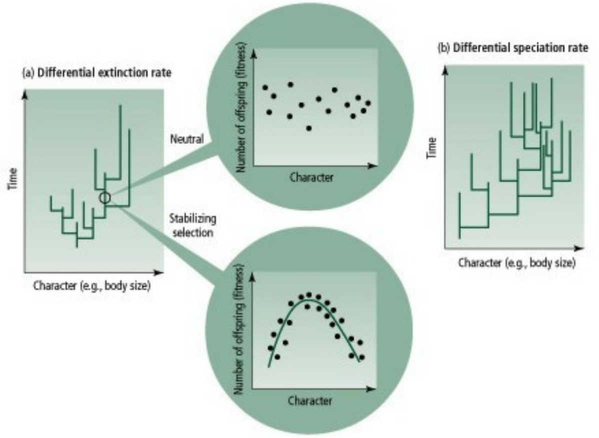
different speciation rates

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