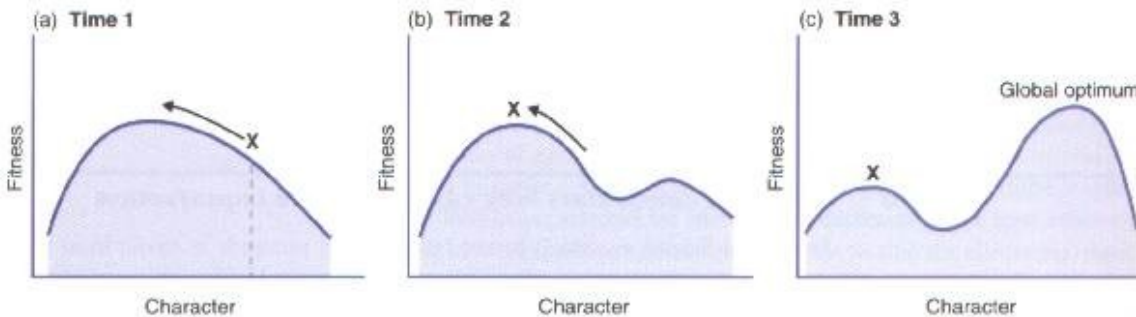
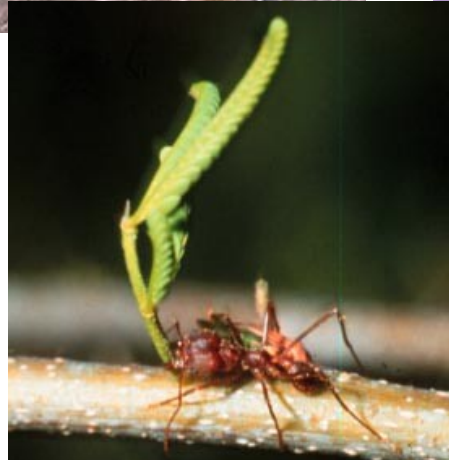
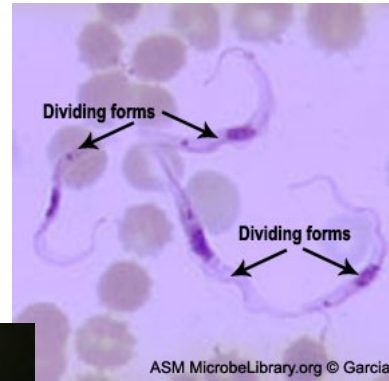
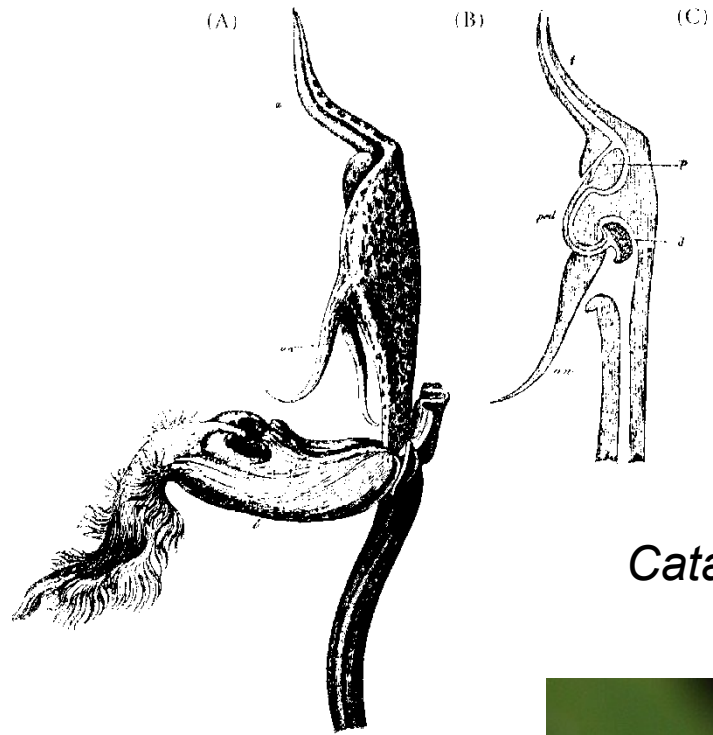


# ADAPTATION AND NATURAL SELECTION



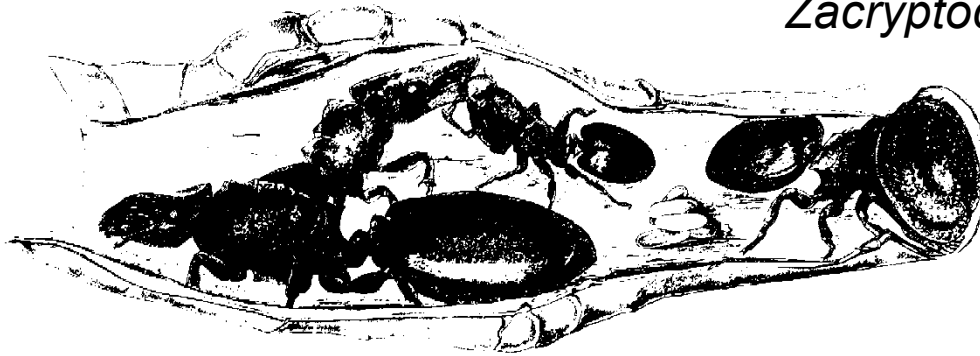
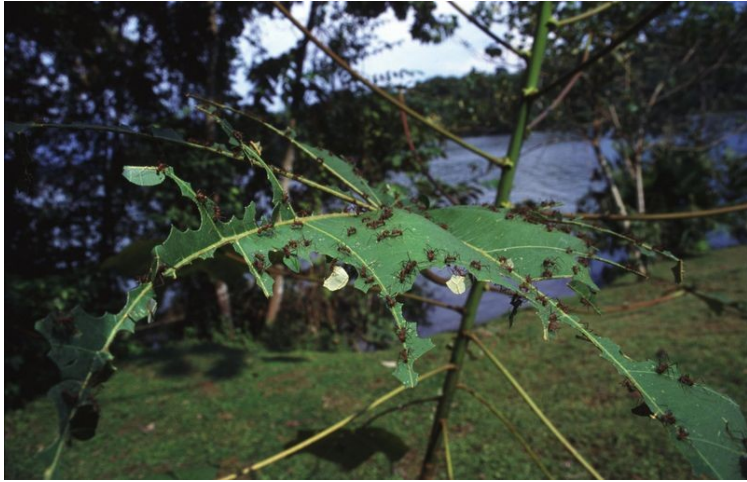


*Catasetum saccatum*



*Chiloglottis formicifera*

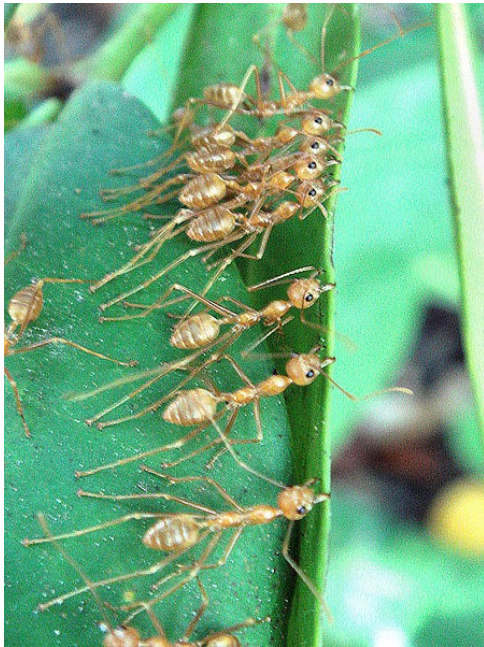
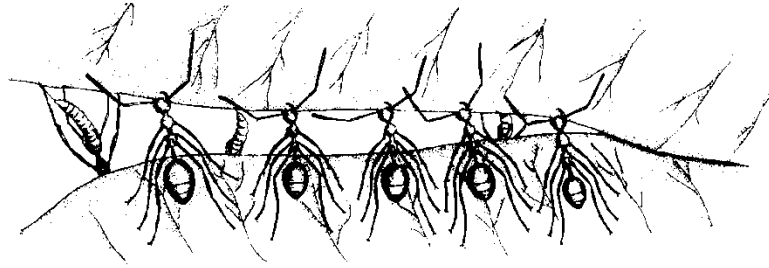
*Atta*, *Acromyrmex*: bigger workers – cutting leaves,  
soldiers – their protection,  
small workers – chewing leaves, growing fungi



*Zacryptocerus varians*



*Oecophylla smaragdina*



parasites × hosts

**life-history strategies** = timing and way of investing to survival and reproduction through the whole life of an individual

eg. timing of sexual maturity, aging,  
number and size of offspring,  
semelparity vs. iteroparity

