Homologie a analogie jedno jsou...?

O společném původu ***s různým stupněm*** modifikací

Organismus 2016

Homologie a analogie jedno jsou...?

O společném původu ***s různým stupněm*** modifikací

- dichotomie homologie vs. analogie

- analýza prostoru mezi *homologií* a *analogií* ve smyslu společného vs. nezávislého evolučního původu, resp. *hloubky/hlubinnosti* takového původu

- od Darwinova "common descent with modification" po "common descent with *various degrees* of modification" (Brian K. Hall)

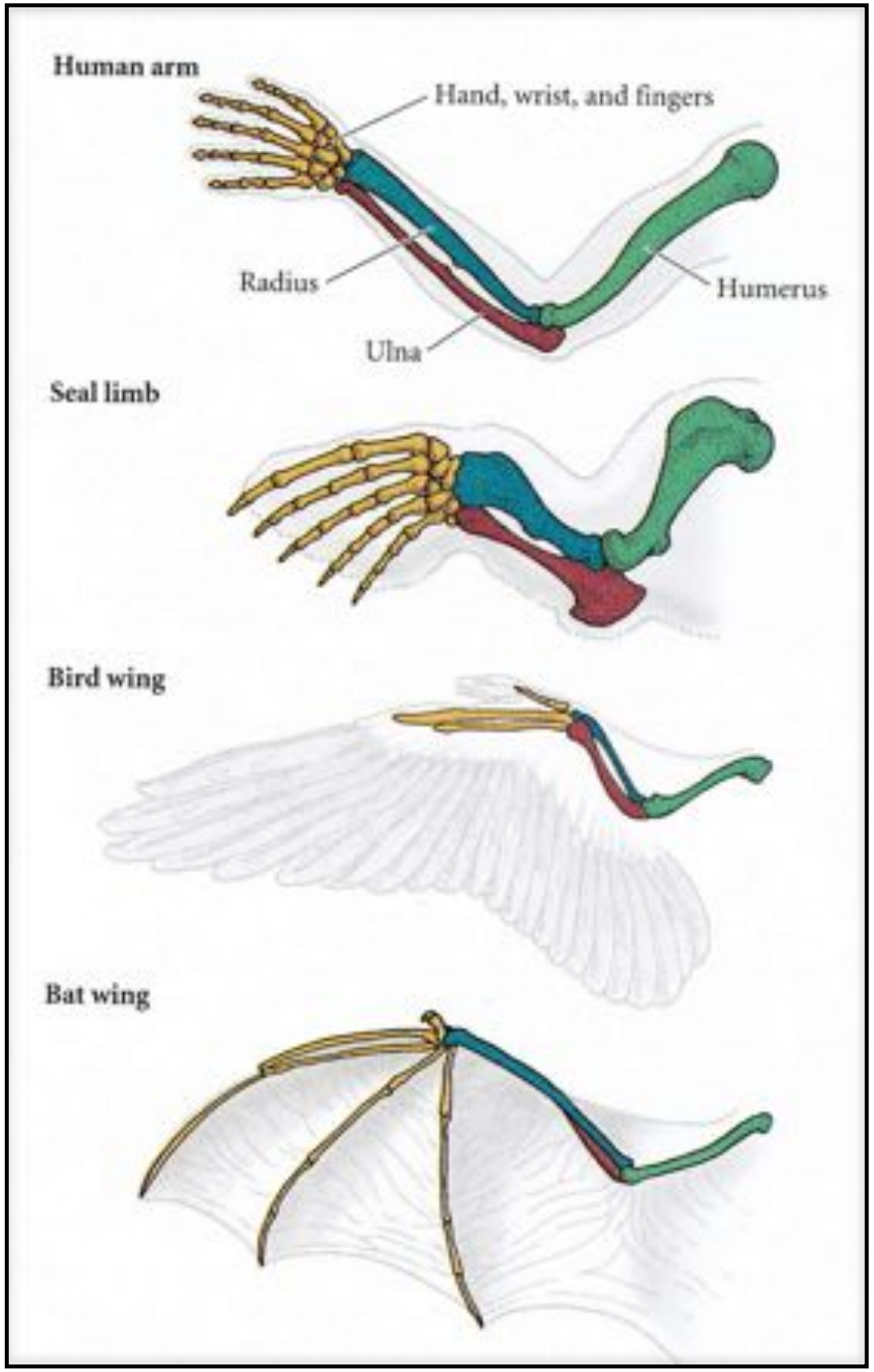
Homologie: typické pracovní definice

Homologie: *společná evoluce znaků*

- **podobnost díky společnému původu; "**příbuzenská podobnost"
- přítomnost /korespondence/ "stejného znaku" u dvou organismů, zděděná od jejich společného předka

Analogie: *ne-společná evoluce znaků*

- **podobnost díky nezávislé evoluci, "**falešná homologie"
- podobnost znaků, která není jednoduše vysledovatelná ke společnému předkovi, tento ji neexprimuje



klasický příklad:

Homologie

vs.

analogie

Přední končetiny čtyřnožců a jejich elementy (srv. barvy) jsou si navzájem **homologické**, odvozené od společného předka tetrapod.

Křídla ptáků a natopýrů představují nezávislé adaptace na let, jsou jakožto létadla **analogická**, neboť společný předek těchto skupin tuto adaptaci neměl.

Homologie: pozor na úrovně, typy a přístupy!

2 základní typy přístupů ke studiu homologií:

- **taxatický (taxický) přístup** – synapomorfie/ synplesiomorfie, W. Hennig; testovatelné kongruencí fylogenetické analýzy (*srv. J. Zrzavý: homologie jako výsledek fylogenetické analýzy).*

(vzpomeň příklad násobné ztráty/evoluce křídel u strašilek *s. lato!)*

- **transformační přístup** – evoluce homologií, sledování proměn a procesů, které je generují; odlišná kriteria a spíše přístup vykazovací nežli testovací.

(kupř. evoluce/transformace končetin z ploutví…)

Approaches to analysis of similarity in different biological fields[1]

Field	Concept	Mode of analysis
Phylogenetics and systematics	Historical homology (synapomorphy)	Character distribution in phylogenetic trees
Phenotypic evolution	Biological homology	Mechanisms of character evolution
Comparative developmental biology	Generative homology[2]	Mechanisms of development and the evolution of development

Homologie: *suma sumarum*

Homologie: *společná evoluce znaků*

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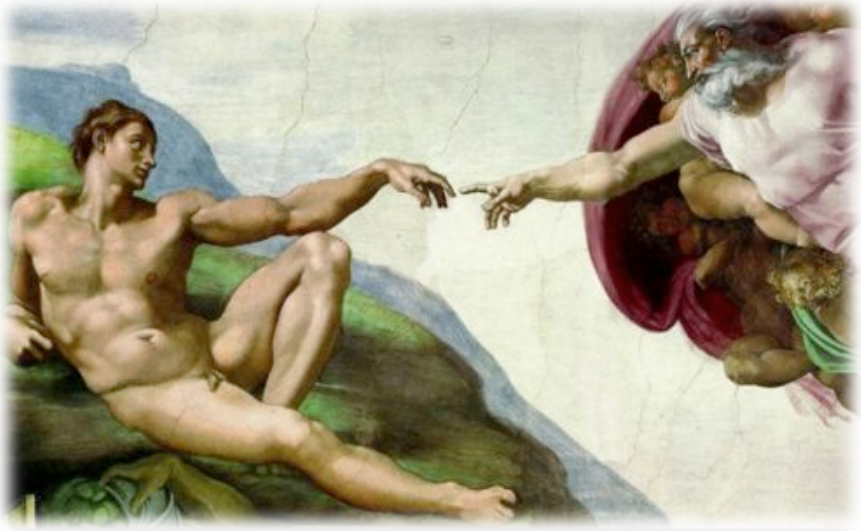
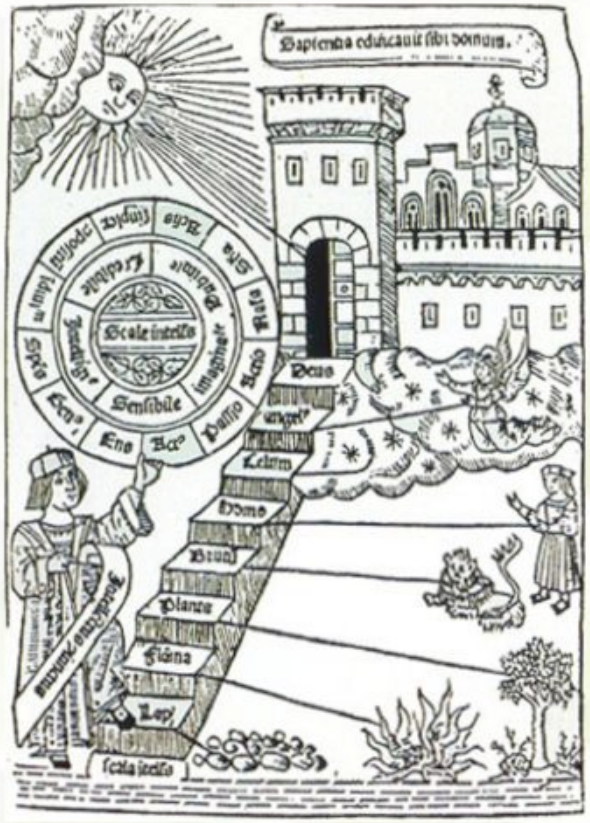
- homologie představuje "správný znak" – umožňující srovnávání a mající hodnotu pro evoluční a fylogenetické analýzy

- homologie představuje základ pro <u>každé</u> hierarchické srovnávání v biologii

Kategorizace podobností a Systém





Přirozené uspořádání organického světa:

v předevolučních dobách se lidé snažili rozklíčovat Boží zámysl a tomu odpovídalo dělení organismů - viz systém C. von Linného - *Systema Naturae* (1758)

ON

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

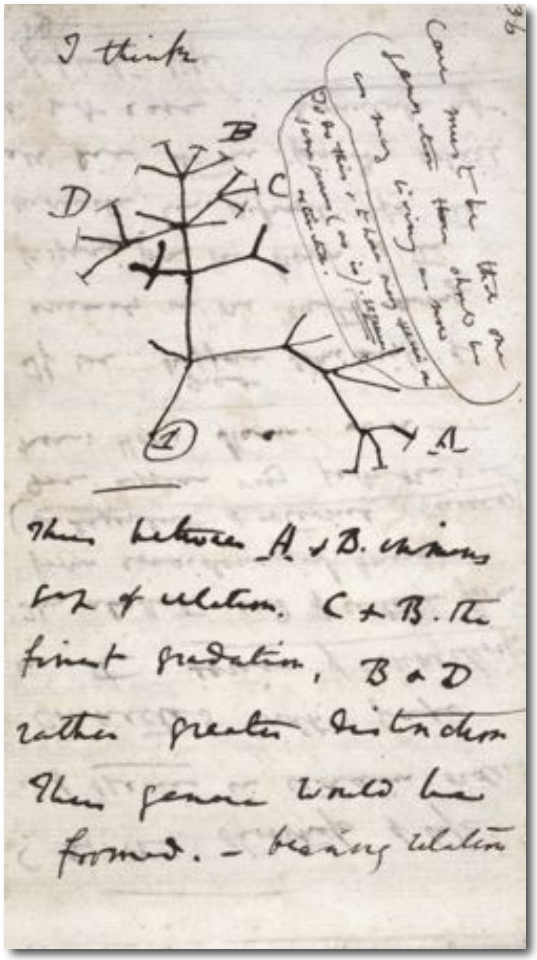
OR THE

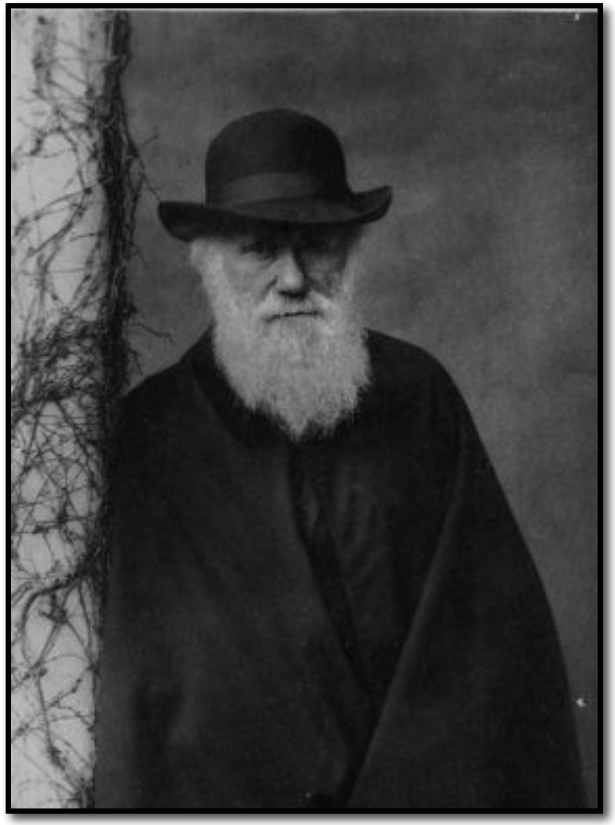
PRESERVATION OF FAVOURED RACES IN THE STRUGGLE FOR LIFE.

By CHARLES DARWIN, M.A.,

LONDON:
JOHN MURRAY, ALBEMARLE STREET.

Kategorizace podobností a Evoluční systém





Přirozený = evoluční systém představuje sled diversifikací linií během evoluce od společného předka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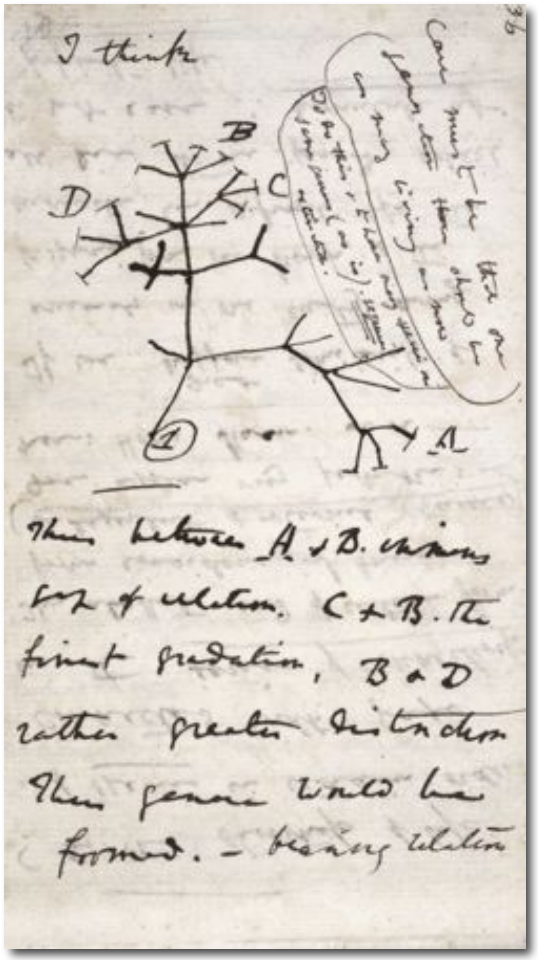


K.K.: ...biologická klasifikace odhaluje podstatnou rovinu našeho světa vůbec...

rozlišení homologie/analogie představuje základ pro všechny srovnávací studie od úrovně genů až po fenotyp a kamkoliv dále

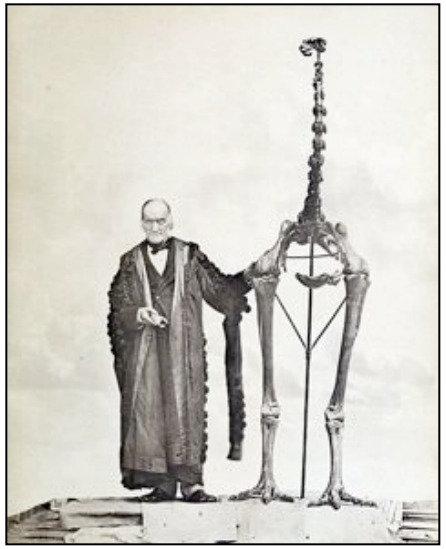
Původní rozlišení: sir Richard Owen

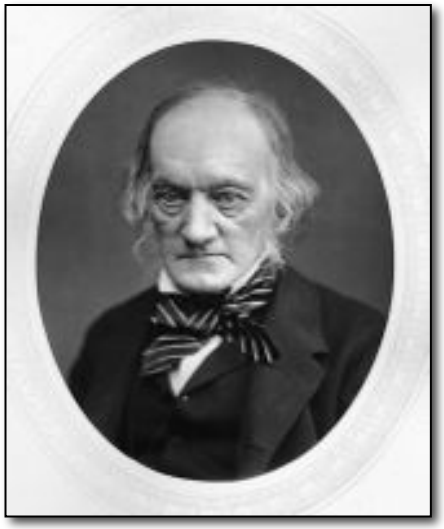
R. Owen (1843):

homologue: „the same organ in different animals under every variety of form and function“.

analogue: „a part or organ in one animal which has the same function as another part or organ in different animal“.

...neblahé problémy se *stejností (sameness)*

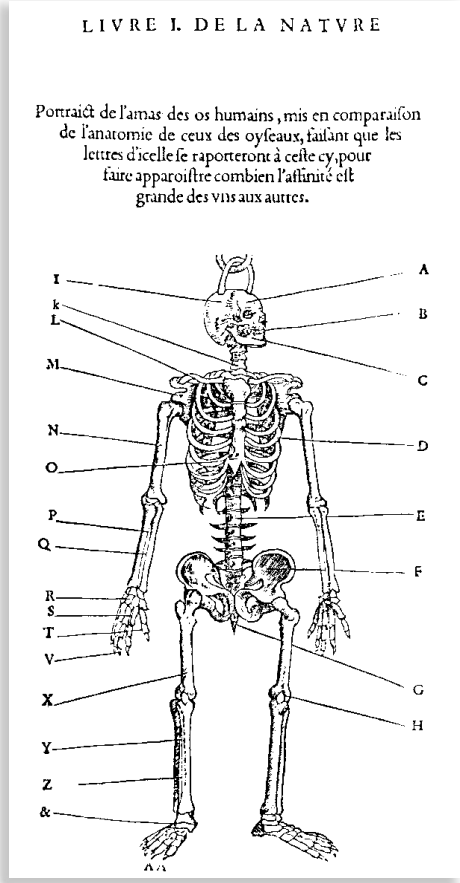


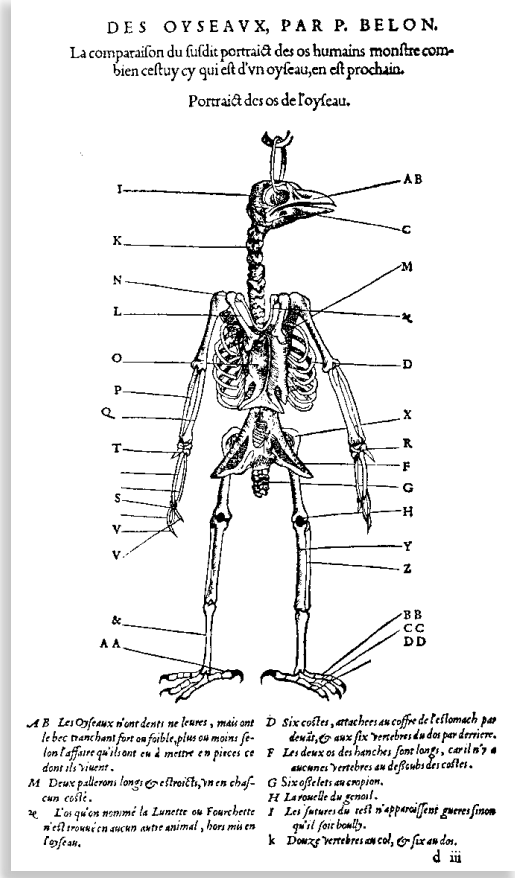


sir Richard Owen (1804-1892)

zakladatel moderní morfologie; **definoval poprvé homologie vs. analogie**

Kritéria k rozlišení homologie: vzájemná pozice a spojení





"Evoluční definice" homologie: sir Ray Lankester

R. Lankester (1870) /srv. C. Gegenbaur/
rozlišil dvě třídy podobností **podle sdílené nebo naopak nezávislé evoluční historie**:

homogeny:
features shared by two organisms and present in their nearest common ancestor
– similarity due to common descent

homoplasy:
other resemblances involving convergent evolution
– similarity arising from independent evolution

☒ podobnost vs. povrchová podobnost,
☒ stejná struktura vs. stejná funkce,
☑ **sdílená vs. nezávislá evoluční historie!!!**

Edwin Ray Lankester (1847-1929)

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Homogenie i homoplasie definovány jako dvě třídy homologie!

srv. S.J. Gould (2002) či B.K. Hall (2003); etc.

