COMPARATIVE BRAIN EVOLUTION

Introduction to Evolution and Vertebrate Phylogeny

Ask questions!

Books:

Comparative Vertebrate Neuroanatomy: Evolution and Adaptation, 2nd Edition

Ann B. Butler, William Hodos

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The Central Nervous System of Vertebrates

Authors: **Nieuwenhuys**, Rudolf, **Donkelaar**, Hans J. ten, **Nicholson**, Charles

Vertebrate Brain Evolution course: outline

- Introduction to evolution and vertebrate phylogeny
- Basis of comparative neuroanatomy (brain structure, cell types)
- Comparative neuroembryology
- Comparative histogenesis
- Evolution, adaptation and brain behavior
- Cerebral cortex in mammals and reptiles
- Laboratory techniques and Talks (Pick your paper!)

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Lecture 1:

1. Introduction to Evolution

2. Vertebrate Phylogeny

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What is Evolution?

Change through time during generations

Diversity — Genetic diversity (mutations, etc.) ⟵ Natural selection

driving force

Example of natural selection: Peppered vs black moth during industrialism

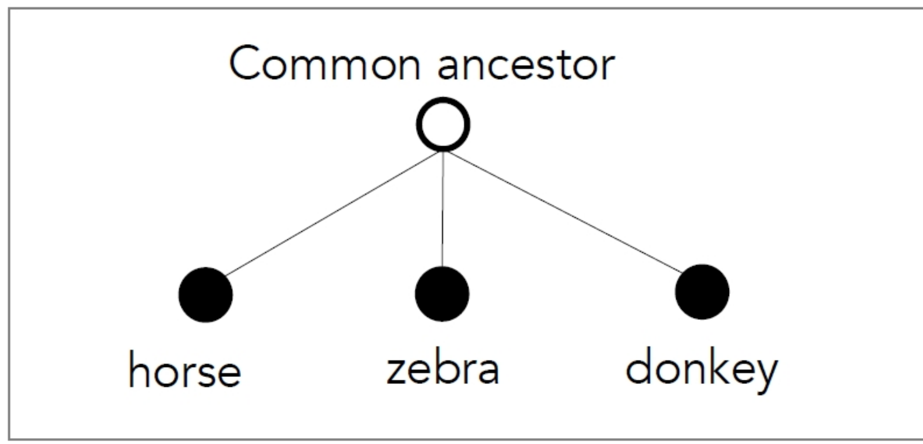
Theory of Evolution: not just a “theory”

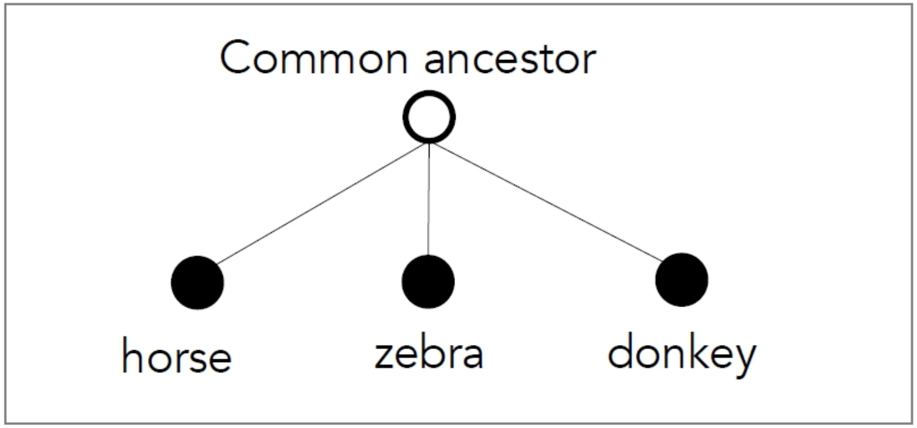
Fundamental processes:

1) Change within a lineage

Ancestor horse → Modern horse

2) Formation of new lineages





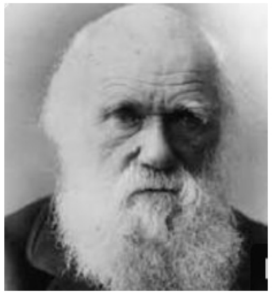
ancestor

Trait, character, species

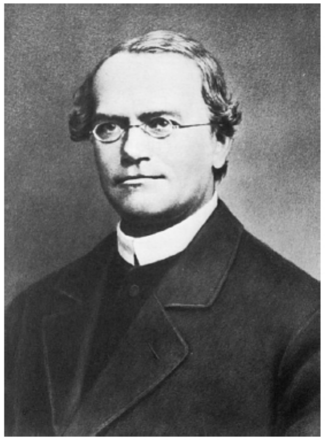
derived

Species: naturally interbreeeding set of individual organisms; they have special "features".

- All species share common ancestry
- Transitional fossils: <u>we expect transitions from ancient forms to modern forms</u>



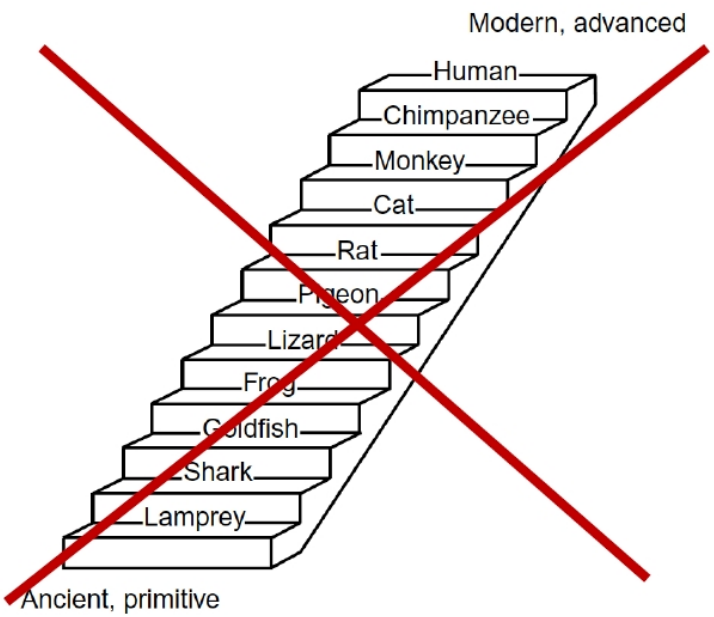
Charles Darwin
Theory of evolution through natural selection



Gregor Mendel
Principle of inheritance,
by the means of transmitted genes

Julian Huxley
"Evolutionary synthesis"
Gradual and larger evolutionary changes (e.g. speciation)

Evolution does not create superior or inferior taxa, it simply creates diversity.



"scala naturae":
an old, anthropocentric term

Do NOT say Higher primates, higher mammals, etc.

All the extant (living) animals are just as successful and well-adapted to their environments as humans.

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Evolutionary mechanisms

Evolution: change over time

What drives evolution?

1. Genetic factors — random, creates variability
2. Natural selection — not random, acts on variability

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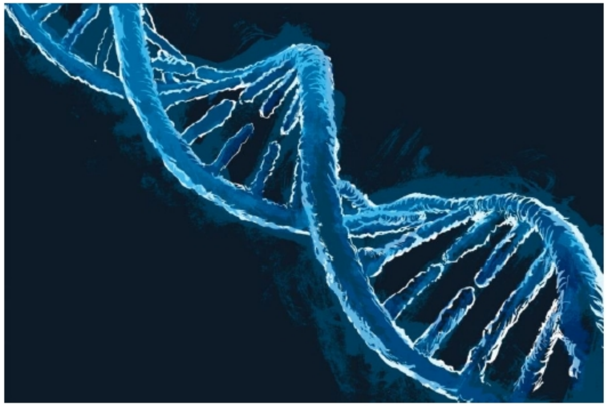
1. Genetic factors



- Mutations
- Genetic recombinations — Changes in genome of different individuals
- Gene flow — Change in frequency of alleles in a population caused by
  - individuals migrating
  - Interbreeding
  - Isolation of one population from another

Geographic isolation   Reproductive isolation

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2. Natural selection

- Acts on populations (not on individuals)

- Fitness of a variant — How strongly that variant will be selected for (how adaptative)

- Gene alleles are pleiotropic — Adaptation often based on combination of multiple genes

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Different types of changes

1. Gradual evolutionary changes

2. Sudden changes

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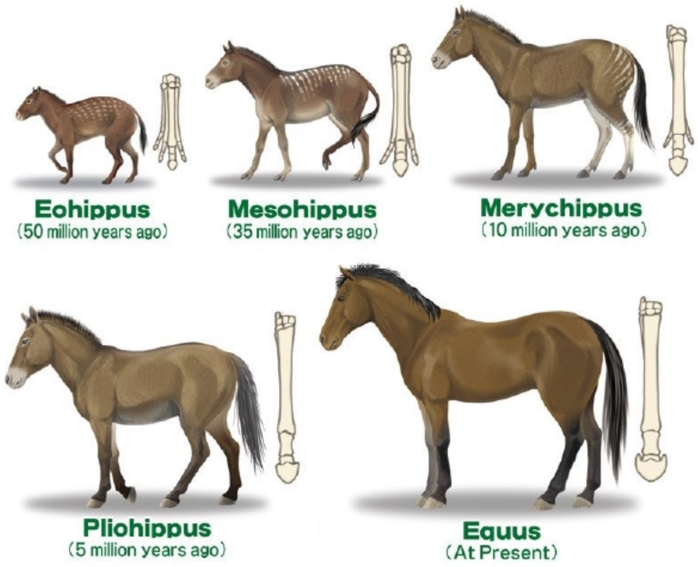
1. Gradual evolutionary changes

- **Microevolution**

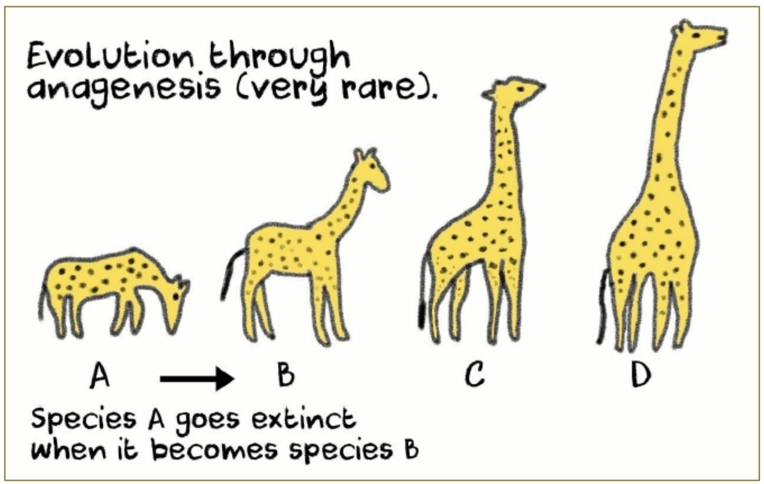
  divergence of populations within a species

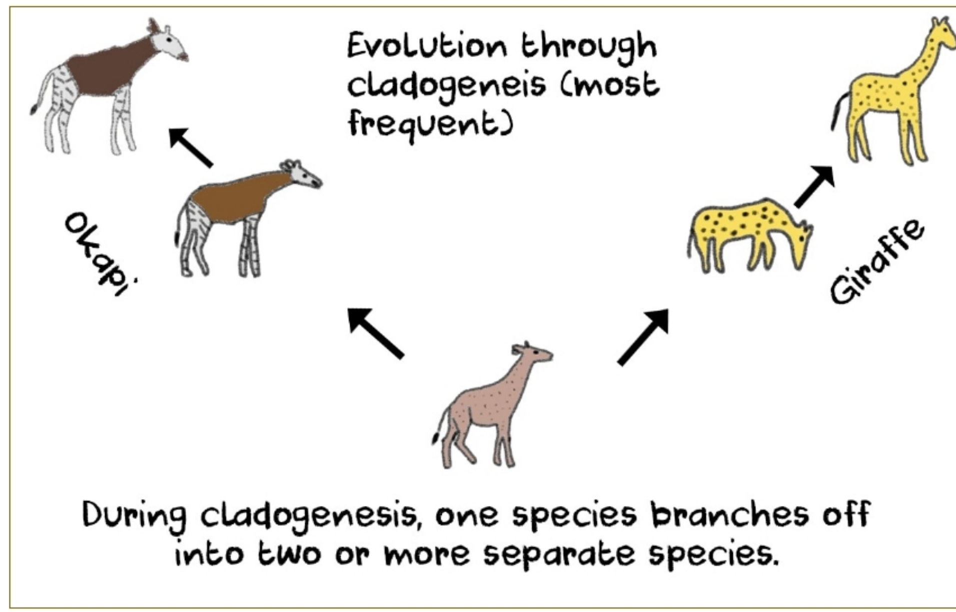


- **Phyletic evolution (anagenesis)**

  A single lineage (without branching out) Becomes another species

Anagenesis vs Cladogenesis





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2. Sudden changes

- Punctuated equilibrium

  a morphology changes abruptly after a long time

  ↓

  macroevolution

- Speciation =formation of a new species (reproductively isolated)
- Heterochrony =changes in developmental processes, e.g. in the relative timing of related developmental events
  → affect adult phenotype

