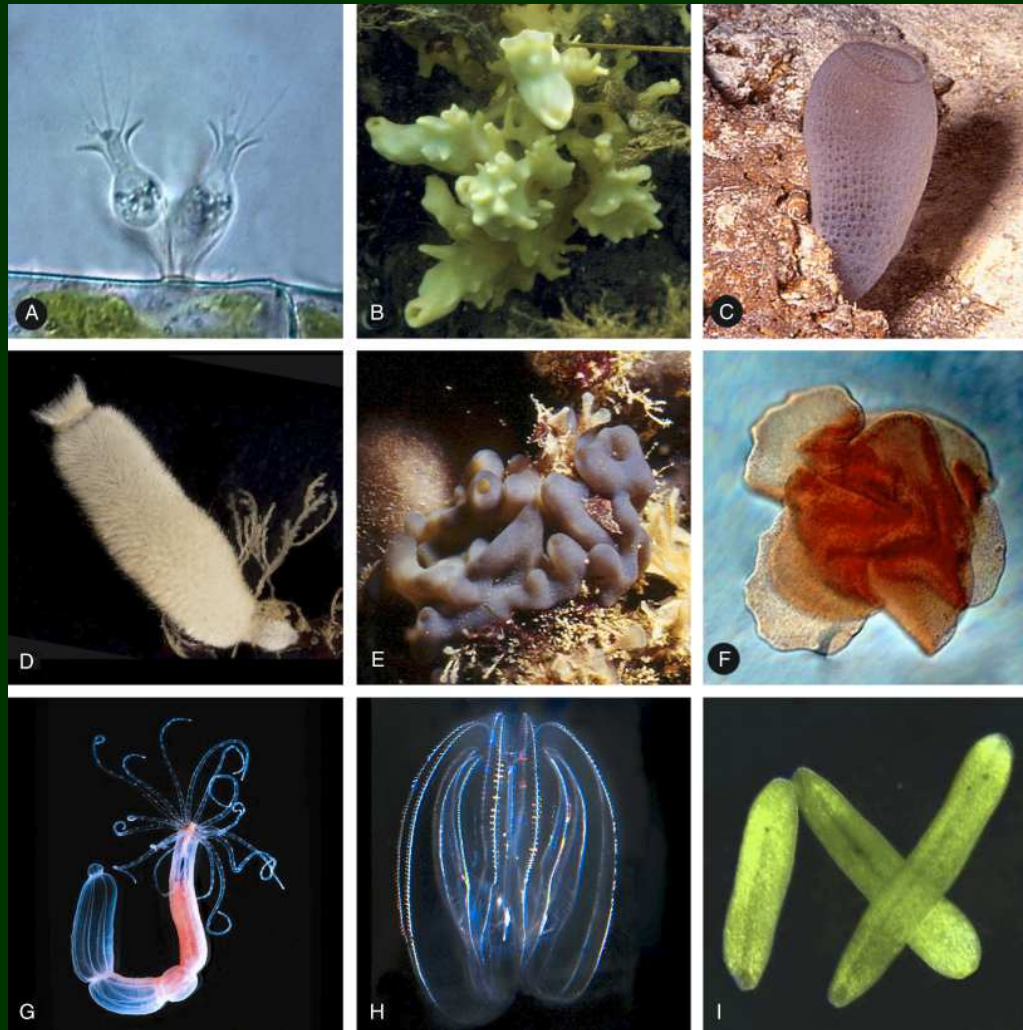
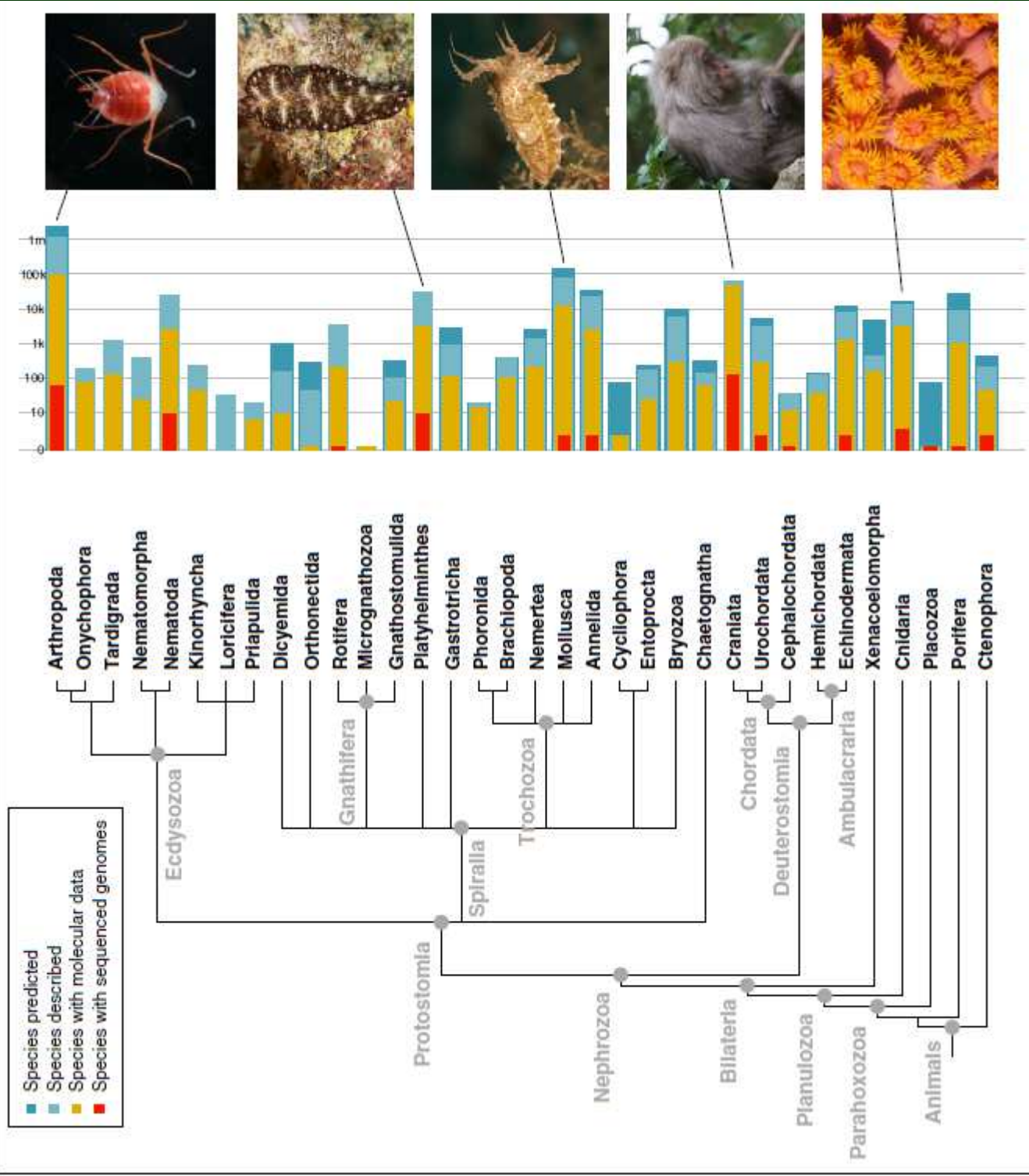
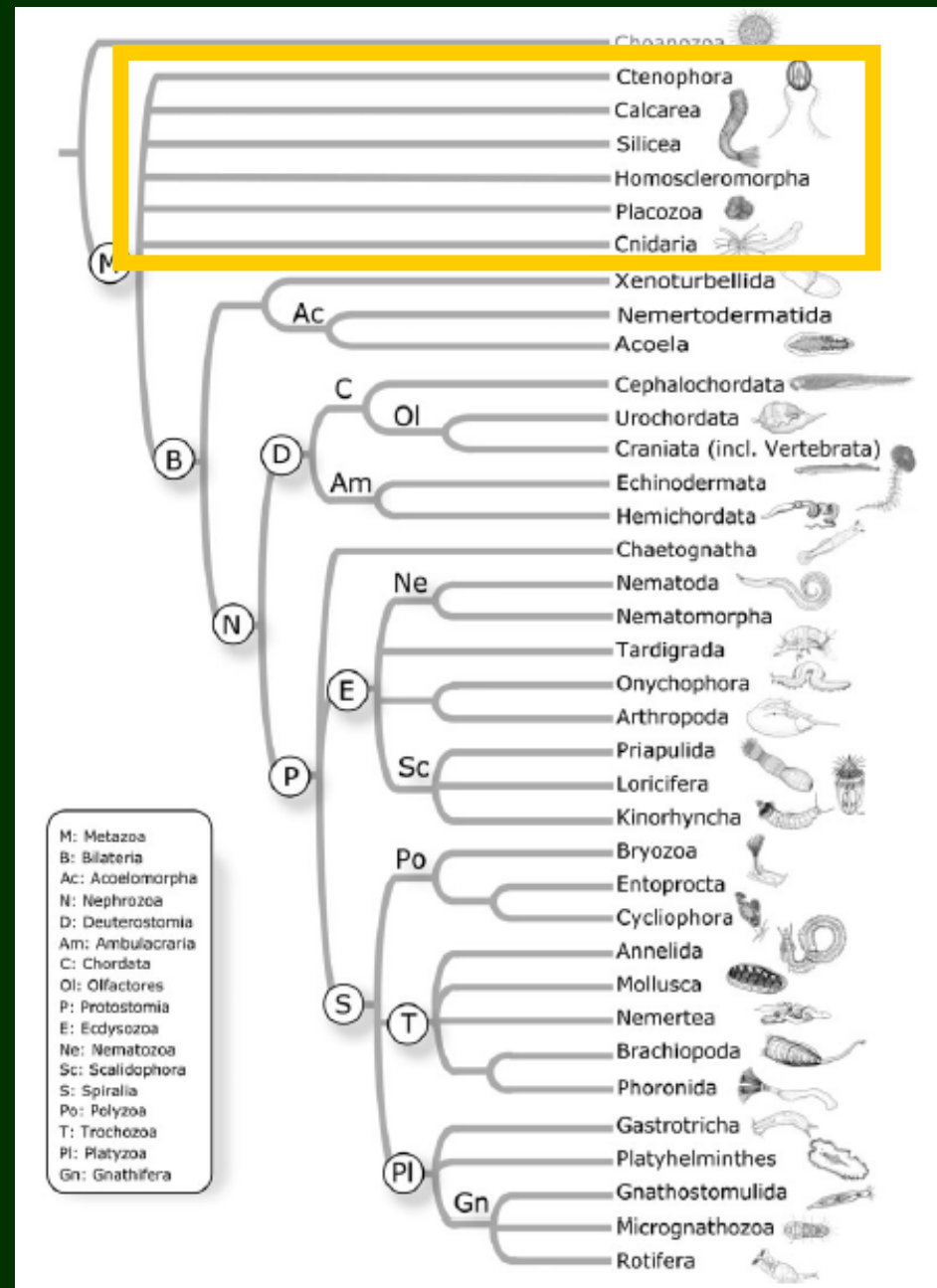


Bazální Metazoa

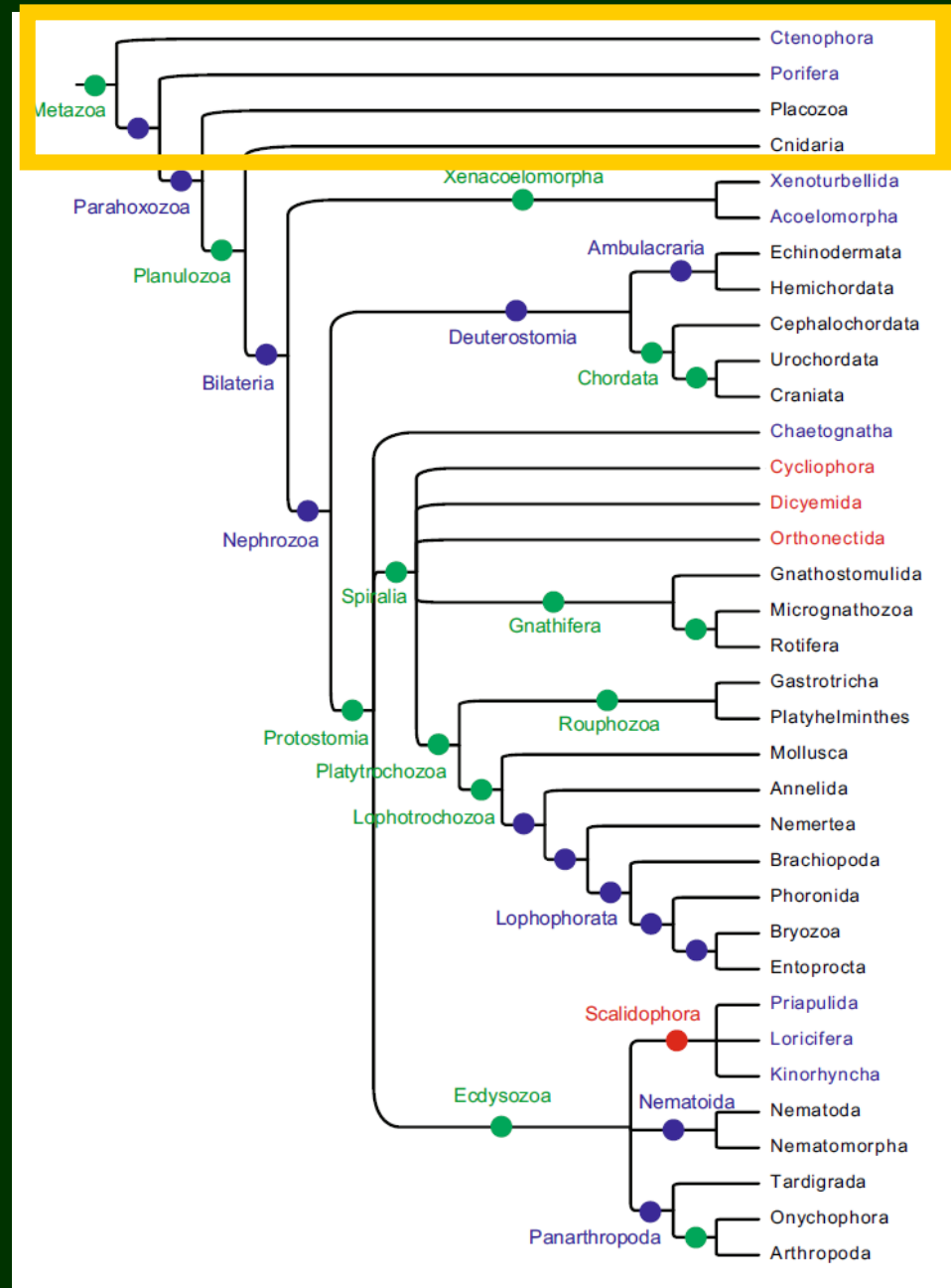




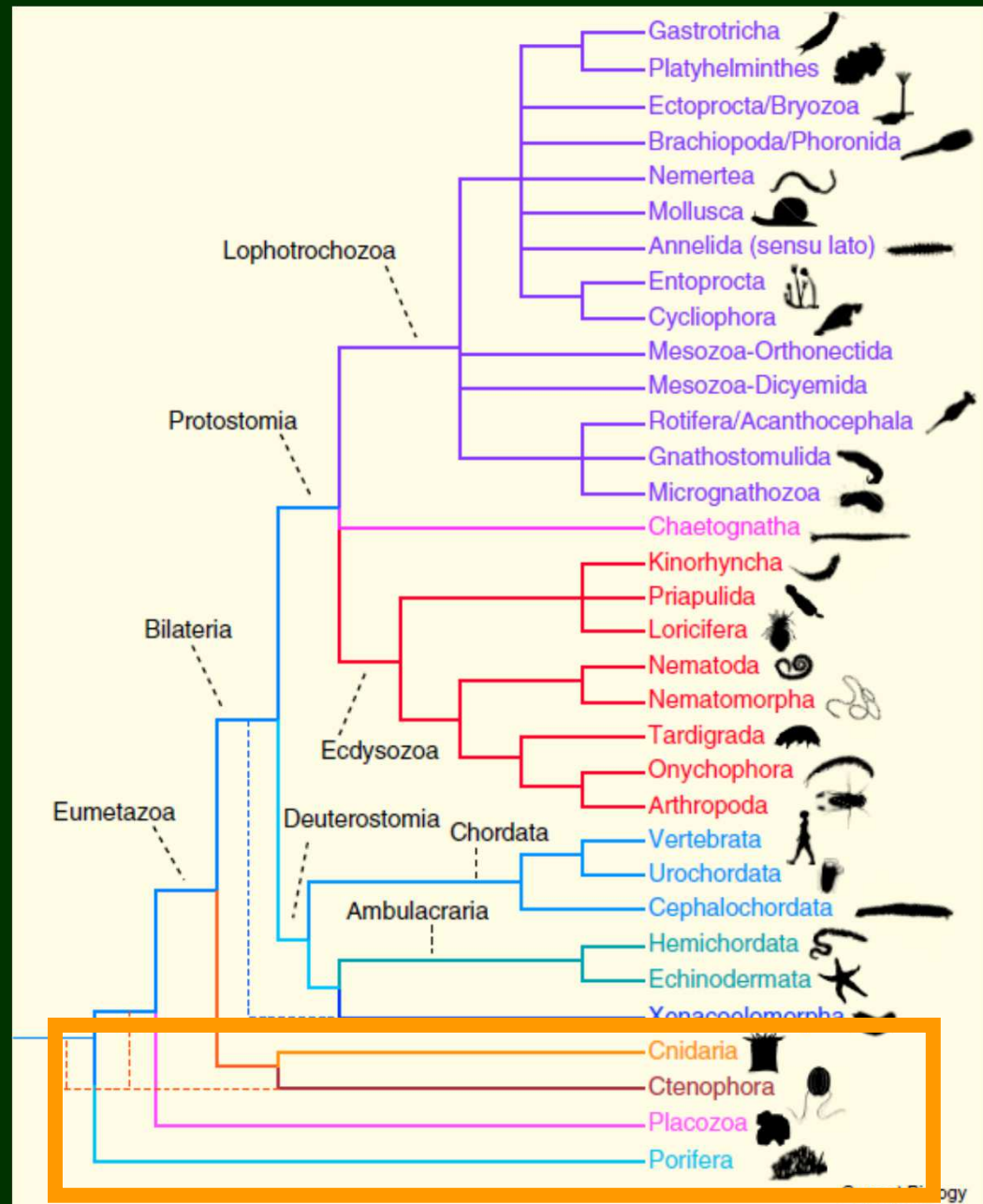
Fylogeneze metazoí (2011)

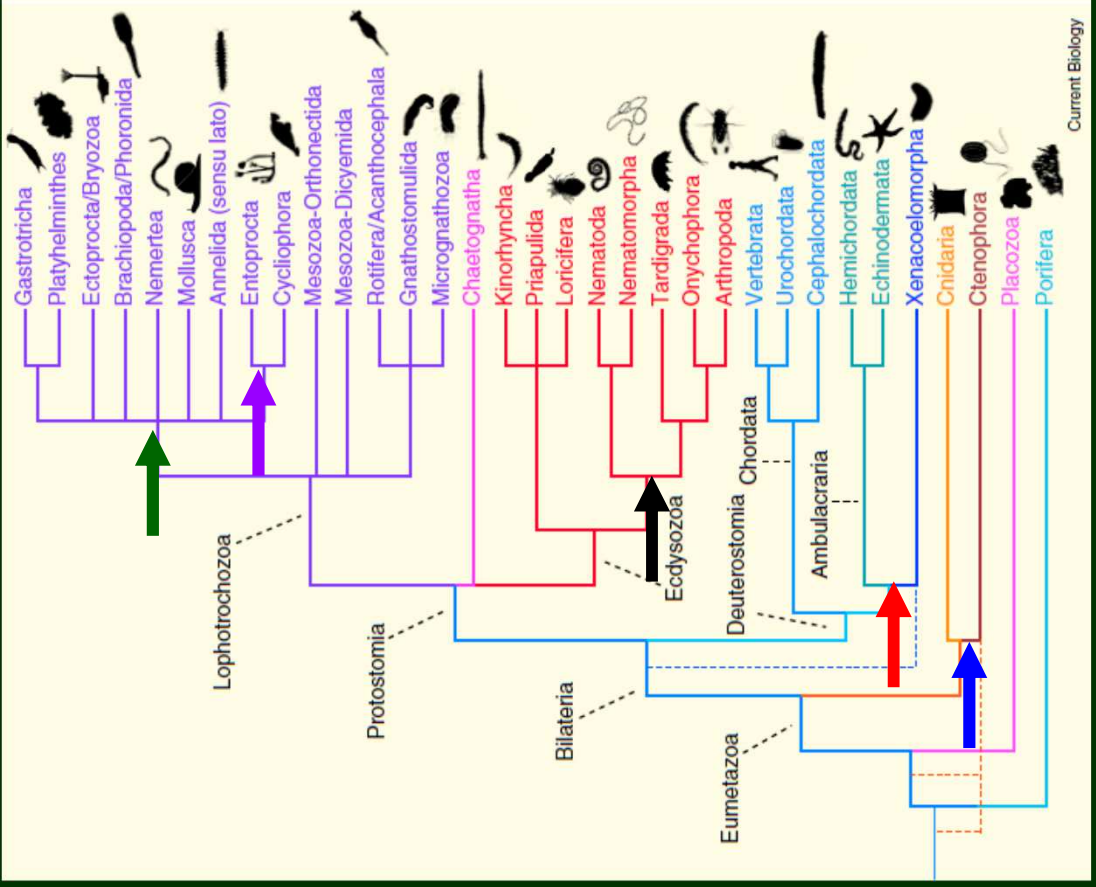
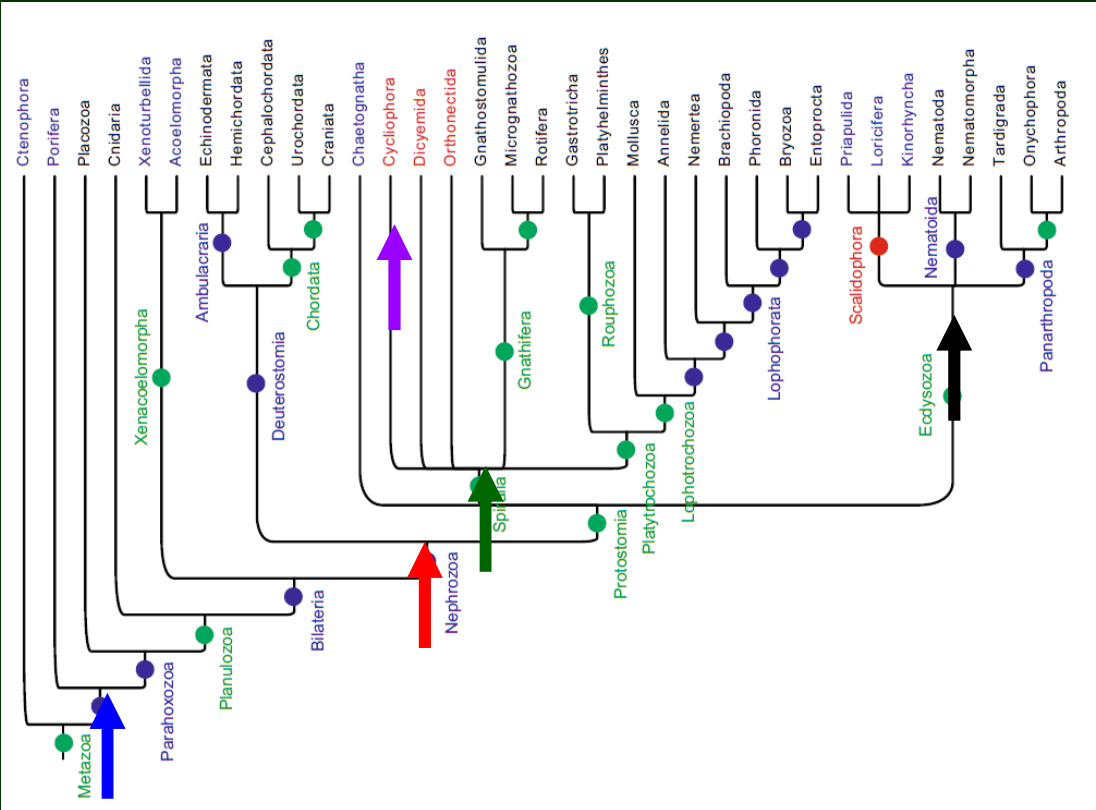


Fylogeneze metazoí (podzim 2015)

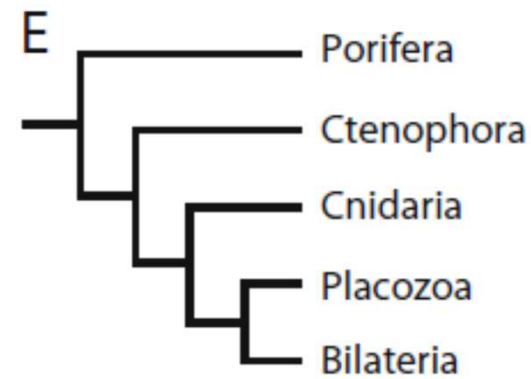
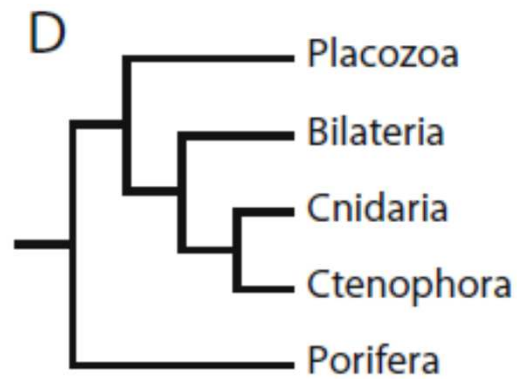
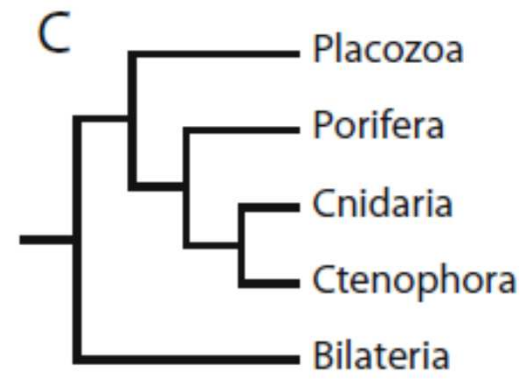
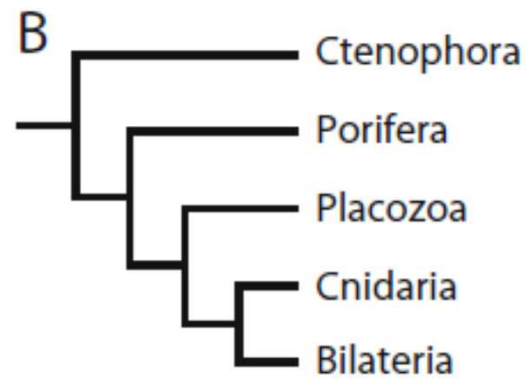
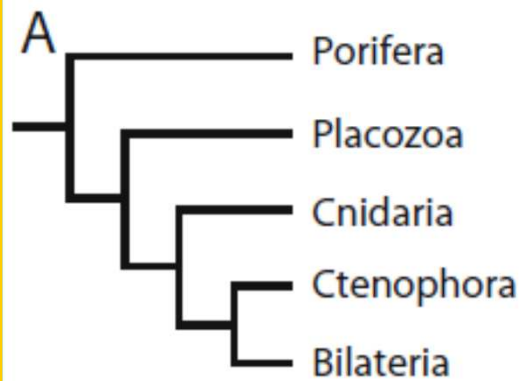


Fylogeneze metazoí (podzim 2015)



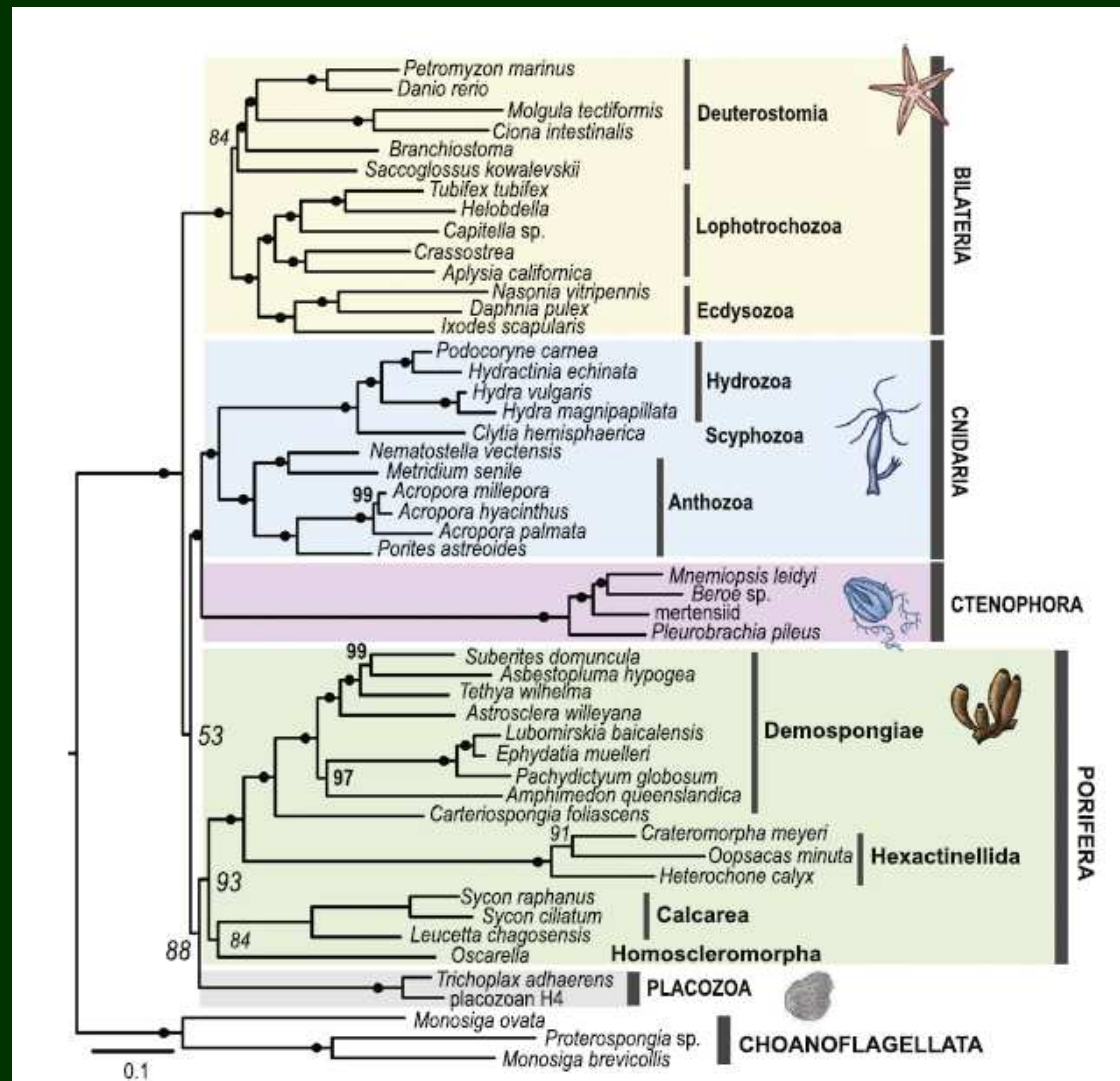


Fylogeneze metazoói

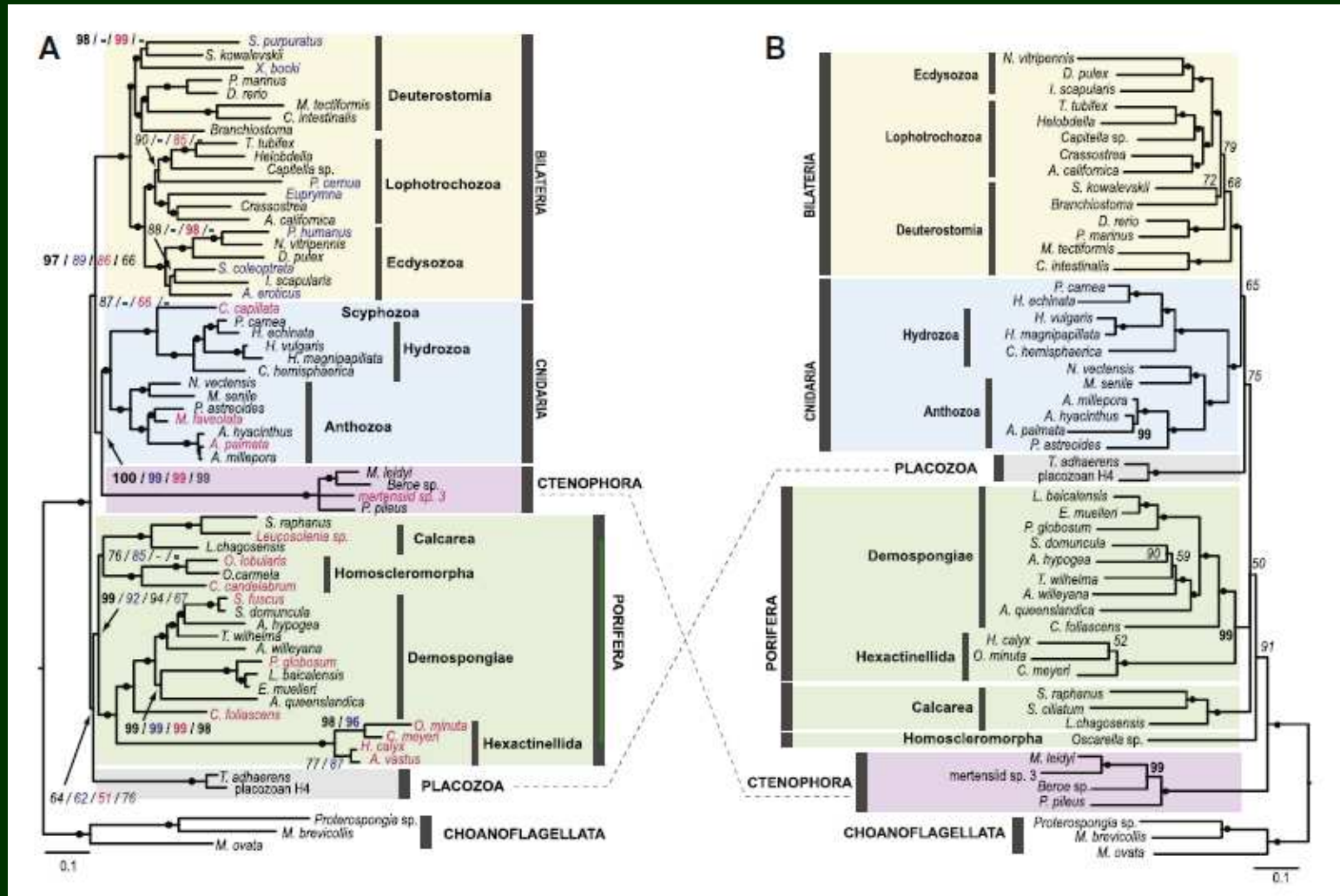


„Coelenterata“

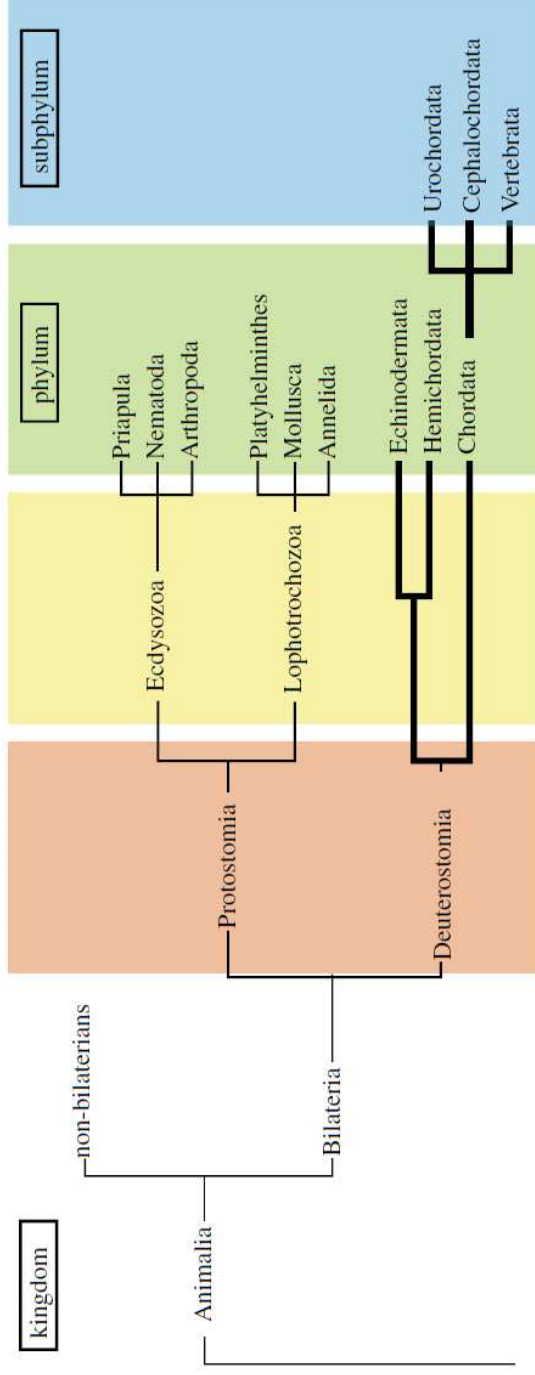
- 122 ribosomálních i neribosomálních genů



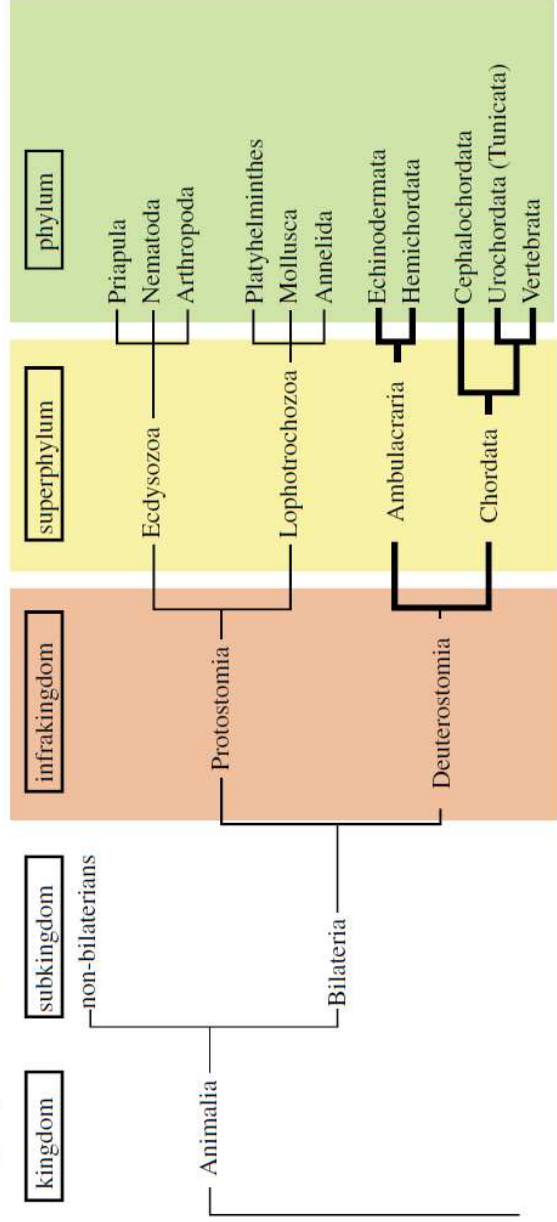
„Coelenterata“: rozpor mezi ribosomálními a neribosomálními geny