"Evoluční definice" homologie: sir Ray Lankester

homogeny:

"Structures which are genetically related, in so far as they have a single representative in a common ancestor, may be called *homogenous*. We may thace an *homogeny* between them, and speak of one as the *homogen* of the other ... details not traceble to, and inherited from the ancestor cannot be *homogenous.*"

(Lankester, 1870)

homoplasy:

"Homoplasy includes all cases of close resemblance of form which are not traceble to homogeny, all *details* of agreement not homogenous in structures which are broadly homogenous, as well as in structures having no genetic afinity."

(Lankester, 1870)

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(Lankester, 1870)

Edwin Ray Lankester

He summarized his approach in the article on Zoology in the 11th edition of the *Encyclopædia Britannica*:

Owen's definition of analogous structures holds good at the present day. His homologous structures are now spoken of as 'homogenetic' structures, the idea of community of representation in an archetype giving place to community of derivation from a single representative structure present in a common ancestor … Darwinian morphology has further rendered necessary the introduction of the terms 'homoplasy' and 'homoplastic' to express that close agreement in *form* which may be attained in the course of evolutionary changes by organs or parts in two animals which have been subjected to similar moulding conditions of the environment, but have not close genetic community of origin [ancestry], to account for their similarity in form and structure, although they have a certain identity in primitive quality which is accountable for the agreement of their response to similar moulding conditions. (Lankester, 1911, vol. 28, p. 1029)

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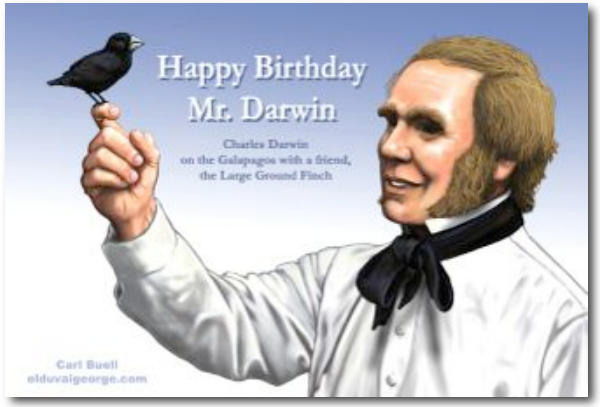
1859.

Homologie DNES

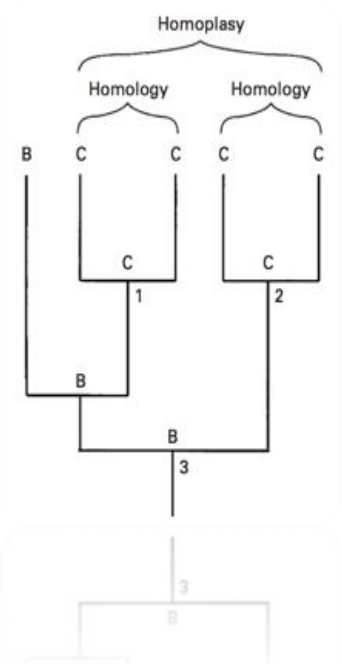


Po r. 1859

(*On the origin of species…*)

ARCHETYP » PŘEDEK

JEDNOTA PLÁNU » SPOLEČNÝ PŮVOD



☒ ☑

- homogenie ➔**homologie** ➔ podobnost díky společnému původu, struktura zděděná od společného předka

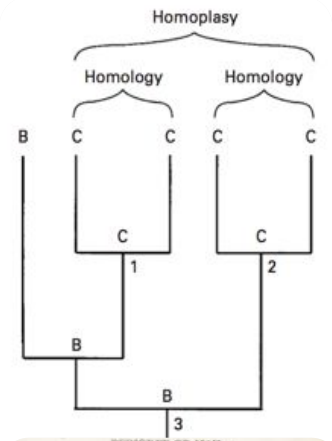
  (*společná evoluce znaků*)

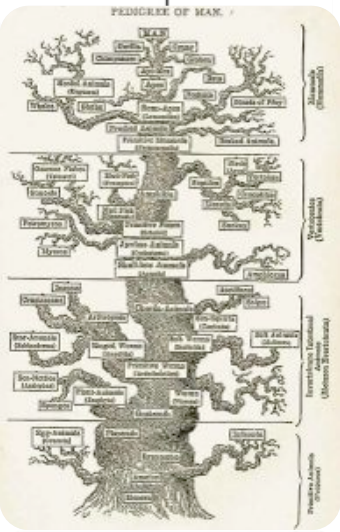
- **analogie(=homoplasie!)**: evoluční paralelismy či konvergence nezávislé na společném původu, dány do souvislosti s adaptací prostředí

  (*ne-společná evoluce znaků*)

Klasickým prizmatem tedy homologie a analogie představují dichotomii

Homologie a analogie: dichotomie vs. kontinuum?





Homology distinguished from homoplasy
At the level of traits/features
Homology is the persistence of similarity in evolution
Homoplasy is the recurrence of similarity
Within a phylogenetic context
Homology reflects the presence of a feature in the most recent common ancestor of two species
Homoplasy reflects: (1) the presence of a feature in two species that do not share a recent common ancestor (convergence), or (2) the presence of a feature in two species when the feature is not found in their most recent common ancestor but is present in a more distant (basal) ancestor (parallelism)

Homology and homoplasy are terms that travel together; homoplasy being close to, but not quite, the inverse of homology. If homology is "the same thing" … homoplasy is the *appearance* of "sameness" that results from independent evolution (Wake, 1996: xvii).

Homologie jako korespondence díky *kontinuitě informace* (Van Valen 1982)

- **Jak hluboko tato kontinuita informace jde ?!?**
- **Homologie i analogie <u>obě</u> reflektují "*descent with modification*": recentnost děděného fenotypu vs. přerušená kontinuita objevování se /chybění znaku.**

Poznání úrovní analogie–homoplasie

(konvergence, paralelismus, atavismy)

je zásadní pro pochopení evoluce!

The three classes of homoplasy and their relationship to developmental pathways

Class	Definition	Development
Convergence[1]	Superficial similarity arising through independent evolution	Different developmental pathways
Parallelism	A feature present in closely related organisms but not present continuously in all the members of the lineage	Similar developmental pathways[2]
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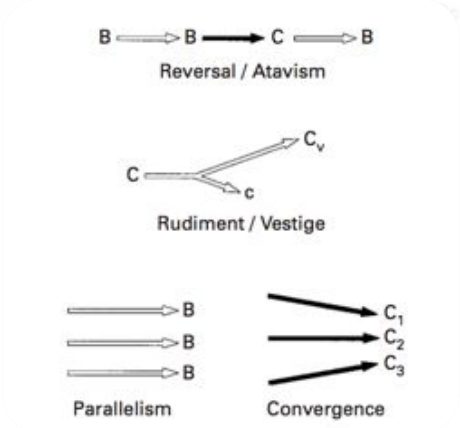

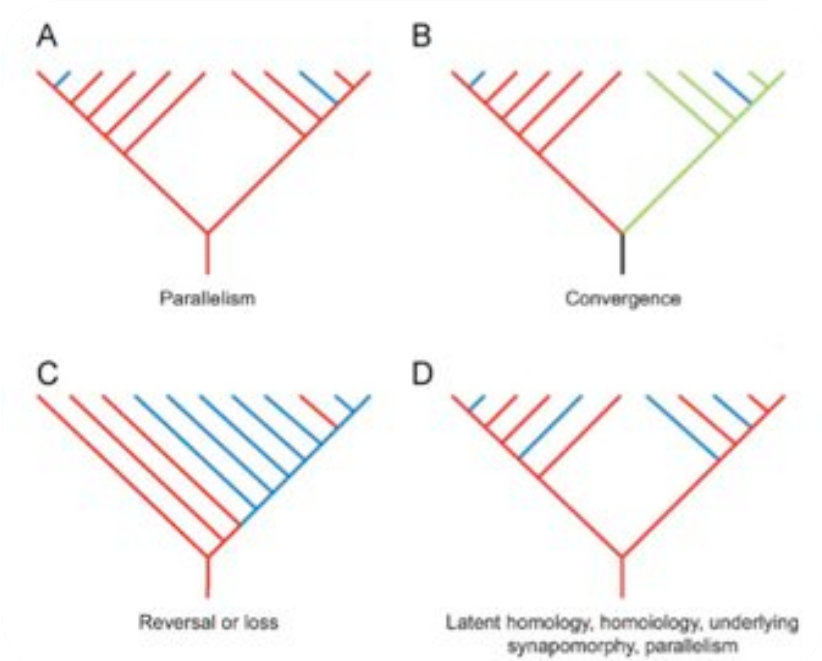

Konvergence:

- podobnost získaná nezávislou evolucí, díky <u>odlišným</u> vývojovým mechanismům;

prodlužování těl mločíků, křídla ptáků a hmyzu (?), hydrodynamický tvar těl vodních obratlovců (??)

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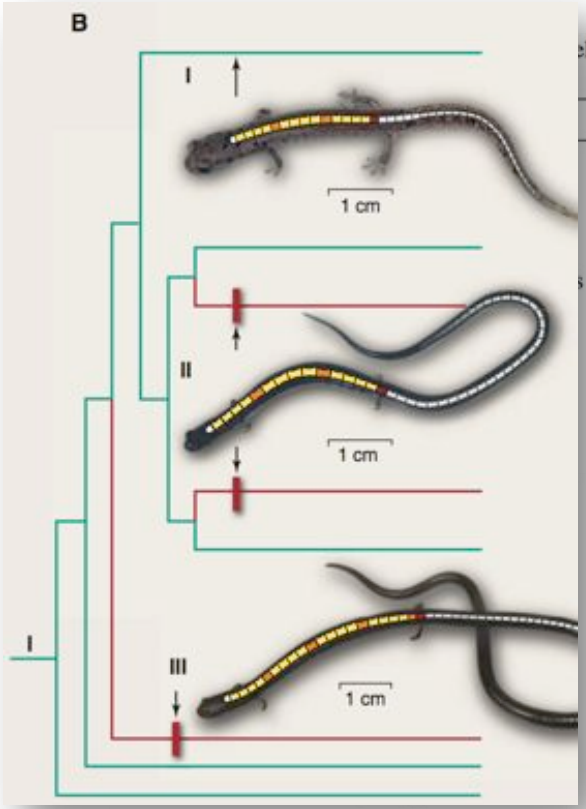

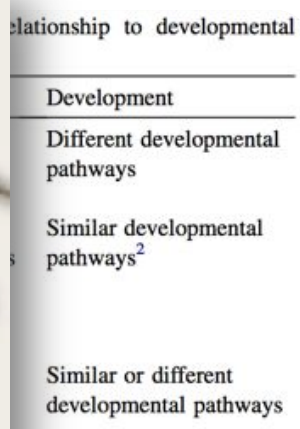

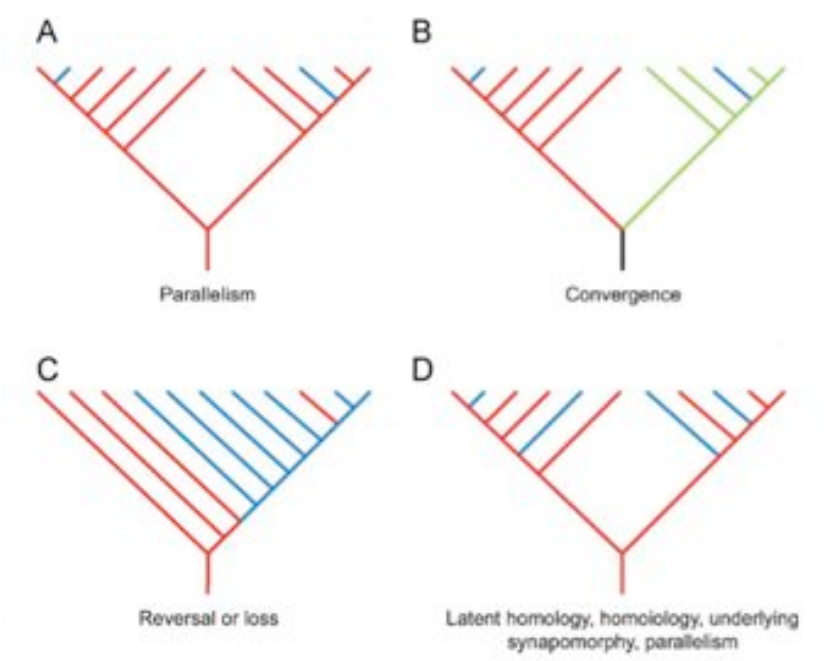

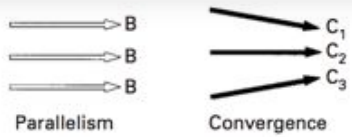

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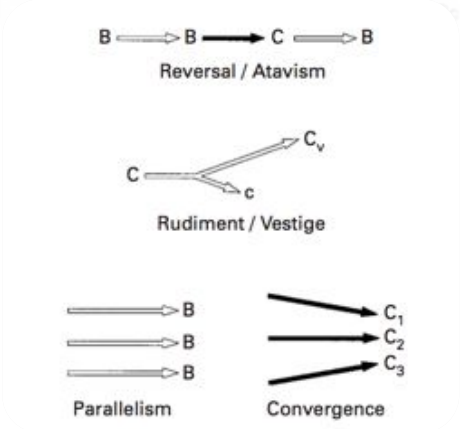

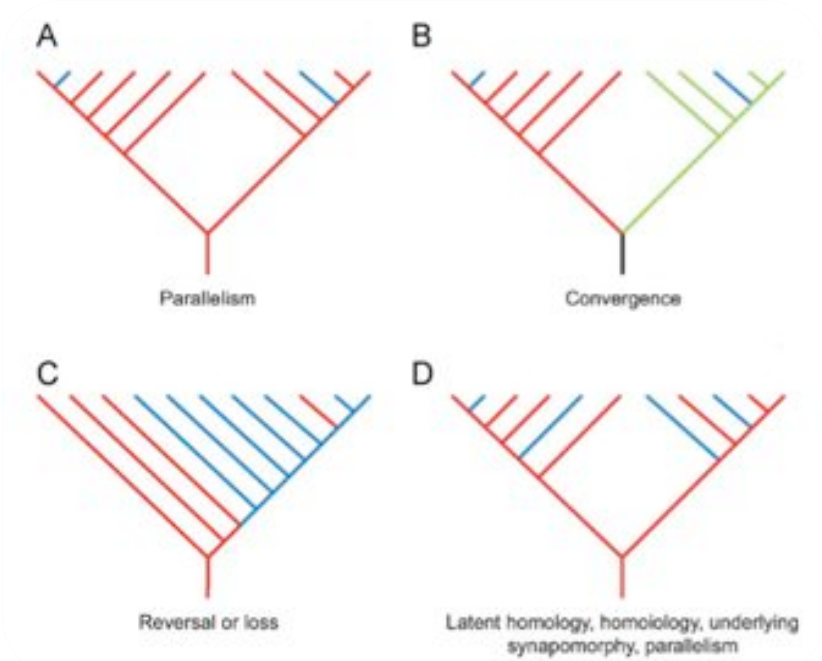

Paralelismy:

- podobnost získaná nezávislou evolucí, díky <u>stejným</u> vývojovým mechanismům;

prodlužování těl mločíků (taktéž i zde!), exprese "meče" samců mečovek na ocasní ploutvi, ...

Poznání úrovní analogie–homoplasie

(konvergence, paralelismus, atavismy)

je zásadní pro pochopení evoluce!

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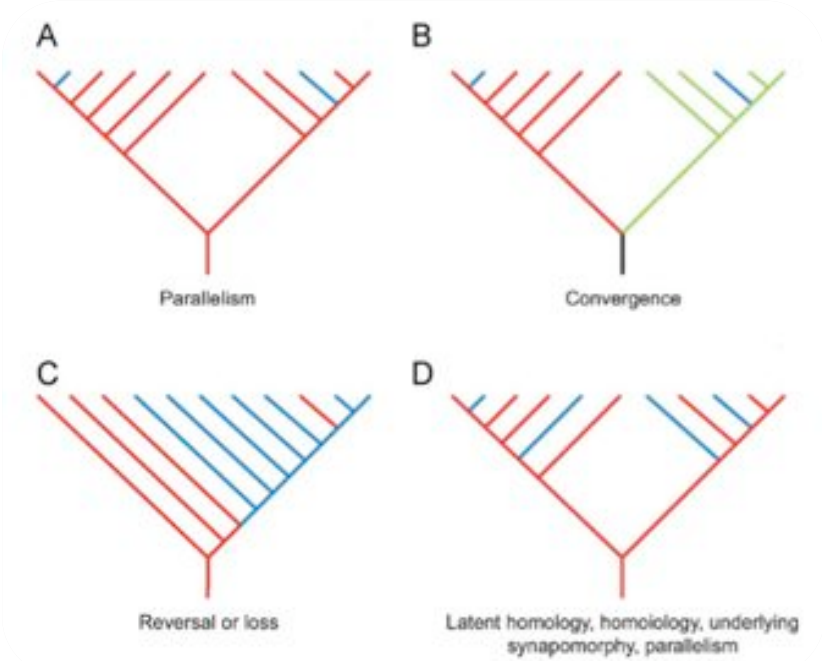
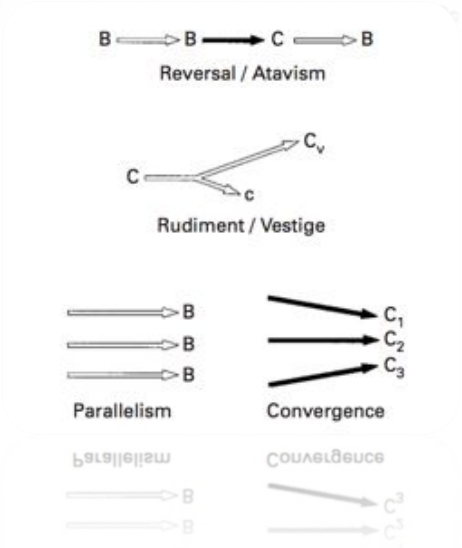




Atavismy (u všech, hlubinné)**, rudimenty** (u některých, jen mladší výv. stadia znaku), **reversaly** (u všech)**:**

- exprese stejného znaku, který však dříve ve fylogenezi vymizel;

maxilární zuby žab & Gastrotheca sp. (vs. latentní homologie?)