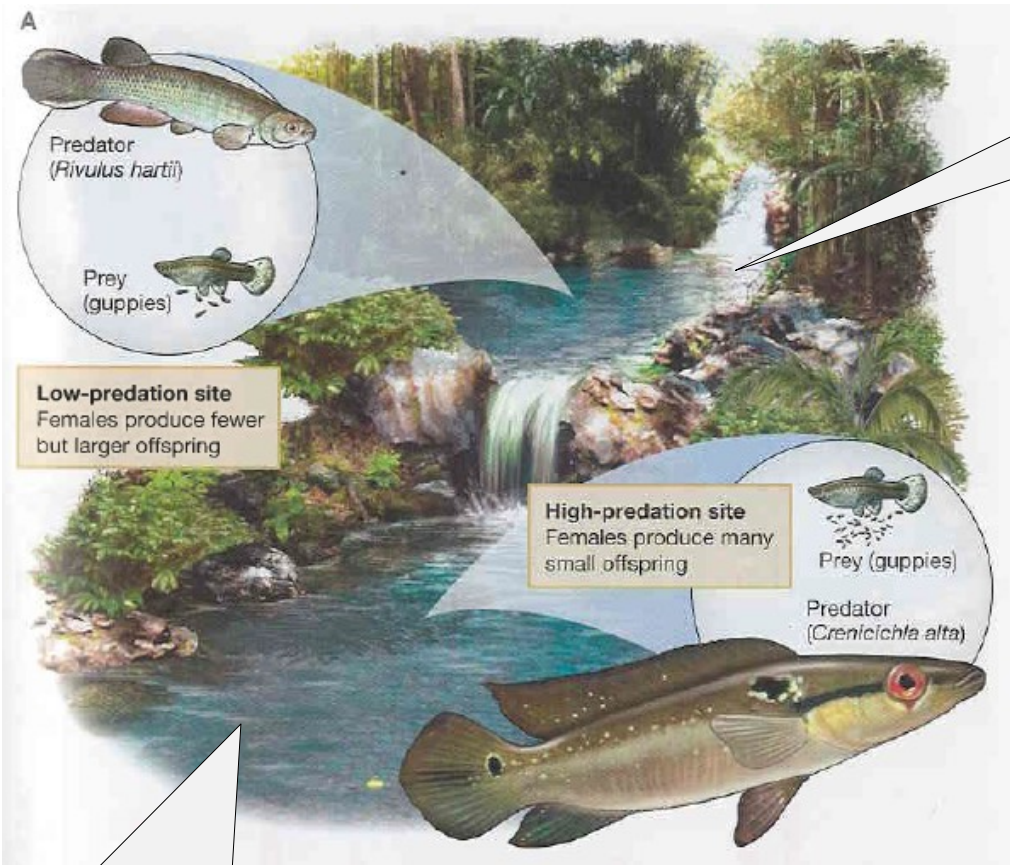
Eg.: guppies, northern Trinidad and Tobago:

upper and lower part of the river separated by waterfalls → barrier both for guppies and predators

upper: moderate predation pressure (*Rivulus hartii*)

lower: strong predation pressure (eg. *Crenicichla alta*)

→ different coloration, antipredatory behaviour, life-history parameters (different number and size of offspring, age of the first reproduction, timing of senescence)



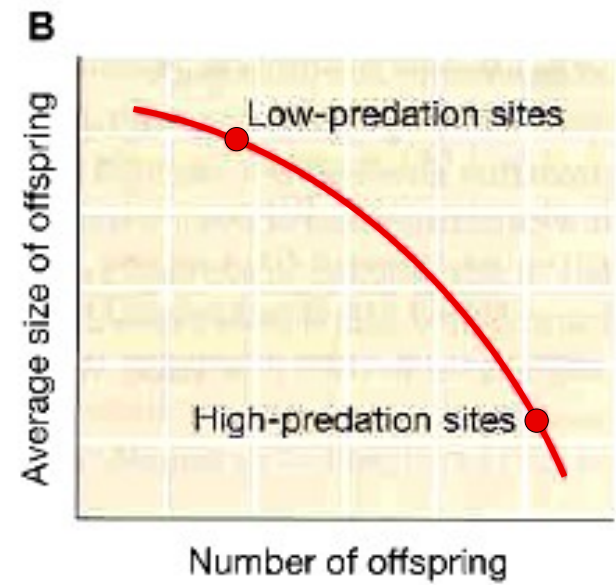
**Low-predation site**  
Females produce fewer but larger offspring

**High-predation site**  
Females produce many small offspring

fewer but larger offspring, later reproduction

many small offspring, early reproduction

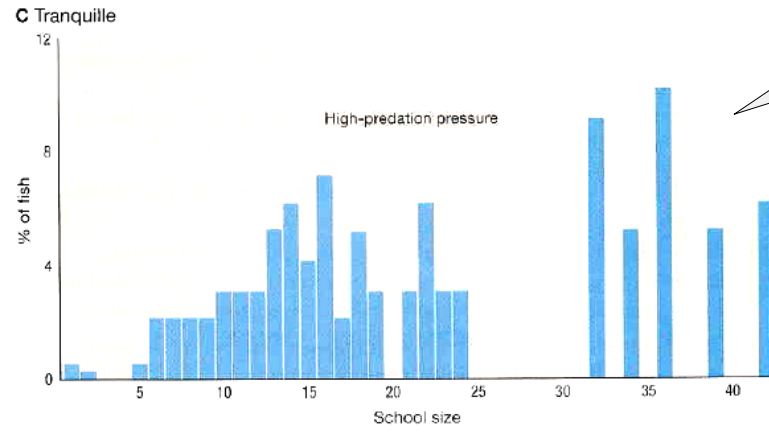
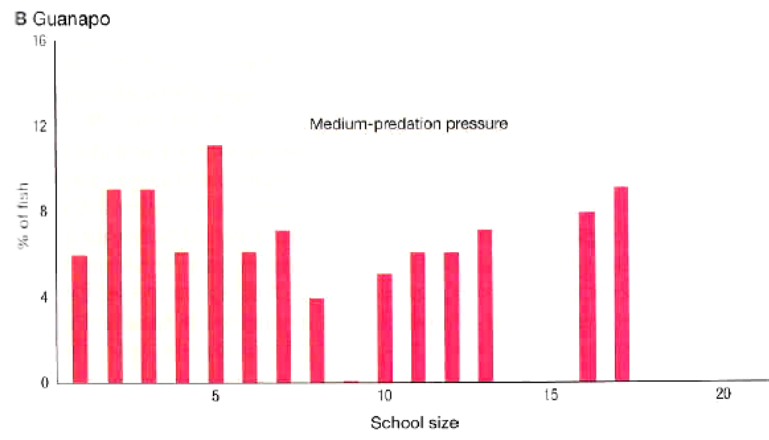
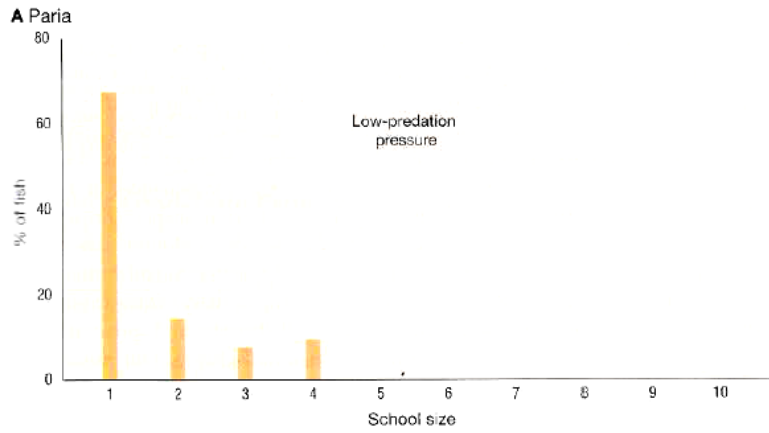
evolutionary trade-off



David Reznick, John Endler et al. (1990):

transfer of 100 males and 100 females from high-predation site to  
low-predation site → after 5 and 12 years females produced fewer  
larger offspring  
this characteristic heritable





high-predation site  
guppies form larger and  
tighter shoals



# What the evolutionary theory must explain:

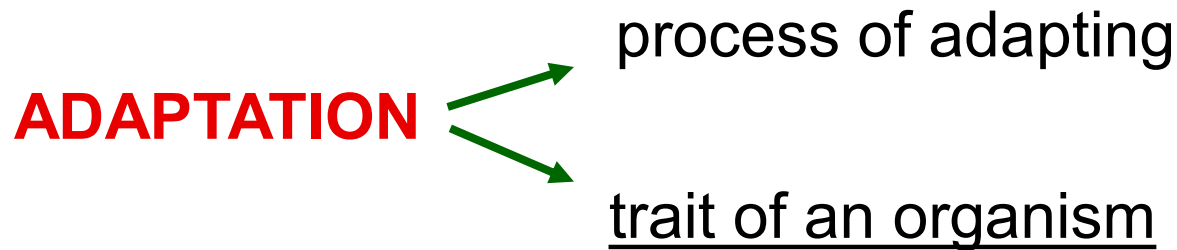
origin of complex adaptation

origin of traits such as recombination, sexual reproduction, programmed life span including senescence and death, segregation distortion etc. which do not (or seemingly do not) provide organisms any benefit

cooperation within and between × antagonism within species (eg. infanticide) and between species (eg. host castration by parasites)