  ↑

  developmental fields

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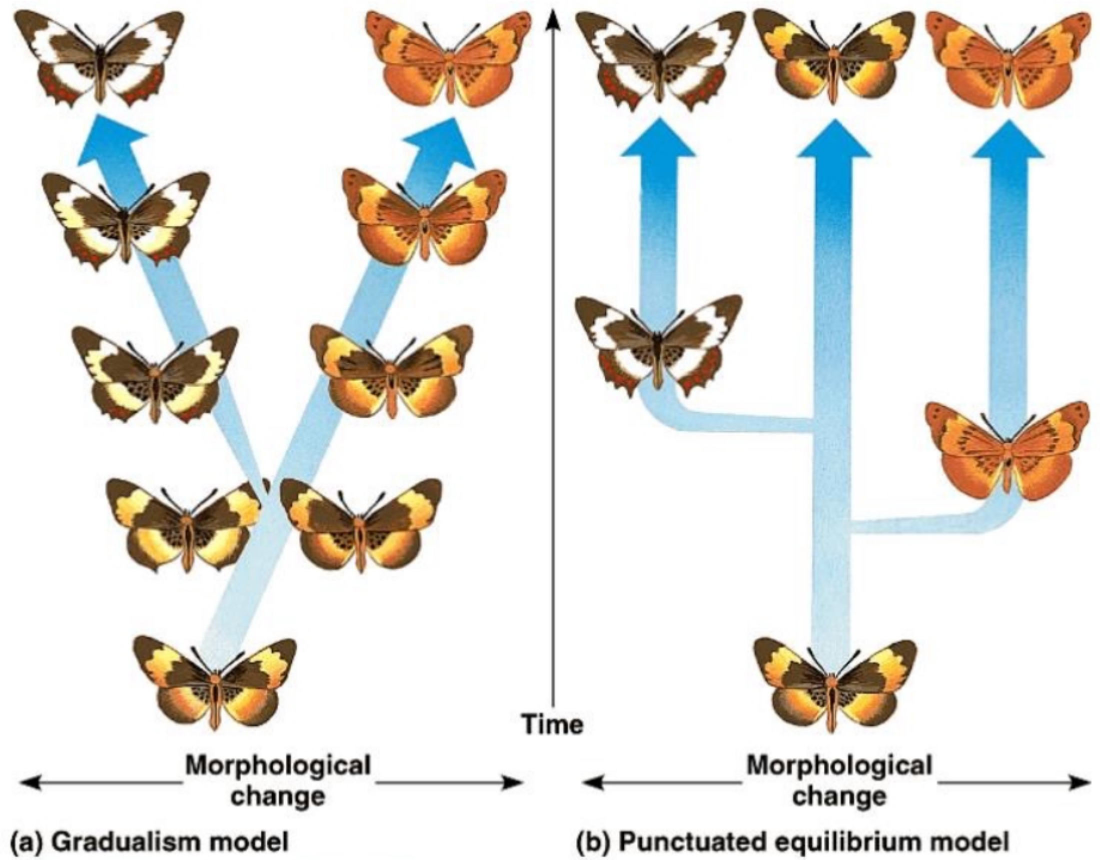
Gradual changes vs Punctuated equilibrium



Evo-Devo synthesis

Evolutionary Developmental Biology

Evolution and Development interact with each other

Example:

Changes in patterning genes can be selected by evolution.

Developmental (or morphogenetic) fields

- Discrete units of embryological development
- Genetically specified
- "**building blocks**" of development

- If altered, adult phenotype will change

- Changes in them may account for saltatory, macroevolutionary changes (sudden changes)

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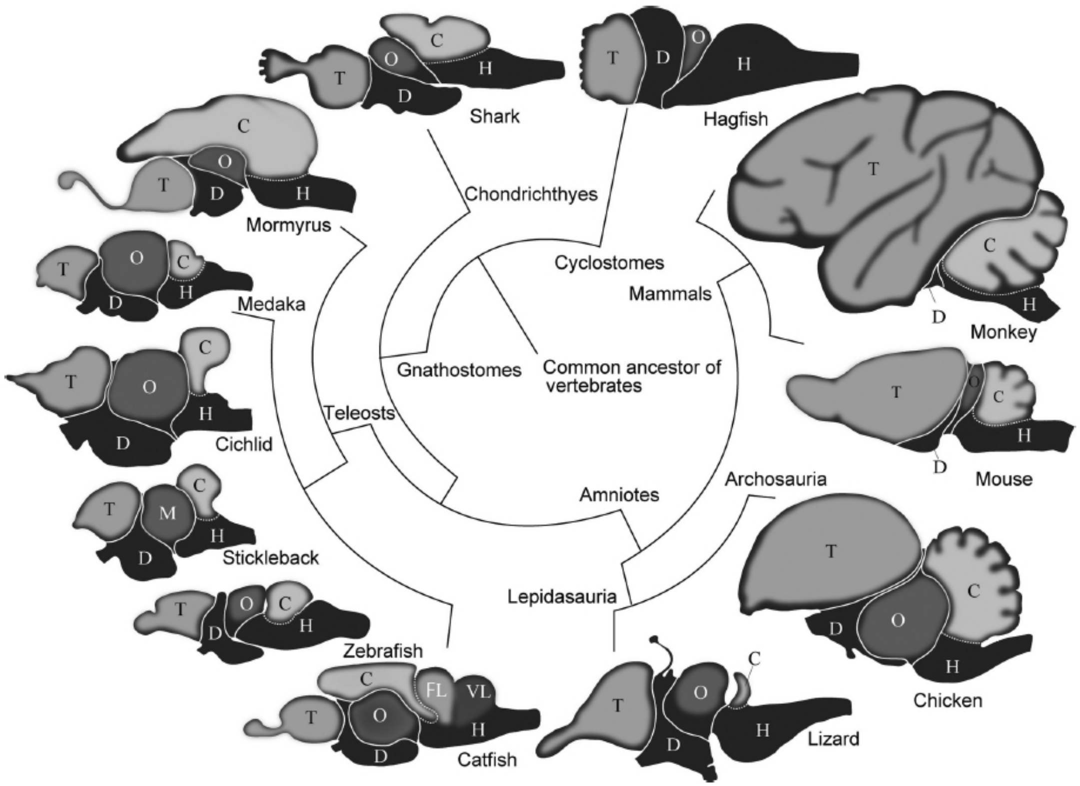
Evolution of the Vertebrate Central Nervous System



CHANGES depend on:

- Morphogenetic fields
- Cell proliferation length
- Migration patterns
- New cell types

Some features are constant, some vary A LOT!

ANALOGY vs HOMOLOGY

ANALOGY

Similarity of function,

Independently from phyletic relationships

HOMOLOGY

Similarity

Inherited from **common ancestry**

Owen introduced the word "homologous"

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Different Types of Homology

- **Discrete (or strict, or historical) homology** — Structures with common ancestry
- **Serial homology** — Structures derived from same ontogenetic division (e.g. vertebrae)
- **Field homology** — Structures derived from the same ontogenic source

Different Types of Homology

- Biological Homology

common ancestry

Takes into account **genetic and morphogenetic continuity**

Focuses on Developmental pathways

HOMOPLASY

- Structural similarity without phyletic continuity (opposite of strict homology)

- Can occur in divergent lineages due to a similar adaptation

Convergence | Parallelism | Reversals

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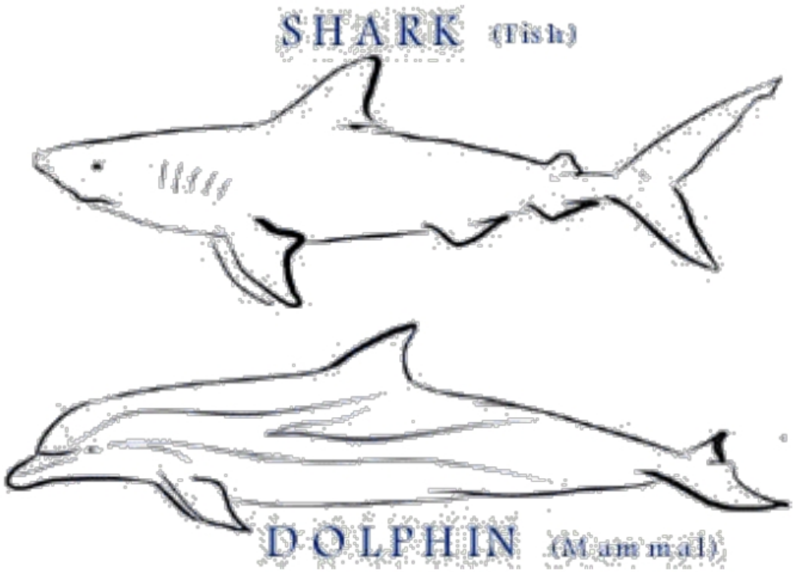
HOMOPLASY

Convergent evolution



2 species from different lineages evolve similar characters due to similar adaptation.

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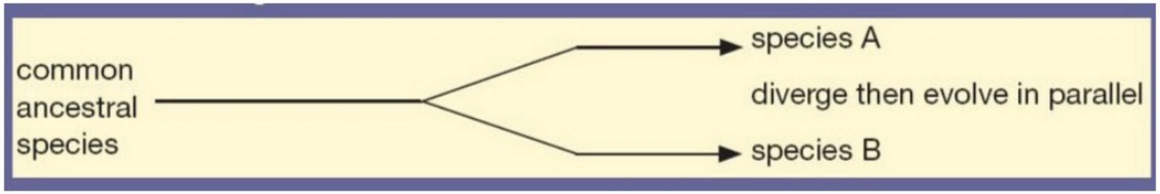
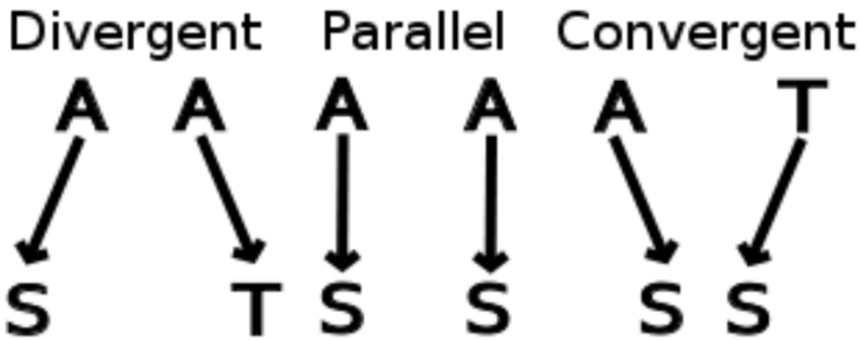
HOMOPLASY

Parallel evolution



Very similar to convergent evolution,
but it occurs when related species evolve similar features independently.