Poznání úrovní analogie–homoplasie

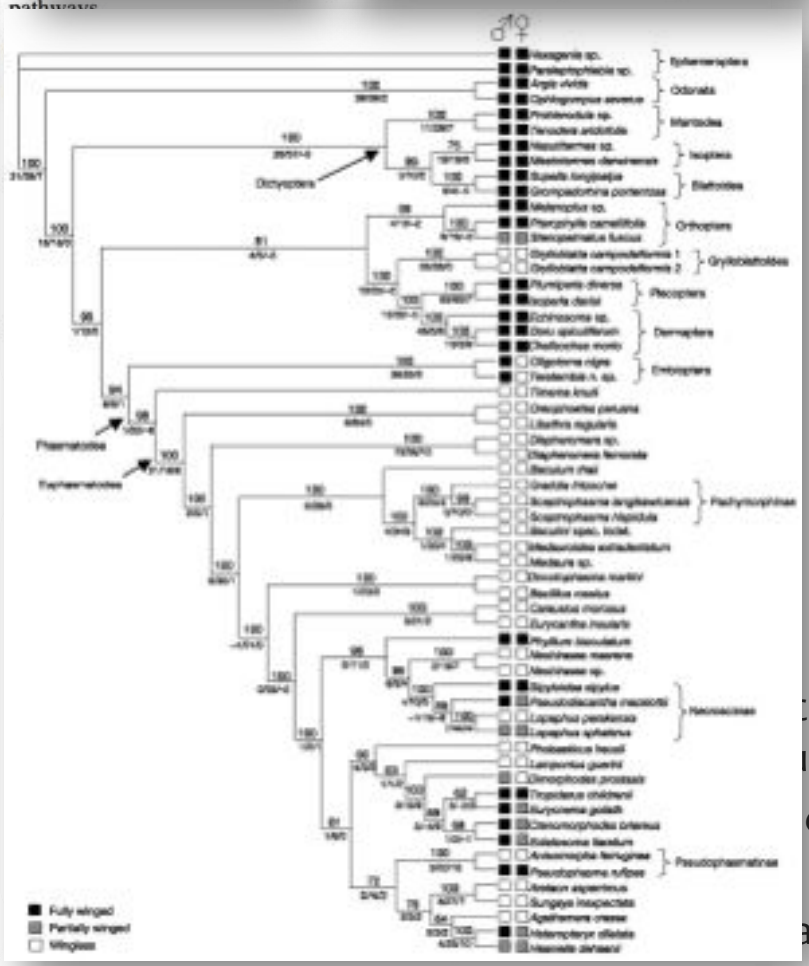
Loss and recovery of wings in stick insects

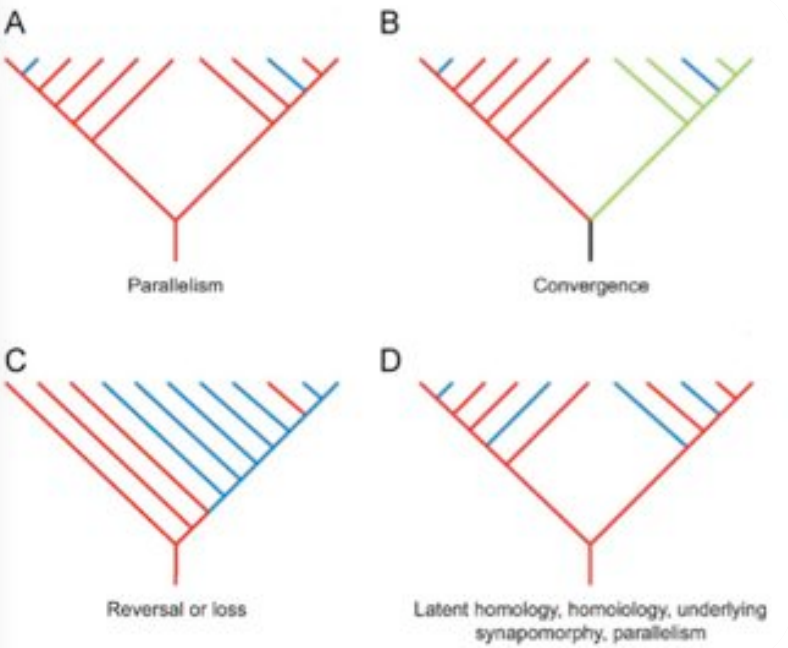
Michael F. Whiting*, Sven Bradler† & Taylor Maxwell‡

* Department of Integrative Biology, Brigham Young University, Provo, Utah 84602, USA
† Institut für Zoologie und Anthropologie, Georg August Universität Göttingen, Germany
‡ Washington University, Department of Biology, St Louis, Missuori 63130, USA

ralelismus, atavismy)

ochopení evoluce!





ch, hlubinné), **rudimenty** (u některých, jen mladší
), **reversaly** (u všech)**:**

ého znaku, který však dříve ve fylogenezi

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Poznání úrovní analogie–homoplasie

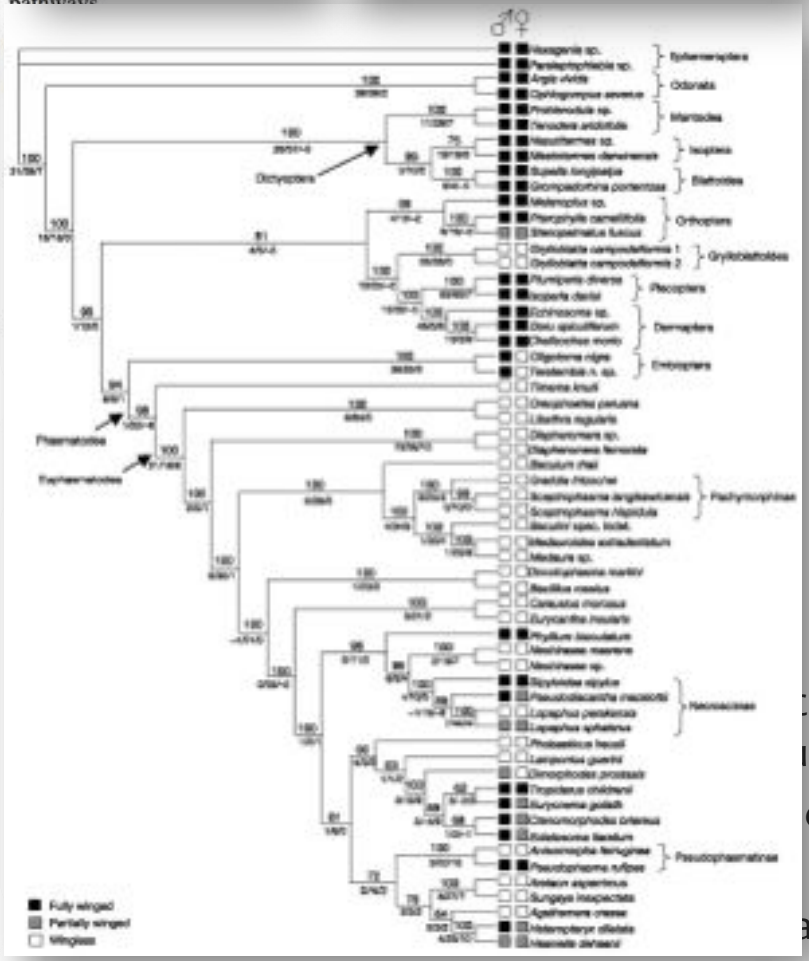
Loss and recovery of wings in stick insects

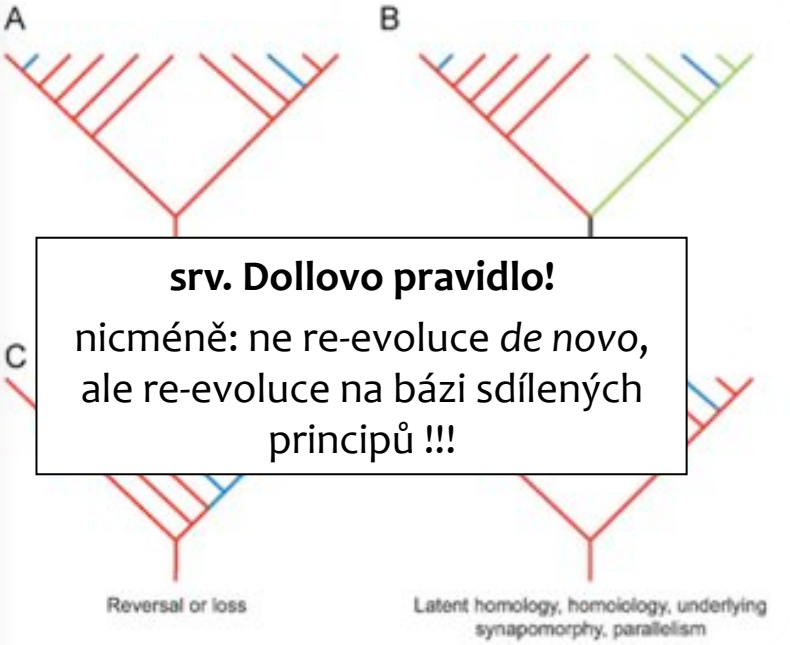
Michael F. Whiting*, Sven Bradler† & Taylor Maxwell‡

* Department of Integrative Biology, Brigham Young University, Provo, Utah 84602, USA
† Institut für Zoologie und Anthropologie, Georg August Universität Göttingen, Germany
‡ Washington University, Department of Biology, St Louis, Missuori 63130, USA

ralelismus, atavismy)

ochopení evoluce!





srv. Dollovo pravidlo!

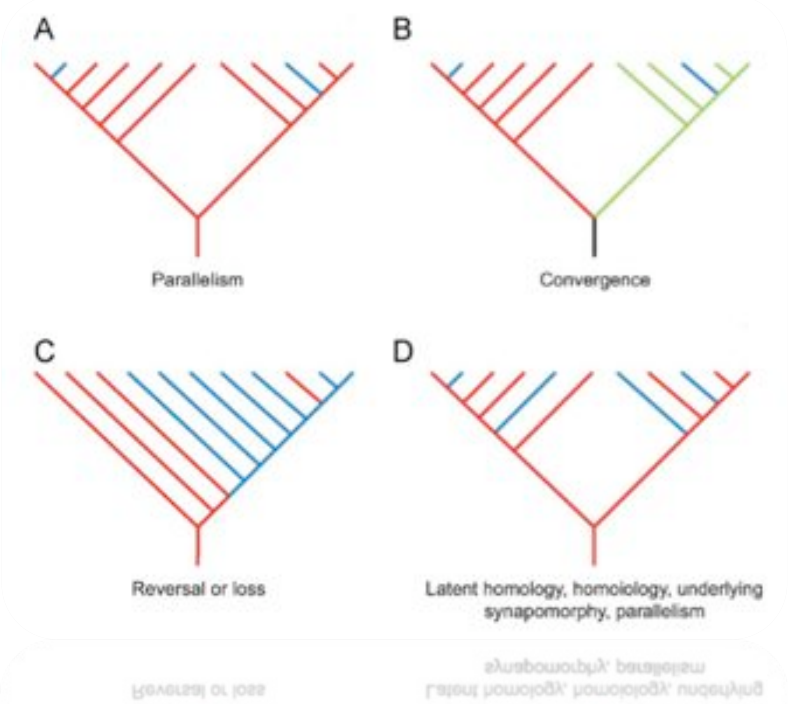
nicméně: ne re-evoluce *de novo*, ale re-evoluce na bázi sdílených principů !!!

ch, hlubinné), **rudimenty** (u některých, jen mladší
), **reversaly** (u všech)**:**

ého znaku, který však dříve ve fylogenezi

ab & Gastrotheca sp. (vs. latentní homologie?)

Rozpoznání úrovní podobností (konvergence, paralelismus, atavismy) je **zásadní pro pochopení cest, příčin a možného opakování evoluce!**



- fenotypy a evoluční linie během evoluce divergují (*descent with modification*)
  - fenotypová podobnost v diversifikovaných a nepříbuzných liniích?
- studováním vývojových mechanismů dokážeme odlišit, zdali similarita vznikla díky objevení se nového mechanismu, či zdali se jedná o opakované využívání archetypálních/hlubinných mechanismů a procesů
  - co je to znak, jak vzniká, evolvuje a udržuje se!

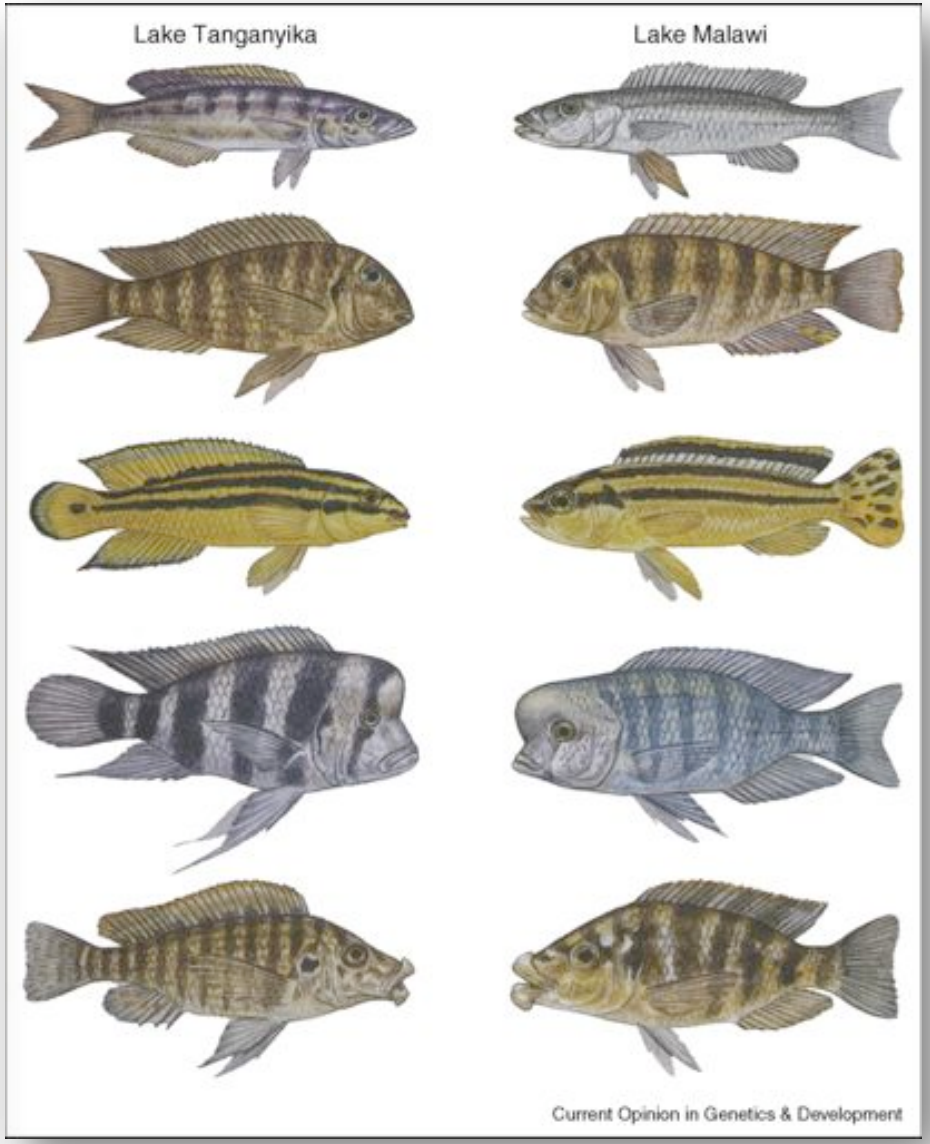
Nezávislá evoluce paralelních znaků na bázi hlubinně společného původu, využívající *stejné* vývojové mechanismy

Roles for Bmp4 and CaM1 in Shaping the Jaw: Evo-Devo and Beyond

Kevin J. Parsons[1] and R. Craig Albertson[2]

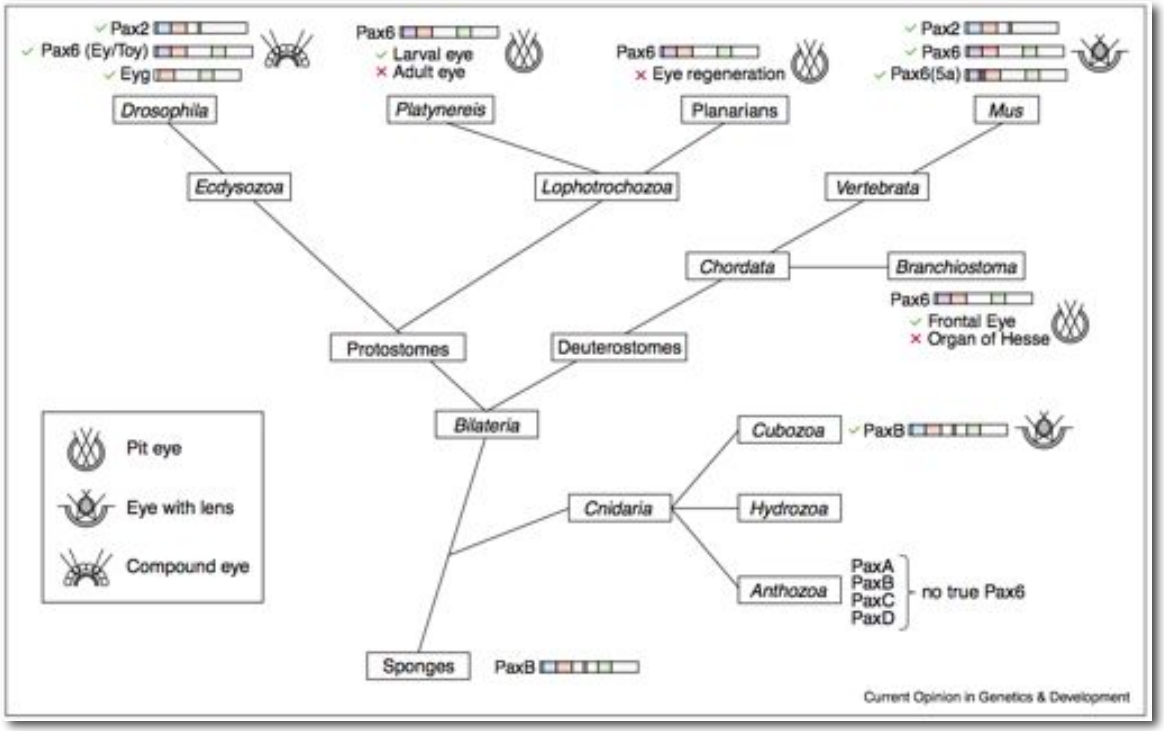
Department of Biology, Syracuse University, Syracuse, New York 13244;
email: kjpars01@syr.edu; rcalbert@syr.edu

Nezávislá evoluce paralelních znaků na bázi hlubinně společného původu, využívající *stejné* vývojové mechanismy



Nezávislá evoluce paralelních znaků na bázi hlubinně společného původu, využívající *stejné* vývojové mechanismy

Deep homology



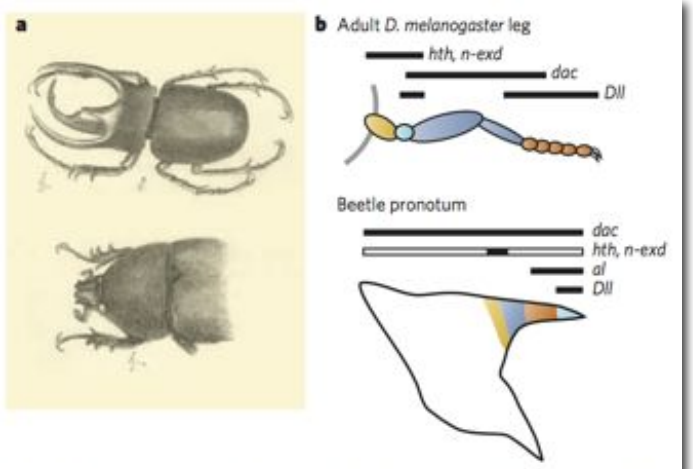


Figure 3 | The evolution of beetle horns by co-option of a limb-outgrowth program. a, Illustration from Darwin's *The Descent of Man* showing the male (top) and female (bottom) forms of the Atlas beetle, *Chalcosoma atlas*. Note the large horns extending from the head. **b,** Similarities in the expression of limb proximodistal axis-patterning gene expression in the adult leg of *Drosophila melanogaster* (top) and the developing horns of *Onthophagus* dung beetles (bottom). Coloured regions denote segments of the leg and regions of the developing horn. Black bars denote gene-expression patterns, indicating the relationship between the expression domains of individual genes in the developing outgrowths. The white bar shows where the listed proteins are co-expressed at only low levels. The expression of outgrowth-promoting genes in beetle horns indicates that these structures evolved by the co-option of an ancient outgrowth program and its deployment at novel anatomical sites. (Panel **a** reproduced from ref. 32; panel **b** modified, with permission, from ref. 35.)

Homologie a analogie jedno jsou...?