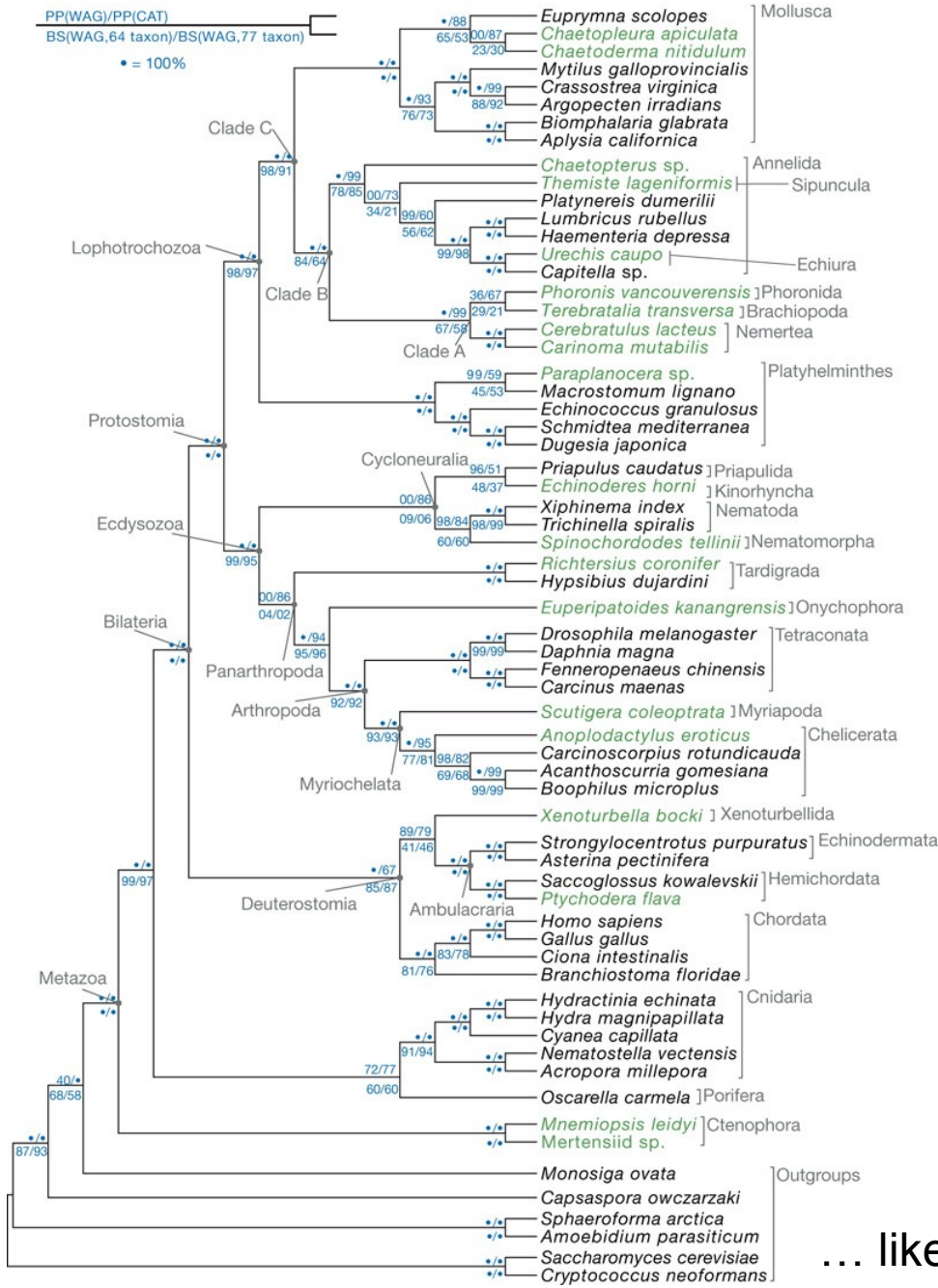
„harmful“ adaptations (eg. bee sting)

# ADAPTATION



trait which allows better survival and reproduction

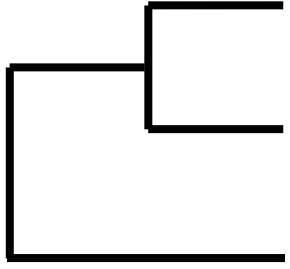
natural selection necessary but also considering history  
(flea winglessness × Collembola)



springtail has no wings because all its ancestors were wingless



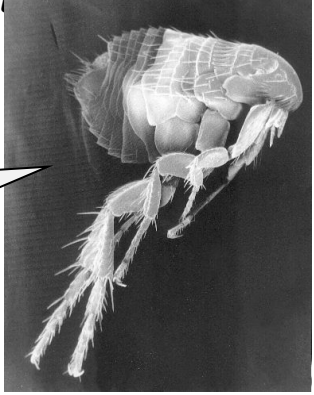
Collembola



Protura

Insecta

flea has lost its wings secondarily



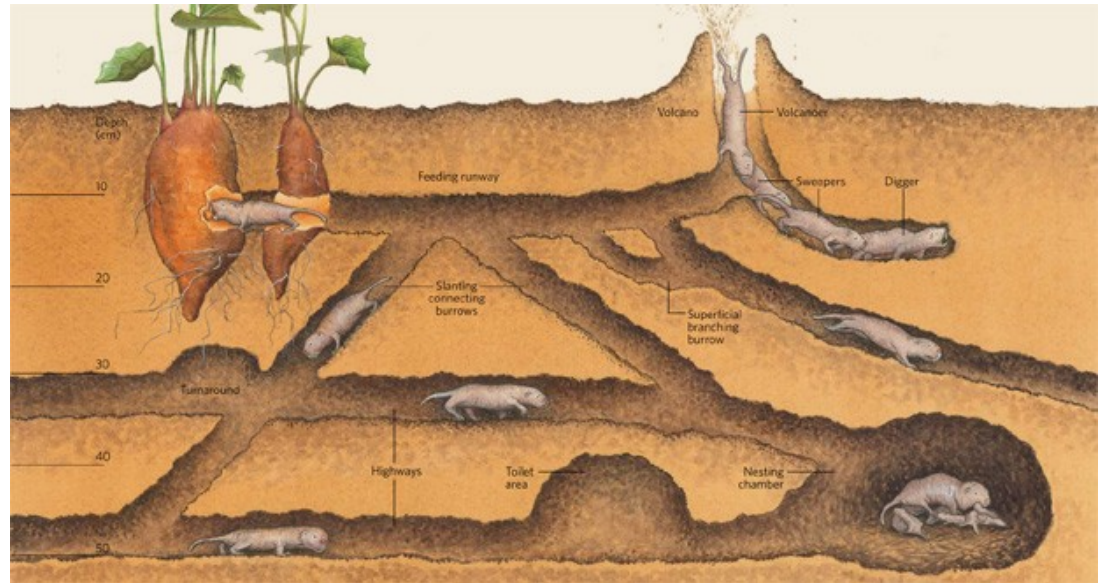
... likewise wingless species of fruit flies etc.



*Heterocephalus glaber*



*Fukomys* sp.



adaptations known for a long time - philosophers,  
natural theologians (St. Augustine, St. Thomas Aquinas, William Paley)

notion of a watchmaker, today „argument from design“

× David Hume

Richard Dawkins: Blind Watchmaker

Explaining adaptations:

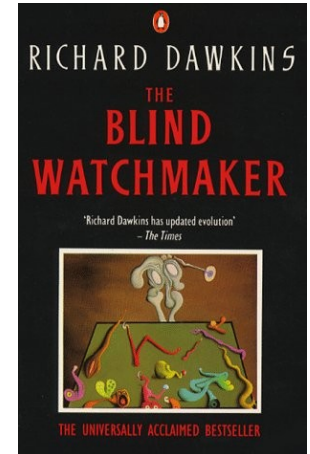
supernatural being

lamarckism, adaptive mutation

zebra and lion: the ability of muscle strengthening is itself adaptive

orthogenesis ... mechanism?

natural selection



# Coadaptation

= complex adaptation requiring coordinated changes of more than 1 part

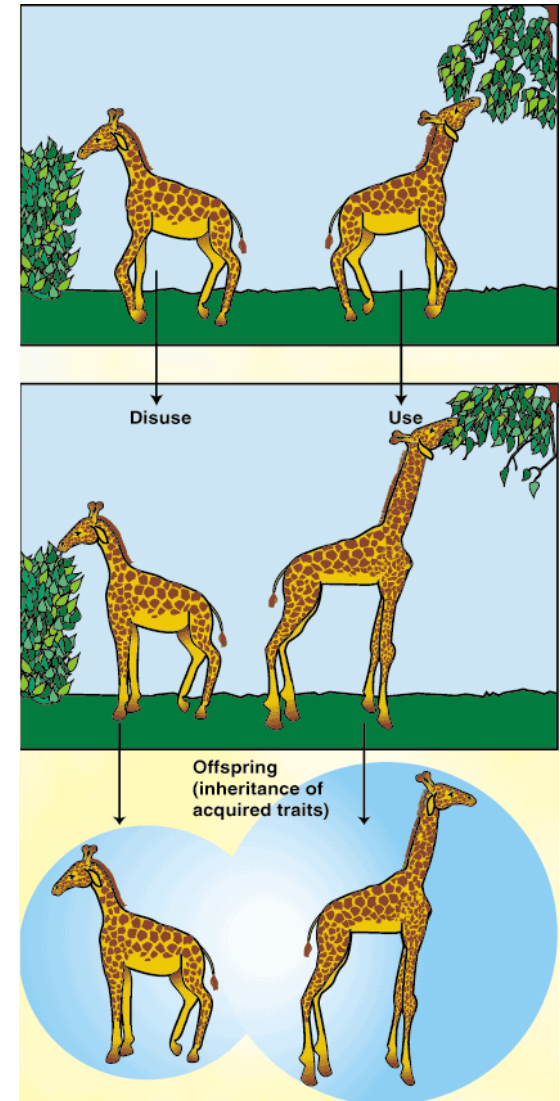
**Herbert Spencer:** giraffe's neck – parallel changes of bones, muscles, and vessels