HOMOPLASY

Reversals

Degeneration of a complex structure

(e.g. loss of a derived feature: forelimbs)

Leg-less lizards

Snake

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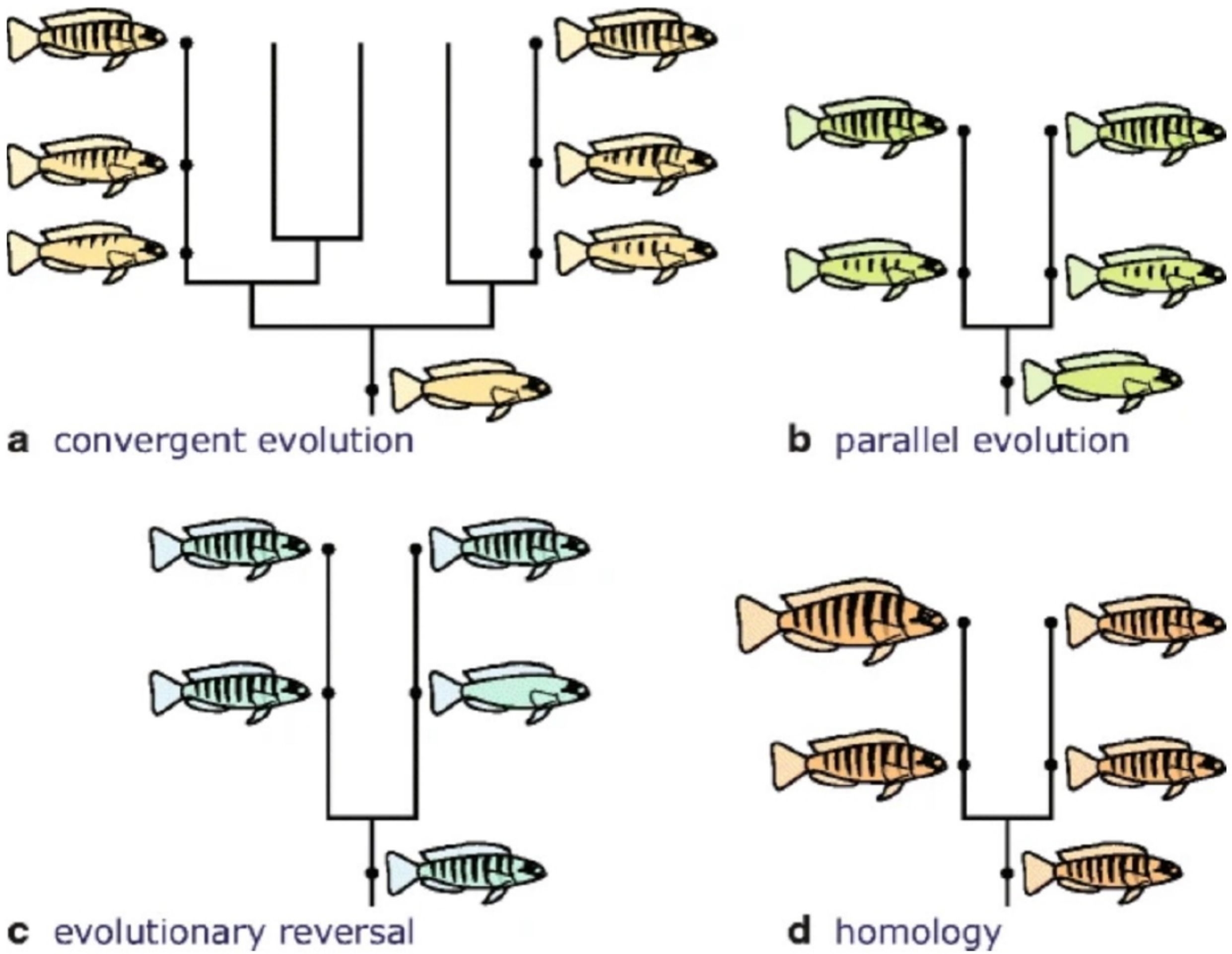

Thanukos, 2008

GENERATIVE HOMOLOGY or SINGENY

(latent homology)

Characters that occur only in few members of a taxon,
and may not have been expressed in the common ancestors.

- Close to biological homology (it recognizes similarity based on shared genetic/morphogenetic pathways)
- It comprises parallelisms, reversals, and most cases of historical homology
- Relevant when studying patterning genes (e.g. similar in Bilateria)

Historical homology → phylogenetics and systematics

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Biological homology → character evolution

↓

Generative homology → Comparative developmental biology

How do we reconstruct evolution?

Cladistics and analysis of variation

Cladistic analysis

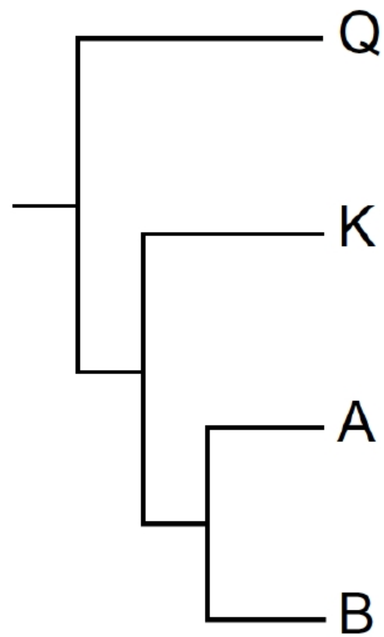

FIGURE 1-1. Cladogram showing the distribution of a trait, indicated by +, among the theoretical extant taxa Q, K, A, and B.

Each branch point (node) represents a common ancestor, and the traits listed along the branches are shared derived characteristics.

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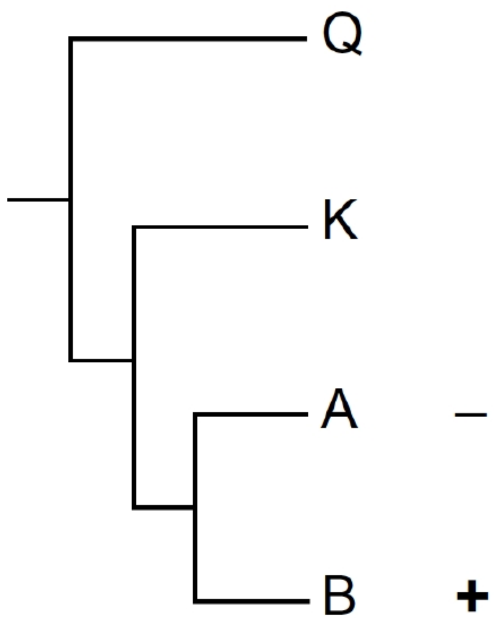
1. Cladistics is a method of classifying organisms based on **common ancestry**.
2. It focuses on **shared derived traits** (synapomorphies), not just similarities.
3. Organisms are grouped into **clades**, which include an ancestor and all its descendants.
4. Each clade represents a **branch** on the evolutionary tree.
5. Relationships are shown in **cladograms**, tree-like diagrams.
6. Cladograms reflect **evolutionary relationships**, not time or complexity.
7. Cladistics avoids **paraphyletic** and **polyphyletic** groups.
8. It uses **morphological, genetic, and molecular data**.
9. The goal is to reconstruct the **evolutionary history** of life.
10. Cladistics has transformed biological classification into a more **objective, evolutionary-based system**.

Cladistics and analysis of variation



Plesiomorphic trait — ancestral

Vs

Apomorphic trait — derived

Is this trait plesiomorphic or apomorphic?

Plesiomorphic Traits

•These are **ancestral traits** inherited from a distant common ancestor.

•They are **primitive** in the context of a particular group.

•Example: Having a backbone is plesiomorphic for mammals, because it's inherited from earlier vertebrates.

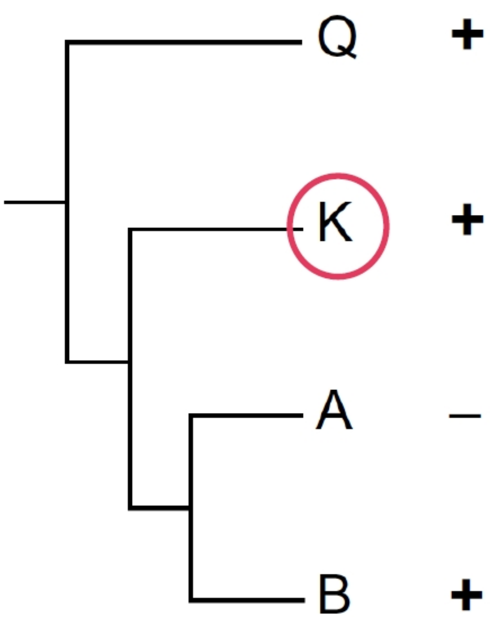
Apomorphic Traits

•These are **derived traits** that evolved more recently in a specific lineage.

•They are **newer** compared to the ancestral condition.

•Example: Having hair is apomorphic for mammals, because it evolved after the divergence from other vertebrates.

Cladistics and analysis of variation



Plesiomorphic trait — ancestral

Vs

Apomorphic trait — derived

Outgroup to A and B

Outgroup comparisons

Summary:

•**Plesiomorphy** = ancestral, shared with distant relatives.

•**Apomorphy** = derived, unique to a more recent group.

Principle of PARSIMONY

Generating an hypothesis of historical homology based on the smallest number of phylogenesitc transformations

Principle of minimum increase in complexity

Also the genome follow parsimony: the simpler the alteration to produce a variant, the greater the probability of its occurring and becoming established in a population.

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Phylum ← Taxon (or Clade, if monophyletic)

Class

Order

Family

Genus

Species

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Phylum: Chordata

Class: Mammalia

Order: Primates

Family: Cercopithecidae

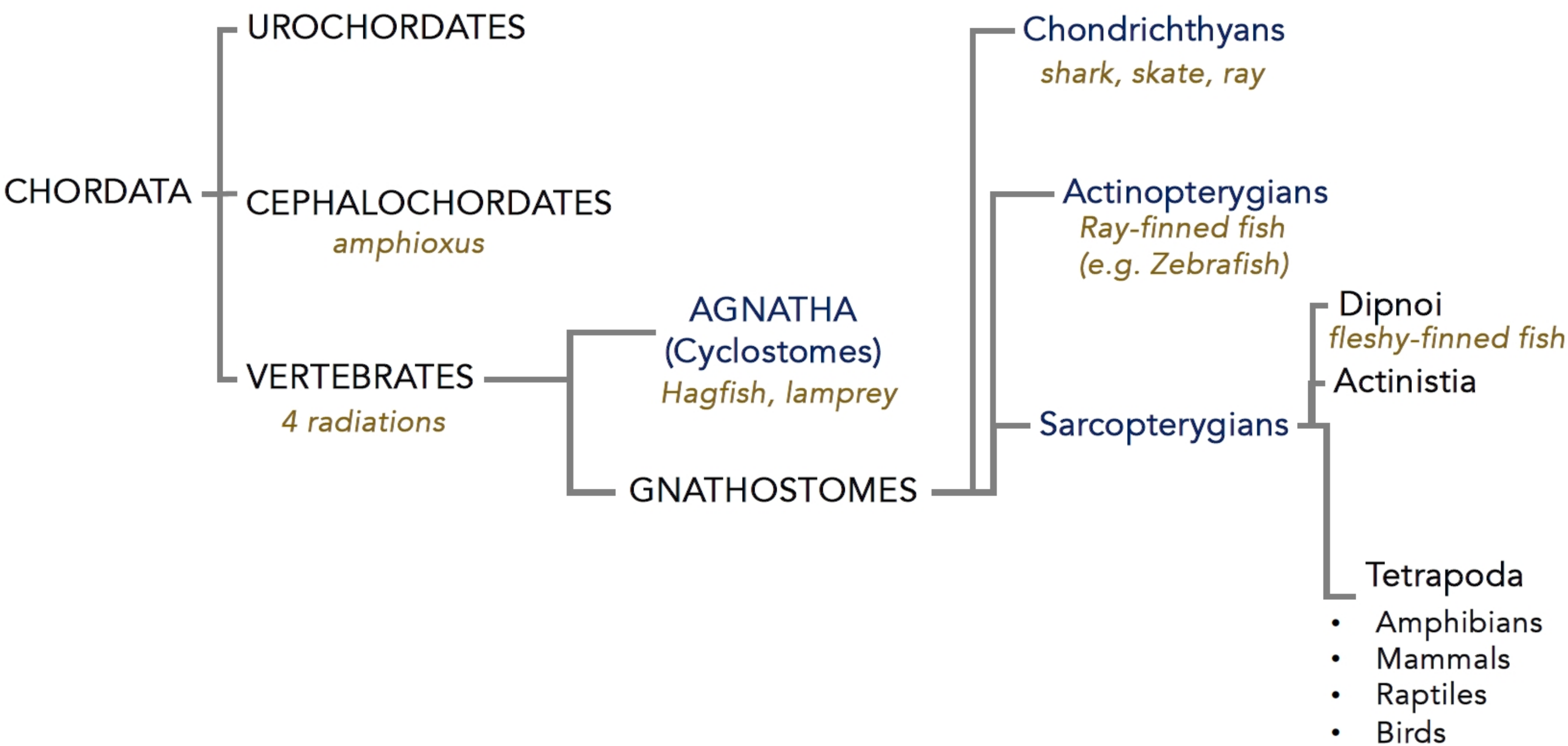
Genus: Macaca

Species: Mulatta

Scientific name: *Macaca Mulatta*

Scientific name: Rhesus macaque, macaque monkey

Vertebrate Phylogeny



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CHORDATA
Characterized by a notochord