O společném původu ***s různým stupněm*** modifikací

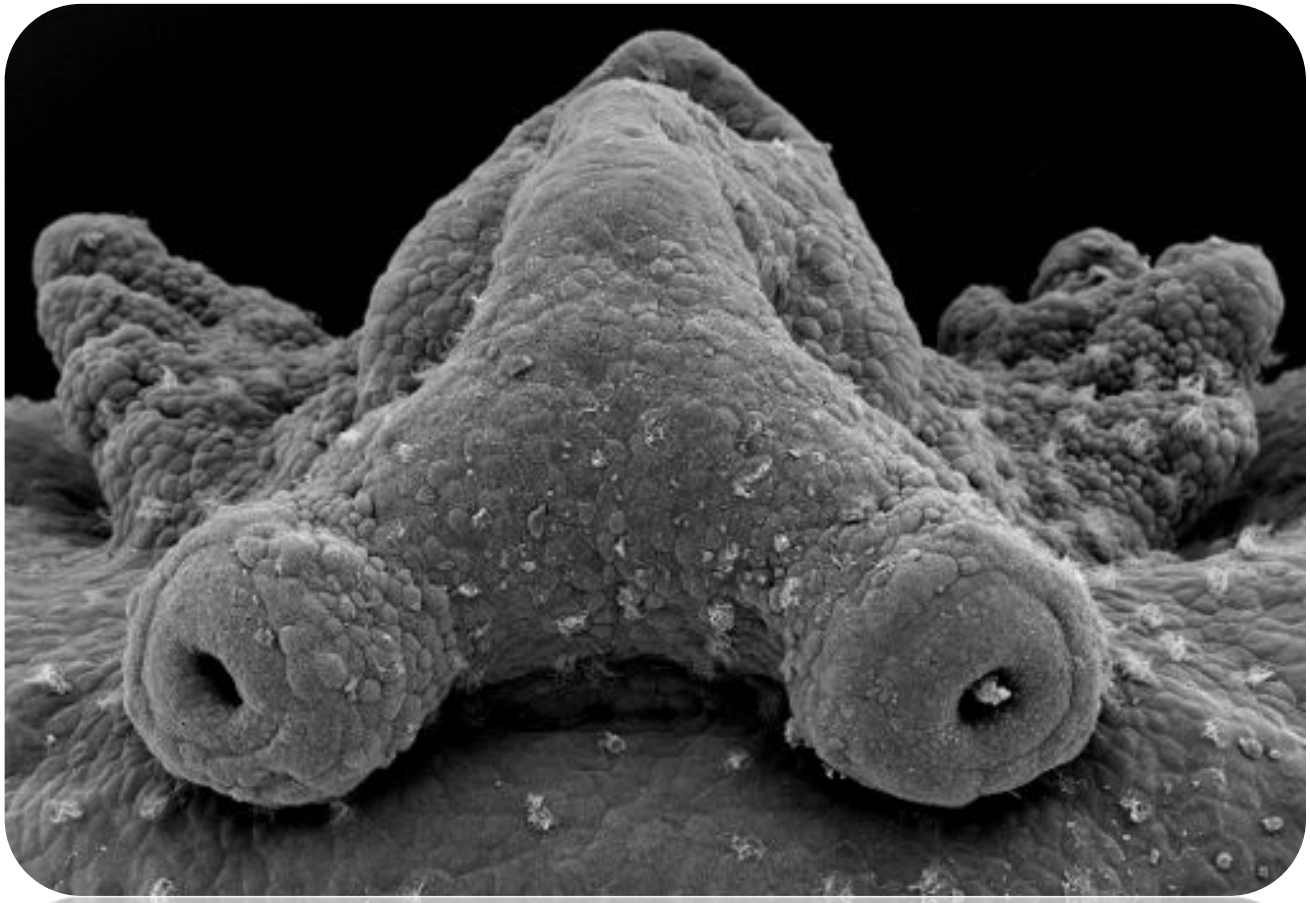
- dichotomie homologie vs. analogie

- analýza prostoru mezi *homologií* a *analogií* ve smyslu společného vs. nezávislého evolučního původu, resp. *hloubky/hlubinnosti* takového původu

- od Darwinova "common descent with modification" po "common descent with *various degrees* of modification" (Brian K. Hall)

Hledání kontinuity informace, homologie vs. (?) analogie:

larvální adhezivní orgány strunatců



Attachment organs (cement-, mucus-producing glands) are common adaptations of larval vertebrates

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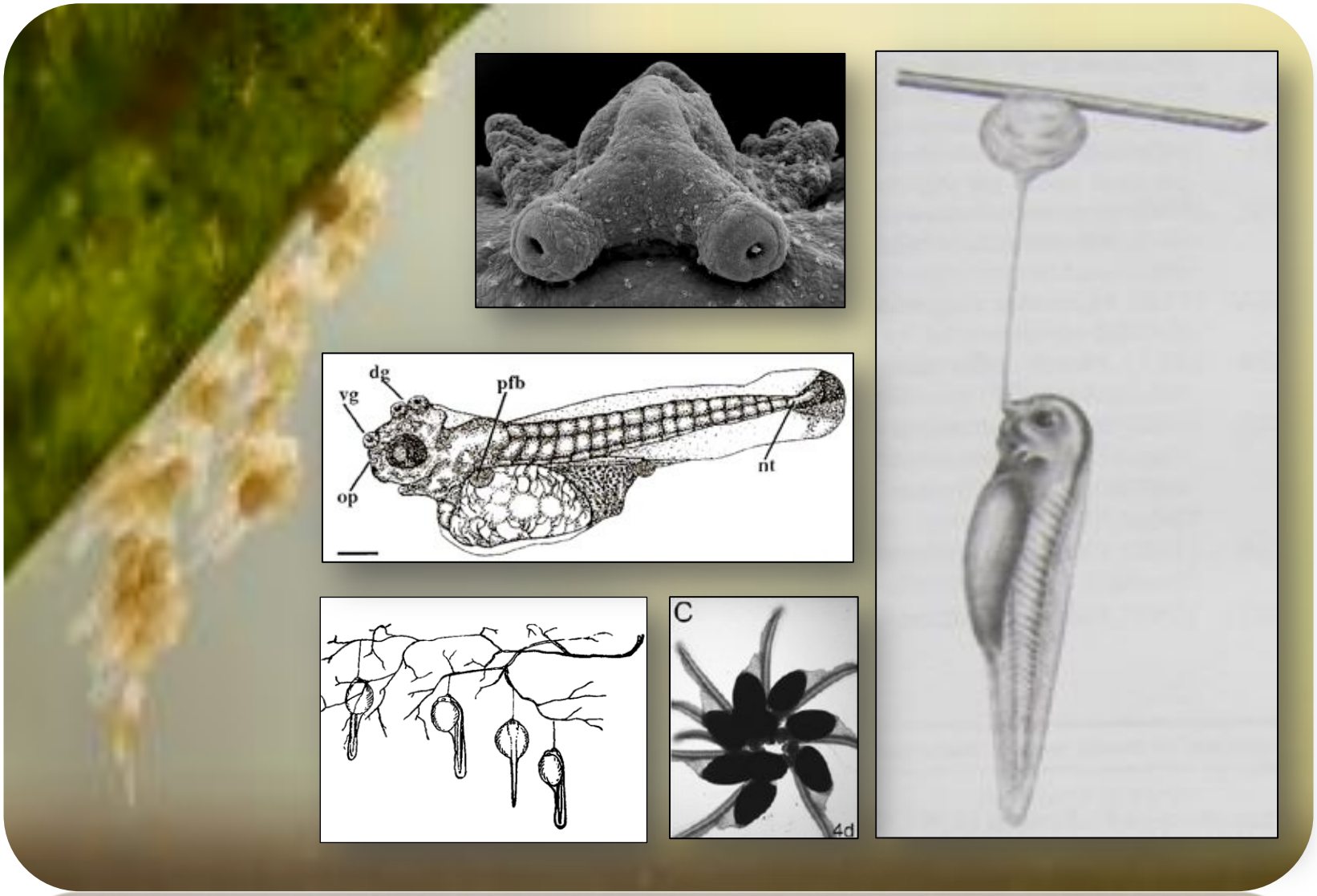
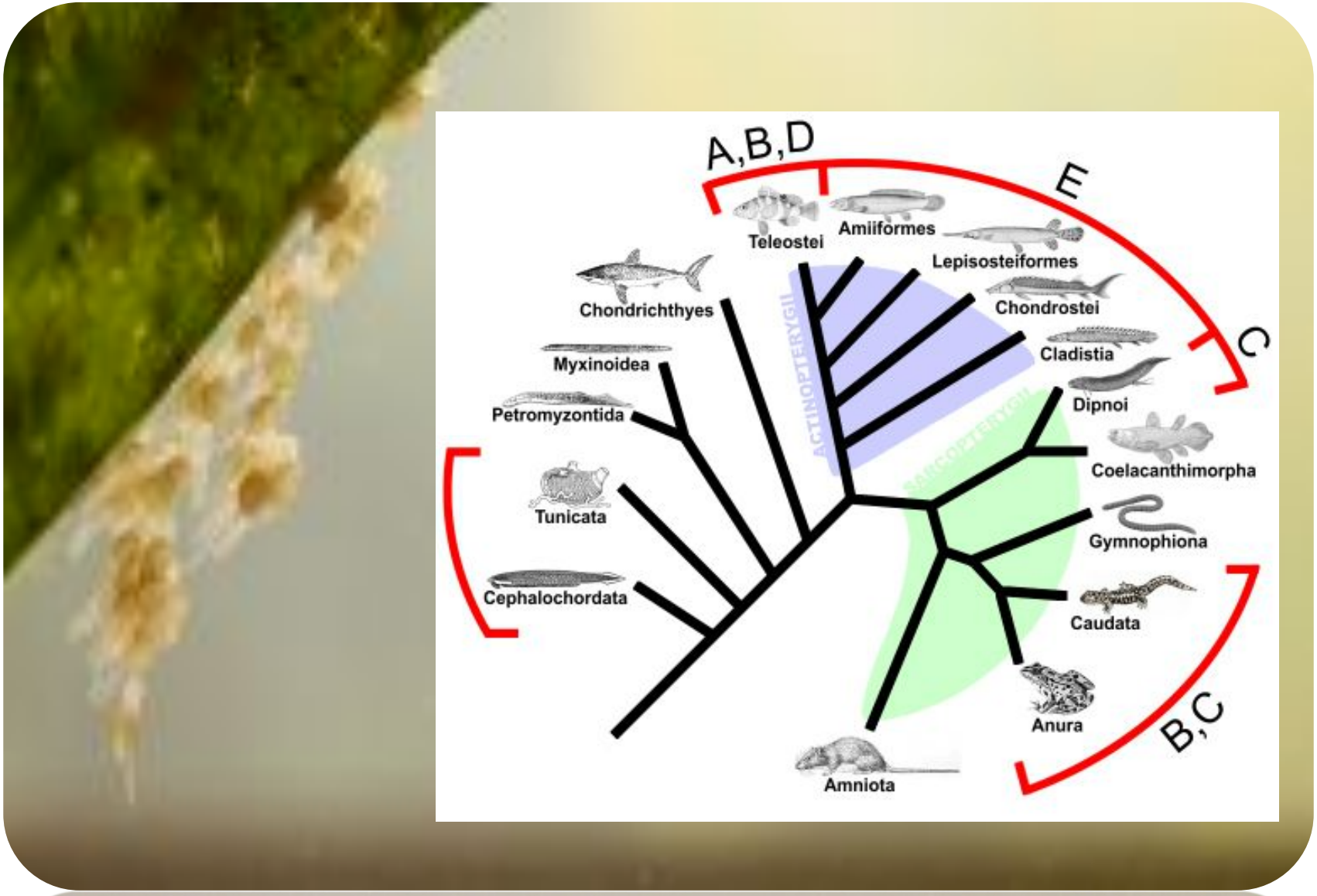
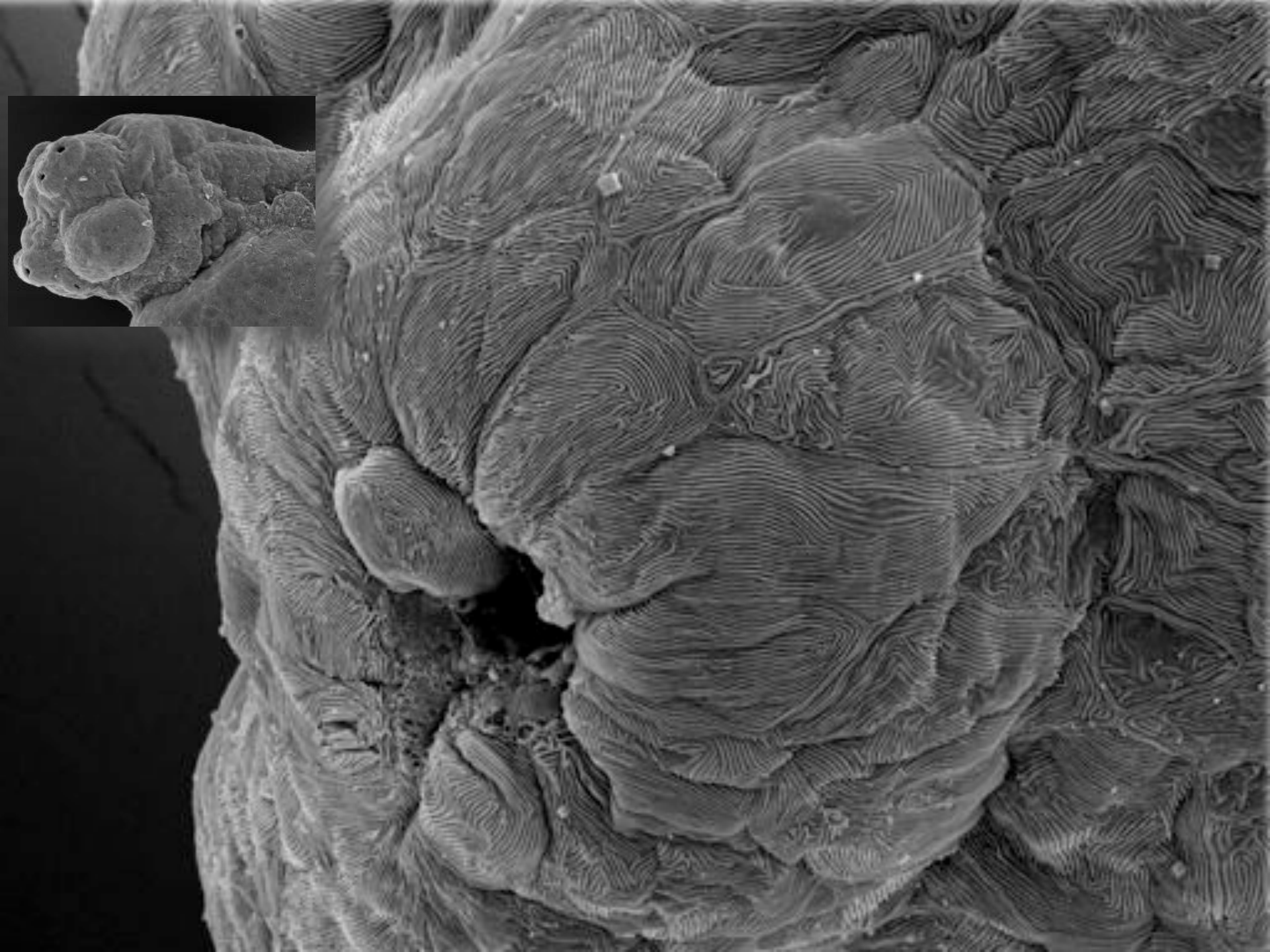
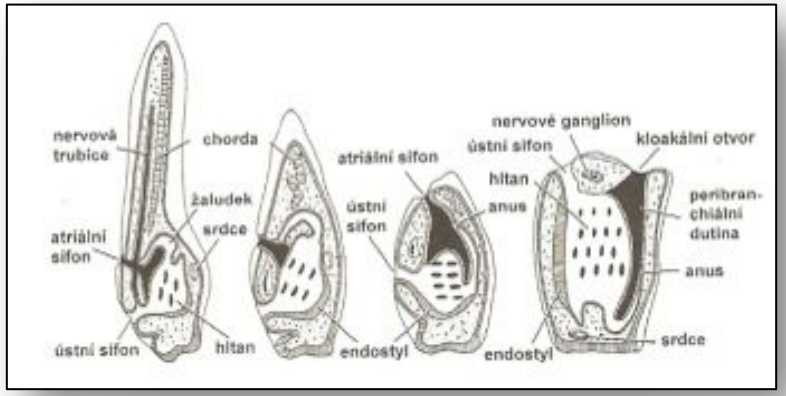


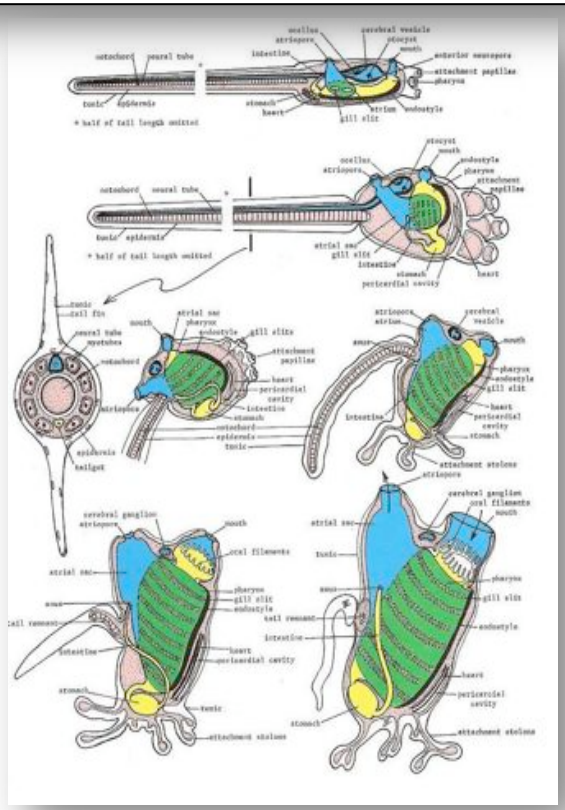
Attachment organs in chordates/vertebrates are ancient and widespread



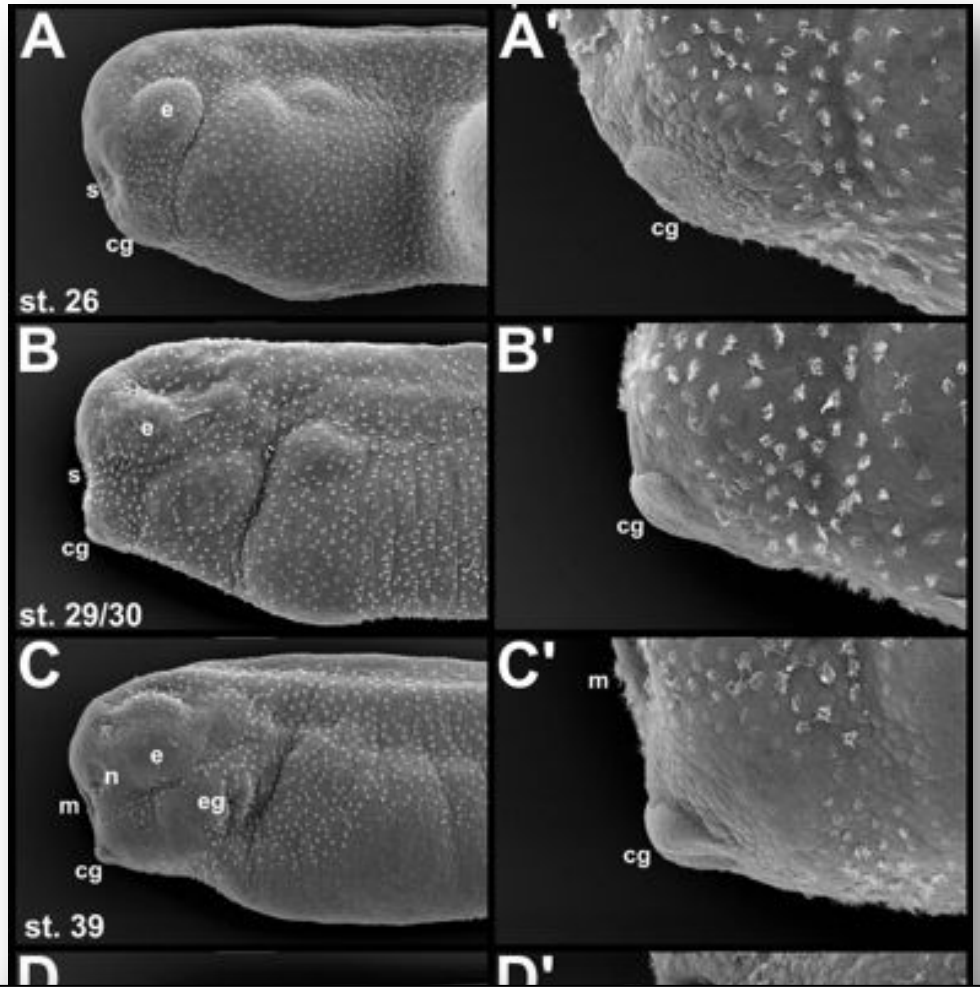


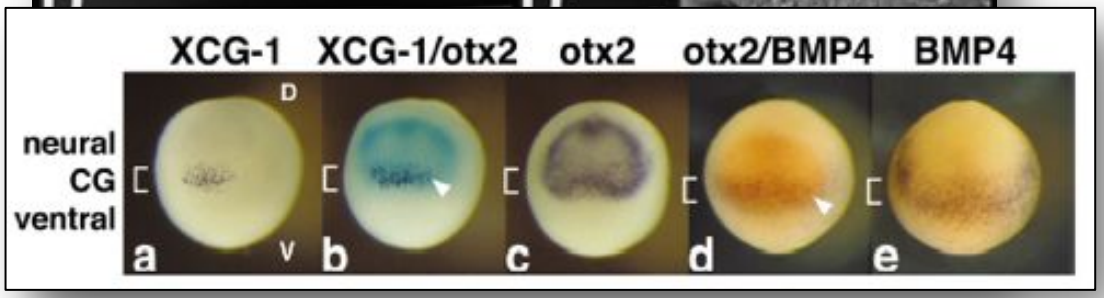
Attachment organs are basal features of chordates: attachment papillae of tunicate larva