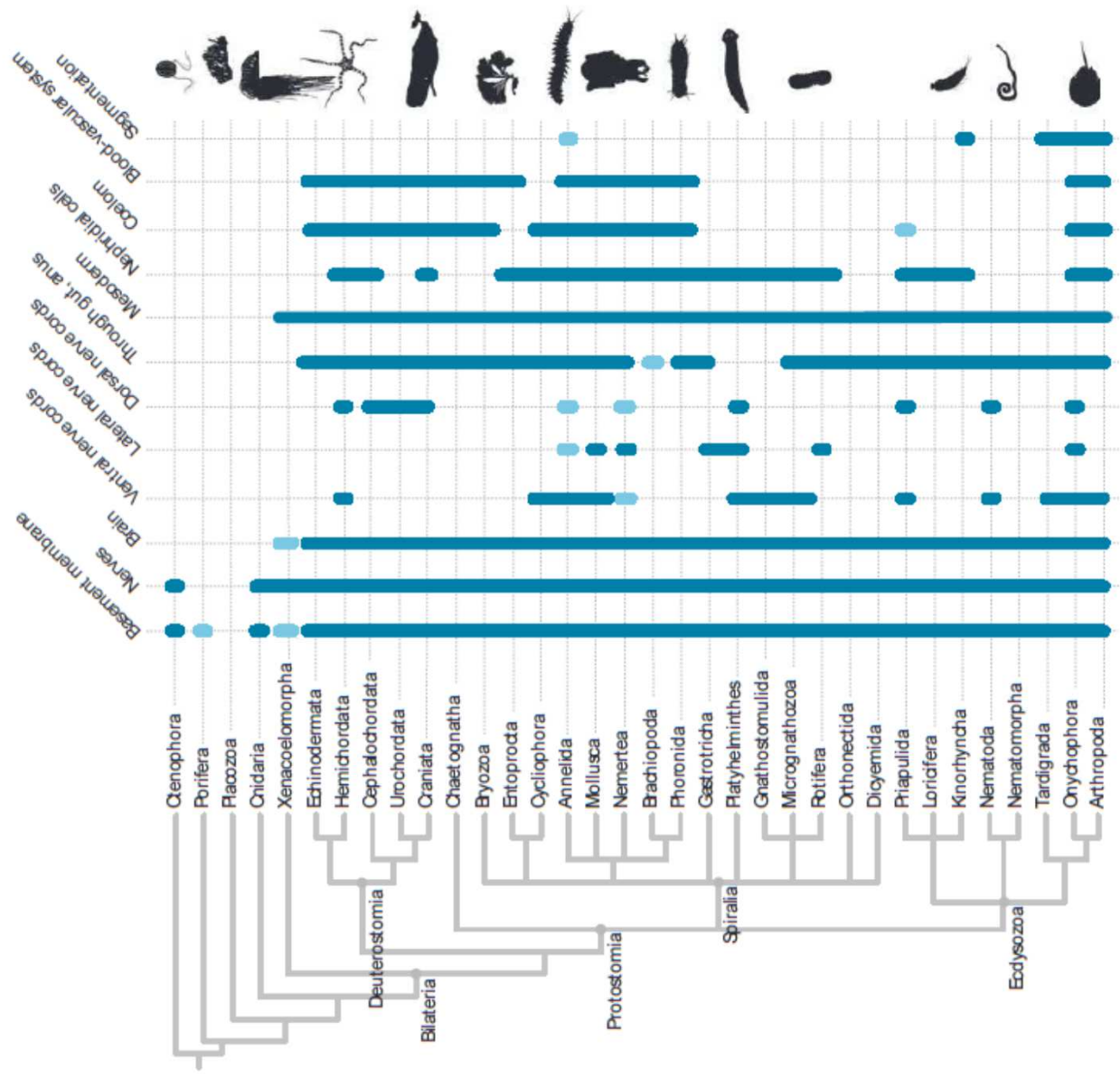


(b) current view

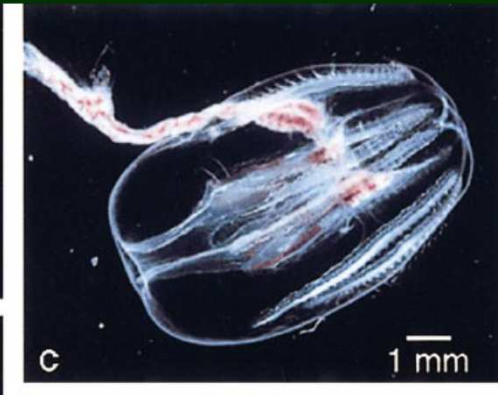
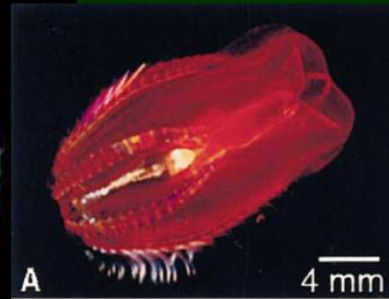
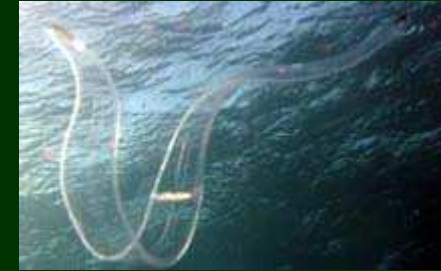


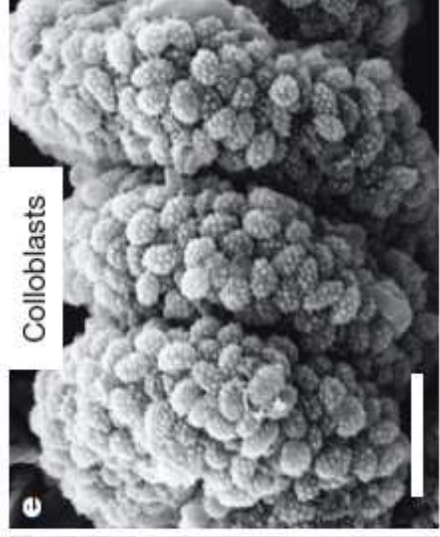
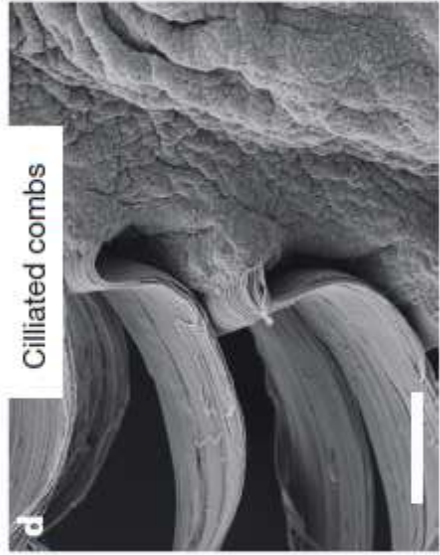
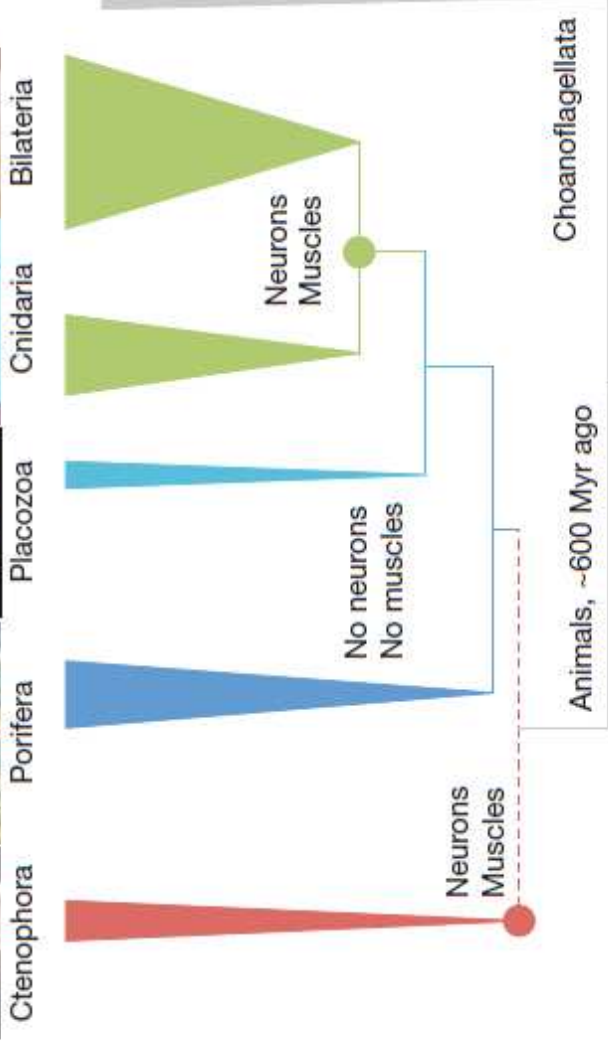
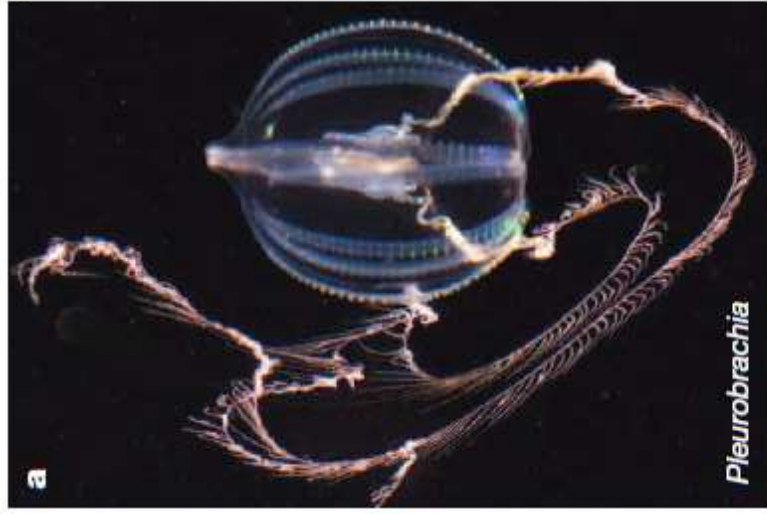
(c) a proposed view



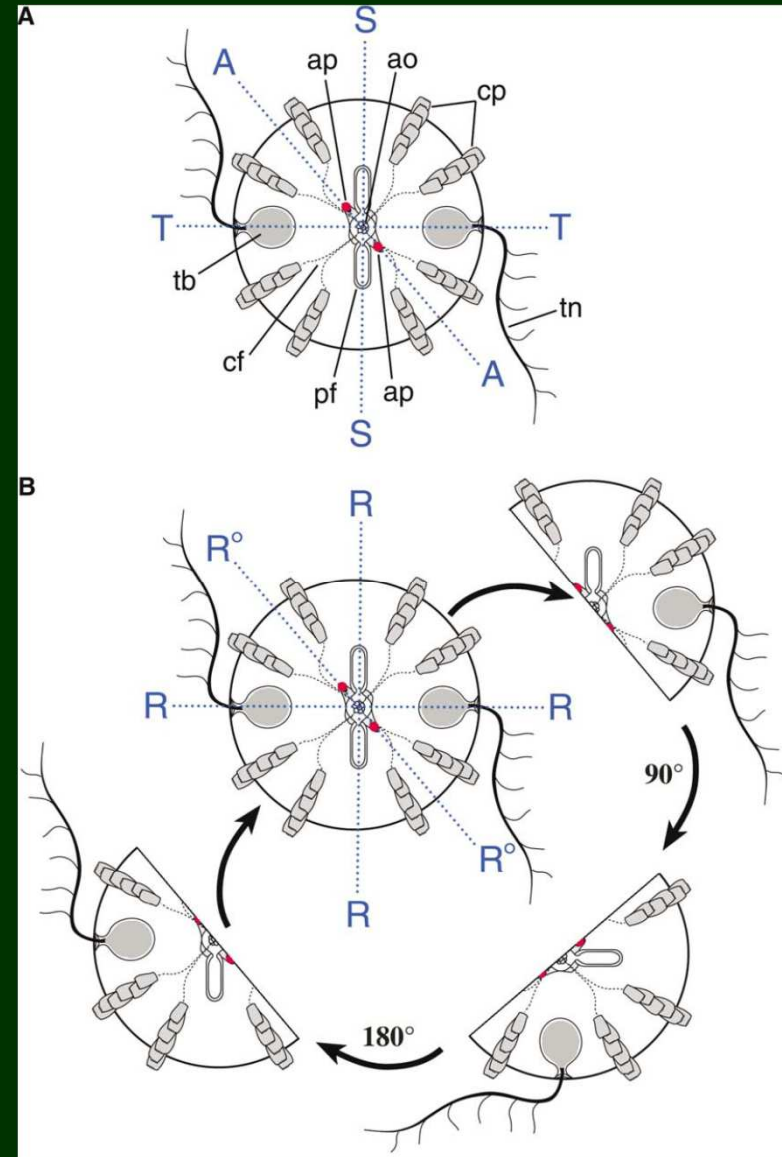
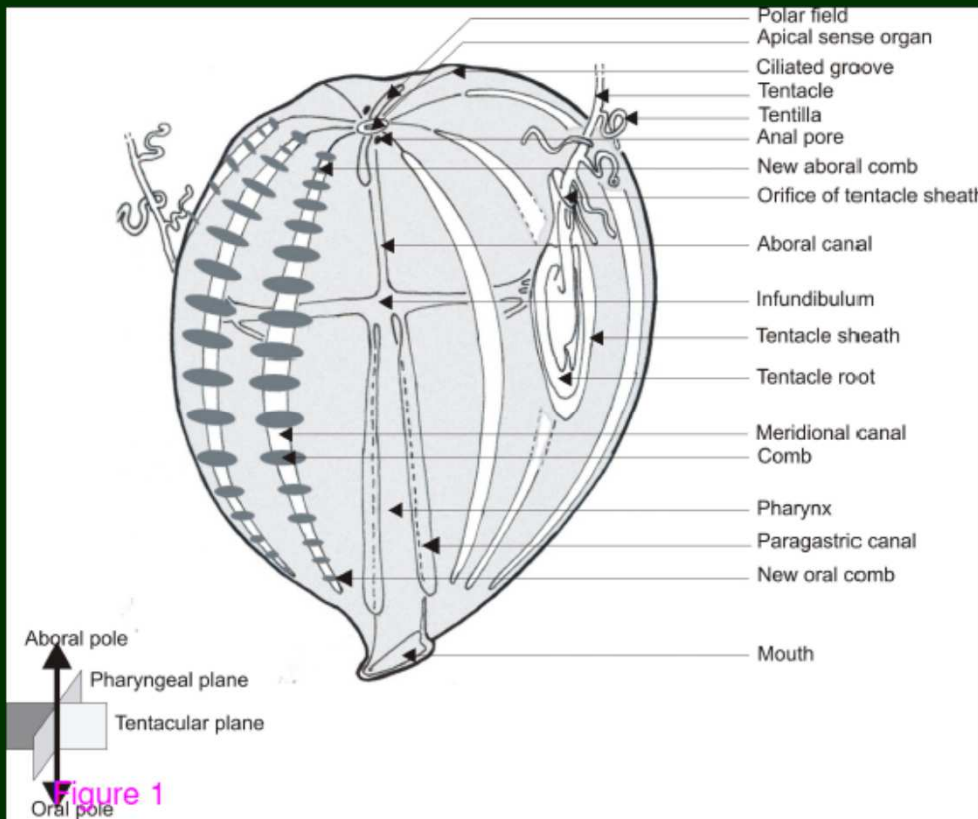


Ctenophora

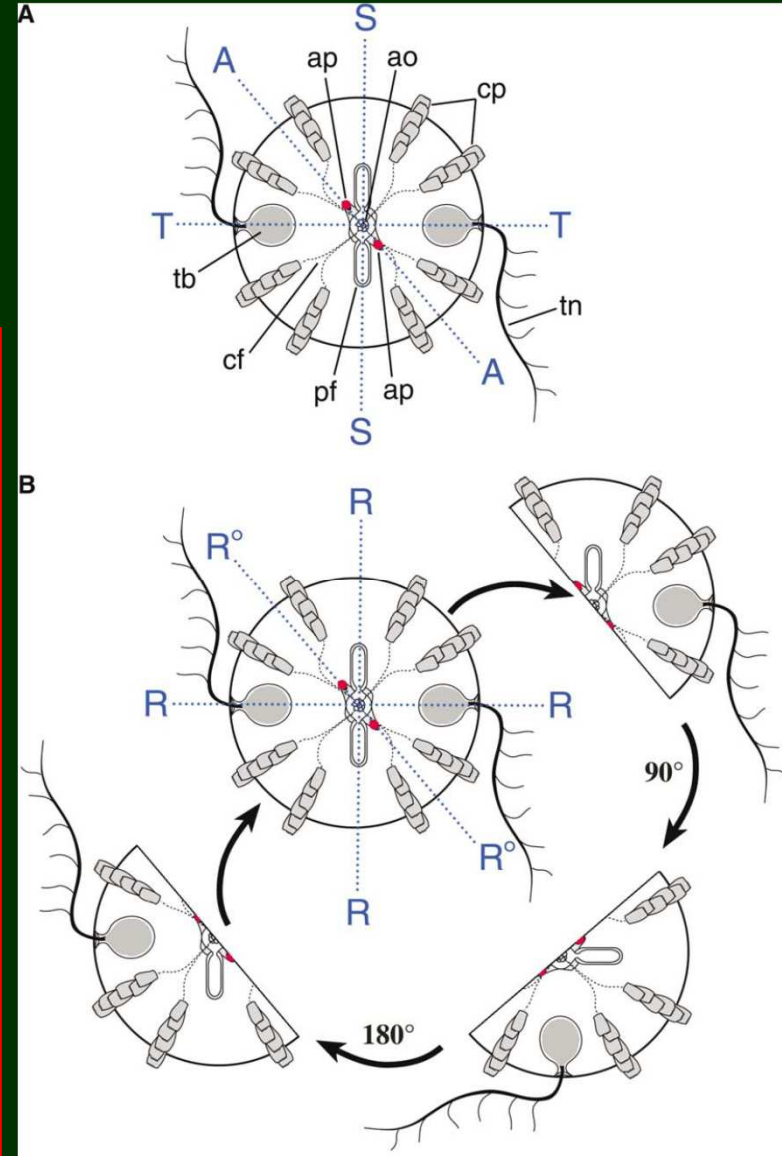
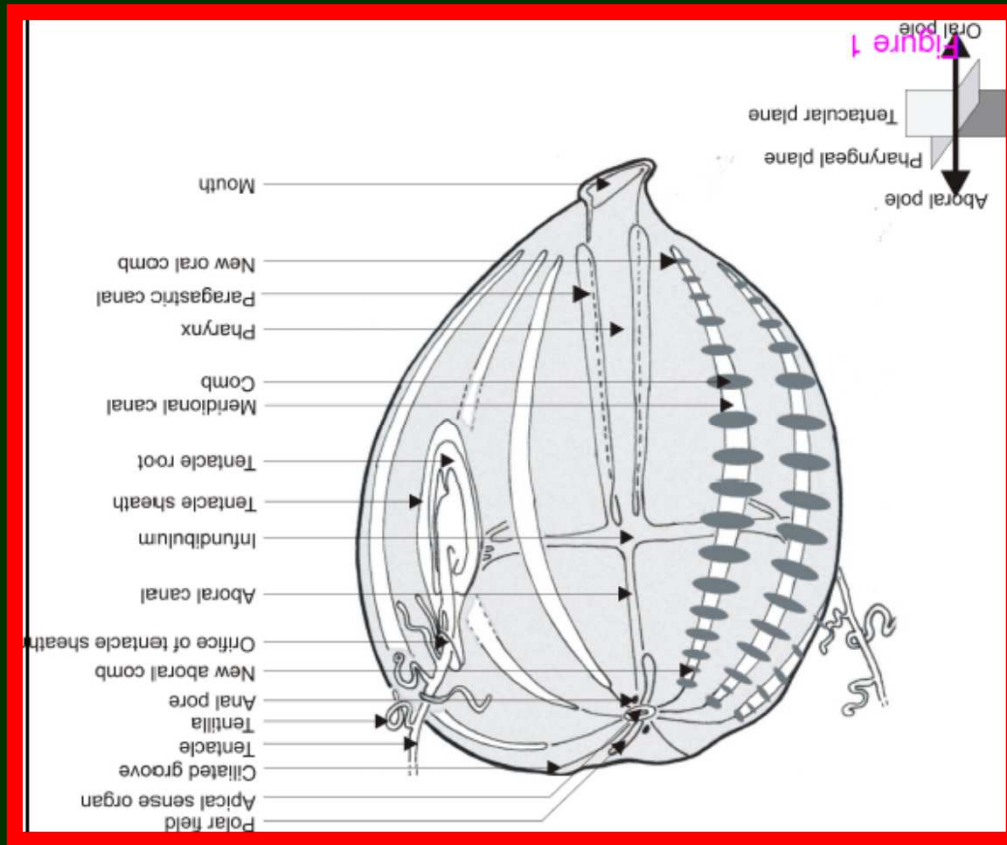




Ctenophora

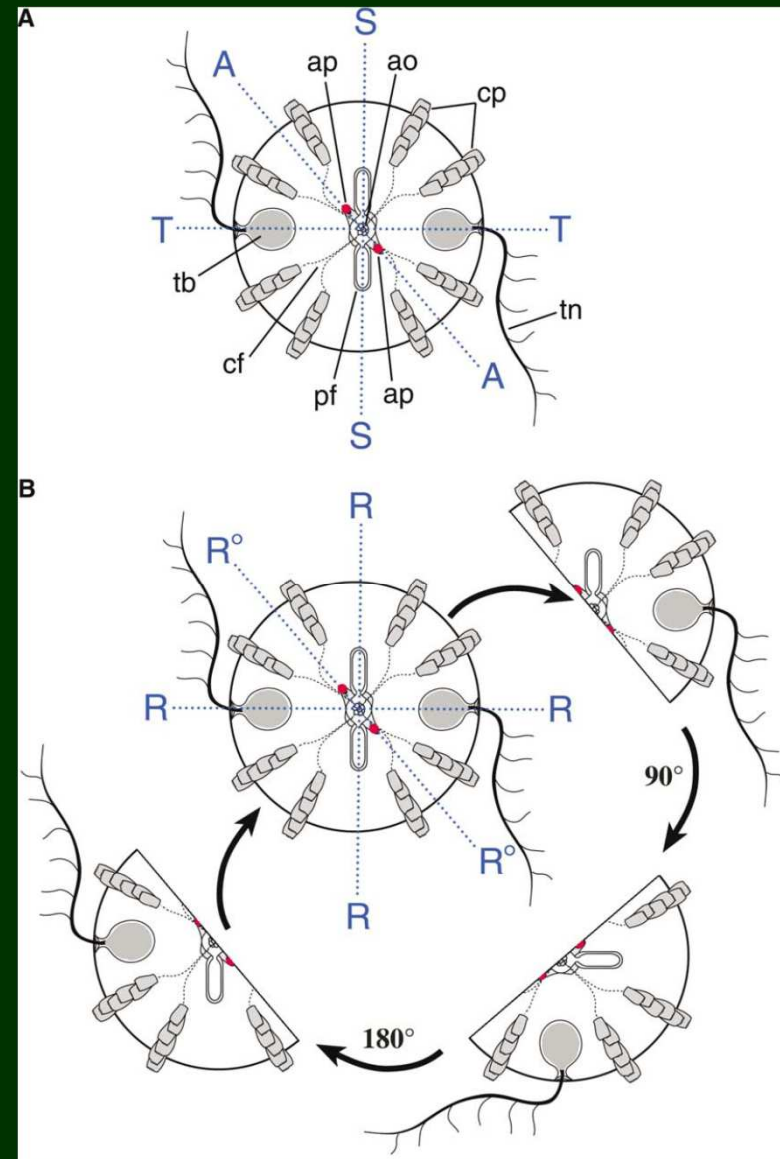


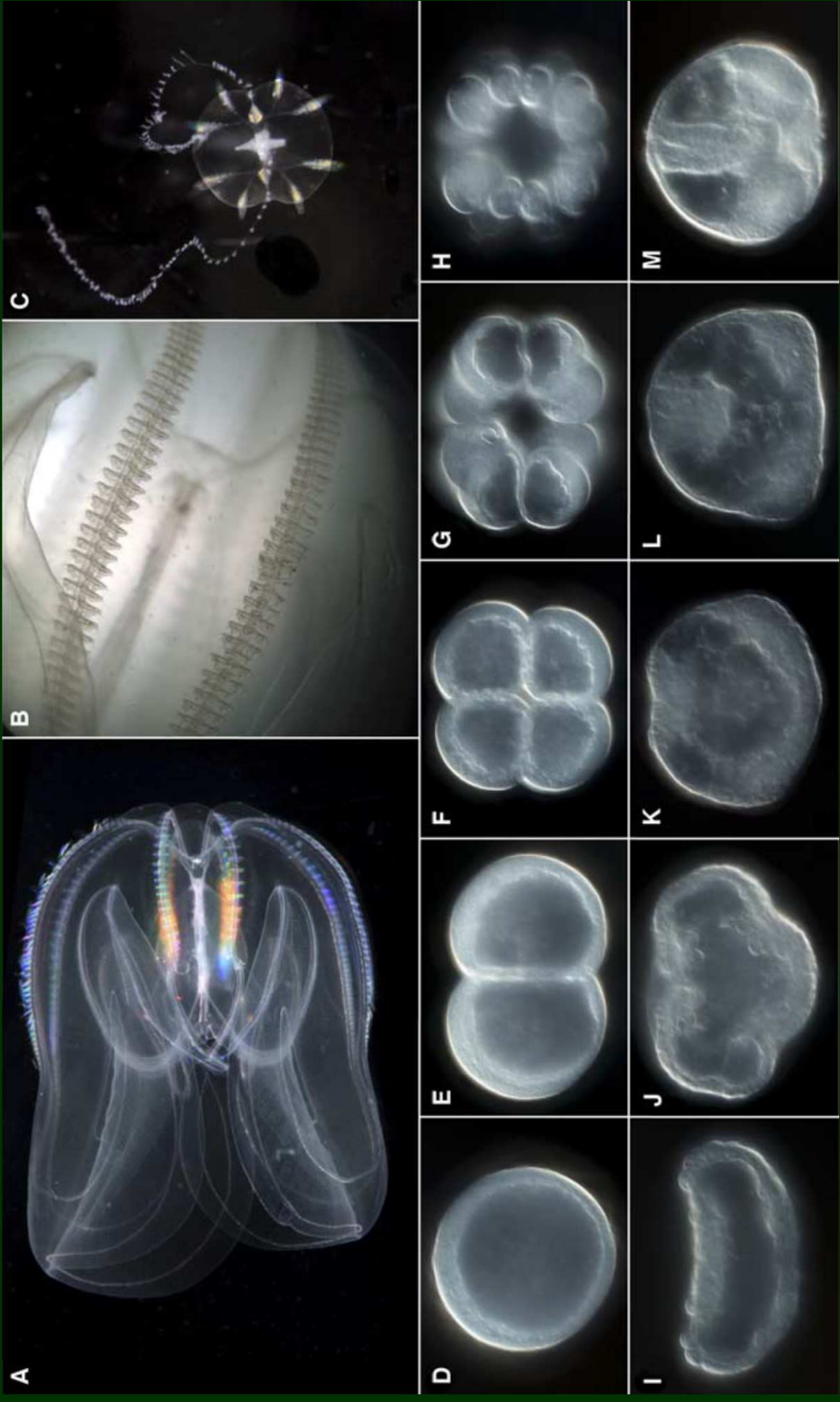
Ctenophora



Ctenophora

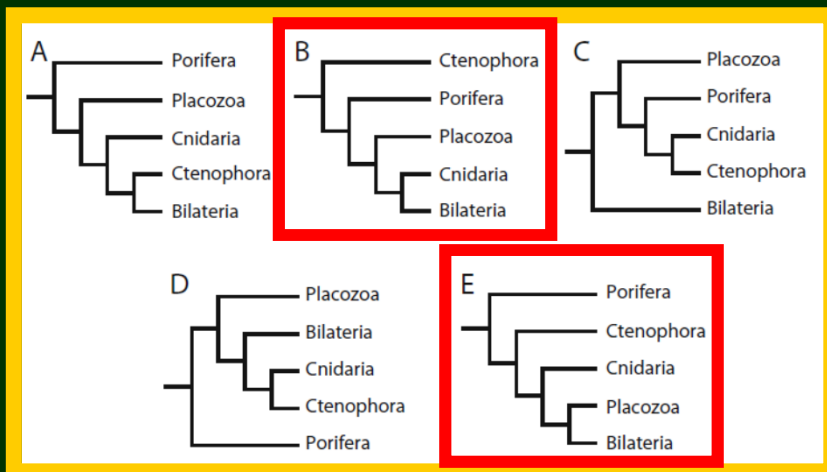
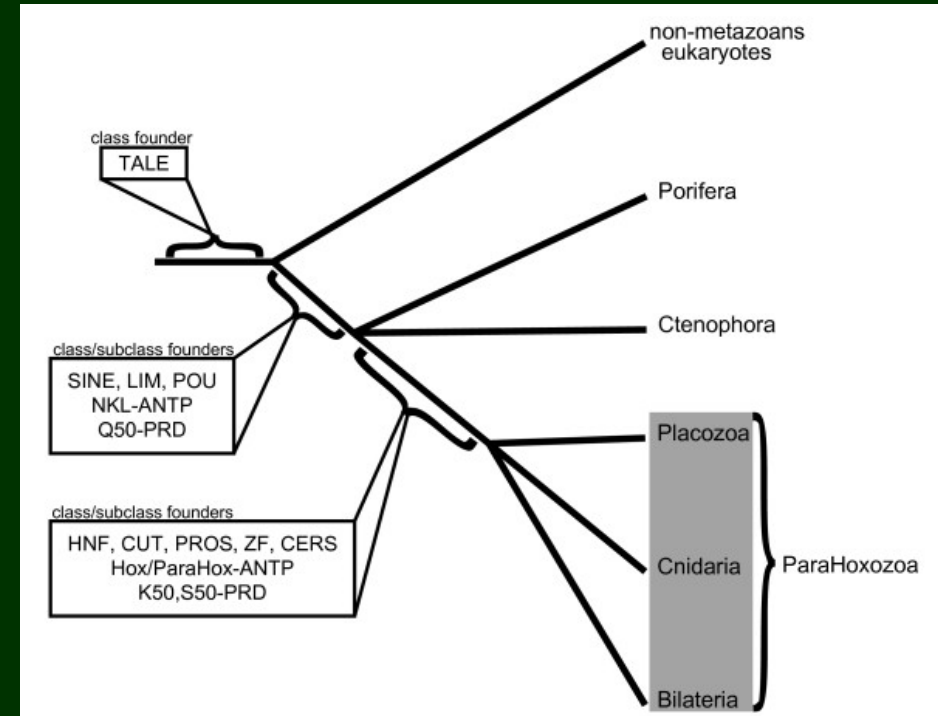
- rotační symetrie – každá plocha procházející orálně-aborální osou dělí zvíře na dvě stejné poloviny, ale otočené o 180°





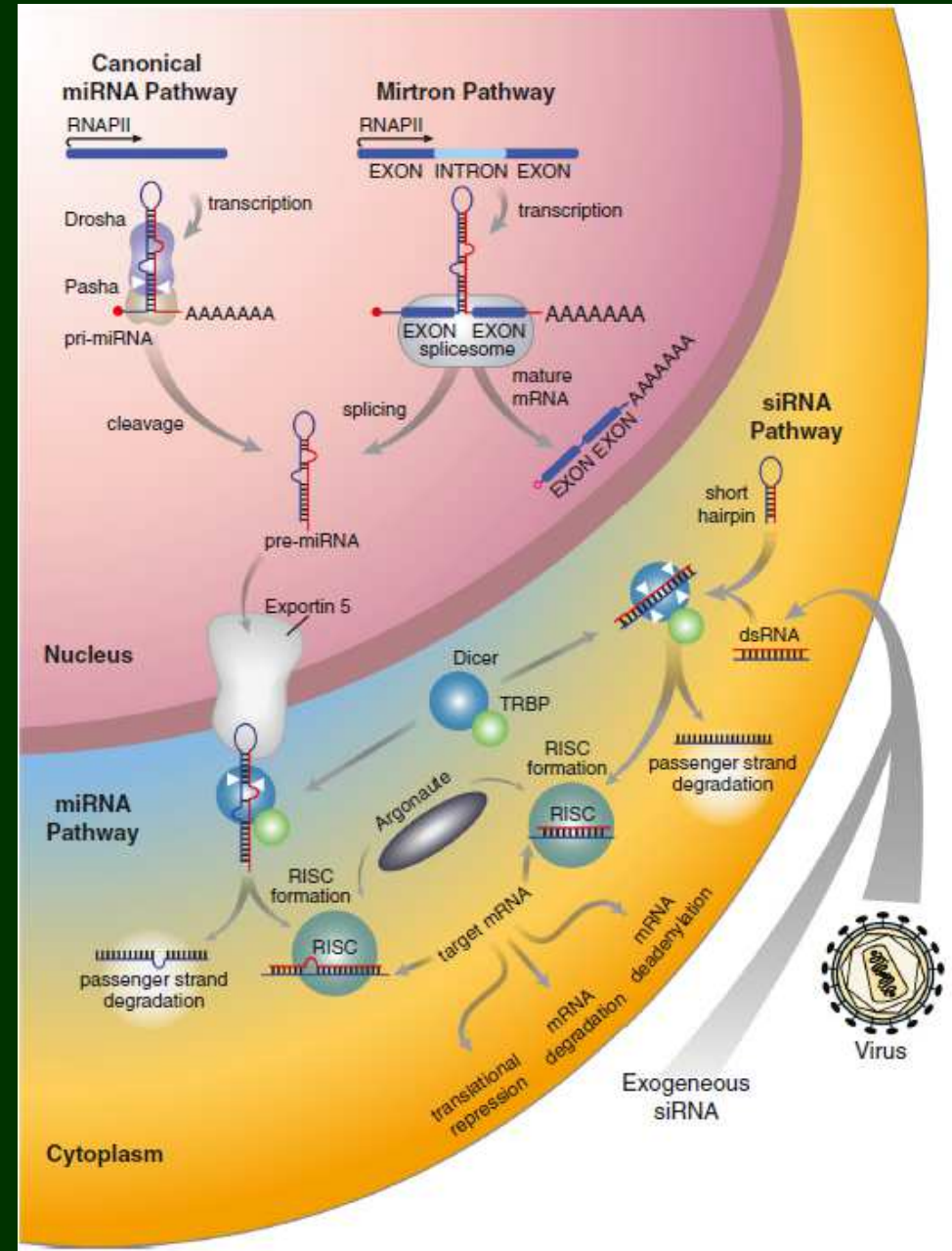
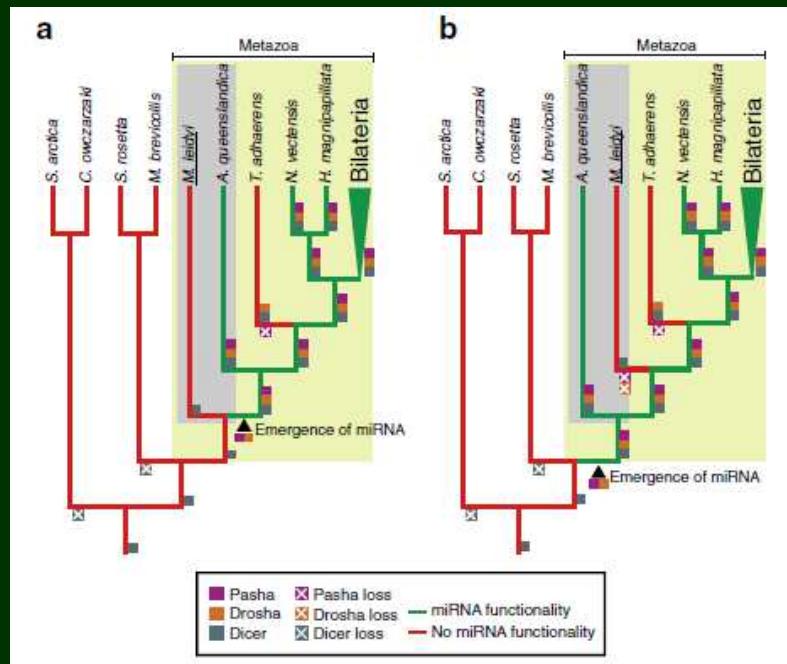
Ctenophora – genom

- nemajú Hox geny, *prd* geny, nukleární receptory se zinc-finger doménami → „**ParaHoxozoa**“ (= Placozoa + Cnidaria + Bilateria)???