× genes do not act independently

**gene** level (→ gene complexes, „supergenes“)

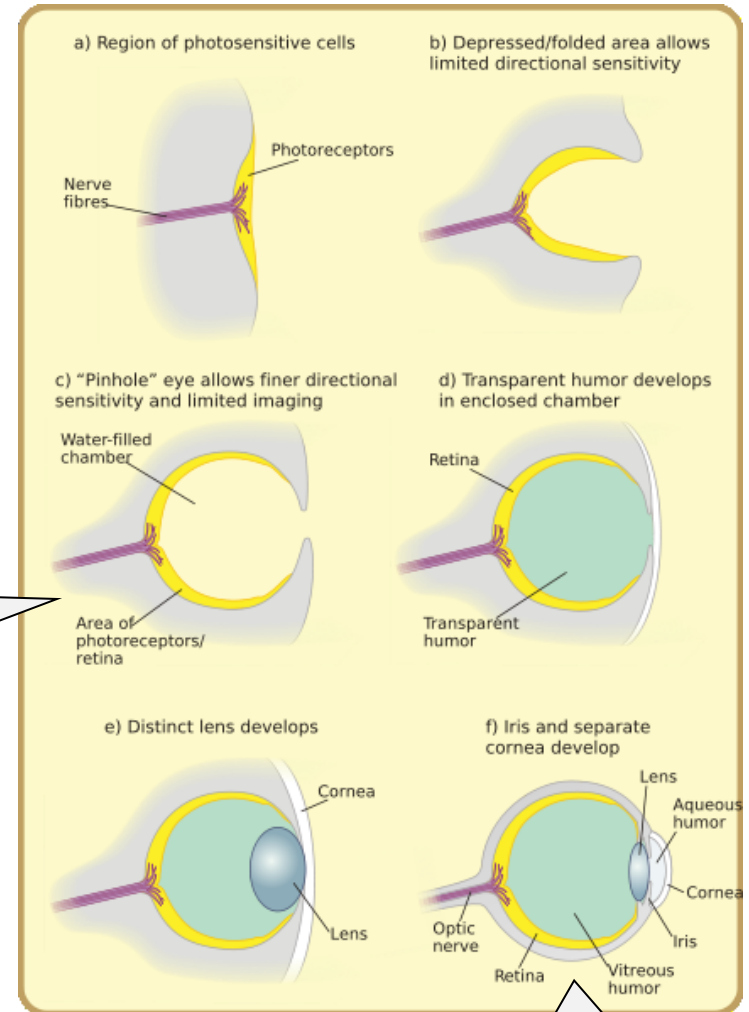
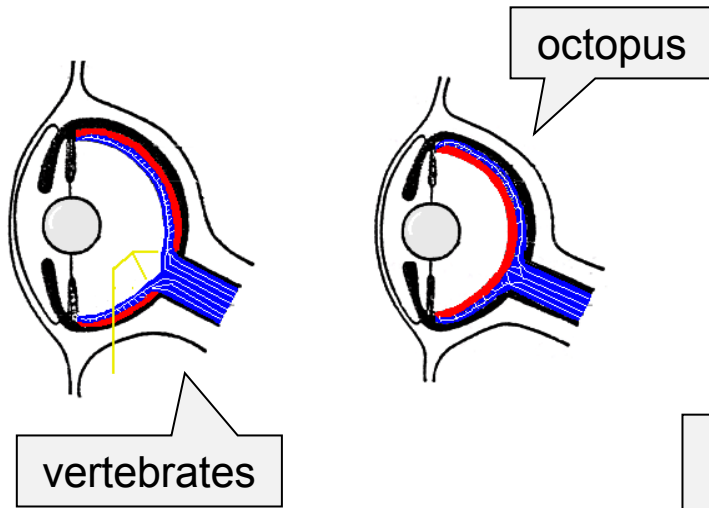
**organ** level

**species** level ... see also Origin of sexual reproduction



# EVOLUTION OF COMPLEX TRAITS

## 1. Functional intermediary traits

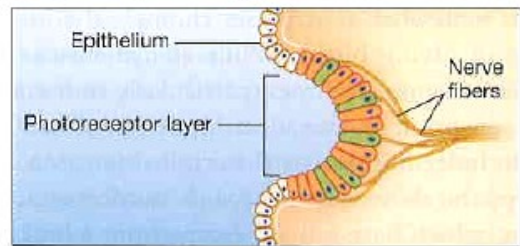
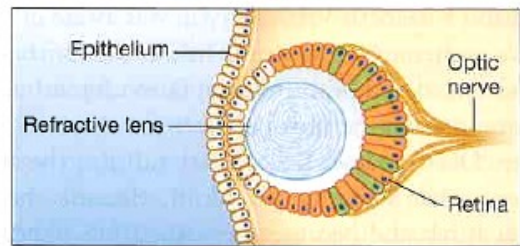
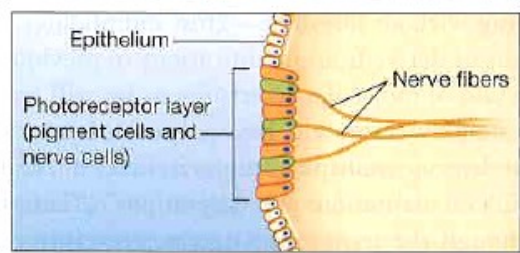
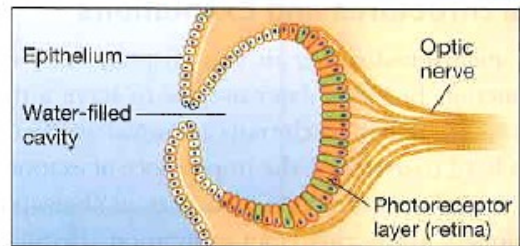
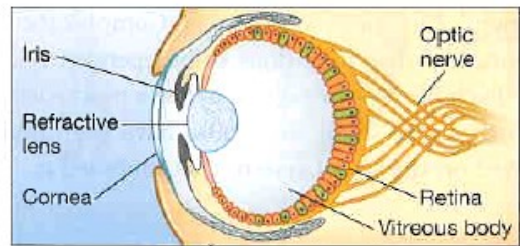
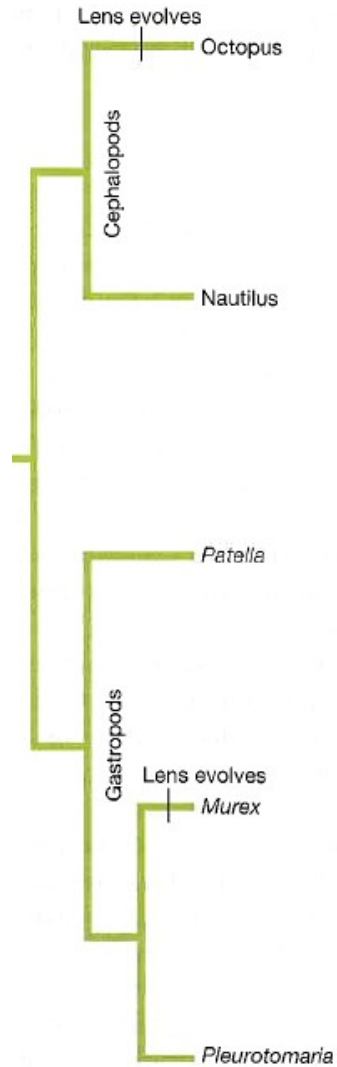


Evolution of camera-type eye:

How can a half-eye be functional?

cephalopods,  
vertebrates

# cephalopods:





## Evolution of a complex camera-type eye – computer simulation:

photosensitive organs → independent origin 50-100× in different groups of invertebrates