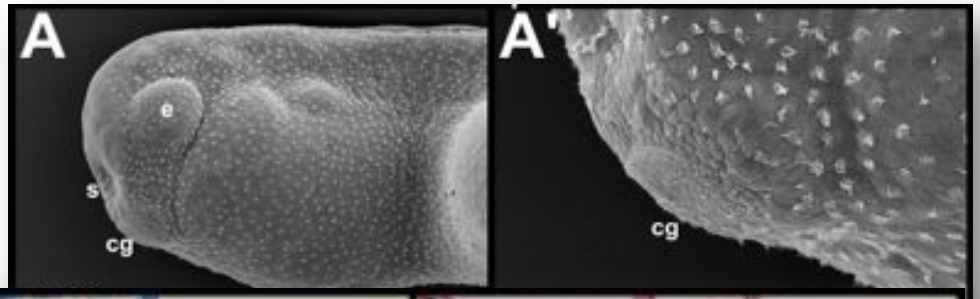


A paradigmatic cement (attachment) organ of *Xenopus* tadpoles





(Gamill & Sive, 1999)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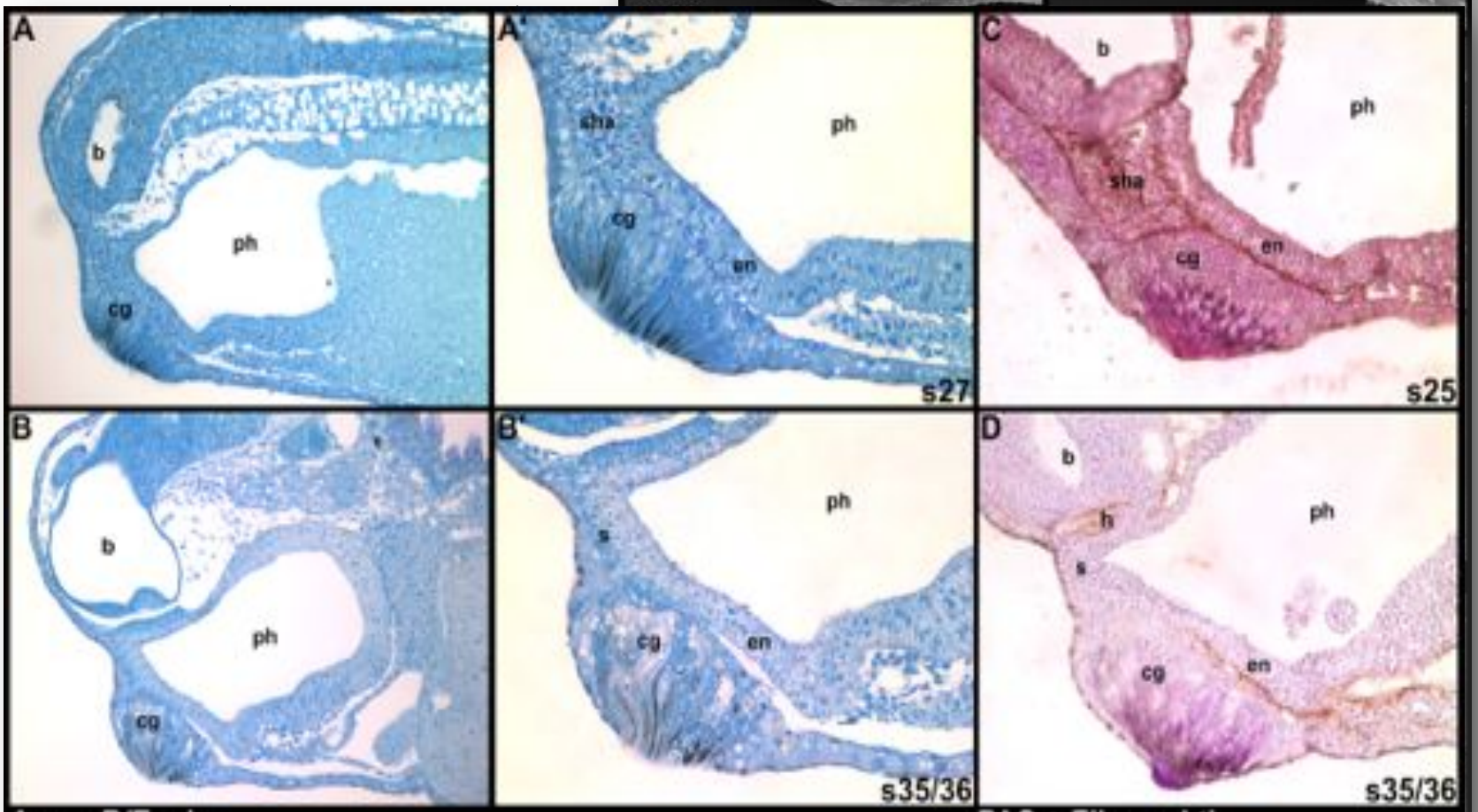
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s35/36
Azure B/Eosin
PAS + Fibronektin

JOURNAL OF MORPHOLOGY 263:270–283 (2005)

Larval Cement Gland of Frogs: Comparative Development and Morphology

M. Nokhbatolfoghahai[1,2] and J.R. Downie[1]*

[1]*Division of Environmental and Evolutionary Biology, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, Scotland, UK*
[2]*Biology Department, Faculty of Sciences, University of Shiraz, Shiraz, Iran 71345*

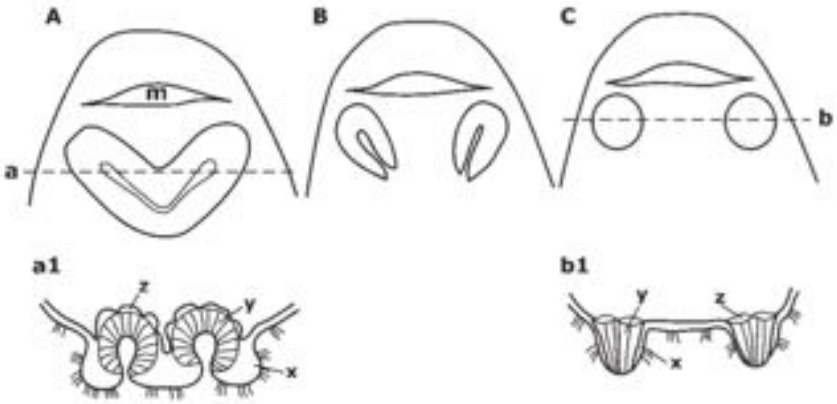


Fig. 1. General organization of the anuran cement gland, showing a common pattern of morphological transformation from V-shaped (**A**) through double horseshoe (**B**) to conical (**C**). Sections through a and b are illustrated in a1 and b1, respectively. m, mouth; x, bordering cells, some ciliated; y, columnar secretory cells; z, basal cells.

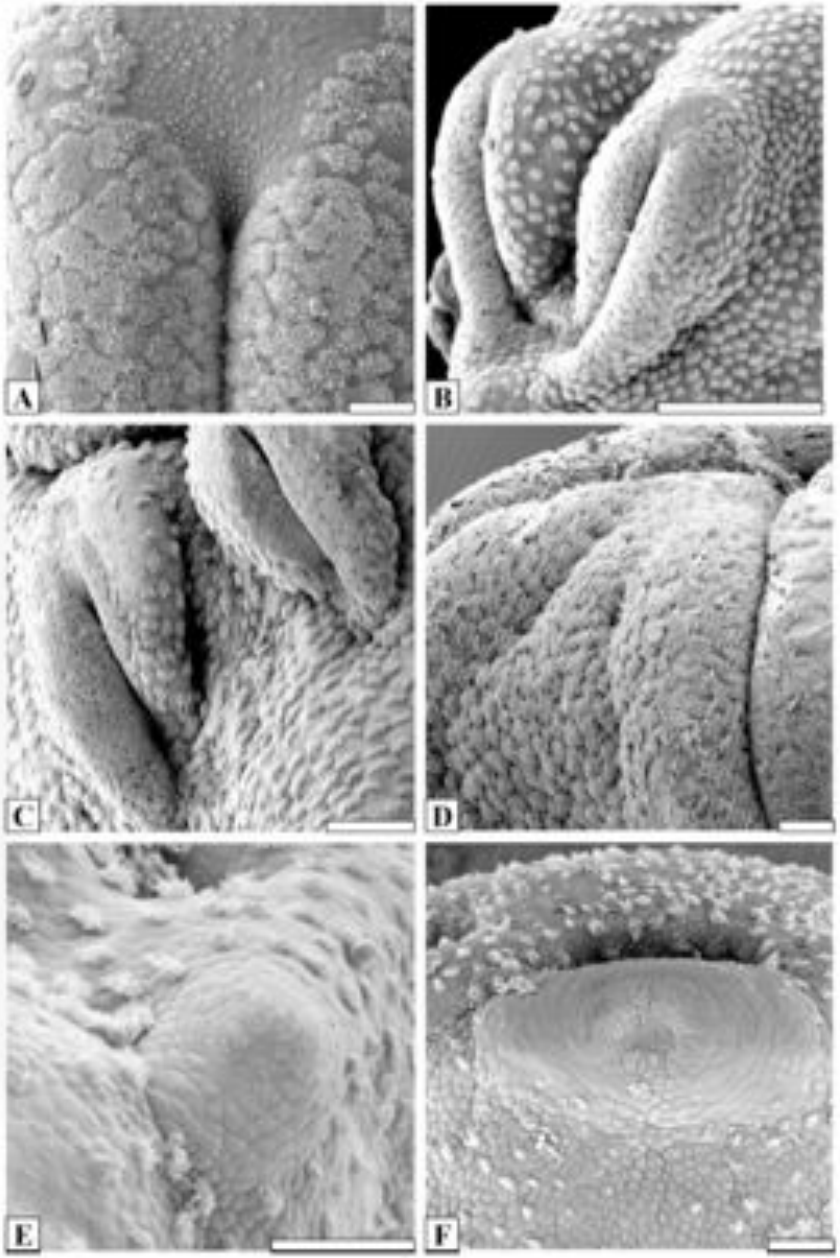
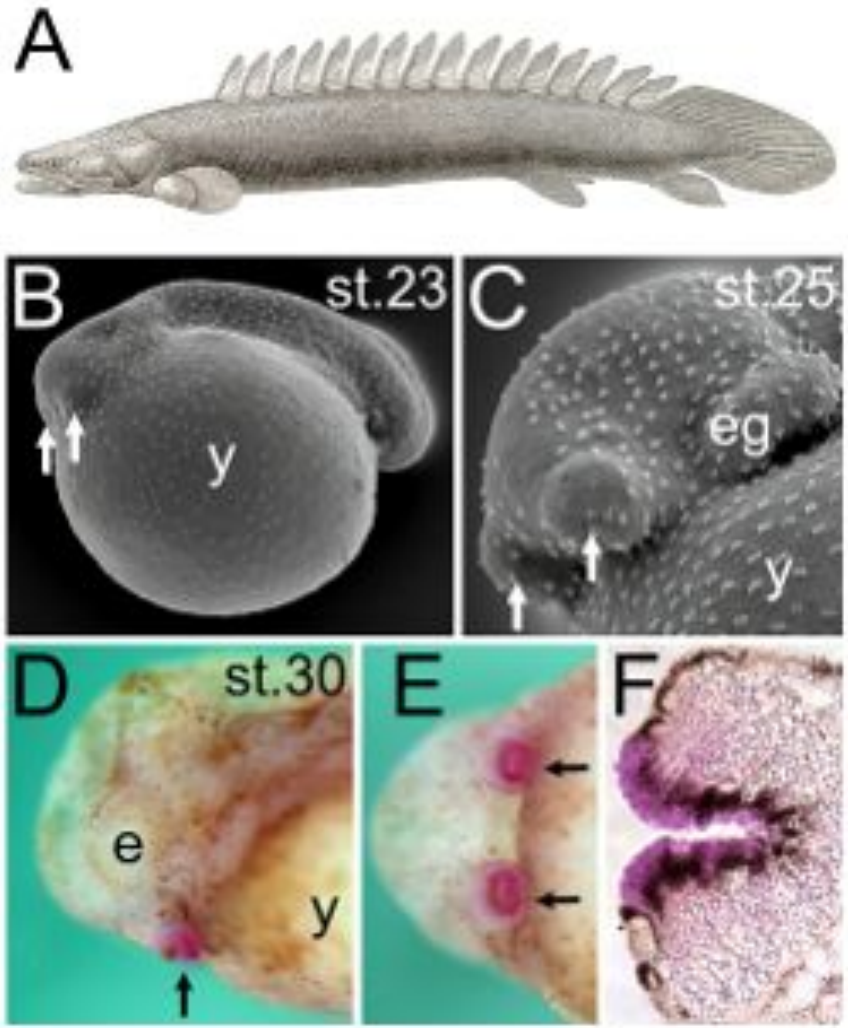
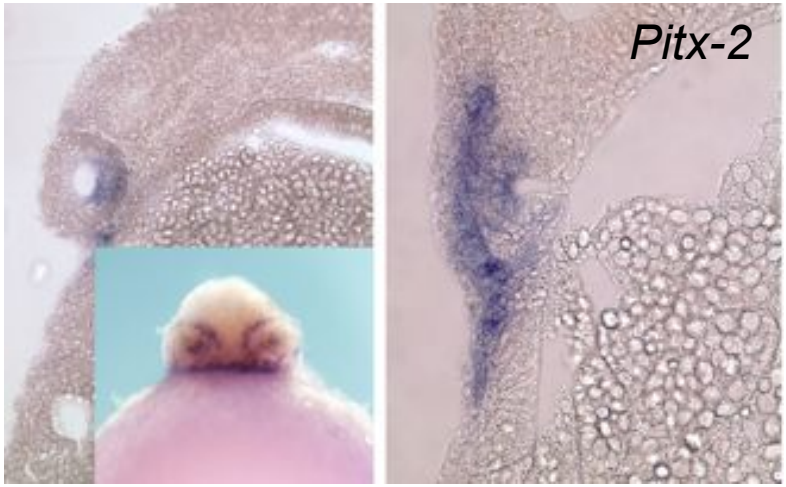
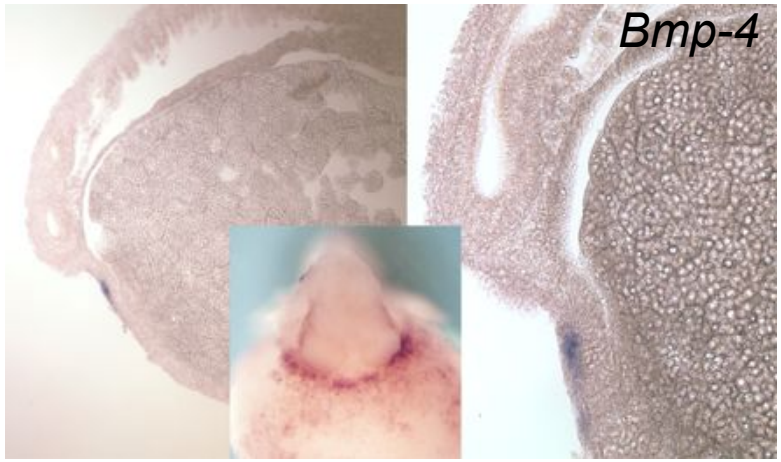


Fig. 7. Ciliated cell patterns associated with the CG visualized by medium resolution SEM. **A–C:** *Rana temporaria*, Stages 18, 19, and 22, all showing dense ciliation. **D:** *Bufo bufo*, Stage 19, dense ciliation. **E:** *Hyla microcephala*, Stage 20, very dispersed ciliation. **F:** *Xenopus laevis*, Stage 22/23, very dispersed ciliation. Scale bars = 60 μm in **A**; 500 μm in **B**; 250 μm in **C**; 120 μm in **D–F**.

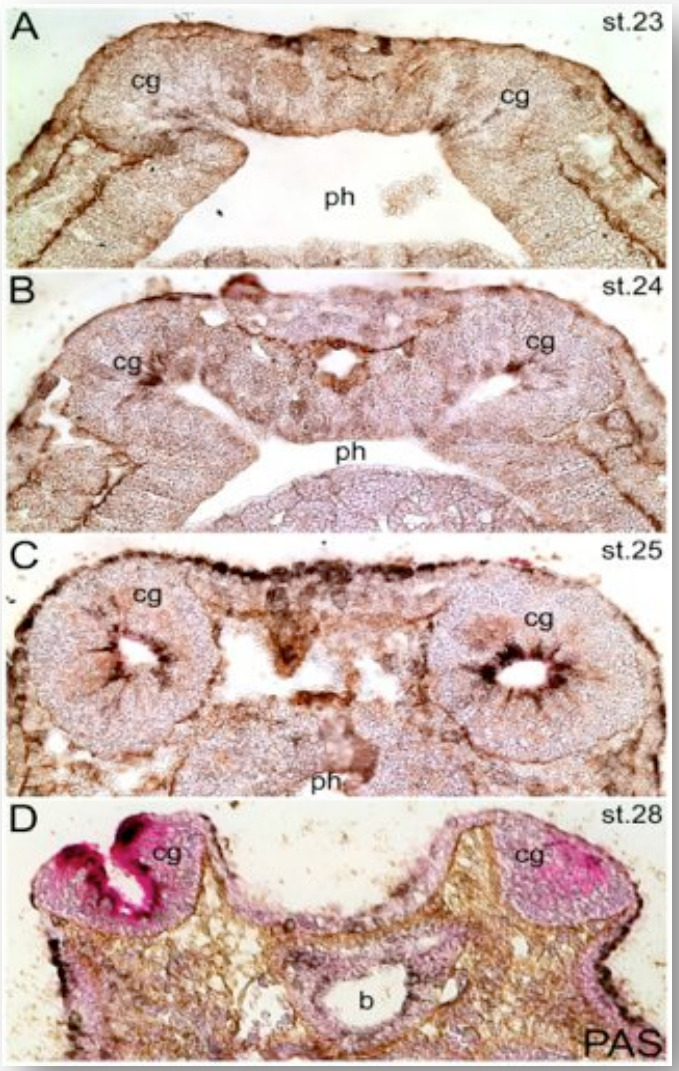
Attachment organs of bichir (Polypterus) produce mucus and express *Otx-2*, *Pitx-2* and *Bmp-4* as in *Xenopus*