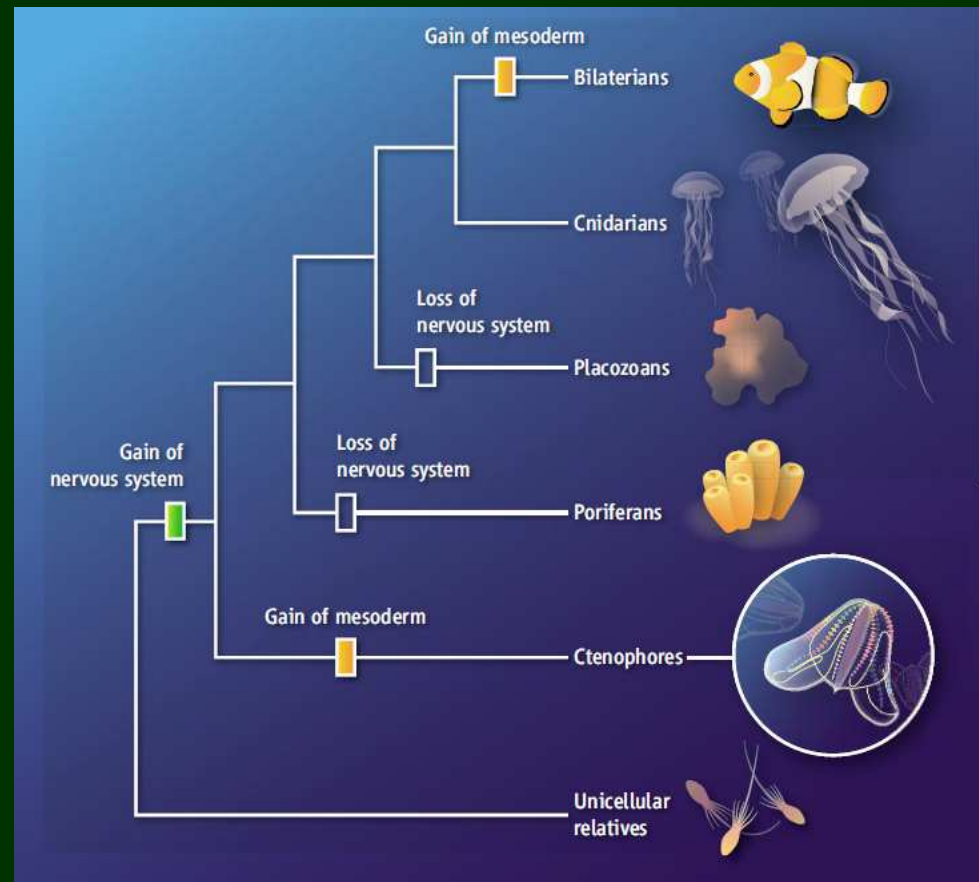
Ctenophora

chybějí geny pro miRNA a příslušnou mašinerii



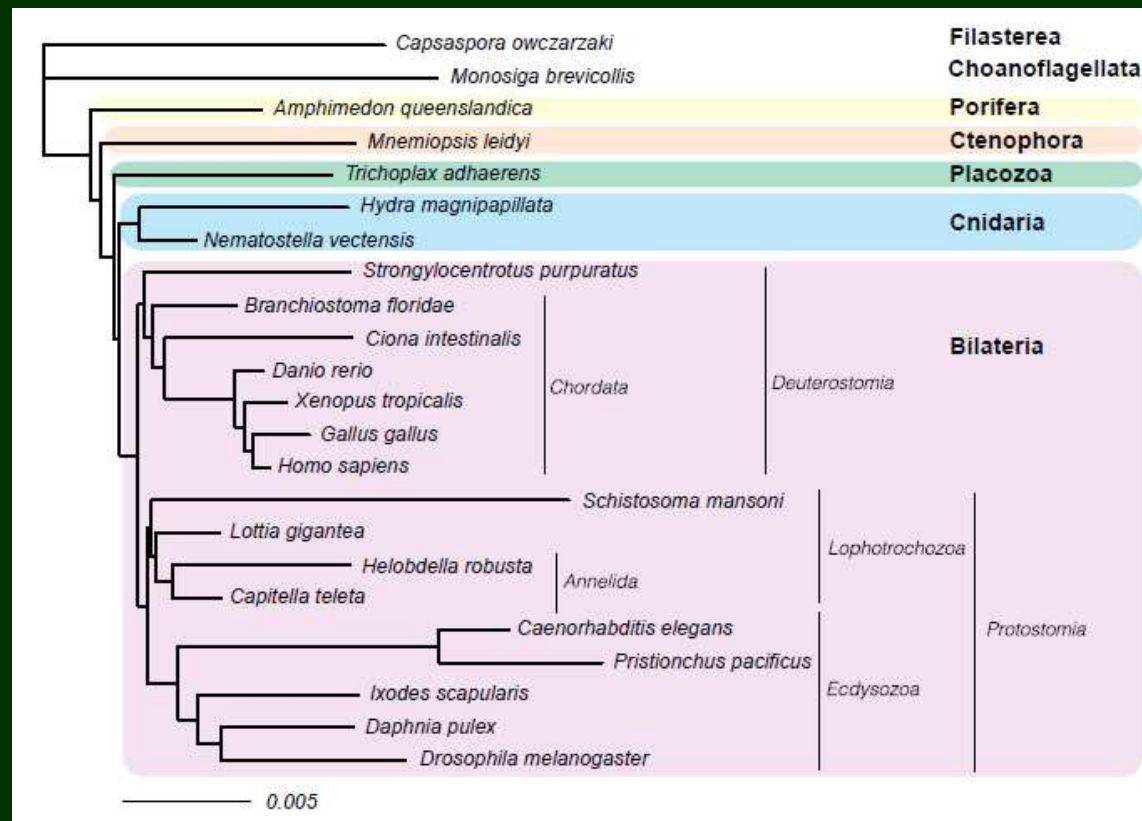
Genom žebernatek (2014)

- sdílená
prezence/absence
genů pro NS:
Ctenophora ~ Porifera
→ NS u předka
metazoí?
- x nic takového pro
mezodermální geny



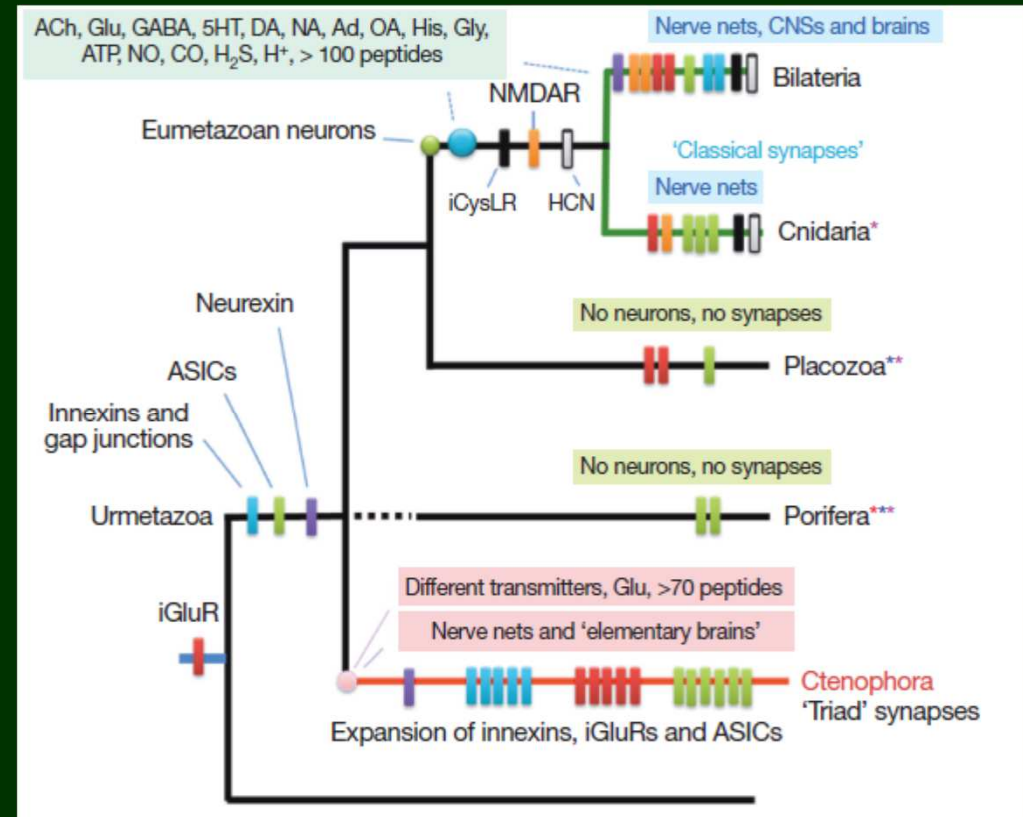
... anebo ne?

- ovšem pozor: i tak je NS buď difyletická, anebo druhotně redukováná u plakozóí



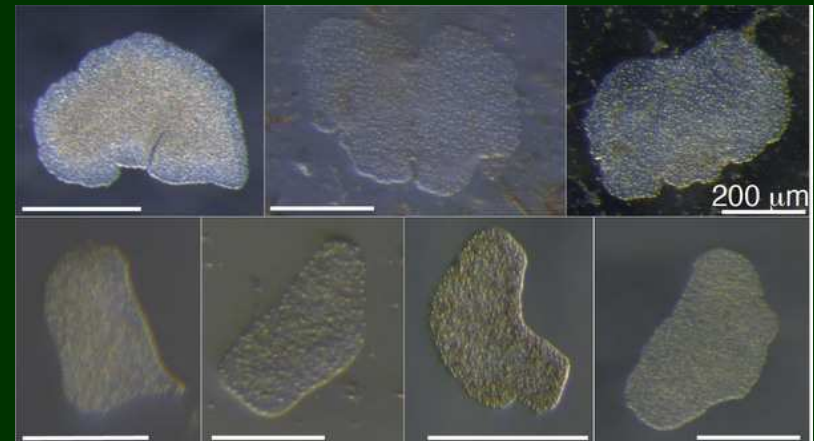
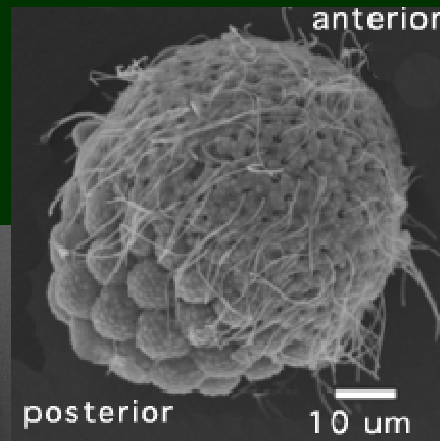
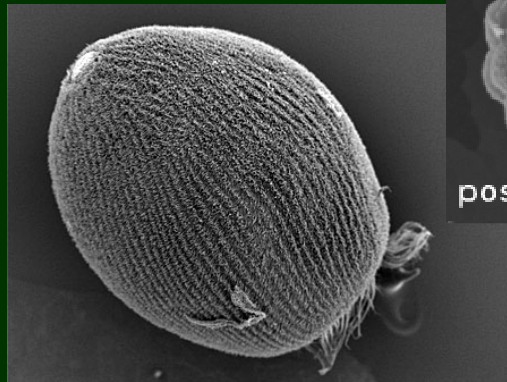
- konvergentní vznik NS?
- mnoho látek (serotonin, acetylcholin, histamin, dopamin, adrenalin, noradrenalin) neužívají jako mezibuněčné posly, chybějí ionotropní receptory
- x transmitery: L-glutamát – výjimečná diverzita glutamátových receptorů i genů pro syntézu a transport glutamátu
- velká diverzita elektrických synapsí
- několik pan-neurálních markerů přítomno (ale neexprimují se v neuronech)
- konvergentní vznik mezodermu a svalů (geny chybějí)

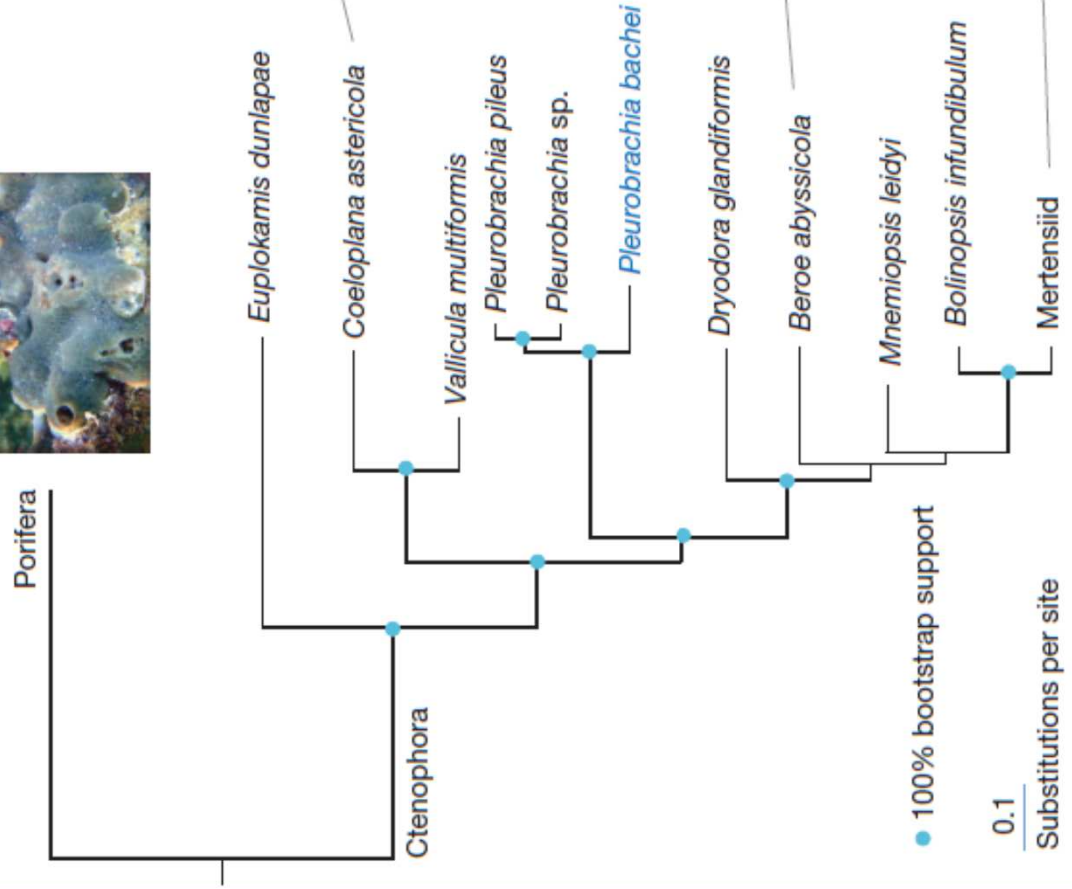
Evolution of metazoans



Zánik nervové soustavy?

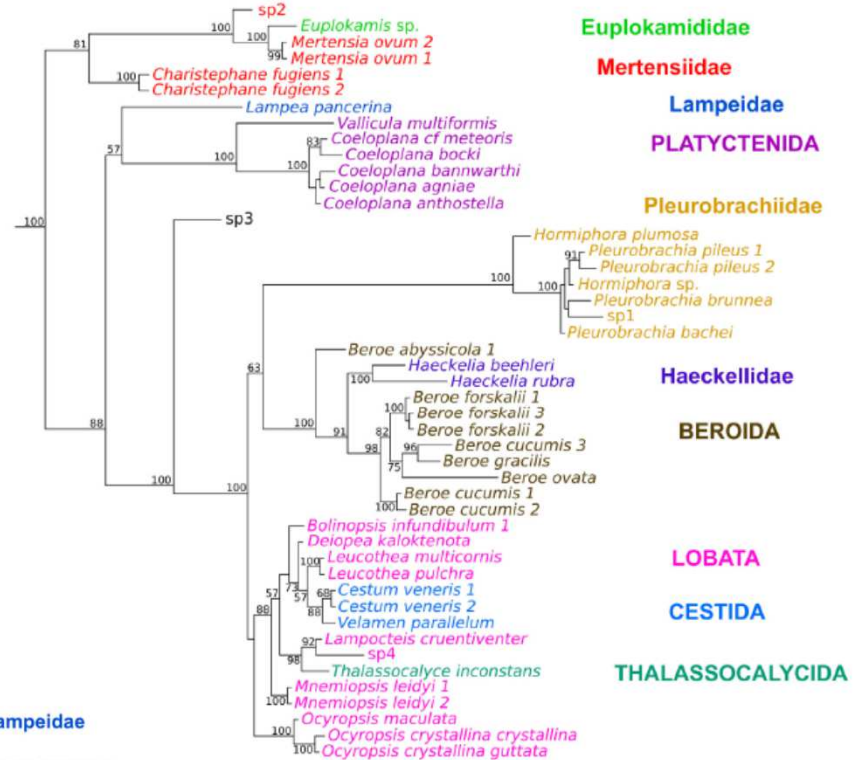
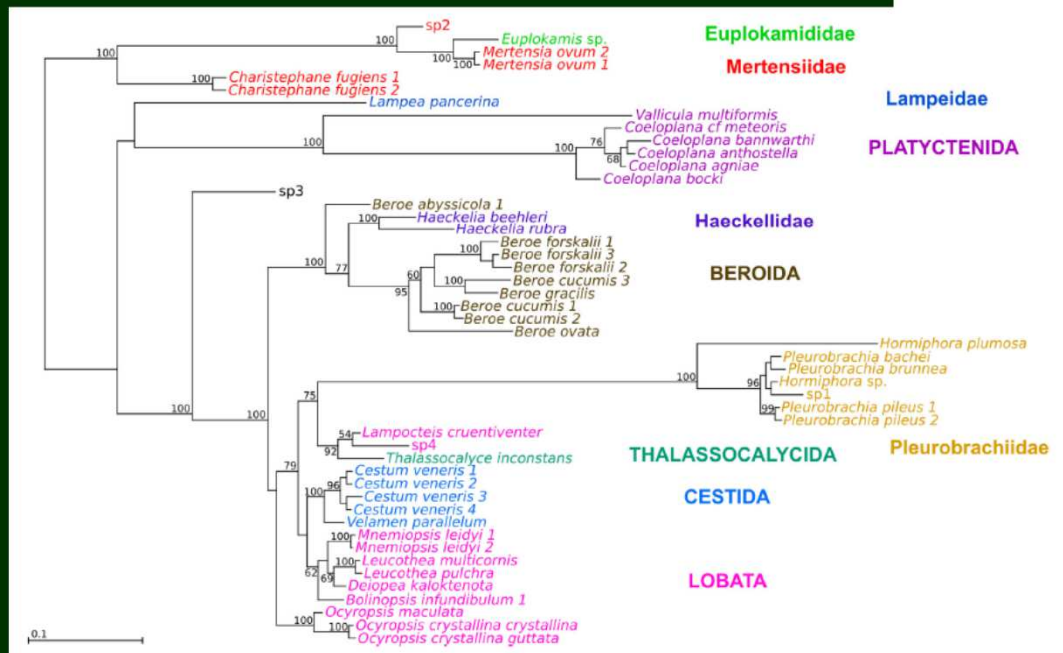
- x Placozoa i Porifera mají aspoň jedno stadium, které se pohybuje aktivním ciliárním pohybem – tj. zánik NS by jim škodil (x Myxozoa, Dicyemida, Rhizocephala)





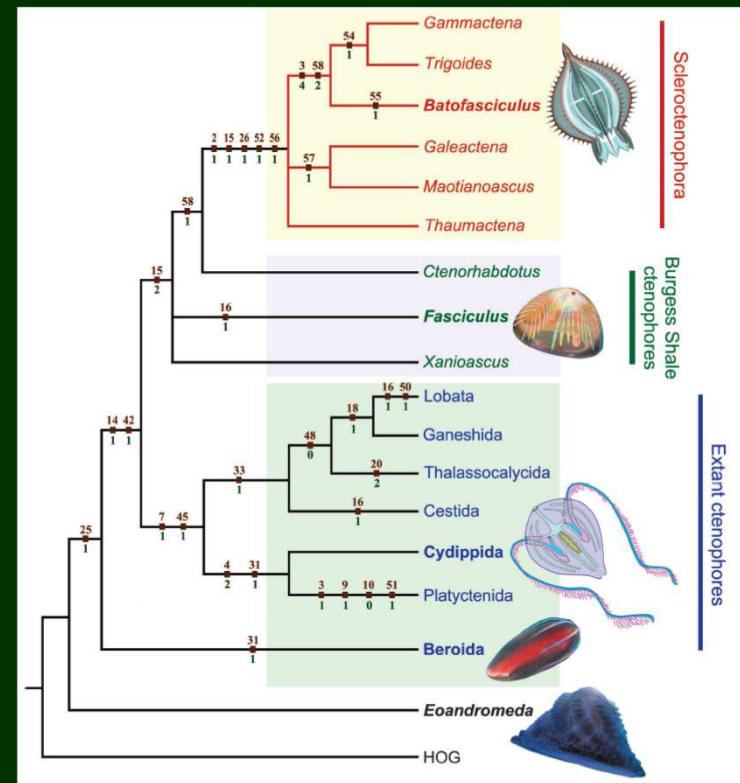
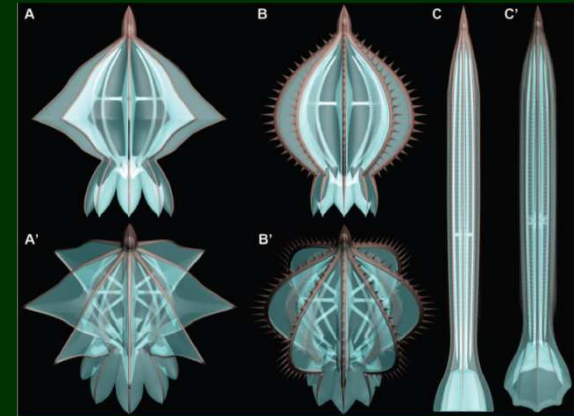
Fylogeneze žebnatek

18S x 18S + ITS1-5.8S-ITS2

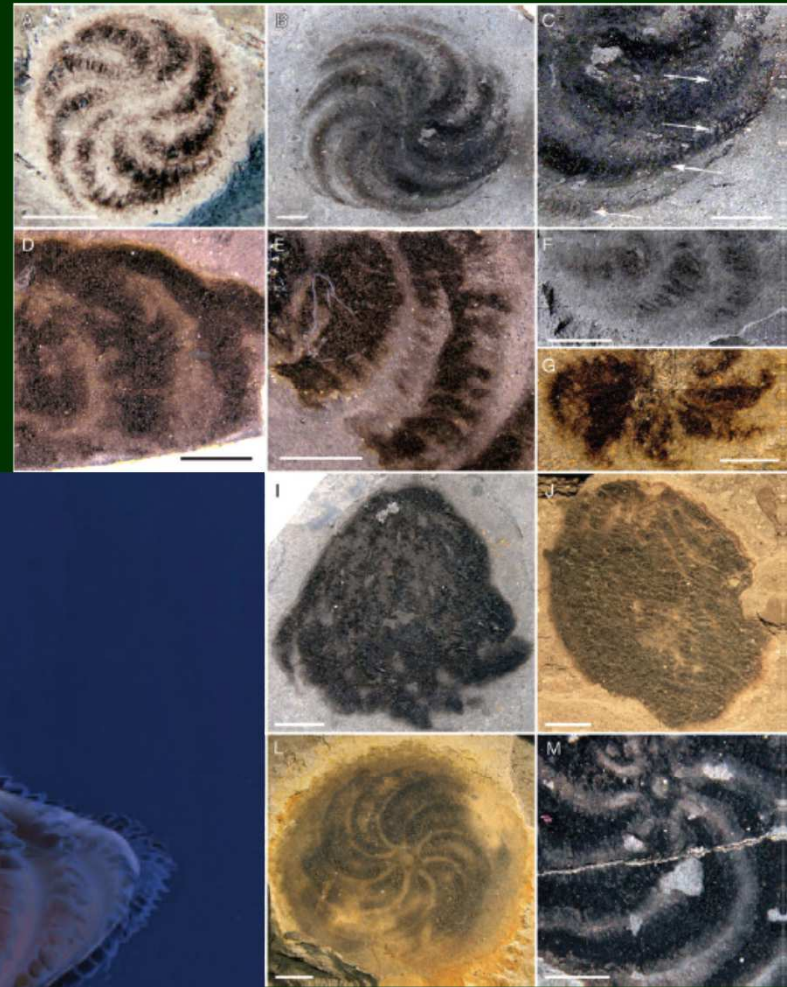


Scleroctenophora

- Chengjiang: kambrijské rody *Gemmactena* (A), *Thaumactena* (C), *Galeactena* a *Batofasciculus* (B)
- skelet, bez chapadel, radiální symetrie
- funkce a složení skeletu neznámé
- skelet patrně ektodermální – buď pod nebo uvnitř epidermis, anebo epidermální exkrece (~ periderm/ perisark většiny korálů)

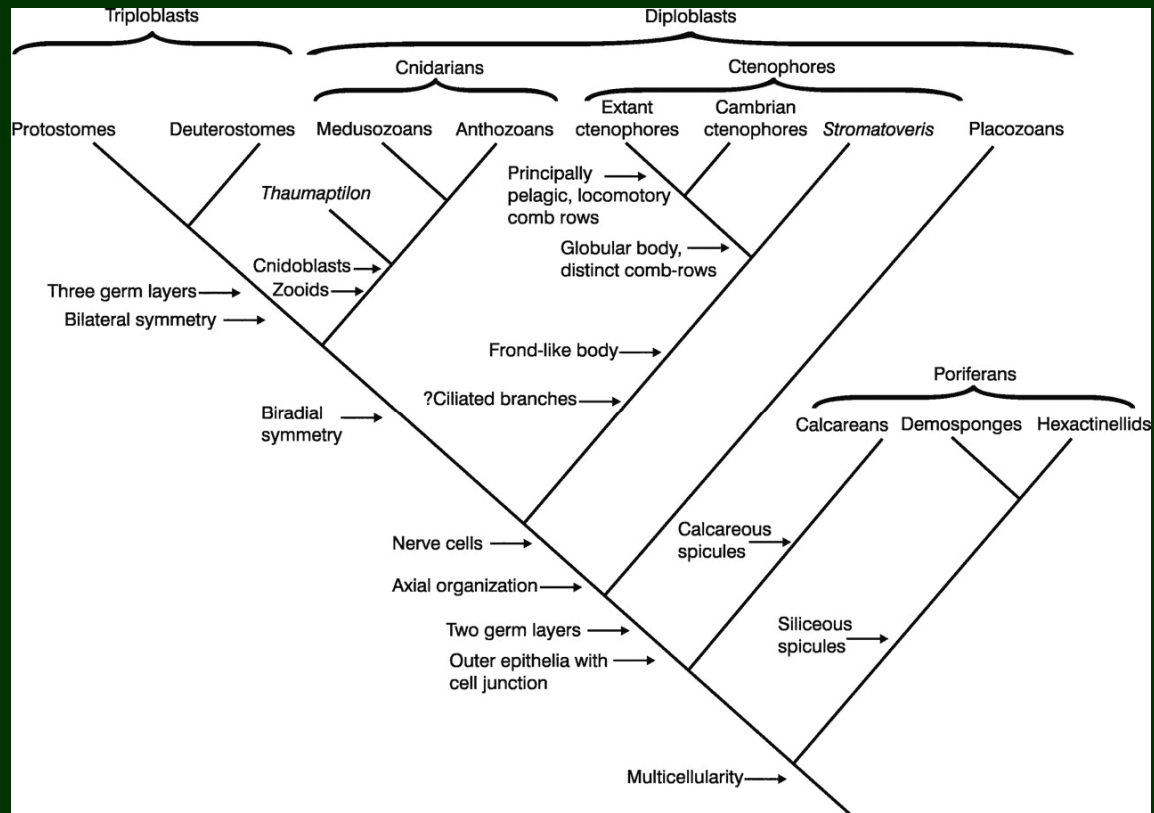


Eoandromeda (ediakara)



Stromatoveris

- kambrijský „vendobiont“
- příbuzný žebnatkám?



Trilobozoa

- ediakarská skupina
příbuzná
žebnatkám???



Porifera

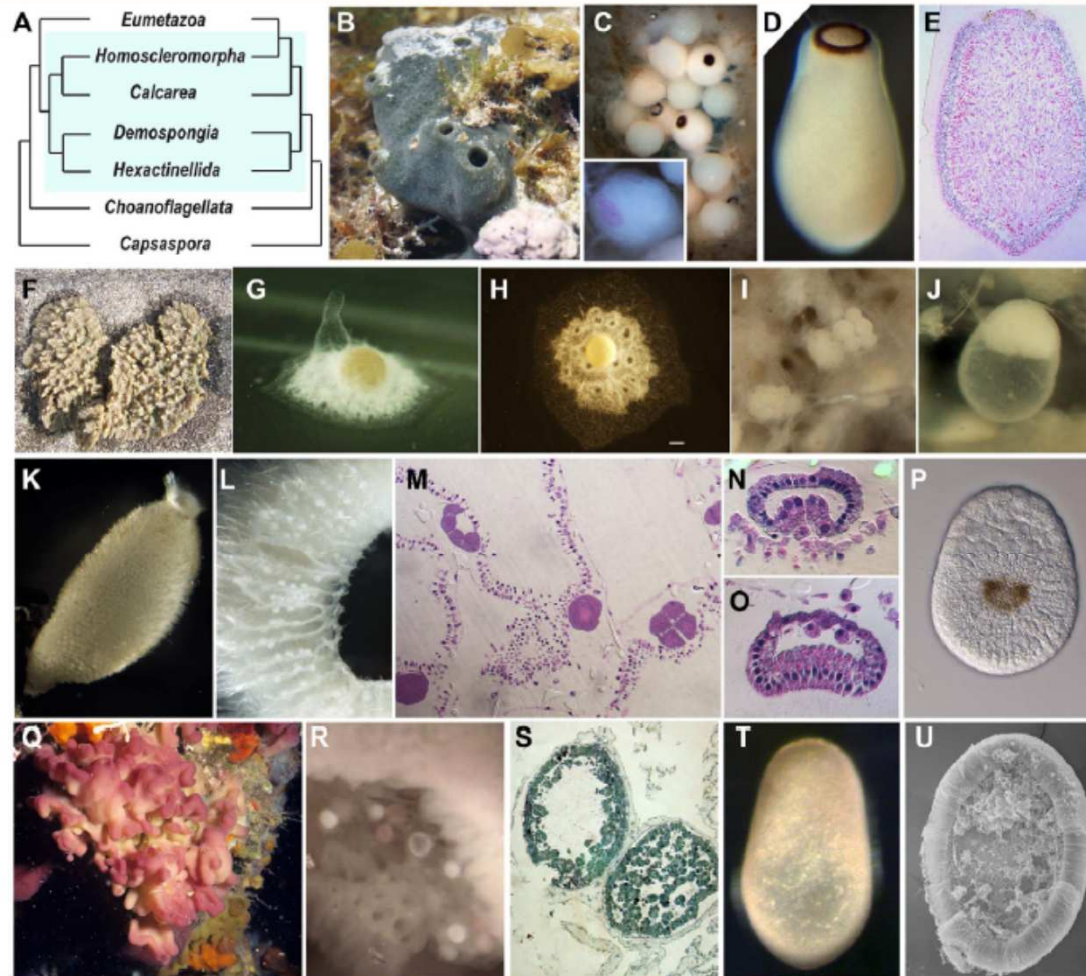
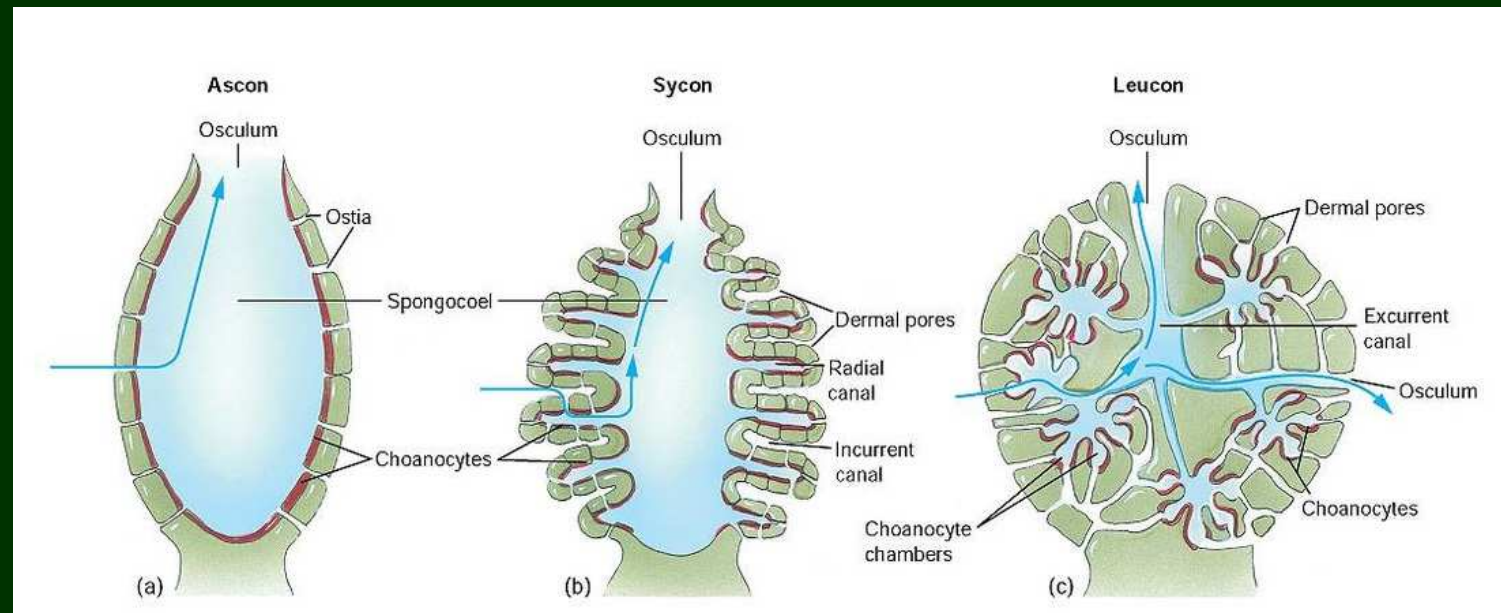
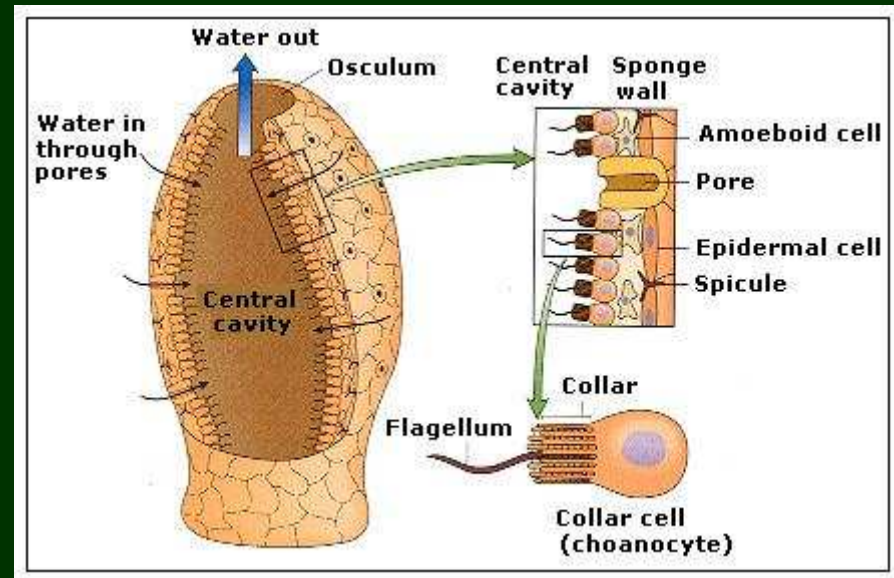


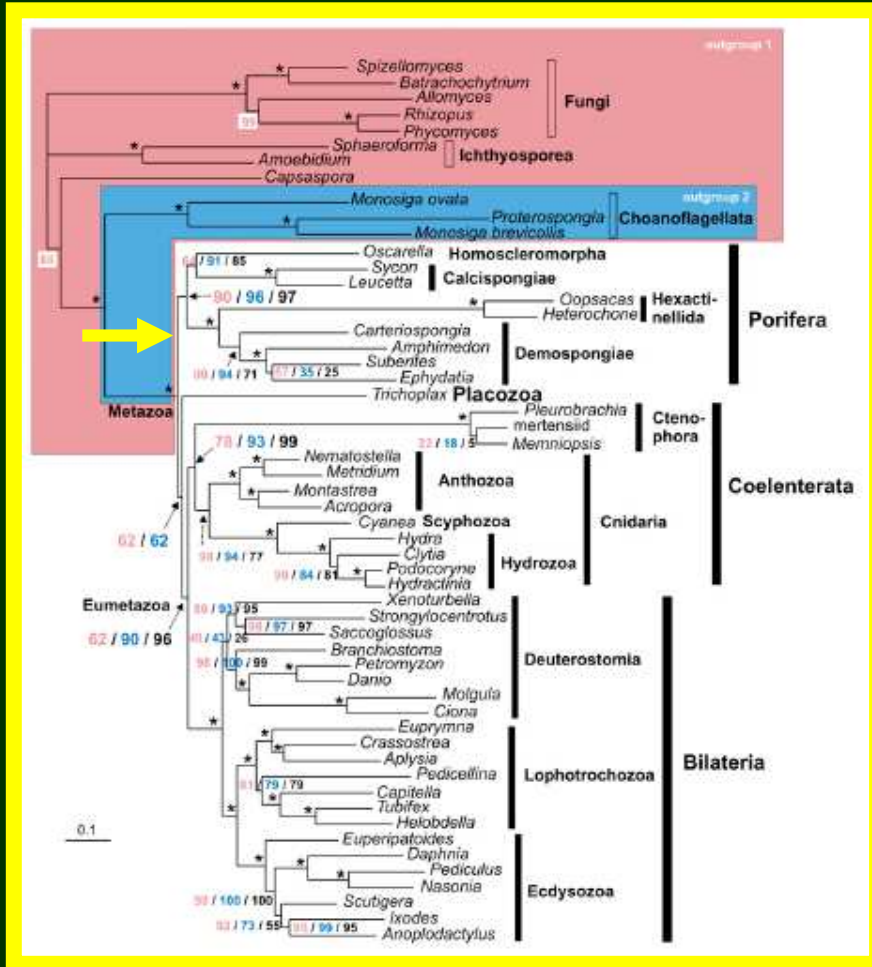
Fig. 2. (A) Two scenarios of sponge evolution: sponge monophyly on the left and sponge paraphyly on the right. (B–U) Examples of model sponges. (B–J) Demosponges: *Amphimedon queenslandica* (B–E) and *Ephydatta fluviatilis* (F–J); (K–P) a calcareous sponge: *Sycon ciliatum*; (Q–U) a homoscleromorph: *Oscarella lobularis*. (B, F, K, Q) Live adult specimens; (G, H) live gemmule-hatched juveniles (side and top view); (C, I, L, R) live embryos in situ; (D, J, P, T) live larvae; (M–O, S) histological sections of tissues with developing embryos; (E) histological section of a larva; (U) scanning electron microscopy image of a larva. Photo credits: M. Adamski (B), G. Richards (E), N. Funayama (F–J) and A. Ereskovsky (Q–U).

Porifera

- velmi podivný a jiným živočichům nepodobný tělní plán
- „něco mezi kolonií a tělem“

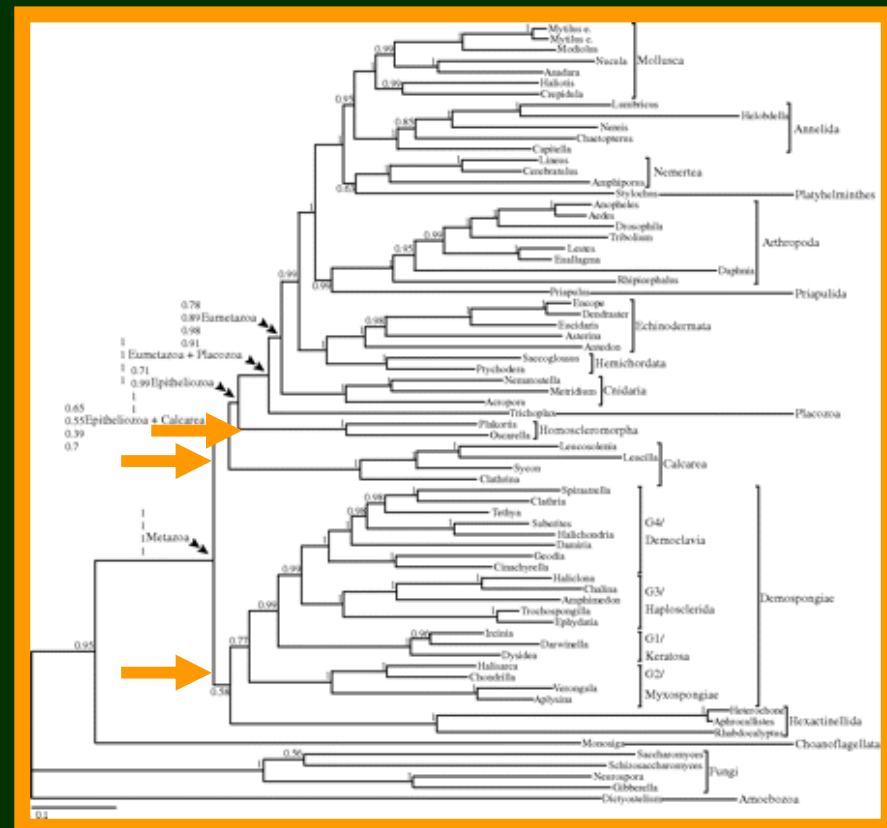


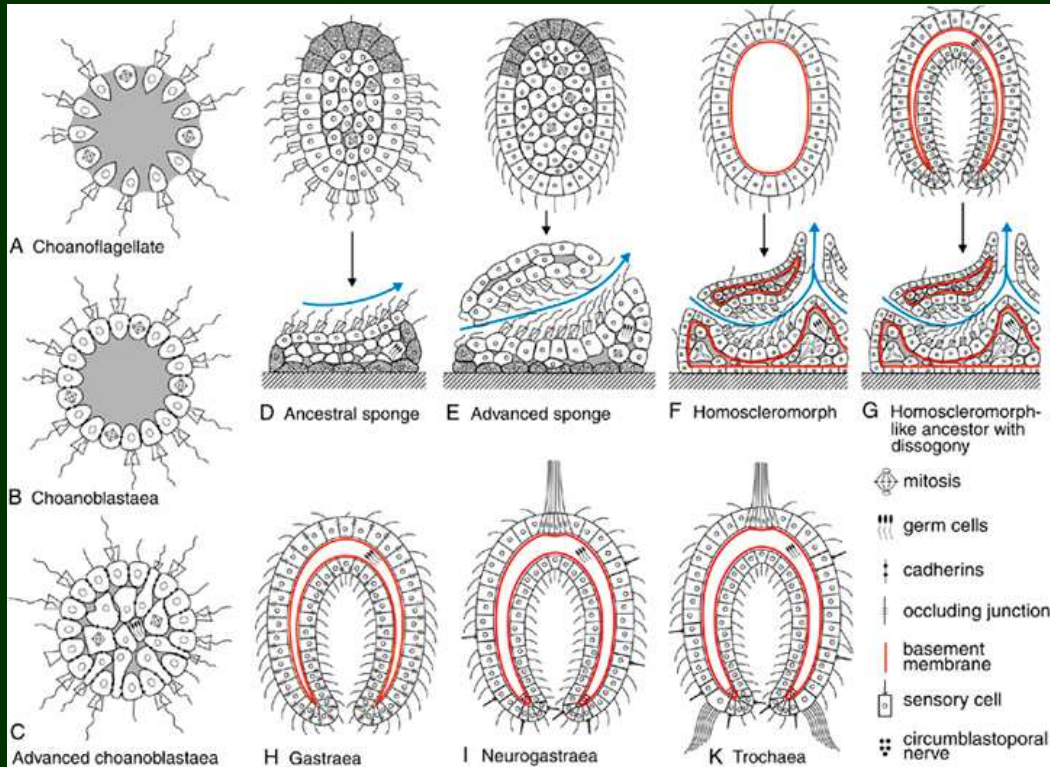
Monofylie nebo parafylie?