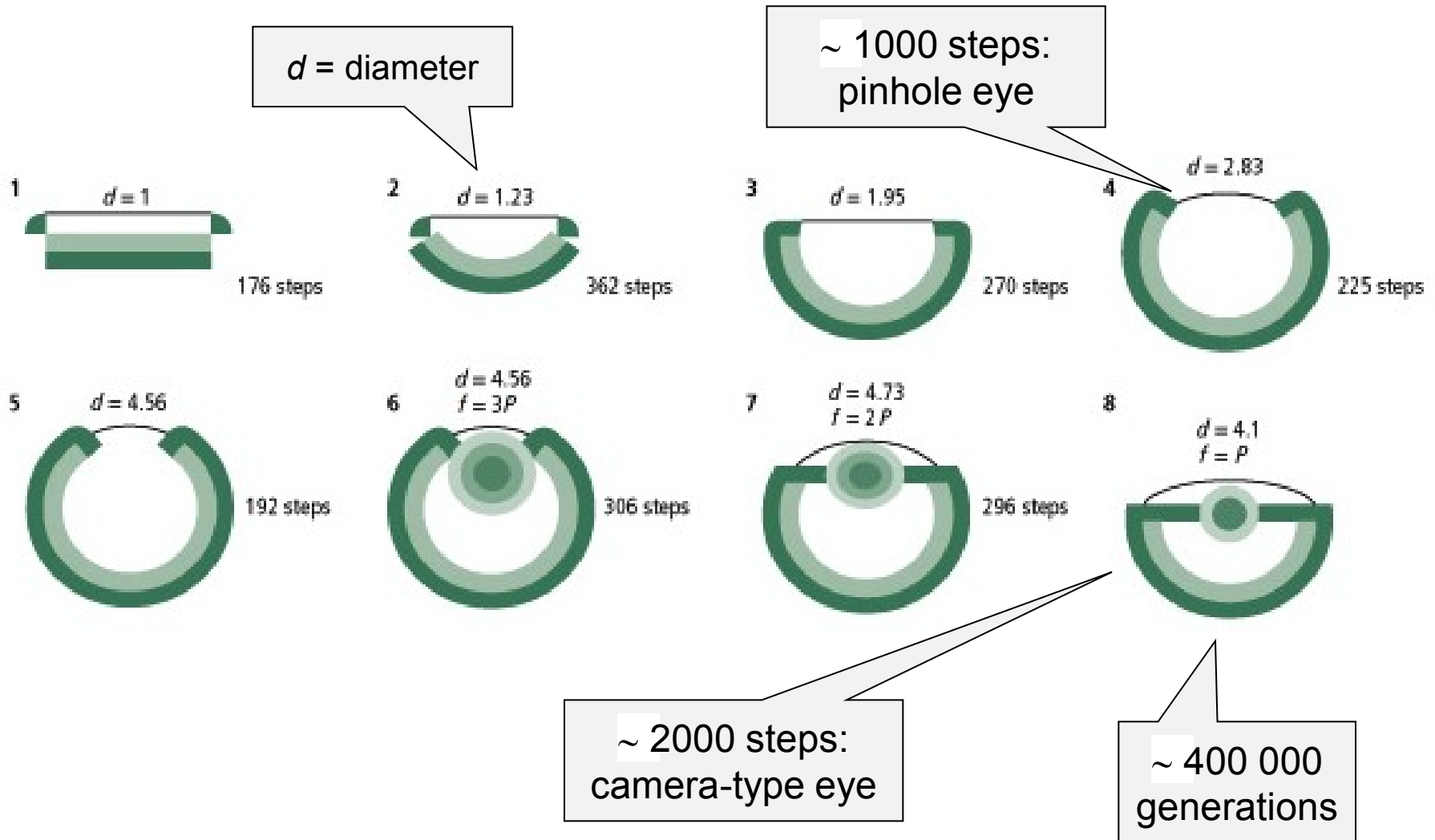
Nilsson & Pelger (1994):

layer of photosensitive cells between dark cell layer below and transparent protective layer on top

random changes <1% → less advantageous changes rejected

criterion = ability to distinguish objects in space (optical physics → potential for quantification)

# Evolution of a complex camera-type eye – computer simulation:



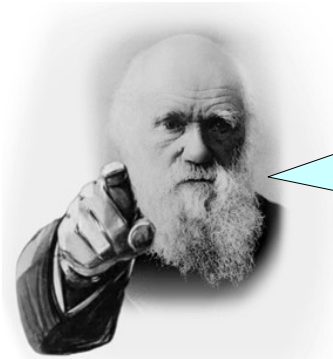
## 2. Exaptation

Complex traits seldom originate *de novo*, rather modification of existing structures

François Jacob (1977): evolutionary tinkering

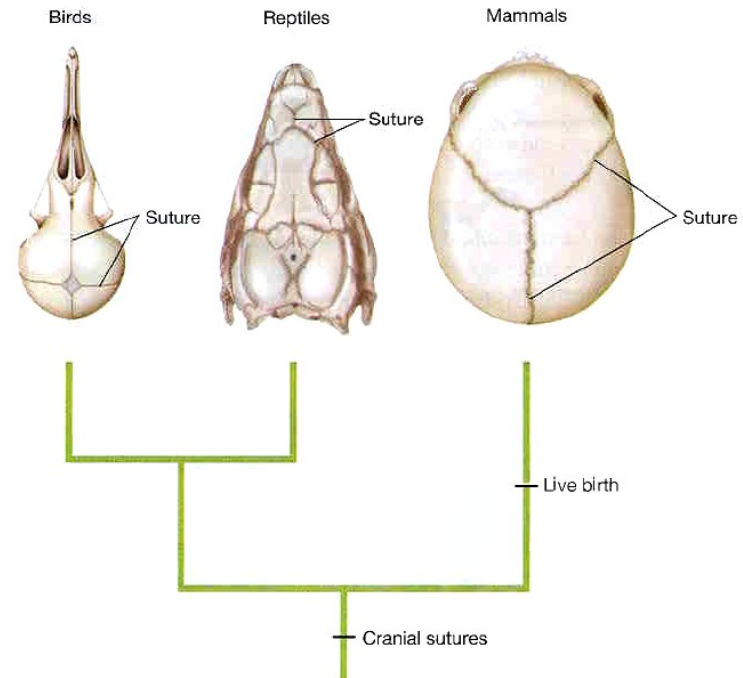
**exaptation** = function shift,  
ie. usage of a trait for another purpose

Eg.: mammal cranial sutures (birth relief)



must have been  
other purpose!

suture probably enabled brain growth



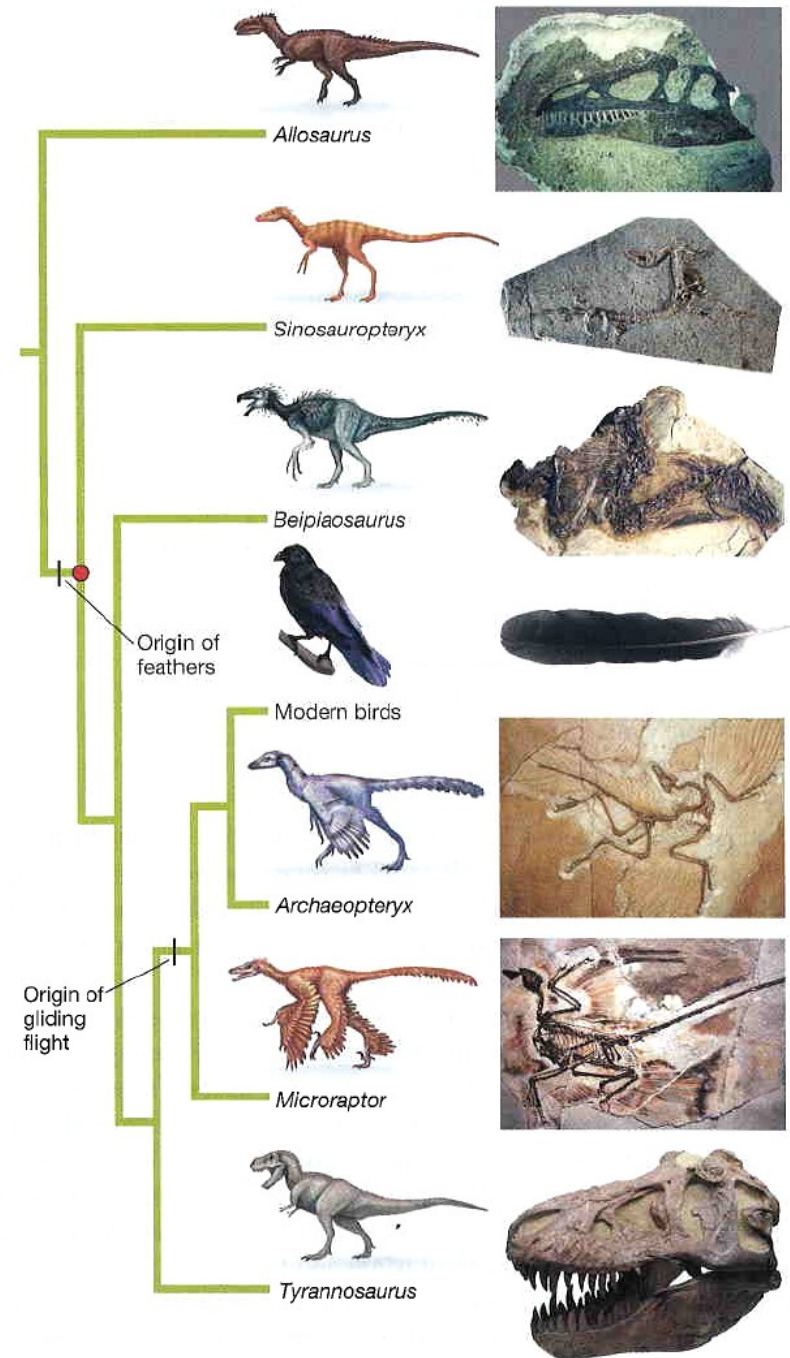
Eg.: bird feathers

single origin

theropod dinosaurs

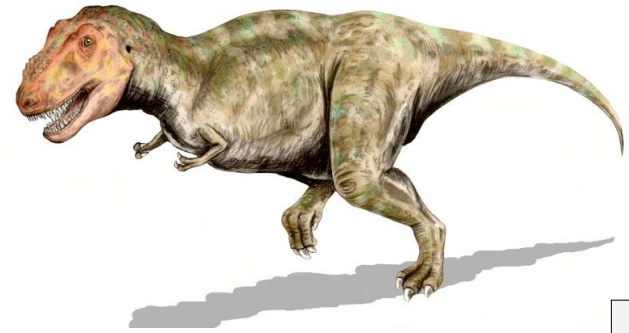
Prum and Brush (2002):