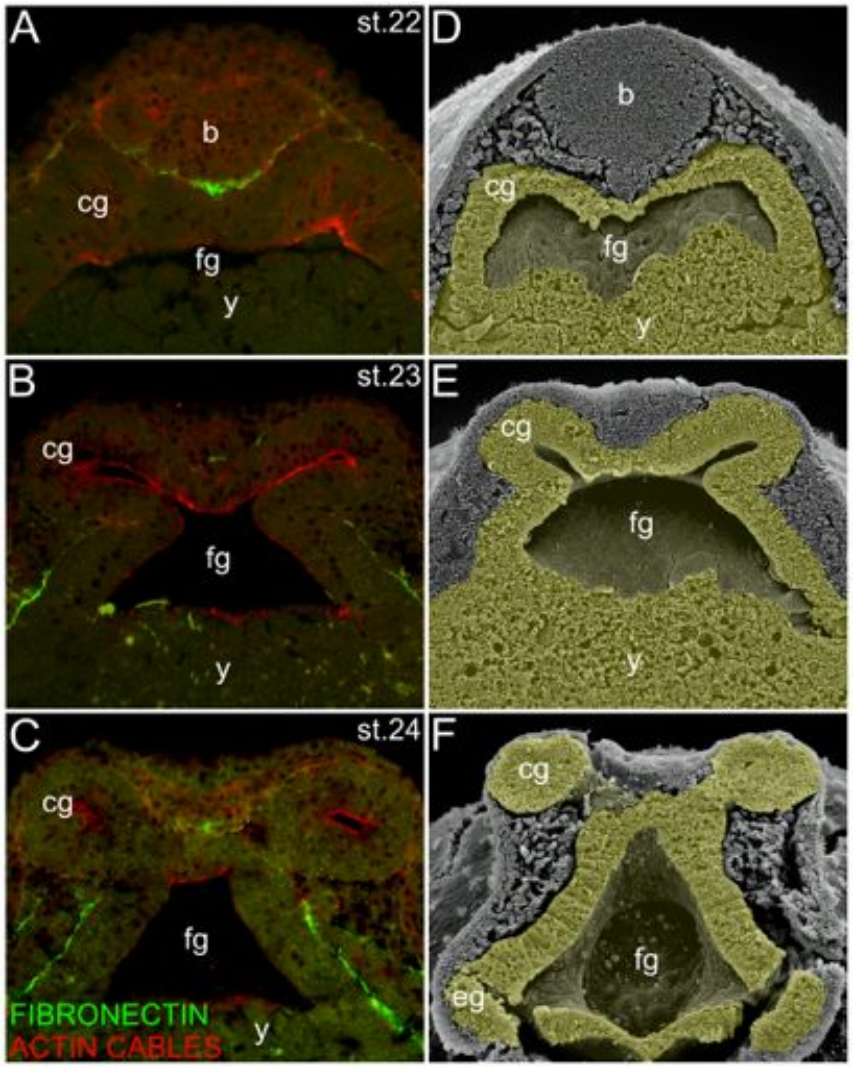




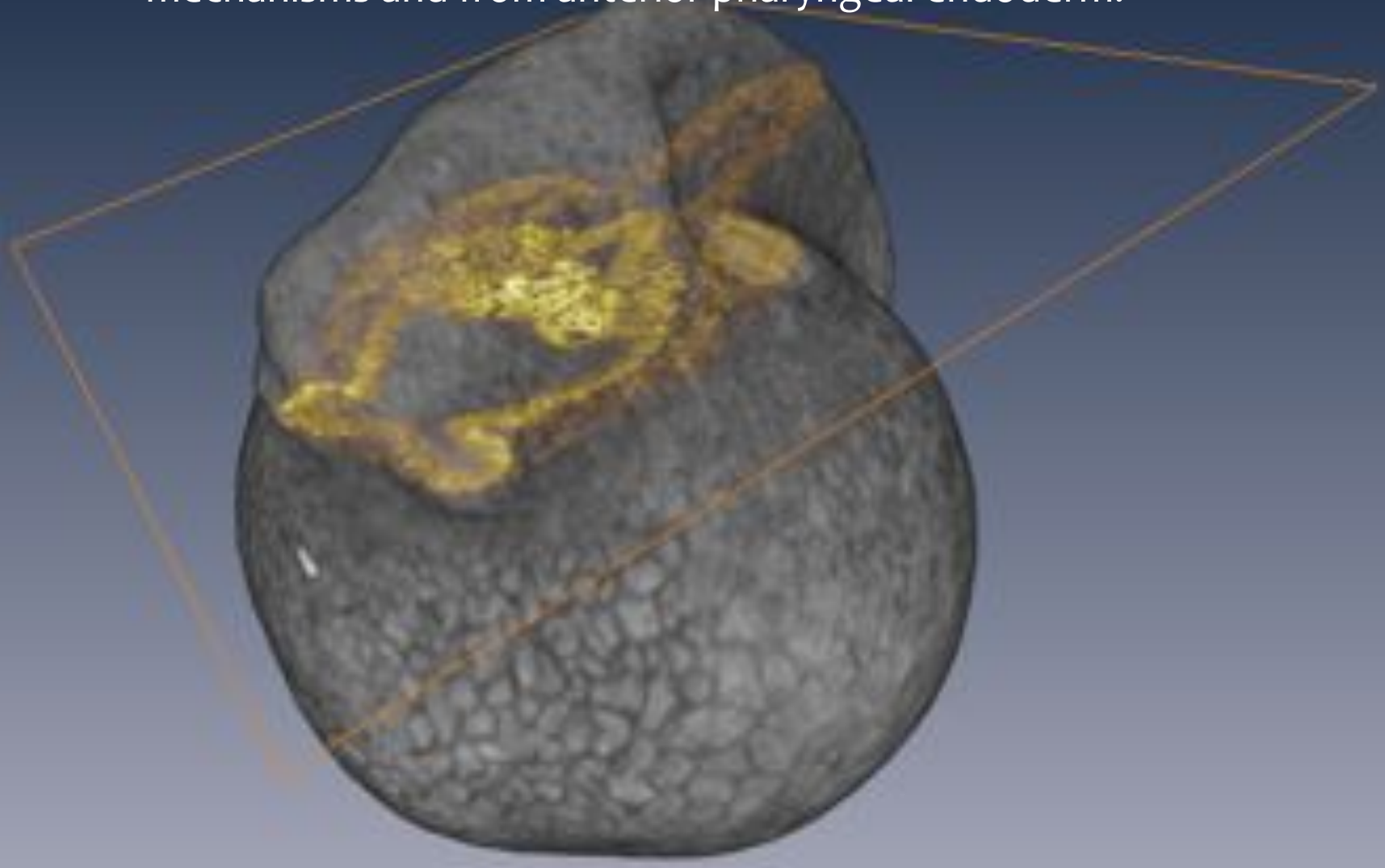


Attachment organs of bichir (Polypterus) develop by pouching mechanisms typical for pharyngeal endoderm

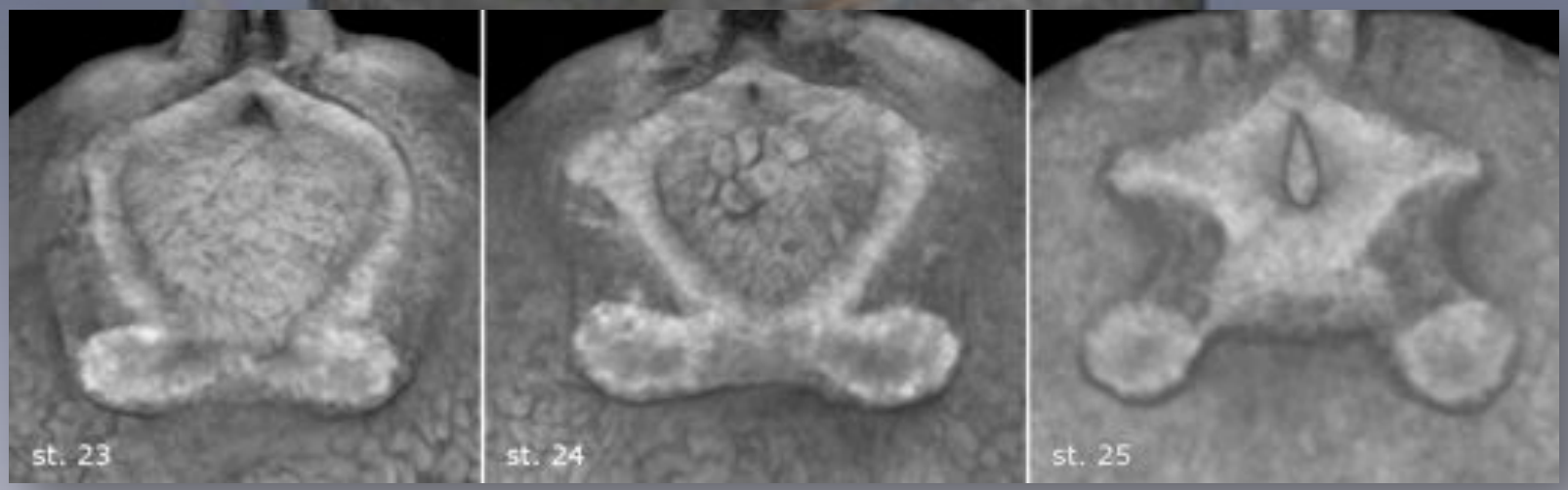




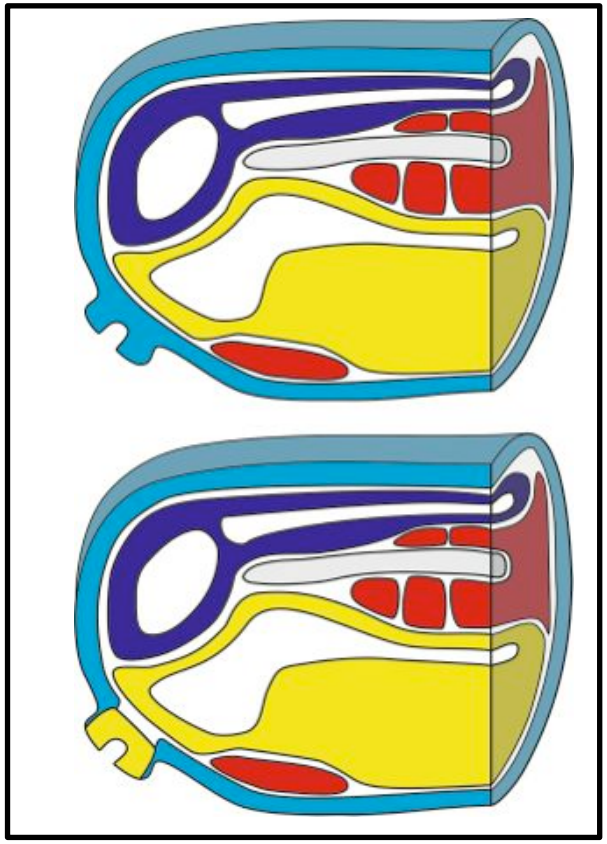
Attachment organs of bichir (Polypterus) develop by pouching mechanisms and from anterior pharyngeal endoderm!



Attachment organs of bichir (Polypterus) develop by pouching mechanisms and from anterior pharyngeal endoderm!



Attachment organs of vertebrates are plastic traits generated by dissimilar processes that always reach a similar shape of their secretory epithelia



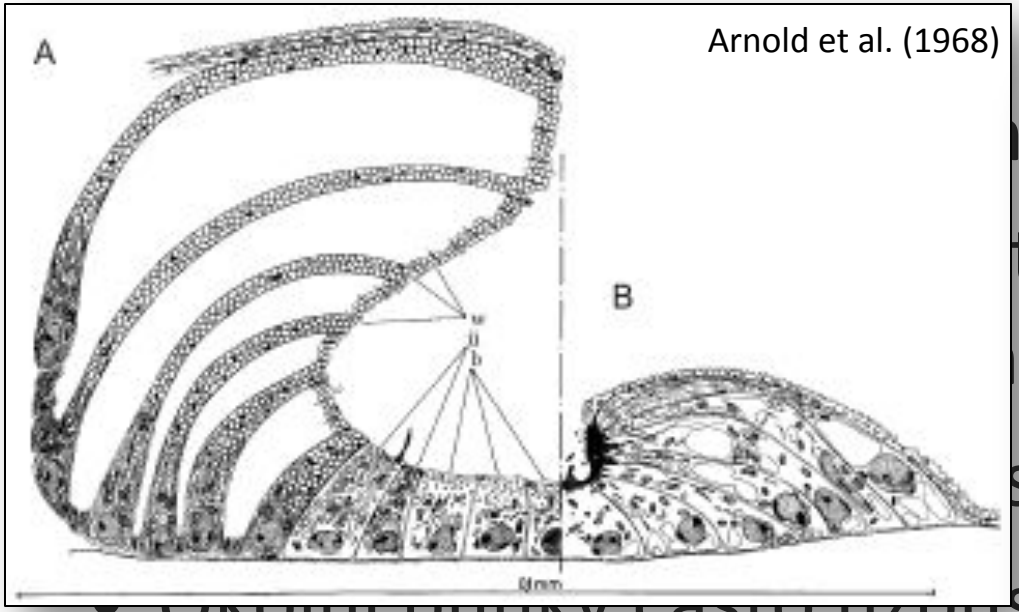
developmental considerations (plasticity):

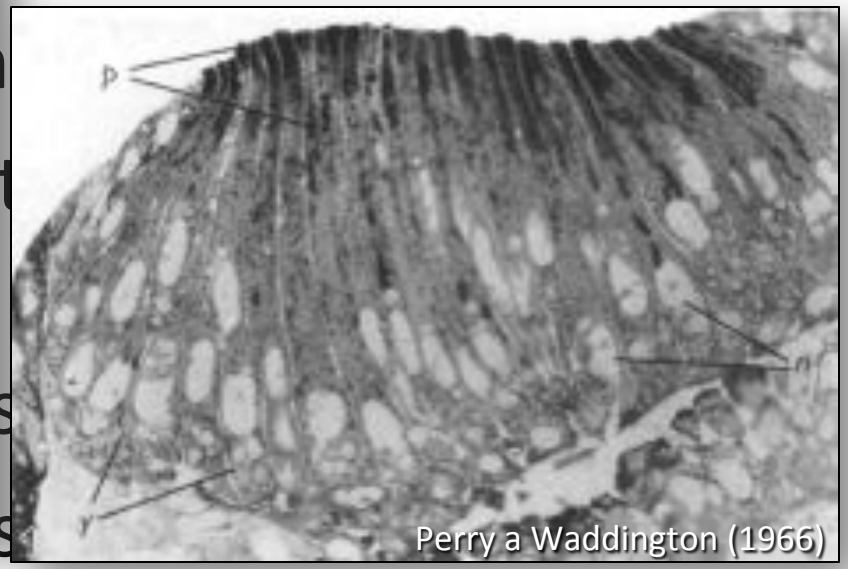
- **Xenopus cement glands** develop via placodal ectoderm morphogenesis and are paradigmatic structures of an extreme anterior; whereas **bichir organs** are derived from endoderm and develop by typical pharyngeal formation including action of actin cables.

evolutionary considerations (modularity):

- Attachment organs of vertebrates probably evolved separately (convergent evolution), but they might share some homology due to deep common ancestry (a deep homology module; possibly responsible for mucus-formation?)

Společné znaky





- Okolní buňky často uzpůs
  adhezivního sekretu
- Shodná inervace

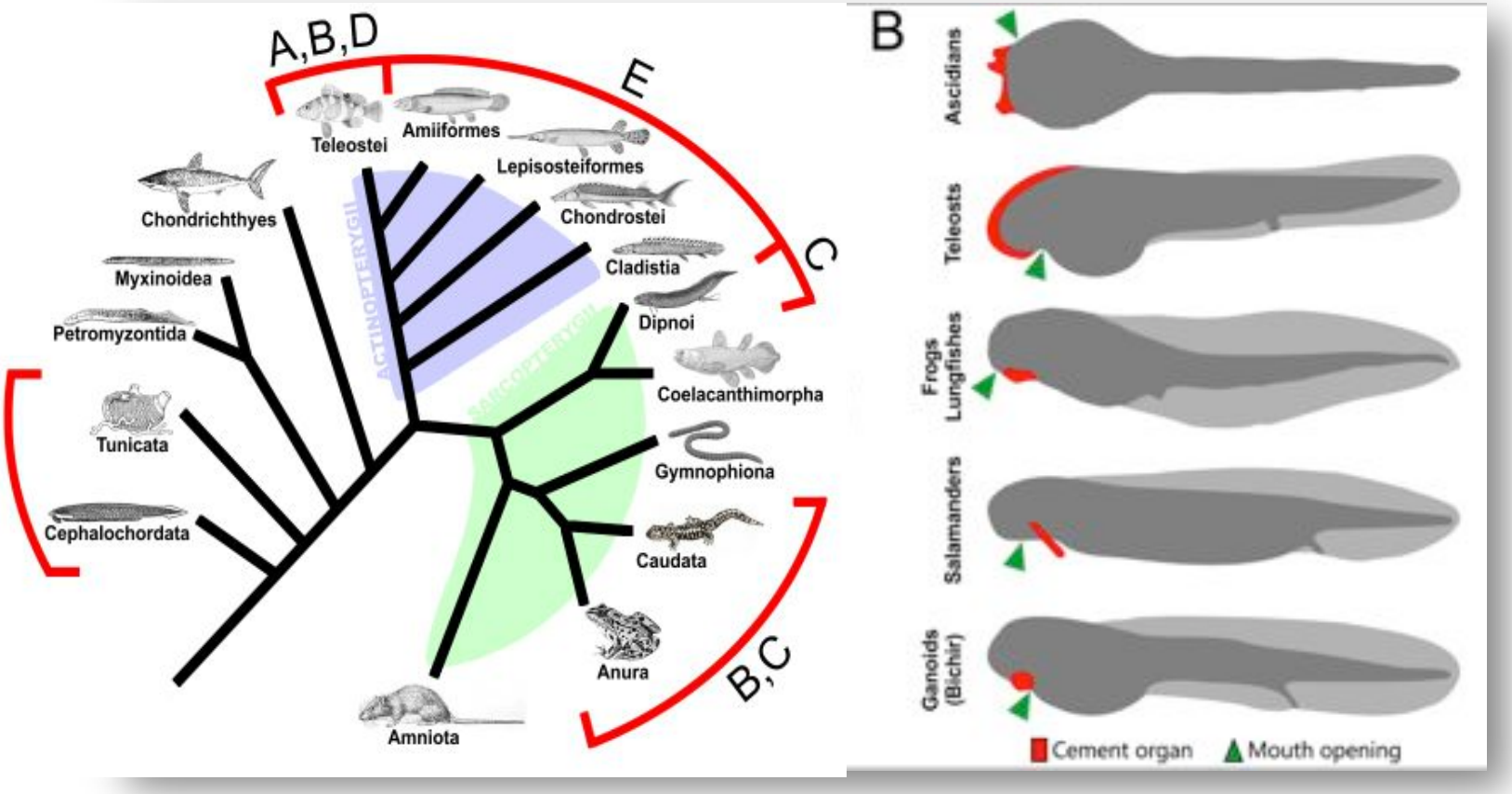
Homologie (přítomnost znaku u <u>posledního společného předka</u>)

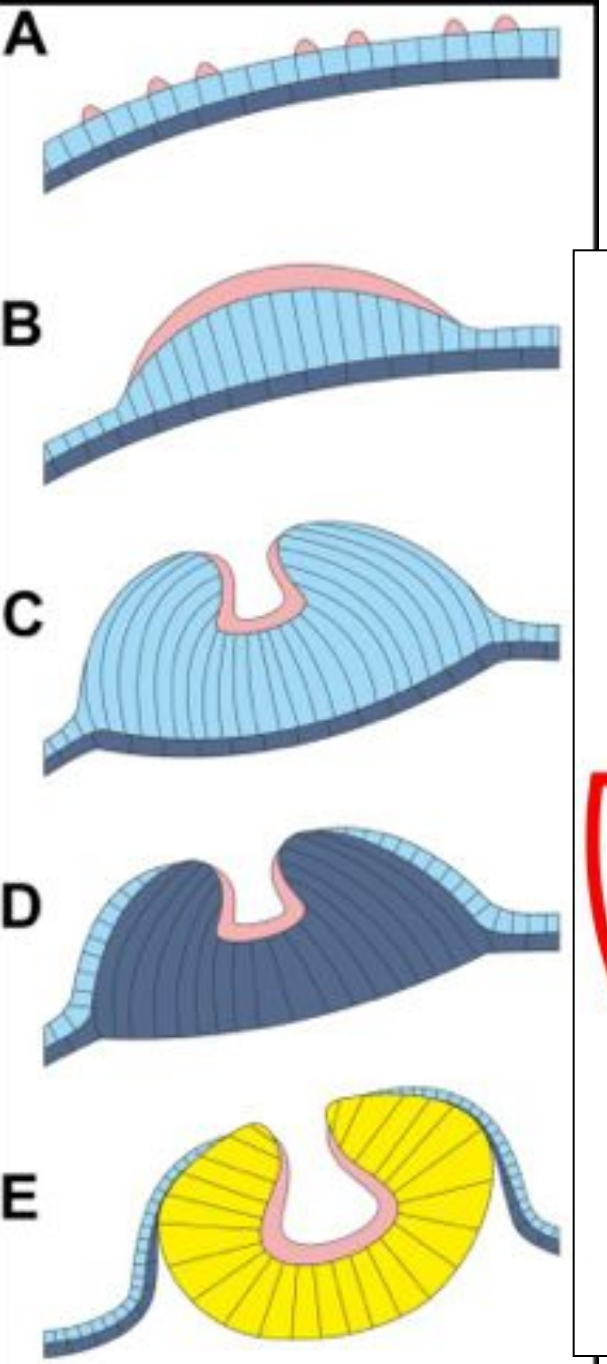
Analogie (<u>nezávislý</u> vznik… larvální adaptace)