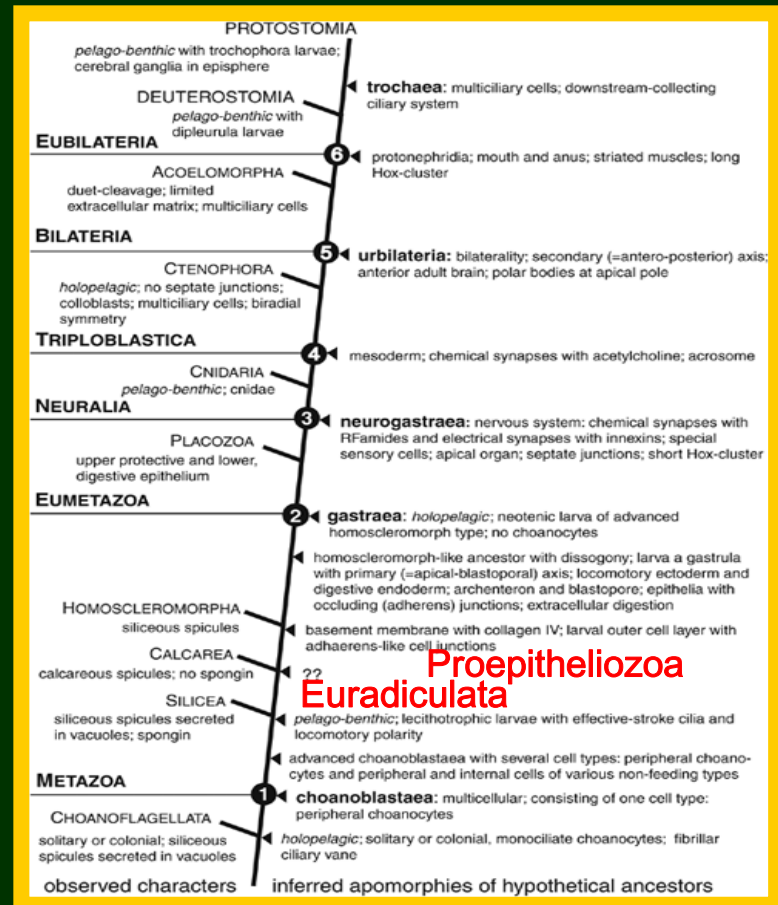
128 genů

7 housekeeping genů





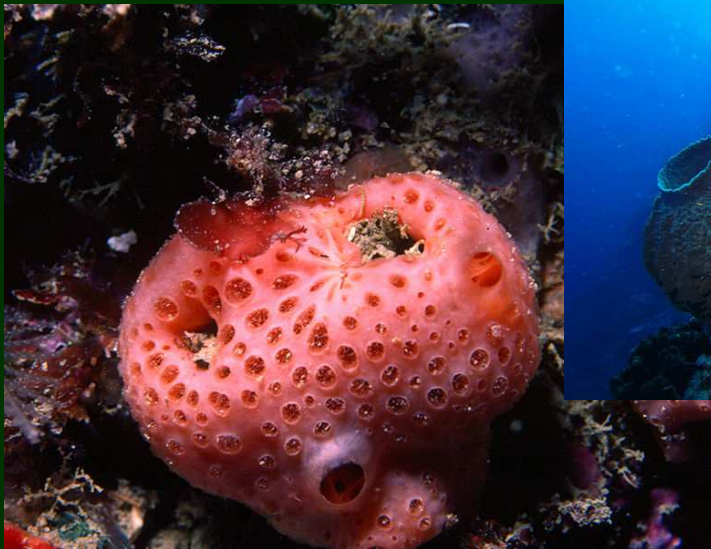
Parafylie houbovců – Epitheliozoa v novém smyslu?



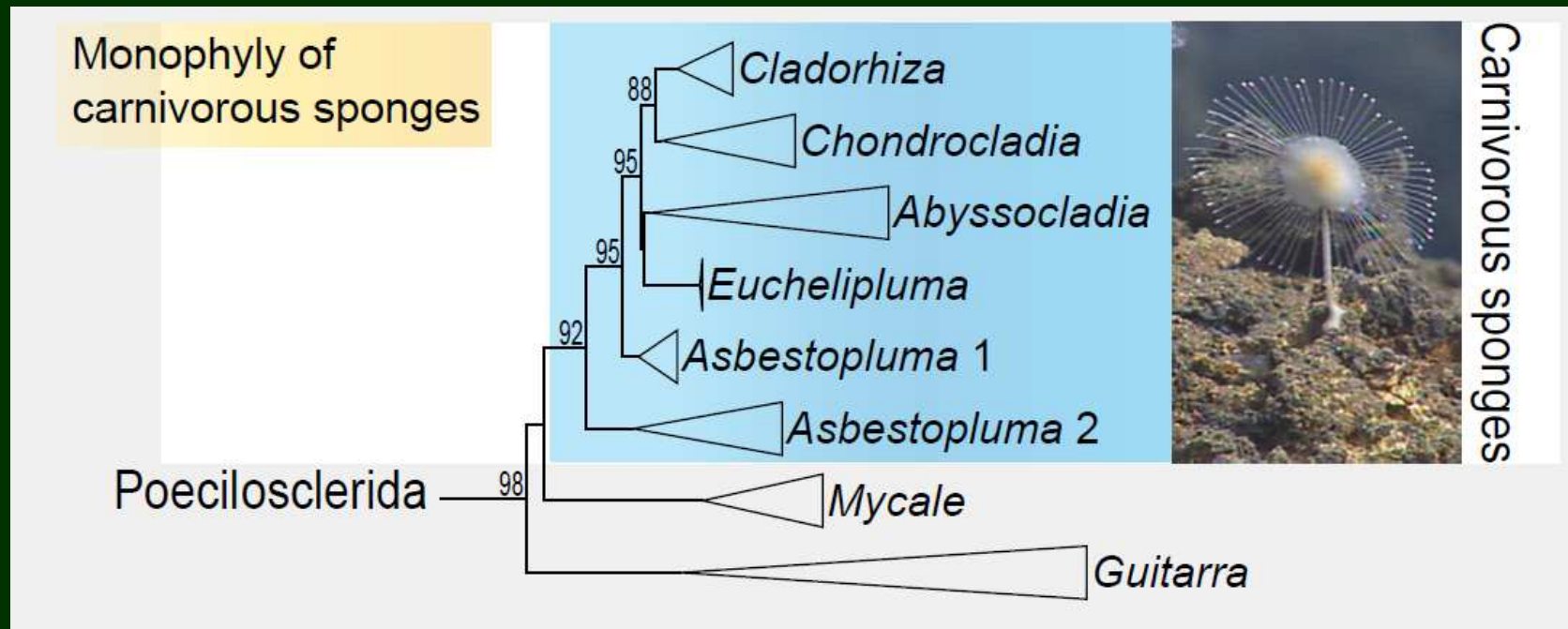
Author	Molecular marker	Inference method (Model)	Sponge lineages included (number of taxa)					Bilateria included	Monophyly, support	Paraphyly, support
			Demospongiae	Homoscleromorpha	Hexactinellida	Calcarea				
Lafay <i>et al.</i> (1992)	Partial 28S rDNA	NJ, MP, ML	9	-	-	2	No		Yes, high	
Cavaller-Smith <i>et al.</i> (1996)	18S rDNA	NJ, MP, ML	4	-	1	3	Yes		Yes, low	
Van de Peer and de Wachter (1997)	18S rDNA (secondary structure)	Distance	2	-	-	2	Yes		Yes, low (BS 67)	
Zrzavy <i>et al.</i> (1998)	18S rDNA	MP	3	-	-	3	Yes		Yes, low	
Collins (1998)	18S rDNA	MP, ME, ML	5	1	1	3	Yes		Yes, low	
Kruse <i>et al.</i> (1998)	cPKC	NJ	2	-	1	1	Yes		Yes, low	
Schütze <i>et al.</i> (1999)	Hsp70, cPKC, calmodulin, tubulin	NJ	2	-	1	1	Yes		Only with Hsp70 and cPKC, low	
Kim <i>et al.</i> (1999)	18S rDNA	MP, ME, ML	3	-	-	3	Yes	Unresolved	Unresolved	
Adams <i>et al.</i> (1999)	18S rDNA (secondary structure)	MP, ME, ML	7	-	2	4	No		Yes, low	
Medina <i>et al.</i> (2001)	18S rDNA, 28S rDNA	ML with KH tests	2	-	1	1	Yes		Equivocal	
Peterson and Eernisse (2001)	18S rDNA	MP	8	-	2	4	Yes		Yes, low	
Rokas <i>et al.</i> (2003)	a-tubulin, b-tubulin, EF-2, HSP90, HSP70	ML	4	-	1	2	Yes		Unresolved	
Manuel <i>et al.</i> (2003)	18S rDNA	MP, ML	9	-	2	17	Yes		Equivocal	
Rokas <i>et al.</i> (2005)	50 genes	ML, MP, BI	1	-	1	1	Yes		Unresolved	
Borchellini <i>et al.</i> (2001)	18S rDNA	NJ, MP	12	-	5	2	No		Yes, high (BS: MP 83/NJ 85)	
Peterson and Butterfield (2005)	Seven nuclear housekeeping genes	MP, ML, distance	3	-	-	2	Yes		Yes, medium (BS 76)	
Peterson <i>et al.</i> (2005)	Seven nuclear housekeeping genes, mtDNA	MP	3	-	-	2	yes		Yes, low (BS 62)	
Sperling <i>et al.</i> (2007)	COI, 18S rDNA	Partitioned BI	9	1	-	2	Yes		Yes, high	
Dohrmann <i>et al.</i> (2008)	housekeeping genes, 18S rDNA, 28S rDNA, 16S rDNA (mt)	Partitioned BI, secondary structure	6	2	32	4	No		Yes, low (PP 0.6/0.7, BS 74)	
Dohrmann <i>et al.</i> (2009)	18S rDNA, 28S rDNA, 16S rDNA (mt)	Partitioned BI, secondary structure	6	2	43	4	No		Yes, low-moderate (PP 0.59/0.84)	
Sperling <i>et al.</i> (2009)	Seven nuclear housekeeping genes	BI (CAT-GTR)	20	2	3	4	Yes		Yes, low (PP 0.65/0.71)	
Sperling <i>et al.</i> (2010)	Seven nuclear housekeeping genes	BI (CAT-GTR)	20	2	3	5	Yes		Yes, moderate to low (PP 0.92/0.75)	
Philippe <i>et al.</i> (2009)	128 genes	BI (CAT)	4	1	2	2	Yes		Yes, high (Bayesian BS 96)	
Pick <i>et al.</i> (2010)	150 genes	BI (CAT)	6	2	3	2	Yes		Yes, moderate (PP 0.91)	
Erwin <i>et al.</i> (2011)	Seven nuclear housekeeping genes, 18S rDNA, 28S rDNA	Partitioned BI (GTR)	14	2	-	5	Yes		Yes, high	

Silicea (= Silicispongia)

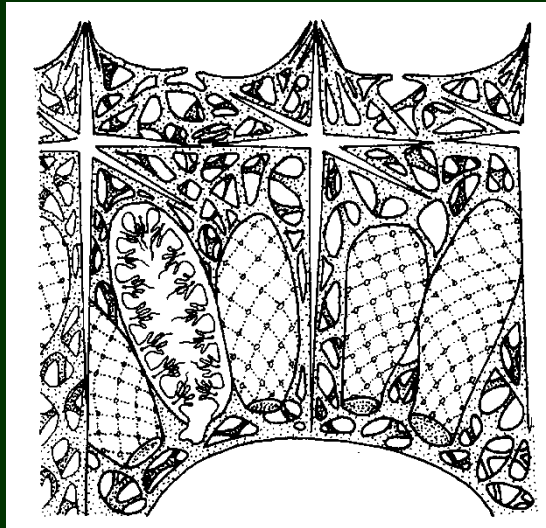
- monofyletická skupina
- Demospongia
- Hexactinellida



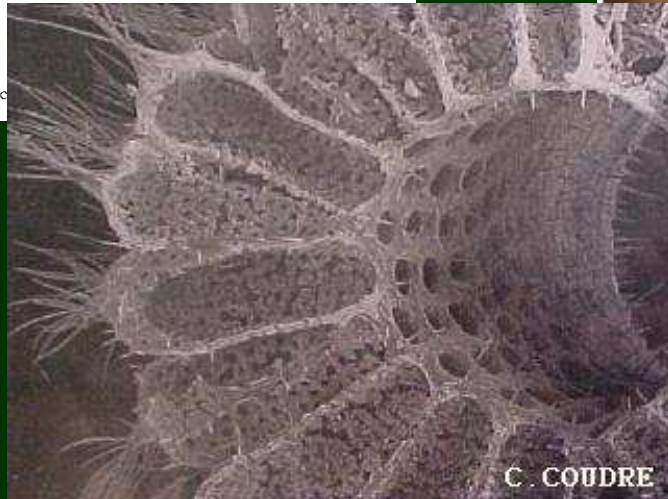
Karnivorní houbovci (Demospongia)



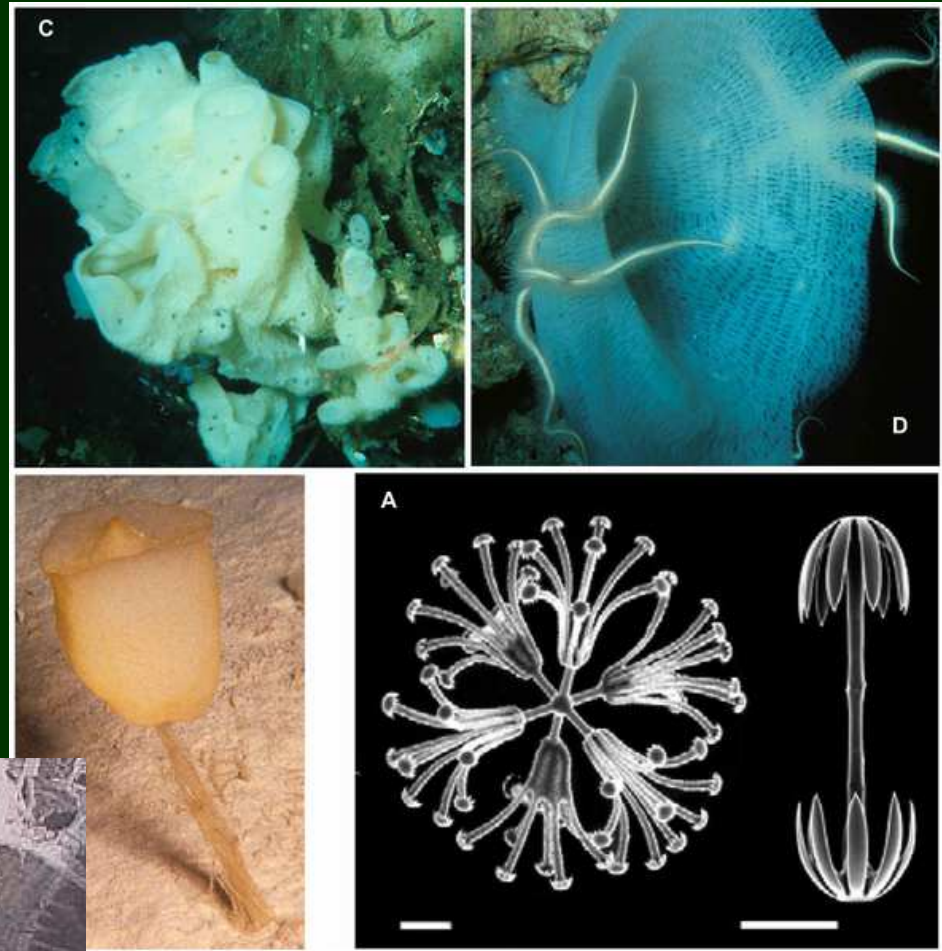
Hexactinellida



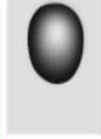
Livingstone, ? BIODIDAC



C. COUDRE



A



Oocyte

B



2-cell Stage

Equal holoblastic cleavage

C



4-cell Stage

equatorial cleavage plane

rotational cleavage

or

or

Start of cleavage plane

Start of cleavage plane

D



6-cell Stage

Start of asynchronous divisions

E



8-cell Stage

radial cleavage

spiral cleavage

or

or

radial cleavage

radial cleavage

F



Blastula

Unequal cleavage results in smaller micromeres that are wedged between the larger macromeres. Cilia begin to differentiate on some micromeres.

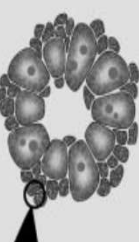
plugged junction

plugged junction

plugged junction

plugged junction

Cytoplasmic bridges, with proteinaceous plugged junctions, form between micromeres.

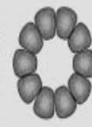


G



16 to 32-cell Blastula

Blastomeres are uniformly sized and tenuously held together by filopodia at their surfaces



cross section



lateral view

H



Gastrula

Micromeres are produced at the periphery and macromeres, which remain more central, gradually fill in the blastocoel. Macromeres start to fuse with each other. Epithelium starts to develop.

Plugged junctions form between micromeres and macromeres.

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I



Early Larval Development

The macromeres, extending around the micromeres, fuse with each other to form a single giant syncytium that completely envelops the micromeres and forms a continuous epithelial membrane.

Sclerocytes and multiciliated cells differentiate from micromeres.

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Spicules start to form within sclerocytes.

multiciliated cell

multiciliated cell

multiciliated cell

multiciliated cell

multiciliated cell

multiciliated cell

multiciliated cell

multiciliated cell

multiciliated cell

multiciliated cell

multiciliated cell

multiciliated cell

multiciliated cell

multiciliated cell

J



Elongation of Larva

As the larva elongates it polarizes with lipid inclusions towards the anterior pole and sclerocytes towards the posterior. In the middle, the cilia of the multiciliated cells pierce the covering syncytium to form a broad "skirt" around the "waist" of the larva.

lipid

lipid

lipid

lipid

lipid

lipid

lipid

lipid

lipid

lipid

lipid

lipid

choanocyte

choanocyte

choanocyte

choanocyte

choanocyte

choanocyte

choanocyte

choanocyte

choanocyte

choanocyte

choanocyte

choanocyte

Internally, micromeres differentiate into choanocytes, which form early central flagellated chambers. The single collar-and-flagellum structure of each choanocyte branches to form several of these structures per cell.

trabecular reticulum

trabecular reticulum

trabecular reticulum

trabecular reticulum

trabecular reticulum

trabecular reticulum

trabecular reticulum

trabecular reticulum

trabecular reticulum

trabecular reticulum

trabecular reticulum

As the sclerocytes elongate to envelop each developing spicule, they become multinucleated. Each sclerocyte connects to the syncytium by cytoplasmic bridges. As the spicules grow, they develop points under the syncytial epithelium.

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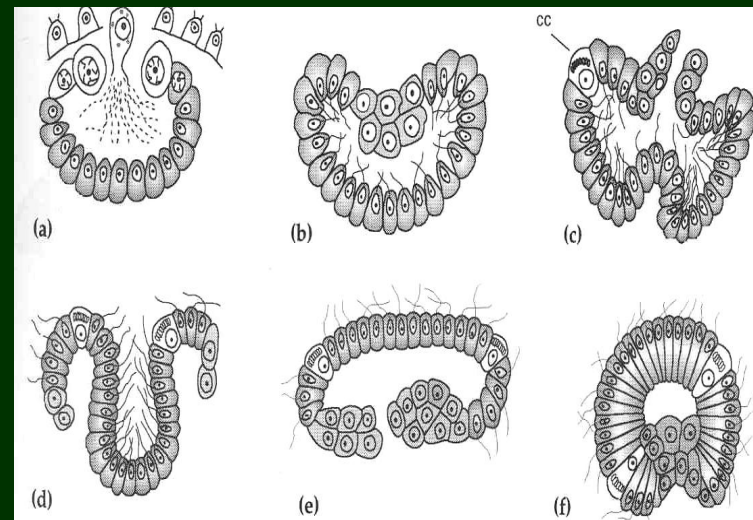
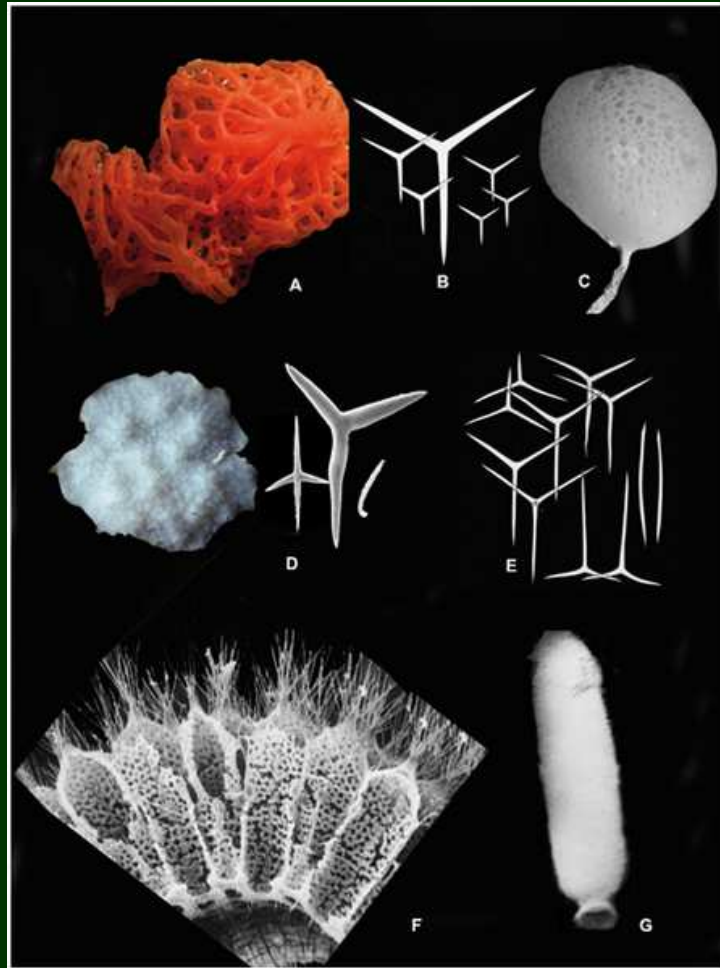
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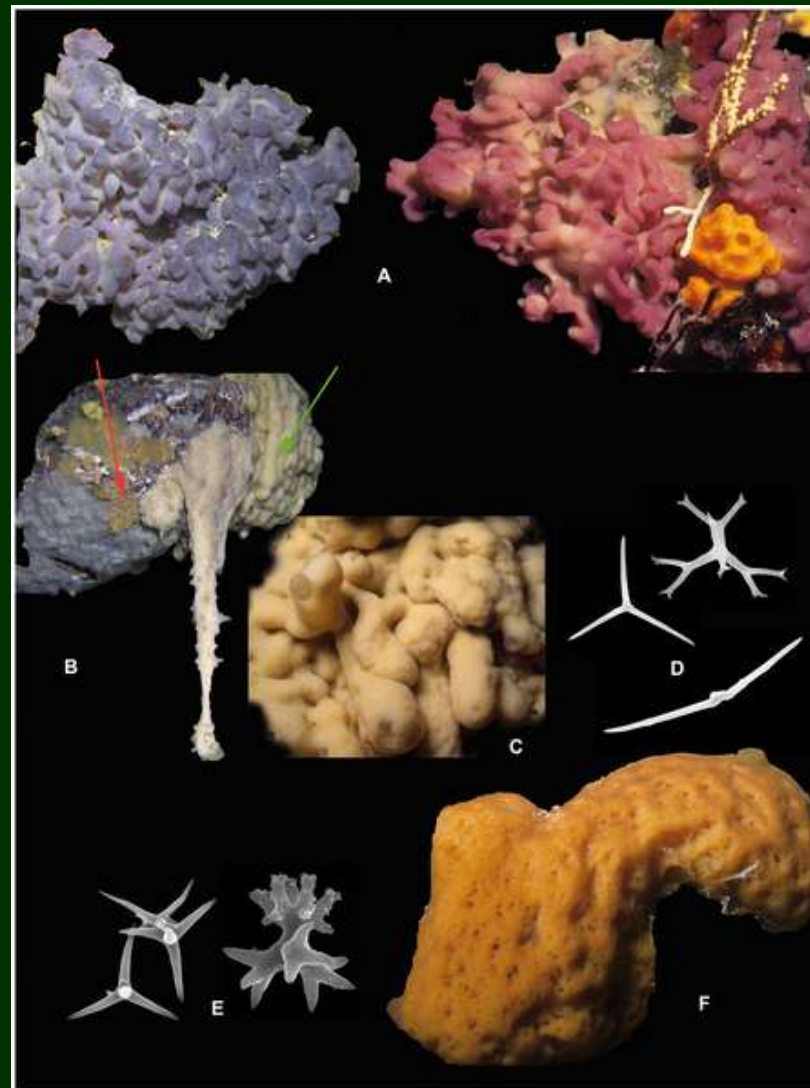
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Calcarea (= Calcispongia)

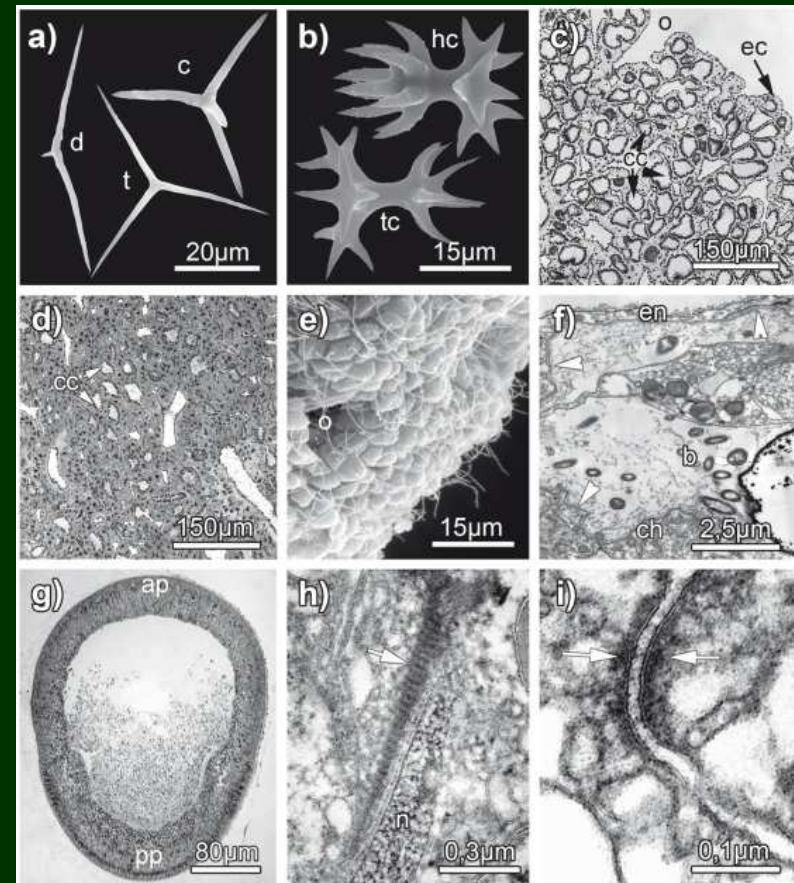
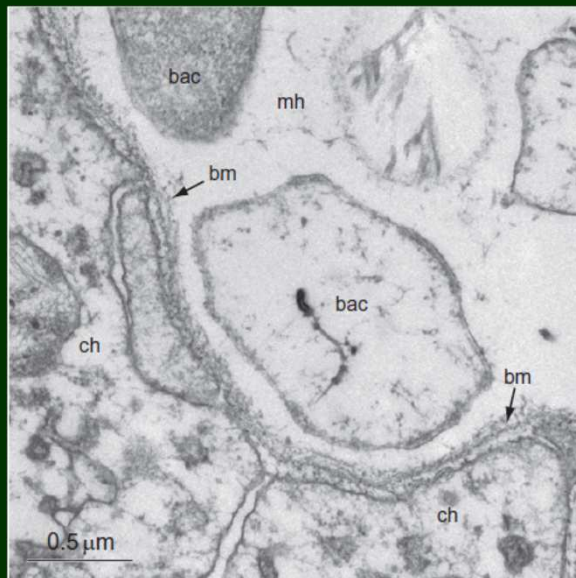


Homoscleromorpha



Homoscleromorpha

- pravé epitely s kolagenem
- povrchový epitel larev z mezibuněčnými spoji typu *adhaerens*



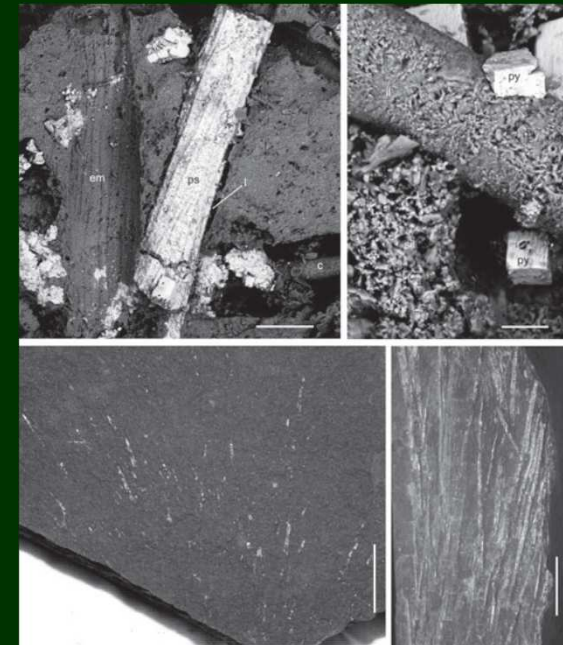
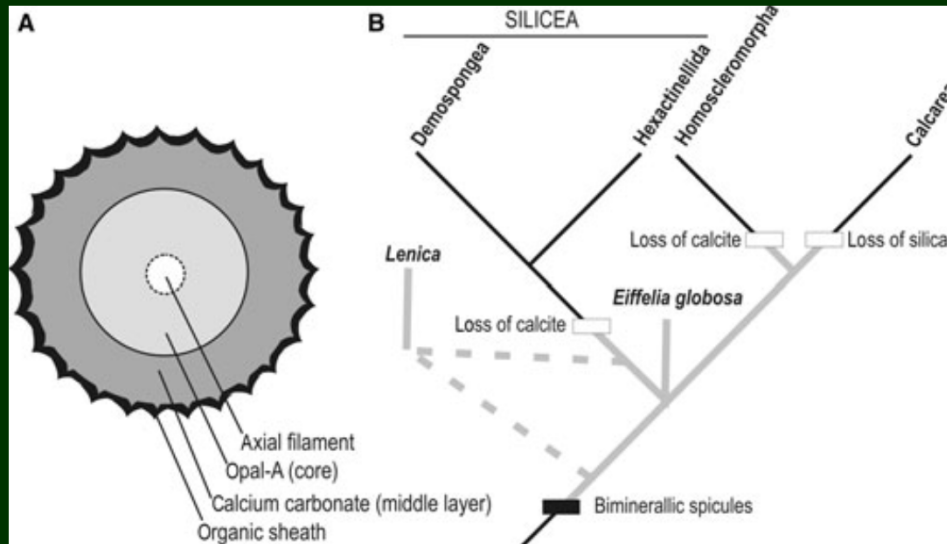
Calcarea + Homoscleromorpha

- synapomorfie: rootlety larválních obrvených epitelů (cinktoblastul, amfiblastul a kalciblastul)
- **Homoscleromorpha**: spikuly intracelulární (v sklerocytech, ale i v buňkách epitelů), bičíkaté pinakocyty a apopylární buňky, inkubovaná cinktoblastula
- **Calcarea**: extracelulární spikuly, vždy živorodé



Biminerální spikuly kambrijských houbovců

- homologie spikul???
- x extra- a intracelulární → dva typy sekrece u původních forem? (*Eiffelia*, kambrium)
- „Sclerospongia“???



„Sclerospongia“

- „korálové houby“ – křemičitý skelet na robustním vápenatém endoskeletu
- *Ceratoporella*,
Stromatospongia, *Hispidopetra*,
Goreauiella, *Merlia*
- demospongie, ale vzájemně nepříbuzné

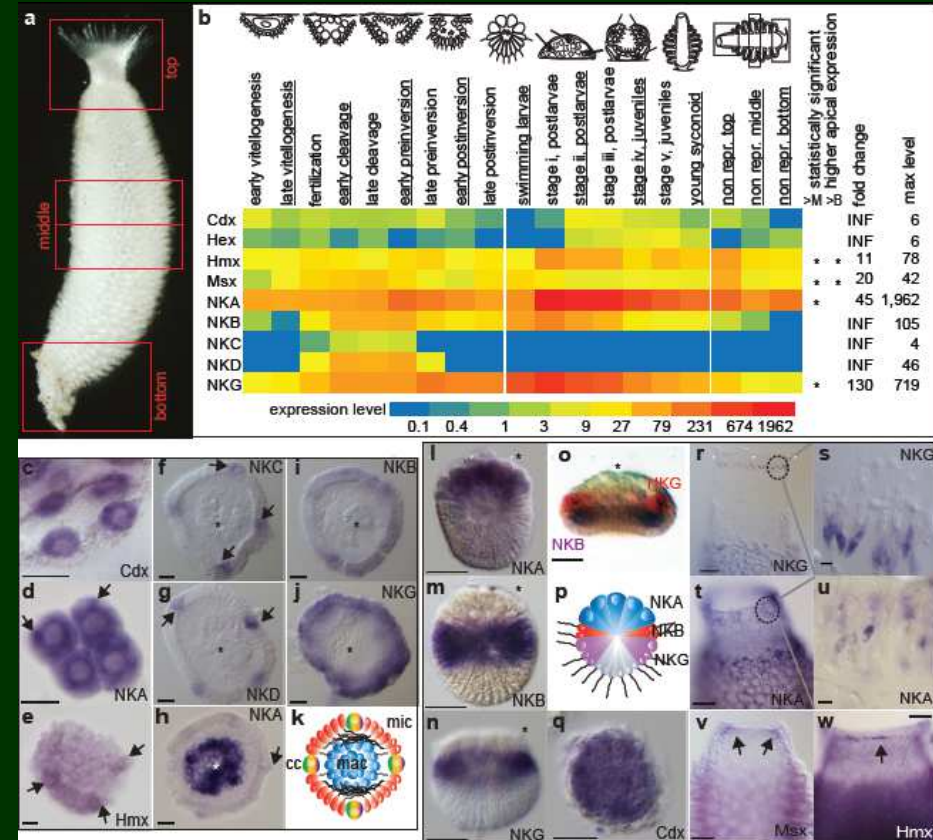


Porifera

- transkriptomy: naprostá většina zásadních genů je *přítomná*



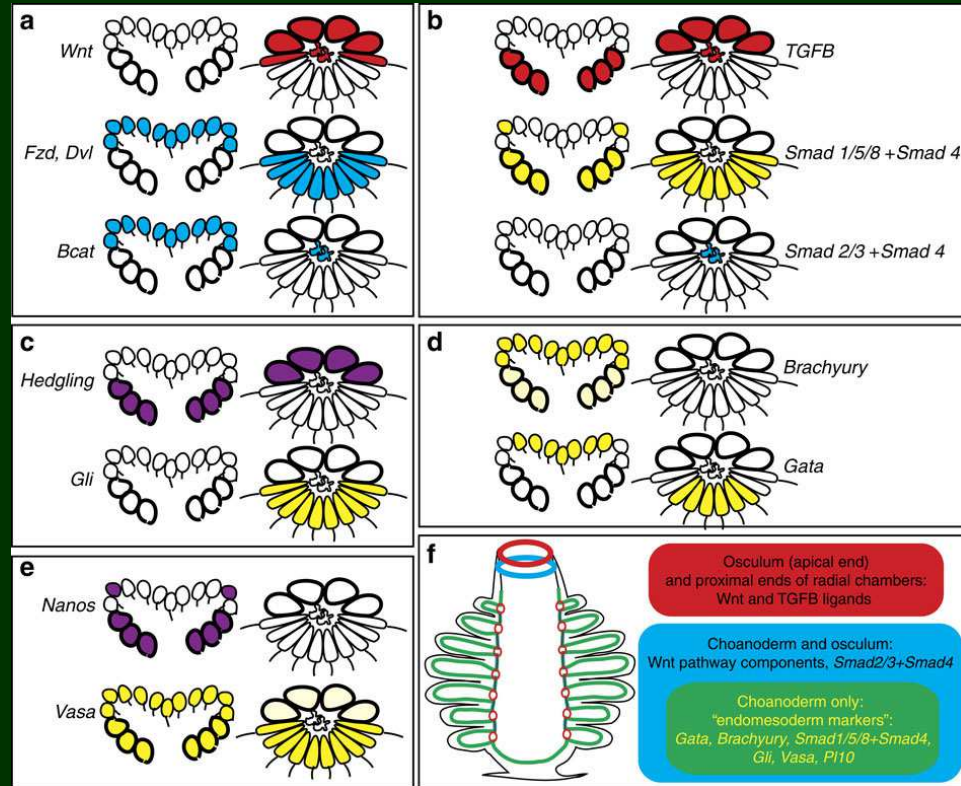
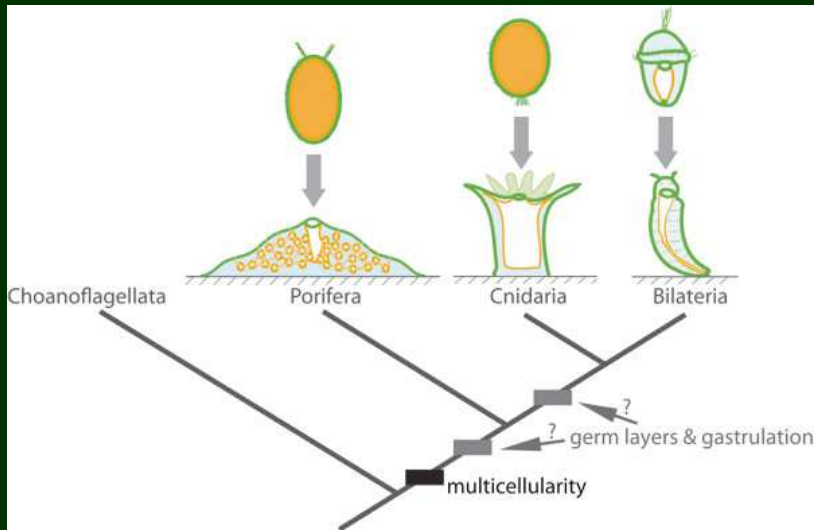
Calcarea: homeoboxové geny (ParaHox a NK)

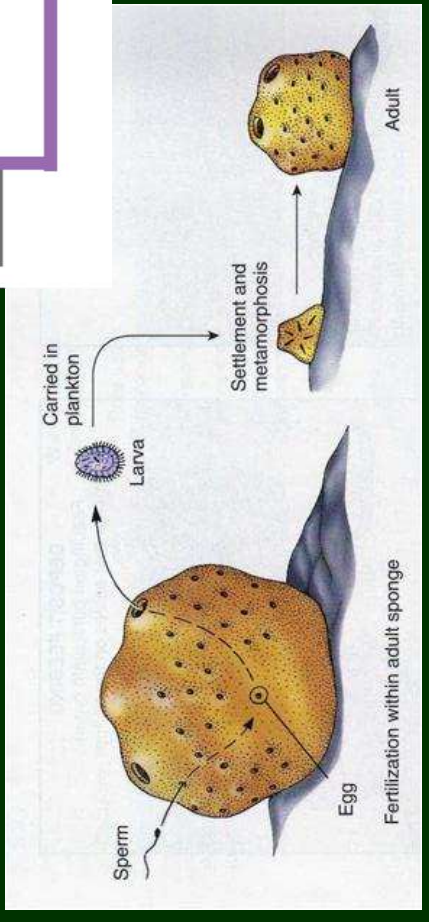
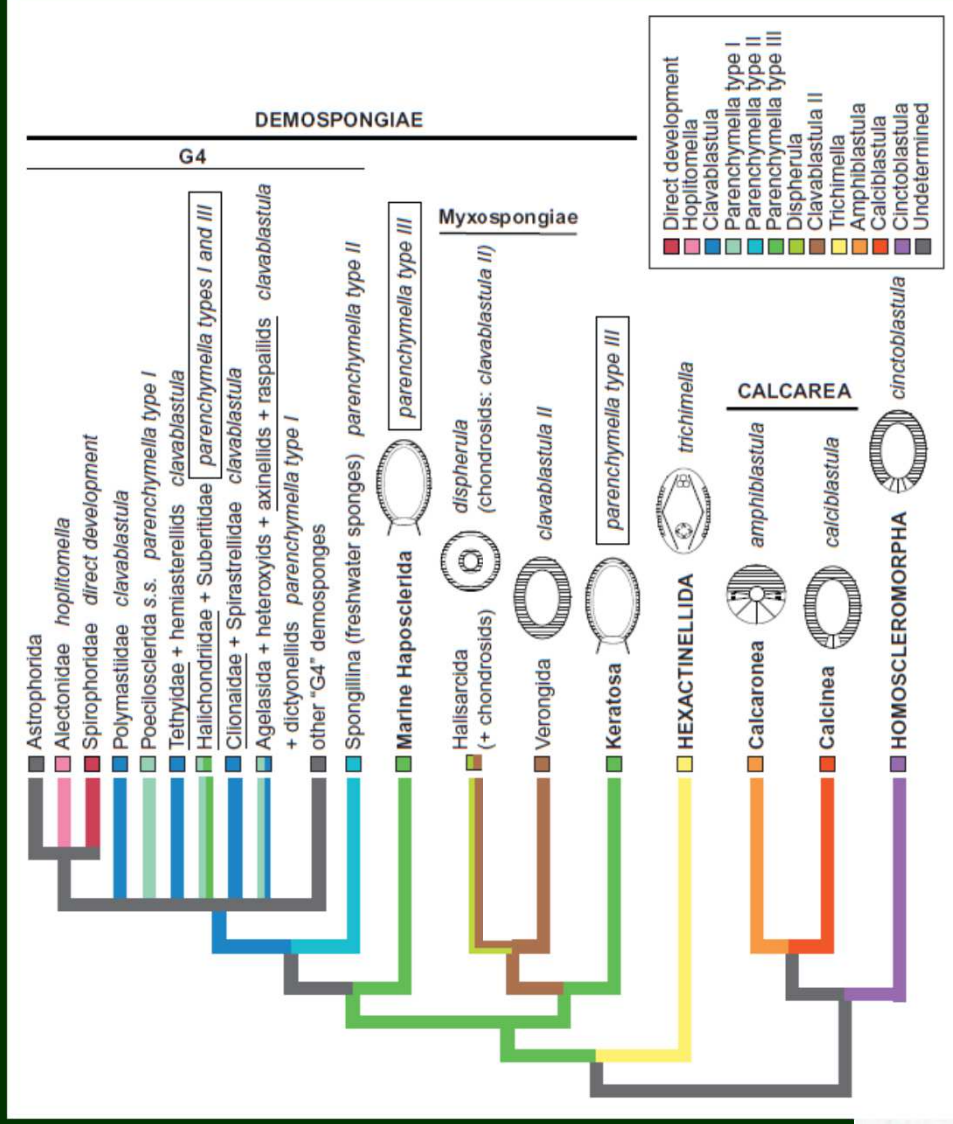
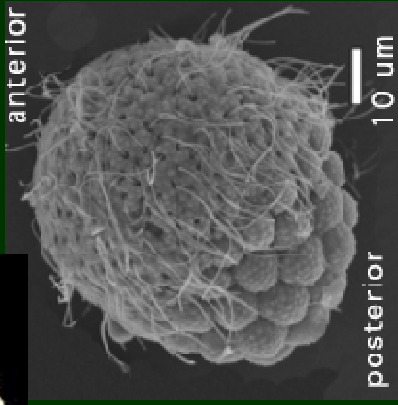


- *Amphimenodon*: 8 NK, ale žádný Hox ani ParaHox → „ParaHoxozoa“
- x nebo druhotná ztráta? („ghost loci“)
- x *Calcarea* (*Sycon*, *Leucosolenia*) mají NK i ParaHox (ale žádný Hox) → název „Parahoxozoa“ je nevhodný...