UROCHORDATES	CEPHALOCHORDATES	VERTEBRATES
Tunicates (ascidians)	Branchiostoma (Amphioxus)	

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VERTEBRATES

hagfishes

1) AGNATHANS (Cyclostomes)

lampreys

2) Chondrichthyans

GNATHOSTOMES

3) Actinopterygians

4) Sarcopterygians

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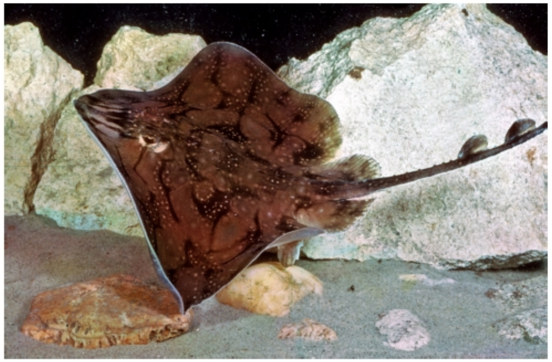
2) Chondrichthyans

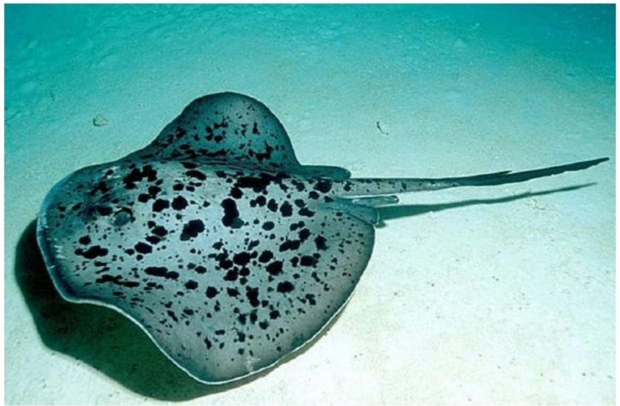
ratfishes

HOLOCEPHALI



skates

ELASMOBRANCHI



rays

sharks

3) Actinopterygians

Ray-finned fishes
(e.g. Zebrafish)

Dominant class of vertebrates: 99% of 30,000 species of fish
Widely distributed.

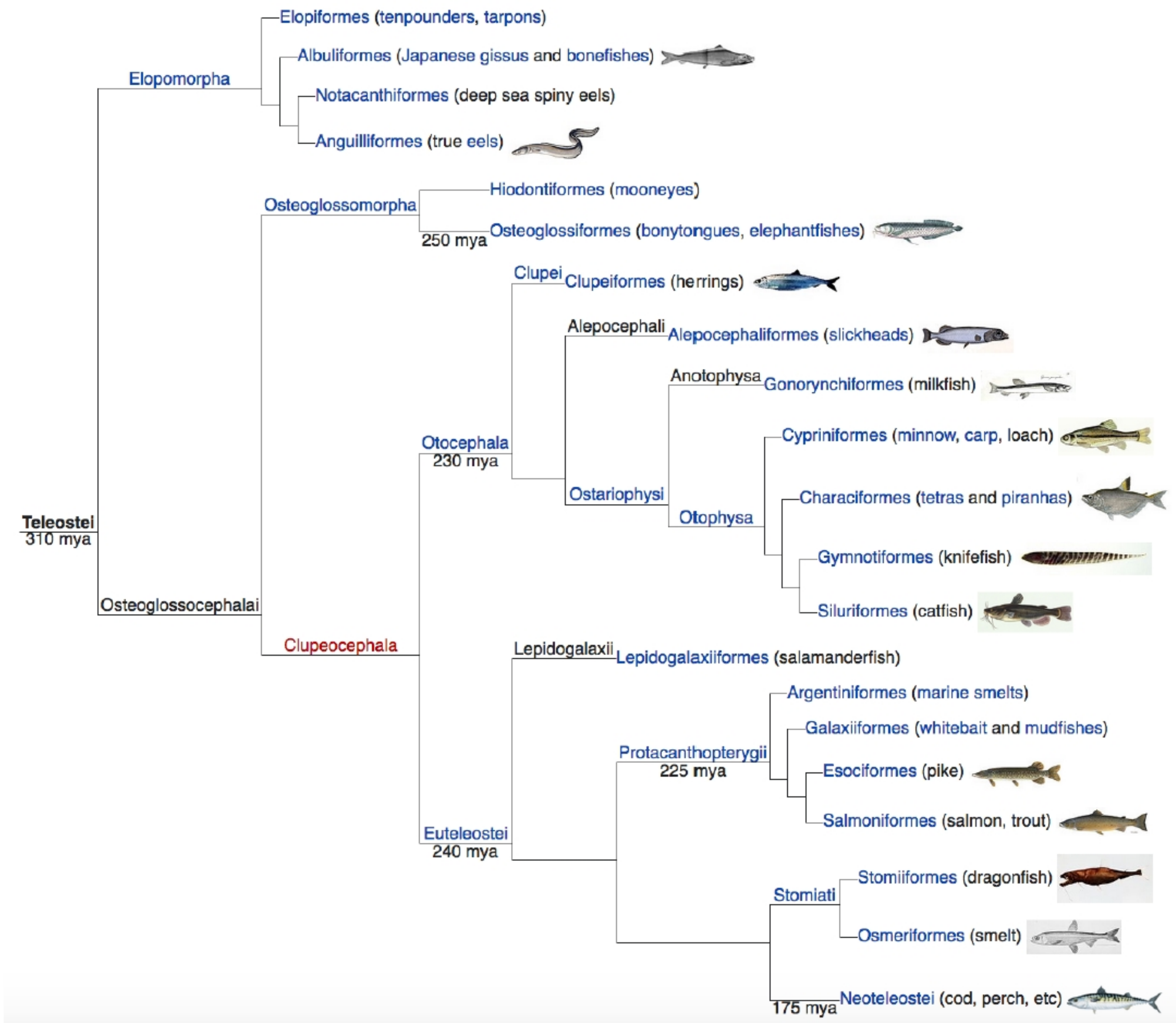
sturgeon

CHONDROSTEI

TELEOSTEI

Zebrafish

TELEOSTEI



Elopiformes (tenpounders, tarpons)
Albuliformes (Japanese gissus and bonefishes)
Elopomorpha
Notacanthiformes (deep sea spiny eels)
Anguilliformes (true eels)
Hiodontiformes (mooneyes)
Osteoglossomorpha
Osteoglossiformes (bonytongues, elephantfishes)
250 mya
Clupei
Clupeiformes (herrings)
Alepocephali
Alepocephaliformes (slickheads)
Anotophysa
Gonorynchiformes (milkfish)
Cypriniformes (minnow, carp, loach)
Otocephala
230 mya
Ostariophysi
Characiformes (tetras and piranhas)
Otophysa
Teleostei
310 mya
Gymnotiformes (knifefish)
Osteoglossocephalai
Siluriformes (catfish)
Clupeocephala
Lepidogalaxii
Lepidogalaxiiformes (salamanderfish)
Argentiniformes (marine smelts)
Galaxiiformes (whitebait and mudfishes)
Protacanthopterygii
225 mya
Esociformes (pike)
Salmoniformes (salmon, trout)
Euteleostei
240 mya
Stomiiformes (dragonfish)
Stomiati
Osmeriformes (smelt)
175 mya
Neoteleostei (cod, perch, etc)

4) Sarcopterygians

Dipnoi — Fleshy-finned fishes

Tetrapods — Amphibians

Mammals
Reptiles
Birds
AMNIOTES

AMNIOTES: with amniotic membrane, that envelops embryo during development

Amphibians

- Gymnophionans Caecilians (worm-like)

- Urodeles salamanders

- Anurans

Frogs

Toads

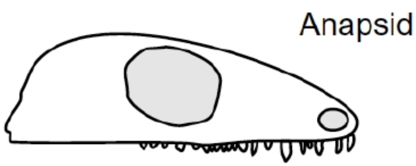
Skull Openings as a marker of evolutionary relationships

The classification into **anapsid**, **synapsid**, and **diapsid** skull types is important because it helps us understand the **evolutionary relationships** and **adaptations** of vertebrates, especially amniotes (reptiles, birds, and mammals).

Skull Openings and Evolution

- These terms refer to the number and position of **temporal fenestrae** (holes behind the eyes) in the skull.
- These openings allow for **stronger jaw muscles** and **lighter skulls**, influencing feeding and behavior.

AMNIOTES: Mammals, Reptiles and Birds



Anapsid

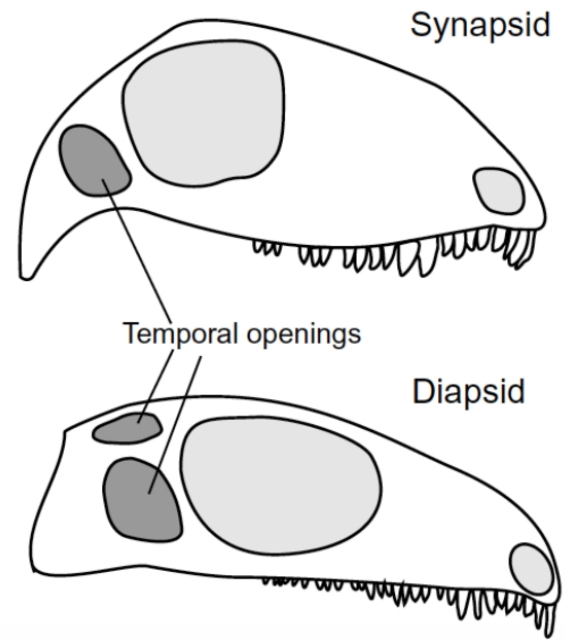
the earliest amniotes;
no openings in the skull

Synapsid

Gave rise to mammals

Diapsid

Reptiles and Birds



Summary:

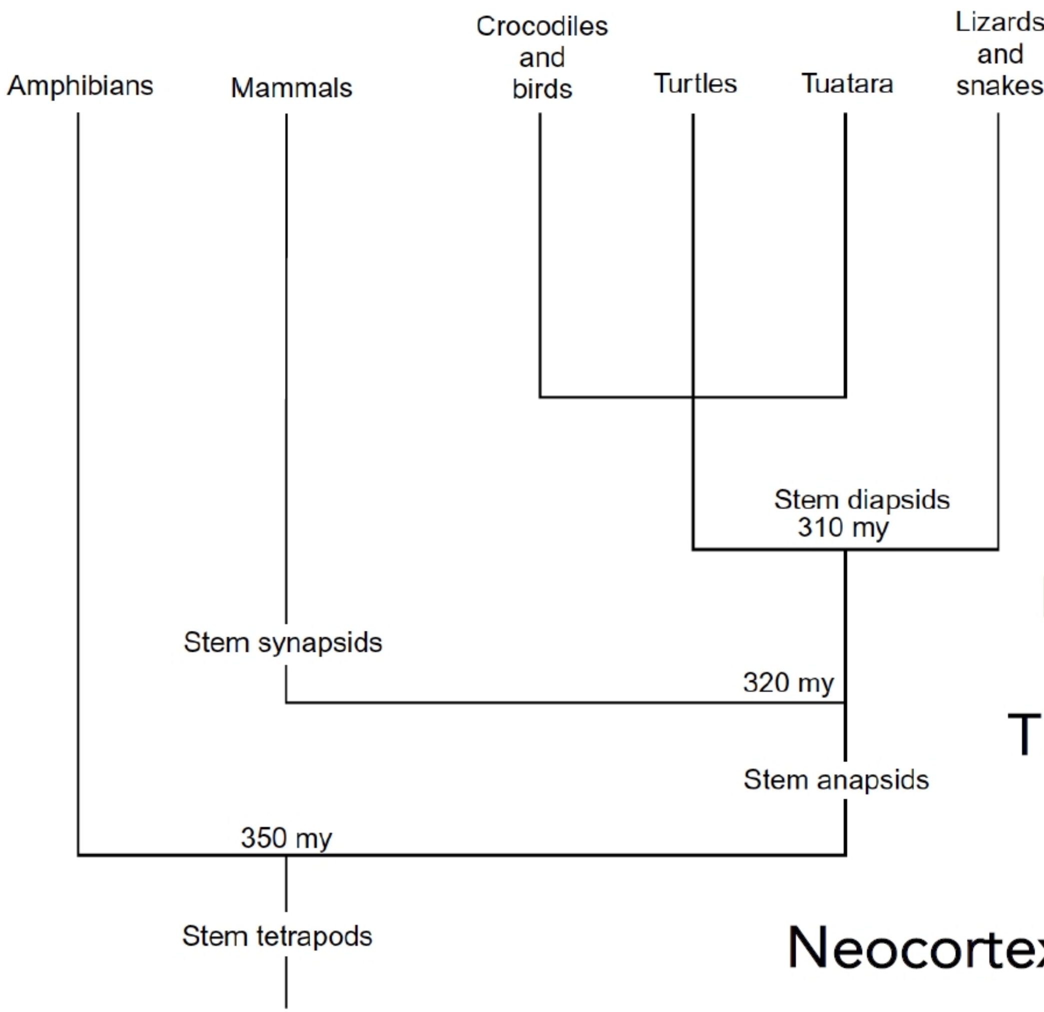
•**More openings = more space for muscles** → stronger bite and more complex feeding strategies.