Deep homology (hlubinná homologie – srv. oko)

Modularita

Developmental System Drift (DSD)




A
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D
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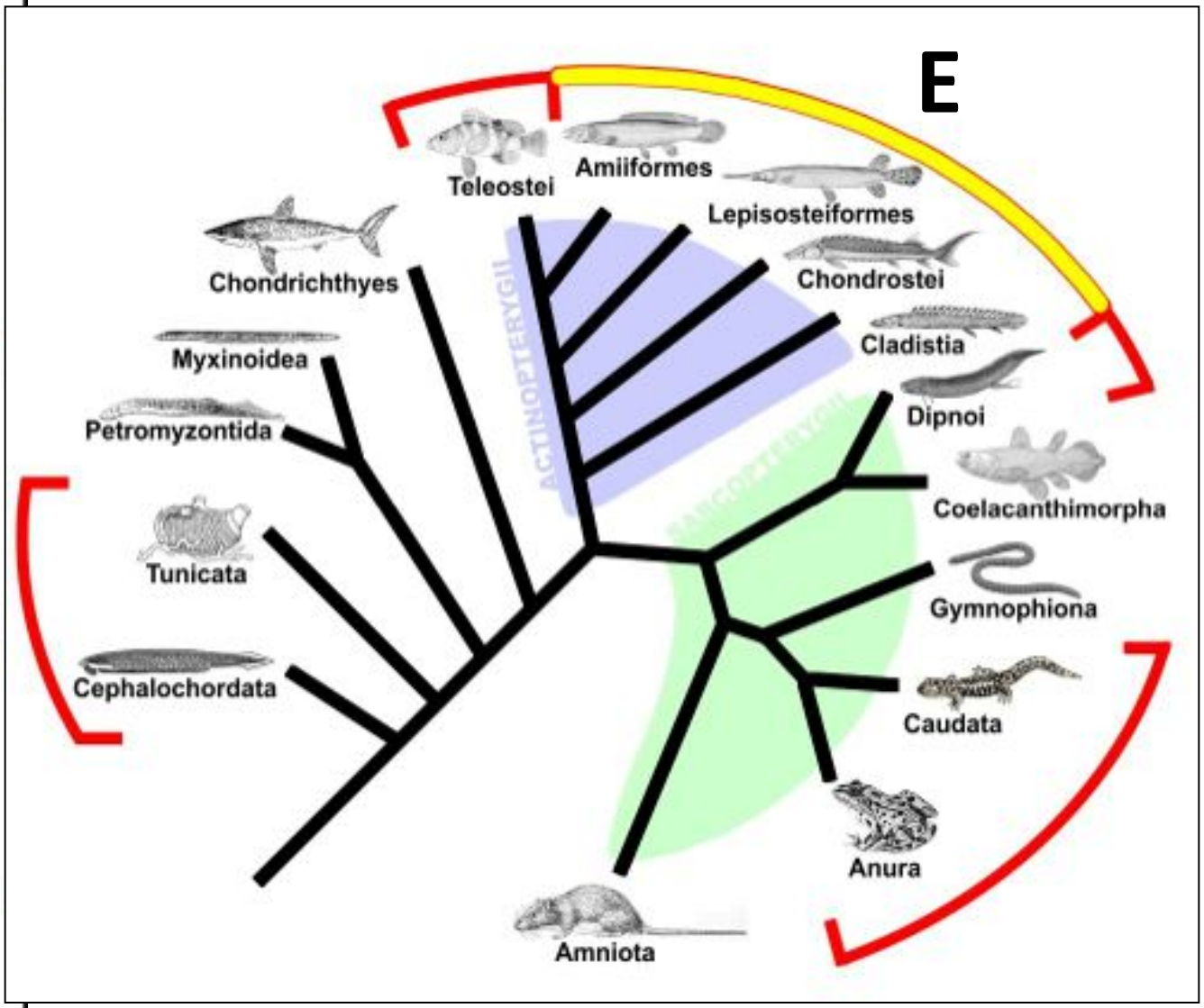
OEct
IEct
End
Mucopolysaccharide secretion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Lepisosteiformes
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Chondrostei
Cladistia
Myxinoidea
Dipnoi
Petromyzontida
Coelacanthimorpha
Tunicata
Gymnophiona
Cephalochordata
Caudata
Anura
Amniota
ACTINOPTERYGII
SARCOPTERYGII

Homologie (přítomnost znaku u <u>posledního společného předka</u>)

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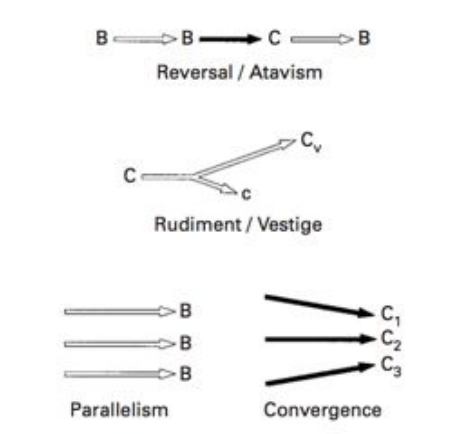
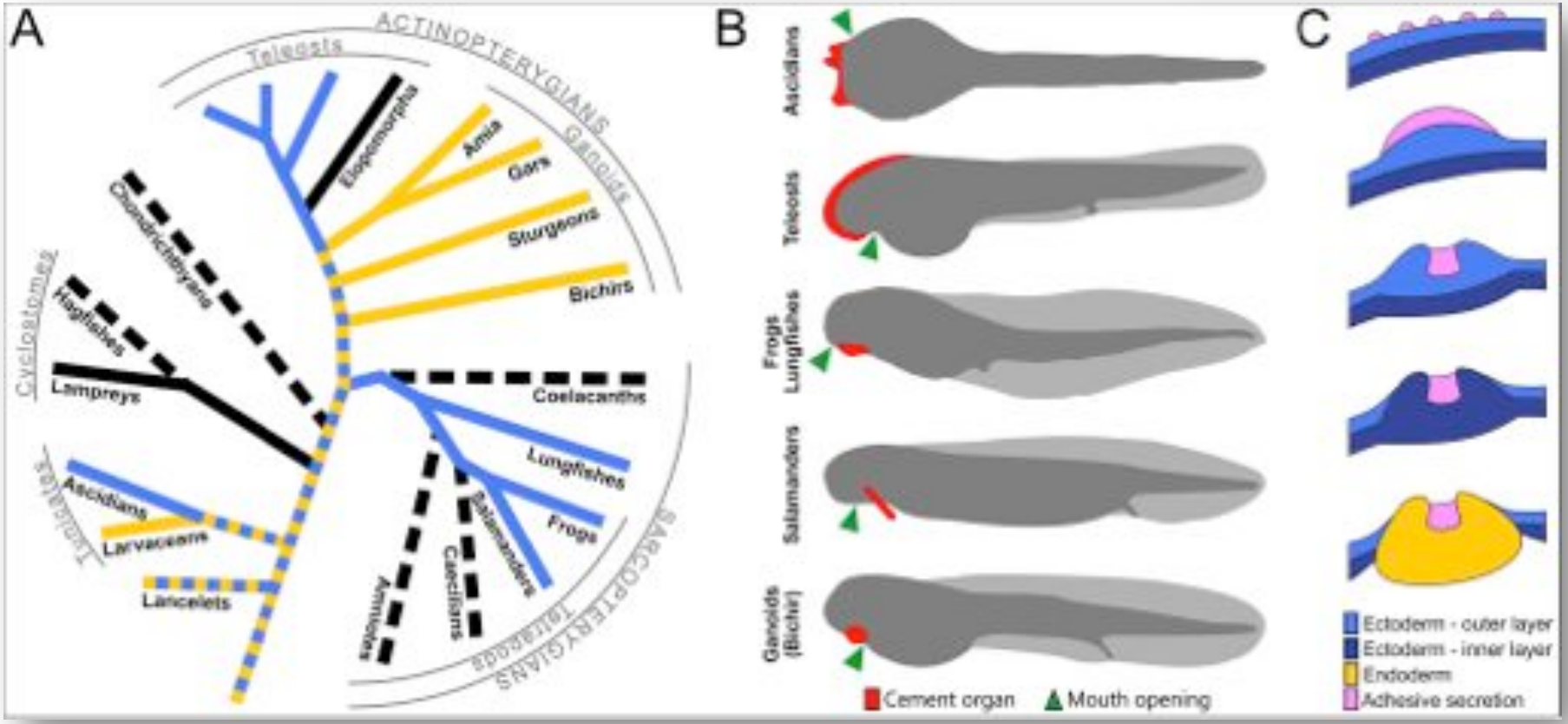
Modularita

Developmental System Drift (DSD)





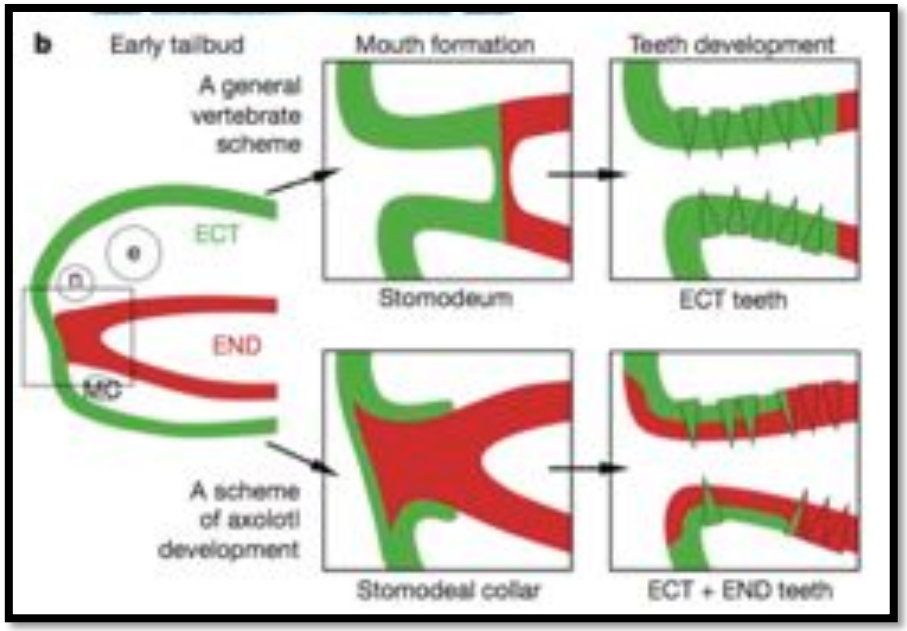
doi:10.1038/nature07304

nature

LETTERS

Dual epithelial origin of vertebrate oral teeth

Vladimír Soukup[1], Hans-Henning Epperlein[2], Ivan Horácek[1] & Robert Cerny[1]

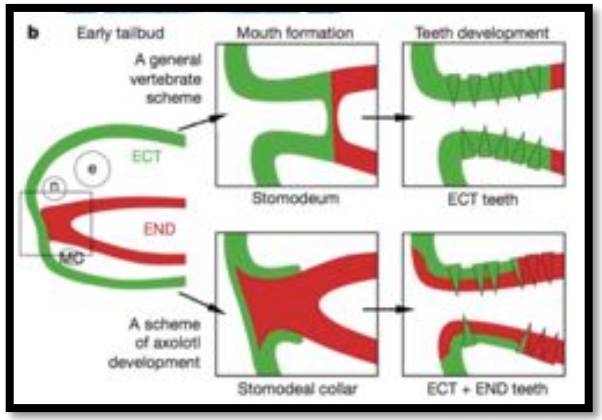


doi:10.1038/nature07304

LETTERS

Dual epith

Vladimír Soukup[1], Han



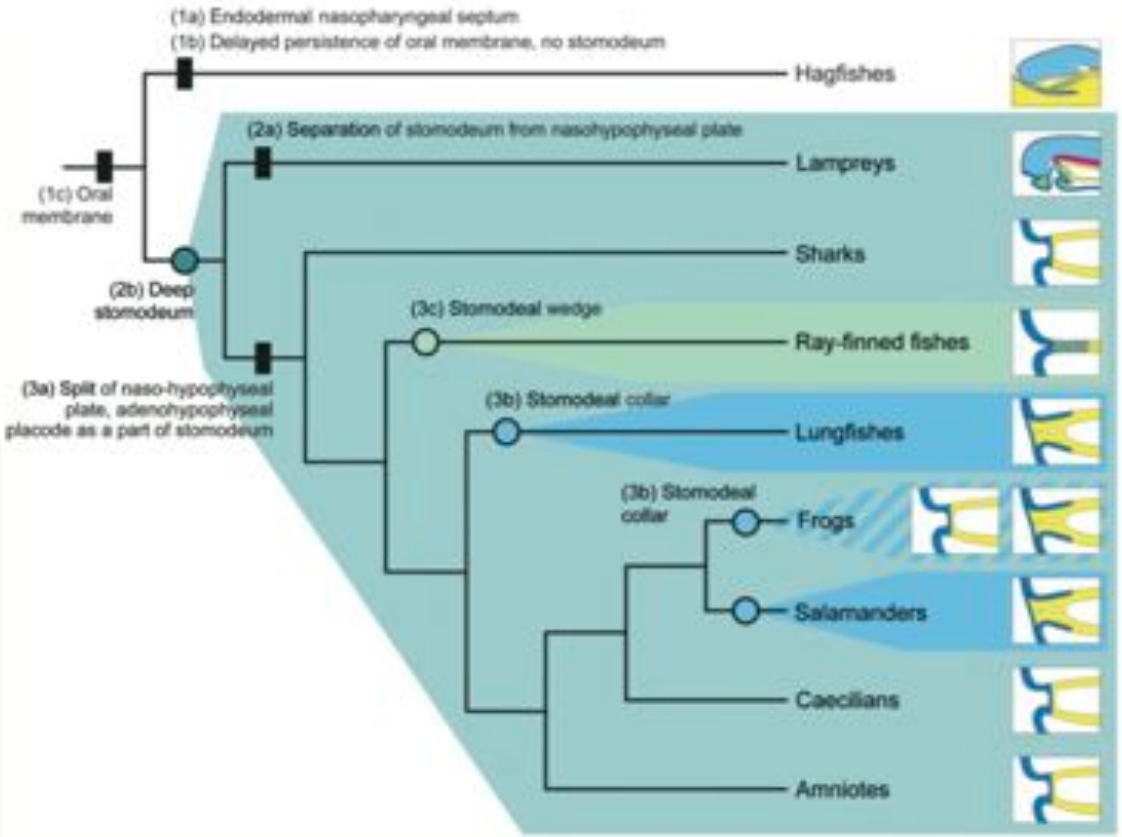
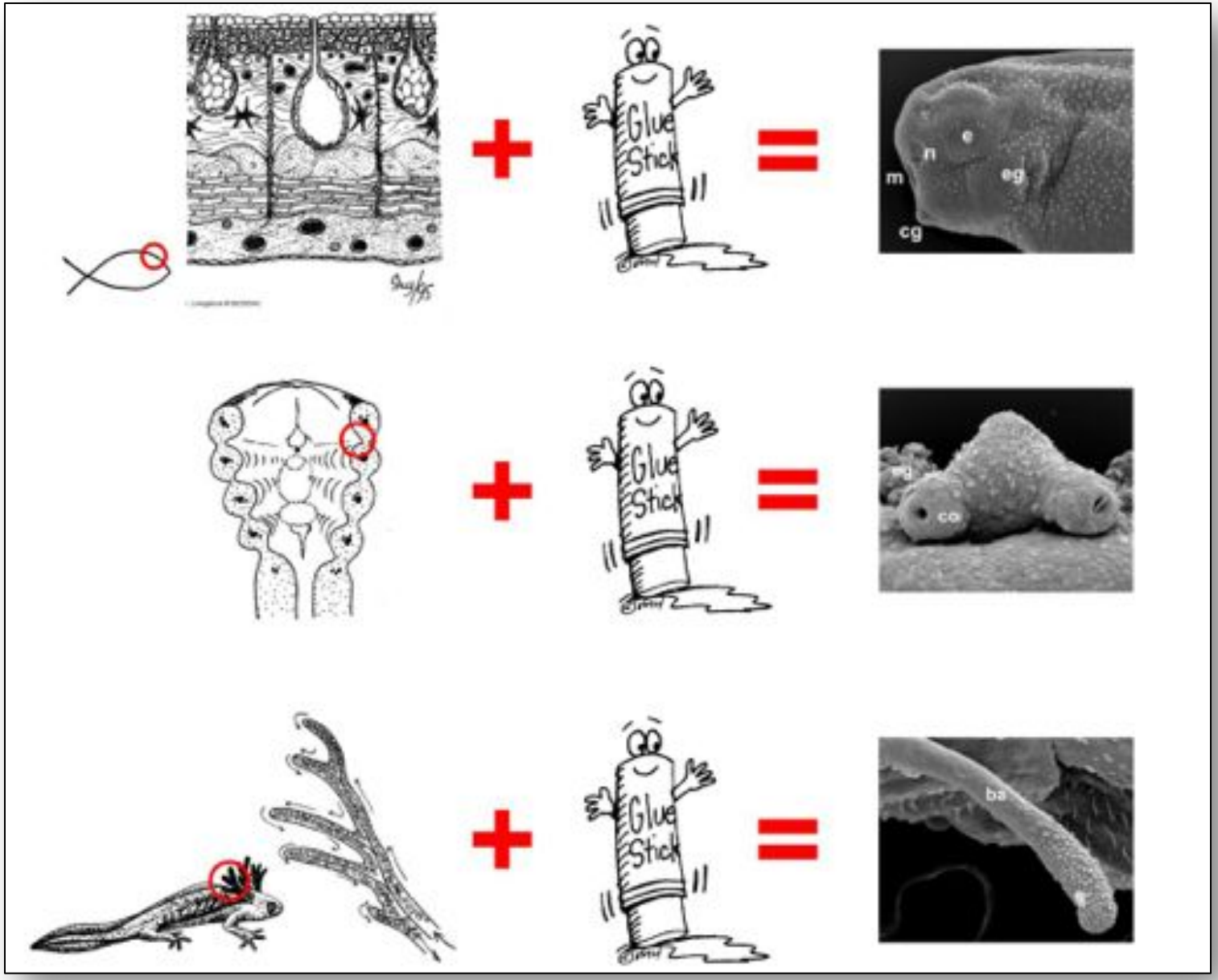
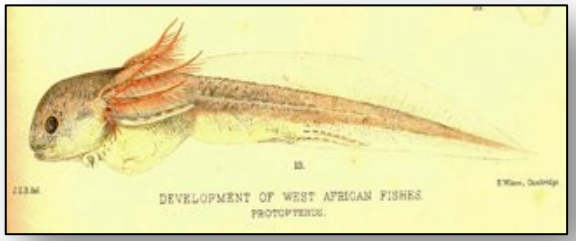


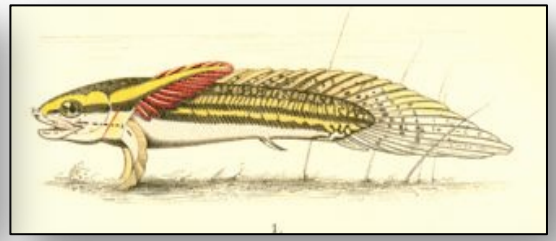
Fig. 6 Phylogenetic distribution of the primary mouth formation characteristics. Phylogenetic relationships after Near (2009), where the 'craniate hypothesis' is preferred with hagfishes as a sister group to lampreys + gnathostomes. See the text for coding of the characters. Opening of the primary mouth via rupture of the double-layered oral membrane (character 1c) is an ancient plesiomorphic character of craniates. Stomodeal invagination (character 2b) is probably apomorphic for lampreys and gnathostomes, while it was further modified once into the stomodeal wedge (in the ray-finned fish lineage and most notably in teleosts, character 3c) and separately several times into the stomodeal collar (in lungfishes, salamanders and some frogs, character 3b).