Vývojové geny (Calcarea)

- vývojové geny: základní plán kalcispongií a žahavců je homologický





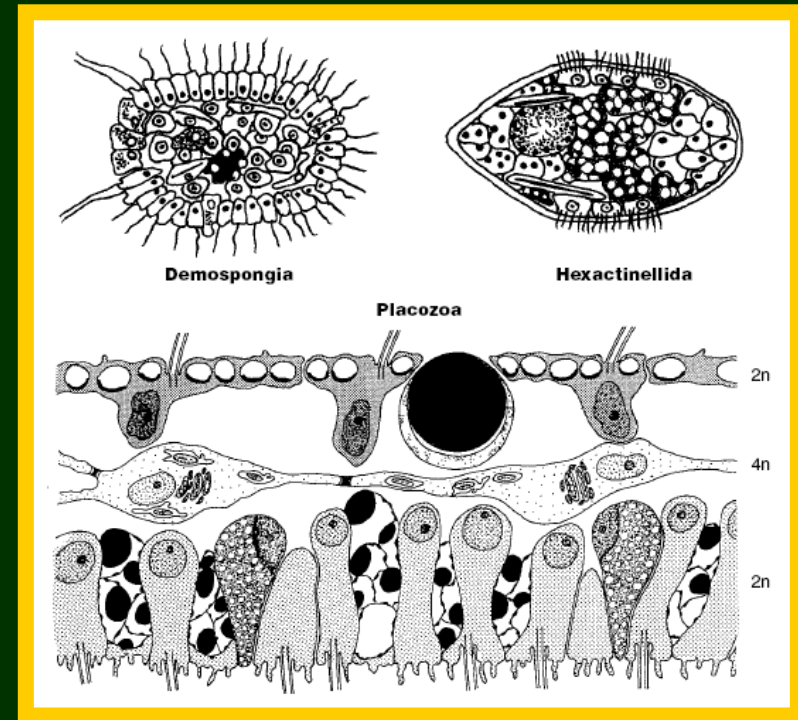
Porifera

problémy a oprava bludů

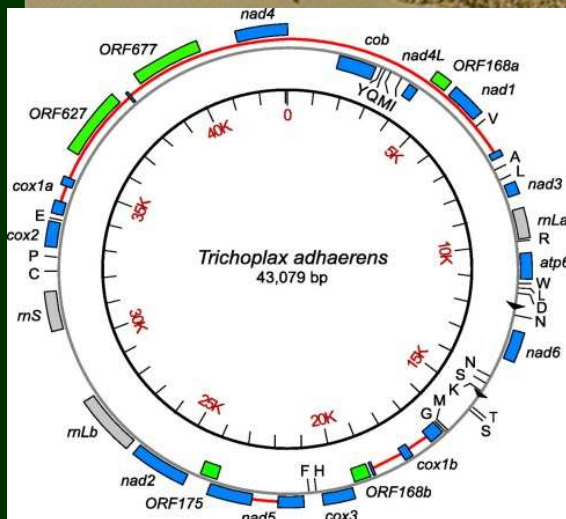
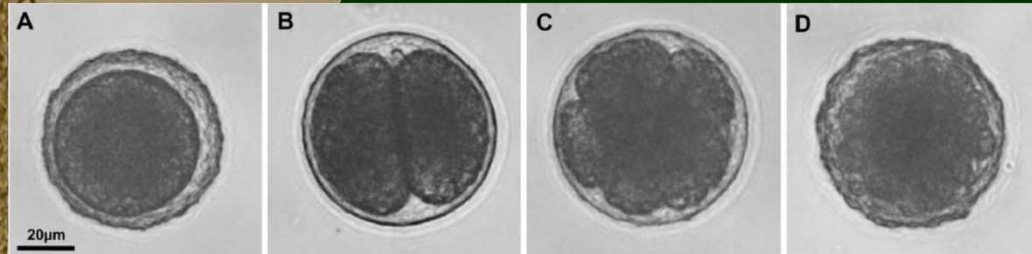
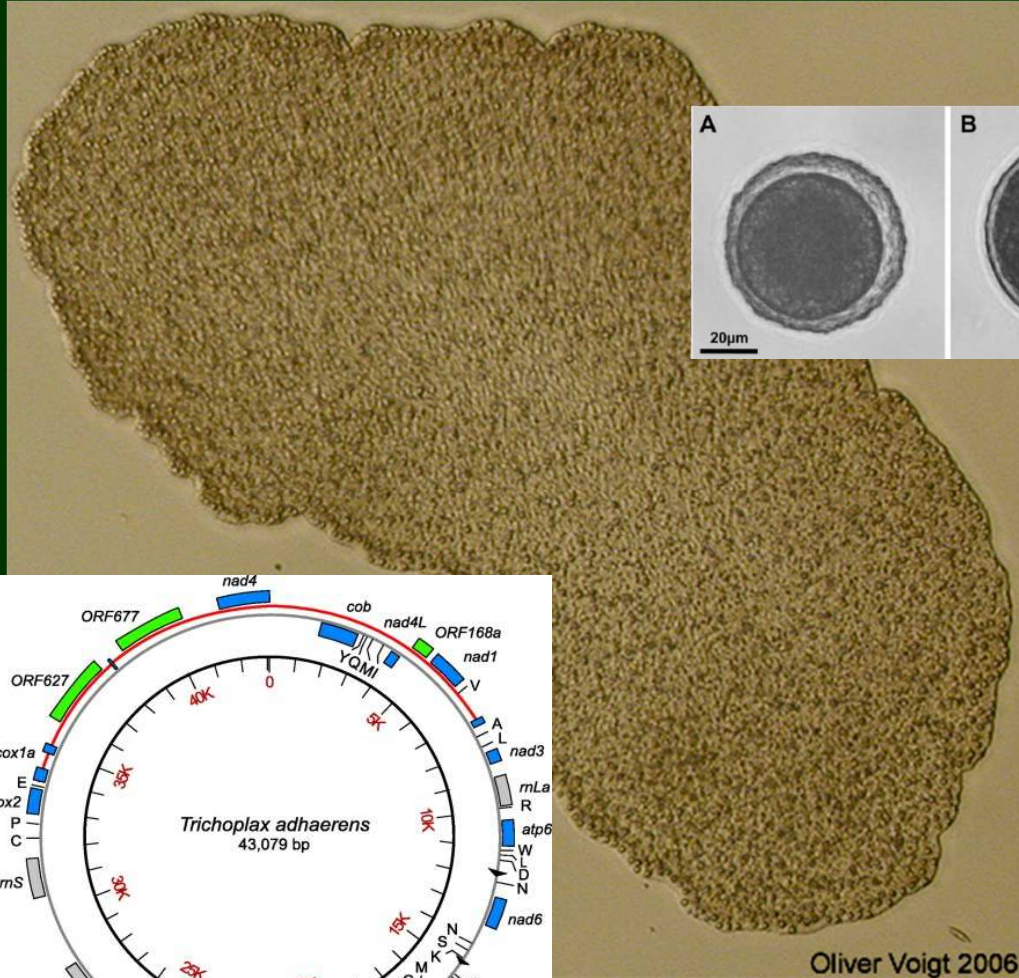
- mají epitely (kontrolují tok iontů do mezohylu) – tj. není to „velká kolonie“
- nejasná homologie choanocytů a buněk choanoflagelátů
- mají ciliární smyslové orgány (larvy, oskulum)
- kontrakce myoidních buněk existují, ale jsou příliš pomalé na signalizaci pomocí neurotransmiterů
- mají glutamatergní signalizaci (kontrakce) a Ca/K akční potenciály (v syncytiích Hexactinellida: regulace přijímání potravy)
- mají geny pro mnoho sekrečních molekul specifických pro NS
- vznik larev metodou třídění jednotlivých buněk x polarizace (larvy, akviferní systém) řízená pomocí *Wnt* signalizace

Porifera – shrnutí

- 1. sesterská skupina „parahoxozoi“
- 2. monofyletická skupina (Silicea x Calcarea + Homosclerea)
- 3. mnohem složitější a „normálnější“, než jsme si mysleli
- 4. pro fylogenezi metazoi jsou důležité larvy, ne aberantní dospělci

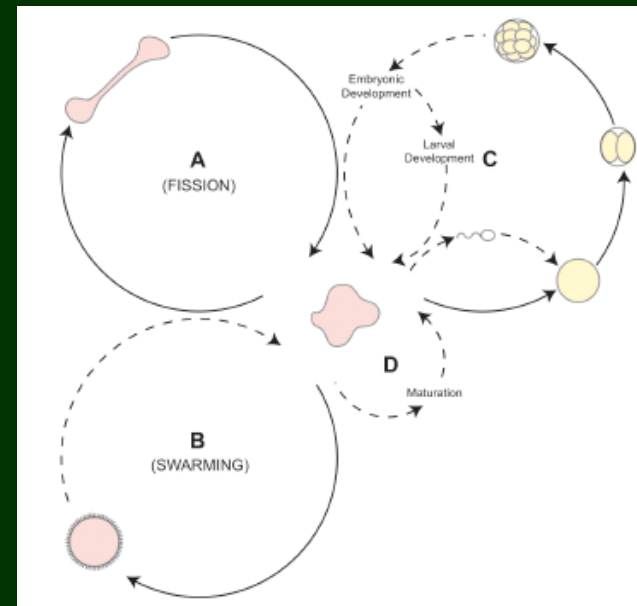


Placozoa

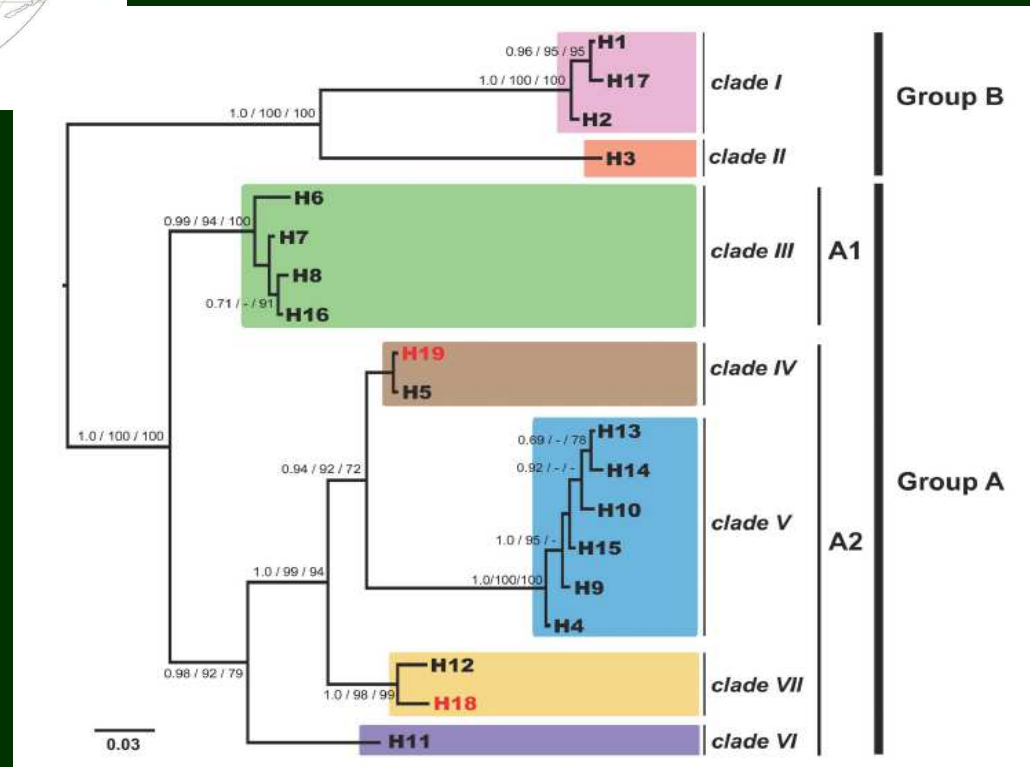
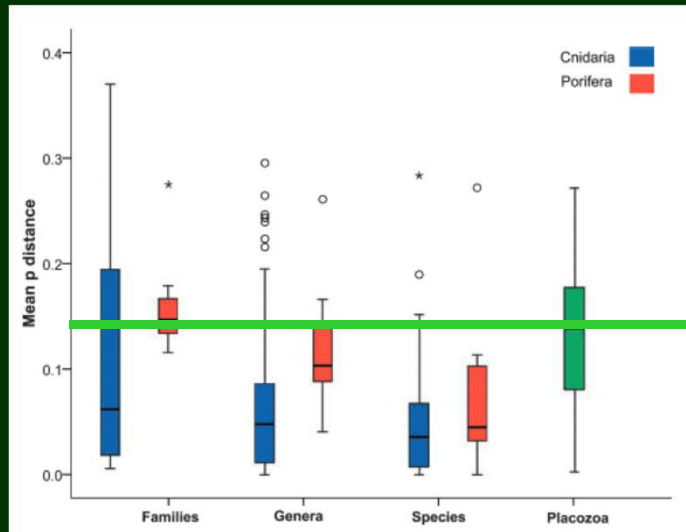
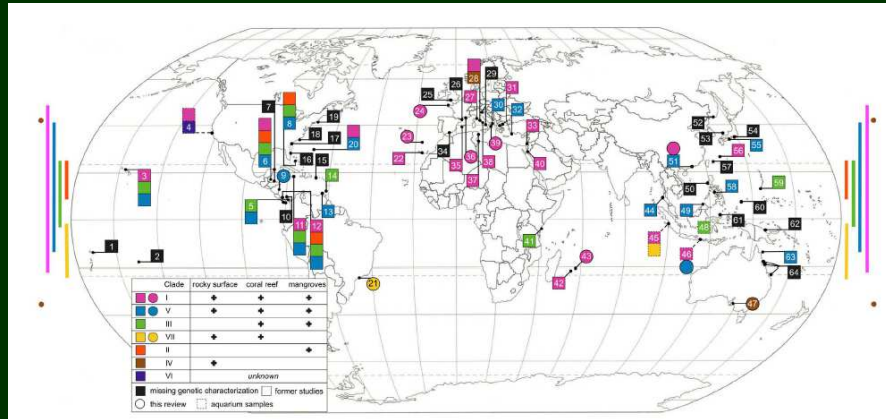


Oliver Voigt 2006

Trichoplax

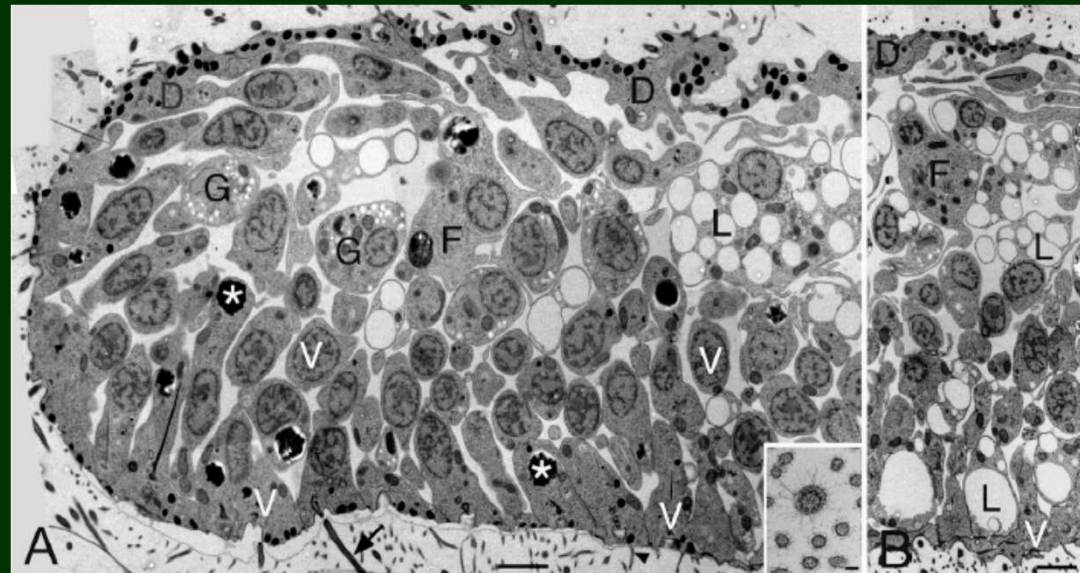
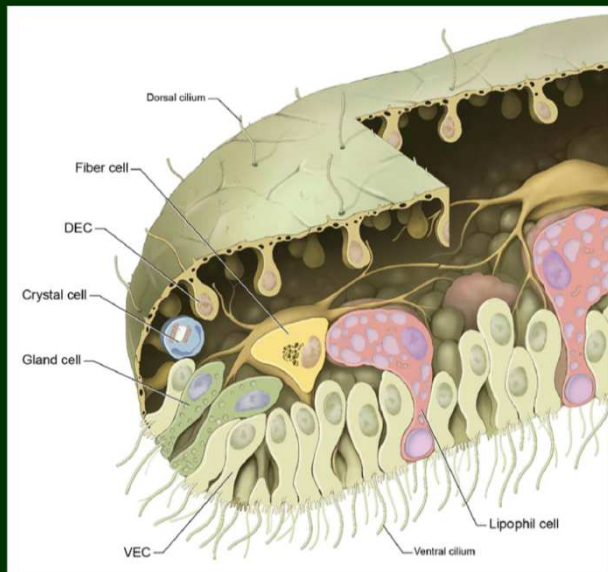


Placozoa: diverzita

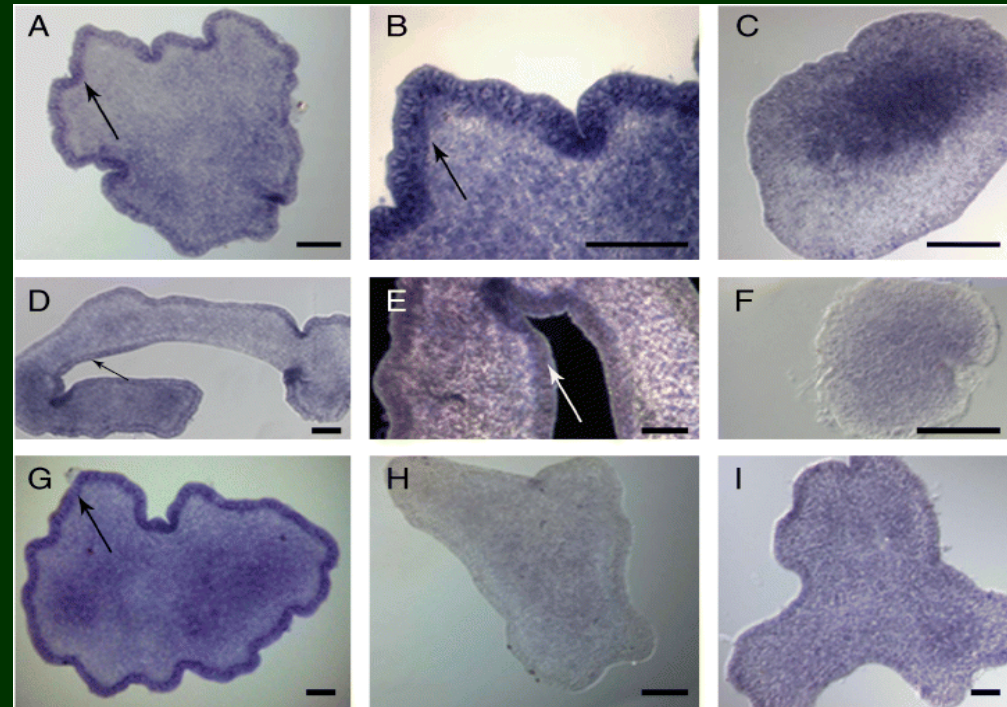


Placozoa

- epitely bez bazálních lamin
- žlázaté buňky ~ neurosekrece (+ kolem okraje sekretují neuropeptidy podobné FMRFamidům)
- morfologie: lipofilové ve spodním epitelu (~ trávicí buňky), krystalové a žlázaté buňky kolem obvodu
- příjem potravy: bičíky se koordinovaně přestanou hýbat, lipofilní buňky koordinovaně produkují trávicí enzymy (ale jen v bezprostřední blízkosti řas)



Homeoboxové geny a *Trichoplax*



Bilateria



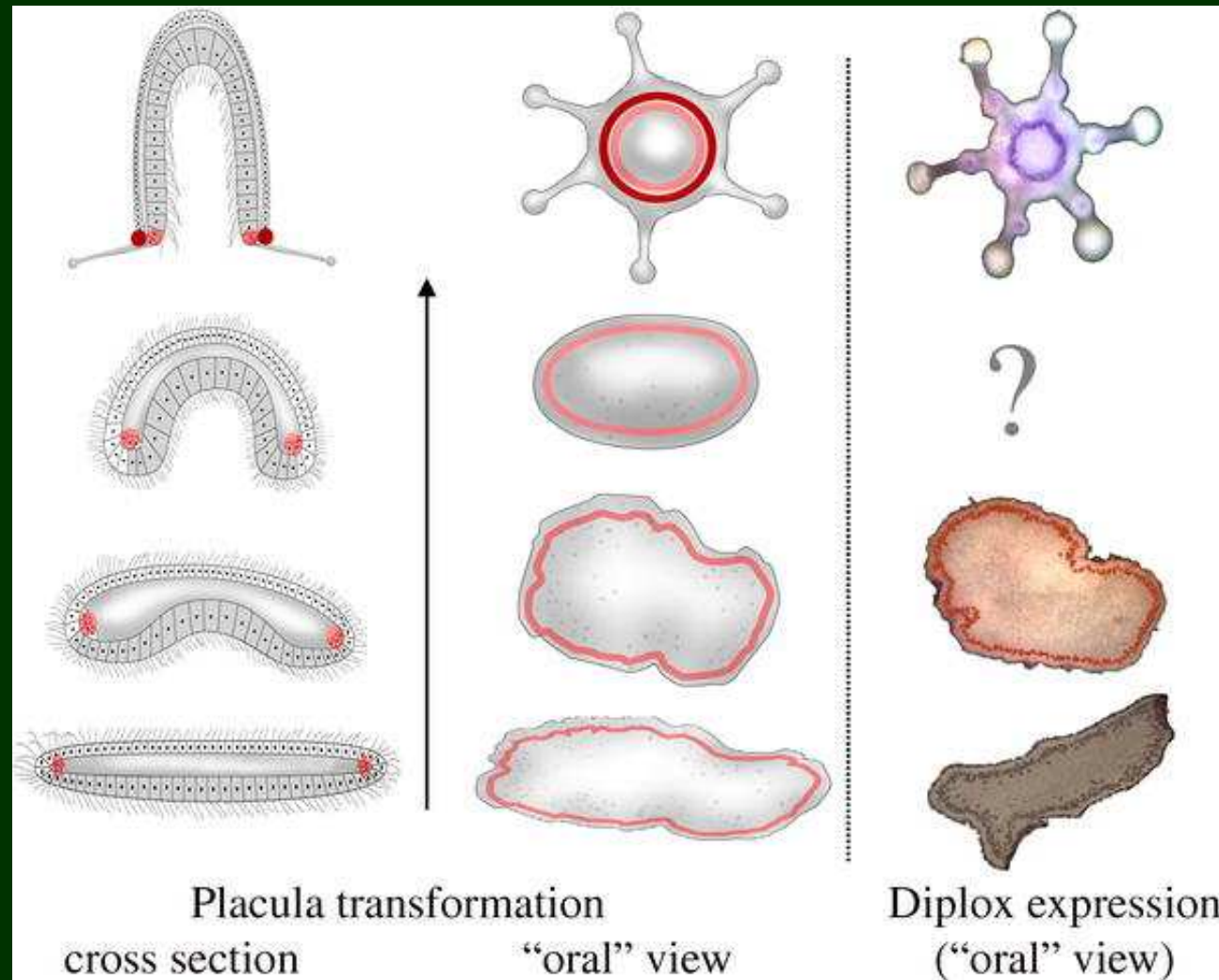
Cnidaria



Placozoa

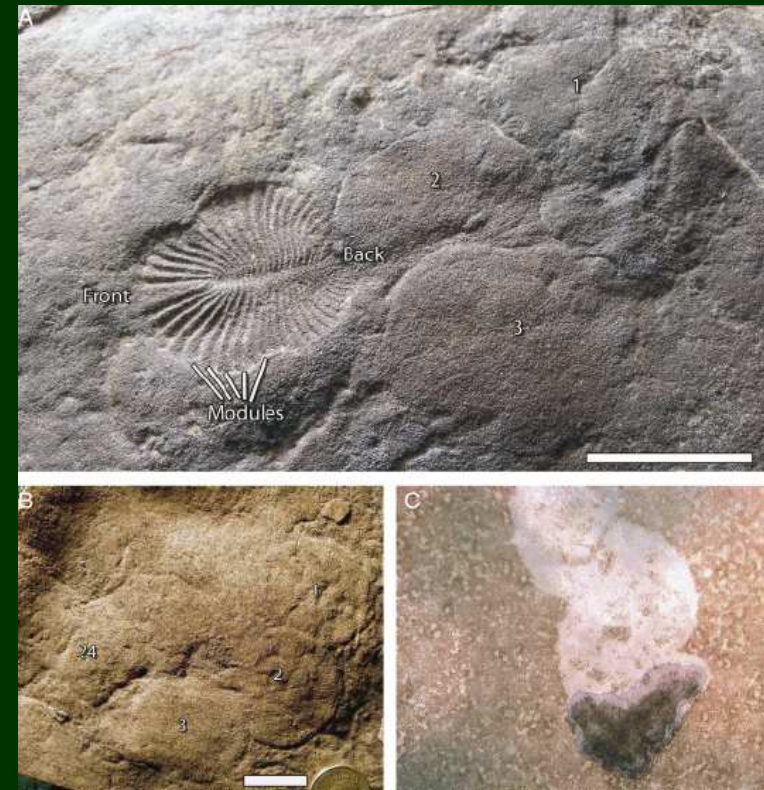
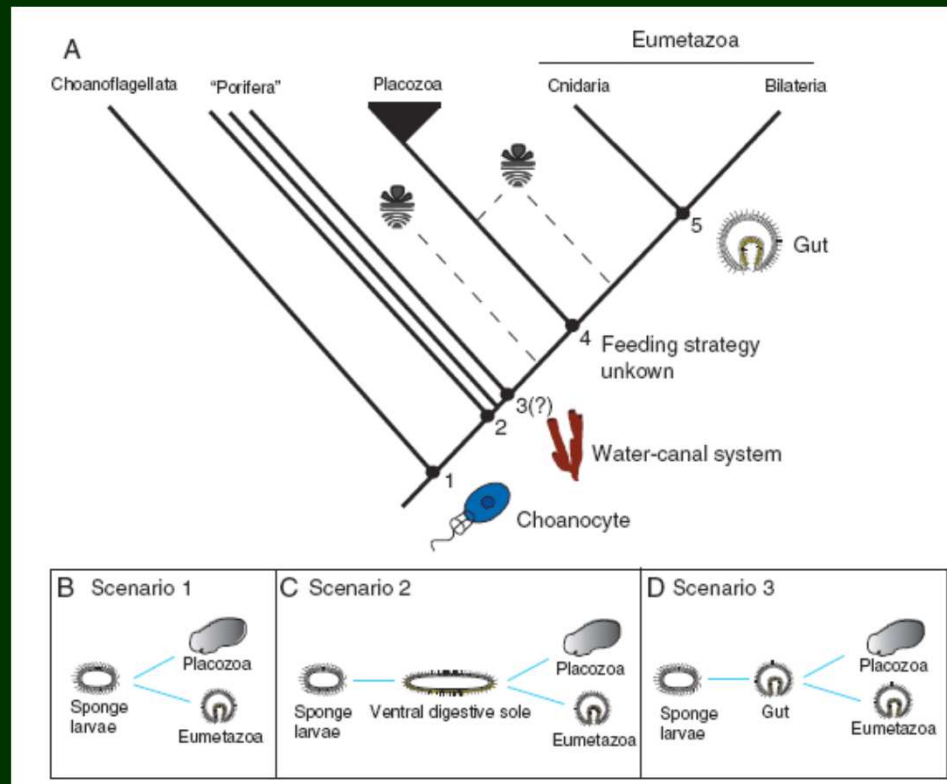


plakula → tělní symetrie metazoí



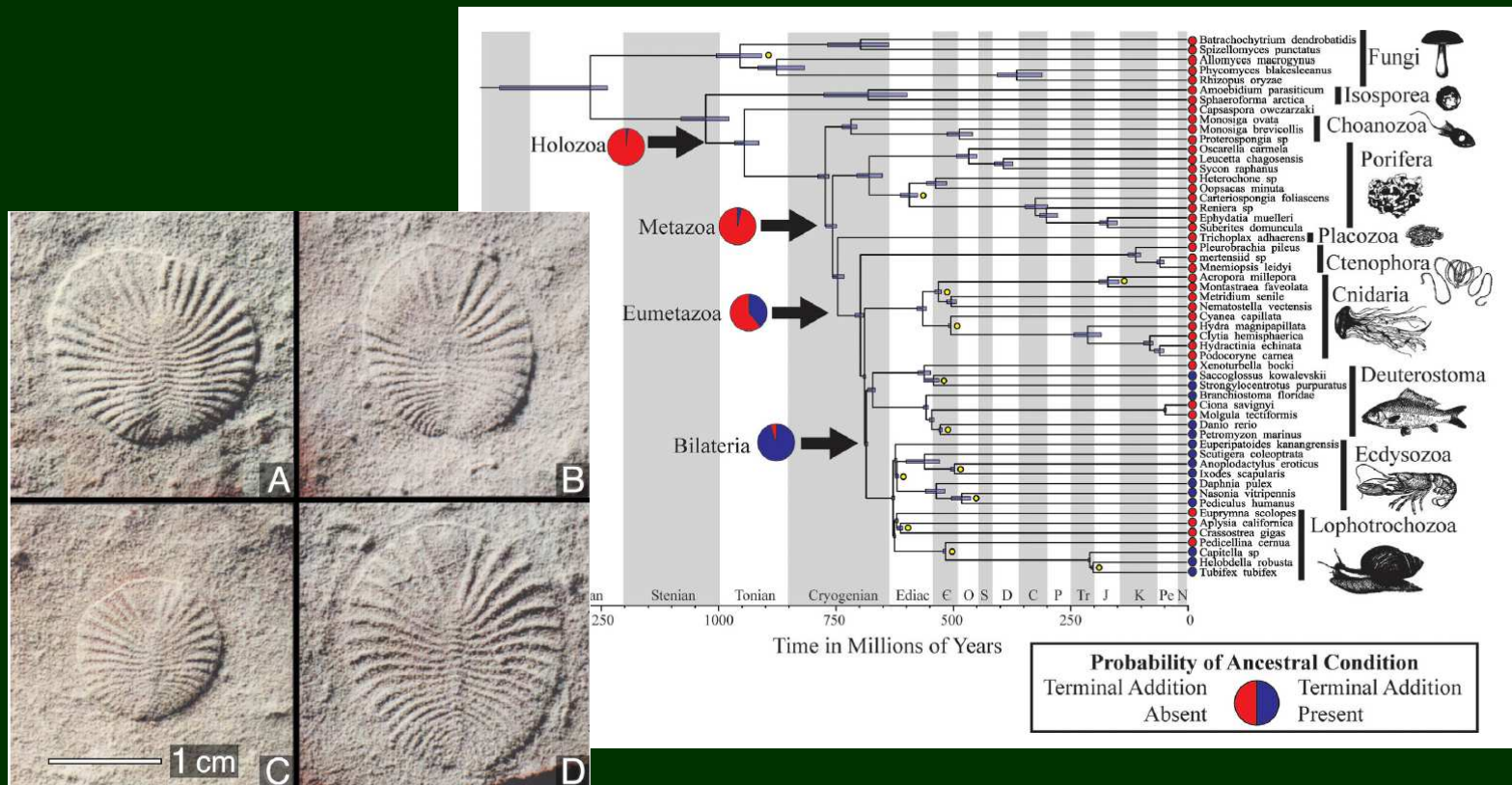
Placozoa v prekambriu?

- *Dickinsonia*???
- x 500krát větší než *Trichoplax*

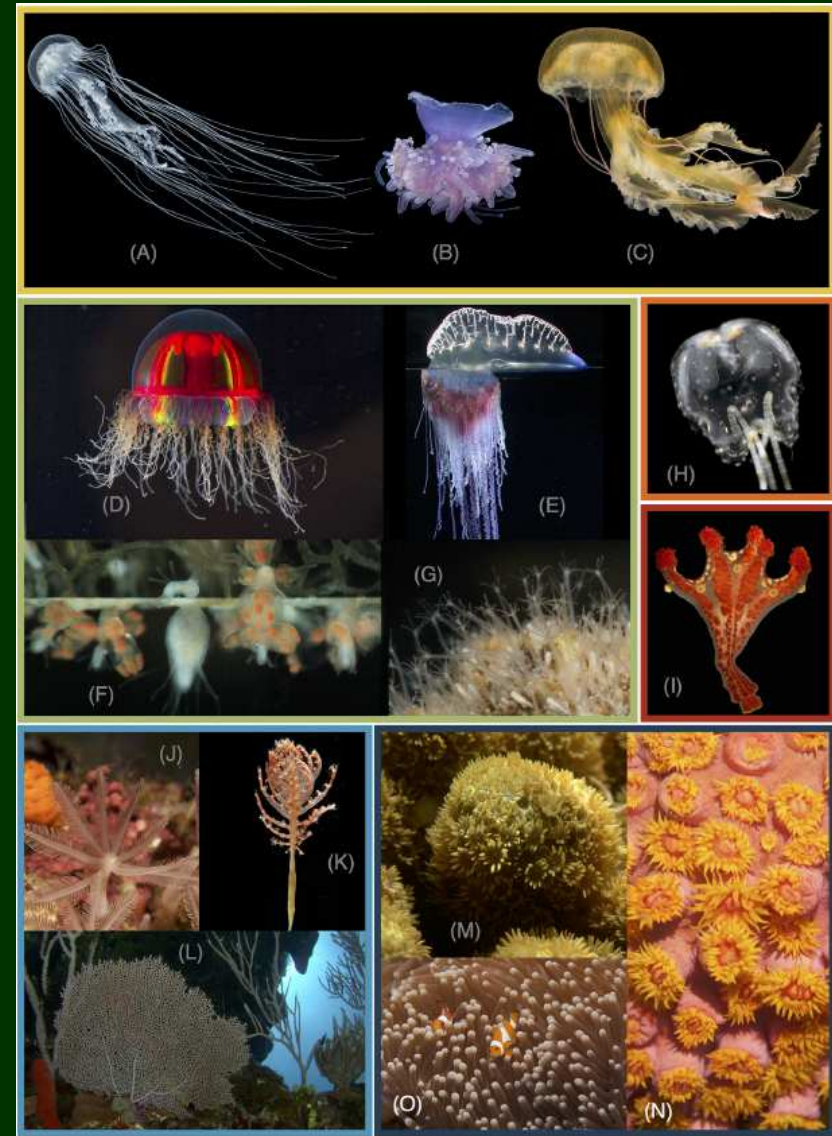
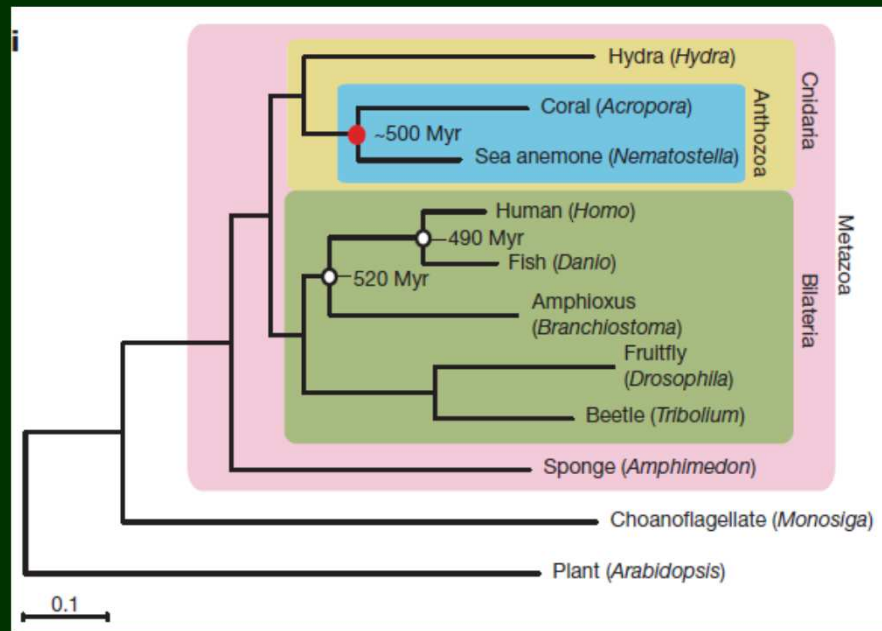


Dickinsonia jako Bilateria?