•These differences reflect **adaptive evolution** to different ecological roles and diets

Anapsids
No temporal openings.
Traditionally associated with **early reptiles** and **turtles** (though turtle classification is debated).
Synapsids
One temporal opening.
Includes **mammals** and their extinct ancestors (like Dimetrodon).
Important for tracing the evolution of **mammalian traits**.

Diapsids
Two temporal openings.
Includes **modern reptiles** (like lizards, snakes, crocodiles) and **birds**.
Crucial for understanding the evolution of **flight**, **vision**, and **predation**. Anapsids were once thought to include turtles, but molecular data suggests turtles may be **modified diapsids**, showing how morphology and genetics can conflict.

Phylogenetic Insight
These skull types help reconstruct **cladograms** and **phylogenies**, showing how major vertebrate groups diverged.



Mammals branched out earlier!

Mammals are not "superior",

They are not on top of any scale

Neocortex is a relatively recent structure

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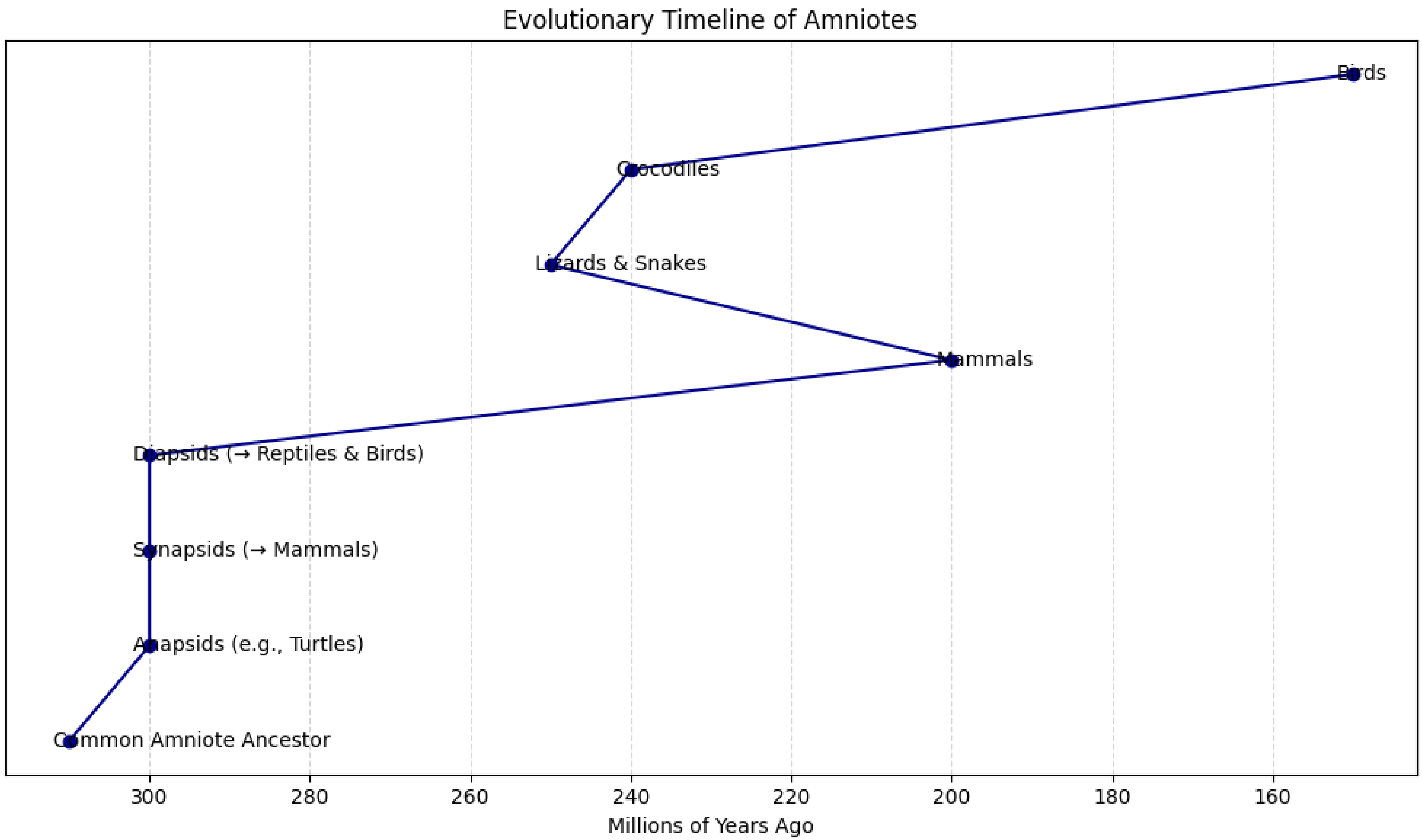


Key Points:

- **310 million years ago**: Common amniote ancestor.
- **Anapsids** (e.g., turtles) diverged early.
- **Synapsids** led to mammals.
- **Diapsids** split into reptiles and birds, including lizards, snakes, crocodiles, and eventually birds.

Mammals

Prototheria (monotremes) lay eggs

Metatheria (marsupials) Viviparous,
skin pouch for embryo development

Eutheria (placentals) Placenta,
Embryo develops fully inside
Very diverse radiation (several habitats)

Reptiles (6,000 species)

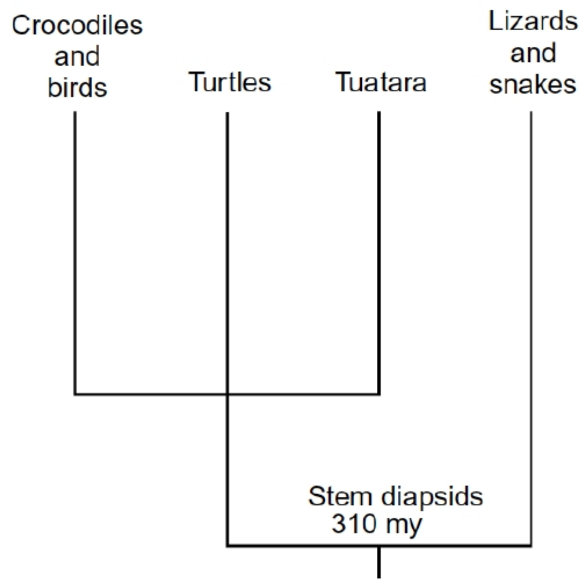
Crocodiles

Turtles

Lizards and snakes

Birds

- Feathers
- Numerous species (8,700 species)



Mammals have 4,500 species

SUMMARY Lecture 1

- **Evolution: diversity, genetic background/changes and natural selection**

- **Ancestor vs derived** (scala naturae does not exist)

- **Gradual vs sudden changes in evolution**

(microevolution,anagenesis, cladogenesis, punctuated equilibrium, speciation, heterochrony)

- **Evo-devo intro**

- **Homology vs Homoplasy vs Analogy**

(convergence, parallelism, reversals)

- **Vertebrate phylogeny diversity** (all animals adapted to their environment)

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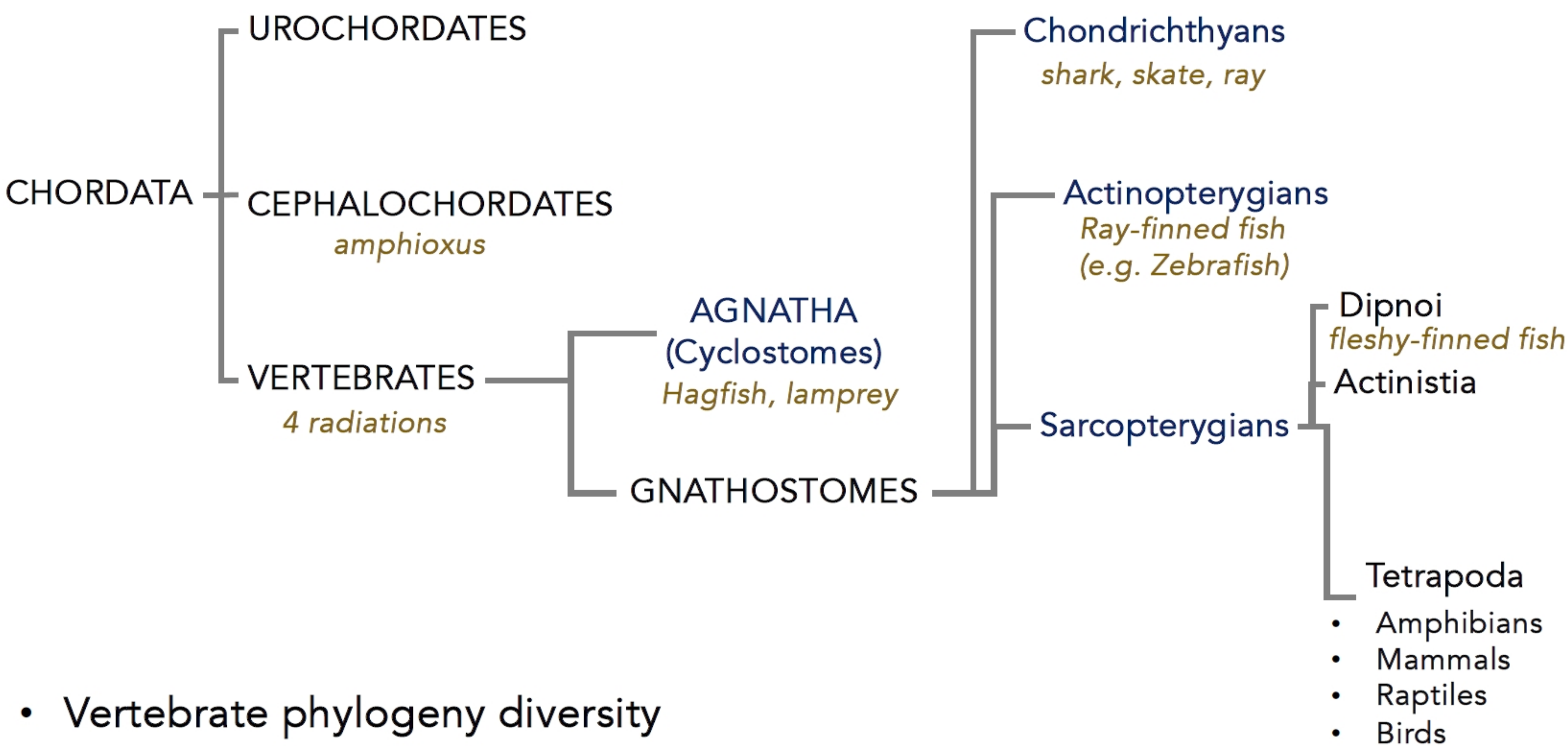
Vertebrate Phylogeny (SUMMARY)



- Vertebrate phylogeny diversity

Lecture 2:
Principles of Comparative Neuroanatomy

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Lecture 2:
Principles of Comparative Neuroanatomy (I)

1. Definition and nomenclature

2. Comparative neuroanatomy studies

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Comparative Neuroanatomy: definition

Aim: elucidate and interpret form and structure of the nervous system

Anatomy is easier when you compare species!