„Concluding that feathers evolved for flight is like maintaining that digits evolved for playing the piano.“

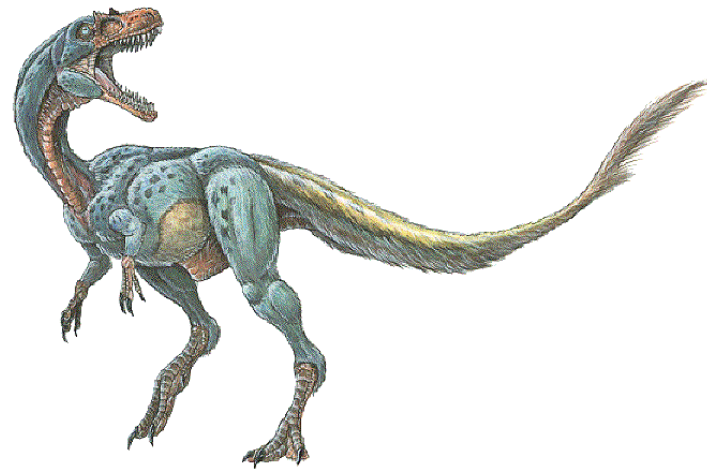


## Bird feathers:

1. thermoregulation
2. protection against solar radiation
3. signaling
4. sense of touch (like vibrisses)
5. prey catching
6. defence
7. water protection



*T. rex*



Spinosaurus  
thermoregulation

*Microraptor gui:*  
gliding



birds:  
active flight

Eg.: lobe-finned fishes – seabed movement → shore climbing



*Panderichthys (Rhipidistia)*



*Tiktaalik*



*Acanthostega*

Eg.: insect cuticle (integument → skeleton); mammalian mammary glands (sweat glands)

Stephen J. Gould, Elizabeth Vrba (1982):

avoiding teleology: the term „preadaptation“ → **exaptation**  
= broader meaning – including originally neutral traits

likewise term co-option

# Evolutionary constraints

Are adaptations always optimal?

**time lag:** neotropical anachronisms

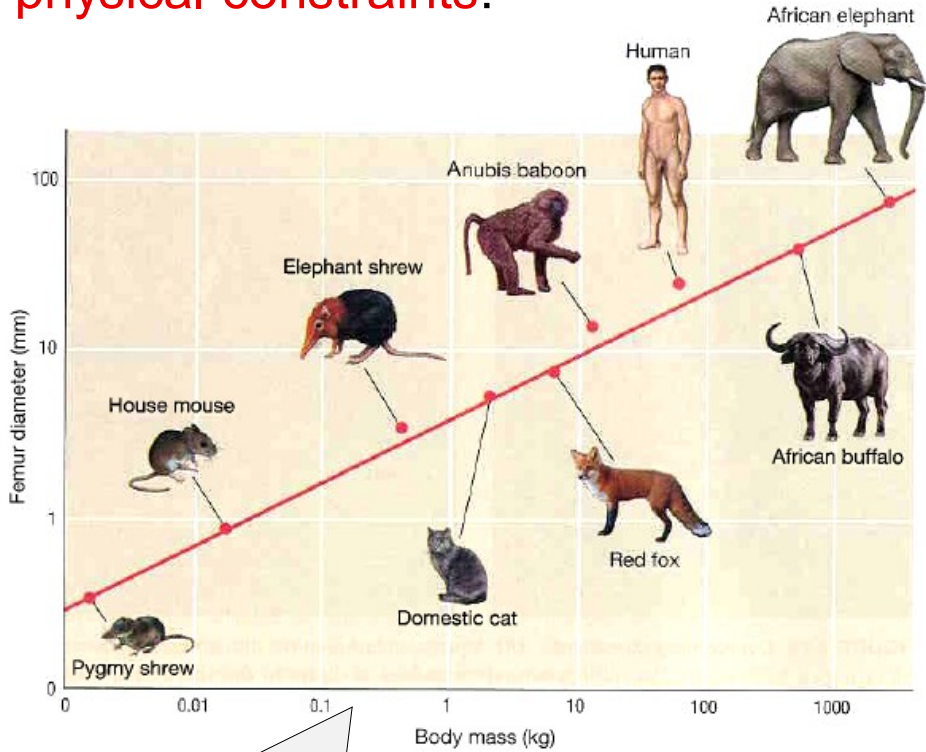
**genetical constraints:** overdominance  
(lethal system of chromosome 1 in *Triturus cristatus*)



*Crescentia alata*

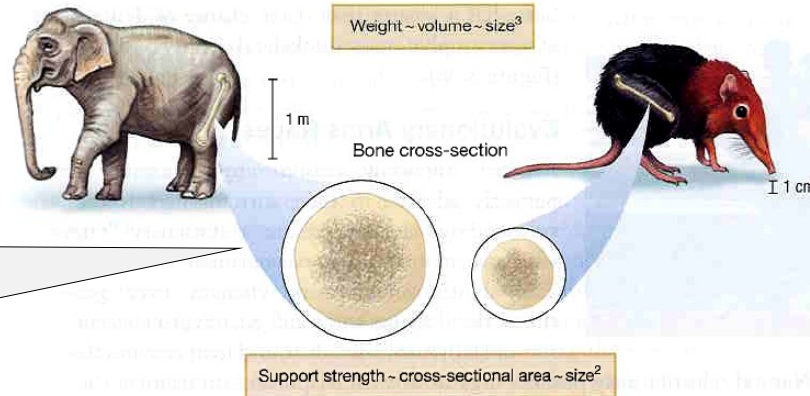


# physical constraints:



mass grows with third power

bone strength grows with second power (bone cross-section)



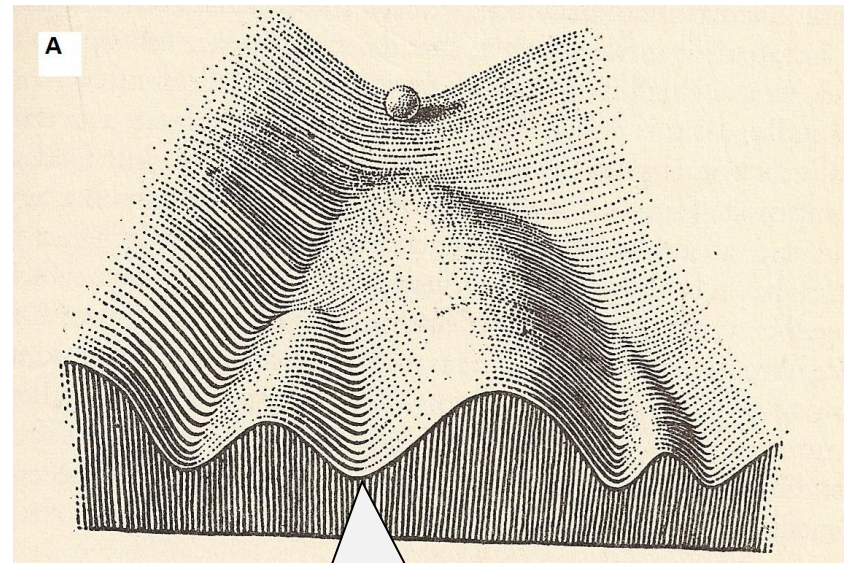


## ontogenetic constraints:

deviation of production of various phenotypes or restriction of phenotypic variation caused by structure, character, composition or dynamics of the ontogenetic system