- ontogenetická terminální adice (anamorfóza) je typický bilaterální znak

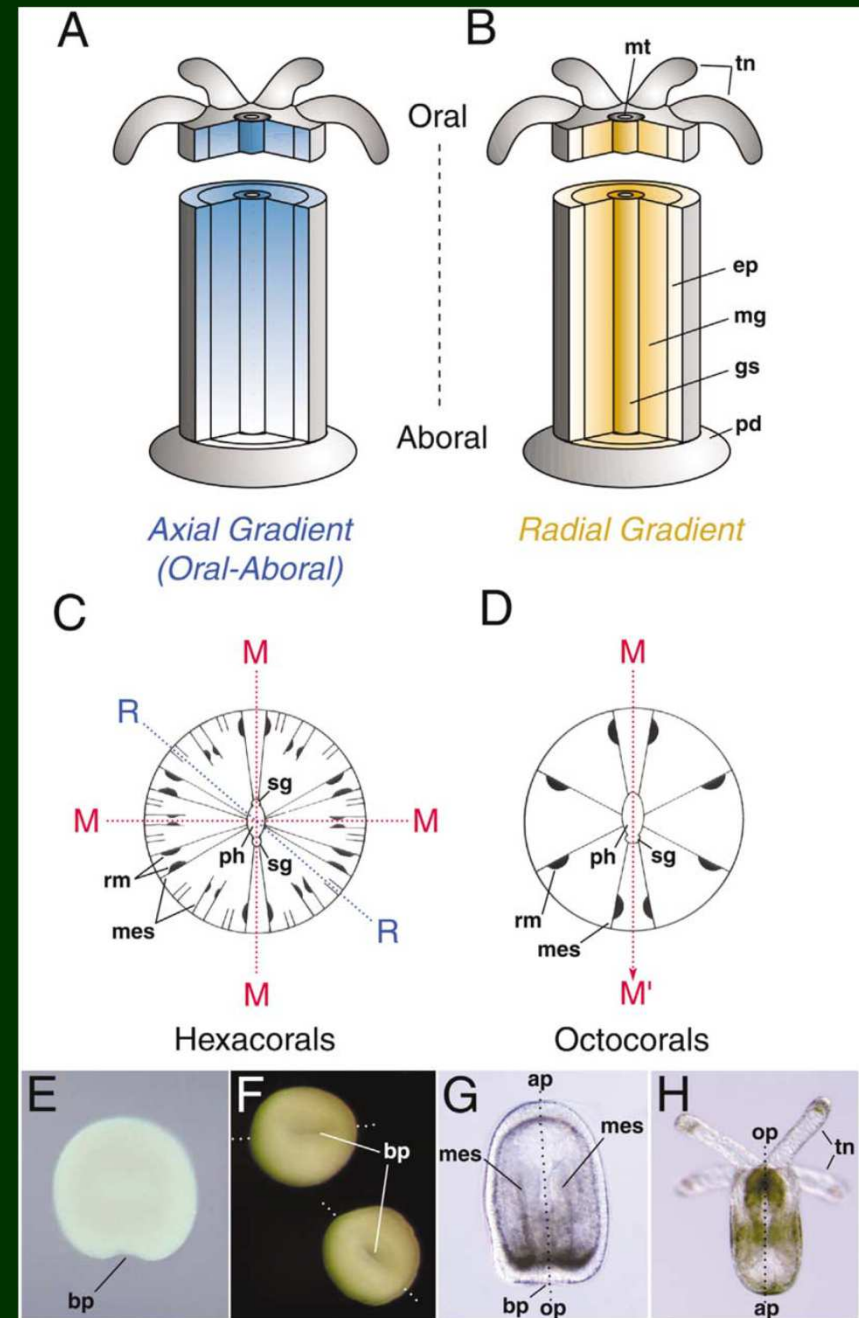


Cnidaria



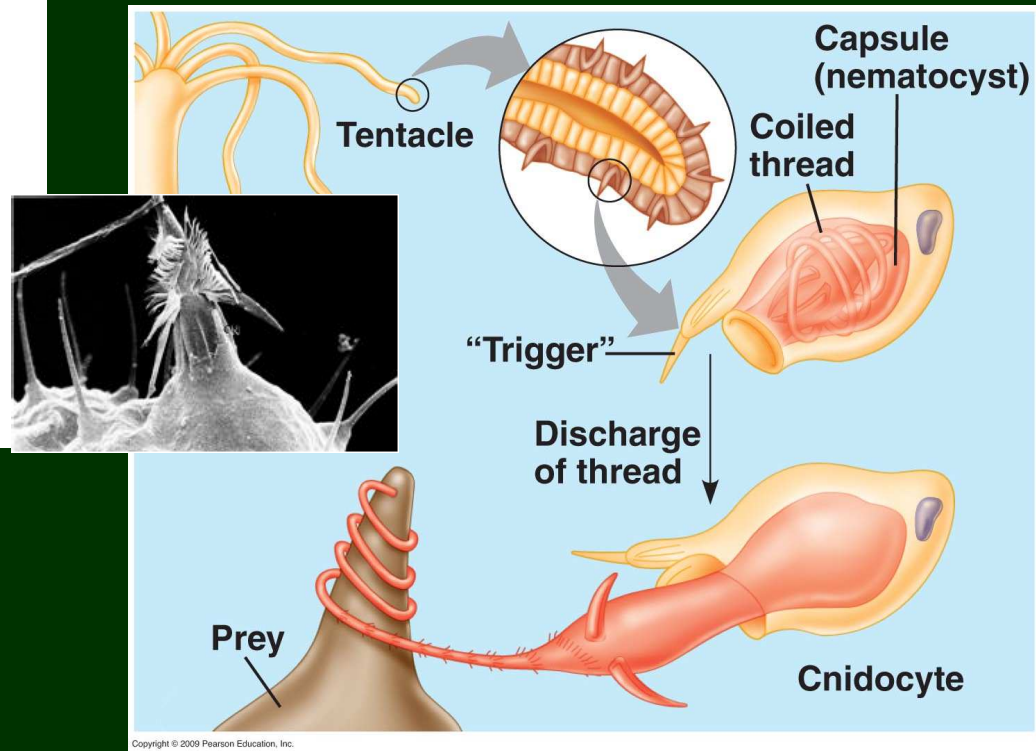
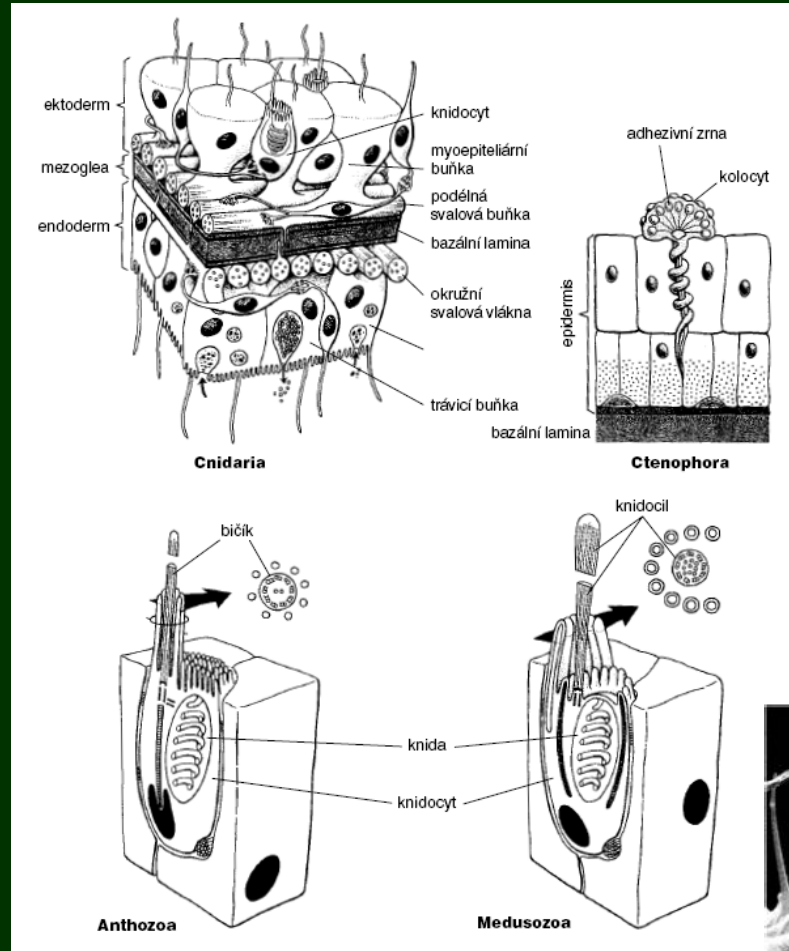
Cnidaria

- biradiální symetrie



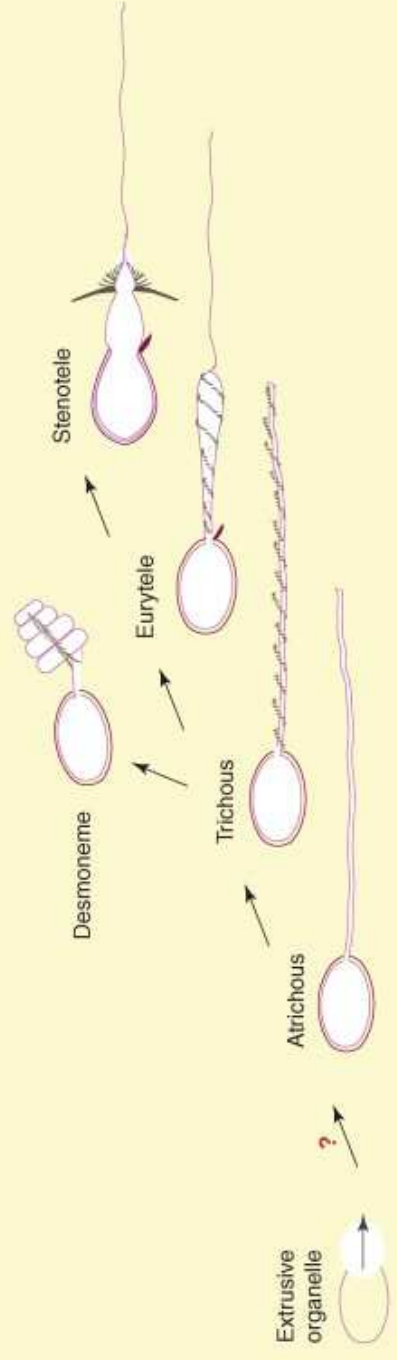
Cnidaria

žahavé buňky

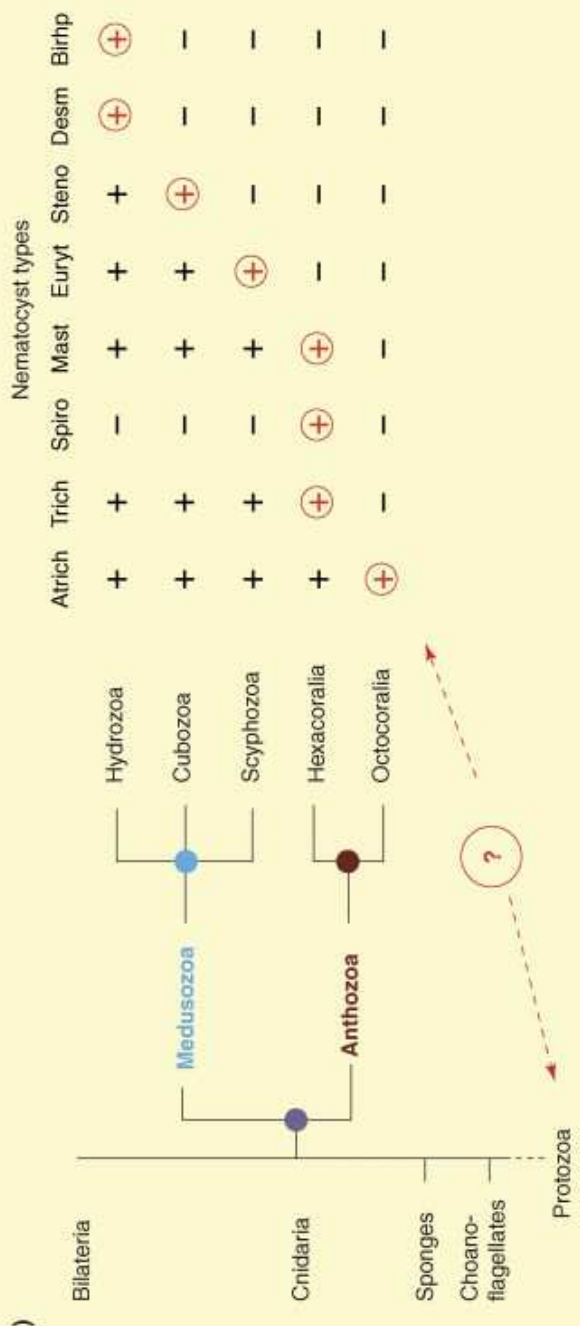


- modifikované neurony
- NS i endodermální (primitivní???)

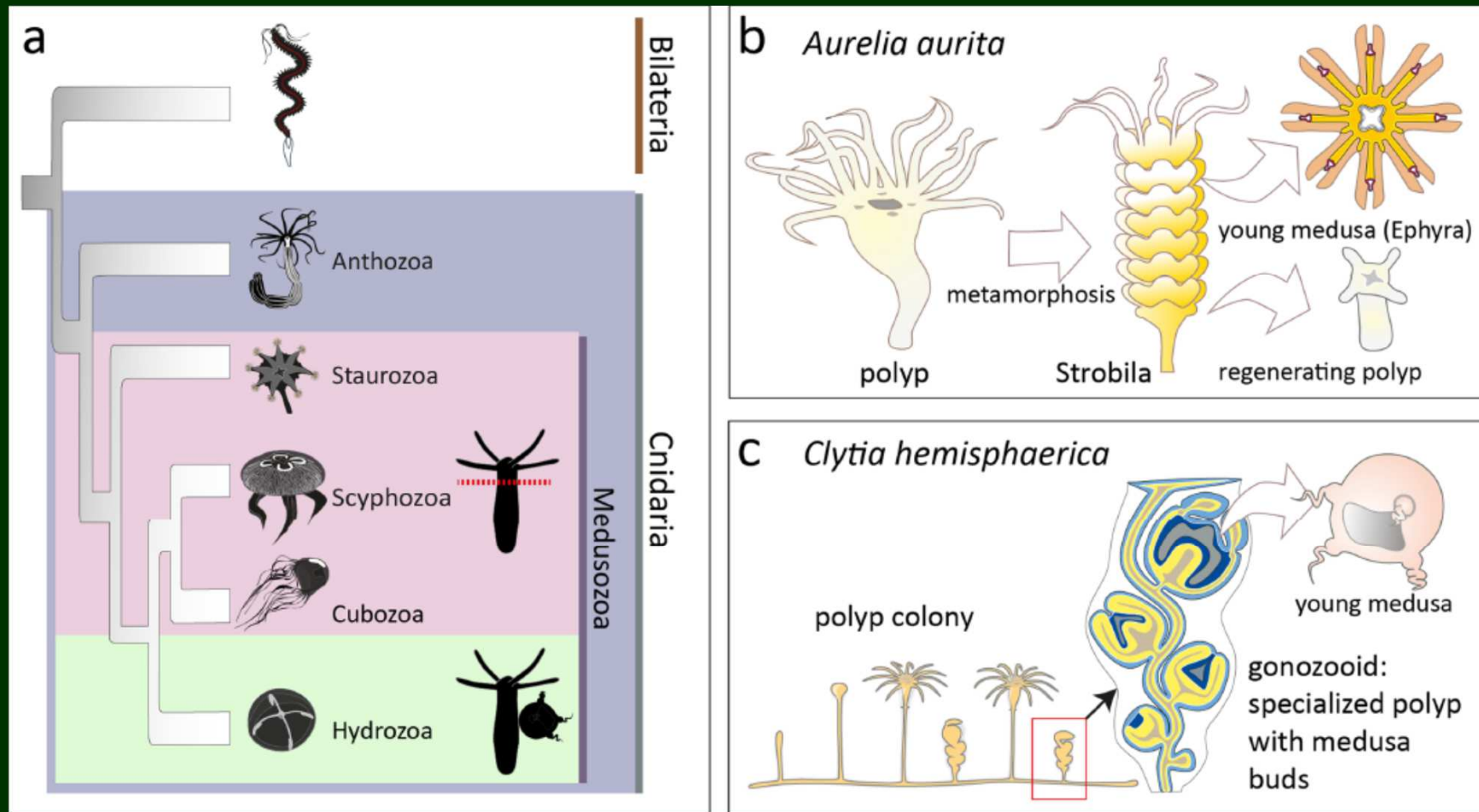
(a)



(b)

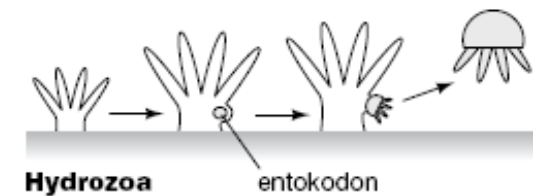
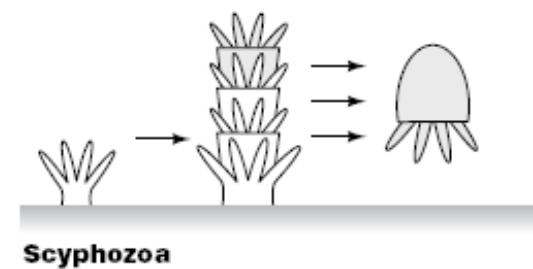
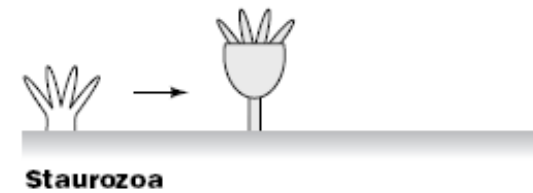
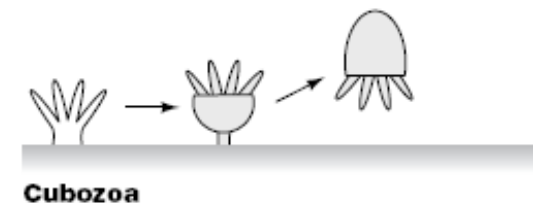
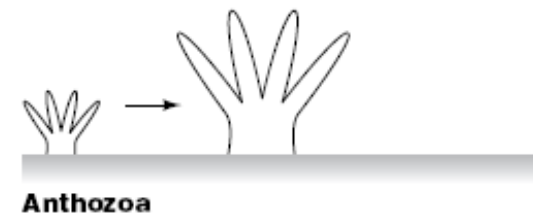


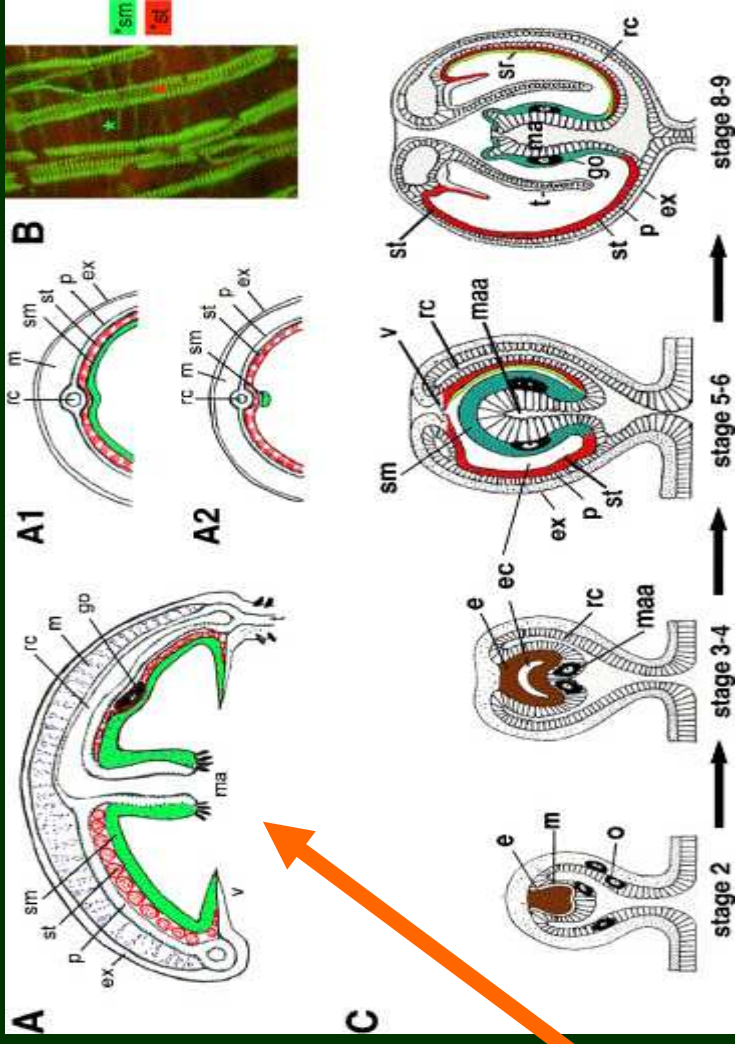
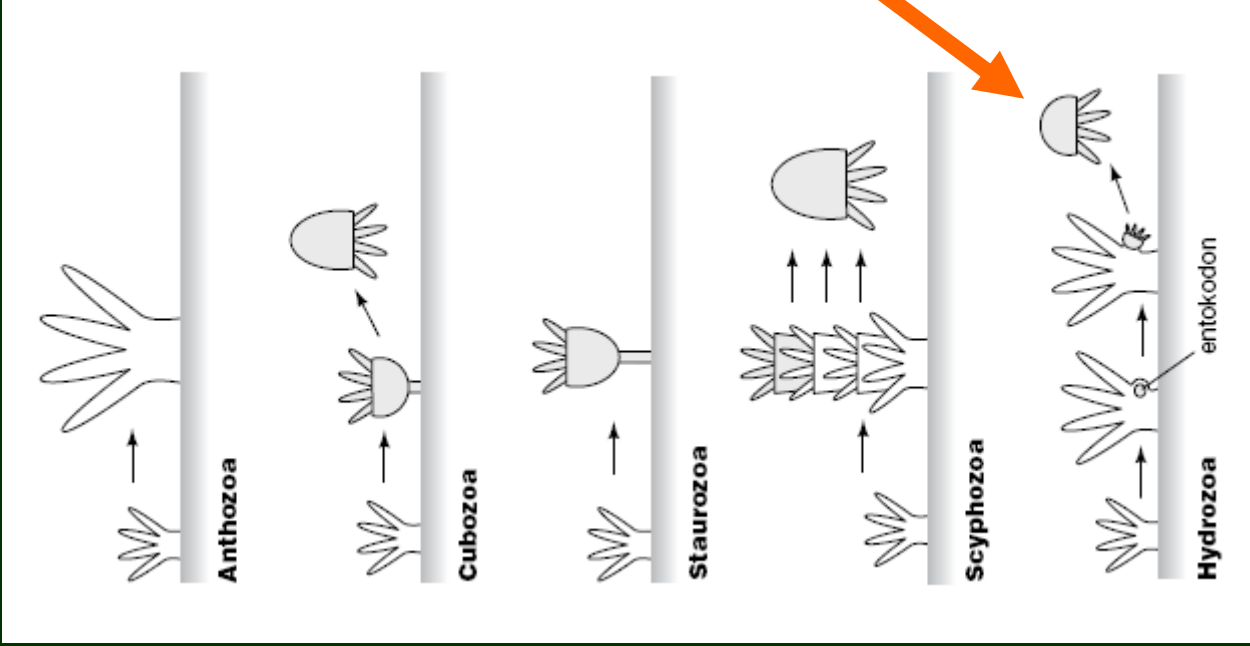
Cnidaria – vývojové cykly



Cnidaria

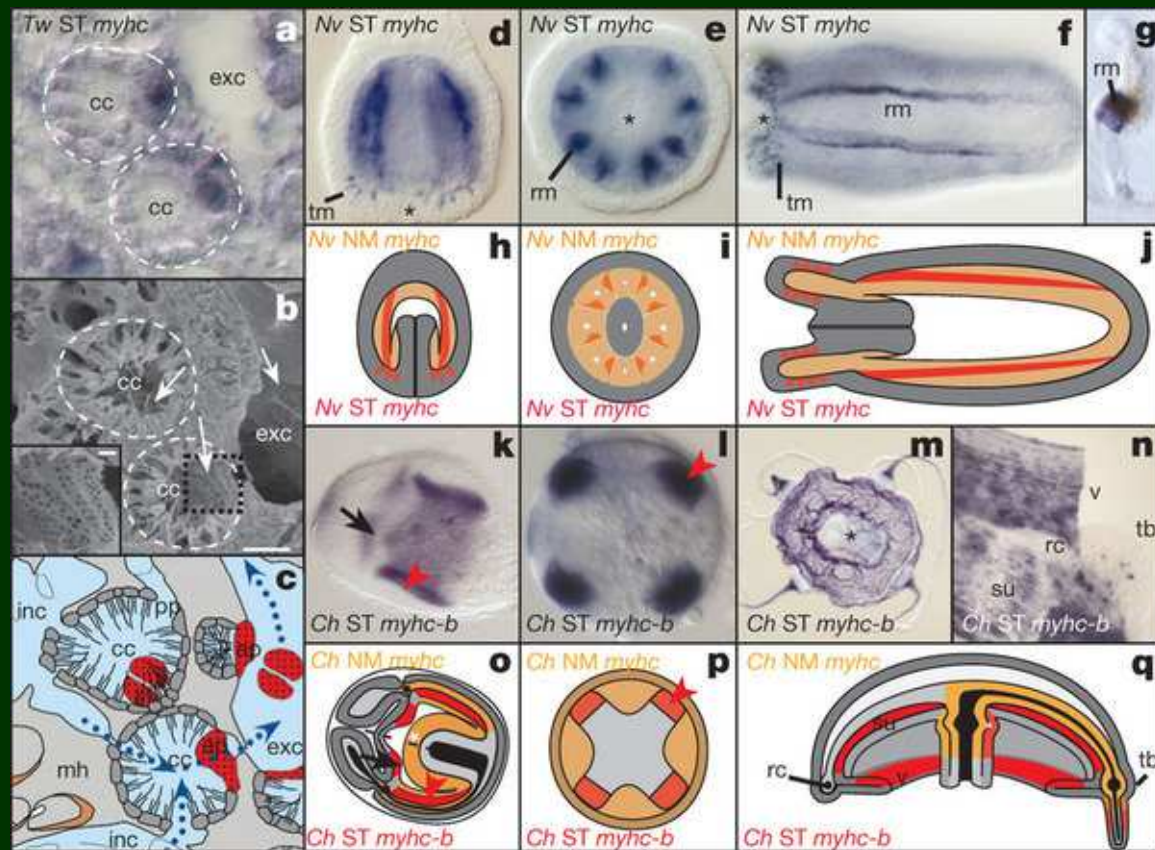
vývojové cykly



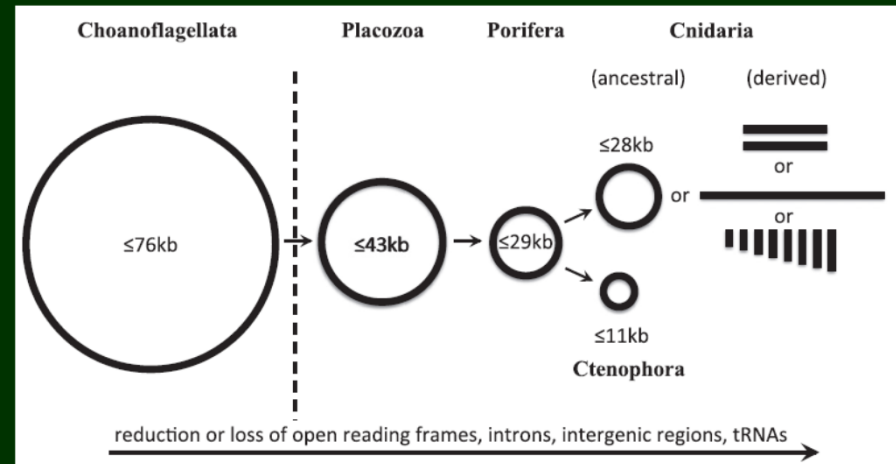
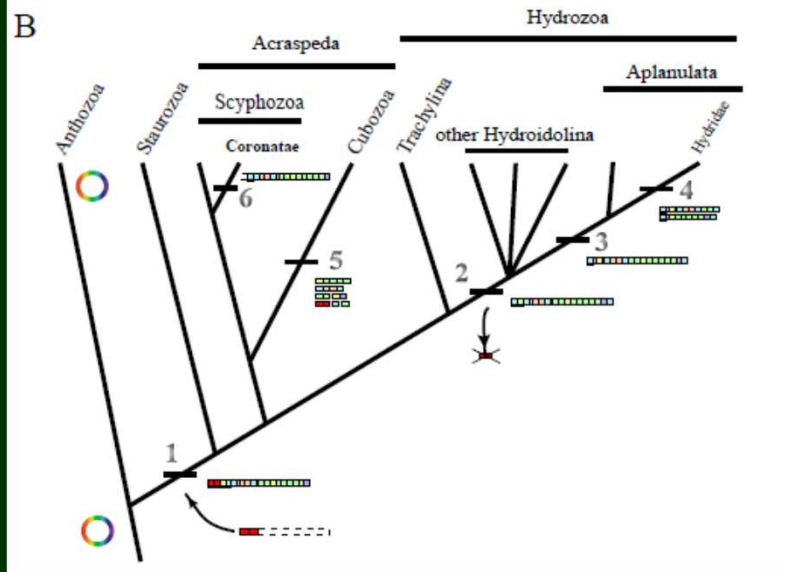
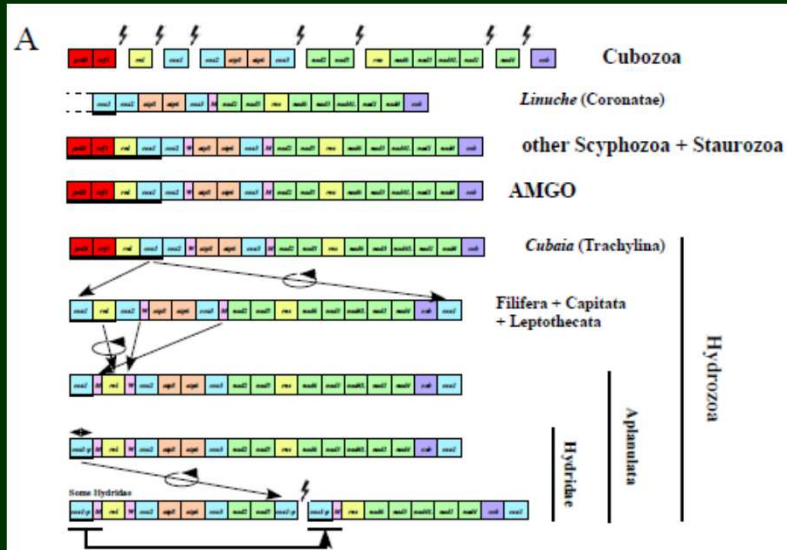


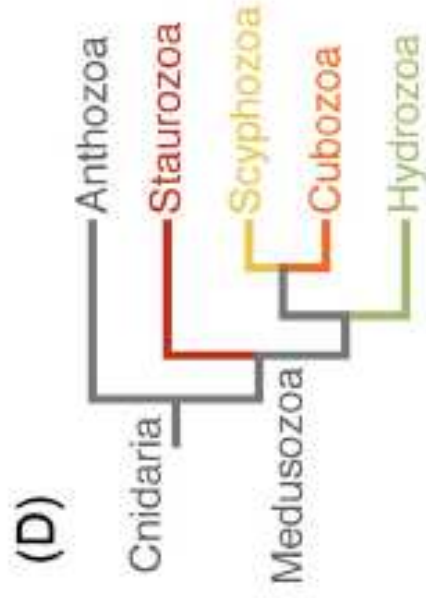
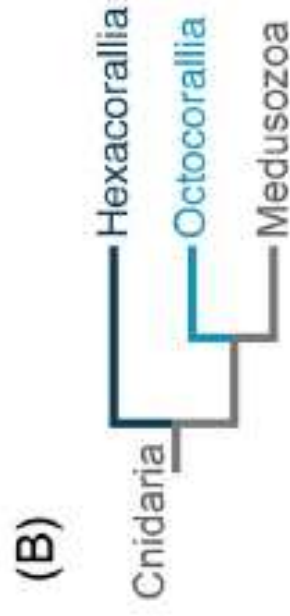
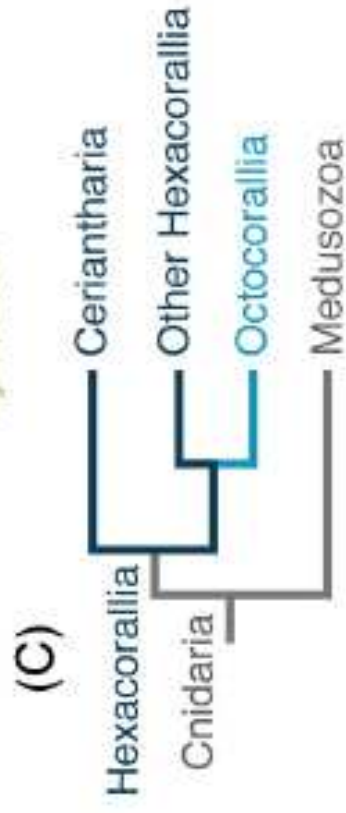
Evolve (příčně pruhovaných) svalů

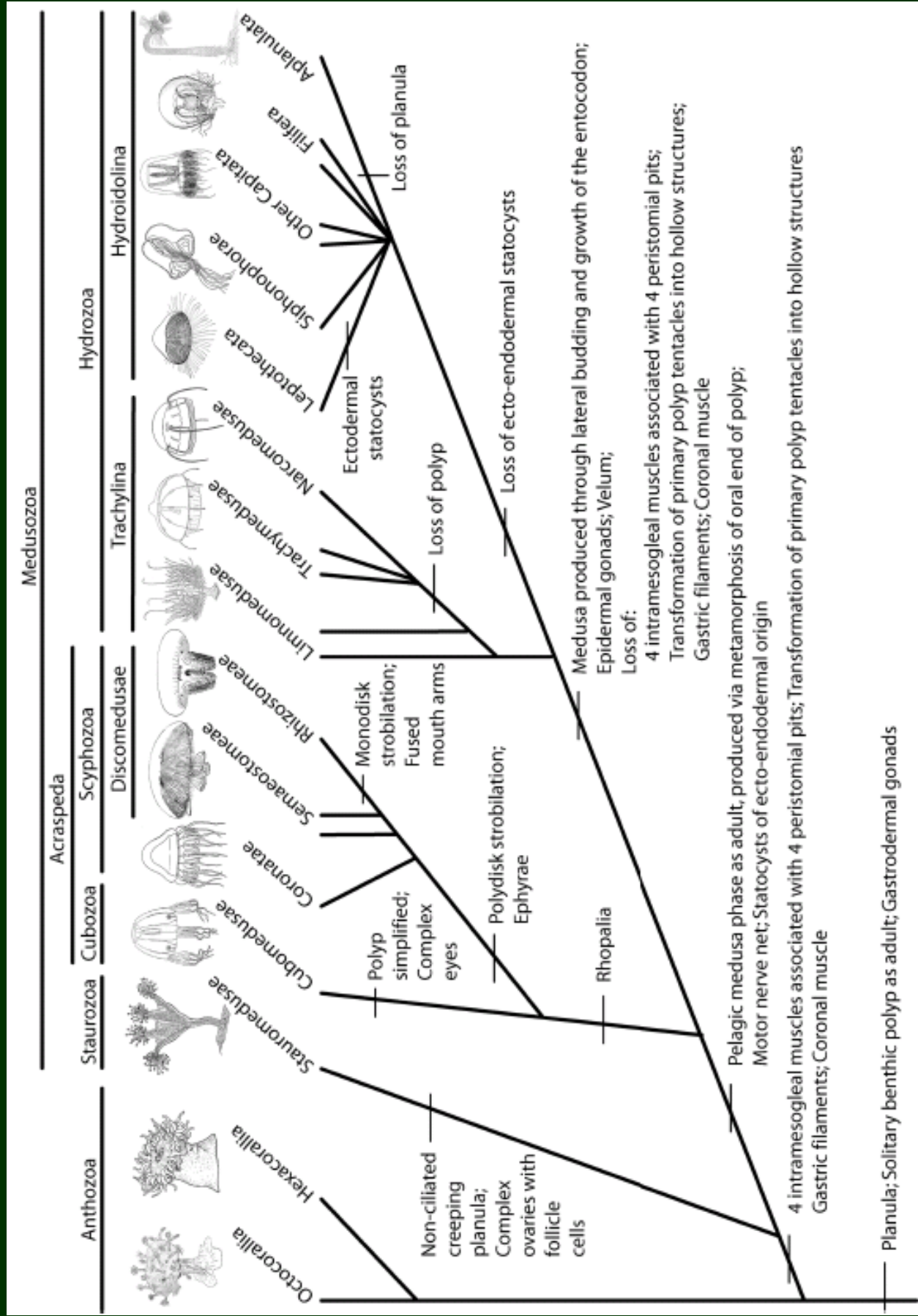
- příčně pruhované svaly medúz a bilaterií vznikly nezávisle
- těžký řetězec svalového myosinu (ST MyHC) vznikl duplikací (paralog NM MyHC: dělení a migrace buněk)
- ST MyHC u houbovců v choanocytech



Cnidaria mtDNA

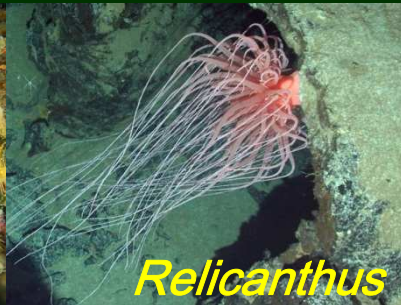






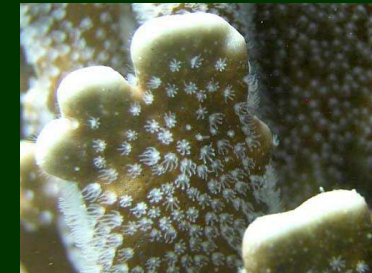
Anthozoa

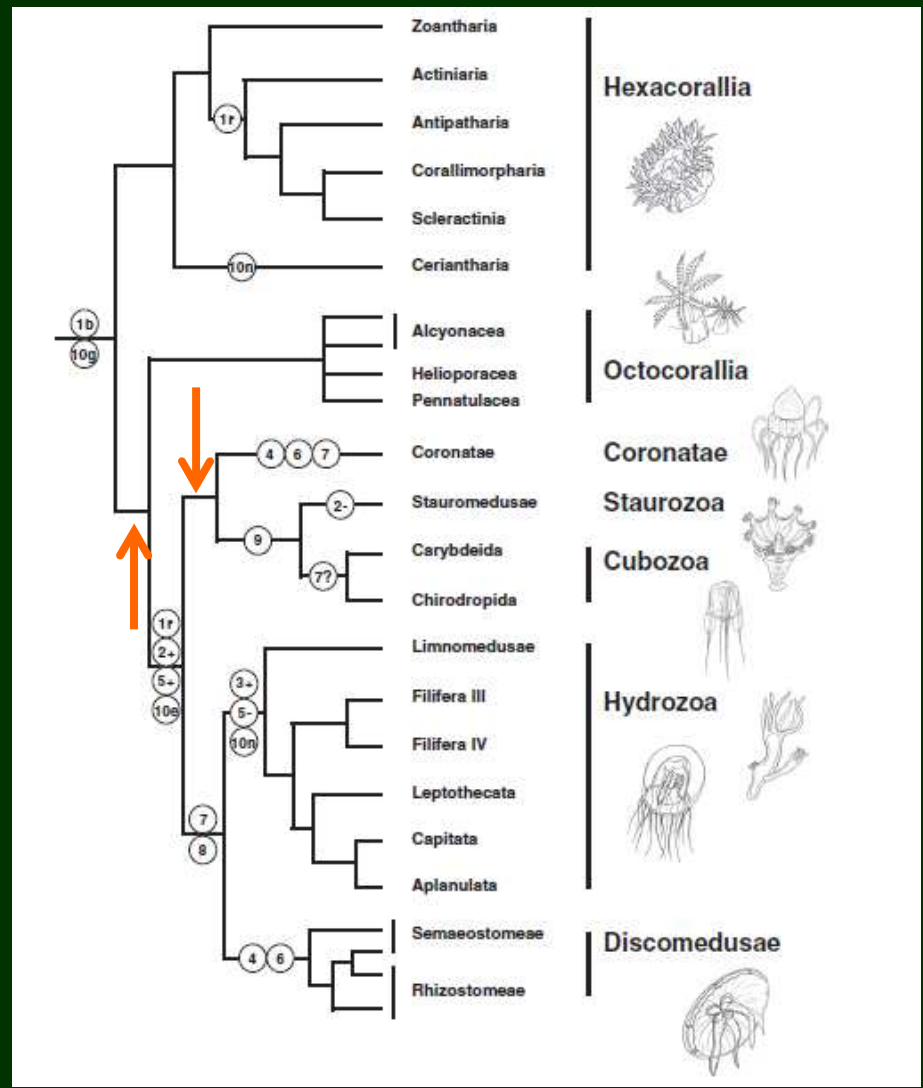
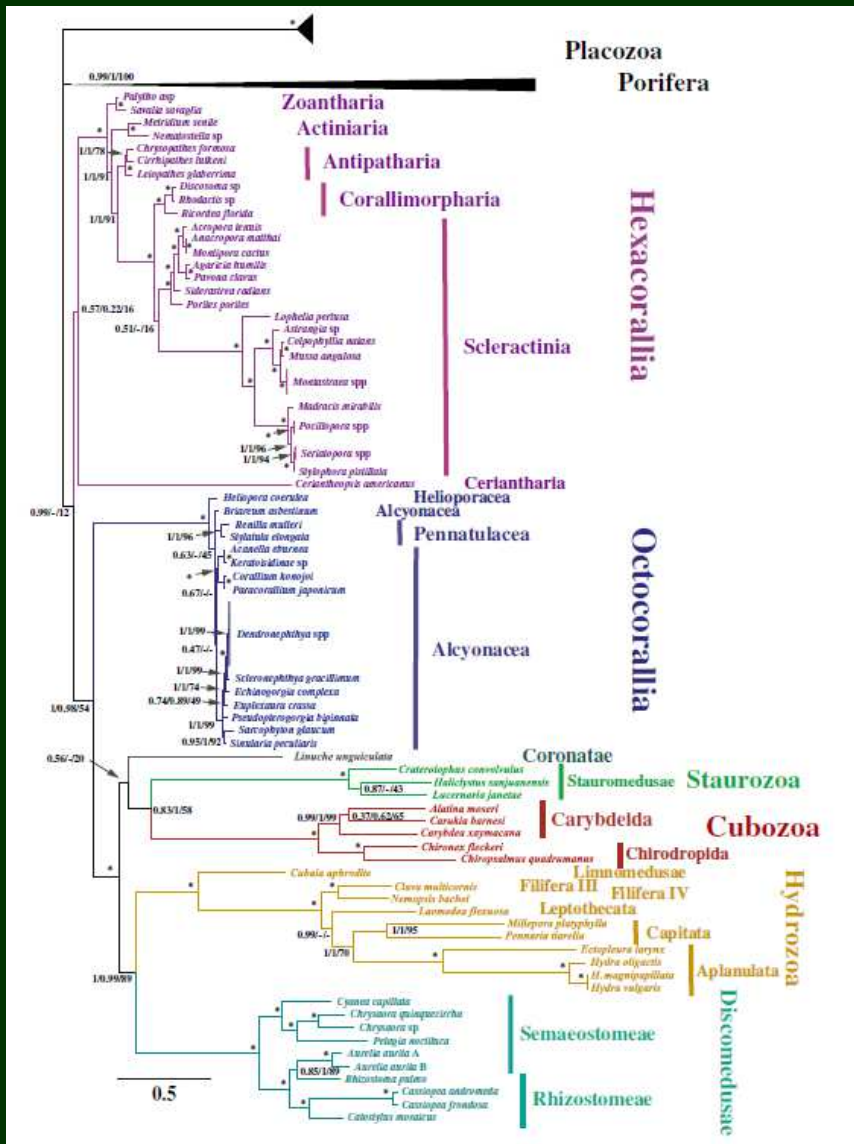
Hexacorallia



Relicanthus
není sasanka!