It encompasses various fields of research:

- Comparative neuroembriology
- Formal (pure) comparative neuroanatomy
- Phylogenetic comparative neuroanatomy
- Functional comparative anatomy
- Evolutionary morphology

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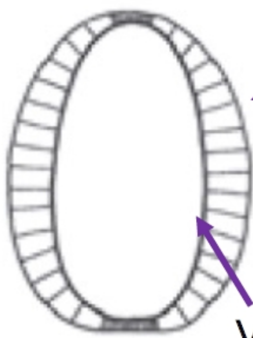
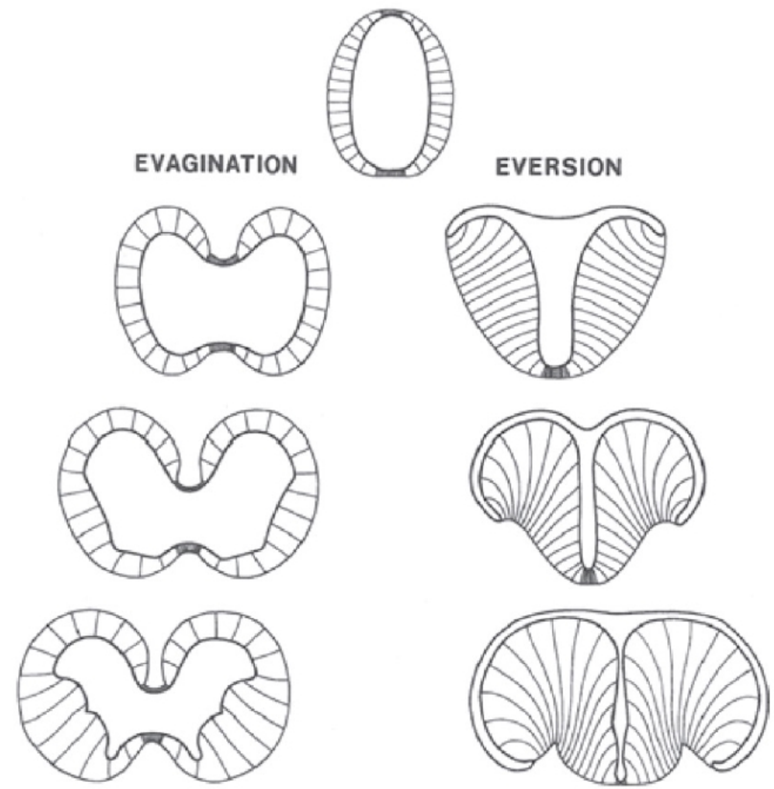
Principles of Comparative Neuroanatomy

Embryonic neural tube



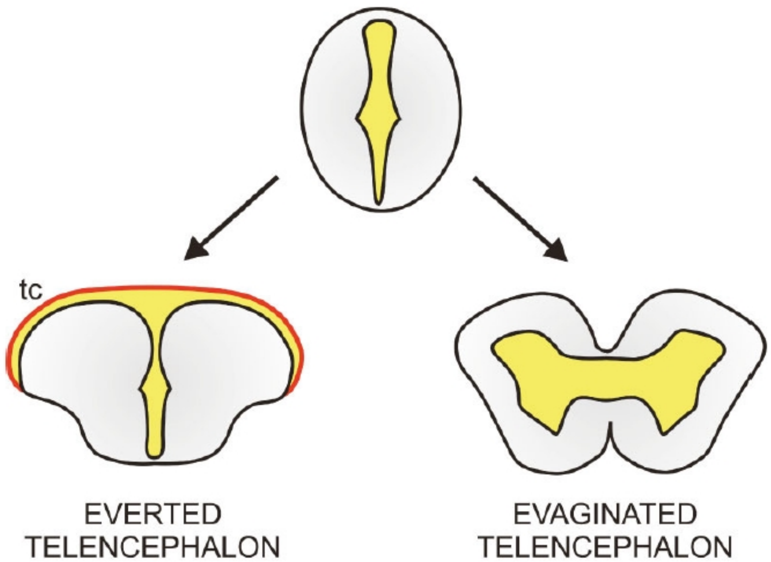
Radially oriented neuroepthelium

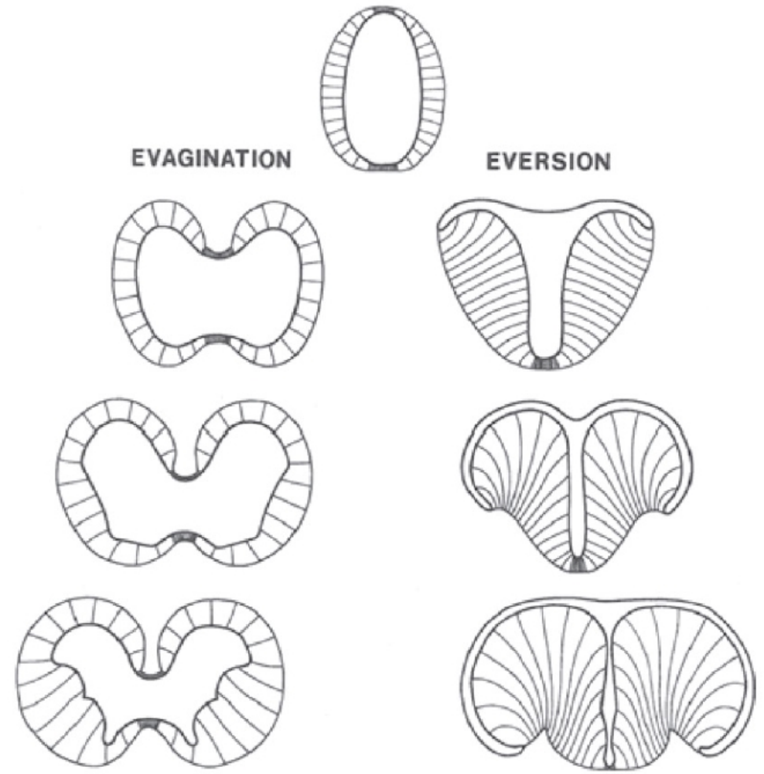


e.g. Mammals

Ray-finned fishes

Principles of Comparative Neuroanatomy





e.g. Mammals

Ray-finned fishes

Neural coordinate system

3 axes:

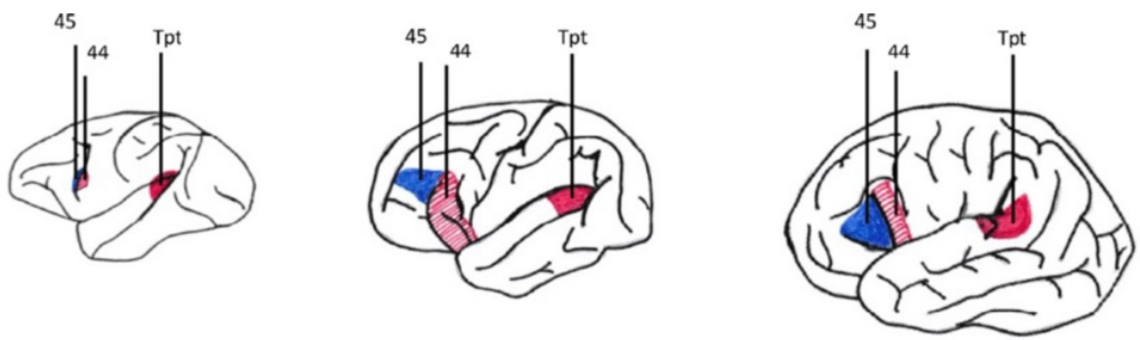
1. Anterio-posterior
2. Dorsal-ventral
3. Medial-lateral

Brodmann areas

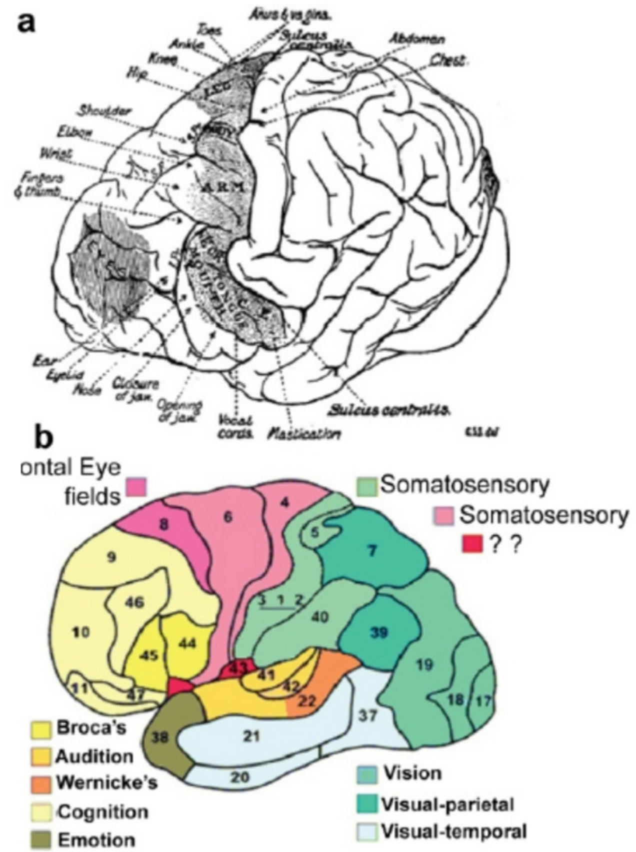
Coronal section

Neural coordinate system

Brodmann areas in different primates



macaque chimpanzee human



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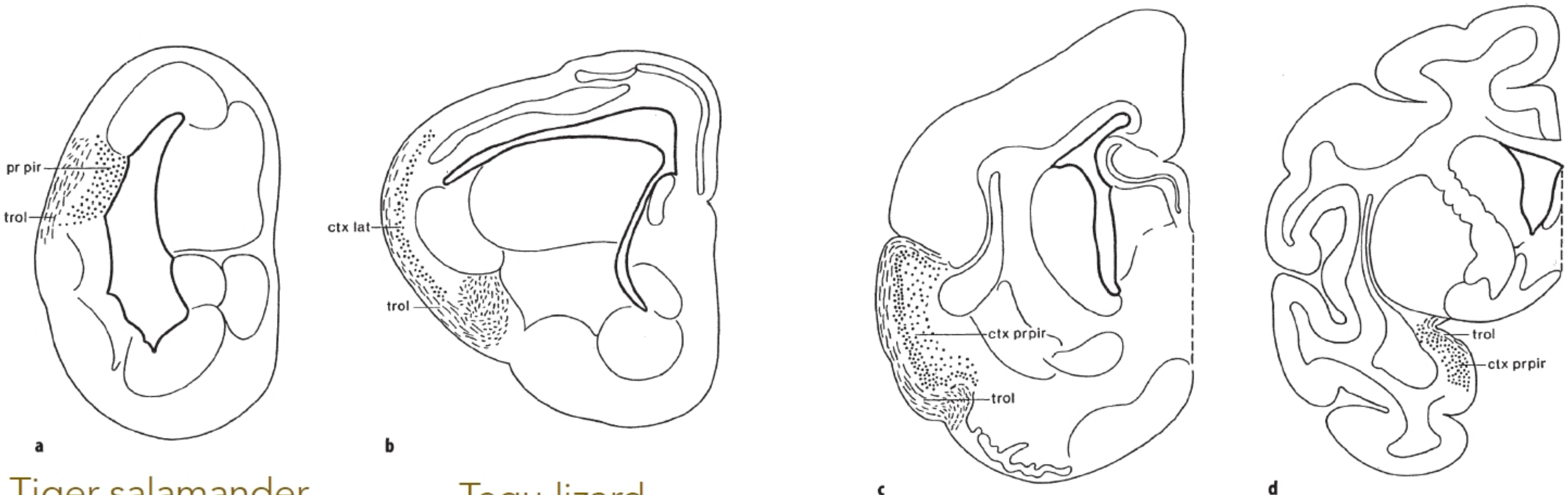
The importance of recognizing boundaries

Same areas (similar functions) change position in different vertebrates.