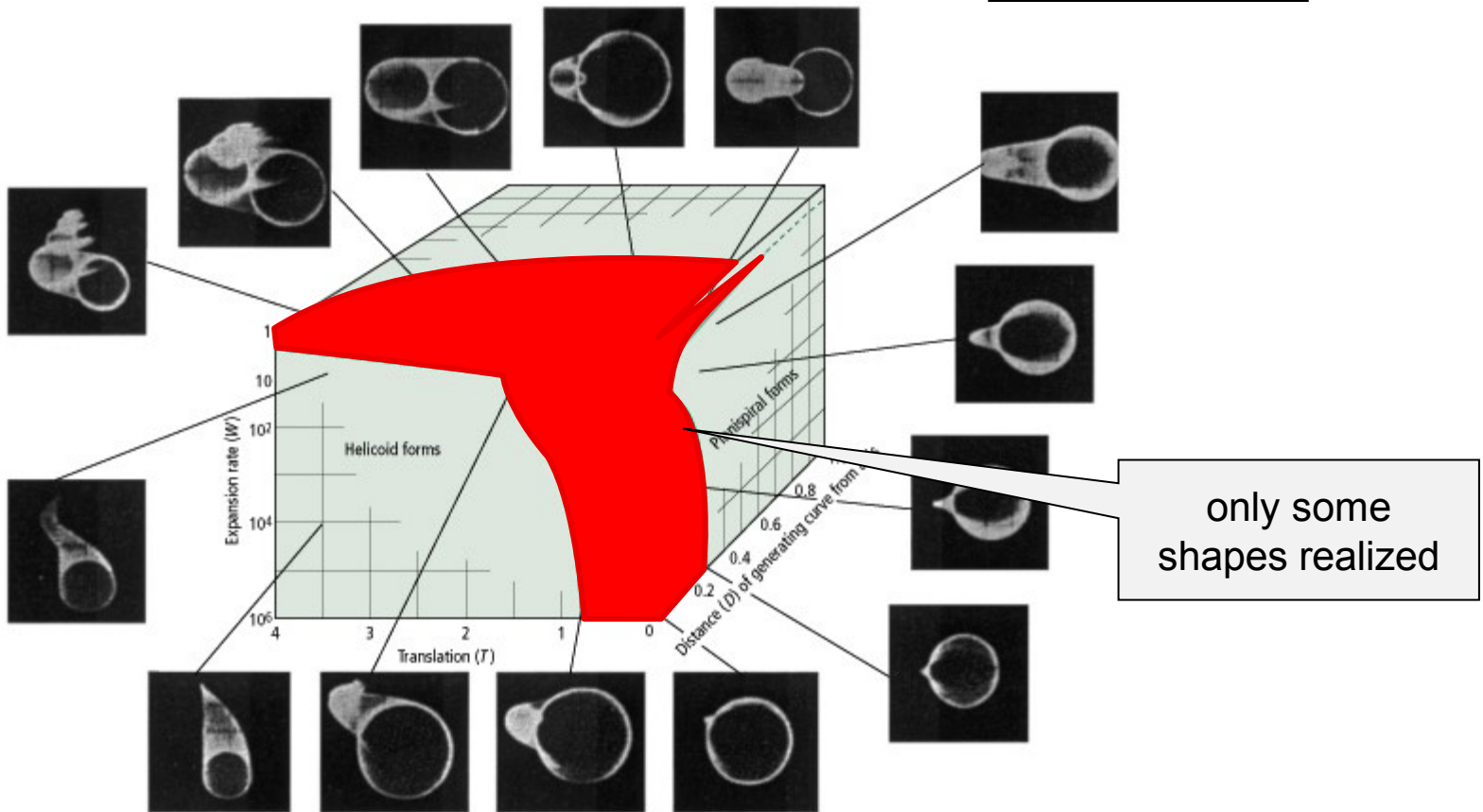
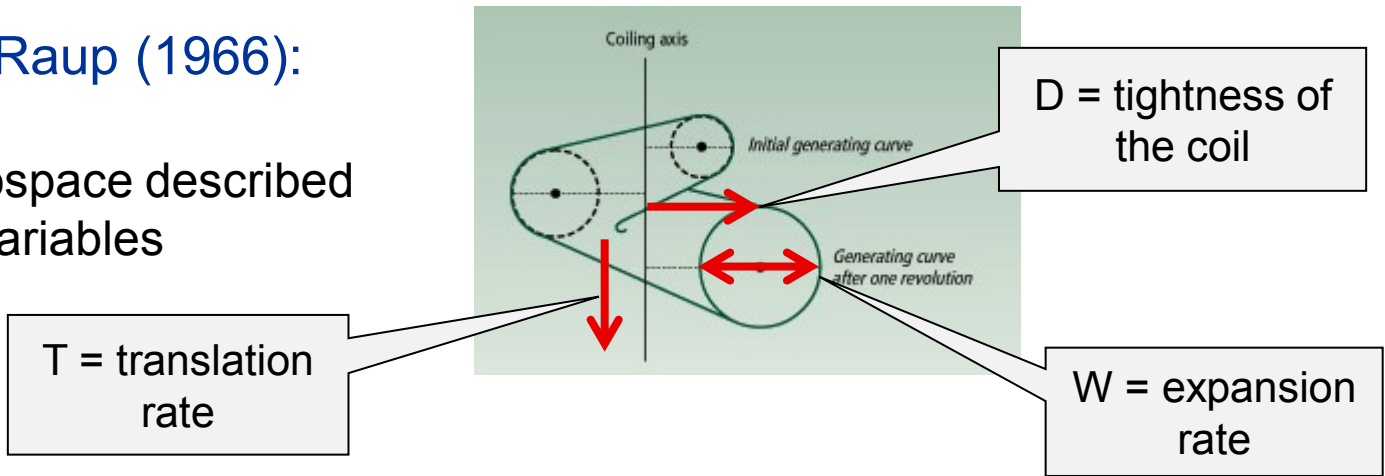
Pegasus's wings cannot arise *de novo*



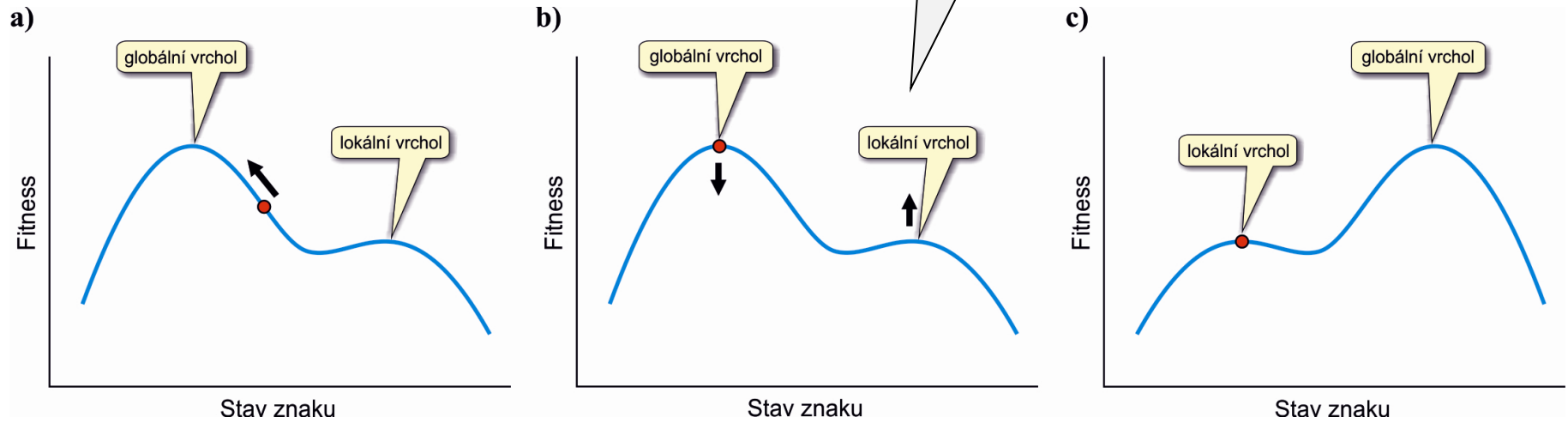
ontogeny is „canalized“

David Raup (1966):

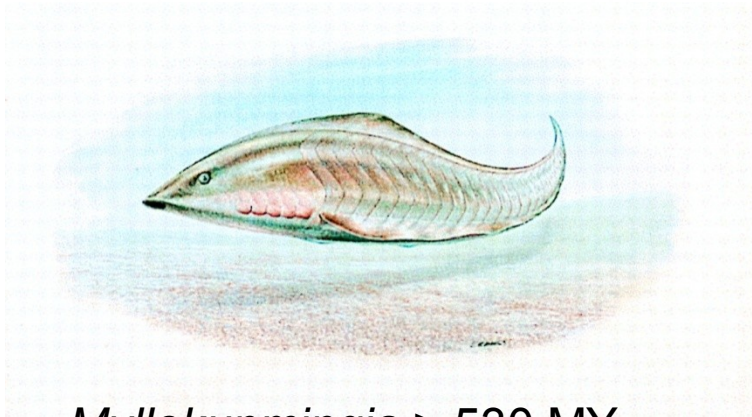
morphospace described  
by 3 variables



# historical constraints

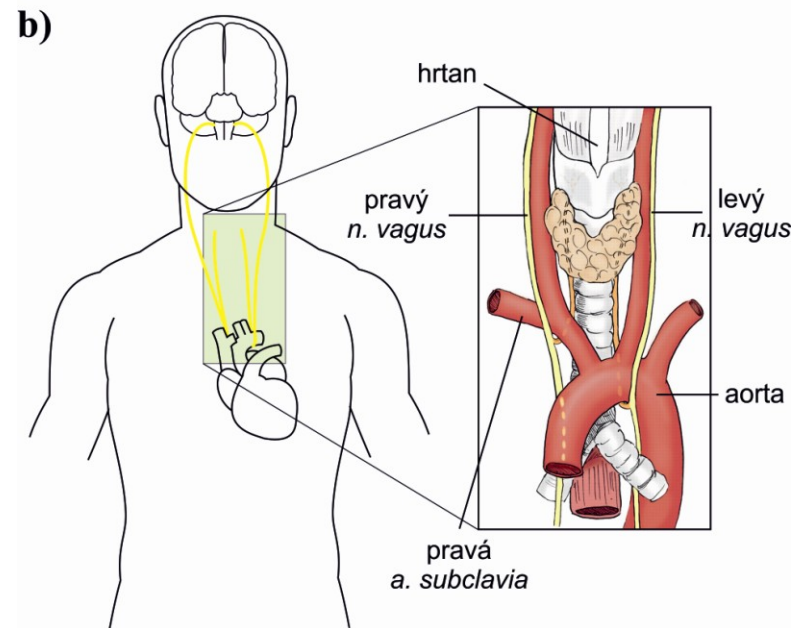
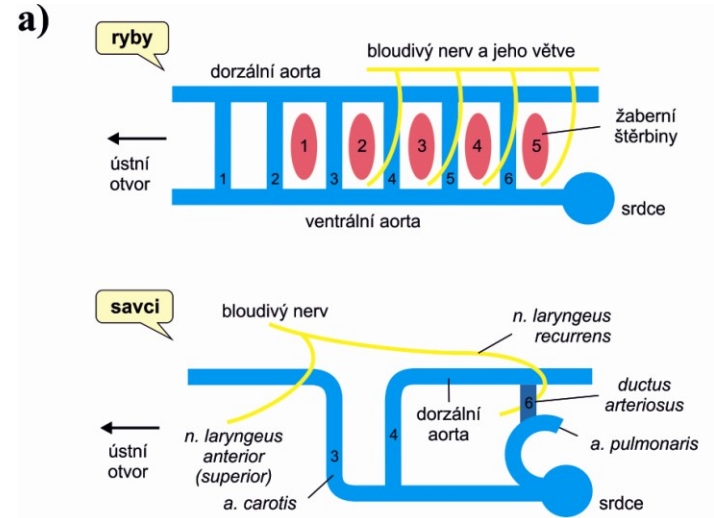
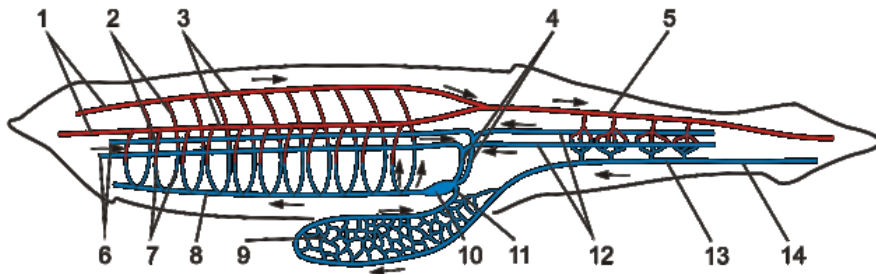