Octocorallia

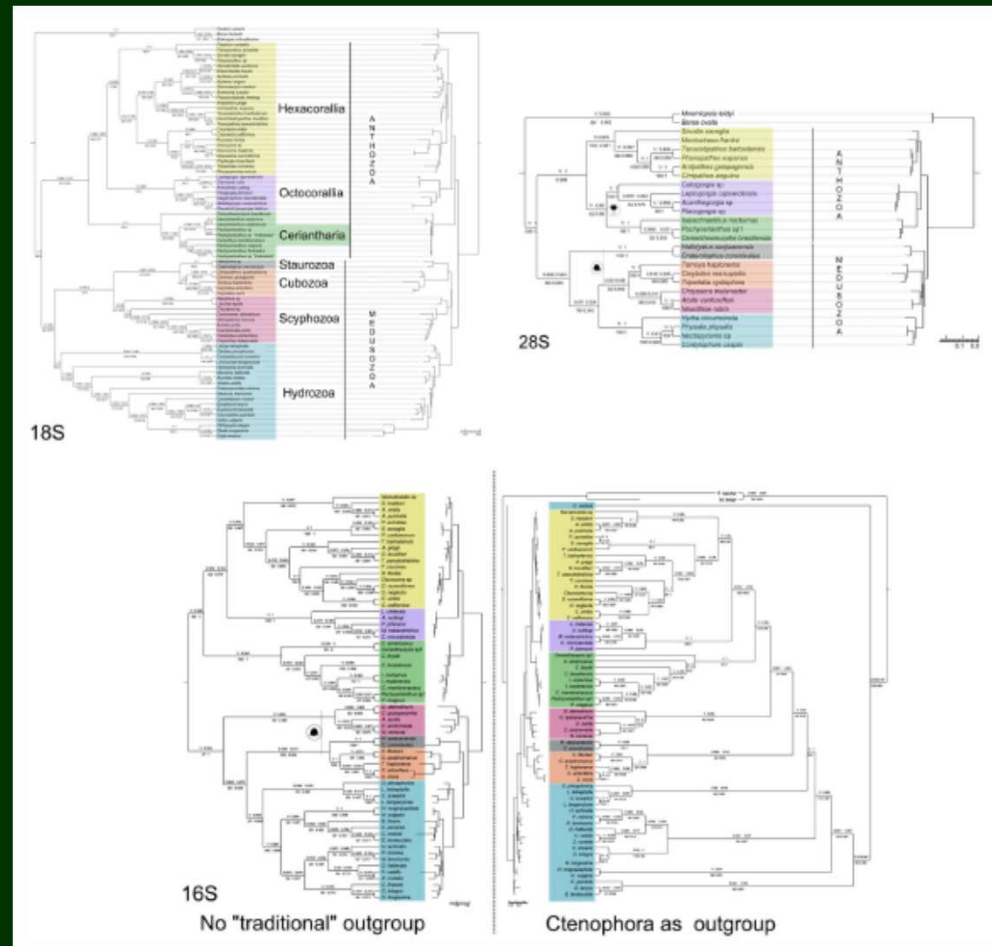




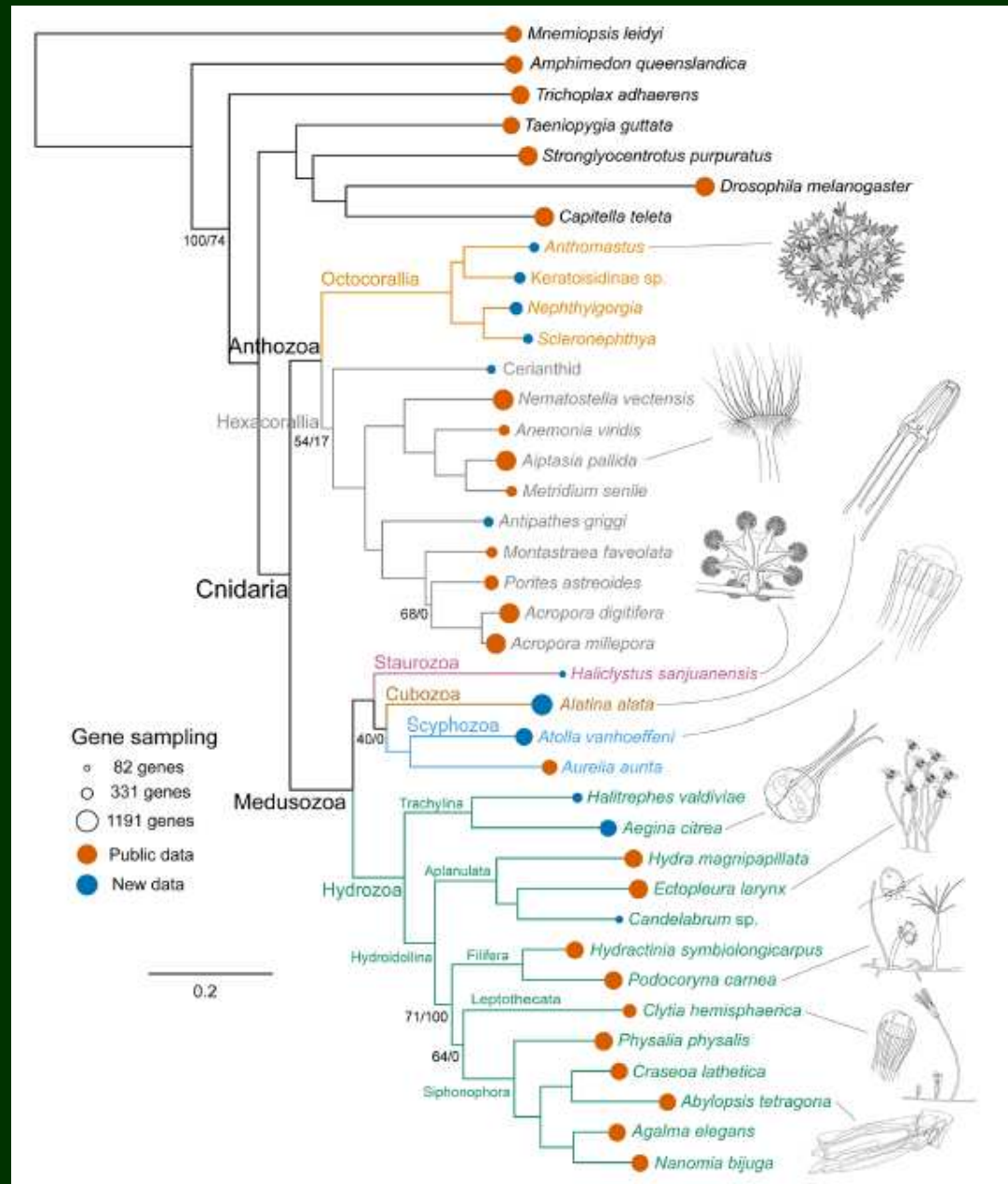
- mtDNA skupiny: bez morfologických apomorfii

Anthozoa

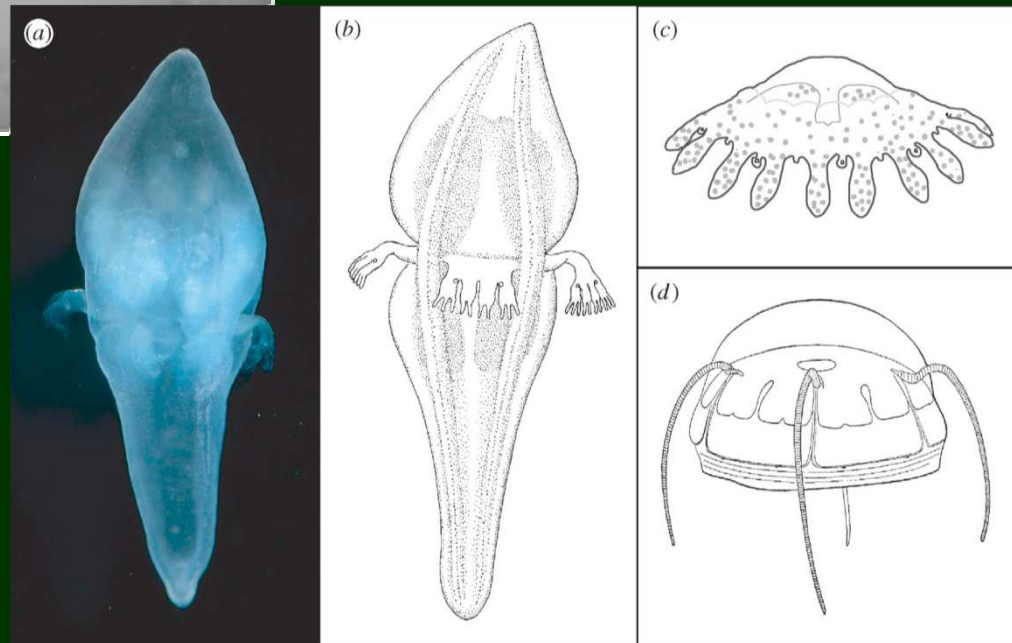
- nejasné postavení ceriantarií – parafylie hexakorálů???



fylogenomika

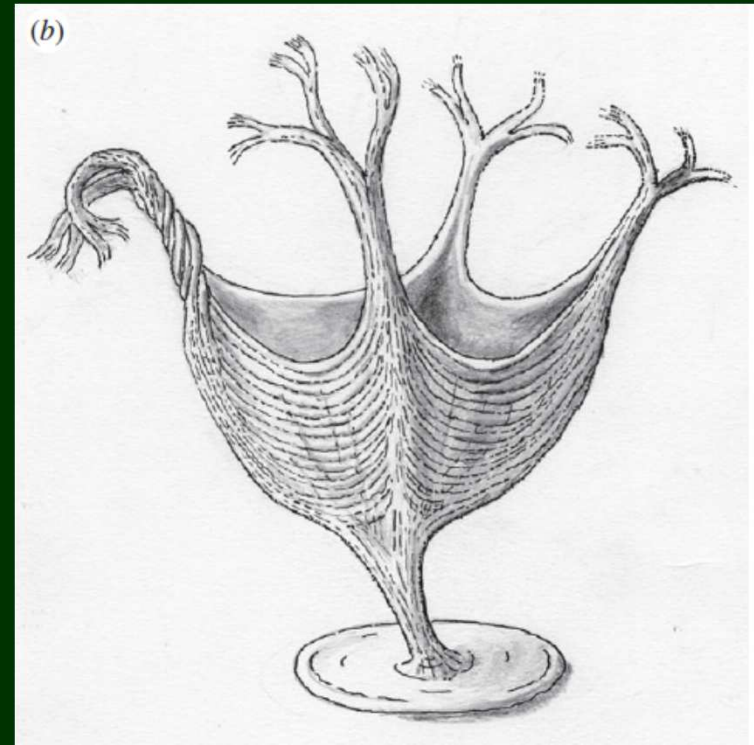
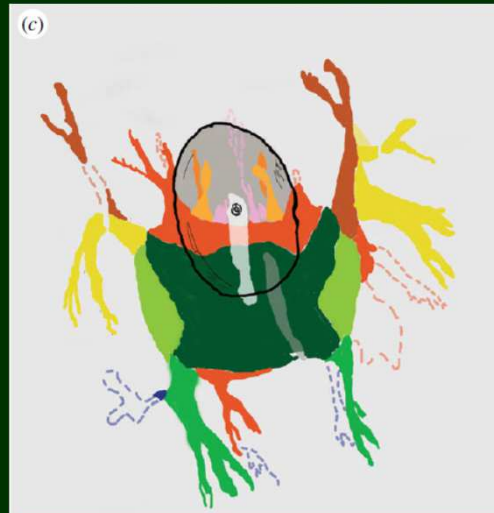


Hydrozoa



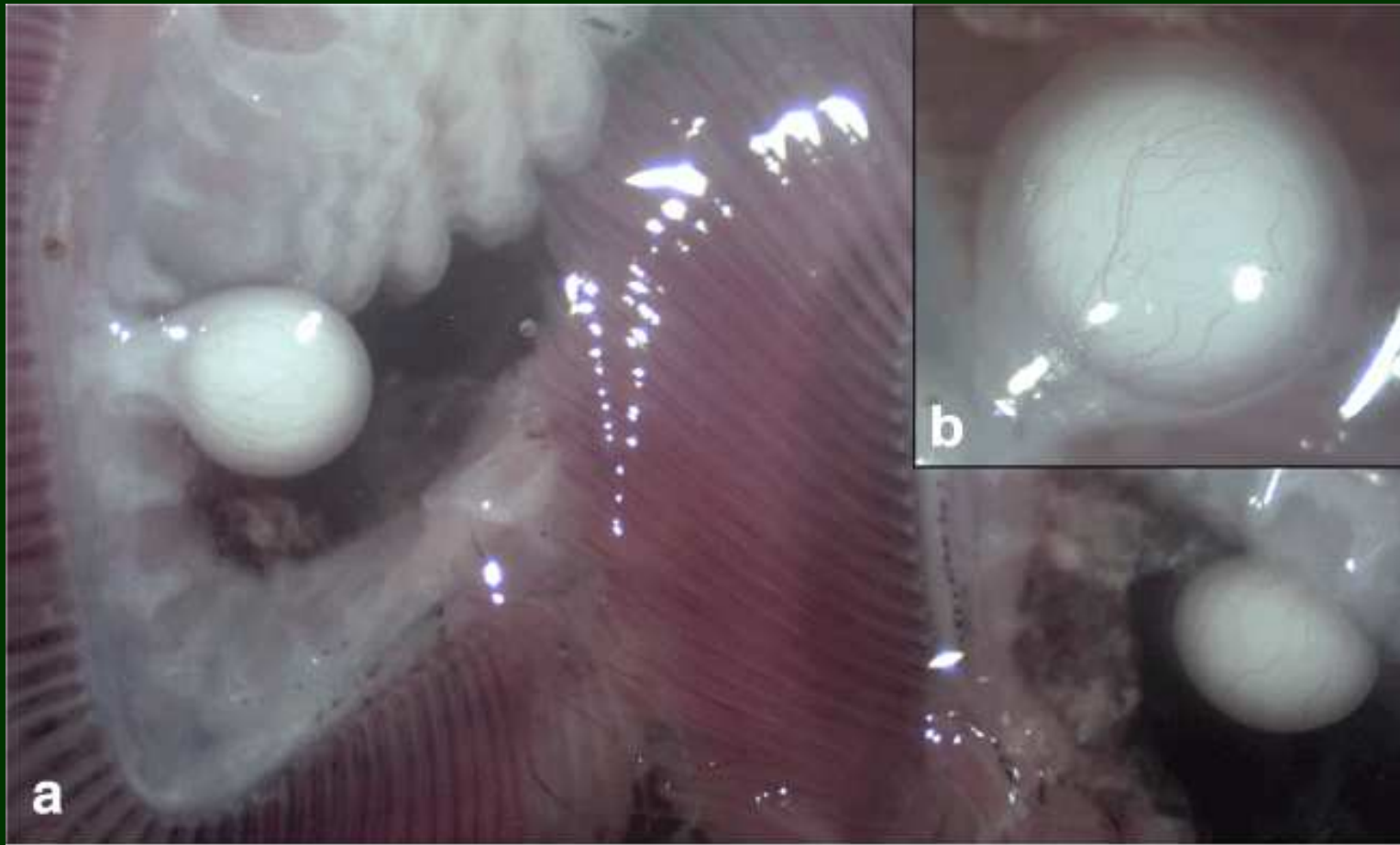
Tetraplattia a *Narcomedusae*

Haootia



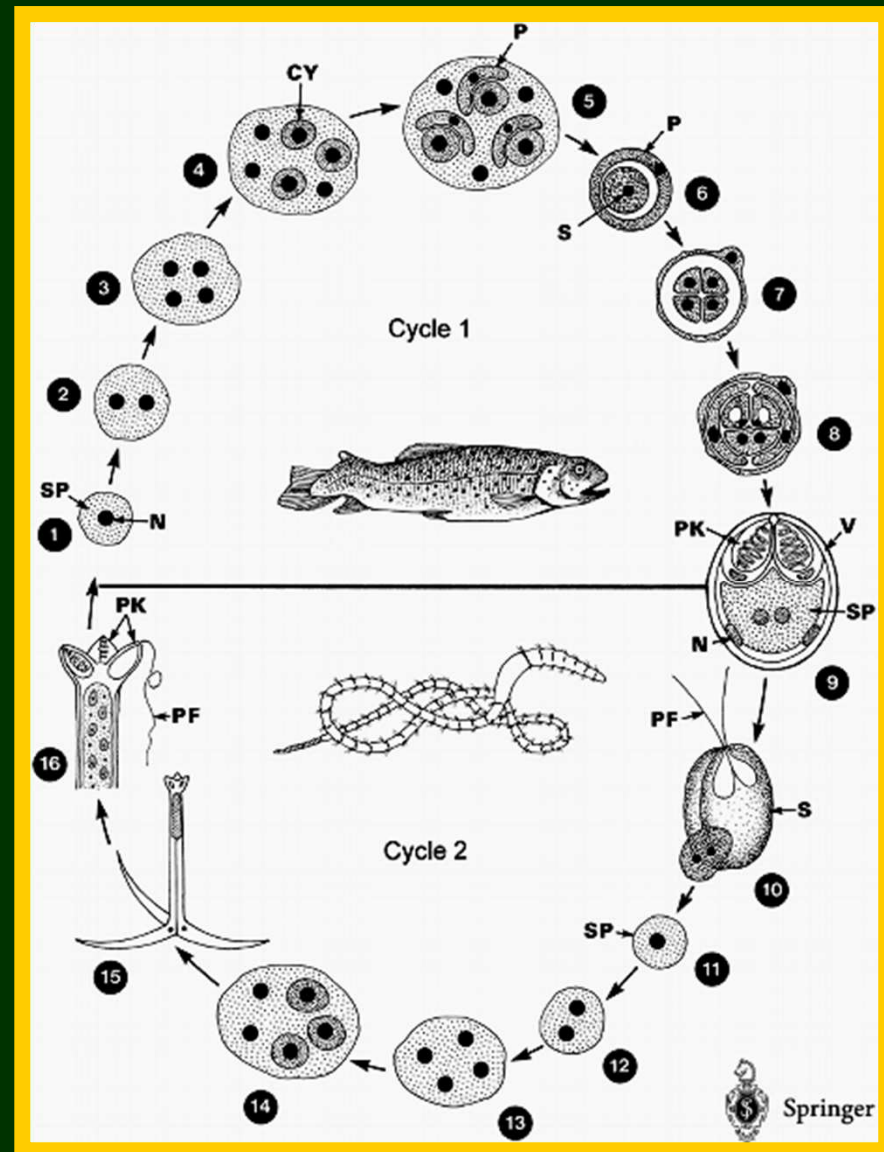
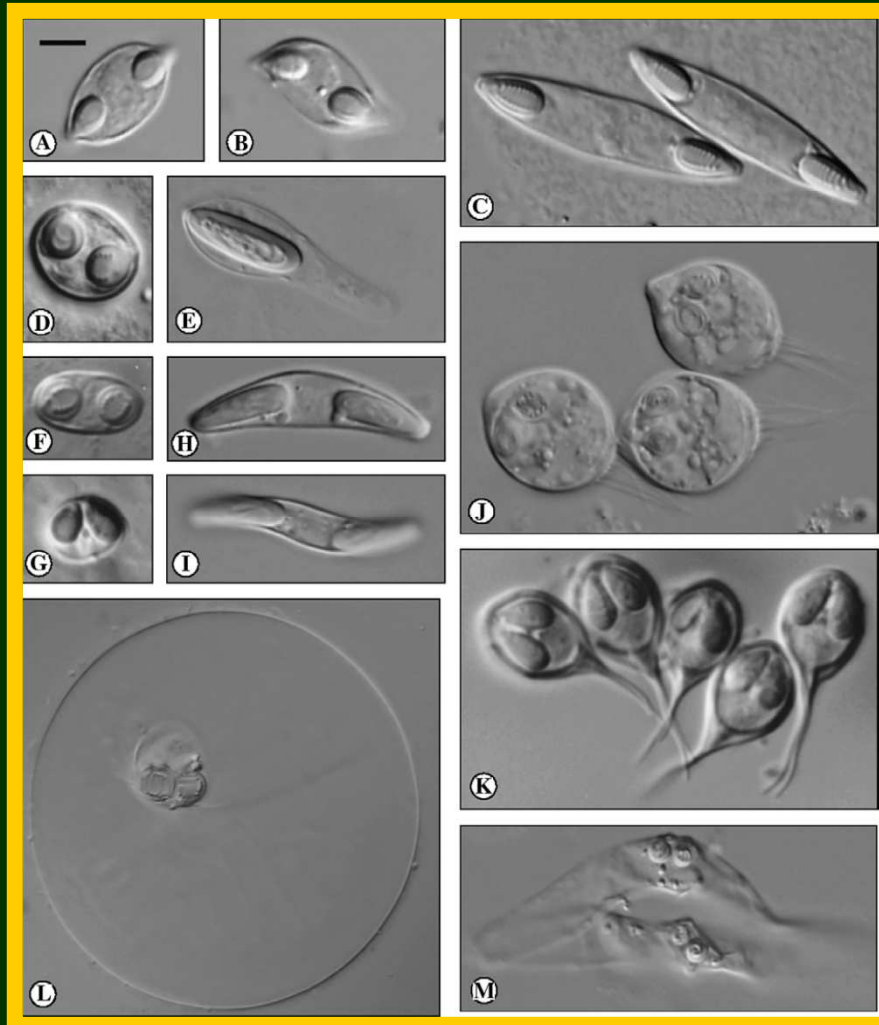
- ediakarský žahavec (?)
- 560 Mya
- Newfoundland

Myxozoa

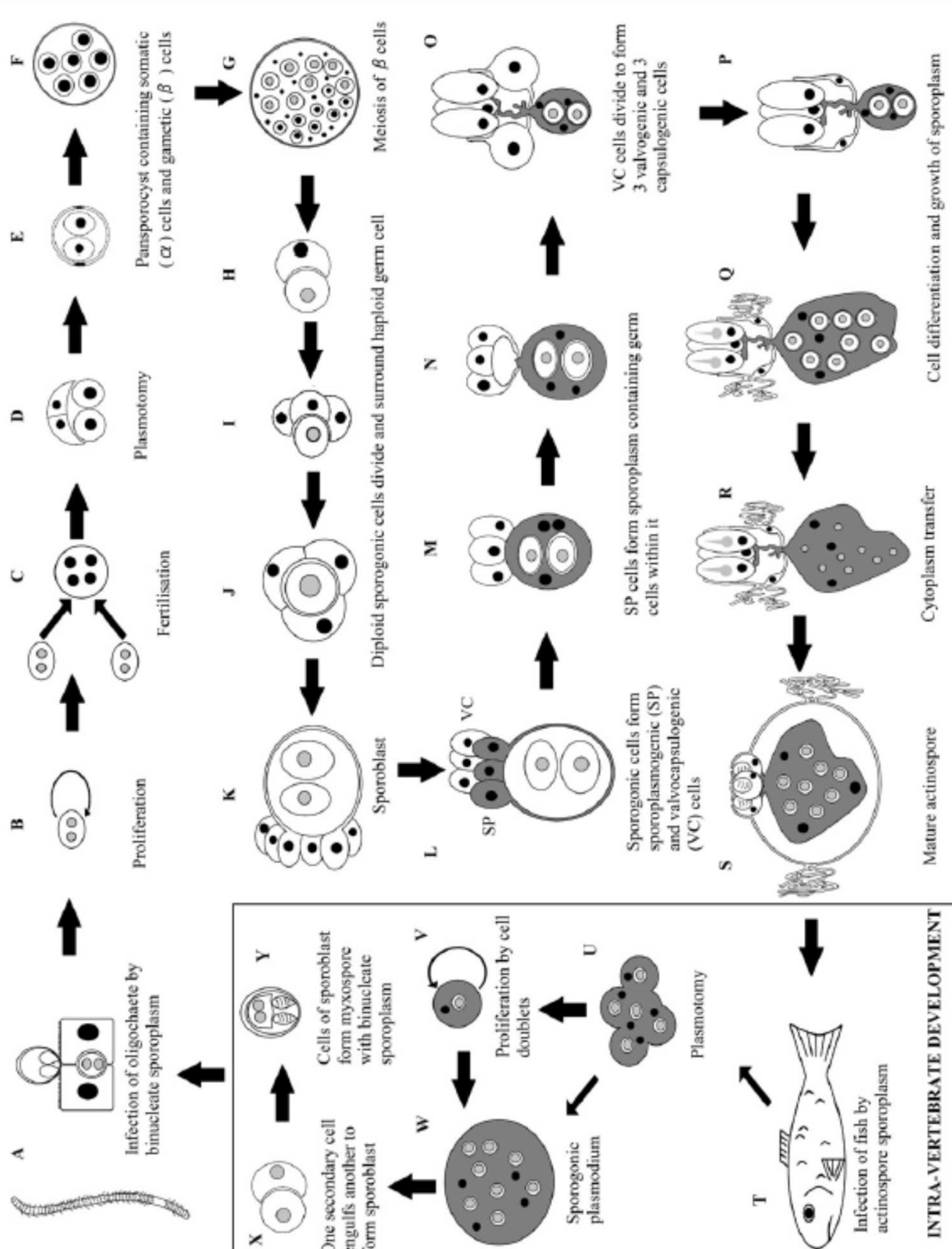


Cnidaria

Myxozoa



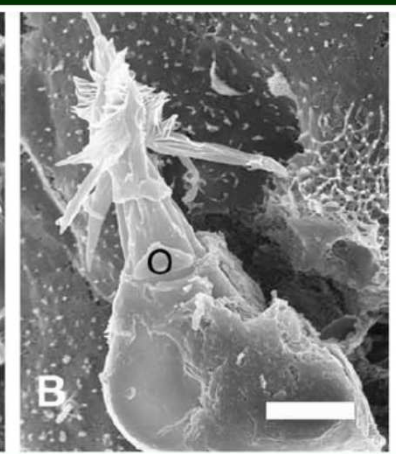
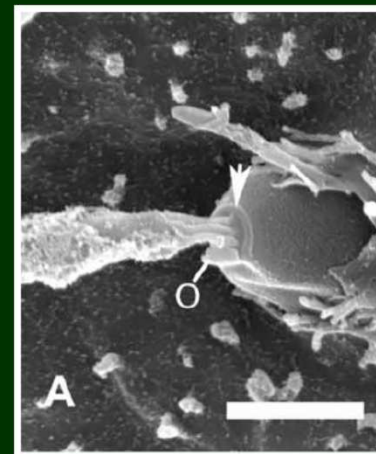
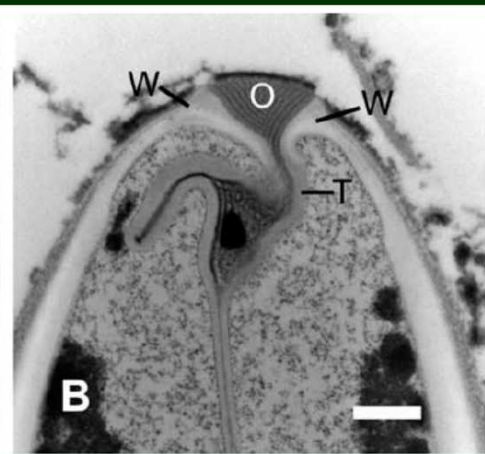
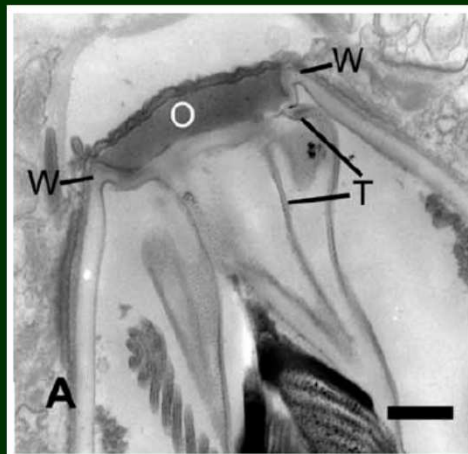
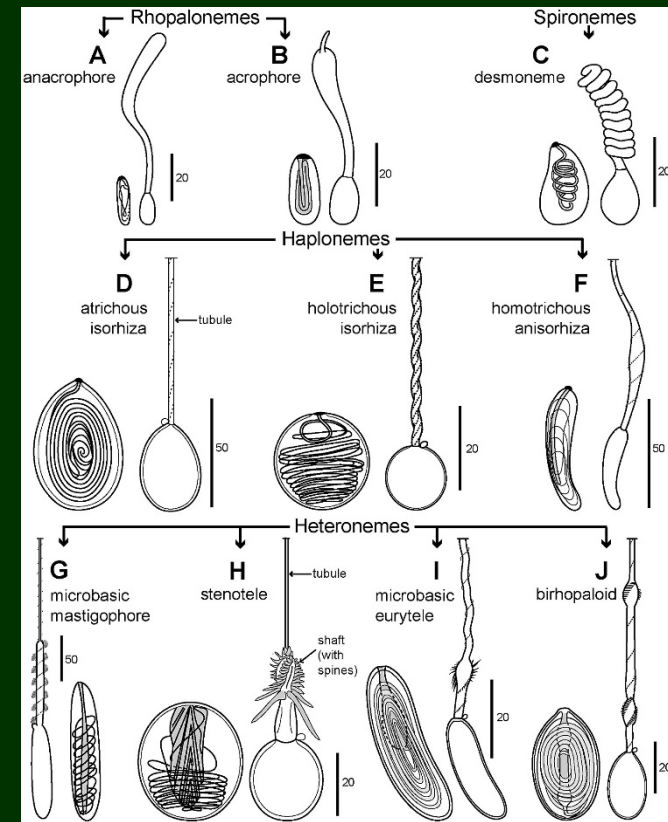
Myxobolus



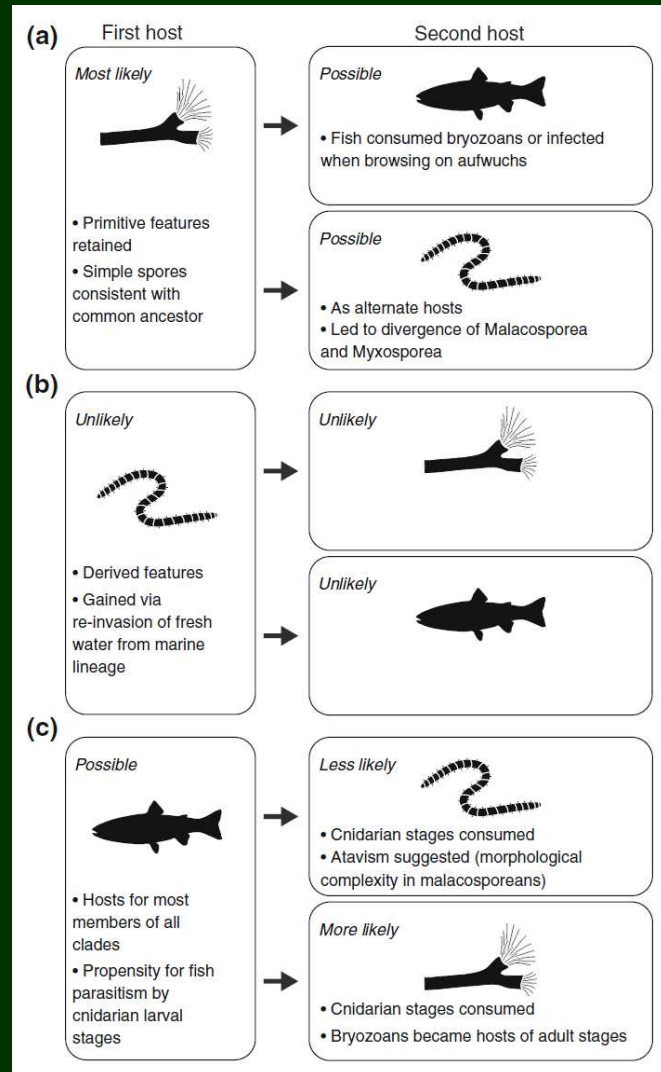
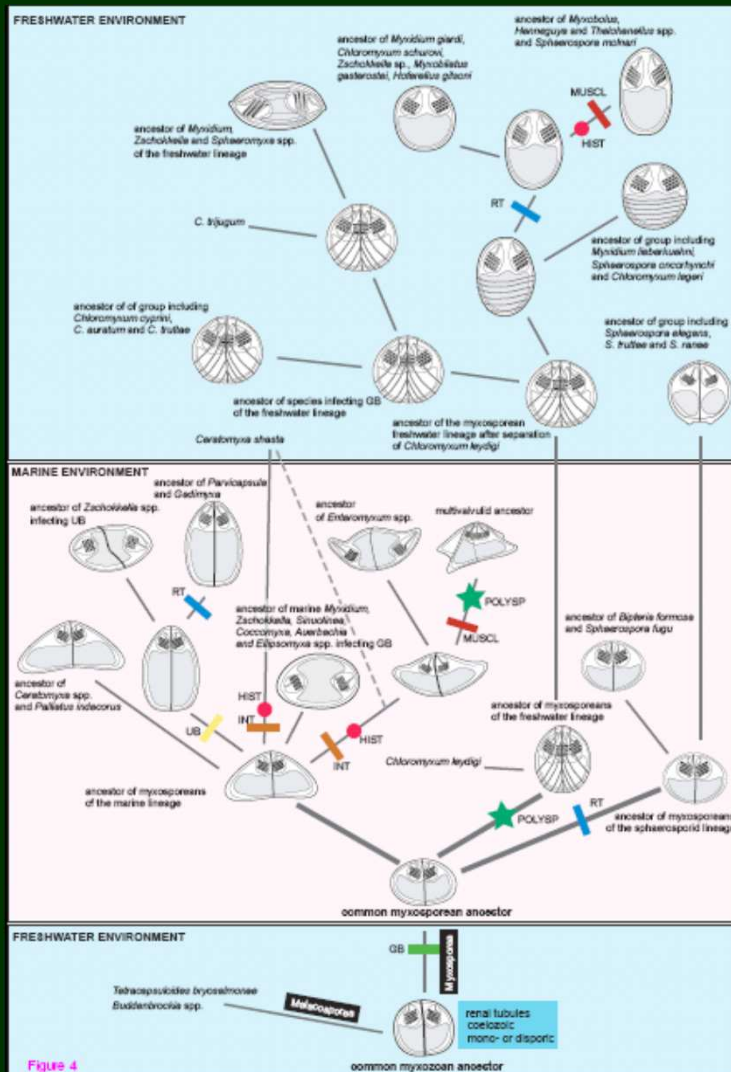
INTRA-VERTEBRATE DEVELOPMENT

Knidy myxozoi

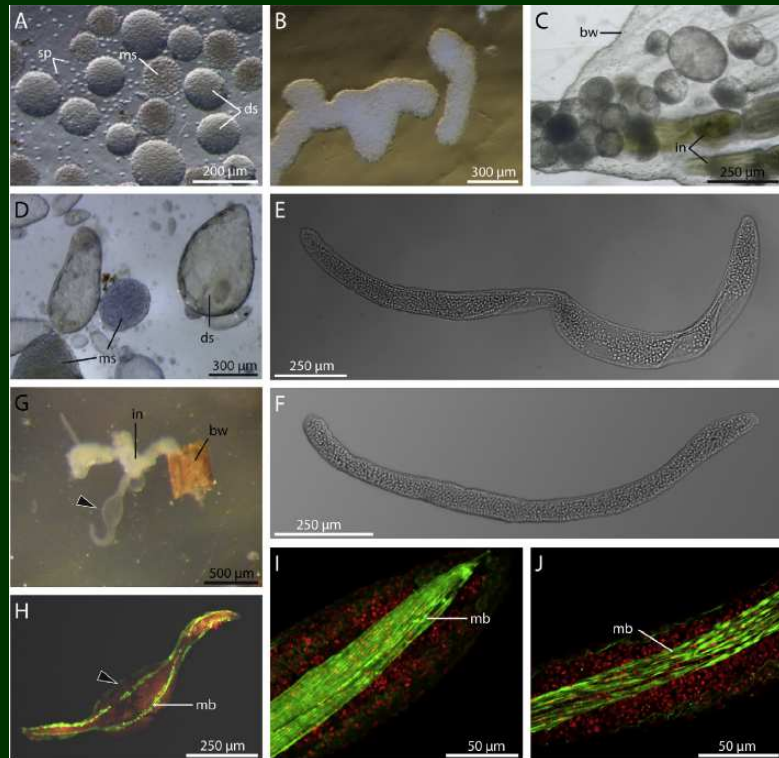
- atrichní a holotrichní izorhizy
- operkulum: Medusozoa a Myxozoa