Modularita ve vývoji adhezivních orgánů... DSD či analogie?



Vnější žábry jako klíčová adaptace larev obratlovců





Embryonic and Larval Development in the Caecilian *Ichthyophis kohtaoensis* (Amphibia, Gymnophiona):

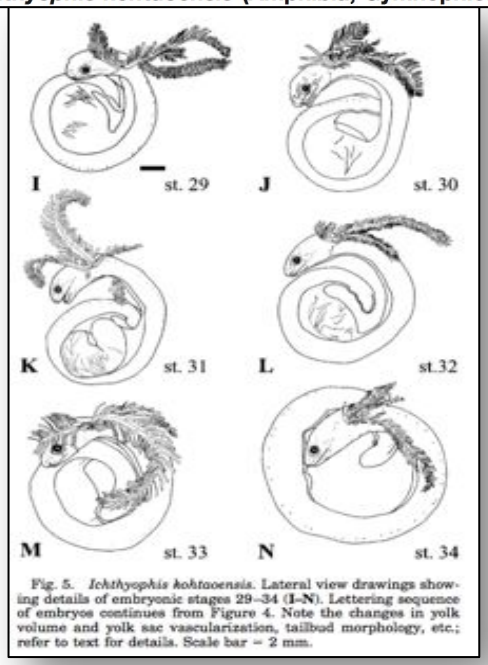
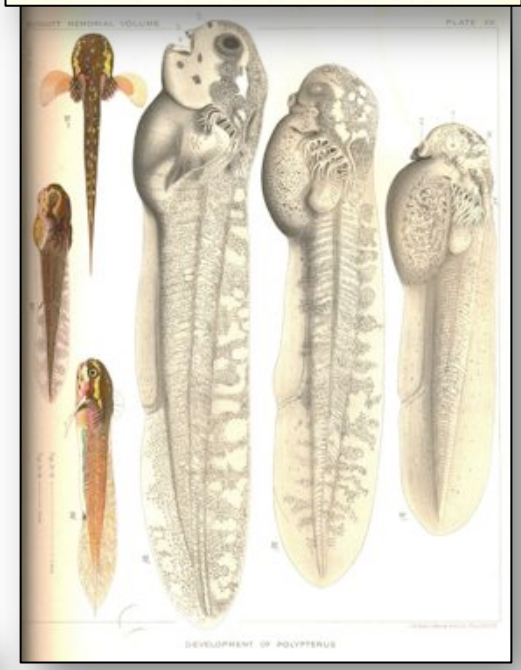


Fig. 5. *Ichthyophis kohtaoensis*. Lateral view drawings showing details of embryonic stages 29–34 (I–N). Lettering sequence of embryos continues from Figure 4. Note the changes in yolk volume and yolk sac vascularization, tailbud morphology, etc.; refer to text for details. Scale bar = 2 mm.

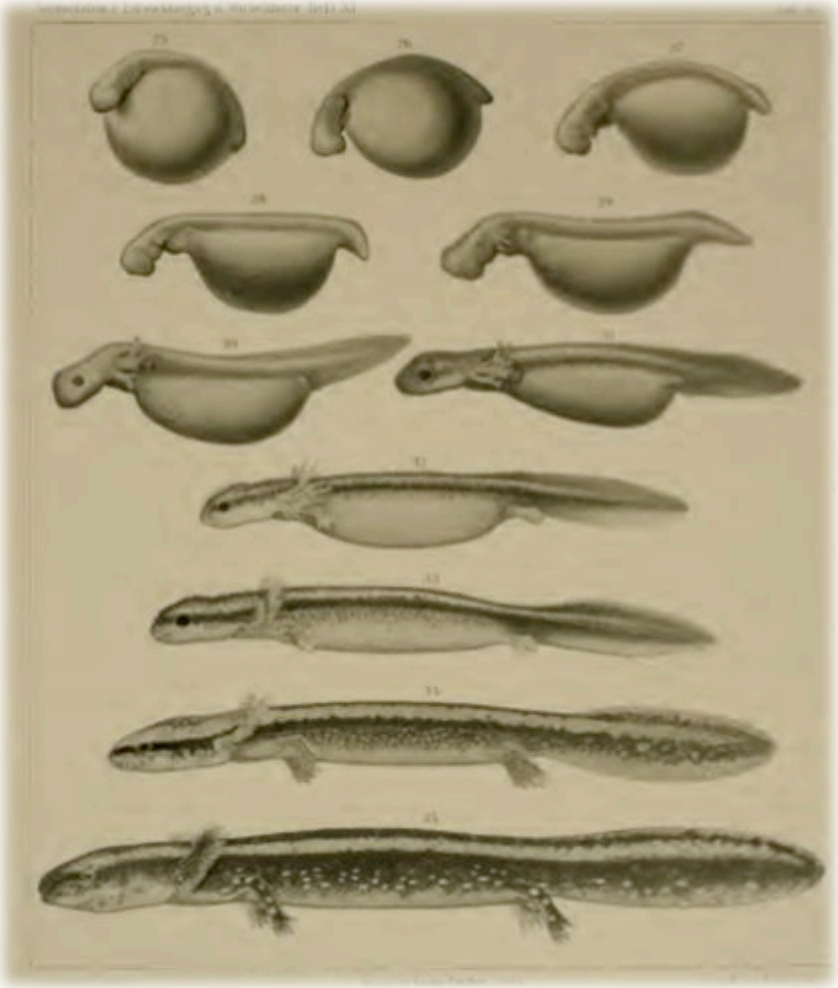
THE DEVELOPMENT OF LEPIDOSIREN PARADOXA, FITZ.

The development of Polypterus senegalus Cuv.

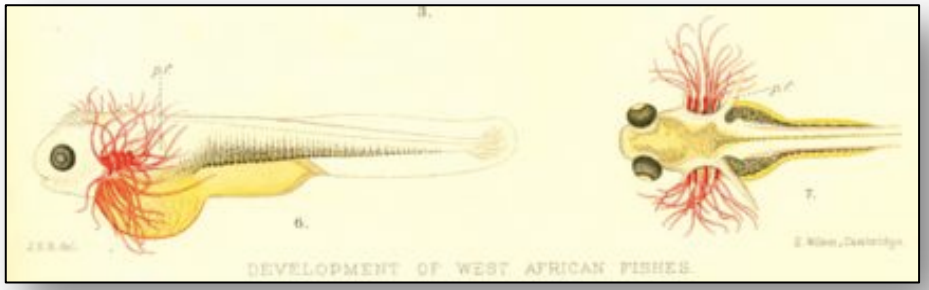


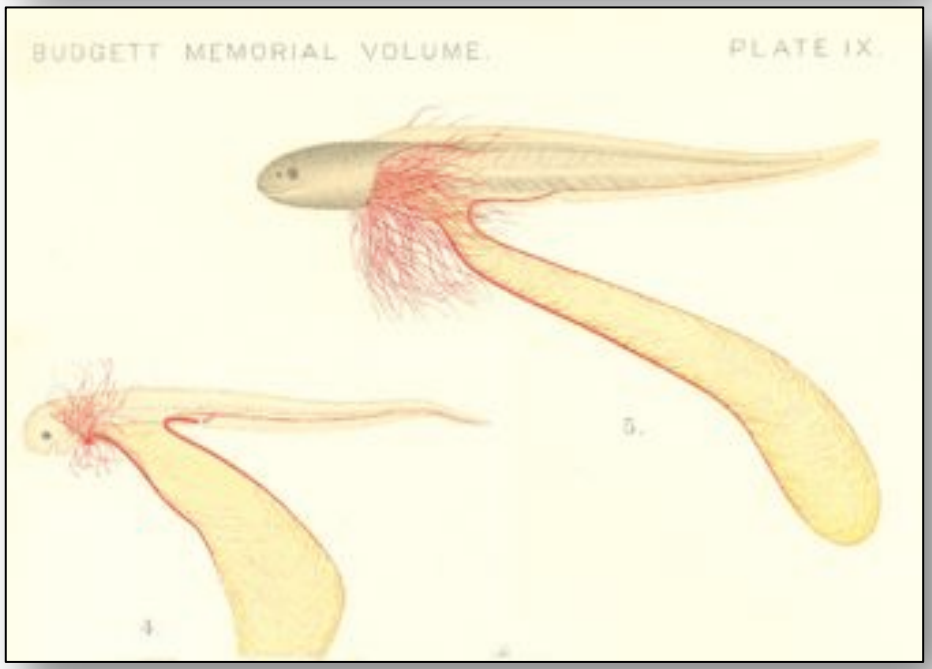
External (outer) gills are key adaptations of many larval vertebrates

- a common adaptation of embryos and larvae of lower vertebrates; transient, but very similar structures
- serve for gass exchange in less-oxygenated water environments; include capillary loops
- develop on head surface in association with branchial arches; plausibly from the outer ectoderm



External gills & external gill filments are key adaptations of many larval vertebrates





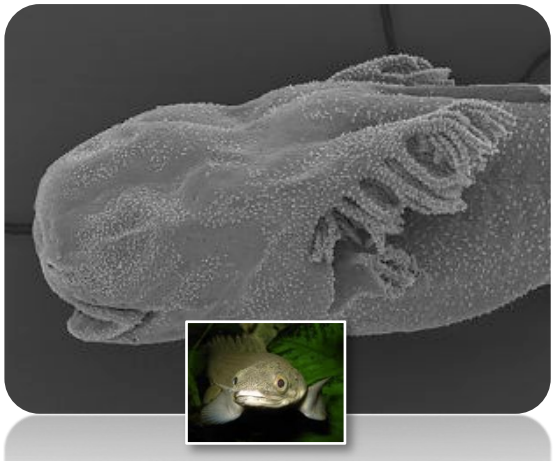
External gill filaments

may also serve for nutrient absorption (*histotrophy*)

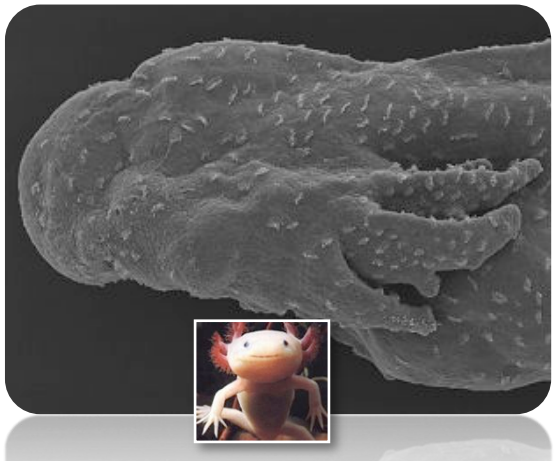
- in some **Actinopterygians** (e.g., Gymnarchus, Heterotis, Misgurnus, Acipenser)
- in some **Chondrichthyans** (e.g., Raja, Heterodontus, Callorhinchus)

Vnější žábry představují klíčovou adaptaci larválních stadií mnoha linií obratlovců: tyto jsou však strukturálně a vývojově nehomologické...

the Senegal bichir
Polypterus senegalus

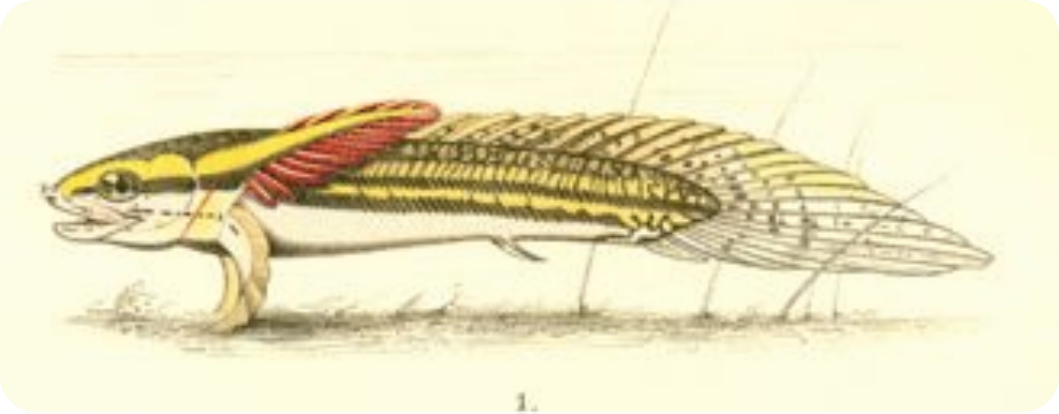


the Mexican axolotl
Ambystoma mexicanum



the Weather loach
Misgurnus fossilis

Vnější žábry představují klíčovou adaptaci larválních stadií mnoha linií obratlovců: tyto jsou však strukturálně a vývojově



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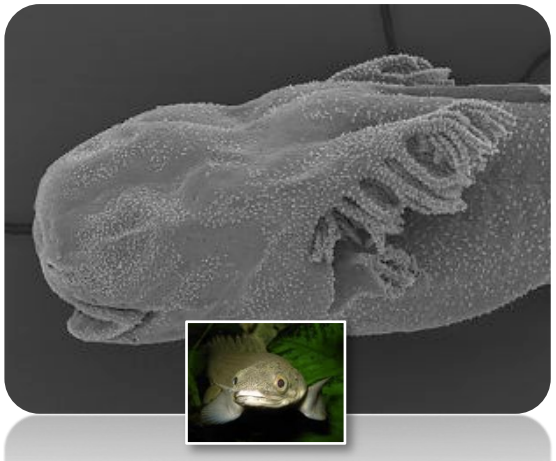
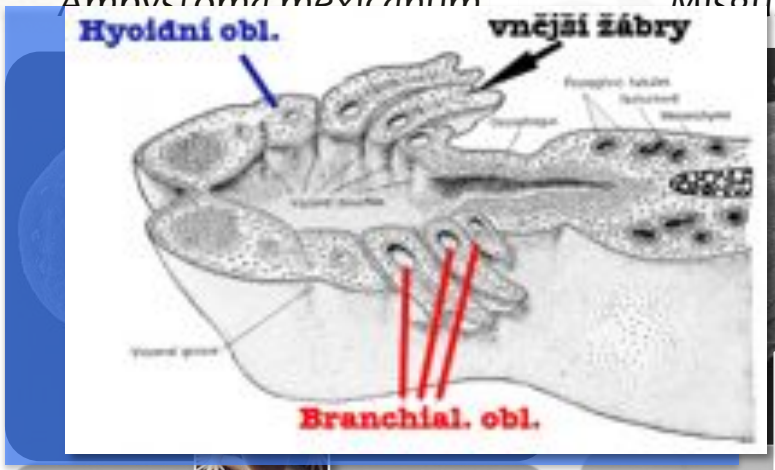
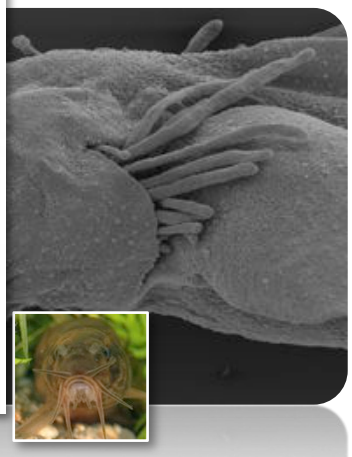
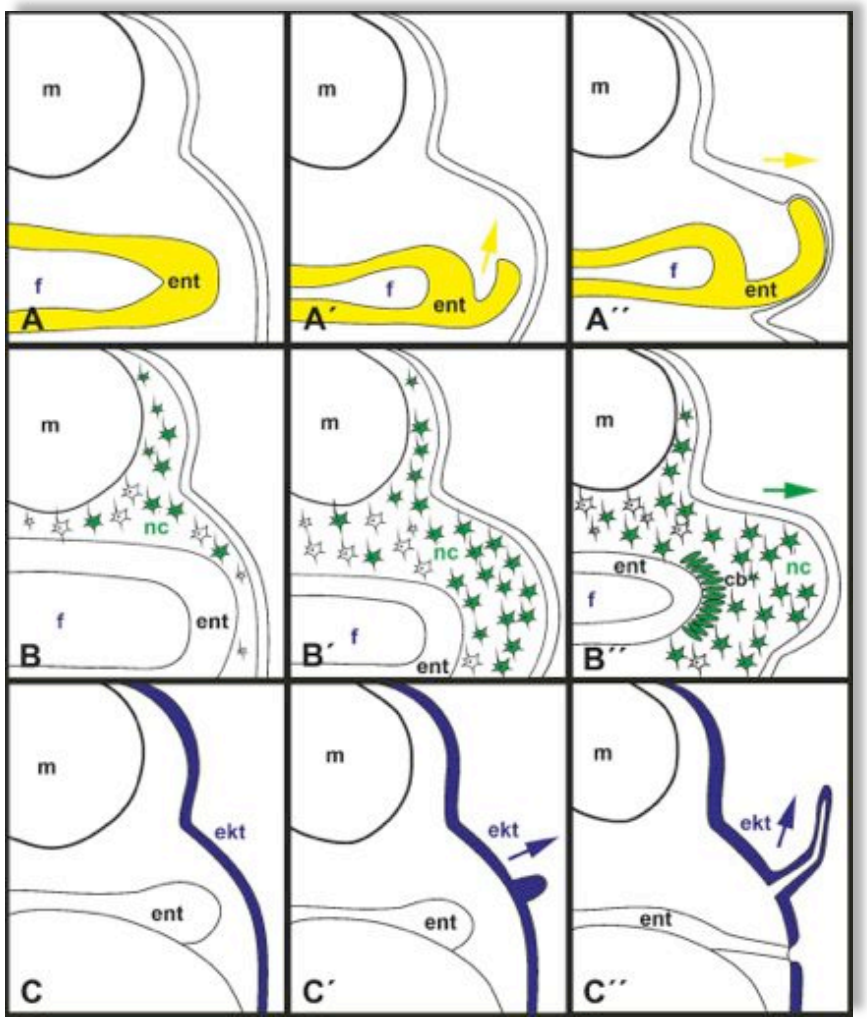






Homologie a stejnost vnějších žaberních struktur:

paralelní evoluce na bázi hluboce sdílené homologie (deep homology), nebo konvergence z odlišných základů ke stejnému „vnějšímu zjevu“?



bichir EG:

- hyoid arch structures
- lateral outpouching of pharyngeal endoderm layer due to their mode of gastrulation

axolotl EG:

- branchial arch structures
- neural crest cells seem to be the major source of gill tissues

loach EGF:

- outer ectoderm lining with no supporting tissue, no muscles
- displaced inner gills

Homologie a stejnost vnějších žaberních struktur:

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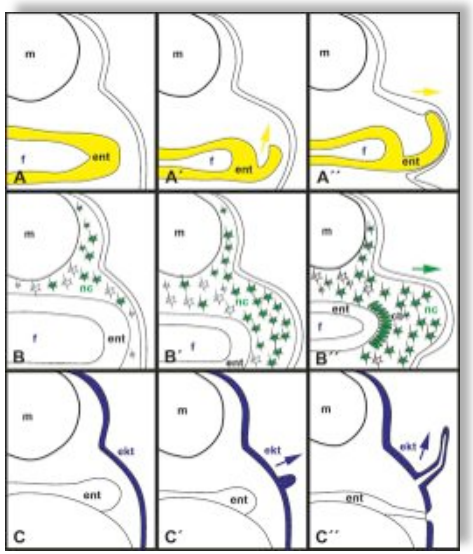

- strong distinction between <u>external gills</u> and <u>external gill filaments</u>
- structurally, <u>true external gills</u> studied are dissimilar in number, position and form
- developmentally, they are formed by dissimilar developmental processes

these distinctions should categorize E.G as <u>analogous structures</u> ariving via independent evolution

E.G. may share some "deep homology module" dealing with gass exchange

alternatively, E.G. can be seen as attractor – the outcome stays <u>same</u> but developmental processes underlying its formation can change during evolution
(Developmental system drift: G. Müller)