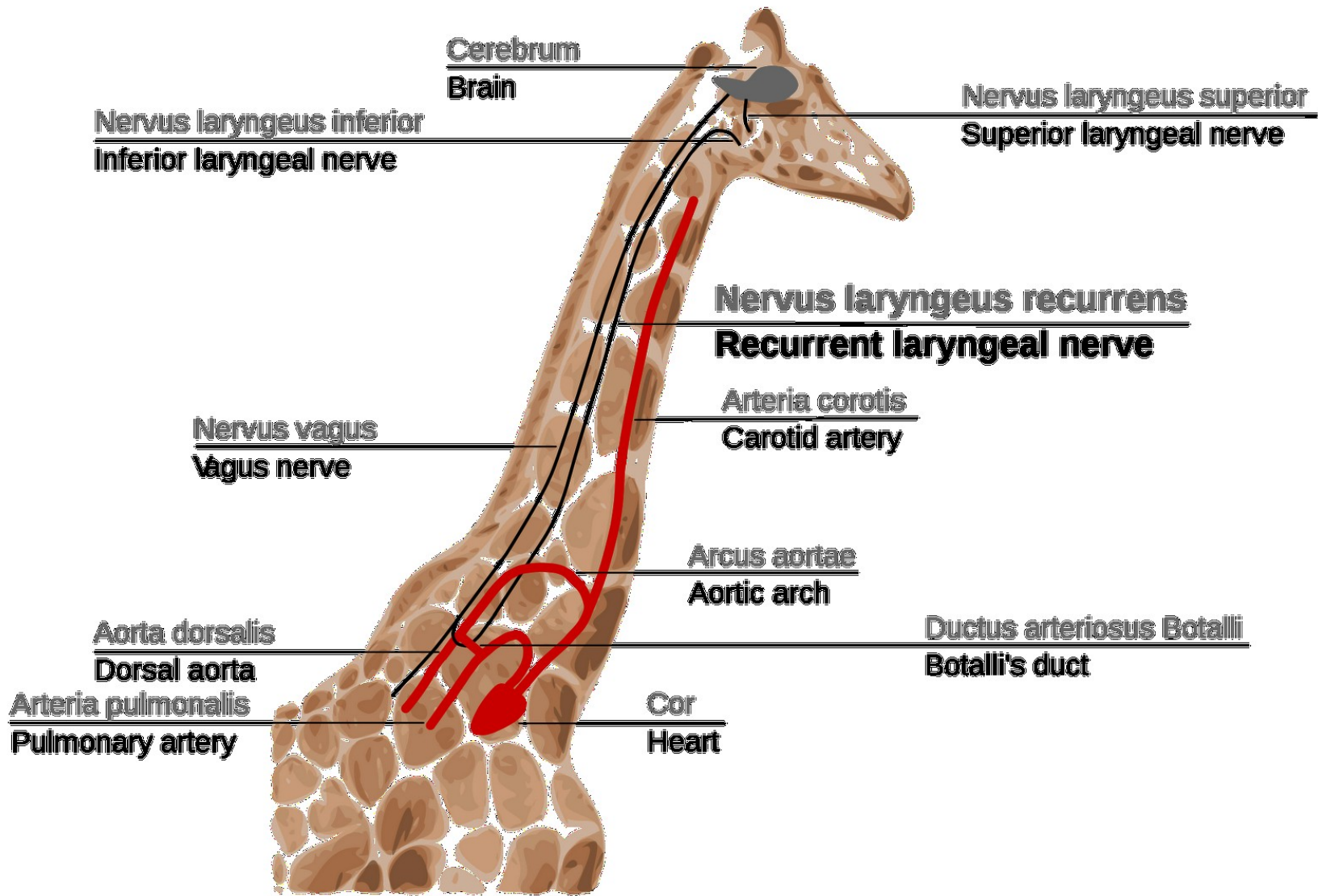
Eg.: laryngeal nerve – one of branches of the vagus nerve (*nervus vagus*)



*Myllokunmingia* > 530 MY

amphioxus





## conflict at different levels:

selection at the gene level vs. selection at the organismal level

## trade-off of various adaptive needs:

parallel breathing and eating when the secondary palate is absent

trade-off between life-history parameters (number of offspring  $\times$  age of the first reproduction)

time distribution between various activities (eating, recreation, ...)

# Methods of study of adaptation:

## structural complexity:

the more complex, the higher probability of a trait being adaptive



## usefulness, demonstration of function

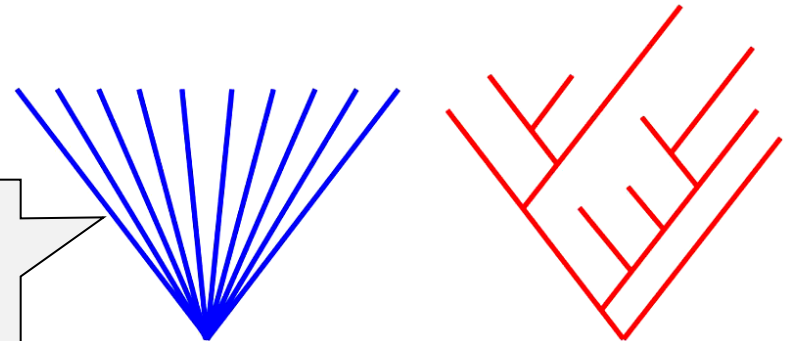
Bergmann and Allen rule,  
falcon wing  $\times$  accipiter wing etc.

## comparative method:

association with phylogenetic analysis

## experiment

non-phylogenetic statistical methods assume that all the compared species are equally related ...



Sometimes even an experiment is not conclusive whether the trait is adaptive  $\rightarrow$  danger of confusing function and effect:  
eg. alkaloids and terpenes of plants (repelling insects  $\times$  waste products of metabolism)

# Is every trait adaptive?

physical and chemical laws:

hemoglobine colour, return of a fish to water

cultural inheritance of some behavioural patterns

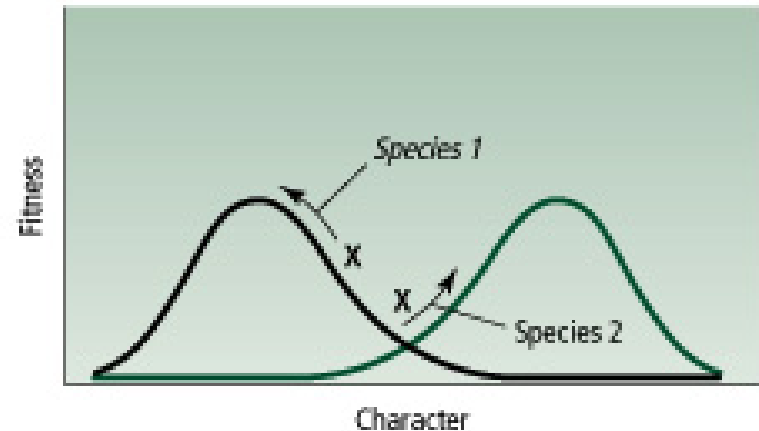
drift:

pseudogenes; shift to parthenogenesis in *Drosophila mercatorum*;  
loss of structures due to accumulation of lethal mutations

correlation with the selected trait:

hitchhiking, pleiotropy

multiple peaks in the adaptive landscape





# Is every trait adaptive?

multiple peaks in adaptive landscape:  
cryptic or aposematic colouration;  
locomotion of kangaroos × zebras



skunk



zorilla

antelope



kangaroo

phylogeny:  
winglessness,  
eusocial behaviour of mole rats

Stephen Gould, Richard Lewontin (1979): The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London, Series B*, 205: 581-598.