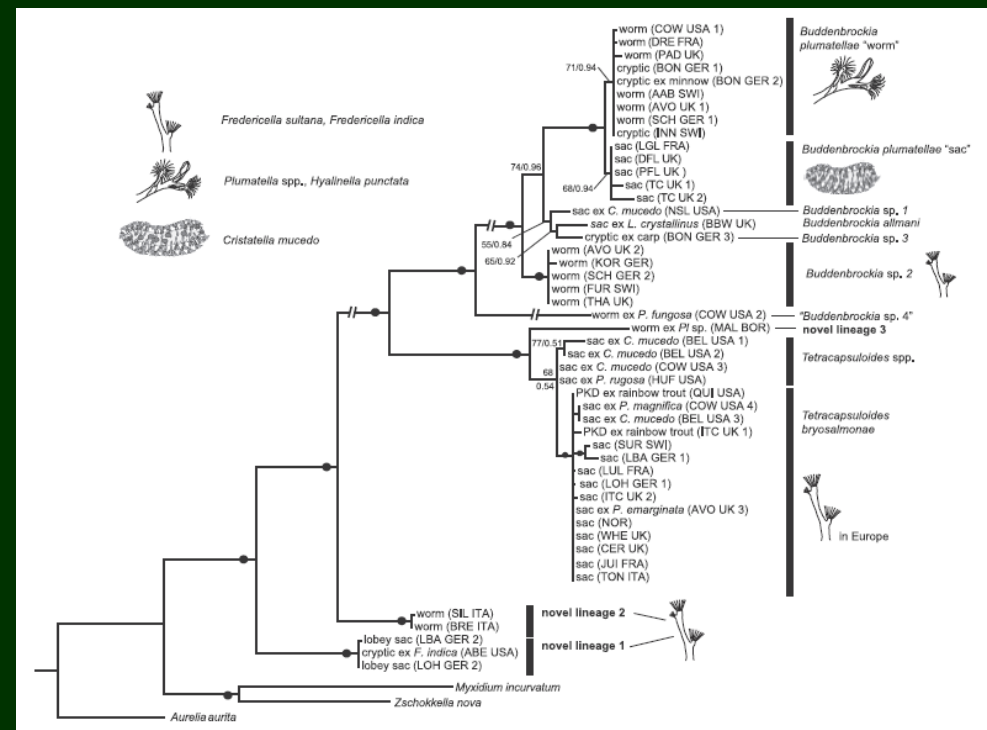
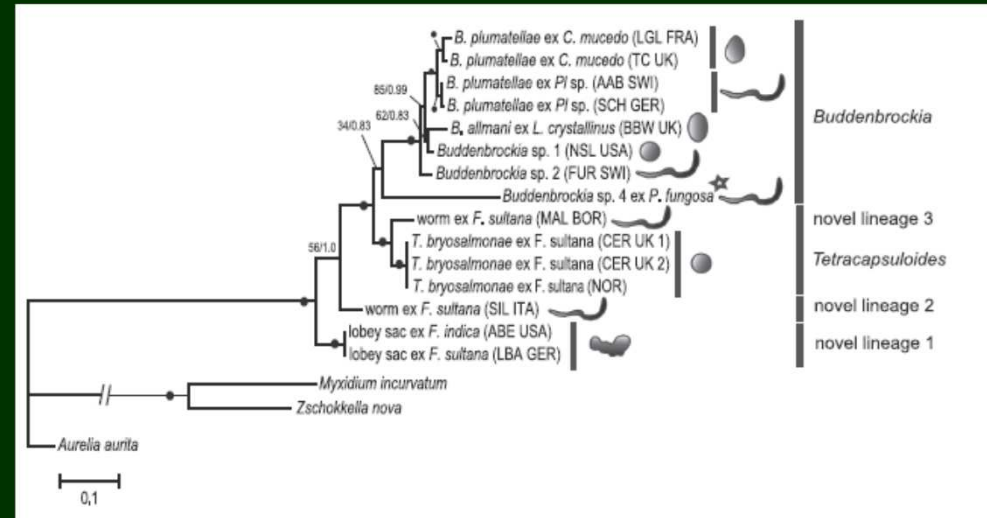
Myxozoa



Malacosporea

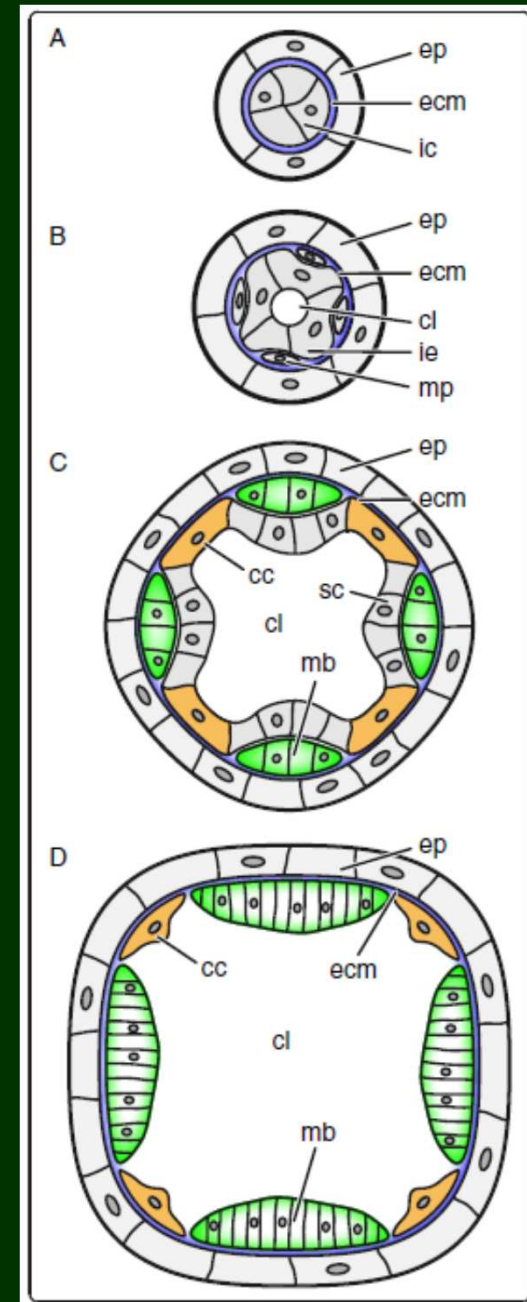


18S x 18S+28S



Myxozoa: Malacosporea

- epitely
- spory bez kutikuly
- Ectoprocta + ryby (lososi, cyprinidi?)
- *Buddenbrockia*: vnitřní epitel tvoří spory
- svaly: myocyty
- tetraradialita ~ Medusozoa
- A/P (nebo orální/aborální) polarita: diferenciaci buněk pokročilejší na distálním (volném) konci



Polypodium hydriforme

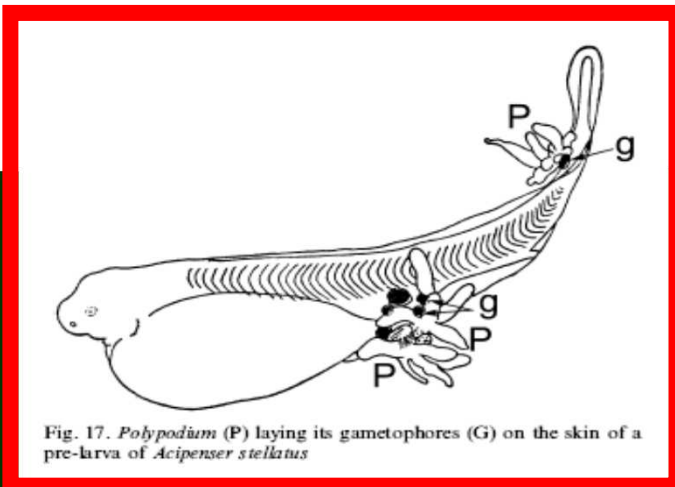
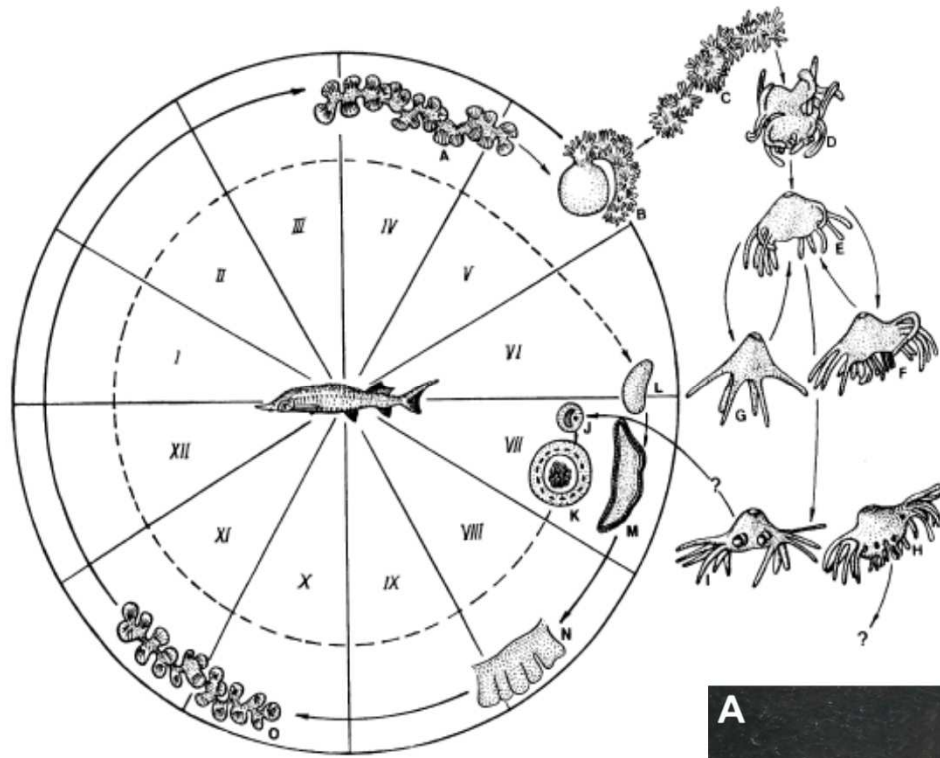
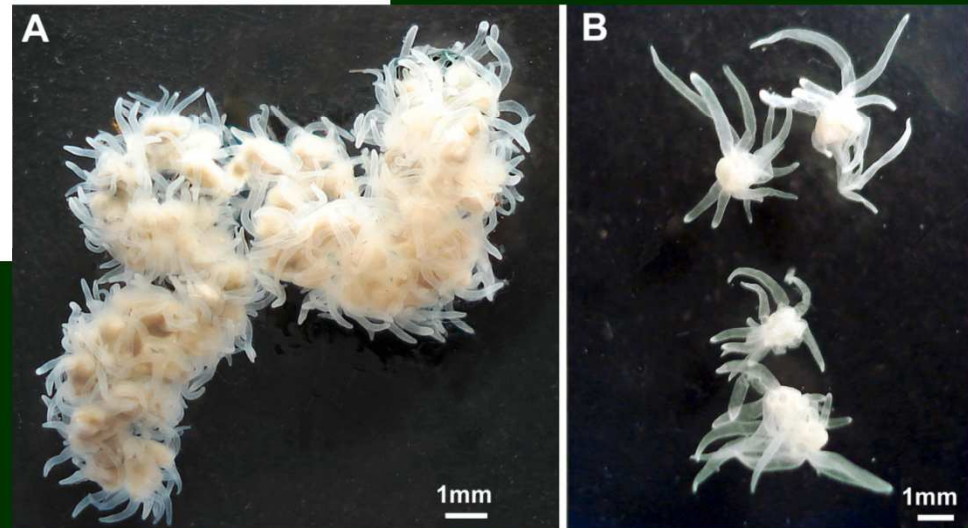
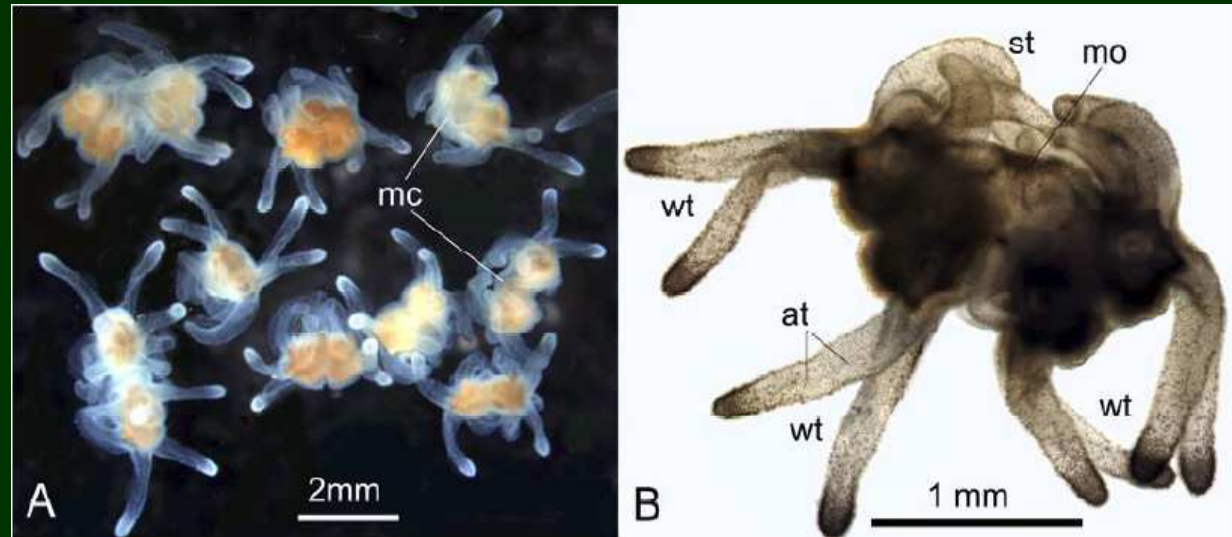


Fig. 17. *Polypodium* (P) laying its gametophores (G) on the skin of a pre-larva of *Acipenser stellatus*



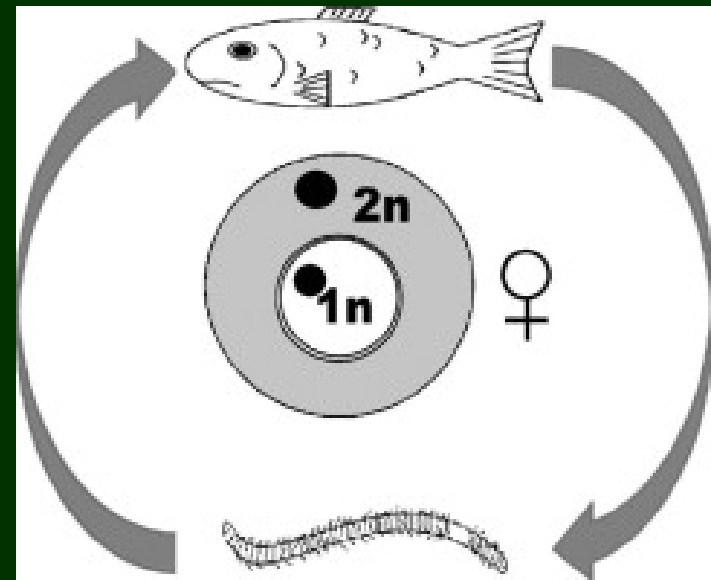
Polypodium

- jediný vnitrobuněčný parazit (x Myxozoa)
- „medusoidi“ lezou po chapadlech
- po strávení žloutku z oocytů se prolamují ústa v místě, kde medusoid přirůstal ke stolonu
- nemají myoepitely, ale svaly (~ *Haeotia*?)
- atrichní/holotrichní izorhizy (~ Myxozoa) – i na chapadlech

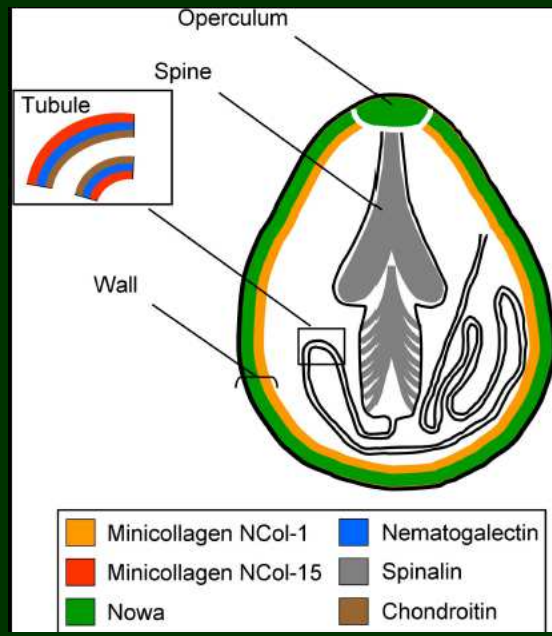
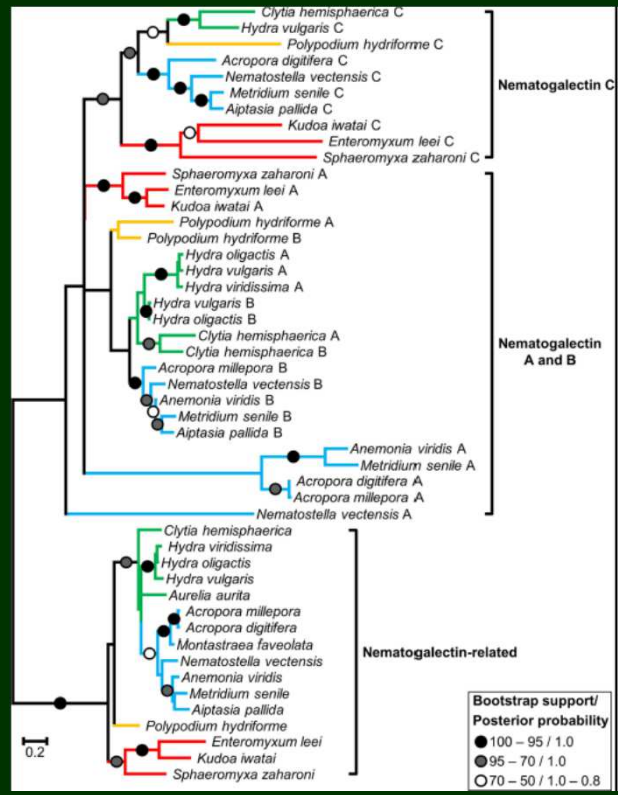
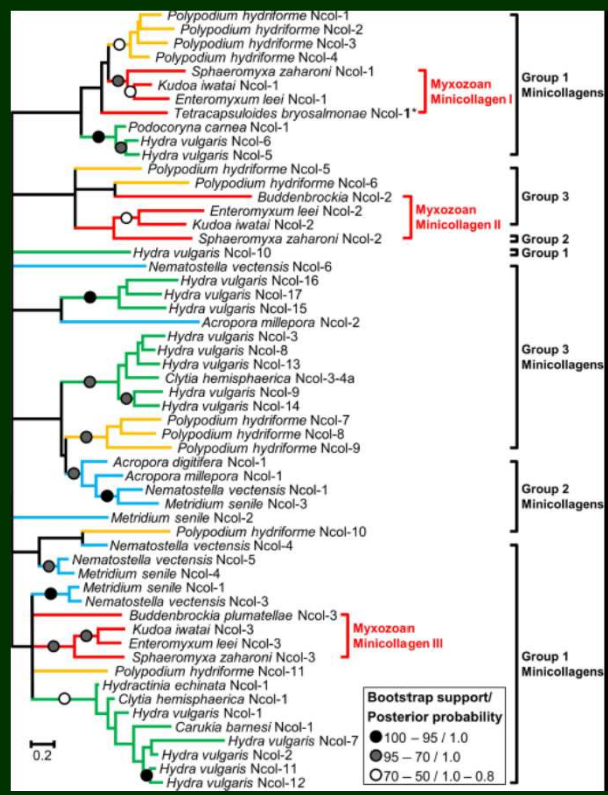


Endocnidozoa (= *Polypodium* + Myxozoa)

- somatické buňky obklopující a vyživující zárodečnou buňku („*cell-in-cell*“)
- gametofor s knidocyty
- tubulární mitochondriální kristy
- ztráta spermatozoí
- x *Polypodium* má NS, gonády, bičíkatý gastroderm, chapadla s knidocyty, centrioly a knidocil

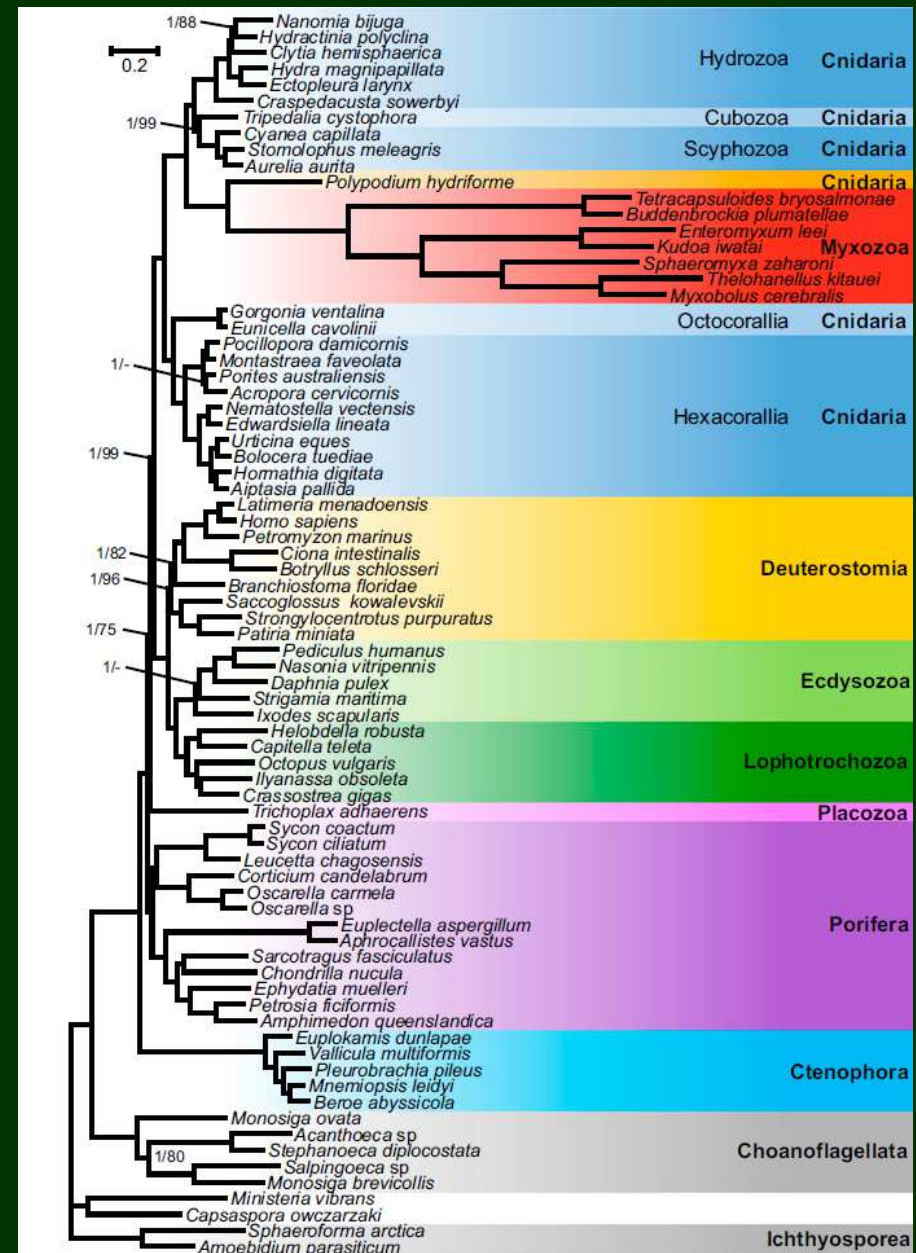


minikolageny a nematogalektiny



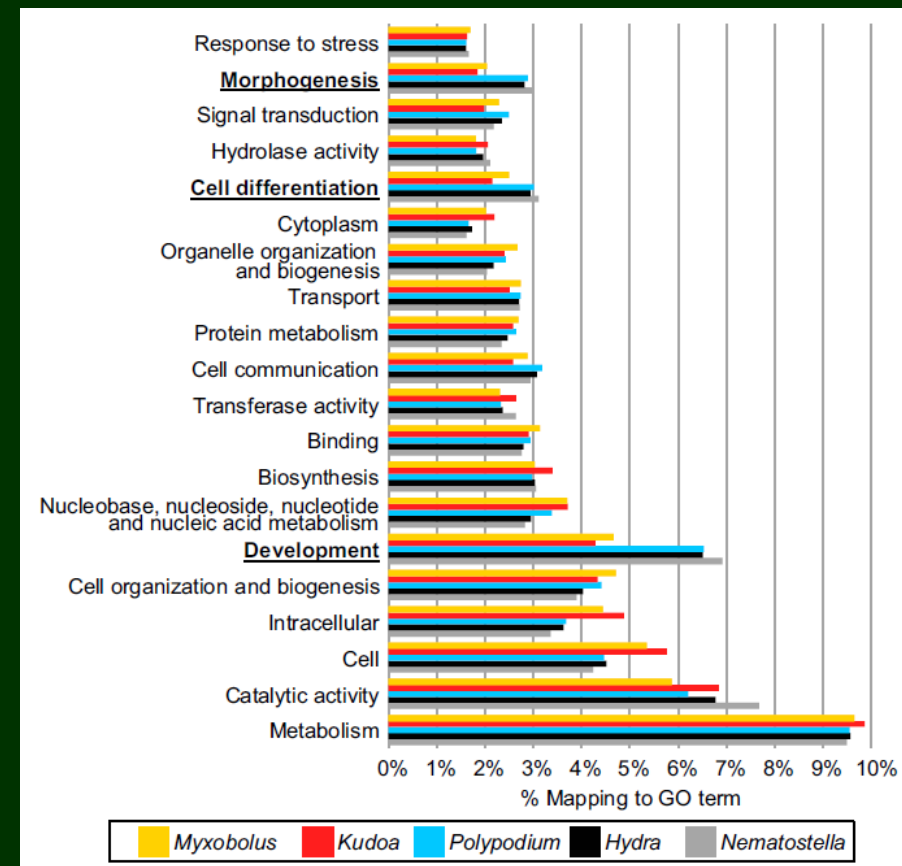
• Endocnidozoa (?) jako třetí linie žahavců (???)

- fylogenomika:
- monofyletická Endocnidozoa
- sesterská skupina (pravých) medusozoi



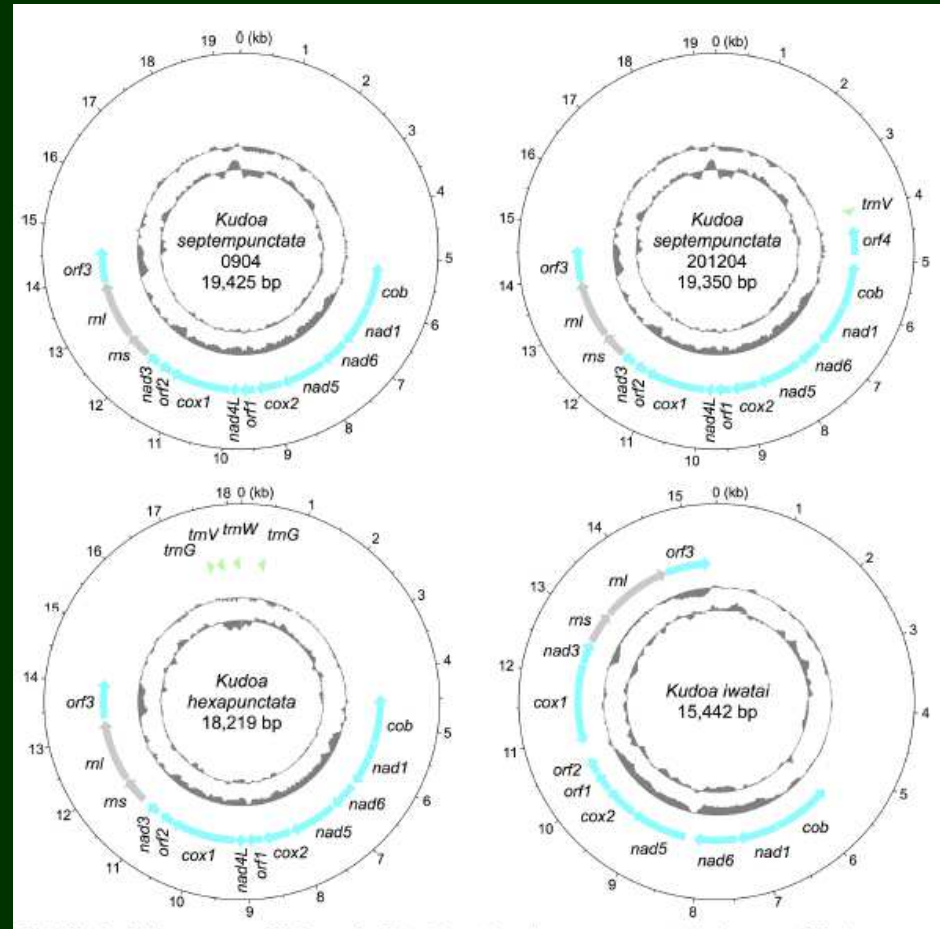
Genom endoknidozoí

- *Polypodium* je ještě normální žahavec
- Myxozoa – chybí např. Hox geny



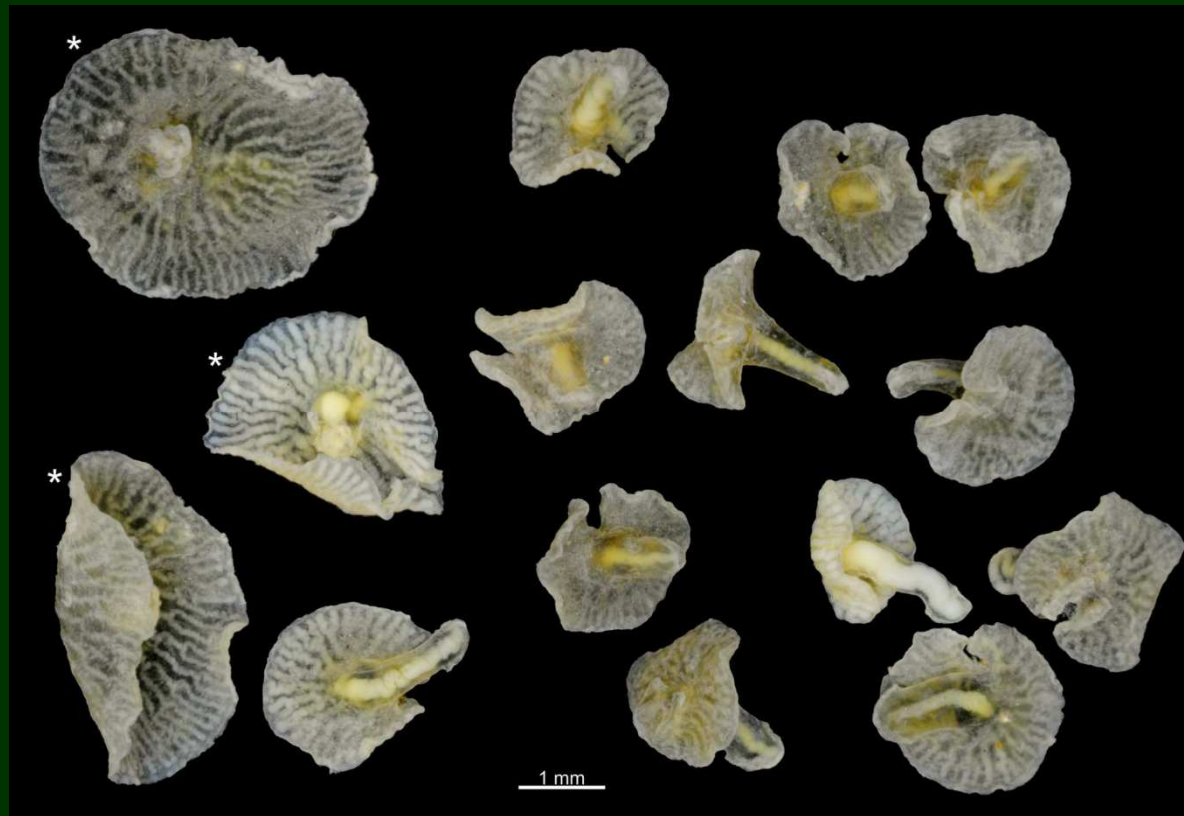
Mitochondriální genom myxozoi

- kruhová mtDNA
- *Polypodium*: neznámé
- tj. Endocnidozoa nepatří přímo mezi Medusozoa
- 3 „podkmeny“



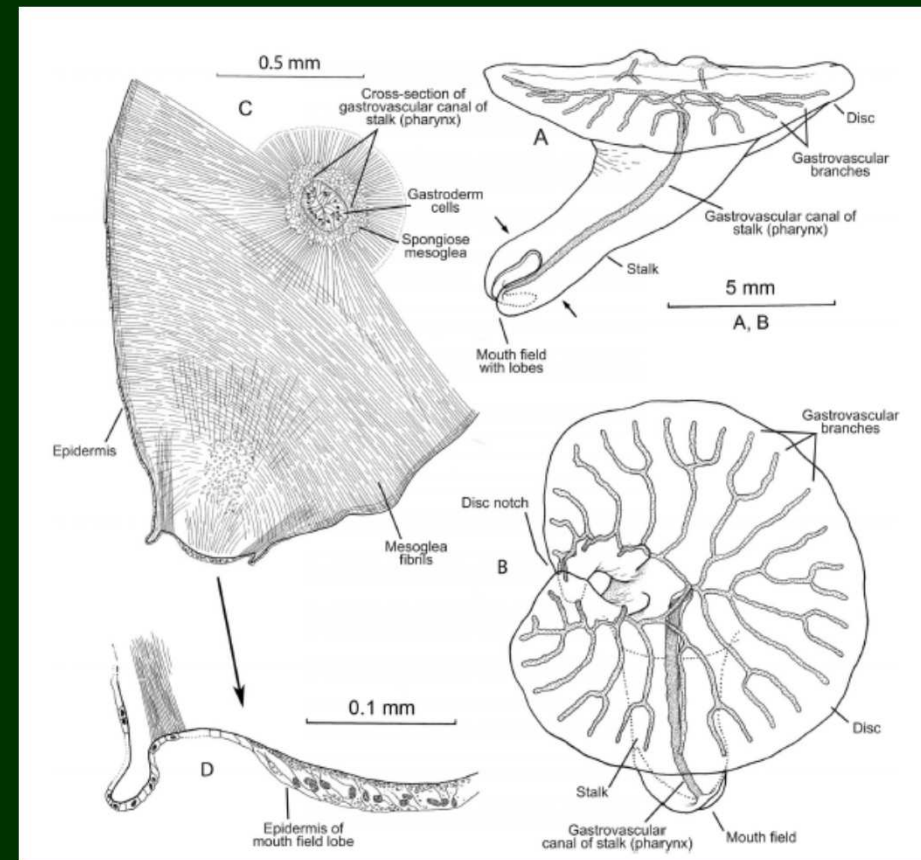
Dendrogramma

- 1986 – JV Austrálie, 400–1000 m
- 2 druhy: *D. discoides** a *D. enigmatica*

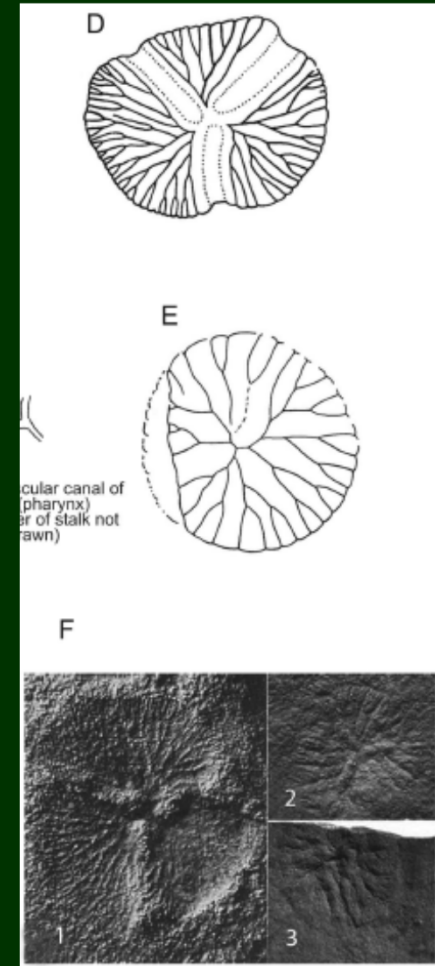
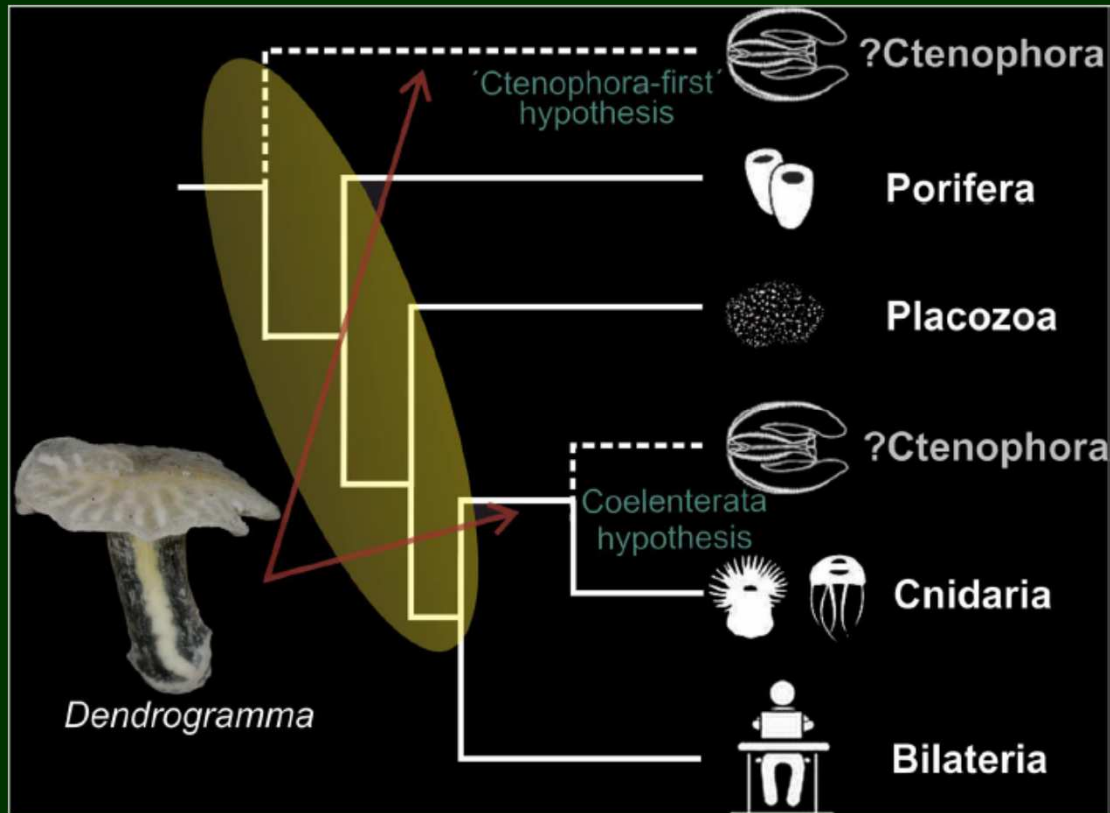


Dendrogramma

- žádné bičíky, morfologie epitelů (?) nejasná
- žádné gonády
- patrně aktivně neplavou
- náznaky bilaterie???
(laloky kolem ústního otvoru, dichotomické větvení kanálů)



Dendrogramma jako ediakarský reliktný (???)



~ *Albumares*,
Rugoconites, *Anfesta*