Tiger salamander

Tegu lizard

Opossum

Rhesus macaque

Primodium piriforme

Cortex lateralis

Piriform cortex

Olfactory tract (trol)

Topology

The CNS of all vertebrates are topologically equivalent.

Topology: geometry of distorsion, investigates the properties that remain unchanged when geometric configurations are subjected to one-to-one continuous transformations.

Changes allowed: distances, bend, stretch, twist

Not allowed: tear

Orientation is hard to identify sometimes!

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Implications of topological studies:

Do evolution always increase complexity?

New structures might be derived from general primordia or homologues in other vertebrates, and might be adding features and become more complex.

Regressions/reductions: specific areas disappear (e.g. anosmatic cetaceans lack olfactory bulbs)

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Implications of topological studies:

What do topology reveal?

YES

morphological correspondance

NO

Ancestral relationships

↓

TAXONOMY

Taxonomy

Identify the **taxonomic position** of chosen species is important in all comparative studies.

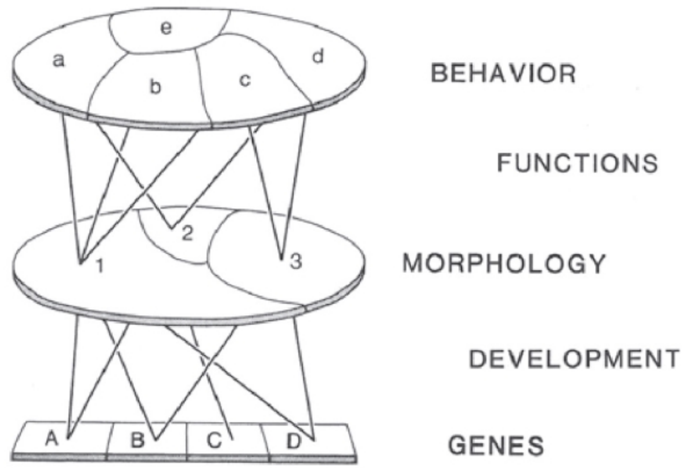
Important to recognize **homology** and **analogy** in Comparative Neuroanatomy.

Homology vs Analogy in Comparative Neuroanatomy

Homology

What it is,
not what it does

- Same relative positions and connections to structures;
- Even without morphological similarity, structures genetically related and with a common ancestor are homologous



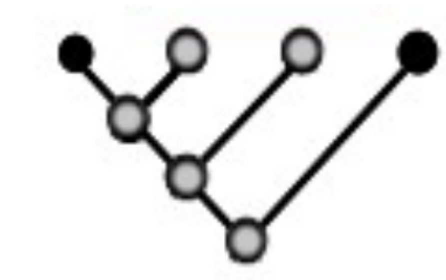
Analogy

Same function

Do not confuse Homology with Homoplasy!

Homoplasy When a trait has been gained or lost indipendently in separate lineages over evolution (parallel or convergent homoplasy).

similar selection pressures



Ancestral trait (○)
Derived trait (●)

What is the ancestral trait and what is the derived one?

Criteria for Determination of Homology in the CNS

- Principal criterion: Similarity in position

- Auxilary criteria:
  - Similarity in fiber connections
  - Similarity in "special quality"
  - Continuity of similarity through intermediate species

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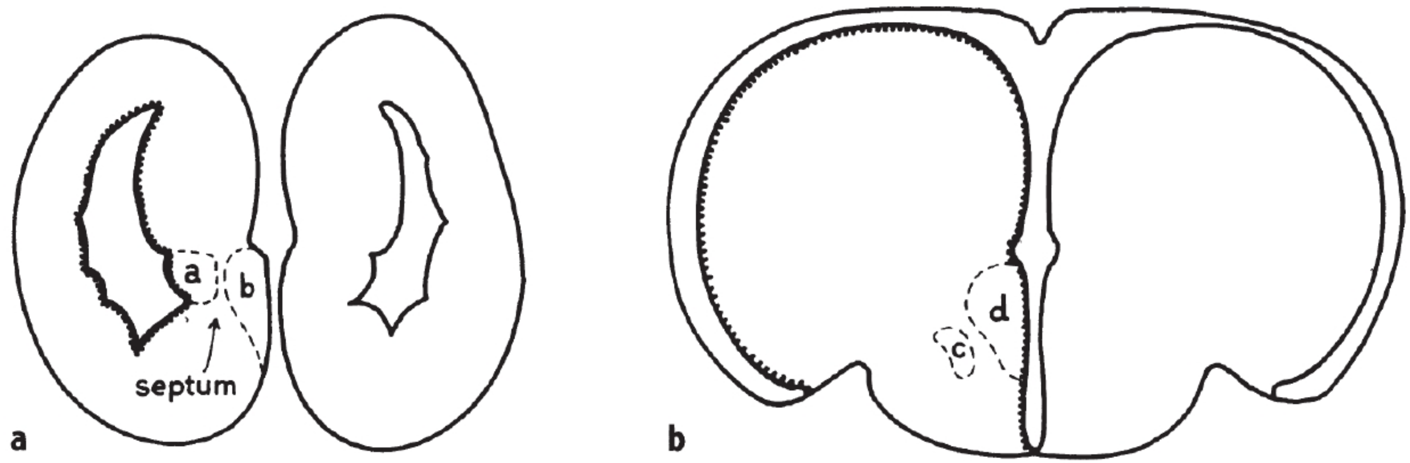
- Principal criterion: Similarity in position



Urodele amphibian

Teleost

Relative topological position: Mutual cytoarchitectonic boundaries

Other landmarks:
- Ventricular sulci
- Cell-free zones
- Commissures
- Fiber bundles

Which “letters” are homologous?

Principal criterion: Similarity in position

Consider ontology (=development)

Cell masses ("nuclei" in anatomy)/structure can be homologised based on their **primary position** (rather than secondary position).

↑

Trace structure back to the topological position they occupied at the beginning of development.

WHY is this more difficult to do with MAMMALS?

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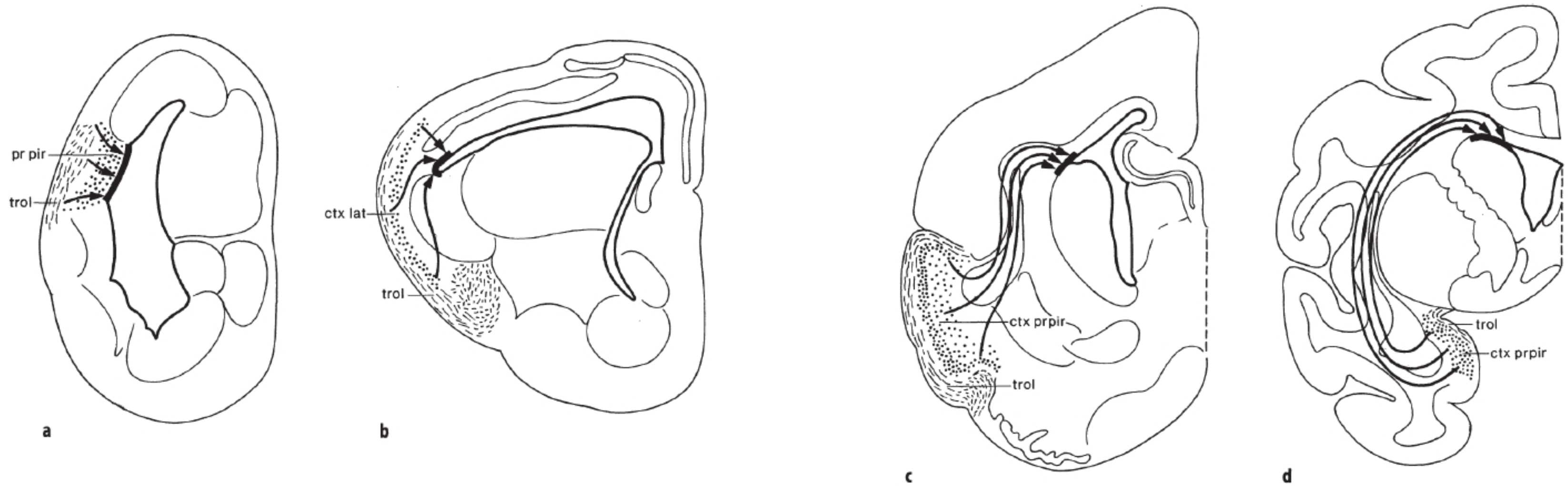
WHY is this more difficult to do with MAMMALS?



Tiger salamander

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Opossum

Rhesus macaque

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Similarity in fiber connections

A controversy: why?

Many pathways of fibers are conserved phylogenetically

- When a structure in a species has the same connections to another species, they concluded they were homologous: NOT ALWAYS TRUE!

- Fibers can seem similar, but they can connect to structures that are not homologous

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Similarity in fiber connections

A controversy: why?

- Many structures do NOT have well-defined connections.

- A neural structure may change its connections without losing its morphological identity

Fiber connections are **not decisive factors**, but they might be supplementary arguments to primary criterion (morphology, embryonic development).

Criteria for Determination of Homology in the CNS

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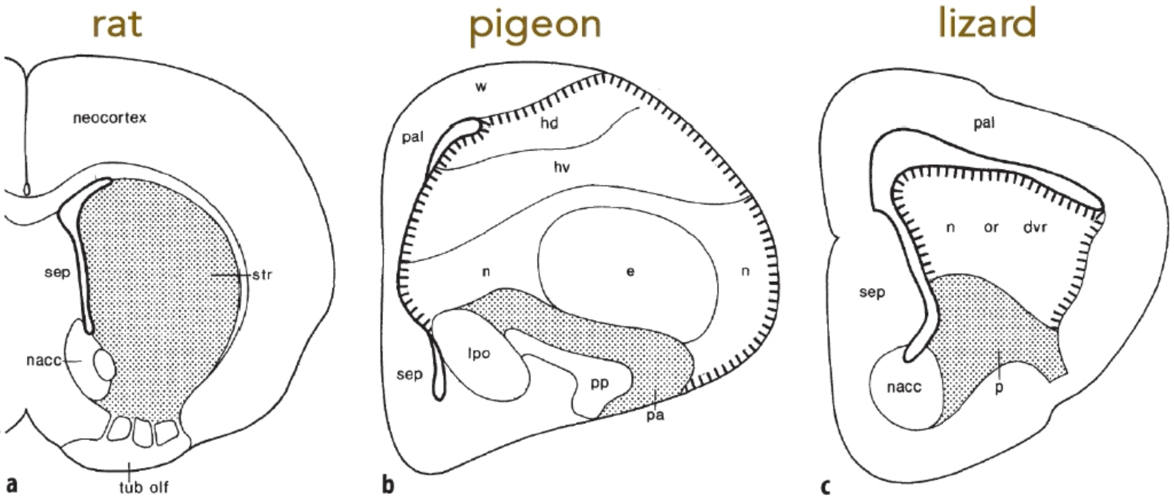
Similarity in special quality: immunohistochemistry

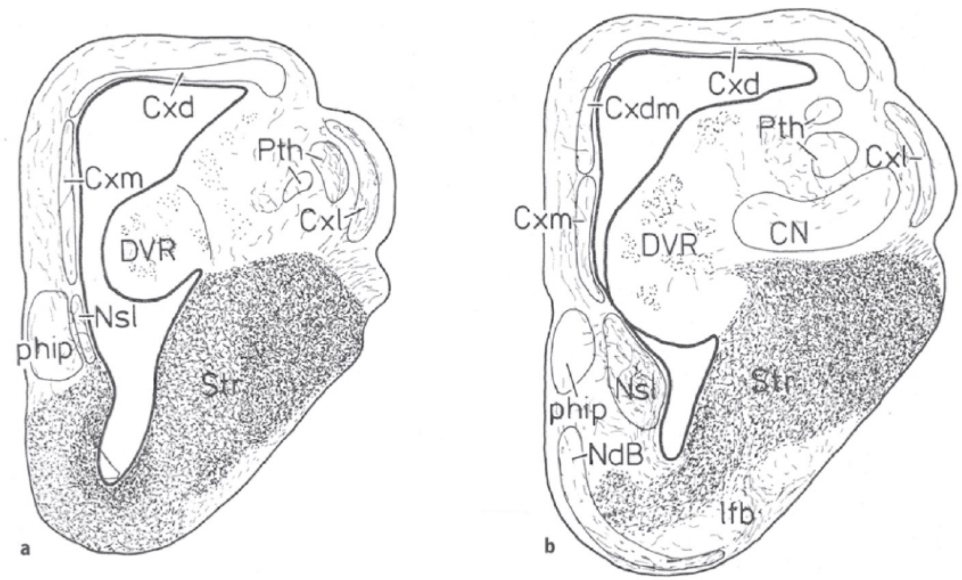
Identify highly specific morphological histochemical features
with immunohistochemical/IF techniques.
(e.g. presence of a particular neurotransmitter, neuromodulator or enzyme)

Example:

Identification of the Avian and Reptilian homologues of the mammalian caudate-putamen complex



turtle



Example 2:

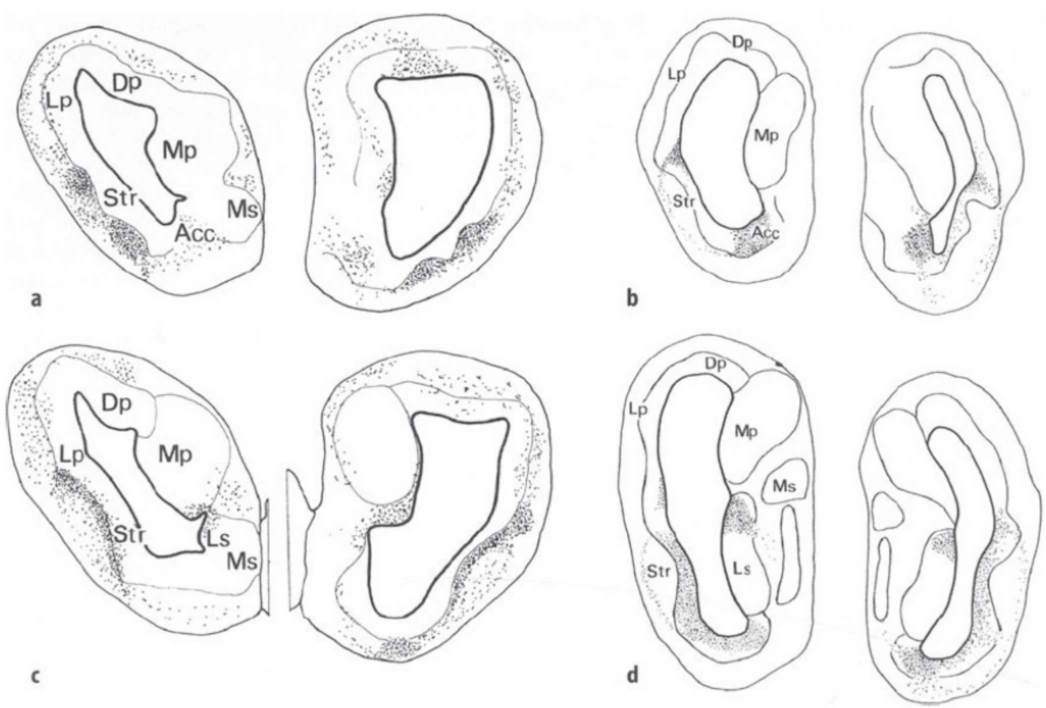
Distribution of dopaminergic fibers reveals the striatum in different species.

URODELA

newt

ANURA

frog



Tyrosine hydroxylase IHC

Dopamine IHC

Example 3:

Localisation of the striatum and nucleus accumbens in amphibians

Criteria for Determination of Homology in the CNS

- Principal criterion: Similarity in position

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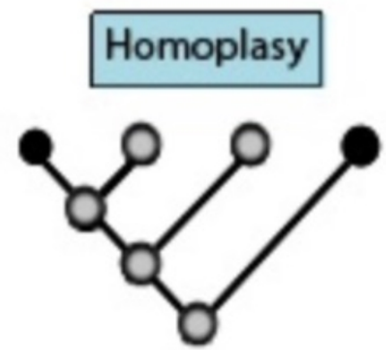
Continuity of similarity through intermediate species

Used when homologous structures differ in position and IHC qualities,
Or to exclude homologies of structures with similar form/position.

Useful to distinguish homologous vs homoplastic.



Example: Electrosensory system

The fact that electroreceptors and a dorsal octavolateral nucleus are lacking in holosteans (the group of actinopterygian fishes standing taxonomically in between chondrosteans and teleosts) makes it likely that dorsal octavolateral nucleus found in most amniote groups and the teleostean electroreceptive lateral line lobe are homoplastic rather than homologous.

Comparative Neuroanatomy (Neuromorphology)

- Formal (pure) comparative neuroanatomy
- Comparative neuroembriology
- Phylogenetic comparative neuroanatomy
- Functional comparative neuroanatomy
- Evolutionary neuromorphology

Pure Comparative Neuroanatomy/Neuromorphology

Aim: establishment of homology.

Nomenclature based on topology

Phylogenetic Neuroanatomy

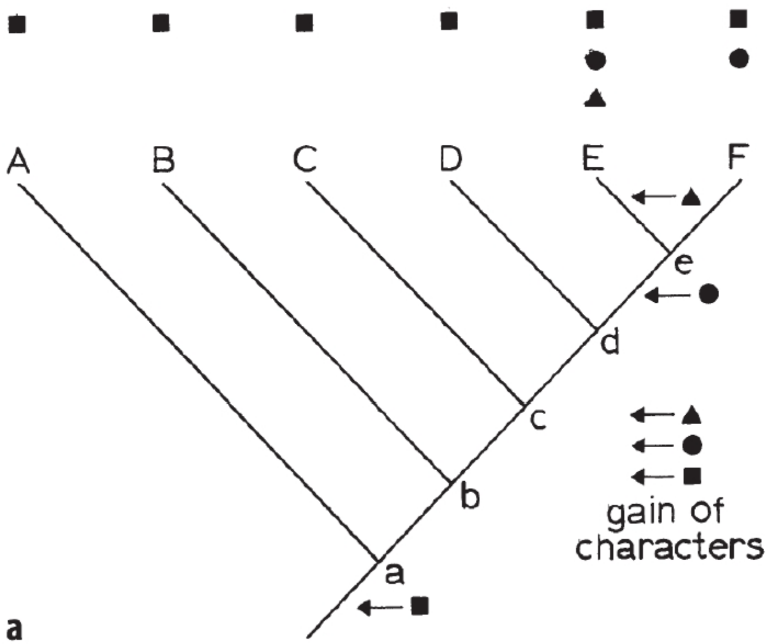
Aim: Place results of neuromorphological studies in a historical context (build **cladograms**).

↓

Neurocladistics

Takes into account phyletic interrelationships

Neurocladistics



monophyletic Descendants of one last common ancestor

plesiomorphic Primitive or ancestral trait

apomorphic Derived trait

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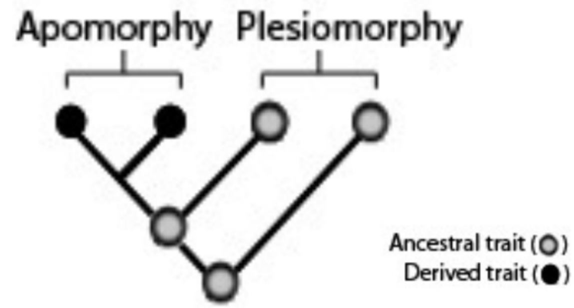
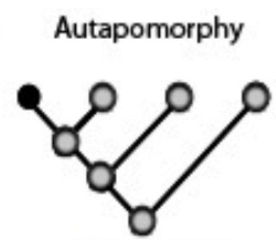
plesiomorphic Primitive or ancestral trait

apomorphic Derived trait

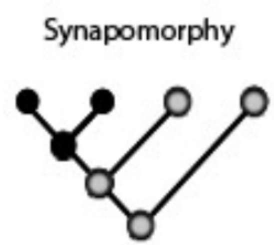


- symplesiomorphic characters present in sister groups and in the out-groups

- autapomorphic characters present in only a single terminal taxon



- synapomorphic Characters present in sister groups but not in the neighboring taxa (i.e. outgroups of the sister groups)

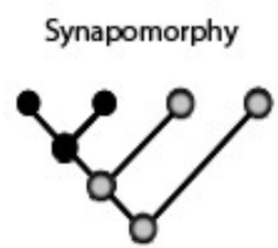


Which ones are homologous?

Symplesiomorphy and Synapomorphy also give info about the **POLARITY** of the homologous characters.

- symplesiomorphic characters present in sister groups and in the out-groups

- synapomorphic Characters present in sister groups but not in the neighboring taxa (i.e. outgroups of the sister groups)

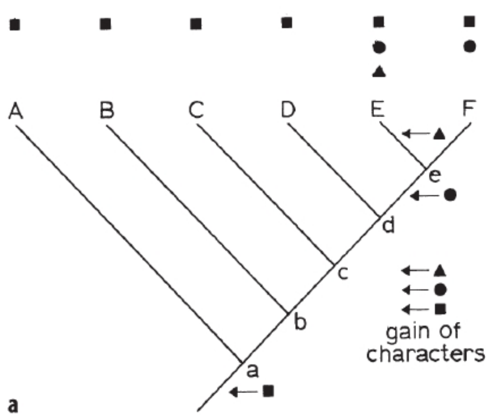


Which ones are **homologous?**

Symplesiomorphy and Synapomorphy also give info about the **POLARITY** of the homologous characters.

How to determine the polarity of transformations?

1. Out-group analysis



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2. Developmental analysis

Early embryos of animals from related groups resemble each other, and the degree of resemblance decreases as development proceeds

early in development: plesiomorphic
late in development: apomorphic

Functional neuromorphology

It uses a nomenclature that takes into account functions.

Example: Functional columns in amniotes

Somatosensory, viscerosensory, visceromotor, somatomotor (rhombencephalon)

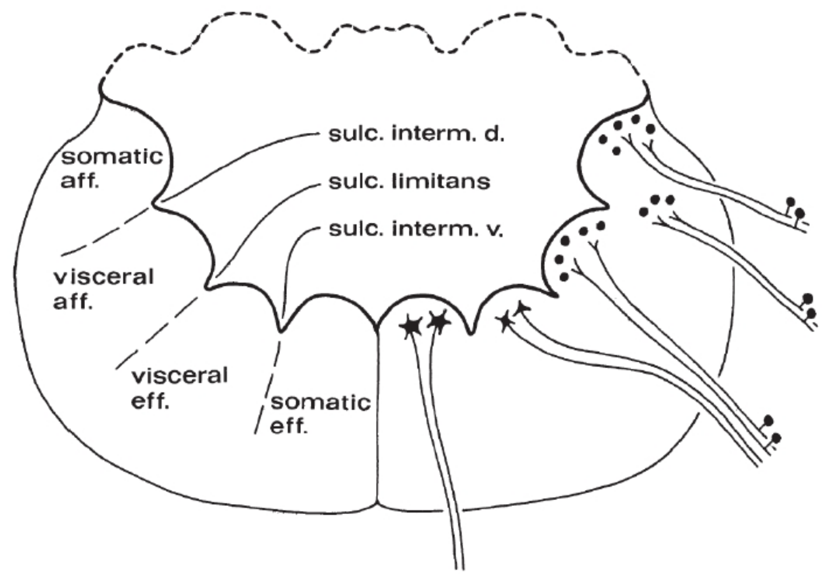

Fig. 6.29. The functional columns in the rhombencephalon according to Herrick and Johnston

A complete functional subdivision of CNS is difficult in comparative neuroanatomy.

Behavior and environment.

Summary

- Axis of the CNS
- Topology
- Taxonomy
- Homology in Comparative neuroanatomy
- Criteria for determination of homology in the CNS
(similarity in position, development, fiber connections, IHC, intermediate species)
- Neurocladistics
- Functional neuromorphology

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Review

The economics of brain size evolution in vertebrates

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Your Brain Is Not an Onion With a Tiny Reptile Inside

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